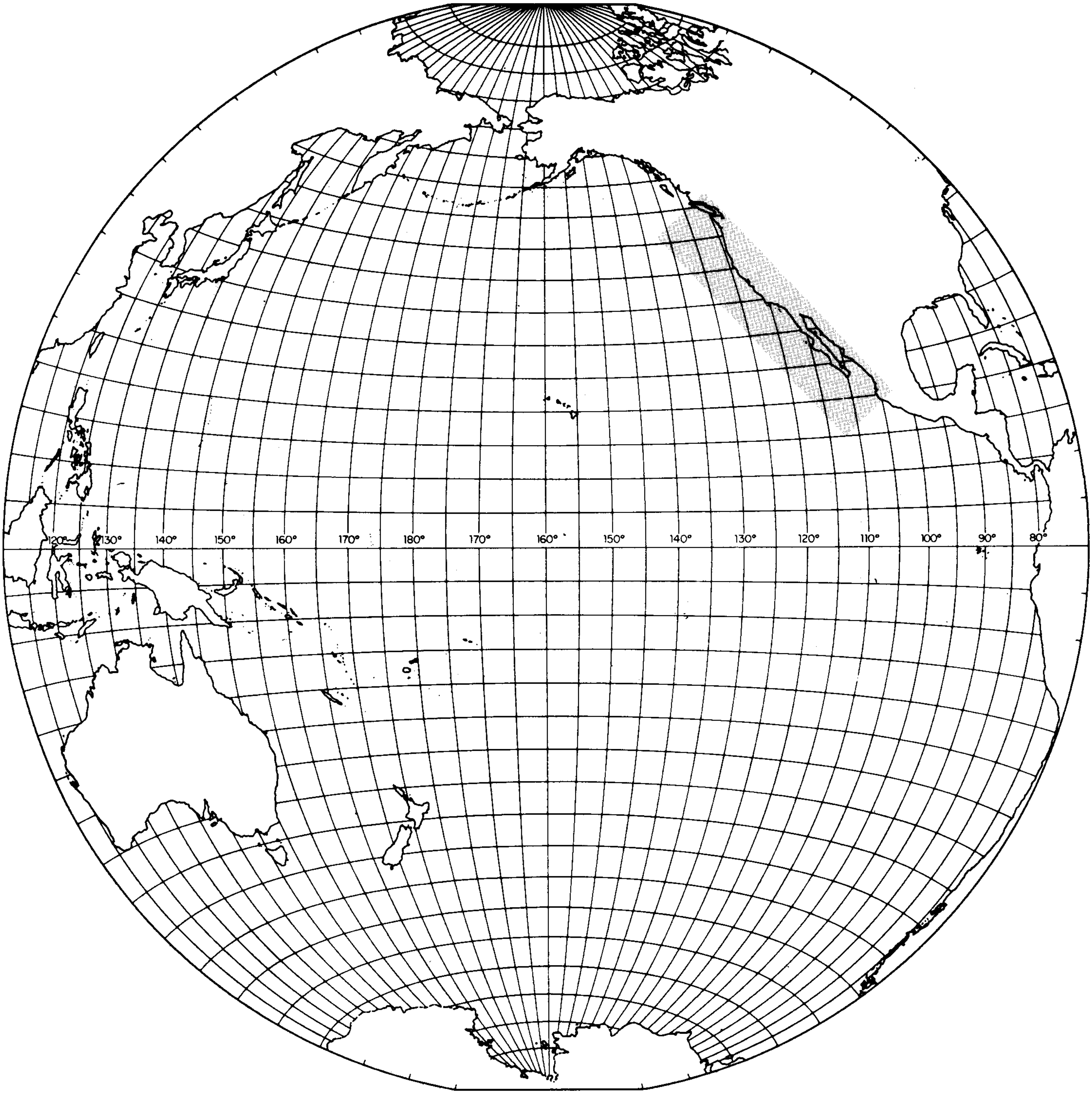

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

VOLUME XXVIII
OCTOBER 1987

CALIFORNIA
COOPERATIVE
OCEANIC
FISHERIES
INVESTIGATIONS

Reports

VOLUME XXVIII
January 1 to December 31, 1986

Cooperating Agencies:

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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Published October 1987, La Jolla, California

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IN MEMORIAM

Frances N. Clark

1894–1987

With the death of Frances Clark a few months after her ninety-second birthday, the fellowship of CalCOFI old-timers lost one of its stalwarts. Although small in physical size, she stood out among her colleagues because of her achievements in the fields of science and conservation. Already well known in the early 1920s, she can be counted among the first generation of marine biologists.

Frances Clark was not only one of the pioneers in the field, but also the first woman fishery researcher to receive worldwide respect and acclaim. For most of her career she was alone in a field dominated by men. However, much to her pleasure (and ours) she lived long enough to see a great many seagoing women scientists follow in her footsteps.

Clark retired from the California Department of Fish and Game in 1956, after 32 years of outstanding work with that agency, including 17 years as director of the California State Fisheries Laboratory. Through her many publications, beginning with a doctoral thesis on the life history of the grunion, she became well known to fisheries workers everywhere. Most of her reports deal with the sardine and the California Current system.

Perhaps the finest testimonial to Clark's leadership as a scientist and administrator is the roster of well-known fisheries workers who received their training under her guidance and who have served the public through the Department of Fish and Game and other agencies. In fact, many of the people she trained have long since retired. Many of them were originally attracted to the laboratory for the opportunity to work with her.

Clark was in on the early planning phases of CalCOFI—in fact, she participated in the first exploratory meetings in 1947. She was a member of the technical committee for the California Marine Research Committee from its inception to her retirement. Long after retiring she continued her interest in CalCOFI, attending many annual meetings and providing counsel to her successors. Those of us who attended the 1981 conference will never forget her recollections of the early days. Significantly, there was more than a sprinkling of women scientists from both sides of the U.S.-Mexican border in the audience, and during the sessions several women presented papers. We can be sure that Frances Clark approved.

Richard Croker

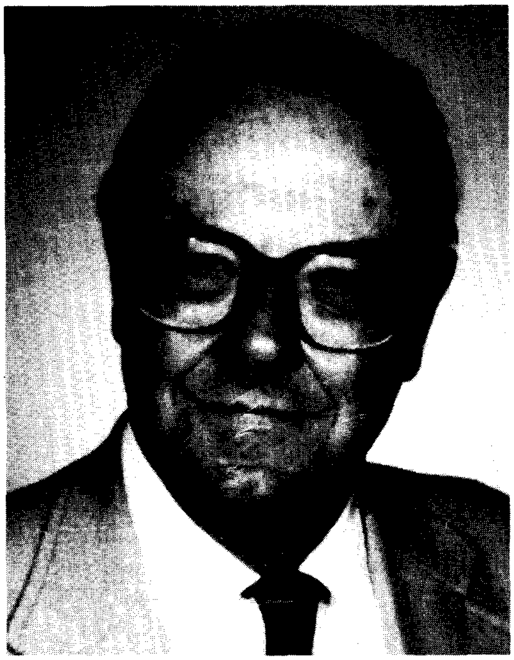
Philip M. Roedel

1913–1985

Philip M. Roedel died on March 30, 1985, ending a distinguished fisheries career of almost 50 years. Roedel played a significant role in Marine Research Committee (MRC) and CalCOFI affairs, from the organizations' inception until 1970. He was particularly active and influential in MRC and CalCOFI programs during the late 1950s and the 1960s.

Roedel began his career with California Department of Fish and Game (CDFG) at the California State Fisheries Laboratory, Terminal Island, in 1936, after graduating from Stanford University. He received a Master of Science degree from the same institution in 1952. From 1936 to 1954, with time out for Army service during World War II, he was a marine biologist at the Terminal Island Laboratory, where he did significant research on Pacific mackerel and served as editor of *California Fish and Game,* among other duties.

From 1954 to 1957, Roedel was regional manager of an inland region of CDFG, but returned to Terminal Island in 1957 as regional manager in charge of marine fisheries research and management programs. Roedel served in this capacity for 12½ years and led his unit through a period of great growth and change, earning everyone's respect for his outstanding work as a scientist and administrator. From 1963 through 1969, Roedel also served as MRC secretary, and for a short period in the mid-1960s was acting CalCOFI Coordinator. Roedel's detailed minutes of MRC meetings represent a comprehensive history of MRC and CalCOFI affairs during that important period. He was most active in fiscal, policy, and management activities affecting CalCOFI. In July 1969, CDFG appointed him Chief, Marine Resources Branch, with headquarters in Sacramento.



Roedel retired from CDFG in December 1969 to accept appointment as director of the U.S. Bureau of Commercial Fisheries (now National Marine Fisheries Service). In 1973, he was named Coordinator, Marine Recreation Programs, of the National Oceanic and Atmospheric Administration and later served as senior fisheries advisor to the U.S. Agency for International Development, a position that took him all around the world. He retired from that position in 1980, but continued to work as a consultant on international fisheries until his death.

John Baxter

Marston Sargent
1906–1986

Marston C. Sargent, CalCOFI Coordinator from 1971–74, died on August 28, 1986, at age 80.

Sargent was associated with Scripps Institution of Oceanography for more than 40 years, during which time he primarily investigated photosynthesis and the growth requirements of marine planktonic algae. Sargent received his A.B. degree in biology from Harvard University in 1929 and his doctoral degree in biophysics from the California Institute of Technology in 1934. He was a research assistant at Caltech for three years before joining Scripps as a biology instructor in 1937.

Sargent served on active duty in the U.S. Navy from 1942 to 1946, during which time he was assigned to the Office of the Chief of Naval Operations and the Navy's Bureau of Ships. He helped coordinate oceanographic research to support Navy needs, chiefly through development and operation of underwater sound equipment. He rose to the rank of lieutenant commander in the Naval Reserve.

In 1946 he returned to Scripps as an assistant professor. That same year, during the biological studies associated with the atomic bomb test in the Bikini Atoll, Sargent and Thomas S. Austin of Scripps made the first measurements of organic production on a coral reef. From 1951 to 1955, Sargent was head of training at the Navy Electronics Laboratory, after which he became an oceanographer and scientific liaison officer with the Office of Naval Research (ONR). For the following 15 years he was located at Scripps, except for a two-year stint in the ONR branch office in London. He served as scientific liaison for the Office of Naval Research with all West Coast oceanographic organizations during 1955–70.

Sargent was appointed CalCOFI Coordinator in early 1971. Under his guidance, CalCOFI began its longstanding and fruitful relationship with Mexico's Instituto Nacional de Pesca. This relationship has produced many cooperative fisheries investigations cruises in U.S. and Mexican waters, training courses and workshops on marine science methods and techniques, and many joint meetings in the U.S. and Mexico. By 1972, the annual CalCOFI conferences for sharing research ideas and results were conducted with simultaneous Spanish-English, English-Spanish translations. Dr. Sargent resigned from his post on July 1, 1974. He continued as a research associate with the Marine Life Research Group at Scripps until 1980.

George Hemingway

Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

The agencies that constitute CalCOFI have continued to cooperate in the use of human and material resources and infrastructure during 1986 and 1987, fielding four CalCOFI survey cruises of 15 days' duration, two young-fish trawl surveys, one anchovy age-composition trawl survey, one prawn trawl survey, and three combination trawl-and-egg survey cruises targeting sardines. The recently developed egg production method was refined in its application to these latter cruises' data (see Wolf et al., this volume). In addition to those surveys, seven cruises were carried out for the purpose of evaluating billfish stocks. Swordfish and striped marlin were tagged and sonically tracked for the first time off California.

International cooperation remains a very important characteristic of CalCOFI's scientific endeavors. Many of the fisheries stocks with which CalCOFI deals are transboundary species. The last year has seen a broadening of the base of interinstitutional cooperation with Mexican research laboratories. The symposium of the annual CalCOFI Conference, held at the UCLA Lake Arrowhead Conference Center during the last week of October 1986, focused on the status and prospects for Mexican west coast fisheries. The papers from that symposium are printed in this volume. In addition, the Sardine-Anchovy Recruitment Program (SARP) has resulted in the participation of Spanish and Portuguese fisheries scientists on CalCOFI cruises, as well as in laboratory activities at the Southwest Fisheries Center, National Marine Fisheries Service.

These and many other international connections reemphasize the importance of a global view of ecosystems and fisheries problems and their resolution. To understand how human intervention changes ecosystems, we must first have some understanding of how natural systems work, and of the magnitude and character of their natural fluctuations. The large-scale, multivariate time series of physical, chemical, biological, and meteorological data from the eastern North Pacific that has been assembled by CalCOFI researchers since 1949 constitutes one of the world's most significant data bases against which to evaluate change. Data from approximately 40,000 stations and 300 cruises have been entered into the CalCOFI online data system at the Southwest Fisheries Center. The base has been analyzed by Scripps Institution and Southwest Fisheries Center personnel, as well as other investigators, for oxygen content of water, temperature, salinity, zooplankton volume, and the eggs and larvae of several hundred species of fish. Output is available in the form of tables and graphs printed on a CRT, on paper, or written to magnetic storage media. Work is continuing to make these files easily accessible. The papers in this volume by Moser et al., Huato-Soberanis and Lluch-Belda, and Roesler and Chelton represent the type of work that is only possible within the context of the dedicated maintenance of a series of multivariate observations over a long time.

The CalCOFI Committee is saddened to report the deaths of three scientists of great vision who began and sustained this time series: Frances Clark, Philip Roedel, and Marston Sargent.

The Committee wishes to express its appreciation to the officers and crews of the University of California RV *New Horizon*, the National Oceanic and Atmospheric Administration RV *David Starr Jordan*, MV *Pacific States*, MV *Lakeside*, Occidental College RV *Vantuna*, Southern California Ocean Studies Consortium RV *Yellowfin*, and MV *Pacific Clipper* for their able assistance in operating the platforms from which the work of CalCOFI was performed this year, as well as the individuals from the member agencies, and the many student volunteers and scientists from the United States, Mexico, Spain, and Portugal who collected data.

The Committee also wishes to thank *CalCOFI Reports* editor Julie Olfe, Spanish editor Patricia Matrai, and the dozens of peer reviewers who have all worked to make Volume XXVIII another excellent report. The reviewers and editorial consultants for this volume were James Allen, Angeles Alvariño, George Boehlert, John Butler, Gregory Caillet, David Checkley, Edward DeMartini, Stephen Goldberg, Jed Hirota, Ralph Larson, Robert

Lavenberg, Richard Lee, Alec MacCall, John McGowan, Alan Mearns, Michael Mullin, William Pearcy, Michael Prager, Thomas Smayda, Paul Smith, Gary Stauffer, John Stevens, George Sugihara, Elizabeth Venrick, and Patricia Wolf. Ten of the 17 manuscripts submitted for publication in this volume were accepted by the editorial board.

Finally the CalCOFI Committee wishes to congratulate George Hemingway as he completes his second two-year term as CalCOFI Coordinator.

The CalCOFI Committee:
Izadore Barrett
Richard Klingbeil
Joseph Reid

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1986

California Department of Fish and Game
Marine Resources Division
245 West Broadway
Long Beach, California 90802

Total 1986 landings of fishes, crustaceans, and mollusks posted the first increase (6%) since the recent decline began in 1981. Even though landings remained below the ten-year average, some hopeful signs were noted.

Pelagic wetfish landings continued the upward trend first observed in 1985 after a four-year decline (Table 1). There was a particularly large increase in market squid landings. Both jack and Pacific mackerel posted gains relative to last year, and sardines apparently continued the long road back that has been evident in recent years.

Mixed returns were noted in other fisheries. Pacific ocean shrimp landings improved greatly. Dungeness crab landings also showed a significant increase.

A slight decrease was noted in groundfish landings; but although halibut landings were down from 1985, the total was still above the ten-year average. Albacore fishing was very poor during the 1986 season.

Lobster catch per unit of effort improved, while the total catch was similar to 1985 because of a decrease in the number of fishermen. Sportfish catch, in general, reflected a decrease in rockfish and pelagic species and an increase in nearshore species.

PACIFIC SARDINE

The opening of a 1,000-ton fishery for Pacific sardines (*Sardinops sagax*) on January 1, 1986, marked the first directed take of sardine since a moratorium went into effect in 1974. A cooperative survey in May 1985 by the California Department of Fish and Game (CDFG) and the National Marine Fisheries Service, Southwest Fisheries Center

TABLE 1
Landings of Pelagic Wetfishes in California in Short Tons

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1964	6,569	2,488	13,414	44,846	175	8,217	75,709
1965	962	2,866	3,525	33,333	258	9,310	50,254
1966	439	31,140	2,315	20,431	121	9,512	63,958
1967	74	34,805	583	19,090	136	9,801	64,489
1968	62	15,538	1,567	27,834	179	12,466	57,646
1969	53	67,639	1,179	26,961	85	10,390	106,307
1970	221	96,243	311	23,873	158	12,295	133,101
1971	149	44,853	78	29,941	120	15,756	90,897
1972	186	69,101	54	25,559	63	10,303	105,266
1973	76	132,636	28	10,308	1,410	6,031	150,489
1974	7	82,691	67	12,729	2,630	14,452	112,576
1975	3	158,510	144	18,390	1,217	11,811	190,075
1976	27	124,919	328	22,274	2,410	10,153	160,111
1977	6	111,477	5,975	50,163	5,827	14,122	187,570
1978	5	12,607	12,540	34,456	4,930	18,899	83,437
1979	18	53,881	30,471	18,300	4,693	22,026	129,389
1980	38	47,339	32,645	22,428	8,886	16,958	128,294
1981	31	57,659	42,913	15,673	6,571	25,915	148,762
1982	145	46,364	31,275	29,110	11,322	17,951	136,167
1983	388	4,740	35,882	20,272	8,829	2,010	72,121
1984	259	3,258	46,531	11,768	4,241	622	66,679
1985	653	1,792	38,150	10,318	8,801	11,326	71,040
1986*	1,310	2,051	44,824	12,172	8,405	23,124	91,886

*Preliminary

(NMFS-SWFC) detected a sardine spawning area that was determined to be characteristic of a spawning biomass of at least 20,000 tons. Since current law allows a 1,000-ton quota when the spawning biomass reaches this level, a fishery was initiated. A second survey conducted in August 1986 detected a spawning area of 955 n. mi^2., which was about 43% larger than the spawning area observed the year before. As a result, a 1,000-ton quota was established for the second season, which opened on January 1, 1987.

Landings of sardines in the 1986 fishery were steady and relatively high, averaging about 150 tons per month through June. The fishery was closed on July 11, when the 1,000-ton quota was reached. Sardines landed incidentally with mackerel in both northern and southern California accounted for 58% of the landings. The southern California catch, both incidental and directed, constituted 93% of sardine quota landings. Directed landings were used primarily as cut bait for the central California striped bass fishery.

Following the close of the season, sardines continued to be landed incidentally under a 15% tolerance limit. An estimated total of 867 tons was landed incidentally with mackerel during the year, which is an increase of 33% over incidental landings in 1985. This is higher than catches of the last 20 years, and continues the trend of increasing occurrences of sardines in the mackerel fishery. Similarly to last year, sardines constituted 1.5% of the overall mackerel catch, and occurred in 60% of observed landings. Total landings of sardines, including both quota landings and incidental landings made after the season closure, reached 1,310 tons (Table 1). Preliminary otolith readings indicated a slightly older age composition in the incidental catch (mostly of 2- and 3-year-old fish, with a small proportion of 4-year-olds) than in the directed landings (mostly 2- and 3-year-old fish, with a few 1-year olds).

Landings of sardines in live bait increased compared to 1985 estimated landings, but were well below the 150-ton annual quota. As in 1985, the availability of squid, which are often preferred as live bait for big game fish, resulted in a decreased demand for sardines.

As in 1984 and 1985, CDFG young-fish surveys in October found little evidence of sardine recruitment. Trawling success for both adults and juveniles declined. In recent years, only the 1983 year class has been captured in high numbers as young-of-the-year and 1-year-olds in these surveys. Young-of-the-year sardines caught in 1986 were considerably larger than their counterparts last year, suggesting that they originated from a spring rather than a summer spawning.

NORTHERN ANCHOVY

Landings of northern anchovy (*Engraulis mordax*) for reduction purposes during the 1985–86 season totaled 909 tons through December 1985. All landings were made in the Morro Bay area, against the northern permit region quota of 10,000 short tons. No landings were made in the southern permit region because of poor market conditions for fish meal and more lucrative fishing for mackerel, tuna, and squid.

A single boat delivered 14 loads totaling 402 tons to the northern area reduction plant in May and June 1986. The 1985–86 reduction season closed on June 30 with 1,511 tons landed (Table 2).

Using a stock synthesis biomass estimation model, National Marine Fisheries Service biologists estimated the 1986 spawning biomass of northern anchovy to be at least 848,770 short tons. The U.S. optimal yield was set at 159,723 tons and the U.S. reduction harvest limit at 154,350 tons. Northern and southern permit area allocations for the 1986–87 reduction season were unchanged from the 1985–86 season, at 10,000 and 144,350 tons, respectively. The fishery opened on August 1 in the north and on September 15 in the south. The northern area processor issued unlimited orders

TABLE 2

Anchovy Landings for Reduction Seasons in the Southern and Northern Areas, in Short Tons

Season	Southern area	Northern area	Total
1966–67	29,589	8,021	37,610
1967–68	852	5,651	6,503
1968–69	25,314	2,736	28,050
1969–70	81,453	2,020	83,473
1970–71	80,095	657	80,752
1971–72	52,052	1,314	53,366
1972–73	73,167	2,352	75,519
1973–74	109,207	11,380	120,587
1974–75	109,918	6,669	116,587
1975–76	135,619	5,291	140,910
1976–77	101,434	5,007	106,441
1977–78	68,467	7,212	75,688
1978–79	52,696	1,174	53,870
1979–80	33,383	2,365	35,748
1980–81	62,161	4,736	66,897
1981–82	45,149	4,953	50,102
1982–83	4,925	1,270	6,195
1983–84	70	1,765	1,835
1984–85	78	0	78
1985–86*	0	1,511	1,511

*Preliminary

for anchovy throughout the first half of the season, but landings were not anticipated because of a price per ton of less than $30. Northern area boats fished primarily for mackerel, salmon, herring, and squid. The southern permit region experienced a decrease in processing capacity when one former reduction plant closed and two others expressed no interest in this market. No reduction landings were made in either permit region through December of the 1986–87 season.

Total landings of anchovy during 1986 included 402 tons for reduction, 1,649 tons for nonreduction, and 4,942 tons for live bait. The decrease in live bait landings from the 1985 total of 5,055 tons was due to the failure of the summer albacore sport fishery in waters accessible to the large San Diego-based fishing fleet.

Trawl surveys conducted by CDFG during 1986 indicate that the 1985 year class is weak; not since the 1981 year class have 1-year-olds constituted a lower percentage of age-composition samples. The 1986 year class, however, made the strongest showing as young-of-the-year fish since 1980. Young-of-the-year fish also appeared abnormally small relative to recent year classes, which may be attributable to late spawning. Mexican reduction fishery representatives reported a continuation of the decline in anchovy landings since the most recent El Niño, with small, young fish dominating the catch.

JACK MACKEREL

An estimated 12,172 tons of jack mackerel (*Trachurus symmetricus*) were landed during 1986 (Table 1). Similarly to last year, jack mackerel accounted for 21% of total mackerel landings. Since 1979, jack mackerel have contributed less than Pacific mackerel to the California mackerel fishery. In the last three years, the proportions of annual mackerel landings composed of jack mackerel have been the lowest since this fishery began in the late 1940s.

Jack mackerel did not dominate statewide landings at any time during 1986, probably because Pacific mackerel landings were unrestricted. Jack mackerel are in less demand than Pacific mackerel, and were generally less available throughout the year. In northern California, however, jack mackerel dominated landings from October through December. The composition of the total 1986 catch varied, with jack mackerel constituting from 5% to 43% of the landings. Nearly 94% of all jack mackerel landings occurred in southern California. Calculated throughout the year, jack mackerel made up 22% of the total mackerel landings in northern California, and 21% of the total mackerel landings in southern California.

Sea surveys conducted in 1986, and the occurrence of large numbers of young-of-the-year fish in the mackerel fishery suggest that the 1986 year class is fairly strong.

PACIFIC MACKEREL

The year began with 22,933 tons of Pacific mackerel (*Scomber japonicus*) already landed through the first half of the 1985–86 fishery season. No quota restrictions were in effect because the total biomass had been estimated to range between 178,000 and 260,000 tons, and current law allows an open fishery when the biomass exceeds 150,000 tons. Landings during January were limited by extended closure of southern California processing plants over the holiday season. Monthly landing totals increased beginning in February. Catch locations through May ranged along the coast of southern California between Long Beach and Ventura. Pacific mackerel constituted 70% or less of monthly catch totals through April, as 1-year-old jack mackerel made a strong showing in the fishery. During the second half of the season, southern California processors set landing limits between 40 and 60 tons per boat per week, and the price per ton was steady at $150–$155. The 1985–86 season closed on June 30, 1986, with a total catch of 41,400 tons of Pacific mackerel, down slightly from the previous season's total of 43,255 tons. Pacific mackerel contributed 75% to statewide landings of mackerel, and 93% of all Pacific mackerel landings were made in southern California.

The 1986–87 season opened on July 1, 1986, with no quota restrictions, based on a total biomass estimated to exceed 500,000 tons. Catches were very low in July, because the southern California purse seine fleet concentrated its efforts on bluefin tuna. Southern California processing plants lifted all landing limits on mackerel from July through September, resulting in catches of over 5,500 tons per month. Varied landing limits and plant closures for holidays reduced landing totals in November and December. Catch locations from July through December included coastal waters between Long Beach and Ventura, and off San Clemente, Santa Catalina, and Santa Cruz islands. Pacific mackerel constituted over 80% of total mackerel landings each month. By the end of December, 26,317 tons of Pacific mackerel had been landed toward the 1986–87 season total. Landings of Pacific mackerel for the year totaled 44,824 tons. This is the third highest annual catch since the Pacific mackerel fishery reopened in 1977, and exceeds the average annual landings for the previous five years. This is also the first year during which no quota restrictions were in effect, which may in part account for the relatively high annual catch under conditions of cannery landing limitations and low price. Northern California landings contributed only 6% to the year's total, down from 8% in 1985 and 18% in 1984.

The 1980, 1981, and 1982 year classes together accounted for 44% of fish landed. The 1985 year class, which was first thought to be very weak, made a good showing as 1-year-olds in the fishery, contributing 14% to the year's catch, and over 35% of fish landed in October and December. Young-of-the-year also made a strong showing, first appearing in the fishery in October, and contributing 11% to December's catch and 1% to total landings for the year.

MARKET SQUID

Landings of market squid (*Loligo opalescens*) in 1986 totaled 23,124 short tons. These landings exceeded any since 1981, and were 65% higher than the 10-year average of 13,998 tons (Table 1).

Only 20% of this year's total was landed in northern California ports (north of Morro Bay). It was hoped that squid would return to Monterey Bay in great numbers this second season after an El Niño so sharply reduced squid growth and survival. However, the 5,544 tons landed in Monterey Bay in 1986 was a far cry from the 10,000 to 14,000 tons expected in a good year. On the positive side, landings were 24% better than in 1985, and more than ten times higher than landings in either 1983 or 1984.

Monterey fishermen began landing squid on April 11 at $300 per ton, but the price dropped to $200 per ton by the second week of the season. In complete contrast to the large squid landed early in the 1985 season, the first squid landed this year were small, averaging 16 per pound. Later in April, the average size increased, producing a count of 13 per pound. In May counts improved slightly, to about 11 per pound.

Fishermen experienced highly variable success early in the season. Throughout May, fishermen had several good days among the many very poor days. Fishing became even worse during the next two months. Boats averaged less than two tons per day, putting a severe crimp in the incomes of fishermen, who work for a share of the catch rather than a fixed wage. Some boat owners had so much trouble finding crew members that they quit fishing for the remainder of the season.

The remaining fishermen found greater concentrations of squid north of Monterey Bay near Pigeon Point, and fished there for the rest of the season. The squid caught there in 1985 were larger, better-quality squid than those caught near Monterey. In 1986, however, the quality of the Pigeon Point area squid was similar to that caught near Monterey—11 per pound. For the remainder of the year fishing was spotty at best. August produced the greatest catch (1,259 tons), followed by July (884 tons), November (822 tons), and May and June (more than 500 tons each month).

In keeping with its typical fall-winter abundance pattern, the 1986 southern California market squid fishery was most active during the months of January, October, November, and December. Of the total 16,450 tons landed in southern California, 88% was brought in during these months. Over 5,000 tons was estimated to be used as live bait during the year.

Fishing effort this season was primarily at Catalina and the northern Channel Islands, with a good deal of effort occurring at Santa Cruz Island. Approximately 42 vessels worked the squid grounds during the season, including several from the Monterey area, and one from as far as Washington. Many boats worked in pairs at night, one attracting squid to the surface with lights, the other wrapping the school with a purse seine or lampara net.

In spite of excellent landings, fishermen did not claim a bonanza season. Boats working in teams split profits between two crews. In addition, markets were essentially flooded with squid, keeping the price fairly low. The going price for squid at the San Pedro markets, where 40% of southern California squid was landed, was $200 per ton, except for March and April when it jumped to $400. Prices elsewhere ranged widely, but were primarily within $120 to $240 per ton. Because of high local availability, some squid was trucked north to Monterey, Moss Landing, and even Newport, Oregon, for processing.

PACIFIC HERRING

In the 1985–86 season (December–March) 8,139 tons of Pacific herring (*Clupea harengus pallasi*) were caught. This represents a quota shortfall of 451 tons. Fishing was generally excellent in most areas. In San Francisco Bay, however, herring spawned in areas that were closed to round-haul gear, and fishing during February was largely curtailed by a series of storms. Most of the shortfall resulted from the fact that herring were subsequently not available to purse seine or lampara boats. The annual catch totaled 8,247 tons, down slightly from 1985 (Table 1). Base price for 10% roe recovery was $1,200 per ton for gill netters and $800 per ton for round-haul boats. The estimated ex-vessel value of the 1985–86 herring catch was over $11 million.

Population estimates from 1985–86 spawning-ground surveys indicate that herring spawning biomass in San Francisco Bay increased 3,000 tons, to 49,000 tons, but in Tomales Bay the biomass decreased 600 tons, to 6,000 tons.

During the past four seasons, recruitment of 2-year-old herring into the San Francisco Bay round-haul fishery has been relatively good, and the trend of increasing abundance is expected to continue. Recruitment of recent year classes in Tomales Bay is unknown. Tomales Bay is a gill net-only fishery, and herring are not fully recruited until 5 or 6 years old. However, a major change in the status of the Tomales Bay fishery is unexpected.

No adjustment was made to the 1986–87 herring quota, which remains at 8,590 tons, based on relatively stable 1985–86 biomass estimates. Early 1986–87 season catches have been very good, but a lower base price of $600 to $800 per ton for 10% roe recovery will reduce the value of the 1986–87 catch.

GROUNDFISH

California's 1986 commercial harvest was 41,795 metric tons (MT), valued at $31,000,000 ex-vessel. The 1986 catch declined by 1,935 MT, or 4% from the 43,730-MT catch in 1985 because of landing decreases for most of the major species. The major share of the catch, 78% and 32,469 MT, was taken by trawlers. Setnet landings were 12% of the total (4,983 MT). The line catch followed at 7% (2,856 MT), and other gear accounted for 1% (629 MT).

Rockfish (a multispecies group), Dover sole (*Microstomus pacificus*), and sablefish (*Anoplopoma fimbria*) were the leading species in 1986 landings (Table 3). Trawl landings of major groundfish species, with the exception of sablefish and Pacific whiting, declined 1%–35% from 1985 levels. A shift of trawl effort from groundfish to the rejuvenated pink shrimp fishery off northern California and Oregon resulted in less groundfish effort and an 8% decrease in trawl landings. Market demand for groundfish, particularly sablefish, remained strong throughout the year. The elimination of the directed Japanese sablefish effort in U.S. waters off Alaska in 1985, together with Japanese market demand, stimulated U.S. fishing effort. Higher prices for all sablefish size categories resulted.

TABLE 3
California Groundfish Landings (Metric Tons)

Species	1985	1986*	Percent change
Dover sole	12,159	10,987	−10%
English sole	1,073	1,074	—
Petrale sole	863	711	−18%
Rex sole	906	840	−7%
Thornyheads	2,975	2,939	−1%
Widow rockfish	3,065	2,468	−19%
Other rockfish	11,812	11,505	−3%
Lingcod	696	514	−16%
Sablefish	5,167	6,099	18%
Pacific whiting	3,023	2,982	−1%
California halibut	574	549	−4%
Other groundfish	1,991	1,127	−43%
Total	44,304	41,795	−4%

*Preliminary values as of March 16, 1987.

In contrast to trawl landings, line groundfish catches increased by 76% (1,236 MT), and setnet catches by 25% (1,005 MT) over 1985 landings. These increases resulted from higher effort and not from increases in resource abundance. Rockfish and sablefish were the major species taken by these fixed gear.

Federal and state groundfish regulations for the Washington-Oregon-California (WOC) region affected the California harvest of sablefish and widow rockfish (*Sebastes entomelas*). Coastwide catch ceilings and optimum yield (OY) for sablefish and widow rockfish were 13,600 MT and 10,200 MT, respectively. Vessel-trip and trip-frequency limits were management measures used to provide a year-round fishery within the optimum yields. The 1986 widow rockfish fishery began with a trip limit of 30,000 lbs. By late September, a reduction to 3,000 lbs was necessary to keep the widow rockfish landings below the OY. Sablefish landings were unrestricted except for a 5,000-lb limit north of Point Conception on fish smaller than 22 inches. By late August, 61% of the OY was attained, and the remaining 5,304 MT were allocated 55% to trawlers and 45% to fixed gear. The fixed-gear allocation was caught in October, and the fishery was closed. The trawl allocation was accompanied by an 8,000-lb trip limit. In late October this trip limit was increased to 12,000 lbs to allow attainment of the OY.

DUNGENESS CRAB

The 1985–86 California commercial Dungeness crab (*Cancer magister*) season yielded 5.92 million pounds, which exceeded 1984–85 seasonal landings by more than 1 million pounds.

Production for the northern California ports of Crescent City, Trinidad, Eureka, and Fort Bragg was 3.08, 0.63, 1.60, and 0.23 million pounds, respectively.

A total of 353 vessels fished for a December 1 opening price of $1.25 per pound. The price rose rapidly to $1.75 per pound as catches diminished after the first three weeks. The season closed on July 15.

Dungeness crab landings for the San Francisco region totaled 384,000 pounds. This is a decrease from the 600,000 pounds landed the previous season and well below the ten-year average of 574,000 pounds.

Half of the season's landings occurred in November 1985, and the price ranged from $2.00 to $2.85 per pound.

PACIFIC OCEAN SHRIMP

Ocean shrimp (*Pandalus jordani*) landings increased to over 5.8 million pounds in 1986. This represents the third successive annual increase in both Area A (California-Oregon border to False Cape) and Area C (Pigeon Point to the Mexican border).

Shrimp landings from Area A totaled 5.0 million pounds during the April 1 to October 31 season. This was a substantial increase over the 2.9 million pounds caught in 1985, and the third highest poundage ever landed in Area A. Ports in Area A also received an additional 0.91 million pounds that had been caught off Oregon (Pacific Marine Fisheries Commission areas 88 and 86). The ex-vessel price started at $.45/lb in April; there were five subsequent increases to a high of $.75/lb at the end of September.

A total of 42 vessels (28 single-rigged and 14 double-rigged) delivered shrimp to Area A ports during the season, an increase of 11 boats over 1985 (12 additional single-rigged vessels and one less double-rigged vessel). Single-rigged boats had an average seasonal catch rate of 288 lb/hr, down from 398 lb/hr during 1985. Double-riggers averaged 465 lb/hr, down from 573 lb/hr in 1985.

One-year-old shrimp again constituted a very high percentage (55.0%–92.1%) of the catch throughout the season. The most notable catch statistic, however, was that the 1986 year class made up 33.6% of the catch in October. This is the highest ever seen in California and indicates potentially good 1987 and 1988 seasons, barring adverse oceanic conditions.

Ocean shrimp landings in Morro Bay and Avila (Area C) in 1986 totaled 839,649 pounds, including approximately 800 pounds taken incidental to prawn trawling. This was a tremendous increase over the 22,889 pounds landed in 1985 and was the most pounds landed since 1983, when 944,695 pounds were unloaded.

Seven single-rigged vessels made 51 trips and caught an average of 306 pounds of ocean shrimp per hour of fishing. Four double-rigged vessels made 28 trips with an average per-hour catch of 548 pounds. However, one single-rigged vessel switched to double nets after the first month, to bring the total number of vessels for the year to ten.

The catch per hour for both types of rigs started very high in April (383 lb/hr for single-rig and 758 lb/hr for double-rig) then declined steadily through June. The scarcity of shrimp in late June caused most of the fishermen to switch to other fisheries, and in July only six landings of ocean shrimp were made. By mid-July all effort had ceased.

The price per pound started at $.45 and stayed around that level throughout the short season except for some small purchases at $.65 per pound.

In the April market samples 51% of the shrimp were two years old, either in the transitional or young female stages. In May this group constituted 38% of the shrimp in the samples and only 30% by June. By contrast, the ratio of the 1-year-old males in the market samples increased from 37% in April to 66% in June. These 1-year-old shrimp should compose the bulk of the catch in the early part of the 1987 season. This follows the catch pattern of 1986 and other years for Morro Bay and Avila, where 2-year-old shrimp dominate the fishery early in the season.

PELAGIC SHARK AND SWORDFISH

During 1986, 264 permits were issued for harpooning swordfish (*Xiphias gladius*), and 240 drift gill net permits were issued for taking pelagic sharks and swordfish.

Harpoon fishermen, assisted by spotter aircraft, caught 0.5 million pounds of swordfish, equalling last year's landings.

Drift gill netters reported 22,737 swordfish on logbooks during 1986. This approximately equals the number of fish reported for 1985. However, there was a significant difference in the average size of fish landed. During 1986, the average dressed weight of swordfish was only 105 pounds, compared to a 160-pound average for the previous year. Accordingly, total landings for 1986 amounted to only 3.62 million pounds, compared to the 5.25 million pounds in 1985.

Also noteworthy were differences in the areas where swordfish were taken. During the previous two years, large numbers of swordfish were taken along the outer escarpment adjacent to the Southern California Bight. The 1986 season was labeled an "inside year" by gill net fishermen, because most fish were taken around southern California islands.

Common thresher shark (*Alopias vulpinus*) landings fell sharply during 1986: only 0.56 million pounds were taken. This decrease was due in large part to the establishment of a closed season (June 1–August 14) in an attempt to take pressure off what is believed to be a depressed stock.

Of special significance during 1986 was the participation by California-based vessels in an experimental fishery for thresher sharks conducted by the states of Oregon and Washington. Approximately 0.7 million pounds of large thresher sharks were taken. These fish represent the adult segment of the thresher stock, in contrast to the mostly immature fish taken in the California fishery.

CALIFORNIA HALIBUT

California halibut (*Paralichthys californicus*) landings for 1986 were 1 million pounds, which was less than the 1.26 million pounds taken in 1985. The ten-year average from 1976 to 1985 was 0.88 million pounds (Table 4). Following a low catch of 0.27 million pounds in 1973, halibut catches have increased steadily, averaging 1.19 million pounds for the last five years. Nearly 70% of the 1986 halibut landings occurred south of Point Conception, compared to 60% during the El Niño period of 1982–84. Traditionally, the spring and summer months have produced the highest halibut catches; this was again the case in 1986.

TABLE 4
California Halibut Landings (1,000s of Pounds)

Year	North of Pt. Conception	South of Pt. Conception	Total
1976	74	553	627
1977	56	412	468
1978	77	364	441
1979	120	454	665
1980	199	511	710
1981	360	902	1,262
1982	456	748	1,204
1983	566	547	1,113
1984	338	762	1,100
1985	319	946	1,265
1986*	302	734	1,036

*Preliminary

Entangling nets (trammel and set gill net) accounted for 80% of all halibut taken. The remainder were taken by trawl net, pot, and hook-and-line gear. Average ex-vessel prices for California halibut ranged from $1.80 per pound in Monterey to $3.00 per pound in the San Francisco area.

Beginning August 15, 1986, a new regulation for trammel and set gill nets was implemented to increase minimum mesh size from 8 to 8½ inches in waters that encompass the major halibut fishing grounds. In addition, these nets were limited to 6,000 feet in length, and a moratorium was established on the issuance of new general gill and trammel net permits.

CALIFORNIA SPINY LOBSTER

The 1985–86 (first Wednesday in October to first Wednesday after March 15) southern California commercial fishery for California spiny lobster (*Panulirus interruptus*) made a resilient comeback from record low levels in 1984–85. Catch per unit of effort (CPUE) levels documented median seasonal success in 1985–86 when compared to the 13-year data base recorded from daily onboard logbooks.

Because of poor catches the previous season, participation declined 20%, to 354 permittees. The 181-boat fleet was down 10%. However, the logged effort of 451,000 traps hauled was only 4% below the previous season, probably reflecting the improved catch success.

The traps continued retaining sublegal-sized ("short") lobsters in large numbers. The 407,000 shorts represent a catch-per-trap rate of 0.9 animals, a level maintained for the past three years. A total catch of 264,000 legal-sized lobsters was logged. Landing receipts documented a total weight of 421,000 pounds.

Catch success, in terms of pounds-per-hundred-trapping-hours (PPHTH) averaged 1.7, an improvement over the previous season's rate of 1.4. Monthly catch success was highest in October (2.5), declined to 1.1 in December, then recovered steadily to a 2.2 rate by the March closure.

Regionally, the Channel Islands (San Clemente, Santa Catalina, Santa Barbara, San Nicolas, Anacapa, Santa Cruz, Santa Rosa) continued to produce at the same 2.2 PPHTH rate recorded in 1984–85, with 29% of the effort accounting for 38% of the total landings. Fluctuating catch success levels are typical along the mainland coast. During 1984–85 the most depressed success levels (1.0 PPHTH) occurred along the lightly trapped coastline north of Santa Monica Bay. In 1985–86, northern fishermen enjoyed a 2.3 PPHTH success rate to produce 8% of the state's catch with 5% of the effort. Catch success along the mainland coast south of Santa Monica Bay improved modestly (1.4 PPHTH compared to 1.1 PPHTH in 1984–85), with 65% of the effort producing 54% of the southern California catch.

Despite the indication of a healthy resource with sublegal standing stock at a continued high level, regional catch success is subject to annual variations as high as 55%, probably because of environmental changes that affect catchability. Relatively warm overwintering temperatures in 1983–84 may have enhanced exploitation levels that season, decreasing the harvestable surplus for 1984–85. By 1985–86, recruitment of an additional year class had returned catches to a median level of success.

High variation in catch success has created an unstable financial basis for individual fishermen, and the fishery has long been characterized by transient participation. In the 1985–86 season only about half the fishermen were "veterans" returning from the previous season. Veteran fishermen seeking relief from this persistent turnover, with its inherent problems of territorial disputes, escalating effort, and overcapitalization, successfully sponsored legislation that would allow the establishment of a limited-entry fishery. Section 8259 of the Fish and Game Code authorizes the Fish and Game Commission to place a statewide or geographically selected limit on the number of lobster permits in order to "prevent overutilization or to ensure efficient and economic operation of the fishery."

Although subject to uncertain catch success from environmental change, and reaching out for legislated stability, the lobster fishery has achieved at least a recent economic peak. Commercial landing receipts available from six years since the 1980–81 season record the following achievements in 1985–86: (1) the highest ex-vessel price of $4.48/lb, 35% above the 1980–81 price and 10% above a year ago; (2) a total fishery value of $1.9 million, second only to the $2.1 million value of 1983–84; (3) the highest per capita gross income—$5,322; and (4) the highest gross income per unit of effort—$4.18 per trap hauled.

ALBACORE

The 1986 California albacore (*Thunnus alalunga*) season was a disappointing one. Effort was low, prices were down, and fish were scattered and farther offshore than usual.

Landings for the season totaled approximately 3,509 tons. This total is half of last year's landings of 7,205 tons and only 32% of the 25-year average of 10,850 tons. Few boats contributed to the fishery this year. Approximately 448 boats participated, but only 244 made landings totaling over one ton. In 1985, 832 vessels landed albacore, and of these 456 made landings of over a ton. These numbers, however, are still low compared to the fishery's peak of over 3,000 vessels in 1950.

The 1986 season began in late June and early July, when boats fishing north of the Hawaiian Islands landed fish in California ports. Albacore made only sporadic appearances in southern California waters for the duration of the season; most commercial boats headed north in late July, and sportfishing boats in the area suffered from canceled charters and low participation throughout much of the season.

Commercial boats fishing 800 to 1,000 miles off Cape Mendocino in July and August did well, with catches of 200 to 600 fish per day, but from late August through September most offshore effort occurred off Oregon and Washington. The only persistent nearshore fishery occurred off Morro Bay, where large, 20-pound fish appeared in August, supporting trolling vessels with catches of generally 100 fish per day. In late September, bait boat activity began to increase in this area, and by October some vessels were reporting catches as high as 900 large fish per day. By the end of October most bait boats had made their final trips for the season. Many nearshore trollers ceased albacore fishing much earlier in the season, and others never switched from salmon gear at all, as a result of an excellent salmon season.

In recent years, 75%–80% of the total sampled catch occurred in nearshore waters (inside 140°W). In 1986 less than 50% of the sampled catch was caught in this region. Although reduced effort partly contributed to this, oceanic condition in southern California was an important factor as well. The cold, turbid waters of the California Current extending south from Point Conception acted like a barrier to albacore, keeping them farther offshore than usual.

Many factors affect participation in the fishery, and one is certainly price. Albacore prices have steadily declined since 1981, when they peaked at $1,800 per ton. This year the Western Fishboat Owners Association and Pan Pacific, the one cannery on the coast still processing albacore, agreed to a starting price of $1,100 per ton for fish 9 pounds and over, and $750 for those under 9 pounds. In 1985 prices began at $1,300 and $950 per ton, respectively, but dropped by season's end to only $1,000 per ton. Prices are low because albacore is highly available on a worldwide scale, and canneries must compete with inexpensive foreign imports and low tariffs.

Fishermen in northern ports received some encouragement when Pan Pacific began absorbing trucking costs in midseason. Instead of the $200–$250 per ton trucking fee, fishermen were charged only a $75 handling fee per ton.

This season, sales made directly off the boat to the public were estimated at 100 tons, or 3.0% of the total landings. Fish sold for as little as $.65, but generally between $.80 and $1.00 per pound. Most direct sales this season occurred in Fort Bragg and Eureka.

RECREATIONAL FISHERY

The catch record of sport anglers fishing on commercial passenger fishing vessels (CPFVs, or partyboats) roughly reflects the success of oceangoing anglers on private boats. These two groups account for the vast majority of the marine sportfish catch.

This catch record has demonstrated wide fluctuations in relative catch success for many species during the past five years as a result of the 1982–84 El Niño phenomenon. Water temperatures along the coast of California returned to "normal" in 1986.

The 1986 recorded catch of some warm-water fishes shows a decline from the 1985 catch. For example, the yellowtail (*Seriola lalandei*) catch was down 10%, to 41,051 fish; Pacific mackerel (*Scomber japonicus*) down 14%, to 601,664; and bluefin tuna (*Thunnus thynnus*) down 86%, to 676 fish. The recorded catch of other warm-water fishes increased in 1986. California barracuda (*Sphyraena argentea*) increased 13%, to 85,304; Pacific bonito (*Sarda chiliensis*) increased 179%, to 334,693; skipjack tuna (*Euthynnus pelamis*) increased 782%, to 2,098; and yellowfin tuna (*Thunnus albacares*) increased 40%, to 5,474 fish. Especially significant is a 57% increase in the catch of white seabass (*Cynoscion atractoscion*), to 1,629. The catch of this fish actually dropped during the 1982–84 El Niño, although in previous warm-water years the catch usually improved as a result of northward shifts of fish from Mexican waters. Albacore (*Thunnus alalunga*) continued to decrease from near record catches in 1984, to 26,955—down 84% from the 1985 catch.

The temperate-water, resident fishes that were recorded in fewer numbers in 1986 were barred sandbass (*Paralabrax nebulifer*) down 12%, to 264,513 fish; the rockfish complex (*Sebastes* spp.) down 12%, to 1,797,378; the salmon complex (*Oncorhynchus* spp.) down 18%, to 88,614; and ocean whitefish (*Caulolatilus princeps*) down 13%, to 73,410.

The temperate-water resident fish with increased catches are predominately nearshore, kelp bed-related species including kelp bass (*Paralabrax clathratus*) up 58%, to 430,572 fish; halfmoon (*Medialuna californiensis*) up 646%, to 66,720; opaleye (*Girella nigricans*) up 832%, to 589; sargo (*Anisotremus davidsonii*) up 653%, to 881; and spotted scorpionfish (*Scorpaena guttata*) up 7%, to 71,432. The catch of some flatfish also increased: for example, sanddab (*Citharichthys* spp.) was up 118%, to 5,432 fish, and California halibut (*Paralichthys californicus*) was up 11%, to 7,823 fish. Two species associated with rocky reefs in central and northern California also increased: lingcod (*Ophiodon elongatus*) was up 24%, to 25,485 fish, and cabezon (*Scorpaenichthys marmoratus*) was up 148%, to 4,373 fish.

The 1986 total catch decreased 2%, to 4,046,659 fish, and the number of anglers declined 8%, to 653,668; in general, this means a slightly better catch per angler.

Several species had size limits or seasons imposed on sport anglers in the early 1980s. Such regulations generally reduce the catch immediately, because the undersized fish that are caught must be released, but the goal is to provide increased catches during the following years. In light of this, the following species show promising trends. California barracuda show a general increase since 1981; California halibut are increasing to levels recorded before El Niño; and lingcod are increasing from a slump coincident with El Niño. Although the white seabass increased slightly, the resource is still at a low level. The worst news is that the rockfish catch has not been this low (1.7 million) since 1966, when the fishery was in a development phase that peaked in 1974 with a catch of more than 4 million fish.

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THE RELATIVE MAGNITUDE OF THE 1986 PACIFIC SARDINE SPAWNING BIOMASS OFF CALIFORNIA

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ABSTRACT

The spawning biomass of the Pacific sardine off southern California during 1986 remains at or above 20,000 short tons[1]. This determination was made using an egg production area method, which estimates the area over which eggs of a specified spawning biomass (20,000 short tons) would be expected to occur. The area method was developed from the egg production method, which estimates adult biomass from measurements of egg production in the spawning area and from the egg production rate of the adult population. From estimates of components of egg production rate and specific fecundity for sardines, we expected that 20,000 tons of spawning biomass would cover a spawning area of about 500 n.mi^2.

The August 1986 survey extended from Point Conception to San Diego and ranged from the 10-fathom isobath to offshore approximately 25 miles. A total of 266 sardine eggs was collected at 59 of 330 stations. Spawning extended from Santa Barbara to Dana Point and out to the Santa Barbara Channel Islands and Santa Catalina Island, and covered an estimated 955 n.mi^2. This spawning area is 43% larger than the spawning area observed in 1985.

RESUMEN

En 1986, la biomasa de desove de la sardina del Pacífico frente a California del Sur se mantuvo en o por encima de las 20,000 toneladas cortas[1]. Esta determinación fue hecha mediante el método del área de producción de huevos, el cual estima el área en la cual se espera encontrar los huevos correspondientes a una determinada biomasa de desove (20,000 toneladas cortas). El método del área se baso en la método de producción de huevos el cual estima la biomasa de los adultos a partir de las mediciones de producción de huevos en el área de desove y de la tasa de producción de huevos de la población adulta. Dadas las estimaciones de componentes de la tasa de producción de huevos y la fecundidad específica de las sardinas, esperábamos que 20,000 toneladas de biomasa de desove cubrieran un área de desove de aproximadamente 500 millas náuticas^2.

El muestreo realizado en agosto de 1986 se extendió desde Point Conception hasta San Diego y cubrió desde la isóbata de 10 brazas hasta 25 millas mar adentro. Un total de 226 huevos de sardina fue colectado en 59 de las 330 estaciones. El desove abarcó desde Santa Barbara hasta Dana Point y, mar adentro, hasta las islas del canal de Santa Barbara y la isla Santa Catalina y, se estimó que cubrió 955 m.n^2. Este área de desove es un 43% más extensa que la observada en 1985.

INTRODUCTION

In this report we evaluate the magnitude of the 1986 spawning biomass of the Pacific sardine relative to 20,000 tons. The California Department of Fish and Game (CDFG) is required to determine annually whether the spawning biomass is above or below this level. Earlier assessments of the spawning biomass were based on ichthyoplankton surveys, incidental landings in mackerel and live bait fisheries, trawl surveys, and aerial observations. From 1974 through 1985, a moratorium on the fishing of sardines was in effect because the biomass remained below 20,000 tons.

The egg production area technique was developed (Wolf and Smith 1985) and applied to sardines in 1985 (Wolf and Smith 1986). This technique allows an objective determination of whether the spawning biomass has exceeded 20,000 tons. The Pacific sardine fishery was reopened in 1986 with a 1,000-ton quota, since regulations permit a low rate of mortality due to fishing (.05) when the spawning stock recovers to 20,000 tons.

We used the egg production area technique to assess the relative magnitude of the sardine spawning biomass during 1986. Details of the method, including procedures for estimating egg production parameters, are described in Wolf and Smith (1986). An adult survey was conducted simultane-

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

[Manuscript received February 5, 1987.]

ously with the egg area survey, in order to develop current estimates of adult parameters for Pacific sardines. Results from this survey, however, are not yet available. Design and results of the 1986 egg survey are presented in the following sections.

EGG PRODUCTION METHOD

The egg production method (Lasker 1985) was developed by Parker (1980) and applied by Picquelle and Hewitt (1983, 1984) and Hewitt (1984) to estimate northern anchovy biomass. This method estimates spawning biomass as

$$B = P_o A \frac{kW}{RFS}$$

where B = spawning biomass (MT),
P_o = daily egg production, number of eggs produced per 0.05 m^2 of sea-surface area,
W = average weight of mature females (g),
R = sex ratio, fraction of population that is female, by weight (g),
F = batch fecundity, number of eggs spawned per mature female per batch,
S = fraction of mature females spawning per day,
A = total area of survey (0.05 m^2), and
k = conversion factor from grams to metric tons.

EGG PRODUCTION AREA METHOD

In the egg production area method, the spawning biomass is specified and the equation solved for A_1:

$$A_1 = \frac{B_1 RFSm}{P_o k_1 W}$$

where A_1 = spawning area of biomass B_1 in nautical miles^2,
B_1 = spawning biomass, in short tons,
k_1 = conversion factor from grams to tons,
m = conversion factor from 0.05 m^2 to nautical miles^2.

In the egg production method, daily egg production and population fecundity parameters are measured during the survey. Daily production of eggs, P_o, is estimated from the density and embryonic developmental stages of eggs collected in an ichthyoplankton survey. Daily specific fecundity parameters W, F, S, and R are estimated from samples of adult fish collected during the survey.

In the egg production area method, we adapted existing information from previous studies (Table 1) concerning sardines and related species to estimate parameters P_o, W, F, S, and R for sardines. This range of parameter estimates—presented and described in Wolf and Smith (1986)—was used in the egg production area equation to produce a range of estimates of A_1. We selected 500 n.mi^2 from the range of values as a useful estimate of spawning area.

SURVEY DESIGN

The 1986 survey was conducted in August, rather than in May, as in 1985. Several sources of information, including nearshore egg and larval surveys in the Southern California Bight (R.J. Lavenberg, Los Angeles County Museum of Natural History, pers. comm.) indicated that sardine spawning in recent years has occurred in late summer and fall rather than in spring. CDFG surveys of young fish did not detect evidence of sardine recruitment until September 1985. Adult sardines captured in these sea surveys and incidentally in

TABLE 1
Values of Parameters Used to Estimate Spawning Area, and Resulting Estimates

B_1	W	R	F	P_o	S	A_1
Spawning biomass (short tons)	Average female weight (g)	Sex ratio (females/total)	Batch fecundity (eggs/batch/ female)	Egg production (eggs/.05m^2-day)	Spawning fraction (spawning females/ total females)	Spawning area (nautical miles^2)
20,000	120	0.5	32,000	5.0	0.02	141
					0.05	353
					0.10	706
					0.15	1,058
				1.5	0.02	470
					0.05	1,176
					0.10	2,352
					0.15	3,528

the mackerel fishery were in progressively more advanced prespawning states in summer and fall during 1985.

The location of the survey area was based on results of the 1985 survey, which indicated that sardine spawning took place relatively close to shore and was prevalent in the eastern portion of the Santa Barbara Channel. Stations were more concentrated in 1986, and were spaced 4 n.mi. apart offshore and 4 n.mi. alongshore, in an attempt to obtain a greater number of positive stations to improve information on the sampling distribution of eggs. The survey covered approximately 5,000 n.mi^2. As in 1985, the critical spawning area, A_1, was estimated to be 500 n.mi^2., or approximately 10% of the 1986 survey area. Because each station represented 16 n.mi^2., the calculated spawning area that 20,000 tons of sardines would cover was expected to produce at least 31 stations with eggs present.

SURVEY DESCRIPTION

The survey was conducted aboard the Occidental College research vessel *Vantuna,* from August 4 through August 12, 1986. Stations were occupied north to south from Point Conception to the Mexican border, from the 10-fathom isobath to approximately 25 n.mi. offshore (Figure 1). Samples were collected at all hours, and, in contrast to the 1985 survey, stations occurring within shipping lanes were occupied. Plankton samples were collected at 330 stations using a 25-cm-diameter CalVET net (vertical egg tow) of 150-micron mesh. The net was retrieved vertically from 70 meters where depth allowed. Plankton samples were preserved in 5% buffered Formalin solution at sea. In the laboratory, sardine and anchovy eggs and larvae were identified, sorted, and counted.

The 1986 survey collected a total of 266 sardine eggs from 59 stations, with the number of eggs per station ranging from 1 to 18 (Figure 2). The mean number of eggs per station was 4.51 (standard error = 0.548) (Table 2). Positive stations occurred along the coast between Santa Barbara and Ventura; in the eastern portion of the Santa Barbara Channel out to and around Santa Cruz Island; in Santa Monica Bay and offshore in the Santa Monica Basin to approximately 30 miles; and between Seal Beach and Dana Point, along the coast and out to Santa Catalina Island in the San Pedro Channel. A total of 413 sardine larvae was collected at 113 stations, from approximately the same areas as sardine eggs (Figure 3). The number of sardine larvae per positive tow ranged from 1 to 22.

Evidence of anchovy spawning was much less

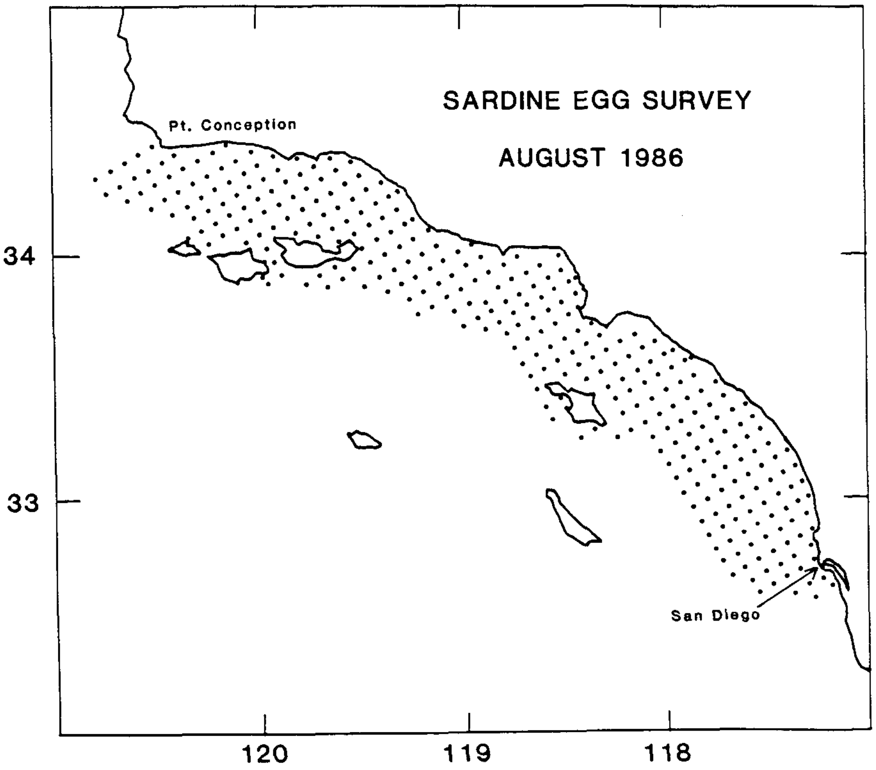

Figure 1. Stations occupied during sardine survey, August 1986.

TABLE 2

Pacific Sardine Egg Sample Frequency Distributions at Different Levels of Estimated Spawning Biomass[a]

#/10 m²		Net types and years						
x	ln (*x*)	CalVET 1986	CalVET 1985	CDFG 2-m 1931–32	1-m 1941	0.5-m 1941	Hi-speed 1950	1-m 1959
.125	−2.08	—[b]	—	2	—	—	—	—
.5	−0.69	—	—	4	—	—	—	—
2	0.69	—	—	6	21	—	—	28
8	2.08	—	—	7	22	8	—	28
32	3.47	—	—	14	16	15	—	30
128	4.85	19	4	12	31	29	77	23
512	6.24	22	4	13	27	14	20	12
2,048	7.62	18	2	5	17	10	7	5
8,192	9.01	0	1	2	3	2	1	4
Estimated mean		902	1,564	544	569	619	406	410
(Biomass (10⁶ MT)[c])		0.02	0.02	3.9	2.7	2.7	1.0	0.2

[a] (Smith and Richardson 1977)
[b] Value below sampler threshold
[c] (Murphy 1966)

common, probably because most anchovy spawning occurs in February and March. Only 39 eggs and 240 larvae were collected, from 27 and 106 stations, respectively. Furthermore, anchovy eggs and larvae were more concentrated in the southern portion of the survey area, between Point Fermin and San Diego.

SPAWNING AREA

The spawning area was determined by multiplying the number of positive egg stations by the area represented by each station (16 n.mi^2.). Slight adjustments were made by including half of the unsampled areas that were adjacent to positive stations, averaged along lines by order of occupation.

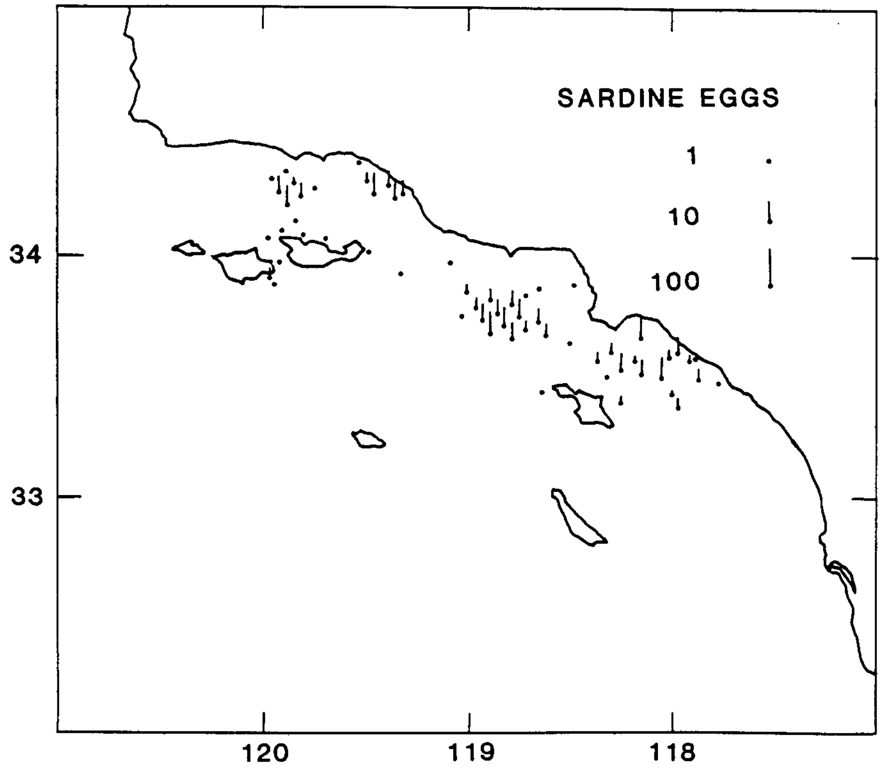

Figure 2. Stations with sardine eggs.

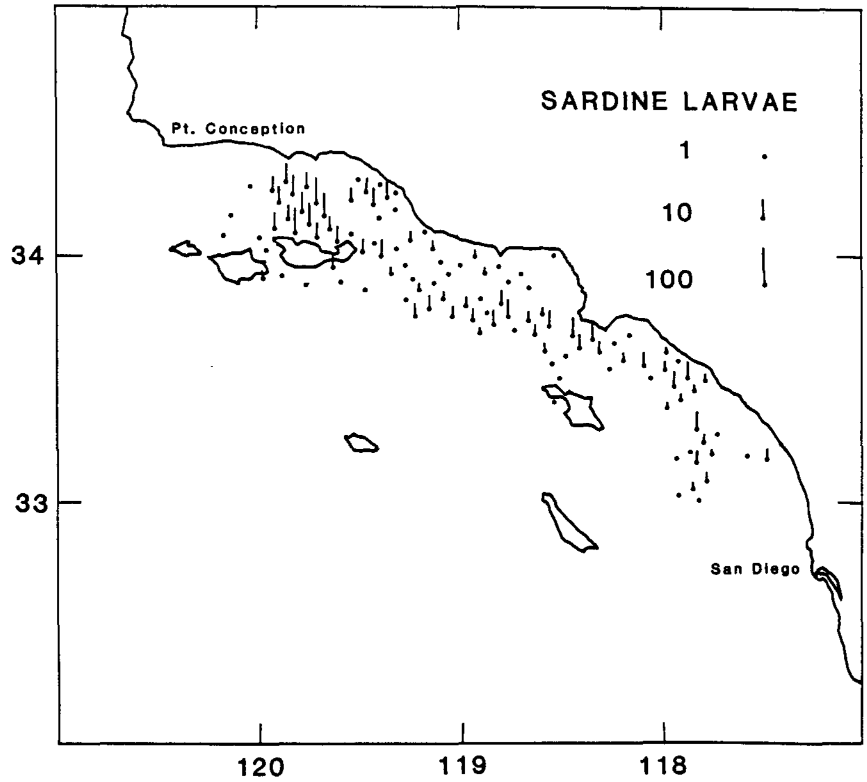

Figure 3. Stations with sardine larvae.

The area of positive stations too near to shore to include an entire 16 n.mi^2. was also adjusted to include only the portion actually sampled (Figure 4). The adjusted estimate of the 1986 spawning area is 955 n.mi^2., which is within the range of spawning area calculated for 20,000 tons of spawning biomass, and greater than the selected estimate of 500 n.mi^2. for A_1. This year's spawning area is 43% larger than the spawning area determined in May 1985.

DISCUSSION

Because the spawning area detected during the survey exceeds that predicted for 20,000 tons of adult sardines, the spawning biomass of sardines off California is considered to be at least 20,000 tons. As a result, the 1,000-ton fishery for sardines was reopened on January 1, 1987. This is the second year of a limited fishery for sardines, and is a continuation of the first directed harvest of sardines allowed in California since the moratorium was enacted 12 years ago.

Although a substantial (43%) increase in spawning area was observed in 1986 compared to the spawning area detected in 1985, the estimate of spawning area for 1986 is probably conservative. Our observations were limited to the survey area, and additional spawning probably occurred elsewhere. We observed evidence of spawning at the offshore edge of the survey, and spawning could have extended beyond those bounds. Fishermen reported large schools of sardines near Santa Barbara Island at the time of the survey. The offshore banks (Tanner and Cortez) were historical spawning grounds for sardines and, although we saw no evidence of spawning there in 1985, it is not known whether spawning occurred in those areas during the 1986 survey. CDFG young-fish surveys in October 1986 detected juvenile sardines near Tanner Bank. Young-of-the-year sardines were observed in Monterey Bay in 1985, and in San Francisco Bay in 1986, indicating that some spawning occurred north of Point Conception in both years.

Our estimate of spawning area for 20,000 tons of adults (500 n.mi^2.) is based on estimates of the adult reproductive parameters. Daily egg production and spawning fraction are not yet known for Pacific sardines. Two other parameters—average female weight and batch fecundity—were estimated from the historical population. An adult survey, in which sardines were collected by purse seine, was conducted simultaneously with the egg survey during 1986 in order to improve our estimates of these parameters. Results from this survey, however, are not yet available. At low biomass levels, existing techniques for biomass

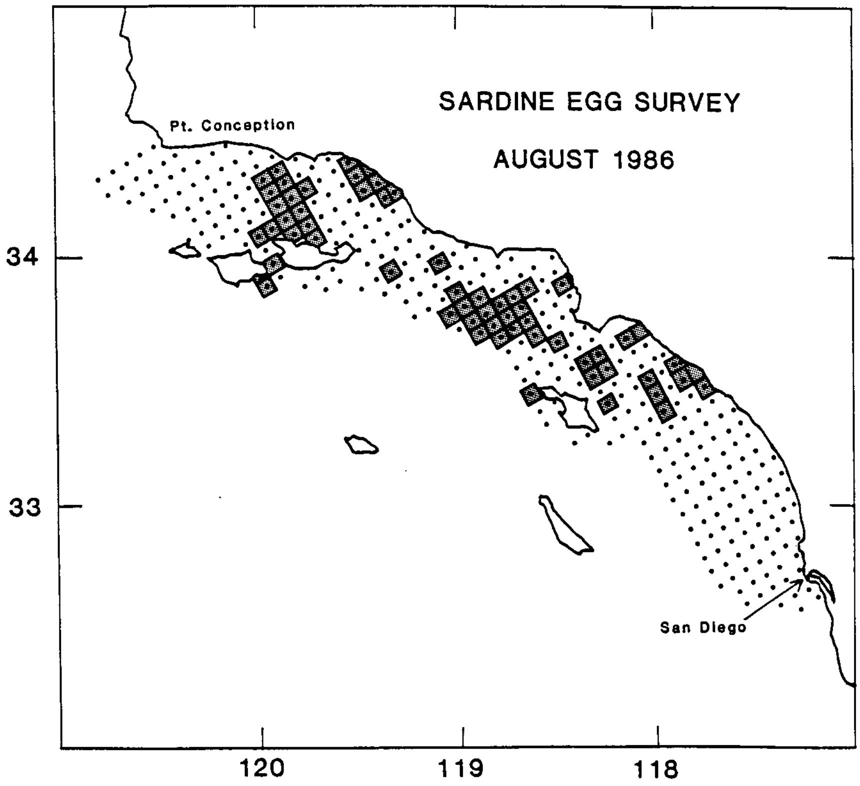

Figure 4. Squares outline the 4-by-4-n.mi. areas represented by each positive station in order to illustrate the spawning area adjustment. Shaded area is the adjusted sardine spawning area.

estimation cannot provide adequate precision. Evaluation of spawning area for biomass assessment is the best available tool where there are low levels of a recovering stock. For sardines, however, the actual relationship between spawning biomass and spawning area is not yet known.

Although the estimated mean of positive samples in the CalVET surveys is high relative to samples taken in the 1930s and 1950s, the 1986 estimated mean appears to be more realistic. This reflects the increased number of positive samples, but still points to technical problems (sampling threshold and scale of integration of the CalVET net relative to other samplers) that cannot be resolved with small numbers of samples.

ACKNOWLEDGMENTS

We thank the crew of the Occidental College RV *Vantuna* and the captain, M. Kibby. B. Flerx and D. Abramenkoff of the National Marine Fisheries Service (NMFS) provided assistance with cruise logistics and equipment. The scientific crew participating in the cruise included A. Enami, G. Lang, J. Patman, and P. Simon of Occidental College. L. Dunn, M.A. Lumpkin, M.E. Farrell, F.R. Pocinich, and M.J. Haddox of Scripps Institution of Oceanography sorted the CalVET plankton samples, and B. Sumida MacCall, E.M. Acuna, E.G. Stevens, and D.A. Ambrose of NMFS staged the sardine eggs under the supervision of Dr. H.G. Moser. C.S. Methot and C. Meyer of NMFS entered and edited the data.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

LAKE ARROWHEAD, CALIFORNIA

OCTOBER 21, 1986

PERSPECTIVES ON MEXICAN FISHERIES SCIENCE

FISHERIES ACTIVITIES IN THE GULF OF CALIFORNIA, MEXICO

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ABSTRACT

The Gulf of California fisheries are of great economic importance to Mexico. In 1981, 500,000 metric tons (MT) were taken in the gulf, representing 33% of the total catch of Mexico. Of the total catch in the gulf, 94% is landed in the ports of Sonora and Sinaloa; 6% is unloaded in Baja California. Of the 31 ports where fish are unloaded, only Guaymas in Sonora and Mazatlán in Sinaloa are equipped with adequate fishing infrastructure. The humble fisheries development on the western coast of the gulf is due to the scarcity of drinking water. In this paper, mention is made of the development of the fishing fleet, the processing plants, fishing arts, and main species exploited in the zone. Sardines are, by far, the most important group, because of the size of the catch (360,000 MT in 1981). It is estimated that the catch of neritic species will not increase significantly in the near future, and therefore any fishing increases will depend on the exploitation of species that have not traditionally been fished in Mexico.

RESUMEN

Las pesquerías del Golfo de California son de gran importancia económica para México. En 1981, se pescaron 500,000 TM en el golfo representando 33% de la captura total de México. Un 94% de la captura total del golfo proviene de los puertos de Sonora y Sinaloa, y un 6% de Baja California. De los 31 puertos de descarga de pesca, sólo Guaymas en Sonora y Mazatlán en Sinaloa tienen una infraestructura pesquera adecuada. El bajo desarrollo de las pesquerías en la costa oeste del golfo se debe a la escasez de agua potable. En el presente trabajo se menciona el desarrollo de la flota pesquera, las plantas procesadoras, las artes de pesca y las principales especies explotadas en la zona. Las sardinas son claramente el grupo más importante dado el tamaño de la captura (360,000 TM en 1981). Se estima que la captura de especies neríticas no aumentará significativamente en un futuro cercano y, por lo tanto, un incremento en la pesca dependerá de la explotación de especies no pescadas tradicionalmente en México.

STATUS OF FISHERIES DEVELOPMENT

Mexican fisheries have shown a great increase in the last few years. However, the increases have not been of the same magnitude in the Gulf of Mexico as in the Pacific Ocean: the catch in the gulf reached a little more than 300,000 MT in 1981; the catch in the Pacific reached about 1,000,000 MT in 1984 (Figure 1).

Considerable increases are reported for the northwestern region of the Mexican Pacific coast (Figure 2). In 1973 a little over 220,000 MT were landed, in contrast with 900,000 MT in 1981.

The greatest increases were observed in the Gulf of California, reaching up to 500,000 MT in 1981 (Figure 3), and representing 33% of the total catch of Mexico for that year. Thus, the Gulf of Califor-

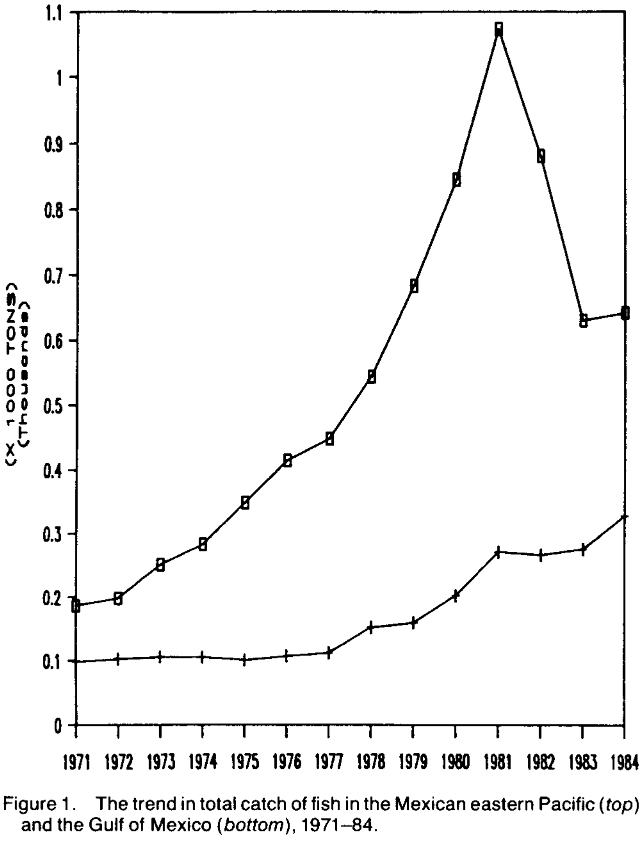

Figure 1. The trend in total catch of fish in the Mexican eastern Pacific (*top*) and the Gulf of Mexico (*bottom*), 1971–84.

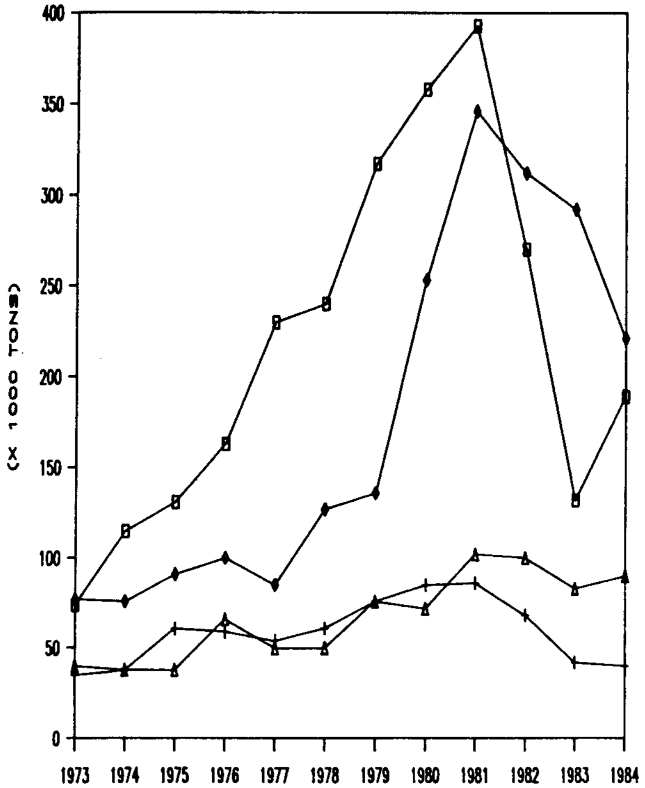

Figure 2. Total catches for the northwestern Mexican Pacific coast, 1973–84. □ = Baja California Norte; ◇ = Sonora; △ = Sinaloa; † = Baja California Sur.

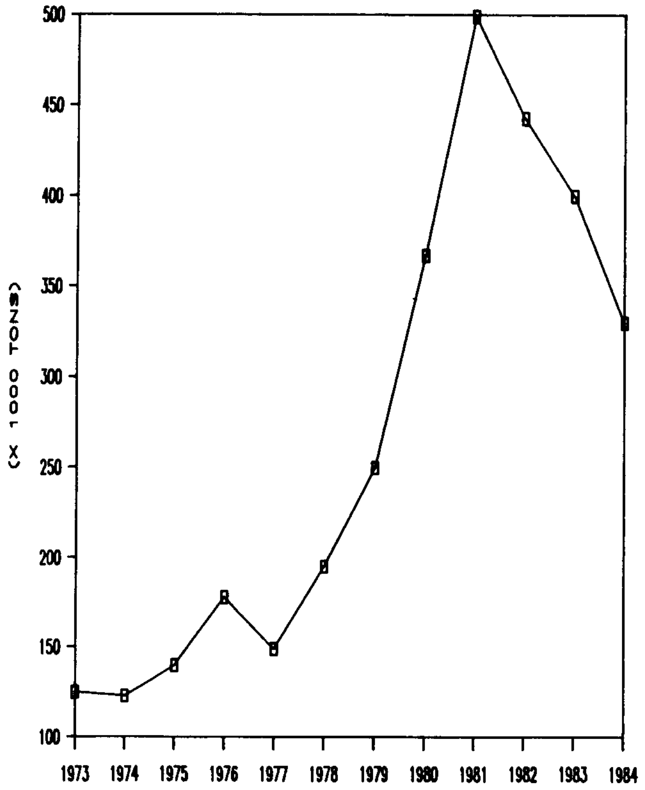

Figure 3. Total catch in the Gulf of California, 1973–84.

nia has become the most important body of water in Mexico for fisheries.

Although the fishermen and most of the boats are distributed along the length of the gulf coasts, the delivery and unloading of the fisheries products is carried out in 31 ports, of which only Guaymas in Sonora and Mazatlán in Sinaloa have sufficient infrastructure to receive and process large volumes. However, the existing infrastructure on the eastern coast of the gulf is underused; e.g., the Port of Guaymas uses only 12.5% of its freezing capacity.

The unevenness of the fisheries development could suggest that concentrations of marine products are greater along the eastern than the western coast of the Gulf of California, especially if we consider that 94% of the total catch reported for the area is delivered to ports in Sonora and Sinaloa. The low volumes unloaded in the ports of Baja California Norte and Sur are due to the scarcity of water, which has limited the development of towns and fishing ports on the western coast.

The neritic species of the Gulf of California are characterized, among other things, by their high species diversity, low volumes, and high economic value. The pelagic species are characterized by low species diversity, high volumes, and low price.

HISTORY OF THE FISHERIES

Fishing activities in the northern part of the Gulf of California date back to the exploitation of the totuava (*Totoaba macdonaldi*), which started at the beginning of the century. These fish were caught mainly for their stomachs, which were in demand among the Chinese population. As a result of this activity, three ports were established: San Felipe; el Golfo de Santa Clara; and Puerto Peñasco. During the 1940s the demand for sharks increased because their livers are rich in oil. Therefore the demand for the totuava increased, since its liver is also a source of oil. In the middle 1940s the exploitation of shrimp, (*Penaeus stylirostris, P. californiensis*), began (this fishery is discussed by Magallon in this volume). The shrimping activity within the totuava's area of reproduction takes many young totuava, and this may affect recruitment. However, incidental capture continues. When the catch of this species decreases, fishing activities tend to stabilize, since in this zone other resources are not abundant. At the end of the 1960s the three ports experienced a sharp increase in tourism, and fishing activities began to take second place.

In the central part of the Gulf of California, fisheries exploitation is further supported by the capture of turtles (*Lepidochelys olivacea*), especially in the Bahía de los Angeles and at the ports near Isla Tiburón (a Seri Indian settlement), where this species is the principal fishing target. To date, Desemboque and Kino are ports that still handle mainly sharks.

In contrast with the ports of San Felipe, Puerto Peñasco, and Golfo de Santa Clara, those of Baja California Sur were established for reasons that have nothing to do with fishing. Loreto, Mulegé, and La Paz were missions founded by friars who colonized the Baja California peninsula. These towns have never been prominent in fishing activities, but in the middle of the nineteenth century La Paz was one of the principal pearl markets of the world. Commercial activity began in 1615 and developed up to 1938, when a high natural mortality of the stocks of mother of pearl (*Pintada mazatlanica*) occurred in few months. Total production at that time was about half a million oysters during the eight-month fishing season. With present-day stocks it is not possible to obtain more than 20,000 oysters, consequently exploitation is prohibited.

The port of Santa Rosalía, Baja California Sur, was founded as a result of mining activities that developed in the beginning of the nineteenth century and continued up to 1980. The appearance of high volumes of Spanish mackerel (*Scomberomorus* spp.) in the years 1978, 1979, and 1980 supported the initial fishing activities, which continued during 1981, 1982, and 1983 for the squid fishery.

In the port of Guaymas, Sonora, before the mid-1940s, fishing was only for totuava and shark. Later the shrimp fishery and, since 1968, the sardine fishery began. Other fish landed in Guaymas are dogfish (*Mustelus* spp.), mullet (*Mugil* spp.), snapper (*Lutjanus* spp.), and giant squid (*Dosidicus gigas*), which are exploited in the years when they are abundant close to the coast. Shrimp (*Penaeus* spp.) and lobster (*Panulirus gracilis*) are species of the highest economic value.

PRESENT STATUS OF FISHERIES

Sardines are the most important pelagic species exploited in the Gulf of California. This fishery consists of small epipelagic species: the Monterrey sardine (*Sardinops sagax caerulea*); the thread herring (*Opisthonema libertate* and *O. bulleri*); the Japanese sardine (*Etrumeus teres*); mackerel (*Scomber japonicus*); the anchoveta (*Cetengraulis mysticetus*); the pineapple sardine (*Oligoplites* spp.); and the Spanish mackerel (*Scomberomorus* spp.). During cold years the Monterrey sardines and mackerel (*Scomber*) predominate the catches; during temperate years the thread herring and other species dominate.

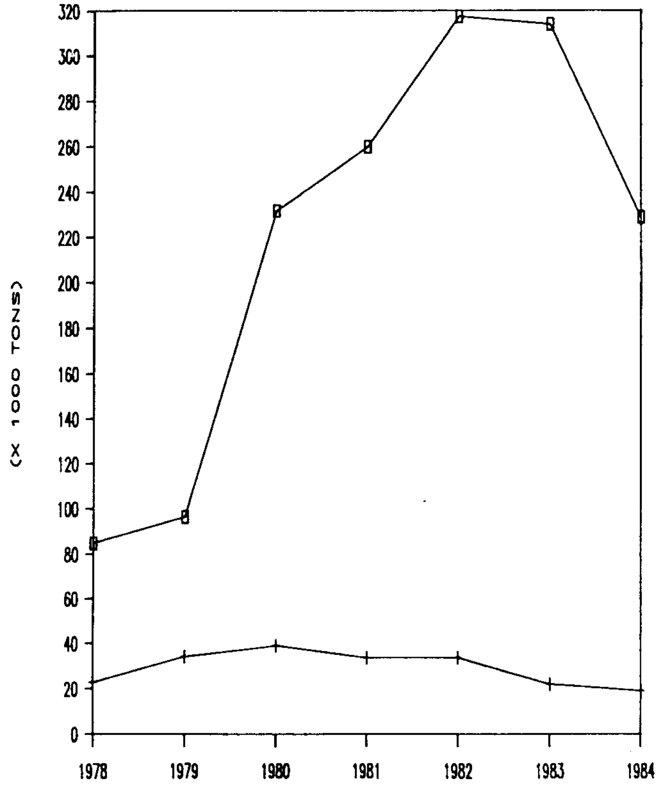

Figure 4. Landings of the six most important species at Guaymas, Sonora, 1978–84. □ = sardine; † = other fishes.

If we contrast the sardine catch unloaded at Guaymas with the catch of other species, the difference is considerable (Figure 4).

Mazatlán and Topolobampo stand out as the fishing ports of importance in the state of Sinaloa. Volumes unloaded in Mazatlán are not as great as those of Guaymas. In 1981 Mazatlán reported a decrease (in contrast with other ports of the gulf, which reported high increases), but in 1984 Mazatlán's volume increased. The catch of six principal species—thread herring (*Opisthonema libertate, O. bulleri, O. medirastre*); anchoveta (*Cetengraulis mysticetus*); Spanish mackerel (*Scomberomorus* spp.); and corvina (*Cynoscion* spp.)—surpass all the other species. In 1981 many uncommon species began to be sold as part of the commercial catch. These species are normally found in the southern part of the area.

Sardine fishing in the Gulf of California was initiated on a massive scale in 1971. Rapid development made it possible to capture 50,000 MT in

1976, 263,000 MT in 1980, and 381,000 MT in 1982. At first it was intended that fishing should be directed in a large part toward canning, but the great tendency toward reduction to fish meal forced federal authorities to obligate fishermen to process a certain percentage of the catch for canning. A point of equilibrium appeared reachable by using the Monterrey sardine mainly for packing, and the thread herring (*Opisthonema* spp.) mainly for meal. At present, this concept has been modified, and now any one of the species is canned.

In 1978 sardines were reduced to fish meal in 31 plants and canned in 13. In 1984 reduction occurred in 40 plants and canning in 14, an increase of almost 30% in reduction and 7% in canning.

The Monterrey sardine concentrates in summer months near the large islands of the Gulf of California (Ángel de la Guarda and Tiburón), and moves along the coast of Sonora during the winter. The southernmost penetration was reported in 1972, when the Monterrey sardine was caught in the port of Mazatlán, Sinaloa. From 1984 to 1986 Monterrey sardines were distributed from Tepopa Bay, Sonora, to Bahía de Santa María, Sinaloa, and from San Luis Gonzaga, Baja California, to Punta Chivato, Baja California Sur. Sizes ranged from 120 to 181 mm with a mean size of 147.5 mm. This size class constituted 15.8% of the total catch.

The Monterrey sardine has a characteristic yearly migratory pattern. Spawning occurs during the winter months south of Sonora, and eggs and larvae are dispersed by currents to the area between Bahía Concepción and Isla San Marcos. The juveniles move along the coast to Isla Ángel de la Guarda, arriving there around August. In September–October juveniles arrive at the "blue zone" off Isla Tiburón, and then in October–November, juveniles and adults move to southern Sonora. After spawning, adult fishes are dispersed along Sonora and northern Sinaloa; in April–May they return to the islands of the Gulf of California.

In the period 1984–86, distribution of this species on the western coast was from San Luis Gonzaga, Baja California, to Bahía Santa Ines, Baja California Sur, and on the eastern coast to El Datil river in Teacapan. Sizes varied from 71 to 245 mm, with a mean of 152.5 mm; this size class constituted 24% of the catch.

Mackerel (*Scomber japonicus*) for the period 1984–86 presents a similar distribution to that of the Monterrey sardine, but in smaller volumes. On the eastern coast of the gulf it is caught between Bahía Tepopa, Sinaloa, and Bahía Santa Maria, and on the western coast from Bahía de las Animas, Baja California, to Isla San Marcos, Baja California Sur. Sizes of mackerel ranged from 131 to 300 mm, with a mean size of 157.5 mm; this size class constituted 17% of the catch.

During 1984–86 fishing for round herring (*Etrumeus teres*) occurred between Bahía Santa Barbara and Santa Cruz, Sinaloa, which means that this species is primarily caught by the Mazatlán fleet, although it is also captured near Isla San Marcos. The length varied from 86 to 195 mm during brief periods, but for most of the season it varied from 106 to 170 mm, with a mean of 122.5 mm. This size class constituted 41% of the catch.

The future of the sardine fishery seems to point toward a stabilization of volumes taken within the Gulf of California; if an increase should occur in these fisheries, it would come from the region to the south of Mazatlán or from the exploitation of other species that coincide geographically with sardines.

Among the neritic species, the coastal species are submitted to the greatest fishing pressure. The volume does not exceed 5,000 MT. Mullet (*Mugil* spp.), sea bass (*Serranidae*), snapper (*Lutjanidae*), porgies (*Sparidae*), and sierra (*Scomberomus* spp.), are caught by fishermen in *pangas* (small boats) along the coasts of the gulf.

Another neritic component, which is presently being caught and used in very low quantities, is the fauna that accompanies the shrimp catch. Volumes varied between 130,000 and 250,000 MT: it is estimated that 109,000 to 152,000 MT are fish; the remainder are invertebrates. The shrimp fishermen take a small part of this volume and sell that which has some market value as fresh fish. The remainder of the fish, perhaps 100,000 MT, are of no value because the fishes are small and weigh very little; the product is not homogeneous, either in size or species; the meat content is generally very low; the meat is of poor quality; and some species are toxic.

The unprofitable fish are dumped into the sea. Undoubtedly, this fauna has a potential use that is now wasted. It would be desirable to take advantage of the entire catch, but the cost is, at present, prohibitive. Nevertheless, fishing statistics show that the volume of by-catch landed reached 25,000 MT in 1976. This was mostly transformed into fish flour and, in smaller quantities, into fish pulp with different commercial uses. This year, with Japanese investment, an attempt will be made to produce *surimi* from the fishes of the shrimp by-catch. The problem is that fishes must be at least 20 centimeters long to be useful for *surimi*, but 80% of the fishes in the catch are less than 15 cm long.

Another fishery that may be exploited in the future is that below 50 fathoms. This is suggested by the fact that the Mexican-Korean trawlers in the Gulf of California capture a good number of species that are the normal components of the shrimp catch, but of a greater size, which would make it possible to obtain a greater amount of fish pulp to make *surimi*. For the time being, however, the magnitude of this resource is unknown, and therefore it is not possible or advisable to make predictions.

Apart from what has been stated previously, it does not seem probable that volumes in the future will rise considerably, especially if we consider the structure of the present fisheries.

The fleet in the Gulf of California fell into four main classifications in 1984. First were the numerous *pangas* (dories and rowboats) dedicated to fishing along the coast or in lagoons or streams. These boats are most numerous in Sinaloa, where there are many lagoons and streams. Second were the sardine boats, designed especially to capture large volumes of fish in the epipelagic zone along the coast. Third were the boats designed to capture shrimp. Finally there were the ships dedicated to the capture of "scaley" fish (some are old shrimp boats and others were designed especially for this activity).

The Mexican government has tended to increase the volume of total catch to levels close to 6.3 million MT per year. However, the government has not taken into consideration the cost represented by these increases, especially with respect to the 1.9 million MT of mesopelagic fish. To date, there is a lack of research on the magnitude of the resource and the size of the fleet necessary to achieve that goal.

On some of the expeditions carried out in the Gulf of California by U.S. research ships, a high number of mictophids, such as *Triphoturus mexicanus*, have been found, raising the possibility that they may become an exploitable resource in the future.

THE MEXICAN TUNA FISHERY

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ABSTRACT

A global overview of different types of gear for tuna fishing is given in terms of species importance. The development of the tuna fishery in the eastern Pacific since 1903 is summarized, with an analysis of two methods: bait boat and purse seine fishing. At present, purse seine fishing in the eastern Pacific extends from the U.S.-Mexican border to southern Chile.

More detail is given on the development of the bait boat and purse seine fishery since 1970. The Mexican purse seine and bait boat fleet reached its maximum in the period from 1978 to 1986. Accordingly, tuna production of this fleet has increased in the last eight years. Historical analysis of tuna production of the Mexican tuna purse seine fleet components is presented, and the efficiency of the Mexican tuna industry is analyzed. Internal consumption and exportation of Mexican tunas tend to equilibrate. Some critical aspects in the development of the fishery are pointed out, and future projections are presented.

RESUMEN

Se presenta una visión global de los distintos tipos de arte de pesca utilizados en la captura de atunes, y las especies de mayor importancia capturadas con cada una de ellas. Se hace un resumen histórico del desarrollo de la pesquería del atún en el Océano Pacífico Oriental a partir de 1903. Se describen fundamentalmente dos etapas: la de la pesca con carnada y la de la pesca con red de cerco, alcanzando esta última una distribución desde la frontera de México con Estados Unidos en el norte hasta el Sur de Chile. Con mayor detalle se describe el desarrollo de la pesquería mexicana de atún con particular énfasis a partir de 1970. La flota mexicana del atún, compuesta por barcos de carnada y de red de cerco, ha alcanzado un máximo entre 1978 y 1986. De igual forma, las capturas se han incrementado considerablemente en los ultimos ocho años. Se analiza históricamente la producción de acuerdo a los sectores participantes en ella en relación a la flota. También se describe la situación actual de la industria atunera en términos de eficiencia. Se presenta un análisis del mercado tanto de consumo interno como de exportación, los cuales tienden a equilibrarse. Finalmente, se discuten algunos puntos críticos en el desarrollo de esta pesquería, y se ofrecen proyecciones para el futuro.

GLOBAL OVERVIEW OF TUNA FISHERIES

Tunas are found in almost every ocean in the world, and they have been the focus of some of the more important fisheries in terms of volume and commercial value. Tunas inhabit temperate and tropical waters of the Atlantic, Pacific, and Indian oceans. They live in the mixed layer, from 10 to 150 m deep, depending on the ocean and the time of year.

Tunas have been exploited mainly by three different types of gear: "pole-line" in bait boats; purse seine; and long-line. These methods of fishing have, respectively, reached approximately 40%, 30%, and 30% of the total world tuna production. The pole-line method has been used mainly to catch yellowfin, bigeye, albacore, northern bluefin, and southern bluefin. In this method of fishing, saury, mackerel, squid, and small coastal pelagic fishes like sardines are used as bait. The purse seine method is the more recent and is one of the most important methods for catching tuna today. The long-line method differs from the other two in that, depending on the target species, the lines can be set from 55 to 150 m deep. Additionally, with this type of fishing, considerable quantities of billfish and sharks are taken.

The average production of tunas in the world oceans is 70% from the Pacific Ocean, 20% from the Atlantic, and 10% from the Indian Ocean. Additionally, big tunas and billfish support important sport fisheries around the world.

TUNA FISHERIES IN THE EASTERN PACIFIC OCEAN

This document will refer exclusively to the bait boat and purse seine tuna fisheries.

The tuna fishery in the eastern Pacific had its origin in the United States in 1903. Fishing started with bait boats, and the U.S. began canning albacore tuna in California. The product was well accepted in the internal U.S. market, and developed rapidly. In 1914, catches were above 18 million

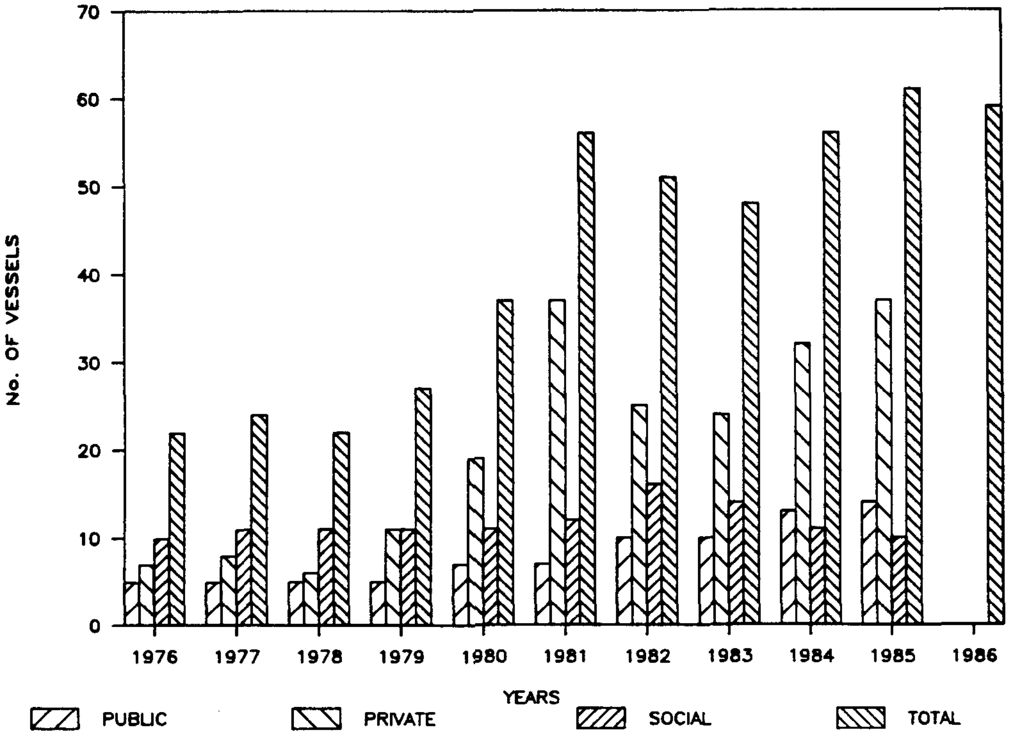

Figure 1. Historical development of the Mexican purse seine tuna fleet by three components: public, private, and social.

pounds. However, because of the nature of the albacore fishery, annual production varied, and in 1916 the catch was low. Producers thus decided to start canning small amounts of yellowfin and skipjack tuna from California. After the First World War, demand for canned tuna increased considerably in the U.S., and it was not possible to meet the demand with albacore alone. As an alternative, the U.S. industry processed large amounts of yellowfin and skipjack. In 1918, these two species accounted for 77% of the total tuna canned in the U.S.

In order to increase its tuna production, the U.S. tuna fleet began to explore southern waters of the Californias to find yellowfin and skipjack. In 1922, small boats, together with large refrigerated boats, made fishing trips during the spring months to Cabo San Lucas, searching for yellowfin tuna. In fall these boats explored near Bahía Tortugas, Baja California. As a result of these operations, fishing was very productive, and in 1923 catches from these areas exceeded those obtained in U.S. waters. In 1929, the U.S. tuna industry expanded its fleet with larger boats, and the California fleet unloaded 64 million pounds. This fleet discovered new tuna banks in Rocas Alijos, Revillagigedo Islands, and Tres Marías Islands, where fishing was possible year-round.

In the 1930s the U.S. fleet made exploratory trips to Clipperton and Cocos islands in Central America, the Galápagos Islands off northern South America, and along the coasts of Guatemala, El Salvador, and Panama. In 1934, the southern region of Panama and the Galápagos Islands were heavily exploited. During the 1950s, tuna fishing by bait boats continued to increase, reaching its maximum at the end of that decade.

Since the 1960s, as a consequence of the development of new gear (purse seine), storage capacity, and the length of trips of the international purse seine fleet, the fishery has expanded from the U.S.-Mexico border to 30°S, off Chile, and to 140°W–150°W at the equator.

THE MEXICAN TUNA FISHERY

There are records of the Mexican tuna fishery since 1937. From 1937 to 1965, catches fluctuated between 340 and 3,528 metric tons (MT); the most abundant catches occurred in 1950 and 1960. This fishery developed in the states of Baja California Norte and Baja California Sur. In 1970, the Mexican tuna fleet had 15 vessels, which caught 11,328 MT. This production level was sustained through 1972. In 1973 the fleet was increased to 19 tuna vessels, which caught 17,495 MT; in 1974 there were 23 vessels producing 21,615 MT of tuna.

After Mexico declared its Exclusive Economic Zone, the Mexican tuna fleet expanded rapidly, taking an average of 35,000 to 40,000 MT of tuna from 1975 to 1981. In 1981, Mexico had 55 tuna

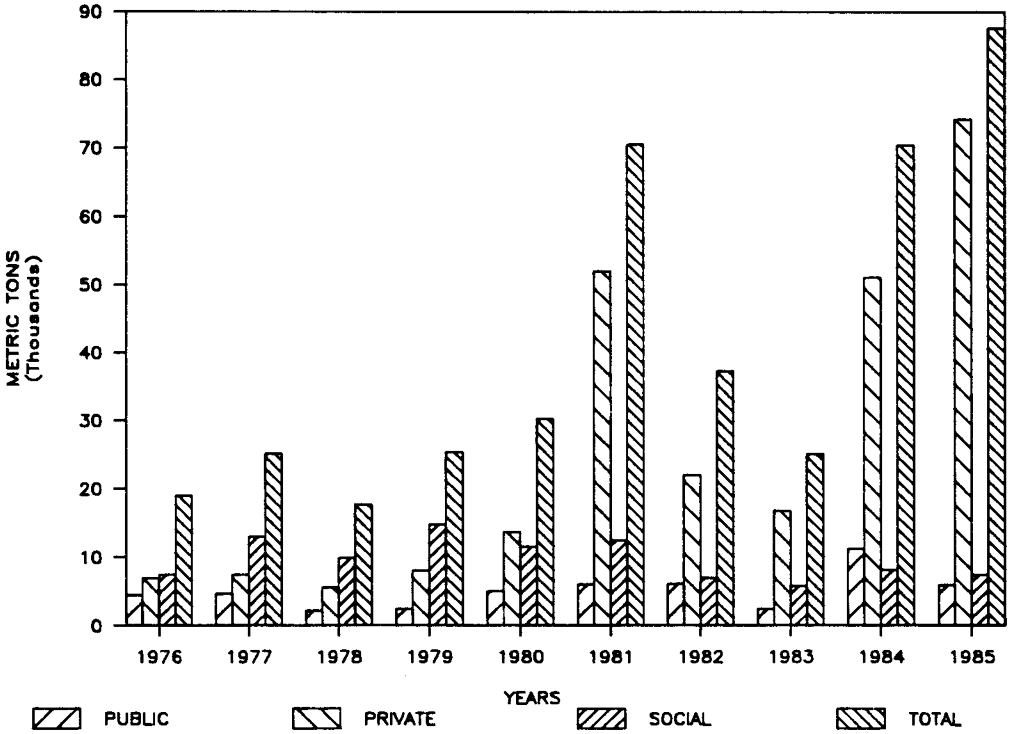

Figure 2. Production of tuna by the purse seine and bait boat fleets of Mexico in metric tons, 1976–85.

vessels and 37,000 MT of carrying capacity. In accordance with the Mexican tuna fleet expansion program, Mexico continued increasing its fleet, and in 1985 there were 61 vessels, with a total carrying capacity of 46,200 MT. In 1986 the fleet decreased to a total of 59 vessels and 49,000 MT of carrying capacity.

Figure 1 shows the historical development of the Mexican tuna fleet and its structure in three components: social, private, and government. Fishing organizations (cooperatives) financed by the federal government are referred to as the social component. The public component comprises fishing companies (Productos Pesqueros Mexicanos) whose industry and fleet are federal government property. This component is also referred to as "government." The private component comprises companies or associations using 100% Mexican capital, or joint ventures using Mexican and foreign capital in accordance with Mexican law. The main increase in the fleet occurred in the period from 1979 to 1985: carrying capacity increased from 14,000 MT in 1979 to 46,000 MT in 1985.

Figure 2 illustrates the development in terms of production. In 1976 Mexico produced around 20,000 MT, and in 1981, about 70,000 MT. However, in 1982 and 1983 there was a considerable decrease. In 1984 and 1985, a new increase in production was observed, reaching about 88,000 MT in 1985. In 1986, Mexico continued increasing its production, and by October had caught more than 80,000 MT. It was estimated that the catch would reach more than 100,000 MT by the end of 1986.

At the beginning of the development of the fishery, from 1976 to 1979, the social component of the Mexican tuna fleet contributed a major proportion of the catch. However, since 1981 the principal contribution of the catch has come from the private component of this fleet, which caught 50,000 MT, or 73% of the total production, in 1981.

Figure 3 shows the historical development of the fleet in terms of carrying capacity. The private sector expanded the most. Social and public components remain stable and low relative to the private sector. The fishing effort of the purse seine fleet has increased considerably in recent years; however, the bait boat fleet has stabilized (Figure 4). As illustrated in Figure 5, from 1983 to the present, the Mexican purse seine tuna fleet has increased its yield per trip and, consequently, its carrying capacity (Figure 6). In 1986, this trend seems to continue. The bait boat tuna fleet has tended to stabilize, but in low proportion to the purse seine component. The main Mexican tuna ports are Ensenada, Mazatlán, La Paz, Puerto Lopez Mateos, Isla de Cedros, Bahía de Tortugas, and La Reforma. Exporting ports are Ensenada and Mazatlán.

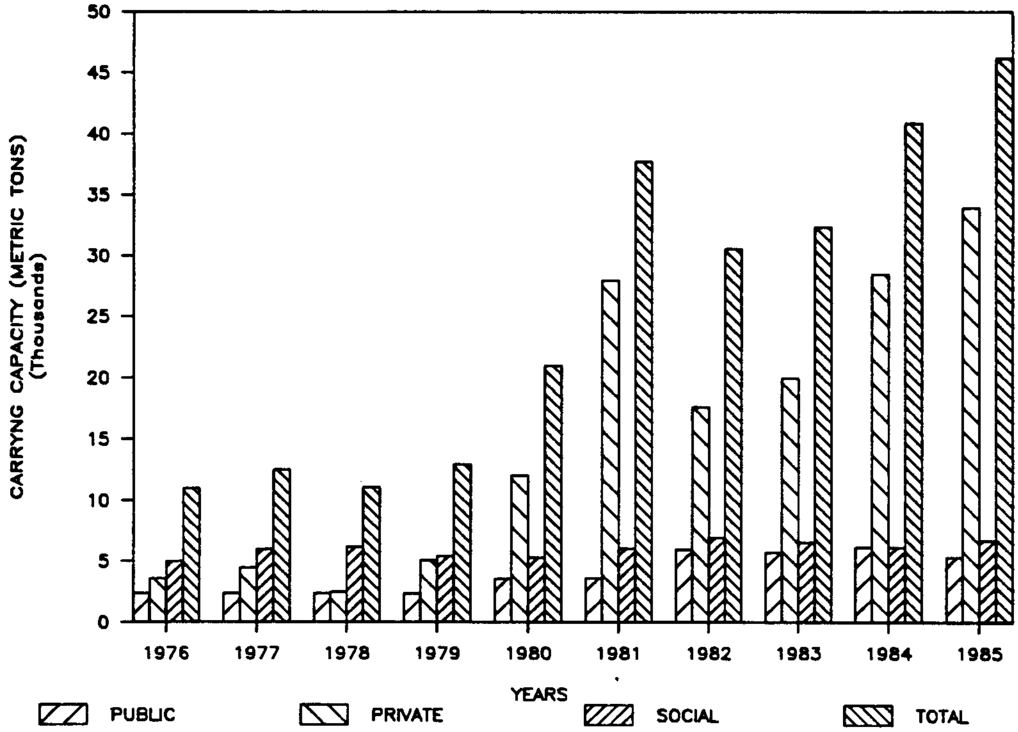

Figure 3. Development of the Mexican purse seine and bait boat tuna fleets in terms of carrying capacity.

FISHING AREAS OF THE MEXICAN TUNA FLEET IN 1985 AND 1986

The Mexican tuna fleet in 1985 covered the entire distribution of the eastern Pacific tuna fishery, according to the following seasonal pattern. In spring the fleet operated around the tip of the Baja California Peninsula and central Mexico as far as 140° west longitude and 5°–15° north latitude; in autumn the fleet concentrated in central Mexico and the mouth of the Gulf of California; in winter it spread out around the Mexican coast and Central America to the north of Peru. In 1986 the pattern of operation of the Mexican fleet was very similar to that of 1985; however, winter operations were extended far offshore of central Mexico.

TUNA INDUSTRY OF MEXICO

In 1985, 70% of the Mexican catch was sold as canned tuna. The national production of canned tuna reached about 3 million cases of 48 cans each. Most of this was packed in oil or water. The public sector produced 58%, the private sector 42%. In 1985 the internal market consumed about two-

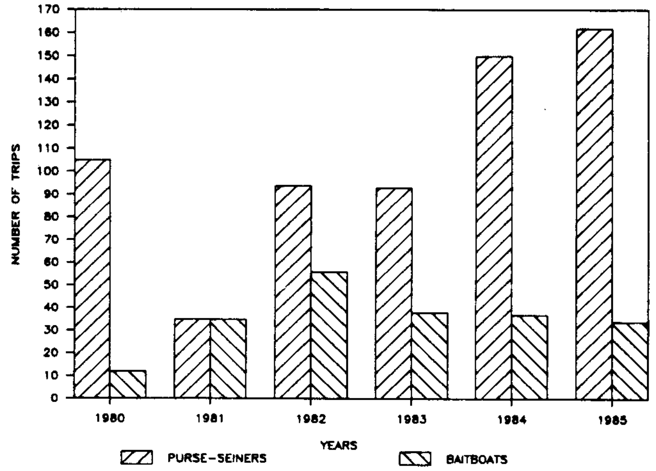

Figure 4. Total number of trips by type of fishing (purse seine and bait boat) shows a considerable increase in the purse seine fleet and stabilization of the bait boat fleet.

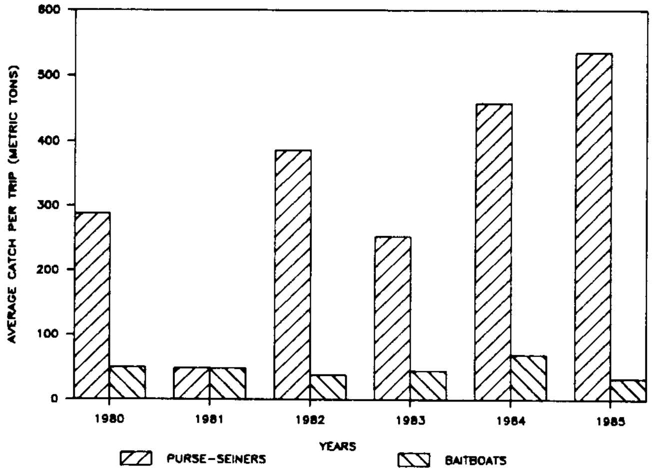

Figure 5. Catch and effort of the Mexican purse seine and bait boat fleets, 1980–85.

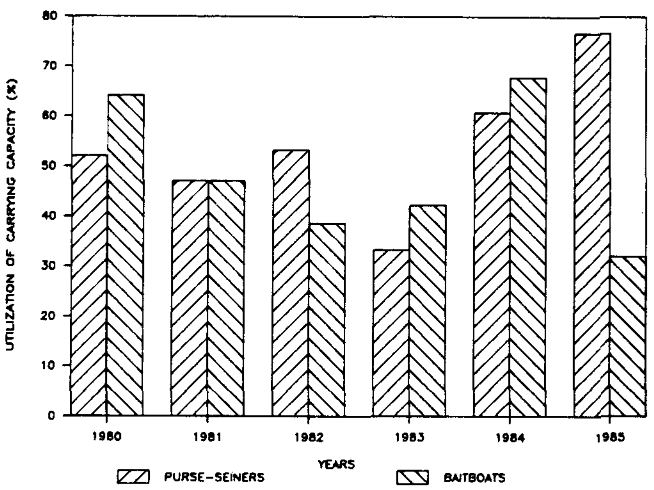

Figure 6. Yields in terms of carrying capacity of the Mexican purse seine and bait boat fleets, 1980–85.

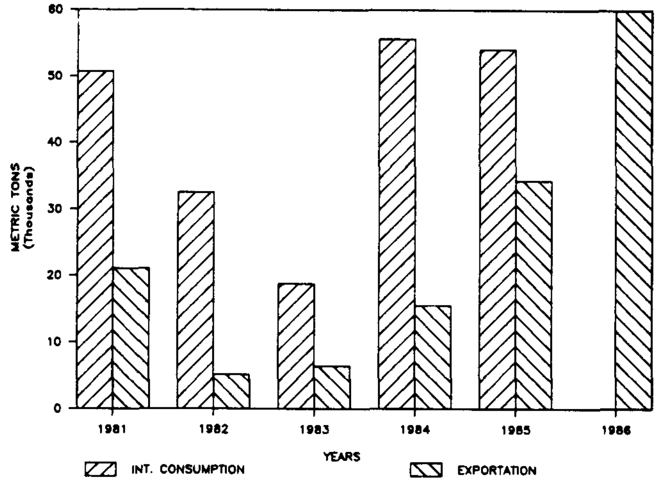

Figure 7. Mexican internal consumption and exportation of tuna, 1981–86.

thirds of the total production of tuna; about 1 million cases remained in storage at the beginning of 1986.

The efficiency of the Mexican tuna industry seems to be below 60% of its capacity if oriented exclusively to canned tuna. However, most of the canneries produce products such as sardine, shrimp, lobster, abalone, tomato sauce, beans, and many other canned vegetables. From January to October 1986, Mexico caught more than 80,000 MT of tuna. Up to June 1986, Mexico had canned about 33,000 MT, which is equivalent to 47% of the national production (1.7 million cases). If this production level continues, by the end of 1986 Mexican tuna production could reach approximately 3.3 million cases. To October 1986, the public sector produced 58.83% of the total, and the remaining 42.17% was produced by the private sector. Both sectors had efficiencies below 60%, but in 1985 other products were produced.

PROCESSING CAPACITY

The public sector of the tuna industry has 313 MT capacity for each 8-hour workday. This is equivalent to 51.65% of the national processing capacity. This sector can pack 87,460 MT in a year of 280 working days, but because of the variety of products, its production remains below the optimum. Another factor affecting efficiency is the social orientation of this industry. Some canneries have been located in isolated areas so as to develop new communities. Some of these canneries, however, reach yields above 70% of their capacity in terms of days worked.

The private sector has a tuna-processing capacity of 293 MT for each 8-hour workday, or 48.35% of the national capacity. The optimum yield is around 82,000 MT for a year of 280 working days. The private sector is affected by the same circumstances as the public sector, and its production remains below the optimum.

COOLING STORAGE CAPACITY

The public sector has 12,400 tons of cooling storage capacity, equivalent to 70% of the national capacity. However, one 3,000-ton facility is under repair, so the present capacity is down to 9,400 tons. This capacity can be increased by contracting to use the cooling facilities of ANSA in Ensenada and Mazatlán. The Mazatlán ANSA facility has a 3,000-ton capacity.

The private sector has 5,300 tons of cooling storage capacity, equivalent to 30% of the national capacity. This can also be increased by contracting with private companies like COPEL in Mazatlán.

INTERNAL AND EXPORT MARKET

Mexico has developed an internal consumption market in the last 10 years. This market reached a maximum in 1986 on the order of 50,000–60,000 MT. However, in 1982 and 1983 there was a decrease, mainly due to a considerably reduced operation of the fleet in 1982, and to financial problems.

Mexico's external market increased 121% in 1985, from 15,470 MT in 1984 to 34,265 MT in 1985. An important factor in this increase was the reopening of the Canadian market. 1985 exports represented 30% of the national production. From January to September 1986, Mexico exported more than 40,000 MT of tuna, or more than 50% of its national production at that time. According to these figures, Mexico could export about 30,000 MT more in 1986, therefore increasing its exports to 200% of that of 1985. Figure 7 shows the Mexican tuna consumption and export from 1981 to 1986.

COMMENTS

The carrying capacity is being better employed, and it can be improved with more efficient unloading operations and a greater use of the unloading ports. There are many aspects that delay production of canned tuna in both private and public industry. These can be corrected by eliminating bottlenecks in the packing operations. It is recommended that the internal and export markets be brought into equilibrium through new strategies for marketing, industry, and fleet operation.

THE PACIFIC SHRIMP FISHERY OF MEXICO

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ABSTRACT

The Pacific shrimp fishery is the most important Mexican fishery in terms of foreign exchange and employment. This fishery comprises an offshore and a lagoon fishery, like other tropical shrimp fisheries of the world. The offshore fishery[1] supports the largest fleet; the lagoon fishery supports the most fishermen.

The lagoon fishery began in pre-Hispanic times, with native barriers called *tapos*. This fishery has become very important in coastal lagoons of the Pacific, and nowadays cast nets such as *atarrayas* and *suriperas* are also used. The catch has stabilized at around 4,000 to 6,000 metric tons (MT) in the last 25 years, with some fluctuations.

The offshore fishery was developed in the 1930s with modified sardine boats. The fleet grew rapidly to 800 boats, and remained stable until 1971. From 1971 to 1981 it increased to 1,700 boats. This important increase in the fleet was made without any increase in the catch. The present catch level is 25,000 to 27,000 MT, with important stock fluctuations in the last 25 years. In the early 1960s and 1980s the catch reached similar maximum levels. During the late 1960s and 1970s the annual catch per boat decreased to a minimum from 40 to 15 MT.

Total catch in both fisheries has reached 40,000 to 55,000 MT in the last five years (1980–84). Regionally, Sonora and Sinaloa provided the main part of the catch. A similar but less important area is that of Oaxaca and Chiapas.

RESUMEN

La pesquería de camarón del Pacífico de México es la más importante del país desde el punto de vista de obtención de divisas y generación de empleo. Está integrada por una pesquería de altamar y otra de aguas protegidas como lo están también otras pesquerías tropicales en el mundo. La primera sostiene la mayor flota pesquera del país, mientras que la segunda sostiene la mayor parte del empleo.

La pesquería de aguas protegidas se ha desarrollado en los sistemas lagunarios costeros desde la epoca prehispánica, con barreras llamadas "tapos." Actualmente es una pesquería muy importante en la mayoría de los sistemas lagunarios del Pacífico, e incluye, además de los tapos, redes denominadas atarrayas y suriperas. La captura en aguas protegidas se ha estabilizado en 4,000–6,000 ton en los últimos 25 años, y se han observado importantes fluctuaciones en la captura a través de los años.

La pesquería de altamar se desarrolló en los años 30 gracias a la introducción de sardineros modificados. Desde esa época hasta los años 60 la flota camaronera mexicana del Pacífico creció rápidamente hasta alcanzar una flota de 800 barcos, la cual permaneció estable hasta 1971. En la década de 1971–81, la flota creció hasta alcanzar 1,700 barcos. Este importante crecimiento de la flota ocurrió sin ningún incremento paralelo en la captura. Los niveles actuales de captura se encuentran entre las 25,000 y 27,000 ton, con importantes fluctuaciones en los últimos 25 años. A principio de los años 60 y 80 se lograron capturas máximas similares y, a finales de los años 60 y durante los años 70, las capturas alcanzaron sus niveles mínimos, descendiendo de 40 a 15 ton por barco por año.

La captura total en ambas pesquerías alcanzó unas 40,000–55,000 ton en el período 1980–84. Desde el punto de vista regional, los estados de Sonora y Sinaloa aportan la mayor parte de las capturas. Una zona similar aunque de menor importancia es la de Oaxaca y Chiapas.

INTRODUCTION

The Pacific shrimp fishery is the most important fishery for the country of Mexico, from both economic and social standpoints. More than 80% of the total catch is exported, which results in an important contribution to foreign exchange. The fishery has an offshore and a lagoon component, as do most other tropical shrimp fisheries in the world. About 1,600 trawlers operate in the offshore fishery. This is the largest fishing fleet in the country, and represents an important investment. The lagoon fishery is the main support of many communities established near the numerous lagoons along the Pacific coast.

During 1980–84, the total catch fluctuated from

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[1] In this paper, offshore shrimp fishery is defined as that occurring in bottom depths ranging from 5 to 60 fathoms.

TABLE 1
Pacific Shrimp Catch by States (MT, Heads on)

State	1980	1981	1982	1983	1984
Baja California	1,698	1,780	1,818	1,162	965
Baja California Sur	579	211	563	1,070	427
Sonora	16,880	14,177	15,053	15,605	12,001
Sinaloa	22,944	16,536	28,318	25,303	25,962
Nayarit	872	711	1,659	2,266	1,121
Jalisco	0	0	0	32	3
Colima	114	94	381	657	532
Michoacán	0	0	0	0	1
Guerrero	133	122	114	121	106
Oaxaca	5,494	5,872	5,734	5,771	6,862
Chiapas	1,546	2,208	1,495	1,803	2,984
Total	50,260	41,711	55,135	53,790	50,964

TABLE 2
Pacific Shrimp Fleet by States

State	1980	1981	1982	1983	1984
Baja California	51	68	60	64	58
Baja California Sur	13	21	34	38	38
Sonora	664	743	712	593	593
Sinaloa	509	557	580	570	570
Nayarit	4	3	5	24	24
Jalisco	0	0	1	13	13
Colima	74	77	31	29	29
Michoacán	7	0	6	8	8
Guerrero	14	11	8	8	8
Oaxaca	166	164	187	181	181
Chiapas	38	48	33	35	35
Total	1,540	1,692	1,657	1,563	1,557

40,000 to 55,000 MT (heads on), the main part of it (up to 80%) from the offshore fishery. Of that, more than 80% is caught in the Gulf of California, 15% in the Gulf of Tehuantepec, and less than 5% on the west coast of Baja California and the central Pacific coast of Mexico (Table 1).

Within the Gulf of California, Sonora and Sinaloa support the main part of the fishery (76% of the total catch), mainly because of the great number of lagoons and the excellent trawling areas on the continental shelf.

Fleet size contributes to the relative importance of this fishery; 75% of the shrimp trawlers were originally based in these two states, mostly at Guaymas and Mazatlán (Table 2). This fleet operates through the entire Pacific area, switching from ground to ground as a function of the minimum commercial densities available at each of them. The same is true for the rest of the fleet during the fishing season.

In the Gulf of Tehuantepec, Oaxaca supports the main part of the total shrimp catch, taken mostly by the Salina Cruz fleet. There are also important lagoon areas here.

The Pacific shrimp fishery is mainly based on three species: brown shrimp (*Penaeus californiensis*), blue shrimp (*Penaeus stylirostris*), and white shrimp (*Penaeus vannamei*). Other species commonly found in the landings are the red shrimp (*Penaeus brevirostris*) and other species of *Xiphopenaeus* and *Sicyonia*. Their landings have become increasingly important as the fleet grows.

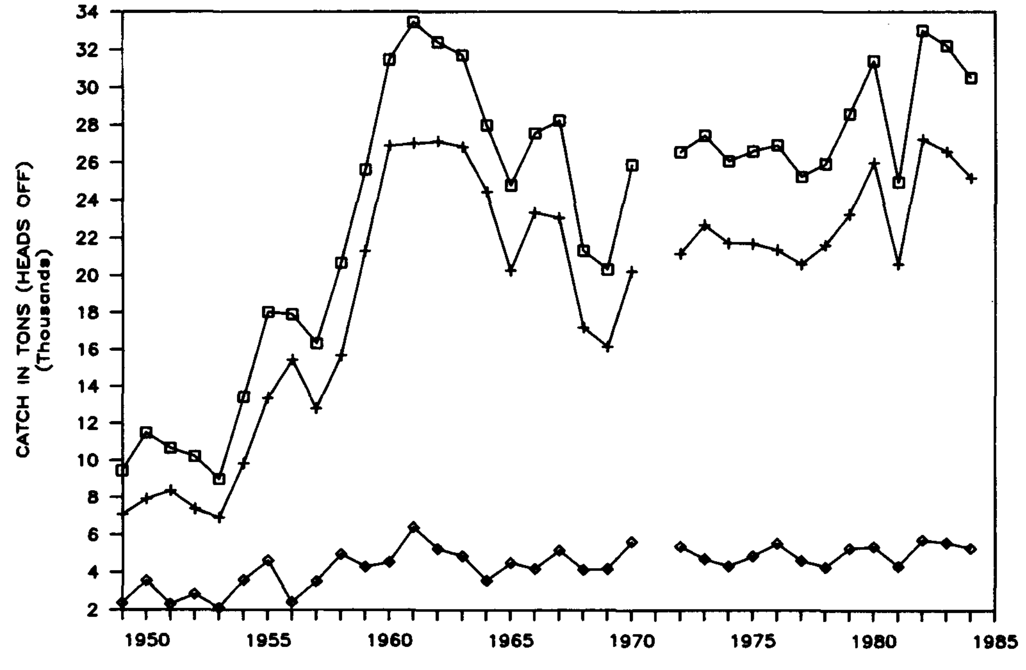

Figure 1. Catch trends in the Pacific shrimp fishery of Mexico. □ = total; † = offshore fishery; ◇ = lagoon fishery.

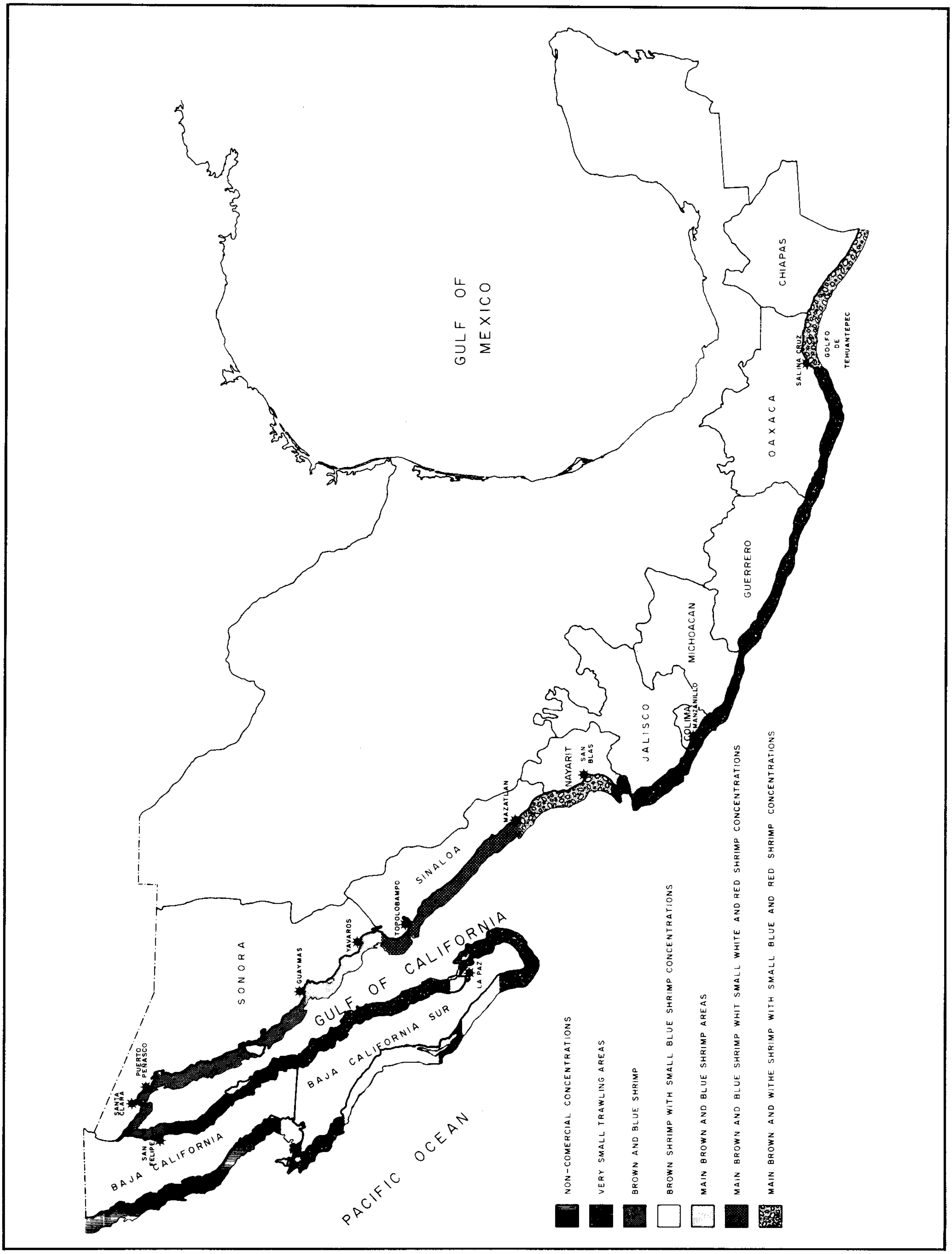

Figure 2. Geographical distribution of commercially important shrimp species in the Pacific fishery.

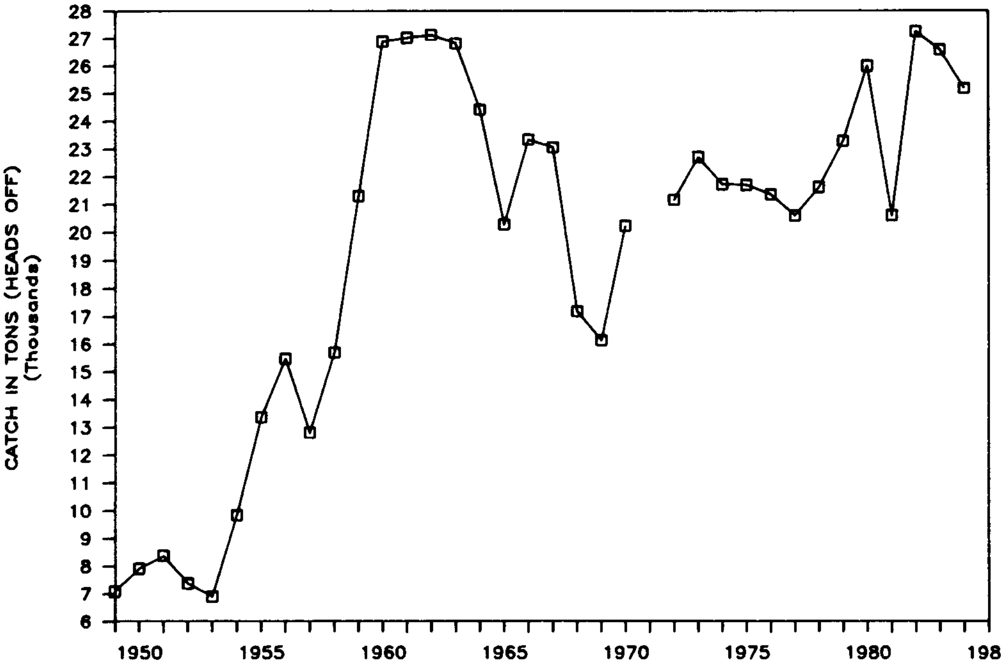

Figure 3. Catch trends in the Pacific shrimp offshore fishery.

TABLE 3
Pacific Shrimp Offshore Fishery

Year	No. of boats	Catch (MT)	Catch per boat (MT)
1949		7,086	
1950		7,920	
1951		8,370	
1952		7,369	
1953		6,902	
1954		9,841	
1955		13,372	
1956	458	15,474	33.79
1957	514	12,806	24.91
1958	838	15,697	18.73
1959	730	21,315	29.20
1960	807	26,900	33.33
1961	694	27,030	38.95
1962	688	27,136	39.44
1963	819	26,820	32.75
1964	867	24,431	28.18
1965	880	20,285	23.05
1966	653	23,356	35.77
1967	710	23,072	32.50
1968	731	17,186	23.51
1969	754	16,150	21.42
1970	762	20,242	26.56
1971	845	—	—
1972	919	21,182	23.05
1973	1,041	22,719	21.82
1974	1,196	21,738	18.18
1975	1,192	21,705	18.21
1976	1,237	21,362	17.27
1977	1,329	20,606	15.50
1978	1,358	21,635	15.93
1979	1,515	23,290	15.37
1980	1,540	26,016	16.89
1981	1,692	20,621	12.19
1982	1,657	27,257	16.45
1983	1,681	26,592	15.82
1984	1,557	25,195	16.18

THE LAGOON FISHERY

The lagoon fishery was developed in pre-Hispanic times by natives, mainly in Sinaloa and Nayarit in the southeastern Gulf of California. They mostly used the *tapos*, barriers built with mangrove sticks across the channels and mouths of estuaries and lagoons. Shrimp juveniles (mainly blue and white shrimp) are trapped during their seasonal migration from the nursery areas in the estuaries to the spawning grounds offshore. The *tapos* system was described by Nuñez and Chapa (1951). Recently, *tapos* have been built with concrete and wood.

The *atarraya* (throw-net) and the *suripera* cast net are also commonly used nowadays. Both are usually made by the fishermen and operated from a small boat (12 m being the most common length) with an outboard engine of typically 45 hp. These nets were introduced around 1920.

The lagoon fisheries of the northern part of the Gulf of California and Magdalena Bay on the west coast of Baja California are based on the catch of blue shrimp juveniles, but in the southern part of the gulf this fishery comprises mostly blue and white shrimp juveniles. In the Gulf of Tehuantepec, white shrimp juveniles predominate.

The Gulf of California lagoon fishery operates from September to December in the north, and from August to February in the south. It operates throughout the year in the Gulf of Tehuantepec. The differences are mainly because recruitment regimes vary in each area.

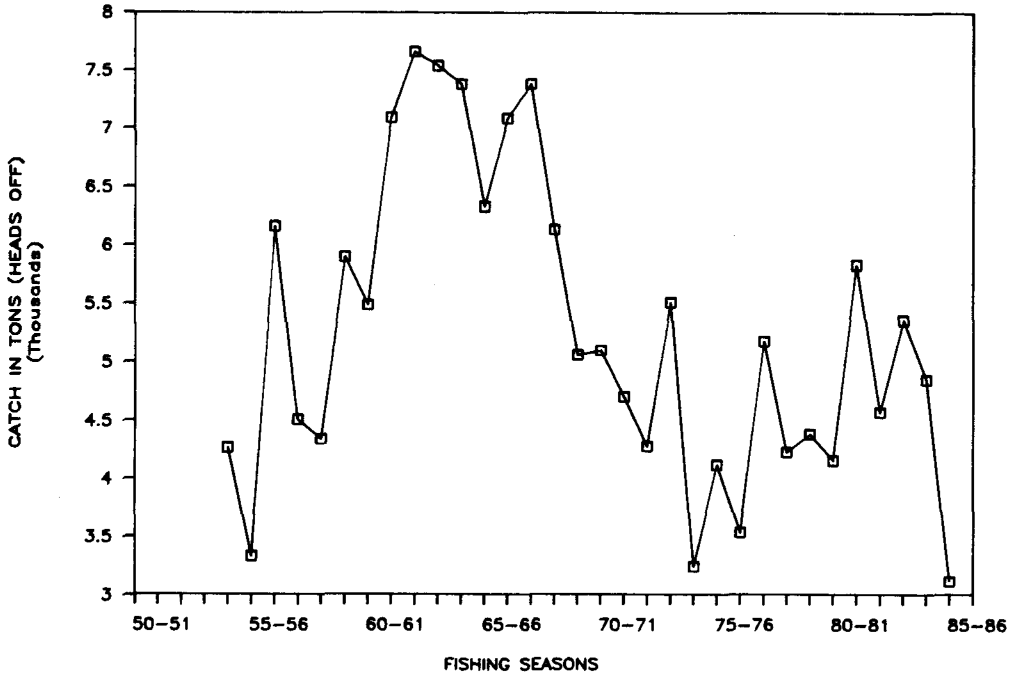

Figure 4. Catch trends in the Guaymas shrimp offshore fishery.

TABLE 4
Guaymas Shrimp Fishery

Fishing season	No. of boats	Catch (MT)	Catch per boat (MT)
1953–54	164	4,267	26.02
1954–55	133	3,329	25.03
1955–56	136	6,161	45.30
1956–57	166	4,506	27.14
1957–58	183	4,336	23.69
1958–59	165	5,899	35.75
1959–60	170	5,487	32.28
1960–61	184	7,092	38.54
1961–62	200	7,663	38.32
1962–63	227	7,543	33.23
1963–64	234	7,381	31.54
1964–65	233	6,331	27.17
1965–66	225	7,086	31.49
1966–67	239	7,386	30.90
1967–68	219	6,131	28.00
1968–69	269	5,059	18.81
1969–70	289	5,097	17.64
1970–71	282	4,703	16.68
1971–72	273	4,275	15.66
1972–73	274	5,511	20.11
1973–74	281	3,242	11.54
1974–75	342	4,119	12.04
1975–76	444	3,535	7.96
1976–77	429	5,177	12.07
1977–78	438	4,225	9.65
1978–79	429	4,383	10.22
1979–80	495	4,154	8.39
1980–81	481	5,833	12.13
1981–82	392	4,569	11.66
1982–83	349	5,360	15.36
1983–84	383	4,850	12.66
1984–85	337	3,115	9.24

The historical catch is shown in Figure 1. During the last 30 years catches have stabilized at around 4,600 MT (heads off), with fluctuations of approximately 25%. This fishery now covers most of the lagoons. An increase in the catch by mere fishery management techniques seems unlikely. Dredging of sand bars at lagoon mouths, promoted during the last 15 years, has apparently helped maintain the catch levels, but has not resulted in an increase.

In the long term, reduced river runoff because of dams and agricultural irrigation has had, apparently, little or no effect on the lagoon shrimp catch. The main prospect for increasing catch in the lagoon shrimp fisheries lies in shrimp aquaculture, which has been promoted for the last five years in experimental and commercial operations, mostly in the gulfs of California and Tehuantepec.

THE OFFSHORE FISHERY

The offshore shrimp fishery has been documented by Ferreira (1965). It began in 1921 at Guaymas with two United States boats. During the 1930s, 17 California sardine boats were modified to trawl, and were incorporated into the fleet. Japanese trawlers explored the Mexican Pacific coast and located the main trawling areas in the same decade.

During the 1940s and 1950s the fishery expanded to the entire Gulf of California and the Gulf of Tehuantepec. During the late 1950s, double-rig trawls were introduced. By 1960, fishing opera-

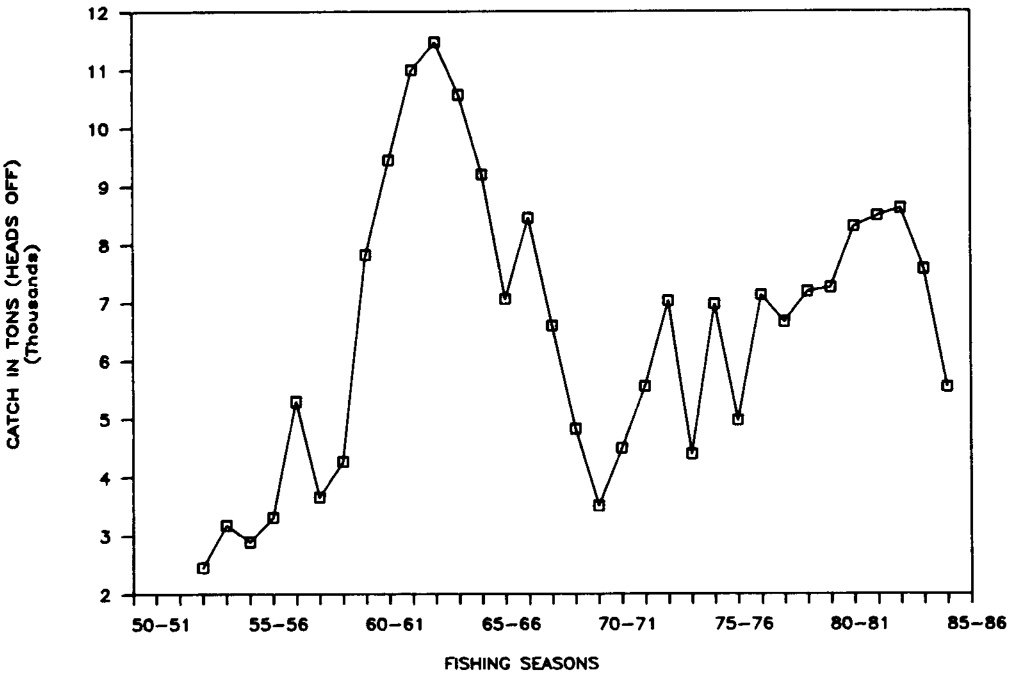

Figure 5. Catch trends in the Mazatlán shrimp offshore fishery.

tions extended to the southwest coast of Baja California. During the late 1960s and early 1970s, the fishermen gradually reduced mesh size (Lluch 1977). In 1977, mesh size regulation was introduced as a management measure.

Nowadays the fleet is equipped either with semi-balloon trawls or flat trawlnets. Official mesh size is 2¼ inches for the body and wings, and 1¾ inches in the cod end. Headrope length averages about 64 feet. Common vessel length ranges from 18 to 23 m. Wooden trawlers are usually powered by 200–250 hp diesels, and new steel trawlers with 350–500 hp motors.

The offshore fishery catches mainly brown shrimp along the coast, from Baja California to the Guatemala border, at depths ranging from 5 to 50 fathoms. Blue and white shrimp are caught from 5 to 20 fathoms. Red shrimp is obtained in the range

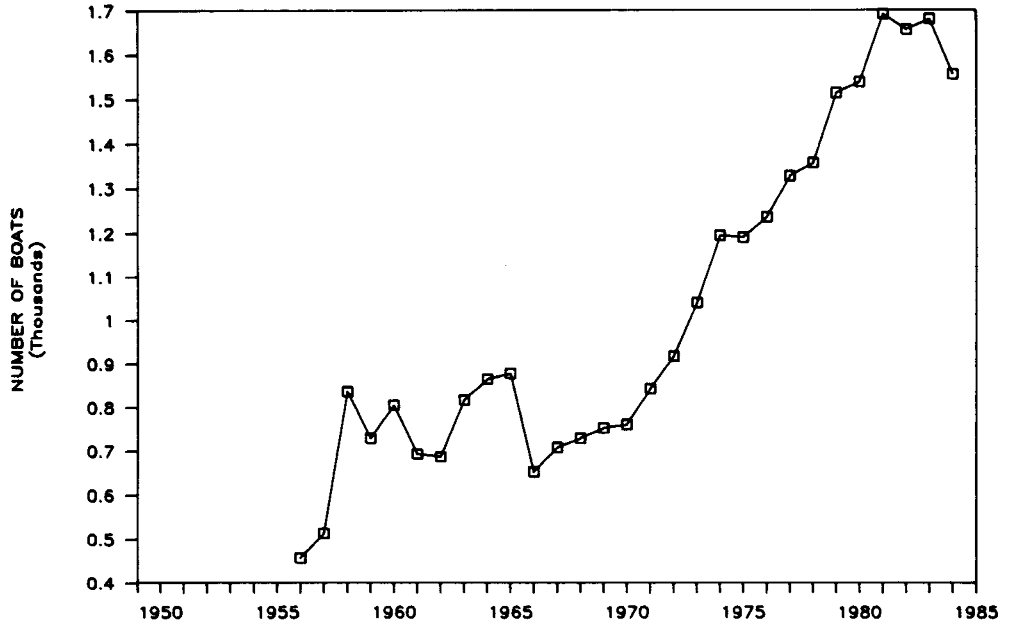

Figure 6. Historical evolution in the Pacific shrimper fleet.

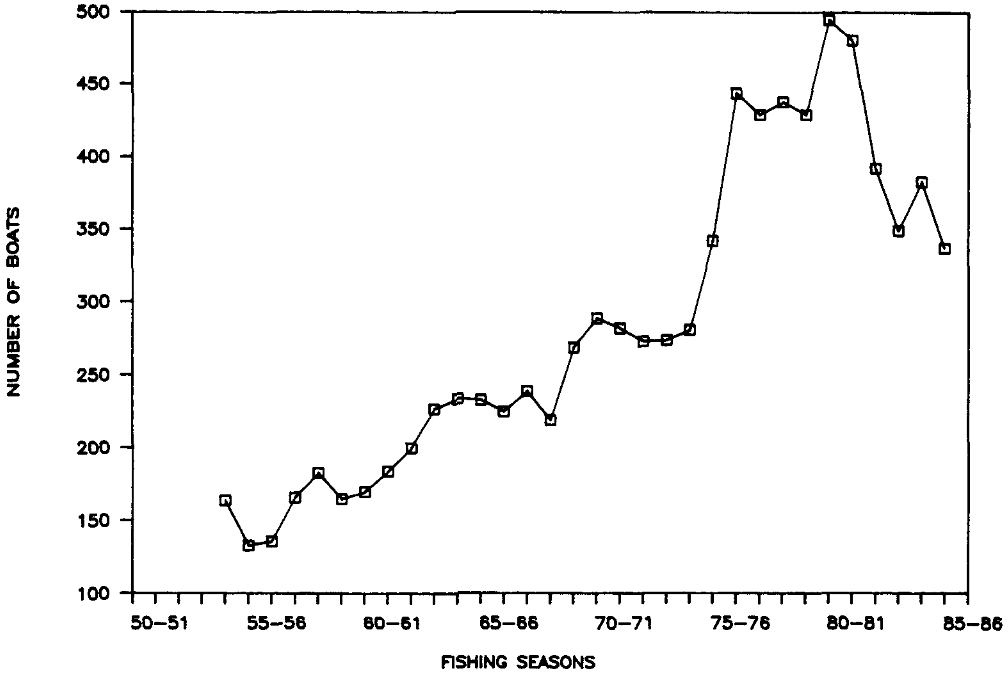

Figure 7. Historical evolution in the Guaymas shrimper fleet.

of 8 to 60 fathoms, in the southeastern part of the Gulf of California and all of the Gulf of Tehuantepec.

The fishery operates mainly from October to June, with a closed season during the remaining months. About 60% to 70% of the total season's landings is obtained during the first three months of the open season, mainly because of fleet size.

Both the main trawling areas and the species distribution are shown in Figure 2. Normally, when the open season begins, the fleet operates intensively in the central and eastern parts of the Gulf of California. As abundance declines in these areas, the fleet spreads its operation to other parts of the Pacific coast. The end of the open season is officially declared around May or June, but the vessels generally stop when shrimp density falls below that which is economical to fish.

For the last 12 years, shrimp stocks have been monitored by the Instituto Nacional de la Pesca

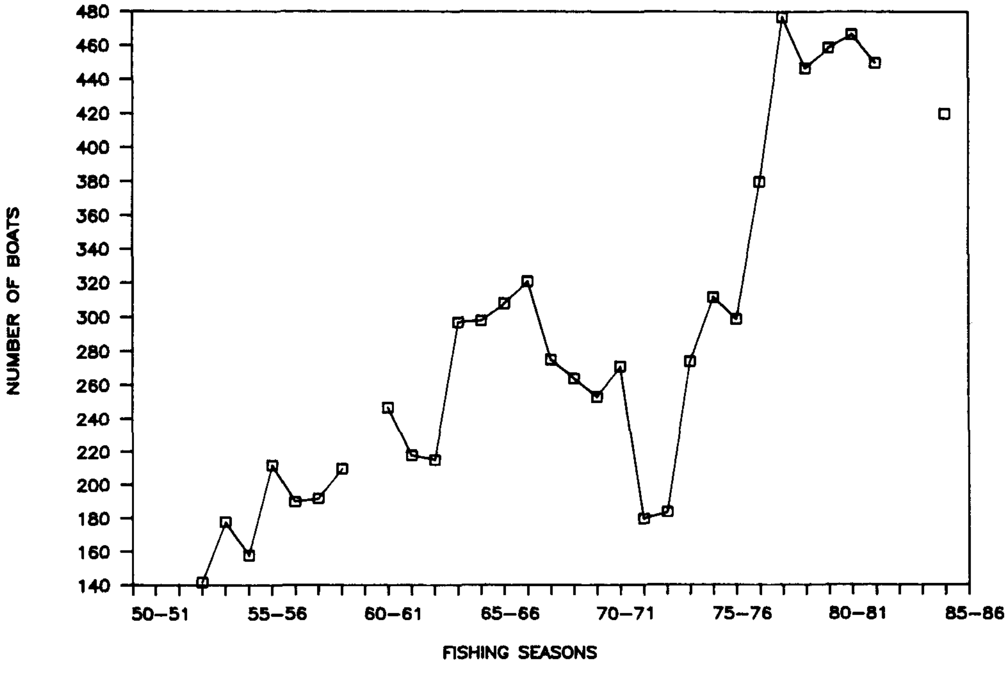

Figure 8. Historical evolution in the Mazatlán shrimper fleet.

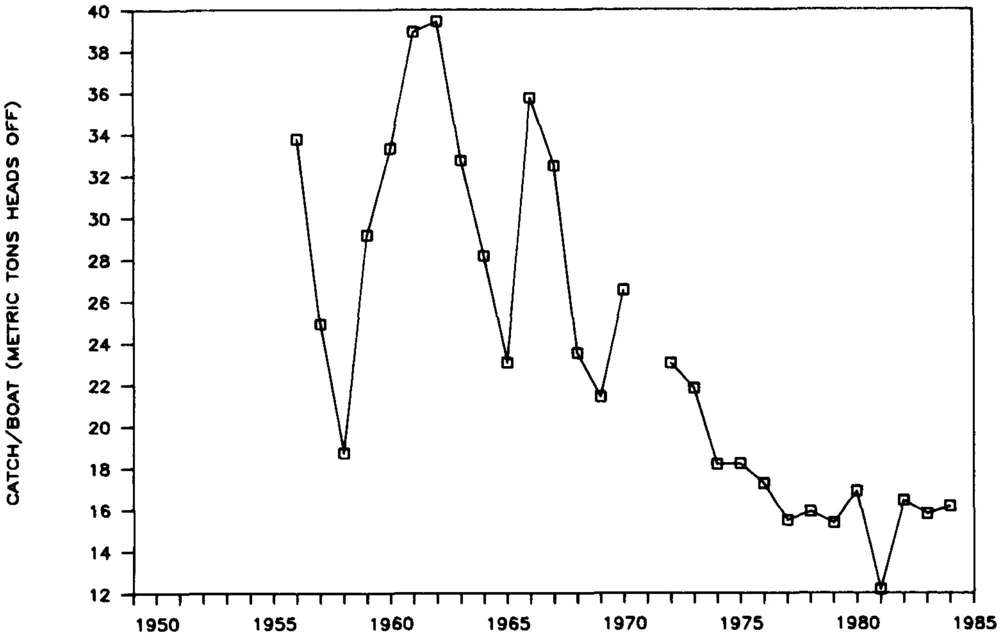

Figure 9. Catch/boat trends in the Pacific shrimp offshore fishery of Mexico.

(INP), together with other research and educational institutions, in order to recommend the beginning of the next open season. During these monitoring programs, spawning and recruitment areas are mapped each year.

Figure 1 shows the evolution of the total annual shrimp catch, which is influenced mainly by the offshore catch. During the last 30 years the offshore catch fluctuated widely. Beginning in the late 1950s, there was a rapid increase, reaching 26,000–27,000 MT (heads off) in the early 1960s. From 1965 to 1979 there was a sharp decline in catch, followed by an increase in the early 1980s that reached levels similar to the peak ones (Figure 3; Table 3). Interannual changes are masked by the aggregation of data of two different seasons into one year. The increase in catch observed during 1979–84 followed the aforementioned regulation in mesh size.

The first maximum, observed during the early

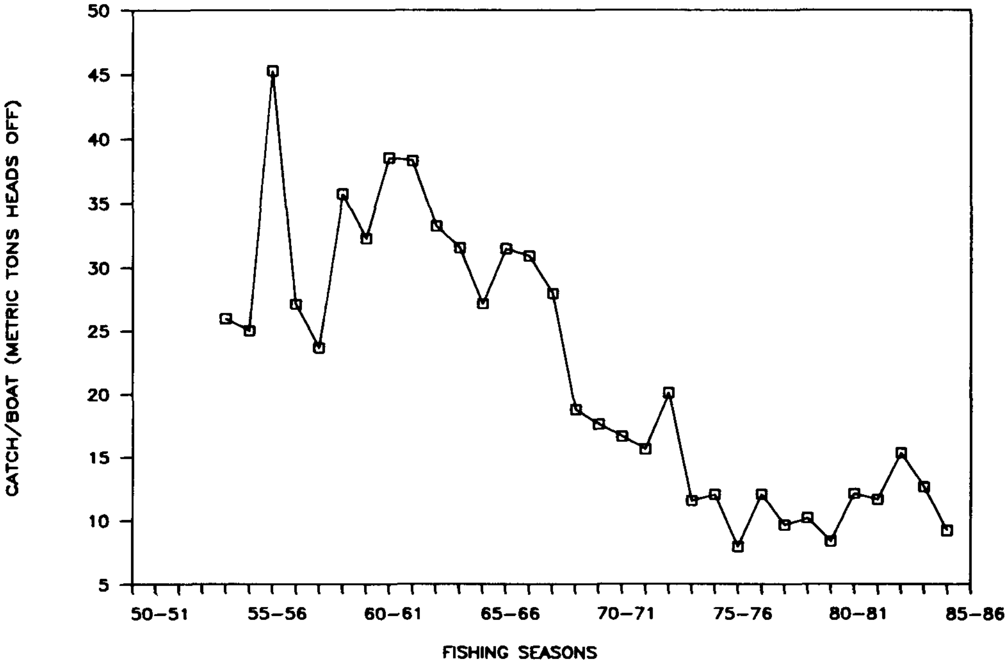

Figure 10. Catch/boat trends in the Guaymas shrimp offshore fishery.

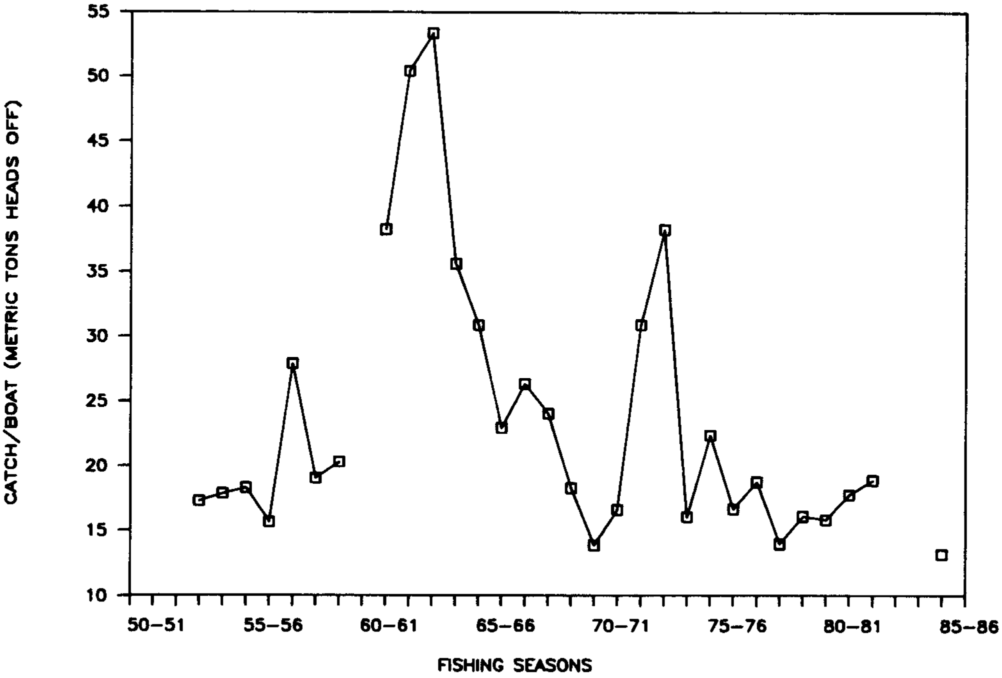

Figure 11. Catch/boat trends in the Mazatlán shrimp offshore fishery.

TABLE 5
Mazatlán Shrimp Fishery

Fishing season	No. of boats	Catch (MT)	Catch per boat (MT)
1952–53	142	2,454	17.28
1953–54	178	3,181	17.87
1954–55	158	2,893	18.31
1955–56	212	3,317	15.65
1956–57	190	5,302	27.91
1957–58	192	3,660	19.06
1958–59	210	4,267	20.32
1959–60	—	7,824	—
1960–61	247	9,451	38.26
1961–62	218	11,000	50.46
1962–63	215	11,480	53.40
1963–64	297	10,575	35.61
1964–65	298	9,200	30.87
1965–66	308	7,065	22.94
1966–67	321	8,458	26.35
1967–68	275	6,609	24.03
1968–69	264	4,829	18.29
1969–70	253	3,509	13.87
1970–71	271	4,499	16.60
1971–72	180	5,563	30.91
1972–73	184	7,038	38.25
1973–74	274	4,398	16.05
1974–75	312	6,983	22.38
1975–76	299	4,978	16.65
1976–77	380	7,138	18.78
1977–78	477	6,674	13.99
1978–79	447	7,204	16.12
1979–80	459	7,268	15.83
1980–81	467	8,312	17.80
1981–82	450	8,501	18.89
1982–83	—	8,628	—
1983–84	—	7,585	—
1984–85	420	5,550	13.21

1960s, was due mainly to the Guaymas and Mazatlán fleet operation; similar catch trends are observed in both fisheries (Figures 4 and 5; Tables 4 and 5). Interannual changes in catch are clearly seen in the Guaymas fishery (catch data are aggregated by fishing seasons). The recent maximum (early 1980s) was reached by all of the fishery; the Guaymas and Mazatlán fisheries contributed in smaller proportion to it, in contrast to the former maximum.

Fleet evolution shows an increase from the beginning of the time series and up to 1958, and a stable fleet size of around 800 boats during the next 13 years (Figure 6).

From 1971 to 1980 the fleet increased to 1,700 boats, clearly apparent in the Guaymas and Mazatlán fleet (Figures 7 and 8) and in other small fleets in the Gulf of California. The fleet doubled without any increase in the total catch, and the catch per boat diminished from 39 MT (heads off) per year in 1971 to 15 MT in 1980 (Figures 9-11). This decrease in catch per boat is observed in both the Guaymas and Mazatlán fisheries. During the declining phase, the Mazatlán fishery and the Pacific fishery were analyzed by Lluch (1977) and Lluch et al. (internal report, unpublished); the Guaymas fishery was analyzed by Rodriguez de la Cruz (1973, 1981) and Rodriguez de la Cruz and Rosales (1977). Following these reports, shrimp fleet growth was stopped in 1981. From then on, the

Pacific shrimp fleet stabilized; furthermore, a decreasing trend is observed in the Guaymas and Mazatlán fleets.

The main problems that remain in the Pacific shrimp fishery are the interseasonal and long-term stock fluctuations observed in the last 30 years. These changes are particularly important in the Gulf of California.

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PESQUERIAS PELAGICAS Y NERITICAS DE LA COSTA OCCIDENTAL DE BAJA CALIFORNIA, MEXICO

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México

RESUMEN

Este trabajo trata sobre las principales pesquerías de la costa occidental de la Península de Baja California, México, pretendiendo dar una idea general sobre el desarrollo, situación actual y perspectivas de las mismas. Así mismo, brevemente se abordan los posibles recursos pesqueros potenciales de la región. Finalmente, se señala la posible relación del abatimiento de los volúmenes de captura de esta zona con los fenómenos de calentamiento a gran escala del Océano Pacífico Oriental.

ABSTRACT

This review will present a general view of the development, present state, and future of the main fisheries of the eastern North Pacific off Baja California, Mexico. Potential fishing resources will be discussed. Finally, a possible relationship between the decline of regional landings the large-scale warm events of the eastern North Pacific will be suggested.

INTRODUCCION

La costa occidental de la Península de Baja California, México (Figura 1) está bañada por la Corriente de California, de origen templado-frío, que le confiere sus características. La mayor parte de los recursos vivos que se encuentran en ella son de origen templado, y se caracterizan por ser más abundantes pero menos diversos, a diferencia de los mares tropicales. Esta característica, en parte, impone una estrategia de explotación de tipo industrial, orientada a capturar y procesar grandes volúmenes de recursos pesqueros.

En términos generales, la costa occidental de la Península puede dividirse en dos zonas: una al Norte de Punta Eugenia, muy similar en condiciones oceanográficas a las áreas más al Norte con características eminentemente templadas, y otra al Sur, con características marcadas de zona de transición templado-tropical. Esta zona Sur presenta, especialmente en años cálidos, intrusiones importantes de especies tropicales.

Con el fin de ser breve, en este trabajo se tratará solamente aquellos recursos pesqueros que a mi juicio son los más importantes. Estos se dividen en

1. Recursos pesqueros costeros accesibles y de alto valor comercial: abulón, langosta
2. Recursos pesqueros masivos de bajo precio: sardina y anchoveta
3. Algas (*Macrocystis* y *Gelidium*)
4. Recursos pesqueros costeros de mediano y bajo precio (cabrillas, tiburones, Scianidos, almejas, etc.).

El impacto de los fenómenos a gran escala, como "El Niño," repercute en las capturas globales de esta región; así, en 1978, un año "normal," esta región contribuyó con el 41.6% de las capturas totales nacionales, mientras que en 1983, un año anormalmente cálido, la contribución de esta zona fue de un 17% (Tabla 1).

ABULON

El abulón es uno de los recursos pesqueros de más alto valor comercial. Los precios se han incrementado velozmente, al combinarse una demanda

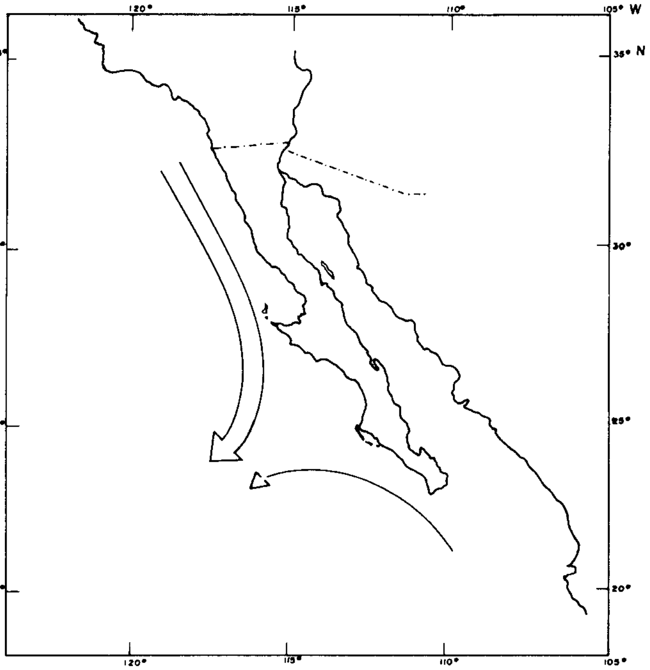

Figura 1. Diagrama de la circulación general superficial en la costa occidental de la Península de Baja California, México.

TABLA 1
Importancia Relativa de las Pesquerías en la Costa Occidental de la Península de Baja California, México

	Porcentaje	
	1978	1983
Pelagicos menores (anchoveta y sardina)	66.0	61.0
Algas (*Macrocystis* y *Gelidium*)	9.2	2.0
Alto valor comercial (abulon y langosta)	1.7	1.2
Atunes	6.4	10.0
Otros (tiburon, almejas, pargo, etc.)	16.7	25.8
Total	100.0	100.0
En relacion a las capturas nacionales	41.6	17.0

siempre presente con una escasez de productos cada vez más crítica.

El descenso de las capturas ha ocurrido no solo por explotación excesiva de los bancos, sino por la captura masiva de individuos pre-reproductores.

Se han puesto grandes esperanzas en el cultivo para recuperar los niveles de explotación de abulón. Hay, sin duda, un considerable esfuerzo para implementarlo; sin embargo, el lento crecimiento y la considerable mortalidad de los juveniles hacen difícil el éxito a corto plazo, e indudablemente deberá complementarse con un manejo muy eficiente de la pesquería natural. De cualquier modo, la disminución de la captura es una tendencia que se hará sentir aún por algunos años. (Figura 2).

LANGOSTA

El la costa occidental, el recurso langostero parece estar en un grado máximo de explotación, o cayendo ya en un problema de sobrepesca. Se capturan anualmente menos de 2,000 ton y la pesquería no parece tener grandes perspectivas de crecimiento a corto plazo (Figura 3).

Figura 2. Captura anual de abulón en la costa occidental de Baja California.

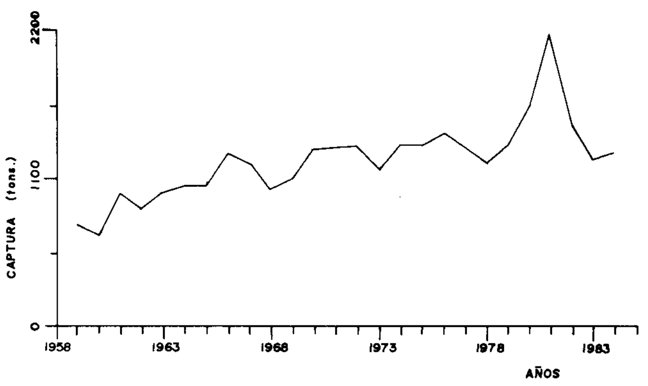

Figura 3. Captura anual de langosta en la costa occidental de Baja California.

SARDINA

Por lo que se refiere a la costa occidental, la pesquería de sardina es la de mayor volumen en Baja California Sur, considerando las descargas que se hacen en Bahía Magdalena y Matancitas, además de lo que se descarga en Santa Rosalía.

La pesquería de sardina en toda la costa de California y Baja California disminuyó considerablemente en años anteriores, al grado de desaparecer como explotación al Norte de Isla Cedros. Afortunadamente para Baja California Sur, los indicadores muestran que hay una tendencia al aumento de la abundancia de sardina en toda la costa occidental del Estado (Figura 4).

ANCHOVETA

La pesquería de anchoveta es una de las de más reciente desarrollo en México, pasando de alrededor de 10,000 ton en 1963 a unas 250,000 en 1981 (Figura 5). La explotación se ha centrado en Ensenada y, aparentemente, se extiende al Sur hacia San Quintín. En México se presentan dos poblaciones de anchoveta, la central, que se distribuye al Norte de Isla Cedros, y la sureña, que va de Punta Eugenia a Bahía Magdalena, principalmente.

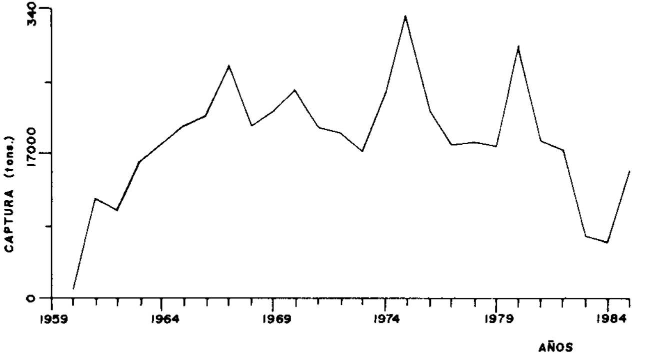

Figura 4. Captura anual de sardina en la costa occidental de Baja California.

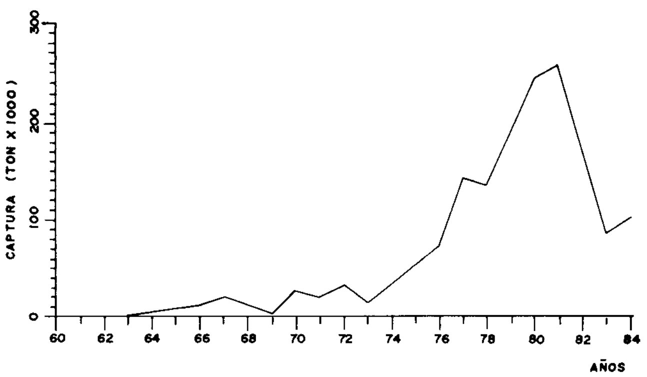

Figura 5. Captura anual de anchoveta en la costa occidental de Baja California.

El potencial estimado de la población central, actualmente explotada, es de medio millón de toneladas conservadoramente. Sin embargo, para tener acceso a la parte que aún no se pesca, la captura deberá hacerse en áreas cada vez más alejadas de la costa. Por otra parte, la población sureña no ha sido tocada aún, y permanece como un potencial de gran interés. Aún cuando parece ser muy variable, un rendimiento de alrededor de 150,000 ton anuales es un cálculo moderado. Estando la tecnología ya disponible, es de esperar que este recurso pueda explotarse en breve plazo.

ALGAS

El recurso algal más importante de la costa occidental de la Península es, sin duda, el llamado "sargazo gigante" (*Macrocystis pyrifera*). Se distribuye desde la frontera hasta el Norte de Bahía Magdalena. En la actualidad, solo se explota este recurso alrededor de Ensenada, B.C. (Figura 6). Al Sur de este puerto, se tiene una estimación del orden de 50,000 ton cosechables al año. Este recurso tiene una gran importancia ya que de él pueden obtenerse productos de gran importancia en la industria alimenticia, farmacéutica, y de cosméticos.

PECES COSTEROS

Un número considerable de especies de escama, que incluyen lisas, tiburones, meros, cabrilla, pargos, sierra, chopas, mojarras, etc., son pescados esencialmente por pescadores ribereños a lo largo de la Península. Los volúmenes descargados no son muy altos y, desgraciadamente, no parece haber muchos motivos para pensar que puedan elevarse sustancialmente. Muchos de los incrementos actuales se deben más a la inclusión bajo el mismo nombre en las estadísticas pesqueras de especies que antes no se capturaban por considerarse de menor calidad.

Figura 6. Cosecha anual de *Macrocystis pyrifera* en la costa occidental de Baja California.

RECURSOS POTENCIALES

Langostilla

La langostilla constituye una expectativa importante de la pesca, debido fundamentalmente a su gran abundancia en algunas áreas. Bahía Magdalena, en la costa occidental, parece ser el centro de distribución más importante.

El potencial de este recurso, simplemente en esta área, ha sido calculado en por lo menos medio millón de toneladas. El problema esencial de su explotación no es, por cierto, la captura. La langostilla es uno de los mayores problemas de los camaroneros que operan en la zona, ya que la red de arrastre queda completamente llena en unos minutos y se recobra con gran dificultad.

La elaboración de harinas que ocasionalmente se ha intentado con este recurso resulta en un producto de bajo contenido de proteínas, lo que da escaso valor en el mercado. Es posible, sin embargo, que parte de esta pobre calidad se deba a la muy acelerada degradación que sufre la materia prima, a partir del momento de la captura. Otras alternativas, como utilizarla para la elaboración de colorantes naturales, para la alimentación de salmones y truchas de criadero y, más recientemente, para la elaboración de fibras de quitosán, derivadas de la quitina, no han sido abordadas aún más que a nivel de posibilidades.

Merluza

La merluza es un recurso inexplotado de gran abundancia en la costa occidental de Baja California Norte. El área del Pacífico de California y Baja California parece ser la zona en que se lleva a cabo la reproducción de la merluza, que proviene de las costas boreales de los EE.UU. y Canadá. Conservadoramente, el potencial de captura de la merluza ha sido calculado en medio millón de toneladas.

Este mismo recurso ha sido explotado en el

Norte por flotas de barcos fábrica soviéticos, que congelan sus filetes. Una prospección que se llevó a cabo durante 1974 por barcos arrastreros alemanes arrojó resultados desalentadores. No obstante, es posible que el año particular en que se llevó a cabo, más cálido de lo normal, haya influído negativamente.

En cualquier caso, la potencial explotación de merluza se enfrenta a varios problemas: (a) La profundidad a que se encuentra durante la temporada de reproducción (250–300 m) está fuera del alcance de los arrastreros que existen en México, lo cual implica fuertes inversiones en barcos especiales; (b) la temporada es corta (unos tres meses de invierno-primavera), lo cual determinaría la necesidad de ocupar los barcos en otra pesquería; (c) los individuos se encuentran más dispersos durante el tiempo de reproducción lo que reduce la eficiencia de la pesca; y (d) la carne tienda a aflojarse rápidamente, perdiendo calidad.

CALAMAR CHICO DEL PACIFICO

Actualmente la pesquería de calamar en la costa occidental de la Península es de carácter incidental, ya que *Loligo opalescens, Loliopsis chiroctes, Lolliguncula panamensis* son capturados particularmente por los barcos camaroneros con las redes de arrastre; *L. opalescens* es explotado en la actualidad particularmente por los pescadores de California, EE.UU., con volúmenes de 11,000 ton por año. Se considera, no obstante, que están muy debajo del rendimiento probable, ya que el mercado es el principal limitante. La captura en la costa occidental en los últimos veinte años ha tenido un valor promedio de 155 tons para todas las especies de calamar explotadas. Tomando como referencia por un lado los valores estadísticos reportados por el Estado de California, EE.UU., que muestran que los volúmenes de captura de *Loligo* se incrementan hacia el Sur; y por otro lado tomando las observaciones realizadas por los barcos de investigación en el Pacífico de Baja California, se suponen fuertes concentraciones de calamar en la zona de Rosarito, B.C., y en la parte Norte de Bahía Sebastián Vizcaíno. Podemos pensar en forma tentativa que en esa zona existen volúmenes considerables quizá comparables por lo menos a los que se obtienen actualmente en California, EE.UU., es decir, entre 10 mil–15 mil toneladas.

Part III

SCIENTIFIC CONTRIBUTIONS

ZOOPLANKTON VARIABILITY IN THE CALIFORNIA CURRENT, 1951–1982

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ABSTRACT

Seasonal and nonseasonal variations in zooplankton biomass in the California Current system are examined from CalCOFI measurements over the period 1951–82. Seasonal signals indicate that total biomass and degree of seasonality are greater in the northern regions, and springtime blooming is initiated in the northern nearshore regions up to two months earlier than in the southern and far offshore regions. Semiannual variability in both zooplankton biomass and geostrophic flow is a common feature throughout the CalCOFI sampling region, suggesting a relationship between zooplankton variability and advection of nutrients and zooplankton biomass. Throughout most of the study area maxima/minima in seasonal zooplankton biomass lag maxima/minima in seasonal alongshore geostrophic flow by one month or less. This indicates that seasonal advection of biomass into the CalCOFI sampling area dominates the observed seasonal fluctuations in local zooplankton abundances.

Nonseasonal zooplankton biomass variability is examined using empirical orthogonal function (EOF) analysis. The principal EOF pattern of $\log_e$ transformed zooplankton volumes is dominated by low-frequency (interannual) variability that is clearly coupled to variations in the transport of the California Current. The timing of zooplankton biomass variations relative to variations in southward advection suggests that nonseasonal zooplankton biomass variations are controlled by two processes: (1) the response of local zooplankton populations to advection of zooplankton biomass—the dominant process in the north—and (2) the response of local zooplankton populations to nutrient advection or the development of more favorable environmental conditions caused by changes in advection—processes that become increasingly dominant from north to south. Examination of the biogeographic boundaries of 15 of the dominant zooplankton species in the survey area during periods of strong current variations also indicate that these mechanisms control the low-frequency zooplankton variability.

The variability of non-$\log_e$ transformed zooplankton biomass is dominated by episodic pulses with time scales less than three months. The spatial pattern associated with the first EOF of untransformed zooplankton suggests a northern source of variability centered offshore in the core of the California Current. The ephemeral nature of the signal suggests a response to nutrients and phytoplankton injected into the core of the California Current by one or more coastal jets or filaments, resulting in an isolated population that dies out relatively quickly (two to three months) for lack of continued food supply in offshore regions.

RESUMEN

Las variaciones estacionales y no-estacionales en la biomasa de zooplancton colectada por CalCOFI son examinadas para el período 1951–82. Los marcadores estacionales indican que la biomasa total y el grado de estacionalidad son mayores en las regiones del norte, y que el aumento en la primavera comienza dos meses o menos antes en las regiones costeras del norte que en aquellas al sur o mar adentro. La variabilidad semianual tanto en la biomasa zooplanctónica como en el flujo geostrófico es una característica común a toda la zona muestreada por CalCOFI, sugiriendo una relación entre la variabilidad del zooplancton y la advección de nutrientes y biomasa zooplanctónica. Los máximos y mínimos estacionales de la biomasa zooplanctónica están atrasados en un mes o menos con respecto a los máximos y mínimos estacionales del flujo geostrófico a lo largo de la costa. Esto indica que una advección estacional de biomasa hacía el área de muestreo de CalCOFI domina las fluctuaciones observadas en las abundancias locales de zooplancton.

La variabilidad no-estacional en la biomasa zooplanctónica es examinada por medio del análisis de una función empírico-ortogonal (FEO). El patrón principal del FEO de los volumenes de zooplancton transformados logarítmicamente está dominado por una variabilidad de baja-frecuencia (interanual) la cual está claramente relacionada con variaciones en el transporte de la Corriente de California. La relación temporal de las variaciones de la biomasa zooplanctónica en relación a las varia-

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[Manuscript received March 11, 1987.]

ciones en el proceso de advección con dirección sur sugiere que las variaciones no-estacionales de la biomasa zooplanctónica son controladas por dos procesos: (1) la respuesta de las poblaciones locales de zooplancton a la advección de la biomasa de zooplancton—el proceso dominante en la zona norte—y (2) la respuesta de las poblaciones locales de zooplancton a la advección de nutrientes o el desarrollo de condiciones ambientales más favorables causado por cambios en la advección—aquellos procesos que cobran mayor importancia de norte a sur. El examen de los límites biogeográficos de quince de las especies de zooplancton dominantes en el área investigada durante aquellos períodos de grandes variaciones en las corrientes corroboran el control de la variabilidad de baja frecuencia del zooplancton por estos mecanismos.

La variabilidad de la biomasa de zooplancton no transformada logarítmicamente está dominada por pulsaciones episódicas con escalas de tiempo inferiores a tres meses. Los patrones espaciales asociados con el primer FEO del zooplancton sin transformar sugiere una fuente de variabilidad ubicada al norte, mar adentro, en el centro de la Corriente de California. La naturaleza efímera de esta señal sugiere una respuesta a los nutrientes y fitoplancton inyectados al centro de la Corriente de California por uno o más chorros o filamentos costeros, la cual produce una población aislada que perece en forma relativamente rápida (dos o tres meses) debido a la falta de una fuente de alimentación continua en las regiones mar adentro.

INTRODUCTION

The waters off the west coast of North America have long been observed to be some of the more biologically productive in the world ocean (Reid 1962; Wooster and Reid 1963). The physical processes responsible for the complexity of the eastern boundary current structure and mixture of regional water masses greatly influence the magnitude of biological production in the region. Of utmost biological importance is the source of nutrients to support the high production. This study reviews the processes responsible for the distribution of nutrients in the California Current system (advection and upwelling) and examines how variations in the supply of nutrients affect local biological production. In particular, the seasonal and nonseasonal signals observed in zooplankton displacement volumes from the CalCOFI 32-year time series (1951–82) are analyzed to investigate physical and biological controls.

The upper-ocean water-mass characteristics of the California Current are largely controlled by the source waters in the Alaskan Subarctic Gyre (Hickey 1979). The subarctic water mass is characterized by cold temperature, low salinity, high nutrients, and large standing stocks of zooplankton (Reid 1962). Charting the southern extent of subarctic water influence in the California Current gives some indication of the degree of equatorward transport of nutrient-rich northern waters into the subtropical water mass (characterized by higher temperatures and salinities and smaller standing stocks of zooplankton). An individual water mass is identifiable by some conservative and distinct property. Bernal (1979, 1981) and Bernal and McGowan (1981) have identified characteristically low salinity values (33.4‰) with the subarctic water mass, to distinguish it from the subsurface equatorial/subarctic mixture that is upwelled with salinities greater than 33.8‰ (also characterized by low temperatures and high nutrients).

Salinity maps constructed by the NORPAC Committee (1960) for July through September (the period of strong equatorward transport in the California Current) indicate that the 33.4‰ isohaline can be traced from the surface to depths greater than 200 m. At 10 m below the surface the isohaline extends southward to San Diego in a tongue approximately 1,000 km wide. At 100-m depth the subarctic mass, still a tongue, narrows and extends as far south as the tip of Baja California. At 200 m—the approximate depth of the core of the poleward-flowing undercurrent (Hickey 1979)—the 33.4‰ isohaline is nonexistent in the California Current region. Thus, the zone of subarctic water-mass influence is a large-scale tongue extending from the subarctic gyre thousands of kilometers equatorward (to 25°N), and from the surface to depths shallower than 200 m. The low-salinity subarctic water mass is associated with high nutrients (Reid 1962); clearly, variations in equatorward transport in the California Current could have considerable impact on the biology of the region.

Previous studies of zooplankton variability in the California Current system have found significant correlations between zooplankton biomass and advection (Bernal 1979, 1981; Bernal and McGowan 1981; Chelton et al. 1982; Hemingway 1979). These earlier studies have suggested that zooplankton biomass responds locally to changes in primary productivity caused by variations in the supply of nutrients by advection from the north. However, in all of the studies, the coarseness of the temporal or spatial scales meant that only associative relations could be resolved.

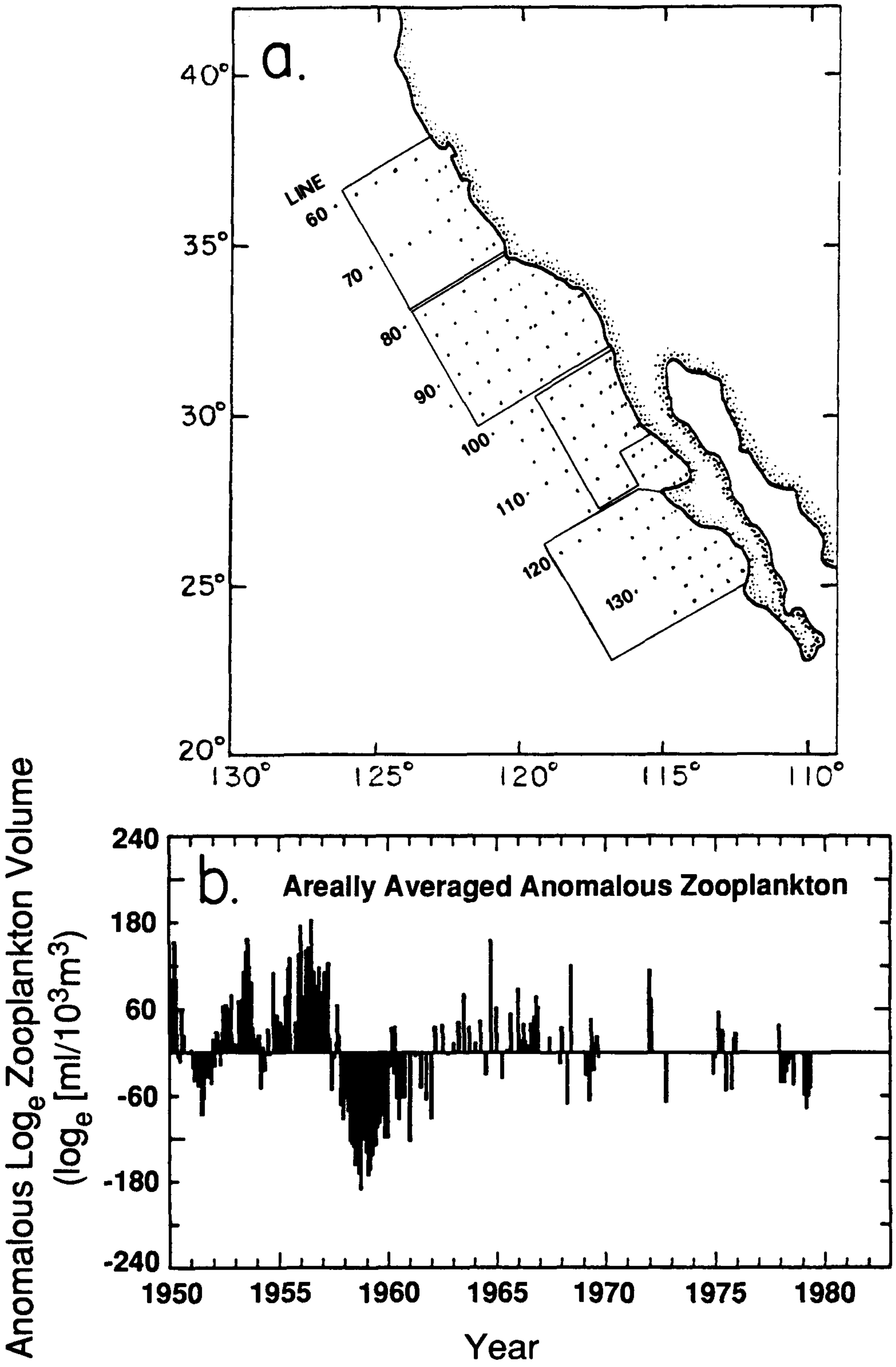

Figure 1. *a*, CalCOFI grid pattern (indicated by dots) and the four regions of average zooplankton volumes used in the study of Chelton et al. (1982). Cardinal lines are denoted by their numbers (60–130). *b*, Areally averaged time series of seasonally corrected (anomalous) zooplankton volumes for the four regions outlined in *a* (also from Chelton et al. 1982).

From a detailed analysis of CalCOFI data for the period 1955–59, Colebrook (1977) showed that large-scale variability in zooplankton was coherent between the taxa, suggesting that fluctuations must result from some physical process rather than from a purely biological interaction. He also concluded that the source of the variability must originate in the north or must affect northern populations to a greater extent. It is noteworthy that Colebrook did not remove the seasonal cycle in his analysis, so his

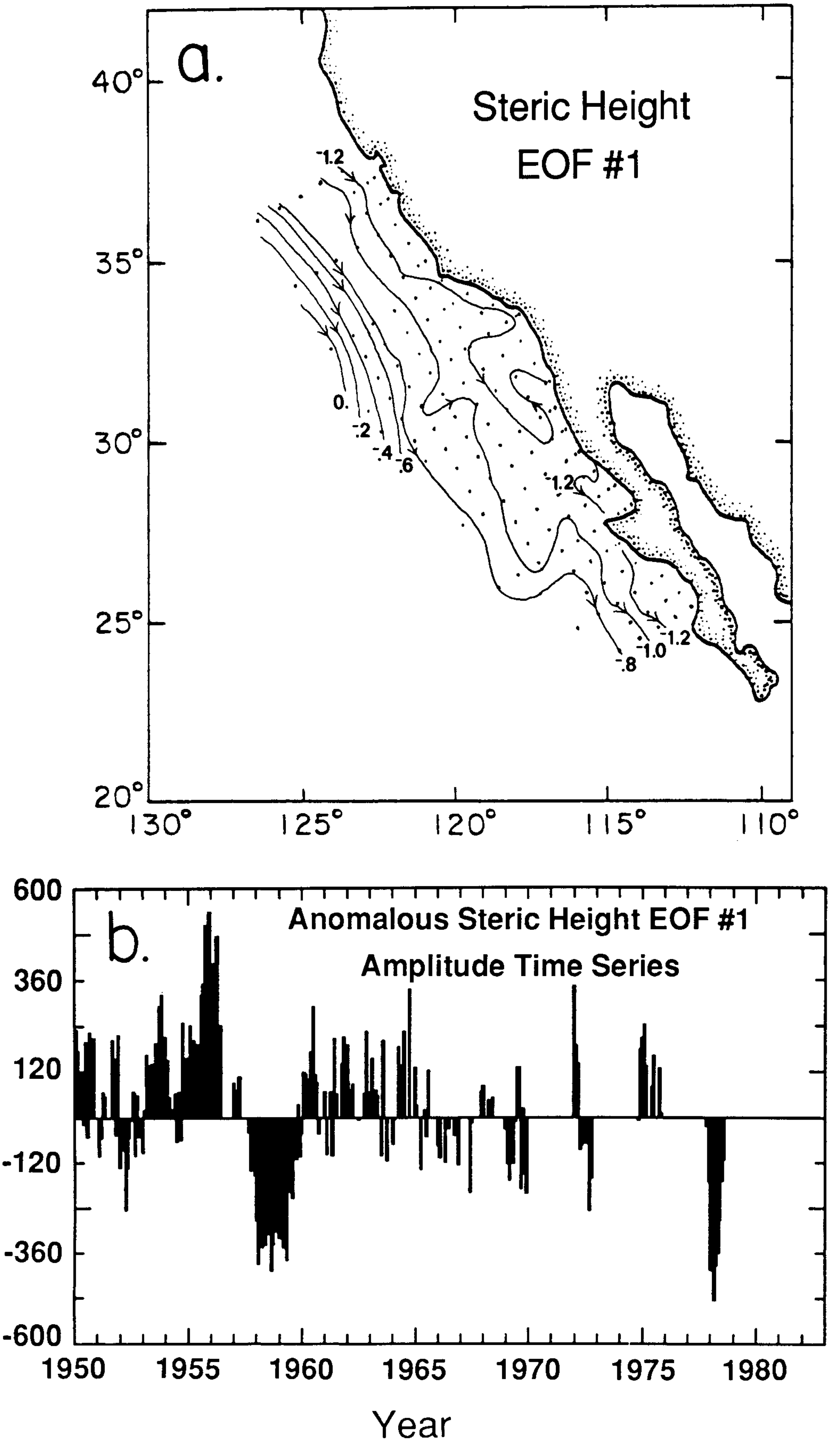

Figure 2. *a*, Spatial pattern of the dominant-mode EOF of anomalous 0/500 db steric height computed from stations (denoted by dots) occupied more than 34 times in the record (1950–78). *b*, The amplitude time series of the dominant EOF mode of steric height. This mode is an index of southward transport in the California Current (from Chelton et al. 1982). Arrows in *a* indicate the direction of the flow when the time series is positive. Weakened or reversed flow occurs when the time series is negative.

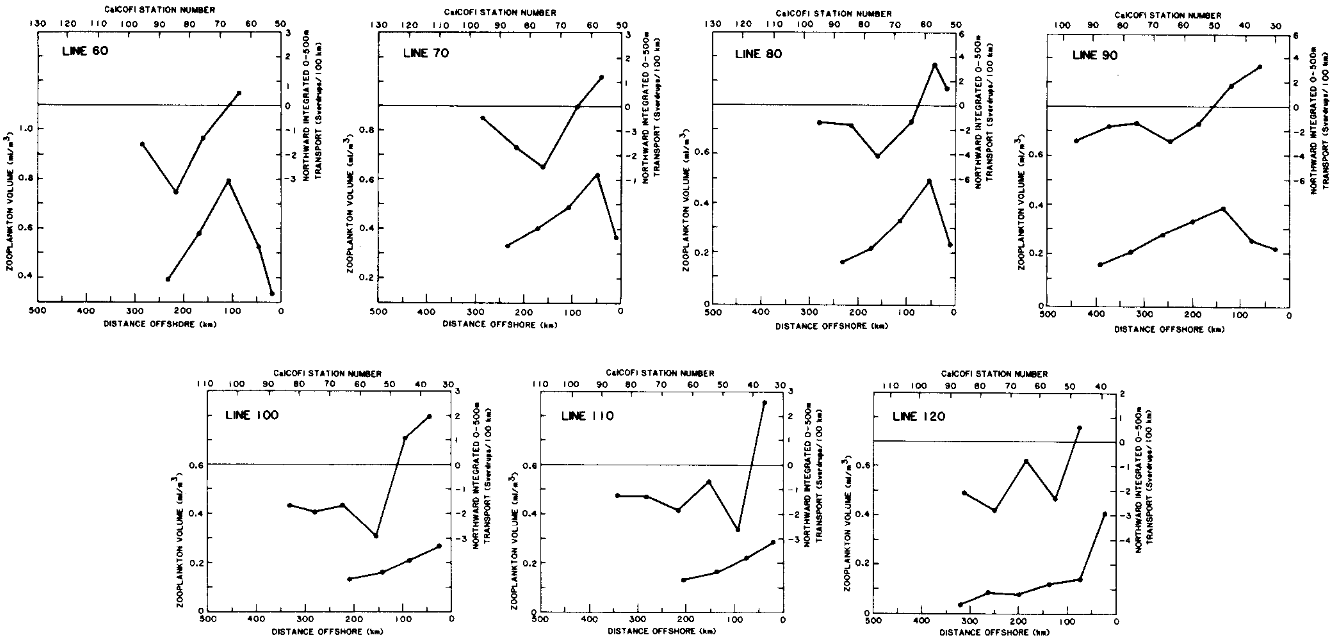

Figure 3. The seasonal values (computed from long-term averages) of the April-through-August averaged zooplankton volumes (ml/10^3m^3), *lower panel*, and the July alongshore integrated transport (in Sverdrups/100 km), *upper panel*, along the CalCOFI cardinal lines. Crossing of the zero axis indicates horizontal shear in the flow (from Chelton 1982a).

results may be strongly influenced by normal seasonal fluctuations in zooplankton biomass.

Chelton et al. (1982) examined large-scale variability in the seasonally corrected total zooplankton displacement volume time series pooled into four areal averages (Figure 1a). Within each of the four areas they found a low-frequency signal of variability with autocorrelation time scales ranging from 14 months in the northern region to 24 months in the southern region (these time scales correspond to periods of about 2.5 to 4.0 years). In order to extract the very large-scale variability, the four regional time series were averaged (Figure 1b). This large-scale average zooplankton time series was found to be significantly correlated with an index of large-scale, nonseasonal advection in the California Current. This index of advection (Figure 2b) was the amplitude time series of the dominant empirical orthogonal function (EOF) of dynamic height at the surface relative to 500 db. Because of the coarse areal averaging of the zooplankton volumes, the detailed spatial structure of the variability was never resolved for comparison with the spatial structure of the advection index (Figure 2a). Furthermore, the detailed mechanisms by which the advective processes affect zooplankton were not defined.

A second study of the CalCOFI zooplankton data by Chelton (1982a) suggested a possible relationship between seasonal geostrophic flow, wind stress curl, and zooplankton abundance. Figure 3 shows the cross-shore signals of averaged zooplankton for April through August (lower panel) and the averaged, vertically integrated, alongshore transport for July (upper panel) in the California Current. Note the horizontal shear in alongshore transport as indicated by poleward transport nearshore and equatorward transport offshore. Between San Francisco and San Diego (CalCOFI lines 60–90), peak zooplankton biomass is found in the region of strongest horizontal shear (the zero crossing of the alongshore transport curve; also found by Bernal 1981). Chelton (1982a) hypothesized that this offshore maximum zooplankton biomass may be related to an offshore maximum wind stress curl causing surface-water divergence and upwelling of deeper waters. This Ekman pumping process leads to an upward tilting of the isopycnals and the nutricline, which brings nutrient-rich deep waters into the euphotic zone. Although spatial correlation between the summer seasonal signals of zooplankton biomass and horizontal shear in the flow is evident from Figure 3, no statistical analyses have yet been performed to establish temporal correlations between the signals.

There are a number of unanswered questions from these earlier studies of CalCOFI zooplankton data: What is the detailed spatial structure of nonseasonal zooplankton variability? Is the low-frequency signal in zooplankton variability identified by Chelton et al. (1982) a response to variability in advection of nutrients and subsequent local growth, a local response to changing temperature and salinity conditions caused by variability in the advection of northern waters, or the result of actual transport of northern stocks of zooplankton biomass? Finally, is there temporal coherence between the offshore zooplankton maximum and horizontal shear in the flow? These questions are investigated in this study using time series of total zooplankton volume on a sampling grid of greater spatial density than was available for the earlier studies.

DATA DESCRIPTION AND METHODS

One of the important features of the CalCOFI zooplankton sampling strategy has been the maintenance of a fixed sampling grid throughout the measurement program, which began in 1951. Surveys are conducted along parallel lines, approximately normal to the coast and separated by 74 km. The lines separated by 222 km, called cardinal lines, are sampled more frequently (Figure 1a). The first ten years of data were collected at monthly intervals with few interruptions. In 1961, the nearly continuous monthly sampling was replaced with quarterly sampling (every three months). This sampling strategy continued until 1969, when CalCOFI switched to monthly samples every third year. As a consequence of this temporal sampling pattern, any time series analysis of CalCOFI data will be largely dominated by the patterns that occurred in the first ten years of uninterrupted collection. A further description of the sampling strategy and its limitations can be found in Chelton (1981) and Chelton et al. (1982).

Zooplankton displacement volumes are measured by oblique net tows from depths of 140 m to the surface. The 5-m-long nets have a 1-m-diameter opening and are made of 500-μm mesh. With a ship speed of two knots, the nets are retrieved at 20 m per second, filtering a total volume of approximately 500 m^3 of water. The zooplankton volumes used in this study consist of the total amount of zooplankton biomass retrieved from the nets minus all zooplankton exceeding 5 cc and all adult and juvenile fish. For a more complete description of the methods of collection and techniques in processing the zooplankton displacement volumes see Smith (1971) and Kramer et al. (1972).

Zooplankton displacement volumes measured in the CalCOFI region during the period of January 1951 through March 1982 were kindly provided by Paul E. Smith at the National Marine Fisheries Service in La Jolla, California. Monthly averages were provided for the 23 spatial regions (Figure 4) originally proposed by Smith and used by Colebrook (1977) to filter out short-term fluctuations (such as vertical migration) and small-scale spatial variability (patchiness). Fourteen of the 23 regions were deemed to have adequate temporal coverage over the 32-year record to be useful in this study. Although 9 regions were omitted from the analyses presented here, the remaining 14 regions more than triple the spatial resolution of previous studies of zooplankton variability in the California Current, with little sacrifice of the temporal resolution.

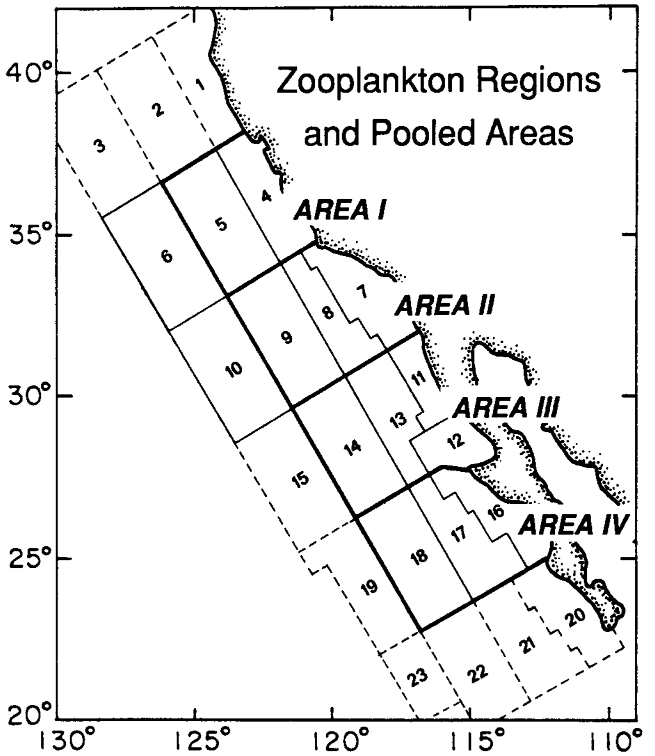

Figure 4. Location of the 23 geographical regions for which spatially averaged CalCOFI zooplankton time series are available (provided by Paul E. Smith). The 14 regions outlined by the solid borders form the basis for the analysis presented in this study; the remaining 9 regions (dashed lines) were deemed to have too few observations over the 32-year record to be useful in this study. The four large-scale areas outlined by heavy borders and labelled as areas I, II, III, and IV are used in the temporal analyses of nonseasonal zooplankton and large-scale advection. These areas are essentially the same as those used previously by Chelton et al. (1982); see Figure 1.

It is customary in analysis of biological data to apply a $\log_e$ transformation to the observed values before analysis. One of the motivations for this transformation is to normalize frequency distributions (Chatfield 1975) in order to place confidence limits on statistical analyses (see Appendix 1). In addition, biological data bases involve, in most cases, exponential growth and decay in the time series. Log_e transforms of data values reduce exponentials to linear representations. Another motivation, and the most biasing, is to de-emphasize spurious or noisy data points; the $\log_e$ transformation reduces the relative amplitude of extreme values. Thus, applying the $\log_e$ transformation is effectively equivalent to presupposing that peak values are not significant. This is misleading in that a true signal of spiky values will be obscured under the transformation and lost in the analysis (see Appendix 1 for further explanation and examples). In order to determine the consequences of taking the $\log_e$ transformation of the displacement volumes, all analyses presented here were performed on both raw and $\log_e$ transformed time series of total zooplankton volumes for the 14 regions.

The CalCOFI hydrographic stations occupied more than 34 times between 1950 and 1978 are shown in Figure 2a. Temperature and salinity profiles at these stations were used to compute density and specific volume (the reciprocal of density) profiles at each station. The difference between the observed specific volume at each sampled depth and the specific volume of a standard seawater sample (with temperature of 0°C, salinity of 35‰) at the same depth is the specific volume anomaly. Integration of this quantity over the pressure range 0–500 db results in values of steric height of the sea surface relative to the 500-db reference level.

Gradients in steric height from station to station are proportional to the magnitudes of geostrophic flow at the surface relative to the flow at the 500-db level (assumed small). Since alongshore flow in the CalCOFI study area is predominantly equatorward (Hickey 1979; Chelton 1984), the alongshore geostrophic flow in all but the three northernmost zooplankton regions was computed along the northernmost cardinal line located in each region; in regions 4, 5, and 6, line 70 was used rather than line 60 because sampling along line 60 was much less frequent over the 32-year measurement program. The regional alongshore component of geostrophic flow was computed from steric height gradients using the equation:

$$v = \frac{-g}{f}\frac{\Delta h}{\Delta x}$$

where v is the geostrophic velocity, Δx is the distance separating the two stations, f is the Coriolis parameter ($2\Omega\sin\phi$, ϕ is the mean latitude), g is the gravitational acceleration, and Δh is the steric height difference relative to 500 db (offshore minus inshore station).

It should be noted that small errors in steric height at one station are amplified in the geostrophic flow computation to a much greater degree when the stations are close together. For example, in a region of 10 cm/sec flow, a 0.5-cm error in steric height at one station results in a computed flow of 10.5 cm/sec if the stations are separated by 100 km; for stations separated by 10 km, the computed flow is 15.0 cm/sec, an order of magnitude increase in error. Sampling error manifestations in geostrophic flow can be effectively reduced by careful selection of station pairs. In this study, station separations of 74 km were used for the narrow, nearshore zooplankton regions, and 158-km spacings were used for the wider, offshore stations.

The time series of zooplankton volumes and steric height are dominated by seasonal variability. The method used here to estimate the seasonal cycles of zooplankton and steric height is the same as that used previously for the CalCOFI steric height data by Chelton (1981, 1982a) and Chelton et al. (1982). The seasonal cycles in each of the 14 regions shown in Figure 4 were defined by harmonic analysis in which the 12 monthly seasonal values are estimated by multivariate regression of the full 32-year time series on an annual and semiannual cycle. With gappy time series such as the CalCOFI zooplankton and steric height data, a small number of spurious points can significantly alter the harmonic seasonal cycle. Chelton (1984, appendix) discusses this problem in detail. In essence, the fewer the number of samples used in the regression, the more unstable the seasonal cycle. The regions in Figure 4 excluded from analysis in this study were rejected on the basis of too few samples to reliably resolve the seasonal cycles. It should be noted, however, that the reliability of the seasonal cycles for the regions retained for analysis may still be questionable in some cases.

Although seasonal fluctuations are important to a large range of applications, they cannot be analyzed statistically to infer cause-and-effect relationships with any degree of reliability. This is discussed in detail in Chelton (1982b). Briefly, the problem is that seasonal cycles consist of only 12 non-independent data values, so that statistical relationships between two seasonal cycles are based upon a very limited number of degrees of freedom. When the annual and semiannual cycles are used for the harmonic analysis, the seasonal cycles contain only four degrees of freedom, and thus anything less than nearly perfect correlation is not statistically significant. It is therefore essential that seasonal cycles be removed from the raw data before statistical analysis. Removal of the zooplankton seasonal cycle from the respective regional time series results in 14 time series of anomalous zooplankton volumes. Defining $\hat{z}_n(t)$ to be the $\log_e$ transformed raw zooplankton volume in region n for the month t, and $s_n(t)$ to be the seasonal $\log_e$ transformed zooplankton volume in region n for the corresponding calendar month, the nonseasonal or anomalous $\log_e$ zooplankton volume is given by:

$$z_n(t) = \hat{z}_n(t) - s_n(t).$$

Anomalies of non-$\log_e$ transformed zooplankton volumes are defined similarly. The seasonal cycles of zooplankton and geostrophic flow are presented and discussed in the next section. Statistical analyses of anomalous zooplankton and steric height variability are presented in subsequent sections of this paper.

SEASONAL VARIABILITY

Contour maps of the seasonal cycles of zooplankton displacement volumes are shown in Figure 5. The expected north-south gradient in zooplankton biomass is apparent throughout the year, with northern values being one to six times larger than southern values. Superimposed on the persistent, north-south gradient is a strong cross-shore gradient that begins to intensify in March, reaches a maximum in May, and decreases through September. Highest values of zooplankton biomass are found near shore. The cross-shore gradient is always strongest in the northern regions. The most southerly regions (at 25°N) and the offshore regions (500 km offshore) show comparatively little seasonality. This is perhaps due to the low mean biomass in these areas, which limits the potential range of seasonal fluctuations compared to potentially large fluctuations in areas of higher mean biomass.

The seasonal cycle time series of zooplankton for each of the 14 regions are shown in Figure 6. The 32-year overall mean value of zooplankton biomass for each region is included in the figure to illustrate the alongshore and cross-shore gradients in the annual average zooplankton biomass. The range of seasonal zooplankton variability is much larger in the north. Not surprisingly, the maximum zooplankton biomass generally occurs in the springtime in response to phytoplankton blooms after the onset of increasing daylength and a high supply of nutrients from upwelling and alongshore advection. A noteworthy feature is the presence of a secondary fall or winter maximum in many of the regions. There is no evidence for such semiannual variability in the wind field in this region, so some other mechanism must be responsible for the observed semiannual zooplankton variations.

It is apparent from Figure 6 that spring blooms occur in the northern regions one to two months earlier than in the southern and offshore regions, notably out of phase with the seasonal progression of upwelling winds from south to north (Nelson 1977; Hickey 1979). These results conflict with the conclusions of Loeb et al. (1983), who found only spring blooms of zooplankton occurring in the southern regions first, synchronous with seasonal coastal upwelling. However, their results were based upon only one year of data (1975) and are apparently not representative of the long-term average pattern. Their conclusion that spring blooms of zooplankton are controlled by coastal upwelling is not true for the 32-year average seasonal pattern, observed on the large spatial scales resolvable by the 14 areal averages analyzed here (Figure 4). Factor analysis of a single year of samples by Hemingway (1979) also supports this claim. He found that standing stocks of zooplankton are not associated with coastal upwelling factors or with the standing stocks of phytoplankton confined to the coastal upwelling band.

The conclusion that seasonal variability of zooplankton is not predominantly controlled by upwelling is rather surprising. A number of previous studies have presented evidence that maximum upwelling zones are coherent with maximum zooplankton volumes. Traganza et al. (1981) found microplanktonic blooms (comprising bacteria, algae, and microzooplankton) at the frontal zones of upwelling regions and upwelling plumes. In addition, Smith and Eppley (1982) found zooplankton associated with peak primary productivity at the coast during upwelling times. Smith et al. (1986) found blooms of *Calanus pacificus* occurring in the nutrient- and phytoplankton-rich upwelling frontal zones off Point Conception. They hypothesized that strong upwelling advects postdiapausal individuals into the surface waters of the frontal zones, and they suggest that offshore movement of these frontal zones may contribute to the offshore zooplankton biomass peak observed by Bernal (1981) and Chelton (1982a).

The apparent discrepancies between this study and these earlier studies is most likely due to the different spatial scales addressed in the respective data sets. The boundary of the frontal zones associated with coastal upwelling is determined by the spatial scale of deformation of the density field of the coastal waters caused by wind stress (Pedlosky 1979). This scale, termed the Rossby radius of de-

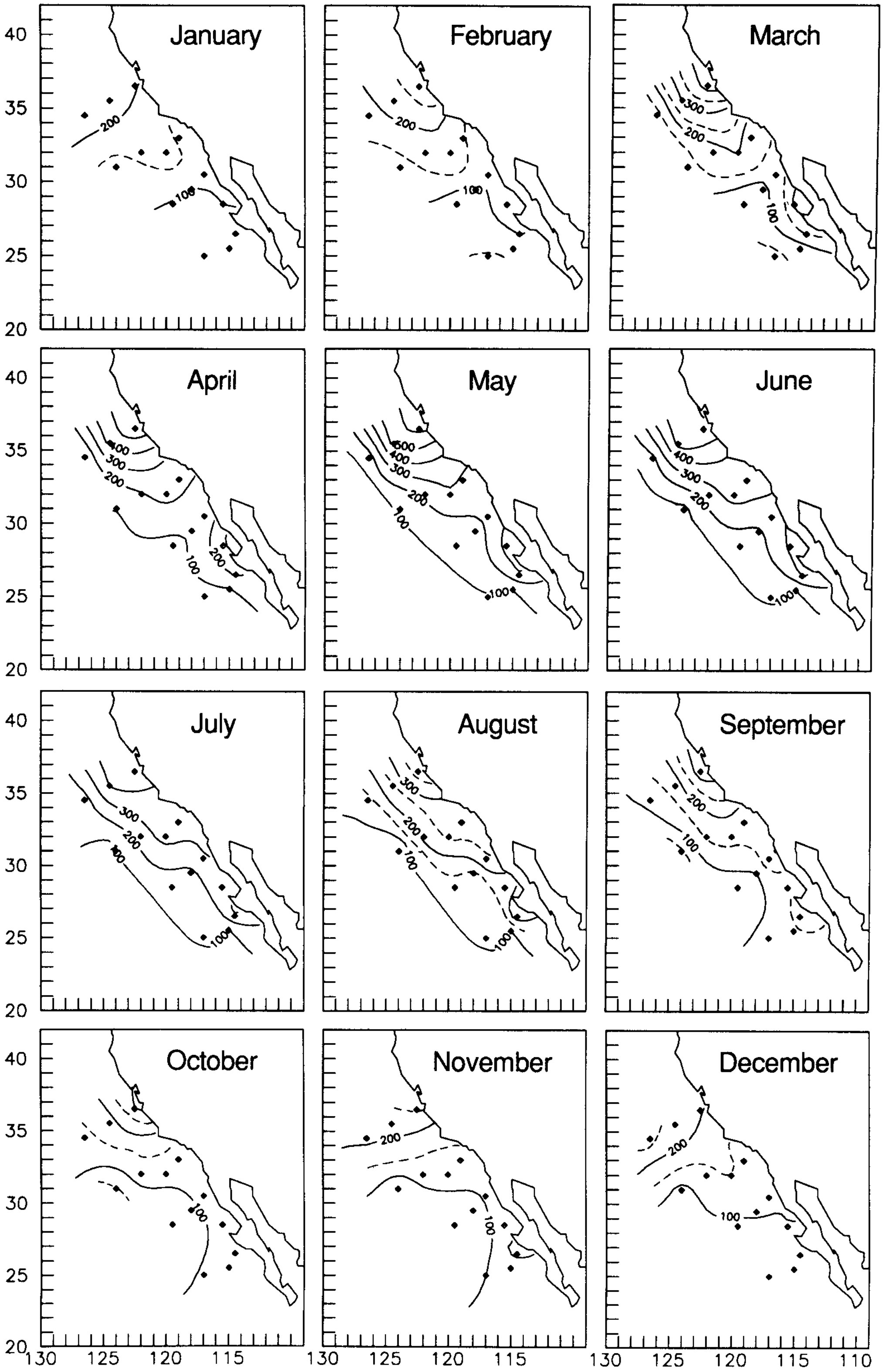

Figure 5. Contour maps of monthly norms of zooplankton displacement volumes in the study area computed from harmonic analysis of the 32-year record. Contour intervals are 100 ml/10^{3}m^3. In months of low biomass, median-valued contours (*dashed lines*) are included for detail of biomass distribution.

formation, is much smaller than the spatial scale of the wind stress and is proportional to water depth. The effective horizontal scale of coastal upwelling is 20 km (Barber and Smith 1981), and the associated offshore transport of upwelled waters is usually within 50 km of the California Coast (Allen 1973; Barber and Smith 1981; Yoshida 1967). Therefore, vertically advected zooplankton in the

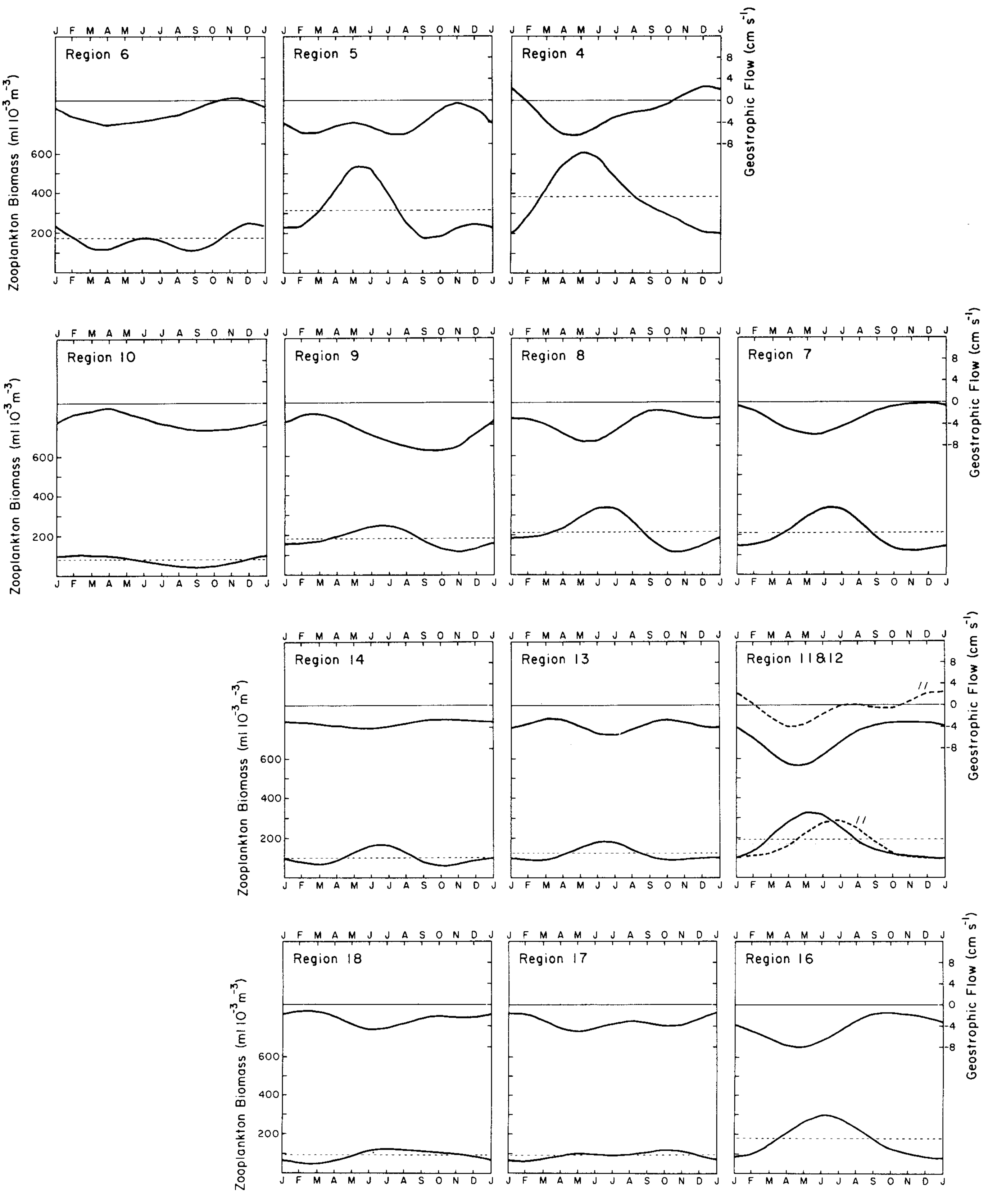

Figure 6. Seasonal cycles of zooplankton displacement volumes (ml/10^{3}m^3) and alongshore geostrophic flow (cm/sec) for each of the 14 zooplankton regions in Figure 4. Seasonal cycles are computed from harmonic analysis of the 32-year record. The mean value of zooplankton is represented by the dotted lines. Graphs are positioned to represent the geographic location of the regions in Figure 4. Regions 11 (*dashed*) and 12 (*solid*) are superposed on the same graph.

upwelling zone, and populations associated with the frontal zone should be confined well within this 50-km boundary. The spatial averaging scheme of this study can only resolve larger-scale fluctuations in offshore populations, since the cross-shore width of the region shown in Figure 4 is 100 km or larger.

Because coastal upwelling is apparently not the impetus behind the large-scale seasonal variability in the offshore zooplankton populations, another driving force must exist. A noteworthy feature of the seasonal zooplankton time series in Figure 6 is the strong presence of semiannual variability in many of the regions. Previous analysis of the seasonal variability of geostrophic flow in the California Current (Hickey 1979; Chelton 1984) has shown that semiannual variability is an energetic component in the seasonal cycle. This suggests a possible causal mechanism for semiannual zooplankton variability. The California Current originates from the West Wind Drift, at approximately 45°N, which comprises mostly subarctic water, rich in both nutrients and zooplankton biomass. Thus variations in transport could result in variations in zooplankton biomass in the California Current.

The seasonal time series of alongshore geostrophic flow are shown in Figure 6 for the 14 zooplankton regions. Careful examination reveals a strong similarity between seasonal variations in alongshore geostrophic flow and zooplankton biomass. With the exception of the four northernmost offshore regions (5, 6, 9, and 10, discussed below), there is a direct correspondence between maxima/minima in zooplankton biomass and maxima/minima in equatorward geostrophic flow. Generally, regions of strong semiannual zooplankton variability coincide with regions of strong semiannual variability of geostrophic flow. In five of the regions (4, 12, 13, 14 and 17), the fluctuations in the cycles of zooplankton and flow are simultaneous. In four regions (7, 8, 16, and 18) changes in zooplankton biomass lag changes in flow by one month. In region 11, changes in zooplankton biomass lag changes in flow by three months.

The high coherence between seasonal cycles of zooplankton and alongshore geostrophic flow is remarkable, particularly in view of the fact that there is regional variation in both the magnitude and timing of the cycles. The springtime maxima of equatorward flow vary by as much as three months from north to south and from nearshore to offshore locations. Secondary winter maxima in equatorward flow become more pronounced in the offshore regions and differ in timing by one or two months in adjacent regions. The magnitudes of the maxima range from 4–12 cm/sec over the CalCOFI domain. These regional variations in the magnitude and timing of seasonal alongshore geostrophic flow are well portrayed in the regional zooplankton cycles.

Two mechanisms have been suggested for observed variations in zooplankton biomass: (1) local zooplankton production in response to nutrient advection and subsequent phytoplankton production, and (2) alongshore advection of zooplankton biomass from northern waters. The time scales of these two processes are quite different. Previous studies of seasonal cycles of nutrient, phytoplankton, and zooplankton concentrations in regions of weak currents (Raymont 1980; Walsh 1977) have found phase lags of two to five months between maximum phytoplankton and zooplankton concentrations, and four to five months between maximum nutrient and zooplankton concentrations. These lags are much longer than the observed lags of zero to one month between zooplankton biomass variations and changes in the alongshore flow. This rapid response is more consistent with advection of zooplankton biomass, which would occur on much shorter time scales, as the dominant mechanism controlling seasonal distributions of zooplankton biomass.

As noted above, seasonal variations in zooplankton biomass and geostrophic flow in the four northern offshore regions (5, 6, 9, and 10) are not as closely coupled as the more nearshore and southern regions. Although the phasing of zooplankton cycles in these regions does not differ notably from the nearshore cycles, the seasonal cycles of the geostrophic flow in these four regions are distinctly different from the seasonal cycles of flow nearer to the coast and to the north and south, both in terms of timing of maximum equatorward flow and in the predominance of the annual or semiannual variability (Figure 6). The alongshore flow along line 70 in region 5 has two maxima in the equatorward transport (February and July) and a single dominant minimum (November). Farther offshore (in region 6) there is a single broad maximum that persists from approximately February through August. Along line 80, just 220 km to the south (in regions 9 and 10), the cycle is quite the opposite, with the maximum equatorward flow occurring in September–October, and the minimum flow occurring in February–March.

This confused picture of seasonal variations in the alongshore component of geostrophic velocity is an artifact of seasonal fluctuations in the speed, location, and orientation of the core of the Califor-

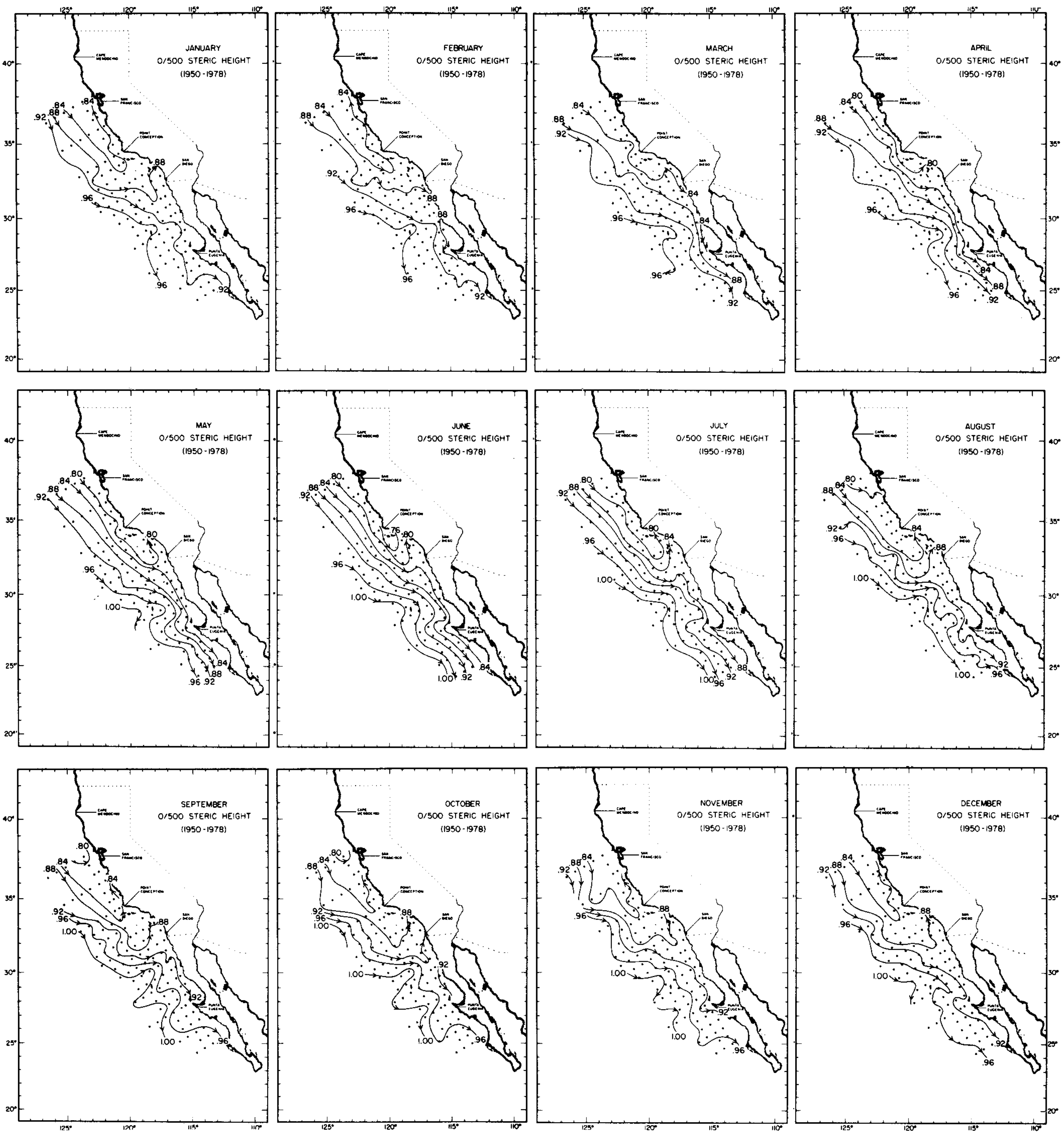

Figure 7a. Contour maps of seasonal mean value of 0/500 db steric height in the CalCOFI survey area. Contour values are in meters, and arrows indicate the direction of geostrophic flow.

nia Current. Meanders in the surface equatorward flow are clearly evident in the contour maps of seasonal steric height (Figure 7a). For comparison, the geostrophic flow at 200 m relative to 500 m is shown in Figure 7b. The quasi-permanent California Undercurrent is apparent in this latter figure. Arrows on the contours in Figure 7a indicate the direction of geostrophic flow, and contour spacing indicates the strength of the flow. From line 70 to line 80, equatorward surface flow is strong in May–July. In August a meander in the surface flow occurs offshore at line 70, introducing a cross-shore

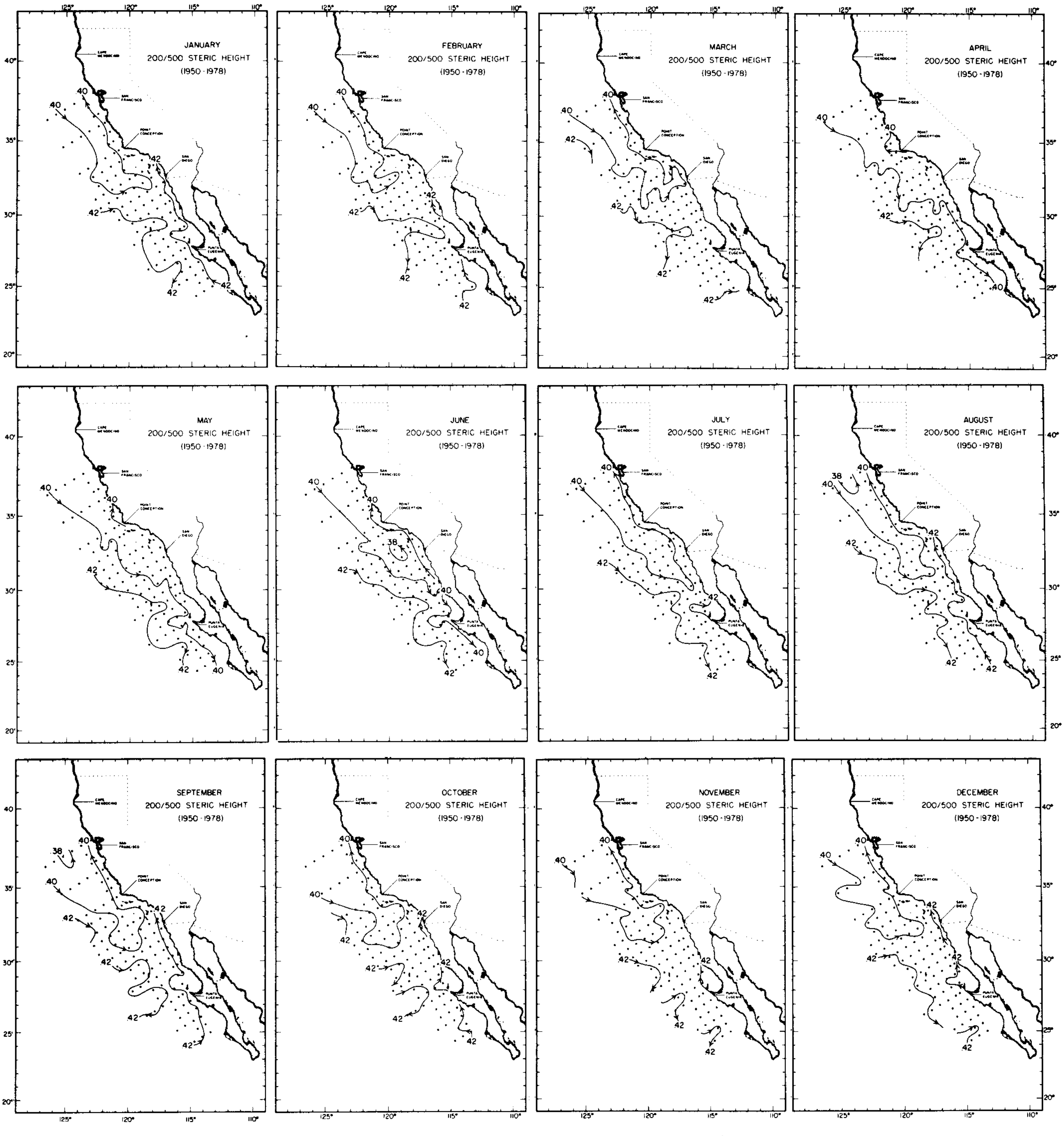

Figure 7b. Contour maps of seasonal mean value of 200/500 db steric height in the CalCOFI survey area. Contour values are in meters, and arrows indicate the direction of geostrophic flow.

component to the flow, and weakened equatorward flow (in regions 5 and 6). The meander persists at this location until December, when it begins to shift southward to line 80. Alongshore surface flow at line 80 (regions 9 and 10) is weak from January to May. The complexity in this region created by the considerable, localized seasonal and spatial variability of the alongshore component of flow may explain the breakdown of the relationship between zooplankton biomass and alongshore geostrophic flow in these four regions. More detailed analyses of both the alongshore and cross-

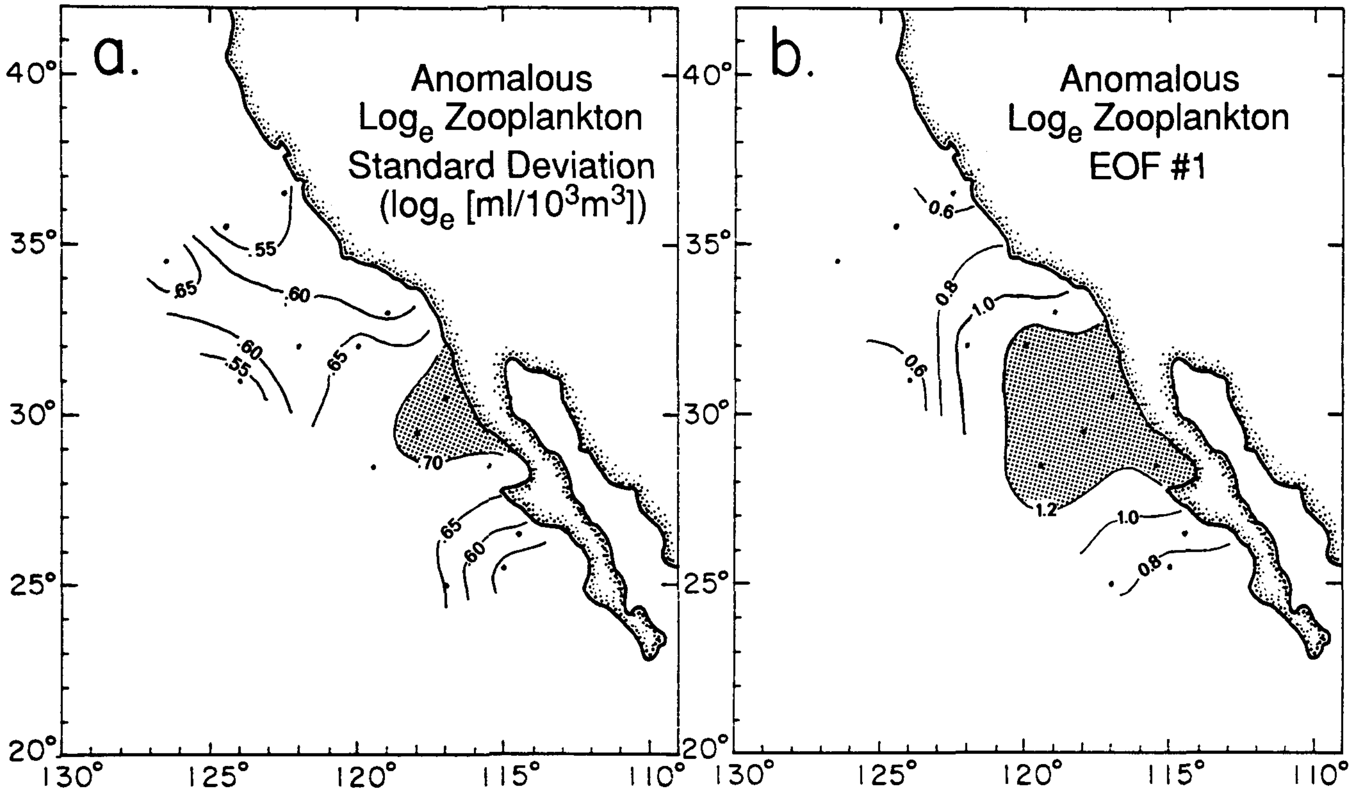

Figure 8. *a*, Standard deviation of $\log_e$ transformed, seasonally corrected zooplankton displacement volumes in the 14 regions denoted by dots. *b*, The dominant EOF of $\log_e$ transformed zooplankton volumes computed over the 14 regions from seasonally corrected time series.

shore components of geostrophic flow may be necessary to understand the seasonal biogeophysical dynamics of this northern offshore area.

NONSEASONAL VARIABILITY

The variance (σ^2) of $\log_e$ transformed, nonseasonal zooplankton volume was calculated for each region by computing the mean of the sum of the squared anomaly values, $z_n(t)$,

$$\sigma^2 = 1/N \sum_{n=1}^{N} z_n^2(t)$$

A contour map of standard deviations (the square root of the variance), Figure 8a, shows that the region of maximum variance is located in a cross-shore band approximately 500 km wide in the alongshore direction, near the coast at about 29°N. This band coincides with the biogeographical boundary between high-biomass northern and low-biomass southern species of zooplankton (Bernal 1979; McGowan and Miller 1980). The significance of the coincident bands is discussed later in this section.

Empirical orthogonal functions (EOFs; see Davis 1976) of the $\log_e$ transformed time series were computed. The first-mode EOF (Figure 8b), representing the dominant recurring pattern of spatial variability in the 32-year record, accounts for 49.6% of the total variance. The pattern is strikingly similar to the standard deviation distribution in Figure 8a. Although the standard deviation map in Figure 8a indicates the spatial distribution of variability, it gives no information about the spatial coherence of this variability. The close agreement between the spatial structure of the EOF and the variance distribution indicates that much of the variance in Figure 8a is spatially coherent over the entire CalCOFI region.

The amplitude time series associated with the first EOF of nonseasonal $\log_e$ transformed zooplankton volume (Figure 9c) defines the temporal dependence of the dominant spatial variability. When the time series is positive, there is anomalously high zooplankton biomass throughout the study area; conversely, when the time series is negative, there is anomalously low biomass, with the largest-amplitude fluctuations occurring in the stippled region of high variance in Figure 8b. The EOF amplitude time series is significantly correlated (correlation = 0.94) with the time series of areally averaged zooplankton volume computed by Chel-

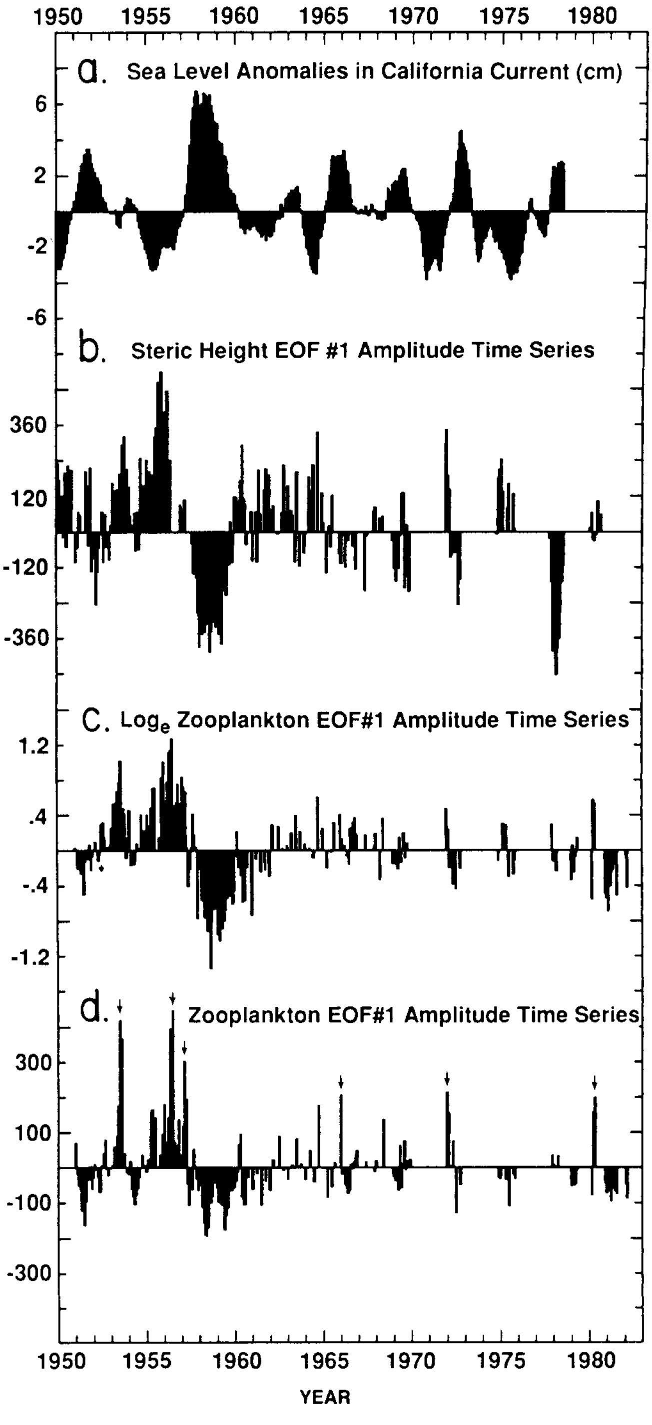

Figure 9. *a*, Time series of sea level anomalies in the California Current (averaged over San Francisco, Los Angeles, and San Diego and corrected for inverse barometric effects of atmospheric pressure) in centimeters. This time series has been smoothed with a double 13-month running average filter. *b*, The amplitude time series of the first EOF of steric height shown in Figure 2b (from Chelton et al. 1982). This time series represents the time dependence of the dominant mode of variability in equatorward advection in the California Current. *c*, The amplitude time series of the dominant EOF of $\log_e$ transformed zooplankton displacement volumes shown in Figure 8b. When the time series is positive (negative) zooplankton biomass is anomalously high (low) over the full CalCOFI region (with the largest amplitude variability in the stippled region in Figure 8b). *d*, The amplitude time series for the dominant EOF of untransformed zooplankton displacement volumes. The spatial pattern for this mode is shown in Figure 16b. Arrows indicate the six episodic events discussed in the text.

ton et al. (1982), shown in Figure 1b. This signifies that the large-scale averaging used in that earlier study very effectively draws out the dominant mode of zooplankton variability in the California Current. Figure 8 shows in greater detail how the large-scale variability is distributed spatially. The time-lagged autocorrelation of the amplitude time series of $\log_e$ zooplankton (dashed line in Figure 10) indicates a time scale of about 18 months for the dominant signal represented by the first-mode EOF, implying periods on the order of three years.

As noted previously by Chelton et al. (1982), the low-frequency signal in the amplitude time series of the nonseasonal $\log_e$ transformed zooplankton is also found in the time series of both sea-level anomalies along the California coast (averaged over San Diego, Los Angeles, and San Francisco) and in the index of southward advection in the California Current (the first-mode EOF of the anomalous steric height). These two time series are shown in Figure 9a and 9b for the 34-year period 1950–83. Cross-correlations between the three time series are statistically significant at better than the 95% confidence level (computed as in Chelton 1982b). Maximum correlations occur when advection lags sea level by three months (correlation = -0.77); $\log_e$ zooplankton (EOF amplitude time series) lags advection by two months (correlation = 0.65); and $\log_e$ zooplankton lags sea level by five months (correlation = -0.59).

These lagged correlations indicate that, statistically, the order of events begins with an anomalous sea-level signal along the California coast, which

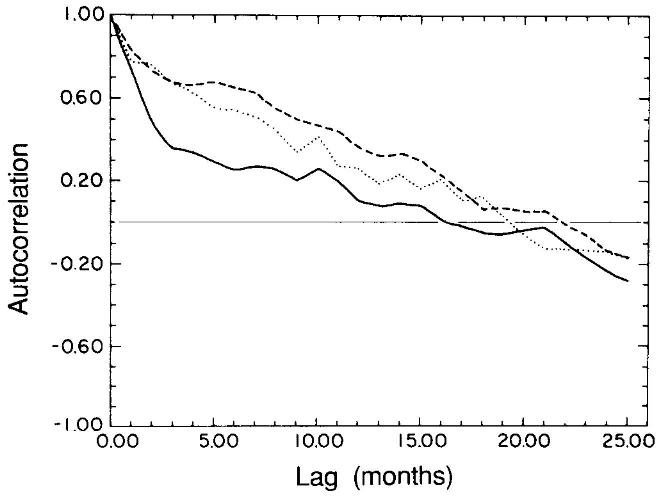

Figure 10. Autocorrelation of the amplitude time series of the dominant EOF of steric height in Figure 9b (*dotted line*); the amplitude time series of the dominant EOF of $\log_e$ transformed zooplankton volume in Figure 9c (*dashed line*); and the amplitude time series of the dominant EOF of untransformed zooplankton volume in Figure 9d (*solid line*).

may be transmitted by low-frequency, poleward-propagating, coastally trapped waves (Enfield and Allen 1980; Chelton and Davis 1982). Theoretical arguments and analyses of sea level and current-meter data off the coasts of Oregon (Cutchin and Smith 1973) and central California (Denbo and Allen 1987) suggest that a time period of one to two weeks is required for coastally trapped waves to propagate through the CalCOFI sampling region. In the monthly averages analyzed here, such a propagation of the sea-level anomaly can effectively be taken as an instantaneous event over the CalCOFI sampling region. Three months after the initiation of a positive (negative) sea-level anomaly, equatorward advection in the current is anomalously low (high), followed two months later by anomalously low (high) zooplankton volumes.

From the lagged correlation analysis presented above, it is not possible to unambiguously resolve the biophysical processes linking advection and zooplankton biomass variability. A lag of two months between variations in large-scale zooplankton biomass and advection might be sufficient to account for local zooplankton growth in response to nutrient advection and subsequent phytoplankton production. In this case, the conclusion would be that anomalous advection of nutrients drives anomalous fluctuations in the local zooplankton biomass. Alternatively, the two-month lag between the very-large-scale variability represented by the EOFs of zooplankton and steric height may merely represent the areally averaged response time of local zooplankton abundances to variations in advection of zooplankton biomass. Anomalous fluctuations in biomass analyzed on smaller spatial scales may exhibit regional variations in the lag between variations in advection and zooplankton response. It is undoubtedly true that both processes (advection of nutrients followed by local phytoplankton production and advection of zooplankton biomass) influence zooplankton biomass in the California Current. The challenge is to isolate which, if either, mechanism is dominant.

The EOF analysis presented above describes only simultaneous variations in each of the 14 regions. A regionally varying response time of zooplankton would not be apparent in the EOF analysis. To resolve this type of response it is necessary to examine the relative timings between advection and zooplankton variability on smaller spatial scales. Ideally, a comparison between zooplankton and advection at each of the 14 regions would indicate the precise responses on very small spatial scales. However, the sampling of steric height and zooplankton within each region is too sparse over the 32-year period to accurately resolve the signal of variability on these small spatial scales. It is necessary to average the zooplankton observations over four regions (essentially the same pooled regions previously used by Chelton et al. 1982; see Figure 1a) to investigate regional response of zooplankton biomass to variations in advection. These four areas are indicated by the heavily outlined boxes in Figure 4.

The areally averaged nonseasonal zooplankton time series are shown in Figure 11 for each of the four areas. In area I the time series appears somewhat "noisy." This is due to a combination of biophysical phenomena (this region is highly variable both biologically and physically) and sampling variability (there were fewer surveys of this area than in the more southern areas because of more frequent rough weather). The zooplankton time series for the three southern areas are more "well behaved." The autocorrelation time scales (Figure 12a) of these four time series become progressively longer from north to south, consistent with the results of Chelton et al. (1982).

The lag time between zooplankton biomass fluctuations and alongshore advection is best determined from the phase spectrum in the frequency domain. A simple lagged response is manifested as a linear change in phase with increasing frequency, and the lag time is determined from the slope of the phase spectrum. (For an example of such an application of phase spectra, see Enfield and Allen 1983.) However, the gappy nature of the 32-year CalCOFI time series makes analysis in the frequency domain impossible. The lag time for zooplankton response to advection must therefore be determined from cross-correlations between zooplankton volume and alongshore advection. Because of the inherent long time scales of the nonseasonal $\log_e$ transformed zooplankton volumes and steric height EOF amplitude time series, time-lagged cross-correlations will exhibit broad maxima. It is therefore difficult to ascertain with any statistical reliability the lag of maximum correlation from the gappy time series. Small changes in sample size (adding or removing a few observations) can shift the lag of maximum correlations by a month or two. One must therefore exercise caution when drawing conclusions from lagged correlation analysis.

The cross-correlations between the averaged zooplankton time series for each of the four areas and the index of large-scale advection (the steric height EOF amplitude time series in Figure 9b) are shown

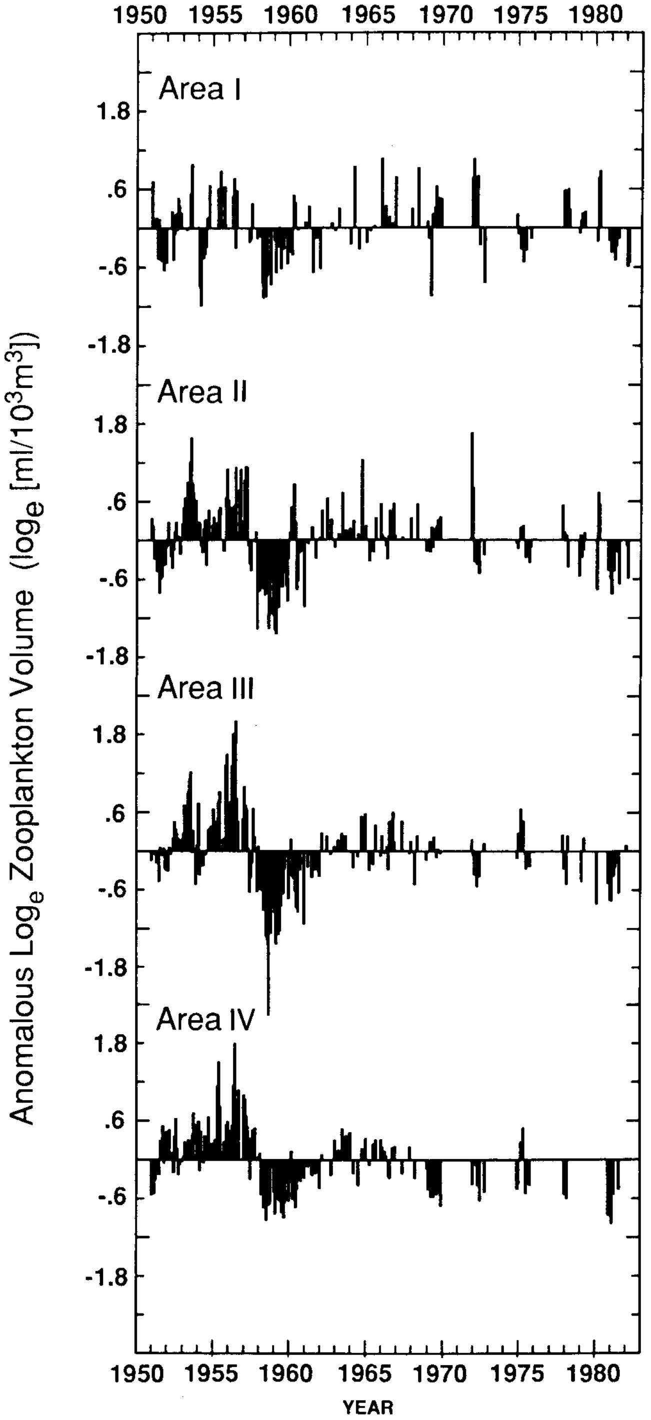

Figure 11. Areally averaged, nonseasonal zooplankton displacement volume time series for the four areas heavily outlined in Figure 4.

in Figure 12b. The correlations for areas I and II are maximum when zooplankton biomass lags advection by one month. The lag of maximum correlation becomes progressively longer for areas III and IV (three and five months, respectively). The rapid response time in areas I and II suggests that advection of zooplankton biomass is the dominant mechanism controlling zooplankton abundance in the northern CalCOFI region. The much slower response time in areas III and IV is too long to be explained by simple advection of biomass, suggesting that local zooplankton response to advection of nutrients (followed by phytoplankton production) and to related changes in other environmental conditions (temperature and salinity) is the dominant mechanism controlling zooplankton abundance in the southern CalCOFI region. The shift to longer response time from north to south indicates a shift in importance from advection of zooplankton biomass in the north, to local response to advected environmental conditions in the south.

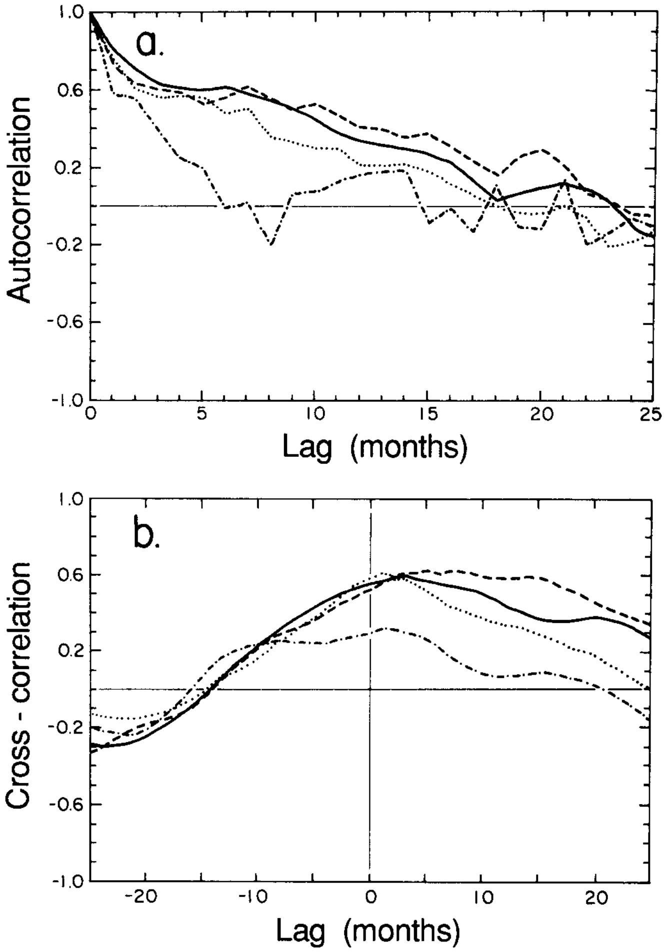

Figure 12. *a*, Autocorrelation of the four areally averaged log$_e$ zooplankton time series (Figure 11) with a dash-dot line for area I, a dotted line for area II, a solid line for area III, and a dashed line for area IV. *b*, Cross-correlation between the four areally averaged zooplankton time series in Figure 11 and the amplitude time series of the dominant EOF of steric height (Figure 9b). The line format convention is the same as that used in *a*.

This relatively simple explanation of the mechanisms controlling zooplankton biomass in the California Current could be somewhat confused if the crustacean component of total zooplankton population is dominated by larval and juvenile stages.

Biomass fluctuations from larval and juvenile growth-rate response to variable food supply are much more rapid than biomass fluctuations from adult reproductive response to variable food supply, because only changes in growth of the individuals and not a complete generation cycle are required to change the total zooplankton volume. It would then be possible that the one-month lag between total zooplankton biomass and advection in areas I and II could be due to larval and juvenile response to advected nutrient concentrations and subsequent phytoplankton production. This mechanism for controlling zooplankton biomass was suggested to us by J.A. McGowan (pers. comm., 1987).

The relative importance of larval and juvenile response to nutrient advection versus advection of total zooplankton biomass can be investigated from maps of larval versus total zooplankton distributions of the genus *Euphausia*. If advection of zooplankton biomass is the primary mechanism governing zooplankton distributions, relatively few established zooplankton (adults and existing juveniles) would be advected equatorward in years of low transport. Most of the zooplankton biomass would result from local new production, and the total zooplankton biomass would be dominated by the larval populations. During years of strong equatorward transport, zooplankton biomass would be dominated by established zooplankton populations, without an increase in productivity, because the biomass is advected equatorward in a water parcel without injection of new food supply. (In fact, the food supply within the parcel of water would decrease with time, as the nutrients were consumed by phytoplankton.) In this case, larval populations would account for a small fraction of the total biomass.

Larval and total zooplankton distributions of *E. pacifica* have been published by Brinton (1967) for 1955 and 1958. Distributions during April (Figure 13a), when zooplankton biomass and equatorward flow are normally high, indicate that year-to-year variations in larval versus adult dominance in response to advection are important in the northern CalCOFI region. During 1955 (a year of strong equatorward advection) the distribution of *E. pacifica* was dominated by adult populations. During 1958 (a year of weak equatorward advection), the *E. pacifica* populations were dominated by larval stages. If these examples are typical for the subarctic species, years of strong equatorward transport are characterized by a dominance of adult populations, and years of weak equatorward transport are characterized by dominance of larval stages of local populations of subarctic species. This is consistent with the interpretation that advection of zooplankton biomass is the dominant mechanism controlling zooplankton abundance in the northern CalCOFI region.

Distributions of larval and total zooplankton biomass of the subtropical euphausiid *E. eximia* during years of strong and weak equatorward advection are very different from the subarctic species (Figure 13b). The populations are dominated by larval stages in both years. Clearly, some other mechanism must be controlling zooplankton biomass in the southern CalCOFI region. Phytoplankton (and hence zooplankton) productivity are more nutrient-limited in the southern half of the CalCOFI domain than in the north. When food supply is low (periods of weak equatorward advection) zooplankton biomass will be dominated by larval and juvenile stages. Input of higher food supply during years of strong equatorward advection would lead to local new production, which also results in a dominance of larval populations in the total zooplankton biomass. Assuming that these distributions of larval versus total zooplankton biomass are typical of subtropical species and representative of years of strong and weak advection, the observed zooplankton variability in the southern CalCOFI region is consistent with the hypothesis that local zooplankton response to advection of nutrients and changes in environmental conditions is the dominant mechanism controlling nonseasonal zooplankton abundances. This result is intuitively sensible: equatorward advection of biomass cannot increase the abundances of the subtropical species in this region because, unlike subarctic species, subtropical species decrease in abundance from south to north.

As noted previously, the region of largest variability of nonseasonal zooplankton biomass (Figure 8a) coincides with the region of transition from subarctic to subtropical species. This suggests that the dominant variability of total zooplankton biomass may be due to simple meridional migrations of biogeographical boundaries (defined here to be the region of strongest gradients in zooplankton biomass). Our premise that the processes controlling zooplankton abundance are advection of zooplankton biomass in the northern area and local zooplankton response to advection of nutrients and changes in environmental conditions in the southern areas can be further investigated by examining the locations of the biogeographical boundaries of subarctic and subtropical zooplankton populations during years of anomalously high

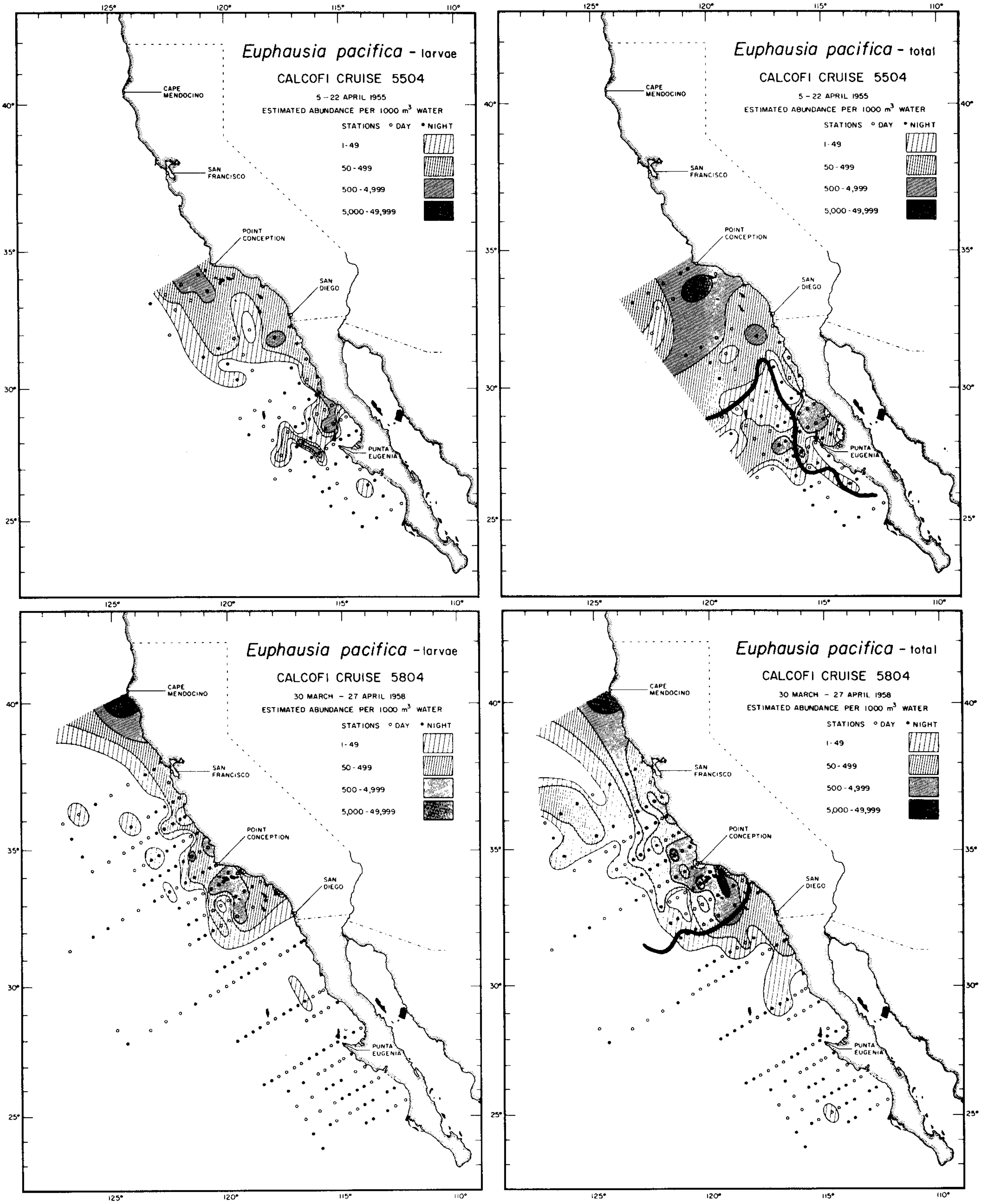

Figure 13a. Larval versus total zooplankton distribution of *Euphausia pacifica*, a subarctic species, for April 1955, an anomalously cold year, and April 1958, an anomalously warm year (Brinton 1967). The black line on the total distributions indicates the approximate location of the 15.5°C isotherm for each date (Anonymous 1963).

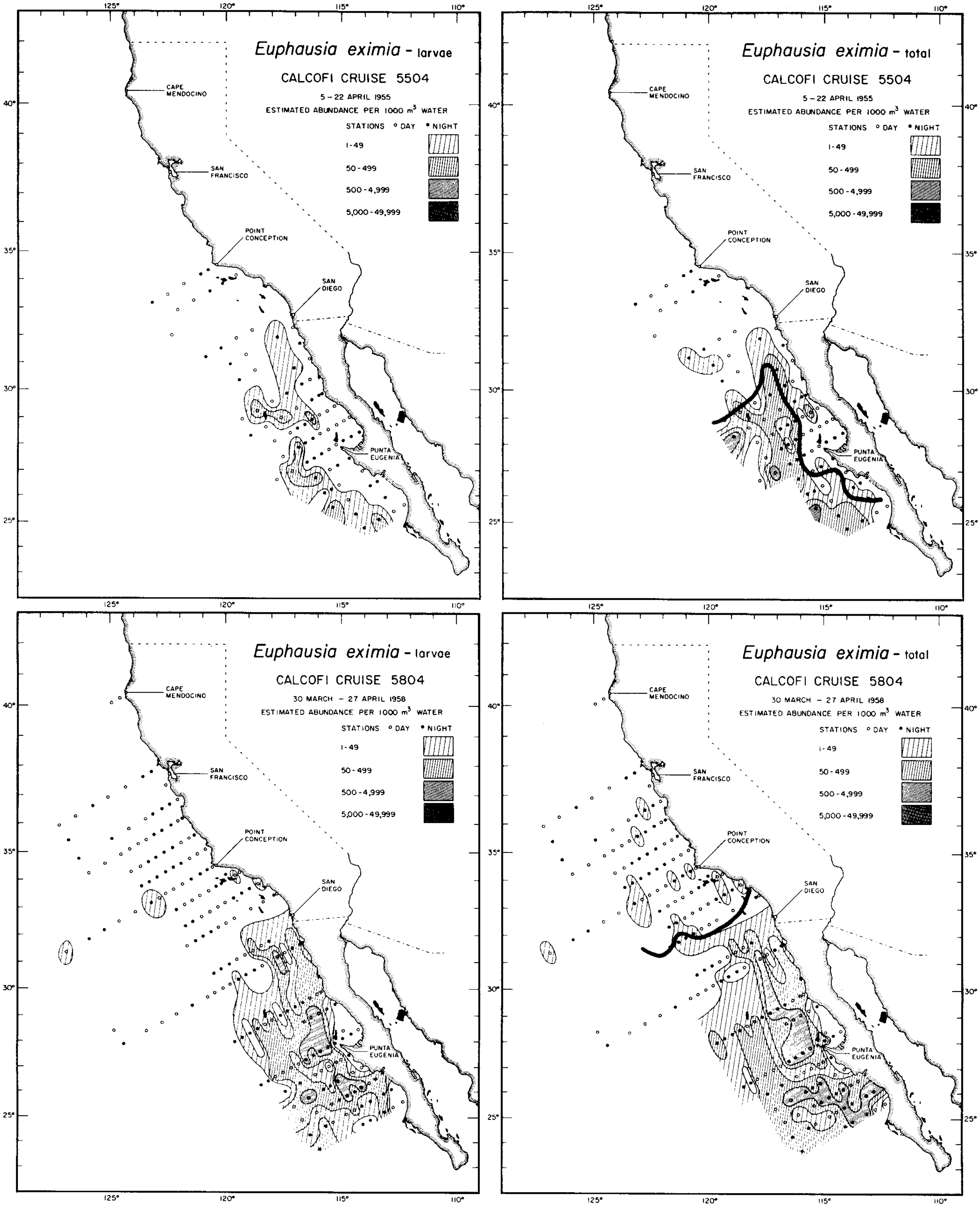

Figure 13b. Larval versus total zooplankton distribution of *Euphausia eximia*, a subtropical species, for April 1955, an anomalously cold year, and April 1958, an anomalously warm year (Brinton 1967). The black line on the total distributions indicates the approximate location of the 15.5°C isotherm for each date (Anonymous 1963).

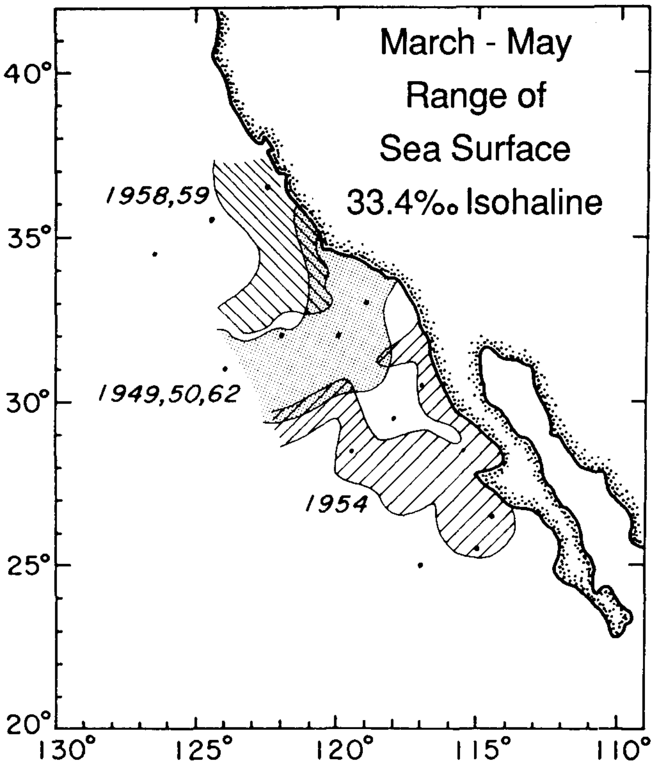

Figure 14. March-through-May averaged range of the sea-surface 33.4‰ isohaline in the CalCOFI survey area for cold years (1949, 1950, 1954, and 1962) typified by strong equatorward transport of subarctic water, and warm years (1958 and 1959) typified by weak equatorward transport. (Data taken from Wyllie and Lynn 1971.)

and low transport. High equatorward transport (positive values in the EOF amplitude time series of steric height, Figure 9b) is characterized by an insurgence of cold, low-salinity subarctic water, rich in nutrients and populated by transition-zone and subarctic zooplankton species (Bernal 1979). Low equatorward transport (negative values in the steric height EOF amplitude time series) is characterized by decreased equatorward advection of cold, low-salinity subarctic water, and in some cases, a reversal in the normal equatorward flow of the California Current resulting in poleward advection of equatorial water, higher in temperature and salinity, lower in nutrient concentrations, and inhabited by subtropical zooplankton species (Bernal 1979).

As noted in the Introduction, Bernal (1979, 1981) and Bernal and McGowan (1981) have identified the 33.4‰ isohaline as the boundary separating the subarctic and subtropical water masses. The location of this isohaline can thus be used to identify year-to-year variations in the equatorward penetration of the subarctic water mass. The range of positions of the 33.4‰ isohaline for March through May of years with weak (1958 and 1959) and strong (1949, 1950, 1954, and 1962) equatorward transport is shown in Figure 14. (These years coincide with years for which maps of zooplankton abundance distributions have been previously published: see discussion below.) The water mass boundary shifts north and south with changes in equatorward transport of the California Current.

The distributions of total biomass of the subarctic species *E. pacifica* and the subtropical species *E. eximia* are shown for April 1955 and 1958 in Figures 13a and 13b (Brinton 1967). These correspond to anomalously cold and warm years, characterized by anomalously weak and strong equatorward advection (see Figure 9b). The dark line on each map indicates the approximate location of the 15.5°C isotherm for each year (Anonymous 1963). As expected, the location of this isotherm fluctuates north and south depending on the strength of advection in the California Current. It is evident from Figures 13a and b that the biogeographic boundaries of both the subarctic and the subtropical species of euphausiids migrate north and south synchronously with the isotherm. Maps of distributions for other dominant species in the CalCOFI region are shown in Appendix 2 for years of weak and strong equatorward advection in the California Current. They show the same patterns of meridional biogeographic boundary migrations that are seen in Figure 13a for *E. pacifica* and 13b for *E. eximia*.

Equatorward shifts in the boundary of the northern transition and subarctic species occur during years of anomalously strong equatorward advection. Similarly, poleward shifts occur during years of weak equatorward advection. As noted previously, the time lag between zooplankton biomass and equatorward advection is short (one month) in areas I and II (Figure 12b). The boundary shifts, synchronous with changes in advection, and the rapid response of zooplankton biomass to advection are all consistent with the interpretation that advection of zooplankton biomass is the dominant mechanism controlling zooplankton variability in the northern half of the CalCOFI domain.

Figures 13a, 13b, and the figures in Appendix 2 show that the biogeographical boundaries of southern species of zooplankton also move north and south in response to changes in alongshore advection. Equatorward shifts in boundary location associated with increased advection could be interpreted as alongshore advection of zooplankton biomass (as in the northern regions). However, northward shifts of the subtropical species' boundary locations during periods of weak equatorward advection are more difficult to explain by simple advection of zooplankton biomass. This mechanism requires actual reversals of the normally equatorward flow south of 32°N (see Figure 7a) in order to advect southern species northward. Such reversals do occur near the coast (within 100–200 km) during highly anomalous years (Wyllie 1966) but are not general broadscale features when the equatorward advection index in Figure 9b is negative. Another possible mechanism for northward advection of subtropical zooplankton biomass is the poleward undercurrent present throughout the year at depths greater than 100–150 m (see Figure 7b). Wroblewski (1982) has suggested a mechanism by which the undercurrent can control the alongshore position of zooplankton. Adult copepods are known to undertake diel vertical migrations to depths exceeding 200 m (Brinton 1962). During years of weak equatorward transport in the near-surface waters, these diel vertical migrations could result in net northward advection of subtropical species.

From the discussion above, it is tempting to explain the observed meridional shifts in location of subtropical zooplankton species boundaries by simple advection of zooplankton biomass, similar to the mechanism proposed for the subarctic species. However, this interpretation is inconsistent with the lagged correlation analysis in Figure 12b, which implies a long response time (three to five months) between zooplankton biomass and alongshore advection in areas III and IV. This lag is too long to be explained by simple advection of zooplankton biomass. From the maps of zooplankton distributions in Figure 13 and Appendix 2, it is evident that isolated populations of subtropical species of zooplankton are always found north of the biogeographical boundary of the species (as defined by the region of strong gradient from high to low abundance). However, these isolated populations are sparse and consist of relatively low biomass, presumably because of unfavorable environmental conditions. Weakened equatorward transport results in a northward shift of the high temperature and salinity usually associated with southern waters and subtropical zooplankton species. Northward shifts of subtropical species boundaries during periods of weak equatorward transport could therefore represent blooms of these isolated populations in response to more favorable conditions for the subtropical species farther north. Such a mechanism for controlling zooplankton biomass would account for the observed slower response (three to five months) of zooplankton to changes in advection in areas III and IV.

From Figure 13 and the figures in Appendix 2, it is apparent that the region of high zooplankton variability in Figure 8a does indeed represent meridional shifts in subarctic and subtropical species boundaries. Geographical fluctuation of the southern boundary of the subarctic water mass and its associated groups of zooplankton defines the spatial structure of the dominant EOF of nonseasonal, $\log_e$ transformed zooplankton biomass (Figure 8b). This is consistent with the results of McGowan and Miller (1980). In the northern CalCOFI region they found low diversity and high species dominance by subarctic and transition species. They found low diversity and high species dominance by subtropical species in the southern CalCOFI region. In the region that we have identified as the highly variable zone inhabited by both zooplankton groups, they found high diversity and low species dominance.

We conclude that the low-frequency signal in zooplankton biomass is closely related to variability in the equatorward advection of the California Current, as previously pointed out by Chelton et al. (1982). It appears that these zooplankton fluctuations are not solely local responses to changes in nutrient advection, as hypothesized in the earlier study. The timing of the low-frequency zooplankton response to advection inferred from lagged correlation analysis indicates that both advection of zooplankton biomass and local zooplankton response to advection of nutrients and changes in environmental conditions drive the variability of zooplankton biomass in the California Current system. In the northern regions, advection of biomass seems to be the dominant process. In the southern regions, it appears that zooplankton biomass is dominated by local responses of zooplankton to advection.

HIGH-FREQUENCY NONSEASONAL VARIABILITY

As noted previously, zooplankton data are generally $\log_e$ transformed before analysis. In part, this is to reduce or eliminate spikes in the zooplankton time series; the spikes are often believed to be due to sampling variability from patchiness in the spatial distribution of zooplankton biomass. As an example, the time series of seasonally corrected raw zooplankton volumes and $\log_e$ transformed zooplankton volumes for region 8 are shown in Figure 15. Note the underlying similarity in the low-frequency aspects of variability. Also note the spikes in the raw zooplankton time series that do not appear in the $\log_e$ transformed data.

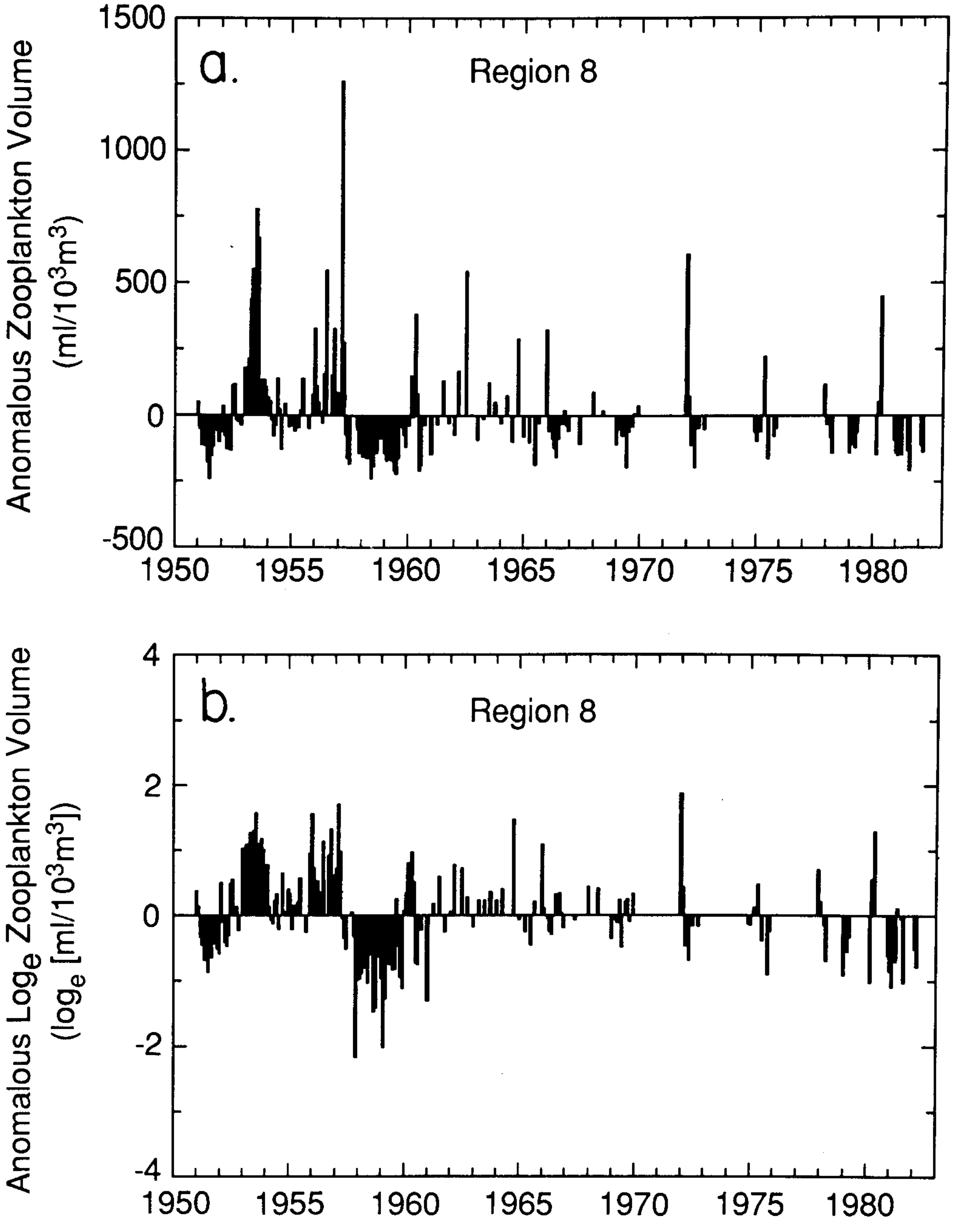

Figure 15. *a*, Seasonally corrected zooplankton displacement volume time series for region 8. Note the episodes of exceptionally high biomass superimposed upon the underlying low-frequency signal. *b*, Seasonally corrected log$_e$ transformed zooplankton displacement volume time series for region 8. Note the dominant low-frequency variability as seen in the previous time series, and the absence of the episodic signals.

Careful inspection of Figure 15a shows that these energetic pulses often have time scales of two to four months (e.g., June–August 1953; May–July 1956; March and April 1957; January and February 1972; and April and May 1980). This implies that, rather than being spurious data points resulting from sampling variability, these spikes probably represent important physical and biological processes. The raw (untransformed) zooplankton data are analyzed in this section to investigate the nature of these episodic events in zooplankton biomass.

A contour map of the standard deviation of untransformed data is shown in Figure 16a. The spatial structure is surprisingly different from the standard deviation map of log$_e$ transformed zooplankton (Figure 8a). Rather than the local concentration of variability at the biogeographical boundary separating northern and southern zooplankton species in the transformed data, the spatial structure of untransformed zooplankton variability consists of a tongue extending from the northern regions southward to approximately 27°N. Evidently, there are physicial and biological

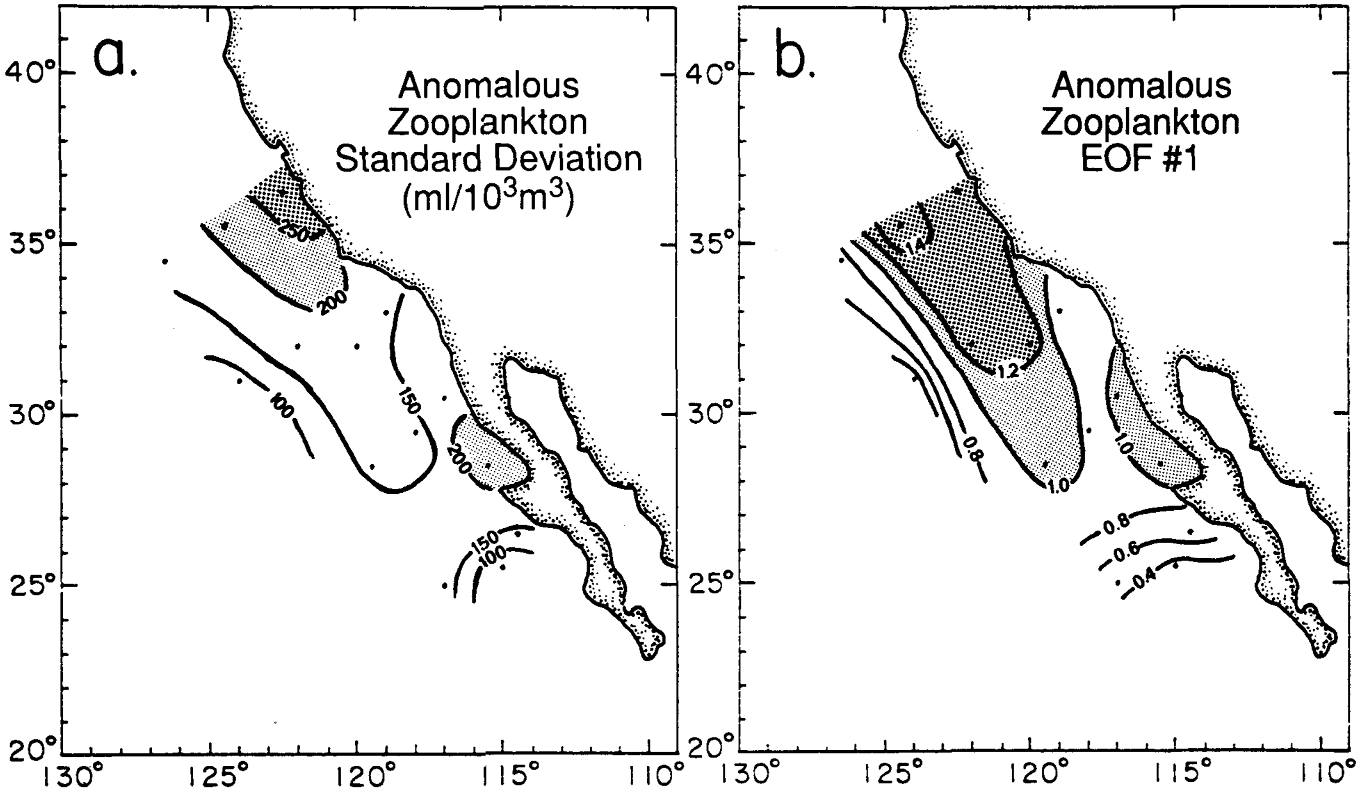

Figure 16. *a*, Standard deviation of the seasonally corrected untransformed zooplankton displacement volumes over the 14 regions. *b*, The dominant EOF of untransformed zooplankton displacement volumes over the 14 regions. When the amplitude time series (in Figure 9d) is positive (negative), anomalously high (low) biomass occurs over the full CalCOFI region, with the largest amplitude fluctuations occurring in the stippled regions.

processes that appear in the untransformed zooplankton volumes but not in the $\log_e$ transformed zooplankton volumes.

The dominant EOF of untransformed zooplankton volume is shown in Figure 16b. It is apparent from this EOF pattern that the variability shown in Figure 16a is spatially coherent over the CalCOFI domain. The spatial structure of untransformed zooplankton variability is very different from that of the $\log_e$ transformed zooplankton variability. The effects of noise in time series of zooplankton biomass on the spatial structure of EOFs are discussed in detail in Appendix 1. It is shown that the spatial EOF pattern is unaffected by spatially and temporally random spikes in the time series. Thus the differences between the first EOFs of $\log_e$ transformed and untransformed zooplankton volumes must be attributable to the spikes in the untransformed data, and these spikes must be coherent spatially. This is an important conclusion, for it implies that the pulses of biomass in Figure 15a are not spurious data points. The spatial structure of these variations in untransformed zooplankton biomass indicates a northern origin extending equatorward as far south as about 27°N in a tongue approximately 600 km long, with the region of highest variability centered about 350 km offshore in the southern region. An important point to note is that the EOF pattern represents spatially coherent pulses of zooplankton biomass along the axis of the tongue. That is, the pulses of zooplankton biomass are evidently not random in space and time, but rather are a relatively large-scale process.

The amplitude time series of the first EOF of untransformed nonseasonal zooplankton volume is shown in Figure 9d. Over the period 1951–82, six large-scale pulses of zooplankton biomass were observed with magnitudes exceeding 200 ml/10^3m^3 (indicated by arrows in the EOF amplitude time series). All six of these episodic events occurred between January and June and persisted for two to three months. That is, these anomalous large-scale features in zooplankton biomass, observed in the untransformed zooplankton volumes on two to three consecutive CalCOFI cruises, are not spurious data points. The time-lagged autocorrelation of the untransformed zooplankton EOF amplitude time series is shown as the solid line in Figure 10. The zero crossing at large lag (16 months) indicates an underlying low-frequency signal in the untransformed zooplankton variability. The rapid drop in autocorrelation from zero lag to three months indicates the short (two-to-three-month) time scale associated with episodic events. The dominant EOF of untransformed nonseasonal zooplankton variability thus represents two separate biophysical processes.

In the California Current, total zooplankton volume is sometimes dominated by large gelatinous zooplankton (Berner 1967). A bloom of gelatinous zooplankton, known to have doubling times on the order of weeks (Mark Ohman, pers. comm., 1986), would certainly skew a total zooplankton displacement volume count because of the larger size of the individuals. We examined all of the published maps of Thaliacea (salp) distributions (Berner 1967). There are no published maps concurrent with any of the six large-scale episodic zooplankton events in Figure 9d, so it is not possible to say definitely whether these pulses represent blooms of all components of total zooplankton volume or blooms of only the gelatinous zooplankton. However, from published maps at times when anomalous blooms of Thaliacea did occur, values of the untransformed, nonseasonal zooplankton volume amplitude time series did not exceed 100 ml/10^3m^3. (Anomalously large abundances of Thaliacea were observed for the following species: *Dolioletta gegenbauri* on CalCOFI cruises 5106, 5206, 5209, and 5806; *Cyclosalpa bakeri* on cruise 5111; *Salpa fusiformis* on cruises 5203 and 5404; and *Thalia democratica* on cruises 5109, 5110, 5111, 5206, and 5804.) It is therefore unlikely that the six observed large-scale pulses of zooplankton biomass are the result of a bloom of only the gelatinous zooplankton. An examination of the zooplankton volumes collected during the six episodic zooplankton events is necessary to ascertain this conclusively.

We have been unable to resolve the mechanism responsible for the generation of these episodic events in zooplankton biomass. They are not significantly correlated with the index of advection in the California Current, wind stress curl over the region, or horizontal shear in the alongshore flow (as defined by the second EOF of steric height; Chelton 1982a). One possible process that could produce the observed pulses in zooplankton biomass is the injection of coastal water, rich in nutrients and phytoplankton, into the California Current by coastal filaments or jets, which have been frequently observed off the California coast (e.g., Tragazna et al. 1981; Kosro 1987; Chelton et al. 1987; Abbott and Zion 1987; Mooers and Robinson 1984). Local zooplankton populations responding to the resultant ideal feeding conditions would be expected to increase relatively rapidly. Subsequent detachment of the filaments, possibly in the form of cold-core rings (e.g., Haury 1984; Simpson 1984; Haury et al. 1986), results in separation from the coastal source of nutrients. As the detached coastal filaments are advected equatorward by the California Current, rapid uptake by phytoplankton populations would diminish the nutrient concentrations so phytoplankton production, followed by zooplankton production, would subsequently crash because of consumption of the limited food supply. The original lower abundances of zooplankton would then be restored on a time scale of one to three months.

Filaments originating off Cape Blanco, Point Arena, and Cape Mendocino (Kosro 1987; Kosro and Huyer 1986) could account for zooplankton events that appear to originate offshore in the northern regions. Filaments off Monterey and Point Conception (Traganza et al. 1981; Atkinson et al. 1986; Chelton et al. 1987; Abbott and Zion 1987) could account for events originating off the central and southern California coast. The characteristics of detached filaments (duration, location, and extent into the current) would determine the fate of the isolated zooplankton populations.

This hypothesis can be tested with historical satellite-derived estimates of phytoplankton biomass inferred from surface chlorophyll concentrations estimated from ocean color measurements by the Coastal Zone Color Scanner (CZCS), and sea-surface temperature measurement by the Advanced Very High Resolution Radiometer (AVHRR). Pelaez and McGowan (1986) have analyzed patterns of seasonal development from selected CZCS and AVHRR images of the California Current region from July 1979 to April 1982. One of these sequences coincides with an observed pulse of zooplankton biomass in April and May of 1980 (Figure 17). A CZCS image from February 7, 1980, shows three fully developed rings located 400–500 km offshore. Three additional rings appear to be in the process of forming from filaments off Monterey, Point Conception, and San Diego (Pelaez and McGowan 1986). The locations of these rings and filaments are superimposed as stippled patterns on the zooplankton distribution for April and May 1980. In April, the high zooplankton biomass in the northern CalCOFI region coincides with the location of the large filament off Monterey. In May, the zooplankton biomass is highest off Monterey, and there is a tongue of high zooplankton biomass located 150 km offshore extending south-

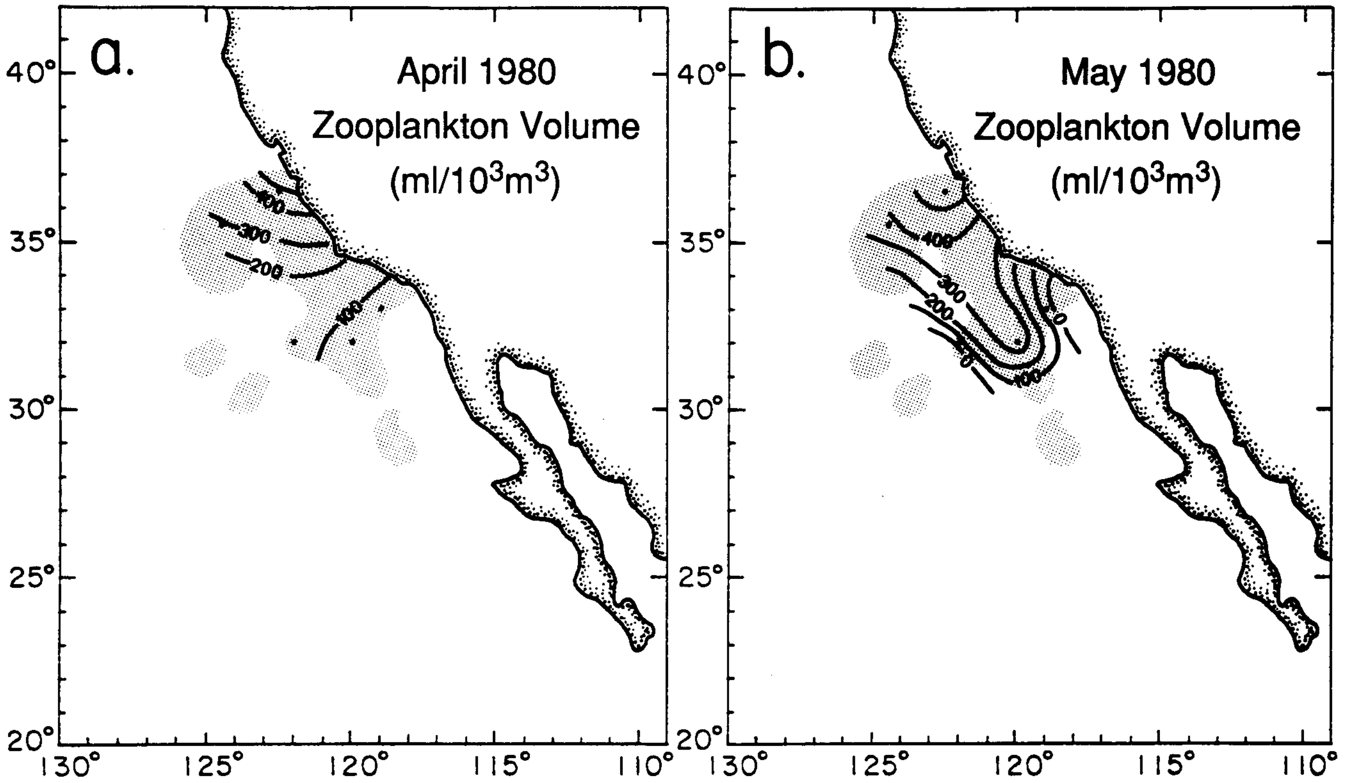

Figure 17. The anomalous zooplankton distributions for the pulse event in April and May of 1980. Contour lines are in intervals of 100 ml/10³m³. The stippled pattern indicates the location of the developing rings located on the February 7, 1980, CZCS image (from Pelaez and McGowan 1986).

ward at least as far as 31°N. (The May 1980 CalCOFI cruise did not sample the region farther south.) When two months' lag is allowed for zooplankton to respond to increased phytoplankton and nutrient input in the offshore waters, the relationship between zooplankton and coastal filaments of high phytoplankton concentration appears to be strong.

CONCLUSIONS

Analysis of the 32-year CalCOFI record of zooplankton displacement volumes has identified recurring patterns of variability. Seasonal variability of large-scale zooplankton biomass appears to be predominantly controlled by advection of zooplankton biomass over most of the CalCOFI sample region. The co-occurrence of maxima (minima) of zooplankton biomass with maxima (minima) of equatorward geostrophic flow in the seasonal cycles does not allow sufficient lag time for zooplankton response to changes in nutrient input from advection.

Nonseasonal variability of $\log_e$ transformed zooplankton volume is dominated by a very-low-frequency signal, with periods of three to five years associated with variations in large-scale equatorward transport in the California Current. In the northern half of the CalCOFI domain, the biogeographical boundaries of subarctic species of zooplankton shift north and south synchronously with variations in alongshore transport, and the response of zooplankton biomass to advection is rapid (one-month time lag). The total zooplankton biomass is dominated by adult stages during periods of strong equatorward advection and by larval stages during periods of weak equatorward advection. This evidence is all consistent with an interpretation that alongshore advection of zooplankton biomass is the dominant mechanism controlling zooplankton abundance in the northern CalCOFI region.

The behavior of subtropical species of zooplankton in the southern half of the CalCOFI domain is fundamentally different. The time scales of variability are much longer, and the biomass appears to be always dominated by larval and juvenile stages. The biogeographical boundaries of subtropical species migrate north and south in response to changes in alongshore advection, but the response time is much longer (three to five months) than in the northern regions. This evidence is more consistent with an interpretation that zooplankton abundance is controlled by local biomass response to changes in environmental conditions associated with changes in alongshore advection.

Intuitively, this explanation for the relation between advection and zooplankton biomass is appealing. In the northern CalCOFI region, the food supply for zooplankton is plentiful (high nutrient and phytoplankton concentrations). Consequently, the zooplankton populations thrive and are not generally food-limited. Then changes in alongshore advection simply transport the biomass distributions. In the southern CalCOFI region, the nutrient (and therefore phytoplankton) concentrations are generally much lower (except very near the coast, where upwelling is important). Since the food supply is less plentiful, adult stages of subtropical zooplankton are less populous, and the biomass is dominated by larval stages. Abundances of subtropical zooplankton species decrease northward, so increased equatorward advection does not increase zooplankton abundance by simple advection of zooplankton biomass. The subtropical zooplankton populations are more sensitive to changes in environmental conditions (increased nutrient supply during periods of strong equatorward advection, and more favorable temperature and salinity conditions during periods of weak equatorward advection).

Analysis of non-$\log_e$ transformed zooplankton volumes reveals a second, higher-frequency signal in nonseasonal zooplankton variability, which is lost in the $\log_e$ transformation. Episodic bursts of zooplankton biomass with durations of three to four months have occurred six times in the 32-year record. These events may be linked to coastal filaments injecting nutrient- and phytoplankton-rich coastal waters off Oregon and northern California into the California Current. Zooplankton biomass would be expected to increase in response to the high food supply. When the source of this coastal water is cut off by detachment of the filaments from the coast (perhaps in the form of cold-core rings) the zooplankton populations decrease relatively rapidly over a period of a few months because of rapid use of the unreplenished nutrient content. This interpretation is supported by an example presented in the previous section, showing the relation between an episodic zooplankton event and satellite-inferred chlorophyll concentrations during the late winter and early spring of 1980.

ACKNOWLEDGMENTS

We are indebted to Paul Smith for graciously supplying us with the CalCOFI zooplankton data used in this study and for helpful comments on an early version of the manuscript. We also thank Larry Eber for providing us with the CalCOFI hydrographic data and John McGowan, Mark Abbott, and Tim Cowles for all of their constructive comments on the manuscript. Special thanks go to Charlie Miller for first suggesting the possibility of advection of biogeographical boundaries in the California Current and for his careful reading of the manuscript. This research was supported by NASA Grant NAGW-869 and NSF Grant OCE-831521.

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APPENDIX 1

The Effects of Spurious Data on Empirical Orthogonal Functions

A perhaps surprising result from the analyses presented in this paper is the significant differences between the dominant recurring patterns of zooplankton variability with and without a log$_e$ transformation. The first EOFs of zooplankton (Figure 16b) and log$_e$ zooplankton (Figure 8b) are very different, and in fact suggest that very different processes control zooplankton variability. One of the motivations for using the log$_e$ transformation in analyzing biological data is to normalize frequency distributions of observed concentrations of biological variables (Figure A1) in order to place statistical confidence limits error bars on correlations with other variables. Another common motivation is to reduce the effects of spurious outlyer data points, often attributed to sampling errors caused by patchiness in the biological variable. Although very effective as a noise filter, the transformation may also act as an effective screen for a true signal consisting of occasional pulses with anomalously large values. In this appendix, we present the results of some simulations intended to determine whether the differences between the EOFs of zooplankton and log$_e$ zooplankton could be due to spurious observations of zooplankton volume (i.e., noise in the measurements).

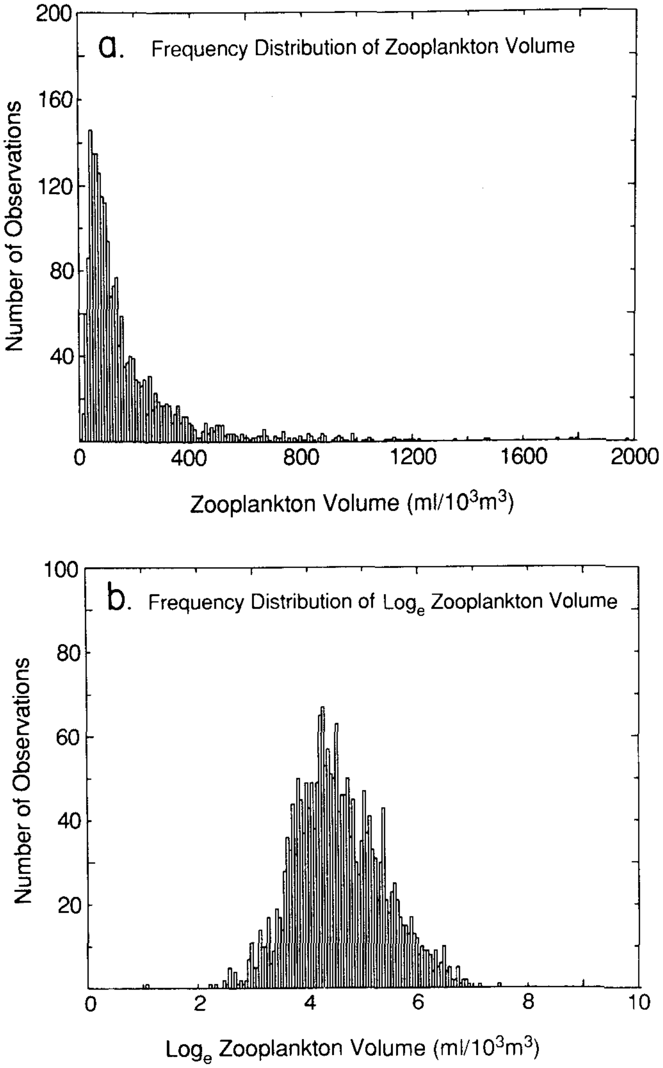


Figure A1. Frequency distributions of all samples of zooplankton displacement volumes (ml/10^{3}m^3) taken over the 32-year record in all 14 regions. Untransformed values (*a*) have a non-normal distribution; the log$_e$ transformed values (*b*) have a normal distribution. The significance of untransformed values greater than 500 ml/10^{3}m^3 is reduced from representing 28% of the total collected zooplankton volume in the 32-year record to just over 4% of the total collected volume.

The nature of EOF analysis is to extract modes of variability that are coherent in space and time, and effectively filter out extraneous noise from each signal. If a single data set is composed of two distinct and uncorrelated signals, the analysis separates these signals into two separate modes of variability. For this reason, the addition of random uncorrelated noise to a data set does not change the spatial structure of the dominant modes extracted by the EOF analysis. It only increases the total variance of the system (and, in particular, increases the variance that is unexplained by the modes of physical or biological variability), and thus reduces the percentage of the total variance explained by the dominant modes. This capability of EOFs to extract signal from noise is shown by an example below.

The dominant EOF of the log$_e$ transformed, seasonally corrected time series of zooplankton displacement volumes discussed in the text and shown in Figure 8b is reproduced here in Figure A2a. Spikes in zooplankton volume were randomly added to the 14 regional time series, with amplitudes ranging from two to six standard deviations from the norm. The corresponding EOF spatial patterns for these increasing noise amplitudes are shown in Figure A2b–d. The dominant EOF remains essentially unchanged, regardless of the magnitude of the added noise. EOF analysis thus very effectively extracts the underlying large-scale signal from noisy data. Figure A3 shows the percent of variance explained by the first EOF mode

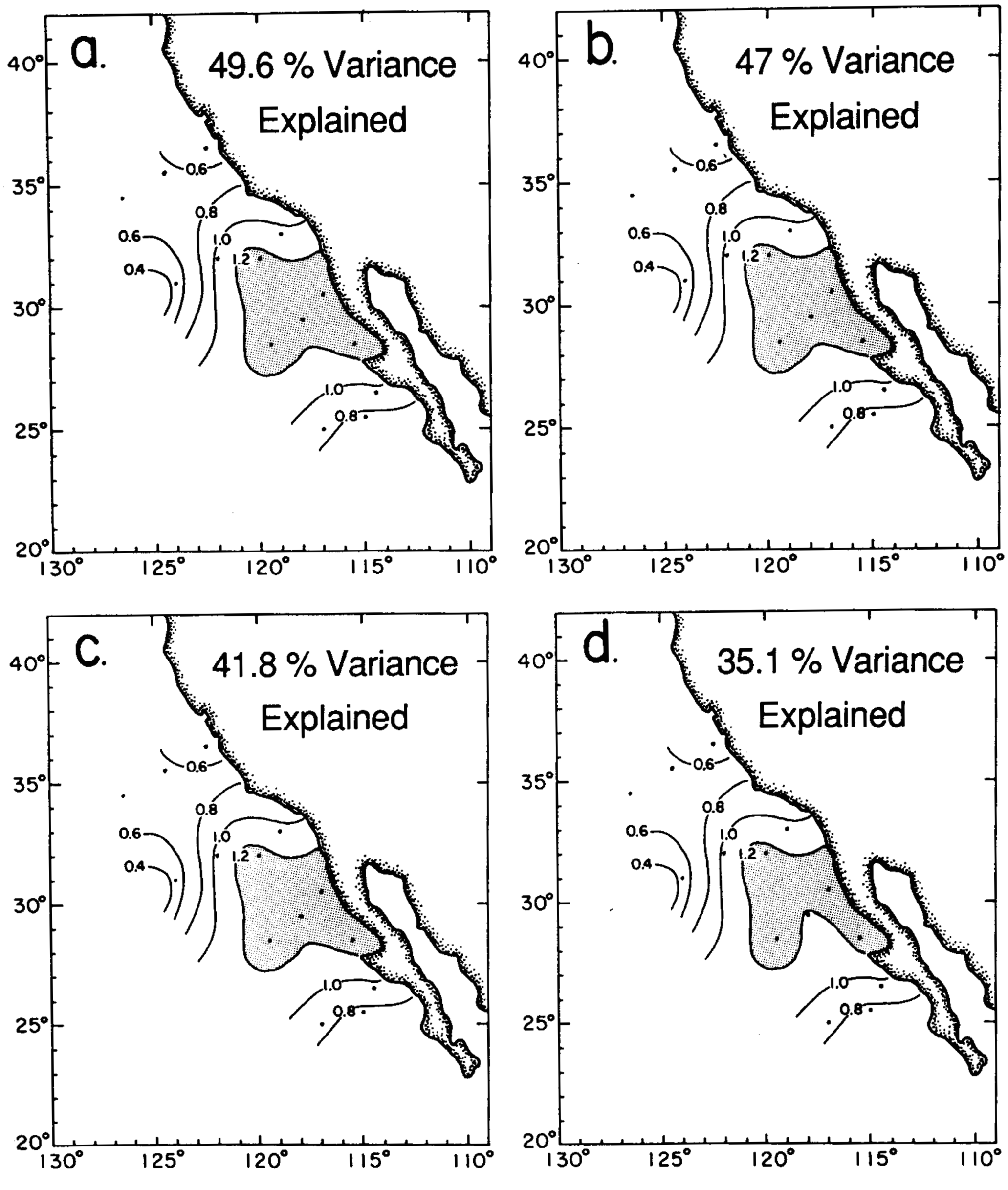


Figure A2. *a*, The dominant EOF of $\log_e$ zooplankton volume over the 14 regions denoted by dots (same as Figure 8b). The 14 time series were randomly spiked with artificial noise with amplitudes of two, four, and six standard deviations from the norm. The EOFs were recomputed from the spiked time series and are shown in *b*, *c*, and *d*.

versus the amplitude of the noise in the artificially spiked time series. The total variance explained by the first mode decreases with increasing noise amplitude. This is because the total variance unexplained by the underlying large-scale signal (i.e., the artificially added measurement noise) increases with increasing noise variance.

It can be concluded that the significant differences between the EOFs of $\log_e$ transformed and untransformed zooplankton volumes are not the result of spurious observations in the time series. The pulses present in the untransformed CalCOFI zooplankton data must therefore represent a biophysical signal that is spatially and temporally coherent throughout the CalCOFI region.

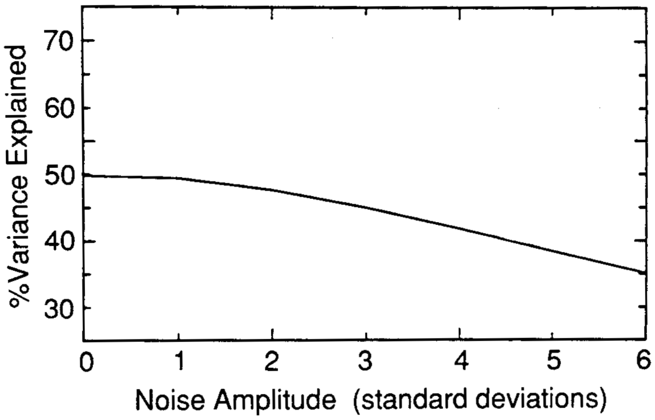


Figure A3. Percent of total variance explained by the EOFs of time series in Figure A2 versus the amplitude (in standard deviations) of the artificially added noise.

APPENDIX 2

Meridional Shifts in Zooplankton Biogeographical Boundaries in the California Current

In this appendix, distribution maps for the dominant zooplankton species in the California Current region are presented to show the interannual meridional migration of biogeographical boundaries (Figures A4–A11). These maps have been published in CalCOFI atlases 2, 3, 5, 8, 18, and 19. The dominant species in the region are broken down by taxa into four species of Chaetognatha (Alvariño 1965), four species of Thaliacea (Berner 1967), two species of Euphausiacea (Brinton 1967, 1973) and five species of Calanoid copepods (Fleminger 1964; Bowman and Johnson 1973).

During cold years (1949, 1950, 1954, and 1962) southward advection in the California Current is high, and species' biogeographical boundaries shift equatorward. During anomalously warm years (1958 and 1959) boundaries of the northern species shift northward. Southern species also shift northward, in some cases as much as 1,000 km. The implications of these shifts are discussed in detail in the text.

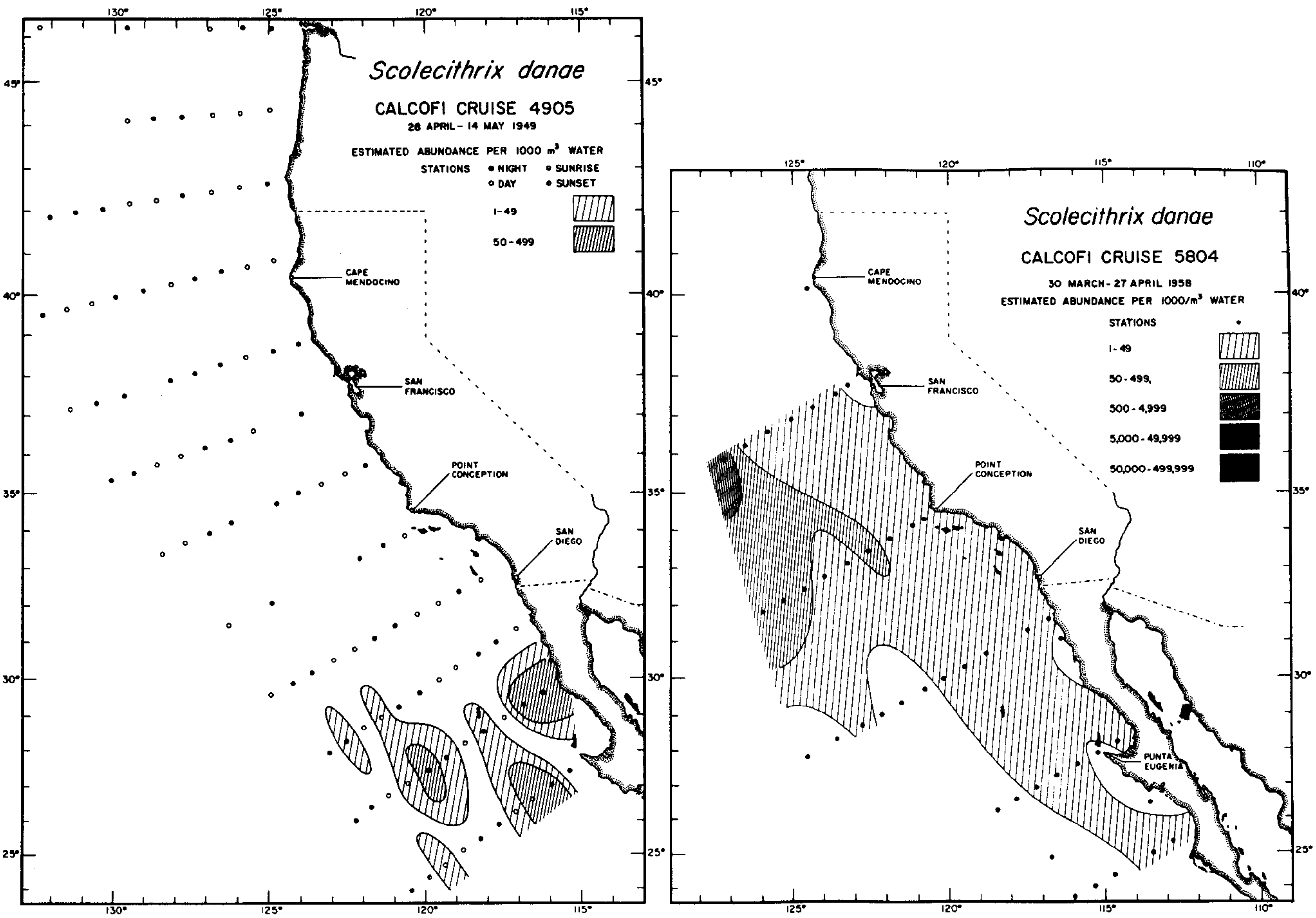


Figure A4. Distribution of *Scolecithrix danae* for May 1949 and April 1958 (Fleminger 1964; Bowman and Johnson 1973). This copepod appears to migrate northward in the low-transport year (1958).

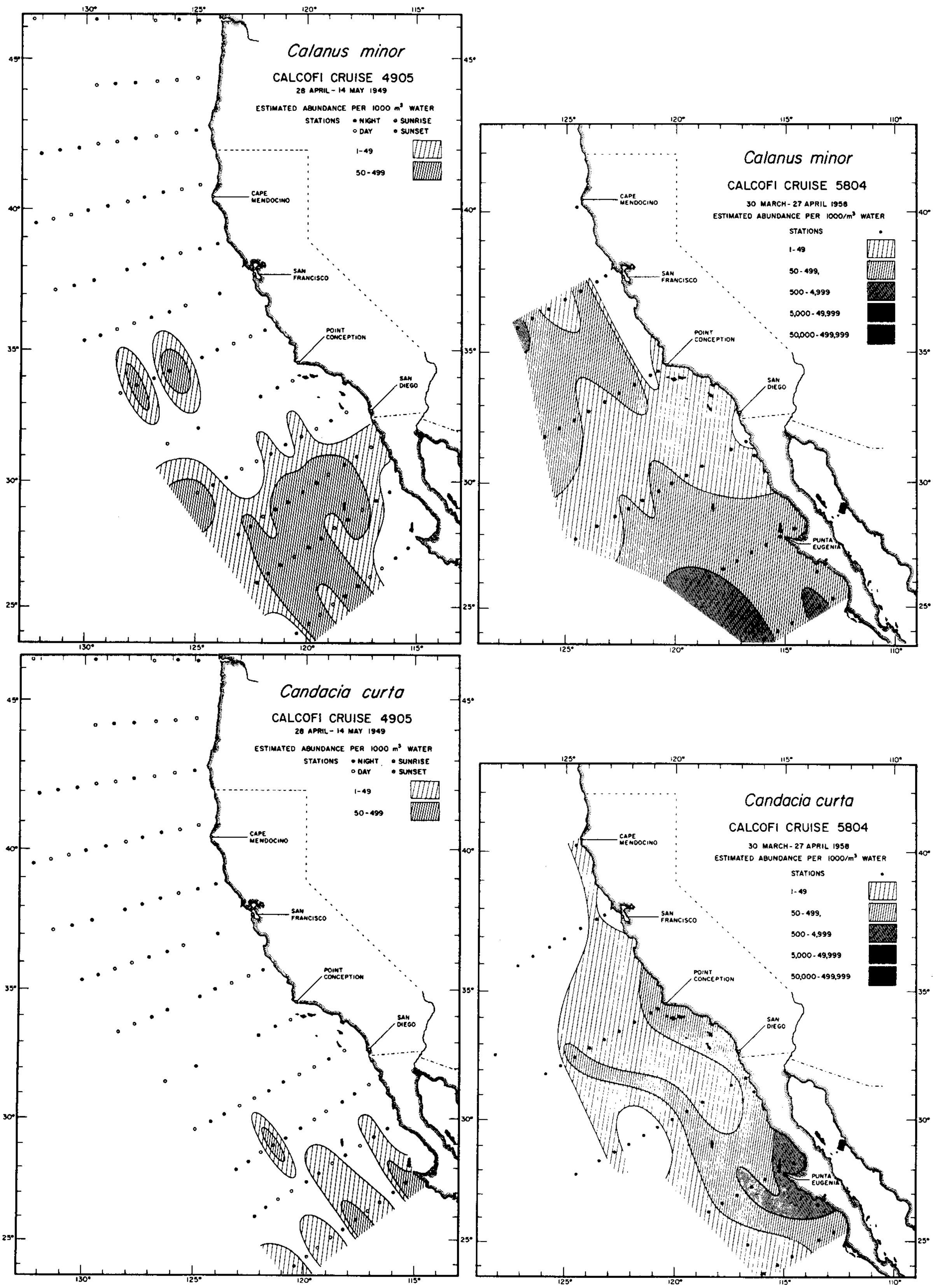


Figure A5. Distribution of *Calanus minor* and *Candacia curta* for May 1949 and April 1958 (cold and warm years, respectively; Fleminger 1964; Bowman and Johnson 1973). Note the apparent northward shifts of the biogeographical boundaries of these two southern species of copepods during the low-transport year (1958).

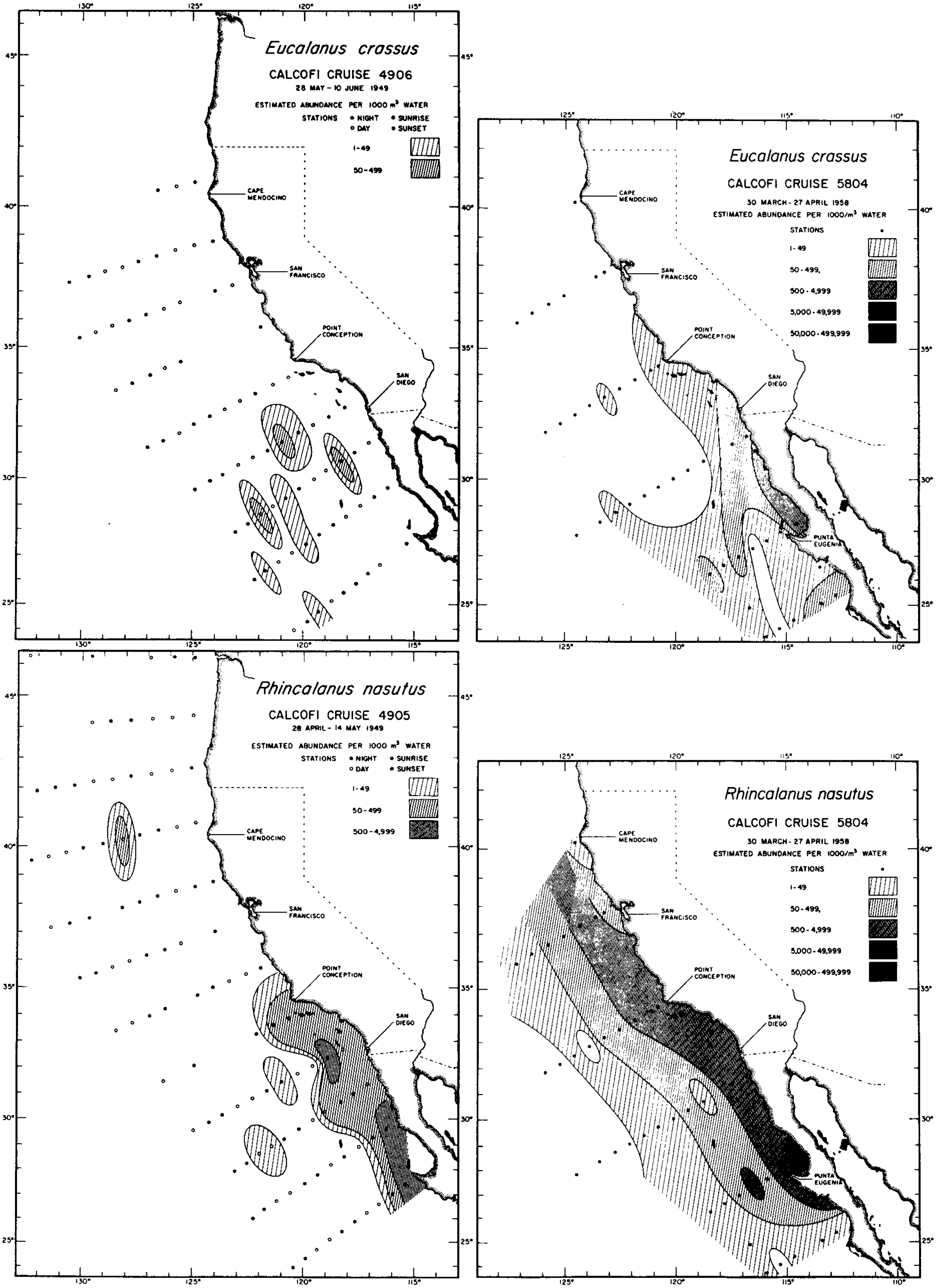


Figure A6. Distribution of *Eucalanus crassus* and *Rhincalanus nasutus* for June and May 1949 (respectively), and April 1958 (Fleminger 1964; Bowman and Johnson 1973). Contrary to what is indicated in the previous figure, these southern species appear to sustain local abundance increases during the low-advection year (1958).

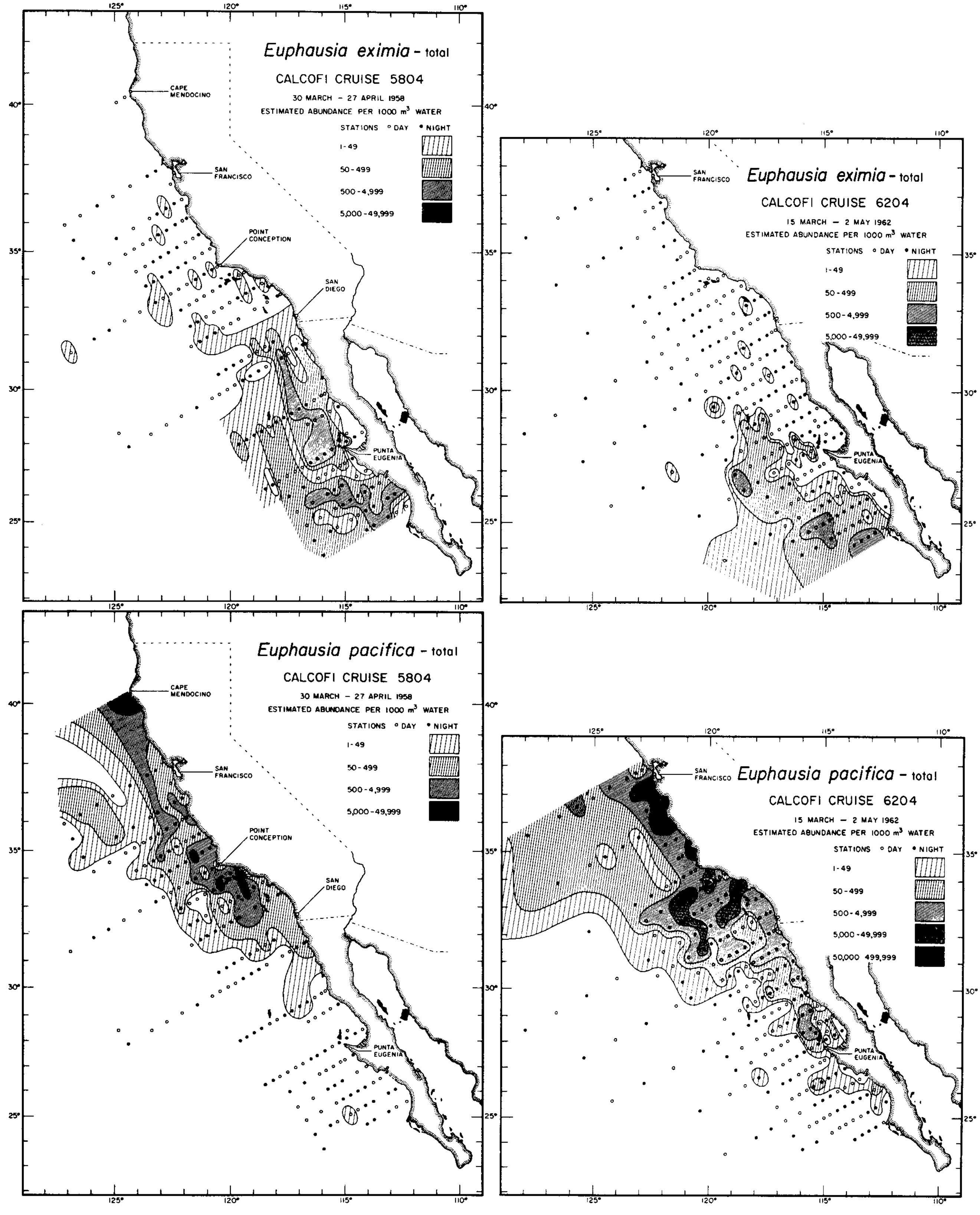


Figure A7. Distribution of *Euphausia eximia* and *Euphausia pacifica* for April of 1958 and 1962 (warm and cold years, respectively; Brinton 1967, 1973). Strong equatorward transport in 1962 pushes the species boundaries southward; weakened transport in 1958 does not bring *E. pacifica* as far equatorward, and local populations of *E. eximia* appear to increase in response to local conditions.

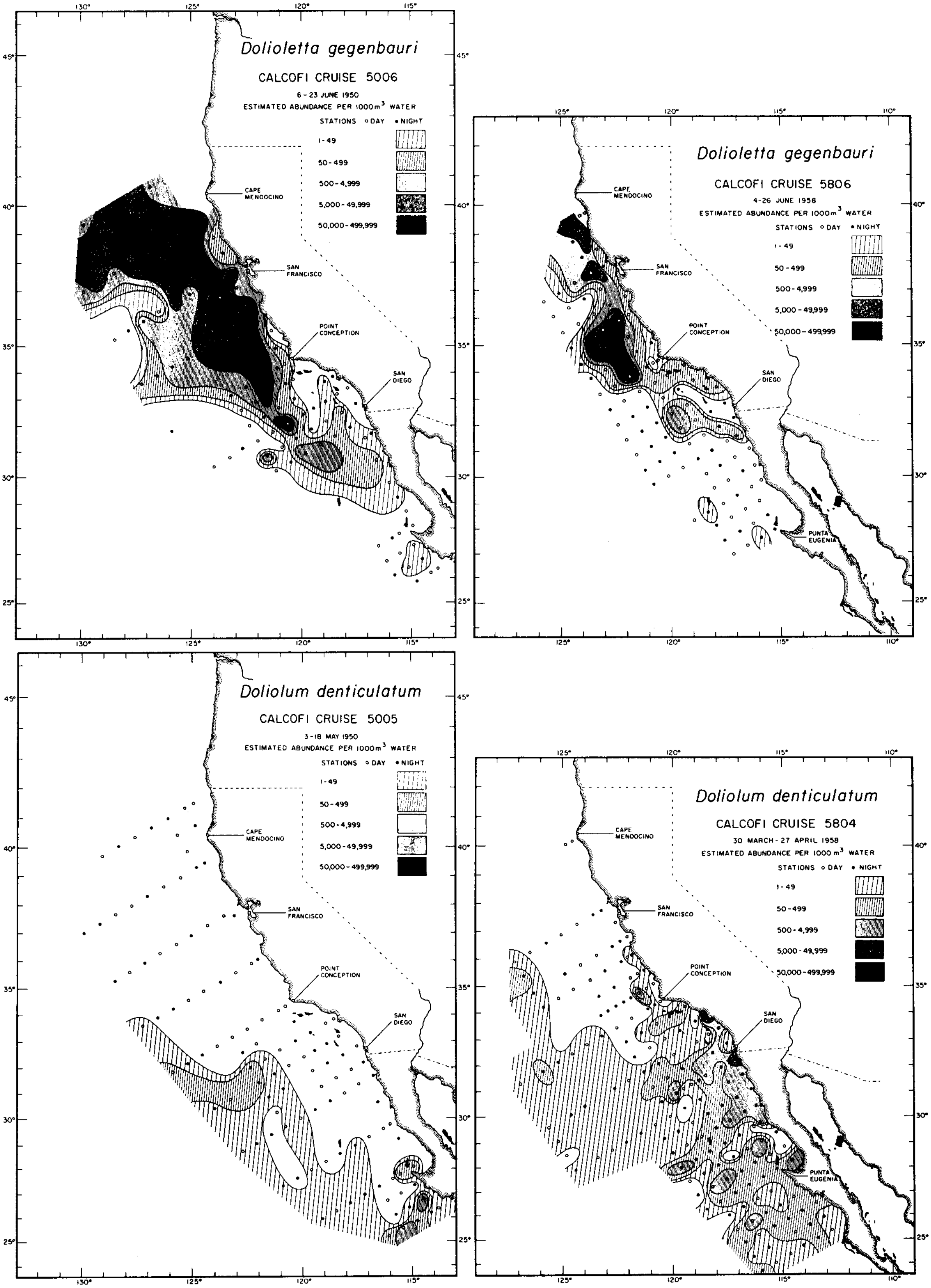


Figure A8. Distribution of *Dolioletta gegenbauri* for June 1950 and 1958, and distribution of *Doliolum denticulatum* for May 1950 and April 1958 (cold and warm years, respectively; Berner 1967). These species exhibit similar responses to advection as those in Figure A7.

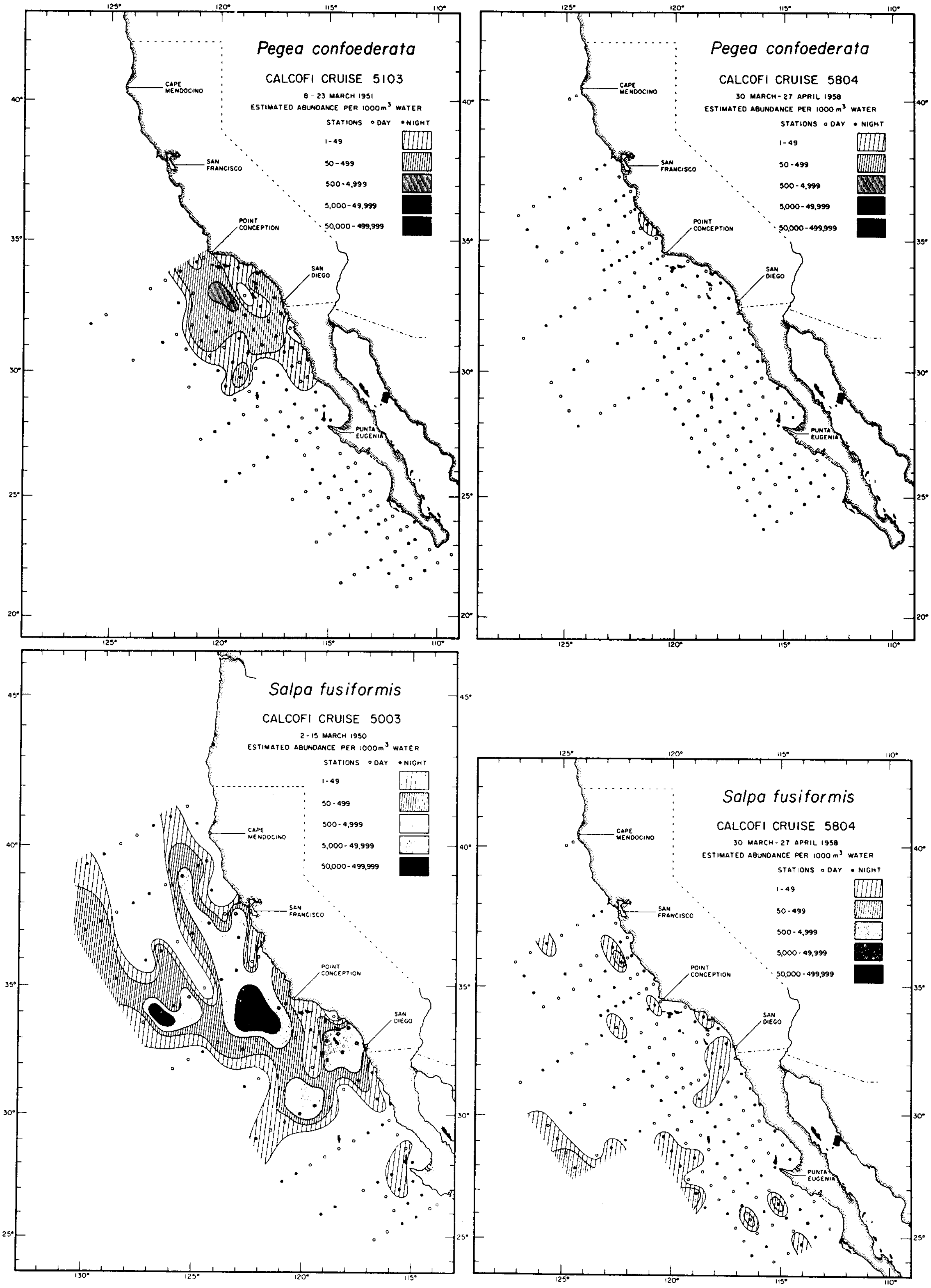


Figure A9. Distribution of *Pegea confoederata* for March 1951 and *Salpa fusiformis* for March 1950 (both cold years) and April 1958 (a warm year; Berner 1967). *P. confoederata* is present in the survey area only during the high-transport year. *S. fusiformis* undergoes a large reduction in abundance when equatorward transport decreases, leaving isolated populations in the survey area.

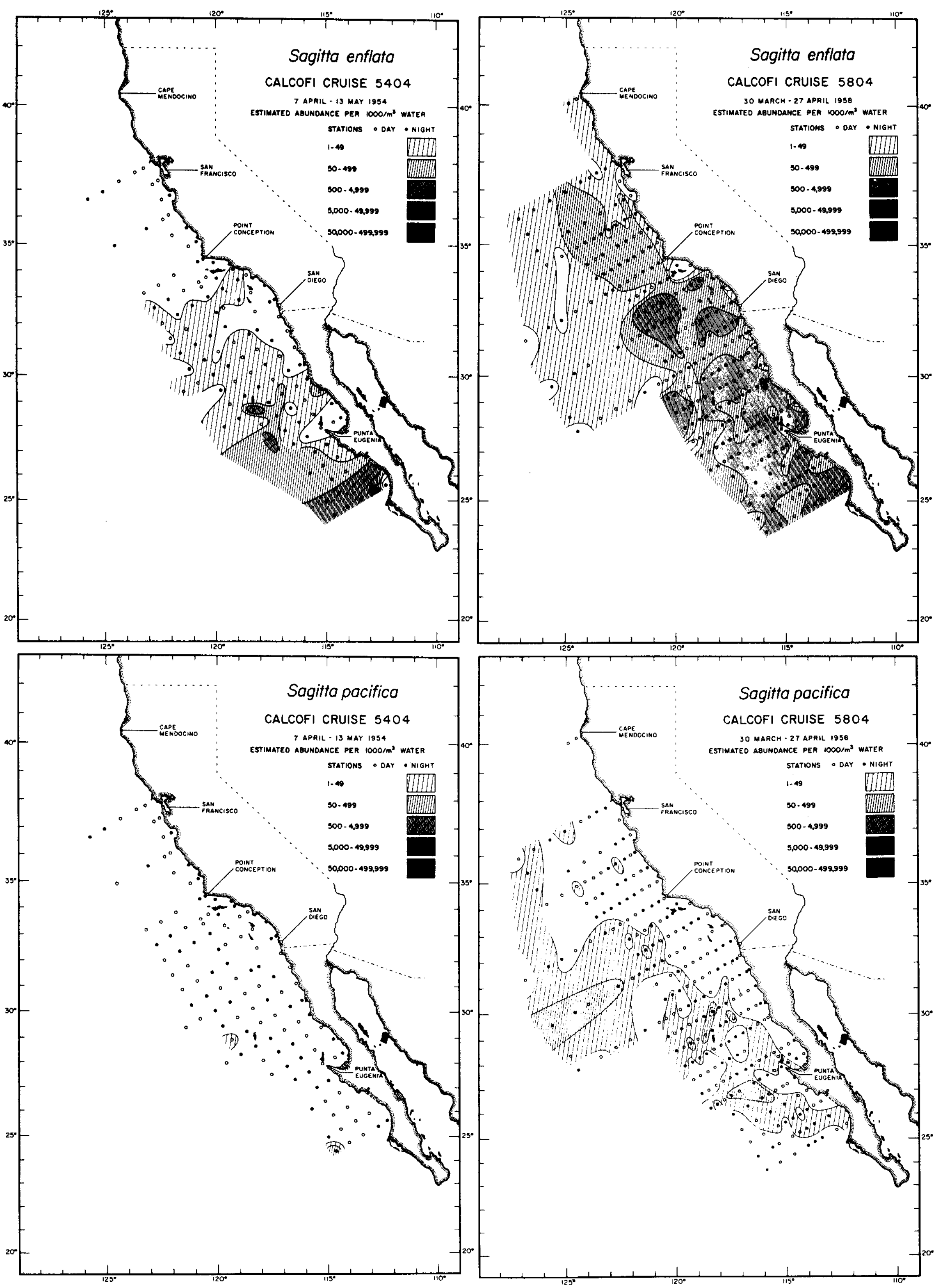
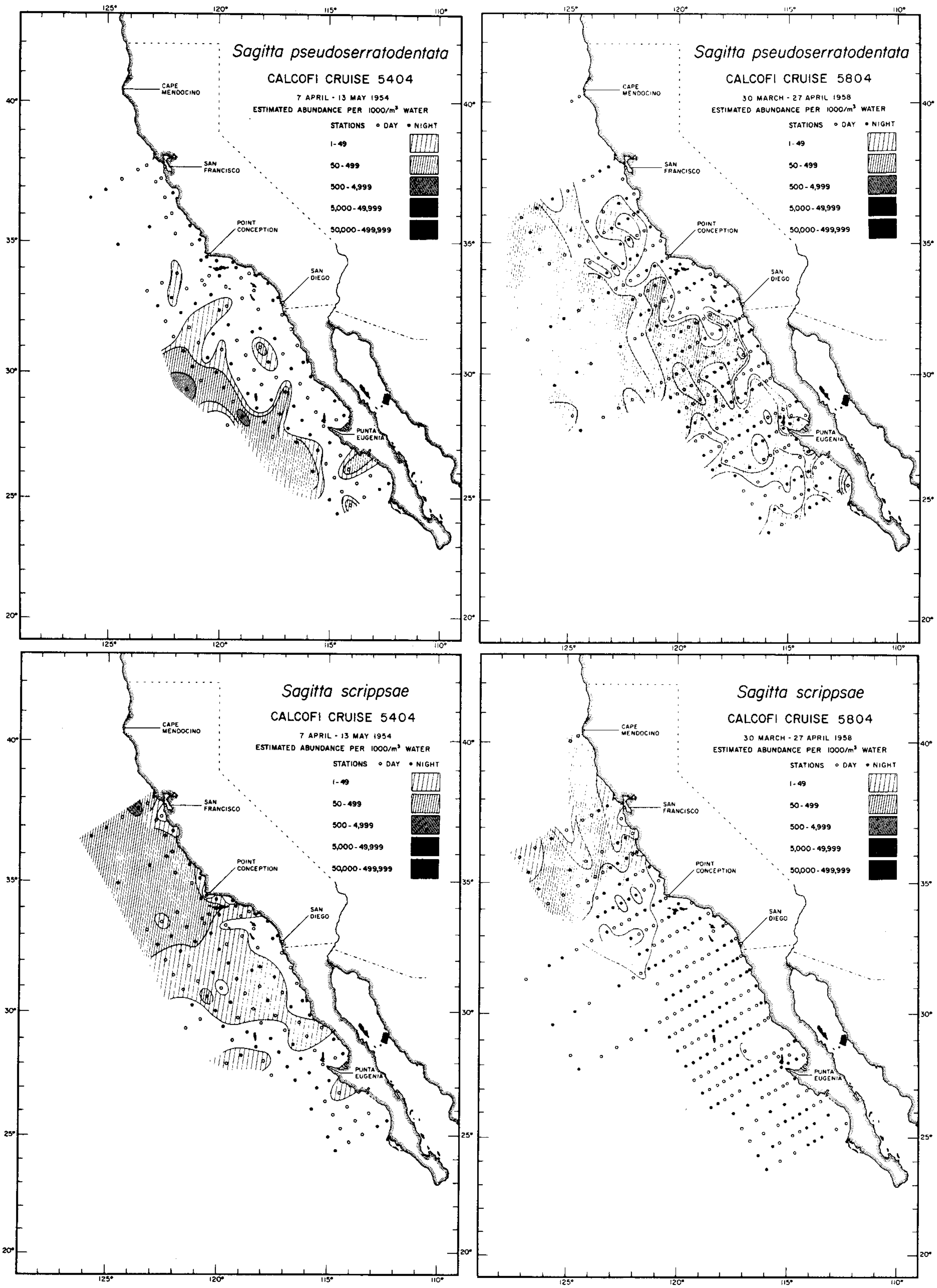


Figure A10. Distributions of *Sagitta enflata* and *Sagitta pacifica* for April of 1954 and 1958 (cold and warm years, respectively; Alvariño 1965). The biogeographical boundary of *S. enflata* appears to migrate northward during the low-transport year, compared to *S. pacifica*, which appears to move inshore, locally increasing population abundances.



Sagitta pseudoserratodentata
CALCOFI CRUISE 5404
7 APRIL - 13 MAY 1954

Sagitta pseudoserratodentata
CALCOFI CRUISE 5804
30 MARCH - 27 APRIL 1958

Sagitta scrippsae
CALCOFI CRUISE 5404
7 APRIL - 13 MAY 1954

Sagitta scrippsae
CALCOFI CRUISE 5804
30 MARCH - 27 APRIL 1958

Figure A11. Distribution of *Sagitta pseudoserratodentata* and *Sagitta scrippsae* for April of 1954 and 1958 (Alvariño 1965). *S. pseudoserratodentata* locally increases abundances during the low-transport year (1958). *S. scrippsae*, a northern species, is not transported as far equatorward in the low-transport year.

LARVAL FISH ASSEMBLAGES IN THE CALIFORNIA CURRENT REGION, 1954–1960, A PERIOD OF DYNAMIC ENVIRONMENTAL CHANGE

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ABSTRACT

Analysis of nearly 200 taxa of fish larvae from CalCOFI surveys in 1954–60 placed 30 taxa into nine recurrent groups. Two complexes of four recurrent groups each were formed by extensive interlinking among the groups. A "northern" complex represents the subarctic-transitional fauna and the coastal pelagic fauna and its associates. A "southern" complex incorporates transitional, warm-water cosmopolite and eastern tropical Pacific taxa. One recurrent group was associated with the extensive continental shelf area of Bahía Sebastián Viscaíno and the Punta Abreojos-Cabo San Lázaro Bight. Oceanographic changes between the cold 1955–56 period and the warm 1958–59 period changed the boundary between the two pelagic complexes and altered the onshore-offshore distribution of the fauna. There was much variability in the constitution of the recurrent groups within the complexes and some change in the degree of overlapping species distributions among the complexes over the seven-year period from 1954 to 1960. The northern-southern complex structure was similar to that described in a previous analysis of data from 1975.

RESUMEN

El análisis de casi 200 taxa de larvas de peces colectados por CalCOFI durante los años 1954–60 ubicó 30 taxa en nueve grupos recurrentes. Extensas interrelaciones entre los grupos recurrentes dieron como resultado dos complejos con cuatro grupos recurrentes cada uno. Un complejo "norteño" representa la fauna subártica-transicional y la fauna pelágica costera y sus asociados. Un complejo "sureño" incorpora taxa cosmopolitas transicionales de aguas cálidas y taxa del este del Pacífico tropical. Un grupo recurrente está asociado con la extensa plataforma continental en el área de las bahías Sebastián Vizcaíno y Punta Abreojos-Cabo San Lázaro. Los cambios oceanográficos ocurridos entre el período frío de 1955–56 y el período cálido de 1958–59 modificaron el límite entre los dos complejos pelágicos y alteraron la distribución perpendicular a la costa de la fauna. Durante un período de siete años, 1954–60, la formación de los grupos recurrentes dentro de los complejos presentó gran variabilidad; a la vez, se observó algunos cambios en el grado de superposición de las distribuciones de especies entre los complejos. La estructura norte-sur de los complejos es similar a aquella descrita en un previo análisis de datos.

INTRODUCTION

A principal task of ecologists is to define the boundaries of communities. In pelagic ecology the task is made difficult by fluid boundaries controlled by meteorological, bathymetric, and oceanographic factors. The composition and structure of planktonic and nektonic communities of the California Current and adjoining regions have been studied extensively over the past 50 years. Broadscale community analyses (Fager and McGowan 1963; McGowan 1971) and distributional studies (Brinton 1962; Ebeling 1962; Alvariño 1964; Reid et al. 1978) showed that water masses in the North Pacific have highly characteristic faunas, confirming the findings of earlier workers (see Sverdrup et al. 1942; Ekman 1953). Subsequent distributional and community studies provided additional faunal definitions of these water masses: central—McGowan and Walker (1979), Venrick (1979), Loeb (1979, 1980), Barnett (1983, 1984); eastern tropical Pacific—Ahlstrom (1971, 1972a), Brinton (1979); subarctic—Parin (1961), Richardson and Pearcy (1977), Richardson et al. (1980), Kendall and Clark (1982), Willis (1984).

The transitional nature of the California Current region is reflected in its fauna, which is a mixture of species that occur in adjacent water masses, and some endemic species (Figure 1). The fish fauna has been studied intensively, leading to community analyses of the nearshore environment (Horn and Allen 1978; Allen 1985); the Southern California Bight region (Gruber et al. 1982); the coastal demersal habitat (Mearns 1974; Allen 1982); and the offshore mesopelagic zone (Ebeling et al. 1970). Loeb et al. (1983) examined the composition and structure of the ichthyoplankton occurring in the

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[Manuscript received March 12, 1987.]

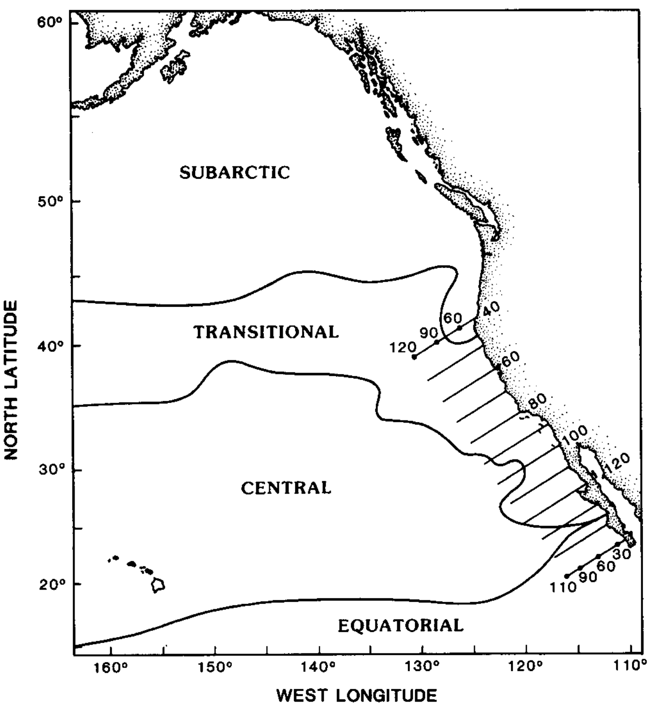

Figure 1. Four major zoogeographic zones in the northeast Pacific as defined by Brinton (1962). The boundaries represent the 50% margins of incidence of the euphausiid shrimp species that characterize these faunal zones. Cardinal lines and selected stations of the basic CalCOFI sampling pattern are shown.

California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling area during 1975.

This paper is the first step in analyzing community dynamics over the entire CalCOFI time series, from 1949 to the present. Recent progress in establishing a computer data base for CalCOFI ichthyoplankton time series has allowed us to study the seven-year period from 1954–60, which was characterized by maximum areal and seasonal sampling coverage during a sequence of anomalously cold and warm oceanographic regimes. In this paper we describe the ichthyoplankton assemblages of the California Current region represented by the 1954–60 data base and examine the changes in these assemblages in relation to major oceanographic changes during that period.

Interannual and seasonal oceanographic changes in the California Current region have been studied extensively (Reid 1960; Chelton 1981; Lynn and Simpson, in press), and much attention has been directed to how these changes affect the distribution and abundance of organisms (Bakun 1985; Bakun and Parrish 1982; Chelton et al. 1982; Fiedler et al. 1986; Lasker 1978; Mullin and Brooks 1970; Smith 1985; Smith and Eppley 1982; Smith and Lasker 1978). For our analysis we assembled the CalCOFI oceanographic data from the 1954–60 period into unique sets of files. This allowed us to describe oceanographic changes in relation to changes in larval fish assemblages and their component taxa.

MATERIALS AND METHODS

This study was based on 907,000 fish larvae from 11,500 plankton net tows taken on annual CalCOFI surveys during the seven-year period from 1954 to 1960. Larvae were identified to species or the lowest taxon possible. Of 191 taxa there were 97 species and 39 generic, 51 familial, and 9 ordinal categories. The distribution of taxonomic categories differs from the original set because identifications were improved during the editing and verification of the data base (Ambrose et al., in press a, b; Sandknop et al., in press; Stevens et al. in press a, b; Sumida et al., in press a, b).

Detailed descriptions of the field and laboratory methods employed in sampling the fish larvae used in this study were described in Kramer et al. (1972). Almost all samples can be associated with 10-m temperature and salinity data taken from the same ship within the hour and within hundreds of meters. (Anon. 1963) Geostrophic flow has been analyzed from most of these cruises from approximately a third of the stations (Wyllie 1966).

In this study, larval fish assemblages were described by recurrent group analysis (Fager 1957, 1963; Fager and McGowan 1963). This analysis determines groups of taxa that occur together relatively frequently and are consistently part of each other's environment. Two major procedures are involved in the analysis—the calculation of an index of affinity (program name AFFINITY) for each pair of taxa that ever occur together in a plankton sample, and the formation of groups of taxa (program name REGROUP) based on a chosen minimum index value (0.3 for this work)[1]. The category "group member" is supplemented by the term "associate" for taxa that have significant affinity indices with one or more but not all group members in one or more groups, and "affiliate" for any remaining taxon that is related to a group by having its highest affinity index (always < 0.3) with a group member. To gain a hierarchical view of the relationships of the principal taxa, the REGROUP procedure was applied to the combined 1954–60 data set at three higher critical affinity levels (0.4, 0.5, and 0.6).

The equation for the affinity index is:

$$I = \frac{N_j}{\sqrt{N_a \cdot N_b}} - \frac{1}{2 \cdot \sqrt{N_b}}$$

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[1] Programs, written in Turbo-Pascal, are available from the authors.

where I is the affinity index,

N_j is the number of joint occurences;

N_a is the number of occurrences of taxon a, the less common taxon, and

N_b is the number of occurrences of taxon b, the more common taxon.

The second term in the equation is a correction factor, which adjusts the affinity index according to the sample size. The correction factor is small for the more common taxa. The first term is the geometric mean coincidence. The consequence of the correction factor is that a pair of organisms would have to coincide 52% of the time to have an affinity index of 0.3 if number of occurrences of the commoner taxon were 5; 37% of the time if the number of occurrences of the commoner taxon were 50; but only 31% of the time if the number of occurrences of the commoner taxon were 5,000.

The oceanographic data used in this study are a compilation of physical and chemical observations made in conjunction with the plankton net tows on CalCOFI survey cruises. The data were processed by the Scripps Institution of Oceanography and published in a series of data reports (cited in Eber and Wiley 1982). For the purpose of documenting the changes in oceanic conditions that occurred during the 1957–59 El Niño, the CalCOFI oceanographic data were separated into two periods: 1955–56 (13 cruises) and 1958–59 (24 cruises).

Over much of the region, the largest differences between the two periods did not occur at the surface, but at depths varying from 30 to 100 meters. Therefore, rather than selecting discrete depths for this overview, we computed averages of oceanographic parameters for the upper 100 meters using data from five standard depths: 10, 30, 50, 75, and 100 meters. For mapping the parameters, we rejected stations at locations where depth to bottom was less than 100 meters to avoid bias associated with vertical gradients. We used harmonic coefficients to compute mean values for oceanographic parameters at each CalCOFI station. These coefficients, based on data from all CalCOFI cruises from 1950 to 1978, were computed for each CalCOFI station by the method of least squares fit to a mean annual cycle.

Anomalies of oceanographic parameters for standard depths on individual CalCOFI cruises were determined by computing deviations from the harmonic means. Anomalies of temperature and salinity were obtained in this way for cruises in each of the selected periods. We analyzed each group of anomalies on a two-dimensional grid fitted to the CalCOFI station pattern. We then subtracted the grid, or matrix, of 1955–56 anomalies from that for the 1958–59 anomalies to obtain charts of differences between the periods.

We examined the association between species distribution and oceanographic characteristics in two adjacent offshore areas of the CalCOFI survey region, between Point Conception, California, and Punta Eugenia, Baja California. These areas include that portion of the CalCOFI station pattern between lines 80 and 120, separated by line 100. The northern area is in the southern fringe of the habitat of two subarctic-transition species, *Stenobrachius leucopsarus* and *Tarletonbeania crenularis*. The southern area is in the northern fringe of the habitat of two eastern tropical Pacific species, *Vinciguerria lucetia* and *Diogenichthys laternatus* (Moser and Ahlstrom 1970; Ahlstrom 1972b). CalCOFI net-tow data from cruises conducted during 1954–56 and 1958–60 were scanned for occurrences of these species in the respective areas.

The data for each of the four species were separated into two categories, one representing samples containing no larvae of the targeted species and the other representing samples containing larvae in excess of a fixed threshold number for each species. The threshold (positive) counts were 10 for *S. leucopsarus* and *V. lucetia*, and 3 for *T. crenularis* and *D. laternatus*. The CalCOFI station codes and cruise dates for each category were then used to separate the oceanographic data into two corresponding groups for each species.

The purpose of this exercise was to test whether the presence or absence of these species provided sufficient criteria to partition the oceanographic data into distinctively different groups. Accordingly, all of the data collected at each station within each area were combined into two temperature-salinity profiles for each species, corresponding to the two categories of larval occurrence (zero or positive). After discarding those stations not represented by both categories (for each species), to avoid geographical bias, we combined the station profiles into a single pair of area profiles for each species.

OCEANOGRAPHY

General Description

The California Current region is bordered by three water masses: subarctic to the north, Pacific central to the west, and equatorial to the south (Tsuchiya 1982). The California Current begins as

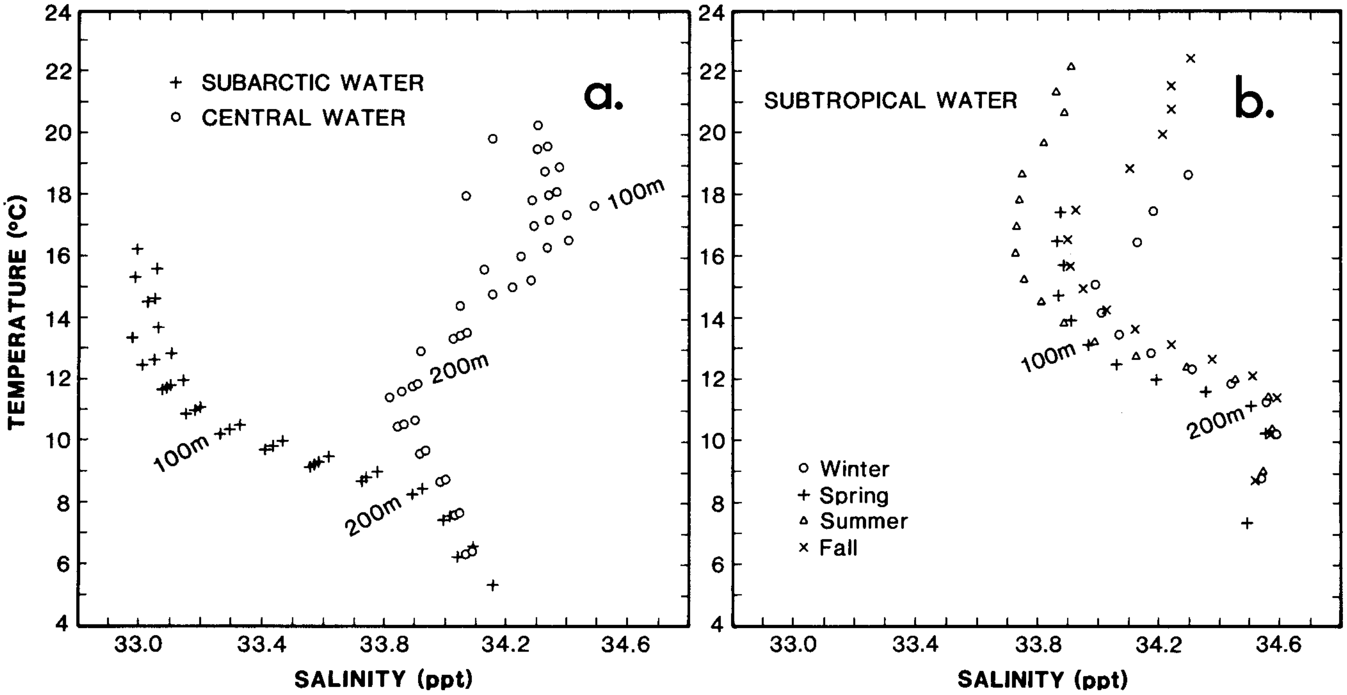

Figure 2. Mean seasonal temperature-salinity plots for modified subarctic water and Pacific central water (*a*) and subtropical water (*b*) in the California Current region. The symbols are plotted for discrete values of sigma-t at intervals of 0.2 g/l.

the southward-turning branch of the transpacific West Wind Drift, with characteristics of subarctic water. As the current proceeds southeastward, these characteristics are modified by excess heating, evaporation, and by intrusion of water from the west and south (Hickey 1979). Further modification is caused by entrainment of mesoscale eddies of upwelled water from coastal areas (Lynn and Simpson, in press).

The peripheral water masses' influence on California Current water can be seen in mean temperature-salinity (T-S) relationships in the upper few hundred meters at different locations (Figure 2). The symbols on the T-S curves were plotted at constant intervals of sigma-t (0.2 g/l). Each symbol represents a seasonal mean, so that their spread along constant sigma-t lines is a measure of seasonal variation. This variation is particularly large in the upper 100 m of modified subtropical water and shows the reciprocating influences of the California Current in summer, and of intrusion from the south in winter. The core of the California Current in the northern portion, 330–370 km off San Francisco on CalCOFI line 60, reflects subarctic water, with cool temperatures and low salinities near the surface. Below 100 m the salinity increases rapidly with depth. The effect of mixing with central water is evident farther west, 1,040–1,180 km seaward from the Southern California Bight along lines 80 and 90. This area reflects the warm temperatures and high salinities of central water in the upper 100 m, with salinities decreasing with depth to a minimum at about 200 m. Equatorial water moving northward along the Baja California coast also mixes into the California Current and is most evident in the southern portion, about 300 km offshore, along lines 133 and 137. Like central water, equatorial water is warm near the surface, but in the layers below 100 m, salinities increase rapidly with depth.

The southern boundary of the subarctic water mass is called the subarctic front. It is found at 40°–43° north, west of 150° west. To the east of that longitude it turns southeast and forms the western boundary of the California Current, where it has been called the California front. The northern boundary of the North Pacific central water is called the subtropical front. It is found at about 31° north, west of 140° west, and also bends southeast at its eastern end. In the transition zone between these fronts is another front, described by Lynn (1986) as the northern subtropical front. At their southern extremes, these fronts become diffuse, and the extension of the California Current turns westward and joins the North Equatorial Current.

It is important to note that the positions of these boundaries may fluctuate. During the period of this study, in particular, the position of the subarctic front at the North American coastline shifted from 40° north before 1957 to 53° north in 1957–58. Moreover, the waters of the California Current and adjacent zones may contain eddies of tens to hundreds of kilometers in extent. Thus there is a considerable amount of exchange and mixing that must be considered in describing a planktonic fauna in terms of water-mass characteristics and boundaries.

Changes during 1955–60

Long-term annual means in the upper 100 m range from 11° to 18°C for temperature and from 33 to 34 ppt salinity. (Figure 3a, b). The temperature pattern shows the expected warming from north to south and also from inshore to offshore. Salinity increases from north to south and, in the northern part of the pattern, decreases from inshore to offshore out to the core of the California Current. The latter appears as a trough in the salinity field about 330 km from the coast.

A chart of temperature anomaly differences (Figure 3c) reveals that the 1958–59 period was warmer than the 1955–56 period throughout the region. The differences were greatest (exceeding 3°C) in the southern portion and, except for an area south of Punta Eugenia, were greater offshore than inshore. The corresponding chart for salinity anomaly shows that salinities were higher in 1958–59 in the southern portion of the region, with positive differences exceeding 0.4 ppt in the farthest offshore area (Figure 3d). The northern portion, however, had higher salinities in 1955–56 in inshore areas and out to nearly 200 km from the coast.

These charts reflect a northward shift of the contours from 1955–56 to 1958–59, particularly in the temperature field. The displacements of the 12°, 14°, and 16° contours between these periods were approximately 220 km (Figure 4). This shift is reflected by changes of temperature and salinity anomalies along CalCOFI line 100 (off Ensenada, Baja California) during the two periods (Figure 5).

It has been suggested that the lower temperatures in 1955–56 might be associated with stronger northwest winds that would contribute to increased upwelling inshore, and to southward transport offshore in the California Current. We attempted to compare southward transports in the 1955–56 and 1958–59 periods by mapping dynamic height anomalies for the sea surface, relative to 500 m, as a representation of geostrophic flow. The principal differences between the two periods were found in the values of dynamic height; those representing the 1958–59 period were larger by up to 0.08 dynamic meters over much of the region. However, a comparison of gradients of dynamic height anomalies (as indices of transport) along CalCOFI lines 60 to 110 was inconclusive.

RECURRENT GROUPS

Recurrent group analysis was applied to the entire data set of 192 taxa for the seven-year period from 1954 to 1960 and also to each of the seven years (Figures 6 and 7). From the recurrent group analysis of the composite seven-year set, 30 taxa formed 9 groups (2 groups with 5 taxa each, 2 with 4, 2 with 3, and 3 with 2), and 8 other taxa formed associate relationships with taxa in 1 or more of the 9 groups (Figure 6).[2] Intergroup affinities formed 2 large complexes, each consisting of 4 recurrent groups, and 1 isolated southern shelf recurrent group (SYNODUS). We refer to these as the northern and southern complexes, since their member taxa had predominately cold- or warm-water distributions, or affinity indices linking them to cold- or warm-water taxa. The SYNODUS group was the primary constituent of a southern shelf complex, which was more fully characterized in analyses of individual years. There were 12 recurrent group members in the northern complex, 14 in the southern complex, and 4 in the isolated SYNODUS recurrent group (Table 1). There were 2 unique associates in the northern complex, 5 unique associates in the southern group, and 1 unique associate in the SYNODUS group. There were 53 affiliated taxa in the northern group, 68 affiliates in the southern complex, and 33 in the SYNODUS recurrent group (Appendix). The significant affinity index between *Engraulis mordax* and *Triphoturus mexicanus* was the only link between the northern and southern complexes.

Northern Complex

In the northern complex the LEUROGLOSSUS group had 5 taxa, CITHARICHTHYS had 3 taxa, and TARLETONBEANIA and SARDINOPS had 2 taxa each (Figure 8). Members of the northern complex over the seven-year period can be found through the survey area in the north-south plane but were more likely to be found nearshore when in the southern reaches. The LEUROGLOSSUS and TARLETONBEANIA groups

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[2] Two additional pairs of taxa formed two isolated groups. One of these, comprising Serranidae and Carangidae, was based on relatively few (43) occurrences; the other, comprising Balistidae and Fistularidae, was formed by a single co-occurrence.

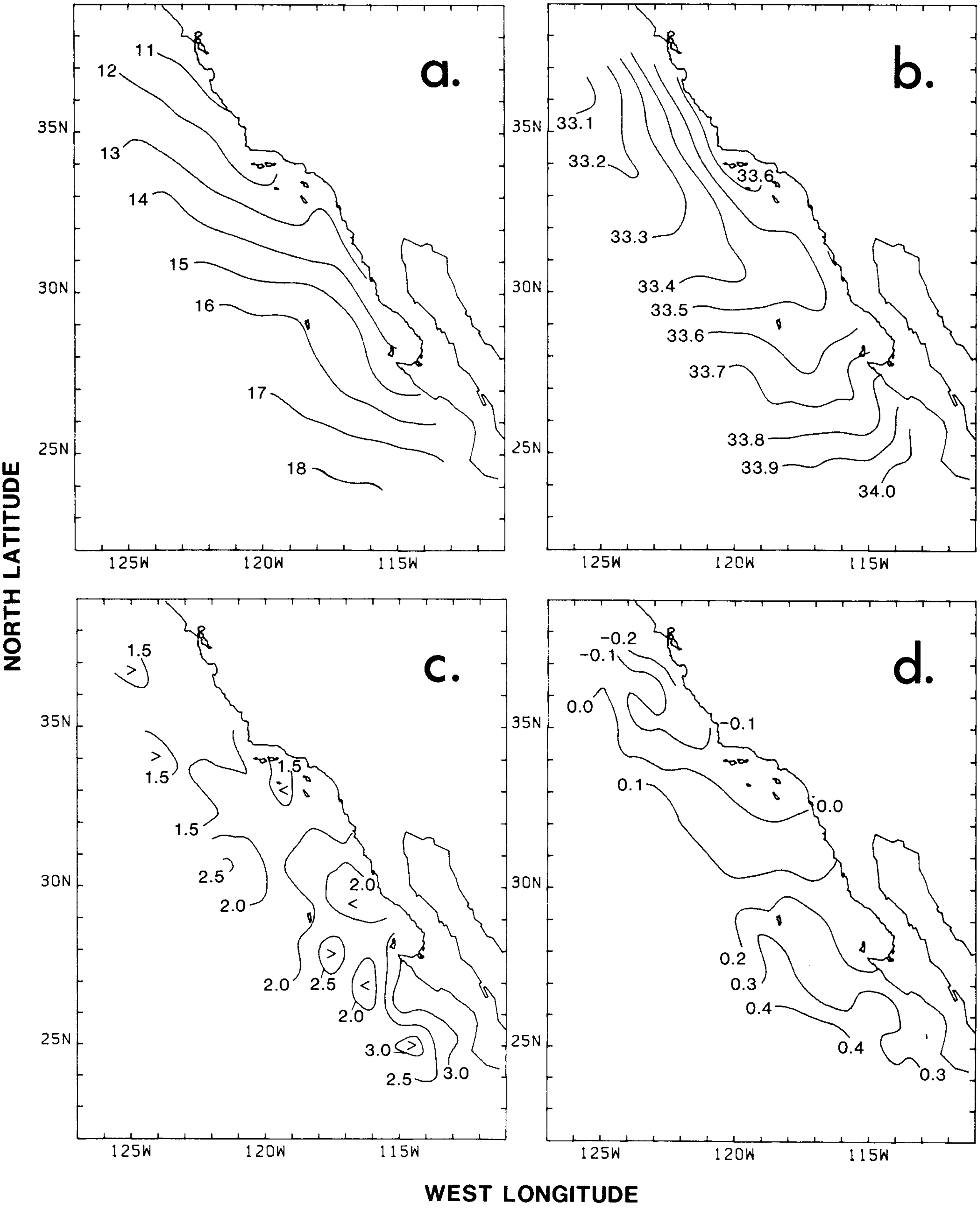

Figure 3. Mean annual temperature (*a*) and salinity (*b*) of the upper 100 meters computed at 5 standard depths (10 m, 30 m, 50 m, 75 m, and 100 m) from harmonic coefficients based on data from CalCOFI cruises from 1950 through 1978. Change, or difference, in the deviations of temperatures (*c*) and salinities (*d*) in the upper 100 meters from the harmonic means, between the periods 1955–56 and 1958–59.

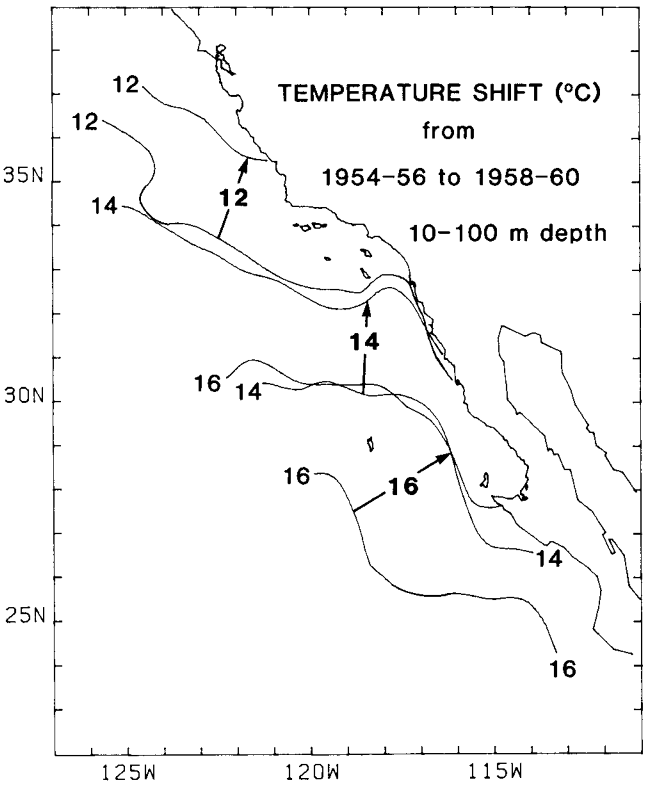

Figure 4. Temperature change in the upper 100 meters between 1955–56 and 1958–59 as depicted by the displacements of the 12°, 14°, and 16°C isotherms between the two periods.

were separated in part by the tendency of the former group to spawn in summer (Table 2). There were significant affinities between *Tarletonbeania crenularis* and 3 of the 5 members of the LEUROGLOSSUS group. Although the distribution of the TARLETONBEANIA group leads one to believe that it was somewhat more northerly than the LEUROGLOSSUS group, this may be because the cruises proceeded farther north in summer, when this group was spawning.

LEUROGLOSSUS recurrent group. This group is made up of 2 mesopelagic argentinoid smelts (*Bathylagus ochotensis* and *Leuroglossus stilbius*), a vertically migrating mesopelagic myctophid (*Stenobrachius leucopsarus*), a schooling gadoid (*Merluccius productus*), and the scorpaenid genus (*Sebastes* spp.), which includes about 60 species in the survey area (Table 2). Faunal associations of the 4 species are subarctic-transitional or transitional; their spawning is highly seasonal, with winter or spring maxima (Table 2). The fifth taxon, the rockfishes of the genus *Sebastes*, is broadly distributed from boreal to transitional waters and has a composite fall-to-spring spawning season with a February peak in the survey area (Table 2).

The distribution for the LEUROGLOSSUS group in the survey area was centered in the Southern California Bight region (Figure 9), reflecting the geographic distribution of *L. stilbius* larvae (Table 3). Populations of *B. ochotensis* and *S. leucopsarus* have more northerly distributions, extending across the subarctic Pacific; their larvae were found predominately in the northern part of the survey pattern, off northern and central California (Table 3). Larvae of *L. stilbius* and *S. leucopsarus* have a more shoreward distribution than *B. ochotensis* larvae. Adults of *M. productus* have a broad distribution from the boreal region to Baja

TABLE 1

Numbers of Larval Fish Taxa That Are Members, Associates, or Affiliates of Recurrent Groups in an Analysis of Pooled Data from CalCOFI Surveys, 1954–60

Complex	Group name	Members	Associates	Unique associates	Affiliates
Northern					
	LEUROGLOSSUS	5	4	0	19
	CITHARICHTHYS	3	7	1	21
	SARDINOPS	2	3	0	5
	TARLETONBEANIA	2	3	0	8
	Subtotal	12	*	1	53
Southern					
	SYMBOLOPHORUS	5	7	1	16
	VINCIGUERRIA	4	6	2	32
	TRIPHOTURUS	3	10	0	9
	CERATOSCOPELUS	2	4	0	10
	Subtotal	14	*	3	66
Southern shelf					
	SYNODUS	4	0	1	32
Total		30	*	5	151

*Not unique sets

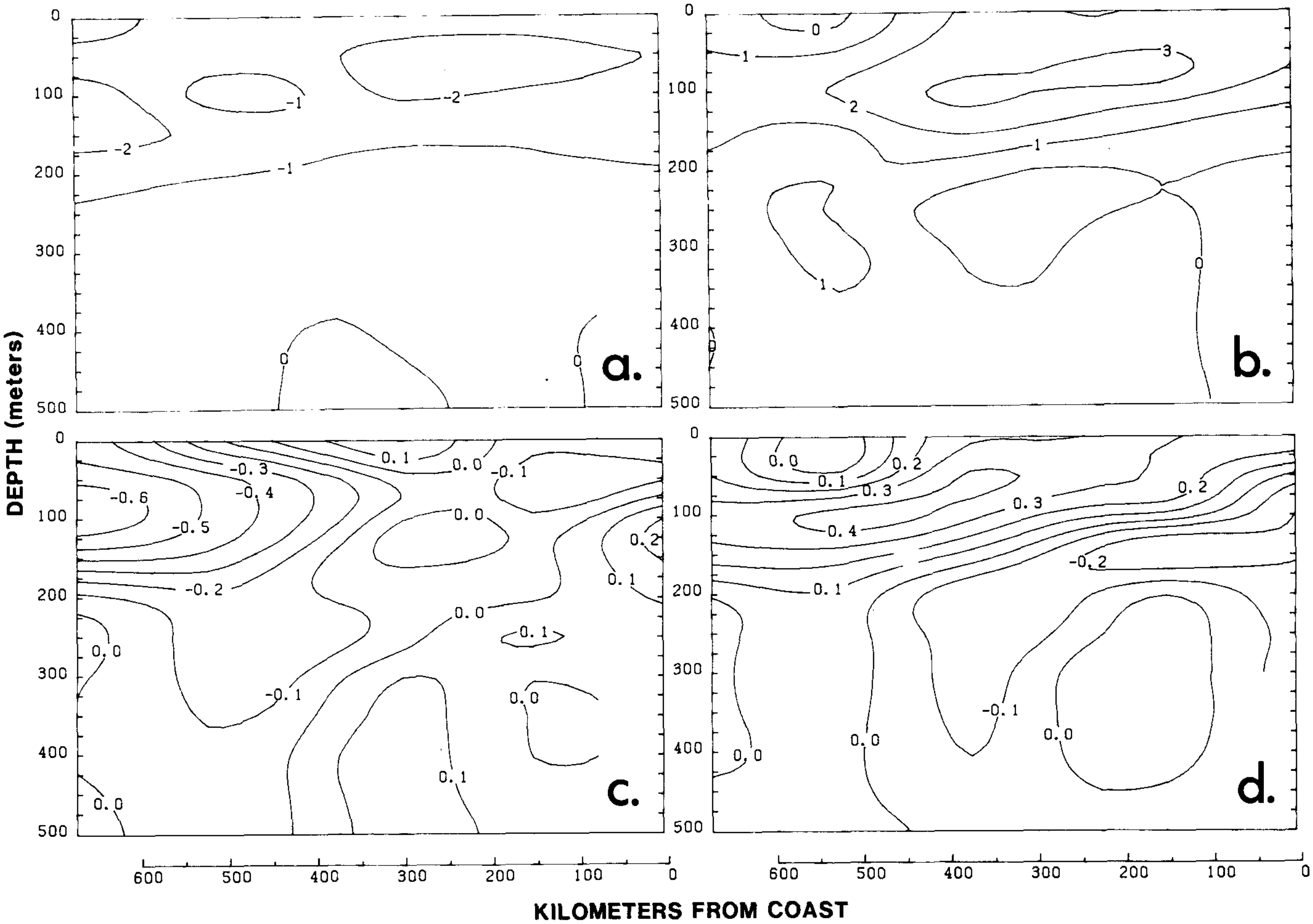

Figure 5. Mean temperature anomaly pattern along CalCOFI line 100 in the upper 500 meters, 1955–56 (*a*), and 1958–59 (*b*). Mean salinity anomaly pattern (computed in the same way) for 1955–56 (*c*) and 1958–59 (*d*). The isopleths represent deviations from harmonic means based on the period 1950–78.

California, with a postulated migration to spawning grounds off southern California and northern Baja California. The high mean abundance off southern Baja California may represent a few anomalously large collections in winter (Table 3). Larvae of *Sebastes* spp. were concentrated in the shoreward regions off California and northern Baja California.

The LEUROGLOSSUS group was strongly connected with other groups of the northern complex. Four of the group taxa had strong affinities with *Engraulis mordax*; 3 had affinities with *Sardinops sagax*; and 3 had affinities with *Tarletonbeania crenularis* (Figures 6 and 8).

TARLETONBEANIA recurrent group. This group comprises a vertically migrating mesopelagic myctophid (*Tarletonbeania crenularis*) and an epipelagic oceanic stromateoid (*Icichthys lockingtoni*). Adults of *T. crenularis* range from British Columbia to central Baja California. The range for *I. lockingtoni* is similar in the south, but extends westward to the Gulf of Alaska and Japan. These two species have well-defined spawning seasonality, with summer maxima (Table 2).

The distribution of the group was coincident with the LEUROGLOSSUS group (Figure 9), and members of the 2 groups would have higher affinity indices if the spawning seasons were coincident. Larval distributions for the 2 species in the TARLETONBEANIA groups were concentrated heavily in northern and central California, with a strong peak in northern California for larvae of *T. crenularis* (Table 3).

CITHARICHTHYS recurrent group. This group comprises a coastal pelagic anchovy (*Engraulis mordax*) and 2 shallow-water paralichthyid flatfishes (*Citharichthys fragilis* and *C. xanthostigma*). *E. mordax* has a broad coastal distribution from

TABLE 2

Taxonomic Composition of Recurrent Groups, Number of Observations (1954–60) and Distribution and Spawning Seasons of Members

Recurrent group taxa	Number	Faunal association	Adult habitat	Spawning season /peak month
Northern Complex				
LEUROGLOSSUS group				
Bathylagus ochotensis	1172	S-T	MP (49–901 m)	Win-Spr/May
Leuroglossus stilbius	3011	T	MP (to 690 m)	Spr/Mar
Stenobrachius leucopsarus	2440	S-T	MP (MEP)	Spr/Feb-May
Sebastes spp.	4486	S-T,T	D (to 732 m)	Fall-Spr/Feb-Mar
Merluccius productus	3027	S-T	D (to 914 m)	Win-Spr/Feb-Mar
TARLETONBEANIA group				
Tarletonbeania crenularis	1044	S-T	MP (MEP)	Spr-Sum/May-Jul
Icichthys lockingtoni	634	S-T	EP (to 91 + m)	Sum/Jun-Jul
CITHARICHTHYS group				
Engraulis mordax	5098	T	CP (to 219 m)	Ext/Feb-Mar
Citharichthys fragilis	819	T,SbTr	D (18–347 m)	Bim/Aug,Feb
Citharichthys xanthostigma	980	TtoTr	D (2–200 m)	Bim/Aug,Feb
SARDINOPS group				
Sardinops sagax	1479	T	CP	Ext/Jan-Mar, Aug-Sep
Scomber japonicus	513	T,SbTr	CP	Sum/Aug
Southern Complex				
SYMBOLOPHORUS group				
Bathylagus wesethi	1913	T	MP (40–1,001 m)	Spr-Sum/May
Cyclothone spp.	1784	WWC	MP	Sum-Fall/Aug
Diogenichthys atlanticus	734	WWC	MP (MEP)	Bim/May,Sep-Oct
Lampanyctus ritteri	2288	S-T	MP (MEP)	Spr/May
Symbolophorus californiensis	966	T	MP (MEP)	Spr/May
TRIPHOTURUS group				
Triphoturus mexicanus	4648	SbTr	MP (MEP)	Sum/Aug
Protomyctophum crockeri	2303	T	MP	Spr/May
Trachurus symmetricus	2096	T	EP (to 183 m)	Spr-Sum/May,Jun
CERATOSCOPELUS group				
Ceratoscopelus townsendi	988	T	MP (MEP)	Sum/Aug
Lampadena urophaos	307	SbTr	MP (MEP)	Sum/Aug
VINCIGUERRIA group				
Vinciguerria lucetia	4288	ETP	MP (MEP)	Ext/Aug
Diogenichthys laternatus	2203	ETP	MP (MEP)	Ext/Jan-Feb,Aug-Oct
Gonichthys tenuiculus	537	ETP	MP (MEP)	Ext/Feb
Hygophum atratum	444	ETP	MP (MEP)	Bim/Jan,Aug
Southern Coastal Complex				
SYNODUS group				
Synodus spp.	402	SbTr,Tr	D (to 50 m)	Fall/Sep-Dec
Prionotus spp.	132	SbTr,Tr	D (15–110 m)	Sum-Fall/Aug-Sep
Ophidion scrippsae	192	T,SbTr	D (3–70 m)	Sum-Fall/Aug-Sep
Symphurus spp.	351	T,Tr	D (1–201 m)	Sum-Fall/Aug-Sep

Abbreviations:

S = subarctic, T = transition, SbTr = subtropical, Tr = tropical, WWC = warm-water cosmopolite, ETP = eastern tropical Pacific, MP = mesopelagic, MEP = migrates to epipelagic, EP = epipelagic, D = demersal, CP = coastal pelagic, Bim = bimodal, Ext = extended.

Information on the distribution of adult fishes summarized from Miller and Lea (1972), Eschmeyer et al. (1983), Wisner (1976), and original data.

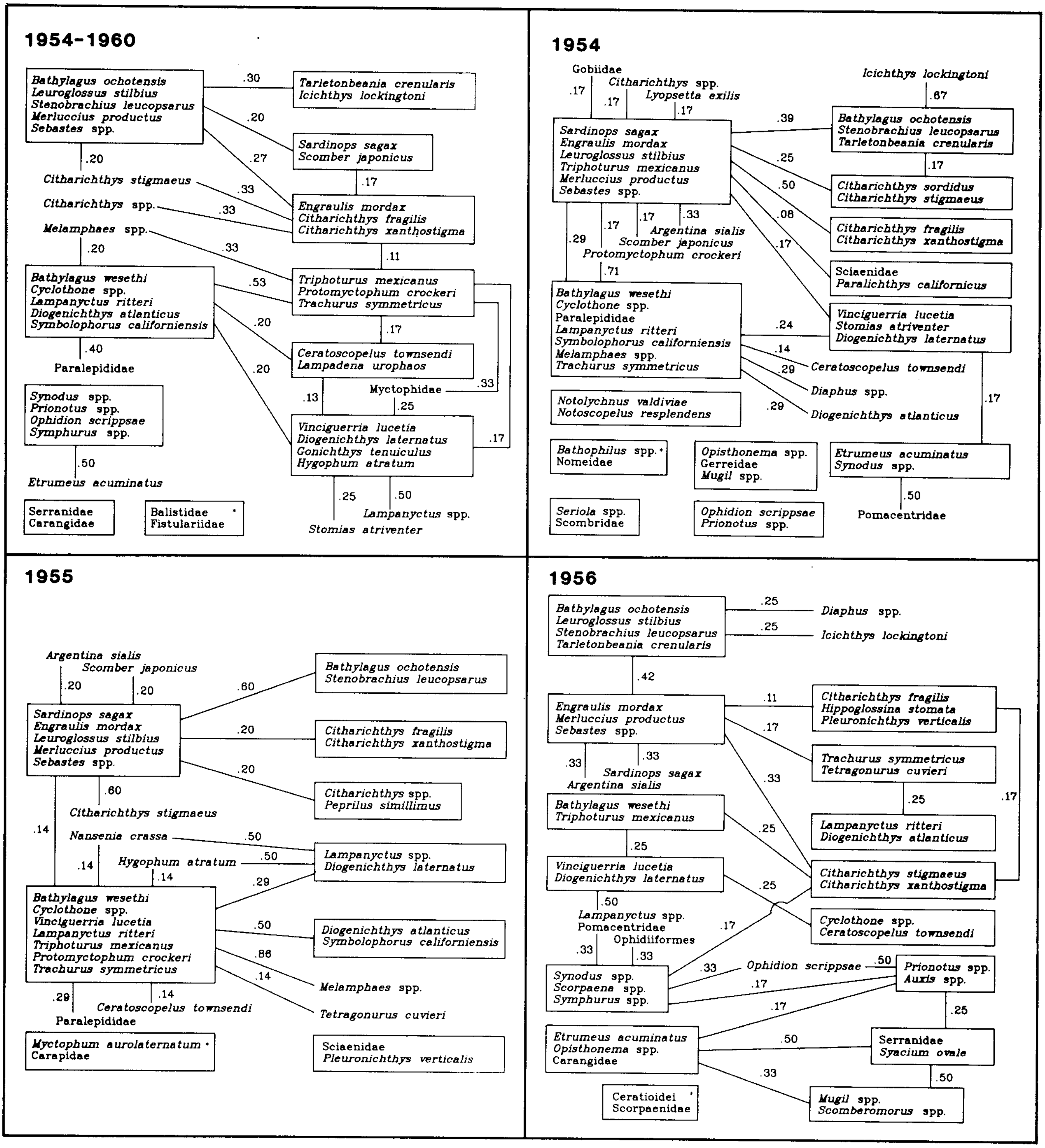

Figure 6. The composition and interrelationships of recurrent groups and their associates in the CalCOFI survey area for pooled 1954–60 data and for three individual years. A line between two recurrent groups indicates that there are intergroup pairs with significant affinity indices (≥ 0.3). The number represents the fraction of significant affinity pairs divided by the possible number of pairs. Recurrent groups represented by a single co-occurrence are indicated by an asterisk.

British Columbia to southern Baja California; however, there are apparently three subpopulations—a northern population extending from central California northward, a central population distributed from central California to central Baja California, and a southern stock from central Baja

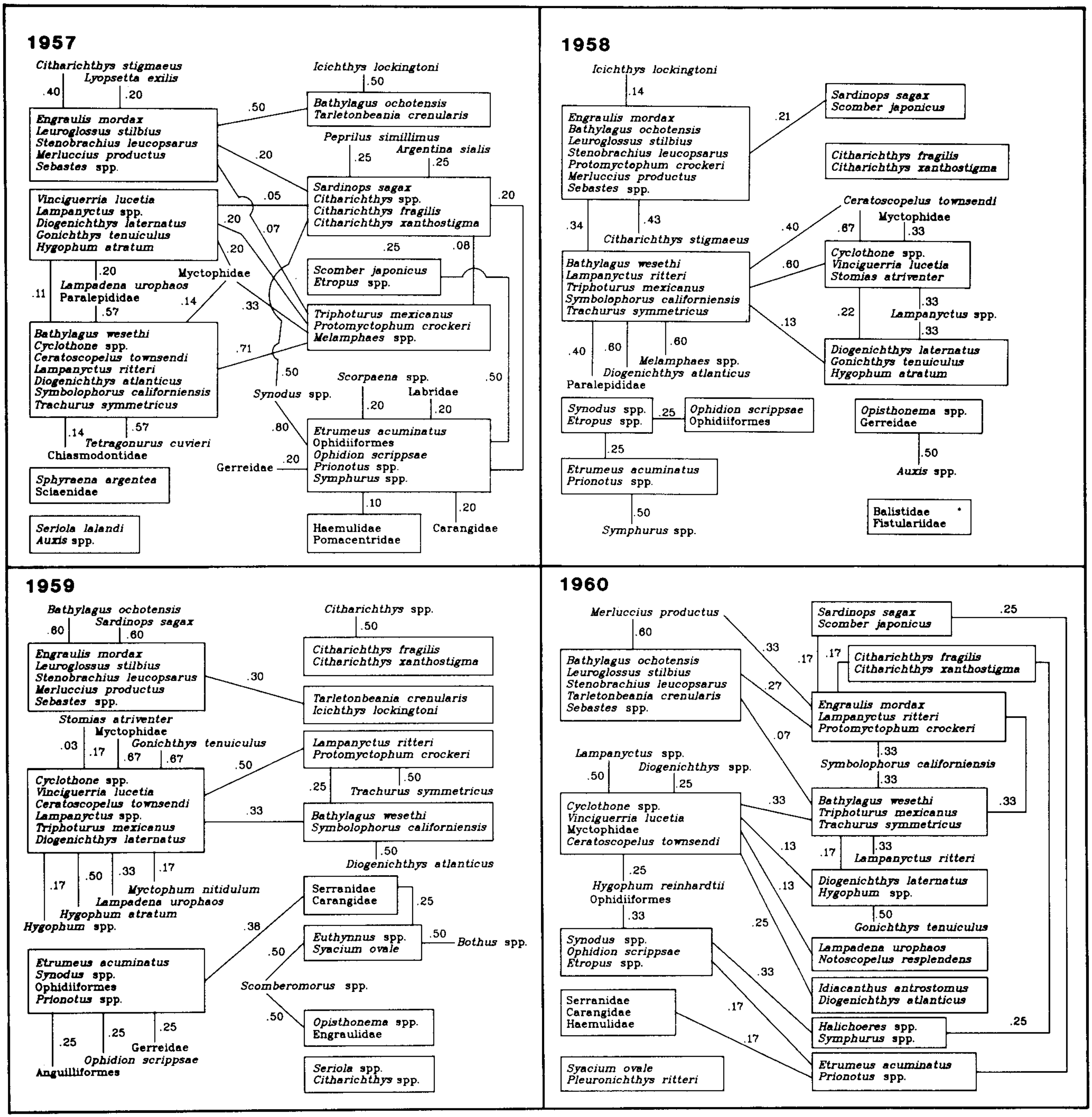

Figure 7. The composition and interrelationships of recurrent groups and their associates in the CalCOFI survey for 1957–60. A line between two recurrent groups indicates that there are intergroup pairs with significant affinity indices (≥ 0.3). The number represents the fraction of significant affinity pairs divided by the possible number of pairs. Recurrent groups represented by a single co-occurrence are indicated by an asterisk.

California to Cabo San Lucas. The 2 flatfishes have warm-water faunal affinities, with ranges extending from southern California south to the Gulf of California, and were included in the northern complex because of their strong affinity indices with *E. mordax*. Two other flatfish taxa form associate relationships with *E. mordax*—the genus *Citharichthys* as a unique associate and *Citharichthys stigmaeus* as an associate shared with *Sebastes* spp. in the LEUROGLOSSUS group[3]. *C. stigmaeus* is more temperate than its group congeners, with a range extending from Alaska to southern Baja California. A third associate relationship is with the

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[3] The category *Citharichthys* spp. consists of small, damaged specimens of the four common species of this genus present in the CalCOFI region, and is of limited significance in this analysis.

TABLE 3
Geographic Distribution (Percent of Total Abundance) of Recurrent Group Larval Fish Taxa in Eleven Areas of the CalCOFI Sampling Pattern, 1954–60

	CCal		SCal		NBCal			CBCal		SBCal	
Taxon	In	Off	In	Off	In	SVB	Off	In	Off	In	Off
Northern Complex											
LEUROGLOSSUS group											
Bathylagus ochotensis	17	43	8	25	2	1	4	T	0	0	0
Leuroglossus stilbius	12	6	38	22	5	3	5	4	4	T	T
Stenobrachius leucopsarus	20	32	22	24	1	0	2	T	0	0	0
Sebastes spp.	27	7	32	10	6	7	2	5	2	1	T
Merluccius productus	6	11	8	26	6	4	15	4	2	19	T
TARLETONBEANIA group											
Tarletonbeania crenularis	22	57	3	17	T	T	T	0	0	0	0
Icichthys lockingtoni	19	48	3	26	T	T	3	T	T	T	0
CITHARICHTHYS group											
Engraulis mordax	4	2	26	7	9	17	5	17	7	6	T
Citharichthys fragilis	0	0	T	0	2	68	1	17	10	1	T
Citharichthys xanthostigma	T	0	T	T	2	38	4	29	22	2	T
SARDINOPS group											
Sardinops sagax	T	T	10	6	3	24	9	21	4	21	1
Scomber japonicus	0	T	6	3	3	30	9	14	4	29	2
Southern Complex											
SYMBOLOPHORUS group											
Bathylagus wesethi	T	3	T	22	3	3	47	1	18	T	2
Cyclothone spp.	T	1	T	12	T	T	43	2	39	T	T
Diogenichthys atlanticus	T	10	1	27	2	1	44	T	13	0	0
Lampanyctus ritteri	3	16	2	26	2	2	32	T	15	T	1
Symbolophorus californiensis	1	11	1	31	3	1	44	T	6	0	0
TRIPHOTURUS group											
Triphoturus mexicanus	T	T	1	5	5	5	32	7	41	T	3
Protomyctophum crockeri	4	21	3	25	3	2	26	2	13	0	T
Trachurus symmetricus	7	16	2	41	2	1	27	T	4	0	T
CERATOSCOPELUS group											
Ceratoscopelus townsendi	T	2	T	7	T	T	45	T	42	T	2
Lampadena urophaos	0	0	0	5	T	1	38	5	45	T	4
VINCIGUERRIA group											
Vinciguerria lucetia	T	T	T	4	T	T	24	2	38	6	26
Diogenichthys laternatus	0	0	T	T	T	T	7	6	36	12	38
Gonichthys tenuiculus	0	0	T	T	T	T	10	4	42	10	33
Hygophum atratum	0	0	0	0	T	T	3	2	23	11	61
Southern Coastal Complex											
SYNODUS group											
Synodus spp.	0	0	T	0	2	30	T	32	2	32	2
Prionotus spp.	0	0	0	0	0	1	0	64	T	20	T
Ophidion scrippsae	1	T	3	T	T	28	T	42	6	16	T
Symphurus spp.	T	0	3	T	T	23	3	28	24	4	13

Abbreviations:
CCal = Central California (CalCOFI lines 60–77)
SCal = Southern California (CalCOFI lines 80–97)
NBCal = Northern Baja California (CalCOFI lines 100–117)
CBCal = Central Baja California (CalCOFI lines 120–137)
SBCal = Southern Baja California (CalCOFI lines 140–157)

In = Inshore portion of section (usually less than 100 km)
Off = Offshore portion of section (about 100–400 km)
SVB = Bahía Sebastián Viscaíno
T = Trace amounts of larvae (less than 0.5%)

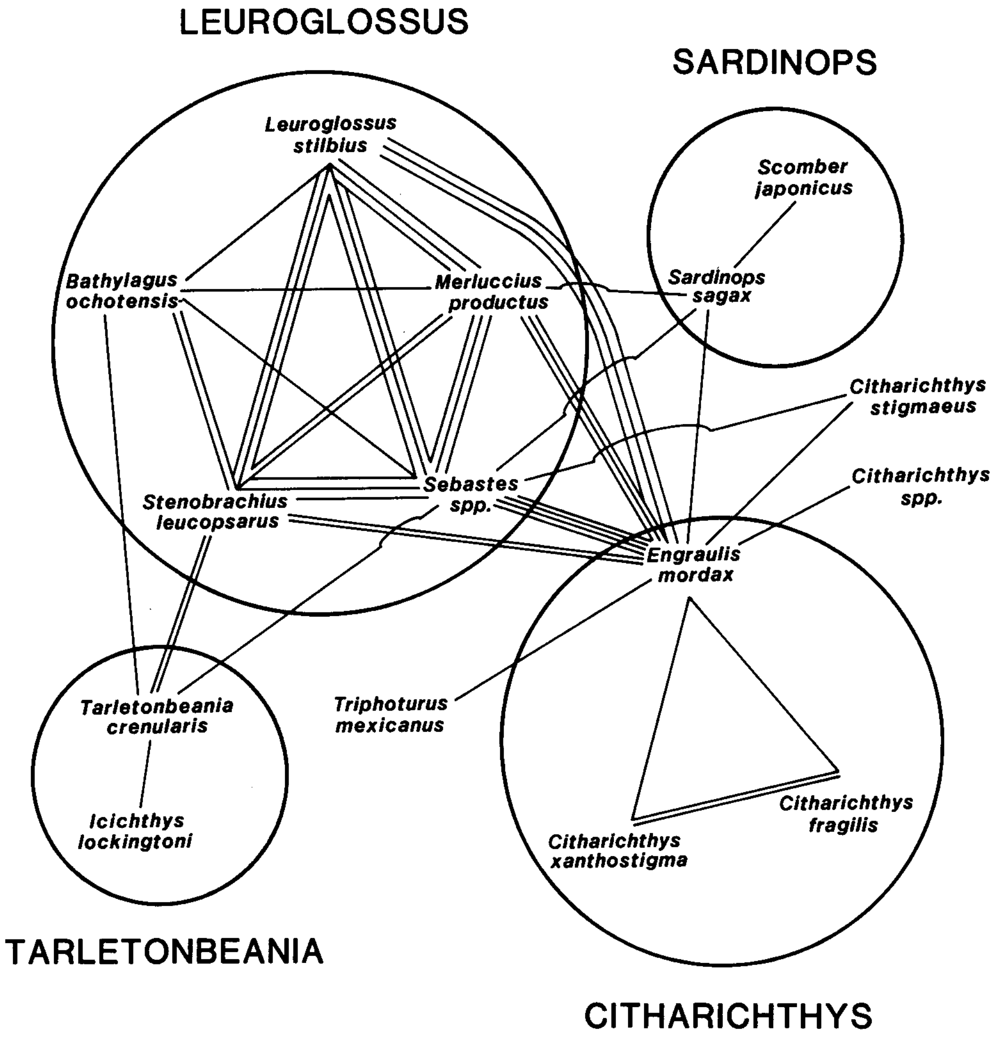

Figure 8. The northern complex of recurrent groups and associates from pooled (1954–60) CalCOFI data. The number of connecting lines indicates the approximate affinity index value. A single line represents an affinity index from 0.30 to 0.39; a double line is 0.40 to 0.49; a triple line is 0.50 to 0.59; and four lines represent an affinity index of 0.60 or greater.

myctophid *Triphoturus mexicanus* in the southern complex. *Engraulis mordax* has a protracted spawning season with a February-March maximum, and the 2 species of *Citharichthys* in the group have bimodal spawning seasons with February and August peaks (Table 3).

The group distribution was centered off coastal northern and central Baja California (Figure 9). Larvae of *E. mordax* were broadly distributed along the coast of the entire survey area, with highest abundance from southern California to central Baja California. Larvae of the two *Citharichthys* species were essentially confined to Baja California, with peak abundance in Bahía Sebastián Viscaíno and the adjoining region to the south.

SARDINOPS recurrent group. The group comprises 2 coastal pelagic species—a clupeid (*Sardinops sagax*) and a scombrid (*Scomber japonicus*). The Pacific sardine, *S. sagax*, is primarily distributed off California and Baja California and in the Gulf of California. In the southern hemisphere another subspecies occurs off Chile and Peru. The chub mackerel, *S. japonicus,* has a worldwide distribution in temperate and tropical waters, particularly in boundary-current regions. *S. sagax* formed associate relationships with *Sebastes* spp. and *M. productus* in the LEUROGLOSSUS group and with *E. mordax* in the CITHARICHTHYS group. *S. sagax* has a protracted, almost year-round spawning season, with apparent peaks in late winter and late summer; *S. japonicus* has a restricted summer spawning season (Table 3).

The SARDINOPS group has a broad coastal distribution from Point Conception, California, to Cabo San Lucas, Baja California (Figure 9). Larvae of the two species had their highest mean abundance in Bahía Sebastián Viscaíno and along the coast south to Cabo San Lucas (Table 3).

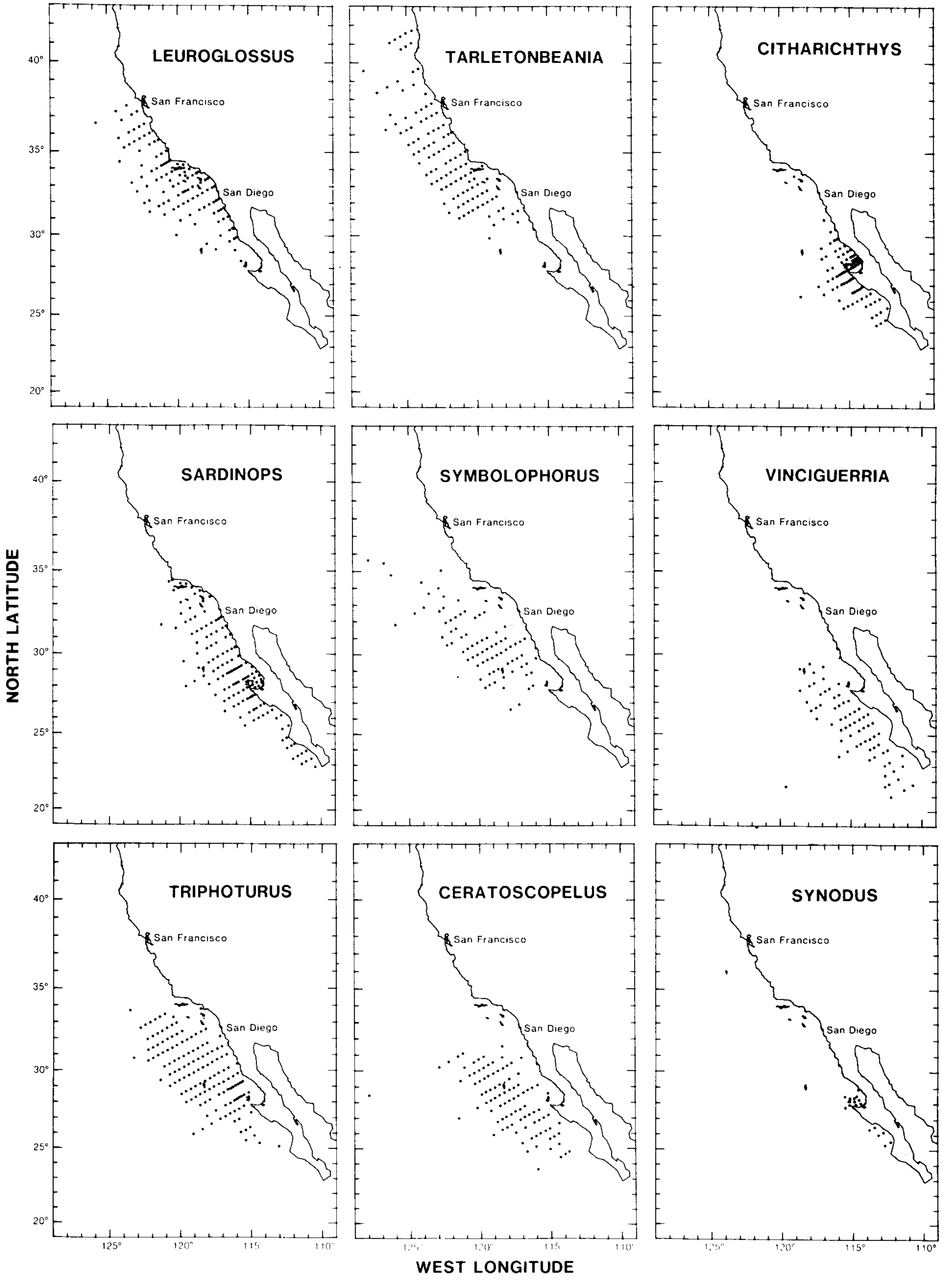

Figure 9. Geographic distribution of recurrent groups of larval fishes in the CalCOFI survey area. The general area for each recurrent group has been approximated by the dots, which represent station positions in which at least one sample in seven years (1954–60) had all recurrent group members present.

Southern Complex

The southern complex was made up of 4 recurrent groups: SYMBOLOPHORUS, TRIPHOTURUS, VINCIGUERRIA, and CERATOSCOPELUS (Figure 10). As in the northern complex, the largest group was connected by shared associates in all the other groups. SYMBOLOPHORUS had 5 member taxa, 7 associates in other recurrent groups, and 1 unique associate. VINCIGUERRIA had 4 member taxa, 6 associates in other recurrent groups, and 2 unique associates. TRIPHOTURUS had 3 member taxa, 8 associates in other groups, and 2 unique associates. CERATOSCOPELUS had 2 members, 4 associates in other groups, and no unique associates.

SYMBOLOPHORUS recurrent group. The group comprises 5 mesopelagic taxa—an argentinoid smelt (*Bathylagus wesethi*), 3 vertically migrating myctophids (*Diogenichthys atlanticus, Symbolophorus californiensis, Lampanyctus ritteri*), and the stomiiform genus *Cyclothone* (Table 2). *B. wesethi* and *S. californiensis* are transitional species characteristic of the California Current region, with distributions extending from the subarctic boundary to central Baja California. *L. ritteri* has a broader subarctic-transitional distribution that includes the Gulf of Alaska. *D. atlanticus* is a warm-water cosmopolite that enters the California Current region off southern California and northern Baja California. Seven species of *Cyclothone* are known from the California Current region. Adult samples are dominated by 2 species, *C. signata* and *C. acclinidens*, and preliminary identifications indicate that this is also true for ichthyoplankton samples. Both species have primarily equatorial distributions in the Pacific; these extend northeastward into the California Current region. Members of the SYMBOLOPHORUS group express a strong spawning seasonality, with *B. wesethi, L. ritteri*, and *S. californiensis* peaking in May and *Cyclothone* in August. *D. atlanticus* is bimodal, with peaks in May and September-October.

Group members form a strong affinity network with all other recurrent groups in the southern complex, which includes 7 groups and 2 individual associates (Figure 10). *L. ritteri* and *B. wesethi* were associates of the mesopelagic genus *Melamphaes*, which was also associated with *Trachurus symmetricus* in the TRIPHOTURUS group. Two species are common in the California Current region: *M. parvus*, which is restricted to this region, and *M. lugubris*, a subarctic-transitional form that ranges westward across the North Pacific. Spawning in *Melamphaes* is highly seasonal, with a peak in May. Paralepididae, a family of mesopelagic predators, was an associate with *B. wesethi*. One paralepidid species, *Lestidiops ringens*, predominates in the adult and larval samples from the California Current region.

The SYMBOLOPHORUS group had an offshore distribution in the central portion of the survey area, impinging on the coast of northern Baja California (Figure 9). Except for *L. ritteri*, all species had their highest larval abundances in the southern California-northern Baja California offshore region (Table 3). *L. ritteri* larvae were slightly more abundant in the northern Baja California offshore region (Table 3).

VINCIGUERRIA recurrent group. This group comprises 4 mesopelagic vertical migrators—the stomiiform lightfish *Vinciguerria lucetia* and 3 myctophine lanternfishes, *Diogenichthys laternatus, Gonichthys tenuiculus*, and *Hygophum atratum* (Table 2). All are eastern tropical Pacific species that range northward to the Gulf of California and the outer coast of Baja California. All have extended spawning seasons: *V. lucetia* peaks in August; *D. laternatus* and *H. atratum* have winter and summer maxima; and *G. tenuiculus* peaks in February (Table 2).

Group members form a strong affinity network with all other groups in the southern complex, including 5 group associates and 3 individual associates (Figure 10). *V. lucetia* and *D. laternatus* are associates of the myctophid genus *Lampanyctus*, which includes at least a dozen species from the California Current region; the unidentified Myctophidae is an associate shared with *T. mexicanus* of the TRIPHOTURUS group. Unidentified larval Myctophidae in our collections are either small or disintegrated specimens that represent a spectrum of the 40 or more species reported from this region. *Stomias atriventer*, a mesopelagic predator, is a unique associate of *V. lucetia*. *S. atriventer* is found from central California to mid-Mexico and has an extended spawning season with a winter-spring maximum.

The VINCIGUERRIA group is distributed principally in the offshore central Baja California and inshore-offshore southern Baja California regions (Figure 9). Only *V. lucetia* occurs in appreciable numbers in offshore northern Baja California waters (Table 3).

TRIPHOTURUS recurrent group. This group comprises 2 mesopelagic lanternfishes (*Protomyctophum crockeri* and *Triphoturus mexicanus*) and

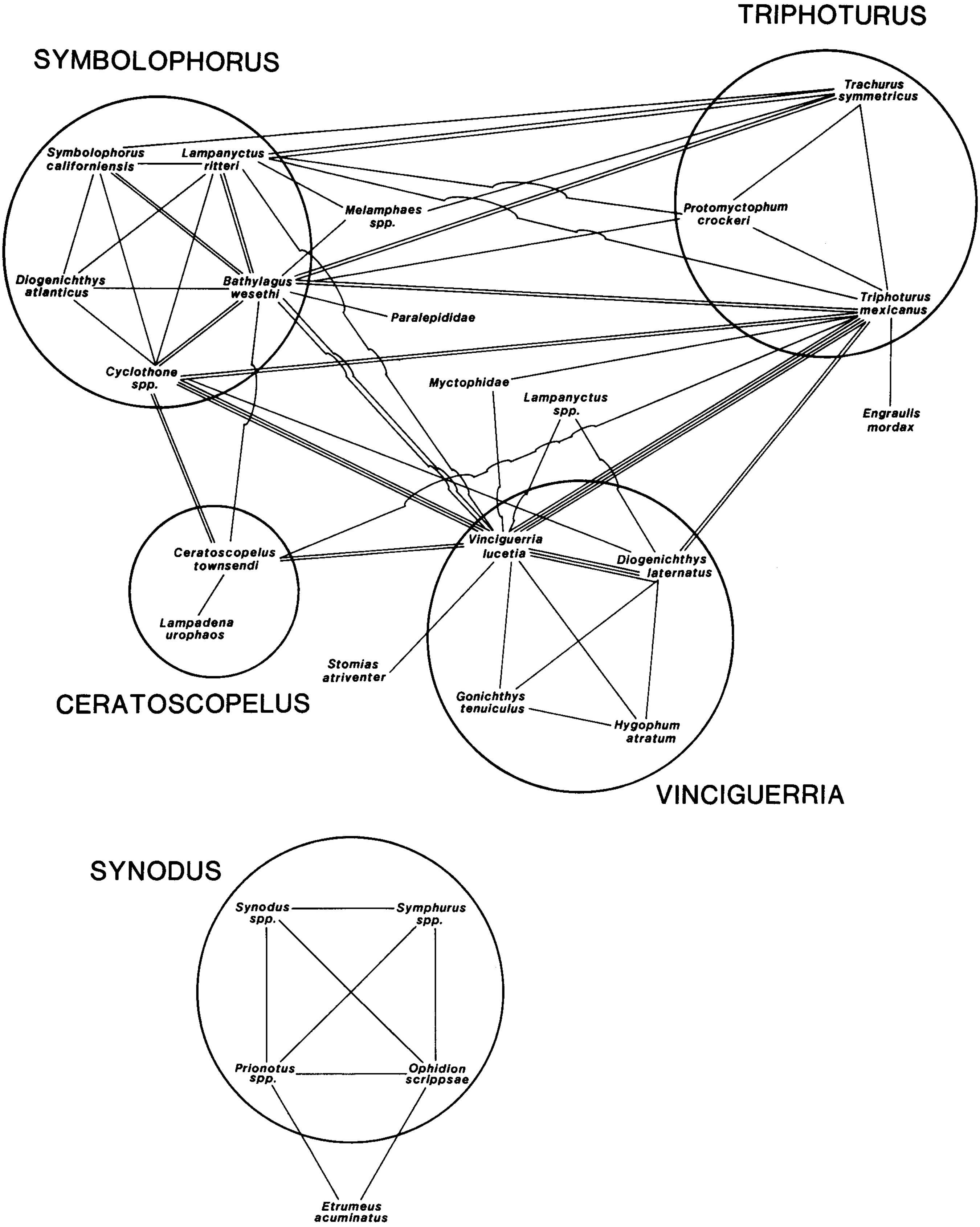

Figure 10. The southern complex and southern coastal complex of recurrent groups and associates from pooled (1954–60) CalCOFI data.

an epipelagic carangid (*Trachurus symmetricus*). *P. crockeri* is a transitional species ranging from central Baja California northward to the coast of Washington and westward to Japan. *T. mexicanus* occurs between 38° and 20°N in the California Current region and in the Gulf of California, with disjunct populations across the tropics (Hulley 1986). The jack mackerel, *T. symmetricus,* occurs from the Gulf of Alaska southward to Cabo San Lucas, Baja California, and has a principal distribution from southern California to central Baja California. Older year classes are noted for their offshore distribution, which can extend 2,400 kilometers seaward. *P. crockeri* has a bimodal spawning pattern with peaks in May and November; *T. mexicanus* peaks in August; and *T. symmetricus* in May–June (Table 2).

The TRIPHOTURUS group was strongly connected with the 2 larger recurrent groups of the southern complex and weakly connected to the CERATOSCOPELUS group (Figure 10). Associations were formed with 7 members of these groups and with 2 individual taxa. The association between *T. mexicanus* and *E. mordax* linked the northern and southern complexes (Figures 6 and 10).

The group had a broad inshore-offshore distribution in the survey area, extending from central California to central Baja California; this reflected the broad distributions of larvae of these species (Figure 9; Table 3).

CERATOSCOPELUS recurrent group. This group comprises 2 vertically migrating myctophids, *Ceratoscopelus townsendi* and *Lampadena urophaos. C. townsendi* is a resident of the California Current region, between 45° and 20°N latitude; *L. urophaos* has a more subtropical distribution that extends westward to Hawaii. Both are highly seasonal spawners, with summer maxima (Table 2).

Affinities exist with all other groups in the southern complex, although only weakly with TRIPHOTURUS (Figure 10). The group's distribution was centered off northern and central Baja California and distinctly offshore, reflecting the areal abundance patterns of both species (Figure 9; Table 3).

Southern Shelf Complex

Four shallow demersal taxa from 4 separate orders form the SYNODUS group—the myctophiform genus *Synodus,* the scorpaeniform genus *Prionotus,* the pleuronectiform genus *Symphurus,* and the ophidiiform species, *Ophidion scrippsae* (Figure 6). In our survey area adult collections of the 3 generic taxa are dominated by 3 species: *Synodus lucioceps, Prionotus stephanophrys,* and *Symphurus atricauda. S. lucioceps* and *O. scrippsae* are temperate-subtropical species ranging from central California to the Gulf of California. *P. stephanophrys* has a broad distribution that extends from the Columbia River (rarely north of Mexico) to Chile, and *S. atricauda* ranges from Oregon (rarely north of southern California) to Panama. The taxa have well-defined summer-fall spawning seasons, peaking in August-September. Spawning in *Synodus* spp. appears to be bimodal, with peaks in September and December (Table 2).

Although this group borders on all groups of the southern complex, no associate affinities were formed with any other recurrent group; the group had one unique associate, *Etrumeus acuminatus,* a coastal pelagic clupeid (Figure 6). This species ranges from central California to Chile and spawns during the summer.

Coincident samples for this group were found only in the widest continental shelf region in the survey area, Bahía Sebastián Viscaíno and southerly along the Punta Abreojos-Cabo San Lázaro Bight (Figure 9). Mean larval abundances were high in both these regions, except for *Prionotus,* which had a low abundance in Bahía Sebastián Viscaíno (Table 3).

The application of the REGROUP procedure to the combined 1954–60 data set at three higher affinity levels (0.4, 0.5, 0.6) provided a hierarchical view of the relationships of the principal larval fish taxa. At a critical level of 0.4, two large groups representing the northern and southern complexes were formed. The northern group included *E. mordax, L. stilbius, S. leucopsarus, M. productus,* and *Sebastes* spp., with *B. ochotensis* as an associate. The southern group consisted of *B. wesethi, Cyclothone* spp., *V. lucetia,* and *T. mexicanus,* with *C. townsendi, D. laternatus,* and *S. californiensis* as associates. This group was linked to a group pair, *L. ritteri-T. symmetricus,* by 3 out of 8 possible intergroup pairings. *Citharichthys fragilis* and *C. xanthostigma* formed an isolated group pair.

At a critical affinity index value of 0.5, the groups were reduced and fragmented. The northern complex consisted of 2 small groups—*E. mordax-L. stilbius-M. productus* and *S. leucopsarus-Sebastes* spp.—linked by 4 of 6 possible intergroup pairings. The southern complex was represented by a group pair—*V. lucetia-T. mexicanus*—with *Cyclothone* spp. and *D. laternatus* as associates. At a critical level of 0.6 only 2 group pairs remained: *E. mordax-Sebastes* spp. and *V. lucetia-T. mexi-*

canus, representing the northern and southern complexes, respectively.

INTERANNUAL VARIATION IN RECURRENT GROUPS

A total of 76 taxa were either group members or associates during the individual years over the seven-year period (Figures 6 and 7). The numbers of recurrent groups ranged from 8 in 1955 to 14 in 1956 and 1960. Number of taxa per group ranged from 2–4 in 1956 to 2–7 in 1954, 1955, 1957, and 1958. The average number of taxa per group was lowest in 1955 (2.4 taxa/group) and highest in 1957 (3.5/group). The total number of taxa contributing to recurrent groups ranged from 24 in 1955 to 39 in 1957. Associate taxa ranged from 8 in 1956 and 1960 to 14 in 1957. There were 2 shared associate taxa (those which form associate links with 2 or more groups) in 1957 and 1 in each of the other years.

There was considerable rearrangement of recurrent groups and group components during the seven-year period; however, the northern and southern complexes, as described in the preceding analysis of the composite seven-year data set, were generally conserved (Figures 6 and 7). In four of the years, group members of one complex became group members of another complex. In 1954 the southern complex species, *Triphoturus mexicanus,* formed a group with 5 northern complex taxa, and in 1958 another southern complex species, *Protomyctophum crockeri,* combined with a similar group of 6 northern taxa. In 1960, *Engraulis mordax* formed a group with 2 southern complex species, *P. crockeri* and *Lampanyctus ritteri.* In 1957 the northern complex and southern coastal complexes were linked by the recurrent group pairing of *Scomber japonicus* and the paralichthyid flatfish, *Etropus* spp. (Figures 6 and 7).

The complexes were also linked when significant affinity indices were formed between northern and southern taxa. In 1954 the high proportion (0.29) of associate linkages between the largest northern and southern groups resulted from the inclusion of *T. mexicanus* in the northern group (Figure 6). This species was an associate of all taxa except Paralepididae in the 7-member southern group. Other pairs contributing to this intergroup connection were *Sebastes* spp.-*T. symmetricus, M. productus-T. symmetricus, B. wesethi-M. productus, S. sagax-L. ritteri,* and *S. sagax-T. symmetricus.* The inclusion of *T. mexicanus* in the northern group was also responsible for the other northern-southern linkages, since it was an associate of *P. crockeri* and formed associate relationships with each member of the group formed by *V. lucetia, S. atriventer,* and *D. laternatus* (Figure 6). In 1955, *T. symmetricus* in the 7-member southern group was largely responsible for the north-south linkage, since it formed associate relationships with *S. sagax, L. stilbius,* and *Sebastes* spp. of the 5-member northern group. The northern species *L. stilbius* also formed associations with *T. mexicanus* and *P. crockeri* of the southern group (Figure 6).

In 1956 the northern-southern connections were keyed to the group formed by the sanddabs *C. stigmaeus* and *C. xanthostigma,* and also involved the southern coastal complex. The two species formed associate relationships with *T. mexicanus* in the *T. mexicanus-B. wesethi* group and with *Symphurus* spp. in the 3-member southern coastal group. Another northern-southern linkage was between *T. symmetricus* of the *T. symmetricus-Tetragonurus cuvieri* group and *M. productus* of the *E. mordax-M. productus-Sebastes* spp. group (Figure 6).

In 1957, northern-southern linkages also involved a group predominated by sanddab taxa (*Citharichthys* spp.-*C. fragilis-C. xanthostigma-S. sagax*) and a 5-member southern coastal group (Figure 7). *Symphurus* spp. of the latter group formed associate ties with all but *C. fragilis* in the northern group, and *O. scrippsae* of the southern group was an associate of *Citharichthys* spp. The shared associate, *Synodus* spp., further linked the two groups; it had significant affinities with all but *E. acuminatus* in the southern coastal group and also with *S. sagax* and *C. xanthostigma* in the northern group. The intercomplex group formed by *Scomber japonicus* and *Etropus* spp. was strongly linked with the large southern coastal group; *S. japonicus* was an associate of *E. acuminatus, O. scrippsae,* and *Symphurus* spp.; *Etropus* spp. had associate ties with the latter two. The *S. japonicus-Etropus* spp. group was connected to the sardine-sanddab group through the pairings of *S. japonicus* with *S. sagax* and *Citharichthys* spp. The sardine-sanddab group was linked to two other southern groups through intergroup associateships involving *C. xanthostigma.* This species was an associate of *T. mexicanus* in a 3-member southern group and also with *D. laternatus* in a 5-member group. The remaining northern-southern link was formed between a 5-member northern group and a 3-member southern group through the associate relationship of *E. mordax* and *T. mexicanus* (Figure 7).

In 1958 the northern and southern complexes were linked by associate relationships formed between a 7-member northern group and a 5-member southern group (Figure 7). The relatively high proportion (0.34) of intergroup associates resulted largely from the inclusion of the southern complex species *P. crockeri* in the northern group. It had significant affinities with all taxa except *T. mexicanus* of the southern group. Also, *T. symmetricus* of the southern group formed associate relationships with *E. mordax, S. leucopsarus,* and *M. productus* of the northern group. The myctophid *L. ritteri* also had associate links with these 3 species and with *B. ochotensis*. The two groups were further linked by the associate pairing of *E. mordax* and *T. mexicanus* (Figure 7).

In 1959 the northern and southern complexes were connected by the single associate pairing of *E. mordax* and *T. mexicanus;* however, in 1960 a group formed by the northern species *E. mordax* and two southern complex species (*L. ritteri* and *P. crockeri*) was responsible for extensive intercomplex linkage (Figure 7). *E. mordax* formed associate relationships with *Sebastes* spp., *S. leucopsarus, L. stilbius, M. productus, S. sagax,* and *C. fragilis* from 3 northern complex groups and with a 3-member southern group through an associate tie with *T. mexicanus*. The latter species also had a significant affinity with *P. crockeri*. The pairing of *L. ritteri* and *T. symmetricus* further linked the 3-member southern group and the *E. mordax-L. ritteri-P. crockeri* group. Other intercomplex links were through the associate pairs *L. stilbius-P. crockeri* and *L. stilbius-T. mexicanus*. Connections between two northern complex groups and two southern coastal complex groups were formed by associate pairings of *C. xanthostigma-Symphurus* spp. and *S. sagax-E. acuminatus*.

Interannual variability of the constituents and structure of the recurrent groups was more variable than that found in the complexes. In the northern complex, recurrent group analysis of the combined 1954–60 data (Figure 6) produced 4 groups. The largest group contained *B. ochotensis, L. stilbius, S. leucopsarus, M. productus,* and *Sebastes* spp. *Engraulis mordax* formed a group with *C. fragilis* and *C. xanthostigma; S. sagax* formed a group with *S. japonicus;* and *T. crenularis* formed a group pair with *I. lockingtoni* (Figure 6). The group diagrams for individual years showed that *E. mordax* and *S. sagax* were closely allied with the 5 members of the LEUROGLOSSUS group and that these 7 taxa were present in each year. In most of the years these taxa formed one or two groups with one or more of the taxa arranged as associates. *T. crenularis* was either included in one of these groups or was absent from the diagram. An exception was in 1959 when it paired with *I. lockingtoni* to form a group, as it did in the combined data set. The sanddabs *C. fragilis* and *C. xanthostigma* were retained as a group for most of the years. Exceptions were in 1956 when they separated to become members of two other flatfish groups and in 1957 when they combined with *S. sagax* and *Citharichthys* spp. to form a 4-member group (Figures 6 and 7).

The 7 principal taxa of the northern complex co-occurred consistently during the seven-year period. The following pairs had significant affinity indices (>0.30) for each of the seven years as well as for the combined data set: *S. sagax-E. mordax, E. mordax-L. stilbius, E. mordax-Sebastes* spp., *E. mordax-M. productus, B. ochotensis-L. stilbius, B. ochotensis-S. leucopsarus, L. stilbius-S. leucopsarus, L. stilbius-Sebastes* spp., *L. stilbius-M. productus, S. leucopsarus-Sebastes* spp., *Sebastes* spp.-*M. productus*. Two other pairs, *E. mordax-S. leucopsarus* and *S. leucopsarus-M. productus,* had significant affinity indices in all but one year, when the index fell just short of 0.30.

The high degree of co-occurrence in the 13 pairs listed above was shown by their high affinity indices. For the seven-year series 71% of the indices were above 0.40, 47% were above 0.50, and 8% exceeded 0.60. Affinity indices exceeded 0.40 for each of the seven years in *E. mordax-L. stilbius, E. mordax-M. productus, L. stilbius-S. leucopsarus, L. stilbius-Sebastes* spp., *L. stilbius-M. productus, S. leucopsarus-Sebastes* spp., and *Sebastes* spp.-*M. productus*. In *E. mordax-Sebastes* spp. the index exceeded 0.50 for all years. The other pair of the northern complex that had significant affinity indices for all seven years was *C. fragilis-C. xanthostigma*.

Interannual variability in recurrent group structure was greater in the southern complex than in the northern complex. Recurrent group analysis of the combined seven-year data set produced 5 groups from 18 midwater taxa and *T. symmetricus*. Five other midwater taxa were associates of these groups. Most of these taxa were present in recurrent group analyses of individual years, although group composition and arrangement were highly variable (Figures 6 and 7). In 1954, 1955, and 1959 there were one large group of 5–7 taxa and two smaller groups of 2–3 taxa. In 1957 there were two large groups of 5 and 7 taxa and a 3-member group. The largest group in 1960 contained 4 taxa with connecting links to 4 smaller groups. Group structure in 1956 was the most divergent and was limited to 5 paired taxa; moreover, only 11 of the 19 southern complex taxa from the 1954–60 combined data set contributed to these groups (Figure 6).

Only the following 6 southern complex pairs had significant indices (> 0.30) for all years: *B. wesethi-T. mexicanus, Cyclothone* spp.-*V. lucetia, Cyclothone* spp.-*C. townsendi, V. lucetia-D. laternatus, V. lucetia-T. mexicanus,* and *L. ritteri-T. symmetricus.* Of these pairs, only *V. lucetia-D. laternatus* had affinity indices higher than 0.40 for all years. Seven other pairs had affinity indices greater than 0.30 for six of the seven years (*B. wesethi-V. lucetia, B. wesethi-S. californiensis, Cyclothone* spp.-*T. mexicanus, V. lucetia-Lampanyctus* spp., *D. laternatus-T. mexicanus, L. ritteri-P. crockeri,* and *L. ritteri-S. californiensis*). In all but one of these pairs the nonsignificant affinity index occurred in 1956. Low affinity indices occurred throughout the southern complex in 1956; in a list of 67 taxon pairs, more than half had their lowest index in 1956. Of the mixed northern-southern complex pairs only *E. mordax-T. mexicanus* had consistently high affinity indices, ranging from 0.26 to 0.50 for the seven years.

The southern coastal complex was highly variable in the structure and composition of its recurrent groups and associate taxa. In the combined seven-year data set, 4 demersal taxa from 4 different orders formed an isolated group with one associate from a fifth order. Two family taxa, Serranidae and Carangidae (all jacks except *Trachurus* and *Seriola*) formed a second isolated group (Figure 6). Four of the taxa from the large group (*Synodus* spp., *Prionotus* spp., *Ophidion scrippsae,* and *Etrumeus acuminatus*) were persistent annually, occurring as group members or associates in six of the seven years (Figures 6 and 7). The fifth taxon, *Symphurus* spp., was present in only four of the seven years. Another key taxon, Ophidiiformes (all cusk-eels except *O. scrippsae* and *Chilara taylori,* and all brotulas except *Brosmophysis marginata*), was present as a group member or associate in five of the seven years. The Carangidae-Serranidae group was less prominent. These taxa occurred as a group in 1959 and 1960 and in separate recurrent groups in 1956. The thread herrings, *Opisthonema* spp., occurred in recurrent groups in four of the seven years. Gerreidae, the mojarras, appeared in four of the seven years: as a group member with *Opisthonema* spp. in 1954 and 1958 and as an associate in two other years. Pomacentridae (damselfishes other than *Chromis*), *Auxis* spp., and *Syacium ovale* occurred as group members or associates in three of the seven years, and 19 other taxa occurred once or twice during the seven-year period.

Group structure changed markedly from year to year. In 1954, 9 taxa were arranged in 4 groups with one of these (*E. acuminatus-Synodus* spp.) connected to the southern complex through an associate linkage between *Synodus* spp. and *Vinciguerria lucetia* (Figure 8). Incidence of southern coastal taxa was anomalously low in 1955, and they did not appear in the recurrent group analysis for that year. The isolated pair, Sciaenidae-*Pleuronichthys verticalis,* had a more northerly coastal distribution. In 1956, 13 taxa formed 5 highly interconnected groups (Figure 6). One of the 3 associate taxa, *O. scrippsae,* was shared by 2 of the groups, and the *Synodus-Scorpaena-Symphurus* group was linked to the northern complex through a *Symphurus* spp.-*Citharichthys xanthostigma* associateship. In 1957, 5 of the key southern coastal taxa formed a group linked to 5 associates and a 2-member group (Figure 7). The extensive associate linkages of this group to the northern complex were described earlier in this section. In 1958, 8 taxa formed 4 group pairs; 3 of these were interconnected, but there was no associate linkage with the northern or southern complexes. Similarly, in 1959, 12 species formed a cluster of 4 linked groups and an isolated group, with no associate connections to the northern or southern complexes (Figure 7). In 1960, 12 species formed a cluster of 4 interconnected groups and one isolated pair (Figure 7). Two groups within the cluster were connected to the northern complex through associate pairings (*C. xanthostigma-Symphurus* spp., *S. sagax-E. acuminatus*) with members of two northern complex groups.

The highly variable nature of incidence and co-occurrence of southern coastal taxa was shown in the list of annual affinity indices for selected pairs. Only 3 pairs had significant affinity indices for four of the seven years: *E. acuminatus-Synodus* spp., *Prionotus* spp.-Carangidae, and *Prionotus* spp.-*O. scrippsae.* Ranges of indices for the seven-year period were wide, and there was no obvious interannual trend except that values for 1955 were either zero or extremely low for selected pairs.

ENVIRONMENTAL CHANGE AND THE DISTRIBUTION OF RECURRENT GROUPS

The dynamic environmental changes that occurred during 1954–60 in the CalCOFI region markedly affected the distribution of larval fishes. These geographic shifts, in concert with changes in the amount and seasonal extent of spawning, re-

TABLE 4
Percent Change of Incidence of Taxa in the Central Part of the CalCOFI Survey Area between 1955–56 and 1958–59

	SCal		NBCal		
	In	Off	In	SVB	Off
Northern complex					
LEUROGLOSSUS group					
Bathylagus ochotensis	-8	-16	-2	-2	-4
Leuroglossus stilbius	-16	-24	-33	-20	-21
Stenobrachius leucopsarus	-23	-20	-18	0	-9
Sebastes spp.	-15	-28	-17	-22	-14
Merluccius productus	11	-3	-25	-28	-25
TARLETONBEANIA group					
Tarletonbeania crenularis	-14	-28	-4	0	-3
Icichthys lockingtoni	-4	-12	-4	-1	-3
CITHARICHTHYS group					
Engraulis mordax	2	12	-4	-9	-4
Citharichthys fragilis	0	0	-4	-3	-1
Citharichthys xanthostigma	0	1	-8	-15	-1
SARDINOPS group					
Sardinops sagax	17	-7	-9	-3	-17
Scomber japonicus	6	1	2	-4	-4
Southern complex					
SYMBOLOPHORUS group					
Bathylagus wesethi	3	19	10	-3	-6
Cyclothone spp.	2	23	6	7	24
Diogenichthys atlanticus	0	0	6	15	17
Lampanyctus ritteri	4	23	-2	-1	-16
Symbolophorus californiensis	3	22	2	0	-2
TRIPHOTURUS group					
Triphoturus mexicanus	15	30	23	23	17
Protomyctophum crockeri	0	4	2	-2	-17
Trachurus symmetricus	5	7	-3	-14	-26
CERATOSCOPELUS group					
Ceratoscopelus townsendi	1	10	7	4	23
Lampadena urophaos	*	2	1	2	8
VINCIGUERRIA group					
Vinciguerria lucetia	9	52	37	29	54
Diogenichthys laternatus	0	0	6	15	17
Gonichthys tenuiculus	*	0	1	3	11
Hygophum atratum	*	*	0	2	5
Southern coastal complex					
SYNODUS group					
Synodus spp.	*	*	0	-5	0
Prionotus spp.	*	*	*	2	*
Ophidion scrippsae	0	*	1	3	0
Symphurus spp.	2	0	1	-1	0

Abbreviations:
SCal = Southern California (CalCOFI lines 80–97)
NBCal = Northern Baja California (CalCOFI lines 100–117)
In = Inshore (usually <100 km)
Off = Offshore (about 100–400 km)
SVB = Bahía Sebastián Viscaíno
* = No specimens found in region in any year

sulted in changes in the structure and composition of recurrent groups. Distributional shifts for recurrent group taxa are shown in Table 4, which lists the percent change in incidence of larvae between 1955–56 and 1958–59 in five subareas of the CalCOFI survey region. These areas off southern California (SCal) and northern Baja California (NBCal) had the most consistent and equitable monthly sampling effort and greatest environmental effect during the period.

In general, taxa of the northern complex declined, and their southern distributional limits contracted northward during El Niño, while taxa of the southern complex showed a relative increase and a concomitant northward expansion of their northern distributional limits. Members of the LEUROGLOSSUS group, with the exception of *M. productus,* decreased in all five subareas during this period (Table 4). Of the three midwater species, *B. ochotensis* had the smallest decline, with a maximum decrease of 16% in the SCal offshore area. *L. stilbius* decreased in all subareas, and *S. leucopsarus* showed a 43% decrease off SCal. *Sebastes* spp. decreased in all subareas, most notably in the SCal offshore area. *M. productus* decreased consistently in all subareas of NBCal, only slightly in offshore SCal, and showed a substantial increase in the SCal inshore area.

The two taxa of the TARLETONBEANIA group were poorly represented off NBCal and showed only slight decreases there during El Niño (Table 4). They were well represented in the SCal area, particularly offshore, and the decrease there reflected a northward contraction of spawning in these subarctic-transitional species during this period.

Members of the CITHARICHTHYS group decreased in all subareas off NBCal (Table 4). This is particularly noteworthy for the two warm-water sanddab species, whose distributions are concentrated in Bahía Sebastián Viscaíno (SVB) and more southerly shelf areas. *E. mordax* also decreased off NBCal but increased off SCal, particularly in the offshore region, reflecting a northward and seaward expansion of spawning distribution during El Niño.

The two species of the SARDINOPS group have coastal distributions that peak in the SVB area. Both decreased slightly in this area during El Niño (Table 4). *S. sagax* decreased in other areas, particularly in offshore NBCal, but showed a distinct increase in the SCal inshore area. The decrease of *S. sagax* in the four subareas could be attributed to the general decline of the stock during this period, as well as to El Niño effects. *S. japonicus* also increased slightly in SCal and inshore NBCal.

In the southern complex, the members of the SYMBOLOPHORUS group are midwater taxa that occur principally in offshore areas (Table 3). The two warm-water cosmopolite taxa, *D. atlanticus* and *Cyclothone* spp., increased markedly in the NBCal area, particularly offshore, and the latter taxon showed a strong increase in the SCal offshore region; this indicates a shoreward and northerly expansion of its spawning range (Table 4). The two transitional species *B. wesethi* and *S. californiensis* increased substantially in the SCal offshore area, increased to a lesser degree in the SCal and NBCal inshore areas, and decreased slightly in the NBCal offshore area. *L. ritteri* has a broad subarctic-transitional distribution; it increased in the SCal area, particularly offshore, and decreased off NBCal.

In the TRIPHOTURUS group, the warm-water myctophid *T. mexicanus* occurs relatively infrequently north of Baja California. During El Niño it expanded northward throughout the Southern California Bight, where its incidence increased by 15%–30%; it also increased substantially in the other four areas (Table 4). The two transitional species *P. crockeri* and *T. symmetricus* had less striking changes during El Niño. *T. symmetricus* increased slightly off SCal, but decreased off NBCal, particularly in the offshore region. *P. crockeri* experienced little change off SCal and inshore areas of NBCal, but decreased in the NBCal offshore area. The two members of the CERATOSCOPELUS group are myctophids with offshore distributions, centered off Baja California. During El Niño their incidence increased markedly in the NBCal offshore area, reflecting a shoreward and slight northerly expansion of their spawning distribution (Table 4).

In the VINCIGUERRIA group, *V. lucetia* had the greatest distributional change of all recurrent group taxa during El Niño. It is an abundant eastern tropical Pacific mesopelagic with a usual northern limit of about CalCOFI line 100 (Figure 1) off Ensenada, Baja California. During El Niño it expanded to north of Point Conception, California, showing increases greater than 50% in the offshore areas of SCal and NBCal (Table 4). Although it increased substantially in the inshore areas of NBCal, it increased only slightly in the inshore area of SCal and appeared to be excluded from that area. The other three species are eastern tropical Pacific myctophids with more southerly northern limits; *D. laternus* occurs infrequently north of Isla Guadalupe, Mexico, and *H. atratum* and *G. tenuiculus* are rarely found north of Punta Eugenia. During El Niño, *D. laternatus* and *G. tenuiculus* increased off NBCal, largely in the offshore area (Table 4). *H. atratum* increased in SVB and in the NBCal offshore area.

Larvae of the SYNODUS group in the southern coastal complex occurred in the shelf regions of SVB and the Punta Abreojos-Cabo San Lázaro Bight to the south. *Symphurus* spp., *O. scrippsae*, and *Synodus* spp. occurred in small numbers on the SCal shelf; only *Symphurus* spp. showed a slight increase in this area during El Niño (Table 4). *Prionotus* spp. and *O. scrippsae* increased slightly in SVB during this period, while *Synodus* spp. and *Symphurus* spp. decreased.

The fine-scale association of selected larval fish taxa and their environment was examined by identifying the temperature-salinity (T-S) characteristics correlated with the presence and absence of these species in a region of mixed water types. The study area for two subarctic-transitional species, *S. leucopsaris* and *T. crenularis*, was bounded by CalCOFI lines 83 to 100, and the area for the two eastern tropical Pacific species, *V. lucetia* and *D. laternatus*, was bounded by lines 100 to 120.

The T-S profiles (Figure 11) represent stations that were either positive or negative for the four species during a period of highly variable oceanographic conditions (1954–60, excluding 1957). These profiles showed a positive correlation between the presence of larvae of the two northern species and cooler, less saline water. Presence of the southern species was correlated with warmer, more saline water in their area. The depth at which the "positive" and "negative" curves were separated was about 150 m, except for *D. laternatus*, where the curves were separated throughout the water column (Figure 11).

The differences in temperature-salinity characteristics associated with the presence or absence of these species reflect the differences in oceanographic conditions before and after the onset of El Niño in 1957. More than two-thirds of all the samples with positive counts for the two subarctic species (*S. leucopsarus* and *T. crenularis*) were taken during 1954–56. Conversely, more than two-thirds of the samples with zero counts for these species were taken in 1958–60.

In the southern area, more than seven-eighths of the samples with positive counts for *V. lucetia* were taken in 1958–60, whereas three-fourths of the samples with zero counts were taken in 1954–56. The data for the other subtropical species, *D. later-*

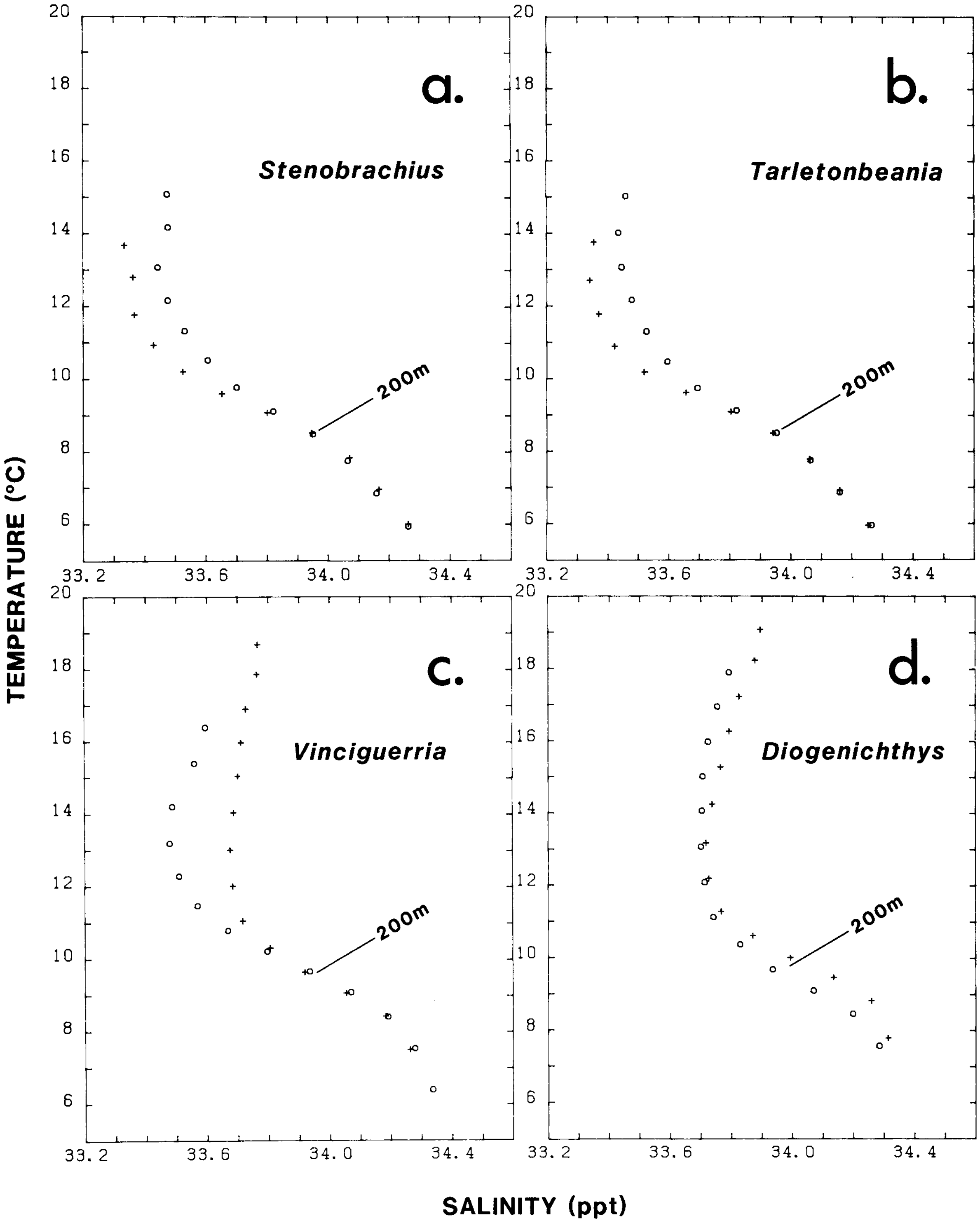

Figure 11. *a.* Mean temperature-salinity curves depicting differences in watermass characteristics associated with the absence (○) or presence (+) of *Stenobrachius leucopsarus* larvae in CalCOFI net tows. The plots represent combined data from 16 offshore stations on lines 83–100 (see Figure 1) occupied during 1954–60. *b.* Same as *a* for *Tarletonbeania crenularis* larvae. The data represented in the figure are from 14 offshore stations on lines 83–100. *c.* Same as *a*, for *Vinciguerria lucetia* larvae. The data represented in this figure are from 21 offshore stations on lines 100–120. *d.* Same as *a*, for *Diogenichthys laternatus* larvae. The data represented in this figure are from 17 offshore stations on lines 103–120.

natus, show less distinction between the pre- and post-1957 periods. Although four-fifths of the samples with positive counts were taken in 1958–60, more than two-thirds of those with zero counts were also taken in that period. Consequently, the T-S curves for both positive and zero counts of *D. laternatus* reflect mainly 1958–60 conditions. The curious separation of these curves below 200 meters is an unexplained feature.

DISCUSSION

The CalCOFI surveys were designed to encompass the areal and temporal limits of the Pacific sardine and its principal ecological associates. The fact that this was accomplished by a monthly sampling program sensitive to mesoscale oceanographic and biological events makes this time series unique. The seven-year period from 1954 to 1960, analyzed in this paper, was of special interest because it contained a major El Niño that was immediately preceded by an anomalously cold period. The recent efforts to reidentify much of the larval fish material from these years and establish a computer data base for it gave us the opportunity to study the structure of fish assemblages in the California Current region during a period of great environmental change.

Recurrent group analysis establishes the co-occurrence of taxa in time and space. When such analysis is applied to an oceanic plankton survey like the CalCOFI sampling program, co-occurrences of larval stages reflect all life-history stages of epipelagic taxa, from egg to adult. Co-occurring taxa experience similar biotic and abiotic environmental conditions and are themselves part of each other's environment. Knowledge of the degree of co-occurrence is a basis for studying trophic relations and competitive interactions between taxa. We view this analysis as a first step in studying the population ecology of these taxa from the standpoint of early life-history stages. Analysis of fluctuations in abundance of these taxa (Smith, Moser, Eber, in prep.) will provide insight into how environment and species interactions affect the populations. Some of these data have been used to estimate population trends of fishery stocks for the past 50 years. These analyses can now be broadened to the ecosystem scale to further define the role of environment, species interaction, and fisheries on the fish stocks of the California Current region.

How well does recurrent group analysis define the larval fish assemblages of the California Current region? Analysis of the pooled data set for 1954–60 identified three major faunal complexes that reflect the transitional nature of the ocean and its zoogeographic components in this region. In the northern complex the CalCOFI surveys define the southern and seaward spawning boundaries of the subarctic-transitional and transitional taxa that make up LEUROGLOSSUS and TARLETONBEANIA, two groups separated by displaced spawning seasons. The pattern also circumscribes the northern spawning limit for *Merluccius productus* in the LEUROGLOSSUS group[4]. Seaward and latitudinal spawning boundaries for the two major clupeoids (*Engraulis mordax* and *Sardinops sagax*) were also defined by the CalCOFI pattern[5]. Larvae of *E. mordax* were pervasive in the CalCOFI sampling region; this in combination with an extended spawning season ensures that larvae of most common species in the CalCOFI region co-occur with anchovy larvae at some time during the year. Indeed, affinity indices with members of the LEUROGLOSSUS group were consistently high, and *E. mordax* was included as a group member with those species in all but one of the single-year analyses during the seven-year period. This same pervasive areal and temporal distribution pattern appears to have characterized *S. sagax* before the collapse of the stock; however, sardine spawning was centered off central Baja California during 1954–60. In the analysis of the pooled 1954–60 data set, *E. mordax* was grouped with two warm-water sanddab species, and *S. sagax* was paired with *Scomber japonicus.* The sanddab species *Citharichthys fragilis* and *C. xanthostigma* are clearly not "northern" species; however, they were linked to the northern complex through their consistently strong affinities with *E. mordax, S. sagax,* and *Sebastes* spp. Likewise, *S. japonicus* is not a "northern" species but was linked to the northern complex through its strong affinity with *S. sagax.*

In contrast to the northern and coastal character of the northern complex, the principal constituents of the southern complex are mesopelagics that inhabit more southerly and offshore waters. Although the taxa were partitioned into 4 groups in the pooled analysis, the various taxa mixed freely and combined to form a variety of groups in analyses of individual years. The 5-member SYMBOLOPHORUS group is faunistically diverse. *Bathylagus wesethi* and *Symbolophorus californiensis* are

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[4] Subpopulations of *M. productus* spawn in the Straits of Georgia, British Columbia, and in Puget Sound, Washington.

[5] The degree of genetic interchange between Gulf of California and outer coast stocks of these two species is unknown.

inhabitants of the California Current region, with distributions centered off Point Conception to Punta Eugenia; their latitudinal and inshore-offshore spawning limits are essentially defined by the CalCOFI pattern. The warm-water cosmopolite *Diogenichthys atlanticus* extends into the CalCOFI area between Point Conception and Punta Eugenia, where its latitudinal limits are well defined. *Cyclothone* spp. has a similar distribution in the CalCOFI area; however, it is primarily equatorial, and only its northern spawning limits are defined by the CalCOFI survey pattern. *Ceratoscopelus townsendi* and *Lampadena urophaos* have distributions similar to *D. atlanticus* and *Cyclothone* spp. in the CalCOFI region. They pair to form a separate group because of the extremely close areal overlap and spawning seasonality, with a sharp peak in August.

TRIPHOTURUS is the most zoogeographically disparate group in the southern complex. *Trachurus symmetricus* and *Protomyctophum crockeri* are transitional species with distributions extending to the western Pacific, and are clearly not "southern" species. In the CalCOFI region their larval distributions have broad temporal and spatial overlap with that of the warm-water myctophid *Triphoturus mexicanus*, particularly in the region between Point Conception and Punta Eugenia. *T. mexicanus* also overlaps broadly with *E. mordax*, with whom it forms consistently high intercomplex affinity indices. It may be viewed as a kind of latitudinal mirror image of *E. mordax* in the southern part of the CalCOFI region. The transitional nature of the TRIPHOTURUS group was shown by the strong affinities its members had with taxa of the northern complex and by the inclusion of *T. mexicanus* and *P. crockeri* in northern complex recurrent groups in 1954 and 1958 (Figures 6 and 7).

VINCIGUERRIA is the most faunistically coherent group in the southern complex. The northern spawning boundaries of its 4 eastern tropical Pacific species are clearly defined by the CalCOFI pattern. *V. lucetia* is abundant and widespread off the entire Baja California coast. *D. laternatus* is widespread but less abundant. *Hygophum atratum* and *Gonichthys tenuiculus* are even less abundant, and chiefly south of Punta Eugenia.

The presence of a southern coastal complex in the CalCOFI data set results from the interplay of coastal bathymetry and the survey pattern. Bahía Sebastián Viscaíno and the Punta Abreojos-Cabo San Lázaro Bight are the only large shelf areas in the station pattern. Taxa in this southern coastal complex are the northern representatives of the shorefish fauna of the tropical-subtropical eastern Pacific. Their northern distributions are sharply curtailed by the narrow shelf of northern Baja California and by the depressed water temperatures of this region that result from coastal upwelling. This complex was isolated from the other complexes in the pooled analysis but formed linkages with the southern and northern complexes in some of the annual analyses.

The descriptions of larval fish assemblages of the CalCOFI region are both informative and conservative. The analysis of pooled data of the northern complex shows the relationship between the subarctic-transitional core group and the pervasive coastal pelagic species with southerly linkages. Likewise the offshore, the California Current region endemic, and the eastern tropical Pacific components of the southern complex are well demonstrated, along with the taxa that bridge the two major complexes. Some of the groupings (e.g., SARDINOPS, CITHARICHTHYS, and TRIPHOTURUS) are not intuitively obvious. Taxa of these groups bind together the divergent fish assemblages of the region by extensive co-occurrence. Annual variation in group composition and in intergroup and associate linkages generally supports the overall scheme described by the pooled data set. Forthcoming analyses of additional yearly surveys and a larger pooled data set will allow further refinement.

The conservative quality of the faunal assemblages is shown by examining the effect of El Niño on recurrent group structure. The cooling trend, which peaked in 1956, resulted in lowered affinity indices among southern-complex species and produced depauperate southern-complex groups. Only about half of the group taxa present in the seven-year pooled analysis were present in 1956. With the onset of the warming trend in 1957 these taxa regained their prominence; northern-complex taxa, however, did not show an analogous decrease in representation as the El Niño peaked in 1958 and 1959, despite lowering of affinity indices for some northern-complex pairs. Neither was there major intermixing of northern and southern recurrent groups resulting from northward and shoreward expansion of spawning of the latter. Taxa of the TRIPHOTURUS group (*T. mexicanus, Trachurus symmetricus, Protomyctophum crockeri*) were the central figures in intercomplex linkages throughout the seven-year period, because of their inclusion in northern recurrent groups or their extensive associate pairings with northern group members. Intercomplex connections were also caused by *E. mordax* and *S. sagax,* particularly through affinities of the former with *T. mexicanus.*

The interconnections of northern and southern complexes made through the sanddab *C. xanthostigma* in 1957 and 1960 were an expression of the warm-water distribution of this species and the absence of its indirect connection to the northern complex through *E. mordax*. The same was true for *S. japonicus,* which paired with the flatfish *Etropus* spp. instead of *S. sagax* in 1957. Interestingly, the sanddab recurrent group, *C. xanthostigma* and *C. fragilis,* was isolated from all other groups in the peak El Niño years 1958 and 1959. This was apparently related to the marked reduction of their numbers during this period, the opposite of what one would expect for warm-water species. Perhaps increased larval mortality associated with reduced productivity was the cause.

We anticipated that species assemblages arising from presence-absence techniques like the Fager recurrent group analysis (Fager 1963) would be more robust than those techniques which use the estimates of the quantities of organisms (MacDonald 1975). This is so because within the habitats of these species, spawning products are patchy and the chance co-occurrence of large numbers of two patchy organisms would assume greater importance than may be warranted. Fager (1957) also pointed out that, in analyses based on abundance, inverse quantities of organisms resulting from predation or competition could be misinterpreted by quantitative analysis so as to displace one of the organisms from an assemblage.

One possible disadvantage of the Fager recurrent group analysis relates to the method of resolving ties in the assembly of large groups. It appears that the more ubiquitous of two alternate group members may tend to be eliminated because it could eventually form a larger group than the less ubiquitous alternate. One example was *E. mordax*. Within the LEUROGLOSSUS group *E. mordax* had high affinities with every group member but *Bathylagus ochotensis*. If *E. mordax* had been selected as the member, *B. ochotensis* would have been displaced and made a member of the TARLETONBEANIA recurrent group; *Icichthys lockingtoni* of that group would have been displaced to an associate of that group; CITHARICHTHYS would have been diminished to two group members; and all of the associates of CITHARICHTHYS would have been transferred to LEUROGLOSSUS. Only in 1958 were *E. mordax* and *B. ochotensis* in the same recurrent group.

The northern and southern complexes were preserved when recurrent group analysis was applied to the combined 1954–60 data set, using a series of high critical affinity values (0.4, 0.5, 0.6). One can observe in the northern complex diagram (Figure 8) that the removal of the 0.3 links (single lines) leaves only a group of five taxa with an associate and an isolated pair. The southern complex (Figure 10) dissolved similarly into one group of four taxa with several associates. Almost all the diversity is gone when both 0.3 and 0.4 (double) lines are removed, and only two isolated pairs remain when the 0.5 line (triple) is also removed. It appears that in this analysis of larval stages of fish taxa, the critical values of 0.3 maintained the structure of the common fish assemblages and permitted the description of associations like the southern coastal complex, SYNODUS, near the sampling threshold.

Considering the possibilities for chaos with several faunal groups contributing to the California Current region, it appears that the structure of the system is clear when several years are pooled. These seven years were selected because they had two cold years, 1955 and 1956; had two warm years, 1958 and 1959; were bounded by two relatively "normal" years, 1954 and 1960; and were separated by one transitional year, 1957. The recurrent group analysis of 1975 clearly separated the same northern and southern complexes as this set (Loeb et al. 1983). It remains to be seen whether the 1954–60 set can be considered to be representative or whether new forms of assemblages will arise from the other 16 years yet to be analyzed. It is probable that another complex, representative of the central water mass, will be defined from analysis of extended cruises in 1972. Also, it may be possible that more intensive coastal sampling of the recent decade (Barnett et al. 1984; Lavenberg et al. 1986) may define a "northern coastal complex" similar to that found by Gruber et al. (1982) in the Southern California Bight.

Lastly, the distinctions among the complexes are exceedingly clear, considering that the system is embedded in a current which is moving several thousand kilometers each year and mixing with coastal temperate, subarctic, and subtropical waters. There is much to be learned from the study of the necessary physiological, behavioral, and oceanographic mechanisms that maintain these groups of populations in one locale.

ACKNOWLEDGMENTS

This study would not have been possible without the dedicated efforts of many people. We are indebted to David Ambrose, Elaine Sandknop, Elizabeth Stevens, and Barbara Sumida for correcting historical data records and reidentifying much of the larval fish material. Richard Charter designed and administered the data base. Cindy Meyer and Larry Zins wrote programs, and Celeste Santos and Debby Snow checked written data and data files. Jim Ryan rewrote the Fager recurrent group analysis in Pascal so that this large data base with several hundred taxa could be analyzed with a microcomputer. For the excellent time series we are indebted to the founders of the CalCOFI program and the many scientists, technicians, and ships' crews who carried it out.

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APPENDIX
Larval Fish Taxa That Constitute Recurrent Groups, Associates, and Affiliates, from Pooled CalCOFI Survey Data, 1954–60

Taxon	Incidence (11,551 total)	Associate group
Northern Complex		
LEUROGLOSSUS recurrent group		
Leuroglossus stilbius	3,010	
Bathylagus ochotensis	1,172	
Stenobrachius leucopsarus	2,439	
Sebastes spp.	4,485	
Merluccius productus	3,027	
Associates (members or associates of other recurrent groups)		
Engraulis mordax	5,097	CITHARICHTHYS
Citharichthys stigmaeus	1,322	CITHARICHTHYS
Sardinops sagax	1,477	SARDINOPS
Tarletonbeania crenularis	1,044	TARLETONBEANIA
Affiliates		
Osmeridae	4	
Nansenia spp.	3	
Bathylagus milleri	7	
Bathylagus pacificus	54	
Valenciennellus stellatus	1	
Macrouridae	40	
Brosmophycis marginata	80	
Hexagrammidae	4	
Oxylebius pictus	38	
Cottidae	250	
Scorpaenichthys marmoratus	53	
Agonidae	78	
Cyclopteridae	41	
Lyopsetta exilis	485	
Microstomus pacificus	147	
Parophrys vetulus	297	
Pleuronichthys coenosus	51	
Pleuronichthys decurrens	22	
Psettichthys melanostictus	22	
TARLETONBEANIA recurrent group		
Tarletonbeania crenularis	1,044	
Icichthys lockingtoni	633	
Associates (members or associates of other recurrent groups)		
Bathylagus ochotensis	1,172	LEUROGLOSSUS
Stenobrachius leucopsarus	2,439	LEUROGLOSSUS
Sebastes spp.	4,485	LEUROGLOSSUS
Affiliates		
Leuroglossus schmidti	3	
Danaphos oculatus	1	
Chauliodus macouni	421	
Diaphus spp.	628	
Bathymasteridae	1	
Pholididae	1	
Icosteus aenigmaticus	6	
Glyptocephalus zachirus	62	
CITHARICHTHYS recurrent group		
Engraulis mordax	5,097	
Citharichthys fragilis	821	
Citharichthys xanthostigma	980	
Associates (members or associates of other recurrent groups)		
Leuroglossus stilbius	3,010	LEUROGLOSSUS
Stenobrachius leucopsarus	2,439	LEUROGLOSSUS
Sebastes spp.	4,485	LEUROGLOSSUS
Merluccius productus	3,027	LEUROGLOSSUS
Citharichthys stigmaeus	1,322	LEUROGLOSSUS
Sardinops sagax	1,477	SARDINOPS
Triphoturus mexicanus	4,648	TRIPHOTURUS
Associates (unique)		
Citharichthys spp.	904	
Affiliates		
Argentina sialis	438	
Gobiesocidae	4	
Atherinidae	18	
Syngnathus spp.	29	
Ophiodon elongatus	7	
Zaniolepis spp.	39	
Caulolatilus princeps	55	
Sciaenidae	499	
Clinidae	118	
Gobiidae	592	
Sarda chiliensis	18	
Peprilus simillimus	216	
Blennioidei	5	
Pleuronectiformes	109	
Citharichthys sordidus	424	
Paralichthys californicus	244	
Hippoglossina stomata	258	
Pleuronichthys spp.	100	
Pleuronichthys ritteri	19	
Pleuronichthys verticalis	178	
Hypsopsetta guttulata	5	
SARDINOPS recurrent group		
Sardinops sagax	1,477	
Scomber japonicus	513	
Associates (members or associates of other recurrent groups)		
Sebastes spp.	4,485	LEUROGLOSSUS
Merluccius productus	3,027	LEUROGLOSSUS
Engraulis mordax	5,097	CITHARICHTHYS
Affiliates		
Girella nigricans	17	
Hypsypops rubicundus	2	
Sphyraena argentea	107	
Semicossyphus pulchrum	5	

(continued)

APPENDIX (*continued*)
Larval Fish Taxa That Constitute Recurrent Groups, Associates, and Affiliates, from Pooled CalCOFI Survey Data, 1954–60

Taxon	Incidence	Associate group
Southern Complex		
SYMBOLOPHORUS recurrent group		
Bathylagus wesethi	1,935	
Cyclothone spp.	1,784	
Diogenichthys atlanticus	734	
Lampanyctus ritteri	2,288	
Symbolophorus californiensis	966	
Associates (members or associates of other recurrent groups)		
Protomyctophum crockeri	2,303	TRIPHOTURUS
Triphoturus mexicanus	4,648	TRIPHOTURUS
Melamphaes spp.	1,309	TRIPHOTURUS
Trachurus symmetricus	2,095	TRIPHOTURUS
Vinciguerria lucetia	4,288	VINCIGUERRIA
Diogenichthys laternatus	2,204	VINCIGUERRIA
Ceratoscopelus townsendi	988	CERATOSCOPELUS
Associates (unique)		
Paralepididae	772	
Affiliates		
Microstoma microstoma	176	
Tactostoma macropus	31	
Aristostomias scintillans	45	
Idiacanthus antrostomus	161	
Alepocephalidae	1	
Scopelarchidae	327	
Scopelosaurus spp.	36	
Myctophum nitidulum	268	
Centrobranchus spp.	1	
Electrona rissoi	4	
Poromitra spp.	111	
Trachipteridae	145	
Sebastolobus spp.	45	
Apogonidae	11	
Chiasmodontidae	294	
Isopsetta isolepsis	1	
VINCIGUERRIA recurrent group		
Vinciguerria lucetia	4,288	
Diogenichthys laternatus	2,204	
Gonichthys tenuiculus	537	
Hygophum atratum	444	
Associates (members or associates of other recurrent groups)		
Bathylagus wesethi	1,935	SYMBOLOPHORUS
Cyclothone spp.	1,784	SYMBOLOPHORUS
Lampanyctus ritteri	2,288	SYMBOLOPHORUS
Myctophidae	1,078	TRIPHOTURUS
Triphoturus mexicanus	4,648	TRIPHOTURUS
Ceratoscopelus townsendi	988	CERATOSCOPELUS
Associates (unique)		
Lampanyctus spp.	966	
Stomias atriventer	803	
Affiliates		
Anguilliformes	163	
Stomiiformes	50	
Nansenia crassa	326	
Bathylagus spp.	29	
Bathylagus nigrigenys	9	
Gonostomatidae	3	
Diplophos taenia	93	
Ichthyococcus spp.	165	
Sternoptychidae	428	
Bathophilus spp.	34	
Myctophiformes	2	
Evermannellidae	10	
Diogenichthys spp.	250	
Hygophum spp.	248	
Loweina rara	82	
Myctophum aurolaternatum	30	
Antennariidae	1	
Moridae	5	
Physiculus spp.	20	
Bregmaceros spp.	60	
Carapidae	11	
Macroramphosus gracilis	6	
Fistularidae	1	
Scorpaenidae	6	
Seriola spp.	3	
Uranoscopidae	5	
Gempylidae	20	
Thunnus albacares	10	
Nomeidae	20	
Citharichthys platophrys	1	
Bothus spp.	24	
Balistidae	1	
TRIPHOTURUS recurrent group		
Protomyctophum crockeri	2,303	
Triphoturus mexicanus	4,648	
Trachurus symmetricus	2,095	
Associates (members or associates of other recurrent groups)		
Bathylagus wesethi	1,935	SYMBOLOPHORUS
Cyclothone spp.	1,784	SYMBOLOPHORUS
Lampanyctus ritteri	2,288	SYMBOLOPHORUS
Symbolophorus californiensis	966	SYMBOLOPHORUS
Melamphaes spp.	1,309	SYMBOLOPHORUS
Vinciguerria lucetia	4,288	VINCIGUERRIA
Diogenichthys laternatus	2,204	VINCIGUERRIA
Myctophidae	1,078	VINCIGUERRIA
Ceratoscopelus townsendi	988	CERATOSCOPELUS
Engraulis mordax	5,097	CITHARICHTHYS

(*continued*)

APPENDIX (*continued*)

Larval Fish Taxa That Constitute Recurrent Groups, Associates, and Affiliates, from Pooled CalCOFI Survey Data, 1954–60

Taxon	Incidence	Associate group
Affiliates		
Nansenia candida	104	
Aulopus spp.	1	
Lampanyctus regalis	164	
Exocoetidae	18	
Cololabis saira	177	
Medialuna californiensis	47	
Oxyjulis californica	23	
Scombridae	57	
Tetragonurus cuvieri	417	
CERATOSCOPELUS recurrent group		
Ceratoscopelus townsendi	988	
Lampadena urophaos	307	
Associates (members or associates of other recurrent groups)		
Bathylagus wesethi	1,935	SYMBOLOPHORUS
Cyclothone spp.	1,784	SYMBOLOPHORUS
Vinciguerria lucetia	4,288	VINCIGUERRIA
Triphoturus mexicanus	4,648	TRIPHOTURUS
Affiliates		
Notoscopelus resplendens	227	
Hygophum reinhardtii	111	
Hygophum proximum	2	
Notolychnus valdiviae	21	
Ceratioidei	105	
Scopeloberyx robustus	3	
Scopelogadus mizolepis	165	
Howella brodiei	1	
Brama spp.	39	
Southern Coastal Complex		
SYNODUS recurrent group		
Synodus spp.	402	
Prionotus spp.	132	
Ophidion scrippsae	195	
Symphurus spp.	353	
Associates (unique)		
Etrumeus acuminatus	172	
Affiliates		
Albula vulpes	1	
Opisthonema spp.	13	
Engraulidae	5	
Anotopterus pharao	1	
Porichthys spp.	1	
Lophiidae	1	
Ophidiiformes	318	
Chilara taylori	62	
Hemiramphidae	2	
Scorpaena spp.	111	
Serranidae	190	
Priacanthidae	1	
Carangidae	81	
Seriola lalandi	118	
Coryphaena hippurus	77	
Gerreidae	34	
Haemulidae	48	
Mullidae	6	
Pomacentridae	75	
Chromis punctipinnis	125	
Mugil spp.	16	
Labridae	549	
Halichoeres spp.	24	
Hypsoblennius spp.	235	
Trichiuridae	266	
Euthynnus spp.	3	
Scomberomorus spp.	7	
Auxis spp.	56	
Etropus spp.	70	
Syacium ovale	22	
Xystreurys liolepis	32	
Tetraodontidae	1	

MESOSCALE CYCLES IN THE SERIES OF ENVIRONMENTAL INDICES RELATED TO THE SARDINE FISHERY IN THE GULF OF CALIFORNIA

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ABSTRACT

Cyclical fluctuations in mean sea level and sea-surface temperature recorded at northwestern Mexican shore stations are compared to Gulf of California sardine fishery data. Sardine abundances correspond to 2-year and 5-year sea-level and sea-surface temperature cycles.

RESUMEN

Fluctuaciones cíclicas en el nivel promedio del mar y la temperatura superficial de estaciones costeras del noroeste de México son comparados con datos de pesquería de la sardina del Golfo de California. Abundancias pesqueras corresponden a ciclos de 2 y 5 años del nivel del mar y de la temperatura.

INTRODUCTION

During recent years, there has been a renewed interest in analyzing the periodic fluctuations of certain natural phenomena, particularly those of large geographic scale. El Niño events and their seeming relation to the Southern Oscillation have been analyzed by various authors (e.g., Wooster and Fluharty 1985). The relationship between oceanographic-climatic periodic fluctuations and natural populations has also been analyzed (Mysak 1986).

Cyclic fluctuations of 5+ years have been reported on mean sea level (MSL), sea-surface temperature (SST), and salinity as related to catches of herring and salmon in the northeast Pacific Ocean by Mysak et al. (1982). Mysak (1986) also proposes a mechanism that explains the connection of such a cycle to El Niño-Southern Oscillation (ENSO) events, through the propagation of Kelvin

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[Manuscript received February 23, 1987.]

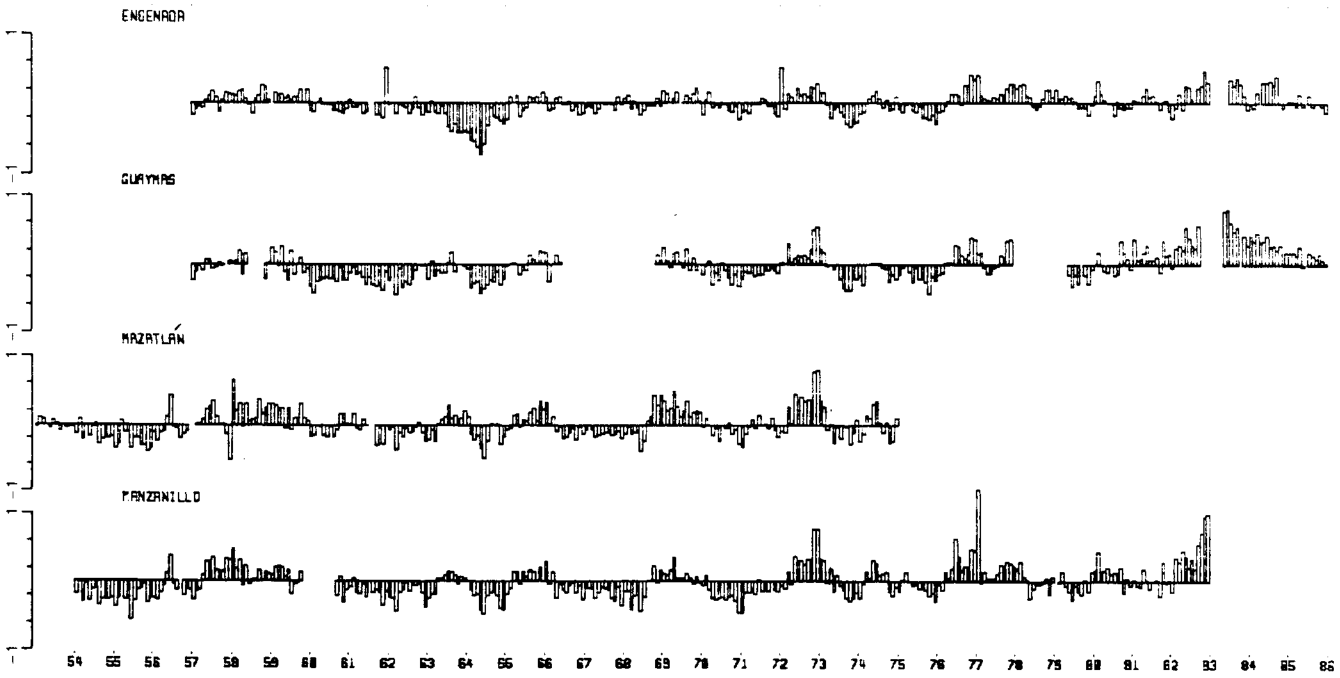

Figure 1. Monthly series of mean sea-level anomalies.

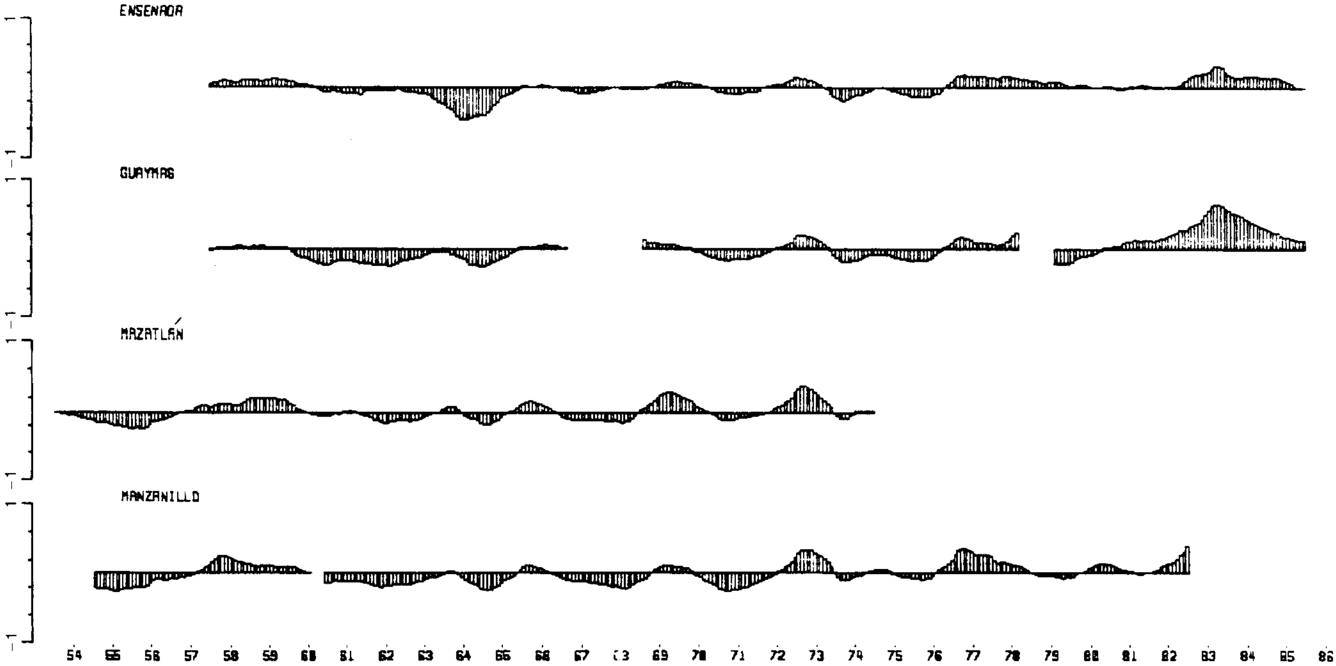

Figure 2. Smoothed monthly series of mean sea-level anomalies.

and Rossby waves along the west coast of North America.

Cyclic fluctuations have also been observed in the sardine fishery of Baja California's west coast (Casas-Valdez 1983), as well as in Baja California's rainfall series, which is used as a climatic indicator (Rueda-Fernández 1983).

We report on cyclic fluctuations of mean sea level and sea-surface temperature from Ensenada, Guaymas, Mazatlán, and Manzanillo, on the west

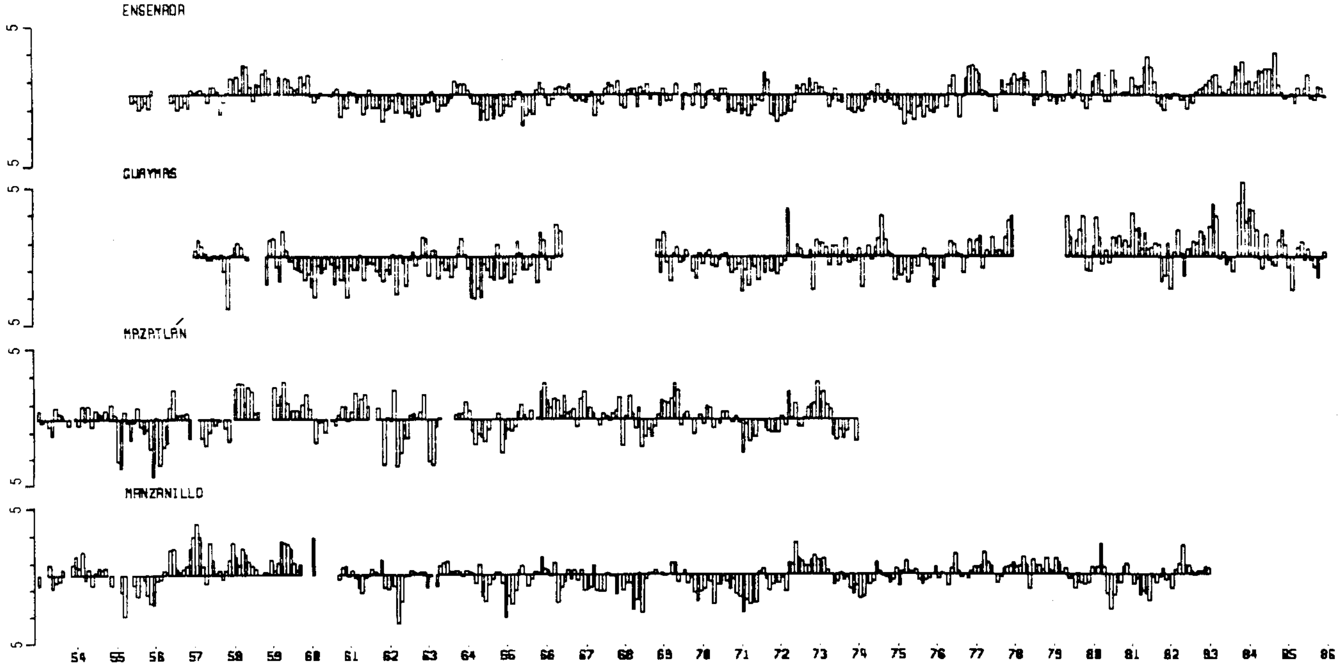

Figure 3. Monthly series of sea-surface temperature anomalies.

TABLE 1
Common Harmonic Parameters and Maxima for Mean Sea Level Series

Period in years	Amplitude	Phase	Peaks (year-month)					
Ensenada								
3.593	0.0721	−2.8336	5808	6203	6510	6905	7212	7607
			8003	8310	8705			
5.278	0.064	0.58722	6110	6701	7205	7708	8211	8803
2.422	0.048	−2.25853	5711	6004	6209	6502	6707	6912
			7205	7410	7703	7908	8202	8407
			8612	8905				
20.996	0.0335	−0.09193	5704	7804	9904			
Guaymas								
5.052	0.0954	−0.98318	5710	6211	6711	7212	7712	8301
			8802					
25.703	0.075	−0.5462	5903	8412				
2.962	0.0676	−0.77293	5705	6004	6304	6604	6903	7202
			7502	7802	8101	8401	8612	8912
3.499	0.0556	3.04577	5810	6204	6510	6904	7210	7604
			7910	8304	8609	9004		
Mazatlán								
3.177	0.095	−0.86458	5306	5608	5910	6212	6602	6904
			7207	7509	7811	8201	8503	8805
5.221	0.0545	−0.39012	5304	5807	6310	6812	7403	7906
			8408	8911				
2.223	0.0546	1.93914	5407	5610	5812	6103	6306	6508
			6711	7002	7204	7407	7610	7812
			8103	8306	8508	8711		
Manzanillo								
3.341	0.0796	2.12008	5603	5907	6211	6603	6907	7212
			7604	7908	8212	8604	8908	
4.817	0.0966	0.54975	5805	6303	6801	7211	7708	8206
			8704					
22.471	0.0632	−0.82863	5612	7906				
2.751	0.0885	3.07264	5505	5802	6011	6308	6605	6902
			7111	7409	7706	8003	8212	8509
			8806					

coast of Mexico, as well as on the average size of sardines caught in the Gulf of California fishery.

METHODOLOGY

Mean sea level (MSL) and sea-surface temperature (SST) data series for Ensenada, B.C.; Guaymas, Son.; Mazatlán, Sin.; and Manzanillo, Col. were published by Grivel-Piña (1975, 1977, 1978) for the years 1950 through 1974. Later data were furnished by the Centro Regional de Investigaciones Pesqueras (CRIP) at Guaymas, as were monthly size averages of Monterrey sardine (*Sardinops sagax*) landed at Guaymas from November 1971 through December 1984.

Time series analysis techniques were used to determine the internal structure of the data series. Because these methods decompose the series into elements that are caused by different phenomena (not necessarily independent), hypotheses on causal effects may be established (Chatfield 1980), as well as statistical criteria for forecasting relevant variables.

Preliminary analysis was conducted by means of anomalies; noise was filtered by using a 12-order running means. After trend filtering, the program SPECTRA, supplied by the Centro de Investigación Científica y Enseñanza Superior de Ensenada (CICESE) was used to estimate the frequency spectra of the series and to determine the main harmonics. Once the frequencies were determined, a cosine model of harmonic components was used to determine both amplitude and phase by least squares, using Bloomfield's (1976) program modified to operate with incomplete data vectors.

RESULTS

The positive anomalies in the MSL series (Figure 1) occur during the years 1957–59, 1965–66, 1972–73 and 1982–83, all of which correspond to moderate-to-strong ENSO events (Mysak 1986). Thus we may estimate an average period of 5.5 years for a moderate-to-strong ENSO event to occur.

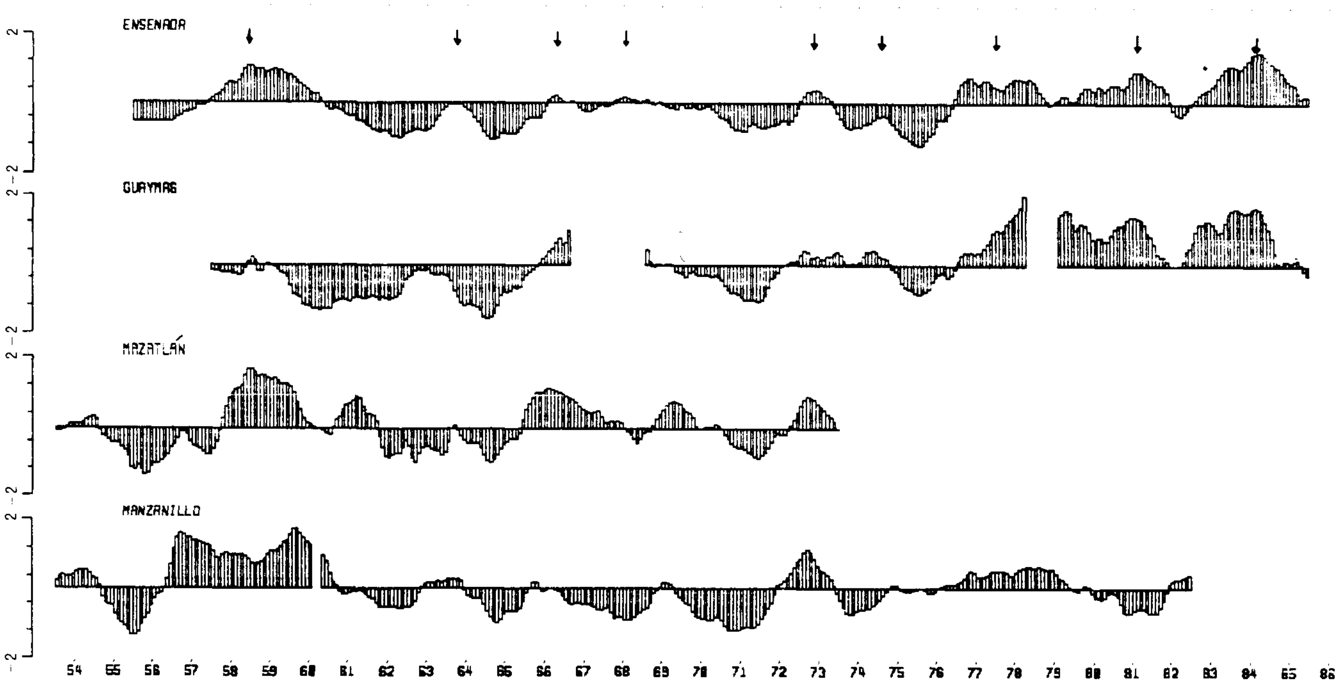

Figure 4. Smoothed monthly series of sea-surface temperature anomalies.

Anomalies at Mazatlán and Manzanillo show other maxima during 1963, 1974, and 1980 (the last one showing only in the Manzanillo series), of which only the first has been reported as a low-intensity ENSO event (Mysak 1986). If we consider all of these, a periodicity of 3.66 years may be estimated for an ENSO event of any intensity. Mysak does not report on the 1974 and 1980 anomalies.

When the series is smoothed by means of moving averages (Figure 2), dominance of sign on longer periods becomes evident. Negative anomalies thus

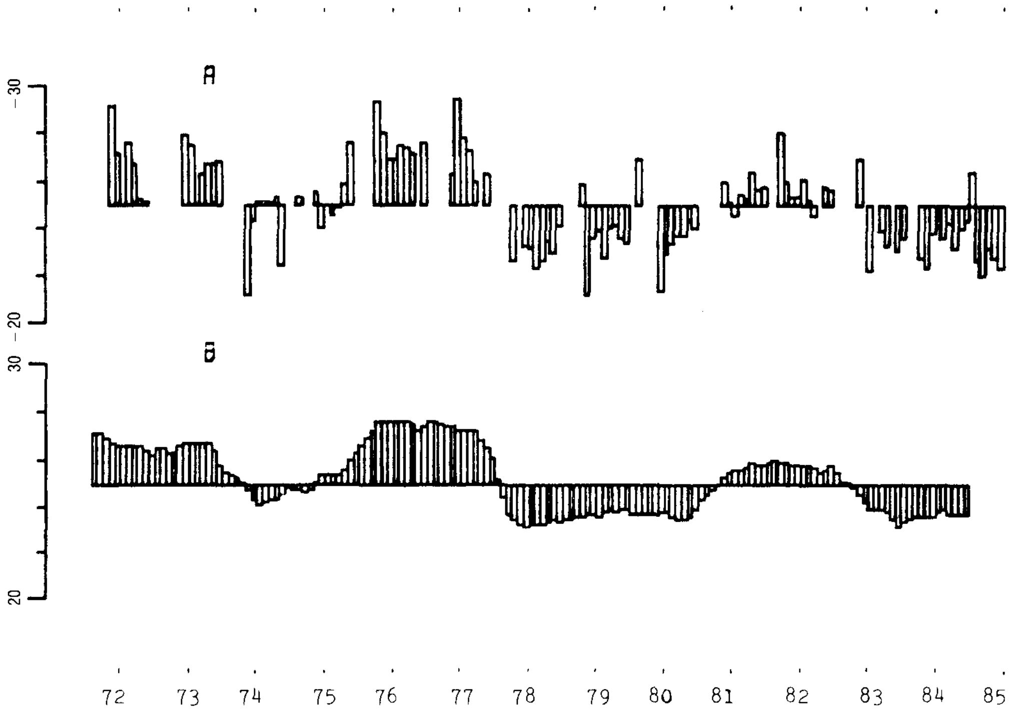

Figure 5. *A*, Monthly mean series of length anomalies for Pacific sardine in the Gulf of California. *B*, Smoothed monthly mean series of length anomalies.

predominate between 1960 and 1971, following a period of normal years through 1981; from 1982 there are only positive anomalies, with a maximum during 1982–83. A component of longer than 25 years is suggested.

When we filtered the linear trend, the spectral analysis showed 14 harmonic components in the Ensenada series, accounting for 80.71% of the total variation; 13 components in the Guaymas series, accounting for 93.75% of the total variation; 10 in the Mazatlán series, accounting for 83.14%; and 11 in the Manzanillo series, accounting for 77.37%. This analysis validated the preliminary findings.

Three of these components are shared by all the series; another is common to only three of them. These components are possibly generated by macroscale phenomena, since they show up in spite of the distance between points, and in spite of the different local current systems. Parameters and maxima estimated for these harmonics are shown in Table 1.

SST anomalies (Figure 3) fluctuate much more randomly. When 12-month running averages are used (Figure 4), two cycles are suggested. The first is shown by the trends toward positive anomalies (shown by arrows in the figure), with an approximate period of 3.6 years, coincident with ENSO events. The second cycle, deduced through sign dominance, has an approximate period of 26 years.

Of the harmonic components detected by spectral analysis—10 for Ensenada (91.81% of the variation), 9 for Guaymas (96%), 8 for Mazatlán (90.53%), and 11 for Manzanillo (84.53%)—there is coincidence in one component for all the series with a period of 3+ years (also found in the MSL series). A second component, of longer period, is not totally consistent, since it does not appear in the Mazatlán series. Furthermore, although in Manzanillo there is a 19.5-year period, Guaymas shows a 26.4-year period, and Ensenada a 25.7-year period (Table 2).

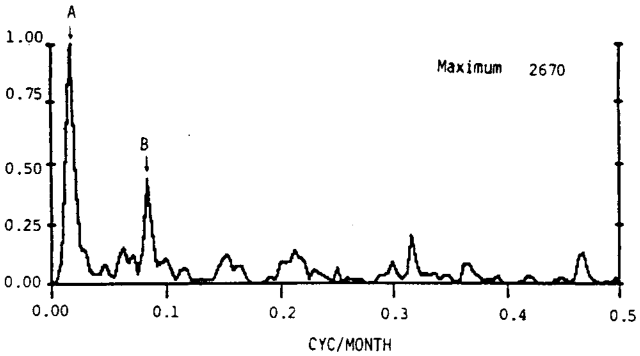

Figure 6. Mean length frequency normalized spectrum of Pacific sardine: *A*, frequency 0.0153 cycles/month (5.4383 years/cycle); *B*, frequency 0.0831 cycles/month (12.03 months/cycle). Maximum is for the main harmonic variance.

Size anomalies (Figure 5A) show an evident cycle, with maxima during 1971–72, 1975–76, and 1981–82—all of them one year ahead of moderate or strong ENSO events. Frequency is estimated at 4.66 years. The anomalies, smoothed by running averages (Figure 5B) show another smaller amplitude cycle that shows up twice for every time the former one appears. This smaller cycle has a period of 2.3 years.

Spectral analysis of this series yielded a model with 11 harmonic components, explaining 82.96% of the total variation. Of all the components, three are major contributors to variance, with periods of 5.44, 1, and 2.8 years. The first and last com-

TABLE 2
Common Harmonic Parameters and Maxima for Sea-Surface Temperature Series

Period in years	Amplitude	Phase	Peaks (year-month)					
Ensenada								
25.762	0.3286	−0.92495	5810	8407				
3.575	0.3181	−1.0592	5508	5903	6210	6604	6911	7306
			7701	8008	8403	8709		
Guaymas								
3.564	0.4599	2.83911	5812	6207	6601	6908	7303	7610
			8005	8311	8706			
26.465	0.3318	0.28934	8203					
Mazatlán								
3.658	0.3798	−2.96814	5409	5805	6201	6509	6905	7301
			7609	8005	8312	8708		
Manzanillo								
19.567	0.5283	−1.71554	5805	7711	9706			
3.139	0.5104	−1.61298	5310	5612	6001	6303	6605	6906
			7208	7510	7811	8201	8503	8804

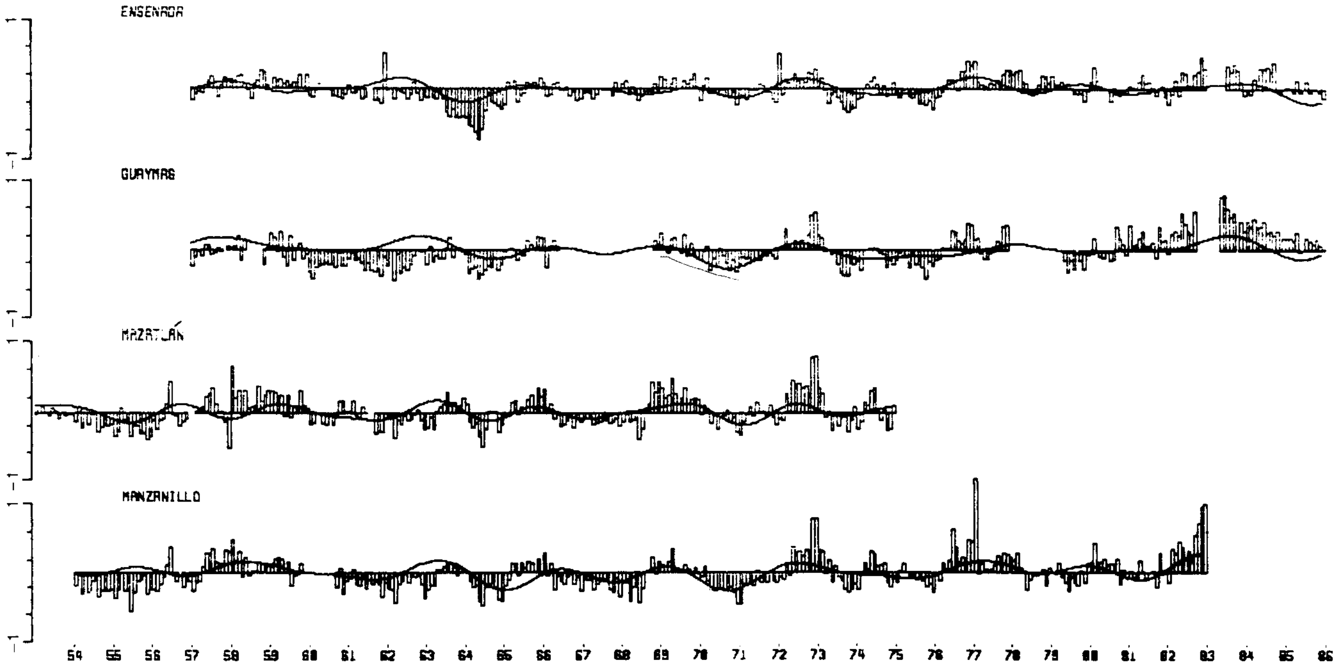

Figure 7. Observed anomalies (bars) and common harmonics in the mean sea-level series (continuous line).

ponents coincide with components on the MSL series.

DISCUSSION

The analysis showed, besides the obvious annual component, four more components that are coherent (in the sense that they appear in most of the series) with 2+ years, 3+ years, 5+ years, and 20+ years. Not all of the components appeared in every series. SST series are less clear, particularly inside the Gulf of California, possibly because of the particular dynamics of the area.

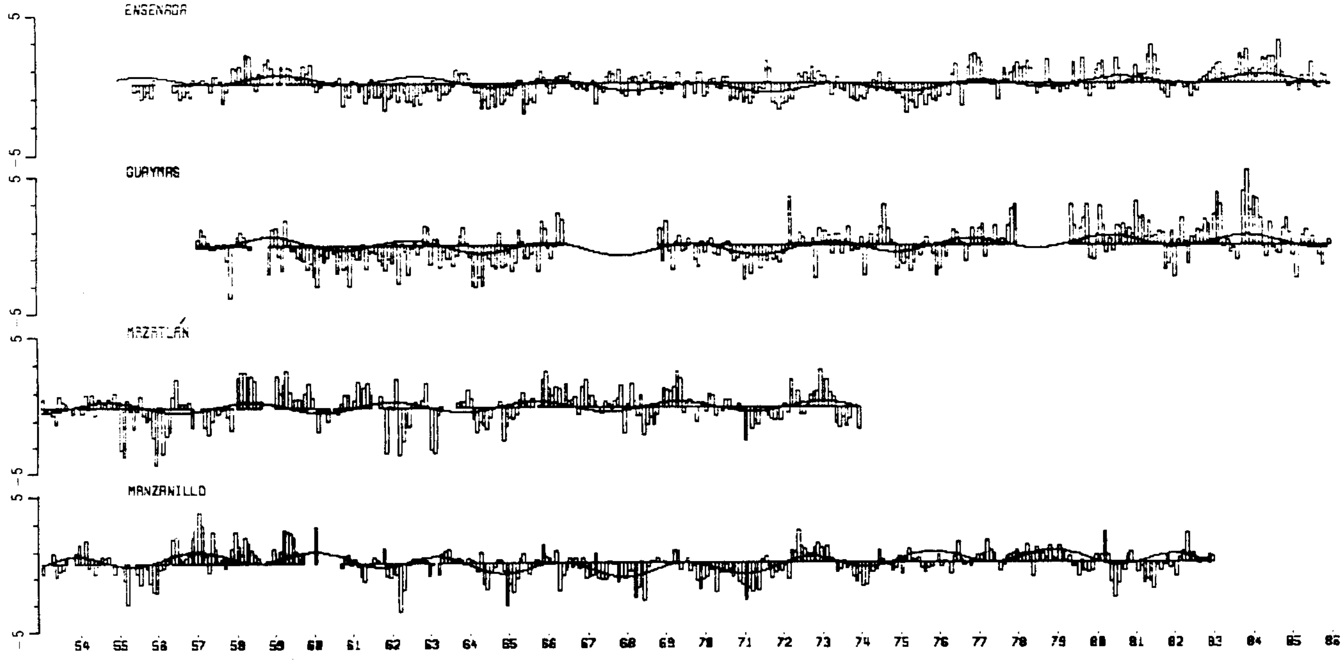

Figure 8. Observed anomalies (bars) and common harmonics in the sea-surface temperature series (continuous line).

The cycle of 5+ years is the one most clearly reflected in the series of sardine average size (Figure 5A). The signal of this cycle is so strong in the sardine size series that it overrides the annual component (Figure 6). We suggest that this is due to abnormally strong recruitment. Similar length-frequency distributions have been reported for Pacific sardines off California (Clark 1936). This cycle also coincides with the cycle of 5+ years reported by Mysak (1986). Besides the cycle of 5+ years, the sardine series also shows the cycle of 2+ years that has been related to El Niño (Monin et al. 1977).

The cycles of 3+ years and 20+ years are not previously reported, possibly because distance attenuation precludes their being detected as far north as British Columbia. They show up in our series because they have been recorded in areas that are considerably closer to the equatorial belt, where the phenomenon seems to originate.

We show the interaction of the anomalies of the four MSL and SST series to simulate their general behavior (Figures 7 and 8). In particular, the strong ENSO events are coincident with years in which the three cycles are in phase (such as 1958–60 and 1982–83). Weak events are associated with years during which cycles are out of phase. Events of intermediate strength are, as expected, associated with partially out-of-phase years at varying degrees.

Thus we suggest that the four cycles detected originate independently from each other and that they determine the ENSO events, with a strength proportional to their degree of coincidence.

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A HISTORICAL REVIEW OF FISHERIES STATISTICS AND ENVIRONMENTAL AND SOCIETAL INFLUENCES OFF THE PALOS VERDES PENINSULA, CALIFORNIA

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ABSTRACT

A synopsis of partyboat and commercial fish and invertebrate catches is presented for the Palos Verdes region. Fifty years (1936–85) of partyboat catch, in numbers of fish and angler effort, and 15 years (1969–83) of commercial landings, in pounds, are reviewed.[1] Several hypotheses are proposed to explain fluctuations in partyboat (commercial passenger fishing vessel) and commercial fishery catches. Where possible, comparisons are drawn to relate catch information to environmental and societal influences. This report documents trends in historical resource use and fish consumption patterns, and is useful for regional fisheries management. The status of several species has improved since the early to mid-1970s. This correlates with other findings of noteworthy environmental recovery and may be associated with reduced contamination of the coastal marine environment.

RESUMEN

Una sinopsis de la pesca de peces y mariscos por barcos comerciales y de recreo es presentada para la región de Palos Verdes. Las capturas de las embarcaciones de recreo (embarcaciones comerciales dedicadas a la pesca hecha por pasajeros) recopiladas durante 50 años (1936–85), en cuanto a número de peces y esfuerzo, así como los desembarques comerciales, en libras, recopilados durante 15 años han sido estudiados. Varias hipótesis han sido propuestas para explicar las fluctuaciones observadas en las capturas por embarcaciones de recreo y de pesca comercial. Las capturas han sido comparades con factores ambientales y sociales en los casos disponibles. Este informe presenta tendencias, a través del tiempo, en el uso de los recursos y en los patrones de consumo de pescado y es de gran utilidad para la administración pesquera regional. Los desembarques de varias especies han aumentado desde principios a mediados de los años 70. Este aumento presenta cierta relación con otros indicadores de una recuperación ambiental significativa y puede estar asociado con una reducción en la contaminación del medio ambiente marino costero.

INTRODUCTION

Our goals were to summarize long-term fish and invertebrate catch statistics gathered by the California Department of Fish and Game (CDFG) for the Palos Verdes Peninsula, to infer relative fish abundance and human consumption rates, and, where possible, to better understand influences from natural and human environmental perturbations. We examined total catches and common and economically important species, in addition to species with reported elevated body burdens of contaminants such as DDT and PCBs.

CDFG fish catch data from blocks 719 and 720 (Figure 1) were analyzed; together they encompassed the entire Palos Verdes Peninsula, a small portion of southern Santa Monica Bay, and northern San Pedro Bay. Block 719 covers a smaller marine area, mostly over the shelf, whereas much of block 720 is above deep canyon and channel waters. Block 719 includes the historically important Horseshoe Kelp Bed in San Pedro Bay (Schott 1976). The Los Angeles County Sanitation Districts' submarine outfall system is located at the junction of blocks 719 and 720. In this analysis, Palos Verdes total catch refers to blocks 719 and 720 combined.

The coastline of the Palos Verdes Peninsula is mainly rocky. Offshore sediments vary from gravels to silt. Sediment within the blocks is as variable as that between blocks. Around the outfall, sediments are very silty as a result of the deposition of fine-grained effluent particulates. Sediments to the east of 719 and west of 720 are also silty. The southwestern section of block 719 is sandy. Coarse sands are found near the shore from southern Santa Monica Bay to the outfall area, grading into finer sand and silt offshore (Uchupi and Gaal 1963). Gorsline and Grant (1972) further detail sediment textural patterns and hydrography. Sediment contaminant burdens vary with distance (from input sources such as the wastewater outfalls or the harbor) and with time (1975–85 levels are substantially lower than the previous decade; Stull and

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[1] Pound and short ton usage was approved in order to allow direct comparisons to historic, statewide California Department of Fish and Game catch data.

[Manuscript received February 2, 1987.]

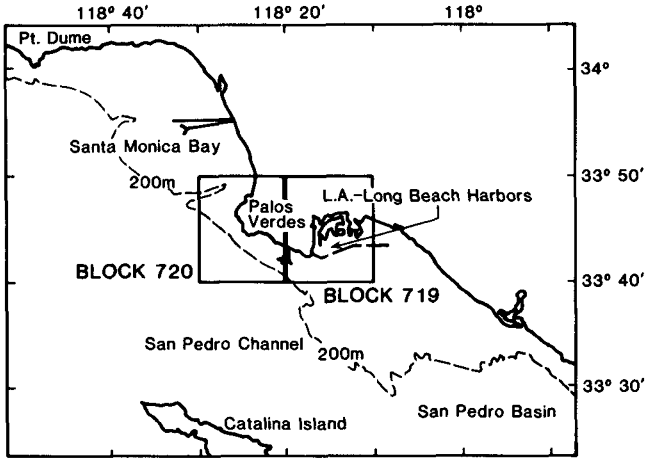

Figure 1. Study area and catch blocks off Palos Verdes Peninsula, Los Angeles County, California.

TABLE 1
Fish and Shellfish Species Analyzed in Palos Verdes Catch Records

Common name	Scientific name
Northern anchovy	*Engraulis mordax*
California scorpionfish	*Scorpaena guttata*
Rockfish complex	*Sebastes* spp.
Lingcod	*Ophiodon elongatus*
Kelp-sand bass complex	*Paralabrax* spp.
Ocean whitefish	*Caulolatilus princeps*
Yellowtail	*Seriola lalandei*
White seabass	*Atractoscion nobilis*
White croaker	*Genyonemus lineatus*
California (or Pacific) barracuda	*Sphyraena argentea*
California sheephead	*Semicossyphus pulcher*
Pacific (or chub) mackerel	*Scomber japonicus*
Pacific bonito	*Sarda chiliensis*
California halibut	*Paralichthys californicus*
Red sea urchin	*Strongylocentrotus franciscanus*
Purple sea urchin	*Strongylocentrotus purpuratus*
Rock crab	*Cancer* spp.
Market squid	*Loligo opalescens*
California spiny lobster	*Panulirus interruptus*

Baird 1985; Stull et al. 1986a, b). Moreover, available fish habitats (e.g., kelp distribution) have fluctuated markedly over the past 50 years (State Water Resources Control Board 1964; Meistrell and Montagne 1983; Wilson et al. 1980; Wilson and McPeak 1983; Wilson and Togstad 1983).

A number of environmental factors, both natural and societal, which potentially affect fisheries will be briefly discussed. Natural events such as temperature fluctuations, upwelling, storms, rainfall and runoff, and attendant alterations in habitat or productivity will be addressed, and some societal impacts such as environmental contamination, dumping, fishing practice, and economic forces will be reviewed.

Data on many potentially relevant factors affecting fish catches were not available. Selective and increasingly efficient fishing (and changes over time), fish migration, weather and ocean conditions, and inaccurate or inconsistent data collection may skew results. The age or size of fish caught was generally unavailable. Partyboat catches do not represent the total sport fishery, since many anglers fish from private boats, piers, and the shoreline.

Because of the many environmental and societal variables influencing fish catches, we cannot overemphasize the tenuous nature of any suggested cause-effect relationships made herein.

METHODS

Environmental Factors

To better visualize the relationships between possible causes of variation in fish catches, we plotted the following physical factors, recorded from the 1960s to 1985: water temperature at 10 m, upwelling index, rainfall, extreme wave episodes, water transparency (by Secchi disk), and wastewater mass emission rate (MER) of suspended solids, DDT, and chromium. The importance of these and other recognized or potential influences (reviewed from the literature) are alluded to in the individual species summaries.

Fisheries Data

The California Department of Fish and Game (CDFG) gathered data from personal surveys, commercial catch landing receipts, and required partyboat catch logs (Cal. Dept. Fish and Game 1952; Heimann and Carlisle 1970; Young 1969).

Species discussed in this report (ordered phylogenetically in Table 1) were selected based on catch record, economic importance, and potential significance to public health. Species importance varies with habitat and catch method. Shellfish contribute only 0.02% to partyboat totals but form 7% of commercial landings.

Partyboat data. Data from CDFG's computer printouts of partyboat catch (number of fish), 1936–85 (excluding 1941–46 because partyboat fishing was suspended during World War II), were entered into computer files by month, year, block, and species. Monthly data were available for 1936–40 and 1947–78; we used annual data from 1956 through 1985. Data were analyzed by species and counts. The partyboat data included 13 of the 17 target fish species.

Although catch statistics do reflect the consumption of marine fish, they rarely provide a direct measure of fish abundance. An important influence on catch is the amount of effort expended. In this paper, partyboat fishing effort is the number of anglers carried each year. Since the partyboat fishery in the Palos Verdes area rarely targets on one species, only the total catch per total anglers can be considered to be catch per unit of effort (CPUE) in the strict sense. Examining the catch of any one species or species complex per angler reveals, at best, a measure of relative abundance between species; it does not take into account how much effort during the year could possibly have taken that species.

Angler effort was recorded differently over the years. Before 1962, one angler day was recorded if the angler went on an 8-hour trip, but half an angler day was recorded for a 4-hour trip. In 1960 and 1961, angler days and number of anglers were recorded. Number of anglers remained the effort statistic from 1962 on. In order to standardize the effort, we calculated 1960–61 conversion ratios that included both angler days and number of anglers. This approximation may skew pre-1960 data, here presented as calculated number of anglers. The equations for converting the pre-1960 data are:

Block 719 angler = 0.576 angler days (SD = 0.14)
Block 720 angler = 0.628 angler days (SD = 0.08)
Palos Verdes (719 + 720) angler = 0.602 angler days (SD = 0.12)

This is the only modification made to the raw data (Figure 2).

Commercial data. Commercial data files (as pounds of fish per month) were created by date and by species for the period 1969–83. CPUE could not be calculated. No data manipulations were performed.

ENVIRONMENTAL FACTORS

Specific environmental data for the Palos Verdes Shelf are limited, and therefore the following overview will first review potential (and confounding) factors affecting fisheries. Available relevant data will then be summarized. It is difficult to specifically correlate catches to natural variability or human influences, and our intent here is not to confuse the reader, but rather to list the spectrum of forces acting on the fisheries. Mearns (1978, 1980, 1984) has also summarized long-term ocean conditions, particularly for Santa Monica Bay, which lies immediately to the north of Palos Verdes.

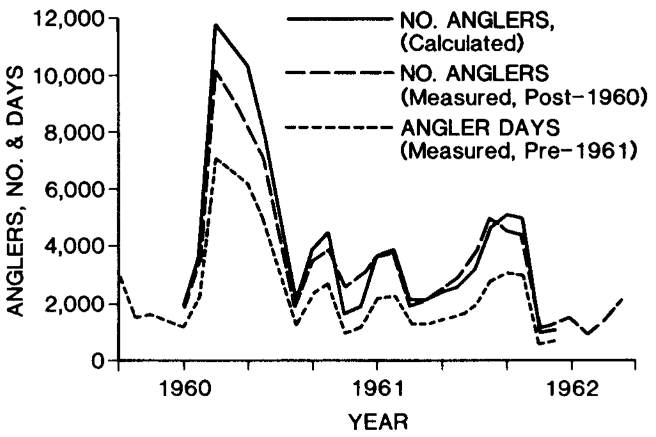

Figure 2. Conversion of Palos Verdes angler data (pre-1961) from angler days to number of anglers.

Natural Events

Temperature changes affect community structure, reproductive success, and food and habitat availability. El Niño events extend the ranges of warm-water species northward, and enhance the local pelagic fishery (e.g., Radovich 1961). Such anomalous warm-water events occurred in 1940–41, 1957–58, 1972–73, 1976–77, and 1982–84 (McLain et al. 1985).

Upwelling of cold, deep, nutrient-rich but less-oxygenated water is a seasonal phenomenon on the Palos Verdes Shelf and is strongest in the spring, although it can occur infrequently at other times of the year. It is generally suppressed by warm-water El Niño events. Fish distributions are altered by upwelling: mobile fish are forced to migrate from some shelf areas, either to shallow water or to surface layers because of unfavorable (but natural) low oxygen and temperature (SCCWRP 1973; Mearns and Smith 1976).

Rainfall and runoff were unusually heavy in 1941, 1952, 1965, 1969, 1978, 1980, and 1983 (National Climatic Service data for Los Angeles Civic Center and Long Beach, California). Nearshore habitats are most influenced by these events.

It has been estimated that there were 45 storm events with extreme wave episodes (exceeding 3 m) between 1935 and 1984 (Seymour et al. 1985). These significantly correlate with El Niño events. Fourteen of the wave episodes exceeded 6 m, and 8 of these occurred between December 1982 and February 1984, during the unusually strong El Niño event. These major storms can create exceptional damage to the coastal region, affecting fish habitats and populations (e.g., U.S. Army Corps. of Engineers and State of California 1984).

Societal Impacts

Environmental contamination in these blocks includes the discharge of treated wastewaters via Los Angeles County Sanitation Districts' (LACSD) outfalls at Whites Point off Palos Verdes. Discharge began in 1937, and daily flows have been approximately 360 million gallons (15.8 m^3/sec) since the late 1960s. Improvements in effluent and environmental quality since 1970 are documented: for effluent, see SCCWRP reports (1973, 1974–84); for fish, Moore and Mearns (1980) and Cross (1985); for kelp, Meistrell and Montagne (1983) and Wilson et al. (1980); and for sediments and benthos, Stull and Baird (1985) and Stull et al. (1986a, b). Significant contaminants also emanate from harbors (Los Angeles-Long Beach), ocean dumping, terrestrial runoff, and other point and nonpoint sources (SCCWRP 1973; Bascom et al. 1979). Mearns (1977) found that nearly half the 1973 Southern California Bight coastal partyboat catch and one-third of the total bight catch was taken within 20 km of the largest municipal wastewater outfalls. Fishing pressure was ten times greater near outfalls than for the coast as a whole, probably because of proximity to marinas. These human impacts could contribute to changes in fish and prey populations.

In 1985, the California Department of Health Services (CDHS) posted warnings of DDT and PCB contamination of some local fish. Consumption guidelines were given for white croaker, and it was recommended that fish from certain regions, including the ocean outfall area and parts of Los Angeles-Long Beach harbors, be avoided. DDT had been discharged into LACSD sewers from 1953 until 1971, when the ecological impact of the pesticide was recognized. The diverse literature on ecological effects, distribution, and persistence of DDT is reviewed by Young (1982). Accumulation of DDT in a sediment reservoir is an acknowledged source to the biota. Matta et al. (1986) and Smokler et al. (1979) summarize declining trends in body burdens of DDT and PCBs in Palos Verdes and West Coast fauna, and Schafer et al. (1982) report on bioaccumulation and biomagnification in food webs. Surveys by Gossett et al. (1982) of sportfish contamination raised concerns for human health, particularly for those consuming white croaker. The 1985 posting was not the first time that DDT residues impacted local fishing efforts or were brought to public attention. In 1970 canned jack mackerel were condemned, and white croaker were seized by the U.S. Food and Drug Administration. In 1971 jack mackerel were withheld from distribution by packers, and jack mackerel and Pacific bonito were condemned (MacGregor 1974). Edible fish tissues in these catches exceeded the FDA's 5 ppm DDT maximum tolerance for commercial fish products. In 1985 the partyboat industry reported a loss of customers as a result of CDHS warnings.

Dumping affects fish habitats and populations. For example, pre-1930 dumping of rock, shale, and mud during harbor expansion is thought to have contributed to the deterioration of the Horseshoe Kelp Bed in San Pedro Bay (Schott 1976). Contaminant dumping has also been reported off Palos Verdes (Chartrand et al. 1985).

Fishing practice and regulations affect catches. During this century there have been a series of detailed restrictions on commercial gear types (nets, mesh sizes), which vary by species. Regional prohibitions or quotas often apply to commercial fishing, and bag limits regulate partyboat takes.

Economic influences impact catches. For example, fuel shortages of 1975–77 altered angler activity: fewer anglers fished block 720, and more fished block 719 instead of the more distant Catalina Island. Also, commercial fishing is strongly driven by economic realities.

Societal impacts on fish species depend partially on biology, habitat, food habits, and behavior. For example, demersal fish living on or near the ocean bottom are more likely to accumulate toxicants from sediments (or benthos) than are wide-ranging pelagic fish. Long-lived residents are more likely to show the effects of overfishing. Certain species are attracted to outfalls or constructed reefs (Allen et al. 1976).

Data interpretation is complicated by lag time: for example, overfishing or environmental influences on fish reproduction (e.g., Cross and Hose 1986) may not be manifested for several years, whereas other effects such as El Niño can occur within a season.

Environmental Data

Figures 3 and 4 summarize Palos Verdes environmental data.

Annual mean water temperature at 10 m (from approximately weekly profiles at a 60-m Palos Verdes site near the outfall) was generally higher after 1975 (Figure 3). The more detailed monthly temperature profiles computed from bathythermograph records at the same 60-m site at the junction of blocks 719 and 720 show that positive anomalies are more prevalent in 1976–85 than in the previous decade (Figure 4). Warmest, most pro-

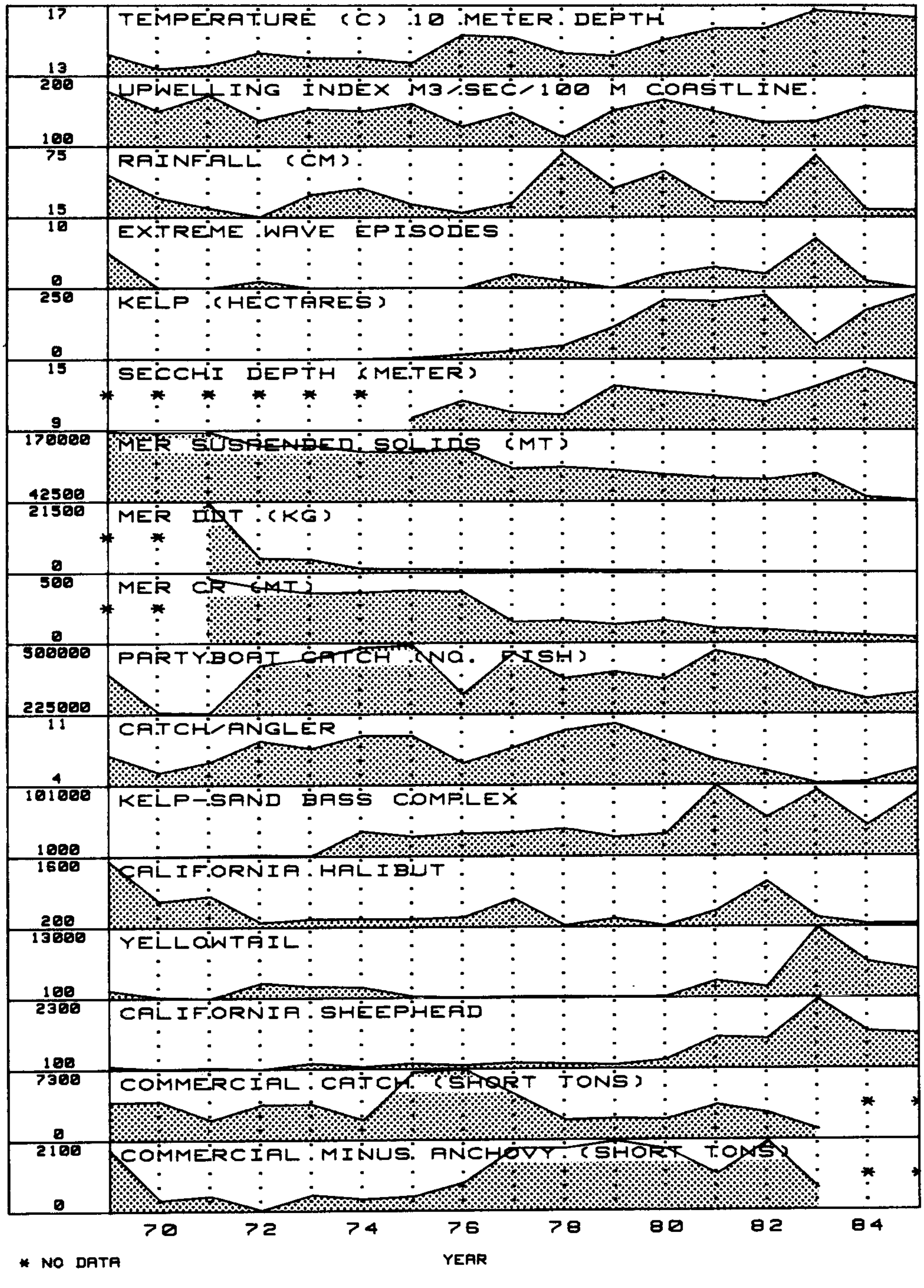

Figure 3. Temporal trends in environmental factors and representative fish catches, 1969–85. All data are annual means; ranges shown are maximum/minimum.

longed, and deepest thermal structure occurred during the 1982–83 El Niño.

Upwelling was suppressed during El Niño years 1972, 1976–78, and 1982–83 (Figure 3). (These data are annual means for 33°N 119°W from Jerrold Norton, National Marine Fisheries Service, Monterey, Calif.). Rainfall and runoff were heaviest in 1978, 1983, and 1980 (National Climatic Service data for Long Beach).

Extreme wave episodes (higher than 3 m) occurred most often during the major El Niño of 1983 and in 1969 (McLain et al. 1985).

Kelp was virtually absent from Palos Verdes through the mid-1970s and sustained major losses from 1983 storms, after which it rapidly returned to the shelf (CDFG data; Wilson and Togstad 1983).

Water clarity (Secchi depth at a 60-m site near

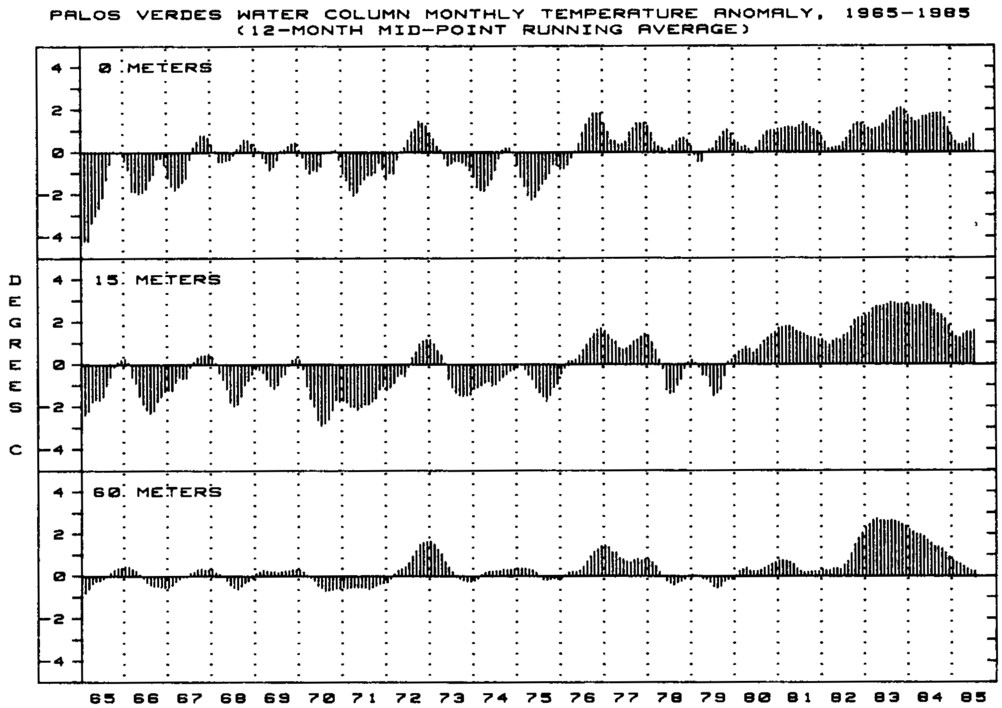

Figure 4. Palos Verdes water column temperature anomaly, 1965–85.

the ocean outfall) improved from 1978 to the mid-1980s. This Secchi trend was also observed in Santa Monica Bay, and Mearns (1984) suggests that possible reasons may be reduced phytoplankton density (from less upwelling or nutrients), low runoff, or reduced wastewater emissions (particulates and nutrients).

Mass emission rates of three wastewater constituents are shown. (1) Suspended solids, which decreased steadily from 1960 to 1985, can affect fish and their habitats by reducing light transmissibility, increasing organic matter in the water column and sediments, and transporting contaminants. (2) DDT, a persistent and bioaccumulating pesticide, was discharged into the sewer system from 1953 to 1971. (3) Chromium represents metals emission patterns, which have all decreased with improved industrial waste source control and solids removal. Effluent quality improved significantly in all components monitored between 1969 and 1985.

ANNUAL PARTYBOAT CATCH

Between 1978 and 1984, the Palos Verdes fishery accounted for 6.8% of California's total partyboat catch (2.65 million of 38.78 million fish), while anglers represented 7.9% of the state total (418,000 of 5.28 million). The average catch per angler day was lower off Palos Verdes (6.3 versus 7.3), but varied from year to year. Data were examined as total fish for Palos Verdes, by species, and by catch block.

Palos Verdes Total

Table 2 lists the Palos Verdes (blocks 719 + 720) partyboat catches in five-year increments, 1936–85, for total fish and for key species (ranked by overall abundance). Rockfish were the dominant group taken (35% of the total) over the half century; bonito, mackerel, kelp-sand bass complex, and barracuda each contributed at least 10% to the sport catch, and eleven species each generated over 1% of the total. The partyboat fishery grew from 300,000 for 1936–40 to nearly 2 million fish per five years after the late 1960s. Largest gains occurred in the late 1950s and the late 1960s–early 1970s.

The annual partyboat catch from Palos Verdes reflects an overall upward trend, with the exception of a half-dozen ephemeral decreases (Figure 5). From 1965 to 1985, approximately 400,000 fish were taken per year in the two blocks combined. Annual data for 1981–85 (Table 3) reflect the recent catches.

Total fish availability and, indirectly, total population size, are better portrayed by fish per angler (a measure of CPUE) than by numerical catch (which is strongly influenced by the number of fishermen). Generally, number of partyboat anglers is inversely related to the catch per angler (Figure 5).

The total catch per angler appears to have decreased from 1936 through 1950 (although early data may not be as representative); it rose steadily from 1951 through 1980, then decreased from 1981

TABLE 2
Partyboat Fish Catch (in Numbers) and Effort (in Anglers), Palos Verdes Region, in 5-Year Increments

	1936–40	1947–50*	1951–55	1956–60	1961–65	1966–70	1971–75	1976–80	1981–85
Rockfish complex	6,177	91,295	395,545	443,505	86,101	391,024	1,443,729	901,386	306,448
Pacific bonito	3,324	10,200	7,062	297,952	427,181	506,664	191,922	213,200	321,596
Kelp-sand bass complex	121,038	141,580	112,218	127,165	290,042	386,756	182,176	129,109	343,061
Pacific mackerel	19,134	62,040	42,654	34,159	61,050	55,527	42,861	435,079	572,181
California barracuda	141,359	94,508	56,791	333,672	84,535	285,782	15,404	35,259	123,101
California scorpionfish	4,759	15,292	13,788	8,932	28,283	38,977	60,708	58,329	51,421
Ocean whitefish	493	1,224	807	1,677	6,084	13,824	20,943	52,475	21,066
California halibut	8,934	39,808	20,145	6,627	30,690	10,702	2,220	2,001	2,532
Yellowtail	2,780	202	807	60,431	5,506	4,340	7,654	1,329	29,987
White croaker	4,790	14,052	11,702	3,089	8,243	4,200	3,356	6,650	6,232
California sheephead	2,678	2,195	1,091	671	672	839	993	1,372	6,799
White seabass	2,420	2,859	2,101	2,247	873	434	1,373	426	693
Lingcod	387	833	396	254	56	74	1,845	1,561	185
Block 719	35,141	122,880	101,748	76,975	151,376	390,731	707,001	722,793	658,526
Block 720	286,990	373,737	635,353	1,261,590	915,807	1,261,590	1,352,640	1,154,259	1,162,477
Total fish	322,131	496,617	737,101	1,338,565	1,067,183	1,740,590	2,059,641	1,877,052	1,821,003
Total anglers	57,735	159,080	193,876	274,085	177,426	267,862	253,582	229,153	352,020
Catch per angler	5.58	3.12	3.80	4.88	6.01	6.50	8.12	8.19	5.17

*No data, 1941–46; 1947–50 is a 4-year increment.

to 1985. The 1951–80 rise could suggest growing fish populations, but improved fishing strategies may also be important. The decreases in the 1980s could be attributable to (1) El Niño and severe storms in 1982–83, which decimated kelp beds, severely impacted nearshore regions, and caused hundreds of millions of dollars in damage to local coastal areas (U.S. Army Corps of Engineers and State of California 1984), and (2) public awareness of contaminated fish tissues (1984–85).

Block 720 generated 76% of the total Palos Verdes catch since the 1930s (Figure 6), although percent taken in the two blocks varies by species (Table 4). Scorpionfish and ocean whitefish catches were higher in block 719, perhaps because these species are prevalent in the edge-effect zone provided by the Horseshoe Kelp Bed environment (Schott 1976), which consists of rock outcrops scattered on a sandy shoal. Also, wastewater discharges influence the ecology of block 720 more than block 719. Block 720's higher catch is likely due to the greater marine area, more diverse habitats, and especially the higher angler effort from more boat marinas.

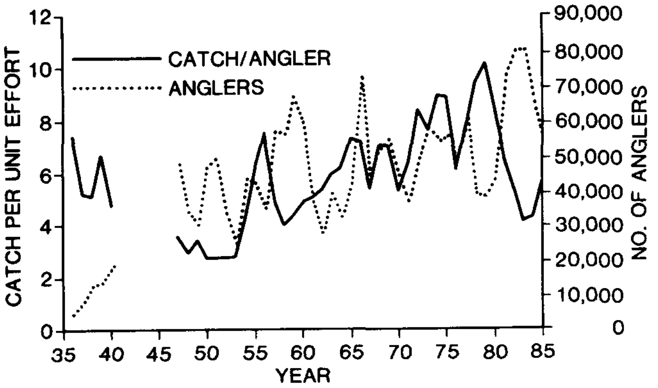

Figure 5. Partyboat anglers and catch per angler, Palos Verdes Shelf, 1936–85.

TABLE 3
Annual Partyboat Catch for Palos Verdes Region

	1981	1982	1983	1984	1985
Rockfish complex	103,773	78,442	31,442	32,897	60,226
Pacific bonito	123,670	30,886	74,052	75,451	17,537
Kelp bass*	50,416	27,870	46,861	22,238	45,107
Barred sand bass*	22,293	18,263	44,853	18,447	46,713
Pacific mackerel	126,347	208,388	74,040	80,298	83,108
California barracuda	23,810	17,730	30,412	27,614	23,535
California scorpionfish	10,589	12,117	10,468	7,721	10,526
Ocean whitefish	2,298	4,345	1,989	2,458	9,976
California halibut	524	1,100	386	255	267
Yellowtail	3,182	2,025	12,968	6,624	5,188
White croaker	1,399	1,336	1,080	2,212	205
California sheephead	1,088	1,027	2,253	1,248	1,183
White seabass	59	79	97	87	371
Lingcod	24	34	22	46	59
Total fish	471,036	427,351	332,553	283,129	306,934
No. of anglers	72,578	79,470	80,117	65,765	54,140
Catch per angler	6.49	5.38	4.15	4.31	5.67

*Reported separately in these years

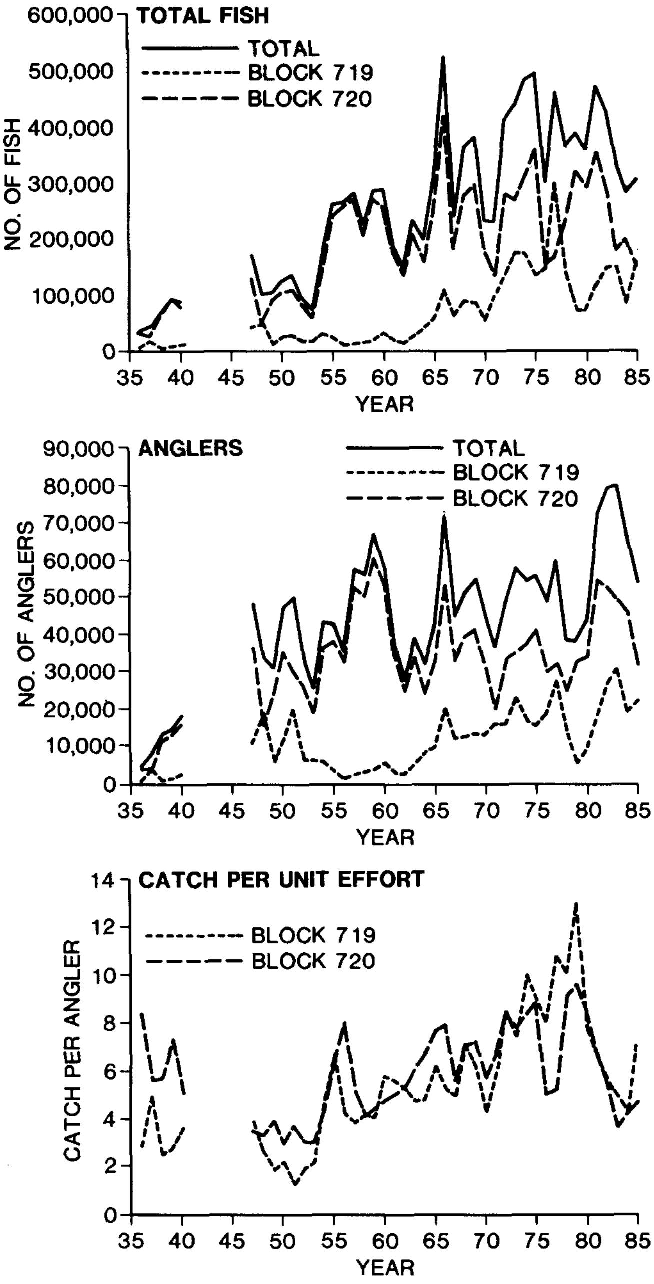

Figure 6. Annual partyboat catch, anglers, and catch per unit of effort for blocks 719, 720, and combined Palos Verdes totals, 1936–85.

Block 720 catch has fluctuated around 250,000 fish per year since 1955; previously fewer than 100,000 fish were reported taken. Block 719 generated fewer fish (under 40,000) through 1965; catch rose rapidly through 1977 to peak at about 300,000; then in the 1980s the average take was approximately 125,000. The pre-1965 rises in Palos Verdes catch were largely from block 720, whereas after 1965 the increase in regional total was from block 719. This reflects relative angler activity in the two blocks (Figure 6).

TABLE 4
Partyboat Percentage of Total Number of Fish (1936–85)

	Block 719	Block 720	Palos Verdes*
Rockfish complex	35	35	35
Pacific bonito	11	20	17
Kelp-sand bass complex	9	17	16
Pacific mackerel	16	10	12
California barracuda	10	10	10
California scorpionfish	5	2	2
Ocean whitefish	2.5	0.5	1
California halibut	2	0.9	1
Yellowtail	0.4	1	1
White croaker	0.9	0.4	0.5
California sheephead	0.2	0.1	0.2
White seabass	0.1	0.1	0.1
Lingcod	0.04	0.05	0.05

*Block 719 + block 720

Total fish and total anglers were about three times higher in block 720; however, catch per angler was more similar in the two blocks (Figure 6), with 720 slightly higher before 1971, and 719 higher more recently.

Individual Species

Partyboat catch records of 13 species (95% of total Palos Verdes 1936–85 catch) were examined (Table 2). In the material that follows, species are ordered by abundance in the combined 50-year catch.

Individual species trends are typically independent of total catch trends, because of differences in habitat requirements, angler selection, angling regulations, and environmental conditions. Trends in blocks 719 and 720 are not identical. In some cases, dominant influences on species abundance can be separated; often, the factors are too complex for any to be isolated.

Catch per angler is not as useful an indicator of species population sizes; relative availability is a more appropriate term. Partyboat effort is multispecific and largely opportunistic: the species represented in the day's catch are a function of habitat, and different habitats are not fished with equal effort each year.

It is important to data interpretation that catch per angler in block 719 is almost always higher or at least equivalent to that in block 720 for all target species except three. The pelagic bonito and yellowtail have a slightly higher overall catch per angler in block 720, as does the kelp-sand bass complex. This may be related to physical structure—e.g., more offshore area and kelp in block 720.

Rockfish complex. Rockfish ranked highest in total partyboat catch (1936–85). Many biologically diverse *Sebastes* species are combined in this complex, including bocaccio, chilipepper, vermillion, cow, and olive. Rockfish became popular after the 1950s, with peak take in the mid-1950s (over 200,000) and mid-1970s (over 400,000). The percentage of the total partyboat catch rose from near zero in the 1930s to over 50% in the early 1950s, and 70% in the early 1970s. Low catches from 1958 to 1964 could be related to environmental deterioration (including the absence of kelp beds or sediment contaminants), to overfishing, or to El Niño effects. Poor 1980s catches may be associated with storm-related kelp losses or El Niño effects. Although catch per angler was similar in the two blocks, more fish were taken from block 720.

Pacific bonito. Bonito catch showed two periods of increase (post-1955 and post-1977) and low values before 1955 and from 1974 to 1977. Average take in block 719 was about 12,000 per year, as compared to about 50,000 in block 720. The relative availability was only slightly higher in block 720, and variable temporal patterns in the two blocks are similar.

Kelp-sand bass complex (kelp bass, barred sand bass, spotted sand bass). The status of the kelp-sand bass complex resource has been closely monitored for 50 years. *Paralabrax* spp. were first regulated in 1939, when a 15-fish limit was imposed for an aggregate of species including these bass. No *Paralabrax* could be sold or purchased from 1953 on, when the first size limits (10.5 inches, or 27 cm) were instituted. The size limits were gradually increased to 12 inches (30.5 cm) by 1959, with a limit of 10 fish in 1979.

Unfortunately, before 1975, data did not reliably or consistently differentiate between kelp bass (*Paralabrax clathratus*), barred sand bass (*P. nebulifer*), and rock bass (*Paralabrax* spp., also including the spotted sand bass, *P. maculatofasciatus*). Relative proportions of the kelp bass and barred sand bass from 1935 to 1975 cannot be estimated.

The combined total take peaked in 1968 (approximately 110,000 fish) and again in 1983 (100,000 fish); the 1968 peak was preceded (before 1960) and followed (1973–80) by catches one-third or less that size. In 1985, approximately 45,000 kelp bass and 47,000 barred sand bass were taken (Table 3).

The rise in kelp bass-barred sand bass complex from 1974 to 1985 parallels the increase in geographic distribution of kelp (*Macrocystis*) off Palos Verdes; both showed greatest recovery in 1980. Kelp forests had disappeared from the Palos Verdes nearshore region during the early 1960s, and reestablishment was largely unsuccessful until 1974. Natural environmental fluctuations and wastewater discharge are believed to have caused kelp's temporary demise (Mearns et al. 1977; Wilson et al. 1980; Meistrell and Montagne 1983). The low 1984 catch is likely related to temporary habitat loss (kelp canopy was virtually destroyed by winter storms in 1983; Wilson and Togstad 1983); by 1985 there were up to 325 hectares of kelp on the peninsula. The lack of correlation between declines of kelp and kelp-sand bass complex may be ascribed to either lag in response time or to dominance by sand bass, which are not associated with kelp.

Higher kelp bass in block 720 correlates with relative kelp/rock habitat. Between 1980 and 1985, 40,000–50,000 kelp bass were taken from the two blocks combined, with block 720 accounting for 50%–60% of the total. Before 1980, block 720 accounted for a greater proportion of the catch. Relative availability was higher in block 720 until 1979; thereafter relative availabilities were similar.

Block 719 generated more barred sand bass than did block 720. This is also a shallow-water species, but it prefers rocky, hard-bottom or sand areas. On the average, 30,000 barred sand bass were taken from the two blocks in the 1980s. Relative availability was considerably higher in block 719 after 1974.

Pacific mackerel. Catch of the nearshore, pelagic, migratory Pacific mackerel increased from the mid-1970s, and approximately 100,000 fish were taken in the 1980s (block 720 dominated the take). Catch was lower in 1983–85 than in 1977–82, but still surpassed pre-1976 by several orders of magnitude. Higher catches coincide with El Niño events, suggesting mackerel migration into the region (e.g., 1966, 1976–78, 1982–83). Relative availability patterns follow similar trends in the two blocks, but 719 values are generally higher. Mackerel are not always preferred or consumed by humans, and there are no bag limits.

California barracuda. Barracuda catches fluctuated over the half century. The 1971 decrease correlates with the imposition of a 28-inch (71-cm) size limit. The regulatory history for this species dates back to 1935 (not more than 5 fish weighing less than 3 pounds) and 1939 (inclusion in the maximum of 15 for aggregate species). The 28-inch (71-cm) size limit was introduced in 1949 (no more than

5 smaller individuals) and became more stringent in 1957 (daily maximum of 2 smaller individuals) and 1971 (none below size limit). Commercial restrictions have been consistent since 1940. The 1971 regulation may be promoting population recovery, because the catch of legal-size individuals has gradually risen. Catch appears to be related to migration from the south in warmer El Niño years: note the peaks in 1958, 1966, 1976, and 1983 (Figure 7a). Since 1971, total partyboat catch is on the order of 20,000 fish per year. Catch in block 719 was generally lower than in block 720 until 1980; the difference is accentuated in peak population years. Perhaps the rockier open coastline of block 720 is preferred. Almost identical relative availability patterns were observed in blocks 719 and 720 for over 40 years; however, availability in block 719 increased more rapidly after 1980.

California scorpionfish (sculpin). Fishermen were, on the average, four times more successful at catching the bottom-dwelling sculpin in block 719 than in block 720 through most of the 1970s (Figures 7a and 8); 1980–85 relative availability values were more comparable, although fewer fish were taken in block 719. Sediment contaminant burdens (Stull and Baird 1985; Stull et al. 1986 a, b) and reduced food availability (crabs, fish such as anchovies, cephalopods, shrimp; Allen 1982) may be reflected in the lower catch for block 720 and the relative availabilities of the late 1960s to late 1970s. Surface sediments in block 720 supported higher concentrations of wastewater-derived DDT, PCBs, metals, and organic matter, and less diverse infaunal and epifaunal communities. Sculpin are attracted to outfall structures (Allen et al. 1976). From 1970 to 1984 availabilities have opposite trends in the two blocks.

Ocean whitefish. Very few ocean whitefish were caught before 1960. In the succeeding 25 years, this species was more abundant during El Niño years, perhaps as a function of migration with warmer waters. Whitefish were more prevalent in block 719. Peak annual catch was in 1977, with about 35,000 fish taken. The typical average annual catch was less than 5,000. Block 719 had a higher relative availability, especially since 1966.

California halibut. Sportfishing regulations for halibut date back to 1949 (daily maximum, 10) and have been modified in response to concern for the population: 1956 (10 maximum, no more than 5 under 4 pounds); 1957 (no more than 2 shorter than 22 inches, or 56 cm); 1959 (2 maximum, no size limit); and 1971 (none shorter than 22 inches, or 56 cm, bag limit of 5). Imposition of the minimum size limit in 1971 probably explains more recent low counts of this sand-preferring bottom species. An earlier low catch (1956–57) coincided with El Niño conditions. Environmental degradation and loss of coastal and estuarine nursery areas may also impact this species. The total partyboat catch after 1971 was generally less than 500, as compared to highs of 15,000 in 1948 and 11,000 in 1964.

Yellowtail. Yellowtail catch was higher in major El Niño years (e.g., 1957, 1983); peak catch is consistently higher in block 720. Maximum total catch, in 1960, was approximately 32,000; the most recent peak (in 1983) was approximately 14,000 fish. In intervening years fewer than 4,000 were taken. Relative availability patterns were parallel in the two blocks, although availability in block 720 was higher, especially in 1960.

White croaker. In block 720, relative availability of white croaker was low from 1954 to 1961, from the mid-1960s to 1973, and in 1978. Catch generally increased after 1973, then plunged in 1985.

In block 719, relative abundance of white croaker was highest from 1950 to 1968, except for smaller catches in 1956, 1959, and 1966. Catch was generally lower in the 1970s and 1980s. The annual average partyboat take for block 720 in the 1970s and 1980s was about 750 croaker, and for block 719 was about 500. Relative abundance was clearly higher in block 719 until 1981, when it decreased below that in block 720. Since the 1950s, relative availability for block 720 has been more consistent.

White croaker are common in harbors and open coastal areas, particularly over organically enriched sediments. They are a ubiquitous, high biomass, easily taken species (Love et al. 1984). These omnivores inhabit a broad depth range. Tissues are fatty, and the lipophilic behavior of DDT and PCBs has resulted in elevated tissue concentrations of these chlorinated hydrocarbons. In 1985, the CDHS posted warnings along the shore advising that Palos Verdes and Santa Monica Bay white croaker should be avoided, and other sportfish consumption should be reduced to 1–2 meals per week. CDHS's interim guidelines further advised avoiding any fish from areas immediately around the Whites Point outfall, Gerald Desmond Bridge, and Cabrillo Pier (in Long Beach-Los Angeles harbors).

Reproductive abilities of white croaker may have been inhibited by environmental contaminants such as DDT or PCBs from treated waste-

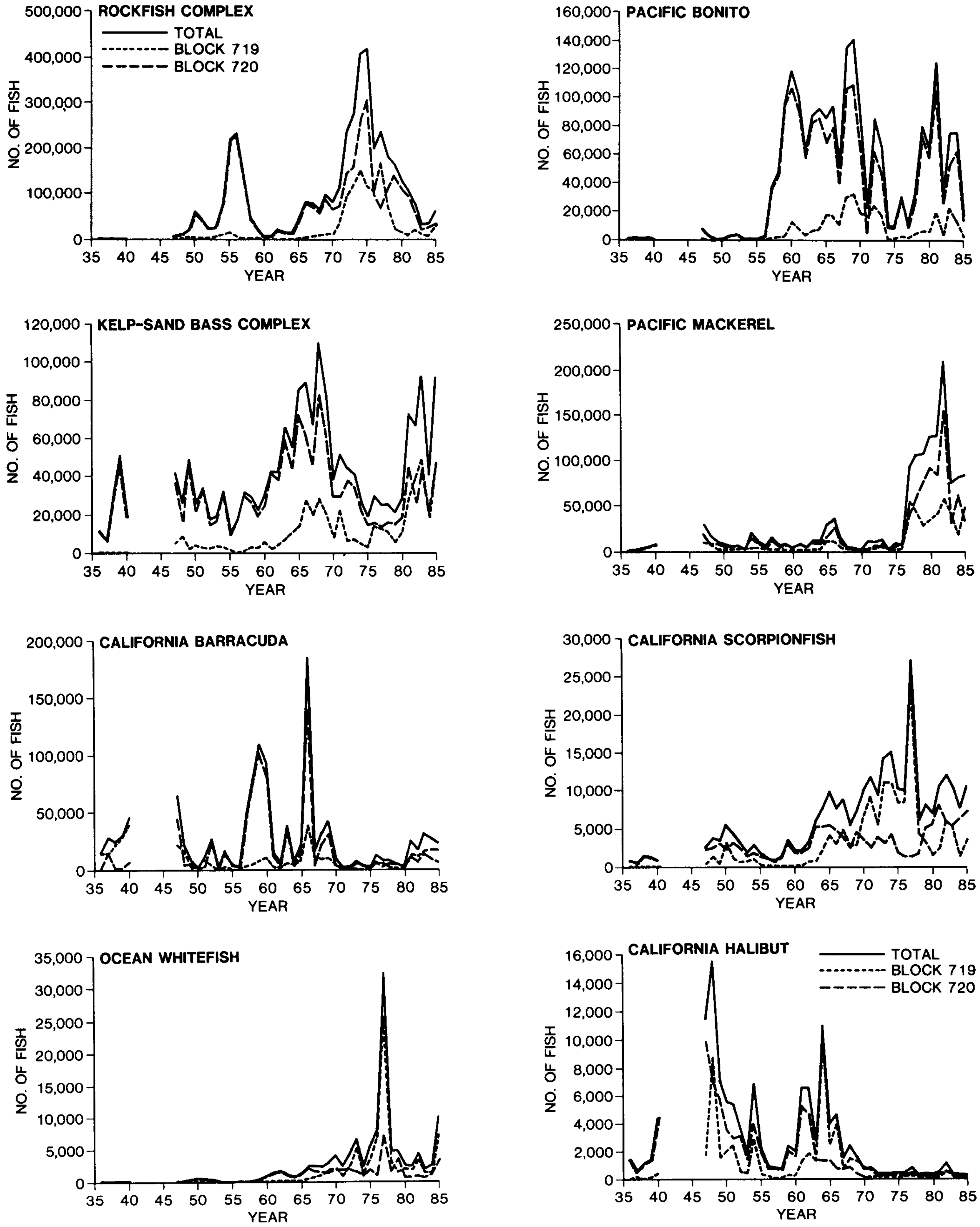

Figure 7a. Annual partyboat fish catches from Palos Verdes blocks 719 and 720, 1936–85.

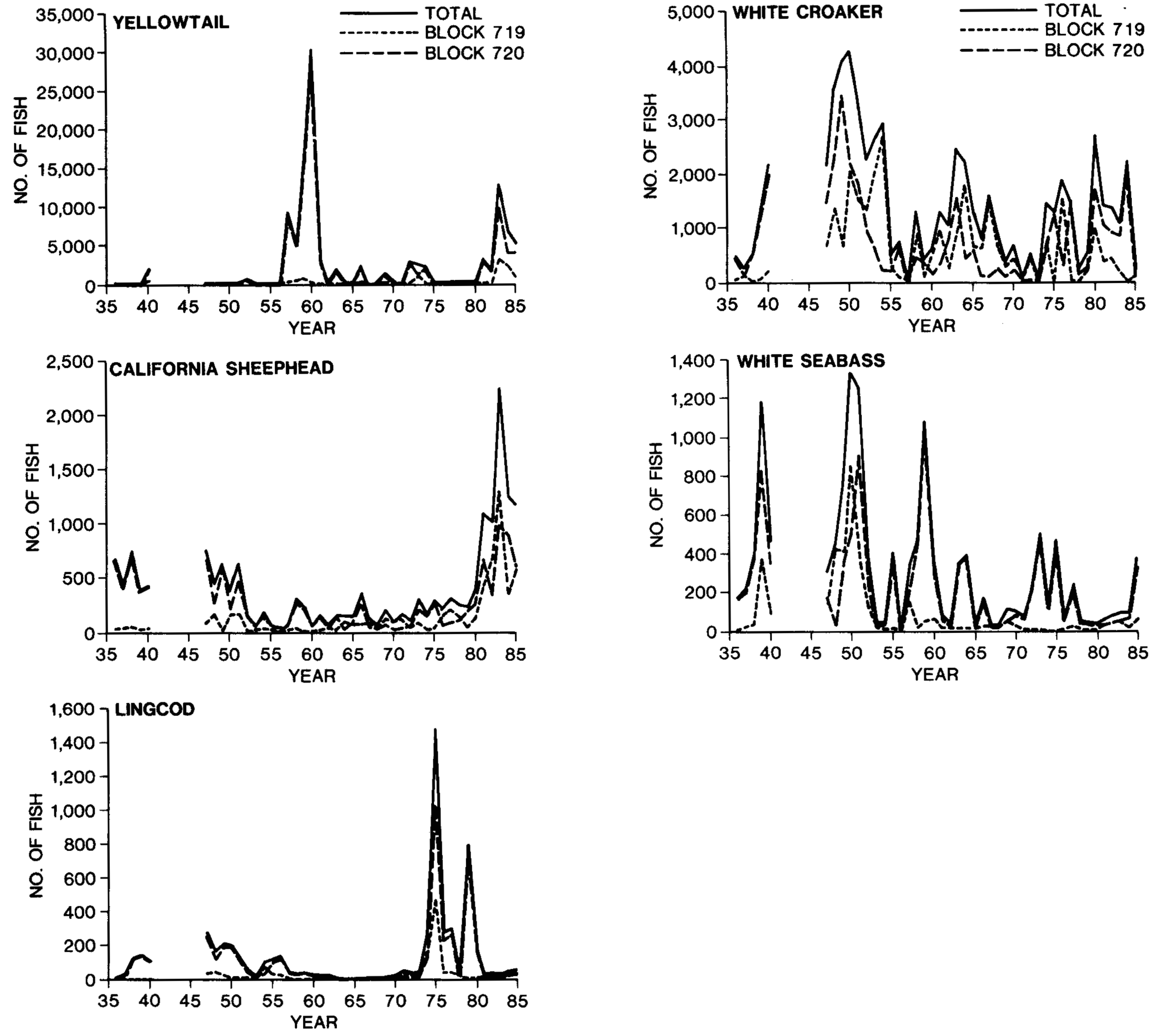

Figure 7b. Annual partyboat fish catches from Palos Verdes blocks 719 and 720, 1936–85.

waters, dumping, runoff, and aerial sources; these constituents accumulated in sediments and biota but decreased during the 1970s.

White croaker is not held in high regard by most experienced partyboat anglers. Two other potential reasons for an increase in recent recorded catches are the fish's appeal to Asian-Americans, whose numbers are probably increasing on partyboats, and increased use as bait for halibut or other predators. The recorded catch may include those kept for bait in addition to those taken home. There are no bag or size limits.

California sheephead. Sheephead take decreased in the 1950s and rose in the late 1970s and the 1980s. An improved nearshore environment (kelp, rocky regions) probably contributed to its stronger status (Figures 3 and 7b). Sheephead are more commonly taken in warmer years. Block 720 usually produced higher catches, and after 1955 relative availability was typically about twice as high in block 719. In the 1980s, approximately 2,300 sheephead were taken annually in the two blocks combined.

White seabass. White seabass catch fluctuated over the five decades, but in general its population appears to have declined off Palos Verdes, as elsewhere in the state (Vojkovich and Reed 1983). This shallow-water species has been rare in block 719

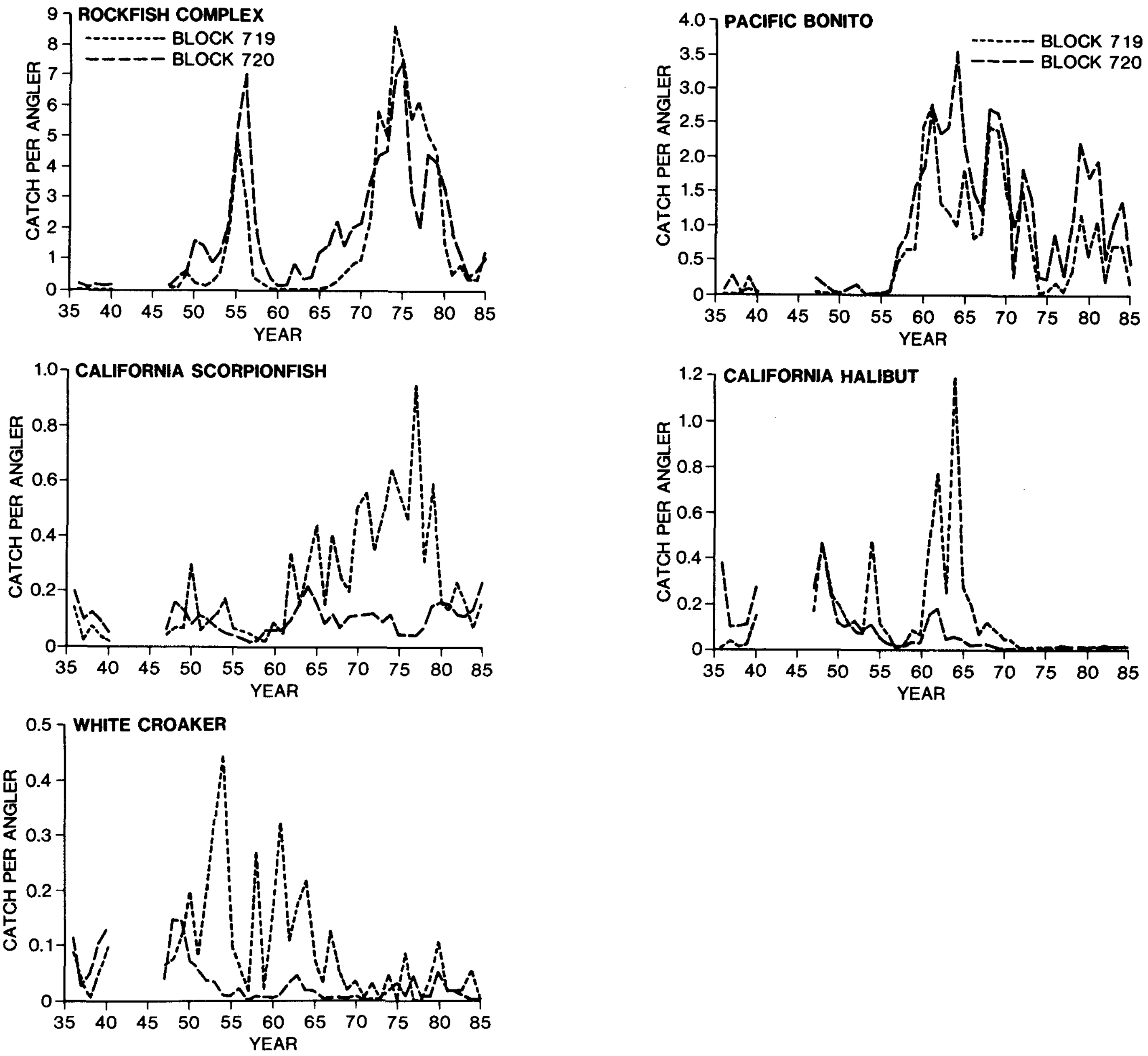

Figure 8. Relative availability of fish species off Palos Verdes, 1936–85.

since 1950; it may prefer the kelp and rocky points of block 720. Annual partyboat catch was usually less than 400 fishes from 1955 (except about 1,000 in 1959), and relative availability was low for both blocks.

Lingcod. Lingcod are not abundant in southern California; they are a more common game fish north of Point Conception or in areas of localized cold-water upwelling. Partyboat catch was highest from 1973 to 1980; 1975 and 1979 had sharp peaks in block 720, but there was only a 1975 peak in block 719. Maximum catch for the two blocks in 1975 and 1979 was 1,500 and 800, respectively; earlier and more recent annual catch was usually under 200 fish. There is no consistent pattern in relative availability or catch in the two blocks.

Several species (rockfish complex, sheephead, lingcod) displayed low catch records in both blocks from the late 1950s to early 1970s, and higher catch before and after this time. The low catches coincide with maximum effluent contaminant emissions and less control on other discharges into the marine environment. Kelp was virtually absent (Wilson et al. 1980; Meistrell and Montagne 1983). On the other hand, the pelagic bonito catches were highest during this period and may have diverted anglers' effort.

MONTHLY PARTYBOAT CATCH

Palos Verdes Total

There is an annual cycle of increased total catch and number of anglers during the late summer, and a decrease during the winter, shifting greatest catch availability to winter. A boat with a few experienced, resident anglers fishing for rockfish (15-fish limit, easily caught) in the winter will have a higher catch per angler than a boat filled with tourists seeking kelp bass or yellowtail (10-fish limit, high loss) during the summer. Palos Verdes fish catches and catch per angler generally show an inverse relationship: the 1970–78 portion of the catch history is magnified in Figure 9.

Individual Species

Patterns vary by species. The most distinct annual catch cycle, with seasonal vulnerability, is found for bass. A similar pattern exists for halibut, barracuda, sheephead, and white croaker. Other species from Table 1 have more uniform vulnerability. Migratory habits (north/south, inshore/offshore), temporary habitat changes (e.g., kelp bed destruction by winter storms), or seasonal changes in targeted species may explain the cyclical catch patterns.

ANNUAL COMMERCIAL CATCH

Commercial landings (in pounds or short tons), 1969–83, were also summarized by total catch, by species, and by block. Commercial fisheries are highly species selective, and more technological advancement in gear has increased fishing efficiency over the years. All commercial net fishing is prohibited in Santa Monica Bay, including a small section of block 720 north of Palos Verdes Point. Some species of fish cannot be harvested commercially (e.g., the kelp-sand bass complex, *Paralabrax* spp., since 1953). Often commercial catches parallel those from partyboats; however, economic pressures are more important in determining commercially targeted fish and effort, making it more difficult to correlate commercial catch and environmental parameters.

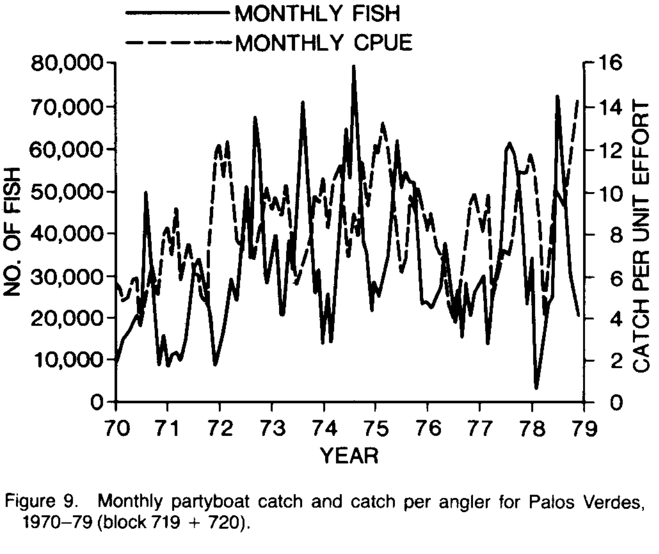

Figure 9. Monthly partyboat catch and catch per angler for Palos Verdes, 1970–79 (block 719 + 720).

Palos Verdes Total

Approximately 5 million pounds of fish and invertebrates were taken commercially from blocks 719 and 720 between 1969 and 1983, with peaks of over 14 million pounds in 1975 and 1976. Almost 70% of the catch, 1969–83, was northern anchovy; in 1975–76, 90% was anchovy (Figure 10). After 1978, anchovy's contribution decreased to 42%. Non-anchovy total poundage fluctuated with anchovy catch, rising in the mid- and late 1970s, and then declining in 1983, perhaps as a result of El

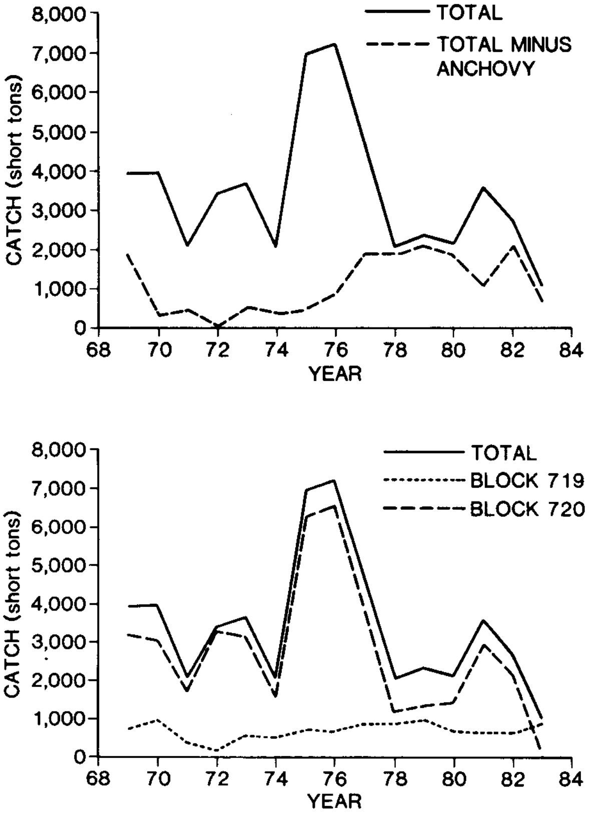

Figure 10. Annual commercial catch taken from the Palos Verdes region, including and excluding anchovy landings, 1969–83. Total catch represents a combination of blocks 719 and 720.

TABLE 5
Commercial Percentage of Total Landings (1969–83)

	Block 719	Block 720	Palos Verdes*
Northern anchovy	40	76	69
Pacific mackerel	9	4	5
Pacific bonito	5	2	3
White croaker	5	0.3	1
White seabass	0.3	0.3	0.3
California halibut	1.2	0.06	0.3
Rockfish complex	0.2	0.1	0.1
California barracuda	0.4	0.02	0.09
California scorpionfish	0.2	0.02	0.06
California sheephead	0.02	0.003	0.006
Sea urchin	3	3	3
Rock crab	0.8	2	2
Market squid	0.7	0.7	0.7
California spiny lobster	0.2	0.2	0.2

*Block 719 + block 720

Niño. Peak non-anchovy take was 4 million pounds.

Block 720 dominates both the partyboat and commercial catches. Anchovy predominates in both blocks, especially in block 720 (Table 5). A relatively steady annual catch of 500–1,000 short tons is taken from block 719; the catch from block 720 fluctuated up to 7,000 tons in peak anchovy years.

Individual Species

Commercial catches of ten common fish species and four invertebrates summarized below represent approximately 85% of the total poundage (Figures 11a, b).

Northern anchovy. From 1969 to 1983, the anchovy—a pelagic, mostly filter-feeding species—has supported an important fishery. Natural population fluctuations (especially in relation to sardine and mackerel abundances); usage (mostly as bait, meal, oil); and economic factors partly determine catch size. Forty percent of block 719 landings (0.5 million pounds) and 76% of block 720 landings (approximately 4 million pounds) were anchovy. Since 1978, catch has been below 1 million pounds, except for 1981's peak of 5 million pounds.

Pacific mackerel. The mackerel catch pattern reflects partyboat data and statewide trends (Klingbeil 1983) in its large rise from 1977: peak take (1.4 million pounds) occurred in 1982; the poundage plunged in 1983 (to about 175,000 pounds), possibly because of El Niño. The two blocks contributed equally.

Pacific bonito. Total bonito landings declined after 1969, when exceptionally high catches (almost 700,000 pounds) were taken from block 720. Total take was approximately 100,000 pounds per year from 1971, with 1975, 1982, and 1983 relatively unproductive.

White croaker. Eighty percent of the total commercial catch of white croaker was from block 719. Average total take over the 15 years was 75,000 pounds, with peaks in 1974 and 1979. The commercial catch pattern paralleled partyboat records. Increased use of monofilament gill nets may contribute to higher landings. Most white croaker are sold fresh, but some are used in Asian food products (Love et al. 1984).

White seabass. Highest numbers of white seabass were taken from 1971 to 1973 (60,000–85,000 pounds); the following decade typically generated 10,000–25,000 pounds of seabass. As with the partyboat data, block 720 was considerably more productive (82% of the 15-year catch).

California halibut. Commercial catch of halibut generally rose from 1974 to 1982. In 1981–82, 65,000 pounds were taken; in 1983, 50,000 pounds were collected. Eighty-three percent of the 15-year catch derived from block 719; only since 1979 have 5,000 pounds of this bottom-dwelling species been taken from block 720.

Rockfish complex. Annual commercial catch of rockfish showed an increasing trend from 1969 to 1980, with a maximum of 15 short tons. A statute effective in 1981 ruled that no rockfish could be taken commercially within the 50-fathom contour, unless incidentally: this probably contributed to the significant declines of the 1980s.

California barracuda. This species made up only 0.09% of the total 15-year Palos Verdes catch; however, its contribution has risen steadily since the early 1970s. Maxima were in 1980–82; in 1982 approximately 17,000 pounds were taken. Gear restrictions apply: no purse seining is allowed, but gill nets over 3.5 inches have been allowed since 1940.

California scorpionfish. On the average, total take was 1,000 pounds of sculpin between 1969 and 1980. Higher landings in 1981 (block 720, approximately 10,000 pounds) and 1982 (block 719, approximately 24,000 pounds) suggest selective fishing, as does the notable lack of sculpin in the 1970s, especially from block 719, when it was commonly taken by partyboats, although it was rarely a target species.

California sheephead. Total annual sheephead take was less than 200 pounds until 1978; about 600

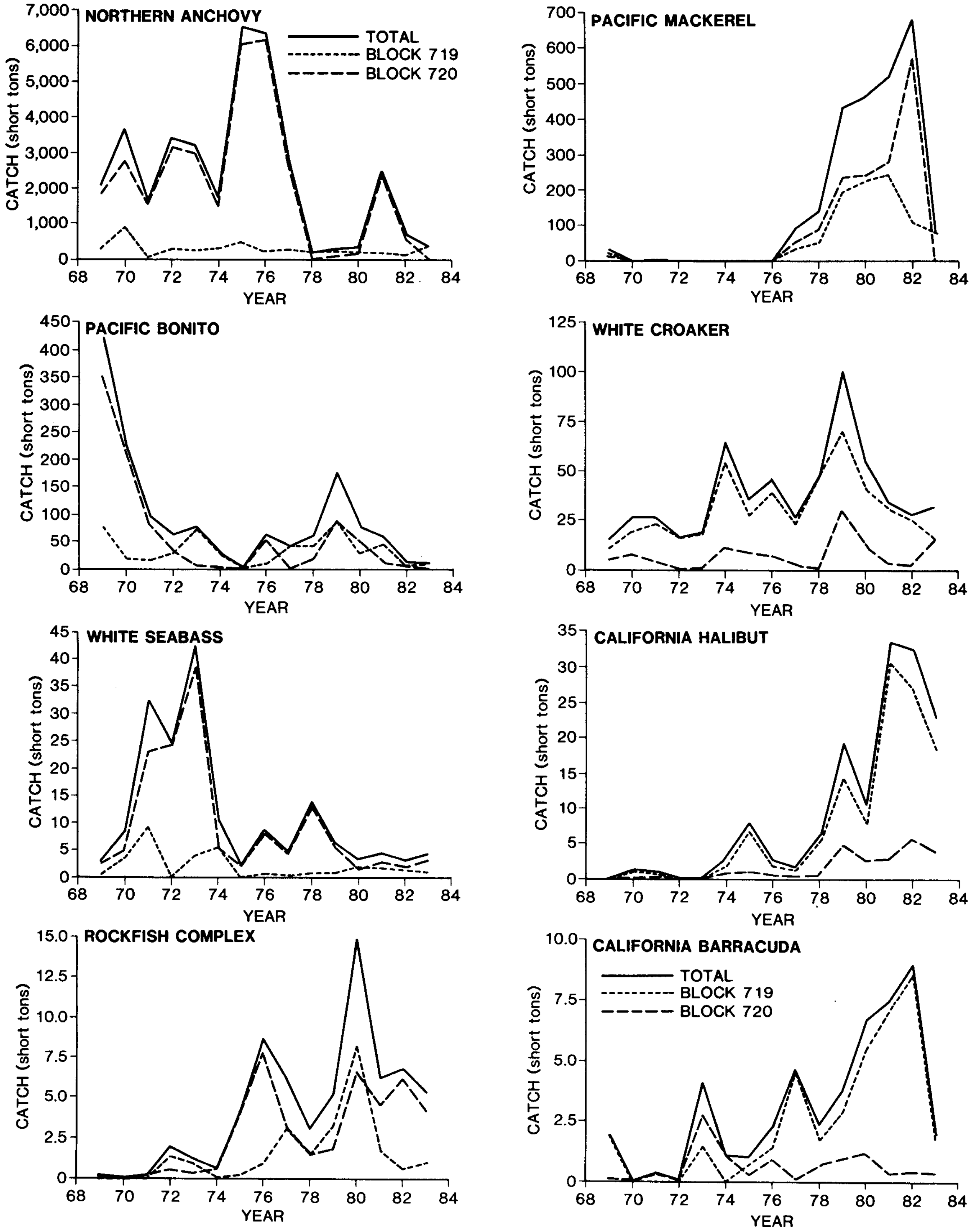

Figure 11a. Annual commercial catch of fishes and invertebrates from Palos Verdes, 1969–83: blocks 719, 720, and combined total.

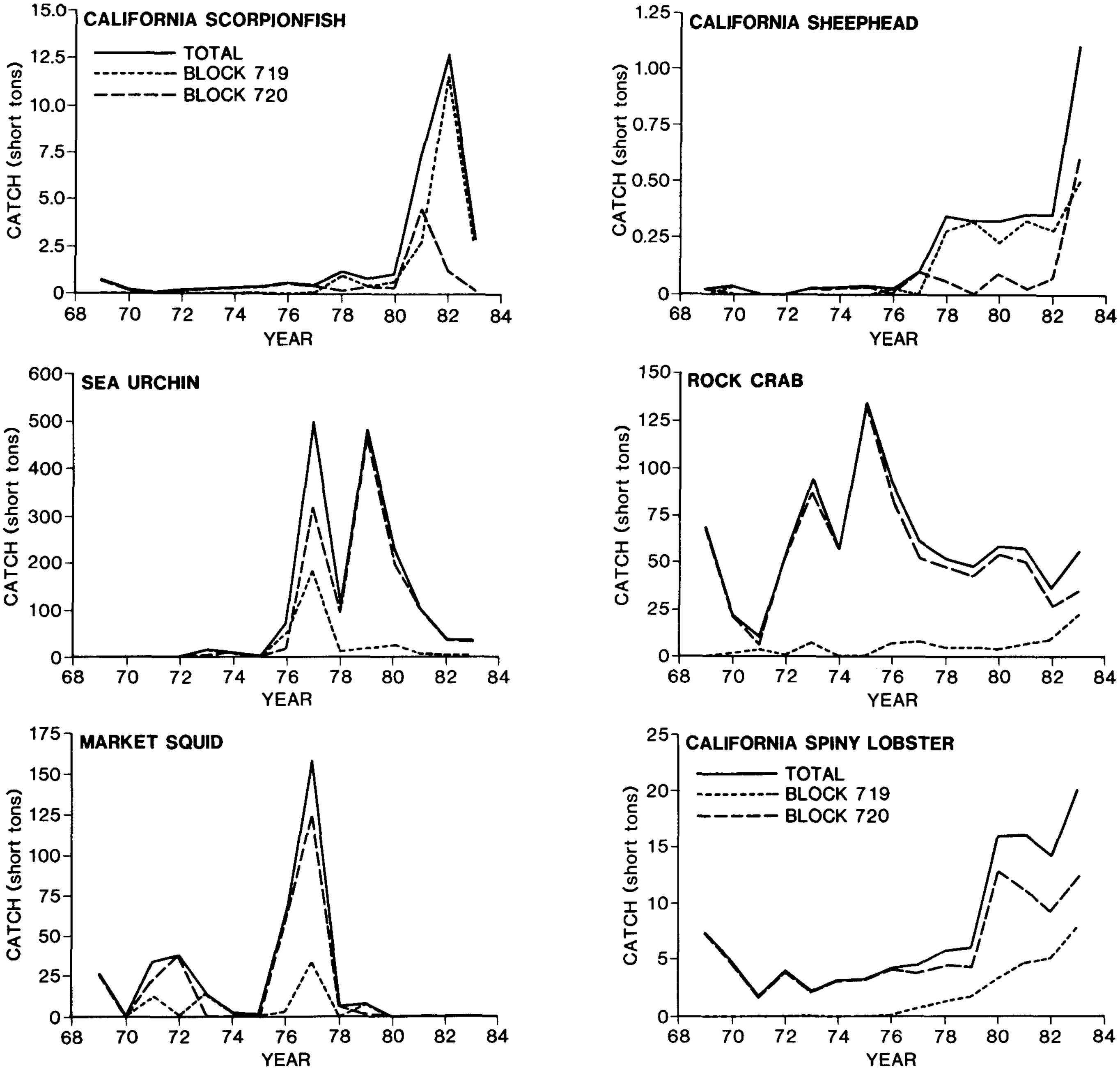

Figure 11b. Annual commercial catch of fishes and invertebrates from Palos Verdes, 1969–83: blocks 719, 720, and combined total.

pounds were taken per annum from 1978 to 1982; and 1983 generated 2,400 pounds. Block 719 catch generally exceeded that of block 720 (65%:35%); the discrepancy was most apparent from 1978 to 1982.

Sea urchin. The preferred species is the red sea urchin, *Stongylocentrotus franciscanus,* but the purple urchin, *S. purpuratus,* is taken coincidentally. Harvesting of sea urchins began on a large scale in 1976, and up to a million pounds were taken in 1977 and 1979. By 1982 fewer than 100,000 pounds were taken, mostly from the kelp bed regions of block 720. Only in 1977 were many taken from block 719. Both purple and red urchins were abundant on the shelf and were systematically removed (not commercially) in large numbers during initial kelp transplant efforts on Palos Verdes in the early 1970s. Red sea urchins became a harvestable resource (in terms of biomass and roe quality) following kelp restoration, when clearance and control efforts were directed toward purple urchins

(Wilson and McPeak 1983). Overharvesting of red urchins diminished stocks and gave purple urchins the competitive advantage: in the 1980s reds are scarce, and purples occupy much of the niche formerly occupied by red urchins. Severe storms in 1982–83 displaced many purple urchins. White urchins (*Lytechinus anamesus*) have also moved onto the shelf in large numbers in the 1980s (Wilson, pers. comm.).

Rock crab. Block 720 yielded most of the rock crabs (*Cancer* spp.) taken from the Palos Verdes region. Maximum harvest, in 1975, was over 125 tons; average take is under 50 tons.

Market squid. The erratic appearance of *Loligo opalescens* in the catch is probably related to water temperature and vagaries of spawning areas, where squid are caught commercially. Maximum landings occured in 1977 (over 300,000 pounds), but typical catch is less than one-third this peak. Most squid were from block 720.

California spiny lobster. Lobster landings increased from the early 1970s, and highest catches in the 1980s averaged over 15 tons. Monthly catch records show seasonally controlled harvesting.

Kelp. The giant kelp (*Macrocystis pyrifera*) was commercially harvested from four CDFG-designated kelp beds ringing the Palos Verdes Peninsula between 1916 and 1954 (State Water Resources Control Board 1964). Tonnage information is confidential; however, relative values are available as annual percentage harvest from various beds, using the year of maximum yield as 100%. Data on areal coverage of the canopy and percentage harvested show that the first thinning and disappearance occurred in areas closest to the ocean outfalls; subsequent deterioration was observed at greater distances (State Water Resources Control Board 1964). The complex combination of factors influencing the decline and subsequent restoration of kelp forests (from the mid-1970s) is summarized in Wilson and McPeak (1983). Kelp canopies provide food and refuge for larval and adult fish and for invertebrates such as urchins, lobster, and abalone. The availabilities of many potentially harvestable marine resources are related to kelp coverage.

MONTHLY COMMERCIAL CATCH

There is a pronounced monthly cycle for commercial catch data. For most species, there is either a relatively large catch or none, depending on legal seasons, seasonal fishing effort, species availability, fish migratory patterns, and other factors. The highest totals occur in the summer.

SUMMARY

Among the partyboat catch data, the 13 fish taxa may be grouped into several temporal patterns:

Rockfishes, ocean whitefish, sculpin, and lingcod all peaked sharply in the mid- to late 1970s, followed by steep declines and slight rises by 1985. Rockfish had an earlier maximum in 1956–57. Lingcod had a second peak in 1979.

Three pelagic fish—mackerel, bonito, and yellowtail—showed steep increases in catch in the early 1980s, but other catch histories are poorly related. For mackerel, all recorded catches were relatively low until 1977, when a rising trend began (peak of 210,000 taken). The 1983–85 catches were half that of 1982. Bonito was commonly caught from 1957 to 1973, but the catch was low in the mid-1970s and 1985. Yellowtail catches are most closely associated with water temperature: peaks in 1960 and 1983 were higher than others.

The kelp-sand bass complex declined in the 1970s but rose in the 1980s with notable habitat improvements (kelp canopy increased, sediment contamination decreased). Comparably high bass catches were recorded in the mid-1960s. Similarly, sheephead rose in the 1980s, following low counts since the early 1950s.

Halibut and barracuda takes decreased in 1971, when minimum size limits were imposed. Barracuda limits appear to have helped restore the resource, as reflected in rising catches. This species clearly prefers warmer waters. Halibut population recovery is not observed in these data. Young fish prefer estuaries and coastal wetlands, which are greatly diminished habitats in southern California.

White croaker catch fluctuated a great deal over the half century. Lows in the late 1950s, early 1970s, and 1978 may be attributed to differences in recruitment success, desirability by consumers, or reporting criteria. However, the 1985 decrease clearly coincides with concern for human health generated by CDHS warnings of chlorinated hydrocarbon contamination in fish tissues.

White seabass have generally declined since the 1950s; the appearance of this "good year-bad year" species may be related to migration, but overall this species is a source of concern.

The period from 1981 to 1985 has been characterized by higher than 50-year average takes for mackerel, sheephead, kelp-sand bass complex, yellowtail, scorpionfish, ocean whitefish, and bonito. The 1981–85 catches were lower than average for halibut, lingcod, white seabass, and rockfishes, and similar to the 50-year average for white croaker and barracuda. The mackerel represents the greatest resurgence in a fishery resource, although significant rising trends in the kelp-sand bass complex and sheephead are encouraging.

Among the commercial catches (1969–83), shorter-term temporal patterns are as follows.

Mackerel, halibut, sculpin, and barracuda landings increased steadily until 1982, and then declined sharply in 1983, possibly because target species changed during El Niño conditions. Barracuda takes rose from 1973, halibut catches rose from 1974, mackerel from 1977, and sculpin from 1981.

Rockfish take also increased over the 15 years, and landing trends were often the inverse of those for halibut.

Sheephead landings also began a rise in 1977; the best year was in 1983.

Poundage of anchovy and white croaker fluctuated continuously, but 1982 and 1983 catches were low in all cases.

Bonito take, also low in 1982–83, dropped sharply between 1969 and 1972 and never recovered to previous weights.

White seabass poundage peaked in the early 1970s, decreased in 1974–75, and low catches were reported through 1983.

The Palos Verdes Shelf has provided a substantial resource to southern California fisheries over the past half century. Total reported partyboat catches were 11.5 million fish from 1936 to 1985; commercial landings were 52,000 short tons for 1969–85. Relative species takes fluctuated in response to many environmental and societal factors, and caveats are implicit in any suggested correlations between species catches and underlying sources of variability. A multivariate analysis of long-term data might contribute to a better understanding of specific causal relationships. Also, Palos Verdes fisheries data should be compared to other urban and "control" regions, and to Southern California Bight and statewide data. Unfortunately, this was beyond the scope and effort allocated to this project.

ACKNOWLEDGMENTS

Joyce Underhill and the personnel of Marine Fisheries Statistics, Department of Fish and Game, were helpful in providing commercial fisheries catch records. CDFG reports, including Marine Biological Consultants (1985), gave substantial guidance. Tsam Wong plotted hydrographic data. Irwin Haydock's advice and constructive reviews are appreciated.

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DEMERSAL FISHES OF THE UPPER CONTINENTAL SLOPE OFF SOUTHERN CALIFORNIA

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ABSTRACT

This study covers the composition, distribution, and abundance of fishes collected by otter trawl and longline between 290 m and 625 m. Fifty-four species of fish were collected: 42 species were caught in trawls, and 30 species were caught on longlines. Only 18 species were caught by both types of gear. The number of species decreased with increasing depth in the trawls but not on the longlines. There were no depth-related trends in abundance or biomass for either gear. Fewer fish were caught during the summer by both types of gear.

Trawl catches were dominated by *Sebastolobus alascanus, Sebastolobus altivelis, Sebastes diploproa, Microstomus pacificus, Glyptocephalus zachirus,* and *Lyopsetta exilis.* Composition of the trawl catches was consistent between areas, seasons, and years.

Longlines were used on mud and banks. Catches on the mud were dominated by *Sebastolobus alascanus, Anoplopoma fimbria,* and *Sebastolobus altivelis.* Catches on the banks were dominated by *Anoplopoma fimbria, Sebastes melanostomus,* and *Sebastolobus alascanus.*

RESUMEN

Este estudio examina la composición, distribución, y abundancia de peces colectados con red de arrastre y espinel entre 290 y 625 m. Cincuenta y cuatro especies de peces fueron colectadas, de las cuales 42 fueron capturadas en redes y 30 en rastras. Solamente 18 especies fueron capturadas con ambos métodos. El número de especies disminuyó con el aumento en profundidad en las redes pero no en las espineles. No hubo una relación entre abundancia o biomasa y profundidad para cualquiera de las técnicas.

Las capturas de las redes estuvieron dominadas por *Sebastolobus alascanus, Sebastolobus altivelis, Sebastes diploproa, Microstomus pacificus, Glyptocephalus zachirus,* y *Lyopsetta exilis.* La composición de la captura por las redes fue consistente entre áreas, estaciones, y años.

Los espineles fueron usadas sobre lodo y bancos. Las capturas en el lodo estuvieron dominadas por *S. alascanus, Anoplopoma fimbria,* y *S. altivelis.* Las capturas en los bancos estuvieron dominadas por *A. fimbria, Sebastes melanostomus,* y *S. alascanus.*

INTRODUCTION

The demersal fish fauna from depths greater than 200 m off southern California is not well known (Horn 1980). The fishes were first sampled by beam trawl from the steamer *Albatross* during U.S. Fish Commission surveys from 1888 to 1911 (Fitch and Lavenberg 1968; Allen and Mearns 1977). Few surveys have been conducted and published since then. Four otter trawl samples were taken between 439 m and 658 m off Catalina Island (Fitch 1966). Fifteen otter trawl samples were taken between 200 m and 610 m (Allen and Mearns 1977), and eight were taken between 550 m and 915 m off Los Angeles (Mearns et al. 1979). Deepwater fishes off southern California have also been photographed by baited and unbaited cameras (Isaacs and Schwartzlose 1975; Edwards 1985) and observed from submersibles (Barham et al. 1967; Smith and Hamilton 1983).

This paper presents the results of extensive otter trawl and longline fish collections on the upper continental slope off southern California. The objective of the study was to summarize the composition, distribution, and abundance of fishes on the upper slope.

METHODS

Trawl samples were taken with a single-warp semiballoon otter trawl with a 7.6-m headrope, 8.8-m footrope, 4.1-cm body mesh (stretched), and 1.3-cm cod-end liner (stretched). The net was towed along a depth isobath at approximately 2.5 knots for 10 min (measured from the time the cable was completely deployed to the start of its retrieval) at scope ratios between 2:1 and 3:1. At sea,

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[Manuscript received December 8, 1986.]

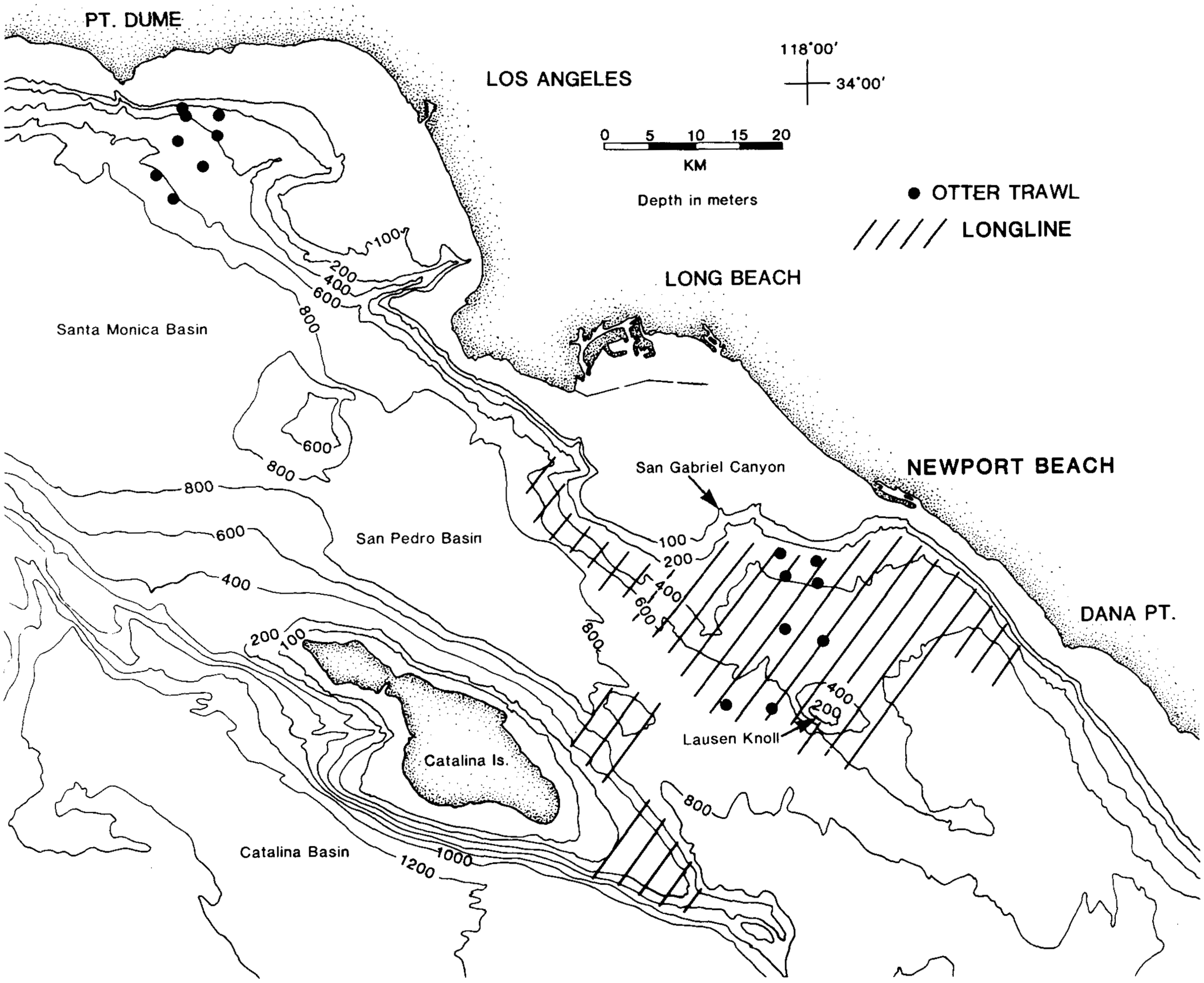

Figure 1. Map of the study area.

the fishes were identified, counted, measured to the nearest mm total length (TL), and weighed by species to the nearest 0.1 kg.

Trawl samples were taken during the day at four stations along each of two lines off Newport Beach and off Point Dume (Figure 1). One sample was taken at each station during each sampling period. Off Newport Beach, 8 trawl samples were taken in winter (Dec.-Jan.) and 8 in summer (July-Aug.) for two consecutive years (1981–82 and 1982–83) for a total of 32 trawls. Off Point Dume, 8 trawl samples were taken in winter and 8 in summer of 1982–83 for a total of 16 trawls.

Data were also obtained from longline catches of commercial fisherman. Their gear consisted of a groundline comprising three to six separate lines of no. 72 twisted cord. Each line of the groundline was approximately 650 m long and, after baiting, was coiled in a wooden tub. (During the set, the individual lines were tied end-to-end.) Hooks (4/0 and 5/0 rockcod) were tied on short leaders and spaced about 1 m apart. Salted pieces of *Engraulis mordax*, and to a lesser extent *Scomber japonicus*, were used as bait.

Sinking and floating longline sets were made. On sinking sets, weights (bricks) were tied to the groundline at the beginning or end of each tub. On floating sets, weights and floats (soda bottles) were alternately tied to the groundline; the distance between two weights encompassed 50–60 hooks. Anchors and buoy lines were attached to each end of the groundline.

Seventy-one trips were made with the commercial fishermen from June 1983 to November 1984. The lines were usually set between 1000 and 1400 hrs and pulled between 0600 and 1000 hrs the following day. Most lines were set within 20 km of Newport Beach, although trips of 50 km were not unusual (Figure 1). The catch of each tub of line was recorded separately. Each fish was measured to the nearest mm TL, and randomly selected individuals were weighed to the nearest 0.1 kg at sea. Weight-length regressions were determined for each species. Weights of fish not weighed were estimated from the regressions, and the weight of the total catch was reconstructed.

Data Analyses

A unit of effort for the otter trawl was one trawl. The number of species, number of individuals, and weight of fish caught in trawls off Newport Beach in 1981–82 and 1982–83 were compared in a three-way fixed-effects analysis of variance (ANOVA; SAS Institute Inc. 1985) with year, depth, and season as the main effects. The number of species, number of individuals, and weights of fish caught in trawls off Newport Beach and Point Dume in 1982–83 were compared in a three-way fixed-effects ANOVA with area, depth, and season as the main effects. The data were transformed to $\log_{10}(x + 1)$ to stabilize the variance. Cell sizes were equal for all analyses. Parallel analyses of raw and transformed data produced qualitatively similar results.

A unit of effort for the longline was one tub of line fished overnight (soak time generally 18 to 20 hrs). For each set, the average catch per tub was determined by averaging the catches of the constituent tubs. The number of species, number of individuals, and weight of fish caught per tub were compared by analysis of covariance (ANCOVA; SAS Institute Inc. 1985) with habitat and season as the main effects and depth as the covariate. The data were transformed to $\log_{10}(x + 1)$ to stabilize the variance. Cell sizes were unequal. Parallel analyses of raw and transformed data produced qualitatively similar results.

Catch parameter means were calculated from all trawls and longline sets taken at specified depths, times, or habitats. Individual species' catch means were calculated from all trawls and sets taken at specified depths, times, or habitats. Percent frequency of occurrence means were calculated from all trawls and sets taken at specified depths and times.

Parametric correlations between individual fish size and depth of capture were determined for the common species. Fish size distributions were compared by the Kolmogorov-Smirnov two-sample test (Siegel 1956). The size-depth relationship for *Sebastolobus alascanus* was examined.

STUDY AREA

Sediments of the upper continental slope are predominantly green silty clays. Sand content was fairly constant downslope (mean = 12% by dry weight); areas around the offshore banks and the shoulders of the submarine canyons were sandier (25%–50% by dry weight). Organic content increased from 5%–7% (as total volatile solids) at 290 m, to 11%–14% at 625 m (SCCWRP 1983).

The longline fishermen recognize two habitats on the slope: hard substrate banks and soft, relatively featureless (on a fathometer) mud bottom. Surface sediments on the banks are a mixture of coarse sand and calcareous organic debris with occasional rocks. Banks, as used herein, include isolated mounds as small as a few hundred meters across and 20–30 m high, shoulders of submarine canyons, and submerged mountains. The mud habitat is the green silty clay described above and is the predominant habitat on the slope.

Temperature, dissolved oxygen, and salinity measured in the water column over the slope off Newport Beach showed weak and decreasing gradients with increasing depth. The mean annual temperature was 8.2°C (SD = 0.4, N = 21, min = 7.5, max = 9.1) at 300 m, and 6.5°C (SD = 0.2, N = 17, min = 6.0, max = 6.9) at 500 m. Mean annual dissolved oxygen was 1.22 ppm (SD = 0.26, N = 18, min = 0.76, max = 1.94) at 300 m, and 0.47 ppm (SD = 0.10, N = 16, min = 0.31, max = 0.72) at 500 m. Some of the variation in these parameters resulted from seasonal changes related to upwelling. In the spring, temperature and dissolved oxygen decreased and salinity and density increased in water shallower than 350 m (SCCWRP 1983).

RESULTS

Fifty-four species of fish were collected during the study (Table 1). Eighteen species were collected by both otter trawl and longline.

Otter trawls collected 42 species; *Sebastolobus alascanus, Sebastolobus altivelis, Sebastes diploproa, Glyptocephalus zachirus, Microstomus pacificus,* and *Lyopsetta exilis* dominated the catches (Table 1). Twenty-four species occurred only in trawls—these were generally small demersal species (agonids and zoarcids), small nektobenthic

TABLE 1
Fishes Collected by Otter Trawl (n = 48) and Longline (n = 71) off Southern California between 290 and 625 m

		Otter trawl		Longline	
Family	Scientific name	Number collected	Percent frequency of occurrence	Number collected	Percent frequency of occurrence
Myxinidae	*Eptatretus deani*	87	33	486	80
	Eptatretus stoutii	1	2	139	59
Chimaeridae	*Hydrolagus colliei*	23	25	138	62
Hexanchidae	*Hexanchus griseus*			1[a]	—
Scyliorhinidae	*Apristurus brunneus*	4	6	475	70
	Parmaturus xaniurus	2	2	223	75
Squalidae	*Squalus acanthias*			148	41
	Somniosus pacificus			2	1
Torpedinidae	*Torpedo californica*			1	1
Rajidae	*Bathyraja kincaidi*	7	15	14	7
	Raja inornata	2	4	1	1
	Raja rhina			20	14
Nettastomatidae	*Facciolella gilberti*	4	6		
Alepocephalidae	*Alepocephalus tenebrosus*	2	2	2[a]	—
Moridae	*Physiculus rastrelliger*	19	19		
Merlucciidae	*Merluccius productus*	62	35	306	63
Macrouridae	*Nezumia stelgidolepis*	24	23	177	46
Bythitidae	*Cataetyx rubrirostris*	57	19		
Batrachoididae	*Porichthys notatus*	19	6		
Scorpaenidae	*Sebastolobus alascanus*	1405	98	2830	99
	Sebastolobus altivelis	3063	52	979	80
	Sebastes aleutianus			3	3
	Sebastes aurora	6	6	588	87
	Sebastes babcocki			1	1
	Sebastes diploproa	403	58	297	18
	Sebastes elongatus	2	4		
	Sebastes gilli			2	3
	Sebastes goodei	5	4	1	1
	Sebastes helvomaculatus			102	7
	Sebastes hopkinsi	1	2		
	Sebastes jordani	32	6		
	Sebastes levis	1	2		
	Sebastes melanostomus			1279	65
	Sebastes paucispinis	3	4		
	Sebastes phillipsi			5	4
	Sebastes rosenblatti	7	10		
	Sebastes rufus	52	15	1	1
	Sebastes saxicola	41	4		
Anoplopomatidae	*Anoplopoma fimbria*	104	58	3799	99
Zaniolepididae	*Zaniolepis frenata*	1	2		
Agonidae	*Bathyagonus pentacanthus*	15	13		
	Xeneretmus latifrons	38	19		
	Xeneretmus triacanthus	1	2		
Cyclopteridae	*Careproctus melanurus*	7	10		
Zoarcidae	*Bothrocara brunneum*	1	2		
	Lycodapus fierasfer	5	4		
	Lycodes pacificus	92	46		
	Lyconema barbatum	3	6		
Bothidae	*Citharichthys sordidus*	1	2		
Pleuronectidae	*Eopsetta jordani*			6	4
	Glyptocephalus zachirus	324	54		
	Lyopsetta exilis	737	50	2	3
	Microstomus pacificus	590	94	49	28
	Parophrys vetulus	11	13		
Total		7,264		12,074	

[a] Caught during the study but on a trip in which I did not participate; not counted in totals.

species (scorpaenids), and some larger demersal species (pleuronectids).

Longlines collected 30 species; *Sebastolobus alascanus*, *Sebastolobus altivelis*, *Sebastes melanostomus*, and *Anoplopoma fimbria* dominated the catches (Table 1). Twelve species occurred only on

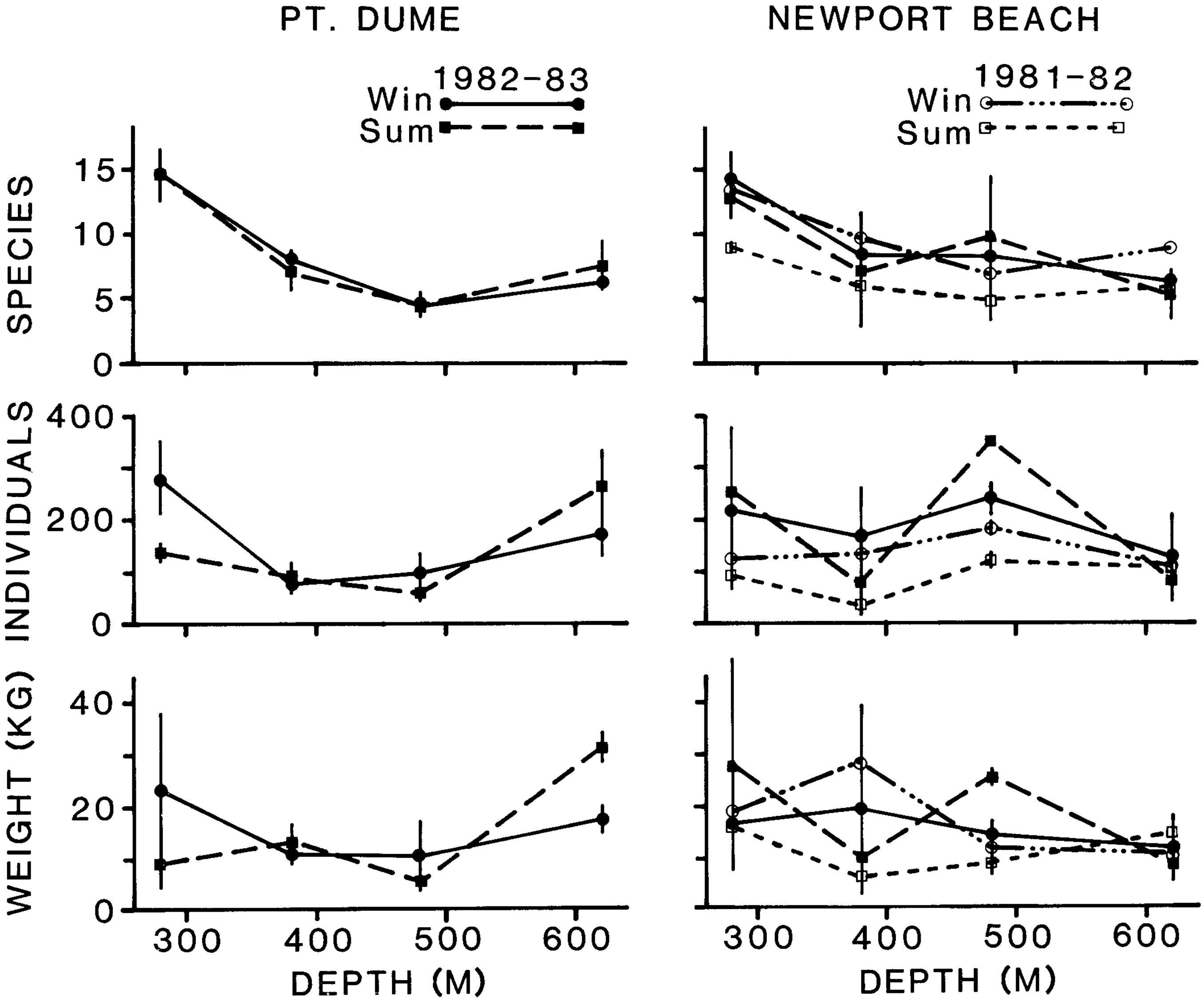

Figure 2. Mean number of fish species, number of individuals, and weight of fish per 10-min trawl off Newport Beach and Point Dume by season, year, and depth. Vertical bars are one standard deviation.

longlines—these were generally large, mobile species (squalids and scorpaenids).

Otter Trawls

The number of species collected per trawl varied with depth and season. Significantly more species were collected at 290 m than at the deeper stations in both areas (ANOVA, $P < 0.05$; Figure 2). Significantly more species were collected during the winter than during the summer off Newport Beach (ANOVA, $P < 0.05$; Figure 2).

The number of individuals collected per trawl varied with depth, year, and season (Figure 2). Off Newport Beach, catches were significantly larger in the winter than in the summer, and catches in 1982–83 were significantly greater than in 1981–82 (ANOVA, $P < 0.05$).

Weight of the catch was the most variable of the three catch parameters and the least consistent between seasons and areas (Figure 2).

Of the six dominant species in trawl catches, all except *Sebastolobus alascanus* showed significant trends in abundance with depth (ANOVA, $P <$ 0.05; Figure 3). *Lyopsetta exilis*, *Microstomus pacificus*, and some *Sebastes* spp. decreased in abundance downslope. *S. alascanus* and *Glyptocephalus zachirus* were more abundant at mid-depths than either shallower or deeper. *Sebastolobus altivelis* increased in abundance downslope.

S. alascanus, *M. pacificus*, and *L. exilis* were

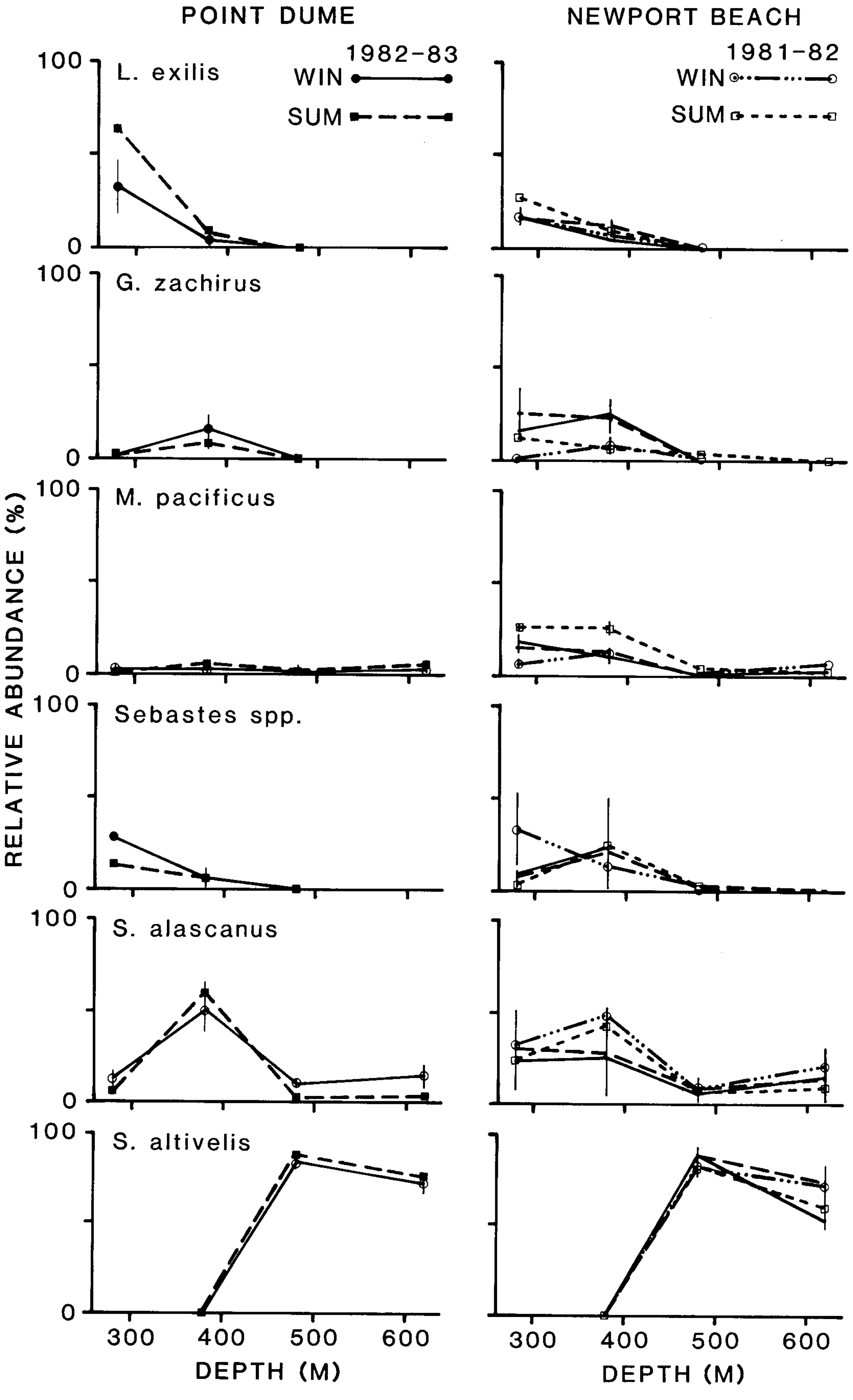

Figure 3. Mean percent abundance of the dominant fish species in trawls off Newport Beach and Point Dume by season, year, and depth. Vertical bars are one standard deviation.

TABLE 2
Composition of Trawl Catches between 290 and 380 m (*n* = 24) and between 480 and 625 m (*n* = 24)

	290–380 m			480–625 m		
	PO	No	Wt	PO	No	Wt
Eptatretus deani	17	0.4	<0.1	50	3.2	0.4
Hydrolagus colliei	42	0.8	0.3	8	0.1	<0.1
Physiculus rastrelliger	38	0.8	<0.1	0	—	—
Merluccius productus	63	2.5	0.8	8	0.1	<0.1
Nezumia stelgidolepis	4	<0.1	<0.1	42	1.0	0.1
Cataetyx rubrirostris	0	—	—	42	2.4	<0.1
Sebastolobus alascanus	100	42.6	3.6	96	15.9	2.6
Sebastolobus altivelis	4	<0.1	<0.1	100	127.5	6.7
Sebastes diploproa	92	16.1	1.8	25	0.7	0.3
Sebastes rufus	29	2.2	0.4	0	—	—
Anoplopoma fimbria	42	0.8	0.8	71	3.5	2.1
Bathyagonus pentacanthus	21	0.6	<0.1	0	—	—
Xeneretmus latifrons	38	1.6	<0.1	0	—	—
Lycodes pacificus	75	3.3	0.4	17	0.5	0.1
Glyptocephalus zachirus	96	12.9	2.5	13	0.6	0.2
Lyopsetta exilis	100	30.7	0.7	0	—	—
Microstomus pacificus	100	19.5	3.8	88	5.1	1.8
Parophrys vetulus	25	0.5	0.1	0	—	—

These species constituted more than 97% of the number and weight of fish caught. PO = percent frequency of occurrence; No = mean number per 10-min trawl; Wt = mean weight (kg) per 10-min trawl.

more abundant in 1982–83 than in 1981–82, and *S. alascanus* and *G. zachirus* were more abundant off Point Dume than off Newport Beach. Despite differences in catches, the relative abundances of the dominant species were consistent between areas and years (Figure 3).

The composition of otter trawl catches changed markedly between 380 m and 480 m (Table 2). Of the 42 species caught by trawls, only 12 were collected at all four depths. Thirty-four species were caught at 290 m and 380 m; 22 occurred only between those depths. Twenty species were caught at 480 m and 625 m; 8 occurred only between those depths.

Longlines

There were no trends in the number of species caught per tub with depth, and there were no differences between bank and mud sets, but the number of species was significantly lower in the summer (ANCOVA, $P < 0.05$; Figure 4). There were no trends in the number of fish caught per tub over depth, and there were no differences between habitats, but the catch was significantly lower in the summer (ANCOVA, $P < 0.05$). There were no trends in weight per tub with depth, but weight was significantly higher on bank sets than on mud sets and was significantly lower in the summer (ANCOVA, $P < 0.05$).

Of the 30 species of fish caught on longlines, 27 were caught on banks and 20 were caught on mud. Catches on banks were dominated by *Anoplopoma fimbria, Sebastes melanostomus,* and *Sebastolobus alascanus* (Table 3). Catches on mud were dominated by *Sebastolobus alascanus, Anoplopoma fimbria,* and *Sebastolobus altivelis.* Ten species, including seven *Sebastes* spp., were caught only on banks; three species were caught only on mud.

TABLE 3
Composition of Longline Catches from Mud (*n* = 38) and Bank (*n* = 33) Habitats

	Bank			Mud		
	PO	No	Wt	PO	No	Wt
Eptatretus deani	70	1.3	0.1	90	2.9	0.4
Eptatretus stoutii	46	0.2	<0.1	71	1.0	<0.1
Hydrolagus colliei	73	0.9	0.5	53	0.5	0.3
Apristurus brunneus	61	1.4	0.5	79	2.9	1.1
Parmaturus xaniurus	73	1.4	0.4	76	0.8	0.3
Squalus acanthias	39	0.9	2.1	42	0.5	1.0
Merluccius productus	85	2.0	1.7	45	0.9	0.6
Nezumia stelgidolepis	12	0.1	<0.1	76	1.5	0.4
Sebastolobus alascanus	97	5.6	2.9	100	20.2	11.2
Sebastolobus altivelis	58	1.7	0.1	100	7.4	0.8
Sebastes aurora	88	2.7	1.0	87	2.8	1.4
Sebastes diploproa	36	2.5	1.0	3	0.2	<0.1
Sebastes melanostomus	100	15.2	17.8	34	0.6	0.9
Anoplopoma fimbria	97	21.1	24.2	100	17.0	20.3
Microstomus pacificus	39	0.2	0.1	40	0.2	0.1

These species constituted more than 97% of the number and biomass of fish caught. PO = percent frequency of occurrence; No = mean number per tub; Wt = mean weight (kg) per tub.

Size of Fish

Nine of 12 trawl-caught species and 6 of 13 longline-caught species showed significant positive size-depth correlations (Table 4). *Sebastes diploproa* showed a positive correlation for trawl captures

TABLE 4
Correlation between Individual Fish Size and Depth of Capture

	Otter trawl			Longline		
	r	*p*	*n*	*r*	*p*	*n*
Hydrolagus colliei	–.369	ns	23	.013	ns	114
Apristurus brunneus				.062	ns	408
Parmaturus xaniurus				.263	**	167
Squalus acanthias				–.187	ns	92
Merluccius productus	.567	**	59	.054	ns	175
Nezumia stelgidolepis				–.112	ns	142
Cataetyx rubrirostris	–.070	ns	49			
Lycodes pacificus	.586	**	69			
Sebastolobus alascanus	.199	**	1240	.167	**	2361
Sebastolobus altivelis	.178	**	2648	.240	**	882
Sebastes aurora				.541	**	469
Sebastes diploproa	.446	**	384	–.157	*	182
Sebastes rufus	.402	*	52			
Sebastes melanostomus				.234	**	843
Anoplopoma fimbria	–.001	ns	73	.140	**	3015
Glyptocephalus zachirus	.341	**	292			
Lyopsetta exilis	.300	**	738			
Microstomus pacificus	.485	**	603	.233	ns	34

r = correlation coefficient; *p* = probability; *n* = number of fish; * = significant at 0.05; ** = significant at 0.01; ns = not significant

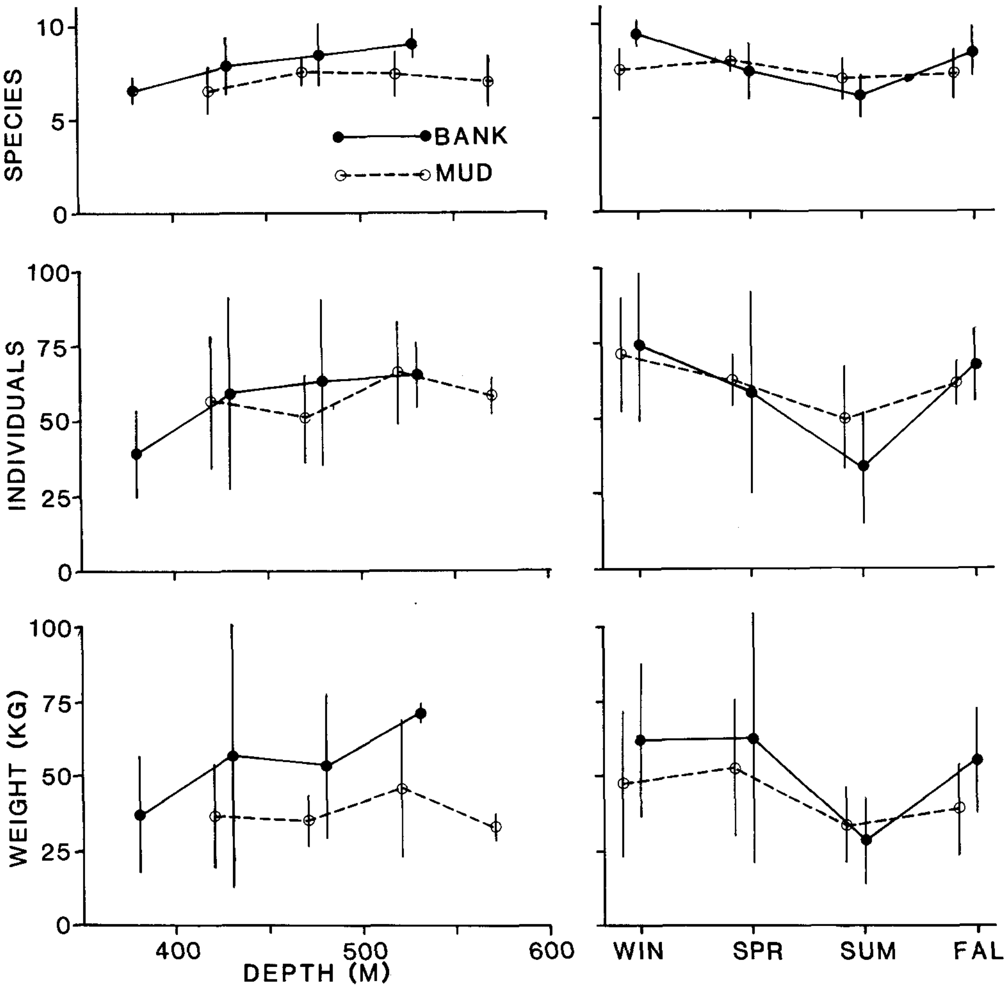

Figure 4. Mean number of fish species, number of individuals, and weight per tub of longline by depth and season. Vertical bars are one standard deviation.

and a negative correlation for longline captures. The remaining species showed no significant size-depth relationships.

The size distributions of eight species were significantly different between trawls and longlines (Kolmogorov-Smirnov two-sample test, $P < 0.05$). In each case, the otter trawl collected smaller individuals (Figure 5).

Trawl collections on the upper slope encompassed most of the vertical range commonly occupied by *Sebastolobus alascanus* (Moser 1974), and captured fish ranged in size from transforming benthic juveniles (< 50 mm TL) to adults (> 400 mm TL). Recently settled individuals were most abundant at the deepest and shallowest stations (Figure 6). Midsized individuals were more abundant at the shallower stations, and large individuals were more abundant at the deeper stations.

DISCUSSION

Gear selectivity substantially affected catch composition. Only 18 (33%) of the 54 species collected were caught by both types of gear. Large mobile fishes dominated longline catches, and small sedentary fishes dominated trawl catches. Small trawls are ineffective samplers of large demersal fishes (Day and Pearcy 1968; Haedrich et al. 1975). Avoidance of the otter trawl is suggested by the larger size of individuals captured by longline.

Otter Trawls

The total number of species collected, the number of species per trawl, and the number of fish per trawl were lower on the upper slope, 290–625 m, than on adjacent areas on the outer shelf, 130–230 m (Table 5). Catch weight per trawl was similar on the upper slope and outer shelf.

All trawl-catch parameters on the slope were higher than those in the adjacent basins, 715–915 m[1] (Table 5). The low number of species, number

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[1] Trawl catch parameters for the basins probably are overestimates. Assuming the net continues to fish for some time after retrieval begins, distance fished during deeper tows probably is underestimated compared to shallower tows.

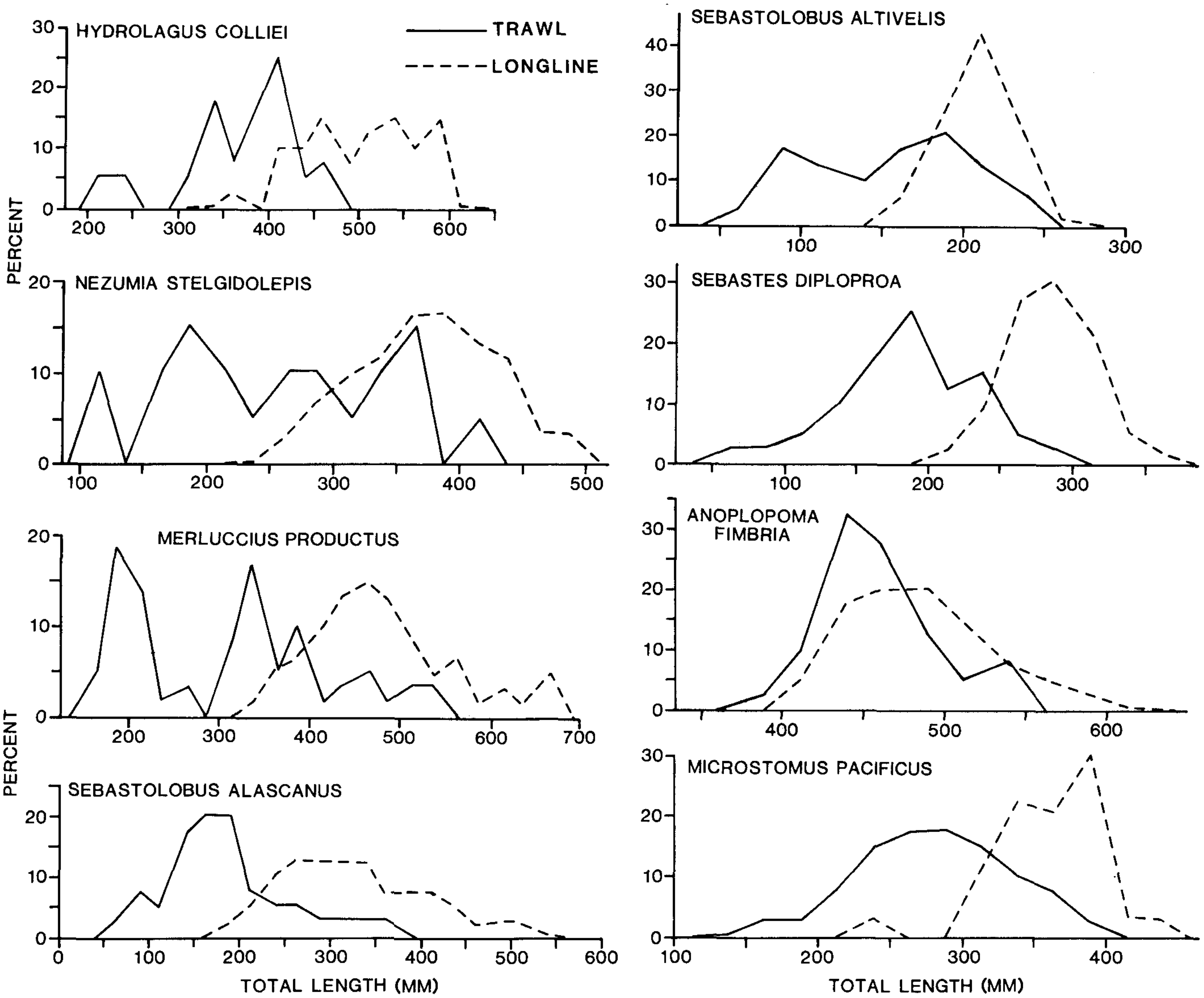

Figure 5. Size distribution of eight species collected by trawl and longline.

of individuals, and weight of fish in the San Pedro and Santa Monica basins is probably related to low dissolved-oxygen levels. Water entering the basins at the depth of the sills (about 700 m) comes from the oxygen minimum layer (0.3 ml l^{-1}) in the ocean waters to the southeast. The oxygen content of the water in the basins ranges from less than 0.1 to 0.3 ml l^{-1} with a mean of about 0.2 (U.S. Department of Interior 1968). The abundance of animals in the bottom of the basins parallels the abundance of oxygen (Rittenberg et al. 1955). Macrofauna and megafauna are scarce in the San Pedro and Santa Monica basins and very abundant in the Catalina Basin, an offshore basin with an average oxygen content about twice that of the nearshore basins (Hartman 1955; Emery 1960; U.S. Department of Interior 1968; Smith and Hamilton 1983).

Estimates of fish abundance (3.4–3.8 fish 100 m^{-2}) and biomass (3.5–3.9 g m^{-2}) on the upper continental slope off southern California (Table 5) are higher than estimates obtained from a 3-m beam trawl (0.6–1.1 fish 100 m^{-2} and 2.0–2.9 g m^{-2}) fished between 515 m and 805 m off Oregon (Pearcy et al. 1982), and lower than biomass estimates obtained from a 23-m trawl (approximately 6–11 g m^{-2}) fished between 250 m and 750 m off Oregon (Alton 1972; Fig. 6 in Pearcy et al. 1982). Differences among net types and accuracy of area-swept estimates preclude anything but a casual comparison.

Longlines

Among the longline catches, the number of species and biomass per tub were higher on banks than

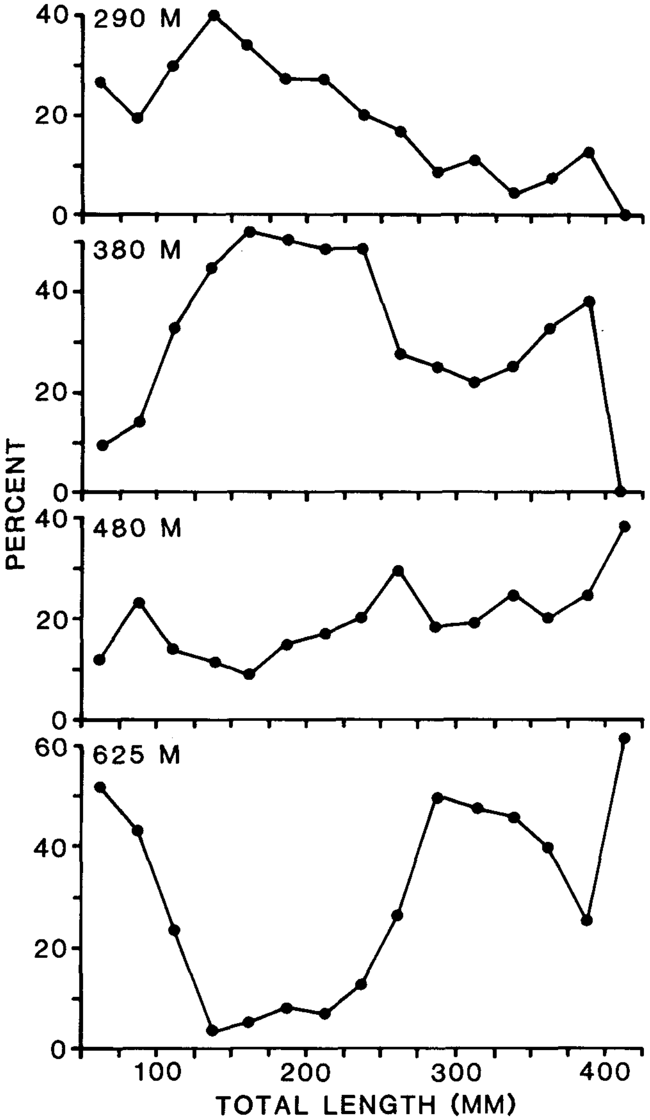

Figure 6. Percent of trawl-caught *Sebastolobus alascanus* in 25-mm TL size class intervals by depth. For example, 52% of the 50–74-mm fish were collected at 625 m, 12% at 480 m, 9% at 380 m, and 27% at 290 m.

TABLE 5

Otter Trawl Catch Parameter Means for the Outer Continental Shelf (130–230 m)[a], the Continental Slope (290–625 m), and the Nearshore Basins (715–915 m)[b] off Southern California

	Depth (m)			
	130–230	290–380	480–625	715–915
Number of trawls	18	24	24	10
Total species	46	32	20	11
Species per trawl	15.4	10.6	6.8	3.3
Fish per trawl	514	138	156	58
[c]Fish 100 m^{-2}	12.5	3.4	3.8	0.7
Biomass (kg) per trawl	15.6	15.8	14.3	2.3
[c]Biomass (g) m^{-2}	3.8	3.9	3.5	0.3

[a]County Sanitation Districts of Orange County, P.O. Box 8172, Fountain Valley, CA 92728; unpublished data.

[b]Southern California Coastal Water Research Project, 646 W. Pacific Coast Hwy., Long Beach, CA 90806; unpublished data.

[c]Estimated area swept 4,100 m^2 assuming effective net opening of 5.3 m (0.6 x 8.8-m footrope length) and distance covered of 772 m (2.5 knots for 10 min).

All trawls were made with a 7.6-m (headrope) net and were 10 min in duration, except between 715 m and 915 m, which were 20 to 25 min. Trawls from 130 m to 230 m and from 715 m to 915 m were made between 1981 and 1985.

mud. The higher number of species on bank sets is probably related to topographic complexity. Because banks provide the only vertical relief on an otherwise featureless habitat, they may attract and concentrate nektobenthic fishes. This hypothesis is supported by the distribution of *Sebastes* species between the two habitats. Ten species of *Sebastes* were caught on the banks, accounting for 34% of the species and 36% of the individuals collected. Three species of *Sebastes* were caught on the mud, accounting for 16% of the species and 7% of the individuals collected. The greater catch-weight of bank sets was due primarily to the abundance of *Sebastes melanostomus* and their large average size (Table 3).

The upper continental slope off southern California is not a uniform habitat. Faunal differences between bank and mud habitats might have been greater if the longlines had been shorter (groundlines were generally 1.5 to 2.0 km long). On several sets on smaller banks, species composition of some tubs was typical of mud sets.

Seasonal and Annual Variation

Summer catches of fish on the slope were generally smaller than during the rest of the year. Among otter trawl catches, fewer species and individuals were caught off Newport Beach during summer than winter. Among longline catches, fewer species and individuals and less weight were caught in both habitats in the summer than during the rest of the year. The seasonal catch patterns may be due, in part, to changes in the bathymetric distributions of some of the fishes. *Microstomus pacificus,* for example, are more abundant on the shelf off southern California in spring and summer than in fall and winter (Cross 1985). In northern California and Oregon, *M. pacificus* move onto the shelf in summer to feed, and move back onto the slope in winter to reproduce (Hagerman 1952; Alton 1972).

Winter catches of fish on the outer continental shelf and upper slope (91–411 m) off Oregon were smaller than those in summer (Alton 1972). Alton attributed this to bathymetric movements of some species (e.g., *M. pacificus* and *Anoplopoma fimbria*) and latitudinal movements of other species (e.g., *Merluccius productus*) related to feeding and reproduction.

Microstomus pacificus, Lyopsetta exilis, and *Sebastolobus alascanus* were significantly more abundant in trawl catches in 1982–83 than in 1981–82. The increase in numbers was not a result of increased recruitment; there were no significant differences in size distributions between years (Kolmogorov-Smirnov two-sample test, $P > 0.05$).

Size

The size of several species captured by both types of gear increased with increasing depth. More species caught in trawls (9 of 12) than on longlines (6 of 13) had significant positive size-depth correlations; the difference, however, was not significant ($x^2 = 1.13$, $P > .25$).

The "bigger-deeper" phenomenon has been observed in several studies (Haedrich and Rowe 1977; Polloni et al. 1979; Haedrich et al. 1980), although the relationship does not always hold for the same species in different areas (Wenner and Musick 1977; Snelgrove and Haedrich 1985) or the same species in the same area on different types of gear (*Sebastes diploproa* in this study). The relationship may also be confounded by sampling gear bias and differing depth distribution of adults and juveniles.

Small trawls are biased against large demersal fishes (Day and Pearcy 1968; Haedrich et al. 1975), a bias that apparently changes with depth. Pearcy (1978) and Pearcy et al. (1982) found a large disparity in species composition and estimates of biomass between a 3-m beam trawl and a 23-m (footrope) commercial otter trawl fished on the continental shelf off Oregon; the disparity did not exist below 1,000 m.

Differences in the distribution of adults and juveniles may be responsible for apparent bigger-deeper relationships. Immature individuals may concentrate at the shallow end of the depth range while adults distribute across the depth range (Snelgrove and Haedrich 1985).

The depth distribution of *Sebastolobus alascanus* (Figure 6) suggests that settling individuals head for the bottom regardless of depth. It is not surprising that some settle in deep water; time spent in the water column from spawning to settling is about a year, and larvae can occur more than 300 km offshore (Moser 1974). If *S. alascanus* settle in deep water, they move up the slope. As they grow, they move into deeper water.

Zonation

Otter trawl collections suggest a faunal break between 380 m and 480 m. The ranges of 22 species ended, and the ranges of 8 species began between these depths. *Sebastolobus alascanus, Lyopsetta exilis, Microstomus pacificus, Glyptocephalus zachirus,* and *Sebastes diploproa* dominated trawl collections between 290 m and 380 m. Juveniles of these species constituted about half of the individuals collected in trawls on the outer shelf (130–230 m). *Sebastolobus altivelis* dominated trawl collections between 480 m and 625 m and in the basins (715–915 m).

Pearcy et al. (1982) noted a rapid change in the benthic fish fauna between 400 m and 900 m on the continental slope off Oregon. The ranges of 34 shelf and upper slope species ended, and the ranges of 24 slope species began between these depths.

Temperature, dissolved oxygen, and salinity decrease with increasing depth on the slope off southern California. Dissolved oxygen drops below 1 ppm between 380 m and 480 m (SCCWRP 1983). The higher respiration rates of active shallow-water fishes may restrict them to depths with higher dissolved oxygen (cf. Sullivan and Somero 1980; Siebenaller et al. 1982).

There are no obvious physical discontinuities between 380 m and 480 m on the slope off southern California. Sediment grain size decreases and organic content increases with increasing depth over the slope (Thompson and Jones 1987). Macroinvertebrate assemblages on the slope off southern California show a similar zonal pattern. Polychaetes dominate the infauna between 161 m and 632 m. Small molluscs and crustaceans dominate the infauna between 480 m and 851 m (Thompson and Jones 1987). The absence of suitable polychaete prey deeper on the slope may restrict polychaete-feeders, such as the pleuronectids[2], to shallower depths.

The causes of species replacements among the macrofauna and megafauna are not well understood but probably include a variety of physical and biotic factors that change gradually and continuously with depth (Rex 1981).

El Niño

A major California El Niño occurred during 1982–83, causing increased sea-surface and subsurface temperatures, a depressed thermocline, and reduced upwelling. Temperature anomalies were, however, small at upper-slope depths off southern California (Lynn 1983; Simpson 1983, 1984).

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[2] Cross, J.N. Food habits of the demersal fishes of the upper continental slope off southern California. Manuscript in preparation.

During El Niño years, tropical species frequently move into southern California, and species from southern California often move into northern California and beyond (Radovich 1961). No tropical fishes were collected on the upper continental slope off southern California during the study. Two species that range south of Baja California were more abundant during the El Niño year: 3 of the 4 *Facciolella gilberti* and 18 of the 19 *Physiculus rastrelliger* were collected in 1982–83. Also present in trawl catches in 1982–83 but not in 1981–82 was *Pleuroncodes planipes*. During past El Niño events, this galatheid crab extended its range from Baja California into southern California (Radovich 1961; Longhurst 1967).

Zoogeography

The fish assemblage of the upper continental slope off southern California is dominated by fishes with northern affinities. (Most ranges were obtained from Miller and Lea [1972]; additional ranges were obtained from Fitch and Lavenberg [1968], Hart [1973], and Pearcy et al. [1982]). Of the 54 species collected during the study, 42 have northern range endpoints off British Columbia or Alaska and southern range endpoints off southern California or northern Baja California. Twenty-nine of these species accounted for 98% of the individuals collected in trawls. Twenty-three of these species accounted for 88% of the individuals collected on longlines. *Sebastolobus alascanus, Sebastolobus altivelis, Anoplopoma fimbria, Microstomus pacificus,* and *Eptatretus deani* constituted 72% of the individuals in 48 trawls on the upper slope off southern California and 86%–90% of the individuals in 49 trawls on the upper slope off Oregon (Pearcy et al. 1982).

Nine of the 54 species collected during the study have ranges that do not extend north of California: *Parmaturus xaniurus, Facciolella gilberti, Physiculus rastrelliger, Sebastes gilli, Sebastes hopkinsi, Sebastes levis, Sebastes phillipsi, Sebastes rosenblatti,* and *Sebastes rufus*. Three of the 54 species have ranges that extend south of Baja California: *Facciolella gilberti, Alepocephalus tenebrosus,* and *Physiculus rastrelliger.* Two species have antitropical distributions: *Hexanchus griseus* and *Squalus acanthias*.

Previous deepwater (200–915 m) trawl studies off southern California produced species lists and dominance rankings nearly identical to the present study (Fitch 1966; Allen and Mearns 1977; Mearns et al. 1979). For the studies that included catch lists, only two species—*Embassichthys bathybius* (Pleuronectidae; Fitch 1966) and *Gnathophis catalinensis* (Congridae; Mearns et al. 1979)—were not collected during the present study.

ACKNOWLEDGMENTS

This study was supported in part by a contract from the County Sanitation Districts of Orange County (CSDOC). H. Stubbs, B. Thompson, and M. Moore (SCCWRP) and T. Pesich (CSDOC) assisted in trawl collections aboard R/V *Vantuna* and R/V *Westwind*. Special thanks go to the dory fishermen of Newport Beach for their cooperation. R. N. Lea, California Department of Fish and Game, identified *Sebastes aleutianus*, and Y. Jiminez translated the abstract. Early versions of the manuscript were reviewed by J. Allen, M. Horn, A. Mearns, W. Pearcy, D. Somerton, and two anonymous referees; their comments improved the manuscript and are appreciated.

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TESTS OF OVARY SUBSAMPLING OPTIONS AND PRELIMINARY ESTIMATES OF BATCH FECUNDITY FOR TWO *PARALABRAX* SPECIES

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ABSTRACT

Hydrated-state ovaries of a few individuals of two species of "rock bass"—the barred sand bass (*Paralabrax nebulifer*) and the kelp bass (*Paralabrax clathratus*)—were analyzed. For both sand bass and the compound taxon, fecundity estimates were indistinguishable based on subsamples taken from anterior, middle, or posterior sections of either member of the ovary pair. Batch fecundity was proportional to the cubic power of body length, and a linear function of somatic weight. These preliminary data strongly suggest that it will be relatively straightforward to calculate the number of eggs per gram of ovary-free body weight in these fishes. Therefore, application of the egg production method (Parker 1980) for estimating stock biomass of rock bass is unlikely to be hindered by problems in estimating batch fecundity.

RESUMEN

Los ovarios en estados de hidratación fueron analizados en un bajo número de individuos de dos especies, *Paralabrax nebulifer* y *P. clathratus*. En ambos casos, similares estimaciones de fecundidad fueron obtenidas en submuestras tomadas en las secciones anterior, central o posterior de uno u otro ovario. La fecundidad de la puesta resultó proporcional al cubo de la longitud corporal y, además, una función linear del peso somático. Estos datos preliminares sugieren una cierta facilidad en el cálculo del número de huevos por gramo de peso corporal (excluyendo ovarios) de estos peces. Por lo tanto, la aplicación del metodo de producción de huevos (Parker 1980) para estimar la biomasa de la población de *Paralabrax* probablemente no se verá afectada por problemas relacionados con la estimación de la fecundidad de la puesta.

INTRODUCTION

The kelp bass (*Paralabrax clathratus*) and the barred sand bass (*Paralabrax nebulifer*) together formed more than 90% of the general "rock bass" (Frey 1971) recreational catch in southern California waters during the first half of this decade (U.S. Dept. Commerce 1985, and references therein). Although rock bass still constitute a significant fraction of the sport catch, the absolute magnitude of the harvest has declined in recent years (Oliphant 1979; U.S. Dept. Commerce 1985). Accordingly, there has been a growth of interest in mariculture and in the development of improved stock assessment techniques to aid in the future management of these fishes (J. Crooke, CDFG, Long Beach, pers. comm.).

The egg production method (EPM) of Parker (1980, 1984) is the state-of-the-art technique for assessing stock size in pelagic-spawning fishes, particularly species of "serial" or "fractional" spawners whose egg production is seasonally indeterminate (Lasker 1984). Batch fecundity (i.e., the number of eggs released per individual spawning) is a key input parameter for modeling stock size using the EPM.

The purpose of this note is twofold. First, I test several basic assumptions of ovary subsampling protocols necessary for future work on fecundity of these basses. Second, I provide preliminary data on the batch fecundity of rock bass.

METHODS AND MATERIALS

Fish and Ovary Sampling

Female kelp bass and barred sand bass whose ovaries contained visibly "hydrated" (ready to spawn: Hunter et al. 1984) eggs were saved whenever encountered on routine trawl and scuba diving surveys (DeMartini and Allen 1984; Roberts et al. 1984) in the San Onofre-Oceanside area (33°15′N, 117°25′W) during the June through August periods of 1982–85. Freshly collected specimens were measured (total length, TL, in mm); both ovaries were excised and weighed (to 0.1 g); and ovary-free body weight (1 g) was determined, if possible. Ovaries were placed in modified Gilson's fluid (Bagenal and Braum 1971) to free and harden ova for subsequent examination.

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[Manuscript received January 26, 1987.]

TABLE 1

Results of ANOVA Testing the Potential Effects of Ovary (Right or Left) and Ovary Subsection (Anterior, Middle, or Posterior) on Batch Fecundity

Barred sand bass only

Source	*df*	*MS*	*F* value	Significance	*R*-square
Model	4	2.20	28.21	$P < 0.0001$	0.627
TL	1	8.76	112.47	$P < 0.0001$	
Ovary	1	0.01	0.15	$P = 0.70$	
Subsection	2	0.01	0.10	$P = 0.90$	
ERROR	67	0.08	—	—	

Barred sand bass and kelp bass

Source	*df*	*MS*	*F* value	Significance	*R*-square
Model	4	2.76	38.64	$P < 0.0001$	0.662
TL	1	10.98	153.62	$P < 0.0001$	
Ovary	1	0.02	0.33	$P = 0.56$	
Subsection	2	0.02	0.31	$P = 0.74$	
Error	79	0.07	—	—	

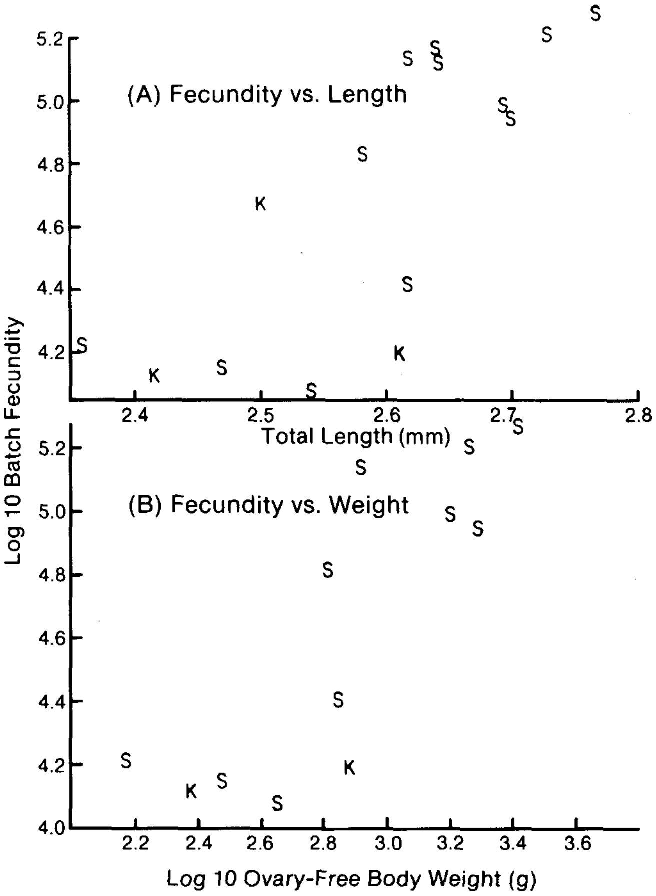

Figure 1. Log-log scatterplot of the relation between estimated batch fecundity and (*A*) total length or (*B*) ovary-free body weight. Regressions were calculated using all 15 pairs of data in *A* and all 12 pairs of data in *B*. Barred sand bass data are indicated as "S" and kelp bass data as "K" on plots.

Each pair of preserved ovaries was blotted dry on bibulous paper and reweighed (0.01 g); one subsample was then sectioned from the anterior, middle, and posterior thirds of each member of the pair. Sections were immediately weighed (0.0001 g) and vialed for microscopic examination. Hydrated ova were recognized by their relatively large size and translucent appearance (Hunter et al. 1984). Batch fecundity was estimated from the mean number of hydrated ova present in the three weighed subsamples (Bagenal and Braum 1971), with subsample counts representing the error of the estimate (Hunter et al. 1984).

Statistical Analyses

Two-way ANOVA was used to test whether that member of the ovary pair and position of the ovary subsection might affect the fecundity estimate. The logarithm of total length was used as covariate. The relation between batch fecundity and length and body weight of fish was evaluated by least-squares regression on log-transformed data.

RESULTS

Four kelp bass and 13 barred sand bass whose ovaries contained ova in hydrated condition were collected. An additional female sand bass was in running ripe (ovulated) condition. Body lengths, body weights, and ovary weights were recorded for all kelp bass. Ovary weights were noted for 12 of the 13 hydrated-state sand bass; body weights were available for 10 of those 12 sand bass. Three out of four pairs of kelp bass ovaries provided quantitative samples.

For 12 barred sand bass with quantitative ovary subsections, neither the position of the subsection nor member of the ovary pair significantly influenced the fecundity estimate (Table 1). The same qualitative pattern persists if the two kelp bass with ovary subsection data are included and the data reanalyzed for the pooled rock bass category (Table 1). The coefficient of variation of the three within-ovary estimates averaged about 15%.

Batch fecundity was related to the cubic power of TL (Figure 1A), according to the relation

$$\begin{aligned} \text{Log 10 } F &= 3.02 \text{ Log10 TL} - 3.13, \\ \text{where } F &= \text{batch fecundity}, \\ TL &= \text{total body length}, \\ r &= 0.78, \\ n &= 15, \\ \text{and } P &< 0.001. \end{aligned}$$

Fecundity was linearly related to ovary-free body weight (Figure 1B) by the relation

$$\begin{aligned} \text{Log10 } F &= 1.01 \text{ Log10 } W + 1.76, \\ \text{where } W &= \text{ovary-free body weight}, \\ r &= 0.83, \\ n &= 12, \\ \text{and } P &< 0.001. \end{aligned}$$

Fecundity ranged over a factor of 15 from about 12,000 eggs (in a 447-g fish) to > 185,000 eggs (in the heaviest, 2,625-g fish) (Figure 1B). The smallest fish (a 148-g sand bass) contained 16,500 eggs (Figure 1). Sample females contained a mean (± SEM) of 760 ± 80 eggs per g ovary and 70 ± 12 eggs per g ovary-free body weight.

The running ripe barred sand bass was collected between 0930 and 1100 hrs (Pacific standard time). Time of collection of the other 13 sand bass whose ovaries contained ova in hydrated condition ranged from 0900 to 1100 hrs and from 2100 to 0300 hrs, with 8 collected during the day and 5 at night. All 4 hydrated-state kelp bass were collected during daylight (0830–1300) hours.

DISCUSSION

Despite the large inaccuracies (relative to measurement error) that were likely introduced by pooling species and years, these data strongly suggest that batch fecundity is linearly related to ovary-free body weight in rock bass. It is, therefore, meaningful to express fecundity in terms of ovary weight or ovary-free body weight for basses of a range of body sizes (see Hunter and Macewicz 1980). Fecundities can be estimated using tissue sections subsampled randomly from throughout either or both members of an ovary pair.

These data on number of eggs produced per gram body weight might be used as trial input to preliminary egg production method estimates of stock size, once other key parameters have been estimated (Parker 1980, 1984). Future comprehensive stock assessments would require concurrent data on batch fecundity, field abundance of eggs (or yolk-sac larvae), female spawning incidence, and the biomass sex ratio of adults.

Recognizably hydrated eggs were present within ovaries of female basses collected during almost the entire diel period. This observation suggests that either (1) ripe oocytes undergo hydration over a period of many hours in these fishes, or (2) individual females exhibit large diel variation in time of spawning. I suggest that (1) is more likely, and (based on time of collection of the one running ripe female) that barred sand bass spawn during late afternoon or evening. Further studies are needed to determine if and how time of collection affects estimates of batch fecundity and female spawning incidence in these fishes.

ACKNOWLEDGMENTS

Many thanks go to Fritz Jacobsen, Carl Thies, and Steve Lagos of UCSB for saving fish that they captured while doing other field studies. I also thank the numerous individuals who helped collect sample fish for a bass food habits study. The latter study was funded by the Marine Review Committee of the California Coastal Commission, and I gratefully acknowledge their support.

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EFFECTS OF SAMPLE SIZE AND CONTAGION ON ESTIMATING FISH EGG ABUNDANCE

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ABSTRACT

Because pelagic fish eggs are usually distributed contagiously, the mean and variance estimated from egg surveys are often driven by a few samples of very high abundance. "Sampling" from simulated negative binomial data sets ($n = 20$ to 1,000, $k = .1$ to .4) showed that the sample mean and variance were both highly dependent on the maximum observed value. As contagion (k^{-1}) increased, or n decreased, the chance of a sample including rare, high values decreased. In consequence, nominally 95% confidence limits excluded the population mean more than 5% of the time and tended to underestimate the mean more often than to overestimate it. Log-based parametric estimates were superior to those assuming a normal distribution of sample means, but only at $k = .4$ and $n \geqslant 500$ did the error rate approach 2.5% in both tails. Since contagion in pelagic fish egg distributions is often greater than this ($k < .4$), and affordable sample size usually small ($n < 1{,}000$), a method was sought that would improve accuracy by increasing the asymmetry of confidence bounds. One potential methodology is Easterling's "consonance regions," applied here to samples from a large set of *Engraulis mordax* egg data.

RESUMEN

Debido a la distribución contagiosa de los huevos de peces pelágicos, el promedio y la varianza estimados de recuentos de huevos son a menudo determinados por un bajo número de muestras con alta abundancia. Los "muestreos" de varios conjuntos de datos simulados de distribución binomial negativa ($n = 20$ a 1000, $k = 0.1$ a 0.4) indican que el promedio y la varianza de la muestra son ambas altamente dependientes del máximo valor observado. A medida que el grado de contagio (k^{-1}) aumenta o n disminuye, la probabilidad que una muestra contenga valores altos, de baja frecuencia, disminuye. Consecuentemente, los límites de confidencia del 95% excluyen el promedio de la población en un 5% de los casos y tienden, en general, a subestimar el promedio. Aun cuando las estimaciones paramétricas con distribución logarítmica resultaron ser superiores a aquéllas para las cuales se supuso una distribución normal, el error alcanzó únicamente un 2.5% en cada cola cuando $k = .4$ y $n \geqslant 500$. Dado que el grado de contagio en las distribuciones de huevos de peces pelágicos es generalmente mayor ($k < .4$), ye el tamaño de muestra es generalmente pequeño ($n < 1000$), se buscó un método que mejorara la exactitud por medio de un aumento en la asimetría de los límites de confidencia. El método de Easterling o "método de regiones consonantes" ha sido usado en este trabajo con muestras provenientes de un alto número de datos de huevos de *Engraulis mordax*.

INTRODUCTION

The usual method of computing confidence intervals rests on the assumption that the distribution of (theoretical) sample means is normal (i.e., that the central-limit theorem applies). Robust as this assumption is, the patchy distribution of fish eggs and larvae can give rise to sufficient contagion in survey data to cause significant departures (e.g., the mean of northern anchovy egg samples of $n < 60$ tends to be skewed).

Although statistics texts treat the problem lightly, if at all, proposals for measuring precision in contagious data do appear in the fisheries literature (e.g., Taft 1960; Zweifel and Smith 1981; Pennington 1983; Pennington and Berrien 1984; Jahn, in press). All the proposed methods deal in some way with the asymmetric distribution of sample means, but little has been done to quantify the error rates inherent in each. This has moderate consequences in most fisheries applications, because sample size is typically held large to counteract the effects of contagion and achieve good precision. However, in research that enjoys less financial support, such as environmental impact studies, sample size is often set by factors external to the nature of the variability and is nearly always smaller than the investigator would wish for.

For a given level of abundance, the definition of "small" sample size depends on the desired precision and the degree of contagion. In this paper we demonstrate the interdependence of estimated

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[Manuscript received January 27, 1987.]

mean and variance, and use simulation to quantify the actual precision obtained from such estimates over a range of sample sizes and degrees of contagion common in coastal ichthyoplankton work. The simulation results, based on completely specified negative binomial distributions, are compared with samples from large "populations" of real anchovy egg data. We also briefly explore an alternate method of estimating precision that shows promise for small samples.

METHODS

Statistics

Skewness ($g1$) and kurtosis ($g2$) were calculated according to procedures in Sokal and Rohlf (1969). Formulas used in computing parametric confidence limits were:

$$m \pm t_{\alpha} \cdot \mathrm{SE} \tag{1}$$

$$m \cdot \exp\{\pm\, t_{\alpha} \surd\, [\ln(1 + \mathrm{SE}^2/m^2)]\} \tag{2}$$

where m is the sample mean, t_{α} the standard normal deviate (here approximated as = 2), and SE the standard error of the mean. Formula 1 is the familiar method, which assumes a normal distribution of m. Formula 2, from Zweifel and Smith (1981), assumes the log-normal distribution of m.

Another method explored was the procedure of simultaneous model fitting and parameter estimation suggested by Easterling (1976), in which an array of parameters is employed in goodness-of-fit tests to define a two-dimensional region in which the data are consonant with the specified model. A full description of this procedure, as applied here using the negative binomial frequency distribution and x^2 goodness-of-fit tests, is given in Jahn (in press).

It should be said at the outset that Easterling's proposal was not specifically for making population inferences, but rather for obtaining an objective description of data. Our motivation for applying the technique to a problem of inference was that it produces an asymmetry of fiducial limits that has the desired properties for small samples from contagious distributions. Easterling (1976) has shown that, for a given probability level, consonance regions will tend to be wider than parametric confidence intervals, the difference depending on the nature of the data. We have found that, with small sets of ichthyoplankton data as treated here, a probability of 0.2, or an 80% consonance region, gives an interval of comparable size to a 95% confidence interval, but with more appropriate asymmetry, as will be shown.

Simulations

To obtain an empirical estimate of the accuracy of parametric confidence limits, "sampling" was carried out on three simulated data sets, each distributed as a negative binomial completely specified by the parameters m (the mean, set = 10 in all cases) and k (an inverse contagion parameter, set = 0.1, 0.2, and 0.4). The simulated populations, generated according to procedures given in Elliott (1971), consisted of 50,000 numbers each, sufficient to produce variances > 99% of asymptotic values ($s^2 = m + m^2/k$). From each population, 1,000 random samples of n = 20, 50, 100, 200, 500, and 1,000 were taken, and their mean, variance, and maximum value recorded.

Egg Data

Real fish-egg abundance data came from surveys employing a 0.05 m^2 vertically towed net, the CalVET sampler (Smith et al. 1985). The six CalVET surveys for 1980–85 took 5,338 samples, of which 2,311 were positive for northern anchovy (*Engraulis mordax*) eggs. Ages of all eggs from each sample were estimated from stage of development and field temperature (Lo 1985). For subsampling purposes, the 3,027 (5,338 − 2,311) negative stations were considered outside the spawning area and omitted as "false" zeros[1]. The first (A) and second (B) whole days after spawning, and total eggs (T), were the three "populations" from which random subsamples of n = 20, 46, 100, 200, and 500 were taken. The two smallest sample sizes correspond to the number of samples per cruise in a program of nearshore egg and larval surveys, wherein mean abundances have been reported with various measures of precision, including some methods used here (Brewer and Smith 1982; Lavenberg et al. 1986; Jahn, in press).

RESULTS AND DISCUSSION

Simulations

For a given level of contagion, the range and symmetry of the distribution of sample means were (as expected) strongly related to sample size (Figure 1). The width of the range of the central 95% of sample means was well predicted from population parameters as 4 standard errors of the mean

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[1] By "false" zeros we mean that these observations were taken outside the spawning area and not by chance from within it. (For a more thorough treatment see Smith 1973.) This oversimplification will have slight consequences for the biological character of our example data sets, but the allocation of zeros is a problem in fisheries practice that rivals that of precision.

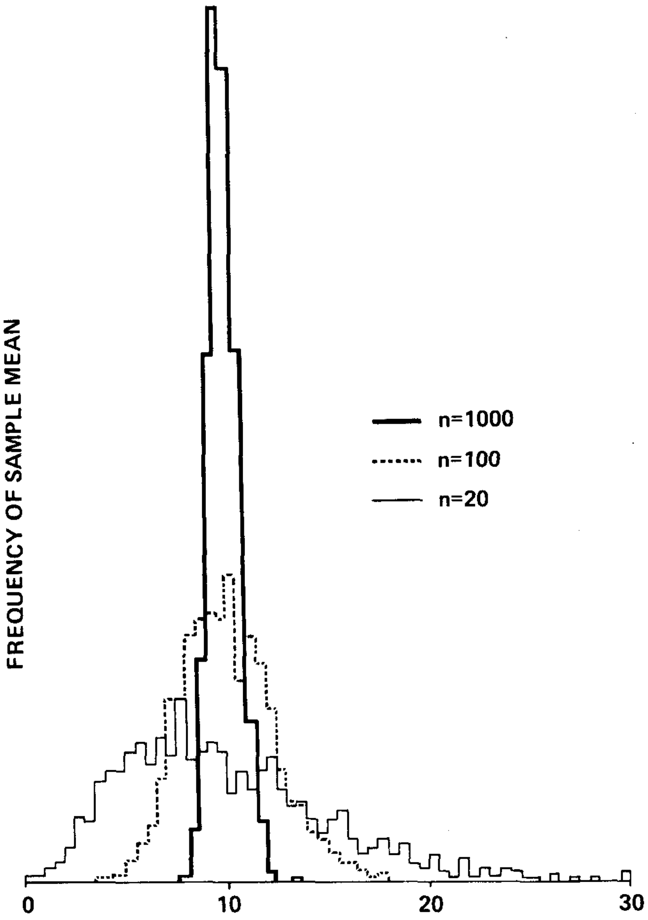

Figure 1. Superimposed histograms of 1,000 sample means for three sample sizes from a negative binomial population with $m = 10$, $k = .2$.

TABLE 1

Summary Statistics of Sample Means from Negative Binomial "Populations" of 50,000 Numbers with $\mu = 10$ and Parameter k as Indicated

	n	m	LL	UL	w	$4\mu(kn)^{-1/2}$	$\frac{UL - \mu}{\mu - LL}$
$k = .1$	20	9.9	1.15	26.25	25.1	28.3	1.84
	50	10.3	3.44	20.92	17.5	17.9	1.66
	100	9.9	4.90	16.66	11.8	12.6	1.31
	200	9.9	6.06	14.67	8.6	8.9	1.19
	500	10.0	7.51	13.07	5.6	5.7	1.23
	1000	10.0	8.06	12.01	4.0	4.0	1.04
$k = .2$	20	9.9	2.70	21.70	19.0	20.0	1.60
	50	9.9	4.72	16.64	11.9	12.6	1.26
	100	10.0	6.10	14.89	8.8	8.9	1.25
	200	10.0	7.075	13.475	6.4	6.3	1.19
	500	10.0	8.07	12.01	3.9	4.0	1.04
	1000	10.0	8.66	11.37	2.7	2.8	1.02
$k = .4$	20	9.9	4.05	18.70	14.65	14.1	1.46
	50	10.0	6.00	14.78	8.8	8.9	1.20
	100	9.9	7.02	13.10	6.1	6.3	1.19
	200	10.0	7.87	12.265	4.8	4.5	1.06
	500	10.0	8.58	11.56	3.0	2.8	1.10
	1000	10.0	9.01	11.03	2.0	2.0	1.04

LL = 2.5th percentile; UL = 97.5th percentile; w = UL − LL; n = sample size; m = average of sample means.

(approximated as $4\mu/\sqrt{kn}$, Table 1), but this interval was never precisely centered on the population mean. The asymmetry of the interval [(upper limit − μ)/(μ − lower limit)] varied inversely with both n and k (Table 1 and Figure 2). Although the distribution of sample means is interesting and informative in a theoretical context, the real problem in practice is estimating population parameters from the information contained in a single sample.

For all three simulated populations, as in the marine sampling environment, parameter estimates were highly dependent on relatively rare, high values. In small samples these extreme observations can dominate parameter estimates; on the other hand, their absence can lead to severe underestimates of the mean and variance. The dependence of these parameter estimates on the maximum observed value is shown in Figure 3 for the case $k = 0.2$, $n = 50$.

Overestimating the variance (and concomitantly, the mean) produces wide confidence intervals which, though imprecise, tend to be accurate in that they include the population mean. Conversely, underestimating the variance often leads to confidence intervals that are too small and exclude the true mean. These trends account in principle for the distributions of samples producing confidence limits that were too low or too high (Table 2). For the same reason that the "curves" in Figure 2 are not smooth, the numbers in Table 2 yield only approximate probabilities, but these should serve as useful indicators of the effects of sample size and contagion on measuring precision.

Ideally, 95% confidence limits should be higher than the true mean 2.5% of the time and lower

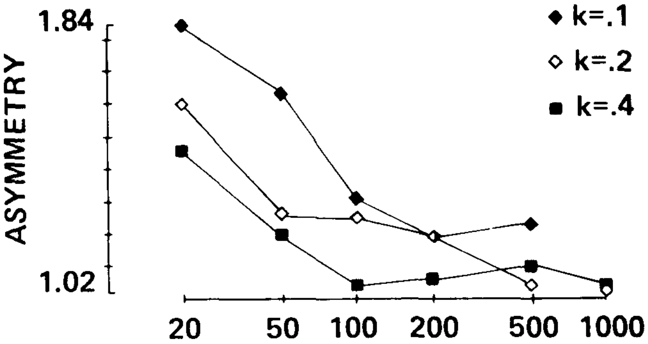

Figure 2. Asymmetry (see Table 1) of the distribution of sample means as a function of sample size (n) for three levels of contagion, k.

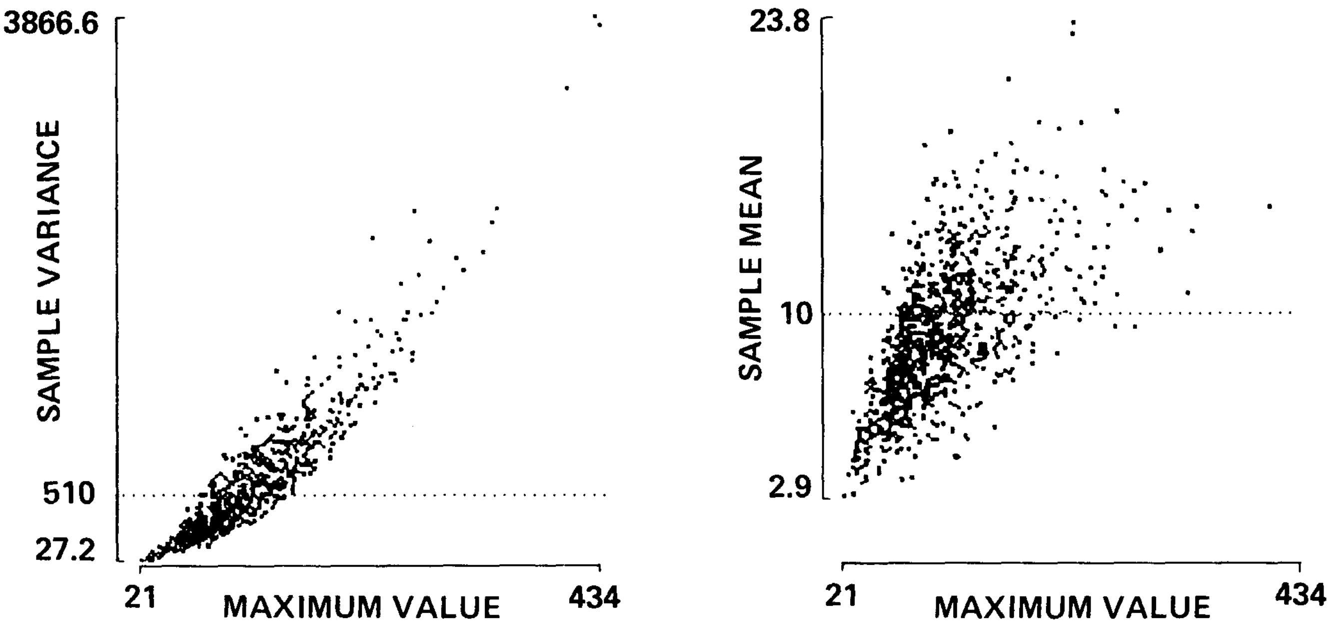

Figure 3. Dependence of estimates of the variance and mean on maximum observed value. All samples were of $n = 50$ from a negative binomial population with mean = 10, variance = 510 ($k = .2$).

TABLE 2

Summary of Samples (from 1000 Iterations) Giving Computed 95% Confidence Limits (CL) That Excluded the Population Mean (μ).

	k	$n=20$		$n=50$		$n=100$		$n=200$		$n=500$		$n=1000$	
		L	H	L	H	L	H	L	H	L	H	L	H
Formula 1	.1	249	1	151	3	110	1	86	4	60	7	50	5
	.2	188	4	119	5	71	3	57	6	59	9	34	12
	.4	144	4	82	8	62	3	50	7	37	20	33	16
Formula 2	.1	162	22	90	22	66	14	54	14	42	15	36	20
	.2	117	26	66	19	42	23	35	27	42	21	30	18
	.4	89	25	50	19	41	11	38	22	29	28	28	22

Formula 1: $m \pm t_\alpha \bullet \mathrm{SE}$

Formula 2: $m \bullet \exp\{\pm t_\alpha \surd[\ln(1 + \mathrm{SE}^2/m^2)]\}$
where t_α was approximated as = 2.

L = number of upper CL's that were lower than μ; H = number of lower CL's higher than μ.

than the mean 2.5% of the time; i.e., the "tails" should be equal and add to 5%. For the simulations presented here (1,000 samples each), the tails should each average 25 samples. As shown in Table 2, the low tail (L) was always > 25, and the high tail (H) usually < 25. The log-based method (formula 2) was superior to the conventional symmetrical limits (formula 1), but approached equal tails only at high n (≥ 500) and k (.4). Because the simulated values of k are realistic, and larger values of n are often not, it is desirable to find a method that will further increase the asymmetry (shorten the low tail and lengthen the high) of computed confidence intervals. One promising approach is applied to real data, below.

Real Data

The three "populations" of real anchovy-egg data (summarized in Table 3) were all positively skewed and peaked (leptokurtic), with large differences between mean and median values. In all cases the variance exceeded the mean squared, implying a high degree of contagion with values of the negative binomial parameter $k < 1$. For various reasons, including the truncation of zeros and the composite nature of the data sets (amalgamation of several years' sampling), the negative binomial distribution is only an approximate model for these

TABLE 3

Characteristics of Three Populations of Anchovy Egg Data Compiled from 2,311 Positive CalVET Tows from 6 Surveys, 1980–85

Population	Mean	Median	Maximum	s^2	Skewness	Kurtosis	k	Freq(0)
A	9.88	2	261	426	5.36	42.45	.343	678
B	7.93	2	468	296	10.84	235.32	.394	632
T	24.22	10	605	1448	4.34	35.92	.656	0

A, B = first and second whole days after spawning. T = total eggs.

populations. This can be verified, for instance, by comparing the maximum likelihood estimates of k (Table 3) with the asymptotic moments relationship, $k' = m^2/(s^2 - m)$. However, as will be seen below, small samples from these distributions will tend to be negative-binomial-like enough that the null hypothesis in goodness-of-fit tests will seldom be rejected.

Ten random samples at each of five sample sizes (20 to 500, Table 4) were drawn from each of the three populations. At sample sizes < 500, the sample mean bore an approximately linear relationship to the maximum observations, shown for the A samples in Figure 4. Only one T sample (#7 at $n = 20$) produced a confidence interval that excluded the mean, but 16% of samples from the more positively skewed A and B populations (which also had $> 25\%$ zeros, Table 3) at $n \leq 200$ produced estimates of the mean that were more than 2 standard errors below the true value. The

TABLE 4

Mean (m), Median (md), Maximum (max), and Standard Error (SE) of Samples of *Engraulis mordax* Eggs

	m	md	max	SE		m	md	max	SE		m	md	max	SE
A20	11.25	1	71	4.57	B20	4.55	1	27	1.59	T20	19.30	8	127	6.85
	11.85	3	71	4.09		4.25	1	47	2.33		15.55	7	83	4.31
	10.30	4	48	3.43		4.00	2	15	0.99		29.10	17.5	173	8.63
	7.25	1	37	2.67		7.05	1	34	2.22		24.95	9.5	144	8.09
	7.90	4.5	39	2.29		9.80	1.5	38	2.98		19.00	3	177	10.81
	7.45	3.5	47	2.89		9.95	5.5	61	3.32		25.10	15	114	6.55
	10.80	5	46	3.17		11.05	3	46	3.41		11.45	6	61	3.12
	10.30	7	39	2.35		6.70	1	34	2.40		46.70	19	252	14.58
	9.65	1.5	79	4.35		8.45	3	36	2.42		18.45	13.5	60	3.97
	7.10	1	55	3.31		3.75	1	27	1.44		23.40	11	106	7.14
A46	10.30	1	99	3.16	B46	10.09	3	86	2.57	T46	31.89	15	201	6.10
	5.80	1	71	1.86		4.44	1	37	1.20		21.52	11.5	97	3.84
	4.85	2	26	1.01		9.13	2.5	74	2.36		32.13	16	166	6.20
	12.15	6	71	2.57		15.91	2.5	468	10.15		25.54	8.5	140	4.91
	17.54	3	247	6.52		8.17	1	55	2.00		25.67	14.5	242	6.06
	11.35	4	94	2.53		10.74	3	119	3.03		19.96	8.5	117	3.65
	10.67	3	127	3.25		10.59	2	142	3.62		20.63	9.5	167	5.17
	7.96	3	109	2.54		7.78	1.5	88	2.23		30.67	15.5	177	6.07
	5.35	1.5	53	1.37		10.48	2.5	83	2.77		31.13	19	157	5.49
	10.80	3.5	84	2.78		6.37	2.5	35	1.28		28.94	16	248	6.27
A100	10.20	2	102	1.91	B100	8.19	2	128	1.73	T100	22.35	6.5	174	3.59
	9.38	3	119	1.69		5.71	2	39	0.88		24.04	13	147	2.92
	11.83	3	170	2.42		6.15	3	45	0.83		29.03	12	342	5.08
	11.93	3	244	2.94		12.35	1	468	4.94		25.27	7	382	4.70
	10.44	3	201	2.45		8.94	3	87	1.63		21.66	7.5	168	3.35
	7.46	2	87	1.38		10.71	3	201	2.61		24.34	9	217	3.82
	13.50	2	229	3.22		5.85	2	59	0.94		23.43	8.5	252	3.59
	9.54	3	118	1.76		14.15	3	468	4.89		22.52	11	171	2.83
	10.69	4.5	170	2.02		10.24	2.5	201	2.64		21.27	11	273	3.47
	10.12	4	65	1.35		6.86	2	69	1.15		27.46	10.5	173	3.80
A200	9.80	2	126	1.34	B200	8.60	3	131	1.10	T200	26.72	10.5	605	3.86
	12.28	3	245	1.88		7.95	1.5	142	1.20		22.05	9	174	2.22
	11.35	3	157	1.47		7.41	3	119	0.94		22.11	7	168	2.24
	13.43	3	261	2.12		9.94	4	140	1.24		22.49	9	273	2.42
	7.52	3	64	0.78		7.29	2	131	1.09		21.27	9	174	2.09
	9.26	3.5	157	1.28		5.98	2	42	0.60		25.77	9	273	2.82
	10.15	3	157	1.40		7.71	2	88	1.00		21.25	7	217	2.40
	7.96	2	94	1.05		7.23	3	64	0.81		23.05	10	252	2.42
	9.52	3	132	1.27		7.65	2	75	0.92		23.61	8	211	2.46
	10.59	2.5	261	1.69		7.62	2	142	1.08		21.33	10	195	2.06
A500	9.48	2	229	0.95	B500	7.79	3	120	0.61	T500	23.52	10.5	249	1.49
	9.52	2	229	0.91		8.49	2	468	1.13		24.26	9	251	1.70
	10.10	2	261	0.97		7.89	2	142	0.66		23.16	10	342	1.60
	10.40	3	261	0.97		8.49	2	128	0.67		22.20	10	342	1.45
	10.28	2	245	1.03		8.31	2	201	0.72		21.36	9	382	1:55
	8.88	2	245	0.83		8.19	3	140	0.64		26.23	11	605	2.06
	10.79	3	170	0.95		9.81	2	468	1.23		22.11	9	215	1.39
	10.82	3	261	1.04		8.11	3	201	0.68		23.51	10	251	1.54
	11.38	3	247	1.18		8.15	2	468	1.15		24.90	9	605	1.96
	10.66	3	201	0.98		7.86	2	142	0.67		23.35	11	342	1.59

A = first whole day, B = second whole day after spawning; T = total eggs. Number after age designation is sample size.

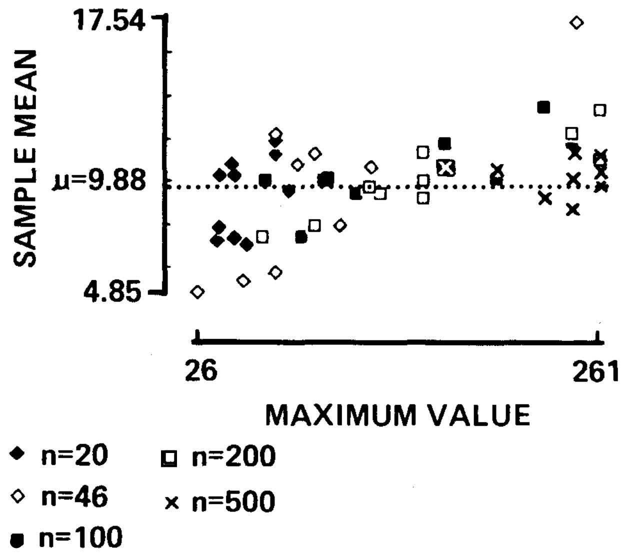

Figure 4. Dependence of the sample mean on the maximum observed value of samples drawn from a "population" of northern anchovy eggs (population A, Table 3).

worst case was sample A46#3, with sample mean = 4.85 and standard error = 1.01. The 95% confidence limits by formula 2 for this sample are 3.2–7.3, well below the true mean value of 9.9. However, the adaptation of Easterling's "consonance region" produced an interval estimate for the mean (3.5–10.5) that included the true value (Table 5). This method thus shows promise of reducing the frequency of samples in the "low tail," found above to be several times too high at sample sizes < 500.

At the other extreme among A samples was A46#5, with mean = 17.54 and standard error = 6.52. The high mean and variance of this small sample were strongly affected by the maximum value of 247 (Table 4; Figure 4), giving a wide confidence interval by formula 2 of 8.54–36.02. The consonance region for this sample gives credence to a narrower range of values for the population mean (approximately 7–14, Table 6), excluding the sample mean but still containing values above and below 9.9, the true mean. The effect of the very high maximum value on estimates of central tendency and dispersion was therefore moderated by the shape of the rest of the data in the sample. Besides the maximum value, sample A46#5 also chanced to have two other values > 100 but a median of only 3, characteristics that contribute to the bilobed nature of the consonance region as computed here.

The goodness-of-fit results of Table 6 also suggest that the negative binomial may be a poor general model for the data of sample A46#5, as no $p \geqslant .5$ region was found. If these data were all that we knew about the population, with what confidence could we make statements about its parameters? Before such questions can be answered, work must be done to quantify the distribution of consonance regions for contagiously distributed data, and to work out the robustness of the method to departures from completely specified distribution

TABLE 5

Chi-Square Probabilities of Goodness of Fit to Sample A46 #3 (See Table 4) of Negative Binomial Models with Parameters *m* and *k*

m	*k*														
	.2		.3		.4		.5		.6		.7		.8		.9
12.5			.1												
12.0			.1	.1											
11.5			.1	.1	.1										
11.0			.1	.1	.1										
10.5			.2	.2	.1	.1									
10.0			.2	.2	.2	.1		.1							
9.5			.1	.2	.2	.2	.2	.1							
9.0			.2	.2	.2	.2	.2	.2	.1						
8.5			.2	.2	.2	.2	.2	.1							
8.0			.2	.2	.5	.2	.2	.2	.1	.1					
7.5			.2	.2	.5	.5	.2	.2	.1	.1					
7.0			.2	.2	.5	.5	.5	.2	.2	.2	.1				
6.5			.2	.2	.5	.5	.5	.2	.2	.2	.2	.1			
6.0		.1	.2	.2	.5	.5	.5	.5	.2	.2	.2	.1			
5.5		.1	.2	.5	.5	.5	.5	.5	.5	.2	.2	.1			
5.0		.1	.2	.5	.5	.5	.5	.5	.5	.2	.2	.2	.2	.1	.1
4.5		.1	.2	.5	.5	.5	.5	.5	.2	.2	.5	.2	.2	.2	.1
4.0			.2	.2	.5	.5	.5	.2	.5	.2	.1	.1		.2	.1
3.5			.1	.2	.1	.2	.2	.2	.2	.2	.2	.1	.1		
3.0					.1	.1			.1	.1	.1				

TABLE 6

Chi-Square Probabilities of Goodness of Fit to Sample A46 #5 of Negative Binomial Models with Parameters *m* and *k*

m	*k*										
	.25		.35		.45		.55		.65		.75
15.0			.1								
14.5			.1								
14.0		.2	.1								
13.5		.2	.1								
13.0		.2	.1								
12.5		.2	.1								
12.0		.2	.1								
11.5		.2	.1								
11.0		.2	.1								
10.5		.1	.1	.1							
10.0		.1	.1								
9.5		.2	.1				.1				
9.0		.1	.1		.2	.1					
8.5		.1		.2	.2						
8.0		.1	.2	.2	.2				.1	.1	
7.5		.1		.2	.2	.2	.2	.1	.1		.1
7.0			.1	.2	.2	.1	.1	.1	.1		
6.5					.1	.1	.1				
6.0											

models. Because of the astronomical number of computations required, it is very unlikely that generally applicable tables will be forthcoming. However, solutions to specific situations, with a few models over a limited range of parameters, should be producible for a given research application.

One obvious limitation of the consonance region approach is that as sample size increases, the statistical power to reject the null hypothesis (i.e., no difference between sample and specified frequency distribution) increases as well. The consonance region will become correspondingly small until some practical limit is reached. At such a point it may be plausible to use models with more parameters, as suggested by Easterling (1976), but as sample size increases, so does the suitability of simpler fiducial methods, such as formula 2.

When, as in pelagic fish-egg and larval census work, the potential exists for a few observations to dominate parameter estimates, the best insurance against wrong estimates is large sample size. In some applications, the costs of increasing sample size may seem too high, and the lower precision of small samples may be acceptable. We have emphasized here that special methods are needed in these cases in order to make correct probability statements about the population. We are not advocating the use of small samples. Rather, it is hoped that the above examples and the data of Table 2 will be helpful to planners who must weigh the costs and benefits of various approaches to sampling contagiously distributed organisms.

ACKNOWLEDGMENTS

We thank James Petersen for his helpful comments on several versions of the manuscript. Two anonymous reviewers also made useful comments. Helga Schwarz helped prepare the manuscript. The first author thanks the Southern California Edison Company for financial support.

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SAMPLING FOR EGGS OF SARDINE AND OTHER FISHES IN THE COASTAL ZONE USING THE CALVET NET

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ABSTRACT

In 1986, vertical tows for fish eggs (using the CalVET sampler) were taken at standard southern California monitoring stations, which range from Ormond Beach in the north to San Onofre in the south and represent the 8-, 15-, 22-, 36-, and 75-m contours. Data for six cruises in even months (120 tows in all) indicate the certain or very probable identification of eggs of at least 18 species or species complexes. *Engraulis mordax, Sardinops sagax, Genyonemus lineatus, Symphurus atricauda, Citharichthys* spp., *Seriphus politus,* and *Pleuronichthys verticalis* were (in descending order) most abundant. *Engraulis* and *Symphurus* were concentrated at the deepest stations, *Seriphus* at the shallowest, the other four at midshelf (15–36 m). The three flatfishes were about evenly distributed alongshore, but 73% to 100% of clupeoids and croakers were concentrated at our two central transects (Santa Monica Bay and Seal Beach). Only one *Paralichthys californicus* and six *Paralabrax* spp. eggs were taken.

RESUMEN

Durante 1986 se realizaron arrastres verticales con un muestreador CalVET para colectar muestras de huevos de peces en estaciones de monitoreo estándar en el Sur de California, las cuales cubren el area desde Ormond Beach en el norte hasta San Onofre en el sur a lo largo de las isóbatas de 8-, 15-, 22-, 36-, y 75-m. Los datos colectados en seis cruceros realizados durante meses pares (120 arrastres en total) permitieron identificar con certeza parcial o total al menos 18 especies o complejos de especies. *Engraulis mordax, Sardinops sagax, Genyonemus lineatus, Symphurus atricauda, Citharichthys* spp., *Seriphus politus,* y *Pleuronichthys verticalis* fueron, en orden decreciente, las más abundantes. *Engraulis* y *Symphurus* se concentraron en las estaciones más profundas, *Seriphus* en las menos profundas y las restantes cuatro sobre la plataforma (15–36 m). Los tres lenguados se distribuyeron uniformemente a lo largo de la costa, mientras que un 73%–100% de los clupeidos y sciaenidos se concentraron a lo largo de nuestras dos transectas centrales (Bahía de Santa Monica y Seal Beach). Un solo huevo de *Paralichthys californicus* y seis huevos de *Paralabrax* spp. fueron colectados.

INTRODUCTION

Recently, much interest has focused on the apparent recovery of the Pacific sardine (*Sardinops sagax*) resource off California and on the use of egg survey data to monitor the stock (Wolf 1985; Wolf and Smith 1985, 1986). Wolf and Smith (1986) estimated that a spawning biomass of 20,000 short tons of sardine, given characteristic values of fecundity and egg production per unit area, would occupy an area of approximately 500 nautical miles^2, or 1,715 km^2. The total area of the continental shelf between Point Conception and the border with Mexico, out to a depth of 75 m, is about 2,800 km^2. The nearshore zone thus has the potential to harbor a substantial portion of the sardine spawning stock in its early stage of recovery.

Year-round collection of egg and larval data from the very nearshore zone showed an increase in sardine spawning beginning in 1982, with a seasonal peak in summer–fall that varied from the expected predominantly springtime pattern (Ahlstrom 1967; Lavenberg et al. 1986). Discussions with P. Smith of the National Marine Fisheries Service (NMFS) and P. Wolf, K. Mais, and R. Klingbeil of the California Department of Fish and Game (CDFG) pointed to the desirability of rapid intercalibration of offshore and nearshore sampling. Accordingly, we integrated the CalVET net, now standard in the NMFS/CDFG sardine egg surveys, into our coastal zone cruise schedule in 1986. This note presents data on sardine and other abundant taxa of which eggs could be identified.

METHODS

The sampler used was the bongo-type PAIROVET version of the CalVET net (Smith et al. 1985), consisting of paired cylindrical-conical nets, each of 0.05-m^2 mouth opening, fitted with 150-μm

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[Manuscript received February 2, 1987.]

TABLE 1
Ranking of Taxa from CalVET Samples for 1986

	Sum	Frequency
1. *Engraulis mordax*	269	39
2. *Sardinops sagax*	170	27
3. *Genyonemus lineatus*	147	38
4. *Symphurus atricauda*	84	18
5. *Citharichthys* species	83	51
6. *Seriphus politus*	41	17
7. *Pleuronichthys verticalis*	33	20
8. *Pleuronichthys ritteri*	16	14
9. *Etrumeus teres*	15	7
10. *Sphyraena argentea*	10	5
11. *Synodus lucioceps*	8	7
12. *Paralabrax* species	6	2
13. *Leuroglossus stilbius*	3	1
14. *Paralichthys californicus*	1	1
15. *Merluccius productus*	1	1
16. *Ophidion scrippsae*	1	1
17. *Pleuronichthys coenosus*	1	1
18. *Pleuronichthys decurrens*	1	1
Subtotal	890	
Other designated types	51	
Unidentified eggs	1,015	
Total	1,956	

mesh netting in one side and 333-μm mesh in the other. The nets were towed vertically from a depth of 70 m, or from the bottom in shoaler waters, at a rate of 70 m min^{-1}. Cruises were in even-numbered months from February to December 1986. Across-shelf transects consisting of samples over the 8-, 15-, 22-, 36-, and 75-m contours were taken from north to south off Ormond Beach, Playa del Rey, Seal Beach, and San Onofre, all in the Southern California Bight (see Lavenberg et al. 1986). Samples were fixed at sea in buffered 5% seawater Formalin. Tows were made in the evening, principally between 1800 and 2200 hrs, and each tow was accompanied by a surface temperature reading.

The 20 paired samples from each cruise were sorted in the laboratory, and then all fish eggs were examined by an experienced technician. Although northern anchovy and Pacific sardine eggs can be readily identified, the eggs of relatively few other local species can yet be identified with absolute certainty. Published descriptions exist for about two-thirds of the taxa listed in Table 1, and an evolving system of designated types is gradually improving the state of fish-egg taxonomy. The identifications used in this report were all made with a high degree of confidence. Staging of sardine and anchovy eggs was done by the methods of Ahlstrom (1943) and Moser and Ahlstrom (1985).

After the fourth cruise, paired t-tests indicated no difference in capture by the two sides of the sampler for either anchovy eggs or all eggs combined. We have therefore added the counts from both nets, so that abundances tabulated here are eggs per 0.1 m^2.

RESULTS

On the six bimonthly cruises, 120 samples produced 1,956 eggs, about half of which were identified to 18 species or species complexes (Table 1). The patterns (places and months of capture) of abundance of the seven most abundant taxa are given in Table 2. Northern anchovy (*Engraulis mordax*) and white croaker (*Genyonemus lineatus*) displayed characteristic winter-spring seasonality; Pacific sardine (*Sardinops sagax*) and the sanddab complex (*Citharichthys* spp.) spawned essentially year-round; hornyhead turbot (*Pleuronichthys verticalis*) and queenfish (*Seriphus politus*) appeared in spring and summer; and California tonguefish (*Symphurus atricauda*) appeared in late summer–fall. Anchovy and tonguefish were most concentrated over the outer shelf, where the abundance of other species tapered off. All species except queenfish and sanddabs became less abundant at the 8-m contour.

An interesting feature of these data is the concentration at the two central transects of four of these species, particularly during their months of peak spawning (73%–100% of all eggs of anchovy, sardine, white croaker, and queenfish occurred at Playa del Rey and Seal Beach). The exceptions to this trend were, perhaps coincidentally, all flatfishes—*Symphurus, Citharichthys,* and *Pleuronichthys* (54%–60%). The extreme case of mid-bight concentration was Pacific sardine, which was not taken at all in the north (Ormond Beach) or south (San Onofre) in 1986.

These data allow some comparisons to the more offshore sardine work of CDFG. In this study, sardine eggs were always taken in a contiguous block of stations (Table 2), roughly representing from about 270 km^2 to 580 km^2 (Table 3). The total ocean area represented by the Playa del Rey and Seal Beach transects, 927 km^2, is roughly half the area estimated by Wolf and Smith (1986) to be occupied by a spawning population of 20,000 tons, the criterion biomass for opening a directed sardine fishery. Taking the comparison further, the average egg abundance at positive stations ranged from 1.4 to 7.2 eggs per 0.05 m^2. Since nearly all eggs were at least a day old (see below), the total count can be considered a crude minimum estimate of daily production (unless mortality was much less than normal); thus the range found here is similar to that used by Wolf and Smith (1.5 to 5 eggs per .05 m^2) in their inverse biomass estimate.

TABLE 2
Counts (Eggs per 0.1m²) of the Seven Most Numerous Egg Taxa

	Engraulis mordax					*Sardinops sagax*					*Genyonemus lineatus*					*Symphurus atricauda*					*Citharichthys* spp.					*Seriphus politus*					*Pleuronichthys verticalis*				
Depth (m)	8	15	22	36	75	8	15	22	36	75	8	15	22	36	75	8	15	22	36	75	8	15	22	36	75	8	15	22	36	75	8	15	22	36	75
February																																			
Ormond Beach	–	–	1	6	6	–	–	–	–	–	1	–	–	1	1	none taken					1	1	–	–	–	–	–	1	–	–	–	–	–	–	–
Playa del Rey	–	1	–	7	14	–	1	2	3	–	–	–	1	3	–						–	2	4	–	–	–	–	–	–	–	–	–	–	4	–
Seal Beach	1	5	4	28	105	–	–	2	7	–	3	7	37	26	–						–	1	3	5	–	–	–	–	–	–	–	–	1	–	–
San Onofre	–	–	–	–	–	–	–	–	–	–	1	2	3	1	1						–	1	2	1	–	–	–	–	–	–	–	–	–	–	–
April																																			
Ormond Beach	–	–	22	4	–	–	–	–	–	–	–	–	–	–	–	none taken					–	1	1	2	–	–	1	1	2	–	–	–	–	–	–
Playa del Rey	1	6	2	–	–	3	15	27	–	–	–	4	3	–	–						3	1	–	–	–	4	5	5	1	–	–	1	1	–	–
Seal Beach	–	–	1	2	3	–	13	14	–	–	1	2	–	–	–						1	1	–	1	–	3	–	–	–	–	–	–	2	–	–
San Onofre	2	–	1	1	1	–	–	–	–	–	–	5	1	–	–						2	1	–	–	–	3	2	–	–	–	–	2	–	–	–
June																																			
Ormond Beach	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	none taken					2	–	–	–	–	–	–	–	–	1	–	3	4	1	1
Playa del Rey	1	2	10	–	–	–	–	–	–	–	–	–	–	–	–						–	–	–	–	–	–	–	1	–	–	–	–	–	1	–
Seal Beach	5	1	–	–	–	–	3	7	2	1	1	–	–	–	–						–	–	–	–	–	4	3	3	–	–	–	–	2	–	–
San Onofre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–						–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
August																																			
Ormond Beach	none taken					–	–	–	–	–	none taken					–	–	–	1	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–
Playa del Rey						–	–	–	–	–						–	–	1	11	3	–	1	–	1	1	1	–	–	–	–	–	1	2	–	–
Seal Beach						1	2	3	28	1						1	–	2	4	3	3	–	1	1	–	–	–	–	–	–	–	1	–	1	1
San Onofre						–	–	–	–	–						–	–	–	–	–	1	2	–	3	–	–	–	–	–	–	–	–	–	–	–
October																																			
Ormond Beach	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	14	2	1	1	–	–	none taken					–	1	–	–	–
Playa del Rey	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	1	11	2	4	1	1	–						–	–	–	–	–
Seal Beach	–	–	–	–	2	–	1	6	10	1	–	–	4	1	–	1	1	–	2	5	1	1	1	2	–						–	–	–	–	–
San Onofre	–	–	–	–	–	–	–	–	–	–	1	2	2	2	1	–	–	–	1	17	2	–	–	–	–						–	2	–	–	–
December																																			
Ormond Beach	–	2	1	–	–	–	–	–	–	–	–	1	3	1	–	none taken					–	2	–	–	–	none taken					none taken				
Playa del Rey	–	–	–	2	–	–	–	–	–	–	–	1	–	2	–						–	1	–	1	–										
Seal Beach	–	7	5	–	–	–	3	3	8	3	–	–	12	4	–						2	–	2	1	–										
San Onofre	1	1	2	2	–	–	–	–	–	–	–	2	1	–	–						–	–	–	1	–										
	11	25	49	53	131	4	38	64	58	6	8	26	67	43	3	2	1	3	25	53	22	23	16	21	1	15	11	11	3	1	0	12	12	7	2

Column totals show overall abundance at the five depth contours.

Because most sampling was done during evening (1800–2200 hrs) and because *Engraulis* and *Sardinops* both spawn at night (Ahlstrom 1943; Hunter and Macewicz 1980), there was a 24-hr pulse in the age structure of these species, with most specimens being at least a day old at the time of capture (Figures 1 and 2). (In April, over half of the anchovy eggs were taken at Ormond Beach, where the temperature was only 15°C, accounting for the somewhat younger calculated age.) Age-stage relationships have not been worked out for other abundant species.

Finally, it is apparent from the frequency-of-occurrence and overall abundance data (Table 1) that the sampler used in this study, specifically designed for use in northern anchovy egg production work, is ill-suited to studies on certain other important species: for instance, the bass complex *Paralabrax* occurred in only two samples (six eggs), and California halibut (*Paralichthys californicus*) in only one.

DISCUSSION

The temporal spawning pattern of Pacific sardine, with peaks in April and August, was similar in 1986 to the pattern previously reported and discussed for the years 1978–84 (Brewer and Smith 1982; Lavenberg et al. 1986), except that the spring peak appeared to be the stronger of the two in 1986. Ahlstrom (1967) noted that an August peak was generally found only off central Baja California and represented a southern subpopulation. The greater abundance in April 1986 may signal a return to the expected pattern for a northern stock.

Perhaps important from a management perspective was the consistent appearance of sardine eggs in waters 36 m deep or shallower, particularly off

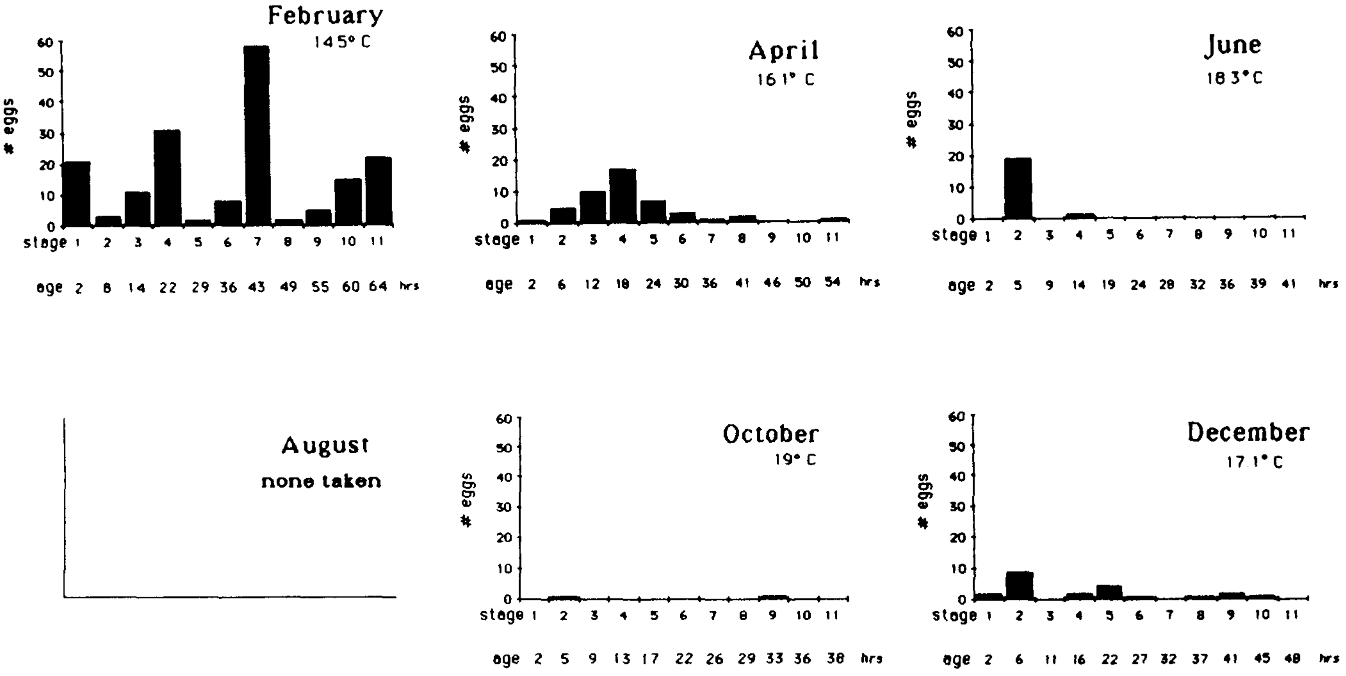

Figure 1. Estimated age in hours of *Engraulis mordax* eggs, based on bightwide mean surface temperature, by the method of Lo (1985).

Seal Beach. Although the total area of shallow habitat used by spawning sardine appeared smaller than the critical area (1,715 km^2 for 20,000 tons spawning biomass) estimated by Wolf and Smith (1986), it constituted a substantial fraction of it. Egg abundance within this shallow area is indistinguishable from that obtained offshore (Wolf, pers. comm.). The consistent appearance of eggs off Seal Beach, along with the observation that the abundance at 75 m was generally less than that

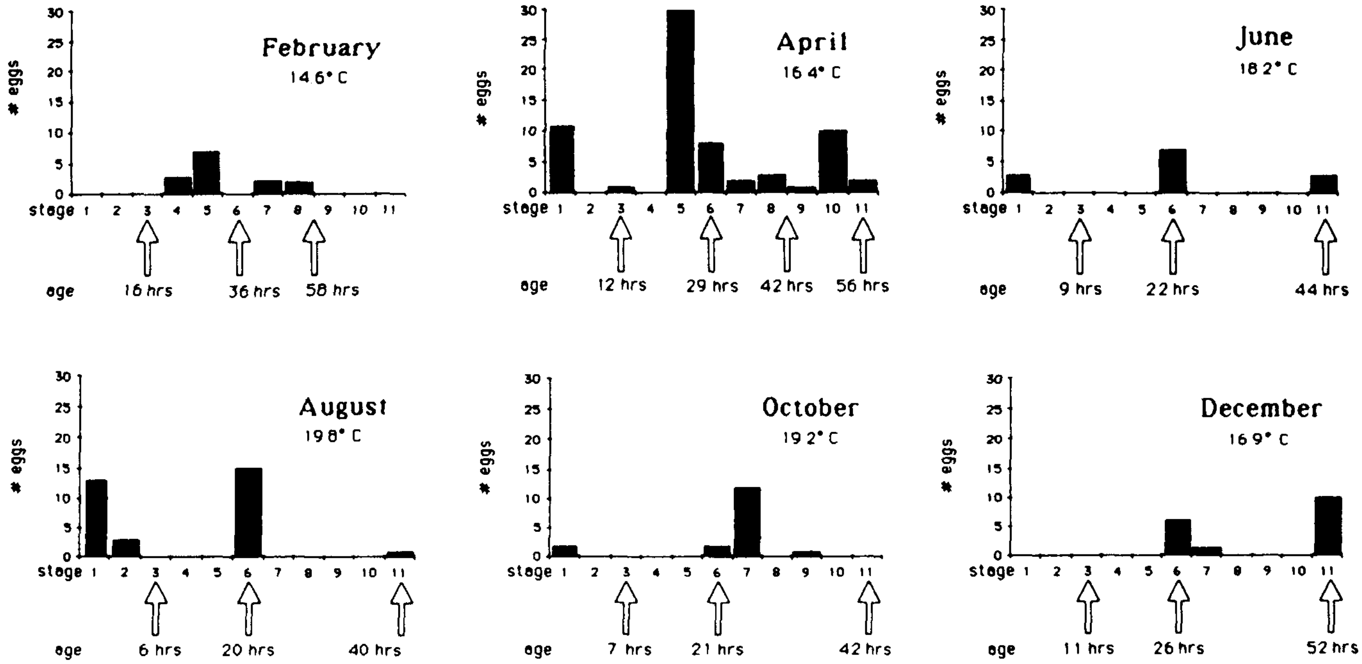

Figure 2. Estimated age in hours of *Sardinops sagax* eggs, based on mean surface temperature at the Playa del Rey and Seal Beach transects, by the temperature-development relations of Ahlstrom (1943).

TABLE 3

Subareas, in km², of the Continental Shelf Represented by Collecting Stations at the Two Central Transects

	Depth (m)					
Transect	0–8	8–15	15–22	22–36	36–75	Total
Playa del Rey	31	35	36	60	185	347
Seal Beach	67	79	91	163	180	580
Total						927

From Lavenberg et al. 1986, Table 4.

between 15 and 36 m, further suggests the importance of this continental shelf locality to a contracted sardine population.

The small numbers of Pacific halibut and bass eggs prove (not unexpectedly) that the techniques used here were inadequate for monitoring these resources. It is obvious that both gear and survey design should be tailored to the spawning habits of these important fishes.

ACKNOWLEDGMENTS

We thank the *Vantuna* field crew, especially Mickey Singer, for work at sea; Paul Smith for getting us all started; Debra Carlson-Oda, Lauma Jurkevics, Fiona Lewis Mackert, and Jim Rounds for processing specimens; Terry Garrett for managing the data; and Helga Schwarz for work on the manuscript. Financial support from the Southern California Edison Company is gratefully acknowledged.

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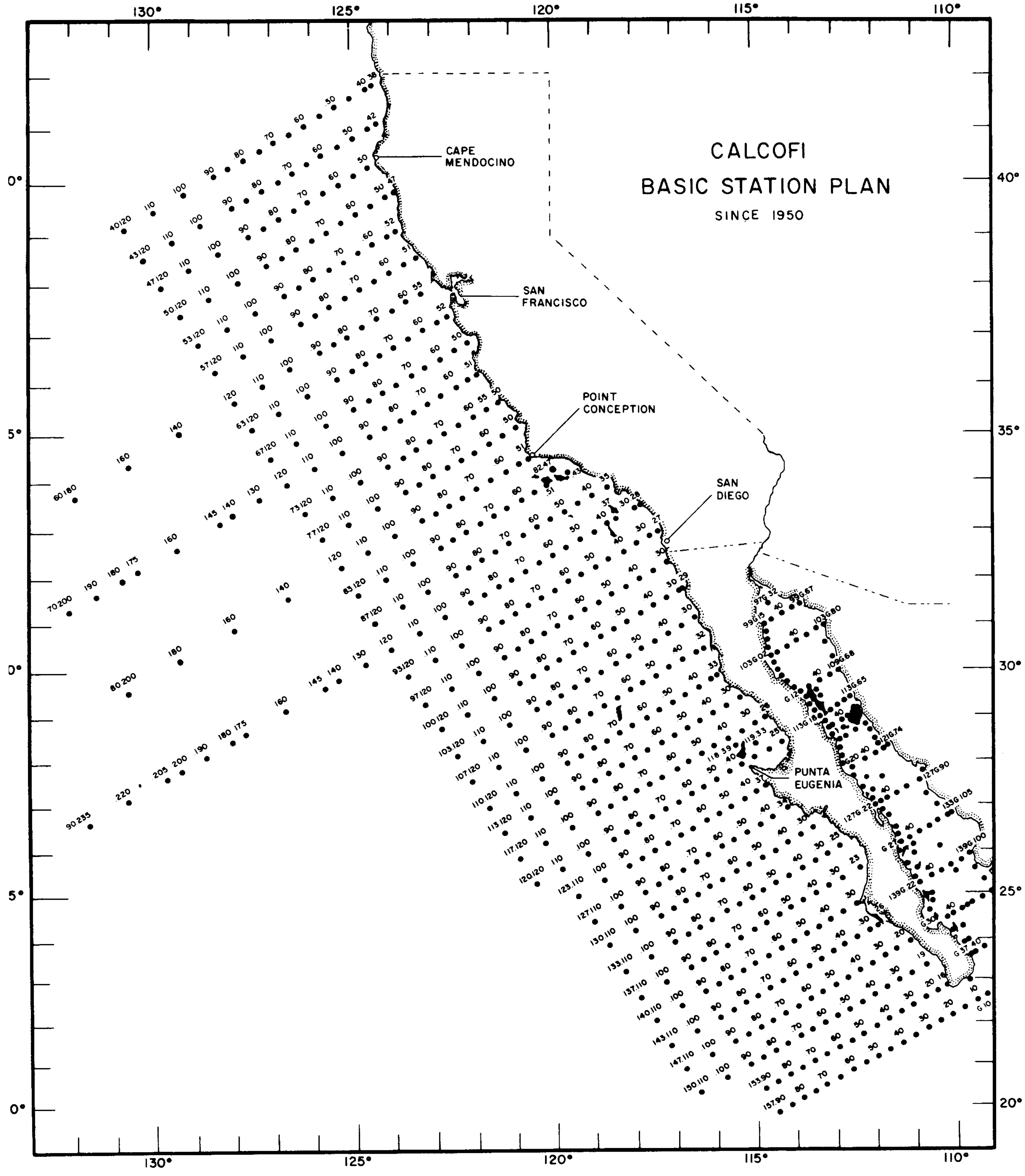

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