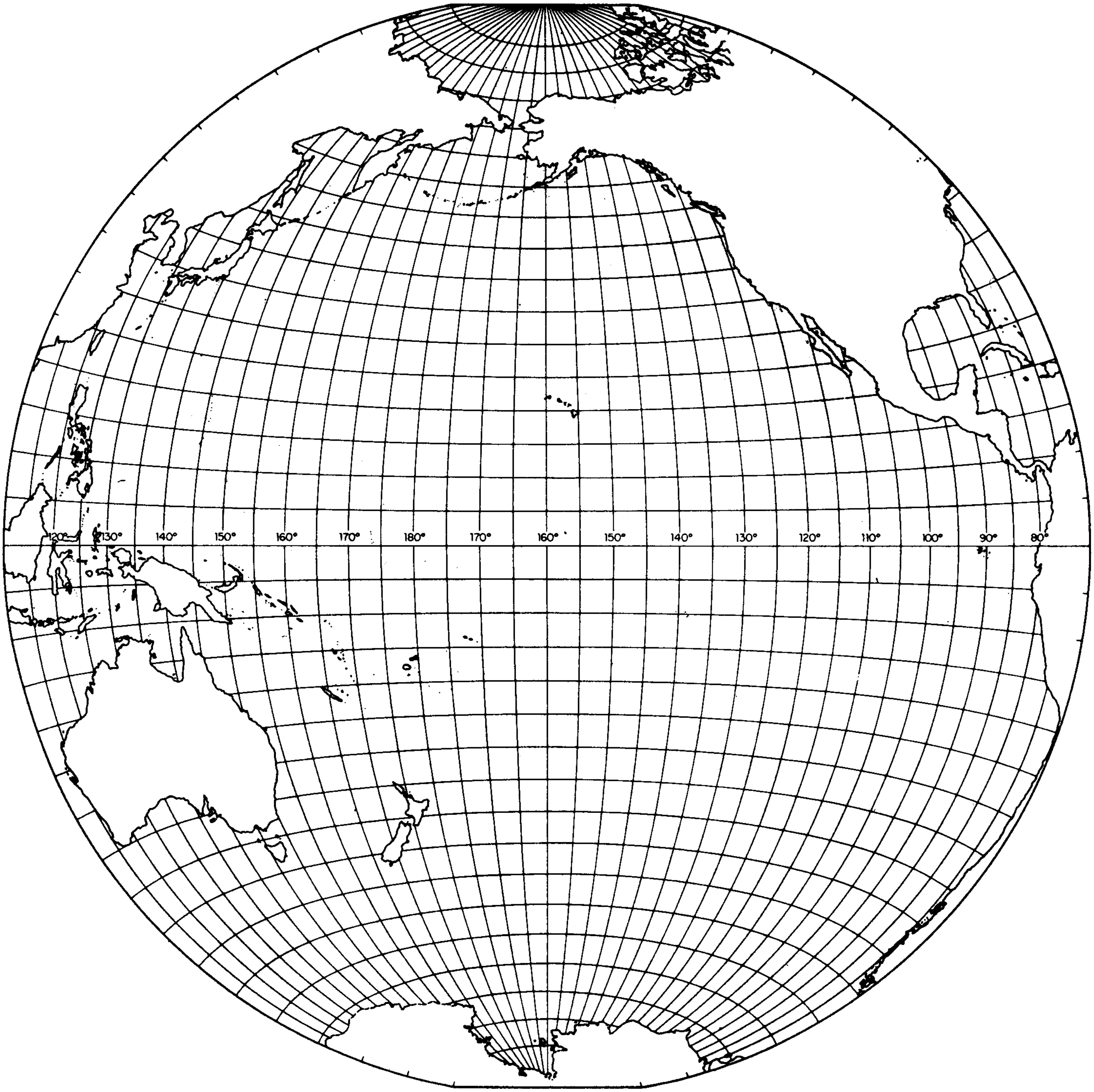

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

VOLUME XXIX
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CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

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

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IN MEMORIAM

Abraham Fleminger
1925–1988

Abraham Fleminger's scientific career was a partnership with his copepods, focused on causes and manifestations of the differentiation of species. Abe was born in New York City 63 years ago. He died on January 13, 1988, after a long and difficult, up-and-down bout with kidney failure. He worked with vigor in his laboratory until the last days. His accomplishments in systematics, zoogeography, and ecology were fundamental—consistently framed in the broad picture of phylogeny and evolution. He was forever generous in sharing insights when he and his colleagues grappled with differing views of the shapes and ways of crustaceans in the vast ocean.

Abe Fleminger came to the Marine Life Research Program at Scripps in 1960 after a period of zooplankton research with the National Marine Fisheries Service in Galveston, Texas. He had earned graduate degrees at Harvard, stimulated and challenged—but not molded—by the provocative evolutionary biologists E. O. Wilson and Ernst Mayr. Speciation processes in the calanoid copepods had captured his attention, never to let go.

The first Fleminger papers were a series of species descriptions tackling gaps and confusion in knowledge of calanoid families including Euchaetidae, Stephidae, and especially Pontellidae in the Gulf of Mexico. Biogeographical evidence was a regular part of his means of arriving at taxonomic conclusions. Abe was impatient, even then, with ecologists who were less than exacting when distinguishing and labeling reproductively distinct populations.

As details of distributions were worked out, Abe became fascinated by the role of population interactions in enhancing morphological differentiation. He was the first to recognize that character displacement in reproductive structures of closely related zooplankton species is a key mechanism in differentiation, appearing when there has been geographical reassociation of young species pairs.

A series of works on species and species groups within the pontellid genus *Labidocera* around the rims of the world's oceans became Abe's most compelling and satisfying endeavor. As this study evolved together with his understanding of variation among coastal environments, he became increasingly successful in predicting places where specific differentiation remained to be discovered. This led to the finding of a "species swarm" in the Caribbean, and of ordered groups in the Indian Ocean and in home waters along the west coast of North America. A study of speciation in the Indo-Australian archipelagos concluded that long-term, local sea-temperature anomalies may well have established Wallace's Line.

Abe pioneered the study of minute integumental organs, called supernumerary pores, in copepods, recognizing the relationship of their sensory function to species-specific arrangements in *Eucalanus*. He used these organs to distinguish a recently evolved species of *Calanus* in the Black Sea and its relationship to Mediterranean species. His discovery of environmentally induced sex reversal in certain calanoid species has prompted a rethinking of aspects of their population biology.

Abe Fleminger's voyages carried him from the California coast to the Caribbean, to the Eastern Pacific Ocean and the archipelagos of the Indo-Pacific regions. He also served as an adviser on marine studies for several nations through UNESCO and other international agencies and universities. He was curator of the Scripps Institution's zooplankton collections—the most extensive and diverse in the world, in part because they include the CalCOFI samples. He also served as editor of the CalCOFI atlas series.

Abe's gift of enthusiasm for the curiosity of students and colleagues and for worthwhile questions helped develop ideas and careers. He was not nominally a teacher, but young and old students of copepods gravitated to his laboratory from many lands. Discussions there sometimes called to mind the Tower of Babel, with Chinese, Japanese, Spanish, and German accents in spirited competition. By the end, though, information and ideas had been exchanged and knowledge generated.

A colleague has observed that now that Abe is gone the available information on copepods is vastly reduced, but we will have to muddle through as best we can. We are in debt for his humanity and for his scientific life.

Edward Brinton

Reuben Lasker
1930–1988

Reuben Lasker has left us, and it will not be easy to fill the gap in our lives or in our science. Born 58 years ago in New York, and proud of it, he came a long way in a tragically short life. The drive and single-mindedness he brought to his research in no way diminished him as a warm colleague and friend. He spoke ill of nobody, and where others might have seen the work of colleagues as competition, he delighted in their success and took every opportunity to assist their careers and research.

From postgraduate studies at Stanford, Reuben Lasker followed a consistent search for generalization in the energy balance of small organisms. Starting with studies of the nitrogen balance of insects (*Lepisma*) whose diet is dominated by cellulose, he transferred his interest rapidly to the metabolism of marine invertebrates after his recruitment to the Bureau of Commercial Fisheries laboratories on Point Loma in 1958. His studies of the energy budgets of clupeids in relation to their potential planktonic food supply have deservedly become classics, and they soon led him on to what was to occupy him until his death: the physiological and ecological factors determining year-class strength in pelagic fish. Reuben Lasker most unusually combined the skills of an experimental physiologist with those of a biological oceanographer, and it was this combination that led him in 1975 to formulate the first comprehensive hypothesis for what might determine year-class strength.

He was the first to point out what should have been obvious long before: that larval fish food is not uniformly distributed in the sea and is only likely to be in abundance higher than some critical threshold if it is aggregated in layers in a stratified water column. He was also among the first—together with his colleague of many years, John Hunter—to realize that there was another side to the same coin. There are situations when predation on larvae is likely to be more critical than lack of food, and his studies with Kurt Lillelund broke new ground in this field.

Undoubtedly, "Lasker events," quiet periods when the coastal sea stratifies and the food organisms of larval fish are concentrated in layers sufficiently abundant to support the growth of larval anchovies, will gain wide currency in the literature of the coming decades, just as Hjort's "critical period" dominated the literature for the previous half century. Reuben Lasker was always the first to point out that the general problem of recruitment had not, in fact, been solved by his model and indeed might not be susceptible to a general solution. Nevertheless, his concept is now the basis of several models that successfully predict recruitment in various clupeid stocks. A paper sent to him for comment by ORSTOM friends in Senegal in the last weeks of his life built on his concept to propose a "recruitment window" for sardines at times when coastal wind stress produced a critical balance between upwelling and stability. Apparently such a model can predict recruitment in several stocks off Morocco, Mauretania, and the Ivory Coast.

The small team of experimental biologists (Hunter, Theilacker, Leong, Metoyer, and others) who grouped themselves around Reuben Lasker from the late sixties onwards became a powerhouse of research on the behavior, physiology, and ecology of larval fish, and rapidly became appreciated worldwide, attracting a stream of visiting workers to La Jolla. Reuben Lasker had, of course, close involvement not only with his home laboratory—which became the Southwest Fisheries Center of the National Marine Fisheries Service—but also with the Scripps Institution of Oceanography, where he held an adjunct professorship, and where he taught, supported graduate students, and participated in faculty committee work. He was an enthusiast for the potential offered to both laboratories by their close association. He played a crucial part in fostering creative collaboration between Scripps and the federal laboratory on the hill just above it; we can be confident that the spirit he engendered will survive his passing.

Reuben Lasker had a gusto for life and wide enthusiasms that were endearing. Though never a country boy, and always more at home in the city, he delighted in his travels wherever they took him, and always wanted to see how people really lived, whether in rural England or in the Far East. But he was always glad to return to his family and the home that he loved so much on his hillside overlooking San Diego and the ocean; he often said how lucky he was to have that to come back to. In recent years, his work in planning international research on larval fish made him known to scientists from many countries; all spoke of him with affection and respect, and he will be widely missed both as a man and a scientist.

Along the way, his qualities were recognized not only informally by all he met, but also formally by the awards and grants he received; his distinguished service to his laboratory earned him silver and gold medals from the departments of the Interior and Commerce, respectively. From Canada came the Huntsman Medal for excellence in biological oceanography, and from Scripps the Lalor Faculty Fellowship. His research, and that of his many students and associates, was supported not only by his home laboratory, but also by many other federal and state agencies.

Reuben Lasker's last task, a few days before his death, was typical of the man. Weak and suffering severe lung disfunction, he introduced a thesis defense at Scripps, speaking wittily and to the point, but with the greatest difficulty. We have lost a dear friend and an exceptional colleague, and we are the poorer for his going.

Alan Longhurst

Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

Participants in the CalCOFI program continue to study the fishery resources of the California Current. In 1987 the egg production method was again applied to examine the resurgence of the sardine. Sardine surveys extended from Point Conception to the Mexican border and out to about 75 miles. The spawning biomass estimate was approximately double the 1986 estimate, and the California Department of Fish and Game (CDFG) again permitted a 1000-ton sardine quota. The season opened on January 1, 1988; the quota was caught within two weeks; and the Fisherman's Cooperative canned sardines for the first time since the 1966–67 season.

Fishery-oriented cruises this year included a 42-day groundfish trawl survey; three 10-day sardine surveys that combined the use of two ships (one for egg collections and one for adult collections); two night-lighting recruitment cruises to assess juvenile Pacific mackerel; and four 15-day surveys of the California Current. For future surveys of the California Current, the CalCOFI Committee is considering taking continuous, underway measurements to increase spatial coverage, identify mesoscale processes, and generate ground-truth measurements for satellites. Initial measurements will be near-surface, but an ultimate goal is to obtain data for at least the entire mixed layer. It is likely that electronic sensing will replace physical sampling.

Data from this year's surveys extend the CalCOFI time series to 38 years. CalCOFI's extensive data base is on line and user-friendly, and a manual describing the menu-driven system was published this year. In addition, all ichthyoplankton data have been reviewed and edited over the last four years, culminating in the publication of 23 data reports covering 1951 to 1981. The utility of the data and value of this time series in attaining CalCOFI's main objective—understanding the variations of fish populations and their biotic and physical environment in the California Current—are discussed in the symposium papers published in this issue.

Cooperative research is paramount in meeting CalCOFI objectives. During the year the U.S. and Mexican governments signed a formal agreement for cooperative fisheries research on the west coast, establishing the Mexus-Pacifico committee to implement the agreement. Mexus-Pacifico contains two binational subcommittees: one to gather and exchange data and one to assess stock. Both subcommittees were productive during the year. Mexican and U.S. scientists also participated in several workshops this year—two on the egg production method for determining spawning biomass, one on age determination, and one on sampling. Scheduled for next year is a Mexican sardine cruise from Cabo San Lucas to Ensenada, a continuing routine interchange of fisheries and biological data, and a workshop on stock synthesis. Finally, Mexus-Pacifico agreed to present a symposium dealing with the sardine "recovery" at the 1990 CalCOFI Conference.

CalCOFI continued to support the U.S. and Spanish Sardine-Anchovy Recruitment Program (SARP). Spanish scientists were trained by NMFS and CDFG personnel in physical oceanographic techniques, population dynamics, the egg production method (EPM) used for biomass assessment, and recruitment-directed assessment techniques (e.g., histopathology and serological assays that define predator-prey relations). A cruise was completed to estimate the sardine spawning biomass off the Atlantic coast of Spain and Portugal. In the next year scientists will compare the sardine birthdate distribution to the spawning season and cube of the wind-speed time series.

To increase the visibility of *CalCOFI Reports* in the marine science community, our publication will be abstracted for *Aquatic Sciences and Fisheries Abstracts (ASFA) and Oceanic Abstracts* retroactively to 1986, and beginning with this issue, *CalCOFI Reports* will be indexed in *Current Contents/Agriculture, Biology & Environmental Sciences*, and covered in the *Science Citation Index, Automatic Subject Citation Alert*, and an online data base SCISEARCH. In addition, *CalCOFI Reports* now carries an International Standard Serial Number (ISSN) from the Library of Congress.

We sadly report the deaths of two dominant figures in fishery and marine science, and champions of CalCOFI—Abe Fleminger and Reuben Lasker. A scholarship fund, The Reuben Lasker Memorial Fund, has been established for graduate students to attend the annual CalCOFI Conference.

Many thanks to the officers and crews who assist us in our work on the University of California RV *New Horizon*, the National Oceanic and Atmospheric Administration RV *David Starr Jordan*, RV *Yellowfin*, FV *Lakeside*, RV *Shana Rae*, and the FV *Vitina-A*.

The Committee also thanks all of those who have worked so hard on this 29th volume: *CalCOFI Reports* editor Julie Olfe for her continuing proficient work; Spanish editor Patricia Matrai; Coordinator Gail Theilacker; and the following reviewers who spent time and effort making this an excellent report: Mario Aguayo, Angeles Alvariño, Kevin Bailey, Ed Brinton, John Butler, Bob Francis, Michael Fogarty, John Graves, Loren Haury, Roger Hewitt, Ed Houde, Bill Lenarz, Nancy Lo, Ron Lynn, Alec MacCall, Roy Mendelssohn, Richard Methot, Beatriz Morales Nin, Richard Parrish, William Pearcy, James Simpson, Paul Smith, Gary Stauffer, Gary Winans, and Patricia Wolf.

Finally the Committee thanks past CalCOFI Coordinator George Hemingway for his support, and current Coordinator Gail Theilacker, who has moved so quickly and positively into her new position.

The CalCOFI Committee:
Izadore Barrett
Richard Klingbeil
Michael Mullin

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1987

California Department of Fish and Game
Marine Resources Division
330 Golden Shore, Suite 50
Long Beach, California 90802

Total landings of fishes, crustaceans, and mollusks increased (4%) for the second year in a row, following a decline from 1981 to 1985.

Pelagic wetfish landings continued to increase (Table 1). Market squid landings were relatively high for the second year in a row; landings of Pacific and jack mackerel increased slightly; and sardines continued their recovery.

Landings of ridgeback and spot prawns both declined, although catch per unit of effort in the spot prawn fishery has improved since 1984.

A slight decrease was noted in groundfish landings, and although the halibut catch decreased for the third year, the annual total was still above the 10-year average.

Albacore landings were very poor for the second year in a row, and in fact hit a 50-year low.

Lobster landings were the third highest of the last 20 years. The sport catch was similar to the catch of the last 3 years.

PACIFIC SARDINE

The Department of Fish and Game, in a cooperative effort with the National Marine Fisheries Service, conducted sea surveys in August 1986 to determine the spawning biomass of Pacific sardines (*Sardinops sagax*). These surveys consisted of (1) evaluating the spawning biomass relative to 20,000 tons, based on the spawning area (egg production area method), and (2) estimating sardine reproductive parameters for use in an egg production method (EPM) to estimate spawning biomass. This was the first attempt at an EPM biomass estimate for sardines; methods used were adapted from a model developed for northern anchovy. Results of the egg production area survey indicated that the spawning biomass of sardines remained above 20,000 short tons in 1986, based on an observed spawning area of 970 nautical miles^2 (n.mi.^{2}). This provided for the opening of a commercial fishery of 1,000 tons on January 1, 1987. This was only the second year of directed fishing allowed since the moratorium on fishing sardines was enacted in 1974.

The first EPM application for sardines was completed in March 1987. Estimated reproductive pa-

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

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
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	1,283	2,105	45,503	12,188	8,405	23,454	92,938
1987*	2,309	1,595	45,890	13,055	9,258	21,578	93,685

*Preliminary

rameters, which included daily egg production rate, average female weight, batch fecundity, spawning fraction, and sex ratio, differed markedly from north to south. The resulting biomass estimate within the survey area was 8,400 tons. The new parameter estimates, when used in the egg production area technique, suggested that the spawning biomass might still have been lower than 20,000 tons. In addition, it appears that the area of egg occurrence indicative of a 20,000-ton spawning biomass is much larger than previously estimated.

The directed catch of sardines was used primarily as dead bait for the central California striped bass sport fishery. All landings were made to southern California commercial markets. Total landings of sardines averaged 325 tons per month through April 1987. The directed fishery was closed on April 17, when the 1,000-ton quota was reached. In contrast, the fishery extended until July 11 in 1986. Incidental landings of sardines in the mackerel fishery accounted for 68% of the 1,000-ton directed quota in 1987. The incidental tolerance limit for sardines mixed with other species was increased from 15% to 25% by weight following the closure of the directed fishery. State law provides for a 10% increase in the tolerance limit if the overall incidental catch of sardines in a fishery for any month averages one-third of the current tolerance limit. Sardines constituted 5% of total landings of mackerel in March 1987, providing for the increased tolerance.

Sardines were an important component of the live bait fishery for the first half of 1987, primarily because of the unavailability of schools of northern anchovy. In May, sardines constituted 60%–70% of the bait catch from Dana Point to San Pedro. In an effort to alleviate the effects of poor availability of anchovy, the allowable catch of sardines for live bait purposes was increased from 150 tons to 350 tons in September 1987. The live bait catch for 1987 totaled 250 tons, according to fishermen's voluntary logs, but information from Department observers on partyboats suggested that live bait catches exceeded 850 tons.

A second set of egg production cruises was conducted in July and August 1987. An attempt was made to survey farther offshore than in the previous year for evidence of sardine spawning. The spawning area detected from occurrence of eggs was 1,850 n.mi.^{2}, including a 50% increase in spawning within the region surveyed in 1986. The detected spawning area was only about 75% of the critical area estimated for a 20,000-ton spawning biomass, according to 1986 EPM results. However, because the 1986 survey was the first EPM application for sardines and consisted of small sample numbers from a restricted geographic area, the spawning area estimate was considered conservative, and a commercial fishery of 1,000 tons was opened on January 1, 1988.

Total reported landings of sardines in 1987 are estimated at 2,560 tons and include 425 directed tons in the open fishery, 1,885 tons incidental to mackerel, and 250 tons for live bait. Incidental landings constituted 3% of total mackerel landings for the year. Comparative figures for 1986 include 445 tons of directed take, 840 tons incidental to mackerel (1% of mackerel total), and 20 tons for live bait.

NORTHERN ANCHOVY

Landings of northern anchovy (*Engraulis mordax*) for reduction purposes in 1987 were limited by poor market conditions for fish meal and by poor availability of fish schools. Anchovy were rarely found in any abundance close to shore, and fishermen would not travel far offshore for the $30 per ton being offered for anchovy. Two boatloads totaling 42 tons were landed for reduction purposes in April 1987. These landings were made in the northern permit area against the 1986–87 season quota of 10,000 short tons for the northern region. The fish were used in an experimental production of trout pellet food for hatcheries. The product was well received, and the Richmond-based processor was hopeful that large-scale production would begin in the 1987–88 reduction season. No landings were made in the southern permit region during the 1986–87 reduction season, although a new processor issued reduction orders. Southern California purse seiners concentrated instead on more lucrative mackerel and squid. The 1986–87 reduction season closed on June 30 with 42 tons landed.

National Marine Fisheries Service biologists estimated the 1987 spawning biomass of northern anchovy to be at least 1,335,988 tons (1,212,000 MT), based on a stock synthesis model. The U.S. harvest quota for reduction was set at 154,322 tons, with allocations of 10,000 tons for the northern permit region, and 144,322 tons for the southern. The fishery opened on August 1 in the north and on September 15 in the south. Landings totaling 122 tons were made during September and October in the northern permit area, and were delivered to the Salinas reduction facility. The Richmond processor did not issue orders for anchovy for trout food production. No landings were made in the south-

TABLE 2
Anchovy Landings for Reduction Seasons in the Southern and Northern Areas (Short Tons)

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

*Preliminary

ern region through December 1987. The price for fish meal almost doubled during the first half of the 1987–88 season because of poor import markets. However, this increase did not result in a higher price for anchovies.

Total landings of anchovy during 1987 (Table 2) included 164 tons for reduction, 1,431 tons for nonreduction purposes, and 4,920 tons for live bait. The live bait fishery was heavily impacted for the first half of the year by the offshore schooling patterns of anchovy. Most bait haulers could not effectively fish anchovy with their shallow-water lampara nets.

JACK MACKEREL

Approximately 13,055 tons of jack mackerel (*Trachurus symmetricus*) were landed during 1987. This is the third consecutive year that jack mackerel constituted 21% of total mackerel landings. Since 1979, jack mackerel have contributed less than Pacific mackerel to the California mackerel fishery. Over the last four years, the jack mackerel proportion of total annual mackerel landings has been the lowest since the fishery began in the late 1940s.

Jack mackerel dominated statewide landings in only one month during 1987, and then only by a small margin. This is probably due to unrestricted Pacific mackerel landings. In northern California, jack mackerel never dominated the mackerel landings, but did occur in fairly equal proportions to Pacific mackerel about half the time. The rest of the year they contributed only a very small proportion to the mackerel fishery. The monthly composition of jack mackerel in the total 1987 mackerel catch ranged from 1% to 50% of the landings, and 97% of all 1987 jack mackerel landings occurred in southern California. Calculated throughout the year, jack mackerel made up 29% of the total mackerel landings in northern California, and 21% in southern California.

Sea surveys conducted during 1987 suggest that the jack mackerel 1987 year class may be weak. The 1986 year class appears fairly strong.

PACIFIC MACKEREL

The year began with 26,973 tons of Pacific mackerel (*Scomber japonicus*) already landed through the first half of the 1986–87 season. Current law allows an open fishery when the biomass exceeds 150,000 tons. Since the biomass was estimated at the beginning of the season to range between 375,000 and one million tons, no quota restrictions were established.

A substantial change in the mackerel fishing industry occurred when Starkist, the major southern California processor, closed its canning facility on Terminal Island in April. The plant was sold to the San Pedro-based Fisherman's Cooperative Association, a group of about 30 boat owners, which reopened the facility in early June under the name United Food Processors (UFP). Landings at UFP have been high and relatively steady, and management is making improvements to take advantage of a promising international market for mackerel. Starkist moved to a secondary plant, where mackerel landings have been low. Processors continued to impose landing limits (40–50 tons per boat per day, on average) most of the year. The ex-vessel price for mackerel was steady at $155 per ton.

During the first three months of 1987, Pacific mackerel landings were high, because fish were available on traditional fishing grounds and Starkist accumulated a large inventory before moving. Landings dropped during the second quarter of the year, primarily as a result of the changes in plant ownership and lulls in operation. The 1986–87 season closed on June 30, 1987, with a total catch of 48,830 tons. This is the highest seasonal total since the fishery reopened in 1977. Pacific mackerel contributed 84% to statewide landings of mackerel, and 96% of all Pacific mackerel landings were made in southern California.

The 1987–88 season opened on July 1, 1987, with no quota restrictions, based on a biomass estimated to be about 290,000 tons. This estimate is considerably lower than the range of estimates calculated the previous year, and is the result of a stricter set of assumptions regarding the use of cohort analysis.

Landings during July, August, and September were the highest since 1981, as processing reached full levels and landing limits were often lifted. Fish were available at southern California islands, along the coast, and at the offshore banks. Landings during October, November, and December were limited by rough weather, by poor availability of fish, and because fishermen directed their efforts towards bonito, squid, and herring. By the end of the year, 24,032 tons of Pacific mackerel had been landed toward the 1987–88 season total. Landings of Pacific mackerel for the year totaled 45,890 tons. This is the second highest annual catch since 1977 and exceeds the average annual landings for the previous five years. Northern California landings contributed only 2% to the year's total. The proportion of the Pacific mackerel catch occurring in Monterey has declined steadily since 1984, when it was 18%.

The 1985 and 1986 year classes, both strong, together accounted for 71% of the fish landed during the year. The 1987 year class also appears to be strong, since it occurred in both the third and fourth quarters of 1987 as yearlings. The consistently high annual catches of Pacific mackerel during the last decade have been the result of several strong year classes, which have sustained the fishery in spite of weak recruitment in a number of years, particularly the successive years of the 1982–84 El Niño.

MARKET SQUID

The current California squid (*Loligo opalescens*) fishery is best described as two separate fisheries: the northern California (or Monterey) fishery, and the southern California fishery. In Monterey, the fishery normally follows a summer-fall season. The southern fishery typically has a fall-winter season. Most squid is frozen for human consumption or bait, or used as live bait.

There are three main gear types used to fish squid in California. In Monterey, nearly all squid are caught with lampara gear. In southern California, brail, or night-light, boats are used. This is a fairly simple method, using bright lights to attract the squid and then brailing, or dipnetting, them into the vessel. The local purse seine fleet, which typically catches mackerel, sardine, and bonito, or tuna when it is available, also participates in the southern California squid fishery. A purse seine can be used in deeper water than a lampara net, since it has heavy rings at the bottom so the net can be pursed closed. Squid caught in this manner are generally of poorer quality than squid taken by the more gentle night-lighting technique, and therefore often bring a lower price. It is not uncommon for a night-light boat and purse seiner to work together, with the night-light boat attracting the squid to the surface and the seiner wrapping around them.

Biologists in northern California have been concerned with the amount of damage to the spawning grounds caused by the lampara net's lead chain. Sometimes large quantities of squid eggs are torn from the bottom and brought up in the net. When squid are in high supply, one or two sets are adequate, and damage to the spawning grounds is limited. However, when squid are in poor supply a dozen sets may be needed; most of the spawning squid are then caught, and the gear denudes the grounds of eggs. Experimental gear permits were issued this season to two boats in Monterey with a modified purse seine. It is called a half-ring net, and has a regular rope with a lead core to help weight it. A Department observation program has been established to evaluate the effectiveness of this new gear relative to egg-case mortality and habitat destruction.

Over the last 25 years, southern California landings have been less than half of the total squid landings. But in the last 2 years this has changed, and southern California landings have been more than double the northern California squid landings. In 1985, squid landings in southern California resumed a normal pattern and increased greatly over the previous 2 years' poor landings, which were associated with El Niño. Landings approximated 7,000 tons in 1985 and reached nearly 16,500 tons in 1986 in southern California. This was the highest annual landing ever to occur in southern California, and more than double the 10-year average. Southern California squid landings for 1987 are estimated to approximate 15,000 tons, at a price that remained stable throughout the season at $200 per ton.

During the 1985 Monterey fishery, squid were scarce. Although 4,300 tons were landed, a recovery from the poor landings associated with El Niño years, this was 35% below the last 10-year average for Monterey. In 1986, the northern California fishery caught most of their 7,000 tons of squid north of Monterey Bay in the Año Nuevo-Pigeon Point area, instead of Monterey Bay. This was the first time in the history of the fishery that large numbers of squid were caught in this area, although it had been known that squid spawn there. During most of the 1987 season in Monterey, the price remained a relatively low $200 per ton, compared to as high as $400 per ton in the previous two seasons, and the squid were small, of poor quality, and primarily frozen for bait. However, near the end of the season during the first week of September, large, high-quality squid were brought in, and the price rose to $240 per ton. These squid were used for human consumption, and brought the season total to about 6,500 tons. Landings for 1986 and 1987 are considered mediocre.

Historically, market squid have been regarded as an underutilized resource off California. There seem to be no major concerns about the status of the squid resource in southern California, where landings have increased to above their pre-El Niño levels. However, in Monterey, squid fishing has not fully recovered. It is thought that perhaps, after the initial decline from El Niño, the fishery has failed to come back to previous levels of the late 1970s and early 1980s because of the fishing gear's destructive action on egg cases and spawning habitat.

PACIFIC HERRING

The 1986–87 fishing season (December–March) was successful in all areas except Crescent City Harbor, where herring (*Clupea harengus pallasi*) did not spawn as expected. The statewide herring catch for the 1986–87 season totaled 9,036 tons. There was a quota overrun of 446 tons, primarily because of short periods of intense fishing in San Francisco Bay. The 1987 annual catch of 9,258 tons is the highest since 1982 (Table 1).

Ex-vessel value of the 1986–87 herring catch was about $8 million, down from $11 million last season. Japanese herring buyers offered $600 to $800 per ton for 10% roe recovery this season, a 30% decrease in price from the 1985–86 season.

Population estimates from spawn deposition surveys indicate that the San Francisco Bay biomass increased 8,000 tons, to 57,000 tons. Tomales Bay experienced a nearly normal season, with biomass estimated at 5,800 tons. This represents a dramatic recovery from 1985–86, when the biomass estimated from spawn surveys was only 1,200 tons. Similar biomass estimates were made in 1984 and 1985. Repeated fluctuations of this magnitude indicate a change in the distribution of Tomales Bay herring.

Four strong year classes—1982 to 1985—are responsible for the increased abundance of San Francisco Bay herring. The apparent change in the distribution of Tomales Bay herring, however, is cause for concern and could potentially affect the future of that fishery.

Based on biomass estimates in the 1986–87 season, catch quotas were adjusted for the 1987–88 season. The San Francisco Bay quota was increased 1,000 tons, to 8,500 tons; Tomales Bay was reduced 250 tons, to 750 tons. The overall 1987–88 season quota was increased to 9,340 tons.

Initial herring catches in the 1987–88 season were very good in San Francisco Bay, where fishing usually begins in December. However, fishing in Tomales Bay typically does not begin until January. Herring buyers were offering $1,200 per ton for 10% roe recovery at the beginning of the season.

GROUNDFISH

Commercial landings of groundfish by California fishermen totaled 41,363 metric tons (MT), which were valued at $32,944,000 ex-vessel. Trawlers landed 34,042 MT (82%), and other gear vessels landed the remaining 732 MT (18%) of the 1987 total.

Rockfish, a multispecies group; Dover sole (*Microstomus pacificus*); Pacific whiting (*Merluccius pacificus*); and sablefish (*Anoplopoma fimbria*) were again the leading species in landings. Changes in landings of these species from 1986 to 1987 were less than 10%, except for the increase of 52% for Pacific whiting. Overall, 1987 landings declined 1%, or 432 MT, from those of 1986 (Table 3).

State and federal coastwide quotas for widow rockfish (*Sebastes entomelas*) and sablefish were

TABLE 3
California Groundfish Landings (Metric Tons)

Species	1986	1987*	Percent change
Dover sole	10,987	10,758	−2%
English sole	1,074	1,318	23%
Petrale sole	711	818	15%
Rex sole	840	824	−2%
Thornyheads	2,939	2,954	1%
Widow rockfish	2,468	2,245	−9%
Other rockfish	11,505	10,931	−5%
Lingcod	514	813	58%
Sablefish	6,099	4,339	−29%
Pacific whiting	2,982	4,518	52%
California halibut	549	534	−3%
Other groundfish	1,127	1,310	16%
Total	41,795	41,363	−1%

*Preliminary

12,500 MT and 12,000 MT, respectively. Management measures for trip frequency, trip limits, and gear allocation failed to prolong these fisheries throughout the year. The widow rockfish fishery was closed on November 25, 1987; the sablefish fixed-gear fishery was closed on October 22, 1987; and the sablefish trawl fishery was closed on November 4, 1987, when respective gear quotas of 5,800 MT and 6,200 MT were reached.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1986–87 season totalled 8.4 million pounds, an increase of 2.5 million pounds from the 1985–86 seasonal landings.

In the north coast region, the ports of Crescent City, Trinidad, Eureka, and Fort Bragg received 4.16, 0.79, 1.64, and 0.20 million pounds, respectively. Fishing began on December 1, after a price agreement of $1.25 per pound. The bulk of production (87%) occurred in December, and the price peaked at $1.75 per pound in January as supply greatly diminished. The season closed off the north coast on July 15.

Commercial fishermen in the San Francisco region caught 1.6 million pounds of Dungeness crab during the 1986–87 season. This is more than four times the 0.38 million pounds landed the previous season and is the largest season total in the past 26 years. Landings for Bodega Bay, San Francisco, and Half Moon Bay were 0.48, 0.57, and 0.56 million pounds, respectively. Landings for November 1986, the first month of the season in the San Francisco region, were 0.72 million pounds—45% of the seasonal total. Landing totals decreased monthly, with only 0.03 million pounds being landed in June 1987, the last month of the season for this region.

Fishermen were paid $2.10 per pound from the start of the season in the San Francisco region until the north coast season opened in December at $1.25. As a result, the San Francisco price dropped to $1.35 per pound but soon began climbing. The ex-vessel crab price was $1.80 by early January and $2.00 by February. By the end of the season fishermen were receiving $2.30 per pound.

PACIFIC OCEAN SHRIMP

Statewide landings of Pacific Ocean shrimp (*Pandalus jordani*) in 1987 totaled 7.8 million pounds, which is an increase from the 6.7 million pounds landed in 1986, and is the third highest total ever. Areas of production were Area A (Oregon border to False Cape), Area B-1 (False Cape to Point Arena), and Area C (Pigeon Point to the Mexican border). The ex-vessel price started at $0.65 per pound coastwide on April 1, increased to $0.85 per pound two months later, then decreased to $0.70 per pound in August, where it remained until October 31, the end of the season.

Area A started off with a record month, when 2.8 million pounds were landed in April, the best start of a season ever. However, catches did not hold up, and the total of 5.6 million pounds, the third largest total ever for Area A, was only a 14% increase over the 4.9 million pounds caught in 1986. An additional 0.87 million pounds, which had been caught off Oregon, were landed in Crescent City. A total of 60 vessels (43 single-rigged and 17 double-rigged) delivered shrimp to Area A ports during the season (April 1 through October 31). This represents the greatest number of vessels since 1981.

One-year-old shrimp constituted a high percentage (81%–87%) of the catch throughout the season. The incoming year class (0's) constituted 21.1% of the samples in October. This was surpassed only by October 1986, when 24.8% of the unweighted samples were made up of 0's. With such strong recruitment, 1988 should be a good season.

Area B-1 produced 743,000 pounds this season, up from 9,799 pounds during 1986. The last year that Area B-1 yielded any significant landings was in 1978, when over 2 million pounds were produced. Three local single-rigged boats, along with one single-rigged and five double-rigged vessels from Crescent City, fished Area B-1 this year.

A total of 664,828 pounds of Pacific Ocean shrimp was landed during the 1987 season in Morro Bay and Port San Luis (Area C), a decrease from 1986, when over 800,000 pounds were landed. Thirteen vessels landed more than 419,000 pounds in April, but fishermen began to drop out in favor of other fisheries or areas in May, and landings dropped to less than one-quarter of April's. The decline continued as boats left the fishery because of decreased catches and an increase in net fouling by salps. Landings were virtually nonexistent in this area from late July to the end of the season in October.

Catch per unit of effort (CPUE) in Area C was only slightly lower this year for single-rigged vessels compared to last year (291 lb/hr versus 306 lb/hr), but double-rigged vessel CPUE declined substantially from 548 lb/hr in 1986 to 316 lb/hr in 1987. For the second year the Morro Bay-

Avila fleet contained more single-rigged (9) than double-rigged (3) vessels. One additional vessel tried both types of rigging.

In the April market samples, 69% of the shrimp were two years old, and that year class continued to dominate the samples through May (56%), June (69%), and July (69%). In contrast, the one-year-old shrimp peaked in percent composition in May (35%) and declined through July (23%). This relative lack of one-year-olds in the fishery may indicate a poor year for 1988.

PELAGIC SHARK AND SWORDFISH

During 1987, 228 permits were issued for harpooning swordfish (*Xiphias gladius*), and 241 drift gill net permits were issued for taking pelagic sharks and swordfish.

Harpoon fishermen reported landing 1,681 swordfish, a significant decline from their 1986 landings of 2,581 fish.

Drift gill netters reported only 10,858 swordfish taken during 1987. This was less than half the number reported for each of the previous two seasons. Although the average size of fish landed during 1987 was quite good (about 160 pounds) only 2.68 million pounds were landed overall. This represents a significant decline from the previous two seasons, when 5.25 million pounds were taken in 1985, and 3.62 million in 1986. No clear reason for this decline in landings by both gears is evident. It should be noted, however, that historically the harpoon-only fishery was subject to similar fluctuations.

Common thresher shark (*Alopias vulpinus*) landings off California remained low during 1987, with only 0.43 million pounds being reported by fish wholesalers.

A quota of 0.82 million pounds was established for the Oregon-Washington experimental shark fishery for 1987. Only 0.24 million pounds of this quota were actually landed.

The bonito shark (*Isurus oxyrinchus*) has surpassed the common thresher shark as the second most important shark species to California fishermen, with the Pacific angel shark (*Squatina californica*) registering the highest landings. During 1987, 0.6 million pounds of bonito shark were landed by drift gill net vessels and by a growing hook-and-line fishery.

Markets are just beginning to open for the blue shark (*Prionace glauca*). In future years, the importance of this species to the commercial industry is likely to overshadow all other shark species off the California coast, if the industry can solve the marketing problems associated with the poor quality of blue shark flesh as it is currently handled.

CALIFORNIA HALIBUT

California halibut (*Paralichthys californicus*) landings for 1987 were 537 MT, which is 3% less than the 552 MT taken in 1986. The 10-year average from 1977 to 1986 was 423.3 MT (Table 4). Following a low catch of 122 MT in 1973, catches have steadily increased, averaging 534 MT for the last five years. In 1987, 64% of the halibut landings occurred south of Point Conception, compared to 49% in 1983 during the El Niño period. Traditionally, spring and summer months have produced the highest halibut catches; this was again the case in 1987, with the high occurring in March (78 MT) and the low in September (20 MT).

Entangling nets (trammel and set gill nets) accounted for 63% of all halibut taken. Average ex-vessel prices for California halibut ranged from $1.44 to $3.51 per pound.

Beginning in September, two new regulations were implemented. Senate Bill 40 (effective September 28, 1987) set restrictions on areas and seasons where gill and trammel nets may be used off central and northern California. Assembly Bill 1094 (effective September 29, 1987) prohibits the use of gill and trammel nets within a specified distance of shore around several points between San Diego and Santa Barbara.

CALIFORNIA SPINY LOBSTER

California spiny lobster (*Panulirus interruptus*) landings during the 1986–87 season (first Wednesday in October through the first Wednesday after March 15) were about 494,000 pounds, a 17% increase from the 1985–86 season. This is the third highest level of landings in the last 20 years, behind 1978–79 (566,800) and 1983–84 (520,850).

TABLE 4

California Halibut Landings (Metric Tons)

Year	North of Pt. Conception	South of Pt. Conception	Total
1977	25	186	211
1978	34	165	199
1979	54	205	259
1980	90	231	321
1981	163	409	572
1982	206	339	545
1983	256	248	504
1984	153	345	498
1985	144	429	573
1986	240	312	552
1987*	191	346	537

*Preliminary values as of March 21, 1988

The lobster permit fee was increased from $100 to $200, and there was a 6% increase in permits issued. The 376 permittees made an estimated minimum 500,000 trap hauls, an 11% increase over the 1985–86 season.

Catch per unit effort of legal-sized lobsters was estimated at 0.99 pounds per trap haul. Sublegal-sized lobsters, retained by the traps and released at the surface, continued to be captured at a rate of 0.9 animals per trap haul.

Forty-four percent of the catch was made in October, 19.5% in November, 17.4% in December, and 19.1% in January, February, and March combined.

The San Diego region accounted for about 40% of the catch; the Los Angeles and Santa Barbara regions trailed with about 35% and 25%, respectively.

Ex-vessel price averaged $4.55 per pound, only a 1.5% increase above 1985–86 prices. The estimated 494,000 pounds landed give the fishery a value of $2.27 million to the fishermen.

ALBACORE

In 1987, albacore (*Thunnus alalunga*) landings in California hit a 50-year low. Only 1,545 tons of albacore were brought in, approximately 15% of the previous 25-year average. Effort was low, and although 331 vessels participated in the fishery, only 180 boats landed more than a ton of fish during the season.

The season began late in July with a few landings from the Midway Islands and occasional catches from central and northern California. In August the best catches were 900 to 1,600 miles off northern California, although fishing improved during the month around central California seamounts. A commercial fishery in southern California failed to materialize, in spite of some good sportfishing outside the San Juan Seamount. By September, most offshore vessels were working off Oregon and Washington, and fishing in California occurred primarily between Morro Bay and San Francisco. Activity toward the end of the month was hampered by poor weather. October effort was primarily by drift gill net vessels off Morro Bay; they landed up to a ton per trip of very large fish.

Demand for albacore was higher this year than in 1986, when a worldwide market glut caused cannery prices to drop to $1,100 per ton for fish over nine pounds. Price agreements in 1987 between the Western Fishboat Owners Association and Pan Pacific, the only albacore cannery on the coast, began at $1,400 per ton for fish over nine pounds, and $950 for those nine pounds and under; by the end of the season, prices had increased to $1,450 and $975, respectively. No trucking fee was charged for fish unloaded at northern ports, but Pan Pacific (located in southern California) began offering $1,500 per ton for quality fish delivered to the cannery. Other buyers in northern ports offered this price or higher for high-quality albacore. Because of high prices from buyers, few fishermen sold directly off their vessels to the public this year.

Low landings in California are attributable to a general lack of effort, as well as poor fish availability. Very few vessels attempted to fish in southern California waters, with most traveling north to more productive waters off Oregon and Washington. A large body of cold water in the mid Pacific, which showed surface temperatures up to 7° colder than normal, may have contributed to poor fish availability in southern California. Because of high prices and no trucking fees, vessels unloaded in northern ports rather than bringing fish directly to the Pan Pacific cannery. Many vessels were lured away by another excellent salmon season, both in terms of price and availability. A number of larger vessels traveled to fish albacore in the South Pacific this winter.

RIDGEBACK PRAWN AND SPOT PRAWN

Ridgeback prawn (*Sicyonia ingentis*) landings for 1987 totaled 233,000 pounds, which was a 66% decline from the 1986 total of 672,000 pounds (Table 5). The majority (77%) of landings occurred in the Santa Barbara-Ventura area, the rest at San Pedro.

Trawl gear is the primary method of capture, and CPUE is measured in pounds per hour. During 1987, there were 15 trawlers engaged in the fishery, and CPUE declined to 82 pounds per hour from a high of 240 pounds per hour in 1985. This dramatic drop probably resulted from several factors: poor recruitment of succeeding year classes of prawns; an increase in predators such as hake, sole, and

TABLE 5
Ridgeback Prawn and Spot Prawn Landings (1,000s of Pounds)

Year	Ridgeback prawn	Spot prawn
1979	356	48
1980	276	69
1981	193	369
1982	141	300
1983	157	109
1984	623	49
1985	905	64
1986	672	102
1987	233	88

rockfish; and an increase in fishing mortality. Declining catches in the Santa Barbara Channel precipitated interest in other areas, such as Santa Monica Bay. Additional management measures are being considered to stabilize and improve the fishery.

During 1987, 88,000 pounds of spot prawns (*Pandalus platyceros*) were landed, as compared to 102,000 pounds in 1986. During the last nine years, this fishery was characterized by record landings in 1981 and a dramatic decline in following years (Table 5). CPUE also declined from 52 pounds per hour in 1980 to 20 pounds per hour in 1984. These dramatic declines in landings, coupled with decreasing CPUE and the results of biological studies, initiated Departmental recommendations for new regulations. A seasonal closure for the trawl fishery was adopted and implemented in 1984. Gradually, the landings began to increase as a result of successful recruitment of new year classes of prawns and increased effort to develop a trap fishery and new fishery grounds accessible to trap gear.

By 1986, trap gear accounted for 58% of spot prawns taken in southern California; the other 42% was taken by trawl gear. CPUE for trawl gear increased dramatically, rising from 20 pounds per hour in 1984 to 82 pounds per hour in 1987. It appears that the spot prawn resource has recovered from the effects of overfishing and of El Niño, thanks to spawning success, management measures, and improved environmental conditions.

RECREATIONAL FISHERY

Carrying passengers to fish for a fee in California probably began around the turn of the century. The earliest boats carried few passengers, were very expensive, and were available only to the affluent. As time went on, the vessels became larger, more affordable, and available to the general public. Through the 1920s and 1930s the fleet grew to around 200 boats. World War II brought a virtual halt to commercial passenger fishing vessel (CPFV or partyboat) operations. After the war there was a rapid expansion and modernization of the fleet, introducing more powerful engines and better accommodations. Vessels registered as partyboats peaked in the 1951–53 period at over 1,000 boats. Today there are 450 vessels registered. Boats range in size from 20 feet to luxurious vessels of over 100 feet. The smaller vessels carry six or fewer passengers, require no formal U.S. Coast Guard inspection, and have less rigorous regulations.

CPFVs are located throughout California. San Diego is generally considered the saltwater sportfishing capital of the western United States, with five major landings: three at Point Loma and two in Mission Bay. Between San Diego and Crescent City, there are no fewer than 35 locations where partyboats operate.

In 1935 the California legislature passed a law requiring partyboats to report their fishing activities to the Department of Fish and Game on logbooks. The California Administrative Code spells out specific items to be reported, such as number of hours fished and number of fishermen. This has provided a fairly good long-term record of the fishery.

The CPFV fishery underwent a period of rapid growth from the post-World War II period to the late 1970s, when the statewide catch peaked at over 6 million fish in 1979. In 1987 the statewide total catch was just over 4.1 million fish (Table 6). This is about the same catch level as for the past three years. The overall decline from 6 to 4 million fish is mainly attributable to a decline in rockfish.

Rockfish catches have declined more than 50% since the mid 1970s. The 1974 catch of rockfish alone was just over 4 million fish. In 1987 the rockfish catch totaled only 1.7 million fish (Table 6), and was still a major contributor to the total statewide catch.

The kelp/sand bass complex, which has historically been a major contributor to the CPFV catches, peaked at over a million fish in the 1960s. In more recent years, the catches have ranged between 400,000 and 700,000 fish. In 1987, 734,000 kelp bass (*Paralabrax clathratus*) and sand bass (*Paralabrax nebulifer*) were taken by partyboats. It was an exceptional year for sand bass (409,000 fish) and an increase of 54% over 1986. The kelp bass catch declined 23% (to 325,000 fish), reversing the historical relationship in numbers.

TABLE 6
1987 Commercial Passenger Fishing Vessel Catch

Species/ species group	Number of fish (thousands)	Rank
Rockfish	1,700	1
Kelp/sand bass	734	2
Bonito	518	3
Pacific mackerel	517	4
Barracuda	158	5
Salmon	125	6
Yellowtail	59	8
Albacore	7	18
Others	258	
Total	4,103	

Salmon (*Oncorhyncus* species) is the most highly prized and intensely regulated species group. It came under the jurisdiction of the Pacific Fishery Management Council by the Magnuson Act of 1976. Regulations are very strict and well enforced. The two high years of CPFV salmon catches were in 1955 (129,000 fish) and 1972 (172,000 fish). Catches in more recent years have ranged between 55,000 and 110,000 fish. In 1987 salmon landings from CPFVs were 125,000 fish; this was only the sixth time in the past 40 years that the 120,000-fish mark was exceeded.

Barracuda (*Sphyraena argentea*) is a latitudinally migratory species, and partyboat catches are subject to wide fluctuations. For the past 15 years catches have remained in the 50,000—90,000-fish range; however, in 1987 158,000 fish were caught.

Yellowtail (*Seriola lalandei*) is another migratory species also subject to great variability in catches, which generally increase during periods of warmer ocean temperatures. In the 1959 warm-water year, a record 457,000 yellowtail were landed. More recently, 178,000 fish were landed in 1983. In 1987 the partyboats caught 59,000 fish.

Albacore (*Thunnus alalunga*) is a highly migratory transoceanic species prized by southern California sportfishermen and noted for its vagaries. During the 1959 warm-water period only 39 fish were logged by CPFVs. In 1987, 7,000 albacore were caught; this is the poorest year since the 1959 disaster.

The six aforementioned species and species groups—rockfish, kelp/sand bass, salmon, barracuda, yellowtail, and albacore—are sought by CPFV sport fishermen and make up large proportions of their catches. In 1987 they constituted 68% of the catch, and with bonito (*Sarda chiliensis*) and Pacific mackerel (*Scomber japonicus*) made up 93% of the total CPFV catch.

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Patricia Wolf, Pacific mackerel
Karen Worcester, albacore
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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

LAKE ARROWHEAD, CALIFORNIA

NOVEMBER 3, 1987

THE CALCOFI SAMPLING PROTOCOL AND TIME SERIES, POINT/COUNTERPOINT

What are the CalCOFI data? What was measured? How often? And where? What exactly was Wib Chapman referring to when he so often said that the California Current was the most intensively sampled piece of ocean in the world? And what do we know of its physics and its inhabitants as a result of this effort?

As the CalCOFI program approached its fortieth birthday, a symposium was convened at the 1987 CalCOFI Conference to discuss these questions. The following three papers were part of the proceedings.

In the first paper I attempt to place the CalCOFI effort in the larger context of the collapse of the sardine fishery. Scientific attention had been directed toward this fishery, once the largest in the world, since 1915. The vagaries of recruitment compounded by society's tendency to overexploit were generally recognized as coconspirators in the demise of the sardine. The CalCOFI program augmented ongoing work and marshalled additional resources to distinguish the relative influences of exploitation and the environment on the production of fish. The primary sampling tools employed at sea were the plankton net and the hydrocast bottle.

The CalCOFI data set is not homogeneous. The sampling protocol was changed several times throughout the history of the program, producing uneven temporal and spatial sample densities. I describe these sampling regimes and attempt to set them in the context of the dramatic emergence of the northern anchovy population and the response of the program's organizers.

In the next paper Joe Reid reviews the contributions of CalCOFI from the viewpoint of a physical oceanographer. Analysis of the CalCOFI data confirmed earlier descriptions of the California Current as offshore southward flow balanced by a countercurrent and upwelling. The CalCOFI surveys, when combined with large-scale surveys of the North Pacific, established broad correlations between circulation, nutrients, and zooplankton. The CalCOFI data also revealed seasonal fluctuations, aperiodic events, and eddies.

Reid notes that CalCOFI's intent was to relate variations in the circulatory pattern to changes in the biota. The first decade, however, was monotonously invariant, offering little opportunity for comparison. The steady decline in the numbers of sardines, which had started in the early 1940s, continued through this period. On the other hand, zooplankton abundance was correlated with the strength of the California Current. This correlation continued through the 1957–58 El Niño (the first major oceanographic event to be observed by the CalCOFI program) as well as through subsequent cold- and warm-water periods.

In the final paper Paul Smith and Geoff Moser review the contributions of CalCOFI from the viewpoint of biological oceanographers. Analysis of ichthyoplankton from surveys bracketing the 1957–58 El Niño revealed biogeographic patterns that moved in concert with major changes in the circulatory patterns. Recruitment to pelagic fish populations was shown to be autocorrelated over several years; trends in population abundance were shown to be autocorrelated over several decades. Contrasted with long-term temporal correlations, changes in population abundance do not appear to be concordant over the geographic range of the population.

Smith and Moser also note that recruitment to the northern anchovy population is much more variable than the anchovy's reproductive output, suggesting that prerecruit predation may control population growth. In this regard the multispecies nature of the CalCOFI data holds great potential.

With computer-aided analytical tools, trophic relationships can now be teased from the CalCOFI data set. The data, previously available only as atlases and research reports, have recently been assembled into a computer data base, and a series of ichthyoplankton data reports have been published. The data base can also be accessed through the CalCOFI On-Line Data System, making it possible for any researcher to explore the extent of the ichthyoplankton and hydrocast data, review the sampling methodology, and extract desired subsets of the data.

Still to be addressed is the future of the CalCOFI sampling program and how the sampling design can be improved to address current research questions. What should be measured, with what techniques, how often, where, and why? Would it be appropriate to develop high-speed plankton sorting and identification techniques (e.g., species-specific DNA probes, antibody assays [ELISA], and image analysis)? Would it be useful to use satellite imagery to describe the dynamics of primary production? Should we sacrifice spatial resolution and species precision for insight into temporal dynamics? And, most promising of all, should we investigate the use of genetic tools to describe population structure and the spatial dynamics of recruitment?

Whether we call it "biodynamics of the sea" or "the ecosystem approach," the essence of biological oceanography is to link the physics of the ocean with biological processes. Unfortunately, there are appallingly few demonstrations of this linkage. Walter Munk tells us that physical oceanographers are just now beginning to measure things on a scale that reflects the ocean's true variability; the implication is that biological oceanographers must do the same in order to make any sense of the world. Some linkages may prove irrelevant to the prediction of population growth. Lasker's elegant demonstrations that successful feeding by larval fish is dependent on a stable mixed layer was offset by the conclusion that survival through the larval stage was not the sole determinant of recruitment. But until we extrapolate from the individual animal and its ambit to the population and its habitat, we will be relegated to simple (and sometimes misleading) correlations between physical and biological variables.

Roger P. Hewitt

HISTORICAL REVIEW OF THE OCEANOGRAPHIC APPROACH TO FISHERY RESEARCH

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ABSTRACT

For the last 70 years either one or both of the major clupeoid stocks off the Californias (the Pacific sardine and the northern anchovy) have been the subjects of almost continual study. This attention was stimulated by the need for information to manage the local harvest of these fishes and by the realization that the successful management of clupeoid stocks was a goal with worldwide implications.

During the 1920s, 1930s, and 1940s the California Department of Fish and Game (CDFG) conducted field studies in cooperation with the Scripps Institution of Oceanography (SIO), the California Academy of Sciences (CAS), and the U.S. Bureau of Commercial Fisheries (USBCF, now known as the National Marine Fisheries Service—NMFS). In the late 1940s, when the future of the sardine fishery became problematic, the industry funded a more intensified program of research. Endowed with an infusion of money and political support, agency scientists laid out an ambitious plan of attack.

Their plan became known as the oceanographic approach to fishery research (today we might call it an ecosystem approach) and was made synonymous with the CalCOFI program. Monthly cruises were conducted to collect plankton and water samples from a grid of stations; laboratory studies were undertaken to describe developmental stages of the young and behavior of the adults; the fishery was sampled to determine adult demography and vital rates; and new instruments and techniques were developed to enhance data collection and analyses. A more detailed understanding of the physical dynamics of the California Current and of the population dynamics of the sardine began to emerge, and the central question of the "sardine problem" came into clearer focus: What was the relative influence of exploitation versus the environment on the productivity of the sardine population?

In spite of this new understanding, the abundance of sardines declined steadily, while that of anchovies increased. The original focus of the CalCOFI program tended to diffuse, and major program reviews were conducted in 1957, 1961, and 1966. As the objectives changed, so did the field-sampling protocols.

When the state charter for the CalCOFI program ended in 1979, CDFG, SIO, and NMFS entered into an agreement to continue the field surveys, albeit on a smaller scale; to continue sponsoring annual conferences; and to continue publishing the *CalCOFI Reports* and Atlas series. The extensive time series of ichthyoplankton data, together with complementary measurements of the physical environment, constitute a major portion of the CalCOFI legacy. On-line computer display and extraction of these data is now available to the research community interested in the pelagic ecology of the California Current.

RESUMEN

Durante los últimos 70 años, ya sea uno o ambos stocks principales de clupeidos presentes frente a California (la sardina del Pacífico y la anchoveta del Norte) han sido estudiados en forma continua. Este interés fue estimulado por la necesidad de obtener información para el manejo de la producción local de estos peces y por el reconocimiento que el manejo exitoso de los stocks de clupeidos es un objetivo con implicaciones mundiales.

Durante las décadas de 1920, 1930, y 1940, California Department of Fish and Game (CDFG) llevó a cabo estudios de terreno en cooperación con Scripps Institution of Oceanography (SIO), California Academy of Sciences (CAS), y U.S. Bureau of Commercial Fisheries (USBCF, ahora conocido como National Marine Fisheries Service—NMFS). A fines de la década de 1940, cuando el futuro de la pesquería de la sardina se tornó problemático, la industria respaldó económicamente un programa de investigación más intenso. Ayudados por una infusión de dinero y apoyo político, los científicos de estas agencias prepararon un ambicioso plan de ataque.

Este plan se hizo conocido como el enfoque oceanográfico en investigación pesquera (hoy en día probablemente denominado enfoque de ecosistema) y fue hecho sinónimo del programa CalCOFI. Se efectuaron cruceros mensuales para colectar plancton y muestras de aguas en una red de estaciones; estudios de laboratorio fueron completados con el fin de descubrir los estadíos de desarrollo de los juveniles y el comportamiento de los adultos; la pesquería fue muestreada para determinar la demografía y las tasas vitales de los adultos; nuevos instrumentos y technologías fueron desarrollados para mejorar tanto la colección de datos como el análisis delos mismos. Un entendimiento más preciso de la dinámica poblacional de la sardina comenzó a emerger, y la pregunta central del "problema de la sardina" se definió: "Cuál es la influencia relativa del hombre en comparación con la del ambiente sobre la producción de la población de la sardina?"

A pesar de este nuevo entendimiento, la abundancia de las sardinas disminuyó continuamente, mientras que la de las anchovetas aumentó. El objetivo original del programa CalCOFI se volvió difuso y, como consecuencia, importantes reevaluaciones del programa ocurrieron en 1957, 1961, y 1966. A medida que cambiaban los objetivos, cambiaron los programas de muestreo en terreno. Cuando el apoyo del estado para el programa de CalCOFI terminó en 1979, CDFG, SIO, y NMFS acordaron continuar los programas de muestreo, aunque a menor escala, al igual que el apoyo a las conferencias anuales, y a la publicación de las serie de Reports y Atlas de CalCOFI. La extensa serie de tiempo de datos ictioplanctónicos, junto con las mediciones complementarias de parámetros físicos constituyen una parte importante del legado de CalCOFI. Estos datos están ahora disponibles a través de computadoras para el uso por la comunidad de investigadores interesados en la ecología pelágica de la Corriente de California.

INTRODUCTION

Welcome to the symposium of the 1987 CalCOFI Conference. We're here today to discuss the heart of CalCOFI: the 37-year time series of data collections—its extent, utility, and, ultimately, its value. The California Current has been referred to as the most intensively studied piece of ocean in the world. This reputation is enjoyed for two reasons: one, because the large number of marine institutions located along the coast of North America have each conducted many and varied field research programs; and two, because of the CalCOFI program.

The CalCOFI program was initiated to determine what happened to the sardines—the population declined rather precipitously in the 1930s and 1940s—and to determine the relative influences of exploitation and the environment on that decline. I will describe what was sampled, how often, over how large an area, and for what reason; that is, the extent of the CalCOFI data. Other speakers will describe the data's usefulness in depicting physical and biological processes.

In addition, we hope to encourage discussion on how the sampling design may be improved to address current research questions. Consideration should be given to new tools, new techniques, the geographic coverage, and how frequently we should make observations. We also wish to encourage discussion of a more fundamental question: Do we understand the California Current well enough now to abandon these large-scale surveys in favor of more focused research, or will we always need large-scale surveys to provide a context for our field experiments and to monitor trends and low-frequency variability? And a final question is: Have we exhausted the information content of this time series, or is there more to learn?

EARLY SARDINE RESEARCH

Research on the California sardine began in the early part of this century. There was an explosive demand for canned sardines starting in 1915, as well as an increasing high return for sardine meal and oil. At the same time the mechanization of the fishing fleet allowed boats to venture farther offshore. Salmon and albacore were targeted first, and then the sardine. The California Fish and Game Commission, founded in 1870, was well funded and respected by the turn of the century.

In 1915, the Commission established the Department of Commercial Fisheries under N. B. Scofield. He was originally recruited to study the albacore, and he immediately hired W. F. Thompson to look at the sardines. Thompson set up the nation's first state-operated fisheries laboratory. He began a systematic collection of landing statistics, known from then on as the "pink tickets." He also trained several fisheries biologists who went on to work in the federal government—people such as Elmer Higgins and Oscar Sette.

In 1920, Thompson published a plan for studying the sardine. He was concerned about both stock overfishing and growth overfishing. But more important, he was concerned about the synergistic effects of the environment and harvest on the population. In 1929 and 1932, the Department of Commercial Fisheries collaborated with Hopkins Marine Station and conducted oceanographic and biological surveys of the early life stages of sardines. In 1937 the Department collaborated with Scripps to study surface currents off southern Cal-

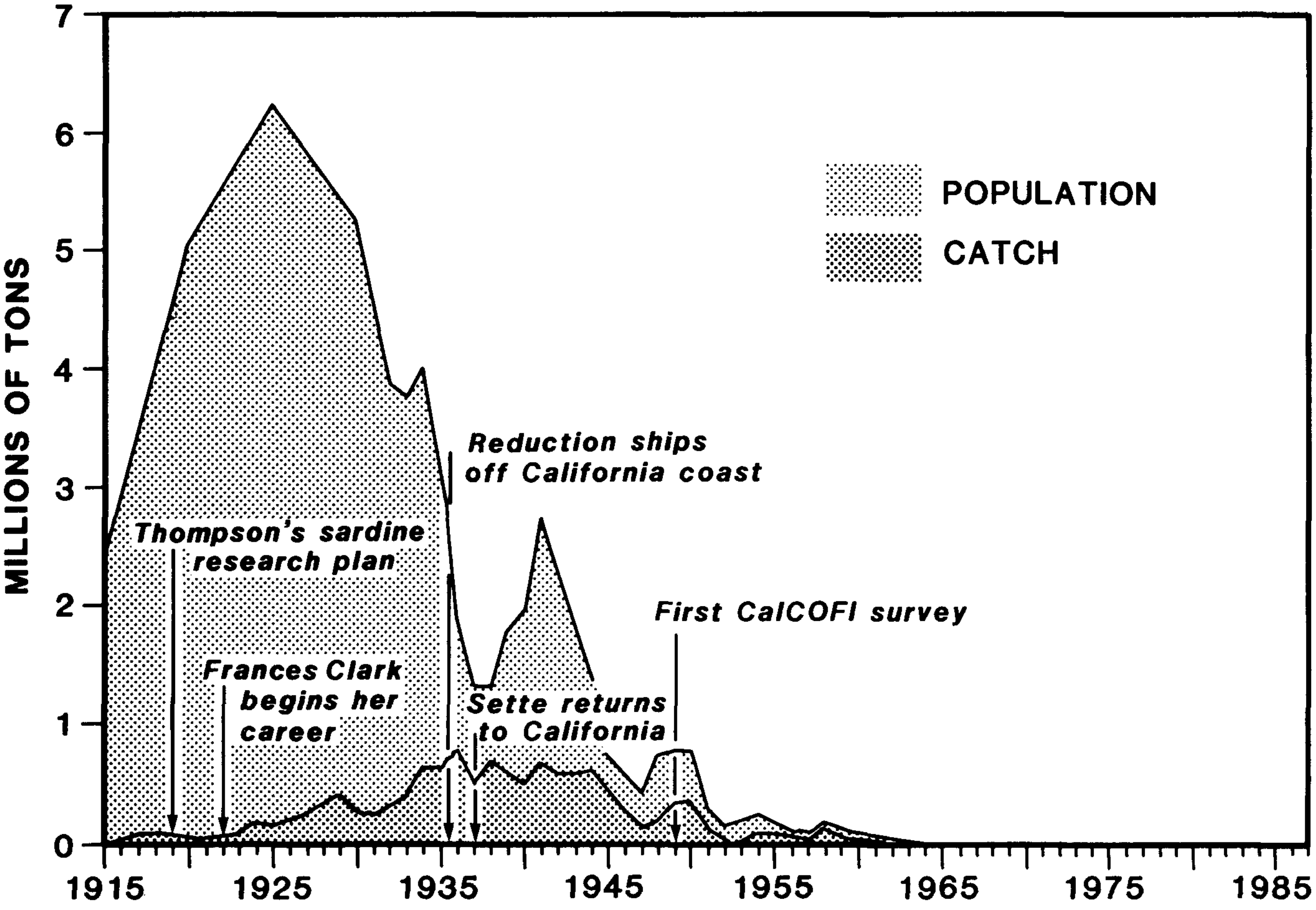

Figure 1. Pacific sardine abundance and commercial catch, since 1915 (from McEvoy 1986).

ifornia. But by the late 1920s, both Scofield and Frances Clark, who by this time had replaced Thompson, were concerned about depletion. They felt they were unable to control the fishery; the catch per unit of effort was down; and there were few older fish. In 1936 several bills were introduced to the U.S. Congress to prohibit offshore reduction ships, which were landing sardines outside the three-mile limit of California waters and reducing the fish to meal. At this time the harvest approached 790,000 tons per year. Congress asked the U.S. Bureau of Commercial Fisheries what it thought of the proposal, and Higgins, who was director at the time, refused to prohibit reduction ships on the grounds that there was insufficient evidence to curtail the commercial enterprise. The situation was further complicated in the late 1930s when there were several good year classes and the stock appeared to be recovering (Figure 1).

From 1937 through 1941 a series of ichthyoplankton cruises was conducted (Figure 2). The California Department of Fish and Game, the U.S. Bureau of Commercial Fisheries, and the Scripps Institution of Oceanography jointly participated in these cruises, which were conducted in the Southern California Bight—that is, between Point Conception and the international border. As a result of the sardine fishery's having been brought to the attention of Congress, the federal government decided to send Oscar Sette to California. Sette contributed to these cruises and eventually published a plan to determine how fishing affected the resource (Sette 1943). This plan is noteworthy because it considers all life stages of the sardines (Figure 3).

By this time, however, older fish were disappearing, and mortality was very high. With the onset of World War II, Sette was given full authority to set sardine quotas. There was a high demand for fish, and in September 1945 there were record sardine landings at Monterey. In October 1945, only one month later, the northern fishery completely collapsed. Steinbeck (1954) described this time by writing: "the canneries themselves fought the war

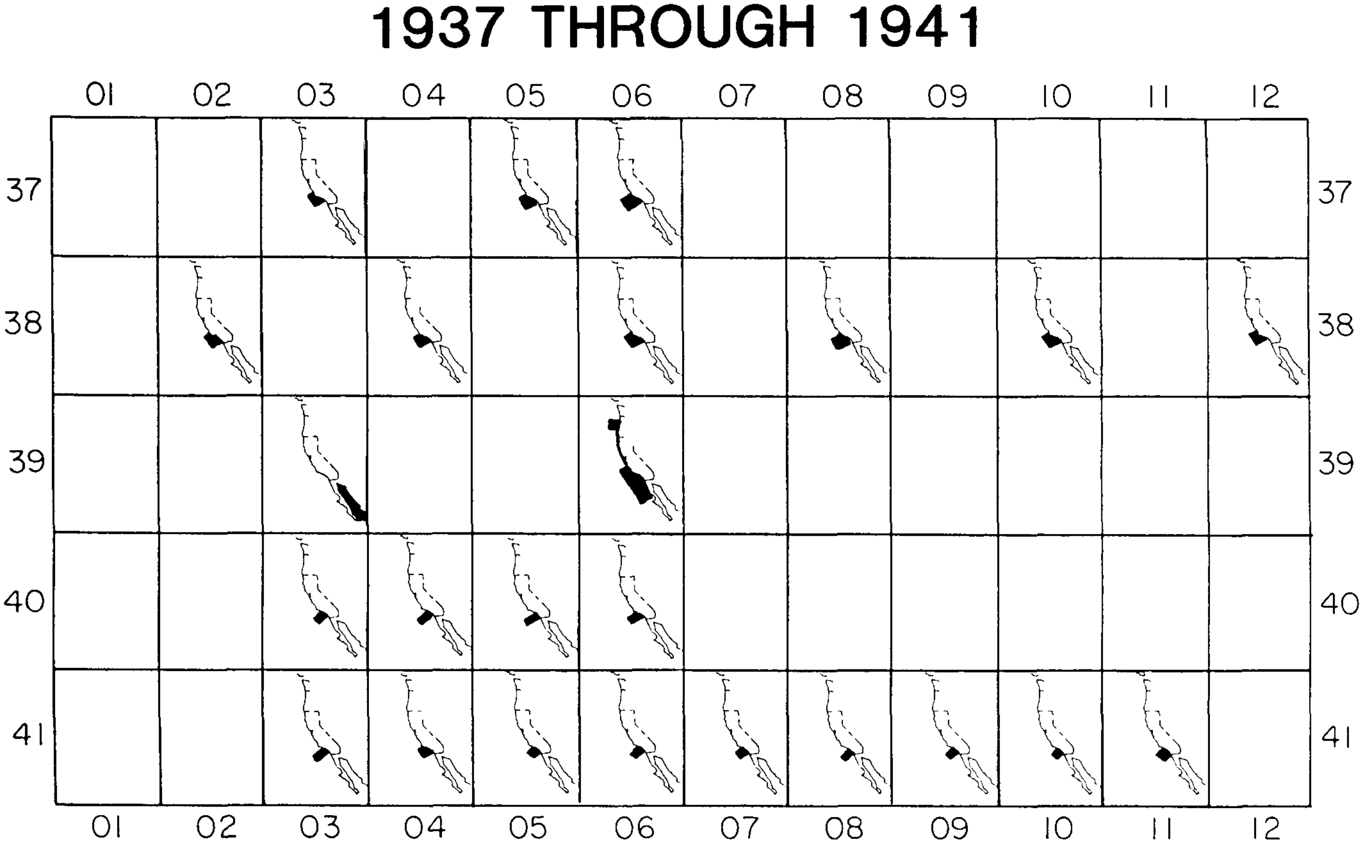

Figure 2. Ichthyoplankton cruises, 1937–41, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

by getting the limit taken off the fish and catching them all. It was done for patriotic reasons, but that didn't bring the fish back."[1]

There were a few moderately successful spawnings after the war, but 1949 through 1951 produced reproductive failures, and the southern fishery was dead by 1952. As the sardine catches declined in the late 1940s, industry leaders became increasingly alarmed. They wanted a more coordinated focus among the several agencies that were independently working on the sardine.

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

At the same time, Governor Earl Warren established several committees to aid industry after World War II. Robert Sproul, president of the University of California, headed one of these committees on natural resources. An informal meeting was convened at the California Academy of Sciences to discuss the problems of the sardine industry. The industry—that is, the canners—wanted help, but they weren't sure how to go about getting it. Sproul's representative was willing to put a big item in the university budget, but only if the U.S. Bureau of Commercial Fisheries and the California Department of Fish and Game cooperated. He further conditioned that the industry would have to tax itself for a matching set of funds, and stipulated that the research could not be dictated by the industry. The industry responded that it would lobby the legislature for a landing tax to be spent solely on ocean research. It wanted these expenditures, however, to be governed by a board made up of industry representatives (the Marine Research Committee). The scientists themselves, from state, federal, and academic agencies, agreed to cooperate and to form a technical committee to guide the research. Each agency, however, insisted that it would govern its own research using its own money. The governor's representative agreed to all of this, only if it was in accordance with a law passed by the legislature, and only if the governor had the authority to appoint the Marine Research Committee. Thus began a tentative confederation

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[1] Art McEvoy (1986) quoted this same passage, which succinctly captures the last major blow to the sardine population.

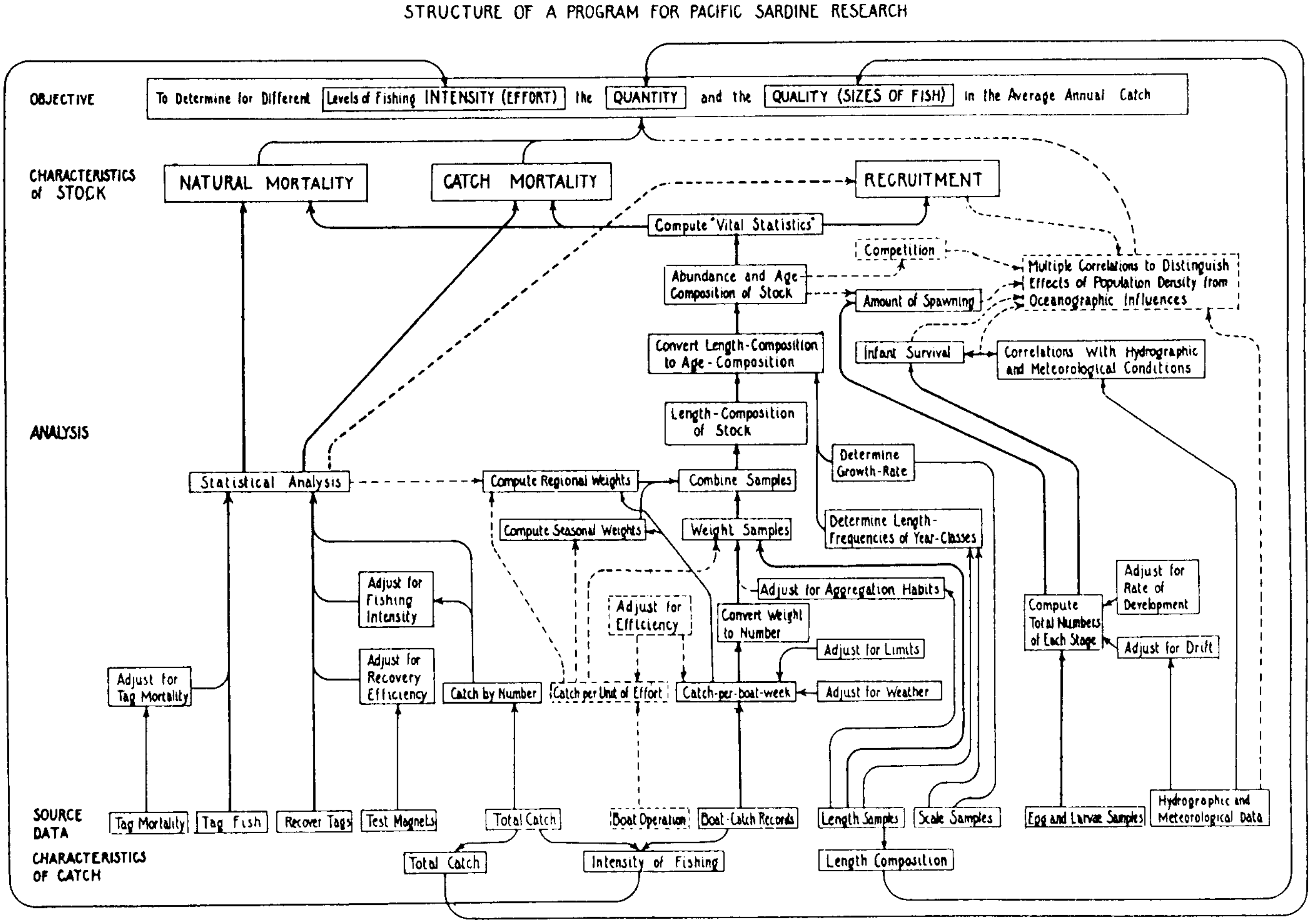

Figure 3. Conceptual model of how fishing affects the sardine resource (from Sette 1943).

among people and institutions with very different motives and objectives; it is a confederation that has productively endured for 40 years.

In 1949 the Marine Research Committee was established, and the CalCOFI program started; at that time it was called the California Cooperative Sardine Program. The technical committee—composed of scientists from the California Department of Fish and Game (CDFG), the U.S. Bureau of Commercial Fisheries (USBCF), the Scripps Institution of Oceanography (SIO), and the California Academy of Sciences (CAS)—laid out a rather ambitious program. The technical committee wrote that

> in order to develop plans for the responsible management of the sardine resource, and to attempt to derive workable methods of predicting where sardines will be found, and in what quantities, it is imperative to know certain underlying principles which govern the sardine's behavior, availability, and total abundance.

They further wrote that the four agencies participating in the program are

> investigating the sardine in relation to its physical and chemical environment, its food supply, its predators and its competitors, in attempting to evaluate the findings in terms of the survival of the young, and in terms of the distribution and availability of the sardines when they reach commercial size. (*California Cooperative Sardine Research Program Progress Report*, 1950)

This outline became known as the oceanographic approach to fisheries research. Essentially what the scientists wished to do was to correlate changes in water conditions with changes in sardine spawning, availability, and abundance. CAS researchers conducted laboratory studies on sardine behavior. CDFG staff monitored fishing effort and the size and age of the catch, as they had done since 1916. They also indexed recruitment from their bait-fishery surveys, collected adults for stomach analysis and reproductive condition, and conducted acoustic surveys for both juveniles and adults. SIO scientists estimated currents, correlated upwelling and wind fields, measured nutrient content, and—most important—developed new instruments for biological and oceanographic observations. USBCF researchers attempted to get the plankton sorted within one month, so as to adjust the survey scheme for changes in the spawning pattern of the sardines. Hopkins Marine Station joined in 1951; its researchers began weekly surveys of Monterey Bay.

The CalCOFI field sampling protocol is essentially a collection of plankton and water samples obtained over a fixed grid of stations (Figure 4) at periodic intervals. In the early days, other studies were made as well, although not as consistently. Phytoplankton tows were conducted; dip net fishing was done under night lights; and albatross and marine mammal counts were maintained. All three agencies acquired new research vessels to support the CalCOFI cruises. In 1954 the landing tax was extended to mackerel, anchovy, and herring. In 1955 the Marine Research Committee was expanded to include recreational fishermen and fishermen's unions.

The program was reviewed in 1957, 1961, and 1966. Each of these reviews resulted in a change in the sampling protocol. The cruises conducted in 1949 and 1950 were essentially exploratory surveys, and the sampling grid was fixed in 1951. Almost every month was sampled in every year throughout the 1950s (Figure 5). Twenty-five percent of the money spent on marine fisheries research in California was spent on the sardine, and half of that money was for vessel time. By 1955, approximately $4 million had been spent on sardine research. Of that, $800,000, or one-fifth, had been dispersed by the Marine Research Committee, with three-quarters going to SIO and USBCF.

By 1957 it was apparent that research directions among the three agencies had diverged, and a committee—John Marr from USBCF, John Radovitch from CDFG, John Isaacs from SIO, and Oscar Sette as a consultant—was formed to review the program. They suggested that a permanent coordinator be hired to provide some cohesiveness to the program, and that a permanent three-person committee, now known as the CalCOFI Committee, be established. They urged more data processing, analysis, and reporting.

By 1961 the CalCOFI Committee was in place, and Garth Murphy was the CalCOFI coordinator. The surveys had changed to quarterly, and covered larger areas, less frequently (Figure 6). By this time, it had been suggested that the anchovy was replacing the sardine, based on the assumption that they were ecological equivalents. It was widely acknowledged that several cold springs plus an intense fishery may have contributed to the sardine's decline.

The CalCOFI Committee stated that the sardine should not be studied as isolated from its ecological associates. The Committee wrote that "the sardine is like the gold of California—a conspicuous, valuable, easily harvested element in the midst of less-conspicuous riches of far greater potentiality."

The Committee also wrote that the "research should be responsible to the needs of society, and that the ultimate goal was to gain sufficient understanding to guide society in its use of natural resources."[2]

In 1966 the CalCOFI Committee decided that more thorough seasonal coverage was necessary to describe the spawning cycles of several species. Quarterly cruises every year were replaced with monthly or bimonthly cruises every three years (Figure 7). The Committee decided to document and study the developing anchovy fishery, which it had proposed a couple of years earlier, and secondly, to continue large-scale surveys of the California Current. Species of particular interest included hake, jack mackerel, and squid.

EMERGENCE OF THE ANCHOVY

During this time, the northern anchovy emerged as a major coastal pelagic stock (Figure 8). In 1951, when the systematic surveys began, there were two sardine spawning centers—one off Cedros Island in southern Baja California, and another off northern Baja California and southern California. At this time, anchovy larvae and sardine larvae were equally abundant. By 1952 it was clear that the 1948 year class of the sardine was moderately strong, but that the 1949, 1950, and 1951 year classes were very poor—about one-sixth of the 1948 year class. The outlook of the fishery was "very bleak." By 1953, "very bleak" became catastrophic as the population contracted farther southward with a reduced age structure. In 1954 warm water appeared off California, sardines came north to spawn, and there were good catches along the coast. By this time, however, anchovy larvae had doubled in abundance, while sardines and Pacific mackerel continued to decline.

In 1955 Clark (CDFG) and Marr (USBCF)

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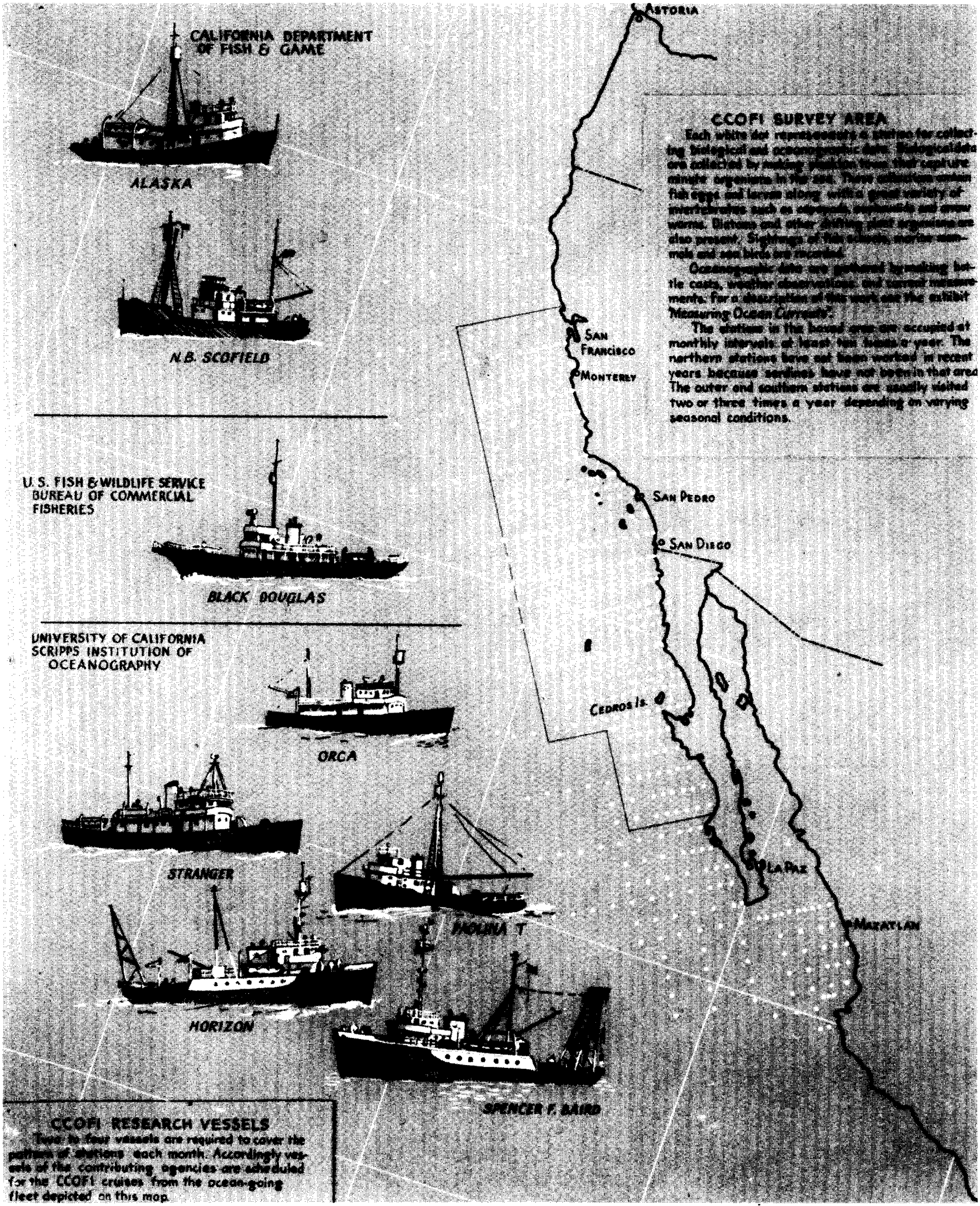
[2] *Calif. Coop. Oceanic Fish. Invest. Rep.* 8 (1961).



CCOFI SURVEY AREA

Each white dot represents a station for collecting biological and oceanographic data. Biological data are collected by making plankton tows that capture minute organisms in the sea. These collections contain fish eggs and larvae along with a great variety of invertebrates such as copepods, euphausiids and arrow worms. Diatoms and other drifting plant organisms are also present. Sightings of fish schools, marine mammals and sea birds are recorded.

Oceanographic data are gathered by making bottle casts, weather observations and current measurements. For a description of this work see the exhibit "Measuring Ocean Currents".

The stations in the boxed area are occupied at monthly intervals at least ten months a year. The northern stations have not been worked in recent years because sardines have not been in that area. The outer and southern stations are usually visited two or three times a year depending on varying seasonal conditions.

CCOFI RESEARCH VESSELS

Two to four vessels are required to cover the pattern of stations each month. Accordingly vessels of the contributing agencies are scheduled for the CCOFI cruises from the ocean-going fleet depicted on this map.

Figure 4. CalCOFI station grid, from 1951 to present.

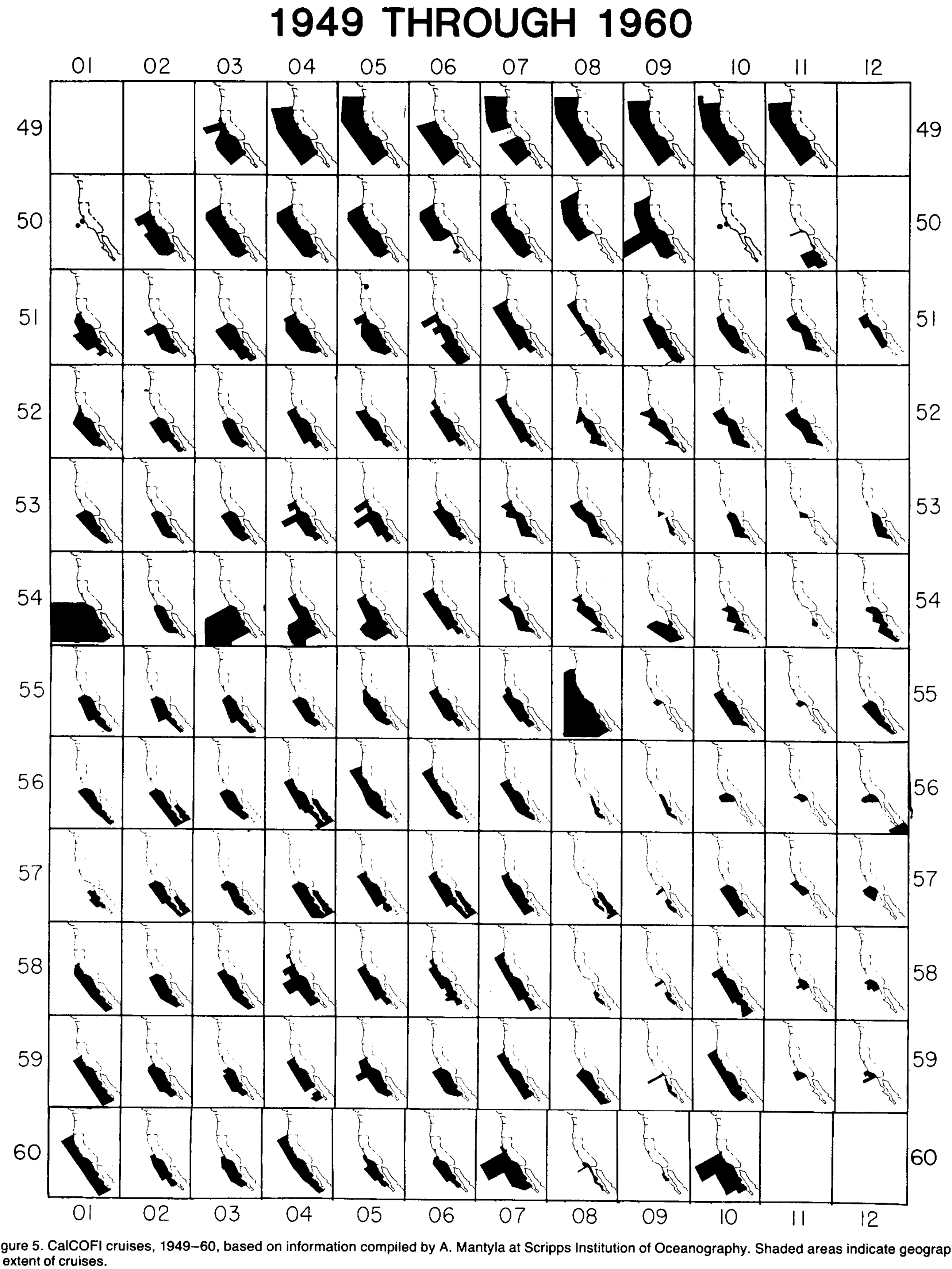


Figure 5. CalCOFI cruises, 1949–60, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

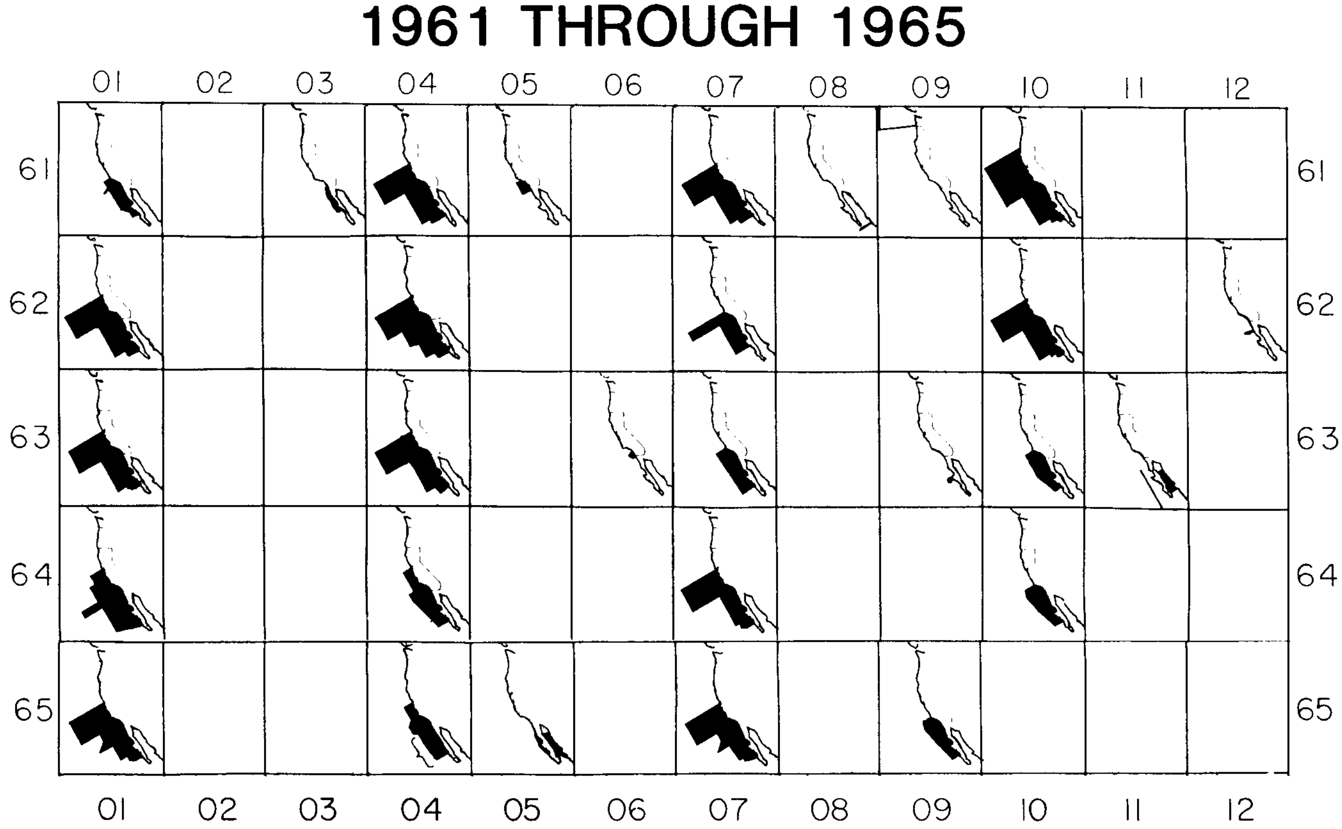


Figure 6. CalCOFI cruises, 1961–65, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

jointly published a paper in which they agreed to disagree on the population dynamics of the sardine. The disagreement was essentially whether or not a relationship existed between sardine spawning stock size and recruitment—that is year-class strength. The arguments implied that either overfishing (Clark) or an adverse environment (Marr) caused the decline in sardine population. 1957 and 1958 brought another warm period, and the sardines spawned as far north as Monterey. There were good catches all along the coast.

In the late 1950s a picture began to emerge. Sardines spawning off southern California were thought to migrate north to Oregon and Washington; sardines spawning off Baja California were thought to migrate to northern California. The lack of spawning success off southern California since 1943 was probably the cause of the collapse of the northern fisheries. Poor spawning success was further thought to be due to low spring temperatures. In 1958, Reid, Roden, and Wyllie published their paper on the physics of the California Current. They suggested that increased winds, enhanced upwelling, and cooler temperatures may have been associated with spawning failures. Later that year CalCOFI sponsored a symposium on the changing Pacific Ocean, and most participants agreed that 1957 had terminated a monotonous decade of low temperatures and high winds in the North Pacific.

By the early 1960s, there was a general acknowledgement that overfishing for sardines had occurred, and the anchovy-sardine replacement hypothesis began to receive some interest. Both Isaacs (1965) and Ahlstrom (1967) published papers on the strong association between anchovy larvae and sardine larvae. By 1958 and 1959, anchovy larvae were three times as abundant as they had been in 1951, and they doubled again in the early 1960s. The anchovy-to-sardine ratio was 3 to one in 1952. By 1956, it was 10 to one; by 1959, 45 to one; and by 1962 there were 80 anchovy larvae for every sardine larva. The suggestion was made at that time that anchovy and sardine may together act as a single population, and that a large sardine-anchovy population may depress year-class strength.

In 1964 the CalCOFI Committee proposed an experimental anchovy fishery. They suggested annual harvests of 200,000 tons of anchovy and

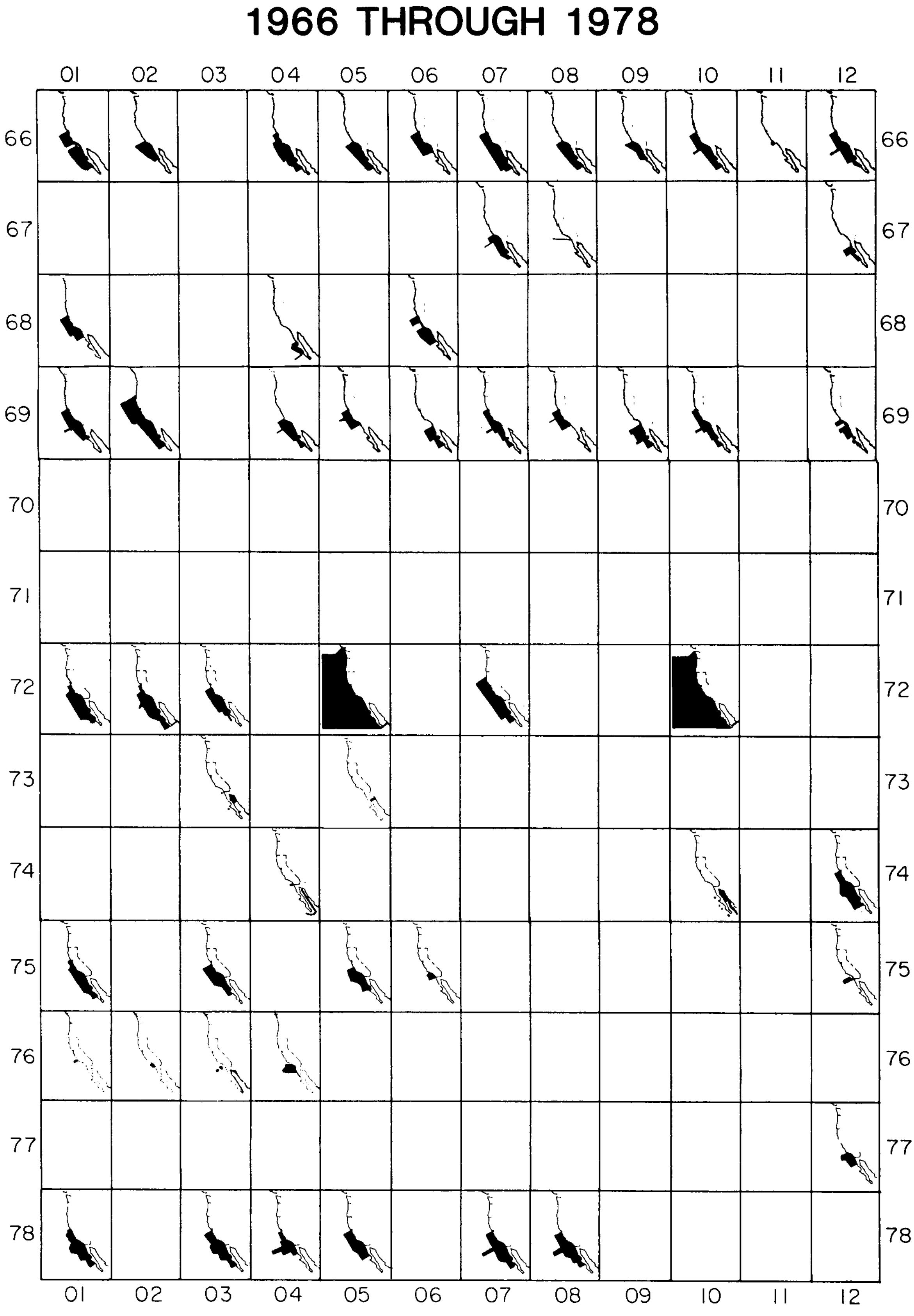


Figure 7. CalCOFI cruises, 1966–78, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

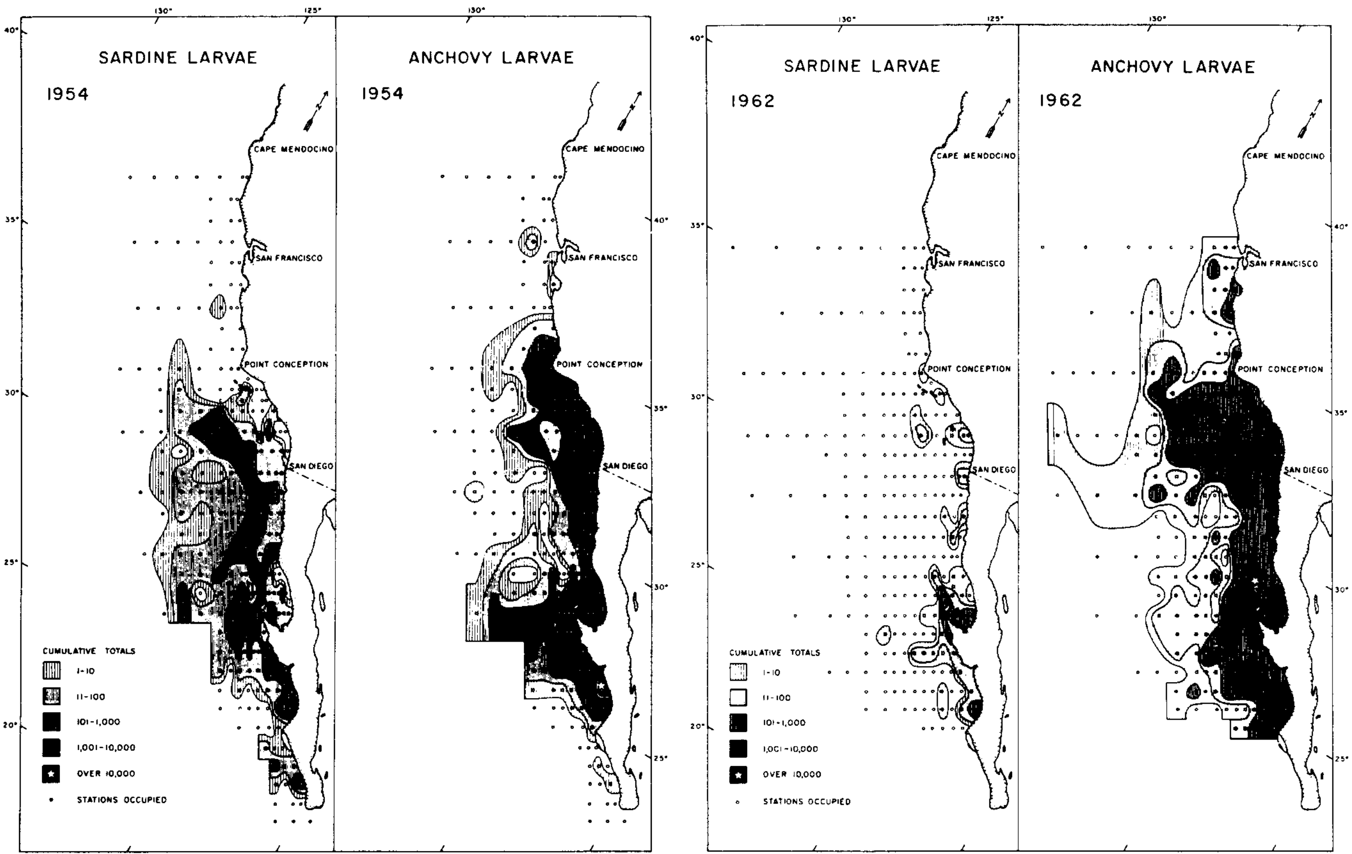


Figure 8. Distributions of sardine and anchovy larvae, 1954 and 1962 (from Ahlstrom 1966).

10,000 tons of sardines. These catches would be sufficient to reduce the anchovy biomass, and still monitor the sardine response. There was a strong negative reaction across the state, and the experiment never got off the ground.

Instead the CalCOFI Committee decided to continue work on the sardine-anchovy relationship, as well as to expand broadscale studies of the pelagic environment. Attention was directed toward other species such as saury, hake, jack mackerel, and squid. The Marine Life Research Program at Scripps expanded its studies into the North Pacific, and Joe Reid convened the 1966 CalCOFI symposium on wide-scale studies of the Pacific Ocean.

In the late 1960s the CalCOFI Committee was frustrated that the anchovy fishery had failed to develop, and they proposed research to identify factors that constrained the use of living marine resources in California. In 1967 CalCOFI sponsored a symposium on the magnitude, distribution, and susceptibility of living marine resources in the California Current. In 1968 the CalCOFI symposium covered the legal, sociological, and technical problems associated with the use of marine resources in the state of California. The 1969 symposium was on world population growth and the role of marine fisheries in providing food. The CalCOFI Committee wrote that there was an understanding of pelagic resources in the California Current sufficiently adequate for the scientific management of multiuse domestic fisheries, and yet the resources remained little used.

The committee suggested two reasons for this: the first was a general failure to appreciate the long-term economic benefits of a healthy domestic fishing industry; the second was misunderstanding and mistrust between users of the resource—essentially, a widespread apprehension that the state could not control a fishery once it got started. This fear was not groundless, given the sardine experience.

EXPORT OF TECHNOLOGY

By the 1970s, however, CalCOFI began to turn outward. In the 1950s, we were concerned about the decline of the sardine. In the 1960s we were concerned about the increase of the anchovy. In the 1970s, we were concerned about exporting what we knew. CalCOFI became an international model for the study of pelagic populations and the large-scale oceanographic and meteorological events that affect them. USBCF became part of NOAA, an agency with a strong tradition of environmental mapping and monitoring. The MARMAP program was established to assess pelagic stocks off the eastern and gulf coasts; it was modeled after CalCOFI. The CalCOFI Committee established a relationship with Instituto Nacional de Pesca in Mexico, and eventually a Mexican anchovy fishery developed. The Sardine Anchovy Recruitment Program (SARP) is also an example of the worldwide influence of CalCOFI ideas.

In 1979 the Marine Research Committee was retired, and an abbreviated CalCOFI program continued by agreement between the state and federal agencies. Surveys and ship time were reduced to what was necessary to monitor certain populations (Figure 9), and a search was made for "indicator stations," that is, stations that could be routinely sampled to represent a much larger survey. By this time, the Marine Research Committee had distributed $3.5 million over its 30-year existence. A little less than $1 million of that came from the sardine, $1.2 million from the anchovy, $1 million from the mackerels, and $⅓ million from squid and herring.

CalCOFI continued as a forum to bring researchers together to collaborate and present results. *CalCOFI Reports*, published once a year, became a peer-reviewed journal. The CalCOFI Committee sponsored symposiums on nonconsumable resources in the California Current, climatic regimes and low-frequency events, mesoscale patterns and processes, eastern boundary currents as a class of phenomena, and nearshore patterns and processes. The goals were restated: to understand the physical and chemical environment and how it changes, to determine the productivity of the California Current ecosystem, and to make this information available in the form of *CalCOFI Reports*, conferences like this one, and data bases. The ultimate goal is still to understand and predict fluctuations in marine populations and to provide a basis for the wise use of these resources.

EGG PRODUCTION SURVEYS

We have changed some of our methods as well. In 1972 Paul Smith gave us a way to determine absolute abundance from ichthyoplankton surveys when he regressed larval census on Murphy's population estimates of the sardine. In this formulation, the numbers of larvae found in the sea are thought to be proportional to the adult spawning biomass. This assumes two things: (1) that every year there is a constant reproductive output per unit weight of adult, and (2) that the mortality of the young is constant from year to year. This technique became known as the larval census method.

The larval census method eventually evolved into the egg production method (Lasker 1985), by which the spawning biomass is proposed to be the quotient of the daily production of eggs in the sea and the daily specific fecundity of the adults. This method directly measures both the reproductive output of adults and the mortality of the young. The only assumption required is that we can sample without bias.

Reproductive output of adults is determined from a sample of adult fish. Various reproductive parameters are measured and combined to estimate the daily specific fecundity—the number of eggs spawned per day per unit weight of adult fish.

Egg production, the number of eggs spawned per day, is determined from high-density surveys conducted over the spawning habitat. Each of these surveys (Figure 10) comprises approximately 1,000 vertical egg tows yielding a rather precise estimate of egg abundance by developmental stage, from which we can determine egg production. These surveys are also part of the CalCOFI data base.

CALCOFI ON-LINE DATA SYSEM

CalCOFI data are available in a variety of hard-copy reports and papers. There are approximately 300 data reports, 30 atlases, and 29 volumes of *CalCOFI Reports*. In addition, at the Southwest Fisheries Center we have developed a computerized data search-and-retrieval system called the CalCOFI On-Line Data System. It is intended to give researchers the opportunity to explore the extent of the CalCOFI data set and to extract desired portions. Although it does not provide access to every CalCOFI data set, the major portion of the CalCOFI data (ichthyoplankton counts and hydrocast profiles) is available in this initial version.

The researcher is guided through the system by a series of menus (Figure 11). The main menu offers four options: (1) station index, (2) methodology, (3) ichthyoplankton data, and (4) hydrocast data. The station index option allows a researcher to peruse the extent of the data, providing access to information on the various cruises, the geographic sampling density (the extent of the area sampled during a particular cruise), and the temporal sampling density (how often a specific area was sampled throughout the time series). The

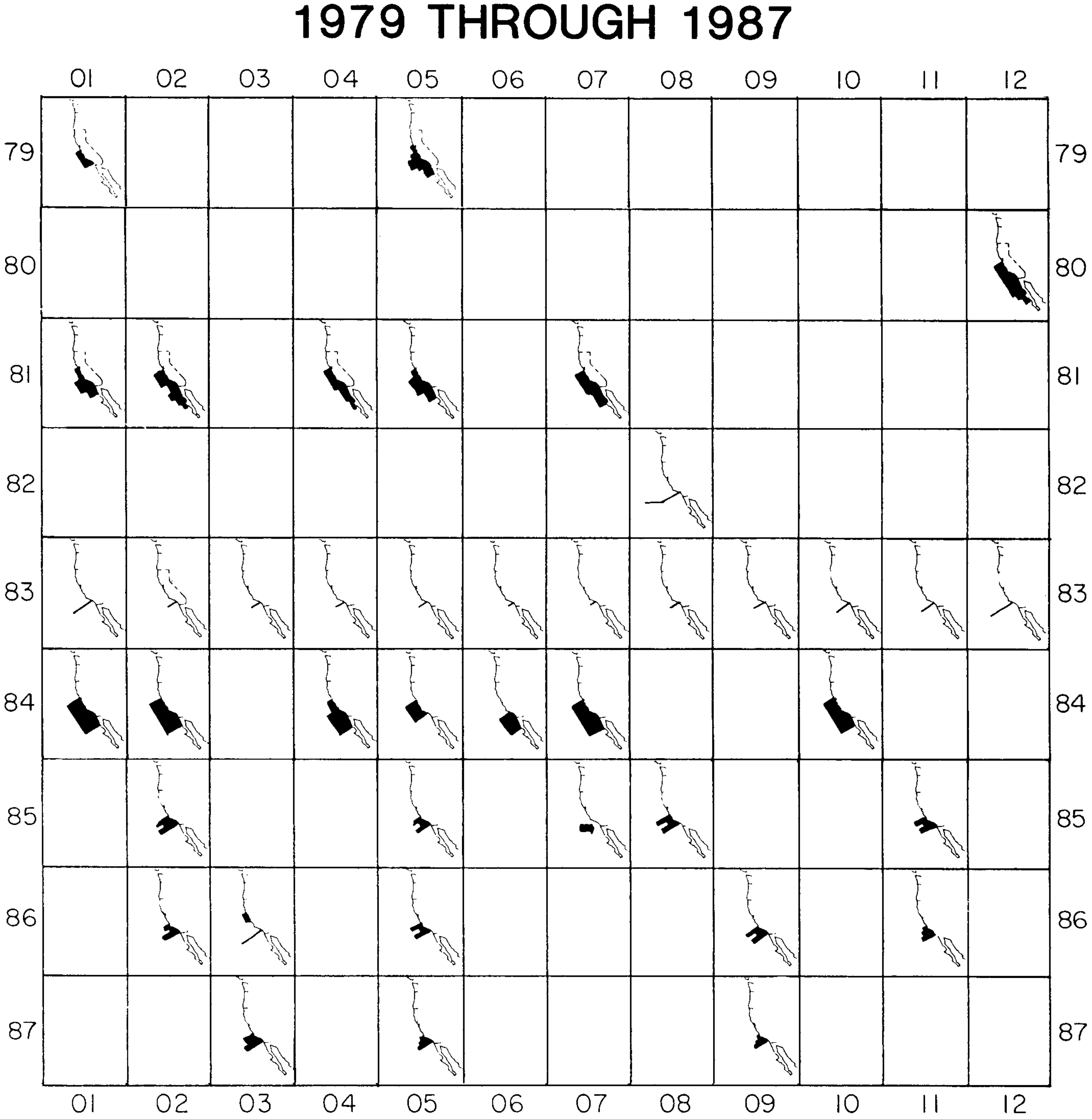


Figure 9. CalCOFI cruises, 1979–87, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

methodology option allows a researcher to peruse descriptions of the data sets currently on line, cruise frequency and geographic coverage, gear design, sample sorting and archiving procedures, identification notes, and annotated references. The ichthyoplankton data option allows a researcher to actually extract data. Data are available on five major species of fish larvae enumerated by length, anchovy eggs enumerated by developmental stage, and the extensive collection of fish eggs and fish larvae identified to over 200 taxonomic categories. The hydrocast data option allows access to a data set of vertical profiles of temperature, salinity, oxygen, oxygen saturation,

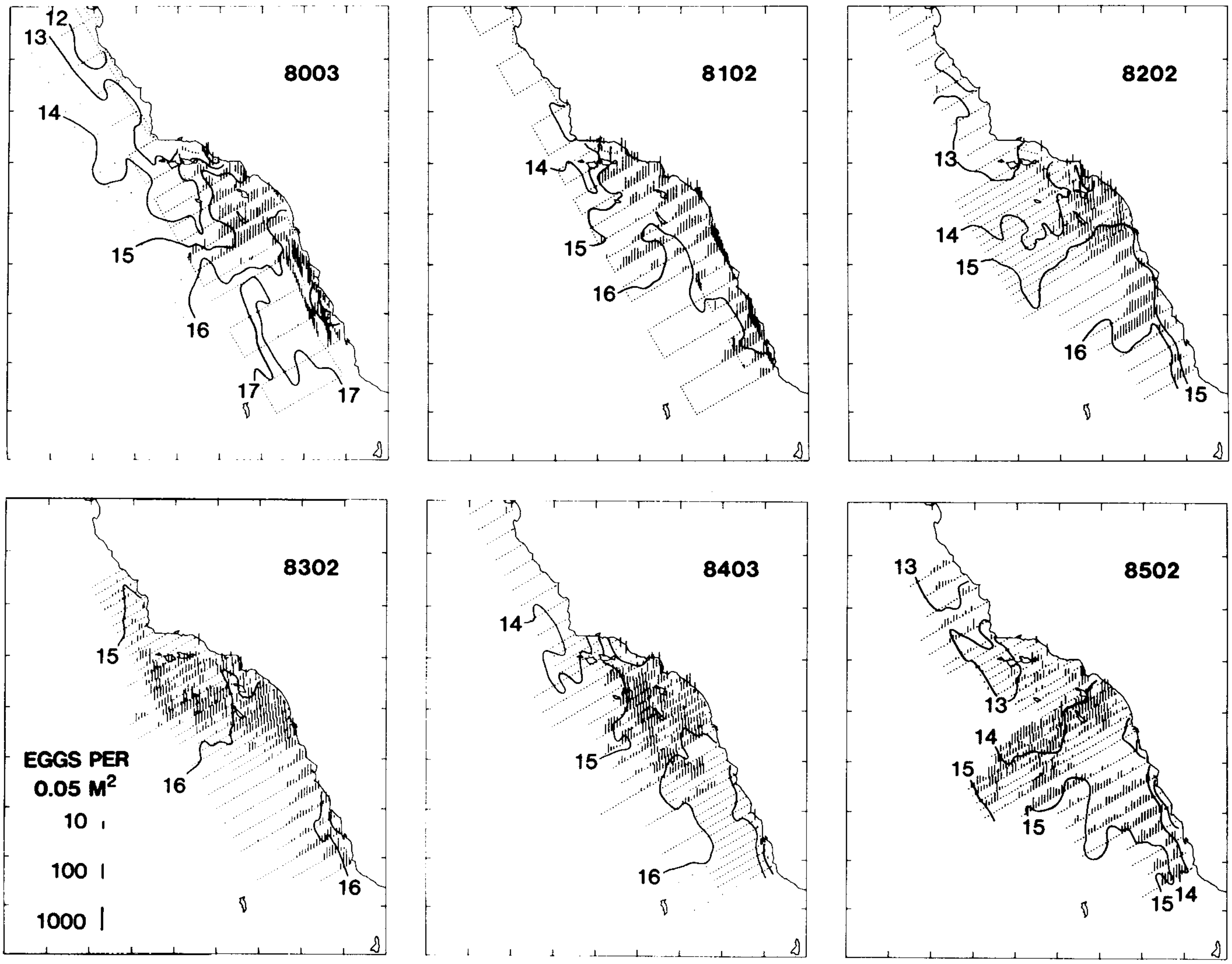


Figure 10. Northern anchovy egg production surveys, 1980–85 (from Fiedler et al. 1986).

density, and dynamic height determined at standard depths.

The data are the results of approximately 300 survey cruises during which 50,000 plankton tows and 10,000 hydrocasts were conducted. The data are displayed on a terminal screen in the form of tables and maps; they can also be written to a computer file for subsequent analysis or printing.[3]

LARGE-SCALE SURVEYS

I close by listing three reasons for conducting large-scale surveys and building a long-term time series like CalCOFI: (1) to determine what species reproduce when and where, what their distribution is, and something about how they recruit themselves—where survival is high and where it is low; (2) to characterize physical habitats, their seasonal and interannual change; and (3) to monitor long-term population trends and variability. These were the intentions of the first CalCOFI surveys, and I believe that they are still valid. Consideration should be given, however, to updating the sampling schemes and the tools that we use.

* * *

Question: Are the Gulf of California data in the CalCOFI On-Line Data System?

Hewitt: Not at the present time. That doesn't mean that the data can't be added later, but they are not there now. The Gulf of California cruises were

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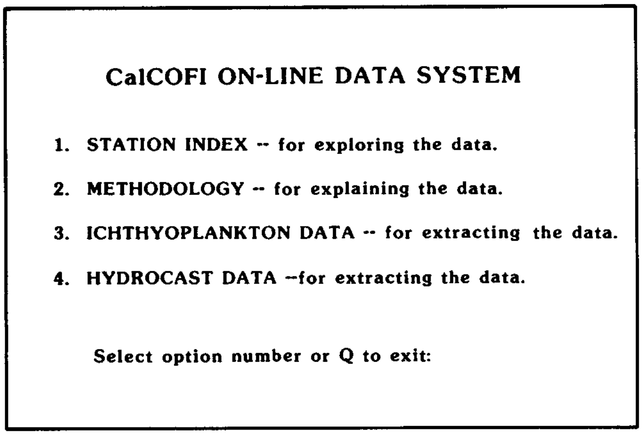
[3] User's manuals for the CalCOFI On-Line Data System may be obtained from the Southwest Fisheries Center, P.O. Box 271, La Jolla CA 92038.



CalCOFI ON-LINE DATA SYSTEM

1. STATION INDEX -- for exploring the data.
2. METHODOLOGY -- for explaining the data.
3. ICHTHYOPLANKTON DATA -- for extracting the data.
4. HYDROCAST DATA --for extracting the data.

Select option number or Q to exit:

Figure 11. Main menu from the CalCOFI On-Line Data System (from Hewitt et al. 1988).

rather sporadic and don't constitute a continuous time series.

Dick Schwartzlose: One of the many things I would like to say, having been in CalCOFI for many years and having been in the administration of the Marine Life Research Program at Scripps for those many years also, is that you notice changes in the cruise frequency from almost every month to every quarter. A lot of people criticized the change and said that we should have continued the monthly cruises. Of course that would have been very nice to do, but at the time all of the agencies were coming under financial stress, and it was impossible to continue the ship operations at a high level, and also to supply the number of people necessary to go on all those cruises. The decision to shift the cruises to a quarterly frequency was not made just because we thought we didn't need them. There was also a consideration of what finances were available. This occurred again in the 1970s as more money and people were diverted to process-oriented cruises, and so there were other ships in the pattern of cruises. Since that time CalCOFI has been criticized for not continuing the monthly cruises. But of course we can't peer into the future to see what's best and what's going to happen.

Hewitt: One of the things that I hoped would come out today is a more rational discussion of what should be measured, how often, over how large an area, using what tools, and so forth. It would be based on a more rational approach to the problem at hand rather than an irrational response to budget restrictions.

Paul Smith: I think it should be pointed out that in 1957, when the Russians launched the Sputnik, the government of the United States launched a series of expenditures on oceanography which tended to double every year from 1957 to 1965. It was during this same period that the CalCOFI surveys were reduced to quarterly. So instead of a reduction in the absolute availability of funds, there was a reduction of the will to conduct the work. Individuals were awarded funds and carried out the work under the names of spin-off organizations. The money was carried away, as were a lot of the people at that time. So I don't think it was the shortage of funds; rather it was a shortage of will.

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PHYSICAL OCEANOGRAPHY, 1947–1987

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The charter of the Marine Life Research Program, as stated in 1958 by Roger Revelle, Director of the Scripps Institution of Oceanography, is as follows:

> The objectives of the Marine Life Research Program at Scripps are to support, foster, stimulate, and carry out coordinated investigations leading to an understanding of the continuity and changes of the nature, environment, ecology, and general biology of the pelagic fishes and associated organisms of the eastern North Pacific . . . .

I would like to review for you something of what has been done, beginning with the earlier work. Most of you were not active in this field when the Marine Life Research Program began, and therefore it is necessary to tell you that techniques and instrumentation were quite primitive at that time. Meteorological data over the ocean were very few, and without computers even these few had to be arrayed by hand.

What was known or proposed about the ocean, and about the California Current in particular? George Davidson had published several papers dealing with the flow, and Richter (1887) had studied coastal temperature. Many of the major concepts about ocean circulation, including the California Current, are of long standing. Early in the century, Thorade (1909) related the temperature to the general circulation; George McEwen (1912) discussed upwelling as a consequence of Ekman transport, and later the effect of the circulation upon climate; and Marmer (1926) presented measurements of coastal currents made from lightships.

Skogsberg (1936) noted that near the coast the water at 50–100-meter depths was warmer from December through February than in summer; he attributed this to summer southward flow and upwelling and the Davidson Current in the winter, which he called the oceanic period.

Sverdrup and Fleming (1941) discussed the circulation of the Southern California Bight, and noted that the conventionally accepted notion of uniform upwelling and offshore flow seemed to be interrupted by eddies at the outside edge of the upwelled water. Tibby (1943) presented maps of geostrophic flow covering the area from northern Washington to Punta Santa Eugenia. McEwen (1948) published a study on eddies in 1948.

These gave the concept of a California Current moving southward, an inshore flow that was southward in summer, above a northward countercurrent that was present during most of the year, and a surface northward flow in winter along the coast. The southward surface flow was geostrophically balanced and was therefore accompanied by coastal upwelling that began in March or April off central Baja California and moved northward, with its maximum effect off northern California in July and August. That the deeper waters in the countercurrent, or undercurrent, had come from farther south had been shown by their higher temperature and salinity, their nutrients, and their lower oxygen. Eddies had been noted and discussed by Sverdrup and Fleming, and in a paper written by McEwen (1948) on their nature, though he emphasized the semipermanent Southern California Bight circulation rather than the smaller-scale and less regular features to the north and south.

This represents what had been learned or conjectured about the California Current at the time CalCOFI began. Sverdrup had had a major part in proposing CalCOFI, but both Sverdrup and Fleming, who had contributed so much, had left Scripps before CalCOFI went to sea for the first time.

Carl Eckart was director of Scripps at the time the field work began, and Roger Revelle was on hand to manage it. Dale Leipper was in charge of the physical oceanography, aided by Bob Reid and later by Paul Horrer. Dave Carritt and Warren Wooster handled the chemistry. An early method of chlorophyll measurement was proposed by Marston Sargent, but it was not satisfactory and was soon dropped. The biological sampling was in the hands of Laurie McHugh at Scripps and Ahlie Ahlstrom of the U.S. Fish and Wildlife Service.

Scripps acquired the two ships *Horizon* and *Crest*, which, with the *E. W. Scripps* and the California Fish and Game vessel *N. B. Scofield*, carried

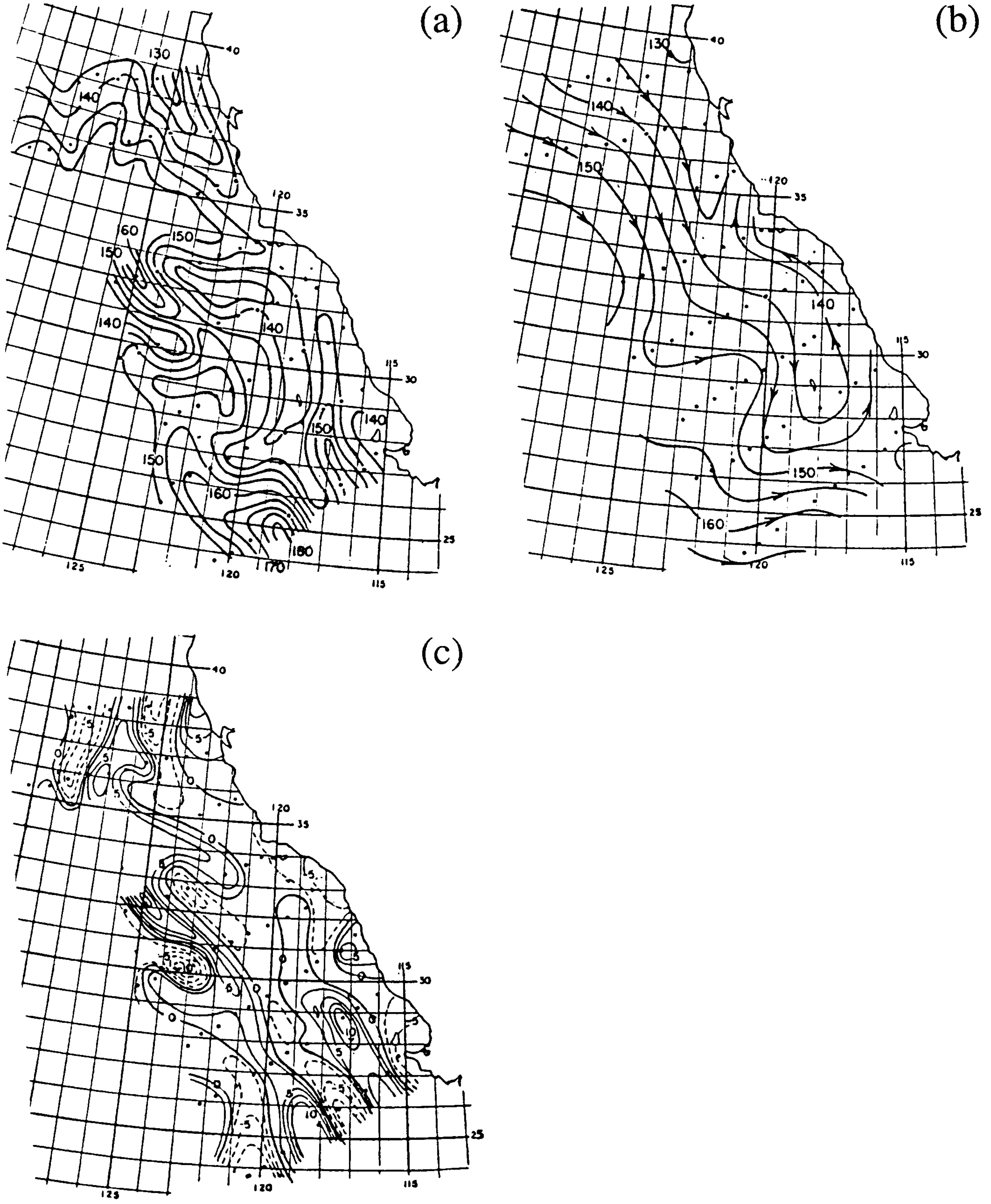

Figure 1. Marine Life Research Cruise 1 (Feburary 28–March 15, 1949): (*a*) dynamic height anomalies (0 over 1000 decibars); (*b*) dynamic height anomalies after elimination of tidal effect; (*c*) deviations in dynamic heights caused by tides. Contour interval 2½ dyn cm. Dashed lines indicate negative values. (Defant 1950a).

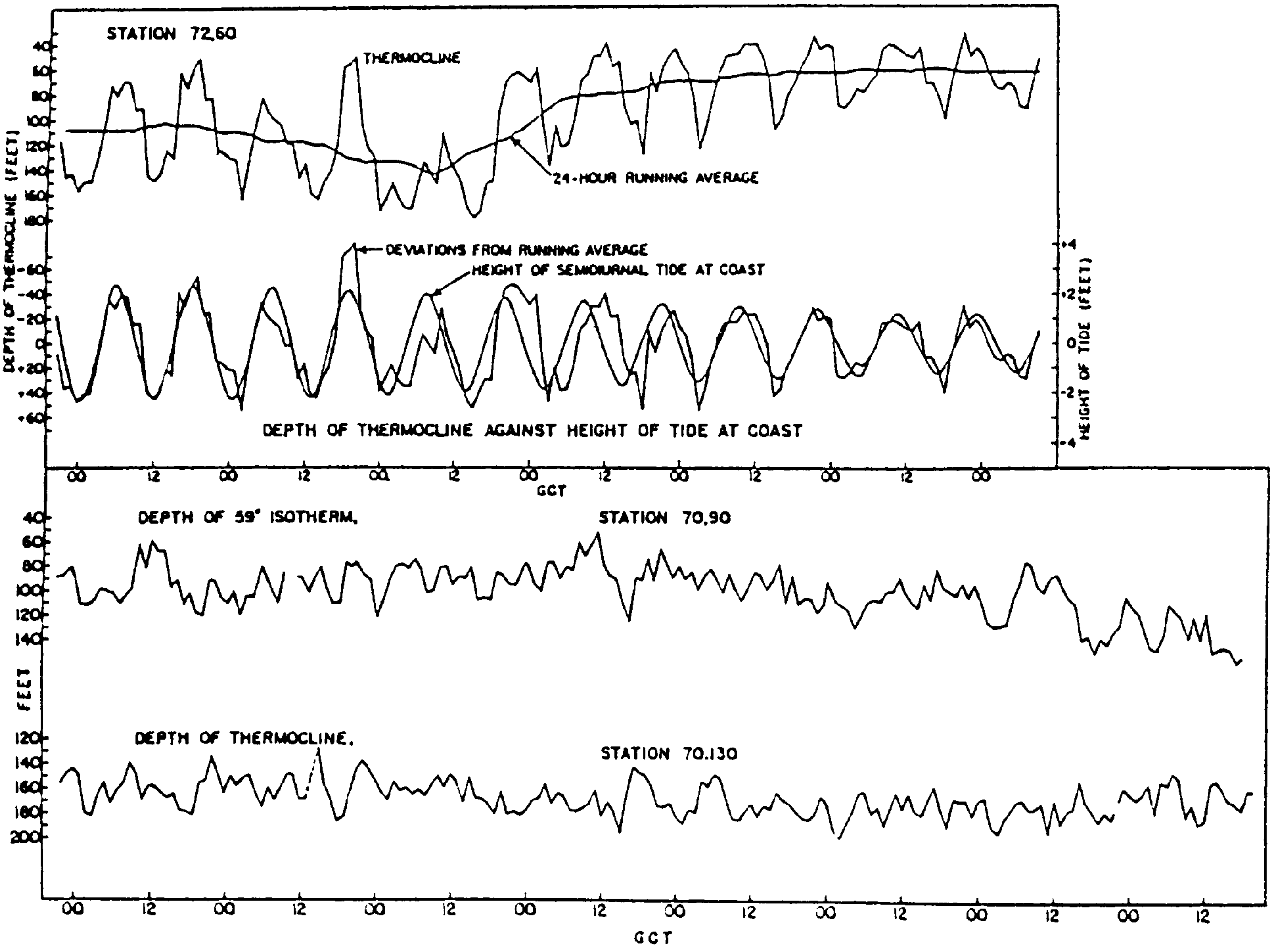

Figure 2. Data from the three anchor stations in October 1950 (Reid 1956).

out the first cruise in March 1949. Setting up the operation for three or four ships at once, in a period of about six months, was not easy. From a core of one experienced technician and two new hires in June of 1948 and enough gear for one ship, they had to expand rather quickly to equip and man three ships by March of 1949. Much of the work on the first cruise was done by students (I was one of those) and a few professors.

Thus began the field work that later became known as the CalCOFI cruises. It was based at first on an extension of work by earlier investigators, and its first pattern had stations widely spaced to permit broad coverage, and to allow the work to be carried out by small technical parties. During the first year it became clear that closer spacing was needed, and intervening lines of stations were added; also the stations were more closely spaced inshore. The requirements of broad-area coverage and small technical parties did place a lower limit, however. Quite often it was not possible to measure both oxygen and phosphate. Vertical spacing and depth range of samples changed from 12 samples in the upper 1000 meters in 1949 to 15 in 1950, to 16 samples in 500 meters in 1953, 17 from 1954 through 1959, and 18 samples from 1960 through 1981; it is now 20 samples in the upper 500 m.

This program, which was to deal with biology as well as physical and chemical oceanography, was planned for a broad coverage of the California Current in order to study the major circulation and its seasonal and year-to-year variations, including upwelling and the countercurrent, and the relation between these and the organisms over a substantial

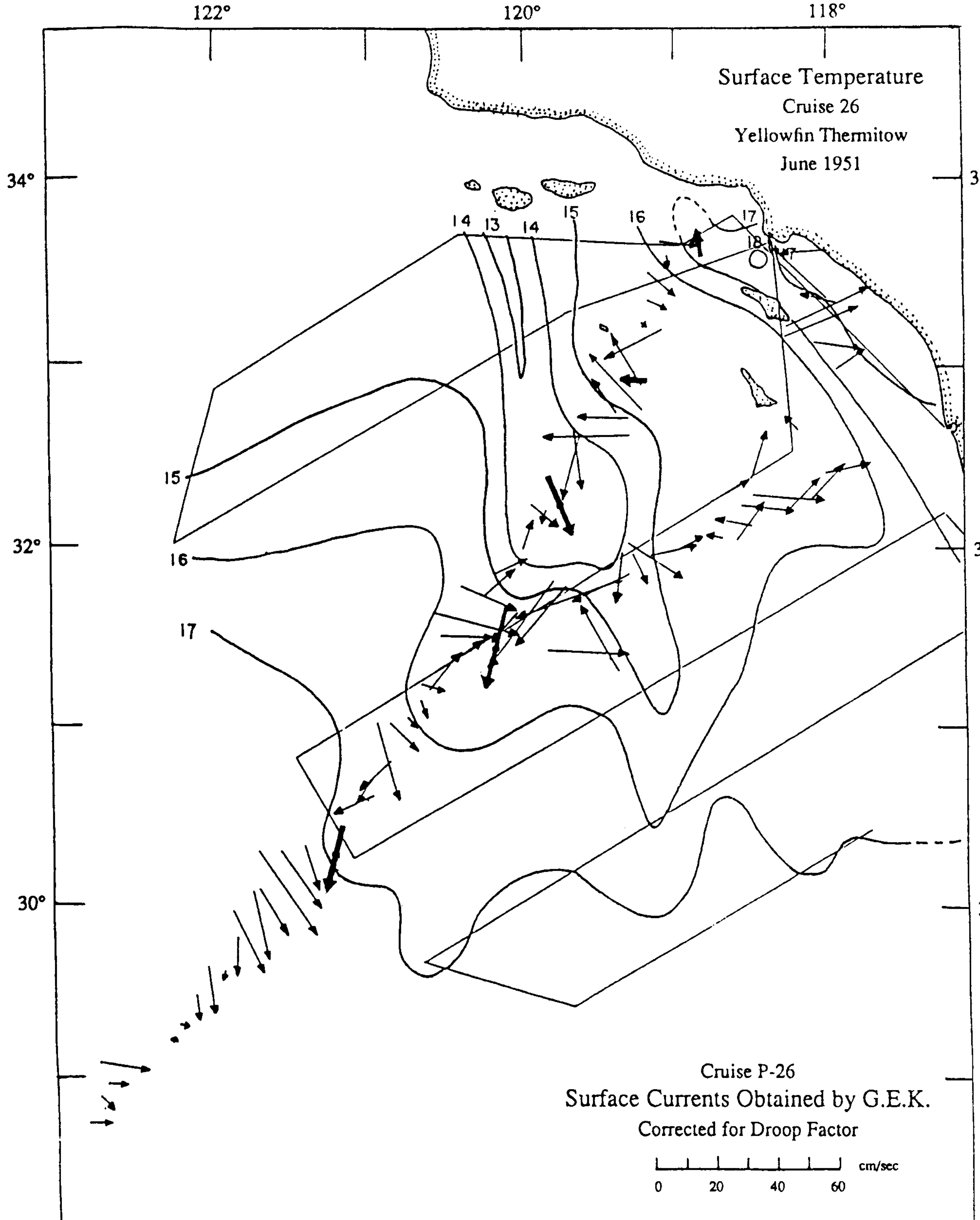

Figure 3. Surface temperature, from the California Department of Fish and Game vessel *Yellowfin* thermitow measurement, in June 1951, and surface currents obtained by GEK on the Scripps vessel *Paolina T* in June 1951. Heavy arrows indicate 24-hour averages (SIO unpublished).

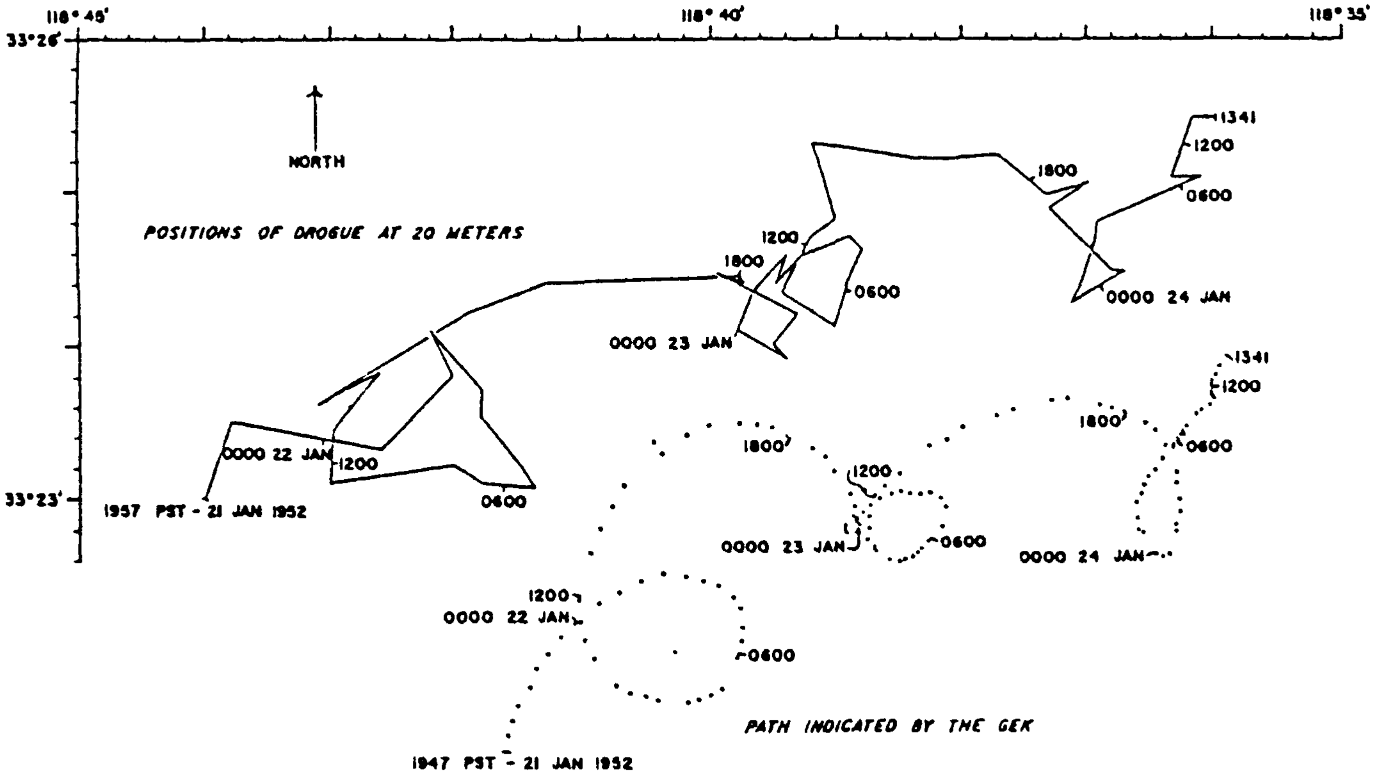

Figure 4. Trajectory of drogue near Santa Catalina Island and path indicated by the integrated GEK velocity measurements (starting points offset to avoid overlap) (Reid 1958).

area. Among the first published papers based upon the 1949 data were studies of upwelling by Yoshida (1955 and 1958) and by Yoshida and Mao (1957). Yoshida continued his interest, and one of his last papers (1980) dealt with coastal upwelling.

The circulation as revealed by the dynamic topography showed various irregularities, and these were at first ascribed to the effect of internal waves of semidiurnal period. Albert Defant (1950a,b) spent six months at Scripps in 1949–50 studying the data, and attempted to develop a method of eliminating the tidal effect. He took part in a brief anchor-station study in January 1950. Data from the first cruise (Figure 1a) showed various bumps and troughs. After Defant had applied his methods to the data, the pattern was much smoother (Figure 1b). The adjustments he made, which he interpreted as internal waves, were as large as 10 dynamic centimeters (Figure 1c).

After Defant left, I was assigned the job of continuing his method. Anchor stations were carried out in October 1950 with three ships (Figure 2). These stations did not show enough amplitude inshore, where the waves were clearly recognizable. Offshore the signal was not clearly present and, in any case, was of even lower amplitude. But it did not seem to account for the amplitude of some of the various smaller-scale features in the data. It was obvious that these features were not simply internal waves, but were something else. Several drogue studies were carried out, but it was not possible with the techniques available in 1952 to follow drogues except by ship, and this could not be done for more than a few days. Positions accurate enough to determine velocity during only a few hours could be determined only by coast piloting, within sight or radar range of the coast or of islands.

In early 1950, a new instrument—the Geomagnetic Electro-Kinetograph (GEK, or jog-log)—became available. In case you don't remember, this instrument allowed measurement of surface current from a ship underway. The measurement required a brief excursion from the ship's course, and we made the measurements hourly underway during many of the cruises. Some results of such measurements made in 1951 are shown in Figure 3. The thin arrows are single measurements made underway, and the wide arrows are the average of 24 hours of measurement in one position. It is clear

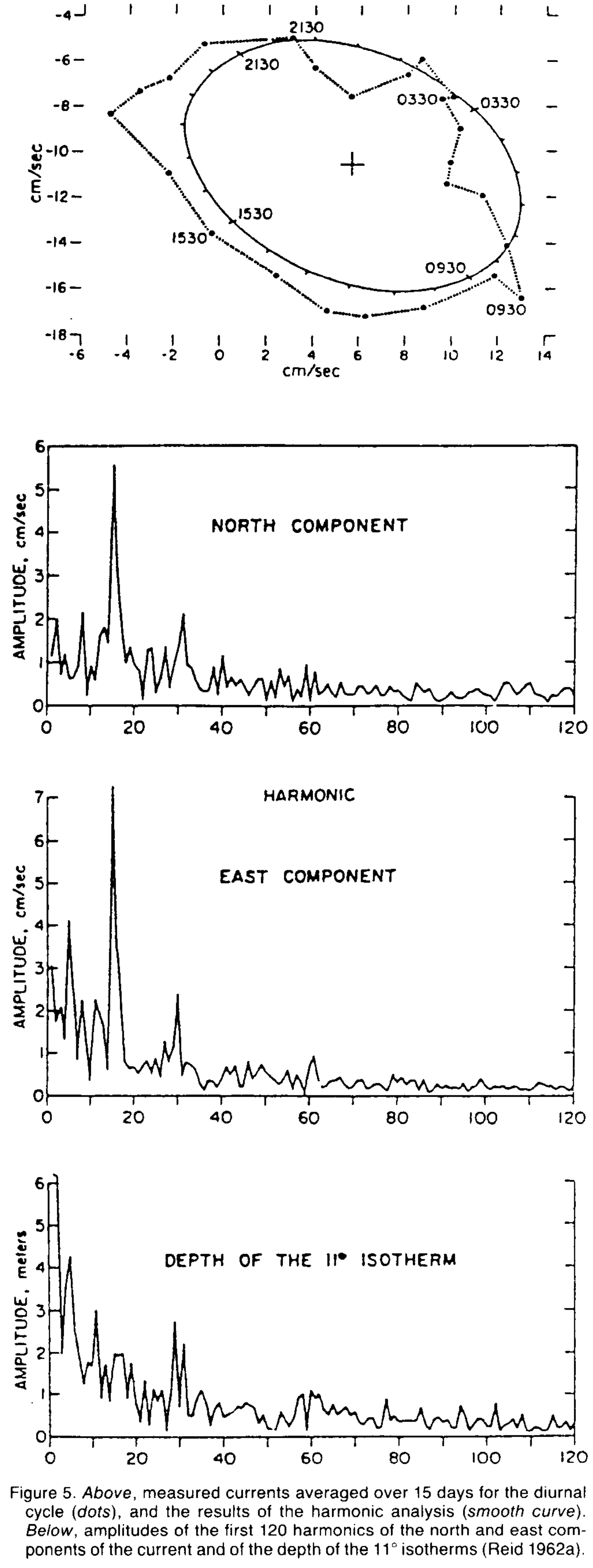

Figure 5. *Above*, measured currents averaged over 15 days for the diurnal cycle (*dots*), and the results of the harmonic analysis (*smooth curve*). *Below*, amplitudes of the first 120 harmonics of the north and east components of the current and of the depth of the 11° isotherms (Reid 1962a).

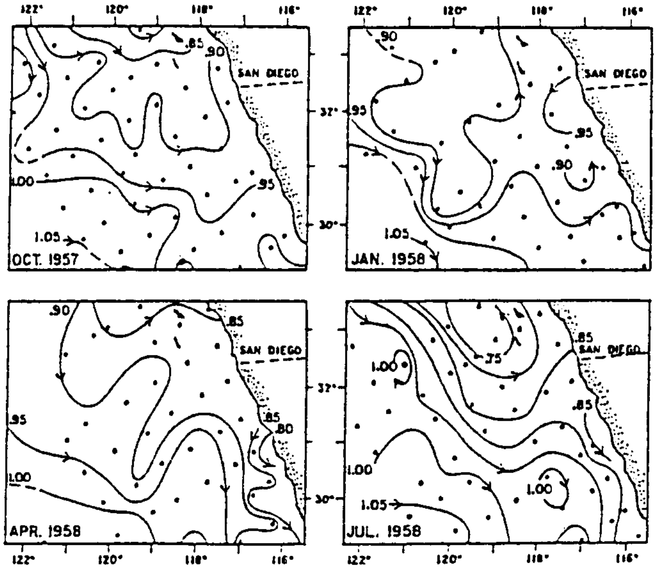

Figure 6. Surface flow (steric height of the sea surface with respect to the 500-decibar surface, in dynamic meters) of the California Current in four seasons (Reid et al. 1963).

that the space and time variations are so large that single measurements made hourly underway do not define the mean large-scale flow.

As a check on the accuracy of the measurements, two series of GEK measurements were made around a drogue (Figure 4). Rather ragged fixes of position were made from bearings taken on Santa Catalina and San Clemente islands, using a magnetic compass on the ship's bridge and a bearing circle on the forecastle. The results seemed to find the GEK a little short, but the diurnal and semidiurnal paths real. GEK measurements were made for 15 days at one position—30°N and well offshore—to investigate the inertial flow, which should have a period of 24 hours there, possibly augmented in amplitude by the tide (Figure 5).

Thus the flow field seemed even more complicated and peculiar than the earlier cruises had indicated. There seemed to be oscillations of semidiurnal and diurnal or inertial periods. Horizontal oscillations were both inertial and semidiurnal inshore but predominantly inertial offshore. Vertical oscillations had already been seen to be predominantly semidiurnal but of lower amplitude offshore than inshore. Wave length could not be established, and series of GEK observations along the tracks of the CalCOFI cruises could not be resolved into a coherent flow pattern. The acoustic Doppler log seems not to have this problem, though it is measuring much the same quantity. I haven't yet worked out why.

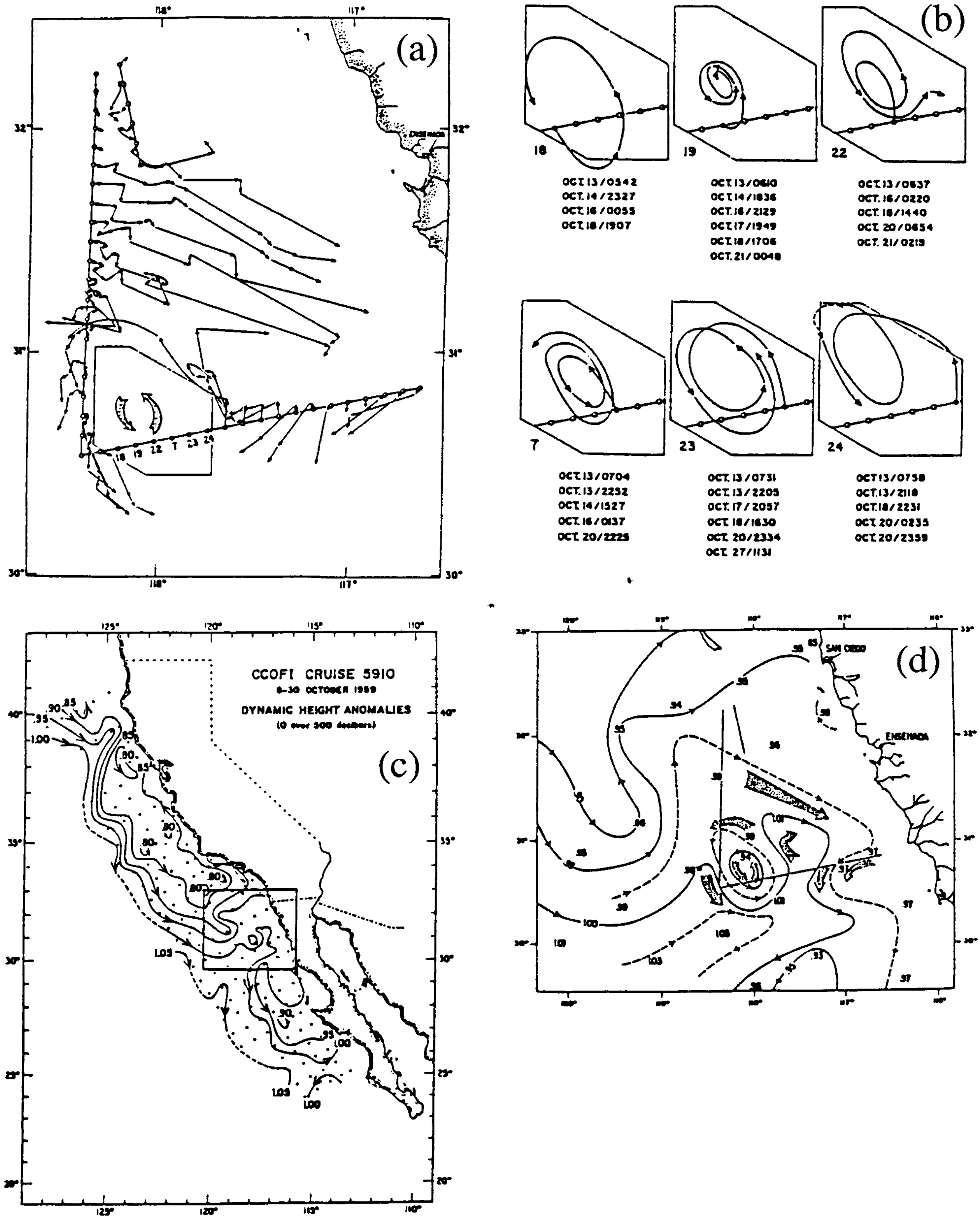

Figure 7. (*a*) Positions of launching (*open circles*) and of subsequent observations (*arrowheads*) of surface drogues in October 1959. The open arrows indicate the general motion of the numbered drogues, given in detail by (*b*). (*b*) Positions of the six drogues launched within the eddy. Circles indicate launching positions (9.3 km apart) and arrowheads indicate subsequent observed positions at the times listed below. (*c*) Surface flow (steric height of the sea surface with respect to the 500-decibar surface, in dynamic meters) in October 1959. The box includes the area of the drogue study. (*d*) The boxed area of (*c*) enlarged, with the drogue movements indicated by open arrows. The value of 0.94 dynamic m within the eddy is at the supplementary station (Reid et al. 1963).

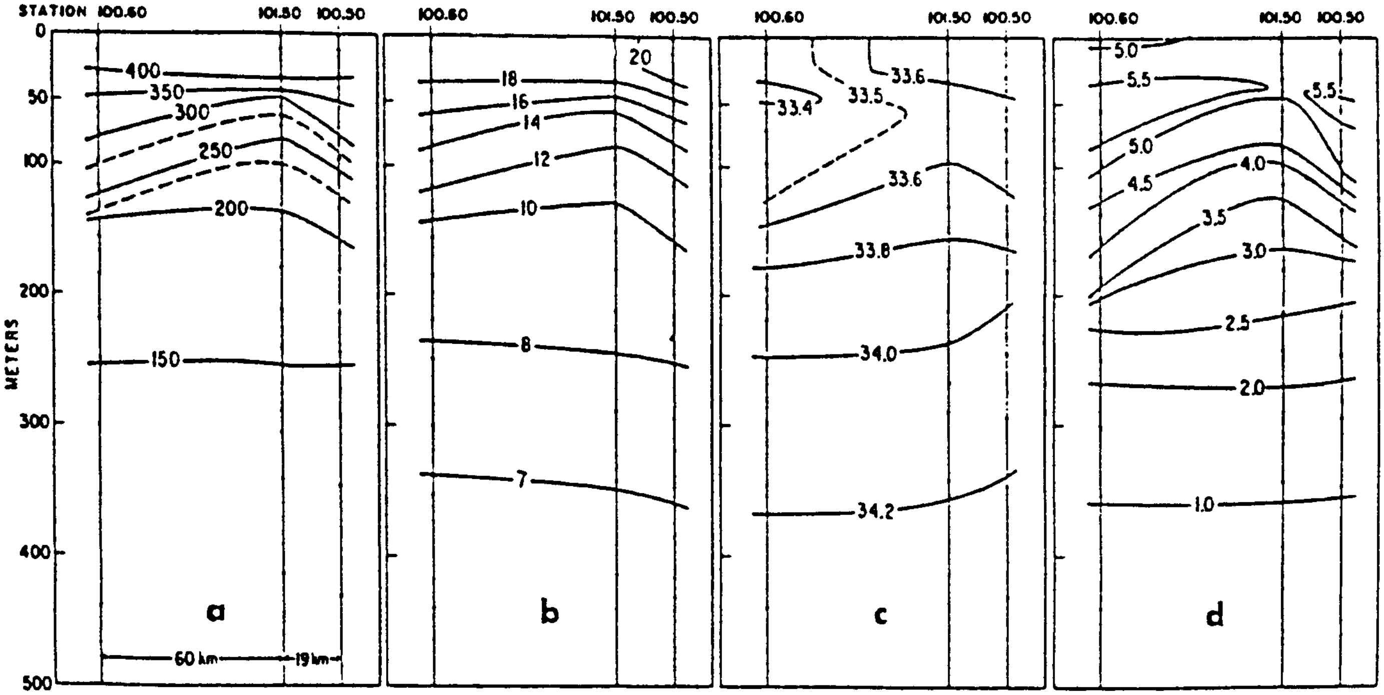

Figure 8. Vertical section across the eddy, including the eddy station and the adjacent inshore and offshore stations, in the upper 500 m. *a*, Thermosteric anomaly in centiliters/ton. *b*, Temperature in degrees Celsius. *c*, Salinity in parts per mile. *d*, Dissolved oxygen content in milliliters per liter (Reid et al. 1963).

To study the eddy features, we carried out quite a number of what would now be called process-oriented cruises, and found the features everywhere we went. In one of our most interesting studies, a set of drogues was laid out and tracked for us by a naval vessel (they were easier to borrow in those happy days). We had noted an inshore turn of the California Current toward Ensenada (Figure 6), as part of the Southern California Eddy, and wished to look at it more closely.

The drogues confirmed the inshore turn, but also found a cyclonic eddy (Figure 7a). Some of the drogues could be followed through several cycles (Figure 7b). We managed to get an extra cast at what seemed to be the center of the eddy (Figure 7c). The geostrophic flow, the general path of the drogues, and the eddy, which had a magnitude of about 5 dynamic centimeters, are shown together in Figure 7d. It is curious that there was no surface manifestation. There was no interruption in mixed-layer depth, and no outcropping of denser, colder water (Figure 8). All the shear associated with the flow of the eddy took place below the mixed layer. Satellite thermal sensors would have found no signal.

In that distant past the gear was primitive and the work both difficult and expensive, but we seemed to find eddylike surface flow wherever we followed drogues (Figure 9).

The first general study of the CalCOFI physical, chemical, and biological data (Reid et al. 1958) began with the best wind data available at the time (Figure 10), and the surface and subsurface flow as given by the relative geostrophic flow, and tried to relate the zooplankton volume to the nutrients (Figure 11), and delineate the boundaries of various species of zooplankton.

One of the purposes of CalCOFI was to observe and account for year-to-year variations. Although there had been very large variations observed in the years before 1950, it was hard to see a strong interannual signal in the early years, which seemed much the same—slightly colder than the long-term mean, with some suggestion of warming in the first half of 1957 (Figure 12). It had been eight soggy years, frustrating to contemplate. While surface temperatures from years before CalCOFI showed some strong anomalies, the 1949 through 1956 differences were small. In the first half of 1957 temperatures were higher, but not enough to make a case for strong interannual variation. Some correspondence between variations of zooplankton abundance and temperature could be detected, though not yet enough to be conclusive (Figure 13).

These cruises began to give us more information about the density field, the geostrophic shear, salinity, phosphate, and zooplankton volume within

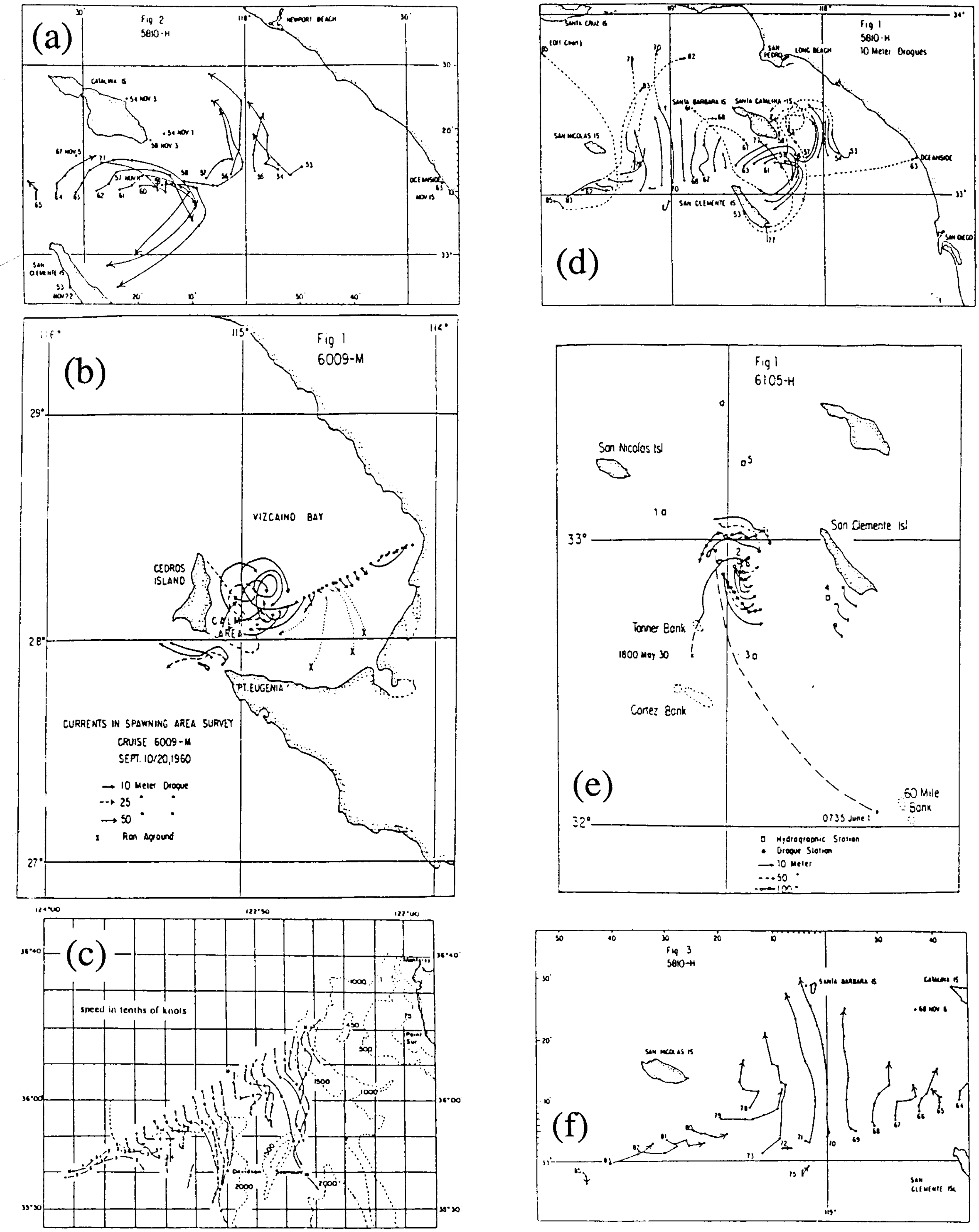

Figure 9. (*a*) Eastern part of the October 23–27, 1958, deployment (SIO 1962). (*b*) Drift of parachute drogues at 10 m on September 10–20, 1960 (SIO 1962). (*c*) Drift of parachute drogues at 10 m, March 23–26, 1958 (Jennings and Schwartzlose 1960). (*d*) Drift of parachute drogues at 10 m, October 23–27, 1958 (SIO 1962). (*e*) Drift of parachute drogues, June 1, 1961 (SIO 1962). (*f*) Western part of the October 23–27, 1958, deployment (SIO 1962).

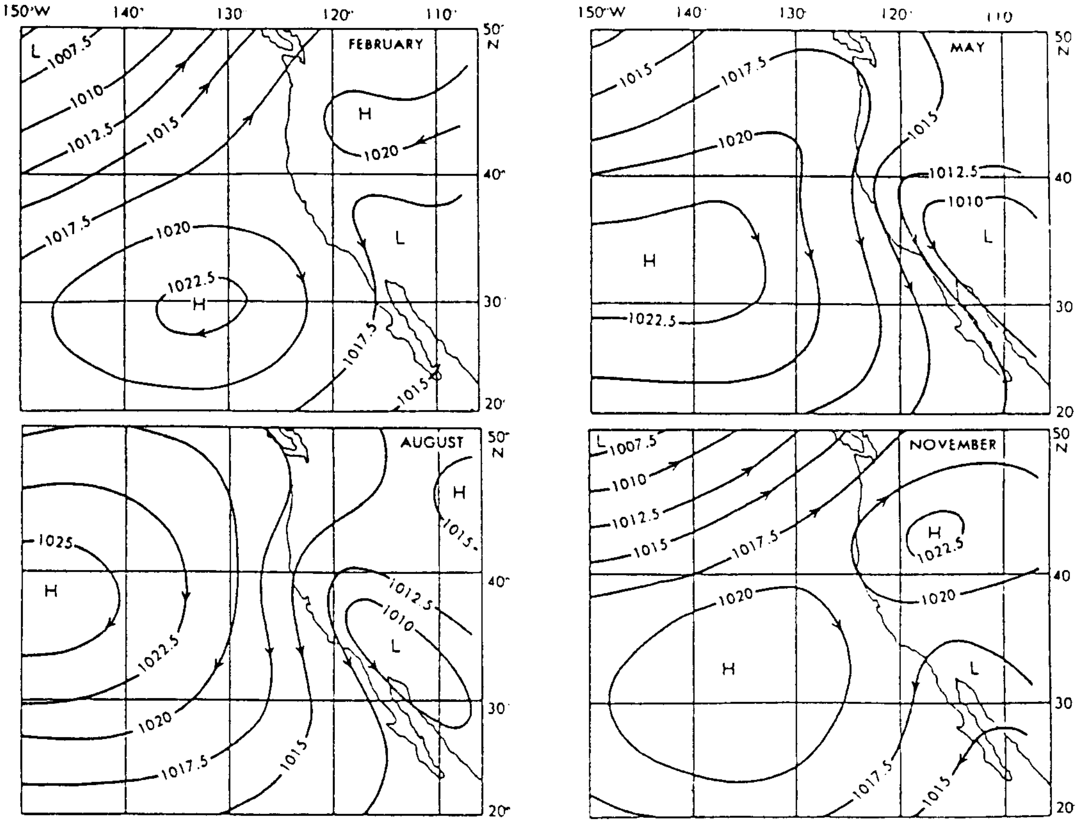

Figure 10. Average monthly atmospheric sea-level pressure (in millibars) over the eastern North Pacific Ocean and the western coast of North America during four months of the year (Reid et al. 1958).

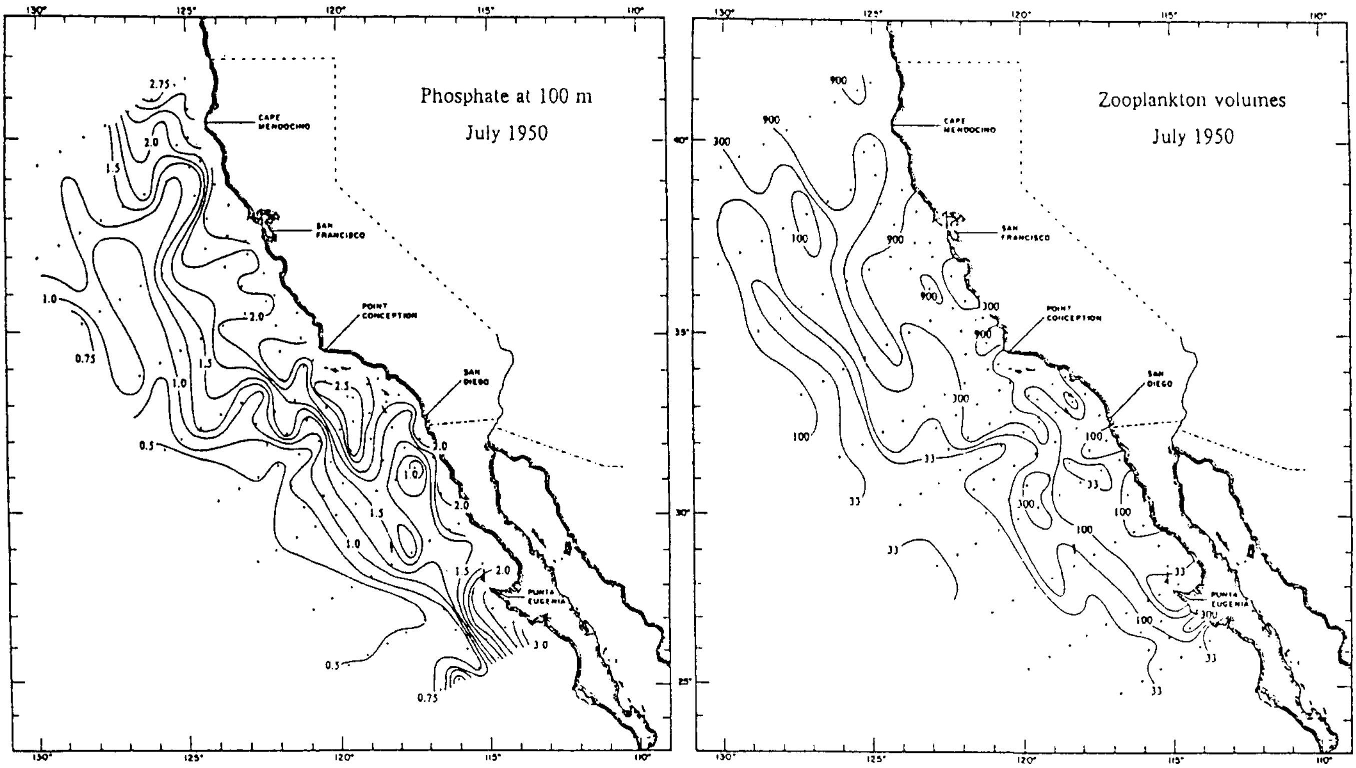

Figure 11. Distribution of phosphate-phosphorus (microgram-atoms per liter at 100 m) and zooplankton volumes (cubic cm per 1000 cubic m) in July 1950 (Reid et al. 1958).

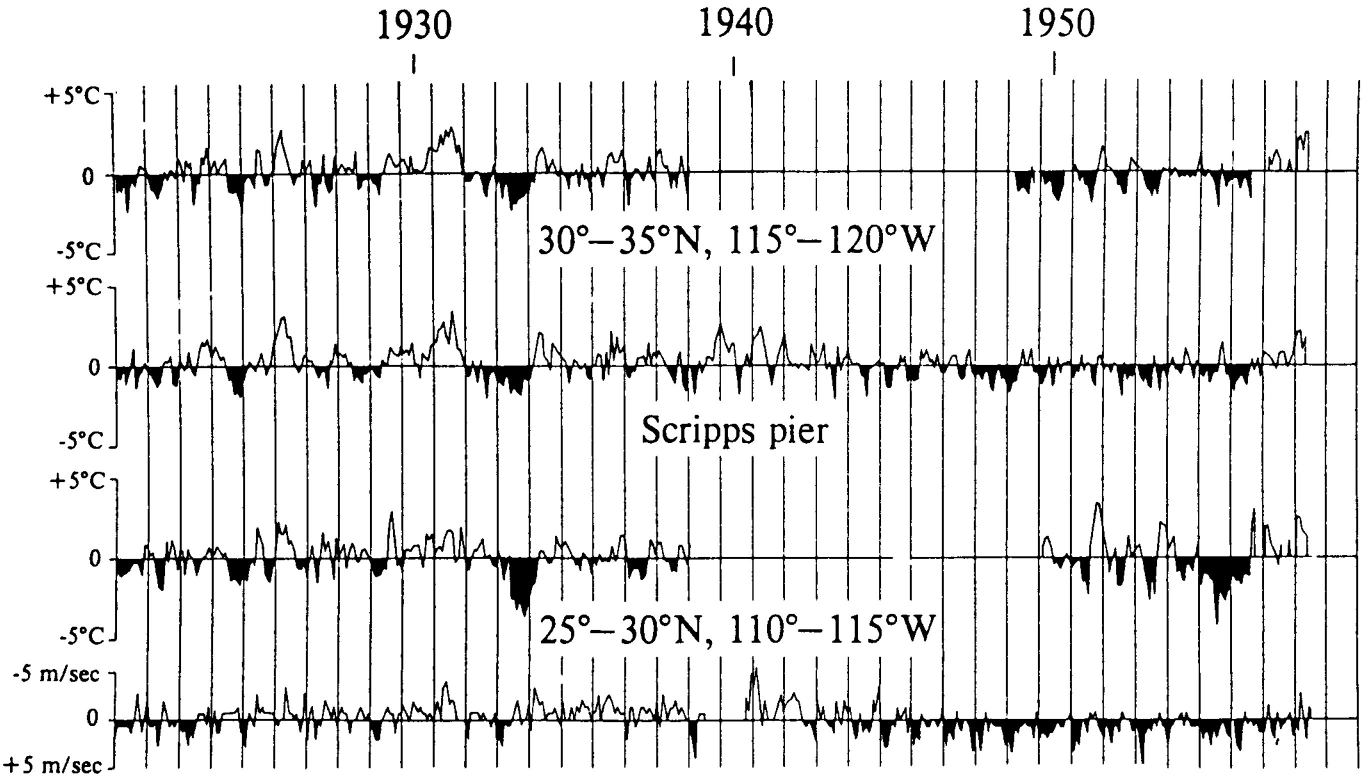

Figure 12. Monthly differences from average sea-surface temperatures (degrees C) at 30°–35°N, 115°–120°W; Scripps Pier; and 25°–30°N, 110°–115°W. *Bottom line*, monthly differences from average northerly wind component at 30°N, 110°–130°W. The period 1921–38 was taken as the average (Reid 1960).

the California Current. All of these were interesting and informative in themselves. But they seemed to suggest relations between these fields that could be examined more effectively if data could be collected over a larger area. We found there was enough interest in the field, and enough resources to carry out, at least once, a coverage of much of the North Pacific Ocean.

With ships and parties from CalCOFI, the University of Washington, the Canadian Pacific Oceanographic Group, the Pacific Oceanographic Fisheries Investigations in Hawaii, and many universities and government agencies from Japan, the entire area north of 20°N was covered in July–September 1955, and the geostrophic flow at the surface relative to 1000 decibars could be mapped for the North Pacific (Figure 14).

Later in the year the Eastropic Expedition added the area east of 140° between 20°N and 20°S, and in the summer of 1956 another expedition involving the United States, Japan, and France extended the tropical work westward to the Philippine Islands. With these background data, many of the relations between nutrients, circulation, and zooplankton seemed much better established throughout the Pacific (Figure 15).

As more data became available, numerous studies were carried out on the flow (Schwartzlose 1963; Wyllie 1966; Brown 1974; Hickey 1979; Chelton 1980; Gomez-Valdez 1984); on the seasonal variation of flow and characteristics (Roden 1961; Anonymous 1963; Lynn 1967; Pavlova 1966; Kindyushev 1970; Wyllie and Lynn 1971; Eber 1977;

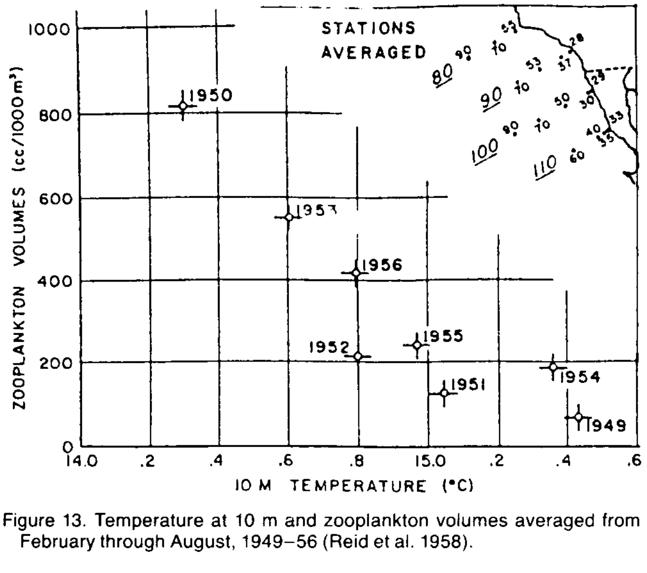

Figure 13. Temperature at 10 m and zooplankton volumes averaged from February through August, 1949–56 (Reid et al. 1958).

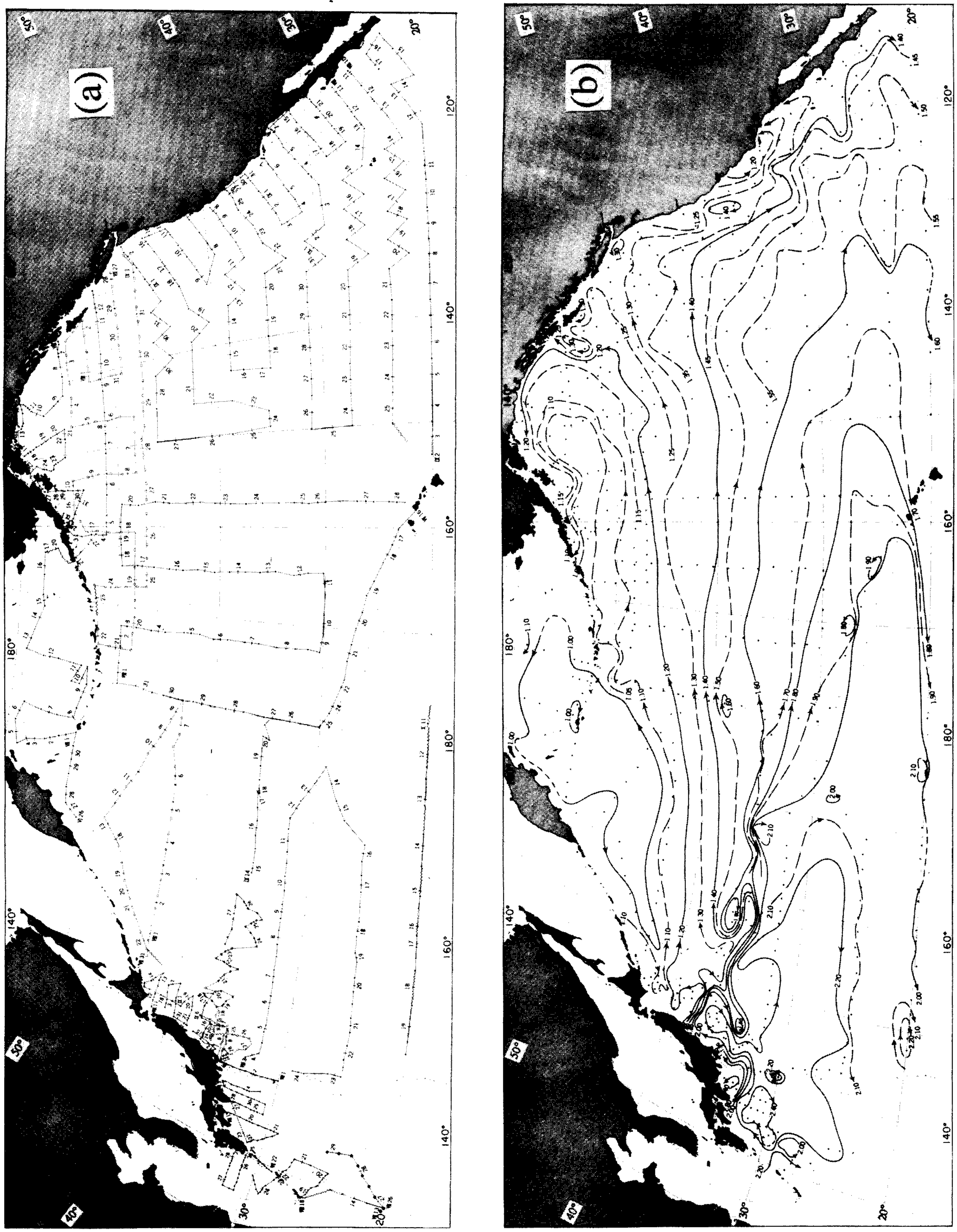

Figure 14. (*a*) NORPAC Expedition track, July–September 1955. (*b*) Steric height at the sea surface relative to 1000 decibars (NORPAC Committee 1960).

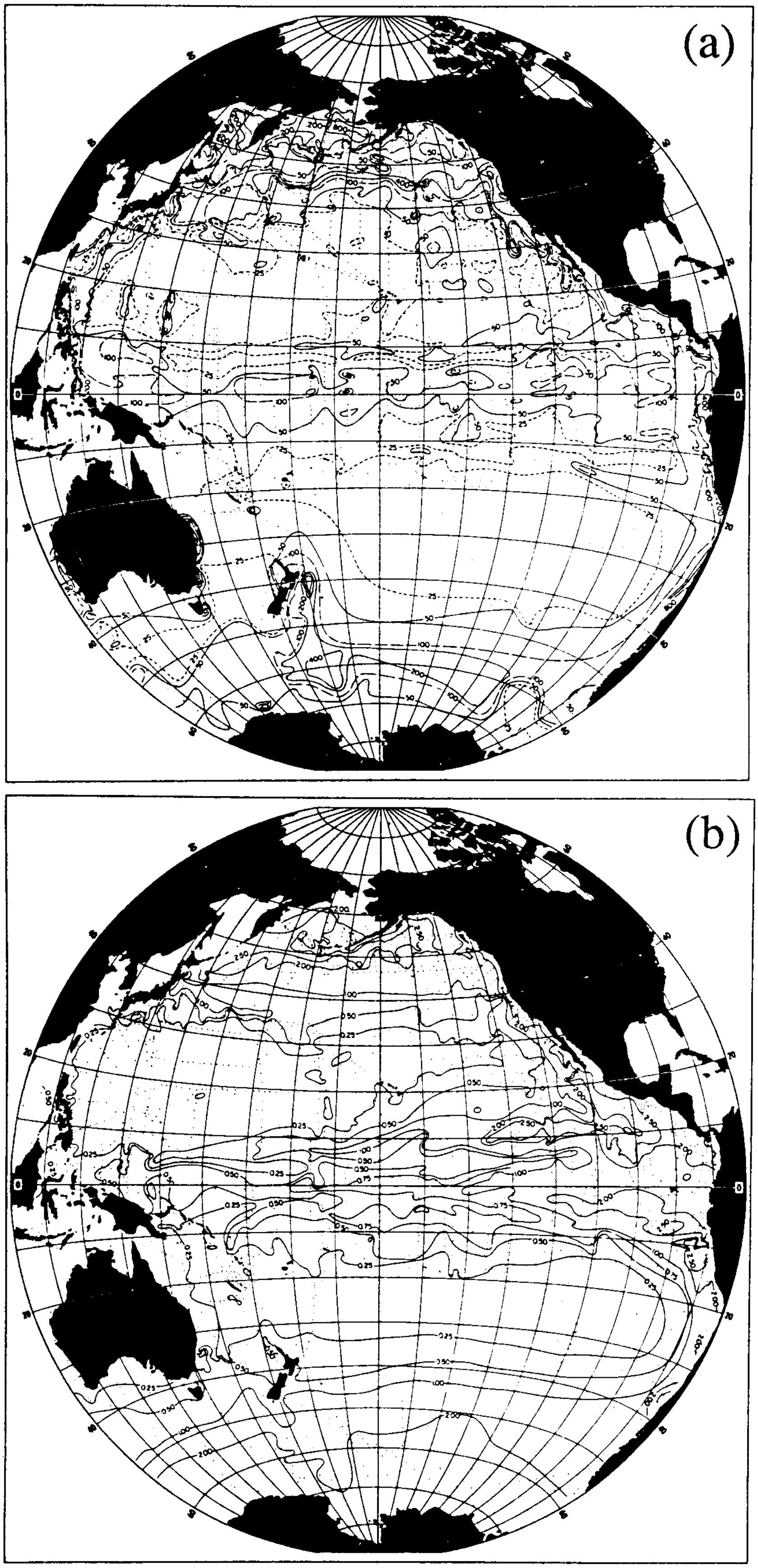

Figure 15. (*a*) Distribution of zooplankton volume (parts per 10^9 by volume) in approximately the upper 150 m of the Pacific Ocean. (*b*) Distribution of PO_4-P at a depth of 100 m in the Pacific Ocean (μg-at./l) (Reid 1962b).

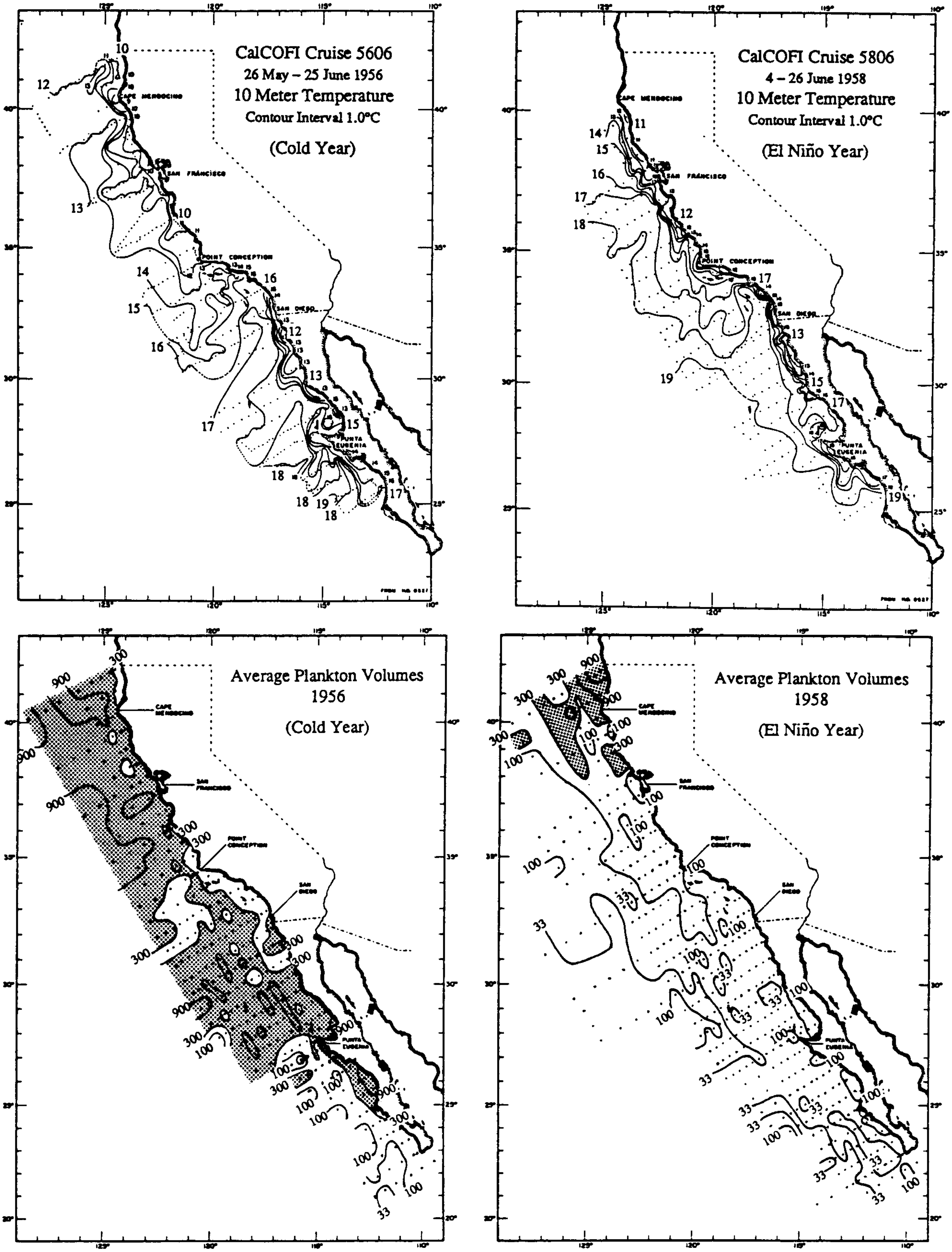

Figure 16. *Top*, Ten-meter temperature in June of a cold year (1956; cruise 5606) and in June of a warm, El Niño year (1958; cruise 5806) (Anonymous 1963). *Bottom*, Zooplankton volumes during a cold year (1956) and the warm, El Niño year (1958) (Reid 1962b).

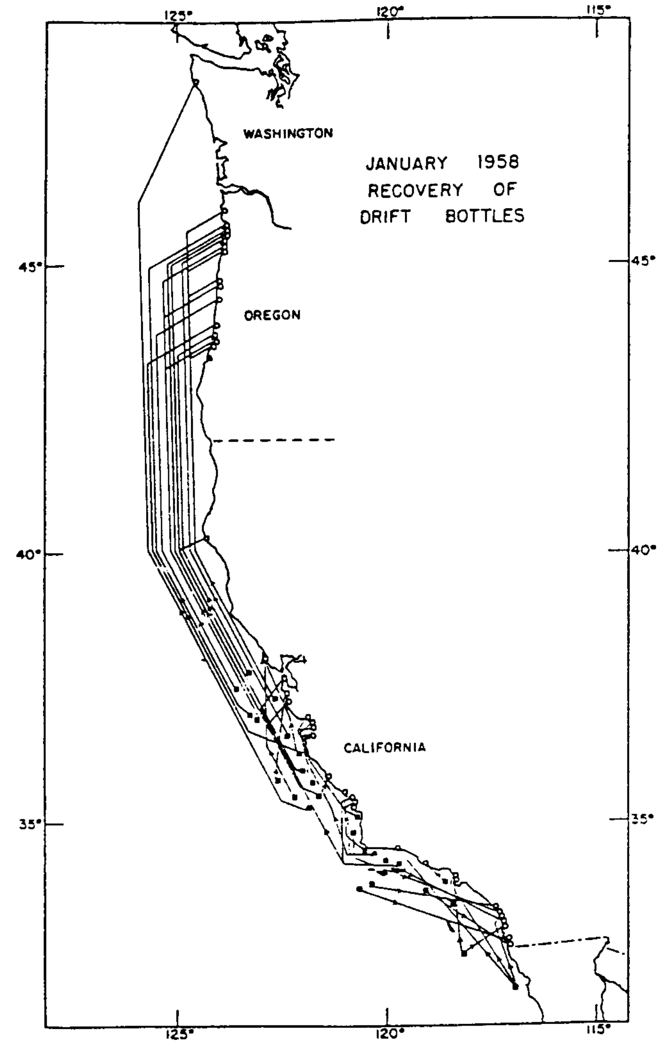

Figure 17. Recoveries of some drift bottles released in January 1958. Black squares show the release points; circles show the recovery points (Crowe and Schwartzlose 1972).

Alvarez-Borrego and Schwartzlose 1979; Lynn et al. 1982); on the heat and salt balance (Roden 1959); and on the deep characteristics (Mantyla 1969). Burkov and Pavlova (1980) described the eddy field. Coastal elevations of the sea surface were discussed by Roden (1960), Sturges (1967), Reid and Mantyla (1976), Enfield and Allen (1983), and Hickey (1984). Early theoretical studies included those by Arthur (1965), Behringer (1972), and Muraki (1974). Larger-area studies were carried out by Wooster and Reid (1963), Wyrtki (1965, 1975), Robinson (1976), and Reid et al. (1978).

EL NIÑO

By the end of 1957, the warming of the California Current had continued, and similar warming signals were being reported from all of the areas of the eastern and equatorial Pacific, wherever measurements were being made.

In particular, in the CalCOFI data, we noted such things as a continued warming of the coastal waters, beyond the slight warming reported in 1957 and extending over the whole area, with a decrease in zooplankton volume (Figure 16). The tentative relation seen through 1956 (Figure 13) held up in the later years. Drift bottles were found much farther north from the January 1958 release (Figure 17). The temperature anomaly was even greater at thermocline depth than at the surface (Figure 18). The ordinary seasonal variation noted in all years (Figure 19) shows values of dynamic height higher in January than July, decreasing monotonically offshore, but the interannual variation in the 1958 El Niño showed higher values inshore and offshore, with a long, narrow trough of low values in the middle (Figures 20a–c). This meant that during El Niño there was more northward flow inshore, as expected, but also more southward flow offshore. Temperature and salinity anomalies were high inshore, dropping offshore.

We tried to account for these variations in terms of the wind system. Previous El Niño events and anti-El Niño events had been accompanied by shifts in the winds, as in 1931, when temperatures were high in the northeastern Pacific, with an anomalously high wind from the south, and in 1933, when low temperatures seemed to follow from a stronger-than-normal wind from the northwest (Figure 21). Gunnar Roden and I tried to pursue this further, by relating temperature off southern California to a wind index across 30°N (Figure 22). But it didn't work out with the wind data we had, or the simple concept we tried.

The El Niño events during the CalCOFI period have been as extreme as any in the longer-term record, but we have not yet found anything as cold as the 1917, 1921, and 1933 record. We still have something to look forward to.

The data were such that a CalCOFI symposium was held in June 1959, attended by—among others—Jule Charny as chairman, and Nick Fofonoff, Elton Sette, Carl Eckart, Fritz Fuglister, John Isaacs, John Marr, Walter Munk, Jerome Namias, Roger Revelle, Benny Schaefer, Henry Stommel, Frances Clark, and Ahlie Ahlstrom.

I quote from John Isaacs's introduction to *CalCOFI Report VII* (1960)

> By the fall of 1957, the coral ring of Canton Island, in memory of man ever bleak and dry, was lush with the seedlings of countless tropical trees and vines.

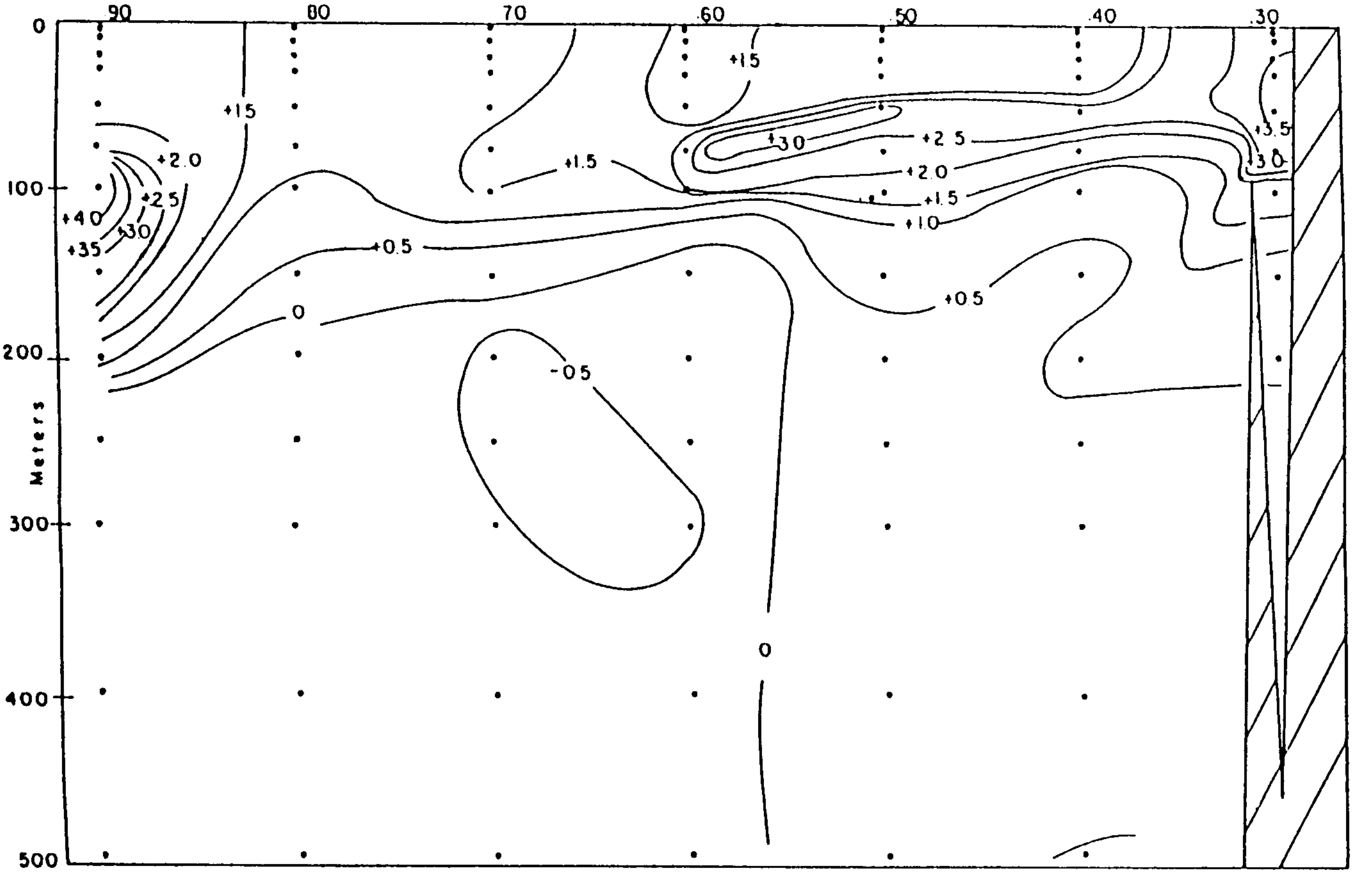

Figure 18. Temperature anomaly on a vertical section extending 250 miles offshore. The values are those measured in January 1958 minus the CalCOFI mean (Reid 1960).

Two remarkable and unprecedented events gave rise to this transformation, for during 1957 great rafts of sea-borne seeds and heavy rains had visited her barren shores.

One is inclined to select the events of this isolated atoll as epitomizing the year, for even here, on the remote edges of the Pacific, vast concerted shifts in the oceans and atmosphere had wrought dramatic change.

Elsewhere about the Pacific it also was common knowledge that the year had been one of extraordinary climatic events. Hawaii had its first recorded typhoon; the seabird-killing *El Niño* visited the Peruvian coast; the ice went out of Point Barrow at the earliest time in history; and on the Pacific's Western rim, the tropical rainy season lingered six weeks beyond its appointed term.

The 1957–58 El Niño had a tremendous impact on both oceanography and meteorology. The data off California made available by CalCOFI, and the data assembled from other areas made it possible to consider in a useful manner the relation between winds, current, temperature, nutrients, and biomass. In particular, the meteorologists began to

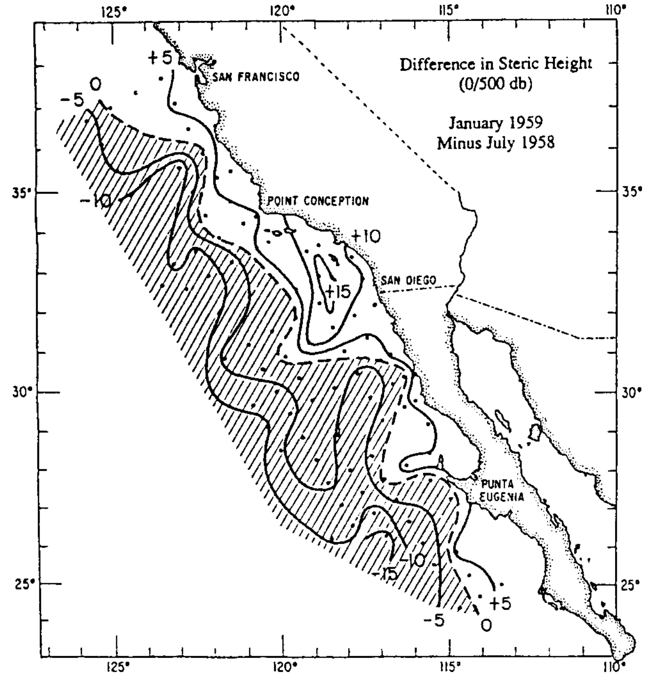

Figure 19. Seasonal difference in steric height, January 1959 minus July 1958. Shaded area indicates negative values (Lynn and Reid 1975).

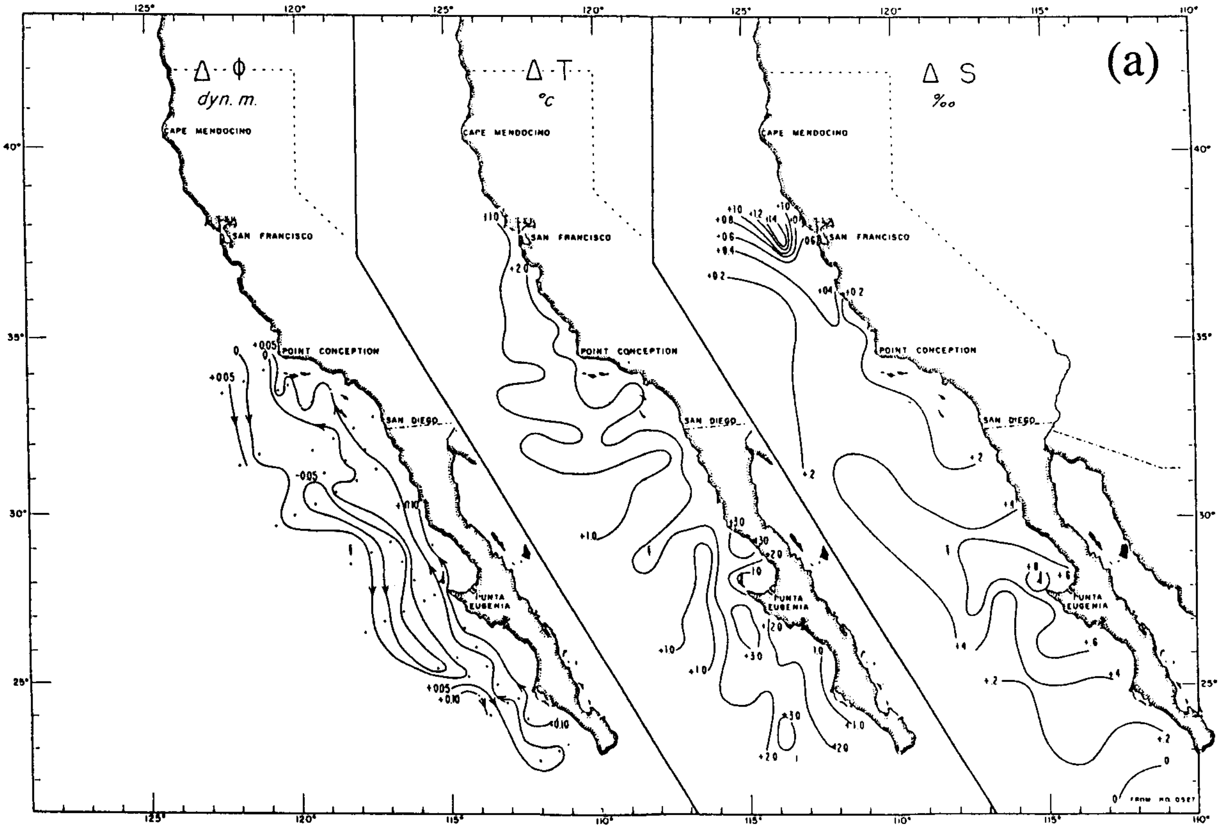

Figure 20a. January 1958 Φ, T, and S anomalies (ΔT and ΔS refer to 1949–54 mean; ΔΦ refers to 1953 only) (Reid 1959).

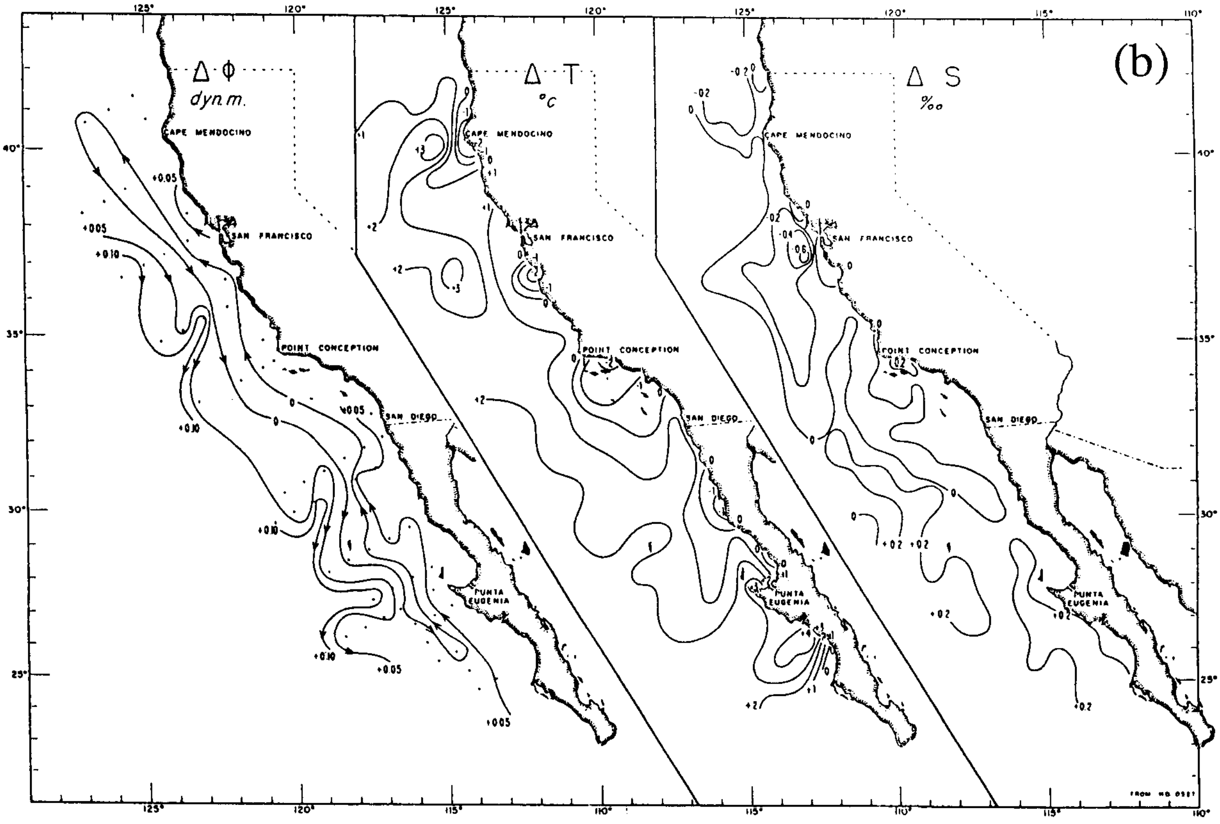

Figure 20b. July 1958 Φ, T, and S anomalies (ΔT and ΔS refer to 1949–54 mean; ΔΦ refers to 1952 only) (Reid 1959).

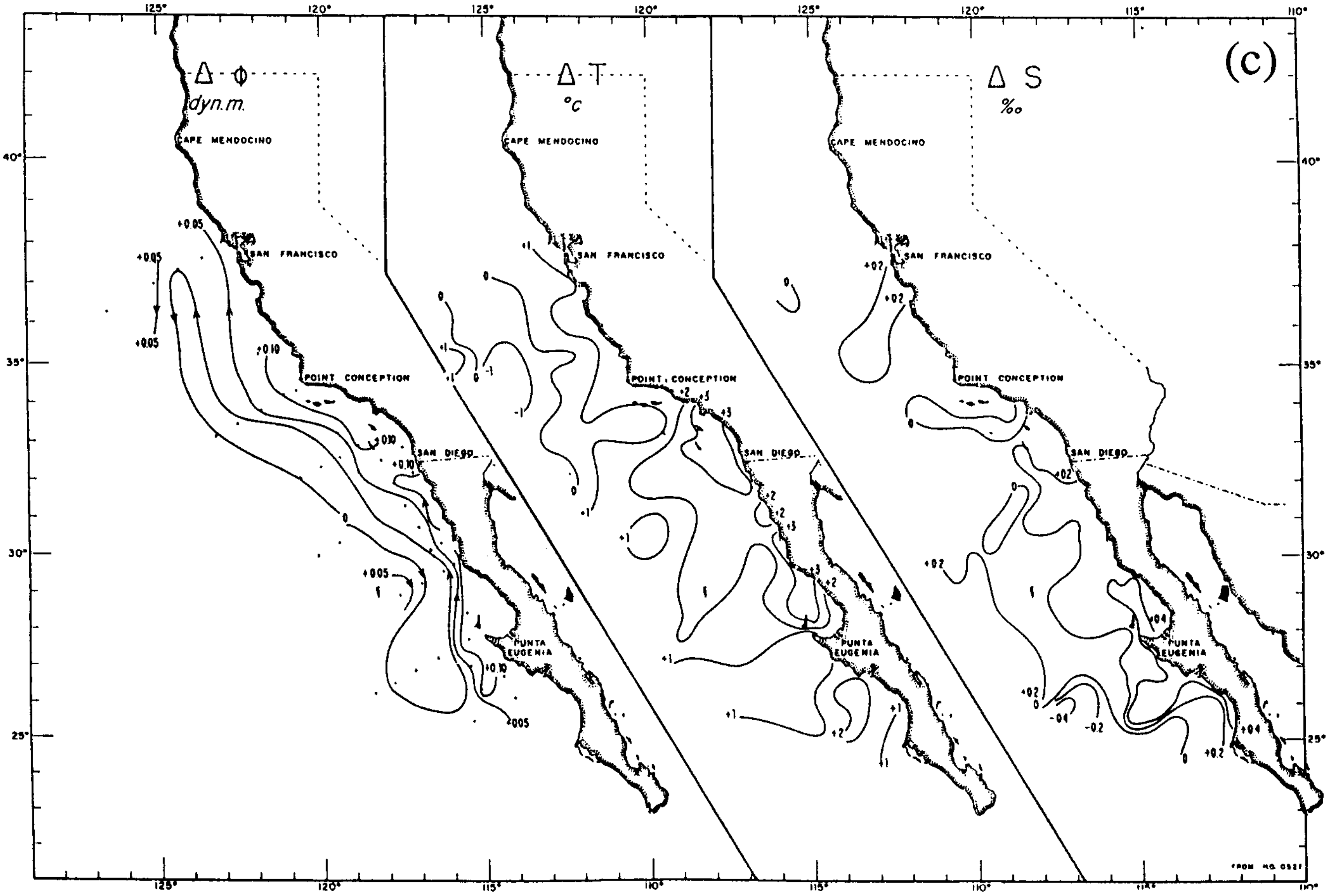

Figure 20c. October 1958 Φ, T, and S anomalies (ΔT and ΔS refer to 1952 only) (Reid 1959).

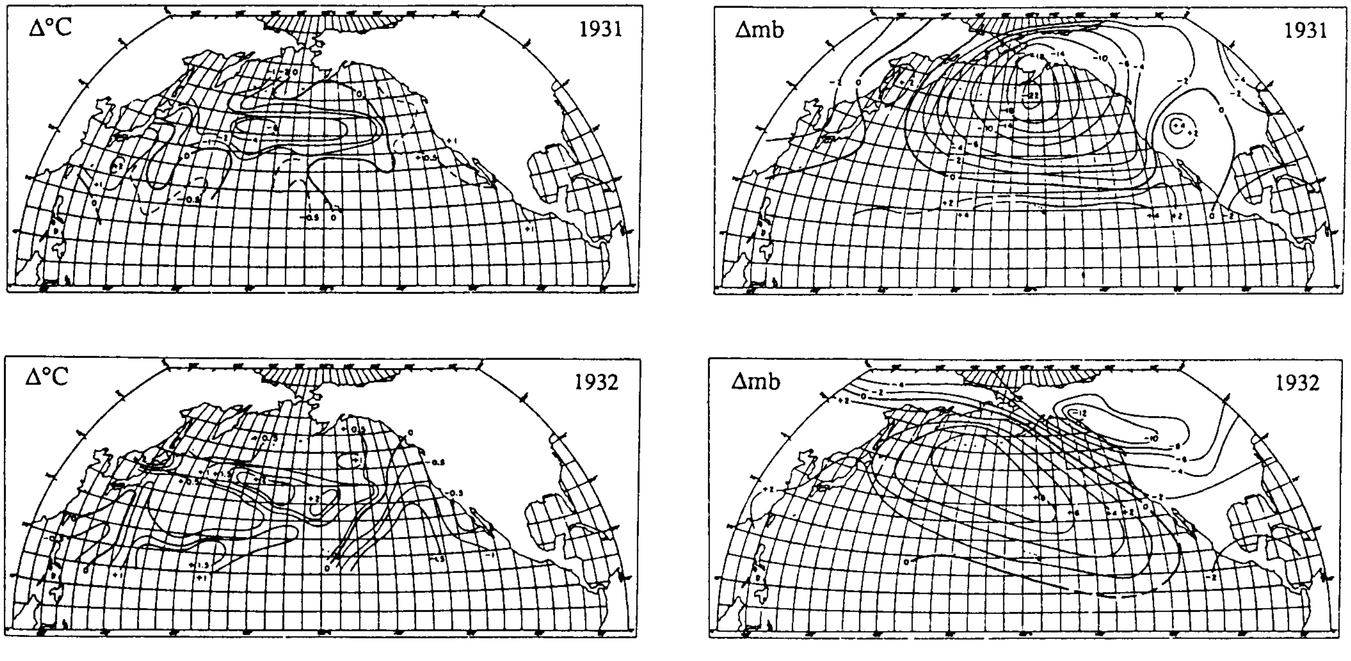

Figure 21. Anomalies of sea-surface temperature (*left*) and atmospheric pressure (*right*) in January of a warm year and a cold year (Reid 1960).

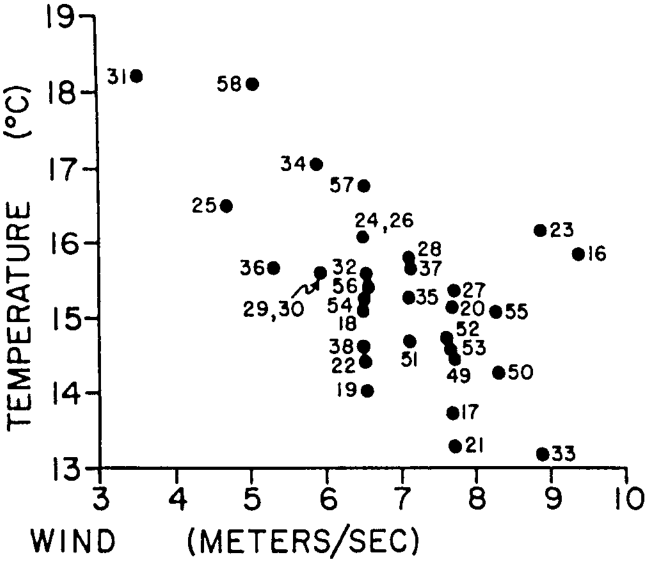

Figure 22. May temperature, 30°–35°N, 115°–120°W, and wind at 30°N, 1916–38, 1949–58 (Reid 1960).

use the increasing information about ocean temperatures in predicting weather and trying to understand climate. I might say that neither oceanography nor long-range weather prediction has ever been the same.

It is also noteworthy that some of the Atlantic people were reluctant to accept these phenomena in the Pacific as real. This was partly because the Atlantic, for reasons we don't know, does not have large-scale year-to-year variations of the magnitude we see in the Pacific. But it may be simply that they didn't like oceans to behave that way, when the large-scale variations were harder to model, any more than they liked our eddies at that time. But 30 years later the large variations in the upper layer are found to be easier to model than the general circulation itself, and we have dozens of modelers, even from the Atlantic, trying to account for Pacific El Niño events.

AFTER EL NIÑO

In the 30 years since the 1957–58 El Niño, a great deal of change and improvement has occurred in instrumentation. Drogues and drifters are no longer tortuously tracked by ships, but by satellites (Figure 23). Analysis of variations in the flow of the California Current can be carried out far more elegantly with the larger series of data and modern computers.

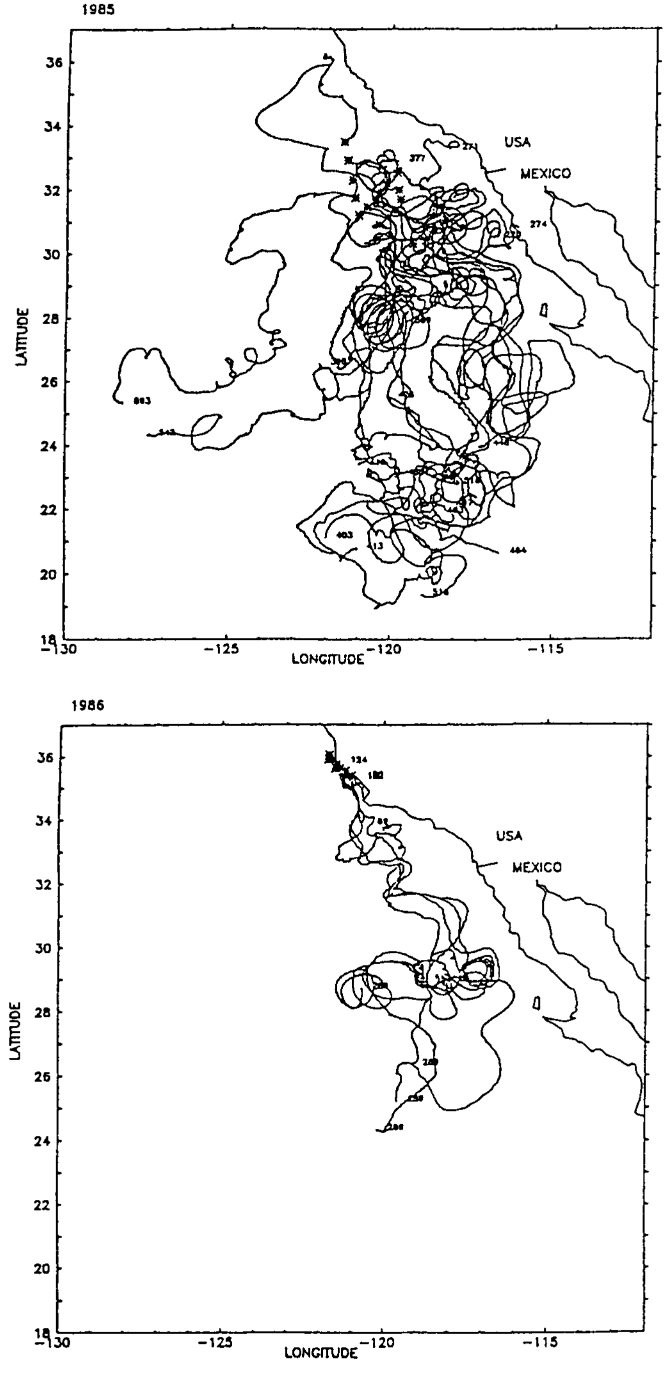

Figure 23. Drogue trajectories, 1985 (*top*), and 1986 (*bottom*) (Poulain et al. 1987).

The early studies of seasonal variation (Anonymous 1963; Wyllie 1966; Wyllie and Lynn 1971; Reid 1959) are seen to be statistically justified, and El Niño differences, with a long, narrow trough in the center of the pattern (Figure 20; and Lynn and Reid 1975) are revealed much more clearly and securely by the longer time series (Figure 24).

The zooplankton-temperature relation has been extended and related to circulation (Figure 25). Surface measurements have been improved and can be made continuously from vessels underway

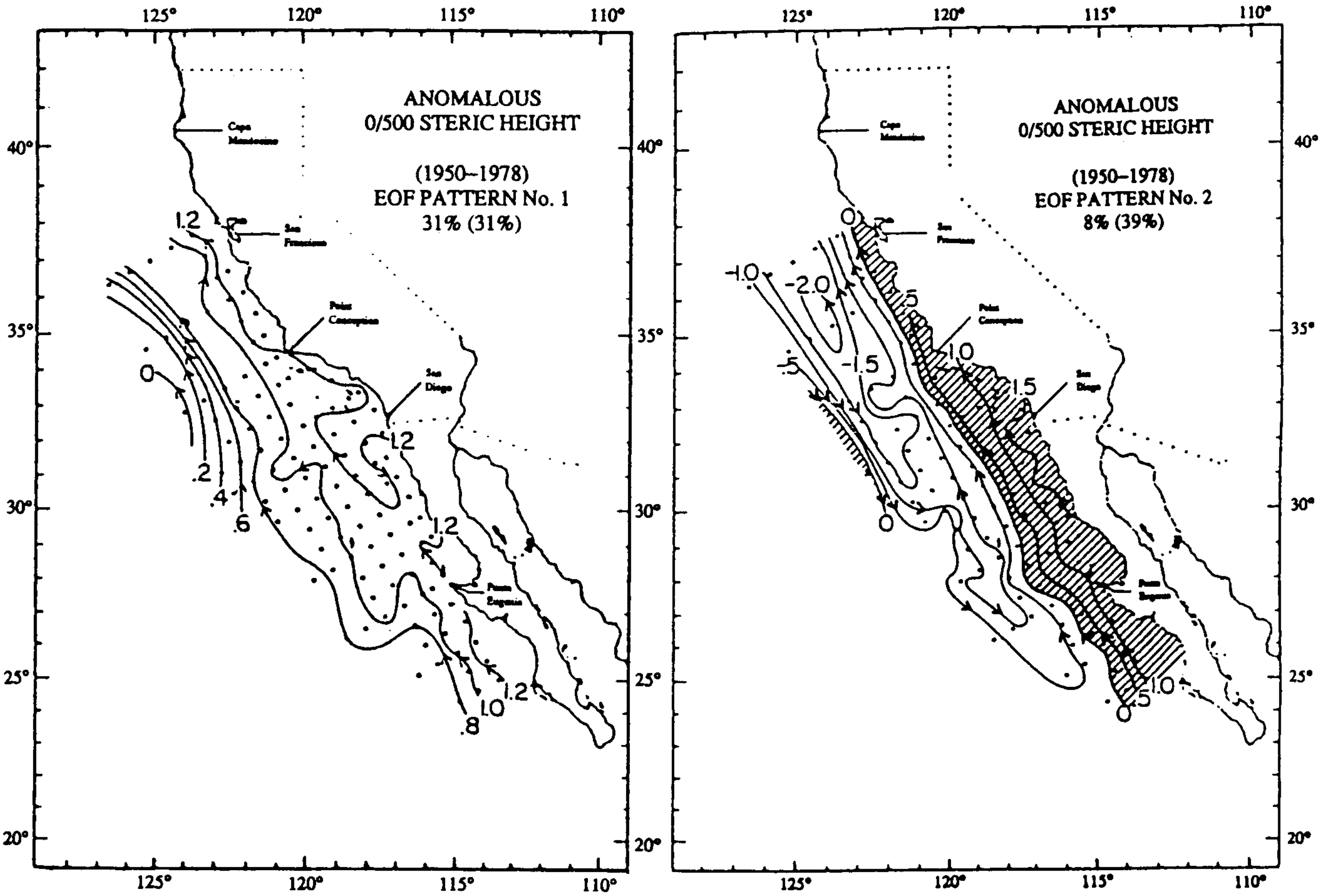

Figure 24. Anomalous 0/500 steric height, 1950–78: *left*, EOF pattern no. 1; *right*, EOF pattern no. 2 (Chelton 1980).

(Figure 26), providing tighter coverage and greater detail, and satellite measurements extend a tight coverage for surface chlorophyll to larger areas where it can be seen to correspond in some cases to the circulation at the surface (Figure 27). In particular, the frontal feature at the latitude of Ensenada that had been seen in the earlier flow pattern (Figure 6) is seen here in chlorophyll.

Variability has been shown to occur over a wide range of time and space scales, and we should not lose track of them. But I do not see how these phenomena can be examined usefully without considering also the background ocean upon which they are imposed. The real question is, How does the whole system operate; how is the biomass sustained in such a varying system?

John Hunter tells me that off southern California alone, each year the mackerel eat as much as 350,000 tons of anchovies, and the anchovies eat about 30 million tons of copepods. How many tons of smaller forms have those 30 million tons of copepods eaten?

And Alec MacCall estimates that 200 years ago, before the millions of seals and sea otters were killed off by the fur hunters, they must have taken an enormous biomass each year to sustain themselves. How were the nekton and plankton arrayed in the great web then?

These are some of the findings from the CalCOFI program. Other programs, such as NORPAX, CUEA, CODE, and various others have followed, pursuing in greater detail and with greater facilities and work force some of the same sorts of studies. But CalCOFI has been, and is still, the only program that has really been interdisciplinary. What have we done, and what have we done wrong? We have the greatest, and the most complete, array of ecological data ever assembled over such a large ocean area.

The most important question is, what should we do now? Should we maintain our present schedule of monitoring cruises and process-oriented cruises? Or divert to an entirely different sort of study? What should be added that can be added to

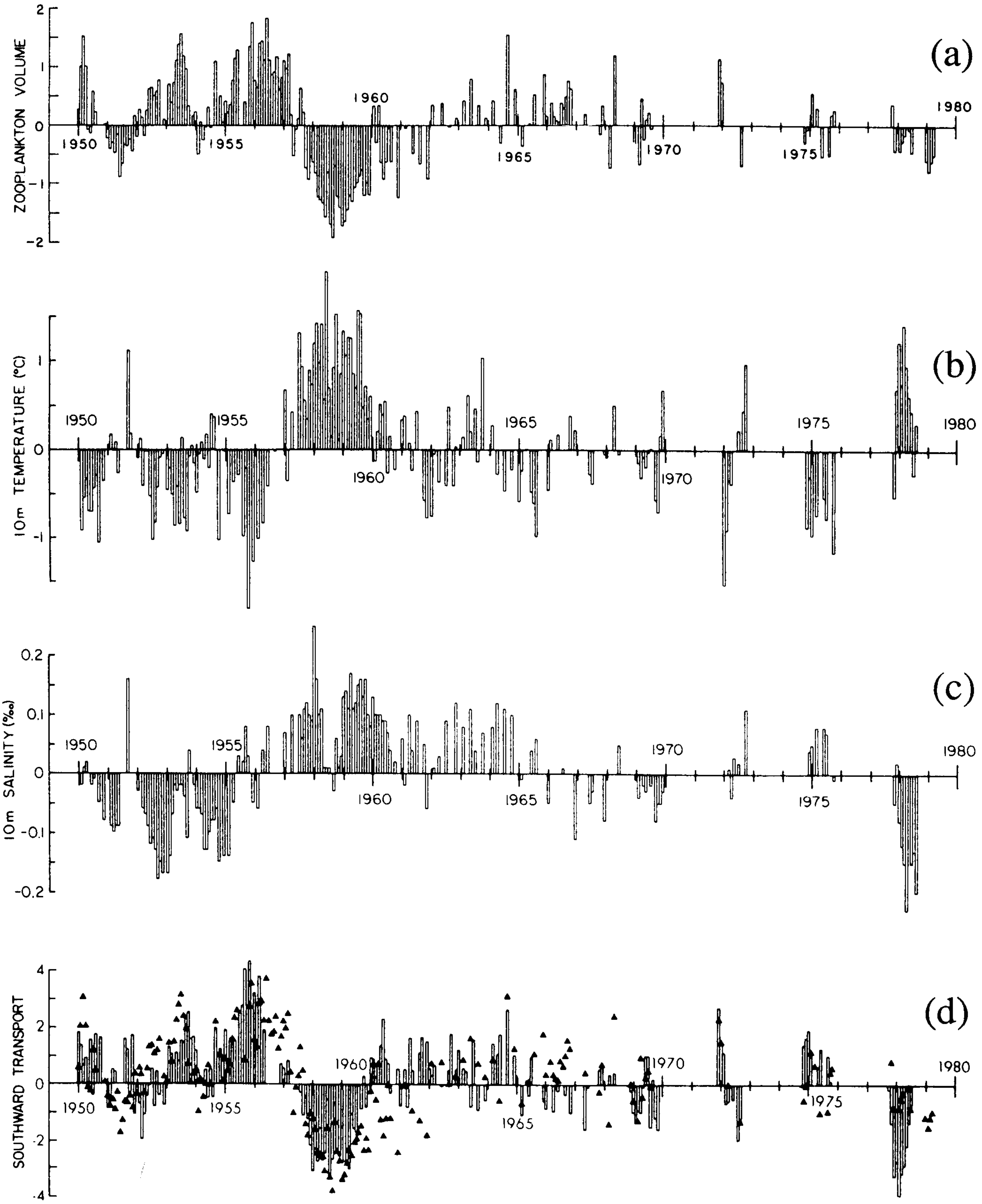

Figure 25. Time series of nonseasonal values of four parameters in the California Current: (*a*) the average of the individual zooplankton time series; (*b*) the average 10-m temperature over 150 hydrographic stations; (*c*) the average 10-m salinity over 150 hydrographic stations; (*d*) the amplitude time series of the principal EOF of 0/500 steric height. Triangles in (*d*) represent the zooplankton time series shown in (*a*) (Chelton et al. 1982).

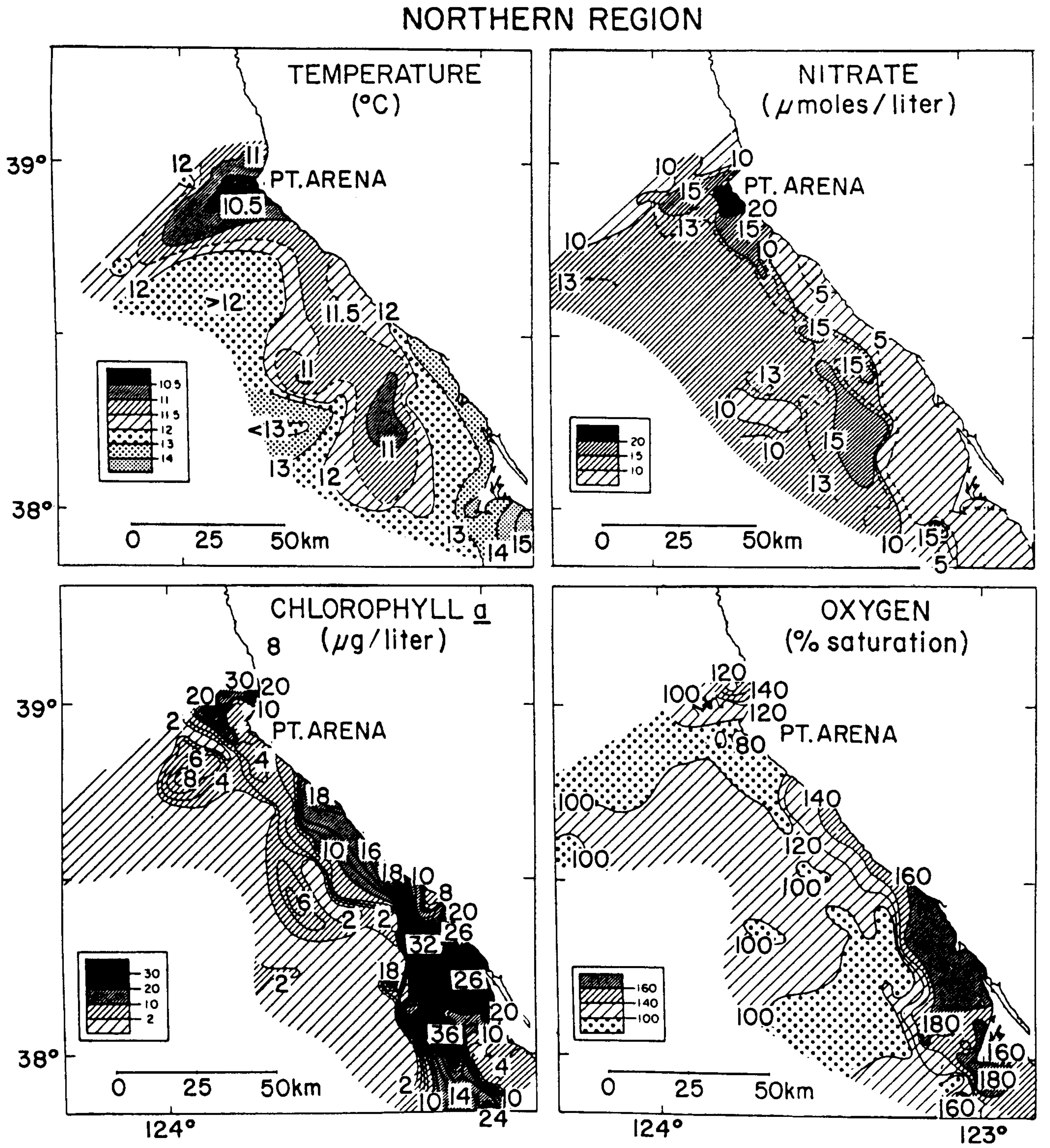

Figure 26. Northern region temperature, nitrate, chlorophyll-a, and oxygen (Simpson 1985).

our investigations? When will the technology be developed to allow us to deal with phytoplankton? Our problems, and these questions, are not unique to the CalCOFI program, but to any investigations of marine ecology. Please give us your thoughts.

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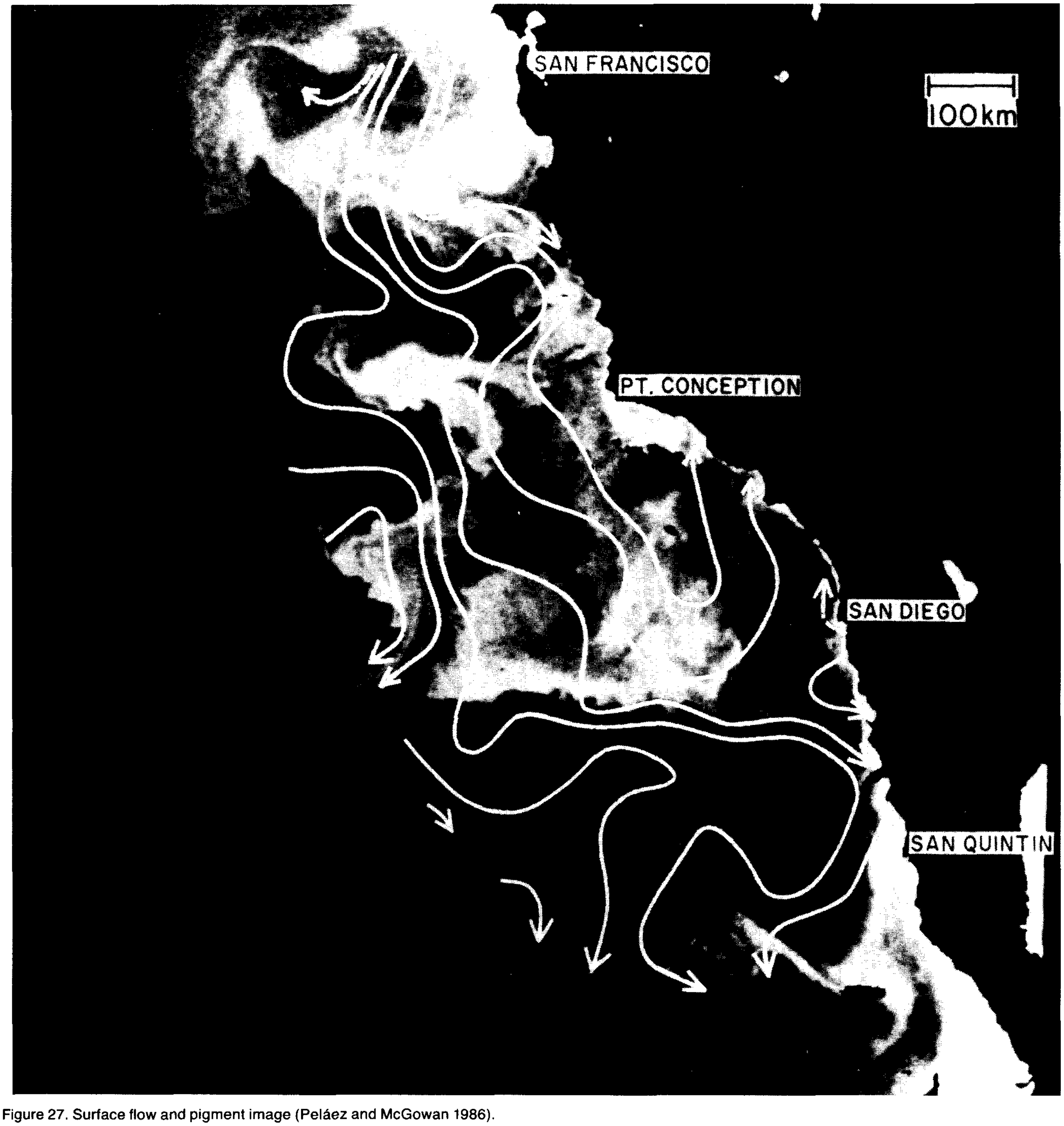

Figure 27. Surface flow and pigment image (Peláez and McGowan 1986).

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CALCOFI TIME SERIES: AN OVERVIEW OF FISHES

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POPULATION PROCESSES

The stated objective of CalCOFI is "to determine what controls variations in population size and availability in oceanic fishes off the west coast of North America." The chief disciplines to be applied to this work are fishery biology—the study of population and biological community reactions to commercial harvest—and biological oceanography—the study of how the biological and physical environment affects biological populations and communities.

Murphy (1966, p. 69) concluded that the Pacific sardine was overfished and that the virtually unfished anchovy had increased to fill its niche as a regionally dominant planktivore. However, the fossil-scale record (Soutar and Isaacs 1974), which is considered to be a useful index of population size and availability, shows that precipitous declines in the Pacific sardine population between 1930 and 1960 off southern California were exceeded between 1850 and 1870, when there was no fishery, and between 1900 and 1915, when the fishery was small.

Smith (1972) reviewed the time series of sardines and anchovies as indexed by their larvae and concluded (p. 873) that the size-frequency curves of the larvae of the two species were so invariant among years that competition between the two species, if any, would most likely occur at the juvenile and prerecruit stages of either species. This was contrary to the argument of Isaacs (1965) that the recruitment of anchovy and sardine could be projected from day/night differences in the early larval stages. Smith (1972) also recommended that the ideas should be tested with surveys of larger larvae and juveniles. He pointed out that the number of batches of spawn per unit time might be plastic (Smith 1972, p. 873). This biases the indices of population size by failing to estimate the degree of interannual variation in the amount of spawning per unit time per unit of adult biomass. In this connection it was pointed out that the decline of sardine spawning in the spring and summer has coincided with an increase of spawning in spring by the anchovy. Current estimates of historical biomass (Lo 1985) indicate that apparent increase in anchovy spawning biomass following the collapse of the sardine population could result from increased repetitive spawning as well as increased anchovy spawning biomass.

Another element in variations in population size and availability of fishes is the biological community structure. Moser et al. (1987) showed that there were major changes in mesopelagic and epipelagic fish recurrent groups during climatic changes. But data from only seven years centered on the 1957 El Niño were analyzed, so the long-term coherence of the changes cannot yet be assessed. For the same period, Colebrook (1977) showed that there were major shifts in the types of zooplankton, with particularly significant shifts in the north-south distribution of zooplankton and secondary changes in the onshore-offshore abundance.

What are the critical time and space scales for understanding the fluctuations in abundance of oceanic fishes off the North American Pacific coast? Haury et al. (1978) suggest a rationale and design:

> Since the study of the causes of variation in population size is one of the chief objectives in ecological research, one reasonable approach is to select for study those scales where the variation seems to be the greatest . . . . the [length scale between] . . . 50 and 1000 km and the [time scale of] . . . one half to 80 years is such a scale. This scale is remarkably similar to the one of Stommel's [time and space variation diagram] showing the most "energetic" part of the ocean. Further, it is about the size of many populations or stocks of planktivorous fish. This may not be purely coincidental.

While the Murphy (1966) proposal that the northern anchovy biomass has replaced the sardine cannot be supported by current biomass estimates of the period he studied (1932–65) or the longer period of scale-deposition rates (Soutar and Isaacs 1974), he did demonstrate an interesting coherence in spawning success rate lasting 3–5 years (Murphy 1966, p. 53). Simple population theory would suggest that a population at the carrying capacity of the environment would have an alternation of spawning success rates, and that populations over

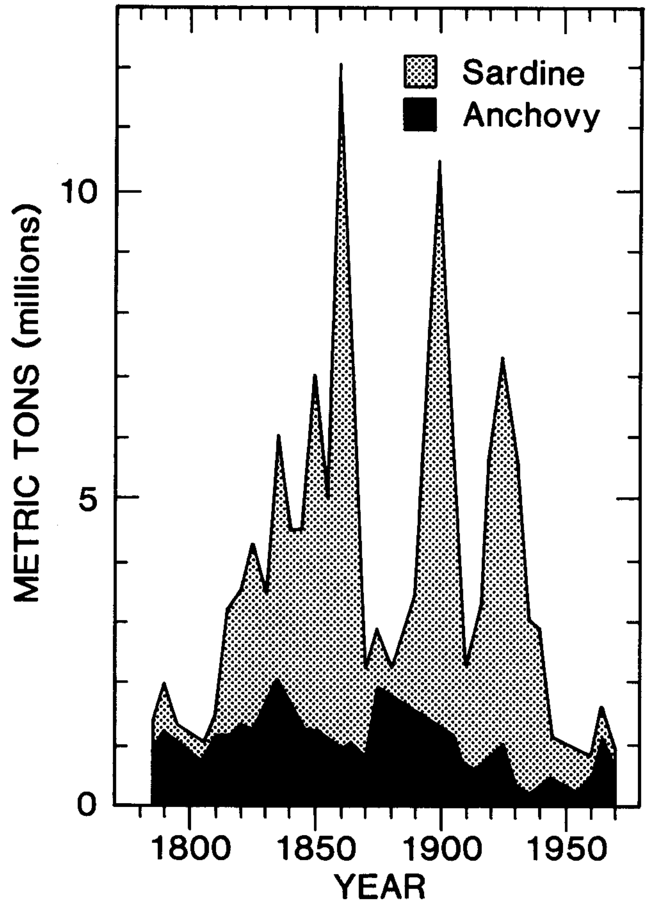

Figure 1. Revised estimate of the spawning biomass of northern anchovy between 1790 and 1970 (180 years at 5-year intervals) derived from the scale-deposition rate in two anoxic basins (Soutar and Isaacs 1974) and adjusted to the spawning biomass determined between 1980 and 1985 for northern anchovy (Methot and Lo 1987), and estimated between 1951 and 1969 (Lo 1985). The Pacific sardine biomass remains the same as in Smith 1978.

the carrying capacity would have poor spawning success. Murphy described multiyear sets of spawning success or failure as indicating population growth mediated by changes in the carrying capacity rather than as a population equilibrium about a fixed carrying capacity. In addition to the 3–5-year coherence in spawning success, there appear to be long-term trends in the sardine and anchovy populations in the scale-deposition record of Soutar and Isaacs (1974) (Figure 1).

It is the purpose of this paper to speculate on the future directions of CalCOFI field work as it relates to processes and patterns that control the variations in population size and availability of oceanic fishes. Many new opportunities are afforded by the technical advances of the last 50 years. The precision and accuracy of primary production estimates have grown steadily. Lasker (1970) specified the level of production necessary for maintaining the Pacific sardine population. The population dynamics and energetics of several other important herbivorous and omnivorous species in the area have been elaborated. The key ecosystem boundaries, and the fauna and their temporal shifts have been described. The scientific basis for conducting ecosystem management exists for some groups of species, but there are formidable technical problems in implementing management.

How Do Population Parameters Vary in Northern Anchovy?

Population maintenance includes the processes of growth, survival, and reproduction. There is important new work on these processes for the massive local population of northern anchovy. Hunter and Leong (1981) found that northern anchovy females spawned 20 batches per year. The energy for only 2 batches was resident in the ovaries; about 13 could be formed from stored fat; the rest would therefore have to be derived from local contemporaneous primary and secondary plankton production. Smith and Eppley (1982) found that the abundance of anchovy larvae in the Southern California Bight region was positively associated with zooplankton standing stock in the previous summer and with primary production in the same quarter.

Theoretically, it is possible to specify all the variations in the northern anchovy population by knowing the variations of reproductive effort of the adults, and growth and survival of all stages (Smith 1985a). Current methods of estimating reproductive effort in anchovy do not depend on index correlations, but directly estimate the reproductive parameters (Lasker 1985, Introduction) and also allow the estimation of embryonic and larval survival. The short 6-year period for which this has been done is not adequate for time-series analysis, but it may be interesting to compare the variations in reproductive and early life-history parameters with the actual variation in spawning biomass. This 6-year period includes 2 years before and after the 1982–1983 El Niño (Chelton et al. 1982; Smith 1985b; Fiedler et al. 1986).

One can see from Table 1 that there are many variables in the reproductive process which may be responsible for a considerable fraction of the recruitment variability. In this 6-year period, the absolute recruitment in numbers of fish varied 64%. The relative recruitment rate in terms of number of recruits per ton of spawners varied 104%. The reproduction parameters varied from a low of 14%

TABLE 1
Interannual Variation of Population Parameters of the Northern Anchovy (*Engraulis mordax*), 1980–85

Parameter	Mean	Standard deviation	Interannual coefficient of variation	Ref.*
Spawning biomass (thousand metric tons)	567	198	35%	1-6
Spawning area (naut. sq. mi.)	25,167	7,679	31%	1-6
Density (grams per sq. m.)	7	3.3	47%	1-6
Spawning female wt (grams)	14.5	3.1	21%	1-6
Specific fecundity (eggs per gram per batch)	513	71.7	14%	1-6
Batch fecundity (eggs per batch)	7,476	2,079	28%	1-6
Interval (days between batches)	8	1.7	21%	1-6
Mean age (years on Feb. 1)	1.8	0.4	23%	8
Year class (10^9 fish)	51	33	64%	8
Juvenile length (mm on Oct 1)	82	7.6	9%	7
Egg production (10^{12} eggs/day)	18	5	28%	1-6
Egg mortality (daily instantaneous)	0.24	0.09	38%	1-6
Yolksac mortality (daily instantaneous)	0.08	0.018	22%	7
Firstfeed mortality (daily instantaneous)	0.14	0.019	14%	7
2-8 mm mortality	1.7	0.36	21%	7
8 mm larvae production (10^{12}/day)	0.19	0.05	27%	7
Eggs to 8 mm (eggs per 8 mm)	102	35	34%	Derived from 7
Year class (thousand fish per MT of spawner)	116	121	104%	Derived from 7

*References:
1. Bindman 1986; 2. Hewitt 1985; 3. Picquelle and Hewitt 1984; 4. Picquelle and Hewitt 1983; 5. Stauffer and Charter 1982; 6. Stauffer and Picquelle 1981; 7. Fiedler et al. 1986; 8. Methot 1986.

for specific fecundity and first-feeding mortality to about 30% for egg mortality, egg production, and batch fecundity. We have not considered any environmental factors, but these internal population factors seem large enough so that combining them with unlisted factors could well account for the observed recruitment variation.

What is missing is a data set designed to partition the relative importance of controls on recruitment. In particular, it remains to be seen how the strong environmental controls interact with the weak population size controls and where in the life cycle these interactions take place. Early life stages can occasionally form part of the variation in recruitment, but much expanded work must be done to sample late larvae and juveniles in addition to (not instead of) early larvae and embryos.

The major problems in sampling late larvae and juveniles (which have been largely solved for embryos and early larvae) are: (1) they are widespread geographically, and there is no way to detect which larvae or juveniles will eventually contribute to recruitment; (2) the late larvae and juveniles are extremely mobile and in schooled patches, thus more sophisticated samplers and more numerous samples will be needed to determine abundance of these stages; and (3) their growth rate is much more plastic than embryos and early larvae, so that regional and seasonal differences in growth rate will require many age and size determinations. In short, analysis of these late larval and juvenile stages will not add to the understanding of the entire life cycle until more money, ship time, and personnel are available for their study. Obviously, as Peterman et al. (1988) point out, the prediction of recruitment could improve as the time between the prediction and recruitment is shortened; this will come about only as it becomes economically feasible.

Another deficiency of all analyses of recruitment variability to date is the inability to assemble the sources of variability that arise from other spatial elements and in other time periods. For example, in addition to being fished, the northern anchovy is preyed upon by a wide variety of fishes, birds, marine mammals (which migrate here from the tropics and from the Arctic, thousands of miles outside the anchovy habitat), and by temperate and tropical tunas (some of which are spawned in the western Pacific 6000 miles away). Some major predators on the anchovy at different stages have life cycles of the order of weeks or months; others have life cycles of years to decades. It would not be unusual, then, for population responses to additional predation pressure on sardines or anchovies to take a decade if the population undergoing change were the northern fur seal; years if predatory populations were Pacific mackerel or one of the mesopelagic fishes; or months if the predatory population were euphausiids or copepods.

Are Time Series of Populations off California Stochastic or Coherent on Long Time Scales?

In Table 2 we have listed measures of periodicity of the fossil-scale series of Soutar and Isaacs (1974). The technique was to count and identify the scales in 5-year intervals for 190 clearly marked varves. We analyzed the time series with an integrated periodogram to determine whether the

TABLE 2

Coherence of Successive Scale Deposition Rates

	5-yr periods	Frequency[a]	Significance[b]	Period[c]
Anchovy	38	low	>0.95	50 yr
Sardine	38	low	>0.95	40 yr
Pacific hake	38	low	>0.75	65 yr
Pacific mackerel	38	low	>0.75	50 yr
Pacific saury	38	low	>0.75	30 yr
Other scales	38	low	>0.95	50 yr

[a] Low frequency of change in trend equals high coherence.
[b] Significance of deviation from random in an integrated periodogram.
[c] Major period in a time series.

series deviated from the random on the low-frequency or high-frequency side and to determine the significance of the cumulative deviation. Each time series was categorized as low-frequency if all periods were above white noise. If they were below the 0.75 probability line the time series was labeled < 0.75; if the series was between the 0.75 and 0.95 probability lines the time series was labeled < 0.95; and if the series projected above the 0.95 line the series was labeled > 0.95. The period was chosen from the maximum peak (10 sample units = 50 years) on the periodogram when there was more than one peak.

We can see from Table 2 that there is major agreement among the species as to the spectral composition of the time series. To varying degrees of significance, the spectrum is of low frequency. The period of change is long, ranging from 30 years in the Pacific saury to 65 years in the Pacific hake. One may assume that the mechanism is environmental, because the generation time of these species is always less than 10 years. In addition to the 3–5-year scale detected in spawning success of sardine (Murphy 1966), we must now be alert to mechanisms operating on a much longer scale. In particular, for management purposes we will need criteria for determining changes in regime from periods of successful reproduction to unsuccessful reproduction.

How Do the Time Series of the Species Compare from Two Collection Sites 1000 km Apart?

Soutar and Isaacs (1974) reported two time series, one from the Santa Barbara Basin at 34°N and one from the Soledad Basin at 26°N. We examined cross-correlations with lags from −5 to 5 representing a period of 55 years. In Table 3 we have the correlation coefficient at the 0 lag or contemporaneously. We have also listed the minimum and maximum cross-correlation coefficients with the lag at which this was achieved.

TABLE 3

Comparison of Cross-Correlation between the Scale-Deposition Time Series at the Santa Barbara Basin and the Soledad Basin (1000 km Southeast)

	Zero lag *R*	Min *R*	Lag	Max *R*	Lag
Northern anchovy	0.26	−0.28	5	0.43	−3
Pacific sardine	−0.02	−0.21	−3	0.24	1
Pacific hake	−0.17	−0.37	−4	0.50	5
Pacific mackerel	0.37	−0.15	−5	0.57	−1
Pacific saury	0.65	−0.09	2	0.66	−1
Other	0.03	−0.33	−5	0.18	1

The Pacific saury, with a transpacific distribution, shows the most cross-correlation between these sites 1000 km apart. The Pacific sardine shows the least. One may conclude from this that the relationships between the sites are generally weak. This could be interpreted to mean that the tendency for these populations to range north and south with long-term changes in climate is nil and that population changes at one site are neither in phase nor out of phase with populations at the other site.

At a Scale-Deposition Site, Do Population Trends of the Major Species Show Interactions Affecting Population Abundance?

To what degree do these populations change at the two sites in response to one another? Table 4 for the Santa Barbara Basin scales and Table 5 for the Soledad Basin scales list the zero-lag correlation coefficients, the minimum cross-correlation coefficient and its lag, and the maximum cross-correlation coefficient and its lag. Here again, as in the species comparisons between basins, most of the correlation coefficients are low. This suggests that within the scale-deposition area of a basin the population densities of the species are unrelated. Some exceptions at the Santa Barbara Basin include the zero-lag (same 5-year period) correlation of 0.66 between the anchovy and hake populations. This means that 40% of the biomass series of either species is controlled by the other or by a common environmental factor. The correlation coefficient between Pacific mackerel and Pacific saury is 0.65 with a lag of 3 (15 years). The largest negative influence is between the northern anchovy and Pacific mackerel at −0.43 with a lag of −1. This suggests that a high biomass of Pacific mackerel is followed in the next 5-year period by a low biomass of anchovy; however, the control is low (about 20%).

At the Soledad Basin there appears to be a bit more structure among the species. Here the an-

TABLE 4
Cross-Correlation Coefficients among Several Species at the Santa Barbara Basin Site

	Pacific sardine	Pacific hake	Pacific mackerel	Pacific saury	Other
No lag					
Northern anchovy	0.33	0.66	−0.36	−0.38	0.03
Pacific sardine		0.38	−0.06	−0.26	−0.21
Pacific hake			−0.18	−0.24	0.01
Pacific mackerel				0.14	−0.11
Pacific saury					0.24
Minimum (lag)					
Northern anchovy	−0.02(−2)	−0.02(−5)	−0.43(−1)	−0.45(1)	−0.19(4)
Pacific sardine		−0.29(4)	−0.35(−4)	−0.31(−2)	−0.29(−2)
Pacific hake			−0.36(−5)	−0.34(−1)	−0.40(4)
Pacific mackerel				−0.19(−3)	−0.33(−4)
Pacific saury					−0.21(−4)
Maximum (lag)					
Northern anchovy	0.41(4)	0.66(0)	0.17(2)	0.04(5)	0.36(−5)
Pacific sardine		0.46(−1)	0.14(2)	0.13(5)	0.18(4)
Pacific hake			0.25(5)	−0.01(−5)	0.53(−4)
Pacific mackerel				0.65(3)	0.18(1)
Pacific saury					0.24(0)

Analysis of data from Soutar and Isaacs 1974.

chovy and hake are negatively correlated at all lags. The correlation is most negative at −1 lag ($r = -0.50$), and it is generally the same at zero lag (−0.45). Sardines are positively correlated with Pacific mackerel ($r = 0.68$, lag 2) and Pacific saury ($r = 0.79$, lag 3). Pacific mackerel is also positively correlated with Pacific saury ($r = 0.64$, lag 1). Anchovy is positively correlated at all lags with the category "other" scales, with a maximum correlation of 0.81 at 0 lag. Hake is also correlated negatively ($r = -0.56$) with "other" scales at a lag of −2 in the Soledad Basin area.

From this analysis, it appears that controls of fish populations on each other are weak, and common responses to environmental changes are similarly weak. Thus although Murphy (1966), Lasker (1970), and Smith and Eppley (1982) all agree that the major pelagic schooling stock, either sardine

TABLE 5
Cross-Correlation Coefficients among Several Species at the Soledad Basin Site

	Pacific sardine	Pacific hake	Pacific mackerel	Pacific saury	Other
No lag					
Northern anchovy	−0.26	−0.45	−0.19	−0.29	0.81
Pacific sardine		0.24	0.38	−0.10	−0.22
Pacific hake			0.44	0.33	−0.22
Pacific mackerel				0.31	−0.19
Pacific saury					−0.17
Minimum (lag)					
Northern anchovy	−0.33(−5)	−0.50(−1)	−0.35(−3)	−0.34(3)	0.11(5)
Pacific sardine		−0.24(−5)	−0.25(−5)	−0.21(−4)	−0.33(−4)
Pacific hake			−0.11(−3)	−0.18(−5)	−0.56(−2)
Pacific mackerel				−0.15(−4)	−0.35(3)
Pacific saury					−0.31(−3)
Maximum (lag)					
Northern anchovy	−0.13(−2)	−0.17(5)	−0.18(1)	0.00(−5)	0.81(0)
Pacific sardine		0.46(−2)	0.68(2)	0.79(3)	−0.12(−2)
Pacific hake			0.44(0)	0.47(1)	−0.06(5)
Pacific mackerel				0.64(1)	−0.06(5)
Pacific saury					−0.01(4)

Analysis of data from Soutar and Isaacs 1974.

or anchovy, is a massive consumer of production relative to the total produced in the California Current system, there does not seem to be any evidence from the fossil-scale record that they compete within a habitat or migrate from one end of the habitat to another. Competition, if any, must be part of a vast and changing array of as yet unmeasured population controls on the major species. It seems possible that abundant mesopelagic populations which migrate to the epipelagic zone and are piscivorous and planktivorous could exert predatory control on the larvae and juveniles of the common epipelagic fishes.

COMMUNITY PROCESSES

The work of Scofield (1934) revealed that the sardine spawned throughout a large proportion of the California Current region, and this was confirmed by Ahlstrom (1948) during the beginnings of the CalCOFI program. Thus a plankton survey designed to comprehensively sample sardine spawning had the potential to yield biogeographic information on a large array of marine organisms. This potential was realized only through the research efforts of dedicated scientists.

Dr. Elbert Ahlstrom was in charge of ichthyoplankton, and from the beginning was determined to identify each sample as far as his knowledge would allow. This knowledge grew rapidly; he soon became preeminent among the small group of people working on ichthyoplankton around the world. Thus, while the primary focus was on the early life history of the sardine and later its relation to the anchovy (Ahlstrom 1966), he was steadily building a fund of information on the ontogeny, systematics, and biogeography of eastern Pacific fishes. His series of definitive papers on early life history and his active role in training and guiding young researchers were principal factors in building a once modest group of devotees into a major field of ocean science. His contributions to the ontogeny and systematics of fishes culminated in an international symposium and a book that summarized and integrated the existing knowledge of these fields (Moser et al. 1984).

The patterns of distribution and abundance of larvae of the principal fish taxa in the California Current and adjoining regions have been reported by Ahlstrom and his co-workers in the CalCOFI Atlas series (Ahlstrom 1969, 1972a; Ahlstrom and Moser 1975; Ahlstrom et al. 1978; Kramer 1970; Kramer and Ahlstrom 1968; Hewitt 1980) and in individual research papers (Ahlstrom 1961, 1965, 1971, 1972b; Ahlstrom and Ball 1954; Ahlstrom and Counts 1955, 1958; Ahlstrom and Stevens 1977; Ahlstrom et al. 1976; Ambrose et al. 1983; D'Vincent et al. 1980; Kramer 1960; Loeb et al. 1983a, b, c; Moser and Ahlstrom 1970; Moser et al. 1973, 1977, 1983, 1986; Stevens and Moser 1982; Sumida et al. 1979, 1985). Lack of a computer data base for CalCOFI has limited our ability to analyze the time series. Since 1983 (Charter et al. 1986[1]) we have been working to remedy this and in the near future will publish 23 ichthyoplankton data reports covering CalCOFI surveys from 1951 to 1981 (see Appendix); the computer data base will be made available to the public through the on-line system described by Roger Hewitt in this volume.

Concurrently with the development of the data base, we have begun to analyze the larval fish assemblages of the California Current region. The northern anchovy, *Engraulis mordax*, has increased in relative abundance throughout the three decades from 1951 to 1981 and accounts for about half the larvae collected over this span (Table 6). Next most numerous are three taxa that consistently rank 2d, 3d, or 4th through this time span: the Pacific hake (*Merluccius productus*), the eastern tropical Pacific gonostomatid *Vinciguerria lucetia*, and the rockfish genus *Sebastes*, which includes over 70 species in the survey area. These 4 top-ranking species represent 72% of all larvae taken. Next in overall rank are 3 midwater species: the deepsea smelt *Leuroglossus stilbius* and two mesopelagic lanternfish, *Triphoturus mexicanus* and *Stenobrachius leucopsarus*. Eighth in overall rank is the sanddab genus *Citharichthys*, which includes 6 species in the CalCOFI region. The remaining 2 species in the top 10 are the Pacific sardine (*Sardinops sagax*) and the jack mackerel (*Trachurus symmetricus*), both of which have shown a relative decline throughout the time series.

The faunal affinities of these top-ranking taxa reflect the transitional nature of the CalCOFI region. Congeners of the anchovy, sardine, jack mackerel, and hake are also abundant in the three other eastern boundary currents of the Pacific and Atlantic. *S. leucopsarus* is a subarctic-transitional species, and *L. stilbius* has a transitional distribution, *sensu* Johnson and Brinton (1965), extending northward from the California Current across the Pacific in a narrow zone between the subarctic and central water masses. *Sebastes* is a subarctic-tran-

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[1] Charter, R., D. A. Ambrose, H. G. Moser, E. M. Sandknop, P. E. Smith, E. G. Stevens and B. Y. Sumida. The CalCOFI ichthyoplankton data base and data reports. Poster presented at CalCOFI Annual Conference, Lake Arrowhead, California, October 21–23, 1986.

TABLE 6

Relative Abundance of the 10 Top-Ranking Larval Fish Taxa Taken on CalCOFI Cruises, Shown as Standardized Counts Pooled for Each Decade

Taxon	1951–81			1951–59			1960–69			1972–78			1980–81		
	Rank	Count	Percent	Rank	Count	Percent	Rank	Count	Percent	Rank	Count	Percent	Rank	Count	Percent
Engraulis mordax	1	5,645,276	49.0	1	1,195,566	33.0	1	2,473,787	54.0	1	1,491,654	57.7	1	484,269	65.5
Merluccius productus	2	1,014,627	8.8	2	523,588	14.4	3	268,044	5.9	2	204,259	7.9	5	18,736	2.5
Vinciguerria lucetia	3	905,814	7.9	3	335,862	9.3	2	384,025	8.4	4	149,191	5.8	3	36,736	5.0
Sebastes spp.	4	718,841	6.2	4	251,065	6.9	4	259,938	5.7	3	157,430	6.1	2	50,408	6.8
Leuroglossus stilbius	5	444,399	3.9	5	176,671	4.9	6	165,733	3.6	5	76,312	3.0	4	25,683	3.5
Triphoturus mexicanus	6	396,178	3.4	6	165,238	4.6	5	170,755	3.7	8	47,799	1.8	7	12,386	1.7
Stenobrachius leucopsarus	7	313,131	2.7	8	132,683	3.7	7	104,316	2.3	6	60,492	2.3	6	15,640	2.1
Citharichthys spp.	8	275,176	2.4	9	128,342	3.5	8	81,621	1.8	7	56,498	2.2	8	8,715	1.2
Sardinops sagax	9	218,722	1.9	7	136,883	3.8	10	62,845	1.4	16	12,946	0.5	13	6,048	0.8
Trachurus symmetricus	10	206,235	1.8	10	116,148	3.2	9	69,959	1.5	14	16,115	0.6	14	4,013	0.5
			87.9			87.3			88.3			87.9			89.6
All taxa		11,532,013			3,628,396			4,578,555			2,586,250			738,812	
No. stations		30,296			14,025			11,256			4,037			978	

sitional shorefish group, and the various species of *Citharichthys* are found in coastal waters from the subarctic through the tropics. *T. mexicanus* is a subtropical species abundant in the southern reaches of the California Current, and *V. lucetia* is an eastern tropical Pacific species. Central water mass species are not abundant in the CalCOFI samples; however, warm-water cosmopolites such as the myctophids *Diogenichthys atlanticus*, *Hygophum reinhardtii*, and *Myctophum nitidulum* appear where central water impinges on the California Current off southern California and Baja California. The distributional patterns of the principal and less-abundant larval fish taxa in the CalCOFI region are closely tied to water masses, clearly affirming what has been shown for a wide array of zooplankton species (Reid et al. 1978).

As a first step in studying potential environmental effects and species interactions, we performed a recurrent group analysis on the 7-year span of the time series from 1954 to 1960 (Moser et al. 1987). This period was chosen because there was maximum areal and seasonal sampling coverage during a sequence of anomalously cold and warm oceanographic regimes. Also, initial identifications of the samples were fairly reliable, and these were improved during the editing and verification of the data base. The recurrent group method identifies groups of taxa that occur together frequently and are consistently part of each other's environment. This method tends to avoid potential misinterpretations that can arise from abundance analyses of patchy organisms.

Analysis of nearly 200 taxa from the composite 7-year data set produced 9 recurrent groups formed by 30 taxa. Intergroup affinities produced two large complexes of 4 recurrent groups each. We refer to these as the "northern" and "southern" complexes, since their constituents had primarily warm- or cold-water taxa or were linked to warm- or cold-water taxa through affinity indices. Spawning was seasonal in most species, with winter or spring maxima in the northern complex and spring or summer maxima in the southern complex. Each complex consisted of a 5-member group with strong connections to the smaller groups in the complex.

The large group in the northern complex was a mix of abundant subarctic-transitional (*L. stilbius, S. leucopsarus, Sebastes* spp.) and transitional (*M. productus, Bathylagus ochotensis*) taxa, which were strongly interlinked with *E. mordax* and *S. sagax* in two other groups. In contrast to the northern and coastal nature of this complex, the southern complex comprised primarily mesopelagic species that inhabit more southerly and offshore waters. The 5-member group included transitional species (*Bathylagus wesethi, Lampanyctus ritteri, Symbolophorus californiensis*) and warm-water cosmopolites (*Cyclothone* spp., *Diogenichthys atlanticus*) that were strongly linked to an eastern tropical Pacific group (*V. lucetia, Diogenichthys laternatus, Hygophum atratum, Gonichthys tenuiculus*) and a group comprising transitional (*Trachurus symmetricus, Protomyctophum crockeri*) and subtropical (*T. mexicanus*) species. A third complex was associated with the extensive coastal shelf region of central Baja California and consisted of a group of four subtropical shorefish taxa.

The structure and composition of the groups varied in analyses of individual years, more so in the southern complex; however, the northern and southern complexes were generally conserved. The two complexes were linked by a single pairing

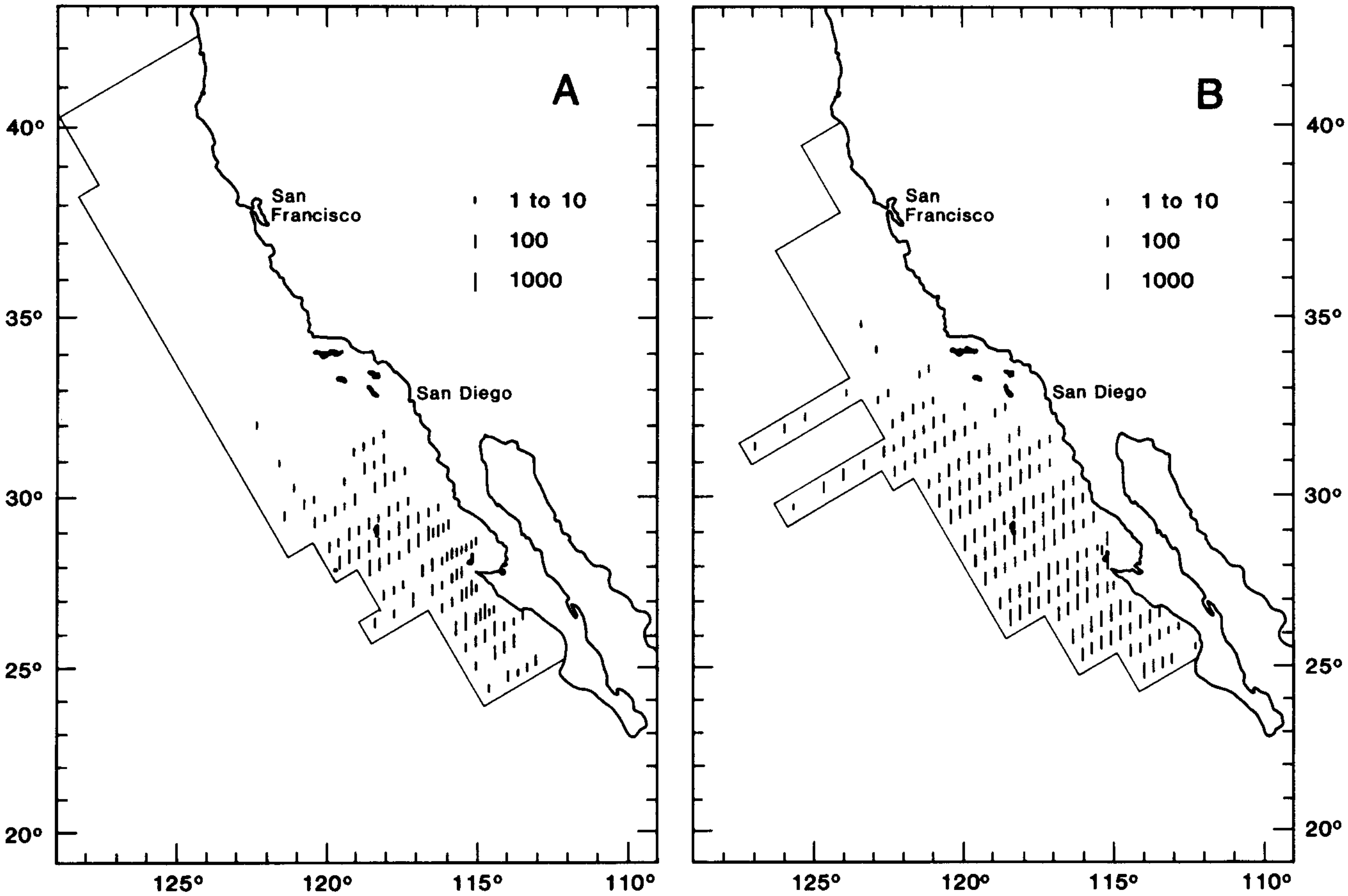

Figure 2. Change in distribution of larvae of *Vinciguerria lucetia* during cold (*A*) and warm (*B*) temperature regimes in the California Current region. Pooled numbers of larvae for three cold years (1954–56) and three warm years (1958–60) are indicated by exponentially scaled bars. The survey pattern for each series of years is outlined.

(*E. mordax-T. mexicanus*) in the composite analysis, although in some years the links between the two complexes were stronger and more numerous, and there was some switching of group members between complexes. Where this occurred, the southern complex group of *T. mexicanus-P. crockeri-T. symmetricus* and the northern complex group of *E. mordax-Citharichthys* were usually involved, emphasizing the transitional position of these taxa in the CalCOFI region.

Variation in the structure and composition of the complexes and their constituent groups was, in part, related to the major oceanographic changes that occurred during 1954–1960. Conditions in the first half of the 1950s were generally cool, culminating in the strong negative temperature anomaly during 1956. A warming trend began in 1957, leading to a major El Niño event in 1958 and 1959. Mixed-layer isotherms were shifted northward more than 200 km, shifting the distribution and abundance of some larval fish taxa northward, (Figure 2) and causing the above-mentioned changes in recurrent groups. These changes were not as great as those associated with the anomalously cold year of 1956, when affinity indices were lowered among southern complex species, and recurrent groups in this complex were markedly depauperate (see Moser et al. 1987 for details).

From this brief summary it is clear that the CalCOFI surveys reveal the major faunal associations and broadscale environmental interactions in the California Current region. This was particularly true for the 1950s, when monthly sample coverage extended over the full length of the pattern. Biogeographic information has diminished since 1960, with the areal and temporal shrinkage of the survey pattern; however, even the present minimal quarterly coverage of the Southern California Bight is sensitive to changes in ocean regimes because subtropical, eastern tropical Pacific, and central water mass species expand their spawning boundaries into this region. The original extensive coverage was also essential in defining the broad spawning ranges of commercial species such as Pacific hake, jack mackerel, Pacific mackerel, and the rockfishes. Fishery scientists have relied heavily on CalCOFI data in developing the knowledge required to manage these populations.

The early surveys also showed that many important coastal recreational and commercial species spawn off Baja California. Ocean whitefish (*Caulolatilis princeps*) appears to spawn exclusively off Baja California, since larvae have not been taken north of the Mexican border (Moser et al. 1986). White seabass (*Atractoscion nobilis*), yellowtail (*Seriola lalandi*), and bonito (*Sarda chiliensis*) spawn primarily off Baja California, with small numbers of larvae appearing off southern California (Moser et al. 1983; Sumida et al. 1985; original data). Barracuda (*Sphyraena argentea*) and California halibut (*Paralichthys californicus*) spawn off southern California, but the greater part of their spawning range extends the entire length of Baja California (Kramer and Smith 1973). Recruitment of these transboundary stocks to southern California is either dependent on or strongly influenced by stocks off Mexico. The United States and Mexico are highly interdependent in the use and management of these stocks, and if CalCOFI is to be involved in studies of their production and recruitment, the present survey pattern will have to be expanded south of the Southern California Bight.

During the past ten years there has been increased ichthyoplankton research on shorefish populations, primarily because of potential impacts of power plants and urban development (Brewer et al. 1981; Gruber et al. 1982; Schlotterbeck and Connally 1982; Barnett et al. 1984; Lavenberg et al. 1986; Walker et al. 1987). These workers have used CalCOFI ichthyoplankton techniques to study the zone between the most shoreward CalCOFI stations and the beach. One of their key findings is a distinct nearshore ichthyoplankton fauna, which peaks at about 40 – m bottom depth and is poorly sampled at the most shoreward CalCOFI stations. Many of these species settle to the bottom at early larval stages, apparently as an adaptation to remain nearshore, and there is a general tendency in these larvae to move downward and shoreward ontogenetically. Some species are neustonic and may be transported shoreward in surface slicks associated with tidally forced internal waves (Shanks 1983). Larvae of the nearshore assemblage are comparatively rare in CalCOFI samples, generally occur well seaward of their zone of settlement, and may represent reproductive wastage rather than potential recruits. Alternatively, they may possess behavioral mechanisms that allow far-ranging planktonic stages to recruit to the nearshore habitats of the adults. This question can be addressed by analyzing the CalCOFI and nearshore ichthyoplankton data bases that are presently being assembled, but it probably cannot be answered without concentrated field surveys in the transition region between the two zones.

An initial objective of the CalCOFI program was to determine the environmental and biotic factors that affect production, recruitment, and population fluctuations of the sardine. During the past 40 years the program has provided spawning biomass indices of the sardine, anchovy, and mackerels (Ahlstrom 1966; Smith 1972; Parrish and MacCall 1978; MacCall and Stauffer 1983) and has documented the continued decline of the sardine and concomitant increase of anchovy in the CalCOFI region. A recent modification of CalCOFI sampling design has allowed direct estimation of anchovy and sardine spawning biomass (Lasker 1985; Wolf et al. 1987). CalCOFI has been the foundation for a number of hypotheses: sardine-anchovy competitive exclusion (Murphy 1966; Ahlstrom 1967; Isaacs 1965); ocean transport-larval survival (Parrish et al. 1981; Simpson 1987); Lasker's (1975) stable ocean-larval survival hypothesis; and MacCall's density-dependent habitat selection model (MacCall 1980; Lasker and MacCall 1983). Correlation techniques support Lasker's hypothesis that wind-driven turbulent mixing increases mortality of early-stage anchovy larvae by dissipating food patches (Peterman and Bradford 1987) but do not support the hypothesis (Lasker 1981) that recruitment and year-class strength are determined by mortality of early-stage larvae (Peterman et al. 1988). The latter authors suggested that recruitment variability would depend on survival during the late larval-prerecruit stages, which are virtually absent from CalCOFI samples.

Our research on interannual variation of incidence and abundance of CalCOFI ichthyoplankton (Moser et al. 1987) suggests that a multispecies approach might provide recruitment information on species such as sardine and anchovy. These species co-occur and interact with a wide array of other species during each life-history stage. Dominant mesopelagic species (Table 6) are not sampled by fisheries, and CalCOFI provides the only synoptic sampling of their populations. Our interpretation of the conclusions of Peterman et al. (1987) emphasizes predation during the late larval and prerecruit stages as a major determinant of recruitment. This occurs widely in the complex species assemblages sampled by CalCOFI surveys, and its relation to recruitment may be revealed by our correlation analyses in progress.

CONCLUSIONS

The early decades of biological oceanography in CalCOFI were marked by the identification of the oceanic regions and currents that impinged on the California coastal area. Johnson and Brinton (1965) used physical oceanography and analysis of planktonic species to describe the primary boundaries. The time series of the major epipelagic fish species—sardine and anchovy—by Murphy (1966) and Soutar and Isaacs (1974) have drawn attention to two scales of change: one at the scale of 3–5 years and another that acts over periods of 3–6 decades. Recent analyses of species assemblages (Moser et al. 1987) will offer time series comparisons for additional species at the decadal scale when the analyses under way are complete. In summary:

1. Spectral analysis of the fish-scale record indicates long-lasting population trends in sardine and anchovy and does not suggest equilibrium phenomena as population controls; the period of change is of the order of a half-century for several pelagic species.
2. The reproductive parameters of the northern anchovy show variations that are much less than the variations in specific recruitment rate.
3. Scale-deposition indices at two sites separated by 1000 km show little agreement, suggesting that the critical spatial scale of the events leading to species biomass changes is less than 1000 km.
4. Species biomass interactions among the major fish populations are weak at both scale-deposition sites.
5. Analysis of fish species assemblages suggests that predation by major mesopelagic species of the California Current region could affect survival rates of ontogenetic stages of epipelagic populations (e.g., sardine and anchovy) and thus influence recruitment variations.

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APPENDIX
CalCOFI Ichthyoplankton Data Reports

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Part III

SCIENTIFIC CONTRIBUTIONS

REVISED ESTIMATES OF HISTORICAL SPAWNING BIOMASS OF THE PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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ABSTRACT

We present revised spawning biomass estimates for the Pacific mackerel stock off southern California for the years 1929–69. These new estimates include corrected assumptions about fecundity, individual growth, underreporting of catches, and the distribution of fishing effort throughout the season. The time series of new estimates shows a more pronounced spawning population decline preceding the population's collapse.

Spawning appears to be more limited to the older fish than previously thought; cumulative egg production curves reveal an increased impact of exploitation on spawn production. Such a pattern might reduce the stock's stability at high levels of exploitation. In examining the weight-at-age time series, we observed clear evidence of density-dependent growth; fish attained much higher weights at age when the population size was small.

RESUMEN

Re-estimaciones de la biomasa de desove de la macarela del Pacífico frente al sur de California son presentadas para el período 1929–69. Estos nuevos valores incluyen suposiciones actualizadas en cuanto a fecundidad, crecimiento individual, declaración de capturas inferiores a las reales, y distribución del esfuerzo pesquero a través de la temporada. La serie de tiempo de las nuevas estimaciones indica una disminución más pronunciada de la población de desove que precedió al colapso de la población.

El desove parece estar más restringido a los peces de mayor edad, con respecto a análisis previos. Las curvas acumulativas de producción de huevos revelan un mayor impacto de la explotación sobre la producción de desove. Un patrón de este tipo puede reducir la estabilidad de la población cuando es expuesta a altos niveles de explotación. La serie de tiempo de peso por edad entrega clara evidencia de crecimiento dependiente de la densidad de la población; los peces alcanzaron mayores pesos a cierta edad cuando el tamaño de la población era chico.

INTRODUCTION

The California stock of *Scomber japonicus*, known locally as Pacific mackerel and elsewhere as chub mackerel, is one of the most closely monitored fish stocks in the world. A remarkably long record of fishery data has made it possible to compute virtual population analyses for the period from the beginning of the fishery in 1929 until the stock's collapse in the late 1960s. After the California legislature closed the fishery in 1970, the stock rebounded, and the fishery reopened in 1977. This provided a second period of catch data. The stock's population dynamics have been described by Parrish and MacCall (1978), MacCall et al. (1985), and Prager and MacCall (1988).

Recent advances in virtual population analysis (Sims 1982; MacCall 1986; Prager and MacCall 1988), new research about the Pacific mackerel's fecundity by Dickerson and Macewicz[1], and a critical reanalysis of the existing growth data (this paper) allowed us to compute corrected historical abundance estimates of the stock's spawning biomass. These estimates differ in several respects from the previous ones.

COMPUTATION OF SPAWNING BIOMASS ESTIMATES

The following formulation was used to compute each year's spawning biomass.

$$B_i = \sum_{j=1}^{5} N_{ij} w_{ij} m_j \tag{1}$$

where i = an index of year,
j = an index of age,

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[1] Dickerson, T. L., and B. J. Macewicz. MS. Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus*, during 1985. Available from B. J. Macewicz, Southwest Fisheries Center, P. O. Box 271, La Jolla, CA 92038.

B_i = the spawning stock biomass estimate in year i,
N_{ij} = the number of fish of age j in the population at the beginning of year i,
w_{ij} = the mean weight of a single fish of age j in year i,
m_j = an index of the relative weight-specific egg production (fecundity) of female fish at age j.

Equation 1 relies upon two main assumptions. First, egg production per gram of total weight is assumed constant for the ages in question, except for the effects of m_j. Second, the sex ratio is assumed to remain constant. With these assumptions met, B_i gives relative values of egg biomass spawned from year to year. This quantity is intrinsically relative, both because m_j is a relative index and because no attempt is made to estimate actual egg production per gram of fish weight. Pacific mackerel exhibit indeterminate fecundity (i.e., the total number of eggs to be spawned is not fixed at the beginning of the season, and new oocytes are recruited if feeding and environment are favorable); therefore actual egg production from a given spawning biomass may vary from year to year.

Estimated spawning biomass, then, comprises three elements (numbers, weights, and fecundities at age), which are treated in the following three sections. We report fish weights and biomasses in the English system of measurement because management and monitoring of this fishery have not yet converted to the metric system.

NUMBERS AT AGE

Methods

The estimates of numbers at age were obtained by virtual population analysis (VPA), as in past analyses of this stock's population dynamics (Parrish and MacCall 1978; MacCall et al. 1985). Our first change to past methods was to obtain an estimate of underreporting in the catch statistics. Because no theoretical framework existed for doing this, we relied upon estimates by those involved in management of the fishery (R. Klingbeil, Calif. Dept. of Fish and Game, 245 W. Broadway, Long Beach, CA 90802, pers. comm.). We believe that this approach, while not ideal, is preferable to assuming that no underreporting has taken place (or, almost equivalently, assuming that the degree of underreporting has been constant). Table 1 indicates the degree of underreporting assumed to have taken place, and by which we corrected the catch data before performing VPA.

TABLE 1
Underreporting Percentages Used for Analysis of Pacific Mackerel Catch Data

Years	Underreporting
1929–47	10%
1948–49	9%
1950–51	8%
1952–57	7%
1958–61	6%
1962–69	5%

Our second revision concerned the VPA methodology used to estimate numbers at age from the catch data. VPA methodology has been well described (Murphy 1965; Pope 1972; MacCall 1986), and thus is not reviewed here. However, we made several modifications to the VPA techniques used in prior analyses of this stock. VPA, since it assumes that the fishing effort is uniformly distributed throughout the fishing season, can produce biased results in a fishery with strongly seasonal fishing effort (Sims 1982). We accommodated this fact by using a variant of MacCall's (1986) approximation that took the seasonal nature of the fishery into account. We used the VPA estimator:

$$\hat{N}_i = N_{i+1} \exp(M) + kC_i \tag{2}$$

where $\hat{N}_i$ = the estimate of population (in numbers) at the start of year i,
C_i = the catch (in numbers) during year i,
M = the instantaneous rate of natural mortality (assumed constant),
k = a constant depending on M and the temporal distribution of catch throughout the year.

In most VPA applications, k is held constant. In contrast, we developed a procedure to find annual values of k fitting the distribution of each year's catch, which increased the accuracy of our population estimates. To do this, we performed an iterative monthly VPA on the unaged catch data, and found for each year the k_i that caused equation 2 to hold on an annual basis (MacCall 1986). These values of k_i were then used in the analysis of the aged annual catches by equation 2. Since the Pacific mackerel fishery is highly seasonal, this gave more accurate estimates of population number than did the standard iterative solution based on constant fishing effort over the full year.

Results of Virtual Population Analysis

The catch data after correction for underreporting are given in Table 2. The new VPA estimates of population number (Table 3) are slightly higher than the estimates of Parrish and MacCall (1978), especially in the years before 1940. This occurs because the correction for underreporting slightly outweighs the seasonal VPA correction in those years.

WEIGHTS AT AGE

The second data component used to estimate spawning biomass was the matrix of age- and year-specific weights at the nominal mean spawning date, May 1. This section describes our procedures for revising these weights for the years 1928–69 and 1974–84. Although spawning biomass estimates were not computed for the years 1974–84, weights for these years were needed to estimate earlier values.

The weight data fell into three groups: (1) no data for 1929 to 1938; (2) average weight of the season's catch by age for 1939 to 1969; (3) monthly weights at age beginning in 1977. Accordingly, we divided our analysis into the same three groups of years. For ease of narrative, we begin with the most recent period.

Years 1977–1984

Weights at age for each year, 1977–84, were based on monthly weight measurements of fish from the catch (R. Klingbeil, California Dept. of Fish and Game, unpubl. data). These were recorded from April through June of each year; we estimated May 1 weights as means of the recorded April and May entries (which, as monthly means, approximate mid-month weights). In years missing data from April or May, we assumed linear growth in weight during the season, interpolated the missing values, and took the mean of April and May

TABLE 2
Adjusted Catch Statistics for Pacific Mackerel in Numbers of Fish (Multiply by 1000)

Year	Age 1	Age 2	Age 3	Age 4	Age 5^+
1929	12,743	23,027	21,338	5,338	9,073
1930	1,360	6,996	4,724	1,871	721
1931	942	9,834	6,093	1,287	1,310
1932	144	3,221	5,843	1,393	1,701
1933	4,162	17,132	28,727	21,048	11,286
1934	3,743	40,807	27,227	31,211	18,610
1935	8,468	9,921	48,061	49,709	33,609
1936	1,894	17,197	14,664	27,866	36,522
1937	1,414	2,484	7,701	15,249	36,690
1938	12,262	33,859	17,506	4,564	22,422
1939	30,304	31,916	42,246	12,711	13,757
1940	24,051	80,182	29,219	15,674	3,582
1941	15,093	31,924	30,967	6,180	1,833
1942	35,770	11,208	15,462	6,418	1,318
1943	15,378	66,767	12,532	8,802	1,822
1944	19,600	22,550	40,140	9,130	2,439
1945	16,941	12,233	12,152	12,216	5,681
1946	11,588	32,072	14,746	5,789	5,939
1947	1,867	10,816	14,831	6,894	4,839
1948	77,374	3,879	924	1,351	881
1949	26,987	60,924	5,292	851	1,102
1950	5,064	25,268	20,798	1,232	278
1951	1,920	5,371	16,825	13,497	451
1952	60	677	1,672	12,334	3,627
1953	1,102	774	951	262	1,237
1954	65,034	6,324	338	115	63
1955	6,986	41,490	11,806	400	278
1956	75,425	22,852	22,341	5,556	95
1957	7,273	35,604	13,234	9,530	3,871
1958	1,428	6,614	12,148	3,905	1,583
1959	62,281	4,618	1,151	1,407	612
1960	22,049	24,804	9,579	2,504	839
1961	35,576	18,143	12,934	2,719	381
1962	31,826	14,669	10,585	4,071	462
1963	4,042	23,458	13,626	8,315	1,272
1964	7,375	5,695	10,747	14,239	1,992
1965	1,321	801	1,777	5,772	10,698

weights as in other years. Values of w_{5+} were estimated as weighted means of weights at ages 5 and 6, namely

$$w_{i5+} = 0.8w_{i5} + 0.2w_{i6}$$

This ad hoc relationship was suggested by the relative frequencies of 5- and 6-year-old fish in the catch.

Years 1940–1968

For the 1939–69 seasons, publications of the California Department of Fish and Game tabulated each season's catches in weight and numbers by age (Fitch 1951, 1953a, 1953b, 1955, 1956, 1958; Hyatt 1960; Knaggs 1972; Parrish and Knaggs 1971, 1972). From these publications, each season's average (not May 1) weights w^*_{ij} at age were obtained by dividing catches in weight by catches in numbers. To estimate weights on May 1, we first calculated the mean harvest date of each fishing season from the monthly distribution of landings. We then assumed that the recorded mean weights at age occurred on that date. Finally, by assuming linear growth from one mean harvest date to the next, we estimated the May 1 weights at age (w_{ij}) by interpolation. Because 1939 was the first season with weight information, the first interpolation was for 1940. To estimate weights at age 5^+, we increased weights at age 5 by 5%, a value suggested by examining a few years for which both w_5 and w_{5+} were known.

The interpolation could not be done for age 1 in 1943 and 1945 because we lacked catch data for age 0, and for age 5 in 1954 because we lacked catch data for age 5. Therefore, these mean weights were estimated indirectly by referring to the relative weight of an adjacent cohort at the same age. For example, in 1953 the age 4 mean weight was approximately equal to the mean of age 4 weights in the preceding and following years; thus the age 5 mean weight in 1954 was estimated as the mean of

TABLE 3
Revised VPA Population Estimates of Pacific Mackerel in Numbers of Fish (Multiply by 1000)

Year	Age 1	Age 2	Age 3	Age 4	Age 5^+
1929	352,430	224,170	168,150	27,994	47,584
1930	754,120	204,480	119,190	86,449	33,317
1931	987,320	456,360	118,690	68,694	69,940
1932	1,094,400	598,120	269,220	67,294	82,159
1933	768,830	663,650	360,380	158,940	85,224
1934	276,090	463,280	390,010	197,600	117,820
1935	120,520	164,720	251,200	216,680	146,500
1936	151,650	66,824	92,559	116,750	153,020
1937	325,570	90,604	28,064	45,508	109,500
1938	237,380	196,400	53,076	11,199	55,014
1939	380,930	134,600	93,238	18,810	20,357
1940	246,870	206,630	55,927	22,517	5,146
1941	215,060	130,690	61,836	10,785	3,200
1942	458,450	118,680	54,396	13,380	2,747
1943	166,870	249,720	63,104	20,742	4,294
1944	150,350	89,142	99,071	28,440	7,597
1945	157,890	76,000	36,590	28,980	13,478
1946	47,175	82,465	36,491	12,651	12,979
1947	39,432	19,372	24,441	10,374	7,281
1948	396,570	22,498	3,527	3,548	2,316
1949	216,890	182,590	10,741	1,447	1,875
1950	24,255	111,590	65,693	2,601	588
1951	10,167	10,932	48,826	24,324	813
1952	6,226	4,737	2,630	17,082	5,023
1953	126,370	3,734	2,394	414	1,950
1954	311,330	75,759	1,641	686	378
1955	131,130	138,890	41,094	736	512
1956	229,670	74,130	52,130	15,787	269
1957	44,260	80,090	27,023	14,080	5,719
1958	67,801	21,210	20,994	6,137	2,488
1959	221,770	39,991	7,618	3,097	1,346
1960	192,800	85,817	20,645	3,721	1,247
1961	330,760	99,062	31,939	4,756	666
1962	168,500	173,080	46,041	9,360	1,063
1963	28,322	77,701	93,687	19,778	3,025
1964	16,632	14,205	29,875	46,802	6,546
1965	6,644	4,762	4,503	10,358	19,199

the preceding and following age 5 weights. A similar procedure was used for age 1 fish in 1943 and 1945; variations in relative weight of age 2 fish were used as the basis for comparison.

Years 1929–1939

Because no weight data had been collected, Parrish and MacCall (1978) had assumed that weights at age were constant before 1939. However, an examination of data from other years indicated that *Scomber japonicus* weights at age are quite variable, and appear to be density-dependent. The use of constant weights during a period of high abundance is likely to have produced biased estimates of spawning biomass.

To eliminate this source of bias, we estimated the 1929–39 May 1 weights at age by using linear regression models of known May 1 weights on May 1 abundances at age. The modeling procedure was similar for estimating weights at each age. (Although all weights are year-specific, the subscript for year is omitted below unless required for clarity.) The procedure for modeling w_1 was:

1. We computed all possible regressions of weight on population numbers of each age. (That is, $\hat{w}_{i1} = f\{N_{i1} \ldots N_{i5}\}$.)
2. By examining goodness-of-fit statistics, including Akaike's information criterion (Akaike 1969), Mallows's C_p (Mallows 1964), and the R^2 and adjusted R^2 statistics (Kvålseth 1985), we chose one or two potential models from those computed for each age.
3. We plotted the selected models to examine goodness of fit and detect any possible outliers or other ill behavior.
4. Favoring simpler models, we chose one regression model and computed predicted values of w_1 where missing.

Models of w_2 through w_{5+} were constructed in a similar way, except that the weight of the same cohort at the previous age was included among the independent variables. For example, in predicting w_{i3}, we included $w_{i-1,2}$ among the possible regressors. In addition, we found it useful to include the same year's weight at the next younger age among the possible regressors. May 1 weights used for fitting the models were from the procedures described above for 1940–68 and 1977–84.

Special cases. The model for w_1 included N_2, which was unrecorded before 1926. Therefore no weight at age 1 was estimated for 1925. Similarly, the model for weight at age 2 included the population number at age 4, which was unrecorded before 1928. In order to estimate w_2 in 1927, we used a separate regression not including N_4. This made it possible to estimate w_3 starting in 1928, w_4 starting in 1929, and w_{5+} starting in 1930.

A value of w_{5+} for 1929 was necessary so that the year's data could be used for further analysis. A separate regression of w_{5+} on w_4 was used for 1929 only. This was possible because, for the older fish, the weights at age were correlated within a single year—in this case, Pearson's $r = 0.85$.

The w_{5+} value for 1965 (1.228), derived as discussed above through interpolation, was considered an outlier. The value of w_{5+} predicted from the regression model (1.495) was substituted for the interpolated 1965 value.

Results of Weight Analysis

The new series of estimated May 1 weights is given in Table 4. Equations for the regression models used to estimate pre-1939 weights are given in Table 5, with model statistics in Table 6. A plot of weight versus population size (Figure 1) illustrates the density-dependence in the stock.

FECUNDITIES AT AGE

Because of data limitations, we used estimated mean fecundities (m_j) that were not year-specific. This is similar to the methodology of Parrish and MacCall (1978), who used the following vector of age-specific fecundities, corresponding to age groups 1, 2, 3, 4, and 5^+:

$$m = \{\Phi_i, 0.77, 0.88, 1.0, 1.0\} \qquad (3)$$

Here Φ_i, the fraction of age 1 biomass which is mature (m_{i1}), was the only year-specific element. It was given by:

$$\Phi_i = 0.54 \exp(-0.00717\, B^*_i) \qquad (4)$$

where B^*_i is the total stock biomass, in millions of pounds, in year *i*.

This *m* vector was based on gonad observations from samples of the catch taken in 12 fishing seasons from 1958 through 1969 (Knaggs and Parrish 1973). Female mackerel gonads from those samples were classified into three categories: immature ("I," no eggs present); maturing ("g," eggs present); and mature ("G," large translucent eggs present). To derive the *m* vector, Parrish and MacCall combined the mean proportions of fish of each age falling into the g and G categories, which they considered to be equal indicators of maturity, and mul-

TABLE 4
Revised May 1 Weights (Pounds) at Age of Pacific Mackerel

Year	Age 1	Age 2	Age 3	Age 4	Age 5^+
1925	—	—	—	—	—
1926	0.396	—	—	—	—
1927	0.369	0.705	—	—	—
1928	0.348	0.613	0.918	—	—
1929	0.368	0.655	0.887	1.152	1.355
1930	0.306	0.664	0.931	1.127	1.330
1931	0.252	0.609	0.880	1.161	1.337
1932	0.178	0.611	0.836	1.121	1.332
1933	0.182	0.442	0.660	1.087	1.289
1934	0.313	0.436	0.513	0.950	1.186
1935	0.409	0.479	0.553	0.836	1.041
1936	0.425	0.626	0.745	0.867	0.998
1937	0.389	0.700	0.945	1.016	1.107
1938	0.383	0.683	0.988	1.172	1.284
1939	0.371	0.695	0.986	1.206	1.389
1940	0.429	0.575	0.795	0.984	1.280
1941	0.482	0.685	0.883	1.113	1.322
1942	0.381	0.703	0.900	1.143	1.465
1943	0.479	0.617	0.944	1.132	1.384
1944	0.461	0.739	0.903	1.182	1.422
1945	0.369	0.728	0.965	1.181	1.440
1946	0.411	0.654	0.966	1.204	1.423
1947	0.510	0.796	1.048	1.211	1.450
1948	0.351	0.741	1.060	1.275	1.484
1949	0.327	0.577	0.864	1.262	1.480
1950	0.462	0.564	0.804	1.059	1.437
1951	0.353	0.692	0.846	1.051	1.311
1952	0.611	0.785	1.058	1.213	1.442
1953	0.438	0.790	0.959	1.219	1.471
1954	0.342	0.740	1.075	1.227	1.484
1955	0.350	0.556	0.889	1.159	1.497
1956	0.398	0.652	0.899	1.092	1.403
1957	0.453	0.662	0.931	1.134	1.342
1958	0.413	0.697	0.844	1.093	1.294
1959	0.414	0.735	0.968	1.136	1.409
1960	0.364	0.690	1.044	1.285	1.521
1961	0.389	0.668	1.017	1.236	1.455
1962	0.508	0.751	1.039	1.236	1.480
1963	0.642	0.873	1.093	1.291	1.560
1964	0.576	0.827	1.119	1.312	1.616
1965	0.402	0.745	1.008	1.254	1.289
1966	0.371	0.717	1.070	1.292	1.715
1967	0.413	0.605	1.004	1.266	1.583
1968	0.427	0.712	1.051	1.240	1.524
1969	0.557	0.801	1.044	1.371	1.614
1970	—	—	—	1.250	1.524
1971–74 No data					
1975	0.465	—	—	—	—
1976	0.465	0.741	—	—	—
1977	0.415	0.940	1.840	—	—
1978	0.473	0.880	1.730	1.920	2.221
1979	0.195	0.865	1.255	1.715	2.205
1980	0.230	0.420	1.010	1.340	1.732
1981	0.265	0.610	0.650	1.250	1.537
1982	0.210	0.500	0.660	0.860	1.357
1983	0.300	0.520	0.745	1.010	1.222
1984	0.300	0.455	0.690	0.855	0.991

tiplied the resulting m vector by a constant α to scale k_5 to unity.

$$m_j = \alpha\{P_j(g) + P_j(G)\} \qquad (5)$$

where m_j = the estimated mean proportion mature at age j.
α = the scaling constant described above,
$P_j(g)$ = the fraction of fish of age j in classification g,
$P_j(G)$ = the fraction of fish of age j in classification G.

TABLE 5

Regression Models of Pacific Mackerel Weights at Age[a]

$$\hat{w}_{i1} = 0.469 - 0.000208N_{i1} - 0.000252N_{i2}$$
$$\hat{w}_{i2} = 0.166 + 0.651w_{i1} + 0.585w_{i-1,1} + 0.000243N_{i1} - 0.00087N_{i4}$$
$$\hat{w}_{i3} = -0.313 + 1.055w_{i2} + 0.829w_{i-1,2}$$
$$\hat{w}_{i4} = 0.435 + 0.780w_{i-1,3}$$
$$\hat{w}_{i5+} = 0.122 + 0.613w_{i4} + 0.544w_{i-1,4}$$

[a] Subscripts refer to year and age, in that order. Symbols are defined in the text.

TABLE 6

Statistics from Regression Models of Pacific Mackerel Weights at Age

Weight estimated	n	Adjusted R^2	F statistic	Prob. of larger F
w_{i1}	35	0.443	14.9	< 0.0001
w_{i2}	35	0.79	33.4	< 0.0001
w_{i3}	35	0.63	30.4	< 0.0001
w_{i4}	34	0.89	282	< 0.0001
w_{i5}	33	0.84	89.0	< 0.0001

Recent histology by Dickerson and Macewicz[2] indicates that the three gonad classifications have a different interpretation from that of Parrish and MacCall. Examination of gonads taken during the 1985 spawning season showed that the G category represented hydrated eggs, indicating spawning imminent within a few hours, whereas the g category was the normal state of mature, spawning fish. Dickerson and Macewicz also report that, in the 1985 spawning season, the average mature female's mean spawning frequency was about once per 12 days, while fish at maximum egg production spawned approximately once per 1.3 days. We assumed that fish in category g were average mature females, and that those in category G were at maximum egg production. (This interpretation, although it may not be accurate, appears better than the previous assumption that g and G represent equally important indicators of maturity.) This leads to a new expression, replacing equation 5, for establishing the m vector, and a new interpretation; i.e., that m_j reflects relative fecundity, not just maturity, at age. The new expression is:

$$m_j = \frac{P_j(\mathrm{g})}{12} + \frac{P_j(\mathrm{G})}{1.3} \qquad (6)$$

where m_j = the new relative fecundity index for age j,
$P_j(\mathrm{g})$ = the fraction of fish of age j in classification g,
$P_j(\mathrm{G})$ = the fraction of fish of age j in classification G.

Equation 6 allowed us to reevaluate the m vector (equations 3 and 4) established by Knaggs and Parrish (1973); their original data were kindly provided us by Richard Klingbeil (Calif. Dept. of Fish and Game, Long Beach, pers. comm.). The 12 years of data were tabulated by the five age groups (1 through 5^+) and eight months (March through October) in which spawning tends to occur. Of these 480 cells, only 280 contained data, of which 86 were zero observations; thus, only 40% of the cells contained nonzero values for m.

We postulated a model in which multiplicative year and age parameters produce a predicted value for the annual spawning output, defined as the sum of the monthly cells for the year. The age factors of this model form the m vector. Although the model could have been fit directly to the data by maximum likelihood, the effort for that approach exceeded our resources, so we chose instead to estimate parameters by analysis of variance (ANOVA) of log-transformed data. To remove month effects, we conducted the ANOVA on yearly sums.

It was necessary to fill missing cells before computing the yearly sums. To accomplish this, we used a second ANOVA based on additive year, month, and age effects to estimate values for the empty cells. This ANOVA was weighted according to the square root of the number of observations in each cell. (Independence of data would warrant weighting by the number of observations; however, the samples of fish came from schools, within which spawning condition was probably corre-

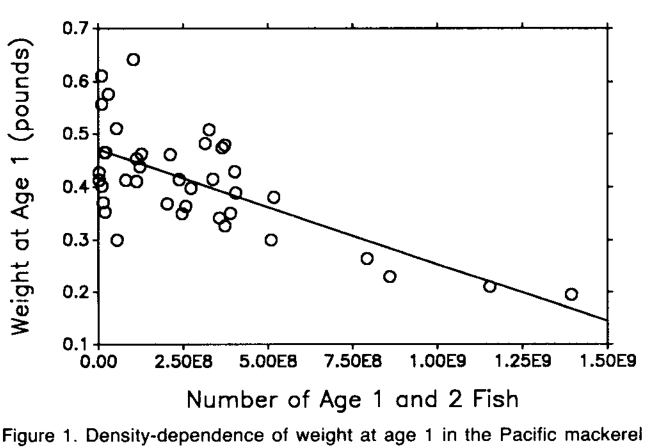

Figure 1. Density-dependence of weight at age 1 in the Pacific mackerel stock. Data shown cover years 1940–84, and do not include weights estimated by regression analysis. The regression line is shown for illustration. Other ages are similar.

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[2] Dickerson, T. L., and B. J. Macewicz. MS. Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus*, during 1985. Available from B. J. Macewicz, Southwest Fisheries Center, P. O. Box 271, La Jolla, CA 92038.

lated. By means of the square root weighting, we attempted to acknowledge this fact while also recognizing that larger sample sizes should nonetheless provide more precise index values.) Very large *F* statistics from this ANOVA suggested that year, month, and age effects were all meaningful; however, lack of normality, the nonstandard weighting scheme, and the additive model, which is probably misspecified, prevented computation of parametric significance probabilities.

After empty monthly cells were replaced by predicted values, the yearly sums formed a data matrix of 12 years by five ages. Negative values in this matrix were treated as missing values. Because abundances from 1966 to 1969 were the lowest on record, and spawning activity the highest, these years were deleted as possibly reflecting an atypical level of spawning activity. Data from 1958 and 1965 were also deleted, because their yearly indices were based on fewer than seven actual (i.e., not estimated) monthly values. The six-year period from 1959 to 1964 remained as the data available to estimate the age specific *m* vector.

Results of Fecundity Analysis

The model of year and age effects was estimated by ANOVA of log-transformed values with equal cell weights. Large *F* values, although not strictly statistically significant, indicated likely biological significance. Exponentiating the age effects from the ANOVA gave an *m* vector of:

$$m = \{0.0586, 0.4837, 0.9107, 0.9118, 1.0\} \qquad (7)$$

Because the age 3, 4, and 5^+ elements of equation 7 were all very similar, we averaged them and rescaled them to unity. This gave a final *m* vector of

$$m = \{0.062, 0.514, 1.0, 1.0, 1.0\} \qquad (8)$$

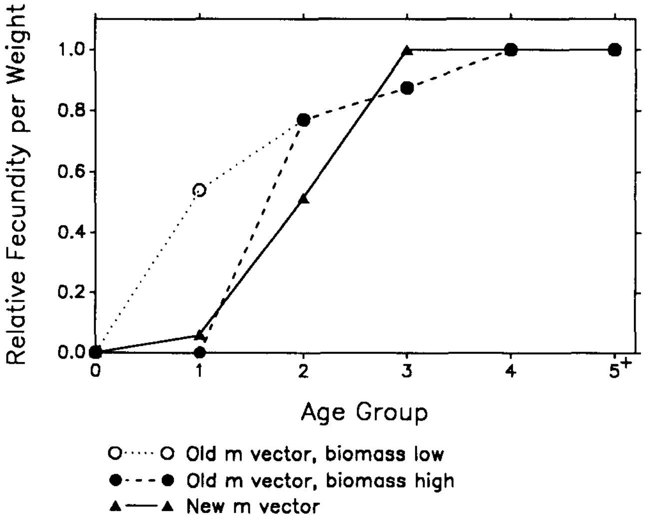

Figure 2. Spawning ogives under new and revised fecundity schedules (*m* vectors). The new schedule reveals that spawning is more concentrated among the older ages.

We found little evidence of density-dependent changes in m_1. Its small magnitude supports Fry's (1936) observation that yearling fish do not spawn.

In view of the new fecundity schedule (*m* vector), it appears that Parrish and MacCall overestimated the contributions of ages 1 and 2 to egg production, even though it was correct that relatively large fractions of these age groups were mature and capable of spawning. The new schedule shifts the spawning biomass to a slightly older mean age, as illustrated in Figure 2, which gives spawning ogives under the old and new *m* vectors.

Figure 3 compares eggs-per-recruit (EPR) curves (fecundity multiplied by survivorship; Prager et al. 1987) for unexploited and exploited populations under old and new schedules, given fishing availabilities from MacCall et al. (1985). The EPR curves with no fishing were scaled to unity; exploitation was at $F = 1.0$; Φ_i was set to 0.26, an average

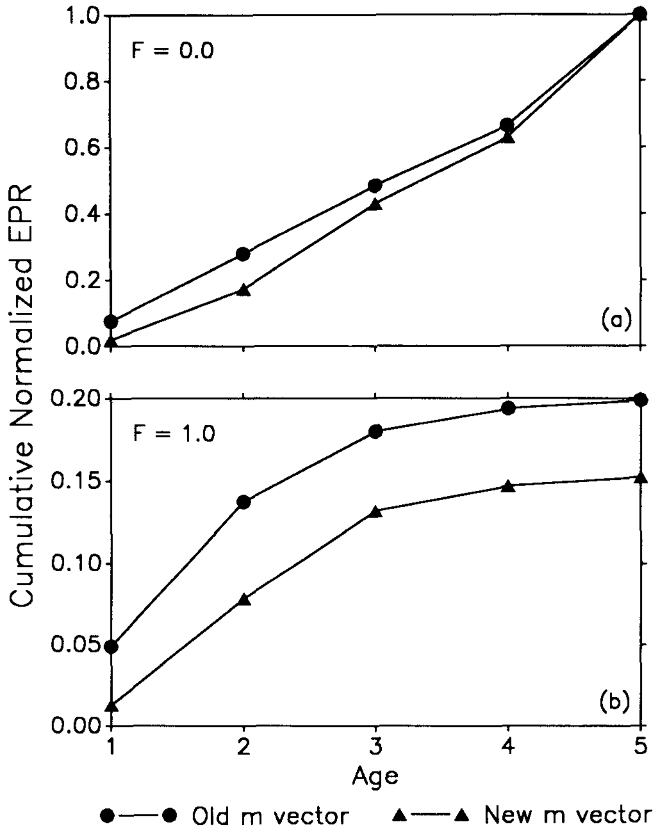

Figure 3. Cumulative eggs-per-recruit (EPR) curves for the Pacific mackerel stock under old and new fecundity schedules (*m* vectors). Curves have been normalized so that each yields EPR = 1.0 with no exploitation. (*a*), Unexploited stock; (*b*), stock exploited at annual $F = 1.0$.

value, for the old *m* vector. With exploitation, the new cumulative EPR curve reaches 0.15, whereas the old curve reaches 0.20. In other words, at $F = 1.0$, spawning output is about 75% of what we thought under the old schedule; thus, slightly less harvestable productivity might be expected. Certainly, these results suggest that the population's spawning productivity is more affected by fishing than was previously believed.

SPAWNING BIOMASS ESTIMATION

The final spawning biomass estimates (Table 7) are presented with approximate 95% confidence intervals in Figure 4. The standard deviation of the estimates was computed by the delta method (Seber 1973; Prager and MacCall 1988); we assumed a 5% coefficient of variation on each element of the *m* vector; confidence intervals were computed as ± 2 standard deviations. Figure 5 presents the old (Parrish and MacCall 1978) and new (this paper)

TABLE 7
Revised Spawning Biomass Estimates for Pacific Mackerel in Pounds (Multiply by 1000)

Year	Spawning biomass	Std. deviation of sp. biomass	Coefficient of variation
1929	329,400	308,350	93.6%
1930	336,800	299,583	89.0%
1931	435,900	318,591	73.1%
1932	609,800	370,675	60.8%
1933	679,900	344,674	50.7%
1934	636,700	277,471	43.6%
1935	516,100	192,120	37.2%
1936	348,400	114,978	33.0%
1937	234,400	67,535	28.8%
1938	210,700	53,703	25.5%
1939	199,700	46,787	23.4%
1940	140,800	17,804	12.6%
1941	123,300	21,347	17.3%
1942	122,000	29,215	23.9%
1943	173,100	35,539	20.5%
1944	172,000	30,077	17.5%
1945	121,000	20,888	17.3%
1946	97,870	13,122	13.4%
1947	57,910	6,829	11.8%
1948	28,900	6,046	20.9%
1949	72,430	11,925	16.5%
1950	89,460	14,244	15.9%
1951	72,050	9,346	13.0%
1952	32,890	3,986	12.1%
1953	10,620	2,858	26.9%
1954	38,580	9,596	24.9%
1955	80,690	13,513	16.7%
1956	94,990	12,919	13.6%
1957	77,290	8,817	11.4%
1958	36,980	4,969	13.4%
1959	33,590	6,777	20.2%
1960	63,020	10,635	16.9%
1961	81,320	18,218	22.4%
1962	133,100	34,943	26.3%
1963	168,600	36,878	21.9%
1964	112,000	19,593	17.5%
1965	44,270	5,828	13.2%

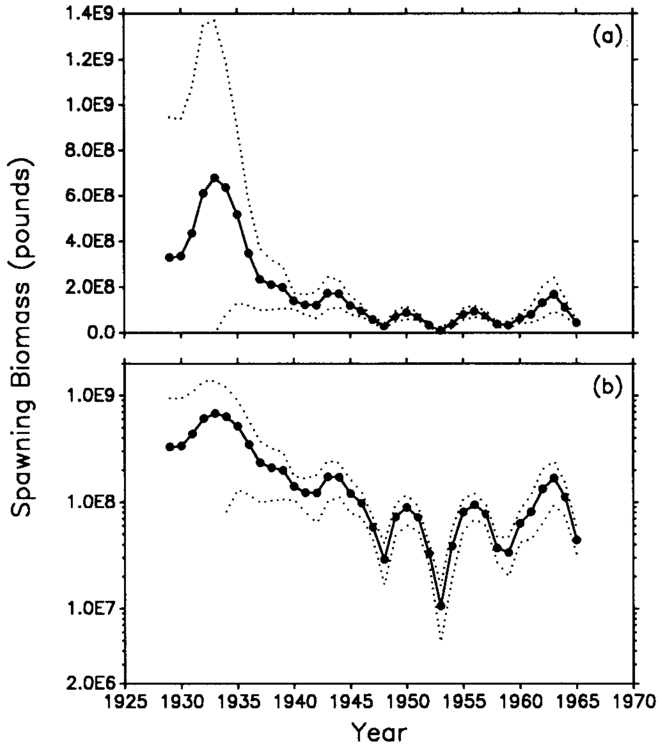

Figure 4. Revised spawning biomass estimates for Pacific mackerel stock, with approximate 95% confidence interval (*dotted line*). (*a*), Linear scale; (*b*), log scale. Large confidence bounds before 1940 reflect less precise knowledge of age structure and weights at age.

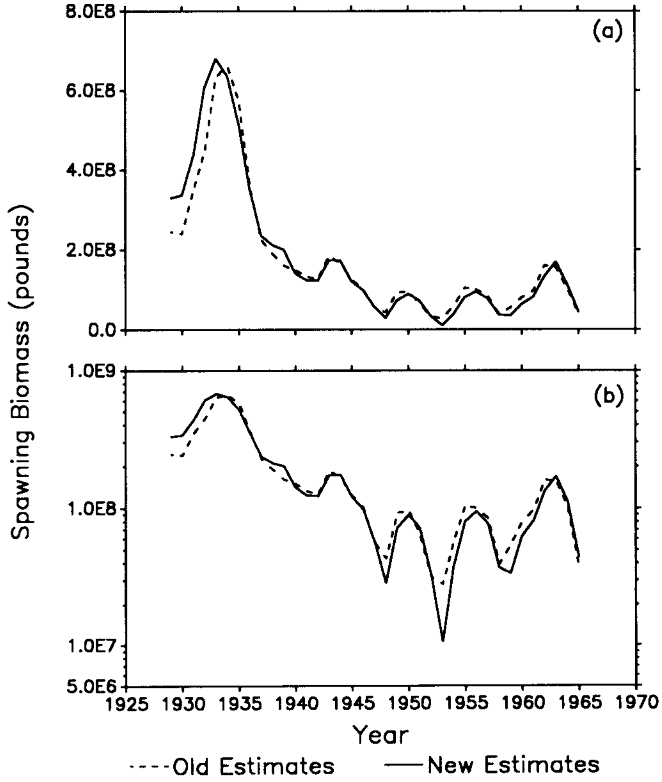

Figure 5. Old and revised spawning biomass estimates for Pacific mackerel stock: (*a*), linear scale; (*b*), log scale.

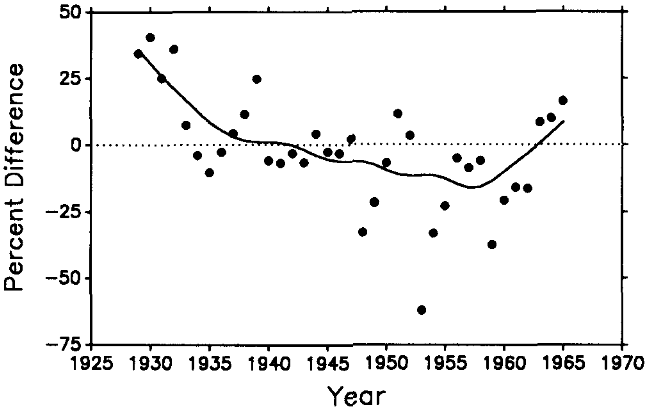

Figure 6. Difference between old and revised spawning biomass estimates, expressed as percent difference from the old to the new estimate [i.e., (old − new) × 100 / old]. Smoothed line is locally weighted robust regression (LOWESS).

spawning biomass estimates. Although they appear quite similar, a closer look presents a different picture. Figure 6, which shows the differences (between new and old estimates) as percentages of the old estimates, illustrates that the declining trend of the spawning biomass from 1925 to 1962 is more clearly seen under the new estimates. This clearer vision is a direct result of increased knowledge of the Pacific mackerel's spawning biology. We hope that our clearer view of the stock's population dynamics will help to lessen the probability of another collapse.

ACKNOWLEDGMENTS

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HISTORICAL CHANGES IN ABUNDANCE OF SIX FISH SPECIES OFF SOUTHERN CALIFORNIA, BASED ON CALCOFI EGG AND LARVA SAMPLES

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ABSTRACT

We have developed annual indexes of larval abundances for five species sampled by the CalCOFI ichthyoplankton surveys from 1951 to 1985: northern anchovy, Pacific sardine, Pacific mackerel, jack mackerel, and Pacific whiting (or hake). We used a similar method to calculate annual indexes of egg abundances for a sixth species—Pacific saury. We pooled observations of larval densities within six geographic regions off southern California and northern Baja California, summarizing the data into region-month-year cells. We then used a multiplicative model of independent region, month, and year factors to predict the abundance in each cell. Under log-transform, the model becomes additive (i.e., log-linear) and was solved by analysis of variance (ANOVA). The ANOVA solution has the added advantage of accommodating missing values (43% of the possible 2160 cells lack observations). The antilogged month factors provided estimates of the mean temporal distribution of larvae over the months of the year. Antilogged region factors similarly provided the mean geographic distribution. Antilogged year factors from an ANOVA weighted by the monthly and regional distributions provided the annual indexes of abundance.

Abundance indexes for all six species show large fluctuations over the 35-year period. The index of northern anchovy larvae increased 50-fold from 1951 to the mid 1960s; since then it has fluctuated widely but without a trend. Indexes of Pacific sardine and Pacific mackerel decline from 1951 to the mid 1970s, and rise sharply thereafter, consistent with known increases in abundance. Indexes of jack mackerel and Pacific whiting are highly variable, and trends are difficult to identify. The index of Pacific saury eggs is high in the 1950s, is slightly lower for the next two decades, and drops severely in the 1980s. Changes in indexes of the latter three species are probably associated with environmental influences that have produced large-scale geographic shifts in spawning.

RESUMEN

Indices anuales de producción de larvas han sido desarrollados para 5 especies muestreádas por las expediciones de ictioplancton de CalCOFI: anchoveta del Norte (*Engraulis mordax*), sardina del Pacífico (*Sardinops sagax*), macarela del Pacífico (*Scomber japonicus*), jurel (*Trachurus symmetricus*), y merluza (*Merluccius productus*). Un método similar fue usado para calcular índices anuales de abundancia de huevos para una sexta especie, *Cololabis saira*. Las observaciones de densidad de larvas dentro de 6 regiones geográficas frente al sur de California y la region norte de Baja California fueron combinadas y resumidas en categorías de region-mes-año. En cada categoría se usó un modelo multiplicativo con factores independientes de región, mes y año para predecir su abundancia. Con una transformacion logarítmica, el modelo se volvió aditivo (i.e., lineal en escala logarítmica) y fue solucionado con un análisis de varianza (ANOVA). La solución ANOVA tiene la ventaja adicional de permitir la ausencia de datos (un 43% de las 2160 categorías posibles carece de observaciones). La función antilogarítmica de los factores mensuales entregó estimaciones de la distribución temporal promedio de larvas durante los meses del año. Similarmente, la función antilogarítmica de los factores regionales entregó la distribución geográfica promedio. La función antilogarítmica de los factores anuales de un ANOVA, ponderados por las distribuciones mensuales y regionales proporcionó índices anuales de abundancia.

Los índices de abundancia para las 6 especies muestran grandes fluctuaciones durante el periodo de 35 años. El índice de las larvas de la anchoveta del Norte aumentó 50 veces entre 1951 y mediados de la década de 1960; desde entonces ha fluctuado enormemente pero sin una tendencia clara. Los índices de la sardina y la macarela del Pacífico disminuyeron desde 1951 hasta mediados de la década de 1970, para después aumentar abruptamente, en forma consistente con aumentos en abundancia previamente establecidos. Los índices de *T. symmetricus* y *M. productus* son altamente variables y es difícil establecer un patrón. El índice de los hue-

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vos de *C. saira* es alto en la década de 1950, levemente inferior en las dos siguientes décadas, y cae considerablemente en la década de 1980. Los cambios en los índices de las últimas 3 especies están probablemente relacionados con factores ambientales que han producido desplazamientos geográficos de gran escala en el desove.

INTRODUCTION

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) have sampled fish eggs and larvae off the coast of California and northern Baja California since 1951. One of the goals of these and similar ichthyoplankton surveys has been to compile time series of abundances of the parent fish species (Moser et al. 1987; Smith and Moser 1988). In developing such abundance estimates there are many difficulties, ranging from uncertainty about the physiology of spawning activity to the statistics of highly patchy populations and incomplete sampling.

The present attempt to derive abundance time series from the CalCOFI data emphasizes development of a uniform methodology that can be applied to all species, independent of the amount of supplemental knowledge. We emphasize that these time series represent a first attempt for most of these species, and additional knowledge should lead to improved estimates for individual species. For example, Lo (1985) used information on growth rates and the size-frequency distribution of anchovy larvae to estimate their mortality rates and rates of parental egg production. The latter provided an improved index of adult abundance. However, we lack such supplementary information for most species. By comparing this "information-poor" analysis with complex, more reliable analyses of the same and/or supplementary data for well-studied species, we can infer the relative performance of this simple approach.

DATA AND METHODS

We summarized the CalCOFI egg or larval data by six geographical regions (Figure 1), for each month and year in which samples were taken. Although these regions were originally defined for purposes of stratifying distributions of anchovy larvae (Smith 1972; see Lo 1985 for current region definitions), they suffice for initial investigations of other species. It is important to note that the geographic regions used in this study do not necessarily cover the full spawning range of some of the species treated here. Because many sets of CalCOFI cruises began in November, we used a sampling year of November through October in this analysis.

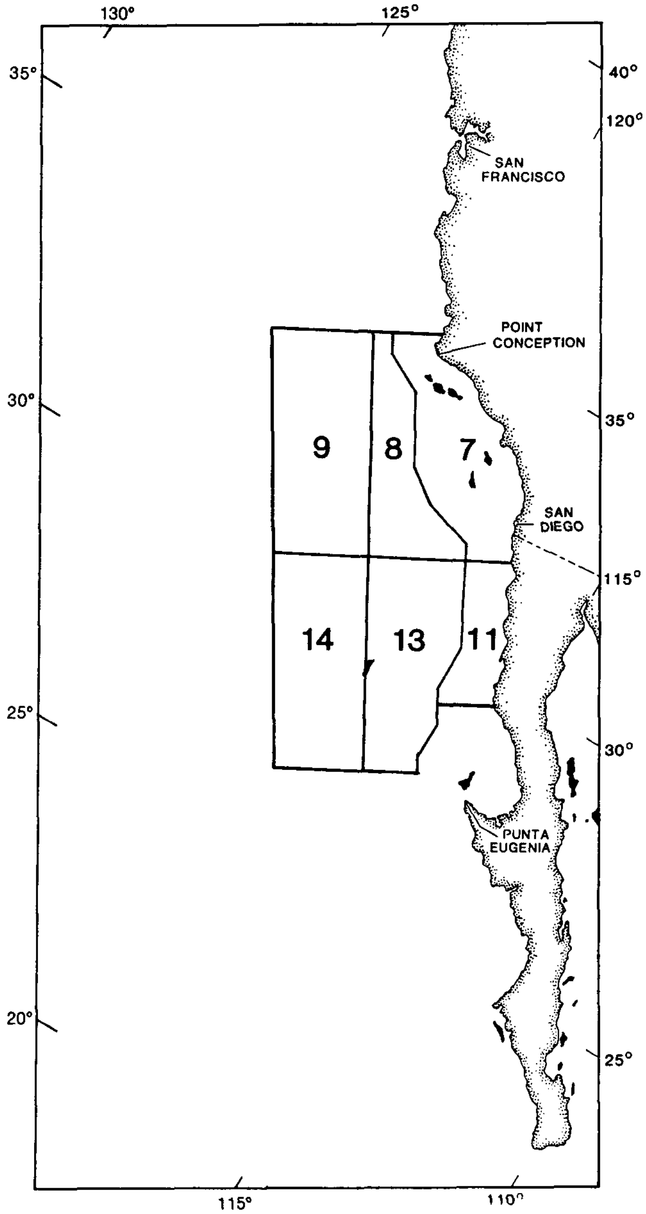

Figure 1. Location of the six geographic regions (7, 8, 9, 11, 13, and 14) used for pooling observations of larval densities.

Following the approach of Smith (1972), we calculated the average larval density for each of these year-month-region strata, or "cells," as the mean of the individual density estimates for all stations occupied within the cell[1] (see Kramer et al. 1972 for a general description of sampling methods; detailed data and changes in sampling are described

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[1] In cases where a cruise extended slightly into a second month, with very small numbers of stations occupied, we nominally combine the data under the adjacent principal month. These months were 11–62, 12–67, 5–68, 11–72, 11–74, 11–77, 4–82, 2–83, and 11–84. Data from 11–75, 12–75, and 11–85 were not used in the analysis.

in a series of publications beginning with Ambrose et al. 1987). During the study period 1951 to 1985, only six years (1970, 1971, 1973, 1974, 1976, and 1977) were not sampled at all. Many years were sampled thoroughly, especially 1951 through 1960. In the 30 "survey years" during the study period, a total of 1238 cells were sampled, which is about 57% of the possible 2160 cells. Missing values in the remaining 43% of the cells present statistical difficulties in developing reliable abundance estimates.

A good solution to the problem of missing values is the method of maximum likelihood, but that method requires developing a complicated probabilistic model based on individual observations. The sheer number of observations (nearly 12,000) would present difficult computational problems. A simpler approach is to use an established model and statistical method that naturally accommodate missing values. For example, previous abundance indexes have used summation of data aggregated on a quarterly basis (Smith 1972), and linear interpolation has been proposed as a basis for estimating missing values (Smith 1978). Here we advocate use of a linear model, or analysis of variance (ANOVA), as an alternate approach that preserves monthly detail. For this application, ANOVA was used as an estimation tool rather than as a tool for testing statistical hypotheses. All computations employed a "main-effects" specification of the GLM procedure of SAS (see SAS Institute 1985 for technical details).

The ANOVA model predicts each cell value as the product of its respective month, region, and year factors. In effect, the month factors reflect the annual spawning cycle (shifted by the average age of the larvae, which usually is less than 0.5 months), and the region factors reflect the average geographic distribution of larval densities or spawning. The year factors reflect relative changes in overall production of eggs and their subsequent survival, and provide a tentative abundance index that may be useful for identifying long-term trends in abundance of the spawning stock within the geographic range of the sampling. In order to cast this multiplicative model as an ANOVA problem, the mean larval abundances were log-transformed (using natural logarithms). The resulting additive (log-linear) model is

$$\ln(N_{ijk} + 0.01) = \ln(R_i) + \ln(S_j) + \ln(T_k) + \text{constant} + \text{error} \qquad (1)$$

where R_i is the region factor ($i = 1, \ldots, 6$), S_j is the month factor ($j = 1, \ldots, 12$), and T_k is the year factor ($k = 1, \ldots, 30$). The solution is not unique, and the fitted constant depends on the scaling of the estimated factors; however, the relative relationships within a set of factors are independent of that constant (which is subsequently ignored), allowing their use as indexes. The quantity N_{ijk} is the mean abundance of larvae per 10 m^2 of sea surface. Because many observed values of N_{ijk} are zero, a constant was added before log transformation. Use of such a constant is a necessary evil in this log-linear approach and can distort the values of the estimated factors, especially for seasons or years with very low larval abundances. The added constant of 0.01 larvae/10 m^2 was near or slightly smaller than the smallest nonzero larval density measurable for a cell at typical sampling densities. Because the model is estimated under log transformation, the factors reflect geometric mean effects.

A further limitation of the simple ANOVA model is its disregard for interactions among factors. These interactions, such as geographic shifts in spawning areas as the season progresses, are known to occur (e.g., Kramer and Smith 1970). They can be addressed by a model such as

$$\ln(N_{kl} + 0.01) = \ln(C_l) + \ln(T_k) + \text{constant} + \text{error} \qquad (2)$$

where C_l is a combined month-region factor ($l = 1, \ldots, 72$). We used this model to examine month-region interactions for the peak months of spawning.

Moreover, the estimated time series of abundance indexes (T_k) were compared for the two models, providing a check on the amount of distortion introduced by the lack of interaction terms in equation 1. Shifts in spawning seasons or areas over the years also are known to occur, but formal recognition of these interactions in a model similar to equation 2 requires an excessive number of estimated parameters. Moreover, sample sizes for some individual factors become rather small, and a strong year-versus-region pattern of missing values makes estimation problematic; this is an area for further investigation.

In this log-linear ANOVA model with equal weighting of all cells, the year factors are highly influenced by months and regions that account for relatively few larvae. Accordingly, we used a weighted ANOVA to estimate the year factors. We chose a weighting scheme that allowed the influence of various months and regions to be made roughly proportional to their average contribution to the total year's spawning. Thus we approximated the weighting implicit in an additive "larval census" treatment, which is a sum of larvae over regions and seasons within a year (Smith 1972). Note that this weighted ANOVA should tend to be robust to error arising from variations in the duration of the spawning season (to the extent that duration is independent of spawner abundance), but may not be robust to error arising from overall shifts in spawning season or location among years.

In determining cell weights, we did not include the number of stations contributing to the cell mean; this modification is worth further consideration, but is somewhat more complicated than would first appear. For example, individual stations can vary substantially in amount of water filtered, as well as probable extrusion and/or avoidance by the larvae. The solution to these variable sample volume problems is likely to take the form proposed by Zweifel and Smith (1981), who weighted individual observations before averaging.

In addition to weighting the ANOVA to obtain the year factors, we restricted the months used in the ANOVA to peak spawning months. These months tend to have more and larger nonzero observations, reducing distortion due to addition of a constant for logarithmic transformation. On the other hand, using a small number of months increases difficulties arising from missing observations. Except for Pacific whiting, which has a brief spawning period, we included at least four months in the nominal peak spawning period in order to balance these two considerations.

The antilogged month and region factors from the previous unweighted ANOVA were used to calculate the weights for the weighted ANOVA, as well as to identify the peak spawning months. In accordance with equation 1, weights were calculated as the product of a month-weighting contribution and a region-weighting contribution. The month contribution consisted of the antilogged factors for the peak months, taken from the unweighted ANOVA and scaled to a unit sum. The region contribution was calculated similarly, except that antilogged region factors were first multiplied by the area of the corresponding region, in order to represent relative abundance of larvae in keeping with the analogy to a larval census (Smith 1972). The regions are shown in Figure 1, and their areas (taken from Lo 1985) are given in Table 1. Because of the month and region weights, observations in some cells are more important than others. A rough index of "effective sample size" is provided by the sum of cell weights for nonmissing values in each year (Table 2).

The added constant of 0.01 larvae/10 m^2 created a minimum possible abundance index, i.e., an index value obtained if no larvae were observed in any cell. We determined the approximate value of this minimum by supplying the ANOVA with an additional year of artificial data containing no positive observations. We assigned exceedingly small weights to these artificial data to avoid influencing the ANOVA results for the actual data.

The comparison of time series of year factors (T_k) as estimated by the simple and interaction models in equations 1 and 2 followed a procedure identical to that described above: We used an unweighted "main effects" SAS GLM procedure (ANOVA) to identify the peak months, and to provide cell weights accordingly. Weighted ANOVAs then produced time series of abundance indexes for the two models. We used the same cell weights for both models. Our use of peak months was especially important in this comparison, because the added constant in the logarithmic transformations in equations 1 and 2 would tend to create erroneous interactions in months and regions where larval densities were low. For a similar reason, the comparison was restricted to years that

TABLE 1
Region Factors from ANOVA with Equal Cell Weights, Reflecting Average Distribution of Larval Densities

	Region					
	7	8	9	11	13	14
Northern anchovy	0.828	0.024	0.007	0.121	0.020	—
Pacific sardine	0.478	0.053	0.078	0.173	0.144	0.074
Pacific mackerel	0.273	0.090	0.153	0.106	0.219	0.159
Jack mackerel	0.050	0.084	0.272	0.033	0.318	0.243
Pacific whiting	0.458	0.128	0.249	0.072	0.063	0.028
Pacific saury	0.214	0.129	0.336	0.036	0.157	0.128
Region area (10^3 n.mi.^{2})	20	12	29	9	21	29

TABLE 2
Effective Annual Sample Sizes for the Abundance Indexes

Species	Northern anchovy		Pacific sardine		Pacific mackerel		Jack mackerel		Pacific whiting		Pacific saury	
Year	N cells	Sum weights	N cells	Sum weights	N cells	Sum weights	N cells	Sum weights	N cells	Sum weights	N cells	Sum weights
1951	20	1.000	36	1.000	24	1.000	—	—	18	1.000	30	1.000
1952	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1953	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1954	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1955	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1956	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1957	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1958	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1959	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1960	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1961	12	0.601	24	0.659	18	0.707	18	0.595	12	0.540	18	0.652
1962	13	0.851	21	0.482	12	0.416	15	0.265	13	0.925	15	0.549
1963	15	0.691	24	0.654	18	0.733	18	0.620	15	0.540	18	0.741
1964	10	0.586	21	0.567	15	0.553	15	0.370	10	0.540	15	0.565
1965	9	0.653	23	0.656	18	0.683	20	0.567	9	0.515	17	0.580
1966	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1967	—	—	9	0.277	9	0.394	9	0.203	—	—	3	0.096
1968	—	—	—	—	—	—	6	0.319	—	—	6	0.141
1969	15	0.939	29	0.860	21	0.847	23	0.721	15	0.810	23	0.835
1972	15	0.859	24	0.539	12	0.492	18	0.428	15	0.970	18	0.557
1975	10	0.414	24	0.710	18	0.840	24	0.833	10	0.460	18	0.531
1978	16	0.942	30	0.868	21	0.847	24	0.738	16	0.925	24	0.875
1979	17	0.943	—	—	—	—	—	—	17	0.928	18	0.708
1980	15	0.946	—	—	—	—	—	—	15	0.913	15	0.619
1981	17	0.983	31	0.892	21	0.847	25	0.743	17	0.872	25	0.858
1982	10	0.537	10	0.187	—	—	—	—	10	0.790	10	0.194
1983	5	0.309	5	0.095	—	—	—	—	5	0.447	5	0.103
1984	17	0.958	32	0.891	—	—	—	—	17	0.975	26	0.909
1985	11	0.595	11	0.299	—	—	—	—	11	0.743	11	0.358

are relatively well sampled, i.e., that lacked no more than about one month's observations during the peak spawning period.

RESULTS

In all six species cases, the time series of abundance indexes estimated from equation 1 and the month-region interaction model of equation 2 are nearly indistinguishable, indicating that no serious distortion results from the model in equation 1. Because of the lack of differences, we do not include detailed results of these comparisons in this report.

*Northern Anchovy (*Engraulis mordax*)*

The unweighted ANOVA showed a protracted spawning season (Figure 2), with the peak months of February through May accounting for 85% of the larvae seen during the year. The two inshore

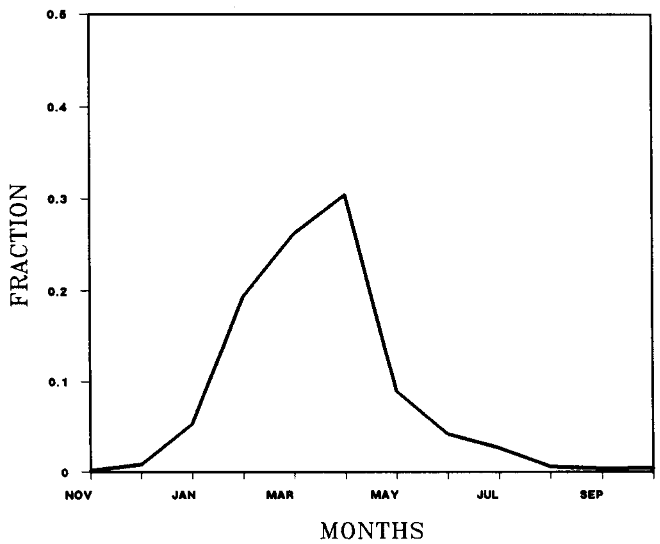

Figure 2. Seasonal distribution of northern anchovy larvae.

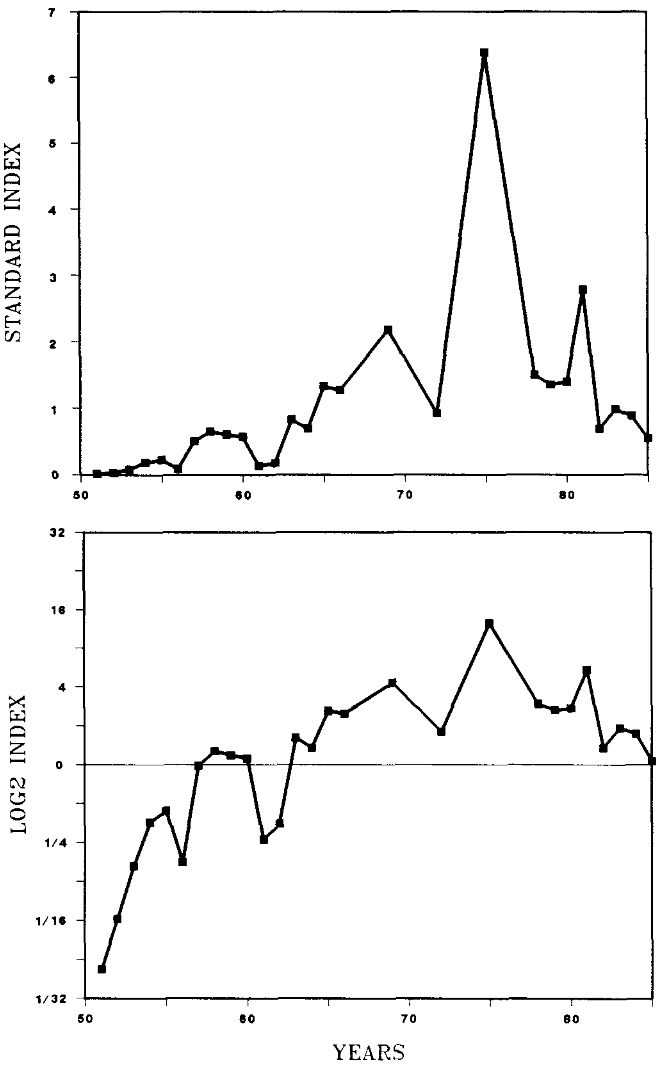

Figure 3. Time series of abundance indexes for northern anchovy larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale.

regions account for 95% of the total larvae (Table 1). Because the southern, offshore region 14 accounts for very few larvae (less than 0.1%), we omitted it from the weighted ANOVA.

Overall, the abundance indexes (Figure 3) were quite similar to the historical egg production time series developed by Lo (1985) from much more complete information including the size distribution of larvae. The main exception was the index value for 1978, which we estimated to be much lower than Lo's value. However, Lo's estimate for 1978 (unlike other years in the series) is based on an assumed preliminary value regarding egg retention by the bongo net (Lo 1983). This value was later revised based on experiments conducted in 1984 (N. Lo, SWFC, pers. comm.); the updated egg retention value was used by Methot (1986) and gives a 1978 value that is similar to the index value developed here.

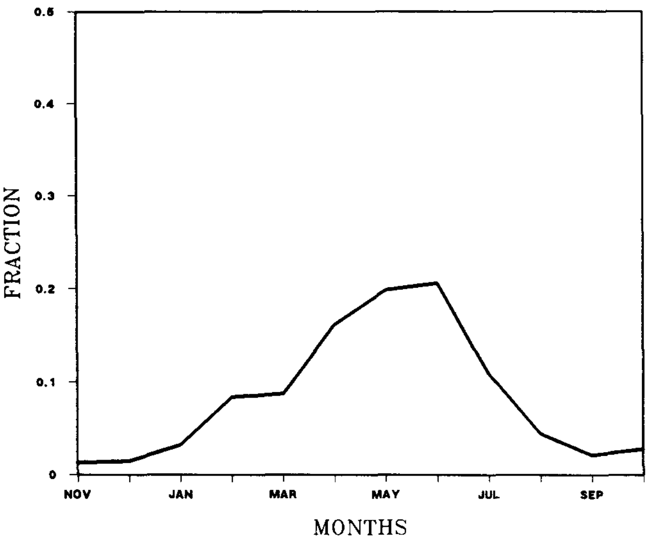

Figure 4. Seasonal distribution of Pacific sardine larvae.

Pacific Sardine (Sardinops sagax)

The long apparent spawning season (Figure 4) is partially an artifact of the added constant; sardine larvae have been scarce for many of the 35 years covered by the surveys. The main spawning period is April, May, and June, but a broad peak appears to extend from February through July and includes at least 85% of the larvae seen during the year. About half of the larvae occurred in inshore southern California waters (region 7), and 80% occurred in combined nearshore regions 7, 11, and 13 (Table 1). As in the case of nonpeak spawning months, the importance of the offshore regions (8, 9, and 14) was probably exaggerated because of the added constant.

The minimum abundance index corresponding to "no larvae" was only slightly below the estimates obtained for the 1970s ($\log_2$[minimum] = −3.99; Figure 5). Our abundance estimates for this low period are therefore not reliable, and the population may well have reached lower levels of abundance than those suggested by our analysis. However, for the first half of the time series, the indicated decline is in agreement with the trend in estimates of abundance derived from fishery catch data (MacCall 1979).

Pacific Mackerel (Scomber japonicus)

As in the case of the sardine, the long apparent spawning season is partially an artifact of the added constant and the low abundance of larvae experi-

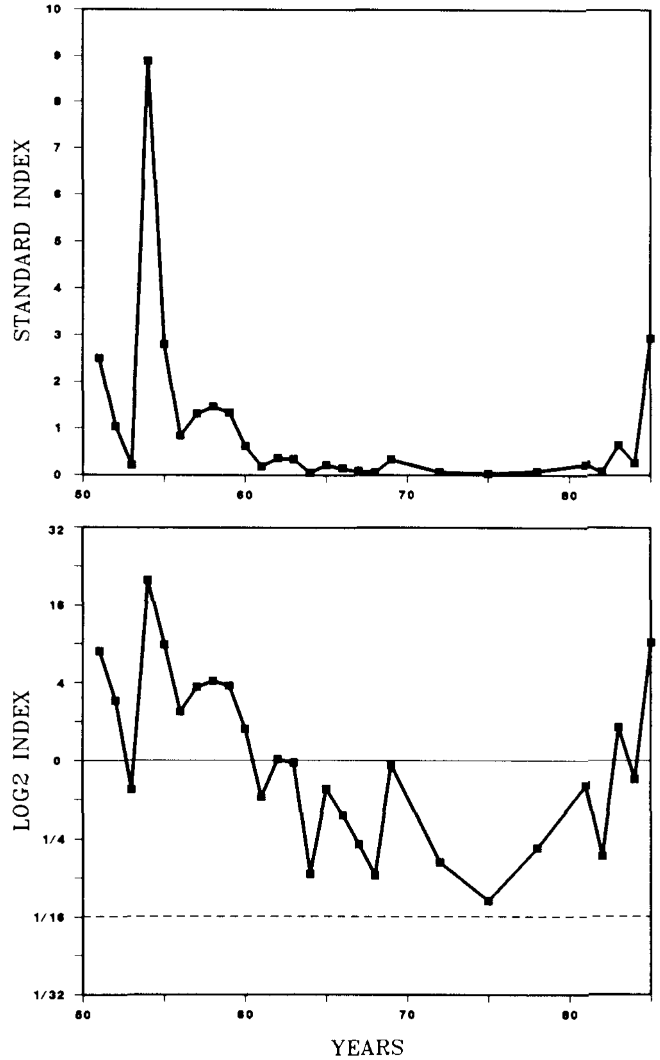

Figure 5. Time series of abundance indexes for Pacific sardine larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale. Dashed line indicates minimum abundance index due to added constant.

enced over much of the time series. Peak spawning is in May through July (Figure 6); however, we included April as a fourth month to increase the sample size. The period April–July accounts for at least 68% of the larvae seen during the year (the true average spawning season is probably more peaked than that calculated here, because of the added constant). Larvae were distributed rather evenly among the six regions (Table 1), but again this evenness also may be exaggerated by the added constant. The index value for 1975 is very near the minimum possible estimate ($\log_2$[minimum] = −4.26; Figure 7); as in the case of the sardine, lower levels of abundance may have been reached than are indicated by our analysis. The sudden increase in 1978 and 1981 is consistent with the recent resurgence of the population (MacCall et al. 1985).

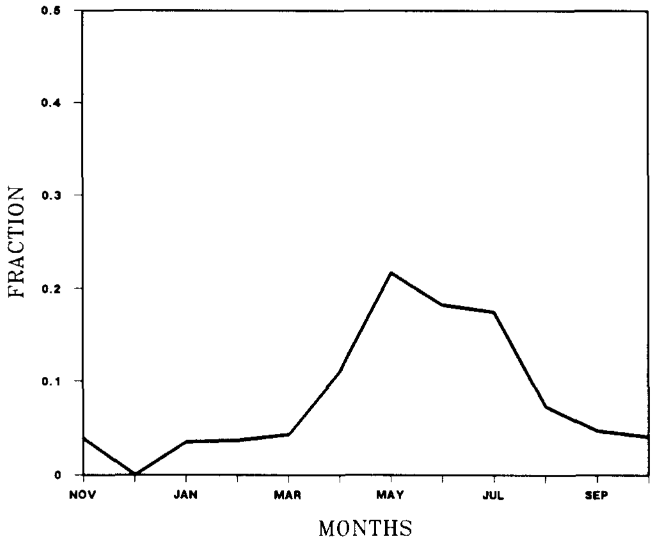

Figure 6. Seasonal distribution of Pacific mackerel larvae.

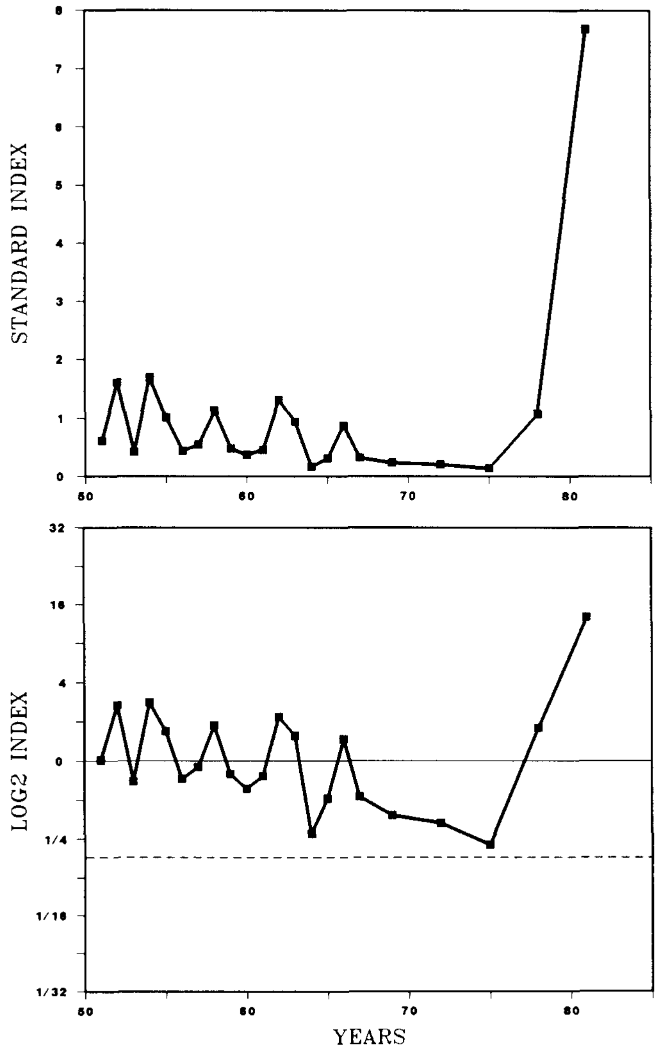

Figure 7. Time series of abundance indexes for Pacific mackerel larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale. Dashed line indicates minimum abundance index due to added constant.

Jack Mackerel (Trachurus symmetricus)

There is a sharp peak of larval abundance in May and June (Figure 8), but for purposes of the ANOVA, we used a peak spawning season of March through July, accounting for 97% of the annual total. Larvae are mostly offshore, with regions 9, 13, and 14 accounting for 83% of the total (Table 1). At the time this study was conducted, the CalCOFI data for 1951 were incomplete, so 1951 was not included in the calculations. The time series of larval abundance indexes (Figure 9) is highly variable, and does not correspond closely to the time series of mean larval abundances compiled by MacCall and Stauffer (1983), which included information from waters off central California. We also note for jack mackerel as well as for some other species that the variability in this index must be far greater than the true variability of a population composed of long-lived individuals.

Pacific Whiting or Hake (Merluccius productus)

The very short spawning season of whiting (Figure 10) prevents extending the analysis beyond February, March, and April, during which 97% of the larvae are observed. Also, 84% of the larvae were observed in the northern three regions (Table 1). Ahlstrom (1969) notes that through 1966, the standard CalCOFI plankton samples, which reached a maximum depth of about 140 m, "evidently do not encompass the complete vertical distribution of hake eggs and larvae at some stations." The depth of the standard CalCOFI plankton samples was extended to about 210 m beginning in 1969, at which time the netting was also changed from silk to an equivalent but more uniform nylon

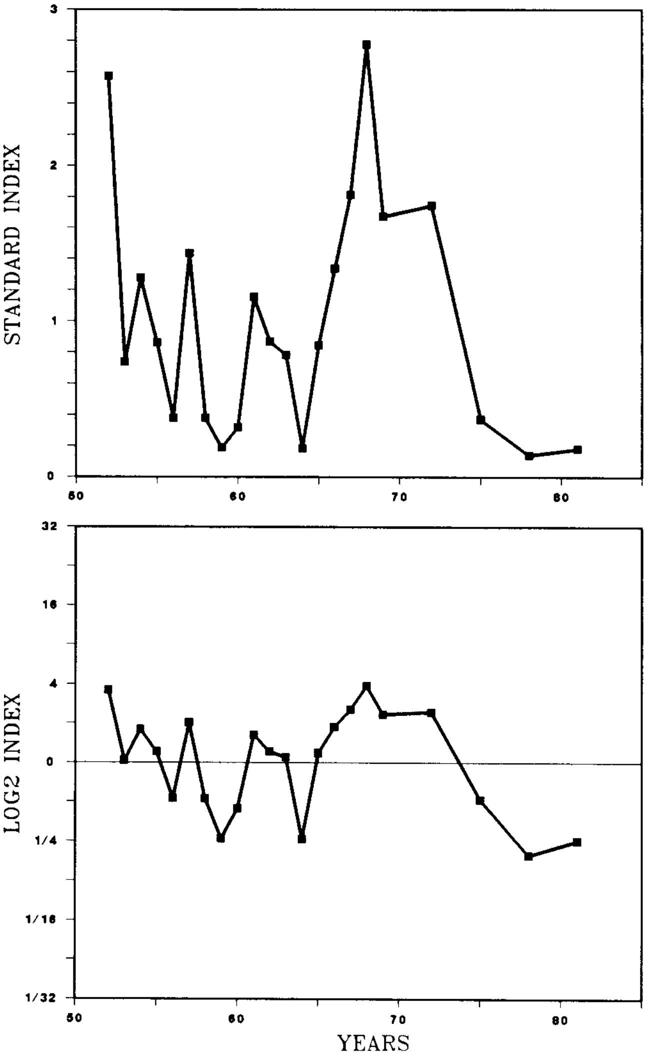

Figure 9. Time series of abundance indexes for jack mackerel larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale.

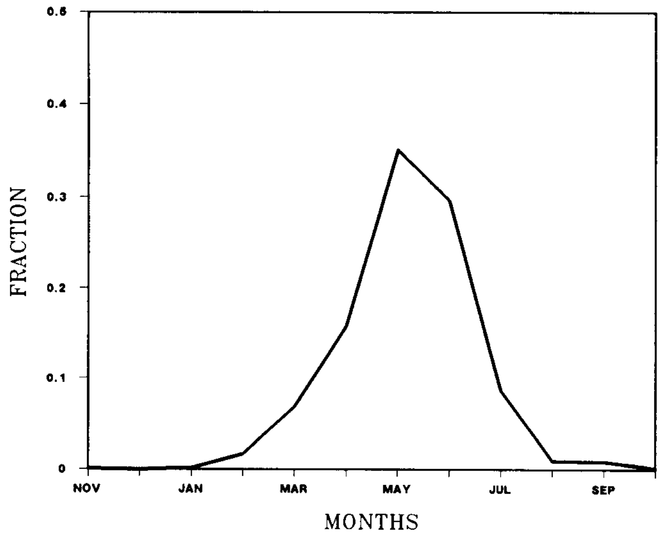

Figure 8. Seasonal distribution of jack mackerel larvae.

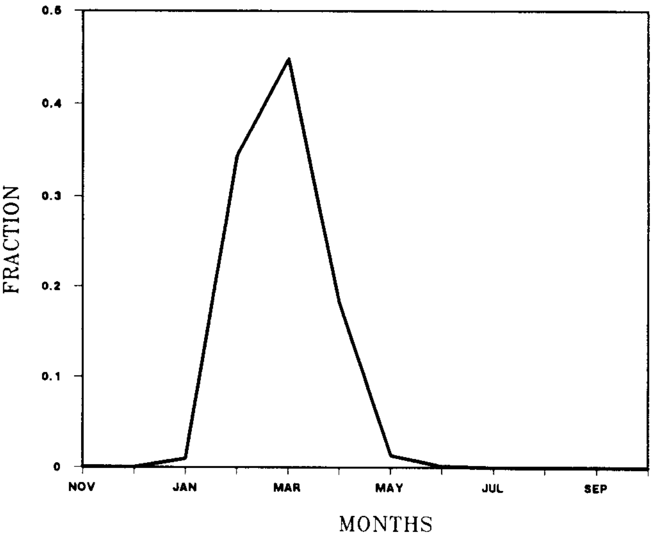

Figure 10. Seasonal distribution of Pacific whiting larvae.

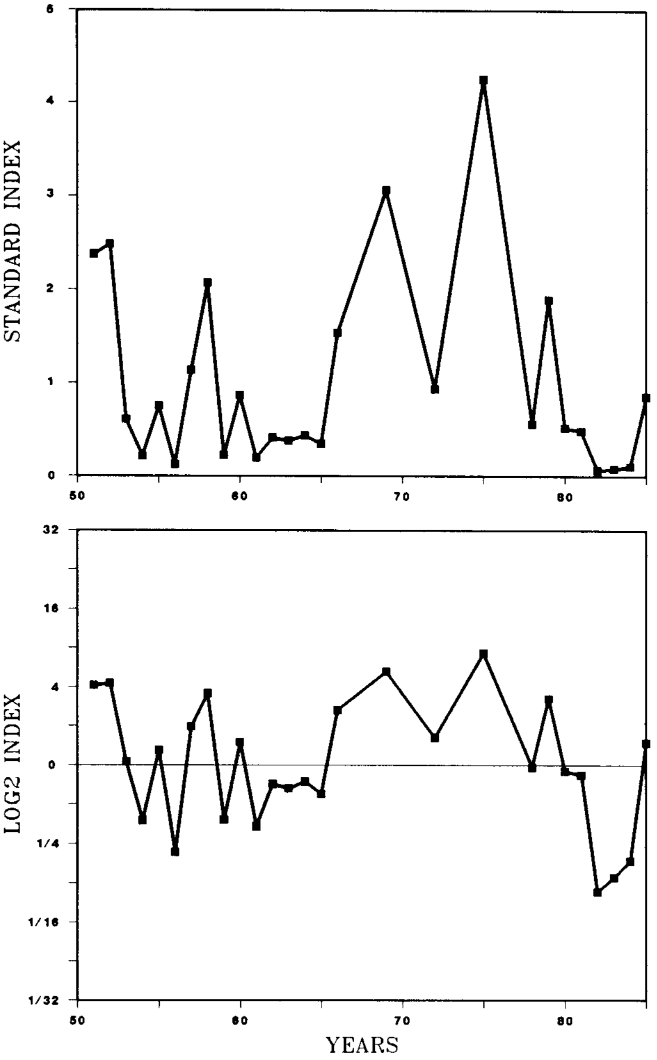

Figure 11. Time series of abundance indexes for Pacific whiting larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale.

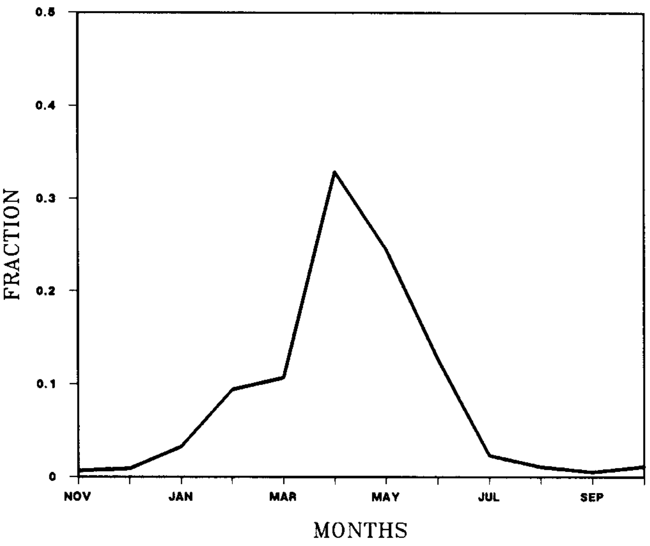

Figure 12. Seasonal distribution of Pacific saury eggs.

mesh (Smith 1974). The index of whiting abundance (Figure 11) is higher during the period following these sampling changes, but changes in actual abundance cannot be discounted; the index increases in 1966, immediately prior to the sampling changes, and the low levels of 1982–84 are lower than any seen previously. The index for whiting is highly variable, and does not agree with abundance estimates based on fishery data (Hallowed et al. 1987), which show a major increase during the 1980s.

Pacific Saury (Cololabis saira)

Egg abundance is very high in April (Figure 12), but we assumed a more extended peak spawning season of February through June, covering 90% of the annual total eggs observed. The geographic distribution of eggs is fairly even, except for a scarcity in region 11 (Table 1). There has been an irregular decline in abundance of saury eggs in the study area since the early 1950s, with eggs being nearly absent since 1980 (note that the latter indexes approach the minimum value possible in this analysis, $\log_2$ [minimum] = -5.24; Figure 13). We cannot determine from internal evidence if the change is due to a northward contraction of the spawning distribution, or if it is a population decline. Few years during the transition period were sampled; the southern regions are incompletely covered; and the geographic coverage of this study is very limited with respect to the overall distribution of saury spawning.

DISCUSSION

The ANOVA method is successful in that it accommodates missing values and produces easily derived indexes of abundance. The method does have shortcomings, especially in treating geographic or seasonal shifts in distribution among years, which seems to be a major source of error. Inclusion of data from waters off central California might have clarified some northward shifts, but that area has a high incidence of missing values, and its contribution would be correspondingly imprecise. In the case of rare larvae, results are biased by the added constant in equation 1. Of course, there is little information content in years where few or no larvae are encountered.

Several improvements on this log-linear or ANOVA approach should be investigated. Missing values may be better accommodated by the EM algorithm (Haberman 1974). Even better would be the maximum likelihood approach, which would include variable sample sizes among cells, but re-

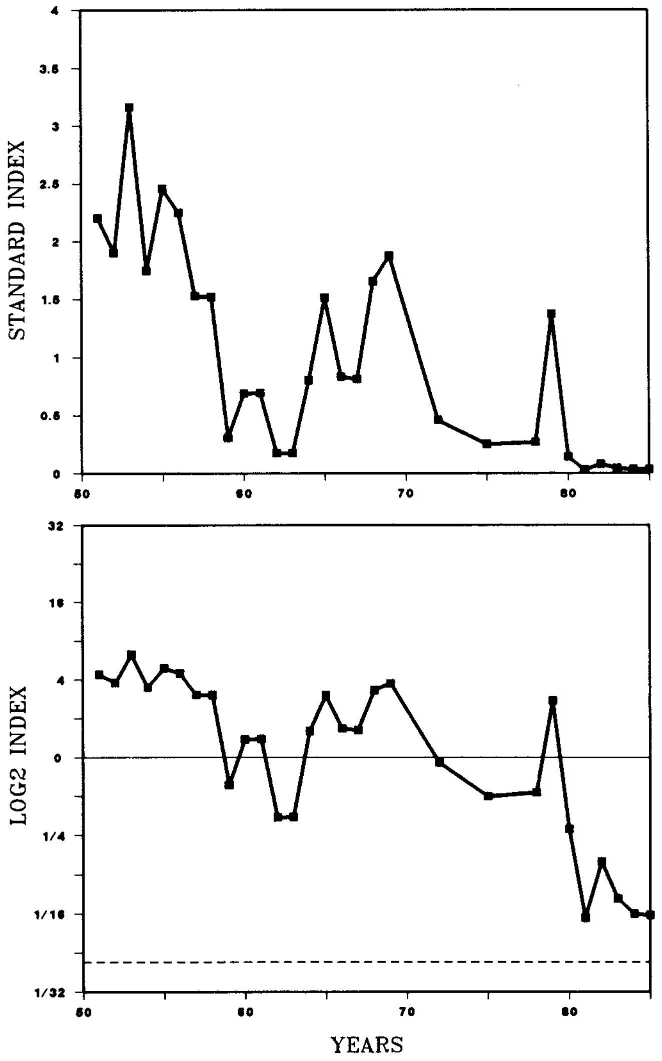

Figure 13. Time series of abundance indexes for Pacific saury eggs. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale. Dashed line indicates minimum abundance index due to added constant.

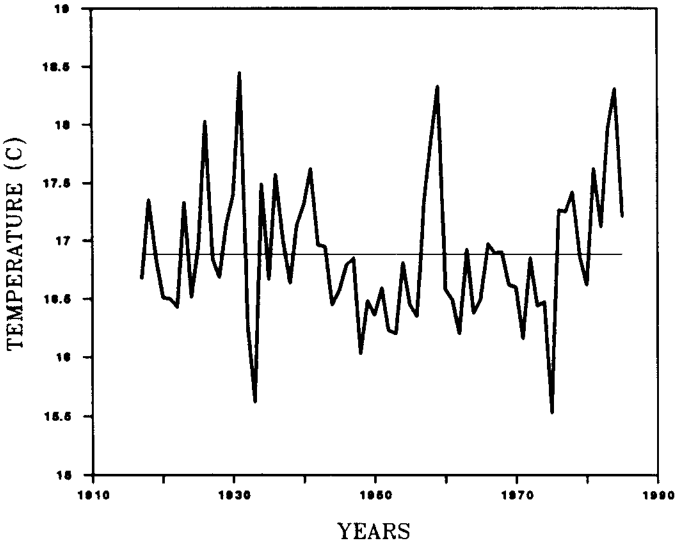

Figure 14. Time series of annual average Scripps Pier water temperatures. Horizontal line is long-term mean.

sults would still be imprecise. Methods for accounting for region-year and region-month interactions should be investigated. The performance and robustness of various approaches could be investigated by means of simulated data. Regions could be redefined in a manner appropriate for each species, and regions off central California should be included.

Major changes in the indexes of three species—Pacific sardine (increase), Pacific mackerel (increase), and Pacific saury (decrease)—have occurred in the last decade, and there is a suggestion that the indexes for Pacific whiting and jack mackerel also have decreased. The California Current has tended to be warmer since the mid 1970s. Annual average Scripps Pier temperatures (Figure 14) have risen by about one-half a degree Celsius, ending a cool period extending from the early 1940s. The warming has been more consistent in the offshore regions of the California Current (Cole and McLain, in press). Pacific saury and jack mackerel spawn relatively northward and offshore, and we speculate that the declines in abundance indexes for these two species are probably the result of northward spawning shifts in response to this warming. For this reason, we prefer to interpret the recent declines in these indexes as shifts in distribution rather than decreases in population abundance.

The spawning area of Pacific whiting similarly shifted northward in recent years (Paul Smith, SWFC, pers. comm.), presumably also in association with the oceanic warming. We also interpret the recent decline in the abundance index for whiting as the result of a northward shift in spawning, with a substantial portion of the population now spawning off central California. Contrary to the decrease in this larva-based index, fishery-based estimates of whiting abundance show a substantial increase during the 1980s, but declining sizes at age in the U.S. fishery independently suggest a northward shift of the resource (Hallowed et al. 1987).

On the other hand, the increases in indexes for sardine and Pacific mackerel, which also coincide with the warming, are definitely associated with respective increases in population abundance (Wolf and Smith 1986; MacCall et al. 1985). Again, these increases have been accompanied by northward shifts in the spawning distributions as indicated by the larval distributions.

The time-series of these six species underscores the importance of long-term monitoring. Had the CalCOFI surveys ceased in 1975, these time series would be far less interesting. Of the six species, only the index for anchovy shows little change after 1978, and that index shows a very large change in the first decade of the time series. Thus, a time series spanning only 25 years would risk missing major population or environmental changes, whereas a series spanning 35 years seems, at least in this case, to have detected major changes.

Isaacs (1976) emphasized the importance of "regimes" in contrast to the usual assumptions of stability (or stable distributions of environmental conditions) underlying fishery models. The temperature history in Figure 14 suggests three major temperature regimes: warm from the beginning of observations in 1916 to the early 1940s (>30 yr), cold to the mid 1970s (ca. 35 yr), and then warm again. The earlier warm regime preceded the era of physical and biological monitoring. The physical and biological changes associated with the recent warming indicate that Isaacs's concern with regimes was justified. Long-term monitoring, such as has been conducted by CalCOFI, is vital to understanding these phenomena.

ACKNOWLEDGMENTS

In addition to the many people who have contributed to the CalCOFI program over the past 35 years, we wish to thank several people who contributed particularly to the present paper. Celeste Santos Methot compiled the source data from the CalCOFI data files. Rich Charter, John Michno, and Kevin Colwell provided computer programming and data base management support. Geoff Moser and his co-workers provided summaries of larvae from recent CalCOFI cruises virtually as the identifications were being completed. Finally, we thank the Ocean Assessments Division, National Ocean Service, NOAA, for supporting this investigation.

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COUPLING OF THE PACIFIC SARDINE (*SARDINOPS SAGAX CAERULEUS*) LIFE CYCLE WITH THE GULF OF CALIFORNIA PELAGIC ENVIRONMENT

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ABSTRACT

The distribution of the Pacific sardine (*Sardinops sagax caeruleus*) in the Gulf of California led others to a conceptual model of the migration patterns over its life cycle. We examine the model in light of our recent understanding of the physical processes in this marginal sea. There appears to be a remarkable coupling between the two. The adult spawning migration from the northern feeding grounds and the subsequent spawning in the Guaymas Basin occurs in winter and early spring, at which time strong northwesterly winds predominate, and strong coastal upwelling is observed along the eastern margin of the gulf. The well-defined squirts and jets that result off the main capes appear to transport eggs and larvae across the gulf towards the Baja California coast, where juveniles concentrate. The summer conditions of southeasterly winds coincide with the migration of juveniles to the adult feeding grounds, thus closing the migratory life cycle. There are indications that the availability of adult Pacific sardines to the fishery depends on the intensity of the upwelling-favorable northwesterly winds and on interannual changes of thermal conditions occurring in the central gulf associated with the El Niño/Southern Oscillation (ENSO) phenomena. Density-dependent food competition among juveniles, and cannibalism on eggs and larvae are proposed as two possible mechanisms affecting recruitment during ENSO events, when the habitat of the Pacific sardine is compressed to the north.

RESUMEN

Un modelo conceptual del ciclo migratorio de la sardina (*Sardinops sagax caeruleus*) en el Golfo de California ha sido formulado por Sokolov y Wong basado en la distribución de los estadios juveniles y adultos. Este modelo es examinado incorporando el entendimiento reciente acerca de algunos procesos físicos que predominan en esta región. Notamos una correspondencia considerable entre ambos. La sardina adulta emigra del alto golfo hacia la cuenca de Guaymas para desovar en invierno y principios de primavera, cuando predominan los vientos del noroeste y se registran surgencias pronunciadas a lo largo del margen oriental del golfo. Los penachos de agua fría que se forman en extensión de los cabos y promontorios principales proporcionaría el mecanismo para transportar huevos y larvas hacia la costa de Baja California, donde se concentran los juveniles. Las condiciones de verano, con vientos del sureste, coinciden con la migración de los juveniles hacia las regiones donde se alimentan en su etapa adulta, cerrando así el ciclo migratorio. Existen indicaciones que la disponiblidad de sardina Monterrey a la pesquería depende de la intensidad de los vientos del noroeste, favorables a los procesos de surgencia, y de los cambios interanuales observados en la configuración térmica de las capas superficiales del golfo central como occurre, por ejemplo, durante un evento de El Niño. La competencia entre trófica juveniles, que depende de la densidad de la población, y el canibalismo de huevos y larvas por juveniles y adultos son propuestos como posibles mecanismos que afectan el reclutamiento durante eventos de El Niño, cuando el hábitat de la sardina Monterrey se encuentra reducido al norte.

INTRODUCTION

The Gulf of California is a semienclosed sea about 1000 km long and 100 to 200 km wide, bounded by the Baja California Peninsula on the west and by the states of Sonora and Sinaloa on the Mexican mainland to the east. The upper gulf, roughly one-third of its total length, is separated from the lower gulf by two large midriff islands and an irregular sill. The lower gulf comprises a series of basins, which deepen from approximately 2000 m off Guaymas to over 3000 m at the mouth. Most of the upper gulf is shallower than 200 m, except for the basins surrounding the pedestal of Ángel de la Guarda Island. Surface waters at the sill are typically cooler year-round than those of the lower gulf because of strong tidal mixing (Roden 1964; Badan-Dangon et al. 1985). The principal difference between the waters inside the Gulf of California and those of the adjacent open Pacific is the additional presence of a high-salinity water mass at or near the surface in the gulf. This water

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is formed by evaporation in the upper gulf and appears to be modified by mixing with subsurface water from the eastern tropical Pacific (Roden and Groves 1959; Alvarez-Borrego and Schwartzlose 1979).

The Pacific sardine, *Sardinops sagax caeruleus*, is distributed from the Gulf of California to Kamchatka, Alaska (Miller and Lea 1972). In the Gulf of California, it is found principally in the central region, where it supports, in terms of biomass, the most important pelagic fishery in the gulf. A hypothesis for the migration patterns of this species over its life cycle in the Gulf of California has been proposed by Sokolov and Wong-Rios (1973) and by Sokolov (1974). The purpose of this paper is to examine this migration hypothesis in light of recent observations augmenting our current knowledge of the physical variability in the pelagic ecosystem of the Gulf of California. We suggest that the general migration pattern of the Pacific sardine in the gulf can be explained by the seasonality of near-surface temperature and circulation patterns. We hypothesize that similar mechanisms will also vary the pattern of migration on an interannual scale and may thus affect adult availability to the fishery (as suggested by Lluch-Belda et al. 1986) as well as juvenile recruitment to the adult stock.

SATELLITE IMAGERY

Satellite data were received, archived, and processed at the Scripps Satellite Oceanography Facility. Infrared radiation propagating spaceward from the Gulf of California was measured with the Advanced Very High Resolution Radiometer (AVHRR) on the polar-orbiting NOAA-6 satellite. The spatial resolution of the AVHRR is 1.1 km at nadir. Visible radiance data from the Coastal Zone Color Scanner (CZCS, Nimbus-7 satellite) was used to calculate average chlorophyll *a* and phaeopigment concentration (one attenuation depth) using an algorithm based on Gordon et al. (1983). Without simultaneous shipboard measurements it is difficult to estimate the accuracy of pigment concentration calculated from satellite-measured sea-surface color; estimates should be taken as approximate. Relative spatial accuracy, however, is very good. The spatial resolution of the CZCS is about 0.8 km at nadir.

We chose to study April 7, 1980, because Badan-Dangon et al. (1985) showed this to be a day when the central gulf's frontal systems were very well developed and because both clear infrared irradiance and ocean color data were available. Although there is a time lag between surface temperature and the biological response (for example, between initial upwelling and increased primary production), we used both infrared and CZCS images from the same day because no other CZCS data were available until April 23. All images were contrast-enhanced to improve pattern recognition, and were mapped so that warmer temperatures and lower pigment concentrations are associated with darker grey shades. The positional accuracy of the processed images is approximately ± 2.2 km.

VARIABILITY IN PHYSICAL ENVIRONMENT AND MIGRATION PATTERNS

The general circulation of the Gulf of California appears to be dominated by the regional wind field. During winter months, northwesterly winds predominate (Roden 1964; Candela et al. 1984, 1985); they are favorable for coastal upwelling along the eastern coast. During spring, the winds and resulting upwelling intensify, producing well-developed plumes of upwelled water across the gulf from off the capes near Guaymas and Yavaros (Badan-Dangon et al. 1985). During late spring, the wind changes to a southeasterly regime, which dominates throughout the summer months; summer upwelling occurs off the western Baja California coast, but is less intense than spring upwelling. Geostrophic calculations by Rosas-Cota (1977) indicate that the net flow at the surface is to the south during winter and spring, and to the north during summer and fall.

Figure 1 presents Sokolov and Wong-Rios's (1973) hypothesis in the line drawing beside an infrared satellite image indicating the surface thermal patterns of April 7, 1980. The remarkable similarity between the proposed larval transport pattern and the observed surface temperature pattern suggests a strong coupling of the two. Sokolov and Wong-Rios (1973) gathered information showing both adult and juvenile migration patterns. Because spawning was thought to be mostly on the east coast of the gulf, and juveniles were found concentrated on the west coast, they postulated that eggs and larvae are transported by the dominating surface circulation from the east to the western nursery grounds, but no mechanism was suggested. The satellite image presented in Figure 1 shows the formation of surface jets of cool water extending from the Guaymas and Yavaros spawning areas to the west coast of the gulf, thus providing a specific mechanism for such east-west egg and larval transport.

Adults migrate along the east coast of the gulf

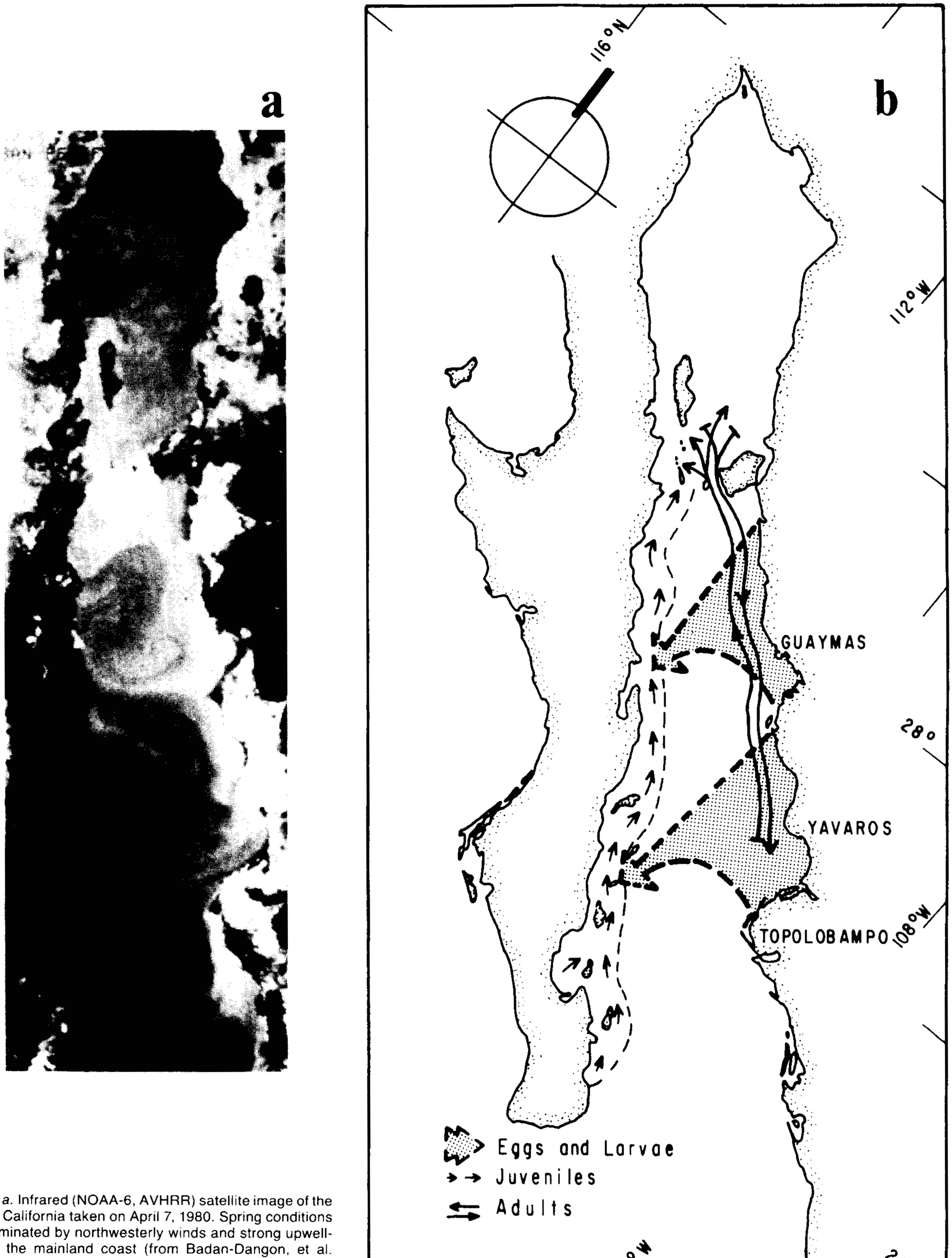

Figure 1. *a.* Infrared (NOAA-6, AVHRR) satellite image of the Gulf of California taken on April 7, 1980. Spring conditions are dominated by northwesterly winds and strong upwelling off the mainland coast (from Badan-Dangon, et al. 1985). *b.* Schematic representation of the life cycle of the Pacific sardine in the Gulf of California as proposed by Sokolov and Wong-Rios (1973).

from their summer feeding grounds in the northern gulf toward their spawning grounds, principally in the region of Guaymas and Yavaros, from January to April. Spawning generally occurs during this period (Wong-Rios 1974), although recent work has found spawning as early as November (Cisneros-Mata et al. 1987); after spawning, the adults return north. This adult southern migration occurs during the period of cool southerly flow and intense coastal upwelling along the eastern coast; the return north coincides with summer warming and the decreased upwelling off the eastern coast associated with the general flow to the north shown by Rosas-Cota (1977). Juveniles are found on the west coast during the period of western upwelling; they migrate north to join the adults in the northern gulf with the late-summer northern flow.

Although the similarity between the larval transport pattern proposed by Sokolov and Wong-Rios (1973) and the thermal patterns on Figure 1 are quite striking, it is important to recognize that sea-surface temperature derived from infrared satellite imagery originates only from a thin surface film (approximately 0.02 mm), and may not represent the temperature and thus the flow at greater depths (Stewart 1985). Therefore it is important to examine more closely whether the circulation patterns reported by Badan-Dangon et al. (1985) could represent a net transport of the eggs and larvae throughout a significant depth in the near-surface layers of the gulf. Because sea-surface color results from processes integrated approximately over the euphotic zone (Morel and Gordon 1980), color is helpful for gauging a minimum depth of these circulation patterns. The concentration of chlorophyll-like pigments in the surface layer (one attenuation depth) greatly contributes to the observed color (Stewart 1985). Sea-surface color, therefore, should better represent net transport of water in the surface layer and may therefore be a better indicator of egg and larval transport. Clearly, pigment concentrations also indicate the relative food availability for first-feeding larvae.

A pattern in the satellite image of sea-surface color is quite similar to that observed in surface temperature (Figure 2), suggesting that the circulation pattern extends down through at least the surface layers. Figueroa and Robles (1987) have shown evidence that the surface patterns are part of a deep baroclinic circulation that may extend to the bottom of the gulf. That the coolest water shows the highest pigment concentration indicates that upwelled, nutrient-rich water from the eastern coast of the gulf is carried by the jets, resulting in higher productivity within the filaments and lower productivity in the surrounding waters.

Temperature and phytoplankton pigment concentration are important measurements to represent the general surface environment. Mean surface temperatures at Guaymas range from about 17.5°C in January to roughly 32°C in August (Cisneros-Mata et al. 1987). Tibby (1937) found the optimum temperature range for Pacific sardine spawning to be between 15° and 18°C for the Pacific coast population. Satellite imagery shows that the surface temperatures on April 7, 1980, ranged from approximately 16° to 19°C (Figure 2). Although typical chlorophyll *a* concentrations have not been reported for the Gulf of California, an average concentration of approximately 5.6 mg chlorophyll *a* m^{-3} was found near Guaymas in March 1983 during the 1983–84 El Niño event (estimated from vertical profiles in Valdez–Holguin 1986); the depth of maximum chlorophyll *a* concentration at this station was about 17 m. A year later, during March 1984, the average concentration was approximately 1.8 mg chlorophyll *a* m^{-3}, and the depth of maximum chlorophyll concentration was about 60 m, below the depth of 1% surface irradiance. Average surface-layer chlorophyll-like pigment concentrations as determined by satellite imagery ranged from approximately 0.5 to 3.0 mg chlorophyll *a* + phaeopigments m^{-3}; very near the coast, over 6.0 mg chlorophyll *a* + phaeopigments m^{-3} were found (Figure 2).

DISCUSSION

The observation of Pacific sardine spawning in the Gulf of California in areas of intense upwelling is quite different from the spawning of pelagic fishes in the California Current. Parrish et al. (1981) suggested that northern anchovy avoid spawning in strong upwelling areas to prevent their eggs and larvae from being transported offshore. Smith and Lasker (1978) wrote that the effect of upwelling should favor northern anchovy adults but would be detrimental to their embryos and larvae. In the gulf, the Pacific sardine seem to spawn preferentially in these areas to enhance the cross-gulf transport of their eggs and larvae. Of course, this does not simply move them offshore, as would be the case in the California Current, but takes them to the western shore. Satellite imagery suggests that eggs and larvae are entrained in cross-gulf squirts and are transported to the west along with high-productivity water. Similar offshore entrainment for eggs and larvae has been described by Fiedler (1986) for the northern anchovy in the

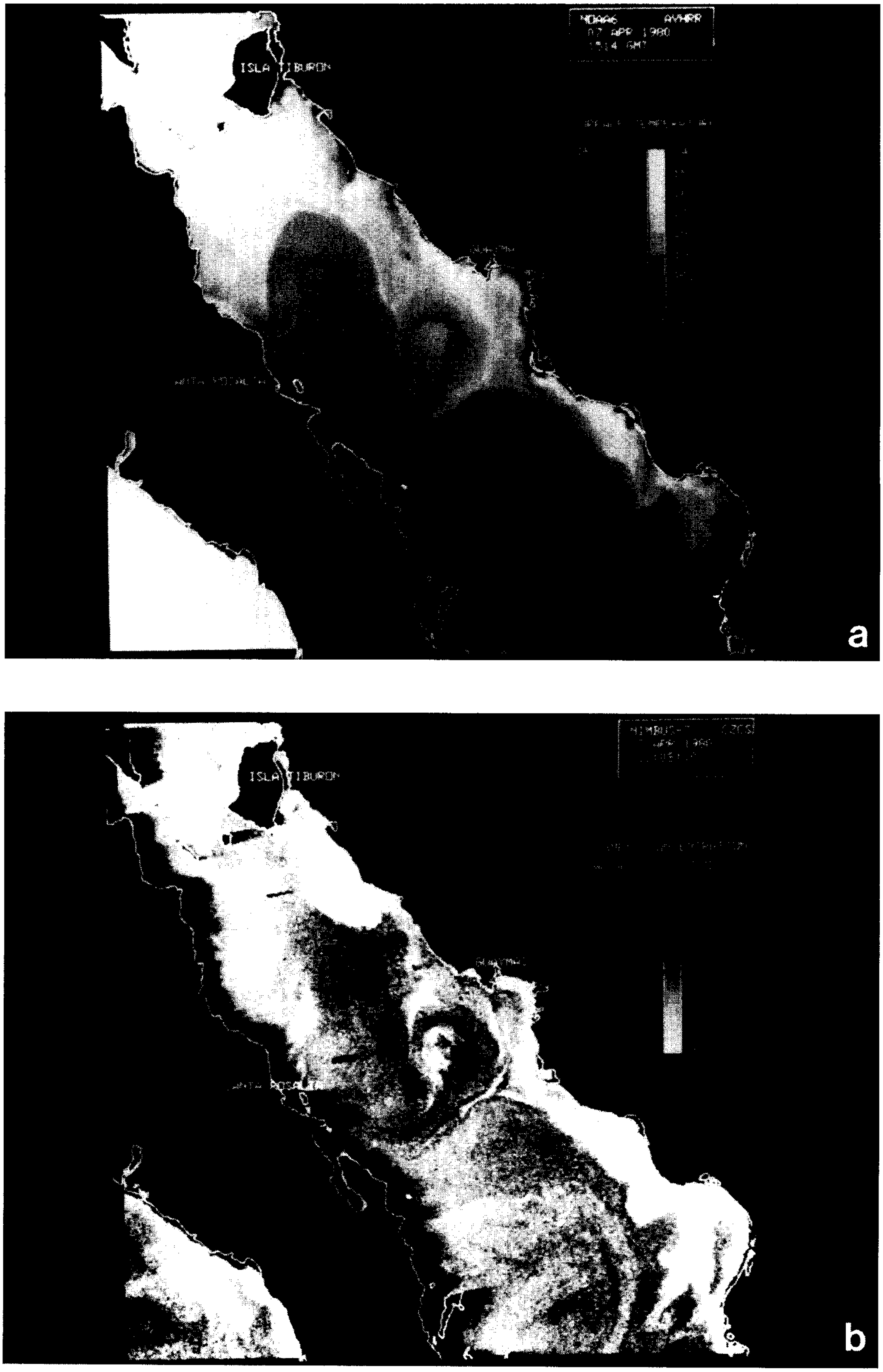

Figure 2. Satellite images of the central Gulf of California on April 7, 1980. *a*. A portion of Figure 1*a* calibrated to derive surface temperature. *b*. The corresponding NIMBUS-7 Coastal Zone Color Scanner Image showing the distribution of chlorophyll-like pigments, corresponding markedly to the pattern of surface temperature shown in *a*.

California Current, but this is not a normal occurrence.

Although the estimated distribution and abundance of Pacific sardine eggs and larvae in the Gulf of California during 1956–57 (Moser et al. 1974) did not reflect the surface patterns in temperature and chlorophyll *a* content shown by satellite imagery, or the pattern of transport proposed by Sokolov (1974), the spatial scale of the stations was too coarse to detect such directed transport. The surface jets seen in the satellite images were also not observed in the surface geostrophic flows (Rosas-Cota 1977) calculated from data collected from the same cruises in which Moser et al. (1974) sampled the ichthyoplankton. This emphasizes that satellite imagery is very important to adequately define the surface structure of the ecosystem over the temporal and spatial scales that are meaningful to the Pacific sardine. Additional habitat and ichthyoplankton survey data would also greatly help in this regard.

Larval mortality may also be affected by variability in surface conditions. Increased pigment concentrations in the jets suggest an increased food supply. Nevertheless, food may not be limiting outside the jets. Butler (1987) has shown that for larval northern anchovy, the growth rate was not affected by the low food availability that occurred with the 1983 El Niño event. For the northern anchovy population on the Pacific coast, the 1982–83 El Niño did, however, greatly affect the growth rate of juveniles (Fiedler et al. 1986; Butler 1987).

Most fishing effort for the Pacific sardine in the Gulf of California occurs near the eastern coast, principally offshore of the port of Guaymas. Data for the period 1969–80 show that interannual variation in the landings and catch-per-unit-effort (CPUE) of Pacific sardine are correlated with the El Niño/Southern Oscillation (ENSO) phenomena; during El Niño events, the landings and CPUE decreased. The reverse was found to be the case for the more tropical *Opisthonema* spp. (Huato-Soberanis and Lluch-Belda 1987). Lluch-Belda et al. (1986) proposed that fluctuations in Pacific sardine catches can be explained almost entirely by temperature-induced fluctuations in their availability. Under cooler, more temperate conditions during anti-El Niño years, the Pacific sardine can move farther south for a longer period and thus be available to the fishery for more time over a larger area, resulting in increased landings. If this is true, variation in current fishery landings for Pacific sardine in the Gulf of California may not reflect recruitment variation.

Since 1977, larger boats with greater range have been added to the sardine fleet in the Gulf of California; these vessels have the capability to fish where Pacific sardine are available. This has tended to reduce the correlation between the ENSO anomalies and Pacific sardine catch and CPUE; the catch of the smaller, limited-range vessels may still reflect this relation, however. This relation may also be due to changes in recruitment to the stock or to changes in the stock's availability to the fleet. Cisneros-Mata et al. (1987) have reported that the Pacific sardine population in the gulf is beginning to show signs of overexploitation (e.g., reduction in average age and length in the fishery). Huato-Soberanis and Lluch-Belda (1987) suggested that 5+ year cycles in mean sea level and mean surface temperature associated with the El Niño-Southern Oscillation are reflected in stock recruitment, as suggested by a similar cycle in the average length of commercially landed sardines. Nevertheless, one cannot escape the disadvantage of working with spatiotemporally selective commercial landings.

At present, the rate of Pacific sardine recruitment in the Gulf of California is not known. If decreased landings and CPUE during El Niño events, for example, are in part due to a decrease in recruitment, one could suggest the following: with the northern penetration of tropical, warm surface waters during an ENSO event (Baumgartner and Christensen 1985; Robles and Marinone 1987), the spawning area of the Pacific sardine in the gulf will be confined to the cool waters in the north, and thus be compressed. Furthermore, the nursery areas of the larvae and juveniles will be compressed northward. Santander and Flores (1983) also described similar adjustments in the distribution of spawning of both anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) with El Niño conditions off Peru.

Although food concentrations in the gulf are very high, an increased population density in a decreased habitat area may cause food to limit growth or fecundity. Butler (1987) showed that limiting food resources for juvenile northern anchovy greatly affects their growth rate and may increase their mortality. Also, when juveniles and adults coexist with eggs and larvae, cannibalism and predation of eggs and larvae by other species may increase in importance. The potential of egg and larval cannibalism as a density-dependent mechanism to control the populations of northern anchovy (Hunter and Kimbrell 1980) and Peruvian anchovy (Santander et al. 1983; Alheit 1987) has been clearly demonstrated. Typically, the adult migration of the Pacific sardine separates them from their eggs and larvae. Under compressed habitat conditions, as may occur with an El Niño event, they may continue to coexist.

Although cannibalism has not been reported for the Pacific sardine, it is unlikely that they would be capable of selecting against their eggs and larvae in the particulate food field. For Pacific sardine in the Gulf of California, Wong-Rios (1974) reported the occurrence of unidentified fish eggs in the stomach contents of over 25% of those analyzed. Off Peru, individual sardines were reported to consume three times the number of anchovy eggs compared to individual adult anchovies, and the degree of consumption was related to the abundance of eggs in the water (Santander et al. 1983). On a per-weight basis, Alheit (1987) found that sardines were more efficient at consuming eggs than anchovy. Therefore, the potential for cannibalism in Pacific sardine in the Gulf of California under compressed habitat conditions is very high. Mechanisms like those described here may partly explain the relation between ENSO conditions and Pacific sardine landings as recruitment becomes more important than adult availability to the fleet in the future.

CONCLUSIONS

We have shown that the general pattern of migration for the Pacific sardine in the Gulf of California proposed by Sokolov and Wong-Rios (1973) and Sokolov (1974) is consistent with the seasonal changes in near-surface temperature and circulation. We have also suggested a mechanism by which interannual variations in recruitment may be related to the occurrence and strength of El Niño/Southern Oscillation events. Nevertheless, these hypotheses imply various assumptions that must be tested.

First, because most information on the adult spawning area is derived from gonad analysis of fishery-caught animals, it is not known if adults spawn where the fleet does not fish; when sardines are available near the port of Guaymas, the vessels do not search farther. Second, the relation between mesoscale oceanographic structures like the cross-gulf jets and eddies shown here, and egg and larval transport has not been verified by ichthyoplankton collections; samples taken on more meaningful time-and-space scales are necessary. Third, it is not known how often the cross-gulf jets that coincide with the spawning season of the Pacific sardine occur in the Gulf of California. Serial analysis of satellite images will allow us to better describe the temporal as well as the spatial spawning habitat. Finally, our discussion here has ignored the importance of competition with or predation by other pelagic species in the environment. Butler (1987) described important interactions between the Pacific sardine and the northern anchovy in the California Current; northern anchovy has been recently reported in the Gulf of California (Hammann and Cisneros-Mata, in press), but its ecological role in the gulf is still not clear.

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BIOCHEMICAL GENETIC AND MORPHOLOGICAL DIVERGENCE AMONG THREE SPECIES OF THREAD HERRING (*OPISTHONEMA*) IN NORTHWEST MEXICO

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ABSTRACT

Three sympatric species of thread herring (*Opisthonema*) important in Mexican fisheries have been described solely on the basis of differences in numbers of gill rakers, taking standard length and geographic variation into account. Because the validity of these species has recently been questioned, we sought to reevaluate their taxonomic status. A combined electrophoretic and multivariate morphometric study of *Opisthonema* from northwest Mexico verifies the diagnostic accuracy of gill-raker number, confirms the status of the three species on biochemical genetic evidence, and suggests that external morphological characters might also be used to discriminate these species in the fishery. We infer from biochemical genetic data that *O. bulleri* diverged from the line leading to *O. medirastre* and *O. libertate* much before the separation of these last two species. How these three morphologically and genetically very similar, sympatric species of thread herring evolved in the eastern Pacific is problematic, particularly in light of evidence that *O. bulleri* and *O. medirastre* occasionally hybridize in nature.

RESUMEN

Las tres especies simpátricas de la sardina crinuda (*Opisthonema*), importantes en la pesquería mexicana, han sido descritas basandose sólo en el número de branquiespinas, pero tomando en cuenta la longitud patrón y el sitio geográfico de su captura. Debido a dudas recientes en cuanto a la validez de estas especies, hemos reevaluado su posición taxonómica. Una combinación de estudios electroforéticos, morfológicos multivariados de *Opisthonema*, provenientes de la región noroeste de México, verificó la precisión diagnóstica del número de branquiespinas y confirmó la validez taxonómica de las tres especies. Este análisis permitió además medir la divergencia evolutiva relativa entre estas especies y sugirió que características morfológicas externas podrían servir para distinguirlas. En base a los datos bioquímicos de la genética de estas tres especies, se infiere que *O. bulleri* se separó de la línea evolutiva de *O. medirastre* y *O. libertate* mucho antes de que estas últimas se separaran. La evolución de estas tres especies de sardina crinuda, simpátricas en el Pacífico Este, y muy semejantes en su genética y morfología es confusa, particularmente en vista de evidencia que *O. bulleri* y *O. medirastre* son ocasionalmente capaces de formar híbridos en la naturaleza.

INTRODUCTION

Five morphologically similar species of thread herring (*Opisthonema*) are recognized on the basis of their geographical distributions and numbers of gill rakers in relation to standard length (Berry and Barrett 1963). One species, *O. oglinum*, occurs in the western Atlantic and Caribbean; another, *O. berlangai*, is restricted to the Galápagos Islands; and the remaining three species, *O. bulleri, O. medirastre*, and *O. libertate*, are sympatric in the eastern Pacific from the Gulf of California to Peru. The sympatric species may be separated using Berry and Barrett's (1963) tabular key, which requires information on location of capture, standard length, and the number of ceratobranchial gill rakers on the first gill arch. For specimens captured in northern Mexico and exceeding 130 mm standard length, for example, ranges in numbers of gill rakers are 25–32 for *O. bulleri*, 40–69 for *O. medirastre*, and 59–109 for *O. libertate*. Individuals of the last two species having the same number of gill rakers have very different lengths. Berry and Barrett (1963) also examined eight meristic and six morphometric traits, but concluded that appreciable overlap in the ranges of these characters for species precluded their use in taxonomic separations. They did note, however, that "... some females tended to have slightly deeper bodies ... than males."

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Before the development of purse seining, thread herring had economic significance as live bait in the tuna fishery. They regained value after 1971, when a large sardine fishery was initiated in the Gulf of California (Arvizu-Martinez 1987). Today, this sardine fishery contributes 27% of Mexico's total fisheries landings (M. G. Hammann, pers. comm., calculated from FAO 1986). Landings of thread herring in the northwest region of Mexico are usually much less than those of the Pacific sardine (Cisneros-Mata et al. 1987), but *Opisthonema* dominates landings in El Niño years and tends to be more abundant in the Mazatlán area in most years (Lluch-Belda et al. 1986). Because of the growing economic importance of this sardine fishery, scientific interest in *Opisthonema* has revived. Recently, the validity of the three Pacific coastal species of *Opisthonema* has been questioned (Rodriguez-Sanchez 1985; Lopez-Lemus 1986), although Rodriguez-Dominguez (1987) supports the classification of Berry and Barrett (1963).

In order to settle this taxonomic controversy and to contribute new information on speciation in the genus *Opisthonema*, we applied the techniques of biochemical genetics (allozyme electrophoresis) and multivariate morphometry—tools not available to Berry and Barrett in 1963—to the systematics of thread herring in northwest Mexico. The results we present here fully support the taxonomy of Berry and Barrett. We verify the diagnostic accuracy of gill-raker counts on the basis of congruent, diagnostic, biochemical genetic differences and suggest further that the three species may have distinctive body shapes. Discriminant functions based on a few traits may provide a more practical means than gill-raker counts for species identifications by fisheries biologists working in the field. Finally, from biochemical genetic data, we estimate times of divergence among these closely related species. *O. bulleri* apparently diverged from the line leading to *O. medirastre* and *O. libertate* about 3.2 million years ago, nearly 2 million years earlier than these last two species separated from each other.

MATERIALS AND METHODS

Collections and Samples

Thread herring were obtained from Bahía Magdalena, Baja California Sur (9 collected from a boat at the dock in San Carlos in July 1985); Guaymas, Sonora (21 taken by panga, March 3, 1987); and Mazatlán, Sinaloa (48, 44, and 45 taken in separate trawls by the vessel *Calafia* on the night of March 3, 1987; 44 taken by the vessel *Hapemsa III* on March 27, 1987).

Samples from Bahía Magdalena were frozen and returned whole to Bodega Marine Laboratory (BML), where they were stored in an ultracold freezer at −65° to −70°C until May 1987. The Gulf of California samples were returned on ice to Centro de Investigaciones Biologicas, La Paz, where their first gill arches were removed for gill-raker counts; a numbered label was attached to a gill cover on each specimen in order to maintain identity; and the fish were then stored in an ultracold freezer until transport to the BML in May 1987.

Subsequently, 200 of these fish were classified to species using the gill raker-standard length tabular key of Berry and Barrett (1963) for northern Mexico. Gill-raker counts were not obtained for 11 fish. Of these, 10 were assigned to species on the basis of allozyme phenotypes found to be congruent with the gill-raker diagnoses of the first 200 fish (see Results); one fish was inferred to be a hybrid between *O. bulleri* and *O. medirastre* (see Results). The species compositions of the six collections were as follows: Bahía Magdalena (7 *O. medirastre*, 2 *O. libertate*); Guaymas (all *O. libertate*); *Calafia* 1 (4 *O. bulleri*, 6 *O. medirastre*, 37 *O. libertate*, and 1 hybrid); *Calafia* 2 (6 *O. bulleri*, 5 *O. medirastre*, 33 *O. libertate*); *Calafia* 3 (2 *O. bulleri*, 7 *O. medirastre*, 36 *O. libertate*); and *Hapemsa III* (all *O. bulleri*). Summing the collections, 56 *O. bulleri*, 25 *O. medirastre*, 129 *O. libertate*, and 1 hybrid were obtained.

Electrophoresis

Samples of eye, heart, liver, and epaxial muscle tissues were dissected from each specimen after morphometric and wet-weight measurements were taken (see below). Tissue samples were placed in labeled plastic well trays with equal volumes of 0.5 M Tris-HCl pH 7.1 buffer; trays were covered and frozen in an ultracold freezer at −60°C. Sample trays were removed from the freezer the day before their first use and placed on trays of ice so that tissues thawed slowly. Homogenization of thawed tissue samples was done by hand-held ground-glass pestle. Trays with homogenized samples were refrozen overnight in the ultracold freezer.

Methods for horizontal starch-gel electrophoresis, protein assays, and genetic interpretation of zymograms were substantially the same as those described previously (Ayala et al. 1973; Tracey et al. 1975; Utter et al. 1987). The protocol used to separate and resolve 19 enzymes and proteins is

TABLE 1
Starch-Gel Electrophoretic Protocol Used To Reveal Variation among Thread Herring (*Opisthonema*)

Enzyme or protein (abbr.)	E.C. no.	Tissue[a]	Buffer[b]	No. of loci
Aspartate aminotransferase (AAT)	2.6.1.1	E,L	B	1
Alcohol dehydrogenase (ADH)	1.1.1.1	E	F	1
Esterase (EST)	(nonspecific)	L	E	1
Fumarate hydratase (FUM)	4.2.1.2	M	C,D	1
Glucose-6-phosphate isomerase (GPI)	5.3.1.9	M	B	1
Glyceraldehyde-3-phosphate dehydrogenase (GAPDH)	1.2.1.12	E,L,M	C,D	1
Isocitrate dehydrogenase (IDH)	1.1.1.42	L	D	1
Lactate dehydrogenase (LDH)	1.1.1.27	E+L+M	B	3
Malate dehydrogenase (MDH)	1.1.1.37	M	F	1
Malic enzyme (ME)	1.1.1.40	H	F	1
Di- and tri-peptidases				
(GL) L-gly-leu	3.4.13.11	E	B	1
(LGG) L-leu-gly-gly	3.4.13.11	E	B	1
(LV) L-leu-val + L-leu-tyr	3.4.13.11	E	B	2
(PP) L-phenylalanyl-proline	3.4.13.9	E	B	1
Phosphoglucomutase (PGM)	2.7.5.1	M	A	1
6-phosphogluconate dehydrogenase (6PGDH)	1.1.1.44	E,L	C,D	1
General proteins (PROT)	(nonspecific)	E+M	A	8
Superoxide dismutase (SOD)	1.15.1.1	L	B	1
Triosephosphate isomerase (TPI)	5.3.1.1	M	B,F	1
Totals 19 proteins				29 loci

[a] E, eye; H, heart; L, liver; M, muscle.

[b] Buffers A, B, C, and D as described by Tracey et al. (1975); buffer E is the lithium borate discontinuous buffer system 2 of Selander et al. (1971); and buffer F is the Tris-maleate-EDTA buffer XVIII of Shaw and Prasad (1970).

summarized in Table 1. Proteins are referred to by capitalized abbreviations (Table 1), loci by these same abbreviations italicized in upper and lower case. The isozymes of LDH are distinguished by suffixes A, B, C (Shaklee et al. 1973). Numerical suffixes distinguish among isozymes or multiple proteins in order of increasing anodal migration. Alleles are symbolized by italicized numerals that express millimeter differences in electrophoretic separation of variants from the most common electromorphs observed for each protein. Alleles encoding common electromorphs are arbitrarily designated *100*. Specimens from different population samples were included in every electrophoretic run so that repeated comparisons of the relative mobilities of their allozymes could be made.

For statistical analyses, individuals were grouped into the following nine population samples:

(1) 12 *O. bulleri* pooled from the *Calafia* samples
(2) 44 *O. bulleri* from the *Hapemsa III* sample
(3) 7 *O. medirastre* from Bahía Magdalena
(4) 18 *O. medirastre* pooled from the *Calafia* samples
(5) 21 *O. libertate* from Guaymas
(6) 2 *O. libertate* from Bahía Magdalena
(7), (8), and (9) 37, 33 and 36 *O. libertate* from *Calafia* samples 1, 2, and 3, respectively.

There was no evidence for genetic heterogeneity among the small collections pooled to obtain populations (1) and (4). After testing for heterogeneity of allelic frequencies, conspecific samples were pooled for calculation of interspecific genetic similarities and distances.

Single-individual genotypes were recoded as alphabetical characters, and entered into the BIOSYS-1 program of Swofford and Selander (1981) for calculations of allelic frequencies; average proportions of heterozygous individuals per locus (observed by direct count, H_o, and expected, H_e, according to Nei's [1978] unbiased estimate); proportions of loci polymorphic per population (P, where a locus is considered polymorphic if the frequency of the most common allele does not exceed 0.99); goodness-of-fit tests to Hardy-Weinberg-Castle (H-W-C) equilibrium phenotypic proportions using Levene's (1949) correction for small sample size; and Nei's (1978) unbiased measures of genetic similarity (I) and distance (D). Log-likelihood ratio (G) tests of differences in allelic frequencies among population samples of *O. libertate* were calculated from absolute frequencies after appropriate pooling of rare alleles. The unweighted pair-group method with arithmetic averaging (UPGMA) in the CLUSTER subroutine of BIOSYS was used to estimate genetic distances for the linkages among species.

Morphometrics and Meristics

Measurements were made with vernier calipers on the left side of each frozen fish after its surface had thawed. Sixteen segments of a box truss network (Bookstein et al. 1985) were defined by eight anatomical landmarks: tip of snout, posterior edge of the supraoccipital at the midline, origin of the dorsal fin, anteroventral edge of the preopercular, origin of the pectoral fin, origin of the pelvic fin, origin of the anal fin, and the end of the medial hypurals (Figure 1). Measurements between landmarks are denoted by syntheses of landmark abbreviations; e.g., the distance from the origin of the dorsal fin to the origin of the pectoral fin is called DORFPELV. In addition, measurements were made from tip of snout to the anterior edge of the orbit (SNTORBIT), of standard length (tip of snout to end of the medial hypurals: STANDARD), and of interorbital width at posterodorsal orbit margins (INT). We also recorded whole body and gonad wet weights, sex, and a subjective index of reproductive condition, ranging from 0 (completely undifferentiated) to 4 (ripe).

Statistical analyses of these data were performed with the BMDP statistical software package (Dixon 1981). Natural logarithms of the 19 length measurements were entered into programs 4M, Principal Components Analysis (PCA), with no rotation of factors and extraction of eigenvalues greater than 0.5 specified, and 7M, Step-Wise Discriminant Analysis (SDA), with F-to enter = 4.0 and F-to remove = 3.999. Bivariate plots and one- and two-way ANOVA routines were also used to examine the relationships of single traits with PCA factors and to test the effect of sex and sexual condition on body-depth measures that appeared to be important in species discrimination.

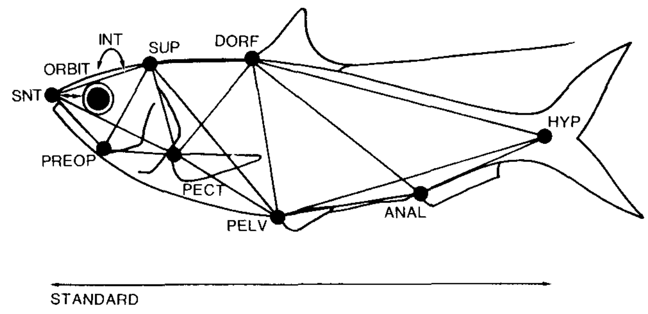

Figure 1. Morphometric measure of *Opisthonema*. Dots mark eight anatomical landmarks defining a three-box truss network of 16 measured chords, each labeled by two end points: ANAL, anal fin origin; DORF, dorsal fin origin; HYP, posterior margin of medial hypurals; PECT, pectoral fin origin; PELV, pelvic fin origin; PREOP, anteroventral edge of preopercular bone; SNT, tip of snout; SUP, posterior edge of supraoccipital bone at the midline. Arrowheads denote ends of three additional measurements: INT, interorbital width at posterodorsal margin of orbit; SNTORBIT, tip of snout to anterior orbit margin; STANDARD, standard length (SNT-HYP).

The numbers of ceratobranchial gill rakers for the Gulf of California specimens were counted by Mr. Ruben Rodriguez-Sanchez (CICIMAR, La Paz, B.C.S.); gill rakers for the Bahía Magdalena fish were counted by L. G. L.-L. Morphometric measurements were done by K. N.; dissection, tissue preparation, electrophoresis, and enzyme assays primarily by L. G. L.-L.; zymogram interpretation and genotype scoring by L. G. L.-L. and D. H. jointly; and statistical analyses of genetic and morphometric data by D. H.

RESULTS

Gill-Raker Counts

Ceratobranchial gill-raker counts for 199 of the 211 specimens in our study fall clearly into three groups as previously described by Berry and Barrett (1963) for *O. bulleri, O. medirastre,* and *O. libertate*. One individual from Mazatlán has a count of 46 (and a standard length of 162 mm), exactly intermediate between the *O. bulleri* and *O. medirastre* means (Figure 2).

Allozyme Variation within and between Species

Starch-gel electrophoresis resolves 29 proteins, each inferred to be encoded by a single locus. A summary of the genetic variability found in our survey of *Opisthonema* is given in Table 2. There are an average of 1.2–1.6 alleles per locus, and 17.2%–37.9% of loci are polymorphic in the nine population samples. On average, individuals are observed to be heterozygous at 5.1%–10.8% of the loci examined; in no case is there a significant

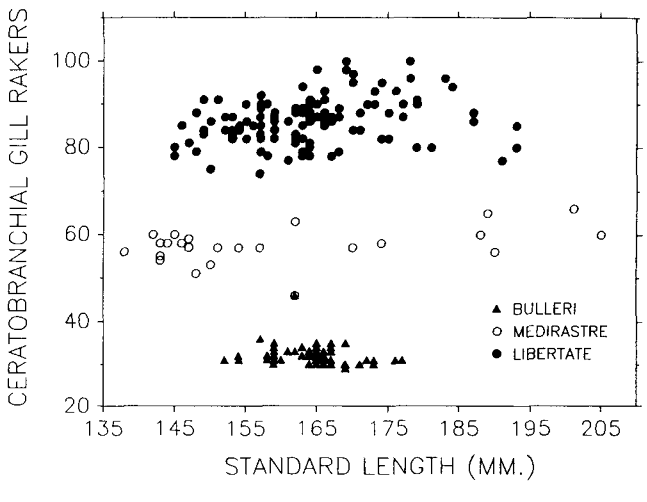

Figure 2. Numbers of gill rakers on the ceratobranchial segment of the first gill arch in relation to standard length for 200 specimens of *Opisthonema* from northwest Mexico. Species identified according to Berry and Barrett (1963), except for an apparent hybrid between *O. bulleri* and *O. medirastre*, which is labeled with the symbols for both species.

TABLE 2

Genetic Variability in Nine Population Samples and in Three Species of Thread Herring (*Opisthonema*) from Northwest Mexico

Species and population	Mean sample size per locus	Mean no. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosities Direct count	H-W-C expected
O. bulleri	50.1	1.4	20.7	0.054	0.055
	(1.5)	(0.1)		(0.025)	(0.026)
Mazatlán, *Calafia*	10.6	1.2	17.2	0.051	0.057
	(0.4)	(0.1)		(0.027)	(0.027)
Mazatlán, *Hapemsa III*	39.6	1.4	31.0	0.054	0.055
	(1.2)	(0.1)		(0.025)	(0.026)
O. medirastre	20.2	1.3	27.6	0.085	0.077
	(1.1)	(0.1)		(0.035)	(0.030)
Bahía Magdalena	4.8	1.2	17.2	0.108	0.076
	(0.5)	(0.1)		(0.049)	(0.033)
Mazatlán, *Calafia*	15.7	1.3	27.6	0.076	0.078
	(0.7)	(0.1)		(0.032)	(0.030)
O. libertate	106.0	1.6	31.0	0.063	0.067
	(5.6)	(0.2)		(0.025)	(0.026)
Guaymas	15.0	1.4	27.6	0.072	0.070
	(1.6)	(0.1)		(0.028)	(0.027)
Bahía Magdalena	1.6	1.2	17.2	0.069	0.109
	(0.1)	(0.1)		(0.041)	(0.046)
Mazatlán, *Calafia 1*	26.4	1.4	31.0	0.061	0.067
	(2.8)	(0.1)		(0.028)	(0.028)
Mazatlán, *Calafia 2*	29.9	1.4	37.9	0.065	0.070
	(1.5)	(0.1)		(0.026)	(0.026)
Mazatlán, *Calafia 3*	34.0	1.3	27.6	0.055	0.056
	(1.1)	(0.1)		(0.022)	(0.023)

Standard errors are shown in parentheses. Sample sizes per locus are numbers of individuals; percentage of loci polymorphic, and heterozygosities are defined in text.

difference between observed and expected heterozygosity (H_e ranging from 5.5% to 10.9%), suggesting that mating is random within populations. The species harbor similar levels of genetic variability, although our small samples of *O. medirastre* apparently tend to have higher heterozygosity than the other two species.

Differentiation among populations within species is slight, although small sample sizes preclude valid statistical tests for most loci. Log-likelihood ratio (G) tests for independence in $r \times c$ tables of allelic frequencies by localities are nonsignificant for four loci tested in *O. bulleri* and in *O. medirastre*. Except for the two fish from Bahía Magdalena, which we initially wanted to keep separate from Gulf of California samples, sample sizes for *O. libertate* populations are large enough to permit tests of independence for six polymorphic loci. These G-tests are all nonsignificant, although the Guaymas and *Calafia* 1 samples appear to have more *103* alleles and fewer *96* alleles at the *Lv-1* locus than the other two *Calafia* samples (tests for the three most heterogeneous loci are shown in Table 3).

Because allelic frequencies appear to be homogeneous among conspecific *Opisthonema* populations sampled in northwest Mexico, we pool conspecific individuals to examine biochemical genetic divergence among species. Frequencies of alleles at 14 loci that are either polymorphic in at least one of the species or have fixed differences between species are given in Table 4. The remaining 15 loci, which are defined as monomorphic within species, share the same allele (at frequencies greater than 0.99) in all three species.

The species are genetically quite similar at the 29 loci studied: Nei's I statistics are 0.89 for *O. bulleri* × *O. medirastre*, 0.84 for *O. bulleri* × *O. libertate*, and 0.93 for *O. medirastre* × *O. libertate* (Table 5). Nei's distance statistics, D—estimates of the number of amino acid substitutions per locus between species—are 0.164, 0.173, and 0.069 for these same three pairwise species comparisons (Table 5).

Between *O. bulleri* and the other two species, fixed allelic differences are found for the *Aat* and *Est* loci, together with marked differences in allelic frequencies for *Fum, Gpi, Ldh-A, Me, 6Pgdh*, and *Sod* (Table 4). No fixed differences distinguish *O. medirastre* from *O. libertate*, but markedly different allelic frequencies occur between these two species for *Fum, Gpi, Mdh-M, Lv-1*, and *Sod*.

Allozymes can be used for taxonomic diagnosis whenever the distributions of phenotypic frequen-

TABLE 3
Log-Likelihood Ratio Tests of the Independence of Allelic Frequencies for Three Loci and Sites of Collection for Four Population Samples of *Opisthonema libertate*

Locus	Alleles	Population samples				Totals	r × c G
		Guaymas	*Calafia* 1	*Calafia* 2	*Calafia* 3		
Gpi	*95*	8	11	14	10	43	
	100	26	43	39	53	161	
	105	8	20	11	9	48	
	Totals	42	74	64	72	252	G = 7.25 6 df, ns
Lv-1	*96*	1	0	5	4	10	
	100	35	63	61	66	225	
	103	6	11	0	2	19	
	Totals	42	74	66	72	254	G = 27.62[a]
Sod	*87*	35	64	61	68	26	
	100	7	10	5	4	228	
	Totals	42	74	66	72	254	G = 4.99 3 df, ns

[a] Significance test not valid because value of first cell (frequency of allele *96* in the Guaymas sample) is expected to be only 1.65 from marginal totals. Pooling frequencies of alleles 96 and 103 in all samples yields G = 3.64, 3 df, ns.

cies are sufficiently nonoverlapping between taxa (Ayala and Powell 1972). Based on our samples of *Opisthonema*, for example, thread herring having the allozyme phenotypes AAT-97 or EST-101 may be unambiguously assigned to *O. bulleri* because these phenotypes do not occur in the other two Pacific coastal species. Two specimens for which we did not obtain gill-raker counts were assigned to *O. bulleri* on the basis of AAT phenotype. In the absence of fixed differences between *O. medirastre* and *O. libertate*, we use the probabilities of multilocus allozyme phenotypes to classify individuals. These probabilities are calculated from the allelic frequencies in Table 4, assuming that phenotypic frequencies are determined independently for each locus (linkage equilibrium) by the Hardy-Weinberg-Castle binomial expansion. For expansion, the composite phenotype {FUM 100, GPI 100, MDH-M 100, SOD 100}, i.e., an individual homozygous for the common allele at each of these four allozyme-coding loci, is expected to occur in 21% of the *O. libertate* population but in only 0.00005% of the *O. medirastre* population. Four specimens missing gill-raker counts but having this composite allozyme phenotype were so assigned to *O. libertate*. The remaining five individuals missing gill-raker counts were also assigned to *O. libertate* based on similar disparities in their expected frequencies of occurrence in the two species. Two, for example, were heterozygous for the Gpi^{95} allele, which does not occur in *O. medirastre*.

The single fish with the exceptional gill-raker count of 46 had an AAT 97/100 phenotype, consistent with its being an interspecific hybrid between *O. bulleri* and one of the other two species. Its composite phenotype for four other allozymes {FUM 104, GPI 100, LV-1 96/100 and SOD 87/100} suggests that this individual most likely resulted from hybridization between *O. bulleri* and *O. medirastre*. This individual was a sexually mature, ripe male. We cannot tell whether it represents an F_1 or a backcross progeny, although the intermediate gill-raker number (Figure 2) suggests the first possibility.

Morphometric Variation and Species Discrimination

A principal components analysis (PCA) of 19 log-transformed morphometric measurements (Figure 1) on each of 206 specimens of *Opisthonema* (3 fish had missing values) produces three factors that account for 88.9% of the variation in data space. Factor I, accounting for 85% of variance in factor space, is correlated strongly and positively with all 19 traits (0.644 to 0.962) and is probably, thus, a reflection of morphometric variation owing to variation in body size (Bookstein et al. 1985). Factor II, accounting for 11.1% of variance in factor space, is substantially, positively correlated with six traits (PECTPELV [0.266], DORFPECT [0.288], STANDARD [0.298], PELVHYP [0.350], ANALHYP [0.522] and SUPDORF [0.645]) and correlated negatively with four others (SUPPREOP [−0.255], DORFPELV [−0.416], SUPPECT [−0.424] and SNTPREOP [−0.426]). Factor III accounts for only 3.9% of

TABLE 4
Allelic Frequencies for 14 Loci That Are Either Polymorphic in at Least One Species or Have Fixed Differences between Species

Locus	Sample size alleles	Species		
		O. bulleri	*O. medirastre*	*O. libertate*
Aat	*N*	55	25	120
	97	1.0	0.0	0.0
	100	0.0	1.0	1.0
Est	*N*	28	4	19
	100	0.0	1.0	1.0
	101	1.0	0.0	0.0
Fum	*N*	56	25	129
	100	0.0	0.42	0.953
	104	1.0	0.58	0.047
Gpi	*N*	56	25	128
	95	0.0	0.0	0.172
	100	0.973	0.16	0.633
	105	0.027	0.84	0.191
Ldh-A	*N*	56	25	129
	93	0.464	0.0	0.0
	100	0.536	1.0	1.0
Ldh-B	*N*	56	25	129
	100	0.98	1.0	1.0
Ldh-C	*N*	55	19	122
	100	1.0	0.974	1.0
	102	0.0	0.026	0.0
Mdh-M	*N*	55	25	128
	100	0.055	0.04	0.848
	103	0.945	0.96	0.152
Me	*N*	39	12	69
	100	0.385	1.0	0.964
	102	0.615	0.0	0.036
Pp	*N*	56	23	127
	95	0.0	0.022	0.0
	100	1.0	0.978	0.972
	102	0.0	0.0	0.028
Lv-1	*N*	56	24	129
	96	0.196	0.375	0.039
	100	0.786	0.604	0.884
	103	0.018	0.021	0.078
Pgm	*N*	56	25	129
	100	0.991	1.0	0.984
6Pgdh	*N*	54	24	108
	100	0.991	0.708	0.620
	103	0.009	0.292	0.375
Sod	*N*	56	25	129
	87	0.0	0.76	0.105
	100	1.0	0.24	0.895

Alleles with frequencies less than 0.01 in all species omitted.

variance in factor space and is correlated substantially only with PELVANAL (−0.265), DORFPELV (−0.261), and SNTORBIT (0.444).

A bivariate plot of Factors I and II, in which individuals are classified to species by gill-raker count or allozyme phenotype (Figure 3), shows remarkable coherence of conspecific individuals. *O. medirastre*, befitting its specific name, lies in a cleft between *O. bulleri* and *O. libertate*. In the upper right corner are Bahía Magdalena specimens of *O. medirastre*, which are substantially larger than specimens from the Gulf of California on the left. The hybrid is centrally located along both axes, and five *O. libertate* and one *O. bulleri* also appear to lie in the cleft between the points for these two species.

Stepwise discriminant analysis (SDA) on the same log-transformed morphometric data set produces, in 12 steps, discriminant functions utilizing 10 variables and yielding a posteriori correct classifications in 96%–100% of cases (Table 6A). Inspection of the order of entry for traits and of trait correlations with Factor II led us to select three traits (SUPPECT, DORFPECT, and DORFPELV) for a second SDA, which produces correct assignments in 84%–95% of cases (Table 6B). Plots of canonical variate scores (linear combinations of the original variables that best discriminate

TABLE 5
Genetic similarity[a] (above Diagonal) and Distance[b] (below Diagonal) among Three Species of Thread Herring (*Opisthonema*)

Species	*O. bulleri*	*O. medirastre*	*O. libertate*
O. bulleri	—	0.894	0.841
O. medirastre	0.164	—	0.934
O. libertate	0.173	0.069	—

[a] Nei's (1978) unbiased *I* statistics
[b] Nei's (1978) unbiased *D* statistics

among groups) for individuals identified to species by either gill-raker count or allozyme phenotype illustrate the discrimination achieved by these two SDA's (Figure 4).

Neither sex nor gonadal condition affects size-corrected body-depth measures. To test the effects of these factors on body depth, which appears to play a big role in the discriminant functions, we constructed two indices:

DEPTH (body-depth index) = $\log_e$ (DORFPECT + DORFPELV + DORFANAL) $-\log_e$ (PECTPELV + PELVANAL)

GONDEX (gonad condition index) = $\log_e$ (GONADWWT) $-$ $\log_e$ (WETWGTH).

First we performed a one-way ANCOVA on *O. libertate* only, grouping males (N = 87) and females (N = 39) separately. Slopes of the regressions of DEPTH on GONDEX within sexes are equal (F = 0.826, 1/122 d.f., p = 0.365) and are not significantly different from zero (F = 2.913, 1/123 d.f., p = 0.090; indeed, the slopes tend to be negative: -0.006 and -0.018, for males and females, respectively). Mean DEPTHs for the two sexes, adjusted by regression on GONDEX, are not significantly different (0.652 for males vs. 0.647 for females, F = 0.326, 1/123 d.f., p = 0.57). Small sample sizes preclude a similar analysis for the other two species.

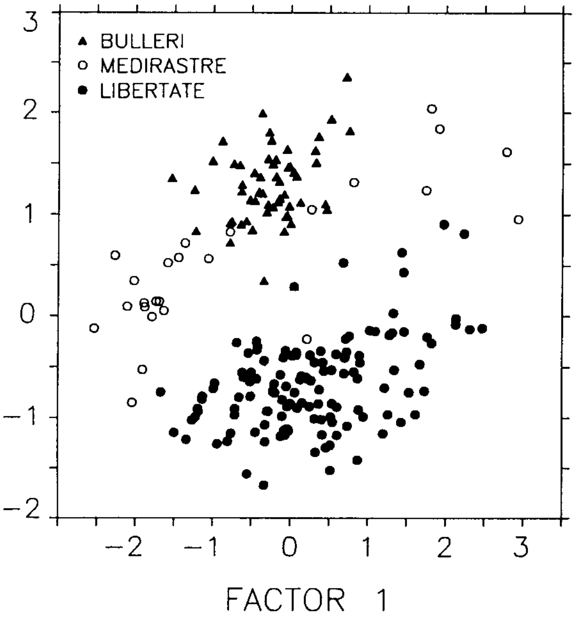

Figure 3. Bivariate plot of scores on the first two principal components extracted from data on 19 morphometric traits measured on 208 *Opisthonema* from northwest Mexico. Species identified either by gill-raker count or allozyme phenotype. An apparent hybrid between *O. bulleri* and *O. medirastre* is labeled with the symbols for both species.

Next, we made a two-way ANOVA of body-depth indices for 207 thread herring, grouping cases by species and by sex. Species contributes almost 95% of total variance (F = 55.47, 2/201 d.f., $p < 0.005$), while sex and interaction of species by sex contribute nonsignificant, 2.5% and 1.3% portions of total variance (F = 1.47, 1/201 d.f., p = 0.23 and F = 0.77, 2/201 d.f., p = 0.46, respectively). Histograms of the index of body depth for males and females of the three species are presented in Figure 5.

TABLE 6
A Posteriori Classifications by Stepwise Discriminant Analyses Using Morphometric Traits of 207 Thread Herring (*Opisthonema*)

Species*	No. of cases	Percent correct	Number of cases classified into group B	M	L
A. SDA using ten traits					
B	56	98.2	55	1	0
M	25	96.0	0	24	1
L	126	100.0	0	0	126
	207	99.0	55	25	127
B. SDA using three traits					
B	56	92.9	52	4	0
M	25	84.0	1	21	3
L	126	95.2	0	6	120
	207	93.2	53	31	123

*B = *O. bulleri*, M = *O. medirastre*, L = *O. libertate*.

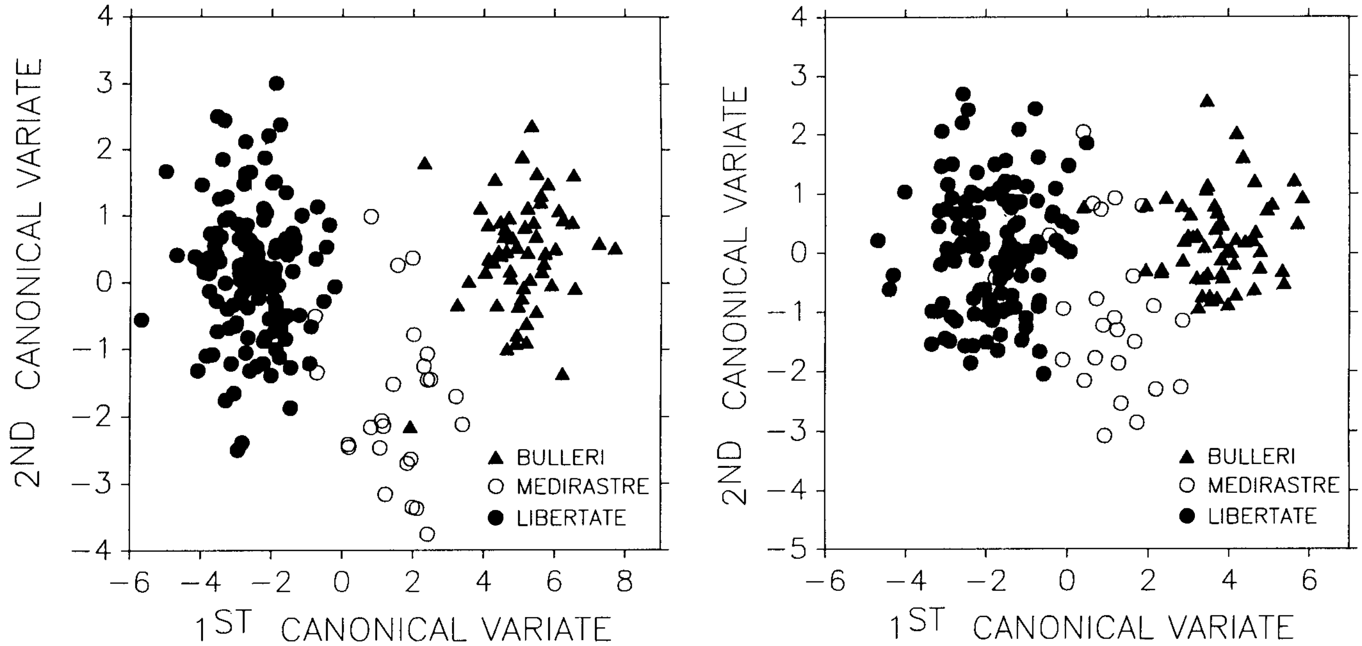

Figure 4. Bivariate plot of scores on the first two canonical variates (orthogonal linear combinations of morphometric traits providing the greatest statistical separation of species) obtained from stepwise discriminant analyses of (*left*) 19 morphometric traits and (*right*) three of these traits—SUPPECT, DORFPECT, and DORFPELV—measured on 207 *Opisthonema* from northwest Mexico. Species identified either by gill-raker count or allozyme phenotype. Hybrid individual omitted.

DISCUSSION

The Three Coastal E. Pacific Species of **Opisthonema** *Are Valid*

The results of our study fully support the taxonomy of coastal Pacific *Opisthonema* put forward by Berry and Barrett (1963). The three species that they described from the coastal eastern tropical and subtropical Pacific Ocean—*O. bulleri, O. medirastre*, and *O. libertate*—are still best separated by the number of gill rakers on the ceratobranchial segment of the first gill arch, taking standard length into account (Figure 2). These species are genetically distinct, as evidenced by fixed allozyme differences between *O. bulleri* and the other two species and by marked differences among the three

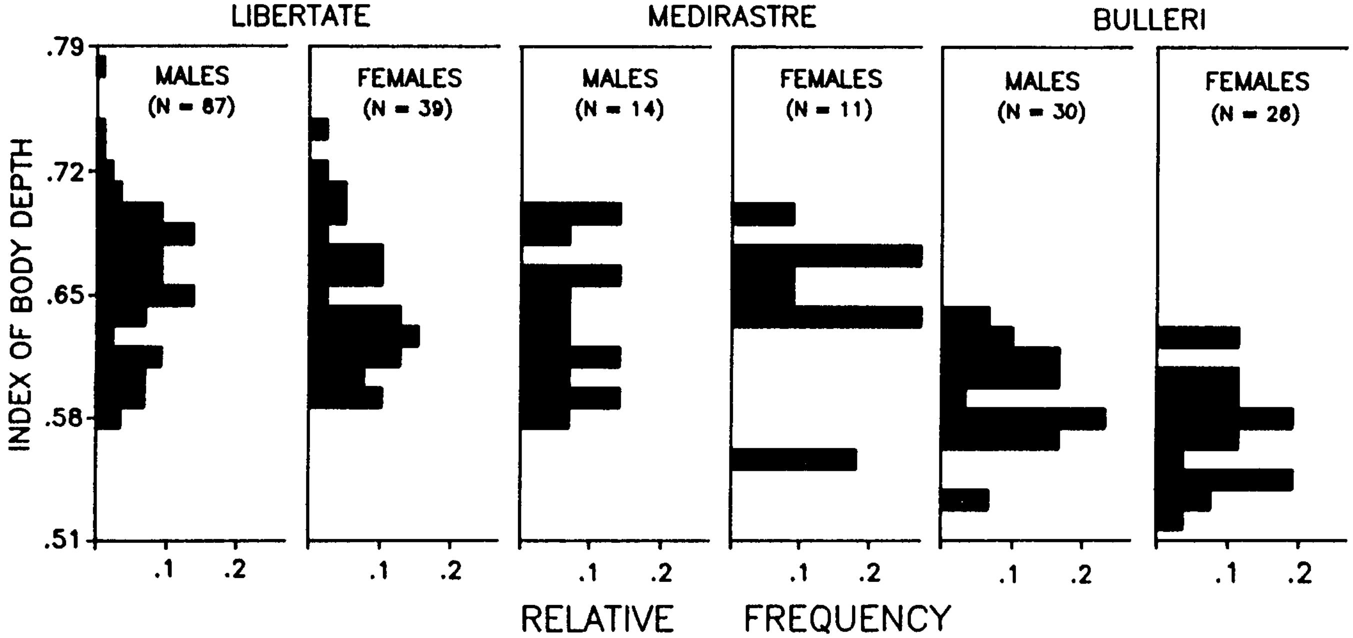

Figure 5. Histograms of an index of body depth for males and females of three species of *Opisthonema* from northwest Mexico.

species in allelic frequencies at several other allozyme-coding loci (Table 4). Indeed, allozymes can be reliably used to classify individuals to species in the absence of data on numbers of gill rakers. Doubts about the taxonomic validity of these species (Rodriguez-Sanchez 1985; Lopez-Lemus 1986) can clearly be laid to rest.

In addition to confirming the status of the three coastal Pacific species of *Opisthonema*, we have shown what Berry and Barrett could not demonstrate using univariate statistics—that these species may be reliably discriminated by multivariate statistical analysis of morphometric traits, particularly by measures of body depth. Although confounding of size and shape variation in morphometrical data generally presents serious difficulties for drawing taxonomic conclusions (Bookstein et al. 1985), a comparison of the results of PCA and SDA suggests that discrimination among *Opisthonema* species depends more on differences in body shapes than on differences in size. It is apparent—both from the large, positive correlations of all morphometric traits with PCA Factor I and from comparison of Figures 2 and 3—that Factor I represents morphometric variation related to size variation. Variance along the orthogonal Factor II axis, then, probably represents mostly variation in shape. Thus the primary use made by SDA of traits that correlate strongly, both positively and negatively, with Factor II suggests that morphometric species discrimination is achieved primarily because of differences in body shape, not size.

In contrast to the remark by Berry and Barrett (1963) that "some females tended to have slightly deeper bodies . . . than males," we have shown that body depth of thread herring is statistically not related to sex or to gonad condition. This further supports our contention that external morphometry, particularly size-corrected measures of body depth, can be used effectively for species discrimination. It may even prove possible to use as few as two or three easily measured traits to identify species in the field or in fishery catches. For example, three traits—SUPPECT, DORFPECT, and DORFPELV—selected because of their behavior in entering the SDA and their strong correlations with Factor II, yield correct classifications ranging from 84% to 95% in a posteriori tests (Table 6B). Other two- and three-character combinations may prove even more accurate, but larger sample sizes from more localities will have to be examined in order to specify optimum least-character discriminant functions.

Geographic Variation in Gene Frequencies and Morphometry

We have examined population samples of *Opisthonema* from only the northern limits of their vast geographical ranges in the eastern Pacific. Three species of *Opisthonema* are clearly distinct in northwest Mexico, but amounts and patterns of intraspecific geographical variation in allozyme frequencies and body shapes must still be considered. Geographical variation is a potential source of error in separating species and also a possible source of insight into the process of speciation in the genus.

Allozyme data give little evidence of geographical variation. No deficiencies of heterozygotes with respect to H-W-C phenotypic proportions result from pooling the *Calafia* samples for *O. bulleri* and *O. medirastre*, but sample sizes are too small to detect much deficiency owing to mixtures of individuals from populations having different allelic frequencies (Chakraborty and Leimar 1987). Genetic differences on such a small geographic scale would be surprising anyway, although we have observed such heterogeneity in proximate samples of northern anchovy, *Engraulis mordax* (Hedgecock and Li 1983; Hedgecock 1986). More rigorous tests of the independence of allelic frequencies over localities are possible for *O. libertate*, but in no case is the null hypothesis rejected. At the *Lv-1* locus, the frequencies of two rare alleles in the *Calafia* 1 sample do resemble those in Guaymas sample, but significance cannot be tested owing to expected frequencies less than 3.0 in two cells (Table 3).

Geographical variation in body size and in body shape, independent of size, occurs in Pacific sardine (*Sardinops sagax*) in the absence of spatial variation in allozyme frequencies (Hedgecock et al. 1985). The anomalous positions of several individuals on the plot of PCA factors (Figure 3) are perhaps similarly explained by differences in the geographic provenance of these particular fish, although we have no evidence for this. The one *O. bulleri* and five *O. libertate* that seem to lie in the cleft occupied by *O. medirastre* in Figure 3 were examined in a series of scatter plots of individual traits against PCA factors. We cannot attribute the positions of these fish to anomalies in particular traits; rather, their differences are multivariate. Interestingly, these individuals are, for the most part, not the same ones misclassified by a posteriori discriminant function assignments. The anomalous *O. bulleri* is misclassified by the SDA done with three traits, but not by the SDA done on all traits. The anomalous *O. libertate*, which, incidentally, were collected over all localities, are never misclassified. Study of fish from widespread locations might help resolve the causes of intraspecific heterogeneity in morphometry.

Divergence and Speciation in Opisthonema

A correspondence between allozyme differences among species and time since speciation has been observed in many organisms (Nei 1987). Grant (1987) reviews the application of molecular clocks to estimating divergence times for fish, pointing out the large errors associated with these estimates but also their apparent congruence for well-dated divergences below the generic level. We use Grant's (1987) calibration of 19 million years per unit of Nei's D to estimate divergence times for the species of *Opisthonema*. This rate is supported by a substantial data base on the divergence of closely related fishes isolated by the Isthmus of Panama (Gorman et al. 1976; Gorman and Kim 1977; Vawter et al. 1980), a barrier that finally separated the Atlantic and Pacific oceans 3.0–3.5 million years ago (Keigwin 1982). For 12 comparisons reported by these authors, average genetic distance between pairs of species or conspecific populations separated by the Isthmus of Panama range from 0.131 to 0.418, with an average of 0.242.

UPGMA clustering produces an estimate of $D = 0.168$, or 3.2 million years, for separation of the line leading to *O. bulleri* from the line leading to *O. medirastre* and *O. libertate*. Compared to previous estimates of teleost divergence across the Isthmus of Panama, our results suggest that the first divergence of *Opisthonema* in the Pacific took place around the time that separation of the Atlantic and Pacific oceans was completed. Examination of the genetic distances between coastal Pacific *Opisthonema* species and the Atlantic species *O. oglinum* should reveal whether *O. bulleri* is most closely related to *O. oglinum*, as hypothesized by Berry and Barrett (1963), or whether the divergence of Caribbean and Pacific species was essentially trichotomous. For the separation of *O. medirastre* and *O. libertate*, we estimate $D = 0.069$, or 1.3 million years, almost 2 million years after the first split of *Opisthonema* in the Pacific. We know of no geological or major oceanographic changes that might be associated with this time of divergence. It would also be interesting to examine the genetic relatedness of these three Pacific species to the one confined to the Galápagos Islands, *O. berlangai*.

How these three morphologically and genetically very similar sympatric species of thread herring developed reproductive isolation is problematic. That number of gill rakers is the best morphological character separating all five species of *Opisthonema* implies that dietary specialization on different size classes and types of plankton was important in the speciation of this genus. Stomach analyses indicate that *O. libertate* feeds primarily on phytoplankton or small zooplankton, whereas *O. bulleri* and *O. medirastre* feed predominantly on larger zooplankton (Berry and Barrett 1963; Rodriquez-Dominguez 1987). Of course the evolution of alternative feeding morphologies in fishes need not be accompanied by speciation, as shown by Sage and Selander (1975) for *Cichlosoma*. Nevertheless, coastal Pacific *Opisthonema* proves not to be a single species polymorphic for alternative feeding types, contrary to Lopez-Lemus's (1986) preliminary conclusion. Differences in the distributions of these species in the Gulf of California, in their seasonal abundances, and in their reproductive cycles have also been described (Rodriguez-Dominguez 1987); these are the ecological differences that will be important in assessing the separate contributions of the three species to the sardine fishery.

Our discovery of a sexually mature interspecific hybrid between *O. bulleri* and *O. medirastre* presents another problem in understanding speciation in the genus *Opisthonema*. The distinctive gill-raker number (Figure 2) and morphometry (Figure 3) of the *bulleri* × *medirastre* hybrid raises the possibility that, rather than representing geographical variants, those *Opisthonema* occupying anomalous positions in the plot of principal components of morphometric variation (Figure 3) may have resulted from introgression. It will be important in the future to quantify how often interspecific hybridization occurs in nature. If hybridization between the more closely related species *O. medirastre* and *O. libertate* also occurs, it may be very difficult to detect by allozymes because of their great similarity and lack of fixed differences. Analysis of restriction fragment-length polymorphisms of mitochondrial DNA might provide crucial evidence for introgression (Ferris and Berg 1987).

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ZOOPLANKTON BIOMASS AND COPEPOD COMMUNITY STRUCTURE IN THE GULF OF CALIFORNIA DURING THE 1982–1983 EL NIÑO EVENT

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ABSTRACT

From March 11 to 23, 1983, we studied zooplankton biomass distribution and copepod community structure in the Gulf of California. Maximum biomass occurred in the eastern side of the central gulf; in general, biomass did not show the reduction typically reported for other ecosystems during El Niño events. Copepods and cladocerans were the dominant taxa, with copepodite stages of *Oithona* sp. and *Penilia avirostris* the most abundant populations. We identified 76 species of copepods: 60 calanoida, 14 cyclopoida, and 2 harpacticoida. Of these, 17 are reported for the first time in the gulf. Calanoid copepods with tropical-subtropical affinity composed 69% of the total, while those with equatorial and temperate affinities were 17% and 14%, respectively. Of the copepods with tropical-subtropical and equatorial affinities, those from oceanic habitats were the most abundant, whereas the most abundant temperate-water species were coastal habitat types. The spatial pattern of the copepod community structure showed two main assemblages, one in the central and the other in the southern parts of the gulf. These two regions correspond to zones with different physical and primary production characteristics.

RESUMEN

La distribución de la biomasa y la estructura de la comunidad del zooplancton del Golfo de California fueron estudiadas del 11 al 23 de marzo de 1983. La máxima biomasa se registró en la costa oriental del golfo central. En general, la biomasa del zooplancton no disminuyó como ha sido reportado para otros ecosistemas durante eventos El Niño. Los grupos dominantes fueron copépodos y cladóceros, siendo los copepoditos de *Oithona* sp. y *Penilia avirostris* las poblaciones más abundantes. Dentro del grupo de los copépodos se registraron 76 especies: 60 calanoides, 14 ciclopoides y 2 harpacticoides. Diecisiete de estas especies se reportan por primera vez para el Golfo de California. Entre las especies de copépodos calanoides, las de afinidad tropical-subtropical constituyeron el 69%, mientras que las de aguas ecuatoriales y templadas registraron 17% y 14%, respectivamente. Dentro de las especies de afinidad tropical-subtropical y ecuatorial, las de hábitat oceánico fueron las más abundantes, mientras que la máxima abundancia de las especies de afinidad a aguas templadas correspondió a las de hábitat costero. La distribución espacial de las poblaciones de copépodos mostró dos grandes regiones faunísticas en las zonas central y sur del golfo, las cuales corresponden a diferentes características ambientales del Golfo de California.

INTRODUCTION

Climatic and oceanographic anomalies in the eastern tropical Pacific at the end of 1982 indicated the beginning of an El Niño event that has been considered the strongest of the century (Cane 1983; Rasmusson 1984). The 1982–83 El Niño event caused drastic changes in phytoplankton biomass and productivity in Peruvian waters (Chávez et al. 1983, 1984), as well as in the availability of fisheries resources (Barber and Chávez 1986). In the California Current, zooplankton abundance was also decreased (McGowan 1983, 1984).

Thermal and sea-level anomalies in the Gulf of California at the end of 1982 indicated that the El Niño phenomenon extended into the gulf (Robles-Pacheco and Christensen 1984; Robles-Pacheco and Marinone 1987). In contrast to the California Current, however, phytoplankton biomass and productivity was increased, with rates up to seven times higher than in normal years (Valdéz-Holguin and Lara-Lara 1987; Lara-Lara and Valdéz-Holguin 1987).

In this paper we describe the zooplankton biomass and copepod community structure in the Gulf of California during the 1982–83 El Niño event.

STUDY AREA

The Gulf of California is located in an arid environment between the Baja California Peninsula

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[Manuscript received February 1, 1988.]

and mainland Mexico (Figure 1). It is a large evaporative basin, with free connection to the Pacific Ocean (Roden 1964). Length is about 1000 km, and average width is about 150 km. Topographically, the gulf is divided into a series of basins, with main hydrographic provinces separated by Ángel de la Guarda and Tiburon islands. There is a shallow basin to the north, and a sequence of deeper basins to the south (Alvarez-Borrego 1983). Strong, semicontinuous tidal mixing and seasonal upwelling occur in the central gulf, near the more northern islands; northwesterly winds cause upwelling on the eastern shore during winter and spring, and southerly winds cause upwelling on the west coast during summer (Roden and Groves 1959; Badán-Dangon et al. 1985).

METHODS

From March 11 to 23, 1983, zooplankton samples were collected at 22 stations (Figure 1) from R/V *El Puma* using a 60-cm-mouth-diameter, 0.333-mm mesh bongo net equipped with a flowmeter and towed obliquely between 250 m and the surface. Samples were preserved in 4% formaldehyde neutralized with sodium borate. Zooplankton biomass was estimated by displacement volume (Kramer et al. 1972) and by wet and dry weight measurements (Omori and Ikeda 1984). Subsamples were prepared with a Folsom splitter. Copepod species were identified from 11 representative stations (Figure 1) using Rose (1933), Grice (1961), Motoda (1963), Frost and Fleminger (1968), Nishida et al. (1977), and Alameda de la Mora (1980) as taxonomic references. Only 89% of the total copepods were identified to genus or species level because of the relatively high abundance of many copepodite stages that could not be identified. The copepod species diversity was calculated using the Shannon and Weaver (1949) index. Faunistic associations were assessed by estimating the similarity between stations with the Jaccard index, followed by a grouping technique, as described by Davis (1973). Surface temperature was measured with reversing thermometers, and

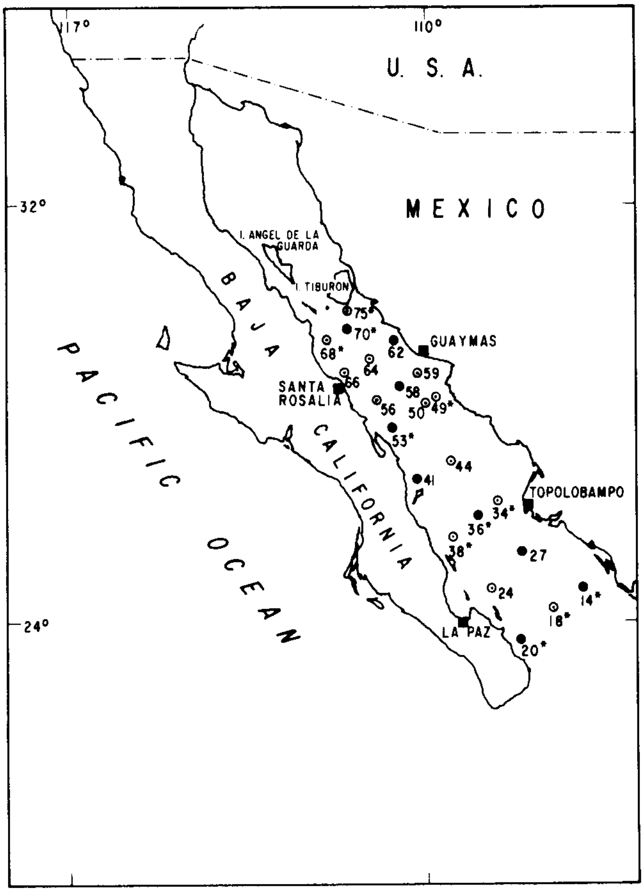

Figure 1. Stations sampled during March 1983: (⊙) day, (●) night. Asterisks denote stations where copepod species were identified.

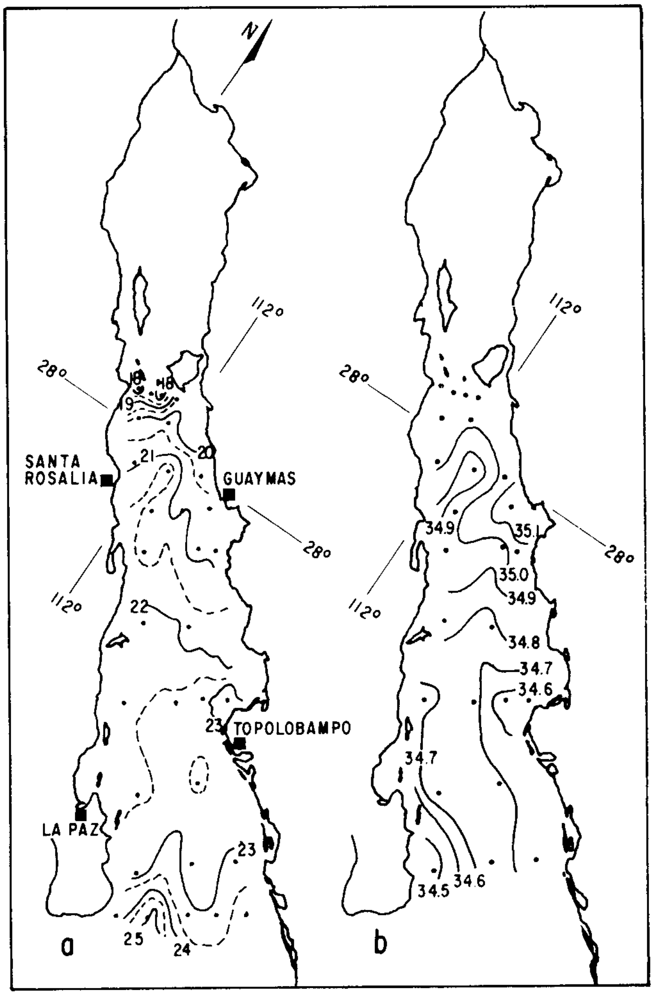

Figure 2. Surface temperature (*a*) and salinity (*b*) distributions in the Gulf of California during March 1983.

surface salinity with a Plessey 6230 salinometer from water samples collected in Niskin bottles.

RESULTS

Temperature and Salinity Distributions

March surface temperature (Figure 2a) ranged from 17.9° to 25.4°C, decreasing from the mouth to the central region; lowest temperatures occurred south of the Tiburon and San Esteban islands. A tongue of colder water extended southward in the eastern portion of the central gulf off Guaymas.

Surface salinity (Figure 2b) varied from 34.4 to 35.2‰, with lowest salinities at the mouth, and highest in the central gulf. A band of more saline water coincided with the cold water found off Guaymas.

Zooplankton Biomass

Zooplankton displacement volumes (Table 1) were higher in the eastern portion of the central gulf (Figure 3); biomass expressed in wet and dry weight (Table 1) showed much the same distribution. Average biomass in the central gulf (north of 27°N) was over twice that in the southern gulf (south of 27°N) (Table 1). Biomass values from stations in neritic waters (< 200 m deep) averaged about three times higher ($\bar{X}$ = 988 ml/1000 m^3) than stations located in water of greater depths ($\bar{X}$ = 295 ml/1000 m^3). Biomass differences between night ($\bar{X}$ = 383 ml/1000 m^3) and day ($\bar{X}$ = 378 ml/1000 m^3) tows were not statistically significant ($p > 0.05$).

Community Structure

Zooplankton abundance by number of individual animals averaged 767 individuals/m^3. Highest abundances were found in the central gulf ($\bar{X}$ = 1009 ind/m^3); the southern region averaged 564 ind/m^3 (Table 2). Copepods were the most important group, with 44.4% of total zooplankton abundance, followed by cladocerans (30.5%), chaetognaths (7.2%), and ostracods (6.5%). The remaining groups represented less than 3% of the total number of zooplankters.

TABLE 1
Zooplankton Biomass in the Gulf of California during March 1983

	Station	Displacement volume (ml/1000 m^3)	Wet weight (mg/m^3)	Dry weight (mg/m^3)
South	14	221.7	172.8	22.07
	18	141.2	94.2	12.17
	20	314.2	239.2	27.02
	24	352.4	201.7	25.99
	27	250.1	209.8	31.28
	34	123.4	64.9	7.96
	36	194.0	165.8	22.95
	38	170.2	87.2	9.63
	41	154.4	133.9	15.33
	44	174.9	117.5	15.07
$\bar{X}$		209.6	148.7	18.95
s		75.5	58.3	7.99
Central	49	257.4	230.9	26.85
	50	446.2	330.3	32.31
	53	289.1	260.1	28.50
	56	239.6	172.7	18.90
	58	266.6	244.2	26.30
	59	440.9	316.5	27.90
	62	1,814.4	1,402.1	103.00
	64	252.8	211.2	23.10
	66	350.5	343.4	32.20
	68	943.2	611.0	37.00
	70	141.9	156.7	13.70
	75	918.0	1,173.0	78.60
$\bar{X}$		532.3	454.3	33.36
s		486.0	410.0	26.20
$\bar{X}$	Total	385.0	315.3	29.01
s	Total	392.0	337.0	21.80

Stations are divided at 27°N lat.

TABLE 2

Zooplankton Taxonomic Group Abundances (ind/m³) at Eleven Selected Stations in the Gulf of California during March 1983

	Stations											
	South						Central					
Taxa	14	18	20	34	36	38	49	53	68	70	75	$\bar{X}$
Siphonophores	2	4	17	—*	5	7	14	34	6	15	22	10
Chaetognaths	33	47	68	34	84	47	54	73	48	30	85	52
Medusae	—	2	4	—	—	2	22	—	1	6	6	4
Copepods	155	87	391	292	297	342	429	550	231	214	710	336
Euphausiids	6	1	2	2	3	—	1	—	—	3	21	4
Amphipods	4	1	11	—	3	—	—	—	—	1	4	2
Cladocerans	240	7	31	90	243	153	421	614	240	155	359	231
Ostracods	35	49	42	46	134	61	53	67	26	30	22	51
Tunicates	3	7	21	2	—	16	13	12	27	25	10	12
Euphausiids (larvae)	—	—	—	—	—	—	10	7	14	36	120	17
Others	27	17	33	27	132	20	42	45	23	3	101	34
Total abundance	505	222	620	493	901	648	1050	1402	616	518	1460	767

*Dashes indicate abundance less than 1 ind./m³

Two species clearly dominated the zooplankton composition during March 1983: copepodite stages of the cyclopoid copepod *Oithona* sp. were most abundant in all samples except at stations 70 and 75, and the cladoceran *Penilla avirostris* was second in abundance at most of the stations. Of the copepods, the calanoida constituted 73% of total abundance, while the cyclopoida registered 26.8%, and harpacticoida only 0.2%.

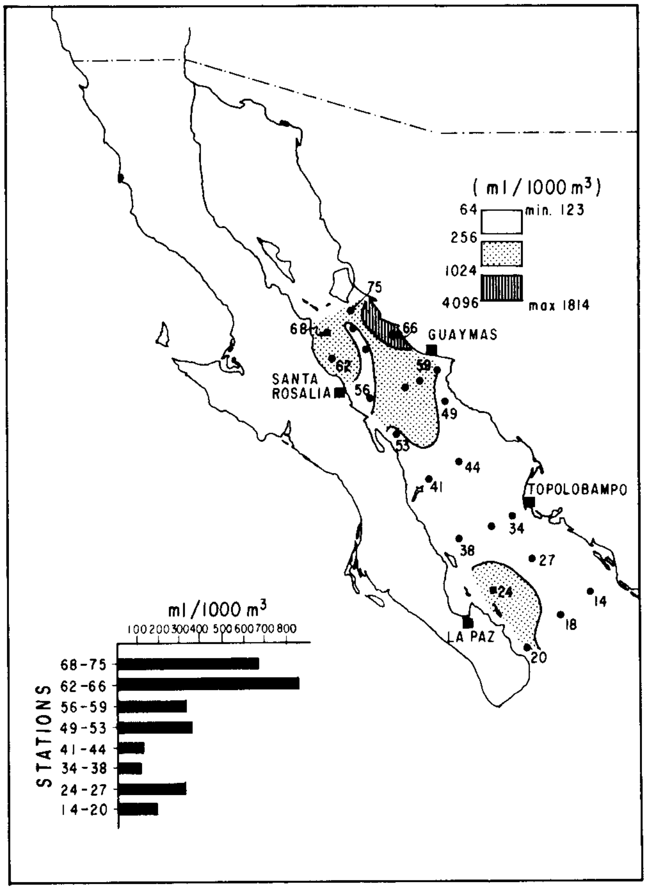

Figure 3. Total zooplankton biomass (displacement volume, ml/1000m³) for the Gulf of California, during March 1983. Bar graph shows average displacement volumes for the lines.

We identified 76 species of copepods (Table 3): 60 were calanoida, 14 cyclopoida, and 2 harpacticoida. The list of copepods reported for the Gulf of California by Brinton et al. (1986) does not include 12 of these species of calanoida, 3 cyclopoida, and the 2 harpacticoida. There was no difference ($p \geq 0.05$) in the number of species taken in night or day tows. In terms of relative abundance, among the calanoida, *Pleuromamma gracilis* was the most abundant (12.5%), followed by *Eucalanus subtenuis* (9.4%), *E. pileatus* (6.89%), *Acartia tonsa* (6.86%), and *Clausocalanus arcuicornis* (6.31%).

The calanoid copepod community was represented by species of tropical, equatorial, and temperate affinities (69%, 17%, and 14% relative abundance, respectively) (Figure 4a). We found that 78% of the tropical species were oceanic, 10% were from neritic waters, and 12% preferred coastal waters (Figure 4b). Of equatorial species, those with neritic and coastal affinities represented 25% and 17%, respectively; oceanic species (58%) were the most abundant (Figure 4c). Among the temperate species, 45% were from coastal environments, 37% from neritic waters, and only 18% perferred the oceanic habitat (Figure 4d).

Species diversity (Shannon index) decreased from the mouth (1.25 decits/ind) to the northernmost stations (1.0 decits/ind). Species richness was

TABLE 3
Copepod Species Found in Gulf of California, March 1983

Calanoida
Acartia danae o, trop
A. negligens o, trop
A. tonsa c, temp
Acrocalanus longicornis n, equat
Aetideus armatus n, trop
Calocalanus pavo o, trop
Candacia curta n, trop
*_C. aethiopica_
C. catula n, equat
C. pachydactila o, equat
*_C. varicans_
Canthocalanus pauper c, equat
Centropages furcatus n, trop
Centropages sp. n, trop
Clausocalanus furcatus o, trop
C. mastigophorus o, trop
*_C. arcuicornis_ o, trop
C. farrani o, trop
C. jobei o, temp
Calanus pacificus n, trop
C. tenuicornis o, temp
*_Euaetideus bradyi_ n, trop
*_E. giesbrechti_ o,
Eucalanus subtenuis o, equat
E. attenuatus o, equat
E. inermis o, equat
*_E. mucronatus_ o, equat
E. pileatus o, trop
E. subcrassus o, trop
Euchaeta acuta o, trop
*_E. marina_ o, equat
E. media o, trop
E. longicornis o, equat
Euchirella sp. o, trop
*_Ischnocalanus tenuis_
Labidocera acuta n, equat
L. diandra c, equat
Lucicutia flavicornis o, trop
Nannocalanus minor
Paracalanus parvus c, trop
Phaenna spinifera
Pleuromamma abdominalis/edentata o, equat
P. abdominalis/typica o, equat
P. gracilis o, trop
Pontellina plumata o, trop
Pontellopsis sp. o, trop
Rhincalanus nasutus n, trop
*_R. cornutus_ o, trop
Scolecithricella ctenopus
S. abyssalis o, equat
*_S. marginata_ o
S. tenuiserrata o, trop
Scolecithrix bradyi o, trop
S. danae o, trop
*_Spinocalanus_ sp. o
Temora discaudata n, trop
Undinula darwinii o, equat
U. vulgaris n, trop
*_Xanthocalanus_ sp.

Cyclopoida
Corycaeus brehmi
C. clausi
C. flaccus
C. latus
C. lautus
C. ovalis
C. robustus
C. specious
Copilia mirabilis
Oithona spp.
*_Oncaea media_
*_O. venusta_
*_Sapphirina darwinii_
S. nigromaculata

Harpacticoida
*_Clytemnestra_ sp.
*_Microsetella norvegica_

*Species reported for the first time in the Gulf of California.
The abbreviations signify favored habitat and biogeographic affinities following Fleminger's categories (Fleminger 1967; and Fleminger in Brinton et al. 1986).
Habitat: c = coastal waters; n = neritic waters; o = oceanic mixed layer.
Biogeographic affinities: temp = temperate; trop = tropical to subtropical; equat = equatorial.

also greater at the southern gulf stations (29 to 37 species) than in the central area (18 to 30 species) ($p < 0.05$). Copepod species richness presented a positive correlation with the sea-surface temperature ($r = 0.83$; $p < 0.01$) and negative correlation with salinity ($r = -0.63$; $p < 0.01$); no significant correlations were obtained between the diversity index and temperature or salinity. Two very distinct faunistic associations (Figure 5) were evident in the grouping analysis: a group was distinguished at six stations in the southern gulf, and there was a central group at the stations north of 27°N.

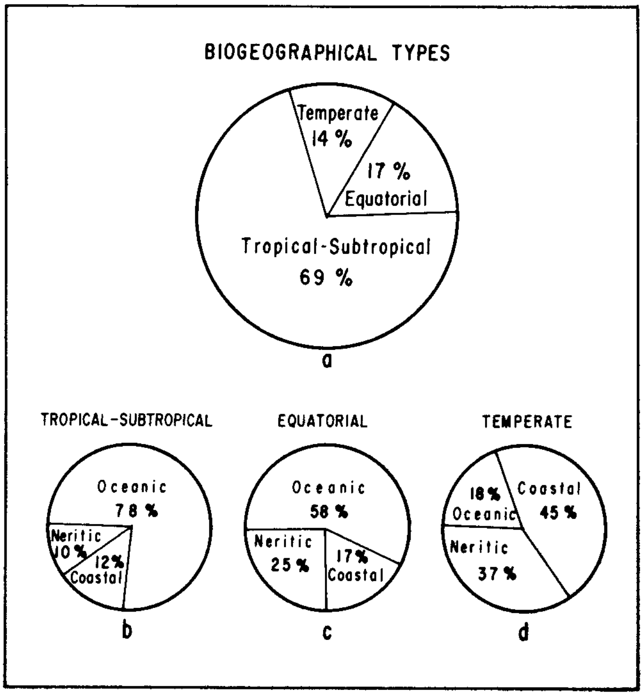

Figure 4. Biogeographical (_a_) and habitat qualities (_b–d_) of Gulf of California calanoid copepod fauna.

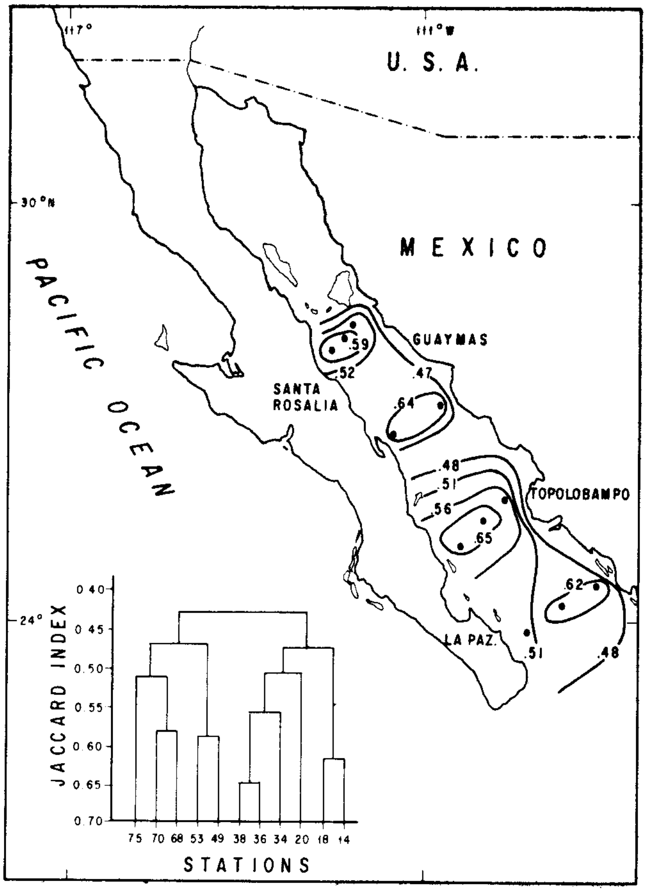

Figure 5. Spatial distribution of station similarity.

DISCUSSION

Temperature data indicates that unusual oceanographic conditions were recorded in the gulf during 1983 (Robles-Pacheco and Marinone 1987). For example, at 10-m depth, temperature readings were generally 2°C warmer than those registered by Brinton and Townsend (1980) during April 1957 in the mid-gulf region (between Isla Tiburon and 26°–27° N), and more than 3° in the eastern side at the mouth of the gulf.

Zooplankton biomass in the Gulf of California was not greatly decreased during the 1982–83 El Niño event, in contrast to that reported for Peru waters (Chávez et al. 1984) and the California Current (McGowan 1984). Our displacement volume values were of the same order as those reported by Brinton et al. (1986) for the Gulf of California during 1956–57 (relatively cold years in the California Current) and are comparable to those found in productive regions of the California Current in the coastal waters of California and Baja California (Brinton et al. 1986). Phytoplankton biomass and primary productivity rates in the gulf during spring 1983 and 1984 were higher than during normal years (Valdéz-Holguin and Lara-Lara 1987; Lara-Lara and Valdéz-Holguin 1987).

Although zooplankton biomass was not reduced, the community structure appeared to be affected. For example, the two dominant species throughout the gulf were the cyclopoid *Oithona* sp. and the cladoceran *Penilla avirostris*. The great abundance of these two species may have resulted from the domination (> 75%) by the nannoplankton (cells < 20 μm) of the phytoplankton biomass during this period (Valdéz-Holguin and Lara-Lara 1987). Experimental studies by Gore (1980) and Poulet (1978) have shown that these two species feed mainly on small particles. Large-particle grazers like *Calanus pacificus* (Frost 1972) were abundant only in the northernmost central region of the gulf, where microplankton dominated (Valdéz-Holguin and Lara-Lara 1987). This suggests that the phytoplankton size structure could have directly affected the population structure of copepods during March 1983.

The 12 species of calanoid copepods found in March 1983 and not reported by Fleminger (in Brinton et al. 1986) occurred in low abundances. Of these 12 species, 7 have been reported by Alameda de la Mora (1980) for the Gulf of Tehuantepec, and 10 by Grice (1961) for the Pacific equatorial waters region. The 3 cyclopoid and 2 harpacticoid species found in the gulf but not reported by Fleminger (in Brinton et al. 1986) also were reported by Alameda de la Mora (1980) from the Gulf of Tehuantepec. We suggest that copepod population structure is affected only during strong El Niño events because of the large invasion of tropical-subtropical waters. We also found that, in contrast to results reported by Manrique (1977) from a long-term study of zooplankton populations off Guaymas, the number of species from oceanic habitats doubled, another possible effect of El Niño events.

Two main copepod species assemblages were defined. In the first group there was a relatively large contribution of species with temperate affinities; this group occurred mainly in the central region of the gulf, where tidal mixing and upwelling are common and cause the cool water in this area (Badán-Dangon et al. 1985). The second assemblage comprised stations south of 27°N, where tropical and equatorial species were dominant. The species richness distribution, with a maximum in the southern gulf, agrees well with the two assemblages found. The two copepod assemblages correspond to the division of the gulf by Valdéz-Holguin and Lara-Lara (1987) into two zones: (1) the central gulf, in which, in several stations, the large contribution to total chlorophyll *a* and primary productivity was due to the microplankton size fraction (cells > 20 μm), associated with a particularly dynamic environment with high turbulence; and (2) the southern gulf, in which most of the chlorophyll *a* and primary production contribution was by the nannoplankton fraction (cells < 20 μm); this is related to a relatively stable environment with more oceanic influence.

We conclude that during our sampling period, El Niño had little effect on zooplankton biomass in the Gulf of California. The zooplankton population structure was, however, altered to some degree.

ACKNOWLEDGMENTS

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TROPHIC RELATIONSHIPS OF THE SHORTBELLY ROCKFISH, *SEBASTES JORDANI*, OFF CENTRAL CALIFORNIA

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ABSTRACT

The shortbelly rockfish, *Sebastes jordani*, the most numerous species of *Sebastes* off central California, feeds primarily on *Euphausia pacifica* and other euphasiids. This rockfish forages in the water column at night, and even more intensively near the bottom during the day. Its major prey, *E. pacifica*, normally inhabits deeper water outside the shelf, where it occurs at depths of 200–400 m during the day. At night, however, *E. Pacifica* migrates upward in the water column, and many are transported over the shelf by prevailing currents. In the morning, when they attempt to descend to their normal daytime depths, many become trapped on the relatively shallow shelf, where *S. jordani* probably find these organisms especially vulnerable.

RESUMEN

Sebastes jordani, la especie más numerosa de *Sebastes* en la costa central de California, se alimenta principalmente de *Euphausia pacifica* y otros eufáusidos. Este pez se alimenta en la columna de agua durante la noche, y más intensamente cerca del fondo durante el día. Su presa principal, *E. pacifica*, vive normalmente en aguas profundas fuera de la plataforma continental, en profundidades de 200 a 400 m durante el día. Sin embargo, durante la noche, *E. pacifica* migra hacia la superficie donde numerosos individuos son transportados hacia la costa por las corrientes predominantes. En la mañana, cuando estos organismos intentan completar su migración hacia las profundidades diurnas normales, se encuentran atrapados en las aguas costeras menos profundas donde son particularmente vulnerables a la predación por *S. jordani*.

INTRODUCTION

The shortbelly rockfish, *Sebastes jordani*, a potentially rich but unfished resource off California (Lenarz 1980), occurs on the continental shelf from northern Baja California, Mexico (lat. 31°N), to Vancouver, British Columbia, Canada (50°N). It is most numerous off central California, where its biomass between San Francisco and Monterey has been estimated to be 295,000 metric tons—more than 10 times the estimated combined biomass of all other species of *Sebastes* within that area (Gunderson and Sample 1980). The adults of this relatively small scorpaenid (to about 32 cm TL) occur at depths from about 90 to 280 m (Miller and Lea 1972).

In making tentative management recommendations, Lenarz (1980) cautioned that the trophic relationships of this species should be better understood before its exploitation is permitted. The shortbelly is an important prey of chinook salmon, *Oncorhynchus tshawytscha* (Merkel 1957), and current study at the National Marine Fisheries Service Tiburon Laboratory has shown that it is also seasonally important to other coastal predators, including coho salmon (*Oncorhynchus kisutch*) (P.A. Adams, Tiburon Laboratory, pers. comm. Jan. 1983); lingcod (*Ophiodon elongatus*); and black rockfish (*Sebastes melanops*) (E. S. Hobson, J. R. Chess, and D. F. Howard, Tiburon Laboratory, unpubl. data 1985). Little is known about its predatory habits, however, beyond the report that adults feed exclusively on macrozooplankton, primarily euphausiids (Phillips 1964).

Here we describe the diel feeding pattern of the shortbelly relative to variations in the availability of potential prey. We then discuss how the shortbelly's distribution on the coastal shelf off central California is influenced by mechanisms affecting the distribution of its prey.

METHODS

Study Area

This study is based on collections and observations made during 10 cruises involving 74 days at sea between 1979 and 1982. Exploratory surveys during November 1979 and March 1980 used hydroacoustics and trawls to locate concentrations of shortbellies in the area between Point Sur (36°18′N) and Point Reyes (38°4′N). These explo-

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TABLE 1

Areas Trawled during Each Cruise, Showing Number of Positive *S. jordani* Catches/Total Number of Trawl Sets Taken

	Month/year of cruises										
	11/79	3/80	7/80	11/80	3/81	5/81	9/81	1/82	3/82	9/82	11/82
Pescadero Point	7/14	4/7	2/6	0/3	—	2/5	0/4	0/1	—	—	—
Ascension Canyon	3/6	—	2/3	5/12	2/4	0/5	4/11	4/7	3/8	4/11	0/6
Monterey	—	2/4	—	—	—	0/2	—	—	—	—	—
Point Sur	—	2/4	—	—	2/2	0/1	—	—	—	—	—

rations found the species concentrated where the coastal shelf extended offshore, often near submarine canyons (the same areas where Gunderson and Sample [1980] had found them abundant during a 1977 coastwide rockfish survey). They were most numerous at depths between 120 and 240 m along about 40 km of the coastal shelf's outer edge offshore of Pescadero Point (at approximately 37°13′N), and the areas immediately north of Ascension and Sur canyons (Figure 1 and Table 1). Work was concentrated at these locations following the exploratory cruises of 1979 and 1980, but exploratory surveys were continued elsewhere as opportunities arose. Although these additional surveys located small concentrations at other places, usually on the outer shelf, the more than 340 hours of additional hydroacoustic search and exploratory trawling between Point Sur and Point Reyes failed to locate concentrations that matched those in the primary study areas defined above.

Collections

The collections were scheduled to define diel and geographical patterns in trophic relationships. The diel feeding patterns discussed below are based on stomach contents of shortbellies trawled from the Ascension area during the hours immediately before sunset and sunrise—times that have been found most effective in defining diel feeding patterns of predatory fish (e.g., Hobson 1974; Hobson and Chess 1976). The geographical patterns are based on shortbellies collected at the various stations during all periods of the diel cycle. Scheduled plankton collections were made during midday (1100–1400 h) and midnight (2200–0100 h) at the Ascension area to define diel variations in prey abundance and distribution.

Shortbellies were collected with a three-bridle midwater trawl that had 30.5-m headropes and footropes. We used a Furuno MkII net monitor with an acoustic link to position the trawl at the depths of the strongest acoustic targets. Often, however, the trawl followed a course offset from that of the ship (due either to the effects of subsurface currents on the trawl, or winds on the ship), which hampered attempts to position the trawl on specific acoustic targets located by shipboard echo sounders. Most sets were made on aggregations that had been located hydroacoustically, but blind sets made where we had found shortbellies earlier were often successful even in the absence of acoustic targets. The standard trawling duration was 20 minutes, but the net was retrieved sooner if there were indications (hydroacoustic or otherwise) that it had passed through a large aggregation of fish. Each catch, or a portion of the catch, was grossly subdivided by size, and from each size group 10 fish were retained for stomach-content analysis. (Fish with any evidence of everted stomachs, an unusual condition, were not included.) A total of 977 specimens were measured (standard length). Their stomachs were removed and preserved, and the contents were analyzed later in the laboratory.

Zooplankton were collected with a messenger-activated, opening-closing 1-m^2 Tucker trawl (Hopkins et al. 1973) fitted with two 0.335-mm mesh nets. Because the net frame was inclined 45° while fishing, its 1 × 1.4-m opening was in effect reduced to 1 m^2. A total of 84 plankton samples stratified by depth were taken during seven cruises. Each cruise included a series of three plankton collections made on two successive days and nights ($n = 12$). The three collections of each series were replicated at estimated depths of 18, 55, and 119 m along the 137-m (75-fm) isobath. (The ship sometimes drifted off course over depths that varied from about 128 to 145 m.) Sampling depths were determined by wire angle and length, and were standardized by maintaining the wire at 45° (which required a speed of approximately 127 cm $^{\text{sec}^{-1}}$) for the 15-minute collection periods. Four test runs using digital flowmeters indicated that this procedure filtered about 1,114 m^3 of water. We used elapsed time and wire angle, rather than a flowmeter, to standardize our samples.

For later analysis in the laboratory, a measured proportion, usually about a 500-ml aliquot of each collection (settled volume) was preserved in 4% buffered formaldehyde. (The entire collection was preserved if smaller than 500 ml.)

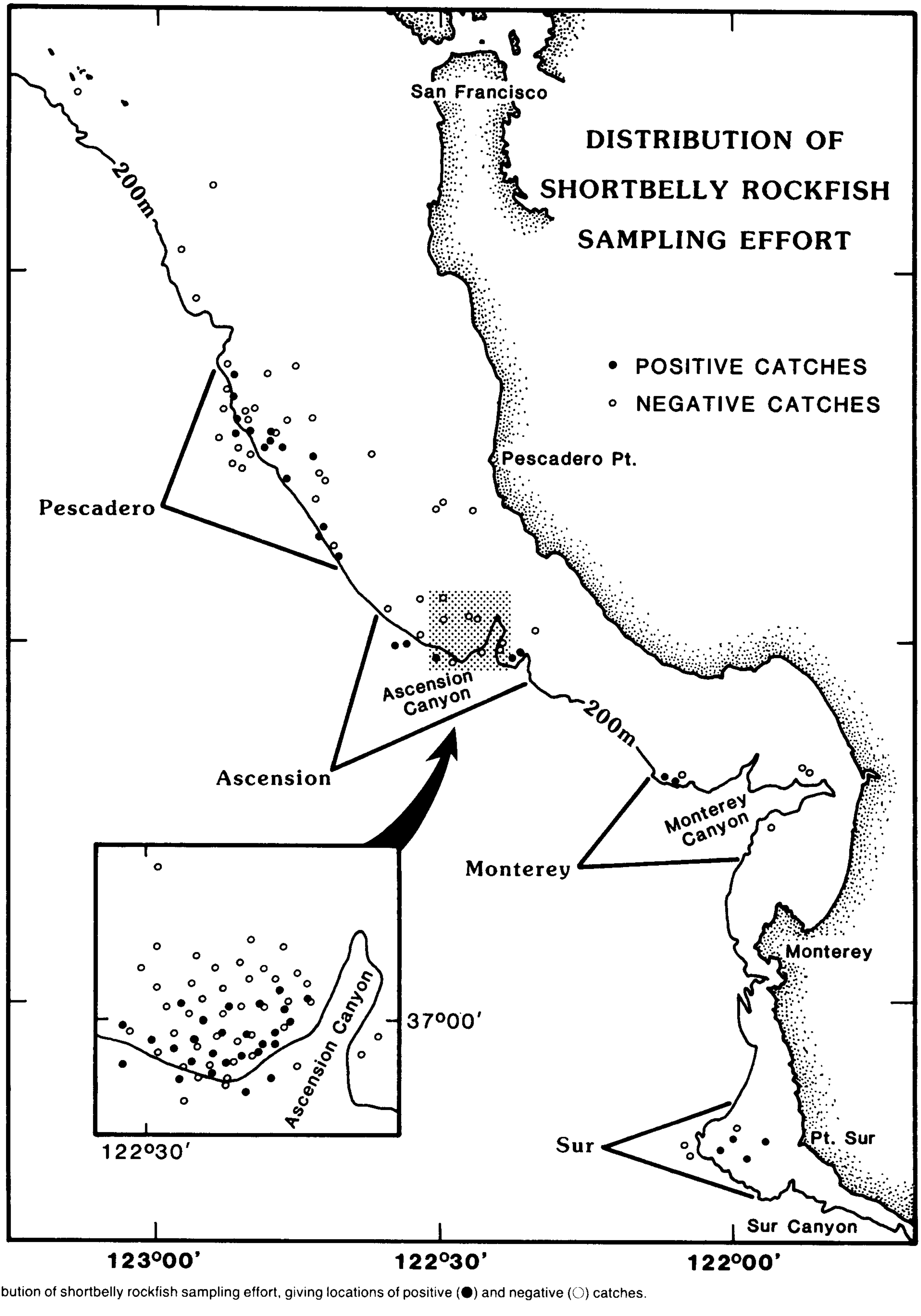

Figure 1. Distribution of shortbelly rockfish sampling effort, giving locations of positive (●) and negative (○) catches.

Additional plankton samples were taken to determine the horizontal distribution of zooplankton within the Ascension study area. These were oblique hauls taken with the Tucker trawl from a depth of 106 m to the surface at specific distances from the canyon. A more complete description of this sample series is presented below.

Laboratory Procedures

In the laboratory, food items from the stomachs were identified to the lowest taxon feasible. For each taxon the following was noted: number, size range, extent of digestion (on a scale of one to five, with one being fresh), and an estimated proportion of the total volume of stomach contents that it represented. An estimate of fullness also was made, although probably this was of questionable value owing to the elasticity of the stomach.

The settled volumes of the preserved plankton aliquots were again determined after the large gelatinous forms had been removed, and workable aliquots of 7–10 ml (settled volume) were obtained with a Folsom plankton splitter. The remainder of each sample was then searched for taxa absent from the aliquoted portion, and these were included in the analysis. For each taxon the following was noted: abundance, estimated volumetric proportion of total sample, and the range of sizes represented. The numbers of organisms in the aliquots were extrapolated to represent the entire sample.

RESULTS

Distribution of Sebastes jordani

Of 126 trawl sets made at depths from 70 to 275 m between Point Sur and Point Reyes, 48 (38.1%) caught shortbellies. Most of the successful sets were near the outer margin of the shelf at depths of about 150 m, on the north sides of submarine canyons (Figure 1).

During the day, shortbellies were found near the bottom in dense aggregations that often extended 15 m and more into the water column (Figure 2, upper). At night, however, they were more dispersed—20 to 70 m above the bottom—but still 30 m or more below the water's surface (Figure 2, lower). Consistent with this pattern of nocturnal dispersion, our catches after dark took shortbellies more frequently, but in smaller numbers than during the day. At the Ascension Canyon site, for example, 14 (64%) of 22 nocturnal hauls took $\bar{x}$ = 122.9 kg (SE 58.2) of *S. jordani*, whereas 10 (30%) of 33 diurnal hauls took $\bar{x}$ = 1,904.0 kg (SE 687.5).

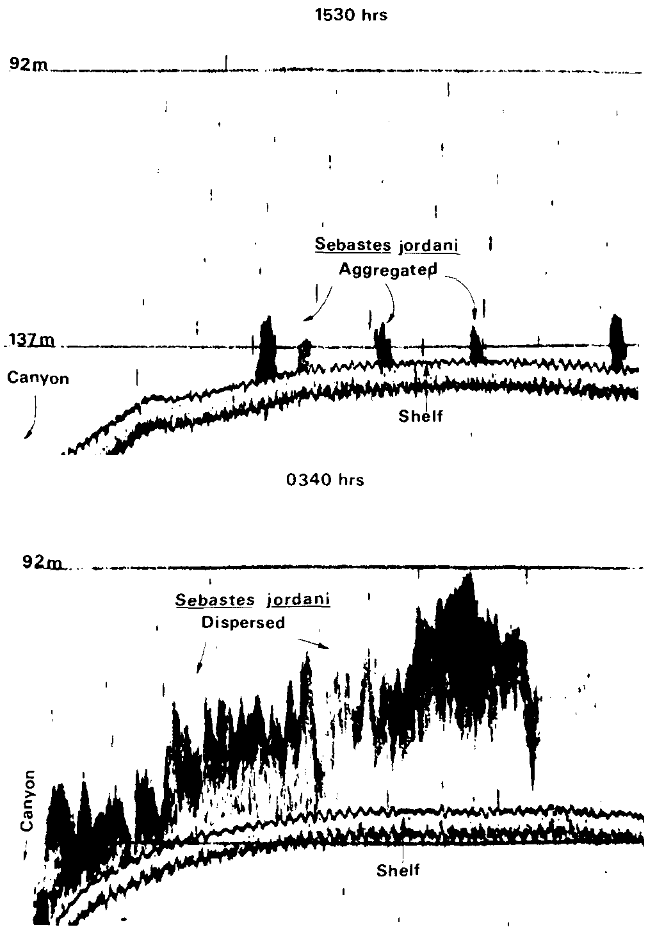

Figure 2. Distribution of shortbellies in the water column during the day (*upper*) and night (*lower*) on the shelf adjacent to Ascension Canyon, January 1982.

Diet of Sebastes jordani

Of the 977 shortbellies (99–272 mm SL, $\bar{x}$ = 175 mm) collected for gut analysis (under the wide variety of circumstances sampled during this study), 694 (71%) contained food. Although 87 prey taxa were consumed, only 24 of them occurred in 14 or more ($\geq$ 2%) of the shortbellies examined (Table 2). The primary prey species was *Euphausia pacifica*, but another euphausiid, *Thysanoessa spinifera*, was also important. Most of the prey were relatively large: 68% of the items exceeded 10 mm, and only 7.7% were less than 2 mm (this fact reflected the prominence of euphasiids in the diet). Some minor items, however, were as small as 0.5 mm (e.g., fish eggs). The size and species composition of prey taken by any given shortbelly was influenced by that fish's size. Although the relative importance of euphausiids was greater in larger fish (Table 3), euphausiids and calanoid copepods were the first- and second-ranked prey in all size groups examined.

TABLE 2
Important Prey of *Sebastes jordani*: Taxa Occurring in at Least 2% of the Stomachs That Contained Food

Prey taxa	Freq. occurr.	$\bar{x}$ *n* stom.	Mean % volume	Size range (mm)
Polychaeta				
Tomopteris spp.	.02	0.08	0.385	7.0–15.0
Ostracoda				
Halocypridae	.07	0.14	0.281	1.5–4.0
Calanoida				
Calanus pacificus	.25	1.79	1.590	2.1–2.8
Candacia bipinnata	.03	0.06	0.072	2.5–4.0
Candacia spp.	.02	0.02	0.062	2.8–4.0
Eucalanidae	.05	1.14	1.050	3.0–9.0
Eucalanus californicus	.06	0.24	0.704	3.5–7.0
Euchirella rostrata	.12	0.55	0.859	2.3–5.0
Metridia pacifica	.17	6.17	2.091	1.4–3.5
Pleuromamma abdominalis	.04	0.09	0.084	3.0–4.5
Pleuromamma spp.	.14	0.65	0.899	1.5–4.5
Rhincalanus nasutus	.08	0.36	0.555	1.4–7.0
Undeuchaeta bispinosa	.02	0.03	0.157	4.0–6.0
Undetermined	.20	1.28	3.165	0.9–6.3
Hyperiidea				
Paraphronima spp.	.02	0.04	0.196	5.0–12.5
Hyperiidae	.04	0.12	0.050	4.0–5.5
Undetermined	.06	0.09	0.768	1.0–15.0
Euphausiacea				
Euphausia pacifica	.49	10.48	25.228	10.0–24.0
Nematoscelis difficilis	.05	0.34	1.284	6.0–22.0
Nyctiphanes simplex	.07	0.22	0.845	7.0–19.0
Thysanoessa spinifera	.25	4.15	11.821	8.0–29.0
Fragments (digested)	.71	—	36.923	9.0–23.0
Chaetognatha				
Undetermined	.02	0.08	0.034	2.0–25.0
Other				
Undetermined digested material	.14	—	4.13	—

TABLE 3
Dietary Proportions of Euphausiacea and Calanoida in Three Size Groups of *Sebastes jordani*

Size of fish (mm)	Mean % diet volume Euphausiacea	Calanoida	Other
99–160 (n = 305)	68.5	17.2	14.3
161–200 (n = 199)	78.6	10.5	10.9
201–272 (n = 190)	86.3	4.5	9.2

The shortbellies fed during both day and night. This was demonstrated by fresh prey in gut content samples taken late in the day and shortly before dawn. The 182 individuals (112–261 mm SL, $\bar{x}$ = 167 mm) examined from among those collected at the Ascension Canyon site during the three hours immediately before sunset had consumed $\bar{x}$ = 37.8 prey of $\bar{x}$ = 4.6 taxa, whereas the 237 fish (99–253 mm SL, $\bar{x}$ = 155 mm) collected in the same area during the three hours immediately before sunrise had consumed $\bar{x}$ = 10.2 prey of $\bar{x}$ = 2.1 taxa. Numbers of prey and numbers of taxa are both significantly different (t-test—$\bar{x}$ no. prey: $P \leqslant 0.01$; $\bar{x}$ no. taxa: $P \leqslant 0.01$). The incidence of empty stomachs was consistent with these data, because only 12.1% of the day feeders were empty, compared to 26.6% of the night feeders (2 × 2 contingency table, x^2 = 12.4, 11 df, $P = 0.005$). Stomach fullness showed the same pattern: the mean fullness of the day feeders was 35.6% (means of individual estimated percent), whereas the night feeders were 28.4% full (Wilcoxon sign rank test, $z = 2.58$, $P \leqslant 0.001$). Thus although feeding occurred during both day and night, it was more intensive by day.

In relating diel feeding patterns of shortbellies to available prey organisms in the environment, we limited our list of prey taxa to those that occurred in at least 5% of the stomachs examined. We determined that each of these taxa was taken in numbers that differed between day and night (Table 4). While the primary prey, *Euphausia pacifica*, was most numerous in fish collected during the day, two other euphausiids—*Thysanoessa spinifera* and *Nyctiphanes simplex*—were most numerous in fish collected at night.

TABLE 4
Diel Variations in the Major Prey Taxa* in Stomachs of *Sebastes jordani* Collected at the Ascension Study Area within the 3 Hours Preceding Sunset and Sunrise

Major prey taxa	Day (N = 158) Freq. occurr.	Day $\bar{x}$ *n* stom.	Day Mean % diet vol.	Night (N = 174) Freq. occurr.	Night $\bar{x}$ *n* stom.	Night Mean % diet vol.
Halocyprid ostracods	.17	0.39	0.93	.01	0.02	0.02
Calanus pacificus	.33	2.61	3.17	.14	1.42	1.38
Eucalanus californicus	.16	0.66	2.18	.01	0.01	0.01
Euchirella spp.	.22	1.27	3.06	—	—	—
Metridia pacifica	.30	3.61	2.19	.04	0.06	0.04
Pleuromamma spp.	.32	0.85	1.03	.01	0.02	1.05
Rhincalanus nasutus	.15	0.94	1.11	.03	0.03	0.63
Euphausia pacifica	.54	18.43	27.24	.39	2.90	19.16
Nyctiphanes simplex	.09	0.13	0.64	.06	0.33	1.20
Thysanoessa spinifera	.14	0.47	1.85	.21	2.97	11.22
Other Euphausiacea	.04	0.05	0.36	.04	0.44	1.30
Euphausiacea (digested)	.83	—	37.78	.75	—	47.67

*Taxa that occurred in ⩾ 5% of all stomachs examined.

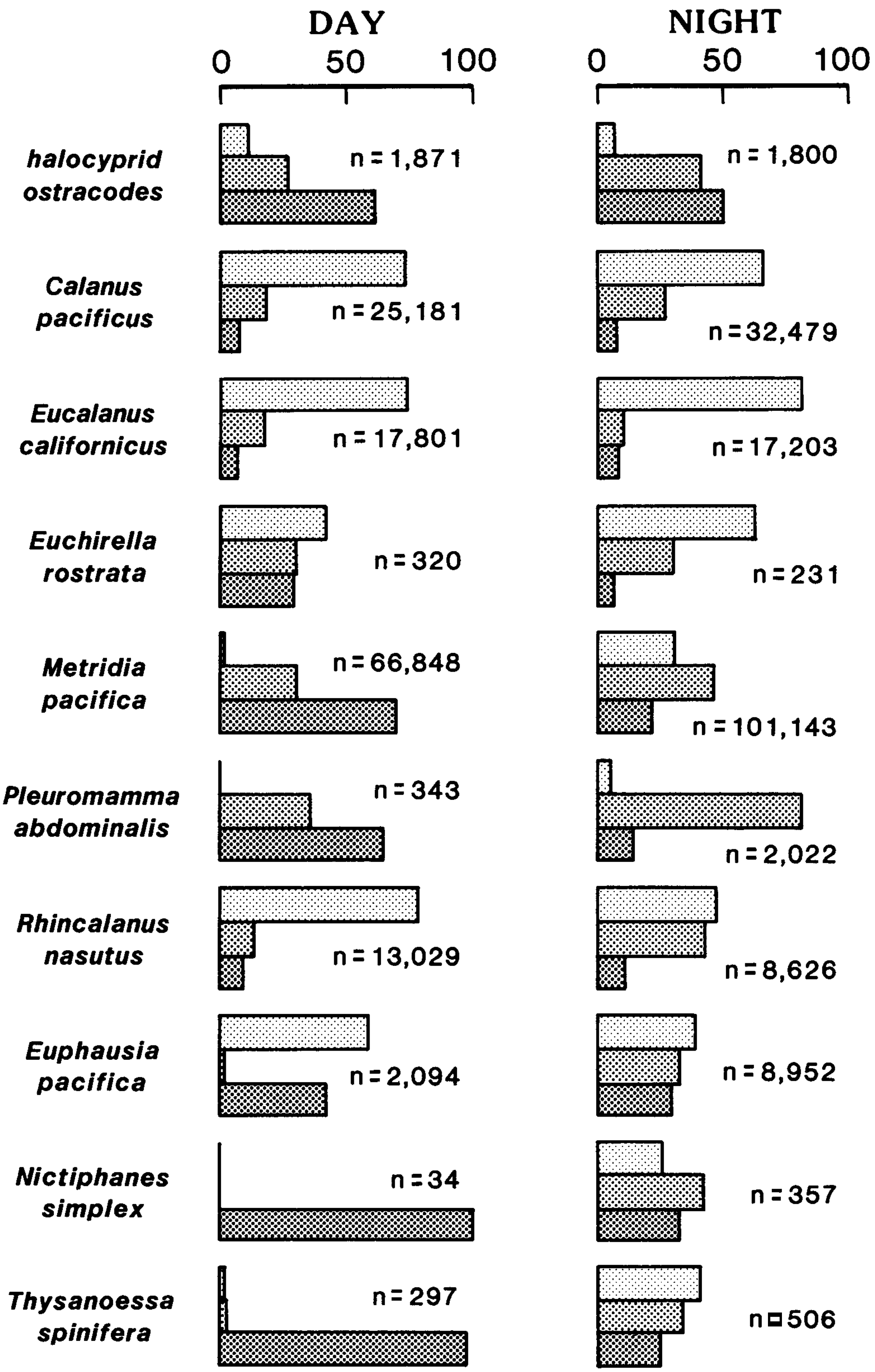

Figure 3. Diel vertical distribution patterns of the major prey taxa (those taxa occurring in ≥ 5% of the *S. jordani* that contained food). Values are the percentage of mean numbers of each taxon collected from each depth: upper (*light*), 18 m; mid (*medium*), 55 m; and lower (*dark*), 119 m. *n* = the sum of the mean numbers collected from each depth.

Distribution of Prey

Most of the major prey taxa were more numerous at higher levels of the water column at night than during the day (Figure 3). (The many *E. pacifica* in the upper level by day, shown in Figure 3, resulted from a single large collection of 5–11-mm juveniles; those shown at the lower levels were 5–24-mm juveniles and adults.) Although net avoidance may have contributed to the discrepancy between day and night *n* values in Figure 3, we have no evidence of this. Most collections were taken at least 18 m above the bottom, but one plankton collection taken over the shelf during midday (15 min. at a depth of 218 m) inadvertently sampled close to the bottom (striking it at least once, as evidenced by a variety of strictly benthonic organisms in the catch). This collection, which included 46,720 *E. pacifica* (nearly four times the number we took in any other plankton collection) suggests that members of this species and perhaps others are more abundant close to the seafloor on the shelf during the day.

A series of collections at the Ascension Canyon site provided some detail on the nocturnal horizontal distribution of *E. pacifica* and other euphausiids over the shelf in relation to the canyon. During seven cruises between November 1980 and September 1982 we made 10 series of four successive oblique hauls, including 3 series that were replicated (all collections were taken between 2300 and 0330 h). Each haul was from a depth of 106 m to the surface and lasted 10 minutes; the first haul of each series sampled over the canyon; the next three sampled at 3.7-km intervals away from the northern rim of the canyon along the 137-m depth contour on the adjacent shelf.

The numerical proportion of *E. pacifica* collected above the canyon was significantly greater than that from any of the stations above the shelf. The mean proportions were: above canyon—46.77%; at 3.7 km—22.87%; at 7.4 km—18.02%; and at 11.1 km—18.68% (analysis of variance of arc sin transformations of percentages $F = 3.96$, $P = 0.02$, df 3,24; Newman-Keuls multiple comparison of means for gap order 2, difference = 19.95; for gap order 3, difference = 24.14; and for gap order 4, difference = 26.66). But although the proportions of *E. pacifica* collected from the shelf stations tended to be progressively less with distance from the canyon, the differences were not significant. In contrast, *Thysanoessa spinifera*, the euphausiid second in importance in the diet of *S. jordani*, was more evenly distributed over both the canyon and shelf, because there was no significant difference in its abundance among these collections ($F = 1.16$, df = 3,24).

Additional information on the distribution of prey species comes from comparing the diet of *S. jordani* between different areas. For example, the generally oceanic *E. pacifica* (Brinton 1962) dominated the diet of shortbellies taken near Ascension and Sur canyons, but the more neritic *T. spinifera* was more important to the diet of shortbellies taken off Pescadero Point and near Monterey Canyon (Table 5).

TABLE 5

Mean Numbers of *Euphausia pacifica* and *Thysanoessa spinifera* in Gut Contents of *Sebastes jordani* from Different Areas

	Ascension Canyon (n = 516)	Sur Canyon (n = 18)	Pescadero Point (n = 104)	Monterey Bay (n = 56)
E. pacifica	13.93	13.56	4.91	1.99
T. spinifera	0.78	0.05	14.13	3.47

DISCUSSION

It is evident that *S. jordani* was distributed on the coastal shelf in relation to the distribution of its prey. This appeared true even though the normal habitat of its major prey, *Euphausia pacifica*, is beyond the shelf break at depths below 200 m (Brinton 1976). This could explain why shortbelly rockfish were concentrated along the shelf margin, especially adjacent to certain submarine canyons (Figure 1). Certain other shelf predators are known to feed heavily on deepwater organisms when these intermittently enter the shelf habitat. For example, *Sebastes pinniger* and *S. flavidus* off central Oregon feed primarily on *E. pacifica* above the outer shelf, with the former foraging mainly by day near the bottom (Brodeur and Pearcy 1984).

It is known that some oceanic organisms that perform diel vertical migrations are carried or disperse over the coastal shelf when in the surface waters at night. It has been suggested that when these organisms attempt to regain their normal daytime depths in the morning, many become trapped on the relatively shallow shelftop, where they are vulnerable to shelf-dwelling predators (Isaacs and Schwartzlose 1965; Pereyra et al. 1969; Clarke 1984). Apparently this mechanism is important in the trophic dynamics of *S. jordani*, because despite foraging at night on a variety of organisms in the water column, members of this species that were examined during this study had fed most intensively by day near the bottom—primarily on *E. pacifica* (Table 4). Clearly *E. pacifica* is especially vulnerable in this setting, probably because it is an open-water species that is maladapted to conditions close to or on the seafloor. On the other hand, *Thysanoessa spinifera* and *Nyctiphanes simplex*, which appear to be more neritic, did not share the diurnal vulnerability of *E. pacifica*. (*S. jordani* preyed most intensively on these two species in the water column at night; Table 4.) As shelf residents, they would be expected to possess adaptive defenses against threats characteristic of that habitat.

Probably *E. pacifica* is transported above the shelf at night by the coastal undercurrent. This current flows poleward above the shelf or upper continental slope throughout the year, but during most years reaches the surface only during fall and winter. At other times of year it is usually submerged, reportedly at depths of 200 to 500 m during the summer (Wyllie 1966; McLain and Thomas 1983). Chelton et al. (1987) found the undercurrent's velocities to be poleward at depths between 70 and 470 m throughout an 18-month period. So most of the time, at least, this current should be expected to impinge most directly on and flow over those parts of the shelf that extend offshore. This would account for the concentrations of *E. pacifica* at the Ascension and Sur canyon sites (Table 5). The dominance of *E. pacifica* near the northern rims of the canyons is consistent with this view. Because these locations are prominent projections in the path of the undercurrent (Figure 1), euphausiids ascending from the depths of adjacent canyons or downstream offshore areas would be expected to be carried over the shelf.

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EGG PRODUCTION ESTIMATES OF ANCHOVY BIOMASS IN THE SOUTHERN BENGUELA SYSTEM

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ABSTRACT

The spawning biomass of the southern Benguela anchovy (*Engraulis capensis*) stock has been estimated annually since 1984 by means of acoustics and the egg production method (EPM), both techniques being integrated into one survey. In 1985 and 1986 the survey area was stratified on the basis of expected fish distribution patterns, and the transects were randomized within limits to allow rigorous investigation of the survey variance of both the EPM and acoustic estimates. The acoustic estimates of relative fish density in the vicinity of trawl stations were incorporated to weight individual trawl parameters for the egg production method, and within-stratum variances were estimated from the weighted mean parameter values for each transect. In 1986 the acoustic and EPM estimates agreed within 15%, but in 1985 the acoustic estimate was about 30% greater than the EPM estimate. High coefficients of variation of 0.35 to 0.41 were associated with the EPM estimates, mainly reflecting imprecision in the estimation of egg mortality rate and female spawning fraction. This paper briefly presents the results of the surveys, and provides a complete description of the statistical methods appropriate to a randomized, stratified design for egg production surveys, incorporating the necessary weighting factors for trawl parameters.

RESUMEN

La biomasa de desove de la anchoveta del cabo, *Engraulis capensis*, ha sido estimada anualmente desde 1984 por medio de detección acústica y el método de producción de huevos (MPH); estas técnicas fueron usadas conjuntamente en nuestros cruceros. En 1985 y 1986, el área investigada fue estratificada en base a la distribución esperada de peces, y los transectos fueron distribuidos al azar dentro de ciertos límites, permitiendo estudiar rigurosamente la varianza de los valores estimados a través de detección acústica y por el método de producción de huevos. Las estimaciones de la densidad relativa de peces por medio de detección acústica en la vecindad de las estaciones de pesca fueron usadas para ponderar los parámetros de la red de arrastre necesarios para el método de producción de huevos. Dentro de cada estrato, las varianzas fueron estimadas a partir de los valores promedios ponderados para cada transecto. En 1986, las estimaciones acústicas y las por el método de producción de huevos coincidieron dentro de un 15%, pero en 1985 la estimación acústica fue alrededor de un 30% mayor que aquella obtenida por el método de producción de huevos. Coeficientes de variación entre 0.35 y 0.41 asociados con el método de producción de huevos, reflejan imprecisión en la estimación de la tasa de mortalidad de huevos y en la fracción de hembras que desova. Este trabajo presenta brevemente los resultados de los cruceros de investigación. Además, se provee una descripción completa de los métodos estadísticos apropiados para un diseño estratificado y aleatorio de cruceros específicamente programados para estimar la producción de huevos, incorporando los factores de ponderación necesarios para los parámetros de la red de arrastre.

INTRODUCTION

The estimation of population size by means of surveys plays an increasing role in fish stock assessments, either within some form of management plan in which recommended yields are a function of stock size (e.g., MacCall 1980) or to provide auxiliary information in catch-at-age analyses (e.g., Methot 1986). Pelagic fish surveys have employed vertical echo sounding (e.g., papers in Nakken and Venema 1983; Hampton 1987), mapping of schools by means of side-directed sonar (Hewitt et. al. 1976) or aircraft-borne remote sensors (Cram and Hampton 1976), and estimation of the abundance of eggs or larvae in the plankton. The latter method includes both the estimation of total annual egg or larval production by integrating over the results of repeated within-season surveys (Lockwood et al. 1981; Smith and Richardson 1977) and the more recently developed egg produc-

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tion method (EPM), in which egg production and specific fecundity are measured daily during a single survey (Parker 1980).

The utility of any survey method depends on its accuracy and precision. Sampling error may be minimized by appropriate survey design and sufficient sampling intensity, but some methods require parameters that are not estimated during each survey and therefore have unquantified variances (for example, the values of specific fecundity at different times during the spawning season in the integrated larval abundance method, or the proportion of schools detectable by aircraft-borne sensors). In the egg production method, all the parameters and their variances are estimated from a single survey, and the sampling intensity required to achieve a desired precision can be considered in the survey design (Picquelle 1985). Egg production surveys of engraulid biomass have been implemented in three of the major eastern boundary current systems: off California (e.g., Bindman 1986), off Peru (Alheit et al. 1984), and off southern Africa (this study).

The spawning population of the southern Benguela anchovy, *Engraulis capensis*, has been surveyed annually since 1983 by means of vertical echo integration (Hampton 1987), and egg samples have been collected during these cruises at regular stations along the acoustic survey grids for the estimation of daily egg production. From 1985, the proportion of the female population spawning each night (the spawning fraction) has been estimated by histological examination of ovaries (Hunter and Macewicz 1985), and in 1985 and 1986 the egg production method provided second biomass estimates in addition to the acoustic estimates. In 1984 the spawning fraction was estimated from the incidence of females with hydrated oocytes, but this was found to be an unacceptably biased method, and the spawning biomass in that year can only be roughly estimated from assumed values of spawning fraction. However, an approximate value can be obtained by comparing the incidence of hydrated females in 1984 with observations in other years when the histological method was also implemented.

Assuming the egg production biomass estimate to be less subject to bias than the acoustic estimate (a direct estimate of target strength has not yet been obtained for *E. capensis*), a method has been developed (Hampton et al., in press) in which the acoustic estimate in 1986 was adjusted by the ratio of egg production to acoustic biomass estimates in 1985 to allow the two 1986 estimates to be combined directly. The combined estimate was expected to be more accurate than either of the separate estimates. The results of the direct surveys of southern Benguela anchovy biomass initially allowed the identification of appropriate levels of yield for the resource (Armstrong and Butterworth 1986), and catches have subsequently been increased from 300,000 tons in 1986 to 600,000 tons in 1987, largely on the basis of the biomass estimates presented here.

In this paper we describe the methods and results of the egg production surveys of anchovy biomass in the southern Benguela Current system during 1984, 1985, and 1986, and provide a detailed account of the parameter and variance estimation procedures appropriate for a stratified random survey. Our method differs from that employed off California and Peru in that the fish densities estimated by means of vertical echo sounding are incorporated as weighting factors for the spawning parameters, and the survey transects, rather than the individual stations, are considered to be the basic sampling units for variance estimation.

METHODS

Biomass Model

The egg production method of estimating the spawning biomass of a fish population (Parker 1980) involves determining the average total number of eggs spawned per day by the population (the daily egg production) and the average number of eggs spawned daily per unit mass of the population (the daily specific fecundity). These estimates are obtained from simultaneous collections of fish and planktonic eggs across the spawning grounds. Biomass is calculated from the expression:

$$\hat{B} = \hat{P}_o A \frac{\hat{W}}{\hat{F}\hat{S}\hat{R}} \qquad (1)$$

where

$\hat{B}$ = estimated spawning biomass,
$\hat{P}_o$ = estimated mean daily egg production per unit area,
A = area within which $\hat{P}_o$ is estimated,
$\hat{W}$ = estimated mean mass of individual females,
$\hat{F}$ = estimated mean batch fecundity (eggs per female),
$\hat{S}$ = estimated mean fraction (by number) of the female population spawning each night, and
$\hat{R}$ = estimated mean ratio of female to total spawning biomass.

Defining a further variable $\hat{Q}$ as the ratio $\hat{W}/\hat{F}$ ($\hat{F}$ is obtained from a linear relationship between batch fecundity and female mass in the surveys described here), the approximate normalized variance of $\hat{B}$ is given by:

$$\frac{\mathrm{V}(\hat{B})}{\hat{B}^2} = \frac{V(\hat{P}_o)}{\hat{P}_o^{\,2}} + \frac{\mathrm{V}(\hat{Q})}{\hat{Q}^2} + \frac{\mathrm{V}(\hat{S})}{\hat{S}^2} + \frac{\mathrm{V}(\hat{R})}{\hat{R}^2}$$

$$+ 2\left[\frac{\mathrm{COV}(\hat{P}_o\hat{Q})}{\hat{P}_o\hat{Q}} + \frac{\mathrm{COV}(\hat{R}\hat{S})}{\hat{R}\hat{S}} - \frac{\mathrm{COV}(\hat{P}_o\hat{R})}{\hat{P}_o\hat{R}} - \frac{\mathrm{COV}(\hat{P}_o\hat{S})}{\hat{P}_o\hat{S}} - \frac{\mathrm{COV}(\hat{Q}\hat{R})}{\hat{Q}\hat{R}} - \frac{\mathrm{COV}(\hat{Q}\hat{S})}{\hat{Q}\hat{S}}\right] \tag{2}$$

The ratio estimate of spawning biomass from equation 1 is subject to small-sample bias arising from the asymmetry in the distribution of products or quotients of variables which themselves have more or less symmetrical distributions. The larger the coefficients of variation, the larger will be the bias. The bias is given as:

$$E(\hat{B}) - B' = B'\left[\frac{\mathrm{V}(\hat{R})}{\hat{R}^2} + \frac{\mathrm{V}(\hat{S})}{\hat{S}^2} + \frac{\mathrm{COV}(\hat{P}_o\hat{Q})}{\hat{P}_o\hat{Q}} + \frac{\mathrm{COV}(\hat{R}\hat{S})}{\hat{R}\hat{S}} - \frac{\mathrm{COV}(\hat{P}_o\hat{R})}{\hat{P}_o\hat{R}} - \frac{\mathrm{COV}(\hat{P}_o\hat{S})}{\hat{P}_o\hat{S}} - \frac{\mathrm{COV}(\hat{Q}\hat{R})}{\hat{Q}\hat{R}} - \frac{\mathrm{COV}(\hat{Q}\hat{S})}{\hat{Q}\hat{S}}\right] \tag{3}$$

where $E(\hat{B})$ is the expected value of the estimate from equation 1 and B' is the true biomass. An approximate estimate of bias is obtained by substituting $\hat{B}$ for B' in the right-hand side of equation 3. The estimated spawning biomass from equation 1 can then be corrected by subtracting the bias value given by equation 3.

Survey Design

The parameters for the southern Benguela anchovy stock were estimated during surveys lasting between two and three weeks, timed to coincide with peak anchovy spawning, which occurs around November each year (Shelton 1986). The surveys were conducted on board the Sea Fisheries Research Institute research ship *Africana*, a 76-m stern trawler capable of aimed midwater trawling to a depth of about 500 m.

The survey design in 1984 was based on a systematic grid of transects running approximately perpendicular to the coastline and spaced 37 km (20 n.mi.) apart at the inshore stations (Figure 1). A total area of 125,700 km^2 was surveyed from November 5 to 23. In 1985 and 1986 the survey area was stratified according to consistent patterns of fish distribution observed in previous spawning surveys, and in 1986 the density of sample transects was increased in strata with expected high fish densities. Within each stratum, the spacing between transects was randomized within limits to allow variances to be estimated on the assumption of random sampling (Figures 2 and 3). Full randomization was avoided to reduce the risk of large areas being left unsampled. A two-stage randomization procedure was adopted to provide a compromise between unrestricted random and equally spaced transects, without invalidating the variance estimates (Jolly and Hampton, MS in prep.) The 1985 and 1986 surveys covered areas similar to those in the 1984 survey, from November 11 to 26 and November 12 to 28, respectively. The egg production survey area A in each year excluded an outer zone of zero egg density in order to minimize the variance estimate. The positive egg strata were terminated within the offshore or inshore boundaries of the survey grid after two successive zero egg stations beyond the last positive egg station on each transect. Embedded areas of zero egg density were not excluded.

A Simrad EK-S 38-kHz scientific echo sounder was run continuously between egg stations, and the echoes were integrated in 1-m depth strata by means of a custom-built digital data logger. In addition to providing a further estimate of biomass, the acoustic density estimates were used to weight the egg production survey trawl parameters, as described later. A full description of the acoustic system and data analysis is given by Hampton (1987).

Collection of Eggs

Anchovy eggs were sampled at stations spaced 9.3 km (5 n.mi.) apart by means of vertical hauls of a CalVET net (Smith et al. 1985) from 200 m or near the seabed, depending on the sounding. In areas of zero egg abundance, the distance between stations was frequently extended to 18.6 km (10 n.mi.) to save time. Temperature profiles were recorded from an electronic temperature/depth sensor suspended below the net. The number of CalVET stations occupied in the positive egg strata of the 1984–86 surveys were 281, 245, and 271, respectively.

Collection of Fish

Pelagic fish were caught, both for acoustic target identification and for estimation of spawning parameters, by means of an Engels-308 midwater trawl with an 8-mm cod-end liner, towed on 32-mm

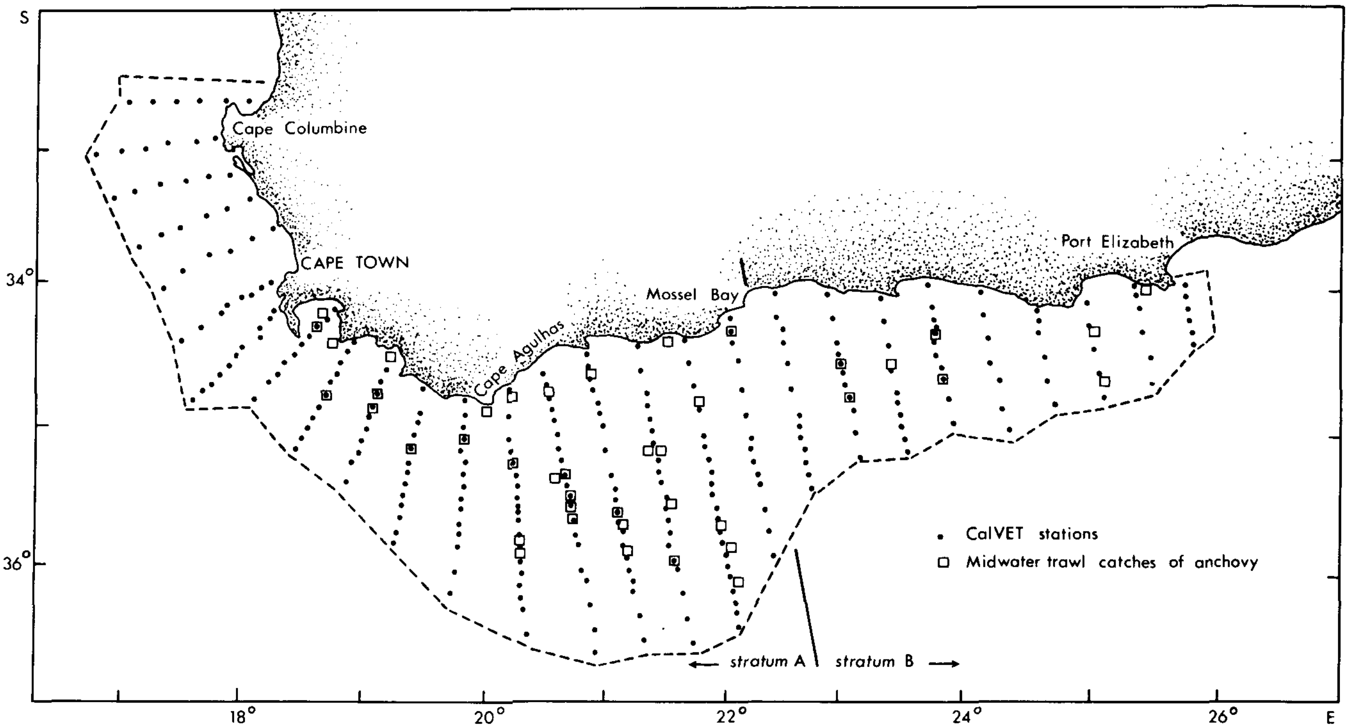

Figure 1. Position of egg stations and midwater trawl catches of anchovy in November 1984. The *post-hoc* delimitation of strata is indicated.

steel warps with 32-m sweeps and 6-m^2 steel doors. A mouth opening of approximately 15 m was recorded with this net at average towing speeds of 3–4 knots (depending on currents). Fishing operations were carried out during day and night when targets were sufficiently abundant to require identification or to provide usable information on spawning parameters. Nighttime trawling was facilitated by the dispersal of the anchovy into diffuse layers, usually just above the thermocline, which varied in depth from about 20 m in shallow water to over 50 m offshore.

The performance of the gear and the entry of fish into the net were monitored by means of a 49-kHz net-sonde mounted on the top panel of the net; the duration of the tows could therefore be varied according to the apparent catch rate. Nighttime tows generally consisted of a double oblique haul through the scattering layer, and all tows were completed in the shortest possible time in order to bring the fish to the surface alive. Catches of anchovy averaged 40–80 kg.

Parameter Estimation for Daily Egg Production

The CalVET net samples of anchovy eggs were sorted and staged according to the criteria given by Moser and Ahlstrom (1985). The average age of eggs in each stage was estimated from egg development-temperature relationships obtained by means of incubation experiments carried out on field-collected eggs during the 1984 survey, and described in Valdes et al. (1987). The relationship between the average age t_p of an egg in development stage p and the ambient temperature v°C was described by the exponential function:

$$t_p = \exp(A_p - B_p v) \qquad (4)$$

Values of A_p and B_p for egg stages 3 to 11 were obtained from the experiments carried out during the 1984 survey (Table 1). The parameters for stage 2 could not be determined from the field-sampled eggs, and the relationship for this stage was there-

TABLE 1

Parameters of the Relationship (Equation 4) Estimated from Incubation Experiments Carried Out on Field-Collected Eggs during the November 1984 Spawner Biomass Survey

Development stage p	Parameter	
	Ap	Bp
2	3.755	0.1183
3	5.197	0.1576
4	5.559	0.1586
5	5.941	0.1600
6	5.875	0.1390
7	5.915	0.1286
8	5.914	0.1206
9	6.387	0.1428
10	6.215	0.1298

Development stages are after Moser and Ahlstrom (1985).

fore assumed to be similar to that of the California anchovy (Lo 1985).

Temperatures in the upper mixed layer were generally uniform, and values at 5 m were used to determine the ages of eggs at each station. (Previous studies of the vertical distribution of anchovy eggs in the survey area [Shelton 1986; Shelton et al., MS in prep.] showed that the eggs occurred at various depths from near the surface to just above the thermocline.)

Spawning was assumed to occur synchronously at 2200 h, based on the incidence of anchovies with both hydrated oocytes and new postovulatory follicles in trawl samples (Melo et al., MS in prep.). The eggs in each developmental stage could therefore be allocated to one of up to three previous nights' spawnings, according to the estimated ages of the eggs in the various stages. The earliest time of spawning each night was taken to be 1700 h; if the age estimated for a given egg stage from equation 4 indicated that spawning occurred before 1700 h, the eggs were assumed to have been derived from the preceeding night's spawning, but having developed more slowly than expected from the temperature at 5-m depth. Because this temperature represents the warmest that the eggs are likely to have encountered in the water column, there is a much higher probability that an egg would be underaged than overaged. The egg stages at each station were grouped by spawning night, and the number of eggs in each group was determined. The mean age of eggs in each group was then reestimated as the time elapsed between spawning at 2200 h and the time of sampling. Zero egg abundance was recorded if a batch of eggs from a previous night's spawning was expected, but not observed.

Egg numbers were assumed to decline at a constant exponential rate according to the model:

$$P_t = P_o \exp(-Z\,t) \qquad (5)$$

where

P_o is the mean total daily egg production and
P_t is the mean egg abundance at age t.

The mean hourly instantaneous rate of egg mortality, Z, was estimated by regressing the natural logarithms of the estimated total abundances of eggs in one-hour age classes against age with weighting values equivalent to the inverse of the variance of each abundance value (see Appendix 1).

The mean density of eggs in each age class (expressed as eggs m^{-2}) was first estimated for separate survey strata by averaging the station values for that age class within each stratum, giving 10-mile stations twice the weighting of stations spaced 5 miles apart to allow for the greater area represented by the 10-mile stations. These mean densities were then multiplied by the stratum areas and summed to give overall abundance of eggs of age t to $t+1$ h. None of the one-hour age classes had zero total abundance of eggs in the 1984–86 surveys, but in the event of this occurring, the age classes could be further amalgamated to eliminate the zeroes. Alternatively, an equivalent nonlinear regression package could be employed, provided the regression data could be weighted as described. Details of the linear regression procedure are given in Appendix 1. Only the abundances of eggs aged between 5 and 50 h were included in the regression to avoid biases caused by hatching or incomplete recruitment of the eggs to the plankton.

In the above procedure, the estimates of egg density in each age class were weighted by stratum area to estimate total egg abundance at each age. This procedure was adopted to reduce any bias that may have arisen if egg mortality varied between survey strata with different fish densities or environmental conditions, even though such variations are unlikely to be detectable at the present sampling rate. A slight reduction in the variance of the egg mortality estimate could have been obtained by abandoning stratum weighting on the basis that between-stratum variations could not be detected with acceptable levels of confidence.

Weighting Procedures and Variance Estimation for $\mathbf{P_o}$

The values of abundance of eggs at age 5 to 50 h at each CalVET station were divided by the estimated survival rate $\exp(-Zt)$ to provide up to three estimates of daily egg production (depending on the number of batches expected at the ambient temperature and time of sampling). These values were averaged to give a station value $\hat{P}_{o_{ijk}}$, and a weighted mean value of age was computed. (Parameters for strata, transects, and stations are suffixed i, j, and k respectively.) The station values were then averaged to give transect estimates $\hat{P}_{o_{ij}}$ and $\bar{t}_{ij}$, with any missing 5-mile station values being obtained by interpolation between adjacent 10-mile stations on the same transect. Stratum mean values $\hat{P}_{o_i}$ were calculated as weighted means of the transect values, with weights equal to the lengths L_{ij} of the transects (weighting expressions for transect and stratum values of spawning parameters are summarized in Table 2 for easy reference):

$$\hat{\bar{P}}_{o_i} = \frac{\Sigma_j L_{ij} \hat{\bar{P}}_{ij}}{\Sigma_j L_{ij}} \tag{6}$$

$V_o(\hat{\bar{P}}_{o_i})$, the approximate variance of $\hat{\bar{P}}_{o_i}$ ignoring at this stage the additional variance associated with the estimation of Z, was obtained from the following equation, which is derived from the formula for the variance of a ratio estimator for subsampling given in Cochran (1977):

$$V_o(\hat{\bar{P}}_{o_i}) = \frac{\frac{n_i}{n_i - 1} \sum_j L^2_{ij} (\hat{\bar{P}}_{o_{ij}} - \hat{\bar{P}}_{o_i})^2}{\left(\sum_j L_{ij}\right)^2} \tag{7}$$

where n_i is the number of sample transects in stratum i. Since each transect provides a random sample of the stratum mean, the sampling variance is fully expressed in the variance between transects, irrespective of the variation within the transects. This does not imply that the within-transect variation (and hence the station allocation) is immaterial, for the variation between transects will be affected by the within-transect variation.

The survey mean value $\hat{\bar{P}}_o$ was obtained by averaging over strata with weights equal to A_i, the areas of the strata:

$$\hat{\bar{P}}_o = \frac{\Sigma_i A_i \hat{\bar{P}}_{o_i}}{\Sigma_i A_i} \tag{8}$$

The component of variance in $\hat{\bar{P}}_o$ arising from sampling error in the estimation of egg abundance was given by:

$$V_o(\hat{\bar{P}}_o) = \frac{\Sigma_i A^2_i V_o(\hat{\bar{P}}_{o_i})}{(\Sigma_i A_i)^2} \tag{9}$$

The overall variance of $\hat{\bar{P}}_o$, $V(\hat{\bar{P}}_o)$, was obtained by including the error associated with the estimation of egg mortality:

$$\frac{V(\hat{\bar{P}}_o)}{\hat{\bar{P}}_o^2} = \frac{V_o(\hat{\bar{P}}_o)}{\hat{\bar{P}}_o^2} + (\hat{\bar{t}})^2 V(Z) \tag{10}$$

where $V(Z)$ is the variance of the hourly egg mortality estimate, and $\hat{\bar{t}}$ is the weighted mean age of eggs over the survey area. The component $(\hat{\bar{t}})^2$ $V(Z)$ expresses the uncertainty involved in back-calculating egg abundance at age zero from station values of egg abundance at age, where the average time elapsed from age zero in the samples is $\hat{\bar{t}}$ h.

Spawning Parameter Estimation

A random sample of 150 anchovies was taken from each midwater trawl catch where possible for estimation of sex ratio and mean female mass; an additional 25 females were taken at random and preserved in 10% Formalin for estimation of spawning fraction. The caudal lengths (Lc) of the 150 fish were recorded, and each fish was slit along the abdomen to allow the sex and maturity stage to be determined. The females were separated from the males and immature fish, and blast frozen in sealed plastic bags with as much air excluded as possible. Hydrated females were excluded, but were measured to the nearest millimeter. The samples were weighed ashore while still frozen, and the sex ratios $(\hat{R}_{ijk})$ and mean female masses $(\hat{\bar{W}}_{ijk})$ were determined. The masses of hydrated females were estimated from a length-mass relationship for females with active but nonhydrated ovaries (to adjust for the temporary gain in mass), and included in the estimation of $\hat{\bar{W}}_{ijk}$ and $\hat{R}_{ijk}$. Because this procedure was necessary only for a small fraction of the sampled female fish, errors in this approximation were considered to have a negligible effect on the estimates of R and $\bar{W}$. Very few immature anchovies were recorded, even in 1986, when a relatively large component of late-recruiting fish of 8–10-cm Lc were present in the survey area. Thus the 1984–86 EPM estimates represent total biomasses at the times of the surveys.

The spawning fractions $\hat{S}_{ijk}$ were estimated from the incidence of females with day-1 postovulatory follicles in the random samples of 25 females, according to the methods given by Hunter and Macewicz (1985). Day-0 females were found to be oversampled by the midwater trawl to an extent similar to that observed off California (Picquelle and Stauffer 1985). Samples in which most females contained hydrated ovaries were regularly taken

TABLE 2
Weighting Expressions for Transect and Stratum Mean Values of Spawning Parameters

		Parameter	
	P_o	W,S	R
Transects j	L_{ij}	$L_{ij} \hat{\bar{d}}_{ij} \frac{\hat{\bar{R}}_{ij}}{\hat{\bar{W}}_{ij}}$	$L_{ij} \hat{\bar{d}}_{ij}$
Strata i	A_i	$A_i \hat{\bar{d}}_i \frac{\hat{\bar{R}}_i}{\hat{\bar{W}}_i}$	$A_i \hat{\bar{d}}_i$

Where L_{ij} = length of transect j, stratum i
A_i = area of stratum i
$\hat{\bar{d}}_{ij}$ = mean density of fish along transect j, estimated by acoustics
$\hat{\bar{d}}_i$ = mean density of fish in stratum i, estimated by acoustics

during the evening spawning period, and these samples were often characterized by anomalous sex ratios. To correct for oversampling of day-0 females and the consequent undersampling of day-1 and day-2+ females, the method given by Picquelle and Stauffer (1985) was applied. In this method, it was assumed that the proportion of day-0 and day-1 spawners in the population should on average be equivalent. Hence the number of day-0 spawners in a sample was replaced by the number of day-1 spawners, and the overall sample size was adjusted accordingly. If the number of day-1 spawners in a sample was N^1_{ijk} and the number of day-2+ spawners was $N^{2^+}_{ijk}$, the spawning fraction $\hat{S}_{ijk}$ was calculated as:

$$\hat{S}_{ijk} = \frac{N^1_{ijk}}{2\,N^1_{ijk} + N^{2^+}_{ijk}} \tag{11}$$

Batch fecundity could not be estimated for each trawl station because of the small proportion of trawls containing hydrated females. However, the batch fecundity was found to be a linear function of ovary-free female mass in each year, and a linear regression allowed the population mean batch fecundity $\hat{\bar{F}}$ to be predicted from the mean female mass $\hat{\bar{W}}$, with a suitable adjustment for the discrepancy between the mass of live and preserved specimens. The variance of this predicted value was then a function of the variance of the regression slope, the residual sums of squares of the regression data, the number of observations and the mean mass of the females in the regression, and the between-transect variation in $\hat{\bar{W}}$. (Had a nonlinear relationship been obtained, $\hat{\bar{F}}$ would of necessity have been estimated by computing an $\hat{\bar{F}}_{ijk}$ for each trawl station.) Females that were hydrated but not yet ovulated were collected during each survey and preserved in 10% buffered Formalin. The batch fecundities were determined by means of the hydrated oocyte method described by Hunter et al. (1985), the sample sizes ranging from 53 to 81 in the three surveys.

Weighting Procedures and Variance Estimation for Spawning Parameters

The procedure described in Picquelle and Stauffer (1985) for averaging station values of spawning parameters of the northern anchovy is based on the assumption that the number of samples in a given area will be proportional to the abundance of fish in that area, providing self-weighted estimates of the parameters. Equal subsample sizes are attempted, but as this is not always attained in practice, the station parameter values are weighted by subsample size on the premise that departures from the target subsample size represent errors in judgment sampling. This argument depends on the method of trawling adopted in the surveys described by Picquelle and Stauffer (1985), in which a midwater trawl with a large mouth opening is towed at a constant depth for a fixed period at locations where anchovy are indicated by sonar targets or eggs in the plankton (P. E. Smith, Southwest Fisheries Center, pers. comm.)

This method of station weighting was considered inappropriate for the surveys described here because the trawling operation was varied on the basis of the net-sonde or vertical echo-sounder record to ensure an adequate sample size, and because the ratio of number of samples to the abundance of females (as estimated from acoustics and values of sex ratio and female mass from midwater trawl samples) was found to be up to four times greater in strata with low female abundance than in strata with high female abundance. This was partly a consequence of the requirement for regular identification of acoustic targets. Further, the adoption of transects as sampling units meant that the individual station values of spawning parameters were obtained as weighted means of the station values (as described below), and transect weighting factors that would allow unbiased estimation of stratum means and variances of the parameters were then derived.

The most appropriate weighting factors were the anchovy density estimates obtained from vertical echo integration. Surface schooling was rarely encountered during the spawning stock surveys to an extent sufficient to bias the density estimates, and tended to be more a feature of the eastern Agulhas Bank, where the fish and egg densities were both generally low. The thermocline was comparatively shallow in this region (Largier and Swart 1987), resulting in a greater proportion of the fish occupying the near-surface region of the upper mixed layer. This problem was partially corrected for by discarding acoustic density estimates from intervals during which schools were frequently detected on the side-directed sonar but not recorded by the vertical echo sounder. Errors in the target strength expression were considered to be unimportant in the derivation of weighting factors, because only relative values of fish density were required.

Transect values $\hat{\bar{W}}_{ij}$, $\hat{\bar{R}}_{ij}$, and $\hat{\bar{S}}_{ij}$ were derived by linking each acoustic interval (the section of transect surveyed between egg stations) with the trawl samples that were considered to provide a reliable identification of the acoustic targets. Each trawl sample was therefore allocated to a segment of transect for which a "biomass" value was calculated as the sum of the products of the interval lengths and the mean fish densities for the intervals, as determined acoustically. These values were used as weighting factors w_{ijk} for the station values $\hat{R}_{ijk}$, but were multiplied by the ratio $\hat{R}_{ijk}/\hat{W}_{ijk}$ to give weighting factors in terms of female numbers for the parameters $\hat{W}_{ijk}$ and $\hat{S}_{ijk}$. The station parameters were averaged, incorporating these weighting factors, to give the transect values $\hat{W}_{ij}$, $\hat{R}_{ij}$, and $\hat{S}_{ij}$.

Stratum values of the spawning parameters were obtained by averaging over transects with weights $w_{ij} = L_{ij}\,\bar{d}_{ij}$ for sex ratio and $w_{ij} = L_{ij}\,\bar{d}_{ij}.\,\hat{R}_{ij}/\hat{W}_{ij}$ for the other parameters, L_{ij} and $\bar{d}_{ij}$ being the length of transect j and the mean anchovy density (g m^{-2}) for transect j, respectively, as determined during the acoustic survey.

Thus for a given trawl parameter $\hat{\mu}$:

$$\bar{\mu}_i = \frac{\Sigma_j\, w_{ij}\, \hat{\mu}_{ij}}{\Sigma_j w_{ij}} \qquad (\hat{\mu}_{ij} = \hat{W}_{ij}, \hat{R}_{ij}, \hat{S}_{ij}) \tag{12}$$

where w_{ij} is the weighting factor for a transect parameter value $\hat{\mu}_{ij}$.

Variances were estimated as:

$$V(\hat{\mu}_i) = \frac{\dfrac{n_i}{n_i - 1}\Sigma_j\, w^2_{ij}\,(\hat{\mu}_{ij} - \hat{\mu}_i)^2}{(\Sigma_j\, w_{ij})^2} \tag{13}$$

where n_i = number of transects in stratum i.

Finally, the stratum values $\hat{R}_i$ were averaged with weights w_i equal to the acoustically derived biomasses $A_i\,\bar{d}_i$ (where A_i is the stratum area and $\bar{d}_i$ is the stratum mean density), and stratum values $\hat{W}_i$ and $\hat{S}_i$ were averaged with weights equivalent to female numbers ($A_i\,\bar{d}_i\,\hat{R}_i/\hat{W}_i$). The variances were then computed as weighted means over strata:

$$\hat{\mu} = \frac{\Sigma_i w_i\, \hat{\mu}_i}{\Sigma_i w_i} \qquad (\hat{\mu}_i = \hat{W}_i, \hat{R}_i, \hat{S}_i) \tag{14}$$

$$V(\hat{\mu}) = \frac{\Sigma_i\, w^2_i\, V(\hat{\mu}_i)}{(\Sigma_i\, w_i)^2} \tag{15}$$

The relationship between batch fecundity and female mass was described by a linear regression, allowing the overall mean batch fecundity to be predicted at this stage from the value $\hat{W}$. The independent variable in the regression was ovary-free preserved mass. The estimate of mean weight was divided by the factor 1.0224 to adjust for a predicted 2.7% increase in mass after 60 days in 10% Formalin (Hunter 1985) and for the removal of the ovaries, which prior to hydration were determined to weigh on average 5% of the ovary-free live mass in the most abundant size classes of females.

To facilitate variance computations in the present situation, in which batch fecundity was a linear function of female mass, a variable $\hat{Q}$ was defined as the ratio $\hat{W}/\hat{F}$. The variance of $\hat{Q}$ arising from sampling error in the estimation of $\hat{W}$ was estimated as:

$$V_o(\hat{Q}) = \left[\frac{1 - b\,\hat{Q}}{\hat{F}}\right]^2 V(\hat{W}) \tag{16}$$

where b was the slope of the batch fecundity regression. Equation 16 is a shorthand method for obtaining the variance of the ratio $\hat{W}/\hat{F}$ when $\hat{F}$ is a linear function of $\hat{W}$. (Expansion of the bracketed term with $\hat{Q}$ replaced by $\hat{W}/\hat{F}$, and multiplication through by $V(\hat{W})$, retrieves the separate expressions for the variances and covariances of $\hat{W}$ and $\hat{F}$.) The total variance of $\hat{Q}$ was estimated by including the component of variance arising from estimation error in the fecundity-mass relationship:

$$\frac{V(\hat{Q})}{\hat{Q}^2} = \frac{V_o(\hat{Q})}{\hat{Q}^2} + \frac{1}{\hat{F}^2}\left[\frac{S^2_{FW}}{n_{FW}} + S^2_b\,(\hat{W} - \bar{W}')^2\right] \tag{17}$$

where S^2_{FW} = the residual sums of squares of the regression,
S^2_b = the variance of the slope b,
n_{FW} = the number of observations in the regression,
$\hat{W}$ = the adjusted estimate of mean female mass in the population, and
$\bar{W}'$ = the mean ovary-free mass of preserved females in the regression.

Combination of Strata

If a stratum has fewer than about eight sampled transects, the estimates of variance for that stratum will tend to be unreliable. Since most sampling effort should be concentrated in the higher-density strata, small numbers of transects will usually occur in low-density strata, particularly when the absence of targets or rough sea conditions result in no trawl samples being taken to estimate spawning parameters on some transects. Rather than obtain estimates of parameters that are highly variable and have unreliable variance estimates, it is advisable to group these strata so as to have about ten or more transects in each group. Average parameters and variances are then estimated for each group. The advantage of stratification is retained in full, the variances of the estimated mean parameter values being based on within-stratum variation.

The principle is described in Cochran (1977), where the resulting estimates are called "combined" in contrast to "separate" estimates for each stratum. An adaptation of Cochran's method suitable for egg production survey parameters is described in Appendix 2. A number of low-density strata were combined in this manner during the 1985 and 1986 surveys, as indicated on Figures 2 and 3.

Covariance Estimation

An advantage of working with transect-based values of parameters is that the covariances between all parameters can be easily worked out. For two parameters $\hat{\mu}(1)_i$ and $\hat{\mu}(2)_i$ estimated for stratum i, in which the transect weighting factors are $w(1)_{ij}$ and $w(2)_{ij}$, the covariance for stratum i is given by:

$$\mathrm{COV}\,(\hat{\mu}(1)_i\, \hat{\mu}(2)_i) = \frac{\frac{n_i}{n_i-1}\sum_j w(1)_{ij}\, w(2)_{ij}\, (\hat{\mu}(1)_{ij} - \hat{\mu}(1)_i)\,(\hat{\mu}(2)_{ij} - \hat{\mu}(2)_i)}{\sum_j w(1)_{ij}\, \sum_j w(2)_{ij}} \tag{18}$$

Covariances were determined for the parameters $\hat{P}_{oi}$, $\hat{W}_i$, $\hat{R}_i$, and $\hat{S}_i$ in each stratum.

Using the same notation as above, the overall covariance values are derived as weighted averages over strata:

$$\mathrm{COV}(\mu(1)\, \mu(2)) = \frac{\sum_i w(1)_i\, w(2)_i\, \mathrm{COV}\,(\hat{\mu}(1)_i\, \hat{\mu}(2)_i)}{\sum_i w(1)_i\, \sum_i w(2)_i} \tag{19}$$

Covariance estimates involving $\hat{W}$ were then adjusted to give the corresponding covariances involving $\hat{Q}$ (the ratio estimate $\hat{W}/\hat{F}$) by multiplying by the factor $(1 - b\hat{Q})/\hat{F}$. The final covariances were accordingly those involving the parameters $\hat{P}_o$, $\hat{R}$, $\hat{S}$, and $\hat{Q}$ (see equations 2 and 3).

RESULTS

Distribution Patterns

The egg distribution patterns were very similar during the three surveys, with the bulk of the

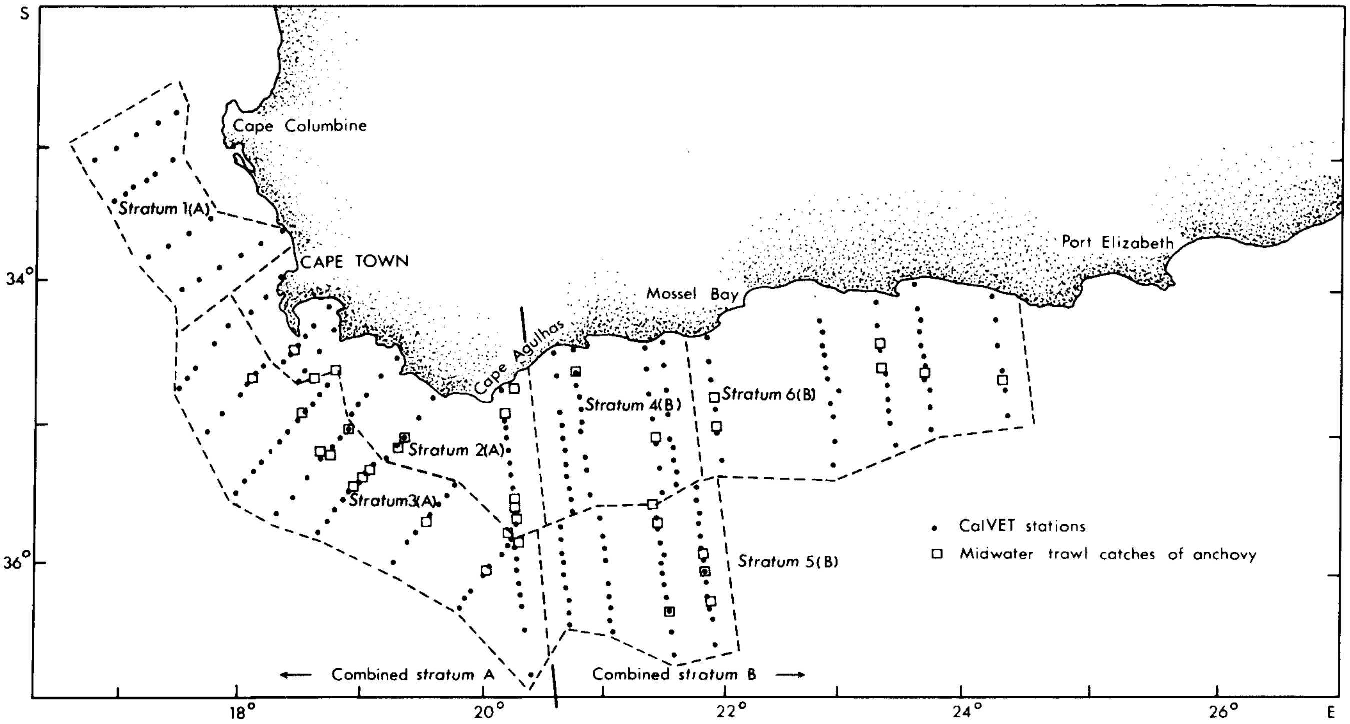

Figure 2. Position of egg stations and midwater trawl catches of anchovy in November 1985. The boundaries of six predefined strata are indicated; the original strata 1–3 and 4–6 were subsequently combined to form the redefined strata A and B for analysis.

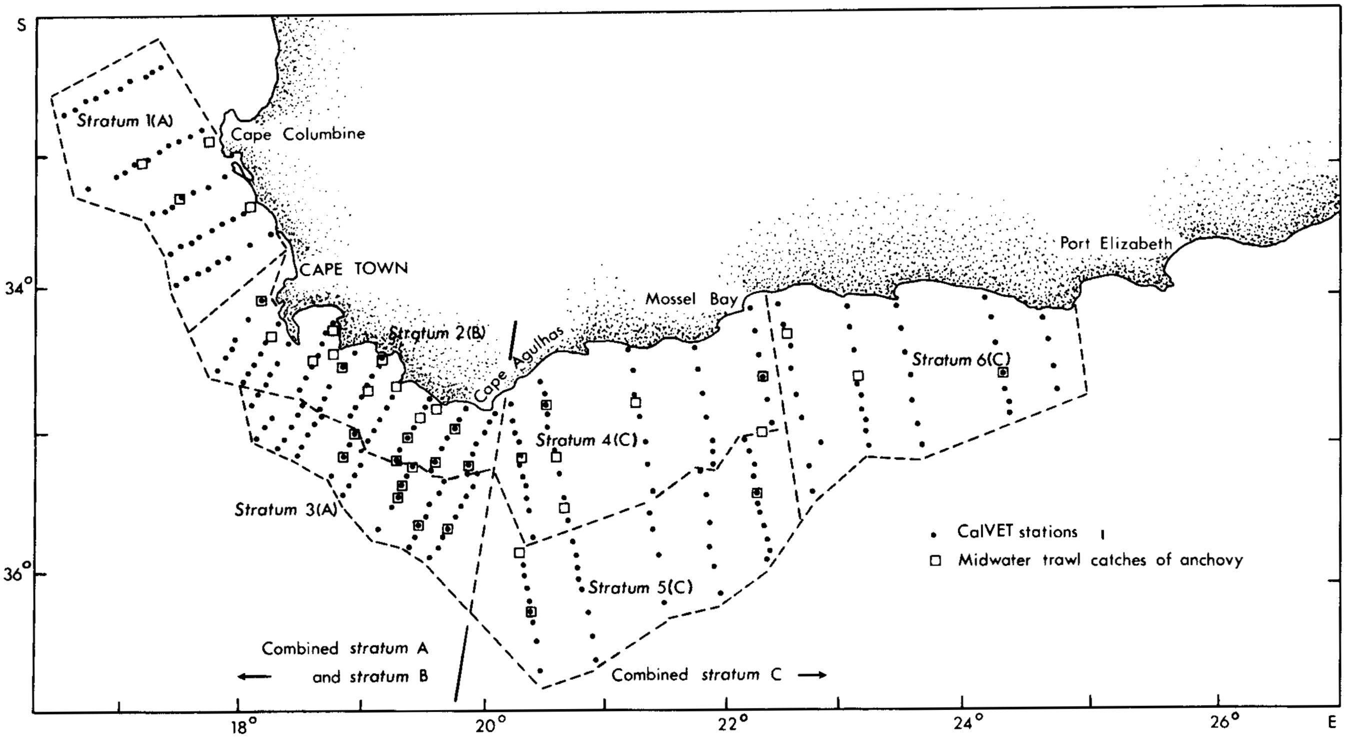

Figure 3. Position of egg stations and midwater trawl catches of anchovy in November 1986. The boundaries of six predefined strata are indicated; strata 1 and 3 and 4–6 were subsequently combined to form the redefined strata A and C for analysis.

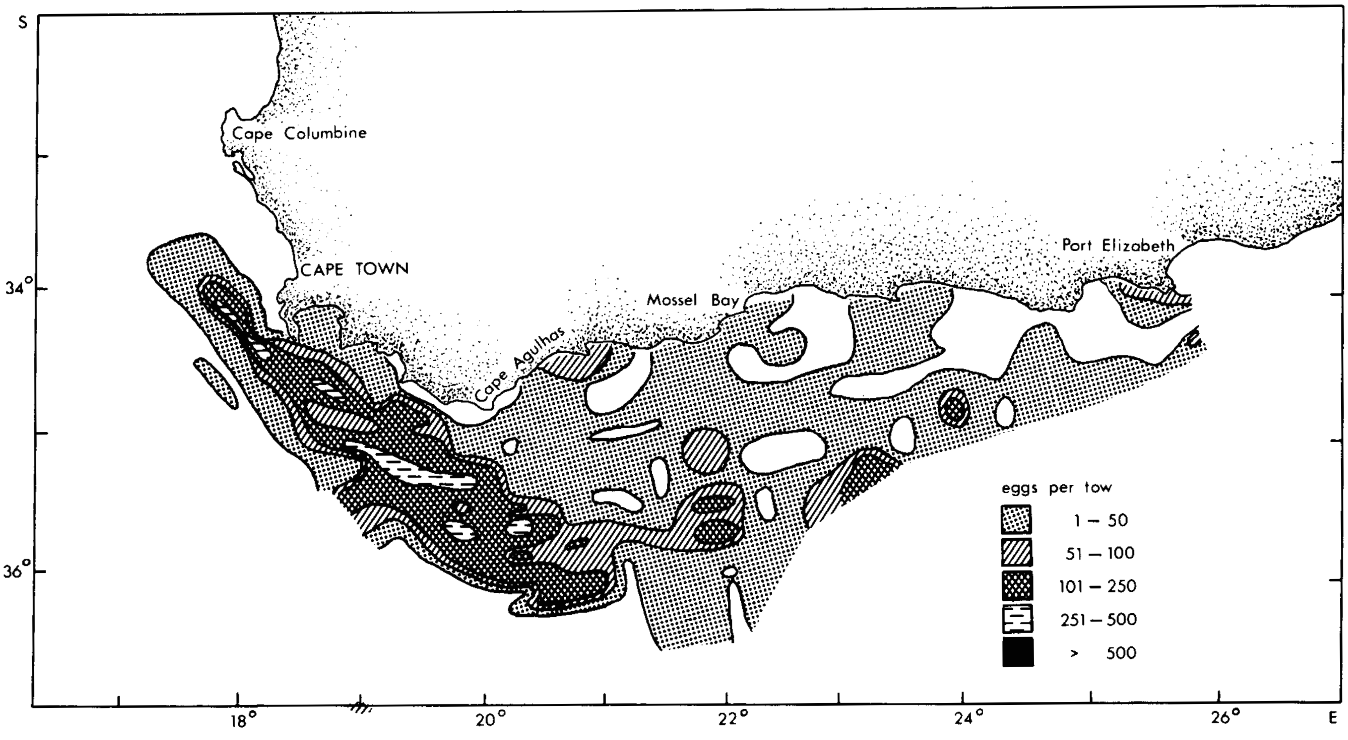

Figure 4. Anchovy egg distribution in 1984.

spawning occurring offshore over the western Agulhas Bank (Figures 4–6). There was evidence of advection of eggs around Cape Point and northwards along the west coast, supporting the hypothesis of Shelton and Hutchings (1982) that fast currents associated with the upwelling and shelf-

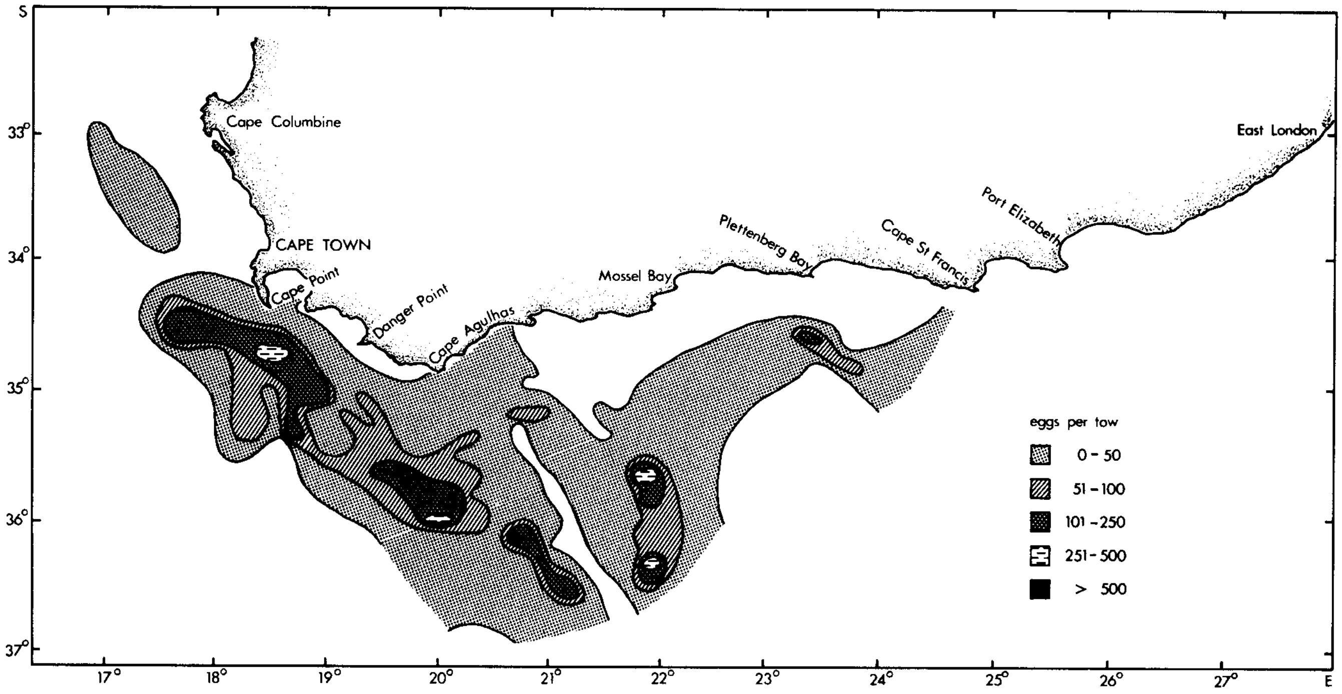

Figure 5. Anchovy egg distribution in 1985.

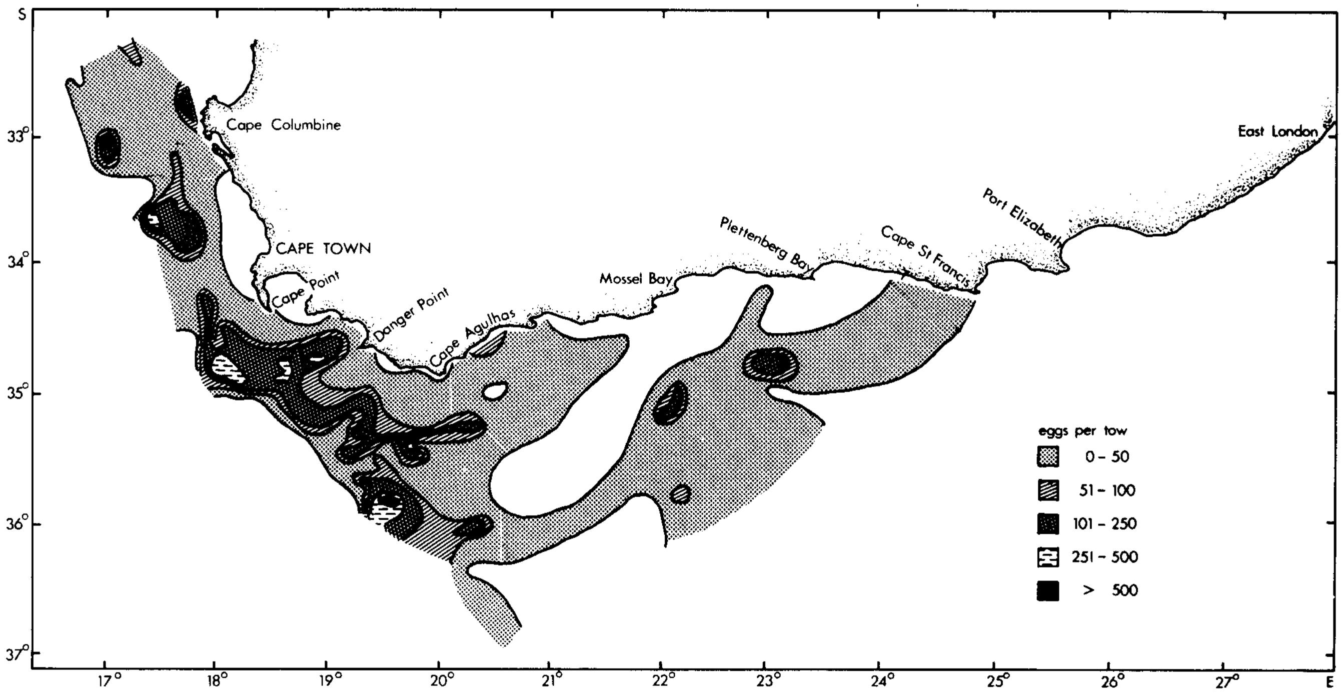

Figure 6. Anchovy egg distribution in 1986.

edge fronts are important for the rapid transport of eggs and larvae toward the west coast nursery areas. There was evidence, however, that spawning in 1986 was also taking place to the north of Cape Point. A remarkable feature of the three surveys was that the areas of the positive egg strata remained roughly constant at 106,000 to 110,000 km^2. Surface temperatures over the spawning area were fairly uniform at 17°–19°C (Figures 7–9), with the great majority of positive egg stations occurring within these temperature limits.

In 1984 and 1985, the fish distribution patterns

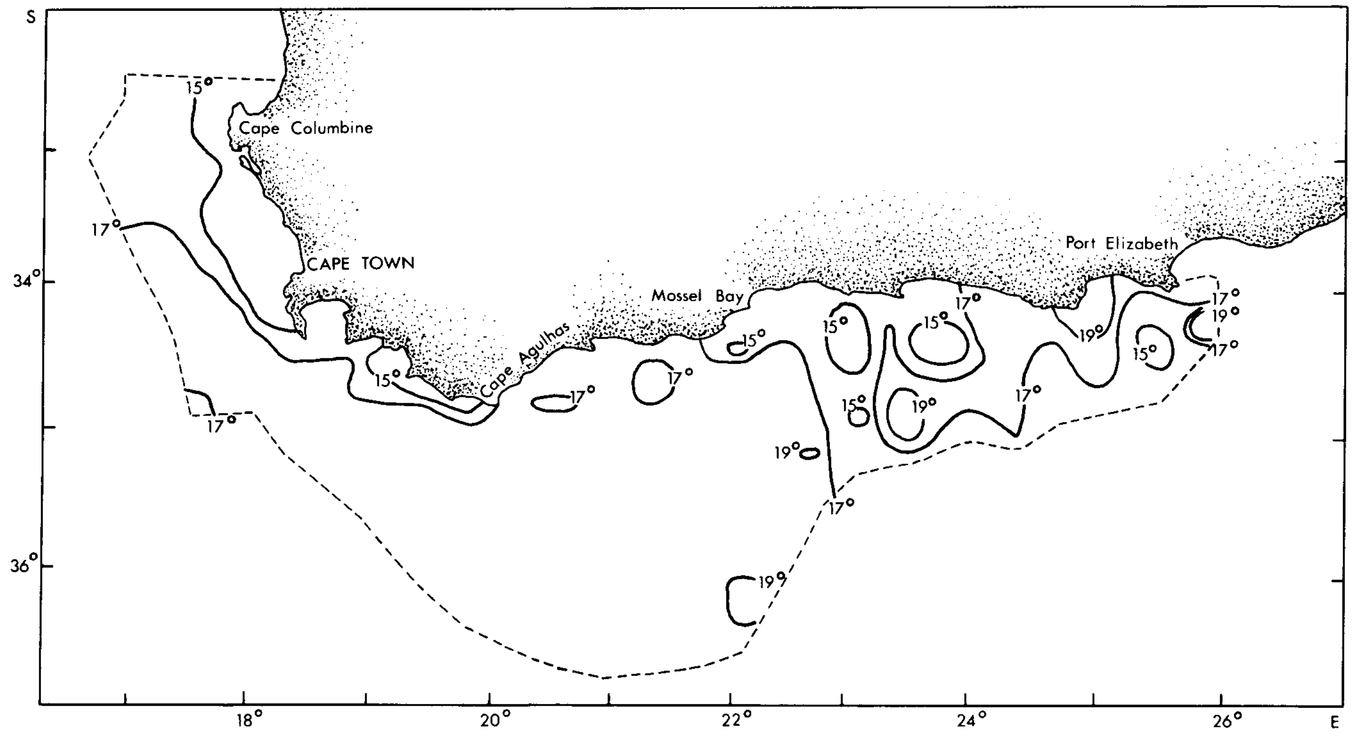

Figure 7. Temperature isotherms at 5-m depth, November 1984.

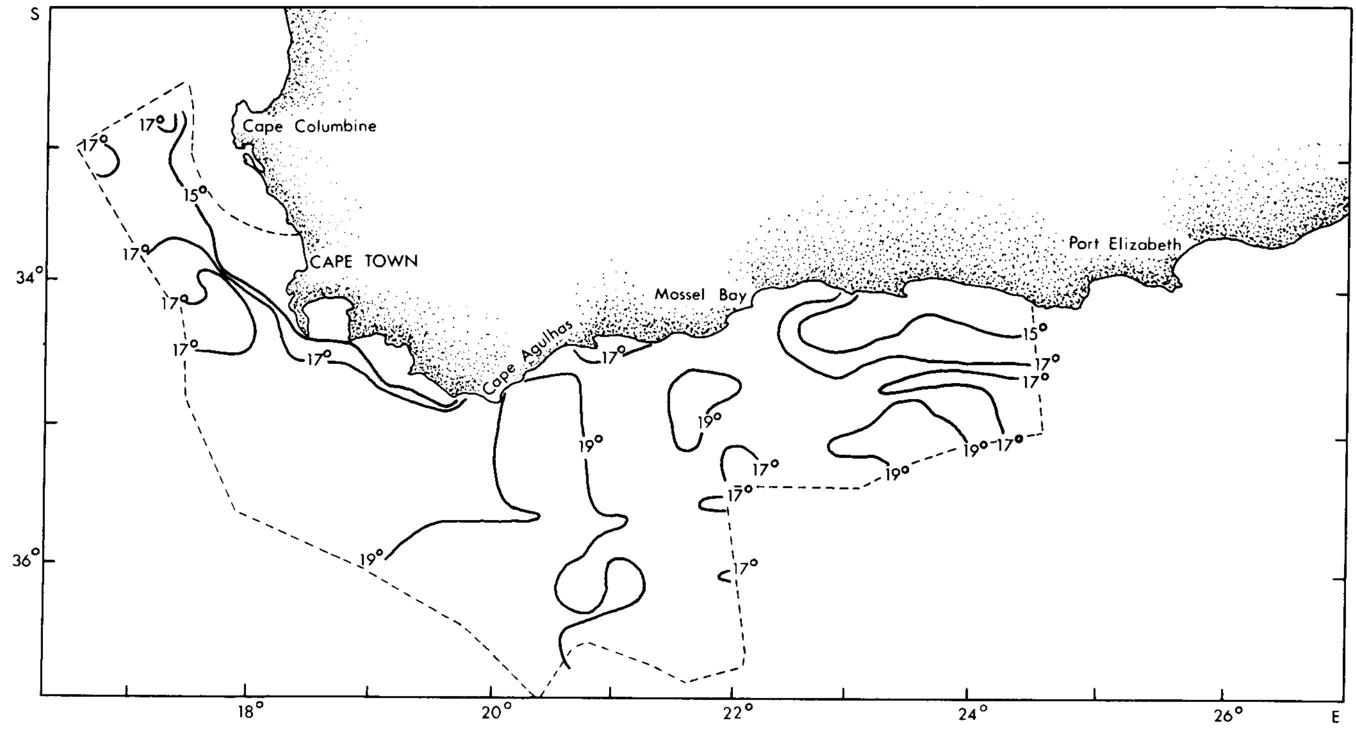

Figure 8. Temperature isotherms at 5-m depth, November 1985.

determined from the acoustic surveys were very similar to the egg distributions, although there was a tendency for the area of high egg density over the western Agulhas Bank to occur slightly offshore of the region of high fish density (Figures 10 and 11). The situation in 1986 was different in that high concentrations of young adult anchovy occurred close to the coastline along the south coast, with shoals

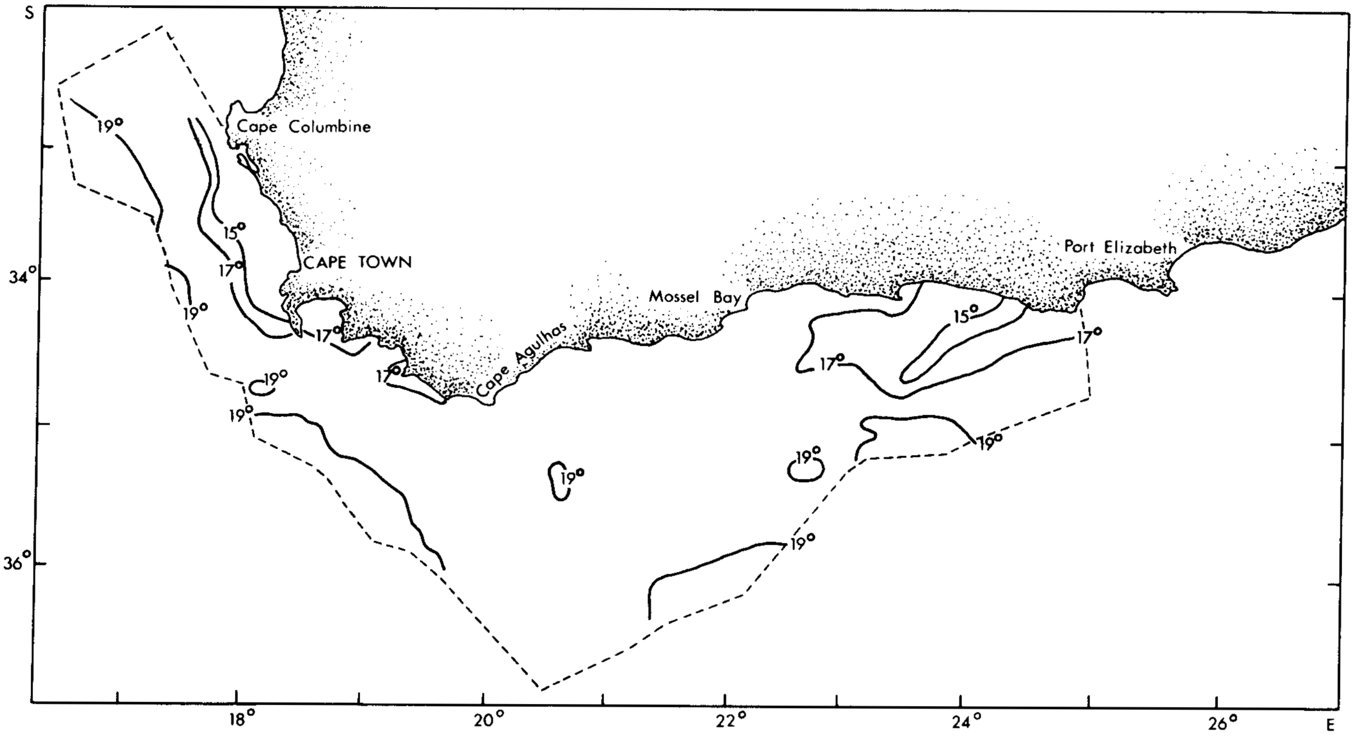

Figure 9. Temperature isotherms at 5-m depth, November 1986.

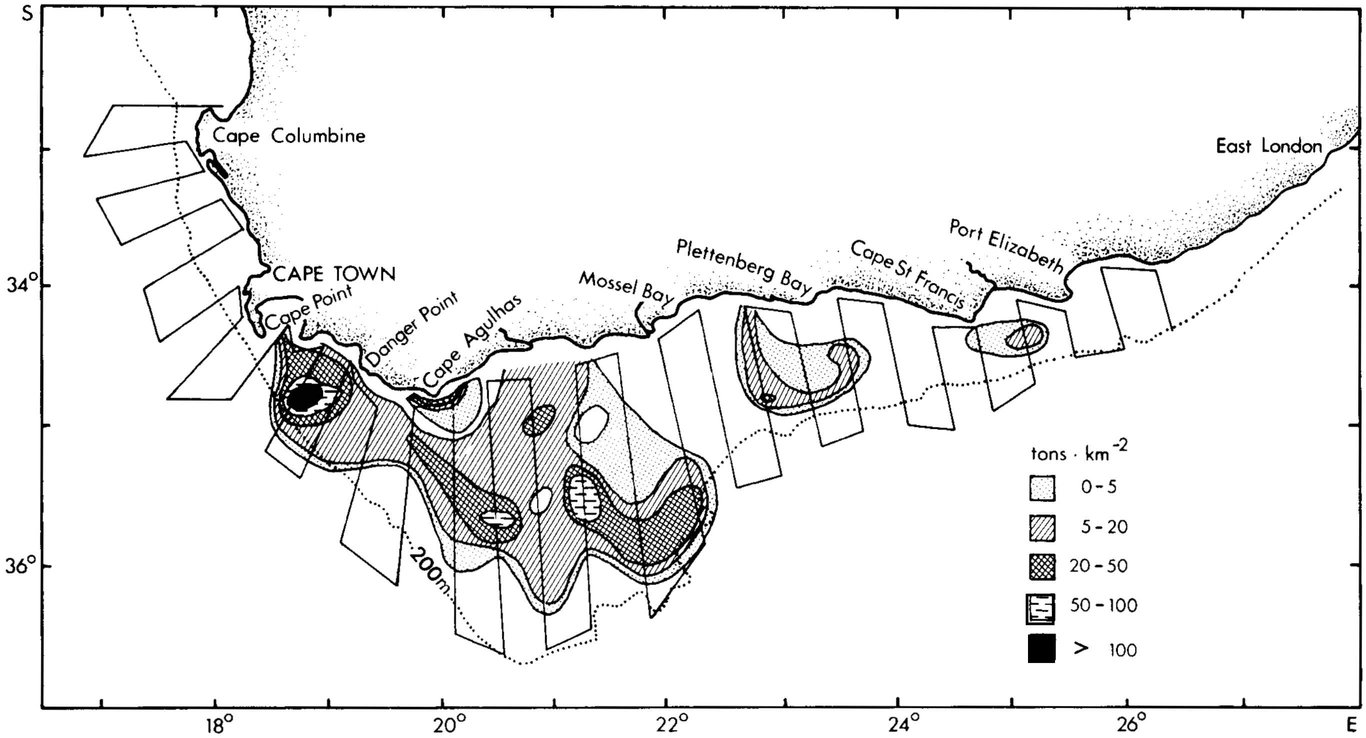

Figure 10. Anchovy density distribution in November 1984, as determined from acoustic data (after Hampton 1987).

also being distributed along the west coast between Cape Point and Cape Columbine (Figure 12). A comparison between the weighted length frequencies of anchovy in the three years (obtained by weighting the sample length frequencies by the same general procedure described for the spawn-

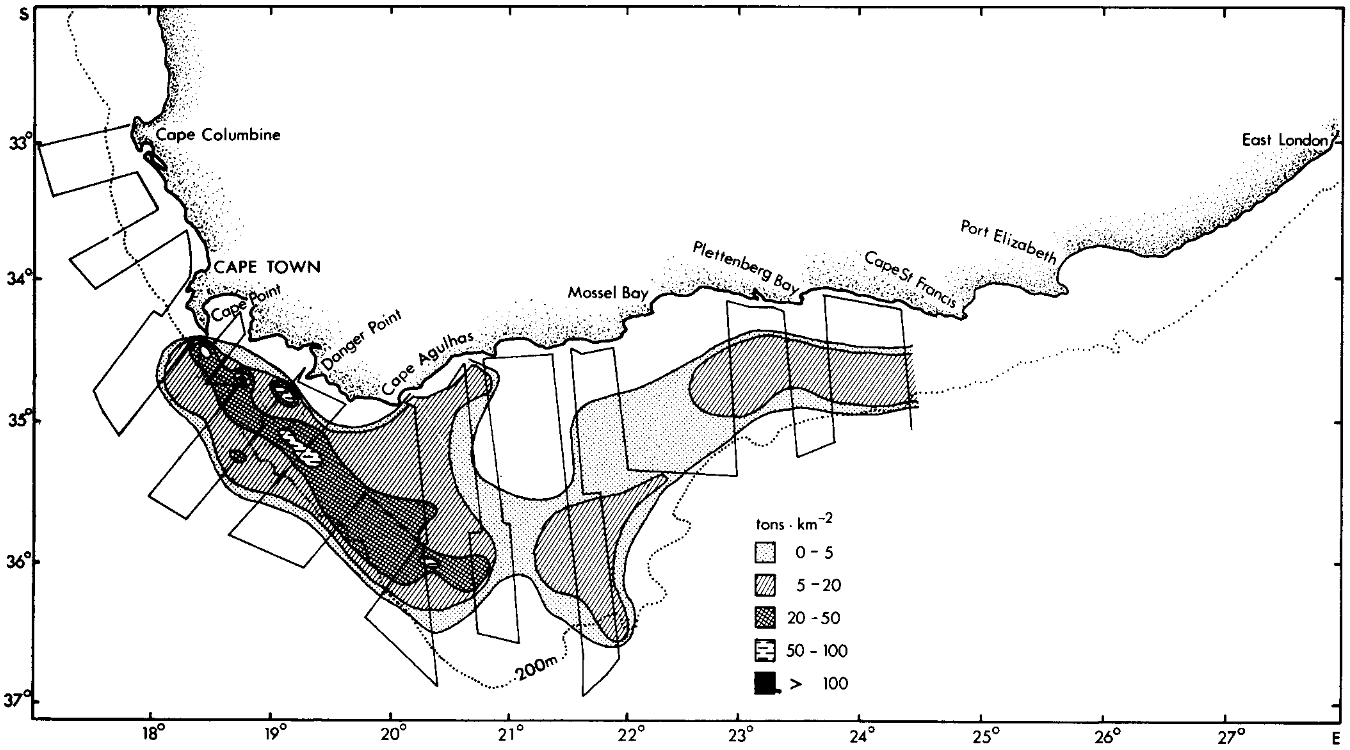

Figure 11. Anchovy density distribution in November 1985, as determined from acoustic data (after Hampton 1987).

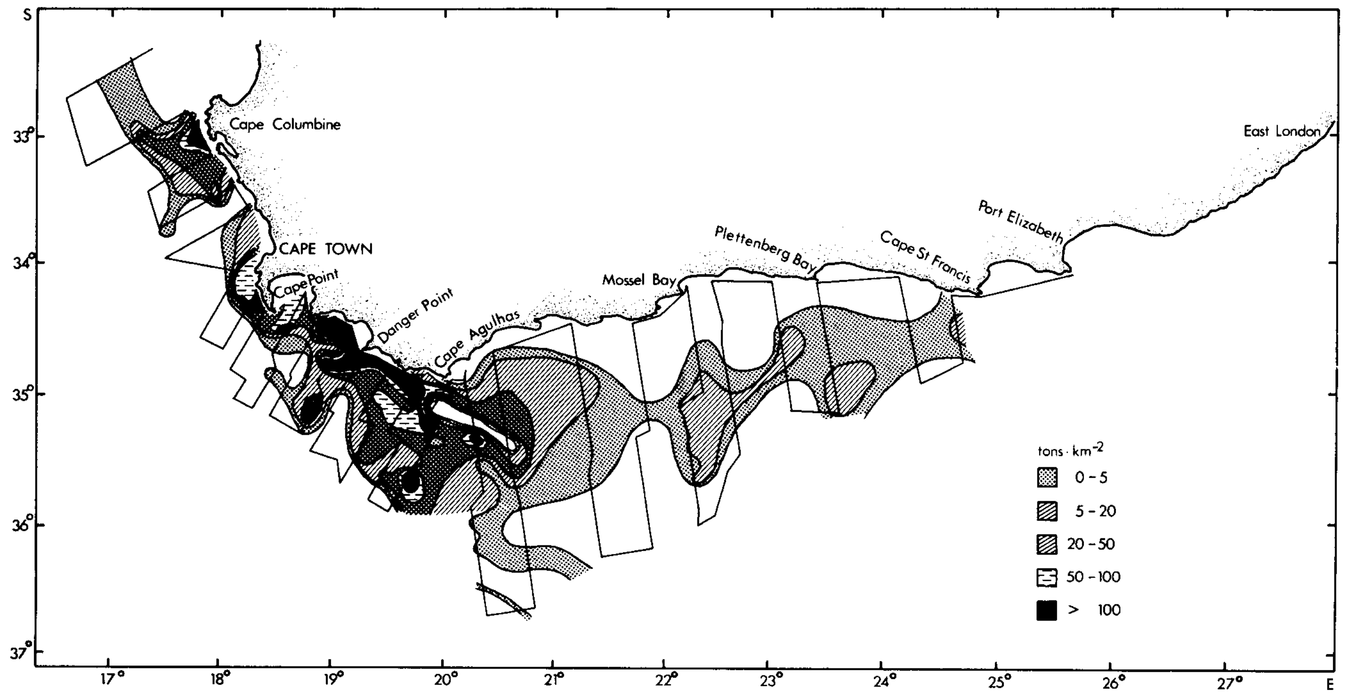

Figure 12. Anchovy density distribution in November 1986, as determined from acoustic data.

ing parameters) shows the presence of these smaller fish in much greater numbers in 1986 than in the previous years (Figure 13).

A consistent tendency for a zone of low egg and fish density to separate areas of spawning over the western and eastern regions of the Agulhas Bank, and for two-year-old and older anchovies to be found mainly in the eastern area provided a clear

TABLE 3
Estimates of Hourly Instantaneous Mortality Rate (Z) of Anchovy Eggs

Year	Z (h^{-1})	Variance	95% confidence limits	
1984	0.0010	8.39×10^{-5}	−0.0170	0.0190
1985	0.0093	3.00×10^{-5}	−0.0014	0.0200
1986	0.0115	6.96×10^{-5}	−0.0049	0.0279

basis for stratification of the survey grid. The systematic grid in 1984 was stratified *post hoc* on this basis, whereas in 1985 and 1986 the surveys were stratified at the design stage, as described earlier. It was subsequently found that some of the strata in 1985 and 1986 contained insufficient transects for reliable variance estimates to be obtained, and strata were combined as described in Appendix 2 (Figures 2 and 3).

Parameter and Variance Estimates

Estimates of hourly egg mortality rate Z and the variances of these estimates in each year are given in Table 3, and the regressions of *Ln* (abundance at age) against age are shown in Figure 14. The 95% confidence intervals were very wide, encompassing zero mortality in each year. The 1985 estimate exhibited the smallest variance, but it was clear that the intensity of sampling, or the method of estimating Z, was, in most years, inadequate for reliable estimation of the average hourly mortality rate.

The daily egg production for the various strata in each year is given in Table 4, and shows the greater amount of spawning over the western region of the Agulhas Bank. Weighted mean $\hat{P}_o$ values for each survey are given in Table 5. Total daily egg production was lowest in 1985, but also had the lowest variance of the values from the three surveys. The variances of $\hat{P}_o$ in 1984 and 1986 were inflated by imprecise estimates of Z, but a substantial decline in the between-transect normalised variance of $\hat{P}_o$ from 0.032 in 1984 to 0.012 in 1986 was evident. This may, to a large extent, reflect improvements in survey design and the increase in sampling effort in the high-density strata in 1986.

The spawning parameters of mean female mass, batch fecundity, sex ratio, and spawning fraction are given for separate strata in Table 4, and as weighted means for the entire survey areas in Table 5. Spawning fraction values based on histological examination of ovaries were not available for 1984. The mean female mass was 2–3 g lower in 1986 than in 1984 or 1985, because of the abundance of small fish of 8–10 cm Lc inshore in stratum B in 1986.

The spawning fraction in 1985 was estimated to be nearly 20% of the female population, nearly

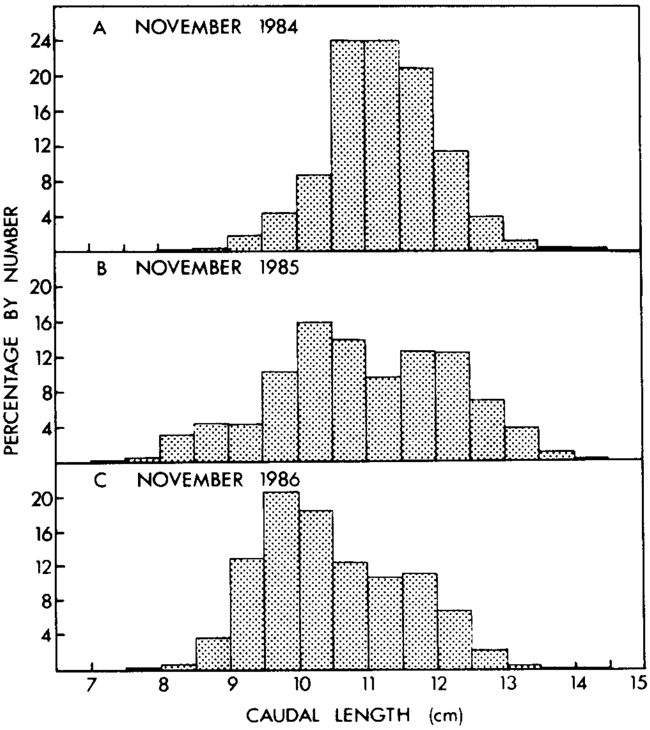

Figure 13. Weighted population length frequencies for the anchovy stocks surveyed in November 1984, 1985, and 1986.

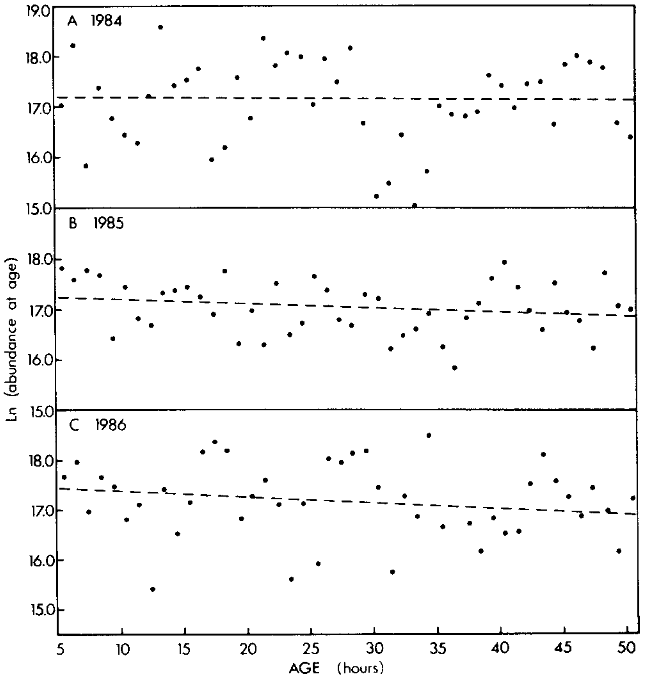

Figure 14. Egg mortality curves for anchovy in November 1984, 1985, and 1986. (See Table 3 for mortality parameters.)

TABLE 4
Estimates of Parameters and Coefficients of Variation for Separate Strata

	Stratum *i*					
	A		B		C	
Parameter $\hat{\mu}_i$	Mean	CV	Mean	CV	Mean	CV
November 1984*						
$\hat{P}_{o_i}$ (eggs $d^{-1}m^{-2}$)	511	0.20†	133	0.35†	—	—
$\hat{W}_i$ (g)	14.95	0.03	17.94	0.02	—	—
$\hat{F}_i$ (eggs $female^{-1}$)	7,820		10,032			
$\hat{R}_i$	0.509	0.05	0.493	0.35	—	—
Area (km^2)	72,223		34,103			
Biomass from acoustics (kt)	903		68			
November 1985						
$\hat{P}_{o_i}$ (eggs $d^{-1}m^{-2}$)	392	0.15†	256	0.30†	—	—
$\hat{W}_i$ (g)	13.68	0.06	15.89	0.13	—	—
$\hat{F}_i$ (eggs $female^{-1}$)	7,510		9,548			
$\hat{R}_i$	0.485	0.06	0.469	0.13	—	—
$\hat{S}_i$ (day^{-1})	0.181	0.40	0.205	0.30	—	—
Area (km^2)	55,133		51,575			
Biomass from acoustics (kt)	717		264			
November 1986						
$\hat{P}_{o_i}$ (eggs $d^{-1}m^{-2}$)	1,082	0.15†	884	0.17†	155	0.30†
$\hat{W}_i$ (g)	13.53	0.06	10.51	0.03	12.85	0.11
$\hat{F}_i$ (eggs $female^{-1}$)	7,026		4,714		6,506	
$\hat{R}_i$	0.573	0.03	0.528	0.04	0.583	0.03
$\hat{S}_i$ (day^{-1})	0.101	0.50	0.108	0.27	0.064	0.52
Area (km^2)	28,568		13,777		67,496	
Biomass from acoustics (kt)	369		842		425	

*No histologically derived estimate of $\hat{S}$ is available in this year.
†Between-transect variation only.

double the value obtained in 1986. The variance of the spawning fraction was, however, very high in 1985, and was the dominant source of uncertainty in the 1985 EPM biomass estimate (Table 5). The estimates of spawning fraction for the combined strata A and B in 1985 were very similar (Table 4).

TABLE 5
Estimates of Mean Spawning Parameter Values and Normalized Variances and Covariances

	Year					
	1984		1985		1986	
		Variance		Variance		Variance
Parameter $\hat{\mu}$	Mean	$\hat{\mu}^2 \times 10^{-3}$	Mean	$\hat{\mu} \times 10^{-3}$	Mean	$\hat{\mu} \times 10^{-3}$
$\hat{P}_o$ (eggs $d^{-1}m^{-2}$)	389.4	97.0	326.5	41.1	487.6	62.4
$\hat{W}$ (g)	15.12	—	14.20	—	11.70	—
$\hat{F}$ (eggs)	7,953	—	7,991	—	5,627	—
$\hat{Q}$ $(=\hat{W}/\hat{F})$	—	1.5	—	2.8	—	3.0
$\hat{R}$	0.508	2.8	0.481	3.1	0.553	0.4
$\hat{S}$ (day^{-1})	—	—	0.186	95.9	0.095	45.9
2 Σ covariances	—	6.7		19.2		8.4
Area (km^2)	106,326	—	106,708	—	109,841	—
EPM biomass estimate (kt)[a]	—	—	614	162.1 (CV = 0.41)	2,006	120.0 (CV = 0.35)
Biomass from acoustics (kt)[b]	1,067	(CV = 0.23)	975	(CV = 0.16)	1,747	(CV = 0.14)

[a] Adjusted for small sample bias.
[b] Final estimates, adjusted for fish inshore of the survey grid (Hampton 1987).

TABLE 6

Estimated Parameters of Regressions of Batch Fecundity against Ovary-Free Preserved Fish Mass ($F = a W + b$)

Year	a	b	S^2_{FW}	S^2_b	$\bar{W}'(g)$	N_{FW}
1984	759.31	−3295.0	4.156×10^6	7581.7	15.909	53
1985	942.60	−5102.0	6.373×10^6	3722.7	16.686	80
1986	782.79	−3332.9	4.744×10^6	3973.3	13.684	81

Between-stratum variations were also relatively small in 1986, despite the increased occurrence of young adult fish in the inshore strata.

The relationships between batch fecundity and ovary-free mass of preserved females were very similar in the three years (Figure 15; Table 6). The variance components of the regressions and the between-transect variation in $\bar{W}$ made a relatively minor contribution to the final variance of the biomass estimate (Table 5).

The sex ratio $\hat{R}$ was close to 0.5 in each survey, and although the coefficient of variation of the estimates was relatively small, much of the variation was attributable to the anomalous values obtained in some catches taken during the evening spawning period.

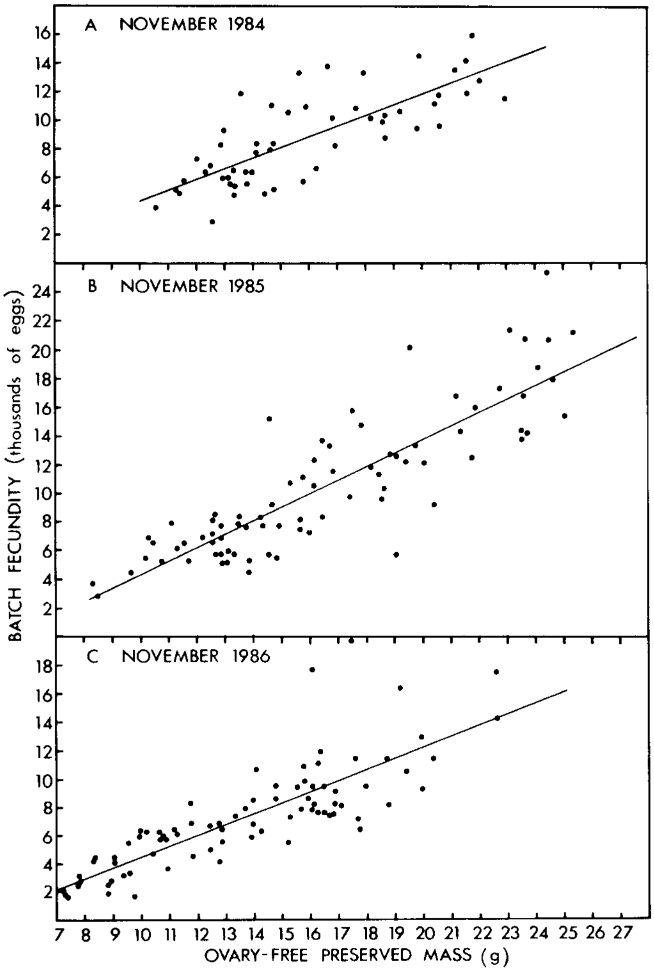

Figure 15. Regressions of batch fecundity against ovary-free mass of preserved female anchovy in November 1984, 1985, and 1986. (See Table 6 for regression parameters.)

The estimates of biomass and coefficient of variation (CV) in 1985 and 1986 are given in Table 5. A 50% increase in total daily egg production between 1985 and 1986, and a reduction in the estimated spawning fraction in 1986 compared to 1985, implied a trebling of the biomass from approximately 0.6 to 2.0 million tons. In comparison, the estimate from acoustics of 1.7 million tons in 1986 was only 80% greater than the corresponding estimate in 1985. The CV's of the EPM estimates were, however, relatively high at 0.35 to 0.41, and consequently the biomass estimates from the two methods are unlikely to differ significantly each year. Poor precision of the spawning fraction estimate in 1985 was largely responsible for the high CV in that year (Table 5).

The spawning biomass in 1984 can be only roughly estimated by assuming a range of possible spawning fraction values. A comparison of the occurrence of hydrated female anchovy (determined macroscopically) in the three surveys indicated that the incidence of such females in 1984 was intermediate between the incidences in trawl samples taken in 1985 and 1986. Thus by taking the 1985 and 1986 spawning fraction estimates as bounding the range of possible 1984 estimates, a range of 1984 biomass estimates of 0.8 to 1.5 million tons is obtained, with an average of 1.2 million tons. In comparison, the 1984 estimate from acoustics was 1.1 million tons. It should be noted that the relatively low CV estimates for the acoustic survey results reflect only the sampling error, and do not include the variance associated with the target strength expression (Hampton 1987).

The differences between the results obtained by adopting the transect rather than the individual trawl stations as the sampling unit, and by incorporating acoustic data to weight the sample means, are shown in Table 7. In both 1985 and 1986, the mean female mass was greater when the values from individual trawl stations were weighted only by sample size. This was caused by oversampling of the low-density strata on the eastern Agulhas Bank, where most of the two-year-old and older

TABLE 7
Estimates of Means and Coefficients of Variation of Spawning Parameters Obtained from (A) the Transect Method with Acoustic Weightings and (B) Averaging Individual Station Values with Weights Proportional to Subsample Size

	1985				1986			
	A		B		A		B	
Parameter	Mean	CV	Mean	CV	Mean	CV	Mean	CV
$\hat{\bar{W}}$ (g)	14.20	0.05	16.09	0.05	11.70	0.04	12.67	0.05
$\hat{R}$	0.48	0.06	0.48	0.07	0.55	0.02	0.58	0.03
$\hat{\bar{S}}$ (day^{-1})	0.19	0.31	0.15	0.14	0.10	0.21	0.12	0.20

anchovy were encountered, and resulted in a 5% to 8% increase in the estimated batch fecundity per unit female mass. Sex ratio and spawning fraction were not significantly correlated with female mass, and were not consistently affected by the weighting procedure. The CV's of the mean female mass and sex ratio were very similar between the two methods, whereas the CV of the spawning fraction tended to increase when acoustic weightings were applied. Although the two methods did not produce substantially different results in 1985 and 1986, the acoustically weighted estimates are less likely to be biased in situations where the fish density and spawning parameters are correlated.

DISCUSSION

The egg production method has proved to be a valuable, if labor-intensive, method for obtaining biomass estimates each year for the southern Benguela anchovy stock, in addition to the estimates obtained from acoustic surveys. The major sources of uncertainty in the egg production biomass estimates have been associated with the estimation of egg mortality rate Z and spawning fraction $\bar{S}$, which together accounted for more than 80% of the sum of the squared CV's of the egg production survey parameters in 1985 and 1986. Improvements in the survey design involving stratification and intensification of survey effort in areas where high densities of fish were expected were implemented in order to minimize sampling error, but it is clear that the ±300 CalVET stations have been insufficient for acceptable precision in estimating egg mortality by the regression procedure adopted each year.

Although an increase in the number of egg stations through additional transects would be expected to reduce the estimate of variance, there may be more appropriate methods of estimating Z than by incorporating all values of egg abundance and age into a single regression. This is particularly the case if egg mortality varies nonrandomly between stations and transects. Recent studies of egg cannibalism in the southern Benguela anchovy stock have provided evidence of density-dependent cannibalism rates (Valdes et al. 1987), and such a mechanism could be expected to cause patchy variations in egg mortality rate related to the density-distribution of spawning adults, their daily specific fecundity, and the local abundance of other food items.

A bias in the estimation of daily egg production may occur if processes such as cannibalism on newly spawned eggs invalidate the assumption of constant egg mortality rate between spawning and hatching. The study of Valdes et al. (1987) showed that within an area of intense spawning where sampling took place, eggs were most frequently encountered in anchovy stomachs during the evening spawning period. Although these eggs could not be staged, the possibility remains that dense aggregates of newly spawned eggs may elicit a feeding response, particularly in the areas of intense spawning. The mortality on these eggs may therefore be higher than on the eggs of age 5 to 50 h, which are represented in the egg mortality regression, resulting in an underestimate of abundance at the time of spawning for certain batches of eggs sampled. It would be necessary to stage the eggs in the stomachs of predators to adequately address this problem.

Improved estimates of spawning fraction and daily egg production would primarily result from increased sampling effort in the high-density strata. In 1986 the sampling effort in terms of the density of transects was about twice as great in the high-density strata as in the low-density strata. However, to reduce the CV of the spawning biomass from 35% to 20% would require at least a further doubling of the overall survey effort by increasing the density of sample transects. Weighed against this reduction in estimated variance would be a substantial slowing down of the survey vessel across the spawning grounds, with a resultant danger of temporal trends in spawning intensity introducing a further component of variation into the final estimate. An additional consideration at present is that the biomass estimates are required for input into management procedures three months after completion of the survey in November. Any substantial increase in survey effort would therefore be limited by the time required to process the samples. Ultimately, the level of uncertainty in the biomass estimate that is acceptable in a stock assessment context will relate to how much the estimate influences future harvests, and how much the stock is being exploited. Such considerations may be explored through stochastic modeling exercises like those of Armstrong and Butterworth (1986) and Bergh and Butterworth (1987).

Hampton et al. (in press) demonstrate that using acoustic information to weight the spawning parameters imposes no additional covariance between the biomass estimates obtained from the two methods, and that the covariance between the egg and acoustic estimates in both 1985 and 1986 was low. The two estimates can therefore be treated as independent, and the similarity between them gives some confidence in the target-strength expression adopted for the acoustic survey. However, until the target strength of *Engraulis capensis* is determined by a reliable method, and its contribution to the error quantified, the acoustic estimates must be regarded as having a potentially large and unknown bias, precluding the direct combination of the acoustic and egg production estimates. However, a method has been developed (Hampton et al., in press) for combining the results of the two surveys, making use of the ratio of the egg production and acoustic biomass estimates in year i to adjust the acoustic estimate in year $i+1$, providing a less-biased estimate to combine with the egg production estimate of biomass in year $i+1$. An optimum combination is obtained of the acoustic method, which provides estimates with high relative precision but potentially low accuracy, and the egg production method, which is assumed to be accurate but has provided relatively imprecise biomass estimates. Hampton et al. discuss appropriate methods for minimizing the variance of the combined estimate.

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APPENDIX 1

Estimation of *Z* by Linear Least Squares Regression

An efficient estimator of the mean hourly instantaneous egg mortality rate Z is required to allow the station values of egg abundance at age (P_t; equation 5) to be raised to the expected abundance at age zero. In the surveys described in this paper, the abundances of eggs in 1-hour age classes were estimated for separate survey strata and then summed over strata to give total estimated abundance at age. The natural logarithms of the abundance estimates $\hat{P}_t$ were then regressed against age for ages $t = 5$ to 50 h. The estimate of the slope, $\hat{Z}$; the variance around the regression line, S^2_{yt}; and the variance of $\hat{Z}$ were obtained from the following expressions:

$$\hat{Z} = \frac{\Sigma_t\, w_t\,(y_t - \bar{y})(t - \bar{t})}{\Sigma_t\, w_t\,(t - \bar{t})^2} \qquad (20)$$

$$S^2_{yt} = \frac{N}{(N-2)\,\Sigma_t w_t}\left[\Sigma_t w_t\,(y_t - \bar{y})^2 - \frac{[\Sigma_t w_t\,(y_t - \bar{y})(t - \bar{t})]^2}{\Sigma_t w_t\,(t - \bar{t})^2}\right] \qquad (21)$$

$$\mathrm{V}(\hat{Z}) = \frac{S^2_{yt}}{\dfrac{N}{\Sigma_t w_t}\,\Sigma_t w_t (t - \bar{t})^2} \qquad (22)$$

where t = mean age in each one-hour age class,
$y_t = \mathrm{Ln}\,(\hat{P}_t)$,
w_t = weighting factor for y_t, and
N = the number of age classes in the regression.

For each 1-hour age class, the natural logarithm of the abundance value was weighted by $n_t \exp(-Z\,t)$, where n_t is the number of egg batches contributing to age class t (including zeros), and t is the age in hours. It can be easily shown that, on the assumption that the abundances of eggs in the nightly batches sampled at each station approximately follow a Poisson distribution, the reciprocal of the variance of $\mathrm{Ln}(P_t)$ for a given t is approximately $n_t \exp(-Z\,t)$. The weighting values were iteratively adjusted using successive estimates of Z until convergence was attained, the initial estimate of Z being obtained with weighting by n_t only.

APPENDIX 2
Averaging over Strata with Few Sampled Transects

A method is required for combining strata in which there are too few transects to allow reliable estimates of variances. The method must retain the advantages for minimization of variance afforded by the original stratification. An adaptation of the method given in Cochran (1977, pp. 165–167), suitable for egg production surveys, is provided here.

Let $\hat{\mu}_{ij}$ be the mean value of parameter μ (= P_o,W,R,S) for transect j in stratum i, calculated with appropriate station weighting, and let w_{ij} be the weighting factor for $\hat{\mu}_{ij}$. A new variate is formed as:

$$y_{ij} = w_{ij}\hat{\mu}_{ij} \tag{23}$$

The principle is to replace the separate stratum means, $\hat{\mu}_i$, by an average μ formed by summing the y_{ij} values over transects and strata, with appropriate stratum weighting, and dividing by the corresponding sum of the w_{ij}. Applying this principle to the group of strata to be combined gives a $\hat{\mu}_c$ (c for "combined") identical to that derivable from equations 6 and 8 or 12 and 14.

To estimate the variance of $\hat{\mu}_c$, unweighted stratum means are formed of y_{ij} and w_{ij} as:

$$\bar{y}_i = \frac{1}{n_i}\Sigma_j w_{ij}\hat{\mu}_{ij} \tag{24}$$

$$\bar{G}_i = \frac{1}{n_i}\Sigma_j w_{ij} \tag{25}$$

where n_i is the number of transects in stratum i.

The stratum mean value of the parameter μ is simply the ratio y_i/G_i (equivalent to equations 6 and 12), and the mean value $\hat{\mu}_c$ over the strata to be combined is obtained, as before, from equations 8 and 14. The variance of $\hat{\mu}_c$ is given by:

$$\mathrm{V}(\hat{\hat{\mu}}_c) = \frac{\sum_i\left(\frac{w_i}{\bar{G}_i}\right)^2\frac{S_i^2}{n_i}}{\left[\sum_i\left(\frac{w_i}{\bar{G}_i}\right)\bar{G}_i\right]^2} \tag{26}$$

$$= \frac{\sum_i\left(\frac{w_i}{\bar{G}_i}\right)^2\frac{S_i^2}{n_i}}{\left(\sum_i w_i\right)^2}$$

where $\mathrm{S}^2{}_i = S^2{}_{iy} - 2\hat{\hat{\mu}}_c S_{iyw} + \hat{\hat{\mu}}^2{}_c S^2{}_{iw}$,

and $$S^2{}_{iy} = \frac{1}{n_i-1}\Sigma_j(y_{ij}-\bar{y}_i)^2 \tag{28}$$

$$S_{iyw} = \frac{1}{n_i-1}\Sigma_j(y_{ij}-\bar{y}_i)(w_{ij}-\bar{G}_i) \tag{29}$$

$$S^2{}_{iw} = \frac{1}{n_i-1}\Sigma_j(w_{ij}-\bar{G}_i)^2 \tag{30}$$

The w_i are the stratum weighting factors for $\hat{\hat{\mu}}_i$ as defined in Table 2.

The "combined" stratum is treated exactly as an independent single stratum in further computations of means and variances of the egg production parameters. The full benefit of stratification is retained because the variance represents only the variation within strata.

CHANGING THE SIZE LIMIT: HOW IT COULD AFFECT CALIFORNIA HALIBUT FISHERIES

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ABSTRACT

The minimum legal size limit for California halibut (*Paralichthys californicus*) is 559 mm TL for all fisheries. There appears to be a conflict of allocation among user groups, with recreational catches being preempted by intense commercial fishing. We evaluate two possible solutions: a uniform change in the minimum size limit to 660 mm for all fisheries, or a differential size limit (recreational = 559 mm, commercial = 660 mm).

The commercial fishery takes from 60% to 80% females, which grow longer than males. Because sexes are not identified in most of the fishery data, we examined two alternative interpretations. In one case we treated the catch as consisting entirely of female fish; in the other case we treated catches as a combination of males and females, with a common, intermediate growth curve. We also examined two possible levels of natural mortality rate: $M = 0.1$ and $M = 0.2$. The virtual population analysis gave average total biomass estimates of 2,600 to 6,000 MT, and average recruitment (age 1) estimates of 0.5 to 1.0 million fish.

Yield-per-recruit (Y/R) analysis indicates that overall fishing effort is about twice the optimum level and that Y/R would likely increase with reduced fishing effort. Our analysis of proposed size limit assumed present levels of fishing effort. Under a differential size limit the recreational fishery shows an increased Y/R, both in weight and in numbers, whereas the commercial fisheries experience a net loss. Under a uniform 660-mm size limit for all fisheries, if $M = 0.1$, the Y/R for both recreational and commercial fisheries increases in weight but not in numbers. For a higher natural mortality rate ($M = 0.2$), the Y/R is reduced in the combined sex analysis, but the case of a female-based catch shows slight gain. The yield-per-recruit analysis suggests that the California halibut fishery is currently utilized at the point of maximum yield and that proposed changes in minimum size are not likely to resolve allocation conflicts among user groups.

RESUMEN

El tamaño mínimo legal para *Paralichthys californicus* en todas las pesquerías es de 559 mm LT. Parece haber un conflicto en cuanto a las cuotas de captura asignadas a ciertos grupos de usuarios, dado que una intensa pesca comercial se apropria de las capturas recreativas. Dos posibles soluciones son evaluadas: un cambio general del tamaño mínimo a 660 mm para todas las pesquerías o un límite diferencial (recreacional = 559 mm, comercial = 660 mm).

La pesquería comercial captura 60% a 80% de las hembras, las cuales alcanzan un mayor tamaño que los machos. Dado que no se indica el sexo en la mayoría de los informes pesqueros, examinamos dos explicaciones alternativas. En un caso, se consideró una captura compuesta exclusivamente por hembras; en el otro, se consideraron capturas compuestas por machos y hembras, con una curva de crecimiento común e intermedia. Se examinaron además dos niveles de tasa de mortalidad natural: $M = 0.1$ y $M = 0.2$. El análisis de poblaciones virtuales dió estimaciones de la biomasa total promedio de 2,600 a 6,000 TM y del reclutamients promedio (edad 1) de 0.5 a 1 millón de individuos.

El análisis de la producción por recluta (Y/R) indicó que el esfuerzo pesquero general es aproximadamente el doble del nivel óptimo y que Y/R probablemente aumentaría con una reducción del esfuerzo pesquero. Nuestro análisis de los cambios propuestos en tamaño mínimo supone niveles de esfuerzo pesquero similares a los actuales. Si se adopta un tamaño mínimo diferencial, la pesquería recreacional muestra un aumento en Y/R tanto en peso como en número de individuos mientras que la pesquería comercial experimenta una pérdida neta. Bajo el criterio de tamaño uniforme de 660 mm en todas las pesquerías, con $M = 0.1$, el Y/R de ambas pesquerías aumenta en peso pero no en número de individuos. Con una mortalidad natural más alta ($M = 0.2$), el Y/R es menor en el caso de un análisis con sexos combinados, pero en el caso de una captura compuesta sólo por hembras muestra un leve aumento. El análisis de producción por recluta sugiere que, actualmente, la pesquería de

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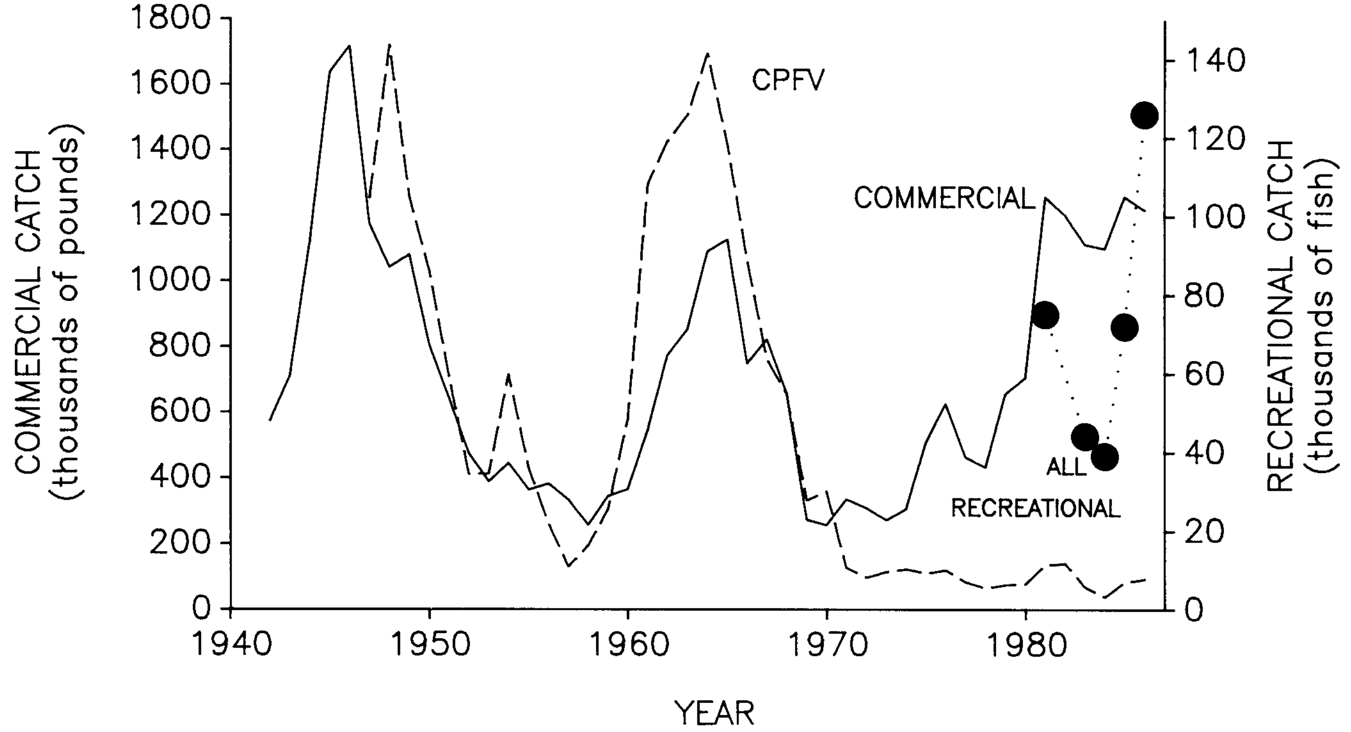

Figure 1. History of California halibut catch, 1947–85. Commercial landings (*solid line*) are reported in pounds. Commercial passenger fishing vessel (CPFV) landings (*broken line*) and total estimated recreational catch (Anon. 1984–87; *dotted line*) are reported in numbers of fish.

P. californicus en California es utilizada a un nivel de producción máximo y que los cambios en tamaño mínimo propuestos probablemente no resolverían los conflictos en cuanto a las cuotas asignadas a los grupos de usarios implicados.

INTRODUCTION

California halibut (*Paralichthys californicus*) is an important food and game fish, utilized heavily by both commercial and recreational fishermen in central and southern California. To prevent overexploitation of the resource, a uniform legal minimum size limit of 22 in. (559 mm) TL was enacted in 1971, with an allowance for a small number of undersized fish for the commercial fisheries. The expected result of this regulation was an initial decrease in the catch with an eventual recovery over the time period required for the halibut to grow to the minimum legal size and for the population to experience recruitment from a larger spawning population. Following this legislation, the recreational commercial passenger fishing vessel (CPFV) catch dropped from 29,451 fish in 1970 to 10,435 fish in 1971 and has continued at this low level, while commercial landings have increased in a pattern typical of historical catches, from 272,000 pounds in 1971 to 1,260,000 pounds in 1985 (Figure 1).

The recreational catch of California halibut includes the catch from four general fishing modes: CPFVs, man-made structures, private boats, and shorelines. Although CPFV catches have been reported annually since 1947, data on all recreational fishing modes are available for only two relatively short periods. These studies indicate that the contribution of CPFV-caught fish to the total recreational halibut catch has decreased from approximately 40% in the mid-1960s (Pinkas et al. 1968) to about 10% in 1981–84 (Anon. 1984, 1985). Thus the recreational halibut catch may have recovered more than the CPFV catch indicates (Figure 1), but not to catch levels previously experienced.

Methot (1983) described the status of the California halibut resource as "uncertain." However, halibut length frequencies observed in commercial fish-market samples are relatively stable, and both the recreational and commercial fisheries have persisted through what appear to be cyclic decreases in the halibut population. Therefore we assume that the fisheries are at approximate equilibrium. But there is a conflict among user groups, with recreational catches appearing to be preempted by intense commercial fishing. Accordingly, the primary management problem is a matter of allocating the catch among the user groups. A management strategy that would improve recreational catches without seriously impacting the commercial yield would reduce the conflict between recreational and commercial users. In this paper we examine increasing the size limit to achieve such a strategy.

Two management alternatives to improve allocation of the California halibut resource are being considered by the California Department of Fish and Game: (1) a uniform size limit of 660 mm (26 in.) to allow the halibut an additional reproductive season before recruitment, or (2) a differential size limit (recreational = 559 mm or 22 in; commercial = 660 mm or 26 in.) to make more legal fish available to recreational anglers. The California halibut catch is presently regulated via a minimum size limit and some commercial gear limitations. The proposed changes in size limit are in keeping with current management strategies for this species, and we presume they could be implemented effectively. To evaluate the effect of these alternatives, we performed a yield-per-recruit analysis for multiple-gear fisheries using the program MGEAR (Lenarz et al. 1974) and data from records of the California Department of Fish and Game.

METHODS

Data

Three different general gear types are used to catch California halibut: (1) recreational hook and line; (2) commercial mobile gear (trawl, purse seine, lampara); and (3) commercial stationary gear (set net, entangling net, longline). The distinctions are made to identify user groups and to partition the fishing mortality rates among fishery segments.

Female California halibut grow faster and thus attain larger sizes at age than males. However, commercial and recreational landings have not been reported by sex categories, and until recently, the length-frequency information from fishery monitoring also has been for combined sexes. The sex of fish sampled from commercial catches was collected opportunistically beginning in late 1985. Females appear to represent 60% to 80% of the commercial landings (Calif. Dept. of Fish and Game, unpubl. data, J. Sunada, Long Beach), but these data contain biases resulting from fish-market cleaning and sampling practices.

Because true sex composition is unknown, we examined two alternative interpretations that include the true sex composition as an intermediate case: Schott[1] compiled a length-age key for combined sexes that included approximately 53% females, 26% males, and 21% unknown sex, as well as keys for individual sexes. This allowed us to base our analysis on Schott's "combined-sex" key as one extreme, and to treat the catch as being entirely female as the other extreme. To estimate population biomass in the latter case, we assumed landings of female fish to be 70% of the total landings.

Because data on female halibut exist only for the most recent years, data used in these two analyses are from somewhat different sources. Length frequencies from the recreational catch were sampled from 1981 through 1984 ($N = 396$; MRFSS 1981–84), but sexes were not identified (Figure 2). Length frequencies for commercial mobile gear were obtained from market samples of trawl-caught halibut; sampling was conducted from 1983 through 1986 ($N = 2{,}072$), but females were identified only in 1986 ($N = 124$). Length frequencies for commercial stationary gear were obtained from direct on-board observations of halibut caught by gill nets; these observations include undersized fish that are legally removed from the population (for personal use, etc.) but are not marketed. Length frequencies of halibut caught by gill nets were taken from 1983 to 1987 ($N = 4, 219$), but females were identified only in 1986 and 1987 ($N = 695$).

The length-frequency information described above was used for two purposes: to convert the commercial catch, which is recorded in weight, to catch in numbers, and to estimate catch by age. We calculated the average weight of the fish in the length-frequency distributions by means of a length-weight relationship developed by Schott (Table 1). For each commercial fishery segment, we divided the average annual catch in weight (1981–86) by the corresponding estimated average fish weight to produce estimates of each segment's catch in numbers (Table 2). Recreational catches are reported in numbers (Anon. 1984–87). We then used the appropriate length-age key[2] to convert each length frequency to an age frequency, and multiplied by the estimated total catch in numbers to obtain the catches at age for use in the virtual population analysis.

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[1] Schott, J. W. Age and growth of California halibut *Paralichthys californicus* (Ayres). (Unpublished manuscript, California Department of Fish and Game files; available upon request from R. J. Reed.)

[2] Ibid.

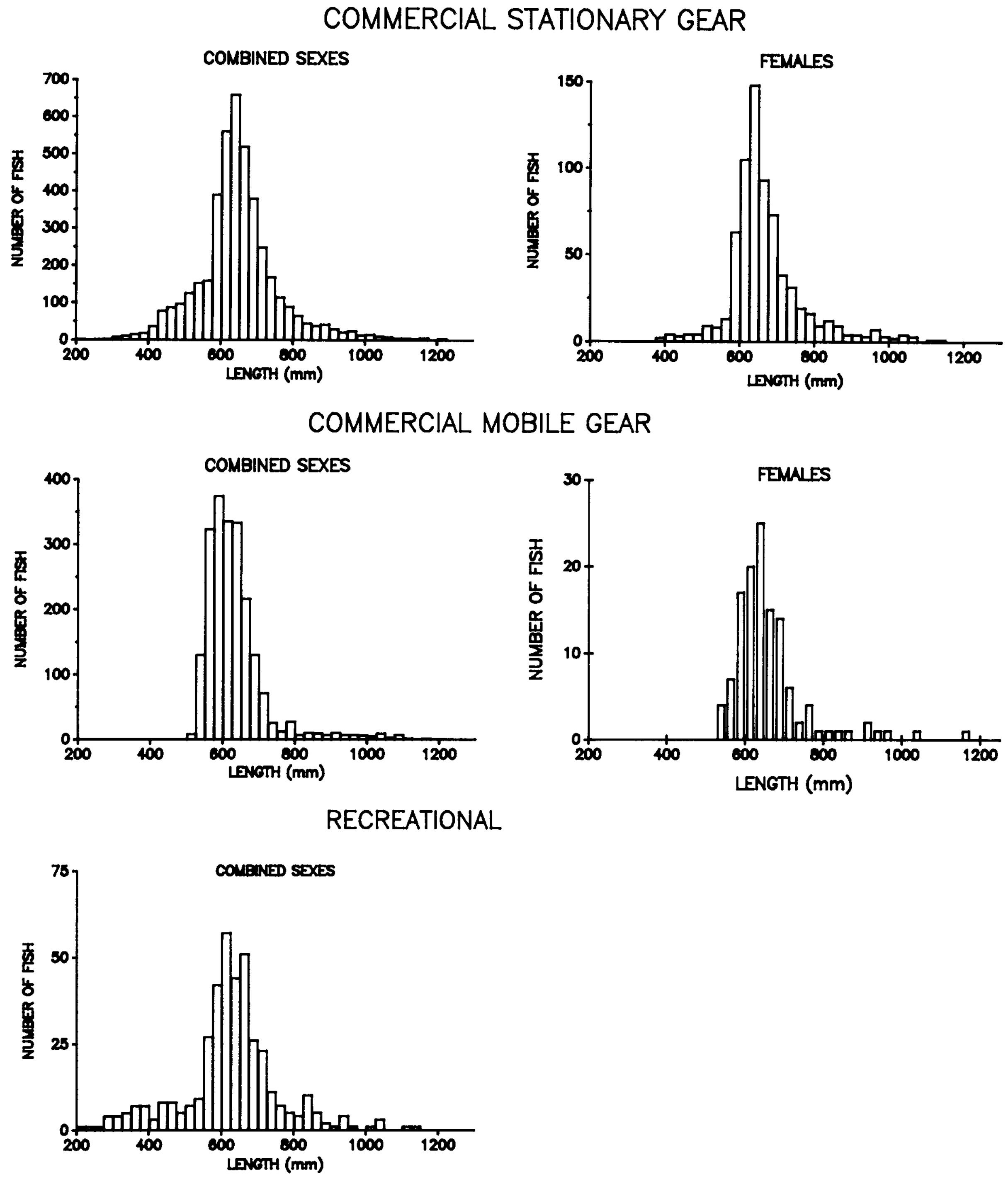

Figure 2. California halibut catch-length frequencies for major fishery segments and sex composition. Note: vertical scales differ.

Virtual Population Analysis

Age-specific fishing mortality rates were derived using virtual population analysis (VPA). In addition to the catches at age, VPA requires estimates of natural mortality and terminal fishing mortality rates. Estimates of the instantaneous natural mortality rate (*M*) ranged from 0.3, on the basis of related flatfish species at similar temperatures (Pauly 1979), to 0.15, on the basis of longevity (Hoenig 1983). We derived the latter estimate from the maximum known age of 30 years, which was obtained from sampling in the mid-1960s[3]. The es-

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[3] Ibid.

TABLE 1
Parameter Values of the von Bertalanffy Growth Equation and Length-Weight Regression for California Halibut

	Growth parameters			Length (mm)-weight (kg) parameters	
	L_{infinity}	k	t_o	a	b
Females and immatures	1417.42	0.1194	0.3801	0.000007768	3.0496
Males and immatures	1137.43	0.1218	0.1004	0.000009216	3.0165
Sexes combined	1217.51	0.1414	0.4073	0.000008807	3.0300

Adapted from Schott, J. W. Age and growth of California halibut *Paralichthys californicus* (Ayres). (Unpublished manuscript, California Department of Fish and Game files; available on request from R. J. Reed.)

timate using Hoenig's method reflects the total mortality rate, and because halibut have been exploited since the early 1900s, M would be expected to be lower than 0.15. In view of the longevity of California halibut, M could not possibly be as high as 0.3. We considered two arbitrary estimates of M (0.1 and 0.2) in order to explore the sensitivity of the yield-per-recruit analysis to a range of probable values of the natural mortality rate.

Our VPA employed a method described by MacCall (1986), which accounts for the seasonal pattern of catches by each segment of the fishery. In the present case, we used the equation:

$$N(t) = N(t+1)\exp(-M) + V_{\text{rec}}C_{\text{rec}}(t) + V_{\text{stat}}C_{\text{stat}}(t) + V_{\text{mob}}C_{\text{mob}}(t)$$

where $N(t)$ is abundance in numbers at the beginning of year t, $C(t)$ is catch in numbers during year t, and V is a coefficient that depends on the seasonal pattern of catches of the respective segment of the fishery (rec = recreational, stat = stationary commercial, mob = mobile commercial). Values of V were based on monthly catches by gill net and trawl gears from 1981 through 1986 (Calif. Dept. of Fish and Game catch records), and on bimonthly catches by the recreational fishery from 1984 through 1986 (MRFSS 1984–86). We calculated coefficients V for each year, and then averaged over the yearly values for each gear separately (Table 3).

TABLE 2
Average Annual Recreational (1980–84) and Commercial (1981–86) Catch of California Halibut

Fishery segment	Average annual catch: Numbers	Average annual catch: Weight (kg)	Average weight per fish (kg)
Recreational	71,200 (15,695)	184,009 (40,016)	2.5844 (0.1040)
Commercial			
Stationary gear	141,066 (7,185)	426,330 (21,715)	3.0222 (0.0359)
Mobile gear	52,201 (7,449)	118,423 (16,900)	2.2686 (0.0438)
Total	264,467	728,762	

Standard errors are in parentheses.

We applied the VPA to the estimated age composition of the catch as a "synthetic cohort," which uses the average age composition of the catch over a relatively short period (3 to 6 years in this case) to approximate the age composition of a cohort over its lifetime. Lacking objective criteria, we calculated terminal fishing mortality rates (F) on the basis of internal consistency. We chose a terminal value (for ages 19 and older) of F that was equal to the average value of F for ages 11 through 18, given that terminal value. This approach gave a unique solution in each case, and depends only on the assumption that F is constant for ages 11 and older. Although we believe that this assumption is reasonable, we lack information by which to test its validity.

Yield per Recruit

Yield-per-recruit analysis requires growth information in addition to the mortality information derived above. Males and females grow at different rates, but, as noted earlier, sex composition of the catch is unknown. For the analysis based on an assumed all-female catch, we used the von Bertalanffy growth curve and length-weight relationship developed by Schott for female halibut. For the combined-sexes analysis, we used Schott's relationships for combined sexes (Table 1).

We modeled yield per recruit using the program MGEAR, which takes into account differences in

TABLE 3
Average VPA Coefficients That Compensate for Seasonality of California Halibut Fishery

	V_{rec}	V_{stat}	V_{mob}
Combined sexes			
$M = 0.1$	1.055437	1.047947	1.048698
0.2	1.114594	1.098704	1.100948
Females only			
$M = 0.1$	1.055437	1.047947	1.048698
0.2	1.114594	1.098704	1.100948

and interactions among fishery segments. Classical yield-per-recruit models have assumed instantaneous, or knife-edged, recruitment to the fishery at a given age. However, recruitment of California halibut occurs over a range of ages because of an allowance for the commercial take of undersized fish and because of differences in gear selectivity among the fishery segments. The program MGEAR allows for fish being recruited gradually and at different ages for different fishery segments by using age-specific F values for each fishery segment.

We estimated the effect of a change in size limit by using a modified set of age-specific F values. Selectivity curves for the various gears are not known, requiring an indirect method: for each gear, we assumed the peak value of F to indicate the age of full availability, and calculated availabilities of younger ages relative to that value. For each of the younger ages, we then used the information in Schott's length-age keys to estimate the length percentile corresponding to the retention rate implied by the availability as if retention were knife-edged.

For example, if availability was 0.8, we calculated the "selection length" at which 80% of the fish were larger. We then assumed that the unknown mechanisms leading to that selection length would change in proportion to the proposed change in size limit, which in the present case is 660 mm/559 mm, or an increase of 18%. Accordingly, we then determined the length percentile corresponding to an 18% increase in the selection length. We assumed that this new percentile represents the modified availability under the new size limit. We multiplied the estimate of modified availability by the peak F that was assumed to represent full availability, thereby obtaining the modified set of age-specific F values for use in the yield-per-recruit analysis (Figure 3). To measure the effect of the uniform and differential size-limit policies, we compare the yield per recruit (Y/R), in weight and in numbers of fish caught, to the Y/R under the current uniform 559-mm size limit to determine the relative percentage change.

RESULTS AND DISCUSSION

Estimates of Abundance

Although our VPA estimates were based on "synthetic" rather than actual cohorts, the results provide estimates of the approximate magnitude of the California halibut resource. The estimates vary with the assumed rate of natural mortality and with the treatment of the sex composition of the catches (Table 4). The probable total biomass is estimated in the range of 2,600 to 6,000 MT. Abundance estimates based on all-female catches must be augmented by a presumed biomass of males, which is somewhat smaller because of their smaller weights at age, but would fall within the above range. Recruitment, in number of fish at age 1, may be treated similarly; estimates based on female catches, which we have assumed to be 70% of the total, should be increased about 30% to include males. Thus we estimate annual recruitment to be between 0.45 and 1.0 million fish (Table 4). The estimates provided by "synthetic" cohorts are, in a poorly defined way, average values. If the record of catches (Figure 1) is any indication, actual

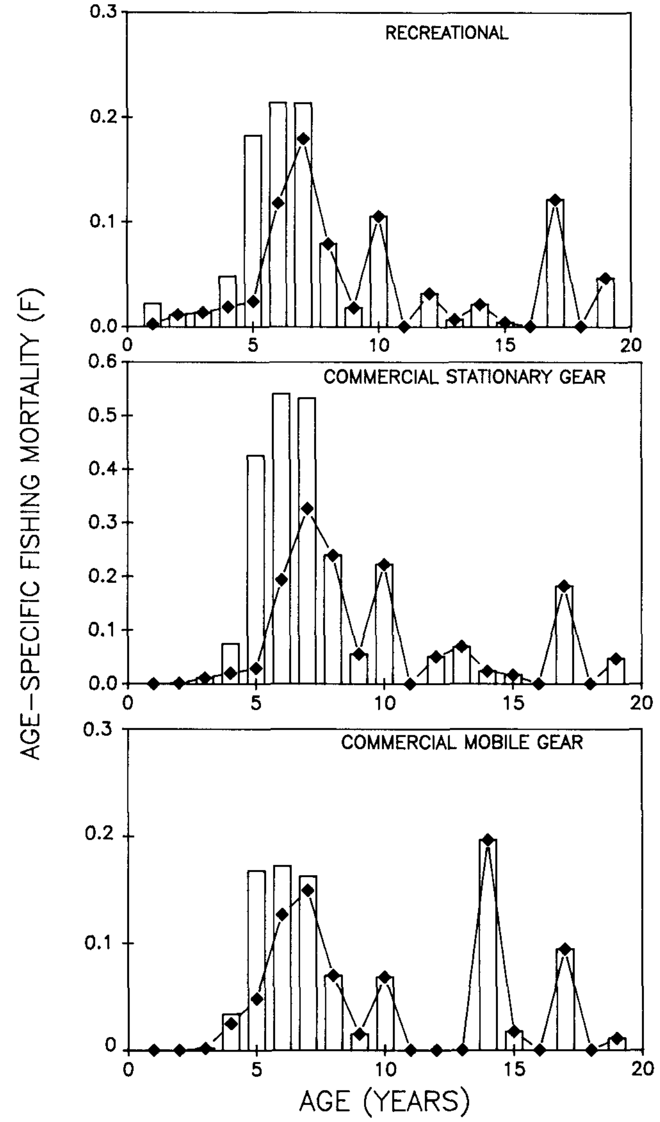

Figure 3. An example of the change in age-specific fishing mortality (F) to simulate the increase of the minimum California halibut size limit from 559 mm to 660 mm. Treatment is all-female catch, $M = 0.1$.

TABLE 4
VPA Estimates of Biomass and Recruitment of California Halibut

Assumed natural mortality rate	Treatment of catches	
	Combined sexes	Females only
$M = 0.1$	$B = 2{,}600$ $R = 450{,}000$	$B = 2{,}300$ $R = 430{,}000$
$M = 0.2$	$B = 6{,}000$ $R = 950{,}000$	$B = 3{,}200$ $R = 750{,}000$

Biomass (B) in metric tons; recruitment at age 1 (R) in number of fish.

biomasses may have varied as much as fivefold, and recruitments have varied much more.

Present Status of the Fishery

Before examining the individual segments of the fishery, it is useful to evaluate the status of the fishery as a whole, particularly with regard to the overall level of fishing intensity. Given the present patterns of size selectivity or age selectivity, and relative intensities of the three fishery segments, the resource is probably overfished (Figure 4); i.e., a reduction in fishing intensity would increase total catch in biomass. Both of the cases where M was assumed to be 0.1 show peak Y/R at fishing intensities lower than present levels. In the cases where M is assumed to be 0.2, the present fishing intensity is at peak Y/R for the all-female case; only for the combined-sexes case is peak Y/R to be found at fishing intensities higher than the present level.

Optimal levels of fishing intensity are nearly always below those that produce maximum yield per recruit. One popular rule of thumb is the $F_{0.1}$ policy suggested by Gulland and Boerema (1973). This policy establishes a nominal upper limit to fishing intensity as the level at which the marginal increment in catch per effort is one-tenth that of a nearly unfished resource. In three out of the four cases shown in Figure 4, the $F_{0.1}$ policy indicates optimal fishing intensities in the vicinity of one-half the present level. Only in the case of $M = 0.2$ and combined-sex treatment of catches is the $F_{0.1}$ level of fishing intensity above the present level. It is our opinion that the latter case is the least likely of the four cases examined, because M is probably much lower than 0.2, and the catch is known to consist mostly of female fish.

Changes in Yield per Recruit

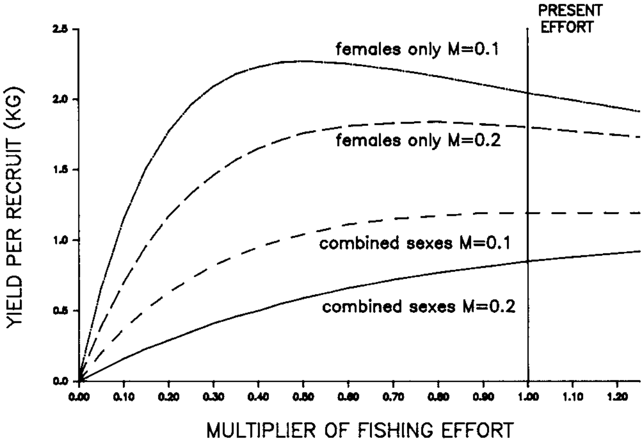

Figure 4. Yield per recruit for California halibut at different levels of fishing effort. Present level = 1.0.

Under a uniform 660-mm size limit for $M = 0.1$, the Y/R increased for all fishery segments, by weight but not by number (Table 5); larger but fewer halibut were caught. When $M = 0.2$, the Y/R shows a loss for all fishery segments in weight and number assuming combined sexes, and no significant gain assuming a fishery based solely on female fish. It would appear that some benefit would be realized under a uniform 660-mm size limit, given the lower natural mortality rate. However, the commercial catch is valued by weight (pounds of fish sold), whereas recreational anglers tend to value their catch based on the number of fish caught (Fritz and Schuler 1984). Therefore we assume that a strategy which reduces the number of fish in the recreational catch would not alleviate the current allocation conflict.

Under a differential size limit, the recreational Y/R increases by weight and by number in all cases (Table 5), but the commercial stationary gear Y/R shows a concomitant decrease. The Y/R for commercial mobile gear increases for a catch based on female fish but tends to decrease for a catch based on both sexes. A differential size limit will improve the recreational fishery segment, but at the expense of commercial fishery segments.

Since females grow faster than males, an increased minimum size limit is expected to increase the percentage of females in the catch. Recent data indicate that the commercial catch is already biased toward females. Of the four cases examined, the least benefit would be expected when the natural mortality is high and males are included in the catch with females. The net change in Y/R for the entire fishery suggests that some benefit would be realized with an increase in size limit, except in the last case.

This analysis simulates an increase in size limit by decreasing the availability of smaller fish, and does not consider the possibility of a concomitant increase in availability of larger fish. Because the

TABLE 5

Percentage Change in Yield per Recruit by Weight and Number ( ) under a Differential Size Limit (559-mm recreational/660-mm commercial) and under a 660-mm Uniform Size Limit Compared to a Uniform 559-mm Size Limit

Male and female combined catch				
	Recreational	Commercial		Entire
		Stationary gear	Mobile gear	
M = 0.1				
Uniform	+17 (−23)	+8 (−30)	+37 (−2)	+16
Differential	+85 (+54)	−21 (−45)	+3 (−22)	+18
M = 0.2				
Uniform	−9 (−29)	−15 (−35)	−53 (−72)	−21
Differential	+41 (+29)	−24 (−41)	−59 (−75)	−28
Female catch only				
M = 0.1				
Uniform	+38 (−11)	+12 (−31)	+69 (+15)	+31
Differential	+90 (+54)	−14 (−45)	+31 (−6)	+21
M = 0.2				
Uniform	+14 (−16)	−12 (−41)	+29 (−4)	+3
Differential	+59 (+37)	−25 (−49)	+13 (−14)	+3

commercial net gears used to catch California halibut tend to be size selective, a possible means of implementing a differential size limit would be via an increase in minimum mesh size. It is possible that, due to differences in mesh selectivity, catch rates of older fish might increase (Hamley 1975). Preliminary comparisons of the performance of commercial halibut gill nets of different mesh sizes indicate an increase in the availability of larger fish (Calif. Dept. of Fish and Game, unpubl. data, K. Miller, Long Beach). This is a case we were unable to analyze with available data. However, any increase in the catch of older fish could compensate for the loss of smaller fish resulting from an increase in the size limit. This would increase the relative percentage change in Y/R for the affected fishery segment. A change in the selectivity of commercial stationary gear or similar increase in the availability of larger fish could change our conclusions regarding the utility of a change in size limit.

CONCLUSIONS

Although Y/R increased by weight under a uniform 660-mm size limit, we assume that this management strategy would increase recreational users' dissatisfaction by decreasing the number of fish in the catch. Alternatively, the differential size limit would be expected to increase recreational satisfaction by increasing the number of fish in the catch. Unfortunately, this increase would substantially impact the commercial fishery segments, particularly commercial stationary gear, which represents over 67% of all commercial landings. The results of this yield-per-recruit analysis indicate that allocation conflicts among user groups are not likely to be resolved by a management strategy that increases the minimum size limit. Instead, the fishery is most likely to benefit from a management strategy that limits fishing effort to $F_{0.1}$ or similar optimum yield level.

ACKNOWLEDGMENTS

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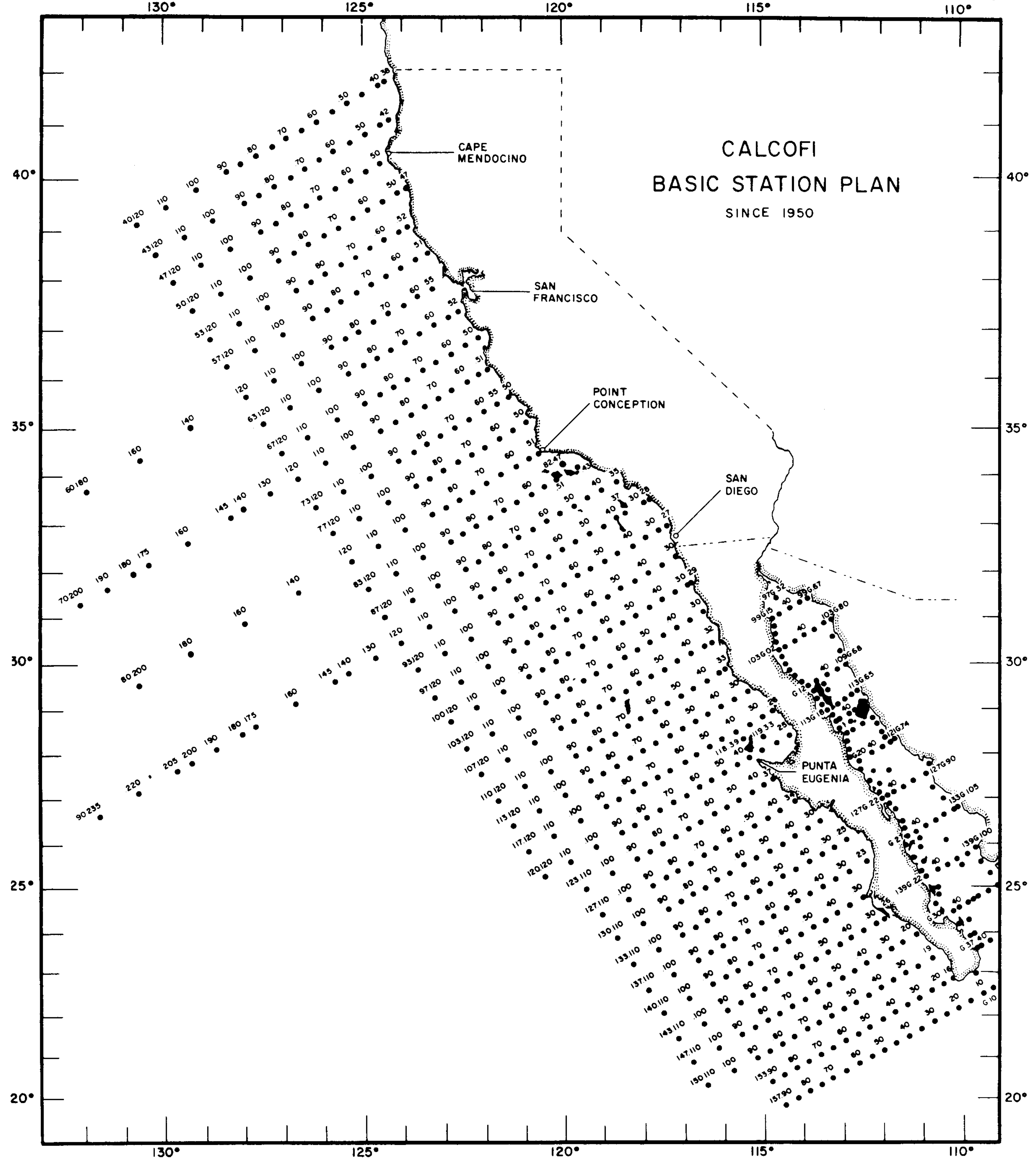

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