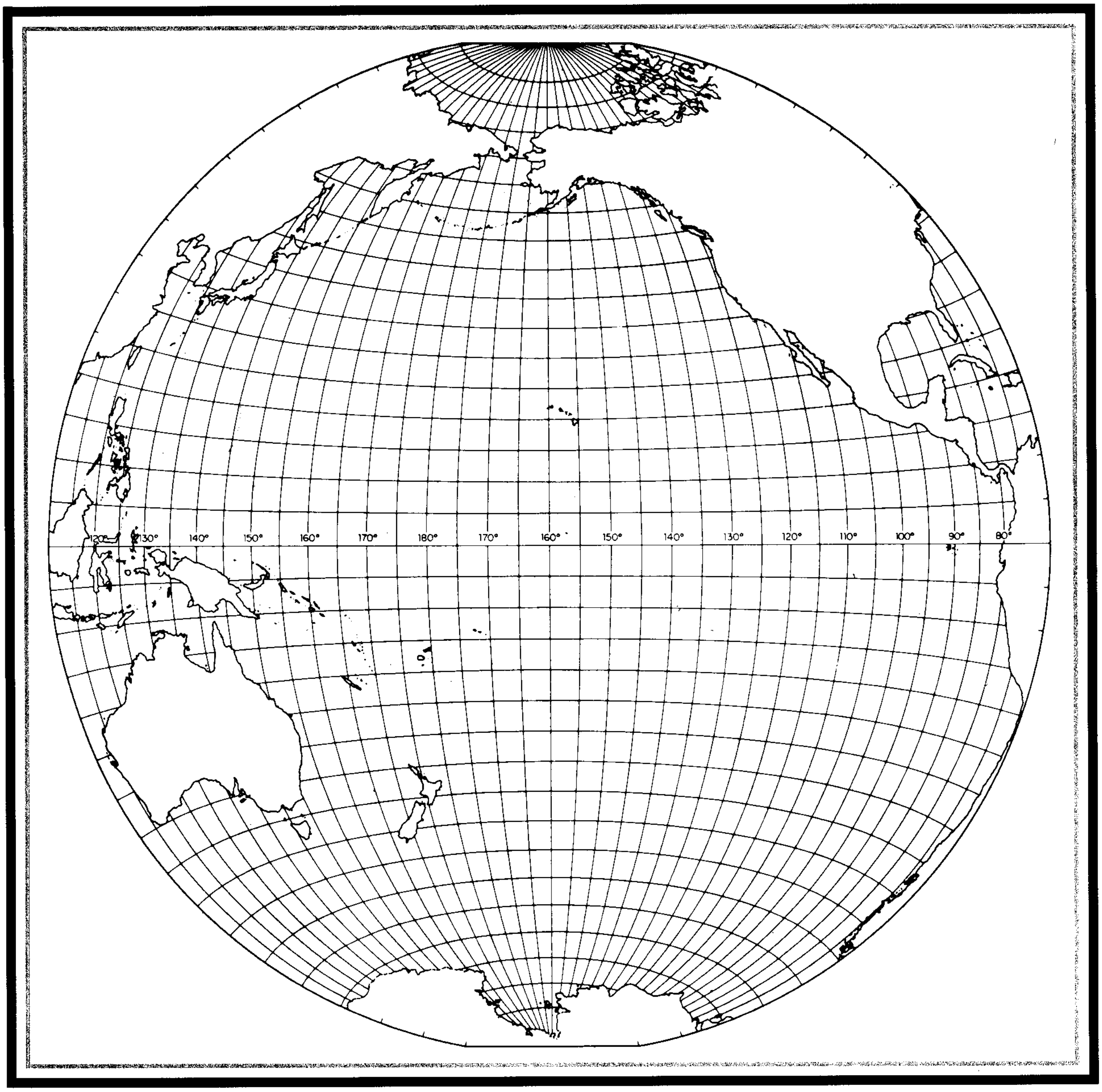

California
Cooperative Oceanic
Fisheries Investigations
Reports

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COOPERATIVE
OCEANIC
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CALIFORNIA DEPARTMENT OF FISH AND GAME
UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL MARINE FISHERIES SERVICE

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CONTENTS

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

Scientists from the California Department of Fish and Game (CDFG), the Southwest Fisheries Science Center of the National Marine Fisheries Service (NMFS), and the Scripps Institution of Oceanography, University of California, San Diego (UCSD), have collaborated for 46 years in the longest-running large-scale study ever undertaken in the ocean. This study was begun in order to understand the causes of changes in population, over time, of commercially important fishes in California's coastal waters. When the study began, the Pacific sardine was by far the most significant species of economic concern to the State of California. Because its population changes were thought to be caused by a diversity of atmospheric, oceanic, and biological variables, a wide array of measurements in the California Current region were begun and have been continued to this day. This long time series of data allows not only a better understanding of the flux of fish populations, but also lays the foundation for understanding interdecadal and secular change in the seas.

Two symposia were held at the 1995 California Cooperative Oceanic Fisheries Investigations (CalCOFI) Conference. The first concerned interdecadal trends in the physics, chemistry, and biology of the California Current region, and was inspired by discoveries published in *Science* magazine by UCSD scientists Dean Roemmich and John McGowan (*Science* 267:1324-1326; 1995). The symposium dealt with time-series data from the California Current and other regions of the Pacific Basin that may help us understand these trends. In preparation for the symposium, a meeting was organized by UCSD scientist Thomas Hayward to discuss the possible changes in sampling and field research strategy that are implied by Roemmich and McGowan's discoveries. The results of that meeting are published at the beginning of the symposium in this volume.

During 1994, scientists of the Instituto Nacional de la Pesca of the Government of Mexico, the NMFS, and CDFG carried out a successful daily egg production method (DEPM) survey to estimate the spawning biomass of the recovering sardine population. A special Sardine Symposium was held at the CalCOFI meeting to discuss the results. One objective of the collaborative research project was to produce a set of peer-reviewed papers. This volume of *CalCOFI Reports* contains nine scientific papers dealing with the DEPM survey, its results, and sardine population dynamics. The survey and papers represent significant advances in the biological understanding of and survey techniques for Pacific sardine.

A hull-mounted continuous egg sampler was tested by NMFS scientists during the first two CalCOFI cruises of 1996. This remarkable device, developed by UCSD scientist David Checkley and colleagues at UCSD's Scripps Institution of Oceanography, allows continuous sampling of ichthyoplankton in the top four meters of the water column while a ship is under way at nine knots. Sardine and anchovy egg catches from the pump were strongly correlated with egg catches in nets towed vertically from 80-m depth to the water surface, and with oceanographic features. The continuous egg sampler may become a routine feature during CalCOFI cruises, and is expected to be used in DEPM surveys as well.

Substantial advances were made by National Oceanographic and Atmospheric Administration and NMFS scientists in a joint project to develop an airborne lidar (laser-based) survey instrument for assessing coastal pelagic fishes. Direct measurements of the reflectivity of fish schools were obtained, and both lidar and sonar data from hundreds of schools were collected for comparison, and published in a report. The next step, to be carried out with scientists of the CDFG during 1997, will test an airplane-mounted lidar unit for rapid surveys over large areas.

During 1995, NMFS initiated a new research program dealing with the reproductive biology and early life history of Pacific whiting. In 1995, cruises were carried out to map physical structure and circulation. Objectives were to: 1) try an adaptive sampling strategy for whiting eggs and larvae (whiting eggs and larvae are extremely patchy in the ocean and hard to survey); 2) measure larval growth rates; 3) compare the distribution of larvae to the distribution of their food; 4) describe the physical structure of larval habitat and the effects of ocean circulation on larval distribution; and 5) measure the size of patches of larvae in the ocean. During 1996, the adaptive approach for sampling whiting eggs and larvae was evaluated on the basis of data from cruises during 1995. Results indicate that considerable increases in precision are possible, but they are complicated by some additional bias.

CDFG's wetfish port sampling program was modified in 1995 to simplify data collection. Other changes may be initiated in order to reduce sampling effort and to accommodate staff reductions.

Pacific mackerel biomass in 1995 was estimated by CDFG scientists to be 56,000 metric tons, consistent with a long-term stock decline apparent since the mid-1980s. A fishery-independent abundance index used in the mackerel assessment model was larval density in the Southern California Bight, calculated from CalCOFI's plankton database. Since the Southern California Bight is at the northern fringe of the mackerel spawning grounds, there was concern that spawning indices derived from it may be insensitive to changes in mackerel abundance at low levels of biomass. Therefore, a mackerel spawning (plankton) survey off Baja California was planned for 1996, in order to obtain data centered in traditional spawning grounds. We hypothesize that these new data will improve the precision of annual mackerel stock assessment. Plankton survey data from Mexican waters should offer additional contributions to sardine assessment work, and to anchovy investigations, and should complement the proposed Inter-American Institute for the Investigation of Global Change (the IAI includes scientists of sixteen American maritime nations).

The total sardine biomass (age 1+) increased dramatically from 1983 to 1995. The July 1, 1995, biomass was estimated to be 353,000 short tons, and CDFG scientists recommended a 1996 sardine quota of 35,000 short tons. To determine the 1996 sardine quota and build consistency for implementing the draft Coastal Pelagic Species–Fishery Management Plan (FMP), the harvest formula selected as the preferred option in the FMP was used. That formula had undergone extensive scientific and user-group review as part of the Pacific Fishery Management Council's adoption process and had the endorsement of the fishing industry, the scientific community, NMFS, and CDFG. Unfortunately, NMFS declined to implement the FMP, and pelagic fishery management remains with CDFG.

In 1995, CDFG scientists conducted a sardine spawning survey off northern and central California during August (3–25). The study was designed to detect the presence and estimate the abundance of sardine eggs in an area from Cape Mendocino to the Channel Islands, and extending from the coastline out to CalCOFI station 90 (approximately 180–200 miles from shore). A total of 480 plankton tows were made during the survey, using CalVET nets deployed from the CDFG RV *Mako*. Of 480 stations sampled with PairoVET net tows, only three contained sardine eggs. The three positive stations were all in the vicinity of Monterey Bay. The scientists concluded that the cruise was too late in the season, despite evidence in the literature that suggested a summer spawning peak (*CalCOFI Atlas* No. 31; and Watson, *CalCOFI Reports* Vol. 33).

Additional research from RV *Mako* during 1995 included a larval hake survey by NMFS scientist Paul Smith; hooking mortality studies for salmon and lingcod; abalone withering foot studies; and shark longline tagging studies.

In early 1996, NMFS scientist Geoff Moser and colleagues at the Southwest Fisheries Science Center completed work on a new CalCOFI Atlas. Together with the CalCOFI Committee and the Allen Press, they have published *CalCOFI Atlas 33*, a definitive identification guide for fish eggs and larvae in the California Current. The guide includes over 1,500 pages, describes about 500 species in 125 families, and represents six years of intensive work by Southwest Fisheries Science Center staff, with cosponsorship of the U.S. Minerals Management Service. The identification guide will serve for decades as a key reference for scientists all over the world, and is available from the Allen Press.

The Committee wishes to thank all those reviewers who have improved the quality of the papers in this volume: Pablo Arenas, Jay Barlow, Tom Barnes, Jon Brodziak, John Butler, David Checkley, Tom Clarke, John Cullen, Paul Fiedler, Rick Fletcher, Ralf Goericke, Loren Haury, George Hemingway, John Hunter, Adriana Huyer, Wim Kimmerer, David King, Rick Klingbeil, Robert Lauth, Bill Lenarz, Nancy Lo, Alec MacCall, Shayne MacLellan, Kenny Mais, Arnold Mantyla, Alan Mearns, Richard Neal, Keith Parker, Richard Parrish, Beatriz Payne, Bill Peterson, I. G. Priede, Kurt Schaefer, Richard Sears, Paul Smith, Yoshiro Watanabe, Joe Weinstein, and Marci Yaremko, as well as the *CalCOFI Reports* editor, Julie Olfe. The field work could not have been accomplished without the superb assistance and professionalism of the officers and crews of the NOAA Ship *David Starr Jordan*, the UC Research Vessel *New Horizon*, and the CDFG Research Vessel *Mako*.

Portions of *CalCOFI Reports* (Table of Contents, Committee Report, Fisheries Review, and State of the California Current), as well as extensive data archives, maps of cruises, animations, operational calendars, and general information, are available online at **http://www-mlrg.ucsd.edu/calcofi.html**.

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REVIEW OF SOME CALIFORNIA FISHERIES FOR 1995

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Total annual landings of fishes, crustaceans, echinoderms, and mollusks in California increased by 29% from 1994, to 192,711 metric tons (MT). Ex-vessel economic value of California's 1995 commercial landings rose 6% from the prior year's level, to $158.5 million.

Pelagic wetfish landings increased 53% from 1994. The largest share of this increase was attributed to a 224% increase in Pacific sardine landings (43,450 MT) and a record level of market squid landings (70,278 MT). Increases were also registered for jack mackerel and Pacific herring, but northern anchovy and Pacific mackerel were on the decline.

Groundfish fisheries reversed an eleven-year decline with an 18% increase in total landings and a 42% increase in total ex-vessel value in 1995. This change was due in part to increased take and higher ex-vessel prices for Dover sole and sablefish. California halibut landings also reflected this reversal with a dramatic increase of 50% from the prior year's level.

Statewide, Dungeness crab landings increased 116%, to 5,931 MT. Sea urchin landings were 7% less than in 1994 and declined 18% in northern California. Spot prawn catches decreased by 11%, and sea cucumber catches by 9%. Commercial abalone landings, primarily red abalone, continued to decline in 1995, to a total of 118.6 MT. Commercial and recreational fisheries for pink, green, and white abalones were closed by the Fish and Game Commission as of March 1, 1996.

Swordfish, thresher shark, and mako shark landings decreased by 32%, 26%, and 20% in 1995. Declines in catch can be partly attributed to decreased effort by both drift gill net and longline fleets. California's longline fleet diminished from 22 vessels to 4 vessels by year's end.

California's live-fish fishery continued to expand in 1995 with respect to total landings, number of target species (54), fishing methods, and markets. Statewide landings of live fish were estimated at 449 MT, with a total estimated value of over $3 million.

PACIFIC SARDINE

Rebuilding of the sardine fishery continued in 1995, with the year's directed landings of 41,490 MT ranking highest since the late 1950s. Total landings statewide were approximately 43,450 MT (table 1). Unlike recent years, throughout 1995 directed sardine fishing remained open in both northern and southern California waters,

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

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1974	6	73,810	60	11,362	2,348	13,111	100,697
1975	3	141,486	129	16,415	1,086	10,715	169,834
1976	24	111,503	293	19,882	2,151	9,211	143,064
1977	5	99,504	5,333	44,775	5,200	12,811	167,628
1978	4	11,253	11,193	30,755	4,401	17,145	74,751
1979	16	48,094	27,198	16,335	4,189	19,690	115,542
1980	34	42,255	29,139	20,019	7,932	15,385	114,764
1981	28	51,466	38,304	13,990	5,865	23,510	133,163
1982	129	41,385	27,916	25,984	10,106	16,308	121,828
1983	346	4,231	32,028	18,095	7,881	1,824	64,405
1984	231	2,908	41,534	10,504	3,786	564	59,527
1985	583	1,600	34,053	9,210	7,856	10,275	63,577
1986	1,145	1,879	40,616	10,898	7,502	21,278	83,318
1987	2,061	1,424	40,961	11,653	8,264	19,984	84,347
1988	3,724	1,444	42,200	10,157	8,677	36,641	102,843
1989	3,845	2,410	35,548	19,477	9,046	40,893	111,219
1990	2,770	3,156	36,716	4,874	7,978	28,447	83,941
1991	7,625	4,184	30,459	1,667	7,345	37,388	88,668
1992	17,946	1,124	18,570	5,878	6,318	13,110	62,946
1993	13,843	1,954	12,391	1,614	3,882	42,708	76,392
1994	13,420	3,680	10,040	2,153	2,668	55,395	85,929
1995*	43,450	1,881	8,667	2,640	4,475	70,278	131,391

*Preliminary

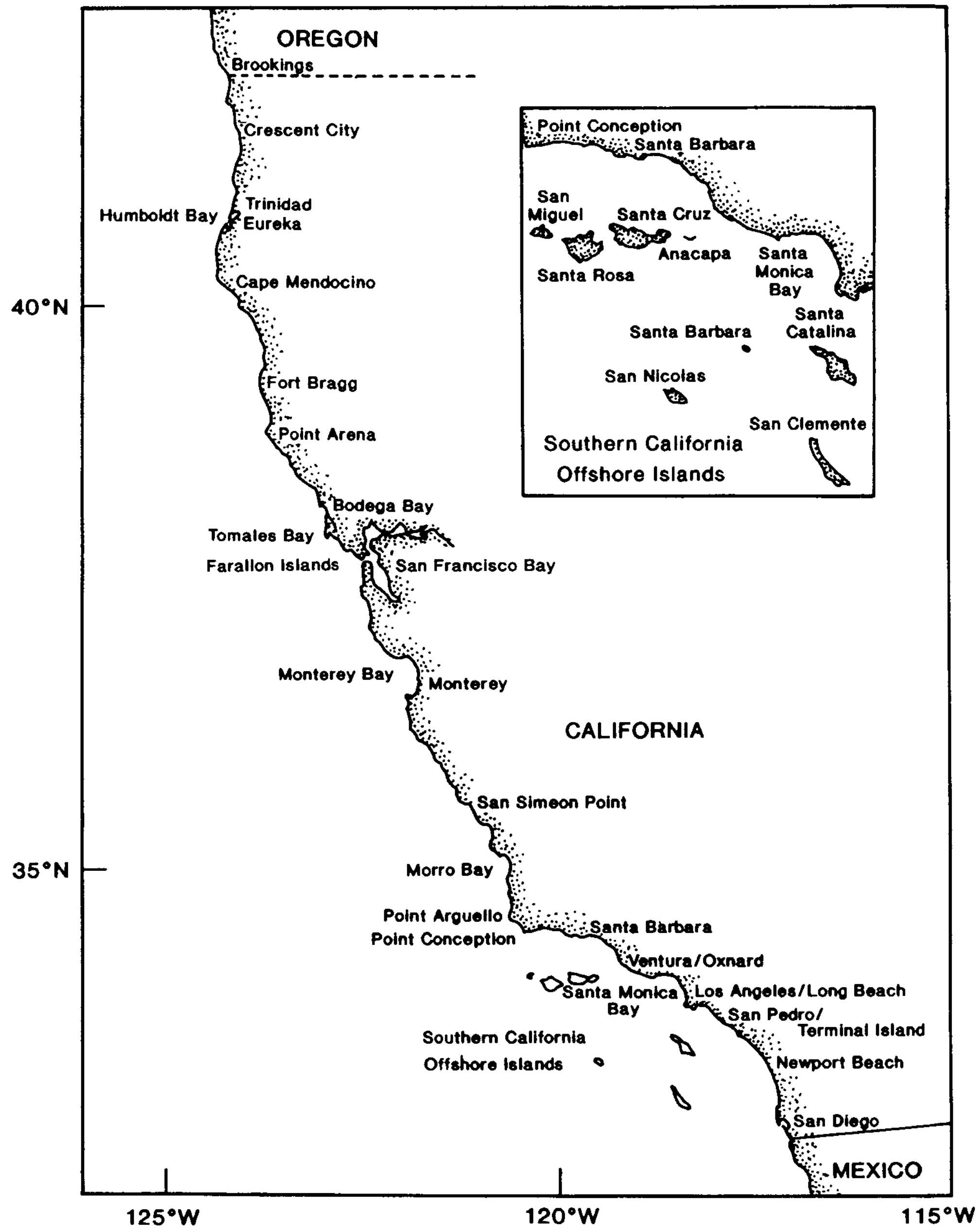

Figure 1. California ports and fishing areas.

because the 48,215 MT quota (up from 9,979 MT in 1994) was not filled by year's end.

Approximately 80% of sardines landed in 1995 were sold at fresh fish markets, while less than 20% were canned as pet food. This ratio has changed dramatically since 1992, when canners were purchasing about 75% of sardines landed.

Fish and Game Code (Section 8150.8) states that annual sardine quotas shall be allocated two-thirds to southern California (south of San Simeon Point, San Luis Obispo County) and one-third to northern California (north of San Simeon Point; figure 1). On October 1, 1995, the California Department of Fish and Game (CDFG) reallocated uncaught quota portions along with 907 MT of incidental reserve and divided evenly between north and south (table 2).

Sardine total biomass as of July 1, 1994, was estimated at 330,493 MT, based on output from CANSAR (Catch-at-age ANalysis of SARdines model). CANSAR, a forward-casting stock assessment model, incorporates both fishery-dependent and fishery-independent data into biomass estimates, including catch and weight-at-age information, landings data, egg and larval abundance, and spotter pilot observations.

TABLE 2
Pacific Sardine Quota Allocations (Metric Tons) for California, 1995

	Initial quota	Reallocated quota	Landings
North	15,768	10,708	4,928
South	31,538	37,507	36,562
Dead bait	454	No limit	0
Live bait	907	No limit	1,960
Total	48,667	48,215	43,450

Current regulations give considerable latitude to CDFG in setting annual sardine quotas. When biomass is estimated to be in excess of 20,000 MT, Fish and Game Code requires that allowable catch must be consistent with resource rehabilitation. The 1995 quota was based on a formula of 15% of total estimated biomass, consistent with pending state sardine legislation.

The price paid to fishermen for sardines held steady this year at approximately $77 per MT at fresh fish markets and $94 per MT at canneries. Two-thirds of this year's sardine catch was landed during the first semester, because tuna availability in summer months and squid availability in November and December shifted fleet attention away from sardine. These species earn a significantly higher market price: $154–$330 per MT for squid and a minimum of $882 per MT for tuna. Industry representatives stated that sardine prices were comparatively low because production costs were high and the end product is of relatively low quality.

In August 1995, the last southern California canner, Pan Pacific, ended production when forced into Chapter 11 bankruptcy. Although Pan Pacific primarily canned tuna, it also canned sardines for human consumption.

While some fish markets are planning to expand production facilities to fill more sardine orders, representatives of others state that they cannot rely on a U.S. quota that could fluctuate widely in volume from year to year because Mexican fisheries are unregulated. Sardine landings from Mexico have equaled or exceeded California's in recent years, and could ultimately affect allowable catch in state waters.

Industry representatives purport that international interest in Pacific sardine is increasing, particularly in China and Japan, which intend to import more sardine. Frozen sardine blocks are increasingly exported for use as fish food in aquaculture facilities. Sardines are also canned abroad for human consumption.

Legislative actions in 1995 also affected sardine fishery management. Most notably, the National Oceanic and Atmospheric Association denied a proposed Coastal Pelagic Fishery Management Plan (CPS). If approved, CPS would have streamlined wetfish management and made it subject to Pacific Fishery Management Council (PFMC) process, shifting management authority of sardines away from California's state legislature. Under development since 1990, CPS had strong support from the commercial fishing industry, CDFG, PFMC, and the sportfishing industry.

During 1995, much effort was devoted to analysis of California State Assembly Bill 76, which proposed several changes in sardine management. Passed in September, the bill eliminated quotas on both live and dead bait fisheries.

PACIFIC MACKEREL

Pacific mackerel (*Scomber japonicus*) landings in 1995 totaled only 8,667 MT, down from 10,042 MT in 1994 (table 1). Since 1990, landings have declined between 14% and 39% annually, with this year's harvest ranking lowest since 1977.

The Pacific mackerel fishing season is specified in Fish and Game Code as July 1 through June 30 of the following calendar year. The 1994–95 fishing season ended with landings of only 9,372 MT against a 14,710 MT quota, and by year's end only 3,428 MT had been landed toward the 1995–96 quota of 9,798 MT.

California Fish and Game Code Section 8412 states that if total Pacific mackerel biomass is less than 18,144 MT, no directed landings are allowed, and if total biomass is greater than 136,080 MT, no limitation on total catch is imposed. A season quota is established for commercial fishing when total biomass determined by CDFG is greater than 18,144 MT, but less than 136,080 MT. Allowable harvest is defined as 30% of total biomass in excess of 18,144 MT.

Despite sharp decreases in allowable take, the 1994–95 fishing season marked the third in a row that the quota was not filled by season's end. Although low mackerel availability is claimed by wetfish fleet representatives to be the largest contributor to lower landings, there was significant wetfish fleet participation in lucrative winter squid and summer tuna fisheries, as well as a fourfold increase in Pacific sardine quota, thus diverting fishing effort from mackerel in 1995.

The ex-vessel price for Pacific mackerel has declined since the early 1980s to almost an all-time low. During 1995, prices ranged from $88 to $198 per MT, and averaged $131. As a result, the 1995 statewide ex-vessel value was $1.2 million, approximately 15% less than in 1994.

Pacific mackerel is a transboundary stock supporting U.S. and Mexican commercial fisheries, and fish have been found as far north as British Columbia in recent years. Several sources of information on the status of Pacific mackerel stocks confirm a decline in biomass compared to late 1970s and 1980s levels. Landing statistics are available since 1978 for both U.S. and Mexican fisheries, and both fleets show reduced catches during recent years. Catch rates for the southern California commercial passenger fishing vessel (CPFV) fleet have also shown declining trends since 1980. Fishery-independent data from aerial observations (spotter pilots) and plankton surveys (California Cooperative Oceanic Fisheries Investigations larval samples) verify declines in abundance compared to the early 1980s. Biomass for July 1, 1995, was estimated at 50,800 MT, based on output from an age-structured stock assessment model known as ADEPT.

A warm-water oceanic regime has dominated the California Current region for about 15 years. This may be responsible for a northern emigration of Pacific mackerel, exacerbating problems of availability to southern California's wetfish fleet. Bycatch of large, presumably older mackerel in Oregon's whiting fishery has been notable in recent years, although incidental catches have remained small (<500 MT) compared to California's directed fishery.

PACIFIC HERRING

Statewide landings for the Pacific herring (*Clupea pallasi*) roe fishery during the 1994–95 fishing season (December to March) totaled 4,475 MT (table 1). Three gill net platoons (376 permittees) in San Francisco Bay's fishery landed a total of 3,155 MT, which was 5.2% over their 2,999 MT quota. Twenty-nine round haul (purse seine and lampara) permittees fishing in San Francisco Bay landed 994 MT, 0.6% less than their 1,000 MT quota. Regulations for Tomales Bay contain provisions for an increased quota based on in-season estimates of spawn escapement. The initial quota of 227 MT for Tomales Bay was increased during the season to 408 MT. Thirty-nine Tomales Bay permittees landed 250 MT. Three of four Humboldt Bay permittees participated in this fishery and landed 49 MT, 9% under their 54 MT quota. Three Crescent City permittees landed one-half ton less than their quota of 27 MT.

Ex-vessel prices for herring caught during the 1994–95 fishing season with 10% roe recovery ranged from $1,200 to $1,400 per short ton; an additional $120 to $140 per short ton was paid for each percentage point over 10%. The total ex-vessel value of roe fisheries was $8.2 million, slightly lower than the 10-year average of approximately $9 million.

Ten permittees participated in the San Francisco Bay herring roe-on-kelp fishery. They harvested 12 MT of roe-on-kelp, which was 15% of the quota. Total estimated ex-vessel value of roe-on-kelp fishing was $310,000, with prices ranging from $12 to $15 per pound.

CDFG biologists estimated spawning biomass for San Francisco and Tomales Bay populations. No estimates were made for Humboldt Bay or Crescent City Harbor. Hydroacoustic and spawn-deposition surveys were used to estimate spawning biomass in San Francisco Bay, and spawn-deposition surveys were used in Tomales Bay.

Herring spawning biomass estimated for San Francisco Bay in 1994–95 was 36,288 MT, identical to last season's estimate but below the long-term average of 49,900 MT. Approximately 66% of the spawning population was composed of two- and three-year-old fish from the 1992 and 1993 year classes. These two year classes, in addition to four-year-olds from the 1991 year class, represented the highest number of two-, three-, and four-year-olds seen in the spawning population in recent years, an encouraging sign for the future.

The 1994–95 spawning biomass estimate for Tomales Bay was 3,610 MT, an increase of 62% from last season's estimate of 2,234 MT. The spawning biomass estimate was slightly above the 13-year (post–El Niño) average of 3,192 MT, but below the 22-year average of 4,574 MT. The increase in spawning biomass was attributable to good recruitment of two- and three-year-old herring as well as to adequate representation of older year classes. Historical data indicate that the spawning biomass in Tomales Bay usually drops following warm water conditions (as occurred in early 1995); thus the spawning biomass in Tomales Bay is expected to drop next season.

MARKET SQUID

California's market squid (*Loligo opalescens*) landings in 1995 were 70,278 MT (table 1), including 67,080 MT (95.4%) in southern California ports and 3,198 MT (4.6%) in central and northern California ports. Total landings are a statewide record high and 26.8% above the previous high record of 55,405 MT in 1994 (table 1). Southern California landings increased 69.9% (27,608 MT) over 1994 total landings of 39,472 MT. Conversely, central–northern California landings decreased 79.9% (12,735 MT) from 1994's total of 15,933 MT.

Southern California squid fishing typically occurs during fall and winter, but landings continued throughout 1995. Southern California landings for the first quarter of 1995 totaled 15,304 MT. April and May were the slowest months, with 163 and 232 MT landed, respectively. From June through September, normally a period when very little or no squid are landed, 6,577 MT were landed. Landings from October through December totaled 44,804 MT.

Three ports received most (98%) of southern California's landings. Port Hueneme received 41,188 MT (61.4%); San Pedro, 17,409 MT (26%); and Ventura, 7,271 MT (10.8%). Port Hueneme dominated landings, primarily because many central–northern California boats fished Channel Island locations near Santa Barbara and made landings there. Squid landed by central–northern

California boats were trucked to Monterey Bay for processing.

Squid fishing in central–northern California typically takes place in spring through fall. In past seasons, squid landings have begun in late April, sometimes continuing into December. In 1995, fishing began in May, when 7 MT were landed. In June, 388 MT were landed; in July, 508 MT. Landings peaked in August with 1,443 MT; 84 MT were landed in October; and 1 MT was landed in November. In 1995, Monterey Bay area landings were 2,449 MT, an 82% decrease from 13,627 MT in 1994. Landings in ports north of Monterey Bay totaled 749 MT, a 68% decrease from 2,306 MT in 1994.

As in previous years, most squid was frozen or canned for human consumption, mostly to supply overseas markets. Exports to Europe continued strong in 1995. Developing markets in other parts of the world, notably China, continued to expand, contributing to increased demand for squid. Internationally, market demand in 1995 far exceeded fishery ability to meet demand. Domestically, a small percentage of squid was used for bait, both live and frozen, and a very small percentage was used for human consumption. Live bait fishing continued to be centered mostly in southern California, with only a minimal amount caught in Monterey Bay.

Ex-vessel prices in 1995 were slightly higher for squid landed in central and northern California than in southern California. This represents a change from previous patterns. Ex-vessel price for squid averaged $282 per short ton in southern California, and about $291 per ton in central–northern California. By comparison, 1994's ex-vessel price averaged $255 per ton in southern California, $294 per ton in Monterey Bay, and $260 per ton in northern California. In 1995, southern California ex-vessel prices fluctuated from $160 to $300 per ton from January through October, depending upon size and availability of squid. In November, prices reached $400 per ton and declined to about $250 per ton in December. In central–northern California, prices were more uniform and fluctuated near annual averages of $291 per ton.

In many years previous to 1995, southern California ex-vessel prices were substantially lower than those in the rest of the state. Southern California's average annual prices have ranged from about $150 to $250 per ton, while in central–northern California, prices have generally averaged around $300 per ton. During the low supply years of 1983–84 (El Niño period), ex-vessel prices in central–northern California averaged approximately $400 and $480 per ton.

In 1995, the total ex-vessel value for squid was approximately $21.9 million, a 35% increase from 1994's $16.2 million. Total ex-vessel value in southern California was approximately $20.9 million, 95.4% of the statewide total.

A growing concern by California fishermen has developed in recent years over expanding fleet capacity spurred on by increased landings in recent years and increased market demand. Because of this, fishermen have attempted to introduce legislation to control the number of boats participating in California's squid fishery. In 1993 and 1994, limited entry was supported mainly by central–northern California fishermen, but no limited-entry regulations resulted from those efforts. In 1995, southern California fishermen took a more active interest and, by the end of the year, limited entry was supported by nearly all squid fishermen as well as by southern California's recreational fishing fleet. By year's end, fishermen were again attempting to introduce legislation to control the number of squid boats. By this time, many previously opposed processors supported limited entry. However, management measures such as limited entry, seasons, and quotas will not control resource fluctuations caused by changing environmental conditions, so bonanza-bust scenarios in squid landings will likely remain.

CDFG is concerned about the rapidly expanding squid fishery, but does not believe that squid resources are overharvested. Although landings are up, the quality and size of squid remain good. Furthermore, in Monterey Bay from Moss Landing south to Yankee Point, 64% of each week is closed to squid fishing (from noon Friday to midnight Sunday and from noon to midnight Monday–Thursday). North of Moss Landing, squid fishing is closed only from noon Friday to midnight Sunday. Closures provide some protection for squid to spawn undisturbed in Monterey Bay. There are no similar restrictions on squid fishing in southern California.

GROUNDFISH

The California commercial groundfish harvest for 1995 was 28,571 MT, with an ex-vessel value of approximately $34 million. Total 1995 landings increased nearly 18%, or 4,415 MT, from 1994. Total ex-vessel value increased by 42%. Dover sole (*Microstomus pacificus*), thornyheads (*Sebastolobus* spp.), sablefish (*Anoplopoma fimbria*), rockfish (*Sebastes* spp.), and Pacific whiting (*Merluccius productus*) continued to dominate harvests. In 1995, downward trends in total harvest since 1990 were reversed in spite of more restrictive Washington-Oregon-California (WOC) landing regulations, and significant increases in harvest were noted for most categories (table 3). Reasons for increases include higher ex-vessel prices for species such as sablefish and thornyheads, and a general increase in market demand for groundfish.

Distribution of 1995 landings by gear showed trends evident during three past years. The bottom and midwater trawl component rose to 84.6%, up from 82.0% in 1994, 77.9% in 1993, and 75.2% in 1992. The line

TABLE 3
California 1995 Groundfish Landings (Metric Tons)

Species	1994	1995	Percent change
Dover sole	4,462	6,043	35
English sole	432	499	16
Petrale sole	524	593	13
Rex sole	548	691	26
Other flatfish	682	1,253	84
Widow rockfish	930	1,712	46
Bocaccio	887	785	−11
Other rockfish	5,406	5,514	2
Thornyhead	3,282	3,609	10
Lingcod	546	538	−1
Sablefish	2,151	2,716	26
Pacific whiting	3,662	4,091	12
Other groundfish	644	527	−18
Total	24,156	28,571	18

portion of the catch continued to drop, from 17.7% in 1992 to 15.8% in 1993, 14.0% in 1994, and 11.4% in 1995. Trap components rose slightly to 1.3% in 1995 from 1.0% in 1993 and 1994. Setnet groundfish landings dropped from 5.3% in 1993 to 3.0% in 1994, and to 2.7% in 1995.

License limitation, implemented by PFMC in 1994, continued in 1995. Annual harvest guidelines were again allocated between a permitted limited-entry (L.E.) fleet and nonpermitted open-access (O.A.) fleet, with separate trip limits for each sector. PFMC continued harvest guidelines that affected California's Dover sole, thornyhead, and trawl-caught sablefish (the DTS complex), *Sebastes* complex, widow rockfish (*Sebastes entomelas*), bocaccio rockfish (*S. paucispinis*), yellowtail rockfish (*S. flavidus*), lingcod (*Ophiodon elongatus*), and Pacific whiting fisheries. In addition, PFMC established a harvest guideline for canary rockfish (*Sebastes pinniger*), and separate harvest guidelines for shortspine thornyhead (*Sebastolobus alascanus*) and longspine thornyhead (*Sebastolobus altivelis*). PFMC continued to use cumulative landing limits as well as trip limits during 1995 in order to meet its objective of staying within annual harvest guidelines while providing a year-round groundfish fishery. Cumulative landing limits were applied to full calendar months during 1995. Lingcod were added to species lists with trip and size limits in 1995.

As in 1992, 1993, and 1994, WOC-area Pacific whiting resources were allocated between at-sea and shoreside processors. This was the second year of a three-year allocation plan which reserves 40% of annual harvest guidelines for shore-based processing after the first 60% is taken in open competition. At-sea processing of whiting was again restricted to waters north of California. In 1995 the WOC area 176,571 MT harvest was near the 178,400 MT harvest guidelines. In California, six midwater trawl vessels fishing off Eureka and Crescent City landed 4,091 MT shoreside, a small increase from the 3,662 MT landed in 1994. A whiting observation program, established in 1992 to monitor bycatch in shoreside whiting landings, continued through 1995. The California salmon bycatch rate was 0.017 salmon per metric ton of Pacific whiting—a slight increase from last year's 0.012 rate. All salmon observed were chinook (*Oncorhynchus tshawytscha*). The nonsalmon bycatch rate in observed landings for 1995 was 28.8 pounds per metric ton of whiting.

One particular problem for PFMC during 1995 was management of the DTS complex. The rate of thornyhead landings increased substantially in 1993 and 1994 due to increased ex-vessel value and reduced opportunities for other species. For two thornyhead species, PFMC decided to establish separate harvest guidelines. This had previously been considered impractical because of the difficulty in distinguishing species. However, preliminary efforts by the trawl industry and processors in late 1994 indicated that most fishermen are able to identify species with a minimum of training. This provided an opportunity to protect less abundant shortspine thornyhead without overly restricting longspine thornyhead landings. For the first time, regulations required sorting of all four DTS species. Sablefish prices remained high, making Dover sole the least valuable of the complex.

Cumulative monthly limits for the DTS complex were initially set at 35,000 pounds for north of Cape Mendocino and 50,000 pounds for south of Cape Mendocino. Within those monthly limits, total thornyhead landings were limited to 20,000 pounds, of which not more than 4,000 pounds could be shortspine thornyhead. Trawl-caught sablefish was initially limited to 6,000 pounds per month. Sablefish was further limited to 1,000 pounds or 25% of the total DTS complex per trip (whichever was greater). Thornyhead landings escalated rapidly in February. In a March conference call, PFMC opted to reduce thornyhead landings to 15,000 pounds, of which no more than 3,000 pounds could be shortspine, effective April 1.

At its April 1995 meeting, PFMC increased trawl-caught sablefish monthly limits to 7,000 pounds, in conjunction with increasing harvest guidelines, effective May 1. Trip restrictions on trawl-caught sablefish were removed on July 14, 1995. In September, PFMC further reduced the total thornyhead monthly limit to 8,000 pounds, of which no more than 1,500 pounds could be shortspine thornyhead. It became evident by October that the sablefish and shortspine thornyhead components of the DTS complex continued to be harvested at a high rate and that harvest guidelines would be exceeded by year's end. As a consequence, PFMC opted to prohibit the take of thornyheads and trawl-caught sablefish, while limiting Dover sole to 3,000 pounds cumulative per vessel during December.

Coastwide catch of Dover sole was 10,618 MT, an increase of 1,278 MT from 1994 landings but still 2,982 MT lower than the 13,600 MT harvest guideline in 1995. Reduced market demand and a redirection of effort toward more valuable sablefish and thornyheads within the DTS complex resulted in reduced production. California 1995 landings of 6,043 MT represent a 35% increase over last year's total, and made up 57% of the total WOC Dover sole landings.

For 1995, PFMC set the shortspine thornyhead harvest guideline at 1,500 MT and the longspine harvest guideline at 6,000 MT. Total WOC-area landings of shortspine and longspine thornyhead were 5,823 MT and 1,782 MT. Shortspine landings exceeded the harvest guideline by 19%. California landed 3,609 MT, or 48% of the total WOC thornyhead catch.

On the basis of sablefish stock assessments conducted in 1994, PFMC recommended that acceptable biological catch (ABC) be increased from 7,000 MT in 1994 to 7,800 MT for 1995 (excluding INPFC Conception area), and an ABC of 425 MT was established for the INPFC Conception area. The WOC-area L.E. trawl/L.E. fixed-gear sablefish allocation remained at 58/42. After respective tribal and open-access allotments of 780 MT and 463 MT were granted, 6,557 MT remained for allocation between L.E. trawl (3,803 MT; 58%) and L.E. fixed-gear (2,754 MT; 42%) fisheries. Total nontribal WOC-area landings of sablefish in 1995 were 7,095 MT, about equal to the combined L.E./O.A. harvest guideline. California accounted for 2,716 MT, or 38% of the total WOC nontribal catch. WOC-area trawl sablefish landings were 3,734 MT, about 2% under trawl harvest guidelines. California trawl vessels landed 1,482 MT, or about 40% of the WOC-area trawl-caught sablefish.

Management of the 1995 L.E. fixed-gear sablefish fishery was substantially different from previous years. In past years, the PFMC attempted to start unrestricted season ("derby") fishing concurrent with Alaska fisheries, forcing vessels to choose between Alaska or the WOC area. In spite of this strategy and the implementation of limited entry for groundfish, the 20-day 1994 season was the shortest yet. In 1995, Alaska went to an individual quota (IQ) system with a longer season, and effort in West Coast derby fishing was expected to increase dramatically. Since there was no longer a reason to tie the derby opening to the Alaska fishery, the fixed-gear industry recommended that PFMC delay the derby until August, when larger fish are more available and wind patterns more favorable. To help keep landings within harvest guidelines, and as a compromise between large and small producers, PFMC intended that the derby be managed to take no more than 70% of the nontrawl L.E. allocation, with the remainder to be taken in a cumulative-limit mop-up fishery. The season was set to last 7 days, August 6–13. The derby fishery took about 78% of the allocation, and a monthly limit for the mop-up fishery was set at 5,500 pounds.

Total WOC-area L.E. fixed-gear sablefish landings of 3,361 MT were about 18% higher than L.E. fixed-gear allocations. The O.A. fishery, limited to 300 pounds per trip, landed approximately 502 MT, exceeding the 460 MT O.A. allocation by about 8%. California fishermen (L.E. and O.A.) landed 1,234 MT, or about 38% of total nontribal WOC-area fixed-gear landings.

On January 1, the L.E. monthly cumulative limit for the *Sebastes* complex (including yellowtail, canary, and bocaccio rockfish; excluding widow rockfish) was set at 100,000 pounds south of Cape Mendocino and 50,000 pounds north of Cape Mendocino to Cape Lookout, Oregon. Within the 100,000-pound limit, no more than 30,000 pounds could be bocaccio rockfish, and no more than 6,000 pounds could be canary rockfish. Within the 50,000-pound limit, no more than 30,000 pounds could be yellowtail rockfish and no more than 6,000 pounds could be canary rockfish. The O.A. cumulative limit was set at an overall 40,000 pounds with no more than 10,000 pounds per trip for vessels using line gear. Bocaccio, yellowtail rockfish, and canary rockfish limits were set equal to L.E. limits.

California's *Sebastes* complex landings (southern harvest guideline) dropped from 8,863 MT in 1992 to 7,315 MT in 1993, and to 6,293 MT in 1994, but in 1995 total landings increased to 7,119 MT. The 1995 rockfish harvest included 785 MT of bocaccio, an 11% drop from 1994's 887 MT.

For 1995, PFMC set widow rockfish harvest guidelines at 6,500 MT and initially set the cumulative limit at 30,000 pounds. Because early landings were well below those for the same time last year, PFMC increased monthly cumulative trip limits from 30,000 to 45,000 pounds on July 14. The fishery was allowed to run at this level through December. The total 1995 landed catch of 6,797 MT in WOC was 297 MT over harvest guidelines. California landings of 1,712 MT were 25% of the WOC total.

A WOC-area harvest guideline for lingcod was set at 2,400 MT. This included 900 MT set aside for recreational gear and 1,500 MT allocated for all commercial gears. The PFMC adopted a 22-inch minimum size limit and a cumulative monthly limit of 20,000 pounds for all commercial gear. Total WOC-area commercial lingcod landings were near commercial allocations at 1,415 MT. California commercial fishermen landed 538 MT, or 36% of the WOC commercial allotment.

In 1996, PFMC will be considering a number of options for long-term management of limited-entry fixed-gear sablefish fishing for 1997 and beyond. Also, the current whiting allocation plan expires in 1996, so during

1996 PFMC will begin to establish a new allocation plan. A new bocaccio rockfish assessment, incorporating information collected during 1995 shelf surveys, is scheduled for 1996, and results will be used to reevaluate harvest guidelines for 1997. PFMC is also working on an analysis of remaining rockfish, to be completed in 1996. Results will be used to derive a quantitative ABC. For the L.E. fishery, PFMC has recommended that all monthly cumulative vessel limits be increased to two months in 1996.

ABALONE

Abalone (*Haliotis* spp.) have historically supported valuable commercial and recreational fisheries in California. In recent times, landings and resources have declined from disease, excessive harvest, and reestablishment of California sea otter populations. Statewide preliminary 1995 landings were: red abalone, 110.0 MT (down 22%); pink abalone, 7.9 MT (up 11%); green abalone, 0.7 MT (down 6%); and white abalone, 17.2 kg (up 15%). Red abalone constituted 92.6% of total commercial landings, with pink making up most of the remaining 6.7%. Green and white abalone made up only 0.06% and 0.01% of total landings. Increased landings of pink abalone were probably due to the anticipated closure of the fishery for this species. Black abalone has been closed since 1993.

A CEQA document describing abalone fishery conditions was completed in 1995, and caused the Fish and Game Commission to close all commercial and recreational harvest of pink, green, and white abalone for two years, beginning March 1, 1996. It is anticipated that this closure will be extended.

The condition of the white abalone resource has been the subject of fishery-independent research. Few live white abalone have been found in the traditional habitat. For example, after a CDFG survey of about 30,600 m^2 of suitable habitat at 15 locations, only three live individuals were found. There is concern that populations of this species have been reduced to levels that would make its continued existence questionable.

Withering syndrome (WS) continues to affect black abalone. It has been detected in central California populations as far north as Cayucos, San Luis Obispo County. Nevertheless, a few large (old) individuals still remain at many locations in the Channel Islands, and there are signs of newly recruited black abalone. These may be significant indications of a WS-resistant strain of black abalone. These abalone would be important in any natural or human-enhanced resource recovery.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during 1994–95 totaled 5,931 MT, an increase of 3,179 MT from 1993–94, and well above the ten-year average of 4,153 MT.

In northern California, crab season opened on December 1, 1994, after a price settlement of $1.40 per pound. A fleet of 385 vessels landed approximately 4,519 MT at Crescent City, Trinidad, Eureka, and Fort Bragg. Crescent City accounted for 2,556 MT, followed by Eureka (1,029 MT), Trinidad (494 MT), and Fort Bragg (440 MT).

San Francisco–area Dungeness crab fishing opened on November 8, 1994, but a price dispute delayed production until November 27, when a price of $1.50 per pound was agreed upon. Total crab landings increased by 1,059 MT from the previous season to a total of 1,304 MT. Crab fishermen landed 595 MT at Bodega Bay and 709 MT at ports in San Francisco Bay. Monterey and Morro Bay contributed 108 MT to total landings.

Significant legislation affected the Dungeness crab fishery; Assembly Bill 3337, signed by Governor Wilson in September 1994, became effective on April 1, 1995. This bill required that vessel permits be issued for commercial Dungeness crab, and established criteria for issuing those permits. The bill also provided for transfer of permits under specified conditions, convened a Dungeness crab review panel to review applications for vessel permits and permit transfers, and permitted the CDFG director to delay opening the Dungeness crab season if such a delay were recommended by the California Seafood Council. Provisions regarding the issuance of Dungeness crab vessel permits and permit transfers were amended in 1995. Additional legislation excluded the Dungeness crab fishery from jurisdiction of the California Seafood Council, and CDFG authorized a quality testing program before the opening of the Dungeness crab season north of Sonoma County.

The CDFG director appointed four Dungeness crab review panel members, who processed over 300 applications for vessel permits and permit transfers. A total of 671 Dungeness crab vessel permits were finally issued for 1995–96.

SPOT PRAWN

Preliminary 1995 spot prawn (*Pandalus platyceros*) landings totaled 176 MT, an 11% decrease from the 198 MT landed in 1994 (figure 2). Approximately 134 MT of spot prawn were harvested by trawl, while 42 MT were taken with trap gear. Eighty-four percent of the combined trawl/trap spot prawn catch was landed and sold live, thereby commanding significantly higher ex-vessel prices. Ex-vessel prices ranged from $4.50 to $12.25/lb live and between $2.50 and $3.50/lb dead. The average ex-vessel price for all spot prawn landed in 1995 was $6.25/lb, up about 50 cents from 1994.

Fifty-one percent of the 1995 spot prawn trawl catch

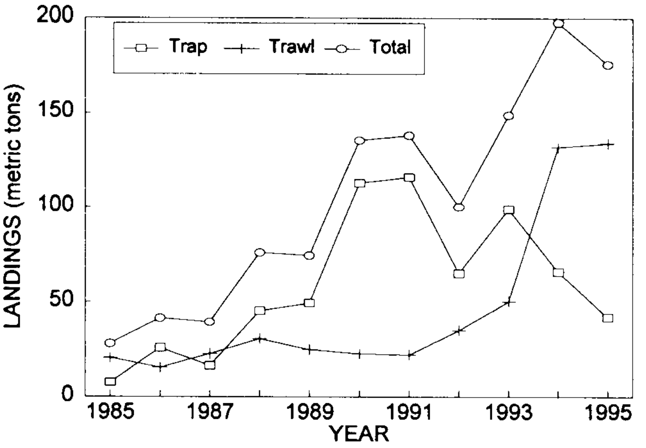

Figure 2. California spot prawn landings, 1985–95.

was taken in Santa Barbara Channel, while trawls conducted between Point Piedras Blancas (San Luis Obispo County) and Point Conception (Santa Barbara County) provided 45% of the spot prawn landings. Unlike previous years, there was little trawl activity along Monterey's coast. Only 4 trawl vessels made landings from this area, as compared to 15 vessels in 1994.

During 1995, southern California spot prawn trappers accounted for 88% of total catch. Southern California trap fishermen continued to fish around the Channel Islands and along submarine canyons (Redondo, Newport, and La Jolla Canyons). Traps were also fished at Tanner and Cortez Banks but were not productive. In northern California, fishermen continued to set traps at Monterey and Carmel Canyons.

In 1995, the Fish and Game Commission modified existing regulations for spot prawn trawl fishing, and adopted regulations for the spot prawn trap fishery, which was previously unregulated. Impetus for these regulations was a reduction of catch per unit of effort (CPUE) in both prawn fisheries despite increases in statewide landings. Trawl fishery CPUE has declined at a rate of about 11% per year since 1989. For trap fishing, CPUE has declined at a higher rate, averaging about 21% per year since 1988.

Changed regulations for trawl fishing expanded area closures to include all waters south of Point Arguello for November 1 to January 15. Before this change, spot prawn trawlers could not fish between Point Arguello and Point Dume from November 1 to January 31. A time/area closure was also initiated in the trap fishery. Trap closures covered the same territory as trawl closure but ran from January 16 to March 31. In addition, spot prawn trap fishermen were limited to 500 traps each, and a mesh size restriction of 2.5 by 2.5 cm was implemented. The Commission also provided for continued use of the commonly used Fathomplus trap until a trap retention study has been completed.

SEA CUCUMBER

Sea cucumber landings statewide were 267.6 MT in 1995, a decrease of 26 MT since 1994. The catch was composed of 75.2 MT of warty sea cucumber (*Parastichopus parvimensis*) and 192.4 MT of California or giant red sea cucumber (*P. californicus*). Commercial trawlers in southern California harvested giant red sea cucumbers, while divers harvested warty cucumbers by hand. Most sea cucumbers were landed at Terminal Island, Ventura, and Santa Barbara Harbors. The main fishing grounds for giant red sea cucumbers were Santa Barbara Channel and Santa Catalina Channel at depths of 30 to 90 fathoms. A small quantity of giant red sea cucumber (2 MT) was taken by divers off central California. Warty sea cucumbers were harvested as far south as San Diego, but most harvesting occurred in waters off four northern Channel Islands at 6 and 10 fathoms.

The average price for both warty and giant red sea cucumbers was $0.70/lb. and ranged from $0.20 to $1.00/lb. The two-tier price structure seen in past years, with a higher price paid for diver-harvested warty sea cucumber, no longer seemed to be employed by dealers. Most of the sea cucumber landings were dried and exported to Hong Kong and Taiwan. The end product, called *trepang*, sold for $4.00 to $13.00/lb. A small portion of total landings was distributed and sold within the United States.

California's sea cucumber fishery began near Los Angeles around 1978, and averaged under 45 MT annually until 1982, when a trawl fishery developed near Santa Barbara. During the next eight years, annual landings increased gradually (figure 3). An influx of trawlers, predominately out of the Los Angeles port area, greatly expanded fishing effort and catch in 1991. From 1991 through 1995, sea cucumber landings exceeded 260 MT (figure 3). Since 1992–93, sea cucumber fishing has been a limited-entry fishery based on previous minimum sea

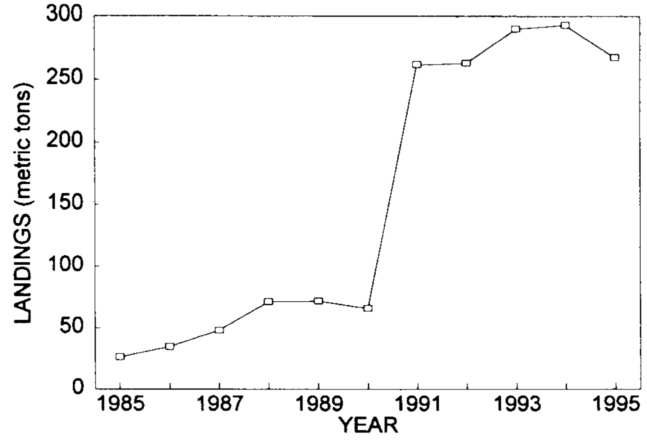

Figure 3. California sea cucumber landings, 1985–95.

cucumber landings of 50 pounds. There were 115 sea cucumber permittees in 1995. Landing receipt data indicate that 79 permittees on 28 trawlers and 39 dive boats actively participated during 1995.

Sea cucumbers have a short life span, low age at maturity, sporadic recruitment, and high natural mortality. Species with these characteristics can be vulnerable to overfishing, but it is expected that southern California populations of warty and giant red sea cucumber can sustain current harvest levels, given the effort-limiting permit restrictions. In central and northern California, giant red sea cucumber is currently caught by a small number of individuals who landed 2.6% of diver-harvested sea cucumbers in 1995.

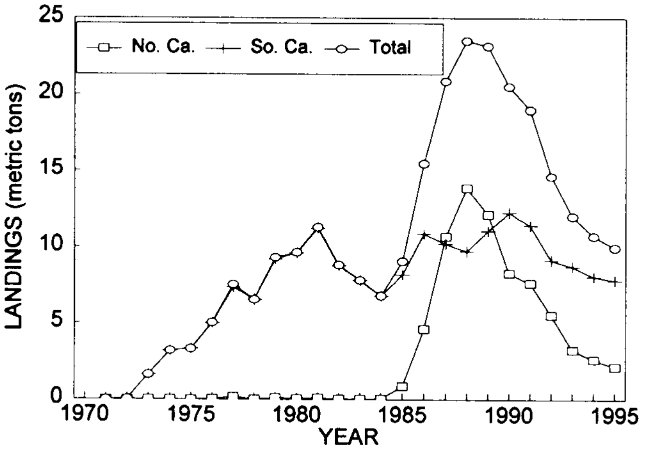

Figure 4. California sea urchin landings, 1970–95.

SEA URCHIN

California's red sea urchin (*Strongylocentrotus franciscanus*) landings peaked at 23,577 MT in 1988. Since then, catches and CPUE have trended downward at different rates in northern and southern California, with 9,991 MT landed statewide in 1995 (figure 4). West coast sea urchin catches and CPUE from British Columbia to Baja California have generally declined during the last half-decade following a period of rapid fishery expansion. The 1995 northern California catch fell by 18% from 1994, while southern California dropped by only 3%, the smallest decline since 1990. Fishing effort in southern California shifted from the northern Channel Islands south to San Clemente Island. Landings in Santa Barbara declined by 38% in 1995, and increased by 91% at Los Angeles area ports, which largely service the southern Channel Islands.

Low average ex-vessel prices and declining harvestable stocks were significant factors driving northern California divers south in 1995 (table 4). Bodega Bay prices fell by an average of 13% from 1994, the sharpest decline in northern California. Despite the drop in catch and value from 1994, $22.2 million ex-vessel made red sea urchin the single most valuable species landed in California, surpassing market squid.

Sea urchin permittees peaked at 915 in the 1987–88 permit year, falling to 576 by 1994. In 1994, 41 northern California permittees out of 207 who fished landed 50% of the 2,630 MT total catch. In southern California, 50% of the 8,063 MT harvested was caught by 104 out of the 450 who fished that region. In 1995 CPUE (kg/diver-hour) ranged from a low of 122 at Bodega Bay and Fort Bragg to 145 kg/hr at Albion. This represents a continued leveling off of CPUE that began in 1993 in northern California. Southern California CPUE ranged from 49 kg/hr in coastal Los Angeles to a high of 155 kg/hr at San Nicolas Island. The relatively minor purple sea urchin fishery represented only 0.4% of the total sea urchin catch (37 MT), split evenly between northern and southern California.

TABLE 4
Preliminary California Commercial Red Sea Urchin Landings, 1995

Port	Landings (MT)	Percentage of catch	Value	$/kg
Crescent City	34.2	.3	$64,789	1.89
Fort Bragg	574.7	5.8	$1,151,550	2.00
Albion	433.5	4.3	$858,822	1.98
Point Arena	727.4	7.3	$1,471,690	2.02
Bodega Bay	340.3	3.4	$597,043	1.75
Other N. Calif.	54.4	.5	—	—
N. Calif. subtotal	2,164.5	21.7	$4,255,722	—
Santa Barbara	2,252.7	22.6	$5,232,803	2.32
Oxnard-Ventura	2,396.7	24.0	$5,549,597	2.32
Los Angeles	2,517.4	25.2	$5,380,950	2.14
San Diego	659.4	6.6	$1,828,690	2.77
S. Calif. subtotal	7,826.1	78.3	$17,991,978	—
Grand totals	9,990.6	—	$22,247,700	—

SWORDFISH AND SHARKS

Swordfish (*Xiphias gladius*) landings were 788 MT in 1995, 32% less than in 1994 (table 5). During the past decade, drift gill net fishing accounted for the majority of total landings. This year, 65% of landings were taken with drift gill nets, up from last year's 45%, as longline landings decreased from 45% to 24%. Although 22 vessels used longline gear outside the U.S. Exclusive Economic Zone (EEZ) and landed swordfish in southern California ports in 1995, only 4 were based out of California by year's end. As usual, harpoon landings constituted 8% of total catch. Sixty-one percent of total swordfish catch was landed in southern California ports.

Gear type affected swordfish ex-vessel prices in 1995. Typically, fishermen landing drift gill net–caught swordfish received $3.00 to $5.00 per pound, whereas longline-caught fish commanded only $2.00 to $4.00 per pound. Fishermen landing harpoon-caught swordfish received the highest prices: $4.00 to $6.00 per pound.

Landings of common thresher shark (*Alopias vulpinus*) declined 20% to 155 MT in 1995, which continues the decade-long declining trend in landings. Thresher sharks are taken primarily with drift gill nets (80%), followed by set gill nets (12%) and assorted other gears (8%). Eighty-six percent of total landings continue to be made in southern California, with San Diego the top port (39%). Ex-vessel prices varied from $1.00 to $2.00 per pound.

Shortfin mako shark (*Isurus oxyrinchus*) landings in 1995 were 65 MT (table 5), a decrease of 26%. Eighty-one percent of total catch was landed in southern California ports, at ex-vessel prices between $0.50 and $1.50 per pound. Mako sharks are caught primarily by drift gill net (76%), with 8% landed by longline vessels operating outside the EEZ, hook and line gear accounting for approximately 7%, and 9% landed incidentally in other fisheries.

TABLE 5
Landings of Swordfish and Selected Shark Species (Metric Tons)

	Swordfish	Common thresher shark	Shortfin mako shark
1985	2,362	700	103
1986	1,749	276	215
1987	1,246	239	274
1988	1,129	250	222
1989	1,296	295	177
1990	851	210	262
1991	711	344	151
1992	1,068	179	97
1993	1,218	162	84
1994	1,165	194	88
1995*	788	155	65

*Preliminary

TABLE 6
Preliminary California Commercial Halibut Landings, 1995

Port	Catch (MT)	Percentage of catch	Value
Eureka	4.35	1.25	$21,299
Bodega Bay	6.69	1.93	$33,203
San Francisco	145.02	41.77	$821,660
Monterey	35.29	10.17	$182,071
Morro Bay	23.29	6.71	$147,894
Santa Barbara	70.04	20.17	$500,269
Los Angeles	49.00	14.12	$353,281
San Diego	13.48	3.88	$106,108
Totals	347.17		$2,165,784

CALIFORNIA HALIBUT

Commercial landings of California halibut (*Paralichthys californicus*) rebounded to approximately 347 MT in 1995 (table 6), a 49.5% increase over the 232 MT landed in 1994 (figure 5). Increased landings in 1995 also marked an end to downward landing trends since 1991. The Marine Resource Protection Act of 1990 (Proposition 132), which restricts gill netting in California waters (out to three miles) south of Point Arguello, has most likely contributed to the lowered landings seen in recent years.

San Francisco led California in halibut landings, with 42% of total catch by weight, followed by Santa Barbara (20%), and Los Angeles (14%). All ports in California experienced an increase in halibut landings over 1994. Trawl gear was the most effective fishing method, landing 50% of the total catch (174 MT), followed by set gill net (25%; 86 MT) and hook and line (22%; 77 MT).

Ports landing mostly with trawl gear include Eureka (68%), San Francisco (62%), Morro Bay (77%), and Los Angeles (56%). Set longline gear contributed the highest percentage by weight for Monterey (50%), Santa Barbara (59%), and San Diego (95%). Only Bodega Bay landings were primarily from hook and line (98%).

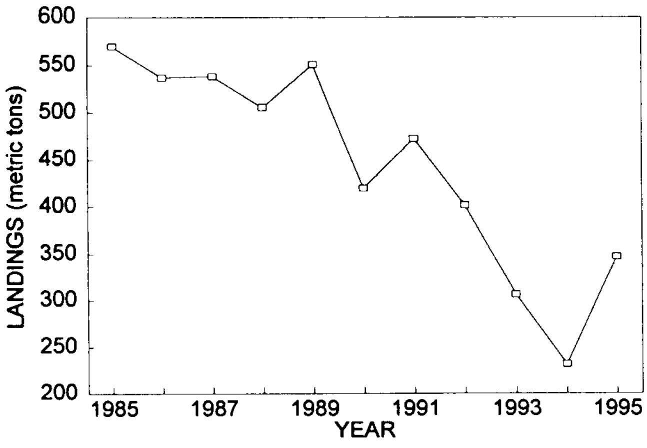

Figure 5. California halibut landings, 1985–95.

Statewide, the ex-vessel price for halibut ranged from \$0.80 to \$5.50 per pound, with an average of \$2.84. Ports south of Monterey averaged \$1.00 more per pound for halibut than ports to the north, probably because of a more developed live-fish market in southern California. The total value for halibut landings in California for 1995 was approximately \$2.17 million.

OCEAN SALMON

In 1995, PFMC again enacted restrictive commercial and recreational ocean salmon regulations in California to (1) protect endangered chinook (*Oncorhynchus tshawytscha*) stocks—Sacramento River winter chinook and Snake River fall chinook, (2) ensure fall chinook spawner escapement goals for Klamath, Sacramento, and Oregon coastal rivers, and (3) protect depressed coho (*Oncorhynchus kisutch*) stocks coastwide.

In California, commercial fishing for ocean salmon was allowed only south of Horse Mountain, with various time and area closures enacted during 1995 (May 1–September 30). A minimum size limit of 26 inches remained in effect. More than 2,741 MT (6 million lbs; 629,300 fish) of dressed chinook were landed by commercial trollers, who fished approximately 21,600 days during 1995. Ex-vessel prices for dressed salmon averaged \$1.76 per pound, and total ex-vessel value exceeded \$10.6 million. Commercial fishing for coho salmon was not allowed during 1995.

Recreational fishing regulations in California were similar to those in 1994, with various time and area closures enacted during 1995 (February 18–November 12). Coho salmon could not be retained after April 30, 1995. In Klamath Management Zone (KMZ; Horse Mountain, California, to Humbug Mountain, Oregon) quotas were also enacted. Statewide, recreational landings more than doubled over the previous year as sport anglers landed a record 397,200 chinook during 378,500 angler trips (CPUE: 1.05 fish/angler). Most salmon were caught south of KMZ, where sport anglers landed 383,600 chinook during 353,800 angler trips on commercial passenger fishing vessels and private skiffs. Anglers were limited to two salmon per day, with a minimum size limit of 20 inches total length.

TABLE 7
Preliminary 1995 Landings of Live Fish (Metric Tons)

	Southern California	Northern California
Rockfishes	126	47
California sheephead	88	0
Cabezon	78	4
California halibut	51	2
Lingcod	14	16
All others	20	3
Total	377	72

In KMZ, three separate seasons were enacted: (1) May 17–July 8, or 10,600 chinook quota, Wednesday through Saturday fishing only, one salmon per day; (2) August 16–31, or 900 total chinook quota, Wednesday through Saturday fishing only, one salmon per day; and (3) September 1–9, no quota, open 7 days a week, one salmon per day, no more than 6 salmon in 7 consecutive days. A 20-inch size limit was in effect during all three seasons. In the California portion of KMZ, anglers landed 13,800 chinook during 24,700 angler trips made primarily on private skiffs.

LIVE-FISH FISHERY

The 1995 statewide landings for live fish were estimated at 449 MT, 10% more than in 1994 (table 7). Fifty-four different fish species were landed live and had an ex-vessel value of over \$3 million. Landings may be underestimated because some fish buyers failed to properly code landings as live fish.

Live-fish fishing began in 1988 mainly to supply the California Asian community. Live fish are now sold to both local and overseas markets. What began as small trapping and hook and line operations has now become a complex, multimillion-dollar fishery using many gear types, targeting a multitude of species, and delivering fish in a variety of ways. For this market, fishes must be visually attractive and able to withstand the rigors of capture and transportation. Optimum individual weights ranged between one and three pounds, a suitable single-entrée size at Asian restaurants. Ex-vessel prices ranged from \$2.00 to \$7.00 per pound. Larger fish were also sold live, but at considerably reduced prices (except for California halibut). Prices fluctuated with market demand, fish size, fish condition, and weather conditions. Hook and line gear was used to capture 63% of the live fish landed statewide; trap gear landed 23%.

Live-fish landings in southern California (Morro Bay

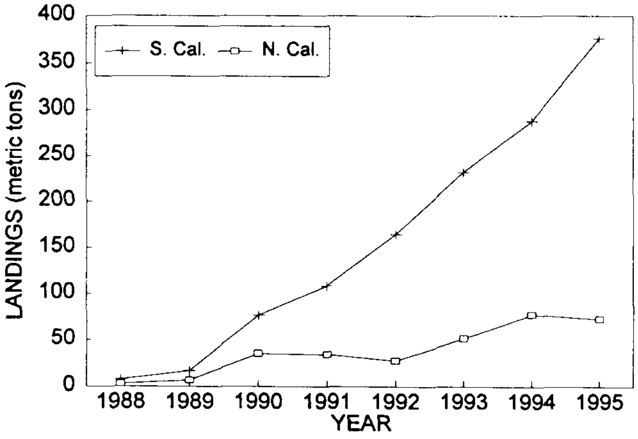

Figure 6. California live-fish landings, 1988–95.

southward) totaled 377 MT, 16% more than in 1994 (figure 6). Target species for all gear types included California sheephead (*Semicossyphus pulcher*), California halibut (*Paralichthys californicus*), California scorpionfish (*Scorpaena guttata*), cabezon (*Scorpaenichthys marmoratus*), lingcod (*Ophiodon elongatus*), and grass (*S. rastrelliger*) and gopher (*S. carnatus*) rockfishes. Most of this year's catch was taken with hook and line (57%) and trap (27%) gear. Trapping accounted for 76% of all live California sheephead taken. Traps used for finfish were originally constructed like lobster traps, but variations flourished as this fishery continued to develop. Fishing pressure for high-value nearshore species intensified as hook and line vessels heavily targeted cabezon and gopher and grass rockfishes. Catches of these fish increased dramatically from 1994: 216% for cabezon, 79% for gopher rockfish, and 56% for grass rockfish. Live California halibut were caught with line, net, and trawl gear, primarily from the ports of Santa Barbara and Morro Bay. Halibut was kept alive to ensure optimum freshness, then bled, iced, and quickly shipped overseas. Two-thirds of all live landings were delivered to Morro Bay and Santa Barbara/Ventura.

Live-fish landings in northern California (north of Morro Bay) totaled 72 MT, 13% less than in 1994 (figure 6). Most landings (94%) were made by hook and line vessels using vertical, horizontal, and troll longlines to harvest rockfish along nearshore rocky reefs and offshore banks. Principal finfishes caught were gopher, china (*S. nebulosus*), and copper (*S. caurinus*) rockfishes. Although finfish traps are not authorized for use in state waters from Pigeon Point (San Mateo County) to southern Mendocino County, fishermen are now exploring trapping options outside the EEZ. Fort Bragg has a rudimentary trap fishery for sablefish and cabezon. White croaker was specifically targeted in San Francisco Bay for the first time this year.

In 1995, legislation created a limited-entry program, which included numbers of traps, trap construction requirements, and incidental catch restrictions. Two Senate bills were also passed to reduce nearshore fishing pressure by limiting hooks used per vessel and to establish weekend closures in designated areas.

RECREATIONAL FISHERY

Northern California

In northern and central California, commercial passenger fishing vessel (CPFV) anglers fish for rockfishes (*Sebastes* spp.), salmon (*Oncorhynchus* spp.), lingcod (*Ophiodon elongatus*), and other nearshore species in ocean waters, and for striped bass (*Morone saxatilus*) and white sturgeon (*Acipenser transmontanus*) in estuarine waters. California halibut (*Paralichthys californicus*) are taken along the coast, but most catch comes from San Francisco Bay. Recreational fishing for coho, or silver, salmon (*Oncorhynchus kisutch*), was closed after April 30, 1995, as it had been in 1994.

Total catch decreased by 12% from reported landings for 1994 (table 8). Twelve primary species or species groups taken in central and northern California, in decreasing proportion, were rockfishes, king salmon, lingcod, California halibut, chub mackerel, striped bass, unspecified flatfishes, cabezon, jack mackerel, unspecified sharks, leopard sharks, and sturgeon. The first four groups made up 98.6% of the total catch. Rockfishes dominated

TABLE 8
Central–Northern California CPFV Landings (Number of Fish) in 1995 and 1994

Species/species group	1995	1994	1995 rank	Percent change
Rockfishes, unspecified	767,313	924,743	1	−17
King salmon	124,489	98,131	2	+27
Lingcod	25,719	25,156	3	+2
California halibut	13,664	4,134	4	+231
Pacific mackerel	3,419	3,433	5	0
Striped bass	3,102	2,247	6	+38
Flatfishes, unspecified	3,099	5,304	7	−42
Cabezon	1,041	1,217	8	−14
Jack mackerel	765	478	9	+60
Shark, unspecified	613	923	10	−34
Leopard shark	468	1,040	11	−55
Fishes, unspecified	348	1,981	12	−82
Sturgeon, unspecified	281	155	13	+81
White croaker	168	317	14	−47
Albacore	135	171	15	−21
All others	135	296	—	—
Totals:				
Number of fish	944,759	1,069,726		−12
Number of anglers	173,093	166,396		+4
Number of reporting CPFVs	121	123		−2

TABLE 9
Southern California CPFV Landings (Number of Fish) in 1995 and 1994

Species/species group	1995 landings Number	1995 landings Rank	1994 landings Number	1994 landings Rank	Percent change
Rockfishes, unspecified	407,678	1	470,549	1	−13
Barred sand bass	350,539	2	286,444	3	+22
California barracuda	326,792	3	268,202	5	+22
Pacific mackerel	267,731	4	333,222	2	−20
Kelp bass	231,687	5	276,086	4	−16
Ocean whitefish	133,655	6	100,420	7	+33
Spotted scorpionfish	94,398	7	90,665	8	+4
Yellowfin tuna	87,347	8	46,831	10	+87
Halfmoon	54,656	9	49,219	9	+11
Skipjack tuna	43,043	10	15,327	13	+181
Pacific bonito	39,995	11	106,280	6	−62
Yellowtail	29,445	12	19,882	12	+48
California sheephead	23,735	13	19,947	11	+19
White croaker	16,916	14	5,725	15	+196
Bluefin tuna	14,646	15	2,309	22	+534
Salmon (Chinook)	9,201	16	3	23	—
Wahoo	5,733	17	4,051	20	+42
California halibut	5,681	18	3,415	21	+66
Jack mackerel	5,330	19	5,425	16	−2
Dolphinfish	5,022	20	5,318	17	−6
Lingcod	4,823	21	5,935	14	−19
Flatfishes, unspecified	4,664	22	4,471	19	+4
White seabass	4,264	23	2,518	22	+69
Blacksmith	3,150	24	5,100	18	−38
All others	17,632	—	7,117	—	—
Totals:					
Number of fish	2,187,763		2,134,461		
Number of anglers	455,545		415,673		
Number of reporting CPFVs	205		155		

CPFV catches in 1995, accounting for 81% of the total catch. In 1995, catch of rockfishes was 17% less than that in 1994, primarily because of an increased salmon catch, up 21% from 1994. During periods of good salmon fishing, recreational anglers shift effort from rockfishes to salmon. The total number of anglers increased by 4% over 1994, primarily because of excellent salmon availability.

Eighty-six percent of total rockfish catch came from port areas from Port San Luis north to Bodega Bay. Lingcod constituted 3% of the total catch, slightly higher than in 1994. There was increased recruitment of juvenile lingcod in 1994 and 1995, and CPUE increased from previous years. Declines in total catch were observed for four other species or species groups including flatfishes (down 42%), cabezon (down 14%), sharks (down 34%), and leopard sharks (down 55%), while catches of jack mackerel increased 38% in 1995.

Landings of California halibut, sturgeon, and striped bass increased from 1994 levels, and were almost exclusively from San Francisco Bay. Halibut catch increased 70% from 1994, and increases in other groups may have been related to a higher influx of Sacramento–San Joaquin Delta runoff than in previous years.

Southern California

Southern California's large marine recreational fishery includes private recreational boat, beach-and-bank, pier, and CPFV modes. CPFV accounts for approximately 40% of California's marine recreational landings. In southern California and Baja California waters, traditional CPFV target species include California barracuda (*Sphyraena argentea*), barred sand bass (*Paralabrax nebulifer*), bluefin tuna (*Thunnus thynnus*), Pacific bonito (*Sarda chiliensis*), halfmoon (*Medialuna californiensis*), California halibut (*Paralichthys californicus*), kelp bass (*Paralabrax clathratus*), Pacific mackerel (*Scomber japonicus*), rockfishes (*Sebastes* spp.), spotted scorpionfish (*Scorpaena guttata*), California sheephead (*Semicossyphus pulcher*), skipjack tuna (*Euthynnus pelamis*), wahoo (*Acanthocybium solanderi*), ocean whitefish (*Caulolatilus princeps*), white seabass (*Atractoscion nobilis*), yellowfin tuna (*Thunnus alalunga*), and yellowtail (*Seriola lalandi*).

In 1995, 2,187,763 fish were landed by CPFV anglers south of Point Conception (table 9). Southern California catch represented 70% of the 3,132,522 fish landed statewide. Reported CPFV landings increased 2.5% in southern California, while decreasing 2% statewide. Angler participation on CPFVs increased both statewide

(8%) and in southern California (10%) in 1995. Approximately 455,545 CPFV anglers fished off southern California, representing 73% of statewide total anglers (628,638) for 1995.

The top ten ranking species made up 91% of total landings by CPFV anglers in southern California (table 9). Rockfishes as a group continued to dominate CPFV landings in southern California and statewide in 1995, but southern California landings decreased by 13%. Barred sand bass landings increased 22%, moving this species from third to second rank of importance in 1995. Barracuda (up 22%) continued a decade-long increase, moving from fifth to third rank. Pacific mackerel decreased in relative importance from rank two to four, with landings down 20%. Kelp bass (down 16%) dropped from position four to five. Ocean whitefish, primarily targeted on rockfish trips, increased by 33% and moved up in importance to rank six. Spotted scorpionfish landings showed little change, but moved from rank eight to seven due to relative decreases of other species. Yellowfin tuna landings were up 87% in 1995, moving this popular species from tenth to eighth place. Halfmoon landings increased 11%, remaining in ninth position. Skipjack tuna jumped from position thirteen to ten, with a 181% increase in landings. Pacific bonito (down 62%) dropped out of the top ten in 1995, moving from rank six to eleven.

Marked changes in landings were observed for a number of other popular sport fish species in 1995 (table 9). Increased landings were reported for several other southern species, including bluefin tuna (up 534%), yellowtail (up 48%), wahoo (up 42%), and white seabass (up 69%). California halibut landings increased 156% statewide and 66% in southern California. Southern California CPFV anglers benefited from chinook salmon, with most of 9,201 salmon landed near Santa Barbara and Ventura, but landings were reported as far south as San Diego. Approximately 1,047 albacore (*Thunnus alalunga*) were landed in southern California, most of which were caught off Santa Barbara in September.

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Note: *This review is available online at*
http://www-mlrg.ucsd.edu/calcofi.html.

THE STATE OF THE CALIFORNIA CURRENT IN 1995–1996: CONTINUING DECLINES IN MACROZOOPLANKTON BIOMASS DURING A PERIOD OF NEARLY NORMAL CIRCULATION

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ABSTRACT

The large suite of environmental data collected routinely in the coastal region of California provides the basis to make timely assessments of environmental structure that can be updated continuously. Here we describe and interpret data collected during the previous 18 months. The emphasis is upon data collected on CalCOFI time-series monitoring cruises and at coastal shore stations. Spatial pattern is described, and the data are interpreted in the context of anomalies from long-term means. The pattern of circulation in the California Current was similar to the long-term mean during most of 1995. Circulation in early 1996 was anomalous in that February was marked by a strong mesoscale structure and a lack of the normal coastal countercurrent in the Southern California Bight. April 1996 was also a period of strong mesoscale structure, and the California Current was displaced farther offshore than normal. The springs of 1995 and 1996 were periods where the surface waters of the coastal region were enriched with cool, high-nutrient water, and the chlorophyll concentration and primary production were high. Indices of environmental structure based upon coastal shore station data provided contradictory signals of the forcing processes causing this biological structure. Sea-surface temperatures at coastal shore stations were warm, and the upwelling index was anomalously low during the springs of 1995 and 1996, suggesting a pattern of low nutrient inputs and primary production. However, direct measurements on the CalCOFI survey cruises showed strong upwelling-favorable wind, and that cool, high-nutrient, and high-production water was present over a large area of the coastal region. It appears that structure during the study period in the coastal waters of central and northern California was similar to that in the CalCOFI study region. In spite of strong forcing and high primary production, macrozooplankton biomass continued the long-term trend of large decline which began in the mid-1970s.

INTRODUCTION

In this report we describe and interpret recent oceanographic and related environmental data from the coastal region of California. The emphasis is upon data collected on the quarterly CalCOFI time-series monitoring cruises, but data from several sources are also considered. This report covers data for the period from April 1995 to April 1996. Data from earlier periods were covered in prior reports (Hayward et al. 1994, 1995). Our objective is to provide an up-to-date assessment of environmental structure. Atmospheric forcing processes, circulation patterns, nutrient distributions, and patterns in the distribution of phytoplankton and macrozooplankton biomass are described. We consider how these patterns differ from the long-term mean structure, and how biological structure is linked to atmospheric forcing and the circulation.

DATA SETS AND ANALYTICAL TECHNIQUES

Coastal data include measurements of temperature and salinity made at a series of shore stations (Walker et al. 1994); data from La Jolla (SIO Pier) and Pacific Grove are shown here as temperature and daily anomalies from the long-term harmonic mean (1916–93 for La Jolla and 1919–93 for Pacific Grove). Coastal sea-level data for San Diego and San Francisco are shown as monthly anomalies from the 1975–86 mean corrected for atmospheric pressure (data courtesy of G. T. Mitchum and K. Wyrtki and the IGOSS program).

Data from quarterly CalCOFI time-series survey cruises in 1994 and 1995 are shown. The CalCOFI monitoring program started in 1949; a brief history of the program is given in Hewitt 1988. The present program consists of quarterly (normally January, April, July, October) survey cruises which occupy a grid of 66 stations in the southern California region. Cruises are designated by the year and month; e.g., cruise 9501 sampled in January 1995. Station locations are designated by a line and station number; e.g., 90.60 represents station 60 on CalCOFI line 90.

The core time-series data set now collected at each station on the quarterly CalCOFI cruises includes a CTD/rosette cast with sensors for pressure, temperature, salinity, dissolved oxygen, PAR (photosynthetically active radiation), fluorescence, and transmissivity. Water samples are collected with ten-liter sample bottles at 20–24 depths in the upper 500 m for determination of salinity, dissolved oxygen, nutrients (NO_3, NO_2, PO_4, SiO_3), phytoplankton pigments (chlorophyll a and phaeophytin), and primary production (^{14}C uptake at one station per day). Oblique and surface (neuston) net tows (0.505 mm mesh) are taken at each station. Continuous near-surface measurements of temperature, salinity, and chlorophyll fluorescence are made from water pumped through the ship, and the data are logged at one-minute intervals. Doppler current profiler (ADCP) data are also recorded continuously. The ADCP data provide a measure of zooplankton biomass based upon acoustic backscatter as well as a measure of upper ocean currents. The most recent data presented here are preliminary, and some changes may be made after the final processing and quality control checks. The methods are described in more detail in the CalCOFI cruise data reports (Scripps Institution of Oceanography 1995). CalCOFI hydrographic data and information about recent activities can be accessed via the World Wide Web (*http://www-mlrg.ucsd.edu/calcofi.html*).

EVOLUTION OF STRUCTURE

Atmospheric and Oceanic Forcing

During the winter of 1994–95, the climate regime over the North Pacific differed greatly from that of the previous year. The tropical Pacific was warm (in a moderate El Niño state), and, somewhat characteristically, the winter and early spring of 1995 featured a deep, eastward-reaching Aleutian Low system with vigorous storms passing the California coast, particularly during January (figure 1) and March. Throughout this period, the westerlies were strengthened with several spates of southerly (from the south) component winds along the California

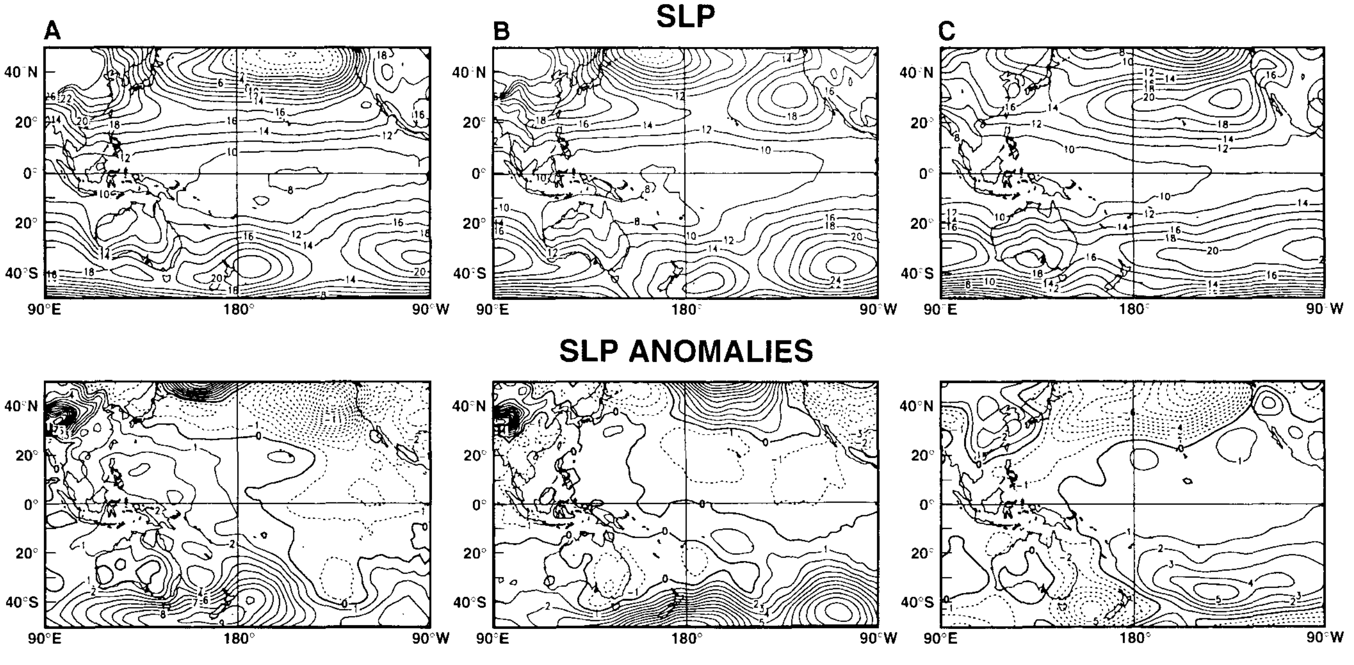

Figure 1. Sea-level pressure (SLP) and SLP anomalies over the Pacific Ocean for (*A*) January 1995, (*B*) January 1996, and (*C*) April 1996 (from the NOAA *Climate Diagnostics Bulletin*).

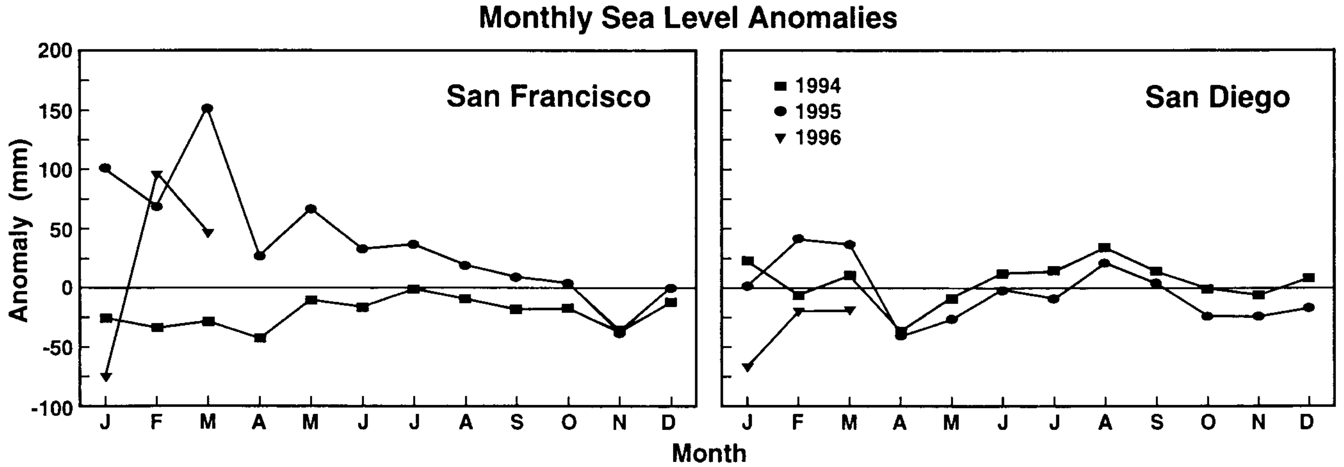

Figure 2. Monthly anomalies in sea level at San Francisco and San Diego for 1994, 1995, and 1996. The monthly anomalies are deviations from the 1975–86 period corrected for atmospheric pressure.

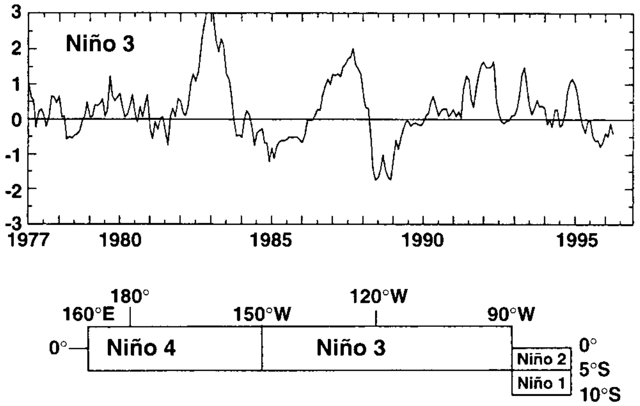

Figure 3. Tropical Pacific SST anomalies from the Niño 3 region (from the NOAA *Climate Diagnostics Bulletin*).

coast. In response, high coastal sea levels (figure 2) and a warming tendency occurred over a broad region along the California coast.

In contrast, during the winter of 1995–96 the tropical Pacific hovered in a weak La Niña state, with slightly cool surface temperatures (figure 3), and there was rather strong anomalously high pressure over the North Pacific (figure 1). However, conditions over the California Current region were changeable over winter and spring of 1996, as the atmospheric circulation wavered considerably across the basin during the winter months. Coastal sea levels (figure 2) alternated between anomalously low elevations during January 1996 to moderate-high elevations during February. These fluctuations corresponded to the accentuated high-pressure, strengthened northerly winds during January, and to lower-pressure, anomalous southerly winds during February. An exceptional feature that developed during winter and continued through spring of 1996 was the unusually warm water temperatures (figure 4) with anomalies exceeding 1°C over most of the eastern North Pacific (also see shore station temperatures at Pacific Grove and SIO Pier in figure 5). This warm regime actually took hold in fall of 1995 and strengthened during winter and spring of 1996. The causes are presumably associated with warming from the previous El Niño episode combined with regional wind and cloud conditions.

During the spring of 1995, the sea-level pressure (SLP) field retained a negative (low-pressure) anomaly feature in the eastern North Pacific. However, because the pressure tended to also be low over the western United States, the pressure gradient was relatively unaltered from its climatological normal, and northwesterly winds took hold along the California coast during April and May 1995. The spring northwesterly wind regime is shown by the vector wind plots from California coastal buoys in figure 6. Consequently, sea level dropped from its winter levels (figure 2), and coastal surface temperatures were cool.

During the spring of 1996, SLP in the region (figure 1) was near its normal levels in March and higher than average in April. The April SLP configuration was such as to weaken the wind field over the southern California coast, which evidently enhanced the warming of the coastal region with near-record warm shore temperatures.

Sea-surface temperature (SST) measured at shore stations at La Jolla and Pacific Grove started 1995 above normal, but a sharp drop in mid-April occurred at both La Jolla and Pacific Grove. SST has been near normal to below normal through the remainder of 1995 and for the first two months of 1996 at Pacific Grove (figure 5). Temperatures at La Jolla fluctuated about normal from April to September 1995. Anomalously warm water was present at La Jolla from October 1995 through March 1996.

Sea level was above normal from January to March 1995 at San Francisco, and above normal during February and March at San Diego (figure 2). Sea level was near

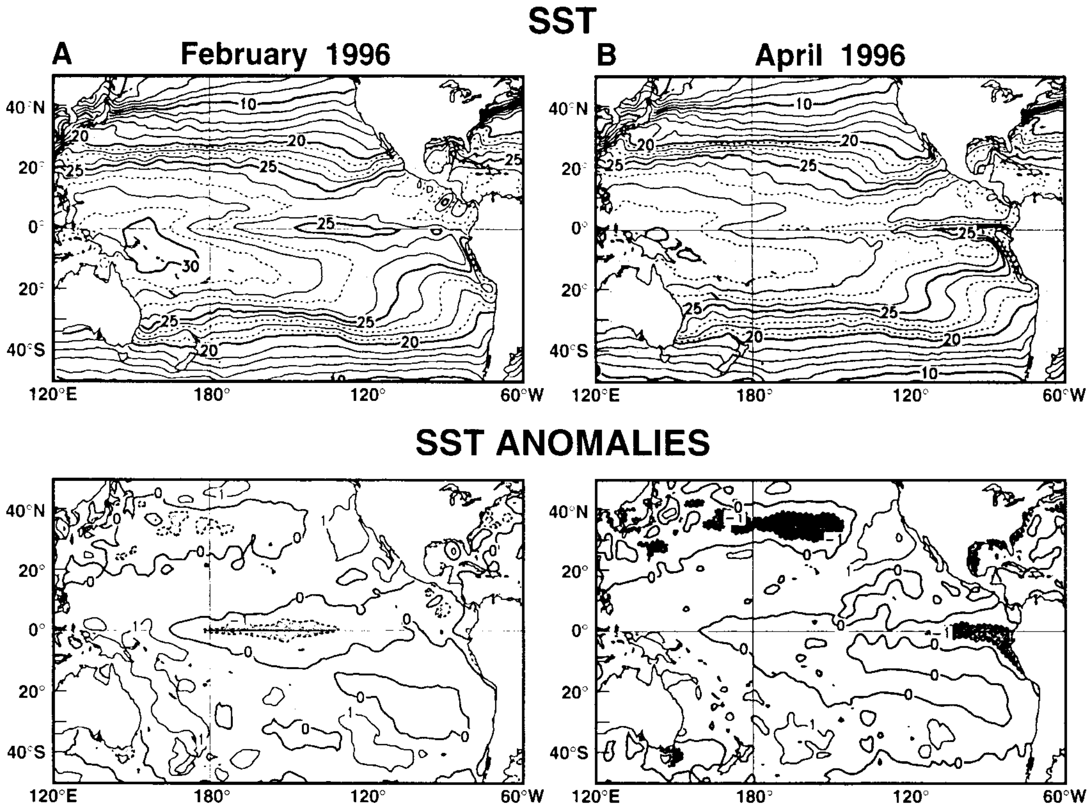

Figure 4. SST and SST anomalies over the Pacific Ocean, February 1996 and April 1996 (from the NOAA *Climate Diagnostics Bulletin*).

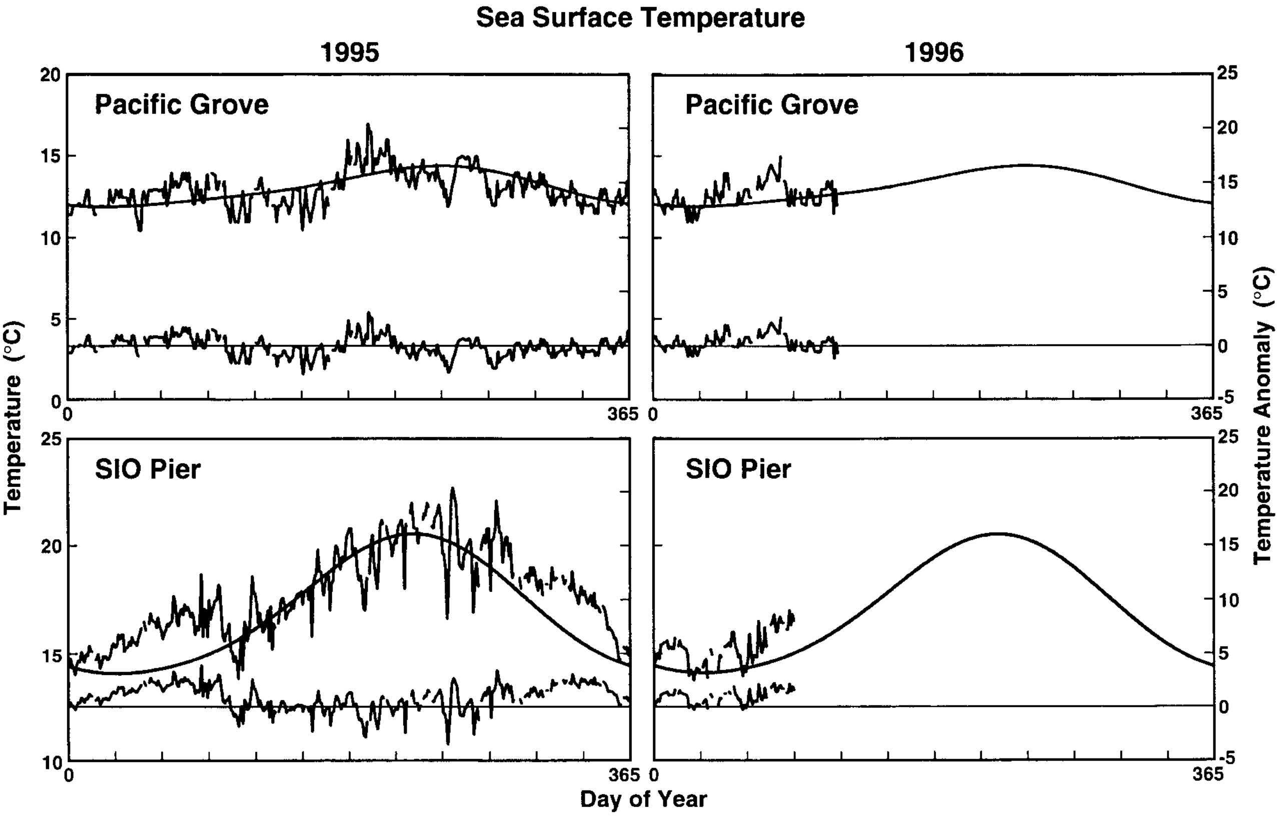

Figure 5. Sea-surface temperature at Pacific Grove and La Jolla (SIO Pier) for 1995 and 1996. Daily temperatures and daily anomalies from the long-term harmonic mean (1919–93 for Pacific Grove and 1916–93 for La Jolla). The *heavy line* shows the harmonic mean annual cycle in SST.

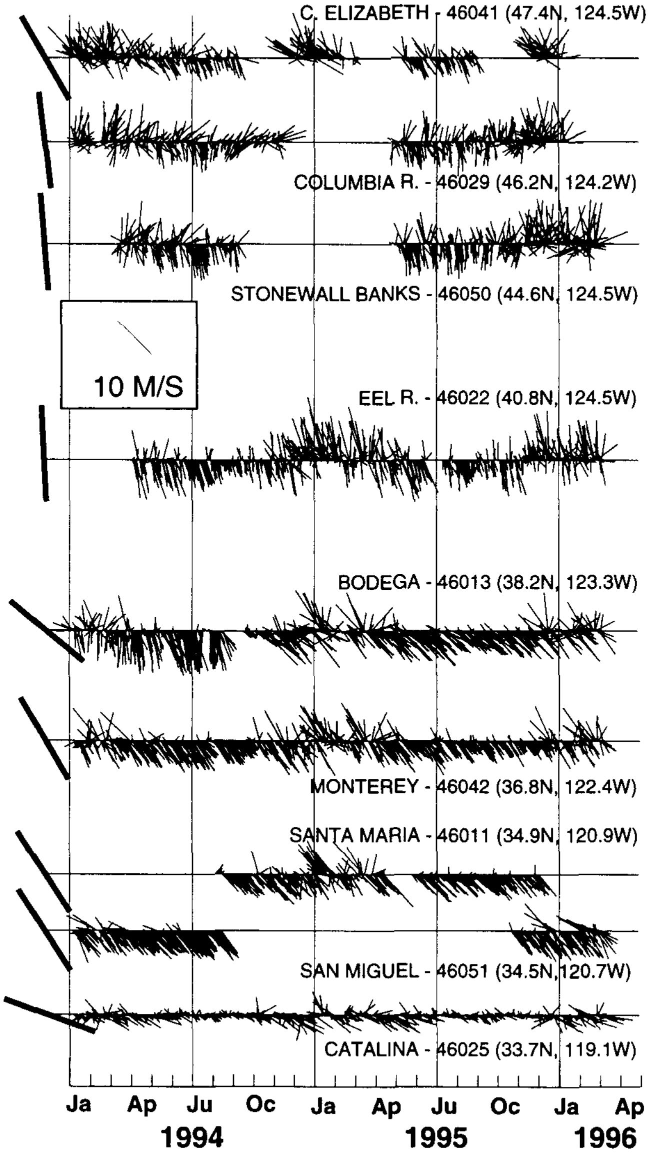

Figure 6. Vector time series of winds at selected National Data Buoy Center meteorological buoys along the U.S. west coast, January 1994–February 1996. Vectors represent daily averages of hourly observations. *Bold lines* to left of each time series denote coastline orientation at the sites.

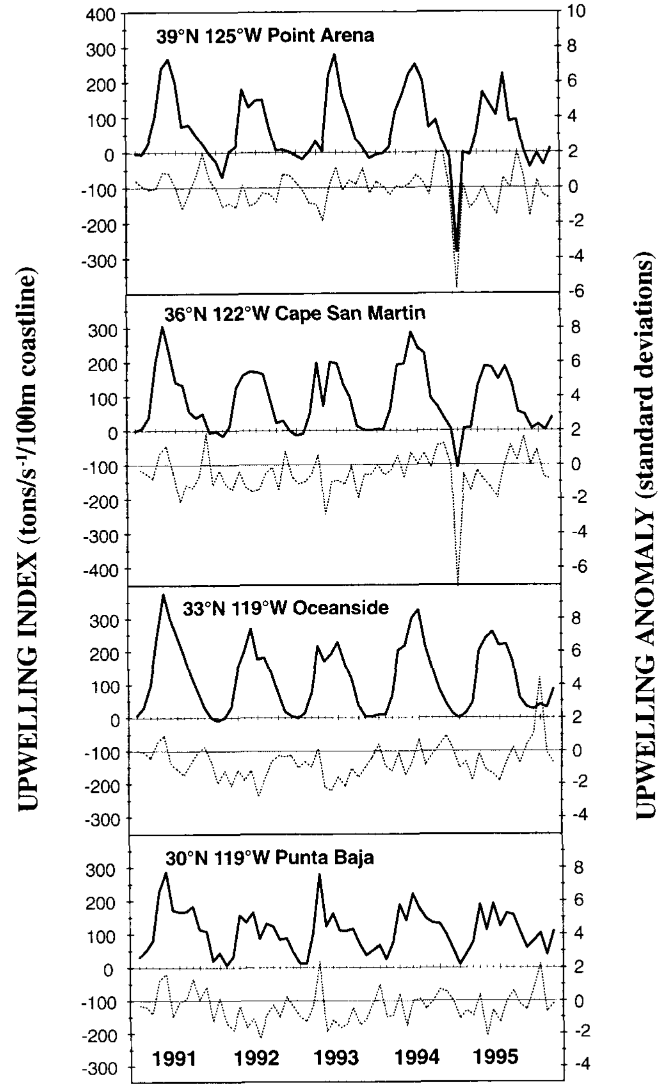

Figure 7. Time series of the monthly average upwelling index (*solid line*) and normalized anomalies (*shaded*) for January 1991 to March 1996 at four coastal locations.

normal at both stations during the remainder of 1995. San Diego and San Francisco both showed a sharp decline to anomalously low values of sea level in January 1996. Sea level increased to normal values at San Diego in February and March, and to anomalously high values at San Francisco. As in early 1995, it is likely that the high values in San Francisco Bay are due, at least in part, to freshwater runoff caused by heavy rains.

The upwelling index (Bakun 1973) measured at 36°N, 122°W (Cape San Martin) and 33°N, 119°W (Oceanside) was anomalously low from January to July 1995 except for April, which was near normal (figure 7). There were anomalously high values in the fall and winter of 1995. The index in February 1996 was anomalously low at both stations. The anomalously low values in the spring of 1995 are important because they occurred when upwelling was approaching its seasonal maximum. The high values of the anomalies in the fall and winter of 1995 occurred when upwelling is normally at the annual low.

Wind data, collected from an array of coastal buoys, provide a more direct measure of regional atmospheric forcing. Harsh environmental conditions make continuity of measurement of wind and other meteorological data from coastal buoys a chronic problem. Plotting a selected number of daily-averaged wind time series along the length of the West Coast, however, gives some indication of seasonal and interannual differences in the large-scale coastal wind field (figure 6). Winter winds are highly variable over short time scales, a result of frequent and vigorously propagating storms. The general direction of winter winds is poleward, especially north of Cape Blanco (42°N). Summer winds are predominantly equatorward, with occasional wind-relaxation events or reversals to poleward flow (Schwing et al. 1991). Wind vectors align strongly with the local coastline, particularly off central and southern California. Winds within the Southern California Bight are weak and variable throughout the year, relative to those north of Point Conception. The seasonal patterns shown here correspond well to a statistical summary of west coast buoy observations by Dorman and Winant (1995). Winds during 1995 and early 1996 appear fundamentally similar to 1994, and to the long-term climatology. Specifically, winds were upwelling favorable (equatorward) through summer 1995 along the entire coast, and there were numerous episodes of equatorward wind throughout winter 1995–96 south of Cape Blanco.

Additional Data Sets from the Coastal Region

The region off central California between Monterey Bay and Bodega Bay was surveyed three times in May–June 1995, as part of the Southwest Fisheries Science Center (SWFSC) Tiburon Laboratory's annual surveys (begun in 1983) of pelagic young-of-the-year rockfish on the RV *David Starr Jordan*. A repeat of the May–June survey was conducted in 1996. In addition, the *Jordan* conducted bongo tows, CTD and PAR casts, and ADCP profiling at CalCOFI station 63.55 for ten days in early February 1995. Preliminary analysis reveals semidiurnal vertical excursions of 25–50 m in the density field. The Tiburon Laboratory can be contacted for further information on these data sets. The SWFSC La Jolla Laboratory's pelagic egg and larval and oceanography surveys extended north to this region in early 1995 (hake) and early 1996 (sardine).

Coastal ocean conditions off central California during May–June 1995 suggest a continuation of the more typical conditions that developed in early 1994 following an extended ENSO, consistent with the results of the CalCOFI surveys off southern California (Hayward et al. 1995). ADCP currents in May–June 1995 off central California showed the meandering southward flow typical of the upper water column during this time of year, highlighted by a strong offshore flow of a cold-water plume off Bodega Bay seen to at least 200 m. The expected northward undercurrent was evident at 200 m. The geostrophic currents inferred from the dynamic topography were similar to the ADCP circulation patterns, although the ADCP data reveal a much more complex current field. Dynamic heights were very similar in magnitude and structure to those in 1994 (Sakuma et al. 1995). The upper ocean was as much as 10 dyn. cm lower than during ENSO conditions in May–June 1992 (Lynn et al. 1995) and 1993 (Sakuma et al. 1994).

Upper water column temperatures and salinities were generally near average for this area for May–June, and cooler and more saline in comparison to 1992 and 1993. Extremely low salinities (values less than 30), a result of high runoff from heavy spring rains and floods in northern California, were limited to the upper 10 m. Otherwise, near-surface temperature and salinity values and distributions imply typical coastal upwelling conditions, despite lower than normal values of upwelling index at this latitude. However, local buoy winds were southward throughout most of the survey (figure 6), consistent with coastal upwelling. Slope water temperatures and salinities at 200 m depth in 1995 were similar to the long-term means, but more saline relative to 1994, a period in which hydrographic conditions suggested a reduced countercurrent, or increased transport in the California Current. Farther offshore, isopycnal surfaces at 200–500 m were uplifted in 1994 and 1995, compared to ENSO conditions when relatively warm, fresh California Current water is displaced shoreward by anomalous poleward wind stress (Simpson 1984; Lynn et al. 1995).

Analysis of data from a program of routine deployment of satellite-tracked drifters in the California Current by the Surface Velocity Program of the Global Drifter Center at SIO provides an additional source of information about the large-scale pattern of upper ocean circulation and the paths of water parcels. The historical data taken since 1985 illustrate the pattern of southward flow and the strong mesoscale variability of the California Current (figure 8). The CalCOFI survey area was not well sampled by the drifter deployments in 1995, but southward flow in the area offshore of the CalCOFI pattern is well illustrated.

The annual pattern of primary production in Monterey Bay has been measured as part of the monitoring program conducted by the Monterey Bay Aquarium Research Institute. A time series of primary production measured by ^{14}C uptake using methods described by Chavez et al. (1990) made from 1992 to 1995 shows a strong seasonal cycle in primary production (figure 9). As expected, values during the spring bloom in Monterey Bay are greater than in most of the CalCOFI survey area except in high-production patches. There was much variability between individual measurements, but the running means did not show strong between-year differences, even when the El Niño years of 1992 and 1993 are compared to 1994 and 1995.

Biological Structure in the CalCOFI Region

During 1995 and early 1996, the mean chlorophyll concentration on the CalCOFI survey cruises was relatively high in the context of measurements made during the last decade in April, and nearly normal in the other months (figure 10). Values in the summer, fall, and

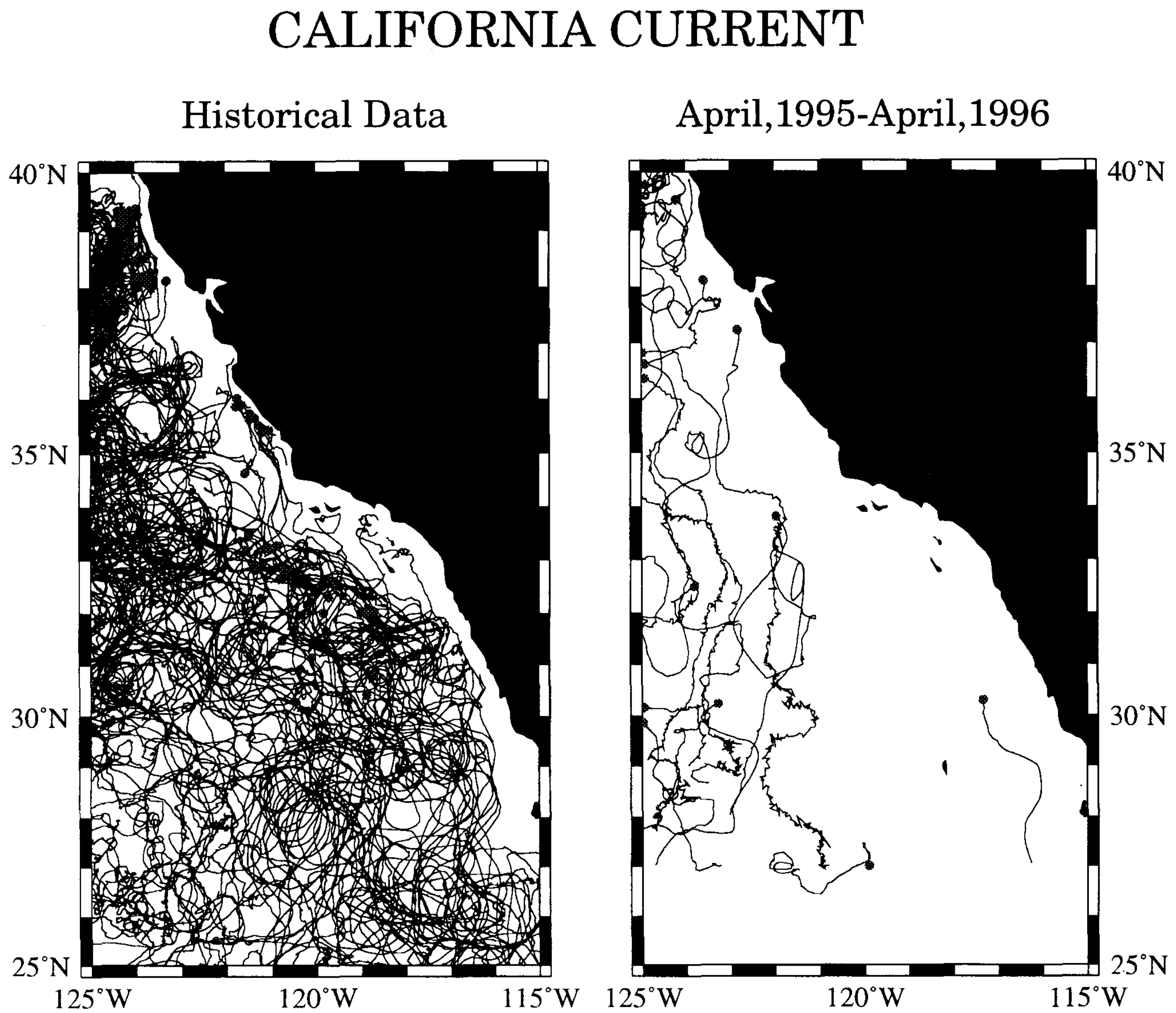

Figure 8. Drifter releases in the California Current region. The *left panel* shows the tracks of the historical data set for satellite-tracked drifter releases in the California Current since 1985. The *right panel* shows the tracks of drifters released from April 1995 to April 1996. The drifters have a drogue set at 15 m depth.

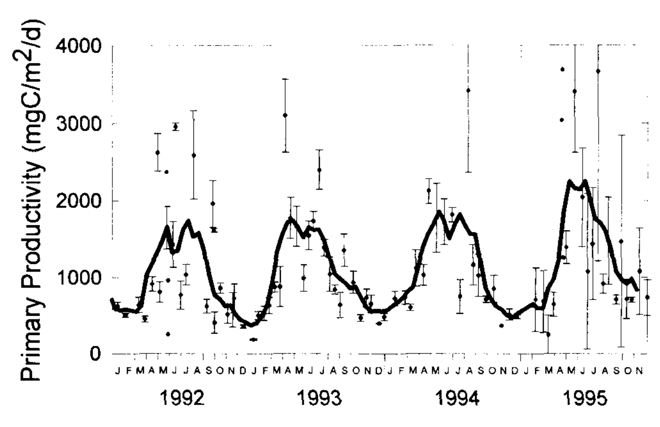

Figure 9. Primary production in Monterey Bay from 1992 to 1995 measured by ^{14}C uptake. Means and standard errors of two to five daily measurements are shown by *filled circles* and *error bars*. The *heavy line* represents a 5-point running mean of the data that was interpolated to biweekly intervals.

early winter were low and relatively constant, as they have been in the last decade. Macrozooplankton biomass continued to show the trend of declining values which has been seen in the last decade (Roemmich and McGowan 1995). The year 1995 was interesting in that in spite of relatively high chlorophyll in April, no strong seasonal maximum in macrozooplankton biomass was observed. It is not known if a seasonal maximum in macrozooplankton biomass was missed by the relatively long intervals between sampling on the quarterly cruises.

Red tide events occurred from San Diego to Monterey in the winter and spring of 1995 (Hayward et al. 1995). A moderate red tide was again evident in the vicinity of La Jolla in April 1996. The April 1996 event was evident as far south as Todos Santos Bay (G. Hemingway, pers. comm.). However, during the spring of 1996 no

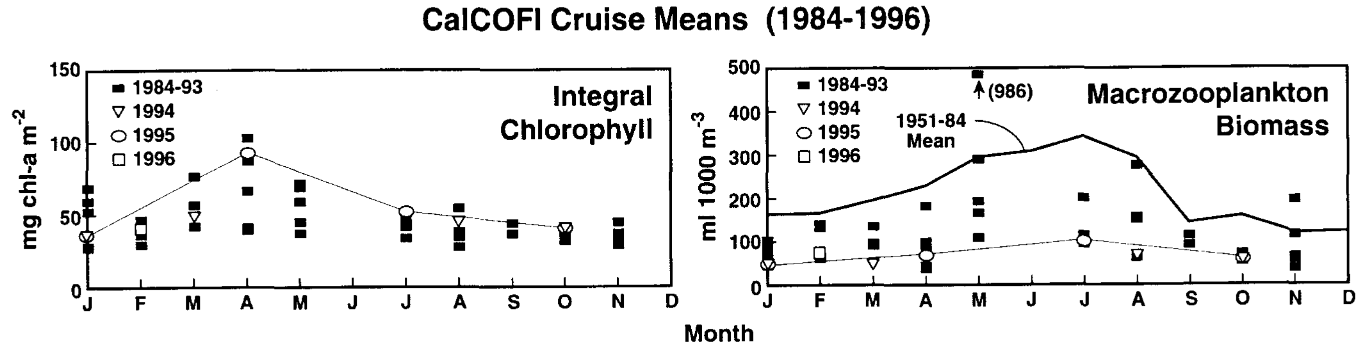

Figure 10. Cruise means of vertically integrated chlorophyll and macrozooplankton biomass plotted versus the month for CalCOFI cruises from 1984 to 1996. Each point represents the mean of all measurements on a cruise (normally 66). The *solid squares* show the cruises that took place from 1984 to 1993. The *open symbols* are cruises from 1994 to 1996; cruises in 1995 are connected with a line. The *bold line* in macrozooplankton biomass indicates the monthly means for the period from 1951 to 1984.

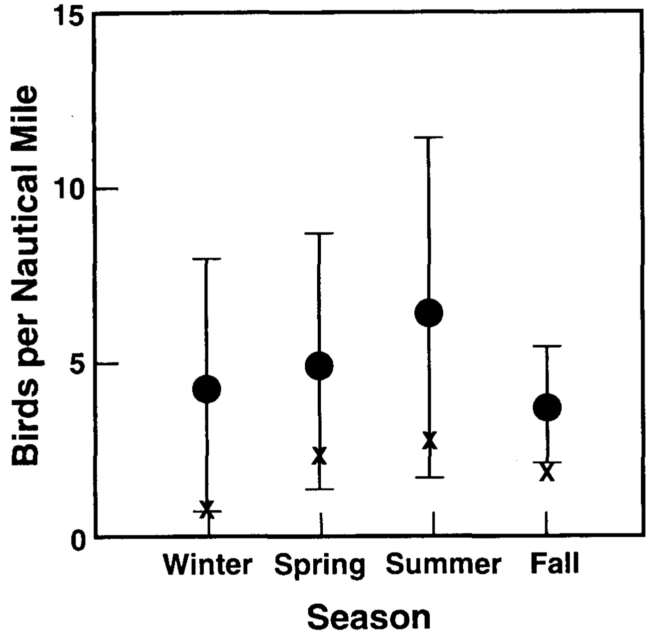

Figure 11. Mean and standard deviation (*filled circles* and *error bars*) of seabird abundance on CalCOFI cruises for the period May 1987 to April 1994. Seabird abundances from the four cruises in 1995 are marked with an *X*.

obvious red tide conditions were apparent at either Monterey or Santa Barbara (B. Prezelin, pers. comm.). In the CalCOFI region on cruise 9604, the primary red tide dinoflagellate (*Gonyaulax polyedra*) was found only in moderate, subdominant abundances (400–500 cells l^{-1}) and only at stations 93.26.7 and 93.28. In contrast, during April 1995, near the end of the red tide, this species was found in equal or greater abundances as far west as station 90.90. The 1996 red tide appears to have been relatively restricted to the immediate coastal environment.

Abundance of oceanic birds in the CalCOFI study region has declined steadily since 1988 (Veit et al., in press). This general decline continued through 1995 (figure 11). Bird abundance increased slightly on the spring and summer cruises of 1995. Seabirds can respond to changing environmental conditions on at least two temporal scales. They can respond to short-term (less than one year) fluctuations through population redistribution, and to longer-term changes through population growth or mortality. The short time scale suggests that the slightly elevated numbers of birds observed in spring and summer of 1995 represent redistribution. Perhaps birds were able to exploit some improved aspect of the environment associated with the elevated primary production in the spring of 1995. Highly mobile predators such as sooty shearwaters could have easily moved to the CalCOFI region from farther north in California, for example. Thus the small increases in 1995 would represent short-term redistribution embedded in a longer-term population decline that has been discussed by Veit et al. (in press).

Spatial Pattern on the CalCOFI Time-Series Cruises

The following section narrates the spatial patterns observed on the five most recent CalCOFI cruises. The circulation patterns on individual cruises are compared to the long-term mean circulation patterns (Lynn et al. 1982), which are shown in Hayward et al. 1994.

9504. Preliminary data from cruise 9504 were presented in Hayward et al. 1995. The dynamic height field (figure 12) from the final data is quite similar to the circulation pattern inferred from the 100 m temperature field (shown in Hayward et al. 1994). This again illustrates the value of this index for inferring the circulation in the California Current region. The circulation pattern was typical of the long-term mean pattern, with a strong cyclonic eddy in the offshore region of southern California superimposed upon it. The cyclonic eddy is also evident in the SST pattern determined from satellite remote sensing (figure 13). Near-surface chlorophyll was quite high in the coastal region throughout the pattern, and this is reflected in the high value of the cruise

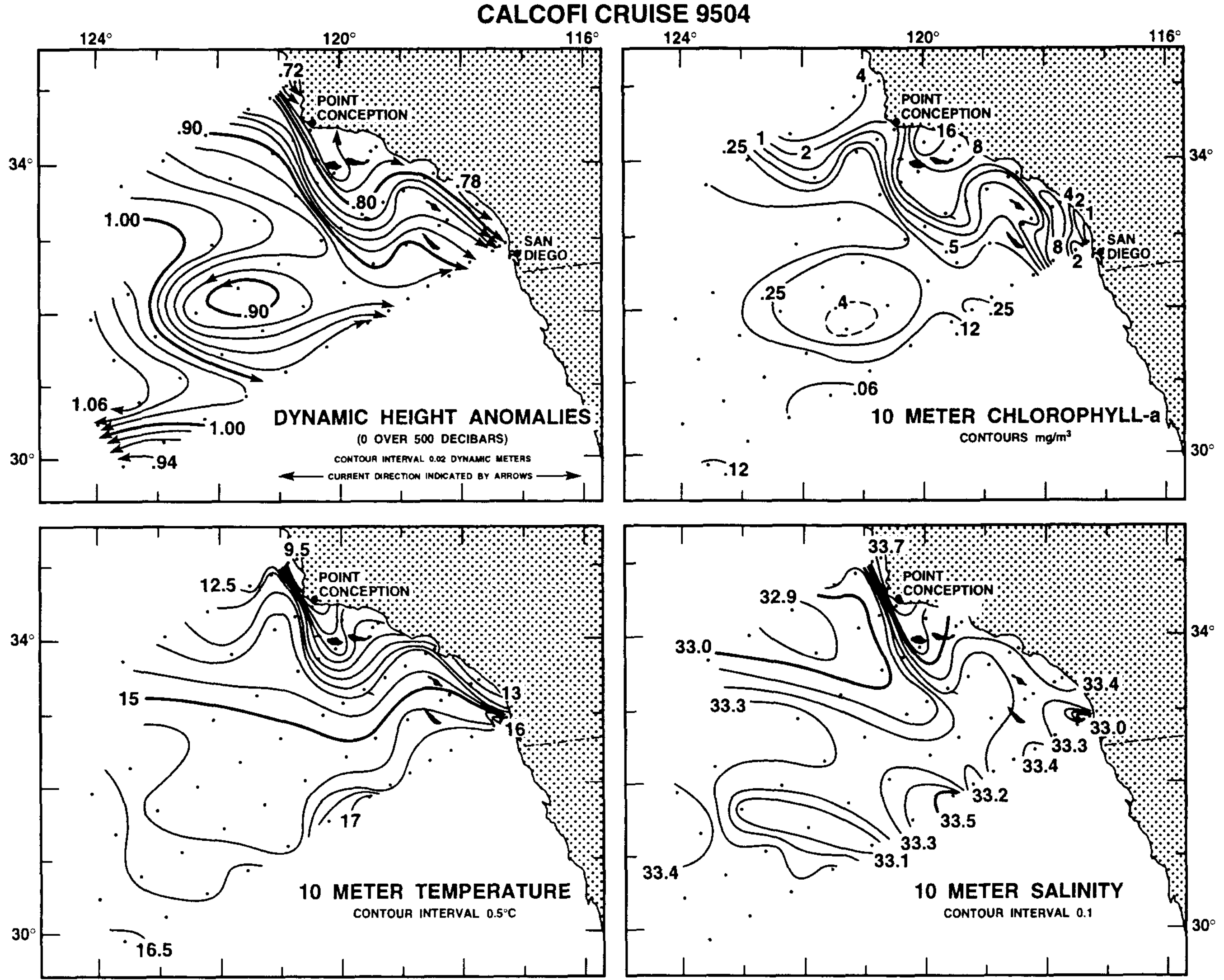

Figure 12. Spatial patterns for CalCOFI cruise 9504 (April 6–22, 1995), including upper ocean flow fields derived from 0 over 500 m dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

mean integral chlorophyll (figure 10). Some of the enrichment was associated with the strong red tide event which affected the coast of California from the U.S.–Mexico border to at least Monterey. However, the enrichment extended much farther offshore than the coastal region where the red tide was evident, and the bloom in the waters offshore of the red tide was dominated by diatoms (Hayward et al. 1995). In spite of the elevated chlorophyll on this cruise, the cruise mean macrozooplankton biomass was low. Strong winds blowing from the north and exceptionally high seas were experienced during this cruise. This was not reflected in the upwelling index, which was anomalously low during most of the spring but near normal in April (figure 7).

9507. The circulation in July 1995 was remarkably similar to the long-term mean pattern. There was strong southward flow of the California Current offshore of the Channel Islands and a well-developed eddy south of the Channel Islands (figure 14). There was northward flow offshore of Catalina and San Clemente Islands and southward flow along the coast in the Southern California Bight. All of these features are in the harmonic mean dynamic height field. Mesoscale structure was weak on this cruise. As expected from the pycnocline topography, chlorophyll was elevated at the inshore edge of the California Current, where the pycnocline slopes sharply upward, and in the coastal waters of the Southern California Bight.

9510. In October 1995 the dynamic height field was quite similar to the long-term mean pattern. There was a strong southward-flowing California Current in the offshore waters and a well-developed coastal counter-

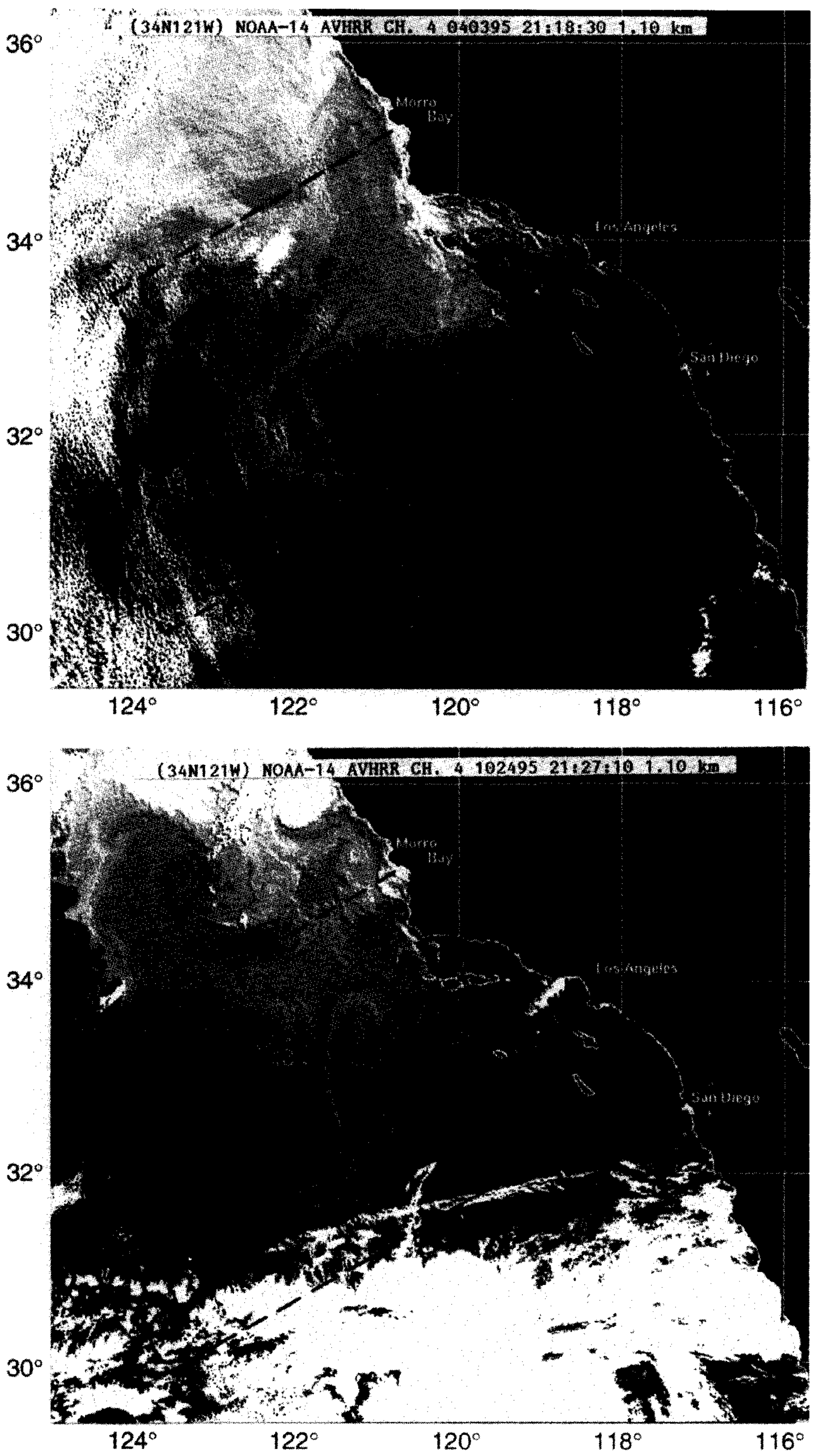

Figure 13. Radiometric temperature from NOAA-14 AVHRR channel 4 for April 3, 1995, 2118 UTC (*upper panel*) and October 24, 1995, 2127 UTC (*lower panel*). Data provided by CoastWatch, West Coast Node.

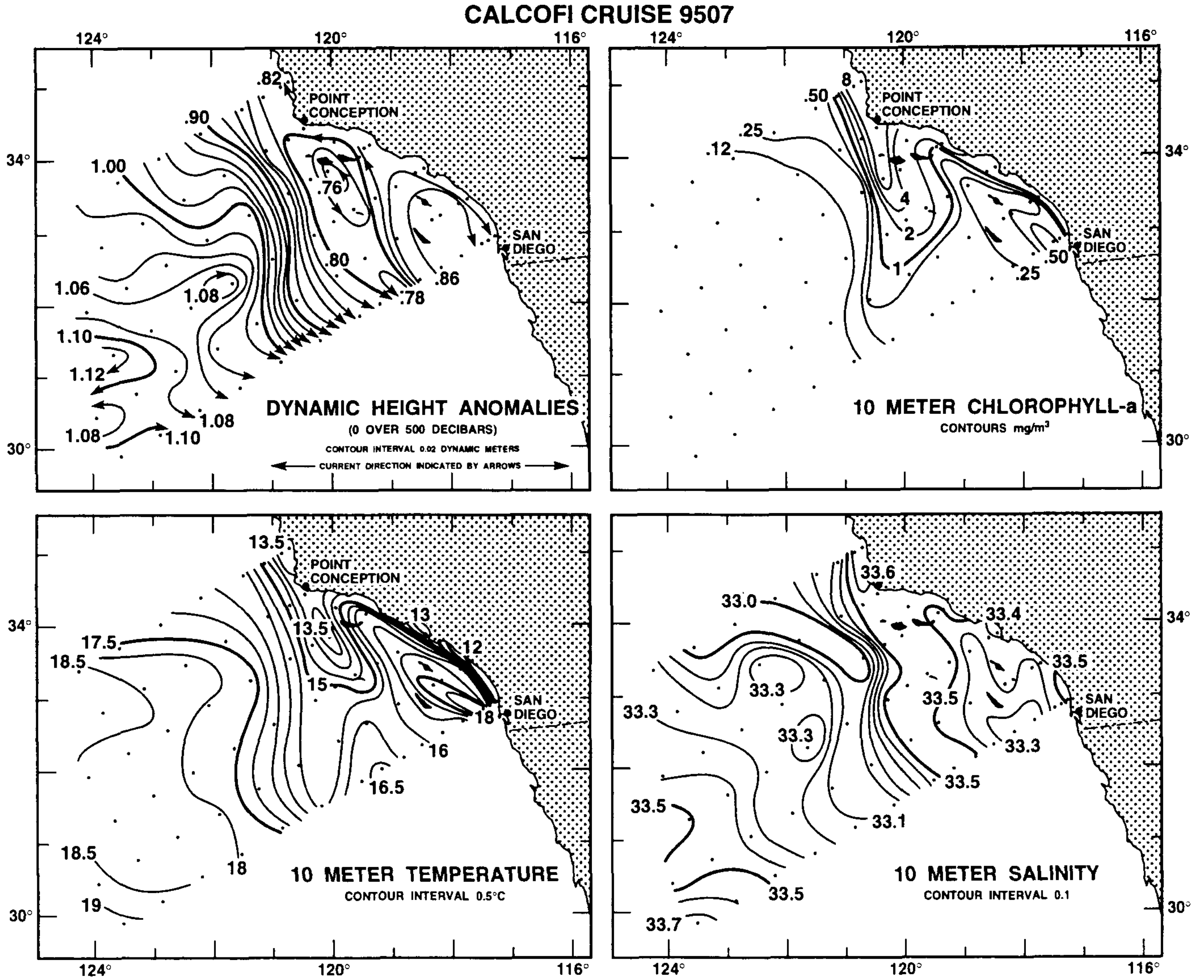

Figure 14. Spatial patterns for CalCOFI cruise 9507 (July 6–23, 1995), including upper ocean flow fields derived from 0 over 500 m dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

current (figure 15). Additional aspects of mesoscale structure are evident in the remotely sensed SST pattern (figure 13). Chlorophyll was relatively low throughout the grid, as is typical of the seasonal pattern. The highest values of chlorophyll were found at the inshore edge of the California Current.

9602. Oceanographic structure had changed by February 1996. In contrast to the preceding year, the circulation pattern (figure 16) differed in several aspects from the long-term mean pattern (figure 17). The normal pattern, in which a low-salinity core of the California Current is evident in the 10 m distributions, was not apparent. A strong mesoscale eddy field nearly masked the large-scale flow. The normal coastal countercurrent was absent in the Southern California Bight, but the typical pattern of a well-developed Southern California Eddy was present. A notable aspect of the circulation was the strong mesoscale eddy field and the strong onshore-flowing jet located in the offshore part of the survey pattern between lines 87 and 90. The absence of the coastal countercurrent and southward flow in the Southern California Bight is consistent with the anomalously low sea level at La Jolla during the winter of 1995–96.

9604. Cruise 9604 was completed on May 3 as this report was being prepared. Preliminary data from this cruise again show an anomalous circulation pattern and very strong physical forcing of biological structure. The flow field inferred from the 100 m temperature distribution shows that the core of the California Current was located anomalously far offshore. As in February, there is a strong mesoscale eddy field. There was strong onshore and offshore flow in the region offshore of southern California.

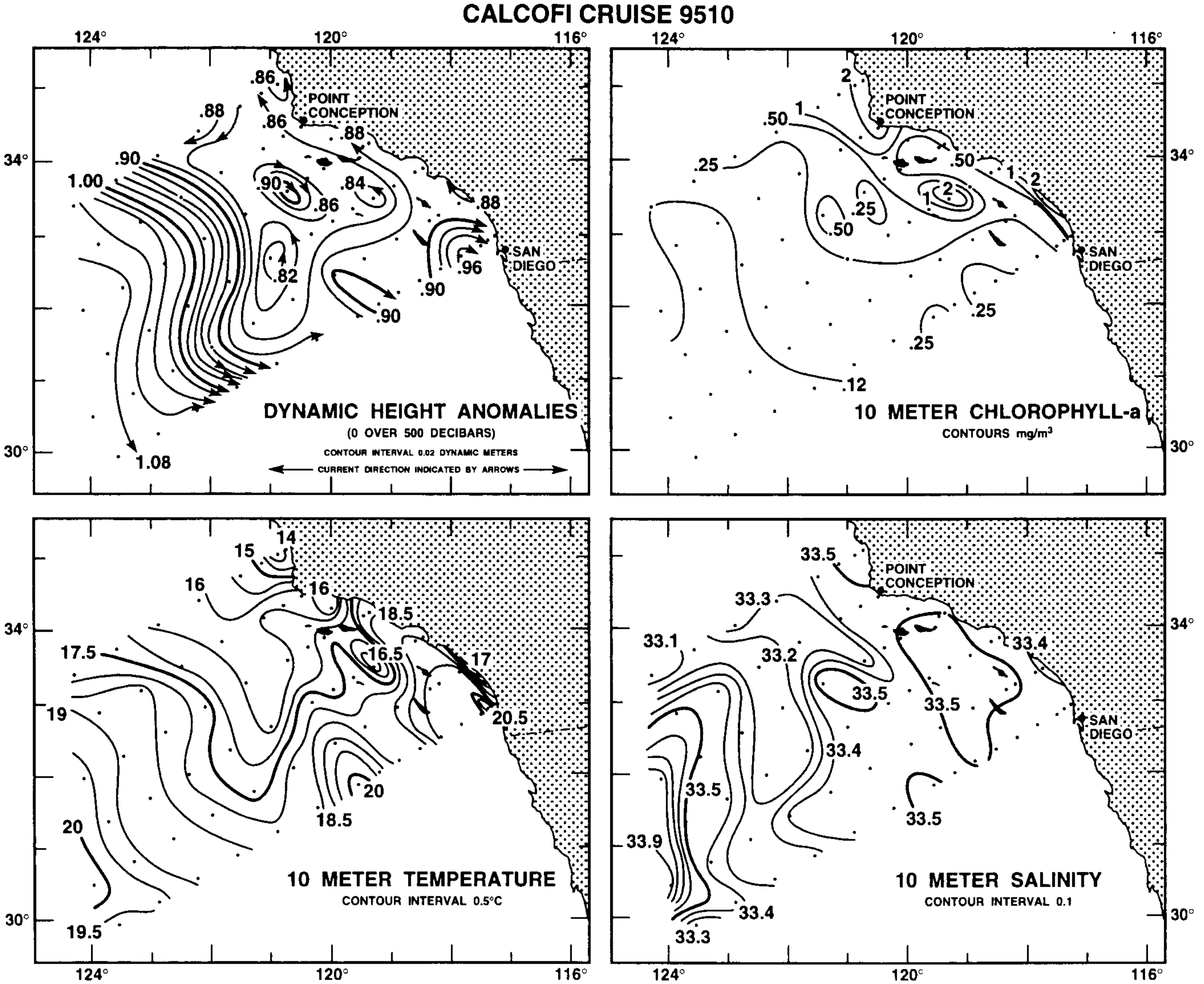

Figure 15. Spatial patterns for CalCOFI cruise 9510 (October 6–28, 1995), including upper ocean flow fields derived from 0 over 500 m dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

The area inshore of the inner edge of the low-salinity jet of the California Current was enriched in both southern and central California. Chlorophyll values were quite high (figure 18) in the surface waters near Point Conception and in the Santa Barbara Channel. The Santa Barbara Channel bloom was dominated by diatoms.

An interesting pattern of sea-surface temperature anomalies emerged on this cruise. The surface waters inshore of the California Current were anomalously cool over most of the pattern (figure 19). The exception was the two stations closest to San Diego at the inshore end of line 93. The offshore waters were anomalously warm. The boundary between the anomalously warm and anomalously cool waters coincided with the inshore edge of the California Current. This was also the boundary of the area with high chlorophyll. This pattern is in contrast to the pattern in February 1996, when the surface waters were anomalously warm over most of the pattern.

DISCUSSION

A large suite of environmental data is now being routinely collected in the coastal region of California. These data provide the basis for timely assessments of the California Current ecosystem. Data are collected at various frequencies, and they differ in the length of time it takes before they become widely available. Only a subset of the data that have been collected is included in this report.

A goal for coastal oceanographers is to interpret these data in a way which improves our understanding of the current state of the ecosystem. Prediction is a longer-

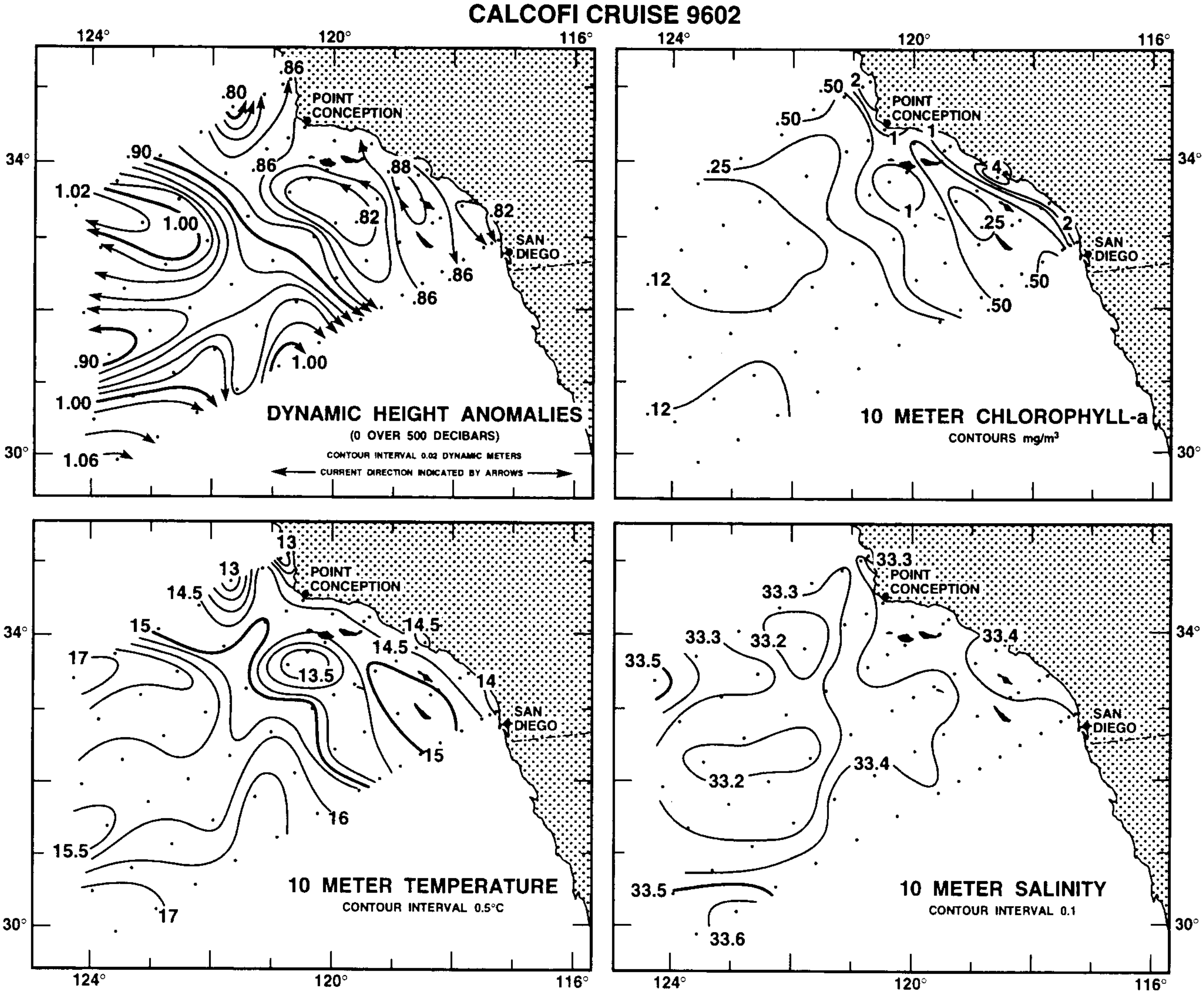

Figure 16. Spatial patterns for CalCOFI cruise 9602 (January 29–February 16, 1996), including upper ocean flow fields derived from 0 over 500 m dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

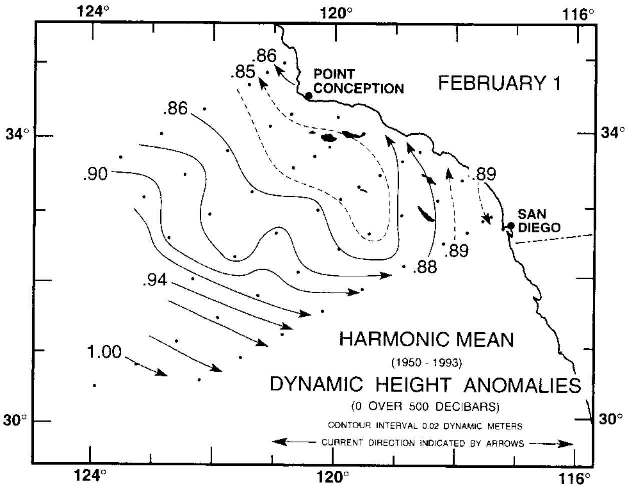

Figure 17. Long-term mean upper ocean flow field for February 1. This plot shows the harmonic mean for 1950 to 1992 of the 0 over 500 m dynamic height field.

term goal. Achievement of both goals will require advances in modeling and in our understanding of how marine populations are linked to environmental structure. It is likely that modeling and predictive ability will improve more rapidly for physical structure, and that successful prediction of biological structure will follow. Interpretation of these data sets requires an understanding of the relation between those aspects of structure which are commonly measured and for which efficient data distribution systems exist and those aspects of ecosystem structure which we wish to assess. Prediction will also require an improved understanding of the linkages between physical and biological structure.

The data which are most rapidly available are those on atmospheric forcing (winds and atmospheric pressure patterns) and temperature, salinity, and sea-level data from coastal shore stations. These are the data which can

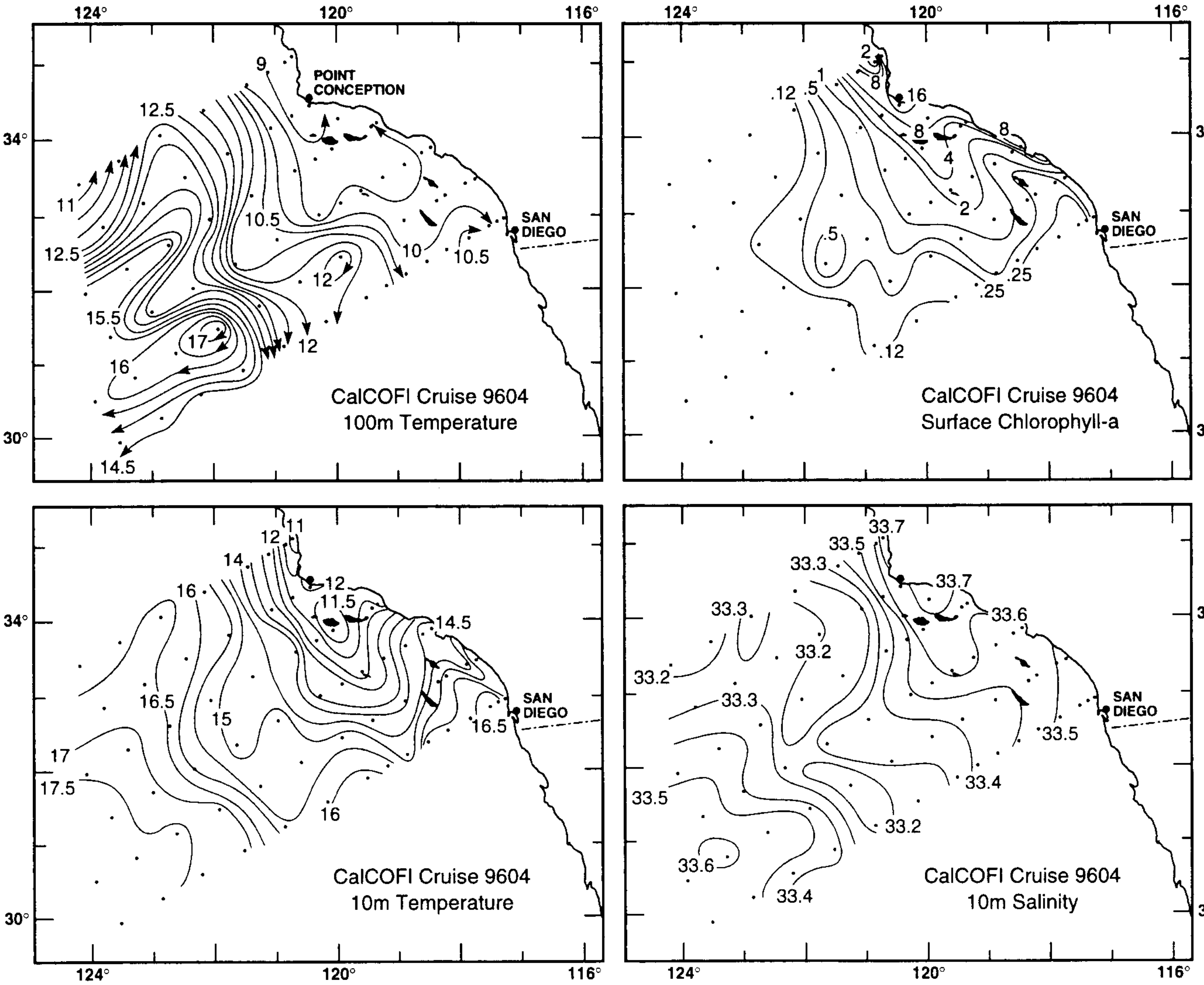

Figure 18. Spatial patterns for CalCOFI cruise 9604 (April 15–May 3, 1996), including upper ocean flow field estimated from the 100 m temperature, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

be used for the most timely assessments of ecosystem structure. During 1995 and early 1996 the upwelling index was anomalously low, especially during the spring, when strong upwelling is initiated. The buoy wind data, however, showed strong upwelling-favorable winds during the spring of 1995, and shipboard data indicated that there were strong upwelling-favorable winds at least during the period of the April 1996 CalCOFI cruise. The anomalously low values of the upwelling index imply that there would have been less upwelling than normal, which may lead to predictions of warmer than normal water in the near-coastal region, and lower nutrient and phytoplankton concentrations. The strong observed upwelling-favorable winds are consistent with the cool, high-nutrient and high-chlorophyll waters that were observed in the coastal region in the springs of 1995 and 1996. During the period considered here, the wind data provided a more useful indicator of ecosystem structure than did the upwelling index.

Elevated sea level in early 1995 (figure 2) is consistent with an enhanced coastal countercurrent, and the near normal sea level later in the year is consistent with a normal circulation pattern. Increased sea level in early 1996 would also be consistent with an enhanced coastal countercurrent. The circulation during the four cruises in 1995 was typical of the long-term mean; February 1996 was anomalous in that the normal coastal countercurrent in the Southern California Bight was absent.

Anomalously warm water was present at La Jolla (figure 5) from October 1995 through March 1996. The anomalously warm water at La Jolla and Pacific Grove during the winter and springs of 1995 and 1996 is consistent with the elevated sea level. The sharp drop in temperature in the spring of each year is consistent with

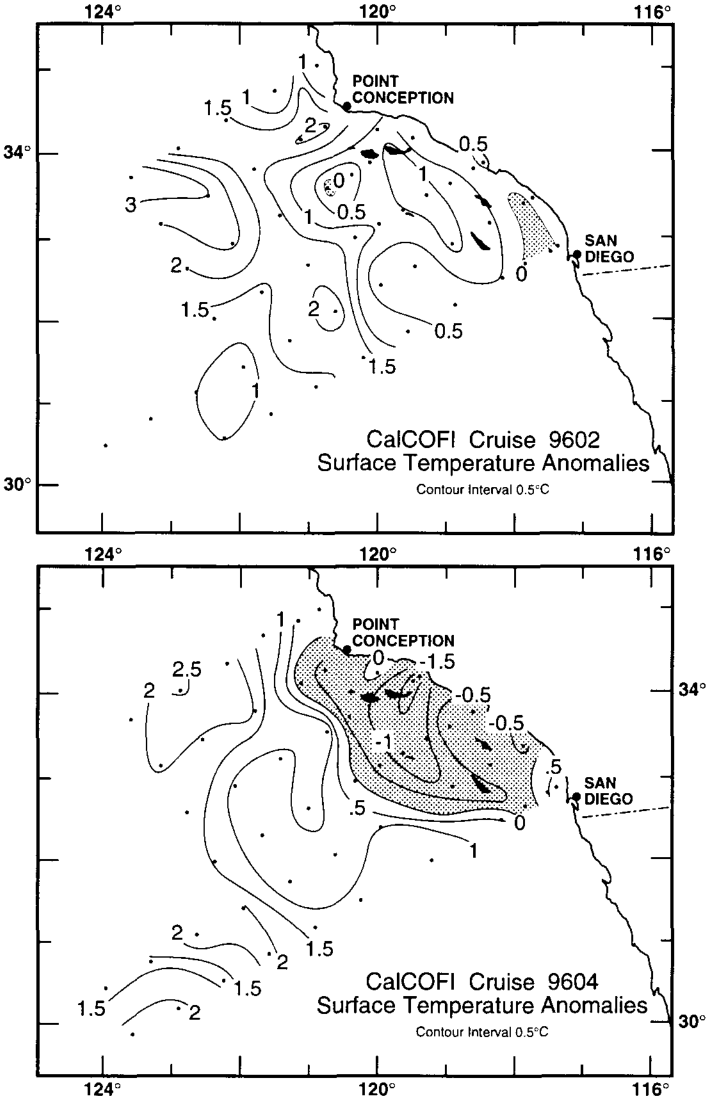

Figure 19. Anomalies in SST (°C) for CalCOFI cruises 9602 and 9604.

the strong winds observed at the coastal buoys. There was a relatively sharp drop in coastal sea-surface temperature and sea level at about the same time as the coastal winds changed from winter conditions with episodic storms and winds from the south to relatively strong winds consistently blowing equatorward along the coast. These changes all occurred about April 1995, and all were coincident with the elevated nutrient and chlorophyll concentrations in the coastal regime of the CalCOFI area during April 1995.

The data from central and northern California suggest that environmental structure to the north was responding in much the same way as in the CalCOFI region. Patterns in wind, coastal temperature, and sea level, as well as anomalies of the upwelling index were generally similar in both regions, and the coastal surveys off central California indicated that the circulation pattern was similar to the long-term mean. This is consistent with the observations that the low-frequency variability in physical and biological structure tends to be spatially coherent in the California Current (Chelton et al. 1982; Roemmich and McGowan 1995).

How are the indices of biological structure measured on the CalCOFI cruises (chlorophyll, primary production, macrozooplankton biomass, bird abundance) related to environmental structure? Spatial pattern and the annual pattern in chlorophyll is generally related to physical structure in the manner expected if phytoplankton abundance is strongly influenced by the nutrient distribution. Chlorophyll concentration is high where there are nutrients in the euphotic zone. Nutrients are generally present in the euphotic zone where they are expected based upon the physical structure. The correlation between spatial pattern in the chlorophyll concentration and physical structure is thus consistent with a relatively uncomplicated link between physical structure and phytoplankton abundance through the nutrient distribution and the relatively short response time of the phytoplankton to nutrient inputs. However, the relation between the available physical proxy variables—such as coastal temperature, sea level, wind, or the upwelling index—and the nutrient distribution is not well established, especially on an interannual time scale.

A more complex pattern of linkages between environmental structure and biological structure emerges when a longer-term view is taken and higher trophic levels are considered. Chlorophyll was relatively high during the spring of 1995 and 1996 in the context of measurements made during spring of the last twelve years. This is consistent with the nutrient distribution observed on these cruises. However, the pattern in higher trophic levels does not appear to be consistent with this. The much longer time series for macrozooplankton biomass shows a large decrease which started in the mid-1970s (Roemmich and McGowan 1995). This decrease continued over the period considered here, and 1995 and 1996 are low even in the context of the preceding twelve years.

The bird data considered here cover the past eight years. These data show an increase in the birds whose range is associated with the offshore waters of the CalCOFI survey area, and a decrease in the seabirds in the inner coastal waters of the CalCOFI survey. The mean abundance of the birds in the inner waters is much greater than the mean abundance of those found farther offshore.

The long-term trends in macrozooplankton biomass and seabird abundance thus appear to be inconsistent with bottom-up forcing. The reasons for this are unclear. It may be that macrozooplankton biomass actually is increasing, but is affected by a long time lag, or that a seasonal increase is missed by the long gaps between the spring and summer CalCOFI survey cruises. It may also be that macrozooplankton biomass and seabird abundance are not tightly coupled to phytoplankton abundance or primary production on this time scale. Ambiguity in the processes that link physical and biological structure makes it difficult to predict patterns in upper trophic levels or to model the consequences of global change in the physical environment.

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Part II

SYMPOSIA OF THE CALCOFI CONFERENCE

Lake Arrowhead Conference Center
October 31 and November 1, 1995

INTERDECADAL CHANGES IN THE ECOLOGY OF THE CALIFORNIA CURRENT: EVIDENCE AND POSSIBLE MECHANISMS

The CalCOFI program was initiated as a result of major change in the California Current—the decline of California's sardine fishery. The detection, description, and understanding of ecological change, including ultimate and proximate causes and implications, have remained central to CalCOFI's research. For example, the 1994 symposium, "The 1991–92 El Niño and Its Impact on Fisheries," emphasized interannual variation.

The present symposium was stimulated by a publication, based on data collected by CalCOFI since its inception, in which major decline in the biomass of macrozooplankton in the southern California sector of the California Current was described, together with an interdecadal rise in seawater temperature (Roemmich and McGowan 1995a, b). Because of the long time scale involved, it is likely that the rest of the California Current System (where data collection has been less regular) has changed. It is also likely that such a change has had consequences for other species, both prey of zooplankton (phytoplankton and microzooplankton) and predators (zooplanktivorous fish and higher marine vertebrates). Geochemical consequences (e.g., change in the vertical flux of particulate carbon) are also imaginable. Finally, Roemmich and McGowan presented evidence inconsistent with several plausible physical causes of the change. Thus the 1995 symposium had the goals of disseminating information about this change, documenting (or at least testing for) its manifestations in components other than zooplankton, discussing its possible driving mechanisms and implications, and identifying research needed to understand these aspects more fully.

A new feature of the 1995 symposium was a preparatory meeting convened by Thomas Hayward, with financial support from CalCOFI and SIO, to discuss the published evidence and its interpretation, to present relevant unpublished or ongoing work, and to recommend augmentation or other change in continuing research to improve understanding. The report of this meeting was distributed at Lake Arrowhead and discussed by Thomas Hayward, and is included in the symposium proceedings on the following pages.

It is also worth noting that other long time series of zooplanktonic biomass have been published (e.g., Tomosada and Odate 1995). Although this data set was obtained by different methods than the CalCOFI set, and did not have truly coincident physical data, it is internally consistent. Superficial examination of the data certainly does not suggest a pattern parallel to that in the California Current, but rigorous testing for frequency-specific coherences in several such data sets could indicate, for example, the spatial scale of causal mechanisms.

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LONG-TERM CHANGE IN THE NORTH PACIFIC OCEAN: A CONSIDERATION OF SOME IMPORTANT ISSUES

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INTRODUCTION

This report summarizes the results of a meeting held in La Jolla on October 12–13, 1995, which was organized by Tom Hayward at the request of the CalCOFI Committee. The purpose of the meeting was to consider recent observations of long-term changes taking place in the North Pacific Ocean, and to make recommendations about whether these observations merit a response by CalCOFI.

Meeting participants: Tim Barnett, Tim Baumgartner, Ed Brinton, Dan Cayan, Francisco Chavez, Karen Forney, Doyle Hanan, Tom Hayward, John Hunter, Ron Lynn, John McGowan, Rick Methot, Art Miller, Dean Roemmich, Frank Schwing, Paul Smith, Mia Tegner, and Amy Weinheimer.

The following people provided helpful written input: Alec MacCall, Dave Mackas, Michael Mullin, and Jeff Polovina.

OBSERVATIONS AND MODEL RESULTS

There is no doubt that important changes have been taking place in atmospheric forcing and in the physical and biological structure of the upper layers of the North Pacific Ocean in the past few decades. Zooplankton biomass and the abundance of pelagic fish and squid in the subarctic Pacific were doubled in 1980–89 in comparison with 1956–62 (Brodeur and Ware 1992). There was also a positive correlation between the intensity of winter winds and zooplankton biomass measured during the subsequent summer in the subarctic Pacific. In the subtropical North Pacific, a doubling of the vertically integrated chlorophyll starting in the mid-1970s is associated with a cooling of SST and an increase in winter winds (Venrick et al. 1987). Decade-scale trends in atmospheric pressure patterns, in mixed layer depth, and in the productivity of several trophic levels has been observed in the subtropical North Pacific (Polovina et al. 1994, in press). Macrozooplankton biomass off Peru declined sharply in the mid-1970s (Pauly et al. 1989), and this was associated with an increase in the strength of upwelling-favorable winds (Bakun 1990). In the California Current, a secular rise in coastal sea level in the last few decades is partly due to warming (and hence expansion) in the top 300 m (Roemmich 1992). A decrease in macrozooplankton biomass (Roemmich and McGowan 1995a, b) and in the abundance of pelagic seabirds (Veit et al., in press) in the California Current is associated with a warming of the surface waters and an increase in stratification.

Much progress is being made in describing and modeling the physical structure of the system, at least in terms of understanding what has taken place. For example, isotherms in the thermocline off the western coast of North America were observed (in XBT data) to deepen in the mid-1970s while the mixed layer concurrently shallowed. This shift in basic-state structure was studied by Miller et al. (1994) in a basin-scale model driven by observed heat flux and wind-stress anomalies. New results from the analysis of that model show that the thermocline deepening off the California coast is part of a basin-scale shift in thermocline structure which is driven by a basin-scale change in wind stress curl. A concomitant weakening of the subtropical gyre (by about 10 percent) occurs in the model as well, but with little long-term change in the California Current transport. Definition of scale is an important issue, since shorter-term interannual changes in thermocline structure associated with El Niño provide a large local signal but a finite lifetime for biological response.

Prediction is still some way away, especially on the mesoscale. Models and mechanisms that may link physical and biological structure on the variety of time and spatial scales involved here need to be developed. Such models must include variations in upwelling and nutrient inputs due to interannual changes in the upwelling-favorable wind field (Bakun 1990), variations in the nutrient input due to a secular trend of increasing stratification (Roemmich and McGowan 1995a, b), and variations in primary production associated with interannual changes in mixed layer depth (Polovina et al., in press). Physical models are improving more rapidly than biological models, and it is highly probable that predictive ability in physical structure will precede that in biological structure.

SOME IMPORTANT QUESTIONS

Basic Science versus Policy and Management Issues

Our meeting emphasized basic science over policy and management issues, probably due to the mixture of those in attendance. In spite of this, it was recognized that there is a real need to make the basic scientific findings of long-term change in the California Current accessible to policy makers and managers in a form that is compelling and useful to them. There was discussion that policy and management issues in the coastal region of California generally seem to be focused upon point-source effects and regional anthropogenic change, while the largest changes we have observed in ecosystem structure are those associated with long-term change which are correlated with changes in the large-scale physical structure. There was general consensus that improving our understanding of the basic science issues will lead directly to increased value for management and policy issues. The group also felt that making the scientific and management communities more aware of these issues would help in gaining research support and seeing more practical application of the findings.

How Is Physical Structure Linked to Biological Structure, Both at the Level of Biomass and Species?

An understanding of how physical structure is linked to biological structure is at the heart of understanding the nature of the changes that have taken place in the California Current, and central to predicting future change. Recent studies have suggested that changes in several different aspects of environmental structure, including mixed layer depth, stratification, and the strength of upwelling-favorable winds, are the cause of changes in primary production. These mechanisms assume that changes in, at least, the biomass of higher trophic levels are forced by bottom-up forcing. Although these physical changes are related, they are also conceptually different mechanisms which may have different regional patterns or different time series. Since time series of several aspects of physical structure are correlated with each other, it is difficult to separate causal mechanisms via time series analysis. Furthermore, the effects of in situ, bottom-up forcing may be masked by apparent changes in population size due to advection, changes in range or preferred habitat of mobile species, and top-down forcing (where changes in predator or grazer populations regulate the abundance of the lower trophic levels). Separating these different mechanisms will be a difficult challenge, especially at the level of individual species. Physical-biological model studies could help to sort out these causalities.

Did Species Structure Change during the Period of Declining Macrozooplankton Biomass?

There are really two questions here. What changes took place in species structure of trophic levels (phytoplankton, macrozooplankton)? How did the population size of selected individual species change? When trophic levels or broad categories such as phytoplankton or macrozooplankton are considered, it is unknown whether species structure changed in addition to biomass. For a few individual species, large changes in population size have been documented. However, in these cases it is difficult to know what caused the changes and whether they are related to long-term environmental change. Most of the discussion focused upon the need to know whether species structure of the macrozooplankton changed, because this is an important response of the ecosystem and it may affect the population dynamics and species structure of higher (and lower) trophic levels.

Are the Changes We See Due to Natural Cycles or Global Change?

One of the most important questions is whether the changes in macrozooplankton biomass are part of a natural cycle or due to anthropogenic global warming. The time rate of change is so small that it is unlikely that this question can be answered by direct measurement of changes in rate processes. However, long time series (10^2–10^3 year) preserved in the sedimentary record can be used to extend the temporal coverage of CalCOFI and estimate scales of natural variability. The paleoceanographic record shows that changes of similar magnitude have occurred in the past. For example, deposition rates of sardine scales over the past 2,000 years show interdecadal–century variability of greater magnitude than has occurred since the initiation of CalCOFI (Baumgartner et al. 1992). Improvement in our understanding of how physical structure changed and how it is coupled to biological structure will help to answer this question.

Can the Present Sampling Scheme Be Improved within the Scope of the Currently Available Resources?

Discussion of the CalCOFI sample scheme focused upon the quarterly time-series cruises. The present scheme does a poor job of characterizing the annual pattern of events. It was observed that attempting to fit the cruises into a specific time window leads to a phase lock, which biases construction of a mean annual cycle. Sampling from south to north on the cruises leads to two-week gaps between sampling the southern and northern lines, and the present scheme leads to gaps in ADCP coverage of the perimeter of the pattern. It was suggested (by Roemmich) that the pattern could be modified to sample the perimeter at the end of the cruise; this would have the advantages of complete ADCP coverage and completing the sampling in a few days. This change would greatly improve the ability to construct a control volume (e.g., Roemmich 1989) and constrain fluxes into and out of the sample grid.

It was also observed that changes within the CalCOFI pattern are forced by physical processes on larger scales, and that populations in different regions may respond differently to changes in environmental structure. Collecting time series of similar data at sites off northern California and Baja California would help to provide a larger-scale view of forcing and indicate whether populations respond to change in the same way.

RECOMMENDATIONS

Nine specific recommendations were made at the meeting. In preparing this list we recognized that recommendations had the greatest chance of being implemented if the costs were modest and if some reasonable source of support were feasible. We did not set priorities on the recommendations because we recognized that priorities will vary depending on the enthusiasm of individuals to pursue the recommendations and on funding priorities of the federal agencies. However, we can state that recommendations with the highest priority were 1 and 2, the general areas of improving our understanding of changes at the species level and increasing modeling efforts in physical models and their coupling to biological structure.

1. Improve Resolution of Zooplankton Species Changes

There was general agreement on the need to understand how species structure of at least some of the major components of the macrozooplankton has changed. It was recognized that several approaches to this—such as counting pooled samples, counting selected years or regions, counting only selected taxonomic groups, or scanning for key species—could reduce the effort required to a more manageable level.

2. Start Putting Biology in Physical Models and Test the Relation to See If the Decline in Macrozooplankton Biomass Can Be Reproduced

One way to gain understanding of the processes linking physical and biological structure will be to include biological processes in physical models of the California Current which are now being developed. The macrozooplankton biomass time series will be ideal for testing such models, and the ongoing data collection program can be used to evaluate predictive ability as it evolves. As a first step in the model-testing process, a very simple model of primary productivity was proposed to be studied by using the mixed layer depth changes hindcast by Miller et al. (1994) as the sole input, with the output compared with historical data on ecosystem productivity.

3. Gain Access to the Output of "Operational" Physical Models Being Developed with Navy Resources

A set of "operational" models is being developed and will be used in the future by the navy for an up-to-date estimate of the upper ocean circulation. The navy will use the model output for its own purposes, but does not have plans to distribute or archive the model output. If the navy is willing to release these data, it would be valuable to distribute the output in a timely manner and to archive the data.

4. Establish a Sample Program off Northern California and Baja California

It would be useful to establish CalCOFI-type field programs off northern California and Baja California. Establishing these would require local resources. It is clear that they would not need to be of the same scope as the present CalCOFI program to be valuable, but it is not clear what the minimum number of stations would need to be (especially to understand changes in macrozooplankton species structure). The CalCOFI data could be used to answer this question.

5. Improve Resolution of Annual Pattern

The annual pattern is poorly resolved by the quarterly sampling on the CalCOFI survey cruises. Additional information about the annual cycle comes from the historical data when cruises were more frequent, ship-of-opportunity cruises made by the cooperating agencies and other regional research programs, coastal shore station data, and coastal mooring data. The annual pattern could be better resolved by including other data sets in the analysis and by establishing moorings at a few selected sites.

6. Have a Meeting on CalCOFI Sampling

People at this meeting felt that there was neither time nor the right group of participants to consider the CalCOFI sample scheme in great detail and to make any recommendations for change. It was recommended that a future meeting deal with this issue. Some focused data analysis may be needed prior to such a meeting. The agenda could include (a) consideration of the present CalCOFI cruise sample scheme; (b) location and sample scheme for additional field programs (e.g., northern California, Baja California); (c) coordination of data distribution and analysis with other sample programs; and (d) location and value of moorings.

7. Better Link the Paleo-oceanographic Record to Water-Column and Current Oceanographic Conditions

There was not sufficient time at the meeting to develop specific recommendations on how to do this, but there was a strong sentiment that it is important to calibrate the paleo-oceanographic record with current water-column conditions. This may require the use of sediment traps and water-column sampling coupled with benthic sampling. It was noted that the Marine Life Research Group has recently increased its level of effort in these areas.

8. Retrospective Data Analysis

The group recognized, as have several other meetings, that much more can be learned by analyzing the existing data from the California Current and at larger scales influencing the California Current (e.g., North Pacific). One specific area which was highlighted was the need to determine if the relation between the nutrient concentration (or dissolved oxygen as a proxy) and temperature/salinity structure has varied in the past few decades. This will be important in understanding how changes in upper ocean physical structure might have affected the nutrient input and primary production.

9. Prepare a Group Synthesis Paper

Most at the meeting were surprised to learn about some aspects of the changes which are taking place in the California Current and felt that the oceanographic community is not generally aware of these changes. It was recommended that a synthesis paper be prepared for a major journal. The paper should focus upon describing change in physical, chemical, and biological (biomass and species) structure in the California Current on a range of space and time scales. This paper would be a useful background citation in grant proposals and a general introduction to the issues. There is no reason why this could not be started now.

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PLANKTON PATTERNS, CLIMATE, AND CHANGE IN THE CALIFORNIA CURRENT

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INTRODUCTION

The Problem

A serious problem facing oceanographers is evaluating the climate's role in the regulation of populations and communities. There can be no doubt that entire ecosystems respond to climate perturbations and that these responses can be large (Chelton et al. 1982; CPR survey team 1992; Frances and Hare 1994; Barry et al. 1995; and this symposium). While evidence for these effects has accumulated, no real theory has developed about the role of climate in population or community dynamics.

Recognizing that climate is important, most marine biologists have emphasized the role of seasonal changes in the regulation of populations. But species tend to adapt well to predictable seasonality. It is the unpredictable anomalies from seasonal norms that we do not understand and that seem to affect populations so strongly. Nor do we understand the driving forces behind such anomalies. It is in the study of climatic and biological anomalies and their interrelationships that a rich field awaits us. After all, we have pretty much known since Copernicus (in 1540) the cause of seasonality.

Our ability to define what is meant by the word *change* is at the root of the problem of understanding climate's role. Populations, communities, temperature, and water movement do vary on a seasonal basis, but they also vary on many other frequencies as well, both higher and lower. These other frequencies of change are of special interest now. Because humans have altered the mix of gases in the atmosphere, there are good reasons to believe that the heat budget of the earth may also be altered and that the consequences will be more variable atmospheric and oceanographic climates. It is expected that these changes will be evident and be felt by ecosystems sometime in the next 10 to 100 years (Martinson et al. 1995).

Defining such temporal changes and understanding their consequences to biological systems are important tasks. But such large environmental temporal changes involve large spatial dimensions as well, so large-scale spatial/temporal ecosystem studies will be necessary because effects due to local changes simply cannot be extrapolated outward to include large areas without evidence for doing so. We can also expect that some changes in time may well include range shifts, and this is a spatial problem as well.

The issue, then, is how will climate change affect marine biological systems? How and in what direction will they respond? There are two basic approaches: (1) local, short-term, process-oriented research, and (2) long-term time-series monitoring. These need not be mutually exclusive, but usually are.

Approaches to the Climate Problem

Process studies. All plants and animals constantly interact with other plants and animals of the same species and other species. Many of those others are competitors, predators, prey, symbionts, or degraders. Because of close spatial/temporal species associations, many biologists have come to believe that at least some of these groupings of species are recurrent and that over time a skein of interactions between species has evolved through natural selection so that there are persistent feedback loops which determine community structure, and regulate energy flow and population dynamics. The introduction of foreign species and the subsequent observed disruption of food webs and established species structure are taken as evidence for this, as are numerous case history studies of coevolved species-species interactions.

If this concept of community is even partially true, then to fully understand the population dynamics of a single species—say the anchovy (*Engraulis mordax*)—some reference to the entire system in which it lives is necessary. But the word *community* and its companion concept *stability* are used in ambiguous ways, and there are still no clear, generally accepted, meanings (Schrader-Frachette and McCoy 1993).

Because of this vagueness of concept and because of the great complexity of even simple communities (that is, many linkages and cross-linkages between co-occurring species populations) many ecologists have chosen to make simplifying assumptions in order to study them. The most common of these assumptions is that various species populations can be aggregated into functional groups. But even here the definition of a functional group is frequently elusive. Many functional designations are synonymous with trophic level. Here the definitions are clear even if the measurements in nature—of, say, the

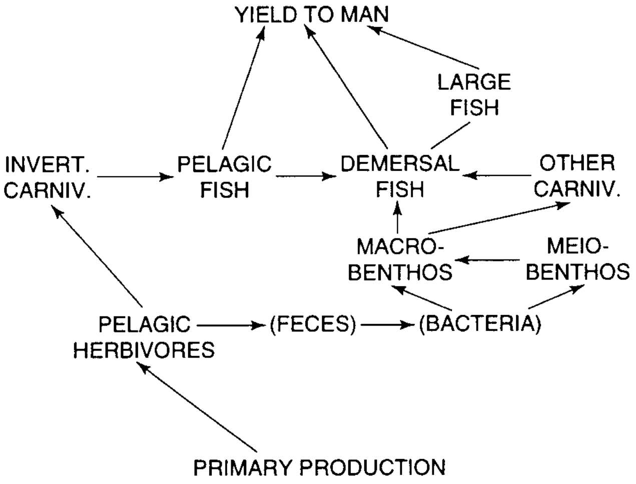

Figure 1. A typical box model of a pelagic food web in which the *arrows* indicate the transfer or "flux" of energy (usually as calories) or biomass or nitrogen or some other index. The emphasis in almost all studies based on this sort of concept is to measure one or more of the rates of transfer either directly or indirectly (as respiration, for example). Some box models are more complex, others are simpler, but very few measure all fluxes at once, so the assumption must be made that the system is in steady state (after Steele 1974).

energy flux through an entire trophic level—are at best dubious. This is especially true if the research objectives are to measure the flux through several or all the levels to some top predator, like the anchovy, in order to determine its potential yield (figure 1).

There are also practical considerations in measuring flux or even just the biomass of entire trophic levels. In order to apply the trophic-dynamic theory of Lindemann or Odum, one generally measures the flux of energy through "representative" species and assumes that the rest of that level is pretty much the same. Alternatively, the respiration of the biomass of what can be captured with a certain mesh-size net is used. But not all herbivores metabolize at the same rates even under identical conditions, and a zooplankton biomass sample may contain as many as three trophic levels.

Trophodynamic studies have not falsified many important hypotheses nor been useful in predictions nor helped us understand the role of climate. But we have learned much from the efforts to understand flux between components, the most important "fact" being the almost universal finding that these fluxes are nonlinear and density dependent. The systems are usually not known to be in steady state when measured. This, of course, makes modeling very difficult.

Ecosystem models are popular, but present models may or may not have much to do with nature. At their worst they are full of untested and untestable assumptions and preconceived ideas. At their best, they are simple quantitative approximations of what we believe we have observed about complex interactions. As such, they stimulate us to think about the potential consequences of such interactions and what might perturb them. Such models should have predictive value and lead to potentially disprovable hypotheses, although there is little evidence for this.

Many contemporary studies in biological oceanography seem to have the mostly unstated objective of providing data for filling in one or another functional role in flux models; i.e., the arrows between the boxes in ecosystem box model depictions (such as figure 1). But this rationale is often unclear. These studies are often referred to as "process oriented" or "case histories," and some of the most decipherable models are based on such observations (e.g., Ross et al. 1993). Many such process studies are reductionist in the extreme, and there are few attempts at true replication, or randomization or controls, and almost never any manipulation of the variables. The more successful of the ecosystem models, based on such studies, have managed to duplicate a seasonal biological signal, but not the sort of responses to anomalies in seasonality that are observed. Such case history or process studies have no doubt enhanced our understanding of some of the details of how the ocean functions and have clear advantages, some of which are:

1. They describe aspects of the dynamics of parts of larger systems and are therefore mechanistic.
2. They can test some specific hypotheses such as: The clearing rate of copepods is not a linear function of food concentrations.
3. They can sometimes provide advice to managers of single-species fish populations.
4. They can sometimes circumscribe or set limits on some rates of transfer of energy or material.
5. They can sometimes provide rough generalizations such as: The rate of growth of individuals is a positive function of temperature; or Phytoplankton growth is limited by nutrients.
6. They are compatible with short funding cycles.
7. They are simple conceptually and therefore popular.

Process studies also have shortcomings, which are:

1. In the context of ecosystem response to climate change, process studies cannot define the word *change* in any meaningful way because of the short duration of the data set.
2. There is no quantitative algorithm for scaling them up in space or forward in time.
3. They are often so highly focused that the relation to the rest of the system is problematical.
4. They are often not really experimental, in the sense that there are usually no replicates, randomization, controls, or manipulation.
5. The ecosystem from which the sample is drawn is seldom in steady state, and the fluxes between boxes are almost always nonlinear.

6. They are often tautological; as such, they are derivative, repetitious questions and add little to our understanding.
7. Conclusions drawn from a process study at one location are not always applicable to other locations; for example, *Calanus* life histories in the North Atlantic versus the North Pacific.
8. There are many untidy system effects. For example, predator switching is a common phenomenon. It has been observed that exogenous perturbations can make prominent players out of system components which were not response variables in the first place.

Time series. Time series are merely the repetitive measurement of some variable over time. The objective is to determine how it varies in magnitude with respect to time in order to define the temporal scales of variability—that is, the frequency spectrum.

Apart from selecting the variable to be measured and the location, time series are designed with few prior assumptions about the behavior of the variable or what may or may not influence its frequency spectrum of variability. Time series are, or should be, empirical. Because they assume little prior knowledge of rates, directions, amplitudes, or frequencies of variation, the sampling should be as frequent as possible for as long as possible. High-frequency changes are just as likely to be the "important" ones as low-frequency under this empiricism.

The main questions asked by a time-series study have been given by Wiebe et al. (1987). What are the temporal scales of variability of basic community ecosystem properties? Are there some frequencies that show the largest and therefore the most ecologically "important" changes? If various components of the biogeochemical system interact to influence each other's magnitude, there should be detectable statistical relationships between them, even in the presence of a large amount of noise. What are the cross-correlations or coherences between system components? We need to know more about what types of atmospheric or hydrographic perturbations affect biogeochemical systems and what types do not. How and in what direction is the response to different kinds of physical events? It seems likely that the mean state of ecosystems is set by the cumulative effects of variability on many space and time scales. But if there are multiple steady states, how are shifts between them brought about? Is it necessary for forcing to change on all frequencies for a shift from one system state to another?

Can a long time series of measurements of the products of nonlinear interactions help us understand the limits of predictability and modeling? Predictions based on models of complex systems about which we have only limited knowledge have not enjoyed great success. But the product of these flexible webs of functional rates, namely changes of the main components of community structure with respect to time, can be easily measured. Changes in structural state can be quantitatively described. Testable null hypotheses can be proposed. We can then construct a sort of inverse model, not based on "first principles" (whatever they are) but on empiricism: what kind of a structure and what kinds of dynamic interactions can result in the system we have observed?

As with the process study approach, there are advantages and shortcomings with the time-series approach. The advantages are:

1. The research is empirical.
2. This research can define what is meant by the word *change.*
3. Dominant frequencies of change can be determined. Frequency spectra can be examined.
4. Time series are on the correct scale for studying ecosystem change on interannual and decadal time scales.
5. If a number of properties at a number of locations have been measured, spatial coherence information can be determined.
6. With a number of well-spaced stations, spatial averaging can be done, thus allowing a smoothing of noisy, high-frequency spatial patchiness.
7. Such series can generate and test higher-order null hypotheses such as: Zooplankton productivity does not respond to changes in coastal upwelling index.
8. Empirical results obtained from time series provide important guidance for designing and developing process studies and ecosystem models. The data can also be used to validate or invalidate models.

The disadvantages of time series are:

1. The results of time series studies provide little information on the intermediary mechanisms of change.
2. Insight into cause and effect depends on correlations.
3. If correlations "fail" there are usually no explanations.
4. Time series are tricky; they can easily be done improperly and are often complicated by practical considerations. If there are frequent gaps or changes in frequency of sampling or if the frequency of sampling is much less than the frequency of variability, the data can be badly aliased, which can lead to misleading results. Single stations do not necessarily tell us about spatial extent of variability or change.
5. Time series require sustained effort over a long period of time.

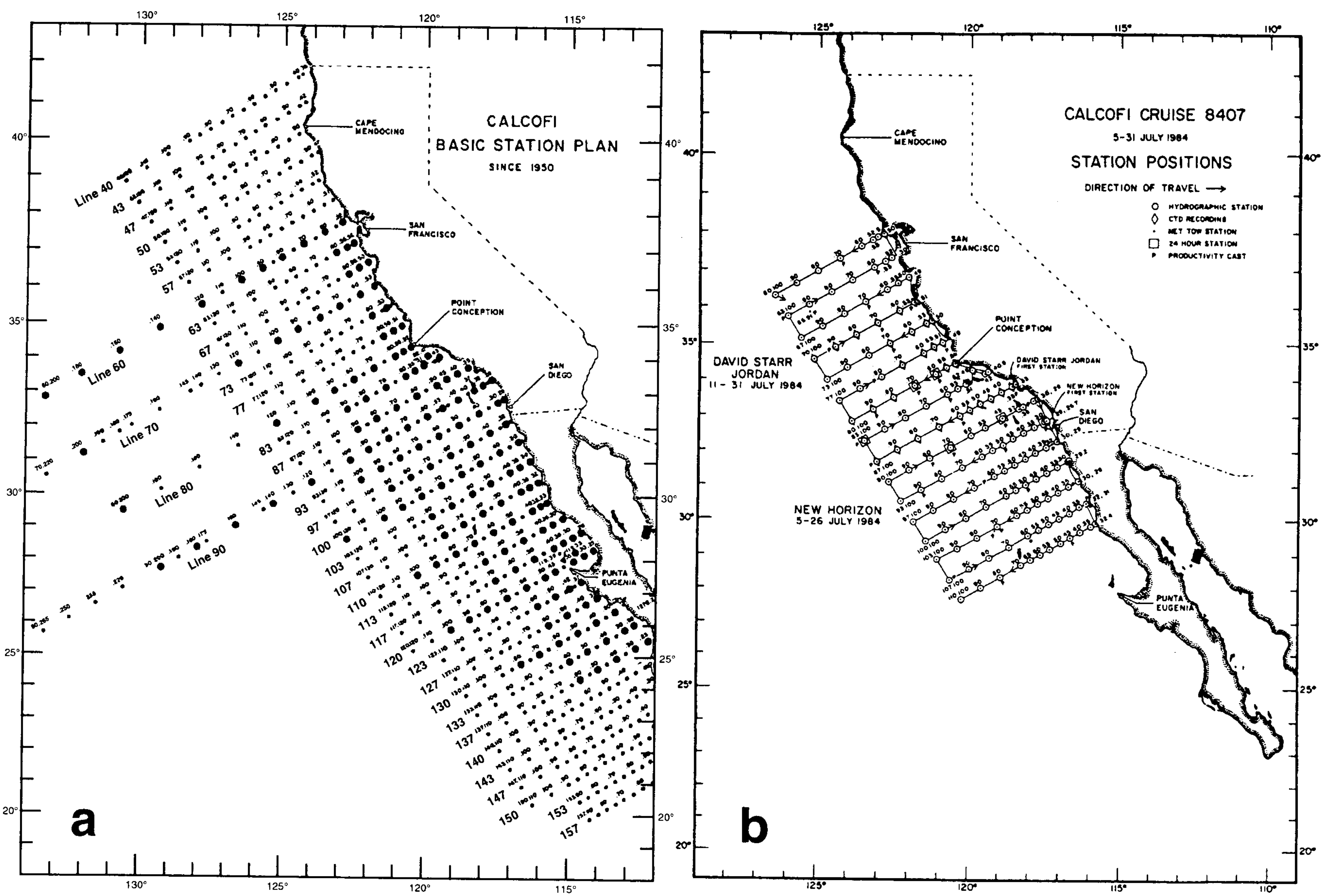

Figure 2. *a*, The basic CalCOFI plan. No one cruise covered this area (*small dots*). The most frequently sampled stations (1950–79) are shown also by *large dots* (after Lynn et al. 1982). *b*, A typical cruise pattern from the 1970s and early 1980s, showing the type of sampling done on each station (SIO Cruise Report).

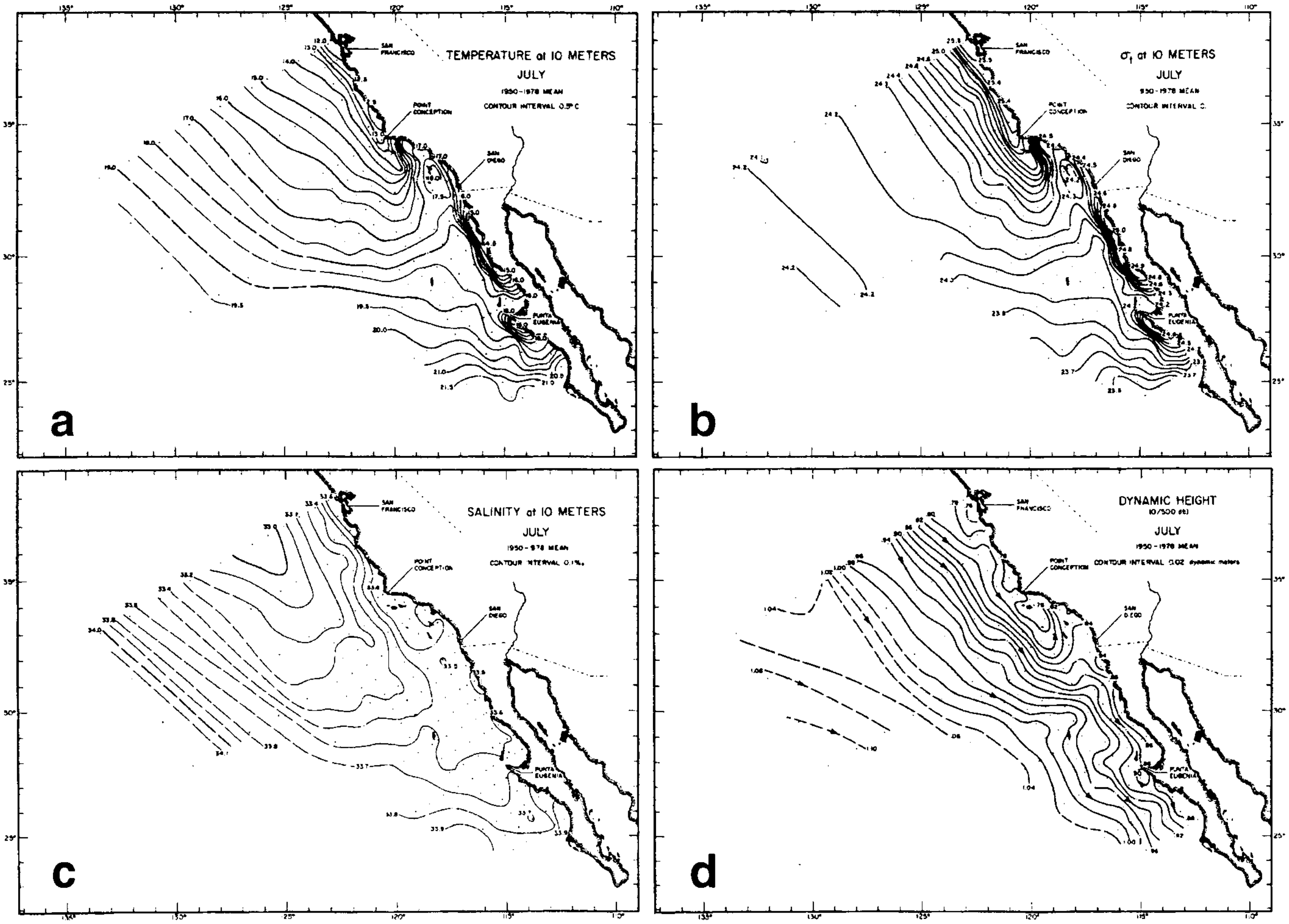

Figure 3. *a*, The 1950 to 1978 mean 10 m temperature for the summer season (July–Sept.). Longshore and onshore-offshore gradients are evident. After about 1977 the California Current warmed significantly. *b*, The 1950 to 1978 mean summer salinities at 10 m. *c*, The mean 10 m summer density patterns, 1950–78. *d*, The mean summer dynamic heights 10/500db for summer. Separation of isopleths indicates speed of current (close together, faster; widely separated, slower). There is a longshore jet in midstream (*a–d* from Lynn et al. 1982).

6. Collecting time series is routine and uninteresting until enough time has elapsed so that natural phenomena can be resolved.

In spite of these shortcomings, time series remain the only way to obtain information on ecosystem variability, and they almost always reveal important new and unexpected results.

THE CALIFORNIA CURRENT

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program was designed in the late 1940s as a time series, chiefly to study the Pacific sardine and its physical and biotic habitat. There were preconceived notions in the selection of variables to be measured and the time and space scale on which to measure them, but these had little or nothing to do with an assumed architecture or dynamics of the system. The program was driven mostly by practical considerations—the decline of the sardine, and what time-space resolution could be afforded that was consistent with understanding the habitat, i.e., the problem posed by Stommel (1965). A grid plan was selected and adhered to; methods, while changing somewhat over time, were intercalibrated and found to be reasonably consistent.

Several of the many advantages of the CalCOFI plan are that it covers a large area that includes most of the spawning area of the sardine and some other fish; important biogeographic and physical features can be seen; and large-sector spatial averaging of the time series can be used to generalize about real temporal changes.

This grid plan is well known (figure 2), as are the long-term spatial means of temperature, salinity, density, and dynamic heights (figure 3). These show considerable spatial variability and strongly imply that time series and spectral analyses are called for in order to investigate the temporal nature of this variability.

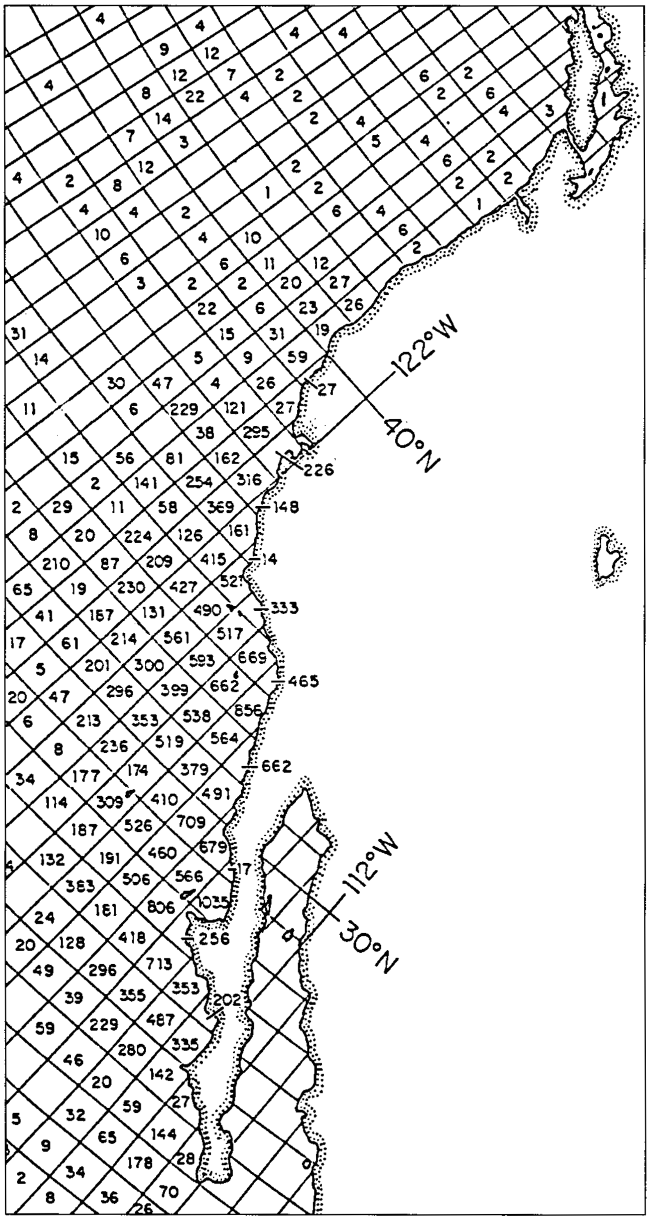

Figure 4. The number of large oblique zooplankton tows per 1° square 1950–88 (see Kramer et al. 1972 for methods).

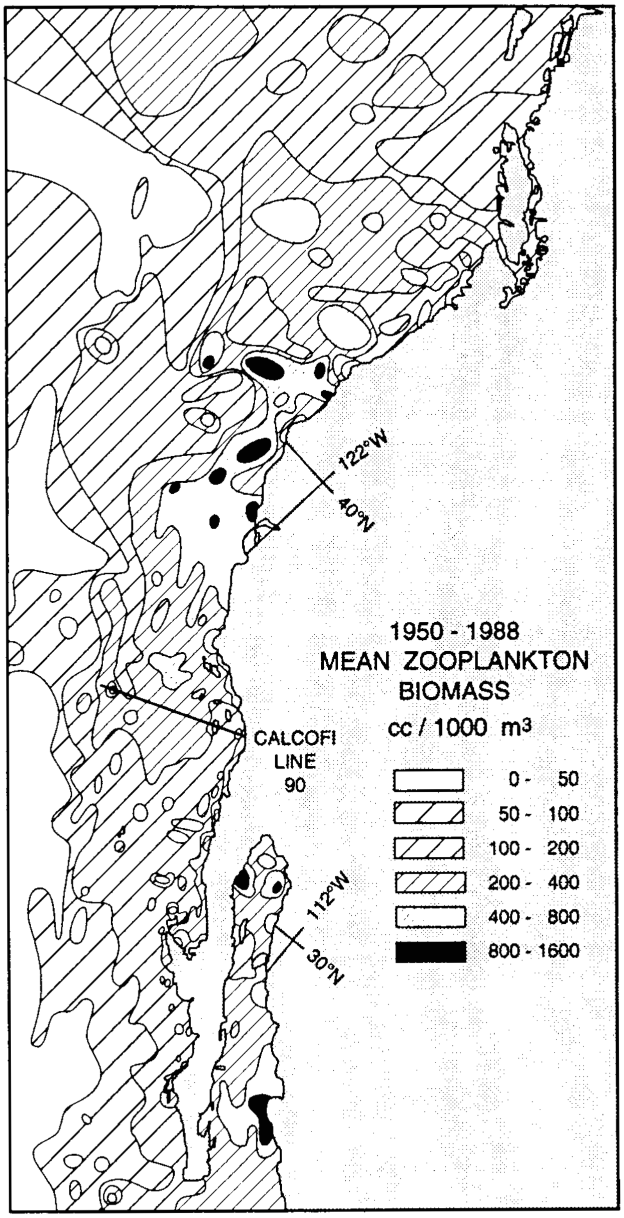

Figure 5. The long-term mean zooplankton biomass. There are onshore-offshore gradients and north-south gradients.

Spatial Patterns

The main purpose of the net tows conducted since 1949 by CalCOFI was to obtain samples for estimating the patterns of abundance of fish eggs and larvae. Since sampling zooplankton at the same time could hardly be avoided, a very large time series of zooplankton has accumulated. Figure 4 shows the number of plankton tows per 1° square over the period 1950–88. Each of these is accompanied by a hydrographic cast to at least 500 m, so that relations between biological and physical variables can be examined on the same frequencies. Although it is clear that there have been wide variations in the intensity of measurement per 1° square, a very large number of measurements do occur in the central sector (the main area of fish spawning), especially on lines 80 and 90.

The long-term spatial mean of zooplankton biomass (figure 5) shows an extraordinarily patchy field despite the long-term temporal averaging. This seems especially true where the sampling intensity is high. Further, most of the plankton is concentrated in a relatively small fraction of the time-spatial domain. But it is clear that there is a north-south gradient off most of California and a well-defined offshore maximum south of Point Conception. The low values off Oregon and Washington may be due to sparse sampling in that region.

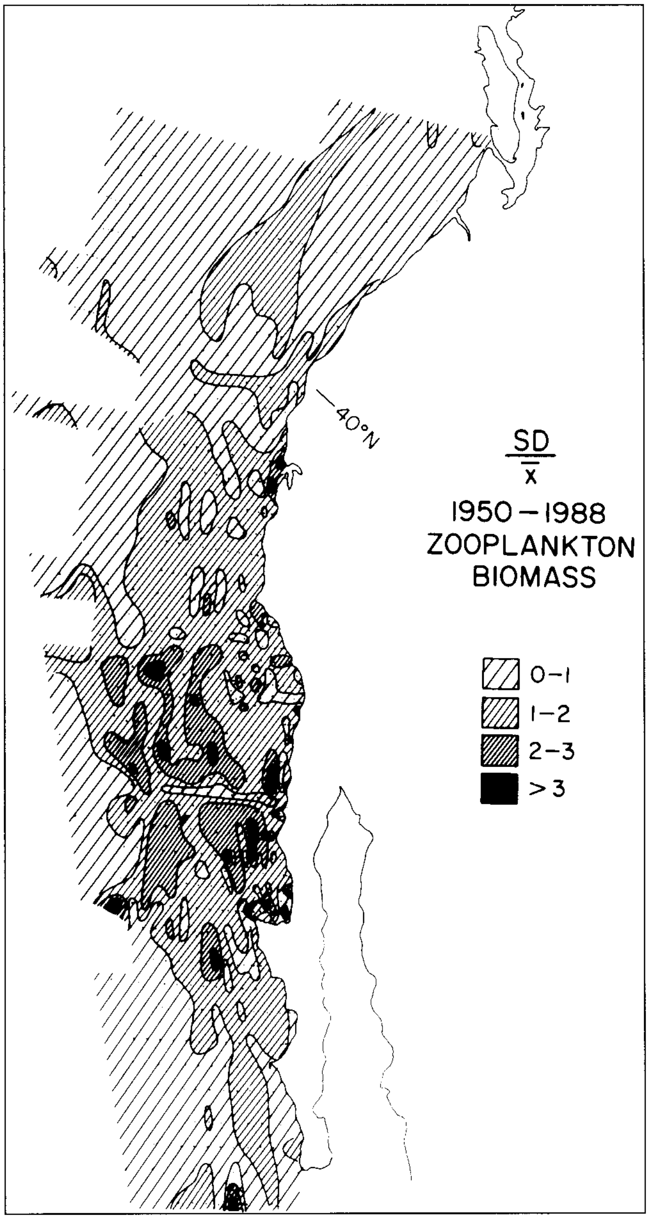

Figure 6. The index of variation (standard deviation divided by the mean) of the zooplankton biomass data in figure 5.

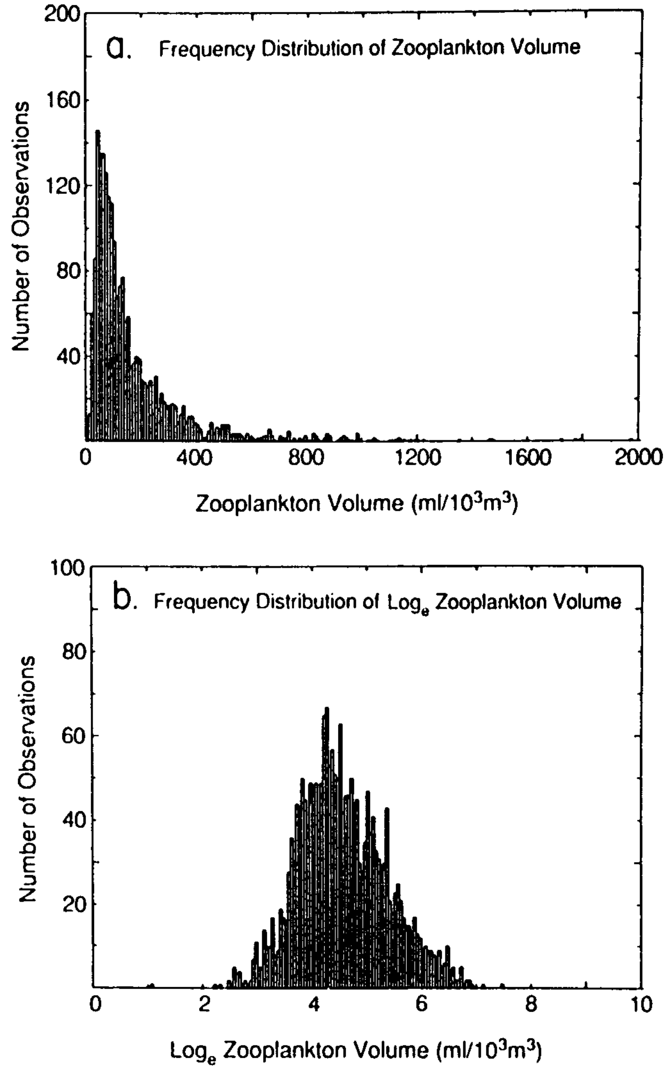

Figure 7. *a*, The frequency distribution of CalCOFI zooplankton biomass estimates; *b*, $\log_e$-transformed data.

In an effort to smooth the data further we used the coefficient of variation ($SD/\bar{X}$) since the magnitude of the variance is dependent on the mean in this case (figure 6). This did smooth the patchiness somewhat and also had the effect of shifting the main area of apparent high spatial variability farther south. The frequency distribution of zooplankton biomass (figure 7) shows many large outliers 4 to 10 times the overall mean. These must represent very dense patches which are episodic in space and time, thus the failure of our averaging and coefficient of variation to effectively smooth the long-term data. This seems clear evidence of the highly variable nature of zooplankton and strongly implies that large but episodic and spatially limited ecological events are features of the California Current System.

The area of high biomass variability is also one of highest species diversity (McGowan and Miller 1980). It is here that species whose populations are continuous with those of the Subarctic, the Transition Zone, and the Central Gyre, and with warm-water cosmopolites mix together (figures 8, 9, 10). This zone of high variability in biomass and diversity (figure 11) is almost certainly due to physical mixing of waters and their faunas from different source regions. Species dominance shifts in the plankton here occur very rapidly and over very short distances as compared to the Central Gyre (McGowan 1990). Such rapid and large shifts in rank order of abundance are unlikely if competitive displacements are the main cause. It seems much more likely

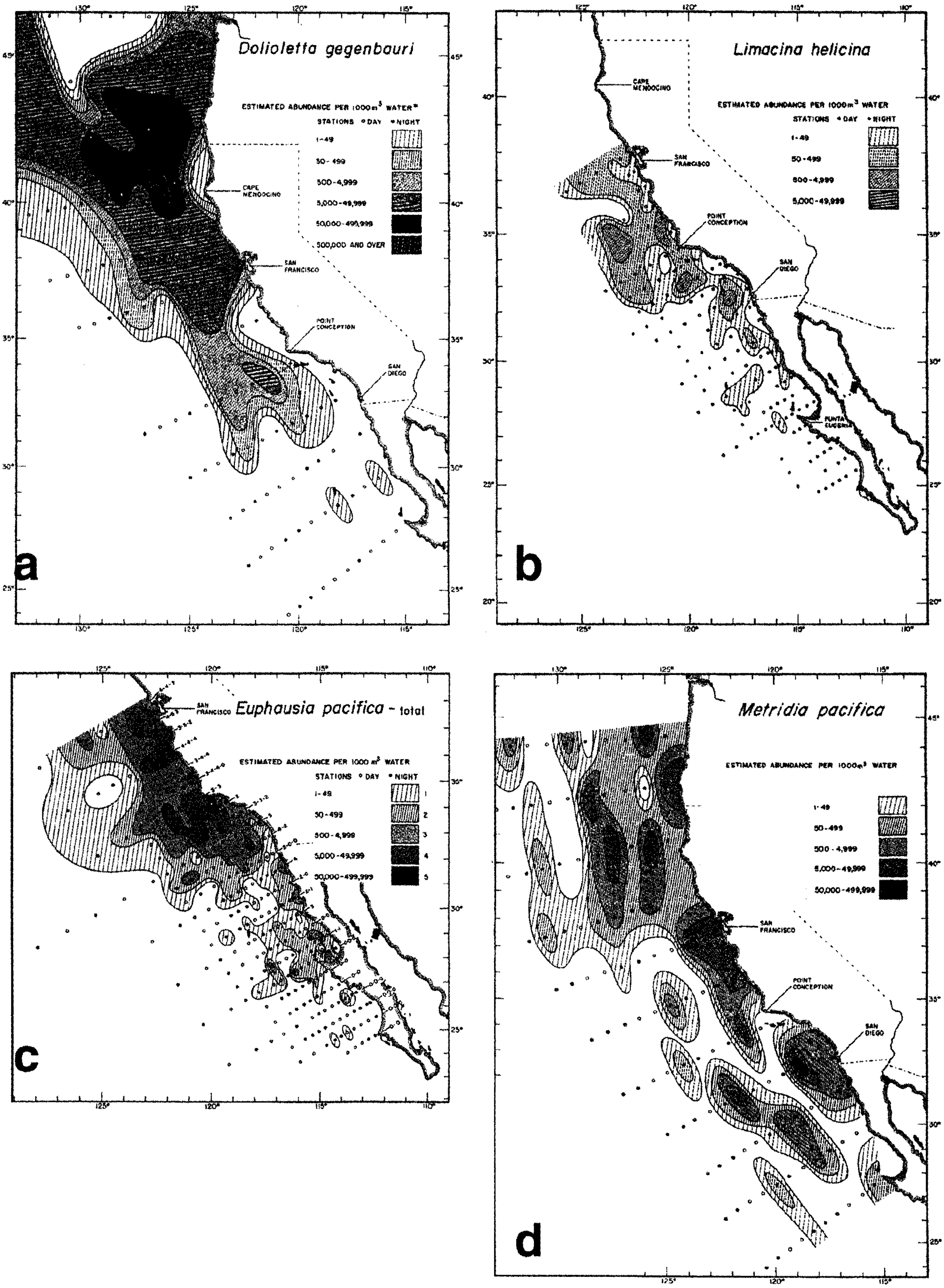

Figure 8. The distribution and abundance of four species of zooplankton that are common in the Gulf of Alaska and the Subarctic North Pacific. *a, Doliolletta gegenbouri* from cruise 4907 (from Berner 1967); *b, Limacina helicina*, a pteropod from cruise 5204 (from McGowan 1967); *c, Euphausia pacifica*, a euphausiid from cruise 4907 (from Brinton 1967); *d, Metridia pacifica* from cruise 4909 (from Bowman and Johnson 1973).

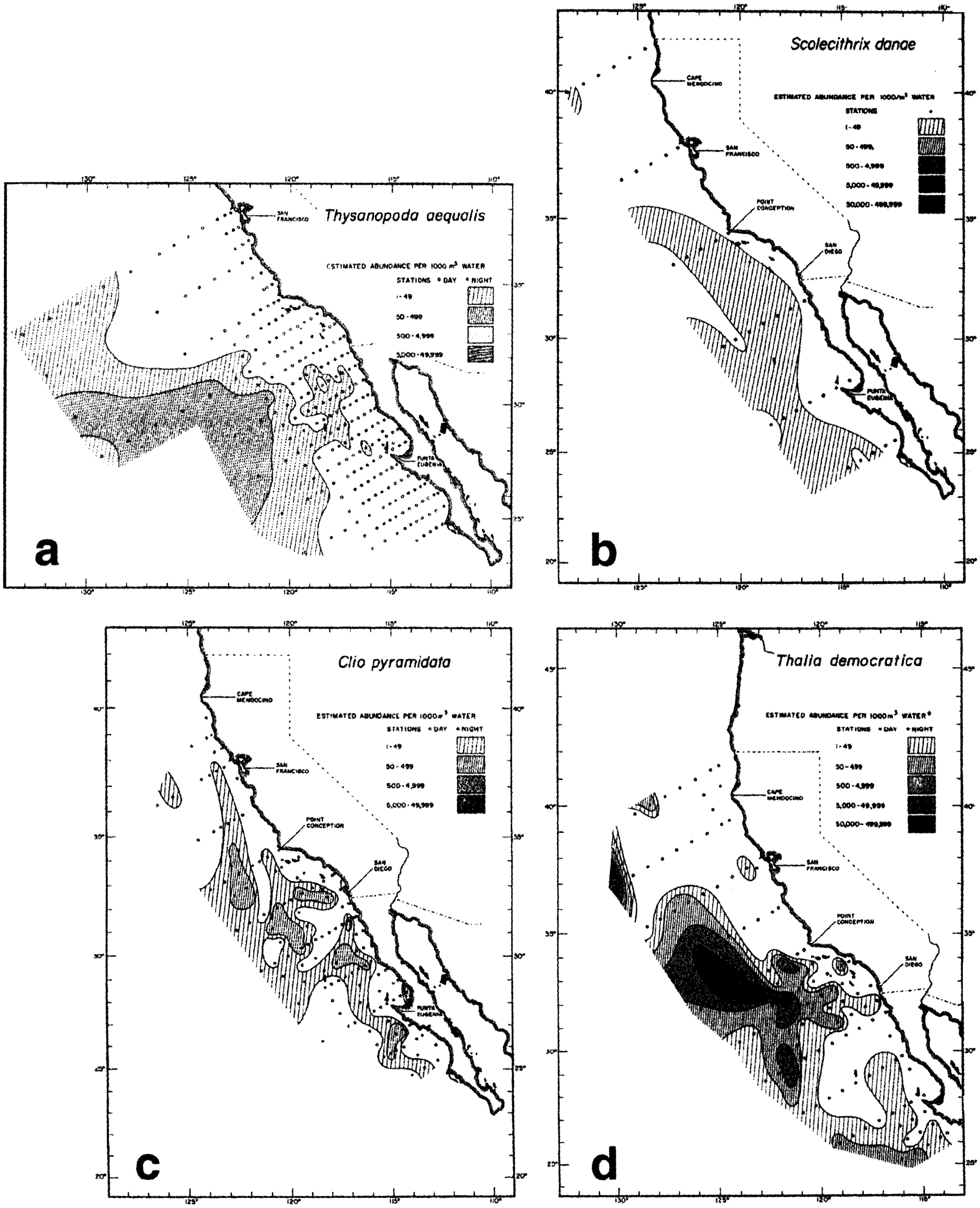

Figure 9. The distribution and abundance of four species that are common in the Central Gyre of the North Pacific and intrude into the California Current from the west. *a*, *Thysanopoda aequalis*, a euphausiid from cruise 6304 (after Brinton 1967); *b*, *Scolecithrix danae*, a copepod from cruise 5807 (after Fleminger 1964); *c*, *Clio pyramidata*, a pteropod from cruise 5206 (after McGowan 1967); *d*, *Thalia democratica*, a thaliacean from cruise 5005 (after Berner 1967).

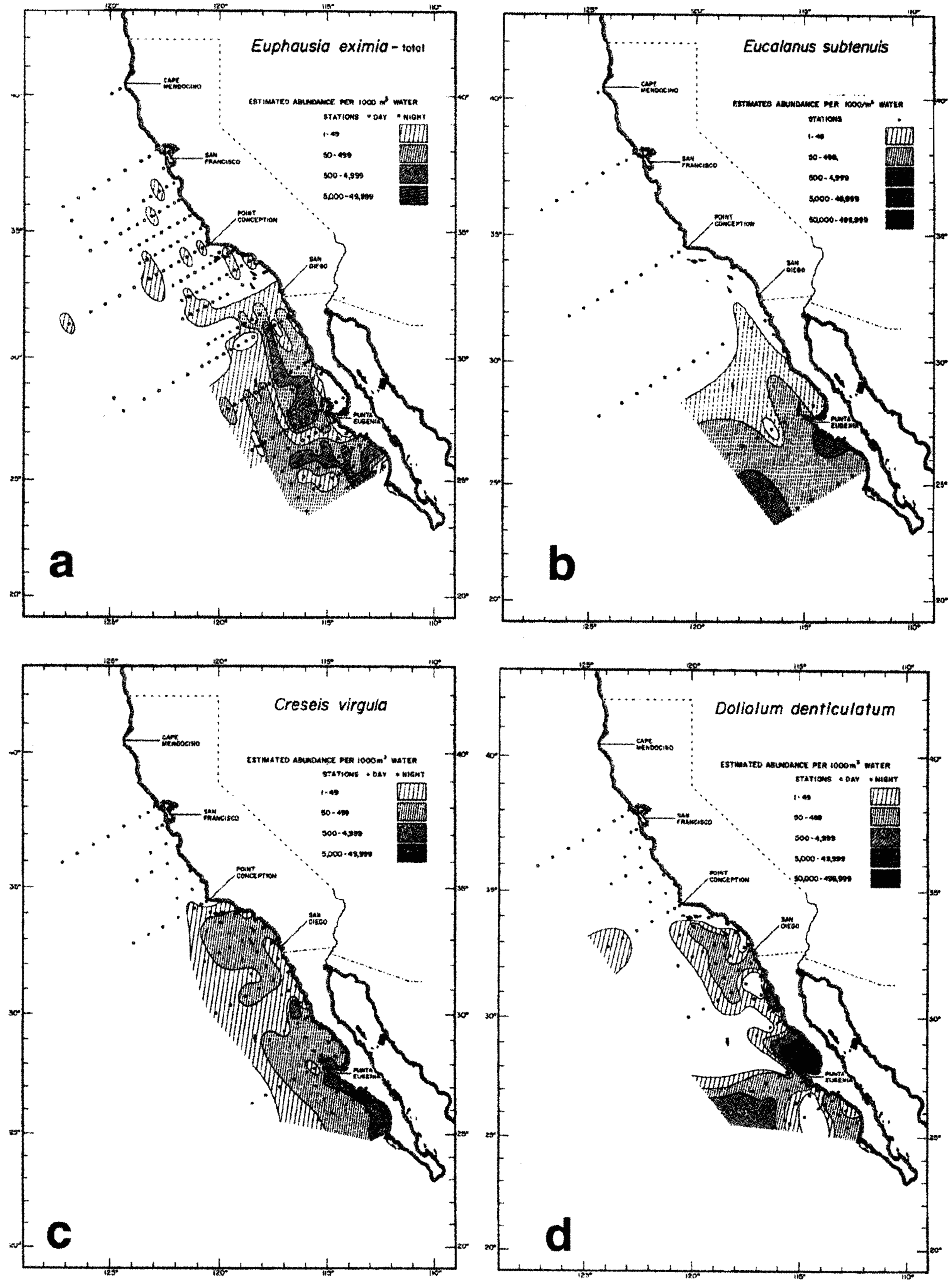

Figure 10. The distribution and abundance of four species of zooplankton that are common in the eastern tropical Pacific and intrude into the California Current from the south. *a*, *Euphausia eximia* from cruise 5804 (after Brinton 1967); *b*, *Eucalanus subtenuis* from cruise 5804 (after Fleminger 1964); *c*, *Creseis virgula* from cruise 5210 (after McGowan 1967); *d*, *Doliolum denticulatum* from cruise 5210 (after Berner 1967).

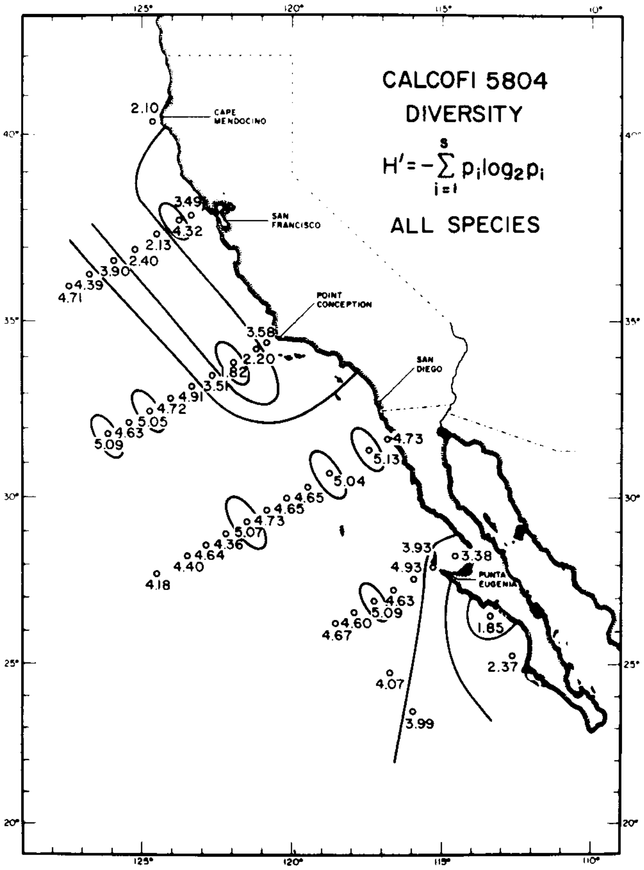

Figure 11. The spatial pattern of zooplankton species diversity in the California Current, from cruise 5804. Over 100 species were used in this study (from McGowan and Miller 1980).

that simple physical mixing of water parcels from different sources with different faunas is the cause behind the nonsignificant species-rank correlation coefficients between samples from this area (McGowan and Walker 1993).

Interannual Patterns

The mean spatial distribution of variables shows the California Current System to be very complex, especially the zooplankton biomass field. But there are reproducible patterns, especially on the large spatial scales. There are also patterns in temporal variations (Bernal 1979; Bernal and McGowan 1981; Brinton 1981; Chelton et al. 1982; Roesler and Chelton 1987; Roemmich 1992; Roemmich and McGowan 1995).

The seasonal temperature signal in the mixed layer was well resolved by the early period of the CalCOFI surveys, when cruises were at approximately monthly intervals (figure 12). It was, and still is, a strong and unambiguous signal. But as the time series progressed, it became evident that there were strong interannual variations as well. Standard deviations of 1.5°C in the monthly mean temperature were common (figure 13). A large El Niño occurred in 1958–59 (Sette and Isaacs 1960). As further low-frequency events occurred, these temperature standard deviations became larger. Eventually it became apparent that a long-term trend of increased temperature of the mixed layer had occurred, but this required about 40 years of data in order to be detected unambiguously (Roemmich 1992). The entire upper layer of the area surveyed up to 1992 had warmed by at least 0.8°C between 1950 and 1990.

Early in the program Reid et al. (1958) showed a negative relationship between zooplankton biomass and 10 m temperature over time. Perhaps because his data set was limited, this observation did not receive much attention, and ecosystem modelers continued to use temperature increase to drive higher production. With the much larger data set now available, we can confirm Reid's point (figure 14). Experimentalists have shown that the growth rate of individuals increases with temperature. This observation has led many to believe that somehow population growth also increases with temperature because larvae and juveniles pass through their vulnerable early stages more rapidly and therefore survivorship is enhanced. The CalCOFI temperature biomass data indicate that this hypothesized relationship is not the dominant mechanism controlling zooplankton abundance in the California Current.

Whereas zooplankton biomass and larval fish have seasonal variations of abundance (figure 15), Chelton et al. (1982) have shown that there are large interannual variations as well and that the magnitude of interannual variability is comparable to or larger than that of the seasonal variability. It is quite clear now that zooplankton biomass and larval fish abundance in the California Current System are both dominated by interannual variability (figure 16). The nonseasonal variations (anomalies from the seasonal signal) are of particular interest since (unlike the causes of the seasonal cycle) the causes of interannual variations are not yet well understood. These interannual variations are indicators of short-term climate changes in the California Current System.

Chelton et al. (1982) have examined lower-frequency changes in both hydrography and plankton. They found that interannual anomalies in temperature, salinity, zooplankton, and mass transport from the north rise and fall together throughout the entire system. The anomalously high zooplankton biomass episodes were correlated with colder, low-salinity episodes which occur during periods of anomalously high transport from the north (figure 17).

The high productivity of the California Current System is a well-known feature in reviews and textbooks, and this richness is almost routinely attributed to the fact that coastal upwelling of deeper water brings nutrients to the surface near shore, enhances primary production,

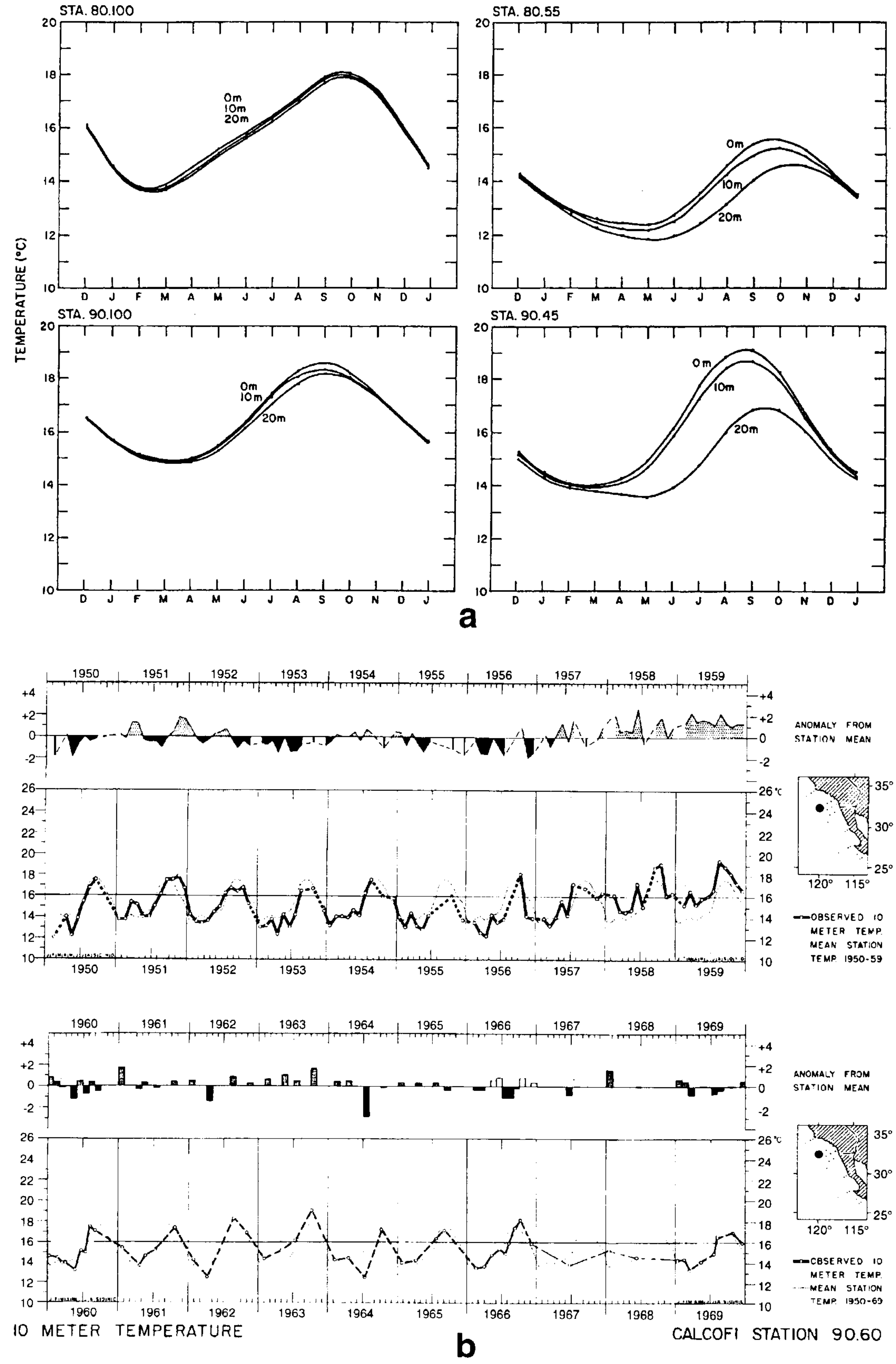

Figure 12. *a*, The seasonal temperature harmonics for four stations at four depths, 1950–80. Stations 80.55 and 90.45 are relatively nearshore; stations 80.100 and 90.100 are offshore. See figure 2 for locations. *b*, The 10 m temperature and temperature anomalies at station 90.60 in the Southern California Bight (see inset) for 1950–69 (after Anonymous 1963 and Wyllie and Lynn 1971).

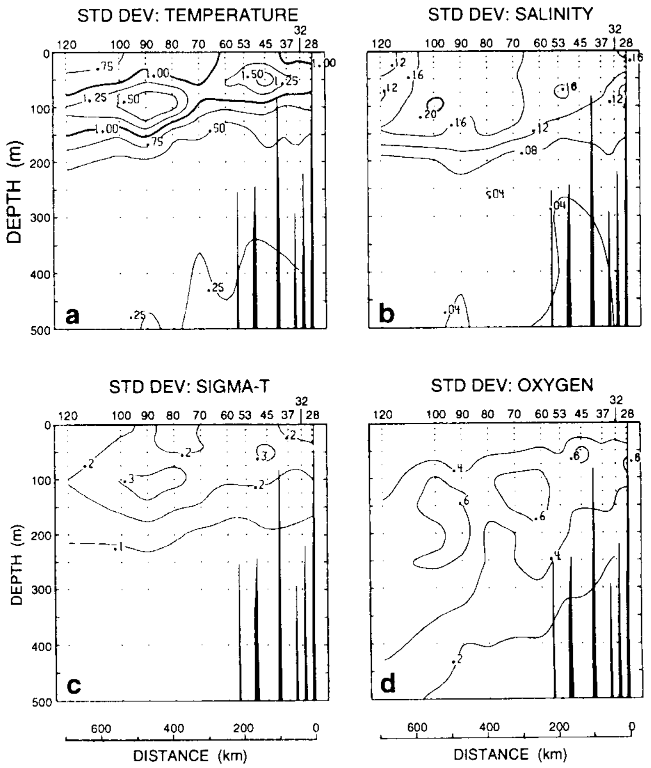

Figure 13. The standard deviation of temperature, salinity, density, and oxygen along line 90 (1950–76, after Eber 1977).

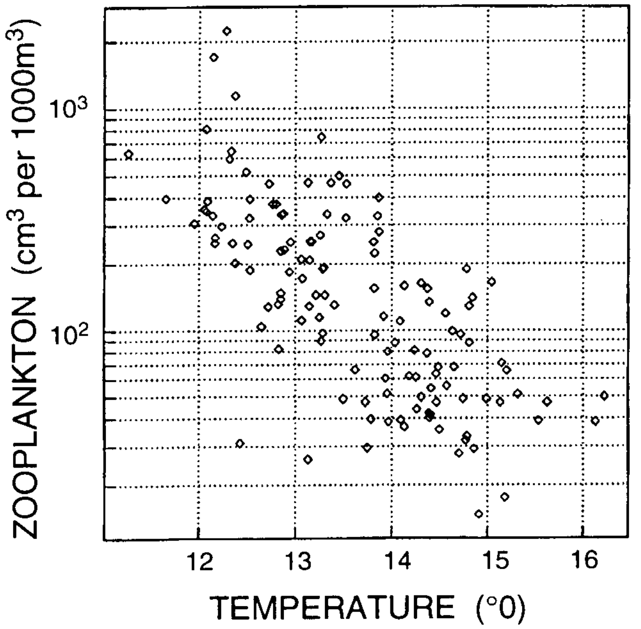

Figure 14. Average California Current zooplankton biomass per cruise, 1950–93, from stations 30 to 120 on line 90 (see figure 2) and the average temperature per cruise of the upper 100 m on that line. There were 10 or 11 stations on this line per cruise.

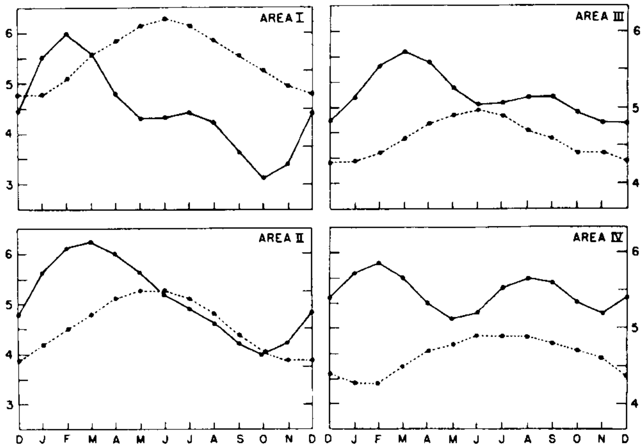

Figure 15. Seasonal cycles of zooplankton displacement volumes in 10^{-3} ml/m^3 (*dashed lines*) and larval fish in units of 10^{-3} individuals/m^3 (*solid lines*) 1950–70. The seasonal cycle is defined here to be the sum of an annual and a semiannual harmonic and a constant offset. The amplitude and phases of these three constituents have been determined by least squares regression.

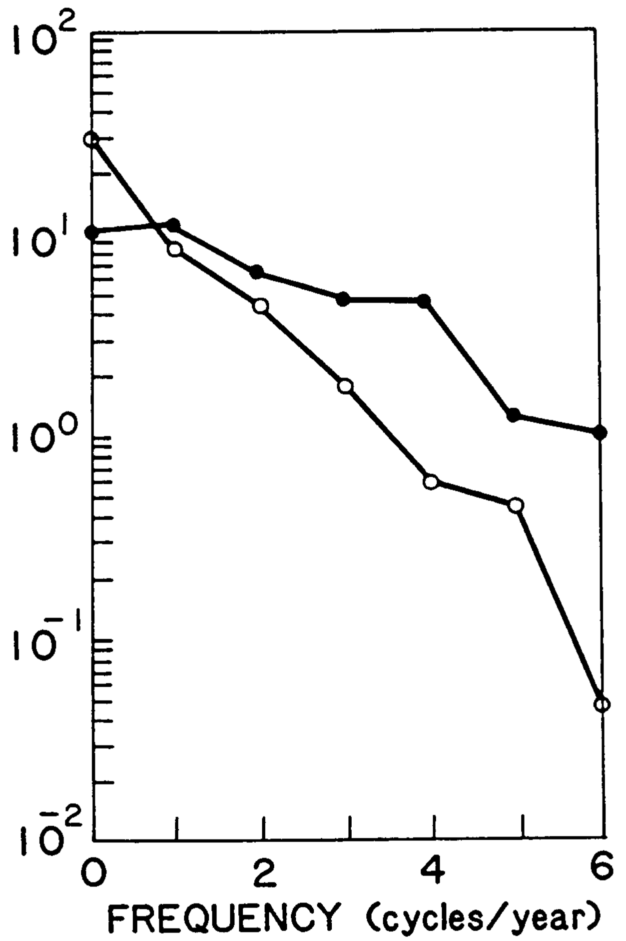

Figure 16. Normalized power spectrum, showing the average, nonseasonal $\log_e$-transformed zooplankton biomass (*open circles*) and the nonseasonal $\log_e$-transformed larval fish abundance (*solid circles*). The fish power spectrum is much more regular than the zooplankton spectrum, and there seems to be a residual broad-bandedness. The small peak of one cycle per year in seasonally corrected fish data may be due to fish having a sharply peaked spawning period but one that varies from year to year.

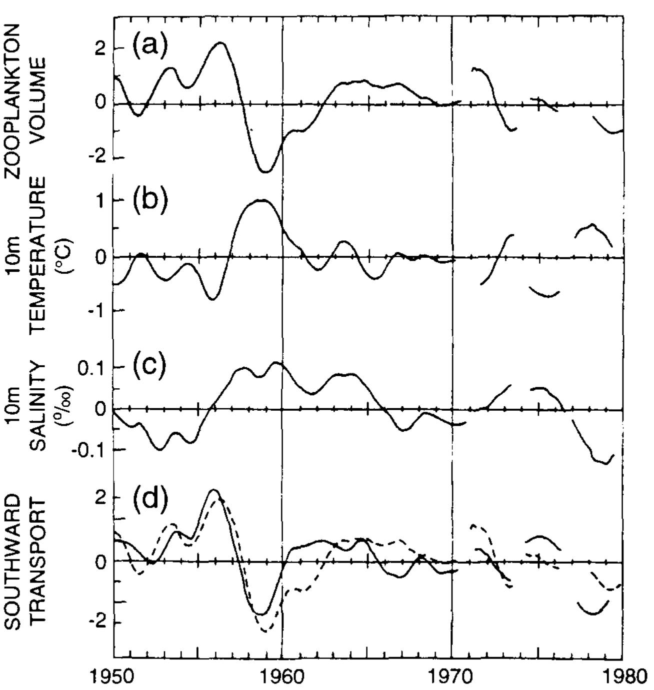

Figure 17. Time series of nonseasonal values of four variables averaged over the entire area: *a*, zooplankton in $\log_e$ were standardized; *b*, average 10 m temperature over the area; *c*, average 10 m salinity; *d*, the amplitude time series of the principal EOF of 0/500 steric height. The raw time series were filtered with a double 13-month running mean. *Dashed line* in *d* represents the zooplankton time series shown in *a* (from Chelton et al. 1982).

and thus enriches the rest of the food web. But direct measures of nutrient upwelling have proven elusive, and the surrogate often used by biologists is the Bakun index of coastal upwelling (Bakun 1973). This index, based on Ekman volume transport dynamics, is reported in both absolute terms of "metric tons per second per 100 m of coastline" and in anomalies. Thus the null hypothesis can be stated: H_0: "Nonseasonal zooplankton biomass anomalies are driven by coastal upwelling." This hypothesis was disproved from time-lagged cross-correlations (figure 18; Bernal and McGowan 1981). This correlation failure is largely due to the fact that the time scales associated with the physical and biological fluctuations are much longer than those of the local wind stress used in calculating the upwelling index.

An alternative null hypothesis is: H_0: "Zooplankton biomass anomalies are driven by mass transport from the north." This hypothesis could not be disproven, because the cross-correlations between transport anomaly and zooplankton are positive and significant (figure 18). Whatever the climatic forcing responsible for interannual changes in the mass transport from the north (otherwise known as the strength of the California Current), they clearly are associated with interannual zooplankton biomass variations off central and southern California. Some of these variations are associated with episodic El Niño events, but some are not.

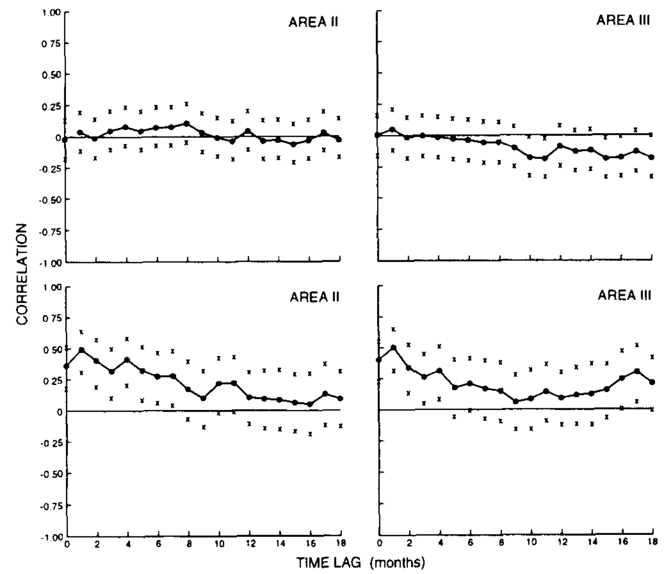

Figure 18. Time-lagged cross-correlations from 0 to 18 months. *a*, Nonseasonal Bakun's upwelling index in Area I leads nonseasonal zooplankton biomass in Area II. *b*, Nonseasonal upwelling index in Area II leads zooplankton biomass in Area III. *c*, Nonseasonal transport from the north (across line 80) leads zooplankton in Area II. *d*, Transport across line 80 leads zooplankton in Area III. *X*s are 95% confidence limits (after Bernal and McGowan 1981).

The nature of the underlying causal mechanisms of the changes in advection are probably quite complex and are not yet understood, but they seem clearly related to climatic changes. Roesler and Chelton (1987) have more closely examined this biological response to physical forcing. They suggest that the timing of the biomass variations relative to variations in southward advection indicates that they are controlled by two processes: (1) the response of local zooplankton to advection of biomass—the dominant process in the north—and (2) the response of local populations to changes in local conditions caused by changes in advection. This latter process becomes increasingly dominant from north to south. Biogeographic species boundary shifts also indicate that these mechanisms control the interannual variability of zooplankton biomass.

The CalCOFI zooplankton samples were taken for the main purpose of capturing fish eggs and larvae. There is thus a 45-year record of variations in larval fish abundance accompanied by a zooplankton biomass volume for each sample. It is possible now to compare temporal variations in larval fish to temporal variations in zooplankton.

Theilacker (1987) and Theilacker and Shen (1993) have documented that sea-caught larval fish may often be badly undernourished, and Houde (1987), Lo et al. (1995), Kendall et al. (1996), and others have shown that the feeding larval and early juvenile stages of many—perhaps most—species of pelagic fish have larger rates of, and variations in, mortality than any other life-history stage. This variability is thought to be one of the important contributions to variations in recruitment. Since larval fish are about the same size as zooplankton, occur together with zooplankton, and frequently have similar diets, it is not unreasonable to assume that they compete with or are preyed upon by members of the macrozooplankton community. This is especially true in view of the fact that many individual species of macrozooplankton, as caught by CalCOFI, are far more abundant than the co-occurring larval fish (McGowan and Miller 1980). But those same macrozooplankton are the diet of the adults that gave rise to the fish larvae. Further, the crustacean zooplankton (at least) give rise to naupliar larvae, which are the food for many fish larvae. The interactions between trophic levels are clearly very complex and nonlinear.

MacCall and Prager (1988) have estimated "Historical changes in abundance of six fish species off Southern California, based on CalCOFI egg and larva samples" by "developing annual indices of larval abundances of the northern anchovy, Pacific sardine, Pacific mackerel, jack mackerel, and Pacific whiting (hake)." These are the most abundant pelagic species in the California Current System. Three of these five (the sardine, anchovy, and Pacific mackerel) had larval abundance indices that agreed well with other estimates of variations in adult population size. The other two species have apparently shifted their spawning range to the north because of the warming trend that began in the mid-1970s. But Hollowed (1992), in an extensive study of hake abundance, has concluded that "production of strong year classes of Pacific hake was regulated by factors influencing survival during early and late larval periods."

Thus there are good reasons to suspect that variations in macrozooplankton abundance can affect larval fish populations in several ways: (1) Adult fish fecundity may vary because of changes in the food supply; (2) Macrozooplankton provide food for larval fish through their own larvae, especially crustacean nauplii; (3) Macrozooplankton may compete for food with fish larvae; and (4) Some species of macrozooplankton are known to prey on larval fish. In cases 1 and 2 we expect macrozooplankton and larval fish abundance to be positively correlated, perhaps with some time lag. In cases 3 and 4 larval abundance changes should be negatively correlated with zooplankton. Large variations in larval abundance should result in variations in recruitment. Therefore large-scale interaction between trophic levels should be occurring. But it is well known that variations in the abundance of different species of harvested fish are not highly cross-correlated. That is, peak abundances occur at different times, and there appears to be a succession of species abundance over time (MacCall and Prager 1988; Sund and Norton 1990; MacCall 1996). It has been suggested several times that interspecific competition for food is a possible explanation of these results. As a consequence, repeated shifts of species dominance occur (Skud 1982), although the standing crop of total "fish" might remain fairly constant.

An important question to be addressed is whether variations in the trophic level represented by larval fish are somehow associated with variations of the trophic level represented by macrozooplankton. It is quite clear that selecting an individual fish species for the test may not yield interpretable results. The same is true if we wish to test whether or not larval abundances are affected by climate. Although variations of one or several species may be correlated with zooplankton or SST or wind-speed variations, these relationships cannot be generalized. If most pelagic fish do replace one another in some sort of competitive succession, then "total larval fish" is likely to be a more appropriate variable to consider.

In view of the evidence that mortality rates are highest during larval stages, that variations in the abundance of larval fish agree with estimates of adult fish, that recruitment depends on survivorship during larval periods, and that fish larvae may often be found to be malnourished, the assumption is made here that "total larval fish" is an index of the status of the next higher trophic level above macrozooplankton. Since the abundance of total fish larvae has been measured over time (figure 19), we can now test two more hypotheses.

Of these two, perhaps the most interesting is the null hypothesis: H_0: "Fish larvae variations in abundance over time are not related to macrozooplankton variations over time in the California Current System." Here we are asking whether both fish and their larvae are food-limited . . . and whether variations in the amount of food available to adults affect the rate of production and/or survivorship of larvae and juveniles. We may test this by asking if temporal variations in larval fish abundance are correlated at any time lag with macrozooplankton over the period 1950 to 1970, when sampling was frequent and before the warming trend to be described. The time lagging is important here because, if larval fish abundance declines occur well after zooplankton, it may mean that poor nutrition of adults in the preceding months has affected their fecundity. If, on the other hand, larval declines are virtually synchronous with zooplankton declines, it is likely that the availability of nauplii is important. Note that this latter result does not really distinguish between an instantaneous response of the adult fish to poor nutrition, and food limitation of fish larvae. If the correlation tends to be negative, then perhaps competition or predation are responsible.

Since nonseasonal, total larval fish variations throughout all four sectors of the California Current System are intercorrelated at low frequencies, we can space-average

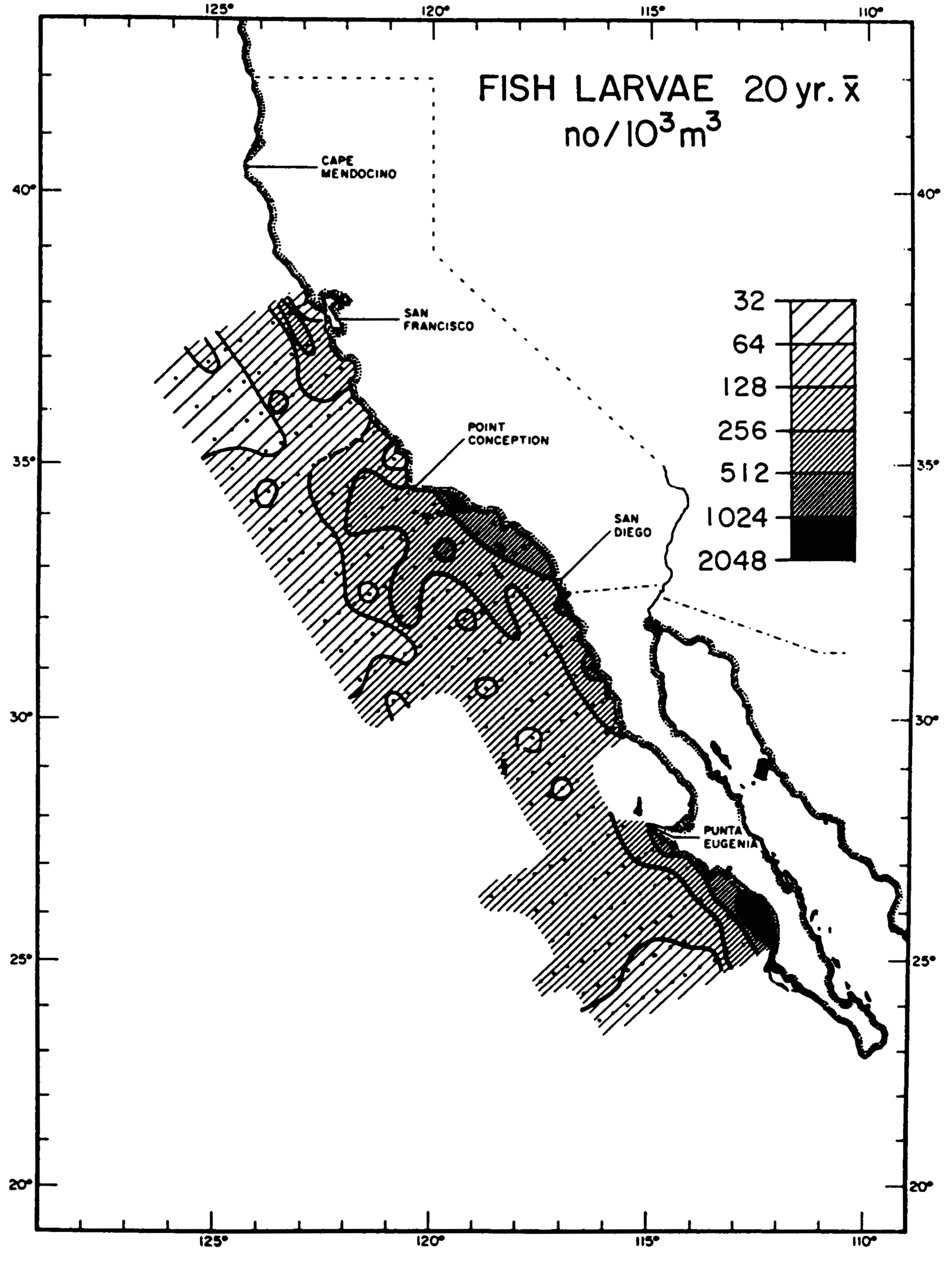

Figure 19. The spatial distribution of estimated number of larval fish of all species averaged per station 1950–70.

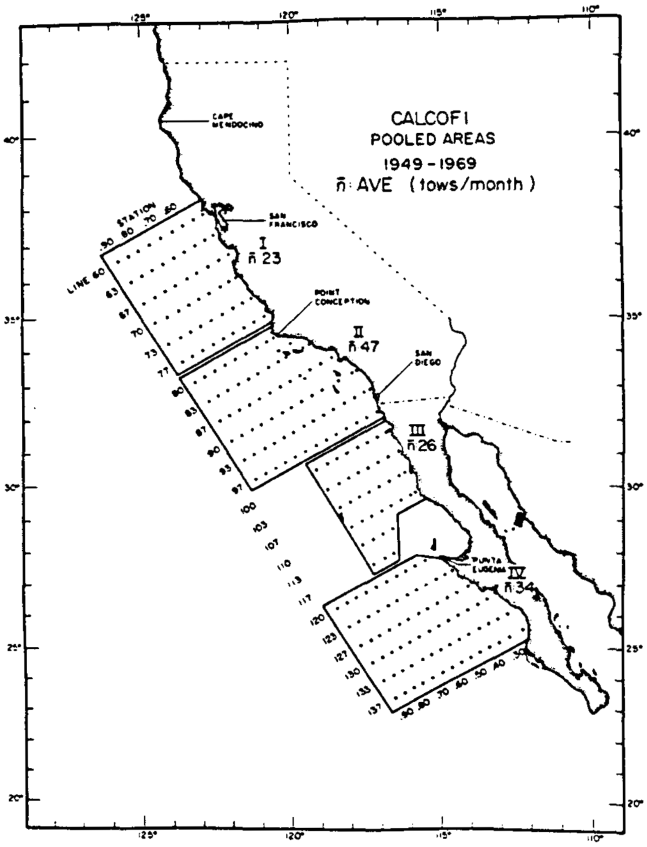

Figure 20. The stations used in the time-series analysis in figures 21, 23, 24, 25. The breaks between areas are not entirely arbitrary but are based on biogeographic and hydrographic patterns (after Bernal and McGowan 1981).

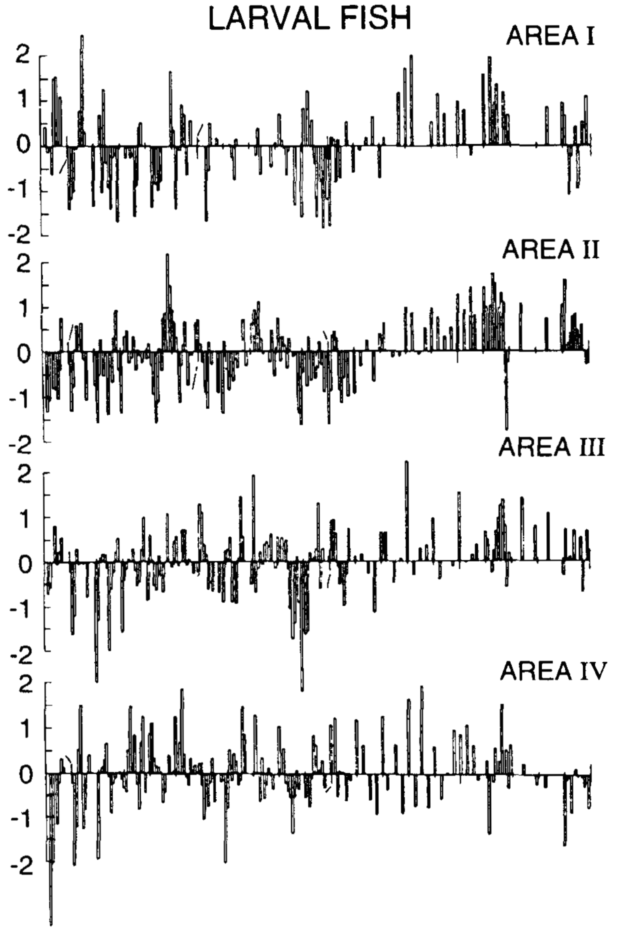

Figure 21. Time series of nonseasonal, $\log_e$-transformed, larval fish data abundance for each of the four areas. Seasonal cycles have been removed, and the time series for each area has been normalized to have a standard deviation of one. *Tic marks* are centered on January of each year.

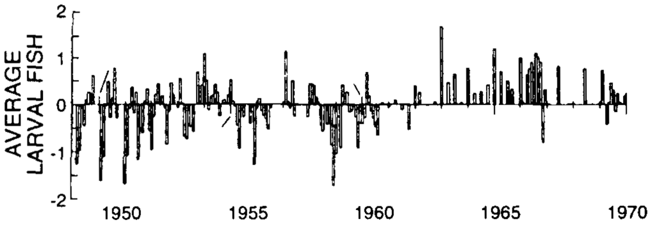

Figure 22. Time series of nonseasonal, transformed, larval fish as in figure 21, but with all four areas averaged.

the estimates throughout the entire system (figures 20–22 and table 1). Although fish and zooplankton abundance both exhibit energetic interannual variability (figure 23), there is little consistent relation between the two time series. This observation is illustrated by time-lagged correlations of the two data sets (figure 24). The maximum correlation between fish and zooplankton occurs when zooplankton leads fish by 4 to 5 months in all sectors but IV. These correlations are small (about 0.3 to 0.4) but are statistically significant even when the statistical significance is adjusted to account for the effective degrees of freedom using the method described by Chelton (1983). Autocorrelations of fish and zooplankton show very different decorrelation time scales (figure 25). That is, fish have a much shorter "memory" of past states than do zooplankton. Although the cross-correlations are weak and the autocorrelations are very different, we have been unable to formally disprove the null hypothesis of no relation between larval fish abundance and that of zooplankton. Further, it appears that the correlation does lag in the direction to be expected if poor nutrition of adult fish has affected their fecundity. But a visual examination of the overall, smoothed fish-zooplankton data shows just how weak this relationship is (figure 26).

Since zooplankton is well correlated, in general, with temperature, salinity, and transport, it seems unlikely that fish will be also, since they are poorly correlated with zooplankton. But we may ask if they are somehow influenced by some more general climate indicator. We may now propose the null hypothesis: H_0: "There is no difference between the time series larval fish and the time series longshore winds." Longshore wind anom-

TABLE 1

A. Cross-correlations of the Nonseasonal, $\log_e$-Transformed Time Series of Larval Fish Abundance in Areas I–IV (see figure 20)[a]

	Area I	Area II	Area III	Area IV
Area I		0.46 (0.25)	0.31 (0.27)	0.10 (0.30)
Area II	0.69 (0.63)		0.50 (0.27)	0.24 (0.26)
Area III	0.41 (0.47)	0.74 (0.40)		0.44 (0.25)
Area IV	−0.20 (0.73)	0.29 (0.50)	0.51 (0.21)	

B. Cross-correlations between the Nonseasonal, $\log_e$-Transformed Zooplankton Biomass Data in Areas I–IV[a]

	Area I	Area II	Area III	Area IV
Area I		0.57 (0.43)	0.42 (0.43)	0.19 (0.41)
Area II	0.75 (0.54)		0.74 (0.31)	0.31 (0.36)
Area III	0.69 (0.47)	0.91 (0.25)		0.55 (0.40)
Area IV	−0.23 (0.57)	0.49 (0.47)	0.71 (0.50)	

C. Correlations between the Large, Spatial-Scale Average, Nonseasonal $\log_e$-Transformed Larval Fish Time Series with Those of Each of the Four Areas

	Unfiltered[b]	Interannual[b]
Area I	0.71 (0.27)	0.72 (0.54)
Area II	0.77 (0.23)	0.93 (0.35)
Area III	0.80 (0.28)	0.87 (0.36)
Area IV	0.65 (0.23)	0.43 (0.29)

D. Correlations between the Large, Spatial-Scale Average, Nonseasonal $\log_e$-Transformed Zooplankton Biomass Time Series with Those of Each of the Four Areas

	Unfiltered[b]	Interannual[b]
Area I	0.75 (0.45)	0.72 (0.46)
Area II	0.85 (0.31)	0.90 (0.36)
Area III	0.88 (0.27)	0.98 (0.35)
Area IV	0.68 (0.44)	0.75 (0.51)

[a] Values above the diagonal are for the unfiltered data; those below are correlations of data filtered with a low-pass double 13-month running mean to emphasize the interannual signal. Parentheses show values required for 95% significance levels with the method described by Chelton (1983).
[b] Values in parentheses are 95% significance levels.

alies are used here because they form the basis for the coastal upwelling model. The reasoning behind this test is that there is a general consensus that coastal upwelling brings nutrients to the euphotic zone, thus stimulating new production and enhancing production in the entire food web. If this mechanism is important, larval fish survival should benefit from upwelling events. On the other hand, Lasker (1975) has proposed that windiness and upwelling may disturb and disperse the layers of food that some larval fish depend on, in which case their survivorship should be reduced. In the first case larval fish abundance should, at some time lag, be positively correlated with longshore winds. In the second case they should, at some time lag, be negatively correlated. Figure 27 shows the time-lagged correlations between local longshore wind and fish larvae. The two are uncorrelated, and both of the hypotheses are there-

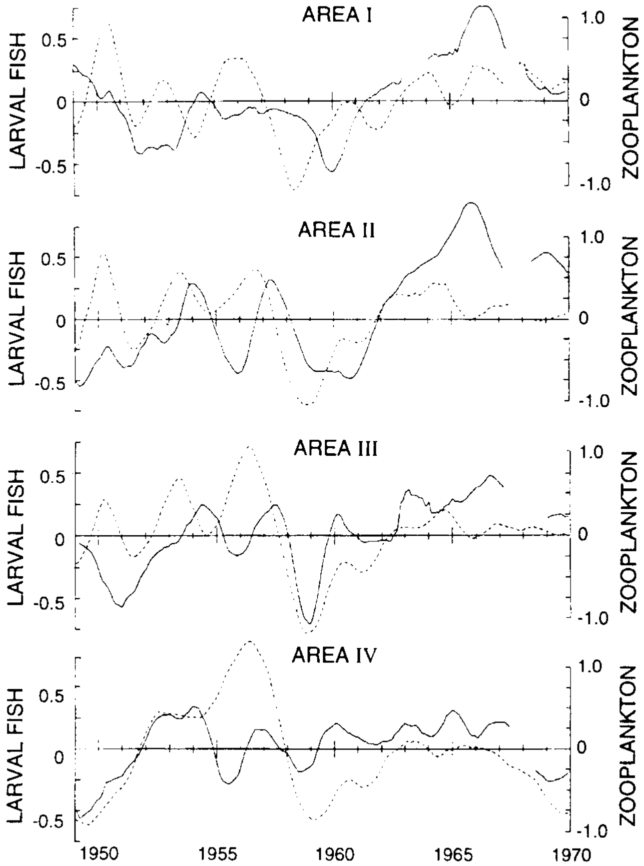

Figure 23. Low-passed filtered, time series of nonseasonal, $\log_e$-transformed larval fish (*solid line*) and zooplankton (*dashed line*) for each of the four areas. The raw, nonseasonal, time series were filtered with a double 13-month, objective, running mean, which effectively extracts the interannual variability.

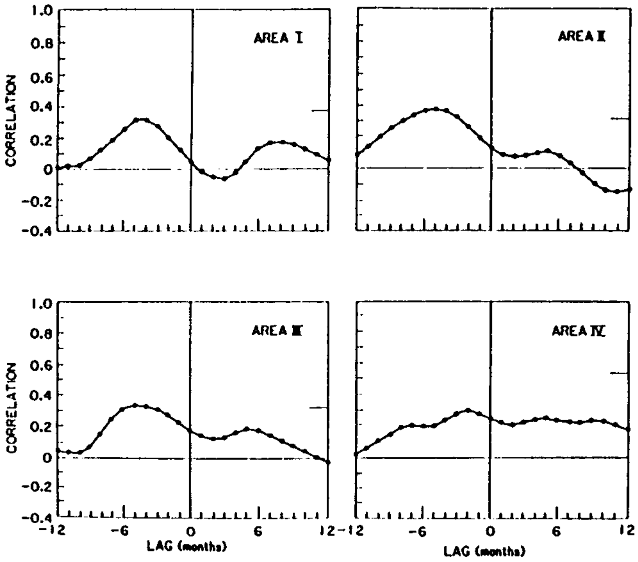

Figure 24. Time-lagged cross correlations between nonseasonal $\log_e$-transformed larval fish at time *t*, and nonseasonal $\log_e$-transformed zooplankton at time (*t* + lag). Negative lags indicate zooplankton leads larval fish. *Tic marks* on right axis represent 95% significance levels.

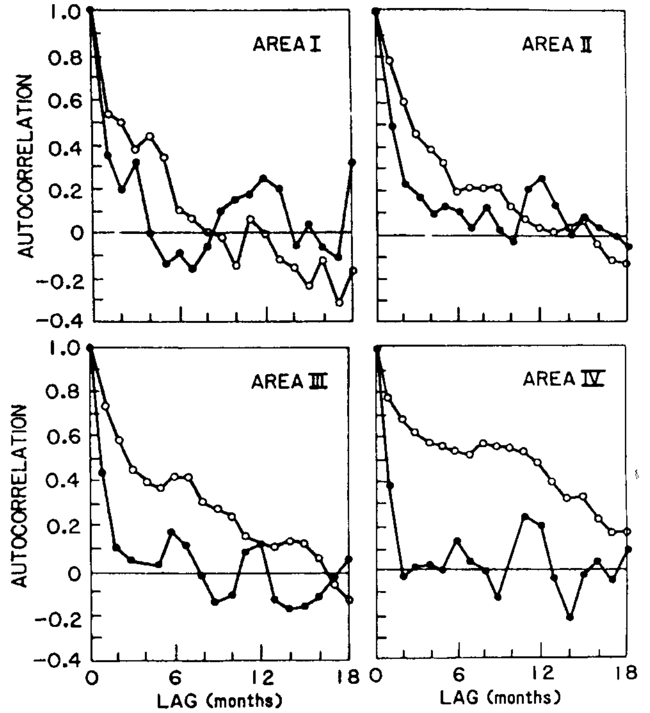

Figure 25. Time-lagged autocorrelations of nonseasonal, $\log_e$-transformed, larval fish (*solid circles*) and nonseasonal, $\log_e$-transformed, zooplankton (*open circles*) data. The secondary peak by fish at 12 months indicates strongly seasonal abundance anomalies.

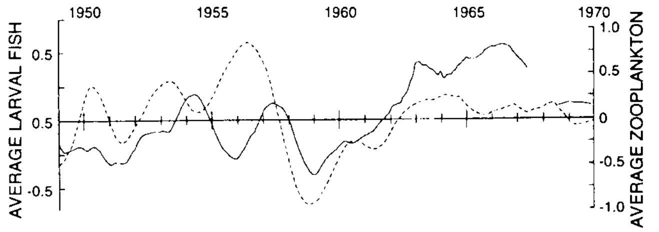

Figure 26. Low-passed filtered time series of nonseasonal $\log_e$-transformed larval fish numbers (*solid line*) and zooplankton displacement volume (*dashed line*) averaged over the four areas shown in figure 20. The nonseasonal time series were filtered with a double, objective running mean. The 1958–59 El Niño effects can be seen clearly. The decline of larval fish abundance tended to lag the decline of zooplankton.

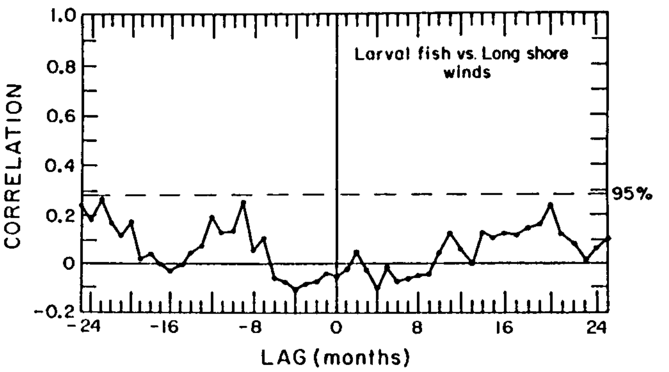

Figure 27. Time-lagged cross-correlation of mean larval fish abundance and longshore winds in Area II, 1950–69. Negative values indicate that winds lag fish. The upper 95% confidence limits are shown.

fore disproved. We thus conclude that the variations in the abundance of zooplankton do not strongly affect adult fish population fecundity or larval mortality. Nor does coastal upwelling affect larval fish survivorship in any simple manner.

The most abundant larvae in the CalCOFI samples are those of the harvested species. Harvesting of adults is an unusual intervention in the normal life histories of pelagic fish, where most natural population regulation seems to come from mortality of larvae. Intensive predation of adults (harvesting) at this point in the life history may so alter normal population dynamics that food limitation or climate-driven perturbations are simply not unambiguously resolvable in a time-series test unless they are large signals. But two further tests of hypotheses are suggested: do the larvae of nonharvested fish respond to plankton changes or weather? A third and unlikely possibility is that larval fish abundance shifts are normally uncoupled from adult population variability.

Interdecadal Patterns

It has become clear that large, spatial-scale environmental changes occur on an interannual (year-to-year) basis and that these variations are often larger than seasonal, monthly, or weekly changes. We are now learning that longer-period variations are also important—the interdecadal. Of course, paleontologists have long known that the thousand- or ten-thousand-year periods or Pleistocene epochs are important ecological and evolutionary milestones. But paleontologists cannot usually resolve any marine fossil frequency of change of much less than a thousand years except in the special circumstances of varved cores. The interdecadal-to-century frequencies of climate change are important in that the magnitudes can be large and there are demonstrable consequences to many environmental variables (Ebbesmeyer et al. 1991).

The 45-year data set of CalCOFI's physical-biological program can, however, be used to investigate interdecadal variability. Roemmich (1992) has shown that over the 42-year period 1950–91 temperature increased by 0.8°C in the upper 100 m of the California Current. An increase is clearly detectable even to depths of 300 m. Concurrently, steric sea level rose by 0.9 ±0.2 mm per year. The fact that the entire upper layer has warmed is of particular significance to marine life, for here is where all the primary productivity takes place and where the greatest fraction of the biomass resides. Roemmich compared the period 1950–56 to the period 1985–91 for changes in steric height. The onshore-offshore steric heights were spatially uniform between the two time periods, but differed systematically from one another by about 3 cm. This spatial uniformity indicates that the

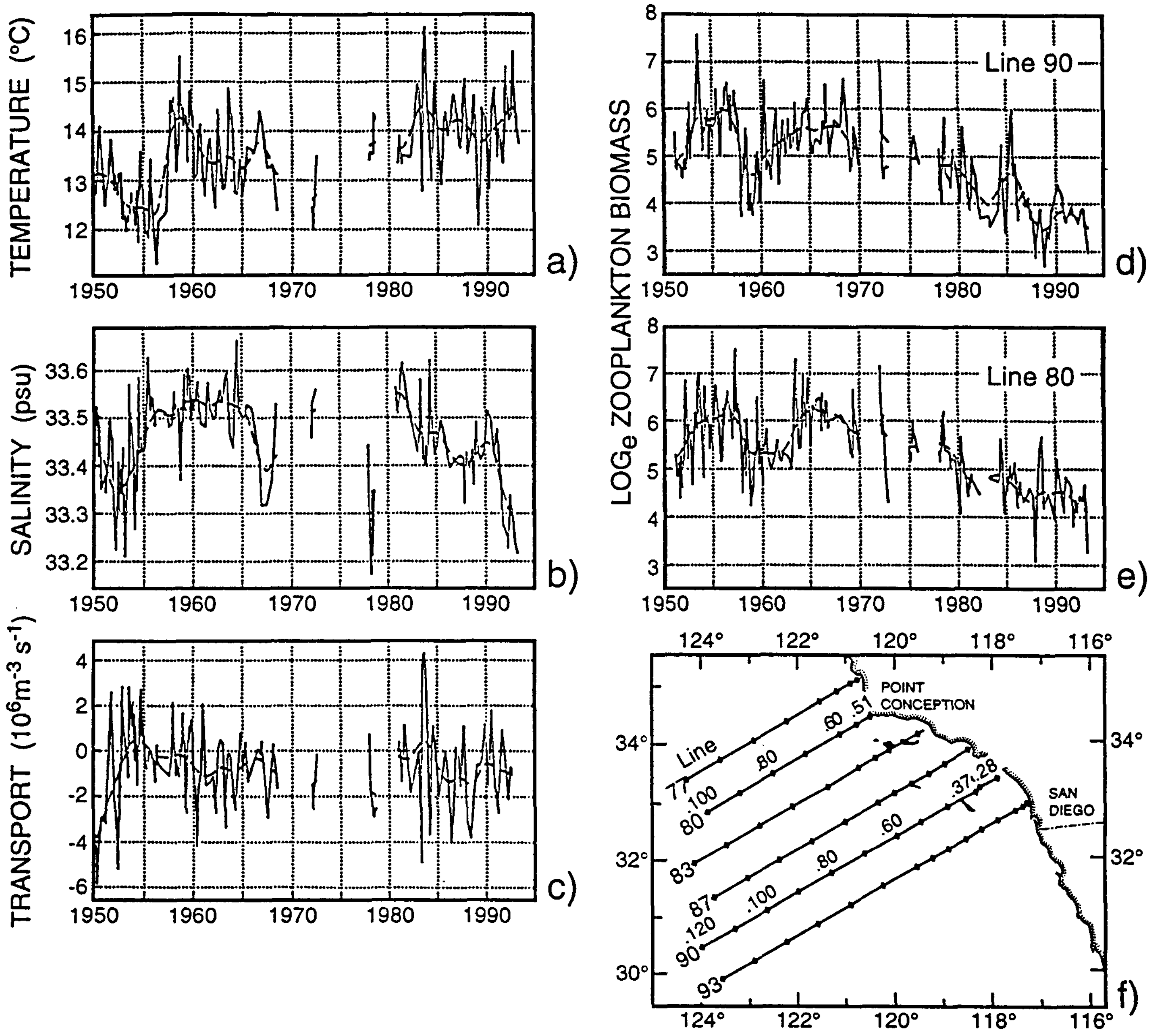

Figure 28. *Left*, Time series of the upper 100 m (*a*) temperature, (*b*) salinity, and (*c*) transport from the north. *Right*, time series of log$_e$-transformed zooplankton volume per 1,000 m^3 of water filtered by the net on CalCOFI line 90 (*d*) and line 80 (*e*). (After Roemmich and McGowan 1995).

large-scale warming and sea-level rise were not accompanied by significant changes in the strength of the surface geostrophic circulation.

Nearshore, daily surface temperature records from Scripps Pier have been taken since 1916. These show a similar warming trend between 1950 and 1991 (Roemmich 1992), but there was no significant trend between 1916 and 1950. The decade of the 1980s was the warmest on record.

Roemmich and McGowan (1995) have reported that the warming of the California Current did affect the plankton populations (and no doubt others) of the upper 200 m. Since 1951, the biomass of macrozooplankton in southern California waters has decreased by over 70% during the same period that the surface layer warmed (figure 28). The temperature difference across the thermocline increased, and this increased stratification resulted in less lifting of the thermocline by wind-driven upwelling. A shallower source of upwelled waters would provide fewer inorganic nutrients for new production and hence support a smaller zooplankton population.

Because of the high energetic interannual variability, it is uncertain whether the zooplankton decline occurred gradually over the entire time series or more rapidly since the 1970s. At both the northern (line 80) and southern (line 90) zones, the onshore-offshore plankton gradients

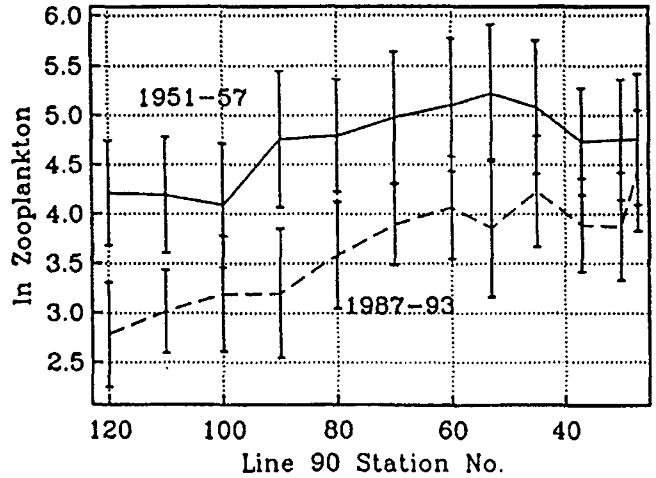

Figure 29. Temporal average and standard deviation (*vertical bars*) of $\log_e$-transformed zooplankton volumes for all cruises in 1951–57 and 1987–93 along line 90. Stations are numbered from nearshore (40) to offshore (120) (from Roemmich and McGowan 1995).

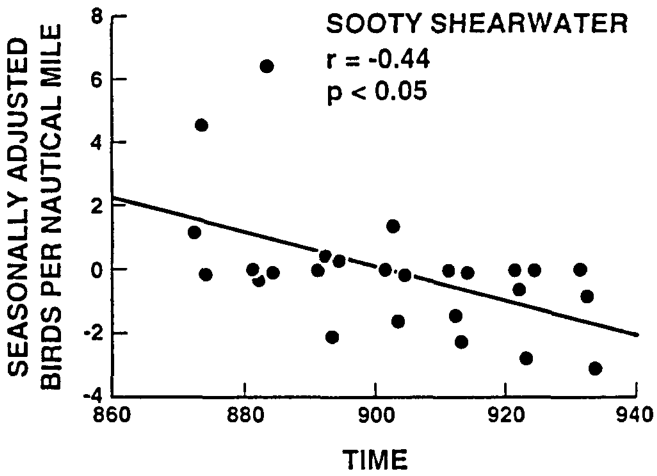

Figure 30. The seasonally adjusted counts of sooty shearwater abundance per cruise from 1987 to 1993. Counts were made during all daylight hours while the ships were underway. Each cruise lasted about two weeks; cruises were made approximately quarterly (from Veit et al., in press).

were approximately constant (figure 2a), as was the north-south gradient (figure 29; Roemmich and McGowan 1995). Geostrophic velocity at line 90 showed an increase in the wind-driven recirculation—greater northward flow nearshore and greater southward flow offshore—but no change in net transport. Bakun (1990), analyzing a combination of directly estimated winds and onshore-offshore barometric pressure differences, concluded that coastal winds off California favorable to upwelling increased substantially from 1946 to 1988. Although his reported increase in alongshore wind is consistent with the increase in recirculation noted above, his predicted consequences—SST cooling and increased production—are the opposite of the observed increased temperature and decreased zooplankton biomass.

The observed rate of decrease in zooplankton biomass is more than $5 \times 10^{-10}\ s^{-1}$ over 43 years. On long time scales, biomass is controlled by the net effect of decreases due to excess mortality over births versus increases through advection from the north. But advective input by currents is estimated to be $\sim 5 \times 10^{-8}\ s^{-1}$ (Roemmich and McGowan 1995), far larger than the observed trend. Thus the long-term trend is a small residual of much larger terms. It cannot be isolated by studies of advection or by process-oriented studies of reproductive rates or mortality. Nevertheless, it is a dramatically large signal when accumulated over 43 years.

These observed trends in the California Current may be related to basin-scale changes in wind forcing. A strengthening of North Pacific winter atmospheric circulation began in the late 1970s (Trenberth 1990; Graham 1994), near the time when the temperature increase and zooplankton decline began to be clearly seen. A number of other effects have been observed in relation to this basin-scale climate shift (Venrick et al. 1987; Miller et al. 1994).

In addition to the plankton decline, there has been a 90% decline in an apex marine predator—the sooty shearwater (*Puffinus griseus*), once the most abundant pelagic seabird in the California Current. Other seabirds have declined as well (figure 30; Veit, Pyle, and McGowan, in press), although not so dramatically (Veit et al., in press).

CONCLUSIONS

Determining the ecological consequences of climate change, whether it is natural or anthropogenic, is one of the most serious problems facing oceanographers today. At the heart of this problem is our limited ability to quantitatively define the word *change*. Because of the paucity of long time series of ecosystem variables, what does this word mean in terms of ecosystem structure and function?

Two Approaches

The departure from some expectation or norm, its sign, amplitude, spatial extent, and temporal persistence are surely essential aspects of the concept of change. A common practice of studying change is to extrapolate from relatively short-term, local, "process-oriented" studies with the expressed goal of providing values for "fluxes" of energy or materials between aggregated categories (sometimes called functional groups) of community ecosystems. These fluxes are assembled in the familiar ecosystem box model. Such inductive models have been used for many years in marine ecology but have not proven useful for understanding variability in system structure and function. In particular, they have provided little insight into the effects of climatic perturbations on system behavior or on the state of its populations. Pelagic community-ecosystem structure is complex, enigmatic, and vacillatory. There are many unknowns, and it has been necessary, therefore, to include untested and often untestable assumptions in such models. But such process-oriented, model-driven research has given us some valuable information. These studies have shown that most, if not all, of the rates of interaction between structural entities are nonlinear and density dependent. The studies have also provided many engaging details about the maze of intermediary mechanics in community function.

It is clear that time series, if they are long enough, can define the word *change*, its sign, amplitude, and persistence. They can also determine the spatial dimensions of change if the correlation length scales are adequately sampled. Anomalies from the baseline seasonal cycle can be calculated and compared with climatic signals by means of the classical methods of null hypothesis testing. However, correlations between climatic anomalies and biological anomalies cannot provide information on the innumerable intermediary mechanisms that link community response to climate change. Although time series, of themselves, do not provide predictive capability, they do offer a wealth of information for testing and validation of ecosystem models. Unless the models can reproduce the observed time series, they cannot be used for predictive purposes.

The California Current Example

The CalCOFI time series has been used to construct long time series over a large portion of the California Current. In spite of highly variable and patchy data, these maps show persistent onshore, offshore gradients and north-south gradients of virtually all physical, chemical, and biological properties. Subarctic and Transition Zone species intrude from the north, along with cool, low-salinity waters. Warm-water cosmopolites come in from the west with warm, high-salinity Central Gyre waters. Equatorial species intrude from the south. These species are mixed together in the central sector of the California Current. It is here that plankton species diversity is the highest of any sector of this current. It seems reasonable to infer that the spatial maximum in diversity is due to simple physical mixing rather than to ecological processes such as resource allocation or disturbance.

The 45-year monitoring study has also allowed time-series and spectral analyses, even though gaps exist in the data. All ecosystem variables show large, nonseasonal, low-frequency variations. Macrozooplankton biomass changes are clearly correlated with interannual, climate-driven changes in mass transport of water from the north. Larval fish are also highly variable in time, but these variations are seldom clearly related to changes in zooplankton (the diet of the adult fish) and, in our data, never to anomalies in longshore winds, the basis of coastal upwelling indices.

Zooplankton also responded to another lower frequency of climate change, the interdecadal. This is manifested as a long-term warming of the entire upper 300 m water column and a coincident decline in zooplankton production. The very large decline in zooplankton (over 70%) with such a "small" temperature signal (~0.8°C) indicates that the organisms were not responding directly to temperature with, say, a change in their thermally regulated metabolism, but rather that the warming is a surrogate index for some greater environmental change. A candidate mechanism is an increase in water column stratification due to the warming (Roemmich and McGowan 1995). This would lead to a decrease in vertical eddy diffusivity, mixing, and upwelling and therefore a lesser input of inorganic nutrients from the deep water. The overall effect would be less primary and secondary productivity, consistent with the observations.

There are several steps in this proposed mechanism as yet to be verified by analyses of the existing observations. But if it is substantially correct, it differs greatly from the mechanism proposed for interannual changes. This mechanism had to do with horizontal advective input to the system proposed for interannual changes (Bernal and McGowan 1981; Chelton et al. 1982). The interdecadal trend in upper-layer temperature may be related to basin-scale wind forcing. A strengthening of the North Pacific winter atmospheric circulation began in the late 1970s (Graham 1994), near the time when the CalCOFI trends began to be clearly seen (figure 28). A number of other effects have been observed in relation to this basin-scale change (Venrick et al. 1987). If the interdecadal decline in zooplankton is part of a natural climatic cycle that reverses itself in coming years, then the impact will be similarly transient. But if the decline is anthropogenic or a natural trend of longer duration, then the magnitude of the decline is a cause for concern (Roemmich and McGowan 1995). For example, if large-amplitude physical perturbations work the way we suggest and if fish populations generally become food limited during such periods, then we may anticipate large-scale declines in the populations that eat macrozooplankton or whose larvae depend upon their larvae.

Thus there are different forcings, amplitudes, and consequences depending on time scales (daily, weekly, monthly, seasonal, interannual, and interdecadal). This demonstrates the dangers of induction. Climate studies dominated by short-term, process-oriented work cannot simply be extrapolated to interannual or decadal time scales where the balance of terms is different from monthly or seasonal balances.

The continuous plankton recorder studies in the North Atlantic (CPR Survey Team 1992), other studies in this volume, and the CalCOFI time series have all shown that the most energetic biotic changes in space and time are of low frequency; that is, the frequency spectra of biological variables are dominated by low-frequency variability. These low-frequency variations in macrozooplankton are all closely associated with large-scale climatic trends in both the Pacific and Atlantic.

If large changes in biomass over time and over large areas are considered to be important ecological and evolutionary events, then the spectra dominated by low-frequency variability have great underlying meaning; there must also be structural and functional changes occurring, and they cannot be understood or predicted by short-term, process-oriented studies. If the consequences of climate and climatic change are of interest, then biotic measurements must be maintained over periods of many decades in order to detect, let alone understand, these consequences.

All of this argues for a new outlook to guide research on marine communities and populations. Apparently little can be inferred about kinematics and dynamics on scales much larger than the scales of measurement. This may be because density-independent forces extrinsic to the internal workings of communities are very important and yet essentially unpredictable from a knowledge of internal dynamics. Further, short-term perturbations such as weather often do not have large or lasting effects on ecosystems. The concepts of stability and resilience are based on this fact.

Since there is legitimate concern that large climate changes are possible in the near future, the time is now to direct more of our effort to defining, detecting, and understanding "change."

Many ecologists are not yet accustomed to thinking about larger scales or doing large-scale research. So the new challenge will require a different outlook and some new approaches. One such approach is to use time series to test some hoary old hypotheses such as zooplankton vs. upwelling index, larval fish vs. zooplankton, or larval fish vs. longshore winds.

It is very clear that there are large interannual changes in total larval fish abundance. This is a fact of considerable interest, for it appears that the entire complex of species is responding over a large area to some forcing other than seasonal. While microscale, fine-scale, or mesoscale studies can suggest some plausible scenarios for these large changes (see Mullin 1993 for a review) the number of potentially testable and falsifiable hypotheses derived from these works, relevant to the climate scale, is small, and the actual number of formal tests of hypotheses is practically nonexistent. Species populations exist on very large spatial scales, and their largest and therefore most energetic variations seem to be interannual or interdecadal. There is no evidence to support the notion that the results of micro- to mesoscale studies can be extrapolated upward and outward to the climate change scale. Time-series measurements can be made on the appropriate scales. They do, however, take time.

Some of the pragmatic details of this new research canon are not well formulated, and we are ill prepared to design a large-scale, long-term monitoring system, since most of our thinking and effort has been dominated by reductionism. But perceiving the problem of scale is necessarily the first step in formulating a new kind of marine ecology.

ACKNOWLEDGMENTS

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RECENT ADVANCES IN CALIFORNIA CURRENT MODELING: DECADAL AND INTERANNUAL THERMOCLINE VARIATIONS

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ABSTRACT

Some recent advances in large-scale modeling of the California Current and its interaction with basin-scale circulation and forcing are summarized. The discussion concentrates on a decadal-scale change and interannual-scale variations identified in the thermocline off the California Coast. The western-intensified decadal-scale change is part of a basinwide change in the North Pacific thermocline from the early 1970s to the early 1980s, which has been observed and modeled. The decadal change is driven by a basin-scale change in wind stress curl (Ekman pumping) and is associated with a deepening of the thermocline off California but no significant change in the strength of the California Current. Interannual variations of the thermocline off the California Coast, which tend to be associated with ENSO, have also been observed and modeled. High-resolution models often exhibit a coastal-trapped Kelvin-like wave arriving from the equatorial zone, but even a coarse-resolution model can capture aspects of the midlatitude wind-forced thermocline signals that propagate westward on ENSO time scales.

INTRODUCTION

Models of the California Current System (CCS) have been in development as long as numerical simulation has been a part of oceanography. Many fundamental issues have been central to the various strategies for formulating models. Among these issues are: why there is an eastern boundary current in the first place (e.g., Philander and Yoon 1982; McCreary et al. 1992); what controls interannual variations of the current (e.g., Pares-Sierra and O'Brien 1989); why such a strong eddy field exists in a relatively weak mean current (e.g., Batteen et al. 1989; Auad et al. 1991; Hurlburt et al. 1992); whether the eddy field can be numerically forecast (e.g., Robinson et al. 1984; Rienecker et al. 1987); what controls the occurrence of cold filaments (e.g., Haidvogel et al. 1991; Allen et al. 1991); and how cold filaments influence biological productivity (e.g., Moisan and Hofmann 1996a, b; Moisan et al., in press).

I can address here only a small subset of the interesting issues and important advances that have occurred in modeling the CCS. Specifically, I discuss in the next two sections a decadal-scale change in the thermocline off the California coast, which has been recently modeled in a coarse-resolution model, and the physics that control observed and modeled interannual variations in the CCS thermocline and velocity field. I concentrate on model results that may be directly compared with observations for validation.

A DECADAL-SCALE CHANGE IN THE NORTH PACIFIC THERMOCLINE

Decadal-scale changes have been observed in numerous physical, chemical, and biological variables in the North Pacific (e.g., Douglas et al. 1982; Ebbesmeyer et al. 1991; Roemmich and McGowan 1995). One especially interesting change occurred in the mid-1970s (e.g., Trenberth 1990; Graham 1994; Trenberth and Hurrell 1994) for which, in previous work (Miller et al. 1994a, b), we have attempted to explain the oceanic physics involved in switching the ocean from a warm central (cool eastern) North Pacific state to an oppositely signed regime after the winter of 1976–77.

A recent observational and modeling study identified a basin-scale change in the oceanic thermocline in the North Pacific.[1] A data set of upper-ocean (to 400-m depth) XBT observations from the period 1970–88 (for details, see White 1995) was compared with the response of an ocean general-circulation model forced by observed fluxes and winds over the same period. The model is a primitive equation formulation constructed with eight isopycnic layers (of variable temperature, salinity, and thickness), which are fully coupled to a bulk surface mixed-layer model. The run is forced by observed monthly mean anomalies of wind stress, heat flux, and turbulent kinetic energy input to the mixed layer. Although the resolution is rather coarse—nominally four degrees but with enhanced resolution near the equator and boundaries (figure 1)—the results are unique in that we are unaware of any other North Pacific Ocean simulation which is forced over such a long period (1970–88) with both wind-stress and surface-flux forcing.

The dominant signal common to both model and observation has decadal scale and is illustrated in figure 2, which shows differences in the upper-ocean tempera-

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[1] Miller, A. J., D. R. Cayan, and W. B. White. A decadal change in the North Pacific thermocline and gyre-scale circulation. MS submitted to J. Clim.

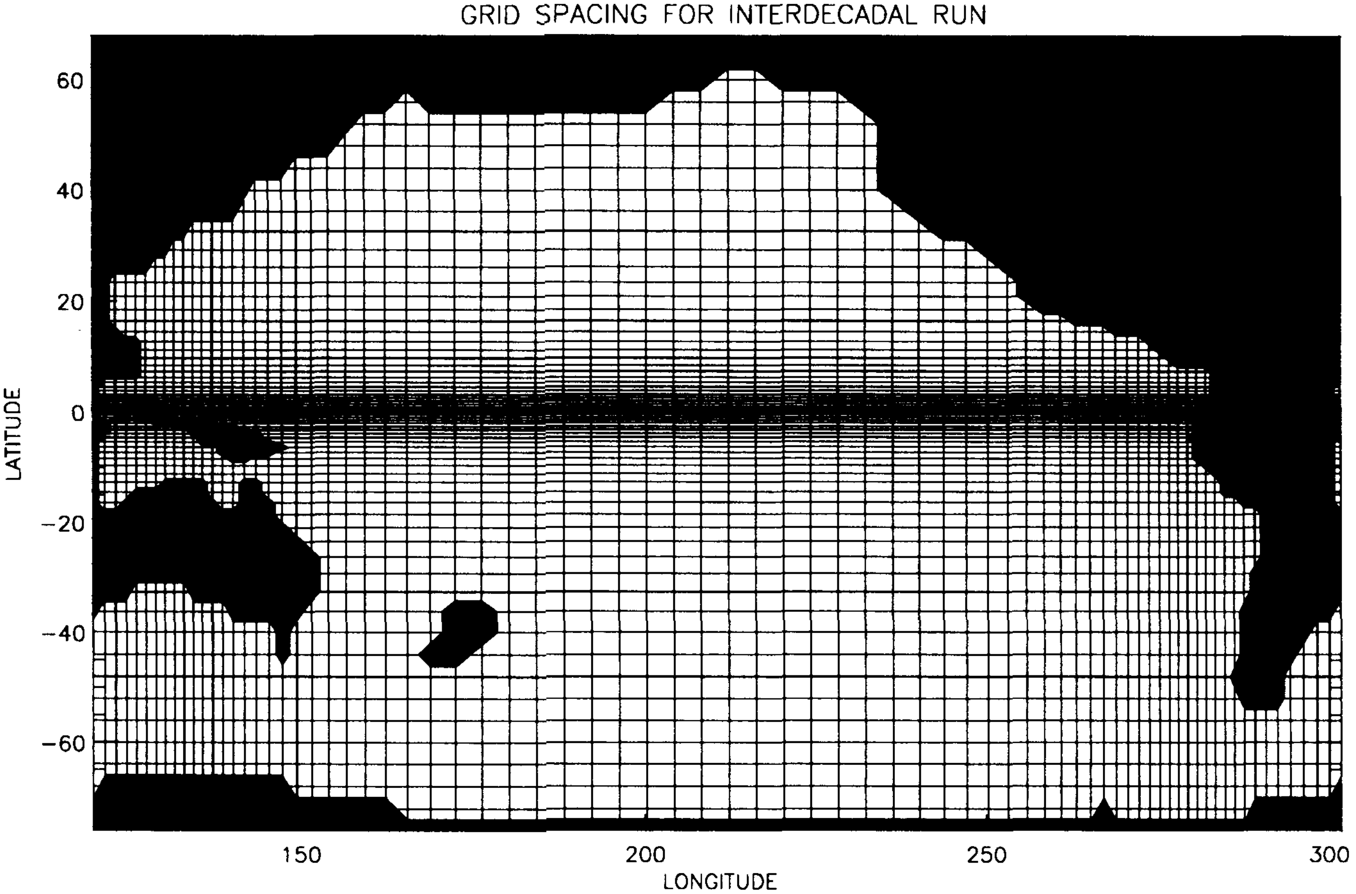

Figure 1. Geometry and grid of the isopycnic coordinate model developed by Oberhuber (1993) and applied by Miller et al. (1994a, b; MSS; see footnotes 1 and 5) for interannual through interdecadal studies of the Pacific Ocean, as discussed in the text.

ture field of the North Pacific from the early 1970s to the early 1980s. In the surface mixed layer, one sees the well-known structure of cooling in the central Pacific and warming of the eastern Pacific. This structure is commensurate with the large-scale structure of the atmospheric variables (heat fluxes and wind stresses) which drive the variability (Cayan 1992; Miller et al. 1994a, b). The time series of sea-surface temperature (SST) variability in a region off western North America (130°W–coast, 24°N–44°N) reveals a good correspondence between model and observations and also the steplike character of the SST change during the winter of 1976–77 (figure 2). Miller et al. (1994a, b) showed that heat fluxes and horizontal advection both contributed to the shift in SST which occurred off western North America during the 1976–77 winter, and that surface heat fluxes were the primary maintenance mechanism for preserving the regimes there before and after the shift.

Looking beneath the mixed layer at 200 m and 400 m (figure 2), where little or no direct contact with the atmosphere occurs, one sees a progression into regions where ocean dynamics are expected to dominate the response. Indeed, the thermal structures at 400 m bear a western-intensified structure reminiscent of gyre-scale circulation theory. Because the mean thermocline is shallower off the coast of California than it is in the middle of the Pacific, I plot temperature anomalies at 120 m (figure 2, bottom) to show that the thermocline deepened from the early 1970s to the early 1980s at the same time that it was raised (cooler 400-m temperature) in the northwestern Pacific. The time series of 120-m temperature variations also shows that the model captures both the deepening of the thermocline as well as interannual variations (to be discussed in the next section). Both data and the model reveal that a more gradual change in temperature occurs at depth (cf. Deser et al. 1996) in comparison to the steplike change in the surface layer.

Difference maps like figure 2 are useful for understanding gross features of the response, but they fail to give a clear picture of the coherency of variations over large spatial and long temporal scales. Empirical orthogonal function (EOF) analysis is useful for just such a purpose. In order to better isolate stationary features from

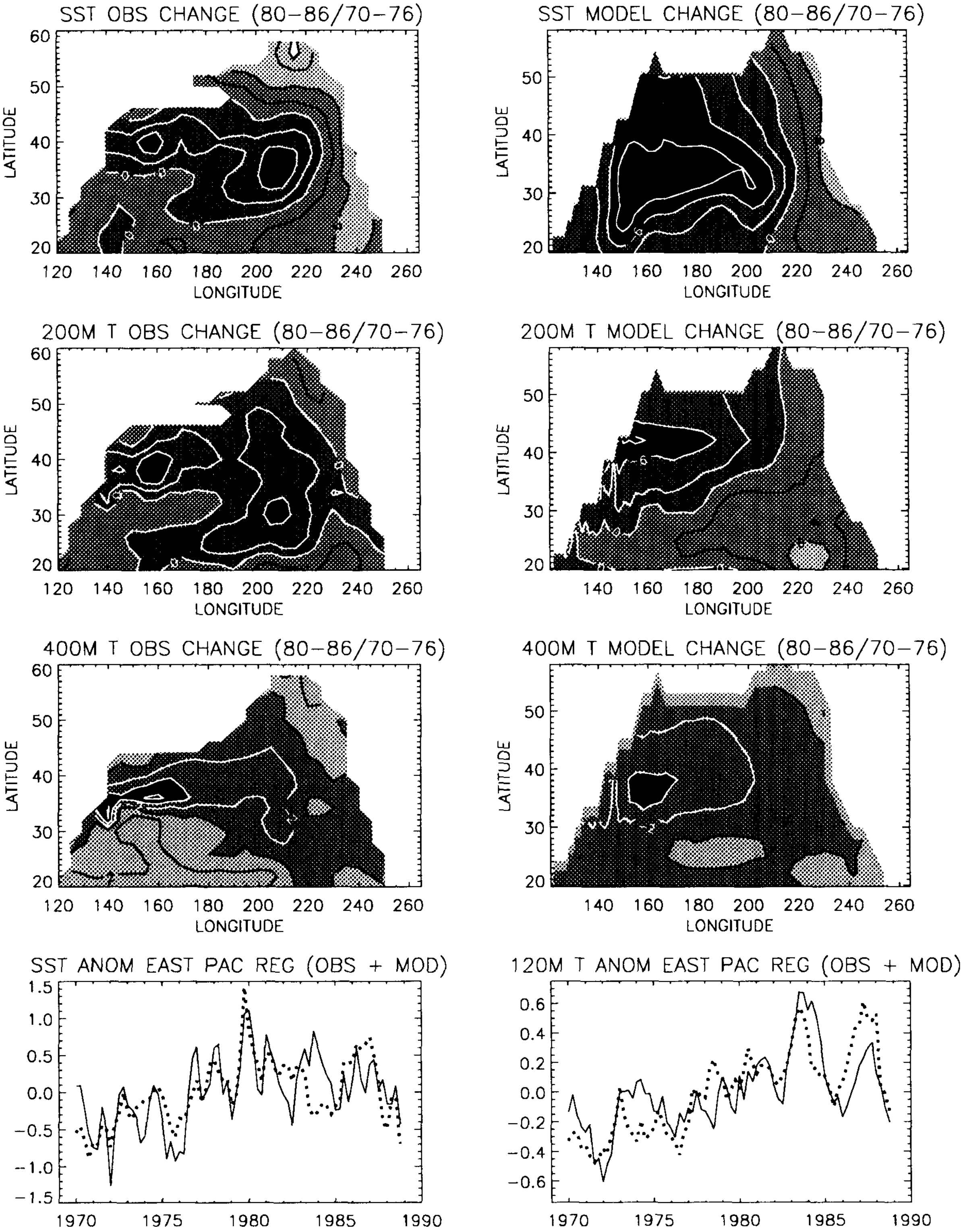

Figure 2. Difference maps of the 7-year periods 1980–86 relative to 1970–76 for (*top*) sea-surface, (*middle*) 200-m, and (*lower*) 400-m temperature for (*left*) observations and (*right*) model. For SST and 200-m temperature, contour intervals are 0.3°C (zero and negative contours white); for 400-m temperature, contour intervals are 0.2°C (zero and positive contours black), with darker shading negative and lighter shading positive. Time series (*bottom*) of observed (*solid line*) and modeled (*dotted line*) temperature at surface (*left*) and 120 m (*right*), averaged over the eastern Pacific region 130°W–coast, 24°N–44°N.

propagating ones, Miller et al.[2] used extended EOF (EEOF) analysis of observed 400-m temperature, model 400-m temperature, model 400-m velocity, and wind stress curl forcing to isolate the decadal-scale signal. Only the region of the North Pacific east of 155°E and north of 20°N was considered in order to avoid including the poorly resolved (in both the model and XBT data set) Kuroshio region and the ENSO-dominated low latitudes.

Figure 3 shows a synopsis of the EEOF view of the basin-scale decadal temperature change in observations and in the model.[3] Since this mode is nearly stationary, we plotted the average of the 13 lags together rather than showing the lags for individual phases. The top two maps show the first combined EEOF of observations and model 400-m temperature, with the time series (scaled amplitude) shown as the thin line in the bottom plot. (The two temperature fields are normalized by 0.25°C and 0.13°C, respectively, because model variability is weaker than observed.) The observed pattern is essentially the same as that of the first EEOF of observations alone (not shown), and the combined EEOF time series has time variation very similar to the EEOF of observations alone. Both the model and observations reveal a cooling of the basin-scale 400-m temperature (a shoaling of the thermocline) from the early 1970s to the early 1980s (as seen in the time coefficient), which is western intensified as expected from inspection of figure 2.

Since this signal explains 29% of the combined variance, it represents a significant deviation of the basin-scale thermocline structure and can be expected to be associated with gyre-scale changes in upper-ocean circulation. Indeed, the combined EEOF of model 400-m temperature and model 400-m velocity (second panel of figure 3 and dotted time series at bottom) reveals that the decadal signal is nearly geostrophically balanced over this 10-year transition time scale. The flow field reveals a 10% increase in the strength of the Kuroshio extension and the subpolar gyre return flow (cf. Sekine 1991; Trenberth and Hurrell 1994). A stronger than normal northward flow into the central Gulf of Alaska (cf. Tabata 1991; Lagerloef 1995) is also seen during the early 1980s in the model diagnosis.

It is interesting to note that little change in the California Current System is associated with this decadal signal, even though the thermocline (figures 2 and 3) did deepen off the west coast of America. A basin-scale change in wind stress curl is the driving mechanism for the thermocline change. Combined extended EEOFs of wind stress curl and north-south transport (integrated from 0 m to 1,500 m) yield an EEOF mode (third panel of figure 3 and dashed time series at bottom) that corresponds to the decadal change in temperature and velocity (panels 1 and 2). Figure 3 indicates that in the eastern basin the flow field is nearly in a local Sverdrup balance (to within a factor of two), and supports the notion that the wind stress is the forcing function of the decadal thermocline change. Note, however, that Meyers et al. (in press) suggest that the thermocline change in the California coastal region may be influenced by waves arriving along the eastern boundary from the tropics.

ENSO-SCALE THERMOCLINE VARIATIONS

The time series in figures 2 and 3 reveal interannual variations in the thermocline associated with time scales of El Niño and the Southern Oscillation (ENSO). Understanding what forces these fluctuations has been a lively subject, and models have successfully reproduced many aspects of the CCS response.

The central question is whether the variations are primarily driven by local forcing such as winds or whether the changes arrive from the equatorial region via coastally trapped Kelvin-like waves. Pares-Sierra and O'Brien (1989) addressed the question directly by using a shallow-water model which resolves the baroclinic deformation radius along eastern Pacific boundary. They compared the results of three simulations with observed sea level. One run was forced by midlatitude winds, a second by oceanic waves propagating north along the eastern boundary from the tropics, and a third by the two effects combined. Pares-Sierra and O'Brien's results demonstrated that local sea level along western North America has an interannual component which arrives through the ocean from the tropics.

Further studies in that modeling framework included those of Johnson and O'Brien (1990)—who showed that an additional component of interannual response is driven by the atmosphere at higher latitudes—and of Shriver et al. (1991)—who identified observed thermocline anomalies along 40°N that corresponded to model baroclinic waves radiated from the coastally trapped signal of equatorial origin. Jacobs et al. (1994, 1996[4]) found that model baroclinic waves radiating from the coastally trapped Kelvin-like waves of the 1982–83 ENSO were able to propagate intact across the Pacific and arrive near the Kuroshio region some ten years later. Ramp et al. (1996) studied a primitive equation model (Smith et al. 1992) forced by ECMWF winds from 1985 to 1994 and found competing effects off California of local winds driving the response, as well as coastal oceanic waves (which may have been scattered into higher vertical

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[2] See footnote 1 on p. 69.

[3] See footnote 1 on p. 69.

[4] Jacobs, G. A., H. E. Hurlburt, and J. L. Mitchell. Decadal variations in ocean circulation, part I: Rossby waves in the Pacific. MS submitted to J. Geophys. Res.

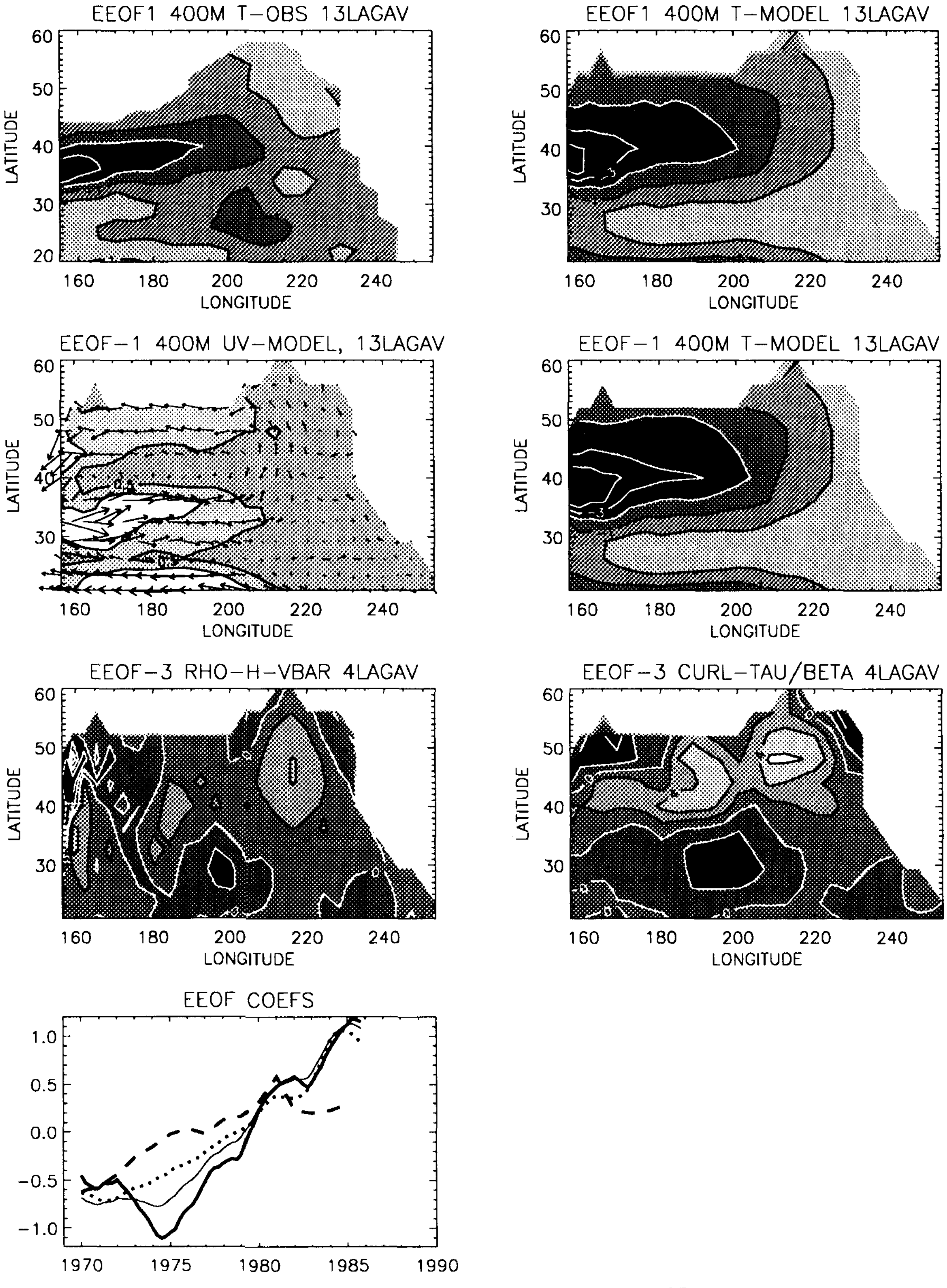

Figure 3. A synopsis of three separate combined extended EOF analyses. *Top*, Combined EEOF-1 of observed (*left*) and modeled (*right*) 400-m temperature, plotted as an average over all 13 lags. *Middle*, Same as top but for combined EEOF-1 of (*left*) model 400-m velocity and (*right*) model 400-m temperature. *Lower*, Combined EEOF-3 of north-south 0–1,500-m transport (scaled by density and depth) and wind stress curl over beta, plotted as an average over all 4 lags (0 to 3 years). *Bottom*, Corresponding principal components of top (*thin line*), middle (*dotted line*), and lower (*dashed line*) EEOFs, along with that of EEOF-1 of the observations alone (*thick line*), each scaled arbitrarily to fit on the same plot.

modes by the Gulf of California) propagating from the tropics.

Although high-resolution modeling studies have suggested that thermocline anomalies off California may be associated with wave radiation from coastally trapped waves of equatorial origin, unambiguous observational evidence has been lacking. In a recent study, however, Miller et al.[5] identified thermocline anomalies which propagated westward on ENSO time scales from western North America to near the dateline. Figure 4 shows maps of the observed fluctuations expressed as EEOFs. Westward-propagating 400-m temperature anomalies are clearly evident from 20°N up to 45°N, and they appear to reach as far west as the dateline, at which point they are either arrested or obscured by the ambient noise of the Kuroshio extension. Anomalies farther south in the analysis domain, near 20°N, propagate faster and farther westward, as anticipated. EEOF-3 leads EEOF-4 by approximately one year, as can be seen in the time series and in the map patterns, which are nearly identical when accounting for the one-year lag. The largest signals in the time series correspond to the mid-1980s and the mid-1970s and have a stochastic periodicity of 3–4 years.

Clearly, the signals in figure 4 are indicators of ENSO time-scale activity and suggest radiated baroclinic Rossby waves, which have been identified in aforementioned high-resolution numerical models in association with coastally trapped Kelvin-like waves of tropical origin. However, the thermocline waves identified here differ from the ones identified in those model studies in several respects. They have longer east-west wavelengths (roughly 3,000 km compared to 800–1,200 km) at 30°–45°N and therefore larger phase speeds (2.4 cm/s) than the thermocline anomalies associated with coastal variability of equatorial origin. Also their amplitude appears to increase away from the eastern boundary. Lastly, Miller et al.[6] show that they also occur in a low-resolution model in which, although it admits a poleward propagating Kelvin-like wave (e.g., O'Brien and Parham 1992), the numerical analogue Kelvin wave is seriously damped as it propagates northward and is trapped to one grid point in the offshore direction.

Miller et al.[7] explored the dynamics of the ENSO-scale thermocline anomalies of figure 4 by studying the model's version of the phenomenon. Figure 5 shows maps of three cases of the combined EEOFs (for brevity, only one lag of the analogue to EEOF-4 of figure 4 is shown; refer to figure 4 for information on phase propagation). The top panel of figure 5 features maps of one phase (cf. figure 4, top right) of the combined EEOF of the observed and modeled thermocline anomalies, which show that the model captures the large-scale westward-propagating behavior and that the time series (bottom, thin line) is coherent with that of the observations alone (bottom; thick line is from EEOF-4 of figure 4). Figure 5 (middle panel, with time series at bottom, dotted line) also shows the combined EEOF of model 400-m temperature and velocity and reveals that the large-scale circulation anomalies associated with the thermocline perturbations are nearly geostrophically balanced. The velocity maps reveal large-scale coherent velocity perturbations that extend several thousand kilometers along the west coast of North America. Their magnitude along the eastern boundary exceeds 0.2 cm/s in the model, suggesting that observed anomalies would reach nearly 0.5 cm/s if we account for the weaker temperature signal found in the model vis-a-vis observations. As the velocity anomalies migrate westward away from the boundary they become more meridional and extend into/from the southern parts of the Alaska Gyre.

The bottom panel of figure 5 shows the combined EEOF of north-south integrated (0–1,500-m) velocity and curl τ scaled to allow for potential Sverdrup balance (time series at bottom, dashed line), as a preliminary investigation of the vorticity dynamics of the thermocline anomalies. Instead of nearly Sverdrup-balanced velocities as seen in the decadal mode, the model thermocline anomalies occur in phase with large-scale deepening and weakening of the Aleutian Low. This suggests that the midlatitude thermocline anomalies seen in the model (which mimic those observed, although the model anomalies are weaker) are significantly driven by midlatitude forcing. It is unclear to what degree the midlatitude waves are forced by signals propagating along the eastern boundary, but, as previously mentioned, this model does not properly resolve this process, and models that do resolve the process yield shorter-wavelength thermocline anomalies.

Basinwide plots (not shown) of the full, unfiltered, seasonal thermocline anomalies for both model and observations reveal that the strongest signal is associated with the 1982–83 ENSO. One can follow the warm thermocline anomaly from the western North American coast across the basin until it encounters the western boundary (at low latitudes) and the Kuroshio region (in middle latitudes). The observed and modeled thermocline anomalies encounter the Kuroshio region in 1987–88, at which point they are no longer discernible because of the high variability there. It is interesting to note that these waves travel twice as fast as those identified by Jacobs et al. (1994; 1996[8]) in satellite-derived

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[5] Miller, A. J., W. B. White, and D. R. Cayan. North Pacific thermocline variations on ENSO time scales. MS submitted to J. Phys. Oceanogr.

[6] Ibid.

[7] Ibid.

[8] See footnote 4 on p. 72.

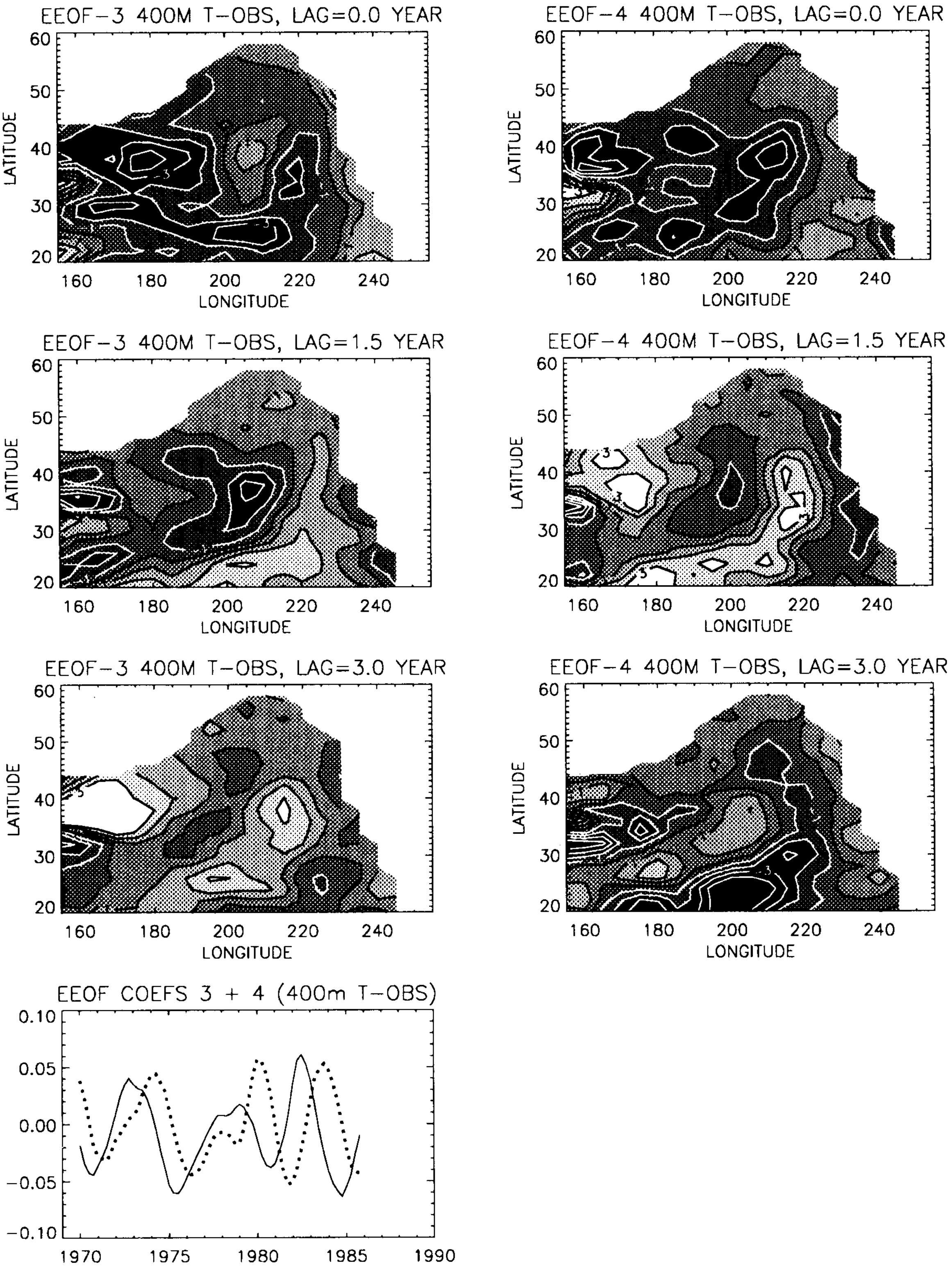

Figure 4. Third (*left*) and fourth (*right*) extended EOFs of the observed 400-m temperature alone for 3 of the 13 lags. *Top*, lag-0; *middle*, lag-1.5 yr; and *lower* lag-3 yr. *Bottom*, Corresponding principal components of third (*solid line*) and fourth (*dotted line*) EEOFs.

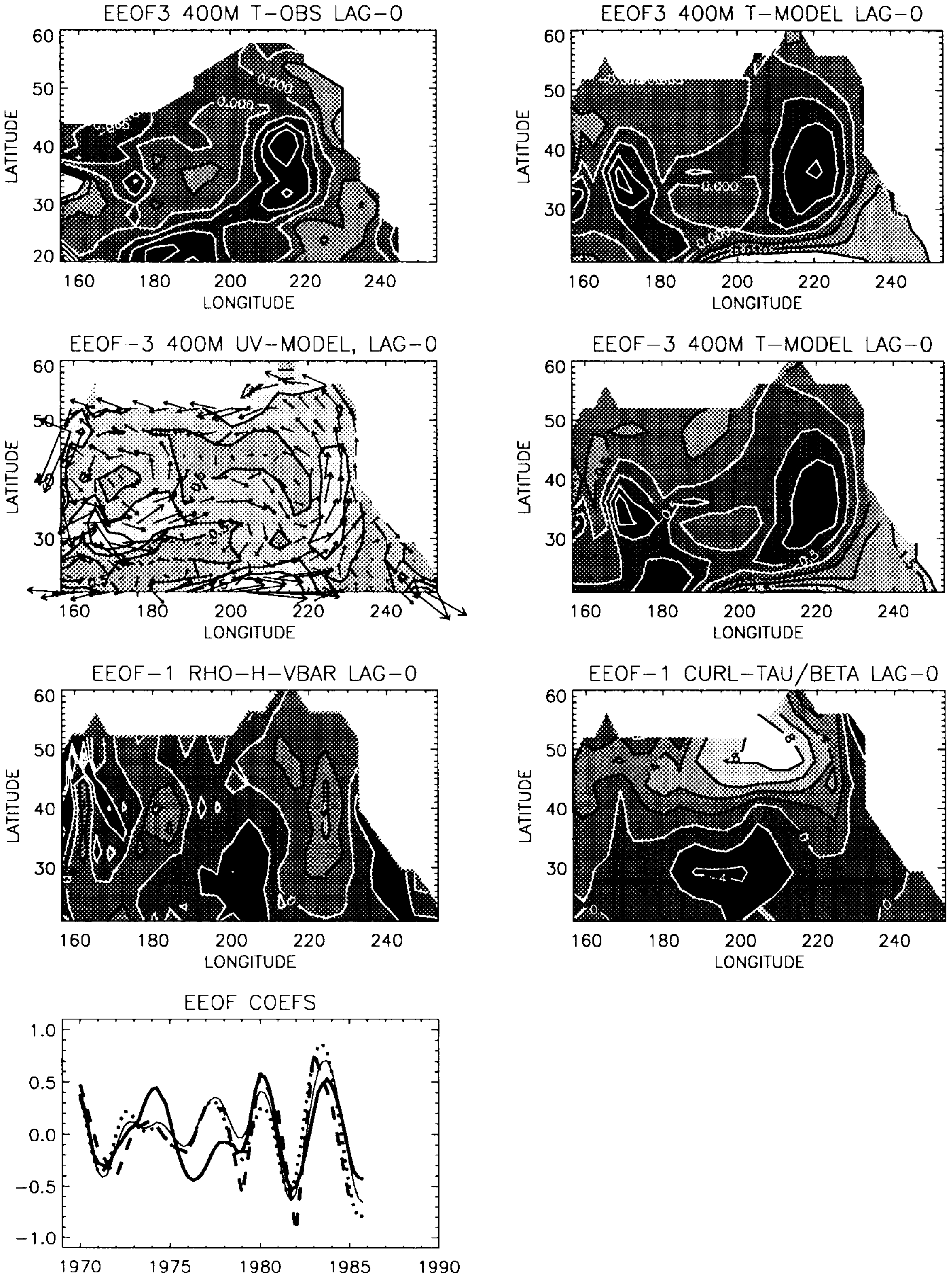

Figure 5. As in figure 3, but for (*top*) EEOF-3, (*middle*) EEOF-3, and (*lower*) EEOF-1, each plotted only for lag-0 (refer to figure 3 EEOF-4 for phase propagation). *Bottom*, Corresponding principal components of top (*thin line*), middle (*dotted line*), and lower (*dashed line*) EEOFs, along with that of EEOF-4 (*thick line*) of the observations alone.

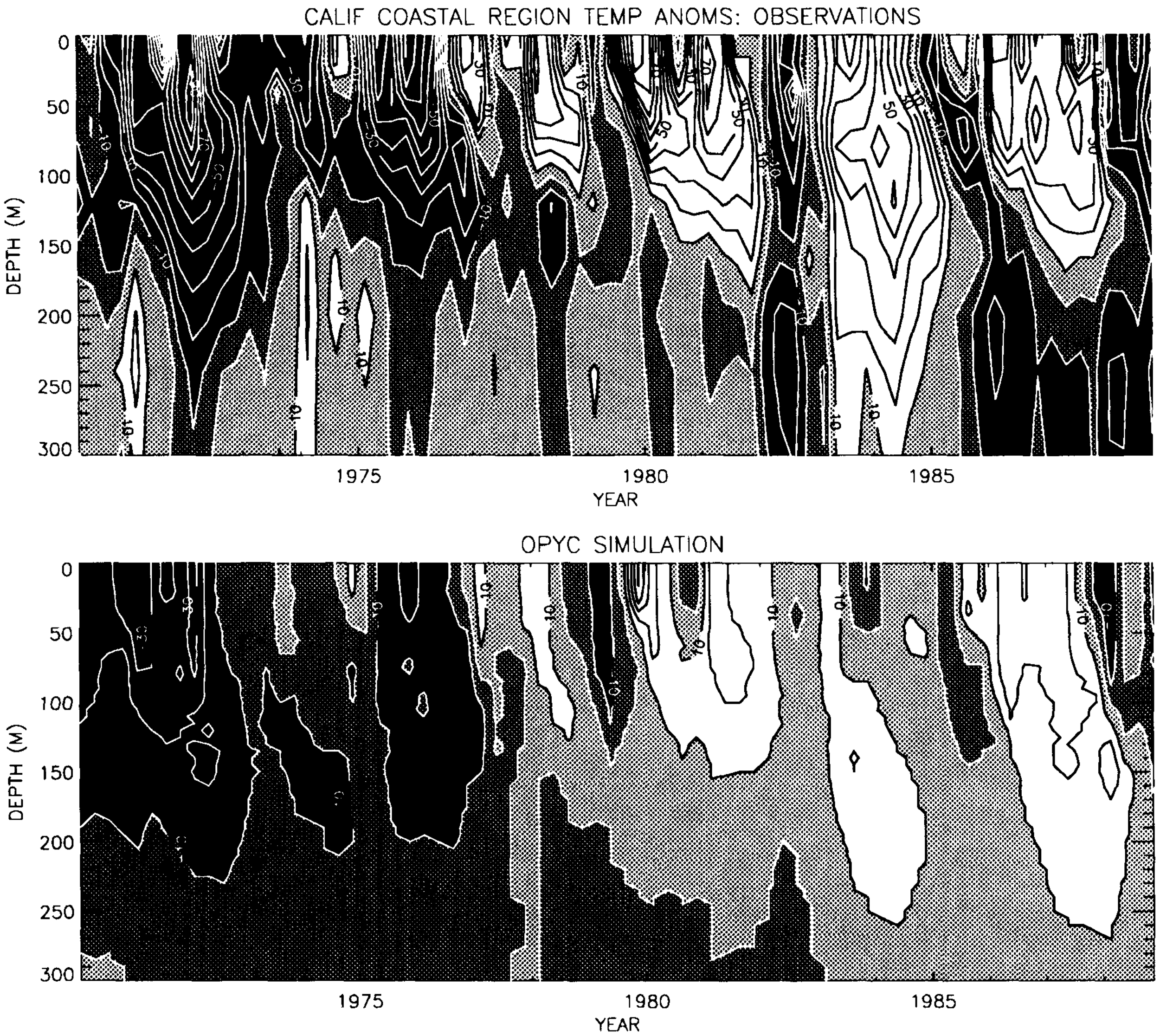

Figure 6. Temperature anomalies averaged over the region 130°W–coast, 25°N–45°N from the surface to 300-m depth from 1970 to 1988 in the observations (*top*) and the model (*bottom*). Contour interval is 0.1°C (scaled by 100), with darker shades cooler and lighter shades warmer.

sea-level observations and high-resolution-model thermocline anomalies, which showed trans-Pacific transit times of nearly ten years of model thermocline anomalies and observed sea-level height anomalies. Chelton and Schlax (1996) also identified sea-level variations that travel twice as fast as their theoretical Rossby wave analogues. Basin-scale atmospheric forcing (e.g., figure 5) is a likely explanation for the increased phase speed.

DISCUSSION

A comparison of a relatively coarse-resolution model of the Pacific Ocean with observations of upper-ocean temperature reveals two dominant signals in the thermocline structure off the coast of California. The first signal is a thermocline deepening associated with a decadal-scale change in the gyre-scale North Pacific thermocline. The second signal constitutes ENSO–time-scale waves propagating westward in the eastern North Pacific. The model suggests that the thermocline variations are both predominantly forced by wind stress curl.

Figure 6 gives a concise depiction of how these signals influence the large-scale thermocline off the California Coast (cf. Roemmich and McGowan 1995). The top panel shows the observations averaged over a region off western North America (130°W–coast, 25°N–45°N) as a function of depth and time, with the bottom showing the model version of reality. Although the decadal thermocline change has its strongest component in the northwestern part of the North Pacific, it is associated with a deepening of the thermocline (warmer ocean above 200 m) along the eastern boundary as well.

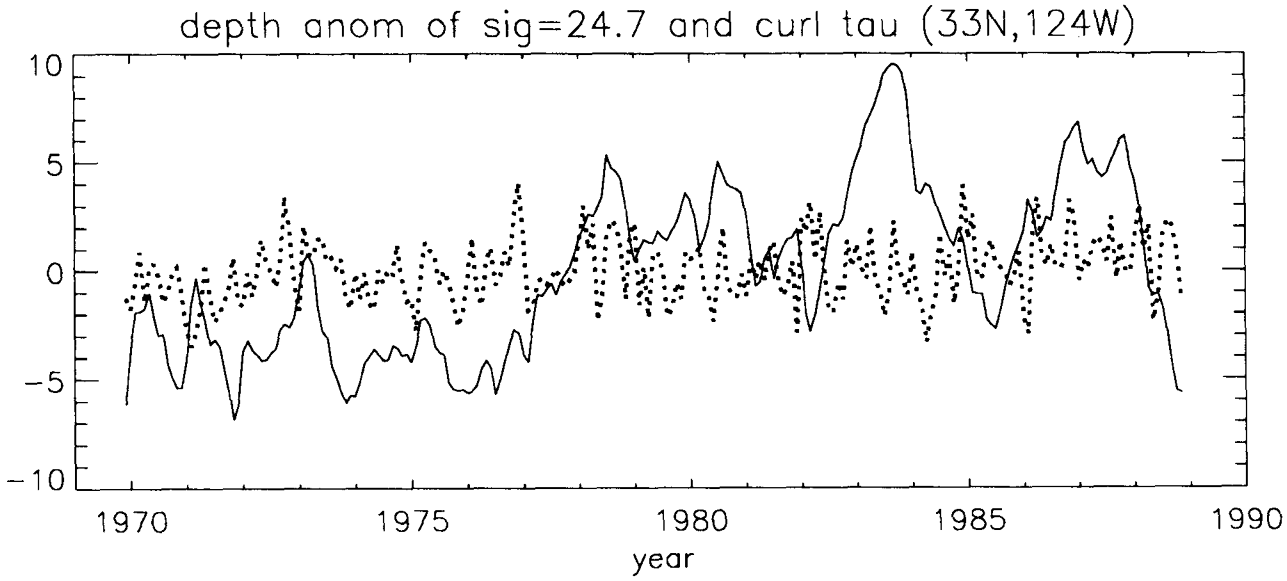

Figure 7. Depth anomalies (*solid line*) of the model isopycnal layer (sigma 24.7) at a grid point off the California coast. Positive anomalies indicate a deeper thermocline at mean level of roughly 180 m. Local wind stress curl anomalies (*dotted line*) at the same point.

Figure 7 shows depth anomalies of a model isopycnal layer (24.7 sigma layer) with a mean depth of roughly 180 m. One can see that the model thermocline deepens by 5–10 meters during the mid-1970s, although in the observations the change is larger and at a shallower depth than in the model (as can be seen in figure 6). Also shown in figure 7 is the local wind stress curl, which reveals no obvious correlation to the local thermocline anomalies; the basin-scale effect of the wind stress curl is instead the key factor.

Besides the decadal change, the ENSO time-scale thermocline fluctuations are evident in figures 6 and 7 as well. These interannual events are dynamically distinct from the decadal change, last for roughly one year, and are associated with temperature anomalies with local maxima at 50–100-m depth in the observations (cf. Norton and McLain 1994) and somewhat deeper maxima in the model (50–150 m).

Several interesting future studies need to be accomplished. There is substantial interest in longer interdecadal simulations with higher resolution than the hindcast discussed here. Such a model could be used for relating present climate variations to those of past centuries and for diagnosing the physical variables that influenced past biological regimes. Further research using idealized interannual forcing is also required to isolate the components of midlatitude ocean response driven by the midlatitude atmosphere versus the eastern boundary-wave propagation mechanism. Particular emphasis in this case should be placed on representing basin-scale atmospheric forcing, allowing interaction with basin-scale circulation, and understanding how thermocline variations affect SST. The most formidable task involves developing models that properly represent the large-scale eddy and small-scale filament formation processes which dominate the synoptic variations of the CCS. Nesting extremely high-resolution models in lower-resolution basin-scale models could aid in understanding how the large-scale flows and temperature variations influence instability processes, as well as their joint effect on associated biological systems.

ACKNOWLEDGMENTS

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INTERANNUAL VARIATIONS IN ZOOPLANKTON BIOMASS IN THE GULF OF ALASKA, AND COVARIATION WITH CALIFORNIA CURRENT ZOOPLANKTON BIOMASS

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ABSTRACT

Large-scale atmospheric and oceanographic conditions affect the productivity of oceanic ecosystems both locally and at some distance from the forcing mechanism. Recent studies have suggested that both the Subarctic Domain of the North Pacific Ocean and the California Current have undergone dramatic changes in zooplankton biomass that appear to be inversely related to each other. Using time series and correlation analyses, we characterized the historical nature of zooplankton biomass at Ocean Station P (50°N, 145°W) and from offshore stations in the CalCOFI region. We found a statistically significant but weak negative relationship between the domains. We investigated whether such a relationship arises from different forcing mechanisms or as an opposite response to the same mechanism. We found that the seasonal peak of both data sets occurred in the summer but that the CalCOFI data lagged the Ocean Station P data. A surface-drift simulation model showed that winter trajectories started at Ocean Station P and along 145°W drifted more into the California Current before the 1976–77 regime shift, and more into the Alaska Current after the 1976–77 shift. We examined physical and biological conditions which may lead to this inverse relationship between the two ecosystems, and we discuss the implications of these results for higher trophic levels.

INTRODUCTION

Substantial temporal and spatial heterogeneity occurs in the production of oceanic ecosystems. Much of this heterogeneity results from seasonal and geographic variations in nutrient availability, mixed-layer depths, or solar radiation. Processes that enhance productivity (e.g., upwelling, wind and tidal mixing) tend to be localized and transient. Physical forcing in the form of the large-scale circulation pattern redistributes the elevated production to areas less favorable for in situ production. Thus production at any location can be affected by both local and remote processes, and it is often difficult to distinguish their relative contributions (Wickett 1967; Chelton et al. 1982; Roessler and Chelton 1987).

It has become increasingly apparent that atmospheric and oceanic conditions are likely to change due to a buildup of greenhouse gases in the atmosphere (Graham 1995). Although there has been much interest in predicting the effects of climate change, especially on fisheries resources (e.g., see papers in Beamish 1995), different scenarios exist for future trends in basic physical processes such as upwelling (Bakun 1990; Hsieh and Boer 1992). Biological processes are more laborious to monitor and difficult to predict because of their inherent complexity.

There are numerous examples showing that large-scale physical and biological changes have occurred throughout much of the Northeast Pacific Ocean over the last few decades (Francis and Hare 1994; Miller et al. 1994). Indices which showed these changes include atmospheric (Trenberth 1990; Trenberth and Hurrell 1994), oceanographic (Royer 1989; Hsieh and Boer 1992; Miller et al. 1994; Lagerloef, 1995; Polovina et al. 1995), productivity (Venrick et al. 1987; Polovina et al. 1994), and biomass of various trophic levels (Brodeur and Ware 1992, 1995; McFarlane and Beamish 1992; Beamish 1994; Hare and Francis 1995; Roemmich and McGowan 1995a, b). A number of studies have suggested that biological changes occurred rather suddenly sometime around 1976–77, concurrent with a dramatic shift in physical regimes (Francis and Hare 1994; Miller et al. 1994).

Documenting the effects of climate change on marine ecosystems requires long time series of sampling to examine low-frequency periodicity. In the Northeast Pacific Ocean, two series are notable not only for their length, but also for the broad suite of biological and physical measurements made at each location. The first of these, Ocean Station P (50°N, 145°W; hereafter called Station P), nominally represents a subarctic oceanic ecosystem that was sampled almost continuously from 1956 to 1980 but only sporadically since then. The second, the CalCOFI grid, is an eastern boundary current ecosystem that has been sampled since the late 1940s, although not always with the same geographic and temporal intensity. Although Ekman pumping of deep, nutrient-rich water is a feature common to both these ecosystems, the mechanisms behind biological production in the two systems differ (Ware and McFarlane 1989).

Over the past few decades, there has been much speculation on the nature of the eastern bifurcation of the Subarctic Current into the Alaska Current and California Current and its possible effects on biological production in these two large ecosystems (figure 1). Wickett (1967), Chelton and Davis (1982), and Chelton (1984) have speculated that the intensities of the flows in the Alaska and California Currents fluctuate in opposition to one another. They hypothesized that north-south shifts in the bifurcation of the Subarctic Current (West Wind Drift) could be forced by physical factors occurring in the western or central Pacific Ocean.

Using environmental indices and fish-recruitment data, Hollowed and Wooster (1992) and Francis (1993) have characterized two alternating interdecadal states of atmospheric and oceanic circulation in the Northeast Pacific Ocean which result in very different components of fisheries production (e.g., groundfish, salmon) in the Alaska Current and California Current domains. Hollowed and Wooster (1992) have characterized these states as lasting 6 to 12 years each. A cold era (Type A) is associated with a weak Aleutian Low, relatively weak circulation in the Alaska Gyre, strong upwelling inshore of the California Current, negative sea-surface temperature (SST) anomalies throughout the coastal Northeast Pacific Ocean, and positive SST anomalies in the central North Pacific Ocean (centered at 40°N). A warm era (Type B) is associated with a strong Aleutian Low, strong gyral circulation, and reduced upwelling and high temperatures to the south (figure 2).

Francis (1993), Francis and Hare (1994), and Hare and Francis (1995) find similar although longer (20–30 year) periods of oscillating "warm" and "cool" regimes, which they relate to the production dynamics of Alaska salmon. In addition, Francis (1993) speculated that the interdecadal variations in salmon production in these two oceanic domains are inversely correlated.

This paper examines factors related to long-term changes in production in the subarctic Pacific Ocean, using examples mainly from Station P. We examine, in particular, trends in zooplankton biomass as an indicator of changes in productivity in this oceanic ecosystem. Using time-series analysis, we then compare these trends to those evident in the offshore region of the California Current to examine the hypothesis of Wickett (1967) that production in both systems may be affected by an

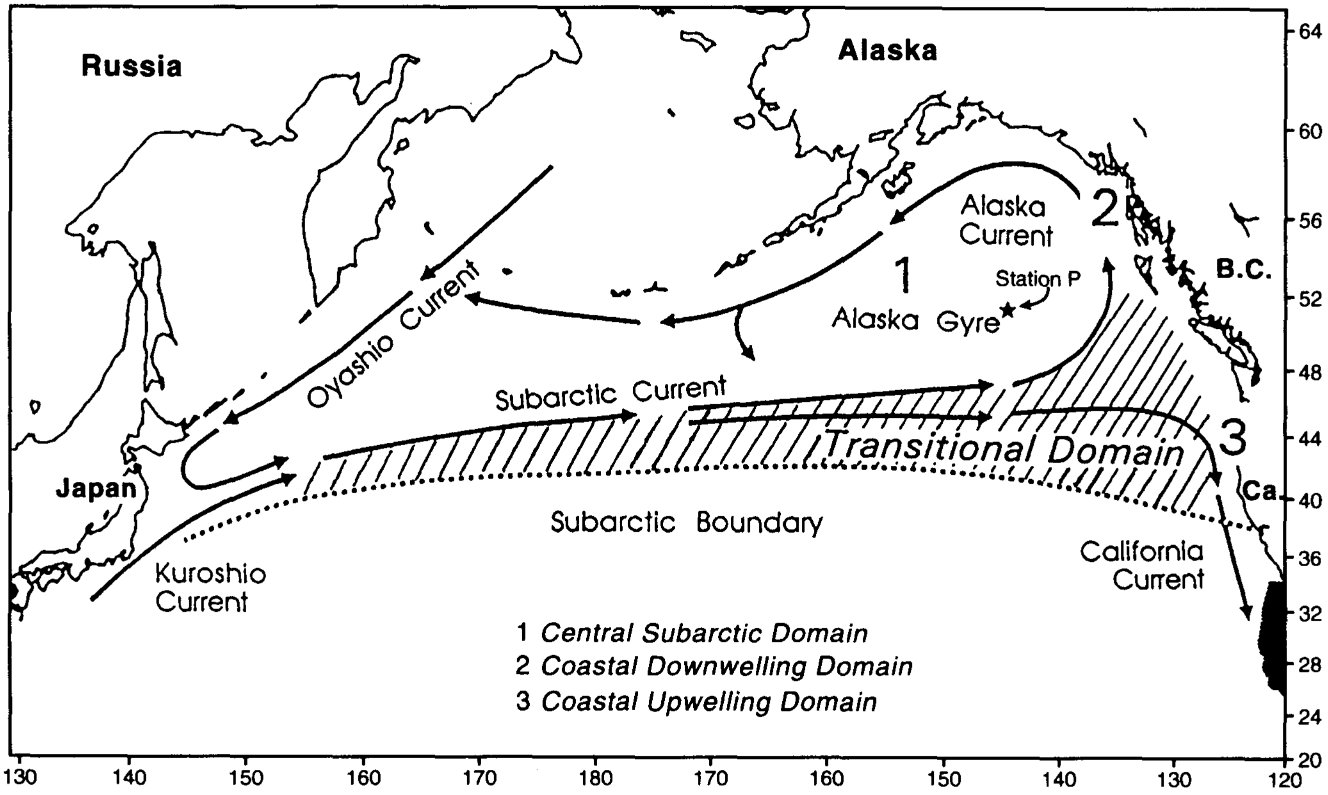


Figure 1. Large-scale near-surface circulation in the North Pacific Ocean, and Ocean Station P (*star*) and the CalCOFI sampling region (*shaded area*). Also shown are the different ocean production domains of Ware and McFarlane (1989) and Pearcy (1991).

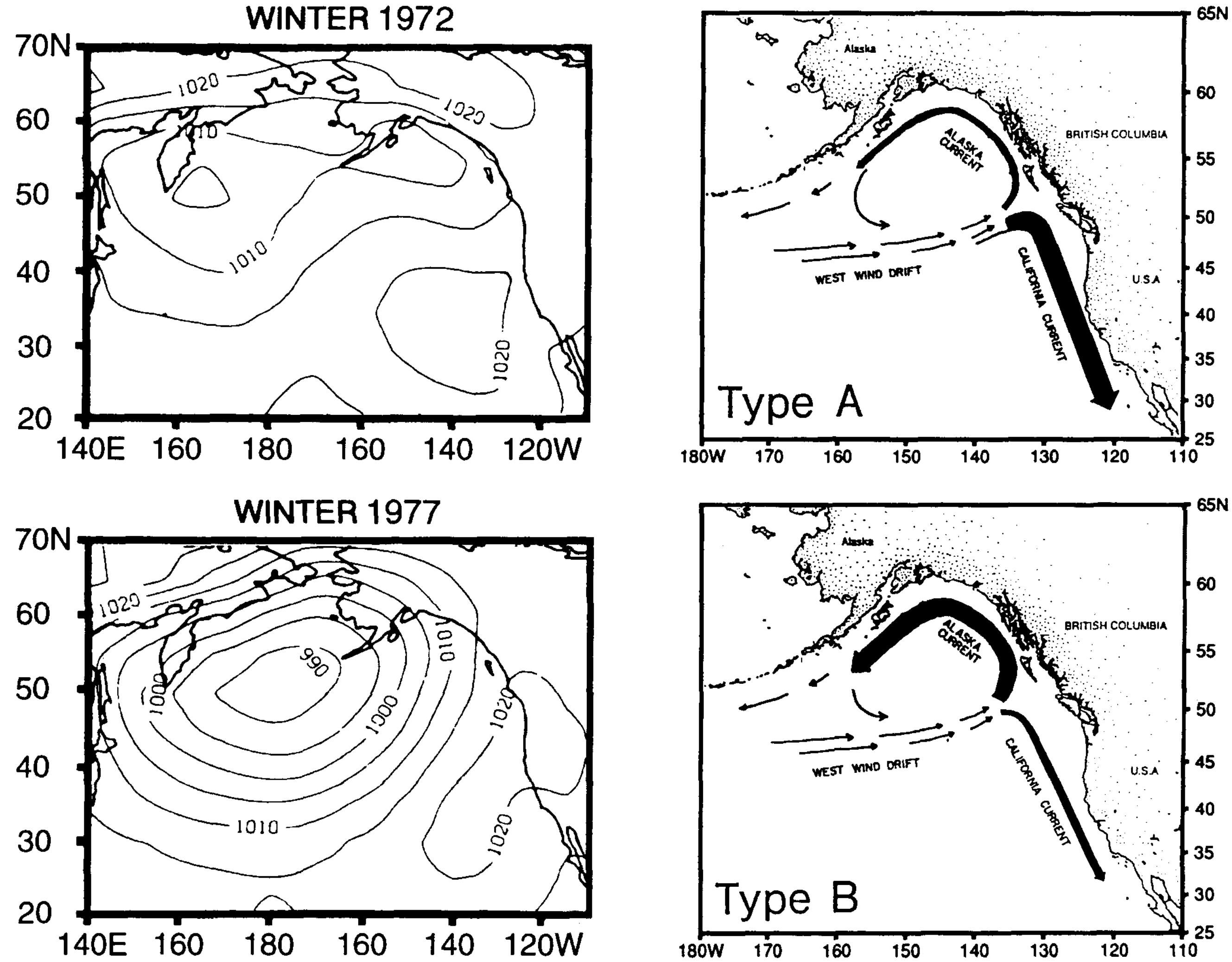


Figure 2. Winter mean sea-level pressure from Emery and Hamilton (1985) for two contrasting years, and the alternate states of atmospheric and oceanic circulation patterns in the eastern North Pacific Ocean proposed by Hollowed and Wooster (1992).

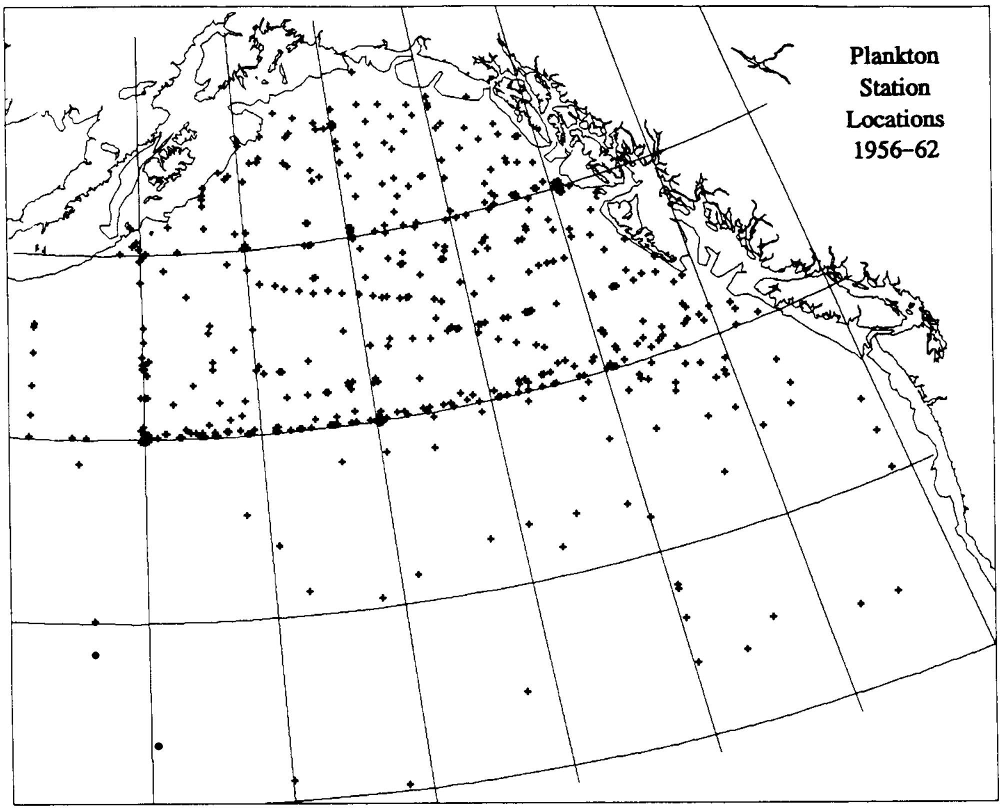
influx of water from the same source—the Subarctic Current. We examine physical data relevant to regime-shift changes in flow between the Alaska Current and California Current. Finally, we discuss implications of regime shifts to higher trophic levels and suggest new hypotheses and further studies that could be undertaken to address these hypotheses.

DATA SOURCES AND METHODS

Zooplankton Data Sets

Zooplankton biomass data from 24 years (1956–80) of vertical net sampling at Station P were used in our analyses (figure 1). Before 1969, sampling was conducted over alternate 6-week periods, but after this time, sampling was continuous (Fulton 1983). Sampling frequency varied from 1 to 29 samples per month over 8 to 12 months of the year (Frost 1983). Hauls were mainly done during daytime, and all were from 150 m to the surface. Sampling gear was changed from a 0.42-m-diameter NORPAC net to a 0.57-m SCOR net in August 1966, although the mesh size remained the same (0.351 mm). Fulton (1983) estimated that the catching efficiency of the SCOR net was 1.5 times greater than the NORPAC net, based on a series of intercalibration tows. But a new estimation based on the original data presented by Fulton (1983) suggests that the correction factor should be higher, somewhere in the range of 1.6–2.1×, with 1.77× being the most likely value (Waddell and McKinnel 1995; Frost, Ware, and Brodeur, unpubl. data), which is what we used in this analysis.

Zooplankton displacement volumes from the central part of the CalCOFI grid (lines 77–93) over a longer time frame (1951–94) were provided by Paul Smith (NMFS, SWFC, La Jolla). The gear and maximum haul depths changed during this period from a bridled 1-m-diameter ring net fished obliquely to 140 m (1951–68) or to 212 m (1969–78) to an unbridled bongo net fished



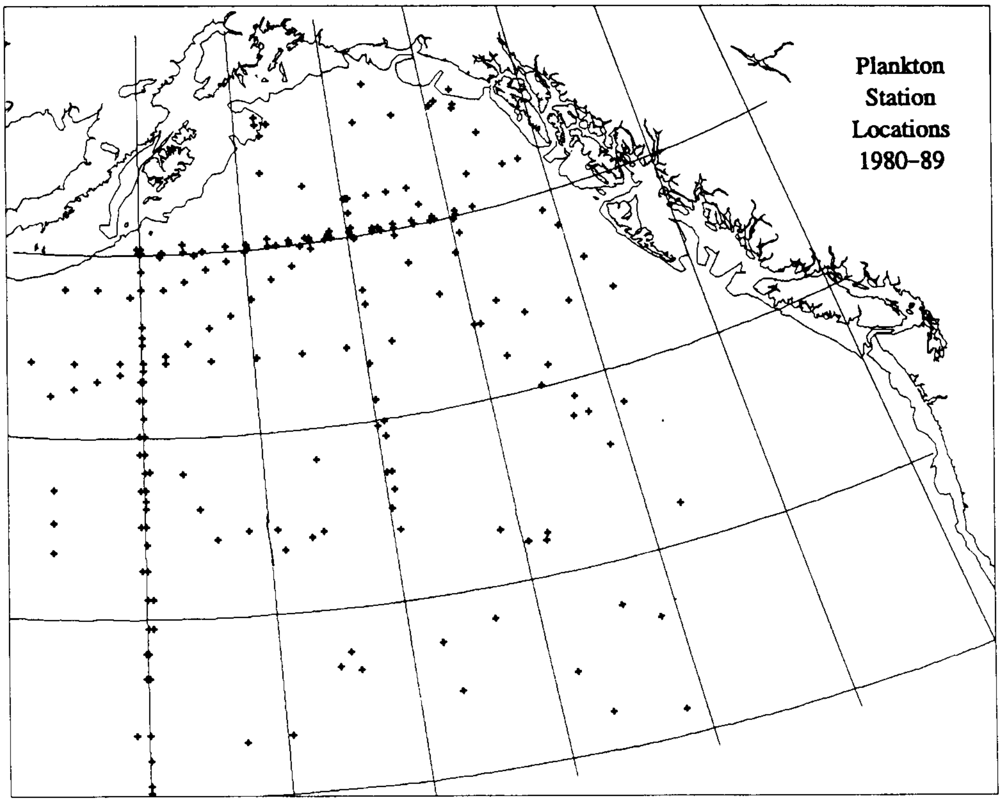


Figure 3. NORPAC zooplankton sampling stations (*plus signs*) during 1956–62 and 1980–89.

down to 212 m (1978–94). An analysis by Ohman and Smith (1995) has determined that the deeper tows with the 1-m net are low by a factor of 1.366 compared with the shallower 1-m nets and the deep bongo tows without bridles, and we adjusted the data accordingly.

Since we were interested in advective rather than local production processes (Chelton et al. 1982), we trimmed the data set to include only those stations farther than 60 km offshore. We initially aggregated the data in several ways, such as by the northern (north of CalCOFI line 80), middle (line 80 to line 90), and southern (south of line 90) parts of the region, as well as by working with only the most frequently sampled transects (lines 80 and 90). We found, however, that the time series utilizing all the data was highly correlated with almost all other combinations of data. Therefore, the CalCOFI data for a given year were combined spatially for all analyses. In addition, the number of missing data points was reduced, though large gaps still existed.

Additional zooplankton biomass data from oceanic areas of the Northeast Pacific Ocean besides Station P exist for two time periods (1956–62 and 1980–89, except for 1986), and are more fully described in Brodeur and Ware (1992). In this analysis, we extended the geographic range of values to 40°N to include the transition region south of the subarctic boundary (Pearcy 1991) for both time periods (see figure 3 for sampling locations). Contour maps of zooplankon biomass (g/1,000 m^3) were generated for both time periods with a raster-based GIS program (Compugrid, Geo-spatial Ltd.). Yearly interpolated means were computed for each year. Since the earlier analysis, an additional 5 years (up to 1994) of data collected by Hokkaido University have become available. Although there is not enough coverage for this later period to map the overall distribution of biomass, many of the same transects were sampled each year so that the interannual variability can be examined. As before, only biomass data collected from 15 June to the end of July and in the same geographic area described by Brodeur and Ware (1992) were included.

Time Series Analyses

We examined the temporal relationship between the Station P zooplankton data and the offshore CalCOFI data using time series cross-correlation analyses (Box and Jenkins 1976). We investigated monthly, seasonal, and annual lagged relationships. The time series of available data for each region shows incomplete temporal overlap, especially for the CalCOFI region, which was intermittently sampled during the 1970s and 1980s (figure 4). The distribution of both the Station P and offshore CalCOFI zooplankton data was highly skewed, and a log-transformation of the data was performed before the time-series analysis. In addition, a pronounced seasonal signal is evident in each region (figure 4). This signal was removed by calculating a yearly average biomass for each month and season (spring = March–May; summer = June–August; fall = September–November; winter = December–February). Both monthly time series exhibited substantial lag-1 autocorrelation, which can result in spurious cross-correlations (Box and Jenkins 1976; Myers et al. 1995). Therefore it was necessary to filter both series by a process known as prewhitening (*sensu* Box and Jenkins 1976) before computing the cross-correlation function (CCF) at lagged periods.

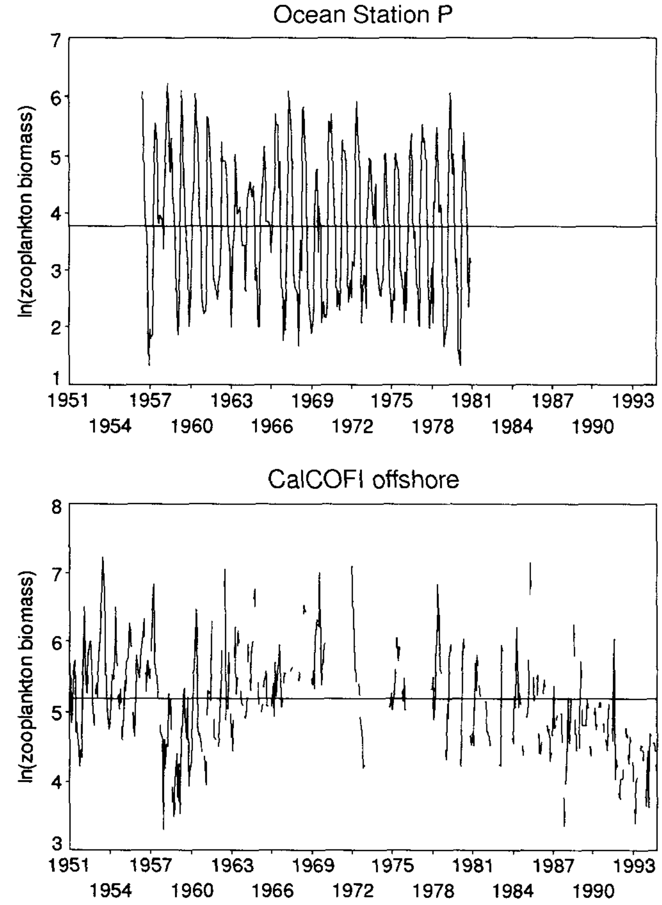


Figure 4. Log-transformed zooplankton biomass time series for Ocean Station P and offshore CalCOFI sampling areas.

Ocean Surface Current Simulations

Due to a lack of time series of open-ocean current data, we used a model developed for the North Pacific Ocean which provided a continuity of surface mixed-layer currents through space and time. The OSCURS (Ocean Surface CURrent Simulations) model uses gridded daily sea-level pressure fields to compute daily winds, and from them to compute daily ocean surface currents (Ingraham and Miyahara 1988). The long-term mean geostrophic current vectors computed from existing temperature and salinity versus depth data are added vectorially to these daily currents, and the model is then tuned to existing satellite-tracked drifter data.

PRODUCTION TRENDS IN THE CENTRAL SUBARCTIC DOMAIN

Phytoplankton and Primary Productivity

Nearly 30 years of observations at Station P indicate no major seasonal variation in phytoplankton biomass (figure 5; see also Wong et al. 1995). There are generally no phytoplankton blooms, and the mean phytoplankton biomass is always very low, averaging about 0.4 mg chlorophyll m^{-3} (figure 5; Banse 1994). There are no indications of long-term increases in chlorophyll over this time period (figure 6) similar to those documented for the central North Pacific Ocean by Venrick et al. (1987).

However, as model studies show (Frost 1993; Fasham 1995), phytoplankton biomass is not necessarily a sensitive indicator of either seasonal or interannual variations of phytoplankton productivity. Depth-integrated productivity at Station P shows a pronounced seasonal cycle, increasing in early spring with the seasonal increase in insolation and peaking in midsummer at levels 4–8 times as high as in winter (Sambrotto and Lorenzen 1987; Welschmeyer et al. 1993; Boyd et al. 1995; Wong et al. 1995). Estimates of phytoplankton production rate at Station P also suggested higher rates in the 1980s than in the 1960s and 1970s, but this is considered inconclusive evidence for interdecadal variation in phytoplankton production rate because of methodological problems prior to the 1980s (Welschmeyer et al. 1993; Wong et al. 1995). Moreover, indirect evidence of changes in phytoplankton productivity based on nitrate removal during the spring-summer period provides no suggestion of interannual trends (C. S. Wong, IOS, Sydney, B.C., pers. comm.). Wong et al. (1995) noted that because availability of dissolved iron may affect phytoplankton production rate at Station P (Martin and Fitzwater 1988), interannual variations in atmospheric input of iron could produce parallel changes in phytoplankton production, but any significant interdecadal changes in phytoplankton production rate induced by this mechanism also should be evident in seasonal nitrate removal.

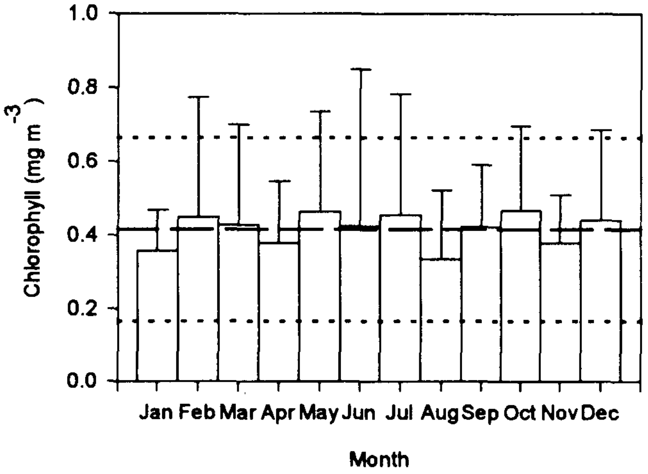


Figure 5. Monthly mean surface chlorophyll a concentration at Ocean Station P. *Error bars* are standard deviations (s.d.) of the mean. Also shown is the overall annual mean (*dashed line*) and ±1 s.d. of the annual mean (*dotted lines*).

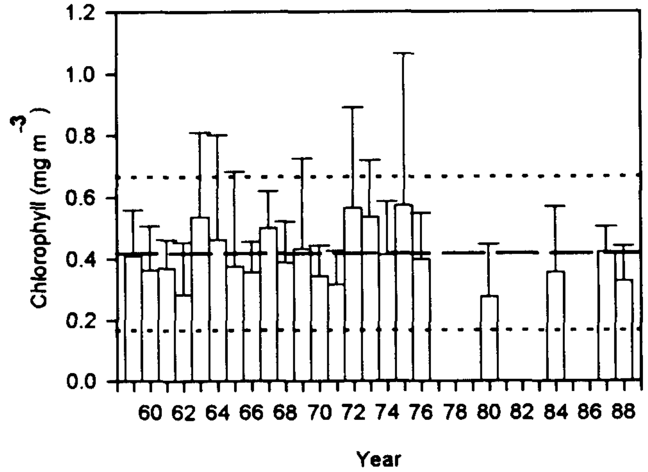


Figure 6. Annual mean and standard deviation of surface chlorophyll a concentration at Ocean Station P. Means for the period 1959–76 are based on data in McAllister et al. (1959), McAllister (1962), and Stephens (1964, 1966, 1968, 1977); two very high values in 1975 (21 June, 26 October) were excluded from the analysis because of lack of supporting evidence from either subsurface depths or preceding and subsequent dates. Sources of other data: 1980 (C. B. Miller, pers. comm.); 1984 (C. J. Lorenzen, unpubl. data rep.); 1987 and 1988 (N. A. Welschmeyer, pers. comm.). Also shown are the long-term mean value (*dashed line*) and ±1 s.d. of the mean (*dotted lines*) for the entire data set.

Zooplankton

Seasonal variability. Zooplankton biomass is highly seasonal at Station P, peaking in May and June and decreasing almost an order of magnitude from late fall to early spring (October to March; figure 7). This contrasts with the situation for the offshore CalCOFI grid, which shows some seasonality but only about a doubling between winter and summer (figure 7). With each month given equal weighting, the annual mean weight of zooplankton at Station P is 82 g/1,000 m^3. The annual mean displacement volume (260 ml/1,000 m^3) for the CalCOFI region converts to a higher wet weight (using wet weight = 0.8 displacement volume; Wiebe 1988) than that seen for Station P.

Interannual variability. In the entire data set of zooplankton biomass from Station P (figure 4), there appears to be no discernible trend over the 26-year period. However, Brodeur and Ware (1992) found a significant long-term increase in biomass for a 6-week period in early

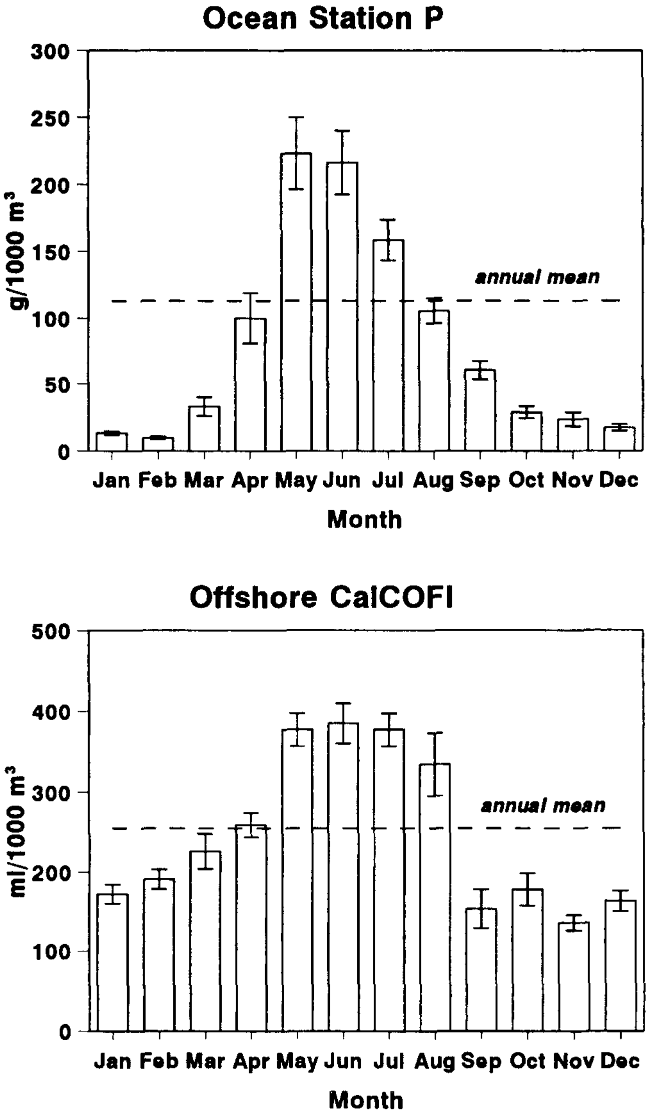


Figure 7. Monthly values of zooplankton biomass at Station P and in the offshore region of CalCOFI. The *bars* represent the means, and the *error bars* represent ±1 standard error. We calculated the Station P data as means of the monthly means for each year (17–23 values per month) rather than using all data within a month (range 104–339 observations per month). The annual means for each area are shown as a *dashed line.*

summer, when biomass is near its annual peak. We reanalyzed these data using the new gear-correction factor (see Methods) and still found a significantly positive relationship ($p = 0.003$) despite the high annual variability and the fact that so few years are represented beyond the 1976–77 regime shift (figure 8). For the large-scale sampling (figure 9), a discernible shift in zooplankton biomass was observed between the earlier period (1956–62) and most of the 1980s (up to 1988). The mean zooplankton biomass for the years after 1988, although above the long-term mean, was generally intermediate relative to the other periods examined, and showed more interannual variability (figure 9).

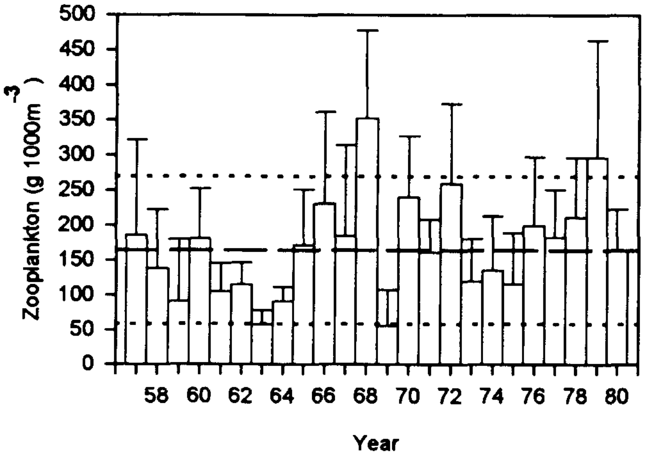


Figure 8. Annual values of zooplankton biomass (means +1 s.d.) at Station P from 1956 to 1980 for the 6-week period beginning June 1. Also shown are the long-term mean value (*dashed line*) and ±1 s.d. of the mean (*dotted lines*) for the entire data set.

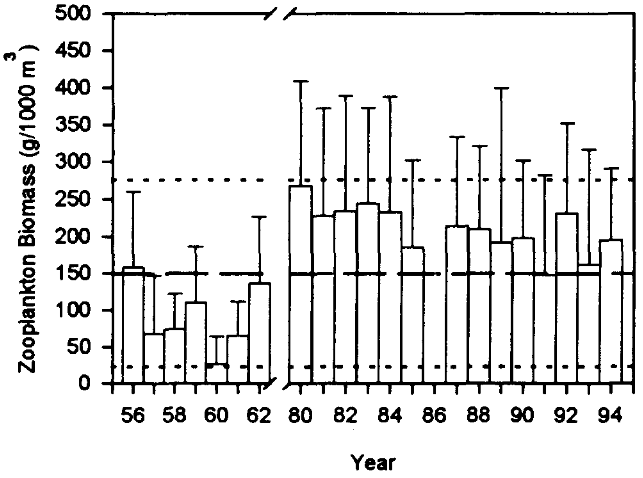


Figure 9. Annual values of zooplankton biomass for the large-scale sampling in the subarctic and transition regions of the North Pacific. Shown are the annual mean (*histograms*) and +1 s.d. (*error bars*). The *dashed line* is the mean for all years, and the *dotted lines* are ±1 standard deviation of the long-term mean.

Geographic variability. The large-scale zooplankton biomass distributions showed dramatic differences between the two periods not only in the overall biomass, as described previously, but also in the distribution patterns for each time period (figure 10). High biomass in the 1956–62 period occurred mainly in the central part of the Gulf of Alaska, with much lower concentrations nearer to the coast. Conversely, during 1980–89 elevated biomass occurred in a continual band from the Transition Zone up to the northern coast of Canada and Southeast Alaska, and then extended westward along the shelf edge (figure 10). The overall pixel distribution of biomass between the periods showed that almost all the biomass values in the later period were above the mean value for the earlier period (figure 10).

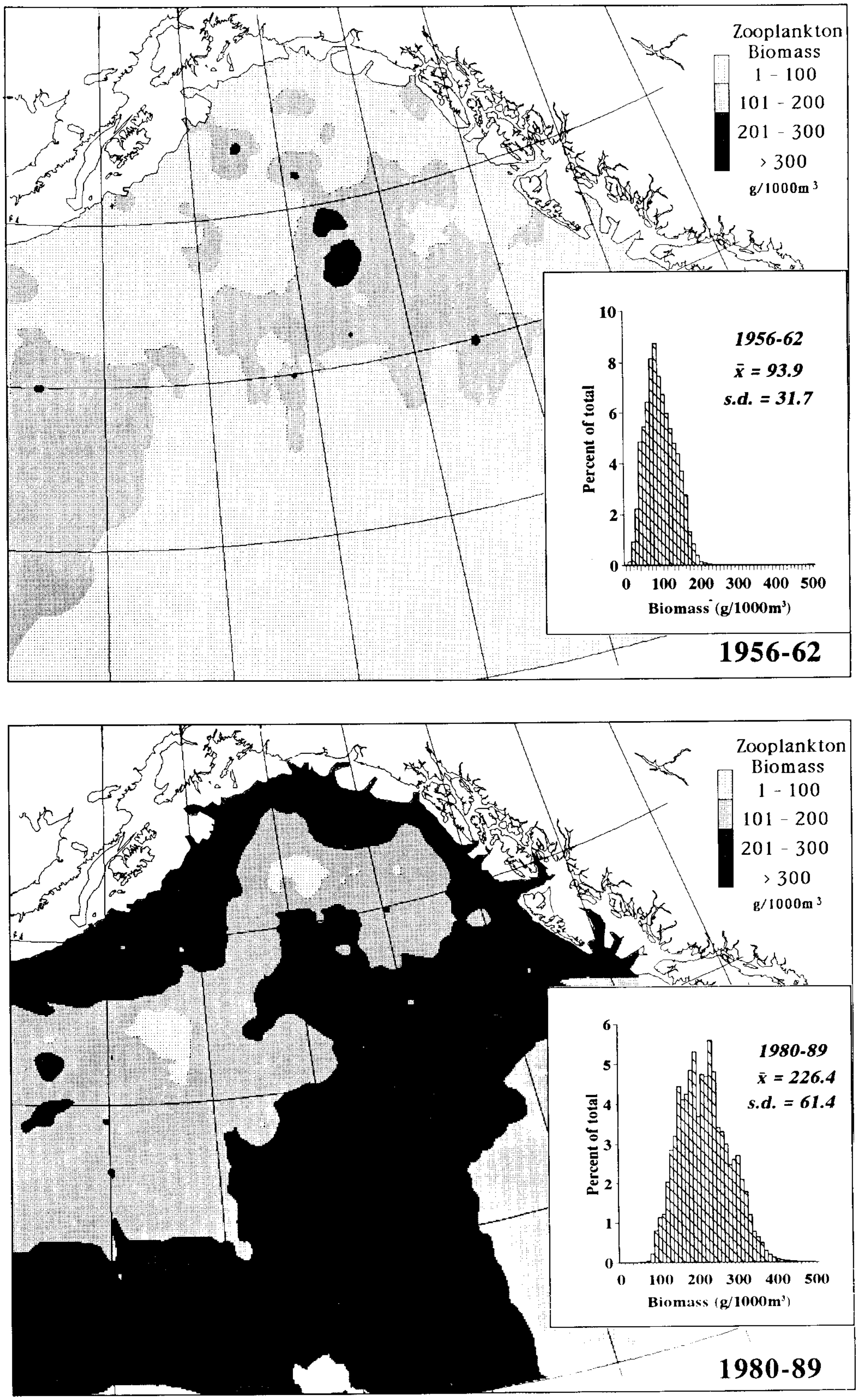


Figure 10. Large-scale distribution of zooplankton biomass from sampling during the 6-week period beginning June 1 for 1956–62 and 1980–89. See figure 1 for locations of sampling stations for each period. The insets show the zooplankton biomass pixel distributions as a percentage of the total number of pixels for each time period. The overall mean and standard deviation of biomass for the time period are given.

ANALYSIS OF COVARIATION IN STATION P AND CALCOFI DATA SETS

The magnitude of anomalous values was similar in both regions, but the CalCOFI data showed an apparent long-term decline in zooplankton biomass over the last two decades (figure 4). Autocorrelation plots were examined to determine whether serial autocorrelation exists within each region (figure 11). Both monthly time series show significant autocorrelation. The CalCOFI data are significantly autocorrelated up to 12 months, and all correlations up to 24 months are positive. Conversely, the Station P data show that anomaly events are much more short-lived (lasting 2–3 months), and little temporal pattern is evident after this time.

The cross-correlation between the autocorrelated data sets shows highly significant lagged correlations in both directions (figure 12). The presence of autocorrelation within both time series, however, renders this relationship highly suspect (Katz 1988; Newton 1988). To ascertain whether there is a real relationship, it is necessary to prewhiten both series—that is, remove the autocorrelation structure—and then plot the CCF of the residual series. Both series were adequately described by a lag-1 autoregressive (AR1) model. Separate filters were used for the two series ("double prewhitening"), and the coefficients were approximately equal to the lag-1 autocorrelation values—0.412 for CalCOFI and 0.524 for Station P. After filtering, almost all the significant lag correlations disappeared (figure 12). The only one that remained (CalCOFI leading Station P by 2 months) was quite small (−0.203) and possibly spurious.

The effect of prewhitening, while statistically justified, may also have the side effect of overcompensating for autocorrelation and removing evidence of an actual signal. As an alternative to prewhitening, an "effective degrees of freedom" is sometimes employed when calculating the confidence intervals around the cross-correlation estimates (Trenberth 1984). In the case of two AR1 time series, the true standard deviation at lag 0 is inflated over the no autocorrelation case by

$$f = [(1 + \phi_X * \phi_Y)/(1 - \phi_X * \phi_Y)]^{0.5},$$

where ϕ_X and ϕ_Y are the lag-1 autocorrelation coefficients (Katz 1988). Thus at lag 0, the standard deviation is approximately 1.25 times greater than that computed on an assumption of independent data points.

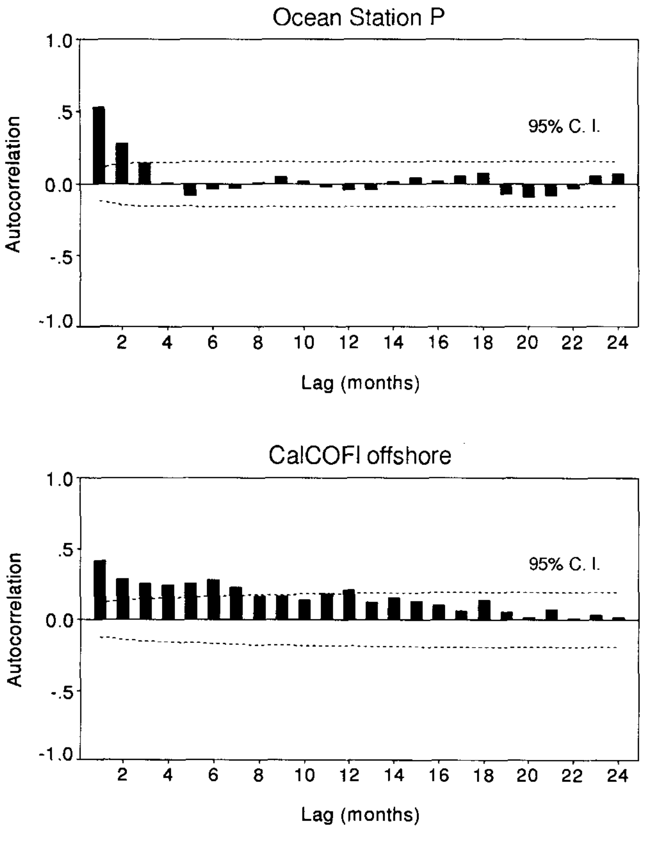


Figure 11. Serial autocorrelation of Station P and offshore CalCOFI zooplankton biomass at various time lags. Upper and lower 95% confidence intervals are indicated as *dashed lines*.

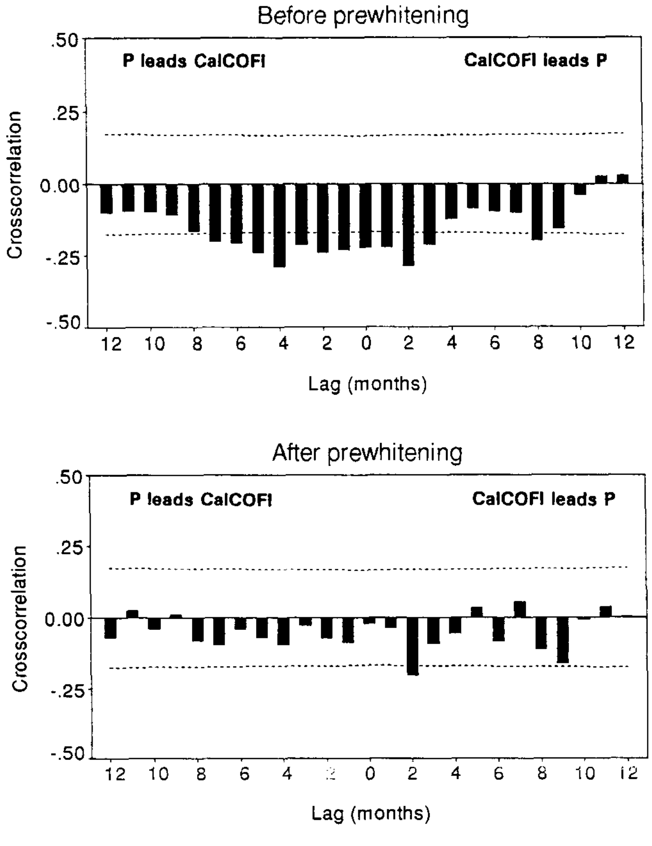


Figure 12. Cross-correlation between Station P and offshore CalCOFI zooplankton biomass at various time lags before and after prewhitening. The upper and lower 95% confidence intervals are indicated as *dashed lines*.

Assuming an approximately equal inflation at other lags, only lags −4 (Station P leads CalCOFI by 4 months) and +2 (CalCOFI leads Station P by 2 months) are significant at the 0.05 level. The −4-month lag is interesting in that it is interpretable in terms of ocean physics. A parcel of water originating upstream in the Subarctic Current would arrive at Station P approximately 4 months ahead of a particle diverted to the CalCOFI region (see next section). The +2-month lag may or may not be spurious, but it has no obvious physical explanation (though see below).

We next examined within- and between-area lag correlations for the yearly 3-month seasonal averages. The seasonal data exhibited almost no autocorrelation among years, a result that can be deduced from the monthly correlations, which die out by 12 months. Therefore, the cross-correlations between seasonal averages did not require a prewhitening step. Most within-region correlations were positive (10 of 12), with the CalCOFI data showing much stronger between-season coherence than the Station P data (table 1).

TABLE 1

Within-Region Correlation Matrices of Ocean Station P and Offshore CalCOFI Seasonal Biomass Time Series (Log-Transformed and Zero-Centered)

	Winter	Spring	Summer	Fall
Ocean Station P				
Winter	1.000	0.221	0.005	0.387
Spring		1.000	$\underline{0.474}$	−0.163
Summer			1.000	−0.032
Fall				1.000
Offshore CalCOFI				
Winter	1.000	$\underline{\underline{0.498}}$	0.242	0.351
Spring		1.000	$\underline{\underline{0.590}}$	$\underline{0.376}$
Summer			1.000	$\underline{0.411}$
Fall				1.000

Single underline indicates significance at the 0.05 level, double underline at the 0.01 level.

We examined cross-region correlations lagged up to a year in each direction (table 2). Out of a total of 36 separate correlations, 32 were negative. Of those 32, 5 were significant at the 0.05 level. There are a few details worth noting about the pattern of correlations. Those where Station P leads CalCOFI tend to be stronger than the converse set, particularly for the winter and spring seasons. If we focus only on the spring months, which is the time when these ecosystems are most likely to respond to variations in the north-south diversion from winter Aleutian Low intensity (figure 13), there is indication of a strong, lag-0 inverse relationship between Station P and offshore CalCOFI ($r = -0.62$; $n = 16$; $p = 0.011$). This relationship remains strong even after the weak autocorrelation in the California Current data is removed ($r = -0.58$).

COMPARISON TO ENVIRONMENTAL VARIABLES

In order to examine variability of surface flow into the Gulf of Alaska, we started OSCURS model runs at Station P on December 1 and ran them for 3 months

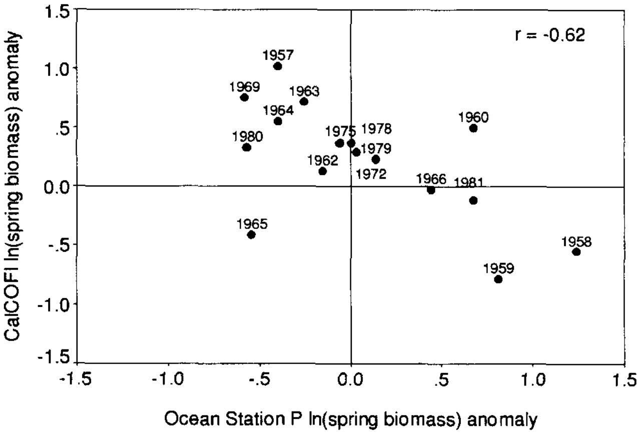


Figure 13. Relationship between Station P and offshore CalCOFI biomass anomalies for the spring quarter (March–May) by year.

TABLE 2

Cross-Region Lag-Correlation Matrices of Ocean Station P and Offshore CalCOFI Seasonal Biomass Time Series: Cross-Region Correlations Are Shown up to 4 Seasons Later

Ocean Station P leads CalCOFI	C winter	C spring	C summer	C fall	C winter+1[a]	C spring+1	C summer+1	C fall+1
P winter	−0.205	−0.315	−0.343	−0.039	−0.182			
P spring		$\underline{-0.615}$	−0.397	−0.463	−0.218	−0.172		
P summer			−0.342	$\underline{-0.506}$	−0.269	−0.055	0.256	
P fall				−0.009	−0.210	−0.376	$\underline{-0.617}$	−0.062
CalCOFI leads Ocean Station P	**P winter**	**P spring**	**P summer**	**P fall**	**P winter+1**	**P spring+1**	**P summer+1**	**P fall+1**
C winter	−0.205	−0.263	0.121	−0.011	−0.018			
C spring		$\underline{-0.615}$	−0.309	−0.026	−0.004	−0.217		
C summer			−0.342	−0.123	−0.322	$\underline{-0.571}$	−0.412	
C fall				−0.009	−0.112	$\underline{-0.610}$	−0.068	0.328

[a] "+1" indicates a season in the following calendar year.

Underlined values are significant at the 0.05 level. The cross-correlations with no lag are repeated in each section of the table for consistency (first diagonal row).

for all years from 1946 to 1994. A substantial divergence of the tracks occurred in the eastern part of the gulf, with some tracks going north into the Alaska Current and others heading into shore or turning south. When the tracks are partitioned into pre-1975 and 1975 and later, some decadal changes become evident (figure 14). In the earlier period, flow into the Alaska Current was more relaxed, and a substantial number of the trajectories veered southward. The later period appeared to show stronger flow into the Gulf of Alaska, and relatively few trajectories went south. The occurrence of either northward or southward flow tends to run in series of various lengths (table 3). Simulations started 5° south of Station P (45°N, 145°W) showed more directed eastward and southward flow but again showed some differences between the two time periods (figure 15).

The model was then used to simulate the north-south divergence of the Subarctic Current along its eastern boundary for equivalent 5-year time periods before and after the regime shift (1971–75 vs. 1976–80) in order to assess changes in circulation between the two regimes. Long-term mean flow tracks begun in January along 145°W showed a more southern diversion before the regime shift than after, with the primary differences in the trajectories starting at or north of 48°N (track 5 in figure 16).

DISCUSSION

For oceanic waters of the eastern subarctic Pacific Ocean, direct evidence for interannual and decadal variations in biological production—that is, phytoplankton production—is weak. However, zooplankton standing stock, when viewed on a basinwide scale, has varied and seems to be higher since the 1976–77 regime shift. Recognizing that primary production might not have changed between the regimes, Brodeur and Ware (1992) hypothesized a causal link between increased wind stress and increased zooplankton stock and production, in that intensified wind mixing would result in deeper mixed-layer depths (MLD) in winter. This would slow the growth rate of the phytoplankton, retard the spring increase in primary production, and allow grazers to make more efficient use of phytoplankton production. Experiments with an ecosystem model (Frost 1993) do not provide support for such a mechanism. Indeed, just the opposite effect should occur. A deeper mixed layer in winter should result in decreased balance between phytoplankton growth and grazing in spring, when the surface layer restratifies. Phytoplankton production should be less efficiently utilized by grazers, and more production should be lost to mixing and sinking below the surface layer.

TABLE 3
Yearly Anomalies of Simulated OSCURS Trajectories from Ocean Station P North or South of the Long-Term Mean Trajectory, in Three-Month (Dec.–Feb.) Trajectories for 1946 to 1994

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But, in fact, there is not much interannual variation in MLD at Station P because of the halocline, and over the observed interannual range of winter MLD (80–130 m), Frost's (1993) model suggests that such variations would have relatively little effect on biological production or zooplankton biomass at Station P (Frost, unpubl. data). Using a 1-D dynamic mixed-layer model (modified Garwood model) coupled to a nitrate-phytoplankton-zooplankton (NPZ) model, McClain et al. (1996) found surprisingly little interannual variation in phytoplankton production rate at Station P.

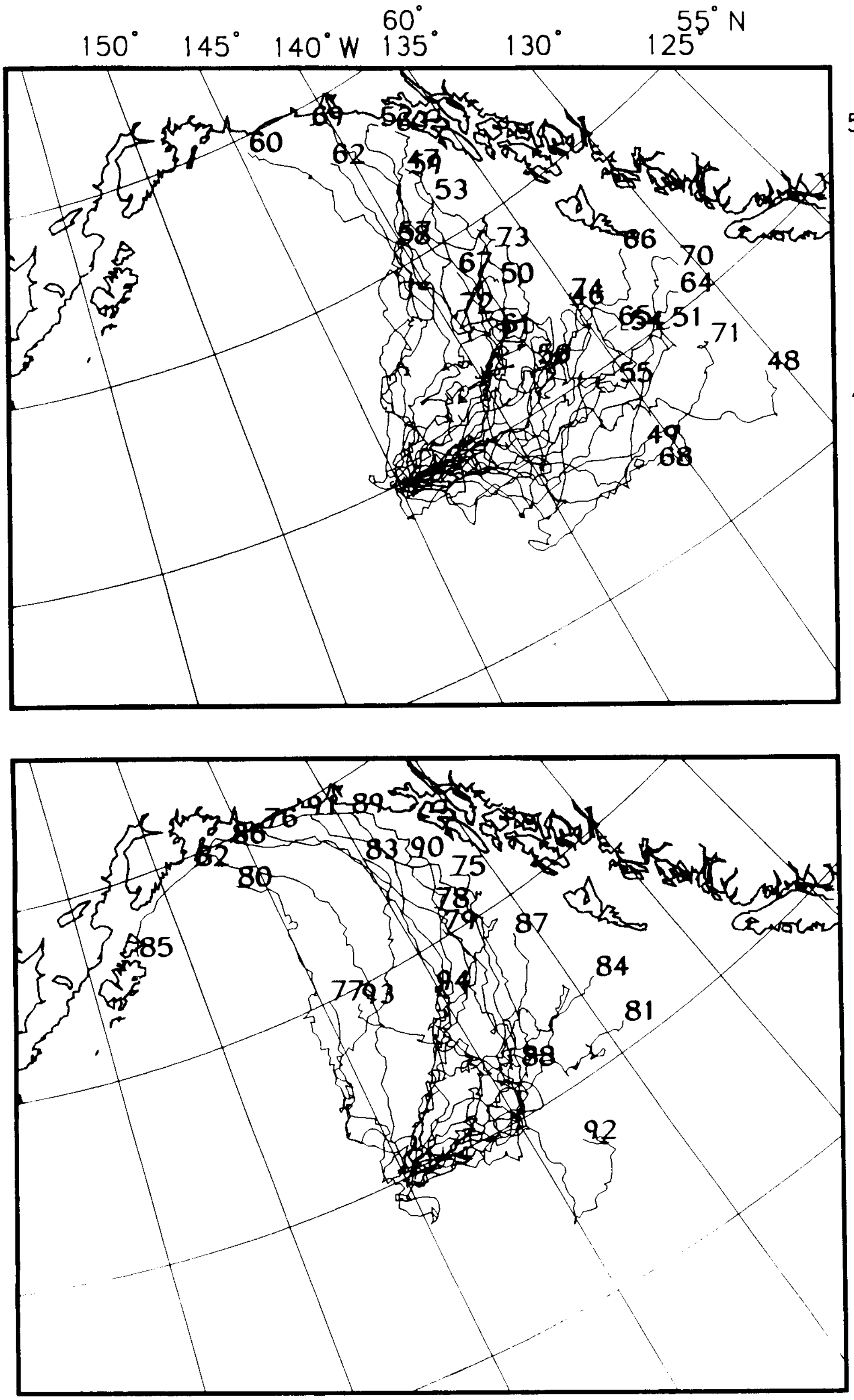

Figure 14. Simulated flow trajectories for the OSCURS model runs from 1946 to 1974 (*top*) and 1975 to 1994 (*bottom*). Each trajectory was started at Station P (50°N, 145°W) on December 1 and run for 3 months, incrementing the positions daily. Each year is marked at the endpoint of its trajectory.

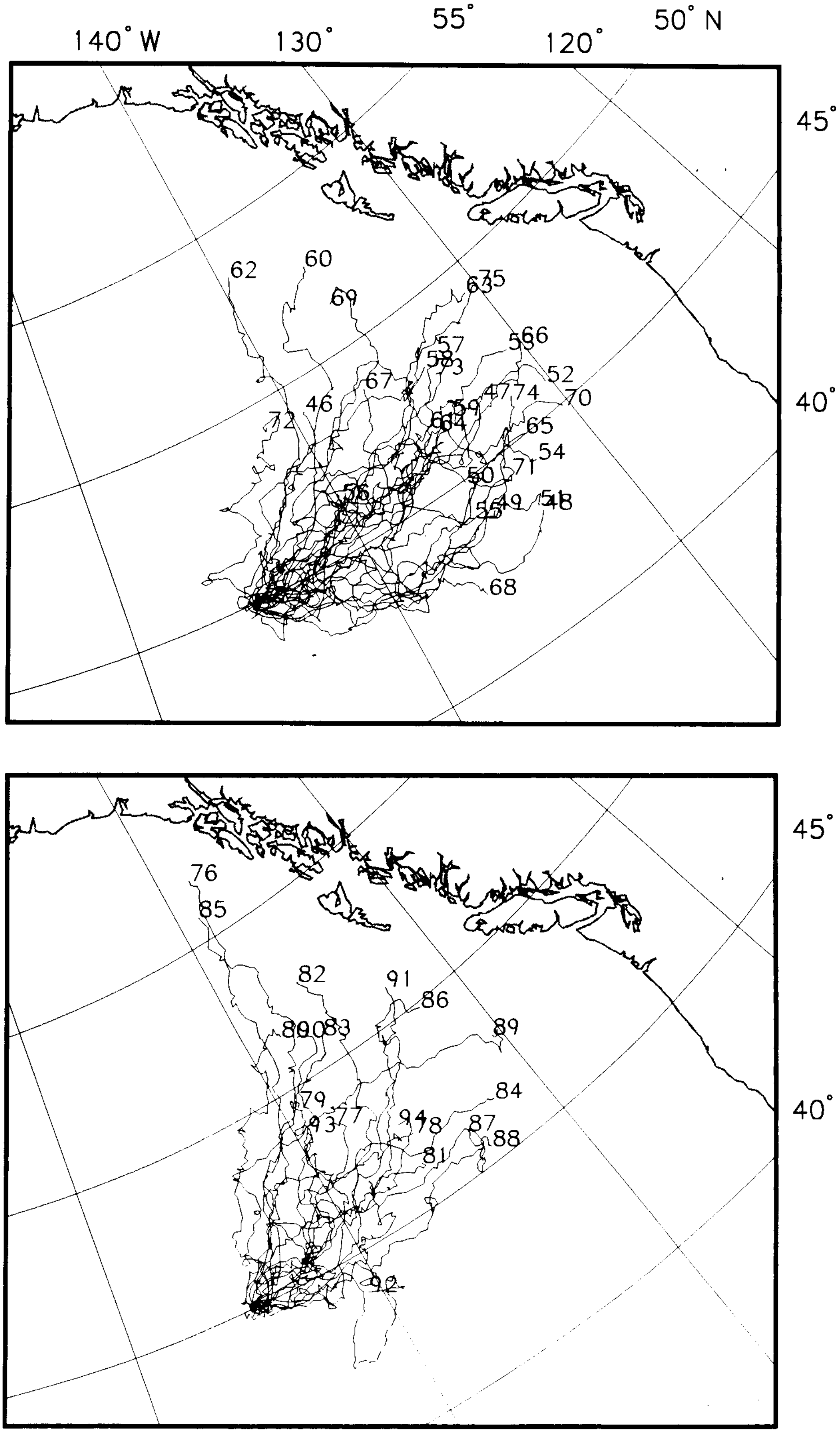

Figure 15. Same as figure 14 but with the simulations started 5° south of Station P (45°N, 145°W).

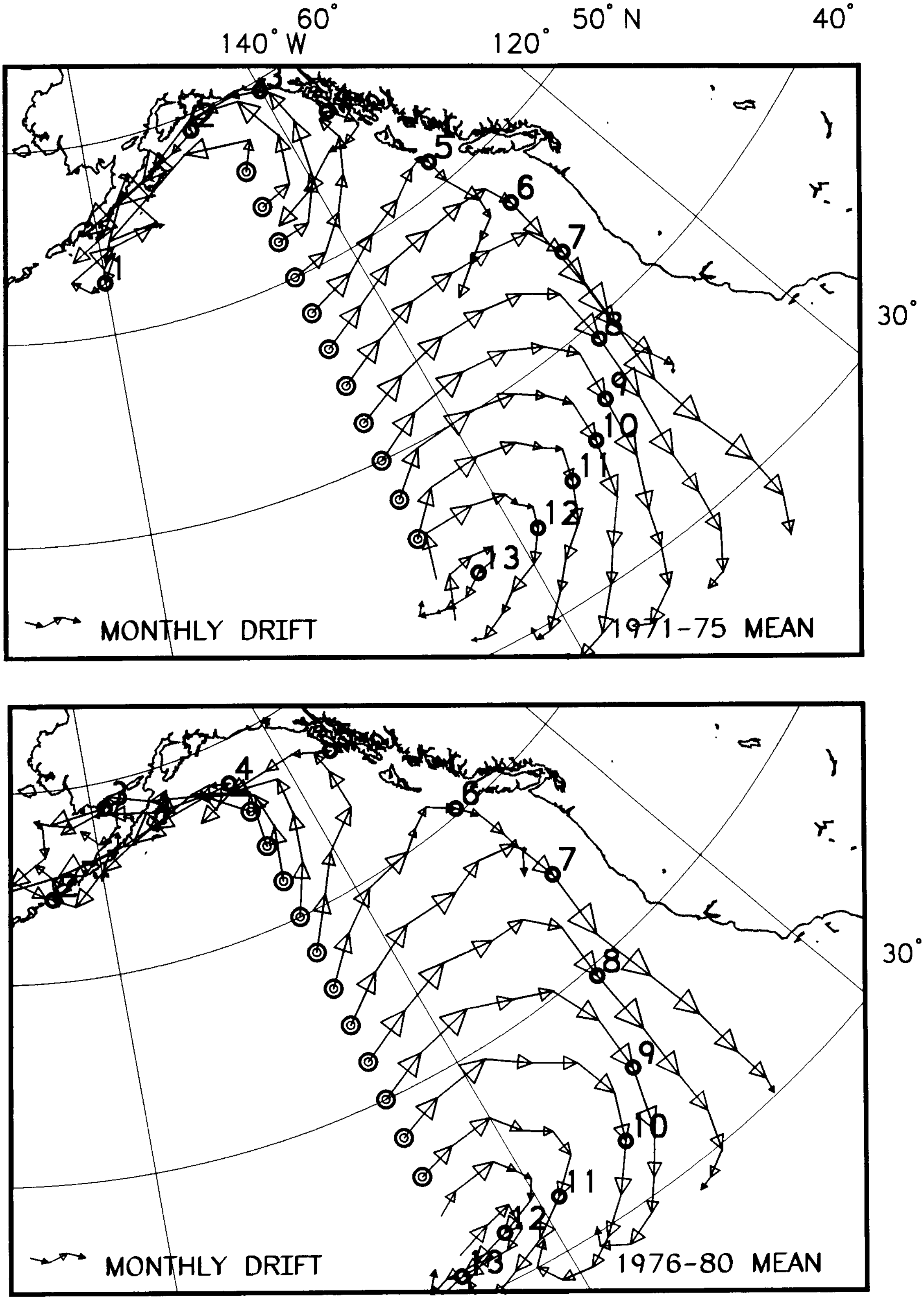

Figure 16. Mean simulated flow trajectories for OSCURS model runs for the 5-year period before (*upper*) and after (*lower*) the regime shift. Model runs were started at 145°W on January 1 and run for 12 months. The size of the arrow head and the length of the shaft indicate the relative current speed. Each trajectory is marked with a circle after 6 months.

It is likely that events at Station P are not generally representative of the entire open Gulf of Alaska, due both to the singularity of the station and its location. Polovina et al. (1995) reported on interannual changes in winter-spring mixed-layer depth throughout the North Pacific Ocean. There was considerable spatial variation in change in MLD, with the region of Station P showing little long-term change but other areas showing rather large changes (e.g., the northeast Gulf of Alaska). Polovina et al. (1995) used an NPZ model to look at the effects of their modeled changes in MLD. The model predicts that large changes in MLD will have little effect on phytoplankton stock, but potentially large effects on phytoplankton production rate and zooplankton stock in the mixed layer. Thus, spatial variation in the processes controlling production rate may explain the apparent increase in zooplankton stock evident on a large spatial scale in the eastern subarctic Pacific Ocean during the 1980s. This hypothesis is difficult to test because there are no basinwide data on nutrient concentrations and biological observations.

To our knowledge, there is no extensive time series of phytoplankton standing stock for the California Current region comparable to the data set from Station P. However, the analysis by Fargion et al. (1993) of Coastal Zone Color Scanner data and in situ chlorophyll measurements indicates little seasonal variation in phytoplankton stock in the offshore area represented by the zooplankton data presented here (30° to 35°N). Moreover, phytoplankton pigment concentrations are similar to those at Station P (cf. Chavez 1995). Because the California Current region covered by the zooplankton data is at considerably lower latitude than Station P, it is probable that higher phytoplankton production accounts for the higher zooplankton standing stock observed (figure 7).

Two factors hinder definitive identification of a lead/lag or "out-of-phase" relationship between zooplankton productivity at Station P and the CalCOFI region. First, as noted earlier, there is a great deal of missing data in both regions. Secondly, the high observed autocorrelation, the robust estimation of which is also hindered by data gaps, needs to be removed. Despite these difficulties, there is evidence that the two regions are negatively related. It is less clear whether there is a consistent lag time between the two regions. The evidence points more toward anomalies at Station P leading anomalies at CalCOFI. It is possible that the inverse relationship is due to differential (i.e., inverse) flow from the Subarctic Current, but that the flow speed within each regime is highly variable, hence the lack of a consistent lag relationship.

El Niño–Southern Oscillation (ENSO) events are another factor that may play a role in the timing and intensity of anomalous zooplankton production. During ENSO events, positive SST anomalies are propagated poleward in the form of coastally trapped Kelvin waves. Roemmich and McGowan (1995a, b) attributed the decline in CalCOFI region zooplankton biomass to sea-surface warming, part of which resulted from a large number of ENSO events since the mid-1970s. While sea-surface temperature anomalies associated with ENSO events have occurred in the Gulf of Alaska (Wooster and Fluharty 1985), as often as not, there has not been any North Pacific Ocean response (Freeland 1990; Bailey et al. 1995). Thus, depending on the magnitude and northward extent of the ENSO event and the Station P zooplankton response to surface warming, there is the potential for a Station P response to lag a CalCOFI response. At the very least, the ENSO factor serves to cloud the relative effects on zooplankton productivity from variations in the Subarctic Current.

It may not be coincidental that the increase in zooplankton shown here in the Subarctic Pacific is opposite to the trend for California Current zooplankton reported by Roemmich and McGowan (1995a, b). Although there is some indirect biological evidence for the ocean-circulation model proposed by Hollowed and Wooster (1992), the hydrographic evidence is more limited. However, several recent papers shed some light on the issue and suggest considerable modification to the model. Tabata (1991), in reexamining the Chelton and Davis (1982) premise, found a correlation between the coastal component of the Alaska Current and California coastal sea levels, particularly during El Niño years. He attributed this correlation, however, to the coastal currents being in phase from Canada to California rather than to changes in the bifurcation of the Subarctic Current. Kelly et al. (1993) analyzed sea-surface height anomalies for the Northeast Pacific Ocean over a 2.5-year period. Their results tended to support those of Chelton and Davis (1982) that the California and Alaska Current systems fluctuate "out of phase," coinciding with variations in wind-stress curl in the North Pacific Ocean and subsequent diversion of flow from the Alaska Gyre into the California Current, as well as with some correlation with ENSO dynamics. Van Scoy and Druffel (1993), in an analysis of tritium (^{3}H) concentrations in seawater from Ocean Station P and a station in the southern California Current, suggest that there is increased advection of subpolar water into the California Current during non–El Niño years and that ventilation of the Alaska Gyre (intensification) occurs during El Niño years.

Lagerloef (1995), in his analysis of dynamic topography in the Alaska Gyre during 1968–90, suggested that after the well-documented climatic regime shift of the late 1970s, the Alaska Gyre was centered more to the east and that its circulation appeared weaker after the shift than before. The implication is that the intensification of the winter Aleutian Low associated with the regime shift did not result in a spin-up of the Alaska Gyre.

Finally, Miller (1996) reviews some recent advances in large-scale modeling of the California Current and its interaction with basin-scale circulation and forcing. He reports the significant deepening of the thermocline off California after the 1976–77 regime shift similar to that described by Roemmich and McGowan (1995a) and attributes this to basin-scale changes in wind stress curl. This is achieved at two time scales—the first at the decadal and North Pacific Gyre scale, forced by significant deepening and weakening of the Aleutian Low, and the second at the interannual ENSO scale, forced by waves propagating through the ocean from the tropics. Miller (1996) also reported that after the 1976–77 regime shift there appeared to be a stronger than normal northward flow into the central Gulf of Alaska but little change in the flow into the California Current system.

If zooplankton biomass is advected preferentially to either region, as the current-simulation model suggests, then this allochthonous biomass should be higher than that produced locally for our results to be valid. There are few comparable measurements of zooplankton biomass in both the Transition Domain and Subarctic Domain. Our data for the large-scale sampling during the 1980s suggest that levels were high in the Transition Domain and are somewhat higher than in the central part of the Alaska Gyre. Data taken in summer for several years from north-south transects in the western subarctic (155°E, 170°E, 175.5°E, and 180°E) show elevated zooplankton wet weights in the transition zone compared with those in the subarctic (Shiga et al. 1995). Sampling along 180° and in the Gulf of Alaska during June and July of 1987 revealed higher zooplankton biomass in transition zone waters than in the central Subarctic Domain, especially in the 150–300-m depth strata (Kawamura 1988).

An alternative explanation for the inverse relationship in zooplankton might be that similar large-scale changes in thermal structure of the western North Pacific (Venrick et al. 1987; Royer 1989; Roemmich and McGowan 1995a; Miller 1996) could have radically different effects on biological production in the two regions. At Station P, the slightly warmer temperature of the mixed layer could directly affect increased zooplankton production rate and standing stock, as suggested by Conversi and Hameed (1996). The same warming and associated deepening of the upper mixed layer (Miller 1996) could cause decreased zooplankton production and standing stock in the California Current region by impeding the supply of nutrients to the surface layer (Roemmich and McGowan 1995a). Our data are not sufficient to allow examination of this alternate hypothesis.

IMPLICATIONS FOR HIGHER TROPHIC LEVELS

The dramatic increase and change in distribution of mesozooplankton biomass seen in the subarctic Pacific Ocean between the periods 1956–62 and 1980–89 would be expected to have important ramifications for higher trophic levels dependent on these food sources. Brodeur and Ware (1995) documented substantial increases in the catch rates of most pelagic nekton (fishes, squids, and elasmobranchs) caught in research gill nets over roughly the same time periods. The only species that showed a decline in catch rates (jack mackerel, *Trachurus symmetricus*) is primarily a California Current species which migrates into the Gulf of Alaska only during periods of peak abundance. Although these authors were not able to convert catch rates to abundance or biomass because of the paucity of collaborative time series of abundances for the noncommercial species, Brodeur and Ware (1995) estimated that total salmon abundance nearly doubled between these two periods.

For the present study, we combined catch data of the 14 species examined by Brodeur and Ware (1995) and plotted nekton catch-rate distributions for roughly the same two time periods over the same geographic range examined previously for zooplankton. Although there are differences between them, the nekton distribution plots (figure 17) showed some similarities to the zooplankton distribution in that most concentrations are offshore in the Alaska Gyre during the 1950s and occur in a band around the outside of the gyre in the 1980s. The magnitude of the increase in catch rate (figure 17 inset) is also similar to that of the plankton. Although this is not cogent evidence of a strong link between these trophic levels, since there is often an additional trophic level (macrozooplankton and micronekton) between the mesozooplankton and the larger nekton, there is enough commonality in the distribution patterns to suggest that the distribution and abundance of zooplankton is positively related to that of higher-level predators.

Coastal fishes in the Gulf of Alaska would be expected to benefit most from the increase in zooplankton biomass that we observed during the 1980s. High rates of upwelling in the center of the Alaska Gyre would push nutrients and subsequent phytoplankton and zooplankton production onto the shelf along the edge of the gulf, thereby stimulating coastal production. Cooney (1986) has suggested that large oceanic species of copepods (*Neocalanus* spp. and *Eucalanus bungii*) are transported onto the shelf in the northern Gulf of Alaska, providing rich food resources for the coastal community. A direct link between atmospheric circulation, oceanic copepod production, and sablefish (*Anoplopoma fimbria*) recruitment has been hypothesized by McFarlane and Beamish (1992), but such mechanisms have not been explored for other demersal fishes.

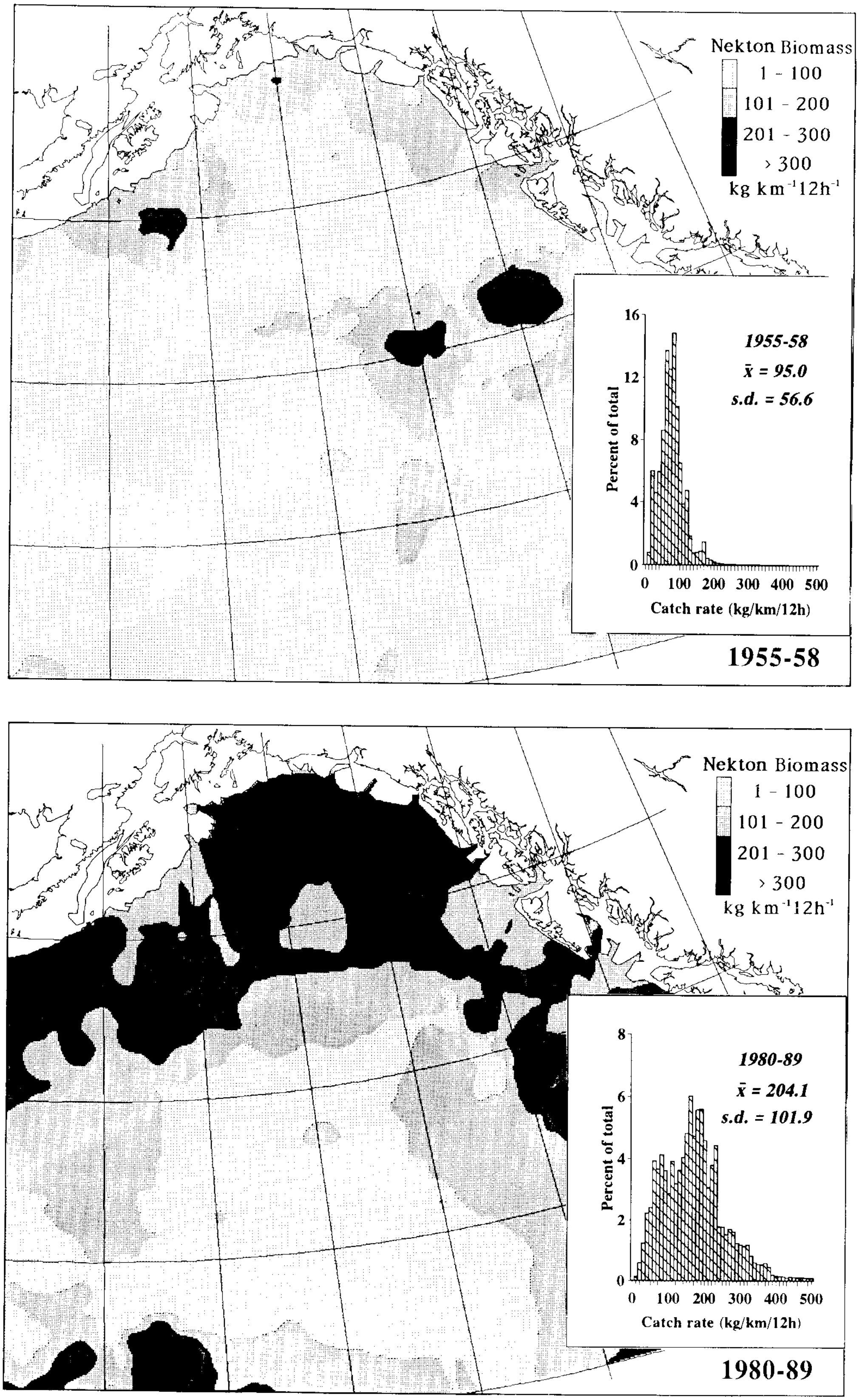

Figure 17. Large-scale catch-rate distribution for 14 species of nekton commonly caught in research gill nets during the periods indicated. See Brodeur and Ware (1995) for sampling methodology, locations of sampling stations, and species included. Insets show nekton biomass pixel distributions as a percentage of the total number of pixels for each time period. The overall mean and standard deviation of biomass for the time periods are given.

For an investigation of ocean effects on fish species, Pacific salmon are an attractive group to study, since they have a relatively short life span, show substantial interannual variability in marine survival, and can be reliably censused at least several times during their life history. As discussed previously, Pacific salmon stocks have substantially increased in abundance since the mid-1970s in Alaska waters, whereas southern stocks have shown opposite trends (Pearcy 1992; Beamish 1994; Hare and Francis 1995). In some cases, the inverse relation between stocks in the two domains is striking (Francis and Sibley 1991). Our analyses suggest that zooplankton biomass in the subarctic region is inversely related to that in the California Current region. A combination of increased transport into the Alaska Current and advection of nutrients and zooplankton onto the shelf would probably increase the carrying capacity for juvenile salmon entering Alaska coastal waters (Cooney 1984).

By studying time lags between atmosphere/ocean and salmon statistics, Francis and Hare (1994) indicated that this regime-scale effect on Alaska salmon production is most likely to be felt during the early ocean life history. If salmonid production and survival are limited by factors occurring early in their marine life history, then the relative flow into the California Current and Alaska Current may profoundly affect their dynamics by enhancing prey production for smolts in the coastal zone. However, the increasing number of salmon surviving to maturation in the open ocean after the regime shift may have imposed an excess burden upon the oceanic zooplankton, which did not appear to increase as dramatically as those in the coastal zone (figure 10). It is likely that the amount of zooplankton available per individual salmon has decreased over this period, as suggested by Peterman (1987), which may be manifested in the long-term decreases in size at age and the older age of maturity witnessed in several salmon stocks (Ishida et al. 1993; Helle and Hoffman 1995).

SUGGESTIONS FOR FURTHER STUDY

1. Examine taxonomic composition of zooplankton over time to see if shifts in species composition have occurred along with the decadal-scale biomass shifts. This objective has been facilitated by the entry of the entire Station P detailed zooplankton data set in digital format that may be amenable to analyses (Waddell and McKinnel 1995).
2. Construct more spatially-explicit coupled physical and NPZ models to account for geographic variability in ocean conditions, nutrient input, and phytoplankton and zooplankton species composition (e.g., as in McGillicuddy et al. 1995).
3. Use models to examine potential top-down control on phytoplankton and zooplankton populations, extending—if possible—some of the presently available models (e.g., Frost 1993) to include nekton.
4. Establish new oceanic sampling sites for comparison with Station P to see whether processes occurring at Station P are representative of the subarctic region as a whole.
5. Continue any present time series sampling, and—if possible—revive discontinued sampling. It is imperative that the methodology does not change substantially during any time series. If it becomes necessary to make changes, then at least a sufficient number of intercalibration studies between old and new methodologies should be conducted to provide a seamless time series.
6. Examine factors that control the production of phytoplankton in the open subarctic Pacific. A major uncertainty concerns the rate of supply of iron, which may stimulate the growth rate of large phytoplankton species, enhance the growth rate of large zooplankton, and produce favorable feeding and growth conditions for pelagic fish.

ACKNOWLEDGMENTS

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PATTERNS OF LOW-FREQUENCY VARIABILITY IN FISH POPULATIONS OF THE CALIFORNIA CURRENT

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ABSTRACT

Long-term data sets include sedimentary fish-scale paleochronologies, faunal surveys from the 1800s, and the records of game fish catches maintained by the Tuna Club at Avalon since 1898. These data suggest a mode of low-frequency biological variability over a cycle of 50 to 70 years that is associated with alternation of warm and cold physical regimes. The very warm conditions in the northeastern Pacific Ocean since 1976 seem similar to conditions experienced from about 1850 to 1870. Coastal pelagic fish abundances since 1930 indicate an orderly sequence of four or five dominant species through these cycles that is very similar to the order and timing of fluctuations in catches of similar pelagic fishes in Japanese waters. The consistency and predictability of this rotation and the biological relationship to low-frequency fluctuations in physical conditions are important areas for further research. These patterns of low-frequency variability result in boom-and-bust fisheries, and pose serious problems for "sustainable development."

INTRODUCTION

With recognition of the worldwide decline in fish stocks, the guideline of "sustainable development" is receiving international support as an explicit goal of fishery and ecosystem management. Ironically, this comes at a time when the biological basis of sustainability in some of the world's major fisheries is itself being questioned because of natural patterns of variability (e.g., Lluch-Belda et al. 1989; Beamish 1995). In a broader context, the science of ecology is moving away from static and equilibrium views of ecosystems. Rather, scientists are coming to perceive ecosystems as pulsing and fluctuating entities, driven by external sources of variability and by internal nonlinear dynamics. Odum et al. (1995) state the possibility that "what is sustainable in ecosystems, is a repeating oscillation that is often poised on the edge of chaos."

At the 1973 CalCOFI Symposium, John Isaacs (1976) took issue with the common implicit assumption in fisheries science that there is "some steady state . . . around which there is a normal distribution of perturbations." He continued,

> This certainly does not seem to be the case. The assumption is that there are some normal statistics to all kinds of conditions. Rather, there are probably a great number of possible regimes and abrupt discontinuities connecting them, flip-flops from one regime to another; multifarious regimes involving biology or climate, or oceanography, or migrations, temperature, or weather, or combinations of these . . . . My main point is that there are no simple statistics in the ordinary sense. There are internal, interactive episodes locked into persistence, and one is entirely fooled if one takes one of these short intervals of a decade or so and decides there is some sort of simple probability associated with it . . . . organisms must respond to more than just fluctuations around some optimum condition. Actually, many of their characteristics and fluctuations of populations must be related to these very large alternations of conditions.

Isaacs coined the term *regime* to describe distinct environmental or climatic states, and *regime shift* has recently gained acceptance as a term for the abrupt transitions between regimes. It is notable that publication of Isaacs' regime concept in 1976 itself coincided with a profound regime shift in the northeastern Pacific. That shift was not apparent at the time, and it required another decade for the oceanic warming (figure 1) to be recognized as a new and persistent condition (MacCall and Prager 1988; Trenberth 1990).

In this paper I examine variability in southern California

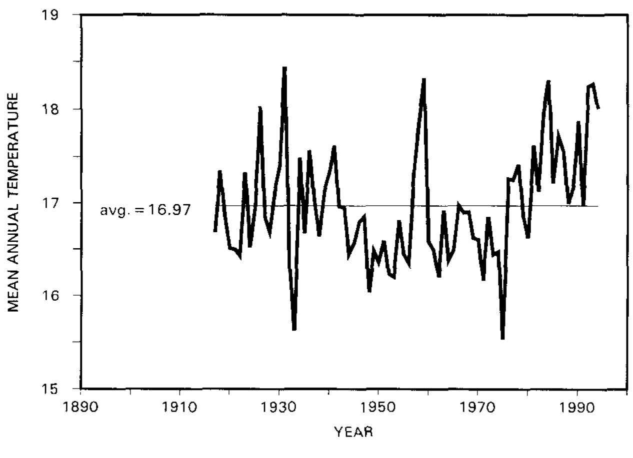

Figure 1. Mean annual temperatures (°C) at the Scripps Institution of Oceanography Pier, La Jolla, California.

fish populations over the longest time scales supported by the qualitative and quantitative information available. Even the quantitative time series are much too short for rigorous statistical analysis. My approach to these data is that of "historical science" (Gould 1989; Francis and Hare 1994); consequently, some of my interpretations are speculative.

Perhaps because fish are an important commodity, better long-term records exist for fishes than for any other biological component of the California Current System. Paleochronologies of fish debris preserved in anaerobic sediments provide invaluable information on prehistoric fluctuations and very-low-frequency variability. The earliest historical records indicative of fish abundance in the California Current are relatively qualitative and begin with the Pacific Railroad Survey of 1856. Quantitative big game fishing records have been maintained since the turn of the century by the Tuna Club at Avalon, on Santa Catalina Island. Although Tuna Club data have seen little use in scientific contexts, these records constitute the longest quantitative and unbroken series of biological observations in this region. The State of California began keeping systematic records of fish landings in 1916, and began comprehensive biological sampling of coastal pelagic fish landings in the 1930s. Good information on ichthyoplankton exists for much of the last 50 years due to the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and other fishery and oceanographic programs that were initiated following World War II.

For the purpose of this paper, I use ocean temperature as a simple proxy for the more complicated and poorly understood suite of oceanographic variables that influences biological populations. Sea-surface temperatures have been monitored continuously at the Scripps Institution of Oceanography Pier (Scripps Pier) in La Jolla, beginning in 1916 (figure 1), forming one of the longest time series of sea-surface temperatures on the Pacific coast. Earlier observations of sea-surface temperature from ships-of-opportunity are provided by the COADS data set (Mendelssohn and Roy 1996), but there are insufficient observations from southern California waters before 1920 to provide annual resolution of temperature fluctuations (R. Parrish, PFEG, NMFS, Pacific Grove, CA, pers. comm. 9/13/95). However, Parrish's examination of the post-1920 COADS data did demonstrate that low-frequency temperature fluctuations in southern California do not necessarily parallel temperature fluctuations off central or northern California. Thus, annual average Scripps Pier temperatures may provide a simplified representation of southern California ocean conditions but may not always be a reliable indicator of conditions in adjacent Pacific coastal regions such as central California.

The major warming that began about 1976 is clearly visible in the Scripps Pier temperature record. This event was widespread and occurred over the entire northeastern Pacific Ocean, from Mexico to Alaska (Cole and McLain 1989). However, the geographic extent of earlier temperature regimes and regime shifts is less clear. An earlier regime shift occurred about 1940, beginning a long period of cold temperatures. Consequently the Scripps Pier record consists of three conspicuous temperature regimes: a moderate and highly variable period from the beginning of the time series to about 1940, a cold period from 1940 to 1976, and a warm period since 1976. Ware (1995) describes similar alternations of temperature regimes off British Columbia.

It is not clear how these low-frequency temperature regimes are related to the El Niño/Southern Oscillation. However, brief warm events related to both El Niño and variability in the Aleutian Low (Wooster and Hollowed 1995) are superimposed on these underlying temperature regimes. Major warm events have occurred at a transition (1940), in the midst of a cool period (1958–59), and in the midst of a warm period (1982–83 and 1992–93).

FISH ABUNDANCES

The anaerobic sediments of the Santa Barbara Basin provide a remarkable paleochronology of fish scale-deposition rates (Soutar 1967). Soutar and Isaacs (1974) developed a 160-year time series of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) scale-deposition rates that indicated large natural long-term fluctuations in both of those species. Baumgartner et al. (1992) extended and refined these studies, and developed a paleochronology spanning the last 1,700 years at a temporal resolution of 10 years (figure 2). Power spectra of these long time series show high variability in both sardine and anchovy scale-deposition rates at a period of approximately 60 years, and at longer periods that differ for the two species. Ware's (1995) analysis of a much shorter physical and biological data set also indicated a spectral peak in the range of 50 to 75 years. Neither Baumgartner et al. (1992) nor Ware (1995) was able to identify a physical mechanism associated with this low-frequency variability.

Anecdotal Information

Biological surveys of the Pacific coast began in the mid-1800s, and provide useful indications of presence or absence of species but have poor resolution for the purpose of estimating the timing and duration of environmental regimes. However, in comparison with conditions during most of the twentieth century, some of the early survey information is so peculiar that Hubbs

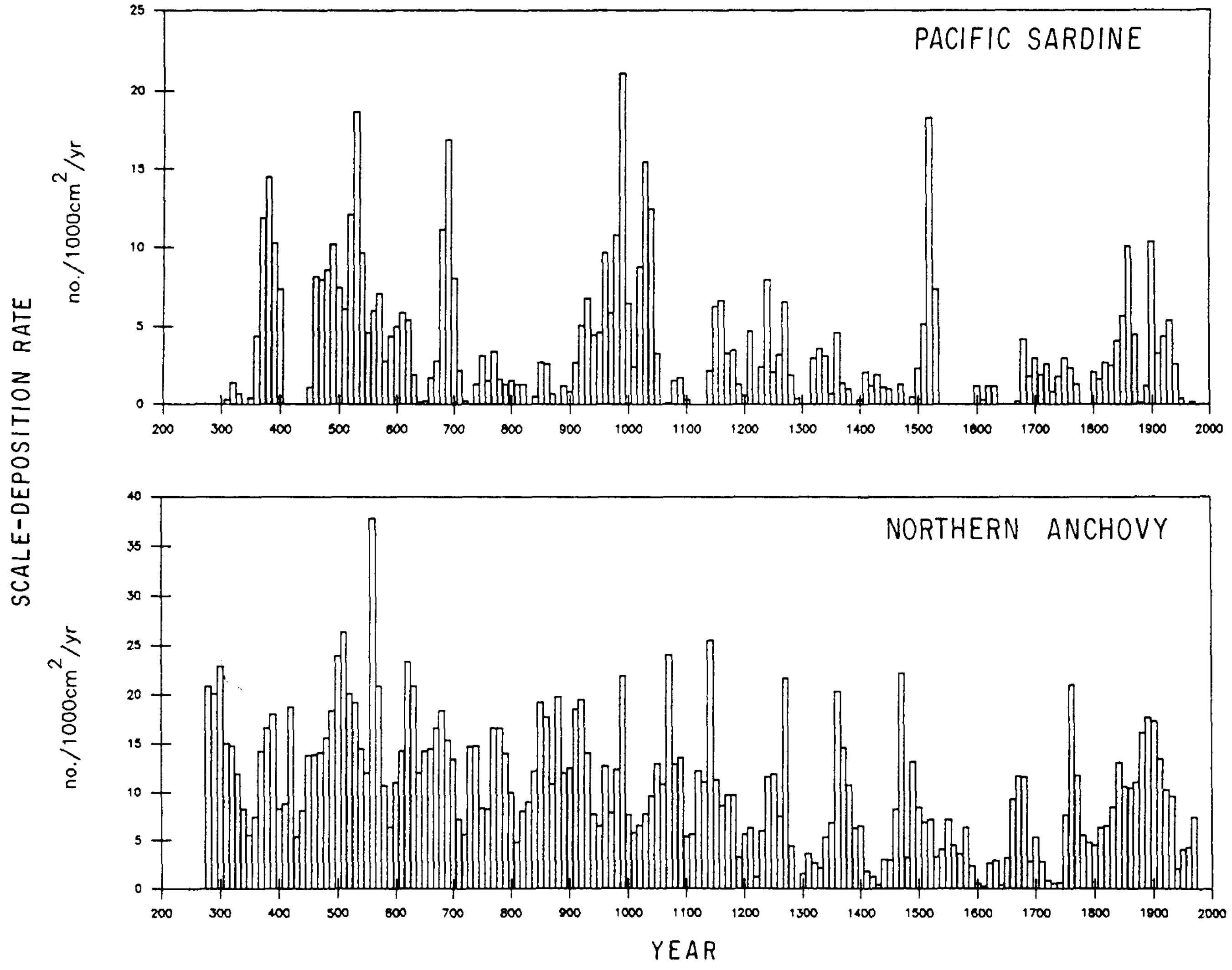

Figure 2. Sardine and anchovy scale-deposition rates in the Santa Barbara Basin (reproduced from Baumgartner et al. 1992).

(1948) was able to infer the existence of an unusually warm ocean climate during the mid 1800s.

According to Hubbs, the Pacific Railroad Survey sampled fish fauna in the San Diego area during the period 1853–57. This superficial survey encountered many "southerly" fish species that no longer occur in southern California. Hubbs reported that when Jordan and Gilbert conducted a thorough sampling of the California coast in about 1880, the fish fauna from Monterey Bay and southern California still had an unusually strong representation of subtropical species. These anomalies led Hubbs to infer that southern California experienced exceptionally warm oceanic conditions from about 1850 to 1870; the beginning and ending dates are imprecise.

In 1857, the Pacific Railroad Survey encountered five specimens of Pacific seahorse (*Hippocampus ingens*) in San Diego Bay (figure 3). This species is normally found much farther to the south and was exceedingly rare in California until a small population reappeared in San Diego Bay about 1984 (Jones et al. 1988). The San Diego Bay population has remained viable over the past decade (R. Burhans, SIO, UCSD, La Jolla, CA, pers. comm. 2/15/96). Hubbs' inference of warm oceanic conditions in the mid-nineteenth century is consistent with reappearance of the Pacific seahorse at San Diego during the warming since 1976.

Tuna Club Records

The Tuna Club was formed at Avalon, Catalina Island, in the summer of 1898, shortly following the discovery of the sport of angling for large ocean game fishes by its founder, Dr. C. F. Holder (Macrate 1948). The club's records, which now span nearly 100 years, document sizes and numbers of several fish species taken in annual tournaments. From 1909 to 1919, a summer tournament was held from May 1 to September 30, and a

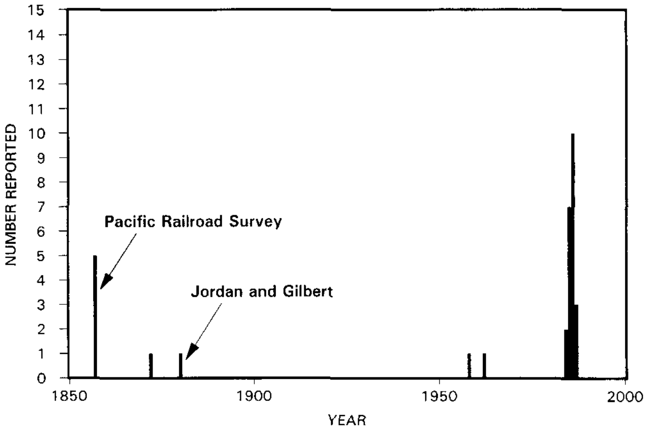

Figure 3. Number of Pacific seahorses reported by various sources (data from Jones et al. 1988).

separate winter tournament was held from October 1 to April 30. From 1920 on, annual tournaments corresponded to calendar years.

The nature of the Tuna Club data differs among groups of fish. Naturally, tunas were of greatest interest, and the club yearbooks provide information on the largest fish caught each year, catch by month, average weight of all fish reported, and date of first catch. Unfortunately the club did not distinguish among several species of large tunas, which include northern bluefin tuna (*Thunnus thynnus*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*). The Tuna Club considered striped marlin (*Tetrapturus audax*) and swordfish (*Xiphias gladius*) to be worthy alternatives to large tuna and kept separate records for those species. Club yearbooks also provide data on the largest fish caught in each annual tournament for a number of "lesser" species, including albacore (*Thunnus alalunga*), white seabass (*Atractoscion nobilis*), yellowtail (*Seriola lalandi*), and giant sea bass (*Stereolepis gigas*).

Tunas were landed in large numbers in many tournaments through the 1920s (figure 4), but were very rare during the extended cold regime from 1940 to 1976. Moderate numbers of tuna reappeared in the annual tournaments following the 1976 warming. The two periods of abundance reflect different species of tuna: pre-1940 catches consisted mainly of northern bluefin tuna, while post-1976 catches have been mostly yellowfin and bigeye tunas. Interpretation is also complicated by the growth of commercial fishing for tunas in southern California during the 1920s (Bayliff 1992; Wild 1992), with consequent declines in abundance and size.

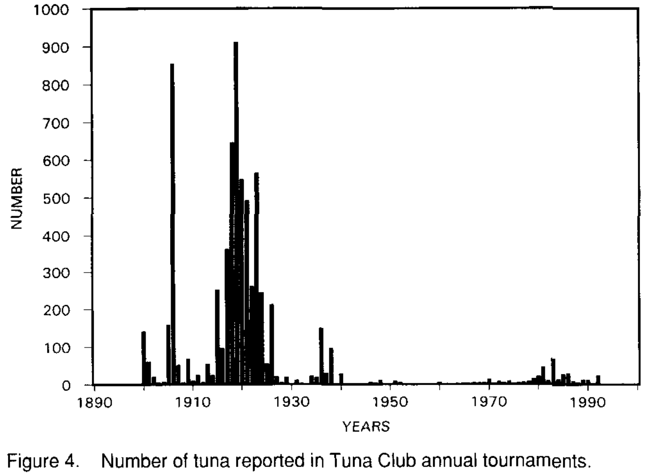

Figure 4. Number of tuna reported in Tuna Club annual tournaments.

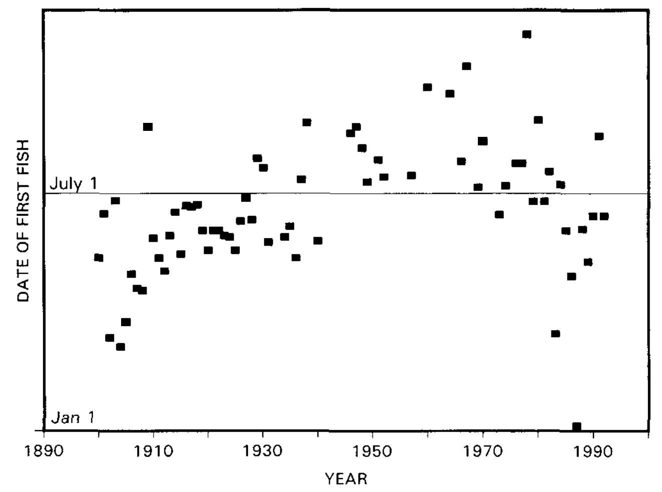

Figure 5. Dates at which first tuna were caught in Tuna Club annual tournaments.

The dates on which the first tuna was taken in the annual tournaments also coincide with the large shifts in Scripps Pier temperatures (figure 5). The post-1976 pattern is similar to that prior to 1940, when the earliest catches were often made in April or May. During the long cold regime, the few tuna that were caught first appeared in July or August. Remarkably, the earliest annual appearance of tuna in club records is March 4, and first appearances were in March of three of the four years 1902–5. Sea-surface temperatures are normally quite cold in March, and immigration of bluefin tuna to southern California would be unlikely at that time of year, suggesting that there may originally have been a small resident population of tuna in southern California. A recent anomaly in figure 5 is a tuna that was caught on January 3, 1987, in waters far to the south of the usual fishing grounds near Catalina Island.

Catches of striped marlin increased sharply in the 1930s, providing an alternative to tuna, which were becoming scarce. Although there is little long-term pattern to annual marlin catches (figure 6), the size of the largest fish dropped conspicuously about 1940. In contrast to many changes associated with the 1940 regime shift, large marlin did not reappear after 1976 (figure 7). And unlike the dates for tuna, the dates of the first marlin caught each year have been virtually constant,

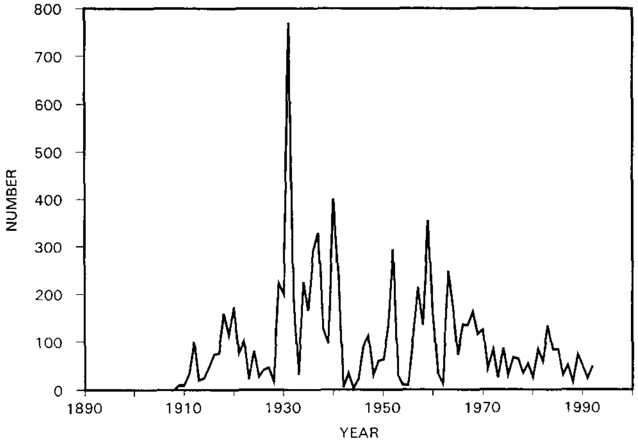

Figure 6. Number of marlin reported in Tuna Club annual tournaments.

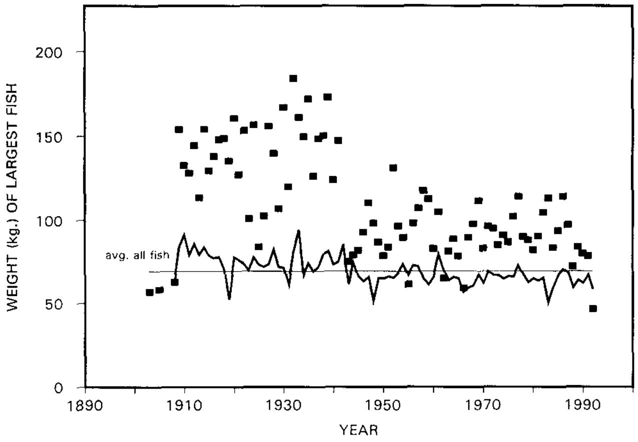

Figure 7. Largest (*points*) and annual average (*solid line*) weight of marlin taken in Tuna Club annual tournaments.

except for one fish caught in southern waters on January 1, 1984 (figure 8). However, marlin appear to be departing southern California waters later in the warm period since the mid-1970s (figure 9).

Tuna Club catches suggest that albacore were abundant in southern California during the first two decades of this century, but catches declined severely in the late 1920s and again declined in the late 1980s, paralleling difficult periods for California's commercial albacore fishery (Laurs and Dotson 1992). From 1910 to 1919, when winter tournament records were kept separately, albacore continued to be caught after October 1, and the largest "winter" fish was consistently larger than the largest "summer" fish (figure 10). This phenomenon cannot have lasted long after the winter tournaments were discontinued, because large albacore disappeared altogether from the annual tournaments shortly after 1920. Large late-season albacore reappeared in southern California waters about 70 years later, and in the mid-

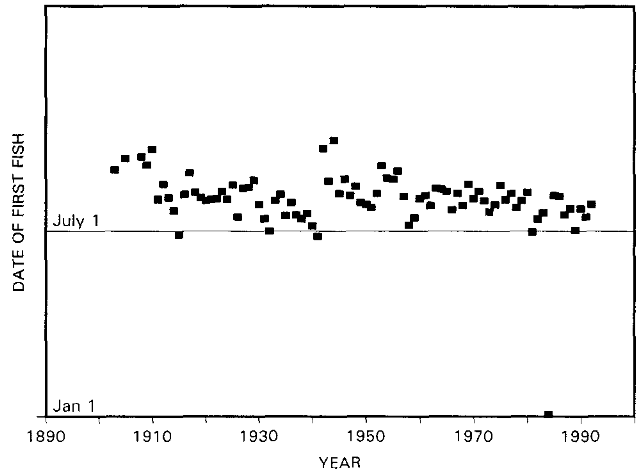

Figure 8. Dates at which first marlin were caught in Tuna Club annual tournaments.

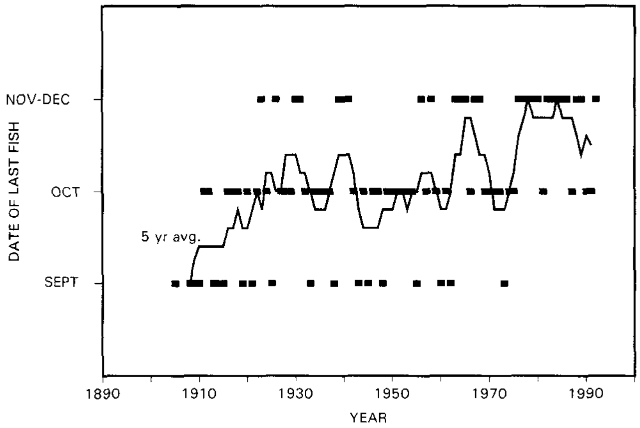

Figure 9. Month in which the last marlin was caught in Tuna Club annual tournaments.

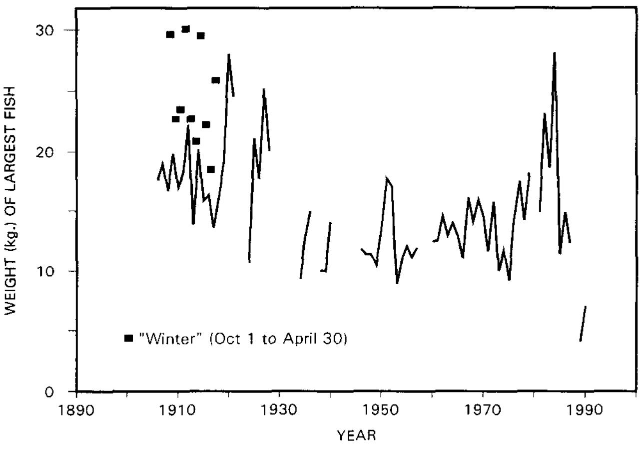

Figure 10. Largest albacore taken in Tuna Club annual tournaments. Winter records were not maintained after 1920.

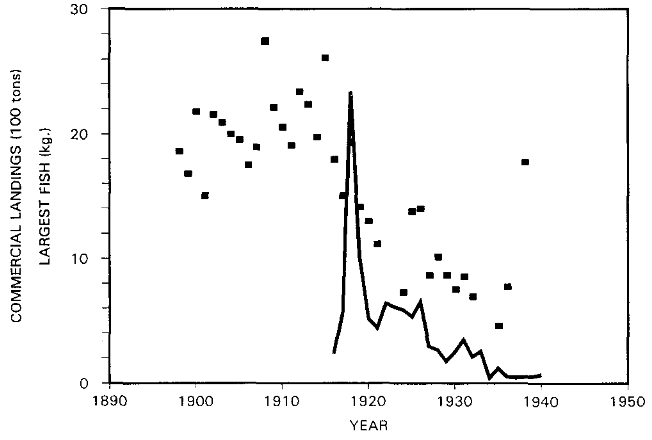

Figure 11. Association of commercial harvesting (*solid line*) with decrease in size of largest yellowtail (*points*) taken annually by Tuna Club members.

1980s once again were encountered very late in the year (T. Foreman, IATTC, La Jolla, pers. comm., 1987). In both the 1920s and 1980s, the appearance of large late-season albacore was followed by a severe decline in southern California catches. The links to climate variability are unclear, and may be related to environmental conditions in distant waters. These albacore fluctuations show a 60-year pattern that seems out of phase with the temperature regimes. An intriguing possibility is that the albacore patterns seen in the 1920s and 1980s consistently lead a regime shift to colder conditions by ten to fifteen years.

Tuna Club records of yellowtail, white seabass, and giant sea bass caught in the annual tournaments do not show clear long-term patterns other than a severe impact from commercial fishing during the period 1916 to 1930. Southern California's giant sea bass were commercially depleted by 1930, after which catches by members of the Tuna Club were rare. For yellowtail, the coincidence of intense commercial harvesting and a decline in size is striking (figure 11). After the 1920s, southern California's catches of these species were maintained by seasonal migration of younger fish from distant waters.

There may have been resident California populations of several species of fish, including bluefin tuna, yellowtail, and giant sea bass. The strongest evidence for a resident population exists for white seabass, which supported continuous harvests in the San Francisco area between 1880 and 1916 (Skogsberg 1939). Ragen (1990)—summarized by Dayton and MacCall (1992)—developed a population model that relates maximum size of fish caught each year to the rate of exploitation, and used the Tuna Club and California commercial catch data to estimate preexploitation abundances of three species. Ragen concluded that initial biomasses of white seabass and yellowtail would have been each about 20,000 tons, and that the initial biomass of giant sea bass was at least 1,300 tons in southern California waters.

Like the Pacific seahorse described earlier, the northern populations of these species are probably established or strengthened during prolonged warm periods, such as occurred during the mid to late 1800s. During cooler regimes, these populations would no longer be self-sustaining, and would slowly decline due to lack of recruitment (cf. Jacobson and MacCall 1995). In the absence of fishing, adults of these species have low mortality rates, and a substantial population could remain resident for decades. However, during cold regimes even a moderate fishery would deplete the population very rapidly.

Small Pelagic Fishes

Patterns and causes of fluctuations in pelagic fish populations of the California Current have long been fundamental issues of study by CalCOFI. Reviews include MacCall (1986) and the Pacific Fishery Management Council (1996). Historical fluctuations in several species of small pelagic fishes are summarized very briefly here.

Scientific monitoring of California's pelagic fish resources began in the 1920s, and useful estimates of sardine landings by age group were provided by the California Division of Fish and Game's Bureau of Commercial Fisheries beginning in 1932. But it wasn't until Murphy (1966) developed a formal technique now known as virtual population analysis (VPA) that consensus could be reached on the detailed historical pattern of sardine population abundance. The Pacific sardine reached a peak abundance in 1934, declined sharply, and recovered to a secondary peak in 1941 before declining to unmeasurably low levels over the following 30 years. The recent sardine recovery was first detected in the early 1980s (Watson 1992; Wolf 1992), and the population has grown steadily since then (Barnes et al. 1992), not yet having shown evidence of a peak in abundance. Jacobson and MacCall (1995) have described a temperature-dependent relationship between recruitment and parental stock for sardines that links the long-term cycle of sardine abundance to the low-frequency variability of sea-surface temperatures.

Pacific mackerel (elsewhere known as chub mackerel, *Scomber japonicus*) experienced two major peaks in abundance, in 1932 and again in 1982 (Parrish and MacCall 1978; MacCall et al. 1985; Pacific Fishery Management Council 1996). The northern anchovy (*Engraulis mordax*) appears to have been at a very low abundance when the CalCOFI ichthyoplankton surveys began in the early 1950s, but increased in the mid-1960s and experienced a brief period of high abundance in the mid-1970s (Methot 1989; Pacific Fishery Management Council 1996). The abundance of northern anchovy is unclear before 1954, but MacCall (1986) interpreted ichthy-

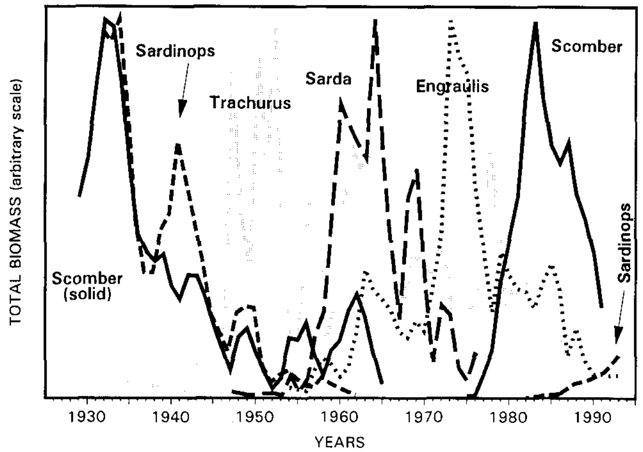

Figure 12. Abundances of major pelagic fishes in southern California, with each species scaled to unit maximum.

oplankton information from 1939–40 as indicating a moderate level of abundance, somewhat higher than was seen during the early 1950s. Pacific bonito (*Sarda chiliensis*) has long been harvested commercially in southern California waters, but recruitment of young-of-the-year was rare before a major increase in southern California abundance that began in the mid-1950s (Collins et al. 1980; MacCall 1986).

Jack mackerel (*Trachurus symmetricus*) abundance has not been monitored, and the history of fishery landings has been strongly influenced by the availability of alternative fishing targets such as sardine, anchovy, and Pacific mackerel. But length distributions reported by MacCall and Stauffer (1983) suggest that there may have been a recruitment pulse in the mid to late 1940s, at about the same time the southern California fishery suddenly increased. The evidence for a large jack mackerel population around 1950 is much weaker than the evidence for other species.

Pelagic fish fluctuations appear to be unpredictable when they are considered individually, but a pattern emerges when the time series of historical abundances of these fishes are viewed simultaneously (figure 12). In order to emphasize the temporal pattern, I have scaled abundances to a unit maximum for each species peak (i.e., where two widely separated peaks occur, each is rescaled separately). Sardine and Pacific mackerel were simultaneously abundant in the early 1930s; unfortunately, pre-1950 information on other species is weak or lacking. In the late 1940s and early 1950s no species appears to have been abundant, with the possible exception of jack mackerel.

Since the 1950s, peak abundances have occurred sequentially at regular intervals of about a decade. Currently, Pacific mackerel is declining in southern California, and Pacific sardine continues to increase. Peak abundances of these pelagic fishes are strongly separated, so that in recent years no two of these species have simultaneously been highly abundant. The sequence of the four well-documented species alternates between piscivores (bonito and Pacific mackerel) and planktivores (anchovy and sardine). An implication of this pattern is that biological interactions may play a substantial role in determining the patterns of peak abundances. Yet the timing of these peaks also appears to be strongly conditional on regime-scale physical fluctuations such as the 1976 transition from cold to warm conditions.

Fishing pressure undoubtedly influences these fluctuations, but its effect is difficult to isolate. In the absence of intense sardine fishing, it is likely that the partial sardine recovery, reaching 2.5 million tons (age 2 and older; Murphy 1966) in 1941, would have produced a much higher abundance, probably exceeding that of 1934 (3.6 million tons). The potential magnitude of the 1941 peak has been estimated quantitatively by MacCall (1979), who simulated historical sardine abundances under alternative fishing pressures. MacCall's simulated 1941 peak was higher than the 1934 peak in scenarios where the simulated fishing intensity was less than about half the actual historical rate. Thus it is reasonable to speculate that a valid sardine peak occurred in 1941, nine years after the Pacific mackerel peak in 1932. Thus the early mackerel-sardine sequence is not necessarily inconsistent with the sequence seen in the 1980s and 1990s, and the coincidence of historical peaks in the early 1930s may have been an artifact of fishery development.

Relationship to the Northeastern Pacific

The southerly portion of the California Current treated in this paper bears a special relationship to the contiguous ecosystems to the north, extending from central California to southwestern Alaska. A large symposium (Beamish 1995) recently addressed climatic effects on fishes in this northern area. Many pelagic fishes (e.g., sardines, Pacific mackerel, jack mackerel, and Pacific whiting, *Merluccius productus*) seem to move to the southern portion of the California Current for reproduction in late winter through early summer. As older adults, these fishes migrate in the summer and fall to northerly waters, especially under conditions of high abundance and warm ocean temperatures. Low-frequency fluctuations in these species are more apparent at the northern and southern ends of the range.

Sardines were abundant off British Columbia in the 1930s, when they supported a substantial fishery (Murphy 1966). Under intense harvesting and a regime shift to colder conditions, they subsequently disappeared from that area for over 40 years. In the 1990s sardines are once again becoming abundant from the Columbia River to British Columbia (Hargreaves et al. 1994).

It is unclear whether *Scomber* was abundant in British Columbia in the 1930s, but in the El Niño events of 1982–83 and 1992–93 it was common enough in the Pacific Northwest to be considered a potentially important predator of young salmon (D. Ware, Pacific Biological Station, DFO, Nanaimo, pers. comm., 1996).

Brodeur and Ware (1995) showed that jack mackerel were abundant in the southern Gulf of Alaska during 1955–58, but were almost entirely absent when the area was resampled in 1980–89.

Salmon (*Oncorhynchus* spp.) in the northeastern Pacific have shown a strong response to regime shifts. Francis and Hare (1994) show that Alaskan salmon catches dropped abruptly with the shift to a cold regime, which they identify as having occurred in 1946, and rose abruptly with the 1976 shift to a warmer regime. Beamish and Bouillon (1995) also examined long-term fluctuations in fish catches from the northeastern Pacific, and found major shifts around 1940 and 1976 for both salmon and nonsalmon species. They conclude that these fluctuations in aggregate catch are closely related to low-frequency fluctuations in the Aleutian Low.

Archaeological evidence shows that giant bluefin tuna have been taken by artisanal fisheries off Vancouver Island and the Queen Charlotte Islands on many occasions during the last 5,000 years (Crockford 1994). Although bluefin tuna have been absent from that area during the twentieth century, Crockford reports an oral account of artisanal harpoon fishing that must have taken place during the decade of the 1880s. The tuna were said to have appeared during brief, exceptionally warm periods in August. Unfortunately, dating of archaeological remains is too imprecise to establish a statistically useful time series, but this pattern is consistent with other evidence of low-frequency variability.

Relationships to Other Ecosystems

Throughout the world, sardine and anchovy stocks exhibit low-frequency fluctuations (Lluch-Belda et al. 1989), many of which appear to be in phase. A remarkable hemispheric coincidence of *Sardinops* spp. fluctuations in Japanese waters and off the west coasts of both North and South America has been described by Kawasaki (1991). In the Peru-Chile system, a large sardine (*Sardinops sagax*) fishery developed following the collapse of the anchoveta (*Engraulis ringens*) fishery in the early 1970s. In the 1990s there is evidence that the sardine resource is declining off Peru and Chile, and that the anchoveta is achieving higher levels of abundance and productivity (R. Parrish, PFEG, Pacific Grove, pers. comm., 1996). Other pelagic fish species in the Peru-Chile system have not been monitored closely enough to discern their relationships to the fluctuations in sardine and anchoveta.

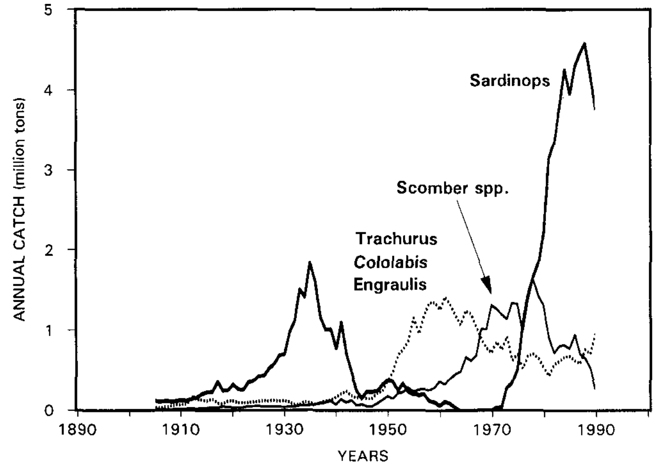

Figure 13. Annual catches of several groups of pelagic fishes in Japanese waters (redrawn from Matsuda et al. 1992).

The waters off Japan have supported harvests of several small pelagic fish species for centuries. Qualitative analysis of historical fish market records kept since 1550 indicates strong low-frequency fluctuations in catches of sardine (*Sardinops melanosticta*), with major peaks occurring every 100 to 120 years (Ito 1961). Reliable pelagic fish catch records exist for most of the twentieth century, but Japanese fishery statistics are maintained separately by many independent agencies, and it is difficult to obtain comprehensive summary statistics. In a study of alternations in pelagic fish abundances off Japan, Matsuda et al. (1991, 1992) proposed a cyclic dominance model (A defeats B, B defeats C, and C defeats A) to explain the temporal pattern of pelagic fish catches off Japan (figure 13). Matsuda et al. identified three pelagic fish groups, consisting of chub mackerels (mostly *Scomber japonicus*), Japanese sardine (*Sardinops melanostictus*), and a mixed-species group composed of anchovy (*Engraulis japonica*), horse mackerels (*Trachurus japonica* and *Decapterus muroadsi*), and Pacific saury (*Cololabis saira*).

There are remarkable similarities between the sequence of pelagic fish species groups in Japanese waters and the sequence of similar groups off California. In both cases, *Sardinops* is followed by *Engraulis*, then by *Scomber japonicus*, and then returns. Matsuda et al. combined *Engraulis* and *Trachurus* into a single group; these two genera may have formed separate peaks in California, but if they were combined, they would occupy the same sequential position as in Japan. The Japanese system does not appear to have an analog of California's Pacific bonito, which intervened between California's tentative *Trachurus* peak and the *Engraulis* peak. In California, sequential peaks in pelagic fish abundance have occurred at near-regular intervals of slightly over a decade (figure 12). In Japan, the peaks in catches of pelagic fish groups are less distinct, but appear to occur at intervals of about

TABLE 1
Dates of Peak Abundance for Similar Pelagic Fishes in Japan and California

Species group	Japan	California
Scomber		1932
Sardinops	1936	1934 (1941?)
Trachurus	combined, 1955–65	late 1940s?
		*Sarda** 1960–64
Engraulis		1973–75
Scomber	1971–78	1983
Sardinops	1988	after 1995

**Sarda* is not present in the Japanese system.

15 years (figure 13); the longer interval may also be related to the smaller number of identified fish groups.

In both systems many pelagic species were at low abundance in the 1940s, following the initial decline of sardine and, in California, immediately following the shift to a cold regime. In the Japanese system, low catches could have been caused by low fishing effort during the post–World War II economic depression. In California actual abundances appear to have been simultaneously low, with the possible exception of *Trachurus*. Future periods of generally low pelagic fish abundance (possibly following a sardine peak or a regime shift) could pose problems for the related industries in both California and Japan.

In California, the peaks in *Scomber* abundance are separated by 51 years (table 1). In Japan, the two peaks in annual harvest of sardines are separated by 52 years. The date of California's second sardine peak has yet to be determined, but the interval will be at least 62 years (i.e., 1934 to 1996 or later). Although the California and Japanese systems appear to have been in synchrony before 1950, a five- to ten-year time lag is now present. If this time lag continues, changes in Japan's pelagic fish populations may presage similar changes in California; if a general predictive relationship exists, the utility of such a predictor would be high, and the phenomenon merits long-term monitoring.

No specific oceanographic or biological mechanisms are known that account for these patterns and phase relationships within and among ecosystems. Caution should also be taken from Baumgartner et al. (1992), who found no consistent phase relationships between anchovy and sardine scale-deposition rates in the southern California paleosedimentary record. However, the timing and sequence of recent species peaks in Japan and California strongly suggest that the mechanisms determining sequences and relative abundance of these species are similar or interrelated.

It is plausible that sharp physical regime shifts, such as from the very cold pre-1976 period to the very warm post-1976 period, would favor distinct sequential changes in dominant pelagic fish species. In contrast, an intermediate and prolonged physical regime (such as pre-1940) could result in less temporal separation of dominant populations, perhaps consistent with the coincidence of high sardine and mackerel biomasses around 1930.

DISCUSSION

Fortunately, the Santa Barbara Basin paleosedimentary record is sufficiently long to establish conclusively that there is low-frequency or interdecadal variability in anchovy and sardine scale-deposition rates (figure 2). Excluding the paleochronologies, even our longest data sets (e.g., Tuna Club records) are inadequate for analysis of very-low-frequency variability, and will remain so for at least another century. Even the 80-year time series of temperatures at Scripps Pier does not yet definitively encompass a complete regime cycle—one more regime shift is still needed.

The most promising approach to extending our time series is to reconstruct conditions between Hubbs' warm period of 1850–70 and the beginning of the Scripps Pier record in 1916. The southern California paleosedimentary record of sardine scales shows a brief but sharp decline in sardine scale-deposition rate around 1890, suggesting very cold temperatures according to the temperature-dependent reproductive model of Jacobson and MacCall (1995). However, Tuna Club records indicate an abundance of warm-water fishes at the turn of the century. If a post-1870 cold period existed, it must have been relatively short (less than 25 years). Alternatively, if there was no distinct cold period in the late 1800s, the pre-1940 moderate temperature regime may have been very long (nearly 70 years).

Although there appears to be a low-frequency warm-cold alternation of physical conditions, this does not necessarily result in only two simple alternative ecological states or regimes. Although the pre-1940 period was warm relative to the subsequent 1940–76 period, it was substantially cooler than the post-1976 warm period The Pacific seahorse population, which presumably was abundant in San Diego Bay during the 1850s, was reestablished there around 1984 (Jones et al. 1988), 127 years after it was first seen by the Pacific Railroad Survey. Notably, a seahorse population was not established in San Diego Bay during the pre-1940 moderate period. As another example, the large marlin recorded regularly by the Tuna Club before 1940 have not reappeared in the post-1976 warm period (figure 7).

Sequences and timing of peak abundances could be modified by interventions by opportunistic species that are not typical elements of the species rotation. The increase of Pacific bonito in southern California during the 1960s may have been such an intervention. Hubbs (1948) reports that surveys conducted at Monterey Bay by Jordan and Gilbert and by others around 1880 encountered remarkable abundances of barracuda (*Sphyraena argentea*), Pacific bonito, and even Spanish mackerel (*Scomberomorus concolor*). In this century, barracuda and bonito have seldom reached Monterey Bay, and catches of *Scomberomorus* have been restricted to southern Baja California.

CONCLUSION

The low-frequency fluctuations of pelagic fish populations in the southern California region are somewhat cyclic, and are related to the alternation of warm and cold temperature regimes on periods of 50 to 70 years. The fluctuations in pelagic fishes are also correlated with fluctuations in other geographical areas such as Peru-Chile and Japan, a phenomenon climatologists call teleconnections. The remarkable similarity of temperate pelagic fish assemblages in these distant areas indicates a larger suite of physical and biological similarities that favor persistence of these particular species types (Bakun and Parrish 1980). Given general physical and biological similarities, we should also expect there to be similarities in the population dynamics of these species and in the interactions among them. From this viewpoint, it is reasonable to hypothesize that the worldwide similarity of fluctuations in sardine and anchovy stocks (Lluch-Belda et al. 1989; Kawasaki 1991) may extend to the full assemblage of major pelagic fishes in those systems. In the near future, the only hope of testing that hypothesis must come from paleochronologies or from long-term data that have already been collected from other comparable ecosystems; within any single system, we otherwise have little hope of gaining further insight during our lifetimes.

It is difficult to resist speculating on what the near future may hold. The present warm regime is now 20 years old, and it has been 56 years since the 1940 shift to a cold regime (figure 1). The appearance of large late-season albacore and the subsequent decline in southern California catches in the mid-1980s resembles events in the mid-1920s that preceded the regime shift by 10 to 15 years. Also, Japanese sardine catches peaked in 1988 and have since declined sharply. If the recent pattern of time lags remains consistent (table 1), we should expect California's peak sardine abundance about a decade later, around 1998. These biological indicators suggest that a transition to a cooler regime is likely in the next decade or so. On the basis of spectral patterns, Ware (1995) has boldly predicted that the transition could occur around the year 2001. Unfortunately, we do not know whether it will be intense or moderate.

Even with the limited understanding provided by historical science, it is clear that the ecosystems and pelagic fish resources of California, Peru-Chile, Japan, and many other ecologically similar locations experience low-frequency variability that is incompatible with a simple interpretation of "sustainable development." However, an analogous principle is vitally needed to guide fishing industries and their management through inevitable boom-and-bust cycles. It is first necessary to recognize the importance of low-frequency variability or regime behavior of ecosystems in contrast to standard steady-state assumptions. This step has taken nearly 20 years (cf. Isaacs 1976), but perhaps some of the delay has been due to the need for a clear object lesson. That lesson was provided by the sharp regime shift in the northeastern Pacific Ocean about 1976.

We are now beginning to understand this low-frequency variability and the corresponding biological responses (e.g., Jacobson and MacCall 1995). Fortunately, there appears to be substantial pattern and statistical predictability in the long-term physical and biological variability of the California Current ecosystem. The scientific problems now faced by CalCOFI are perhaps more complicated than was originally envisioned, and are of fundamental importance to fields such as climatology, oceanography, and ecosystem management. It may be taken as a sign of institutional and intellectual health that as our view of the California Current ecosystem matures, the need for and value of CalCOFI monitoring and research continues to grow.

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IS THERE EVIDENCE FOR LONG-TERM CLIMATIC CHANGE IN SOUTHERN CALIFORNIA KELP FORESTS?

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ABSTRACT

Evidence for long-term natural change in coastal ecosystems has to be separated from the effects of intense anthropogenic impacts, especially in heavily populated areas. The kelp forests of southern California, highly productive ecosystems organized around the giant kelp, *Macrocystis pyrifera*, support a variety of fisheries, and the kelp is harvested for extraction of alginates. Because of the importance of *Macrocystis* itself to the diverse assemblage within the kelp forest community, research in this ecosystem has focused on changes in giant kelp populations. Canopy maps of the Point Loma kelp forest near San Diego illustrate major changes over the last century; these changes have been ascribed to a variety of different causes, including temperature. To understand the role of physical forcing on interannual variability in the *Macrocystis* canopy at Point Loma, we compared two 31-year kelp data sets with available physical records. Annual average surface temperature was significantly correlated with kelp harvest, but explained only 24% of the variance. Because the canopy of giant kelp is susceptible to disturbances that may not affect plant survival, we evaluated two subsurface measures—stipe number as an index of individual plant growth, and stipe density as a measure of carrying capacity. Both stipe measures were sensitive to interannual variability in surface temperature for the period 1983–95 and were more sensitive than plant survival. Plant size and carrying capacity were very low following 1992–93 El Niño conditions and the anomalously warm 1994. Comparison with historical stipe data from 1957, 1973, and 1974 indicates up to two-thirds reductions in standing biomass since 1957. There is a strong inverse trend between median plant size and the sums of anomalies in Scripps Institution of Oceanography Pier surface temperature, calculated quarterly for three years. It appears, however, that these large, interdecadal changes in biomass can be explained by the location of the data sets within multiyear warm and cold periods. We conclude that stipe numbers and stipe density—measures of individual plant size and carrying capacity—are useful tools for evaluating long-term change in *Macrocystis* populations within specific locations. Although limited by the paucity of historical observations, the sensitivity of stipe counts to surface temperature argues strongly for their incorporation into ongoing and future kelp forest research.

INTRODUCTION

Roemmich and McGowan's (1995) report of a 70% decrease in the biomass of macrozooplankton associated with warming of the surface layers off southern California since 1951 suggests that climatic warming may be strongly affecting productivity of the California Current region. Is there evidence for similar long-term change in the nearshore zone of southern California? Such a determination for the nearshore zone faces major confounding factors relative to offshore waters; the effects of climate change on coastal populations have to be separated from those of intense human exploitation, disturbance, and pollution. Further complications for detecting long-term change in the nearshore zone include very different life spans and time scales of some coastal organisms and communities relative to pelagic macrozooplankton. The coastal zone receives nutrients from some sources that may have little to no effect on the California Current; these sources include runoff, sewage discharge, and benthic topographic effects on turbulence and mixing. Even the spatial scale of coastally linked upwelling is within a few km of shore (Jackson 1986). Furthermore, nutrient availability will be different for fixed and free-floating plants; for example, internal waves, which constitute an important nitrogen source for giant kelps (Zimmerman and Kremer 1984, 1986; Zimmerman and Robertson 1985), are inherently less valuable to phytoplankton, which float within a water mass. The importance of coastally linked sources and processes affecting nutrients is supported by satellite studies showing a trend for high chlorophyll in the very near coastal zone in all seasons (Fargion et al. 1993). Thus, for several reasons, long-term change is likely to be more difficult to demonstrate in the coastal zone.

Nevertheless, Barry et al. (1995) reported a long-term shift in invertebrate species composition in a central California rocky intertidal community. Barry et al. relocated fixed quadrats established in the 1930s at Hopkins Marine Station in Pacific Grove, which has been closed to public access since 1917. The abundances of eight of nine species with southerly distributions increased significantly, and the abundances of five of eight northern species decreased significantly between 1931–33 and 1993–94; there was no trend for cosmopolitan species. Barry et al. associated the species shifts with a small, 0.75°C increase in annual sea-surface temperature and a larger, 2.2°C increase in summer temperature.

The kelp forests of southern California are highly productive nearshore ecosystems centered around the giant kelp, *Macrocystis pyrifera*. Kelp forests support sport and commercial fisheries for sea urchins, abalones, spiny lobsters, and various finfishes; the kelp itself is harvested for the production of alginates. Providing the preponderance of the primary productivity and three-dimensional structure to the kelp community, as well as considerable food to adjacent communities, *Macrocystis* is a key species for a diverse assemblage of invertebrates, fishes, and marine mammals. Thus research in this ecosystem has focused not on species composition but on changes in populations of *Macrocystis* itself.

Understanding patterns of productivity and long-term change in giant kelp populations presents a very different set of challenges than for phytoplankton. *Macrocystis* is a very large plant with complex morphology, a life history that involves alternation of generations, and a macroscopic sporophyte which can live for several years, leading to population cycles of three to four years. Macrophytes of rocky shores are generally adapted to vigorous water movement, which allows them to benefit from high levels of turbulent diffusion as well as coastal upwelling; these in turn permit high levels of nutrient uptake, photosynthesis, and growth (Mann 1982). *Macrocystis* forms an extensive surface canopy which allows it to outcompete lower-standing kelps for light but increases its susceptibility to storm damage (reviewed by Murray and Bray 1993). Thus both the morphology and the habitat of *Macrocystis* contribute to its dynamic nature; its populations are highly variable in space and time, and environmental forcing clearly plays a large role in this variability (Dayton and Tegner 1984a, 1990; Tegner and Dayton 1987; Dayton et al. 1992; Tegner et al.[1]).

The health of *Macrocystis* populations in southern California has long been associated with temperature and nutrients. The widespread destruction of populations during 1958 and 1959 and the deterioration of surface canopies during warm summer/fall periods were attributed to long periods of water temperatures greater than 20°C (North 1971). The demonstration of the inverse relationship between temperature and nutrients (Jackson 1977; Zimmerman and Kremer 1984) led to experimental uncoupling of these factors. If nutrients are present, *Macrocystis* can tolerate temperatures at which damage has been observed in the field; both photosynthesis and nutrient uptake occur unimpeded above 20°C (reviewed by Murray and Bray 1993; North 1994). The sensitivity of *Macrocystis* to higher-frequency temperature variation, notably El Niño–Southern Oscillation events (Dayton and Tegner 1984a, 1990; Tegner and Dayton 1987; Dayton et al. 1992; Tegner et al.[2]), may offer some insight into the future, allowing predictions of short-term responses to longer-term global warming (Peterson et al. 1993; Lubchenco et al. 1993).

Here we report changes to *Macrocystis* forests over the last century, evaluate several sets of physical data for their effects on two measures of the kelp canopy in the Point Loma forest near San Diego, propose and evaluate subsurface indicators of plant size and carrying capacity, and consider the evidence for long-term climatic change in giant kelp populations.

CANOPY HISTORY

Against the backdrop of inherent variability, there is well-known evidence for major changes in *Macrocystis* populations. Kelp's importance to sailors as an indicator of shallow water led to many recorded observations and canopy diagrams on nautical charts documenting the entrances to major ports. Concern over dependence on imports for potash—important to farmers for fertilizer and to the munitions industry of the early twentieth century—led to a survey of all kelp forests from Alaska to Baja California by the U.S. Department of Agriculture in 1911–12 (Crandall 1915). Sporadic and eventually annual aerial mapping illustrated long-term changes in canopy coverage. Comparisons of these early maps with recent surveys indicated overall declines of 30%–70% in canopy area of kelp beds in southern California since Crandall's surveys (reviewed by Foster and Schiel 1985). The decline has been attributed to many factors (e.g., Foster and Schiel 1985; Tarpley and Glantz 1992; Neushul and Neushul 1992) including grazing, fisheries on predators of grazers, storms, abnormal oceanographic conditions such as El Niño events, discharge of wastes (sewage, industrial, thermal, oil drilling), harbor dredging, competition for substrate, and different mapping techniques—all of which have to be filtered out of any consideration of long-term change in productivity. Furthermore, kelp has been harvested since 1911 (Tarpley and Glantz 1992); as for any natural resource, the harvest data reflect changing markets as well as natural disturbances and variable productivity.

The Point Loma kelp forest near San Diego, California, one of the largest *Macrocystis* forests in the world, is generally about 8–10 km long by 1 km wide. It is also one of the scientifically best known; the pioneering studies of Wheeler North and colleagues date back to the mid 1950s. North's Kelp Habitat Improvement Program continued until 1975, overlapping with research conducted

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[1] Tegner, M. J., P. K. Dayton, P. B. Edwards, and K. L. Riser. Large-scale, low-frequency oceanographic effects on kelp forest succession: a tale of two cohorts. MS submitted to Mar. Ecol. Prog. Ser.

[2] Ibid.

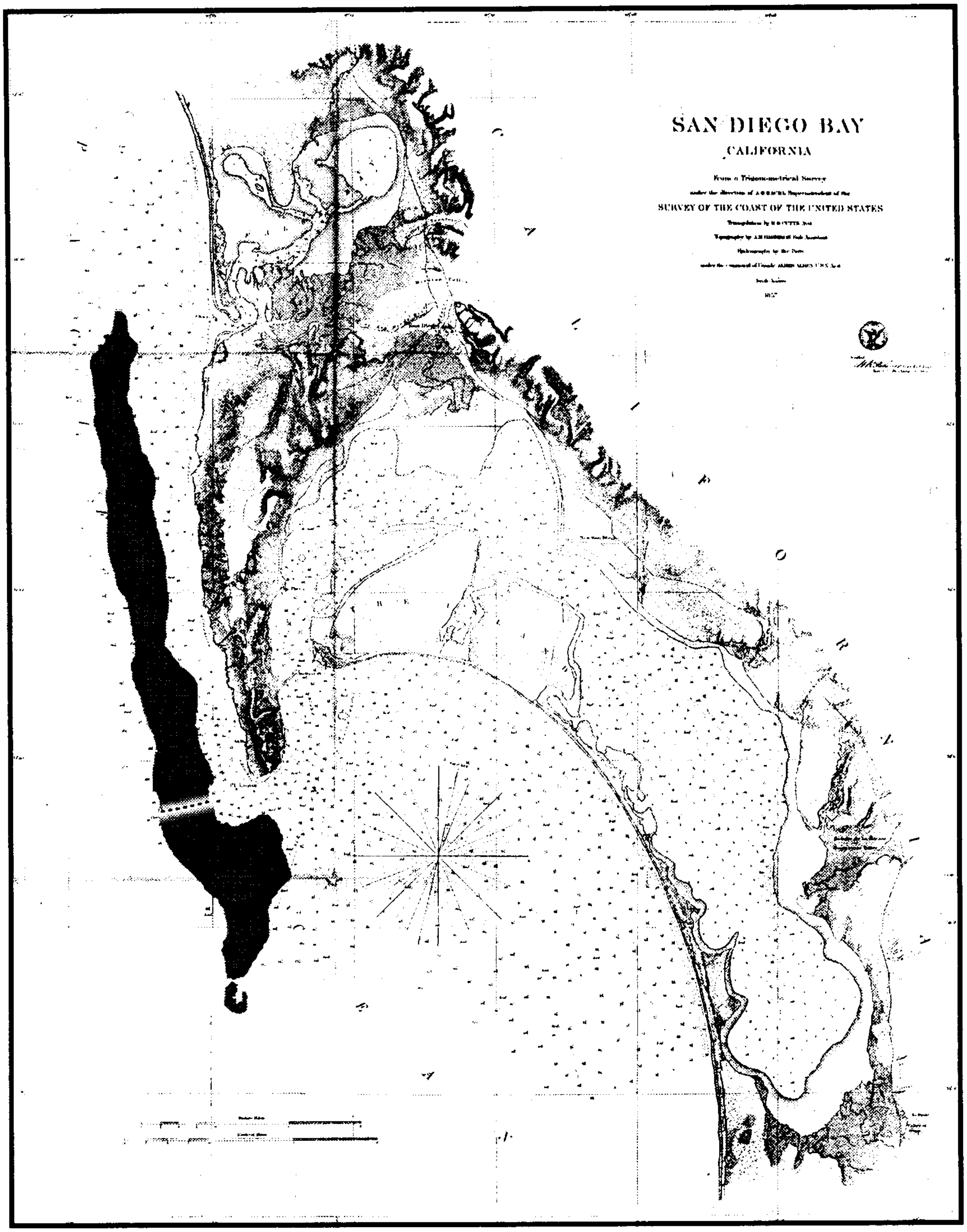

Figure 1. Point Loma in 1857, after a United States Coast Survey chart; the kelp canopy has been shaded to increase its visibility.

by Kelco—the San Diego–based harvesting company—and Scripps Institution of Oceanography (SIO), which began in 1970. Point Loma's proximity to Kelco has led to steady, maximal rates of harvest (the upper four feet is harvested up to three times a year), and the presence of San Diego's sewage outfall has ensured annual photographic assessments of canopy cover for regulatory purposes since 1964.

An 1857 chart of the San Diego Bay region by the United States Coast Survey (figure 1) with sailing directions describes a *Macrocystis* canopy extending three miles south of the tip of Point Loma. Crandall (1915) mapped a similar canopy extent in 1911, but by 1949, the Point Loma kelp forest exhibited considerable decline, which culminated in virtual disappearance of the canopy in the late 1950s–early 1960s (figure 2). The dis-

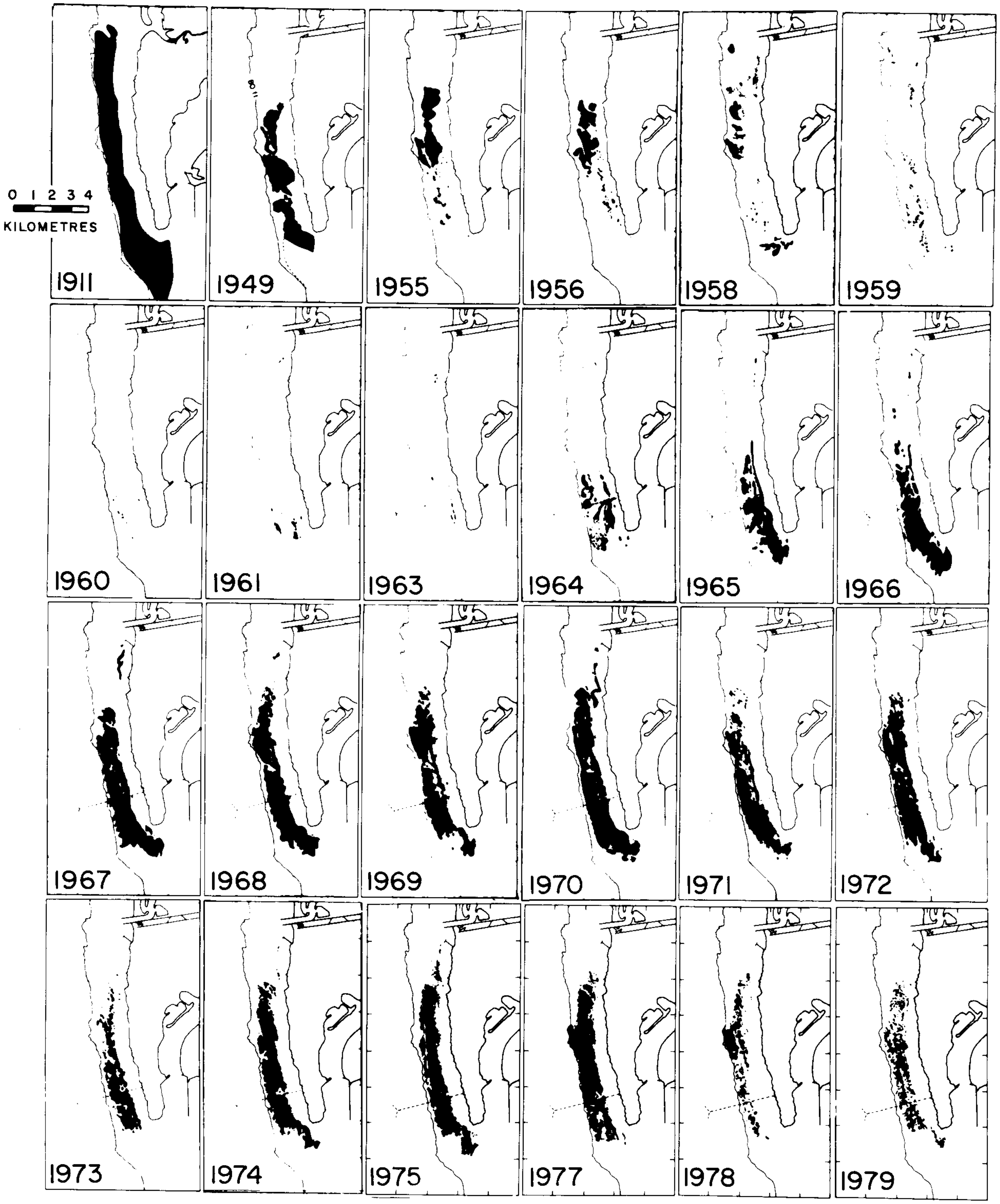

Figure 2. Montage of canopy maps of the Point Loma kelp forest assembled by Wheeler North (see North et al. 1993 for methods). Note the changes in vertical and horizontal extent after 1980. Mission Bay is a recreational bay to the north of the kelp forest; its entrance channel and the westernmost portion of the bay are visible at the top of each panel. The entrance to San Diego Bay, a large natural harbor, is south of the kelp forest and east of the tip of the Point Loma peninsula; the Zuniga jetty forms the eastern boundary of the entrance channel. The Point Loma sewage outfall, the dotted line crossing the kelp forest, was constructed in 1963. Figure 2 continues on next page.

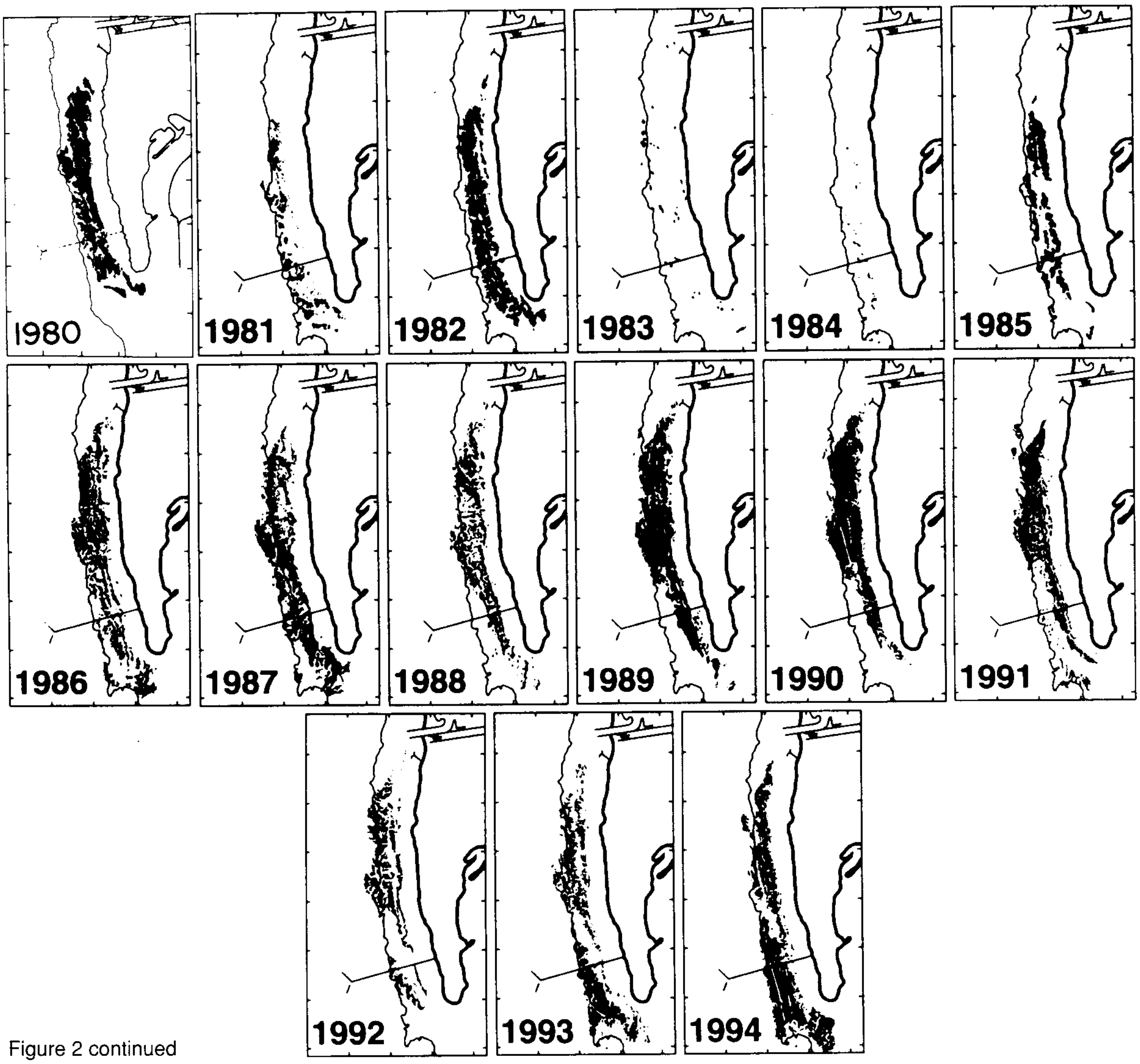

Figure 2 continued

appearance was attributed to intense grazing by sea urchins, the 1957–59 El Niño, and the discharge of poorly treated sewage in San Diego Bay (reviewed by Tegner and Dayton 1987, 1991).

Recovery began after the sewage outfall was moved to a deepwater, offshore location, and kelp restoration efforts began controlling sea urchin populations. There was considerable regrowth, and the *Macrocystis* canopy was relatively stable in the late 1960s–1970s; the sea urchin fishery that began in the 1970s contributed to this stability. The 1980s were marked by the massive 1982–84 El Niño and the 200-year storm of 1988, but the canopy recovered quickly from these natural disturbances. Although the size of the forest has grown considerably from its low points, the Point Loma canopy has not approached the northern or southern maximum extents of 1857 or 1911; these may be permanent changes related to the dredging of Mission and San Diego Bays, and the effects of the Zuniga jetty on tidal outflow from San Diego Bay (see figure 2).

ENVIRONMENTAL CORRELATES OF KELP CANOPY

Kelp Harvest vs. Canopy Area

In an effort to understand the role of physical forcing on interannual variability in the *Macrocystis* canopy at Point Loma, we compared two long-term (1964–94) data sets—annual harvest and annual maximum canopy area—with various long-term physical records. Point Loma kelp harvest data for 1964–94 were provided by D. Glantz of Kelco, a unit of Monsanto Company. To protect proprietary information, the maximum harvest year of this time series (1972) was treated as 100%, and other years were scaled accordingly. Approximate annual maximum kelp-canopy coverage data from Point Loma were compiled from aerial photographs by W. J. North (see North et al. 1993 for methods).

Surface and 5-m depth temperatures were collected daily on the SIO Pier; in situ bottom temperatures were collected from the 18-m Central site at Point Loma (Dayton et al. 1992). Monthly Secchi disk data (a measure of near-surface transparency) from three sites along the outer edge of the Point Loma kelp forest, and annual mass emission rates from the Point Loma wastewater treatment plant were provided by the City of San Diego. A significant (p = 0.02) degree of concordance was found to exist through time among the three Secchi disk stations by testing with Kendall's concordance test (Zar 1984). A Kruskal-Wallis test showed that the Secchi depths at the three sites did not differ (p = 0.12), so the data were pooled to calculate annual averages. Wave data from the Mission Bay buoy (lat. 32°45.9', long. 117° 22.5', about 13 km offshore of the entrance to Mission Bay) were collected by the Coastal Data Information Program. Seymour et al. (1985) detail the data-gathering system and analysis techniques. Significant wave height is defined as the average of the one-third highest waves. Sea-level data for San Diego Bay were downloaded off the Internet from the Integrated Global Ocean Services System (IGOSS) at the University of Hawaii, courtesy of G. T. Mitchum and K. Wyrtki. Anomalies were calculated from the 1975-to-1986 mean annual cycle of sea level and corrected for the inverted barometer effect by IGOSS.

Simple linear regressions were used to compare kelp harvest data with canopy coverage data, and to determine the effect of environmental variables on the kelp forest, with kelp harvest as the dependent variable. In each case, untransformed data met the assumptions of regression analysis. Because these data sets varied in length from 11 to 31 years, individual regressions were run to make use of all available data; this represents more testing than optimal, but appears to be the best way to extract the most information.

To determine the more appropriate measure of *Macrocystis* for these analyses, we compared time series data of annual kelp harvest with the approximate annual maximum canopy coverage (figure 3). Harvest data have the advantages of integrating growth over a longer period and of less measurement subjectivity. Areal coverage offers better spatial information, but is a snapshot in time and a poor indicator of canopy density. The two measures are significantly correlated (r^2 = 0.343, p = 0.0005), but there are differences in maximal years and in the relationship between harvest and coverage. The highest canopy coverage in this time period occurred in 1994, but that year's harvest was relatively low, probably because of warm surface temperatures. In contrast, surface temperatures were relatively cool in the late 1960s through the mid-1970s (e.g., Smith 1995), when harvest rates were high relative to canopy cover. Because of the strong inverse relationship between temperature and nutrients (Jackson 1977; Gerard 1982; Zimmerman and Kremer 1984), we compared both harvest and canopy coverage with surface temperature; both kelp-canopy measures were significantly (p = 0.005 and 0.019, respectively) negatively correlated with surface temperature. Because of the advantages discussed above and because surface temperature explained more of the variance in harvest data (r^2 = 0.24 vs. 0.17), we chose to use harvest data for further comparisons.

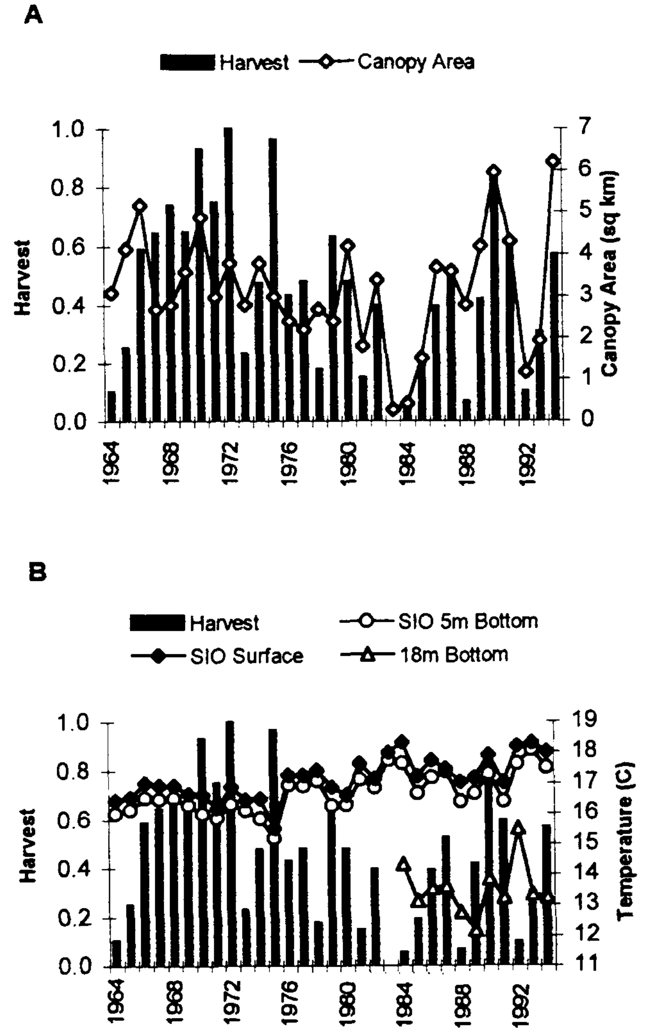

Figure 3. *A*, Comparison of kelp harvest data with canopy coverage, 1964–94. *B*, Relationship between kelp harvest data and the SIO Pier surface temperature 1964–94, SIO Pier 5-m temperature 1964–94, and 18-m in situ bottom temperature 1984–94. Harvest is scaled to the maximum year in this time series—1972.

Kelp Harvest vs. Physical Parameters

Two measures of subsurface temperature were examined: the daily determination at 5 m from the SIO Pier

TABLE 1
Results of Simple Regressions of Relative Kelp Harvest (% 1972), SIO Surface Temperatures, SIO 5-m Bottom Temperatures, and 18-m Bottom Temperatures on Various Environmental Factors Using Yearly Means, Totals, or Maxima

Variable	N*	Intercept	Slope	R^2	P
Harvest					
Canopy area	31	0.083	0.118	0.343	0.0005
SIO surface temperature	31	3.997	−0.207	0.237	0.0050
SIO 5-m bottom temperature	31	4.022	−0.214	0.239	0.0052
18-m bottom temperature	11	1.258	−0.066	0.050	0.5067
Secchi depth	18	0.504	−0.006	0.010	0.6981
Mass emissions	30	0.853	−0.001	0.078	0.1361
Max sig wave height	12	0.538	−0.001	0.054	0.4687
Sea-level anomaly	20	0.394	−0.004	0.231	0.0300
SIO surface temperature					
SIO 5-m bottom temperature	60	0.5915	0.935	0.787	0.0000
18-m bottom temperature	11	10.747	0.507	0.502	0.0147
Sea-level anomaly	20	17.342	0.014	0.466	0.0009
SIO 5-m bottom temperature					
18-m bottom temperature	11	12.149	0.371	0.331	0.0640
Sea-level anomaly	20	16.939	0.014	0.559	0.0002
SIO 18-m bottom temperature					
Sea-level anomaly	11	13.399	0.026	0.636	0.0033

*Number of years of data available.

and the 18-m in situ records. The former has the advantage of 31 years of available data, but is shallow for kelps, and is located some distance from Point Loma in an area where topographic complexities may affect temperature patterns. The latter data set is from the Point Loma kelp forest and is based on eight values per day, but only 11 years of data.

The 5-m temperature was significantly correlated with harvest, as was surface temperature, and explained an identical amount of its variance (figure 3, table 1). Not surprisingly, surface and 5-m temperatures were very highly correlated (r^2 = 0.79). In contrast, in situ 18-m temperature explained very little of the variance in kelp harvest over the shorter period. The deeper measure was significantly correlated with surface temperature (p = 0.015), although less so than 5-m temperature. Nevertheless, while annual averages of surface and bottom temperatures are related, their relationship varied within and between years (figure 3). The implications for kelp harvest, however, are clear: most of the growth of giant kelp is responding to temperature in the upper part of the water column, not at 18 m.

The City of San Diego has collected monthly Secchi disk data immediately offshore of the Point Loma kelp forest for 18 years. There was interannual variability in the averaged Secchi data, with the 1982–84 El Niño years notably clearer (figure 4). Nevertheless, there was no significant relation between kelp harvest and annual Secchi depth averages (table 1). Conversi and McGowan (1992) detected no trends in Secchi depth for the period 1972–87 at these sites, and demonstrated the independence of water clarity, as measured by Secchi depth, and mass emissions rate from the Point Loma outfall. Because of the strong inverse relationship between mass emission rates of suspended solids from the Los Angeles County outfall and the area of the Palos Verdes kelp canopy (Stull and Haydock 1989), we compared these data from the Point Loma wastewater treatment plant with kelp harvest data (figure 4). The relation between mass emissions and kelp harvest was not significant for the period 1965–94 (table 1).

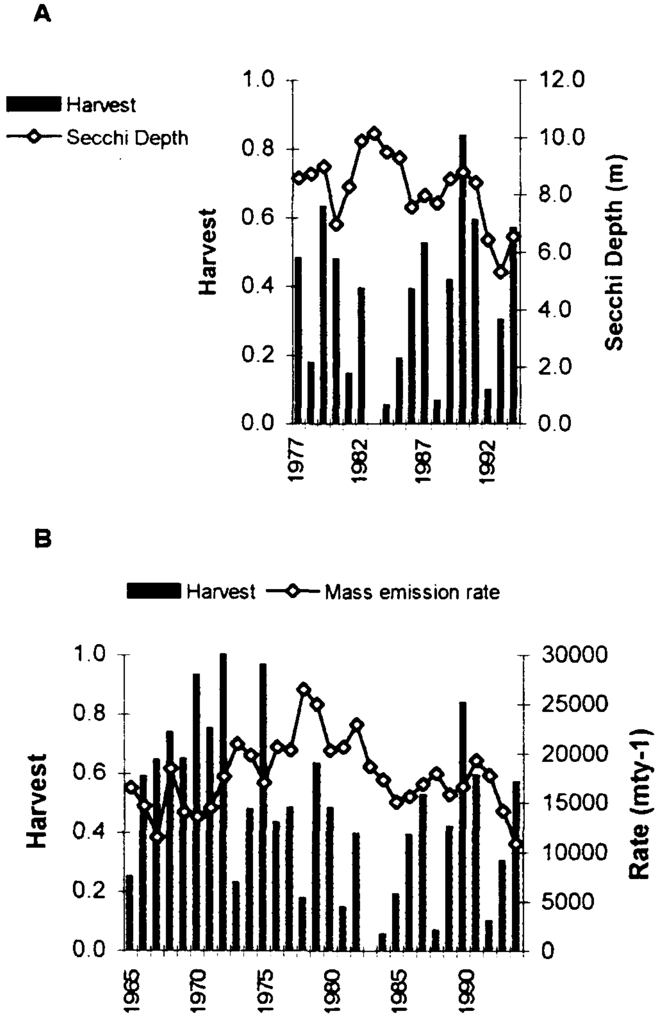

Figure 4. *A*, Kelp harvest data vs. average annual Secchi depth, 1977–94. *B*, Kelp harvest data vs. annual mass emission rate of suspended solids from the Point Loma wastewater treatment plant, 1964–94. Harvest is scaled to the maximum year in this time series—1972.

Wave damage has devastated the Point Loma kelp forest in recent years (Seymour et al. 1989; Dayton et al. 1992), and 1983 and 1988 were peak years of maximum significant wave height; however, the relation between maximum significant wave height and Point Loma kelp harvest was not significant (figure 5, table 1). Other mea-

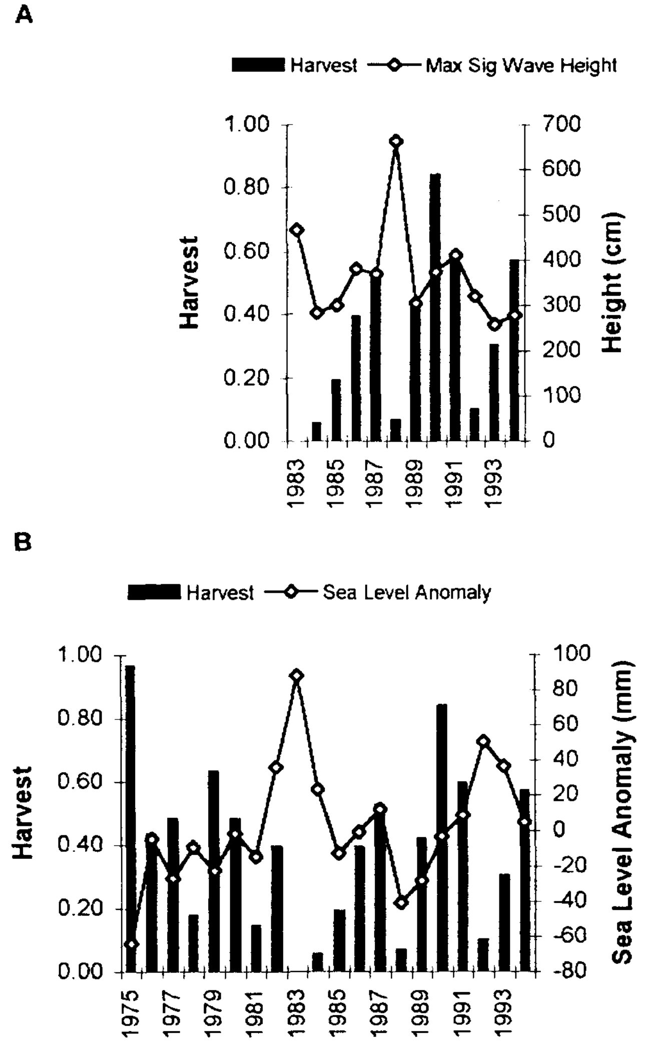

Figure 5. *A*, Kelp harvest data vs. annual maximum significant wave height, 1983–94. *B*, Kelp harvest data vs. sea level anomaly, 1975–94. Harvest is scaled to the maximum year in this time series—1972.

sures of wave energy, including the number of days with significant wave height greater than 2 m, and the average significant wave height for the year, explained even less of the variance; extreme values are apparently the most relevant parameter (e.g., Gaines and Denny 1993).

The productivity of the California Current, as indicated by zooplankton volume, is heavily influenced by large-scale, interannual variations in flow, which are strongly related to the coastal sea-level anomaly (Chelton et al. 1982). There is a significant inverse relationship between sea-level anomaly and Point Loma kelp harvest data for 1975–94 (figure 5, table 1; $r^2 = 0.23$, $p = 0.03$). Sea-level anomaly is also correlated with sea-surface temperature (figure 6, $r^2 = 0.47$, $p = 0.0009$), 5-m pier temperature ($r^2 = 0.56$, $p = 0.0002$), and in situ bottom temperature ($r^2 = 0.64$, $p = 0.0033$). The increasing amount of variance explained with decreasing depth suggests that local processes are relatively more important to surface temperature, whereas deeper temperatures are more influenced by larger-scale phenomena.

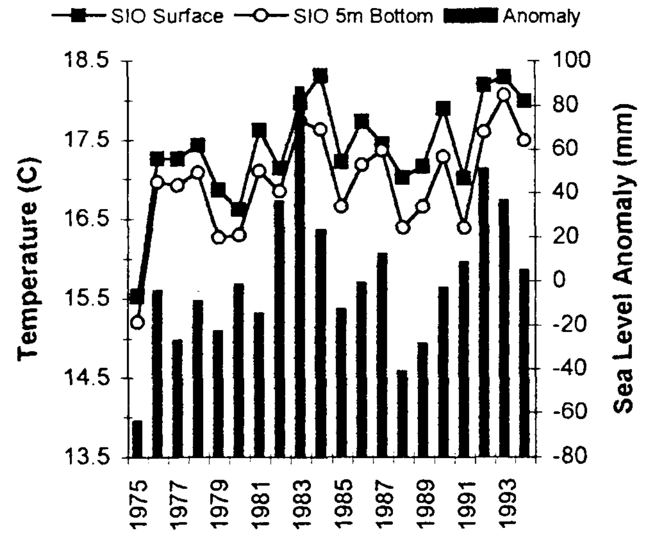

Figure 6. Sea-level anomaly vs. SIO Pier surface temperature and SIO Pier 5-m temperature, 1975–94.

STIPE COUNTS AS SUBSURFACE INDICATORS OF ENVIRONMENTAL CHANGE

Both areal estimates and harvest are correlates of the canopy that can be strongly affected by storms and warm summer–fall sea-surface temperatures with lesser or no impacts on survival of the plants themselves. This suggests that some measure from the less variable bottom environment of *Macrocystis* would be a better indicator. The density of giant kelp plants is generally a function of disturbance history and cohort age (figure 7; Dayton et al. 1992). High levels of disturbance lead to high initial cohort density (Reed et al. 1988; Tegner et al.[3]); after recruitment, intraspecific competition leads to gradual self-thinning (Dayton et al. 1984). Thus, some measure of individual plant status is required.

Giant kelp plants consist of a holdfast, which anchors the plant to the substratum; bundles of fronds analogous to the branches and leaves of a land plant; and reproductive tissues called sporophylls, which are located just above the holdfast. Fronds, made up of stemlike stipes and leaflike blades, originate at the basal meristem above the holdfast and grow up through the water column to form the surface canopy; fronds generally increase in number as plants age. *Macrocystis* plants are perennial, living up to about five years in the San Diego region (Rosenthal et al. 1974; Dayton et al. 1992), but the maximum lifetime of individual fronds is six to nine months (North 1994). The frond population of a plant turns

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[3] See footnote 1 on p. 112.

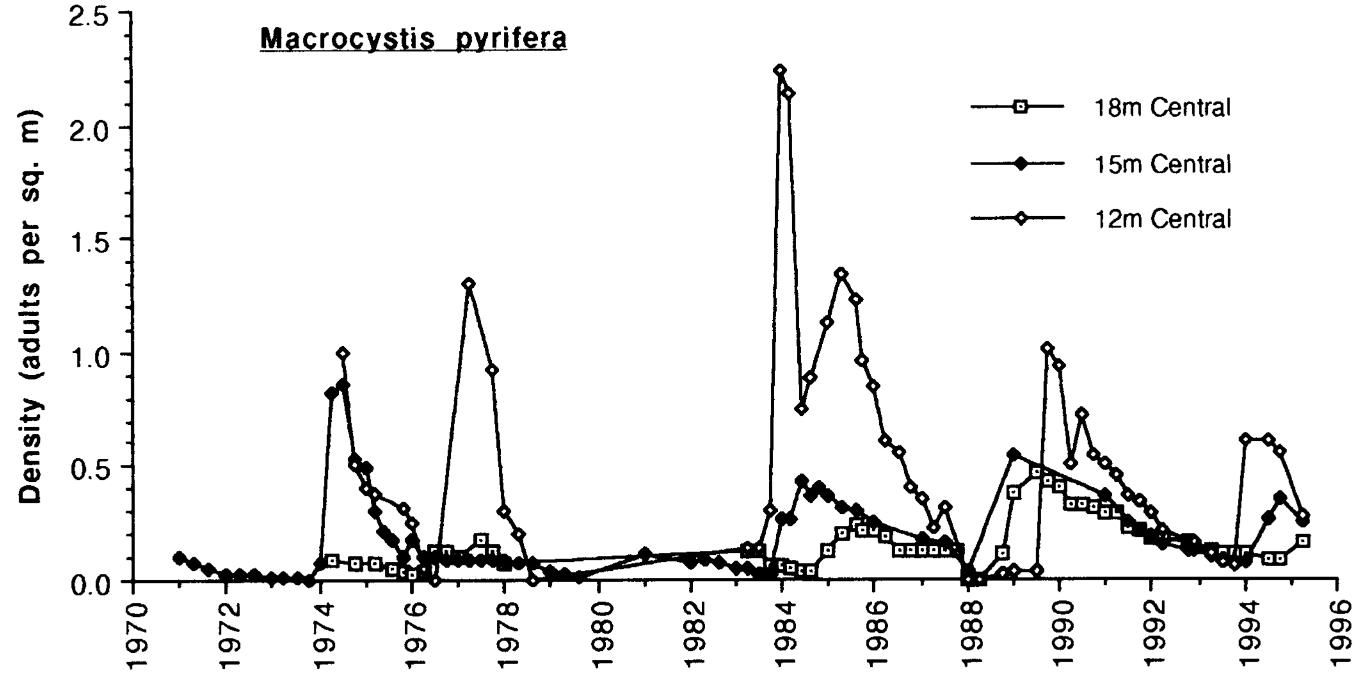

Figure 7. Density of adult (defined as four or more stipes, Dayton et al. 1992) *Macrocystis pyrifera* determined quarterly at long-term study sites in the central Point Loma kelp forest, 1983–94. Continuation of data from Dayton et al. 1992.

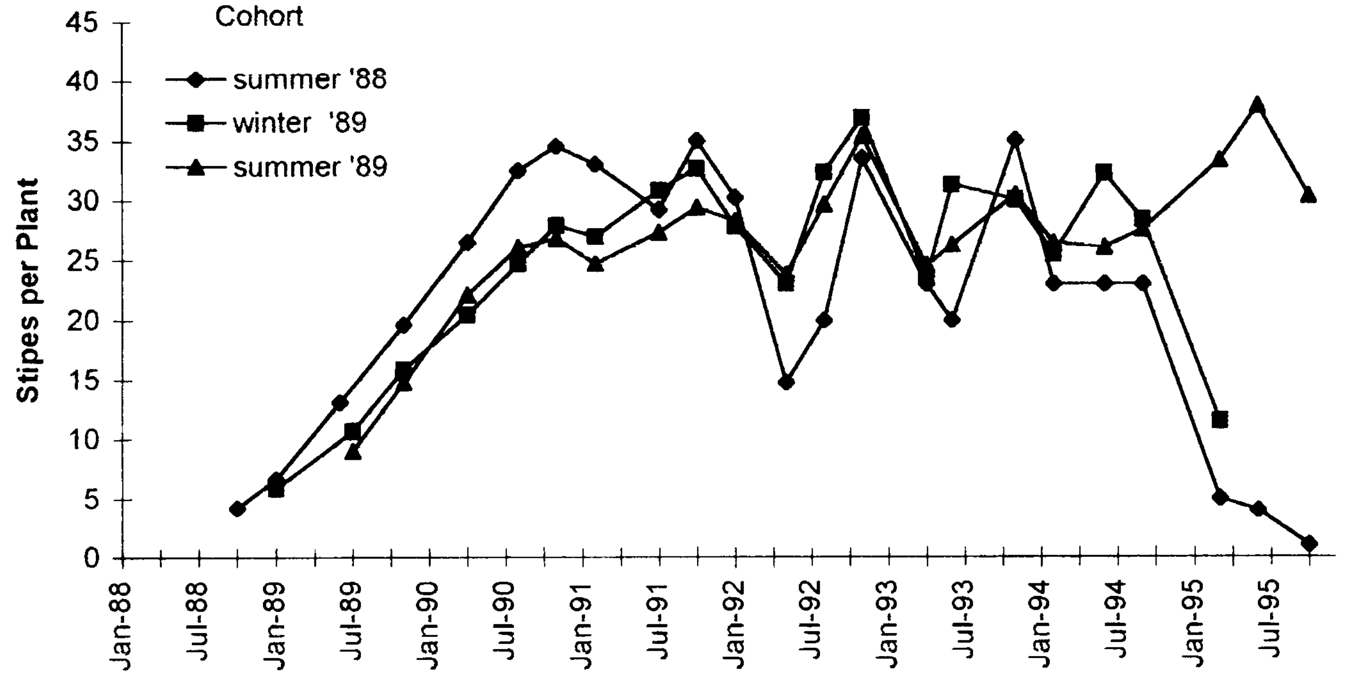

Figure 8. Changes in the mean number of stipes per *Macrocystis pyrifera* plant by cohort at 18-m Central, 1988–94.

over once or twice a year as fronds lost to senescence or disturbance are replaced with juveniles; at any given time the frond population consists of a complex mixture of different ages. This constant turnover of biomass contrasts sharply with terrestrial forests, where biomass in woody trunks and branches of trees often remains fixed for decades (North 1994), and is the basis for the rich invertebrate-grazer fisheries of this ecosystem.

We began regularly collecting stipe data at five permanent sites at Point Loma in 1983 (Dayton et al. 1992;

Tegner et al.[4]). All adult (defined as four or more stipes) giant kelp plants are mapped quarterly in 400 m^2 per site, and stipes are counted at a height of one meter above the bottom. Stipes are not tagged, so stipe number data encompass both attrition and growth. Cohorts are defined as those plants which newly achieve adult status in a quarterly census. Jackson (1987) modeled *Macrocystis* stipe numbers and showed their sensitivity to season, depth, latitude, degree of wave exposure, upwelling, and other factors. Indeed, stipe density decreases with depth at Point Loma, and appears to be a good indicator of carrying capacity (Dayton et al. 1992). Thus stipe data should be compared within locations through time, and the comparative data presented here are all from 15 m in central Point Loma. Generally, frond number varies seasonally, independent of cohort age. In this example from our 18-m Central site (figure 8), there were clear decreases in average stipe number associated with seasonal decrease in light and winter storms, and increases in stipe number with the onset of spring upwelling and longer days in 1992 and 1993. Generally, there is also an inverse relationship between plant density and average plant size, in terms of fronds per plant (North 1994).

The relationships between disturbance, oceanographic conditions, plant density, and stipe carrying capacities have been explored in detail (Dayton et al. 1992; Tegner et al.[5]). Here we summarize these findings to establish the basis for using stipe counts as a useful indicator for long-term change in *Macrocystis* populations. Different stipe patterns were observed following the 1982–84 El Niño in comparison with after the 1988 storm. Data from 15-m Central (figure 9) are typical, although this site had a few adult survivors of both disturbances which led to brief peaks in stipes per plant before these large adults died.

After the extreme warm-water conditions of 1983–84, the number of stipes per plant steadily increased until the catastrophic storm of 1988 caused extensive mortality (Dayton et al. 1992); presumably these plants would have continued to grow in the absence of disturbance. Stipes per plant increased as plant density decreased, and thus stipe density remained relatively stable from 1986 until the storm (figure 9). In other words, there was an apparent stipe carrying capacity of about 5 m^{-2} at the 15-m site between 1986 and 1988 (Dayton et al. 1992; Tegner et al.[6]). After the 1988 storm (excluding the prestorm survivors), there were three years (fall 1988–fall 1991) of steady increase in the number of stipes per plant during cold conditions associated with the 1988–89 La Niña (Dayton et al. 1992), but then this value leveled off except for seasonal variation.

There was widespread sea-surface warming in the California coastal zone during 1992 and 1993 associated with the 1991–93 El Niño (Lynn et al. 1995). During 1994, circulation returned to a more normal pattern, but sea-surface temperatures were again anomalously warm during most of the year (Hayward et al. 1995). This leveling off of stipe number per plant during three years of warm-water conditions contrasts with the relatively steady increase observed after 1984, when water temperatures were closer to the mean. The general decline in stipe density to <2 m^{-2} in early 1994, along with the decline in plant density after summer 1991, as well as the lack of increase in stipes per plant, suggests that warm-water conditions negatively affected growth and carrying capacity. Thus, both plant and stipe densities were much higher in 1988–90 than in 1985–86, but the initial success of these cohorts did not persist, and both indices dropped well below the 1986–88 carrying capacities. New plants recruited in mid-1994 after the decline of the post-1988 storm cohorts, and data from the early stages of the 1994 cohort indicate that the plants are growing in size as plant density decreases, and that the stipe density has remained relatively constant at about 4 m^{-2} under more normal surface temperatures in 1995 (figure 9).

Thus we have two measures of kelp biomass independent of the canopy: stipe number per plant—an index of individual growth—and stipe density per square meter—which appears to reflect carrying capacity of the habitat. These are both very sensitive to water temperature and more sensitive than plant survival; witness the decline in stipe density in 1992–94 (figure 9) without unusual mortality (figure 7).

Analysis of long-term change depends on the availability of historical data; we located three earlier stipe data sets from 15 m in central Point Loma to compare with the last 12 years (table 2). Wheeler North surveyed all plants in an 800-m^2 area in September 1957 (North 1994); Ron McPeak (unpubl. data) of Kelco haphazardly measured 19 plants in September 1973; and Paul Dayton (unpubl. data) measured all plants in 225 m^2 a few months later, in January 1974, after winter storms would have caused some decreases in frond number from when McPeak's data were gathered. To represent our data from the last 13 years, we selected the peaks in number of stipes per plant for each of the post-disturbance populations, June 1986 and September 1993. Figure 10 illustrates the log of plant size (in terms of stipes per plant) plotted against cumulative percentage for four of the size-frequency distributions; the small McPeak data set was left off this figure for legibility. Median plant size has decreased by about two-thirds since 1957. Note also

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[4] See footnote 1 on p. 112.

[5] See footnote 1 on p. 112.

[6] See footnote 1 on p. 112.

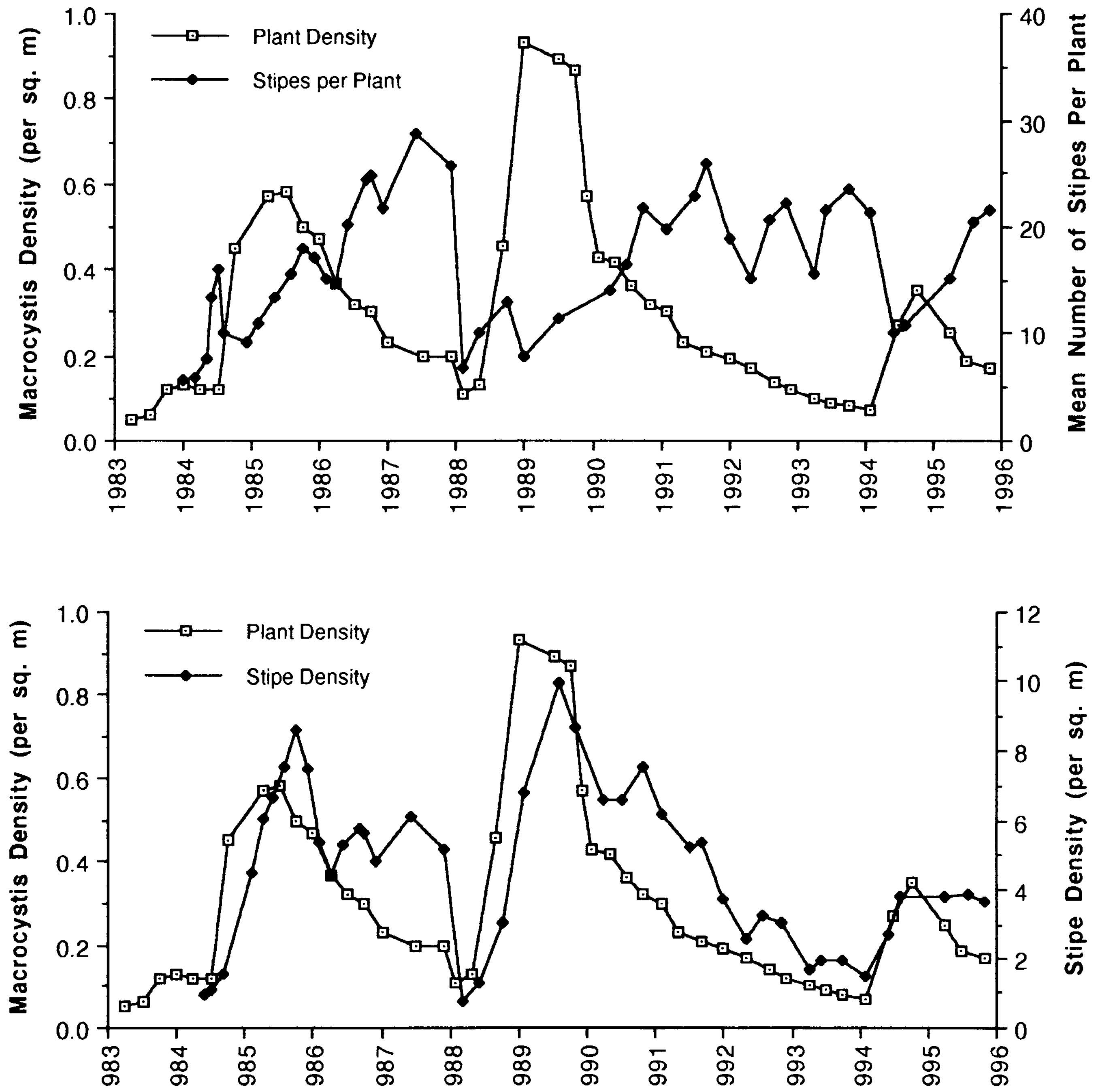

Figure 9. Changes in the mean number of stipes (growth) per *Macrocystis pyrifera* plant and in stipe density (carrying capacity) as functions of plant density at 15-m Central, 1983–94.

the changes in maximum plant size (table 2). Because of the strong inverse relationship between plant size and density (e.g., North 1994), it is important to compare plant densities among these years; despite the large discrepancy in size, the very large plants of September 1957 were found at the same density as the 1993 plants, suggesting very different carrying capacities. We reiterate that the earlier data represent haphazard points in time; only the 1983–95 data are continuous.

Because surface temperature was the best predictor of kelp harvest (table 1) in our data set, and because the plants live for several years, we plotted median stipe number against the sums of anomalies in SIO Pier temperature, calculated quarterly for three years (figure 11). There was a strong inverse trend between the accumulated pier temperature anomalies and median stipe number. Note that four of the five points were collected between June and September; it is probably because

TABLE 2
Data Sets for Comparison of *Macrocystis pyrifera* Stipe Distributions among Years

Date	*N*	Plant density (per sq m)	Stipe number Min	Stipe number Max	Stipe number Med	Mean stipe density (per sq m)	Sum of anomalies (12 quarters)	Source	Notes
Sept. 1957	60	0.08	1	192	55.0	4.11	−3.98	North (1994)	800 sq m
Sept. 1973	19	N.A.	12	194	48.0	N.A.	−4.26	McPeak (unpubl.)	Haphazardly selected plots
Jan. 1974	44	0.20	1	91	40.5	8.89	−5.80	Dayton (unpubl.)	225 sq m
June 1986	79	0.20	5	88	26.0	6.00	8.78	Tegner et al.*	Peak of 1983–88 cohorts (400 sq m)
Sept. 1993	33	0.08	1	69	19.0	1.92	11.40	Tegner et al.*	Peak of 1988–94 cohorts (400 sq m)

All data were collected from 15-m depths in the central Point Loma kelp forest. Anomalies refer to SIO Pier surface-temperature measurements.
*See footnote 1 on p. 112.

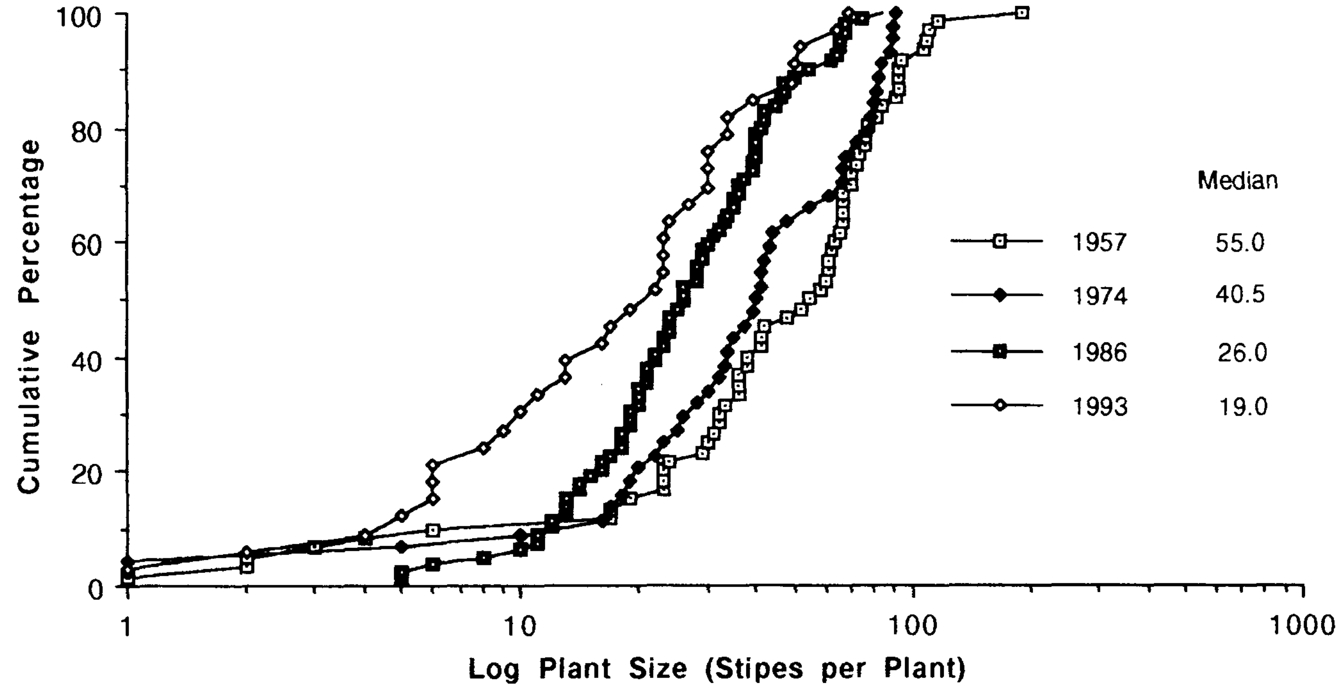

Figure 10. Log of *Macrocystis pyrifera* size vs. cumulative percentage for size-frequency distributions collected in four different years.

of the seasonal cycle in stipe number (figure 8) that the January 1974 data point appears low. Furthermore, because we selected the two peaks in stipe numbers between 1983 and 1995, the slope of this line is conservative. This figure explains the variable relationship between kelp harvest and canopy area (figure 3). The large canopy area but relatively low harvest of 1994 was due to low stipe counts, whereas the relatively high harvests of the late 1960s to mid-1970s almost certainly reflect high stipe counts.

DISCUSSION

Schiel and Foster (1986) review the problems of factor covariance (e.g., with depth) and interactions; changing relationships between abiotic variables and plant responses with the scale of measurement; and differences in responses among life-history stages in simple correlation analyses. Such analyses, problematic when used to deduce cause-and-effect relationships, are useful when based on independent information on mechanisms and within the context of the proper time and space scales. Our analyses of the effects of environmental parameters on kelp harvest offer information on large-scale, interannual variability; these data are not relevant to processes with shorter time scales such as two-week kelp-recruitment windows (Deysher and Dean 1986) or restricted spatial scales (Dayton et al. 1984).

Surface temperature (as a surrogate for nutrient availability) is the best environmental predictor of kelp harvest and canopy area of those parameters for which we have historical data (see also North et al. 1993). The very high correlation between surface and 5-m pier temperatures and subjective evidence of thermocline depth at Point Loma suggest that the 5-m record is too shallow

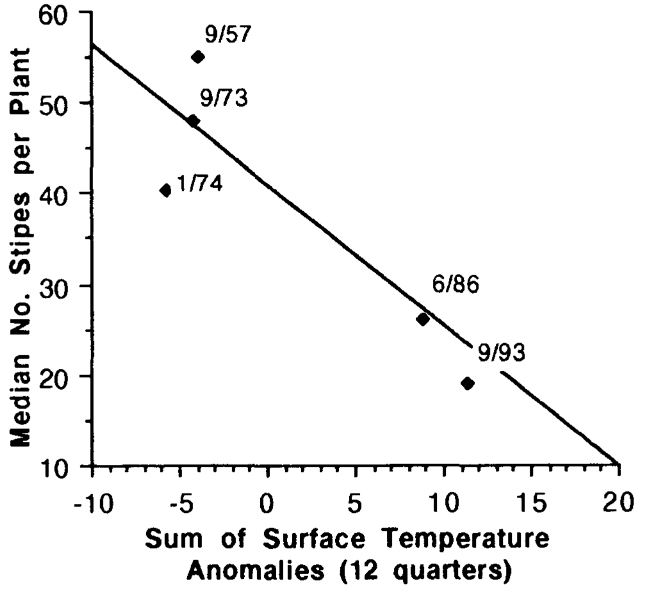

Figure 11. Anomalies in SIO Pier surface temperature, calculated quarterly and summed for three years, versus median stipe number of *Macrocystis pyrifera*.

to represent bottom temperatures in the kelp forest, and a longer 18-m in situ record would be desirable. The predictive value of surface temperature is somewhat counterintuitive—given the long period of the year that surface temperatures are warm; the colder, presumably more nutrient-rich bottom waters; and the importance of thermocline motion to the health of *Macrocystis* plants at Santa Catalina Island (Zimmerman and Kremer 1984, 1986; Zimmerman and Robertson 1985). However, with up to 60% of giant kelp biomass in the surface canopy (North 1968), and more than 98% of the production of *Macrocystis* in the upper 3 m of the water column (Towle and Pearse 1973), the portion of giant kelp plants above the thermocline probably overwhelms capacity for nutrient transport from below much of the time (e.g., Jackson 1977).

The greater importance of surface temperature as opposed to bottom temperature for kelp harvest was supported by R. W. Eppley and R. McPeak (unpubl. MS). They were able to account for less than 10% of the variance in coastal kelp harvest by using the depth of the nitrate concentration gradient (≥ 1 µg atom/L NO_3), which ranged from about 10 to 50 m. North et al. (1993), in their study of kelp forests in Orange and San Diego Counties, illustrate one spatial scale of temperature effects: 10 of the 12 forests in existence in the early 1980s displayed their lowest canopy coverage during El Niño conditions in 1983 or 1984, and 12 of 20 beds in existence in the late 1980s had their highest or next highest coverage during the 1989 La Niña.

The high correlations between all temperature measures and sea-level anomaly (r^2 values from 0.46 to 0.64, table 1) indicate the importance of very large scale events to kelp harvest in coastal forests; Hickey (1993) reviews evidence that more than 75% of the variance in sea level in the Southern California Bight is accounted for by equatorial forcing. Such El Niño and La Niña events affect the California Current and the nearshore, although the largest interannual effects occur nearshore. Regional scales are also important to temperature; for example, sea level in 1984 was greatly reduced relative to 1983, and the tropical El Niño dissipated by fall 1983. However, anomalous conditions, including the warm surface temperatures associated with this event, persisted through 1984 in the California Current region (see references in Tegner and Dayton 1987; Dayton and Tegner 1990).

Some processes supplying nutrients to the nearshore are both temperature and coastally dependent. Coastal upwelling, where the land provides a barrier that forces water to flow away from the coast under appropriate wind conditions, is minimal in the Southern California Bight relative to other regions along the West Coast. However, coastal upwelling does occur within a few km of shore (the scale appropriate for kelp forests) in the bight, and is especially prominent at Point Conception, Palos Verdes, and Point Loma (Jackson 1986). El Niño events depress the depth of the thermocline, and thus may greatly reduce coastal upwelling or render it ineffective (Fiedler 1984; Shkedy et al. 1995). Other sources of nutrients to the nearshore, such as runoff from land, sewage discharge, and benthic topographic effects on turbulence and mixing, are less related to temperature. Thus, nutrients are provided to kelp forests in the nearshore zone by physical processes on a variety of scales, but the lesson of recent years has been the dramatic importance of very large scale events.

The history of Point Loma kelp populations since 1982 leaves no doubt that wave disturbance can decimate this community (Seymour et al. 1989; Dayton et al. 1992). Annual maximum significant wave height alone, however, does not predict kelp harvest. This may not be surprising, given the importance of wave period and wind in addition to significant wave height to kelp damage (Seymour et al. 1989); the strong age dependence of mortality rates for *Macrocystis* (Dayton et al. 1984, 1992); the strong dependence of kelp recovery on temperature; and annual harvest data.

Light is critical for all plants, and successful competition for light appears to explain the dominance of *Macrocystis* over understory kelps (reviewed by Murray and Bray 1993). Gerard and North (1984) report evidence that giant kelp growth is affected by light conditions the week preceding the growth determination, as opposed to the week of the determination. Interannual variability in light, as measured by averages of monthly Secchi depths on the outer edge of the Point Loma kelp forest, however, explained little of the variance in kelp harvest. This is perhaps not surprising, given that canopies, the basis of kelp harvest, capture full sunlight before much radiant energy is absorbed by the water column (North et al. 1986). Secchi data, as an indicator of euphotic depth (the uses of this tool are reviewed by Conversi and McGowan 1992), would be more relevant to earlier life-history stages. Light and temperature requirements for germination and growth of microscopic stages of kelps define recruitment windows (Deysher and Dean 1986), which ultimately affect kelp harvest, but clearly growth conditions affecting intermediate life-history stages have a more direct effect. That understory recruitment events appear to depend on major canopy disruption by storms, sea urchins, or significant self-thinning of *Macrocystis* populations (Tegner et al.[7]) suggests that disturbance and the age structure of giant kelp are more important than interannual variability in water clarity for these lower-standing kelp guilds.

The anthropogenic factor most clearly associated with the health of southern California kelp forests is particulate emissions from sewage outfalls. Past high emissions from the Los Angeles County outfall reduced light penetration, introduced flocculant material and toxicants, and buried the substratum in the Palos Verdes kelp forest (Stull and Haydock 1989). There was a strong inverse relation between annual mass emissions and kelp canopy coverage from the mid-1940s to 1990. At Point Loma, the relation between mass emissions and kelp harvest was not significant for the 1964–94 period for which we have data (figure 4). We note, however, a strong inverse trend over the last three years. Fine-tuning of the advanced primary treatment process has reduced suspended solids emissions annually since 1991 (A. Langworthy, pers. comm.), and the outfall was extended an additional 3.7 km in 1993; the present discharge is 7.1 km offshore in 93 m of water. In this case, however, we know that the recent increase in *Macrocystis* harvest and canopy coverage resulted from release in grazing pressure due to a disease that eliminated a large sea urchin barren in the southwestern portion of the kelp forest and affected about a third of the bed (figure 2; see also figure 2 of Tegner et al. 1995). Subsequent kelp recruitment and growth led to dramatic changes in this region; the canopy at the end of 1994 extended more than a kilometer farther south than we have seen in the last two decades. Finally, the strong recovery of the Point Loma kelp forest after the catastrophic storm of 1988 in comparison with the weak recovery after the 1982–84 El Niño event argues that oceanographic conditions have been the critical determinant of resiliency in this ecosystem in recent years.

Stipe counts appear to be a useful tool for assessing *Macrocystis* carrying capacity and plant response to environmental change. Stipe counts are sensitive to temperature/nutrient conditions, integrate conditions over at least a three-year period, and are much less susceptible to disturbance than are measures of the canopy such as harvest or surface area. But most important, stipe counts are more sensitive to environmental conditions than is plant survival. Unfortunately this tool's usefulness as a historical record is limited because data cannot be compared across sites and depths (Jackson 1987; Dayton et al. 1992). Furthermore, there are few historical data where giant kelp populations have consistently been followed for any length of time, let alone the time-consuming stipe counts made. Nor will this tool be easy to apply, given that the plants in a cohort apparently need to be at least two years old for competition to govern their size and thus make the tool useful. The relationship between plant size, density, and nutrient availability bears further investigation. Nevertheless, the strong trend in the relation between accumulated surface temperature anomalies and median plant size (figure 11) clearly justifies further use of this tool—and constitutes yet another argument that long-term population studies are critical to our understanding of ecology and responses to long-term change (e.g., Dayton and Tegner 1984b).

What is the significance of these large interdecadal changes in giant kelp plant size as determined by stipe counts (figure 10) for the issue of long-term change? These data are inadequate to determine whether the decline in plant size was continuous from 1957 to before 1983, or whether the three historical data sets all happened to fall within cold periods, and the last twelve years have all been in a very warm period. Smith (1995) analyzed monthly SIO Pier temperature anomalies for the period 1940–93 for longer-term variability using a 24-month running mean. His results describe a long 1942–57 cold period followed by the 1957–59 El Niño, a cold period during 1960–66, a brief warm interval, a 1969–76 cold period, and finally the extraordinary 1977–93 warm period. North's 1957 data were from plants that had grown through the longest cold interval in this record before the ENSO had much impact in southern California; the 1973 and 1974 data came from plants which integrated the 1969–76 cold period. Thus much of the change in kelp biomass shown in figure 10 may be due to the location of these sample dates within warm and cold periods. Only time can resolve whether the 17-year warm anomaly that started in 1977, the longest in the 1922–94 period, is a harbinger of long-term increase in temperatures. We note that 1995 temperatures were much closer to the long-term mean and that more normal relationships between plant density, stipes per plant, and stipe density appear to

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[7] See footnote 1 on p. 112.

be establishing with the plants that recruited in 1994 (figure 9).

There was a two-thirds reduction in median plant size as measured by frond number from 1957 to 1993 at the same plant density. Given that the average wet weight of a frond in the 10–20-m depth range is about one kilogram (North 1994), this substantial reduction in *Macrocystis* biomass suggests the possibilities of secondary effects on kelp forest community structure and on the export of material to surrounding communities. The relationship between giant and understory kelps is governed by competition for light (e.g., Dayton et al. 1984, 1992); the range in stipe densities observed since 1957 suggests important effects on benthic light levels. Comparing the structure of the Point Loma kelp forest community following the large-scale disturbances of the winter 1982–83 and the January 1988 storms, we found major differences in *Macrocystis* population dynamics and its competitive interactions with lower-standing species (Tegner et al.[8]). There was intense kelp recruitment after both disturbances. Poor giant kelp growth, canopy formation, and survival during El Niño conditions in 1983–84 apparently allowed the persistence of understory populations. Extraordinary *Macrocystis* growth during 1988–89 La Niña conditions led to the near extinction of understory kelps in our study sites. In both cases, the anomalous oceanographic conditions at the beginning of these cohorts lasted about two years after the disturbances, but the effects on kelp community structure persisted for the lives of the *Macrocystis* cohorts, despite average or poor conditions later.

Once established, understory kelp patches have considerable resistance to invasion (Dayton et al. 1984; Dayton and Tegner 1984a). Thus one scenario for long-term change would be increased understory populations and less *Macrocystis*. This has obvious implications for the giant kelp harvest and is likely to affect animal populations as well, given the enhancing effects of *Macrocystis* on fish recruitment and abundance (reviewed by Cross and Allen 1993) or the importance of giant kelp drift to sea urchins (Tegner and Dayton 1991; Dayton et al. 1992). Kelp detritus exported to surrounding communities supports high secondary production and prey for many fishes (Vetter 1995); thus reduced *Macrocystis* production could have ramifications well beyond the kelp forest.

Differences between high-frequency ENSO events or even these longer-term warm and cold periods and long-term change include the rate of change and the time available for species to acclimate or evolve adaptions to cope with changing conditions (Lubchenco et al. 1993). Perhaps not surprising for a species ranging from central Baja California, Mexico, to north of Santa Cruz, California, *Macrocystis pyrifera* varies physiologically within its range. North (1971) observed giant kelp populations in Bahía Tortugas, near the southern end of the range, flourishing during 1957 when warm temperatures were associated with the deterioration of more northerly forests. Kopczak et al. (1991) demonstrated significant quantitative differences in the physiological responses to nitrate limitation in three geographically isolated populations of giant kelp with different natural patterns of nutrient availability. Kopczak et al. suggest that these populations have undergone genetic divergence that can be explained by ecotypic adaption to widely differing habitat nutrient conditions. Thus, over long time scales, *Macrocystis* may be able to adapt, at least in part, to global warming, as changing conditions select for ecotypes similar to that which Kopczak and colleagues found at their most oligotrophic site.

These rate-of-change and time-scale differences in biotic responses to ENSOs or warm and cold periods and to long-term global change clearly limit our ability to use these higher-frequency events as a look into the future. For the near-term future, however, we believe that *Macrocystis* stipe counts are a useful indicator of temperature effects on the carrying capacity of southern California kelp forest communities.

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[8] See footnote 1 on p. 112.

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SARDINE SYMPOSIUM

THE 1994 MEXICO–U.S. SPAWNING BIOMASS SURVEY FOR PACIFIC SARDINE (*SARDINOPS SAGAX*) AND THE 1995 CALCOFI SARDINE SYMPOSIUM

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INTRODUCTION

Mexican (Instituto Nacional de la Pesca) and U.S. (California Department of Fish and Game and the National Marine Fisheries Service) scientists carried out a daily egg production method (DEPM) survey during 11 April–14 May 1994 to measure the spawning biomass of Pacific sardine (*Sardinops sagax*). The project was the largest and most comprehensive cooperative survey of a transboundary fishery resource ever undertaken by government agencies in the two countries. Five research vessels from both countries (table 1) surveyed 380,000 km^2 along the west coast of the Californias from near San Francisco in the north to San Ignacio Lagoon (near Punta Abreojos), Baja California, in the south. The DEPM survey is described by Lo et al. and Macewicz et al. (this symposium).

Results of the 1994 DEPM survey were presented and discussed at the special Sardine Symposium held during the annual CalCOFI (California Cooperative Oceanic Fisheries Investigations) Conference in 1995 at Lake Arrowhead, California. The following pages contain seven papers that were originally presented at the Sardine Symposium, and one paper (Cisneros-Mata et al.) prepared afterward.

This introduction to the CalCOFI Sardine Symposium offers a historical perspective and outlines primary results from the DEPM survey. We conclude with our perspectives about uncertainties and directions for future research.

HISTORY

The Pacific sardine was once the largest fishery in North America, with peak landings of 664,000 MT during 1936 and peak biomass (ages 2+) of 3.6 million MT during 1934 (Murphy 1966; MacCall 1979). Sardine biomass fell to less than 10,000 MT by 1965; the fisheries collapsed; and the stock did not increase noticeably for about fifteen years (Barnes et al. 1992). Meanwhile, the demise of the Pacific sardine fishery became a well-known, textbook example (Hilborn and Walters 1992) of the boom-and-bust cycles characteristic of clupeoid stocks and fisheries.

As sardine biomass declined, fisheries collapsed in a southerly direction, beginning off British Columbia (Radovich 1982). Small fisheries off central and southern Baja California, at the southern end of the sardine's range, developed and continued after the collapse in the north was complete (Lluch-Belda et al. 1989). In addition, a substantial fishery for sardine developed in the Gulf of California (Cisneros-Mata et al. 1995). By state law, the California sardine fishery was significantly restricted in 1969 and virtually eliminated in 1972 (Wolf 1992).

Sardine science and research during and following the collapse of the historical sardine fishery were of exceptionally high quality. The historical work sets a high standard for current research and, more important, provides data and analyses that are a sound basis for comparison. Research during the historical period included large-scale tagging studies (Clark and Janssen 1945), the development of the CalCOFI program for regular and

TABLE 1
Vessels Used in the 1994 Daily Egg Production Method (DEPM) Spawning Biomass Estimate for Pacific Sardine

	Survey dates			
Vessels	From	To	Sampling	Region
RV *El Puma* (UNAM/INP)	18 April	11 May	Eggs	San Ignacio Lagoon, Baja California–Ensenada, Baja California
RV *MacArthur* (NMFS/NOAA)	18 April	11 May	Eggs	San Francisco–San Diego
RV *David Starr Jordan* (NMFS/NOAA)	14 April	4 May	Eggs	San Diego–Point Eugenia, Baja California
RV *Mako* (CDFG)	11 April	6 May	Adults	Point Conception, Baja California–San Diego
RV *BIP12* (INP)	18 April	12 May	Adults	San Ignacio Lagoon–Ensenada
Mexican commercial vessels	21 April	14 May	Adults	Vicinity of Ensenada
U.S. commercial vessels	4 April	5 May	Adults	Vicinity of Monterey Bay and San Pedro, Calif.

UNAM means Universidad Nacional Autónoma de México (Autonomous National University of Mexico); INP means Instituto Nacional de la Pesca; NMFS/NOAA means National Marine Fisheries Service/National Oceanographic and Atmospheric Administration; CDFG means California Department of Fish and Game.

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intensive ichthyoplankton sampling (Hewitt 1988), and the development of cohort analysis (Murphy 1966), also called virtual population analysis or VPA (Megrey 1989), for estimating trends in stock biomass from fisheries data. Many of these data sets (Roemmich and McGowan 1995; Jacobson and MacCall 1995) and methods (Murphy 1966; Megrey 1989) are used today to address important problems and issues.

RECENT DEVELOPMENTS

In the early 1980s, qualitative information (Wolf 1992) indicated that the Pacific sardine stock along the west coast of California and Baja California had begun to increase. In response to interest in commercial fishing off California, Wolf and Smith (1985) developed an "inverse egg production method" for estimating spawning biomass of sardine based on the area occupied by spawners. The inverse egg production method (Wolf and Smith 1986; Wolf et al. 1987) indicated that spawning biomass of sardine had grown to at least 20,000 MT, and in 1986, as specified in California law, a small quota (908 MT) was allowed for directed fishing in U.S. waters. At about the same time, sardine landings began to increase in Baja California at Ensenada (Jacobson et al. 1995) and as far south as Magdalena Bay (Félix-Uraga et al., this symposium).

Borrowing techniques developed for northern anchovy (*Engraulis mordax*), the California Department of Fish and Game (CDFG) carried out a DEPM survey (Lasker 1985) in 1986 that resulted in a sardine spawning biomass estimate of about 8,000 MT with a coefficient of variation (CV) of about 51% (Scannell et al. 1996). Additional DEPM surveys (Lo et al., this symposium) were attempted in 1987 (1,600 MT, CV 91%) and 1988 (14,000 MT, CV 160%). Imprecision and severe undersampling of adult sardines was a persistent problem in these first attempts to apply the DEPM to Pacific sardine. In addition, the estimates appeared suspiciously low. Difficulties in sampling adult sardine led to development of the high-speed trawl described by Dotson and Griffith (this symposium) for sampling pelagic fish.

Information from the early DEPM surveys (e.g., size of spawning area and estimates of adult reproductive parameters) was an important part of data used to manage the stock (Wolf 1992). As sardine biomass continued to increase, more sophisticated stock assessment models (Barnes et al. 1992; Deriso 1993) based on a wide range of fishery and fishery-independent data were developed. Results from the models verified that sardine biomass was increasing rapidly, but the current biomass was uncertain.

One of the key difficulties in early modeling studies was lack of information about adult reproductive parameters and age-specific net fecundity for sardine. These biological parameters are used to convert CalCOFI and other ichthyoplankton-based survey data to units of spawning biomass, and to convert estimates of spawning biomass to units of total biomass (Barnes et al. 1992; Deriso 1993). Another problem was that abundance data from CalCOFI, fish spotters (Lo et al. 1992), and other sources did not cover the entire range of the sardine, particularly as the stock's geographic range and abundance continued to expand.

Sardine fisheries are managed by the Instituto Nacional de la Pesca (INP) in Mexico, and by CDFG (with technical assistance from the National Marine Fisheries Service, NMFS) in the United States. Parties on both sides of the U.S.–Mexico border became concerned that increased harvest rates in the United States and Mexico would quash the long-awaited recovery of the sardine stock. Consequently, a workshop was convened in Rosarito, Baja California, during 1993 to bring together key persons from both nations to discuss the status of the sardine population and fisheries.[1] The Rosarito meeting included industry representatives, scientists, and government officials. After reviewing all available evidence, the participants concluded that sardine abundance was increasing, but that the size of the population and future trends were uncertain. The meeting was very productive because communication was enhanced, plans for future research were discussed, and the seeds of a shared scientific understanding were sown.

In May of 1993, following up on a proposal made at the Rosarito meeting, NMFS, INP, and CDFG resolved to carry out a cooperative DEPM survey to estimate spawning biomass of the recovering sardine population over as much of the spawning area as possible. Resources and ship time were limited in both countries, so cooperation and efficiency were critical. After many planning and coordination meetings in the United States and Mexico, and after countless phone calls, faxes, and e-mail messages, the joint survey was launched in April 1994.

RESULTS

All eight papers in the Sardine Symposium section of this volume contribute to the understanding of Pacific sardine. Dotson and Griffith's new, high-speed research trawl can be used to obtain better, more representative samples of sardine (and other pelagic fish) than are obtained from commercial purse seine catches. Butler et al. document the rapid individual growth rates and early sexual maturity that have contributed to rapid growth

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[1] Baumgartner, T., G. Hammann, and M. M. Mullin. 1993. A binational workshop for the scientific evaluation of the recovery of the Pacific sardine in the California Current—Final narrative report for the project of UC MEXUS Program on Environmental Issues and the U.S.–Mexican border. Unpubl. Rep. 24 pp.

of the sardine stock in recent years. Macewicz et al. give new estimates of batch fecundity and spawning frequency for sardine and suggest that reproductive data might be used to infer movements of sardine. Bentley et al. estimate that about 50,000 MT of sardine were spawning in the Columbia River plume off the Pacific Northwest during 1994, an area where sardine have been absent for decades. Bentley et al. and Lo et al. report that sardine spawning habitat occurs at temperatures of 14°–15°C along thermal fronts and coastal upwelling areas. Lo et al. hypothesize, based on this information, that sardine use suitable spawning habitat opportunistically. In addition to estimating spawning biomass in the DEPM survey area (111,000 MT, CV 33%), Lo et al. estimate the time of peak spawning for sardine and develop a temperature-dependent egg-development model. Bentley et al. give criteria for distinguishing between sardine eggs and eggs of similar size spawned by other fishes in northern areas. Using DEPM and other data, Deriso et al. estimate that Pacific sardine biomass (age 1+) during July 1995 was about 344,000 MT (CV = 33%) and that sardine biomass, despite fishing, increased by 28% year^{-1}, on average, during 1983–95.

Shifting to the southern end of the California sardine's range, Félix-Uraga et al. give new information about stocks and fisheries off central and southern Baja California (south of the DEPM survey area), an area that may serve as a refuge when sardine are rare in the north (Lluch-Belda et al. 1989). Finally, Cisneros-Mata et al. analyze deterministic effects of fishing, climate change, and other factors on abundance of Pacific sardine in the Gulf of California by using a simulation model and data that have only recently become available.

DISCUSSION

The 1994 DEPM survey demonstrated the ability of agencies in Mexico and the United States to work cooperatively and efficiently on large and complex field studies. Moreover, the survey and subsequent analyses resulted in significant scientific progress.

The 1994 DEPM survey provided answers to many questions, but uncertainties remain, and there are exciting new questions to be addressed. Deriso et al. (this symposium) estimate that DEPM spawning biomass estimates for Pacific sardine during 1994 and earlier years may have measured only 34%, on average, of the actual spawning biomass. We hypothesize that the DEPM survey areas (380,000 km^2 in 1994 and smaller in earlier years) were not large enough to encompass the entire spawning habitat. This hypothesis is supported by the historical geographic range of the sardine population (Mexico to British Columbia, Radovich 1982); spawning sardine in the Columbia River plume off Oregon during 1994 (Bentley et al., this symposium); observations of sardine off British Columbia during 1992–95 (Hargreaves et al. 1994); and the impending development of a small sardine fishery in Canadian waters (D. Ware, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC, V9R 5K6, Canada, pers. comm.).

New techniques of fisheries science are needed for surveying sardine when abundance is high and the geographic range of the stock is large (e.g., from Baja California to British Columbia during 1994) because it may be impossible to survey the entire stock with conventional techniques like the DEPM (Deriso et al., this symposium). Complicated models that measure the degree of undersampling (Butterworth et al. 1993; Deriso et al., this symposium) may be required to interpret DEPM and other data for large stocks. New survey technologies such as aerial lidar (light detection and ranging),[2] continuous underway egg sampling (Checkley[3]), adaptive sampling (Thomson 1992), and remote sensing (Simpson 1994) may provide information for larger areas in less time and at lower cost. New analytical approaches such as Bayesian statistics (Walters and Ludwig 1994) and geostatistics (Pelletier and Parma 1994) may make better use of the data that are collected.

Environmentally driven predictors for habitat size, in addition to new survey methods, may be required to effectively and efficiently survey sardine. It would be easier to devise cost-effective surveys if the boundaries of spawning (Bentley et al., this symposium) and feeding habitats could be predicted on the basis of satellite or other real-time environmental measurements. Despite difficulties in conducting and interpreting survey data, the experience of Deriso et al. (this symposium) indicates that survey-derived information is necessary to assess and manage the sardine fishery.

Sardine fisheries exist once again along the entire coast from Baja California to British Columbia. It is an opportune time for managers and scientists to reevaluate the assumptions about stock structure used to assess and manage the fisheries (Radovich 1982; Hedgecock et al. 1989). Is spawning habitat in northern areas important in terms of recruitment? Bentley et al. (this symposium) found that sardine egg production per unit area in spawning habitat off the Columbia River was as great as in the Southern California Bight, but that oil droplets in eggs were sometimes smaller and dispersed and that the size of eggs was more variable off Oregon. Do differences in eggs from northern areas imply reduced fitness? Peak catches in Magdalena Bay, at the southern

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[2] Lidar surveys use a laser at a frequency that penetrates water to locate fish schools (Hunter and Churnside 1995).

[3] Checkley, D. M., Jr. A continuous, underway fish egg sampler. MS.

end of the sardine's range, occur at much warmer temperatures than in northern areas. Are sardine in the south genetically adapted to their subtropical environments, or are these differences due to phenotypic plasticity? Are growth rates (Butler et al., this symposium) and maturity rates (Deriso et al., this symposium) of sardine in northern areas due to size-specific migration patterns or to localized adaptation? Did Deriso et al.'s (this symposium) estimate of sardine biomass implicitly include the sardine biomass discovered off Oregon by Bentley (this symposium)? Should fishery managers in California consider abundance of sardine off Oregon, Mexico, and elsewhere when regulating the California fishery? Can stocks along the west coast be assumed to mix because of dispersion or because of feeding and spawning migrations (Macewicz et al. and Félix-Uraga et al., this symposium)? Over what time scales does mixing occur? Should managers and scientists regard sardine along the west coast as a metapopulation comprising groups with restricted interchange or as a single, homogenous population? Are complicated, geographically stratified models required for management purposes?

CONCLUSION

Many of our questions and uncertainties about sardine were raised by scientists and managers decades ago. Clark and Marr (1955) proposed, for example, the existence of regional, partially intermixing, groups of sardine that migrate north and south along the coast of North America. It is likely that many questions will be answered as recent data augment historical information and as new statistical techniques are applied (e.g., Jacobson and MacCall 1995). Molecular and other genetic approaches to studying the distribution of fish (Hedgecock 1994), together with historical tagging studies (Clark and Janssen 1945) may, for example, answer questions about mixing of sardine and about localized adaptations. It is clear that the distribution and relationships among sardine along the west coast of North America, from Mexico in the south to Canada in the north, will remain an interesting topic of research in the coming years.

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A HIGH-SPEED MIDWATER ROPE TRAWL FOR COLLECTING COASTAL PELAGIC FISHES

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ABSTRACT

The development and testing of a new high-speed midwater rope trawl (HSMRT) was initiated in the fall of 1992 by the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service, Southwest Fisheries Science Center and the California Department of Fish and Game (CDFG). The HSMRT was designed to collect fishery-independent data for adult coastal pelagic fish species including Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), jack mackerel (*Trachurus symmetricus*), and Pacific mackerel (*Scomber japonicus*). Originally the trawl was constructed as a four-panel net with 53-meter head- and footropes with 6.5-meter meshes in the opening panels tapering down to 5-centimeter meshes in the rear and 10-centimeter meshes in the cod end. The net was modified after several cruises in 1992 and 1993 aboard NOAA's *David Starr Jordan* and CDFG's *Mako*. During fishing operations, targeted speeds of 4 to 4.5 knots were obtained by both vessels. For shallow tows, deployment took approximately 30 minutes with a fairly small crew (4–5 people). Fork lengths of fish captured ranged from 136 to 280 mm for Pacific sardine, 30 to 140 mm for northern anchovy, 50 to 320 mm for jack mackerel, and 60 to 450 mm for Pacific mackerel. Mature hydrated female sardine were taken during April–May, 1994, only by the *Mako*, which generally fished in deeper water than the *David Starr Jordan*. The HSMRT worked well on both the *David Starr Jordan* and the *Mako*, but because the *Mako* had less horsepower, it was unable to maneuver while trawling or to tow the net shallower than 18 meters below the surface.

INTRODUCTION

Fisheries research on coastal pelagic fish species (northern anchovy, *Engraulis mordax*; Pacific sardine, *Sardinops sagax*; jack mackerel, *Trachurus symmetricus*; and Pacific mackerel, *Scomber japonicus*) may require fishery-independent means to sample adult fish. Fishery-independent samples are generally advantageous because scientists are able to regulate sampling protocols and locations. A wider range of sizes or a more representative sample of adult fish may be obtained.

Commercial fisheries for coastal pelagic species typically use round haul fishing gear such as either purse seines or lampara nets near shore to capture coastal pelagic species off California (Browning 1980). Neither the National Marine Fisheries Service's (NMFS) *David Starr Jordan* nor CDFG's *Mako* have the capability to fish with round haul gear, but both vessels are suitable for trawling. Small midwater trawls towed at 2 knots had been used on the *David Starr Jordan* to capture adult and juvenile anchovy, with bycatches of juvenile jack and Pacific mackerel. Adult sardine, jack mackerel, and Pacific mackerel are, however, fast enough to escape a trawl net towed at two knots. Adult Pacific mackerel, jack mackerel, and sardines were caught in large commercial midwater trawls towed at speeds of 4–6 knots by Russian fishermen (Macewicz and Hunter 1993).

A cooperative project between NMFS, Southwest Fisheries Science Center (SWFSC), and CDFG was launched in late 1991 to develop a high-speed midwater rope trawl (HSMRT) capable of collecting the required samples from vessels (*David Starr Jordan* and *Mako*) operated by both agencies. We chose a rope trawl design similar to those used for the pollock (*Theragra chalcogramma*) and Pacific whiting (*Merluccius productus*) fisheries in the Pacific Northwest to provide the greatest mouth opening for herding and capturing fish.

The need to collect juvenile through adult sizes of anchovy, sardine, jack mackerel, and Pacific mackerel meant that the net had to capture and retain fish as small as 50 mm long and potentially as large as 800 mm long. The net had to be towable at depths from near surface to at least 100 m. Based on the experiences of Russian trawlers (Macewitz and Hunter 1993) and fisheries on other pelagic species, we decided that a towing speed of 5 knots would be fast enough to capture adult pelagic fish.

Before the development of our HSMRT, no sampling gear was available that could be used on all vessels operated by NMFS and CDFG to collect adult and juvenile pelagic fish species. The contract to build the net was awarded to Gourock Trawls in Seattle, Wash.[1] The HSMRT (net design no. R2024504) was built and delivered to the SWFSC for testing on November 6, 1992.

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[1] Reference to trade names or businesses does not imply endorsement by the National Marine Fisheries Service, National Oceanic and Atmospheric Administration.

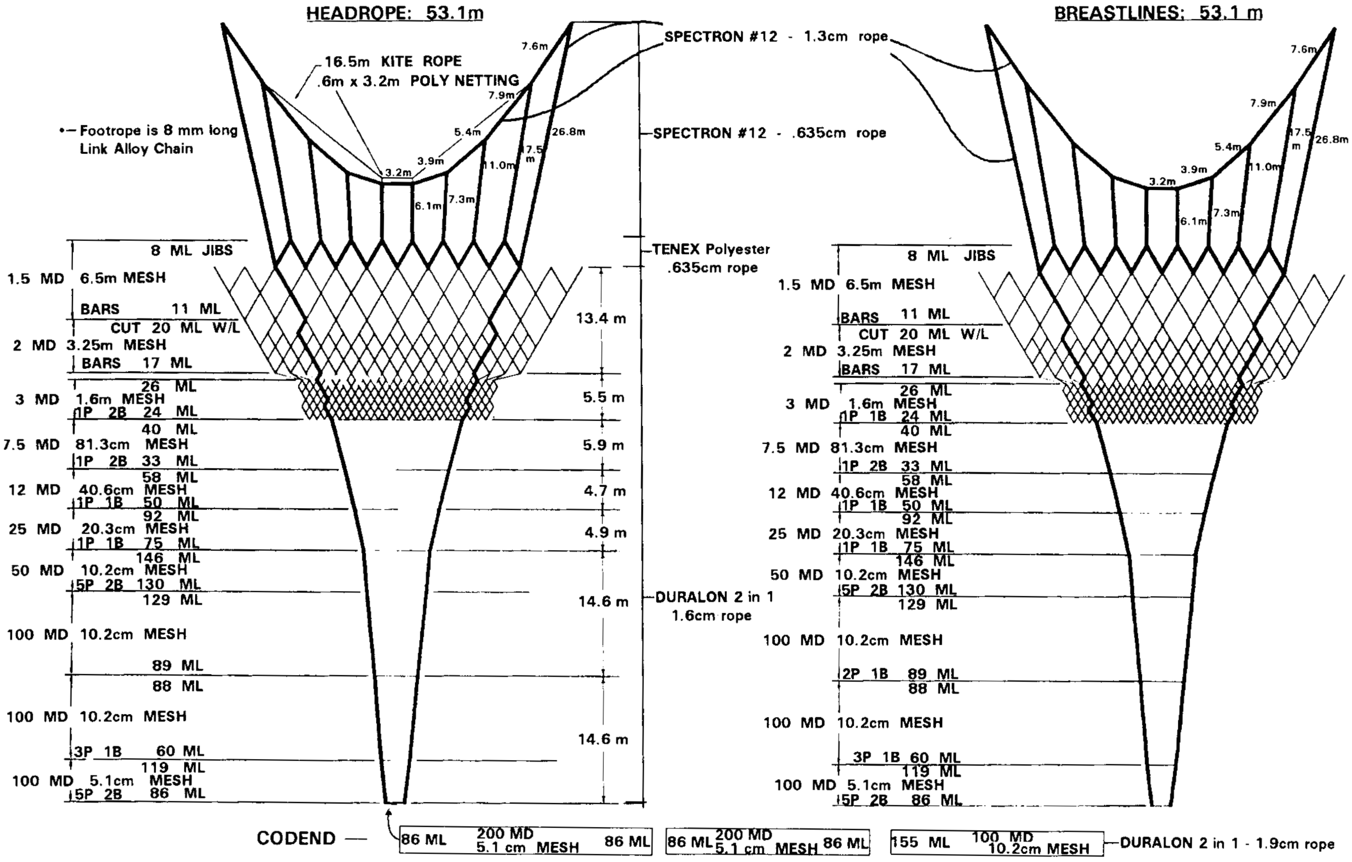

Figure 1. Diagram of high-speed midwater rope trawl (design #R202825A) with final modifications.

MATERIALS AND METHODS

Net Description

The HSMRT is a four-panel net that initially had a 53-m (174-ft) headrope and footrope, with 6,502-mm (256-in) meshes in the forward portion decreasing to 51-mm (2-in) meshes in the rear of the net and ending with a 102-mm (4-in) mesh cod end (figure 1). A funnel of 51-mm (2-in) mesh was built into the center to prevent escapement. Net twines were a combination of Spectra, nylon, and polypropylene.

The net was modified by Gourock Trawls in March 1993 after numerous tests on both the *David Starr Jordan* and *Mako* in 1992. Most of the Spectra twine was replaced with nylon because of excessive abrasion of the Spectra, and a new net design number (R202825A) was assigned. Further testing in 1993 indicated that there was too much drag and poor retention of anchovy and sardine. The 2.3-m^2 double foil Suberkrüb doors were therefore replaced by 1.8-m^2 doors (figure 2). A kite tied into the headrope to increase vertical height of the mouth opening was abandoned after testing indicated it did not work well. In March 1994, NMFS, Alaska Fisheries Science Center (AFSC) staff removed the funnel in the

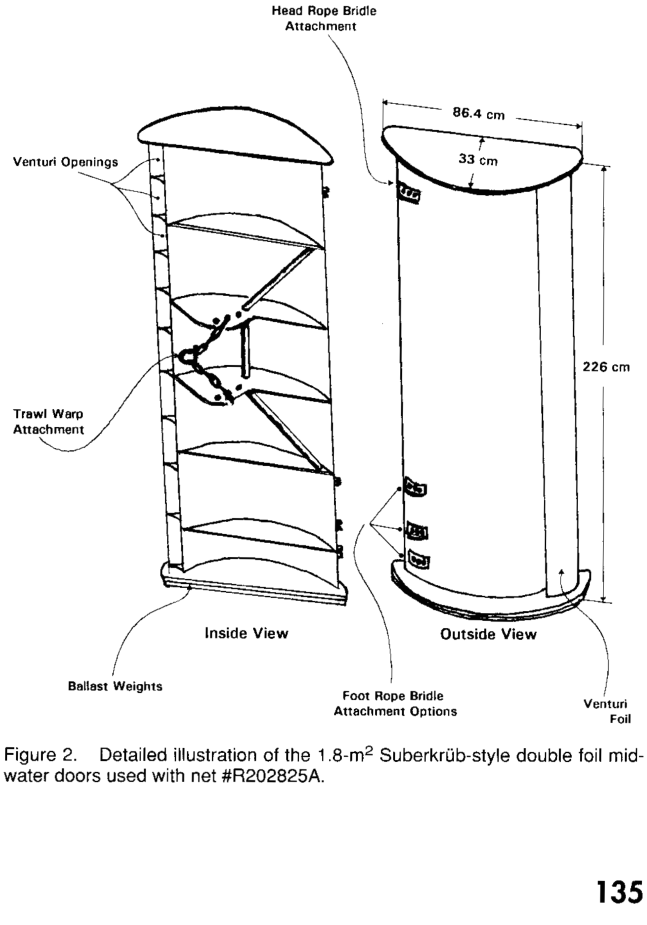

Figure 2. Detailed illustration of the 1.8-m^2 Suberkrüb-style double foil midwater doors used with net #R202825A.

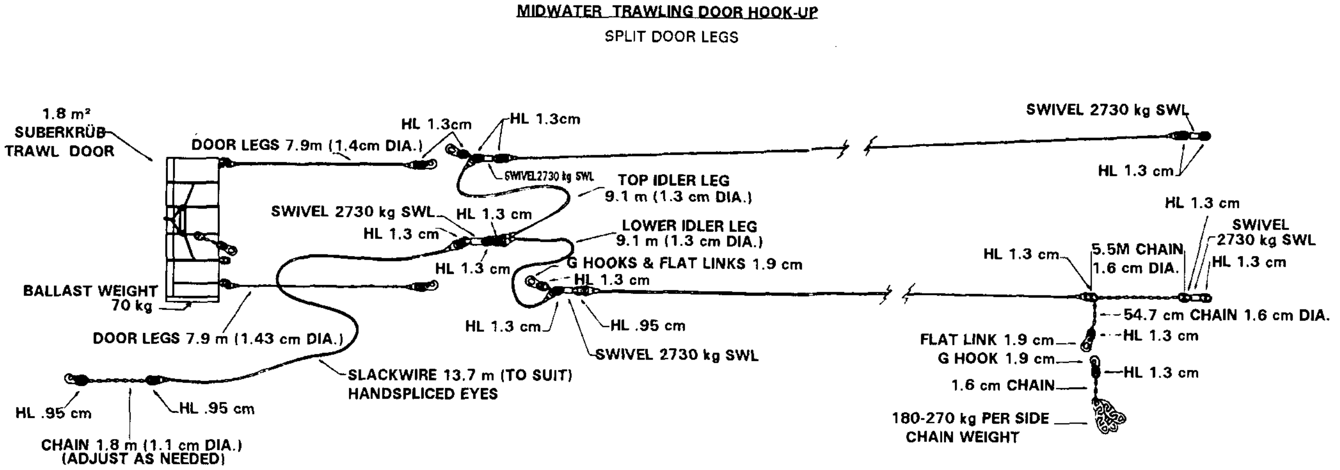

Figure 3. Equalizer bridle rig used with net #R202825A. The *David Starr Jordan* used 270-kg chain weights and 70-kg door ballast weights. The *Mako* fished with 180-kg chain weights and 35-kg door ballast weights. HL = hammer locks; SWL = safe working load.

center of the net to reduce drag, replaced 400 51-mm (2-in) tapered meshes in the rear of the net with 200 102-mm (4-in) tapered meshes, added a square intermediate of 400 51-mm (2-in) meshes just forward of the 102-mm-mesh cod end, and added a 13-mm-mesh liner to retain small fish (figure 1).

A bridle rig with zero setback (short section of chain between bottom bridle and footrope swivel) was used with weight chains of 180–270 kg (400–600 lbs) on the footrope bridles (figure 3). Costs for materials in the HSMRT during 1994, excluding labor, were about $13,000, with an additional cost of $3,825 for the 1.8-m^2 Suberkrüb double foil midwater doors.

Vessel Descriptions

The *David Starr Jordan* has a steel hull, is 52 m long, displaces 873 gross tons, and has twin screws with engines rated at 900hp (combined). The *Mako* has a steel hull, is 24 m long, displaces 146 gross tons, has a single screw with a Kort nozzle, and an engine rated at 503hp. Since the *Mako* was more limited in towing ability, its specifications were used as criteria for the net design.

Fishing the Net

Procedures for fishing the HSMRT were developed during cruises in 1992 and 1993 and during the sardine daily egg production method (DEPM) survey conducted from April 11 to May 14, 1994 (Arenas et al. 1996). A Wesmar scanning sonar (60kHz on the *David Starr Jordan* and 160kHz on the *Mako*) was used to find a target or multiple targets. Large schools of pelagic fishes could be detected at maximum ranges of about 500 meters on the *Mako* and 800 meters on the *David Starr Jordan*. If the schools were located during daylight hours, the position was noted, the immediate area surveyed for other schools, and the track line resumed if sufficient time remained before dark. Fishing was done only between sunset and sunrise because success is minimal during daylight hours (Mais 1974). At dark, the schools were relocated with the sonar and color depth sounder, and fishing began.

A minimum deck crew of four was required to set and retrieve the HSMRT. The total time from starting until all the trawl warp was deployed was about half an hour. The net was set at a speed of 3 knots and would sink to a depth of 80–100 meters before all the trawl warp was deployed and before the ship's speed was increased to raise the depth of the net. Downswell sets minimized entanglement of the large meshes and helped keep the Furuno netsonde on the headrope straight while the net was set.

Headrope depth was recorded on the *Mako*, and both headrope depth and vertical net height were recorded on the *David Starr Jordan*. Vertical net height on the *Mako* was determined with time/depth recorders (TDR, Wildlife Computers Model Mk3e). As the ship approached a school detected by sonar, it changed course to cross over the school. When the school passed under the ship, the depth of school was noted and the fishing depth of the net was adjusted by speeding up or slowing the vessel. It was much easier to lower the net than to raise it, so the net was generally brought in at a shallow depth and dropped slightly, if needed. Both vessels were able to tow at speeds of 4.0–4.5 knots. The duration of each tow was not standard (see below), but we generally retrieved the net once it had passed through a school or schools. Retrieval (until the cod end came on board) took about half an hour. A commercial fish-spotter pilot (Lo et al. 1992) was occasionally used to locate fish and to help set the net.

During fishing trials with the net on both vessels, we experimented with various door settings, chain weights, setbacks (increasing the length of the footrope bridle over that of the headrope bridle), and scopes of trawl warp (amount of cable out) in order to balance the net, maximize towing speed, and determine the best fishing depths and net configuration. Doors were equipped with several attachment holes for the trawl warp and bridles (figure 2). Different attachment points altered the angle of attack of the door's leading edge and changed the spread and lift provided by the door.

To fish near the surface, where most coastal pelagic species were found, the *David Starr Jordan* set 275 meters of 16-mm (0.625-in) trawl warp, 270-kg (600-lb) weight chains, even setback, and both bottom plates on the foot of each trawl door giving them a weight of 300 kg each. The *David Starr Jordan* was able to fish at headrope depths of 10 meters from the surface, and sometimes as little as 5 meters. The vertical height of the net was 15 meters, with a wingspread of 23–25 meters.

The configuration for fishing near the surface from the *Mako* was 137 meters of 16-mm (0.625-in) trawl warp, 180-kg (400-lb) weight chains, even setback, and with one 35-kg plate removed from the foot of each trawl door with a resultant door weight of 265-kg each. With this configuration, the *Mako* was able to fish the headrope within 15 meters of the surface, with a vertical net height of 18 meters and wingspread of 20 meters.

The *David Starr Jordan* was positioned about two miles upswell of the target to allow setting and positioning of the net before reaching the target. It was possible to detect fish entering the mouth of the net when using the Furuno netsonde. When it appeared that a quantity of fish had been captured, the tow was terminated to avoid capturing more than the 200 pounds of fish that was considered adequate for a sample.

The *Mako* positioned itself one mile upswell of the target before setting. The *Mako* netsonde did not monitor the mouth of the net, therefore the net was pulled after a set period of time or if, after large or multiple targets were passed, it was assumed that enough fish had been captured.

The *David Starr Jordan* could maneuver quite well in light to moderate seas, making course changes of 20° when approaching a school, and sometimes turning 180° if the school was missed. While turning, the net would sink; how much it sank depended on the sharpness of the turn.

The *Mako* had very little maneuverability with the net out, and turns often caused one of the doors to break the surface of the water. These differences between the *Mako* and *David Starr Jordan* probably result from the *Mako*'s smaller horsepower rating, smaller rudder, shorter trawl warp lengths, and lighter door weights.

RESULTS

Pacific sardine, northern anchovy, Pacific mackerel, and jack mackerel were all captured with the high-speed trawl during the DEPM survey. The size ranges of fish captured for each species were: Pacific sardine, 136–280 mm; northern anchovy, 30–140 mm; Pacific mackerel, 60–450 mm; and jack mackerel, 50–320 mm (tables 1 and 2).

TABLE 1
Total Catch Weight and Length Ranges for Coastal Pelagic Species Caught by the High-Speed Midwater Rope Trawl Aboard the *David Starr Jordan* during the 1994 DEPM Survey

Haul no.	Northern anchovy	Pacific sardine	Pacific mackerel	Jack mackerel
5		229 kg 200–280 mm	0.7 kg 340 mm	490 kg 240–320 mm
8	670.2 kg 70–100 mm			
9		17.8 kg 180–280 mm	24.1 kg 220–410 mm	3.3 kg 200–300 mm
12	0.2 kg 30–50 mm		0.04 kg 60 mm	0.09 kg 50–60 mm
14	8.5 kg 80–130 mm			
18		0.6 kg 240–260 mm	2.8 kg 300–370 mm	
26		6.1 kg 170–280 mm	115 kg 170–310 mm	2,235.5 kg 160–260 mm
27		9.1 kg 170–200 mm	52.1 kg 190–340 mm	494.7 kg 170–260 mm
29			42.4 kg 370–450 mm	
30			55.1 kg 390–450 mm	
31		58.5 kg 170–200 mm	16.1 kg 210–290 mm	0.4 kg 170–260 mm

TABLE 2
Total Catch Weight and Length Ranges for Coastal Pelagic Species Caught by the High-Speed Midwater Rope Trawl Aboard the R/V *Mako* during the 1994 DEPM Survey

Haul no.	Northern anchovy	Pacific sardine	Pacific mackerel	Jack mackerel
3		0.4 kg 181–187 mm	0.7 kg 220–290 mm	
4		8.8 kg 168–225 mm	0.07 kg 210 mm	
5		14.7 kg 158–200 mm		
6		2.4 kg 156–202 mm		
7		21.2 kg 160–203 mm		
9		49.5 kg 148–202 mm	10.2 kg 170–360 mm	6.6 kg 150–200 mm
10		45.8 kg 148–197 mm	5.3 kg 180–290 mm	2.8 kg 150–190 mm
14	11.9 kg 120–140 mm			
15	10.4 kg 110–140 mm			
16	82.2 kg 100–120 mm			
17	26.2 kg 110–140 mm			
20		0.6 kg 157–179 mm	2.9 kg 180–230 mm	3.9 kg 150–200 mm
21	38.3 kg 110–140 mm	0.1 kg 136 mm		

In addition to the four target species, we captured large numbers of lanternfishes (*Myctophidae* spp.), with ribbonfishes (*Trachipteridae* spp.), snipe eel (*Nemichthyidae* sp.), blackdragons (*Idiacanthidae* spp.), torpedo rays (*Torpedo california*), Molas (*Mola mola*), slender sole (*Lyopsetta exilis*), Pacific sanddab (*Citharichthys sordidus*), Pacific whiting (*Merluccius productus*), California smoothtongue (*Leuroglossus stilbius*), California barracuda (*Sphyraena argentea*), tuna crabs (*Pleuroncodes planipes*), market squid (*Loligo opalescens*), and various medusae and salps.

A disadvantage of sampling with a trawl is that it is impossible to determine from mixed catches whether they represent one school of mixed species or several schools of different species sampled over the course of the trawl. Trawling through an area where no targets were seen with electronics was generally nonproductive, and a few tows made during daylight produced no significant catches.

DISCUSSION

The HSMRT proved to be effective for sampling both young and adult coastal pelagic fish species ranging in size from 40 to 450 mm. The HSMRT was more effective in capturing adults, particularly Pacific mackerel, than the slower and smaller midwater trawls used during surveys of the California Current pelagic fish (Mais 1974). The HSMRT's design is similar to nets used to capture juvenile tunas (Tanabe and Ogura 1995). In areas where fish schools could be located with the sonar and depth-sounding equipment, it was generally possible to trawl with the net through the area and collect samples.

To determine if the HSMRT sampled a broader range of size classes than commercial round haul gear, we compared length-composition data for the HSMRT and purse seine samples from the Southern California Bight during the 1994 DEPM survey. No sardine longer than 230 mm were found in purse seine catches in nearshore areas, but they were caught in the high-speed trawl. Sardine smaller than 150 mm were poorly represented in the offshore trawl catches but made up a significant fraction of the purse seine catch (figure 4).

The primary restriction of the HSMRT is that it must be towed in moderately deep water, usually at least 70 meters. Because it sank during setting and hauling back, we typically set the net in water deeper than 200 meters and hauled back in water deeper than 150 meters. Towing was restricted to waters deeper than 70 meters for fear of the net sinking enough to snag the bottom during a course change or if the ship slowed down. Further experimentation may reduce this minimal bottom depth slightly, but probably to no shallower than 50 meters with the present hardware configuration. Some changes in the present hardware setup, such as adding floats to the headrope or changes in door settings, may

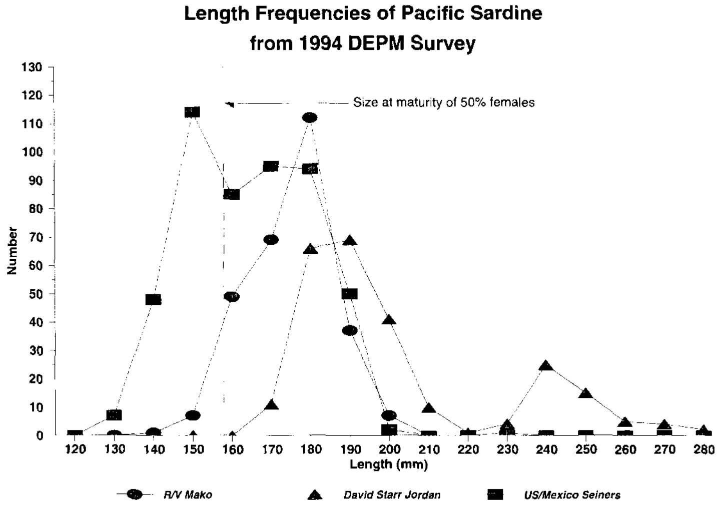

Figure 4. Length frequencies of Pacific sardine (*Sardinops sagax*) sampled during the 1994 DEPM survey within the Southern California Bight (includes Ensenada, Mexico).

allow fishing in shallower water. A fishing vessel must experiment with different door configurations, setback, and scope ratios to determine which are best for that individual vessel and the fishing application.

During the sardine DEPM survey in 1994, the larger and more powerful *David Starr Jordan* fished the HSMRT nearer the surface (as shallow as 5 meters headrope depth) than the *Mako* (minimum headrope depth of 15 meters) and encountered dense schools. These depths and schools fished by the *David Starr Jordan* were similar to those fished with purse seines by the commercial industry. The *Mako*, in contrast, fished on less dense schools of sardine and anchovy at depths of 20 to 40 meters.

Samples of sardine and anchovy collected by the *Mako* consistently contained mature females with hydrated eggs. The *David Starr Jordan*, which generally fished the net at shallower depths, did not capture any females with hydrated eggs. Samples from commercial seiners that fished in the shallow coastal waters were mostly immature females and small males (males not sexed). These preliminary results indicate that hydrated females are found primarily at depths of 20 to 50 meters. These collections of hydrated females, however, may be due to many factors other than depth. Time of collection and area fished were major influences in their occurrence (Butler et al. 1996).

We believe that the effectiveness of this net in capturing fast-swimming pelagics like Pacific mackerel, jack mackerel, and Pacific sardines bodes well for its use in sampling other pelagic species. The design of the HSMRT—which allows relatively high-speed towing by medium-sized vessels; easy deployment and retrieval with standard deck gear; a small crew; and capture of a wide size range of specimens—makes it an attractive sampling tool. The net may also be useful in studies of adult and subadult Pacific whiting (*Merluccius productus*), juvenile salmon (*Oncorhynchus* spp.), and juvenile pollock (*Theragra chalcogramma*) in the open ocean. Our results (figure 4) suggest that the greatest range in lengths of sardine and anchovy might be obtained by combining commercial (purse seine) and HSMRT samples.

ACKNOWLEDGMENTS

We would like to thank Dave King and Jim Smart of the NMFS Alaska Fisheries Science Center, Seattle, for their participation in the early trials of the net, for suggesting modifications, and for making many changes in the HSMRT design. We would also like to thank the officers and crew of the NOAA vessel *David Starr Jordan* and the CDFG vessel *Mako* for their efforts during the testing and early use of this net.

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ADULT REPRODUCTIVE PARAMETERS OF PACIFIC SARDINE (*SARDINOPS SAGAX*) DURING 1994

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ABSTRACT

The average female Pacific sardine, *Sardinops sagax*, spawned about once every 15 days along the Pacific coast off California and Baja California during April–May 1994. The relation between batch fecundity and female weight without the ovary (W_{of}) was best estimated by the equation $F_b = -10{,}585 + 439.53W_{of}$. Fifty percent of the females reached sexual maturity by 158.6 mm standard length (95% CI 155 mm–162 mm). Data from surveys off California during 1986–88 combined with the 1994 data indicated that peak daily spawning occurs between 19:00 and 22:59. The spawning cycle of sardine females with active ovaries averaged about one spawning every 7 days during 1986–94 off California. Our interpretation of the literature on sardine spawning indicates that they may spawn at similar rates in Chile, Japan, Australia, and South Africa. Finally, off California differences existed between months in the fraction of females that had active ovaries. These differences may indicate movements of groups of Pacific sardine away from and into the survey area.

INTRODUCTION

To assess spawning biomass using the daily egg production method (DEPM) of Parker (1980, 1985), one must estimate the following adult fish parameters (averages for the spawning population): daily spawning rate of mature females (spawning frequency), number of oocytes released per spawn (batch fecundity), fraction of the population by weight that is female (weight-specific sex ratio), and average weight of mature females. This paper provides estimates of adult Pacific sardine (*Sardinops sagax*) reproductive parameters for the 1994 season to be used in calculating the DEPM spawning biomass (Lo et al. 1996). We also estimate the probability of sexual maturity as a function of standard length and use histological criteria to examine the atretic state of sardine ovaries. We combine our data with those from earlier fecundity studies (MacGregor 1957; Scannell et al. 1996) and the adult reproductive parameters from DEPM estimates (Wolf 1988a, b; Scannell et al. 1996) to establish general relationships for batch fecundity, spawning frequency, and peak time of daily spawning for Pacific sardine. We compare data on Pacific sardine to that on *Sardinops* from around the world to determine if any general patterns in spawning frequency exist.

METHODS

From April 7 to May 14, 1994, adult Pacific sardine were collected from San Ignacio Lagoon (just south of Punta Abreojos), Baja California Sur, Mexico, to Monterey Bay, California, during a joint U.S.–Mexico DEPM survey (Arenas et al. 1996). Thirty-seven trawl or purse seine collections of sardine (taken at night between 1929 and 0500 hours) were usable for determining adult female reproductive parameters (table 1).

Sardine were randomly sampled from the catch. Up to 50 fish from each collection were sexed, and standard length was measured to the nearest millimeter. The first 5 males and first 25 females in each sample were individually weighed to the nearest gram; otoliths were removed for aging (Butler et al. 1996); and gonads were removed and preserved in 10% neutral buffered formalin. If the first 25 females included females with small ovaries in which yolked oocytes were not visible (female potentially immature), more females were taken with the intention of bringing the total number of mature females to 25.

From time to time additional fish were selected after the random sample because they were small, large, or had hydrated ovaries. These fish were used to increase the size range for aging or the number of fecundity samples but were not used to estimate spawning frequency, which requires a representative or random sample from the population.

The female proportion by weight was determined for each collection. The average weight of males and females (calculated from the first 5 males and 25 females) was multiplied by the number of males or females in the random 50-fish subsample to calculate total female and male weights in each subsample. Thus the female proportion by weight in each collection is calculated as total female weight divided by the sum of total female weight and total male weight (table 1). The estimate of the population's weight-specific sex ratio was calculated by methods given in Lo et al. (1996) and Picquelle and Stauffer (1985).

In some instances, on a few vessels included in the survey, only a piece of the ovary was preserved. It was

TABLE 1
Proportion of Female *Sardinops sagax* by Weight[a] Taken in Trawls (T) and Purse Seines (P) during April–May 1994

Collection number	Gear type	Latitude	Longitude	Month/day	Time (h m)	Proportion of females
667	P	36°52.0'N	121°52.2'W	4/22	0402	0.562
666	P	36°37.4'	121°51.2'	4/21	0345	0.433
664	P	36°37.4'	121°54.4'	4/20	0535	0.426
665	P	36°37.2'	121°51.4'	4/21	0109	0.518
663	P	36°36.8'	121°53.6'	4/20	0125	0.587
643	T	33°55.8'	118°33.8'	4/15	0417	0.540
642	T	33°55.4'	118°34.4'	4/15	0247	0.414
660	P	33°41.5'	118°19.5'	5/04	2330	0.619
659	P	33°41.5'	118°19.5'	5/04	2330	0.683
662	P	33°38.6'	118°15.4'	5/04	0309	0.654
655	P	33°37.8'	118°06.1'	4/28	2200	0.622
661	P	33°36.1'	118°02.6'	5/04	0002	0.621
656	P	33°28.2'	117°45.0'	4/30	2300	0.582
657	T	33°09.8'	118°20.2'	5/02	0445	0.294
649	T	33°03.1'	118°23.2'	4/19	2336	0.653
648	T	33°02.8'	118°24.1'	4/19	2117	0.672
645	T	33°00.4'	119°14.8'	4/17	0408	0.212
644	T	32°55.8'	119°06.9'	4/17	0053	0.023
634	T	32°55.7'	117°26.1'	5/07	2223	0.586
646	T	32°55.1'	119°11.9'	4/18	0054	0.892
629	T	32°39.2'	117°59.5'	5/05	1929	0.790
630	T	32°39.1'	118°00.9'	5/06	0037	0.571
611	T	32°05.9'	118°16.8'	4/22	0100	0.467
623	T	32°04.4'	118°15.4'	5/02	2015	0.714
685	P	32°03.0'	116°57.0'	5/14	0100	0.504
683	P	31°48.0'	116°46.0'	5/05	0155	0.597
682	P	31°48.0'	116°46.0'	5/04	0100	0.510
684	P	31°46.0'	116°44.0'	5/07	0355	0.437
687	P	31°36.0'	116°42.0'	4/07	0500	0.513
679	P	31°36.0'	116°42.0'	4/21	0800	0.437
680	P	31°36.0'	116°42.0'	4/22	0255	0.499
675	T	30°20.5'	115°57.8'	5/03	1955	1.000
615	T	28°31.4'	115°32.6'	4/25	0044	0.175
672	T	28°14.8'	114°13.0'	4/27	2203	0.701
673	T	28°03.0'	115°10.6'	4/29	2034	0.430
670	T	27°42.8'	115°11.0'	4/25	0130	0.545
668	T	26°40.1'	113°29.6'	4/22	2015	0.748

[a] Sex ratio based on average weights (Picquelle and Stauffer 1985).

TABLE 2
Conversion Equations for Pacific Sardine (*Sardinops sagax*) by Location and Maturity

Dependent variable Y	Independent variable X	Area divided at 32°04'N	Mature	Linear equation $Y = a + bX$					Range of X
				a	b	r^2	F	N	
Female wet weight	Ovary-free wet weight	North[a]	Yes	−5.113	1.1055	0.996	79,782.69	362	50.1–269.1
		South	Yes	−1.909	1.0508	0.996	37,802.39	141	19.9–127.4
		North	No	−0.454	1.0136	0.999	132,811.34	28	32.0–88.9
		South	No	−0.1012	1.0079	0.999	861,020.06	68	21.9–108.2
Ovary weight	Ovary-free wet weight	North	Yes	−5.111	0.1054	0.67	725.19	362	50.1–269.1
		South	Yes	−1.820	0.0506	0.49	135.55	141	19.9–127.4
		North	No	−0.437	0.0133	0.47	22.72	28	32.0–88.9
		South	No	−0.1001	0.00791	0.46	56.86	68	21.9–108.2
Ovary weight	Female wet weight	North	Yes	−5.049	0.0994	0.73	971.94	362	53–281
		South	Yes	−1.871	0.0504	0.54	165.60	141	20–133
		North	No	−0.442	0.0134	0.48	24.01	28	32–90
		South	No	−0.102	0.00792	0.47	58.84	68	22–109
Male wet weight	Testis-free wet weight	North	Both	−4.083	1.0954	0.995	17,425.67	96	44.4–203.5
		South	Both	−1.421	1.0408	0.999	283,182.09	173	21.0–240.8

[a] Equation used to predict whole wet weight for females with hydrated ovaries because hydration inflates whole body weight.

therefore necessary to estimate ovary weight from fish weight so that ovary-free female weight could be calculated for females with incomplete ovaries. This is especially important for any mature female used during biomass estimation. In table 2, we provide the conversion equations.

Histological Classification

Each preserved ovary was blotted and weighed to the nearest milligram in the laboratory. A piece of each was removed and prepared as hematoxylin and eosin (H&E) histological slides (Hunter and Macewicz 1985a). All slides were then analyzed and classified.

In Pacific sardine, oocytes develop asynchronously; that is, oocytes in many stages of development occur simultaneously in reproductively active ovaries (Wallace and Selman 1981). Andrews[1] used many histological stages to describe the development and absorption (atresia) of oocytes in Pacific sardine ovaries off southern California. Torres-Villegas (1986), Alarcón et al. (1984), Goldberg et al. (1984), Retamales and González (1984), and Aguilera et al. (1986) used less complex classification systems similar to that developed for the northern anchovy (*Engraulis mordax*) by Hunter and Goldberg (1980) and Hunter and Macewicz (1985a, b) to describe Pacific sardine ovaries off Mexico, Peru, and Chile. We also followed the Hunter and Goldberg (1980) and Hunter and Macewicz (1985a, b) methods of histological classification. With a few modifications for the ovarian structure of Pacific sardine, we recorded the presence or absence of unyolked oocytes; oocytes in early vitellogenic stages (diameters of 0.27–0.6 mm); advanced yolked oocytes (minimum diameter about 0.44 mm); oocytes in migratory-nucleus stage (precursor to hydration, beginning about 0.56 mm in diameter); hydrated oocytes (≥0.8 mm diameter); any atresia; and postovulatory follicles.

Hydrated oocytes in Pacific sardine contain an oil droplet that can be used for staging the ovary. Before vitellogenesis starts, lipid droplets first appear in oocytes of ≥0.25-mm diameter. As the oocyte grows and acquires yolk, the lipid droplets gradually surround the nucleus and begin to fuse. Just before migration of the nucleus, the partially fused lipid droplets move to the side of the nucleus opposite the direction of nuclear migration. The 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, migratory-nucleus-stage oocytes can be detected much earlier in species with an oil droplet—such as Pacific sardine; Pacific mackerel, *Scomber japonicus*, (Dickerson et al. 1992); or jack mackerel, *Trachurus symmetricus*, (Macewicz and Hunter 1993)—than in species such as the northern anchovy, which lack an oil droplet.

We classified atresia in ovarian sections by using the system of Bretschneider and Duyvene de Wit (1947) and Lambert (1970), as modified by Hunter and Macewicz (1985b). The presence or absence of alpha (α) atresia of previtellogenic, early vitellogenic, or advanced-yolked oocytes, and beta (β) atresia was recorded. We use β atresia in ovaries with only unyolked oocytes and without postovulatory follicles to identify postbreeding females. Postbreeding females are mature females that are no longer active and considered to be incapable of further spawning in the season.

Maturity was calculated as the fraction of all females that were histologically classified as mature. Immature females have ovaries with no β atresia and only unyolked oocytes present (a few oocytes in the earliest stage of yolk deposition may be present). Some ovaries classed as immature may contain α atresia of unyolked oocytes. All females not identified as immature were considered mature. Females were grouped into 10-mm length classes, and the length at which 50% were mature was estimated by logistic regression by means of the computer program BMDPLR (Dixon et al. 1988).

Spawning Frequency

We used aged postovulatory follicles to estimate spawning frequency of Pacific sardine, following the methods of Hunter and Goldberg (1980) and Hunter and Macewicz (1985b). The best method for establishing aging criteria for postovulatory follicles is to spawn fish in the laboratory and sample at known times after spawning, but this has not been done for Pacific sardine. All previous investigators (Goldberg et al. 1984; Alarcón et al. 1984; Retamales and González 1984; Aguilera et al. 1986; and Torres-Villegas 1986) developed their aging criteria by examining a time series of field-collected material and by assuming the peak hour of spawning. We also relied on this method; our resulting histological criteria were essentially the same as those described by Goldberg et al. (1984). Thus the presence of hydrated oocytes or new (without deterioration) postovulatory follicles was used to estimate spawning frequency of females spawning on the night of capture, and the presence of older postovulatory follicles (about 20–30 h old) was used to estimate the spawning frequency of females that had spawned the night before capture.

Batch Fecundity

Batch fecundity (F_b, number of oocytes per spawn) was considered to be the number of migratory-nucleus-stage oocytes or number of hydrated oocytes in the ovary (Hunter et al. 1985). Females that may have lost oocytes

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[1] Andrews, C. B. 1931. The development of the ova of the California sardine (*Sardina caerulea*). Unpubl. MS. 88 pp. Stanford University, Stanford, CA 94305.

because they had begun to ovulate and spawn (ovaries with hydrated oocytes and new postovulatory follicles) were not used to determine batch fecundity. We used the gravimetric method to estimate batch fecundity (Hunter et al. 1985, 1992). We teased apart the oocytes in a few drops of 50% glycerin, and identified, counted, and measured them with a digitizer linked by a video camera system to a dissection microscope. We averaged the counts in two or more weighed tissue samples (usually one sample from the central region of each side of an ovary). We estimated mean batch fecundity for 51 females (6 based on counts of hydrated oocytes, and the remaining 45 on counts of migratory-nucleus-stage oocytes) and then determined the relation to female weight (without ovary).

We did not test for how the location of the tissue sample affects batch fecundity estimates. Lo et al. (1986) indicated that such an effect may exist for Peruvian sardine, whereas Clark (1934) and MacGregor (1957) found no such effect for Pacific sardine off California. Our tissue samples came from the central region of the ovary. According to Lo et al. (1986), fecundity estimates based on this location are about 4% higher than the average for hydrated ovaries of Peruvian sardine.

In fecundity preparations from formalin-preserved material, migratory-nucleus-stage and hydrated oocytes are easily identified. Hydrated oocytes are very large and translucent, with faint segmentation 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 may have a wide, clearish, peripheral band that results from the fusion 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. Migratory-nucleus-stage oocytes are detectable in whole oocyte material only after most of the lipid droplets have accumulated and begun to fuse. Earlier stages involving movement and fusion of lipid droplets can be consistently detected only in histological sections.

RESULTS AND DISCUSSION

Size, Sex, and Maturity

Standard length of sardine in the samples ranged from 131 to 284 mm for females and from 128 to 283 mm for males (figure 1). The proportion by weight of the population that was female was 0.537 (Lo et al. 1996). Following the recommendation of Picquelle and Stauffer (1985), we adjusted for bias in female weight caused by females with hydrated ovaries by using the linear regression equation (table 2) for the area north of 32°04'N latitude, where all the hydrated females were taken. The mean whole wet weight and ovary-free wet weight of the mature females (N = 583) used to estimate spawning frequency was 82.5 grams and 79.3 grams, respectively (table 3).

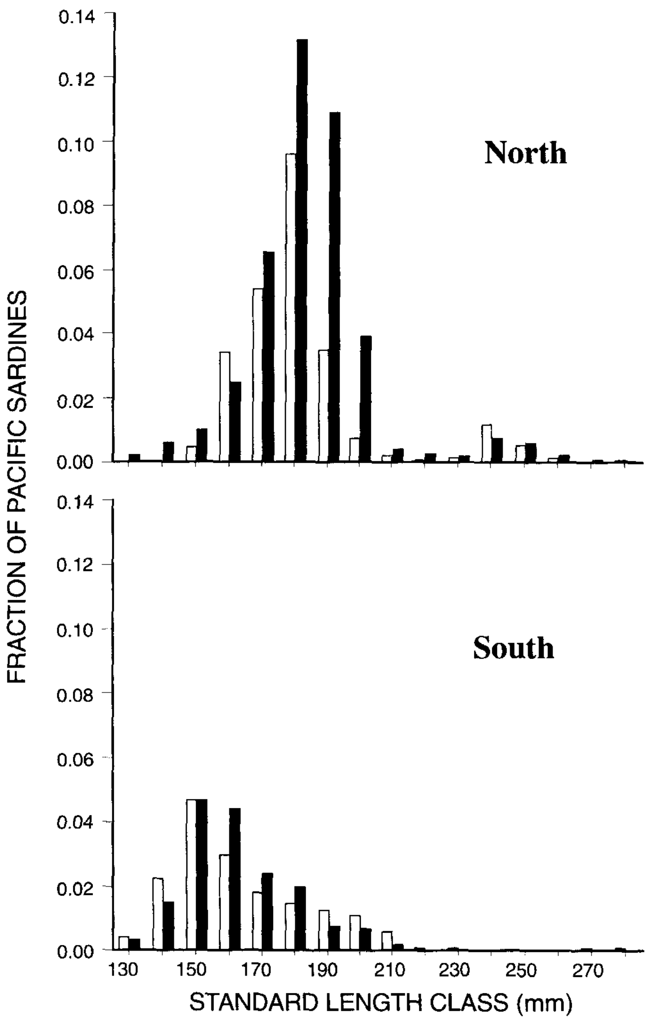

Figure 1. Length distribution for Pacific sardine (total N = 1,343) in the random subsamples taken by trawls and purse seines during 1994, for areas north and south of 32°04'N latitude. Males = *open bar*; females = *closed bar.*

According to logistic regression results (table 4), 50% of the females taken in the survey were sexually mature at a standard length of 158.6 mm (figure 2). We divided the females into the same three latitudinal areas used by Butler et al. (1996) and determined the length at 50% mature and the 95% confidence interval (CI) for each area (table 4). We compared two methods of using CI to detect differences in population means (Lo 1994), and neither detected a difference in the populations. Therefore we feel confident that we can pool the data and that our estimate (158.6 mm) is acceptable over the whole area studied during 1994.

TABLE 3
Parameters for Mature Female *Sardinops sagax* Used in Estimation of 1994 Biomass from Individual Samples

Collection number	Number of mature females	Average whole weight (g)	Average ovary-free weight (g)	Average batch fecundity (oocytes)	Number of females spawning: Night of capture	Number of females spawning: Night before capture
667	23	78.0	75.7	22,704	0	0
666	9	83.8	81.4	25,180	0	0
664	24	98.7	94.6	31,014	0	0
665	25	89.2	86.0	27,196	0	0
663	25	95.6	91.7	29,725	0	0
643	25	79.7	77.4	23,449	6	2
642	2	85.0	82.3	25,593	0	1
660	25	86.4	84.2	26,416	0	0
659	25	87.0	84.6	26,592	0	0
662	22	73.8	71.8	20,953	0	1
655	18	83.9	82.2	25,545	0	0
661	8	77.0	74.0	21,937	0	0
656	15	75.7	74.0	21,956	0	0
657	2	61.0	59.2	15,442	0	0
649	16	70.8	67.1	18,909	2	3
648	25	65.4	62.4	16,827	8	3
645	5	100.2	94.2	30,833	1	2
644	8	88.2	83.7	26,190	5	0
634	25	86.9	83.0	25,907	1	5
646	25	84.6	79.0	24,130	0	0
629	25	80.1	76.9	23,212	0	6
630	25	82.9	79.0	24,148	2	4
611	25	192.9	178.2	67,738	0	0
623	2	215.5	192.8	74,181	0	0
685	4	34.9	34.8	4,694	0	0
683	25	52.6	52.0	12,278	0	6
682	25	36.9	36.7	5,545	0	0
684	1	33.4	33.3	4,043	0	0
687	6	61.8	60.6	16,045	0	0
679	2	29.0	28.9	2,099	0	0
680	3	27.7	27.6	1,551	0	0
675	1	63.0	62.2	16,762	0	0
615	25	106.0	101.6	34,076	11	4
672	25	49.4	48.3	10,630	0	3
673	6	60.0	59.6	15,621	0	0
670	6	51.7	51.2	11,930	0	0
668	25	77.8	77.3	23,382	0	3
All	583	82.5	79.3	24,282	36	43
SE		1.4	1.2	2,617		

TABLE 4
Logistic Model[a] Parameters and Estimated Standard Length at Which 50% of Pacific Sardine Females Were Sexually Mature

Latitudinal area[b]	Length at 50% mature (mm)	95% CI	a	SE	b	SE	N
26°35'–36°55'N	158.6	155–162	−18.16	1.55	0.1145	0.0094	632
36°35'–36°55'N	160.6	128–191	−22.31	4.72	0.1389	0.0277	125
31°35'–33°59'N	159.3	156–162	−19.53	1.92	0.1226	0.0117	443
26°35'–30°25'N	159.1	154–163	−18.60	3.83	0.1169	0.0237	103

[a] $$P = \frac{e^{a+bL}}{1+e^{a+bL}}$$

[b] Data from whole 1994 survey and divided into three areas.

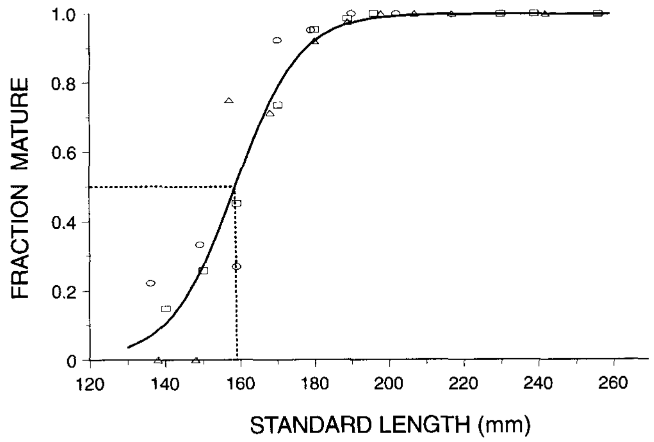

Figure 2. Fraction of Pacific sardine females that were sexually mature as a function of standard length (logistic curve parameters: $a = -18.16$; $b = 0.1145$). *Dotted line*, estimated length at which 50% of the females were mature (158.6 mm). Curve estimated from random females caught within entire 1994 survey area. Symbols represent actual *fraction mature* within 10-mm length classes for females in each latitudinal area: *triangle* = 36°35'N–36°55'N; *square* = 31°35'N–33°59'N; and *circle* = 26°35'N–30°25'N.

Batch Fecundity

The relation between female weight (without ovary, W_{of}) and batch fecundity (F_b) for the 51 females taken in the 1994 survey (table 5), as determined by simple linear regression, was

$$F_b = -10{,}585 + 439.53W_{of}$$

where $r^2 = 0.92$, and W_{of} ranged from 39 to 231 g (table 6). We tried using a power function to model the relationship, but it did not fit the data as well ($r^2 = 0.85$). Additionally, a linear function is easier to use in comparisons and during computations for biomass estimation. Thus we used the above equation to predict batch fecundity for each of the 583 mature Pacific sardine females used to estimate spawning frequency. The mean predicted batch fecundity for these females was 24,282 oocytes (table 3), equivalent to a relative fecundity of 306 oocytes per gram fish weight (24,282 oocytes/79.3-g female).

We used covariance analysis to test for differences in the relation between batch fecundity and female weight (without ovary) in sardine from 1986, 1987, and 1994. California Department of Fish and Game (CDFG) provided the data sets for females collected during past Pacific sardine surveys off southern California in 1986 ($N = 44$) and 1987 ($N = 56$). No statistical difference existed among slopes from the three data sets ($P = 0.234$). Assuming that the slopes were equal, covariance analysis indicated that the adjusted group means were not different at the 5% significant level ($F_{2,147} = 3.00$, $P = 0.053$). Combining the data from all three years (figure 3) yielded the equation

$$F_b = -13{,}677 + 471.79W_{of}$$

TABLE 5
Batch Fecundity[a] of 51 *Sardinops sagax* Females Taken in 1994

Collection number	Fish number	Standard length (mm)	Body weight without ovary (g)	Ovary weight (g)	Batch fecundity (oocytes)
672	26	149	39.13	2.400	6,012
672	65	158	47.20	2.300	8,492
648	63	161	50.00	15.380	19,553
648	23	160	51.83	4.060	12,863
672	63	167	53.74	2.900	7,177
648	37	168	57.63	4.318	16,885
683	02	183	58.00	5.400	13,434
649	40	168	59.88	5.301	17,578
648	51	170	61.06	23.005	28,027
649	29	171	63.78	5.404	17,776
648	10	172	64.56	8.260	22,863
672	70	174	65.57	4.400	19,711
646	15	170	66.50	8.330	23,880
648	22	171	67.42	4.599	14,473
630	27	181	70.66	5.568	16,921
646	30	174	73.70	8.072	24,676
646	07	175	74.15	10.067	25,097
646	06	176	75.22	6.126	22,284
630	39	182	75.81	9.217	27,262
648	27	182	76.59	19.762	22,035
646	24	184	76.71	10.632	29,928
646	28	185	78.36	7.224	25,516
646	02	180	78.69	6.809	23,258
648	05	192	79.76	29.789	31,698
630	18	192	80.20	8.724	29,920
646	10	184	80.76	11.850	26,955
661	07	184	81.49	8.349	25,757
634	08	187	81.71	4.219	12,376
646	13	178	81.90	7.821	24,728
661	05	186	82.99	5.140	23,583
630	21	189	86.84	10.456	25,510
615	11	191	87.25	7.375	22,930
646	12	189	88.40	9.740	26,767
634	05	192	89.47	7.095	25,141
615	19	197	92.24	9.957	28,842
615	57	197	95.48	7.072	21,116
644	55	200	98.22	9.969	31,637
645	30	197	99.17	12.599	31,453
648	01	202	104.85	36.085	32,152
615	37	200	105.69	9.388	30,993
615	59	208	112.78	11.815	32,260
611	37	237	149.73	14.446	48,305
611	30	238	151.93	18.035	51,265
662	54	242	162.49	18.605	57,233
611	66	247	169.00	24.354	75,422
611	39	251	183.12	21.635	60,301
611	18	250	184.95	26.990	76,034
623	02	255	196.88	32.211	82,695
611	59	265	197.20	24.103	64,647
611	27	267	198.87	28.375	91,603
611	52	290	230.67	40.169	94,486

[a] Batch fecundity—number of oocytes to be spawned in the batch—was determined from counts of hydrated oocytes or migratory-nucleus-stage oocytes in the ovary.

TABLE 6
Linear Regression Coefficients for the Relation between Female Weight (W_{of}, Ovary-Free, in g) and Batch Fecundity (F_b) for Pacific Sardine, *Sardinops sagax*, from 1946 (MacGregor 1957), 1986, 1987, 1994, and the Three Recent Years Combined

Year	Linear equation $F_b = a + bW_{of}$								Estimate for 130-g female	Female weight	
	a	SE	b	SE	r^2	F	s[a]	N		Mean	Range
1994	−10,585	1,907	439.53	17.78	0.93	611	5,844	51	46,554	97	39–231
1986	−21,018	9,330	495.76	52.65	0.68	89	11,890	44	43,430	174	103–244
1987	−21,088	10,564	531.83	62.72	0.57	72	14,763	56	48,050	165	97–237
1986–94	−13,677	2,874	471.79	18.73	0.81	634	11,735	151	47,658	145	39–244
1946	3,300	NA	250.00	NA	0.60	NA	5,100	40	35,800	132	95–169

[a] s is the square root of the MS error of the regression line.

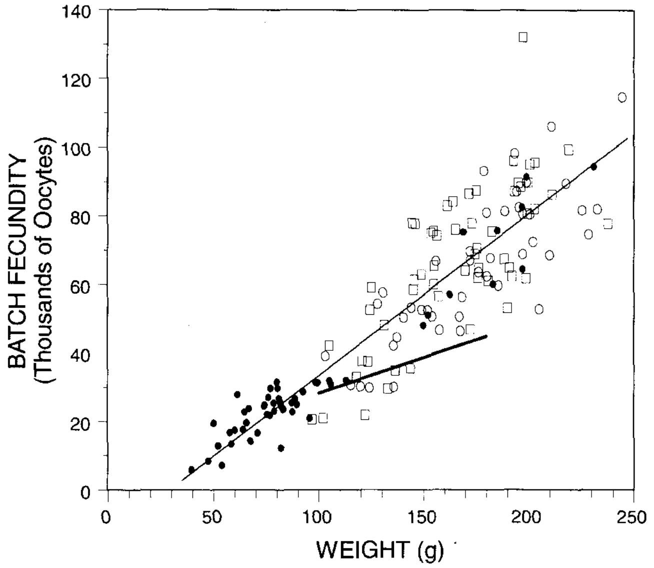

Figure 3. Batch fecundity (F_b) of *Sardinops sagax* as a function of female weight (W_{of}, without the ovary) for 151 females taken during 1994 (*closed circle*), 1986 (*open circle*), and 1987 (*open square*). The batch was estimated from numbers of migratory-nucleus-stage oocytes or hydrated oocytes. The fitted regression line was $F_b = -13,677 + 471.79\ W_{of}$ where $r^2 = 0.81$ (*thin line*). For comparison, we include the regression $F_b = 3,300 + 250W_{of}$ (*thick line*) for 40 sardine females taken in 1946 (MacGregor 1957).

where $r^2 = 0.81$, and W_{of} ranged from 39 to 244 grams (table 6).

MacGregor (1957) estimated that the relation between batch fecundity and female ovary-free weight for 40 Pacific sardines captured in February 1946 was $F_b = 3,300 + 250W_{of}$ ($r^2 = 0.60$). We compared the slope of his regression to the slope of the regression for the combined data ($N = 151$) from the recent studies and the estimated batch fecundity from each model for a 130-g fish (without ovary). Both the slopes and predicted value for batch fecundity differed significantly (slopes, $t = -4.94$; estimated fecundity at 130 g, $t = -9.25$).

It is possible that the difference in batch fecundity may be due to the techniques used by MacGregor (1957). He states that he estimated fecundities only for ovaries with a distinct group of advanced-yolked ova differentiated by size from the smaller-yolked ova. This could cause an underestimate of fecundity if the oocytes destined to form the hydrated batch were not fully recruited into the modal group counted by MacGregor.

Alternatively, this difference may be related to the biomass of the stock, since the estimated biomass of Pacific sardine in 1986, 1987, and 1994 was 44, 69, and 246 thousand MT, respectively (age 1+, Deriso et al. 1996); whereas in 1946, when MacGregor took his samples, it was estimated to be 566 thousand MT (age 2+, MacCall 1979). Both batch fecundity and somatic growth (see Butler et al. 1996) were apparently lower when the population of Pacific sardine was higher. Thus, more food may have been available per sardine in recent times (1986–94) than in the past.

Spawning Frequency

The average percentage of female sardine spawning per day was 6.2% when the estimate was based on females spawning on the night of capture, and 7.4% when based on females that had spawned the night before capture (table 3). Thus both estimates of spawning frequency for sardine were similar. This was not the case for northern anchovy: females spawning on the night of capture were believed to be more vulnerable to the trawl and thus oversampled (Picquelle and Stauffer 1985). Although frequencies estimated for female Pacific sardine spawning on the night of capture may be less reliable (see discussion on time of day and spawning), we found no indication of overestimation due to sampling bias. Combining the rates for the two nights resulted in an average estimate of 6.8% of the mature females spawning per day. Thus in April–May of 1994 the average mature female in the population spawned about once every 15 days.

A geographic pattern may exist in spawning rates, with sardine in the most southern section of the pattern (26°38'N–30°25'N latitude) spawning at nearly twice the rate of females farther north (table 7). Strangely, none of the fish taken at the northern end of the pattern had spawned recently; in fact, most females were in a postbreeding condition. The northern samples were taken on a commercial vessel that fished nearshore in Monterey Bay. Considering the small number of collections and the opportunistic nature of our sampling, it seems premature to conclude that a fixed geographic trend existed

TABLE 7
Average Percentage of Mature Pacific Sardine Females Spawning per Day during 1994 in Three Areas

			Mature females percent spawning		
Latitudinal area	Female ovarian state[a]	Number of females	Night of capture	Night before capture	Average fraction spawning per day
36°35'–36°55'N	Active	13	0.0	0.0	0.000
	All mature	106	0.0	0.0	0.000
31°35'–33°59'N	Active	270	9.3	12.2	0.107
	All mature	389	6.4	8.5	0.074
26°38'–30°25'N	Active	44	25.0	22.7	0.233
	All mature	88	12.5	11.4	0.120
Total	Active	327	11.0	13.1	0.121
	All mature	583	6.2	7.4	0.068

[a] Active mature females are capable of spawning and have ovaries containing oocytes with yolk or postovulatory follicles less than 48 hours old. "All mature" females include mature females that are postbreeding and incapable of further spawning this season.

in reproductive traits. It seems likely, however, that there was strong local patchiness in reproductive traits.

The spawning rates described above are our best estimates of the population rate during the 1994 survey period. The population rate (spawning females divided by all mature females) is a requirement of the DEPM model (Picquelle and Stauffer 1985) and includes in the denominator not only females with reproductively active ovaries, but also mature females classed as postbreeding (inactive). If the postbreeding females are excluded from the denominator, one obtains a measure of the spawning rate of the reproductively active females in the population. The average active female spawning rate was 12.1%, about twice the population spawning rate, because nearly half the females were in postbreeding condition (table 7). Thus the average Pacific sardine female may have spawned once every 8 days during her reproductive season in 1994.

Comparisons of Sardine Spawning Frequency Estimates

In making comparisons, it is better to use the spawning frequency for active females rather than the population rate. Population spawning rates not only depend on the spawning rate of active females but are also a function of the fraction of active females, which varies seasonally. We compared the spawning frequency of active female sardine in the 1994 survey to rates from CDFG surveys in 1986, 1987, and 1988. The average fraction of active females spawning per day (table 8) was 12%–13% in 1986, 1987, and 1994, and 20% in 1988, with a grand mean of 14.9%. The mean based only on females spawning the night before capture, possibly a more reliable method, was 13.7%. Thus, over the 1986–94 period, the average duration of the spawning cycle for active Pacific sardine off California seems to have been about 7 days.

To compare spawning rates for active sardine off California with values from the literature for sardines from around the world, we made the following assumptions:

1. Population rates are equivalent to the active rate of spawning, since they are not usually distinguished in the literature.

TABLE 8
Summary of Estimated Percent Spawning for Pacific Sardine off California and Baja California during 1986–1994

					Mature females percent spawning		
Adult survey midpoint date & organizations[a]	Survey area (# of collections)	Gear type[b]	Female ovarian state[c]	Number of females	Night of capture	Night before capture	Average fraction spawning per day
April 22, 1994 NMFS, INP, CDFG	Monterey Bay, USA, to San Ignacio Lagoon, Mexico (37)	P, T	Active	327	11.0	13.1	0.121
			All mature	583	6.2	7.4	0.068
Aug. 9, 1986 CDFG	Point Conception, USA, to international border (12)	P, T	Active	322	14.0	11.5	0.127
			All mature	323	13.9	11.4	0.127
July 26, 1987 CDFG	Point Conception, USA, to international border (13)	P	Active	409	7.1	17.1	0.121
			All mature	431	6.7	16.2	0.115
May 13, 1988 CDFG	Monterey Bay, USA, to international border (19)	P, HL	Active	557	27.1	12.9	0.200
			All mature	746	20.2	9.6	0.149
All			Active	1615	16.2	13.7	0.149
			All mature	2083	12.5	10.6	0.116

[a] National Marine Fisheries Service (NMFS), Mexican National Fisheries Institute (INP), California Dep. of Fish and Game (CDFG)
[b] Sardine were collected by purse seine (P), midwater trawls (T), or hook and line (HL).
[c] "Active" mature females are capable of spawning and have ovaries containing oocytes with yolk or postovulatory follicles less than 48 hours old. "All mature" females include mature females that are postbreeding and incapable of further spawning this season.

TABLE 9
Comparison of Spawning Rates for *Sardinops* around the World

Species	Area	Percent spawning per day[a]	Reference
S. sagax	California & Baja Calif.	13.7	Table 8, this paper (mean of 1986–94)
S. sagax	N. Chile	17.8	Retamales and González 1984
S. sagax	S. Chile	10.6[b]	Aguilera et al. 1986
S. melanostictus	SW. Japan	11.5[b]	Aoki and Murayama 1993 Murayama et al. 1994 Matsuyama et al. 1994
S. neopilchardus	W. Australia	11.0	Fletcher, in press (mean of 1991–92)
S. ocellatus	South Africa	10.5[b]	Le Clus 1989 (Sept. 1973–Feb. 1974)
	All	12.5	

[a] In these comparisons, we averaged only midseason peak values if multiple values were given.
[b] We calculated the spawning rate from data in the references.

2. A female with migratory-nucleus-stage (MN) oocytes will most likely spawn the night after capture (considered one spawning event).
3. Hydrated, or final-maturation, oocytes and new postovulatory follicles occur only on the night of spawning.
4. When the number of females with postovulatory follicles (not aged separately) is added to the number of hydrated females, two spawning nights are indicated (thus the combined number is divided by 2).
5. "Beyond the commencement of hydration" (Le Clus 1989) includes the earliest stages of MN oocytes as well as fully hydrated oocytes (thus the combined number is divided by 2).

These assumptions lead us to conclude that the overall mean sardine spawning rate from California and Baja California, northern Chile, southern Chile, South Africa, western Australia, and Japan was 12.5%, which is equivalent to each female spawning about once a week (table 9). We assumed that 12.5% spawning per day is a midseason rate for active female sardine.

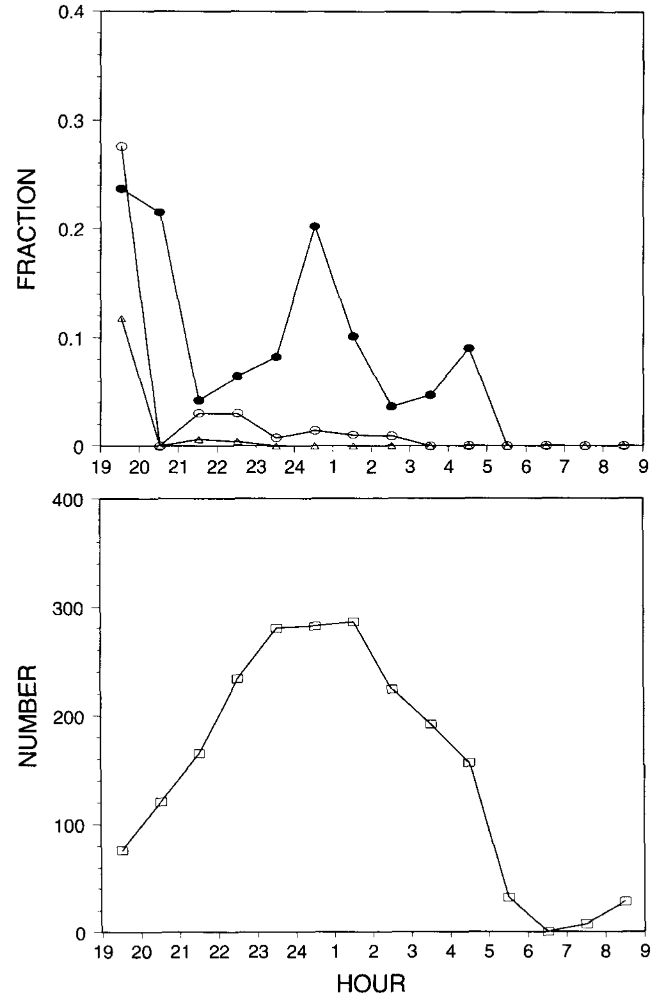

Figure 4. *Top*, Fraction of mature females caught in each hour that were identified as spawning on the night of capture by the histological presence in the ovaries of hydrated oocytes (*triangles*), hydrated oocytes and new postovulatory follicles (*open circles*), or only new postovulatory follicles (*closed circles*). *Bottom*, Number of mature sardine females sampled in each hour; mature females from four surveys taken in 1986, 1987, 1988, and 1994.

Time of Day and Spawning

The time of peak spawning each night is essential to DEPM spawning biomass estimates because the assumed peak time affects how ages are assigned to egg stages, and ultimately the estimates of egg mortality and daily production of eggs (Picquelle and Stauffer 1985). Females identified as spawning on the night of capture (ovaries containing hydrated oocytes, new postovulatory follicles 0–5 h old, or both) can be used to estimate when the time of daily peak spawning occurs (Hunter and Macewicz 1980). The number of females in the 1994 survey was insufficient to carry out a meaningful analysis of occurrence of histological stages by hour. We therefore combined the 1994 data with the original data from the 1986–88 CDFG sardine DEPM surveys off California. The time of day for each collection was assumed to be the midpoint between the time at the beginning and end of the trawl or purse seine set. All sardine were captured between 1929 at night and 0825 in the morning.

Females with hydrated ovaries were caught until 2259, with the highest fraction occurring just after sunset, between 1900 and 1959 (figure 4). Females in the act of spawning (both hydrated oocytes and new postovulatory follicles present in ovary) were captured from 1900 to 0259, with a peak between 1900 and 2259 (figure 4). Analyses of staged Pacific sardine eggs (Lo et al. 1996) indicated that the time of peak spawning was about 2100, which agrees with our findings. Peak spawning time for

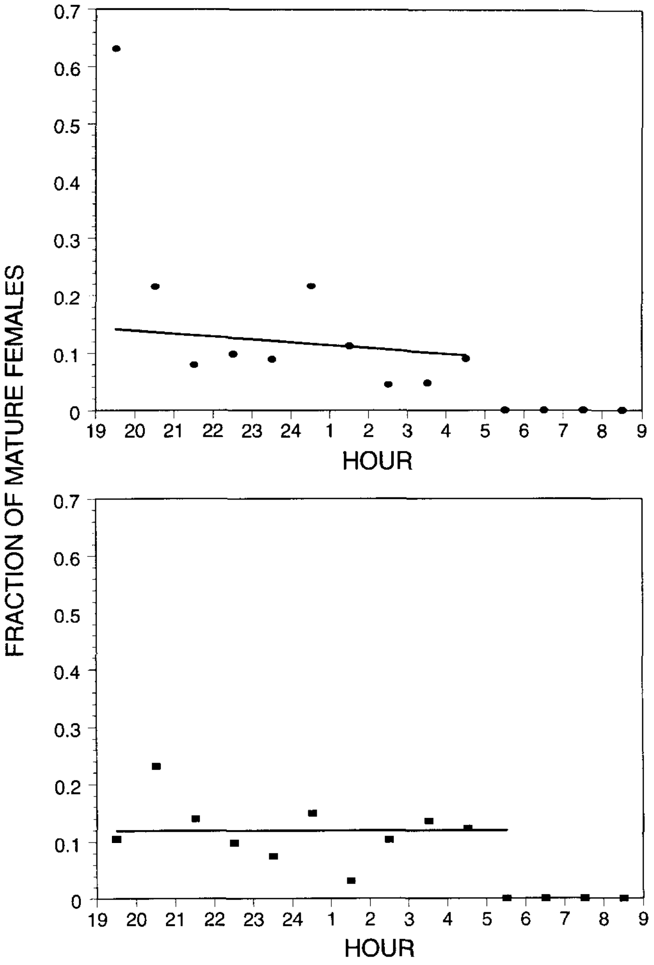

Figure 5. Fraction of mature females caught in each hour that were spawning on the night of capture (*upper panel*) or had spawned the night before capture (*lower panel*). The slope of the regression line was not significant (calculated over 1900–0459 h; $P = 0.417$) for females that spawned the night before capture (ovaries contained 18–31-h-old postovulatory follicles), but for females spawning the night of capture, the line indicated a decreasing trend with time ($P = 0.050$).

sardines off California is similar to the peak times reported for Pacific sardine, *Sardinops sagax musica*, off Ecuador (2000–2300; Coello 1988) and northern Chile (2100–2359; Retamales and González 1984) and for the Japanese sardine, *Sardinops melanostictus*, off southwestern Japan (2000–2300; Morimoto 1993; Matsuyama et al. 1994).

The data for Pacific sardine off California during 1986–88 and 1994 were also examined to determine if biases existed in estimates of reproductive states due to sampling time. The fraction of females judged to have spawned the night before capture (ovaries with ~24-h-old postovulatory follicles) was not affected by time of capture (figure 5, lower panel); in fact, the slope of the trend line did not differ from 0 ($P = 0.417$). This result indicates that the use of females with ~24-h-old postovulatory follicles provides an unbiased estimate of spawning rate.

In some pelagic species, females with hydrated ovaries may be oversampled, presumably because of increased vulnerability to the trawl or purse seine (*Engraulis mordax*; Picquelle and Stauffer 1985; *Engraulis ringens*; Alheit 1985). When the numbers of sardine females with hydrated oocytes, new postovulatory follicles, or both are combined, there is a significant ($P = 0.050$) decreasing slope with time (figure 5, upper panel). If all stages were equally vulnerable to the capture gear at all times, there should be no trend, because the decline in number of females with hydrated ovaries should be offset by an increase in the number of females with new postovulatory follicles (0–5-h old). The trend is largely due to very high values for all three stages during 1900 h (figure 4), when only 2 collections were taken. We recommend that additional adult collections be taken between 1700 h and 2000 h before conclusions about vulnerability of hydrated females are drawn.

Incidence of Postbreeding Females, Indicator of Sardine Movements?

A striking feature of the April 1994 survey was the high incidence of postbreeding females. Since peak spawning of sardine in the Southern California Bight (1951–89) is thought to be May–June (Hernández-Vázquez 1994), these results are counterintuitive. The percentage of postbreeding females by month from surveys during 1986–88 and 1994 was calculated from table 8 as: April (1994) 44%; May (1988) 25%; July (1987) 5%; and August (1986) 0.3%. Thus the three surveys carried out by CDFG also indicate counterintuitive seasonal trends in the incidence of postbreeding females.

Why does the number of postbreeding females decrease as the season progresses? We hypothesize that after spring spawning in the bight, sardine move north, and may be replaced by sardines migrating into the bight from the south. Two sources of information support our hypothesis: first, the peak spawning season of sardine in the south (Punta Eugenia region) is in August and September (Hernández-Vázquez 1994); and second, tagging results and timing of the historical sardine fishery indicate that sardine from the bight migrate north after spawning (Clark 1952).

Another possible hypothesis is that the apparent monthly trend in postbreeding females occurred by chance—the result of the extreme patchiness of reproductive traits (including the seasonality of spawning) and our partially opportunistic sampling of adult sardine in the north and south.

Thus the results can be best explained either by contagion in the regional timing and duration of the spawning season, or by movements of adult sardines along the coast (or by a combination of these effects). Both hypotheses involve levels of biological complexity that we do not yet fully understand.

ACKNOWLEDGMENTS

Our ability to interpret data from the cruise was greatly enhanced by the addition of adult sardine reproductive data from 1986–88 provided by the California Department of Fish and Game (CDFG). We wish to thank the CDFG and, in particular, P. Wolf, T. Dickerson, K. Mais, K. Worcester, R. Reed, E. Konno, T. Bishop, and M. Larson. We thank all on shipboard who helped collect Pacific sardine ovaries during the 1994 survey: A. Ruiz, J. Sanchez, R. Sanchez, M. L. Granados, P. Diaz, B. Leos, T. Barnes, T. Bishop, E. Konno, W. Chou, H. Fish, E. Acuna, D. Ambrose, S. Charter, R. Dotson, and D. Griffith. O. Tapia V. assisted in the laboratory. N. C. H. Lo gave statistical advice. R. Charter and D. Prescott updated computer programs.

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AGE COMPOSITION, GROWTH, AND MATURATION OF THE PACIFIC SARDINE (*SARDINOPS SAGAX*) DURING 1994

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ABSTRACT

In conjunction with a study to estimate biomass based on daily egg production, Pacific sardine (*Sardinops sagax*) were independently aged by four or five readers using annuli in whole otoliths. Agreement among all five readers was only 31%, and an index of precision for estimated ages was 0.24. Ages ranged from one to seven years. The age composition of Pacific sardine in 1994 indicates a growing population or high adult mortality rates. Most of the biomass was in the youngest year classes. Very few fish were older than 4 years. Samples were taken from Baja California (26°40'N) to Monterey, California (36°40'N) during April and May 1994. Latitudinal clines in age of first maturity and size at age were found. Despite problems in age determination, it is clear that some sardines mature before their first birthday. Sardine in the south mature at a younger age than in the north. Most sardine in the current population mature at age one, rather than at age two as reported for the population prior to the collapse of the fishery.

INTRODUCTION

Pacific sardine (*Sardinops sagax*) dominated the Pacific coast fisheries of North America for much of the first half of the twentieth century, prior to successive years of low recruitment and unsustainable fishing mortality (Barnes et al. 1992). Following the collapse of the sardine fishery in the mid-1960s, a moratorium was placed on the commercial harvest of sardine in California (Radovich 1982).

Today the sardine fishery is rebuilding, as biomass during the past decade has increased (Deriso et al. 1996). The stock currently supports directed commercial fisheries in Ensenada (Baja California, Mexico), San Pedro (U.S.), and Monterey (U.S.). Determining the age composition of landings is important for investigating changes in abundance and suggesting management decisions. Unlike many commercial fisheries, age composition of sardine landings in California is relatively well documented for most of the twentieth century (Yaremko 1996). The methods of estimating age composition have varied over time from length-frequency analysis to annuli counts from either scales or otoliths. California Department of Fish and Game (CDFG) and others (Hester 1993) have conducted systematic port sampling and age determination of wetfish landings in the California commercial fishery since 1983.

In accordance with current practice, we chose otoliths over scales (or other hard parts) for determining sardine age. Otoliths are preferred for several reasons. (1) Samples were collected with trawl or purse seine gear, and at the time of collection, handling had abraded off the scales of many specimens. (2) Unlike scales, sardine otoliths do not require mounting or other preparation for ageing and can be stored with relative ease. (3) Otoliths are as reliable as scales (Mosher and Eckles 1954). (4) There is some evidence that annuli in otoliths form on an annual cycle (Barnes and Foreman 1994).

In this study we determined the age, growth, and maturation of Pacific sardine over a broad geographic range from Punta Eugenia, Baja California, to Monterey, California. This is the first attempt to address regional growth and maturation of Pacific sardine, which may show patterns similar to those found in northern anchovy (Parrish et al. 1985).

METHODS

Sampling

A daily egg production method (DEPM) biomass survey (Lasker 1985) was conducted from April 7 to May 14, 1994, to estimate current stock size (Lo et al. 1996). A total of 667 adult sardines were sampled to obtain adult reproductive data for DEPM calculations, and otoliths were removed for age determination. An additional 412 fish were sampled for age determination to encompass the size range of adults. Collection methods are described in Lo et al. 1996 and Macewicz et al. 1996. In most cases otoliths were removed at sea, cleaned, and stored dry in gelatin capsules. For a few samples taken from commercial purse seine catches landed in Ensenada, otoliths were removed in the laboratory from sardines taken at sea the night before.

Otolith Reading

An annulus was defined as one of a series of concentric zones on a structure that may be interpreted as annual markers. For sardine otoliths, an annulus is the interface between an inner translucent growth increment and the successive outer opaque growth increment (Fitch

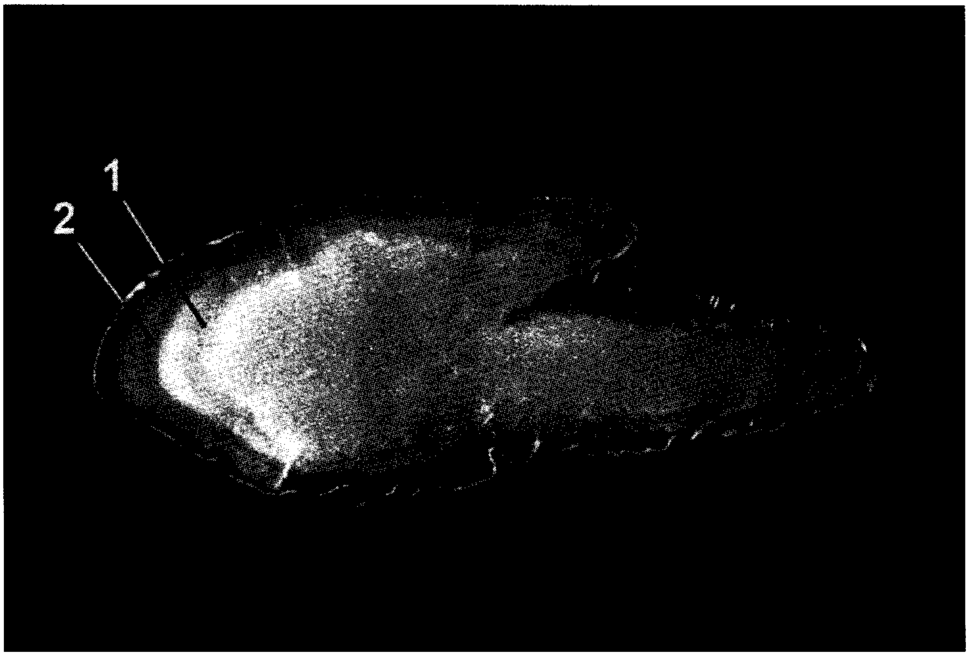

Figure 1. Sagitta of a 182-mm SL California sardine (*Sardinops sagax*), showing two annular increments.

1951; figure 1). Counting successive annuli in an otolith results in an estimate of age. The year class (year of birth) can be calculated by assuming a peak spawning season from the age and sample date. By convention, a year class consists of all fish hatched during a calendar year. Although some sardine spawning takes place year-round, most occurs in summer (Watson 1992). Because the actual hatch date for each individual is unknown, we assume that all individuals in each year class become one year old on January 1. This method differs from that used in California for Pacific sardine in the past. Murphy (1966), Walford and Mosher (1943), and Barnes and Foreman (1994) all assumed a July 1 birth date. The age of each fish reported here was the mean of four or five readers.

Annuli were identified by submerging each pair of sagittal otoliths under a depth of 4–5 millimeters of distilled water in a watch glass with black background to improve distinction between increments (Yaremko 1996). Under a stereoscopic microscope at 12–25× magnification and reflected light, opaque increments appeared white, and translucent increments appeared black or gray.

Age was not determined from otoliths that were deformed or partially crystallized (Blacker 1974). It is not uncommon for one or both members of a pair to be somewhat deformed; therefore both otoliths were examined. Readability of the pair was improved if they were placed in the watch glass side by side, sulcus side down, because annuli may be more distinct on one otolith than the other.

Otoliths were read within three minutes of immersion because water is quickly absorbed, reducing readability. Once saturated, the outermost opaque increments tend to fade or become indistinct from translucent increments. This can be a potential source of error, causing underestimation of true age. (Readability can be restored by drying.)

Each pair of otoliths was read by four independent readers. A portion of the sample was read by a fifth reader. Age reported here is the mean of all readers' results, rounded to the nearest whole number. Means with a decimal of 0.5 were rounded to the next highest whole number. Because of the assumed January birthdate and the date at which sampling was done (in the spring before the spawning peak), all fish that had no complete annulus were assigned to age 1, the 1993 year class. Since the fish were sampled in May, age-1 fish were roughly 10 months old.

The average percent error (*APE*) was calculated from

$$APE = \frac{100}{N} \sum_{j=1}^{N} \left[1/R \sum_{i=1}^{R} \frac{[X_{ij} - \bar{X}_j]}{\bar{X}_j} \right] \qquad (1)$$

where N is the number of fish aged, R is the number of readers, X_{ij} is the ith reader's age determination for the jth fish, and $\bar{X}_j$ is the average age (Beamish and Fournier 1981).

The index of precision was calculated from

$$D = \frac{1}{N} \sum_{j=1}^{N} \frac{1}{\bar{X}_j \sqrt{R}} \sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - \bar{X}_j)^2}{(R-1)}} \qquad (2)$$

where D is the coefficient of variation divided by $\sqrt{R}$ from equation 1 (Chang 1982). We report D times 100 to make it more comparable to *APE*.

We also report the mean and range of percent agreement, *PA*, for combinations of 2–5 readers, where percent agreement is the percentage of otoliths that all readers agree is a given age. There are 10 combinations of agreement between 2 readers with 5 total readers (e.g., R1 with R2, R1 with R3, etc.). Agreement may or may not exist for a particular fish among any combination of readers. For each combination we calculated the percent agreement. To combine data for all combinations of readers, we averaged percent agreement over combinations:

$$\overline{PA} = \sum_{r=1}^{R} \frac{PA_r}{R} \tag{3}$$

where

$$PA_r = \sum_{n=1}^{N} \frac{D_{r,n}}{N}$$

where R is the number of readers, N the number of fish aged, and $D_{r,n} = 1$ if agreement, 0 if disagreement.

Objective Criteria

Weight of the otoliths from sardines has been correlated with age (Pawson 1990; Fletcher 1991, 1995). In an attempt to obtain objective criteria (Boehlert 1985) to aid age determination, whole otoliths were weighed to the nearest 0.001 mg with an electrobalance after they had been cleansed with bleach and dried for two days in a desiccator. Weights of the otoliths and lengths of the fish were plotted by age class to determine whether our age determinations could be improved by cluster analysis or other statistical technique.

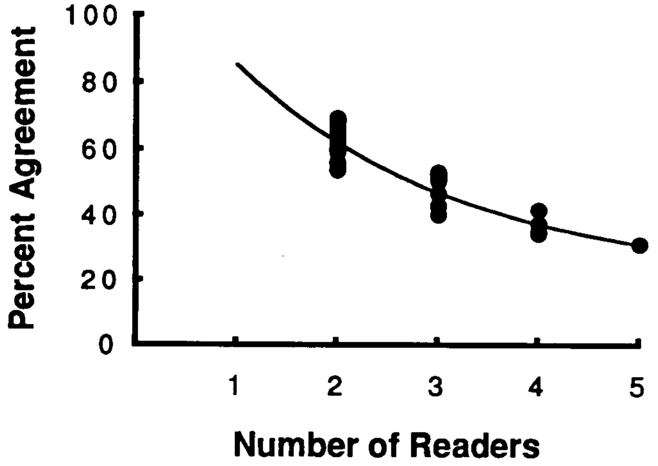

Figure 2. Percent agreement (*PA*) on age determination of Pacific sardine by two, three, four, and five readers. Equation fitted to the line is $PA = 19.6 + 102 * \mathrm{EXP}(-.44 * NR)$

Maturity

Maturation of females was determined from the histological state of the gonads. Presence of postovulatory follicles or yolked eggs was used as an indication of maturity (see Macewicz et al. 1996).

Geographic Areas

Samples were grouped into three regions: Monterey ($N = 152$), Southern California Bight ($N = 710$), and Baja California ($N = 212$). The Southern California Bight samples included all samples from 31°N to 34°N (see figure 3 in Lo et al. 1996). Monterey samples were all collected in Monterey Bay (north of 34°N), and Baja California samples were collected south of 31°N.

RESULTS

Reader Agreement

Age determinations for Pacific sardine were not very precise. The average percent error (*APE*) among readers was 16%, and the index of precision (times 100; Chang 1982) was 9. The mean agreement of five readers was 31%; of four readers, 37% (range 34%–42%); of three readers, 47% (range 40%–53%); and of two readers, 62% (range 54%–69%). Reader agreement was not correlated with experience. The two most experienced readers had the lowest agreement (54%). Agreement approaches an asymptote of about 20% as the number of readers who agree increases (figure 2). The percent agreement among five readers was negatively correlated with mean age ($N = 637$, $P < 0.01$).

Otolith Weight and Standard Length

It was not possible to use otolith weight with other data to estimate age of Pacific sardine. Otolith weight and fish length were plotted by mean age (figure 3). Fish assigned to age 1 and age 2 largely overlap in both length and otolith weight, whereas age-3 fish appear to be separate from younger and older fish. Some fish assigned to age 3 overlap with fish age 2 and also with fish age 5 and age 6. In addition, we were not able to use modal analysis of otolith weight to distinguish year classes (figure 4) as reported by Fletcher (1991, 1995). We decided that cluster analysis would not be a useful approach for estimating sardine ages.

Age Composition

Sardine in DEPM samples ranged from age 1 (1993 year class) to age 7 (1987 year class). Age composition comprised 21.4% 1993 year class; 41.4% 1992 year class; 28.3% 1991 year class; 6.3% 1990 year class; 2.6% 1989 year class; 0.3% 1988 year class; and 0.1% 1987 year class. The age composition of our samples was much younger than that reported for the California fishery during the

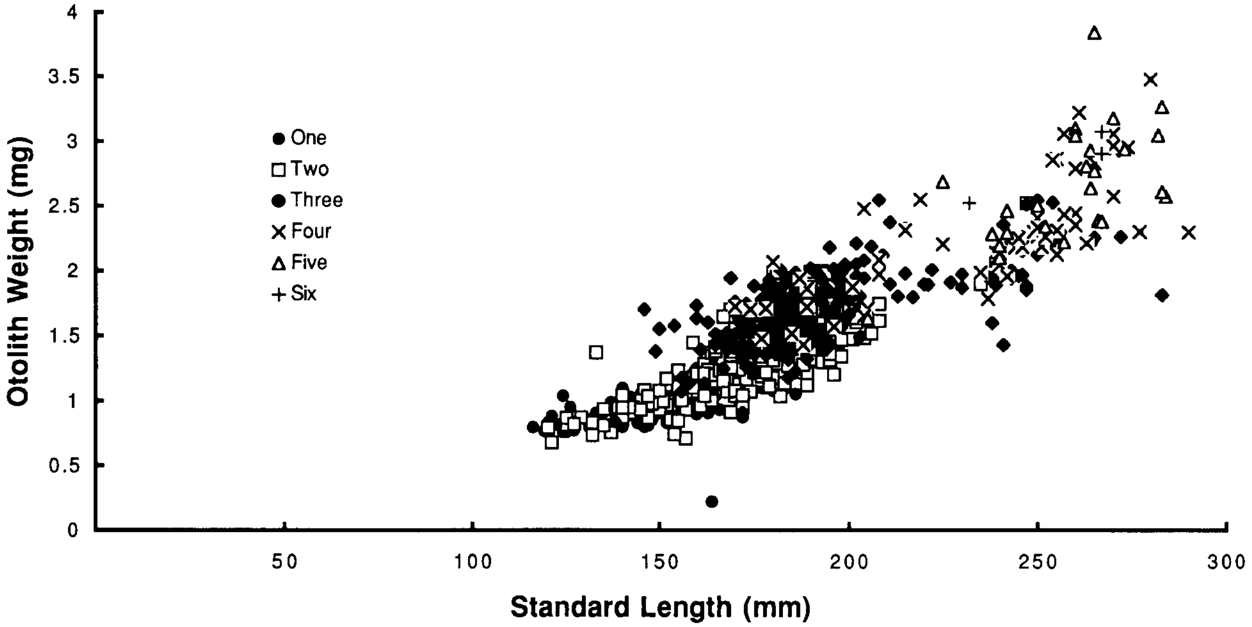

Figure 3. Otolith dry weight and standard length of Pacific sardine collected during the 1994 daily egg production method (DEPM) biomass survey.

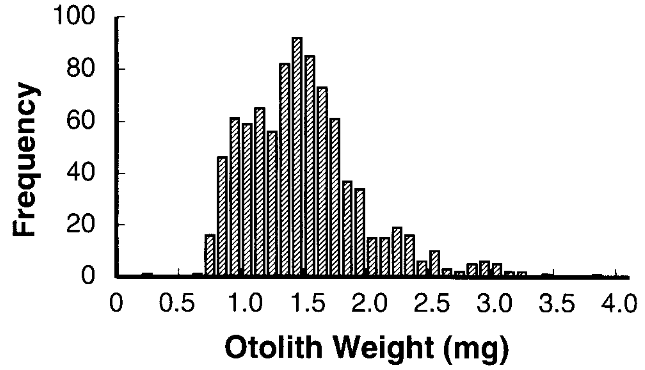

Figure 4. Distribution of otolith weights of Pacific sardine collected from 26°N to 36°N during 1994.

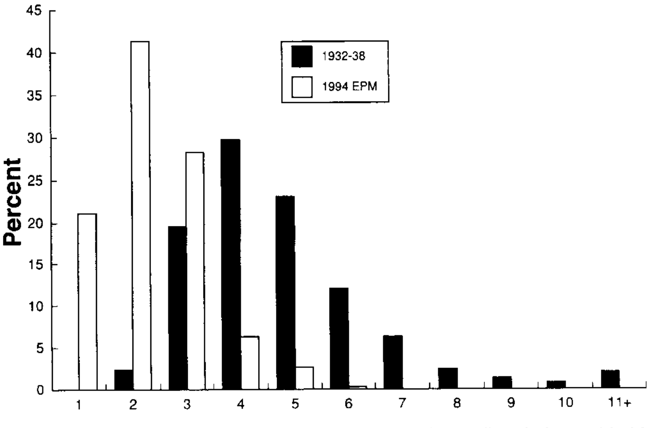

Figure 5. Comparison of age composition of Pacific sardine during 1932–38 (Moser and Eckles 1954) and 1994.

1930s (figure 5). Landings during the 1930s reached a maximum age of over 10, and at that time ages 6 and older accounted for 14.6% of all fish captured. In comparison, no fish older than 7 years were found in the samples collected during the DEPM survey.

Length at Age

Growth was estimated by fitting a von Bertalanffy equation to the size at age for all samples (figure 6). Length at infinity was 205.4 ± 1.6 mm SE; k was 1.19 ± 0.04 SE; and t_0 was fixed at zero because there were no data near the origin, and the parameter was not estimable (R^2 = .37). Length at infinity greatly underestimates the maximum size of sardine, but a large growth coefficient is consistent with fast growth.

Maturity

The age of 50% maturity could not be calculated, since more than 50% of age-1 fish were mature.

Regional Differences

Age composition varied with latitude in our samples. More young fish were found off Baja California than in the Southern California Bight or off Monterey (figure 7).

The length at age for Pacific sardine differed between regions (figure 8), although there was considerable overlap in size for the 1993, 1992, and 1991 year classes in each region. Mean sizes at ages of one-, two-, and three-year old fish indicate that fish were smaller at age off Baja

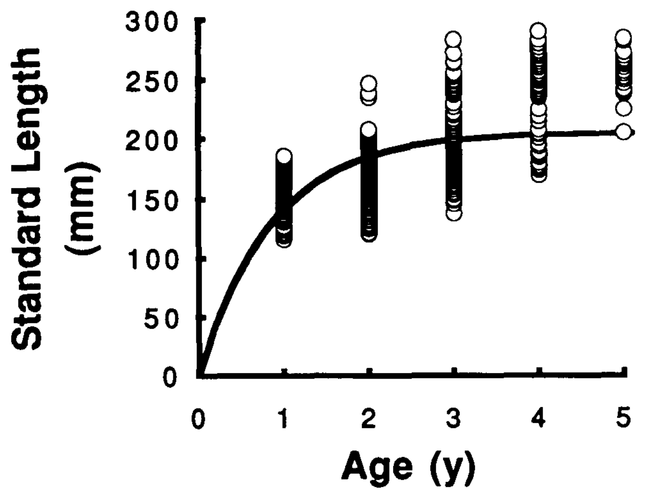

Figure 6. Length at age of Pacific sardine with Von Bertalanffy model. See text for details of the equation.

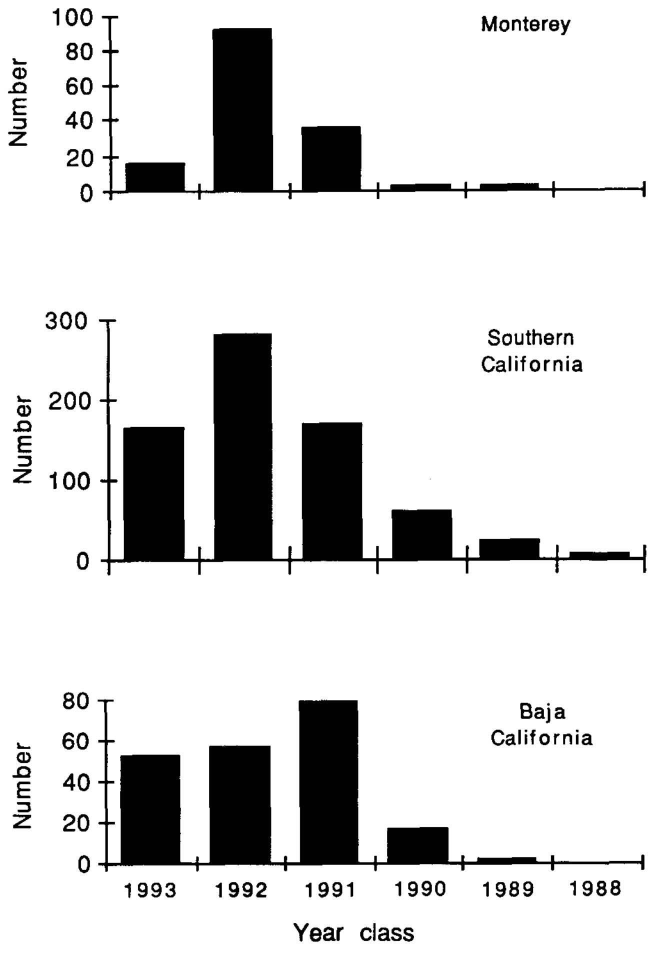

Figure 7. Age composition of Pacific sardine collected north of 34°N (Monterey); from 31° to 34°N (Southern California Bight); and south of 31°N (Baja California).

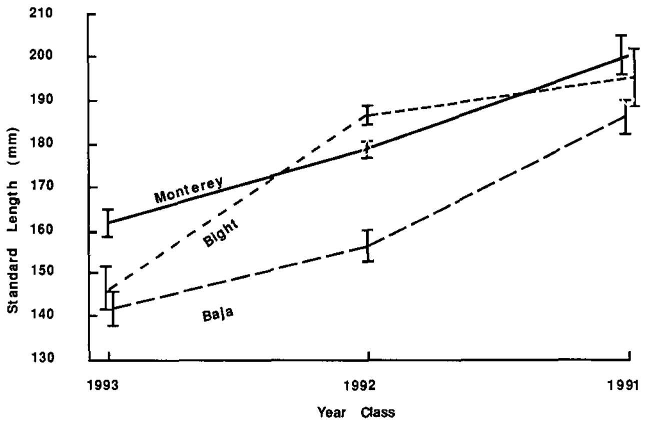

Figure 8. Length at age for Pacific sardine collected north of 34°N (Monterey); from 31° to 34°N (Southern California Bight); and south of 31°N (Baja California).

California and larger off Monterey. The one exception to this apparent cline in growth was age-2 fish collected in the Southern California Bight, which were larger than those collected off Monterey.

Maturation of Pacific sardine females appears to vary with latitude. Fish mature at a younger age in southern California and Baja California than off Monterey (figure 9). However, considering the small numbers of age-1 fish sampled both for age and maturity off southern Baja California (5) and off Monterey (14), these data must be considered as preliminary.

DISCUSSION

Validation

It is essential that the periodicity of annuli formation be validated before ages and year classes can be assigned with certainty. Barnes and Foreman (1994) documented the periodicity of annuli in otoliths of young sardines up to age 3. Their samples were collected from the Southern California Bight during the 1980s, in the early stages of the current resurgence in the population (Deriso et al. 1996). Earlier work by Walford and Mosher (1943) demonstrated an annual cycle in marginal increment width for otoliths taken from southern California landings during 1938 and 1939, implying the formation of annuli during that period.

The studies by Barnes and Foreman (1994) and Walford and Mosher (1943) provide some evidence for the formation of annuli in fish from California waters during different oceanographic regimes. This suggests that marks in Pacific sardine otoliths are not caused by transitory conditions. However, different oceanographic conditions or spawning behavior may cause the formation of two opaque growth increments per year for fish caught in Bahía Magdalena, Baja California Sur (Felix-Uraga and

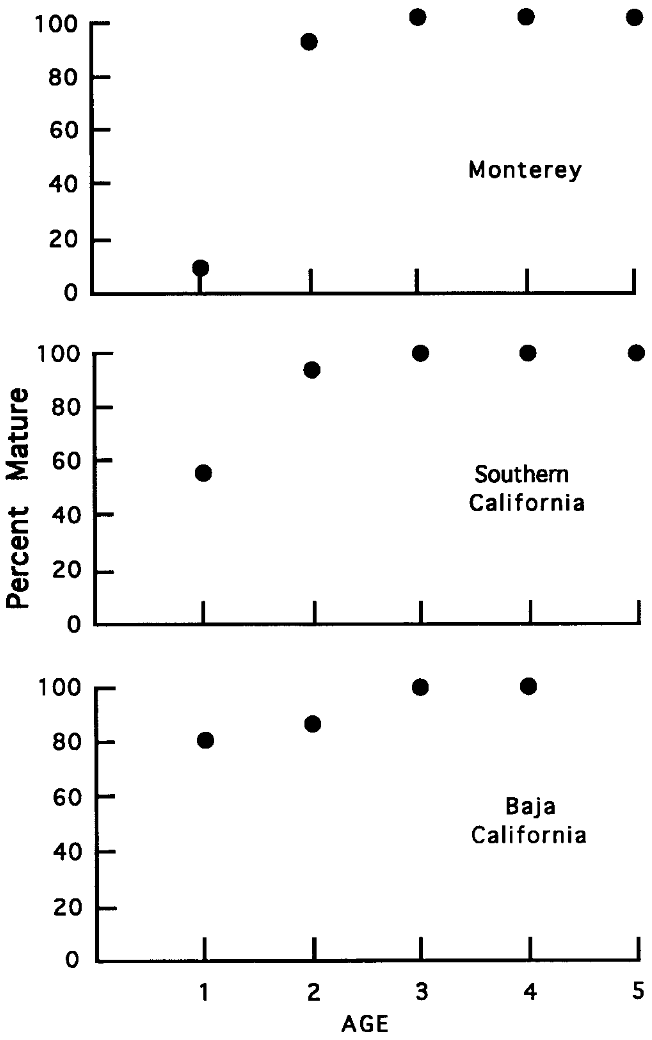

Figure 9. Percent maturity of Pacific sardine by age class for three geographic areas.

Ramirez-Rodriguez 1989). Kimura (1970) reported the formation of checks in scales of sardine reared in the laboratory. Unfortunately, otoliths were not taken from Kimura's samples. Thus errors due to variable periodicity are possible, but are probably associated with the more southern reaches of the population range.

In addition to validation, studies using age-composition data need to demonstrate reproducibility or verification of age assignments. There are two potential sources of ageing error in our study: (1) variable periodicity for major growth increments, and (2) indistinct or ambiguous appearance of major growth increments, complicated by false annuli or spawning checks in the otolith. We suspect that both sources of error are present to some extent in our results, although difficulties in interpreting otolith appearance are thought to be a greater problem than variable periodicity of annuli. Barnes and Foreman (1994) identified variable timing of the spawning peak as another potential source of ageing error, but that was not thought to be significant in this study.

The clarity of the annual pattern varies considerably from specimen to specimen, so interpretation of the annual growth patterns in otolith appearance was to some degree ambiguous in nearly 70% of our samples, as demonstrated by the low degree of agreement between all five readers. Ambiguous sardine otoliths create an element of subjectivity in age assignments, resulting in low precision. In this study two of our readers agreed on 64% of 1,035 otoliths. But in a recent ageing study involving specimens collected during 1988–92 (Hester 1993) the same readers achieved 70%–75% agreement in independent duplicate readings. This suggests that the otoliths in our study were more difficult to read. It is generally assumed that in any sample some fraction of otoliths is so unambiguous that all readers would assign the same age. In our study the fraction of unambiguous otoliths was about 20%.

Some ageing errors associated with simple annuli counts may be corrected by modeling age as a function of annuli count and other measurement data. Errors have been reduced by predicting age for individual Mediterranean sardines, *Sardina pilchardus*, by using otolith weight–fish length relationships for each year class (Pawson 1990). We anticipate that further work along similar lines will improve ageing results for Pacific sardine. But the apparently large variability in Pacific sardine growth rates among areas suggests that direct application of Pawson's (1990) method may not be appropriate for Pacific sardine. We suggest an expanded model for Pacific sardine that includes effects due to annuli counts, otolith weight, fish length, latitude of capture, and radial distance to each otolith annulus. One aspect of further ageing work should include counts of daily growth increments (Butler 1987) and injection with fluorescent dyes that mark the otolith to confirm growth rates and age assignments for different geographic regions.

Independent Criteria

Weight of the otolith and standard length of the fish did not clearly separate fish by assigned age. Fish aged one overlap fish aged as two-year-olds. This may be a result of ageing error for fish sampled over a broad geographic area, or a result of variation in spawning season and juvenile growth rates. Fish from southern California produce one translucent mark per year (Barnes and Foreman 1994), whereas Felix-Uraga and Ramirez-Rodriguez (1989) report that fish from southern Baja California produce two translucent marks per year. DEPM samples covered both regions, and readers used one criterion to assign an age for all samples. An alternate hypothesis is that fish from different regions have different allometric growth of the otolith.

Growth Rates

It is difficult to compare size at age reported here with previous studies (Felin and Phillips 1948; Phillips 1948; Felin et al. 1958, etc.) because our samples are taken in April and May, and previous studies were taken from the commercial fishery, conducted between August and February. Marr (1960) reported calculated size at first annulus formation for year classes from 1934 to 1957. During 1934–43 and 1944–57, length at first annulus formation was 101 mm and 131 mm, respectively. Similar differences in sardine growth rates with population size have been found in Japan (Kawasaki and Omori 1995; Wada et al. 1995).

In this study, age-1 fish that are about 10 months old averaged 142, 162, and 146 mm in southern Baja California, southern California, and Monterey. It is uncertain whether these regional differences are due to differences in growth, small sample sizes, differences in spawning season, or inaccurate age determination. The average of all age-1 fish is 155 mm. This is larger than fish collected from 1934 to 1957 (Marr 1960) or fish reared in the laboratory (120 mm; Kimura and Sakagawa 1972). However, Felix-Uraga (1990) reports that sardine grow to 153 mm in one year in Bahía Magdalena. Thus sardine are apparently growing much faster now than previously reported. However, details of regional growth can best be documented with daily growth increments (Butler 1989), which were not examined in our study.

Age Composition

Age composition varied with latitude. This is consistent with findings from the historical fishery (Mosher and Eckles 1954). Hester (1993) reported similar latitude effects on age composition for samples collected from commercial fisheries in Ensenada, San Pedro, and Monterey during 1987–92.

Estimates of age composition from DEPM samples differ from those estimated from an age-structured stock assessment model of the population (Deriso et al. 1996). Age-2 (1992 year class) fish were most numerous in DEPM samples, whereas the population model indicates that age 1 (1993 year class) is most numerous (Deriso et al. 1996). This discrepancy may be due to assumptions about recruitment in the population model or due to size-specific gear selectivity in the DEPM sample. Lower selectivity for small, young fish results in underrepresentation of the two youngest year classes. Although 45% of DEPM specimens were obtained from commercial purse seine sets, these samples were taken inshore, whereas trawl samples were taken offshore. Perhaps for this reason, size composition did not differ between samples taken with the two gear types (Lo et al. 1996). Barnes et al. (1992) and Deriso et al. (1996) found sardine to be fully recruited to purse seine gear at age 3. Our results indicate that sardine were fully available to the DEPM sampling gear at age 2 or age 3, possibly because the high-speed midwater trawl obtains more representative samples of small, young fish than the commercial purse seines (Dotson and Griffith 1996).

Maturation

The age and size of maturation of sardine is a critical parameter, since the proportion of mature and immature fish is used to calibrate spawning biomass and total biomass (Lo et al. 1996; Deriso et al. 1996). Sardine appear to be maturing at an earlier age than previously reported. Murphy (1966) interpreted Clark's size at maturity for fish collected off Monterey during 1928–31 (Clark 1934) to indicate that 50% matured by age 2. MacGregor (1957) reported that 30% of age-1 fish and all age-2 fish were mature in samples taken off San Pedro during 1945 and 1946. Ahlstrom (1960) reported that Pacific sardine matured at 115 mm SL, with 50% mature at 125 mm in samples taken off Ensenada in 1958. It is important to note that 1958 was an El Niño year, with water temperatures 1°–2°C above normal. These fish were probably less than one year of age and are consistent with our age at first maturity for samples from southern Baja California. Thus maturation of sardine appears to be flexible. Interpretation of biological changes in response to population size or climatic regime is confounded by variation in seasonality and locality of sampling. The 1994 DEPM survey offered the first opportunity for studying maturation of Pacific sardine synoptically over a large geographic range.

CONCLUSION

The age composition of Pacific sardine in 1994 reflects a growing population and/or high adult mortality rates. Most of the biomass is in the most recent year classes. Very few fish are older than 4 years. During the 1930s the sardine population comprised many more year classes, and fish older than 8 years were not uncommon. The age composition of the population should be monitored carefully, because the present population, while growing, is very vulnerable to recruitment failure.

ACKNOWLEDGMENTS

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EGG PRODUCTION AND SPAWNING BIOMASS OF PACIFIC SARDINE (*SARDINOPS SAGAX*) IN 1994, DETERMINED BY THE DAILY EGG PRODUCTION METHOD

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ABSTRACT

The daily egg production method (DEPM) was used to compute spawning biomass of Pacific sardine in a 380,175 km^2 (111,081 n.mi.^{2}) area from San Ignacio Lagoon, south of Punta Abreojos, Baja California Sur, to San Francisco, California, during April–May 1994. The estimated spawning biomass was 111,493 MT (CV = 0.32) with an approximated 95% confidence interval (40,000 MT, 182,800 MT). Daily egg production in the survey area was 0.169 eggs/0.05 m^2/day (CV = 0.22), and daily specific fecundity was 11.53 eggs/gm/day. Estimates for adult parameters were: sex ratio, 0.53 (CV = 0.067); average female weight, 82.49 gm (CV = 0.071); spawning frequency, 0.073 (CV = 0.23); and average batch fecundity, 24,282.52 (CV = 0.11). We estimated peak spawning time for Pacific sardine (9:00 p.m.) and coefficients in a temperature-dependent egg-development model. Egg density in 1994 was similar to that in 1986, indicating that the increase in spawning biomass during 1986–94 was due to expansion of spawning area rather than to increased density of spawners. Most of the eggs collected were found in waters off California and were distributed along temperature gradients formed by upwelling. Surface temperatures of about 13.8°C seemed to limit the inshore distribution of eggs. Food supply, rather than temperature, may have limited the offshore distribution.

INTRODUCTION

The Pacific sardine fishery began to collapse in the early 1950s, and the population declined by the mid-1970s to less than 10,000 MT, or about 1% of the estimated stock in the 1930s (Barnes et al. 1992). The population began to recover in the late 1970s (Watson 1992), and in the 1980s the wetfish fishery began to catch sardine incidentally with mackerel and anchovy (Barnes et al. 1992; Wolf 1992). The sardine population in California waters has increased steadily since 1983 (Deriso et al. 1996).

The daily egg production method (DEPM; Lasker 1985) was first used to estimate sardine spawning biomass off California in 1986–88 when the California Department of Fish and Game (CDFG) conducted surveys off southern California (Wolf 1988a, b; Scannell et al. 1996; table 1). Results from the CDFG spawning biomass surveys were used in conjunction with other information to manage the sardine fishery in U.S. waters (Wolf and Smith 1985, 1986; Wolf 1992).

TABLE 1
Estimates of Egg Production Rates and Adult Reproductive Parameters for Daily Egg Production Method Surveys, 1986–88, 1994

	1986[a]				
Parameters	North	South	1987[b]	1988[c]	1994
Egg production (P_0) (eggs/0.05 m^2/day)	0.276 (.557)[d]	0.513 (.322)	0.657 (.945)	0.33 —	0.169 (0.22)
Area of survey (A) (km^2)	6,616	10,774	37,605	44,339	380,175
Average female weight (W) (gm)	199.9	154.8	163.8	166.3	82.5 (0.07)
Batch fecundity (F)	71,382 (.049)	51,743 (.086)	62,289 (.111)	61,147 (.066)	24,282.52 (0.11)
Spawning fraction (S) (fraction of mature females spawning per day)	.038 (.467)	.189 (.283)	.125 (.062)	.144 (.182)	.0729 (.23)
Sex ratio (R)	.559 (.117)	.603 (.052)	.664 (.062)	.493 (.128)	.537 (.067)
Spawning biomass (B_s) (metric tons)	4,756 (.792)	2,903 (.349)	15,685 (.912)	13,514 —	111,493 (.32)
Daily egg mortality (Z)	Fixed at .05	Fixed at .05			.12 (.97)

[a]Scannell et al. 1996 [b]Wolf 1988a [c]Wolf 1988b [d]Coefficients of variation in parentheses

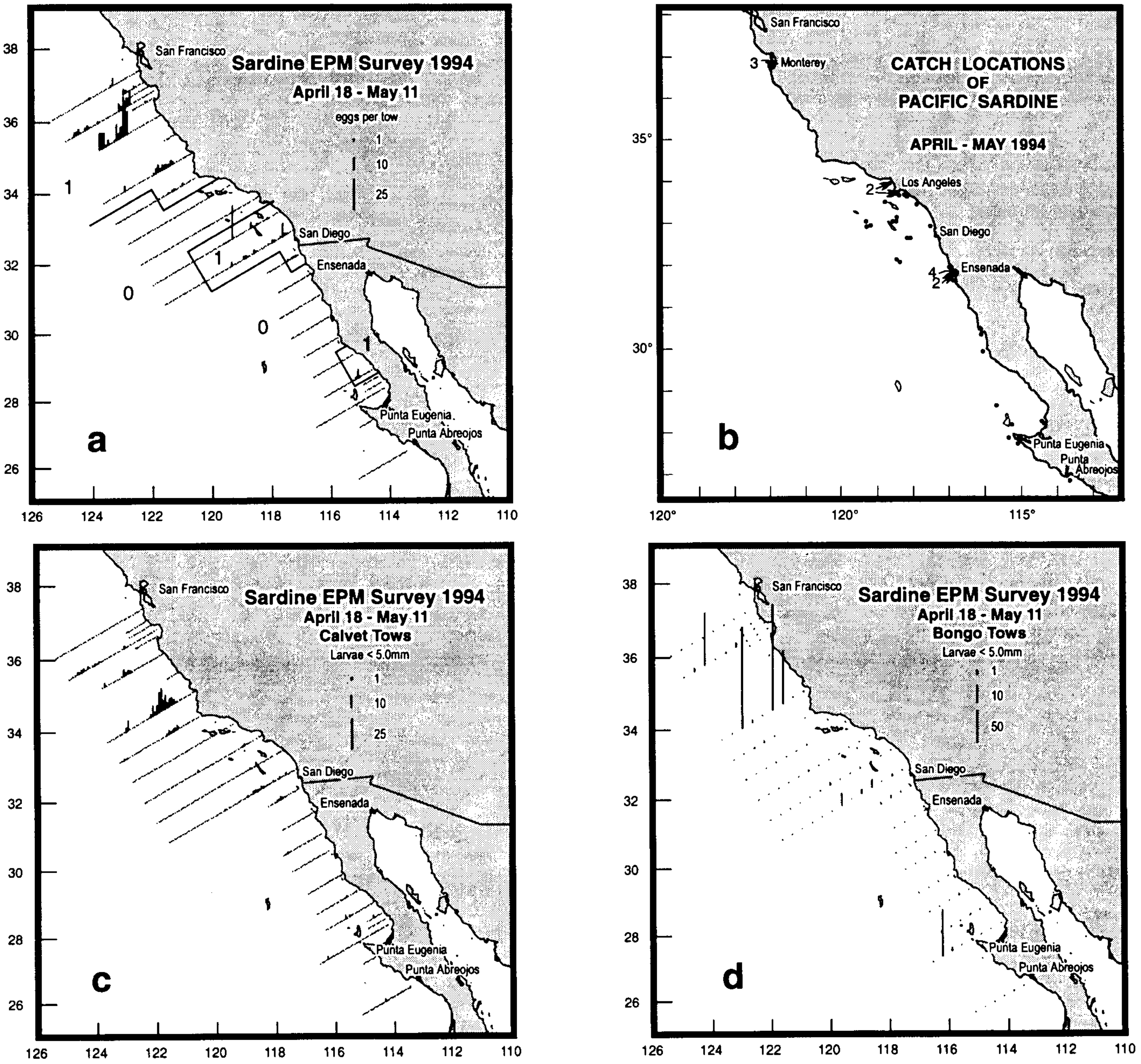

Figure 1. Areas sampled during April–May 1994 daily egg production survey for Pacific sardine. *a*, CalVET stations and egg catches. *b*, Locations for adult samples. *c*, CalVET stations and yolk-sac larval catches. *d*, Bongo stations and yolk-sac larval catches.

In 1994, the National Marine Fisheries Service (NMFS), CDFG, and Instituto Nacional de la Pesca (INP), Mexico, conducted a joint sea survey using the DEPM to assess the spawning biomass of Pacific sardine. The area surveyed extended from San Ignacio Lagoon, south of Punta Abreojos, Baja California Sur, to San Francisco, California (Arenas et al. 1996).

In this paper, we describe the plankton survey design, location of adult samples (Macewicz et al. 1996), the spatial distribution of sardine eggs, and relations with oceanic conditions. We also estimate peak spawning time for Pacific sardine, coefficients in a temperature-dependent egg-development model, daily egg production, egg mortality, and spawning biomass. Macewicz et al. (1996) describe procedures for sampling adults captured in association with the plankton survey and estimate reproductive parameters for adult sardine used to compute the spawning biomass.

MATERIALS AND METHODS

Survey Design

The plankton survey, April 18–May 11, 1994, covered 380,175 km^2 (111,081 n.mi.^{2}) from Punta Abreojos, Baja California Sur, in Mexico to San Francisco, California (table 1, figure 1a). CalVET[1] and bongo nets were used to collect plankton samples (Smith and Richardson 1977; Smith and Hewitt 1985). The survey extended 180 n.mi. offshore in U.S. waters and 80 n.mi. offshore in Mexican waters. The survey grid followed California Cooperative Oceanic Fisheries Investigations (CalCOFI) track lines (east-west transects) at 40-n.mi. spacing. On each line, the distance between stations was 4 n.mi. for CalVET net tows and bucket temperature measurements (except off Monterey, where three short lines were added), 20 n.mi. for bongo net tows (Smith and Richardson 1977; Lasker 1985), and mostly 40 n.mi. for conductivity temperature depth profiler (CTD) casts. The survey was conducted during the primary spawning period for sardine as determined from historical data (Ahlstrom 1966; Hernández-Vázquez 1995).

Two ships were used to collect ichthyoplankton data. The RV *McArthur* started just south of San Francisco on April 18 and ended in San Diego on May 10, covering an area of 253,850 km^2 (CalCOFI lines 63.3 to 93.3). The RV *El Puma* started at Punta Abreojos on April 20 and ended at Ensenada on May 7, covering an area of 126,325 km^2 (CalCOFI lines 130 to 96).

Three research vessels, RV *Mako* (CDFG), RV *David Starr Jordan* (NMFS), and RV *BIP XII* (INP), collected adult sardines (Macewicz et al. 1996). The *David Starr Jordan* and *Mako* used a high-speed midwater trawl (Dotson and Griffith 1996). The *BIP XII* also used a midwater trawl. Also, adult sardine samples were collected from commercial purse seiners. Most adult samples were from the coastal areas or around islands (figure 1b, table 2).

Oceanographic Measurements

CTD casts were made to a nominal depth of 500 m (depth permitting). A Sea-Bird Electronics, Inc. model SBE 911 was used aboard the R/V *McArthur* (calibrated by the Northwest Regional Calibration Center), and a model SBE 19 was used aboard *El Puma*. The SBE 911 data was processed by standard Sea-Bird Seasoft processing software. The data collected by the SBE 19 had sporadic spikes in the conductivity channel (roughly 0.1 to 0.2 Siemens/m) and excessive hysteresis between the down and up casts. Both the conductivity and calculated salinity from the SBE 19 were filtered to reduce the spiking. In addition, the down and up cast data were averaged to eliminate hysteresis. The resulting data were adequate to describe oceanographic conditions.

TABLE 2
Numbers of Trawl and Purse Seine Samples in U.S. and Mexican Waters Used to Estimate Adult Reproductive Parameters for Pacific Sardine during 1994

		U.S.	Mexico	Total
Trawl	Total	35	34	69
	Usable	13	6	19
Purse seine	Total	11	9[a]	20
	Usable	11	7	18
Total	Total	46	43	89
	Usable	24	13	37

[a] One purse seine sample contained only anchovy.

Sorting and Egg Staging

Sardine eggs were sorted from the plankton and identified on the basis of characteristics described by Ahlstrom (1943) and Miller (1952). Each sample of eggs was placed in a watch glass with water and examined with a dissecting microscope. Eggs were assigned to one of 11 stages based on sequential morphological stages that occur during embryogenesis. Stage criteria were modified from those used for northern anchovy, *Engraulis mordax* (Moser and Ahlstrom 1985). These modified criteria were easier to interpret and more practical than those originally described for Pacific sardine eggs by Ahlstrom (1943).

The use of transmitted light in identifying sardine eggs was essential, since fine structures in the egg could not be seen under reflected light. Most of the preserved eggs for the plankton samples were distorted to some degree, and some were shrunken considerably. We assumed that damage to eggs was an artifact of collection. Stages were therefore assigned to all eggs except those that were amorphous and had no morphological features. Amorphous eggs were assigned stages prorated according to the distribution of egg stages in the sample in which they occurred (Moser and Ahlstrom 1985). Staging criteria used in this study are described briefly below (figure 2).

Stage I: Cell division not yet begun; protoplasm accumulated at one pole of the egg or distributed around granular yolk; the perivitelline space may be small to large; the average diameter of the egg shell (in live eggs, Miller 1952) increases from 1.15 mm at fertilization to 1.38 mm at the end of stage I (ca. 1.5 hours after fertilization), to 1.83 mm at the end of stage II (10 hours after fertilization).

Stage II: Begins with the initial division of the cytoplasm into two cells (or blastomeres), first noticeable as a furrow on the cytoplasmic cap and often marked by tiny bubbles (artifacts produced during preservation) along the cleavage plane. The second cleavage plane is at right angles to the first, and subsequent synchronous divisions produce a blastodisc. Mechanical

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[1] The diameter of the CalVET net frame is 25 cm; the tow is vertical to minimize the volume of water filtered per unit depth; the mesh size is 0.150 mm, and the depth of tow is 70 m. The diameter of the bongo net frame is 71 cm; the tow is oblique at a 45° wire angle; the mesh size is 0.505 mm; with 300 m of wire out, the depth of tow is 210 m.

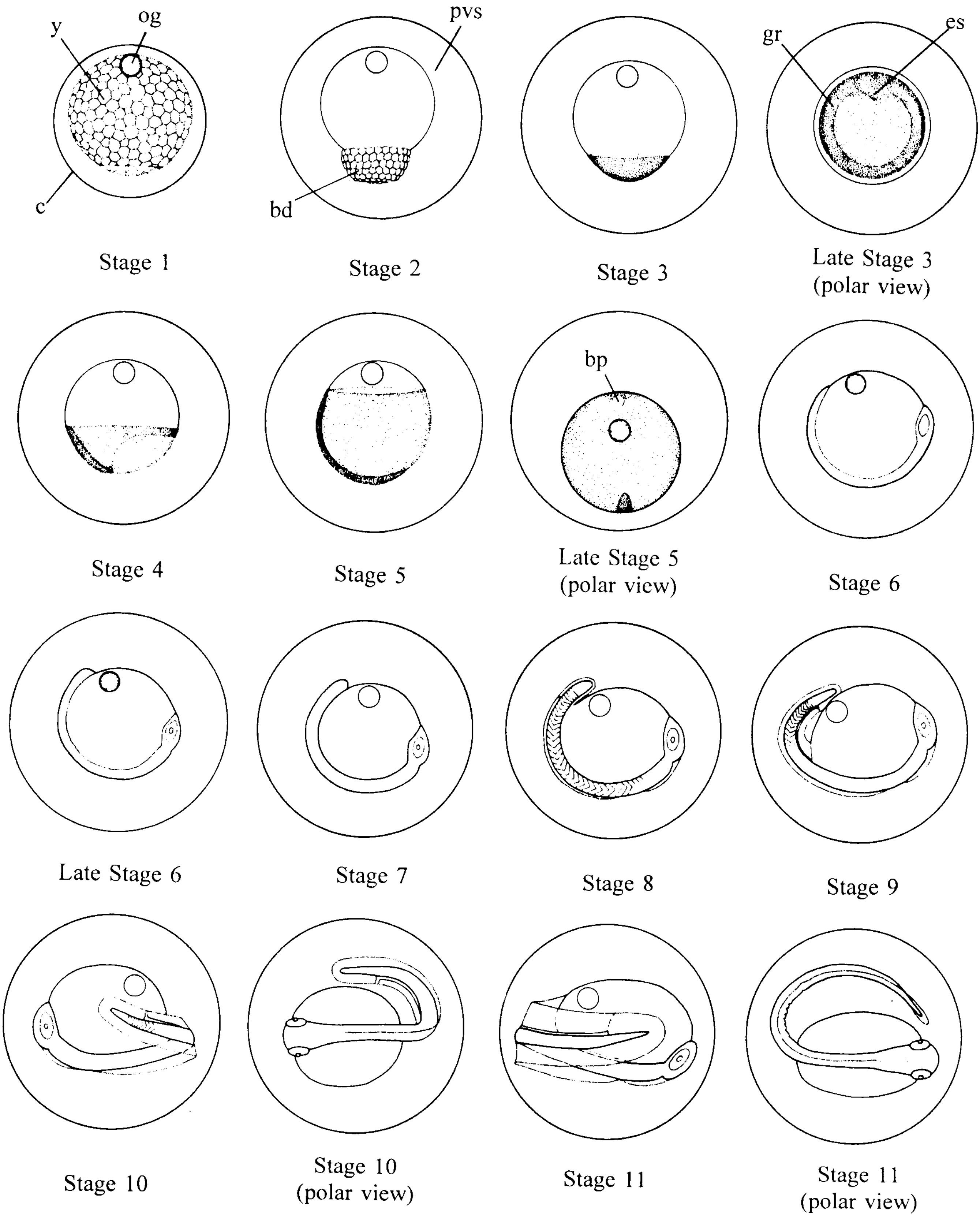

Figure 2. Sardine egg stages. Yolk segmentation is shown only in stage 1. Only a section of the myomeres (muscle segments) is shown beyond stage 8. Symbols: bd, blastodisc; bp, blastopore; c, chorion or shell; es, embryonic shield; gr, germ ring; og, oil globule; pvs, perivitelline space; y, yolk.

stress during the tow may cause the individual cells of the blastodisc to become disassociated and intermingled with yolk granules; however, blastomeres have a different refractive index from yolk granules and appear darker when viewed with transmitted light.

Stage III: Begins when cell division has progressed to the point where individual blastomeres are no longer apparent, and the blastoderm has the appearance of tissue. Late in this stage the cells at the edge of the blastodisc become thickened to form the germ ring; one part of the germ ring becomes thicker to produce an archlike structure (the embryonic shield), which is the first indication of the embryonic axis; the yolk mass begins to be covered by cell proliferation and movement of the blastoderm around the yolk (epiboly).

Stage IV: Begins when the germ ring has enclosed one-third of the yolk mass; embryo forms by further development of the embryonic shield.

Stage V: Begins when the germ ring has enclosed two-thirds of the yolk mass. As epiboly progresses, the uncovered portion of the yolk is referred to as the blastopore. At the end of the stage the brain, optic vesicles, and trunk somites of the embryo are becoming apparent.

Stage VI: Begins with closure of the blastopore at the posterior tip of the embryonic axis. By the end of the stage, somites are present along most of embryo; the brain has begun to differentiate; the lens primordia are forming in the eyes; and the tip of the tail has thickened slightly.

Stage VII: Begins when tip of tail has become rounded and has begun to separate from the yolk mass. The tail becomes pointed as it lengthens.

Stage VIII: Begins when the length of the free section of the tail (the portion that has separated from the yolk mass) is half the length of the head (head length defined for this purpose as the distance from the tip of the snout to the back of the cerebellar lobe of the midbrain).

Stage IX: Begins when the free length of the tail is equal to or greater than the head length.

Stage X: Begins when the free length of the tail has reached halfway around the yolk mass.

Stage XI: Begins when the free length of the tail has reached three-quarters of the way around the yolk mass. The tail continues to lengthen and may extend beyond the front of the head in late-stage specimens just prior to hatching; the stage ends at hatching.

Standardization of Bongo Samples

Counts of eggs and yolk-sac larvae (larvae <5 mm preserved length; Zweifel and Lasker 1976) collected in bongo tows were adjusted for percentage of the sample sorted, multiplied by a standard haul factor (SHF)[2], and adjusted to the units used for CalVET nets (number of eggs or larvae/0.05 m^3/1-m depth). We assumed no extrusion of sardine eggs from bongo tows because the sardine egg diameters (1.35–2.05 mm) were larger than the mesh size (0.505 mm). Some sardine eggs may have been destroyed by the pressure of water in the net during the tow, but we were not able to adjust for this possibility.

Yolk-sac larval production (number/day/0.05 m^2) from bongo tows was computed from the catch in each tow, corrected for larval extrusion and avoidance (Lo 1983; Lo et al. 1989) and the duration of yolk-sac larval stage (Zweifel and Lasker 1976). Extrusion and avoidance correction factors for anchovy larvae were used because this information is not available for sardine. Retention rates for anchovy and sardine larvae are similar (Lenarz 1972; Zweifel and Smith 1981).

Peak Spawning Time within a Day

Peak spawning time of Pacific sardine eggs was estimated to be 10:00 p.m. by Ahlstrom (1950) and midnight by Butler et al. (1993). To refine estimates, we used all available data for sardine eggs collected off California: during 1940–41 (Ahlstrom 1950), 1951–64 (CalCOFI surveys; Smith 1973), 1986–91 (sardine plankton surveys conducted by the CDFG), and 1994 (sardine DEPM survey).

Smith and Hewitt (1985) used 6:00 p.m. as time zero and the proportion of positive tows for anchovy in 2-hour age groups based on tows that caught anchovy eggs to determine the distribution of spawning time within a day. We estimated the peak spawning time based on the peak capture time for stage II sardine eggs. Stage I eggs would be ideal for this purpose, but few stage I eggs were found because of their patchy spatial distribution (Smith 1973, 1981). Cumulative proportions of time-of-tow for stage II eggs were computed starting at sunset (J. R. Hunter, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, pers. comm.). We used cumulative proportions rather than cumulative abundance of stage II eggs to avoid possible bias caused by a few large catches of stage II eggs. The 50th percentile

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[2] SHF is a multiplier used to convert actual catch of a net tow to the equivalent catch per unit of water filtered (catch/10 m^3/1-m depth). SHF = $10/(ab/d)$ where a is the area of the mouth of the net opening in square meters; b is the length of the tow path in meters; d is the maximum depth of tow in meters. The standardized catch is then computed as catch/10 m^3/1-m depth = actual catch * SHF (Smith and Richardson 1977; Zweifel and Smith 1981). To make catches in bongo and CalVET nets comparable, standardized catch in bongo nets was divided by 200 to obtain units of catch per 0.05 m^3/1-m depth (or catch/0.05 m^2).

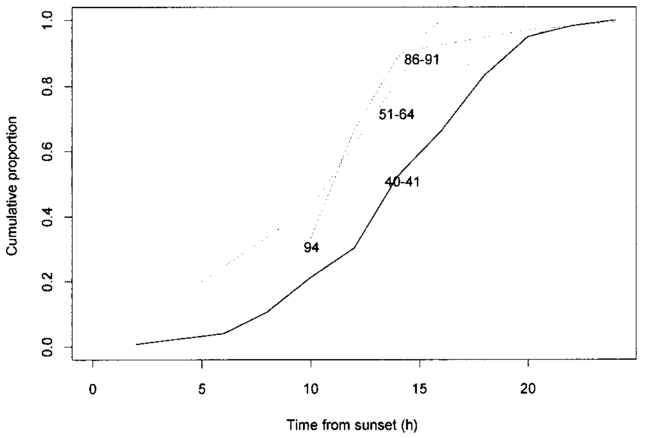

Figure 3. Cumulative proportion of time from sunset (6:00 p.m.) for stage II sardine eggs during 1940–41 (Ahlstrom 1950), 1951–64 (Smith 1973), 1986–91 (Wolf 1988a, b, 1992; Scannell et al. 1996), 1994.

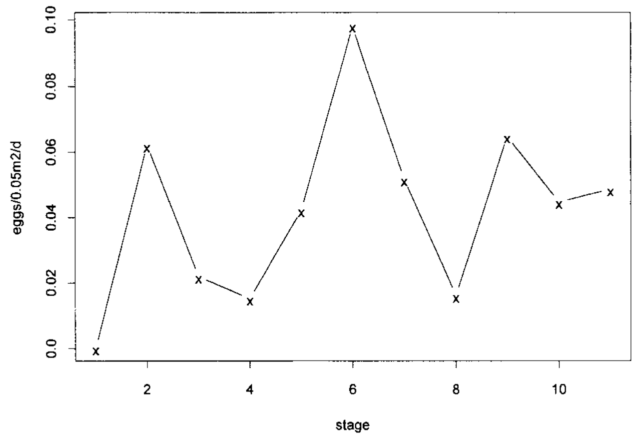

Figure 4. Mean number of Pacific sardine eggs/0.05 m^2 from both CalVET and bongo tows for each developmental stage of Pacific sardine eggs, 1994.

(median) of time from sunset was used to estimate the expected peak capture time for stage II eggs (figure 3). The expected capture time for stage II eggs minus their average age (as estimated by a temperature-dependent egg-development model; see below) approximates the peak spawning time (table 3).

Temperature-Dependent Sardine Egg-Development Model

Nakai (1962) described development rates of Japanese sardine (*Sardinops melanosticta*) eggs at temperatures of 15°, 17°, and 20°C. Zweifel and Lasker (1976) summarized the time to reach stages III, VI, VII–IX, and XI for Pacific sardine eggs at 13.5° to 17° based on field data from Ahlstrom (1950) and laboratory experiments for incubation at 11°–21° (Lasker 1964). We used all the above data sets (table 4) to model the relationship between age and developmental stage for Pacific sardine eggs at various temperatures. The model is (Lo 1985)

$$\hat{y}_{i,t} = \alpha e^{\beta_1 t + \beta_2 i + \beta_{12} it} i^{\gamma} \qquad (1)$$

where $\hat{y}_{i,t}$ is the average age (h) of the ith-stage sardine eggs at temperature t°C; i is egg stage, $i = 1, \ldots, 12$; and stage 12 represents hatching. All coefficients were estimated by nonlinear regression (Chambers and Hastie 1992) assuming additive errors. The coefficient β_{12} is for the interaction between stage i and temperature t.

Egg Production (P_0) and Egg Mortality (Z)

The number of eggs and yolk-sac larvae per day per unit area, their age, and a negative exponential curve were used to estimate daily egg production, P_0, and egg mortality (Picquelle and Stauffer 1985). Sardine eggs collected from both CalVET and bongo net tows were used

TABLE 3

The Median Time from Sunset (6:00 p.m.) for Positive Tows Containing Stage II Pacific Sardine Eggs, the Corresponding Peak Time of Occurrence, Temperature, and Other Estimates from Four Data Sets

Year	1940–41[a]	1951–64[b]	1986–91[c]	1994
Median time from sunset (h)	14	11	11	12
Peak time of occurrence of stage II	8:00 a.m.	5:00 a.m.	5:00 a.m.	6:00 a.m.
Temperature (°C)	15.12[d]	15.54	16.36	13.8
Age (h)[e] of stage II	8.00	8.00	7.00	10.00
Spawning time	Midnight	9:00 p.m.	10:00 p.m.	8:00 p.m.
Positive tows	122	301	35	9
Egg production (P_0)	0.162	0.169	0.123	0.167
CV	0.40	0.22	0.32	0.22
Embryonic mortality (Z)	0.104	0.12	0.044	0.095
CV	1.96	0.97	3.22	1.11

[a] Ahlstrom 1950
[b] Smith 1973
[c] Wolf 1988a, b, 1992; Scannell et al. 1996
[d] 10-m temperature
[e] Rounded to the nearest hour

TABLE 4
Stage and Age of Sardine Eggs Incubated at Various Temperatures (°C) from U.S., Japan, and Mexico Samples

Temperature (°C)	Stage[a]	Age (h)	Data sources
Japan			
20.20	3	5.9	(Nakai 1962)
20.20	4	7.9	
20.20	5	9.9	
20.20	6	12.9	
20.20	6.5	15.9	
20.23	7	18.9	
20.27	8.5	25.9	
20.34	11	33.9	
17.30	3	9.9	
17.30	4	13.4	
17.45	5	16.4	
17.51	6	21.4	
17.50	6.5	26.4	
17.51	7	31.4	
17.56	8.5	42.4	
17.46	11	56.4	
15.21	3	14.6	
15.34	4	19.6	
15.30	5	24.6	
15.24	6	31.6	
15.27	6.5	38.6	
15.28	7	46.6	
15.26	8.5	64.6[b]	
15.23	11	84.6[b]	
United States			
11	12	140	(Lasker 1964)
12	12	115	
13	12	93	
14	12	78.5	
15	12	68.1	
16	12	60.2	
17	12	53.7	
18	12	48.4	
19	12	43.2	
20	12	39.2	
21	12	34	
13.5	3	20.4	
13.5	6	41.8	
13.5	8.5	62.5	
13.5	11	82.6	
14	3	18.9	
14	6	39.1	
14	8.5	58.3	
14	11	77.2	
14.5	3	17.4	
14.5	6	36.6	
14.5	8.5	59.4	
14.5	11	72.2	
United States (continued)			
15	3	16.2	(Ahlstrom 1943)
15	6	34.3	(Zweifel and Lasker 1976)
15	8.5	50.7	
15	11	67.5	
15.5	3	14.9	
15.5	6	32.1	
15.5	8.5	47.2	
15.5	11	63.1	
16	3	13.8	
16	6	30	
16	8.5	44	
16	11	59	
16.5	6	28.1	
16.5	8.5	41.1	
16.5	11	55.1	
17	6	26.3	
17	11	51.5	
Mexico			
19.6	5	2.8	(Ramirez-Sevilla et al. 1992)
19.6	6	7.4	
19.6	7	13.4	
19.6	8	18.0	
19.6	9	18.9	
19.6	10	21.5	
19.6	11	24.8	
19.6	12	26.5	
22.0	5	2.5	
22.0	6	7.0	
22.0	7	12.0	
22.0	8	13.3	
22.0	9	15.3	
22.0	11	19.3	
22.0	12	21.3	
24.0	5	2.5	
24.0	6	6.1	
24.0	7	9.9	
24.0	8	12.0	
24.0	9	13.5	
24.0	10	16.0	
24.0	11	19.4	
24.0	12	20.0	
27.0	5	2.2	
27.0	6	5.1	
27.0	7	8.0	
27.0	8	10.0	
27.0	9	11.1	
27.0	10	14.2	
27.0	11	15.2	
27.0	12	16.0	

[a] Stages of Japanese sardine eggs with decimals are equivalent to multiple stages of Pacific sardine eggs in U.S. data, i.e., stage 6.5 indicates stages 6–7. Stage 12 is end of hatching.

[b] Not used in the analysis because of abnormally high values.

in fitting the negative exponential curve. For a station where both net tows were taken, an average of number of eggs/0.05 m^3/1-m depth for each stage was computed. Yolk-sac larvae were from bongo nets only. Few early-stage eggs were taken in either CalVET or bongo tows during this survey (figure 4), because of their patchy distribution (Smith 1973, 1981). To increase the number of age categories for constructing a mortality curve, we assumed that the mortality rates of eggs and yolk-sac larvae were the same, and we included both in a single embryonic mortality curve (Lo 1986):

$$P_t = P_0 e^{-zt} \tag{2}$$

where P_t is the number of eggs or yolk-sac larvae produced per day per unit area at age t days; P_0 is daily egg production at age zero; and Z is the daily instantaneous mortality rate.

Age of sardine eggs was calculated based on equation 1, the peak spawning time, and time of tow (Lo 1985). Eggs were grouped by half-day categories, excluding eggs younger than 3 h old and eggs older than the expected hatching time; e.g., 3 d at 15°C (equation 1 and see later section; Smith 1973).

Age of yolk-sac larvae from fertilization was estimated from a temperature-dependent growth curve (Zweifel and Lasker 1976). The average temperature for tows with yolk-sac larvae was 14.5°C and 15.5°C in U.S. and Mexican waters. The age of yolk-sac larvae was 5 d with a duration of 3.7 d in U.S. waters, and 4.6 d with a duration of 3.18 d in Mexican waters. The duration for the yolk-sac larvae was computed from the difference between age at formation of a functional jaw and hatching time, both of which depend on temperature (Zweifel and Lasker 1976).

For sardine egg samples, the survey area was post-stratified into stratum 1 (which included the area containing positive tows), and stratum 0 (which was devoid of eggs). Stratum 1 included 64% of the U.S. survey area and 10% of the Mexican survey area (46% of the total area; figure 1a). Egg production in each half-day age group for the whole survey area was obtained as egg production at age in stratum 1 times the fraction of the total area belonging to stratum 1. The stratification was not applied to yolk-sac larvae because yolk-sac larvae are less patchy than sardine eggs.

Biomass Computation

The spawning biomass was estimated (Parker 1985) as

$$B_s = \frac{P_0\,A\,C}{R\,S\,F/W_f} \tag{3}$$

where P_0 is daily egg production per 0.05 m^2; A is the survey area in units of 0.05 m^2; S is the proportion of mature females that spawned per day; F is the batch fecundity; R is the fraction of mature female fish by weight (sex ratio); W_f is the average weight of mature females (gm); and C is the conversion factor from g to MT. P_0A in equation 3 is the total daily egg production in the survey area, and the denominator in equation 3 is the daily specific fecundity (number of eggs/population weight (gm)/day). F, R, W, and S are adult parameters.

The variance of the spawning biomass estimate (B_s) was computed from the Taylor expansion and in terms of the coefficient of variation (CV) for each parameter estimate and covariances for adult parameter estimates (Parker 1985):

$$\begin{aligned} \mathrm{VAR}\,(\hat{B}_s) = \hat{B}_s^2\,[&CV(\hat{P})^2 + CV(\hat{W})^2 + \\ &CV(\hat{S})^2 + CV(\hat{R})^2 + \\ &CV(\hat{F})^2 + 2COVS] \end{aligned} \tag{4}$$

The covariance term on the right-hand side is

$$COVS = \sum_{i}\sum_{i<j} sign\,\frac{COV(x_i,x_j)}{x_i x_j}$$

where x's are the adult parameter estimates, and subscripts i and j represent different adult parameters; e.g., $x_i = F$ and $x_j = W$. The sign of any two terms is positive if they are both in the numerator of B_s or denominator of B_s (equation 3); otherwise, the sign is negative.

We used a ratio estimator (Cochran 1977; Picquelle and Stauffer 1985) for adult parameters F, R, W, and S:

$$\begin{aligned} \bar{y} &= \sum_{i=1}^{n}\sum_{j=1}^{m_i}\bar{y}_{ij}/\sum_{i=1}^{n} m_i \\ &= \sum_{i=1}^{n} m_i\bar{y}_i/\sum_{i=1}^{n} m_i \end{aligned} \tag{5}$$

with sample variance

$$s^2(\bar{y}) = \sum_{i}^{n} m_i^2(\bar{y}_i-\bar{y})^2/[\bar{m}^2 n(n-1)]$$

where y_{ij} is the measurement of the jth female fish in the ith trawl; m_i is the number of mature females; $\bar{y}_i$ is the sample mean for F, S, or W in the ith trawl; and n is number of trawls. For sex ratio (R), m_i is the sample total weight, and $\bar{y}_i$ is the sex ratio in the ith trawl.

The correlation between two adult parameter estimates, say fecundity ($\hat{F}$), and female weight ($\hat{W}$) from equation 5, was

$$correlation\ (\hat{F}, \hat{W}) = \frac{\sum_{i}^{n} m_i(\bar{F}_i-\hat{F})k_i(\bar{W}_i-\hat{W})}{[\bar{m}\bar{k}n(n-1)]se(\hat{F})se(\hat{W})} \tag{6}$$

where m_i and k_i are number of mature females sampled in the ith trawl for each parameter. $\bar{F}_i$ and $\bar{W}_i$ are $\bar{y}_i$ in equation 5 where se is the standard error of an adult parameter estimate.

For simplicity, all estimates will be written in this paper without the symbol ˆ. For example, $\hat{P}_0$ will be written as P_0.

RESULTS

Oceanography and Distribution of Sardine Eggs

Most sardine eggs were distributed in a narrow range of sea-surface temperatures (SST; figures 5 and 6a). Nine percent of the sardine eggs were found at SSTs of 13.7°C and below (only three eggs were found below 13.0°); sixty-five percent were found at SSTs between 13.8° and 14.5°; and the remainder were over a range from 14.6° to 16.6°. All eggs found at SST above 14.5° were within

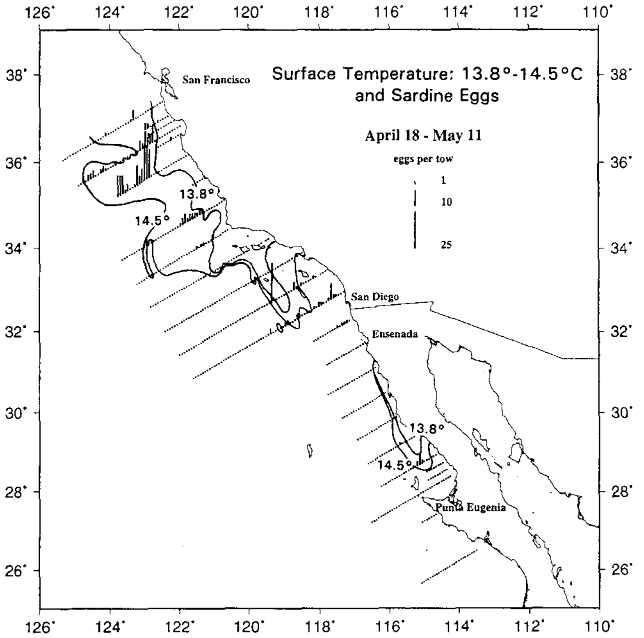

Figure 5. Pacific sardine eggs from CalVET tows and 13.8° and 14.5°C sea-surface isotherms.

and offshore of the southern portion of the Southern California Bight (SCB). The median SST at stations where sardine eggs were found was 14.3°, slightly below the temperature of 14.6° described by Lluch-Belda et al. (1991) as the lower of two peaks in the ratio of frequency distributions for SST and sardine eggs based on 39 years of CalCOFI data.

The greatest number of sardine eggs was found in a region south of Monterey Bay and associated with a filament of relatively cold water. The filament of cold water extended offshore from the coastal headlands north and south of Monterey Bay (figures 6a and 7a). The association of eggs with the offshore extension of the filament was particularly strong in samples along CalCOFI line 70 off Point Sur, where the filament coincided with a station track that extended 240 km offshore. A second, smaller concentration of eggs was associated with a smaller filament south of Point Piedras Blancas. A few sardine eggs were also found at four stations south of the coastal upwelling around Punta San Antonio (figures 5, 6a, and 7b).

Peak Spawning Time within a Day

We chose 9:00 p.m. as the peak spawning time for Pacific sardine, based on data from 1951 to 1964. Our estimate is similar to the 10:00 p.m. stated by Ahlstrom (1950). The cumulative proportion of time from sunset for stage II eggs in the 1940–41 data set was quite different than in the other three data sets (figure 3, table 3). Temperature measurements for the 1940–41 data set were made at 10-m depth. If the sea-surface temperature used in some years of the three other data sets were warmer than the temperature at 10 m, our estimate of the age of stage II eggs, based on surface temperature, would have been smaller, and the peak spawning time may have been earlier (Macewicz et al. 1996).

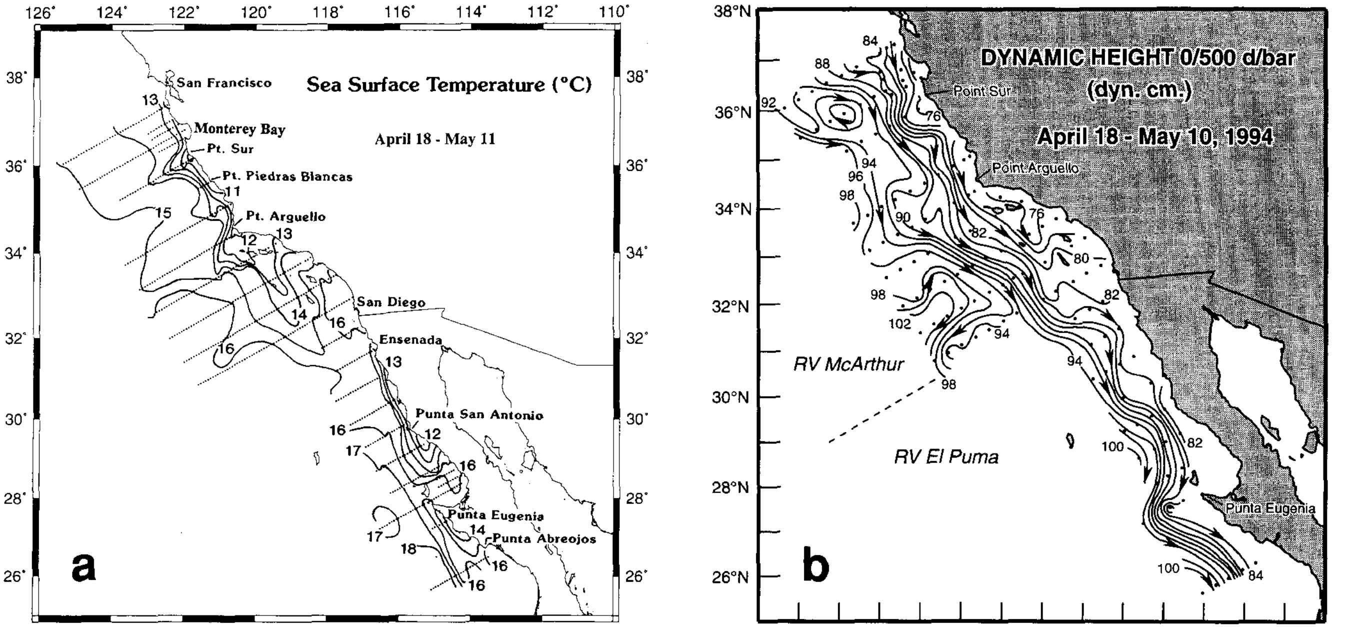

Figure 6. Oceanographic data for daily egg production method survey area: *a*, sea-surface temperature (°C), and *b*, dynamic height of the sea surface relative to a level of 500 decibars (in dynamic centimeters). *Arrows* indicate the direction of geostrophic flow.

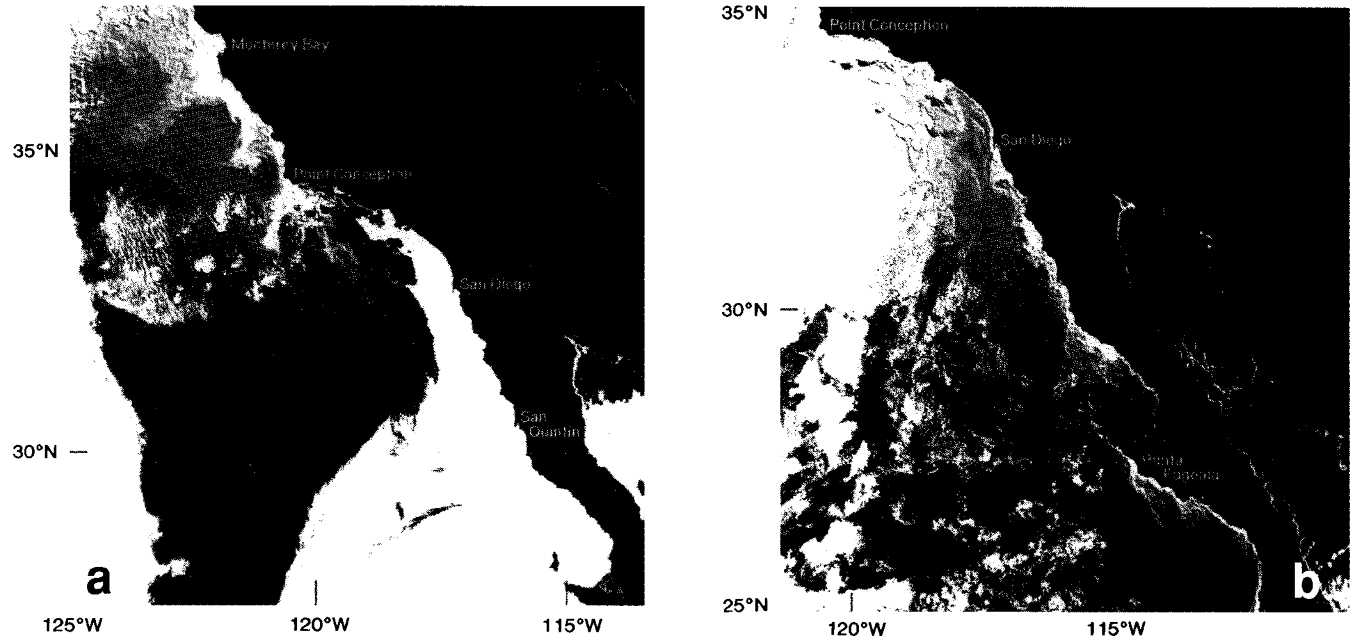

Figure 7. Infrared sea-surface temperature images from NOAA 11 channel 4 AVHRR satellite on (*a*) April 19, 1994, when the RV *McArthur* was at the western end of the northernmost line and (*b*) a combined image for April 28 and 29, 1994, when the RV *El Puma* was at the western end of the station line off Punta Eugenia. The images were provided by the *CoastWatch* node at La Jolla, California.

Temperature-Dependent Sardine Egg-Development Model

Estimates and the standard errors of coefficients for the temperature-dependent egg-development model (equation 1, figure 8) from data of Japan and United States are[3]:

Coefficient	Estimates	CV	*t* values
Intercept (α)	30.66	0.186	5.4
Stage (β_1)	−0.037	0.54	1.8
Temperature (β_2)	−0.145	0.026	38.5
Stage (γ)	1.41	0.12	8.33

The residual standard error was 3.0 on 58 degrees of freedom.

We also computed the expected age (hours) and expected peak time of occurrence for sardine eggs at different developmental stages and temperatures ranging from 10° to 22°C (table 5; Lo 1985). The expected age can be computed directly from equation 1. However, the peak time for each stage at various temperatures is a function of peak spawning time. Therefore the expected peak time, together with field data, can be used for checking the accuracy of staging of field-collected sardine eggs, as well as the accuracy of an assumed peak spawning time.

Embryonic Mortality Curve and Daily Egg Production

A total of 684 CalVET tows were taken, 462 off California and 222 off Mexico (figure 1a). There were 66 CalVET tows positive for sardine eggs off the United States, and 8 off Mexico (figure 1c). Bongo tows were taken at 91 stations off California and at 45 stations off Mexico (figure 1d). When CalVET and bongo tows are combined, the number of positive stations for sardine eggs was 82, of which 74 were in U.S. waters. Sardine eggs were not caught in bongo tows taken off Mexico.

The number of positive CalVET tows for yolk-sac larvae was 49 in U.S. waters and 8 in Mexican waters (figure 1c). Nineteen bongo tows in U.S. waters and 6 in Mexican waters caught yolk-sac larvae (figure 1d). The number of positive stations (CalVET and bongo) was 76, of which 62 were in U.S. waters and 14 were in Mexican waters (table 6).

The estimated daily egg production (P_0) was 0.169 eggs/0.05 m^2/day (CV = 0.22), and the estimated daily embryonic mortality rate (Z) was 0.12/day (CV = 0.97; figure 9 and tables 1 and 7). The relatively high CV of

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[3] Ramirez-Sevilla et al. (1992) reported the development rates of *Sardinops sagax caerulea* from 19.6° to 27°C. We were unaware of this report while we computed the spawning biomass of Pacific sardine. The following estimates of coefficients for equation 1 were computed from combined data of Japan, U.S., and Mexico, and are recommended particularly if temperature is higher than 21°C (table 4).

Coefficient	Estimates	CV	*t* values
Intercept (α)	82.832	0.4	2.47
Temperature (β_1)	−0.1139	0.35	2.80
Stage (β_2)	−0.2103	0.11	9.52
Temperature x Stage (β_{12})	0.0050	0.4	2.52
Stage (γ)	1.4024	0.15	6.55

The residual standard error was 3.82 on 88 degrees of freedom.

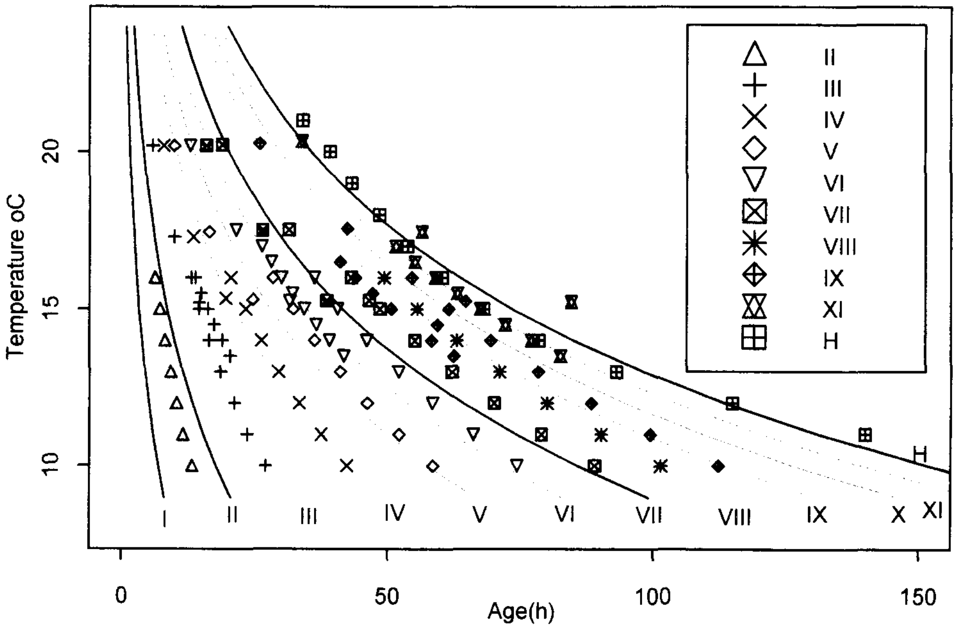

Figure 8. Age for each developmental stage of sardine eggs, based on a temperature-dependent model. Stage XII is end of hatching (H). Symbols are data for Japan and U.S. (table 4).

TABLE 5
Average Age (h) and Expected Time of Peak Occurrence for Pacific Sardine Eggs for Stages I to XI, and Temperatures between 10° and 22°C

Average age (hour)

	Stage										
Temp. (°C)	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
10	6	16	28	40	53	66	80	93	106	118	131
11	5	14	24	35	46	57	69	80	91	102	113
12	4	12	21	30	40	50	60	69	79	88	97
13	4	10	18	26	34	43	51	60	68	76	84
14	3	9	15	22	30	37	44	52	59	66	73
15	3	7	13	19	26	32	38	45	51	57	63
16	2	6	11	17	22	28	33	39	44	49	54
17	2	5	10	14	19	24	29	33	38	43	47
18	2	5	8	12	16	21	25	29	33	37	41
19	1	4	7	11	14	18	21	25	28	32	35
20	1	3	6	9	12	15	18	21	24	27	30
21	1	3	5	8	10	13	16	18	21	24	26
22	1	2	4	7	9	11	14	16	18	20	22

Expected peak time of occurrence (hour)

	Stage										
Temp. (°C)	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
10	3	13	1	13	2	15	5	18	7	19	7
11	2	11	21	8	19	6	18	5	16	3	14
12	1	9	18	3	13	23	9	18	4	13	22
13	1	7	15	23	7	16	00	9	17	1	9
14	00	6	12	19	3	10	17	1	8	15	22
15	00	4	10	16	23	5	11	18	00	6	12
16	23	3	8	14	19	1	6	12	17	22	3
17	23	2	7	11	16	21	2	6	11	16	20
18	23	2	5	9	13	18	22	2	6	10	14
19	22	1	4	8	11	15	18	22	1	5	8
20	22	00	3	6	9	12	15	18	21	00	3
21	22	00	2	5	7	10	13	15	18	21	23
22	22	23	1	4	6	8	11	13	15	17	19

Peak spawning time was assumed to be 9:00 p.m. Each entry was computed at the midpoint of temperature.

TABLE 6
Summary of Data Used to Compute Yolk-Sac (YS) Larval Production for Pacific Sardine from Bongo and CalVET Samples

	YS larvae /d/0.05 m^2	Positive tows	Total stations	% of survey area
United States				
Bongo	0.11	19	91	
CalVET	0.077	49	462	
Bongo and CalVET	0.098	62[a]	462	67
Mexico				
Bongo	0.0312	6	45	
CalVET	0.018	8	222	
Bongo and CalVET	0.024	14	222	33
Total bongo and CalVET	0.0735[b]	76	684	100

The average of standard haul factor for bongo tows was 4.8 for U.S. samples and 9.0 for Mexican samples.
[a] 62 is the number of tows that caught yolk-sac larvae with either or both bongo and CalVET nets.
[b] An average weighted by survey area.

the estimate of egg mortality was due in large measure to patchiness of early-stage eggs (figure 4; Smith 1973, 1981).

Spawning Biomass

Of the 43 collections positive for adult sardine, 37 were usable; most of the positive collections were in coastal or insular areas (figure 1b). The sex ratio for sardine sampled during the survey was 0.53 (CV = 0.068); mean batch fecundity was 24,282.52 eggs/batch (CV = 0.11); spawning frequency was 0.073/d (CV = 0.23); and mean female fish weight was 82.53 gm (CV = 0.071; table 1; Macewicz et al. 1996). The daily specific fecundity was 22.53 eggs/gm/day. The correlation matrix for the adult parameter estimates (equation 3) is:

	F	*S*	*R*
W	.89	−.22	−.29
F		−.2	−.27
S			−.07

The biomass was 111,493 MT (CV = 0.32), with an approximated 95% confidence interval of 40,000 to 182,800 MT.

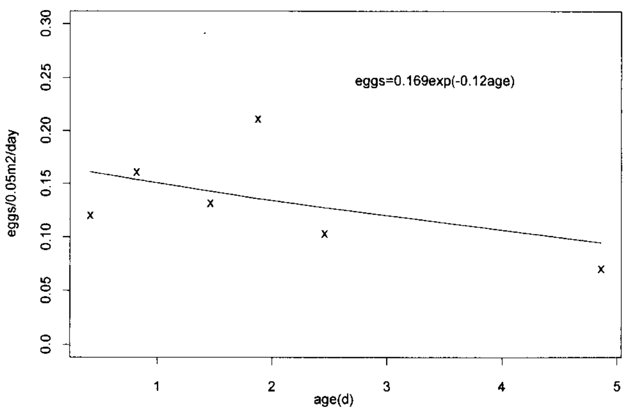

Figure 9. Embryonic mortality curve for Pacific sardine eggs and yolk-sac larvae during the daily egg production method survey, 1994.

TABLE 7
Number of Eggs and Yolk-Sac Larvae Used to Estimate the Parameters of the Embryonic Mortality Curve for Pacific Sardine during 1994 Survey

	Age (d)	Number/0.05 m^2/d	
1	0.41	0.123	Eggs
2	0.82	0.163	
3	1.46	0.134	
4	1.87	0.213	
5	2.45	0.105	
6	2.84	0.206	
7	3.35	0.105	
8	3.80	0.079	
9	4.76	0.073	Larvae

Eggs younger than 3 h and older than 2.8 d were excluded from the analysis.

DISCUSSION

During April 1994, oceanographic conditions were close to seasonal norms. Upwelling as measured by Bakun's index (1973) in April 1994 was very close (within 0.5 units of standard deviation) to its long-term (1963–93) mean value from Oregon to southern Baja California. There is strong evidence that the large-scale cold-water filaments, especially common off northern and central California and Baja California in late spring and early summer, are associated with a meandering current jet (Strub et al. 1991). A strong coastal jet during the survey coincided with nearshore temperature and salinity gradients from San Francisco to Punta Abreojos (figure 6b). Sardine eggs were found mainly in waters between 13.0° and 14.5°C in association with the high-flow region of the current jet. Eggs associated with the eddy in the northwest corner of the survey (figure 7) were found in waters between 14.3° and 14.5°. Eggs found in waters of temperatures above 14.5°C were within the bight in the low-flow region. During July 1994, off Oregon, sardine eggs were found in the 1–10-m depth temperature range of 14° to 16°, which was a sharp temperature gradient (Bentley et al. 1996).

The SST range (13.8°–14.5°) in which most (65%) of the sardine eggs were found occurred within the strong SST and salinity gradients that develop immediately offshore of coastal upwelling centers during spring. With only a few exceptions, sardine avoided spawning in waters of less than 13.0°, a temperature fatal to sardine larvae in laboratory experiments (Lasker 1964). Studies conducted on the large cold-water filaments show that the current jet associated with these features is a boundary between coastal eutrophic waters and the offshore oligotrophic waters (Hood et al. 1991; Mackas et al. 1991). Thus the absence of sardine eggs in warmer water offshore beyond the 14.5° isotherm suggests that the availability of food rather than temperature might limit the offshore extent of spawning. Eggs found within the SCB at temperatures above 14.5° (up to 16.6°) are in a biologically richer environment than eggs found in similar temperature in the offshore waters. Sardine eggs have been found in waters as warm as 27° (Lluch-Belda et al. 1991).

We may have underestimated daily egg production, P_0, and the spawning biomass because sardine eggs destroyed in the net were not accounted for. Future studies are needed to quantify the proportion of eggs destroyed, and to correct spawning biomass estimates for this effect.

The variance for our spawning biomass estimate may be underestimated because the peak spawning time was estimated but its variance not included in the variance estimates for egg production. We computed P_0 and Z for four spawning times: 8:00 p.m., 9:00 p.m., 10:00 p.m., and midnight. P_0 and Z were similar for all estimated peak spawning times except 10:00 p.m. (table 3). There was no trend between P_0 and estimated spawning time. We concluded that the estimates of P_0 and Z were not biased by our assumption about the spawning time. The peak spawning time for sardine estimated by Macewicz et al. (1996; 8:00–10:00 p.m.) was similar to the value we assumed.

The low abundance of sardine eggs off Mexico was probably because our survey was conducted before the peak August spawning time there (Hernández-Vázquez 1995). The low abundance of sardine eggs collected in Mexican waters during our survey does not indicate low Pacific sardine abundance there.

The CV for our spawning biomass estimate (CV = 32%) was due mostly to an uncertainty about the estimated egg production (CV = 0.22) and the estimated spawning frequency (CV = 0.23). Although 684 CalVET tows were taken in the survey, the embryonic mortality rate of 0.12/d was imprecise (CV = 0.97), primarily because eggs at young stages were not captured efficiently because of their patchy distribution (Smith 1973, 1981) and relatively short duration (Picquelle and Stauffer 1985). The patchy distribution of early-stage eggs is primarily due to the aggregation of adult females. The spatial distribution of older-stage eggs becomes less patchy because of dispersal as eggs age (Smith 1973). Smith (1973) computed number of positive tows for 6-hour age groups for sardine eggs and found that 6-hour-old sardine eggs were lowest among all age groups. Smith (1981) computed the number of tows required to estimate production for one-day categories of anchovy eggs for a given level of precision. He showed that sample size should be four times larger for day-one anchovy eggs than for day-two anchovy eggs. Similarly, early-stage sardine eggs will require more tows than later-stage eggs, due to high variance, which is a direct result of patchiness. Other potentially more efficient sampling schemes, like adaptive sampling (Thompson 1992) or Bayesian approaches, might yield more efficient and unbiased estimates of egg production for the youngest sardine eggs.

TABLE 8
Comparison of Sardine Parameters and Estimates during 1986 and 1994

	1986	1994
Area	17,390 km^2	380,175 km^2 253,850 km^2 (U.S.)
North	Point Conception	San Francisco
South	San Diego	Punta Abreojos
CalCOFI lines	80–93.3	63.3–130
Month	August	April–May
Number of CalVET tows (positives)	330 (59)	462 (66) (U.S.) 222 (8) (Mex.) 684 (74) (total)
Eggs/tow	0.78	0.7 (U.S.) 0.07 (Mex.) 0.64 (total)
Peak spawning	10:00 p.m.	9:00 p.m.
Number of positive trawls	11	24
Number of positive purse seine samples	—	19
Batch fecundity		
Intercept	−21,000	−10,585
Slope	495.67	439.53
Density of spawning biomass	0.44 MT/km^2	0.27 MT/km^2 0.4 MT/km^2 (U.S.) assuming 90% of population is in U.S. waters

We compared estimates from our survey with values obtained in 1986 by CDFG (Scannell et al. 1996), the first year when the DEPM was used to estimate the spawning biomass of sardine off California. Significant changes between parameter estimates in 1986 and 1996 may shed light on the dynamics of sardine population in this ten-year period (Wolf 1988a, b, 1992; Barnes et al. 1992).

The survey area in 1994 was 22 times larger than during the 1986 survey, and the 1986 survey covered a more inshore area (tables 1 and 8). The survey in 1994 was conducted in April–May, whereas the 1986 survey was conducted in August. The dates for each survey were based on the best estimates of the spawning season. The spawning time for California sardine has shifted from summer to spring. Based on CalVET tows only, the number of eggs/0.05 m^2 was 0.64 during 1994 (0.7 in U.S. waters) and 0.78 during 1986. Percentage of positive tows was 0.1 during 1994 (0.14 for U.S.) and 0.18 during 1986. The percentage of positive tows during

1986 was higher because the survey area was closer to shore and intentionally near the center of the spawning grounds. Egg production (P_0) was 0.169/0.05 m^2 during 1994 and 0.27–0.513/0.05 m^2 during 1986. In 1994, the estimated egg mortality was 0.12/d (CV = 0.97). An assumed value of 0.05/d was used for 1986.

Most of the adult parameter estimates were similar for 1986 and 1994, except that the average female fish weighed less in 1994 (83 gm) than in 1986 (150–200 gm; tables 1 and 8). Deriso et al. (1996) also report reductions in average weight during 1983–95. The spawning biomass and survey area for 1986 were 7,659 MT and 17,390 km^2, compared to 111,493 MT and 380,175 km^2 in 1994. If one assumes that 90% of the 1994 spawning biomass of sardines was in U.S. waters, then the density in U.S. waters during 1994 would be 0.4 MT/km^2, which is similar to 0.45 MT/km^2 in 1986. Therefore the increase in the spawning biomass of Pacific sardine from 7,659 MT in 1986 to 111,493 MT was due to the expansion of area (either spawning area or survey area) rather than to an increase in the density of spawning biomass.

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CATCH-AT-AGE ANALYSIS FOR PACIFIC SARDINE (*SARDINOPS SAGAX*), 1983–1995

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ABSTRACT

We used CANSAR (Catch-at-age ANalysis for SARdine, an age-structured stock-assessment model) and a wide range of data to estimate biomass and recruitment of Pacific sardine (*Sardinops sagax*) off California and northern Baja California during 1983–95. Daily egg production method (DEPM) spawning biomass estimates and an abundance index from CalCOFI data based on generalized additive models were important new sources of information. Biomass (344,000 MT of sardine age 1+ during July 1995, CV = 33%) increased by 28% year^{-1}. Fishing mortality (particularly for older ages) after 1991 was high and probably not sustainable under average environmental conditions. DEPM data for sardine during 1986–88 and 1994 may have underestimated spawning biomass due to incomplete coverage of spawning habitat. There was a modest potential for bias in the DEPM data due to nonrepresentative sampling of young age groups by survey gear. On the basis of experience with DEPM data for sardine and northern anchovy (*Engraulis mordax*), we make suggestions about how DEPM data should be used for fish stock assessment and fishery management. Size-at-age declined during 1983–95 and was significantly correlated with sardine biomass.

INTRODUCTION

Pacific sardine (*Sardinops sagax*) along the west coast of North America (stock structure reviewed in Hedgecock et al. 1989) is a small (28–30 cm SL), short-lived (less than nine years in recent years), pelagic schooling fish usually harvested near shore with purse seine gear (Wolf 1992). The historical fishery for Pacific sardine developed during the second decade of the twentieth century (Schaefer et al. 1951). It expanded rapidly; landings exceeded 700,000 MT during the 1936–37 fishing season and often exceeded 500,000 MT season^{-1} during the following years (Radovich 1982). Sardine landings fell off sharply after 1944 as abundance declined to low levels and the fishery collapsed. A minor fishery persisted off California during the 1960s and early 1970s until it was prohibited in 1973.

Sardine biomass began to increase in the late 1970s (Barnes et al. 1992), and sardine became common as bycatch in fisheries off northern Baja California and California (Wolf 1992). There was immediate commercial interest, and the prohibition on sardine fishing in California waters was lifted in 1986 when a small quota (1,043 MT) was allowed for directed fishing. California and Mexican landings subsequently increased to 5,000 MT in 1987, 48,000 MT in 1993, and 34,000 MT in 1994 (table 1). In California during 1994, Pacific sardine was, next to market squid (*Loligo opalescens*), the second most important species landed in terms of total landings, and the thirteenth most important in terms of ex-vessel revenues ($2.8 million).[2] During 1995, total landings of sardine along the Pacific coast (excluding Mexican landings from the Gulf of California and south of Ensenada) exceeded 70,000 MT (preliminary data). Thus the sardine fishery had grown to again become one of the largest along the coast from Baja California to British Columbia.

Biomass of Pacific sardine is estimated annually and used to set quotas for the California fishery (Wolf 1992). A variety of models and approaches have been used to estimate sardine biomass (Barnes et al. 1992), but none

TABLE 1

Pacific Sardine Landings (MT) in the United States (California) and Ensenada, Baja California, Mexico, 1983–1995

	First semester		Second semester		
Year	U.S.[a]	Mexico	U.S.	Mexico	Total
1983	263.0	149.5	89.0	124.1	625.6
1984	159.0	0.1	75.0	0.1	234.2
1985	322.0	3,174.2	271.0	548.1	4,315.3
1986	920.0	99.2	244.0	143.4	1,406.6
1987	1,304.0	975.0	791.0	1,456.6	4,526.6
1988	3,020.0	620.2	766.0	1,414.7	5,820.9
1989	2,154.0	461.0	1,528.0	5,761.2	9,904.2
1990	2,132.0	5,900.0	683.0	5,475.3	14,190.3
1991	5,173.0	9,271.0	2,577.0	22,120.8	39,141.8
1992	6,256.0	3,326.5	11,060.0	31,241.7	51,884.2
1993	12,153.0	18,649.0	4,034.0	13,396.0	48,232.0
1994	8,498.6	5,706.2	4,336.4	15,165.0	33,706.2
1995	28,462.6	18,257.0	12,296.2	15,441.1[b]	74,456.9[b]

[a] U.S. landings include commercial landings and commercial bycatch. Live bait catches (less than 500 MT during 1983–92 and less than 2,000 MT in 1993–94) are excluded.

[b] Preliminary.

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[2] Revenues include 1,487 MT of live bait sold at $681/MT and 11,933 MT sold at $148/MT primarily for human consumption.

took advantage of all available fishery and fishery-independent data. The purpose of our paper is to describe a stock assessment model (CANSAR for Catch-at-age ANalysis for SARdine; Deriso 1993) that includes all available data. Additionally, we describe a new index of abundance based on CalCOFI data. We also test assumptions about daily egg production method (DEPM) spawning biomass estimates for sardine and evaluate potential bias in DEPM data (Lo et al. 1996).

DATA

Catch-at-age (numbers of fish at age) and mean weight-at-age data for the California fishery during 1983–95 and for the Mexican fishery around Ensenada during 1990–92 were from random stratified port samples. Where catch-at-age data were unavailable, tons landed (table 1) were used instead (see below). Fishery data were aggregated by semester (January–June or July–December) and area (California or Mexico) because of seasonal and spatial differences in catch and weight-at-age. Before use in CANSAR, catch-at-age data were adjusted so that the sum of catch-at-age times weight-at-age was equal to tons landed for both fisheries in each semester of each year. Sardine were aged by counting annuli in whole sagittal otoliths (Yaremko 1996). A birth date of July 1 was assumed.

We used three indices of relative abundance and DEPM spawning biomass estimates for 1986 (Scannell et al. 1996), 1987–88, and 1994 (Lo et al. 1996) in CANSAR to estimate sardine abundance (table 2, figure 1). Indices of relative abundance were from CalCOFI data, fish-spotter reports, and spawning area surveys.

CalCOFI Index

The CalCOFI index measures annual egg production by sardine on a relative basis from ichthyoplankton data collected during 1984–95 (Hewitt 1988). We used data for sardine eggs and larvae taken in bongo nets within the boundaries of the current CalCOFI sampling grid (Lo and Methot 1989) from shore out to station 67.5. The current CalCOFI grid is smaller than the historical range of sardine but is the largest area occupied by the survey in all years. Data from samples taken farther offshore than station 67.5 were omitted because sardine were seldom taken there and the data were highly variable.

Previous studies used four types of aggregated CalCOFI data for sardine: egg density (mean eggs tow^{-1}),

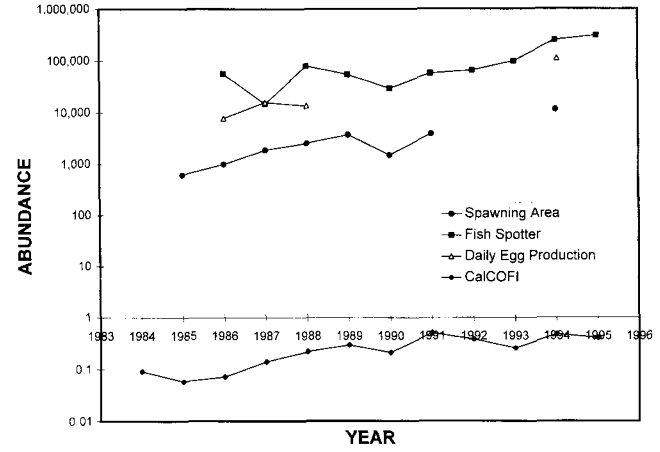

Figure 1. Relative abundance and DEPM data for Pacific sardine used in CANSAR.

TABLE 2
Abundance, Spawning Biomass, and Mean Three-Season Sea-Surface Temperature Data for Pacific Sardine by Fishing Season

Season[a]	CalCOFI	Fish spotter	CV[b]	California spawning area (nm^2)	Daily egg prod. (MT)	CV[b]	Mean three-season[c] Scripps Pier temperature (°C)
1983							17.8
1984	0.0524						17.9
1985	0.0251			670			17.7
1986	0.0175	55,539	0.31	970	7,659	0.51	17.6
1987	0.0519	14,522	0.36	1,850	15,705	0.91	17.2
1988	0.0813	78,605	0.36	2,508	13,526	1.6	17.2
1989	0.1431	54,032	0.39	3,680			17.3
1990	0.0530	29,314	0.36	1,480			17.6
1991	0.2325	56,479	0.32	3,840			17.8
1992	0.1623	65,059	0.32				18.0
1993	0.1370	97,582	0.33				18.0
1994	0.2613	251,862	0.31	11,360	125,537[e]	0.45	18.0[d]
1995	0.2757	306,561	0.34				18.0[d]

[a] Season runs from 1 July of one year to 30 June of the following year; e.g., the 1983 season ran from 1 July 1983 to 30 June 1984.

[b] Coefficients of determination.

[c] Mean three-season sea-surface temperature calculated as in Jacobson and MacCall 1995. For example, the temperature datum for 1983 is used to predict recruitment of age-zero sardine on 1 July 1983 and was calculated from mean daily sea-surface temperatures at Scripps Pier during 1 July 1982–30 June 1985.

[d] Mean three-season temperature assumed to be the same as for 1993.

[e] Preliminary value.

larval density (mean larvae tow^{-1}), proportion of tows positive for eggs, and proportion positive for larvae. A general linear model (GLM) was fit to all four types of CalCOFI data in previous studies to obtain a single index of egg production (Barnes et al. 1992). The index was plagued, however, by problems with trends in residuals, the choice of a small additive constant used to log-transform the data (which includes "zeroes" when no eggs or larvae are taken; MacCall and Prager 1988), and differences in the appropriate statistical distribution for estimating parameters from proportion positive and density data.

To avoid the problems of previous studies, we fit logistic regression models using generalized additive model techniques (GAM; Hastie and Tibshirani 1990) to nonaggregated, tow-by-tow CalCOFI data. The advantages were greater flexibility in modeling, no additive constants, maximum likelihood parameter estimates, and no aggregation of data. The GAM used for sardine presence-absence data was

$$P_{y,m,L,s} = \frac{e^{\eta_{y,m,L,s}}}{1+e^{\eta_{y,m,L,s}}} + \epsilon_{y,m,L,s} \qquad (1)$$

where $P_{y,m,L,s}$ was the probability that a tow in year y, month m, at line L and station s would contain at least one sardine egg or larvae, and $\epsilon_{y,m,L,s}$ was a statistical error. The term $\eta_{y,m,L,s}$ is described below.

The variance of statistical errors in equation 1 was modeled with quasi-likelihood techniques (McCullagh and Nelder 1983):

$$\mathrm{VAR}(\epsilon_{y,m,L,s}) = \phi \hat{P}_{y,m,L,s} (1-\hat{P}_{y,m,L,s}) \qquad (2)$$

where the scale factor (ϕ) measures how large the actual variance [Var($\epsilon_{y,m,L,s}$)] was relative to that expected under the binomial distribution [($\hat{P}_{y,m,L,s}$ $(1-\hat{P}_{y,m,L,s})$], and hats (ˆ) denote model estimates. The binomial distribution was appropriate because data used to fit model 1 were either zero (if no sardine eggs or larvae were taken in the tow) or one (if at least one egg or larva was taken). Results using just eggs or larvae were similar (correlation coefficient $\rho = 0.9$), so we combined data for eggs and larvae and estimated the probability that a tow was positive for either an egg or a larva.

The term $\eta_{y,m,L,s}$ in equation 1 was a "linear predictor" (McCullagh and Nelder 1983):

$$\eta_{y,m,L,s} = X_y + f(m) + g(L) + h(s) \qquad (3)$$

where X_y was a parameter for year y (years were treated as factors), and the components $f()$, $g()$, and $h()$ were smooth, possibly nonlinear, functions of the covariates month, line, and station. Smooth terms were fit with the locally weighted scatterplot smoother (Cleveland et al. 1988; called "loess" in Cleveland and Devlin 1988 and Hastie and Tibshirani 1990) with a neighborhood size of 75% and quadratic local regressions on the data in each neighborhood. Statistical interactions between month, line, and station probably exist but were omitted from model 3 because they are difficult to specify with loess components. MacCall and Prager (1988) found that interaction terms made little difference in estimation of year effects from CalCOFI data for six fish species.

Models like model 1 for egg and larval density data (numbers tow^{-1}) were fit assuming the Poisson distribution with Var($\epsilon_{y,m,L,s}$) = $\phi \hat{P}_{y,m,L,s}$. We did not report or use the results, however, because the variance of residuals was extreme (ϕ = 9,928 for larvae and ϕ = 1,950 for eggs), and estimated trends were erratic. High variance in egg and larvae counts is typical for sardine because of patchiness in the spatial distribution of spawning adults (Mangel and Smith 1990; Smith 1990).

In contrast to results for density data, the variance of residuals for presence-absence data was close to one (ϕ = 0.89 for proportion-positive larvae and ϕ = 1.4 for eggs), and trends over time were similar to other abundance indices (figure 1). The CalCOFI index (table 2, figure 1) was calculated for each year during May at line 80 and station 50 (figure 2).

Fish-Spotter Data

An index of schooling biomass for sardine during 1984–95 (table 2, figure 1) was based on fish-spotter data (Squire 1961) and delta-lognormal models (Lo et al. 1992). We used the same procedures to calculate the index as in Lo et al. 1992, except that (1) data for each flight were weighted by the number of blocks searched so that data from long flights were weighted more heavily than data from short flights; (2) July–June annual periods were used to aggregate data (to match time steps used in CANSAR, see below); and (3) years with fewer than 100 positive flights for sardine were excluded. The fish-spotter information for 1995 included only data for July 1994–March 1995.

Spawning Area Survey

Estimates of spawning area (table 2, figure 1) were used in CANSAR as an index of spawning biomass. The CDFG conducted spawning area surveys in California waters from 1985 to 1991 to measure the surface area of the ocean occupied by spawning sardine (Wolf and Smith 1985, 1986; Barnes et al. 1992). CDFG data were augmented by calculating spawning area during the 1994 DEPM spawning biomass survey (Lo et al. 1996). For consistency, we included only spawning area in California waters during 1994.

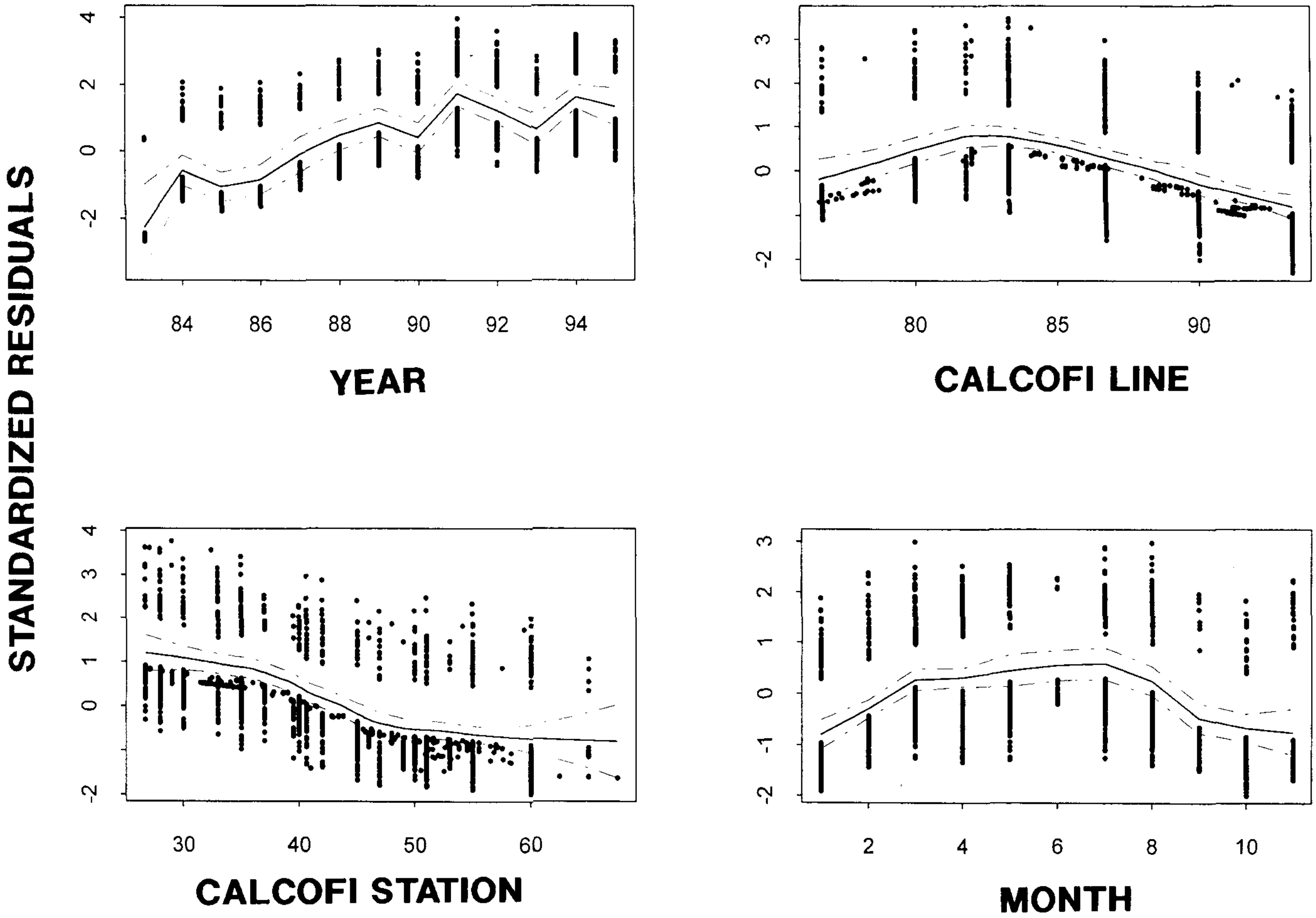

Figure 2. Fitted values and residuals (with approximate 95% confidence intervals) for a generalized additive model fit to CalCOFI data for Pacific sardine. Plots are scaled so that the mean residual is zero. Many negative residuals occur between major CalCOFI lines because the samples were taken when sardine eggs were rare and no eggs were collected.

MODEL

CANSAR was derived from the CAGEAN program (Deriso et al. 1985). All computer calculations and storage were double precision. The original CAGEAN model used only catch-at-age and catch-per-unit-effort data. Deriso (1993) modified the "observation model" component of CANSAR to accommodate fishery-independent indices of relative abundance, estimates of spawning biomass, and aggregate landings data (without age-composition information). With these modifications, CANSAR was equivalent to other modern age-structured stock-assessment models based on a forward simulation approach (e.g., Methot 1990; Jacobson et al. 1994a).

Semesters were used as time steps in CANSAR; ages were incremented between semesters on 1 July; and spawning was assumed to occur on 1 April (the middle of the first semester). In reality, sardine spawn throughout the year, with a broad peak during March–August (figure 2), but new recruits (age-zero sardine from spawning during the current year) are seldom seen in the fishery before July 1. Ages in the model ranged from zero to 5+ (age five and older, a "plus group"; Megrey 1989). Natural mortality was assumed to be $M = 0.4$ yr^{-1} (MacCall 1979; Barnes et al. 1992). There were obvious seasonal and latitudinal differences in sardine catch-at-age and weight-at-age data, so California and Mexican fisheries during the first and second semesters were modeled separately. In addition, California catch-at-age (selectivity parameters, see below) during the first semester of 1991–95 was modeled separately.

Population Dynamics

Abundance of sardine was modeled with standard equations and techniques (Deriso et al. 1985). For example:

$$N_{a,y,2} = N_{a-1,y,1}\, e^{-Z_{a-1,y,1}} \qquad (4)$$

where $N_{a,y,s}$ is the number of sardine age a alive at the beginning of either the first ($s = 1$) or second ($s = 2$) semesters in year y, and $Z_{a,s,y}$ is an instantaneous total mortality rate. Recruitments (age-zero sardine at the beginning of the second semester of each year, $N_{0,y,2}$) were parameters estimated in the model.

Population biomass at the beginning of each semester of each year was calculated by summing the products of abundance at age and population weight-at-age. In most instances, population weight-at-age was assumed to be the same as weight-at-age in the California fishery. Fishery samples overestimated weights of age-zero sardine during the second semester of each year (shortly after hatching), however, because only the largest age-zero sardine were large enough to be captured. We therefore assumed a constant value ($w_{0,y,2,\mathrm{POP}} = 1.5$ g, calculated from length data in Butler 1987 and a length-weight conversion formula) for the weight of age-zero sardine in the population during the second semester of each year.

Observation Model

Predicted catch-at-age in the model was given by

$$\hat{C}_{a,y,s,t} = U_{a,y,s,t} \, N_{a,y,s} \qquad (5)$$

where $C_{a,y,s,t}$ was the predicted catch in number of fish by fishery t (t = 1 for California and t = 2 for Mexico). The exploitation fraction $U_{a,y,s,t}$ was from Baranov's catch equation (Deriso et al. 1985):

$$U_{a,y,s,t} = \frac{F_{a,y,s,t}}{Z_{a,y,s}} \left(1 - e^{-Z_{a,y,s}}\right) \qquad (6)$$

where $F_{a,y,s,t}$ was an instantaneous fishing mortality rate, and $Z_{a,y,s} = M + F_{a,y,s,\mathrm{US}} + F_{a,y,s,\mathrm{MEXICO}}$.

For modeling purposes, fishing mortality was separated into annual mortality and age-specific selectivity components (Megrey 1989):

$$F_{a,y,s,t} = s_{a,y,s,t} \, f_{y,s,t} \qquad (7)$$

where $s_{a,y,s,t}$ was a selectivity parameter for age, year (see below), semester (first or second), and fishery (U.S. or Mexico); and $f_{y,s,t}$ was a fishing mortality rate. Selectivities were scaled to a value of one at age 5+ (Deriso et al. 1985). Selectivities (see below) and fishing mortality rates for each fishery and semester were parameters estimated by the model.

First semester selectivities for the U.S. fishery were assumed constant during 1983–90 and 1991–95. The change from 1990 to 1991 accounted for a change in the United States from a first semester incidental fishery (sardine as a bycatch) to a directed fishery with sardine as the main target species (table 1 in Wolf 1992). Selectivities for the first semester Mexican (directed) as well as second semester fisheries in the United States (incidental) and Mexico (directed) were assumed constant during 1983–95. Preliminary runs with simpler selectivity patterns had trends in residuals. Preliminary runs that assumed more complicated selectivity patterns had convergence problems associated with overparameterization.

Catch-at-age data were not available for Mexican and California fisheries during some semesters, so we modeled total landings instead:

$$\hat{C}_{0+,y,s,t} = \sum_{a=0}^{5+} U_{a,y,s,t} \, N_{a,y,s,t} \, w_{a,y,s,t} \qquad (8)$$

where $\hat{C}_{0+,y,s,t}$ was predicted total landings in weight, and the $w_{a,y,s,t}$ were weights-at-age. Ratios of mean weight-at-age in the Mexican and California fisheries during 1991–92 (first semester) and 1990–92 (second semester) were used to calculate weight-at-age in the Mexican fishery where necessary. For the first semester, the ratio of Mexican to California weight-at-age was 0.74 for age zero and 0.95 for ages 1–5+. For the second semester, the ratios were 0.56 for age zero and 0.89 for ages 1–5+.

In CANSAR, predicted DEPM spawning biomass was calculated:

$$\hat{I}_{DEP,y} = Q_{DEPM} \sum_{a=0}^{5+} m_a \, N'_{a,y} \, w_{a,y,1,US} \qquad (9)$$

where Q_{DEPM} was a scaling parameter; m_a was sexual maturity of sardine age a; $w_{a,y,s,t}$ was weight-at-age in the U.S. fishery during the first semester; and $N'_{a,y}$ was the abundance of sardine (males and females) in the middle of spawning season (April 1). The scaling parameter Q_{DEPM} was theoretically equal to one and unnecessary (because the DEPM method estimates spawning biomass), but we included it so that assumptions could be tested. For modeling purposes, sexual maturity (m_a) is defined as the probability that a female sardine has already spawned, is spawning, or will spawn during the current spawning season.

Data from fishery and research trawl samples during the 1994 DEPM survey indicate that maturity of young sardine was lower for samples collected north of the Southern California Bight near Monterey, California (Butler et al. 1996). Because the number of sardines collected near Monterey during the DEPM cruise was small, we used a larger set of fishery data collected during 1991–93 (Hester 1993) to estimate maturity-at-age for sardine. Results (table 3) confirm that maturity at age zero is lower in fishery samples taken near Monterey.

All of the maturity data available for sardine taken near Monterey were from the fishery, which operates near shore, usually within 10 km of the coast. It is possible that lower maturity for young sardine near Monterey was due to a tendency for smaller sardine (with lower

TABLE 3
Maturity-at-Age Data for Female Sardine in Fishery and Research Catches during March–April, 1994 (Butler et al. 1996) and from Fishery Samples during March–June, 1990–92 (Hester 1993)

	Southern California Bight			Monterey, California			
Age	Mature females	Total females	Estimated maturity	Mature females	Total females	Estimated maturity	Population estimated maturity
0	136	238	0.65	9	29	0.50	0.58
1	720	794	0.87	136	184	0.71	0.79
2	763	798	0.96	48	51	0.86	0.91
3	441	450	0.99	25	30	0.94	0.97
4	244	245	1.00	12	12	0.97	0.99
5+	164	165	1.00	12	13	0.99	1.00

Note: Southern data include sardine collected between 31° and 34° N. Lat., primarily at Terminal Island, Calif., and Ensenada, Mexico. Maturity was determined by visual inspection of gonads (Hjort 1914); females with eggs visible to the eye were recorded as mature. Estimated maturities were by logistic regression; slope and intercept parameters for logistic regressions fit to Monterey and southern samples were significantly different ($p < 0.05$). Population maturities were estimated by averaging southern and Monterey values.

maturity) to occur near shore (Parrish et al. 1985), rather than to effects of latitude on the population (Hedgecock et al. 1989). In addition, we had no way of knowing how to combine maturity estimates for northern and southern areas to calculate age-specific maturity for the sardine population as a whole. We ignored these problems and used the simple average of maturity-at-age for northern and southern samples in CANSAR (table 3).

Predicted values for CalCOFI data in each year ($I_{\text{CalCOFI},y}$) were calculated:

$$\hat{I}_{CalCOFI,y} = Q_{CalCOFI} \, E_y \tag{10}$$

TABLE 4
Estimates of Relative Fecundity-at-Age (f_a) Used in CANSAR for Pacific Sardine

Age (years)	Fecundity-at-age data for mature females (eggs batch^{-1} mature fish^{-1})	Predicted fecundity-at-age for mature females (eggs batch^{-1} mature fish^{-1})	Predicted fecundity-at-age for all females (eggs batch^{-1} fish^{-1})	Rescaled fecundity-at-age for all females (eggs batch^{-1} fish^{-1})
0	15,794 (N = 62)	10,408	6,037	0.075
1	23,101 (N = 256)	24,498	19,354	0.239
2	28,164 (N = 168)	38,588	35,515	0.434
3	52,140 (N = 18)	52,678	51,098	0.632
4	77,777 (N = 6)	66,768	66,100	0.817
5+	76,823 (N = 1)	80,858	80,858	1.00

Note: Fecundity estimates were calculated from data for female sardine collected during the 1994 DEPM survey and aged (Macewicz et al. 1996; Butler et al. 1996). For each female sardine, batch fecundity (B) was calculated from ovary-free body weight (O) using $B = -108585. + 439.53$ O (B. Macewicz, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, pers. comm.). Average batch fecundities for each age class were regressed on age. Predicted batch fecundities from the regression on age were multiplied by maturity-at-age (table 3) and rescaled to a maximum value of 1.0 to calculate relative fecundity for female sardine. The sample size for each age group (N = number of female sardine) is given in parentheses.

where $Q_{CalCOFI}$ was a scaling parameter and E_y was relative egg production on 1 April. Predicted values for the CDFG spawning area index were obtained in the same manner except that a different scaling parameter (Q_{CDFG}) was used.

Relative egg production for sardine was calculated:

$$E_y = \sum_{a=0}^{5+} f_a \, N'_{a,y} \tag{11}$$

where f_a is relative fecundity at age for female sardine in units of eggs batch^{-1} fish^{-1} (table 4). Ideally, fecundities would be calculated from the product of age-specific batch fecundity (eggs batch^{-1}) and spawning frequency (batches day^{-1}), but estimates for spawning frequency were not available. Scaling parameters (e.g., $Q_{CalCOFI}$) made it possible to calculate egg production (equation 11) in terms of male and female abundance ($N'_{a,y}$), assuming that the sex ratio was constant.

Predicted values for the fish-spotter index were calculated:

$$\hat{I}_{SPOTTER,y} = Q_{SPOTTER} \sum_{a=0}^{5+} \bar{s}_{a,y,US} \, N_{a,y,2} \, w_{a,y,2,US} \tag{12}$$

where $\bar{s}_{a,y,US}$ was the geometric mean during year y of selectivities for sardine age a in the U.S. fishery during semester 2 and fish age a-1 during semester 1. Fish spotters locate and direct harvesting operations in the U.S. commercial fishery. Thus it was reasonable to use the same age-specific selectivities for both the U.S. fishery and fish-spotter data.

CANSAR included a modified Ricker (1975) spawner-recruit function that constrained recruitment estimates:

$$\tilde{R}_y = Z_y \, e^{\alpha + \beta Z_y + \gamma T_y} \tag{13}$$

where $\tilde{R}_y$ was the number of age-zero sardine on 1 July of year y predicted by the spawner-recruit model; Z_y

was a measure of spawning biomass during April; and T_y was temperature. The spawner-recruit parameters α, β, and γ could, in principle, have been estimated by CANSAR, but this proved difficult because so few years of data were available. Jacobson and MacCall (1995) fit a model like model 13 to a longer series of spawner-recruit data using biomass of sardine age 1+ in July to measure spawning biomass (S_y), and "mean three season" sea-surface temperatures at Scripps Pier in San Diego, California, to measure temperature (T_y). In CANSAR, we fixed spawner-recruit parameters at values from Jacobson and MacCall (1995) after adjusting for differences in units ($\alpha = -14.02$, $\beta = 3.147 \times 10^{-7}$ MT^{-1}, $\gamma = 0.961°\text{C}^{-1}$). To correspond as closely as possible with Jacobson and MacCall 1995, spawning biomass for spawner-recruit calculations was the biomass of sardine age 1+:

$$Z_y = \sum_{a=1}^{5+} N'_{a,y}\, \bar{w}_{a,1,US} \qquad (14)$$

where $\bar{w}_{a,1,US}$ were average first semester weights-at-age for sardine in the California fishery. The definition of sardine spawning biomass for spawner-recruit calculations was similar, but not identical to, the definition of spawning biomass for DEPM calculations (equation 9).

Parameter Estimation in CANSAR

Parameters in CANSAR (selectivities $s_{a,s,t}$; fishing mortalities $f_{s,y,t}$; scaling parameters $Q_{CalCOFI}$, Q_{CDFG}, $Q_{SPOTTER}$; and recruitments R_y) were estimated by nonlinear least squares as described by Deriso et al. (1985). All parameters were estimated after log transformation, and calculations were mostly log scale (to facilitate calculation of derivatives). Parameter estimates minimized the sum of squares:

$$L = \sum_{r=1}^{R} \lambda_r \sum_{j=1}^{N_j} \delta_{r,j}[\ln(D_{r,j}) - \ln(\hat{D}_{r,j})]^2 \qquad (15)$$

where λ_r was a weight applied to data of kind r; $\delta_{j,r}$ was a weight for observation j of kind r; and $D_{r,j}$ was a datum. For the spawner-recruit constraint, "observed" values were the models' current best estimates of recruitment (R_y), and "predicted" values ($\hat{R}_y$) were from equation 13. By definition (Deriso et al. 1985), λ_1 was one for U.S. fishery data in CANSAR. The search for best parameter estimates was terminated in CANSAR when either the change in the objective function (equation 15) or the relative change in all parameter estimates between steps was less than 10^{-6}. Problems with false minima were reduced by using these relatively stringent convergent criteria. Bootstrap procedures (2,000 iterations) were used to calculate variance and bias of sardine biomass and recruitment estimates from CANSAR (Deriso et al. 1985).

Theoretically, the weights λ_r account for differences in precision among different kinds of data, whereas the weights $\delta_{r,j}$ account for differences in precision or variance among observations of the same kind (Deriso et al. 1985). The theory is simple but difficult to implement because variance estimates for data are difficult to obtain independently of the model (Deriso et al. 1985; Conser and Powers 1989; Jacobson et al. 1994a). In practice λ_r is often used to increase or decrease the influence of a data type on parameter estimates, while $\delta_{r,j}$ is used to increase or decrease the influence of a single observation. We set λ_{SR} for spawner-recruit estimates to a small value (0.1) because recruitment variability is large for sardine (Jacobson and MacCall 1995). Weights (λ_i) for other kinds of data were set to 1.0 except during sensitivity analyses. Weights for individual data and spawner-recruit estimates ($\delta_{r,j}$) were set to 1.0 (but see below).

RESULTS

Initial CANSAR runs gave estimates of sardine recruitment and biomass that were anomalously high for the most recent seasons, and gave estimates of abundance for sardine age 5+ in 1983 that were near zero. Very low abundance of old fish during 1983 was reasonable because the stock had just begun to recover and few old fish were present. In final runs, the abundance of sardine age 5+ during 1983 was fixed at a small value and not estimated in CANSAR.

To obtain more reasonable estimates of recruitment and biomass for sardine during recent years, we increased weights on spawner-recruit predictions in CANSAR for 1993–95 to $\delta_{r,j} = 5.0$, 7.5, and 10.0, which, with $\lambda_{SR} = 0.1$, gave total effective weights on spawner-recruit predictions of 0.1, 0.5, 0.75, and 1.0 for 1993–95. Thus the spawner-recruit calculations for 1995 were given the same weight in parameter estimation as a catch or abundance datum.

An interesting result from our study was evidence that DEPM data for 1986–88 and 1994 underestimated spawning biomass in the sardine population. Preliminary runs with $Q_{DEPM} = 1$ had large positive residuals (predicted DEPM > observed value) for each year (figure 3). This result was not definite, however, because the final scaling parameter estimate ($Q_{DEPM} = 0.34$, CV = 1.5) was not significantly different from one and because spawning biomass estimates from CANSAR were imprecise. Residual patterns from runs with $Q_{DEPM} = 1$ may have been due to model miss-specification, errors in assumptions about maturity (i.e., the relation between spawning and total biomass), or other problems.

We calculated sums-of-squares profiles (Mittertreiner

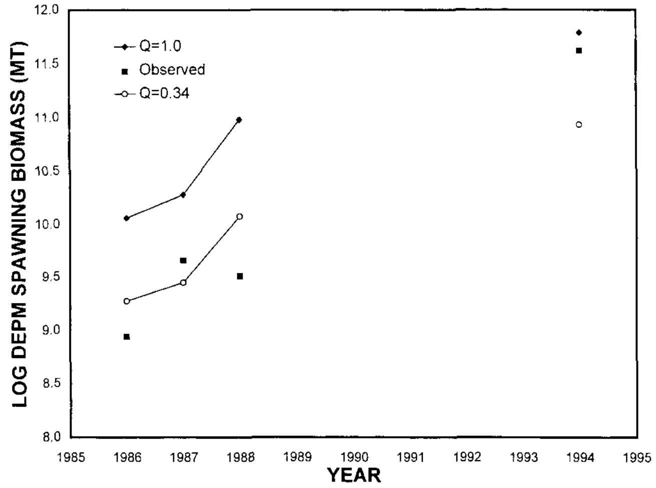

Figure 3. Observed and predicted DEPM data for models assuming DEPM data are an absolute (scaling parameter $Q_{DEPM} = 1$) and relative ($Q_{DEPM} = 0.34$) measure of spawning biomass for Pacific sardine.

and Schnute 1985) for a wide range of maturity-at-age parameters to determine if problems with lack of fit to DEPM data were due to the assumptions about maturity used to interpret DEPM, CalCOFI, and spawning area data. The sums-of-squares surface was relatively flat, indicating that reliable estimates of maturity could not be obtained from our data. Moreover, maturity patterns that gave the lowest sums-of-squares (best fit) corrected the problem with residuals but were biologically unreasonable (i.e., maturity declined with age). In final runs, we used default maturity-at-age values (table 3), estimated Q_{DEPM}, and assumed that DEPM data were a relative, rather than an absolute, measure of spawning biomass for sardine.

Fishery selectivities from final runs made sense with asymptotic selectivity patterns estimated for the directed fisheries in Mexico and in California during the first semester of 1991–95. Selectivity patterns for the incidental California fishery during the first semesters of 1983–90 and second semesters of 1983–95 were domed.

We found that CANSAR sometimes converged to local, rather than global, minima in the sums-of-squares surface, a common problem in complicated nonlinear models estimated from limited data (Jacobson et al. 1994a). We reran CANSAR repeatedly, starting with different initial parameter values to confirm that our final parameter estimates were at the global minima.

The model used for final runs included 104 parameters, of which 101 were actually estimated in CANSAR. Mean squared log-scale residuals (calculated instead of variances because degrees of freedom were unknown; Jacobson et al. 1994a) were similar (0.2–0.4) for all data types except spawning area, which appeared to be more precise than other types of abundance data for sardine (see below). Recruitment estimates for sardine from CANSAR did not fit the spawner-recruit function precisely.

Data type	Number of observations	Mean squared log-scale residual
Calif. fishery	120	0.30
Mex. fishery	50	0.29
CalCOFI	12	0.19
Spawning area	8	0.12
Spotter	10	0.37
DEPM	4	0.24
Spawner-recruit	13	1.3

Like Jacobson et al. (1994a) and Bence et al. (1993), we found that biomass and recruitment estimates for sardine from CANSAR were generally biased high. Final estimates (table 5 and figure 4) were corrected for consistent bias according to Efron (1982) and log-transformation bias (Jacobson et al. 1994a). Consistent bias, measured by comparing biomass and recruitment estimates to mean values from bootstrap runs, ranged 6% to 12%

TABLE 5
Sardine Biomass and Recruitment on 1 July 1983–1995, Corrected for Bias

Year	Biomass (age 1+ MT)	CV[a]	Recruits (10^6 fish)	CV[a]
1983	9,061	0.33	227	0.27
1984	23,533	0.24	246	0.23
1985	32,021	0.22	167	0.24
1986	44,071	0.20	550	0.19
1987	68,683	0.17	414	0.19
1988	83,984	0.16	666	0.17
1989	99,534	0.14	441	0.19
1990	103,333	0.14	1,442	0.20
1991	164,159	0.16	1,648	0.22
1992	151,403	0.17	1,623	0.29
1993	148,191	0.23	3,751	0.29
1994	245,625	0.25	4,863	0.35
1995	344,141	0.33	6,912	0.43

[a] Arithmetic scale coefficient of variation.

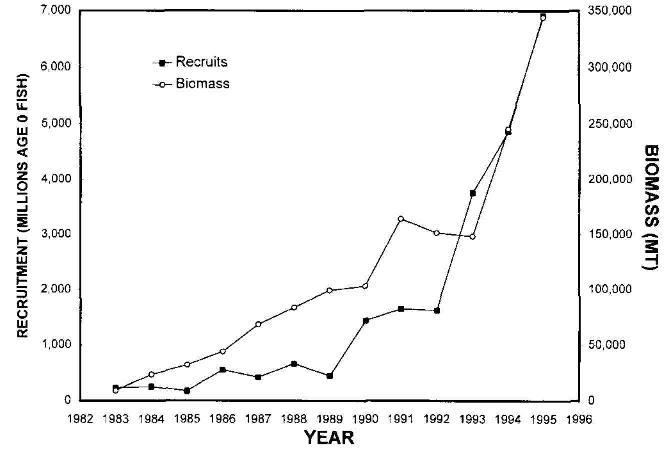

Figure 4. Estimated biomass (MT age 1+ on 1 July) and recruitment (10^6 age-zero fish) for Pacific sardine during 1983–95.

and averaged 8%. Log-transformation bias (from exponentiating log-scale biomass and recruitment estimates in CANSAR) ranged from −9% to −1% and averaged −3%. Consistent and log-transformation biases tended to cancel one another; total bias ranged from 4% to 8% and averaged 6%. All three types of bias in biomass and recruitment estimates were correlated with variance. CVs and bias in estimates from CANSAR were comparable to those from other models for pelagic fish (Lo et al. 1992; Jacobson et al. 1994a, b) and indicate reasonable model performance.

Sensitivity Analysis

We varied weights (λ_t) on different data types to determine how differences among data affected estimates of sardine biomass (ages 1+ on 1 July) during 1990–94 from CANSAR. Results (table 6) indicate that average estimated sardine biomass during 1990–95 was not sensitive (change < 10%) to halving or doubling weights on different types of data or the spawner-recruit constraint. The estimate of sardine biomass during 1995 was, however, sensitive (change > 10%) to halving the weight on fish-spotter data and doubling the weight on CalCOFI data or the spawner-recruit constraint. Biomass estimates were more strongly affected (change >10%) when weights were increased to ten times their default values or set to zero (i.e., the data type was removed from the model; table 6). Results for the spawner-recruit constraint (decreased biomass estimates when the weight on the spawner-recruit constraint was increased) indicate that sardine recruitment in recent years has been stronger than would have been predicted on the basis of Jacobson and MacCall's (1995) spawner-recruit model.

DISCUSSION

The available data (figure 1) and biomass estimates from CANSAR (figure 4) indicate that Pacific sardine increased in abundance and were highly productive during 1983–95. Estimated sardine biomass (fish age 1+ on 1 July) increased exponentially from about 9,000 (CV 33%) to 344,000 MT (CV = 33%) at an average rate of 28% year^{-1} (calculated as in Barnes et al. 1992). This impressive rate of increase occurred in the presence of fishing. Fishing mortality rates for sardine increased (table 7) in 1991 when total landings increased from about 14,000 to almost 40,000 MT year^{-1} (table 1).

Recent fishing mortality rates for sardine probably could not be sustained under average environmental conditions. Average instantaneous fishing mortality rates for sardine age 2+ (weighted by number of fish in each age group) ranged from 0.52 to 0.84 yr^{-1} and averaged 0.68 yr^{-1} during 1991–95. Sardine productivity is positively correlated with sea-surface temperatures (Jacobson and MacCall 1995), and F_{msy} (the fishing mortality rate

TABLE 6
Sensitivity of Biomass Estimates for Pacific Sardine to Weights (λ_t) Used in CANSAR

Multiplier	U.S. fishery	Mexican fishery	CalCOFI	Spawning area	Fish spotter	Daily egg production method	Spawner-recruit
Mean 1991–95 biomass							
0.0	71%	116%	13%	0%	−29%	0%	35%
0.5	1%	−1%	3%	0%	−10%	0%	1%
2.0	−5%	0%	−10%	1%	5%	2%	−7%
10.0	7%	−5%	−34%	15%	56%	27%	−11%
1995 biomass							
0.0	−31%	88%	20%	0%	−48%	0%	96%
0.5	−4%	−3%	5%	0%	−16%	0%	1%
2.0	−9%	−3%	−17%	2%	9%	3%	−15%
10.0	5%	−19%	−54%	22%	87%	32%	−24%

Note: Discrepancies between best fit estimates and estimates with different weights are given in the table as percentages of best fit estimates. For each run, base case weights (λ_t = 0.1 for spawner-recruit calculations and 1.0 for other data types) were scaled by the multiplier in the first column. Bias corrections were not used.

TABLE 7
Annual Fishing Mortality Rates (yr^{-1}) for Pacific Sardine, 1983–95, Estimated in CANSAR

Age	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
0	0.01	0.00	0.04	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.04	0.02	0.04
1	0.18	0.03	0.23	0.01	0.04	0.03	0.05	0.06	0.15	0.19	0.29	0.18	0.30
2	0.59	0.11	0.59	0.04	0.13	0.10	0.18	0.19	0.42	0.62	0.71	0.48	0.65
3	0.57	0.09	0.73	0.04	0.16	0.11	0.24	0.25	0.69	1.08	1.04	0.80	0.93
4	0.40	0.04	0.70	0.03	0.14	0.08	0.20	0.22	0.68	1.02	1.05	0.80	0.94
5	0.46	0.06	0.71	0.03	0.14	0.09	0.21	0.23	0.64	0.94	0.96	0.74	0.82

giving the maximum sustained yield or MSY) at current temperatures (three-season average of 18°C, table 2) is about 0.6 yr^{-1}, so recent fishing mortality rates were near the MSY level. In contrast, F_{msy} at average three-season temperatures (17°C) is about 0.2 yr^{-1} (Jacobson and MacCall 1995).

Weight-at-age data for sardine indicate that individual growth rates decreased as abundance increased. Correlations between sardine biomass and weight-at-ages 2 to 5+ in the second-semester U.S. fishery were, for example, all between −0.7 and −0.9. This result suggests that weight-at-age might be used as an index of abundance for sardine. In addition, it appears that sardine biomass is currently large enough to affect growth rates in the stock.

Uncertainty

Bootstrap CVs for sardine biomass and recruitment indicate substantial uncertainty (table 5), but there were sources of uncertainty in our analysis not included in bootstrap calculations. Parma (1993) found that bootstrap calculations underestimated variances for abundance of Pacific halibut (*Hippoglossus stenolepis*) because serial correlation in residuals (also present in results for sardine) was not included in the bootstrap procedure. Variances from CANSAR probably understated uncertainty about sardine biomass because bootstrap calculations included the spawner-recruit constraint, which reduced variability in biomass and recruitment estimates for recent years. In addition, uncertainties about natural mortality, age-specific fecundity, maturity-at-age, and other parameters estimated outside of the model were not included in the bootstrap procedure (Restrepo et al. 1992).

Sardine age 4+ were seldom observed in the recent fishery but were common in the historical sardine fishery (Murphy 1966; MacCall 1979). Absence of older sardines from recent landings may be due to relatively high fishing mortality rates on older fish (table 7) or movement of large, old sardine to areas outside the range of the current fishery. In statistical terms, effects of movement and fishing mortality may be confounded in selectivity parameters estimated by CANSAR.

Effects of uncertainty about relationships between DEPM data and sardine biomass were substantial. Biomass estimates with $Q_{DEPM} = 0.34$ were larger by 6%–25% than biomass estimates with $Q_{DEPM} = 1$, and the discrepancy was largest for recent years.

Nonlinear relationships between abundance data and sardine biomass are a potentially major source of uncertainty that we were not able to fully evaluate. This source of uncertainty may become more important as sardine biomass expands. Fish-spotter, CalCOFI, and other abundance data for sardine were collected from areas smaller than the current distribution of the sardine stock. Abundance indices will "saturate" to the extent that increased biomass outside the survey area is not reflected by proportional increases in the data. Residuals from final runs were plotted against time and predicted value, and there was no evidence for saturation, but the possibility remains.

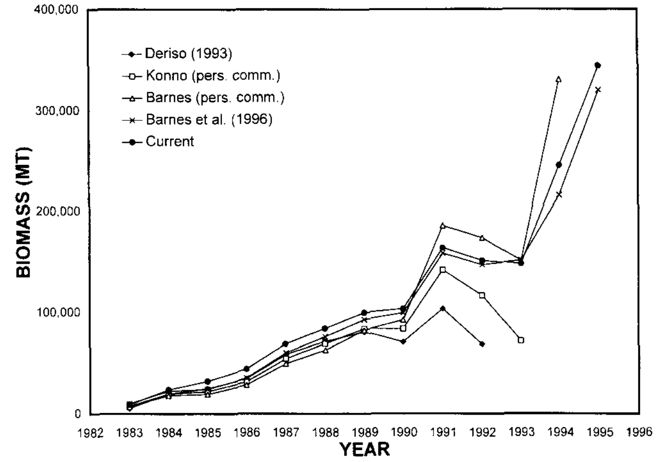

Figure 5. Historical record of biomass estimates (MT age 1+ on 1 July) from CANSAR used to manage the California sardine fishery. Estimates labeled "pers. comm." are from E. Konno (California Department of Fish and Game, 330 Golden Shore, Suite 50, Long Beach, CA 90802) and T. Barnes (California Department of Fish and Game, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038). Estimates labeled "Current" are from this paper.

We evaluated retrospective bias (Sinclair et al. 1991) in CANSAR by running it with 1990–95 data omitted (Jacobson et al. 1994a). Results indicated little or no retrospective bias. Although CANSAR did not suffer from retrospective bias in a statistical sense, there is historical evidence that errors in biomass estimates for recent years are usually correlated (figure 5). In addition, results from CANSAR appear sensitive to changes in data (e.g., the 1994 DEPM observation and information about maturity-at-age), environmental conditions (e.g., 1991–93 El Niño; Lynn et al. 1995), and changes in modeling approaches routinely introduced from one year to the next.

Bias in DEPM Data from Nonrepresentative Sampling

Several studies have investigated bias in DEPM spawning biomass estimates for northern anchovy due to nonrepresentative sampling of adult fish (Parker 1985; Picquelle and Stauffer 1985; Smith and Hewitt 1985; Alheit 1985). We used a different approach to examine this question for sardine. Mathematical symbols used in this section for DEPM calculations are from Parker (1985) and not the same as used elsewhere in this paper.

The DEPM estimator for spawning biomass (Parker 1985; Lo et al. 1996) is proportional to:

$$\frac{W}{FS} \qquad (16)$$

where W is average weight of mature females (g); F is batch fecundity for actively spawning females (eggs batch^{-1} active female^{-1}); and S is spawning frequency (fraction mature females that are actively spawning per day; one batch day^{-1} female^{-1} assumed). Adult parameters (W, F, and S) may vary in sardine with age and size, but the bias in equation 16 is minimal when adult parameters are estimated from representative samples of the mature female population (Parker 1985). Comparison of age-composition data for all sardine (mature and immature) sampled during the DEPM survey (Butler et al. 1996) as well as estimates for the population during April, 1994, from CANSAR indicate that age-zero sardine were undersampled during the DEPM survey by about 70% (see below).

	Age composition		
Age	DEPM	CANSAR	CANSAR CV
0	0.21	0.71	0.29
1	0.41	0.19	0.30
2	0.28	0.073	0.30
3	0.063	0.021	0.39
4	0.026	0.002	0.56
5+	0.003	0.004	0.76

Estimates from CANSAR may be misleading because they were imprecise (CVs > 29%) and affected by a spawner-recruit constraint and other assumptions. It seems likely, however, that age-zero sardine were more common in the population than in the DEPM samples because sardine abundance has been increasing (figure 1) due to strong recruitment during recent years.

Estimates of population maturity-at-age and batch fecundity-at-age (F) were taken from tables 3 and 4. Weight-at-age (W) was assumed to be the same as in the U.S. fishery during the first semester of 1994. Unfortunately, no data were available to estimate age-specific spawning frequency (S). We therefore calculated potential bias under two scenarios: (1) S constant, and (2) S increasing from 1.0 at age 0 to 1.5 at age 5+. The choice of 1.5 at age 5+ was arbitrary.

For each scenario, simulated sample means for adult parameters W, F, and S were calculated assuming representative and nonrepresentative sampling. In our calculations, the age composition for nonrepresentative samples was the same as the population age composition except that

$$q_0 = \pi_0 \kappa \qquad (17)$$

where q_0 was the proportion of age-zero sardine in DEPM samples; π_0 was the proportion of age-zero sardine in the population; and κ measured survey gear selectivity for age-zero sardine. Gear selectivity ranged from $\kappa = 0$ (no age-zero fish sampled) to $\kappa = 1$ (representative sampling).

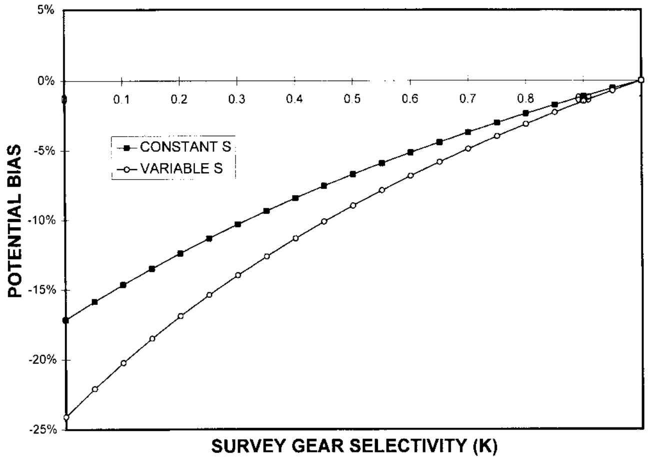

Figure 6. Potential bias in DEPM spawning biomass estimates due to nonrepresentative sampling of age-zero sardine. Age-zero fish are not sampled by survey gear (100% undersampling) when $\kappa = 0$, and are sampled in proportion to their abundance when $\kappa = 1$.

Results (figure 6) indicate the possibility of modest bias in the 1994 DEPM estimate due to nonrepresentative sampling. When the proportion of age-zero sardine in DEPM samples was 30% of the proportion in the population ($\kappa = .30$ for 70% undersampling), potential bias was -10% for the constant S scenario and -14% for the increasing S scenario. Bias due to nonrepresentative sampling was not large enough to account for the difference between DEPM data and spawning biomass estimates from CANSAR.

Bias in DEPM data was probably not as great as indicated in our calculations because mature age-zero sardine were probably undersampled to a lesser extent than smaller, immature age-zero fish. In addition, sampling gear may have taken large, mature age-zero sardine preferentially, leading to estimates of maturity at age zero that were biased high. Maturity-at-age is not important in DEPM calculations but was used in our bias calculations. Potential bias was lower when the assumed maturity at age zero was reduced. On the other hand, our potential bias calculations did not include nonrepresentative sampling of fish ages 1+, which would likely increase estimates of potential bias.

Use of DEPM Data for Fisheries Management

DEPM spawning biomass estimates have been used directly to set catch quotas and manage fisheries (e.g., Priede and Watson 1993). The precision of advice to managers may be enhanced, however, when DEPM and all fishery and fishery-independent information, including DEPM data, are combined in a single stock-assessment model. Estimates of total biomass for sardine from CANSAR during 1986 and 1994 (table 5) were substantially more precise than the DEPM data on which they were based (table 2). Jacobson et al. (1994a) obtained CVs of about 0.14–0.20 for northern anchovy (*Engraulis mordax*) spawning biomass estimates during 1981–86, while CVs for DEPM data ranged from 0.17 to 0.26. In addition, use of DEPM data in a model makes it possible to adjust estimates based on DEPM data for spawning habitat that was not surveyed.

Use of DEPM Data in Stock-Assessment Models

As in Methot (1989) and Jacobson et al. (1994a), DEPM spawning biomass estimates for sardine were used as "tuning" data in CANSAR. A problem with this approach is that there are assumptions about population age structure and adult parameters in both the DEPM estimate (equation 16) and the model (equation 9) which may be contradictory (see above). It may be better to tune future models to total egg production rather than to spawning biomass. Adult parameters could be modeled individually or collapsed into single age-specific parameters (e.g., $s_a = R_a F_a S_a$). External estimates of adult parameters could be used either directly, as starting values for further parameter estimation, or as Bayesian constraints on feasible parameter values (Jacobson et al. 1994a; Dorn 1995). This approach would be more flexible and would allow more consistent interpretation of data. In line with Methot's (1990) approach and recent modeling trends, our suggestion makes the "model look like the data," rather than the reverse.

It seems likely that DEPM data underestimated spawning biomass for the sardine population because of incomplete coverage of the spawning area during DEPM surveys. Sardine occur along the coast to the north (Hargreaves et al. 1994) and south (Félix-Uraga et al. 1996) of the areas surveyed during DEPM cruises. Relative underestimation of spawning biomass by DEPM data (figure 3) was smallest in 1994, when the survey extended over the widest geographic range. In modeling, we chose to assume that DEPM data were proportional ($Q_{DEPM} \neq 1$) rather than absolute ($Q_{DEPM} = 1$) measures of spawning biomass for sardine. A more accurate assumption would probably be that DEPM data measured spawning biomass within the area surveyed in absolute terms. Apparent underestimation of spawning biomass for the population as a whole probably resulted from the fact that not all of the spawning habitat was surveyed.

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THE SARDINE FISHERY ALONG THE WESTERN COAST OF BAJA CALIFORNIA, 1981 TO 1994

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ABSTRACT

Catch data (3,416 MT during 1984 and 56,350 MT during 1994) indicate that abundance of Pacific sardine (*Sardinops sagax*) along the west coast of Baja California has increased dramatically. Increases were closely related to abundant year classes in 1984, 1989, and 1993. The abundant year classes in 1984 and 1993 followed El Niño events. Seasonal patterns in catches lead us to hypothesize that sardine migrate seasonally between Magdalena Bay and Ensenada, moving northward during the summer and fall and southward during winter and spring. The period of highest abundance after 1989 was associated with a northern shift in the distribution of sardine and increased catches in Ensenada. Peak catches occurred in a bimodal pattern at 17° and 20°C near Ensenada in the north, at 17° and 21° near Cedros Island, and at 19° and 24° near Magdalena Bay in the south. This pattern suggests the possibility of three stocks along the west coast of Baja California.

INTRODUCTION

In Mexican waters, Pacific sardine is harvested commercially along the western coast of Baja California and in the Gulf of California. The first recorded catches of Pacific sardine (*Sardinops sagax*) along the western coast of Mexico were in Ensenada during 1951. As the sardine fishery collapsed in California, the Mexican fishery moved progressively southward (figure 1), arriving at Cedros Island in 1961 and Magdalena Bay in 1972 (Murphy 1966).

In this paper we describe some aspects of the Pacific sardine fishery along the western coast of Baja California, emphasizing the period from 1981 to 1994, and three fishing zones: Ensenada in the north, Cedros Island, and Magdalena Bay in the south (figure 1). The principal species in the commercial fishery along Baja California is Pacific sardine, but the fleet also harvests thread herring (*Opisthonema* spp.), chub mackerel (*Scomber japonicus*), and, to a lesser extent, round herring (*Etrumeus teres*), anchoveta (*Cetengraulis mysticetus*), and jack mackerel (*Trachurus symmetricus*) (Hernández-Vázquez 1983; Félix-Uraga 1986). At Magdalena Bay and Cedros Island, around 80% of the catch is used for fish meal, and approximately 20% is canned for human consumption.

The number of canneries and size of the fleet in Magdalena Bay have been relatively constant since 1981. There are two canneries with fish meal plants, one in Port San Carlos and the other in Port Lopez Mateos (figure 1). The number of boats in the Magdalena Bay zone ranges between 5 and 7 per year, with capacities between 60 and 120 MT per boat. The fleet operates mostly within the bay and leaves only occasionally to fish outside near the mouth of the bay.

On Cedros Island there is only one cannery with a fish meal plant and only one boat (150 MT capacity) that catches sardine. The boat operates near the island. Detailed information about canneries and fleet size has not been compiled for Ensenada.

DATA AND METHODS

Data about catch and fishing effort for ports in Lopez Mateos, San Carlos, and on Cedros Island during 1981–94 were obtained from canneries' business records by Centro Interdisciplinario de Ciencias Marinas personnel (table 1). Catch data for Ensenada (table 1) were

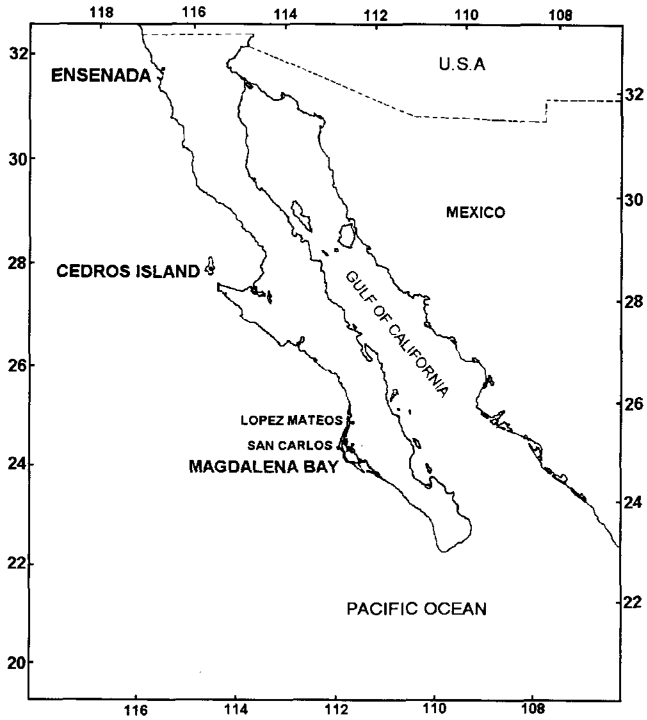

Figure 1. Baja California and its three main fishing grounds for Pacific sardine.

TABLE 1
Annual Landings (MT), Fishing Effort (Trips), and Average Sea-Surface Temperatures (SST) for Three Fishing Zones along the Western Coast of Baja California

	Cedros Island				Magdalena Bay				Ensenada	
Year	Catch Pacific sardine	Catch all species	Fishing effort	SST	Catch Pacific sardine	Catch all species	Fishing effort	SST	Catch Pacific sardine	SST
1981	1,704.6	4,267.3	133	18.8	10,557.0	14,689.1	550	21.4		17.7
1982	2,401.4	6,761.5	176	18.1	9,392.0	12,585.7	364	21.2		17.3
1983	1,595.8	2,824.1	89	19.2	2,386.2	4,945.5	174	22.9	273.6	18.2
1984	962.1	2,401.9	82	18.7	2,453.8	4,604.3	197	21.6	0	17.9
1985	1,023.4	3,356.1	96	17.9	10,979.2	13,278.3	322	20.6	3,722.3	17.2
1986	2,808	4,708.8	128	17.9	14,203.3	15,723.6	364	20.8	242.6	17.3
1987	2,856.1	3,956.7	94	18.2	8,599.3	10,486.3	241	21.3	2,431.6	17.3
1988	846.1	1,257.1	42	18.0	12,080.5	14,248.4	286	20.3	2,034.9	17.2
1989	2,344.3	3,957.9	89	18.2	7,746.1	10,087.5	239	20.9	6,222.2	17.3
1990	2,085.6	2,816.1	80	18.6	16,975.3	22,844.5	449	21.8	11,375.3	17.7
1991	551.3	1,081.0	36	18.8	15,893.5	27,331.8	511	22.8	31,391.8	17.6
1992	348.4	992.3	22	19.8	5,026.0	19,754.4	501	23.2	34,648.2	18.8
1993	1,504.6	1,966.4	36	18.8	7,543.6	18,566.8	501	22.6	32,044.9	18.2
1994	1,685.3	2,329.0	27	18.8	33,787.0	35,921.1	646	22.0	20,877	17.5

TABLE 2
Catch-at-Age data (10^6 Fish) for Pacific Sardine Caught in Magdalena Bay, 1981–1994

	Age groups						
Year	0	1	2	3	4	5	6+
1981	14.824	51.542	64.515	13.058	0.000	0.000	0.000
1982	25.355	50.965	56.860	7.607	2.582	0.000	0.000
1983	0.171	8.162	16.725	1.289	0.215	0.071	0.000
1984	5.879	7.016	17.694	9.748	0.283	0.000	0.000
1985	15.380	119.604	43.722	0.252	0.000	0.000	0.000
1986	3.929	37.047	96.494	52.135	3.863	0.000	0.000
1987	0.000	10.931	53.981	21.107	5.459	0.000	0.000
1988	7.129	34.532	48.205	37.201	3.093	0.218	0.663
1989	31.752	37.307	15.521	6.186	2.311	0.075	0.000
1990	5.195	55.485	57.292	37.047	13.267	11.352	0.102
1991	9.730	61.080	67.911	24.244	8.389	2.042	1.264
1992	1.458	37.689	30.402	5.053	0.679	0.237	0.000
1993	4.980	79.866	56.118	5.663	0.000	0.000	0.000
1994	46.294	341.263	147.834	26.358	9.737	0.000	0.000

provided by Walterio García (Centro Regional de Investigaciones Pesqueras, Ensenada, pers. comm.), but effort data were not available.

Sea-surface temperature (SST) data for Magdalena Bay, Cedros Island, and Ensenada during 1981–90 were obtained from COADS (Comprehensive Ocean Atmosphere Data Set; Roy and Mendelssohn 1994; table 1). SST data for 1991–94 were from Anonymous 1991–1994. The SST data from COADS were average temperatures in 2° latitude × 2° longitude squares. Squares along the coast at 24°–26° N., 28°–30° N., and 30°–32° N. Lat. were used for Magdalena Bay, Cedros Island, and Ensenada. Data from IATTC (Inter-American Tropical Tuna Commission) reports were the temperature at the isothermal nearest each fishing zone. Average annual temperatures were calculated for each region.

Catch-at-age data (number of fish in each age group caught during each year) during 1981–94 were available for Magdalena Bay, but not for Cedros Island and Ensenada. Catch-at-age data for Magdalena Bay in Félix-Uraga 1992 were updated (with the methods of Holden and Raitt 1975) to 1994 (table 2). A recruitment index for sardine in the Magdalena Bay fishery was estimated from catch-at-age data by summing the catch at each age for each year class.

For 1991 to 1994, we estimated a seasonal index of relative catch for each fishing zone (catch increased considerably in Ensenada during this period). The seasonal catch was the catch during a season divided by the catch for the entire year. Seasons were winter (January–March), spring (April–June), summer (July–September), and fall (October–December). To determine temperature preferences for sardine, we summed monthly catches by 1°C intervals and plotted the results.

RESULTS

Catch and Effort

The total catch of sardine along the western coast of Baja California increased from about 12,000 MT in 1981 to about 56,000 MT in 1994 (table 1, figure 2). From 1985 to 1989, total landings averaged 16,000 MT annually, and catch in Magdalena Bay was greater than at Cedros Island or Ensenada. After 1989, the average catch was more than 40,000 MT annually, and catches were greatest in Ensenada, except for 1994, when the catch was higher (34,000 MT) in Magdalena Bay. Thus the period of highest abundance after 1989 seems associated with a northern shift in the distribution of sardine.

The sardine catch at Cedros Island has averaged 1,600 MT annually and has been relatively constant since 1981. In most years, the Cedros Island fishery was the least important in terms of total landings.

Total fishing effort (number of fishing trips) and catch by the sardine fleet at Magdalena Bay and Cedros Island is related to the availability of sardine and other species (table 1). When fish are available, fishing trips and catches increase. The correlation (*r*) between fishing effort and total landings (all species) at Magdalena Bay and Cedros Island during 1981–94 was $r = 0.88$ ($P < 0.00$) and $r = 0.94$ ($P < 0.00$). The correlation between fishing effort and Pacific sardine landings was $r = 0.66$ ($P = 0.001$) for Magdalena Bay and $r = 0.64$ ($P = 0.01$) for Cedros Island.

Year-Class Abundance Index

The year-class index (figure 3) indicates that sardine recruitment increased continuously after 1981, with particularly strong recruitments during 1984, 1989, and 1993. The 1994 year class appears weak, but this is probably due to limited data for the most recent recruitment.

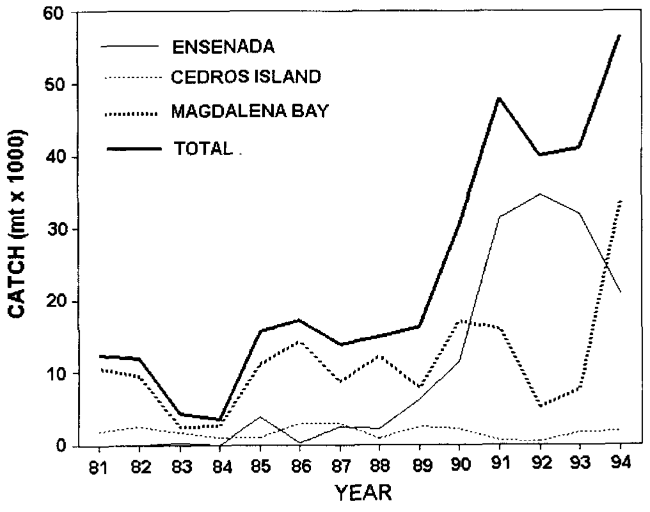

Figure 2. Pacific sardine landings (MT) along the west coast of Baja California.

Figure 3. Recruitment index (sum of catch at age for each year class) for Pacific sardine in the Magdalena Bay fishery.

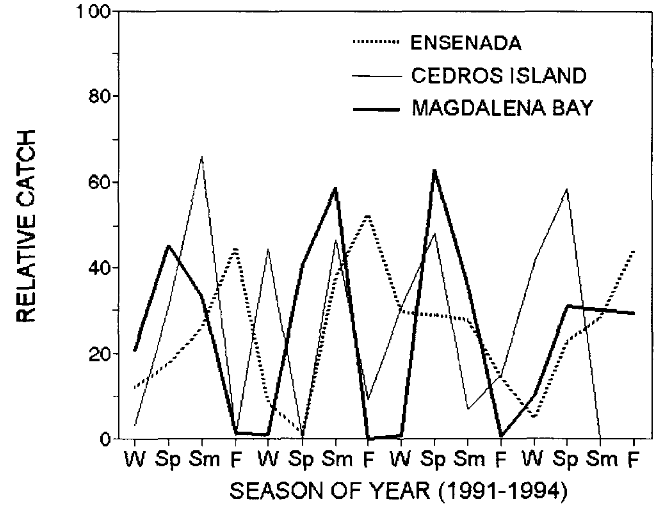

Figure 4. Relative Pacific sardine catch by year, season, and fishing zone, 1991–1994. W = winter; Sp = spring; Sm = Summer; and F = fall.

Seasonal Catch

Seasonal catch during 1991 to 1994 (figure 4) shows that the fishery in Magdalena Bay occurred mainly during spring and summer. In most years, the fishery at Cedros Island also occurred during the spring and summer. During 1991, however, there were peaks during both the summer and winter. In the Ensenada fishery, except for 1993, only one peak occurred in each year, mainly in the fall.

Catch and Temperature Relationship

Annual average SST along the western coast of Baja California was relatively warm in 1983 and 1992 and relatively cool during 1985–90 (figure 5). Trends in temperature at different zones were similar, but Magdalena

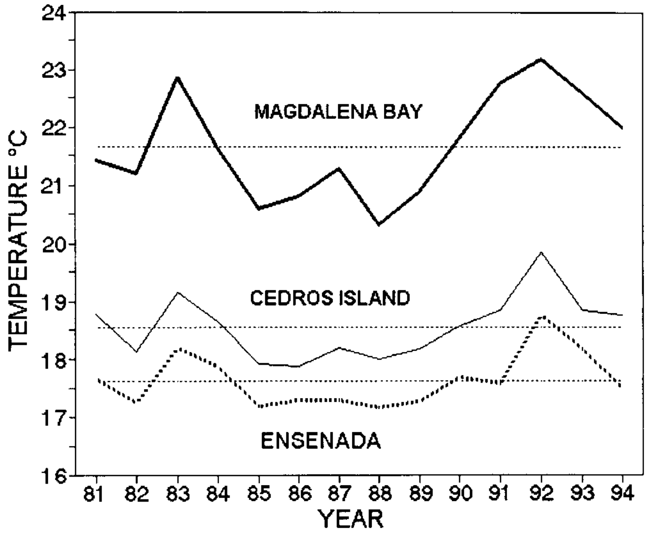

Figure 5. Annual average sea-surface temperatures near Ensenada, Cedros Island, and Magdalena Bay.

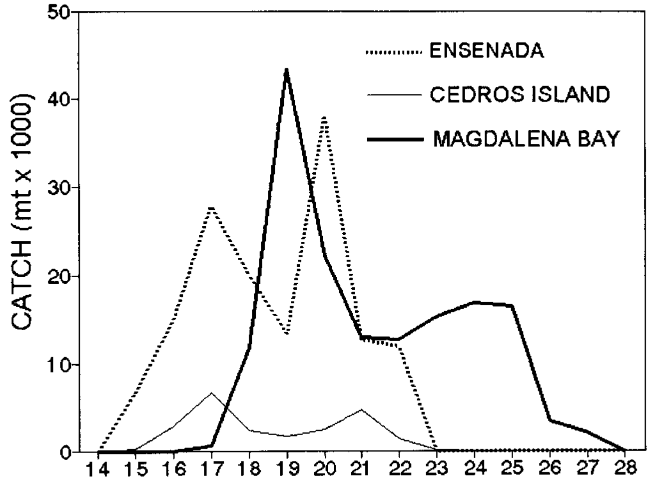

Figure 6. Pacific sardine catch by temperature at Ensenada, Cedros Island, and Magdalena Bay, 1981–1994.

Bay was consistently warmest (average 21.7°C compared to 18.5° at Cedros Island and 17.6° at Ensenada). The difference in average temperature during 1981–94 between Ensenada and Cedros Island was only about 1°, whereas the difference between Cedros Island and Magdalena Bay was about 3°.

Peak catches in the three fishing regions occurred at different temperatures, and there were two peaks at each location (figure 6). At Ensenada, the first peak in sardine catch was at 17°, the second at 20°. The first peak at Cedros Island was also at 17°, but the second was at 21°. For Magdalena Bay, the first peak was at 19°; the second was between 24° and 25°.

DISCUSSION

Increases in total catch (a crude index of abundance for sardine; e.g., Lluch-Belda et al. 1989) during 1985, 1990, and 1994 (figure 2) were associated with strong year classes during 1984, 1989, and 1993 (figure 3). The strong year classes in 1984 and 1993 may be due to El Niño events during 1983 and 1992 (Murphy 1960; Huato-Soberanis and Lluch-Belda 1987; Félix-Uraga 1992).

Increased catches at Ensenada during 1992 coincided with decreased catches at Magdalena Bay in the same year (figures 2 and 5). This could be due to the 1992 El Niño event, which caused northward movements of sardine from Magdalena Bay.

The pattern of highest relative catch by season (spring–summer in the south, and fall in the north) during 1991–94 (figure 4) indicates seasonal migrations of sardine between Ensenada, Cedros Island, and Magdalena Bay. Seasonal migrations may amplify or contribute to increases in abundance of sardine in northern areas when the population is growing (Lluch-Belda et al. 1989, 1991).

Pacific sardine are caught over a wide range of temperatures along the western coast of Baja California (figure 6). Peak catches occurred at three different temperatures: 17°, 20°–21°, and 24°–25°. This pattern suggests the possibility of three different stocks along the coast of Baja California.

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EGG PRODUCTION OF PACIFIC SARDINE (*SARDINOPS SAGAX*) OFF OREGON IN 1994

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ABSTRACT

Since the late 1970s, the Pacific sardine (*Sardinops sagax*) population off the west coast of the United States has been increasing. In 1994, an ichthyoplankton survey to assess anchovy biomass was conducted off the Oregon coast from the Columbia River to the Coquille River (just north of Cape Blanco) and out to 190 km offshore. Samples collected during the survey contained numerous Pacific sardine eggs and larvae, which were used to estimate daily egg production (0.42 eggs/0.05 m^2/day) and egg mortality (0.13/day). The spawning biomass of Pacific sardine was calculated to be about 50,000 MT.

There appears to be an association between geographic distribution of sardine eggs and the 14°C isotherm derived from the 1-m to 10-m depth zone. We hypothesize that the isotherm of 14°C forms a distinct boundary for spawning sardine off Oregon and may prove useful for determining boundaries for future spawning surveys.

INTRODUCTION

The Pacific sardine (*Sardinops sagax*) fishery, which ranged from Baja California, Mexico, to as far north as British Columbia, Canada, was the largest commercial fishery in the Western Hemisphere in the early 1900s (Wolf 1992). During that period, sardine evidently spawned throughout most of their range. Spawning occurred during the summer in Oregon and British Columbia waters (Walford and Mosher 1941; Ahlstrom 1948). Since the decline of the sardine population in the 1940s, no landings have been documented in waters off Oregon and Washington (Radovich 1982; Wolf 1992), and to our knowledge no spawning has been documented in waters north of California.

In 1994, the National Marine Fisheries Service (NMFS) conducted an ichthyoplankton survey off the Oregon coast to estimate northern anchovy (*Engraulis mordax*) biomass. During this survey northern anchovy eggs were rarely collected, but Pacific sardine eggs were abundant throughout the study area. Pacific sardine eggs were found as far north as Tillamook Head, Oregon, indicating that the Pacific sardine may again be using northern portions of its historical spawning range. This apparent expansion of spawning range to Oregon waters is consistent with the rates of increase in biomass and spawning area that have been observed off California since the mid-1980s (Deriso et al. 1996).

In this paper, we describe the geographic distribution of Pacific sardine eggs and larvae and estimate egg production and mortality in our study area off Oregon in July 1994. We also provide a crude estimate of Pacific sardine spawning biomass.

MATERIALS AND METHODS

Survey Description

The ichthyoplankton survey used the egg production methods of Lasker (1985) and was conducted aboard the 17.4-m research vessel *Sea Otter* during 5–26 July 1994. Sampling was conducted over a grid of 234 stations along 12 east–west transects, which encompassed an area of 69,308 km^2 (figure 1). Transects extended

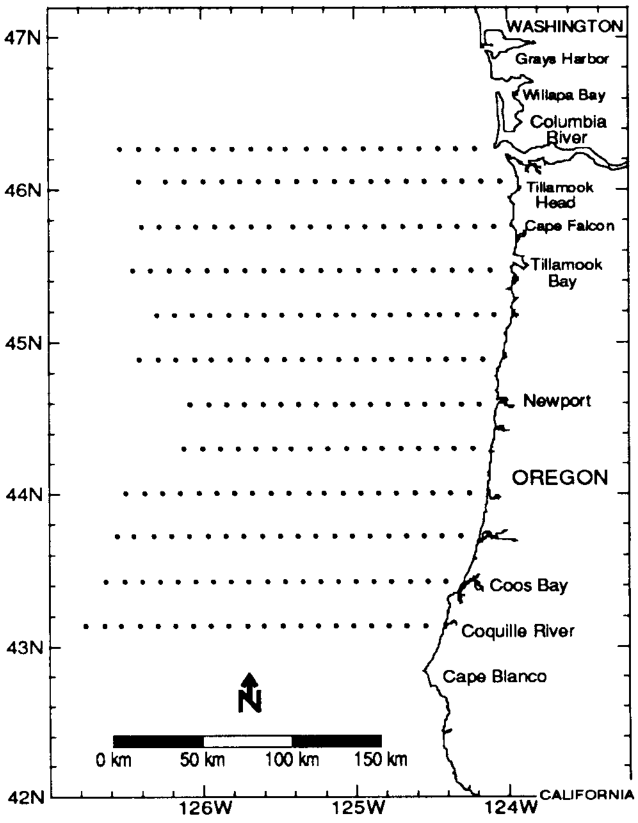

Figure 1. A grid of 234 sampling stations occupied during the ichthyoplankton survey, 5–26 July 1994.

from 9 to 190 km offshore and encompassed a north–south distance of 348 km, from the Columbia River to the Coquille River, Oregon (just north of Cape Blanco). Transects were at 32-km intervals and included 17–20 evenly spaced sampling stations, each about 9 km apart.

Vertical egg tows were made at each station from a depth of 70 m, or just above the bottom, to the surface with a CalVET net that had a mouth area of 0.05 m^2 and a mesh size of 0.15 mm (Smith et al. 1985). In conjunction with each egg tow, temperature and salinity profiles were collected with a Seacat SBE19 profiler. Seawater from the 3-m depth at each station was collected for chlorophyll *a* analysis. Stations were sampled when the boat arrived, regardless of time of day. Vessel speeds of 13–17 km/h between stations allowed for completion of about one transect every 24 h.

Plankton Sample Processing and Egg Identification and Staging

Standard techniques (Smith and Richardson 1977) were used to preserve and sort fish eggs and larvae. Eggs were identified and staged by personnel at the NMFS Southwest Fisheries Science Center in La Jolla, California. Sardine eggs were identified from characters described by Ahlstrom (1943), Miller (1952), and Lo et al. (1996) and assigned to 11 developmental stages based on their morphology.

Egg Mortality and Egg Production

To estimate daily production of age-0 eggs and egg mortality, we first assigned ages to staged eggs from each tow, based on incubation temperature, time of tow, and time of peak spawning. We used a model for temperature-dependent age of each egg stage developed by Lo et al. (1996) to assign an age to each egg stage, aided by a computer program STAGETOAGE (Hewitt et al. 1984; Lo 1985; Picquelle and Stauffer 1985). The peak spawning time for Pacific sardine off California in 1994 ranged from 2000 to 2400 h and was centered at 2100 h (Lo et al. 1996). Silliman (1943) found that most Pacific sardine eggs off California were distributed in the 10-m to 20-m depth zone at temperatures of 14°–16°C, and Ahlstrom (1943) used the mean temperature for this zone to assign an age to each egg based on its stage of development.

Eggs were further grouped by half-day age category (e.g., 4–15 h, 16–27, etc.; table 1), excluding those eggs less than 3 h old or greater than the expected hatching time, which depends on water temperature (3 days, exposed to 15°C waters; Picquelle and Stauffer 1985; Lo et al. 1996). Densities of young eggs, less than 3 h old, tend to be misrepresented because of their contagious distribution and their short duration. Eggs older than the expected hatching time are also biased because of hatching (Lo et al. 1996). Mean number of eggs and mean age in each half-day age group (P_t) were used to estimate daily production of eggs in the sea, P_0, from the following egg mortality equation:

TABLE 1
Observed Egg Densities (Eggs/0.05 m^2/day) and Age Categories (Days) Used to Model the Egg Mortality of Pacific Sardine off Oregon, 1994

Age category (days)	Egg density (eggs/0.05 m^2/day)
0.39	0.170
0.82	0.461
1.42	0.641
1.88	0.435
2.42	0.275
2.83	0.097

$$P_t = P_0 e^{-zt}$$

where P_t = egg production per 0.05 m^2 at age t (day),
P_0 = egg production per 0.05 m^2 at age 0,
z = the daily instantaneous egg mortality rate.

Spawning Biomass

To compute spawning biomass, we used the daily egg production method (DEPM; Lasker 1985). The DEPM computes the spawning biomass as the ratio of estimates of P_0 and daily specific fecundity (number of eggs/population weight/day):

$$B_s = \frac{P_0 A}{Q k}$$

where B_s = spawning biomass (MT),
P_0 = daily egg production per 0.05 m^2,
A = total survey area (in units of 0.05 m^2),
Q = daily specific fecundity (number of eggs/g biomass/day) = RSF/W_f where R is the fraction of mature female fish by weight (sex ratio); S is the proportion of mature females that spawned per day; F is the batch fecundity; W_f is the average weight of mature females (g),
k = constant (g to MT).

Daily specific fecundity (Q) is normally computed from adult samples collected in conjunction with egg sampling. Because no adult sardines were collected during our survey, we decided to use the daily specific fecundity observed for sardine in California in 1994 (11.53 eggs/g biomass/day; Lo et al. 1996; Macewicz et al. 1996) as a crude estimate for adult sardines in our study area. Because of the potential bias in using an estimate for $|Q|$ from California in an estimate for sardine off Oregon, we obtained only the point estimate for the

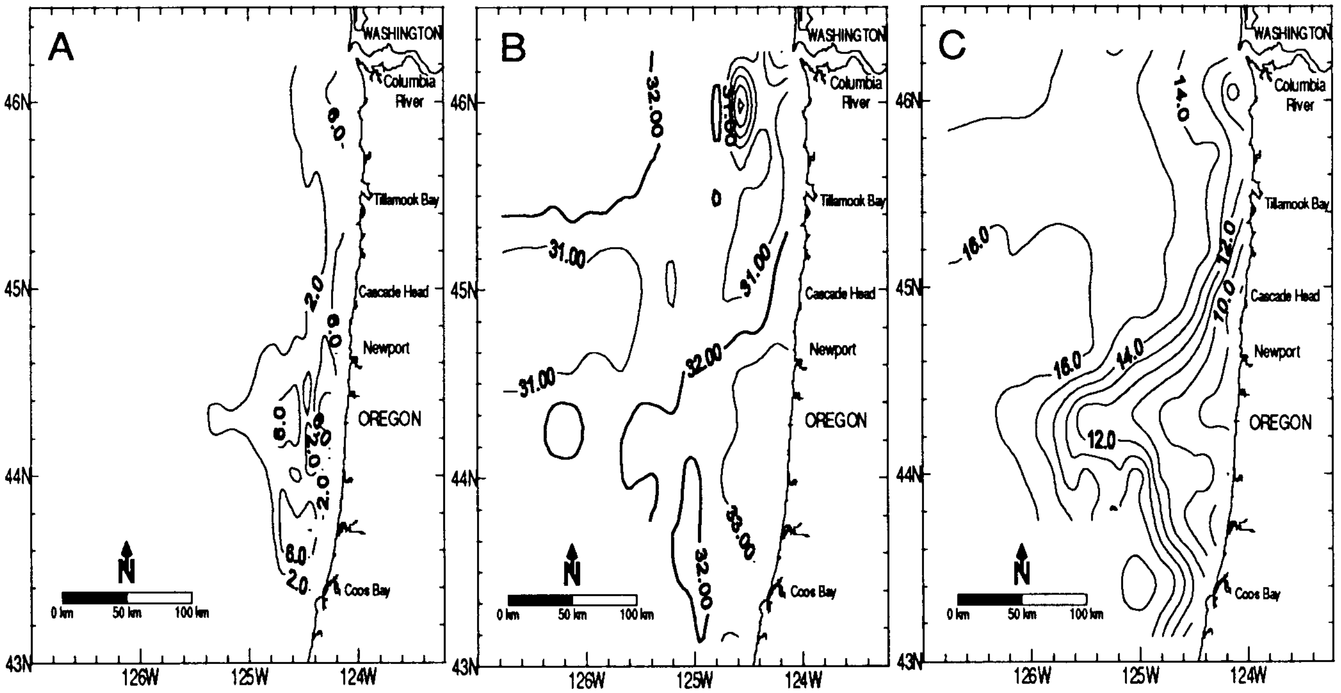

Figure 2. *A*, Chlorophyll *a* (mg/m^3), *B*, salinity (ppt), and *C*, temperature (°C) contours observed during the ichthyoplankton survey off Oregon, 5–26 July 1994. All measurements were taken at the 3-m depth.

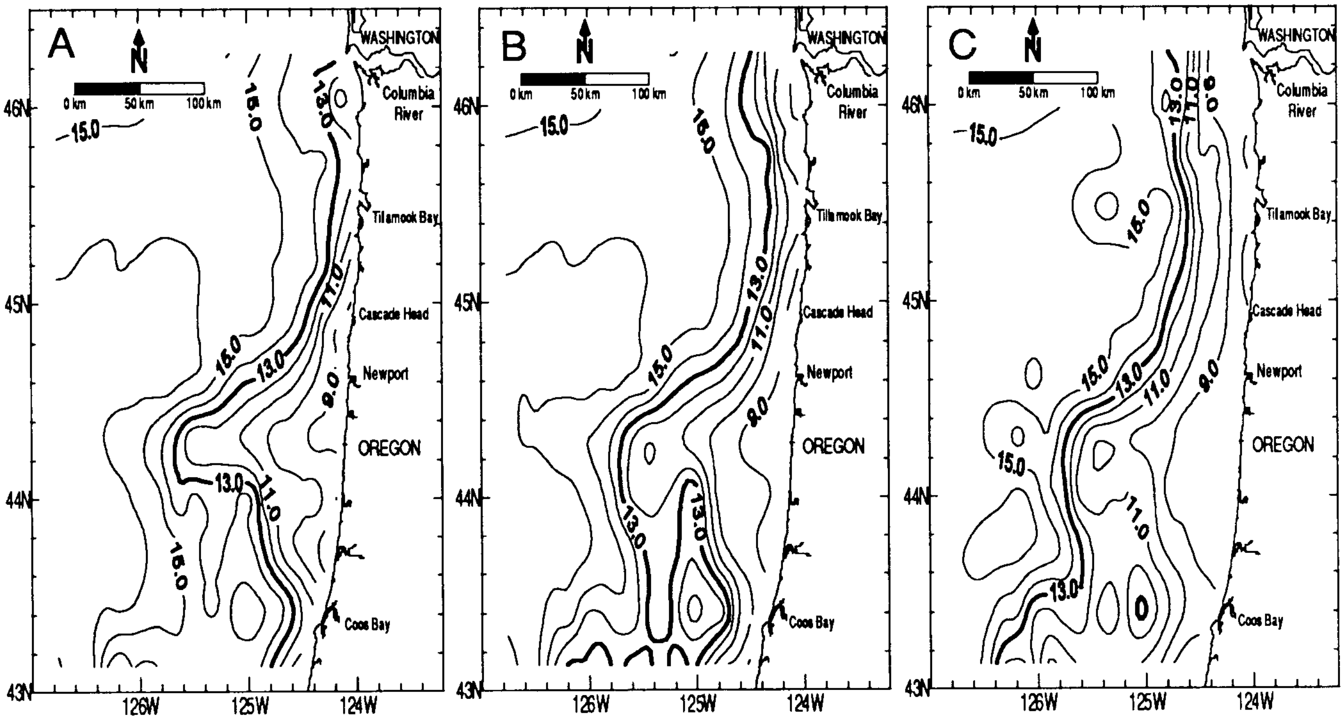

Figure 3. Temperature (°C) contours for the 3-m (*A*), 10-m (*B*), and 20-m (*C*) depths observed during the ichthyoplankton survey off Oregon, 5–26 July 1994.

spawning biomass of sardine off Oregon, and made no attempt to obtain confidence interval estimates for the spawning biomass.

RESULTS

Ocean Conditions

Marine environmental conditions in July 1994 were representative of summer conditions found along the Oregon coast when upwelling, generated by sustained northwesterly winds, causes low ocean temperatures and high salinities in a narrow band along the coast (figure 2; Barnes et al. 1972; Huyer et al. 1975; Huyer 1979). Upwelling calculated for July 1994 at latitude 45°N, longitude 125°W was among the highest on record (data obtained from the Pacific Fisheries Environmental Group, Monterey, Calif.). Low surface temperatures (<10°C) and high surface salinities (>33 ppt) observed along the central Oregon coast were further evidence of strong upwelling. Chlorophyll *a* concentrations reflected the trends in surface temperature and salinity, and increased in areas where nutrient-rich waters were upwelled into the euphotic zone. Highest chlorophyll *a* levels (>10 mg/m^3) were found near shore around the Columbia River mouth and along the central Oregon coast just south of Newport, Oregon.

The 13°C isotherm, the lower limit for successful spawning of Pacific sardine, was observed along the entire coastal portion of the survey grid (figure 3). In the northern half of the survey area, from Newport north to the Columbia River, a mixed layer of 15°C water was observed from about 60 to 190 km offshore and at depths greater than 10 m (figure 4). The Columbia River plume, delineated by lower-salinity surface waters (<32 ppt), usually follows an offshore and southerly direction during the summer (Pearcy and Mueller 1969; Barnes et al. 1972; Hickey and Landry 1989; Fiedler and Laurs 1990), and this pattern was evident during July 1994.

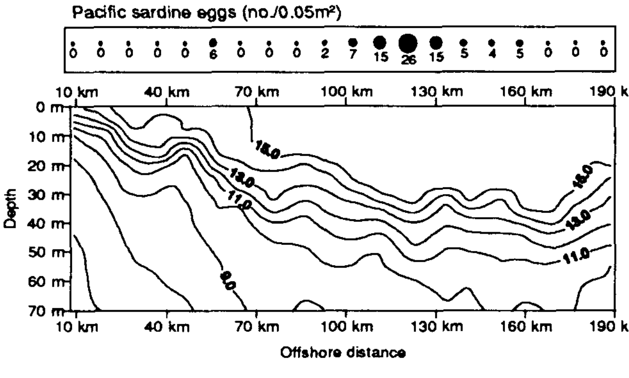

Figure 4. Temperature profile off Cape Falcon, Oregon (45.8°N), and the number of Pacific sardine eggs collected per station.

TABLE 2

A. Summary of Pacific Sardine Egg and Larval Data Collected off the Oregon Coast during July 1994

	Total number	Percent of sampling stations
Number of stations containing:		
Eggs	46	19.6
Larvae	30	12.8
Eggs or larvae	64	27.3
Eggs and larvae	12	5.1
Mean number of eggs/0.05 m^2		
All stations	0.96	
Positive stations	4.87	
Mean number of larvae/0.05 m^2		
All stations	0.38	
Positive stations	3.00	

B. Temperatures (°C) That Eggs May Have Been Exposed to

Depth (m)	Average all tows	Positive tows for eggs	
		Average	Weighted average
1–10	14.16°	15.06°	15.31°
10–20	13.38°	14.39°	14.87°

Egg Identification and Staging

A total of 224 Pacific sardine eggs was collected at 46 (20%) of the 234 stations sampled (table 2). The average number of eggs per tow was 0.96—coefficient of variation (CV) = 0.2—with a maximum of 26 eggs.

Sardine eggs from our samples had a mean size similar to eggs collected off central California during May 1994 (Lo et al. 1996), but they had a slightly higher size variation (table 3; figure 5). We found proportionally more eggs at the high and low extremes of the size range than were found off central California. Also, the oil globule is usually obvious in California sardine eggs but was often difficult to detect in our samples.

Melanostomiid eggs with features similar to those of Pacific sardine (large diameter, wide perivitelline space, segmented yolk, and single oil globule) were found in 24 samples. The size range of these eggs partially overlaps that of sardine (table 3); however, the composition and color of the yolk and size of the oil globule were different from those of sardine eggs. The melanostomiid egg has bright yellow, spherical yolk segments that are smaller than the polygonal, pale orange segments of sardine eggs. Also, the oil globule of the melanostomiid egg (usually dispersed) is at least two times larger than that of sardine eggs. The melanostomiid eggs in our samples were most likely from *Tactostoma macropus*, since this species spawns primarily in summer (Kawaguchi and Moser 1993).

All 11 developmental stages of Pacific sardine eggs were present in our samples, although not all were equally

TABLE 3
Diameters of Sardine Eggs from Oregon and Central California Compared to Those of a Melanostomiid Species from Oregon

Species	Area	Size range (mm)	Mean size	SE ($\times 10^{-03}$)	n
Sardine	California	1.43–2.00	1.75	7.18	150
Sardine	Oregon	1.23–2.00	1.75	9.65	165
Melanostomiid	Oregon	1.32–1.60	1.50	1.13	32

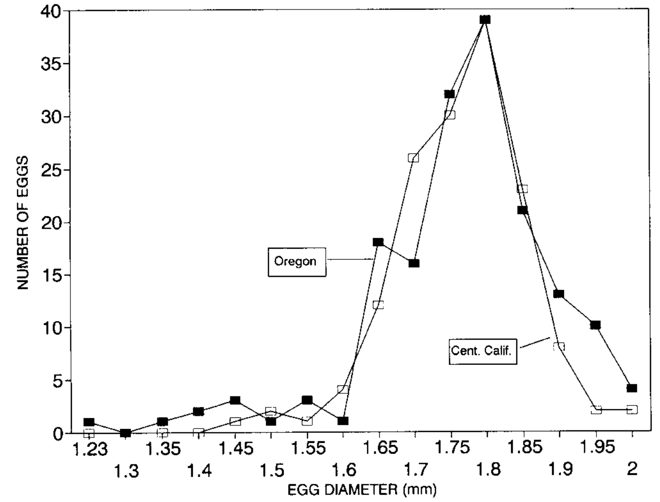

Figure 5. Diameters (mm) of sardine (*Sardinops sagax*) eggs collected off Oregon in July 1994, and off central California in April 1994.

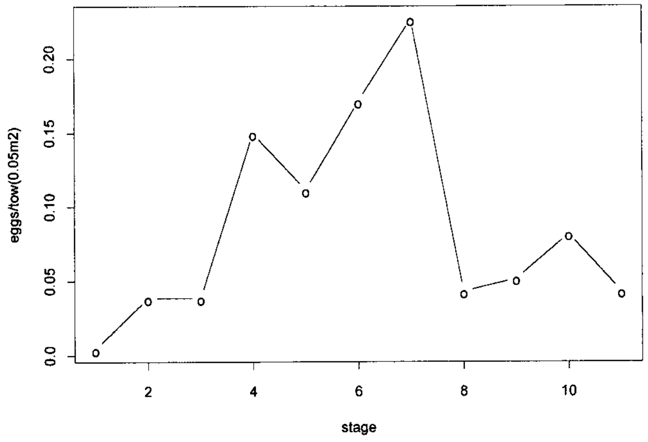

Figure 6. Egg densities categorized by developmental stage for Pacific sardine collected off Oregon, July 1994.

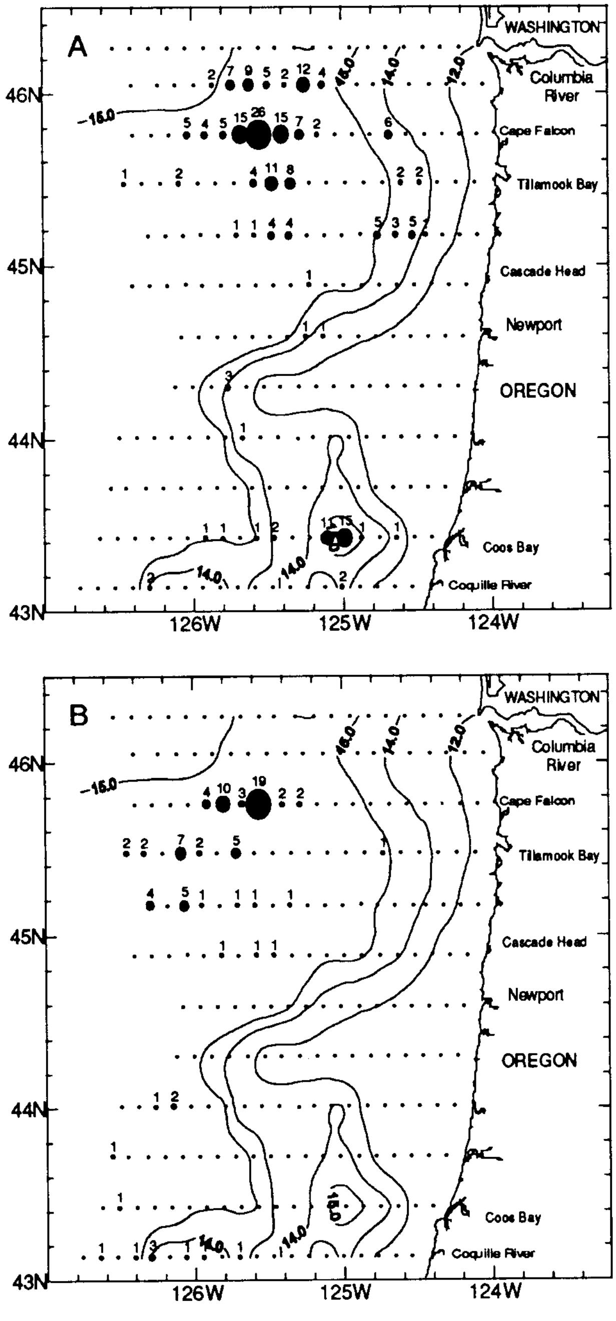

Figure 7. Geographic distribution of Pacific sardine eggs (*A*) and larvae (*B*) collected during the ichthyoplankton survey, 5–26 July 1994. Eggs and larvae are presented as the number per tow (no./0.05 m^2). The 12°, 14°, and 15°C isotherms for the 1-m to 10-m depth profile are also presented.

represented. Due to the contagious distribution and difficulties in sampling young eggs, density was lowest for stage 1, increased with subsequent stages, peaked at stage 7, and decreased thereafter due to mortality and dispersal (figure 6).

Egg and Larvae Distribution

Numerically, Pacific sardine eggs constituted 52.0% of all fish eggs collected. The highest concentration of sardine eggs was found 120 km off Cape Falcon, about 45 km south of the Columbia River, in waters 15°C or warmer (figure 7). Geographically, this is the same region that was preferred by spawning northern anchovy two decades ago, and this region is thought to be strongly affected by the Columbia River plume (Richardson 1981).

Pacific sardine larvae were found less frequently than eggs, occurring at 30 (12.8%) of 234 stations. Sardine larvae made up about 30% (88/292) of all fish larvae collected. The area of highest concentration (>10 larvae/0.05 m^2) was geographically similar to that of highest egg abundance (figure 7).

Egg Production and Spawning Biomass

The developmental rate of sardine eggs is temperature dependent; thus the temperature of the water column where females lay eggs is essential for estimating egg production. Silliman (1943) documented that the most sardine eggs collected off southern California were found to be within the 10-m to 20-m depth zone at temperatures of 14° to 16°C. However, using this depth criterion, we discovered that about 40% of station temperatures (mostly nearshore) were less than 13°C, a temperature at which little spawning occurs (Hart 1973) and at which newly hatched sardine larvae do not survive (Lasker 1964). For the Oregon survey area we chose to use the average temperature of the upper 10-m depth zone at each tow for age assignments. The overall average temperature in the upper 10-m depth zone, weighted by sardine egg abundance, was 15.3°C.

At 15.3°C, Pacific sardine eggs generally hatch about 3 days after being spawned (Lasker 1964; Lo et al. 1996); therefore, only eggs younger than 3 days were included in mortality estimates. Including eggs 3 days or older would overestimate the mortality rate because decreasing abundance after 3 days is primarily due to hatching rather than mortality.

Egg production (P_0) was estimated to be 0.42 eggs/0.05 m^2/day (CV = 0.51), and instantaneous mortality rate (z) was estimated to be 0.13/day (CV = 2.43). The high CV for the instantaneous mortality rate resulted from low catches of eggs in early developmental stages (figure 6). This is not unusual, because stage 2 and stage 3 eggs are patchy in distribution, and have high variance, in particular when the number of sample tows is small and small-volume plankton nets, which may miss patches, are used (Smith 1973, 1981). The egg mortality model, necessary for estimating P_0 (figure 8), fit poorly to the observed egg abundance data as a result of the low catches of young eggs. On the basis of egg production of 0.42 eggs/0.05 m^2/day, we estimated that the spawning biomass of Pacific sardine in the 69,308-km^2 survey area was 50,493 MT. No standard error of the spawning biomass was computed.

DISCUSSION

There appears to be a close association between the geographic distribution of sardine eggs and the 14°C isotherm derived from the 1-m to 10-m depth zone. A similar phenomenon was observed off California, where sardine eggs were concentrated in a narrow range of sea-surface temperatures between 13.8° and 14.5°C (Lo et al. 1996). On the basis of patterns of occurrence of eggs, depth, and temperature, we hypothesize that the isotherm of 14°C may form a distinct boundary which could be used to determine the vertical distribution of sardine eggs and will be a useful stratifying variable in sampling design for sardine egg surveys off Oregon. Sardine eggs off Oregon may have been concentrated in a shallower area of the water column than sardine eggs off California. Further research on the vertical distribution of sardine eggs off the Oregon coast is needed to test this hypothesis.

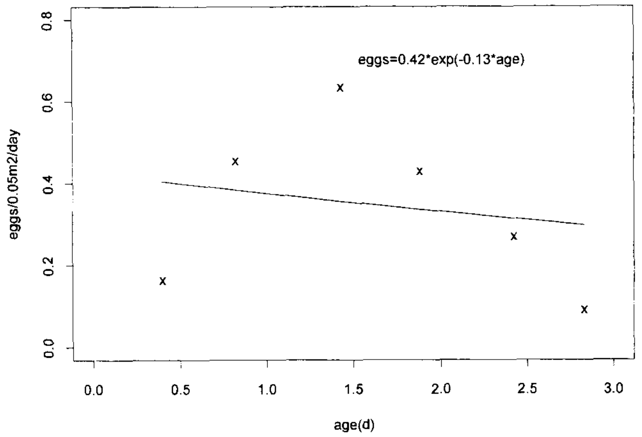

Figure 8. Sardine egg mortality curve and the observed egg density (eggs/0.05 m^2) for each half-day category, July 1994, off Oregon.

The developmental rate of sardine eggs is temperature dependent; thus vertical distribution of sardine eggs and the water-temperature profile are required for estimating egg production. In this study, however, we did not know the vertical distribution of eggs collected, and we assumed that most Pacific sardine were concentrated in the 1-m to 10-m depth zone, in which the temperatures were suitable for spawning and larval survival (i.e., warmer than 13°C; Silliman 1943; Lasker 1964).

The poorly fitted mortality curve is primarily due to the high variances of young eggs (stage 3 and younger). When the sample is small or the population is at a low level, it is common to observe either extremely high or extremely low catches of young eggs because young eggs are patchy (Smith 1973, 1981). A similar phenomenon was observed in the survey for Pacific sardine off California in 1994 (Lo et al. 1996). Other estimation procedures and sampling schemes should be considered for the future. To circumvent the highly variable density of young eggs, Lo et al. (1996) used an embryonic mortality curve which included both eggs and yolk-sac larvae to reduce the variance of the estimates of egg production and egg mortality.

The spawning biomass estimate for the Oregon survey area is speculative, for lack of estimates of adult reproductive parameters, and consequently we did not calculate the error of the estimate. The greatest potential bias is the assumption that the estimate of Q for California in April was the same as for Oregon in July. Since spawning frequency varies each year from zero to the maximum of 1.6 (Macewicz et al. 1996), any number in between is possible. Batch fecundity is linearly related to fish weight, so the fecundity per gram of female may be similar. Even though there is strong evidence of latitudinal clines in age composition of sardine along the west coast, with the age structure increasing northward (Hart 1973; Butler et al. 1996; Deriso et al. 1996), the difference in fecundity per fish weight between two areas is likely to be negligible.

The estimated egg production off Oregon in July 1994 (0.42 eggs/0.05 m^2/day) was more than twice the production estimated off the California coast in May 1994 (0.169 eggs/0.05 m^2/day; Lo et al. 1996). The percentage of tows that yielded eggs (20%) in our survey was also higher than that observed off California (11%). However, when we compared egg production off Oregon with that of stratum 1[1] off California, the results were similar: stratum 1 was 46% of the total area surveyed in California waters, and the egg production in stratum 1 was 0.37 (= 0.169/0.46), which is similar to the egg production we observed off Oregon. Although the egg mortality rates from both surveys had a high CV, their point estimates were similar. The percentage of tows yielding eggs in stratum 1 off California was 23%, which is also similar to the 20% yield we observed off Oregon.

Pacific sardine spawning off Oregon in July 1994 appeared to occupy the same habitat (Columbia River plume) occupied by the northern subpopulation of northern anchovy in the 1970s (Richardson 1981). Although the occurrence of Pacific sardine eggs was high, northern anchovy eggs were rarely observed in our survey area. Whether this indicates displacement of northern anchovy by Pacific sardine is uncertain, and what effect this would have on regional trophic interactions is unknown. However, northern anchovy have been identified as the primary prey off the Oregon coast for many fish species, including salmonids (Fresh et al. 1981; Brodeur et al. 1987). Although salmonids have been known to feed on sardines in the past (Silliman 1941), displacement of anchovy by sardine would have unpredictable effects on the food habits of salmonids. Sardines grow considerably larger (Hart 1973) and evidently swim faster than northern anchovy. The increasing Pacific sardine population, while perhaps compensating for the reduction in anchovy biomass (unpublished data), may not be prey of adequate size range and may be more difficult to capture than northern anchovy.

Whether the spawning of Pacific sardine off Oregon in 1994 was an anomalous event or part of a long-term northward expansion is uncertain. However, there is evidence that Pacific sardine may have spawned as far north as Vancouver Island, British Columbia, in recent years (Morgan Busby, NMFS, Alaska Fisheries Science Center, pers. comm., Nov. 1995). The shift in oceanic regimes (reduced advection from the north and decreased coastal upwelling) in the North Pacific over the past two decades, and the resulting increased surface temperatures may have created an environment more suited for Pacific sardine (Jacobson and MacCall 1995). A long-term data set for coastal Oregon would identify the mechanisms responsible for the northward expansion of the Pacific sardine's spawning distribution.

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[1] In the California survey, the area was poststratified: stratum 1 encompassed the area where eggs were found or were likely to be found based on incidence in surrounding locations, and stratum 0 consisted of the area devoid of eggs.

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MODELING DETERMINISTIC EFFECTS OF AGE STRUCTURE, DENSITY DEPENDENCE, ENVIRONMENTAL FORCING, AND FISHING ON THE POPULATION DYNAMICS OF *SARDINOPS SAGAX CAERULEUS* IN THE GULF OF CALIFORNIA

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ABSTRACT

We used an age-structured deterministic model to investigate how population dynamics of Pacific sardine, *Sardinops sagax caeruleus*, in the Gulf of California are affected by age structure, density-dependent recruitment, environmental forcing, and fishing. Density-dependent recruitment had a very strong effect; it stabilized the population dynamics and caused mesoscale (4–5 year) cycles in abundance. A sinusoidal function was used to vary survival rates with constant period of 60 years and various amplitudes. This representation of environmental forcing caused long-term cycles in the abundance of sardine, similar to the pattern observed in real stocks. A linearly increasing fishing schedule over a period of 25 years on a stock with environmental forcing caused strong reductions in abundance that extended for up to 20 years, and mesoscale oscillations for up to 40 years after the harvest period. The negative impact was longer if harvest started when survival rates were at their maxima, but biomass decreased most when harvest started at the descending node of survival rates. A stability analysis indicated that the sardine stock in the Gulf of California is unstable; however, when age structure is included in the simulations the stock is very resilient and can recover from low levels of biomass. This theoretical result was probably due partly to the absence of stochastic effects in our model.

INTRODUCTION

Variability in abundance is a pervasive aspect of all natural biological populations. Abundance changes over time due to stochastic and deterministic factors; here we focus on the latter. Much of our current knowledge about deterministic effects on population variation comes from theoretical work because most data sets are short and because deterministic effects are obscured by stochastic environmental effects and measurement error. Theoretical studies indicate that in the absence of stochasticity, factors such as age structure, density dependence, and environmental forcing can cause populations to fluctuate with different frequencies (May 1973; Caswell 1989; Botsford 1986).

Some populations experience quasi-periodic oscillations in annual survival rates due to environmental effects on recruitment. Examples may include Pacific sardine in the Gulf of California and off the Pacific coast of North America. Variation in sardine abundance coincides with the mesoscale frequency (5 to 10 years) of El Niño events (Huato-Soberanis and Lluch-Belda 1987), and low-frequency oscillations (50 to 60 years) observed in many clupeoid fish species throughout the world (Lluch-Belda et al. 1989).

As a result of their close relation to the physical environment, short life span, and variable recruitment, small pelagic fish populations (e.g., sardines and anchovies)—the most important group of fish species in the world in terms of volume captured—have complex dynamics (Sharp and Csirke 1983), and their management is particularly difficult. Furthermore, the fact that small pelagic fish populations experienced oscillations of several orders of magnitude long before fisheries existed (Baumgartner et al. 1992) prompts one to ask if fisheries management can affect the dynamics of these important stocks.

PACIFIC SARDINE IN THE GULF OF CALIFORNIA

The Gulf of California (henceforth referred to as the gulf) has many features in common with major upwelling systems. Bathymetric characteristics, strong tidal mixing, and seasonal upwelling result in high productivity and abundance of commercially important marine fish species (Álvarez-Borrego and Lara-Lara 1991). The gulf's most important fishery resources by volume and economic value are small pelagic fish and shrimp. Three species of small pelagic fish are represented in the gulf in a guild similar to those of the California and Humboldt Current systems: Pacific sardine (*Sardinops sagax caeruleus*), northern anchovy (*Engraulis mordax*), and Pacific mackerel (*Scomber japonicus*). A difference is the presence in

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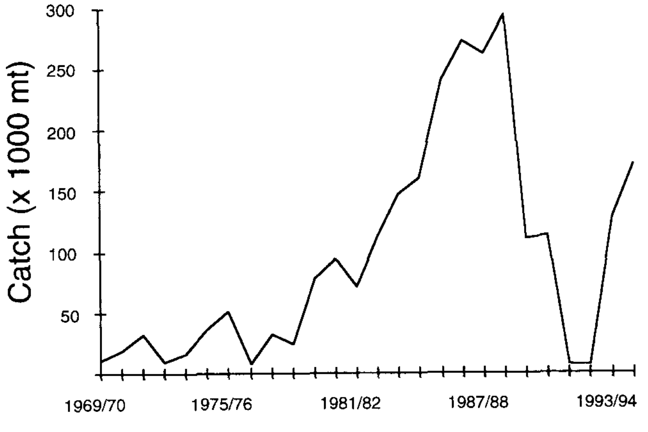

Figure 1. Pacific sardine catch in the Gulf of California, Mexico. Sardine fishing seasons start in mid-October and end the following year. Because of changes in the fishery and in management regulations, the number of months during which fishing occurred changed from 7 to 11 in 1977, to 12 in 1982, and then to 10 in 1989.

the gulf of more tropical species such as thread herring (*Opisthonema* spp.) and round herring (*Etrumeus teres*; Cisneros et al. 1990).

The Pacific sardine in the gulf is the main component of the Mexican fishery for pelagic fish, with maximum annual recorded landings of 292,000 metric tons (MT). Pacific sardine were first harvested in the gulf during the late 1960s after the collapse of the sardine fishery off the west coast of California and Baja California (Lluch-Belda et al. 1986). Sardine landings increased steadily over two decades, peaked in 1988–89, and then declined rapidly to a minimum of about 7,000 MT in the 1991–92 fishing season (figure 1).

Decreased sardine abundance in the gulf before 1991–92 may have been due to excessive fishing during a period of adverse environmental conditions. A shift in the age structure of the stock and catch to younger ages, and excessive harvest rates during the decline indicated overexploitation of the stock (Cisneros-Mata et al. 1990). The appearance in 1985 of northern anchovy in the commercial catch (Hammann and Cisneros-Mata 1989) suggested that anchovy may have been replacing sardine. The species replacement hypothesis can probably now be discarded because recent data indicate that the species have coexisted in the gulf (Holmgren-Urba and Baumgartner 1993), and because both sardine and anchovy presently seem to be increasing in abundance. The potential effect of harvest on the gulf's sardine stock has yet to be clarified, although it has been repeated ad nauseam how excessive fishing in combination with natural phenomena caused the collapse of the Pacific sardine in California and the anchoveta in Peru.

In a study based on virtual population analysis (VPA; Gulland 1965, cited in Pope 1972) it was proposed that both fishing and sardine stock biomass increased in parallel in the gulf during the last two decades (Cisneros-Mata et al. 1995). This hypothesis makes the implicit assumption that fishing started when the sardine stock was at a low point in a long-term cycle of abundance. Analysis of scale deposition in anaerobic sediments indicates that the cycle of sardine abundance in the gulf apparently is not coupled to that of the same species in the California Current (Holmgren-Urba and Baumgartner 1993). The hypothesis that sardine abundance cycles in the gulf is supported by the recent recovery in catches (figure 1) and abundance (unpubl. data).

In this work we analyze how (1) age structure, (2) density dependence, (3) periodically oscillating survival rates, and (4) fishing affect the dynamics of Pacific sardine in the Gulf of California, Mexico. We developed a deterministic age-structured model with density-dependent recruitment for the Pacific sardine stock of the Gulf of California and performed numerical simulations under various conditions. We included sinusoidal variation in survival rates to represent low-frequency environmental forcing. We then analyzed the effects of harvest beginning at different points in the underlying cycle for survival rates to understand how fishing pressure affects a population of small pelagic fish experiencing low-frequency oscillations. Our objective is to understand the importance of deterministic mechanisms in the dynamics of exploited small pelagic populations. Our eventual goal is to develop appropriate management schemes. We address stochastic environmental effects, which are also important, in another paper.

MATERIALS AND METHODS

We consider a time-discrete model for a population with more than one age class. The first age class comprises the juveniles (recruits); the remaining classes comprise the adults. For such a population the total number of individuals in a given year (N_t) is composed of the number of recruits in that year (R_t) plus survivors from the previous year (S_t):

$$N_t = R_t + S_t \tag{1}$$

Assuming constant annual survival rates for recruits and adults, this year's number of adults (S_t) is given by the number of recruits from the previous year that survived to the present year ($p_1 R_{t-1}$), plus adults of last year that survived to the present year ($p_2 S_{t-1}$):

$$S_t = p_1 R_{t-1} + p_2 S_{t-1} \tag{2}$$

where p_1 and p_2 are the net annual natural survival rates of recruits and adults, respectively. Combining equations 1 and 2 we have:

$$N_t = R_t + p_1 R_{t-1} + p_2 S_{t-1} \tag{3}$$

Equation 3 is a discrete time model for population growth; if recruitment is constant, then population size will merely depend on survival rates, the size of annual recruitment, and the adult stock size in the previous year; that is, $N_t = R\ (1 + p_1) + p_2\ S_{t-1}$. If recruitment is not constant, one can include a function in equation 3 to model variation in annual recruitment. We took this approach and included a Shepherd (1982) stock-recruitment function in equation 3. Cisneros-Mata et al. (1995) found that Shepherd's model fit data for sardine in the gulf.

Shepherd's model yields a curve with a dome that is more or less pronounced, depending on the strength of the density dependence:

$$R_t = \frac{aS_{t-1}}{1+(S_{t-1}/b)^c} \tag{4}$$

where R_t is recruitment size in year t, S_{t-1} is parental stock size in the previous year, and a, b, and c are parameters that shape the curve. Here, a is maximum per capita recruitment; b is the parental stock size above which density dependence dominates density-independent factors; and c measures the strength of the density dependence. Inclusion of equation 4 in equation 2 yields the following nonlinear, second order, discrete model for the annual adult stock size as a function of past stock sizes and survival rates:

$$S_t = p_1 \frac{aS_{t-2}}{1+(S_{t-2}/b)^c} + p_2S_{t-1} \tag{5}$$

To determine the stability properties of model 5, we used a standard technique (e.g., Edelstein-Keshet 1988) that consists of a perturbation to the linearized system at an equilibrium point. If the perturbation grows with time, the system is unstable, and vice versa. Briefly, model 5 was transformed into a system of two equations, and the Jacobian was evaluated at steady states to find conditions for stability. (For details, see Appendix.) From this analysis, we found model 5 to be stable over the range of parameters satisfying

$$2 > 1-p_1ab^c \left[\frac{b^c + (\dot{S})^c(1-c)}{\left(b^c + (\dot{S})^c\right)^2}\right] > p_2, \tag{6}$$

where p_1, a, b, and c are the same as described above, and $\dot{S}$ is the equilibrium adult stock size.

We included age structure in our model population of sardine by combining equation 5 with a 7 year-class Leslie matrix; that is, annual recruitment was computed with Shepherd's model and a constant survival rate for the 6 age classes comprising the parental stock.

Parameter values of the Shepherd stock-recruitment relationship for the sardine of the Gulf of California were (from Cisneros-Mata et al. 1995): $a = 2.697$ recruits per adult; $b = 1.471 \times 10^{10}$ adults; and $c = 6.499$, with standard errors of 0.3, 1.13×10^9, and 2.23, respectively.

In all simulations, initial numbers in the population were set arbitrarily as 100×10^6 recruit sardines, and biomass trends were computed over a period of 400 years. Numbers (N_t) were converted to biomass with: $W_t = N_tW_\infty[1-e^{-K(t-t_0)}]^\beta$, where W_t is weight at age t; W_∞ (g) $= \alpha L_\infty{}^\beta$ is maximum weight, and $L_\infty = 204$ mm (standard length); $K = 0.86\text{y}^{-1}$; and $t_0 = -0.014\text{y}$ (Cisneros-Mata et al. 1995) are parameters of the von Bertalanffy individual growth function. The standard errors of L_∞, K, and t_0 are 3.14, 0.07, and 0.04. The parameters of the length-weight relationship, $\alpha = 4.21 \times 10^{-6}$ (SE $= 1.01 \times 10^{-6}$) and $\beta = 3.28$ (SE $= 0.03$) were computed with samples of sardine taken from the commercial landings during the 1994–95 fishing season.

Mean adult annual survival rates (p_2) for the unfished Pacific sardine stock in the gulf were computed as: e^{-M}, where yearly instantaneous natural mortality rate $M = e^{1.46-1.01\ln t_{\max}}$ (Hoenig 1983) and $t_{max} = 7\text{y}$ (Wong 1973) is longevity of sardine. For recruits the survival rate (p_1) was arbitrarily increased by 5% because there is evidence that in clupeids and other fish species survival decreases with age (Hoenig 1983). We used the resulting values, $p_1 = 0.57$ and $p_2 = 0.55$, as baseline survival rates in our analyses.

We investigated the effect of density-dependent recruitment on stability of the sardine population by computing annual biomass trajectories using different values of parameter c of the stock-recruitment relationship. The values chosen for c were one-half and double the baseline value (which we call $c_0 = 6.499$), both within a 95% confidence interval of c_0.

Periodic environmental forcing was simulated by introduction of a sine function of mean annual juvenile and adult natural survival rates. The equation was: $X_t = X_0 + d\ \sin(2\pi \frac{1}{T} t)$, where X_t = survival rate at time t; X_0 = original survival rate (p_1 or p_2); d = amplitude; and T = period of oscillations. We chose a period of 60 years for all trials because we were interested in using a frequency similar to that observed in pelagic stocks (Lluch-Belda et al. 1989; Baumgartner et al. 1992). We conducted a series of trials with three different wave amplitudes d (0.2, 0.3, and 0.4) and observed the effects on dynamics of model sardine population. The values tested for d were chosen to avoid survival rates above one, and zero or less.

To investigate how fishing affects a population of Pacific sardine already experiencing cyclic oscillations in survival due to environmental forcing, we introduced an additional mortality factor affecting survival rates of adults and juveniles. For adults, we used a linearly increasing instantaneous fishing mortality (F) schedule over a 25-

year period, ranging from $F = 0.08$ in year 1 to $F = 2$ in year 25, and $F = 0$ in all other years. For juveniles, we arbitrarily used the same schedule but multiplied by 1/3, based on the idea that juveniles are usually under less fishing pressure than adults. Both the time span and the final fishing mortality were chosen to emulate the fishing schedule experienced by Pacific sardine in the gulf. Computations using length-based cohort analysis (Jones 1981) yielded an F of 1.4 for the mid-1980s (Cisneros-Mata et al. 1990).

The resulting linearly increasing annual fishing mortality coefficients F's were converted to annual survival rates as: $S_F = e^{-F}$; total survival after natural and fishing mortality occurred was computed as $S_T = X_t * S_F$. We simulated fishing during 25 years starting at four points in the baseline cycle of survival rates: increasing, peak, decreasing, and trough. For these trials we arbitrarily fixed the amplitude of oscillations of survival rates to the intermediate value ($d = 0.3$) tested in the previous section.

RESULTS

The stability condition of the system (equation A5 in the Appendix) was not met: $2 > 2.62 > 0.55$; thus we concluded that, for the particular set of parameter values used, our model for Pacific sardine in the Gulf of California is intrinsically unstable. The condition for stability was met when we changed the value of parameter c to $0.5c_0$, but not to $2c_0$, and the null equilibrium (a collapse of the stock) is also stable (Appendix), which makes biological sense. However, adding age structure stabilized the sardine population, as demonstrated in the simulations.

Density-dependent recruitment had a strong effect in the dynamics of the model sardine population. Time series plots of biomass of adults at time t vs. biomass of recruits at time $t+1$ changed from a smooth parabola for $c = 0.5c_0$, to orbital shapes at high population values for c_0 and $2c_0$ (figure 2). Mean size of the stock decreased with increasing density dependence. The trajectories of total biomass with the baseline (c_0) density-dependence value showed a two-point limit cycle with a period of 5 years. The oscillations disappeared when the strength of density dependence was decreased to $c = 0.5c_0$, and increasing c to $1.5c_0$ produced oscillations of the same amplitude as those with c_0 but decreased the period to 4 years (figure 2).

For the three amplitudes tested for the sinusoidal function of survival rates, total sardine biomass over time showed periodic oscillations of mesoscale frequency superimposed on the 60-year period caused by oscillating survival rates (figure 3). Increasing d reduced the frequency of oscillations at low population sizes and increased the amplitude at high population sizes; the largest value of d almost caused the stock to collapse (figure 3). The trough/peak values of juvenile survival for the three values of d used were: 0.37/0.77 for $d = 0.2$; 0.27/0.87 for $d = 0.3$; and 0.17/0.97 for $d = 0.4$. The values for adult survival were: 0.35/0.75; 0.25/0.85; and 0.15/0.95. Thus virtual extinction when $d = 0.4$ was

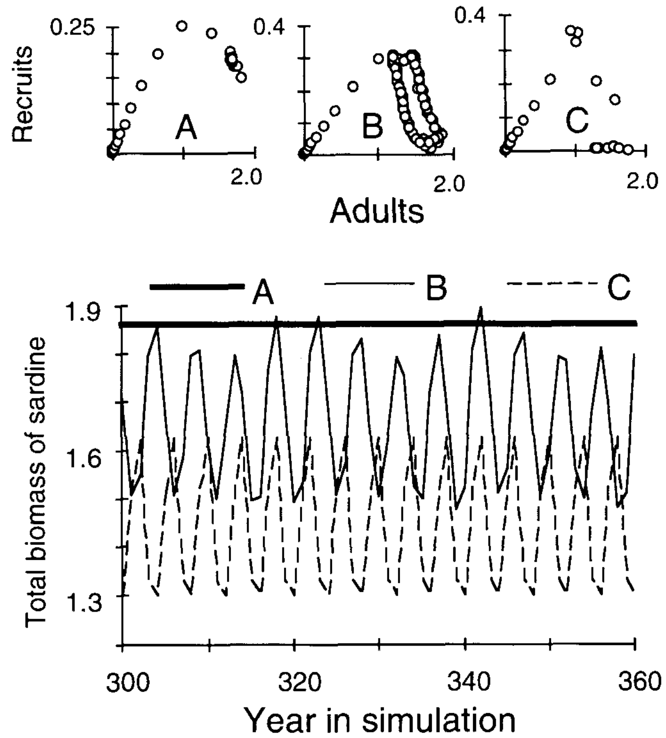

Figure 2. Effects of density-dependent recruitment on the dynamic behavior of a model Pacific sardine population. Baseline indicates the default value $c_0 = 6.499$ (from Cisneros-Mata et al. 1995), which is a measure of the strength of density dependence in Shepherd's (1982) stock-recruitment function. *Top panel*, stock-recruitment trajectories for the three scenarios: 0.5 c_0 (*A*), baseline (*B*), and 2 c_0 (*C*). *Bottom panel*, trajectories of total biomass computed with the same three values of c. All figures are in millions of metric tons.

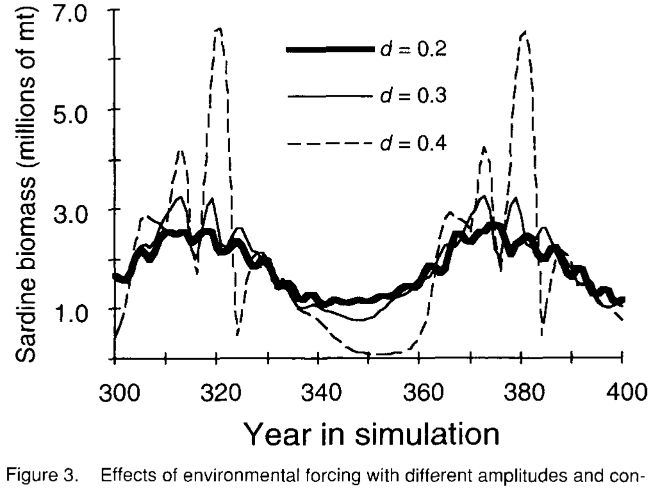

Figure 3. Effects of environmental forcing with different amplitudes and constant period (60 years) on juvenile and adult survival rates in the Pacific sardine population model. Parameter d measures the relative amplitude of the sinusoidal trajectories of annual survival rates.

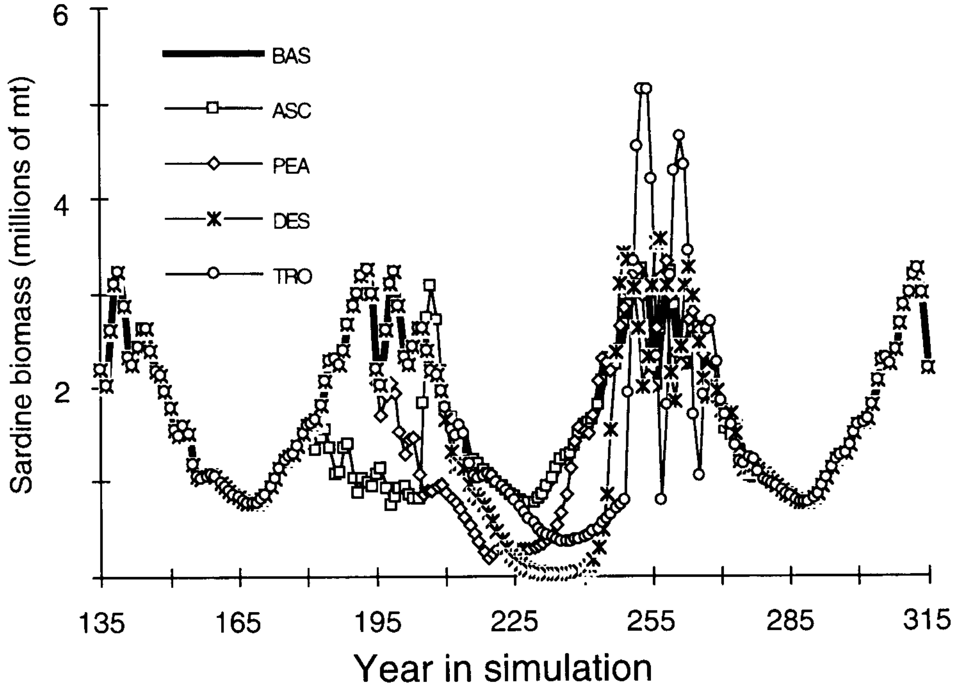

Figure 4. Simulated effect of 25 years of increased fishing pressure starting at four different points of a 60-year cyclic Pacific sardine population. The amplitude of oscillations is $d = 0.3$. BAS indicates an unfished population; ASC corresponds to initial harvest at the ascending node of the cycle, PEA at the peak, DES at the descending node, and TRO at the trough.

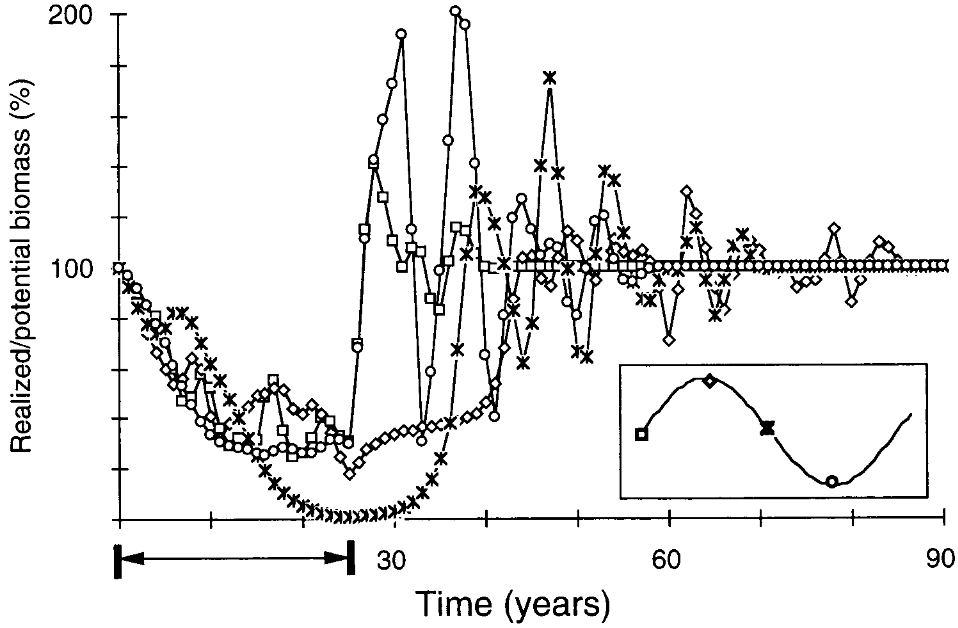

Figure 5. Simulated ratios of realized/potential biomass of a 60-year cyclic Pacific sardine population under 25 years of increasing fishing pressure starting at four different points in the sinusoidal cycle of survival rates. The *double-headed arrow* indicates the period of fishing (*F*). The insert represents the cycle of survival rates causing the oscillations of sardine biomass, and shows the beginning of fishing in the four scenarios.

due to the dynamic behavior of the population, and not to null survival rates due to forcing.

For the four starting points at the 60-year cycle of sinusoidal survivorships, fishing severely decreased population size (figure 4). For a clearer representation, we computed the ratio of realized to potential sardine biomass and scaled all four cases to the same starting point of fishing (figure 5). The stock was significantly affected both during the fishing period and after it had ended. When fishing began at the descending node of the regime, sardine biomass was quite low during the last decade of fishing. The overall effect in terms of time it took to recover after harvest was worst when fishing started at the peak of the regime, and the widest oscillations were caused when fishing started at the trough (figure 5). Oscillations in the ratio of realized/potential biomass continued long after fishing had ceased. Values other than 100% result from baseline and realized trajectories being out of phase, thus oscillations indicate changes in the dynamic behavior of the model population due to fishing pressure.

DISCUSSION

Our analysis indicates that for the underlying assumptions and range of parameter values used, age structure, environmental forcing, and density dependence can strongly affect the long-term dynamic behavior of the sardine population in the gulf. Density-dependent recruitment effects produced cycles of mesoscale frequency. Fishing had a strong impact; it reduced potential biomass and altered the oscillations imparted by a forcing environment.

Oscillations of mesoscale frequency in the biomass of sardine were driven by density-dependent recruitment, as shown in figure 2. The existence of density dependence in small pelagic fishes has been questioned, probably because of difficulty in finding convincingly supportive empirical data (e.g., Armstrong et al. 1989; Koslow 1992). For the Pacific sardine in the California Current, Jacobson and MacCall (1995) found a relation between spawning biomass and number of recruits, suggesting compensatory mortality of juveniles. Recruitment success in these species has been related to ambient indicators such as plankton biomass or annual sea temperature (Ware 1991; Jacobson and MacCall 1995). Cannibalism has also been hypothesized as an important density-dependent factor affecting recruitment in small pelagic fish (Sharp 1987). Smith et al. (1989) concluded that for sardine and anchovy off Peru, cannibalism of adult fish on their eggs could cause low-frequency changes in biomass.

For the Pacific sardine in the gulf no mechanism has been identified to explain the overcompensatory relation found between adults and recruits. Recent studies showed the presence of Pacific sardine eggs in stomachs of adults of the same species (López-Martínez, Centro de Investigaciones Biológicas del Noroeste, Guaymas, Son., pers. comm.), thus suggesting cannibalism. A probable mechanism that results in increased cannibalism in the gulf is the intrusion of anomalous warm-water masses that shorten the spawning season and compress adult distribution northward (Hammann 1991). Strong sardine recruitment has been shown to occur after cool, anti–El Niño years present in the gulf with mesoscale frequency (Huato-Soberanis and Lluch-Belda 1987). These concepts seem to complement each other: expansion of spawning habitat for sardine during cool years results in low cannibalism, increased probability of survival, and good recruitment; the opposite occurs during warm years.

Adding age structure to our sardine model had a stabilizing effect on the population trajectories. This is in agreement with results by Botsford and Wickham (1978) who showed that removing older individuals could destabilize the stock of a model crab population. Before reaching stable age distribution and geometric growth, populations modeled with a Leslie matrix with no density dependence will oscillate with a period equal to the mean generation time (Caswell 1989). For sardine in the gulf, mean generation time—defined as the average age of mature females in a population at stable age distribution (Stearns 1992)—is 3 years as compared to the 4- and 5-year cycles caused by density dependence. Our results show that regulatory mechanisms will override oscillations due to age structure, even when the population increases from a very low level. Nevertheless, it seems likely that the combined effect of a lagged response of total biomass due to age structure (Caswell 1989) and density dependence caused the oscillations after the fishing period.

Environmental forcing on survival rates strongly affected the dynamic behavior of sardine in our model population. No conclusion can be drawn regarding the amplitude and period of oscillations because the values chosen here as baselines were completely arbitrary. Judging by the recovery that the sardine stock is experiencing, it would seem that environmental forcing in the gulf, if it exists, probably has a period of less than 60 years.

Although nonmechanistic, the approach we used here was intended to explore the consequences of cyclic variation of survival rates. Regardless of its nature, an environmental regime will ultimately affect survival rates and probably the fecundity of sardine and other species. Existence of cyclic environmental forcing seems likely, given the low-frequency oscillatory behavior of Pacific sardine in and outside the Gulf of California. Lluch-Belda and collaborators (1991a, b, 1992) provided evidence of a direct relation between sea-surface temperature and abundance and distribution range of Pacific sardine in the California and Humboldt Currents. Smith (1995) discussed the potential effects that warming in the California Current might have on the population growth of Pacific sardine over the past decade. For example, decreased incubation period and maturation time due to high temperature might result in lower mortality and higher biomass.

Our results indicate that harvest strongly affects the sardine stock experiencing environmental forcing. It took up to 20 years after fishing had ended for the stock to recover its baseline biomass level, and up to 40 years for oscillations to subside. Because the scale of recovery is probably similar to the time span of most real fisheries, these results point out the importance of adequate management to prevent economic, if not biological, collapse. Our results also suggest the resilience of the sardine stock in the gulf, because it was able to recover from near collapse after the harvest period. However, random environmental and demographic effects, in addition to density-independent effects, could drive the real population to extinction.

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APPENDIX

To determine its stability properties, model 5 was first reexpressed as a system of two first-order equations:

$$S_t = f(S_{t-1}, Y_{t-1}) = p_1 \frac{aY_{t-1}}{1+\left(Y_{t-1}/b\right)^c} + p_2 S_{t-1} \quad \text{(A1a)}$$

$$Y_t = g(S_{t-1}, Y_{t-1}) = S_{t-1} \quad \text{(A1b)}$$

A steady state (or equilibrium) occurs when, for suitable values $\dot{S}$ and $\dot{Y}$, we have $S_t = \dot{S} = S_{t-1}$ and $Y_t = \dot{Y} = Y_{t-1}$. Thus, $\dot{S}$ and $\dot{Y}$ must satisfy:

$$\dot{S} = f(\dot{S}, \dot{Y}) = p_1 \frac{a\dot{Y}}{1+\left(\dot{Y}/b\right)^c} + p_2 \dot{S} \quad \text{(A2a)}$$

$$\dot{Y} = g(\dot{S}, \dot{Y}) = \dot{S} \quad \text{(A2b)}$$

Note that the null equilibrium ($\dot{S} = 0$ and $\dot{Y} = 0$) is stable. Equation A2a implies that

$$\dot{S} = \frac{p_1 a \dot{Y}}{(1-p_2)\left[1+\left(\dot{Y}/b\right)^c\right]} \quad \text{(A3a)}$$

and

$$\dot{Y} = \dot{S} \quad \text{(A3b)}$$

When values of S_t and Y_t are close to a steady state $(\dot{S}, \dot{Y})$, equation A1 can be approximated as a linear system. Expressed in matrix form, this system is:

$$\begin{bmatrix} s_t \\ y_t \end{bmatrix} = \begin{bmatrix} \partial f/\partial s & \partial f/\partial y \\ \partial g/\partial s & \partial g/\partial y \end{bmatrix}_{\dot{S}, \dot{Y}} \begin{bmatrix} s_{t-1} \\ y_{t-1} \end{bmatrix}, \quad \text{(A4)}$$

where f and g are given by equations A1a and A1b, respectively. s_t and y_t represent small perturbations $S_t - \dot{S}$ and $Y_t - \dot{Y}$ from the equilibrium points $\dot{S}$ and $\dot{Y}$. The matrix of partial derivatives in equation A4 is known as the Jacobian (J), and the condition for stability of the system is (Edelstein-Keshet 1988):

$$2 > 1 + Det(J) > |Tr(J)|, \quad \text{(A5)}$$

where $Det(J)$ is the determinant and $Tr(J)$ the trace of J.

In the particular case of equation A4

$$\partial f/\partial s = p_2, \quad \partial f/\partial y = p_1 a\left[\frac{b^{2c} + b^c Y^c(1-c)}{(b^c + Y^c)^2}\right],$$

$$\partial g/\partial s = 1, \text{ and } \partial g/\partial y = 0$$

Therefore

$$J = \begin{vmatrix} p_2 & p_1 a\left[\dfrac{b^{2c} + b^c Y^c(1-c)}{(b^c + Y^c)^2}\right] \\ 1 & 0 \end{vmatrix}_{\dot{S}, \dot{Y}} \quad \text{(A6)}$$

Finally—for given values of the parameters a, b, c, p_1, and p_2—the equilibrium population size is found by solving system equation A3:

$$\dot{S} = b\left(\frac{ap_1}{1-p_2} - 1\right)^{1/c} \quad \text{(A7)}$$

Part III

SCIENTIFIC CONTRIBUTIONS

DEMERSAL FISH TRAWLS OFF PALOS VERDES, SOUTHERN CALIFORNIA, 1973–1993

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ABSTRACT

Demersal fish and epibenthic macroinvertebrates were monitored on the Palos Verdes Shelf and upper slope, near Los Angeles, 1973–93. Otter trawls were taken at 12 sites: 4 cross-shore transects with 3 depths (23, 61, and 137 m). Dominant soft-bottom demersal fish were Dover sole (*Microstomus pacificus*), stripetail rockfish (*Sebastes saxicola*), slender sole (*Eopsetta exilis*), Pacific sanddab (*Citharichthys sordidus*), plainfin midshipman (*Porichthys notatus*), yellowchin sculpin (*Icelinus quadriseriatus*), and speckled sanddab (*Citharichthys stigmaeus*). Spatial and temporal abundance patterns are reviewed for 28 representative species.

Two decades of dynamic environmental conditions off Palos Verdes are documented. Specific factors causing fluctuations in fish catches cannot be determined. However, water depth greatly influences distributions, and major temperature shifts and associated biological changes correlate strongest with temporal variations. The extreme 1982–83 El Niño event created the largest changes in community composition. Reduced mass emissions of suspended solids and contaminants from the Los Angeles County Sanitation Districts' submarine outfall system contributed to declining sediment contamination, kelp bed expansion, increased food resource diversity, and greater water clarity. Environmental changes associated with improved wastewater quality stimulated recovery of demersal fish assemblages.

Annual incidence of fin erosion in Dover sole at the outfall station decreased from over 50% in the early 1970s to zero since the mid- to late 1980s. Pseudotumors ranged from 0 to 5% in Dover sole near the outfall.

INTRODUCTION

Our goal is to summarize 21 years of demersal fish trawls at 12 sites off Palos Verdes, and to better understand fluctuations in abundance under changing environmental conditions. We examine monitoring data from the Palos Verdes Shelf and upper slope, 1973–93, and natural and anthropogenic environmental factors. Incidence of fin erosion and pseudotumors among Dover sole is summarized.

The Los Angeles County Sanitation Districts (LACSD) serves the sewage treatment and solid waste management needs of 5 million people in 79 cities, including over 70,000 commercial establishments and industries. Each day, 1.25×10^6 meters^3 (330 million gallons) of partial secondary treated wastewater are discharged into the ocean off Palos Verdes. Municipal wastewaters have been discharged off Palos Verdes for 55 years. The submarine outfall system extends about 3 km offshore from Whites Point to a water depth of 60 m (figure 1). Fish trawl surveys are a Los Angeles Regional Water Quality Control Board permit requirement for the discharge of treated wastewaters.

The demersal fish fauna of the Palos Verdes Shelf and slope was first surveyed in 1911 (Ulrey and Greeley 1928). Palos Verdes trawl sampling was initiated in the early 1970s. The sampling grid consisted of up to 7 cross-shore transects (T0–T6), with stations at 3 depths (23, 61, and 137 m). Seventy-six trawls were taken from May 1970 to February 1972 (SCCWRP 1973), and an additional 29 were taken from May 1972 to March 1973. This 21-station grid was used only until May 1977; thereafter a subset of 12 stations was sampled (figure 1). In fall 1971, net size (headrope length and mesh) and trawl speed were changed (SCCWRP 1973; Mearns and Allen

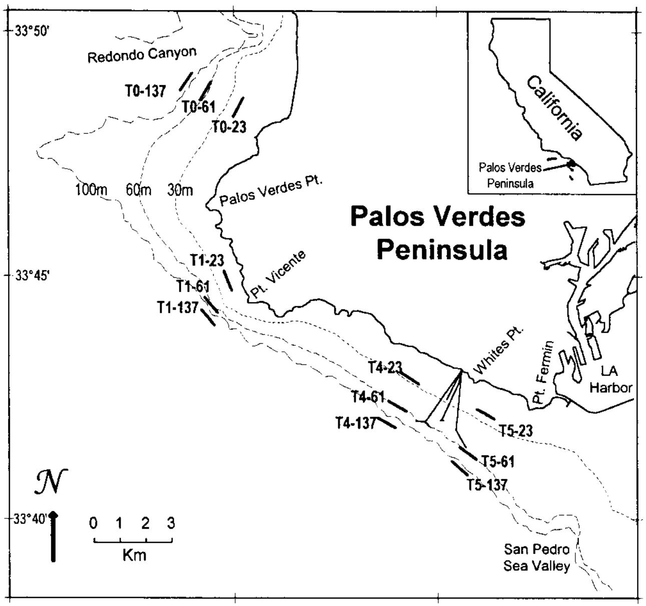


Figure 1. Stations sampled by trawl during Palos Verdes monitoring surveys, 1973–93.

[Manuscript received January 15, 1995.]

1978). Therefore we do not use the entire Palos Verdes trawl database in this report because of changes in sampling methods and stations.

This report summarizes LACSD's semiannual and quarterly trawl surveys, 1973–93, at 12 stations (figure 1), along 4 cross-shore transects and 3 isobaths: 23 m (the inner shelf), 61 m (the midshelf), and 137 m (the upper slope). Characteristic fish assemblages have been reported at each of these depths (Mearns et al. 1976; Allen 1982; LACSD 1993; MBC Applied Environmental Sciences and Applied Management and Planning Group 1993; Cross and Allen 1993).

BACKGROUND

The following discussions of environmental conditions and historic fish communities and external anomalies are important background material for the study of long-term changes in Palos Verdes fish assemblages. Methods and results for LACSD's Palos Verdes trawl surveys follow. In the Discussion section, life-history traits for individual fish species will be reviewed with the catch data, and patterns among similar types of species groups will be reported.

Environmental Conditions

The marine environment and its fish assemblages are very dynamic, and much of the variation is not easily explained. We review seven types of environmental factors that can profoundly influence fish recruitment, abundance, and succession. Natural phenomena predominate. Some of the most extreme oceanographic events of the past century occurred during the last two decades. Also, we hypothesize that changes in Palos Verdes fish assemblages demonstrate recovery as a result of decreasing emissions from the LACSD ocean outfalls and the associated ecological improvements.

1. Water temperature and El Niño events. Temperature anomalies measured off Palos Verdes, 1964–93, reveal the major warming (El Niño) trends of 1972–73, 1976–77, 1981–83, 1987, and 1992–93 (figure 2). Waters were considerably cooler in the 1970s than in the 1980s and early 1990s. During El Niño events, species with

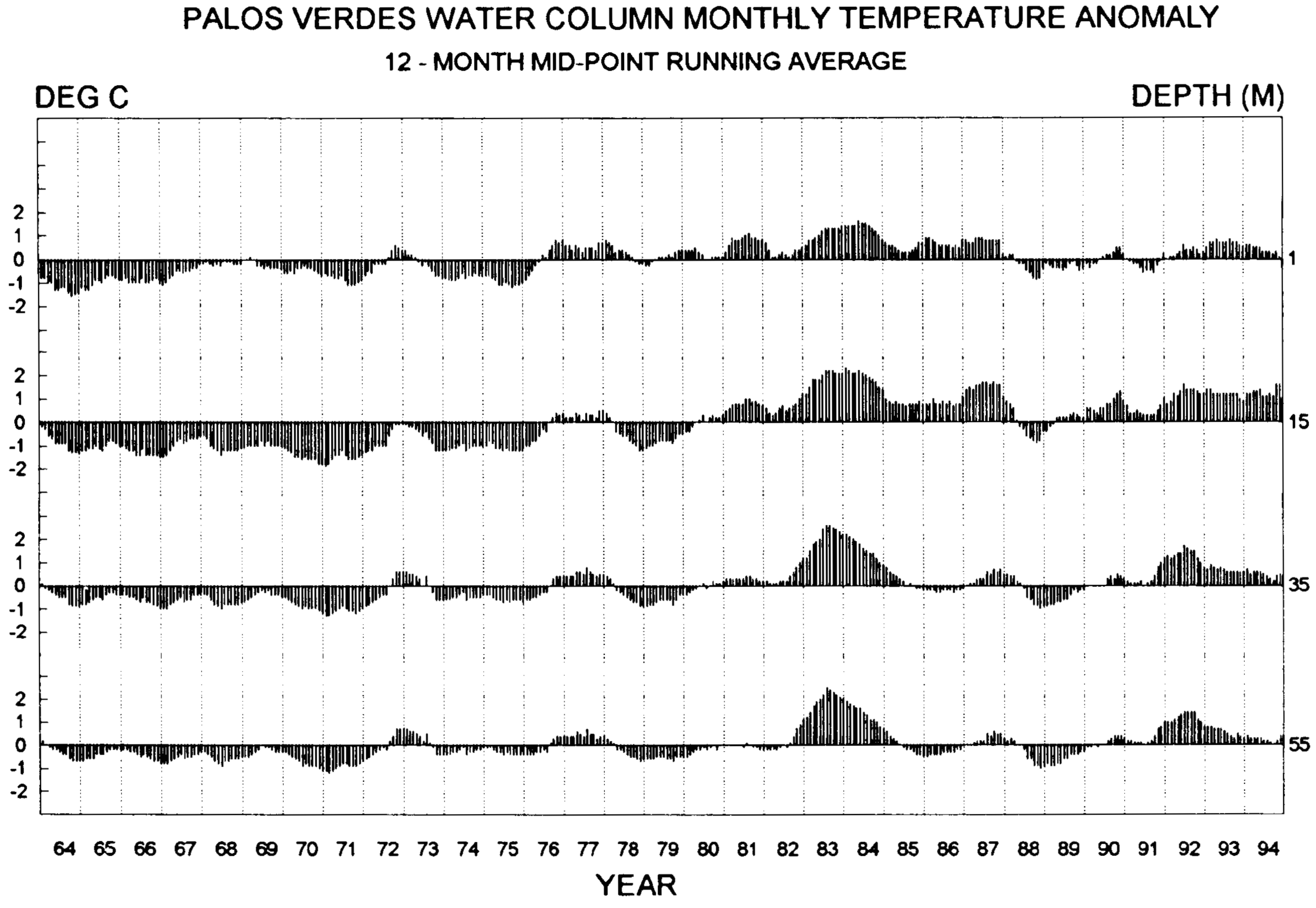


Figure 2. Palos Verdes water column monthly temperature anomaly at water depths 1–55 m from a 60-m near-outfall site. Depth-specific temperature anomaly (12-month midpoint running average) is on left axis; water column depths are on right of figure.

southern distributions are more abundant; shallow-water species occur in deeper waters; and some species with northern distributions become more rare (e.g., Radovich 1961; Mearns 1988). Carlisle (1969) noted major warm water/cold water differences in trawl catches during and after the 1957–59 El Niño. Also, biological productivity in surface waters decreases during El Niño events (e.g., Petersen et al. 1986). Warmer or cooler waters influence spawning, recruitment, and faunal composition for several years (Mearns et al. 1980; Love et al. 1986). Mearns (1979) and Love et al. (1986) report smaller otter trawl fish catches during warm-water events. The major 1982–83 El Niño was accompanied by severe storms, which altered marine habitats substantially (Dayton and Tegner 1984). In 1988, a more intense storm struck the coast, without an associated El Niño (Seymour 1989).

*2. **Movement of water masses.*** Variable currents and water masses influence the recruitment and distribution of organisms (e.g., larval fish, Smith and Moser 1988). Also, more northerly species can live in the cooler waters of upwelling areas south of headlands. The Redondo Canyon brings deeper, colder-water species nearer shore, and its walls, currents, and particle flux influence biota.

*3. **Topography.*** Demersal fish have habitat preferences. The Palos Verdes Shelf is relatively narrow and steep (2–5 km, 1.7–5.5 degrees); the shelf break is at a water depth of 75^+ m; and its steeper slope (9–12 degrees) is irregular (figure 1; Emery 1960). The Redondo Canyon to the northwest and the San Pedro Sea Valley to the southeast separate Palos Verdes from adjacent shelves. Silt sediments predominate over much of the shelf and slope, grading to sand in the nearshore and to sandy silt past Palos Verdes Point and at the outfalls. The rocky inshore area is extensive, and outcrops are common northwest of the peninsula.

*4. **Environmental quality.*** Water clarity over the Palos Verdes Shelf has increased since the 1970s (Conversi and McGowan 1994). Quality of surface sediments has varied greatly both spatially and temporally. Remarkable reductions in distributions of contaminants, organic matter, and hydrogen sulfide between the 1970s and 1990s relate primarily to improved effluent quality discharged through LACSD's ocean outfalls (figure 3, chromium measured in 1985 at most distant and deepest sites; Stull 1995). However, bioaccumulation of historically discharged chlorinated hydrocarbons (specifically DDT and PCBs) is still a concern on Palos Verdes. A partly buried contaminant reservoir persists in Palos Verdes Shelf and slope sediments; DDT and PCBs are bioaccumulated by marine organisms (Mearns et al. 1991; Stull 1995).

*5. **Food availability.*** Sediment-dwelling benthic infauna, especially crustaceans and polychaetes, are favored foods for many demersal fish (Allen 1982). As surface sediment contamination declined over the past two decades, the distribution and composition of benthic assemblages changed dramatically (figure 3; Stull 1995). For example, benthic species diversity, numbers of arthropods, and annelid biomass increased, and mollusc biomass decreased. Pelagic and nektonic benthopelagic prey are favored by some demersal fish, and their availability has also fluctuated (figure 4). Because of the 1982–83 El Niño, extremely large numbers of crustaceans temporarily occupied the Palos Verdes Shelf and slope. Trawl catches of *Pleuroncodes planipes* (pelagic red crab) were highest in 1984 and 1985; the annual average catch from a 10-minute otter trawl at T4-137 in 1985 was 22,000. *Sicyonia ingentis* (ridgeback prawn) densities were highest from 1983 to 1986, with annual 10-minute trawl averages of 14,000 at T0-137 and over 10,000 at T5-137.

*6. **Kelp coverage.*** Kelp beds provide food and habitat to fish. Palos Verdes *Macrocystis pyrifera* virtually disappeared by the late 1950s, in part because of wastewater discharge (State Water Quality Control Board 1964). Local recovery began slowly in the mid-1970s, and, since 1978, growth and coverage have been extensive except after severe coastal storms in 1983 and 1988 (Meistrell and Montagne 1983; Wilson and Togstadt 1983; LACSD 1993).

*7. **Daily and seasonal patterns.*** Activity patterns vary daily (more fish are caught in night trawls on Palos Verdes; LACSD 1983) and seasonally (e.g., Dover sole feeds on the shelf in summer and reproduces on the slope in winter; Hagerman 1952; Cross 1985).

Community Structure and Function

In the early 1970s the Palos Verdes demersal fish fauna showed distinct effects from wastewater discharge, including low numbers of species, diversity, abundance, and biomass in the immediate vicinity of the outfalls (Mearns et al. 1976; Allen 1977). In addition, important members of southern California fish assemblages were missing (as in Santa Monica Bay; Carlisle 1969), and diseases such as fin erosion were common in some species.

Allen (1982) developed a model of the functional structure of the demersal fish communities of the southern California shelf to aid in studying wastewater effects. The model describes the number and type of feeding guilds represented at different water depths from 10 to 190 m, and the species composition (which species of each guild should dominate at different depths). Feeding guilds include species with similar foraging behavior, based on morphology, diet, and behavior. Palos Verdes trawls were compared to the model to determine which expected species and feeding guilds were present or absent at each depth (LACSD 1988–91). For the most part, the functional structure of Palos Verdes assemblages was similar to structures elsewhere in the bight.

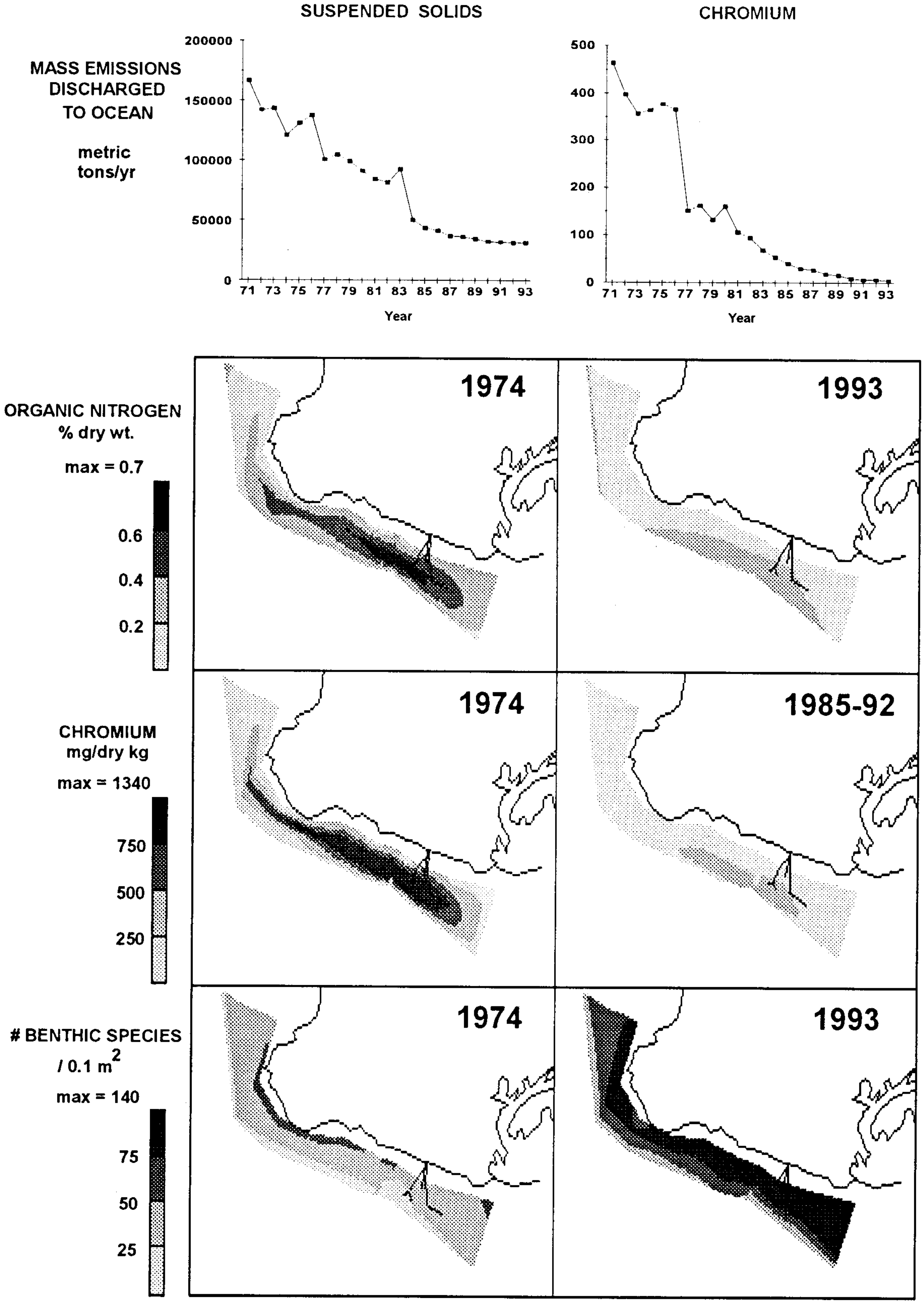


Figure 3. Palos Verdes environmental quality, 1971–93: LACSD effluent emissions of suspended solids and chromium to the ocean; surface-sediment organic nitrogen and chromium concentrations; number of benthic infaunal species per 0.1 m^2.

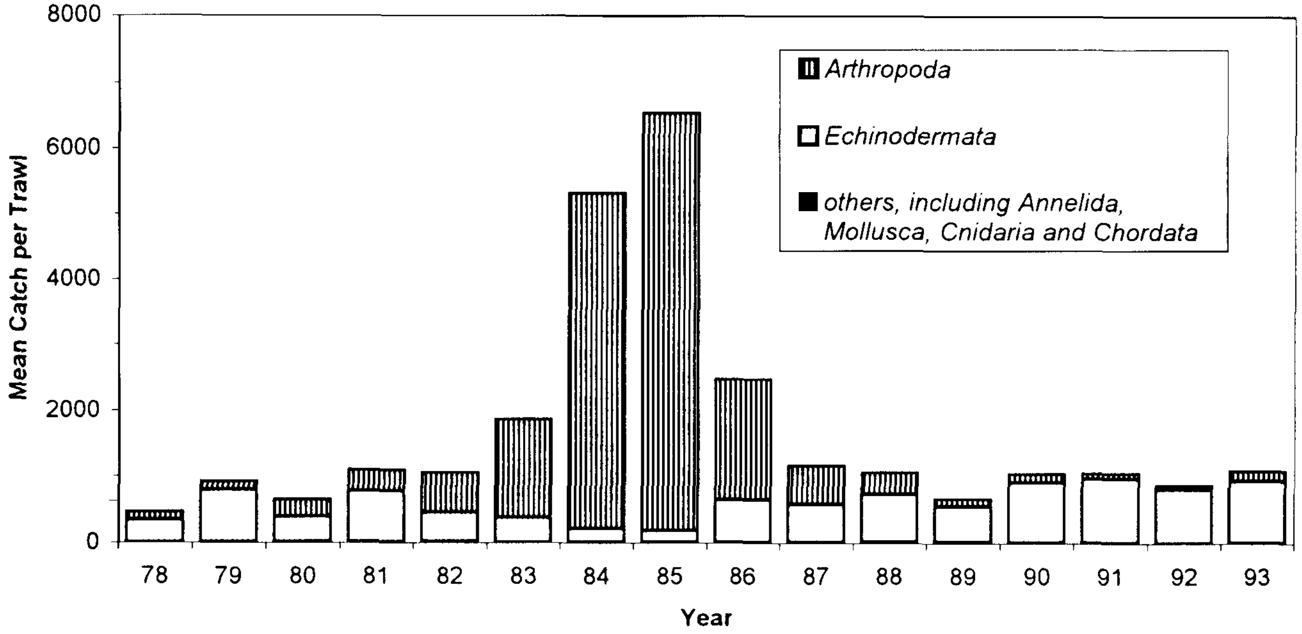


Figure 4. Palos Verdes epibenthic invertebrate abundance, 1978–93. Catch is mean of quarterly 10-minute otter trawls at 12 sites: transects T0, T1, T4, and T5, at depths of 23, 61, and 137 m.

Prager and MacCall (1990) conducted biostatistical modeling of contaminant and climate influences on fish populations of certain Southern California Bight species (northern anchovy, Pacific sardine, Pacific mackerel, Pacific whiting, and California halibut). They could not discern effects of contaminants, but caution that this does not mean that there were no effects. Fish populations are naturally variable, and without multiple events (trends, peaks) it was not statistically possible to distinguish among the numerous potential explanations for changes in abundance or recruitment. Multicollinearity among potential factors was also a complication.

External Anomalies

Dover sole (*Microstomus pacificus*) is typically a deep-water species. Hunter et al. (1990) report 98% of the spawning biomass in central California live in cold, low-oxygen, slope depths (640–1,006 m). Juveniles settle on the shelf and gradually move downslope over their lifetime. Dover sole also migrate seasonally, to the shelf in summer and slope in winter. They feed on benthos (MMS 1987) and may live over 50 years (Hunter et al. 1990).

Among Palos Verdes demersal fish, Dover sole had the greatest frequency of external anomalies, most commonly fin erosion and epidermal pseudotumors. Cross (1988) found fin erosion more common nearer the outfall; 25% to over 30% of the Dover sole exhibited the syndrome in 1971–83. The etiology of fin erosion is unknown, but it has been hypothesized to be related to sediment contamination. Sherwood and Mearns (1977) initiated fin erosion in juvenile Dover sole exposed to contaminated sediments in the laboratory for 13 months.

Epidermal pseudotumors are hypothesized to be a parasitic protozoan condition characterized by unusual mitotic figures (Myers 1981, in press). They are not neoplasms. Per Myers, all fish species with "X-cell epidermal pseudotumors" are in contact with bottom sediments during a large part of their lives. Pseudotumors are most common among flatfish less than a year in age. They are found at both polluted and unpolluted sites. Cross (1988) found frequency higher nearer the LACSD outfalls than elsewhere on Palos Verdes. Incidence as high as 50% was found among juvenile flatfish in the Bering Sea, far from pollutant sources (A. J. Mearns, NOAA, pers. comm., 1990). Younger or previously affected individuals with an immunologic history are more susceptible. The syndrome produces tumorlike lesions on skin, gills, and pseudobranchial glands. Myers postulates that the protozoa exist in marine sediments and that infestation is by contact or feeding. Amoebae morphologically similar to the X-cell are widely distributed.

METHODS

The sampling grid of 12 stations includes 4 transects (T0, T1, T4, and T5), perpendicular to shore and separated by 5 to 8 km, each with 3 water depths (23, 61, and 137 m; figure 1).

Sampling was done with an otter trawl with a 7.6-m headrope, 3.8-cm (stretch) body mesh, and 1.3-cm (stretch) cod-end mesh. The trawl was towed on bottom along the isobath of each station for 10 min at approximately 1 m/sec, thus traversing about 0.6 km. Fish captured during each tow were identified, counted, measured to the nearest cm (standard length for bony fish and total length for cartilaginous fish), examined for external anomalies, and weighed (composites of all individuals of a species) to the nearest 0.1 kg.

RESULTS

Species captured, mean catches, and numbers of occurrences in 1973–93 Palos Verdes trawls are listed in table 1. Common names derive from Robins (1991). Demersal fish populations were highly variable over the 21 years and 73 surveys (876 trawls total).

TABLE 1
Palos Verdes Demersal Fish, 1973–93: All Species Taken, Mean Catches, and Number of Occurrences (Total Number of Fish Taken in 21 Years Was 235,254)

Family name	Scientific name	Common name[a]	Mean number per trawl[b]	% of total abundance	Number of occurrences[c]
Chimaeridae	*Hydrolagus colliei*	Spotted ratfish	1.7	0.05%	51
Heterodontidae	*Heterodontus francisci*	Horn shark	0.2	0.01%	9
Torpedinidae	*Torpedo californica*	Pacific electric ray	0.7	0.01%	49
Rhinobatidae	*Platyrhinoidis triseriata*	Thornback	1.3	0.01%	70
Rajidae	*Raja inornata*	California skate	1.6	0.01%	81
Myliobatidae	*Myliobatis californica*	Bat ray	0.7	0.01%	45
Engraulidae	*Engraulis mordax*	Northern anchovy	18.0	0.56%	19
Argentinidae	*Argentina sialis*	Pacific argentine	5.3	0.17%	88
Synodontidae	*Synodus lucioceps*	California lizardfish	66.7	2.07%	396
Moridae	*Physiculus rastrelligger*	Hundred-fathom codling	0.2	0.01%	9
Gadidae	*Merluccius productus*	Pacific hake	16.8	0.52%	112
Ophidiidae	*Chilara taylori*	Spotted cusk-eel	3.7	0.12%	138
	Ophidion scrippsae	Basketweave cusk-eel	0.2	0.01%	7
Batrachoididae	*Porichthys myriaster*	Specklefin midshipman	1.4	0.01%	76
	Porichthys notatus	Plainfin midshipman	242.9	7.54%	511
Scorpaenidae	*Scorpaena guttata*	California scorpionfish	33.8	1.05%	414
	Sebastes sp.	Unidentified rockfish	0.4	0.01%	15
	Sebastes auriculatus	Brown rockfish	0.5	0.01%	3
	Sebastes chlorostictus	Greenspotted rockfish	1.1	0.01%	31
	Sebastes crameri	Darkblotched rockfish	0.9	0.01%	28
	Sebastes dalli	Calico rockfish	89.9	2.79%	182
	Sebastes diploproa	Splitnose rockfish	132.0	4.10%	261
	Sebastes elongatus	Greenstriped rockfish	3.1	0.10%	105
	Sebastes goodei	Chilipepper	1.2	0.01%	30
	Sebastes hopkinsi	Squarespot rockfish	0.9	0.01%	26
	Sebastes jordani	Shortbelly rockfish	40.6	1.26%	106
	Sebastes levis	Cowcod	1.5	0.01%	56
	Sebastes miniatus	Vermilion rockfish	4.3	0.13%	60
	Sebastes paucispinis	Bocaccio	3.2	0.10%	66
	Sebastes rosenblatti	Greenblotched rockfish	19.5	0.61%	230
	Sebastes rubrivinctus	Flag rockfish	0.3	0.01%	12
	Sebastes saxicola	Stripetail rockfish	289.6	8.99%	452
	Sebastes semicinctus	Halfbanded rockfish	4.9	0.15%	80
	Sebastes serranoides	Olive rockfish	0.2	0.01%	11
	Sebastolobus alascanus	Shortspine thornyhead	4.0	0.12%	67
Anoplopomatidae	*Anoplopoma fimbria*	Sablefish	4.0	0.12%	52
Hexagrammidae	*Zaniolepis frenata*	Shortspine combfish	16.6	0.52%	205
	Zaniolepis latipinnis	Longspine combfish	39.4	1.22%	260
Cottidae	*Chitonotus pugetensis*	Roughback sculpin	19.4	0.60%	176
	Icelinus quadriseriatus	Yellowchin sculpin	222.6	6.91%	287
	Radulinus asprellus	Slim sculpin	0.2	0.01%	9
Agonidae	*Bathyagonus pentacanthus*	Bigeye poacher	0.2	0.01%	4
	Odontopyxis trispinosa	Pygmy poacher	2.3	0.07%	93
	Xeneretmus latifrons	Blacktip poacher	22.6	0.70%	204
	Xeneretmus triacanthus	Bluespotted poacher	0.6	0.01%	27
Serranidae	*Paralabrax clathratus*	Kelp bass	0.2	0.01%	3
	Paralabrax nebulifer	Barred sand bass	2.7	0.08%	80
Malacanthidae	*Caulolatilus princeps*	Ocean whitefish	0.5	0.01%	8
Sciaenidae	*Genyonemus lineatus*	White croaker	132.6	4.12%	147
	Seriphus politus	Queenfish	8.0	0.25%	29
Embiotocidae	*Cymatogaster aggregata*	Shiner perch	33.0	1.02%	75
	Embiotoca jacksoni	Black perch	1.5	0.01%	40
	Hyperprosopon argenteum	Walleye surfperch	0.6	0.01%	9
	Hypsurus caryi	Rainbow seaperch	3.6	0.11%	38

(Table 1 continues)

[a] Common names derive from Robins 1991.
[b] Mean of 876 trawls in 73 surveys (2/yr in 1973–77, 3/yr in 1978, and 4/yr in 1979–93).
[c] In 876 trawls.

TABLE 1 (continued)
Palos Verdes Demersal Fish, 1973–93: All Species Taken, Mean Catches, and Number of Occurrences (Total Number of Fish Taken in 21 Years Was 235,254)

Family name	Scientific name	Common name[a]	Mean number per trawl[b]	% of total abundance	Number of occurrences[c]
Embiotocidae	*Phanerodon furcatus*	White seaperch	6.7	0.21%	61
	Rhacochilus toxotes	Rubberlip seaperch	0.4	0.01%	8
	Rhacochilus vacca	Pile perch	1.7	0.05%	54
	Zalembius rosaceus	Pink seaperch	38.2	1.19%	250
Pomacentridae	*Chromis punctipinnis*	Blacksmith	0.2	0.01%	2
Zoarcidae	*Lycodes cortezianus*	Bigfin eelpout	0.2	0.01%	9
	Lycodopsis pacifica	Blackbelly eelpout	94.0	2.92%	289
Uranoscopidae	*Kathetostoma averruncus*	Smooth stargazer	0.7	0.01%	35
Gobiidae	*Lepidogobius lepidus*	Bay goby	2.6	0.08%	80
Stromateidae	*Peprilus simillimus*	Pacific pompano	0.5	0.01%	13
Bothidae	*Citharichthys fragilis*	Gulf sanddab	39.3	1.22%	257
	Citharichthys sordidus	Pacific sanddab	258.4	8.02%	520
	Citharichthys stigmaeus	Speckled sanddab	202.8	6.30%	311
	Citharichthys xanthostigma	Longfin sanddab	12.7	0.39%	108
	Hippoglossina stomata	Bigmouth sole	20.8	0.64%	397
	Paralichthys californicus	California halibut	13.5	0.42%	297
	Xystreurys liolepis	Fantail sole	11.0	0.34%	272
Pleuronectidae	*Eopsetta exilis*	Slender sole	264.5	8.21%	296
	Eopsetta jordani	Petrale sole	0.4	0.01%	27
	Errex zachirus	Rex sole	54.8	1.70%	204
	Hypsopsetta guttulata	Diamond turbot	1.0	0.01%	57
	Microstomus pacificus	Dover sole	561.2	17.42%	504
	Pleuronectes vetulus	English sole	11.7	0.36%	270
	Pleuronichthys coenosus	C-O sole	5.8	0.18%	141
	Pleuronichthys decurrens	Curlfin sole	10.8	0.34%	165
	Pleuronichthys ritteri	Spotted turbot	4.1	0.13%	88
	Pleuronichthys verticalis	Hornyhead turbot	36.0	1.12%	436
Soleidae	*Symphurus atricauda*	California tonguefish	64.9	2.01%	374

Rare Species Accounting for <0.01% of Total Catch and Taken in <10 of 876 Trawls

Family name	Scientific name	Common name[a]	Family name	Scientific name	Common name[a]
Myxinidae	*Eptatretus stouti*	Pacific hagfish	Hexagrammidae	*Zaniolepis* sp.	Unidentified combfish
Scyliorhinidae	*Cephaloscyllium ventriosum*	Swell shark	Cottidae	*Icelinus cavifrons*	Pit-head sculpin
Carcharhinidae	*Mustelus californicus*	Gray smoothhound		*Icelinus tenuis*	Spotfin sculpin
	Mustelus henlei	Brown smoothhound		*Leptocottus armatus*	Pacific staghorn sculpin
Squalidae	*Squalus acanthias*	Spiny dogfish		*Orthonopias triacis*	Snubnose sculpin
Squatinidae	*Squatina californica*	Angel shark		*Radulinus boleoides*	Darter sculpin
Rhinobatidae	*Rhinobatos productus*	Shovelnose guitarfish		*Scorpaenichthys marmoratus*	Cabezon
Rajidae	*Bathyraja interrupta*	Sandpaper skate	Agonidae	*Agonopsis sterletus*	Southern spearnose poacher
	Raja binoculata	Big skate		*Agonopsis vulsa*	Northern spearnose poacher
Urolophidae	*Urolophus halleri*	Round stingray	Percichthyidae	*Stereolepis gigas*	Giant sea bass
Sternoptychidae	*Argyropelecus sladeni*	Silvery hatchetfish	Serranidae	*Pronotogrammus multifasciatus*	Threadfin bass
Myctophidae	*Stenobrachius leucopsarus*	Northern lampfish	Carangidae	*Trachurus symmetricus*	Jack mackerel
	Triphoturus mexicanus	Mexican lampfish	Sciaenidae	*Sciaenid*	Unidentified croaker
Bythitidae	*Brosmophycis marginata*	Red brotula		*Altractoscion nobilis*	White seabass
Ogcocephalidae	*Zalieutes elater*	Roundel batfish		*Menticirrhus undulatus*	California corbina
Syngnathidae	*Syngnathus* sp.	Unidentified pipefish	Kyphosidae	*Girella nigricans*	Opaleye
	Syngnathus exilis	Barcheek pipefish	Bathymasteridae	*Rathbunella hypoplecta*	Stripedfin ronquil
Scorpaenidae	*Sebastes babcocki*	Redbanded rockfish	Zoarcidae	*Eucryphycus californicus*	Persimmon eelpout
	Sebastes carnatus	Gopher rockfish		*Lyconema barbatum*	Bearded eelpout
	Sebastes caurinus	Copper rockfish	Stichaeidae	*Stichaeid*	Unidentified prickleback
	Sebastes constellatus	Starry rockfish		*Plectobranchus evides*	Bluebarred prickleback
	Sebastes eos	Pink rockfish	Anarhichadidae	*Anarrhichthys ocellatus*	Wolf-eel
	Sebastes macdonaldi	Mexican rockfish	Clinidae	*Heterostichus rostratus*	Giant kelpfish
	Sebastes mystinus	Blue rockfish		*Neoclinus blanchardi*	Sarcastic fringehead
	Sebastes rastrelliger	Grass rockfish	Gobiidae	*Coryphopterus nicholsi*	Blackeye goby
	Sebastes rosaceus	Rosy rockfish	Scombridae	*Scomber japonicus*	Chub mackerel
	Sebastes umbrosus	Honeycomb rockfish	Bothidae	*Citharichthys* sp.	Unidentified sanddab
Hexagrammidae	*Hexagrammos decagrammus*	Kelp greenling	Pleuronectidae	*Pleuronectes bilineatus*	Rock sole
	Ophiodon elongatus	Lingcod		*Pleuronichthys* sp.	Unidentified turbot
	Oxylebius pictus	Painted greenling			

[a] Common names derive from Robins 1991.

[b] Mean of 876 trawls in 73 surveys (2/yr in 1973–77, 3/yr in 1978, and 4/yr in 1979–93).

[c] In 876 trawls.

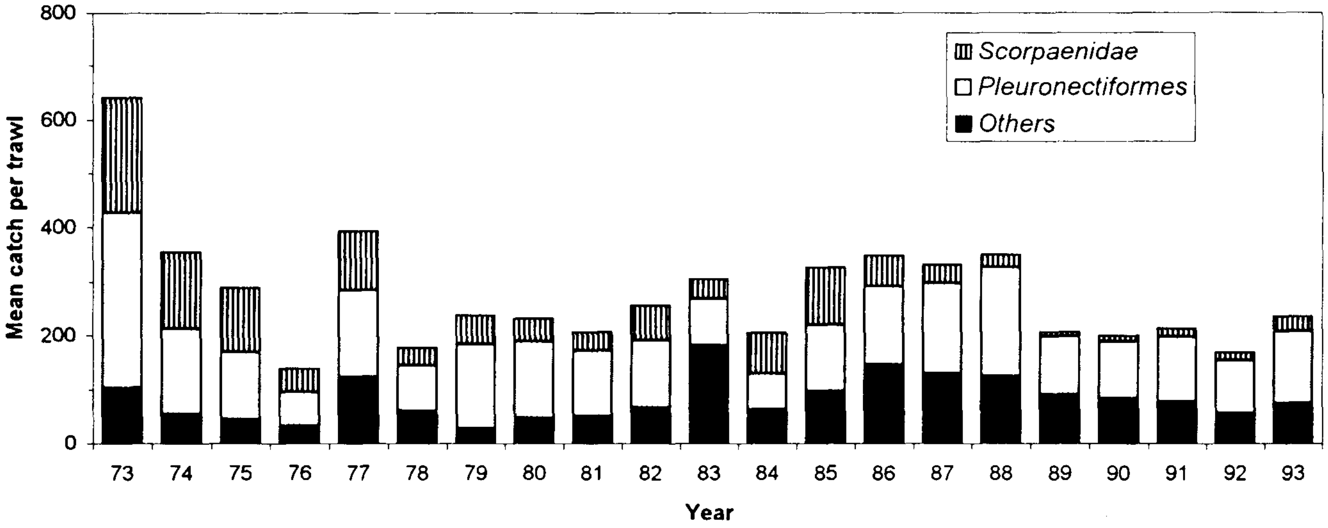


Figure 5. Fish abundance in Palos Verdes trawls, 1973–93. Catch is mean of semiannual or quarterly 10-minute otter trawls at 12 sites: transects T0, T1, T4, and T5 at depths of 23, 61, and 137 m.

Regional History

Pleuronectiformes (flatfish, mostly Pleuronectidae and Bothidae, righteye and lefteye flounders) and Scorpaenidae (scorpionfish, mostly rockfish) dominated the monitored Palos Verdes demersal fish fauna, 1973–93 (figure 5). Mean catch at the 12 sites ranged from 140 in 1976 to 641 in 1973. Flatfish were the most numerous in the 1990s, accounting for 53%–59% of the fish collected; they dominated in all years except 1983–84. The proportion of flatfish increased from 23-m to 137-m water depths. The percentage of rockfish declined over time; they accounted for 4%–12% of the total catch from 1988 to 1993, as compared to over 30% in 1973–76 and 1984–85.

Seven species account for at least 6% of the total number of fish taken in trawls between 1973 and 1993 (table 1): *Microstomus pacificus* (Dover sole, 17%); *Sebastes saxicola* (stripetail rockfish, 9%); *Eopsetta exilis* (slender sole, 8%); *Citharichthys sordidus* (Pacific sanddab, 8%); *Porichthys notatus* (plainfin midshipman, 8%); *Icelinus quadriseriatus* (yellowchin sculpin, 7%); and *Citharichthys stigmaeus* (speckled sanddab, 6%). Together they represent 63% of the 21-year catch. Dominance changed over time.

TABLE 2
Mean Fish Abundance, Biomass, and Number of Species per Trawl, Palos Verdes, 1973–93

	Abundance (mean/trawl)			Biomass (mean kg/trawl)			Species (mean no./trawl)		
Year	23 m	61 m	137 m	23 m	61 m	137 m	23 m	61 m	137 m
1973	538	594	791	5.7	23.9	52.7	10	18	16
1974	197	329	539	2.9	10.5	15.2	10	12	15
1975	125	276	469	2.1	5.6	19.3	8	14	16
1976	37	155	229	2.4	7.2	17.2	7	11	14
1977	179	478	522	13.0	21.6	20.4	13	15	17
1978	44	151	340	6.4	11.7	13.5	8	8	13
1979	99	283	335	6.7	9.0	14.8	11	12	14
1980	77	226	398	3.6	7.7	19.4	7	13	15
1981	71	187	365	8.2	8.9	13.0	9	13	14
1982	133	242	396	8.5	10.9	15.1	10	14	17
1983	199	306	413	19.7	13.9	17.0	13	15	20
1984	45	215	361	4.2	8.0	10.0	9	13	16
1985	156	384	444	8.9	12.8	20.9	11	17	16
1986	101	481	468	10.0	12.3	19.8	10	16	17
1987	148	367	483	12.9	13.2	22.5	11	17	17
1988	100	451	499	9.2	14.2	21.9	10	16	14
1989	77	323	223	8.3	12.8	6.9	9	14	13
1990	61	226	313	8.3	10.9	8.0	10	13	13
1991	66	224	351	5.1	7.7	9.2	9	15	14
1992	39	126	341	4.3	7.1	7.9	8	13	13
1993	58	316	335	5.2	11.8	8.7	9	14	13

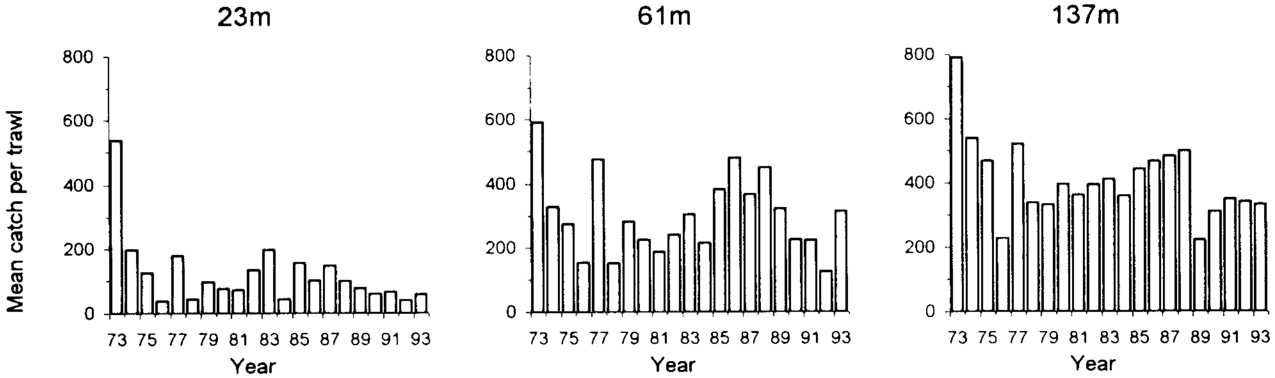


Figure 6. Fish trawled along three Palos Verdes isobaths, 1973–93. Catch is mean of semiannual or quarterly 10-minute otter trawls at 4 sites (T0, T1, T4, and T5) at each depth.

Table 2 lists average abundance, biomass, and number of species at the three depths over time.

Depth and Site Distributions

Fish distributions and abundances are highly depth and habitat dependent. Total abundance increased with depth from 23-m to 137-m isobaths, and abundance and dominance changed over time (figure 6).

In the following material, site-specific distributions are described for abundant fish species, 1973–93 (figures 7–20). The number preceding each species is its rank order in overall abundance for the 21 years. The top 20 fish species and selected other taxa are described. (Data for the other species in table 1 can be provided on request.)

Various life-history traits segregate fish species ecologically. Allen (1982) developed a comprehensive classification of the distributional centers, reproductive modes, refuge requirements, size, morphology, diet, foraging behavior, and relative abundance of southern California soft-bottom fish species. He classifies geographic ranges as warm temperate (San Diegan faunal region, Point Conception to Magdalena Bay); temperate (distribution center north of southern California but ranges to Magdalena Bay); and cold temperate (distribution center north of southern California but ranges to central San Diegan faunal region). Allen (1982) provides detailed specifics, but a brief summary of ranges, feeding habits, refuges (when inactive), and reproductive modes of Palos Verdes dominants is included with the catch histories that follow. The information on life-history traits will be used to show trends in similar types of species groups (Discussion section).

1. *Microstomus pacificus* (Dover sole, figure 7) was the most abundant species trawled off Palos Verdes over the 21 years. It was most common on the slope near the outfalls (T4-137, T5-137) in the 1970s. Numbers declined thereafter. This temperate, upper-slope flatfish is a bottom dweller which stalks benthic infauna such as capitellid polychaetes. When inactive, Dover sole is buried in the sediments. It has pelagic eggs and larvae.

2. *Sebastes saxicola* (stripetail rockfish, figure 7) was a dominant fish at all three depths in the early 1970s. It persisted longer in cooler waters in upper-slope depths (137 m). It was least abundant along the T4 outfall transect, and most common at T0 near Redondo Canyon and at T5-137. At 137 m, catches increased after the 1982–83 El Niño. This temperate, outer-shelf/upper-slope roundfish pursues pelagic prey such as euphausiids. When inactive, the stripetail rockfish is exposed. It has internal eggs and pelagic larvae.

3. *Eopsetta exilis* (slender sole, figure 8) catches at 137 m increased from 1986. It was most abundant near Redondo Canyon (T0-137) and least abundant on transect T4. This cold-temperate, upper-slope flatfish is a bottom dweller which pursues nektonic benthopelagic prey such as shrimp. When inactive, this species buries itself in the sediments. It has pelagic eggs and larvae.

4. *Citharichthys sordidus* (Pacific sanddab, figure 8) has been abundant in 61 and 137 m and nearer the outfall. Smaller catches coincided with El Niño conditions (1976–78, 1983–84, 1989–91). This temperate, outer-shelf/upper-slope flatfish pursues pelagic prey such as euphausiids. When inactive, this species buries itself in the sediments. It has pelagic eggs and larvae.

5. *Porichthys notatus* (plainfin midshipman, figure 9) also prefers outer-shelf/upper-slope habitats, in particular T1-61. Small numbers were caught in the 1970s, and largest catches were at T1-61 following the 1982–83 El Niño. This temperate, outer-shelf/upper-slope roundfish ambushes pelagic prey such as euphausiids. When inactive, its refuge is burial in the sediments. It is nocturnal and has demersal eggs and larvae.

6. *Icelinus quadriseriatus* (yellowchin sculpin, figure 9) peaked at 61 m following the major El Niño (1985–87); it was scarce at T4-61 and common at T1-61. This warm-temperate, outer-shelf roundfish ambushes epibenthic and benthopelagic prey such as gammaridean amphipods.

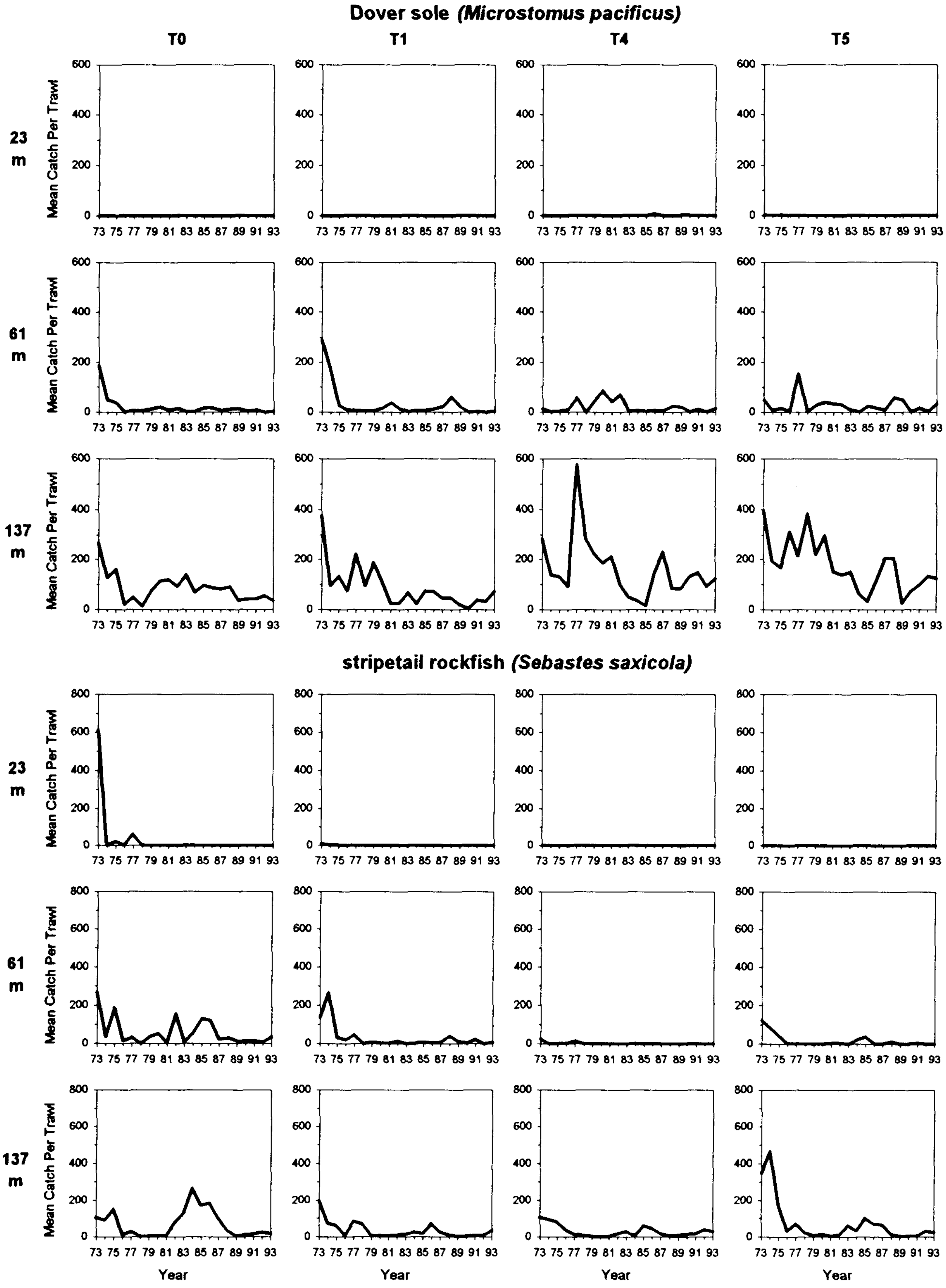


Figure 7. *Microstomus pacificus* (Dover sole) and *Sebastes saxicola* (stripetail rockfish) distributions on Palos Verdes, 1973–93.

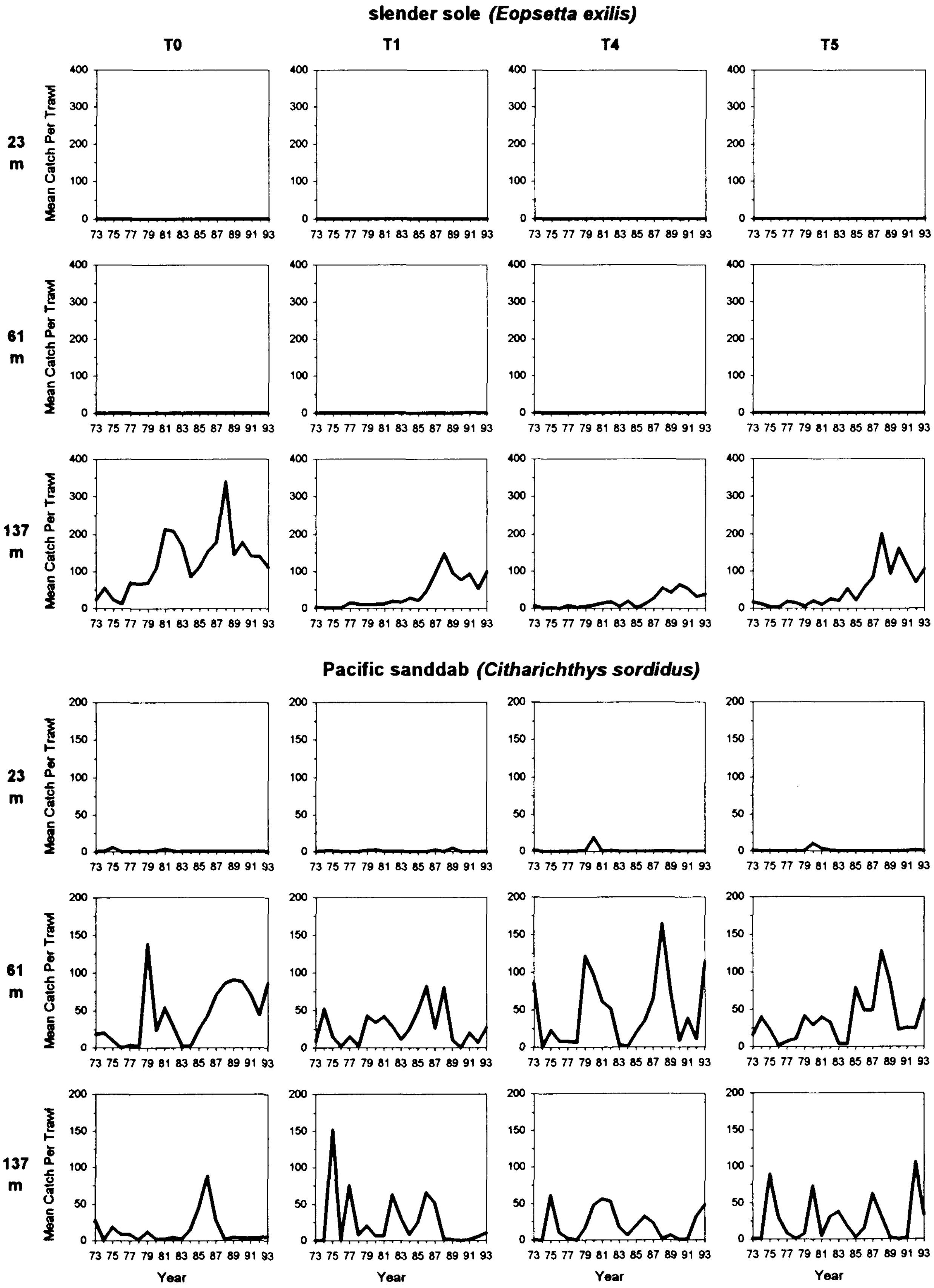


Figure 8. *Eopsetta exilis* (slender sole) and *Citharichthys sordidus* (Pacific sanddab) distributions on Palos Verdes, 1973–93.

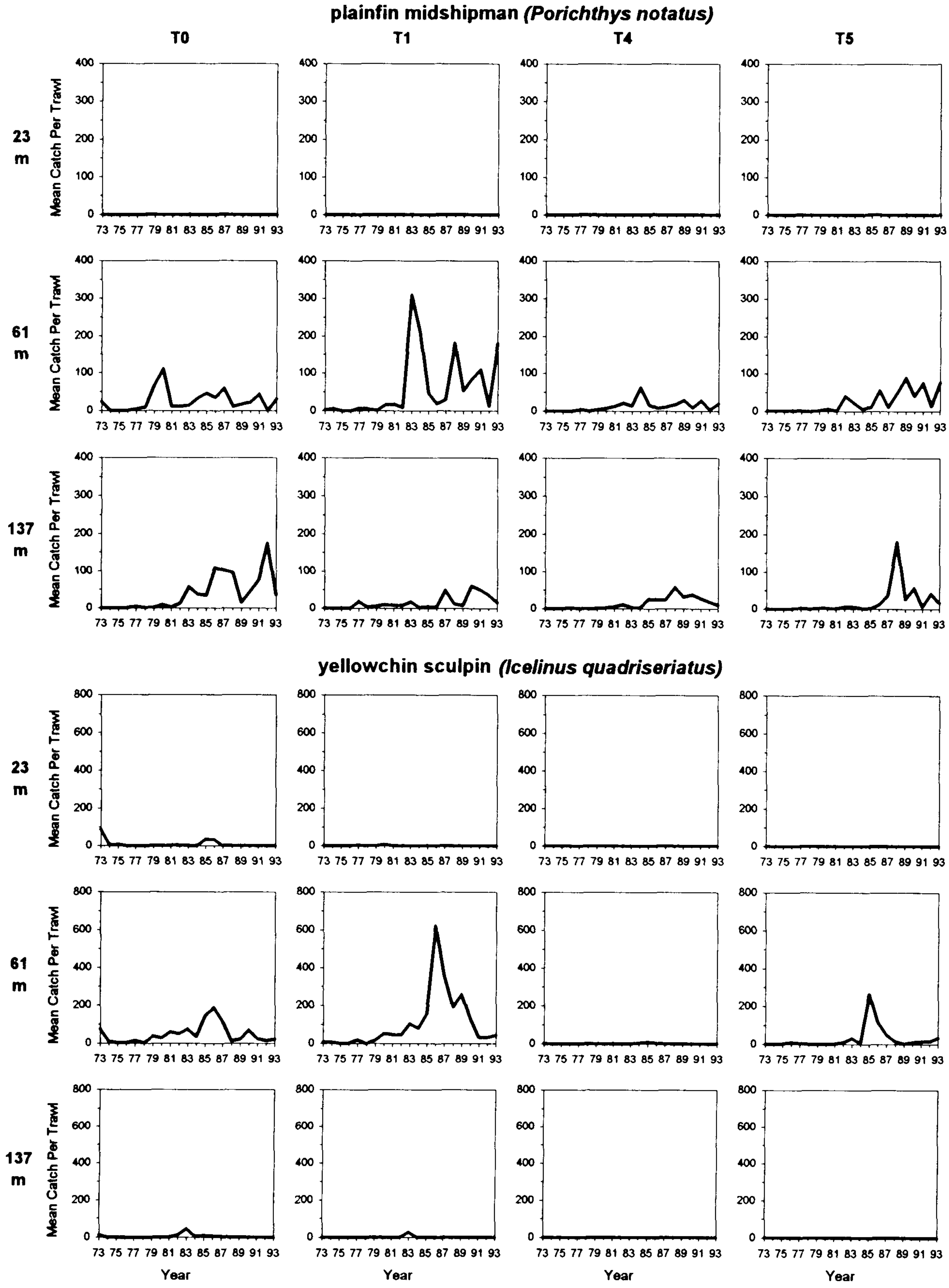


Figure 9. *Porichthys notatus* (plainfin midshipman) and *Icelinus quadriseriatus* (yellowchin sculpin) distributions on Palos Verdes, 1973–93.

When resting, this fish species is exposed. It has demersal eggs and pelagic larvae.

7. *Citharichthys stigmaeus* (speckled sanddab, figure 10) is most common at 23 m (T1-23 and T0-23), and its abundance has decreased substantially since the early 1970s. This temperate, inner-shelf flatfish pursues nekton and benthopelagic organisms such as mysids. When resting, this species is buried in sediments. It has pelagic eggs and larvae.

8. *Genyonemus lineatus* (white croaker, figure 10) is a schooling fish captured sporadically, especially at T4-61 (outfall) and T5-23 and T5-61 (closest to Los Angeles Harbor). Catches were greatest during El Niño events. This temperate, inner-shelf roundfish searches for infauna such as eunicids. Because it is nocturnally active it is most easily caught at night. It has pelagic eggs and larvae. Partyboat and commercial catches of white croaker taken off Palos Verdes are reported in Stull et al. 1987.

9. *Sebastes diploproa* (splitnose rockfish, figure 11) is an upper-slope species, most common at T0-137 and T5-137 and least abundant at T1-137. It decreased in abundance from the early 1970s and was relatively rare from 1986 to 1992. This cold-temperate, upper-slope roundfish species pursues pelagic prey such as euphausiids. At rest, it is exposed. It has internal eggs and pelagic larvae.

10. *Lycodopsis pacifica* (blackbelly eelpout, figure 11) catches are highest at Redondo Canyon T1-137 in El Niño periods. Overall, catches were larger in the 1980s and 1990s than in the 1970s. There was a gradient from north to south along the 137-m isobath. This cold-temperate, upper-slope roundfish searches for epibenthic/benthopelagic prey such as gammarid amphipods. It burrows into sediments. It has demersal eggs and larvae.

11. *Sebastes dalli* (calico rockfish, figure 12) were common in the 1970s at 61 m; populations declined after the 1982–83 El Niño, and they were rare (except at T5-61) in the 1980s and 1990s. This warm-temperate, outer-shelf roundfish pursues pelagic prey such as calanoids. It seeks crevices or is exposed when at rest. Internal eggs and pelagic larvae characterize the species.

12. *Synodus lucioceps* (California lizardfish, figure 12) prefers shelf depths (23-m and 61-m sites); it shows the clearest pattern of high catches during El Niño events (1976–77 and 1982–83), following storm years (e.g., 1988), and at T4-61 and T5-61. This warm-temperate, inner-shelf roundfish ambushes pelagic prey such as anchovies. When inactive, it is buried in sediments. It has pelagic eggs and larvae.

13. *Symphurus atricauda* (California tonguefish, figure 13) has increased steadily at 61 m since the early 1980s, especially at T0-61 and T5-61. Historically, abundances were lower at T4-61 as compared to other 61-m sites. In the 1990s, *Symphurus* catches were not smaller at T4-61. This warm-temperate, outer-shelf flatfish searches for epibenthic/benthopelagic prey such as gammaridean amphipods. At rest it buries itself in sediments. It is nocturnal, and has pelagic eggs and larvae.

14. *Errex zachirus* (rex sole, figure 13) was most abundant in 1973–74, 1979–81, and 1988 at 137 m, especially at T0-137 (Redondo Canyon). It was rare to absent in 1983–84 and 1990–93. This cold-temperate, upper-slope flatfish searches for epibenthic/benthopelagic prey such as gammarid amphipods. When inactive, this species is buried in the sediments. It has pelagic eggs and larvae.

15. *Sebastes jordani* (shortbelly rockfish, figure 14), a cold-temperate, upper-slope neritic roundfish, was more frequent in the 1970s than later. Large numbers were taken at T1-137 in 1985 (1,680 in a single trawl) and 1976 (217 in one trawl).

16. *Zaniolepis latipinnis* (longspine combfish, figure 14) catches were highest at 61 m; they varied considerably. Numbers were lowest nearest the outfall (T4-61) but have increased in the 1990s. This temperate, outer-shelf roundfish pursues epibenthic/benthopelagic prey such as gammarid amphipods. At rest, it is exposed. It has demersal eggs and pelagic larvae.

17. *Citharichthys fragilis* (gulf sanddab, figure 15) were frequently taken at canyon site T0-137, and less frequently off the peninsula face (T1-T5), from 1980. This species is common in the Gulf of California. It is an outer-shelf/upper-slope fish which probably pursues pelagic prey such as euphausiids. When inactive, this species buries itself in the sediments. It has pelagic eggs and larvae.

18. *Zalembius rosaceus* (pink seaperch, figure 15) is common in 61-m catches except at the outfall site (T4-61). This warm-temperate, outer-shelf roundfish searches for epibenthic/benthopelagic prey such as ostracods. At rest it is exposed. It has internal eggs and larvae.

19. *Pleuronichthys verticalis* (hornyhead turbot, figure 16) prefers shelf depths; it was rarest in the 1970s and most common in the mid- to late 1980s, following El Niño. Catches were lower nearer the outfall (T4-61, T5-61). This warm-temperate, inner-shelf flatfish stalks infauna such as polychaete worms (spionids). When inactive, this species is buried in the sediments. It has pelagic eggs and larvae.

20. *Scorpaena guttata* (California scorpionfish, figure 16) was most abundant at 61 m, especially at T4-61. This warm-temperate, outer-shelf roundfish ambushes epibenthic prey such as crabs. It is nocturnal, and at rest adults are usually exposed or in crevices. It has pelagic eggs and larvae.

21. *Cymatogaster aggregata* (shiner perch, figure 17) thrived near the outfall in the 1970s (T4-61, T5-61, T4-23). This cold-temperate, outer-shelf roundfish schools. It pursues pelagic prey such as calanoids. At rest it is exposed. It has internal eggs and larvae.

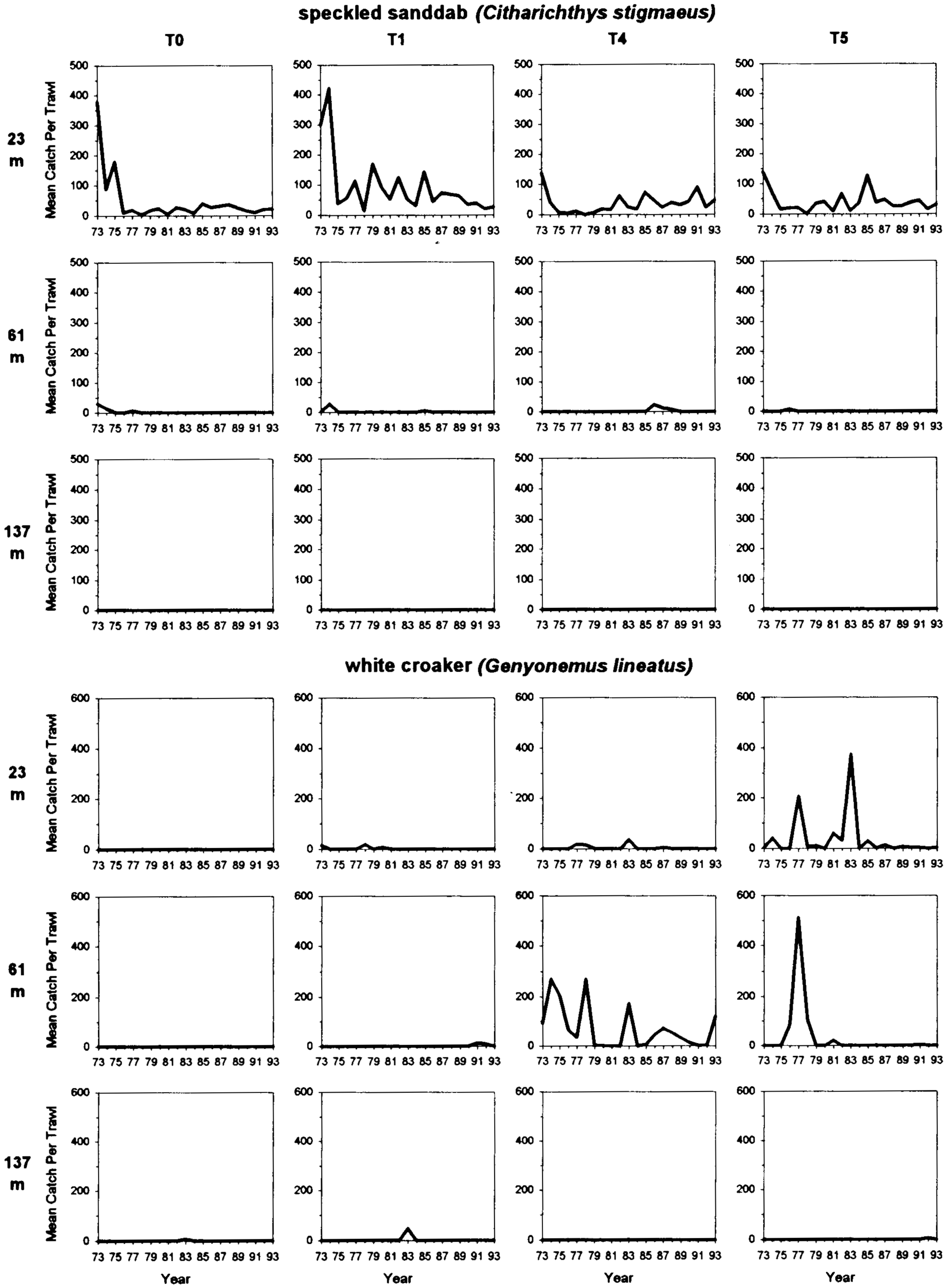


Figure 10. *Citharichthys stigmaeus* (speckled sanddab) and *Genyonemus lineatus* (white croaker) distributions on Palos Verdes, 1973–93.

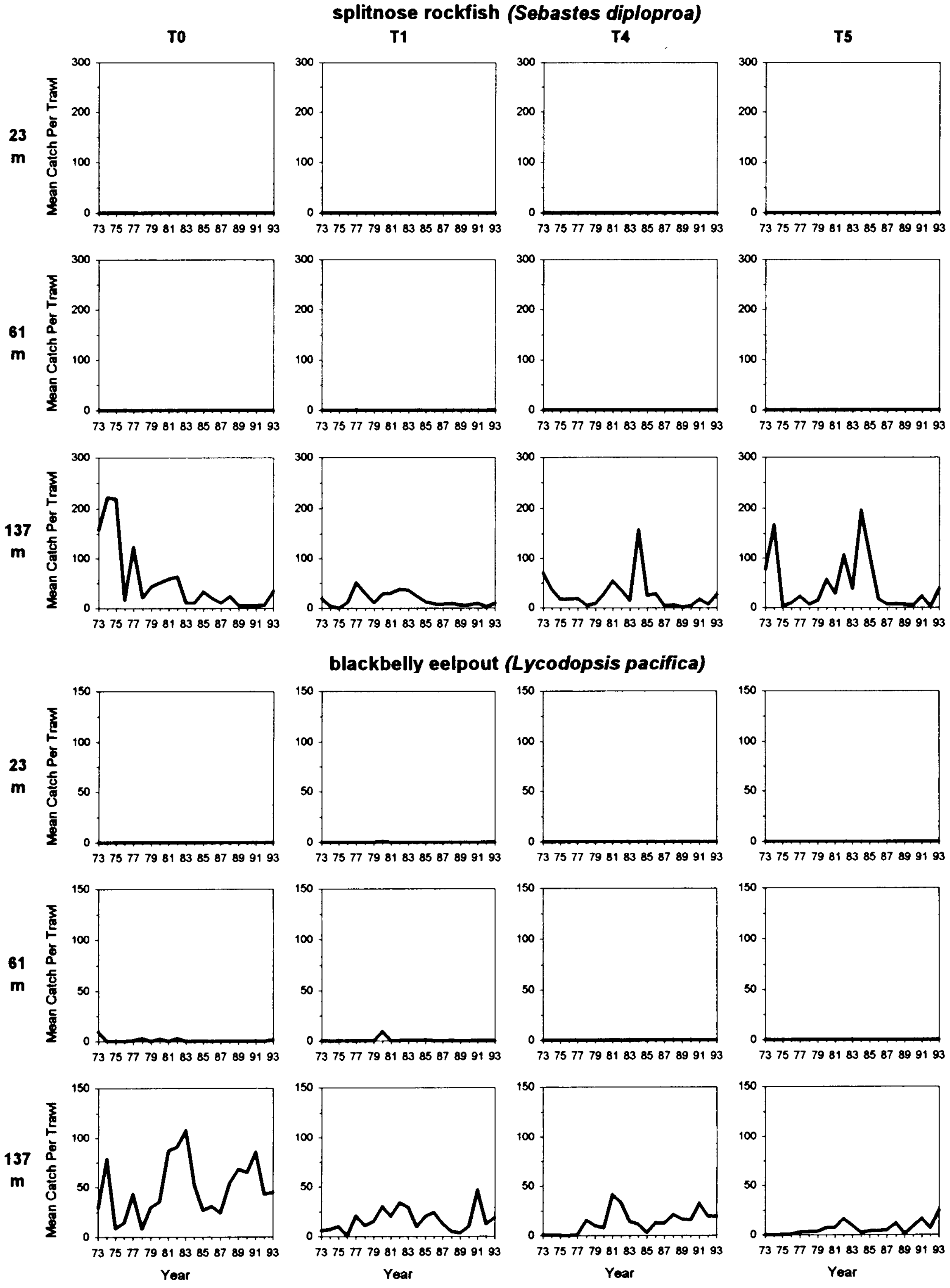


Figure 11. *Sebastes diploproa* (splitnose rockfish) and *Lycodopsis pacifica* (blackbelly eelpout) distributions on Palos Verdes, 1973–93.

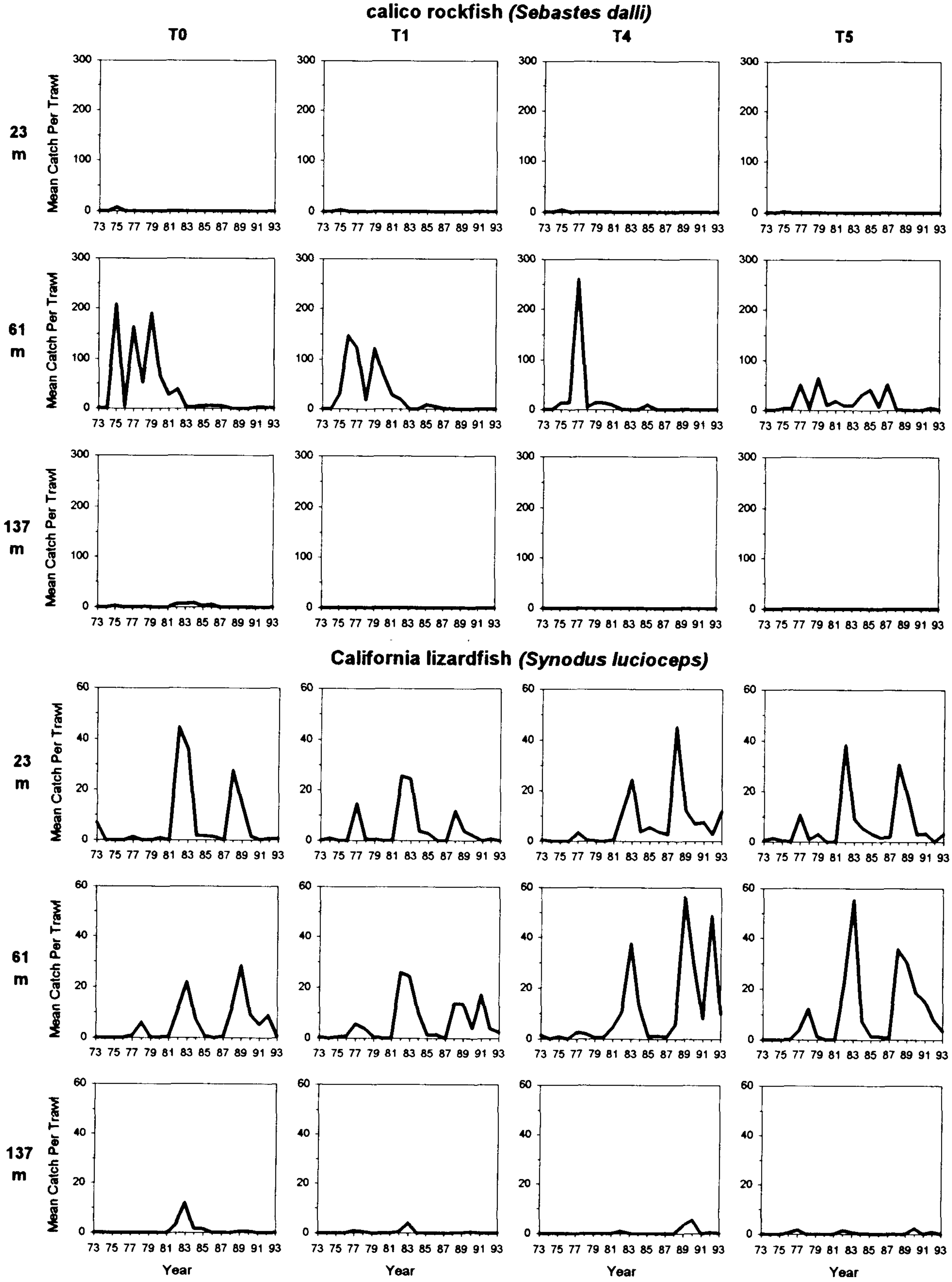


Figure 12. *Sebastes dalli* (calico rockfish) and *Synodus lucioceps* (California lizardfish) distributions on Palos Verdes, 1973–93.

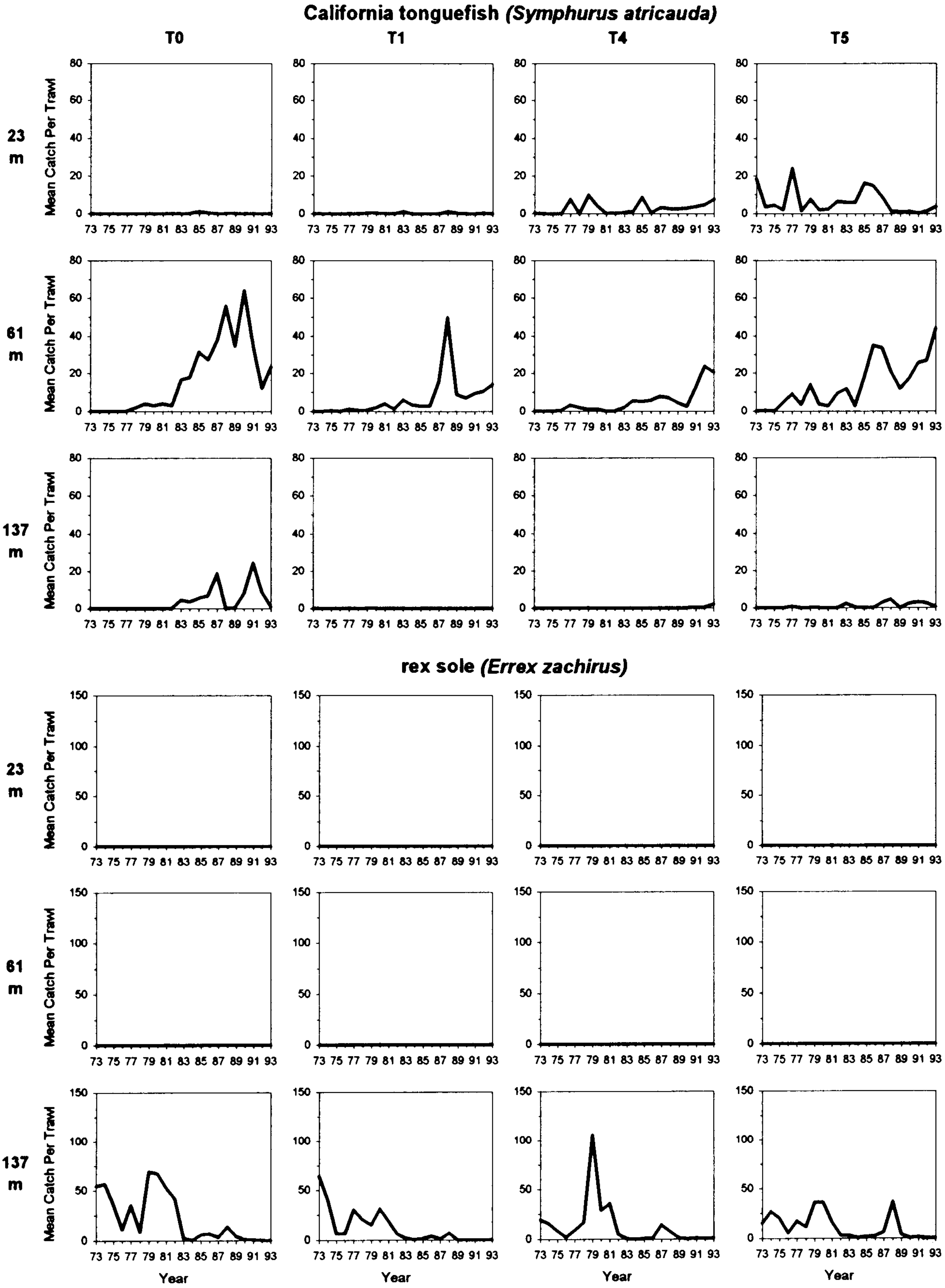


Figure 13. *Symphurus atricauda* (California tonguefish) and *Errex zachirus* (rex sole) distributions on Palos Verdes, 1973–93.

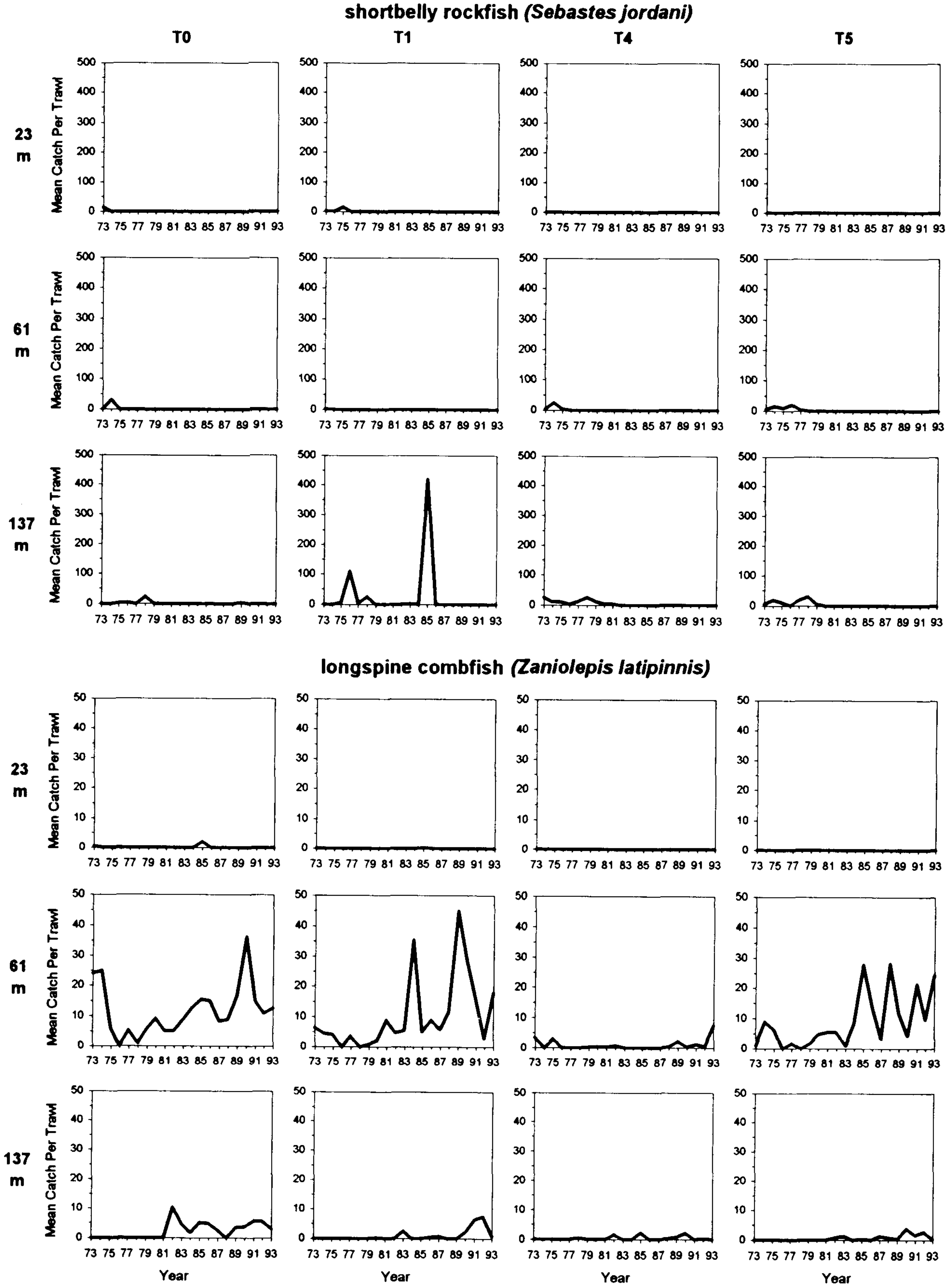
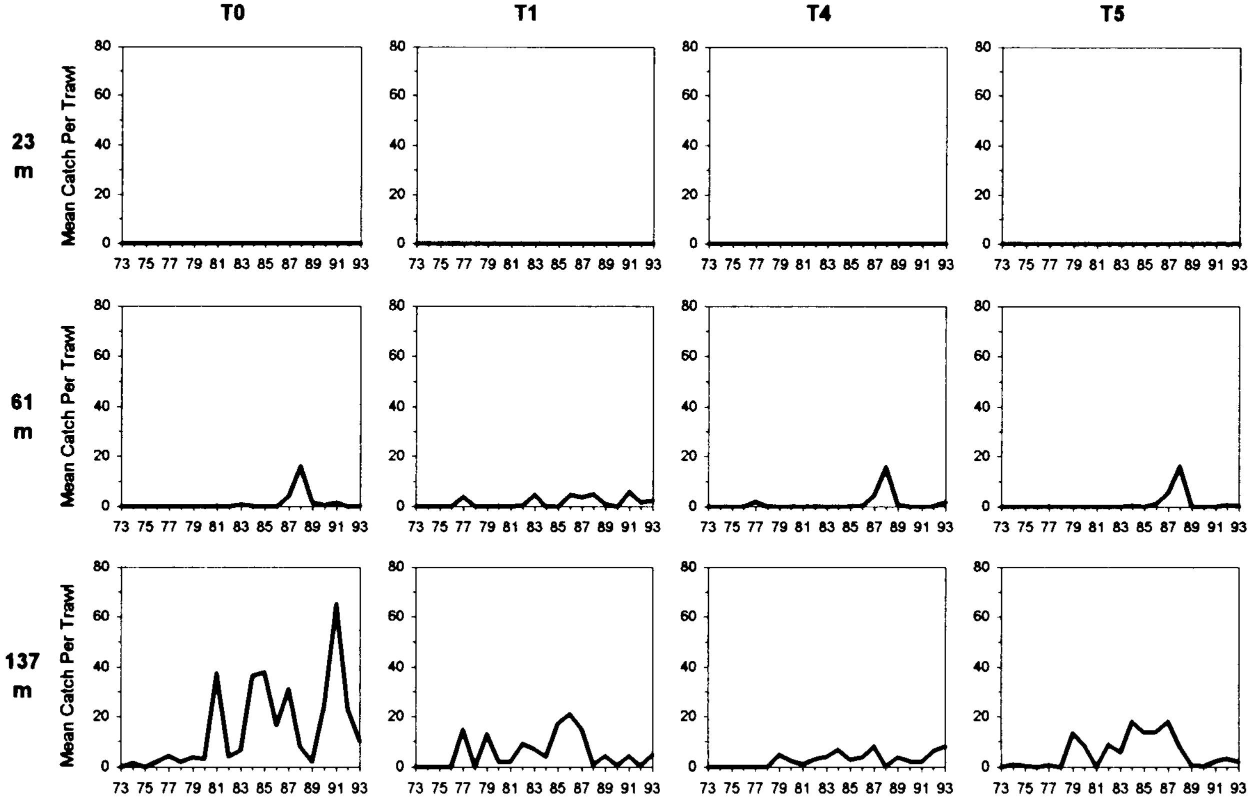


Figure 14. *Sebastes jordani* (shortbelly rockfish) and *Zaniolepis latipinnis* (longspine combfish) distributions on Palos Verdes, 1973–93.

gulf sanddab ***(Citharichthys fragilis)***



pink seaperch ***(Zalembius rosaceus)***

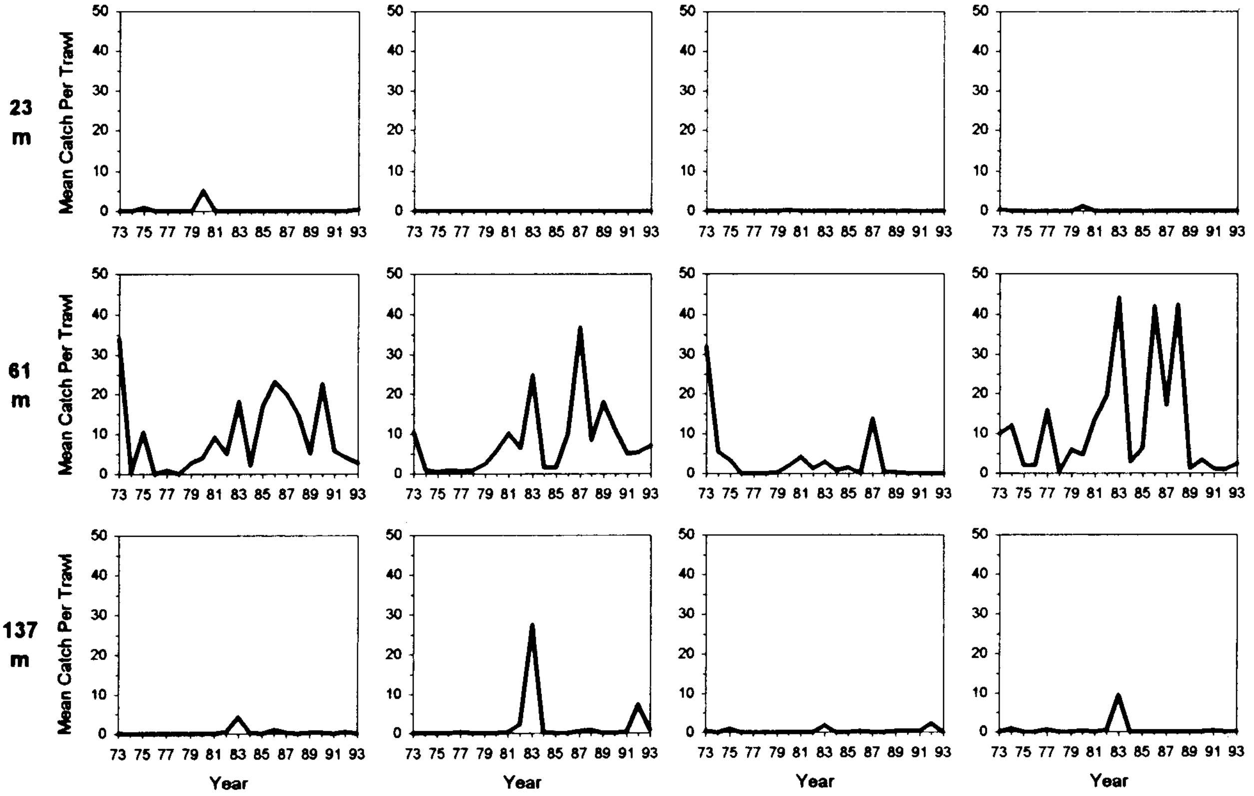
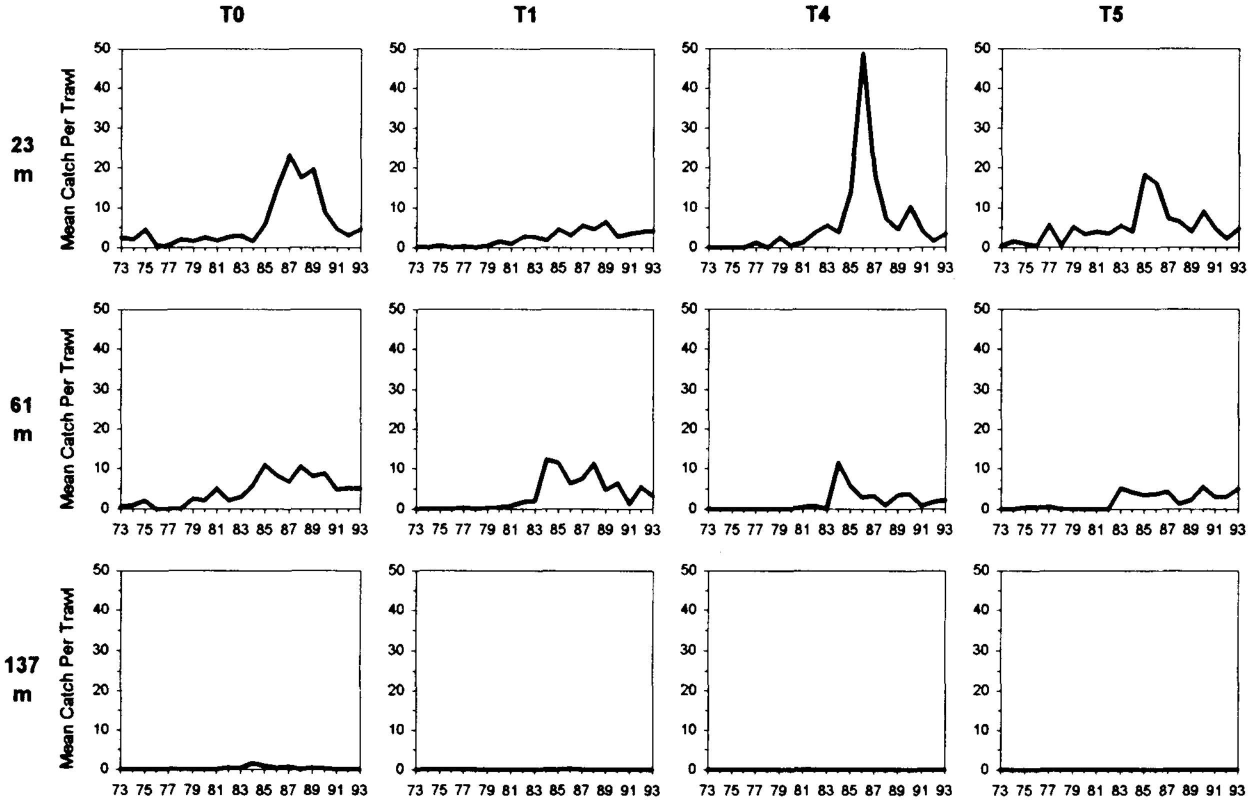


Figure 15. *Citharichthys fragilis* (gulf sanddab) and *Zalembius rosaceus* (pink seaperch) distributions on Palos Verdes, 1973–93.

hornyhead turbot *(Pleuronichthys verticalis)*



California scorpionfish *(Scorpaena guttata)*

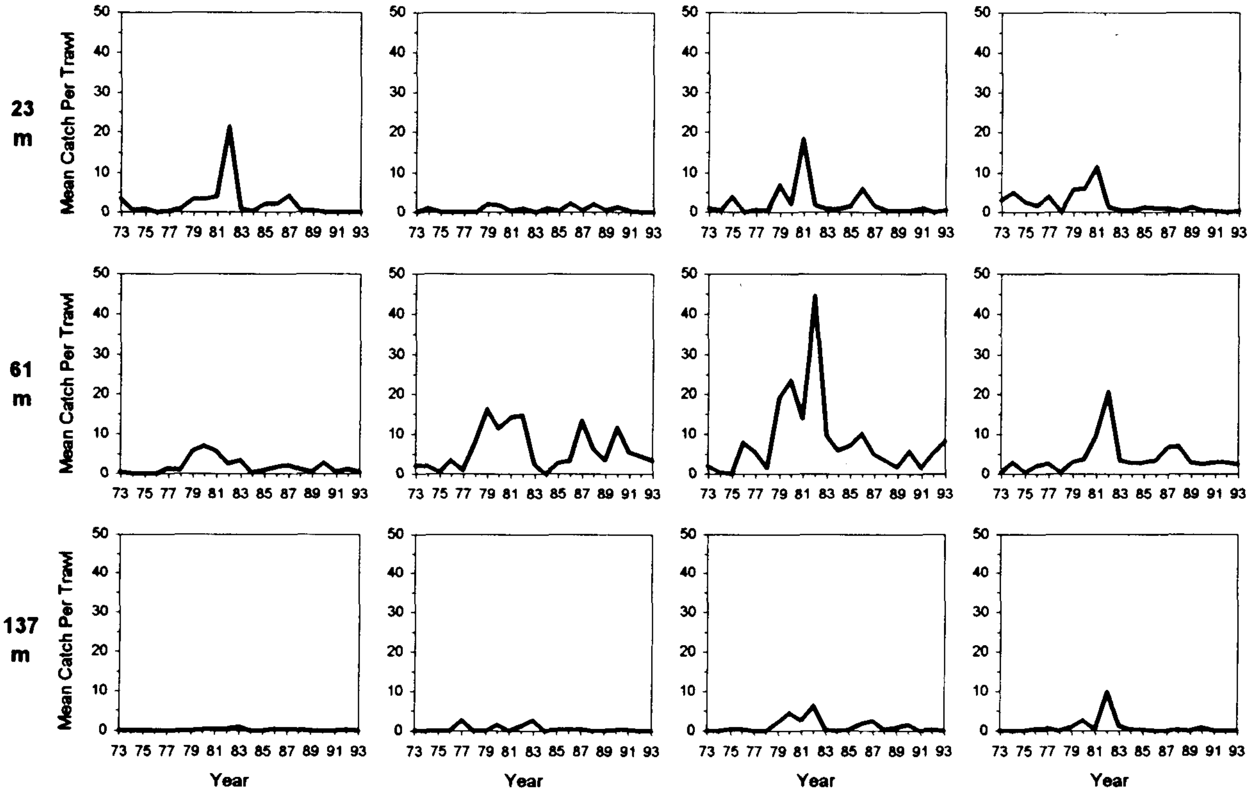


Figure 16. *Pleuronichthys verticalis* (hornyhead turbot) and *Scorpaena guttata* (California scorpionfish) distributions on Palos Verdes at 137 m, 1973–93.

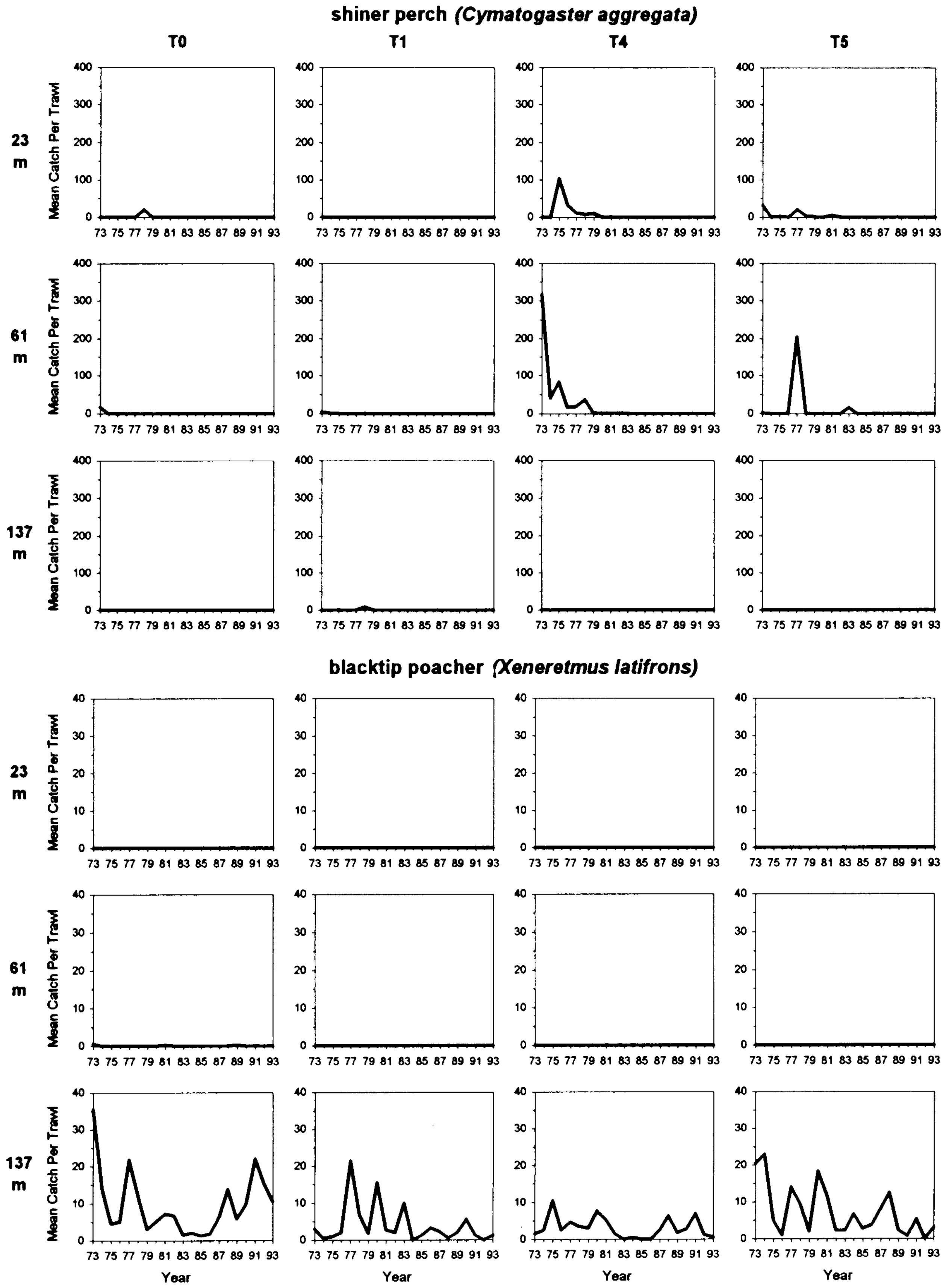


Figure 17. *Cymatogaster aggregata* (shiner perch) and *Xeneretmus latifrons* (blacktip poacher) distributions on Palos Verdes, 1973–93.

22. *Xeneretmus latifrons* (blacktip poacher, figure 17) was frequently taken along the 137-m isobath, but it was less abundant at outfall station T4-137. This cold-temperate, upper-slope roundfish ambushes epibenthic benthopelagic prey such as gammarid amphipods. At rest it is exposed. It has demersal eggs and pelagic larvae.

23. *Hippoglossina stomata* (bigmouth sole, figure 18) was rare in the 1970s, and most common in the mid- to late 1980s, likely in response to El Niño. It was most numerous near Redondo Canyon (T0-61). This warm-temperate, outer-shelf flatfish ambushes nektonic or benthopelagic prey such as mysids. It is buried when at rest. It has pelagic eggs and larvae.

29. *Paralichthys californicus* (California halibut, figure 18) was most common at 23 m in the 1980s, especially at T1-23; it was rare in the 1970s. This temperate, inner-shelf flatfish ambushes pelagic prey such as anchovies. It buries itself in sediments when at rest, and has pelagic eggs and larvae.

31. *Pleuronectes vetulus* (English sole, figure 19) was most abundant in the early 1970s at scattered sites, 23–137 m. In the 1980s and 1990s it was most often caught at outfall station T4-61. This temperate, outer-shelf flatfish searches for infaunal prey such as eunicid polychaetes. It is buried when at rest and has pelagic eggs and larvae.

32. *Xystreurys liolepis* (fantail sole, figure 19) was most common along the 23-m isobath from the 1980s and was abundant only in the mid-1980s at 61 m. This warm-temperate, inner-shelf flatfish ambushes epibenthic prey such as crabs. It is buried when at rest, and has pelagic eggs and larvae.

33. *Pleuronichthys decurrens* (curlfin sole, figure 20) is a shelf species which was most prevalent in the early 1970s at T4-23, T1-23, and T4-61. This cold-temperate, outer-shelf flatfish stalks benthic infauna such as echiurans. At rest it is buried. It has pelagic eggs and larvae.

35. *Phanerodon furcatus* (white seaperch, figure 20) is another inshore species, most numerous in the 1970s at T5-23 and T4-23. This cold-temperate, inner-shelf roundfish searches for epibenthic/benthopelagic prey such as gammarid amphipods. At rest, it is exposed. It has internal eggs and larvae.

Among the species not portrayed, *Sebastes rosenblatti* (greenblotched rockfish), *Zaniolepis frenata* (shortspine combfish), and *Chitonotus pugettensis* (roughback sculpin) were less common near the outfall.

External Anomalies

Dover sole dorsal and anal fins, which are in frequent contact with the sediment surface, showed most fin erosion; the ventral pectoral fin was more affected than the dorsal. Near total losses of most fins were observed in the early 1970s, but the severity of the syndrome declined over time. Data from the 1980s are conservative; very minor fin anomalies were observed, and it was sometimes difficult to distinguish if the damage was from the trawl net or some other source.

Most Dover sole were taken along the 137-m isobath. Figure 21 (dotted line) shows the mean number of Dover sole of four size classes taken annually at the four Palos Verdes 137-m sites. Dover sole were remarkably abundant in the early 1970s, particularly in summer; they were less common from 1980 to 1993.

Figure 21 (bars) also shows the mean annual percentage of Dover sole of the four size classes with fin erosion. Fin erosion was a function of sampling site and fish size. Most frequent and most severe fin erosion incidences were found at near-outfall stations (T4 and T5) in the 1970s. The syndrome was rare at the most distant transect, T0, and infrequent at T1. Frequency has been very low at all sites from the mid- to late 1980s.

Fin erosion declined first among smaller sole; the syndrome has not been observed in the smallest size class since 1980. The syndrome persisted longer in larger individuals; it was rarely observed in the mid-1980s, and not observed in the 1990s.

Historically, fewer Dover sole had X-cell epidermal pseudotumors than fin erosion (figures 21 and 22). But there has not been the same relative reduction in pseudotumors as in fin erosion. Incidence was highest (0–5%) nearest the outfall (T4-137), and lowest among larger specimens (>14 cm standard length).

DISCUSSION

Demersal fish that live both in the water column and on the bottom are commonly taken over Palos Verdes' soft-bottom habitat. Allen's (1982) descriptions of functional aspects of southern California soft-bottom fish communities indicate that the Palos Verdes fish eat pelagic, benthopelagic, epibenthic, infaunal, and other prey. Arthropods are a preferred food, especially euphausiids, gammarids, shrimp, mysids, and crabs. Many fish taken in the 1980s and 1990s bury themselves in the sediments when inactive; others are exposed. The most common reproductive strategy includes pelagic eggs and larvae, although a few dominants have internal or demersal eggs or larvae. For the entire 21 years, total abundances and numbers of species tend to be only slightly lower at outfall station T4 as compared to the other 61-m sites.

It is difficult to establish the causes of the observed spatial and temporal changes in demersal fish catches on Palos Verdes, 1973–93. A multiplicity of hydrodynamic and biological processes influence fish populations on various spatial or temporal scales. Parallel long-term regional data that might serve as a reference are unavailable. Also, the geomorphology of Palos Verdes is unique

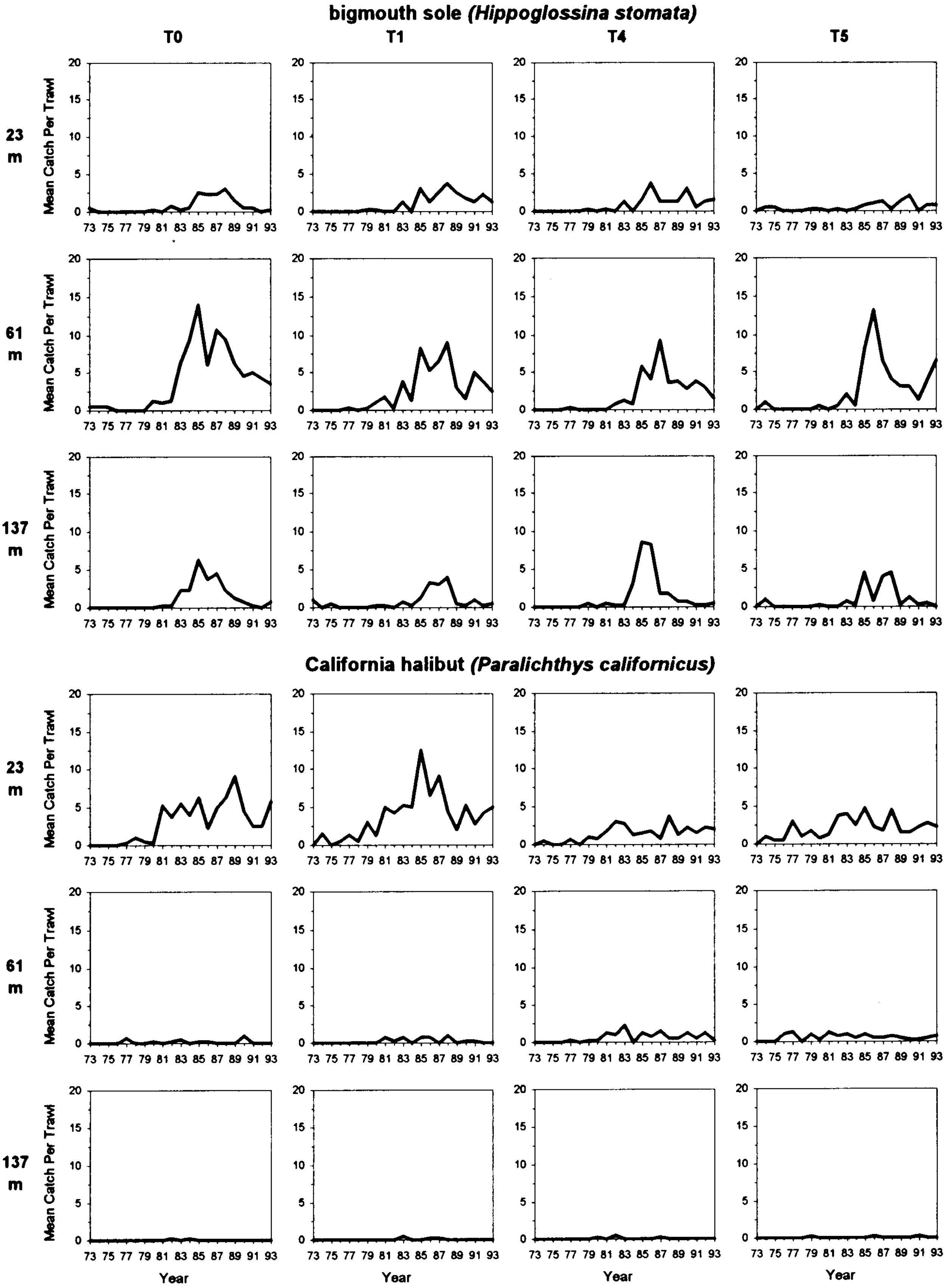


Figure 18. *Hippoglossina stomata* (bigmouth sole) and *Paralichthys californicus* (California halibut) distributions on Palos Verdes, 1973–93.

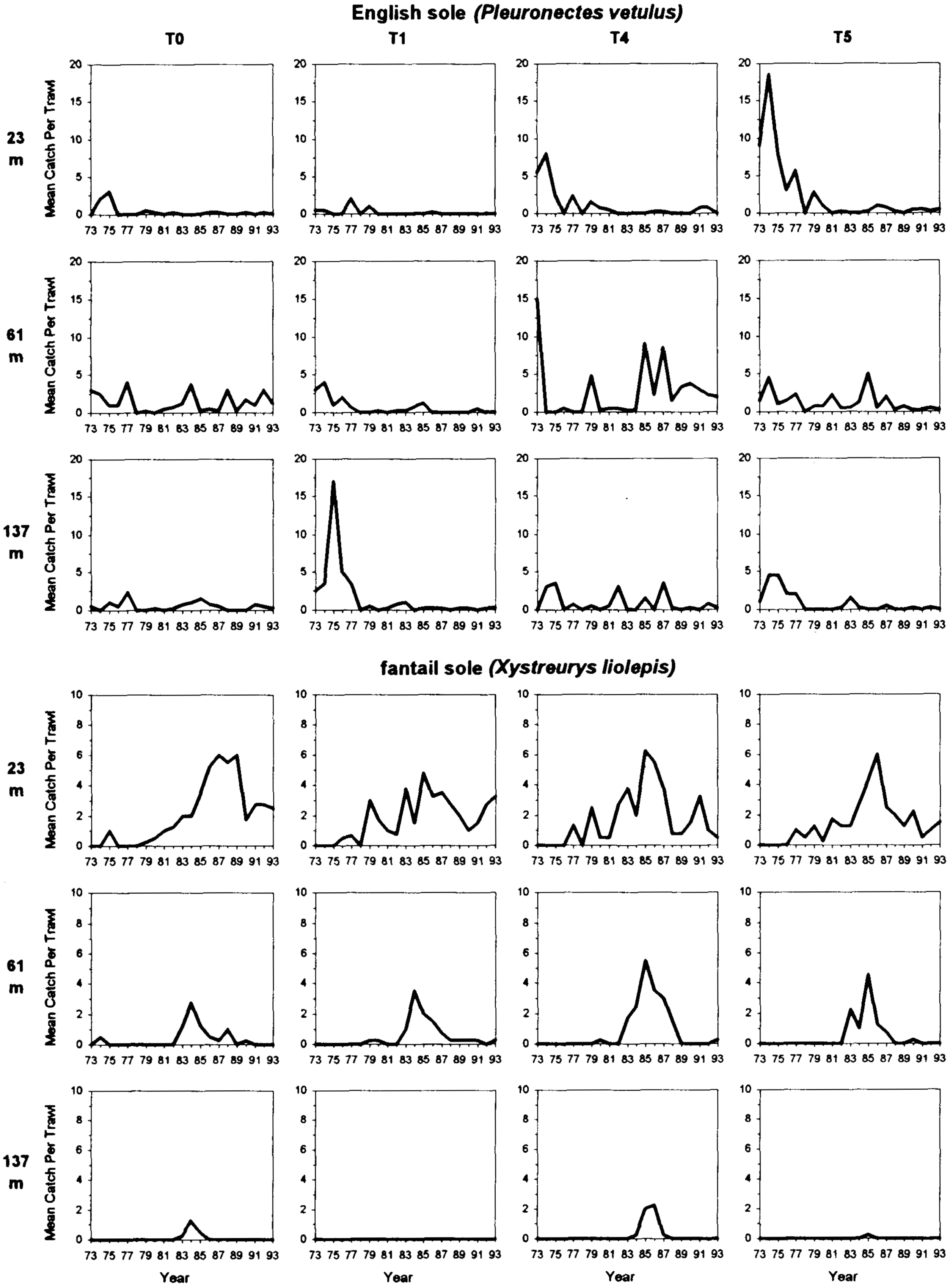


Figure 19. *Pleuronectes vetulus* (English sole) and *Xystreurys liolepis* (fantail sole) distributions on Palos Verdes, 1973–93.

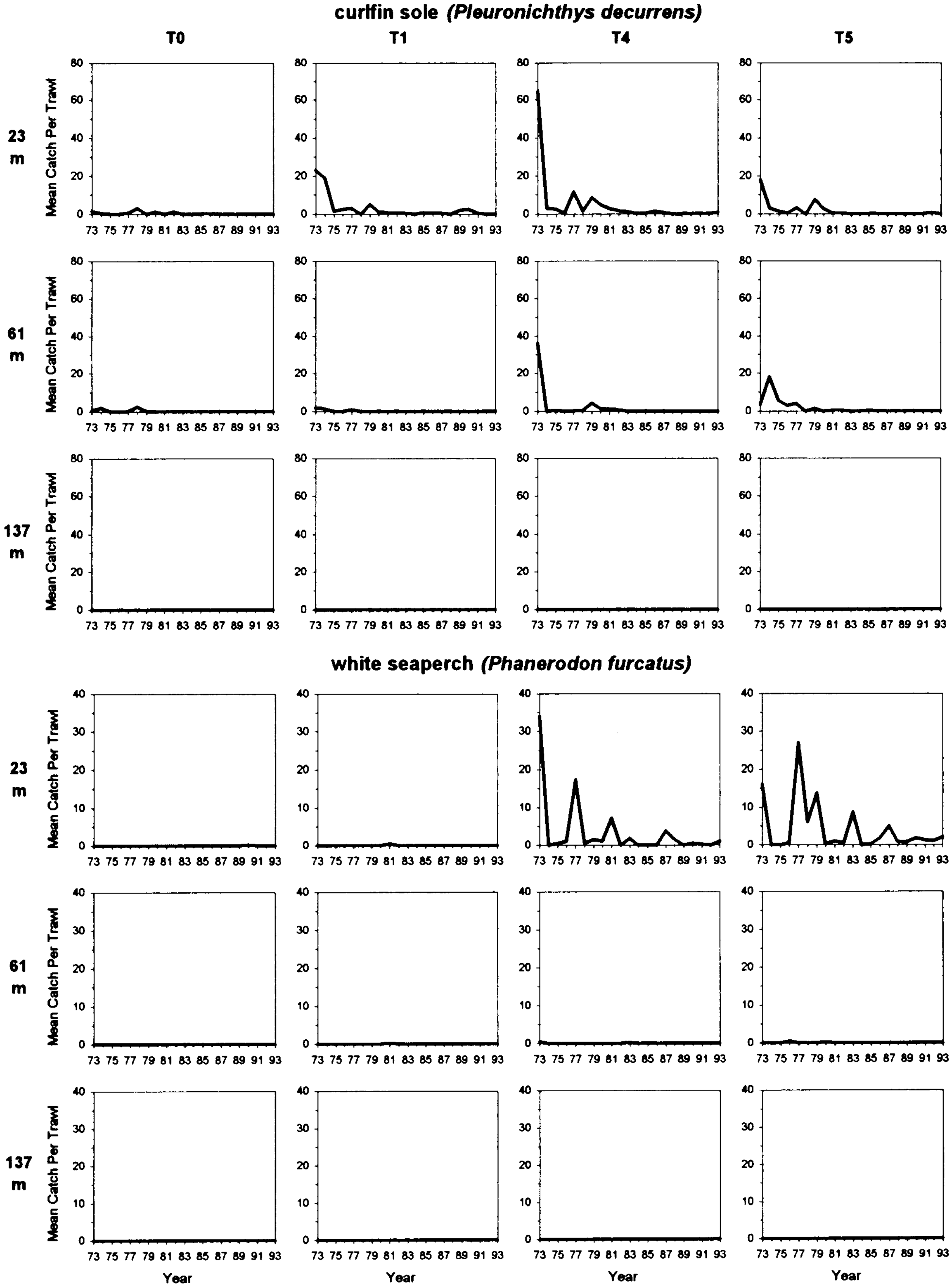


Figure 20. *Pleuronichthys decurrens* (curlfin sole) and *Phanerodon furcatus* (white seaperch) distributions on Palos Verdes, 1973–93.

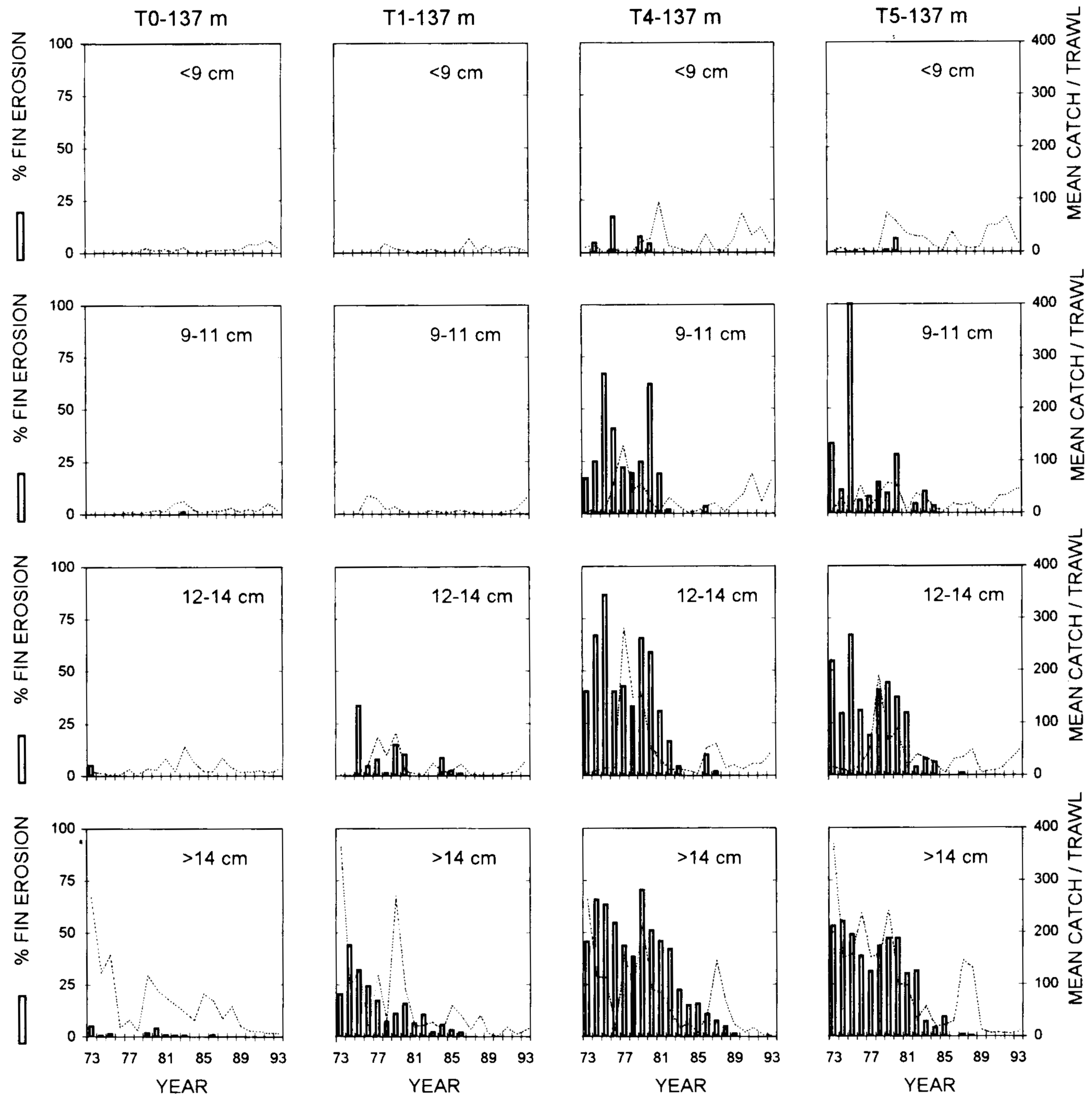


Figure 21. Percentage of fin erosion and number of Dover sole caught at Palos Verdes 137-m sites, by size class, 1973–93.

relative to its regional setting. Moreover, many demersal fish species have pelagic eggs and larvae which can be widely dispersed; thus correlations between local environmental factors and catch data are difficult. Also, fish populations can reflect both present environmental conditions and conditions at the time of settlement from the plankton. Despite these difficulties, one can speculate on the important processes from correlations with specific perturbations or from physical/biological habitat characteristics.

Water depth created the dominant spatial distribution pattern. Species exhibit depth preferences from inner shelf (23 m) and outer shelf (61 m) to upper slope (137 m). Other habitat features that probably influenced fish distributions include sediment type and quality (substrate, and levels of contaminants and organic matter), and topography (coastal promontory with narrow shelf, steep slope, canyons, outfall structure, and seasonal upwelling).

Stochastic natural events appear to play a major role

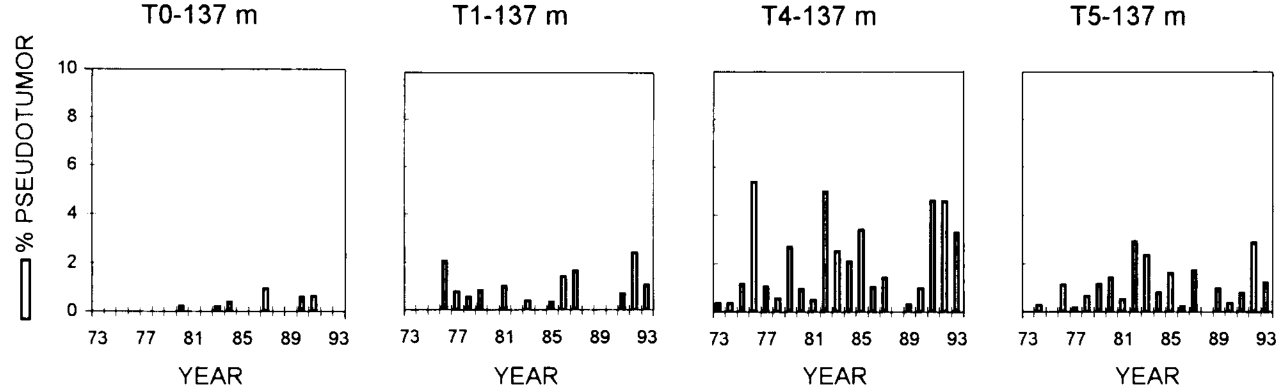


Figure 22. Percentage of pseudotumors in Dover sole caught at Palos Verdes 137-m sites, 1973–93.

in shaping community structure. Most of the changes in species composition and abundance occurred over the entire Palos Verdes study area, and may have been region- or bightwide.

Temperature shifts had the greatest effect on Palos Verdes fish populations. El Niño events, which are related to the strength of the California Countercurrent, were a key factor. Residual effects from the most extreme El Niño (1982–83) persisted in the fish assemblage for several years. The warmer waters of 1982–83, and of the 1980s and 1990s, brought southerly (mostly warm-temperate) species northward, changed recruitment patterns, and displaced some fish farther offshore or to the north.

Species whose catches increased during or after the 1982–83 El Niño include *Merluccius productus* (Pacific hake), *Xystreurys liolepis* (fantail sole), *Seriphus politus* (queenfish), *Chitonotus pugettensis* (roughback sculpin), *Sebastes rosenblatti* (greenblotched rockfish), *Hippoglossina stomata* (bigmouth sole), *Pleuronichthys verticalis* (hornyhead turbot), *Citharichthys fragilis* (gulf sanddab), *Zalembius rosaceus* (pink seaperch), *Zaniolepis latipinnis* (longspine combfish), *Symphurus atricauda* (California tonguefish), *Synodus lucioceps* (California lizardfish), *Sebastes diploproa* (splitnose rockfish), *Genyonemus lineatus* (white croaker), *Porichthys notatus* (plainfin midshipman), and *Icelinus quadriseriatus* (yellowchin sculpin). During this period, there were fewer *Xeneretmus latifrons* (blacktip poacher) and *Errex zachirus* (rex sole), both cold-temperate species.

Most of the fish species whose catches increased during or after the 1982–83 El Niño consume crustaceans such as shrimp, mysids, euphausiids, crabs, gammarids, ostracods, or calanoids (Allen 1982). The prey are primarily benthopelagic or pelagic, and are taken from the bottom or from the water column. During and following the largest El Niño (1983–86), extremely large numbers of *Sicyonia ingentis* (ridgeback shrimp) and *Pleuroncodes planipes* (pelagic red crab) occurred on the shelf and upper slope. It is hypothesized that these were a very important food resource for the fish that flourished during those years.

Following are several other examples of distribution patterns and possible environmental correlates. Some of the changes in catches relate to declining wastewater emissions (solids, trace contaminants) and associated ecological improvements such as better sediment quality, more diverse food resources (e.g., more microcrustacea and fewer small polychaetes), increased kelp, and greater water clarity. The large and ongoing natural variability alters effects from wastewater discharges and tends to confound interpretations.

At 23 m, *Citharichthys stigmaeus* (speckled sanddab), *Pleuronectes vetulus* (English sole), *Pleuronichthys decurrens* (curlfin sole), and *Phanerodon furcatus* (white seaperch) decreased, and *Paralichthys californicus* (California halibut) and *Xysteurys liolepis* (fantail sole) increased. Warmer waters in the 1980s and 1990s were likely a factor; sediment quality and food resources may have played a role.

At 61 m, *Sebastes saxicola* (stripetail rockfish), *Genyonemus lineatus* (white croaker), *Sebastes dalli* (calico rockfish), and *Cymatogaster aggregata* (shiner perch) decreased. These are water-column fish; many are exposed when at rest. The rockfish and shiner perch have internal eggs. *Symphurus atricauda* (California tonguefish), *Zaniolepis latipinnis* (longspine combfish), *Pleuronichthys verticalis* (hornyhead turbot), *Hippoglossina stomata* (bigmouth sole), and *Citharichthys xanthostigma* (longfin sanddab) increased. These have pelagic or demersal eggs, and pelagic larvae. Most are bottom-living fish which bury themselves during periods of inactivity. The increase in bottom dwellers may relate in part to improvements in sediment quality, such as lowered trace contaminants, organic matter, and hydrogen sulfide. Bottom dwellers themselves play a major role in redistributing contaminants by disturbing the sediments.

At 137 m, *Microstomus pacificus* (Dover sole), *Sebastes saxicola* (stripetail rockfish), *Sebastes diploproa* (splitnose rockfish), *Errex zachirus* (rex sole), and *Anoplopoma* *fimbria* (sablefish) decreased. *Eopsetta exilis* (slender sole), *Porichthys notatus* (plainfin midshipman), *Lycodopsis pacifica* (blackbelly eelpout), *Sebastes rosenblatti* (greenblotched rockfish), and *Zaniolepis frenata* (shortspine combfish) increased. Some species with a more northerly distribution were more common in the 1970s, whereas some with a more southern or temperate distribution increased in the 1980s and 1990s.

Nearshore fish appear to have moved offshore during perturbations. *Synodus lucioceps* (California lizardfish) catches at 23 m correspond directly with El Niño and storm events (increases in 1973, 1977, 1982–83, 1988, and 1992). *Cymatogaster aggregata* (shiner perch) decreased steadily, but the largest 61-m populations were also recorded in El Niño years 1973, 1977, and 1983. *Genyonemus lineatus* (white croaker) tended to be more abundant in 61-m catches in El Niño years (1977, 1983, and 1993).

At 137 m, *Porichthys notatus* (plainfin midshipman) was most abundant on the upper slope after the 1988 storms. Two waves of *Sebastes saxicola* (stripetail rockfish) recruitment came with El Niño events.

Some species characteristic of the Palos Verdes outfall area in the early 1970s decreased thereafter, including *Cymatogaster aggregata* (shiner perch), *Pleuronichthys decurrens* (curlfin sole), *Phanerodon furcatus* (white seaperch), *Pleuronectes vetulus* (English sole), and *Microstomus pacificus* (Dover sole). These have cold-temperate and temperate distributions; many prey on various benthic infauna.

Other species that had been absent or rare became more abundant near the outfall, including *Symphurus atricauda* (California tonguefish), *Pleuronichthys verticalis* (hornyhead turbot), *Paralichthys californicus* (California halibut), *Zaniolepis latipinnis* (longspine combfish), and *Lycodopsis pacifica* (blackbelly eelpout). Many are warm-temperate or temperate species, and microcrustaceans such as gammarids are a common food preference.

Some species, such as *Icelinus quadriseriatus* (yellowchin sculpin) and *Zaniolepis latipinnis* (longspine combfish) are rare near the outfall. Both prey on gammarid amphipods, which are less abundant in soft sediments nearer the outfall system. Persistent differences in fish assemblages near the outfall may be due to the nature of the substrate (fine-grained, organically enriched sediments with trace contaminants), topography (e.g., outfall structure), food resources, or the discharge of treated wastewaters. Also, historically discharged contaminants such as DDT and PCBs persist in a partly buried sediment reservoir on Palos Verdes (Stull et al. 1988). These may influence the condition of some fish species (Cross and Hose 1988).

Fin erosion was common in Dover sole near the outfall. But it has not been induced in Palos Verdes Dover sole for many years: in smallest sole (<9 cm) it has not been observed since 1980, and in larger specimens (>14 cm) it was last observed in the mid-1980s (figure 21). Absence of the syndrome may result from improved sediment quality and reduced emissions of effluent solids and contaminants (figure 3).

Pseudotumors were more prevalent in Dover sole nearer the outfall, as reported by Cross (1988). Historically the incidence of pseudotumors was lower than that of fin erosion. Although fin erosion virtually disappeared, pseudotumors continue to occur on Palos Verdes, with lowest frequency in larger Dover sole (>14 cm). The overall incidence ranges from 0–2% at stations distant from the outfall (T0, T1), and 0–5% near the outfall.

CONCLUSIONS

1. Palos Verdes demersal fish catches varied greatly from 1973 to 1993. Spatial and temporal patterns are described, and inferences are made on potentially important environmental processes that influence fish assemblages.

2. Water depth was the primary determinant of spatial distributions. Species exhibited particular preferences for inner-shelf (23-m), outer-shelf (61-m), or upper-slope (137-m) habitats. Wastewater discharge, substrate type, topography, and food resources also influenced distributions.

3. Temperature shifts induced more changes in fish assemblages over time than did any other natural or anthropogenic factors. The 1970s were several degrees cooler than the 1980s and 1990s. The major warming trend of the 1982–83 El Niño, and associated physical and biological perturbations, had the most dramatic effects on demersal fish. Warmer waters, large populations of crustaceans, and more southern fish species were observed. Catches of many fish species increased substantially, while a few decreased. The largest changes persisted for several years.

4. Many other factors also helped shape the fish populations over time, including smaller-scaled oceanographic events, natural hydrodynamic and biological fluctuations, disturbances such as storms, and anthropogenic activities.

5. Fish assemblages recovered in concert with decreasing emissions of wastewater solids and contaminants from the outfalls, and with associated ecological improvements in Palos Verdes habitats. Some species that were abundant near the outfalls in the early 1970s declined; some that had been rare increased. Bottom fish, which bury themselves in sediments during periods of inactivity, became more common, as did species which prey on crustaceans. Several species are still reduced near the outfall as compared to other Palos Verdes sites.

6. The incidence and severity of fin erosion among Palos Verdes Dover sole decreased from the 1970s; it has not been observed since the mid-1980s. Dover sole

epidermal pseudotumors, believed to be a parasitic condition and not a neoplasm, are more frequent (<5%) near the outfall than elsewhere on Palos Verdes. They have also been observed in flatfish distant from pollutant sources.

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We are very grateful to Joe Meistrell and David Montagne, who supervised most trawl surveys, and to April Ford for fish identification and data input. Jim Allen of Southern California Coastal Water Research Project was actively involved in program development and modeling from the 1970s; he prepared several NPDES annual summaries. Among the long-term program participants were Don Cadien, Cheryl Brantley, Irwin Haydock, Doug Hotchkiss, Tom Parker, Bill Power, Kateri Shea, Andrea Smith, Fred Stern, and Tsam Wong, but over the years many others contributed.

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RELATIONSHIP BETWEEN DEEP CHLOROPHYLL MAXIMUM AND SURFACE CHLOROPHYLL CONCENTRATION IN THE CALIFORNIA CURRENT SYSTEM

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ABSTRACT

Empirical relationships were derived to estimate the depth (Z_m) and concentration (Chl_m) of the deep chlorophyll maximum (DCM) in the California Current System (CCS) between 28° and 37°N, using CalCOFI data (1978–92). Because primary productivity may be modeled from remotely sensed ocean color data, it is important to be able to predict Z_m and Chl_m. The DCM is a persistent feature of this system, with the average Z_m generally increasing from north to south, and with distance from shore. Meanwhile, Chl_m is higher inshore than offshore. During ENSO events, Z_m was deeper, and Chl_m was lower than during normal years. The studied area was spatially divided into six subregions, and temporally into warm and cool seasons. Regression models were developed for each subregion and season to estimate Z_m and Chl_m as functions of surface chlorophyll.

INTRODUCTION

Satellites provide the only observational platform by which total and new primary productivity can be monitored at ocean-basin scales (Platt and Sathyendranath 1988; Sathyendranath et al. 1991). Unfortunately, remotely sensed ocean color is limited to depth at which 90% of the backscattered irradiance from the water column originates. Remote sensors provide information on the average photosynthetic pigment concentration for the upper 22% of the euphotic zone (Kirk 1983).

Empirical and semianalytical algorithms to estimate primary productivity from satellite-derived photosynthetic pigments have been compared (Balch et al. 1989, 1992; Platt and Sathyendranath 1993). These productivity models apply to the entire euphotic zone; ideally, they should use the vertical profile of pigment biomass as input. Therefore a gap exists between the limited satellite pigment information and what is needed for modeling. The assumption of a mixed layer with a homogeneous pigment distribution could lead to an over- or underestimation of productivity, depending on the shape of the biomass distribution (Platt et al. 1988, 1991).

A common characteristic of the California Current System (CCS) is the presence of a deep chlorophyll maximum (DCM) (Cullen and Eppley 1981; Hayward et al. 1995). This maximum changes in depth and concentration from inshore to offshore (Hayward et al. 1995). A DCM deeper than the 1% light level may contribute as much as 10% of the total integrated primary productivity (Venrick et al. 1973).

Since the early studies on the DCM (Riley 1949), a large effort has been directed to understanding such features (Varela et al. 1992, and others cited therein). In our study area, the DCM coincides with the upper part of the nitracline, where nitrate concentration is about 1.0 µM (Hayward et al. 1995).

The purpose of our work is to provide empirical algorithms to estimate the DCM concentration (Chl_m) and depth (Z_m) as a function of surface properties that may be estimated with data generated by remote sensors, such as surface chlorophyll concentration (Chl_s) and T °C. The underlying assumption is that for a given area of the CCS, in a given season, the relationships between the surface chlorophyll concentration and Chl_m, and Z_m, are constant or at least predictable.

DATA AND METHODS

All observations fall within the region bounded by CalCOFI line 60 on the north, line 120 on the south, and stations XX.110 on the west (figure 1). We used the CalCOFI database for the 1978–92 period. Chlorophyll *a* concentrations were determined by the standard fluorometric method (Yentsch and Menzel 1963; Holm-Hansen et al. 1965).

Initially, our data base had 4,160 chlorophyll profiles. We discarded 18% of these profiles because they presented two or more maxima. We tabulated the DCM concentration and depth, as well as the surface temperature and surface chlorophyll concentration for each of the remaining 3,410 profiles. Table 1 shows the number of useful profiles available for each year, month, and area.

The study area was divided into three regions following Lynn and Simpson (1987): Central California (CC), Southern California (SC), and Baja California (BC; figure 1). We then plotted Z_m versus distance from shore for each CalCOFI line, and we divided the regions into inshore (i) and offshore (o) subregions (figure 1) according to the behavior of Z_m (figure 2 illustrates examples). These inshore-offshore subregions

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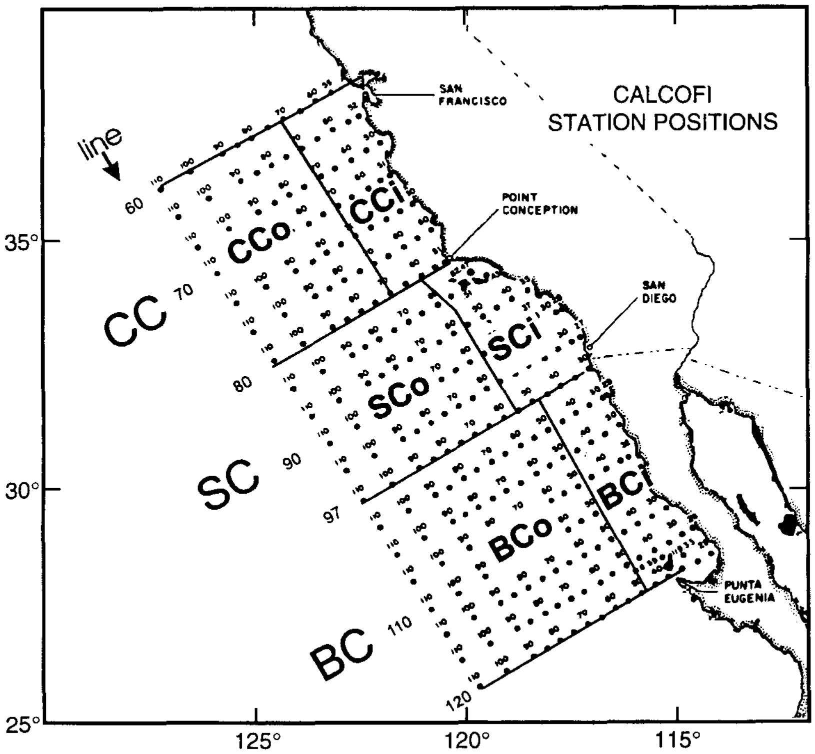

Figure 1. Study area: Central California (CC); Southern California (SC); and Baja California (BC) regions; inshore (i) and offshore (o) subregions.

TABLE 1
Numbers of Chlorophyll Profiles Used for Each Year, Month, and Season for Each Subregion

	CCi	CCo	SCi	SCo	BCi	BCo	Total
Year							
1978	51	49	83	109	93	113	498
1981	1	0	19	26	6	11	63
1983	0	0	70	23	0	0	93
1984	33	65	230	231	98	162	819
1985	12	12	103	89	0	0	216
1986	12	15	113	94	0	0	234
1987	9	10	117	112	0	0	248
1988	23	11	123	99	1	0	257
1989	16	16	112	120	0	0	264
1990	12	10	100	105	0	0	227
1991	13	14	107	108	0	0	242
1992	11	17	100	121	0	0	249
Month							
January	16	25	130	124	43	37	375
February	19	24	93	113	15	27	291
March	18	20	126	94	25	24	307
April	12	16	149	146	25	35	383
May	20	0	143	129	0	0	292
June	0	0	51	35	34	70	190
July	24	44	136	137	22	45	408
August	32	36	112	127	18	27	352
September	9	7	77	70	1	0	164
October	28	29	112	119	9	6	303
November	15	18	141	135	6	15	330
December	0	0	7	8	0	0	15
Season							
Cool	85	85	641	606	142	194	1,753
Warm	108	134	636	631	56	92	1,657
Total	193	219	1,227	1,237	198	286	3,410

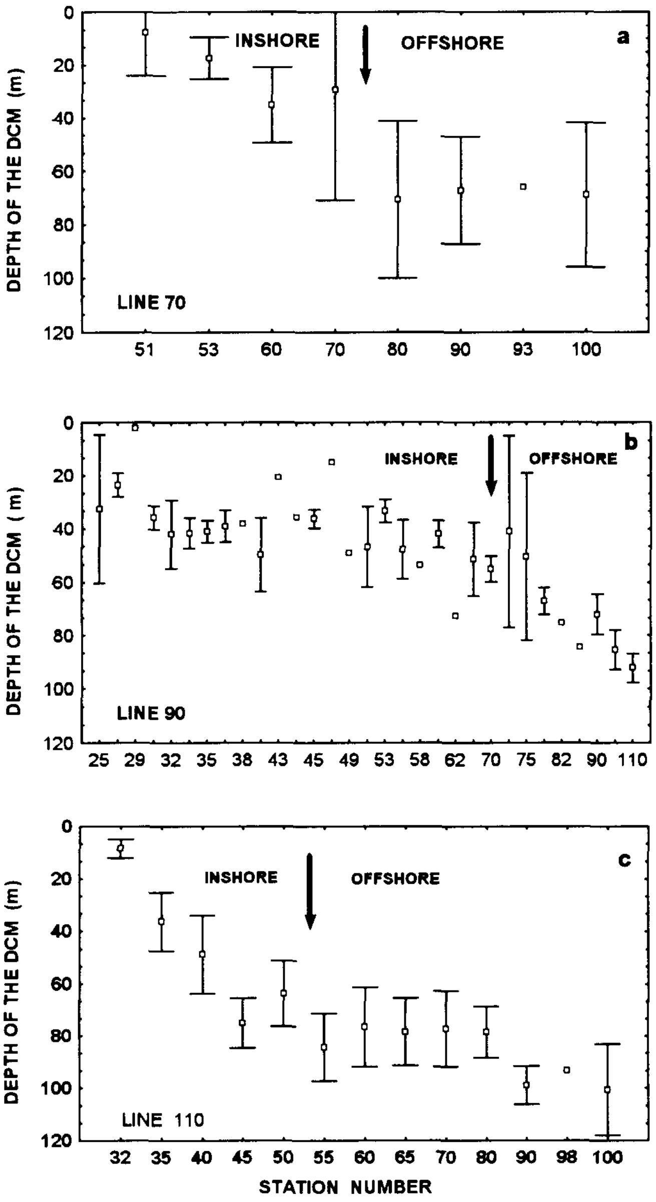

Figure 2. Depth of DCM at each station of CalCOFI lines: *a*, 70; *b*, 90; and *c*, 110. *Arrows* indicate the limit between inshore and offshore subregions.

coincide very closely with those proposed by Lynn and Simpson (1987) based on sigma-t analysis.

We used the 95% range estimate of the surface temperature monthly mean for the whole 1978–92 period, for each subregion, to define seasons (figure 3). The cool season was January through May for CC and SC regions, January through June for the BC region. The rest of the year is considered the warm season.

Surface chlorophyll values were grouped into seven categories (table 2). The criterion for defining these seven categories was that Z_m had to be significantly different at each category, at the 95% confidence level. Categories 4 and 5 had the same Z_m within region CC, thus we grouped them into a single category. Within region BC, categories 4 and 6 presented the same Z_m, but they were kept separate.

TABLE 2
Surface Chlorophyll Concentration Interval for Each Category

Category	Concentration (mg•m^{-3})
1	≤0.1 mg•m^{-3}
2	>0.1 y ≤ 0.2 mg•m^{-3}
3	>0.2 y ≤ 0.5 mg•m^{-3}
4	>0.5 y ≤ 1.0 mg•m^{-3}
5	>1.0 y ≤ 2.0 mg•m^{-3}
6	>2.0 y ≤ 5.0 mg•m^{-3}
7	>5.0 mg•m^{-3}

We built regression models of the means of Chl_m and Z_m for each subregion, season, and category, as functions of the Chl_s mean for each category.

RESULTS AND DISCUSSION

Within the CC region the mean Z_m increased from less than 10 m at station 51 to about 70 m at station 80, and then it remained nearly constant with greater distance from shore (figure 2a). The behavior of Z_m within region SC was different compared to that of regions CC and BC. In this middle region, it changed between 20 and 50 m, from nearshore to station 65, without a particular pattern, and then increased to 95 m at station 110 (figure 2b). The behavior of the mean Z_m within region BC was similar to that in region CC, but the inflection point was closer to shore (station 50, figure 2c). Cullen and Eppley (1981) observed the increase of Z_m with distance offshore.

The mean Chl_s values for the whole year tended to be lower during the 1983, 1987, and 1992 ENSO events than during the other years (figure 4). Also, their 95% confidence intervals tended to be shorter during the ENSO years. The mean of Chl_m showed a similar behavior. The mean Z_m also tended to be larger for ENSO years (not illustrated). Typically, the oceanic effects of ENSO events in the CCS include a strong and broad countercurrent/undercurrent along the continental margin, anomalous poleward winds along the coast, and a depressed thermocline and nutricline, ultimately causing a strong effect on the marine biota (Lynn et al. 1995, and others cited therein). Our Chl_s time series is too short to show a clear interannual tendency (figure 4). Nevertheless, there is some indication of a Chl_s tendency to decrease, resembling the general zooplankton decrease described by Roemmich and McGowan (1995) for the period 1951–93.

The monthly Chl_s means for all regions show the typical seasonal variation in temperate waters, with maxima at the end of winter and spring (figure 5). The average year of Chl_m, for each subregion, generally shows

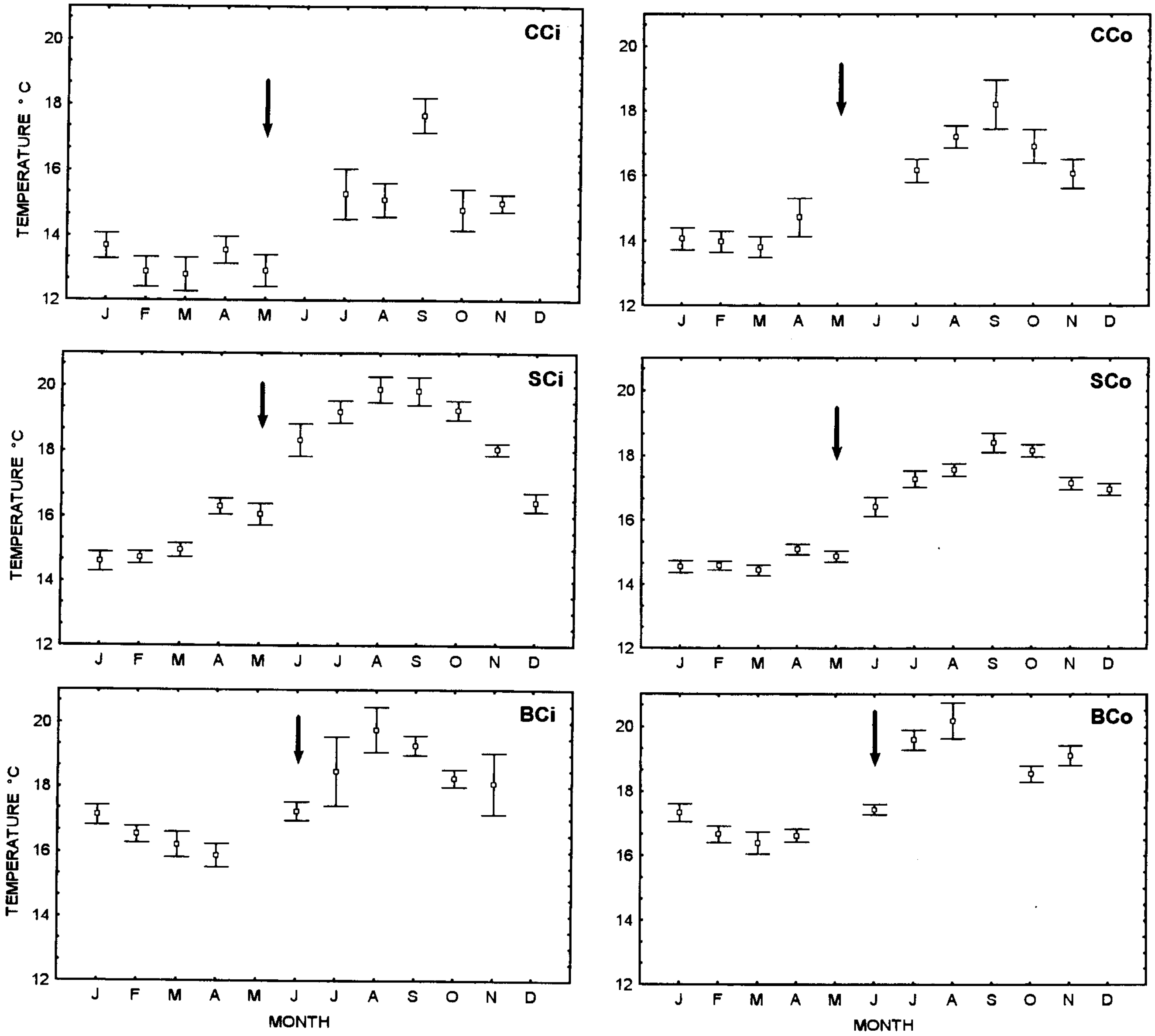

Figure 3. Monthly mean surface T °C for each subregion, and for the whole study period. *Bars* are the 95% confidence intervals. *Arrows* indicate the end of the cool season.

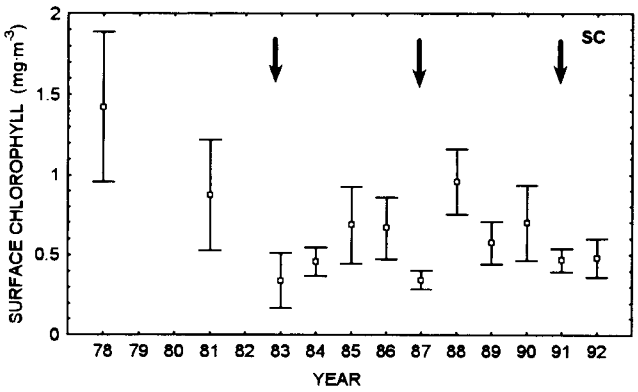

Figure 4. Mean surface chlorophyll for each year for the Southern California region. *Bars* are the 95% confidence intervals. *Arrows* indicate ENSO events.

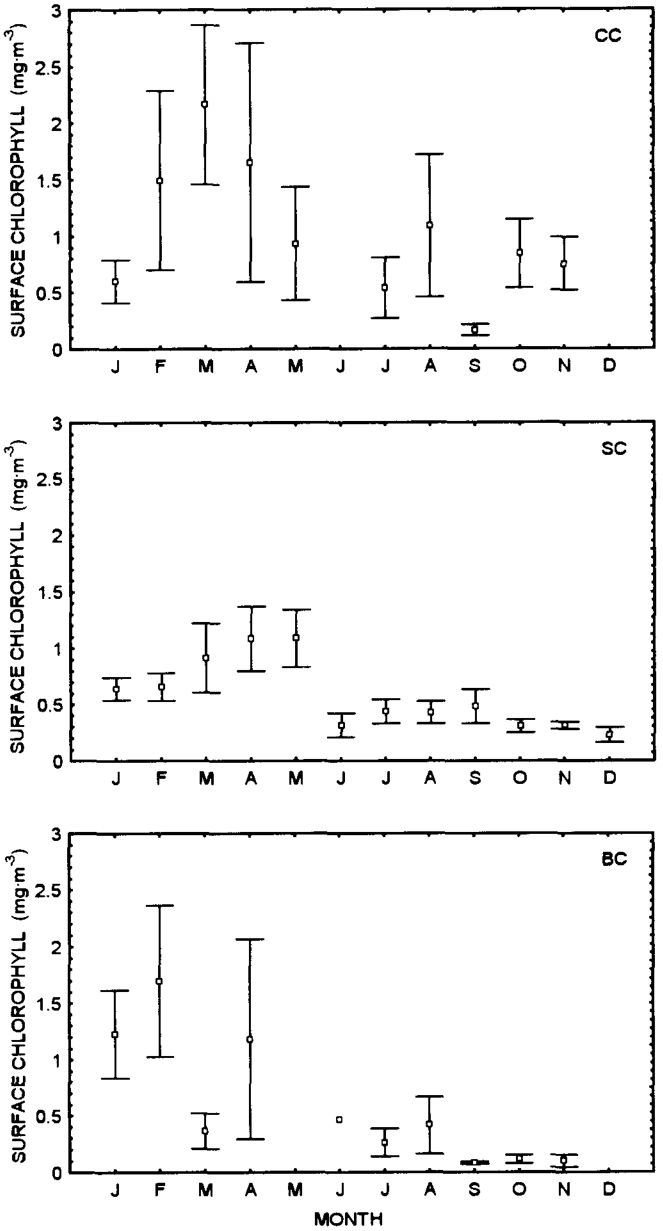

Figure 5. Monthly mean surface chlorophyll for the whole study period, and for each region. *Bars* are the 95% confidence intervals.

a seasonal variation with a spring maximum (figure 6). The maximum mean Chl_m was highest for CCi (7 mg m^{-3}), and it was lowest for SCo and BCo (2.3 mg m^{-3}).

There is no general behavior of the Z_m seasonal variation (figure 7). Within CCi and CCo, Z_m showed lowest values during fall and winter, and maximum values during spring and summer. However, Z_m was largest during summer and fall for SCi, and from the end of spring through December for SCo. Meanwhile, Z_m had minimum values at the beginning of winter and end of summer, and large values during the rest of the year, within BCi and BCo.

The overall mean surface chlorophyll concentration ($MChl_s$) for cool and warm periods was greater for inshore than for offshore subregions (figure 8a, b). The $MChl_s$ was significantly greater for CCi than for SCi and BCi. There was no significant $MChl_s$ difference for the offshore subregions at the 95% confidence level, with the exception of BCo during the warm season, which was lower than the other two (figure 8a, b).

In general, the behavior of the overall mean Chl_m ($MChl_m$) for all cool and warm periods was similar to that of $MChl_s$ (figure 8 a–d). The $MChl_m$ was higher for inshore than for offshore subregions (figure 8c, d).

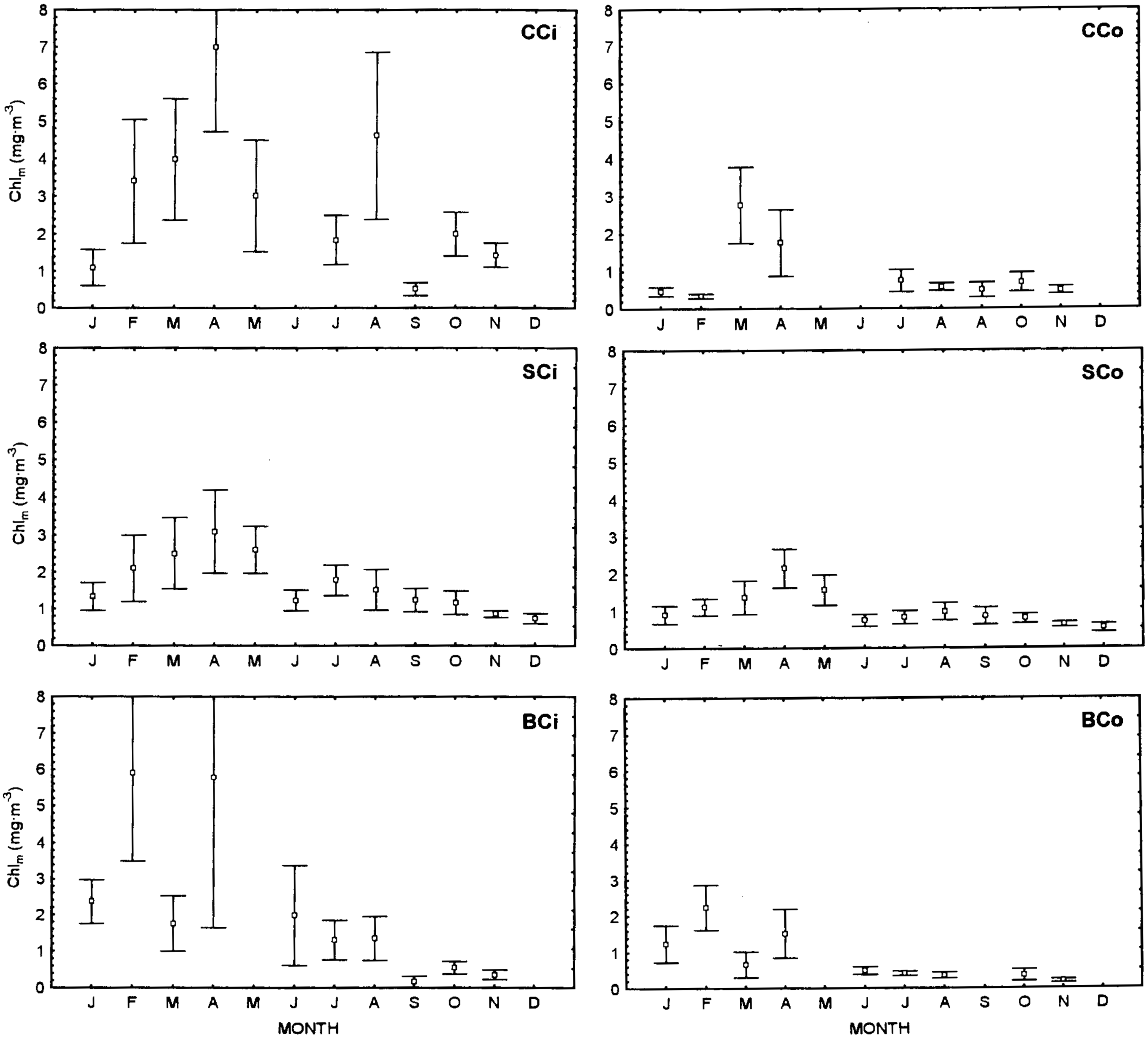

Figure 6. Monthly mean chlorophyll concentration at the DCM for each subregion. *Bars* are the 95% confidence intervals.

During the cool season, there is no significant variation of MChl$_m$ in the north-south direction (figure 8c). Nevertheless, during the warm season there was a significant decrease of MChl$_m$ from north to south (figure 8d). The overall mean of Z$_m$ (MZ$_m$) showed a difference of 30–40 m between inshore and offshore subregions, with larger values for the latter (figure 8e, f). The MZ$_m$ generally increased from north to south.

The MChl$_m$/MChl$_s$ ratio increased both from inshore to offshore and from north to south during the cool season (not illustrated). The largest difference for this season was 1.7 for CCi to 4.5 for BCo. During the warm season, the MChl$_m$/MChl$_s$ ratio did not follow a general trend; it increased from inshore to offshore only in the CC and BC regions (from 3.0 to 4.2); in the SC region there was no significant difference. Also, during the warm season there was no significant change of the MChl$_m$/MChl$_s$ ratio from north to south in the whole study area (not illustrated).

We calculated the mean of all Chl$_m$ and the mean of all Z$_m$ for each subregion and season and for each surface-chlorophyll concentration category (CMChl$_m$ and CMZ$_m$), as well as the mean of all Chl$_s$ values within each category (CMChl$_s$; table 3). In some cases, graphs

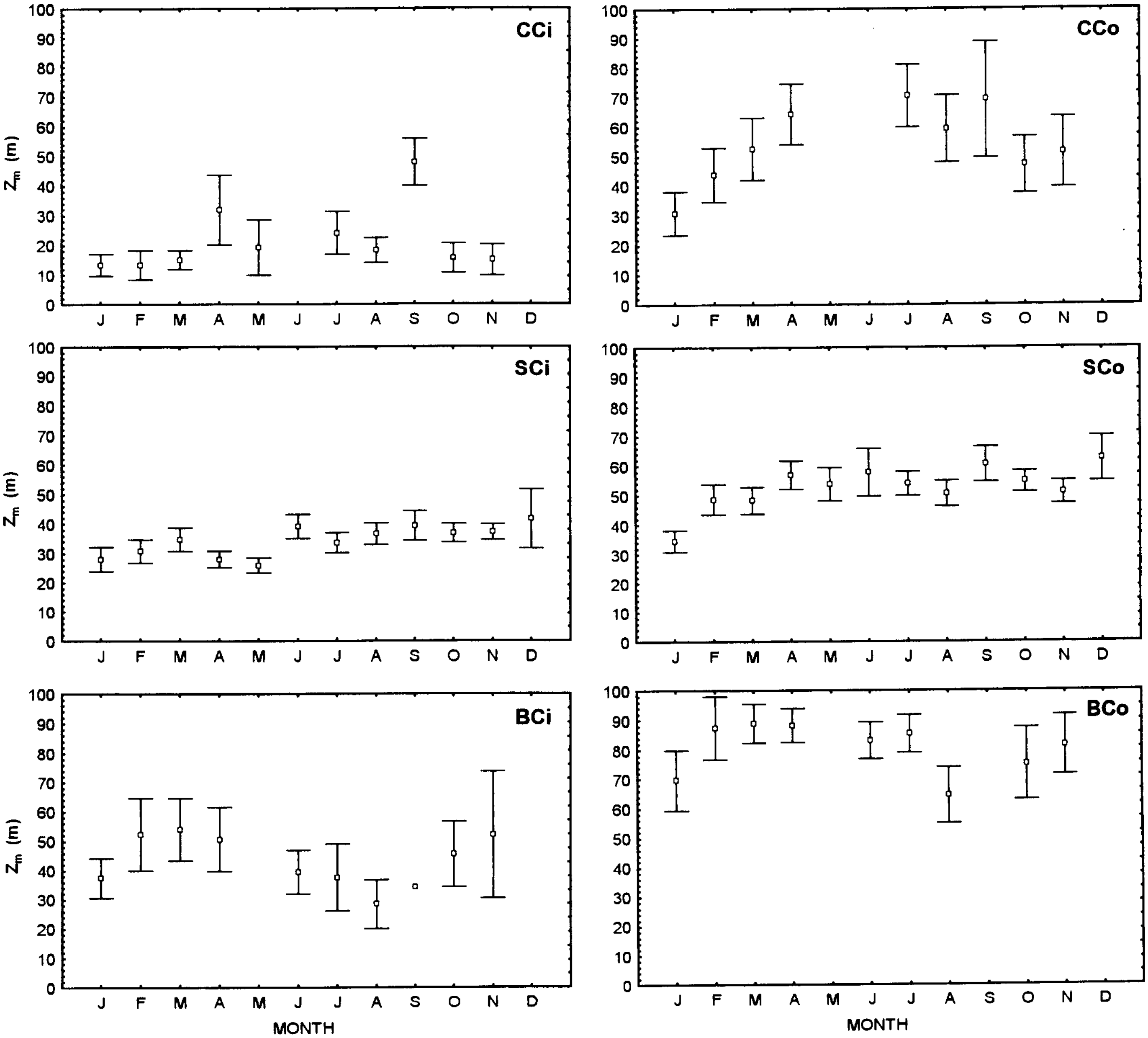

Figure 7. Monthly mean DCM depth (Z_m) for each subregion. *Bars* are the 95% confidence intervals.

of $CMChl_m$ versus $CMChl_s$ suggest a positive exponential relationship, and in other cases they show a linear relationship (not illustrated). Something similar is shown by the mean of all Z_m's for each subregion and season (CMZ_m), but it was either an exponential or linear decrease, instead of an increase (not illustrated).

We built simple linear regression models of $CMChl_m$, or ln $CMChl_m$, as functions of either $CMChl_s$ or ln $CMChl_s$, and we did the same for CMZ_m. Adding surface T °C to the models as one more independent variable did not contribute significantly to the improvement of the correlation coefficient (r) at the 95% confidence level.

Thereafter, we chose the models with the largest r for each subregion and season (table 4). All chosen regression models have r greater than 0.90, except for the CMZ_m models for the cool season of CCo and BCo, and the CMZ_m model for the warm season of CCi. The regression models for the warm season of BCo are strongly limited by the fact that we only had data for chlorophyll categories one, two, and three. Nevertheless, these three points fell close to the straight line ($r > 0.99$).

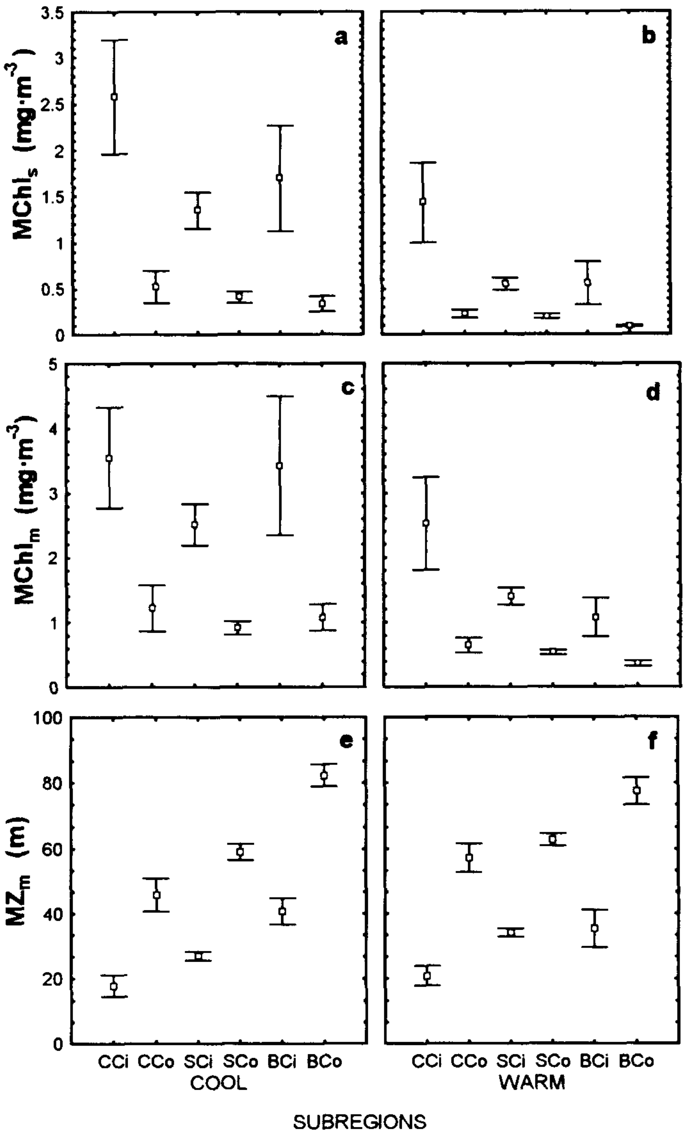

Figure 8. Overall mean for each subregion and season: *a* and *b*, surface chlorophyll concentration; *c* and *d*, chlorophyll concentration at the DCM; *e* and *f*, DCM depth. *Bars* are the 95% confidence intervals.

In most cases, our regression models explain up to 98% of the total sums of squares of CMChl$_m$ and CMZ$_m$ (table 4). Using data from off Southwest Africa, Baja California, and Peru, Lorenzen (1970) found a high linear relationship between ln Chl$_s$ and the logarithm of the integrated Chl for the whole euphotic zone (r = 0.90). Hayward and Venrick (1982) also found Chl$_s$ correlated with integrated chlorophyll (r = 0.86) in the CCS. However, the latter authors reported a lack of correlation of surface and integrated chlorophyll in the central North Pacific. It is necessary to analyze available data from the central North Pacific to study a possible correlation of CMChl$_s$ with CMChl$_m$ and CMZ$_m$.

Our algorithms are not capable of predicting the instantaneous Chl$_m$ and Z$_m$ for a particular geographic location. In other words, when our algorithms are applied to estimate CMChl$_m$ and CMZ$_m$, these predicted values should be used for the whole area with all the Chl$_s$ values within the respective chlorophyll category, within the corresponding subregion, and for the whole season.

ACKNOWLEDGMENTS

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TABLE 3

Means of Chl_s, Chl_m, and Z_m for Each Subregion, Season, and Category

		Cool season				Warm season			
Subregion	Category	$CMChl_s$	$CMChl_m$	CMZ_m	*n*	$CMChl_s$	$CMChl_m$	CMZ_m	*n*
CCi	1	0.07	0.41	69.8	2	0.08	1.39	10.9	2
	2	0.10	0.34	31.6	1	0.14	0.63	47.6	10
	3	0.28	0.52	28.5	6	0.30	0.91	32.1	30
	4	0.99	1.70	16.7	46	1.09	2.73	14.8	49
	6	3.49	5.44	16.7	17	3.06	3.92	9.6	12
	7	7.75	8.95	11.8	13	9.07	9.95	5.1	5
CCo	1	0.07	0.77	75.6	12	0.06	0.38	79.6	41
	2	0.13	0.36	54.5	22	0.13	0.57	60.5	48
	3	0.32	0.50	28.5	26	0.29	0.76	40.5	30
	4	0.98	2.43	43.4	22	0.72	0.87	17.5	14
	6	2.48	6.45	43.1	2	2.27	2.33	8.3	1
	7	6.24	6.81	14.0	1				
SCi	1	0.89	0.71	49.0	10	0.80	0.67	52.3	17
	2	0.15	0.79	48.7	118	0.14	0.82	48.6	202
	3	0.31	1.34	32.5	176	0.29	1.17	34.1	253
	4	0.71	1.27	18.2	124	0.72	1.73	18.2	83
	5	1.39	2.61	16.0	111	1.37	2.41	12.0	47
	6	3.01	5.11	14.0	63	3.27	4.26	8.7	31
	7	9.25	13.01	10.8	39	7.33	8.85	11.0	3
SCo	1	0.72	0.44	90.4	163	0.75	0.34	82.7	229
	2	0.13	0.49	65.4	191	0.13	0.52	62.1	259
	3	0.33	0.59	36.6	109	0.29	0.69	38.4	104
	4	0.68	1.43	36.4	87	0.70	0.83	17.2	23
	5	1.42	2.95	30.6	37	1.33	1.78	12.6	12
	6	2.58	3.92	14.2	16	3.05	3.37	9.8	4
	7	8.34	10.04	15.8	3				
BCi	1	0.82	0.67	68.9	17	0.85	0.29	71.7	4
	2	0.14	0.75	60.7	42	0.13	0.47	48.4	25
	3	0.27	1.19	35.9	14	0.31	1.38	31.5	11
	4	0.72	1.48	18.9	11	0.67	0.93	12.1	6
	5	1.43	3.38	28.6	26	1.28	1.72	11.6	6
	6	3.06	6.53	23.3	19	2.67	4.01	9.4	3
	7	9.75	15.23	11.5	13	5.17	5.17	0.0	1
BCo	1	0.07	0.38	93.0	97	0.06	0.29	84.7	60
	2	0.12	0.45	78.3	52	0.11	0.45	67.4	27
	3	0.29	0.94	60.1	5	0.27	0.62	39.1	5
	4	0.73	3.02	78.3	22				
	5	1.35	4.68	67.8	9				
	6	2.57	3.73	25.4	9				
	7								

TABLE 4

Regression Equations to Estimate $CMChl_m$ and CMZ_m as Functions of $CMChl_s$, for Each Subregion and Season

Province	*n*	Cool season	*r*	*n*	Warm season	*r*
CCi	7	$CMChl_m = 0.4603 + 1.1511 (Chl_s)$ $\ln CMZ_m = 3.0480 - 0.3022 (\ln Chl_s)$	0.99 −0.91	7	$CMChl_m = 0.9855 + 0.9914 (Chl_s)$ $\ln CMZ_m = 3.1286 - 0.1775 (Chl_s)$	0.99 −0.76
CCo	7	$CMChl_m = 3.7055 + 1.5930 (\ln Chl_s)$ $\ln CMZ_m = 3.9875 - 0.2023 (Chl_s)$	0.92 −0.82	6	$\ln CMChl_m = 0.2956 + 0.4713 (\ln Chl_s)$ $\ln CMZ_m = 2.6991 - 0.6469 (\ln Chl_s)$	0.96 −0.99
SCi	7	$CMChl_m = 0.6877 + 1.3436 (Chl_s)$ $\ln CMZ_m = 3.0280 - 0.3576 (\ln Chl_s)$	0.99 −0.97	7	$CMChl_m = 0.7666 + 1.1021 (Chl_s)$ $\ln CMZ_m = 2.8954 - 0.4274 (\ln Chl_s)$	0.99 −0.95
SCo	7	$CMChl_m = 0.5959 + 1.1577 (Chl_s)$ $\ln CMZ_m = 3.3829 - 0.3836 (\ln Chl_s)$	0.99 −0.95	6	$CMChl_m = 0.3273 + 1.0018 (Chl_s)$ $\ln CMZ_m = 2.8177 - 0.6168 (\ln Chl_s)$	0.99 −0.98
BCi	7	$CMChl_m = 0.8380 + 1.5113 (Chl_s)$ $\ln CMZ_m = 3.2888 - 0.3410 (\ln Chl_s)$	0.99 −0.92	7	$CMChl_m = 0.5707 + 0.9679 (Chl_s)$ $\ln CMZ_m = 3.7434 - 0.7169 (Chl_s)$	0.96 −0.94
BCo	6	$\ln CMChl_m = 1.0013 + 0.7648 (\ln Chl_s)$ $\ln CMZ_m = 4.4986 - 0.4244 (Chl_s)$	0.96 −0.88	3	$CMChl_m = 0.9235 + 0.2277 (\ln Chl_s)$ $CMZ_m = -2.3330 - 32.24 (\ln Chl_s)$	0.99 −0.99

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FILTERING APPARATUS AND FEEDING OF THE PACIFIC MACKEREL (*SCOMBER JAPONICUS*) IN THE GULF OF CALIFORNIA

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ABSTRACT

The filtering apparatus and the stomach contents of 350 Pacific mackerel (*Scomber japonicus*) were examined from sizes ranging between 80 and 280 mm standard length (SL). Fish were collected in the Gulf of California in 1993 and 1994. Analysis of the filtering apparatus showed that the adults of the species employ filter feeding because they have a small gill-raker gap, and that juveniles, which have the greatest gill-raker gap, are particle-feeders. Analysis of the stomach contents with the index of relative importance (IRI) showed that the most meaningful prey categories were fish larvae (*Engraulis mordax* and *Sardinops caeruleus*) followed by crustacean larvae (brachyurans and stomatopods), as well as calanoid copepods (*Calanus pacificus*, *Acartia* sp., and *Paracalanus* sp.). This study shows that the Pacific mackerel is a facultative carnivore that prefers zooplanktonic and micronektonic prey whose variability depends on seasonal changes. Because of its feeding habits, the fish is placed on the third and fourth trophic levels in the epipelagic environment of the Gulf of California.

INTRODUCTION

The Pacific mackerel, *Scomber japonicus* Houttuyn 1782, is a cosmopolitan species distributed in tropical and subtropical waters of the Atlantic, Indian, and Pacific Oceans, as well as in their marginal seas (Collette and Nauen 1983).

In the Eastern Pacific, the most important population is distributed in the California Current System, including the Gulf of California, where it is associated with marginal, nearshore upwelling. In the Gulf of California, the fish is distributed in the central and southern provinces in nearshore waters (Roedel 1948; Walker 1953).

Because of the importance of the Pacific mackerel fishery, many studies have been made, mostly related to its fisheries biology. These studies include age and size evaluations, reproductive and growth ratios, and migratory pathways (Kramer 1969; Schaefer 1980). But quantitative studies on its feeding ecology are scarce (Molina-Ocampo 1993).

The main objective of this study is to assess and describe the functional morphology of the filtering apparatus and its implications in food retention, as well as the composition and variability of the diet of the Pacific mackerel during four interannual periods.

METHODS

We collected 350 specimens of Pacific mackerel from four experimental cruises in the Gulf of California carried out in August 1993 (13 stations, 110 fish); November 1993 (5 stations, 80 fish); January 1994 (2 stations, 80 fish); and September 1994 (4 stations, 80 fish). All samples were taken at night in the central and northern gulf (figure 1), with a midwater trawl with an 8-mm-opening mesh net. The size of fish caught was fairly homogeneous within three intervals of standard length (SL): 0–170 mm, 171–200 mm, and >200 mm. Each fish was

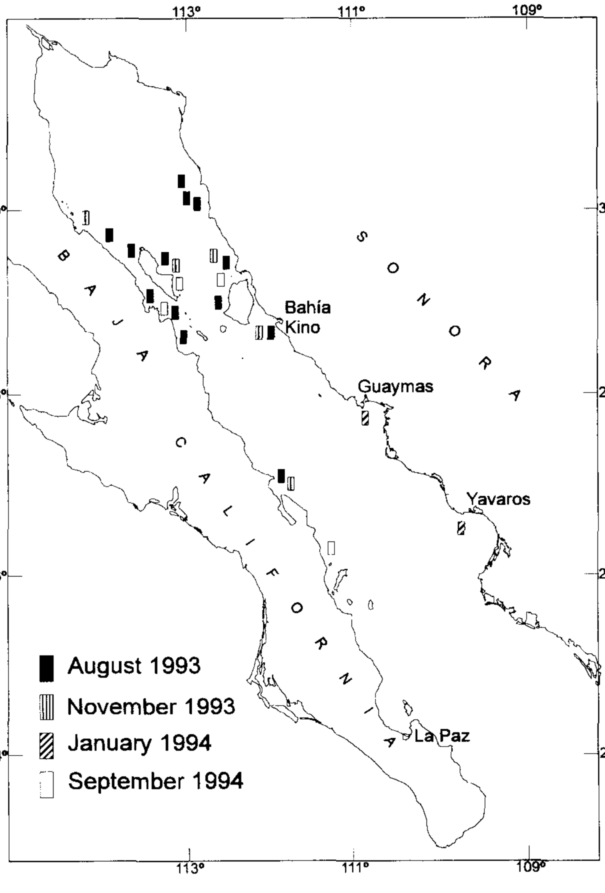

Figure 1. Study area showing locations and dates of collections of Pacific mackerel (*Scomber japonicus*) in the Gulf of California.

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injected with 4% buffered formalin in the gastric cavity to avoid degradation of the stomach contents and loss of food material.

At the laboratory, the fishes were measured and dissected. The head was separated from the body, and the first branchial arch was removed from the main branchial basket in order to make counts and metric measures (Magnuson and Heitz 1971; Hammann 1985). The digestive tract was removed from the gastric cavity to make counts and gravimetric measures (Hyslop 1980; Molina-Ocampo 1993).

The stomach contents were recovered, placed in a 50-ml glass dish, and stained for 24 h in Bouin solution to facilitate the isolation and identification of food items (López-Martínez 1991). All examinations of the stomach contents were made with a stereoscopic microscope; the recognizable food items were identified to the lowest possible taxonomic level. Pielou's sample size method was used to determine the minimum sample size (Hoffman 1978).

We used the index of relative importance (IRI) described by Pinkas et al. (1971) to assess the importance of food items in the fish diet. The IRI equation can be expressed as

$$\mathrm{IRI}_j = (\%N_j + \%V_j) \times \%FO_j$$

where j is a taxon or prey category present in the stomach contents; $\%N$ is the percent number; $\%V$ is the percent volume; and $\%FO$ is the percent frequency of occurrence of j. These values were calculated from the following equations:

$$\%N_j = \frac{n_j}{\sum_{j=1}^{n} \mathrm{N}} \times 100$$

$$\%V_j = \frac{v_j}{\sum_{j=1}^{v} \mathrm{V}} \times 100$$

$$\%FO_j = \frac{e_j}{E} \times 100$$

where n_j and v_j are the numeric and volumetric ratio of j; e_j is the number of stomachs containing j; and E is the total number of examined stomachs. We calculated the unit volume for each prey category by using stereometric equations (Molina-Ocampo 1993).

We performed a chi-square (χ^2) statistical test of the stomach contents to determine if the Pacific mackerel were consuming items at random within the study period. A two-way, $R \times C$, contingency table was used, where R is the number of prey categories and C is the study period (Bernard et al. 1985).

The IRI makes it possible to rank the prey category by this combination index, and is represented in a three-way graph. Here, a rectangle with a vertical axis comprised of $\%N$ and $\%V$, and the horizontal axis, re-zeroed for each prey, representing $\%FO$, indicates the importance of the prey as a food item (Cailliet et al. 1990).

The first branchial arch belonging to each of 53 Pacific mackerel ranging from 80 to 280 mm SL was measured completely and by segments. We measured the length and width of each segment and counted the gill rakers. We also measured the gill-raker gap of 73 specimens ranging from 95 to 260 mm SL, and used the SL for regressions. We used a stereoscopic microscope equipped with an ocular micrometer with sensitivity of 0.01 mm for these examinations.

RESULTS AND DISCUSSION

Filtering Apparatus

The Pacific mackerel's branchial basket is formed by five pairs of branchial arches; the most external and largest has gill rakers on its external margin (figure 2). A feeding function specifically related to food retention is attributed to the gill rakers: they present a series of marginal teeth that, when interlocked with those of the adjacent gill rakers, form an extremely fine sieve. No gill rakers can be seen in arches 2 through 4; instead, there are protuberances that tend to disappear as the arches appear. The fifth branchial arch is completely modified as an epibranchial organ possessing a feeding function.

No significant bilateral differences were found in the development of the first branchial arch; the ceratobranchial segments on both sides of six specimens ranged in size as follows: 149, 157, 166, 187, 196, and 230 mm. Gill-raker length, as well as width ($t = 0.68$; $p = 0.05$), and the dimension of the gill-raker gap ($t = 0.29$; $p = 0.05$) had no significant morphometric variation.

The development of the filtering apparatus, indicated by the growth of the first branchial arch, is faster in the ceratobranchial segment than in the epibranchial and hypobranchial segments, which have very similar growth rates (figure 3). The length and width of the gill rakers measured in the first branchial arch showed a growth rate that increases with increasing development of the arch (figures 4 and 5). Furthermore, since both measures are greater than the growth rate of the branchial arch, the gill-raker gap in the whole filtering apparatus becomes reduced as the fish reaches its maximum length (figure 6). This morphological change is important, since the alimentary quality of smaller particles is greater.

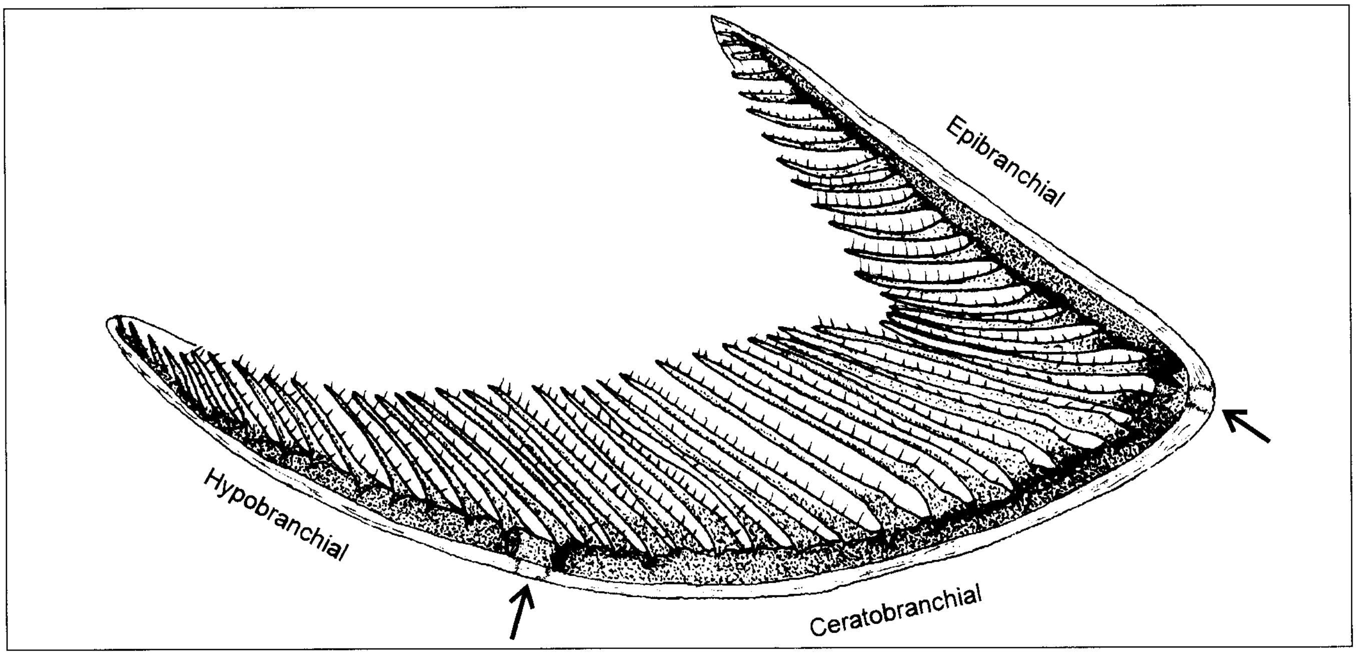

Figure 2. First branchial arch (*left side*) of a 196-mm SL specimen of Pacific mackerel. *Arrows* indicate the cartilaginous junctions of the three segments composing the arch.

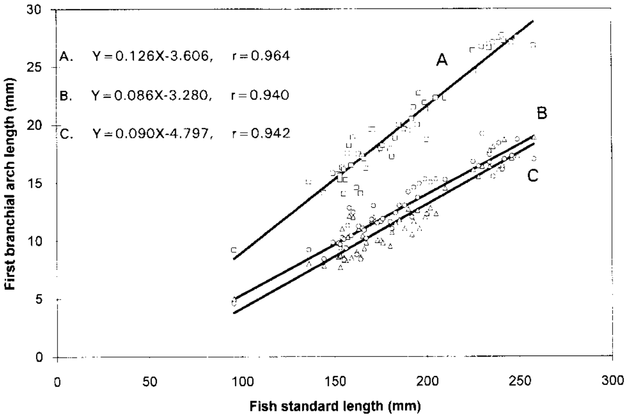

Figure 3. First branchial arch's segment dimensions versus standard length in the Pacific mackerel: *A*, ceratobranchial; *B*, hypobranchial; and *C*, epibranchial segments (*n* = 53).

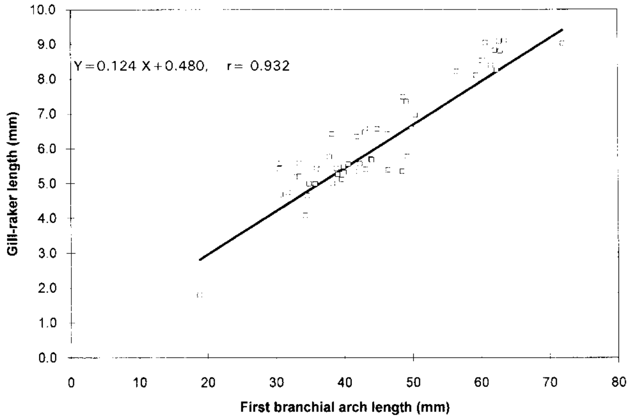

Figure 4. First branchial arch's gill-raker length versus arch length in the Pacific mackerel (*n* = 53).

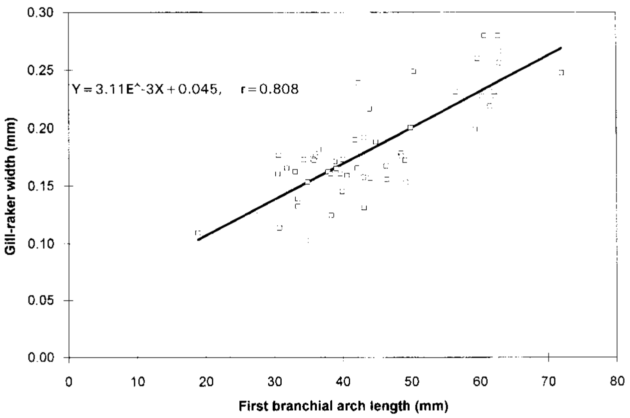

Figure 5. First branchial arch's gill-raker width versus arch length in the Pacific mackerel (*n* = 53).

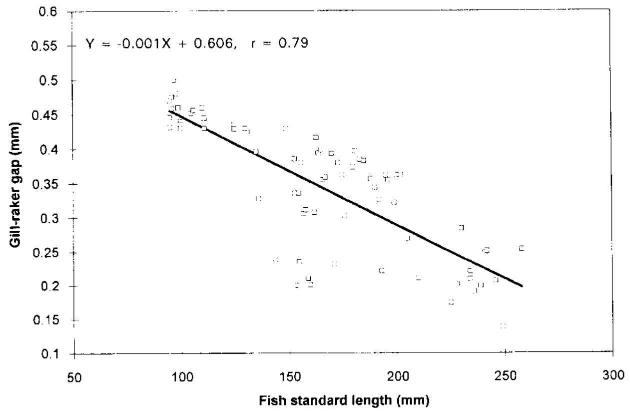

Figure 6. First branchial arch's gill-raker gap versus standard length in the Pacific mackerel (*n* = 73).

TABLE 1
Raw Data (%*N*, %*V*, and %*FO*) for Prey Categories and Index of Relative Importance (IRI) of the Pacific Mackerel (*Scomber japonicus*) Collected in the Gulf of California

	%*N*	%*V*	%*FO*	IRI	%IRI
August 1993					
Fish larvae	16	99.57	100	11,557	60.60
Crustacean larvae	30	0.21	100	3,021	15.84
Copepods	17	0.10	100	1,710	8.97
Euphausiids	6	0.04	75	453	2.38
Amphipods	6	0.03	75	452	2.37
ONI*	25	0.05	75	1,878	9.85
November 1993					
Fish larvae	6	98.45	100	10,445	54.21
Crustacean larvae	35	0.65	100	3,565	18.50
Copepods	7	0.11	100	711	3.69
Euphausiids	41	0.66	100	4,166	21.62
Chaetognaths	4	0.10	50	205	1.06
ONI*	7	0.03	25	175	0.91
January 1994					
Fish larvae	3	96.56	100	9,956	50.62
Crustacean larvae	41	1.63	100	4,263	21.68
Mollusc larvae	1	0.01	75	75	0.39
Copepods	27	0.89	100	2,789	14.18
Euphausiids	24	0.81	100	2,481	12.61
ONI*	4	0.10	25	102	0.52
September 1994					
Fish larvae	24	99.70	100	12,370	68.74
Crustacean larvae	41	0.19	100	4,119	22.89
Copepods	8	0.03	75	602	3.35
Euphausiids	4	0.02	50	201	1.12
Amphipods	5	0.02	50	251	1.39
ONI*	18	0.04	25	451	2.51

*Others not identified

Feeding Habits

The food items found in the stomachs of the Pacific mackerel show a facultative skew on the trophic spectrum, resulting in a high incidence of zooplanktonic and micronektonic prey as single food resources. The index of relative importance (IRI) associates seven prey categories—fish larvae, crustacean larvae, mollusk larvae, copepods, euphausiids, amphipods, and chaetognaths—as the main dietary components for the Pacific mackerel (table 1).

The diet composition based on the IRI during the study period (figures 7 and 8) shows that fish larvae were the largest component, contributing a minimum of 50.49% (for January 1994) and a maximum of 66.97% (for September 1994). The main prey category was the northern anchovy (*Engraulis mordax*), followed by clupeid larvae (probably belonging to the species *Sardinops caeruleus*), as well as myctophids, carangids, and sciaenids (figure 9).

The second group in relative importance was crustacean larvae, mainly composed of brachyuran zoeas and megalopas, as well as stomatopod alimas (figure 9), contributing average values of 19.71%.

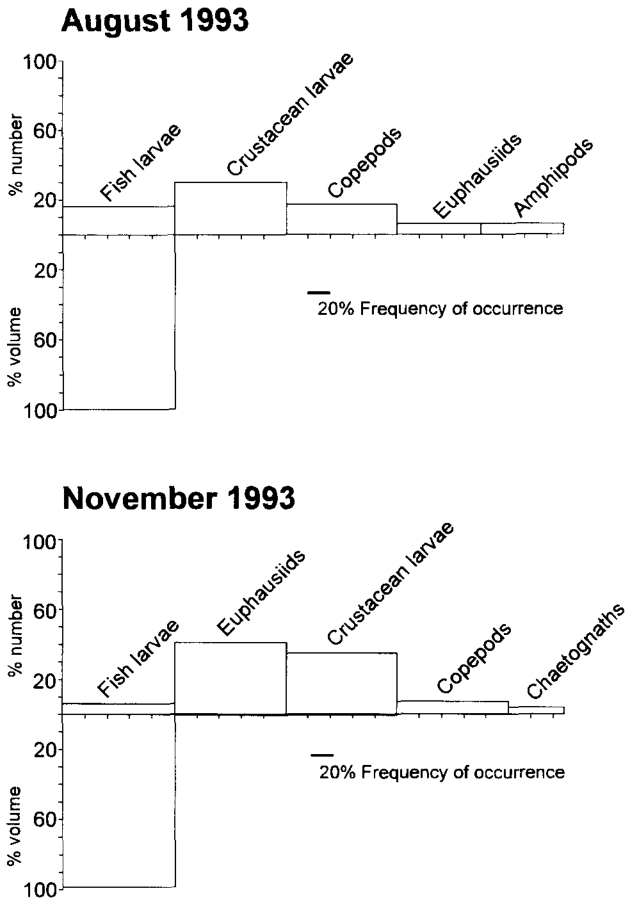

Figure 7. Graphic representation of the index of relative importance for the Pacific mackerel's diet during August and November 1993 ("others not identified" are not included).

The remaining groups were either present or absent at certain times and had a wider variation in IRI values. The copepods make up the transition group.

The taxonomic composition of the three trophic groups that are the major contributors to the diet of the Pacific mackerel is shown in figure 9.

The chi-square analysis for homogeneity showed a dietary variability during the study period (table 2) due to the fact that the abundance and availability of the food resources in the environment are a function of annual seasonal changes.

CONCLUSIONS

These studies on the filtering apparatus of the Pacific mackerel show that this species is a facultative-carnivorous feeder which employs particle feeding in preference to filter feeding. We found that a relation between the gill-raker gap and the ingested particle size could exist: the gill-raker gaps are smaller in the largest fish.

According to the IRI analysis, Pacific mackerel prefer certain prey categories, and consumption depends

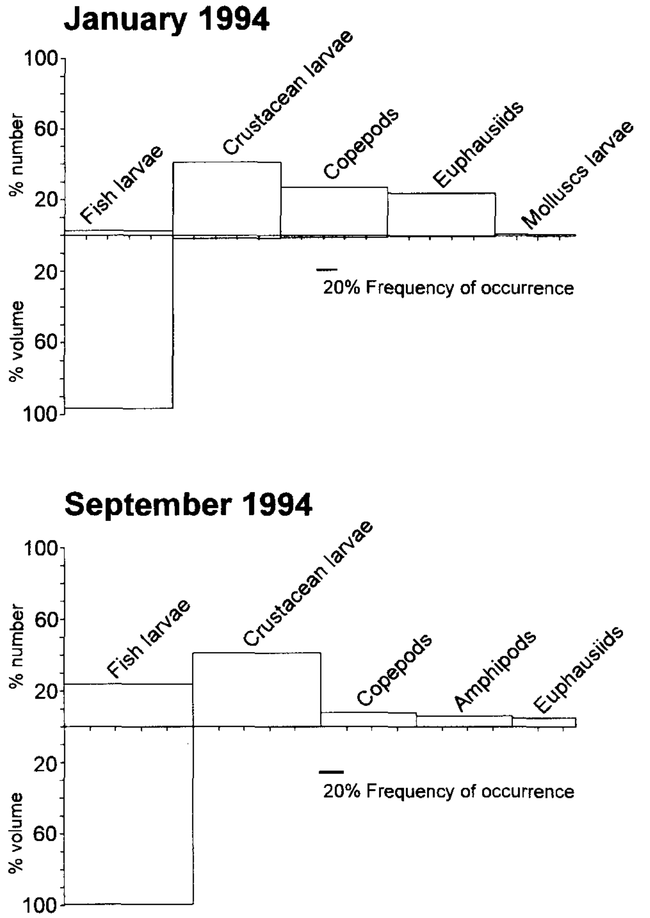

Figure 8. Graphic representation of the index of relative importance for the Pacific mackerel's diet during January and September 1994 ("others not identified" are not included).

TABLE 2
Observed (Upper) and Expected (Lower) Values of the Percent Abundance for Seven Prey Categories of the Pacific Mackerel (*Scomber japonicus*) Collected in the Gulf of California

Prey category	Aug. 1993	Nov. 1993	Jan. 1994	Sep. 1994	Total
Fish larvae	16	6	3	24	49
	10.62	13.17	13.60	11.61	
Crustacean larvae	30	35	41	41	147
	31.86	39.51	40.79	34.84	
Mollusc larvae	0	0	1	0	1
	0.22	0.27	0.28	0.24	
Copepods	17	7	27	8	59
	12.79	15.86	16.37	13.98	
Euphausiids	6	41	24	4	75
	16.26	20.16	20.81	17.77	
Amphipods	6	0	0	5	11
	2.38	2.96	3.05	2.61	
Chaetognaths	0	4	0	0	4
	0.87	1.08	1.11	0.95	
Total	75	93	96	82	346

The prey abundance was shown to be time dependent through the statistical testing of the time independence (null) hypothesis, resulting in its rejection: chi-square (χ^2) = 111.97, degrees of freedom (df) = 18, confidence intervals (p) = 0.01, critical value (α) = 34.81.

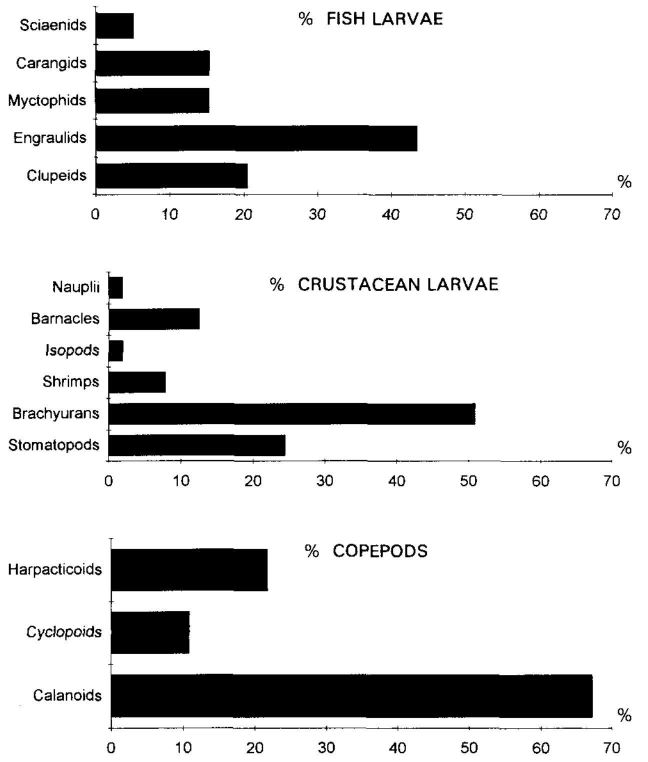

Figure 9. The three most meaningful prey categories (by taxonomic groups) in the Pacific mackerel's diet during the study period.

mostly on prey distribution and availability. These latter factors are consequences of seasonal variations.

The Pacific mackerel, which preferentially uses zooplankton and fish larvae as food, is placed on the third and fourth trophic levels in the epipelagic ecosystem of the Gulf of California.

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ANNUAL VARIABILITY OF OCEAN CURRENTS AT 350-M DEPTH OVER THE CONTINENTAL SLOPE OFF POINT SUR, CALIFORNIA

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ABSTRACT

Currents were measured at 350 m from May 1989 through February 1995 over the 800-m isobath off Point Sur, California. Mean flows were directed toward 334°T at 7.6 cm/s. The pattern of monthly mean flow reveals a distinct annual pattern: the spring transition begins in mid-April and is marked by a tripling of undercurrent speeds, onshore flow, and minimum temperatures. The strong poleward flow persists until mid-July and is accompanied by steady warming. When the flow decelerates, temperatures remain elevated until mid-December, when cooling begins.

El Niño conditions resulted in warming during much of the period between July 1991 and November 1992; no dramatic change of the current pattern was observed.

INTRODUCTION

Several recent attempts have been made to use CalCOFI data to resolve the annual cycle of currents along the central California coast. Chelton (1984) and Lynn and Simpson (1987) used 23 years of CalCOFI hydrographic data to examine the variability of geostrophic velocity relative to 500 db over the outer continental slope off Point Sur. They found poleward deep flow over the slope from June through February, with a maximum in December (about 3 cm/s at 350 m). At depth, weak equatorward flow occurred from March to May (> -2.5 cm/s).

Relatively few current measurements have been made over the slope off central California (Wickham et al. 1987; Chelton et al. 1988; Huyer et al. 1989), and these measurements show the annual cycle to be different than that inferred from geostrophy: poleward flow appears to occur in spring and summer, and is 3–5 times greater than that obtained from hydrographic data. Compared to the hydrographic measurements, the current meter data span only a short period of time (6 months–2 years), and the data reported by Wickham et al. (1987) have many gaps.

In order to better understand both the annual variability and the changes in the currents that occur during El Niño events, we began a program of current measurements over the upper slope near Point Sur, California, in 1989. Although there is considerable year-to-year variability in the observed currents at Point Sur, the six years of data that have been obtained for 350 m reveal a consistent pattern of annual variability, which is described below. This annual pattern will also be used to classify and discuss the observed interannual variability of the flow.

OBSERVATIONS

Since May 1989, the Naval Postgraduate School has maintained a current meter on the continental slope due west of Point Sur, California, at 36°20'2"N, 122°10'2"W, where water depth is 800 m, roughly halfway between CalCOFI stations 67.55 and 70.53, and about 24 km from the coast. Currents, temperature, and pressure were measured with Aanderaa RCM8 vector-averaging current meters. Because of instrument failures, there is a relatively continuous record only at middepth. Unfortunately, two gaps exist in this time series, from February 7 to April 20, 1993, and from November 23, 1993, to February 9, 1994, when the mooring was cut by trawlers.

Table 1 describes the current meter installations used in the present study. The observation depth was close to 350 m, except for the seventh mooring (April 1, 1992, to April 19, 1993), when currents were observed at 260 m. To estimate the effect of the depth difference, we examined the vertical shear at the mooring site; this had been measured with acoustically tracked dropsondes on 34 occasions between April 1989 and April 1991. The mean shear and standard deviation, 260 m–350 m, was -1.0 ± 2.4 cm/s for the east component of velocity, 1.6

TABLE 1
Mid-depth Current Observations at 36°20'2"N, 122°10'2"W

Setting no.	Start date	End date	Meter depth
1	5/12/89	8/26/89	365
2	8/26/89	12/13/89	387
3	12/16/89	4/27/90	350
4	5/15/90	10/8/90	352
5	10/11/90	5/11/91	346
6	5/16/91	4/27/92	353
7	4/30/92	4/19/93	260
8	4/22/93	11/23/93	355
9	2/9/94	2/11/95	350

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± 1.9 cm/s for the north component. Given the uncertainty and small difference, we used the 260-m current data without adjustment. From 19 CTD casts at the mooring location, the temperature difference and the standard deviation of the temperature difference between 260 m and 350 m were 0.76°C ± 0.14°C. The temperature gradient was nearly the same at both depths—0.0084°C/m at 260 m and 0.0082°C/m at 350 m. So we adjusted the 260-m temperature data by simply subtracting 0.76°C.

The Aanderaa current meters acquired hourly data. A ducted paddlewheel is used to measure speed, and a vane to measure direction. Paddlewheel counts are converted to speed, and every 1.2 minutes the speed and direction are converted to north and east velocity components, which are in turn summed over the one-hour sampling period. The speed measurement is accurate to ±1 cm/s for speeds between 2 cm/s and 50 cm/s (the rotor stalls at speeds less than 2 cm/s, and accuracy is 2% of speed when speed is greater than 50 cm/s). The accuracy (precision) of direction is ±3 degrees (0.35 degrees). Temperature and pressure are sampled once per hour with an accuracy (precision) of ±0.05°C (±0.025°C) and ±4 db (±0.4 db), respectively. Compass, temperature, and pressure calibrations are done before and after deployment. Hourly data were filtered to remove tides by means of a cosine-Lanczos filter with a width of 121 hours and a half-power point of 46.6 hours. The resulting time series was decimated to four samples per day and was further subsampled for various plots.

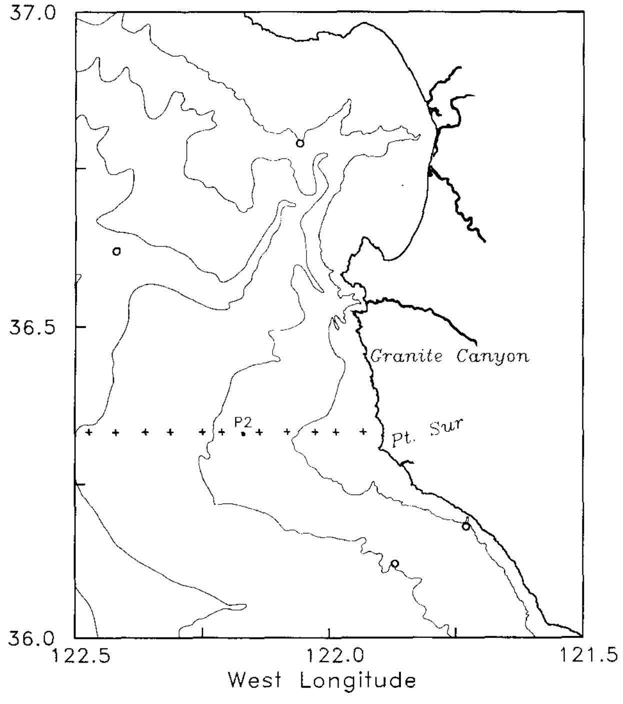

Figure 1. Position of the current meter mooring (P2) off Point Sur, California. Open circles (○) indicate the position, from north to south, of CalCOFI stations 67.50, 67.55, 70.51, and 70.53 (these stations were last occupied in October 1984). Crosses (+) indicate the location of POST hydrographic stations (Tisch et al., 1992). 200-m, 1,000-m, 2,000-m, and 3,000-m isobaths are shown.

Figure 1 shows the mooring location, bathymetry, coastline, nearby CalCOFI hydrographic stations, and stations used by Tisch et al. (1992). The bathymetry to the south reflects the general trend of the California coastline; the Monterey Submarine Canyon modifies the bathymetry to the north. This causes the isobaths near the mooring to tend north-south in contrast to the NNW orientation of the coast. During the upwelling season from mid-March through September, a wedge of cold, upwelled water is found off Point Sur, and offshore-flowing jets of cold water are occasionally observed in AVHRR imagery during July–September (Breaker and Mooers 1986).

RESULTS

Mean Conditions

Figure 2 is the scatter diagram formed by the end points of daily current vectors. The elliptical shape is due to the constraint the coast imposes upon across-shore flow, but differs from those typical of shelf regions (figure 7 in Huyer 1990) in the scattering of points to the southwest because of currents that flow offshore. The mean current was directed toward 334°T at 7.6 cm/s. The principal mode for the speed histogram was 4 cm/s, and the maximum speed was 44.1 cm/s. The principal

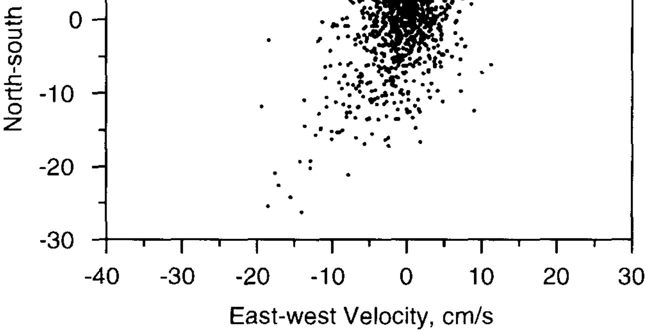

Figure 2. Scatterplot of daily 350-m current observations, May 12, 1989, to February 11, 1995. Dots have been placed at the heads of the vectors representing the currents.

mode for the direction histogram was 338°T, and the principal axis was directed toward 345°T. The direction of the mean flow partakes of the trend of the isobaths upstream of the flow for both poleward and equatorward flow. For poleward flow, this creates a local divergence to the north of Point Sur because the local topography is oriented north–south. This divergence may contribute to anticyclonic flow observed off Monterey Bay (Tisch et al. 1992).

The integral time scales[2] for flow along the major and minor axes were 18 and 8 days, respectively. Standard deviations were 9.7 cm/s and 4.1 cm/s for the major and minor axes. The maximum and minimum for the alongshore (onshore) flow were 43.6 and −21.8 (15.0 and −25.6). Equatorward flow was observed only 22% of the time.

The mean temperature was 7.18°C, and its standard deviation was 0.31°C. The integral time scale for temperature was greater than that obtained for either velocity component—26 days. The maximum temperature—8.14°—occurred on August 9 (year-day 222), 1992, and the minimum temperature—6.26°—occurred on May 1 (year-day 122), 1994.

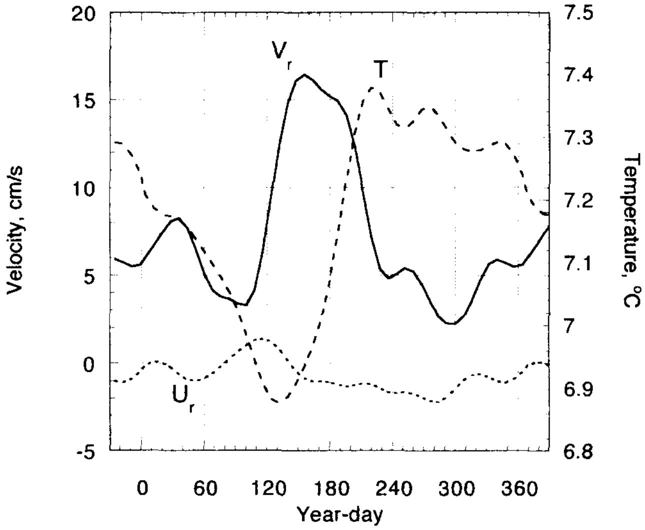

Figure 3. Annual variability of currents and temperature at 350-m depth. Alongshore currents (V_r) are represented by the *solid line*, across-shore (U_r) currents by the *dotted line*, and temperature (T) by the *dashed line*. Data have been averaged for all years in successive 8-day blocks, then smoothed again to represent monthly averages. To clarify the seasonal variability that occurs at the beginning and end of the year, the time has been extended so that 20 days of December data are plotted to the left of January 1, and 20 days of January data are plotted to the right of December 31.

Annual Variability

We constructed an average annual cycle by first collecting the data into calendar years, then averaging across all years in 8-day blocks. No attempt was made to synthesize missing data; the divisor for averaging was simply reduced accordingly when gaps were included. These data were in turn smoothed by a filter with a half-power point at 32 days, resulting in a series of "monthly averages" with 8-day temporal resolution (figure 3).

The alongshore component of velocity (directed toward 345°T) was dominated by a strong pulse in poleward flow that occurred between April 17 (year-day 108) and August 23 (year-day 236). The poleward flow accelerated from 3 cm/s to 16 cm/s between April 9 and May 27 (year-days 100 to 148) and remained greater than 14 cm/s through July 14 (year-day 196). The poleward flow decreased to 5 cm/s on August 23 (year-day 236), and remained at about 5 cm/s for the rest of the year. Before the onset of this large pulse in poleward flow, a smaller pulse of poleward flow occurred on February 5 (year-day 36). The onshore component of velocity was positive (flow toward the coast) at the start of the poleward pulse, but became offshore when the poleward flow reached 16 cm/s. The strength of the offshore flow increased slowly to −2 cm/s on September 27 (year-day 271), thence relaxing to −1 cm/s by November 3 (year-day 308).

Almost all the temperature variability occurred in the first 200 days of the year. Beginning on December 5 (year-day 340) of the previous year, the temperature decreased from 7.29°C to the minimum, 6.87°, on May 11 (year-day 132). This occurrence of a temperature minimum agrees with the mid-May occurrence of maximum density at 350 m at CalCOFI station 70.53 (figure 18 in Lynn and Simpson 1987), which is located southeast of our mooring (figure 1). The temperature minimum occurred one month after the start of the poleward pulse and at the end of the associated onshore flow. Temperature then increased, reaching a maximum of 7.37°C on August 7 (year-day 220). Between August 7 (year-day 220) and December 21 (year-day 356), the temperature remained high, between 7.3° and 7.2°.

Although the monthly average middepth flow over the upper continental slope off Point Sur was poleward all year, the flow had a clear annual character. The poleward acceleration of flow in April, which begins with onshore flow and minimum temperature, marks the beginning of the transition to summer conditions. The acceleration of poleward flow is accompanied by a steady increase in temperature. When the poleward flow decreases in early August, neither the temperature nor the offshore flow changes character. Poleward flow reaches a minimum in early October, and temperatures begin to cool in December. It is unclear which of these latter events represents a fall transition.

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[2] The integral time scale is a correlation time scale and a measure of the period of the process that dominates a given time series. Observations separated by a period of time equal to the integral time scale can be assumed to be independent for statistical purposes.

The relationship between alongshore flow and temperature is complex. Geostrophic adjustment to an increase in poleward flow would cause isopycnals (isotherms) to deepen toward the coast, resulting in a temperature increase at a fixed depth on a mooring. Temperature increases could also be caused by a regional deepening of the pycnocline (thermocline), which involves no change in the alongshore flow. Finally, for a given stratification, advection of equatorial water from the south could increase the temperature (and salinity) on a density surface. Our single current meter and mooring cannot distinguish between these. Evidence that some of the observed warming is associated with advection of equatorial waters has been provided by Lynn and Simpson (plate 2, 1987), who show the seasonal characteristics of σ_t = 26.6 along CalCOFI line 70. At station 70.53, the minimum temperature (about 7.7°C) and shallowest depth (about 210 m) of σ_t = 26.6 occurred in May, warmest temperatures (>8°C) in October, and deepest depth (>260 m) in December and January. This suggests that geostrophic adjustment is responsible for the initial spring warming but that subsequent warm temperatures were associated with advected (equatorial) waters.

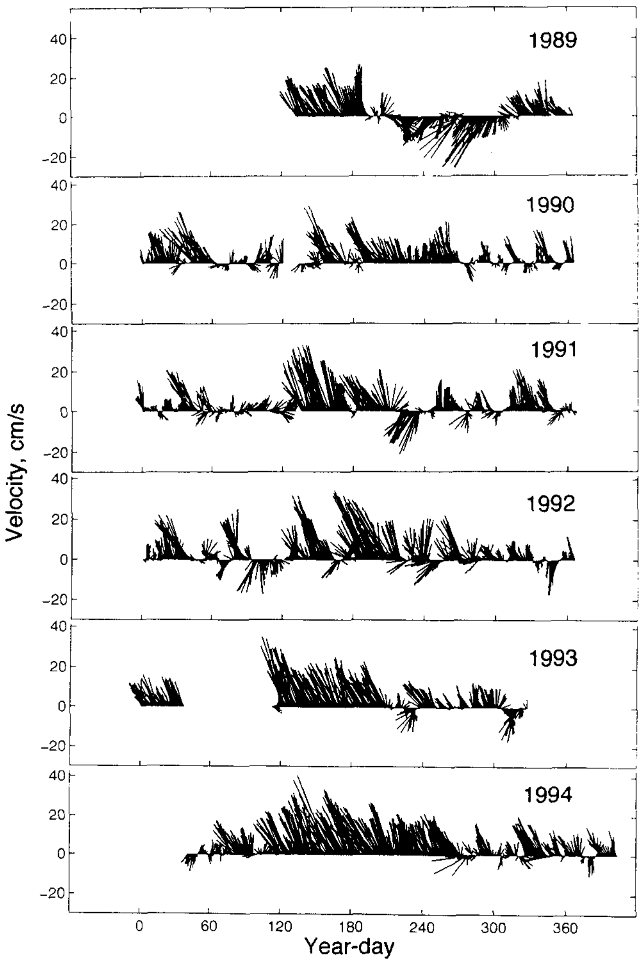

Figure 4. Time series of currents at 350-m depth. Data have been detided with a cosine-Lanczos filter with 121 hourly weights and a half-power point of 46.6 hours. Two vectors are plotted each day.

Interannual Variability

The pattern of annual variability described above provides a canonical description of the flow, which can be used to contrast year-to-year variability. Daily currents and temperatures are shown for the period 1989–94 in figures 4 and 5. In discussing these figures, we will call the strong poleward flow that occurs in the spring and summer the "spring jet," in contrast to shorter-period "poleward pulses" that occur in other months. Short-period events when the alongshore flow is equatorward and the onshore flow is less than −10 cm/s will be referred to as "squirts."

1989. The observations began on May 12, 1989, well after the spring transition. The poleward velocity pulse ended in mid-July (year-day 197), and the temperature maximum occurred shortly thereafter. This was followed by what turned out to be the most anomalous flow of the entire record, a 100-day period of equatorward offshore flow, including three squirts that occurred fortnightly beginning on September 1 (year-day 245).

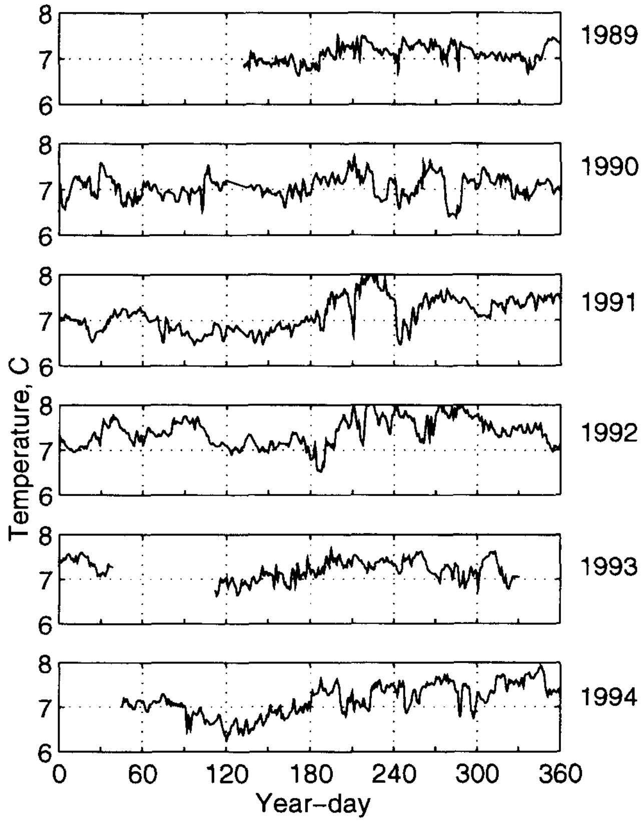

Figure 5. Time series of temperature observations at 350-m depth. Data have been detided with a cosine-Lanczos filter with 121 hourly weights and a half-power point of 46.6 hours. Two data points are plotted each day.

1990. Pulses of poleward flow occurred in January and late February. A strong onshore pulse occurred on April 10 (year-day 100), but the spring jet did not develop until June 1 (year-day 153) and persisted through the summer months until September 26 (year-day 270). The spring jet was accompanied by warming from 6.9° to 7.6°. The coldest temperature, 6.4°, occurred on October 6 (year-day 280), just after a short pulse of equatorward and onshore flow, but the temperature quickly recovered.

1991. After a short pulse of poleward flow in mid-February, the temperature cooled steadily from late February to early April. The temperature minimum, 6.5°, occurred on April 7 (year-day 98), and two weeks later the spring jet began, accompanied by onshore flow. The spring jet extended through July 28 (year-day 210), and warming continued through August 11 (year-day 224), which marked the warmest temperature, 8.0°. A squirt occurred in mid-August (year-day 230).

1992. This was an El Niño year, anomalous both because of the warm winter temperatures and the lack of a period of sustained onshore flow accompanied by equatorward or weak poleward flow during the winter. During winter the poleward flow was maintained by pulses in mid-January to mid-February and again in late March. The spring jet began on April 29 (year-day 120) and lasted until September 6 (year-day 250), although the spring jet was interrupted by equatorward and onshore flow on June 19 (year-day 171; the strongest onshore flow observed during our record). The temperature minimum, 6.5°, occurred 17 days after this onshore event. The temperature rapidly recovered, and the warmest temperature recorded during the entire record, 8.1°, was observed on August 9 (year-day 222). In late September (year-day 270), cooling began and continued through February 1993. Squirts were observed in early April (year-day 100) and in early September (year-day 250).

1993. An instrument failure occurred on February 6, and the mooring was not cycled until April 22. Data recorded on April 22 show equatorward flow, which—coupled with the observed minimum temperature, 6.6°, on April 23 and onshore flow—led us to believe that this was the beginning of the spring jet. The spring jet continued through July 23 (year-day 205), accompanied by steady warming. In mid-August (year-day 230) and early November (year-day 315), squirts occurred. Between September 21 and October 21 (year-days 265 and 295), temperature cooled by about 0.5°, but the warmest temperature of the year, 7.6°, was observed on November 6 (year-day 311). The mooring was cut by a fishing boat on Thanksgiving Day, drifted northward, and was retrieved due west of Moss Landing the following week.

1994. The mooring was reset on February 9. A poleward pulse of amplitude 18 cm/s was observed on March 25 (year-day 85), but the spring jet began on April 19 (year-day 110) and extended through September 26 (year-day 270). The temperature minimum, 6.3°, occurred on April 20 (year-day 120), and the ocean steadily warmed at 350 m through July 7 (year-day 189) to 7.6°. Flow was onshore at the start of the spring jet, and a squirt was observed in early October (year-day 280). Poleward pulses occurred in late October and late November (year-days 295 and 335), and the warmest temperature of the year, 7.9°, was observed on December 12 (year-day 347).

DISCUSSION

Subseasonal Variability

Two features of shorter period appeared in our records—poleward pulses and offshore squirts. Vertical arrays (Wickham et al. 1987; Tisch 1992) show these features to be vertically coherent throughout the water column. Yet coherence with moorings on the shelf (Chelton et al. 1988) and 25 km seaward (Tisch 1992) is low, perhaps due to the short Rossby radius, 15 km (Tisch 1992). The poleward pulses resemble Kelvin waves seen in equatorial current meter records, and Wickham et al. (1987) speculate that these features are Kelvin waves. An onshore-offshore array of current meters and pressure gauges across the upper slope is needed to definitively describe the physical character of these features.

Chelton et al. (1988) note that Point Sur appeared to be a southern boundary of a region of convergence in 1984, with poleward flow and surface waters of equatorial origin to the south, and equatorward and offshore flow and fresher surface waters to the north. Their 70-m current record shows no offshore flow. Satellite images and laboratory studies show that offshore flow of cold, upwelled waters frequently occurs at Point Sur, and the 350-m record at P2 suggests that these flows can penetrate the thermocline. Our data suggest that this occurs most frequently in the fall, after the spring jet ends.

Relationship to Granite Canyon Surface Observations

In order to see how the annual cycle at 350 m compares with surface conditions, we constructed an annual cycle of sea-surface salinity and temperature observed at Granite Canyon (figure 6). The Granite Canyon data consist of daily observations for the period 1989–94, filtered in the same manner as daily detided mooring data. During winter, sea-surface salinity at Granite Canyon was S ≈ 33.5; during March and April, there was a transition to summer conditions. During this transition, salinity increased to S > 33.8 (as a result of coastal upwelling); the rate of cooling increased; and minimum temperatures (10.7°C) occurred at the beginning of May—the

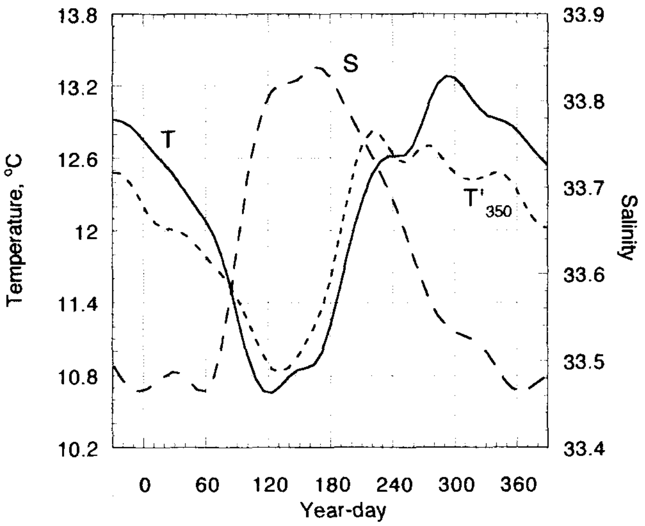

Figure 6. Annual variability of sea-surface temperature (T) and sea-surface salinity (S) at Granite Canyon, 1989–94 (the location of Granite Canyon is shown in figure 1). Data have been processed in the same manner as those shown in figure 3. The annual 350-m temperature (T'_{350}) cycle (figure 3) has been increased and amplified to ease comparison with surface data.

same time that temperature minimums were observed at 350 m.

High salts and low temperatures persisted during May and June at Granite Canyon. Beginning in July, surface waters steadily freshened and warmed. The temperatures reach a maximum of 13.3° in late October, in contrast to the 350-m temperatures, which reach a maximum in August.

Despite the fact that different processes act at the sea surface, it is clear that the spring transition from winter to summer conditions is closely linked at the surface and at middepth over the upper slope. The timing of the onset of this transition is marked by increasing salinities at the surface and by increasing poleward velocities at middepth, the latter lagging the former by 40 days. Although the spring transition has been observed to occur over a few days (Lentz 1987), especially off northern California and Oregon (Strub et al. 1987), the transition may not be as rapid along central California (Strub et al. 1987). Breaker and Mooers (1986) note that a rapid drop in temperature occurred at Granite Canyon in only 6 of the 13 years that they studied.

Annual Variability

Although at the start of this paper it was noted that previous current measurements failed to define an annual cycle (Wickham et al. 1987; Chelton et al. 1988; Huyer et al. 1989), the results of those measurements fit well with the annual cycle documented here. In 1979 and 1980, measurements were made over the continental slope just south of Point Sur at 35°9'N (Wickham et al. 1987). The annual variation that they observed included a spring transition followed by maximum poleward flow in May–June, with velocities exceeding 15 cm/s. Their observations, which spanned the period from January 10 to March 3, 1979, indicated a transition from eastward to northward flow in mid-February. In 1980, the spring transition was marked in mid-March by a southward flow, which rotated counterclockwise, becoming eastward and then poleward in late March. This period was marked by a decrease in temperature from 7.6° to 6.9°.

The measurements of Huyer et al. (1989) include the period April 1981 to August 1982 and were obtained in water 400 m deep over the upper slope at 38°5'N. At 350 m, the mean direction (338°T) was the same as observed at 350 m at Point Sur, but the mean speed (4.2) and variability (standard deviation, 7.5 cm/s) were less than observed at Point Sur. In 1982, Huyer et al. (1989) observed a spring jet in April and May, following a period of onshore flow. Sustained poleward flow also was observed in July 1981 and July–August, 1982.

Chelton et al. (1988) report on current measurements at a much shallower depth, 70 m, over the upper slope off Point Sur for the period March 1–August 1, 1984. Their data show a pulse of poleward flow in early March followed by equatorward flow in mid-March and April. The "spring jet" appears to begin on May 9 (year-day 130). Chelton et al. (1988) also note the disagreement between measured flow and that estimated from geostrophic shear.

Tisch et al. (1992) computed geostrophic currents relative to 1,000 m; these show occasional substantial flow at 500 m, to the degree that use of a 500-m reference results in an apparent surface flow of the opposite sign. It is also clear from our measurements that disagreement between measured and geostrophic flow arises because of the existence of barotropic flow over the upper slope at Point Sur.

The annual cycle appears well defined, especially the variability associated with the spring transition. In response to increased southward wind stress (see figure 7 in Chelton 1984), the thermocline tilts upward toward the coast, accelerating the southward flow of the California Current and simultaneously lowering the temperature at a given depth next to the coast. The southward wind stress also increases the poleward-directed alongshore pressure gradient force at the coast. This eventually accelerates the undercurrent. This, in turn, results in warming at depth, first due to a deepening of isotherms associated with geostrophic adjustment to the poleward flow, and later due to advection of warm (salty) equatorial water. When the undercurrent decelerates, the warm water remains in the area.

It is more difficult to explain deceleration of the spring jet, the timing of the start of winter cooling, and the role of the onshore pulse. Chelton (1984) shows that the local wind stress curl near Point Sur is about 0.02 N m^{-2}/100 km from December through June, and then doubles in July, just as the southward wind stress begins to relax. The 350-m cooling begins as the wind stress curl decreases, and perhaps onshore flow of offshore (subarctic) waters contributes to the observed cooling.

El Niño

The principal source of interannual variability in California's coastal waters is associated with El Niño, and the principal physical manifestation of this interannual variability is subsurface warming next to the coast (Cole and McLain 1989). With respect to the 1992 El Niño, our observations show that waters were anomalously warm during most of the period from July 1991 to November 1992, and the temperature minimum usually associated with the spring transition was not observed in 1992. A comparison of smoothed, monthly mean data (not shown) for this period with the annual cycle shown in figure 3 yields anomalies of as much as 0.5°C.

Given the large year-to-year variability of the velocity field, it is more difficult to identify anomalous velocity behavior associated with this warming. Sustained bursts of poleward flow occurred in November 1991 and January 1992, and onshore flow was almost zero during the winter of 1992. The current meter records of 1992 were also characterized by strong reversals of flow in winter and spring; such reversals were not observed in other years.

Value of Long Time Series

An annual signal has been derived; it would have been ambiguous if there were only a year or two of data available. The currents for any given year or pair of years may be very noisy, dominated by shorter-period events that have much greater energy than the mean flow. For example, Tisch (1992) reasonably concluded after examining the first 17 months of this data set that the data were dominated by a 215-day signal and that no canonical pattern existed to explain temporal means. Once an annual pattern becomes recognizable, it is possible to see changes that occur from year to year, to determine long-term trends, and to quantify interannual variability.

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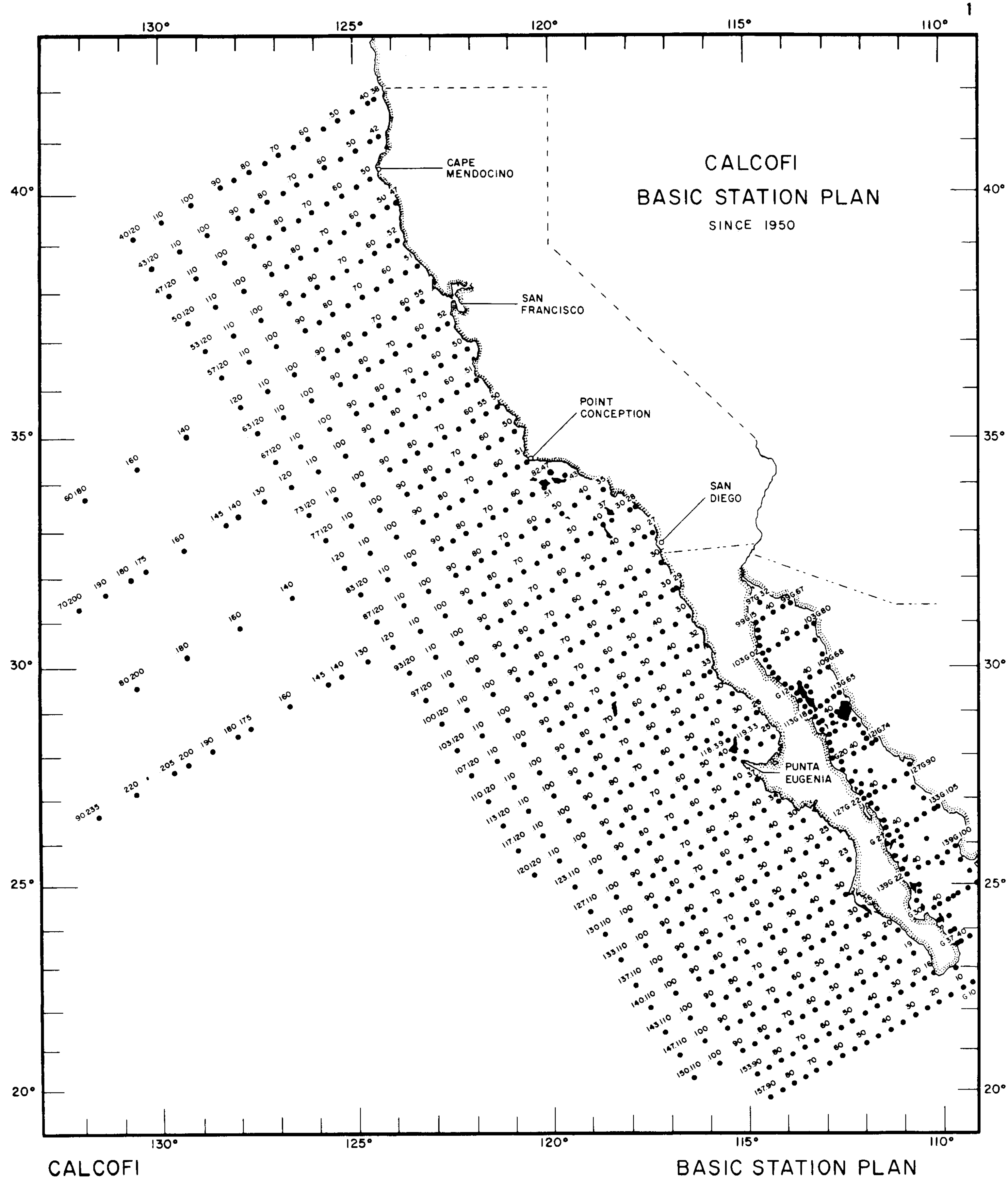

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I. Reports, Review, and Publications

II. Symposia of the CalCOFI Conference, 1995

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Indexed in *Current Contents.* Abstracted in *Aquatic Sciences and Fisheries Abstracts* and *Oceanic Abstracts.*