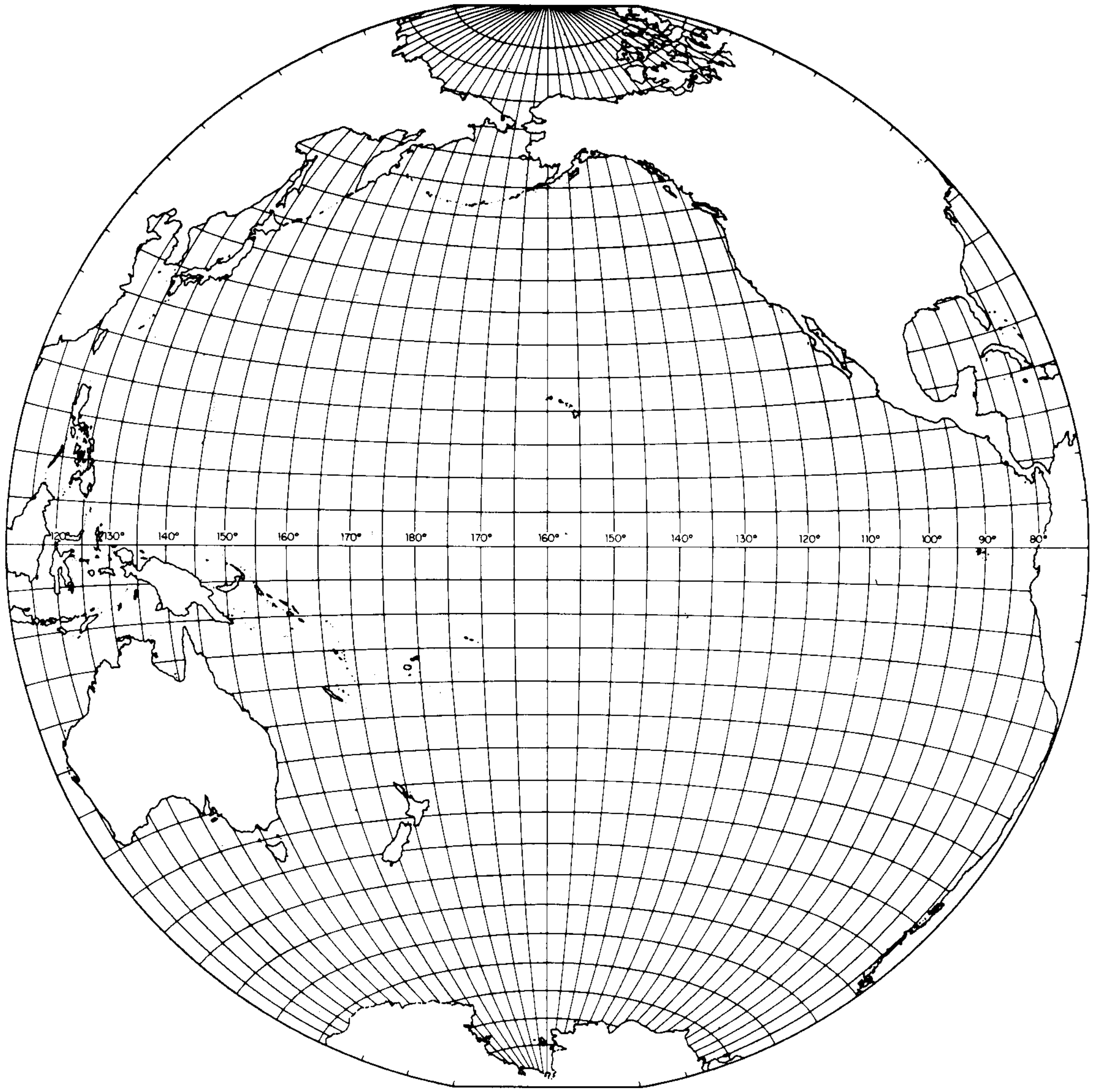

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CALIFORNIA DEPARTMENT OF FISH AND GAME
UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL MARINE FISHERIES SERVICE

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

The year 1998 marks 49 years of CalCOFI's multidisciplinary work in the California Current. In addition, 1998 has been declared by the United Nations and by President Clinton as "The Year of the Ocean." The importance of the oceans to the U.S. economy is underscored by Secretary of Commerce William M. Daley's comment that "One of every six jobs in the U.S. is marine related, and one third of the nation's gross national product is produced in coastal areas through fishing, transportation, and recreation" (Baker 1998).

To CalCOFI researchers, the economic impact of changes in the availability of coastal resources looms large, since CalCOFI was born out of California's policy response to the decline of the sardine fishery (Burnette et al. 1950). For almost five decades federal, state, and University of California scientists and managers, and their many partners, have amassed a formidable array of data related to the biology, physics, chemistry, geology, and atmospheric interactions of the California Current region and its fishes and other living resources. It is hoped that such data will allow us to predict events, or to mitigate the probable results of events that may affect our society and economy.

One such well-known and episodic phenomenon is that known as El Niño. CalCOFI dedicated its 1958 conference to the El Niño of 1956–58 and, at that meeting, began to seriously examine the hemispheric and global oceanic and atmospheric connections implied by the data presented (Sette and Isaacs 1960). The advent of climate and ocean-atmosphere-interaction studies at the Scripps Institution of Oceanography was one direct result of that conference. Subsequent El Niño events have captured the attention of CalCOFI researchers, as well as agencies of the state and federal governments. The forecast that a major California El Niño would appear in the winter of 1997–98, indicated by developments along the equator, stimulated interest in increasing the temporal coverage of the event. Assisted by enhanced funding from NOAA, CalCOFI augmented its quarterly cruises with shorter cruises every month during 1998. Thanks to many hours at sea by CalCOFI staff, this El Niño event will probably be the best documented to this time in history, providing data for correlative studies of processes and for testing models. Continuous underway monitoring of near-surface properties, including fish eggs, provided much more detailed data on mesoscale distributions than was previously available. A presentation of early results may be seen in the paper by Lynn et al. in this volume.

El Niño was not the only phenomenon requiring additional effort in 1997–98. There was considerable interest in mapping the northward expansion of the California sardine. As a result, the quarterly CalCOFI cruises were extended northward to Monterey Bay, reestablishing the time series of physical and ecological data which had been terminated in 1984 for that region. These surveys and the development of small fisheries off Oregon, Washington, and British Columbia show that the population has increased and the distribution has extended northward, beyond the historically sampled CalCOFI grid. As a result, SWFSC and CDFG biologists have developed a crude and speculative stock-assessment model that suggests a coastwide sardine biomass of 570,000 metric tons.

A new program of ocean monitoring off Baja California, Mexico (fig. 1), was initiated in September 1997 by a consortium of seven Mexican institutions. Mexican and U.S. marine scientists have long called for the reactivation of the sampling plan off Baja California (Hayward 1996), abandoned in the 1980s by CalCOFI because of lack of funds. This program is known by the acronym IMECOCAL (Investigaciones Mexicanas de la Corriente de California). The IMECOCAL cruises are coordinated closely with CalCOFI cruises to provide an integrated description of the pelagic ecosystem (see paper by Lynn et al. in this volume). The core observations at each station include a CTD and rosette cast to measure temperature and salinity and to collect water from 10-liter sampling bottles for analysis of salinity, dissolved oxygen, nutrient chemistry, phytoplankton counts, and the pigments chlorophyll a and phaeophytin. Oblique net tows (505-micrometer mesh) are taken: one cod end is used to estimate zooplankton biomass and the other to estimate ichthyoplankton abundance. Continuous, underway measurements of near-surface temperature, salinity, and chlorophyll fluorescence are taken from water pumped through the ship's hull. An acoustic Doppler current profiler (ADCP) is operated continuously between stations.

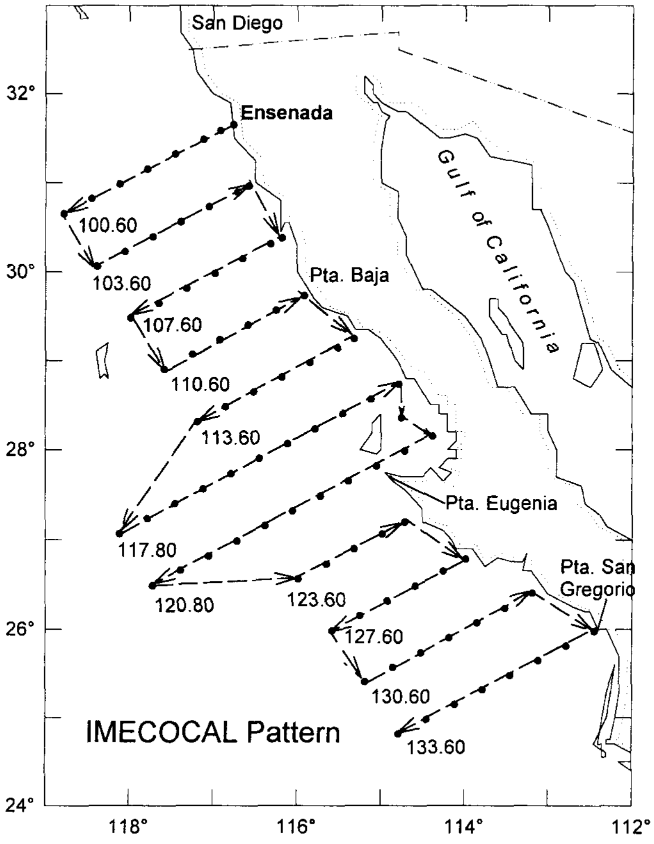

Figure 1. The IMECOCAL cruise pattern, established in 1997.

The market squid (*Loligo opalescens*) became California's most valuable marine resource in 1997, with reported landings valued at $30 million. As a result, the symposium of the 1997 CalCOFI Conference dealt with the biology, economics, and public policy assessment of the market squid. This symposium was cosponsored by CalCOFI, the California Seafood Council, and the Channel Islands National Marine Sanctuary. Workshops in the evenings of the conference brought together fishers, packers, union representatives, policy analysts, and scientists. Subsequently, CDFG and SWFSC completed a research plan for the market squid, and began a joint research program that focuses on the measurement of age, growth, longevity, fecundity, reproductive effort, and the integration of this information into a management strategy.

For several years, scientists of the SWFSC have been investigating the relation between climate variability, solar ultraviolet radiation, and the survival of pelagic fish eggs and larvae. They have discovered that, on days with clear skies, low winds, little mixing, and clear water, ultraviolet light is lethal to northern anchovy larvae to a depth of one meter, and causes measurable damage to DNA of larvae living as deep as 20 m. Scientists at the SWFSC and UC Santa Barbara are modeling the prevalence of such "bad days" in order to evaluate what proportion of total mortality is attributable to UV-induced mortality.

Catches of nearshore, rocky-reef fishes for the live-fish restaurant trade are increasing rapidly, and live fish command a high price. Little is known of the abundance, recruitment, and productivity of these species, and local stocks may have already been depleted in some regions. The SWFSC and CDFG have begun genetic studies of stock structure in nearshore rockfishes (*Sebastes*) to determine how much recruitment depends either on local production of larvae or on larval dispersion from genetically mixed populations located along the entire coast.

Director Jacqueline E. Schafer of the CDFG has announced plans to create a Marine Region with headquarters at Monterey Bay. This action is intended to emphasize the Department's commitment to safeguarding the state's complex and diverse marine ecosystems. The new Marine Region will coordinate policy implementation for all CDFG marine and maritime activities, expand local CDFG services to the public, and seek legislation to protect emergent fisheries.

The CalCOFI Committee extends its thanks to the many reviewers who gave so graciously of their time and expertise in critiquing the manuscripts published in this volume: Johann Augustyn, Barney Balch, Jay Barlow, Tom Barnes, Jon Brodziak, Steven Cadrin, Francisco Chavez, Earl Dawe, Lara Ferry-Graham, Stuart Helleren, George Hemingway, Raleigh Hood, Larry Jacobson, Bob Lavenberg, Beverly Macewicz, Greg Mitchell, Dick Parrish, Steve Ralston, Richard Sears, Ray Smith, Cindy Thomson, Chuck Trees, and Michael Vecchione. The Committee also thanks editor Julie Olfe for her excellent, careful editing of the manuscripts. We are very grateful for the support the directors of the SWFSC and the Scripps Institution for their help in securing additional ship-days and funding for the spatial extensions and temporal infill of the cruise patterns. Special thanks is extended to the officers and crews of the NOAA ship *David Starr Jordan*, the CDFG R/V *Mako*, the UCSD R/V *New Horizon*, and the UCSD R/V *Ellen B. Scripps* for their professional conduct of marine operations in support of CalCOFI's field research and monitoring of the California Current. We also thank the California Seafood Council and the Channel Islands National Marine Sanctuary for their contributions to the 1997 annual conference and to the publication of the symposium section of this volume.

Editor Julie Olfe offers particular thanks to two additional publications experts. Simone Llerandi has been typesetting *CalCOFI Reports* since 1985. Back then she worked at Thompson Type, and typed in every word of every paper. Now freelancing, she handles the disks and enters corrections to edited papers. But she still types the tables from scratch. Her work has been truly excellent for all these years. Designer and production expert

Barry Age took over from Sharon Tallman in 1994. Since then he has eased our transition into the computer age by making sure that each of the various disks we receive can be used, and by scanning in and placing many challenging pieces of art. His commitment to good design is obvious on every page of this book. The reliable dedication of these professionals helps make it possible for *CalCOFI Reports* to appear on schedule each year.

Portions of the *CalCOFI Reports*, as well as extensive data archives, calendars of operations, maps of cruise tracks, animations, links to cooperating agencies, and general information about CalCOFI are available online at *www-mlrg.ucsd.edu/calcofi.html.*

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REVIEW OF SOME CALIFORNIA FISHERIES FOR 1997

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In 1997, commercial fisheries harvested an estimated 219,744 metric tons (t) of fishes and invertebrates from California waters, a 7% increase over the 205,493 t harvested in 1996. Preliminary total commercial landings in California were 222,597 t, 6% greater than in 1996. The preliminary ex-vessel economic value of California commercial landings decreased by 9%, to $168.7 million. Statewide landings by recreational anglers aboard commercial passenger fishing vessels (CPFVs) increased by 17%, to 3,855,900 individual fishes.

The El Niño event of 1997–98 dramatically affected several California fisheries. Elevated water temperatures altered the seasonal availability of several harvested species; this, in turn, caused some fishers to redirect their efforts. Poor weather for fishing, partly resulting from El Niño, was an additional factor. Among the fisheries with suspected El Niño–related declines, none was more dramatic than the fall 1997 southern California market squid fishery. This fishery, usually among the most active and productive in California, was essentially nonexistent because of the almost complete absence of harvestable quantities of squid. This changed the dynamics of the wetfish fishery in California, and was partly responsible for increased landings of other species, especially Pacific mackerel. Other commercial fisheries that declined for a variety of reasons (perhaps including El Niño) were sea urchin, Dungeness crab, white seabass, swordfish, thresher shark, abalone, and ridgeback prawn.

In contrast to these declines, several fisheries increased in 1997, some as a result of El Niño. The continued recovery of the sardine resource suggests that management efforts and industry cooperation are having an effect. Other fisheries with increased landings in 1997 included Pacific mackerel, Pacific herring, groundfishes, shortfin mako shark, and fishes harvested by CPFVs (especially warm-water fishes like yellowtail). Particularly notable was the continued growth of the fishery for live fishes. Efforts by the California Department of Fish and Game (CDFG) to monitor and manage this complex fishery may increase in the future.

PACIFIC SARDINE

Rebuilding of the Pacific sardine (*Sardinops sagax*) fishery continued in 1997, with the year's total landings of 43,632 t ranking highest since the reopening of the directed fishery in 1986 (table 1). The 1997 fishery had

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

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1977	5	99,504	5,333	44,775	5,200	12,811	167,628
1978	4	11,253	11,193	30,755	4,401	17,145	74,751
1979	16	48,094	27,198	16,335	4,189	19,690	115,542
1980	34	42,255	29,139	20,019	7,932	15,385	114,764
1981	28	51,466	38,304	13,990	5,865	23,510	133,163
1982	129	41,385	27,916	25,984	10,106	16,308	121,828
1983	346	4,231	32,028	18,095	7,881	1,824	64,405
1984	231	2,908	41,534	10,504	3,786	564	59,527
1985	583	1,600	34,053	9,210	7,856	10,275	63,577
1986	1,145	1,879	40,616	10,898	7,502	21,278	83,318
1987	2,061	1,424	40,961	11,653	8,264	19,984	84,347
1988	3,724	1,444	42,200	10,157	8,677	36,641	102,843
1989	3,845	2,410	35,548	19,477	9,046	40,893	111,219
1990	2,770	3,156	36,716	4,874	7,978	28,447	83,941
1991	7,625	4,184	30,459	1,667	7,345	37,388	88,668
1992	17,946	1,124	18,570	5,878	6,318	13,110	62,946
1993	13,843	1,954	12,391	1,614	3,882	42,708	76,392
1994	13,420	3,680	10,040	2,153	2,668	55,395	85,929
1995	43,450	1,881	8,667	2,640	4,475	70,278	131,391
1996	32,553	4,419	10,286	1,985	5,518	80,360	135,121
1997*	43,632	5,718	20,718	1,160	11,541	70,929	153,158

*Preliminary

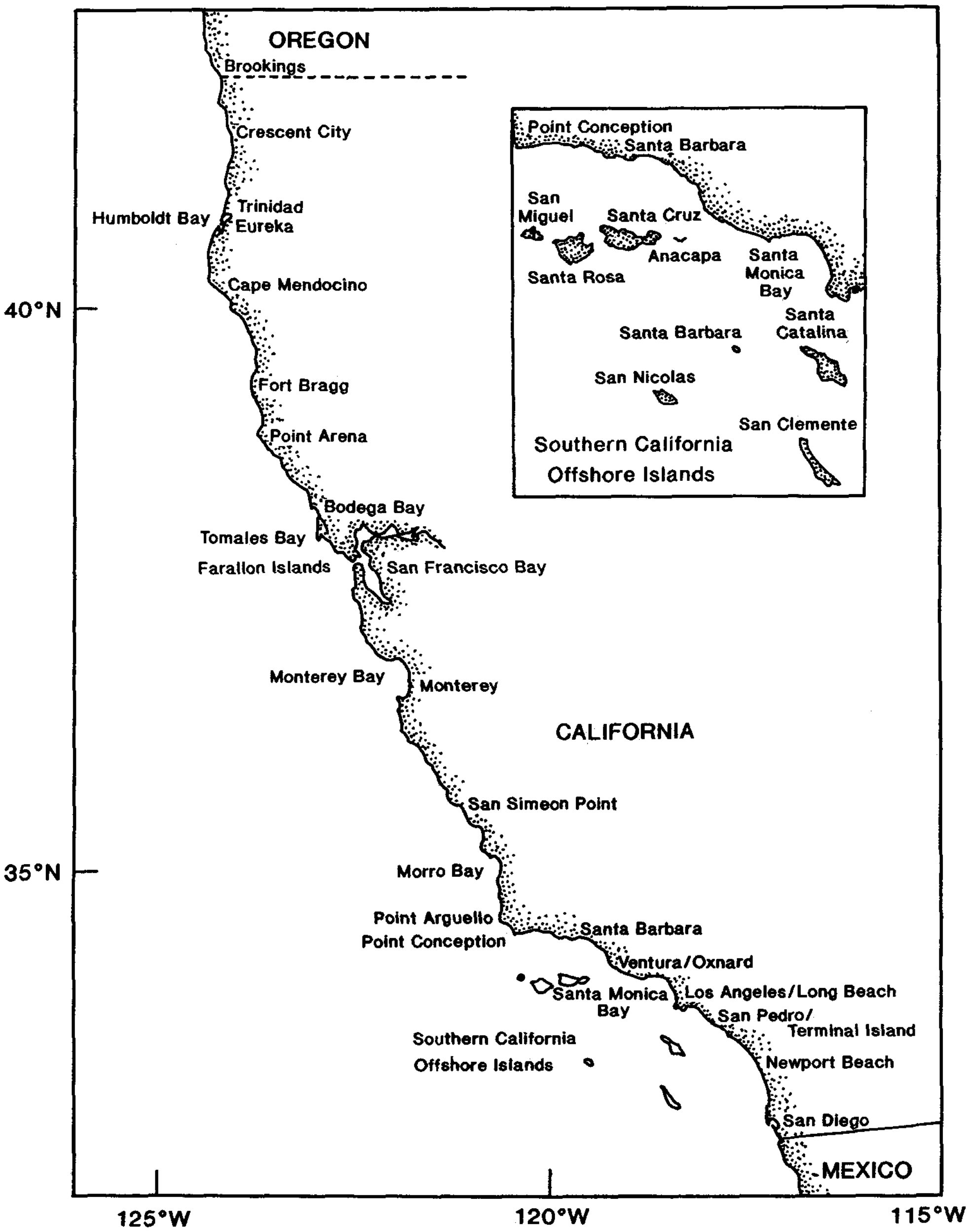

Figure 1. California ports and fishing areas.

an approximate ex-vessel value of $3.9 million, up from $3.11 million in 1996. Only 89% of the 1997 quota was landed, and the directed fishery remained open until the year's end.

Fish and Game Code (Section 8150.8) states that annual sardine quotas shall be allocated two-thirds to southern California (south of San Simeon Point, San Luis Obispo County) and one-third to northern California (fig. 1). Based on a 1 July 1996 biomass estimate of 462,664 t, the formula generated an initial 1997 southern fishery quota of 32,658 t, and a northern fishery quota of 16,329 t. In October, CDFG reallocated uncaught quota portions equally between north and south (table 2). The southern California fishery filled its portion of the reallocation in mid-December, but CDFG did not recommend closure of the southern fishery because only a few weeks remained in the year and several thousand tons were left in the northern allocation. Consequently, 5,336 t of the 1997 allocation was not taken.

Sardine population biomass (age 1+) as of 1 July 1997 was estimated at 421,000 t, based on output from CANSAR (Catch-at-age ANalysis of SARdines model). A forward-casting stock-assessment model, CANSAR produces biomass estimates by incorporating both fishery-dependent and fishery-independent data, including

TABLE 2
Pacific Sardine Quota Allocations (Metric Tons) in California for 1997

	Initial quota	Reallocated quota	Landings
North	16,329	14,349	10,847
South	32,658	14,349	32,785
Total	48,988	28,698	43,632

catch and weight-at-age information, landings data, egg and larval abundance, spawning biomass and area estimates, and spotter pilot observations. In 1997, CANSAR was modified into a two-area model (CANSAR-TAM) to include assumptions about migration and recruitment, and to address effects of net emigration on spawning biomass available to the fishery.

Current regulations give CDFG considerable latitude in setting annual sardine quotas. When biomass is estimated to be more than 20,000 t, Fish and Game Code requires that allowable catch must be consistent with resource rehabilitation. To calculate quotas, CDFG has (since 1996) used a harvest formula originally selected as the preferred option in the draft Coastal Pelagic Species Fishery Management Plan (Amendment 7). Based on the 1997 estimate of total biomass (age 1+), the 1998 sardine fishery opened on 1 January with a quota of 43,545 t for the California fishery. The 1998 quota was 11% less than the 1997 allocation.

Prices paid to fishers (ex-vessel price) for sardines remained relatively low in 1997, but were slightly higher than in 1996. Price ranged from $70 to $110 per t, and averaged $87 per t. Other important target species for the southern California wetfish fleet include Pacific mackerel (*Scomber japonicus*) and market squid (*Loligo opalescens*) in the winter, and tunas during the summer. In northern California, Pacific herring (*Clupea pallasi*) is also an important target species from January to March. Squid and tuna command significantly higher ex-vessel prices than sardines: $140–$300 per t for market squid and $600–$1,400 per t for tuna. During 1997, sardine landings varied by month due to availability, demand, and fleet participation in other fisheries. Over half of the 1997 sardine landings were made during the fourth quarter of the year, probably driven by lack of market squid availability to the southern California fall-winter fishery.

In 1997, about 89% of sardines landed in southern California were sold to market processors (56% frozen whole bait; 33% fresh fish for human consumption), and the remaining amount was canned for human consumption (6%) or pet food (5%). This ratio has changed dramatically since 1991, when canneries purchased about 75% of the landings. No California landings were used for the production of fish meal.

Besides the wetfish fishery for sardine, a small bait fishery exists that is not subject to a quota, and usually takes less than 5,000 t annually. Live bait ex-vessel prices, more than $600 per t in 1996, were approximately seven times greater than prices for the directed fishery. In 1997, the ex-vessel value of the sardine live bait fishery was approximately equal in value to the directed fishery.

Approximately 25% of California's sardine landings were exported in 1997, sold primarily (94%) as frozen blocks. In 1997, 10,977 t of sardines were exported, slightly less than the 1996 total of 12,347 t. Export revenues totaled $5.38 million at approximately $490 per t. The top four importers of Pacific sardine were Australia (73%), Japan (10%), Malaysia (4%), and China (3%). Australia imports sardines for use as fish food in aquaculture facilities, while Japan supplements its catch to meet consumer demand following the recent decline of its sardine resource. Exports to the Philippines dropped significantly in 1997, despite ranking first in 1995 and second in 1996.

In 1997, the Pacific Fishery Management Council (PFMC) voted unanimously to resubmit a draft Fishery Management Plan (FMP) for coastal pelagic species including Pacific sardine. Recent events have increased the need for federal management of this species. Sardine biomass continues to grow by 30% annually, and commercial fisheries are harvesting sardines off Mexico, California, Oregon, Washington, and Canada. The Council is expected to adopt and send out a draft of the amendment for public review in June 1998.

PACIFIC MACKEREL

Landings of Pacific mackerel (or chub mackerel, *Scomber japonicus*) in California increased significantly in 1997, countering a mid-1990s trend of reduced catches attributed to low biomass and lack of abundance on the traditional fishing grounds. Annual landings in California in 1997 totaled 20,178 t, nearly double the 10,286 t caught in 1996 (table 1). The surge in landings was largely due to increased effort by the wetfish fleet, prompted by the absence of a late fall and winter market squid fishery.

The Pacific mackerel fishing season is specified in the Fish and Game Code as the 12-month period from 1 July through 30 June of the following calendar year. Based on an estimated biomass of 47,173 t on 1 July 1996, an 8,709 t quota was set for the 1996–97 fishery, the lowest allocation in two decades. When total biomass is estimated by CDFG to be greater than 18,144 t but less than 136,080 t, allowable harvest is defined as 30% of the total biomass in excess of 18,144 t.

On 12 March 1997 the season quota was filled, and the directed fishery for Pacific mackerel closed for the first time since 1985, although regulations allowed incidental landings of mackerel mixed with other wetfish species. Following the closure, bycatch tolerance was limited to 35% mackerel by weight, resulting in approximately 730 t of mackerel landed incidentally between 12 March and the close of the 1996–97 season on 30 June. Landings for the season totaled 9,787 t, surpassing the 1995–96 season total of 7,615 t, which was the lowest since the commercial fishery reopened in 1977.

Using refinements in assessment methodology such as the age-structured model ADEPT, the 1997–98 quota allocation for mackerel was 22,045 t, based on an estimated biomass of 91.2 t. Landings throughout the summer were consistently higher than in recent years, followed by monthly totals surpassing 4,500 t in both October and November of 1997. Southern California fishers reported generally good availability on the traditional fishing grounds, with many landings at the east end of Catalina Island, and from waters adjacent to the coast from San Pedro to Newport Beach.

During the winter of 1997–98, abnormally high water temperatures associated with an El Niño condition caused a decline in market squid abundance in southern California waters. Consequently, effort that the wetfish fleet would normally have directed toward squid was redirected to Pacific mackerel and sardine. Although closure of the mackerel fishery before 30 June seemed likely (as of April 1998, 20,178 t, or 92% of the quota, had been landed), this did not happen. Total landings for the 1997–98 season approximated the quota.

Nearly 85% of California landings during 1997 were made by the southern California wetfish fleet, with the remainder in the Monterey area. Although no directed commercial fishery for Pacific mackerel exists north of Monterey, it is suspected that the stock has more fully occupied the northernmost portions of its range during recent years in response to a warm oceanographic regime in the northeast Pacific Ocean; schools have been found as far north as British Columbia. There has been notable bycatch of Pacific mackerel in the Oregon and Washington whiting fisheries throughout the 1990s, and interest in developing directed mackerel fisheries in these states is increasing.

The ex-vessel value of the catch of the 1997 Pacific mackerel fishery was approximately $2.99 million paid to fishers, with a mean price of $148 per t. Throughout the year, the price paid to fishers ranged from $66 to $165 per t, with higher-quality fish in the fall months generating higher prices. Approximately 3,700 t were exported (18.6% of the statewide total landed in 1997), earning approximately $3.3 million in revenue for California processors. Australia ranked highest among export nations, followed by Japan and Uruguay. Mean export price was approximately $880 per t.

Age composition of the commercial catch in 1997 changed dramatically, as indicated by routine sampling by CDFG at southern California ports. Over 43% of nearly 3,000 fish sampled were age three or older, compared with only 13% in 1996.

PACIFIC HERRING

Annual statewide landings for Pacific herring (*Clupea pallasi*) were 11,541 t, an increase of 109% from the previous year (table 1). Statewide landings for the roe fishery during the 1996–97 fishing season (December–March) totaled 10,694 t, largest in the history of this fishery. Three gill net platoons (383 permittees) in San Francisco Bay landed 7,774 t, which was 19% under their 9,633 t quota. Twenty-five round haul (purse seine and lampara) permittees in San Francisco Bay landed 2,655 t, exceeding the quota by 1 t. The quota for Tomales Bay was 236 t, and the 39 permittees landed 201 t. The four Humboldt Bay permittees landed 35 t, 35% less than their 54 t quota. Three Crescent City permittees landed 28 t, 4% more than their quota of 27 t.

Ex-vessel prices for herring with 10% roe recovery averaged about $1,000 per short ton during the 1996–97 fishing season; an additional $100 per short ton was paid for each percentage point over 10%. Total ex-vessel value of the roe fishery was $14.7 million, down 26% from last season, but still above the average for the previous eleven seasons (roughly $11 million).

Eleven permittees participated in the San Francisco Bay herring eggs-on-kelp fishery and harvested 190 t, 27% less than their quota of 260 t. Eggs-on-kelp landings were the largest ever recorded, and nearly double the previous record of 97 t. Total estimated ex-vessel value of the eggs-on-kelp fishery was $6.3 million, with prices ranging from $10 to $20 per pound.

To estimate herring spawning biomass in San Francisco Bay and Tomales Bay, CDFG biologists used hydroacoustic and spawn-deposition surveys. No surveys were conducted in Humboldt Bay or Crescent City Harbor. The 1996–97 herring spawning biomass estimate for San Francisco Bay was 81,260 t, down 9.5% from last season, but still one of the three highest ever. The large biomass estimate was attributable to very large numbers of three-, four-, and five-year-old fish from the 1994, 1993, and 1992 year classes. The 1994 year class, one of the largest in the history of the fishery, was fully recruited as three-year-old fish this season. The moderately strong 1995 year class represents the fourth consecutive year of successful recruitment for the San Francisco Bay population.

Spawning biomass estimates have fluctuated widely in Tomales Bay since the reopening of the fishery in the 1992–93 season. The 1996–97 spawning biomass estimate was 1,331 t for Tomales Bay, a 30% decrease from the 1995–96 estimate of 1,892 t. The 1996–97 biomass estimate was below the four-year average of 2,853 t, and well below the 24-season average of 3,968 t. Aside from the weak 1991 year class, other year classes were well represented in the population. Heavy rains beginning in January 1997 reduced bay salinities, which probably inhibited spawning.

A dead-bait-and-animal-food fishery for Pacific herring is usually conducted during the summer in Monterey Bay. However, participation in this fishery was minimal in 1997, with only 45 pounds landed. Increased landings of Pacific sardine in 1997 may have met the demand for dead bait and animal food.

MARKET SQUID

The 1997 market squid (*Loligo opalescens*) fishery suffered as a result of the 1997–98 El Niño event. Nevertheless, market squid remained the state's most valuable commercial fishery. Statewide landings totaled 70,304 t and generated an ex-vessel value of $20.6 million. This was a 13% decrease from the record landings of 80,360 t in 1996 (table 1).

Two fisheries for market squid exist in California: the southern California fishery, conducted primarily in fall and winter, and the central–northern California fishery, conducted primarily in spring and summer. The southern California fishery has accounted for approximately 90% of the statewide landings for the past several years, and 1997 was no exception: landings in southern California were 61,813 t, 88% of the statewide total. Port Hueneme and Ventura were the most active ports, receiving most of the landings (33,222 t and 9,445 t, respectively). This activity, however, occurred mainly during January–March; the southern California fishery was virtually nonexistent the following fall because of the influence of the 1997–98 El Niño (fig. 2). The average monthly landings in southern California for January–March 1997 were 20,124 t; the corresponding average for 1994–96 was 6,287 t. In contrast, total landings in southern California for October–December 1997 were only about 403 t, dramatically less than the average of 12,641 t for October–December 1994–96.

The 1997 central–northern California squid fishery ended before the 1997–98 El Niño event, and was less affected. This fishery, centered in the southern bight of Monterey Bay, began on the last day of March, and by the end of May a total of 6,078 t had been landed. This two-month period accounted for 72% of the area's annual total of 8,490 t. Landings were made through September, then stopped abruptly in Monterey Bay. A few small landings were made in October and December in ports north of Monterey Bay. This year's pattern of landings was unusual; historically, the annual peak of the central–northern California squid fishery occurs in August.

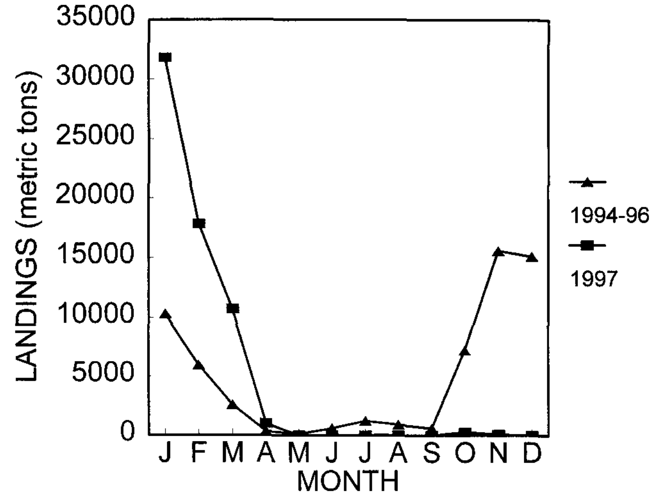

Figure 2. Monthly landings of California market squid during 1997 compared to monthly averages for 1994–96.

A total of 149 boats participated in the 1997 fishery; of these, 120 boats used purse seine and/or brail gear, and the remainder used miscellaneous gears. As in previous years, purse seine boats dominated the fishery, landing over 99% of the statewide total. In central–northern California, 30 vessels used purse seines, the only gear used. In southern California, 106 purse seiners (7 also using brail) landed squid, and 11 other boats landed squid by using brail only. Some boats participated in both regional fisheries.

Annual statewide ex-vessel prices for squid averaged $265 per short ton. As in many previous years, the ex-vessel price per ton in the Monterey Bay area was the highest in the state: it averaged $309 and generated a total of approximately $2.8 million. Ex-vessel prices for squid in the Santa Barbara area averaged $243 per ton and generated $11.8 million, while the ports of San Pedro and Terminal Island averaged $300 per ton and generated $5.7 million.

Demand for squid on the international market once again stimulated the fishery, with China as the dominant foreign market. But industry representatives reported that the success of the 1996–97 southern California squid fishery, coupled with substantial landings worldwide, resulted in saturation of the Chinese market by the middle of 1997. This was due primarily to the limited cold-storage capacity of most of the coastal Chinese processors. Few, if any, squid cold-storage facilities exist in inland China. As a result, at least one California processor repurchased squid and shipped it to European markets in frozen 25-pound blocks during the second half of 1997. The Japanese market remained steady because it is based primarily on a "presentation" product of one-pound packages of squid.

As in previous years, the 1997 squid fishery was essentially an unregulated, open fishery. However, after several years of effort by some fishers and industry members, Senate Bill 364 (Sher) was passed. Among other provisions, this bill requires that all boats landing more than two tons of squid per trip, and all light boats, buy a $2,500 annual permit. Funds generated from the sale of these permits for the next three years are to be used by the California Department of Fish and Game for squid research. The bill also mandated that the CDFG submit a report on the status of the squid fishery, with recommendations for a market squid conservation and management plan, to the legislature by 1 April 2001. It also authorized the director to establish a Squid Research Scientific Committee to help develop research protocols, and a Squid Fishery Advisory Committee.

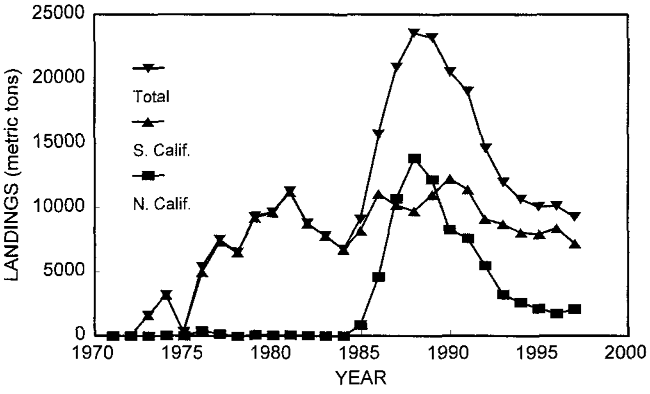

Figure 3. California sea urchin landings, 1970–97.

SEA URCHIN

Overall, red sea urchin (*Strongylocentrotus franciscanus*) landings continued to decline from previous years, a trend that has continued since 1988, when landings peaked at 23,577 t. Total 1997 landings deceased by 8% from 1996. Landings in northern California increased by 16%, while they decreased 14% in southern California (fig. 3). El Niño–related warming of seawater had a devastating effect on kelp, the primary food of urchins, in southern California. This, together with poor weather and sea conditions, was responsible for declining catches in southern California. There was a shift of urchin divers from the south to the north, partly because of sea conditions, but also because of the closure of the southern California abalone fishery. Divers with dual permits for abalone and urchin, who usually dive for abalone at the Farallon Islands and Half Moon Bay, shifted to sea urchin and caused an increase of effort in the north. This is reflected in increased landings at Bodega Bay, the southernmost of the northern California ports.

While northern California landings increased in 1997, they made up about 25% of statewide landings. Santa Barbara continued to be the most active port for sea urchin landings, with about 25% of the statewide total. Sea urchins landed there came from coastal southern California and the northern Channel Islands, as did landings at Oxnard, Ventura, and Los Angeles (table 3).

The statewide value of the 1997 fishery declined to about $15 million, from $17.1 million in 1996, a 15% decrease. This may be due to lower landings, and also to the current economic situation in Japan. The unit price per kg was about $1.80, down from $2.20 in 1995, and caused serious economic hardship for California divers. The number of permits—469—dropped by 50 from 1996 and was the largest drop since 1989.

The outlook for sea urchin is mixed. Detrimental El Niño conditions are likely to dissipate, but the effects were severe, and how long it will take the resource to recover is uncertain. Economic conditions in Japan will determine the final value of the fishery. The changing market will adversely affect the California product, because high-quality California sea urchin brings premium prices, which fewer Japanese are able to afford. The market has turned to a lower-quality, lower-cost product for the general consumer market. Finally, the sea urchin fishery is threatened by expanding sea otter populations, which appear to be extending their range to south of Point Conception (as of March 1998) and also northward to a lesser degree. Past experience suggests that most invertebrate fisheries cannot coexist with persistent populations of sea otters.

GROUNDFISHES

The California commercial groundfish harvest for 1997 was 28,932 t, with an ex-vessel value of approximately $34 million. Total 1997 landings increased 4%,

TABLE 3
Preliminary California Commercial Red Sea Urchin Landings (Metric Tons) for 1997

Port	Landings	Percentage of statewide catch	Value	Price per kg
Crescent City	28.9	0.4	$ 30,267	$1.05
Fort Bragg	646.8	7.9	$ 1,207,110	$1.87
Albion	371.5	4.6	$ 676,531	$1.82
Point Arena	613.3	7.5	$ 1,156,224	$1.89
Bodega Bay	383.1	4.7	$ 660,919	$1.73
Half Moon Bay	10.6	0.1	$ 4,309	$0.41
N. Calif. subtotal	2,054.2	25.2	$ 3,735,360	$1.82
Santa Barbara	2,072.6	25.4	$ 3,672,377	$1.70
Oxnard/Ventura	1,693.5	20.8	$ 3,165,869	$1.87
Los Angeles	1,868.9	22.9	$ 3,109,850	$1.66
Orange County	39.9	0.5	$ 88,937	$2.23
San Diego	417.6	5.1	$ 852,535	$2.04
S. Calif. subtotal	6,092.5	74.7	$10,889,568	$1.79
Grand total	8,146.6		$14,624,928	

or 1,112 t, from 1996. Dover sole (*Microstomus pacificus*), thornyheads (*Sebastolobus* spp.), sablefish (*Anoplopoma fimbria*), rockfishes (*Sebastes* spp.), and Pacific whiting (or Pacific hake, *Merluccius productus*) continued to dominate the harvest. Total landings were similar to those in 1995 and 1996, but the whiting contribution increased sharply while other groups showed modest declines.

Many of the declines shown in table 4 reflect increasingly restrictive Washington-Oregon-California (WOC) landing limitations. This is most apparent for bocaccio: the harvest guideline has been in a step-down mode, and trip limits have been reduced to bring landings in line with lower allowable yields. Nontrawl landings of grenadiers also fell sharply, but in this case, reduced limits on species associated with grenadiers have made the fishery unprofitable.

In 1997, 86% of the groundfishes landed in California were taken with bottom and midwater trawl gear, a slight increase from the 83% observed in 1996. Line gear accounted for 12% of 1997 landings, a decrease from the 15% observed in 1996. The gill and trammel net component stabilized at just under 1% after a steady decline from 5% in 1993. The trap component remained steady at close to 1%.

For 1997, the Pacific Fishery Management Council (PFMC) maintained harvest guidelines (HGs) for Dover sole; shortspine thornyhead (*Sebastolobus alascanus*); longspine thornyhead (*Sebastolobus altivelis*); the *Sebastes* complex; widow rockfish (*S. entomelas*); yellowtail rockfish (*S. flavidus*); and canary rockfish (*S. pinniger*). Also, commercial harvest guidelines (CHGs) were set for Pacific whiting; sablefish; bocaccio (*S. paucispinis*); and lingcod (*Ophiodon elongatus*). For Pacific whiting and sablefish, CHGs do not include the portion of the total allowable catch assigned to Washington treaty tribes of Native Americans; the CHGs for lingcod and bocaccio exclude the portion set aside for the recreational fishery. These HGs and CHGs were allocated between a limited-entry fleet and open-access fleet; furthermore, the limited-entry allocation for sablefish was divided between the trawl fishery (58%) and nontrawl fisheries (42%). The PFMC used two-month cumulative landing limits in the limited-entry fishery and one-month cumulative landing limits in the open-access fishery, as well as trip limits, to stay within the annual HG or CHG while providing a year-round fishery.

TABLE 4
California Groundfish Landings (Metric Tons) for 1997

Species	1996	1997	Percent change
Dover sole	6,379	5,282	−17
English sole	585	648	11
Petrale sole	817	827	1
Rex sole	502	453	−10
Other flatfishes	995	1,107	11
Widow rockfish	1,060	1,336	26
Bocaccio	478	286	−40
Other rockfishes	5,922	5,667	−4
Thornyhead	3,270	2,754	−16
Lingcod	477	502	5
Sablefish	3,172	2,888	−9
Pacific whiting	2,901	6,332	118
Grenadier	1,133	632	−44
Other groundfishes	129	218	69
Total	27,820	28,932	4

The 1997 California shoreside Pacific whiting fishery began on 15 March; the opening in Oregon and Washington was delayed until 15 June. The directed season for at-sea catcher-processors and vessels delivering to mother ships began on 15 May off Oregon and Washington. A new catch allocation formula, expected to be in effect for five years, was determined by PFMC before the season opening. A CHG of 207,000 t was divided among vessels landing at shoreside processing plants (42%), catcher-processors (34%), and vessels delivering to mother ships (24%). Total 1997 WOC-area landings of 207,841 t were just over the CHG. In California, eight midwater trawl vessels fishing off Eureka and Crescent City landed 6,357 t shoreside, an increase over the 2,901 t landed in 1996, but still only 3% of total WOC-area landings. The California salmon bycatch rate was 0.022 salmon per t of whiting, a slight increase from the 1996 rate of 0.008, but well below the 0.05 threshold. All salmon observed were chinook (*Oncorhynchus tshawytscha*). The nonsalmon bycatch rate in observed landings was 5.8 pounds per t, nearly identical to last year's 5.2 pounds per t.

Dover sole, longspine thornyhead, shortspine thornyhead, and trawl-caught sablefish (DTS complex) management was similar to that for 1996. The coastwide Dover sole HG was again set at 11,050 t. The thornyhead HGs for the WOC area north of Point Conception remained at 6,000 t for longspine thornyhead and 1,380 t for shortspine thornyhead. The amount of sablefish allocated to the trawl fishery north of the Point Conception area was 3,803 t.

The coastwide catch of Dover sole was 10,093 t, 957 t under the 1997 HG, and a 2,036 t decrease from 1996 landings. The decreased landings were primarily caused by restrictive management measures, implemented by the PFMC to constrain the take of shortspine thornyhead and trawl-caught sablefish within the DTS complex. California 1997 Dover sole landings of 5,282 t represented a 17% decrease from 1996, and were 52% of total WOC landings (similar to the 53% observed in 1996).

WOC-area landings (north of Point Conception) of longspine and shortspine thornyhead were 4,011 t and 1,323 t, respectively. Shortspine thornyhead landings were very close to the HG, but longspine thornyhead landings were nearly 2,000 t below the 6,000 t allowable harvest. This reduced harvest demonstrates the difficulties inherent in managing mixed-species fisheries. In this case, landing limits designed to constrain shortspine thornyhead and sablefish catches made it uneconomical to maximize catches of the other species in the complex. California landed 2,754 t (52%) of the total WOC thornyhead catch.

The allocation formula in the Groundfish Management Plan resulted in 2,754 t of sablefish for the limited-entry nontrawl fishery and 463 t for the open-access fishery. In an attempt to eliminate the limited-entry nontrawl sablefish derby, the PFMC initially recommended that a primary fishery be managed as a three-week equal cumulative limit. However, the National Marine Fisheries Service (NMFS) determined that the proposal would be classified as an individual quota, which is prohibited until 1 October 2000 by the Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA). At its June meeting, the PFMC adopted an alternate proposal for a nine-day primary fishery with equal cumulative limits. As in previous years, a mop-up fishery would be established to harvest fish left over. In addition, a sablefish endorsement was required for fishing in the primary fishery. The primary season opened 25 August and closed 3 September, with an equal limit of 34,100 pounds for all vessels. The nontrawl limited-entry sablefish fishery outside of the derby and mop-up fisheries was again managed under a daily limit of 300 pounds north of 36°N latitude, and 350 pounds south of 36°N. The open-access sablefish fishery was limited to daily trip limits of 300 pounds north of 36°N, and 350 pounds south of 36°N. The total nontribal WOC-area catch of sablefish (limited-entry trawl and nontrawl, and open-access) in 1997 was 7,536 t, exceeding the overall 7,020 t CHG by 507 t. California accounted for 2,888 t, or 38%, of the total WOC-area nontribal catch (percentage identical to 1996).

A WOC-area CHG for lingcod was set at 1,500 t, and 900 t was set aside for recreational gear. The 22-inch size limit remained in effect during 1997, with a 100 pound-per-trip trawl allowance for fish under 22 inches. Recreational fishers were limited to three fish per bag and the 22-inch size limit. The total WOC-area commercial lingcod landings of 1,562 t slightly exceeded the 1,500 t CHG. California commercial fishers landed 502 t, or 32%, of the WOC-area commercial allotment. The estimated recreational catch for 1997 was 400 t, considerably less than the amount set aside.

New HGs for the *Sebastes* complex (rockfishes other than widow) were established for the northern area (Vancouver-Columbia) at 6,656 t and for the southern area (Eureka-Monterey-Conception) at 9,284 t. The new HGs are substantially below the levels of previous years, and near the levels of recent landings. California's commercial *Sebastes* complex landings were 5,953 t in 1997.

Bocaccio are included in the overall *Sebastes* complex HG, but the species has also been managed with a separate HG since 1991. The 1996 bocaccio assessment indicated a dramatic decline in the stock and recommended the allowable biological catch be set at 265 t for 1997. The PFMC recommended a step-down approach and set the southern-area HG at 387 t for 1997, with the intent of moving to a 265 t HG in 1998. The HG was further divided into a CHG of 231 t, and 55 t was set aside for the recreational fishery based on estimated 1996 catches. The 1997 *Sebastes* complex harvest included 286 t of bocaccio, a 40% drop from the 478 t landed in 1996. Another 60 t was estimated to have been caught in the recreational fishery.

In 1997 the PFMC implemented a new stock-assessment review process to improve public participation, increase the level of scientific peer review, and provide a greater separation between the scientific and management processes. New assessments for Dover sole, shortspine thornyhead, longspine thornyhead, sablefish, widow rockfish, and lingcod indicated that immediate and substantial harvest reductions were needed to prevent further stock declines. The PFMC responded with greatly reduced HGs and more restrictive trip limits for 1998.

In 1998, the PFMC will continue to investigate a groundfish industry capacity-reduction program, and the feasibility of a comprehensive groundfish observer program. Amendments to the FMP required by the MSFCMA regarding essential fish habitat, bycatch, and overfishing are scheduled for adoption by the PFMC. Allocations of lingcod and rockfishes within the limited-entry fishery, and between the commercial and recreational fisheries, will also be considered. New assessments are scheduled for chilipepper (*S. goodei*); blackgill rockfish (*S. melanostomus*); Pacific ocean perch (*S. alutus*); black rockfish (*S. melanops*); sablefish; and shortspine thornyhead.

SWORDFISH AND SHARKS

Swordfish (*Xiphias gladius*) landings were 725 t in 1997 (table 5), 10% less than in 1996. During the past decade the drift gill net fishery has accounted for the majority of the catch. This year, 53% of the catch was taken with drift gill nets, down from last year's 60%. Longline landings constituted 37% of the catch. Nine vessels used longline gear outside the U.S. Exclusive Economic Zone (EEZ) and landed swordfish in southern California ports. Only three of these vessels, however, were based in California. As usual, harpoon landings constituted 8% of the catch. Seventy-two percent of the swordfish catch was landed in southern California ports.

TABLE 5
California Landings (Metric Tons) of Swordfish and Selected Shark Species, 1986–1997

	Swordfish	Common thresher shark	Shortfin mako shark
1986	1,749	276	215
1987	1,246	239	274
1988	1,129	250	222
1989	1,296	295	177
1990	851	210	262
1991	711	344	151
1992	1,068	179	97
1993	1,218	162	84
1994	1,165	194	88
1995	796	155	66
1996	803	181	64
1997*	725	169	88

*Preliminary

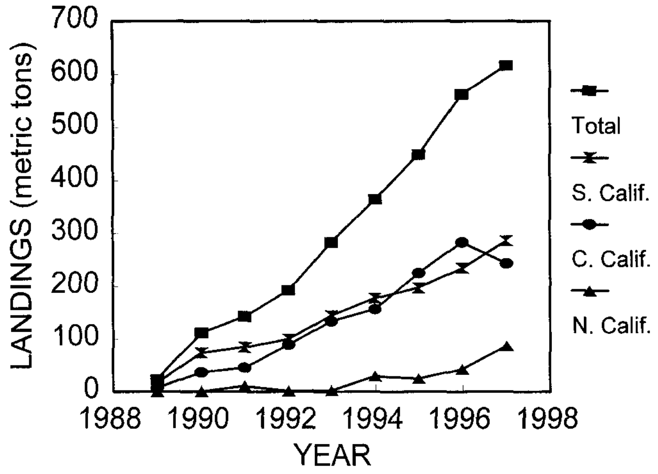

Figure 4. California landings of live fishes, 1989–97.

As expected, gear type affected swordfish ex-vessel prices. Typically, fishers landing drift gill net–caught swordfish received $3.00 to $9.00 per pound (averaging $3.00), whereas longline-caught fish commanded only $2.00 to $4.00 per pound (averaging $2.00). Fishers landing harpoon-caught swordfish received the highest average price of more than $5.50 per pound, with a range of $3.00 to $7.50 per pound.

Landings of common thresher shark (*Alopias vulpinus*) totaled 169 t in 1997 (table 5). This was a slight decrease from 1996. Thresher sharks (*Alopias* spp.) were taken primarily with drift gill nets (81%), followed by set gill nets (14%), and assorted other gears (5%). The greater part (85%) of landings continued to be made in southern California. Typically, ex-vessel prices varied from $1.00 to $3.00 per pound, with an average price of $1.50.

Shortfin mako shark (*Isurus oxyrinchus*) landings in 1997 were 88 t (table 5), an increase of nearly 40%. Most of the catch (80%) was landed in southern California ports, at ex-vessel prices between $0.30 and $4.50 per pound, with an average price of $1.00. Mako sharks were caught primarily by the drift gill net fishery (83%). The remainder of the catch was landed with set gill nets (4%), hook and line gear (3%), longline vessels operating outside the EEZ (2%), and as incidental catch with other gears (8%).

LIVE FISHES

The 1997 statewide landings of live nearshore finfishes were estimated at 617 t, 10% more than in 1996 (fig. 4). Sixty-eight different species of fishes were landed in live form, and had an ex-vessel value of over $3.9 million. Field observations suggest that documented landings underestimate the activity of this fishery. Additionally, many fishes intended for the live-sale market did not survive the rigorous process of capture, transport, and delivery, and were sold as fresh (dead) fishes at reduced prices. These landings, and those of premium-quality fresh fishes (sold at live prices) were not included in estimates of live-fish landings because of the difficulty of collating data. The market for premium-quality nearshore finfishes has evolved to include a variety of options for product delivery, but the origin and ultimate destination of these fishes remains the same. All of these landing options should be considered when attempting to accurately describe current demand. This complex fishery continues to evolve as market interest, fishing success, and participants change, and as new ways to access previously inaccessible fishing grounds are developed.

Ex-vessel prices ranged between $0.50 to $9.00 per pound, with the average price about $3.00 per pound. Larger fishes were popular "large party" specialties at local restaurants. Prices fluctuated with market demand, fish size and condition, and fishing and weather conditions. Hook and line gear were used to capture 63% of the live fish landed statewide; trap gear landed 26%. These values were consistent with those for 1995 and 1996.

Fishing activity in northern California (Sonoma County northward) increased markedly as live-fish landings totaled 87 t, 102% more than in 1996 (fig. 4). As previously, most landings were made with a variety of hook and line gears, but trapping gained in popularity (table 6). The number of fishers making at least one live-fish landing virtually doubled from 1996 (from 71 to 140), as urchin divers reported a downturn in urchin prices and sought a more profitable fishery (table 7). Landings of the original target species continued to climb: rockfishes (*Sebastes* spp.); cabezon (*Scorpaenichthys marmoratus*); and lingcod (*Ophiodon elongatus*) increased 37%, 115%, and 165%. Landings increased for principal species of rockfishes: 82% for China (*Sebastes nebulosus*); 132% for gopher (*S. carnatus*); and 393% for grass (*S. rastrel-*

TABLE 6
Percentages of Annual Landings of Live Fishes by Gear Type in 1996 and 1997

	Northern California		Central California		Southern California	
Gear type	1996	1997	1996	1997	1996	1997
All line	98	97	82	80	34	39
All trap	1	3	14	18	35	39
All trawl	<1	<1	4	2	15	10
All net	0	<1	<1	<1	15	11
All dive	<1	0	<1	<1	1	1

liger). Copper (*S. caurinus*) was the only targeted rockfish with reduced landings (72% of 1996). Statewide fluctuations in landings of rockfishes may be partly due to misidentifications of species on the landing receipts; this possibility is enhanced by markets that prefer to sort their catch by size and condition rather than by species. A dramatic increase of fishing effort was recorded for kelp greenling (*Hexagrammos decagrammus*), as landings grew sevenfold over 1996.

Central California fishers landed 244 t of live fishes, a decrease of 16% from 1996 (fig. 4). Although landings of virtually all target species including rockfishes, cabezon, lingcod, and California halibut (*Paralichthys californicus*) declined, the central coast remained the hub of live rockfish activity; 70% of all rockfishes in California were delivered primarily to Morro Bay and Avila–Port San Luis. Diminished landings of specific rockfishes such as gopher, copper, and grass were also recorded. Kelp greenling was the only market category that increased. Hook and line gear were employed to harvest 80% of the region's live catch, with the predominate device being the "fishing stick." This small, lightweight device consists of weighted plastic tubing or rebar with hooked leaders and a buoy attached. Trapping operations showed only a modest increase from 1996. The anticipated influx of trappers displaced by the full implementation of the limited-entry program for finfish trapping in southern California never materialized.

Live-fish landings in southern California (Santa Barbara southward) totaled 286 t, 22% more than in 1996 (fig. 4). Target species included California sheephead (*Semicossyphus pulcher*); California halibut; cabezon; California scorpionfish (*Scorpaena guttata*); rockfishes; and thornyheads (*Sebastolobus* spp.). Line and trap gear each accounted for approximately 39% of the landings; line users focused on nearshore rockfishes and cabezon; users of trap gear primarily targeted California sheephead. Trapping accounted for 84% of all live sheephead delivered to market, over half of the catch coming from the Santa Barbara–Ventura area (including the northern Channel Islands). The number of trappers making at least one landing of live fishes declined precipitously in 1997 (from 285 to 185), as did fish trap permittees (from 316 to 195). The impending limited-entry program apparently fueled the flurry of trapping and permit purchases in 1996, as fishermen secured their future participation in the fishery. Increases in estimated landings were recorded for California sheephead, California scorpionfish, cabezon, sablefish (*Anoplopoma fimbria*), and thornyheads. However, landings declined for rockfish and California halibut.

Legislation that would further restrict the fishery for live finfishes is pending. In addition, more restrictive federal groundfish regulations now apply to many of the target species such as rockfishes, thornyheads, lingcod, and sablefish. Innovative management options are currently being evaluated by the CDFG to improve conservation of the nearshore ecosystem.

ABALONE

The commercial and recreational abalone fishery in central and southern California was closed to all fishing under emergency action by the Fish and Game Commission in May 1997. Legislative action under Senator Thompson's SB463 extended the closure indefinitely in January 1998. Under the new legislation, the Fish and Game Commission may lift all or part of the closure following completion and acceptance of a detailed Abalone Recovery and Management Plan (ARMP) to be prepared by the Department of Fish and Game on or before 1 January 2003. The ARMP requires scientifically valid evidence of a broad recovery before reopening any of the closed abalone species to harvest.

Commercial landings for red abalone (*Haliotis rufescens*) totaled 50 t, or about half the 102 t landed in 1996. Landings were concentrated in March as fishing effort increased in anticipation of the May moratorium. The Commission and the legislature chose to allow continued

TABLE 7
Number of Participants Making at Least One Live-Fish Landing, by Region, 1989–1997

Region	1989	1990	1991	1992	1993	1994	1995	1996	1997*
Northern California	16	16	20	18	13	45	12	71	140
Central California	26	70	171	273	356	428	356	378	349
Southern California	34	104	82	151	246	315	285	405	361

Note: Some fishers operate in more than one region.
* Preliminary

recreational red abalone harvest north of San Francisco. This action was based on fisheries-dependent and independent data indicating that a sustainable fishery for red abalone still exists in this area.

Laboratory transmission studies indicate that withering syndrome, first observed in black abalone populations, has tentatively been identified as a rickettsiales-like bacteria. Studies continue. Experiments are also being conducted on antibiotics that may be used to treat cultured abalone. DNA-based probes using polymerase chain-reaction technology are being developed to compare the 16S gene sequences of known rickettsiales organisms with organisms observed in symptomatic abalone.

White abalone (*Haliotis sorenseni*) was added to the candidate species list by NMFS. Pending a status review, further action may be initiated. Recent scuba diving and Delta submarine surveys indicate that current population densities are far too low for recovery. Recent densities were one abalone per hectare, compared with historic densities of about one abalone per square meter. Recovery of this abalone may require extensive human intervention.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1996–97 season totaled 1,809 t, a decrease of 5,052 t from the previous season, and well below the ten-year average of 4,226 t. These were the lowest landings in 22 years.

In northern California, the crab season opened on 1 December after a price settlement of $1.35 per pound. The low volume of crabs was followed by escalating prices, which reached $4.00 per pound by the end of the season. A fleet of 498 vessels landed approximately 995 t in northern California, including 383 t at Crescent City, 182 t at Trinidad, 357 t at Eureka, and 73 t at Fort Bragg.

San Francisco–area Dungeness crab fishing opened on 15 November, with fishers settling on a price of $1.75 per pound. Total crab landings decreased by only 80 t from the previous season, to 779 t. Crab fishers landed 249 t at Bodega Bay, and 530 t at ports in San Francisco Bay and Half Moon Bay. Monterey and Morro Bay contributed 35 t to the statewide landings.

The California legislature passed SB 144-Thompson which provides that no person shall take Dungeness crab for commercial purposes in the area from the Oregon border to the Mendocino-Sonoma county line (Districts 6, 7, 8, 9) for 30 days after the opening of Dungeness crab season if there has been a delay in the opening, and if the person has taken Dungeness crab from ocean waters outside of those specified districts before the opening of the season in Districts 6, 7, 8, or 9. The bill also provides that no person shall take Dungeness crab for commercial purposes in ocean waters off Washington, Oregon, or California for 30 days after the opening of the season off these states if both of the following have occurred: (1) the opening of the season has been delayed in Washington, Oregon, or California, and (2) the person has taken crab for commercial purposes in either of the two other states before the delayed opening in the ocean waters off any one of the three states. This "reciprocity" legislation was requested by the Tri-State Dungeness Crab Committee to prevent pulse fishing in association with season-opening delays during years when crabs are soft-shelled.

In MSFCMA of 1996, the U.S. Congress urged the PFMC to develop a fishery management plan for Dungeness crab. The PFMC reviewed an analysis of options for management of Dungeness crab, and heard a report from the Tri-State Dungeness Crab Committee (whose membership includes shellfish biologists and industry representatives from California, Oregon, and Washington). The committee recommended that the PFMC suggest language for the MSFCMA that amends the current interim authority given to California, Oregon, and Washington. Currently, the interim authority extends the states' management authority to the EEZ over season opening and closing dates, and size and sex restrictions, but excludes limited-entry programs. In addition, the proposed language would prevent harvesting and processing of Dungeness crab in the EEZ by a vessel without a permit issued by California, Oregon, or Washington. The PFMC unanimously passed this option in September 1997 in lieu of developing a fishery management plan. Congressional legislation was subsequently proposed for an amendment to the MSFCMA, because the current interim authority expires in October 1999.

SPOT AND RIDGEBACK PRAWN

Preliminary 1997 ridgeback prawn (*Sicyonia ingentis*) landings totaled 174 t. This represented a 37% drop in landings from the 275 t landed in 1996 (fig. 5). Ridgeback prawn are taken exclusively by trawl nets, and there is a closed season from 1 October through 31 May, when an incidental catch of 50 pounds is allowed. All of the 1997 landings were made in southern California ports, and over 95% of all ridgeback prawn were caught within the Santa Barbara Channel. The proportion of ridgeback prawn landed live has increased greatly since 1994. In 1997, the ex-vessel prices were $2.00 per pound for live prawn, and $1.30 per pound for dead prawn. The average ex-vessel price in 1997 increased to $1.80 per pound from $1.33 per pound in 1996; this increase resulted from the greater proportion of higher-priced live ridgeback prawn in the catch (66%, versus 44% in 1996).

Preliminary 1997 spot prawn (*Pandalus platyceros*) landings were 343 t, a 41% increase over the 244 t landed

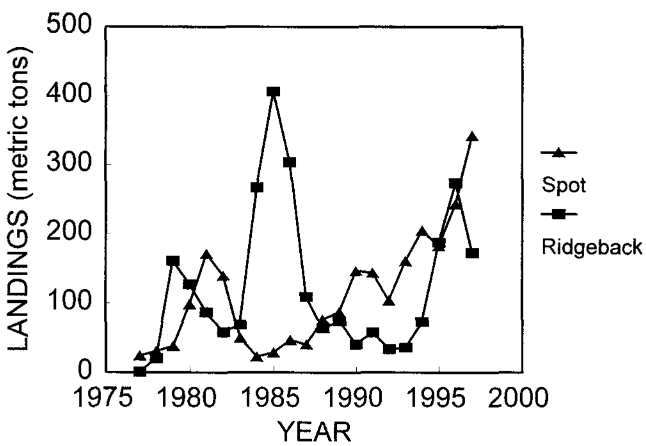

Figure 5. California spot and ridgeback prawn landings, 1977–97.

in 1996. Landings of spot prawn have followed a ten-year upward trend (fig. 5). Spot prawn are caught with both trap and trawl gear. In 1997, 143 vessels (68 trap and 75 trawl) made landings; table 8 shows types of gear and landings for spot prawn by port area. Over 45% of the combined trap and trawl spot prawn landings in 1997 were made in the Santa Barbara area. In the past, boats using trap gear dominated the fishery, but since the mid-1970s the number of boats using trawl gear has increased, and their landings now dominate. Approximately 257 t of spot prawn were harvested by trawl in 1997, while 86 t were taken with trap gear (table 8).

The larger spot prawn commanded a much higher ex-vessel price than the ridgeback, averaging $6.00 per pound. This represented a decrease of $0.77 from 1996. The decrease in average price was partly a result of the increased supply of spot prawn that, at times, exceeded market demand. Also, because 75% of the spot prawn landings were made with trawl gear, which tends to cause mortalities, a larger portion of the catch was landed dead and sold at a lower price. Live spot prawn had an average ex-vessel price of $7.50 per pound, whereas dead spot prawn averaged $4.50 per pound. Thirty-eight percent of trawled spot prawn were sold as dead product, while just 9% of trapped spot prawn were sold as dead product.

During 1997, the trap and trawl spot prawn permit fisheries in southern California (south of Point Arguello) operated under nonconcurrent closures; the trap closure between 15 January and 31 March, and the trawl closure between 1 November and 16 January. To provide more protection for gravid female spot prawn, regulations were enacted in 1997 that changed the southern California trap and trawl seasonal closures; they will run concurrently between 1 November and 31 January, beginning in 1998.

OCEAN SALMON

In 1997, the PFMC enacted restrictive commercial and recreational ocean salmon regulations in California to (1) protect endangered Sacramento River winter chinook (*Oncorhynchus tshawytscha*) and Snake River fall chinook; (2) ensure fall chinook spawner escapement goals for Klamath, Sacramento, and Oregon coastal rivers; and (3) protect depressed coho (*Oncorhynchus kisutch*) stocks coastwide. Among the regulations were reduced seasons and specific gear restrictions for the area between Horse Mountain and Point Conception. Under authority of the Endangered Species Act, NMFS required the PFMC to take specific action to reduce harvest impacts on the endangered Sacramento River winter chinook to increase spawning escapement by 31%.

In 1997, commercial fishing for ocean salmon (all species except coho) in California was allowed coastwide from 1 May to 30 September with various time and area closures. The minimum size limit was 26 inches total length (TL). Approximately 2,360 t (487,500 fish) of dressed chinook were landed by commercial trollers who fished approximately 18,700 days (fig. 6). Ex-vessel prices for dressed salmon averaged $1.38 per pound, and total ex-vessel value exceeded $7.2 million.

Recreational fishing regulations in California were less restrictive than in 1996, with various time and area

TABLE 8
1997 California Spot Prawn Landings (Metric Tons) by Port Area and Gear Types

	Number of fishing vessels by gear type		Spot prawn landings			
Port areas	Trap	Trawl	Trap	Trawl	Totals	Percentage of Total
Eureka	3	7	0.9	10.9	11.8	3.4
San Francisco	6	18	4.9	87.3	92.2	27.0
Monterey	6	10	19.3	14.9	34.2	10.0
Santa Barbara	10	37	18.5	141.5	160.0	46.6
Los Angeles	25	3	25.5	2.5	28.0	8.0
San Diego	18	0	16.9	0	16.9	5.0
Totals	68	75	86.0	257.1	343.1	100.0

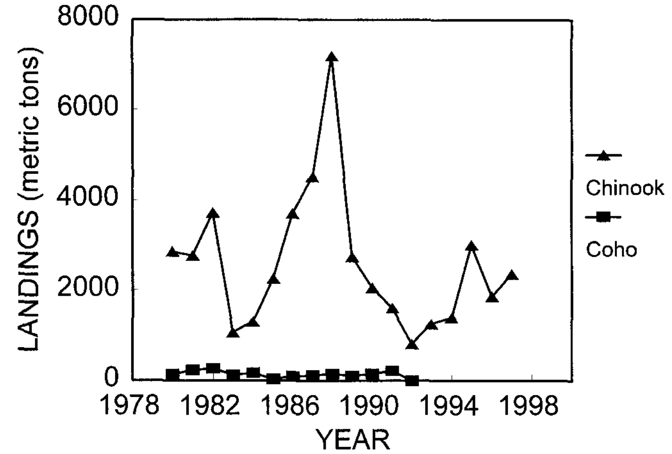

Figure 6. California commercial salmon landings, 1980–97.

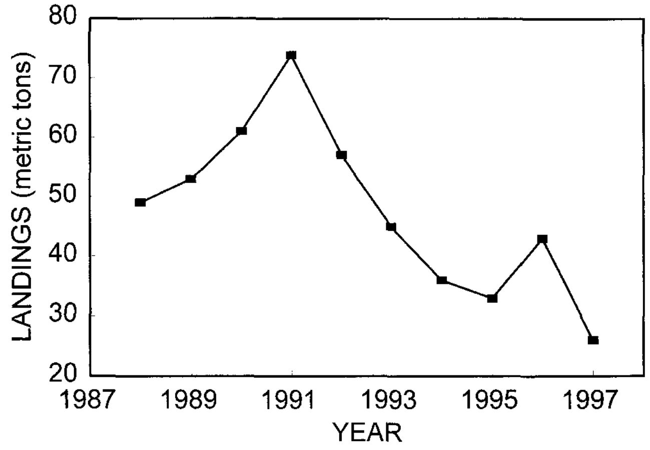

Figure 8. California commercial white seabass landings, 1988–97 (California and Mexican waters).

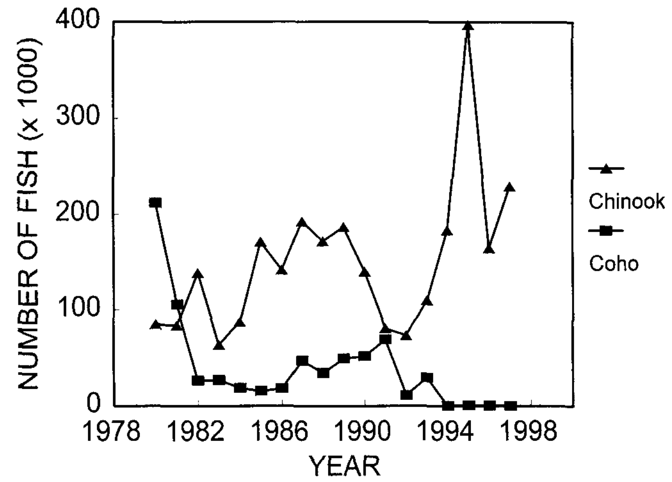

Figure 7. California recreational salmon landings, 1980–97.

closures (15 February–16 November). Statewide recreational landings increased by almost 40% compared to the previous year (fig. 7), totaling 228,900 chinook during 234,300 angler trips (catch per unit angler = 0.98). Anglers were limited to two salmon per day (all species except coho), with a minimum size limit of 24 inches TL, except from 1 July to 1 September between Point Reyes and Pigeon Point, where anglers were required to keep the first two salmon regardless of size. After 1 September, anglers fishing with bait between Horse Mountain and Point Conception were required to use circle hooks and 1 pound or less of weight.

In the Klamath Management Zone (KMZ: Horse Mountain, California, to Humbug Mountain, Oregon) season management, rather than quotas, continued, with fewer fishing days because of reduced abundance of Klamath fall chinook. In the KMZ, three separate seasons were enacted: 24 May–30 May, 17 June–6 July, and 12 August–14 September, open all days of the week. The bag limit was one salmon per day (all species except coho) with no more than four fish in seven consecutive days; a 20-inch TL limit existed north of Horse Mountain. In the California portion of the KMZ, anglers landed 9,000 chinook salmon during 19,000 trips made mostly on private skiffs.

WHITE SEABASS

The 1997 white seabass (*Atractoscion nobilis*) commercial catch was 26 t, with an ex-vessel value of $127,270. This was a 40% decrease from the 43 t landed in 1996 (fig. 8). While most of the commercial catch was taken from southern California waters, 5 t came from fishing areas off San Francisco, Monterey, and Morro Bay. Early in the century, the center of the commercial fishery was off San Francisco, but by the mid-1910s the fishery had shifted to south of Point Conception. The 1997 take of white seabass in central and northern California waters probably reflected the strong El Niño event that resulted in elevated sea-surface temperatures along much of California's coast. White seabass is considered a stenothermal species that prefers warmer water, and is generally most abundant south of Point Conception. The ten-year average take by commercial vessels is 48 t. Set and drift gill nets were the reported method of take for 84% of the catch in 1997, while hook and line gear took 12%. Trawl, seine, and miscellaneous gears took the remainder of the catch. Commercial regulations prohibited take of white seabass in California waters south of Point Conception between 15 March and 15 June. In 1997, 72% of the commercial landings were between 16 June and the end of August. The average ex-vessel value was $2.27 per pound.

Recreational landings reported on commercial passenger fishing vessel (CPFV) logs increased to 2,017 fish in 1997, compared with 1,452 fish in 1996 (fig. 9). Most of the fish were caught in southern California. The ten-

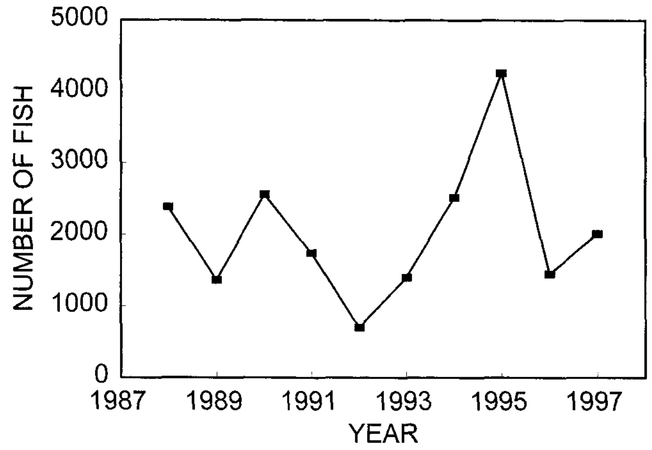

Figure 9. Landings of white seabass by California CPFVs, 1988–97 (California and Mexican waters).

year average number of white seabass taken by CPFVs is 2,057.

The Ocean Resources Enhancement and Hatchery Program, created in 1983 as part of a long-term program to determine if hatchery-produced fish can augment wild stocks, produces juvenile white seabass that are released into the ocean. The fish are raised to approximately three inches at the hatchery, injected with a coded-wire tag, then transported to grow-out pens along the coast. Volunteers then raise the fish to approximately nine inches. At that size, 10% receive an external anchor tag, and all the fish are released either at the pen site or nearby. In 1997, 57,800 hatchery-produced fish were released at eleven coastal sites. Information from tag returns is used to determine habitat preference for the juvenile fish.

RECREATIONAL FISHERY

Southern California

In southern California, saltwater recreational fishing with hook and line gear is conducted from private vessels, piers, shorelines, and CPFVs. Specific information about many of these recreational fisheries is difficult to collect. However, CDFG maintains a large database gathered from mandatory logbook information supplied by CPFVs. Much of our knowledge of recreational fishing in southern California is based on these data. Landings by CPFVs represent approximately 40% of the total landings by recreational fishers.

Traditionally, the taxa targeted by CPFVs in southern California and Baja California waters include Pacific barracuda (*Sphyraena argentea*); serranids, or sea basses (*Paralabrax clathratus, P. nebulifer*); scorpaenids, or scorpionfishes (*Scorpaena guttata, Sebastes* spp.); scombrids, or mackerels, tunas, and wahoo (*Acanthocybium solandri, Katsuwonus pelamis, Sarda chiliensis, Scomber japonicus, Thunnus alalunga, T. albacares*); California halibut (*Paralichthys californicus*); ocean whitefish (*Caulolatilus princeps*); white seabass (*Atractoscion nobilis*); yellowtail (*Seriola lalandi*); halfmoon (*Medialuna californiensis*); and California sheephead (*Semicossyphus pulcher*). The taxa being targeted can vary with season, and also by year. Occasionally, El Niño conditions greatly increase the southern California availability of species normally found off Mexico; 1997 was such a year. Typically, CPFVs are quick to exploit these opportunities to catch subtropical species.

In 1997, 630,669 anglers aboard CPFVs landed 2,883,462 fishes south of Point Conception (table 9). The number of reporting CPFVs was 238. The number of fishes landed represented 75% of the total landings by CPFVs statewide (3,855,900 individuals). The number of fishes landed statewide was 17% greater than in 1996; landings in southern California increased by 13%. Angler participation in southern California rose by 28% over 1996, and represented 79% of angler participation statewide.

As in 1996, 1997 landings of barred sand bass in southern California exceeded those of all other species (table 9). However, the number of individuals landed decreased by 19% from the previous year. Next in rank was yellowtail, which showed a sixfold rise in landings over 1996. This remarkable increase was related to the 1997–98 El Niño event, which produced a great year for southern California anglers who love to fish for *Seriola lalandi*. Among the other species with increased landings, none was more spectacular than albacore, which rose 133-fold over 1996. Additional species with notably elevated landings included Pacific barracuda, Pacific bonito, yellowfin tuna, dolphinfish, skipjack tuna, bluefin tuna, California halibut, blacksmith, and white seabass. Several of these increases were associated with the warm waters of El Niño. The species with the largest decrease in landings was white croaker (−64%), which dropped in rank from twelfth in 1996 to seventeenth.

Northern California

Traditionally, CPFV anglers along the California coast north of Point Conception target rockfishes (*Sebastes* spp.); salmon (*Oncorhynchus* spp.); lingcod (*Ophiodon elongatus*); and, opportunistically, albacore (*Thunnus alalunga*). Cabezon (*Scorpaenichthys marmoratus*) and other nearshore species are also taken. California halibut (*Paralichthys californicus*); striped bass (*Morone saxatilus*); sturgeon (*Acipenser* spp.); and leopard shark (*Triakis semifasciata*) are primarily taken from San Francisco Bay. In 1997, warm oceanic water related to the El Niño event provided some unusual fishing opportunities.

In 1997, 164,356 anglers caught 972,438 fishes, a 31% increase in landings over 1996 (table 10). This increase was primarily due to increased landings of the top five

TABLE 9
Southern California CPFV Landings (Number of Fishes) in 1997 and 1996

	1997 landings*		1996 landings		Percent change
Species/species group	Number	Rank	Number	Rank	
Barred sand bass	489,422	1	604,132	1	−19
Yellowtail	398,248	2	66,763	10	+497
Rockfishes, unspecified	397,094	3	455,040	2	−13
Kelp bass	335,043	4	282,673	4	+19
Pacific barracuda	334,552	5	271,856	5	+23
Pacific (chub) mackerel	224,694	6	329,146	3	−32
California scorpionfish	141,312	7	119,492	6	+18
Pacific bonito	102,423	8	72,664	8	+41
Yellowfin tuna	89,016	9	72,449	9	+23
Ocean whitefish	87,367	10	108,282	7	−19
Albacore	71,503	11	536	—	+13,240
Halfmoon	51,082	12	43,555	11	+17
Dolphinfish (dolphin)	28,606	13	21,939	14	+30
California sheephead	25,772	14	23,450	13	+10
Skipjack tuna	19,156	15	6,356	17	+201
Flatfishes, unspecified	9,602	16	11,052	15	−13
White croaker	9,332	17	25,654	12	−64
Bluefin tuna	7,959	18	2,477	22	+221
California halibut	7,878	19	5,829	18	+35
Blacksmith	7,245	20	4,926	20	+47
Lingcod	6,444	21	6,970	16	−8
Jack mackerel	5,481	22	5,403	19	+1
Wahoo	3,844	23	3,680	21	+4
White seabass	2,010	24	1,448	24	+39
Cabezon	1,468	25	1,501	23	−2
All others	26,909	—	9,635	—	—
Total number of fishes	2,883,462		2,556,372		+13
Number of anglers	630,669		494,091		+28
Reporting CPFVs	238		208		+14

* Preliminary

TABLE 10
Central and Northern California CPFV Landings (Number of Fishes) in 1997 and 1996

	1997 landings*		1996 landings		Percent change
Species/species group	Number	Rank	Number	Rank	
Rockfishes, unspecified	769,598	1	621,070	1	+24
Chinook (king) salmon	110,338	2	60,650	2	+82
Lingcod	30,624	3	22,764	3	+35
Albacore	16,538	4	1,337	9	+1,137
Pacific mackerel	16,253	5	6,094	6	+167
California halibut	7,966	6	13,263	4	−40
Striped bass	6,926	7	6,096	5	+14
Jack mackerel	3,642	8	1,226	10	+197
Flatfishes, unspecified	3,616	9	2,285	7	+58
Cabezon	1,664	10	1,502	8	+11
White croaker	562	11	669	11	−16
Shark, unspecified	439	12	363	12	+21
Sturgeon, unspecified	429	13	308	13	+39
Leopard shark	285	14	179	14	+59
Ocean whitefish	146	15	88	15	+66
Pacific barracuda	105	16	3	18	+3,400
California sheephead	16	17	5	16	+220
Bluefin tuna	15	18	1	—	+1,400
White seabass	7	19	4	17	+75
Skipjack tuna	5	20	0	—	—
Blue shark	3	21	4	17	−25
Dungeness crab	7,148	—	—	—	—
Rock crab	3,939	—	—	—	—
Jumbo squid	686	—	—	—	—
All others	3,261	—	651	—	+401
Total number of finfishes	972,438		738,563		+32
Number of anglers	164,356		138,145		+19
Reporting CPFVs	129		121		+7

* Preliminary

species or species groups. The largest increases in landings among the top ten species or species groups were albacore; Pacific (chub) mackerel (*Scomber japonicus*); chinook (king) salmon (*Oncorhynchus tshawytscha*); and jack mackerel (*Trachurus symmetricus*). Changes in annual landings may reflect shifts in effort among preferred species, or changes in species availability, such as with albacore, Pacific mackerel, and jack mackerel (rather than actual changes in abundance). As in 1996, recreational anglers were not allowed to take coho (silver) salmon (*Oncorhynchus kisutch*).

Warm oceanic water near the coast was responsible for high albacore landings (1,137% over 1996), which increased dramatically from the low levels observed since 1986. Some albacore were taken within 5 miles of shore, but most were caught between 15 and 40 miles offshore. Other species associated with the unusually warm water were Pacific bonito (*Sarda chiliensis*); bigeye tuna (*Thunnus obesus*); bluefin tuna (*Thunnus thynnus*); skipjack tuna (*Katsuwonus pelamis*); jumbo squid (*Dosidicus gigas*); and Pacific mackerel.

Significant landings of crab and squid were reported in 1997. CPFVs caught 11,087 Dungeness (*Cancer magister*) and rock (*Cancer antennarius*) crabs in conjunction with fishing for rockfishes, mainly from the ports of Bodega Bay (76% of landings) and Trinidad (19%). In 1993, CPFVs (primarily from the Bodega Bay area) began running "crab combo" trips on which crab traps were set prior to fishing for rockfishes and lingcod, then pulled at the completion of fishing for the day. Bodega Bay CPFVs targeted giant squid when they became abundant late in the year; 686 were caught.

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THE STATE OF THE CALIFORNIA CURRENT, 1997–1998: TRANSITION TO EL NIÑO CONDITIONS

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ABSTRACT

This report, part of a continuing series of annual reports describing oceanographic conditions in the coastal waters of the Californias, emphasizes the 1997–98 period. The coastal waters of the Californias were strongly influenced by El Niño conditions beginning late in the summer of 1997 and continuing into the summer of 1998. Timely prediction of the onset of this event made it possible for several research programs to augment their observation programs. We review the pattern of atmospheric forcing and changes in the tropical ocean and note the initial impacts upon the California Current system. Sampling being done by the CalCOFI (California Cooperative Oceanic Fisheries Investigations) program is described, and recent data are summarized and interpreted. Data from several other programs including oceanographic sampling off Baja California and central California, and coastal data from buoys, shore stations, and diving programs in kelp forests are reported. There were large and rapid changes in atmospheric forcing and in the upper ocean temperature and salinity distribution and circulation pattern. The pelagic ecosystem was strongly influenced; cruise mean macrozooplankton abundance during the spring of 1998 was the lowest in the 50-year CalCOFI time series. Large changes in the range and abundance of plankton and fish populations were observed. El Niño–induced changes must also be considered in the context of changes on other space-time scales, and the relation of El Niño–related changes and secular trends seen since the mid-1970s regime shift will merit particular attention.

INTRODUCTION

This is the fifth in an annual series of reports (Hayward et al. 1994, 1995, 1996; Schwing et al. 1997) that describe and interpret oceanographic and related environmental data from the coastal region off the Californias. Physical data series are updated and intercompared to explain the prevailing forcing, and biological series and their anomalies are examined in relation to the physical structure. Our intent is to describe observational programs in the region and to provide a preliminary summary and interpretation of their results. The emphasis is on CalCOFI. We have, however, included information from several other programs in order to place the CalCOFI observations in a larger regional context and to provide a brief summary of other programs and a point of contact for additional information about them. The list of additional programs is by no means complete.

In an effort to consider the most timely information that is available, we have included preliminary data in this report; some values may change as the final steps of data processing are completed. We have also had to balance our goals of interpreting and summarizing observations for a timely report with the need to use preliminary data and the brief lead time for their analyses.

We have chosen to include some more speculative interpretation of the most recent data while recognizing that subsequent reevaluation may lead to revision of some of the ideas.

We start by examining the large-scale atmospheric and oceanic conditions that force much of the variability in the California Current. Last year's report (Schwing et al. 1997) described the initial development of strong El Niño conditions in the eastern tropical Pacific Ocean during the first five months of 1997 while in the same period the California Current system was affected by regional forcing. El Niño conditions became the dominant forcing process in the latter months of 1997. This report continues the description of the tropical El Niño and its subsequent effect on the California Current region. However, events on other space-time scales also strongly influence this system, and the effects of El Niño must be considered in the context of longer-term trends, particularly the secular trends of warming of the upper layers and decline in macrozooplankton biomass that have been evident since the mid-1970s regime shift (Roemmich and McGowan 1995). Our emphasis is upon oceanographic conditions and pelagic ecosystem structure, but trends in coastal kelp forest communities and pelagic seabirds are also described. A few fisheries issues are considered as well.

DATA SETS AND METHODS

Coastal data include temperature and salinity at shore stations (Walker et al. 1994). La Jolla (SIO Pier) and Pacific Grove daily temperatures and their anomalies from the long-term harmonic mean (1916–93 for La Jolla and 1919–93 for Pacific Grove) are shown as time series. Coastal sea-level data from San Diego and San Francisco are shown as monthly anomalies from the 1975–95 mean, corrected for atmospheric pressure. Monthly upwelling indices and their anomalies, relative to 1948–67, for the western North American coast are presented. From six representative buoys throughout the California Current region, time series of the daily alongshore wind component and sea-surface temperature (SST; data courtesy NOAA National Data Buoy Center) are plotted against the harmonic mean of each record; the location and base period of each buoy is given in table 1, and the position of all but the most northern one is plotted in figure 1.

Data from quarterly CalCOFI surveys in 1997 and 1998 are described. The CalCOFI monitoring program started in 1949. The present program consists of quarterly (normally January, April, July, October) cruises that occupy a grid of 66 stations off southern California (fig. 1). The core time-series data set now collected at each station includes a CTD/rosette cast with sensors for pressure, temperature, salinity, dissolved oxygen, photosynthetically active radiation, fluorescence, and transmissivity. Water samples are collected at 20–24 depths in

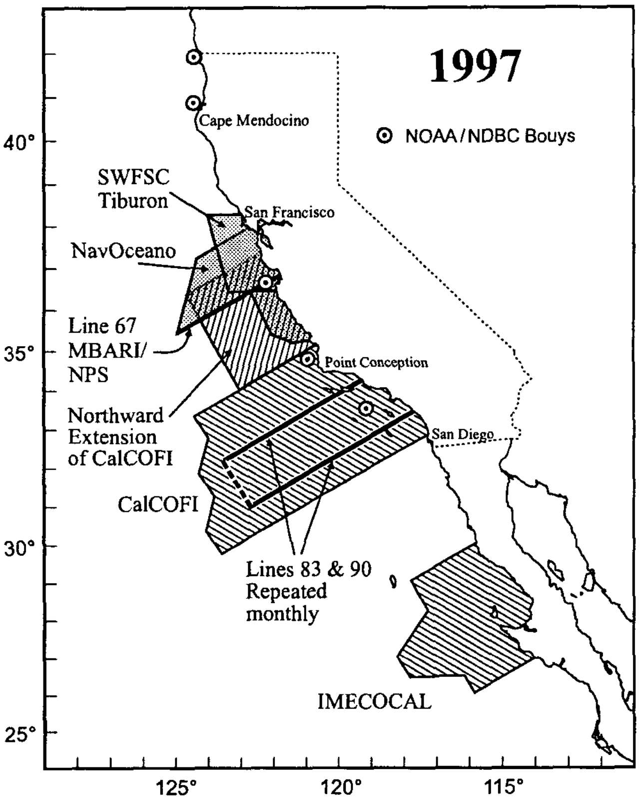


Figure 1. Positions and depiction of coverage for various sampling programs described in this report.

TABLE 1
Locations of SST and Alongshore Wind Time Series

Buoy	Name	Position	Base Period[a]	Alongshore angle[b]
46050	Stonewall Bank, Ore.	44.6°N 124.5°W	1991–98	0
46027	St. George, Calif.	41.8°N 124.4°W	1983–97	341
46022	Eel River, Calif.	40.8°N 124.5°W	1982–98	354
46042	Monterey Bay, Calif.	36.7°N 122.4°W	1987–97	328
46011	Santa Maria, Calif.	34.9°N 120.9°W	1980–98	326
46025	Catalina Ridge, Calif.	33.7°N 119.1°W	1982–98	294

[a] Period of harmonic mean.
[b] Determined from principal-component analysis.

the upper 500 m to determine salinity, dissolved oxygen, nutrients (NO_3, NO_2, PO_4, SiO_3), phytoplankton pigments (chlorophyll a and phaeophytin), and primary production (^{14}C uptake at one station per day). Oblique and surface (neuston) net tows (0.505 mm mesh) are taken at each station. Acoustic Doppler current profiler (ADCP) data are also recorded continuously, providing a measure of upper ocean currents as well as an estimate of zooplankton biomass based upon acoustic backscatter. Continuous near-surface measurements of temperature, salinity, and chlorophyll fluorescence are made from water pumped through the ship. In a separate pumping system, water from approximately 3 m depth is continuously filtered for fish eggs and larvae. Cruise 9604 was the first CalCOFI cruise on which this continuous underway fish egg sampler (CUFES) was used (Checkley et al. 1997). The CUFES has now become a standard CalCOFI sampling device. The most recent data presented here are preliminary, and some changes may be made after the final processing and quality control checks. More details on the methods, information about recent activities, and CalCOFI hydrographic data can be accessed via the World Wide Web (*http://www-mlrg.ucsd.edu/calcofi.html*).

Observations in regions off central California were made by various research groups including CalCOFI, the Monterey Bay Aquarium Research Institute (MBARI), the Naval Oceanographic Office (NAVOCEANO), the Naval Postgraduate School (NPS), the Southwest Fisheries Science Center (SWFSC) at Tiburon, and SWFSC at La Jolla (fig. 1) and are discussed below. A new monitoring program off Baja California by Mexican scientists, Investigaciones Mexicanas de la Corriente de California (IMECOCAL), coordinated by CISESE and UABC (see CalCOFI Committee Report, this issue), was initiated in 1997 and is also described in this report.

OBSERVATIONS

Large-Scale Oceanic and Atmospheric Climate Patterns

During 1997–98, a number of remarkable anomalies occurred in the large-scale distribution of atmospheric and oceanic patterns in the eastern North Pacific. Many of these represented the lingering effects of the 1995–97 La Niña (Schwing et al. 1997), while others were connected to the 1997–98 El Niño in the equatorial Pacific. In the early stages of the El Niño event (March–September 1997) the direct impacts of the event on the extratropical North Pacific appear to have been small. There is some evidence that during this period the extratropical North Pacific anomalies contributed to the development of El Niño anomalies in the equatorial Pacific. During the later stages of the event (November 1997–April 1998) there were major effects from the tropical Pacific on the extratropical North Pacific.

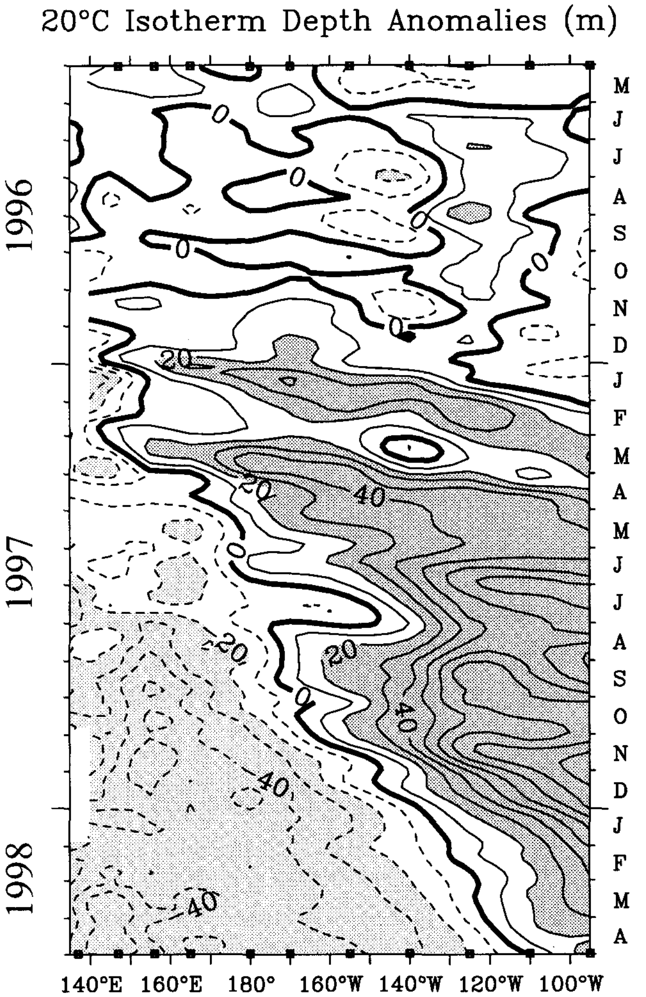


Figure 2. Depth of the 20°C isotherm between 2°N–2°S for May 1996–April 1998. Analysis based on the five-day averages of moored time-series data from the TAO array. Shading denotes isotherm depths more than 20 m deeper than the monthly climatology. The eastward-propagating deep and shallow anomalies indicate the passage of Kelvin waves across the equatorial Pacific (e.g., during December 1996–July 1997). The gradual eastward extension of the shallow anomaly from the western equatorial Pacific during July 1997–April 1998 shows the eastward extension of anomalously cool subsurface water. Adapted from NCEP (1998b).

During December 1996 and into the early months of 1997 the relaxation and reversal of westward winds in the western equatorial Pacific helped to initiate El Niño. Observations of equatorial subsurface temperatures reveal the propagation of a series of ocean Kelvin waves from the western equatorial Pacific to the South American coast during the first half of 1997 (fig. 2). During April–June 1997 El Niño grew very rapidly and reached an intensity rarely seen (fig. 3). By May, intensive and extensive anomalous warming had developed in the eastern equatorial Pacific, as evidenced by the sea-surface temperature anomalies (SSTAs; fig. 4b).

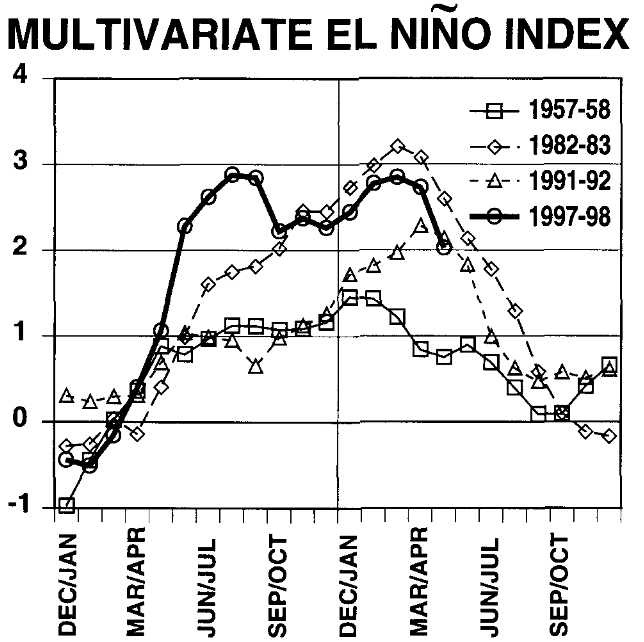


Figure 3. A multivariate El Niño index indicating the intensity of the 1997–1998 event relative to four strong historical El Niño events. Adapted from Wolter and Timlin (in press).

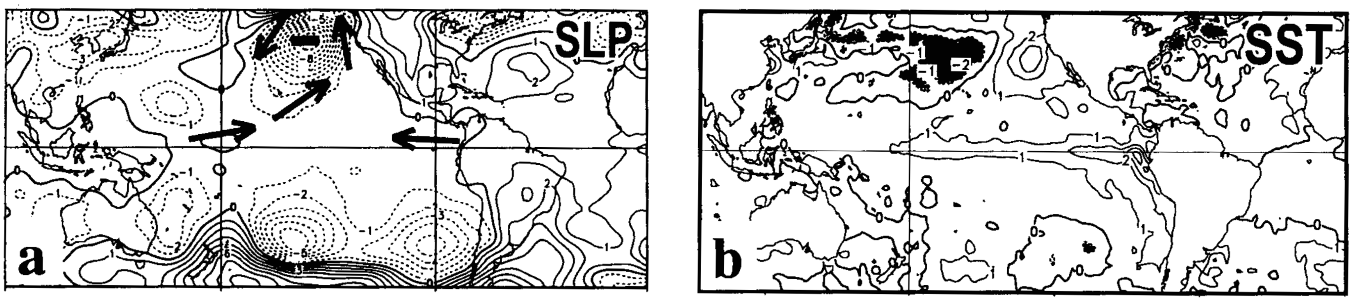
A basic pattern of above-average SST in a broad region off the North American coast and below average SSTs in the central North Pacific existed well before the initiation of El Niño and continued through the early months of 1997 (Schwing et al. 1997). In May 1997 there was a sharp intensification of SSTAs off the North American west coast coincident with the warming in the eastern equatorial Pacific (figs. 3 and 4b). However, the anomalous warming in the eastern North Pacific in spring–summer 1997 appears to have been primarily due to regional wind anomalies and not caused by equatorial Pacific El Niño processes. During April–June 1997, anomalously low sea-level pressure (SLP) in the eastern North Pacific led to a weak North Pacific High (NPH) and weak southwestward trade winds out of the NPH. For much of this period, the usual southward winds along the west coast were exceptionally weak, or even northeastward out of the subtropics. The positive SSTAs strengthened in a roughly triangular region of the northeast Pacific extending between Cabo San Lucas, Hawaii, and Vancouver Island (fig. 4b). This strengthening appears, to a large extent, to have been a response to anomalous surface Ekman transports resulting from the northeastward wind anomalies (fig. 4a; cf. Schwing et al. 1997). Atmospheric teleconnections from the equatorial Pacific to the North Pacific produce most of the significant effects of El Niño events, but these teleconnections are generally very weak in the northern summer and most pronounced during the northern winter. Thus, despite strong El Niño conditions in the equatorial Pacific during April–September 1997, the event appears to have had little direct effect via atmospheric teleconnections on the North Pacific at this time. Instead, the NPH and trade winds may have contributed to the intensification of the equatorial El Niño conditions, especially during April–June 1997 (figs. 3 and 4a, b).

During much of July–September 1997, anomalous atmospheric wave trains emanating from east Asia helped maintain weak SLPs in the eastern North Pacific and weak trade winds into the equatorial Pacific. The SLP anomaly (SLPA) pattern for August 1997 (fig. 4c) shows an example of the influence of this wave-train activity. The alternating positive and negative centers that gently arced across the North Pacific were part of a tropospheric wave train emanating from a region of intense tropical cyclone activity in east Asia (cf. Nitta 1987). This summer teleconnection pattern appears to have helped create anomalous surface Ekman transports and SSTAs across the North Pacific, including strongly positive SSTAs in the triangular region described earlier and along much of the West Coast (fig. 4d). July–September 1997 was also a period of large positive SSTAs in the central equatorial Pacific, and a period in which El Niño reached an initial peak in its intensity (fig. 3).

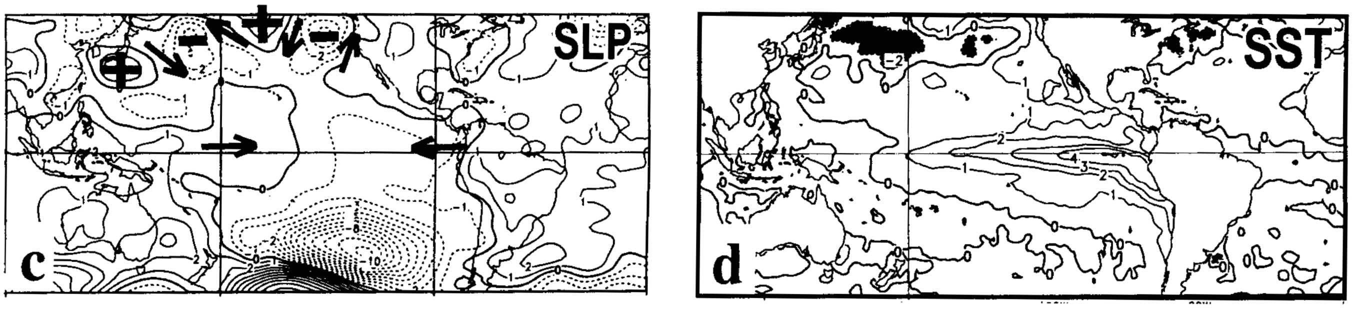
During November 1997–April 1998, the El Niño event reached a second peak in intensity (fig. 3), and the first clear effects on the North Pacific Ocean appeared. These effects were primarily the result of an atmospheric wave train that emanated from the central equatorial Pacific and produced a pattern similar to the Pacific–North American anomaly (cf. Murphree and Reynolds 1995). During much of this period, a similar but oppositely phased wave train emanated from near Indonesia and reinforced the first wave train over the northeast Pacific. Some of the clearest El Niño effects occurred during February 1998, when much of the northeast Pacific was dominated by a strong negative SLPA and strong wind anomalies out of the west-northwest (fig. 4e). The SSTAs in the central and eastern North Pacific were negative, while positive SSTAs were confined to a relatively narrow band next to the West Coast (fig. 4f). December 1997–February 1998 was a period of exceptionally intense winter storm activity along the West Coast, especially during February. These storms and their heavy precipitation represented the anomalous intensification and southward shift of the North Pacific jet stream caused by the impacts of El Niño on the upper tropospheric circulation.

From March through May 1998, El Niño conditions in the equatorial Pacific weakened considerably, with negative SSTAs developing in the central equatorial Pacific during May (NCEP 1998b). During this period, anomalously cool subsurface (50–300 m) temperatures extended along the equator from the western Pacific well into the eastern Pacific. This pattern resulted from the

May 1997 Anomalies



August 1997 Anomalies



February 1998 Anomalies

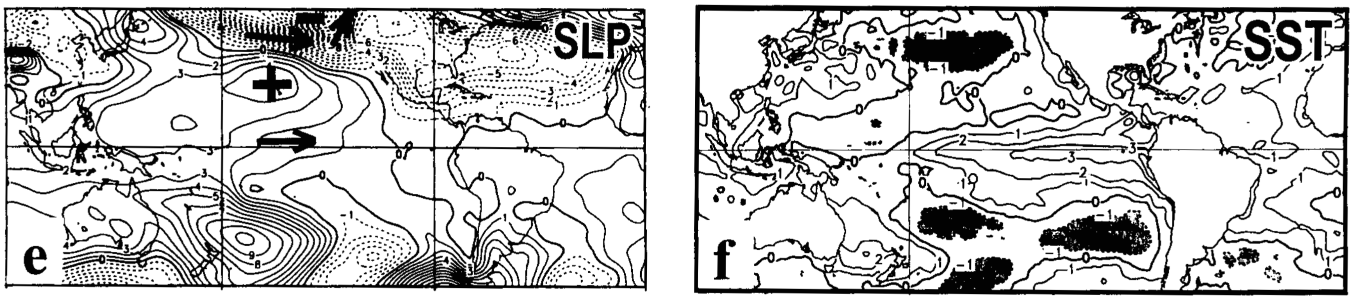


Figure 4. Sea-level pressure anomalies (SLPAs) with idealized surface wind anomalies, and sea-surface temperature anomalies (SSTAs) over the Pacific Ocean: *a*, SLPAs, May 1997; *b*, SSTAs, May 1997; *c*, SLPAs, August 1997; *d*, SSTAs, August 1997; *e*, SLPAs, February 1998; *f*, SSTAs, February 1998. Anomalies are departures of monthly-averaged fields from the 1979–95 base-period mean fields. Positive anomalies denote higher than average atmospheric pressure and warmer than average SST. Contour intervals are 1 mb for SLPA and 1°C for SSTA. The arrows indicate the direction and strength of the wind anomalies. Anomalous surface winds are approximately parallel with SLPA contours, and cyclonic (counterclockwise in Northern Hemisphere) around negative anomalies. Closer-spaced SLPA contours indicate faster anomalous winds. Adapted from NCEP (1997a, b, 1998a).

eastward expansion of a cool subsurface anomaly from the western Pacific beginning in July 1997 (fig. 3). This suggested a clear transition toward La Niña conditions, which several long-lead forecasts have predicted for late 1998 (COLA 1998). However, the equatorial Pacific trade winds were weak during March–May 1998, and some forecasts have predicted weak El Niño conditions extending into early 1999 (COLA 1998).

Coastal Conditions

The monthly upwelling indices (Bakun 1973; Schwing et al. 1996) along the U.S. West Coast during 1997 showed no remarkable long-term displacement from the annual signal (fig. 5). Indices were higher than normal (more upwelling) along southern California in early 1997 and along northern California in summer 1997. Extremely negative (downwelling-favorable) indices af-

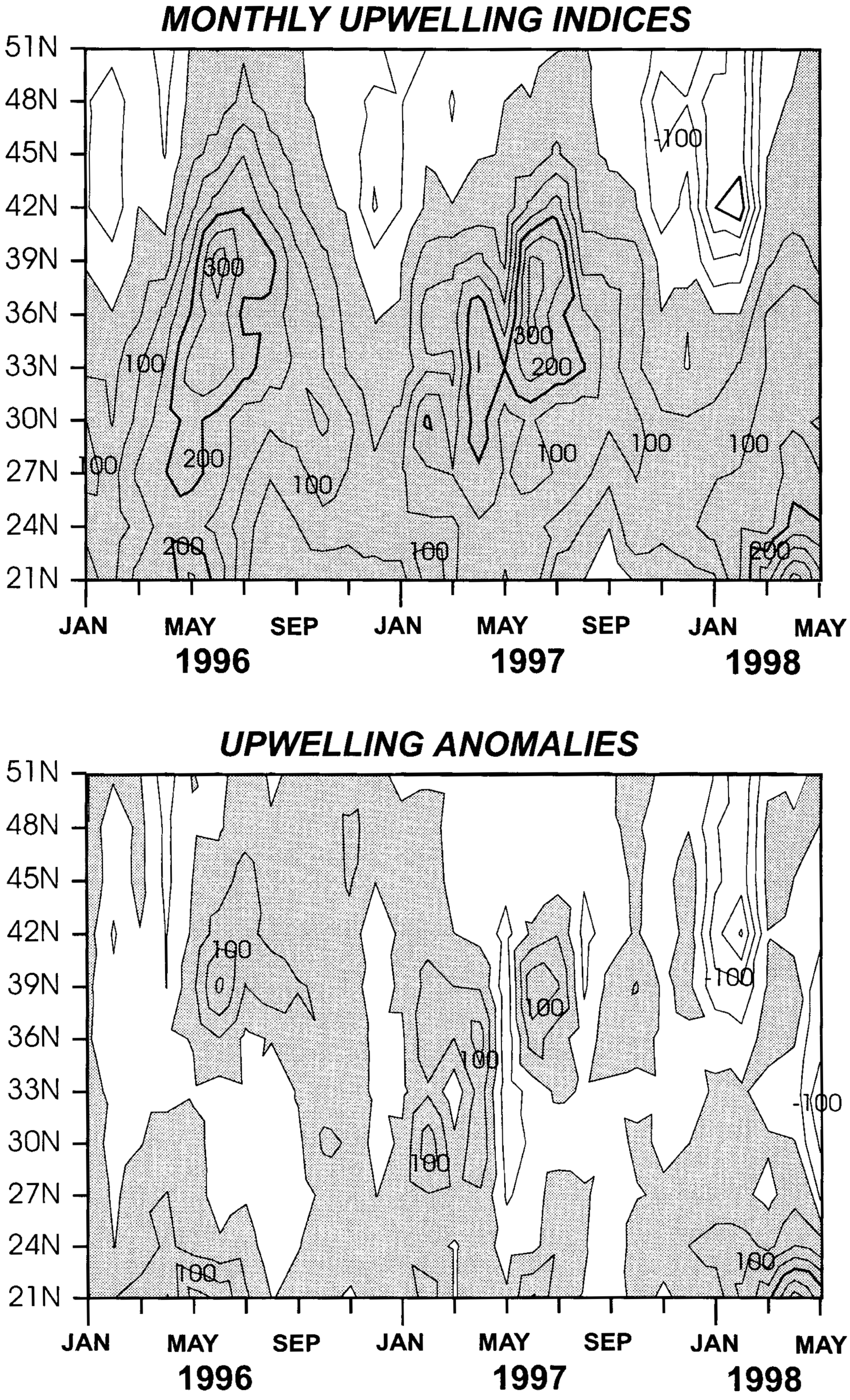


Figure 5. Monthly upwelling index and upwelling index anomaly during 1996–98. Positive values imply coastal upwelling. Shaded areas denote positive (upwelling-favorable) values in upper panel, and positive anomalies (generally greater than normal upwelling) in lower panel. Anomalies are relative to 1948–67 monthly means. Units are in $m^3 sec^{-1}$ per 100 km of coastline.

fected the Washington, Oregon, and northern California coast in early 1998. Unusually weak upwelling developed in April–May 1998 off California and northern Baja California, similar to (but much greater than) the previous May. Southern Baja California experienced abnormally high upwelling during the first part of 1998. Since mid-1997, much of the West Coast has featured a three-month fluctuation in the upwelling anomaly (e.g., minima in May, August, November 1997, and February and May 1998). These fluctuations correspond to a cyclical pattern in the North Pacific High and associated buoy winds across much of the midlatitude and subtropical North Pacific. Conditions in 1996 were detailed in last year's report (Schwing et al. 1997).

NDBC buoy winds at selected available locations along the U.S. West Coast (fig. 6) display the short-term variability associated with synoptic atmospheric events, superimposed on the annual climatological cycle of strong southward winds in summer and northward or weak southward winds in winter. Wind vectors align strongly with the local coastline. Because of budget shortfalls, maintenance to the buoy network has been limited for the past few years, leading to very spotty data returns. Much of the 1996–97 winter featured generally greater than normal northward buoy winds (more downwelling-favorable), but February–March 1997 was a time of stronger than normal southward coastal winds. The following fall and winter (1997–98) exhibited numerous episodes of strong northward winds. This pattern is particularly evident off northern California, and coincides with very heavy winter storm activity and copious precipitation for much of the West Coast. Winds were very strong and oscillated in direction even in the Southern California Bight, where winds are normally relatively weak and variable. The upwelling index anomalies (fig. 5) correspond well with the tendencies of the buoy alongshore winds, with both indicating greater than normal upwelling in early 1997 and spring 1998, and anomalous downwelling in May and August 1997 and early 1998.

After several months of slightly cooler than normal surface conditions, SSTs at the West Coast buoys climbed rapidly beginning in the spring of 1997 (fig. 7). Two periods of particularly intense warming occurred in May and August 1997. These warming events coincided with times of weaker than usual southward buoy winds and negative upwelling anomalies. The absolute SST and its anomaly relative to the climatology peaked in early fall 1997, and remained well above normal through spring 1998. Since mid-1997, coastal SSTs have been 2°–3°C above average, and anomalies as much as +6°C were found in late summer. Since the buoy climatologies extend only to the early 1980s (table 1), the magnitude of the anomalies cannot be compared to those of the coastal shore stations because shore station base periods are much longer and the secular trend of warming has been well documented (Roemmich and McGowan 1995). The same caveats about base periods to determine "normal conditions" also apply to comparisons with the hydrographic data.

The temperature data from the coastal shore station at Pacific Grove (fig. 8) showed that SST fluctuated about its long-term mean from early 1997 through July, and conditions were anomalously warm from August 1997 to March 1998, except for a cold event in November 1997. In contrast to Pacific Grove, the shore station at La Jolla registered larger and more consistent positive SST anomalies. In the early months of 1997 the SST anomaly increased, to more than +4°C in May (fig. 8). From September 1997 through mid-March 1998 the SST anomaly was consistently in the range of +2° to +4°C.

Coastal sea level at San Francisco and San Diego showed similar fluctuations. There was a sharp rise in sea level at San Francisco in December 1996 and January 1997, which may have been partly caused by large inputs of fresh water from river runoff (fig. 9). After a drop to below-normal values, sea level began to rise in March 1997, generally increasing through February 1998. The largest anomalies occurred after September 1997. At San Diego sea level generally increased throughout 1997, starting from small negative anomalies and ending the year at high positive anomalies. In 1998 sea-level anomalies at San Diego declined in both January and February. A speculative interpretation is that the rise at San Diego after July and the rises at both stations after September are caused by strong increases in geostrophic adjustment to an unusually strong poleward coastal countercurrent/undercurrent, the oceanic response (coastally trapped Kelvin waves) to El Niño.

CalCOFI Survey Cruises

9704 (2–20 April 1997). The preliminary data from this cruise, included in last year's report (Schwing et al. 1997), used the 100 m temperature field as an estimate of the circulation pattern. The map of dynamic height (fig. 10), which gives the geostrophic flow pattern, differs from the earlier estimate only in the region very near the coast. Within the Southern California Bight the flow is generally weak with mixed direction. The main flow of the California Current has a very sharp meander that brought the relatively warm low-salinity core of the California Current close to Point Conception. There is a strong offshore sweep to the current core south of Point Conception, and the low-salinity jet which forms the core of the California Current is unusually far offshore in the southern part of the sample grid. (The long-term mean circulation patterns for the time periods coinciding with

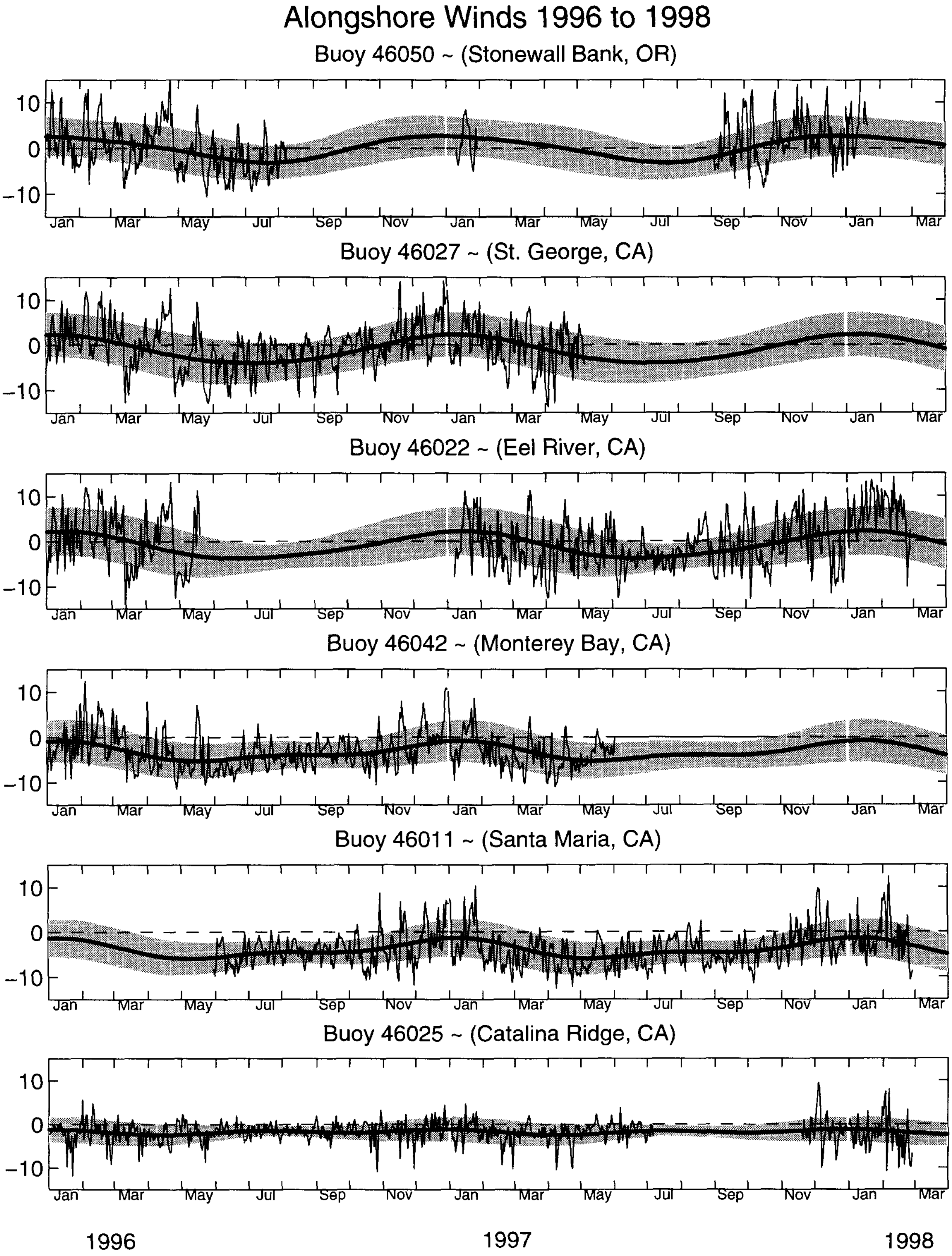
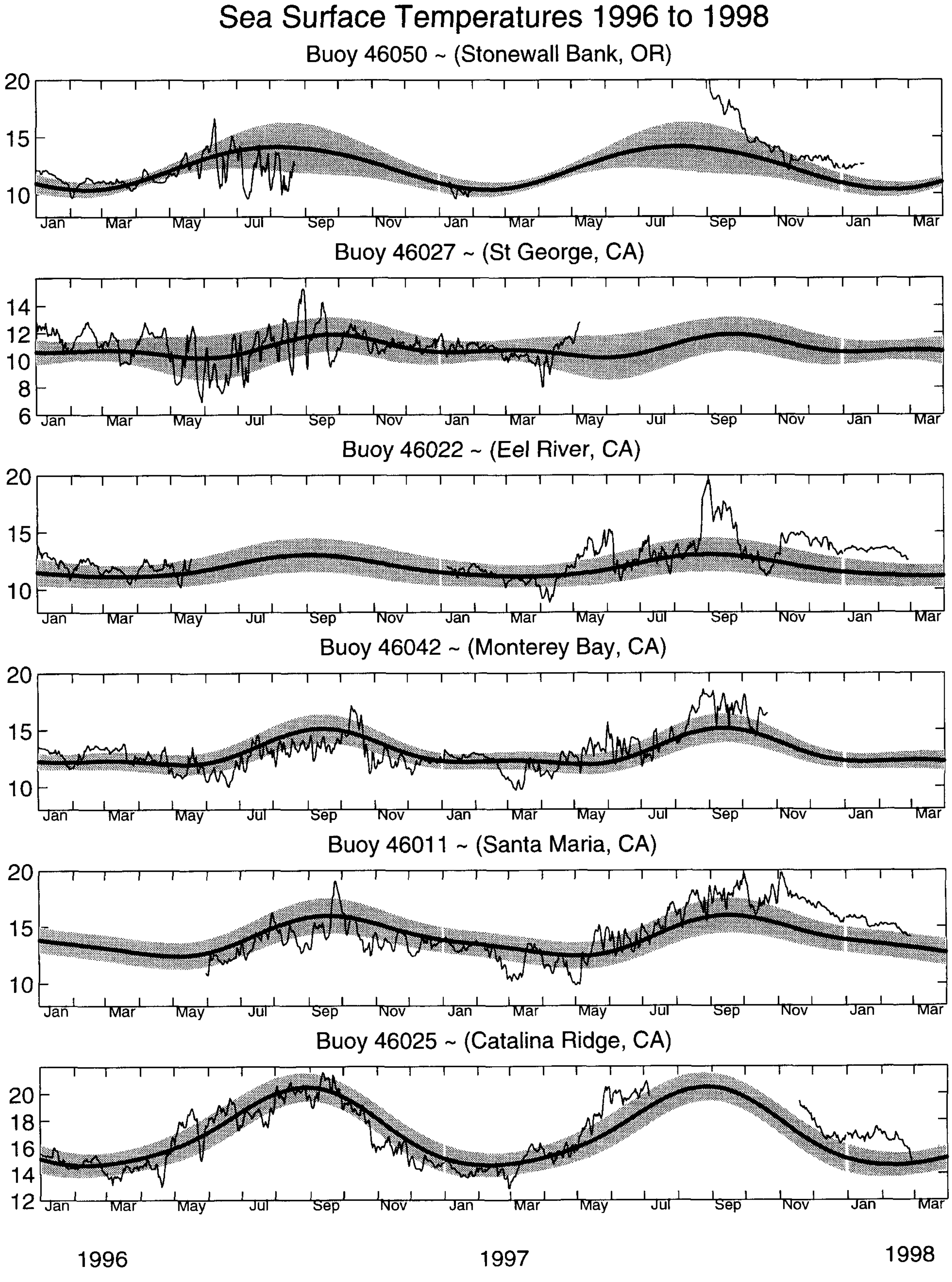


Figure 6. Time series of daily-averaged alongshore winds for 1996–98 at selected NDBC buoys. Bold lines are the harmonic mean annual cycle at each buoy. Shaded areas are the standard error for each Julian day. The period used for calculating the mean at each site and the alongshore angle are shown in table 1.



Sea Surface Temperatures 1996 to 1998

Buoy 46050 ~ (Stonewall Bank, OR)

Buoy 46027 ~ (St George, CA)

Buoy 46022 ~ (Eel River, CA)

Buoy 46042 ~ (Monterey Bay, CA)

Buoy 46011 ~ (Santa Maria, CA)

Buoy 46025 ~ (Catalina Ridge, CA)

Figure 7. Time series of daily-averaged SST for 1996–98 at selected NDBC buoys. Bold lines are the harmonic mean annual cycle at each buoy. Shaded areas are the standard error for each Julian day. The period used for calculating the mean at each site is shown in table 1.

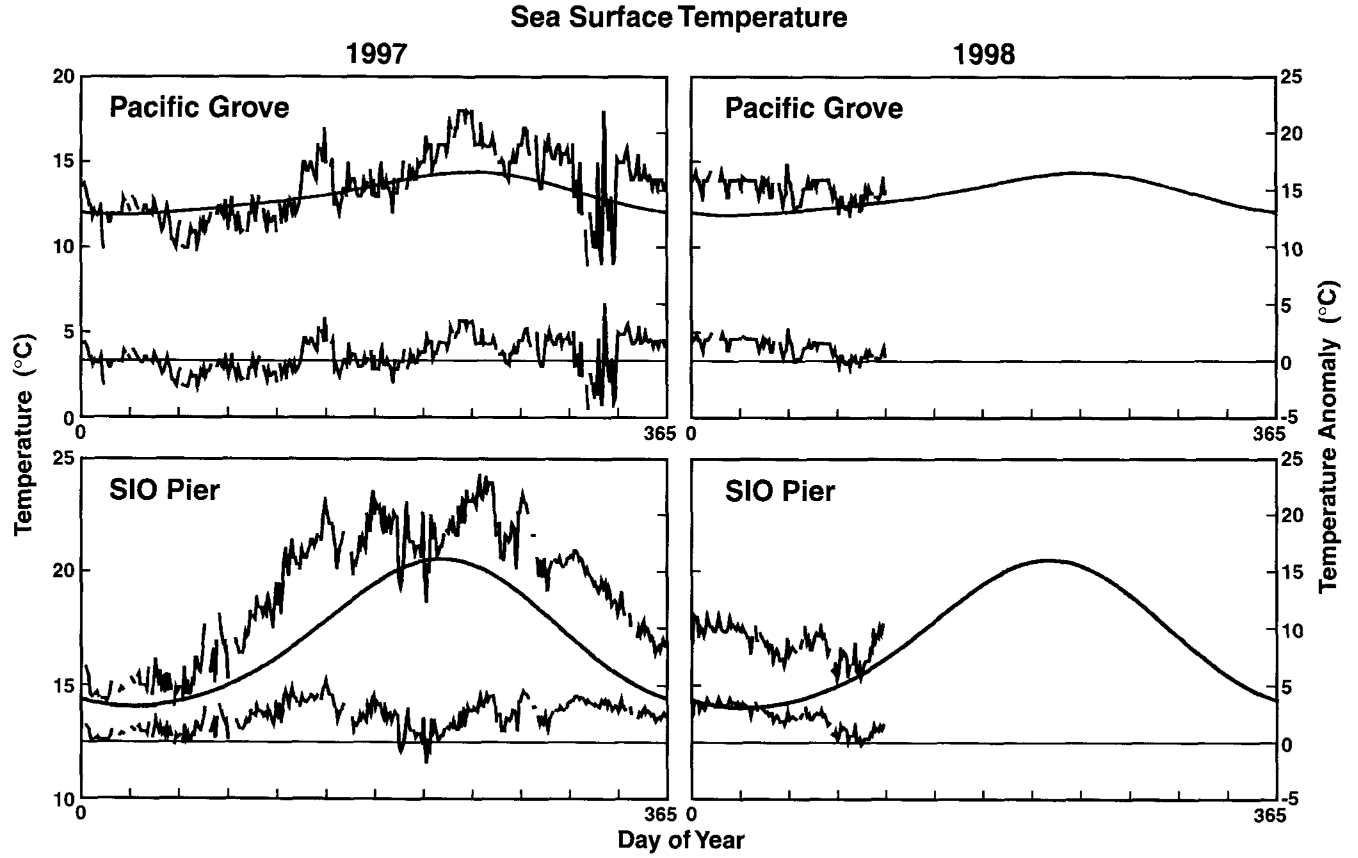


Figure 8. Sea-surface temperature at Pacific Grove and La Jolla (SIO Pier) for 1997 and 1998, and daily temperature and anomalies from the long-term harmonic mean (1919–93 for Pacific Grove and 1916–93 for La Jolla). The heavy line shows the annual cycle of the harmonic mean in SST.

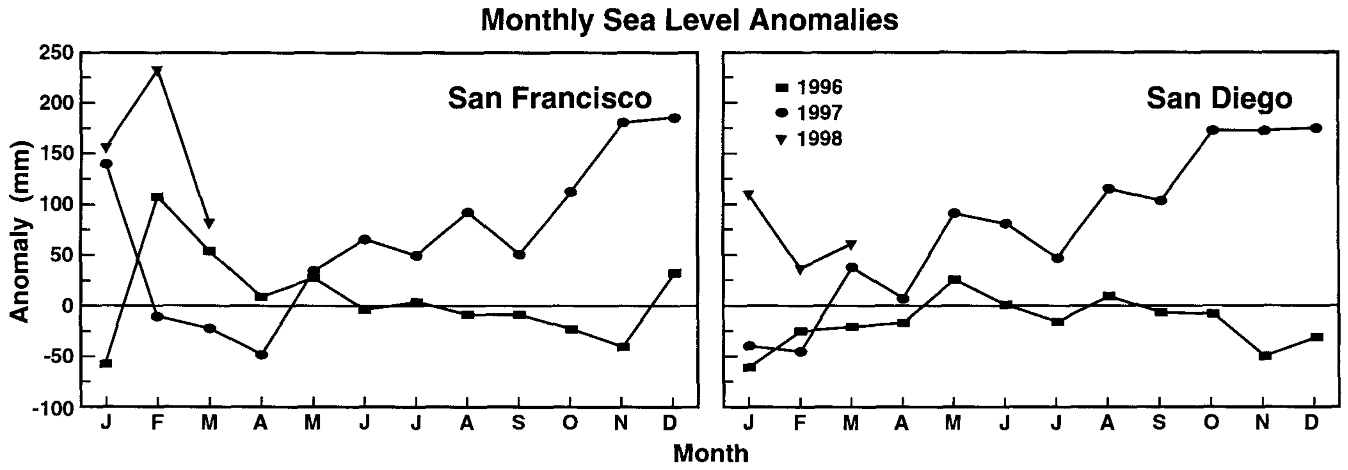


Figure 9. Monthly sea-level anomalies at San Francisco and San Diego for 1996, 1997, and 1998. The monthly anomalies are deviations from the period 1975–95, corrected for atmospheric pressure.

the CalCOFI cruises are shown in Hayward et al. 1994). Within the Southern California Bight, waters at 10 m were anomalously warm and saline. The chlorophyll distribution was typical of spring conditions, with elevated values in the vicinity of Point Conception and the Santa Barbara Channel. The concentration and spatial distribution of chlorophyll was similar to that seen in the springs of 1995 and 1996.

9707 (1–20 July 1997). Except for some minor features, the geostrophic flow field for 9707 (fig. 11) is typical of the normal pattern for summer. The well-defined core of the California Current is, however, slightly far-

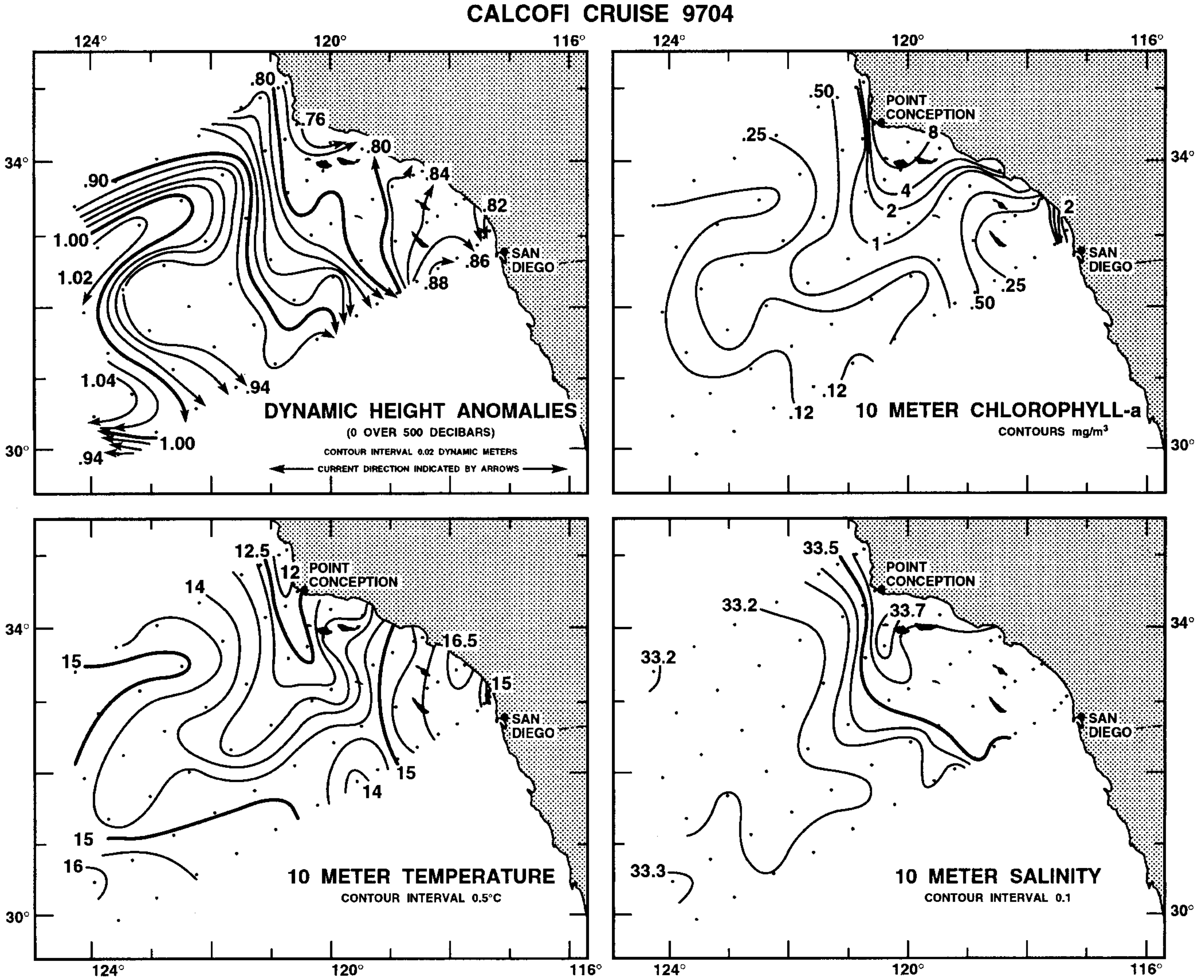


Figure 10. Spatial patterns for CalCOFI cruise 9704 (2–20 April 1997), including upper-ocean geostrophic flow estimated from 0 over 500 dbar dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

ther west than the long-term mean pattern (Lynn et al. 1982; Hayward et al. 1994). The inshore countercurrent is well developed, with greater than average velocities. The Southern California Eddy is small but intense enough to leave a strong signature in both the fields of SST and chlorophyll. With few exceptions the 10 m temperatures are above the long-term average; several areas exceed 1.5°C. Maps of SST anomalies from monitoring projects available on the World Wide Web (e.g., *NOAA/NWS/NCEP* and *NOAA/NESDIS/CoastWatch*) all showed a substantial increase between the months of April and May 1997. The core of low salinity at 10 m aligns with the outer half of the strong jet and is also displaced slightly westward of its long-term mean position. A comparison of cross-sections of salinity (line 93) for April and July shows a remarkable change in waters over or near the continental slope. In July there is a plug of water with salinity exceeding 34.4 where none had existed in April (fig. 12). The large change extends from 150 m to 450 m. Seen on a map of salinity at 300 m (fig. 11), this intrusion appears as a tongue of high-salinity water penetrating the bight from the south. The accompanying plot of ADCP vector flow confirms the southern source. The poleward California Undercurrent is very strong and continuous through the bight and around Point Conception. Waters with salinity exceeding 34.4 at this level are more typically found 550 km (300 nmi) to the south. This remarkable pattern may be part of the oceanic response (Kelvin wave) to the strong El Niño event in the tropics.

9709 (20 September–9 October 1997). The values of dynamic height calculated from this cruise are con-

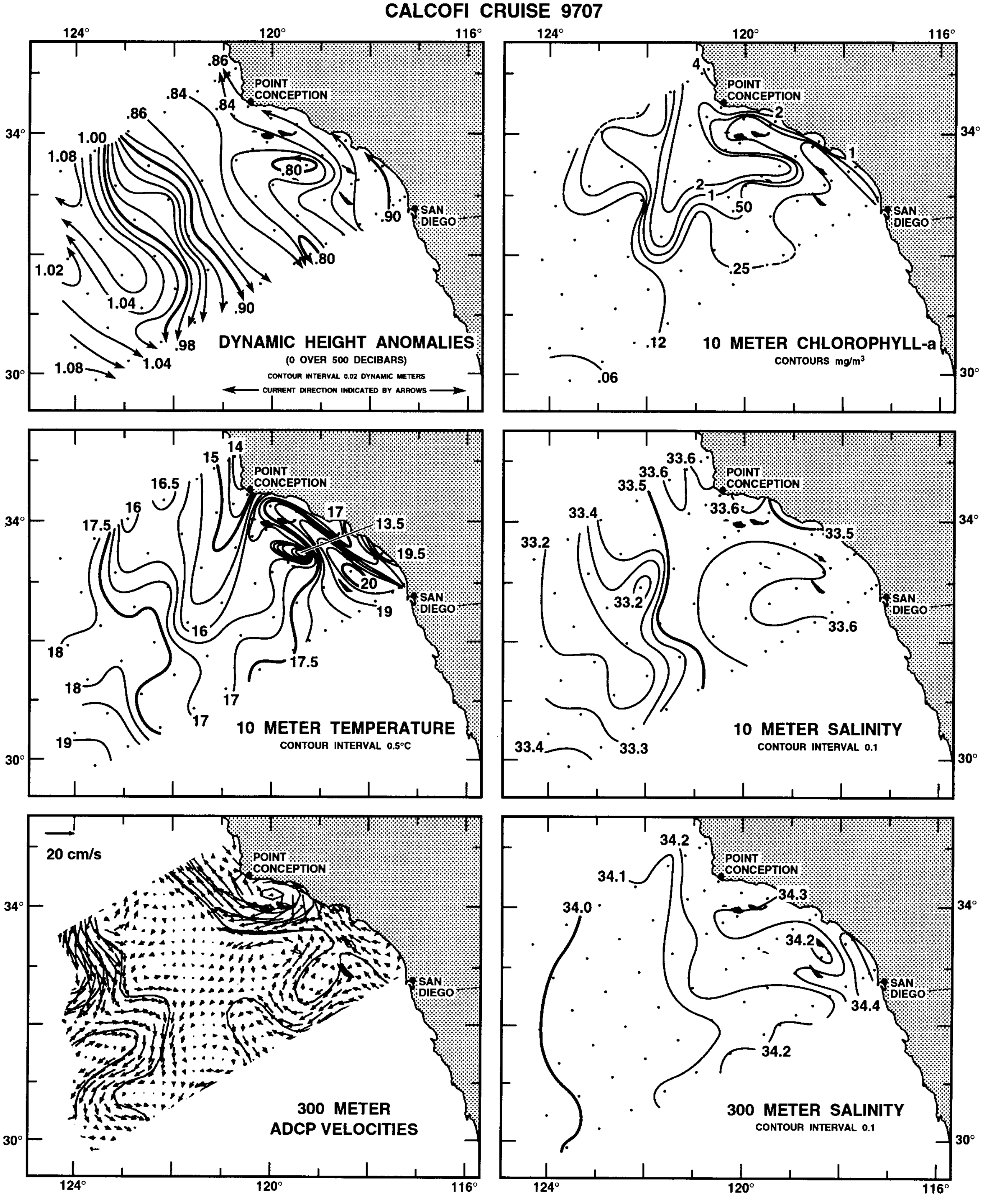


Figure 11. Spatial patterns for CalCOFI cruise 9707 (1–20 July 1997), including upper-ocean geostrophic flow estimated from 0 over 500 dbar dynamic height anomalies, 10 m chlorophyll, 10 m temperature, 10 m salinity, 275–325 dbar ADCP velocity vectors (courtesy of T. Chereskin), and 300 m salinity.

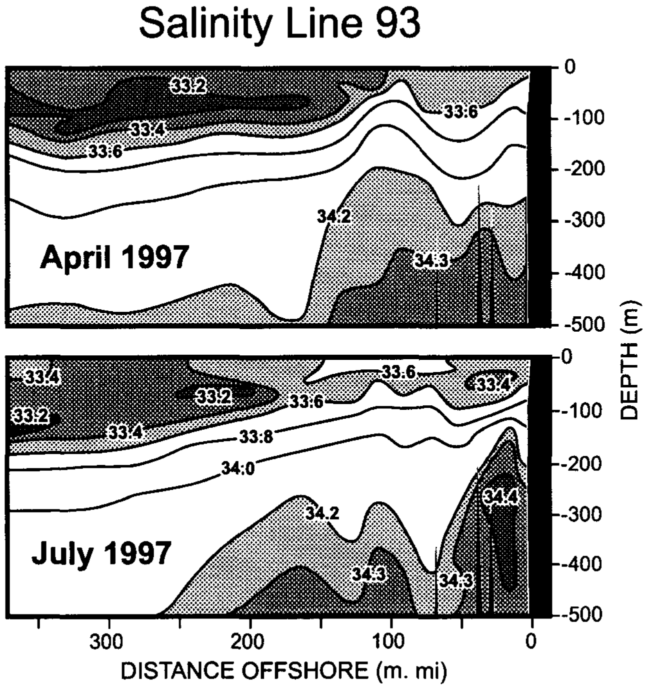


Figure 12. Vertical sections of salinity for line 93 from CalCOFI cruises 9704 and 9707. Salinity below 33.6 and above 34.2 is shaded.

siderably higher (mostly within the range of +0.04 to +0.15 dyn. m) than the long-term mean for October (fig. 13). Of the two strong cyclonic eddies, the one in the Southern California Bight is found in the mean field for October. The lowest temperature (17.15°C) and highest chlorophyll are found within this eddy. Positive 10 m temperature anomalies increased considerably from the previous cruise and are everywhere above normal, with the coastal band well exceeding 3.5°C. The inshore coastal countercurrent is continuous through the bight and around Point Conception, transporting very warm and saline water northward.

9802 (26 January–14 February 1998). Values of dynamic height for this cruise (fig. 14) are considerably higher than the long-term seasonal norm, reflecting both the anomalously higher surface temperatures and generally deeper thermocline; values range from 0.92 to 1.08 dyn. m. (10 J.kg^{-1}) compared to long-term mean values of 0.83 to 1.00 dyn. m. given by Lynn et al. (1982). Two cyclonic eddies characterize the circulation pattern during this cruise. The inshore limb of the shoreward eddy is the inshore countercurrent, and the flow is considerably stronger than normal. The surface water in this current has a salinity anomaly as much as +0.5 and a temperature anomaly greater than +3°C. The center of the California Current jet is displaced farther offshore and is characterized by the tongue of very low-salinity water. Between these two currents there is a large looping flow involving both eddies. A secondary lobe of cool, low-salinity water suggests that a new path may be developing for the main jet (just offshore of the Southern California Eddy), thus pinching off the offshore meander and the western eddy.

9804 (2–21 April 1998). The most dramatic seasonal change in conditions occurs between winter and spring. In April 1998 the California Current as estimated by the field of dynamic height appears as an exceptionaly strong coastal jet (fig. 15) replacing the poleward coastal countercurrent that had been found in February. The coastal jet is balanced by a strong upward tilt (shoreward) of the density structure, which upwells a narrow coastal band of water with very low temperature, high salinity, and high nutrients. The latter is evidenced by the high production of chlorophyll. The spatial pattern of chlorophyll is similar to that observed in the springs of 1997, 1996, and 1995. The California Current jet transports low-salinity waters from the north, appearing in this survey as a narrow tongue penetrating southward. The unusually high salinity in the southern and central portions of the Southern California Bight may be a product of upwelling of southerly waters that had been transported northward during the earlier period.

Additional El Niño Cruises

The timely predictions and early recognition of the El Niño event developing in the eastern tropical Pacific prompted West Coast marine research institutes and agencies to augment various observational programs. Funding has been made available to augment the quarterly CalCOFI cruises with additional abbreviated cruises that fill out a monthly sampling of lines 90 and 83 extending to station 100 for the period from October 1997 through December 1998. Time aboard the NOAA ship *MacArthur* was volunteered to start this new series 17–22 November 1997. The R/V *Robert Gordon Sproul* occupied these lines during 12–15 December 1997, 11–17 March 1998, and 16–21 May 1998. The data from these cruises show that the circulation patterns and plankton distributions can change very rapidly. Highlights (data not shown) include an abrupt deepening of the mixed layer along CalCOFI line 90 between November and December 1997, and a very abrupt change between March and April 1998. In February (CalCOFI) and March (mini-CalCOFI) an anomalously strong, coastal countercurrent was transporting warm, saline, low-nutrient water northward along the coast. One month later in April 1998 (fig. 15) strong southward flow of the low-salinity jet of the California Current was observed in the coastal region, especially in the Point Conception and Santa Barbara Channel region. Coastal SSTs in the Santa Barbara Channel region dropped from about 15° to 13°C, and 10 m surface chlorophyll increased from about 2 μg l^{-1} to greater than 7 μg l^{-1} (an adjacent station had a

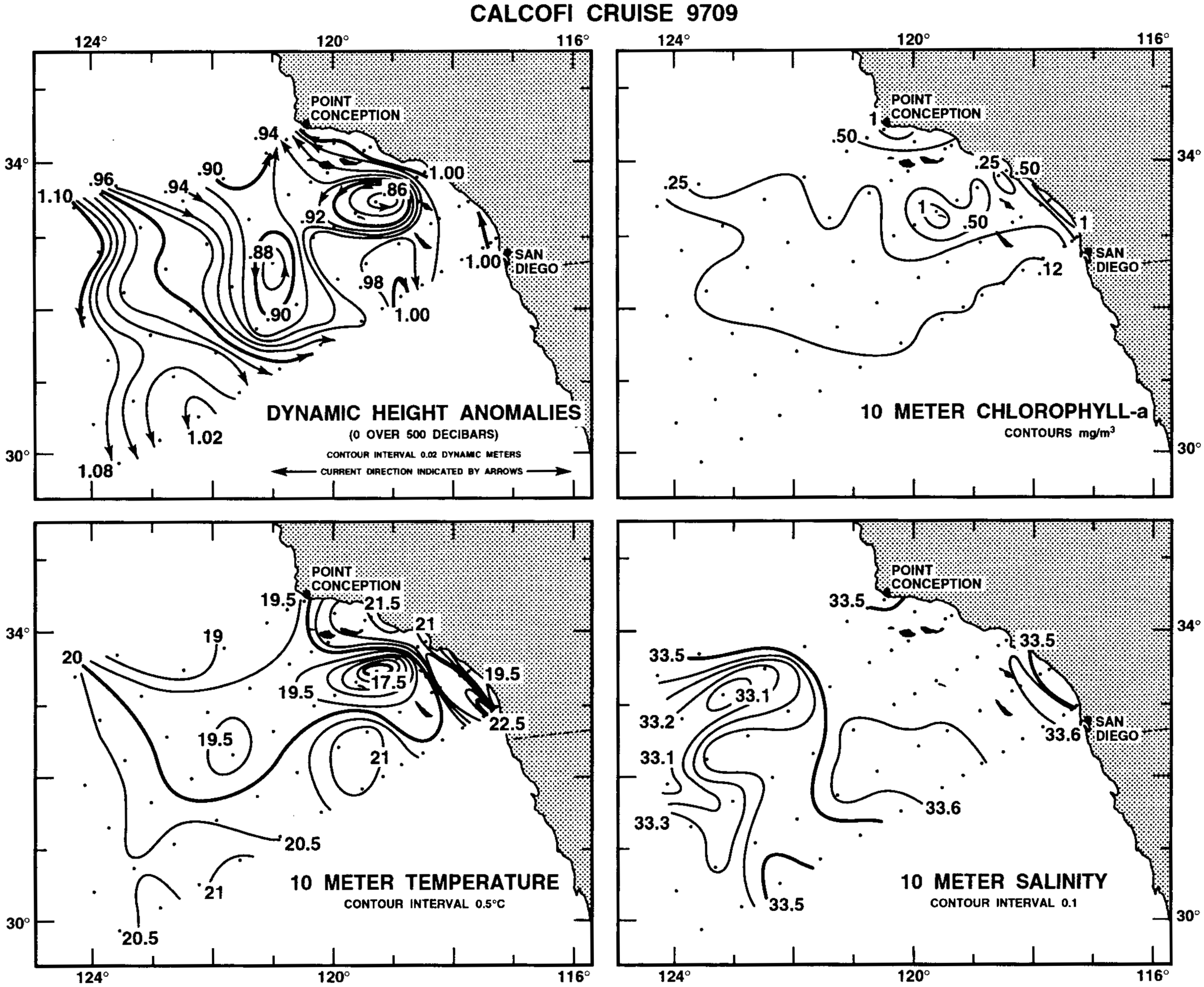


Figure 13. Spatial patterns for CalCOFI cruise 9709 (20 September–9 October 1997), including upper-ocean geostrophic flow estimated from 0 over 500 dbar dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

chlorophyll concentration greater than 14 $\mu g\,l^{-1}$) in this one-month period. The augmentation to monthly coverage will greatly help resolve the temporal pattern of physical forcing and the biological response, as well as the subsequent influences on higher trophic levels.

Central California Sampling Programs

A survey of spawning by small coastal pelagic fish was conducted from most of the CalCOFI station grid (since 1985) and additional northern grid lines (to line 67 off Monterey), 11 March–7 April 1997 (fig. 16). The observations from this survey precede those from CalCOFI cruise 9704 by approximately 3.5 weeks. Because CTD casts were limited to slightly over 200 m depth, the 100 m temperature is used to estimate the pattern of geostrophic flow. The fields of surface temperature, salinity, and estimated flow all indicate conditions prior to the "spring transition." Temperatures are higher and salinities lower than on the subsequent cruise. Coastal upwelling has not started. The California Current jet is in its offshore position typical of late winter. Shoreward of the jet is a broad region of negligible dynamic activity.

The SWFSC Tiburon Laboratory has conducted survey cruises annually since 1983 during May–June off San Francisco (fig. 1; Schwing et al. 1991; Sakuma et al. 1994). The rockfish surveys include a CTD cast with each trawl station. The CTD station grid was enhanced in 1987 and is occupied in three consecutive sweeps. CTD casts are made to 500 m, bottom depth permitting. During 1997 the grid was occupied as follows: sweep 1: 14–23 May; sweep 2: 23–31 May; and sweep 3: 7–18 June. This excellent spring time series will be

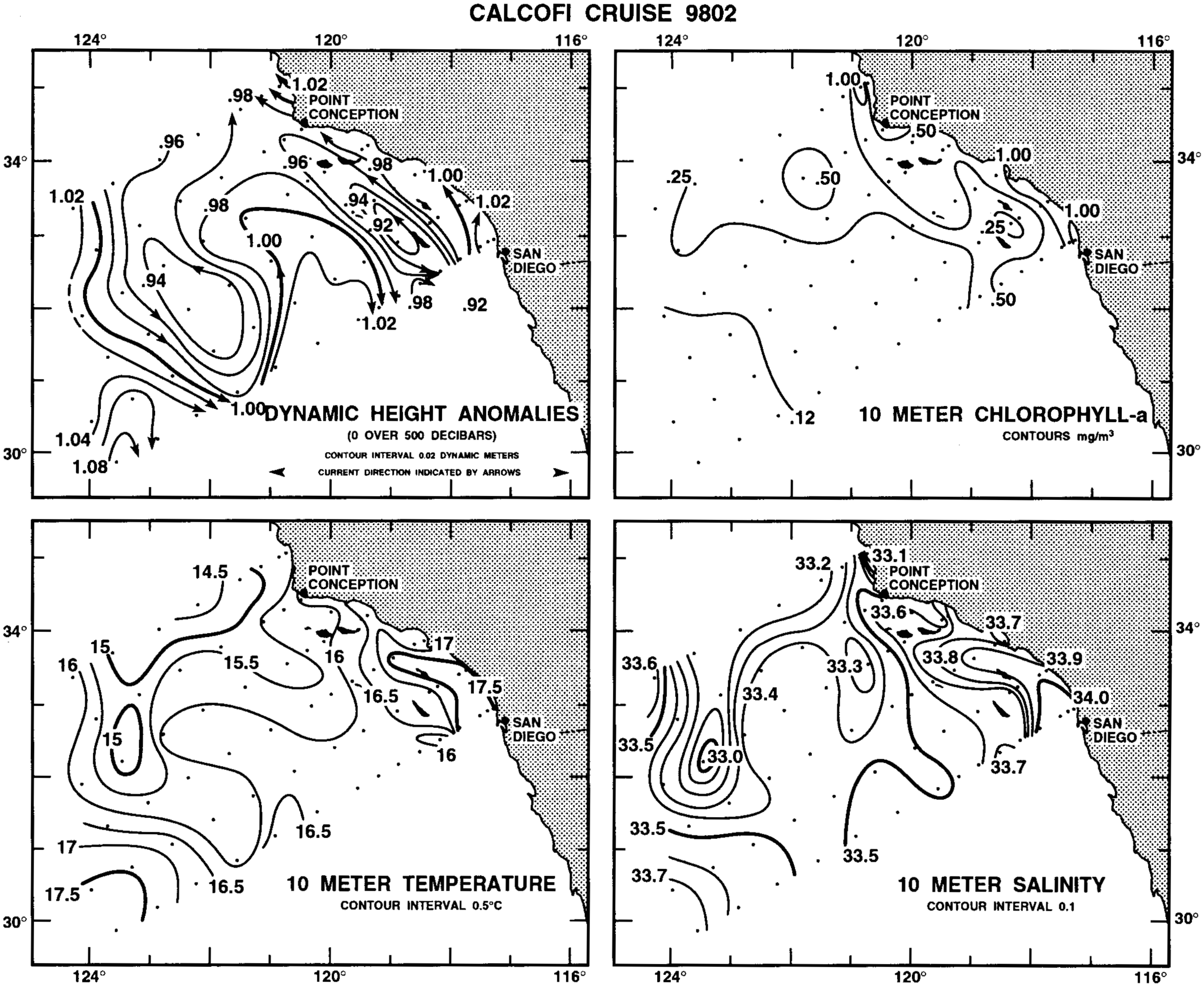


Figure 14. Spatial patterns for CalCOFI cruise 9802 (26 January–14 February 1998), including upper-ocean geostrophic flow estimated from 0 over 500 dbar dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

valuable for a comparative analysis of the 1997 coastal ocean dynamics.

MBARI, NPS, and NAVOCEANO cooperated in a series of cruises off central California. NAVOCEANO (D. Kronen and C. Szczechowski) conducted CTD/ADCP surveys 11–17 February 1997; 21–25 February 1997; and 5–14 March 1997 (NavOceano in fig. 1) which covered the coastal region from Morro Bay to Point Reyes. The surveys included CalCOFI line 67, which was occupied again in late July by the R/V *Point Sur* (MBARI and NPS). Results from this latter cruise revealed a strong poleward flow over the continental slope. At 200 meters poleward velocities reached 30 cm sec^{-1} (fig. 17). In the region immediately west of Monterey, a southward flow occurred to the east of the poleward flow, but this anticyclonic recirculation at the entrance to Monterey Bay is caused by the divergence of the strong poleward flow from the local bathymetry. Along line 67, a much larger anticyclonic feature was seen between 122.8°W and 123.8°W, resulting in poleward flows of 10–20 cm sec^{-1} between 123.8° and 124.2°. Farther offshore, weak equatorward flow associated with the California Current was observed.

Throughout the water column, temperatures were warmer in July 1997 than normal, with the greatest warming (greater than 1°C) found above the halocline and at a depth of 350 m over the continental slope (fig. 17). Within the halocline, the temperatures were slightly greater than normal: by 0.2°–0.4°C. Salinities were greater than normal almost everywhere along line

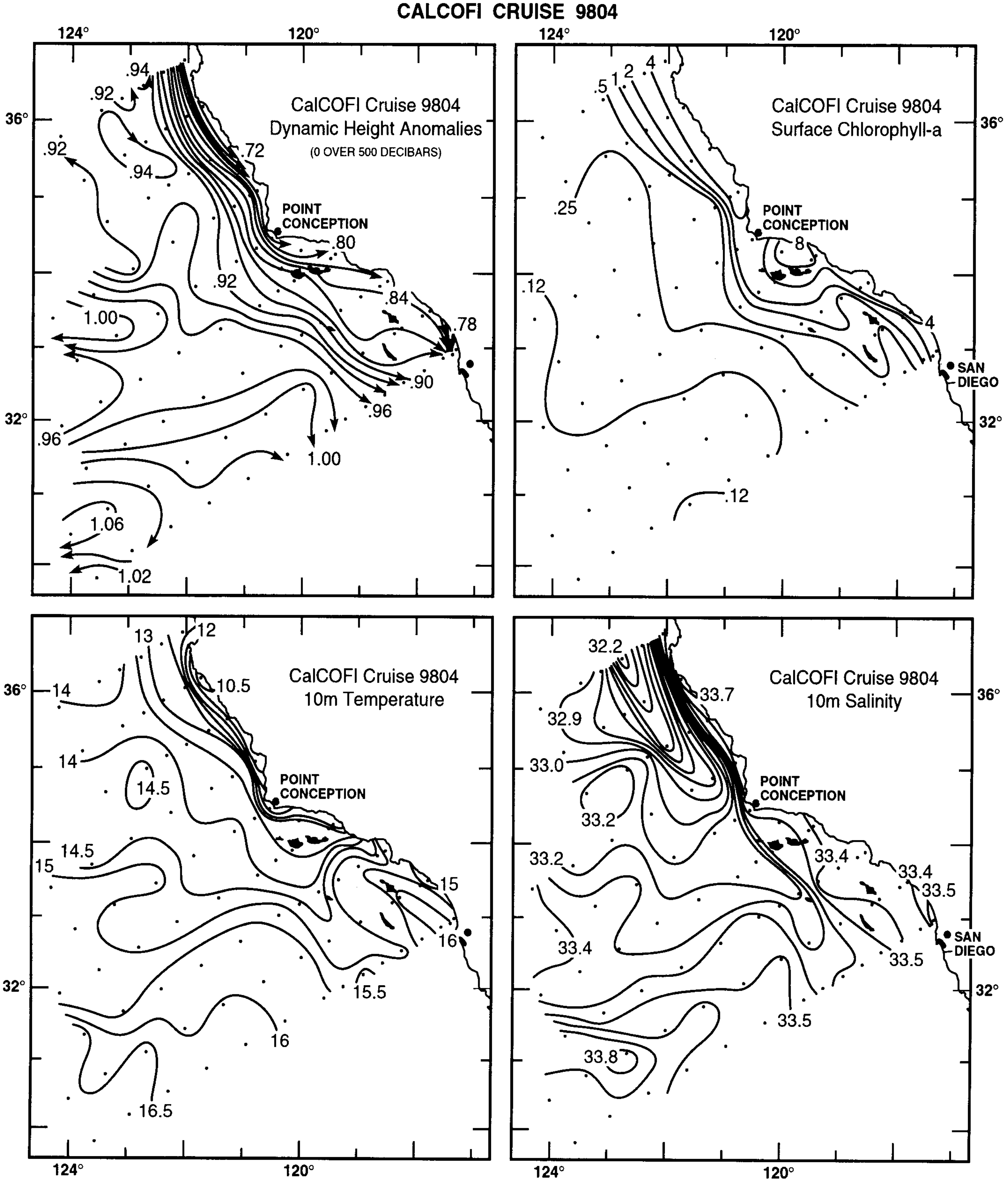


Figure 15. Spatial patterns for CalCOFI cruise 9804 (2–21 April 1998), including upper-ocean geostrophic flow estimated from 0 over 500 dbar dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

67 in July 1997, with the largest anomalies, 0.2, found above 150 m. Unlike the temperature anomaly field, the subsurface salinity field over the continental slope shows only a weak increase above normal.

These findings match in kind those described for CalCOFI cruise 9707 and thus further support the interpretation of a strong poleward countercurrent/undercurrent as an oceanic response to the equatorial ENSO events. The poleward flow was untypically strong and transported anomalously warm, generally higher-salinity waters to northern latitudes.

Baja California

A new program of ocean monitoring off Baja California by Mexican scientists, IMECOCAL (Investigaciones Mexicanas de la Corriente de California), seeks to reestablish sampling on a quarterly basis by using the CalCOFI station grid in the southern sector of the California Current. A brief description of the survey is given in the report of the CalCOFI Committee (this issue).

The initial IMECOCAL cruise, 9709/10 (24 September–5 October 1997) was carried out on the CICESE research vessel *Francisco Ulloa*, with R. Durazo and B. Lavaniegos as cruise leaders. This cruise occupied lines 110, 113, 117, 120, 123, and 127. The farthest offshore station occupied was 70, on lines 117 and 120; the remaining lines extended to station 55. CDT profiles were conducted to near-bottom depths, and surface water samples were collected to determine nutrients and chlorophyll. (Water samples were limited to the surface because of problems with operation of the CTD rosette.) Standard oblique bongo tows were made with 505 mm mesh, with one cod end dedicated to ichthyoplankton and the other to macrozooplankton. Continuous underway surface measurements were made of temperature, salinity, and fluorescence; the shipboard ADCP was used for continuous current profiling.

Temperature and salinity in the upper 500 m along line 120 (off Bahía Sebastián Vizcaíno) were, for the most part, above the seasonal norm (figs. 18 and 19). The anomalies are based on October values for the period 1950–78 from Lynn et al. (1982). In particular the surface layer was highly anomalous. Temperature exceeds 26°C and salinity exceeds 34.8 in the surface layer close to Punta Eugenia. The anomalies of temperature and salinity reach maximum values (8°C and 0.8) near 30–40 m depth at 30 nmi off Punta Eugenia. The core of positive anomalies penetrates offshore as a gradually thinning subsurface lens, particularly visible in the temperature

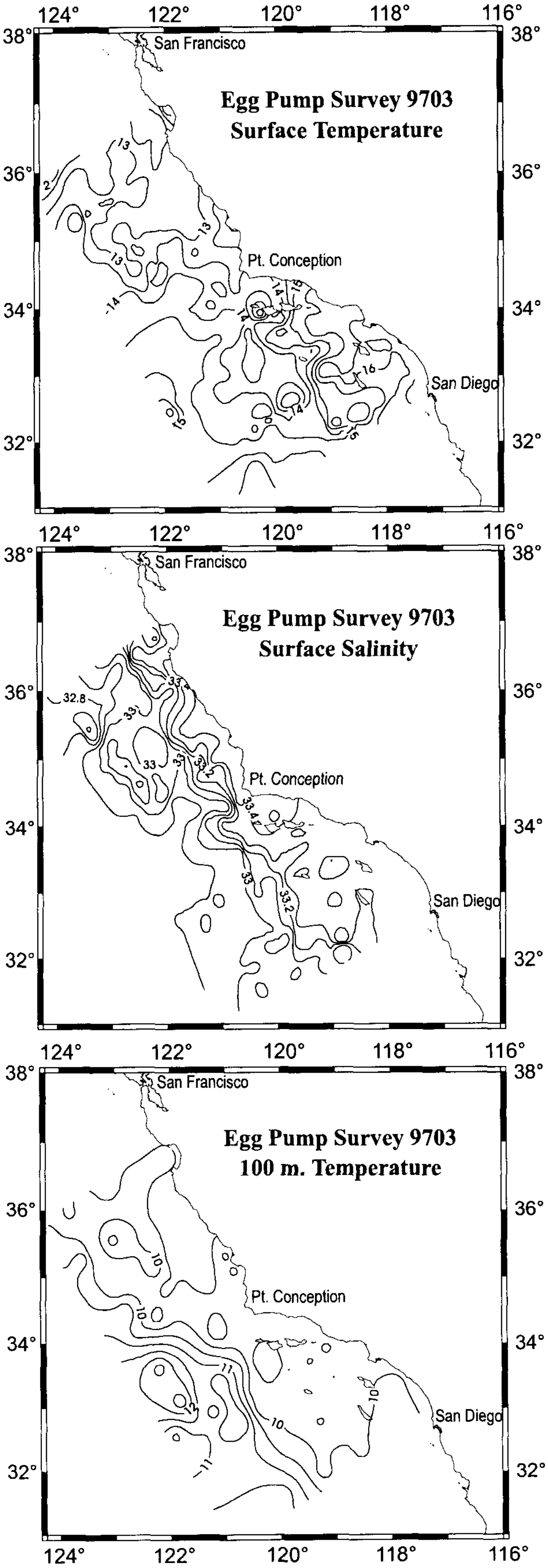


Figure 16. Spatial patterns for an NMFS/SWFSC pelagic fish egg and larvae survey (11 March–7 April 1997) including surface temperature and salinity, and 100 m temperature.

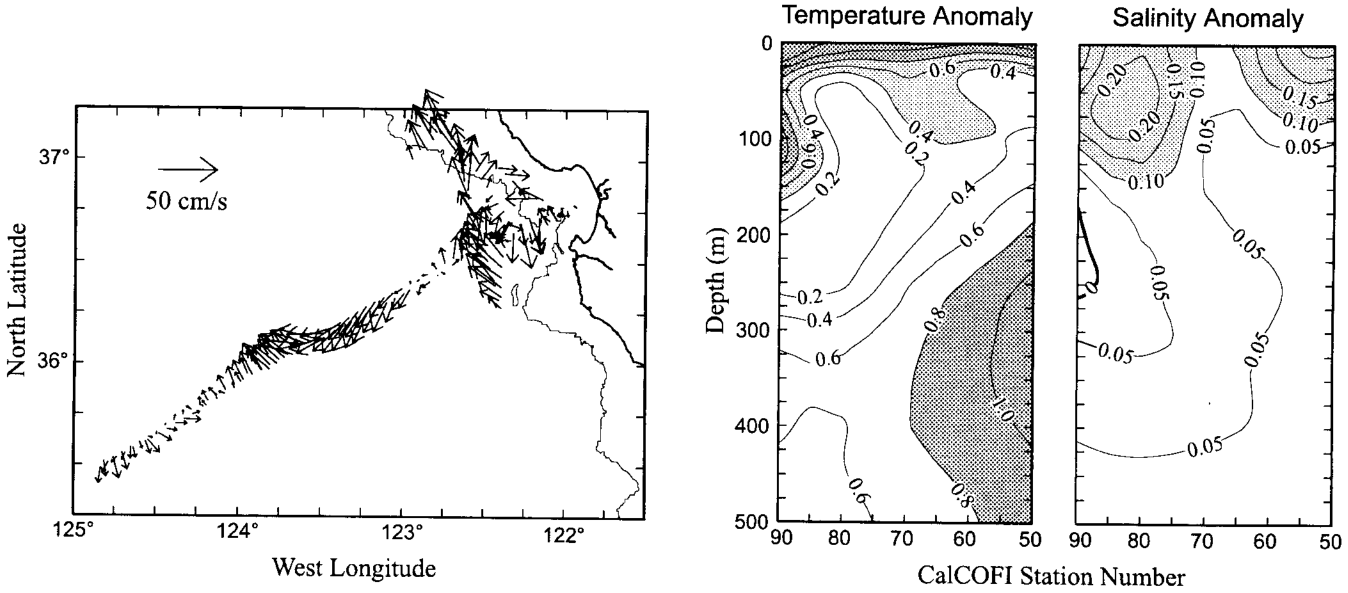


Figure 17. Left panel: ADCP current vectors at 200 m currents, 22–29 July 1997, and the 1,000 m isobath off Monterey Bay. Measurements were made with a vessel-mounted acoustic Doppler current profiler. Right panels: Vertical sections of anomalies of temperature and salinity for the offshore transect of the same cruise (CalCOFI line 67), 26–29 July 1997. Anomalies are based upon summer climatology for CalCOFI line 70 (Lynn et al. 1982).

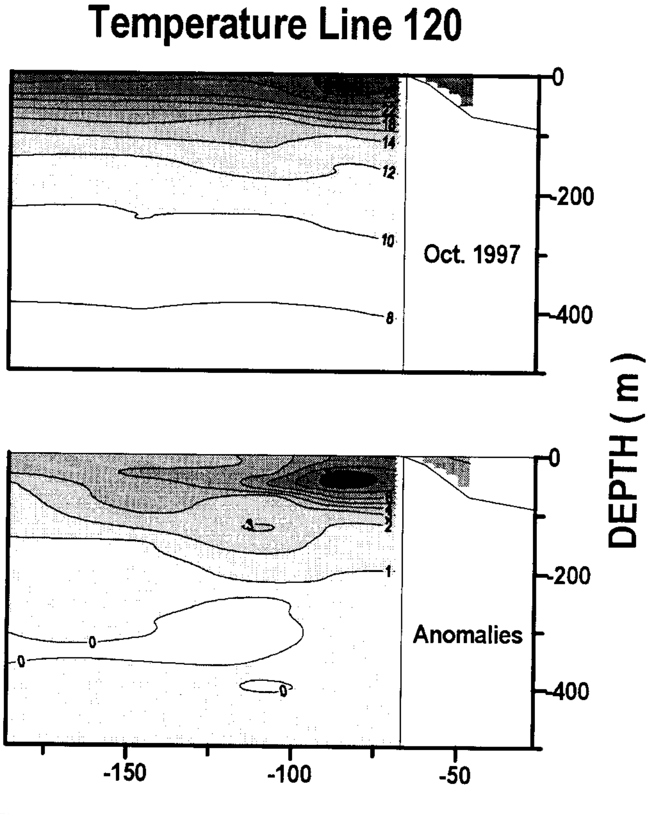


Figure 18. Top, Temperature from IMECOCAL cruise 9709/10 (24 September–5 October 1997) along CalCOFI line 120. Stations (35, 40, 45, 50, 55, 60, 65, 70) spaced at 20 nmi. Bottom, Temperature anomalies calculated from mean values given by Lynn et al. (1982) for the period 1950–78 for even-numbered stations plus nearshore stations 35 and 45.

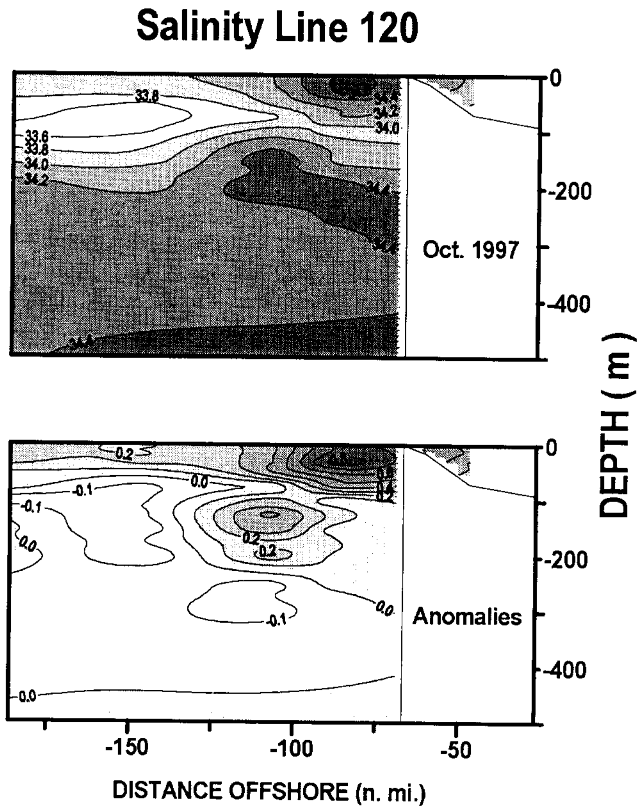


Figure 19. Top, Salinity values along line 120 for IMECOCAL cruise 9709/10. Bottom, Salinity anomalies calculated from mean values given by Lynn et al. (1982) for the period 1950–78 for even-numbered stations plus nearshore stations 35 and 45.

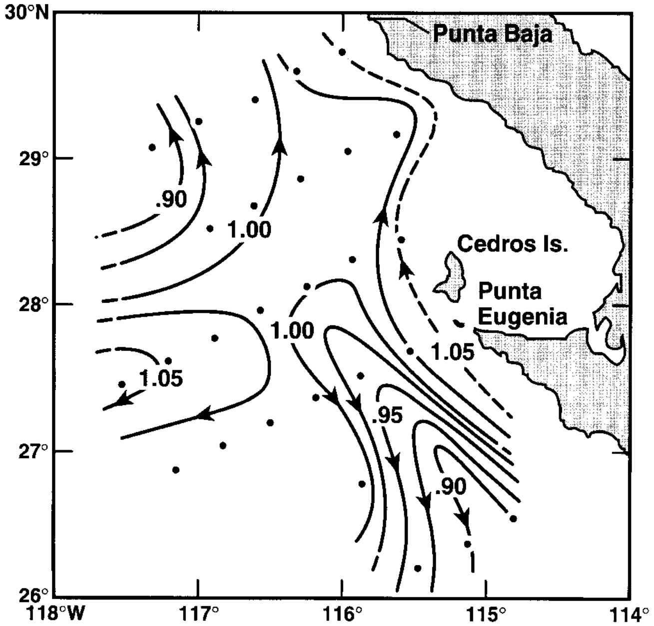


Figure 20. Dynamic height anomaly (10/500 dbar) for IMECOCAL cruise 9709/10. Contour interval is 0.025 dyn. m.

anomalies. The salinity section shows that this high-salinity lens was underlain by a wedge of low-salinity California Current water thinning toward the coast. At lesser extreme values, there is a second and deeper anomalous core lying farther offshore between 100 and 200 m depth. The T-S characteristics of this deeper core indicate subtropical subsurface water, as defined by Wyrtki (1967), mixed with California Current water, a composition expected for the poleward California Undercurrent with its high-salinity source to the south. The very high temperature and salinity anomalies of the near-surface core also indicate the anomalous penetration of coastal water normally found several hundred kilometers to the south (cf. alongshore sections for mean October salinity in Lynn et al. 1982).

Near-surface dynamic heights calculated as 10/500dbar (fig. 20) show a strong near-surface poleward coastal jet along the peninsula south of Punta Eugenia. The effects of this jet extend to depths greater than 100 m on the temperature and salinity sections and in dynamic heights of 125/500 dbar (not shown here). This jet splits into two branches at the latitude of Isla Cedros. A poleward branch follows along the contour of the shelf break, veering toward the coastline and finally leaving the survey area off Punta Baja. The other limb of the coastal jet bends around sharply to reverse its direction and flow equatorward with an offshore component near the southern edge of the survey area. An onshore flow enters the survey area at latitude 28°N from the west, also dividing into two branches. One branch turns north to join the flow along the shelf break, so that poleward flow prevails across the entire length of line 110 at the northern boundary of the survey area. The southern branch of onshore flow entering the survey area at 28°N converges with the offshore limb of the coastal jet and then recurves to flow back offshore.

The warm, high-salinity, near-surface core seen in figures 18 and 19 is located within the poleward coastal jet seen in the dynamic heights and can be followed from south to north across all the tracklines. The onshore flow at 28°N in figure 20 is associated with the low-salinity wedge of California Current water in figures 18 and 19. The dynamic topography for 125/500 dbar indicates that the California Current water is associated with generally southerly to southeasterly flow penetrating onshore as a broad meander forming the low-salinity wedge in figure 19. The presence of a slightly negative subsurface salinity anomaly on line 120 probably results from the onshore transport of California Current water.

BIOLOGICAL PATTERNS

Changes in biological structure over time are evaluated by comparing cruise means of individual cruises with the historical time series. The February and April 1998 CalCOFI cruises had the lowest macrozooplankton standing crops in the long-term (1951 to present) CalCOFI database (P. Smith, pers. comm.). The previous low plankton volume was in March of 1959, 23 months after the onset of the 1957–59 ENSO. The 1998 low was less than a year after the onset of the present ENSO. These patterns are evident in the cruise means of macrozooplankton biomass (fig. 21). It can also be seen that the secular trend of declining macrozooplankton biomass observed since the mid-1970s regime shift (Roemmich and McGowan 1995) is continuing, and the effects of the 1997–98 El Niño conditions are superimposed upon this.

The cruise means in integral chlorophyll also follow the pattern seen in recent years. Integral chlorophyll does not show a trend of declining values, at least since the mid-1980s; nor do the El Niño periods of 1992–93 (Hayward et al. 1994) or 1997–98 (fig. 21) stand out as being anomalous in the context of values measured over the entire 1984–98 time period. Understanding why strong decadal and El Niño trends are apparent in macrozooplankton biomass but not in vertically integrated chlorophyll concentration is an area of active research.

The coastal waters are often affected by red tide events. A phytoplankton bloom resulting in red tide conditions was not expected by many this spring because of the El Niño conditions present. Following the last major El Niño in 1982–83, phytoplankton concentrations were low, always less than 1 × 105 l^{-1} (Reid et al. 1985). However, in 1998 a red tide began in San Diego in late May and lasted several weeks. The bloom was domi-

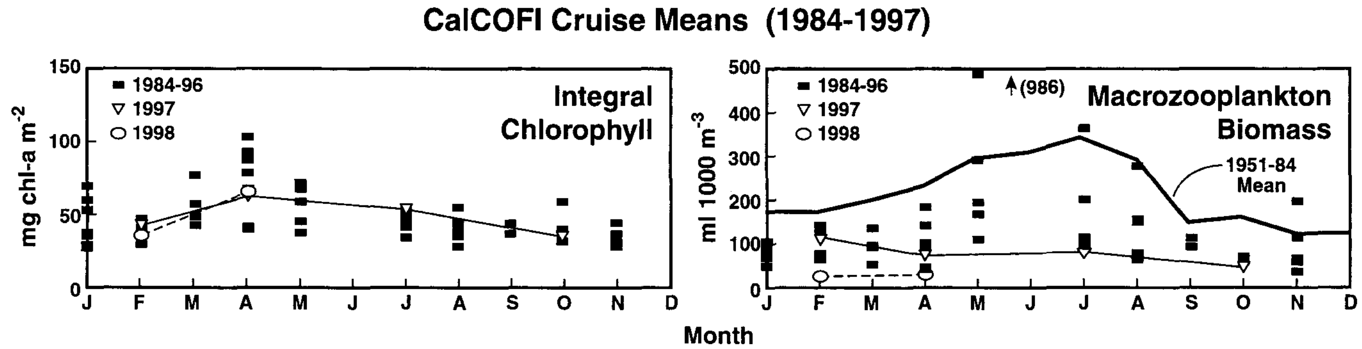


Figure 21. Cruise means of vertically integrated chlorophyll and macrozooplankton biomass plotted versus the month of CalCOFI cruises from 1984 to 1998. Each point represents the mean of all measurements on a cruise (normally 66). The solid squares show results from cruises conducted from 1984 to 1994. The open symbols are results from cruises in 1997 and 1998; cruises from individual years are connected with lines. The bold line in macrozooplankton biomass indicates the monthly means for 1951–84.

nated by the dinoflagellate *Prorocentrum micans*, which reached concentrations in surface waters of at least 5 × 10^5 cells l^{-1}. Blooms of *P. micans* do not appear to be a regular feature of El Niño. In the spring of 1983 *P. micans* was also present as a dominant member of the community (Reid et al. 1985) but was not observed during the 1957–58 El Niño (Balech 1960). The dinoflagellate species *Lingulodinium polyedrum*, the dominant constituent of the extremely large phytoplankton blooms that have occurred the last few years, was seen in only trace concentrations.

One of the exciting new components of the CalCOFI program is the improved ability to sample the distribution of fish eggs. The continuous underway fish egg sampler (CUFES), originally designed and used to sample menhaden eggs off the East Coast (Checkley et al. 1997), was first used in the California Current region in March 1996 (Checkley et al., in press). The large improvement in estimating the spatial extent of spawning habitat and egg production for sardines and anchovies has resulted in the use of the CUFES in fish egg and larval surveys, and its adoption as a standard observational tool in the CalCOFI quarterly cruises. In the CUFES water is pumped from a depth of 3 m at a rate of 640 L min^{-1}, then passed through a concentrator from which 30 L min^{-1} carrying the fish eggs passes to a sample collector. Samples are collected over periods typically ranging from 5 to 30 min (equivalent to 0.75 to 4.5 nmi at 9 knots).

The distribution of sardine eggs was greater off central California than off southern California during the spring surveys of 1997 and 1998 (fig. 22). The egg distributions differ sharply, however, in the broad, offshore extent in 1997 compared to the narrow, near-coastal pattern in 1998. The differences in egg distribution appear to relate to the large differences in the oceanographic patterns described earlier (figs. 15 and 16). The conditions in March 1997 were those of late winter, with

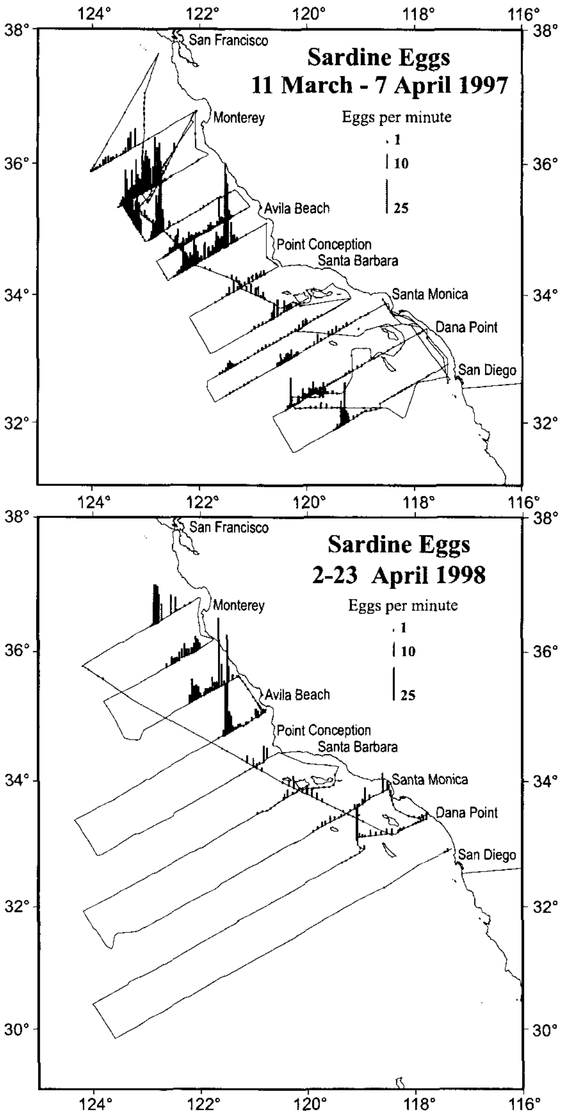


Figure 22. Upper panel, The distribution of sardine eggs as collected by the continuous underway fish egg sampler (CUFES) for an NMFS/SWFSC pelagic fish egg and larval survey (11 March–7 April 1997); and (lower panel) for CalCOFI survey 9804 (2–23 April 1998).

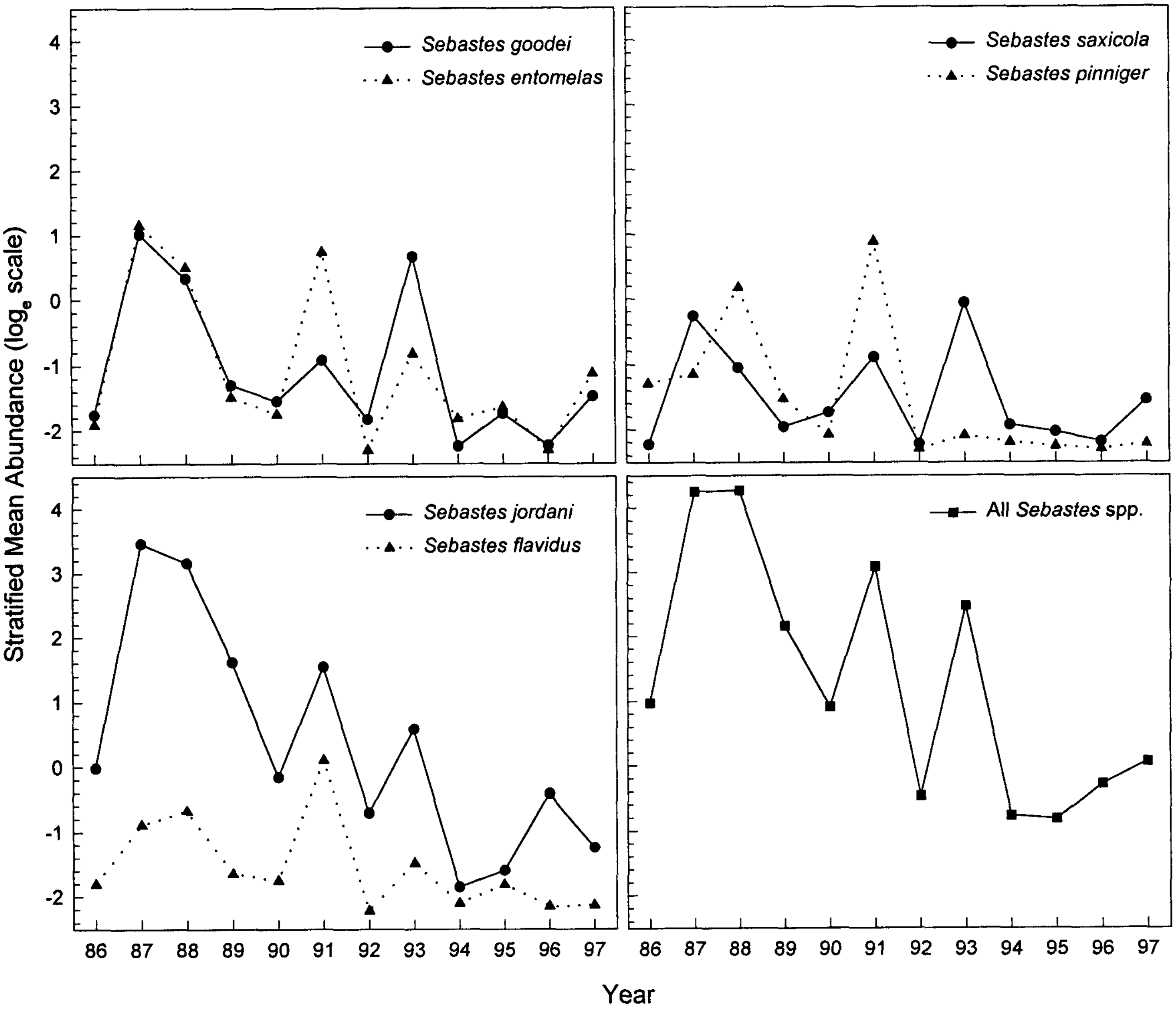


Figure 23. Annual abundance estimates of pelagic young-of-the-year rockfish, *Sebastes* spp., off central California for 1986–97. Abundances were adjusted according to Adams (1995) to account for interannual differences in size structure, and transformed by $\log_e(x + 0.1)$, where x is the length-adjusted catch.

an offshore California Current. In April 1998 the transition to spring conditions had taken place, and a narrow, exceptionally swift California Current was pressed against the coast.

Annual abundance indices of pelagic young-of-the-year rockfish (*Sebastes* spp.) off central California were estimated from midwater trawl collections by the NMFS SWFSC Tiburon Laboratory (see Adams 1995 for methods). Catch rates during May–June 1997 were higher than those observed in 1996, but still relatively low, as they have been since 1994 (fig. 23). The catch rate of *S. jordani* (the most common species collected) was slightly lower in 1997 than in 1996, but abundances of many of the remaining rockfishes showed a slight increase, leading to an overall increase in *Sebastes* spp. abundance. This increase in overall abundance was primarily due to moderate catches of large (>25 mm SL) *S. entomelas*, *S. goodei*, and *S. saxicola*, which occurred within the first week of the 1997 midwater trawl survey. However, as catches of these large specimens decreased substantially over the course of the survey, it appeared that the major recruitment pulse might have preceded the beginning of the survey. VenTresca (California Department of Fish and Game, Monterey, CA) observed that the recruitment of *S. mystinus* to the kelp bed areas of Monterey Bay was unusually early (pers. comm. reported by Schwing et al. 1997). The early transition to upwelling-favorable conditions in the beginning of 1997 may have been associ-

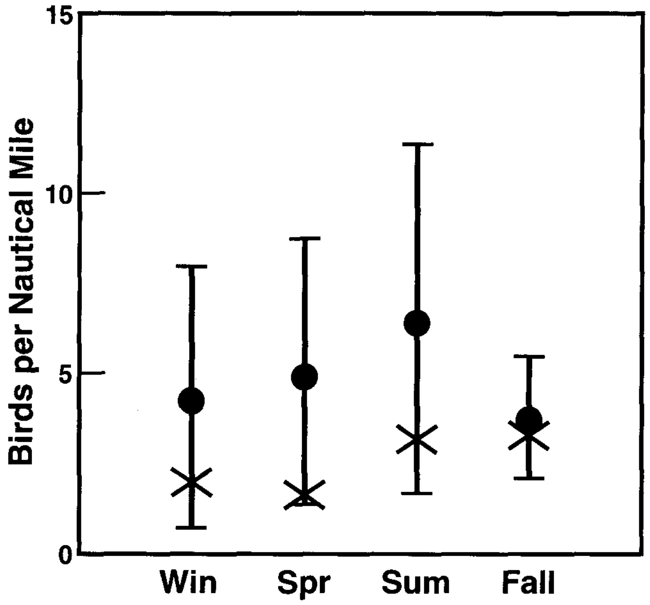


Figure 24. Mean and standard deviation (filled circles and error bars) of seasonal seabird abundance on CalCOFI cruises from May 1987 to April 1994, and abundance for cruises from July 1997 through April 1998 (depicted with an x). Figure modified from Hayward et al. (1996).

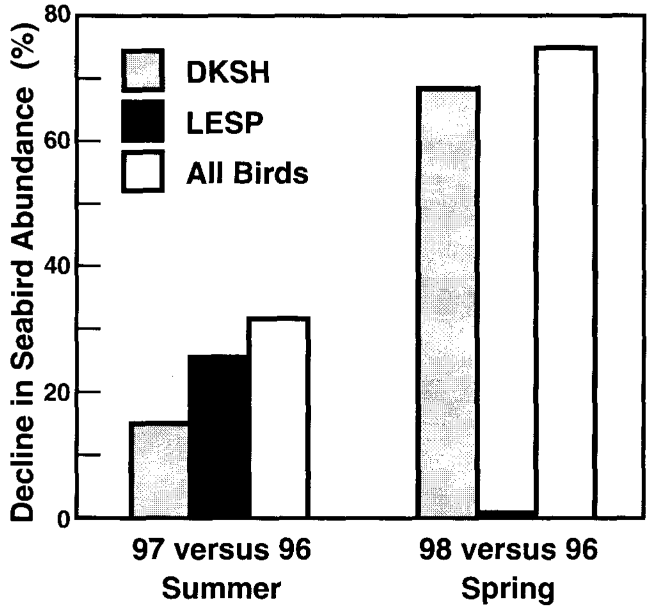


Figure 25. Short-term changes in abundance for numerically dominant offshore seabirds (LESP: Leach's storm-petrel); coastal seabirds (DKSH: sooty and short-tailed shearwater); and all bird species combined (All Birds).

ated with the observed early recruitment of *Sebastes* spp. In contrast, the ENSO conditions that developed later in 1997 (with the associated depression of upwelling) had a detrimental effect on the recruitment of *Sebastes* spp.; preliminary results from the May 1998 survey show that catch rates are the lowest in the history of the survey.

CalCOFI time-series cruises have provided the opportunity for systematic surveys of the distribution and abundance of seabirds, and studies of population trends in relation to oceanographic conditions. The abundance of seabirds in the CalCOFI region has declined steadily from 1987 to 1994 (Veit et al. 1996). Bird abundance during 1997–98 was consistently lower than the long-term mean, suggesting further declines during this period (fig. 24). In addition, the seasonal cycle of seabird abundance was disrupted in 1997–98. Instead of the usual summer peak, bird abundance was highest during fall 1997 and declined to a yearly minimum by spring 1998.

It is unclear to what degree these fluctuations are attributable to the 1997–98 El Niño. The decline in seabird abundance during summer 1997 affected both offshore and coastal species (fig. 25), and may have been related to anomalous physical conditions and low macrozooplankton biomass during the previous year (Schwing et al. 1997). It is likely that the onset of El Niño further affected bird distributions by compounding anomalous conditions in preceding months. For instance, the incursion of southern species during fall was probably related to enhanced poleward flow of the California Countercurrent and elevated sea-surface temperatures (Ainley et al. 1995). Veit and co-workers (1996) documented similar increases of black (*Oceanodroma melania*) and least (*O. microsoma*) storm-petrels during the 1992–93 El Niño. Finally, the decline in overall seabird abundance during spring 1998 was closely related to the failed immigration of shearwater species into coastal waters of the CalCOFI region (fig. 25). These are highly mobile predators capable of adjusting their distributions in response to large-scale changes in ocean productivity and prey biomass (Veit et al. 1997).

CalCOFI is also concerned with better understanding the influences of changes in oceanographic structure on nearshore communities. Kelp forest communities are diverse assemblages organized around the giant kelp, *Macrocystis pyrifera*, which is itself harvested for the production of alginates and whose biological structure and high productivity support numerous fisheries. Dependent on high levels of nutrient input to maintain growth rates and standing biomass, *Macrocystis* populations are very sensitive to interannual variability in sea-surface temperatures, measured as a surrogate for nutrient availability (Tegner et al. 1996). Because of the cascading effects of reductions in kelp on higher trophic levels, kelp forest communities are the temperate benthic community most strongly affected by El Niño events (Tegner and Dayton 1987; Dayton and Tegner 1990).

Anomalously warm sea-surface temperatures in 1997 decimated *Macrocystis* canopies bight-wide; by November the canopy of the Point Loma kelp forest near San Diego was about 10% of normal (D. Glantz, pers. comm.), and

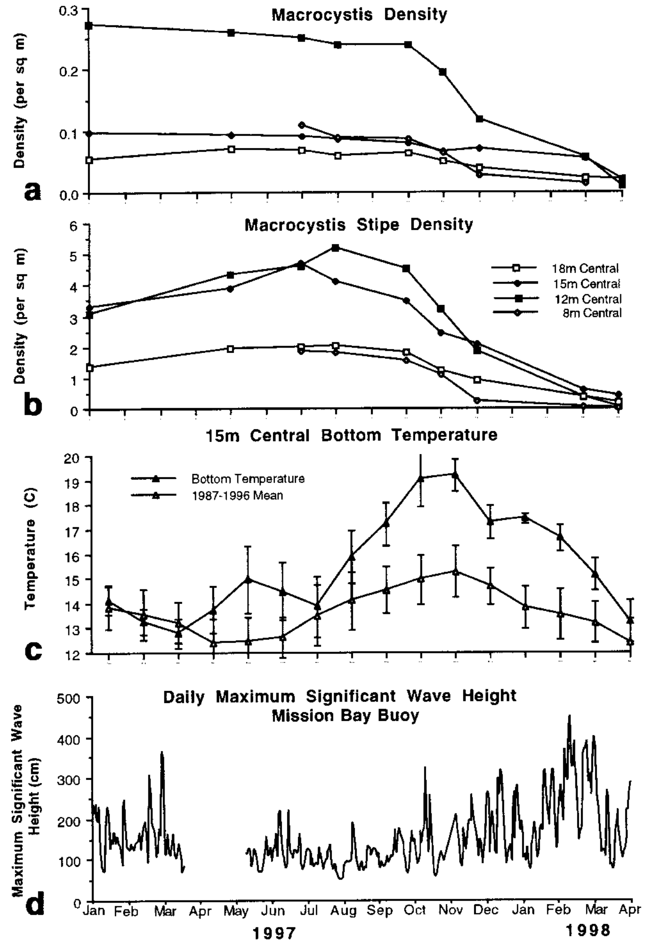


Figure 26. Changes in *Macrocystis* plant density (*a*) and stipe density (*b*) from permanent sites at 18, 15, and 12 m in the center of the Point Loma kelp forest during the 1997–98 El Niño. See Tegner et al. (1997) for sampling details. *c*, In situ temperature at 15 m for 1997–98 and the mean for 1987–96; error bars represent one standard deviation. *d*, Daily maximum significant wave height from the Mission Bay Buoy (Coastal Data Information Program).

it deteriorated further with the winter storms. Figure 26 compares subsurface changes in kelp populations across the depth gradient of this forest with benthic temperature and maximum significant wave height. *Macrocystis* stipe (analogous to branches of land plants) density, an index of carrying capacity for giant kelps, peaked after relatively cool bottom temperatures in July 1997 and then declined precipitously as bottom temperatures soared in fall 1997. Density of giant kelp plants also decreased, but is less sensitive than stipe density (Tegner et al. 1996, 1997). Both measures declined further as the extended period of large waves associated with El Niño conditions (e.g., Seymour 1996) affected the nearshore zone in fall 1997 and especially winter 1998. Note that the effects of warm, nutrient-depleted conditions as well as wave energy are most severe in shallow water and decrease with depth across the forest; the effect of these disturbances is to shift the forest into deeper water. Because canopy deterioration preceded the storm season, plants may have survived better than during the 1982–83 El Niño storm season. The combination of cool temperatures in April 1998 with the considerable open space cleared by the storms led to the onset of kelp recruitment and conditions for regrowth of surviving adults.

DISCUSSION

The period beginning in January 1997 and continuing to the present (May 1998) has been one of unusually large anomalies in physical and biological conditions in the coastal waters off the Californias. Observations show this to be one of the remarkable periods in the 50-year time series of CalCOFI. The coastal SSTs have been above seasonal norms throughout this period, and since May 1997 there have been large displacements in the distribution of many species of fish. Zooplankton levels are at their lowest recorded levels in the long-term CalCOFI time series. In the first half of 1997 the driving forces appear to have been of a local nature, a residual (and unusual) effect of the end of a La Niña period in the tropics. Conditions leading to an El Niño were initiated in the western equatorial Pacific at the beginning of this same period. The initial impact of El Niño upon California waters (July 1997) may have been an increase in the coastal undercurrent, which transported unusually warm and saline waters northward at depths below 100 m. The effects of El Niño on surface waters via the atmospheric teleconnection followed in November 1997. Important processes are taking place on other space-time scales as well. Some anomalies and trends in both physical and biological conditions are, at least in part, of long standing and have led to the recognition of decadal and multidecadal variations. The 1997–98 El Niño is as strong as that of the 1982–83 event, and it has had a strong effect on the California Current system.

The 1997 ENSO was predicted by various models well in advance of its inception (e.g., Barnett et al. 1996; Ji et al. 1996; and Kirtman et al. 1996). Although neither the swiftness of its onset nor its considerable strength of warming were predicted, research and monitoring groups were alerted, and lead time was allowed for preparation to intensify and augment observational programs. One augmentation is the additional observation of two of the standard CalCOFI lines (83 and 90) that, along with the quarterly cruises, will result in nearly monthly coverage for the period October 1997 to January 1999. Sampling is being done in the near-coastal region off San Diego to examine the coupling between offshore waters and kelp forests. The frequency and coverage of central California coastal waters was increased by a number of research groups including MBARI, NPS, NAVOCEANO, CalCOFI, and SWFSC. The initial IMECOCAL cruise was rescheduled to start earlier than originally planned in response to the developing El Niño. This ENSO event has been the most well observed to date. Despite the fact that it has yet to complete its course and will have residual effects on various marine populations for some months and perhaps years to come, analyses and reports are under way. The most dynamic effects occur in the eastern tropical Pacific, where the TAO buoy array has provided detailed temporal and spatial information at the equator since its installation in December 1994. The effects of the ENSO upon the North American Pacific coastal zone, whether through atmospheric or oceanic forcing, are even more complex; the observations to date involve numerous agencies and countries. The task that lies ahead for reasearch scientists is to assemble and analyze these observations (and others not herein reported) to provide a comprehensive understanding of the physical forcings and their effects on the marine biosphere.

The oceanic influences of El Niño became evident in deep California coastal waters by July 1997 as an enhancement of the undercurrent, seen as strong poleward flow in the coastal region at 200–300 meters, transporting water that was much warmer and more saline than normal. Although the surface waters were anomalously warm at this time, thermocline depth was near normal. In late fall the thermocline depth began to deepen, and it abruptly increased between November and December 1997. The data from regions off Baja California and central California will be of great value in determining whether events evolved at the same or differing times and in similar ways along the coast.

Changes in the upper ocean circulation pattern were also reflected in plankton populations. The strong association between the upper ocean physical structure and plankton distributions is well documented. However, it still remains to be determined what physical patterns constitute the presence of El Niño conditions in the California Current region and what aspects of a changing physical structure influence the pelagic ecosystem. The linkages between physical structure and ecosystem structure are now well known, but they may differ between El Niño events. Two important mechanisms are changes in range of populations due to changes in the pattern of circulation and hence transport, and direct trophic effects due to changes in nutrient inputs and primary production caused by changes in thermocline and nutricline depth. The data from Baja California and central California will also be of great value in looking at how advection affects changes in plankton abundance. The relative importance of changes due to advection and local changes in production may differ at different locations along the coast.

The 1997–98 period was also one of great changes in the near-coastal ocean. Kelp forest communities were strongly affected, and strong red tide events along the coast were a concern in early 1998. The causal role of El Niño and how these near-coastal populations are linked to the offshore circulation patterns will be an area of active research. It is important to learn to what extent offshore forcing processes influence the coastal region, and to what extent the higher-frequency measurements made at coastal observing programs can be used to understand changes in structure in the offshore region.

At publication time there are continuing new reports of highly unusual catches of commercial and sport fish. These include unseasonal catches or northward range extensions of yellowtail, bonito, barracuda, calico, sand bass, and albacore. Rockfish are at a historic low.

Seabird abundance during 1997–98 was consistently low, when compared to long-term averages and to surveys conducted in 1996. But it may be premature to ascribe fluctuations in seabird abundance during 1997–98 solely to El Niño. Short-term changes in avian abundance must be interpreted with care. Bird distributions do not reflect ocean conditions instantly, but respond after a time lag of several months. Furthermore, seabirds respond to oceanographic variability at multiple scales. Transient distributional changes in response to short-term forcing are embedded in long-term population trends related to ocean warming. El Niño can affect seabird populations at both short (distribution) and long (demography) temporal scales. Additional surveys will be necessary to elucidate the effects of the 1997–98 El Niño on the avifauna within the CalCOFI study region.

A review of the nine different forecast models published in the Experimental Long-Lead Forecast Bulletin (COLA 1998) suggests a near consensus in predicting a return to near normal conditions in the eastern tropical Pacific in 3 to 6 months and a high likelihood of lower than normal SSTs late in the year. The SST anomaly in Niño3 region reached +4°C during the month of December 1997. This SST anomaly has been declining since, although by May 1998 it was barely below +2°C. The experience of the apparent end of the 1992 ENSO and its surprising return in 1993 suggests some caution in relying on the predictions.

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Part II

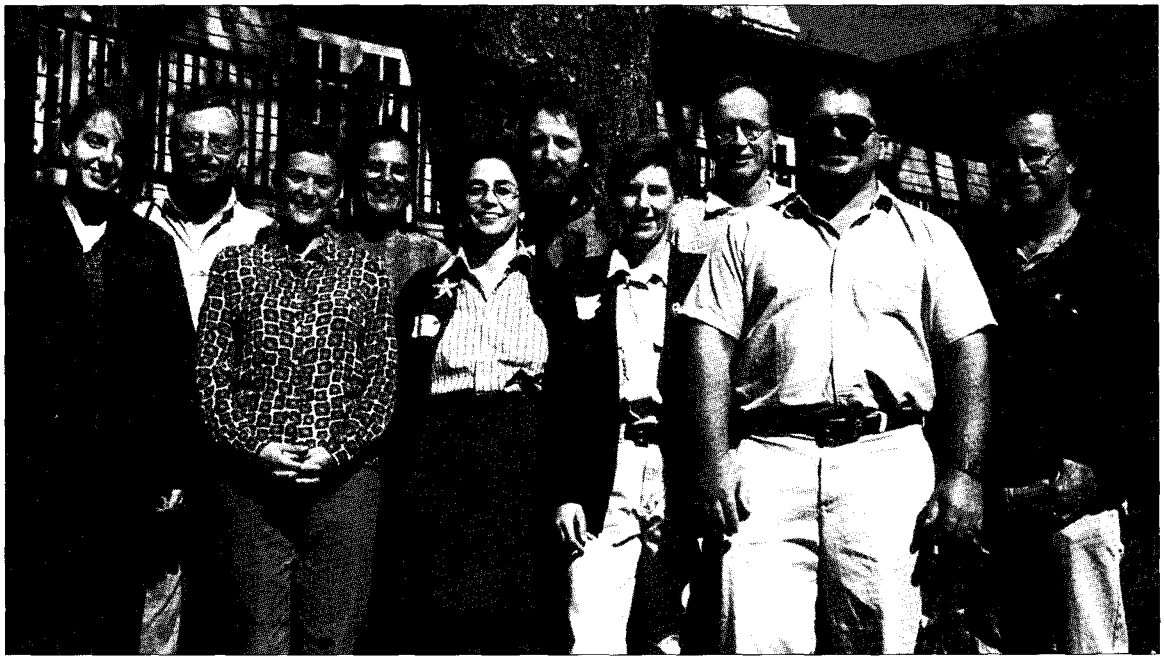
SYMPOSIUM OF THE CALCOFI CONFERENCE

Lake Arrowhead, California
28–29 October 1997

MARKET SQUID: WHAT WE KNOW AND WHAT WE NEED TO KNOW FOR EFFECTIVE MANAGEMENT[1]

Market squid has been harvested in California waters by a variety of methods including hooks and jigs, dip nets, lampara nets, and purse seines. Squid are fished by attracting spawning aggregations to the surface with lights when squid are present in nearshore waters. These techniques have produced commercially viable landings from fishing grounds in Monterey Bay and around Santa Catalina Island for nearly a century. Recently, global markets expanded for California's market squid, and purse seine catches increased dramatically until 1997, when market squid became the largest California fishery by volume landed and by dollar value.

Because of this rapid expansion, mainly at the Channel Islands off southern California, with fishing vessels from as far away as Alaska, the fishing community became concerned about overfishing and overcapitalization. The California state legislature was notified; legislation was prepared and signed into law with significant input from the fishing community working with the California Department of Fish and Game (CDFG). During this process, it became apparent that little was known about the biology or population dynamics of market squid. Consequently, the limited-entry legislation that was passed required CDFG to perform necessary research and provide the legislature with recommendations for managing the market squid resource based on scientific data and input from the fishing community.



Participants in the 1997 Symposium of the CalCOFI Conference: Market Squid: What We Know and What We Need to Know for Effective Management. Left to right, Denise Reichow, Johann Augustyn, Emma Hatfield, Marija Vojkovich, Sophie des Clers, George Jackson, Caroline Pomeroy, Roger Hanlon, Jon Brodziak, and Mark Lowry.

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[1] Supported by the California Seafood Council.

This symposium, sponsored by CDFG and supported by the California Seafood Council, was an initial step in the process of identifying research and management needs for this fishery. Additionally, two evening workshops were held during the conference. They were sponsored by the California Seafood Council and the NOAA Channel Islands Sanctuary to provide an opportunity for conference attendees to participate in dialogue on the topics indicated in the symposium's title.

We sincerely thank the participants for their verbal presentations at the symposium, written papers for the volume, and enthusiastic contributions to the evening workshops. We thank George Hemingway and Mary Olivarria for coordinating logistic support for the symposium and workshops. We thank the anonymous manuscript reviewers and CalCOFI managing editor Julie Olfe for production of the symposium volume. We thank Sean Hastings and Ed Cassano of the Channel Islands Sanctuary for organizing and facilitating the second evening workshop. Finally, we thank Diane Pelshner and the California Seafood Council for providing travel funds for the symposium participants and funds for publishing the symposium.

Doyle Hanan

THE CALIFORNIA FISHERY FOR MARKET SQUID (*LOLIGO OPALESCENS*)

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ABSTRACT

The California fishery for market squid (*Loligo opalescens*) was established over 130 years ago in Monterey Bay, central California. The fishery expanded into southern California after the 1950s, but remained relatively minor until the late 1980s, when worldwide demand for all squid species increased. Landings in California prior to 1987 rarely exceeded 20,000 metric tons. Since then, landings have increased fourfold, and squid is now the state's largest fishery in both tons landed and market value. The number of vessels participating in the fishery has also increased from approximately 85 to over 130.

Industry members have questioned whether such high catches are sustainable. Unfortunately, the California Department of Fish and Game has a paucity of data to determine how best to provide for sustainable harvest. Knowledge and experience from other Loliginid fisheries around the world are sought to guide us in developing a state management plan for the market squid.

INTRODUCTION

For several decades the market squid resource was viewed as vastly underutilized, and many suggested that increased harvest could and should be pursued (Frey 1971; Kato and Hardwick 1975; Recksiek and Frey 1978). Today that view may have changed. A fishery supplying dried product to China during the 1880s–1930s has grown into a fishery providing frozen product worldwide. Squid fishing has grown from a Japan-dominated industry to one of more global involvement. Sonu (1993) indicates that the number of nations landing more than 20,000 metric tons (t) of squid species annually increased from two in 1966 to twelve in 1992. The United States is one of those countries, and contributes approximately 3% to the total world squid catch. *Loligo opalescens* figures prominently in that share. Not only does market squid find its way into restaurants and homes in Spain, Greece, and Japan, it has quite a following in China and here in the United States. Price competitiveness and demand have increased its popularity internationally, and creative recipes and healthy eating campaigns have increased its demand domestically.

Rapidly rising catches and vessel participation over the past four years have focused attention on market squid and California's lack of a plan for sustainable management of the resource. To begin the plan-development process, I will briefly cover some life-history characteristics that make *Loligo opalescens* unique, explain the types of gear and methods employed to harvest squid, provide a brief history of squid catches, and give a general overview of changes in the California squid fishery over the past century.

There is a lot we don't know about market squid, making management of the fishery difficult. I intend to lay the groundwork for further discussions of how we might use knowledge and experience from other *Loligo* fisheries and other research to help develop the Department of Fish and Game's management approach. The papers that follow will likely have major influence on where or how the Department applies its future research and management funding for squid off California.

BASIC LIFE HISTORY

Loligo opalescens is one of 30–40 species of squid in the Loliginidae family (Boyle and Boletsky 1996) and is found from central Baja California, Mexico (Fields 1965), to Southeast Alaska (Wing and Mercer 1990; fig. 1). However, it is rarely available in fishable concentrations north of Vancouver Island, British Columbia, Canada. Although market squid appear to be widely dispersed along most of coastal North America, the areas of greatest spawning activity appear to be off central and southern California (Fields 1965; Kato and Hardwick 1975). In California, it is the only squid species consistently taken for commercial purposes.

Market squid are relatively small. Adults measure up to 305 mm (12 in.) total length and weigh between 56 and 84 g (2–3 oz.). They are short-lived, and are believed to complete their entire life cycle in 12–18 months (Spratt 1979). Mature squid form relatively large spawning aggregations in nearshore waters. Market squid egg capsules are found throughout the year in Monterey Bay, but the greatest concentrations are found in early spring through summer (Fields 1965). In southern California, large spawning aggregations can be observed from November through April (Fields 1965). Egg capsules are usually deposited on a sandy substrate, often at the edges of canyons or rocky outcroppings (McGowan 1954). Mass adult mortalities are evident after spawning events, but it is unclear how long squid live after spawning, or

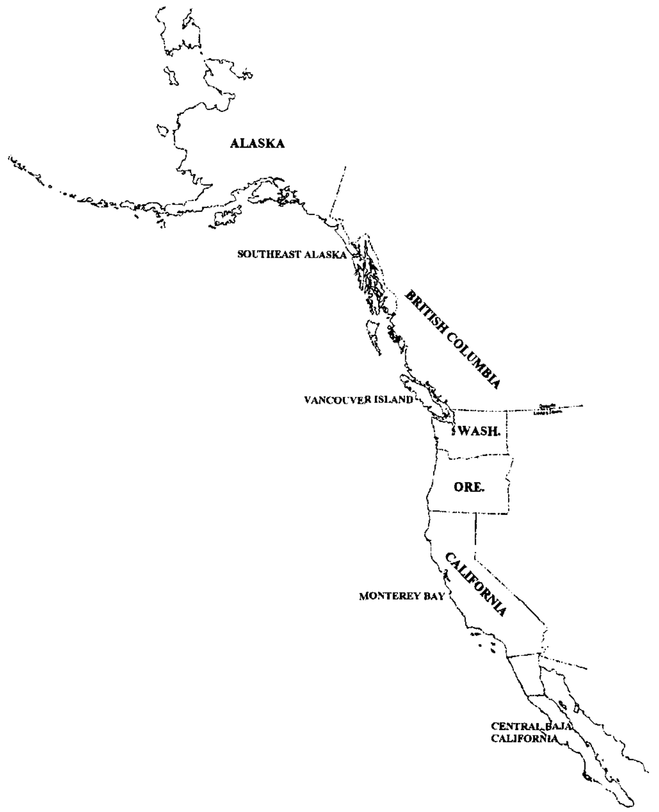

Figure 1. Geographic range of market squid (*Loligo opalescens*).

how many times a squid may spawn (McGowan 1954).

Young squid hatch between 3 and 5 weeks after the egg capsule is deposited, and development is highly correlated with water temperature (McGowan 1954; Fields 1965). Although young squid have been noted in the area of spawning grounds, large concentrations of juveniles have not been found (Okutani and McGowan 1969; Recksiek and Kashiwada 1979). Likewise, distribution information about nonspawning adults is scant, although some information does exist from research cruises (Mais 1974; Ally et al. 1975) and commercial trawler landings. Because *L. opalescens* are highly phototropic (Fields 1965), the fishery often uses lights to attract spawning aggregations.

HISTORY OF THE FISHERY AND GEAR

The Chinese were the first to harvest squid off North America, in Monterey Bay, California. In the late 1800s they used small skiffs, lit torches to attract the squid to the surface, and deployed purse seines to capture the squid (Scofield 1924; Kato and Hardwick 1975; Recksiek and Frey 1978; Dickerson and Leos 1992). They dried their catch and shipped most of it to China, although some was probably consumed locally and in nearby San Francisco (Scofield 1924). In 1905, Italian immigrants introduced the lampara net into the fishery and outcompeted the Chinese, who settled into the processing and exporting business (Scofield 1924; Kato and Hardwick 1975; Recksiek and Frey 1978; Dickerson and Leos 1992).

Both the purse seine and lampara net are round haul nets. The webbing of the nets is laid out to encircle a school of squid (Fields 1965; Kato and Hardwick 1975). A purse seine net has metal rings sewn along its bottom edge, and a cable is passed through the rings. When the cable is drawn tight, the net "purses" (Fields 1965). The lampara net does not have rings, but rather tapered "wings" of webbing on both sides so the body of the net tends to form a bag. When the wings of the net are drawn simultaneously toward the vessel, the bottom of the net essentially closes together and the fish are herded toward the bag portion of the net (Kato and Hardwick 1975). Until the 1970s a small brail net was used to lift squid out of the main net, a couple of hundred pounds at a time, and into the vessel's hold. Now a centrifugal pump is lowered into the bagged school of squid, and water and squid are pumped through a separator and into the hold of the fishing vessel (described in Kato and Hardwick 1975).

Lights, as an attractant, have been allowed and disallowed many times since the fishery began in Monterey (Dickerson and Leos 1992). Lights have never been prohibited in southern California and presently are allowed, with few restrictions, everywhere in the state. Using lights to attract spawning aggregations of squid to the surface of the water column is effective because of the animal's phototropism. Lights are used for both round haul nets and brail fishing (Kato and Hardwick 1975).

In southern California, lights and brail nets were used almost exclusively until the late 1970s (Dewees and Price 1982). Squid were attracted to the surface by high-intensity lights and the brail net was used to scoop the squid aboard; no other net was used (Kato and Hardwick 1975; Dickerson and Leos 1992). Vessels using this method were referred to as "scoop" or "brail" boats. These boats tended to be smaller and required smaller crews than the purse seine or lampara vessels (Kato and Hardwick 1975).

Around 1977 there was a definite shift in fishing gear from brail vessels to purse seine vessels in southern California (fig. 2). Today nearly all of the squid are landed by purse seine nets. Members of the squid industry have indicated that economics forced that change. Tuna and "wetfish"[1] vessels were looking to participate in more

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[1] The term *wetfish* was historically used to describe how a group of small pelagic species (i.e., anchovies, Pacific sardines, mackerels, etc.) was processed at canneries. The species were placed in cans in a "wet," or fresh, condition and then cooked (Frey 1971; Klingbeil 1992). Vessels harvesting such species are typically referred to as the wetfish fleet.

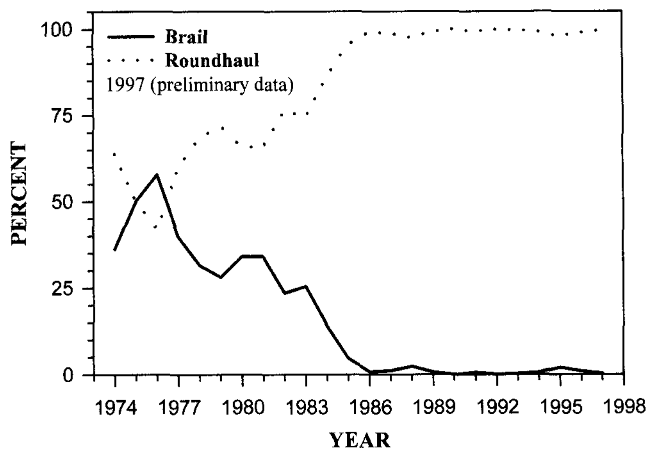

Figure 2. Proportion of squid landings taken with round haul gear (lampara and purse seines) and brail gear, by calendar year.

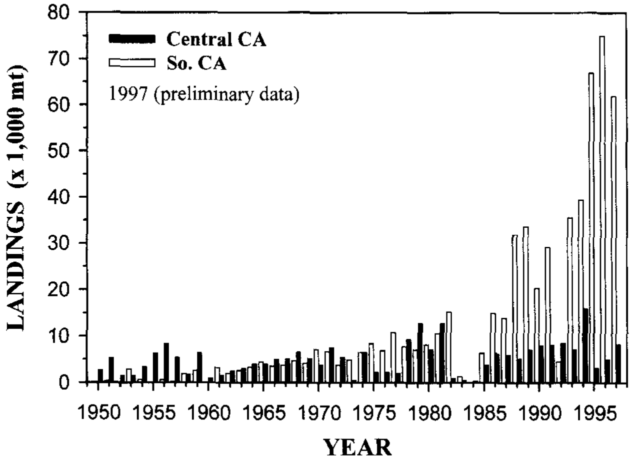

Figure 3. California squid landings (metric tons) by region and calendar year.

lucrative fisheries closer to home. In addition, brail vessels had difficulty competing because seiners could meet the market demand more efficiently. With the current market demand so strong, there appears to be room for every type of gear, but brail vessels haven't reentered the fishery in appreciable numbers.

CATCHES AND FISHERY DYNAMICS

Until the mid-1920s annual squid landings rarely exceeded 270 t (Scofield 1924). A healthy export market to China existed from 1923 to 1932, and catches increased to an average of 1,900 t annually. When the export market collapsed because of adverse financial conditions, most squid were used domestically, and catches averaged about 365 t for the next decade (Fields 1965; Frey 1971; Dickerson and Leos 1992). The central California coast, specifically Monterey Bay, produced nearly all the market squid catches until the early 1950s.

Fishing for squid began in southern California as demand for seafood increased after World War II. Landings were evenly divided between central California and southern California from 1960 until the early 1980s (fig. 3). Since the late 1980s, southern California has far outpaced central California in landings. Annual landings of squid in central California have averaged around 6,000 t since 1950. In contrast, southern California landings have increased from an annual average of 9,000 t during the 1970s and early 1980s to over 41,000 t in the past ten years (fig. 3).

Squid fishermen were paid less than $14 per t in the early 1900s (Scofield 1924). After canning and freezing became the method of preserving squid, fishermen were paid differently depending on which method was to be employed. As late as 1981 fishermen were getting between $105 and $253 per t, depending on how the squid was to be processed (DeWees and Price 1982). Now most squid is frozen and exported. It is used primarily for human consumption, to a lesser extent as animal feed, and as bait in both recreational and commercial fisheries. Most recently, squid has averaged $294 per t, but the price varies throughout the season and geographic location of landing. When supply did not meet the demand, the ex-vessel value rose as high as $452 per t.

FACTORS AFFECTING CATCHES

Within the last few years, market squid has become the number one fishery in California in both tons landed and value (table 1). Two major factors have influenced

TABLE 1
Top Three California Fisheries in Metric Tons and Ex-vessel Value

Metric tons		U.S. dollars (millions)	
1992			
Mackerel	19,733	Red urchin	29.2
Pacific sardine	17,914	Dungeness crab	10.7
Red urchin	14,649	Rockfishes	10.3
1993			
Squid	42,630	Red urchin	26.7
Pacific sardine	15,329	Dungeness crab	13.2
Mackerel	13,469	*Squid*	10.5
1994			
Squid	55,374	Red urchin	25.3
Mackerel	12,698	Dungeness crab	18.5
Pacific sardine	11,610	*Squid*	16.2
1995			
Squid	69,841	Red urchin	22.5
Pacific sardine	40,635	*Squid*	21.8
Mackerel	10,340	Dungeness crab	14.6
1996			
Squid	80,272	*Squid*	33.3
Pacific sardine	32,517	Red urchin	18.7
Mackerel	11,791	Dungeness crab	17.2

Source: California Department of Fish and Game Commercial Fisheries Information System database.

these steeply rising numbers. Most obvious is the increase in market demand, which is fueled by the expanding global economy and the unavailability of export squid species from the Falkland Islands, Japan, and New Zealand (Sonu 1993). Exports of market squid from California to various nations have changed significantly since 1991 (table 2). The greatest changes have been a decrease of exports to Japan and an increase of exports to Europe and Asia. Over 60% of exported frozen squid goes to Asia, and China buys most of it (93%). We assume that the demand will continue as long as market squid prices in California remain competitive to foreign importers.

The second factor affecting squid landings is an increase in fishing effort in southern California. Dickerson and Leos (1992) stated that the expansion of fishing effort to previously underutilized squid spawning habitat has definitely affected catches. If squid availability and demand are high, the southern California fleet does well. The Monterey fishing fleet catches seem to be more stable even when demand is high. This may be because of the limited fishable habitat for squid in central California. Although it is assumed that squid spawn all along the coast, much of the central California coast is rocky, is fully exposed to weather patterns, and has a narrow continental shelf. The topography and weather patterns in southern California, especially the northern Channel Islands, allow for substantially more fishable spawning habitat. Thus when global demand increased (as it did in the last ten years) and squid were available, more of the southern California squid spawning habitat was exploited, and catches increased.

Climatological changes can also affect squid catches (Dickerson and Leos 1992). In the Monterey area, warmer than normal water temperatures appear to have a positive effect on catches 18 months later (McInnis and Broenkow 1978). El Niño events, however, seem to have the opposite effect. Squid landings in California decreased during the two major El Niño events since 1950 (fig. 4). Other, less strong, El Niño years, such as 1973–74 and 1992–93, show some apparent effect on squid catches as well. A strong El Niño developed in the equatorial

TABLE 2

California Exports of Market Squid to Various Countries

1991	
Japan	37%
Europe	29%
Philippines	15%
Other Asia	<1%
All others	~18%
Metric tons exported	12,546
1992	
Japan	16%
Europe	41%
Philippines	21%
Other Asia	5%
All others	17%
Metric tons exported	13,468
1993	
Japan	25%
Europe	53%
Philippines	2%
Other Asia	5%
All others	15%
Metric tons exported	9,003
1994	
Japan	16%
Europe	54%
Philippines	7%
Other Asia	10%
All others	13%
Metric tons exported	24,406
1995	
Japan	11%
Europe	28%
Philippines	6%
Other Asia	51%
All others	4%
Metric tons exported	38,353
1996	
Japan	12%
Europe	16%
Philippines	<1%
Other Asia	67%
All others	~4%
Metric tons exported	51,669
1997	
Japan	5%
Europe	34%
Philippines	4%
Other Asia	53%
All others	4%
Metric tons exported	59,933

National Marine Fisheries Service statistics. Assumes all squid exported through California ports is *Loligo opalescens*.

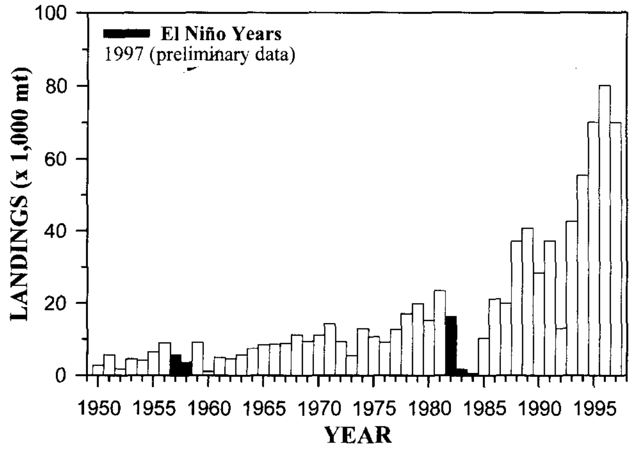

Figure 4. Statewide squid landings (metric tons), with major El Niño events indicated.

Pacific during 1997, and we believe that winter squid catches in southern California will be negatively affected, as in the past.

VESSEL PARTICIPATION

During the 1970s and 1980s, an average of 85 vessels were active in the squid fishery (fig. 5). Since 1993 the number of vessels landing over 0.5 t of squid has increased to nearly 135. The past four years of unmet demand and easily available squid have attracted many to the fishery. Some of the recent increase has come from out-of-state vessels (fig. 5), but many new entrants are from within California. The vessels from out of state have been salmon and herring seiners active at other times of the year in Alaska and Washington fisheries.

Many of the newly arrived vessels are of recent vintage and have sophisticated electronics and refrigerated fishholds. They are typically 17.7 m (58 ft.) long and of steel construction, with a fish capacity of 55 t. Many vessels in the California fleet have upgraded during the past 15 years, but many remain from the wetfish and tuna fishery of the 1950s and 1960s. They tend to be 24.4 m (80 ft.) long, with fishholds of 68–108 t, many of which are not refrigerated. Some processors prefer loads of squid that have been kept refrigerated because they hold up better in transport and provide for a better-quality product. Consequently, this has resulted in a keen level of competition between owners of older or unrefrigerated vessels and owners of more updated vessels.

Participation in the squid fishery has also grown because it has been relatively free of regulation. Because many fisheries (i.e., nearshore gillnetting, salmon, herring) have become more restrictive, and access to them has become tightly controlled, an opportunity to enter an open and profitable fishery is viewed by many as the chance of a lifetime. There are some minor area closures in effect along Santa Catalina Island and a weekend closure in Monterey Bay, but all that is needed to participate in this fishery are a California commercial fishing license and boat registration.

Many participants in California's squid fishery operate on a "statewide" basis. Although Monterey vessels tended to fish only in Monterey Bay in earlier years, the offset fishing "seasons" have made it attractive for them to fish southern California waters also.

SUMMARY

Until recently the fishery for squid has grown at moderate levels. During the mid-1970s some fishing industry members from Monterey voiced concerns that spawning aggregations were being fished very near shore, that squid were low in the food chain, and that we knew next to nothing about them. With monies collected from a special tax levied on the wetfish fleet (begun in the 1940s) to study wetfish, the Department directed some of those funds and some Sea Grant funds to researching squid (H. Frey, San Pedro, Calif., pers. comm., Feb. 1998). A major research cooperative was developed by the Department and Moss Landing Marine Laboratories to answer questions about age and growth, maturity and fecundity, spawning habits and habitats, assessment techniques, population structure, environmental influences, and harvest impacts on squid and its prey and predators. These are necessary bits of scientific information upon which management decisions are made.

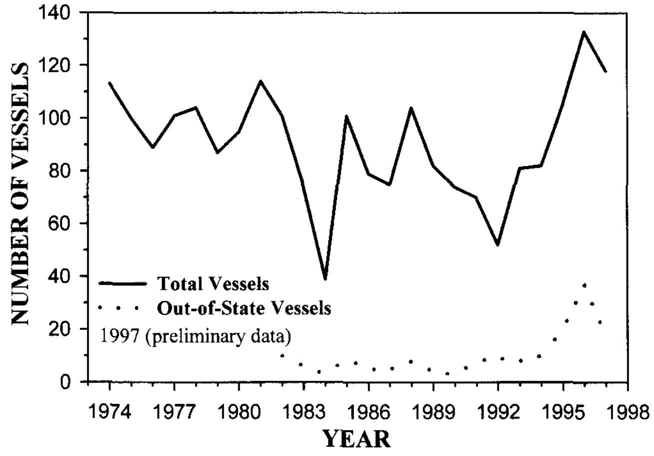

Figure 5. Number of vessels landing more than 0.5 metric tons in California, by calendar year.

Results from some of the research form the basis upon which we presently weigh the "status" of the market squid resource. The studies found that squid are abundant in the waters of the California Current and are a major food source for other marine animals. It was found that squid spawn during only one spawning period. Ageing of statoliths indicates that squid live less than two years.

Other results, however, were not conclusive. Specifically, studies were unable to identify more than one population of squid along the West Coast even though there is a temporal and geographic separation between "fishable" spawning aggregations. There appeared to be a correlation between squid availability and oceanographic conditions, but the results were geographically limited. Some acoustic techniques held promise for assessing squid biomass but needed additional testing (Recksiek and Frey 1978).

In a proactive management move, a draft management plan was prepared by biologists involved in squid research for presentation to and consideration by the newly formed Pacific Fishery Management Council. The council felt that there was no need to federally manage squid, because most of the fishing occurred in state waters, and only during occasional warm-water events like El Niño was there a fishery for squid in Oregon and Washington. Interest in expanded squid exploitation wasn't quick to develop; the fishery appeared to be healthy; and the fishing industry convinced the California legislature to rescind the extra research tax on wetfish (H. Frey, pers. comm., Feb. 1998). Continued interest in squid research was put on the back burner and has remained there until just recently. It is important to note, however, that Recksiek and Frey (1978) concluded that if squid-importing countries began to accept smaller frozen squid, then there appeared to be considerable potential for an expanded fishery for *L. opalescens*. In less than two decades their predictions and vision have become a reality.

So where are we now? We have a major fishery for a species that appears to have unlimited market demand. We have a rapidly increasing squid fishing fleet and a fishery that is technically unmanaged. And we are still asking some of the same questions we asked in the mid-1970s. Is there only one population of squid on the West Coast? How large is the population? Where do squid spawn? What influences population changes or availability? How does exploitation affect the stock(s)? How important is squid in the food web, and how do we factor that into management? How are we to best manage this fishery for sustainable use?

In presenting the lead paper for this symposium, my objective is to set the stage for the papers that follow. The Department's overall goal is to develop a management protocol that will consider this squid fishery from an ecosystem perspective and provide for a sustained fishery. How we are to achieve this objective will likely depend on the information provided in the following papers and the discussions that ensue. We are fortunate to have information about Loliginid fisheries from around the world presented at this 48th CalCOFI Conference.

ACKNOWLEDGMENTS

I thank the members of the squid fishing industry for openly discussing the fishery with me and allowing me to observe their fishing operations. I thank the California Seafood Council for its generous support. I thank Mary Larson and John Ugoretz for producing the graphics used in this paper and other presentations about the squid fishery throughout the year. I also thank Rick Klingbeil for his editorial comments, as well as those anonymous reviewers who give freely of their time and talents to make all of us better communicators.

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REVISED BIOLOGY AND MANAGEMENT OF LONG-FINNED SQUID (*LOLIGO PEALEI*) IN THE NORTHWEST ATLANTIC

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ABSTRACT

New biological information on the growth and life cycle of the long-finned squid (*Loligo pealei*) became available as ageing procedures based on statoliths were applied to this valuable commercial resource in the 1990s. It was found that *L. pealei* grew very rapidly and completed its life cycle in less than one year. This research led to several important changes in management for the *L. pealei* fishery. First, biological reference points were developed for summer- and winter-hatched squid based on differences in growth and maturation rates between seasonal cohorts. Second, a precautionary approach was taken toward determining the annual allowable catch and long-term potential yield. The revised estimate of long-term potential yield of 21,000 metric tons (t) based on a life span of less than one year was less than half of the previous estimate of 44,000 t, which was based on an assumed life span of roughly two years. Third, limited entry was applied to the commercial squid fishery because the stock was fully exploited on the basis of the revised estimate of long-term potential yield. The Mid-Atlantic Fishery Management Council has set the current annual domestic allowable harvest of *L. pealei* to equal the revised estimate of long-term potential yield, and in-season monitoring of landings and enforcement of the domestic allowable harvest level have been planned.

INTRODUCTION

The long-finned squid (*Loligo pealei*) ranges from the Gulf of Venezuela, Venezuela (Summers 1983), to Newfoundland, Canada (Dawe et al. 1990). The *L. pealei* resource in the northwest Atlantic is distributed from its southern zoogeographic boundary of Cape Hatteras, North Carolina, to Georges Bank (NEFSC 1996). Although separate populations of *L. pealei* exist in the Gulf of Mexico (Hixon 1980) and along the Eastern Scotian Shelf (Dawe et al. 1990), these portions of the resource have not been subject to intensive commercial harvest and are outside the scope of this study.

North of Cape Hatteras, the *L. pealei* population undertakes seasonal migrations to avoid cold waters with bottom temperature lower than 8°C (Summers 1969; Serchuk and Rathjen 1974; Vovk 1978; Lange and Sissenwine 1983) and to occupy favorable spawning grounds close to juvenile nursery areas in coastal waters (Vecchione 1981). In early winter *L. pealei* migrate offshore to avoid the autumn cooling of coastal waters. Submarine canyons and areas along the edge of the continental shelf at depths of 100–250 m have warmer water temperatures during winter (9°–12°C) and provide suitable habitat for *L. pealei* (Vovk 1978; Lange and Sissenwine 1983; Summers 1983). During spring, *L. pealei* migrate inshore to continental shelf and coastal waters (<100 m), where they spawn and feed. In general, these migrations can complicate interpretation of length-frequency data and bias estimates of squid growth that are based on localized sampling (Hatfield and Rodhouse 1994).

Diel migrations can also complicate the interpretation of *L. pealei* catch and length-frequency data. Although adult *L. pealei* are primarily demersal (cf. Hanlon et al. 1983), juvenile *L. pealei* migrate vertically upward in the water column at night to avoid predation or to acquire prey (Summers 1968; Brodziak and Macy 1996). As a result of these movements, bottom trawl catches of *L. pealei* juveniles and adults are generally larger during daylight hours, and estimates of the relative magnitude of diel effects on research survey catches of *L. pealei* have been developed (Sissenwine and Bowman 1978; Brodziak and Hendrickson, in press).

New biological information on the growth and life cycle of *L. pealei* became available as ageing procedures based on statoliths were applied to this valuable commercial resource in the 1990s (Macy 1995a). Results showed that *L. pealei* grew very rapidly and completed its life cycle in less than one year (Macy 1995a; Brodziak and Macy 1996). This research led to several important changes in management for the *L. pealei* fishery.

In this paper, I describe how fishery management procedures for the *L. pealei* resource in the northwest Atlantic were revised to account for improved understanding of its life cycle and growth. I begin by describing some previous theories on the life cycle and growth of *L. pealei*. The history of fishery management of this loliginid is also briefly discussed. I then describe the application of statolith ageing techniques to *L. pealei* and identify some important consequences of this research. Revised management measures for the *L. pealei* fishery and their

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rationale are described; these measures include revised biological reference points, estimates of long-term potential yield, and limited entry to the commercial fishery. Last, some areas of future research that may reduce uncertainty in the management of the *L. pealei* resource are discussed.

EARLY IDEAS ABOUT LIFE CYCLE AND GROWTH

Previous researchers assumed that the life span of *L. pealei* exceeded one year (Verrill 1881; Mesnil 1977; Lange and Sissenwine 1983; Summers 1983; NEFSC 1988). Length-frequency data collected from research surveys and other sources generally indicated the presence of multiple cohorts within a year due to a protracted spawning season. But these data also suggested that there were two primary cohorts each year: spring and late summer (Summers 1968, 1971; Mesnil 1977; Lange 1981; Lange and Sissenwine 1983). Analysis of the modes of successive length-frequency samples led to the hypothesis that these two primary cohorts were linked through time (Mesnil 1977; Summers 1983; Lange and Sissenwine 1983).

In the crossover life-cycle model of Mesnil (1977), the spring cohort was expected to return to spawn in late summer of the following year at an age of about 14–16 months. The late-summer cohort was expected to return to spawn in spring two years later at an age of about 20–22 months. Thus the two primary cohorts produced each year were expected to maintain separate breeding lines that successively changed from a spring spawner life cycle to a late-summer spawner life cycle. This was called the crossover life-cycle model and was accepted as the best hypothesis for *L. pealei* until the application of statolith ageing to this species in the 1990s (Brodziak and Macy 1996).

Historically, research on the pattern and rate of growth of *L. pealei* was based on analysis of the progression of modes within successive length-frequency samples (Verrill 1881; Summers 1968, 1971; Cohen 1976; Mesnil 1977; Lange 1980; Lange and Sissenwine 1980; Macy 1980; Hixon et al. 1981). These analyses suggested growth rates of 10–24 mm of mantle length per month (Hixon et al. 1981).

The assumption that growth of *L. pealei* followed a Von Bertalanffy growth curve was used to analyze some inferred length-at-age data (Ikeda and Nagasaki 1975; Lange 1980), where cohort ages were inferred from modes of length-frequency distributions. However, this asymptotic growth model did not seem appropriate for some of the inferred length-at-age data (Lange 1980; Lange and Sissenwine 1983).

Regardless, alternative indirect estimates of growth have been used to calculate yield per recruit for various fishery selectivity patterns. When coupled with estimates of recruitment, these yield-per-recruit estimates provided a rationale for evaluating the potential yield from the *L. pealei* resource under various fishery selectivity patterns and fishing mortality rates (Lange 1981; Lange and Sissenwine 1983).

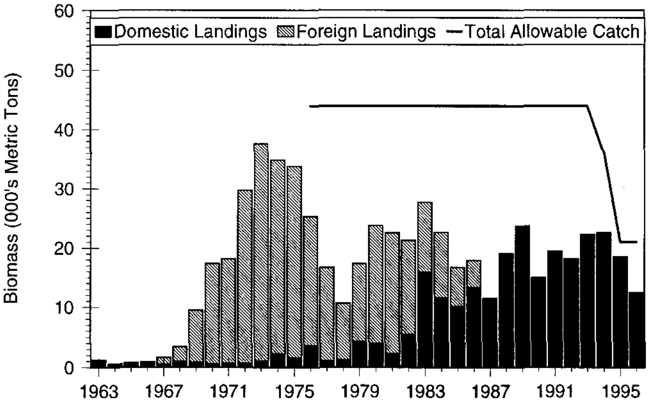

Figure 1. Foreign and domestic landings of *Loligo pealei* from Cape Hatteras to the Gulf of Maine, 1963–96, and total allowable catch.

HISTORY OF FISHERY MANAGEMENT

Before the 1960s, domestic fisheries for *L. pealei* were small-scale, and much of the yield was used as bait. Fleets from Japan, Spain, and the USSR began harvesting the *L. pealei* resource during the late 1960s in offshore waters of New England and the Mid-Atlantic Bight (Lange and Sissenwine 1983). These trawl fisheries were primarily prosecuted in winter, when squid were aggregated near canyons or along the edge of the continental shelf. Eventually, the foreign fisheries were managed on a total allowable catch basis under the auspices of the International Commission for the Northwest Atlantic Fisheries (ICNAF). An initial total allowable catch (TAC) of 71,000 t was established for combined landings of *L. pealei* and northern shortfin squid (*Illex illecebrosus*) in 1974–75 (Lange and Sissenwine 1980); a separate TAC for *L. pealei* was set at 44,000 t in 1976–77. However, the United States withdrew from ICNAF after passage of the U.S. Fishery Conservation and Management Act (FCMA) of 1976, which established national responsibility for fishery resources within 200 miles of U.S. land boundaries. As a result, total landings of *L. pealei* by foreign nations were reduced through the late 1970s and early 1980s as domestic fishers supplanted foreign fishers under auspices of the FCMA (fig. 1). Foreign fishing for *L. pealei* ceased in 1987.

The traditional fishing season for *L. pealei* by domestic fishers extended from late spring through summer, when squid were available inshore (Lange et al. 1984; Brodziak and Rosenberg 1993). Many vessels in the domestic fishery used bottom otter trawl gear to capture squid, although some landings were made inshore with floating traps and fish weirs (McKiernan and Pierce 1995). In the early 1980s, however, the domestic trawl fleet began to expand and to harvest more squid offshore during winter. Most vessels in the winter offshore fishery were stern trawlers (150–2,000 gross registered tons) that harvested *L. pealei* on its overwintering area along the edge of the continental shelf at depths of 100–500 m (Lange and Sissenwine 1983). As a result, the domestic fishery now has two components: an inshore summer fishery and an offshore winter fishery (NEFSC 1996). The development of a domestic winter fishery had important consequences for the management of the *L. pealei* resource because it led to an expansion of domestic fishing effort directed at this species.

STATOLITH AGEING

Squid statoliths are paired calcareous structures that are functionally analogous to fish otoliths (Rodhouse and Hatfield 1990). Fine, ringlike structures within statoliths were observed by Clarke (1966), who suggested that these increments might provide information on squid age. But it was not until the early 1990s that statolith ageing became an accepted method for measuring squid age (Jereb et al. 1991; Jackson et al. 1993; Jackson 1994a). Growth increments in the statolith appear as pairs of light and dark bands formed over a 24-hour period (Jackson 1994a). These increments have been shown to be formed on a daily basis for several squid species (Hurley et al. 1985; Lipinski 1986; Jackson 1990a, b, 1994b; Jackson et al. 1993).

Macy (1995a) applied statolith ageing techniques to *L. pealei* in the early 1990s. Statolith ageing of this species was difficult because of the fine scale of increment structure; as a result, Macy used digital image analysis to improve the resolution of the fine increments. This research indicated that the largest specimens (over 40 cm long) were less than 300 days old (Macy 1995a; Brodziak and Macy 1996). Verification of the one-day one-increment hypothesis was difficult for *L. pealei* because they can be challenging to rear in captivity (Summers 1983; Macy 1995a). Nonetheless, the hypothesis that statolith increments are formed daily in *L. pealei* is the most credible hypothesis on the basis of limited tetracycline marking data and by analogy with other loliginid species (Brodziak and Macy 1996).

The implications of statolith ageing research for squids have been substantial in recent years (Jackson 1994a). Patterns of growth for exploited species such as *L. pealei* appear to be linear or exponential, so that adult sizes do not approach an asymptote (Jackson 1994a; Brodziak and Macy 1996). This contrasts the asymptotic pattern of growth epitomized by the Von Bertalanffy growth curve, which is commonly used for analysis of size-at-age data for marine fishes.

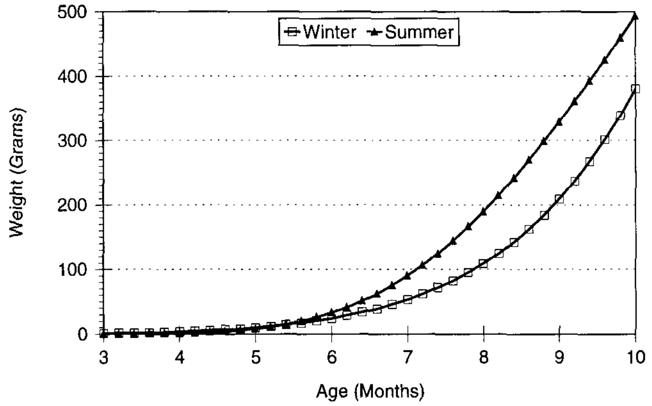

Figure 2. Size at age of winter-hatched (open square) and summer-hatched (solid triangle) *Loligo pealei*. (Data from Brodziak and Macy 1996.)

In part, the acceptance of statolith ageing techniques as valid measures of age has led to the realization that squids, such as *L. pealei*, grow more rapidly than once thought and do not conform to commonly accepted growth models for finfish. Although there is still some debate over the general pattern of growth of squids, the examination of nonasymptotic growth curves is recommended, and objective approaches to determine the most parsimonious growth model have been developed (Brodziak and Macy 1996). For *L. pealei*, the statolith ageing research led to revised estimates of key life-history parameters and to improved interpretations of abundance measures and fishery impact (Brodziak and Macy 1996; NEFSC 1996).

Revised Life-History Parameters

Revised estimates of life-history parameters of *L. pealei* are reported in Brodziak and Macy 1996 and NEFSC 1996. Revised estimates of growth of *L. pealei* in the northwest Atlantic were derived by Brodziak and Macy (1996). They found that seasonal differences in growth were substantial between squid hatched during "summer" (June–October) and "winter" (November–May). Weight at age increased exponentially for both summer- and winter-hatched squid, but growth was slower, on average, for winter-hatched squid, which experienced lower temperatures as juveniles (fig. 2). The slower growth of winter-hatched squid implied that the yield per recruit would differ for the domestic winter fishery, which primarily captured summer-hatched squid, in comparison to the domestic summer fishery, which primarily harvested winter-hatched squid.

Revised monthly estimates of the instantaneous natural mortality rate of *L. pealei* were derived with the new information on life span. Three methods were used to estimate natural mortality (NEFSC 1996). On the basis of Hoenig's regression method (Hoenig 1983) and a maximal age of 296 days, instantaneous natural mortality was

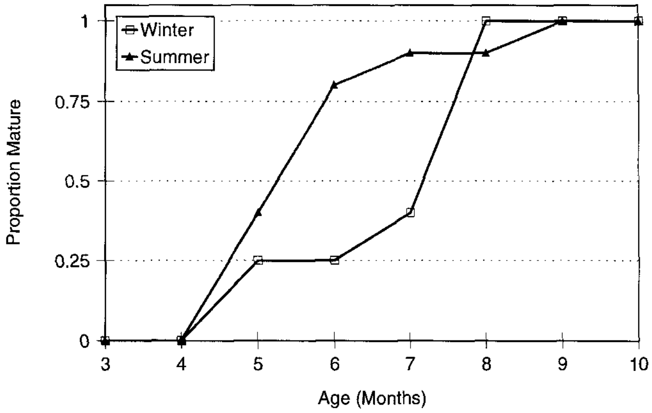

Figure 3. Fraction mature at age of winter-hatched (open square) and summer-hatched (solid triangle) *Loligo pealei*. (Data from Macy 1995b.)

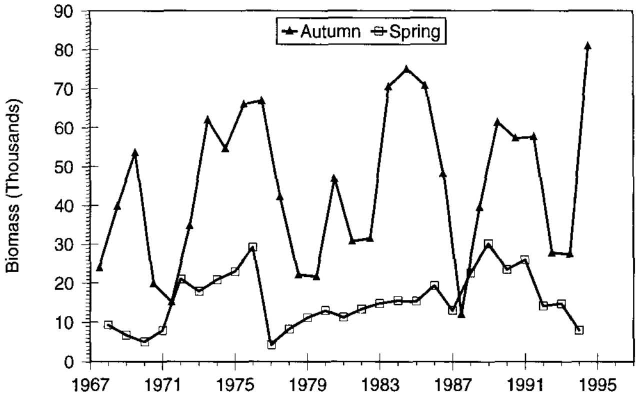

Figure 4. Diurnally adjusted swept-area estimates of *Loligo pealei* biomass (t) during autumn (solid triangle) and spring (open square) NEFSC bottom trawl surveys, 1967–94.

estimated to be $M_m = 0.34$ per month. Another method was based on the analogy that the monthly natural mortality rate of *L. pealei* would be similar to that of other commercially exploited squid species. Rosenberg et al. (1990) reported a monthly natural mortality rate of $M_m = 0.26$ per month for *Illex argentinus*. The third method used the process of Peterson and Wroblewski (1984) to derive a natural mortality rate on the basis of animal size and bioenergetic constraints. With an assumed weight coefficient of growth of $k = 0.018$ per day estimated for female *L. pealei*, and a mean size of 25 g taken from the annual NEFSC autumn bottom trawl survey, it was estimated that monthly natural mortality was $M_m = 0.30$ per month. The average of these three estimates was $M_m = 0.3$ per month, and this value of natural mortality was accepted as the best current estimate for *L. pealei* (NEFSC 1996).

Revised estimates of fraction mature at age by hatch season were developed from statolith ageing and Macy's classification method for determining maturity stage of *L. pealei* (Macy 1982). The classification of squid as mature (stage III or IV) or immature (stage I or II) was accomplished for both summer- and winter-hatched *L. pealei* (NEFSC 1996). Empirical estimates of the fraction mature at age in months (Macy 1995b) were greater for summer-hatched *L. pealei* than for winter-hatched squid (fig. 3).

Interpretation of Abundance Measures and Fishery Impact

Research surveys conducted by the NEFSC during spring and autumn provide measures of *L. pealei* abundance and biomass (Lange and Sissenwine 1980, 1983; NEFSC 1996). These surveys have employed standard bottom trawl gear to sample demersal species composition and abundance on the continental shelf off the northeast United States from Cape Hatteras to the Gulf of Maine since the late 1960s (Azarovitz 1981). Both juvenile and adult *L. pealei* have been routinely captured during the NEFSC spring and autumn bottom trawl surveys since these surveys began in the 1960s. Trends in abundance of *L. pealei* during research surveys were difficult to interpret under the crossover life-cycle model because the expected life span of about two years suggested that there would be more moderate changes in population size over several years than were observed. In contrast, under the annual life-cycle model of *L. pealei*, short-term patterns of above-average or below-average abundance can be observed from the spring and autumn survey series (fig. 4). These patterns are due to the approximate 6-month lag between hatching and recruitment to the sampling gear (Brodziak and Macy 1996, fig. 3).

RESEARCH SURVEYS

Measures of the abundance of the *L. pealei* population north of Cape Hatteras have been developed from the NEFSC spring and autumn bottom trawl surveys on the basis of diurnally adjusted swept-area estimates of biomass (Lange and Sissenwine 1980, 1983; NEFSC 1996). In general, the catchability of *L. pealei* by the bottom trawl survey gear is lower at night than during the day, although the diel effect is more pronounced for juveniles than for adults (Brodziak and Hendrickson, in press). Size-specific correction factors have been developed to adjust nighttime catches of juvenile and adult squid to equivalent daytime units (Sissenwine and Bowman 1978; NEFSC 1996; Brodziak and Hendrickson, in press). For *L. pealei*, the application of correction factors for diurnal catchability leads to a time series of diurnally adjusted swept-area biomass estimates (fig. 4). The diurnally adjusted spring biomass estimate provides an estimate of population biomass at the beginning of the domestic summer fishery (April–September). Similarly, the diurnally adjusted autumn biomass estimate provides a measure of population biomass at the beginning of the winter fishery (October–March).

COMMERCIAL FISHERY

Estimates of standardized landings per unit of effort have been developed for winter and summer bottom otter trawl fisheries that capture *L. pealei* (NEFSC 1996). Here the winter fishery is defined as bottom otter trawl fishing trips during October through March with at least 10% landings of *L. pealei* by weight. Thus, the winter fishery is a contiguous 6-month period that includes fishing trips from October through December of the previous year. The summer fishery is defined similarly, as bottom otter trawl fishing trips during April through September with at least 10% landings of *L. pealei* by weight.

Estimates of standardized landings per unit of effort (LPUE) and standardized fishing effort were derived for both the winter and summer fishery with a general linear model with main effects of year, tonnage class, area, and month. The winter fishery shows increasing trends in LPUE and fishing effort during 1983–93 (fig. 5). In contrast, the summer fishery shows a declining trend in LPUE during 1983–93 and a moderate decline in effort during 1986–93 (fig. 6). When winter fishing effort is compared to LPUE the following summer, there is a significant decreasing trend in summer LPUE with increasing winter effort (fig. 7). Although this trend does not imply causation, since environmental factors may be involved, it does suggest the possibility that high levels of winter fishing effort may have reduced recruitment to the subsequent summer fishery.

Estimates of monthly fishing mortality rates for winter and summer fisheries have also been developed from diurnally adjusted estimates of spring and autumn abundance and fishery landings. In particular, swept-area biomass from the spring survey provides an estimate of population size at the beginning of the summer fishery, whereas biomass from the autumn survey provides an estimate of population size at the beginning of the winter fishery. Estimates of 6-month exploitation rates were obtained by dividing winter or summer fishery landings by estimated population biomass at the beginning of the fishery season. The 6-month exploitation rates were converted to instantaneous monthly rates for comparison with biological reference points (fig. 8). These mortality rates are based on landings and do not account for potential discarding of *L. pealei* in the trawl fisheries.

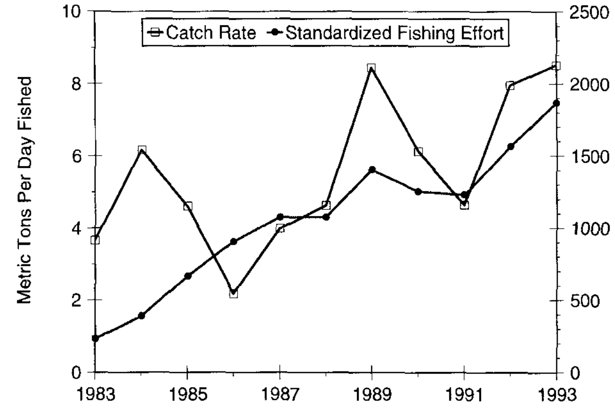

Figure 5. Standardized catch rate (open square) and fishing effort (solid circle) for the domestic winter trawl fishery, 1983–93.

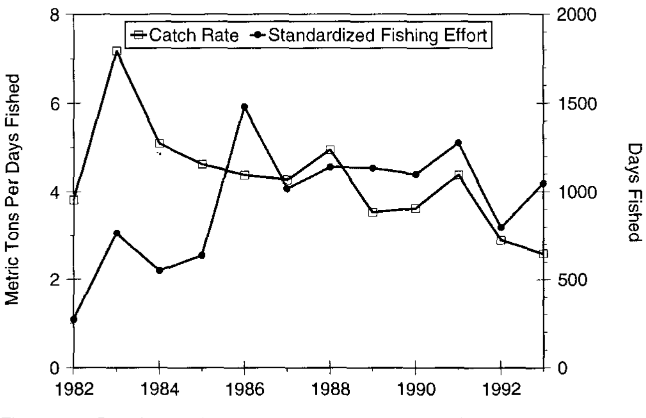

Figure 6. Standardized catch rate (open square) and fishing effort (solid circle) for the domestic summer trawl fishery, 1982–93.

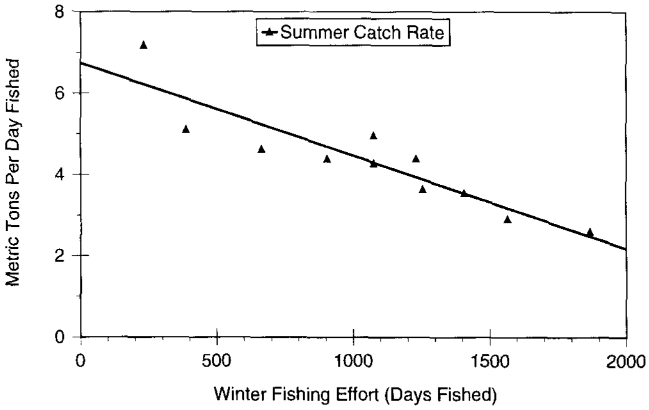

Figure 7. Standardized fishing effort in the winter trawl fishery versus standardized catch rate in the subsequent summer trawl fishery, 1983–93.

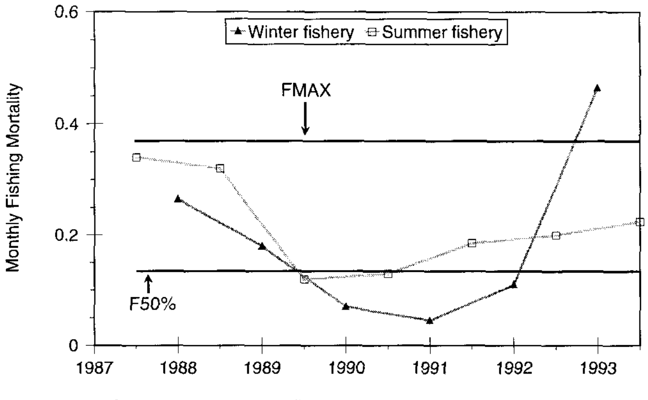

Figure 8. Monthly estimates of fishing mortality in the winter (major tick mark) and summer (minor tick mark) trawl fisheries in comparison to target (F50%) and overfishing (FMAX) fishing mortality rates, 1987–93.

REVISED MANAGEMENT MEASURES

Management measures for the *L. pealei* resource were revised to account for the improved understanding of its life cycle and life-history parameters (Brodziak and Macy 1996; NEFSC 1996). The revisions included changes in biological reference points defining overfishing and target harvest rates, determination of long-term potential yield, and provisions for limited entry to the fishery (MAFMC 1997).

Biological Reference Points

Biological reference points for *L. pealei* were revised to account for the improved estimates of life-history parameters. Of particular importance was revision of the former overfishing definition for *L. pealei.* This definition was based on a 3-year average of the relative abundance of juvenile *L. pealei* captured during the NEFSC autumn bottom trawl survey. In particular, the stock was considered to be recruitment overfished whenever the 3-year moving average of numbers of juvenile *L. pealei* (mantle length less than 9 cm) fell within the lowest quartile of the autumn juvenile time series. This overfishing definition was reviewed by a scientific panel and found to be a risky definition of overfishing for such a short-lived species (Rosenberg et al. 1994).

The fact that growth and maturation of *L. pealei* differed by hatch season complicated the development of biological reference points. Separate analyses of yield and spawning biomass per recruit were conducted for summer-hatched (June–October) and winter-hatched (November–May) cohorts to account for differences in size at age and fraction mature at age between seasonal cohorts (fig. 9). Standard methods to compute yield and spawning biomass per recruit were used (e.g., Gabriel et al. 1989). In these analyses, it was recognized that the winter and summer fisheries operated on a mixture of summer- and winter-hatched *L. pealei* and that the reference points would have to be interpreted cautiously if they differed substantially for summer- and winter-hatched cohorts.

An overfishing rate was defined on the basis of yield-per-recruit analyses for the summer- and winter-hatched *L. pealei.* The fishing mortality rate that maximized yield per recruit (FMAX) was chosen as the overfishing rate on the basis of yield-per-recruit considerations (Beverton and Holt 1957). Fishing in excess of the overfishing rate would result in growth overfishing of the stock. The estimated FMAX for winter-hatched squid was 0.38 per month; FMAX for summer-hatched squid was estimated to be 0.36 per month. The values of FMAX were virtually identical, although the realized yield per recruit at FMAX was higher for summer-hatched squid because of their more rapid growth. As a result, an overfishing rate of FMAX was adopted for seasonal cohorts of the *L. pealei* stock.

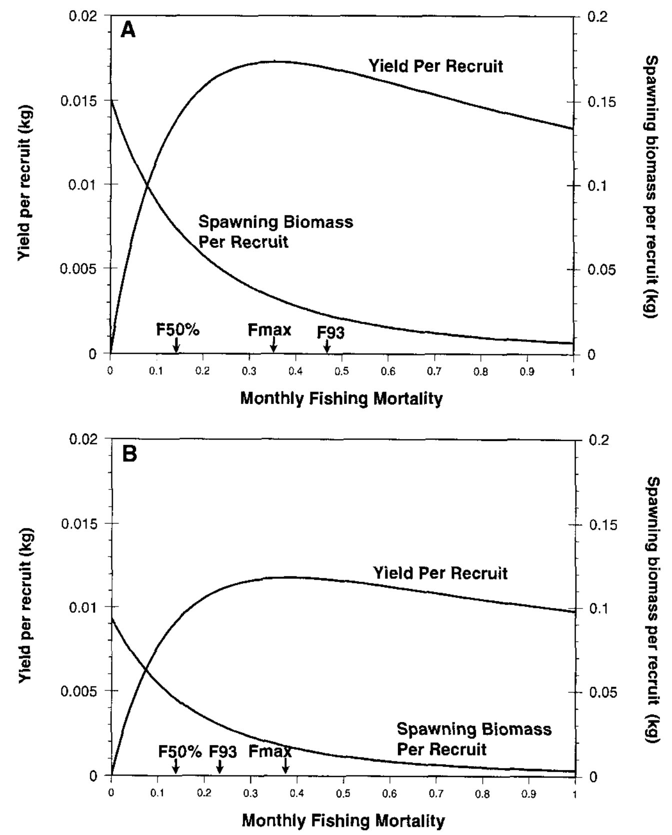

Figure 9. Yield and spawning biomass per recruit for (*A*) summer-hatched and (*B*) winter-hatched *Loligo pealei* as a function of monthly fishing mortality.

Similarly, a target harvest rate was defined from analyses of spawning biomass per recruit for summer- and winter-hatched *L. pealei.* The target harvest rate was chosen to maintain average spawning potential of the *L. pealei* stock in the face of high natural mortality (0.3 per month); moderate fecundity on the order of 10,000 eggs per female (Summers 1971; Vovk 1972, cited in Summers 1983); and a complex mating system (Griswold and Prezioso 1981; Hanlon et al. 1997).

The target harvest rate for the *L. pealei* stock was chosen to be F50%, the fishing mortality rate that would maintain 50% of the maximum spawning potential of a cohort. The 50% level was selected on the basis of analogy with management of *Illex argentinus* in the Falkland Islands, where a proportional escapement goal of 40% determined the target exploitation rate. By analogy, if all *I. argentinus* were equal in their contribution to spawning potential, a proportional escapement goal of 40% would roughly correspond to F40% for a given cohort. The use of the more precautionary F50% level for *L. pealei* was considered reasonable because fecundity of *L. pealei* is roughly an order of magnitude lower than for *I. argentinus.*

It should be noted, however, that analyses of spawning biomass per recruit have generally not been conducted for management of squid resources. As a result, there were no comparative values of percent maximum spawning potential for squids that could be inferred to produce a sustainable target harvest rate. But in their review of how much spawning biomass per recruit could sustain fisheries resources, Mace and Sissenwine (1993) observed that many small pelagic fishery resources may require levels of 40%–60% of maximum spawning potential to maintain themselves. Given that *L. pealei* are subject to high natural mortality rates characteristic of small pelagic fishery resources, it was inferred that the high end (mean level plus two standard deviations) of percent maximum spawning potential reported for small clupeoid fish of roughly 50% (table 3 in Mace and Sissenwine 1993) would likely provide a precautionary level of spawning escapement for *L. pealei.*

The target harvest rate estimates of F50% for winter- and summer-hatched squid were 0.13 and 0.14 per month. Like the overfishing rate, the target harvest rate was virtually identical for both seasonal components. As a result, a target harvest rate of F50% was used for calculating long-term potential yield from two seasonal cohorts.

Long-Term Potential Yield

The annual long-term potential yield (LTPY) for the *L. pealei* resource in the northwest Atlantic was recalculated to account for the revised life-history parameters and improved understanding of the life cycle. The LTPY for the *L. pealei* stock was computed as the sum of the expected long-term potential yields for winter- and summer-hatched squid based on estimates of recruitment taken from the NEFSC spring and autumn surveys and the expected yield at the target harvest rate. Abundance of summer-hatched squid was measured during the autumn survey because they were primarily harvested in the winter fishery. Similarly, abundance of winter-hatched squid was measured during the spring survey because they were primarily harvested in the summer fishery.

Seasonal patterns of recruitment and growth were incorporated in the calculation of long-term potential yield from the *L. pealei* fishery. Estimates of *L. pealei* recruitment to the winter and summer fishing seasons were based on the diurnally adjusted swept-area estimates of total numbers of pre-recruits (squid less than 9 cm in mantle length) from the autumn and spring survey, respectively. Because of the rapid growth of *L. pealei,* all pre-recruits were assumed to be fully available to the commercial fishery during the 6 months following the survey. The expected LTPY for summer-hatched *L. pealei* (autumn pre-recruits) was computed as the average of the predicted yield for summer-hatched squid at the target harvest rate of F50% times the estimated number of pre-recruits in the autumn survey for 1968–94. Similarly, the expected LTPY for winter-hatched *L. pealei* (spring pre-recruits) was computed as the average of the predicted yield for winter-hatched squid at F50% times the number of pre-recruits in the spring survey for 1968–94. As a result, the overall LTPY was estimated to be roughly 21,000 t, with 3,000 t (14%) coming from winter-hatched *L. pealei* and the balance (86%) from summer-hatched squid (fig. 10).

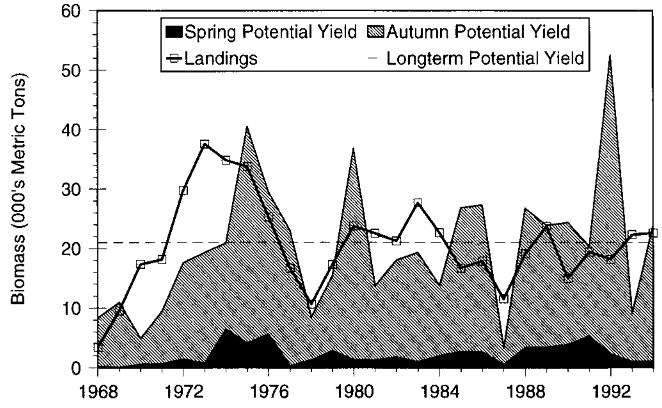

Figure 10. Potential yields of *Loligo pealei* from spring and autumn recruitment in comparison to annual landings (solid line) and long-term potential yield (dashed line), 1968–94.

A precautionary approach was taken to determining LTPY because *L. pealei* are an important component of the northeast ecosystem as predators and prey. In this approach, LTPY was calculated on the basis of average levels of recruitment and the target harvest rate of F50%. This approach was precautionary in comparison to using FMAX as the optimum harvest rate to determine LTPY. Although the application of FMAX would produce the maximal yield per recruit attainable under the current exploitation pattern, this harvest rate would not ensure that spawning potential was maintained for this short-lived, semelparous species. If FMAX were used instead of F50%, the expected maximal yield for *L. pealei* would be about 26,000 t. Historically, landings in excess of 25,000 t have not been sustained by the *L. pealei* fishery because of fluctuations in abundance.

The revised estimate of long-term potential yield of 21,000 t on the basis of a life span of less than one year was less than half of the previous estimate of 44,000 t, which was based on an assumed life span of roughly two years (Lange and Sissenwine 1983). The Mid-Atlantic Fishery Management Council has set the current annual domestic allowable harvest of *L. pealei* to be equal to the revised estimate of long-term potential yield, and in-season monitoring of landings and enforcement of the domestic allowable harvest level have been planned.

Limited Entry

Provisions for limited entry to the *L. pealei* fishery were motivated by two primary considerations. First, the *L. pealei* stock was fully exploited on the basis of a scientific assessment of the resource and a consensus review of that assessment (NEFSC 1996). Because the stock was fully exploited, additional fishing effort directed at the stock would not be expected to increase fishery yields or net national benefits of harvesting the resource. Second, the potential for increased fishing effort on the *L. pealei* stock was substantial, given the amount of displaced fishing effort from the New England groundfish fishery and the increasing trend in winter trawl effort for *L. pealei* during 1983–93. Provisions of Amendment 7 to the Northeast Multispecies Fishery Management Plan were directed to limit fishing effort on New England groundfish stocks in the mid-1990s to reduce chronic overfishing and rebuild groundfish stocks. As a result of effort limitations on groundfish fishers, fishing effort formerly directed at groundfish could be expected to focus on *L. pealei.*

Development of limited-entry provisions for the *L. pealei* fishery was contentious, but permits were ultimately based on historic participation in the *L. pealei* fishery. In effect, vessels that participated in the *L. pealei* fishery during the 1980s or early 1990s were assigned limited-entry permits. This led to approximately 400 limited-entry permits for the *L. pealei* fishery (L. Hendrickson, NEFSC, Woods Hole, Mass., pers. comm.).

FUTURE RESEARCH

The recent application of statolith ageing techniques to *L. pealei* and other squid species has improved the understanding of squid life cycles and life-history parameters (Jackson 1994a). But there is much more research to do because, in comparison to marine finfish whose population dynamics have been studied for over a century (cf. Smith 1994), squids have not been as intensively investigated. Future research can reduce uncertainty and improve fishery management of *L. pealei* and other squid resources.

One primary area for future research is further investigation of the commercial fishery for *L. pealei.* Direct sampling of the age composition of landings and discards from the winter and summer fishery for *L. pealei* is essential to understanding the interaction between these fisheries. In particular, it will be useful to determine whether increased winter effort leads to reduced summer spawning, and whether low levels of summer spawning reduce the probability of high levels of recruitment to the winter fishery. The use of commercial fishery LPUE as a relative abundance index is another area for commercial fishery research. Further, the development of a dynamic assessment model that integrates commercial fishery and research survey data to estimate seasonal fishing mortality rates and population abundance of *L. pealei* is an important topic for future research. Commercial fishery data may also provide more temporal and spatial detail on the seasonal distribution of *L. pealei,* and geostatistics and geographic information systems may have important application.

Another potential area of research is to quantify the importance of density-dependent effects on the population dynamics of *L. pealei* (Brodziak and Macy 1996). Little is known about the relation between spawning stock and recruitment for the *L. pealei* stock. It will be important to quantify the level of density-dependence in this relationship to refine understanding of the levels of spawning biomass needed for sustained resource productivity. Density-dependence as well as seasonal and annual variation in growth and maturation are important for informed management, but reducing uncertainties about these matters will require much more extensive age sampling than has been conducted to date.

Trophic dynamics and the effect of community-level interactions with *L. pealei* predators and competitors are also an important research topic. The northeast shelf ecosystem has undergone profound changes in species composition and abundance since the intensive foreign fisheries of the 1960s and 1970s (Sissenwine and Cohen 1991). How these changes have affected long-term productivity of *L. pealei,* a mid-trophic-level species, would be useful to quantify for management. The current management approach includes an implicit recognition of the importance of *L. pealei* as part of the ecosystem. In effect, the current estimate of long-term potential yield provides an upper bound on annual landings. Under this management approach, potential increases in yield due to exceptional abundance of *L. pealei* are limited, with the consequence that *L. pealei* predators, such as groundfish, would have increased forage. This limitation of harvest may improve the productivity of other fishery resources of the northeast shelf ecosystem.

Finally, the investigation of environmental effects on the population dynamics and population biology of *L. pealei* remains an important research topic. Distribution and growth of *L. pealei* can be influenced by temperature (Murawski 1993; Brodziak and Macy 1996). As a result, potential global warming may substantially affect the productivity and distribution of the *L. pealei* resource. Overall, quantifying the effects of environmental variation on the growth, recruitment, maturation, and distribution of *L. pealei* will remain a challenging research topic for years to come.

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FISHERIES BIOLOGY, STOCK ASSESSMENT, AND MANAGEMENT OF THE CHOKKA SQUID (*LOLIGO VULGARIS REYNAUDII*) IN SOUTH AFRICAN WATERS: AN OVERVIEW

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ABSTRACT

Extensive studies of biology and life cycle, and the application of some stock-assessment techniques to South African chokka squid (*Loligo vulgaris reynaudii*) have contributed toward formulating management approaches for the species. Efforts to clarify the systematics preceded the biological, behavioral, population dynamics, life-cycle, and ecological studies. Management measures have progressed from simple ones designed to order the fishery and control effort, to a more structured approach that uses a closed season as the main management tool. Recent modeling studies have indicated that the stocks are nevertheless under pressure, at a time when there is a political imperative to allow new entrants into the fishery. There is consequently a need to introduce new methods of management (while maintaining effort control as opposed to catch control), which may ultimately lead to the introduction of an operational management procedure.

INTRODUCTION

This paper reviews the progress that has been made in South Africa since the early 1980s in understanding the biology and life cycle of chokka squid (*Loligo vulgaris reynaudii*). It describes how this knowledge has been combined with various stock-assessment techniques to develop a management approach for a species that is one of a group considered to be very difficult to manage effectively (Pierce and Guerra 1994).

Until the mid-1980s chokka squid was taken almost exclusively as a bycatch of the demersal trawl fishery. A small-boat, entrepreneurial, handline jigging fishery was established in 1985 (Augustyn 1986). It grew explosively, but was soon brought under licensed control. Today the chokka squid jigging fishery is based on a relatively small (mean catch: about 6,000 metric tons), but valuable resource (close to R 104 million, or $22 million; Cochrane et al. 1997) which is exploited entirely in South African waters. Catches have fluctuated between approximately 2,700 and 11,000 t per year (fig. 1).

FISHERIES BIOLOGY OF CHOKKA SQUID

Extensive research has been conducted on chokka squid, mostly since the early 1980s. The following aspects have been investigated.

- Morphological and biochemical systematics (Augustyn and Grant 1988; Vecchione and Lipiński 1995)
- Embryological and larval development (Vecchione and Lipiński 1995; Blackburn et al., in press)
- Ageing methods and physiology of statolith deposition (Lipiński 1991, 1993; Lipiński and Durholtz 1994, 1996; Durholtz et al. 1995, 1997; Gerneke et al. 1995; Durholtz and Lipiński 1997; Lipiński et al. 1997; Lipiński, Durholtz, and Underhill, in press)
- Trophic relationships and feeding behavior, feeding physiology (Lipiński 1987, 1990, 1992; Lipiński and David 1990; Sauer and Lipiński 1991; Smale et al. 1995)
- Direct stock-assessment methods, including trawl and hydroacoustic surveys (Hatanaka et al. 1983; Uozumi et al. 1984, 1985; Wallace et al. 1984; Augustyn et al. 1993; Lipiński, Hampton, et al., in press)
- Stock-assessment modeling and methods (Augustyn et al. 1993; Roel et al., in press)
- Management (Augustyn 1986; Lipiński 1990; Augustyn et al. 1992, 1994; Sauer 1995a, b)
- Reproductive histology and fecundity (Badenhorst 1974; Sauer and Lipiński 1990; Peredo et al. 1996; Melo and Sauer 1997, in press)
- Reproductive biology and spawning and schooling behavior (Lipiński 1979; Augustyn 1990; Sauer et al. 1992; Sauer and Smale 1993; Hanlon et al. 1994; Sauer, Roberts, et al. 1997)
- Migration (Sauer et al. 1994; O'Dor, Andrade, et al. 1996; O'Dor, Webber, et al. 1996)
- Short- and long-term environmental effects on availability and spawning (Sauer et al. 1991; Roberts and Sauer 1994; Roberts et al. 1996; Roberts, in press)
- Population dynamics and life-cycle studies (Augustyn 1989, 1991; Sauer 1991, 1993; Sauer et al. 1993; Augustyn et al. 1994; Lipiński 1994; Booth et al. 1997; Sauer, Augustyn, and Roberts 1997)

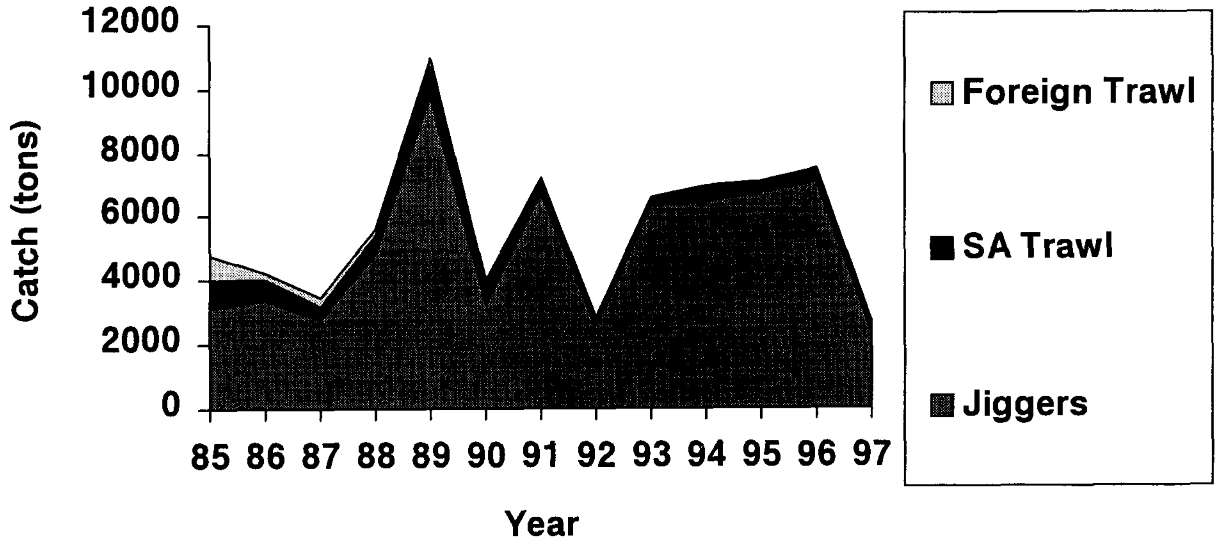

Figure 1. Annual catches of South African chokka squid (*Loligo vulgaris reynaudii*) in three sectors, from the inception of the fishery in 1985 to 1997.

Systematics

Several years before the jigging fishery developed, Sea Fisheries Research Institute (SFRI) recognized that chokka squid was a potential new resource. A fisheries biological research project was launched in the early 1980s. Investigating the systematics became a priority because it was realized that, if a fishery were to be established and properly managed, the stock distribution would have to be delimited and its systematic relationship with its European and West African counterpart, *L. vulgaris*, established. From a study in which morphological measurements, meristic counts, and protein gel electrophoresis were used, it was determined that the South African species was a distinct and isolated one and that genetic differences were at the subspecific, rather than specific level. On that basis, the two species were renamed *L. vulgaris vulgaris* and *L. vulgaris reynaudii* (Augustyn and Grant 1988).

Biological Studies

Initially the trawler bycatch was sampled to collect basic biological information in an attempt to understand development, growth, population structure, maturation cycle, and ecology. Later, the spawning grounds in bays along the southern coast of South Africa were investigated (Augustyn 1989). The main spawning sites were then thought to be located in False Bay, near Cape Town. In the early 1980s, the distribution and relative abundance, as well as basic biology and ecology were directly studied for the first time on the shelf, during three joint Japanese–South African surveys of the South Coast Shelf (Hatanaka et al. 1983; Uozumi et al. 1984, 1985). These were soon followed with regular stratified random sampling surveys by a new South African research vessel. The surveys encompassed the whole coast and established an index of abundance (Augustyn 1989, 1991). The distribution of mature animals and different size classes indicated that the main spawning areas were located farther east than had earlier been suspected. Eventually these surveys made it possible to draw a more complete picture of the life cycle, including aspects such as deepwater spawning and larval distribution.

With the onset of a directed jigging fishery on chokka squid, the focus of the research shifted to the southeast coast, because it was realized that the major spawning grounds were located there. Research based on scuba diving clarified the understanding of chokka squid's mating and spawning behavior and of its seasonality and probable life cycle (Augustyn 1990; Sauer 1991). At the same time, the first steps were taken toward using statolith daily growth rings to determine the age of squid and the basis of ring deposition in statoliths (Lipiński and Durholtz 1994, 1996).

In the late 1980s a Squid Working Group at the SFRI in Cape Town was established, and cooperation with the squid industry began to lend new impetus to the research. New work, including migration and tagging studies (Sauer et al. 1994), acoustic studies, and more advanced behavioral studies using acoustic tags (Sauer, Roberts, et al. 1997), as well as a comprehensive environmental research project made further contributions to understanding the population dynamics of chokka squid.

Our current understanding of the life cycle of this squid is summarized by the diagram in figure 2. The species is relatively short-lived, apparently not exceeding a life span of 18 months. The population is usually made up of at least two, sometimes three, major cohorts. Spawning usually peaks in spring and early summer, with a variable smaller peak in autumn or winter (Augustyn 1989, 1990; Sauer 1991). A large part of the population

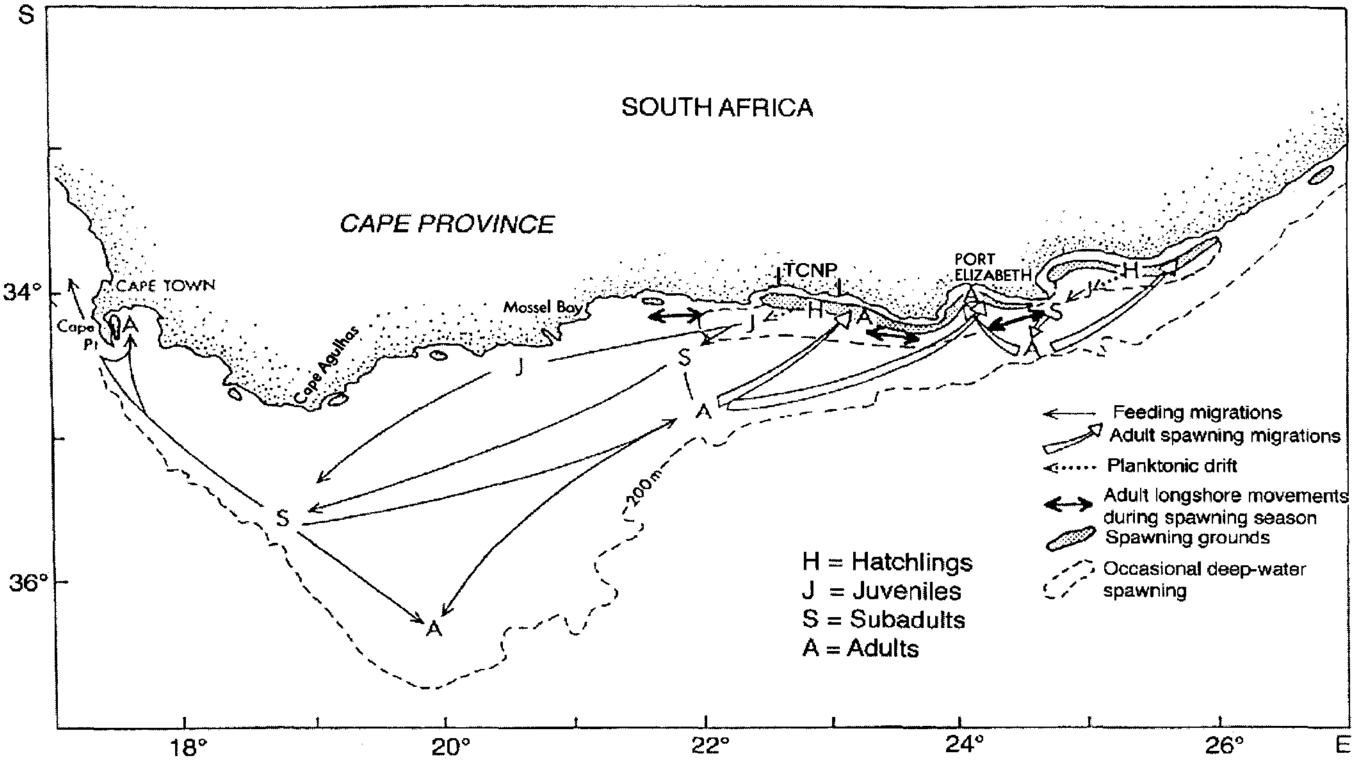

Figure 2. Conceptual diagram of the life cycle of chokka squid (*Loligo vulgaris reynaudii*) in its main area of distribution off the south coast of South Africa. TCNP = Tsitsikamma Coastal National Park.

migrates in waves as mature animals to the southeast coast, where most spawn in the shallow (20–50 m) spawning grounds (Augustyn 1989, 1990; Sauer 1991). These variations are reflected in the catches, as shown in figure 3. Availability on the spawning grounds appears to be linked to cool, clear, upwelled water, a seasonal feature at the capes on the southeast coast, which results from easterly wind forcing (Sauer et al. 1991). When waters are warmer than about 21°C or become turbid, the squid tend to spawn in deeper water, often deeper than 100 m. The squid are then less available to the fishery, and different fishing techniques are applied.

Behavioral studies in maintenance experiments in the laboratory, and scuba diving have established that visual signaling with distinct body patterns plays an integral role in spawning and other behavior (see fig. 4), and it is thought that turbid conditions interfere with this behavior.

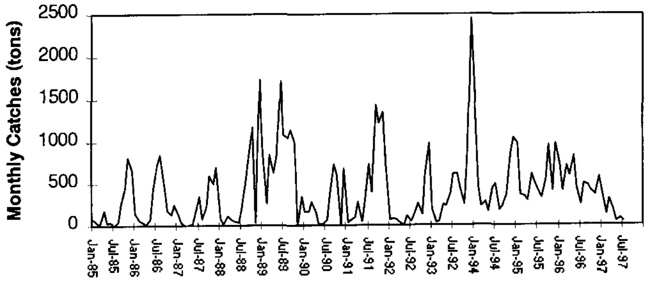

Figure 3. Monthly chokka squid (*Loligo vulgaris reynaudii*) jig catch variations, reflecting changes in availability on the spawning grounds.

Different types of shoaling behavior have been identified on the spawning grounds. Spawning squid often form mushroom-shaped aggregations (Sauer et al. 1992). The structure of these aggregations and the movement around them has been elucidated by acoustic tagging studies (Sauer, Roberts, et al. 1997). Several other types of aggregations have also been observed and are characterized by typical echo-sounder trace types (Sauer et al. 1991).

Tagging with "spaghetti" tags has also made it possible to plot longshore movements of squid. Distances of up to 200 km have been measured between tagging and recapture positions, and a generally eastward direction of migration has been established (Sauer et al. 1994).

Lipiński, Hampton, et al. (in press) have studied the stability of individual spawning shoals through tag-and-release experiments. By comparing several biological parameters, Lipiński (1994) investigated the selectivity of various fishing methods—i.e., jigging, midwater trawling, and purse-seining. Assuming that purse-seining provided the most representative sample of the squid school targeted, jigging proved to be highly selective of large males. No females were caught by this method, whereas the purse-seining ratio of males to females was

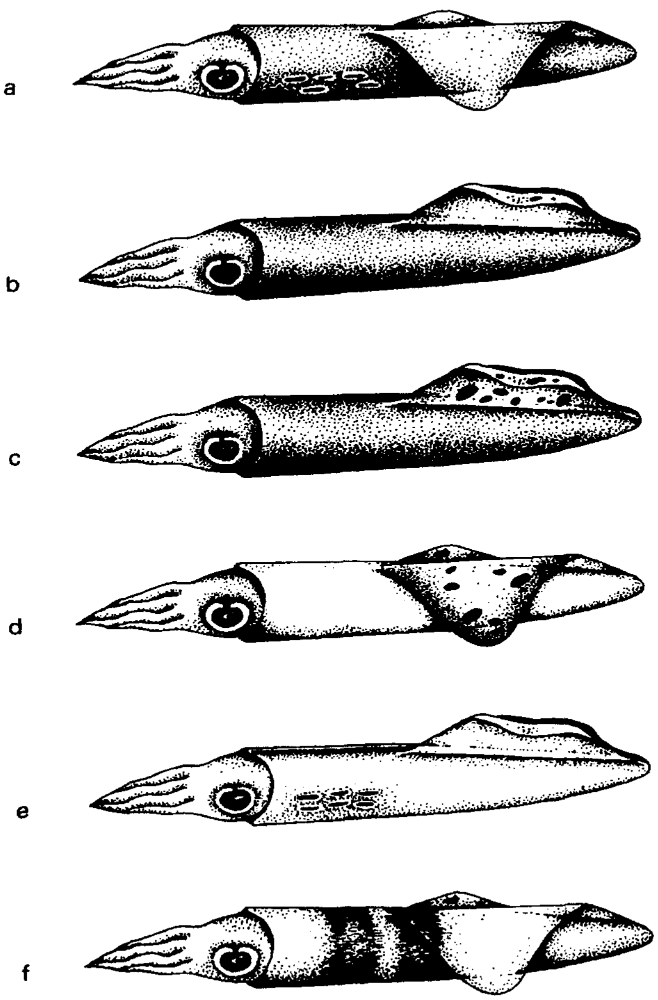

Figure 4. Male chokka squid fin and mantle patterns as observed on the spawning grounds (after Sauer and Smale 1993). *a*, Lateral mantle streaks; *b*, all dark; *c*, fin spots; *d*, dark fin edges; *e*, dorsal stripe; *f*, ring pattern.

2.52 to 1. Commercial jig catches do not, therefore, represent the population, and neither do jigged, or to a lesser extent, midwater-trawled research catches. These conclusions obviously have important consequences for stock-assessment methods based on commercial catch data or on research catches.

Acoustic tracking studies have been carried out by Sauer, Roberts, et al. (1997). Squid were tagged (inside the mantle cavity) with acoustic transponders, the signals of which are detected by transducers on a grid of four buoys. The data are radio-beamed ashore to a second receiver linked to a computer which calculates three-dimensional tracks of up to eight squid at a time. The study elucidated movements of male, female, and "sneaker" males. They showed that the squid tend to move off the egg beds at night to feed in the vicinity and that mating mainly takes place during daylight. These studies support the acquisition of baseline data on population dynamics, which are influenced by reproductive behavior. The study emphasized that management strategies should be aimed at avoiding breakdown of these critical spawning aggregations. Recruitment could, for instance, be adversely affected by increases in the alternative tactic of mating and spawning offshore, where development temperatures and success may be lower. Studies of hatching success at various temperatures can therefore also be justified in terms of management advantages.

More recently, a system is being developed to remotely monitor the behavior of squid in relation to environmental parameters by setting up a video camera system linked to a solar-powered surface buoy (fig. 5) which beams the video and environmental data back to shore where it can be stored and later analyzed (Roberts, in press). This work should contribute to understanding the effects of rapid temperature and turbidity and current regime changes on squid availability and behavior.

STOCK ASSESSMENT AND MANAGEMENT

Introduction

Very few squid fisheries around the world are subject to rigorous standard stock-assessment or operational management procedures. This can probably be ascribed largely to the fact that squid are typically annual species with highly variable stock-recruitment relationships and consequently volatile stock levels (Pierce and Guerra 1994). In upwelling systems such as the southern Benguela and the extremely variable south coast of South Africa, the center of the local chokka squid fishery, food availability and survival in the nursery areas are critical to survival and growth, and predicting recruitment is fraught with difficulties. At the same time, many species aggregate strongly and migrate freely, so the use of catch per unit of effort (CPUE) indices (the basis of most population modeling) must take these characteristics into account. On the practical side, data from the fishery are often inaccurate or missing.

In the following sections we review the South African approach to stock assessment and management, which has been modified and adapted as more knowledge has been gained. Over a period of slightly more than a decade, we have moved from a situation of very limited knowledge and expertise into one based on improving knowledge. Higher complexity and more limited resources in terms of surveying and manpower have forced us to take compensatory pragmatic measures. Future options are also touched on briefly.

Direct Estimates of Biomass

Direct population estimation before the start of or during the main fishing season, such as hydroacoustic, stratified random sampling, or egg production surveys

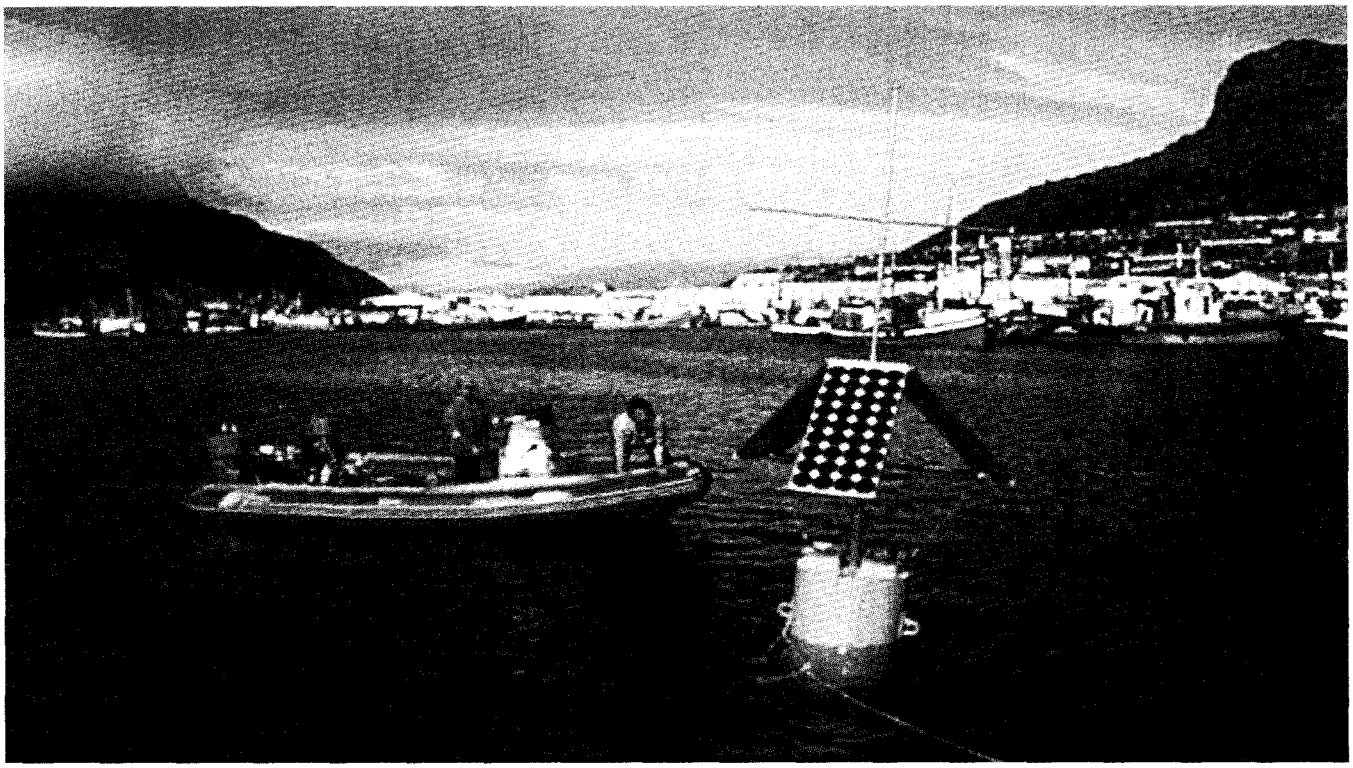

Figure 5. Testing a solar-powered buoy, used to power underwater video equipment that constantly monitors the behavior of chokka squid in the vicinity of egg clusters in response to changes in environmental variables, in South Africa. Photograph reproduced with the permission of Mike Roberts of Sea Fisheries Research Institute, South Africa.

have been used or considered in South Africa (Augustyn et al. 1993). Hydroacoustic methods have not yet been fully developed, and some difficult scientific obstacles still have to be overcome (e.g., how to detect squid when not in large schools). On the other hand, there have been recent successes in directly estimating target strength by using split-beam echo sounders to measure caged squid (M. Soule, pers. comm.).

Stratified random sampling surveys, primarily designed to estimate hake biomass, are currently carried out on the South African south coast in spring and autumn. These surveys also provide estimates of squid biomass, which are useful in determining shelf biomass trends. The surveys do not, however, give an estimate of absolute biomass, because they do not cover the entire area of distribution and because only squid swimming close to the bottom will be caught by the trawl. The proportion missed by the trawl is not known (Augustyn 1991; Augustyn et al. 1993; Roel, unpubl. data). Additional, dedicated squid surveys would be too expensive in terms of vessel time and manpower required, so alternatives for estimating the biomass of the resource are needed.

Practical Management Measures

Since the chokka squid jigging fishery in South Africa began in the mid-1980s, various management measures have been introduced (Augustyn et al. 1992). These have generally taken cognizance of the biology of chokka squid, but they have also been based on pragmatic decisions made in the absence of good information about the level of squid stocks. An early debate about effort control versus catch control (in about 1989) resulted in the adoption of effort control. The main arguments then were that there was no time series of any length from which to determine trends, and that the life cycle was too short to predict and capitalize on good year classes. A total allowable catch (TAC) could not be set with any confidence, given the absence of a proven survey method. Further, if effort could be kept under control, the fishery would largely ride the good years and survive the poor years.

The first steps to limit effort had, in fact, already been taken a few years earlier, when the developing fishery threatened to spiral out of control. In 1985–86, the fishery was developing explosively as a market was discovered in Europe, and a favorable exchange rate made exports very lucrative. Rapidly declining product quality threatened the market (due to poor handling and freezing practices), and there were even reports of dumping. It was realized that we were dealing with a valuable resource that had to be used sustainably and managed properly.

Initial actions were aimed at limiting the hordes of recreational fishermen and favoring the bona fide commercial and semicommercial line fishermen who had developed a catch record over the first two years of the fishery. Those who could demonstrate that they had exceeded the threshold catch levels for each class of vessel were given chokka permits. This resulted in a reduction from more than 500 boats to about 235, of which about 70 were limited to specific areas where they were given rights to catch for bait purposes only. A three-year moratorium on the selling of permits was instituted to prevent short-term profiteering. A public bag limit was set in 1986 (20 squid/person/day). Later, the unit of effort in the fishery became men, and the number of men for each vessel was fixed.

Limitations on vessel size and fishing methods were also considered but discarded, on the grounds that they would lead to inefficient harvesting and therefore introduce economic distortions. Purse-seining was, however, banned outright, being considered too destructive of the spawning habitat. Trawling of spawning squid is also not feasible, because it has been prohibited in all the major spawning areas of squid on the south coast via a ban on trawling in bays since 1987.

Closed Seasons/Areas

Increasing efficiency and declining catch rates of demersal squid bycatch (which reflects abundance of mostly subadults on the shelf) led to a closed season strategy, which reduced effort by shortening the fishing season by several weeks (initially four) and by affording protection to spawning females at the peak of the breeding cycle.

Closing areas, perhaps in cyclic fashion, was also considered. There was, however, already a de facto closed area in the Tsitsikamma Coastal National Park (adjacent to the main spawning areas), and it was necessary to determine its effectiveness by investigating the level of spawning taking place there. Although a thorough evaluation has not yet been completed, there does appear to be considerable spawning activity there. Sauer's (1995b) findings in this regard are unofficially substantiated by occasional prosecution of illegal fishing activities on spawning aggregations within the three-mile-wide national park.

Leslie-DeLury Option

In the early 1990s, the SFRI investigated an effort-based management approach that would allow efficient use of the resource. The possibility of closing the fishery at an appropriate level of escapement, by applying Leslie-DeLury analyses to catch-rate data to determine the peak and subsequent decline of each major influx (Beddington et al. 1990; Rosenberg et al. 1990), seemed a possible option. Its application would have required close-to-real-time monitoring of catch rates each time there was an influx of squid.

The method appears to work well in the Falkland Islands, where the objective of applying a target escapement level is to allow enough squid to escape the fishery at the end of the fishing season so as not to appreciably reduce the probability of good recruitment in the following season. In the South African context, the objective would be to allow sufficient spawning to take place to reach the same goal. In the Falklands the situation is simplified by the fact that a limited number of large vessels supply daily catch (in mass and numbers) and effort data, but in South Africa, almost-real-time monitoring of catch rates on a large number of small vessels would be required (currently beyond our means). The method also works on the assumption of a closed population during the period that the stock is being fished out. Chokka squid populations can display several immigration waves per year (Augustyn 1989; Sauer 1991) and apparently continue to immigrate and emigrate to and from the spawning grounds (the "conveyor belt" concept; des Clers, pers. comm.). As a result, the method was reluctantly rejected as too impractical for the South African fishery. If clear abundance peaks can be defined and a representative sampling method devised (along with rapid collection of data) it does, however, remain an attractive possible future option.

Variable Closed Season

When it appeared that the logistics of the Leslie-DeLury approach were beyond early implementation, the SFRI returned to the closed season as the primary tool of effort management and spawning protection. The closed season was first implemented in 1988, and extended from approximately the last two weeks of October until mid-November. The period coincides with the peak of the spawning season, when squid aggregate inshore and become very vulnerable to the jigging fishery. The duration of the closed season was determined in relation to the perceived resource abundance. The estimate of shelf biomass from the annual spring survey, together with the commercial catch taken in the first seven months of the year, were used as indices of resource abundance after examination of a large number of indices.

A set of decision rules were then put into place to determine the duration of the closed season. This was allowed to vary between three and five weeks, depending on the survey estimate and the catch index (table 1). However, in 1997 it was recommended that the closed season be held at four weeks to allow the implementation of a closed season that would also apply to recreational fishers. This strategy will have to be reviewed in the future.

TABLE 1
Rules for Determining the Duration of the Closed Season for Chokka Squid in South Africa

Rule	Biomass/catch	Duration of closed season (weeks)
1	Spring biomass < 10,000 t or January–July catch < 500 t	5
2	10,000 t < spring biomass < 20,000 t and 500 t < January–July catch < 5,000 t	4
3	10,000 t < spring biomass < 20,000 t and January–July catch > 5,000 t	3
4	Spring biomass > 20,000 t and January–July catch > 500 t	3

Dynamic Biomass Modeling

Direct estimates of stock abundance from demersal surveys and catch per unit of effort data from both the demersal fishery and the jig fishery have been used as indices of stock abundance to assess the stock by means of biomass dynamic models. The indices suggest conflicting trends, so they were also combined to estimate initial biomass, growth rates, replacement yield, and depletion rates. The results indicate that a reduction in effort is required in order to prevent the replacement yield from being exceeded, the size of such reduction being very sensitive to model assumptions (Roel and Cochrane 1996).

The results of modeling also show that biological and economic gains provided by the currently applied closed season are relatively small, consistent with an approximately 9% reduction in effort (Roel et al., in press). Although the benefits may be greater at higher levels of effort than those currently being applied, such levels correspond to high risks of depleting the spawning biomass to levels at which the chance of successful recruitment might be impaired. They are therefore not feasible management options, even with a closed season. However, decisions about the desirability of the closed season should not be taken without considering the desirable effort level in the fishery as a whole.

According to Roel et al. (in press), advice on an appropriate level of effort for the fishery at this stage is difficult because:

1. Although point estimates indicate that the current level of effort is below that which would lead to maximum yield, the estimates are not precisely determined and therefore need to be interpreted with caution.
2. Risk-related statistics (high for the base-case assumptions of these analyses) are very sensitive to the assumptions made in the model and to specification of the spawning biomass level below which average recruitment is likely to fall. There is little information from squid fisheries elsewhere in the world upon which to base an informed opinion on this matter, other than the work done in the Falklands (Basson and Beddington 1993).

Although, therefore, the closed season seems little more than a mechanism for effort reduction on the basis of the assessment results, it would seem prudent, in view of the apparently high levels of risk associated with the current effort level, to maintain it and to limit the effort permitted in the fishery to the current level until greater clarity on the matters raised in points 1 and 2 above is obtained.

Options in the Near Future

The fishery has reached the mature stage of development when a management procedure could be considered and implemented. A management procedure for squid, as for other stocks, would be a set of clearly defined rules (tested by simulation) specifying:

1. How the regulatory mechanism (for example, a total allowable annual effort) is to be set, typically on an annual basis;
2. What data are to be collected for the purpose; and
3. Exactly how the data are to be analyzed and used to this end.

The set of rules is to be preagreed upon by the parties involved, typically the management agency and the fishing industry. The management procedure should be put into place for a number of years (three to five seem to be an acceptable standard period in most fisheries) and left to run for this period. Thereafter, the procedure should be reviewed and modified as necessary in light of changes in understanding of the resource or the fishery that may have developed in the interim. A revised procedure would then be implemented for the next three-to-five-year period.

At a recent international workshop on cephalopod fisheries held in Cape Town (during the 1997 Cephalopod International Advisory Council Symposium) it became clear that very few fisheries of this nature around the world are managed by catch limitation; in most cases it is fishing effort that is controlled. In the only squid fishery known to operate on a TAC (the U.S. New England trawl fishery on *L. pealei*), the number of vessels is also strictly limited (J. A. Brodziak, pers. comm., 1997). The primary reason for preferring effort control is that, in most cases, setting a TAC is extremely difficult in the case of short-lived organisms such as squid, unless real-time monitoring of the resource biomass is feasible. As a result, management is likely to be faced with two equally unsatisfactory options when setting a TAC: (1) a conservative TAC is set and the resource is protected but often underutilized; or (2) a more risk-prone approach is taken, but the resource could be depleted if conditions for recruitment are unfavorable for a few years in succession.

Alternatively, when the effort is held constant (in terms of vessels and men), the same proportion of the stock would generally be harvested each year, with good years being taken advantage of by the fishing industry, and the necessary protection being provided to the resource in years when the biomass is low. Ideally, some mechanisms should be introduced to reduce fishing pressure on the stock in years when clear signs of poor recruitment can be detected. These could take the form of a shortening of the fishing season or limitation of the annual catch. Another advantage of effort control is that misreporting of catches is seldom a serious factor, because there is little or no incentive for fishers to provide incorrect catch statistics.

There are, however, concerns relating to the implementation of fishing effort limitations. These include difficulties in monitoring changes in effective effort and the costs of enforcing regulations such as, for example, the number of men on board. On the other hand, if catch limitations were to be implemented, problems of monitoring and enforcement would be exacerbated even more.

It has consequently been recommended to the South African management authority that effort control should, for the time being at least, remain the primary management tool for chokka squid. An aim of the proposed new South African fisheries policy is to allow previously disadvantaged new entrants into all fisheries, and strategies for doing so in effort-controlled fisheries such as the squid jigging fishery will clearly require some innovative thinking. Such measures should be aimed at redistributing fishing effort while maintaining the current overall level of effort. Possible options could include: (1) allowing new entrants, but curtailing the total time during which the fishery operates in a year; (2) developing mechanisms that could allow new entrants to obtain fishing permits from the present holders; and (3) restricting the area of operation of permit-holders.

The SFRI's proposed strategy for generating scientific solutions to the challenges posed by the new fisheries policy is to initiate debate on the matter, involving all parties associated with the utilization of chokka squid. Such a debate would include scientists, industry representatives, and other interested parties. The ultimate objective would be the development of a management procedure that strikes a balance between effective and fair utilization based on good knowledge of the stock dynamics and trends. It should allow good use of the abundance peaks in the resource with adequate safety measures to keep the risk of stock collapse at a low level.

The South African government's new fisheries policy holds out the promise of a responsible approach toward the use of marine resources, but adequate funding for research and enforcement is required to ensure the future of chokka squid and other resources.

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FISHERIES MANAGEMENT AND RESEARCH FOR *LOLIGO GAHI* IN THE FALKLAND ISLANDS

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ABSTRACT

Two squid species have been the subject of targeted fisheries in the southwest Atlantic since the early 1980s. The two fisheries have been managed in Falkland Islands waters since 1987 and provide an annual license revenue to the Falkland Islands government equivalent to some $35 (U.S.) million. The real-time assessment of the two species, *Loligo gahi* and *Illex argentinus*, is based on the Leslie-DeLury assessment model. The model assumes a single recruitment event before the start of the period used in fitting the model, and a closed population during the period. Early research on the demography and distribution of the Falkland Islands *L. gahi* population demonstrated ontogenetic descent with a probable associated coastward spawning migration. The *L. gahi* fishery concentrates by area and does not follow the migration pattern, indicating that the closed population assumption of the assessment model is invalid for much of the period assessed. Research has confirmed the variable nature of recruitment of microcohorts to the fishery, overstretching the single-recruitment assumption of the Leslie-DeLury model. But research has also shown that there are periods of residency of *L. gahi* on the fishing grounds. The current assessment procedure uses these periods of residency to derive estimates of population depletion and therefore stock size. In this paper the salient features of the fishery for *L. gahi* are presented, and the crucial links between resource assessment, biological research, and management advice are discussed. Finally, directions for further research, needed to refine assessments and achieve some predictability of population processes, are identified.

INTRODUCTION

The productive waters of the Patagonian Shelf around the Falkland Islands support two major squid fisheries and four finfish fisheries. February 1997 marked the first decade of controlled fishing effort management by the Falkland Islands government. In this paper, we present the salient features of the fishery for the Patagonian squid (*Loligo gahi*) by describing the management procedure, followed by the population ecology of *L. gahi*. We then discuss the crucial links between resource assessment, biological research, and management advice. Finally we identify directions for further research to refine assessments and achieve some predictability of population processes.

This paper reviews the biological research carried out to date, and shows how knowledge of the exploited *L. gahi* population has been used to produce the currently held life-history model that serves as the basis for the assessment.

MANAGEMENT

The completion of the first ten years of the Falkland Islands Fisheries management regime provides a timely opportunity to describe the underlying policy and to review some statistics.

Fisheries Policy

From its beginning in 1987, the three objectives of the fisheries policy have been (Anon. 1989):

1. to conserve the resource,
2. to maintain the fisheries' economic viability, and
3. to enable the Falkland Islands to enjoy greater benefit from the resource.

Licenses. Licenses and license fees were introduced as policy measures to limit access to the different fisheries and to raise revenue for assessment, research, management, and enforcement of the fisheries policy.

From 1987 to 1990, access to the fishery for *L. gahi* was through a dedicated "squid south" license from February to June. This separated *L. gahi* vessels from those fishing for the short-finned squid (*Illex argentinus*) under a "squid north" license. Initially both licenses allowed the catch of finfish as well as squid, but restricted vessels to grounds either north or south of 51°20' south latitude.

There has been little overlap between fleets fishing for the two species over the years. The oceanic squid *Illex argentinus* migrates with the Brazilian Current from approximately 45° north latitude on the high seas some 200 miles off the northern Argentinean coast, through the Argentinean Exclusive Economic Zone, down through the northern half of the Falkland Islands fishing zones, and then back north again. In Falkland Islands

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waters, *I. argentinus* has been pursued mainly by jigging vessels attracting feeding aggregations to the surface with powerful lights at night, between January and June.

By contrast, *Loligo gahi* is found in greatest densities only from the northeast (south of 51°20'S) to the south of the islands, in the Falkland Islands Conservation Zone, within 100 nautical miles of the islands (fig. 1). *L. gahi* is a colder-water demersal squid, smaller than *I. argentinus*. It has been pursued by trawlers targeting concentrations near the seabed on the edge of the continental shelf during daytime. Jigging vessels are unlikely to catch finfish species, but demersal trawlers can easily catch finfish and *L. gahi* with no change of gear. In order to avoid the risk of gear interactions between *L. gahi* and finfish fisheries throughout the year, in 1991 a specific *L. gahi* license was created for the second half of the calendar year.

Licenses are usually issued for individual vessels and for one season only, but long-term involvement has been encouraged through 5-year licenses in one or both seasons. "Long-term" licenses for *L. gahi* are awarded to vessel owners contributing to the development of the local fishing industry, according to criteria periodically defined in the fisheries policy. The total allowable effort in "vessel-capacity-units" is determined from an assessment of spawning stock escapement of the previous year, as described later in this paper. Within the estimated total effort, allocation to individual vessels is at the discretion of the fisheries director of the Fisheries Department of the Falkland Islands Government (FIGFD), and follows a ranking of applicants according to a point system published as part of the fisheries policy. The point system formalizes some requirements of the third objective of the fisheries policy by giving an advantage to applications which entail direct commercial involvement of Falkland Islands residents and businesses.

The basis for license fees applied to trawlers is the international gross registered tonnage (IGRT), a measure of the volume displacement of the vessel on the water. In the *L. gahi* fleet, the IGRT provides a very good correlate of vessel length (and beam by definition) and also of engine-brake horsepower and volume of freezer holds (des Clers and Hudson, unpubl. data). Twice a year, the Falkland Islands government publishes (in the official gazette) the terms and conditions, including fishing license fee, that will prevail for the next six-month season. A license fee for the whole season is a linear function of a vessel's IGRT. The coefficients of the fee policy formula are revised, through an analysis of individual vessel production (tonnage and estimated gross value), at the end of each season.

In 1996, 61,360 tonnes of *L. gahi* were caught, and the revenue generated from license fees for *L. gahi* was 4 million pounds sterling (approx. 6.2 million U.S. dollars). This represented about 28% of the total revenue from all squid and finfish licenses (Falkland Islands Government 1997). Assuming an average market price of $900(U.S.)/t of *L. gahi* to vessel owners, this means that an estimated 7% of the fisheries gross revenue was extracted as license fees.

Closed seasons. The fishery for *L. gahi* is currently licensed as two separate fishing seasons, from February to May and from August to October. The seasons were originally chosen to cover the peak of early 1980s commercial catches by Russian, Polish, and Spanish vessels (Csirke 1987; Patterson 1987, 1988; des Clers 1998a). This is still the case in most seasons, when the squid migration through the fishing grounds is entirely framed by the seasons' beginning and end dates. However, fixed dates have served to control fishing mortality on several occasions, which are described in detail in Resource Assessments later in this paper.

An important feature of the management regime is that the fisheries director may decide to close the season early, as a result of real-time catch and effort monitoring and stock assessment throughout the season. This happened once in the first ten years of the fishery. In 1989, the first season, which originally lasted (albeit at a reduced pace) until June, was closed three weeks early at the end of May. The first season's duration has been four months ever since.

Closed areas. Since 1990, the fisheries policy has specified grounds reserved to *L. gahi* fishing. The "Loligo box" extends over some 9,700 square nautical miles. It covers the entire fishing grounds for *L. gahi* on the shelf edge around the islands from the north-northeast of East Falkland to the south of West Falkland (fig. 1). The original purpose of the Loligo box was twofold. The main purpose was to keep trawlers licensed to catch finfish out of the squid fishery. This has been very effective; exemptions have been granted rarely and only to semipelagic trawlers targeting spawning aggregations of southern blue whiting (*Micromesistius australis*). The second purpose was to confine vessels targeting squid, for which there are no prescribed minimum mesh sizes, to fishing grounds where there is the least likelihood for incidental capture of juvenile finfish.

The fishery is conducted in the 80–300 m depth range, but most catches are concentrated along the shelf break at depths between 150 and 200 m. This is a much narrower depth range than that in which the species is found around the Falkland Islands (some 20–400 m; Hatfield et al. 1990).

Some areas are explicitly closed—to certain vessels or to license types or at certain times of the year—by the fisheries conservation policy. An even larger area, however, is currently closed to fishing because there are no coastal fleet or small-scale, local, sea-fishing activities.

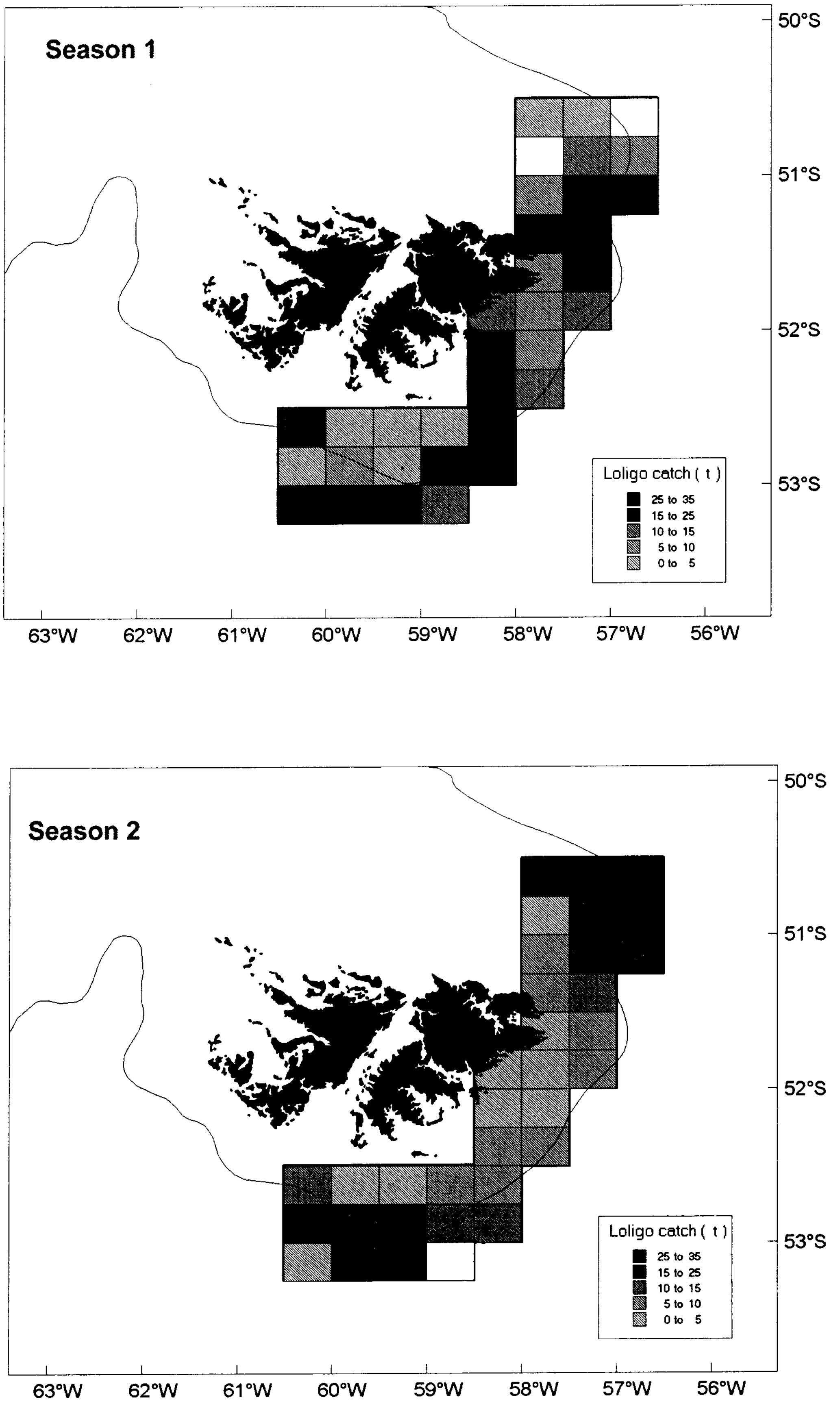

Figure 1. *Loligo gahi.* The "Loligo box" and areas of highest commercial activity in relation to catch season and bathymetry (200 m isobath) around the West (left) and East (right) Falkland Islands.

Therefore, most of the depth range of coastal habitat, between 20 and 100 m, is de facto in a marine protected area because the grounds are not suitable to the current fleet of large factory trawlers.

Other technical conservation measures. There is no other limitation on inputs apart from vessel licensing, closed seasons, and closed areas in the fishery for *L. gahi*. For instance, there is no mesh size or other gear prescription. In terms of output control, there are no minimum landing sizes or specifications for bycatch or discards, but the processing of *L. gahi* into meal is prohibited in all fisheries licensed in Falkland Islands waters.

Fisheries Statistics

The small population and limited scope for rapid onshore infrastructure development on the Falkland Islands in 1987, and the distant operating area of the fleet, meant that output (landings) would have been very difficult to monitor. This was the essential reason for the choice to limit input as a management regime.

From the outset, it was also recognized that the *L. gahi* fishery operated on a short-lived species (Anon. 1989). This meant that management decisions might be needed during the fishing season. In order to build the necessary information base, the FIGFD launched an intensive data-collection exercise as part of the fishing license requirements. This program is still in effect, and includes radio transmission to the FIGFD of detailed information about individual vessel position and catch and effort. Technical details about vessels are gathered at the license application stage, and biological information is collected by scientific observers placed by the FIGFD on board selected vessels.

Catch. Between 1987 and 1996 an annual average of 75,000 tonnes of *L. gahi* was caught in Falkland Islands waters (Anon. 1989; Falkland Islands Government 1997; table 1). These were the highest annual catches of loliginid squid worldwide until 1996, when the fast-developing fishery for California market squid (*Loligo opalescens*) produced 80,272 tonnes (Vojkovich 1998).

A characteristic of squid fisheries is a large interannual variability in fishable biomass (Boyle 1990; Boyle and Boletsky 1996). This is not surprising, given the potentially stronger effect of environmental fluctuations on marine species with short life spans and extensive migrations.

In Falklands Islands waters this variability is reflected by coefficients of variations of annual catches of 29% for *L. gahi* (average catch 75,309 t) and 42% for *I. argentinus* (average catch 136,858 t; table 1). A greater variability of total annual catches for oceanic species compared to demersal squid species has been noted before on the east coast of the United States (*Illex illecebrosus* and *Loligo pealei*, Dawe et al. 1990).

TABLE 1
Historical Catch Figures in the Falkland Islands Squid Fisheries

	Loligo gahi			*Illex argentinus*	
Year	Total annual catch (t)	% annual catch/ average	% catch 1st season/ annual total	Total annual catch (t)	% annual catch/ average
1987	82,547	110	78	142,051	104
1988	53,931	72	90	209,523	153
1989	118,720	158	90	224,022	164
1990	82,990	110	84	102,417	75
1991	53,817	71	69	174,745	128
1992	83,384	111	58	160,016	117
1993	52,279	69	45	145,160	106
1994	65,757	87	54	66,996	49
1995	98,308	131	62	63,843	47
1996	61,360	81	63	79,803	58
Average	75,309	100	69	136,858	100
COV	0.29	0.29	0.23	0.42	0.42

Reported catches are not equivalent to population abundance (the details are discussed later in the paper through an analysis of differences in fishing effort and catch per unit of effort between years). However, catches, which reflect both global population abundance and local availability (itself a function of effort and migrations), may be less variable in squid when demersal feeding aggregations are harvested. The higher apparent stability of targeted feeding aggregations may be expected to break down when the fishery exploits spawning aggregations. Such breakdowns may be seen as either large interannual fluctuations in catch, such as for *Loligo opalescens* on the U.S. west coast (Yaremko 1997), or intra-annual differences, such as for *L. vulgaris reynaudii* off South Africa (Augustyn et al. 1992). Environmental cues such as temperature, current, and turbidity, which are known to influence spawning migrations (Roberts and Sauer 1994), are more likely to vary rapidly and to a greater extent on inshore, shallow spawning grounds than on offshore, deeper feeding grounds. Nonetheless, on the U.S. east coast it seems that the offshore fishery targeting feeding aggregations of *L. pealei* is more variable than the inshore fishery targeting spawning aggregations (NEFSC 1996).

Large interannual variations in total catches have nevertheless been a feature of the Falkland Islands *L. gahi* fishery, and have prompted in-season management decisions on several occasions. Between 1987 and 1996, production ranged between a low of 52,000 t in 1993 and a high of 119,000 t in 1989 (table 1). These variations resulted in adjustments of effort allocation and consequent fluctuations of fee revenues. In its first ten years, the fishery has established and monopolized a predominantly European market. Therefore market prices have often been inversely related to production, and fee policies have had to be appraised in depth before each new fishing season.

Effort. The fishing fleet targeting *L. gahi* in Falkland Islands waters has always been made up of large factory trawlers (West European and initially some East European). Fleet composition, license allocation, and details of changes over the first ten years of the regulated fishery are given in Anon. 1989, Falkland Islands Government 1997, and des Clers 1998b.

Several types of fishing effort descriptors are used routinely in the Falkland Islands *L. gahi* fishery. Weekly averaged numbers of hours fished per day are used to assess the resource. Maximum allowable fishing mortality estimated from assessments is then translated into allowable effort in terms of maximum fleet aggregate tonnage. The total allowable fishing effort is distributed among individual applicant vessels during the licensing exercise. Individual tonnage (IGRT) is the only vessel detail currently used in the fee policy equation. But a wealth of other data collected through the biannual license application rounds are updated into a computerized database at the FIGFD, and routinely checked by fisheries inspectors. Vessel details are also studied through statistical analyses of daily catch rates, and by scientific observers.

An important feature of the *L. gahi* fishing fleet is that average individual vessel size (1,500 IGRT) has remained constant over the years (des Clers 1998b). Total fleet size has decreased, but this does not imply a decrease in fishing effort, because the fewer vessels have fished more during the season. Thus the decrease in total number of vessel-days fishing in the first season has been compensated by an increase in the second season (des Clers 1998a). Furthermore, record catches of 1995 (98,308 t), when compared to those of 1989 (118,720 t), suggest that gradual technological upgrades—whether in finding, catching, or freezing efficiency—have most likely made up for reductions in numbers of vessel-days and hours fished.

The spatial and temporal distributions of fishing activity lend two further dimensions to the matter of effort. In essence, the fixed duration of the two fishing seasons, and the confines of the Loligo box combine to create a narrow window in space and time through which the squid migrate. This creates an intrinsic link between migration and abundance on the fishing grounds. An early migration, for example, may be well under way by the time the fishing season starts at week 5 (first week of February). This is illustrated by the CPUE (catch per unit of effort) time series in the 1990 and 1995 first seasons or in the 1992 and 1993 second seasons (fig. 2). Therefore the fixed frame of the window determines a "perceived abundance," which may in some years be quite different from the actual size of the population moving through the fishing grounds and surviving a fishing season.

Although this difference is not obvious every year (see discussion of CPUE below), it is likely that the bulk of the squid exploited in the first season and the bulk in the second season come from two separate cohorts. Prevailing wisdom considers the population to be homogeneous throughout the Loligo box (Agnew et al., in press), but a recent hypothesis suggests that the two fishing areas support two reasonably distinct populations (Nolan et al., in press).

Scientific Observer Program

The limited-entry management regime chosen by the FIGFD in 1987 relied on the possibility of limiting mortality by closing the fishing season before its usual end if necessary. The decision for a possible early closure is based on evidence from assessments of the squid fishable biomass, or stock size, which is derived from a basic population dynamics accounting exercise on estimated squid numbers. (Details of the stock assessment technique are discussed in the later section Resource Assessments.) Information is collected routinely on squid size, sex, and maturity in order to follow population processes, and on individual weights in order to translate daily catches (tonnes) into numbers of squid.

The data are collected by FIGFD scientific observers who stay on board vessels for three to five weeks at a time to monitor daily catches, effort, and biological parameters. The fishery for *L. gahi* has been the most observed of all Falkland Islands fisheries; for example, in 1997 there were 310 observer-days during the 27-week total duration of the two fishing seasons. In 1997, 132,000 *L. gahi* were measured (equivalent to some 14.8 km) and dissected to determine sex and maturation; a further 7,345 were taken back to shore to be weighed.

In addition to monitoring the fisheries, scientific observers contribute to various collaborative research projects, including squid taxonomy; studies of world bycatch and discards; and surveys of birds and marine mammals. Their observations and activities, described in reports kept by the FIGFD, provide crucial insight for the stock-assessment exercise.

Catch per Unit of Effort

Catch per unit of effort (CPUE) time series statistics are very different data from all of the above in that they are a mathematical construct. There is no such thing as CPUE in the real world; CPUE exists only in terms of fisheries assessment. For this reason, and because CPUE is a ratio and therefore does not vary linearly with either catch or effort, CPUE time series must be interpreted with caution.

These points are examined in detail in the later section Resource Assessments, which discusses theory and practice. However, it is important to keep them in mind, notably when reading about past research and future

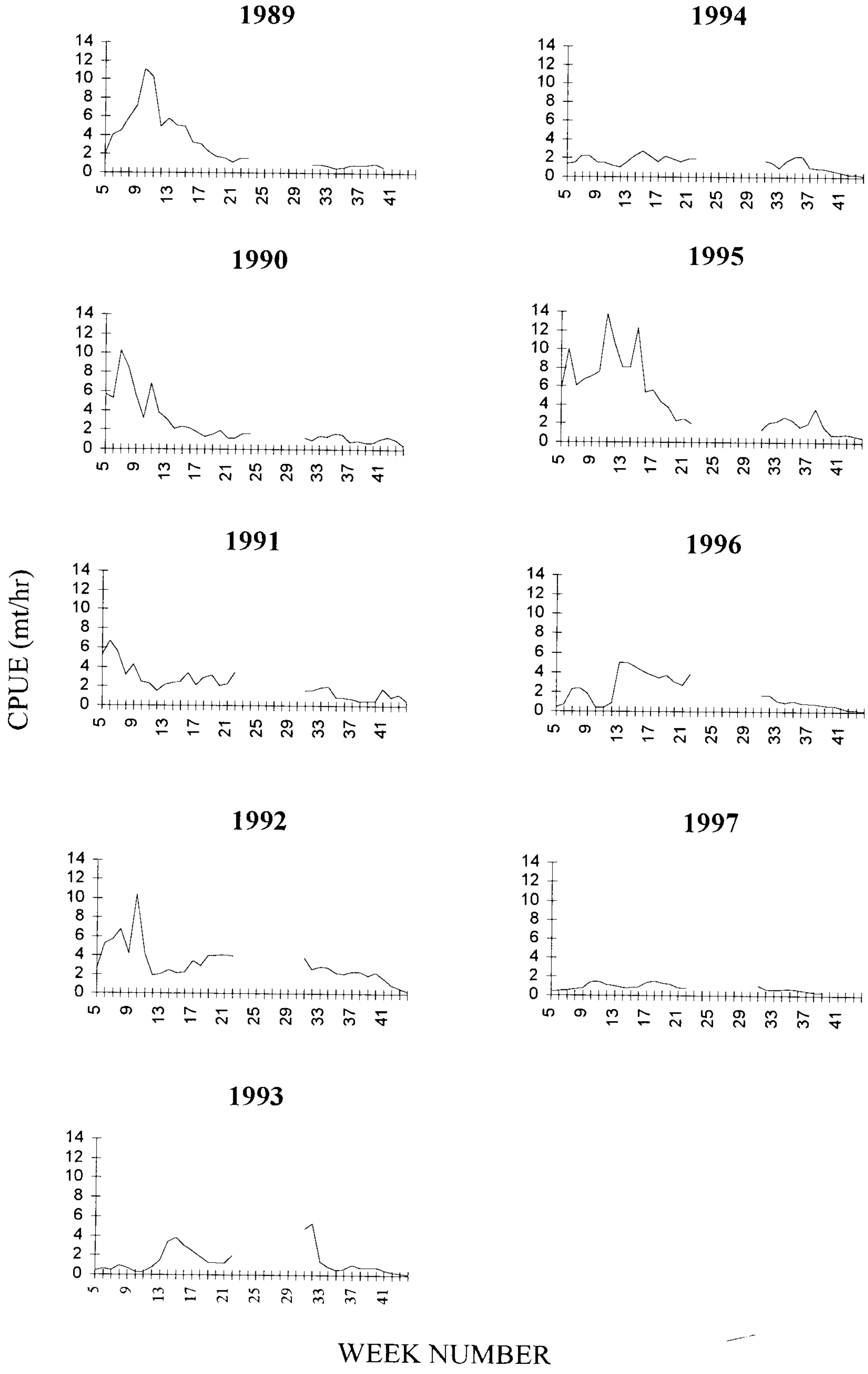

Figure 2. *Loligo gahi.* Patterns in catch per unit of effort (CPUE, tonnes per hour trawled) from 1989 through 1997 in season 1 (week 5 to around week 22) and season 2 (week 31 to end).

needs. Nearly all data on which research has been based so far have been collected from samples taken from the commercial fishery.

RESEARCH

The role of research as an essential pillar of fisheries management has been recognized from the start in the *L. gahi* fishery. In an effort to provide the best possible biological information for assessments and management advice, research thus far has concentrated on the dynamics of the exploited population.

Beyond the need to define priorities, the FIGFD has had to address a less common challenge. Research, which had to be wholly contracted out overseas because of lack of local human resources, had to be steered in ways that allowed a gradual transfer to local development.

The British government, prior to February 1987, commissioned some (unpublished) expert consultations, mainly to evaluate alternative fisheries management regimes for the Falkland Islands (J. Beddington, pers. comm.). Research programs were effectively initiated in 1987.

Population Biology

Population structure. Patterson (1988) made the first attempt at estimating the growth of *L. gahi* and disentangling the population structure of multiple cohorts observed in the two fishing seasons. Using length-frequency and maturity data from samples of commercial catches, he proposed that the exploited *L. gahi* resource comprised two separate stocks, each with an annual life cycle. These stocks were hypothesized to recruit to the fishery in March and November. The stock recruited in March was harvested in the first season (February to May–June) and the second season (August to October). The second stock, recruited to the (closed) fishery in November, was available to the fishery in the first season alone. Thus the presence of two stocks in the first season explained the higher abundances seen in March and April, whereas lower abundances in the second season were explained by the presence of a single stock.

Population structure was further researched through an analysis of the population genetics of the Falkland Islands *L. gahi* population (Carvalho and Loney 1989; Carvalho and Pitcher 1989). The samples analyzed came from commercial catches, notably in the north and south of the Loligo box, and from both seasons. Electrophoretic evidence did not confirm the existence of the discrete stocks proposed by Patterson (1988), although the life-history parameters, such as size and maturity, collected as part of the genetics study confirmed the Patterson (1988) two-stock hypothesis. The population genetics study concluded that genetic evidence favored the existence of a single, interbreeding population of *L. gahi*, and suggested that the lack of genetic evidence for discrete stocks could be due to a combination of migration and extended spawning period for males. An analysis of the population's age structure was recommended to help resolve the issue of stock structure.

Migrations. The geographical distribution and likely life-cycle migrations of *L. gahi* were first mapped during an extensive dedicated research survey in 1988. The survey suggested that *L. gahi* migrated from shallow coastal spawning/nursery grounds into the deeper waters of the continental slope and shelf edge as they fed, grew, and matured, and that there was a probable coastward return migration (Hatfield et al. 1990; fig. 3). Highest feeding concentrations of squid appeared to occur at depths and in areas of the Loligo box where the commercial fishery concentrated its activities.

The extensive survey coverage demonstrated that narrow size ranges of *L. gahi* were associated with narrow depth ranges, and that larger squid were found in deeper waters. This explained the enigma of the apparently constant size of *L. gahi* caught by the commercial fishery during parts of the fishing season, because vessels were focusing on narrow depth ranges. The migratory nature of *L. gahi* also meant that peaks of CPUE in the commercial fishery could be due to pulses of squid moving either offshore to the feeding grounds or inshore to the spawning grounds.

Age and growth. Concomitant research to assess the age structure of the population by using both research and fishery samples (Hatfield 1991) confirmed the hypothesis of the annual life cycle and demonstrated the presence, by back-calculation, of two major peaks of hatch in August/September and December/January. These peaks probably cause two of the major peaks of recruitment, seen as increases in CPUE in February and May, because squid appear to recruit between five and seven months of age.

These initial age data did not explain the changes in CPUE observed in the second season, nor did they agree entirely with the brood structure description of Patterson (1988) and Carvalho and Pitcher (1989). However, these early pieces of research demonstrated that stock assessments could be invalid if interactions between migrations, growth, and population structure were not accounted for. They also showed how further biological research held the key to understanding the structure of the *L. gahi* population in Falkland Islands waters.

A later, more detailed, age study linked migrations to growth of individual broods (Hatfield and Rodhouse 1994a) and suggested periods of residency on the fishing grounds. This study made it possible to determine rates of growth more accurately than had previously been possible (Patterson 1988; Hatfield 1991). The study's findings about migrations have been reinforced by a re-

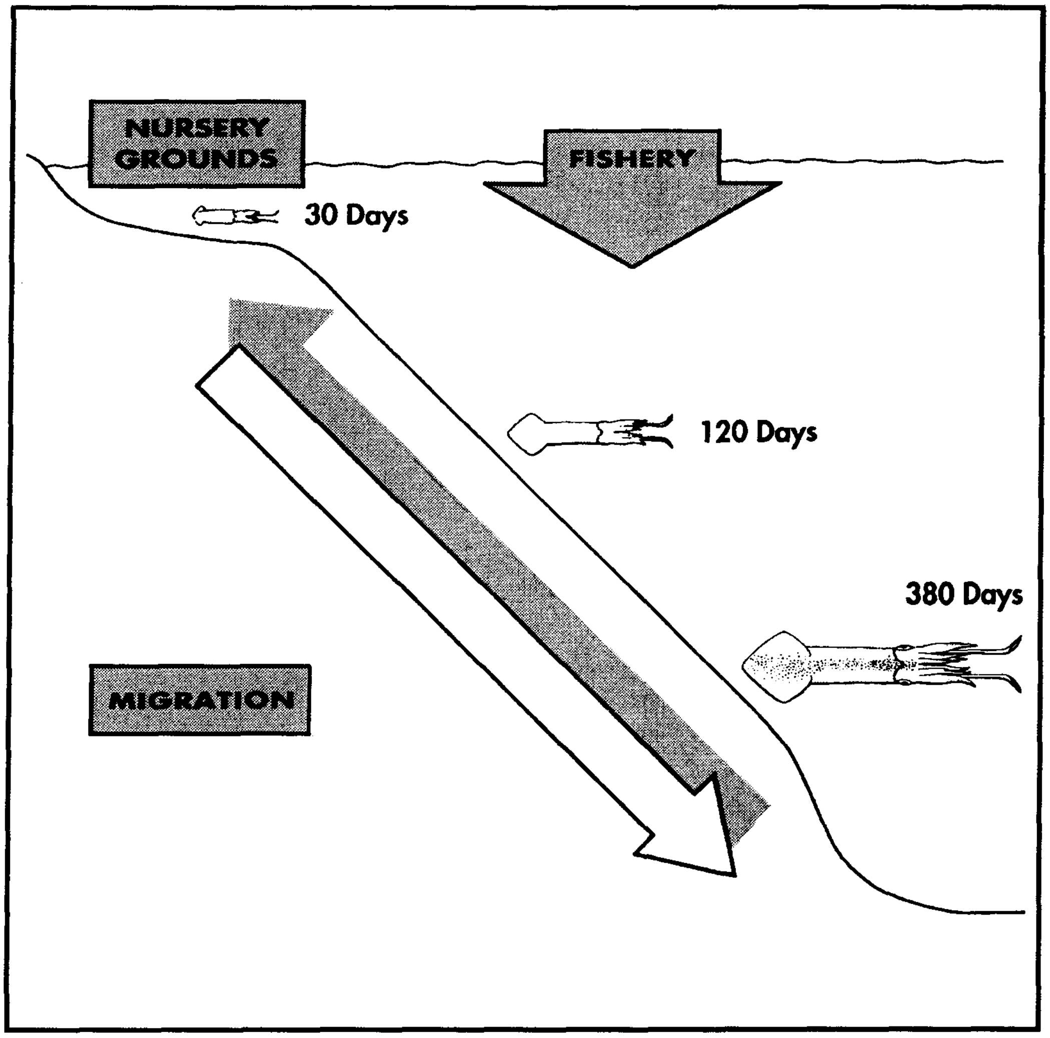

Figure 3. *Loligo gahi.* Diagram depicting migrations over the Patagonian Shelf and the association with the commercial fishery (reproduced by permission of *Antarctic Science*).

cent analysis of length, weight, and maturity data from the commercial fishery, which has confirmed the highly variable pattern of immigration and residency throughout the year (Agnew et al., in press).

Early life history. Data on the early life history of *L. gahi* cannot be collected from the commercial fishery because squid are usually caught only in the second six months of the life cycle.

Four research surveys around the Falkland Islands, employing small research nets generally inshore from commercially fished areas, were conducted between 1988 and 1992 in the austral winter and spring. Reasonable numbers of paralarvae and juveniles of *L. gahi* were caught (Hatfield and Rodhouse 1994b), corroborating the presence of one of the broods seen in the first commercial fishing season and demonstrating the presence of a third brood of squid rarely present in commercial catches, or then only late in the second season.

Life cycle. The research data on early life history, together with growth rates estimated from age studies, were combined to produce a life-cycle model (Hatfield and Rodhouse 1994b). The model proposed that the exploited population usually comprises three broods.

The two major peaks in CPUE in the first season are produced by the immigration of a first and a second brood. The first peak in the second season is due to the continued presence of the second brood from the first season, which for some reason is unavailable to the fishery from June to August. The second peak in the second season, which is not apparent in commercial catches every year, is produced by immigration of a third brood. The proposed third brood corresponds with the brood originally described by Patterson (1988) and Carvalho and Pitcher (1989) as recruiting in the austral spring.

Data analyses of mean length for successive maturity stages and relative proportions of each maturity stage in the population at monthly intervals between 1987 and 1991 provided further evidence of three broods in the population, and confirmed the supposed pattern of entry of each brood into the commercial fishery (Hatfield 1996).

The three-brood hypothesis explains the early genetic findings about panmixia within the exploited Falkland Islands *L. gahi* population, particularly because each of the three major broods can recruit over a relatively extended and variable time period. This may result in a steady trickle of recruitment throughout a large part of both fishing seasons, as evinced by a year-round hatching pattern (Hatfield 1991). More recent age data (as yet unpublished from samples taken in 1994 and 1995) continue to show only two peaks of hatch. The lack of an identified peak for the third brood, likely to be in May, could simply reflect the relatively smaller size and unpredictable occurrence of this brood.

Resource Assessments

Since 1987, the *L. gahi* fishery has been assessed with a modified Leslie-DeLury model originally developed for the Falkland Islands *Illex argentinus* fishery (see Rosenberg et al. 1990; Basson et al. 1996).

The beauty of the technique is its simplicity. As the population is depleted and total catches accumulate, the CPUE decreases. The heart of the assessment is a log-linear regression estimation problem. In the routine assessment for *L. gahi*, input data are the time series of weekly catch, effort, and total catches, and a fixed natural mortality over the period. Provided one has at least three weekly data points, it is possible to estimate the size of the initial population and the vessels' ability to catch, which is assumed to remain constant over the period.

In practice, the analysis is done by subfleet, each assumed to deplete the same population, but each with a separate catchability coefficient. This means that catch and effort data must be available for each group of comparable vessels within the fleet. Also assessed are squid numbers, which are estimated from the tonnage caught on the basis of length-frequency distributions, weight at length by sex, and sex-ratio data. The population data are collected by scientific observers.

Simplicity is conditioned by a few key assumptions. The most basic Leslie-DeLury condition to obtain valid estimates of the initial population size and rate of depletion is that the population is "closed." Closure has to be both demographic (no birth or death) and geographic (no migrations in or out), but only over the period and area of assessment.

The assessment model has been adapted for squid to account for migrations (Brodziak and Rosenberg 1993; Basson et al. 1996; Agnew et al. 1998). However, research has not yet offered a way to define what a *Loligo gahi* population is, let alone to assume that it is closed at any place or time. In particular, a better understanding of what makes a brood or cohort within the fishery and what determines a given brood to replace another is needed, as well as the relative proportions of each brood that are present at the swap-over period.

Although some operational modifications of the assessment procedure have recently been suggested (Agnew et al. 1998), we currently have no predictive understanding of the population processes at play. The exploited *L. gahi* resource is presumed to be one population during the course of a season, and homogeneous throughout the Loligo box (Agnew et al., in press) despite some signs of a north-south divide (Nolan et al., in press). Seasonal assessments still derive very much from an *ad hoc* procedure invoked mostly a posteriori. Their main purpose is to estimate the subfleet catchability coefficients necessary to determine total allowable effort for the following year.

Management Advice

Since 1987, the essential biological assessment management advice has been the determination of total allowable effort. This is carried out for each season based on the assessment of the same season the previous year. The patterns of migration and depletion are analyzed. Initial abundance (and final escapement) and subfleet catchability coefficients are estimated when possible and compared to estimates for the same season from previous years. This is described in some detail in Agnew et al. (1998).

Although early closure has always been an option, it was only considered once in the first ten years of the fishery, in 1991, and for a second time in 1997, when first-season catches were very poor. In each case, projections of conventional stock-assessment estimates indicated a low final percentage escapement from the fishery. In both cases scientific advice proved difficult to formulate, mainly because two broods or cohorts were present in the first season, and because a poor recruitment in the first season does not imply the same for the second season. Halfway through the first season, around week 13 (fig. 2), real-time daily monitoring yields very little information about total catch or CPUE for the coming eight weeks (see figs. 3 and 5 in Agnew et al. 1998).

Originally, the management target was a 40% escapement of the biomass estimated in the absence of fishing. In practice, although this target has been a useful guide, absolute escapement would be a more useful target. It remains impossible to set an absolute escapement target until more is known about *L. gahi*'s population structure and dynamics.

Future Research Needs

It has been argued elsewhere (des Clers 1998b) that, over the first ten years of controlled effort regime, the Falkland Islands *L. gahi* fishery has been managed sustainably. Ten years is a short time, though, in which to accumulate information and knowledge about an annual species such as *L. gahi*. More research is needed to clarify its complex life cycle, and to achieve any degree of predictability. Some directions for future research that are currently being developed are discussed below.

Research on the life cycle and population ecology of *L. gahi* has progressed rapidly since 1987. Two directions have emerged. One, more fundamental, has focused on the essential mechanisms of population dynamics and ecology. Another, more pragmatic, has centered on refining the currently used assessment practices and models. In the first direction, Grist and des Clers (1998) have proposed a new model to link seasonal growth and life-cycle duration. The model, although still preliminary, gives a first hope of predictability, because it predicts the size of a squid entering the fishery as a function of seawater temperature six months previously. It also shows that life-cycle duration of a cohort (or brood) is likely to depend on seawater temperature and, by analogy with many insect populations, may result in one or two cohorts emerging per year. This, combined with Nolan et al.'s (in press) suggestion that the two fishing areas support two reasonably distinct populations, would reconcile the research suggesting three broods (Hatfield and Rodhouse 1994b; Hatfield 1996). At the same time it could explain Agnew et al.'s (1998, in press) suggestions of two broods from research based on an analysis of the two fishing areas and both sexes combined together.

Many crucial aspects of the biology, ecology, and dynamics of *L. gahi* remain unknown. Multiple broods, extended spawning periods, and separate migrations of the two sexes combine to produce a complex picture during the two fishing seasons and between contiguous areas of the Loligo box. The oceanography of the region is little studied, and its effects (e.g., on the biology of *L. gahi* in the spawning grounds around the Falkland Islands) or its importance to recruitment, growth, and maturation of the species have not been studied. The first six months of the life cycle are almost unknown in relation to geographical distribution, growth, or trophic interactions. The role of *L. gahi* within the Patagonian Shelf ecosystem is little studied, and there is little knowledge about population regulation from within (cannibalism); from other species (predation, competition, food limitation); or from the fishery itself (see Murphy et al. 1994; Brodziak and Macy 1996).

Information collected regularly on the distribution of *L. gahi* off-season and outside the Loligo box is likely to yield important understanding of the population biology of this commercially valuable species. Paralarvae could be surveyed, as they are in Japan to predict adult stock size of *Todarodes pacificus* (Okutani and Watanabe 1983). The paralarval distribution of *L. gahi* in the vicinity of the Falkland Islands is only sketchily known, and an efficient method of capture remains to be identified (see McGowan 1954; Clarke 1977; Recksiek and Kashiwada 1979; Vecchione 1981).

On the more pragmatic side, assessment models could be extended along the lines proposed by Agnew et al. (1998), and notably through a statistical rather than a deterministic approach.

From the point of view of the fisheries manager, estimates of seasonal abundance should be obtained independently from the commercial fishery. Independent survey estimates may be the only potential safeguard against errors such as those which plagued the northern cod assessments (Walters and Maguire 1996). Areal expansion methods, for example, have been employed to determine pre-recruit biomass of exploited loliginid species other than *L. gahi* (Augustyn et al. 1992, 1993; NEFSC 1996).

Finally, a variety of aspects will have to be researched in the near future. Among these are the effort dimension of the fishery; optimal fleet size and technological upgrade; economics of vessel operations; and development of fishing gear, product quality standards, new products, and new and existing squid markets.

Future directions of the fisheries policy should also be designed and evaluated. Changes may arise as more Falkland Islanders assume ownership of fishing vessels, or as a result of the universal trend of privatizing fisheries access rights. Some of this research, and some of the biological research, may be funded entirely by, or in collaboration with, vessel owners. In all cases, the FIGFD is likely to play an important steering role.

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MATING SYSTEMS AND SEXUAL SELECTION IN THE SQUID *LOLIGO*: HOW MIGHT COMMERCIAL FISHING ON SPAWNING SQUIDS AFFECT THEM?

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ABSTRACT

The effect of targeted fishing on spawning grounds is central to the management of commercially valuable squids for at least three reasons: (1) the very short life cycle of about one year; (2) dense spawning aggregations, which are easily targeted by fisheries; and (3) fishing techniques that could remove certain sexes or sizes of squids, thus leading to "unnatural" sexual selection processes that affect recruitment. Recent field and laboratory studies on *Loligo vulgaris reynaudii* in South Africa and *Loligo pealei* off the northeastern United States indicate that the mating systems are complex, that sperm competition is a major feature of the systems, and that alternative reproductive tactics may be flexible enough to withstand targeted fishing pressure, provided that the pressure is not so great that it suppresses reproductive behavior. Behavioral studies combined with DNA fingerprinting to assess paternity of individual egg capsules are helping to resolve some of these questions. In this paper, I outline an approach to studying reproductive behavior in the context of fisheries management, and I speculate on features of the mating system of *Loligo opalescens* that should be understood before high levels of exploitation are permitted.

INTRODUCTION

Evolution has forged ingenious ways for animals to reproduce, and squids are no exception. Like all organisms, squids must survive natural selection, and in the process they must succeed in sexual selection to ensure that their individual genes are passed to the next generation. Squids of the genus *Loligo* school for most of their very short life cycle, and during a large portion of this yearly cycle they are engaged in reproductive behavior. Sexual competition, fecundity, and reproductive success of squids of the genus *Loligo* have only recently been studied in any detail by cephalopod biologists (summarized in chapter 6 of Hanlon and Messenger 1996).

Dense aggregations of sexually active squids are common, and they seem particularly vulnerable to harvesting by commercial fishing methods. For example, *L. vulgaris reynaudii* (South Africa), *L. pealei* (NE U.S.), and *L. opalescens* (U.S. west coast) are fished partly, if not mainly, on spawning aggregations, and they are the basis of large and growing fisheries that are being exploited heavily (e.g., Fields 1965; Dewees and Price 1982; Hixon 1983; Sissenwine and Rosenberg 1993; NFSC 1995; Augustyn 1998). Nevertheless, it is possible that the squids' mating systems are flexible enough to withstand such commercial fishing pressure, although this remains to be demonstrated.

In this paper, I explore the possible ramifications of targeted fishing on spawning aggregations in the context of what we have learned recently about sexual selection processes and mating systems in *Loligo*.

METHODS AND APPROACH

It has been productive to combine field and laboratory studies of *Loligo* spp. Fortunately, spawning loliginid squids do not react to divers or machines, so it is easy to approach and film them with little or no period of habituation (e.g., Hanlon et al. 1994, 1997; Hanlon 1996; Sauer et al. 1997). Technological advances have refined the processes for gathering behavioral data. Scuba diving allows underwater observations under natural conditions, and diver-held video allows careful analysis back in the laboratory or aboard ship. Hi-band 8 mm video, super VHS video, and most recently digital video provide increasingly high-resolution images that allow behavioral details to be recorded and analyzed. Remotely operated vehicles (ROVs) with video cameras allow behavioral sampling as well; when sampling routines for divers and ROVs are coordinated, it is possible to obtain a wide range of behavioral data in a relatively short time, especially with refined behavioral sampling rules and methods (Martin and Bateson 1993). Telemetry devices implanted in squids have allowed longer-term movements to be recorded (Sauer et al. 1997). Field studies under natural conditions make it possible to use noninvasive methods to describe generalities of the mating system, and set the stage and the questions for laboratory experiments.

Significant improvements in methods for keeping squids alive in captivity have enabled researchers to study various aspects of reproductive behavior (e.g., Hurley 1978; Hanlon et al. 1983). Perhaps more important, the advent of DNA fingerprinting methods has allowed verification of paternity in sexual selection studies of numerous taxa (e.g., Queller et al. 1993), both in the field and in the laboratory. With *Loligo*, it is now possible to determine multiple paternity of field-collected egg capsules (Shaw and Boyle 1997) and to assign paternity after highly controlled mating trials in which the recent mating history of individual females is known with precision (e.g., Hanlon et al. 1997). These powerful molecular and behavioral techniques will permit rigorous studies of reproductive success in cephalopods for the first time.

MATING SYSTEMS, SEXUAL SELECTION, AND FISHERIES

Within a population, the *mating system* refers to the general behavioral strategy used in obtaining mates. It includes such features as (1) the number of mates acquired, (2) the manner of mate acquisition, (3) the presence and characteristics of any pair bonds, and (4) the patterns of parental care provided by each sex (Emlen and Oring 1977). Mating systems can be viewed as outcomes of the behavior of individuals competing to maximize their reproductive success (Davies 1991). The conceptual beginning point of mating systems is promiscuity (all pairings are random and multiple); monogamy represents the other end of the spectrum (Lott 1991). To our current knowledge, there are no monogamous cephalopods. But we cannot yet predict pairings in squid matings beyond saying that, in most species, both males and females will mate with more than one partner.

Sexual selection is defined as the differences in reproduction that arise from individual variations in traits that affect success in competition over mates and fertilizations (Andersson 1994). Hypotheses about sexual selection were first proposed by Darwin, but hypotheses have been tested and actual mechanisms have been determined mostly in recent decades by behavioral ecologists (cf. Andersson 1994; Eberhard 1996; Krebs and Davies 1997).

Fighting among males is a form of competitive aggression (as distinct from protective or parental aggression) that enables males to gain preferred access to females for mating; this is an example of sexual competition (Archer 1988) and introduces a most important concept. *Sperm competition* was defined originally by Parker (1970) "as the competition within a single female between the sperm from two or more males for the fertilization of the ova," but a current definition in common use was provided by Birkhead and Parker (1997) "... a part of sexual selection ... and includes the adaptations which arise as a result of it; e.g., any behaviour, morphology or physiology associated with multiple mating by females, paternity guards and ejaculate characteristics, all viewed from both a male and female perspective."

Sperm competition can occur whenever a female mates with more than one male in one breeding cycle. Thus there is a strong behavioral component to sperm competition. Specifically, sperm competition involves (1) competition between males for copulations, (2) sperm precedence mechanisms by males (e.g., sperm plugs, last in first out, sperm dilution), as well as (3) possible manipulation of the sperm by inseminated females (Eberhard 1996). Sperm competition is a major component of mating systems in many phyla and is a vigorous field of inquiry for behavioral ecology (cf. Smith 1984; Birkhead and Moller 1992; Andersson 1994; Birkhead and Parker 1997).

Sperm competition typically includes the following features in many phyla: a large testis that can produce large quantities of sperm; sperm packaged in spermatophores; sperm stored by females; appropriate morphologies of the oviduct and spermatheca; polygamous mating systems; multiple styles of mating; delays between mating and egg laying; and intense mate guarding. In squids, many matings can occur over many months, and it is possible that sperm from the most recent matings might displace that from earlier matings. After all, the seminal receptacle of *Loligo* appears to be little more than a series of invaginations and associated glands (Lum Kong 1992), but no one has yet considered the functional anatomy of the seminal receptacle in relation to the hypothesis of sperm competition.

Sexual selection is a vital complement to natural selection (Darwin 1871) and can be a large determinant of the population structure over time. Population structure (i.e., the spatial variation in density and genetic composition of individuals in a species) is affected by fishing techniques and fishing pressure. Because there is a close relation between the population genetic structure and the behavior of individuals in a population (Hewitt and Butlin 1997), the mating system can be altered as population structure is altered, possibly affecting recruitment into the next generation and, ultimately, the fishery.

BEHAVIORAL DYNAMICS OF SPAWNING AGGREGATIONS

Squids of the genus *Loligo* are demersal spawners that usually lay eggs in large communal masses. Spawning aggregations are common for *Loligo vulgaris reynaudii* (e.g., Sauer et al. 1992), *L. pealei* (Arnold 1962; Summers 1983), and *L. opalescens* (McGowan 1954; Fields 1965). Although spawning aggregations are the principal means of reproduction, very small groups or individual pairs of squids also lay eggs in isolation in all three species. Commonly the spawning aggregations comprise hundreds, thousands, or even hundreds of thousands of squids. The behavioral dynamics are at first bewildering, but for *L. vulgaris reynaudii* and *L. pealei* progress has been made in sorting out the general scope of activities (e.g., Hanlon et al. 1997; Sauer et al. 1997).

Figure 1 is a generalized schema of a spawning aggregation of *L. vulgaris reynaudii* in South Africa. The

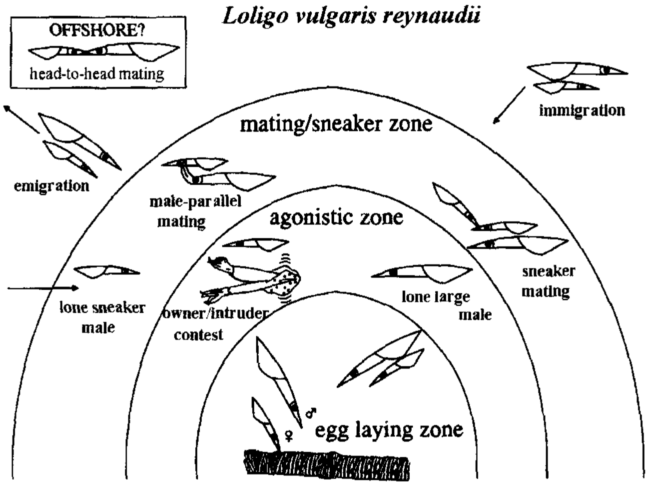

Figure 1. General schema of a spawning aggregation for *Loligo vulgaris reynaudii* off South Africa (modified from Hanlon and Messenger 1996). The "zones" are somewhat arbitrary in their dimensions. "Owners" are large paired consort males, and "intruders" are unpaired large males attempting to become consorts. Offshore head-to-head mating is speculative, but females often have sperm in the seminal receptacle.

main components of the scheme apply generally to the other species as well: (1) an egg-laying "zone" with pairs descending to the substrate and the females inserting individual egg capsules into the communal egg mass; (2) an area with considerable agonistic (fighting) behavior, and (3) an area with mating (several types). In some respects, these aggregations resemble a busy airport in which pairs of squids are circling above and then descending to lay eggs before repeating the cycle. Meanwhile, lone males continually use multiple tactics to obtain mates, both by fighting paired males to replace them as consorts, or by obtaining extra-pair copulations (EPCs); small males are also attempting to gain EPCs. Head-to-head mating has not yet been observed in this species, but it certainly occurs, because females usually have stored sperm in the seminal receptacle; it is possible that this type of mating occurs while the populations are offshore.

Operational Sex Ratios

Although the ratio of males to females is generally 1:1 for *Loligo* populations, in spawning aggregations there appears to be a skew toward slightly more males, which establishes a selection gradient of males competing for females. This aspect of squid biology is poorly known, however, and extensive behavioral observations and quantification are needed to determine the operational ratio of males to females because this is an essential feature of sexual selection processes. Determining how many individuals are actively participating in sexual behavior on any given day or week within a population or restricted geographic area is a challenging task, yet ROVs, telemetry, and divers offer methods to accomplish this.

Multiple Mating Positions and Multiple Mates

Two or three methods of copulation for each individual are known in many loliginid squid and octopus species, and these provide a critical source of variation in cephalopod mating systems. What determines the method to be used by a particular pair of squids at any given mating encounter is unknown. In *Loligo*, it is worth pointing out that in the "head-to-head" position the spermatophores appear to be passed only to the seminal receptacle below the mouth for sperm storage and eventual use by the female (e.g., Drew 1911). By contrast, in the "male-parallel" position the spermatophores are placed inside the female's mantle cavity near the opening of the oviduct (fig. 2). The head-to-head position has been correlated with extra-pair copulations in *L. vulgaris reynaudii* (Hanlon et al. 1994; Sauer et al. 1997) and in *L. pealei* (Hanlon 1996; fig. 3), but no such position has been observed in *L. opalescens*, although there is a seminal receptacle below the mouth as in the other species (see comment in Concluding Thoughts). In the male-parallel position, eggs would have to be extruded and fertilized within minutes or hours to take advantage of those spermatophores, many of which seem to be partially or wholly broken as they are deposited (Drew 1911).

Both sexes have multiple mates, although the absolute number of mates is unknown on natural spawning grounds. In laboratory trials, females of *L. pealei* are known to have up to four mates within several hours, and to lay eggs after mating with several males in succession (Hanlon et al. 1997). These same females lay eggs in bouts that are several days or weeks apart, and in each bout they typically deposit 20–50 egg capsules.

The complexity of sexual behavior in *Loligo* becomes more obvious when the multiple mating positions and mates are analyzed by the different behaviors of each sex. Possibly the most fascinating aspect of this is that female *L. pealei* (U.S. East Coast; Hanlon 1996) and *L. vulgaris reynaudii* (South Africa; Hanlon et al. 1994) perform EPCs with small sneaker males, so that each female may have three or more sources of sperm to fertilize eggs in each egg capsule she deposits (ca. 200 eggs per capsule). These three sources would be from the large paired male, the stored sperm in the seminal receptacle, and the sneaker male, who in *L. vulgaris reynaudii* appears to mate the female when she is holding an egg capsule in her arms. Furthermore, there may be more than one male's sperm stored in the seminal receptacle.

Male Behaviors: Fighting, Courting, Copulating, Sneaking, and Guarding

On spawning grounds, large male *Loligo* strive to form temporary pairs with females, with the goal of having preferred access to copulations. The operational sex ratio

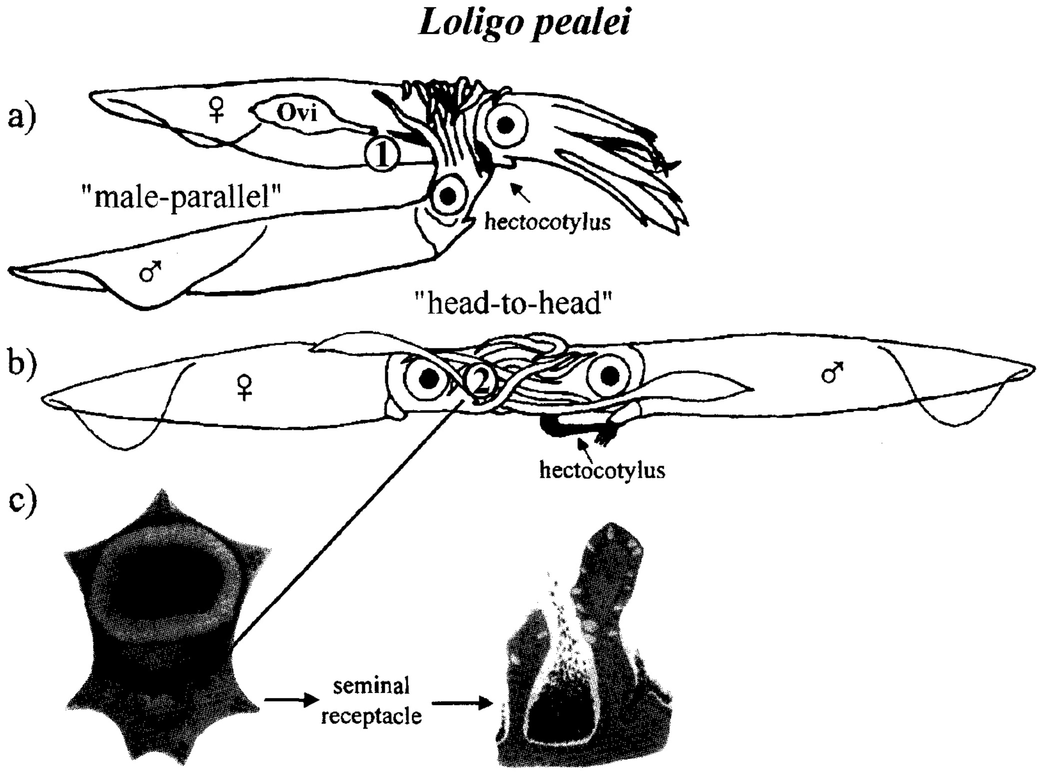

Figure 2. Two sperm sources and their placement during different methods of copulation in *Loligo* spp. Drawing is based upon *L. pealei* (modified from Drew 1911 and Hanlon and Messenger 1996). 1. Spermatophores are transferred by the hectocotylus (darkened) and placed near the external oviduct (Ovi) in the mantle cavity of the female during male-parallel mating (*a*). Eggs are usually laid shortly after this type of mating. 2. During head-to-head mating (*b*), males place sperm directly into a seminal receptacle located just below the mouth of the female (*c*). Note stored sperm in the cross-section of the seminal receptacle. Egg laying does not usually take place soon after head-to-head mating.

is skewed toward males, thus males must fight to obtain a mate and then be able to repel the lone rival males. Thus these "consort males" spend considerable energy and time courting and defending individual females, and they have high mating success (Hanlon et al. 1997). By contrast, lone large males spend time trying to become consort males, and focal behavioral sampling of these males has shown them moving from one pair to another, challenging consort males in agonistic bouts that use multiple visual signals and sometimes escalate to fin beating, which is a physical test of strength (Hanlon et al. 1994; Hanlon and Messenger 1996; DiMarco and Hanlon 1997; Sauer et al. 1997).

Yet on all spawning grounds there are smaller males too, and their tactics are very different. They do not engage in agonistic bouts with larger males, but opt to stay distant from pairs and observe them vigilantly. It is worth emphasizing that some small males are sexually mature and active, so that mating is not reserved for large males. The small "sneaker males" rush in and copulate with paired females in the head-to-head position, often with no resistance from the consort male (fig. 3). In 1997, two additional sneaking tactics were observed for *L. pealei* off Cape Cod (Hanlon et al. 1997). First, small males sometimes became "bold" and moved around the egg mass in groups of 2–4, occasionally darting in for an EPC; thus we have observed both surreptitious and bold sneakers among small males of *L. pealei*. Second, lone large males became "sneakers" on occasion by dashing in and copulating with paired females in the male-parallel position (opposite to that of the small sneakers that mated head-to-head). Overall, five male behaviors have been documented as tactics to obtain copulations (Hanlon et al. 1997).

Finally, the large consort males guard their paired female mates as they descend toward the egg mass to deposit an egg capsule. Such guarding is a common feature of mating systems characterized by sperm competition. However, the degree of vigilance and guarding by consort males varies a great deal, and its meaning remains to be discovered.

Female Behaviors: Choosing Mates and Choosing Sperm

Generally the most obvious behaviors seen in animal mating systems are those of the males, but it is becoming

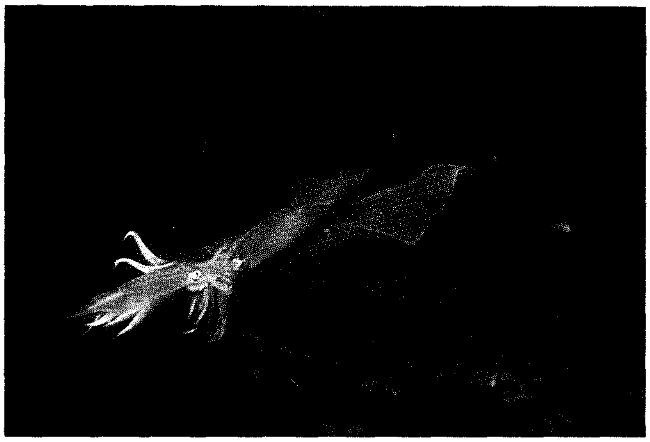

Figure 3. Sneaker male (left foreground) of *Loligo pealei* mating a paired female as the large consort male does not interfere (photo by William K. Macy).

increasingly apparent that females exert several levels of mate choice (Andersson 1994), including methods of sperm manipulation and allotment—a phenomenon known as "cryptic female choice" and elucidated in a provocative book by William Eberhard (1996). Recent studies of sexual selection point out a fundamental discovery: the mechanisms of female choice and their influence on relative paternity by multiple mates are considerable, and may be powerful forces in the ultimate outcome of fertilizations.

Female *L. pealei* (and perhaps the other two species) arrive on nearshore spawning grounds in spring with stored sperm in the seminal receptacle. Thus it is evident that they mate early in their life cycle, and they clearly have at least one source of sperm (a "backup" perhaps). Theoretically they may not need to mate again on the spawning grounds, but squids near shore on Cape Cod engage in high levels of sexual activity.

The curious feature of female *Loligo* behavior is that they appear to be generally receptive to all male mates, and they are relatively passive; i.e., they do not typically show conspicuous behaviors or other obvious signs of rejection of male suitors. Females tend to accept multiple mates even in succession on a single day. But analyses of video tapes of *L. pealei* females on spawning grounds show cases in which females actively jet backwards when males attempt to mate them (Hanlon, Maxwell, and Shashar, unpubl. data). This has happened mostly when sneaker males approach for a head-to-head mating, but has also been seen for male-parallel mating. Such rejections would be cases of "direct" female choice of mate. Most interesting, a recent paper by Wiley and Poston (1996) introduced the concept of "indirect female choice," in which females may set the stage for competition for males before arriving at the spawning grounds, so that any male fit enough to be present and sexually active on the spawning ground has already proved his fitness. In such a system, it might pay females to mate with any male present.

A female *Loligo* may exert choice in the decision of which mating position is used, or whether stored sperm are used when she extrudes each egg capsule, but experimental evidence is lacking for either of these possibilities.

Female fecundity and reproductive output are not well understood in *Loligo* spp., although the information is essential for fishery managers. There is considerable controversy over whether females are terminal "big bang" spawners or "intermittent" spawners over several months (Hanlon and Messenger 1996). Only in *L. opalescens* have dying squids been seen on the mating grounds, which is anecdotal evidence for terminal spawning. There are documented cases in which individual females of *L. pealei* lay eggs over weeks and months in the laboratory. Hixon (1980) documented a case in which a single female deposited 222 egg capsules over 72 days during several bouts of egg laying. Recent trials in our laboratory demonstrate high variability in reproductive output: some small females are as fecund as large females, as determined by measuring the number of mates and egg capsules that are laid over several weeks in captivity (M. Maxwell and R. Hanlon, unpubl. data, 1997). In a single day, one female laid 70 egg capsules; another had at least 6 mating partners over 33 days in the laboratory, so the hypothesis that females commonly have many mates may prove to be true. Clearly more data are required on this subject.

PROBABILITY OF MULTIPLE PATERNITY IN EGG CAPSULES

There is likely to be a rather high degree of multiple paternity in egg capsules of all three of the loliginids considered in this paper, for the following reasons. Pairings of consort males with females are temporary, leading to a high turnover of mates for both males and females. Individuals mate multiple times, often with different mates, even during the same day, and eggs are not always laid after each mating, so that sperm from several males mating in succession could be competing for fertilizations within the egg capsules that are laid that day. There are multiple positions of mating, each with different sperm placement (fig. 2). Females can store sperm for long periods, probably from different males, in the seminal receptacle below the mouth. Females also exercise the option of releasing their stored sperm—or not releasing it—onto egg capsules. When they do release it, however, there is almost certainly going to be multiple paternity.

Sperm competition can take place at multiple levels in such a mating system. First, of course, is the level of whole-animal behavior of males and females that has been outlined above. To demonstrate this, let us follow the probable course of an egg capsule from its extrusion from the oviduct to the time it is laid in the substrate:

- Egg capsule is extruded from the oviduct into the mantle cavity.
- Free-swimming sperm may be present in mantle cavity from male-parallel mating.
- Sperm enter jelly matrix of egg capsule and swim toward ova.
- Sperm swarm at micropyle of ova[1].
- Egg capsule is drawn by the female into her arms.
- Stored sperm from seminal receptacle may be released and enter jelly matrix and swim toward ova.
- Sperm competition at the micropyle of each ovum may be occurring among sperm from the mantle cavity (male-parallel mating) and from the seminal receptacle (from head-to-head mating).
- In some species, a head-to-head mating can occur just as the egg capsule is held in the arms, so direct deposition of spermatophores on the egg capsule would provide another source of sperm.
- The egg capsule is deposited into the substrate.

Collectively then, multiple paternity must be expected in some percentage of the egg capsules. It is important to know paternity between egg capsules as well as within egg capsules. In both cases the question of "how many" is important, both in evolutionary terms to the individual squids as well as to fishery managers who must be concerned about gene mixing within the population.

How is multiple paternity measured? Field samples of eggs can be analyzed by DNA fingerprinting, which can tell us only that multiple paternity has occurred. Complementary laboratory studies of selective mating combined with DNA fingerprinting of all participants provide detailed information that can elucidate mechanisms of sperm competition. In laboratory experiments, my colleagues and I control the mating sequences; we know the recent mating history of each female in captivity; and we have tissue samples of each potential father to measure paternity with accuracy (Hanlon et al. 1997). The practical difficulty is that many DNA samples must be run for each egg capsule (which contains 100–200 ova), and this is both time-consuming and expensive.

DO COMMERCIAL CAPTURE TECHNIQUES SELECTIVELY REMOVE CERTAIN SQUIDS?

If commercial capture techniques selectively remove certain sizes or sexes of squids, they could create an artificial sexual selection gradient. The consequences of this artificial gradient would be manifest as differential gene mixing in the next generation.

In South Africa, jigging is the primary capture method for *L. vulgaris reynaudii*. Lipinski (1994) found that jigs undersampled both the largest and smallest squids compared to purse seines (which were presumed to be sampling all sizes equally); this could be extrapolated to mean that the large consort males and the smallest sneaker males, or possibly the smallest females, were undersampled by jigging. Sauer (pers. comm., 1998) found evidence that large paired consort males are less interested in jigs than are lone large males; furthermore, he noticed that females not actively laying eggs were more interested in jigs. These types of observations need to be quantified because they are important to management decisions.

Loligo pealei off the northeastern United States are captured commercially mostly with trawl nets, but also near shore with weir traps. Weirs (which are passive devices) probably capture entire schools, and it would be expected that they reliably sample the adult population. The largest and fastest squids (males in this species) may avoid trawls, and video cameras affixed to trawl nets are now being used in New England to assess such avoidance behavior (Glass and Wardle 1989).

Loligo opalescens off California are attracted with lights, then captured by various types of surrounding nets (purse seines, lampara nets, etc.). If squids naturally spawn at night, it is possible that only some participants on active spawning grounds might be attracted to the lights and captured, while others remain near the demersal eggs and avoid capture. To my knowledge, such information is not available.

A main point here is that practically no information has been gathered to compare the composition of captured squids with the "normal" distribution of squids in an effort to assess the possible deleterious effects of fishing on their reproductive behavior.

For the same reasons, it would be beneficial to study the behavior of squids in relation to jigs, lights, and nets (both passive and actively fished). In addition, the effects of trawls or lampara nets on demersal eggs should be considered. Finally, it is possible that female fecundity is affected by these methods, especially if fecundity partially depends upon the social interactions of schools of squids engaged in intensive sexual competition.

REPRODUCTION, RECRUITMENT, AND FISHERY MANAGEMENT

Reproduction in loliginid squids is a complex system that encompasses a wide spectrum of behavior, a large anatomical investment, and a long period during the short life cycle. This complexity is one measure of the alternative—and flexible—reproductive tactics that should be expected in a short-lived species that migrates to and

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[1] This process of swarming before fertilization takes up to 10 minutes in laboratory observations (Arnold 1984), which would allow ample time for all the behavioral events of sperm competition to be completed.

from different habitats. What does this mean with respect to managing the fishery?

The underlying notion emerging from this recent work is that the mating systems of squids like *L. pealei* and *L. vulgaris reynaudii* seem to result in genetic diversity in the next generation. This is likely to aid recruitment processes for the next generation, although the dynamics of squid recruitment are not well studied (Rodhouse et al., in press). Much of this diversity appears to result from the multiple paternity that we expect to find not only *among* the many egg capsules (each with 100–200 ova) laid by each individual female, but *within* each egg capsule as well. Ultimately this diversity results from the reproductive behavior of males and females before and during their time on the spawning grounds.

The difficulty of making such assessments should not be diminished. Several other mechanisms might influence paternity, gene mixing, and recruitment. For example, I have been assuming that if a fishing technique selectively removes the large consort males, then gene mixing and subsequent recruitment will be affected insofar as the largest fit males will not be well represented in subsequent populations. But perhaps those same consort males acted as sneaker males months before arriving on the spawning grounds, and their stored sperm were used by some females, perhaps even in precedence over males that the females encountered on the spawning grounds. Although this seems unlikely, it is possible, and DNA studies may turn up cases such as this in laboratory trials. As another example, it is possible that sneaker males are more fit than large consort males, and that recruitment might be strengthened by having more of their genes in the population if large consorts are removed.

As a simple generalization, limited impact on spawning aggregations by targeted fishing will probably not interfere drastically with gene mixing and egg laying, and thus will not have a strongly adverse effect on recruitment. What I mean by "limited impact" is moderate fishing pressure on spawning grounds, and verification that the fishing techniques do not selectively take one segment of the breeding population (e.g., largest consort males, or females, or sneaker males). Unfortunately, such verification is not yet available for any of the three fisheries I have referred to in this paper. This should be a rather high priority for research so that fishery managers will have some biological data upon which to base decisions.

Another practical fisheries consideration is whether commercial fishing takes place during the peak reproductive activity of a species. What sort of disruption would occur if it did? To determine the peak daily time of reproductive behavior, ROVs stationed near communal egg beds could sample around the clock for several days. If, for example, *L. opalescens* spawns predominantly during the day, then commercial fishing at night is likely to disturb mating and egg laying less than daytime fishing directly on spawning squids.

Some of the generalities presented in this paper are likely to apply to *L. opalescens*, but I hasten to add that *L. opalescens* appears to have some differences (Hurley 1978) from the mating systems of *L. pealei* and *L. vulgaris reynaudii*, which have now been studied in some detail (e.g., Hanlon 1996; Hanlon et al. 1997; Sauer et al. 1997). Only one mating position (male-parallel) has been verified in *L. opalescens* (McGowan 1954; Fields 1965). Fields reported that he "might" have observed head-to-head mating once among "scores of encounters," and he noted that it happened to occur "between a small male and a large female." From our knowledge of other *Loligo*, it is likely that Fields observed a sneaker male, but such a concept was unknown at that time.

There is keen competition for mates on the spawning grounds, as highlighted by Hurley's (1978) field observation of five males simultaneously attempting to mate a single female. Furthermore, Fields (1965) noted that "several males may single out one or two females from a group and mate several times with them, ignoring the other females present." Such behavior has not been noted in the extensive observations on the other two *Loligo*.

It is not clear from anatomical studies that female *L. opalescens* can spawn intermittently (Reckseik and Frey 1978), but this requires future behavioral study. Finally, female *L. opalescens* often hold the egg capsule in a horizontal position for long periods of time, even moving it up and down, which would be a plausible way to release stored sperm along the length of the egg capsule, which Fields (1965) suggested. Neither *L. vulgaris reynaudii* nor *L. pealei* have been reported doing this. My colleagues and I have looked for this behavior at communal egg masses of *L. pealei* and have not seen it after dozens of observations.

CONCLUDING THOUGHTS

It is impossible in a short treatise to consider all the features of reproduction that may be affected by, or may themselves affect, a commercial fishery. My point is to highlight the nature of the mating system—particularly its flexibility and multiple tactics—so that fishery managers and teuthologists can consider the possible effects on recruitment if fishing techniques alter the system.

The California fishery for *L. opalescens* is under pressure, not only from commercial fishing but from the influence of El Niño, which has displaced squid populations greatly during 1997 and 1998. It would be prudent to err on the conservative side and protect some known traditional spawning grounds of *L. opalescens* until some features of the mating system are studied, particularly since this species is so short-lived and recruitment could be affected so directly. Recall, for example, that some of the mechanisms that seem to promote genetic mixing (alternative mating positions, intermittent spawning, multiple paternity within egg capsules) have been shown only in other species, not *L. opalescens*. There is substantial recent literature on the precautionary approach to fishery management, which argues for more restrictive management in the face of uncertainty (e.g., FAO 1997; Serchuk et al. 1997).

Nevertheless, fishermen and managers alike should be encouraged that our current knowledge indicates that the mating systems of *Loligo* spp. can probably withstand a moderate amount of targeted fishing on spawning squids, even though solid scientific evidence is needed to verify this. The problems are known, the techniques are available, and hopefully the opportunity to study these issues will be realized as well.

ACKNOWLEDGMENTS

I am indebted to many friends and colleagues for the opportunity to study these issues over the years. Malcolm Smale and Warwick Sauer and their colleagues in South Africa (including the fishermen's cooperative association) were instrumental in arranging diving studies on spawning grounds. In New England, the owners of local weir traps (Mark Simonitsch, Paul Lucas, and Ernie Eldridge) enabled us to film spawning squids. Postdoctoral fellows Mike Maxwell and Nadav Shashar in my laboratory were essential for gathering data in the field and laboratory, and for reviewing the manuscript. Bill Macy kindly provided figure 3. There has been great logistical support at the MBL, especially from Ed Enos and Bill Mebane and their staffs in the Marine Resources Center, and from many summer students. Fishery biologists at the Northeast Fisheries Center, NMFS, Woods Hole, have greatly expanded my knowledge about management issues of squids. I am most grateful for funding from WHOI Sea Grant NA46RG0470, from Saltonstall-Kennedy Grant NA76FD0111, and for the temporary loan of an ROV from the east coast National Underseas Research Center (NOAA), all of which made our studies of *L. pealei* possible. Lastly, I thank Doyle Hanan and George Hemingway for organizing this fine symposium, and the California Seafood Council for its generous support.

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RESEARCH INTO THE LIFE HISTORY OF *LOLIGO OPALESCENS*: WHERE TO FROM HERE?

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ABSTRACT

Statolith ageing techniques have greatly aided our understanding of loliginid squid biology. We now know that life spans of loliginid squids are relatively short: most temperate species live for about a year or slightly more. Many tropical species appear to complete their life spans in fewer than 200 days. Early growth estimates for *Loligo opalescens* based on length-frequency analysis have suggested a life span of around two years. However, preliminary data from statolith ageing and culture of *L. opalescens* have shown that reproductive maturity can be reached in less than a year. Further research is needed to determine the life span of this species, but it is possible that it may not exceed one year. Research is especially needed to validate periodicity in statolith increments and to study latitudinal and seasonal variation in growth and maturity rates. This will provide the necessary data for future management and policy decisions. Other areas of research—the use of predators as sampling tools; investigation of the condition of and degradation of tissue in association with maturity; tracking studies using transmitters, radio acoustic positioning, and telemetry (RAPT) as well as traditional tagging; and light trapping—may yield important biological data about *L. opalescens*.

INTRODUCTION

Loliginid squid stocks occur in most continental shelf areas of the world's oceans except for the extreme polar regions. Some species have a wide latitudinal distribution, such as *Loligo opalescens* off the west coast of North America or *Loligo forbesi* in European/African waters. In contrast, *Sepioteuthis australis*, which is restricted to southern Australia and northern New Zealand waters, is an example of a loliginid with a much narrower distribution. In some continental shelf regions (e.g., northern Australia; Yeatman and Benzie 1993, 1994, or the Gulf of Thailand; Chotiyaputta 1993) there is a diversity of loliginid species, whereas in other regions there is only one loliginid species, such as *L. gahi* on the Patagonian Shelf and *L. opalescens* off California.

Many of these populations are coming under increasing pressure from national and international fisheries. There is a need to obtain information on the biology and life history of these loliginid populations worldwide to provide the necessary building blocks for management and policy decisions. Without such data, management is based only on guesses and approximations. Current knowledge about the age and growth of loliginid squids has revealed that previous life span estimates have led to an inaccurate understanding of the biology of these organisms. One example of this has been the application of length-frequency analysis in an attempt to determine squid growth (see Jackson and Choat 1992; Jackson et al. 1997). The results of such analysis have led to the measurement of life spans in years instead of days. Such errors can have profound implications for interpreting population dynamics and for management decisions.

The collection of accurate data on age, growth, and life history is fundamental for implementing long-term management strategies. This paper reports on past research into the age, growth, and life history of *L. opalescens*; identifies where we are now; and suggests areas where research should be focused. The significance of applying ageing techniques to *L. opalescens* can be appreciated by drawing on the results of studies from other loliginid populations (summarized in table 1) that have used similar ageing techniques to determine important biological features.

Loligo opalescens is not only a valuable fishery resource but also an important ecological species in the California Current. Its predators include at least 19 species of fish, 13 species of birds, and 8 species of marine mammals (Morejohn et al. 1978). Some vertebrates reviewed in Morejohn et al. (1978) that appear to be major predators of *L. opalescens* include the fish curlfin turbot (*Pleuronichthys decurrens*), several specimens of which have been shown to consume more than 600 individual squid; the seabirds rhinoceros auklet (*Cerorhinca monocerata*) and sooty shearwater (*Puffinus griseus*); and the marine mammals harbor porpoise (*Phocoena phocoena*) and the California sea lion (*Zalophus californianus*). Management of *L. opalescens* stocks therefore extends beyond fisheries interests alone; it must also take into account the role of this species in the ecology of California coastal waters.

LIFE HISTORY OF *LOLIGO OPALESCENS*

Loligo opalescens is a nearshore loliginid squid that inhabits continental shelf waters off the west coast of North America. A key feature of its life cycle is the spawning

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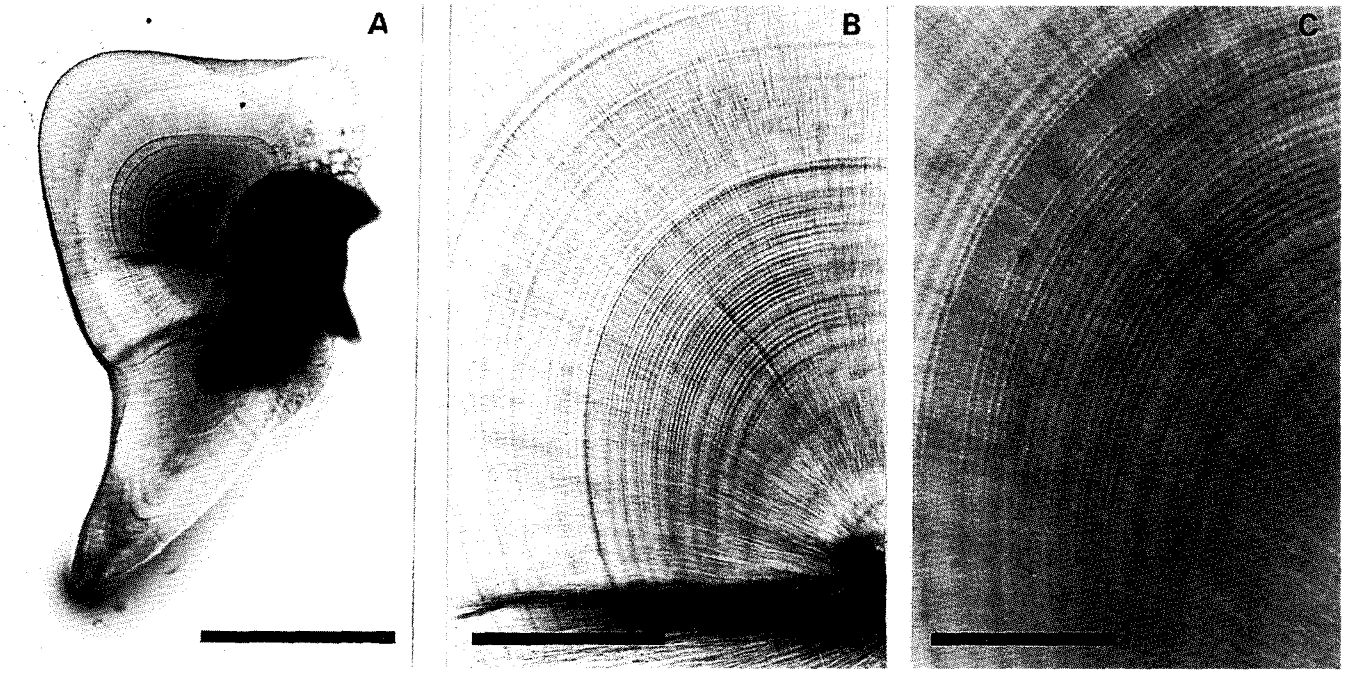

Figure 1. The ground and polished statolith of a female *Loligo opalescens* (128 mm mantle length, age 311 d; see Jackson 1994b) captured off central California in 1990: *A*, whole statolith (scale bar = 500 µm); *B*, close-up of lateral region showing detail of increment structure (scale bar = 100 µm); *C*, close-up of individual increments in the lateral region (scale bar = 50 µm).

aggregation which takes place in relatively shallow waters off California. Before reproducing, squid appear to be more dispersed, with some individuals in deeper water. For spawning, they form huge aggregations and produce benthic egg masses that can be up to 12 m in diameter and over a meter in depth (Hixon 1983).

This species appears to be a true terminal spawner, with death following soon after spawning. Analysis of the reproductive system of males (Grieb and Beeman 1978) and females (Knipe and Beeman 1978) revealed that the maturation process is terminal; there is no sign of renewal of the gametogenic process in males and no stage I preoöcytes in females. There is also a dramatic emaciation of the mantle tissue in association with maturation; its thickness decreases approximately 24% in males and 42% in females (Fields 1965, cited in Hixon 1983).

AGE AND GROWTH

Growth estimates for *L. opalescens* have come from length-frequency analysis, culture data, and limited use of age information. Fields (1965, cited in Hixon 1983) used length-frequency analysis in an early attempt to understand growth. These early results suggested a growth rate of 4 mm/month and a life span of about two years.

Knowledge of squid biology has been greatly enhanced with the discovery of daily statolith increments. There is a growing body of information on growth and life spans of squids based on data obtained from statoliths (Rodhouse and Hatfield 1990; Jackson 1994a). The daily periodicity in production of statolith increments has been validated in a number of species (Jackson 1994a; Jackson et al. 1997). Statolith analysis reveals information on hatch date, individual age, and average growth rates (fig. 1). Analysis of the width of daily rings may also provide information on daily growth. There is now the potential for using the squid gladius to analyze specific daily growth rate (Arkhipkin and Bizikov 1991; Bizikov 1991; Jackson et al. 1993; Bizikov 1995; Perez et al. 1996).

Spratt (1978) highlighted the significance of increments within the statoliths of *L. opalescens* when statolith analysis was in its infancy. Although Spratt identified what he thought were daily increments within the dorsal dome of the statolith, he also suggested that more prominent increments were produced monthly. Enumeration of these daily as well as "monthly" increments also indicated a life span of almost two years.

Culture of *L. opalescens* provided another avenue to understanding growth parameters and life span. Work by Yang et al. (1983, 1986) resulted in a radically different form of growth. Cultured individuals could be modeled by an exponential equation, and maturity was reached in captivity in less than 200 d, with spawning taking place between 196 and 239 d. Culture work yielded considerably different life-span estimates for *L. opalescens* than previous fieldwork, which suggested a life span of about two years (fig. 2).

A second preliminary analysis of statolith growth increments was undertaken by Jackson (1994b), who aged

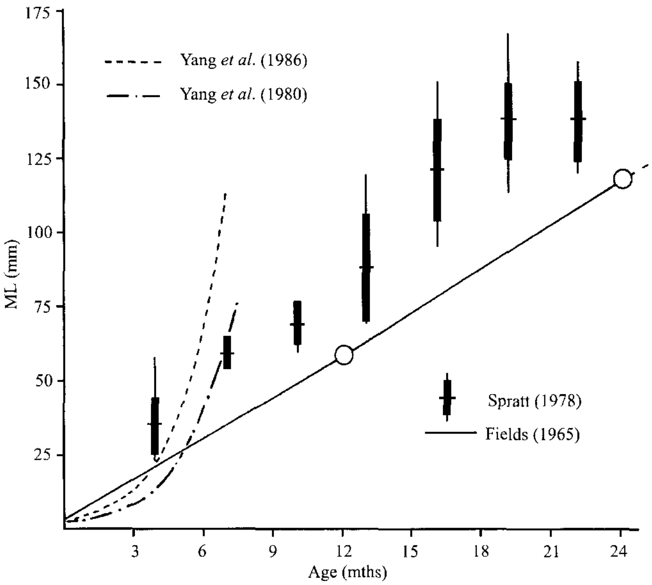

Figure 2. Summary of growth models developed for *Loligo opalescens* (modified from Hixon 1983).

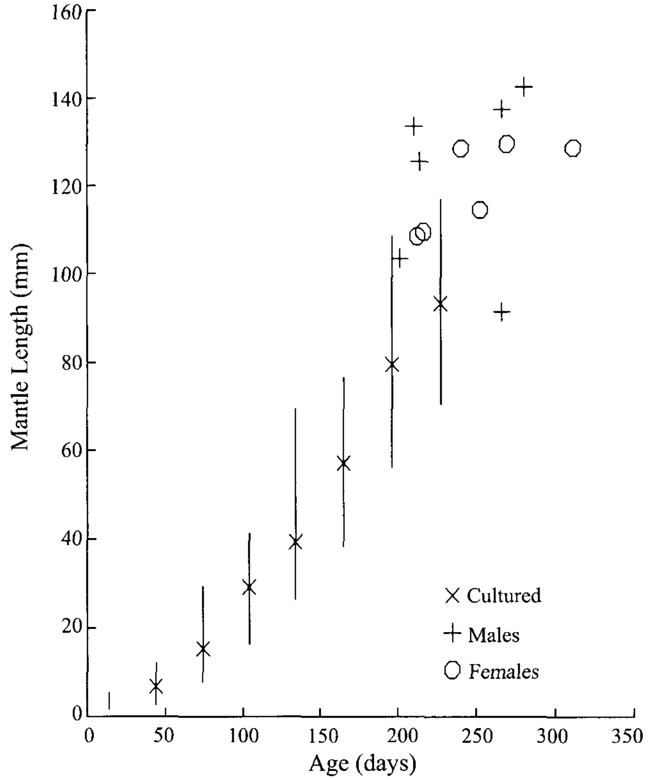

Figure 3. Age estimates for field-captured individuals of *Loligo opalescens* compared to data generated for this species raised in captivity (from Jackson 1994b).

12 individuals of *L. opalescens* captured off Monterey, in central California. This analysis interpreted all increments as daily, in contrast to earlier work by Spratt (1978). The good agreement in the results of Jackson (1994b) and Yang et al. (1986) suggests that *L. opalescens* may complete its life in less than a year off central California (fig. 3).

Such studies underscore the significance and validity of ageing studies for understanding squid growth, and further reveal the inadequacies of applying length-frequency analysis to squid.

INFORMATION FROM OTHER LOLIGINID POPULATIONS

An examination of age and growth parameters from other loliginid populations can provide general features of age and growth of loliginids. Statolith ageing techniques have now been applied to a number of loliginid populations around the world (table 1). The results reveal that loliginid life spans are generally short; only several species live longer than a year, and all species complete their life cycles in fewer than 18 months. *Loligo vulgaris reynaudii* appears to have one of the longest life spans; some large males may live longer than 15 months (Lipinski 1991; Augustyn et al. 1994). Generally, temperate species complete their life cycle in about a year; tropical species can complete their life cycle in <200 d; and very small tropical species such as *Loliolus noctiluca* can reach maturity in 3 months or less and complete their life cycle in 4 months (Jackson and Choat 1992).

Loliginid squids show a marked response to environmental temperature changes because of their short lives (e.g., Forsythe 1993). Age analysis of field-caught individuals (Jackson and Choat 1992) revealed seasonal variation in growth in the tropical loliginid *Photololigo* sp. (referred to as *Loligo chinensis*, but now known to be a new species; see Yeatman and Benzie 1993, 1994), which completed its life span in 115 d in summer but lived longer than 170 d in winter. These differences in growth rates also affected seasonal maturation rates in the species (Jackson 1993).

Ageing work on *Loligo gahi* (Hatfield 1991) and *Loligo pealei* (Brodziak and Macy 1996) also showed that individuals which hatched in different months had different growth rates. Recent work on *Loliguncula brevis* (Jackson et al. 1997) revealed that small, shallow-water loliginids can exhibit marked seasonal differences in growth as a result of pronounced seasonal temperature fluctuations. The age of this species can range from 81 to 172 d, depending on the prevailing temperatures during growth (especially during the early growth period).

Seasonal growth variation is so important that ageing individuals without a knowledge of their past life history would make it virtually impossible to understand the form of growth. For example, figure 4a shows all the age data for *Lolliguncula brevis* from Jackson et al. (1997). Presenting this data without a knowledge of the season of capture can mask the form of growth. The scatter-

TABLE 1
Size and Age Data from Different Loliginid Populations around the World, on the Basis of Statolith Age Analysis

Region	Species	Age (days)	Mantle length (mm)[a]	Environment	Reference
North America	*Loligo opalescens*	280	142	Temperate	Jackson 1994b
	Loligo pealei	296	303–440	Temperate	Macy 1995
	Lolliguncula brevis	172 summer	72	Warm temperate	Jackson et al. 1997
		95 winter	71		
		81 autumn	82		
South America	*Loligo gahi*	439	210–350	Temperate	Hatfield 1991
Europe	*Loligo forbesi*	377 male	431	Temperate	Collins et al. 1995
		359 female	263		
	Loligo vulgaris	~245	~274 (not full size range)	Warm temperate	Natsukari & Komine 1992
North Africa	*Loligo vulgaris*	396 male	498	Tropical	Arkhipkin 1995
		335 female	290		
	Alloteuthis africana	208 male	205	Tropical	Arkhipkin & Nekludova 1993
		187 female	155		
	Alloteuthis subulata	231 male	135	Tropical	Arkhipkin & Nekludova 1993
		172 female	72		
South Africa	*Loligo vulgaris reynaudii*	~540	360	Temperate	Lipinski 1991
Japan	*Photololigo edulis*	350	~404	Warm temperate	Natsukari et al 1988
	Heterololigo bleekeri	385.5 male	320	Warm temperate	Kinoshita 1989
		336.5 female	210		
Thailand	*Loligo chinensis*	172 male	271	Tropical	Chotiyaputta 1997
		151 female	235		
	Loligo duvauceli	98 male	119	Tropical	Chotiyaputta 1997
		95 female	110		
Australia	*Sepioteuthis lessoniana*	188	184	Tropical	Jackson 1990a
	Photololigo sp.[b]	173 winter	167	Tropical	Jackson & Choat 1992
		115 summer	167		
		~102	~92	Tropical	Moltschaniwskyj 1995
	Photololigo sp. 1	157	115	Tropical	Jackson & Yeatman 1996
	Loliolus noctiluca	112	90	Tropical	Jackson & Choat 1992

Age and mantle length values were generally provided in the reference or estimated from size-at-age plots included in it.

[a] The data refer to sizes of oldest individuals, which do not necessarily indicate the maximum obtainable size for each species.

[b] This species was referred to as *Loligo chinensis* in Jackson and Choat 1992. It is now known to be a new, undescribed species of *Photololigo* (see Yeatman and Benzie 1993, 1994).

plot in figure 4a suggests that *L. brevis* might have asymptotic growth, with a slowing after about 100 d, and a life span of about 170 d. However, when the data are plotted with the appropriate seasonal segregation (fig. 4b) it becomes apparent that growth is nonasymptotic; squids that hatched during warmer seasons had faster growth rates and shorter lives.

Results of ageing work on squid suggest that growth is continuous, nonasymptotic, and exponential or linear in form. In many species, growth of the gonad appears to coincide with growth of the soma. We currently do not fully understand all the physiological processes governing how squid grow. They do, however, appear to grow in a fundamentally different way than fish (e.g., O'Dor and Webber 1986; Alford and Jackson 1993). Moltschaniwskyj (1994) has provided a physical mechanism for the observed differences in the form of growth between squid and fish. Fish appear to grow initially by recruitment of new muscle fibers (hyperplasia) and with an increase in muscle fiber diameter (hypertrophy). Their final size may be influenced by the number of muscle fibers present once hyperplasia ceases, and individuals with more muscle fibers have the potential to reach a larger size (Moltschaniwskyj 1994). Squid also show both mechanisms of muscle fiber growth, but with the fundamental difference that hyperplasia does not cease; rather, recruitment of new muscle fibers is a continuous process throughout life. This phenomenon has also recently been documented for *L. opalescens* (Preuss et al. 1997).

FUTURE RESEARCH

Growth and Reproduction

The growth of *L. opalescens* is still poorly understood. Because of its wide latitudinal distribution, this species encounters considerable temperature differences. It is therefore likely to exhibit marked plasticity in growth as a result of varying water temperatures. Growth may also differ depending on the season of hatching or other physical phenomena such as El Niño events.

There appears to be a continuum in squid reproductive strategies, from species that are multiple (or batch) spawners (e.g., *Stenoteuthis oualaniensis*, Harman et al. 1989; *Loligo forbesi*, Boyle et al. 1995) to true terminal spawners that die in association with or soon after spawning (e.g., *L. opalescens*, Grieb and Beeman 1978; Knipe

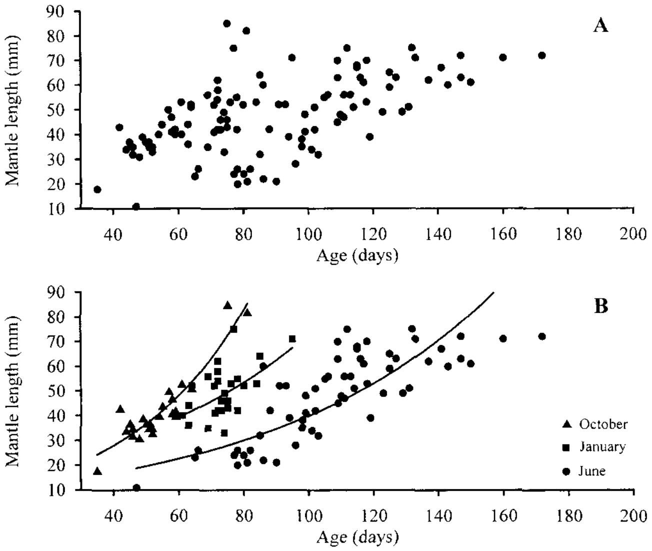

Figure 4. Size-at-age data for *Lolliguncula brevis* from the Gulf of Mexico (Jackson et al. 1997). *A*, The scatterplot resulting from pooling all individuals, with the data suggesting a possible asymptotic growth curve; *B*, the same scatterplot showing the month of collection and the associated exponential growth curves. Note that neither the *x* nor the *y* axis starts at zero.

and Beeman 1978; *Moroteuthis ingens*, Jackson and Mladenov 1994). The physical processes of terminal spawning in *L. opalescens* need to be described in more detail. The deepwater squid *M. ingens* was shown to undergo a dramatic tissue breakdown process in association with maturation and spawning that results in the loss of virtually all mantle musculature, leaving only a collagen matrix. The loss of mantle thickness in *L. opalescens* (Fields 1965, cited in Hixon 1983) may be due to a similar process.

Potential Research Protocols

Although there are some historical data on the biology of *L. opalescens*, there is an urgent need to establish biological parameters for this species. Such life-history data can then be used to develop necessary management models. The following studies would greatly facilitate our understanding of *L. opalescens* biology.

1. Obtain information on age, growth, maturation rates, and life span from analysis of statolith increments. Statoliths are the tools of choice for determining the basic demographic parameters needed for population management. Since *L. opalescens* covers such a large latitudinal range (Alaska to Mexico, Hixon 1983), samples should be taken from a variety of sites covering as large a latitudinal range as possible. This will document the geographic variability in growth rates. Sampling effort should also be conducted year-round, and should span several years from one or more key sites to document differences in growth rates, maturation rates, and life spans of different seasonal cohorts.
2. Validation experiments should be undertaken to document the periodicity of statolith increments. This would involve staining live squid with either tetracycline or calcein (e.g., Jackson 1989, 1990a, b) and maintaining individuals in captivity to verify the one-ring:one-day hypothesis. Alternatively, other techniques such as analysis of marginal increments for individuals captured over a 24 hr period may be possible (Jackson 1994a).
3. Studies into squid condition in association with maturation should be undertaken to describe the dynamics of mantle muscle in association with terminal spawning. If a process of tissue degradation occurs in *L. opalescens* similar to that in *M. ingens*, then females nearing the end of their lives may have very little muscle tissue left.
4. Examine the possibility of using predators as sampling devices. Squid are notoriously difficult to sample, especially the younger stages. But some species such as the curlfin turbot may prove to be excellent sampling devices for juvenile squid. Croxall and Prince (1996) have highlighted the usefulness of seabirds for sampling squids. Some species such as the rhinoceros auklet may also be an effective sampling tool. Species that prey on younger stages may offer a valuable means for sampling the relative abundance of juvenile squid in order to predict future recruitment into the adult population. Alternatively, periodic collections of scats or vomits of the California sea lion may offer an effective way to monitor the population structure of squid in a specific region. Such analysis is especially effective because specific squid species can be identified by undigested beaks (e.g., Klages 1996), and beak size can be related to squid size (Clarke 1986). Examining such remains should make it possible to reconstruct size frequencies of squid.
5. Radio acoustic positioning and telemetry (RAPT) offers one means of obtaining information on movements of individuals within a spawning region over small scales of hundreds of meters to several kilometers (e.g., Sauer et al. 1997). Individual squid can be tracked over longer distances with telemetry (e.g., Nakamura 1991) to obtain information on longer migrations or movements into deeper water offshore. Traditional tagging methods (Nagasawa et al. 1993; Takami and Suzuchi 1993) may also be useful for obtaining information on long-distance migrations along the California coast.
6. Light trapping (Moltschaniwskyj and Doherty 1995) may be a technique for monitoring the abundance and distribution of juvenile squid within the water column.

CONCLUSION

California management agencies are in a unique position to collect basic biological data on *L. opalescens* before fishing pressure increases. As the fishery progresses, ongoing monitoring and assessment will provide basic biological information that can serve as a basis for developing management strategies. We still do not fully understand the importance of *L. opalescens* off the North American coastline. Continued research with a variety of techniques will help to answer important biological questions that are now being asked. Such focused research will also serve ecological and conservation needs because the resulting data will help to clarify the role that *L. opalescens* plays in the California coastal food web.

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INFORMATION NEEDS FOR EFFECTIVE MANAGEMENT OF THE CALIFORNIA MARKET SQUID FISHERY: THE ROLE OF SOCIAL SCIENCE RESEARCH

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ABSTRACT

Recent events in the fishery for California market squid (*Loligo opalescens*), especially the rapid increase in landings and participants, have raised concerns about its socioeconomic as well as its biological sustainability. As management options for the fishery are considered, it is essential to take into account the fishery's social and economic organization, including its structure; its temporal and spatial organization; the relationships among fishers, processors, and others involved in the fishery; and the informal and formal rules and strategies by which its participants operate. These factors will influence how different management options would affect—and be affected by—the fishery. We have begun to explore these aspects of the fishery in a Sea Grant–sponsored study entitled "Socio-Economic Organization of the California Market Squid Fishery: Assessment for Optimal Resource Management." This paper begins with an overview of fisheries social science and its application to fishery management elsewhere. We then provide an overview of the social, economic, and regulatory history of the fishery, followed by an introduction to our study and questions it will address toward contributing to consideration and implementation of management for the fishery.

INTRODUCTION

Since the passage of the Magnuson Act in 1976, there has been growing recognition of the importance of social and economic information to effective fishery management (Orbach 1978; Clay and McGoodwin 1994; Buck 1995). Fisheries social science entails the study of the social, cultural, and economic aspects of fisheries, to afford basic understanding of the human dimensions of fisheries and to contribute to resource management (AFS 1993). The latter goal is based on the idea that fishery management is as much people management as it is biological resource management (Fiske 1990).

Recent events in the fishery for California market squid (*Loligo opalescens*), especially the rapid increase in landings, have raised concerns about its socioeconomic and its biological sustainability, and have led to discussions of management options for this, the last major open access fishery on the West Coast. Questions have been raised about the fishery's social and economic organization, and how different management options would affect—and be affected by—the fishery. We are exploring these questions through a Sea Grant-sponsored study entitled "Socio-Economic Organization of the California Market Squid Fishery: Assessment for Optimal Resource Management."

This paper prefaces that study by providing an introduction to fisheries social science and its application to fishery management elsewhere, followed by an overview of the squid fishery, of social and economic questions relevant to its potential management, and of our plans to address those questions through our study.

FISHERIES SOCIAL SCIENCE

Overview

Several aspects of commercial fisheries interest social scientists. Chief among these are fisheries' direct dependence upon the natural environment, uncertainties associated with fishing, the common-pool nature of fishery resources, and fishers' and processors' individual and collective adaptations to contingencies created by these characteristics.

Fisheries are strongly influenced by environmental, technological, economic, and regulatory uncertainty and risk (see Acheson 1981 for an extensive review). Most marine resources are hidden from direct view; their life histories and interactions with other species are complex; and their availability in space and time is highly variable. Additional environmental uncertainty stems from changeable weather, climate, and oceanographic conditions that influence when and where fish are, and fishers' ability to find, catch, and land them safely. Technological uncertainty stems from fishers' use of heavy, potentially dangerous equipment, and fish-finding and navigation technologies (e.g., radar, sonar, loran). Even with the best gear, the sturdiest and best-equipped vessel, and the best technology, there is no guarantee that fishers will find, catch, and deliver fish to market (and do so safely). Economic uncertainty arises from unpredictable variations in supply, and the changing demand of local and global markets. Finally, changing regulatory and management structures, from the Law of the Sea and the Magnuson Fisheries Conservation and Management Act to state regulations, are an additional source of uncertainty (Maiolo and Orbach 1982; Pollnac and

Littlefield 1983). Although the implementation of standardized management institutions (e.g., the federal fishery management council system) has eliminated some aspects of regulatory uncertainty, others persist because rules change in response to changing environmental, political, economic, and social conditions. Moreover, rules have differential, and often unanticipated, social and economic implications for both harvesters and processors (Pollnac and Littlefield 1983; Hilborn 1985). For example, seasonal closures can result in idled vessels and processing facilities, temporary unemployment, accumulation of or default on debt, and conflict on the fishing grounds when fishing resumes. Similarly, regulatory changes in one fishery (e.g., gear restrictions, closed seasons, limited entry) can displace fishers, prompting them to enter or increase their effort in other fisheries.

Fisheries also interest social scientists because of their common pool resource (CPR) nature.[1] Fish stocks that inhabit a large territory and thus are not easily designated as private property are best used by a group, or "in common." This poses both opportunities and challenges to resource users and managers. Without regulation, almost anyone can catch fish to eat or sell. Yet if everyone does this without restraint, the resource becomes vulnerable to overuse. The resulting tragedy of the commons (Hardin 1968) is marked by resource scarcity, social conflict, and economic hardship. These outcomes are evident, for example, in crowding on the fishing grounds, pressure to fish longer or in more dangerous conditions, and insufficient supplies of fish to keep processing plants running and staff employed.

People in fisheries have found diverse and innovative ways to deal with the uncertainties and challenges associated with CPR use, and to organize life effectively around fishing. Individual and collective adaptations are found in work organization at sea, relationships at the docks, and life on land (Acheson 1981). For example, the share system commonly used in fisheries invests the crew in the process and outcome of fishing. Other adaptations include coordination with other boats while at sea (e.g., through code groups), and other forms of information and skill management (e.g., Orbach 1977; Acheson 1981; Eales and Wilen 1986). Fishers and processors also adapt by acquiring new skills, adopting innovations, managing capital, and maintaining the flexibility to switch among fisheries as conditions and opportunities change interannually, seasonally, and even daily at sea, on the market, and in fishery management. In some cases, resource users cooperate to establish and uphold rules, norms, and strategies to coordinate the use of shared resources. These "institutions for CPR management" have attracted the attention of social scientists and resource managers as alternatives or complements to traditional, state-centered (i.e., top-down) fishery management (NRC 1986; McCay and Acheson 1987; Berkes 1989; Ostrom 1990). They may be locally generated and operated, independent of state management systems, or they may be coordinated (officially or unofficially) with state resource management, as forms of cooperative (or co-) management (Pinkerton 1989).

Applications to Fishery Management

Traditional fishery management tends to focus almost exclusively on the biological resource, to the exclusion of the "human dimension" (Orbach 1980). The rationale for conducting social science research on fisheries is that management decisions informed by an understanding of people's practices, values, and beliefs are more acceptable and successful, and less disruptive (Hanna and Smith 1994).

Social scientific research and the information it produces can play a critical role at various stages of fishery management. For example, social and economic impact assessment can help prepare those who will be affected by a change in the rules (ICGP 1994), and can help managers anticipate resistance or other problems associated with implementing new management policies (Orbach 1980; Fiske 1990; Orbach et al. 1990). Social science research also is useful in situations where the biological condition of the resource is unknown or not clearly an issue, but where social and economic concerns are associated with its use (e.g., where continued growth in that use could threaten both the industry and the resource). Such research can also give managers information to facilitate their work with the industry. As one California Department of Fish and Game (CDFG) biologist noted, "It's not required that we have such information to manage the fisheries, but it sure makes it a lot easier if you know who and what you're working with" (anon. pers. comm.). Social and economic information about a fishery can help those who design and implement policy by giving them a fuller understanding of how management measures will affect *and be affected by* the individuals and groups involved.

Social science disciplines, from anthropology to economics, have increasingly been applied to fisheries. However, the particular interests and approaches across the social sciences differ. In short, anthropology and sociology focus on culture and social organization, geography on the spatial and temporal organization of social and economic life, political science on politics and policy processes, and economics on the costs, benefits, motivations, and behaviors associated with fishing. While

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[1] There is an important distinction between common *pool* and common *property* resources. Whereas the former refers directly to the biophysical nature of the resource and its use, the latter pertains to the resource as the subject of the legal institution of property (Bromley 1991).

political scientists and economists work principally with public data sets and then argue from theory to explain their results, anthropologists, sociologists, and geographers often conduct fieldwork—involving interviews, observation, and archival research—in an effort to understand how, why, and what people are doing. Systematic collection and analysis of this information then enables the detailed descriptive, explanatory, and perhaps predictive characterization of fisheries as a human endeavor.[2]

Fisheries social scientists focus first on elements common to most or all fisheries—direct dependence on a natural resource system, uncertainty, the use of a shared resource, and adaptation. These elements taken together in context have led to the identification of a "subculture of fishing," with reference to the people involved, the work, the communities where fishing is based, and the organization of life around fishing (Poggie and Gersuny 1974). Researchers have examined the occupational, social, and cultural identities of fishers and fishing communities and how these influence perceptions, attitudes, and behavior (Poggie and Gersuny 1974; Orbach and Beckwith 1980; Miller and Van Maanen 1982). The particular values associated with work, family life, and community are found to be common among fishing communities and yet distinct from the larger culture. Even as fisheries have much in common, however, each is unique, owing to the particular life histories, habitats, and ecologies of the species involved, and to the distinct historical, social, and cultural context of the fishery. Fisheries differ also in the nature and extent of their markets, and the ways they have been managed and regulated, both informally (through local institutions) and formally (by state and federal governments).

A growing number of research programs provide social scientific information useful to fishery management (AFS 1993). Notable among these are James Acheson and others' work on the Maine lobster fishery, and Susan Hanna, Courtland Smith, and others' work on Oregon coastal fisheries. Acheson's research on the practices and social organization within the Maine lobster fishery led to the identification of "harbor gangs," port-based groups of lobster fishers along the coast who have a system of shared norms and rules about who fishes, where and how (Acheson 1988). Membership in a harbor gang is contingent upon one's ethnic identity and community ties. Group members set their lobster traps in areas adjacent to their home port, and defend those areas from intrusion by "outsiders." Within this territorial system, Acheson distinguishes between "nucleated" and "perimeter-defended" areas. In nucleated areas, the sense of territoriality is strong close to the harbor mouth (and the core of individual territories), but diminishes with distance from it. Perimeter-defended areas are characterized by a strong sense of territoriality, with sharply drawn boundaries both within and among groups (Acheson 1987).

Ecological and economic analysis of these arrangements showed that perimeter-defended lobster territories had higher catch per unit of effort, larger lobsters, and higher densities of lobsters compared to nucleated areas (Acheson 1975). Acheson argues that "perimeter-defended territories . . . serve both to restrict entry into the fishery in these areas and enable the enactment of local conservation measures" (Acheson 1987:48).[3] Contrary to many observers' expectations, the lobster fishery has remained biologically and economically robust, governed by the local institutional arrangements first described by Acheson in 1975 (Wilson, pers. comm.). In 1995, the Maine Department of Marine Resources recognized those arrangements with a plan to transfer resource management responsibility for the lobster fishery to the local level through the establishment of experimental "lobster zone management councils" (Lobster Institute 1997).

Hanna and Smith's (1994; Smith and Hanna 1993) recent survey of Oregon trawl captains' attitudes about work, resource use, and fishery management challenges key assumptions that underlie much of fishery management. It is often assumed that fishers from a single-gear fleet are homogeneous in their views and practices, and that they have myopic, short-term views of the resource and do not recognize the collective effects of fishing on the resource. Hanna and Smith (1994) found, however, that trawl captains were heterogeneous. Differences in individuals' experience, family associations, education, age, and place of residence contribute to differences in their views on work, environmental and economic risk, and the environment. Individuals differed also in their fishing practices. Whereas some captains make shorter trips in the interest of landing quality, others take longer trips to land quantity. Such differences are important, for example, when considering trip limits and the differential effects they would have on the fleet (Hanna and Smith 1994). Hanna and Smith (1994) also argue that because assumptions of homogeneity among trawl captains and their operations do not hold, the use of landings data (assuming homogeneous links between a fishing

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[2] Although informative, this work is also difficult because of the ethical issues associated with conducting research on human beings. Interviews and observation are intrusive; people feel uncomfortable being studied. Yet the local knowledge they have is important, and can (and should) be brought together with information from other sources and situations to help inform efforts to solve problems both locally and elsewhere.

[3] Fishers have devised and implemented rules such as trap limits, closed seasons, and prohibitions against keeping berried (egg-bearing, i.e., reproductive) females.

trip and fishing effort) may be inappropriate and lead to dangerous results for both the resource and the fishery (see also Hilborn 1985; Smith and Hanna 1990). Hanna and Smith argue that acknowledging these differences when designing management strategies can lead to more appropriate and successful management; failure to do so often leads to unpredictable (and often negative) results.

These and other research programs' attention to the social and economic organization, institutional arrangements, and diversity within fisheries, as well as to their implications for resource management, have informed our approach to the fishery for California market squid. In the remaining sections of this paper, we provide a brief history of the squid fishery, describe recent changes in its social and economic organization and regulatory status, and conclude with an overview of the study we are undertaking.[4]

THE FISHERY FOR CALIFORNIA MARKET SQUID

History

The fishery for California market squid was started in the 1860s at Monterey by the Chinese, who used torches to attract squid and caught them with small purse seines (Dewees and Price 1983; Lydon 1985). In the early 1900s, Monterey's Italian fishers introduced lampara nets into the fishery. The fishery was centered in the Monterey Bay area until the 1960s, when the southern California fishery developed on spawning aggregations near the Channel Islands (Dewees and Price 1983). Since then, landings in southern California have been on the rise, while those at Monterey have remained about the same (LMR 1995).

Through the early 1980s, annual squid landings remained below about 25,000 metric tons (t), largely because of limited demand (LMR 1995). Following record low catches associated with the 1982–83 El Niño, however, landings increased greatly. By 1996, squid ranked first among California fisheries in both volume and value, with landings of more than 86,000 t, worth over $32 million (Vojkovich 1998).

This phenomenal growth in the squid fishery is the result of developments in markets, processing, and fishing strategies over the past 10 to 15 years.[5] Domestic markets have grown as consumers have come to value the nutritional benefits of seafood in general (NMFS 1996), and have developed a taste for squid products marketed under the more appealing name of "calamari." Declines in other squid fisheries (e.g., Falkland Islands) and the opening of new markets have prompted growth in international demand from both traditional consumers such as Greece and Italy and new ones, most notably China (Redmayne 1996). In addition, fluctuating supply and demand in other domestic fisheries have contributed to growing demand for squid.

This growing demand has spurred changes in fishing practices that have resulted in increased catch and in fundamental alterations in the structure and spatial distribution of the fishery. Purse seiners using round haul gear are now the dominant type of operation, although a number of lampara boats still operate in southern California. Some squid fishers use spotter planes, as well as depth sounders and sonar, to locate fishable aggregations of squid. The use of light boats—small vessels that scout for fishable aggregations, and use halogen lamps to attract and hold the squid for a seiner to catch—has become widespread (although they are prohibited in District 10).[6] These innovations have greatly increased the efficiency and scope of squid fishing operations. The central California fishery has spread from the inner waters of Monterey Bay to outer bay waters, while the southern California fishery has expanded its coverage of Channel Islands fishing sites.

The fleet's capacity has increased as well. The CDFG estimates the fleet's maximum capacity in 1995 at 4,520 net tons, compared to 3,640 net tons in 1982 (M. Vojkovich, pers. comm.).[7] Both CDFG and fishers' records show an increase in the number of out-of-state vessels participating in the southern California fishery. Of the 137 vessels that landed squid in 1982, 6 were from out of state and landed 6% of the catch; by 1995, 22 of 117 vessels in the fishery were from out of state, and accounted for 27% of landings (M. Vojkovich, pers. comm.). A list compiled recently by fishers shows that the number of vessels fishing squid on the southern California grounds doubled between 1994 and

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[4] The following is based on preliminary research on the fishery (literature review, informational interviews, and observation) that we conducted in preparation for submitting the proposal to California Sea Grant and in anticipation of receiving funding.

[5] Research on squid biology, processing, and marketing in the 1960s and 1970s stimulated many of these developments (e.g., Fields 1965; Recksiek and Frey 1978; Kato 1970; Brooks 1977; Brown and Singh 1981; Berntsen 1988).

[6] Light boats, as discussed here, are registered vessels, distinct from purse seiners and seine skiffs, that are equipped with lights and are used primarily to scout for, attract, and hold aggregations of squid for capture by the purse seine vessel. Light boats are owned or contracted by a seiner operation, or operate as free-lancers, and receive a percentage of the catch for their services.

District 10 includes the ocean waters and tidelands between the southern boundary of Mendocino County and a line extending west from Pigeon Point Lighthouse in San Mateo County, including Tomales Bay, to a line drawn from the mouth of an unnamed creek about 1,500 feet north of Tomasini Point to the mouth of an unnamed creek at Shell Beach; excluding Bodega Lagoon, that portion of Bolinas Bay inside of Bolinas Bar, that portion of San Francisco Bay east of a line drawn from Point Bonita to Point Lobos, and all rivers, streams and lagoons (CDFG 1998).

[7] Although CDFG data show little change in the number of boats, there have been changes in vessel size, gear, and practices such as the use of light boats, all of which influence the fleet's fishing power and capacity. Spratt and Ferry (1993) have documented such changes in the Monterey fleet.

1996, from 18 to 36.[8] These increases in fleet capacity and in numbers of out-of-state vessels participating in the fishery are attributed to strong demand and good prices for squid, and to limited entry and/or declines in other fisheries in California, Oregon, Washington, and Alaska.

These changes reflect a blurring of territorial distinctions between the Monterey and southern California fleets and fisheries. Many vessels from the Monterey fleet now also fish in southern California, and the central California processors they work with have invested in receiving, transporting, and (in some cases) processing capabilities in southern California to receive catch at those locations. A smaller number of vessels and processors from southern California also participate in the central California fishery.

The fishery's growth notwithstanding, it remains constrained by environmental, technological, and economic uncertainties. It is particularly vulnerable to changing oceanographic conditions (especially temperature), which play an important role in the spawning, distribution, and abundance of squid (Hixon 1983). Declines in the availability of squid appear to be correlated with El Niño events, including the 1997–98 event (Leos 1998). As of early 1998, the southern California fishery had landed reduced numbers of squid, and some fishers were concerned that the same would happen at Monterey in the spring. Technological uncertainty is associated with squid fishers' reliance on fish-finding devices, light boats, and spotter planes to locate fishable aggregations.[9] In addition, once caught, squid is highly perishable, so vessels must have reliable refrigeration systems or be able to deliver the catch within hours of capture, and processors must have dependable squid pumping, cleaning, packing, storage, and transport technologies. Economic uncertainties affect both supply and demand in the fishery. For example, according to one squid processor, the growth in international demand for squid has been dampened by recent downturns in Asian markets.[10]

It is even more important, perhaps, that heterogeneity within the fishery persists, and includes fundamental social, cultural, and economic differences within and among ports. The San Pedro fleet consists primarily of traditional Slav, Italian, and Portuguese skippers; older, wooden-hull seiners and gear; and large (about 8-person) crews.[11] The Ventura/Channel Islands/Port Hueneme fleet is more ethnically diverse, and primarily uses fiberglass or steel-hull vessels, newer gear, and smaller crews. The Monterey fleet is dominated by Italian skippers and increasingly nontraditional crews, which now include many Vietnamese (Spratt and Ferry 1993). The Washington-based fleet, which operates out of several California ports (except San Pedro), consists primarily of Scandinavians and Slavs who run well-equipped steel-hull vessels. In addition, while the San Pedro fleet depends primarily on squid and other coastal pelagic species, many fishers from other ports participate in other nonlocal fisheries (e.g., Alaska salmon, San Francisco Bay herring). Processors also vary in their social and cultural backgrounds, the nature and extent of vertical and horizontal integration, and the relative importance of squid and other fisheries to their operations. These differences underscore the need for detailed understanding of the squid fishery's participants, their social and economic relationships, values, perceptions, and attitudes, and how all of these influence their behavior.

Management

Historically, squid fishing has been regulated by the state with legislative measures that restrict the use of lights to attract squid, limit days or times when fishing is allowed, and for several years prohibited the use of purse seines in Monterey Bay (see Dewees and Price 1983). Current regulation includes a prohibition on the use of light boats in District 10 (Half Moon Bay) and a closure of the fishery from noon Friday until noon Sunday north of Point Conception (California Fish and Game Code Sec. 8399.1 and 8420.5). Many of these regulations have been prompted by harvesters or processors.

The squid fishery has not been regulated under a federal fishery management plan (FMP), but it was taken into consideration in the development of the 1994 Coastal Pelagic Species (CPS, i.e., northern anchovy, Pacific sardine, and Pacific and jack mackerel) FMP. Specifically, the FMP would have allowed squid landings to count toward vessel landings requirements for qualification to participate in the CPS fishery. The rationale for doing this was linked to the fishery's close ecological, economic, and social ties to the CPS fisheries (CPS FMP Development Team 1993a, b; Thomson et al. 1994). Although the CPS FMP was canceled in early 1996, it has been revived as of early 1998.

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[8] Industry members expect many new entrants in 1998 following the passage of SB 364.

[9] According to some squid fishers, seining for squid can be especially dangerous for those accustomed to seining for finfish. Squid respond differently in the net and can shift a vessel's balance quickly, thereby increasing the risk of capsizing.

[10] The nature, extent, and seriousness of recent downturns in Asian markets for California market squid will be explored as part of our Sea Grant–sponsored study of the fishery. See Moo (1998) and Ess (1998) for discussions of international markets for squid and other marine species caught by U.S. fishers.

[11] Jacobson and Thomson (1993) note the changing ethnic composition of crews in their analysis of ethnicity, opportunity cost, and decisions to fish for northern anchovy. They highlight fundamental social and cultural differences between "traditional" European-American and increasingly ethnically mixed crews, and the implications of these differences and changes for the organization and conduct of the fishery.

As the fishery continued to grow, members of the industry called for scientific, regulatory, and managerial attention to the fishery, citing concerns about its biological and economic sustainability. Opponents argued that there was no evidence of a resource problem, and therefore there was no need for regulating the fishery. The CDFG agreed that a resource problem was not evident, but noted that it had insufficient information to make a clear determination. (These positions and arguments are more complex, but are beyond the scope of this paper.) In 1997, the California Legislature passed SB 364 (Sher), instituting a $2,500 permit requirement for fishing vessels and light boats to participate in the squid fishery, with the funds to be used to support a three-year program of research on the resource and the fishery (CFG Code Sec. 8420-8429).

Social and Economic Information Needs

Fishery management in the form of regulations governing human use of fishery resources is often directed toward fisheries in biological crisis or subject to multiple-use conflict. With a lack of clear evidence of biological crisis or multiple-use conflict in the squid fishery, why think about regulating squid now? From a social science perspective, the interest emerges from local knowledge of the observed rapid changes in the fishery, placed in comparative perspective with recollections of other cases where such rapid change led to resource decline or economic hardship (e.g., the sardine fishery; PCFFA 1996). It is not clear that squid can reasonably be compared to other fisheries. What is more important is the articulation of concerns about the social and economic, as well as biological, sustainability of the fishery. The suggestion that squid receive regulatory consideration now—before apparent biological or socioeconomic crisis—is unusual in fisheries, and may provide a rare opportunity to develop management that is more appropriate and workable than it would be if action were deferred until a time of crisis.

In addition to the biological and ecological questions about squid, industry participants and resource managers have articulated many questions about the fishery's social and economic organization. For example: What are the vessel, crew, and work configurations in the squid fishery? What are the social, cultural, and economic relationships between harvesters and processors? How and why have these characteristics, configurations, relationships, and institutions changed over time? For which or what types of vessel configurations, processing operations, or individuals is the squid fishery the (or a) primary fishery in both economic and social terms? What other fisheries do fishers and processors participate in? How is participation in these fisheries coordinated in time and space? What strategies have fishers and processors used to adapt to changing conditions in the fishery? Where are vessels, fishers, and processors based? What is the nature and extent of their geographical mobility in terms of the squid fishery and in terms of other fisheries? How have these spatial factors and relationships changed over time?

We will address these questions in our recently initiated study of the California market squid fishery. The study's objectives are (1) to characterize the changing practices and institutions in the California market squid fishery; (2) to determine the relationship between fishers' and processors' dependence on the fishery and their fishing and processing strategies; and (3) to ascertain the spatial patterns, linkages, and developing relationships between the central and southern California fisheries.

In the two-year project, we will examine the changing (social, cultural, and economic) relations of production, adaptation, and flexibility within the industry, as well as resource dependence. We will collect and analyze data through a combination of archival (background documentary) research; observation of fishing, processing, and other industry activities; and interviews with industry participants and others knowledgeable about the fishery. Using this information, we will compare the present fishery with that of the past; the social and economic institutions which organize the fishery within and among fishing areas and landing ports; and this fishery with other fisheries. The proposed research will give resource managers and industry participants systematic documentation of the fishery as a human enterprise. This information can be integrated with existing and new information on the nature and condition of the resource to contribute to the design and implementation of effective resource management.

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Part III

SCIENTIFIC CONTRIBUTIONS

BIOMASSES OF LARGE-CELLED PHYTOPLANKTON AND THEIR RELATION TO THE NITRICLINE AND GRAZING IN THE CALIFORNIA CURRENT SYSTEM OFF SOUTHERN CALIFORNIA, 1994–1996

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ABSTRACT

Based on twelve quarterly cruises over three years, the relative importance and absolute biomass of phytoplankton retained on an 8 µm-pore membrane filter increased as the depth of the nitricline decreased, even though biomass of macrozooplankton (potential grazers) also increased as the nitricline shoaled. The relative importance of ≥8 µm cells was inversely related to a proxy for their biomass-specific mortality (biomass of macrozooplankton/biomass of ≥8 µm cells), as was their "residual" biomass not predicted from the nitricline depth.

INTRODUCTION

As in many other sampling programs, the biomass of phytoplankton in the region surveyed quarterly by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) is assessed by determining the amount of chlorophyll retained on a GF/F glass fiber filter with nominal retention approximately 1 µm (Venrick and Hayward 1984). This measure is well correlated with other properties of sestonic biomass (Eppley et al. 1977; Napp et al. 1988) and (when integrated through the water column) with primary production (e.g., Eppley et al. 1985; Mullin 1991; Mantyla et al. 1995).

However, biomass of large-celled phytoplankton is more variable in space and time than is that of total phytoplankton, and is relatively more important in eutrophic situations (e.g., Hopkins 1971; Furuya and Marumo 1983; Mitchell-Innes and Pitcher 1992). Further, there is evidence that some planktonic copepods are selective grazers, preferring large cells, and that their reproduction and physiology are better correlated with the biomass of large cells than with that of total chlorophyll (Runge 1985; Bellantoni and Peterson 1987; Durbin and Durbin 1989).

The purpose of this study was to determine the mesoscale spatial and temporal distribution of biomass of large-celled phytoplankton, relative to that of total phytoplankton, and to determine how the size distribution was related to that of the nutrient nitrate, and to grazing by macrozooplankton.

METHODS

At approximately half of the locations sampled on twelve quarterly cruises by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) from January 1994 through November 1996 (see, e.g., Hayward et al. 1995) samples were taken to estimate the biomass of phytoplankton ≥8 µm, defined as chlorophyll retained on a membrane filter of this nominal pore diameter (filter type). On these cruises, samples were routinely taken from several depths with closing water bottles on a rosette with a CTD, and the seston from each bottle retained on a GF/F glass fiber was extracted for chlorophyll, determined fluorometrically (Venrick and Hayward 1984). From each of the shallowest ten of these water bottles (representing samples from the surface to approximately 100 m or shallower), an additional 140 ml sample was withdrawn; these were combined and filtered through the 8 µm membrane filter, which was then extracted and analyzed as were the ten GF/F filters representing the same sampled depths.

Biomasses of chlorophyll per unit volume were then integrated to 100 m for both the total phytoplankton (GF/F filters, ten samples integrated algebraically) and the ≥8 µm phytoplankton (membrane filter, one physically integrated sample) to give biomass in mg chlorophyll · m^{-2}. The biomass of cells <8 µm was calculated as the difference between total and ≥8 µm chlorophyll, although this procedure means that <8 µm chlorophyll is not an independent variable for statistical analysis. In a few cases, the measured biomass of ≥8 µm cells as chlorophyll exceeded that of total chlorophyll, presumably due to subsampling or analytical variability. In these cases, the biomass of large cells was taken to be 100% that of the total. The phytoplanktonic biomass referred to as large cells would, of course, include the biomass of cells firmly attached in colonies or aggregates ≥8 µm in effective size.

The concentrations of NO_3^- were determined in water samples drawn from the same bottles as the samples analyzed for biomass of chlorophyll. The vertical distribution of NO_3^- typically includes a near-surface region of concentrations «1 µM; the nutricline (or, in this case, nitricline), where concentrations increase rapidly with depth; and deep-water concentrations >1 µM. I chose

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[Manuscript received October 31, 1997.]

the depth where $[NO_3^-] = 1.0$ μM as the core of the nitricline (e.g., Eppley et al. 1979), and determined this for each station by linear interpolation between the deepest depth where measured $[NO_3^-] < 1.0$ μM and the shallowest depth where measured $[NO_3^-] \geq 1.0$ μM.

At each station (weather permitting), a tow was made between the surface and 200 m or the bottom (whichever was shallower) with a 505 μm-mesh, bridleless net equipped with a flowmeter. Each sample was preserved in formalin-seawater, and its displacement volume was measured. I multiplied data from samples taken nocturnally by 0.75 to correct for the interaction of the time of day a station was sampled and diel vertical migration (Smith 1974; Mullin 1986), thus creating a data set of "diurnal equivalent" macrozooplanktonic biomasses.

The relation between the catch of 505 μm mesh and smaller zooplankton (passing through 505 μm mesh, retained by 202 μm mesh) in this region was investigated by Ohman and Wilkinson (1989). The 202–505 μm fraction was, on average, half the ≥505 μm fraction, though there was diel and onshore-offshore variability in this relation, the 202–505 μm fraction being relatively more important by day and near shore. However, there was no relation between the size partitioning of the zooplankton and the biomass of chlorophyll. I will therefore use the biomass of ≥505 μm macrozooplankton as a proxy for grazing pressure on ≥8 μm cells, in the sense that variability in this proxy reflects variability in grazing, even if the magnitude of grazing by all zooplankton is underestimated.

Relations between properties are shown below as regressions of various algebraic formulations; these should be interpreted only as indicating trends, not as representing the function forms of causal mechanisms between the properties.

RESULTS

The geographic distributions of total chlorophyll during four seasons of each year, as biomass at 10 m, are shown in Hayward et al. (1995) for January 1994–April 1995; Hayward et al. (1996) for April 1995–April 1996; and Schwing et al. (1997) for August and October 1996. These references also show the associated hydrographic properties and describe the context of each cruise relative to long-term conditions for each season.

The relative importance of ≥8 μm phytoplankton tended to be greatest at nearshore locations north of the Palos Verdes Peninsula (fig. 1) and least offshore. The distribution during January 1995 (cruise 9501; fig. 1) represented the greatest departure from this generalization, when the only two stations at which ≥8 μm chlorophyll exceeded 50% of the total were noncontiguous ones far offshore and southerly. Each of these stations differs so much from its immediate neighbors that the results are suspect. Even so, the absence of large-cell-dominated stations near shore in January 1995 is notable, since a major red tide dominated by the large dinoflagellate *Gonyaulax polyedra* had begun to develop near shore (Hayward et al. 1995). This red tide, notable for its spatial extent and wintertime appearance, probably influenced the results during cruise 9504 as well, though grazing by *Noctiluca miliaris* and dispersion by storms had intervened, and abundant diatoms also contributed to unusually large chlorophyll biomasses then (Hayward et al. 1995).

An hypothesis is that large phytoplankton cells tend to form mesoscale blooms in time or space, and that these are superimposed on a "background" of relatively invariant biomasses of small cells (Hopkins 1971). That is, large cells would be disproportionately abundant in regions or times of elevated total biomass. Figure 2 shows the relation of ≥8 μm chlorophyll to total chlorophyll for all 12 cruises over the 3 years (approximately 430 data points); based on the linear regression, ≥8 μm chlorophyll typically ranges from approximately 3% of total chlorophyll in the most oligotrophic areas (total chlorophyll ≈ 25 $mg \cdot m^{-2}$) to 67% in the most eutrophic ones (total chlorophyll ≈ 500 $mg \cdot m^{-2}$). Chavez et al. (1991, their fig. 13) found similar results in a study of mesoscale circulation and phytoplankton off northern California, as did Mitchell-Innes and Pitcher (1992) in a study of temporal change off western South Africa.

As could be anticipated from the geographical distributions shown in figure 1, in each year the fraction of the total chlorophyll due to ≥8 μm cells was greater where and when the nitricline was closer to the surface (fig. 3). When and where the nitricline was deeper than 75 m, large cells were <25% of the biomass (except for the two instances far offshore during January 1995; fig. 1). When the nitricline was shallow, large cells often dominated the biomass, although not always.

These data also imply that the biomass of large cells is more responsive to variations in the position of a shallow nitricline than is the biomass of small cells. As shown in figure 4, the decrease in ≥8 μm cell biomass with respect to increasing nitricline depth, when this was ≤50 meters, was much more marked than was the decrease of <8 μm cell biomass (shown by the steeper curve and larger negative exponent for the relation concerning ≥8 μm biomass).

Finally, if nutrients whose distributions are unrelated to the nitricline (e.g., NH_4^+), and which affect large cells differentially are more important in some seasons than in others, the relation between the fraction of total phytoplanktonic biomass which is ≥8 μm and the depth of the nitricline might differ between seasons. Averaged over the three years, the relative importance of large phytoplankton was greatest in the spring and least in the

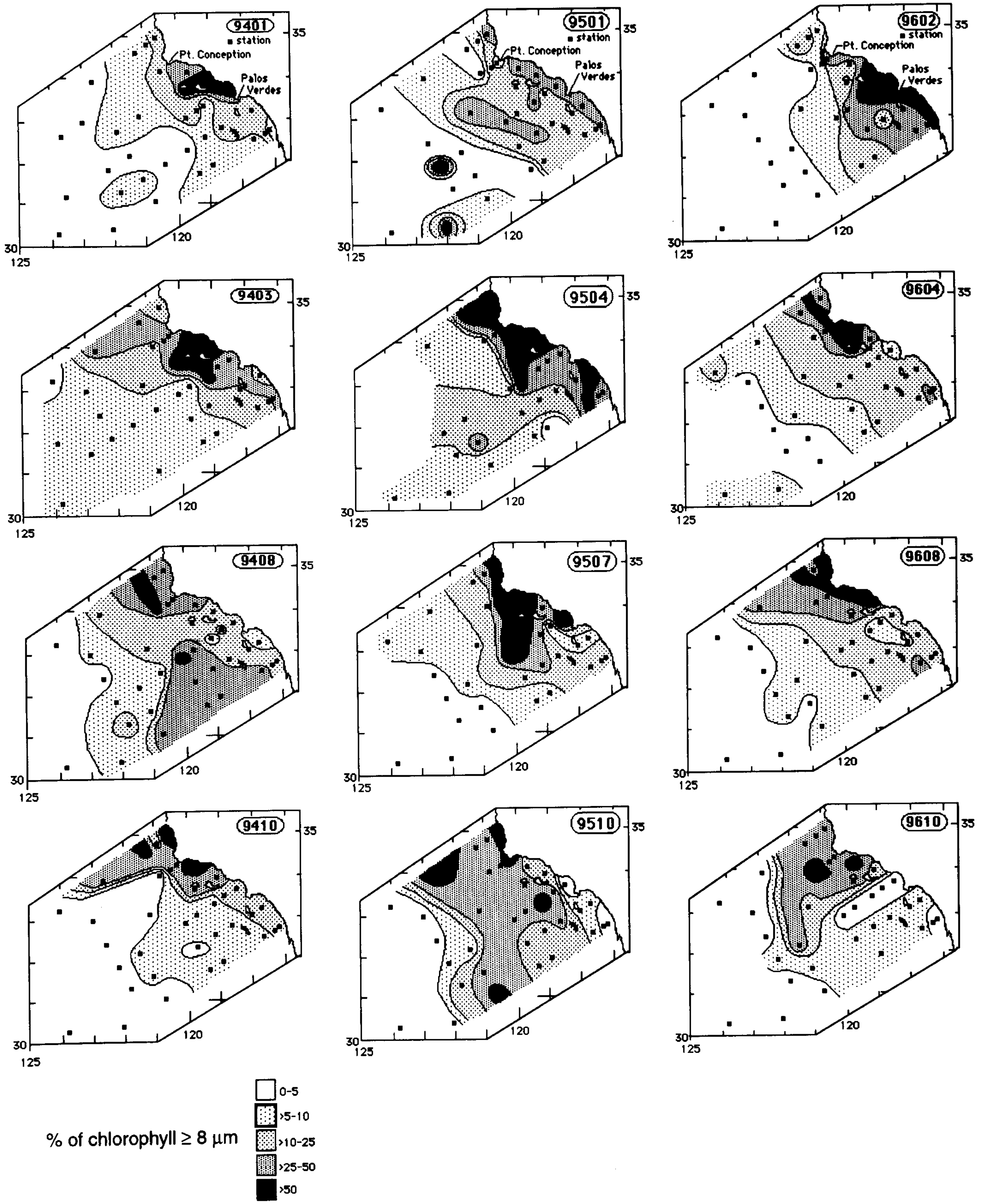

Figure 1. Distribution of the relative contribution of ≥8 µm phytoplankton to total biomass of chlorophyll, 0–100 m, during 12 cruises in 1994–96 (months indicated by last two digits of cruise number). For distribution of total chlorophyll on these cruises, see Hayward et al. 1995, 1996, and Schwing et al. 1997.

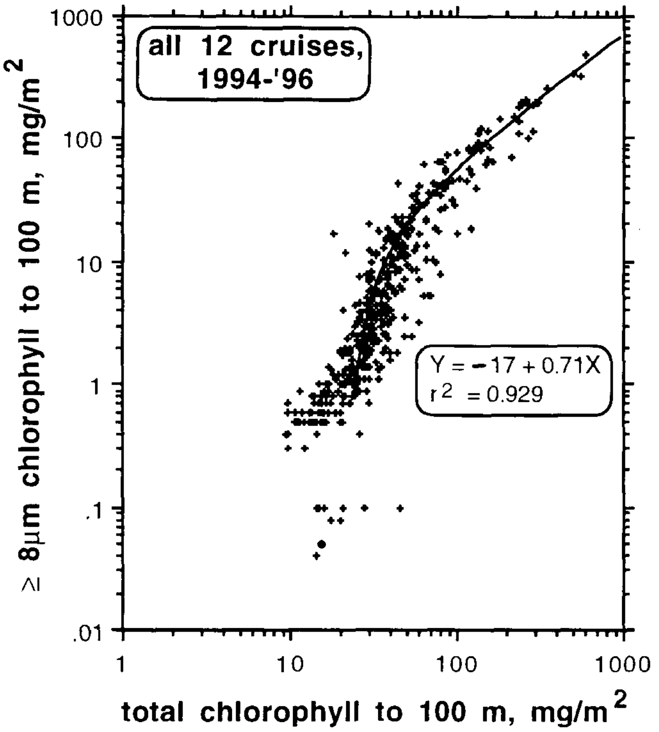

Figure 2. Biomass of chlorophyll in ≥8 μm particles vs. total biomass of chlorophyll (GF/F filter) for 12 cruises over three years. On the double-log plot, the linear regression is curved.

autumn for any given depth of nitricline, though this tendency is probably not statistically significant and does not, in itself, suggest any particular cause.

In principle, grazing by macrozooplankton should reduce the biomass of large cells preferentially, but the increase in ≥8 μm biomass with shoaling of the nitricline (fig. 4) occurred in spite of a similar, but less marked, increase in macrozooplanktonic biomass with a decrease in nitricline depth (compare fig. 5, top, to fig. 4). However, if macrozooplanktonic biomass · (≥8 μm biomass)$^{-1}$ is taken as a surrogate for grazing pressure per unit biomass of large cells, this biomass-specific mortality decreased as the nitricline shoaled (fig. 5, middle), and the relative importance of large cells was greatest where and when the biomass-specific grazing pressure on them was small (fig. 5, bottom).

Because grazing pressure and nitricline depth are themselves related, their relations to ≥8 μm biomass of chlorophyll are convolved. However, if it can be assumed that the depth of the nitricline (presumably affecting growth) is the dominant determinant of the biomass of ≥8 μm phytoplankton, it is possible to determine whether there is a detectable secondary effect of grazing pressure (affecting death). The test is whether departures or residuals of actual biomass of ≥8 μm chlorophyll from the biomass predicted from the depth of the nitricline (i.e., actual data points minus values of the regression line in fig. 4) are related to the surrogate for grazing pressure. As shown in figure 6, there tends to be "excess" biomass (positive residuals) where grazing pressure is low, and a "deficit" (negative residuals) where grazing pressure is high.

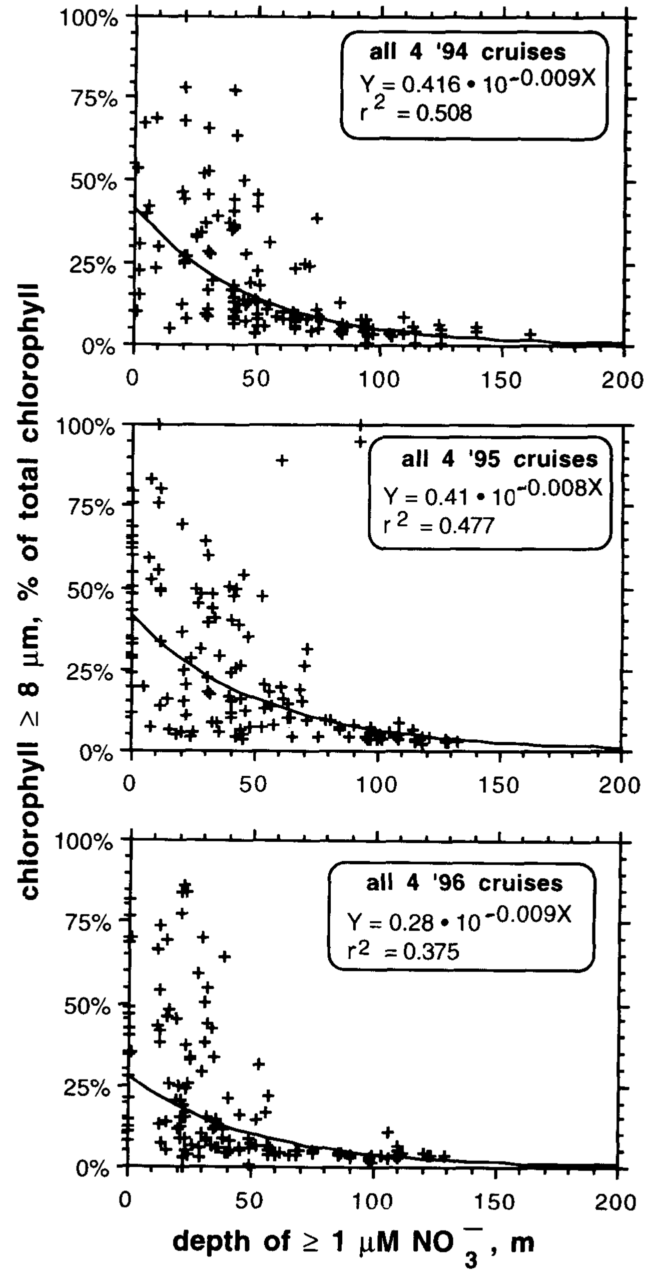

Figure 3. Relative importance of ≥8 μm particles to total biomass of chlorophyll as a function of depth of the nitricline (where NO_3^- first is ≥1 μM) for 1994, 1995, and 1996.

DISCUSSION

The relative importance of large phytoplankton (defined here as ≥8 μm—could also include aggregates of smaller cells) differed considerably in geographic pattern

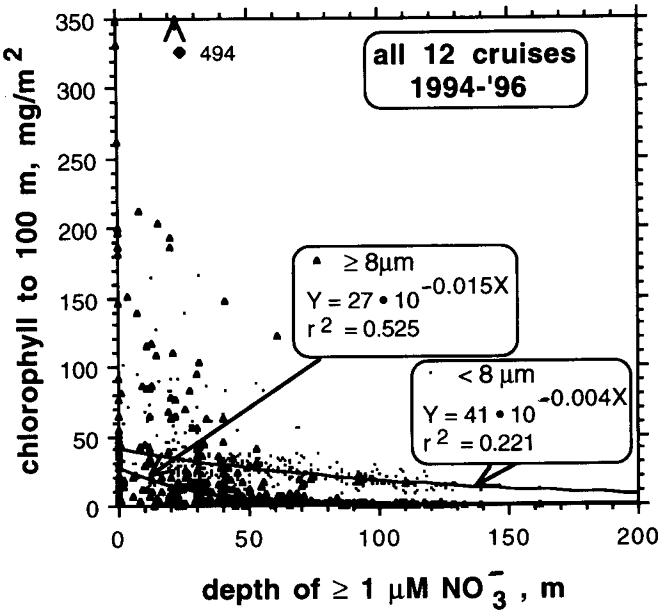

Figure 4. Biomasses of chlorophyll in <8 and ≥8 µm particles as functions of depth of the nitricline for 1994–96. Biomass <8 µm = total biomass – ≥8 µm biomass.

over the three years studied (fig. 1), but this relative importance tended to be greater in eutrophic than in oligotrophic regions (fig. 2). Both the relative importance of large cells (fig. 3) and their absolute biomass (fig. 4) were related to the depth of the nitricline, in agreement with the conclusions of Hopkins (1971), who used a much coarser filter (22 µm mesh) to separate "large" from "small." This finding is consistent with, but does not prove, the hypothesis that "new" production (defined as nutrients supplied from below the euphotic zone) is more important for maintaining an elevated biomass of large cells than it is for small cells. However, Chavez (1989) reported an interesting and important example—the equatorial Pacific—in which elevated surface concentrations of nitrate were not associated with large cells.

Because other oceanographic features (e.g., turbulence) may covary with nitricline depth, other causal influences are possible. Biomass-specific grazing by macrozooplankton is one such covariable (fig. 5, middle), but there is a detectable effect of grazing pressure beyond that related to nitricline depth (fig. 6). Covariables may also have predictive utility; for example, Mitchell-Innes and Pitcher (1992) discussed the role of nitrate in affecting

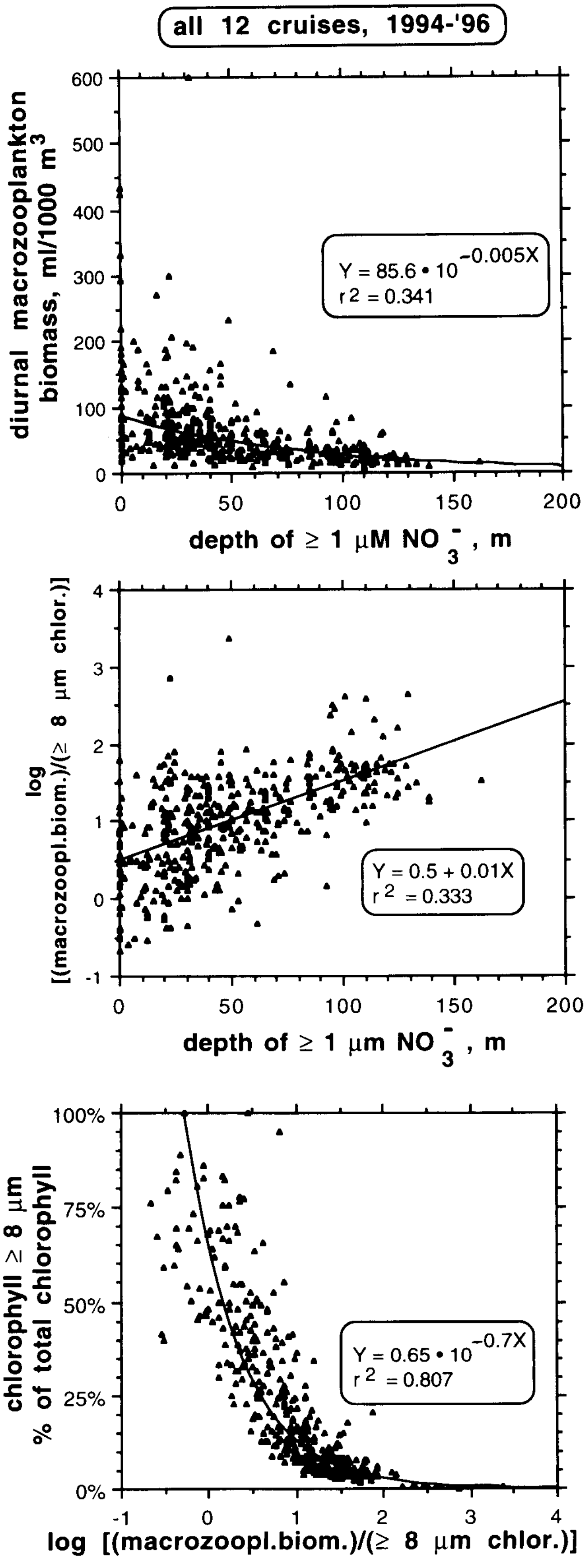

Figure 5. Relations involving macrozooplanktonic biomass, all 12 cruises. Top, Biomasses of macrozooplankton as a function of the depth of the nitricline. Middle, Proxy for biomass-specific grazing mortality of ≥8 µm cells (macrozooplanktonic biomass·(≥8 µm chlorophyll)$^{-1}$) vs. depth of the nitricline. Bottom, Biomass of ≥8 µm cells, as a percentage of total chlorophyll biomass, vs. the proxy for biomass-specific grazing mortality.

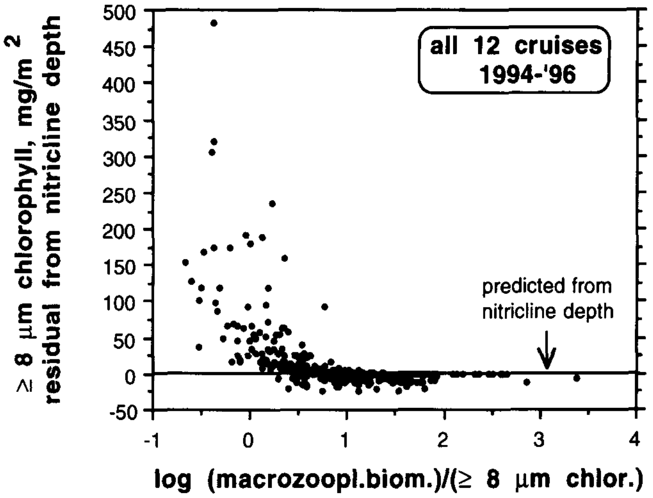

Figure 6. Residual biomasses of ≥8 µm chlorophyll (actual data minus the biomass predicted from nitricline depth; see fig. 4) vs. the proxy for biomass-specific grazing mortality of ≥8 µm cells.

the size distribution of phytoplankton, and therefore the suitability as food by higher trophic levels, but emphasized the use of sea-surface temperature and total biomass of chlorophyll as predictive tools, since these can be remotely sensed.

Given the paradigm that large cells participate in a "diatom-copepod-fish" food chain, while small cells are more likely to pass through a "microbial loop" or microzooplanktonic chain (e.g., Landry 1977; Beers 1986), the results of this study support the hypothesis that the production of zooplanktivorous fish will be related to nitricline depth in a nonlinear way. That is, shallow nitricline depths mean not only a greater total biomass of phytoplankton and macrozooplankton, but also that a greater proportion of this biomass will be passed to fish with relatively few "middleman" costs. This argument has been made elsewhere (e.g., Cushing 1989; Coombs et al. 1994), though definitive tests of the hypothesis are rare. Further, the hypothesis is a gross oversimplification, since the actual relation between nutrient supply and fish production also depends on other aspects, such as timing (e.g., short pulses, possibly leading to sinking of uneaten phytoplankton, vs. steady flux of nutrients), and the species and nutritional value of the phytoplankton (and zooplanktonic herbivores) which develop.

ACKNOWLEDGMENTS

I thank the scientific parties of the CalCOFI cruises in 1994–96 for collecting and analyzing samples, particularly Ed Renger and Sherry Cummings for providing data. I also thank Tom Hayward for suggesting that I explore the relation between the size distribution of phytoplankton and the depth of the nitricline, and Francisco Chavez for comments on the manuscript. This research was supported solely by the Marine Life Research Group, Scripps Institution of Oceanography.

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THE PHYTOPLANKTON OF THE SANTA BARBARA BASIN: PATTERNS OF CHLOROPHYLL AND SPECIES STRUCTURE AND THEIR RELATIONSHIPS WITH THOSE OF SURROUNDING STATIONS

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ABSTRACT

A twelve-year series of chlorophyll data from the CalCOFI station in the Santa Barbara Basin (SBB) shows that pigment is consistently concentrated in the upper 25 m. The annual maximum tends to be in April or May. When temporal fluctuations of mixed-layer chlorophyll are compared with the fluctuations at other CalCOFI stations, the stations most similar lie to the south and west of the SBB. There is one nonadjacent station to the north. Chlorophyll fluctuations west of stations 60 or 70 are negatively correlated with fluctuations at the SBB station.

Phytoplankton species at the SBB during April 1993 and April 1995 were typical upwelling diatoms. When the species structure at the SBB is compared with that at other CalCOFI stations, the stations with similar species structure tend to be those with similar temporal patterns of chlorophyll fluctuations. Species structures of the offshore stations have negative correlations with structure at the SBB.

INTRODUCTION

The Santa Barbara Basin (SBB) is an area of roughly 575 km^2 in the central portion of the elongate Santa Barbara Channel, southeast of Point Conception, California. The channel and basin have been the site of many research programs (Baumgartner et al. 1992; Thunell et al. 1995; Hendershott and Winant 1996; Schimmelman and Lange 1996; Osgood and Checkley 1997). Much of the interest has been prompted by the existence of varved sediments within the basin (Lange et al. 1996; Schimmelman and Lange 1996). These are a consequence of a unique combination of hydrography, biology, and bottom topography, and they have unusual potential for fine-scale reconstruction of climatological and oceanographic history (Schimmelman and Lange 1996).

The accuracy of such reconstruction will depend in part on the degree to which the deposition within the basin can be related to regional oceanographic conditions and to larger-scale processes. On the one hand, the complicated hydrography of the SBB (Harms and Winant 1998) indicates that near-surface conditions in the SBB are highly variable on small spatial and temporal scales and may not always be closely related to conditions outside the basin. On the other hand, sedimentary records from the SBB do appear to reflect historic large-scale phenomena (Lange et al. 1990), suggesting that generalizations are valid, at least over sufficiently broad scales.

Since the early 1950s, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has regularly occupied a station in the SBB as a part of its routine survey of the California Current. To my knowledge, no study has directly compared phytoplankton of the near-surface waters of the SBB with those of the rest of the stations in the CalCOFI grid in order to examine similarities and differences on scales of kilometers and years.

Two recent studies have examined patterns of mixed-layer chlorophyll and floristics from the CalCOFI region. The SBB station provided data for both studies. But because of the synthesis of a large amount of data, the contribution of this one station cannot be identified specifically. Because of the interest in this local region, it is appropriate to examine the data from the SBB station directly.

The first study included an analysis of near-surface chlorophyll concentrations between January 1984 and July 1995 (Hayward and Venrick, in press). On the basis of the temporal fluctuations, three cohesive regimes within the CalCOFI area were identified (fig. 1). Within each regime, primary production is regulated by a different combination of physical processes. Most relevant to the present study is the northern inshore regime, which includes the SBB station at the northern edge. At these stations, chlorophyll in the mixed layer typically peaks between March and May when the euphotic zone is enriched by isopycnal shoaling, which brings nutrient-rich water to the surface.

In the second study (Venrick 1998) the distributions of phytoplankton species in the mixed layer were examined for two spring bloom periods: April 1993 and April 1995. In these years, a spring flora recurred and dominated the northern inshore regime.

The following study extends the previous analyses to examine the conditions at the SBB station with three objectives: to confirm the seasonal cycle of chlorophyll, to determine the species composition during two spring bloom periods, and to determine how large a region is

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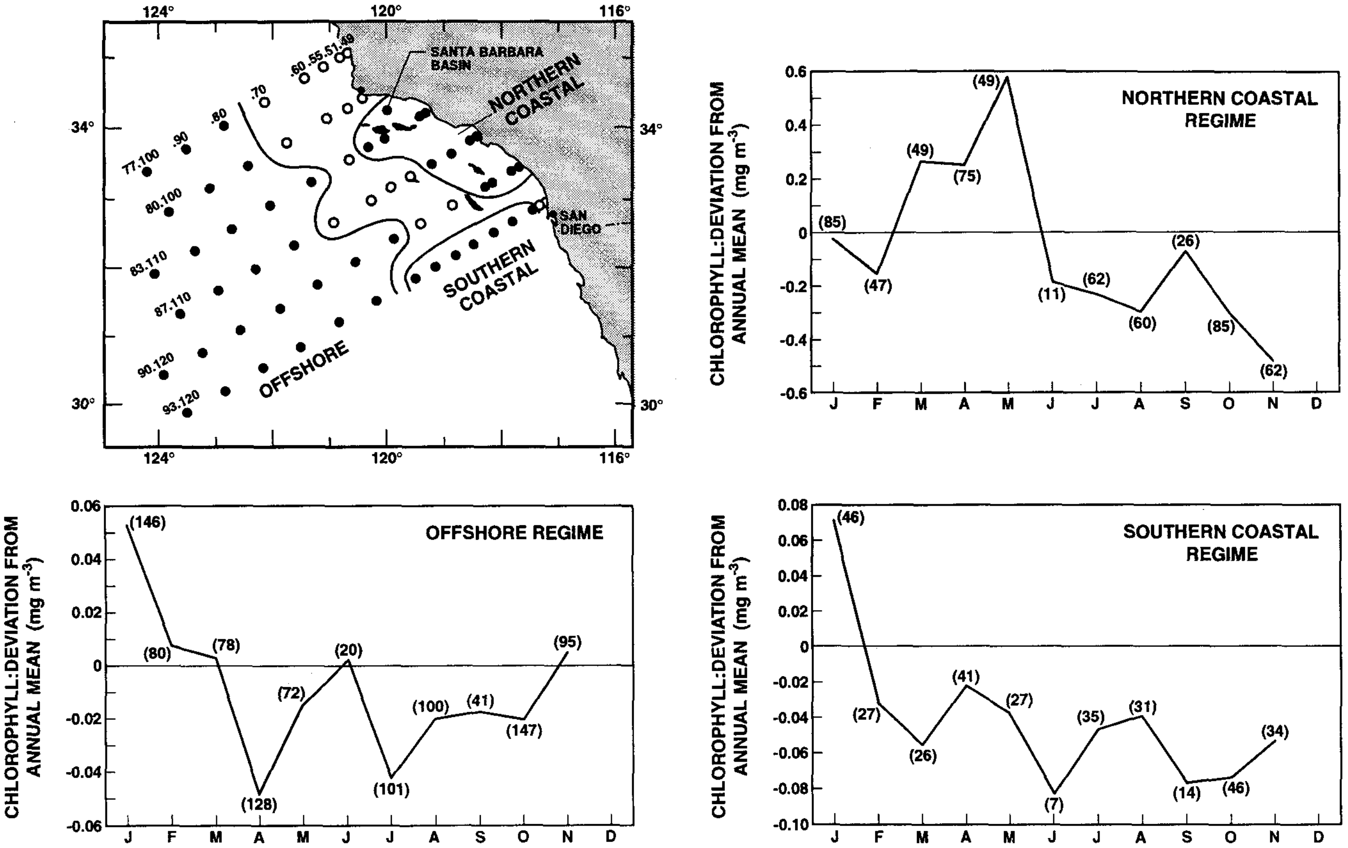

Figure 1. Location of three environmental regimes defined by Hayward and Venrick (in press). The near-surface chlorophyll concentrations at stations within each regime have similar patterns of fluctuations over time. The boundary between regimes fluctuates, so that 16 stations (open circles) are alternately in one regime or another and cannot be classified. The average seasonal variations of chlorophyll within each regime are expressed as the difference between the annual mean at each station and the cruise value, averaged over all stations within a region within a month. Numbers in parentheses indicate the numbers of values in each mean.

represented by chlorophyll fluctuations in the SBB on the interannual scale, and by floral structure on the quasi-synoptic scale.

METHODS

All samples were collected at standard CalCOFI stations. Station positions are given in CalCOFI data reports (e.g., SIO 1993, 1995). For convenience, station numbers have been rounded to the nearest whole number. Thus, station 40.6 on line 83.3 is designated as 83.41.

Since 1984, chlorophyll concentrations have been routinely determined from 10 to 14 depths in the upper 200 m. Samples are filtered through Whatman GF/F filters, extracted in acetone, and analyzed fluorometrically. Details of the procedure are given in CalCOFI data reports (e.g., SIO 1993, 1995). During this period, cruises have occurred quarterly, except for 1984 when there were six cruises. Fifty cruises in 12 years (8401 to 9510) are included in this study. On each of these cruises, a single station was occupied in the SBB, usually station 82.47. The target location of this station is 34°16.5'N, 120°1.5'W. Past stations have been within 15 km of this position.

In April 1993 (cruise 9304) and April 1995 (cruise 9504), phytoplankton samples of 125 ml were collected from the second bottle of the routine hydrocasts. Samples were preserved with neutralized formalin and enumerated under an inverted microscope. The volume counted varied from 0.17 ml to 100 ml. The entire amount settled was counted at 100X for the larger or rarer taxa, and one-sixth of the volume was counted at 250X for small species.

The sample from the second depth comes from the mixed layer when a mixed layer exists. This is the only depth, other than the surface, that has a consistent relationship with the vertical density structure across a broad range of hydrographic regimes. Over the 12-year period, the second depth varied between 3 m and 22 m, with a mean of 12.2 m. At the SBB, the mean depth was 10.8 m.

In order to compare the SBB station to the other stations in the CalCOFI grid, Spearman's nonparametric correlation coefficients (ρ) were calculated between data from the SBB station and from each other station. In the analysis of chlorophyll, the data correlated were the temporal sequences of mixed-layer chlorophyll concentration. In the floristic analyses the data were the rank order of abundance of phytoplankton species from the mixed layer.

In these analyses, ρ is used as a qualitative index of similarity. The numbers of correlations are so great that some are likely to be "significant" by chance alone (multiple testing). Thus the actual probability of any one value cannot be directly evaluated. The null distribution of Spearman's ρ is a function of sample size, and sample size varies with each station pair (i.e., the number of cruises that sampled both stations during the 12-year period, or the number of species in their combined species list). Thus values of ρ based upon samples of different sizes cannot be directly compared. To correct for the effect of sample size, the magnitude of a correlation was evaluated by reference to standard statistical tables. It is important to keep in mind that, in spite of reference to statistical tables, I am interested in relative strengths of relationships and their patterns, rather than statistical significance.

RESULTS

Temporal Patterns of Chlorophyll

The SBB station is one of 7 stations near Point Conception that has a mean mixed-layer chlorophyll in excess of 2 mg m^{-3} (fig. 2). It had the fourth highest single chlorophyll concentration observed during this study: 22.3 mg m^{-3} at 1 m depth in April 1995. The maximum chlorophyll concentration was 29.9 mg m^{-3} at 21 m at station 87.33 in March 1987. Concentrations exceeding 22.3 mg m^{-3} were also found at station 83.41 in May 1985 and at station 77.55 in July 1990.

Elevated chlorophyll concentrations at the SBB station are restricted to the upper 25 m (fig. 3). There is no recurring or persistent subsurface maximum such as characterizes offshore waters (Venrick et al. 1973) or waters farther south in the Southern California Bight (Cullen and Eppley 1981).

Values integrated to 200 m are variable (fig. 4), ranging between 20 mg m^{-2} (Aug. 18, 1985) and 553 mg m^{-2} (April 17, 1995). An estimate of the seasonal cycle is obtained by subtracting from each datum that year's annual mean value (fig. 5). Maximum annual deviations occur between April 11 and May 17. Only four of ten deviations in that period are markedly elevated, although nine of the ten are above the annual mean. Minimum deviations occur between August and January. Maximum values in the spring are characteristic of the northern inshore regime defined by Hayward and Venrick (fig. 1), although some stations in this regime have peak concentrations as early as March. The probability that the four highest annual deviations would occur during the spring (March–May) if, in fact, there is no spring bloom is vanishingly small ($p = 8.7 \times 10^{-10}$).

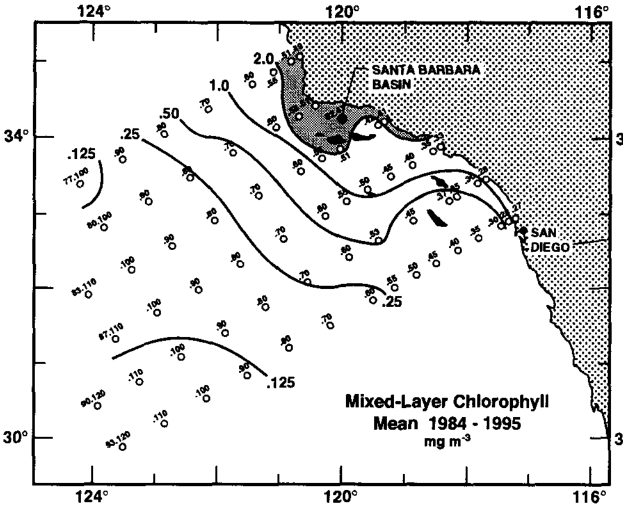

Figure 2. Mean chlorophyll concentration in the mixed layer, 1984–95.

To make the following analysis comparable to the floristic analysis to follow, I have restricted it to the chlorophyll in the second depth of the routine CalCOFI hydrocasts. At the SBB station, this sample most frequently (44%) contains the maximum chlorophyll in the water column, and the concentration from this depth explains 65% of the variability of the total chlorophyll (Spearman's $\rho = 0.81$; I do not give a probability here because of the lack of independence of the two sets of data). Presumably, fluctuations of chlorophyll at the second depth indicate fluctuations in biomass as well as do fluctuations at any single depth.

I have examined the geographical area sharing the pattern of chlorophyll at the SBB station by calculating Spearman's rank order correlation coefficient between the sequence of chlorophyll at the SBB station and the sequence at each of the 65 remaining CalCOFI stations. The highest coefficients of similarity ("p" ≤ 0.001) define a group of 9 stations, which, with one exception, lie south and west of the SBB (fig. 6). The boundary of this cluster is similar to that of the northern inshore regime defined by Hayward and Venrick (fig. 1). On the other hand, the correspondence with the high chlorophyll stations (fig. 2) is weak. The next contour of similarity ("p" ≤ 0.05) includes most of the nearshore stations, east of station 70 in the north but restricted to the immediate coast along lines 90 and 93. This boundary corresponds to the 12-year mean chlorophyll contour of 1.0 mg m^{-3} (fig. 2). Thirty-seven of the 65 CalCOFI stations have positive correlations with the SBB. These

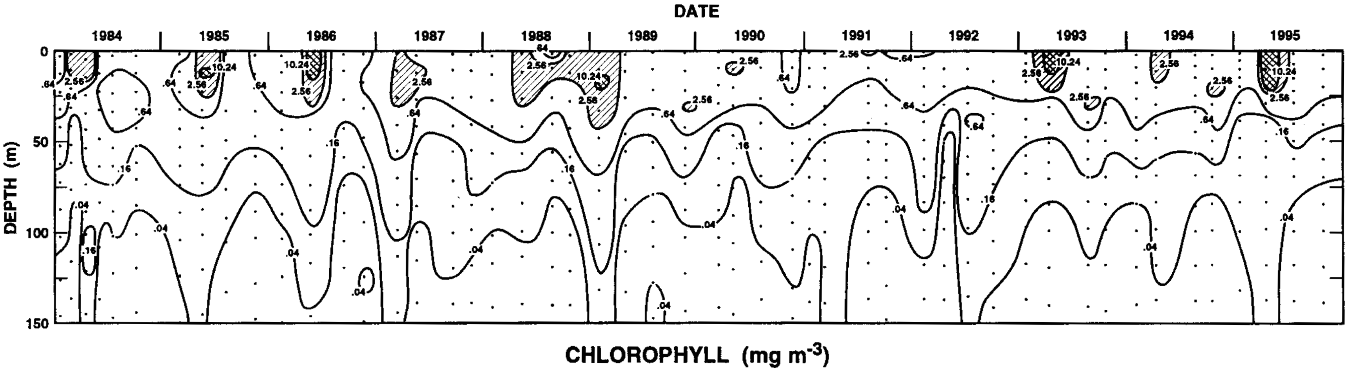

Figure 3. Time/depth plot of chlorophyll concentration at the Santa Barbara Basin station, 1984–95.

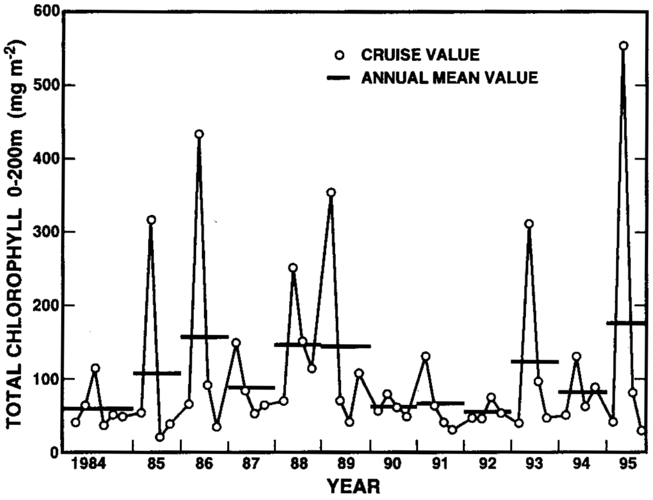

Figure 4. Temporal variability of integrated chlorophyll, 0–200 m, at the SBB station. Horizontal lines indicate annual means.

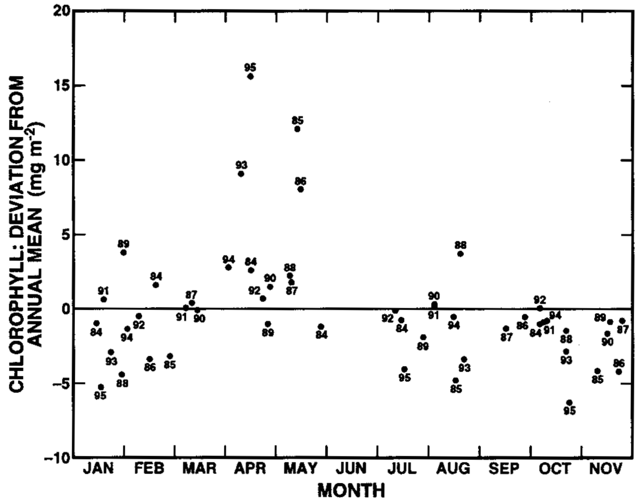

Figure 5. Seasonal cycle of integrated chlorophyll, 0–200 m, at the SBB station. Values are deviations from the annual mean value, by month. Numbers indicate the year.

stations are the inshore portion of the CalCOFI grid. Farther offshore, all but two stations have low but negative correlations with the SBB station. These offshore stations fall in the offshore regime defined by Hayward and Venrick (in press).

Within the region delimited by a positive relationship with SBB (fig. 6), only the SBB station and station 87.45 have eight high correlations with other inshore stations ("*p*" ≤ 0.001). No other inshore station has more. From this perspective, we may say that the fluctuations of mixed-layer chlorophyll at the SBB station are as representative of fluctuations in the inshore region as are those at station 87.45, and are more representative than chlorophyll fluctuations from other stations.

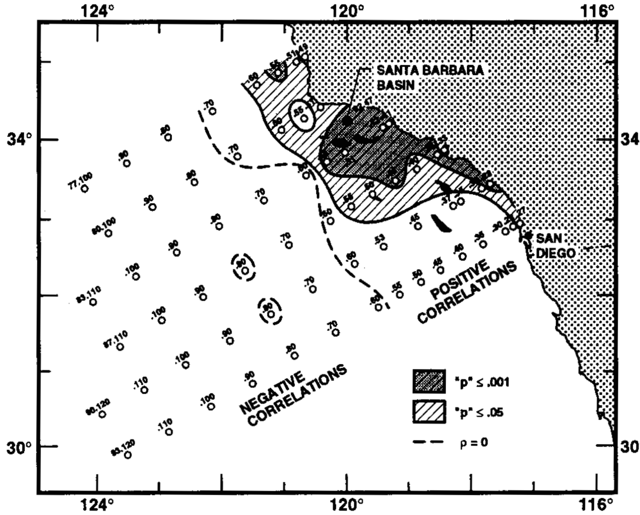

Figure 6. Similarity map for chlorophyll. Contours indicate positive correlations (Spearman's ρ) between chlorophyll fluctuations at the SBB station and surrounding stations at two "probability levels," uncorrected for multiple testing. Dashed contour is the boundary between positive and negative correlations.

Spring Species Composition

El Niño conditions prevailed during most of 1993. However, during the spring of 1993, there was a brief return to more normal circulation patterns (Hayward et al. 1994), so that the environmental characteristics of station 82.47 in April 1993 were similar to those of April 1995 (fig. 7). The pycnocline began near 20 m, and most chlorophyll was shallower. The major differences between years were the lower nitrate and higher chlorophyll in 1995. The profiles suggest that the SBB in 1993 was sampled earlier in the development of the bloom, and that differences between years may be artifacts of the time of sampling.

Temperature, oxygen, nitrate, and chlorophyll data indicate that the most recent upwelling occurred near stations 77.49 and 80.51 in 1993 and near stations 77.49, 77.51, and 80.51 in 1995 (Venrick 1998). Some portion of the water at the SBB station may have been advected from the north. Conditions during these cruises are discussed more fully by Hayward et al. (1994, 1995, 1996). Data have been published in cruise reports (SIO 1993, 1995).

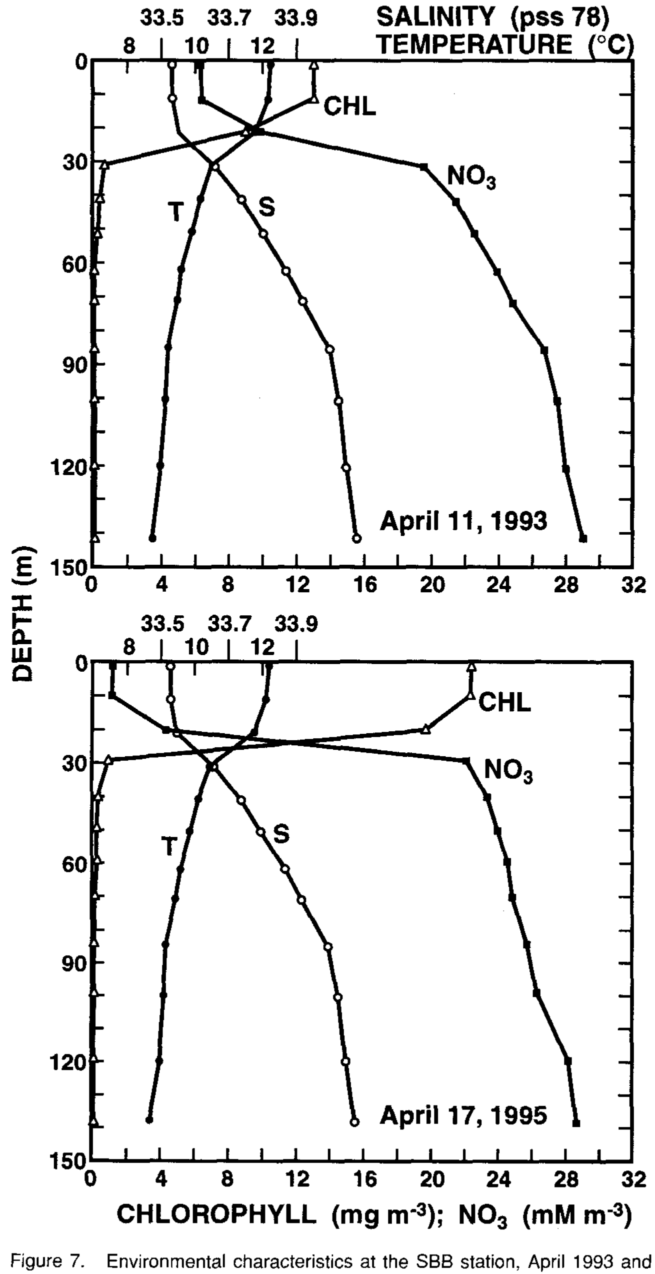

Figure 7. Environmental characteristics at the SBB station, April 1993 and 1995.

A total of 39 species was identified at the SBB station during the April cruises of 1993 and 1995 (table 1). There were 2,556 cells ml^{-1} comprising 27 identified species in April 1993; three additional species were recognized in uncounted material. In 1995 there were 4,181 cells ml^{-1} comprising 25 species. Both flora were dominated by species of *Chaetoceros* in the subgenus *Hyalochaetae*. Five coccolithophorids but no dinoflagellates were present. The major differences between the two floras were the absence of *Skeletonema costatum* in 1993 and the dominance of *Chaetoceros socialis* in 1995. Despite the differences, the correlation between rank orders of abundance of the two spring floras was significant ($\rho = 0.34$, $p < 0.05$). Such temporal consistency is not normal in the CalCOFI pattern. Between the two sampling periods, only three other stations (77.80, 77.55, and 83.55) had a similar consistency of flora over time. It is unlikely that there is anything special about these four stations; more likely, they are random artifacts of the large numbers of possible correlations.

Spearman's ρ was used to examine the floral similarities between the SBB station and the remaining CalCOFI stations. In general, stations with similar patterns of chlorophyll fluctuations over time (fig. 6) have similar species composition (fig. 8). However, the patterns derived from floristics are less spatially and temporally cohesive. The stations most similar to the SBB station were different in 1993 and 1995; the only stations to be correlated with the SBB station with "p" ≤ 0.05 in both years were stations 83.55, 87.50, and 87.33. Relationships with other stations changed; station 83.51 was similar to the SBB station in 1993 ($\rho = 0.40$, "p" ≤ 0.01) and not in 1995 ($\rho = 0.13$, "p" $> .20$). Also, the stations most similar to the SBB station are not always adjacent to it.

The floristic patterns reflect the hydrography. The similarity between SBB and 87.70 in 1993 corresponded to a well-developed offshore eddy that is reflected in the maps of dynamic height and 10 m chlorophyll values. The eddy had transported offshore a parcel of nearshore water and flora. The discontinuous flora along line 83 in 1995 was related to a meander in the California Current, which brought offshore flora into stations 80.60 and 80.55. This is more evident in the 10 m chlorophyll and temperature map (SIO 1995) than in the dynamic heights, perhaps indicating a near-surface feature.

In this study, a negative correlation of species structure usually indicates species replacement. The stations that were negatively related to the SBB station were as abundant as stations with positive relationships. Out of

TABLE 1
Species Found in the Santa Barbara Basin (CalCOFI Station 82.47) in April 1993 and April 1995, Listed According to Mean Dominance

Code number	Species	Cells ml^{-1}		
		1993	1995	Mean
1	*Chaetoceros socialis* Lauder	147	2,031	1,089.0
2	*Chaetoceros debilis* Cleve	636	499	567.5
3	*Chaetoceros radicans* Schutt	566	145	355.5
4	*Pseudo-nitzschia* spp.—delicate forms	356	82	219.0
5	*Skeletonema costatum* (Grev.) Cleve	0	277	138.5
6	*Pseudo-nitzschia* spp.—robust forms	44	231	137.5
7	*Chaetoceros didymus* Ehrenb.	49	195	122.0
8	*Chaetoceros costatus* Pavillard	209	0	104.5
9	"Epiphytic cylinder"	114	54	84.0
10	*Chaetoceros compressus* Lauder	84	54	69.0
11	*Gephyrocapsa oceanica* Kampt. (Grindley & Tayler)	49	82	65.5
12	*Thalassiosira cf aestivalis* Gran	5	118	61.5
13	*Gephyrocapsa* spp.	16	82	49.0
14	*Fragilariopsis pseudonana* Hasle (Hasle)	82	0	41.0
15	*Bacteriastrum delicatulum* (Cleve)	54	18	36.0
16	*Cylindrotheca closterium* (Ehrenb.) Lewin & Reimann	16	54	35.0
17	*Chaetoceros* cf. *vanheurcki* (Gran)	24	45	34.5
18	*Dactyliosolen phuktensis* (Sundstrom) Hasle	24	23	23.5
19	*Thalassiosira cf anguste-lineata* (A. Schmidt) Fryxell & Hasle	0	45	22.5
20	*Thalassiosira cf. bioculata* (Grunow) Ostenfeld	0	45	22.5
21	*Emiliania huxleyi* (Lohm.) Hay & Mohler	+	27	13.5
22	*Thalassiosira cf. eccentrica* (Ehr.) Cl.	0	23	11.5
23	*Thalassiosira rotula* (Meunier)	22	0	11.0
24	*Dactyliosolen fragilissima* (Bergon) Hasle	19	0	9.5
25	*Dactyliosolen blavyanus* (H. Perag.) Hasle	0	18	9.0
26	*Hemiaulus sinensis* (Grev.)	0	14	7.0
27	Pennate 1	10	0	5.0
28	*Leptocylindrus danicus* Cl.	0	9	4.5
29	*Lauderia annulata* Cl.	8	0	4.0
30	*Chaetoceros affinis* Lauder	5	0	2.5
31	*Amphiprora* spp.	5	0	2.5
32	*Ditylum brightwelli* West (Grun.)	0	5	2.5
33	*Thalassiosira cf. nordenskioldii* Cleve	0	5	2.5
34	*Chaetoceros* "fine aequatorialis"	3	0	1.5
35	*Actinocyclus* "small curvatulus"	3	0	1.5
36	*Anoplosolenia brasiliensis* (Lohm.) Deflandre	3	0	1.5
37	*Haslea wawrikae* (Hust.) Simonsen	3	0	1.5
38	*Mastogloia woodiana* Taylor	+	0	+
39	*Helicosphaera carterae* (Wallich) Kamptner	+	0	+
Total		2,556	4,181	3,367.5
	Unidentified cells			
	hyalochaete spp.	745	784	764.5
	spores	0	5	2.5
	Thalassiosira spp.	35	5	20.0
	Pennate diatoms	5	23	14.0
Overall total		3,374	4,998	4,186.0

+ indicates that the species was present in the material but not seen in the fraction counted.

48 and 51 comparisons in 1993 and 1995, 22 and 31 pairs were negative. The boundary between negative and positive correlations varied, but the alongshore orientation agreed with the boundary defined in figure 6 on the basis of positive and negative relationships between temporal patterns of chlorophyll. Both of these, in turn, corresponded with the boundary region between coastal and offshore regimes defined by Hayward and Venrick (fig. 1).

DISCUSSION

Seasonal Cycle

There is a great deal of variability in the chlorophyll data series (figs. 3 and 4). Although much of this may be due to the complicated hydrography in the region, some portion almost certainly arises from sampling error due to the interaction of cruise timing with the seasonal cycle. For instance, the absence of a peak in the spring of 1994

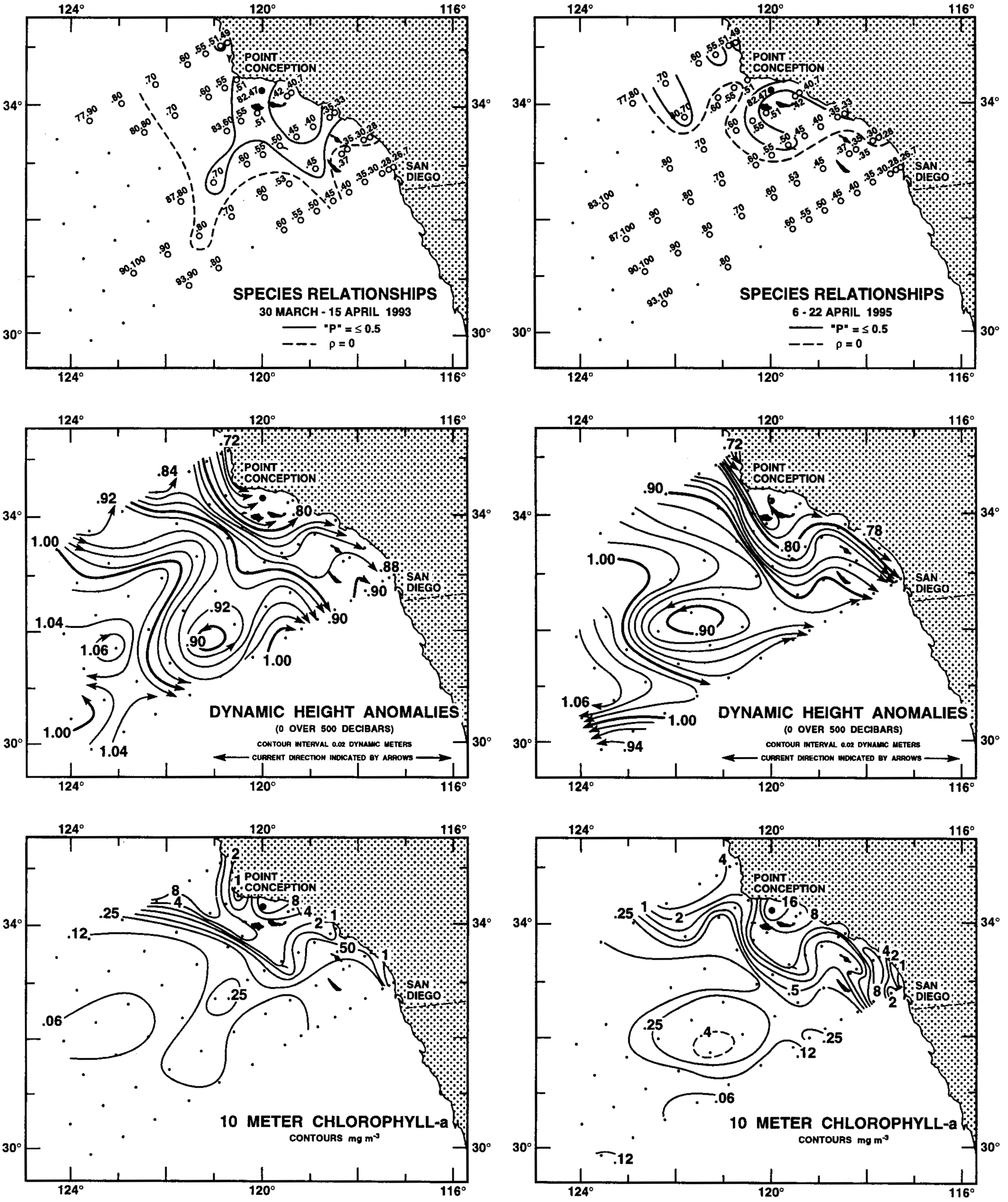

Figure 8. Similarity maps for species structure together with maps of dynamic heights and 10 m chlorophyll concentrations for 1993 and 1995 (SIO 1993, 1995). Solid contours of similarity indicate the positive correlation (Spearman's ρ) between the order of dominance of species at the SBB station and surrounding stations at "p" ≤ 0.05, uncorrected for multiple testing. Dashed contour shows boundary between positive and negative correlations. Stations without floristic samples are unlabeled.

may indicate only that the cruise did not coincide with the spring bloom in the SBB. This sampling error is reflected in both seasonal and interannual variabilities.

With some simplifying assumptions, the sampling error may be used to estimate the probable duration of the spring peak. I define a bloom as an integral chlorophyll concentration greater than 7 mg m^{-2} above the annual mean. There were four such values between April 11 and May 17 (fig. 5). I assume that the peak occurs each year during a 40-day period (e.g., April 10 and May 20); this period was sampled by ten cruises. I also assume that the number of days of elevated chlorophyll is the same each year (although they do not need to be sequential), and that the timing of cruises relative to the chlorophyll peak is random, so that each cruise during that period is equally likely to sample a chlorophyll peak. Then, from the binomial distribution, the 90% confidence interval for bloom duration is between 9 and 24 days. If we permit some years without blooms, this interval becomes longer. For instance, if we assume we sampled every bloom (i.e., six years had no blooms), the shortest likely bloom duration is 18 days. If we assume a bloom each year but enlarge the possible bloom period to include March, then the corresponding 90% confidence interval is 11–33 days. Calculations such as these suggest that the spring bloom at the SBB station (when it occurs) is likely to be longer than one week and shorter than six weeks.

Spring Species Composition

A spring flora—dominated by *Chaetoceros* species in the subgenus *Hyalochaetae*, *Skeletonema costatum*, and *Pseudo-nitzschia* spp.—appeared during April of both 1993 and 1995. These species are the quintessential components of enriched flora throughout temperate oceans (Venrick 1998).

A continuing goal of my work is to provide information on species composition in the water column which can be compared with species from sediment traps and near-surface sediments (e.g., Lange et al. 1997). I need many more than two phytoplankton samples over varying scales of time and space to make this comparison meaningful. Nevertheless, a preliminary observation may be warranted.

On the basis of sediment trap data collected in 1994 from the SBB, Lange et al. (1997) characterized the spring bloom by a high flux of diatom resting spores in the genus *Chaetoceros*, most notably spores of *C. radicans*. In the mixed-layer samples of the present study, species in the genus *Chaetoceros* were dominant, and *C. radicans* was among the top five species in both 1993 and 1995 (table 1). For correct interpretation of the sedimentary record, it is not necessary for the spring flora to be preserved unaltered, only that key elements be preserved and that any transformations between water and sediment be quantified. *Chaetoceros radicans* may prove to be one such key element.

Generality

The area represented by the phytoplankton of the SBB has been examined with different data sets over different time scales. The floristic data are nearly synoptic in each of two years. On this scale there is clearly a great deal of heterogeneity. The stations most similar to the SBB station differ between the two sampling periods, and the floral structure at the SBB fluctuates. Generalizing details from the spring flora of the SBB to surrounding stations at any one point in time is risky.

On the other hand, the analysis of changes in chlorophyll over a 12-year period indicates a group of stations primarily to the south and west of the SBB station that show a common pattern of biomass fluctuations, visible above the small-scale complexity of the area. This is due, at least in part, to a common seasonal cycle. With the present sampling frequency, we cannot define the seasonal cycle accurately enough to examine the residual interannual variability. It is reasonable to expect (but in no way proven) that the floristics behave over time in a way similar to chlorophyll. That is to say, there is a group of stations, including the SBB station, that tend to have similar spring flora on a decadal scale in spite of considerable heterogeneity between years.

Clearly this study is a small fraction of the ideal study. The floristic analyses are limited to April. There is no reason to expect similar results during different seasons, especially since the circulation within the SBB and the rest of the California Current has a strong seasonal component (Hickey 1979; Harms and Winant 1998). Data from additional years are needed. Finally, the study should be expanded to other trophic levels.

Perhaps the most important result from this study is that the SBB represents only a fraction of the CalCOFI area, regardless of the data type or sampling scale. This is the area that roughly corresponds to the northern inshore regime as defined by Hayward and Venrick (in press). Stations in the offshore regime are clearly unlike the SBB. This places limitations on the generalizations that can be made from Santa Barbara Basin data, at least on scales shorter than interdecadal.

ACKNOWLEDGMENTS

This paper was prompted by discussions with Carina Lange and Freda Reid, and by a heated debate with John McGowan. It was made possible by many scientists, technicians, and volunteers who have collected, analyzed, and processed the chlorophyll data and collected the phytoplankton samples. The research was sponsored by the Marine Life Research Group of Scripps Institution of Oceanography, UCSD.

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ALGORITHMS FOR SEAWIFS STANDARD PRODUCTS DEVELOPED WITH THE CALCOFI BIO-OPTICAL DATA SET

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ABSTRACT

Funding from NASA's Ocean Biogeochemistry Program and the Goddard Space Flight Center SeaWiFS Project was used to implement an ocean optics program as part of the routine cruises of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Since August 1993, data from more than 300 bio-optical stations have been acquired, merged with complementary data, and made available for developing remote sensing algorithms. The profiling instrument consisted of a Biospherical Instruments, Inc. MER-2040/2041 radiometer integrated with CTD probes, a transmissometer, and a fluorometer. A detailed calibration time series of the radiance and irradiance sensors has been maintained to ensure maximum accuracy. The data set has been used to develop empirical algorithms for SeaWiFS standard products including chlorophyll a (chl a), "CZCS pigments," and diffuse attenuation coefficient $K_d(490)$. Algorithms using cubic regressions of remote sensing reflectance (R_{rs}) ratios provided the best estimation of chl a and pigments over the full range of chl a (0.05–22.3 mg m^{-3}). Multiple linear regressions of multiple-band ratios proved to be less robust. Relationships between spectral K and chl a suggest that previous K algorithms may have errors due to estimates of pure-water absorption.

INTRODUCTION

The Southern California Bight region, from San Diego to just north of Point Conception, is a region with one of the longest, most comprehensive time series of marine observations—California Cooperative Oceanic Fisheries Investigations (CalCOFI)—which has been jointly sponsored by the National Oceanic and Atmospheric Administration (NOAA), the University of California, and the California Department of Fish and Game for more than 40 years. The Southern California Bight is part of the California Current system, a region which has been well studied with respect to its regional optical properties in an effort to develop regional ocean color algorithms (Smith and Baker 1978a, b; Gordon et al. 1983; Mitchell and Kiefer 1988; Sosik and Mitchell 1995).

The CalCOFI region encompasses a large dynamic range of coastal and open-ocean trophic structure. Optics data have been collected for chl a concentrations at the surface ranging over three orders of magnitude, from 0.05 mg m^{-3} for offshore stations to over 50 mg m^{-3} during a massive red tide bloom at Scripps Pier. The taxonomic composition across the onshore-offshore gradient ranges from a dinoflagellate/diatom-dominated coastal community to a picoplankton-dominated community offshore. The offshore region of CalCOFI is typical of the open-ocean oligotrophic subtropical gyres, with low surface chl a, a deep chl a maximum between 100 and 130 m, and a nutricline between 120 and 150 m.

The current CalCOFI station grid (fig. 1) has 66 stations. On each cruise, approximately 25 of the CalCOFI stations are suitable for remote sensing reflectance measurements during daylight hours.

METHODS

Instruments

An integrated underwater profiling system was used to collect optical data and to characterize the water column. The system includes an underwater MER-2040 radiometer (Biospherical Instruments, Inc., S/N 8738) that measures depth, downwelling spectral irradiance (E_d), and upwelling radiance (L_u) at the following nominal wavelengths: 340, 380, 395, 412, 443, 455, 490, 510, 532, 555, 570, and 665 nm. The E_d block also included PAR (phytosynthetically available radiation); the

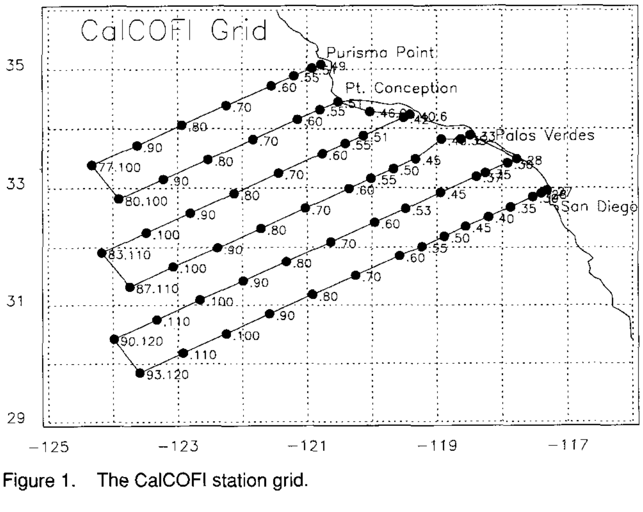

Figure 1. The CalCOFI station grid.

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L_u block included natural fluorescence. A MER-2041 deck-mounted reference radiometer (Biospherical Instruments, Inc., S/N 8739) measured downwelling irradiance at the following nominal wavelengths: 340, 380, 395, 412, 443, 490, 510, 555, 570, 665, 780, and 875 nm, PAR. The MER-2040 was also interfaced to a 25 cm transmissometer (SeaTech Inc.), a fluorometer (Wetlabs Inc.), and conductivity and temperature probes (Sea-Bird Electronics Inc.).

The underwater instrumentation was integrated onto a stainless steel frame. Power was provided to all systems via the MER-2040. Data from all instruments were multiplexed through the MER-2040 for transmission to the surface through submarine 3-conductor cable on an oceanographic winch equipped with a slip ring.

Instrument Characterization and Radiometric Calibrations

The MER-2040/2041 system used in this study has had detailed system characterization and radiometric calibration performed by the manufacturer, Biospherical Instruments, Inc. (BSI), and the Center for Hydro-Optics and Remote Sensing (CHORS) of San Diego State University according to procedures specified by the SeaWiFS Protocols (Mueller and Austin 1995). The unit was characterized by CHORS for spectral bandpass and for the immersion coefficient and cosine response of the cosine collector (Mueller 1995). A calibration and spectral band characterization was also obtained from the University of California, Santa Barbara, Institute for Computational Earth System Science (UCSB ICESS). The instrument specifications called for band centers within 1 nm of the nominal BSI band center. The reported spectral band centers measured by CHORS differ by more than 1 nm from the BSI nominal band centers for 5 out of 12 channels; two of those are SeaWiFS bands. The UCSB calibration found all SeaWiFS bands to be within 1 nm of the BSI nominal band center. The maximum difference found by UCSB is 3.1 nm for the "380" nm channel (table 1). All data are reported in terms of the "BSI nominal" band centers. Experimental determinations by BSI and CHORS were in good agreement for cosine response and immersion coefficient for the cosine collector.

Radiometric calibrations of the instrument were performed relative to National Institute of Standards and Technology (NIST) standard FEL lamps. During the period corresponding to this data set, BSI performed 10 calibrations and CHORS performed 3. The unit was calibrated at BSI, CHORS, and UCSB between May and November 1995. The differences in calibration between BSI and UCSB were within about 1% for E_d and within 2% for L_u; slightly higher differences were observed between BSI and CHORS (figs. 2 and 3). Some of the differences in the UV bands may be attributable to the differences in the spectral bandpass characteriza-

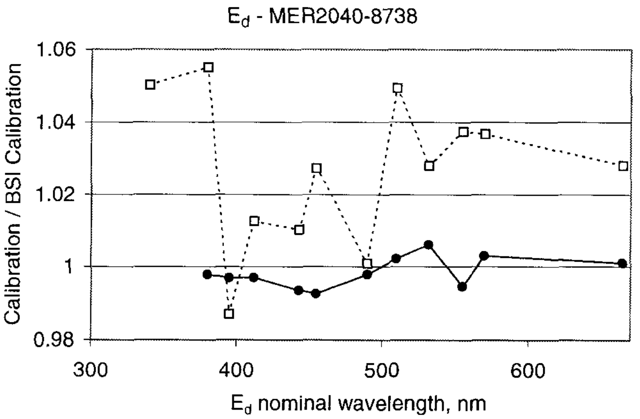

Figure 2. A comparison of MER-2040 E_d calibrations by different laboratories: ratio of UCSB calibration on 18 May 1995 to BSI calibration on 2 June 1995 (filled circles), and ratio of CHORS calibration on 2 Nov. 1995 to BSI calibration on 25 Nov. 1995 (open squares).

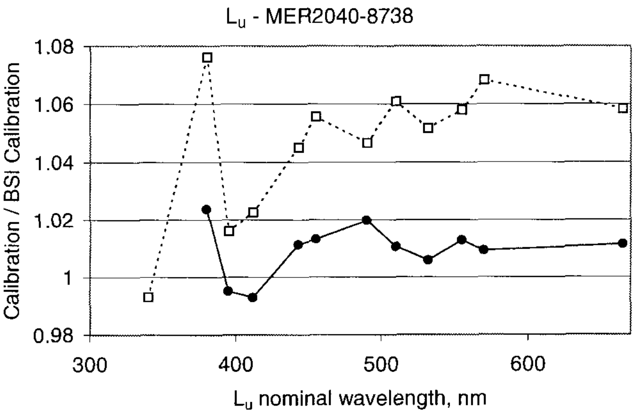

Figure 3. A comparison of MER-2040 L_u calibrations by different laboratories: ratios of UCSB calibration on 18 May 1995 to BSI calibration on 2 June 1995 (filled circles), CHORS calibration on 2 Nov. 1995 to BSI calibration on 25 Nov. 1995 (open squares).

TABLE 1

Measured E_d Band Centers as Determined by UCSB and CHORS, Compared with the Nominal BSI Centers for MER-2040-8738

BSI nominal wavelength, nm	UCSB center— BSI nominal, nm	CHORS center— BSI center, nm
340	−1.7	−1.4
380	−3.1	−2.4
395	0.9	1.6
412	−0.6	0.0
443	0.2	0.8
455	−0.7	0.1
490	0.3	1.1
510	−1.0	−0.1
532	−0.3	0.0
555	0.3	0.0
570	−0.6	0.0
665	0.4	1.5

tion (table 1). Also, lamp energy in the UV is low, causing greater calibration error. Our participation in the NASA SeaWiFS Project SIRREX activities and the multiple calibrations of MER 8738/8739 at different laboratories leads to the conclusion that the overall interlab calibrations approach the minimum requirement set by the SeaWiFS protocols (Mueller and Austin 1995), which call for calibration reproducibility of better than 5%. However, the goal of absolute calibration within ±1% has not been attained. Details of the in-water instrument calibration efforts can be found in Mueller at al. (1994).

Reasonable agreement between BSI calibrations and those of independent laboratories and the fact that more calibrations were from BSI justified using the BSI calibrations exclusively for determining the calibration time series for processing CalCOFI data.

The experimental immersion coefficients for E_d were provided by CHORS (Mueller 1995). The immersion coefficients for the L_u window were based on the window material refractive index and were changed after cruise CAL9308, when the original window composed of Schott glass UBK7 cracked because of mishandling and was replaced with a quartz glass window, which has been used on all subsequent cruises.

The radiometric calibration coefficients for each channel of each cruise were found as linear interpolations to the middle date of each cruise by using all calibrations performed at BSI since the instrument was manufactured. Even for channels that are stable over time, this procedure of interpolating the time series is a superior approach to using the most recent calibration, since each calibration has analytical error of several percent, and some of this is compensated by taking a longer-term statistical fit to the data. For channels with significant trends, a time-series fit of the data is essential.

An example of the scatter of individual calibration results and the resulting linear interpolation used in the processing of the MER data is shown in figure 4. The 95% confidence limits and the trend regression in figure 4 illustrate that individual calibration points can deviate outside the significance bounds of the trend. These are probably caused by NIST standard lamp transfers, calibration lamp degradation, and technical aspects of executing each calibration (Mueller et al. 1994). Several channels show significant trends, most notably the L_u (555 nm) channel example shown in figure 4, but also the 340 nm channel. Because the E_d (340 nm) channel filter/detector assembly was replaced in June 1995, a dual linear interpolation was used for this channel.

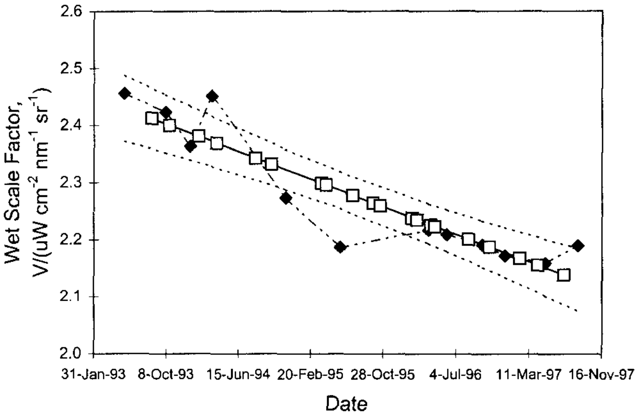

Figure 4. Calibration time series of the MER-2040 L_u (555 nm). Filled symbols are the actual calibrations performed at BSI. The straight line with open symbols is the interpolated wet-scale factor plotted against the middle date of a CalCOFI cruise. Dashed lines are ±95% confidence limits. Similar interpolations are used for all the E_d and L_u channels.

Profiling Procedure

The MER-2040 unit and associated underwater instruments were deployed from the ship's stern A-frame on each station, in accordance with SeaWiFS bio-optical protocols (Mueller and Austin 1995). When skies were clear, partly cloudy, or thinly overcast, the ship was typically oriented with its stern toward the sun to minimize the ship's shadow. This was not always possible because of winds or sea state, so some casts have significant contamination from ship shadow.

The instrumentation was held near the surface for 5–10 minutes before starting the downcast to allow for temperature equilibration and to prime the pump for the Sea-Bird conductivity and temperature system. Winch speed during the cast was kept between 20 and 30 m per minute for most profiles, and the nominal sampling speed of the MER was approximately 2–4 Hz. This achieved a typical sampling density of more than four samples per meter. The MER unit was generally deployed immediately before or immediately after the CalCOFI water bottle cast to ensure minimal offset in time/space for the optics and the pigment data set.

Immediately following each cast, a dark scan of the MER radiometer was run by attaching opaque PVC caps on the radiometer heads and recording the data for several minutes. Dark scan records were evaluated, and the median dark scan for each channel provided the basis for setting lower radiometric thresholds (ten times the dark voltage) for data processing (see below). Dark scans done at the end of profiles differ from dark scans done at BSI during routine calibrations by less than 5% for most channels, but by 10%–20% for several channels. Such differences are negligible for the near-surface data presented here because our exclusion threshold is ten times the median dark voltage for a cruise.

Processing of MER Vertical Profiles

The CalCOFI bio-optical profiles were processed with a modified version of the Bermuda Bio-Optics Project

(BBOP) data-processing system (Siegel et al. 1995). The BBOP system was found most suitable because of its modularity and the ease of adding new filters. The BBOP filters operate on the so-called LCD file format, which is a self-contained ASCII file with the pertinent header, calibration, and processing history included. The implementation of the BBOP processing scheme was adapted and modified in order to increase processing speed, reduce disk access, remove unnecessary complexity, and add new filters. The large set of UNIX shell scripts was completely replaced with a single Perl script, and the proliferating "list" files were replaced with two control files. Modifications were done to the suite of C and C++ programs with the purpose of streamlining the whole process. Added filters include adjustment of the depth of the different variables according to the position of the particular sensor in relation to the depth sensor, and thresholding low radiance or irradiance values in relation to the dark values. Some filters were made more versatile; for example, the binning filter can now produce vertical bins in any float interval starting from 10 cm instead of integer meters. Vertical bins smaller than 1 m were essential for processing profiles with very high attenuation or for very shallow water.

The new processing scheme resulted in almost ten times faster execution speed compared to the original implementation. The speed increase was mostly due to reduced disk access. Because of the increased speed it was found more convenient to do a full reprocessing starting with the raw data whenever a new calibration was implemented, rather than to modify the existing LCD files. All source files of the modified BBOP code as well as the executables for IRIX 5.3 are available for downloading from *ftp://spg.ucsd.edu/pub/bbop*.

In order to ensure compatible depth values with the Marine Life Research Group's rosette-CTD system, we calibrated the MER depth sensor by using linear regression on the depths of a large number of distinct features (e.g., fluorescence maximum, transmission minimum, or bottom of the mixed layer) in profiles measured with both systems.

A typical sequence of operations performed with a set of data files collected with the MER-2040/2041 system consisted of three steps: preprocessing, BBOP processing, and postprocessing.

Preprocessing. Preliminary processing either during a cruise or immediately after the cruise creates hard-copy plots of the vertical profiles. The at-sea procedure is run on a PC under DOS/Windows and includes transforming the MER binary file into a preliminary LCD file, breaking the LCD file into separate downcast and upcast files, and making hard-copy plots of the selected variables. The plots are used for visual quality inspection of the profiles, selecting the depth intervals for the surface extrapolation, and defining the depth of the surface mixed layer. Each profile is given a quality ranking.

Control files listing the MER files to be processed, the filters to be run, and the parameters needed are created either by exporting the necessary fields from a database, or manually with an editor. The auxiliary information includes the corresponding calibration and dark files, dates, coordinates, vertical binning interval, depth range for surface extrapolation, mixed-layer depth range, interval for calculating K, and a quality flag. Calibration files are created for each cruise and MER instrument, and are based on the middle date of the cruise and the calibration history (see earlier section Instrument Characterization and Radiometric Calibrations). The calibration files are updated when new calibration data become available. Time series of the dark scans are created for each cruise. The median dark voltages for each channel for each cruise are used to flag data smaller than ten times the corresponding dark voltage.

BBOP processing. The sequence of the different filters applied to the MER vertical profiles is given in table 2.

Postprocessing and quality control. The MER data from depths corresponding to water samples and the surface extrapolation (0^-) are imported into a relational database (in Microsoft Access). In the database the MER data are linked to results from discrete water samples (e.g., absorption spectra of particulate, detrital, and soluble material) and the hydrographic data from the CalCOFI IEH files.

When measured by an instrument of a finite size, $L_u(\lambda)$ is affected by the instrument's own shadow (Gordon and Ding 1992). The self-shading correction scheme recommended by Mueller and Austin (1995) has been implemented in the analysis since 1997 (see Kahru and

TABLE 2
Summary of the BBOP Processing of Bio-Optical Vertical Profiles

Number	Filter	Description
1	mer2lcdn	Reads binary data file and creates LCD file.
2	insertcastid	Inserts cruise and cast information.
3	mkbin	Bins the data to a regularly spaced vertical grid (typically 1.0 m), partitions the file into down- and upcasts.
4	mkfutil	Deletes unnecessary variables.
5	mkh2o	Calculates salinity and sigma-t.
6	mkshift	Shifts the E_d samples up the number of bins closest to 75 cm.
7	bbopdeflag	Deletes bins with no samples.
8	thresh	Flags values below threshold.
9	mkscalc	Extrapolates some variables to the surface (0^- depth).
10	mkkc	Calculates the diffuse attenuation coefficients K for E_d.
11	ksurf	Extracts the surface diffuse attenuation coefficient K from results of mkscalc and inserts into the surface (0^-) record.

Mitchell, in press, for details). In the analysis reported here the self-shading was ignored. The median error resulting in underestimating L_u for the SeaWiFS bands (excluding 665 nm) of the CalCOFI data was 1%–2%; the maximum error was about 20% for high-pigment water.

For calculating the remote sensing reflectance just above the sea surface $R_{rs}(0^+,\lambda)$, we used the equation

$$R_{rs}(0^+,\lambda) = 0.54\ L_u(0^-,\lambda) / [1.04\ E_d(0^-,\lambda)] \qquad (1)$$

Here $L_u(0^-,\lambda)$ is the upwelling radiance extrapolated to just below the sea surface; $E_d(0^-,\lambda)$ is the downwelling irradiance extrapolated to just below the sea surface; and the coefficients 0.54 and 1.04 are the transfer coefficients of the air-sea interface for, respectively, L_u and E_d (Austin 1974). Calculation of $R_{rs}(0^+,\lambda)$ from the surface irradiance measured by the MER-2041 deck unit $E_s(\lambda)$ was also evaluated:

$$R_{rs}(0^+,\lambda) = 0.54\ L_u(0^-,\lambda) / E_s(\lambda) \qquad (2)$$

Although both equations 1 and 2 gave similar results, the variability of equation 2 was higher, and the number of stations where equation 2 could be applied was smaller (because of missing MER-2041 data on some cruises). The greater variance when equation 2 was applied is attributed to surface phenomena such as ship shadowing and wave focusing, which affect both E_d and L_u on the MER-2040, but not E_s on the MER-2041. Time/space offsets when shadows from clouds or the ship's superstructure affect the above-water and in-water sensors differently can also contribute to errors in equation 2. Therefore, we used equation 1 for the analysis reported here.

We estimated the surface-layer diffuse attenuation coefficients $K_d(\lambda)$ from the depth range that was used to derive the $L_u(0^-,\lambda)$ and $E_d(0^-,\lambda)$ surface extrapolations. For comparison to previous $K_d(490)$ algorithms and the relationship between $K_d(\lambda)$ and $K_d(490)$, we transformed the remote sensing reflectance to the normalized water-leaving radiance as $L_{WN}(\lambda) = R_{rs}(0^+,\lambda)^*\ F_0(\lambda)$, where $F_0(\lambda)$ is the mean extraterrestrial irradiance.

The entire MER data set of $E_d(z,\lambda)$, $L_u(z,\lambda)$, $E_s(\lambda)$ is reprocessed as updated calibration files become available or modifications are found necessary. Current data sets are available from NASA's SeaWiFS project SeaBASS archive *(http://seabass.gsfc.nasa.gov)*.

Water Sampling

The general hydrographic data, including the fluorometric pigment concentrations for the CalCOFI cruises, were collected by the Marine Life Research Group of the Scripps Institution of Oceanography (SIO) and were obtained from the CalCOFI data archives *(http://nemo.ucsd.edu)*. Water sampling during CalCOFI cruises was done with a CTD-rosette system separate from the MER profiler. The time delay between those two casts was sometimes more than 1 hr. The resulting errors introduced into the matching of MER data to the water samples due to the spatiotemporal variability may be significant, especially for coastal stations.

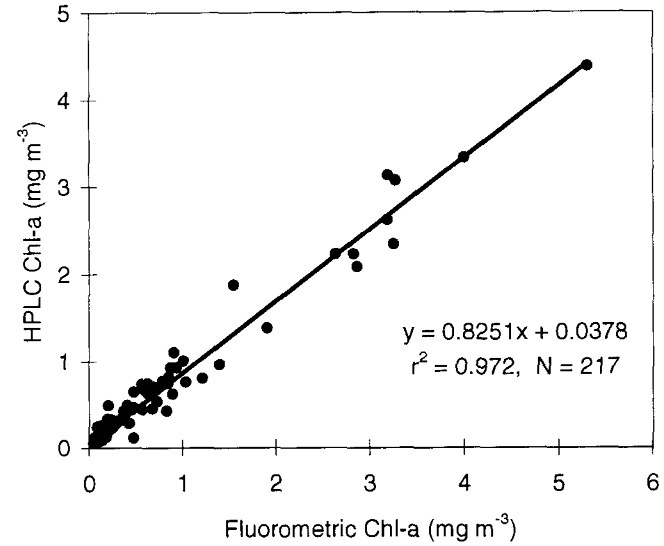

Figure 5. Correlation between fluorometric estimate of chl a and the HPLC estimate. The HPLC estimate is based on the sum of chlorophyll a, chlorophyllide a, allomerized chlorophyll a, divinyl chlorophyll a, and chlorophyll a'. Data presented here are for the upper mixed layer only.

Pigments

The chl a and phaeopigment concentrations used here were determined with the fluorometric method (Holm-Hansen et al. 1965; Venrick and Hayward 1984). High-performance liquid chromatography (HPLC) measurements of chl a with the method of Goericke and Repeta (1993) showed a consistent relationship with the fluorometric results for surface chl a in the range 0.05–5 mg/m^3 (fig. 5). However, the HPLC chl a estimate is about 82% of the fluorometric chl a estimate. This difference is in agreement with the findings of Bricaud et al. (1995). HPLC estimates for chl a are available for approximately half of the optics stations, so we used the fluorometric data for algorithm development.

Statistical Methods

Depending on the variance of a data set, either the reduced major axis (RMA) type II linear regression model (Ricker 1973; Laws and Archie 1981) or the "robust" least absolute deviation linear regression (Press et al. 1990) was used to compute the linear slope and intercept between variables. The "robust" method is preferable in the case of outliers because of various measurement errors. Outliers were usually determined as the points outside two standard deviations of the initial "robust" regression. The remaining points were then run through either the RMA or the "robust" linear regression models. The root mean square (RMS) error formula used was the same as that of O'Reilly et al. (in press).

RESULTS

The CalCOFI Data Set

A total of thirteen CalCOFI cruises made from 1993 to 1996 are summarized in table 3. More than 300 coincident MER profiles and surface pigment measurements were made. Data from a massive red tide event in the spring of 1995 is reported elsewhere (Kahru and Mitchell, in press).

The frequency distribution of chl a in the CalCOFI data set (fig. 6) deviates from an ideal lognormal distribution that has been proposed before (e.g., Campbell and O'Reilly 1988) and may be better approximated by a sum of two or more lognormal distributions corresponding to the different regimes (oligotrophic, coastal).

Surface Irradiance vs. In-Water Irradiance

The relationship between $E_d(0^-,\lambda)$ determined by extrapolation of the MER-2040 underwater profile to just below the surface, and $E_s(\lambda)$ measured by the MER deck unit is shown in figure 7. The relationships at 412–555 nm have a curvature (demonstrated by the slightly better fits of the power function compared to the linear regression). This may be due to the effect of decreasing transmittance of the air-water interface at large solar zenith angle.

Except for 665 nm, the surface loss of $E_d(z, \lambda)$ through the air-sea interface as estimated by the slope of the linear fit is higher than the often quoted 4% value (Austin 1974). Our data have been collected in diverse conditions including early morning, late evening, cloudy skies, and rough seas. All of these factors may contribute to the elevated air-sea loss compared to the 4% for ideal conditions.

The slope coefficients range from 1.07 (at 555 nm) to 1.10 (at 412 and 443 nm). As expected, $E_d(0^-, 665$ nm) data are more noisy as a result of surface extrapolation errors (due to strong attenuation of light at this wavelength) and possible chl a fluorescence. The slope of less than 1.0 may be partially due to natural fluorescence source terms in the underwater data.

TABLE 3
Summary of the CalCOFI Bio-Optical Data Set

Cruise	Starting date	Ending date	Number of MER stations
CAL9308	11 Aug. 93	26 Aug. 93	28
CAL9310	11 Oct. 93	25 Oct. 93	17
CAL9401	17 Jan. 94	8 Feb. 94	30
CAL9403	22 Mar. 94	7 Apr. 94	32
CAL9408	5 Aug. 94	21 Aug. 94	21
CAL9410	30 Sept. 94	16 Oct. 94	25
CAL9504	6 Apr. 95	22 Apr. 95	24
CAL9507	6 July 95	22 July 95	28
CAL9510	12 Oct. 95	26 Oct. 95	29
CAL9602	29 Jan. 96	10 Feb. 96	22
CAL9604	15 Apr. 96	30 Apr. 96	16
CAL9608	7 Aug. 96	25 Aug. 96	20
CAL9610	10 Oct. 96	1 Nov. 96	30
CAL9702	30 Jan. 97	2 Feb. 97	30
CAL9704	2 Apr. 97	17 Apr. 97	22
Total: 17 cruises			419 stations

Remote Sensing Reflectance vs. Chl

For a large dynamic range in surface pigments (chl a from 0.05 to 22.3 mg m^{-3}, [chl a + phaeo] from 0.06 to 27.2 mg m^{-3}) the CalCOFI data exhibit a relatively consistent pigment-reflectance relationship for the SeaWiFS bands (fig. 8). Some of the 304 measurements used for figure 8 were excluded from the final regressions if outside the 2 standard deviation range of the first robust least-deviation regression. The number of points outside the 2 standard deviation limits of the regression ranged from 7 at 665 nm to 19 at 510 nm. Compared to other bands, $R_{rs}(555)$ had the fewest excluded points, because noisier data at that wavelength resulted in a larger tolerance.

Chl Algorithms

When the $R_{rs}(443)/R_{rs}(555)$ and $R_{rs}(490)/R_{rs}(555)$ ratios were plotted against chl a, 11 of the more than 300 stations qualified as outliers because of various anomalies, and are not included in the analyzed data set. Some of the anomalies were explained by features like a shallow chl a maximum at about 10 m that influenced the R_{rs} but was not represented in the surface chl a sample, high soluble or sediment absorption at some coastal

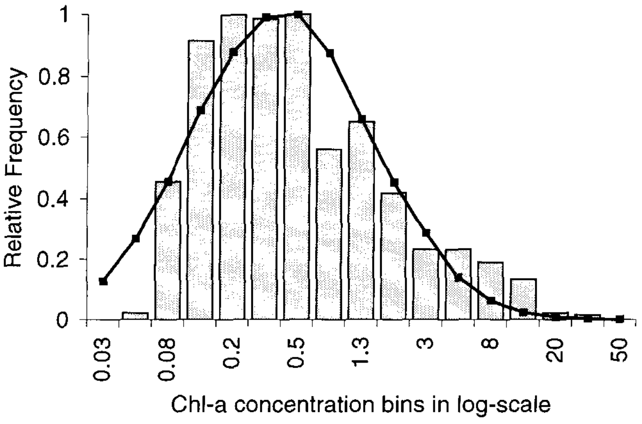

Figure 6. Relative frequency distribution (bars) of fluorometric chl a concentration for the upper 15 m in the CalCOFI data set. In total, 1,910 chl a measurements (all the CalCOFI cruises between 1993 and 1996) have been used, including those for stations with no bio-optical measurements. The mean is 1.07; the median is 0.31 mg m^{-3}. A theoretical lognormal distribution with the same mean and standard deviation is shown for comparison (continuous line).

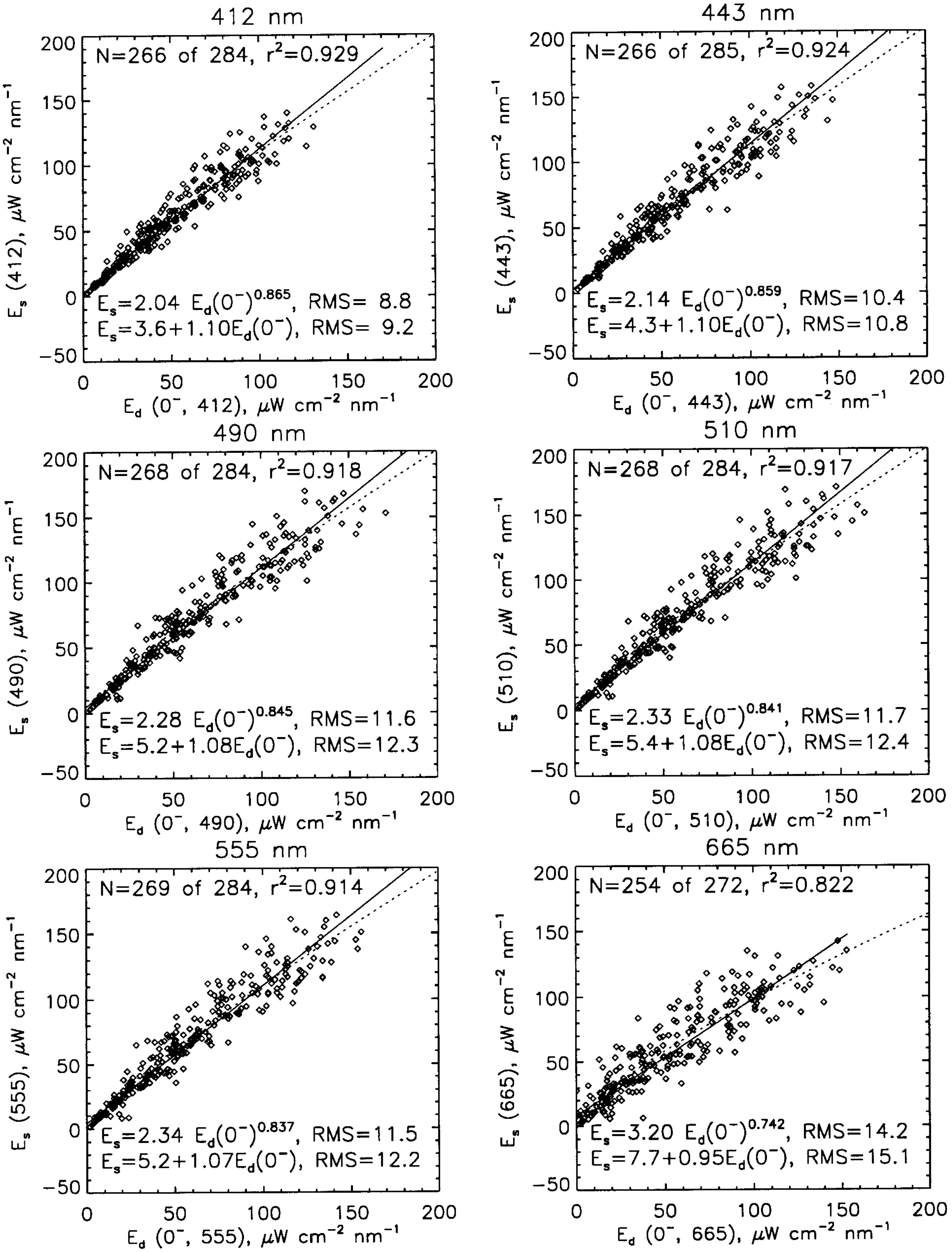

Figure 7. Surface irradiance $E_s(\lambda)$ as a function of the downwelling irradiance extrapolated to just below the surface $E_d(0^-,\lambda)$ from measurements of the underwater MER at the six SeaWiFS wavelengths. All values greater than the corresponding mean extraterrestrial irradiance $F_0(\lambda)$ (caused by wave focusing) were considered errors and were excluded. The remaining N_T points were fit to a linear regression, and all points deviating more than two standard deviations from the regression line (attributed to temporal/spatial offsets of cloud or ship shadow) were excluded. The remaining N points were fit with both reduced major axis linear regression and a power function. The respective sample size ("N of N_T"), coefficients, and root mean square errors are shown.

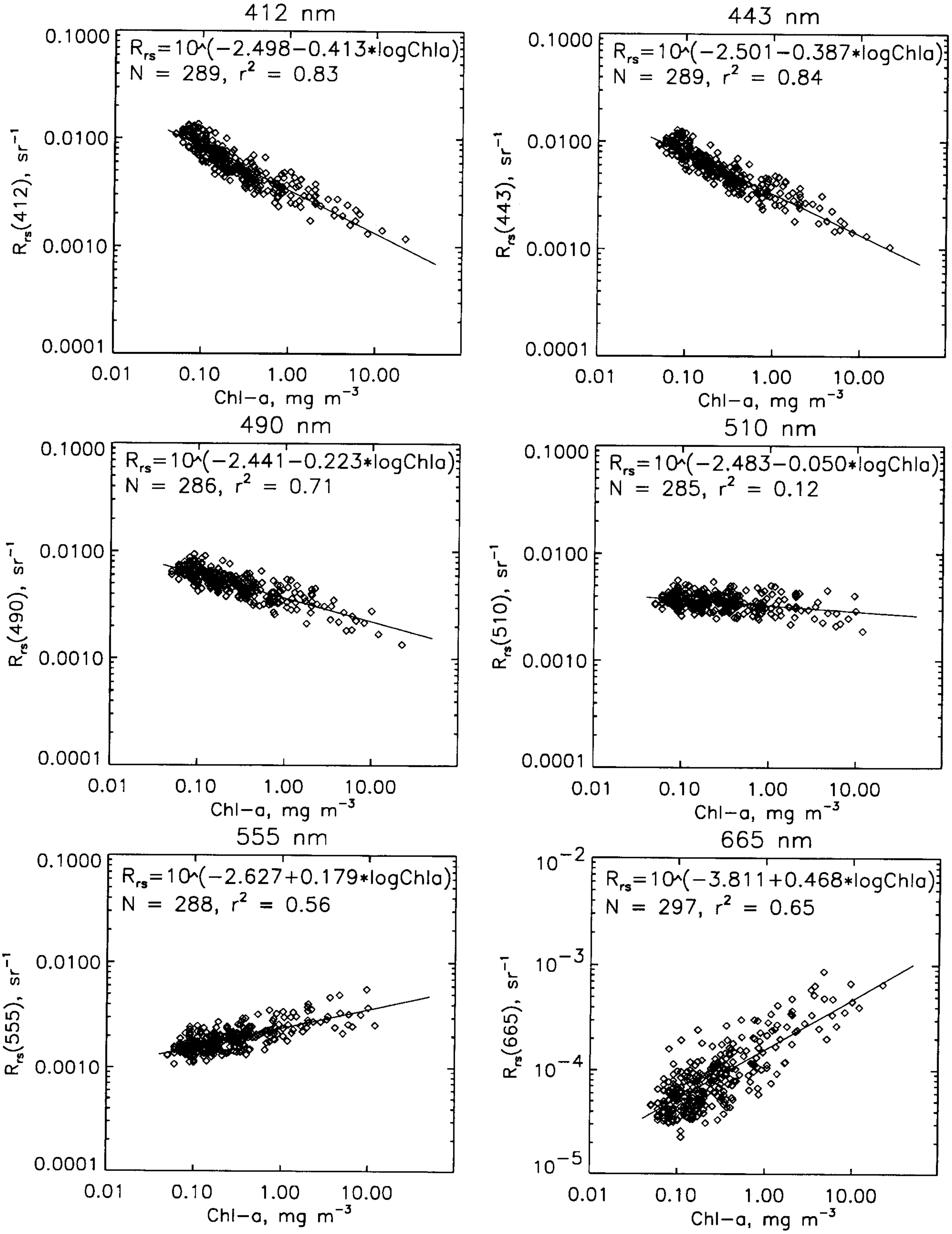

Figure 8. Remote sensing reflectance at the six SeaWiFS wavelengths as a function of chl a concentration. The points deviating more than 2 s.d. from an initial regression were excluded from the plots and the final statistical fit. Because the total data set consists of 304 observations, the number excluded can be determined on the basis of *N* reported for each wavelength.

stations, or high pigment packaging for some diatom blooms. Others had no obvious explanations. Of the 304 stations included in the CalCOFI data set, some surface extrapolated radiometric bands are still suspect, especially at 665 nm. Because of high absorption by water at 665 nm, the depth range that could be used for surface extrapolation was restricted to shallower depths that were more contaminated by ship shadow and other near-surface effects.

The consistency of the data set including all 304 data points is evident by the high linear correlation between log-transformed chl a concentration and reflectance ratios (fig. 9). In the high chl a range the relationship has a significant curvature, especially in the $R_{rs}(443)/R_{rs}(555)$ plot, which is not well described by the linear regression model. The relation between chl a and $R_{rs}(490)/R_{rs}(555)$ is closer to linear in the log-log space, has less variability, and in general has proven to be one of the most useful ratios in chl a prediction. This is attributed to three main causes: detrital and soluble absorption are lower at 490 nm compared to 443 nm, and pigment package effects are less at 490 nm because of weaker total absorption by the phytoplankton.

Linear models of both the log-log-transformed chl a or chl a + phaeo vs. $R_{rs}(490)/R_{rs}(555)$ (table 4, equations 3a, b) achieve r^2 of about 0.955 (fig. 10, upper panel). Although the linear fit in log-log space for the entire data set is practically unbiased (intercept of 0.0 and slope of 1.0), there is systematic underestimation at higher chl a. A quadratic fit was evaluated but did not bend toward the pure water value at low chl a (data not presented). A cubic polynomial fit has more parameters to force it to bend toward the pure water value at low chl a. But because of the absence of chl a concentrations less than 0.05 mg m^{-3}, the downward bend in the CalCOFI data was insignificant (fig. 9), and the least squares fit of a cubic polynomial (table 4, equations 4a, b) curved in the opposite direction.

In order to force the model into the correct direction at low chl a, we added another empirical coefficient to the cubic polynomial (table 4, equations 5a–d), following the Ocean Chlorophyll 2 (OC2) model (O'Reilly et al., in press). The resulting model ("CalCOFI Cubic A4"; fig. 10) improves the estimates at both high and low chl a ranges and reduces the overall RMS error. The sigmoid curvature of the OC2 model of O'Reilly et al. tuned to the global data set seemed to be too strong for the CalCOFI data set and resulted in higher RMS error, 0.129 of the OC2 model vs. 0.101 of the CalCOFI Cubic A4 model. The better fit to the CalCOFI data set of the Cubic A4 model is evident, especially in the middle chl a range of 0.2–3.0 mg m^{-3} (fig. 9, lower panel). Although the exact coefficients of the Cubic A4 model may undergo small changes as more data become available in the high and low chl a domains, models of the OC2 and CalCOFI Cubic A4 type are preferable to other empirical and semianalytical models that have been tested.

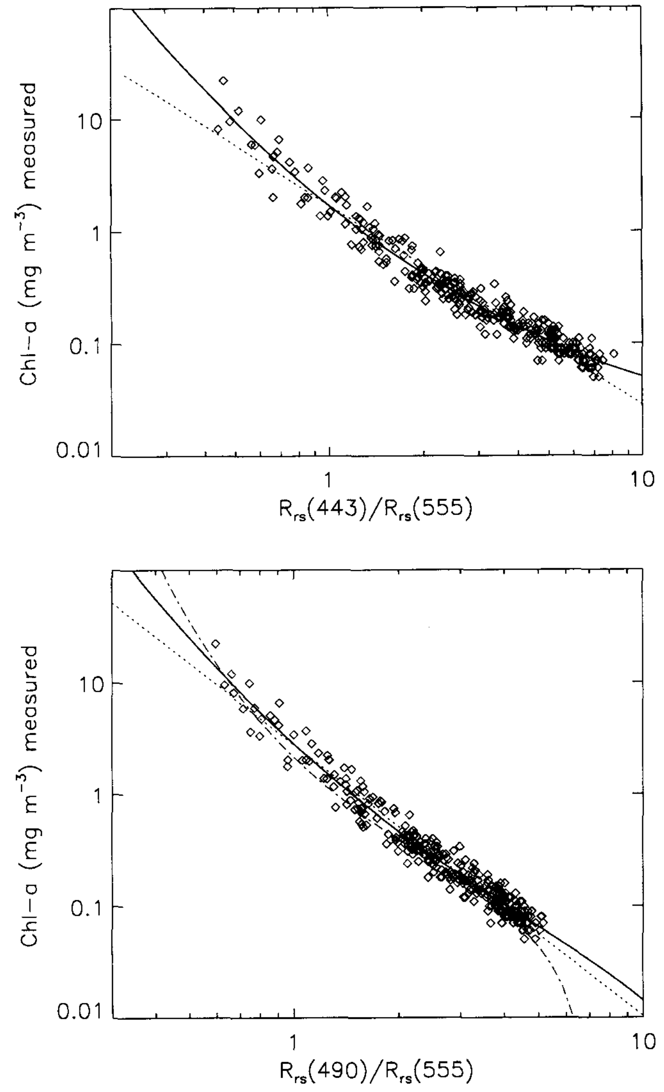

Figure 9. Near-surface chl a concentration as a function of $R_{rs}(443)/R_{rs}(555)$ and $R_{rs}(490)/R_{rs}(555)$ with reduced major axis linear regression (dotted straight line); CalCOFI Cubic A4 model (bold curved line, equations 5a and 5c, respectively, in table 4); and the OC2 model (dash-dot line) proposed by O'Reilly et al. (in press). The regression results are given in table 4.

Even with the coefficient of determination between the measured and predicted chl a above 0.95, there is still substantial variability around the regression line; this variability is even more accentuated in the linear scale than in the logarithmic scale. If part of the variability is due to accessory pigments, colored dissolved organic material (CDOM), or other spectrally dependent phenomena, then appropriate additional bands could explain some of the variability and reduce the RMS error of the prediction. To test this hypothesis, we evaluated multiple linear regressions between two log-transformed

TABLE 4
Evaluation of Algorithms for Estimating chl a and Pigment Concentrations (chl a + phaeo) from Remote Sensing Reflectance Ratios

Model	a intercept	b slope	r^2	RMS error	Equation number
CalCOFI 2-band linear model (*CalCOFI 2-Band*)					
chl a = 10.^{0.444 − 2.431 log[R_{rs}(490)/R_{rs}(555)]}	0.000	1.000	0.955	0.108	3a
chl a + phaeo = 10.^{0.557 − 2.440 log[R_{rs}(490)/R_{rs}(555)]}	0.000	1.000	0.956	0.107	3b
CalCOFI 2-band cubic model (*CalCOFI Cubic*)					
chl a = 10.^(0.450 − 2.860 R + 0.996 R^2 − 0.367 R^3) where R = log[R_{rs}(490)/R_{rs}(555)]	−0.012	0.980	0.960	0.101	4a
chl a + phaeo = 10.^(0.564 − 2.753 R + 0.571 R^2 − 0.002 R^3) where R = log[R_{rs}(490)/R_{rs}(555)]	−0.010	0.980	0.959	0.102	4b
CalCOFI Cubic A4					
chl a = 10.^(0.239 − 2.224 R + 0.888 R^2 − 0.053 R^3) − 0.02 where R = log[R_{rs}(443)/R_{rs}(555)]	−0.012	0.978	0.959	0.103	5a
chl a + phaeo = 10.^(0.357 − 2.185 R + 0.665 R^2 − 0.1018 R^3) − 0.02 where R = log[R_{rs}(443)/R_{rs}(555)]	−0.009	0.979	0.959	0.102	5b
chl a = 10.^(0.455 − 2.842 R + 1.000 R^2 − 0.080 R^3) − 0.02 where R = log[R_{rs}(490)/R_{rs}(555)]	−0.011	0.978	0.960	0.101	5c†
chl a + phaeo = 10.^(0.568 − 2.740 R + 0.571 R^2 − 0.2411 R^3) − 0.02 where R = log[R_{rs}(490)/R_{rs}(555)]	−0.009	0.978	0.959	0.102	5d†
CalCOFI 3-band model					
chl a = exp(1.025 − 1.622 ln[R_{rs}(490)/R_{rs}(555)] − 1.238* ln[R_{rs}(510)/R_{rs}(555)]	−0.013	0.978	0.956	0.106	6a
chl a + phaeo = exp(1.265 − 1.937 ln[R_{rs}(490)/R_{rs}(555)] − 0.737* ln[R_{rs}(510)/R_{rs}(555)]	−0.010	0.978	0.956	0.106	6b
CalCOFI 4-band model					
chl a = exp(0.753 − 2.583 ln[R_{rs}(443)/R_{rs}(555)] + 1.389* ln(R_{rs}(412)/R_{rs}(510)]	−0.013	0.977	0.956	0.106	7a
chl a + phaeo = exp(0.995 − 2.528 ln[R_{rs}(443)/R_{rs}(555)] + 1.285* ln[R_{rs}(412)/R_{rs}(510)]	−0.010	0.978	0.957	0.105	7b
OC2 (O'Reilly et al. 1998)	−0.085	0.976	0.955	0.129	
OC4 (O'Reilly et al. 1998)	−0.045	0.991	0.957	0.112	

†Preferred models for estimating chl a and chl a + phaeo for the CalCOFI data set.

R_{rs} ratios and chl a. We ran all possible combinations of the two R_{rs} ratio combinations, and selected the combinations with highest r^2 and lowest RMS error. The best combination using three bands is given by equations 6a, b; the best 4-band combination is given by equations 7a, b in table 4.

In essence, very little (if any) additional information was gained by including other band ratios besides $R_{rs}(490)/R_{rs}(555)$ to estimate chl a or [chl a + phaeo]. Although the 3- and 4-band combinations resulted in a slightly lower RMS error compared to the single linear $R_{rs}(490)/R_{rs}(555)$ ratio model, they were inferior to the quadratic and cubic fits of the $R_{rs}(490)/R_{rs}(555)$ ratio. Using more than one band ratio may be advantageous in cases of high variability caused by instrumental and environmental noise or for quality control. But it appears that the 3- and 4-band models tend to be specific to the particular data set and not robustly applicable to other data sets. As a result, the best combinations of bands changed when more data points were added to the CalCOFI data set.

For actual satellite applications, algorithms using more bands will be complicated by the need to know the on-orbit calibration time series of all the bands used. Clearly, simple 2-band algorithms will pose a simpler challenge for maintaining robust algorithms during a satellite's mission life. However, the sensitivity of multiband multiple regression models may be used for screening the data set for possible inconsistencies.

In conclusion, it appears that the residual noise is due predominantly to methodological errors and environmental variability and not to other optically significant components that should covary with band ratios other than $R_{rs}(490)/R_{rs}(555)$ (e.g., accessory pigments, CDOM). Bio-optical measurements at sea have significant variability due to illumination conditions, ship shadow, instrument tilt, and other methodological effects that cannot be completely eliminated and contribute to the residual RMS error.

With the coefficient of determination (r^2) greater than 0.96 between the log-transformed variables of a simple R_{rs} ratio model for chl a, it is unlikely that more advanced bio-optical models can produce a significant improvement. However, advanced models may extend the chl a range or provide additional variables besides chl a; e.g., CDOM, $a_{ph}(\lambda)$, coccoliths, backscattering coefficient, suspended sediments (Doerffer and Fischer 1994; Garver and Siegel 1997).

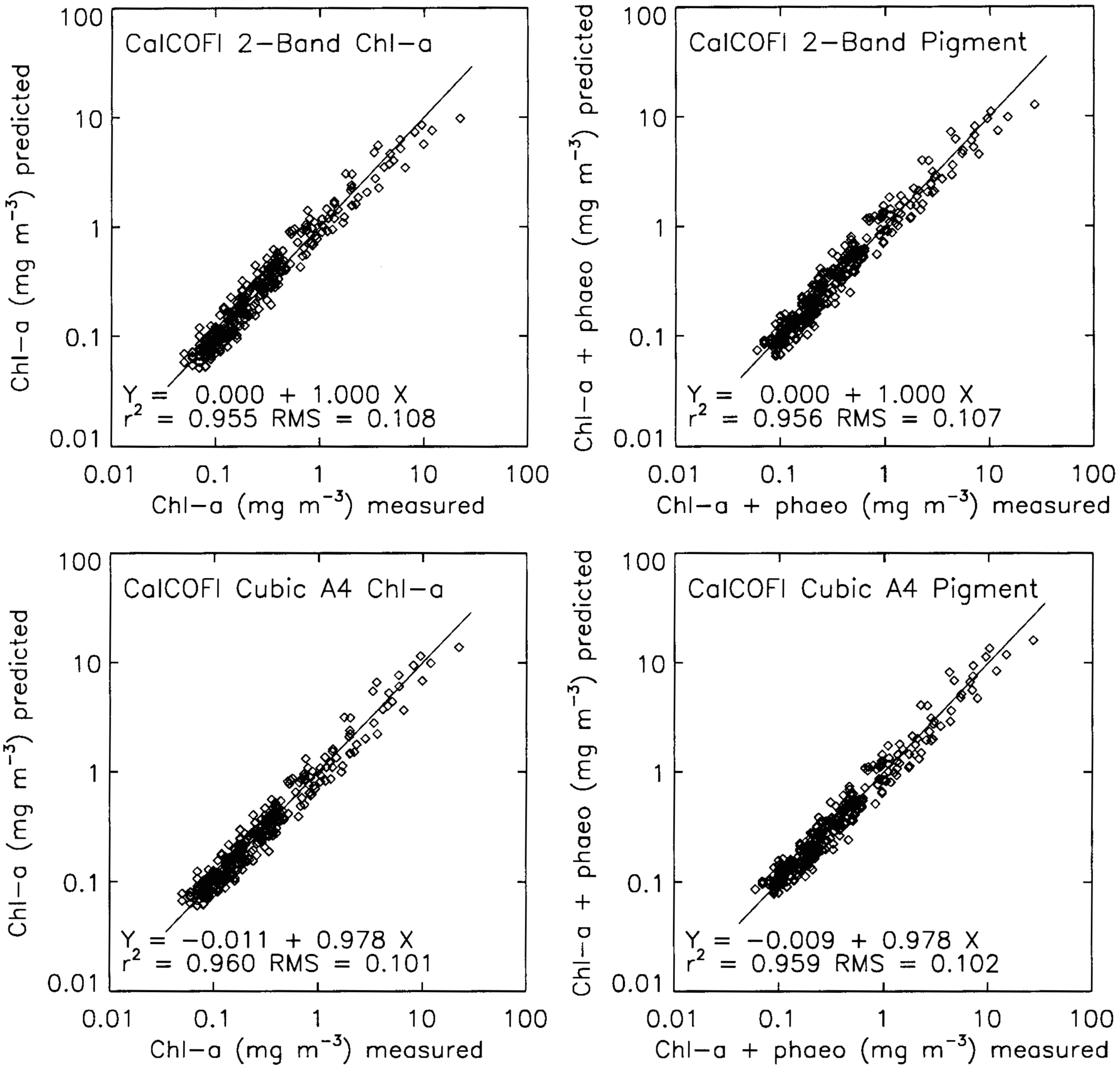

Figure 10. Results of the CalCOFI 2-band linear algorithm (top, equations 3a, b in table 4) and the CalCOFI Cubic A4 algorithm (bottom, equations 5a–d in table 4). Both algorithms use the ratio $R_{rs}(490)/R_{rs}(555)$. The one-to-one lines are shown.

$K_d(490)$ Algorithm

Since the work of Jerlov (1976), it has been assumed that the diffuse attenuation coefficient for downwelling irradiance $K_d(\lambda)$ at any wavelength can be expressed as a linear combination of K_d at a reference wavelength (e.g., 490 nm). At low K_d values this is a good approximation. Austin and Petzold (1984) have tabulated the slopes $M(\lambda)$ from the equation

$$[K_d(\lambda) - K_w(\lambda)] = M(\lambda)\ [K_d(490) - K_w(490)]. \quad (8)$$

They used values of K_w that were very close to those of Smith and Baker (1981) or Morel and Prieur (1977).

New values of pure water absorption have recently been determined with an integrating cavity absorption meter (Pope and Fry 1997), and there are some concerns within the ocean optics community that the values of K_w or a_w used in previous literature may be too high, especially between 400 and 500 nm. For the analysis presented here, we used values of K_w from Morel (1988) for data between 400 and 700 nm and from Smith and Baker (1981) for wavelengths below 400 nm. In figure 11 a comparison between the CalCOFI data set and the results of Austin and Petzold (1984) for the coefficient M indicate good agreement between the CalCOFI data set and theirs, when similar methods were used.

The relation between chl a and $K_d(\lambda) - K_w(\lambda)$ has been studied by many investigators (e.g., Baker and Smith 1982; Morel 1988; Mitchell 1992). Figure 12 indicates that this relation is not well described by a linear fit in the log-log space for SeaWiFS wavelengths 412, 443, and 455 nm. Baker and Smith (1982) fit their data with a nonlinear function in log space, whereas Morel (1988) used a power law model (equivalent to linear in the log-log space). Some of the curvature observed between 400 and 460 nm at low chl a, also observable in the Baker and Smith fit, could be caused by subtraction of K_w that is larger than the true value of K_w. The K vs. chl a and $K(\lambda)$ vs. $K_d(490)$ relationships should be reevaluated with modern estimates of the absorption and K values for pure water (Pope and Fry 1997).

A simple band-ratio approach was used to estimate $K_d(490)$ from the normalized water-leaving radiance data following the original approach for CZCS (Austin and Petzold 1981). In spite of the high variability at low $K_d(490)$ (fig. 13), the equation that we obtained by using the "robust" least absolute deviation linear regression

$$K_d(490) = 0.022 + 10\hat{}[-0.964 - 1.301 * \log (L_{WN}(443)/L_{WN}(555))] \quad (9)$$

is in excellent agreement with the recent estimate of Mueller and Trees (1996). Mueller and Trees concluded that the data set they had compiled (including some CalCOFI data) led to a regression that was significantly different, in a statistical sense, from the regression used for CZCS. This may in part be attributed to the difference between the 550 nm band in CZCS and the 555 nm band used in this data set and in that of Mueller and Trees. The good agreement between Mueller and Trees (1996) and the results presented here indicates that the simple method we used to estimate surface layer K is consistent with the integral least-squares method of Mueller (1991).

The ratio of $L_{WN}(490)/L_{WN}(555)$ instead of $L_{WN}(443)/L_{WN}(555)$ gives a slightly higher r^2 and lower RMS error (fig. 13, lower panel) and proved more reliable for ocean color applications in cases of very high 443 nm absorption (e.g., in red tide or other blooms or when CDOM in coastal waters is very large). The equation using the $L_{wn}(490)/L_{wn}(555)$ ratio is

$$K_d(490) = 0.022 + 10\hat{}[-0.813 - 1.636 * \log (L_{WN}(490)/L_{WN}(555))]. \quad (10)$$

The improvement using the $L_{wn}(490)/L_{wn}(555)$ ratio compared to $L_{wn}(443)/L_{wn}(555)$ ratio is also found for empirical chl a algorithms (see previous section Chl Algorithms). NASA's global processing for chl a exploits the improved empirical regressions using $L_{wn}(490)/L_{wn}(555)$ but uses $L_{wn}(443)/L_{wn}(555)$ for $K_d(490)$. We believe that $L_{wn}(490)/L_{wn}(555)$ provides a sufficiently better empirical fit for $K_d(490)$ and that NASA should consider using it in global processing.

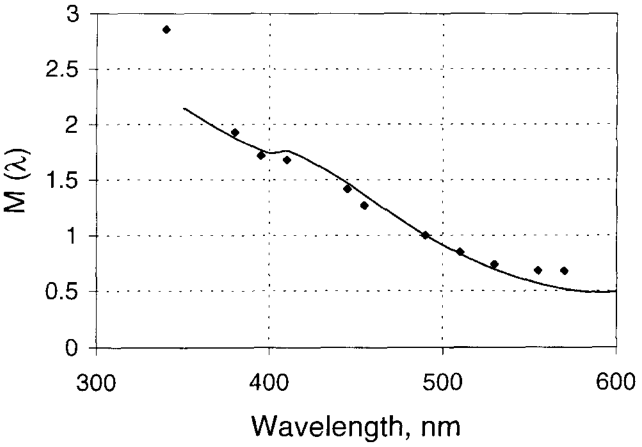

Figure 11. Slope $M(\lambda)$ for equation 8 from Austin and Petzold 1986 (continuous line) compared to CalCOFI data (filled symbols). Only $K_d(490)$ less than 0.1 m^{-1} were used to estimate $M(\lambda)$.

CONCLUSIONS

A set of more than 300 concurrent measurements of remote sensing reflectance, chl a, and diffuse attenuation coefficients has been analyzed. The CalCOFI data set comprises more than 30% of the total "global" data set that was assembled by the SeaWiFS Project for this effort (O'Reilly et al., in press). In general, the CalCOFI data set was consistent with the other global data and covered all but the lowest pigment range (chl a < 0.05 mg m^{-3}).

Evaluation of empirical algorithms and semianalytical models shows that simple empirical algorithms perform better than semianalytical models at this time for SeaWiFS standard products including chl a, chl a + phaeo, and $K_d(490)$. Relatively little, if any, improvement in estimation is attained by using more complex sets of multiband ratios for this type of empirical algorithm. Given the added complexity of accurate knowledge of the on-orbit calibration if multiple spectral bands are used, it seems advisable to use the $R_{rs}(490)/R_{rs}(555)$ ratio as a basis for global processing algorithms for chl a and chl a + phaeo. It may be advisable, as well, to consider this band ratio for the $K_d(490)$ algorithm, given the improvement that was found with the CalCOFI data set using $L_{WN}(490)/L_{WN}(555)$ compared to $L_{WN}(443)/L_{WN}(555)$. It is also important to recognize that previous $K_d(490)$ algorithms depend partly on assumptions about the value of K for pure water. Those assump-

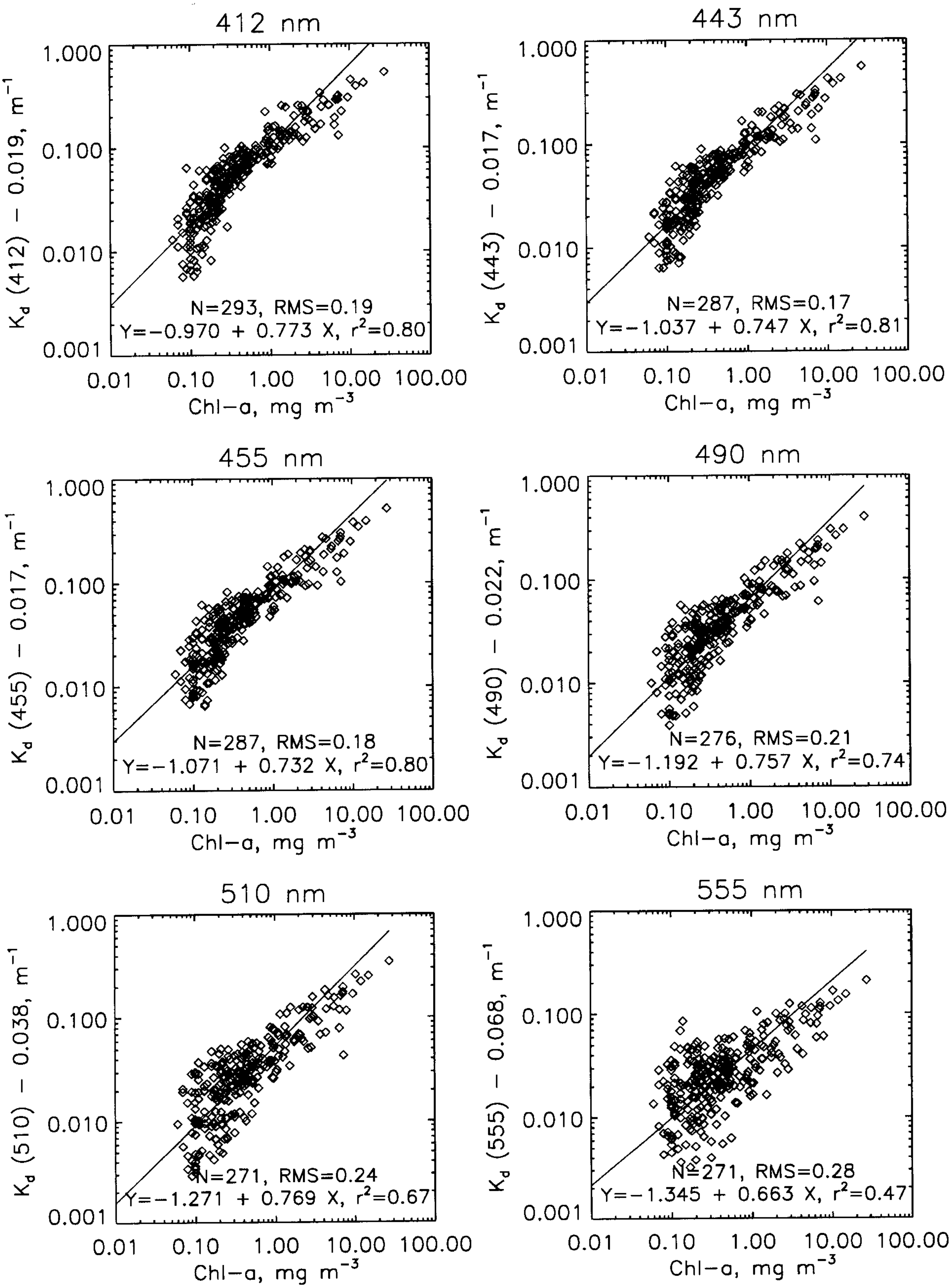

Figure 12. $K_d(\lambda)$ – $K_w(\lambda)$ as a function of chl a concentration. The $K_w(\lambda)$ values are from Morel 1988. The lines are reduced major axis linear regressions in the log-log space.

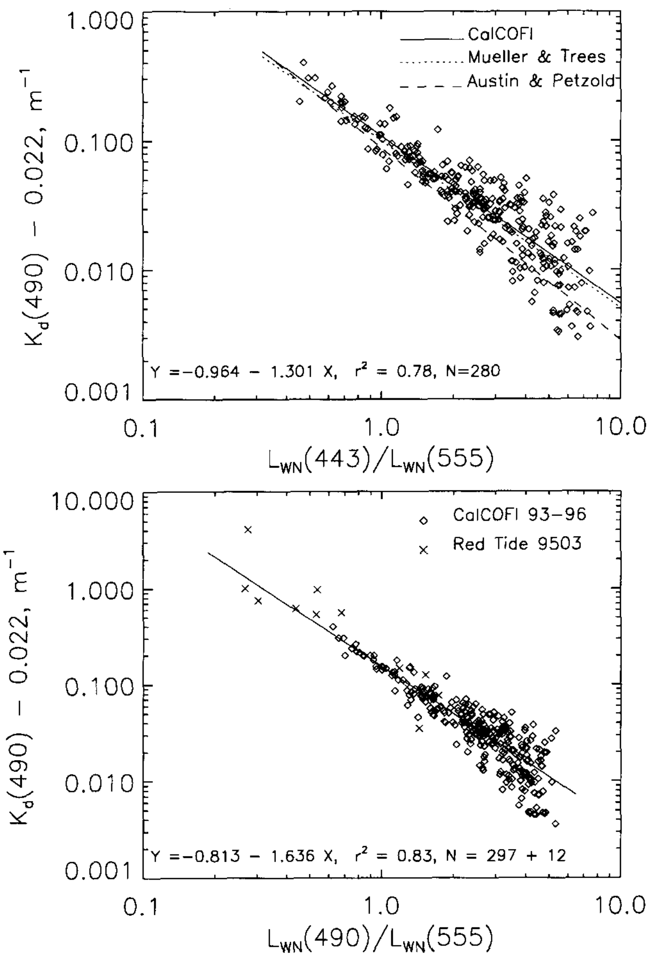

Figure 13. Upper panel, $K_d(490)$ as a function of the ratio of normalized water-leaving radiances $L_{wn}(443)/L_{wn}(555)$. A comparison of the CalCOFI estimate (equation 9) with the results of Mueller and Trees (1996) and Austin and Petzold (1981). Lower panel, $K_d(490)$ estimated from $L_{WN}(490)/L_{WN}(555)$ including data from a red tide cruise RED9503. The root mean square error and r^2 were calculated for the log-transformed data.

tions may now need to be revised, since recent laboratory measurements imply that the *K* for pure water in the region of relevance for SeaWiFS bio-optical algorithms may be smaller than previously reported.

ACKNOWLEDGMENTS

This work was supported by a grant from the NASA HQ Ocean Biogeochemistry Program and a cooperative agreement from NASA GSFC (NAGW-3665, NCC-5-48). We gratefully acknowledge BSI, Inc., CHORS, and ICESS for their efforts in characterizing and calibrating our radiometer; E. Brody and V. Fournier-Sicre for participating in some of the cruises, and for helping with the early development of the calibration time series procedures and processing schemes; the director's office of SIO and the Vettelson Foundation for providing matching funds for the NASA grant for several days of ship time to contribute to CalCOFI for part of the wire time; David Siegel for making the BBOP software available; the CalCOFI Committee for encouraging our participation in the CalCOFI cruises and providing very generous wire time to accomplish our work; the CalCOFI technicians for extraordinary analytical and data-reduction effort, and for their provision of the CalCOFI data sets; the SIO Marine Facility and resident technicians for assistance in configuring winches and laboratory vans for the cruises; and the captains and crews of the R/V *New Horizon* and R/V *David Starr Jordan* for their expert execution of the CalCOFI cruises.

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GLOSSARY

Abbreviations

BBOP	Bermuda Bio-Optics Project
BSI	Biospherical Instruments, Inc.
CDOM	Colored dissolved organic material
CHORS	Center for Hydro-Optics and Remote Sensing (San Diego State University)
CZCS	Coastal Zone Color Scanner
HPLC	High-performance liquid chromatography
ICESS	Institute for Computational Earth System Science (University of California, Santa Barbara)
IEH	File format of the CalCOFI data archive
IRIX	A computer operating system
LCD	Least common denominator (data file format)
MER	Multispectral Environmental Radiometer
Perl	A programming language
RMS	Root mean square (error)
SeaBASS	SeaWiFS Bio-optical Archive and Storage System
SIRREX	SeaWiFS Intercalibration Round-Robin Experiment

Symbols

λ	Wavelength, nm
$a_{ph}(\lambda)$	Phytoplankton pigment spectral absorption coefficient
$a_w(\lambda)$	The absorption coefficient for pure water
$E_d(\lambda)$	Downwelling spectral irradiance
$E_d(0^-,\lambda)$	Downwelling spectral irradiance just below the sea surface
$E_s(\lambda)$	Surface irradiance
$F_0(\lambda)$	Mean extraterrestrial spectral irradiance
$K_d(\lambda)$	Diffuse attenuation coefficient of seawater for downwelling irradiance
$K_d(490)$	Diffuse attenuation coefficient of seawater for downwelling irradiance measured at 490 nm
$K_w(\lambda)$	Diffuse attenuation coefficient of pure seawater
$L_u(\lambda)$	Upwelling spectral radiance
$L_{WN}(\lambda)$	Normalized water-leaving radiance
$M(\lambda)$	The slope coefficient between different spectral K values
phaeo	Phaeopigment concentration
$R_{rs}(\lambda)$	Remote sensing reflectance
$R_{rs}(0^-,\lambda)$	Remote sensing reflectance just below the sea surface
$R_{rs}(0^+,\lambda)$	Remote sensing reflectance just above the sea surface

PHOTOSYNTHETIC PARAMETERS OF PHYTOPLANKTON IN THE CALIFORNIA CURRENT SYSTEM

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ABSTRACT

We analyzed photosynthesis-irradiance (P-E) and phytoplankton absorption data from the coastal waters of the Southern California Bight (SCB) as well as data in the literature for other coastal and oceanic regions of the California Current system (CCS). Since there is substantial variability within data sets, we conclude that it is not possible at this time to predict fine time-and-space-scale variations in photosynthetic parameters. For simple primary production models, we recommend working averages for the CCS between northern California and Bahía de San Quintín (300 km south of San Diego) based on data we summarized from coastal and oceanic waters. For the upper half of the euphotic zone we propose to use the following averages: $\alpha^B = 0.047 \pm 0.004$ mg C (mg chl)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$ (the initial slope of the photosynthesis-irradiance curve); and $P^B_{\max} = 8.60 \pm 0.060$ mg C (mg chl)$^{-1}$ h^{-1} (assimilation number). A linear interpolation for the gradient of α^B and $P^B_{\max}$ is recommended for the lower half of the euphotic zone (10%–1% E_o depths), with values for the 1% E_o depth equal to 25% of the values of the upper euphotic zone: $\alpha^B = 0.012$, and $P^B_{\max} = 2.15$.

INTRODUCTION

The advent of remotely sensed ocean color data has made the synoptic estimation of primary productivity for large geographic areas an attainable goal. Empirical and semianalytical algorithms to estimate primary productivity from satellite-derived photosynthetic pigments have been compared (e.g., Balch et al. 1989; Platt et al. 1995; Sathyendranath et al. 1995). The parameters used in these algorithms belong to three categories (Morel 1991): environmental (e.g., location, atmospheric conditions); ecological (e.g., the chlorophyll vertical profile); and physiological (e.g., the photosynthesis-irradiance curve parameters, the chlorophyll-specific absorption coefficient of phytoplankton, photosynthetic quantum yields).

Given a set of ecological and physiological parameters, the evolution of productivity in response to environmental changes is unambiguously derived, since the physics involved are rather accurately modeled (Morel 1991). On the basis of the CalCOFI data set, Millán-Núñez et al. (1996, 1997) proposed regression models to predict the vertical profiles of chlorophyll (chl) from surface values for the California Current system (CCS). Fewer data exist, however, on the physiological parameters of phytoplankton.

The Southern California Bight (SCB) constitutes a unique physical environment within the CCS. A dramatic change in the angle of the coastline, coupled with the topography of the southern California offshore coastal area results in circulation patterns that differ significantly from other locations of the west coast of the United States and northern Baja California. During summer, the CCS bends shoreward south of San Diego, then poleward, recycling water through the SCB in the large-scale Southern California Countercurrent (Hickey 1993). The growth and productivity of SCB phytoplankton is intermediate when compared to other areas of the world's ocean. It is greater than the growth and productivity in the North Pacific Central Gyre, but less than that in nutrient-rich upwelling regions (Hardy 1993).

Peláez and McGowan (1986) analyzed satellite color imagery and found a sharp zonal boundary just south of San Diego—the Ensenada Front. It coincides with the CCS onshore component and is best defined from about 100 km to 500 km offshore. It is an abrupt transition between two large and different biological water masses, with a threefold change in phytoplankton pigment content over a distance of a few kilometers, with very low surface-pigment concentrations in the southern, warmer, water mass. From June through winter the oligotrophic water mass intrudes into the Southern California Bight. This low-pigment area is located immediately offshore of the narrow coastal band of higher pigment, and it is continuous with the low-pigment region south and west of the Ensenada Front (Peláez and McGowan 1986).

The objective of this work was to characterize the parameters of the P-E curve: its initial slope (α^B), and the maximum rate ($P^B_{\max}$), both normalized to chl, for the coastal region of the Southern California Bight. We also estimated $a^*_{ph}(\lambda)$, the specific absorption coefficient of phytoplankton, which allowed us to derive maximum photosynthetic quantum efficiency ($\phi_{\max}$) from α^B and the spectral distribution of irradiance in our incubator. We analyze here the variability of these parameters at a

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station off Bahía de Todos Santos (100 km south of San Diego) for a period of 20 days, and compare our values with those in the literature for other coastal and oceanic regions of the CCS. Finally, we propose a set of working averages of the physiological parameters to be used in primary-productivity algorithms for the CCS region represented by the various data sets.

METHODS AND MATERIALS

From 20 July to 8 August 1994, daily samples were taken at a station 7 km west of Isla Todos Santos within the CCS (31°50'N, 116°53'W; fig. 1). Bahía de Todos Santos is near the southernmost extreme of the Southern California Bight (fig. 1.5 in Dailey et al. 1993). Sampling was done around noon. Wind speed and direction, and atmospheric temperature were measured at Punta Morro (fig. 1). Once each day we measured profiles of temperature and salinity (CTD; SeaBird Inc.), natural (daylight-induced) fluorescence, and photosynthetically available scalar irradiance (PNF-300, Biospherical Instr.).

We also took water samples from two depths, corresponding to 100% and 10% of the irradiance incident just below the sea surface (E_o^-). Water samples were transported to the laboratory on land, in 20 L glass bottles covered with dark cloth and placed in insulated boxes filled with seawater to maintain constant temperature. We assume that transportation time from the field to the laboratory (maximum, 2 hrs) did not affect the P-E relation of our samples since changes from high to low irradiance result in negligible photoacclimation (change of chlorophyll cell^{-1}) at time scales less than 5 hours (Post et al. 1984).

Upon arrival in the laboratory, chl samples were filtered through Whatman GF/F glass-fiber filters. The samples were later extracted in 90% acetone for 24 hours, and analyzed fluorometrically (Yentsch and Menzel 1963; Holm-Hansen et al. 1965; Venrick and Hayward 1984). Water samples were filtered through GF/F filters for particle absorption, which was measured with a Perkin-Elmer Lambda 6 spectrophotometer. Raw absorbances were corrected for the path-length amplification effect according to Mitchell (1990). Estimates of total particle absorption (a_p) were corrected for detrital absorption (a_d) following Kishino et al. (1985), to obtain an estimate of phytoplankton absorption (a_{ph}). Spectrophotometric phosphate concentration (PO_4) analyses were done following Strickland and Parsons (1972).

To generate the photosynthesis-irradiance (P-E) curves, 420 ml from each water sample were passed through a 333 µm mesh to remove large herbivores, then ^{14}C was added to a final concentration of 0.5 $\mu\text{Ci ml}^{-1}$. A 10 ml aliquot was pipetted into each of 36 scintillation vials, which were incubated for an hour in an incubator similar to the one designed by Talbot et al. (1985). Temperature was maintained at 16°C ± 2° for all samples. Three additional samples were taken for dark incubation, and three more for a time-zero control; the latter were immediately acidified after filtration. After incubation, each sample was filtered through a 0.45 µm Gelman membrane filter, after which 0.2 ml of 1.2 N HCl was added to each filter. Radioactivity was determined with a Beckman LS5000 scintillation counter. Carbon assimilation was estimated according to Strickland and Parsons (1972).

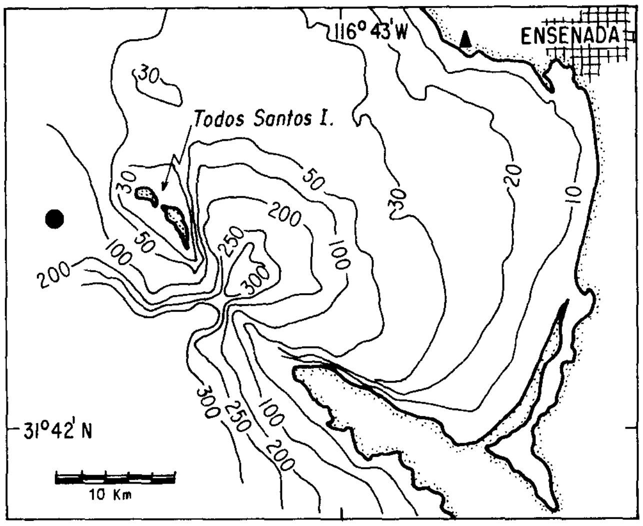

Figure 1. Study area. Sampling site (●) and Punta Morro meteorological station (▲).

The initial slope, α^B, was estimated with a linear regression of the low irradiance points. To estimate P^B_{max}, we fit the data points to Smith's (1936) equation

$$P^B = (P^B_{max}\ \alpha^B E)\ [(P^B_{max})^2 + (\alpha^B E)^2]^{-1/2},$$

using the STATISTICA software package. Maximum photosynthetic quantum efficiency (ϕ_{max}) was calculated by dividing α^B by the $a^*_{ph}(\lambda)$ weighted by the spectral irradiance of the P-E incubator (Schofield et al. 1993; Sosik 1996).

RESULTS

Dominant winds were from the northwest, with large diurnal variations. During the first five days, maximum wind speeds were as high as 9 m s^{-1} (not illustrated). Sea-surface temperature (T °C) was 16.5°–17° the first four days and decreased to 15° the following two days; then, as the winds relaxed to 3 m s^{-1} on the tenth day, T increased to 20°. Thereafter, winds increased without reaching the intensities of the first days, and surface T decreased again to 16.5° on the thirteenth day. Finally, winds decreased toward the end of the sampling period, and surface T increased to 20.6° (fig. 2a). At the 10%

E_o depth T behaved in a similar manner as at the surface. These temperature fluctuations are believed to be caused partly by local upwelling, as indicated by changes in isopycnal depths (fig. 3). Temperature differences from 1.5° to 5° between the surface and the 10% E_o depth suggest strong stratification (fig. 2a).

Very clear skies during the first two days and on day 18 of our sampling period produced high incident scalar irradiance (E_o^-). But on the other sampling days, variable cloudiness caused E_o^- values lower than 500 µmol quanta m^{-2} s^{-1} (fig. 2b). The density field indicates vertical mixing up to 15 m on some dates (fig. 3). The 24.5 σ_t isopycnal fluctuated between 10 m and the surface up to day 18, then subsided deeper than 25 m after day 18. The 10% E_o depth behaved similarly to the 24.5 σ_t isopycnal. Its minimum was near 10 m on the twelfth day, and its maximum was almost 30 m toward the end of our sampling period (fig. 3).

Phosphate concentration (PO_4) varied irregularly with time and was not correlated with T °C. In general, there were slightly higher PO_4 values at the 10% E_o depth than at the surface (fig. 4). For our data set, PO_4 concentration and standard error (s/n$^{1/2}$) were 0.26 and 0.013 µM, respectively. We have used CalCOFI data from the upper 50 m for 1993–97 to derive empirical regressions of

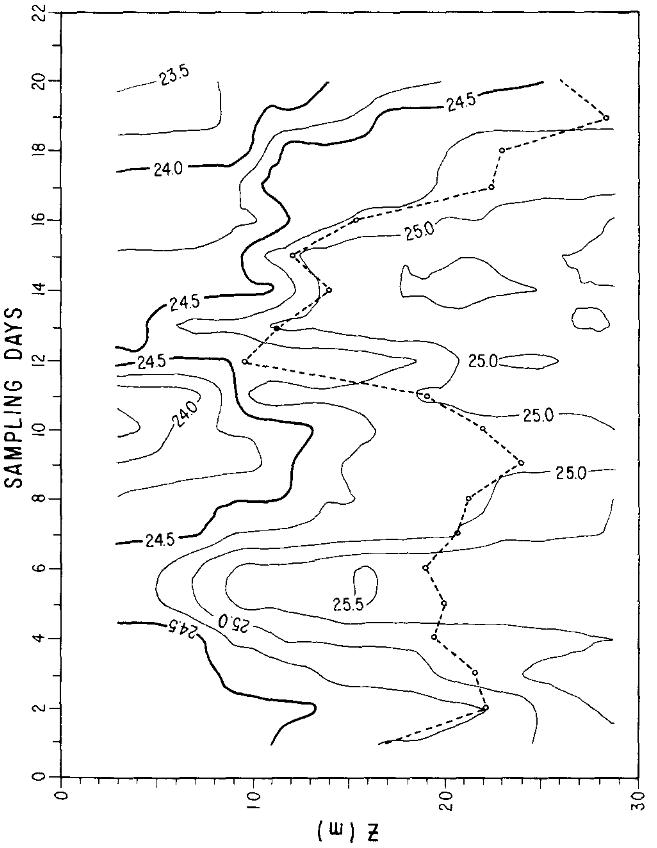

Figure 3. Vertical distribution of density, the 10% E_o depth (dashed line), and the 24.5 σ_t isopycnal (bold line).

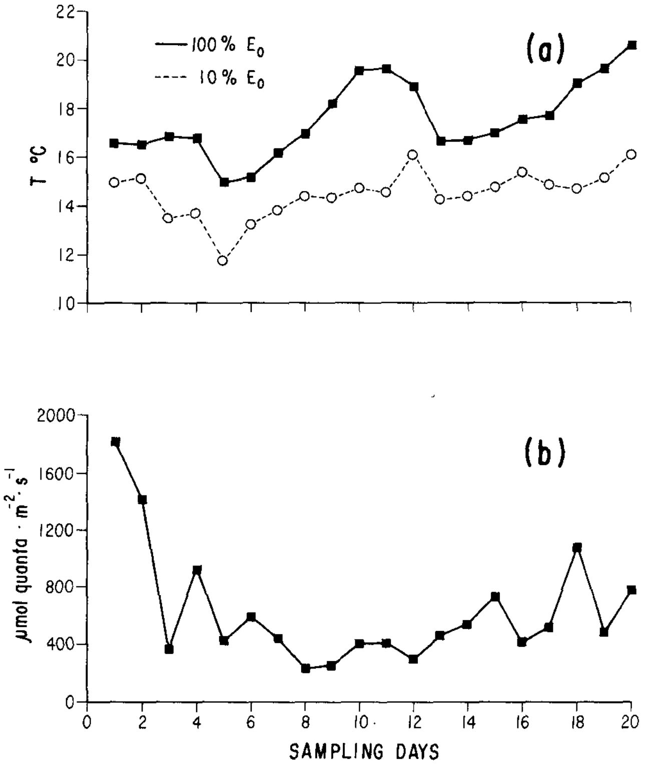

Figure 2. *a*, Temperature time series (surface and 10% E_o depth); *b*, incident irradiance (E_o^-) time series.

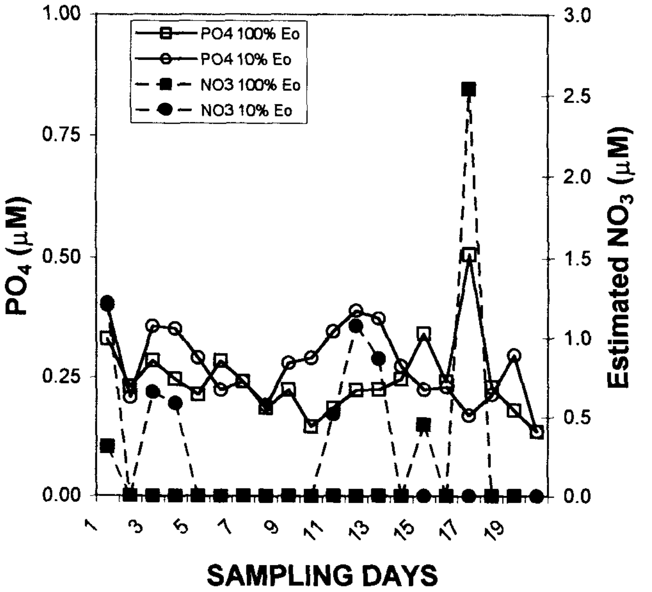

Figure 4. Phosphate concentration (open symbols, µM) for surface and the 10% E_o depth. Nitrate values (closed symbols, µM) are based on regression estimates from CalCOFI data.

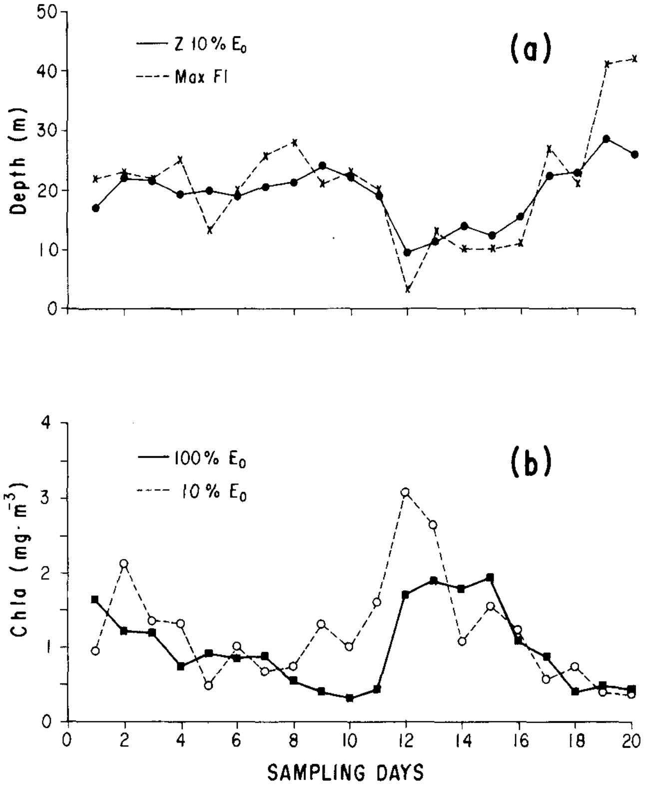

Figure 5. *a*, Fluorescence maximum and the 10% E_o depths; *b*, chlorophyll a time-series (surface and 10% E_o depth).

phosphate vs. nitrate (NO_3) that were used to estimate NO_3 in figure 4. Analysis of the CalCOFI data showed that there is residual PO_4 after NO_3 depletion, thus accounting for the poor correlation of PO_4 with temperatures over this narrow temperature range. In the CalCOFI data set, PO_4 is well correlated with temperatures lower than 15°.

Depth of the fluorescence maximum was not significantly different from the 10% E_o depth ($p \leq 0.10$; fig. 5a). In general, there was no significant difference between surface chl and that at the 10% E_o depth (fig. 5b). However, during sampling days 8–13, chl was higher at the 10% E_o depth than at the surface ($p \leq 0.005$). The minimum and maximum chl values, respectively, for the 10% E_o depth were 0.42 and 3.1 mg m^{-3}; for the surface they were 0.36 and 1.95 mg m^{-3}. We had lowest chl values and highest temperatures in the middle and at the end of the sampling period (figs. 2a and 5b).

The chlorophyll-specific phytoplankton absorption spectra are shown in figure 6. Variations in the spectral shape are represented by changes in the ratios of the blue (440 nm) to red (675 nm) peaks. This ratio differed significantly between the 100% and 10% depths only on day 1 (fig. 6c).

Analysis of P-E response indicated slight photoinhibition with irradiances higher than 600 µmol quanta m^{-2} s^{-1} (for example, surface samples on day 6 and day 8; fig. 7), but in general there was no photoinhibition up to 1,400 µmol quanta m^{-2} s^{-1}. The average saturation parameter of photosynthesis ($E_k = P_{max}/\alpha$) was 246 µmol quanta m^{-2} s^{-1} for the surface and 255 for the 10% E_o depth, with a standard error of 14 and 21 µmol quanta m^{-2} s^{-1}, respectively. These E_k values are not statistically different, and the overall average of 250 µmol quanta m^{-2} s^{-1} can be adopted.

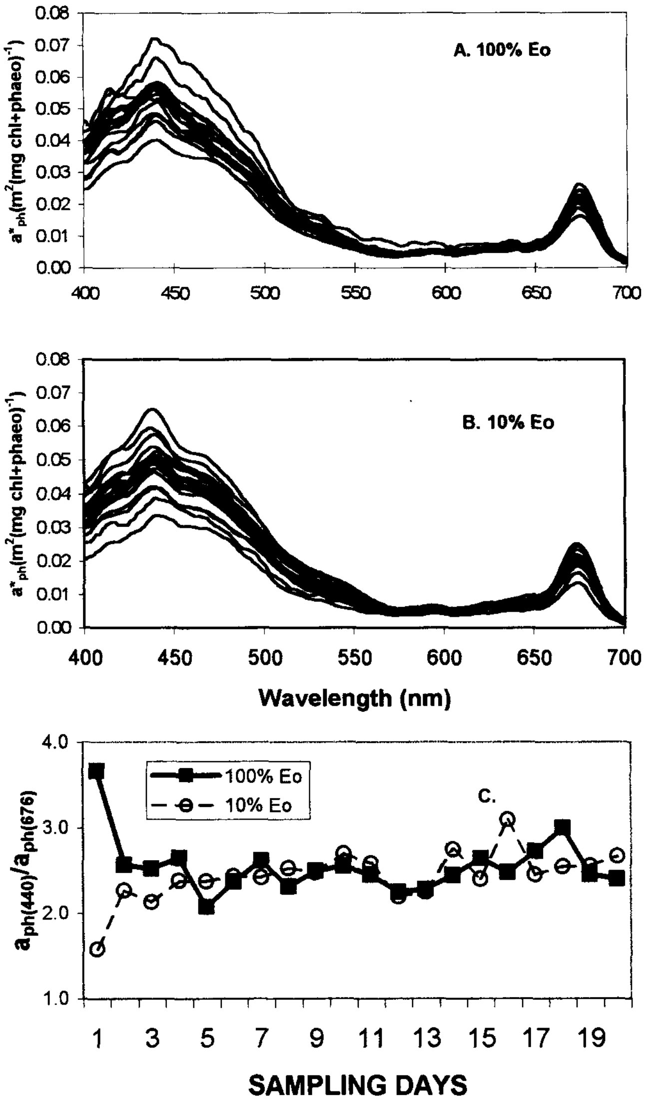

Figure 6. Phytoplankton pigment-specific absorption spectra (a^*_{ph}) for (*A*) 100% E_o depth, and (*B*) 10% E_o depth. *C*, Absorption ratio (440/676) time series.

The initial slope, α^B, was variable; its mean and standard error for our whole data set were 0.039 and 0.005 mgC (mg chl)$^{-1}$ h^{-1} (µmol quanta m^{-2} s^{-1})$^{-1}$, respectively. Except for days 6, 8, 9, and 19, α^B values for both depths were very similar (fig. 8a). The maximum α^B value was estimated for sampling day 8 [0.153 mg C

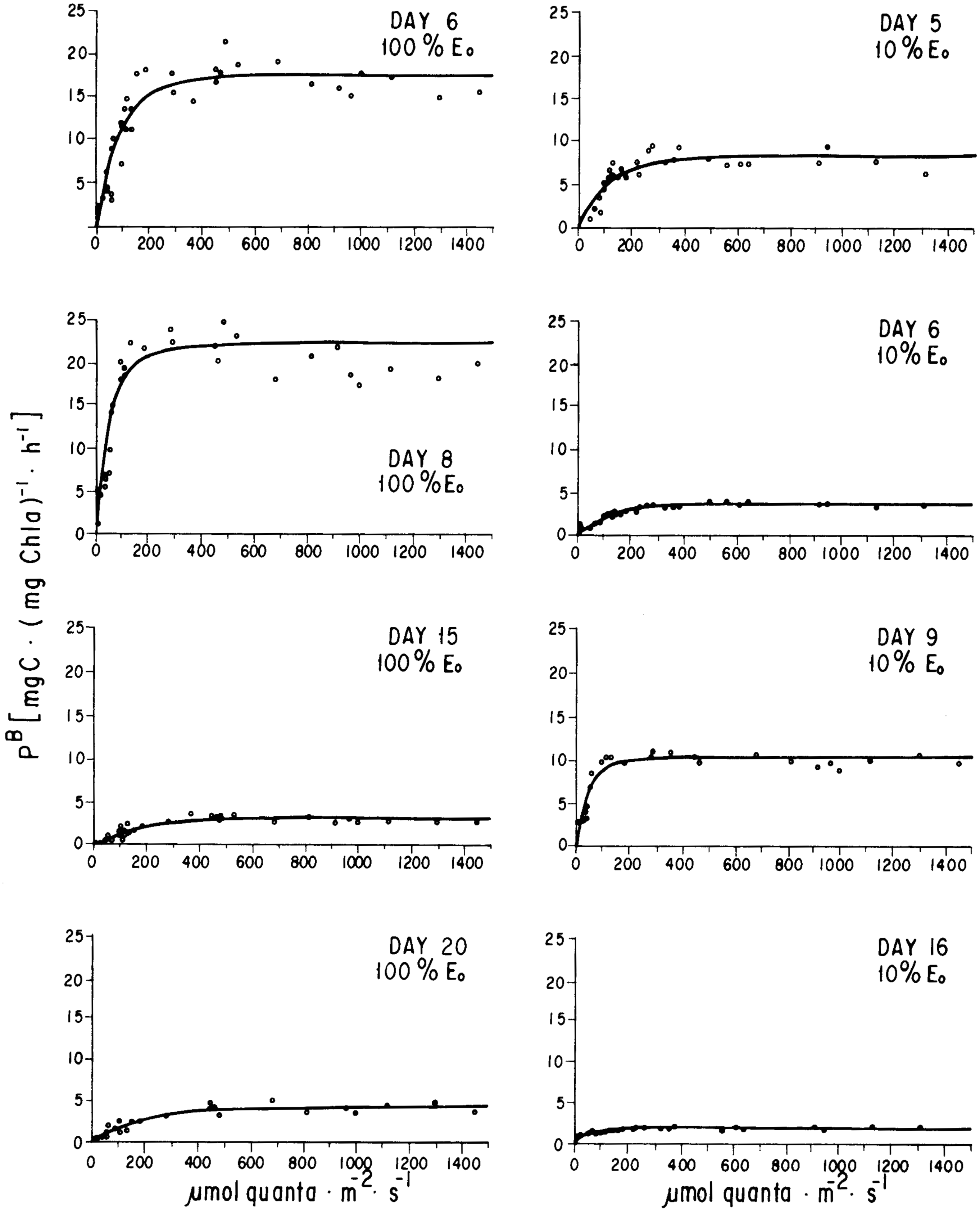

Figure 7. Examples of photosynthesis-irradiance (P-E) curves at 100% and 10% E_o depths for different sampling dates.

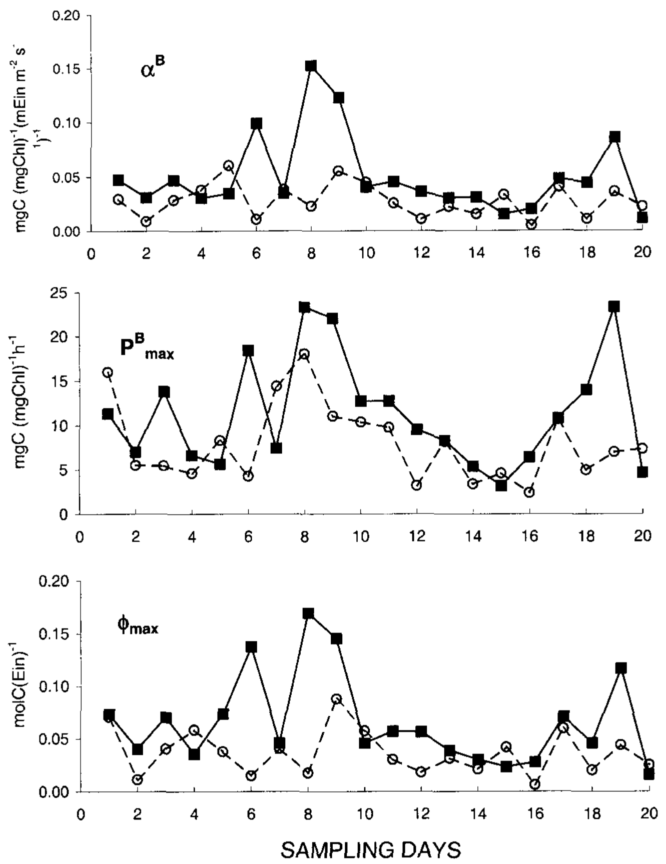

Figure 8. Time series of initial slope (α^B), maximum photosynthetic rate (P^B_{max}), and maximum quantum efficiency (ϕ_{max}).

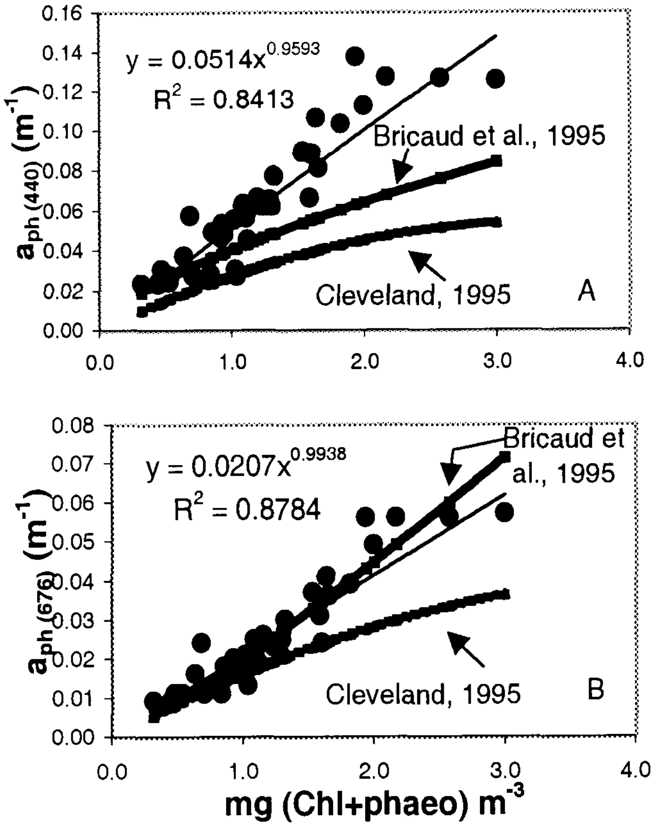

Figure 9. Best fits with a power function model for the phytoplankton absorption coefficients versus chlorophyll a concentration for 440 nm (*A*) and 676 nm (*B*) for our entire data set. The thick lines represent prediction of the models of Cleveland (1995) and Bricaud et al. (1995).

$(\text{mg chl})^{-1}\ \text{h}^{-1}$ (μmol quanta $\text{m}^{-2}\ \text{s}^{-1})^{-1}$] for the surface. On the other hand, α^B values as low as 0.01 were estimated for the 10% E_o depth.

Like α^B, P^B_{max} varied over time but with a greater similarity between the two sampled depths (fig. 8b). For the entire data set, P^B_{max} ranged from 2.5 to 23. The mean and standard error for P^B_{max} were 9.6 and 0.9 mg C mg $\text{chl}^{-1}\ \text{h}^{-1}$, for all P-E data.

Because of its dependence on α^B, and relatively little variability in a^*_{ph}, ϕ_{max} showed the same pattern of variation as α^B (fig. 8c). Minimum ϕ_{max} values for both sampled depths were about 0.01 mol C (mol quanta)$^{-1}$, and maximum estimates were 0.088 for the 10% E_o depth and up to 0.169 for surface waters. The mean and standard error for ϕ_{max} were 0.051 and 0.006 mol C (mol quanta)$^{-1}$ for our whole data set. However, error of individual samples was greater, and the highest ϕ_{max} values were not significantly different from the theoretical maximum of 0.125. None of the three parameters (α^B, P^B_{max}, and ϕ_{max}) were correlated with either chl or T °C.

The phytoplankton absorption was well correlated with pigment (chl + phaeo) concentrations (fig. 9), as found by other investigators (Mitchell and Kiefer 1988; Bricaud et al. 1995; Cleveland 1995; Sosik and Mitchell 1995). But unlike the modeling parameterizations of Cleveland (1995) or Bricaud et al. (1995), our study showed little nonlinearity in the a_{ph} versus chlorophyll relation at 440 or 675 nm, as shown by the exponent of the power fit, which is not significantly different from 1.0 (fig. 9). This may be caused by the relatively narrow range of pigment concentration in our data set. Our data at 675 nm agree well with the Bricaud et al. (1995) model, but both our data and the Bricaud et al. model are higher than the Cleveland (1995) model at this wavelength. At 440 nm our data are greater than either of the previous model predictions.

These differences are partly due to the fact that the earlier models were based on data processed with algorithms dependent on the Mitchell and Kiefer (1988) report, which results in a_{ph} values about 30% lower than the algorithm we used (Mitchell 1990). There is large variance in the source data sets of the previous models, and our data are within the range of those data.

DISCUSSION

Segovia-Zavala et al. (in press) reported maximum PO_4 values of 0.75 μM, and NO_3 values of 1.0 μM for coastal surface waters between San Diego and Bahía de Todos Santos during an intense upwelling event with minimum surface temperatures under 13°. These are relatively low nutrient values for CCS upwelling at this temperature. Our nutrient values are lower because we did not have an upwelling event as intense as theirs (our lowest surface T was 15°). Our higher T's and lower nutrients also indicate that there was not a significant "island mass effect" (Doty and Oguri 1956) due to Isla Todos Santos. Smith et al. (1987) also reported relatively low near-surface nutrients for a transect through the northern extreme of the SCB. Nutrient and surface temperature values from 15° to 20°, similar to our observations, are typical of the SCB region (Sosik and Mitchell 1995; Hayward et al. 1996).

Bahía de San Quintín, 200 km south of Bahía de Todos Santos, is about 100 km south of the point where the oligotrophic intrusion turns back offshore (surface geostrophic flow shown in fig. 27 of Reid 1988). During non–El Niño years, strong upwelling events occur in the area off Bahía de San Quintín, with minimum surface T of 11° in July (Alvarez-Borrego and Alvarez-Borrego 1982), more than 4° lower than our minimum surface T. In Bahía de San Quintín the maximum reported surface PO_4 and NO_3 values for summer are 2.5 and 12 μM (Millán-Núñez et al. 1982). North of the SCB, off Point Sur (35 km south of Monterey Bay), maximum surface NO_3 values reported for an upwelling event in June were around 24 μM (Traganza 1985). Thus, north and south of the bight, nutrients are much higher than inside the bight. Our relatively low nutrient concentrations, and also those of Segovia-Zavala et al. (in press) and Smith et al. (1987), are consistent with the concept that our site was only slightly influenced by coastal upwelling and was dominated by the well-described oligotrophic north-flowing currents (Hickey 1993; Hayward et al. 1996).

In the coastal waters of the bight, chl values are also lower than in the coastal waters off Bahía de San Quintín and off Point Sur. Our maximum surface chl values were near 2 mg m^{-3}, often in the range 0.5–1.5 mg m^{-3} (fig. 5b). Our data are in agreement with the chl time series at Scripps Pier—where chl values are typically in the range 0.5–1.5 mg m^{-3}, with some relatively isolated peaks greater than 5 mg m^{-3}—and with CalCOFI cruise data for within the bight (Sosik and Mitchell 1995; Hayward et al. 1996). Chl values reported for waters off Bahía de San Quintín are often larger than 5 mg m^{-3}, with peaks larger than 15 mg m^{-3} in summer (Millán-Núñez et al. 1982). Similar high chlorophyll concentrations are observed in northern California waters in the upwelling plumes (Hood et al. 1991).

Both photosynthetic parameters, α^B and P^B_{max}, showed great variability over the sampling period. This agrees with a 70-day time series reported by Coté and Platt (1983) for Bedford Basin, and with other reports for the CCS (Harding et al. 1982; Prézelin et al. 1987; Schofield et al. 1991). According to Coté and Platt, phytoplankton cells respond fairly rapidly to changing environmental conditions, close to the order of a generation time. Harding et al. (1982) demonstrated large diel variability in α^B and P^B_{max}. Hood et al. (1991) and Schofield et al. (1991) also found relatively large variability for these two parameters in northern California and at the northern end of the Southern California Bight, respectively.

These reports for the CCS region place considerable doubt on our ability to predict instantaneous primary production rates by using satellite estimates of chl and irradiance. Ecological and physiological models are not yet capable of predicting the short-term P-E parameters. Nevertheless, it is possible to estimate mean values of the P-E parameters to calculate primary productivity for large time and space scales to which the data apply (Sathyendranath et al. 1995).

Millán-Núñez et al.'s (1997) algorithms cannot predict the instantaneous chl profiles for a particular geographic location in the CCS, but they are appropriate at regional and seasonal space and time scales. In a similar manner, we might be able to find acceptable averages of the photosynthetic parameters for the CCS region, in order to apply algorithms to estimate primary productivity from chl and light data. Although there is evident short-term variability in P-E relationships, it has still been proposed by Platt and Sathyendranath (1988) that larger-scale biogeographic provinces can be represented by mean parameters. This approach has been applied to provinces of the Atlantic (Sathyendranath et al. 1995) and to northern California waters by Moisan and Hofmann (1996), who proposed using a regional mean set of P-E parameters based on Hood et al. (1991), with diel variability specified as in MacCaull and Platt (1997).

Two relevant questions are: How large is the region within the CCS biogeographic domain for which our data apply? and, What seasonal and interannual time scales can be represented? Taking into consideration that photosynthetic parameters depend mainly on the phytoplankton light regime, we may explore the possibility that the average values of our photosynthetic parameters are representative of a much larger area than just the southern extreme of the SCB and are also representative of different seasons and years.

Malone (1971) reported phytoplankton assimilation ratios for coastal waters off Monterey and for an offshore area as far as 130°W (about 500 km offshore) and reported a mean assimilation ratio of 7.4 ± 1.0 (95% confidence limits) for coastal phytoplankton and 7.7 ± 1.1

for offshore phytoplankton with no significant difference. Malone (1971) estimated assimilation ratios with incubations under fluorescent light with 0.06 langleys min^{-1}, which corresponds to about 210 μmol quanta m^{-2} s^{-1}. This value is lower than our mean E_k of 250. Thus his "assimilation ratios" may not have been at saturating irradiance like the P^B_{max} values we report.

Gaxiola-Castro and Alvarez-Borrego (1991) tested the hypothesis that greater primary productivity on the cold side of the Ensenada Front is due to higher assimilation numbers. They rejected the hypothesis, finding no significant difference between relative P^B_{max} values from both sides of the front. They attributed the higher primary productivity values on the cold side to the shallower subsurface chl maximum, which causes less limitation of light for the phytoplankton. Unfortunately, the absolute value of the ^{14}C activity added by Gaxiola-Castro and Alvarez-Borrego (1991) to their incubation samples was uncertain (but constant), which is why they used relative assimilation numbers instead of absolute values.

Lara-Lara et al. (1980) and Millán-Núñez et al. (1982) reported phytoplankton assimilation ratios for surface waters off San Quintín, derived from summer in situ ^{14}C incubations carried out in the morning, noon, and afternoon. Possibly at noon they had saturating irradiances, so their noon assimilation ratios should be close to P^B_{max} values. The mean ± standard error of Lara-Lara et al.'s (1980) noon values are 7.0 ± 0.57 mg C mg chl^{-1} h^{-1}; Millán-Núñez et al.'s (1982) noon values are 6.2 ± 0.66 mg C mg chl^{-1} h^{-1}.

We could compare Malone's (1971), Lara-Lara et al.'s (1980), and Millán-Núñez et al.'s (1982) assimilation ratios with our P^B_{max} values to test the hypothesis that lower surface chl values in the coastal waters of the SCB, with respect to those of coastal waters to the north and south, may be associated with lower photosynthetic parameters of phytoplankton. The alternative hypothesis is that photosynthetic parameters are not related to phytoplankton biomass, and their values in the SCB waters are not significantly lower than those of waters farther north and farther south, off San Quintín and off Monterey.

Strictu sensu, we cannot run a proper statistical test, because assimilation ratios for San Quintín and off Monterey may not correspond to optimum irradiances and thus may be lower than P^B_{max} values. Furthermore, when different laboratories generate P-E curves, the reported P-E parameters differ significantly, even when the same water sample is used (Richardson 1991). Nevertheless, we note that with lower nutrient concentrations and phytoplankton biomass values, our mean P^B_{max} values are not lower than assimilation ratios of Malone (1971), Lara-Lara et al. (1980), and Millán-Núñez et al. (1982). At the 95% confidence level our P^B_{max} mean overlaps theirs.

In table 1, we have assembled P-E, $a^*_{ph}(440)$, and ϕ_{max} data that have been reported for the CCS from northern and southern California, including coastal waters and open-ocean waters up to 500 km offshore. Phytoplankton assemblages in coastal California waters seem to behave similarly to those of oceanic waters across the Ensenada Front with respect to photosynthetic parameters. In other words, lower nutrients and chl in the SCB are not associated with lower photosynthetic parameters. This agrees with the conclusion of Cullen et al. (1992) that phytoplankton are acclimated to their irradiance regimes and that nutrition has a small influence on assimilation ratios and P-E parameters. Nutrients appear to be a major factor regulating the standing stock of phytoplankton (Eppley et al. 1979). Thus seasonal and interannual variations in the relative distributions of colder high-nutrient water and warmer low-nutrient water may not strongly influence the P-E parameters.

For our data, P^B_{max} and α^B for surface waters are not significantly different ($P > 0.05$) from those of the 10% E_o depth (fig. 8b, table 1). This agrees with Prézelin et al. (1987), who found similar values for P^B_{max} for the water column between the surface and the 10% E_o depth, at the northern extreme of the SCB. Also, Gaxiola-Castro and Alvarez-Borrego (1991) reported similar relative P^B_{max} values for the water column between the surface and the 10% E_o depth on both sides of the Ensenada Front. Prézelin et al. (1987) and Gaxiola-Castro and Alvarez-Borrego (1991) reported much lower values for the 1% E_o depth—about 25% of the surface values. For the upper half of the euphotic zone (10%–100% E_o), the mean P^B_{max} [8.6 ± 0.60 mg C (mg chl)$^{-1}$ h^{-1}] and α^B [0.047 ± 0.004 mg C (mg chl)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$] values in table 1 are proposed for all the region between San Quintín and Point Sur (near Monterey Bay). Also, the results of others (Malone 1971; Gaxiola-Castro 1991; Hood et al. 1991; Sosik 1996) make it possible for us to extend this region offshore to include the oceanic area of the CCS.

We propose a linear variation of α^B and P^B_{max} for the lower half (10%–1% E_o depths), with values for the 1% E_o depth of $\alpha^B = 0.012$ and $P^B_{\text{max}} = 2.15$ where the 1% irradiance depth values are 25% of the values recommended for the upper euphotic zone (Gaxiola-Castro and Alvarez-Borrego 1991). We have few data in table 1 for the 1% light level or the deep chl maximum. Prézelin et al. (1987) and Schofield et al. (1991) tended to have estimates lower than other reports for the 10%–100% depths, so we believe their deeper data may be an underestimate. When estimating integrated primary productivity, errors for the lower half of the euphotic zone due to errors in P-E parameters will be

TABLE 1
Summary of Photosynthetic Parameters for the California Current System (Standard Error in Parentheses)

Data source	Month and year	Sample time	α^B	P^B_{max}	$a^*_{ph(440)}$	ϕ_{max}
Harding et al. (1982)	May–Aug. 1980	0800–1200	0.052	9.41	—	—
			(0.014)	(2.56)		
	May–Aug. 1980	1200–1600	0.055	8.60	—	—
			(0.010)	(1.81)		
Prézelin et al. 1987						
100% E_o	July 1985	0800–1600	0.053	6.06	—	—
			(0.011)	(1.14)		
10% E_o	July 1985	0800–1600	0.061	6.75	—	—
			(0.010)	(0.68)		
1% E_o	July 1985	0800–1600	0.035	1.25	—	—
			(0.010)	(0.21)		
Hood et al. 1991						
0–50 m	June 1987	1200–1600	0.092	10.98	—	—
			(0.034)	(4.69)		
Schofield et al. 1991						
Surface	July–Aug. 1988	Noon estimated	0.011	4.14	—	0.030
			(0.003)	(0.73)		(0.005)
chl max	July–Aug. 1988	Noon estimated	0.015	1.00	—	0.043
			(0.008)	(0.13)		(0.005)
Sosik 1996						
100% E_o	Jan.–Apr. 1992	1000–1200	—	—	0.062	0.025
					(0.002)	(0.013)
4.5% E_o	Jan.–Apr. 1992	1000–1200	—	—	0.048	0.047
					(0.017)	(0.003)
This report						
100% E_o	July–Aug. 1994	1200–1300	0.050	11.32	0.055	0.066
			(0.008)	(1.36)	(0.002)	(0.009)
10% E_o	July–Aug. 1994	1200–1300	0.028	7.95	0.050	0.037
			(0.003)	(0.96)	(0.002)	(0.005)
		Average values for all reports from 100% to 10% E_o depth	**0.047**	**8.60**	**0.060**	**0.040**
			(0.004)	**(0.60)**	**(0.031)**	**(0.020)**
		Average values for all reports at 1% E_o or chl maximum depth	**0.028**	**1.17**	**—**	**0.043**
			(0.007)	**(0.14)**		**(0.005)**

The units for the parameters are:
α^B mg C (mg chl)$^{-1}$ (mE m^{-2} s^{-1})$^{-1}$
P^B_{max} mg C (mg chl)$^{-1}$
$a^*_{ph(440)}$ m^2 (mg chl+phaeo)$^{-1}$
ϕ_{max} mol C (mol quanta)$^{-1}$

relatively small, because irradiance levels are low (Millán-Núñez et al. 1997). Our proposed averages and the vertical structure of these parameters agree with data reported by others, as summarized in table 1.

For the purpose of estimating primary productivity with absorption-quantum yield algorithms (Kiefer and Mitchell 1983; Smith et al. 1989; Sosik 1996), we propose using the method of Alvarez-Borrego (1996) to estimate the depth dependence of quantum yield: $\phi_{(z)} = \phi_{max}\,[1 + (E_{o(z)}/E_k)^2]^{-1/2}$, where $\phi_{(z)}$ is the actual quantum yield at each depth, and ϕ_{max} is the maximum quantum yield for low-light-adapted phytoplankton. We recommend a ϕ_{max} of 0.1 mol carbon (mol quanta^1), which is slightly lower than the theoretical maximum of 0.125, to account for nitrate-based growth. Sosik (1996) has shown that phytoplankton from the 4.5% light level can have ϕ_{max} of 0.1, and our data from Bahía de Todos Santos also suggest that ϕ_{max} values can approach the theoretical maximum. Using our mean E_k of 250 µmol quanta m^{-2} s^{-1} results in a ϕ of 0.085 and 0.016 at the 10% and 100% light depths, assuming surface irradiance is 1,500 µmol quanta m^{-2} s^{-1}. For most of our sampling period, we had surface irradiance of approximately 500 µmol quanta m^{-2} s^{-1} (fig. 2b), which results in a ϕ value of 0.045.

For algorithms like Kiefer and Mitchell's (1983), we also require values for the a^*_{ph} for the 400–700 nm interval, weighted for the spectral distribution of irradiance. One way to estimate the absorption spectra of phytoplankton is to calculate the two absorption peaks and combine them with a normalized shape. Cleveland (1995) proposed empirical models to predict $a_{ph(440)}$ and $a_{ph(676)}$ for tropical and temperate waters. Bricaud et al. (1995) provide tables that allow estimates of $a_{ph}(\lambda)$ every 2 nm from 400 to 700 nm.

In general, our $a_{ph}(440)$ values are larger than those estimated by Cleveland (1995) or Bricaud et al. (1995; fig. 9). At 676, our data agree well with previous models and with CalCOFI data (Sosik and Mitchell 1995). Differences between our values and those derived from Cleveland's (1995) model could be due to a lower package effect in the blue peak for our samples. It is important that further work be done to reconcile the variations in a_{ph} versus chlorophyll models.

Our proposed values for the physiological parameters may be appropriate for the CCS at large time and space scales. Torres-Moye and Alvarez-Borrego (1987) reported surface chl and primary productivity for waters off San Quintín for 1984, an El Niño year, which were an order of magnitude lower than during non–El Niño years. These latter authors reported assimilation numbers in the range of 2.0–5.4 mg C (mg chl)$^{-1}$ h^{-1}. However, Sosik (1996) reports ϕ_{max} values for a moderate El Niño year that are greater than those of Schofield et al. (1991) for a non–El Niño year. El Niño can cause large perturbation in the CCS, with suppressed upwelling and more extensive intrusion of warm, nutrient-depleted subtropical waters near the coast and in the northern California domain (Lynn and Simpson 1987). These perturbations will cause changes in surface and vertical distributions of chlorophyll biomass. But the data of P-E, a^*_{ph}, and ϕ parameters from various years, seasons, and distances offshore in the CCS, or previous reports of assimilation numbers off San Quintín, Baja California; Monterey Bay; and the Ensenada Front, do not support the implementation of unique El Niño and non–El Niño photosynthetic parameterizations. And there is no evidence for seasonal differentiation based on the data we summarize in table 1. But since table 1 covers spring and summer seasons primarily, the limited data of Sosik (1996) for winter CalCOFI is not sufficient for making final generalizations about seasonal variability. Still, the variance within data sets at small time and space scales is larger than the variance between means for different regions or seasons. Thus it seems reasonable to use simplified working means for photosynthetic parameters for large time and space scales within the CCS. This approach may provide reasonable large-scale estimates, but poor small-scale instantaneous estimates of primary production.

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VARIATIONS IN SPECIFIC ABSORPTION COEFFICIENTS AND TOTAL PHYTOPLANKTON IN THE GULF OF CALIFORNIA

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ABSTRACT

From 15 to 19 October 1994, an oceanographic cruise was carried out in the Gulf of California. Phytoplankton biovolume, pigment concentrations, and taxonomy were examined as functions of location and light depth. The specific absorption coefficient of phytoplankton (a^*_{ph}) showed variability in magnitude and spectral shapes between stations and with depth. The a^*_{ph} values ranged from 0.020–0.056 m^2(mg chl a)$^{-1}$ at 440 nm to 0.013–0.020 m^2(mg chl a)$^{-1}$ at 674 nm. Spectra of phytoplankton belonging to the same taxonomic group tended to have similar shape. At stations where the environmental conditions favored the presence of microphytoplankton populations (cells >20 μm), the lowest a^*_{ph} were found. Of all the variables studied, pigments, particularly the photoprotective pigment zeaxanthin, had the highest correlation with a^*_{ph}. Changes in pigment composition and cellular concentration were responsible for over 70% of the variability of the specific absorption at 440 nm. Including biovolume per cell in a multiple regression improved the model to explain up to 80% of a^*_{ph} variations. The work described here concurrently examined pigment packaging, measured as the cellular concentration of chlorophyll a and as the phytoplankton cell volume, and the confounding effect of the blue-absorbing accessory pigments on the specific absorption coefficient. The a^*_{ph} varied as a function of all three variables, indicating the importance of both taxonomic variations (size and accessory pigments) as well as responses to environmental variations.

INTRODUCTION

Particulate material, including phytoplankton, is responsible for most of the light scatter and absorption in the ocean. The characterization of particle variability provides information about light attenuation, potential primary production, and the phytoplankton pigment biomass. Changes in the optical characteristics of water masses have been associated with biochemical processes that are related to the energy used in photosynthesis (Yentsch 1960; Morel and Prieur 1977; Mitchell and Kiefer 1988a; and Bricaud et al. 1995).

Several authors have reported the distribution of light absorption by particles in the ocean (Maske and Haardt 1987; Yentsch and Phinney 1989; Nelson et al. 1993; and Cleveland 1995), concluding that there is a nonlinear relation between the phytoplankton light-absorption coefficient and the chlorophyll concentration. This relation is a function of the phytoplankton environment, particle form and size, and concentration of pigments and detritus (Morel and Bricaud 1981; Spinrad and Brown 1986; and Bricaud et al. 1995). These authors have argued that cell size and the photosynthetic pigment composition of the phytoplankton are partly responsible for the variability of the specific light-absorption coefficient.

Several analytical models have been developed to estimate primary productivity as a function of the in vivo phytoplankton light absorption (e.g., Kiefer and Mitchell 1983). In these models, the a^*_{ph} values are taken as constants; however, recent studies have shown both horizontal and vertical variations in a^*_{ph} (e.g., Sosik and Mitchell 1995).

The objective of this research was to study the factors that cause variability of the phytoplankton-specific light-absorption coefficient in the Gulf of California. In particular, pigment composition was examined as a possible cause of variable a^*_{ph} at specific wavelengths.

MATERIALS AND METHODS

From 15 to 19 October 1994, an oceanographic cruise was made aboard the R/V *A. Humboldt H-03* in the Gulf of California. Seawater samples were collected from five depths: 100%, 32%, 10%, 3%, and 1% of surface irradiance E_o (fig. 1).

Photosynthetically available radiation (PAR) was measured with a light sensor (Biospherical Instruments, Inc. PNF-300). Temperature and salinity were measured with a CTD recorder. Phosphate concentrations were measured with a Bausch & Lomb (Spectronic 1001) spectrophotometer, following Strickland and Parsons (1972). Phytoplankton species and abundances were analyzed with a Carl Zeiss inverted microscope with 16× and 40× objectives. Phytoplankton cell volume was estimated following relationships developed by Strathmann (1967) and Edler (1979).

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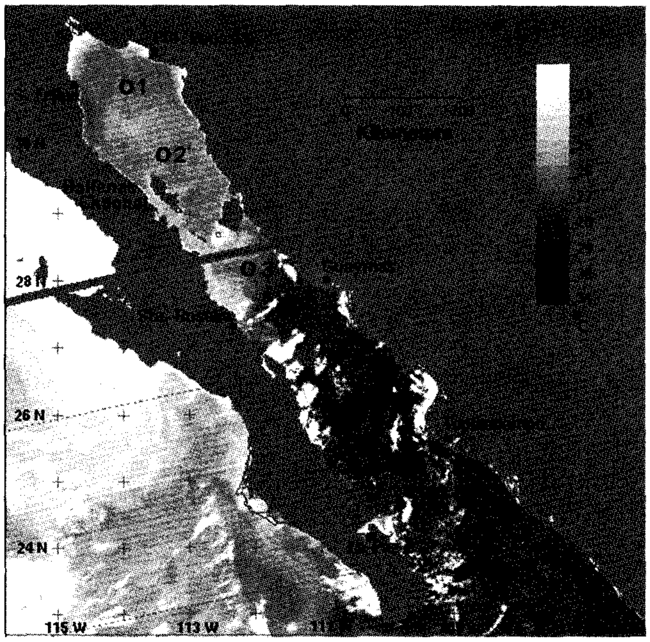

Figure 1. Satellite image of sea-surface temperature in the Gulf of California, and sampling stations 1–5.

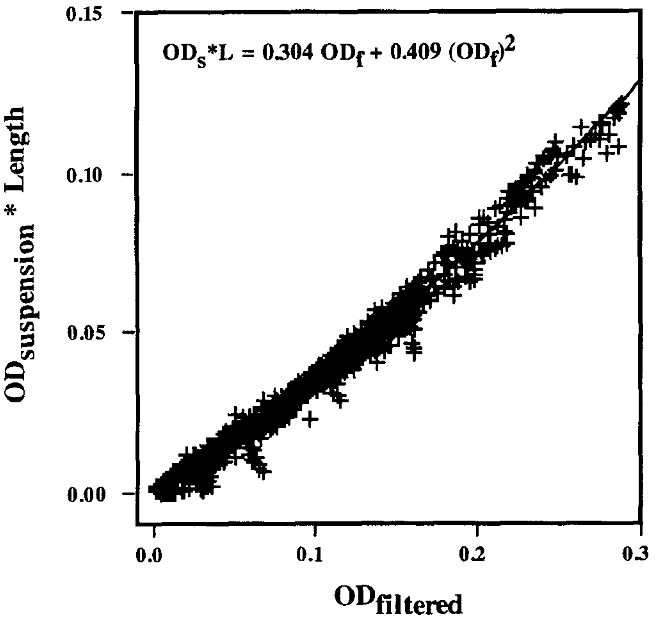

Figure 2. Relationship between the optical density (OD) of cells measured in suspension and on a filter from laboratory culture.

Absorption Measurements

Samples for measurements of phytoplankton light absorption were collected on Whatman GF/F filters and immediately frozen in liquid nitrogen. In the laboratory, the filters were defrosted, then saturated with filtered seawater. Spectral absorption was measured with a Hewlett Packard 8452 diode array spectrophotometer equipped with an integrating sphere (Labsphere RSA-HP-84), following the technique described by Mitchell (1990) and Cleveland and Weidemann (1993). The filtered samples were scanned between 400 and 750 nm with a spectral resolution of 2 nm. The filters were rinsed (~20 minutes) with hot methanol to remove pigments, and a second reading was made to estimate the detritus absorption (Kishino et al. 1985). Phytoplankton pigment absorption was estimated by subtracting the detritus absorption from the total particulate absorption.

We corrected the absorption spectra for the path-length amplification factor (β) by using the algorithm empirically derived from laboratory cultures by Charles Trees (fig. 2) for the HP diode array spectrophotometer. This path-length amplification adjusts optical density for filtered samples OD_{filt} (λ) to equal optical density for an equivalent sample in suspension OD_{sus} (λ).

$$OD_{sus} = 0.3038\ OD_{filt} + 0.4086\ (OD_{filt})^2$$

The specific light-absorption coefficient, a^*_{ph}, m^2(mg chl a)$^{-1}$, was obtained by dividing the phytoplankton absorption coefficient by the chlorophyll a concentration measured in acetone extracts with a Turner Designs 10-005 fluorometer (Yentsch and Menzel 1963).

HPLC Pigment Analyses

Samples for high-performance liquid chromatography (HPLC) pigment analysis were collected on Whatman GF/F filters and frozen in liquid nitrogen for analysis in the laboratory. Chlorophylls and carotenoids were separated by means of the Wright et al. 1991 method. A spectra-focus UV2000 detector with autosampler As3000, with a reverse-phase Radial-PAK C_{18} column (Spherisorb, 25 micron, 25 cm) was used with a flow rate of 1 ml minute^{-1} to separate and quantify the pigments as they eluted off the column. Before injection, a 1,050 µl aliquot of sample extract was mixed with 3 ml of water to help separate dephytolalid pigment compounds. We used canthaxanthin as an internal standard to correct for volume changes during the extract process.

Comparisons of HPLC and standard fluorimetric methods for the determinations of chlorophyll a are shown in figure 3. We found reasonable agreement between chlorophyll a measured by HPLC and fluorimetric methods ($r^2 = 0.89$; $p = 0.05$).

RESULTS

Figure 1 shows the typical distribution of sea-surface temperature during our study. There were two main features: North of the large islands, the temperature varied from 29.5° to 31.0°C. In the southern part of the gulf, a cold front with temperatures from 22.0° to 24.0° was established. In general, these conditions remained in the gulf throughout the entire cruise.

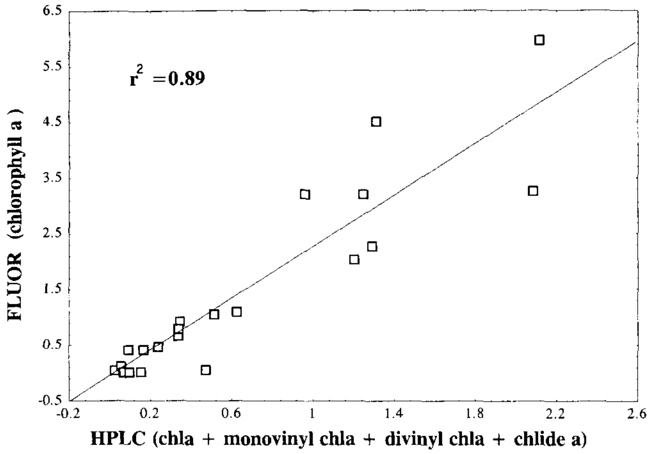

Figure 3. Comparison between HPLC and fluorometrically measured chlorophyll a in the Gulf of California, October 1994 ($r^2 = 0.89$; $p = 0.05$).

TABLE 1
Spatial Distribution of the Main Bio-Optical Variables in the Gulf of California, October 1994

Irradiance	100%	32%	10%	3%	1%
Station 1					
Depth (m)	1	6	14	23	33
Chl a[a] fluor.	1.085	1.162	1.089	1.068	0.921
a^*_{ph} (440 nm)	0.054	0.045	0.047	0.041	0.042
a^*_{ph} (674 nm)	0.023	0.020	0.021	0.018	0.020
Station 2					
Depth (m)	1	6	12	18	25
Chl a[a] fluor.	2.03	2.70	2.34	1.25	0.585
a^*_{ph} (440 nm)	0.026	0.021	0.022	0.023	0.022
a^*_{ph} (674 nm)	0.012	0.010	0.011	0.015	0.013
Station 3					
Depth (m)	1	5	10	16	25
Chl a[a] fluor.	2.764	3.204	—	1.487	0.585
a^*_{ph} (440 nm)	0.020	0.017	—	0.016	0.029
a^*_{ph} (674 nm)	0.013	0.010	—	0.011	0.019
Station 4					
Depth (m)	1	11	26	42	60
Chl a[a] fluor.	0.438	0.479	0.503	0.625	0.184
a^*_{ph} (440 nm)	0.056	0.040	0.036	0.036	0.040
a^*_{ph} (674 nm)	0.016	0.015	0.014	0.017	0.018
Station 5					
Depth (m)	1	7	22	35	45
Chl a[a] fluor.	0.479	0.682	0.804	0.495	0.406
a^*_{ph} (440 nm)	0.031	0.028	0.030	0.037	0.047
a^*_{ph} (674 nm)	0.020	0.013	0.015	0.025	0.027

[a] mg m^{-3}

Variability of a^*_{ph} Values

The vertical distribution of the phytoplankton-specific light-absorption coefficient at 440 nm for stations 1 to 5 (fig. 4) ranged from 0.016 to 0.056 at 440 nm. At 674 nm, a^*_{ph} ranged from 0.010 to 0.027 m^2(mg chl a)$^{-1}$ (table 1). The spatial variability of the phytoplankton-specific light-absorption coefficient between stations showed the maximum differences for stations 1, 4, and 5 at 100%, 32%, and 10% of E_o; stations 2 and 3 were very similar at these light depths. The specific absorption spectrum for station 4 at the 1% light depth was noisy and high, but this may have been an artifact of the low chl a concentrations and the small volume filtered.

Phytoplankton Abundances

We found 15 genera of diatoms with 46 species; stations 2 and 3 showed the highest number of genera (table 2). The average biovolume (μm^3) for diatoms ranged from 19.52 to 22.29 ln biovolume l^{-1}. Stations 2 and 3 showed the highest cell abundance (~90 × 10^3 and ~80 × 10^3 cells l^{-1}, respectively; fig. 5). *Chaetoceros* spp. were the most abundant, with a cellular volume of ~280 μm^3, equivalent to a ~10 µm diameter. However, *Rhizosolenia* spp. showed the maximum cellular volume of ~13.4 × 10^6 μm^3, equivalent to a ~295 µm diameter. In general, stations 1, 4, and 5 showed abundances below 5×10^3 cells l^{-1}.

Photosynthetic Pigments

Photosynthetic pigments were classified into five groups in accordance with Bidigare et al. 1990: (1) "CHLA" chlorophyll a, chlorophyllide a, and phaeopigment a (not including phaeophorbide); (2) "CHLB" chlorophyll b, phaeopigment b; (3) "CHLC" chlorophyll c and c_2; (4) "PSC" photosynthetically active carotenoids, including fucoxanthin, 19' butanoyloxyfucoxanthin, 19' hexanoyloxyfucoxanthin, and prasinoxanthin; and (5) "PPC" photoprotectant carotenoids, including diadinoxanthin, alloxanthin, and zeaxanthin/lutein (table 3). This method does not make it possible to separate zeaxanthin from lutein (they have the same retention time), but there is evidence suggesting that zeaxanthin dominates over lutein in the ocean (Everitt et al. 1990), so we assumed that all the absorption at that particular retention time was due to zeaxanthin. However, these values should be interpreted with care. If chlorophyll b concentrations were low, then the presence of lutein would be minimal.

As expected, the concentration of chlorophyll a exceeded that of any other pigment, with an average range from 0.192 to 1.256 mg m^{-3}, while the ratio zeaxanthin/chl a varied from 0.066 to 0.374. Fucoxanthin pigment showed the same pattern as chlorophyll a, in the ranges of the average ratios (0.19 to 0.692) and concentrations from 0.05 to 0.87 mg m^{-3}.

Shape of the Absorption Spectra

The absorption, at all depths at which measurements were taken, was averaged (fig. 6a). From the averaged absorption spectra, two groups of stations were identified: group 1 includes stations 1, 4, and 5; group 2 includes

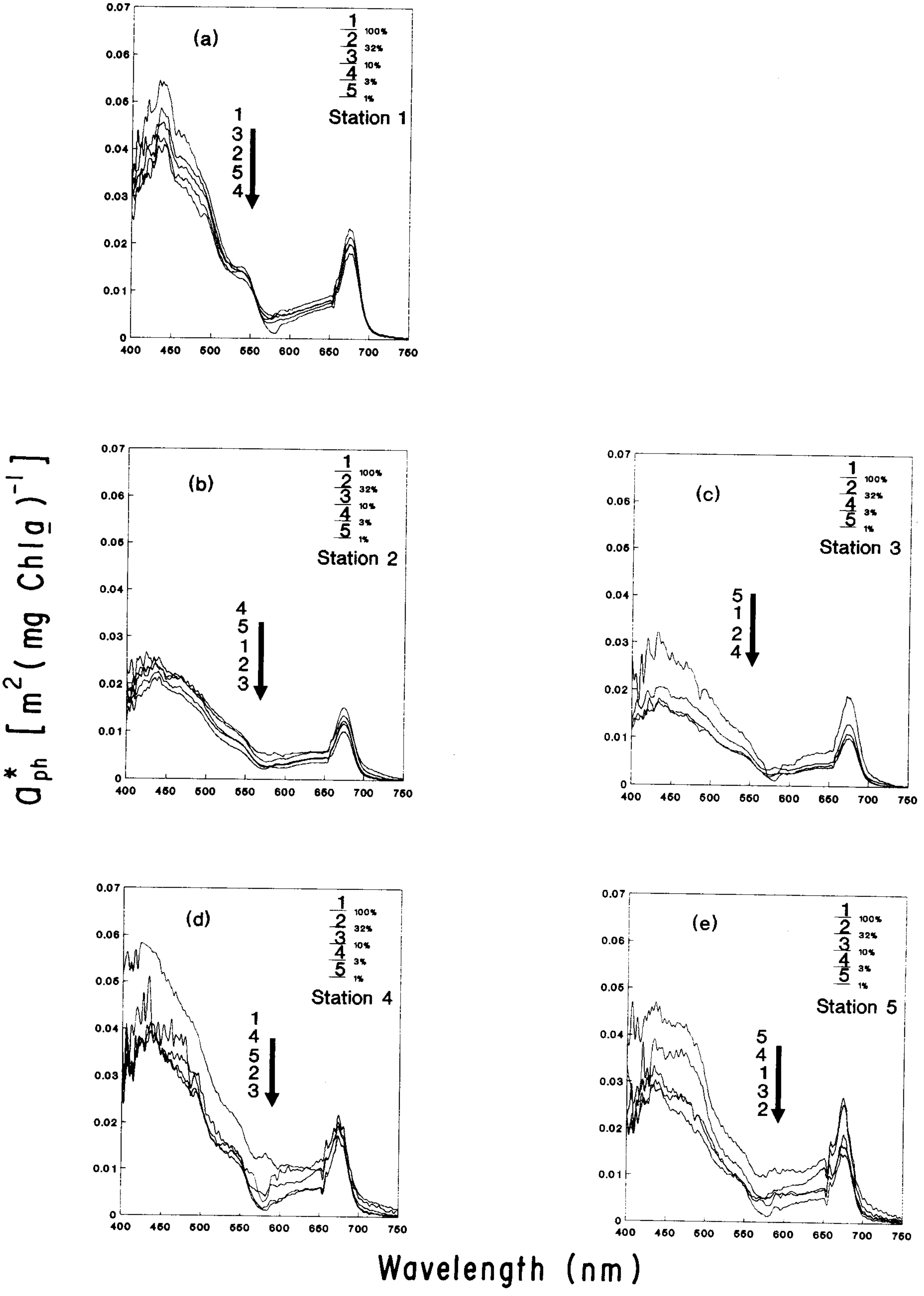

Figure 4. Spectral variability of the specific light-absorption coefficient of phytoplankton (a^*_{ph}) m^2(mg chl a)$^{-1}$ at five light depths (100%, 32%, 10%, 3%, and 1% of E_0): *a*, station 1; *b*, station 2; *c*, station 3; *d*, station 4; and *e*, station 5. Numbers to the left of the arrows indicate the position sequence of the spectral curves.

TABLE 2
Spatial Variability by Stations of Average Cell Volume l_n ($\mu m^3\ l^{-1}$) for Diatoms in the Gulf of California

Diatom genus (average)	Station 1	Station 2	Station 3	Station 4	Station 5
Nitzschia	13.92	13.57	14.92	13.38	13.64
Rhizosolenia	20.01	20.98	22.17	21.15	19.46
Chaetoceros	11.87	15.87	14.66	11.86	11.71
Skeletonema	10.34	11.53	12.08	—	—
Corethron	15.24	16.52	17.39	—	14.85
Bacteriastrum	10.26	12.10	11.55	11.20	—
Thalassiothrix	12.55	19.00	17.92	16.05	14.65
Leptocylindrus	15.31	16.78	17.02	—	15.85
Navicula	11.89	11.70	16.80	10.40	14.51
Ditylum	18.08	19.35	18.77	—	—
Coscinodiscus	15.69	19.72	18.36	13.57	14.21
Pseudoeunotia	—	17.68	18.25	—	—
Hemiaulus	—	16.37	15.69	—	—
Actinoptychus	—	17.60	17.21	—	13.47
Guinardia	—	—	18.09	—	—

TABLE 3
Spatial Variability by Station of Average Chlorophyll and Carotenoid Concentrations (mg m^{-3}) in the Gulf of California

Pigments (average)	Station 1	Station 2	Station 3	Station 4	Station 5
Chlorophyllide a	0.1203	0.2647	0.2969	0.1085	0.1808
Chlorophyll c	0.0691	0.4120	0.5943	0.0388	0.0919
19' But-fucoxant	0.0297	0.0369	0.2398	0.0285	0.0597
Fucoxanthin	0.1495	0.8704	0.7695	0.0531	0.0692
19' Hex-fucoxant	0.1301	0.1067	0.0617	0.0457	0.0522
Prasinoxanthin	0.0294	0.1217	0.1142	0.0190	0.0080
Diadinoxanthin	0.0130	0.0479	0.0547	0.0077	0.0113
Alloxanthin	0.0138	0.0111	0.0344	—	—
Zeax/Lutein	0.2853	0.0923	0.0757	0.0533	0.0470
Chlorophyll b	0.1209	0.0681	0.1040	0.0628	0.0681
Chlorophyll a	0.7621	1.2569	1.1524	0.1920	0.2384
Phaeopigment b	0.0929	0.1910	0.2448	0.0170	0.1227
Phaeopigment a	0.0102	0.0245	0.0262	0.0030	0.0071
Divinyl chl*a*	0.0160	0.0170	0.0130	0.0130	0.0530

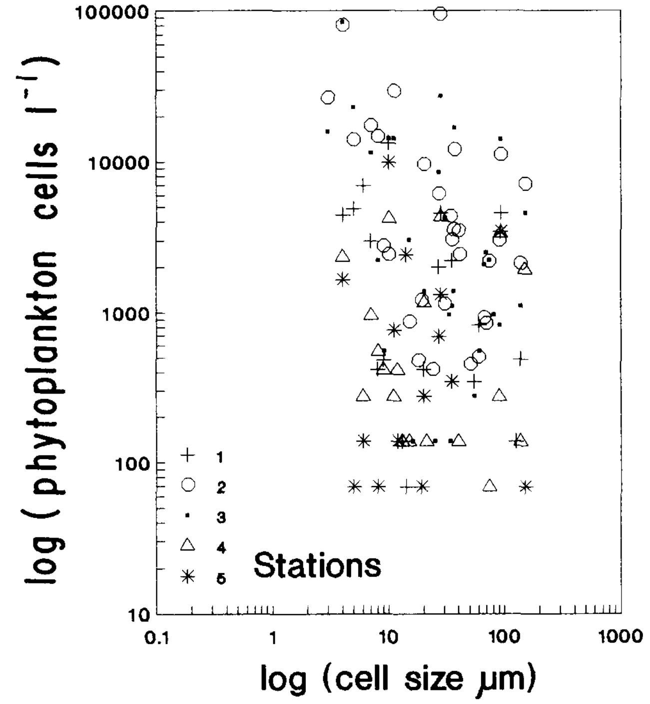

Figure 5. Abundances and cell sizes of phytoplankton by stations for the Gulf of California.

stations 2 and 3. The average spectral shapes, by stations, were determined from phytoplankton absorption normalized to 440 nm ($a_{ph}(\lambda)/a_{ph}$440 nm). The main difference between the two groups was the absorption at wavelengths 480–550 nm and 661 nm. The spectral shoulder observed near 545 nm has been reported as characteristic of cyanobacteria (Bidigare et al. 1989; Moore et al. 1995; Sathyendranath et al. 1996; and Jeffrey et al. 1997). Likewise, the absorption at 661 nm is characteristic of the divinyl chl a pigment and corresponds to the prochlorophytes group (Jeffrey et al. 1997).

In table 4 we show two algorithms, or empirical models, relating specific absorption of phytoplankton with the concentration of key pigments and with cell size. The best model ($r^2 = 0.80$; $p = 0.05$) for a^*_{ph} at 440 nm was achieved when the ratios zeax/chl a, chl a/biovolume, and biovolume cell^{-1} were included. For $a^*_{ph}(674)$, the best model ($r^2 = 0.67$; $p = 0.05$) was achieved when the ratios chl a/biovolume and zeax/chl a were considered.

DISCUSSION

During our study, the phytoplankton-specific absorption coefficient varied both between stations and within stations. Two of the five stations showed that a^*_{ph} was higher for the deeper samples. The values for $a^*_{ph}(440)$ were more variable than the values for $a^*_{ph}(674)$. The values for a^*_{ph}(440 nm) for stations 1, 4, and 5 were higher (~45%) than the values for stations 2 and 3. Stations 2 and 3 were located near the large islands (fig. 1); this region of the gulf has the highest ratios of chlorophyll c and fucoxanthin to chlorophyll a, indicating that diatoms dominate. This region is characterized by intense mixing (winds and tides), and typically has high primary productivity rates and blooms of microphytoplankton (cells >20 µm). Stations 1 and 5 had higher ratios of chlorophyll a/biovolume, fewer diatom genera, and lower ratios of chlorophyll c and fucoxanthin to chlorophyll a, compared to stations 2 and 3. In general, stations 2 and 3, which exhibited the lowest specific absorption coefficient, are located in a region where the environment favors the flourishing of larger species within the phytoplankton community. Our findings agree with previous conclusions about the ecological implications of the variability of absorption efficiencies of natural phytoplankton communities (Lewis et al. 1985; Mitchell and Kiefer 1988b; Yentsch and Phinney 1989; Bricaud

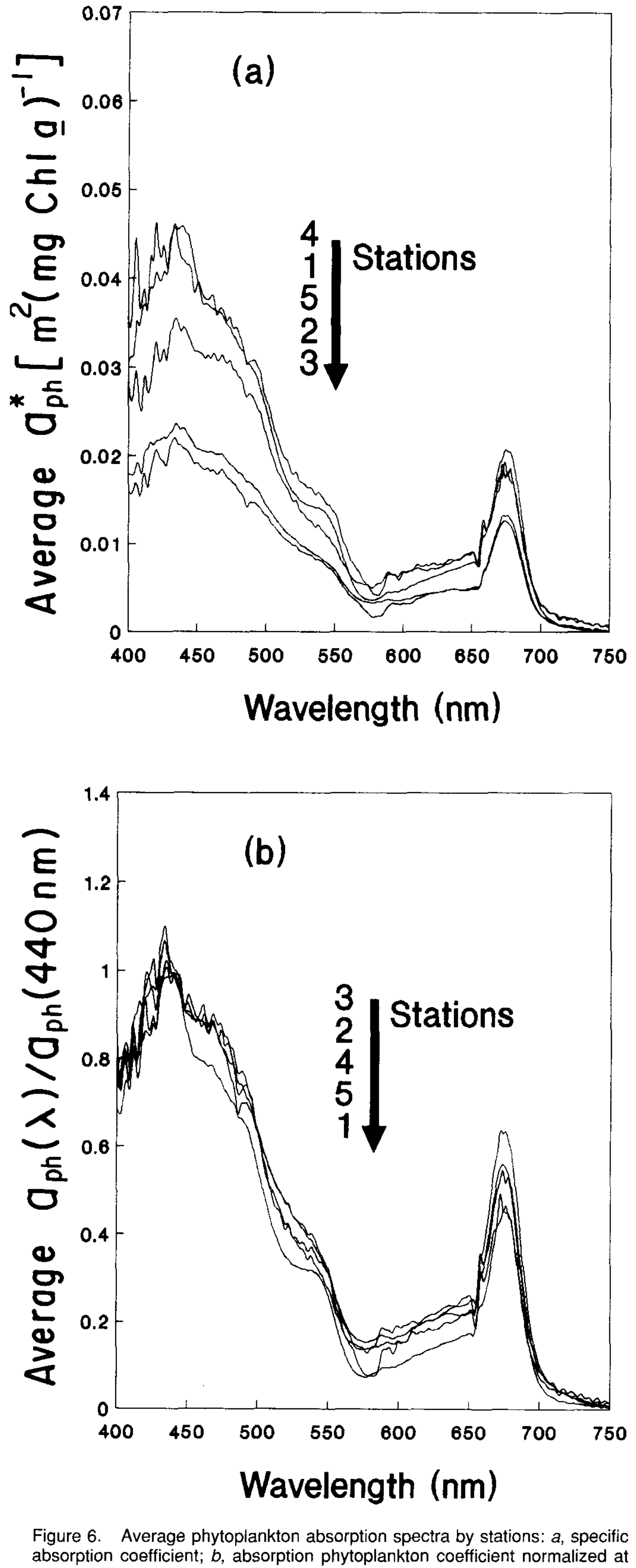

Figure 6. Average phytoplankton absorption spectra by stations: *a*, specific absorption coefficient; *b*, absorption phytoplankton coefficient normalized at 440 nm. The numbers to the left of the arrows show the position sequence of the spectral curves.

TABLE 4

Summary of Stepwise Regression Analysis for the Phytoplankton-Specific Light-Absorption Coefficient a^*_{ph} (440 and 674 nm) as a Dependent Variable

Variables	Partial cor.	R^{2a}	F^b	P level
440 nm				
Zeax/chla	0.778	0.578	20.07	.000624
Chla/biovol	0.716	0.708	13.76	.002642
Biovol/cel	0.563	0.800	6.05	.028801
674 nm				
Chla/biovol	0.800	0.504	22.75	.000334
Zeax/chla	0.683	0.671	11.35	.004994

[a] Multiple coefficient of determination.
[b] Variance ratio of the multiple regression.

and Stramsky 1990; Hoepffner and Sathyendranath 1992; Babin et al. 1993).

One of the main objectives of our study was to elucidate the factors causing variability in the phytoplankton absorption coefficient in the gulf. For instance, several studies (theoretical and laboratory) have reported that the absorption coefficient is not constant, and have argued that the variability is caused by the flattening of the absorption spectra due to particle effect (size, shape, and optical density of the particles) and the pigment composition (Duysens 1956; Morel and Bricaud 1981; Dubinsky et al. 1986; Sathyendranath et al. 1987; Mitchell and Kiefer 1988b; Sosik and Mitchell 1991; Kirk 1994).

Morel and Bricaud (1981) argued that the packing of chlorophyll into a cell physically changes the probability that an individual chlorophyll molecule will absorb a passing photon. As chlorophyll per cell increases at constant cell volume, the specific absorption coefficient decreases. This pattern might occur if a single species were increasing its pigments, perhaps due to photoadaptation, but not changing its size. However, in a natural phytoplankton community where the size spectrum comprises diverse species, it is uncertain whether chlorophyll per cell volume will remain constant as cell size varies. Our data (fig. 7) showed that chlorophyll a per volume [ln(chlorophyll a/biovolume)] decreased as cell size [ln(biovolume cell^{-1})] increased. This pattern indicated that, at least during our sampling, chlorophyll per cell volume was not independent of cell size, as assumed in Morel and Bricaud's (1981) calculations. Because this particular model restriction was not met by the field data, it is not necessary to expect a^*_{ph} to vary inversely with cell size. And, in fact, it did not: When plotted as a function of ln(biovolume cell^{-1}), neither $a^*_{ph}(674)$ nor $a^*_{ph}(440)$ showed any discernable pattern (data not shown), and the relationships were not statistically significant.

A second factor that might be significant in this discussion of cell size is a technical limitation. Only

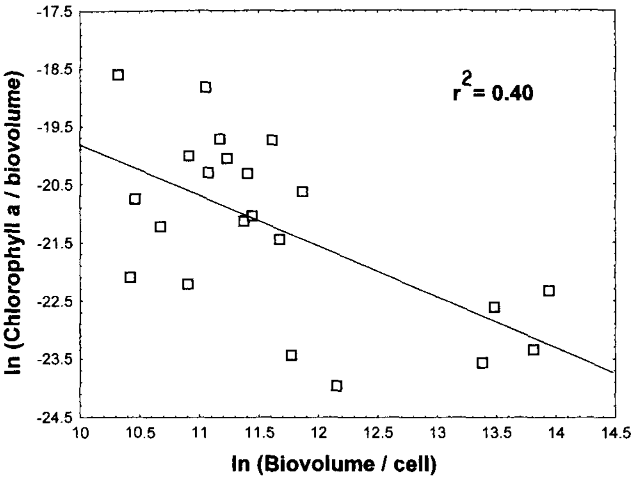

Figure 7. The chlorophyll a/biovolume ln(chlorophyll a/biovolume) as a function of the cell sizes ln(biovolume cell^{-1}) ($r^2 = 0.40$; $p = 0.05$).

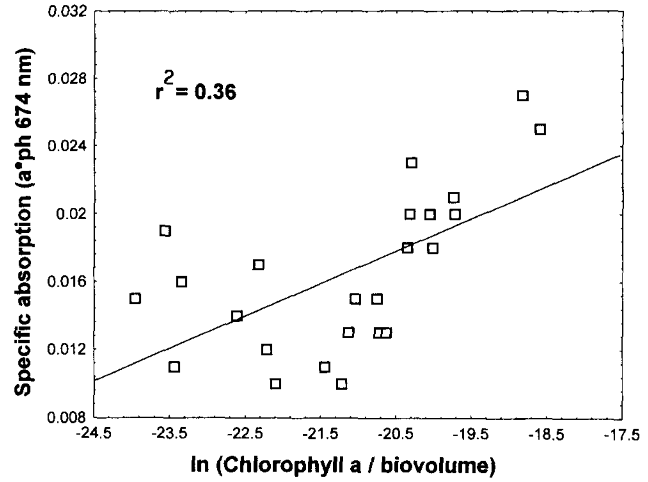

Figure 8. Specific light-absorption coefficients of phytoplankton a^*_{ph} m^2 (mg chl a)$^{-1}$ as a function of the ln(chlorophyll a/biovolume) at 674 nm ($r^2 = 0.36$; $p = 0.05$).

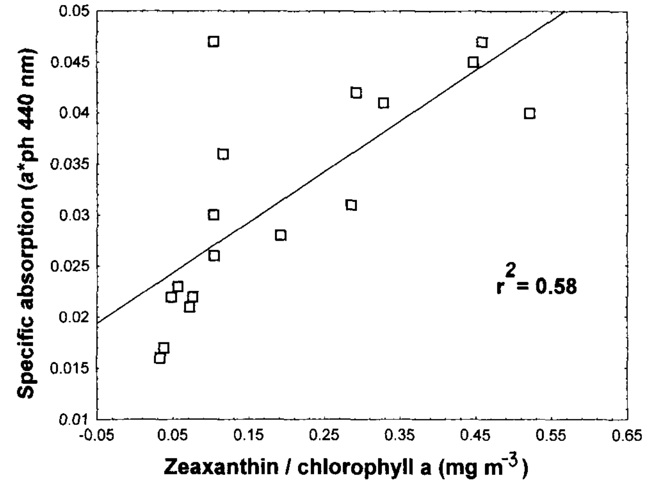

Figure 9. Specific light-absorption coefficient of a^*_{ph} m^2(mg chl a)$^{-1}$ in the blue band (440 nm) as a function of the ratio zeaxanthin/chlorophyll a ($r^2 = 0.58$; $p = 0.05$).

phytoplankton cells >5 µm can be counted and sized with the inverted microscope technique. However, the absorption and pigment measurements could include small cells (>0.7 µm). The observations that >60% of the countable phytoplankton cells in our samples were in the nanophytoplankton (<20 µm) fraction might suggest that the cells in the uncounted <5 µm fraction were abundant. This systematic bias may contribute to the absence of the expected pattern of decreasing specific absorption coefficient with increasing cell size; in this data set we were not able to find a significant slope (data not shown). However, when we used the ratio chlorophyll a/biovolume as an index of the size of the phytoplankton community, we found that the highest specific absorption coefficients (a^*_{ph}674 nm) corresponded to stations 1 and 5, where small-size cells were abundant (fig. 8).

As pointed out before, changes in pigment composition have also been associated with variations in phytoplankton-specific absorption coefficient. In the Gulf of California, the average ratios of zeaxanthin/chlorophyll a were high (up to 0.37). Of all the pigments studied (table 3), the highest correlation ($r^2 = 0.58$; $p = 0.05$) with a^*_{ph} was obtained between the ratio zeaxanthin/chlorophyll a and a^*_{ph}(440) (fig. 9). In general, the ratio zeaxanthin/chl a can be used as a marker pigment for cyanobacteria and prochlorophytes (Kana et al. 1988; Bidigare et al. 1989; Falkowski and Laroche 1991; Bricaud et al. 1995; Moore et al. 1995; and Sathyendranath et al. 1996). The distinctive divinyl chlorophyll a absorption peaks (~661 nm) of prochlorophytes were observed at stations 1, 4, and 5 (fig. 6a).

Cyanobacteria pigments are evident as absorption shoulders at 480 and 550 nm in the spectra from stations 1, 4, and 5 (fig. 6b), indicating that the cyanobacteria group was present. Even though we could not directly count cyanobacteria (typically about 1 µm in diameter) with the inverted microscope technique, the presence of these small cells is evidenced by these absorption and pigment data.

High a^*_{ph} is expected for small cells because of low or absent pigment-packaging effects; the presence of small cyanobacteria where zeaxanthin was high explains part of the pattern between a^*_{ph}(440) and zeaxanthin/chlorophyll a shown in figure 9. Futhermore, zeaxanthin manifests wavelength maxima at 454 and 480 nm (Jeffrey et al. 1997), typical of carotenoids; high at blue and blue-green wavelengths with a broad peak. When present, zeaxanthin is certainly responsible for some of the measured absorption at 440 nm, artificially increasing $a^*_{ph}(440)$, which is normalized to chlorophyll a concentration only. Indeed, $a^*_{ph}(440)$ tended to be high where the pigment group PPC was high. The positive relation between $a^*_{ph}(440)$ and the ratio of zeaxanthin/chlorophyll a is probably due to the combined effects of pigment composition and cell size, and to the related errors in the β factor caused by these small phytoplankton on specific absorption.

At stations 2 and 3, there was less variability in the magnitude of a^*_{ph} with depth in the water column (fig. 4b, c), lower a^*_{ph}, and the lowest ratio of average zeaxanthin/chl a (0.073 and 0.066), with no indication of absorption by cyanobacteria pigments (table 3). We confirmed these observations by examining the exponential curve of methanol-extracted particulate absorption spectra (data not shown).

We used multiple regression analysis to explore whether cell size or pigment composition was more significant in the variability of the specific absorption coefficient (table 4). We found that the variability of $a^*_{ph}(440)$ was most strongly related first to the ratio of zeaxanthin/chlorophyll a ($r^2 = 0.58$; $p = 0.05$), second to the ratio chlorophyll a/biovolume, and finally to biovolume per cell, giving a final r^2 of 0.80; other variables were not significant in the model. Our results are in line with laboratory results of Sathyendranath et al. (1987), who studied the particle and pigment composition effect on the absorption spectra of eight species of phytoplankton. They were able to explain 44% of the variability of the absorption efficiency at 440 nm by changes in the pigment composition. When the pigment packaging was included with pigment composition, the model explained up to 96% of the variation in absorption efficiency.

Our data showed greater variability in a^*_{ph} at 440 nm than 674 nm. This difference results from strong absorption in the blue region by carotenoids; however, their concentrations were not considered in our calculations of the specific absorption coefficient. Variable contributions to $a^*_{ph}(440)$ by carotenoids will increase variability in $a_{ph}(440)$. In the red region (674 nm), the main absorption is due to chlorophyll a. Similar results have been reported by Sathyendranath et al. (1987) for laboratory cultures; Yentsch and Phinney (1989) for the western North Atlantic; Sosik and Mitchell (1991) for the California Current; and Sathyendranath et al. (1996) for the northwest Indian Ocean.

Kiefer and SooHoo (1982) measured values for the specific absorption coefficient in Gulf of California waters in March 1979 and reported a mean value of 0.022 $m^2(\text{mg chl a})^{-1}$ for $a^*_{ph}(440)$. Yentsch and Phinney (1989) reported values for a^*_{ph} (440) of ~0.082 and ~0.047 for $a^*_{ph}(670)$ for the southern part of the gulf in March 1988. Our October values for the central and northern gulf ranged from 0.020 to 0.056 $m^2(\text{mg chl a})^{-1}$ for $a^*_{ph}(440)$ and from 0.013 to 0.020 $m^2(\text{mg chl a})^{-1}$ for $a^*_{ph}(674)$. Yentsch and Phinney's values were higher than ours; they suggested that the high absorption values were due to increased concentration of UV-photoprotective pigments. The data available for the Gulf of California (this paper; Kiefer and SooHoo 1982; Yentsch and Phinney 1989) are not sufficient for interpreting seasonal or interannual variability.

For our data set, pigment composition was more important than cell size for determining the magnitude of $a^*_{ph}(440)$. However, in order to explain 80% of the variability in $a^*_{ph}(440)$, a variable related to cell size was required. Most of the previous field work on the variation of $a^*_{ph}(440)$ has focused on only one of these three variables at a time. Our results are significant because they illustrate the interaction of pigment composition and pigment packaging (through chlorophyll per cell volume and through cell size) in determining the magnitude of $a^*_{ph}(440)$.

CONCLUSION

The spectra of phytoplankton belonging to the same taxonomic group tended to have similar shapes. The specific absorption coefficient of phytoplankton was highly variable (spatial domain) in the gulf. Stations where the environment favors the development of microphytoplankton (cells >20 μm) presented the lowest specific absorption coefficients because of the increased pigment-packaging effect in these biggest cells. Pigments, particularly the photoprotectant pigment zeaxanthin, had the highest correlation with the absorption coefficient. Changes in pigment composition and cellular concentration were responsible for over 70% of the variability in the specific absorption coefficient at 440 nm, and—if biovolume per cell was included—the model explained up to 80% of the variance.

The significance of these results lies in the concurrent quantitative examination of several potential controls of the specific absorption coefficient: pigment packaging (i.e., the cellular concentration of chlorophyll a and the phytoplankton cell volume) and the confounding effect of blue-absorbing accessory pigments. The statistical significance of the resulting multivariate relationships indicates that all three of these factors can influence the specific absorption coefficient.

Chlorophyll per volume [ln(chl a/biovolume)] decreased as cell size (biovolume cell^{-1}) increased; theoretical analysis that holds one variable constant while examining the other does not account for the situation observed in these particular phytoplankton communities. The bigger cells did not maintain the same internal concentration of chlorophyll per cell volume as the smaller cells; therefore, figure 8 shows that as ln(chl a/biovolume) decreased, indicating large cells, the a^*_{ph} decreased. Observations of a nonlinear relationship between $a_{ph}(440)$ or $a^*_{ph}(440)$ and chlorophyll a (e.g., Yentsch and Phinney 1989; Bricaud et al. 1995; Cleveland 1995) may indeed be due to a pigment-packaging effect related to cell size, as postulated. But our results and some of those in Cleveland 1995 show that this situation is not always the case. As previously pointed out by Hoepffner and Sathyendranath (1992), accessory pigmentation plays a significant role in the variability of $a^*_{ph}(440)$. Perhaps it is time for the community to define the specific absorption coefficient in terms that include these other pigments.

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SPAWNING HABITAT OF THE PACIFIC SARDINE (*SARDINOPS SAGAX*) IN THE GULF OF CALIFORNIA: EGG AND LARVAL DISTRIBUTION 1956–1957 AND 1971–1991

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ABSTRACT

The distribution of Pacific sardine eggs and larvae in the Gulf of California was studied from 38 cruises carried out during 1956–57 and 1971–91. Eggs and larvae were found throughout the gulf, but spawning was more intense in the central region. Contrary to previous hypotheses, spawning was not restricted to the coasts. Pacific sardine spawn in the Gulf of California from November to May, most intensely during December and January. Spawning habitat is inferred from the sea-surface temperature (SST) where early-stage (I–III) eggs are present; spawning occurred at 18.9° ± 1.9°C. Water is rarely colder than 14° in the gulf, so cold water is not likely to limit spawning, but the probability of finding Pacific sardine eggs is lower than 5% in waters warmer than 24° at the surface. It is suggested that Pacific sardine spawning in the Gulf of California is limited by the strong seasonality in sea-surface temperature caused in part by the summer intrusion of warm, subtropical water. Furthermore, eggs and larvae appear to be retained by the central anticyclonic gyre found in the gulf during winter, and spawning close to the eastern coast could be detrimental because of transport to the warm, subtropical conditions in the south.

INTRODUCTION

The Pacific sardine, *Sardinops sagax* (Jenyns, 1842), is a coastal pelagic schooling fish found from the Gulf of California, Mexico, to British Columbia, Canada (Whitehead 1985). In the Gulf of California, it has typically been the dominant species in the multispecies "sardine" fisheries. Yearly landings have exceeded 275,000 metric tons, and there is concern that the stock may have been overexploited (Cisneros-Mata et al. 1995). Hedgecock et al. (1989) found no genetic differences between sardine sampled from the Gulf of California and four other widely separated localities on the Pacific Coast. Nevertheless, there may be regional differences in life-history traits and population dynamics that occur on shorter time scales.

The Gulf of California is a semienclosed sea, unique in being the only large evaporation basin in the Pacific Ocean (Roden and Groves 1959). It is characterized by great seasonality in temperature, circulation, winds, upwelling, and productivity (Rosas-Cota 1977; Badan-Dangon et al. 1985; Robles and Marinone 1987; Valdéz-Holguín and Lara-Lara 1987; Bray 1988; Ripa and Marinone 1989; Alvarez-Borrego and Lara-Lara 1991; Paden et al. 1991; Cervantes-Duarte et al. 1993; Castro et al. 1994; Santamaría-del-Angel et al. 1994a, b; Lavín et al. 1995).

There have been many reports of sardine eggs and larvae collected from ichthyoplankton cruises in the Gulf of California (Sokolov and Wong-Ríos 1972, 1973; De la Campa and Gutierrez 1974; Gutierrez 1974; Gutierrez and Padilla 1974; Moser et al. 1974; Sokolov 1974; Wong-Ríos 1974; De la Campa and Ortiz 1975; Molina-Valdez and Pedrin 1975; De la Campa et al. 1976; Padilla-Garcia 1976a, b, 1981; Olvera-Limas 1981; Olguin et al. 1982; Molina-Valdez et al. 1984; Olvera-Limas and Padilla 1986). However, egg stages have not been presented to better define the spawning season, and the overall seasonality of Pacific sardine spawning has not been described.

The purpose of this paper is to analyze the seasonality in the distribution of Pacific sardine eggs and larvae collected on 38 cruises from 1956 to 1991 in the Gulf of California and to determine the relation of spawning to sea-surface temperature. Early-stage eggs are a good index of spawning, and their presence can be used to define the thermal limits under which spawning tends to occur (Tibby 1937; Ahlstrom, 1943; Lasker 1964; Lluch-Belda et al. 1991).

MATERIALS AND METHODS

Historical raw data come from seven California Cooperative Oceanic Fisheries Investigations (CalCOFI,

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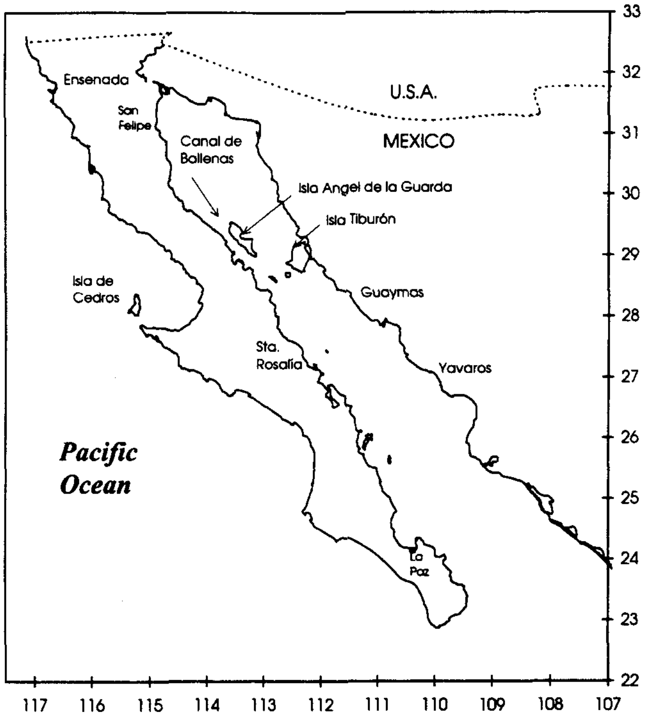

Figure 1. The Gulf of California.

TABLE 1
Cruises in the Gulf of California

Cruise	Institution	Dates	Number of stations
CC5602	CalCOFI, USA	Feb. 1956	93
CC5604	"	Apr. 1956	129
CC5612	"	Dec. 1956	79
CC5702	"	Feb. 1957	70
CC5704	"	Apr. 1957	125
CC5706	"	June 1957	132
CC5708	"	Aug. 1957	81
AA7101	INP, Mexico	Apr. 1971	50
AH7110	"	Sept. 1971	80
AA7204	"	Apr. 1972	77
AH7206	"	Nov. 1972	79
AA7302	"	Mar. 1973	79
AH7303	"	Mar. 1973	15
AA7305	"	Apr.–May 1973	75
AA7308	"	July 1973	103
AA7402	"	Feb.–Mar. 1974	52
AA7403	"	Apr. 1974	12
AA7405	"	Dec. 1974	19
AA7501	"	Jan. 1975	66
AA7503	"	Mar.–Apr. 1975	50
AA7504	"	Apr. 1975	39
AA7601	"	Jan. 1976	65
AH7605	"	Apr. 1976	66
AA7605	"	July 1976	58
AA7701	"	Feb. 1977	24
AH7703	"	Sept. 1977	58
AA7704	"	Aug.–Sept. 1977	50
AA7708	"	Dec. 1977	48
AA7802	"	Feb.–Mar. 1978	59
AA7810	"	Sept.–Oct. 1978	59
AA8103	"	Mar.–Apr. 1981	78
PU8403	"	Mar.–Apr. 1984	87
PU8611	"	Nov. 1986	187
AA8701	"	Jan.–Feb. 1987	56
PU8711	"	Nov. 1987	22
AL9002	CICESE	Feb.–Mar. 1990	200
BIPXI9008	"	Aug.–Sept. 1990	38
PU9109	"	Sept. 1991	110

USA) and 28 Instituto Nacional de Pesca (INP, Mexico) cruises in the Gulf of California (fig. 1) during 1956–57 and 1971–87; three additional cruises were carried out by the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE, Mexico) during 1990 and 1991 (table 1).

The number of cruises per year, number of stations, sampling gear, and station plan varied among cruises (fig. 2, table 2); there were no cruises during the 1960s. During the 38 cruises, 3,631 tows from 2,667 stations were made with a surface neuston net, a standard CalCOFI net, a bongo net, or a CalVET net, following ichthyoplankton techniques described by Kramer et al. (1972), Smith and Richardson (1977), and Lasker (1985).

Pacific sardine eggs and larvae were separated; eggs were staged following Ahlstrom (1943); and larvae were measured to ±0.5 mm. Egg abundance data were standardized to numbers/m^2; larval abundances were standardized to numbers/10 m^2. The high variability of water volume filtered in the surface neuston tows caused by the net breaking the surface, and the overestimation of abundance from surface samples does not allow for standardization, so for neuston samples we used presence or absence, not actual abundance.

During summer months in the Gulf of California, Pacific sardine eggs could be confused with those of thread herring (*Opisthonema* spp.; Matus-Nivón et al. 1989 [for *O. libertate*]), but slight differences between the number of myomeres and pigmentation of the larvae have been reported (Watson and Sandknop 1996). Nevertheless, it is unlikely that thread herring eggs and larvae occurring in the summer would have been misidentified as Pacific sardine for several reasons. Adult distribution of Pacific sardine during the summer is restricted to the region of the large islands, north of the central gulf (Cisneros-Mata et al. 1988). Adult maturity studies have shown that Pacific sardine preferentially spawn in cooler temperatures during winter and spring (Torres-Villegas et al. 1986), and thread herring spawn in warm temperatures during summer (Torres-Villegas et al. 1985; Rodriguez 1987). The relative abundance of thread herring adults in the Gulf of California is usually lower than that of Pacific sardine (Cisneros-Mata et al. 1988). As an example, thread herring scales were not sufficiently abundant to appear in laminated sediments in the Gulf of California (Holmgren and Baumgartner 1993), even though they are quite different from Pacific

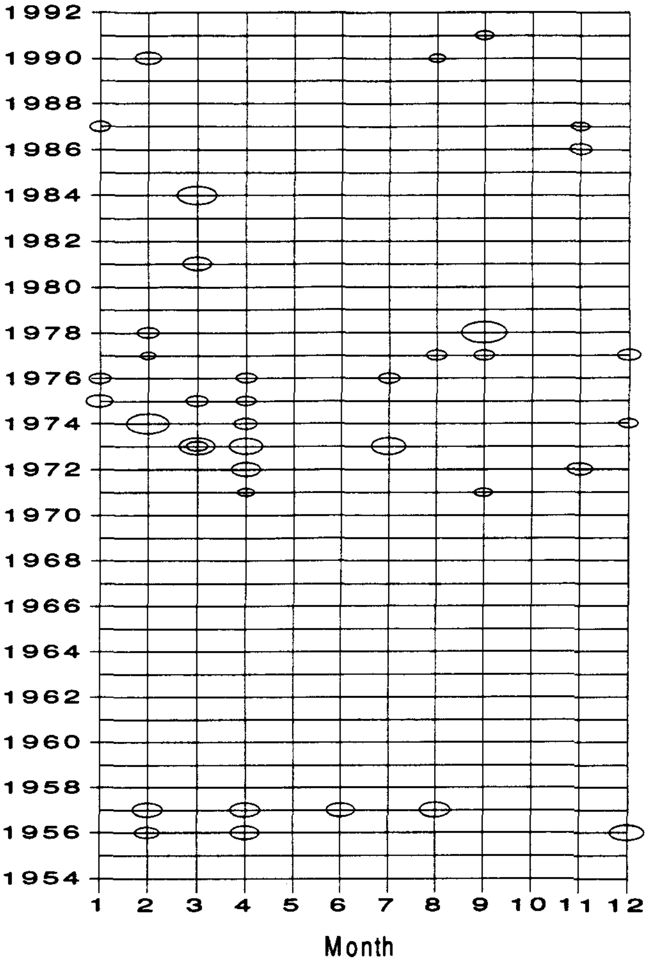

Figure 2. Time distribution of cruises in the Gulf of California. Ellipses indicate individual cruises, with size proportional to cruise duration (5 to 31 days).

TABLE 2
Number of Stations and Tows per Cruise in the Gulf of California

Cruise	Stations	Oblique tows*	Neuston tows
CC5602	93	93	0
CC5604	129	129	0
CC5612	79	79	0
CC5702	70	70	0
CC5704	125	125	0
CC5706	132	132	0
AA7101	50	50B	50
AH7110	80	80C	80
AA7204	77	77C	77
AH7206	79	79C	79
AH7302	79	71C	61
AA7303	15	15C	4
AA7305	75	73C	70
AA7308	103	66C	103
AA7402	52	40C	52
AA7403	12	8C	12
AA7405	19	16C	17
AA7501	66	37C	66
AA7503	50	50C	50
AA7504	39	32C	39
AA7601	65	39C	65
AH7605	66	49C	66
AA7605	58	39C	58
AA7701	24	21C	24
AH7703	58	48C	58
AA7704	50	50C	0
AA7708	48	48C	0
AA7802	59	59C	0
AA7810	59	59C	0
AA8103	78	78C	0
PU8403	87	87B	0
PU8611	187	187CV	0
AA8701	56	56B	0
PU8711	22	22B	0
AL9002	200	200CV	0
AL9002	200	110B	0
BIP9008	47	47M	0
PU9109	79	79B/71M	0

*B = bongo net; C = CalCOFI net; CV = CalVET net; M = Kidd-Methot net.

sardine scales and easily identifiable (Holmgren 1993). During the June cruise clupeoid eggs were found and thought to be thread herring (12.3% positive from NMSF/SWFC raw data notes) because thread herring larvae were the most abundant larval fish and no Pacific sardine larvae were found (Moser et al. 1974); using later life stages as a taxonomic aid for earlier life stages is a common practice. Furthermore, although Pacific sardine eggs and larvae were reported from the two cruises during July, no thread herring eggs were reported. Thread herring larvae were reported for the cruises during August and September, but not thread herring eggs.

Seasonality in the spawning of Pacific sardine is described as the average percentage of positive stations per month for eggs and larvae. Distribution and abundance data for Pacific sardine eggs and larvae in the Gulf of California are combined for all cruises, as well as for each month when spawning occurred.

Sea-surface temperature (SST) was taken at each station during the cruises. Station SST data for the CalCOFI cruises are from SIO (1963 and 1965). The surface thermal characteristics of the spawning habitat were described by comparing the frequency distribution of SST for stations positive for egg stages I–III and IV–XI, and larvae. Eggs are 13 to 8 hours old at the end of stage III at 17° and 21°C, respectively (calculated from data in Lasker 1964). Using all egg stages to increase the sample size, we calculated the probability of finding Pacific sardine eggs at different SSTs.

RESULTS

Average SST in the Gulf of California ranged from 17° in February to 30° in August; no cruises were made in October, so that point was interpolated (fig. 3).

Pacific sardine spawn in the Gulf of California from November to May, most intensely during December and January (fig. 4, table 3). Owing to their more dispersed distribution (Smith 1973; Hewitt 1981), larvae (20%–50%

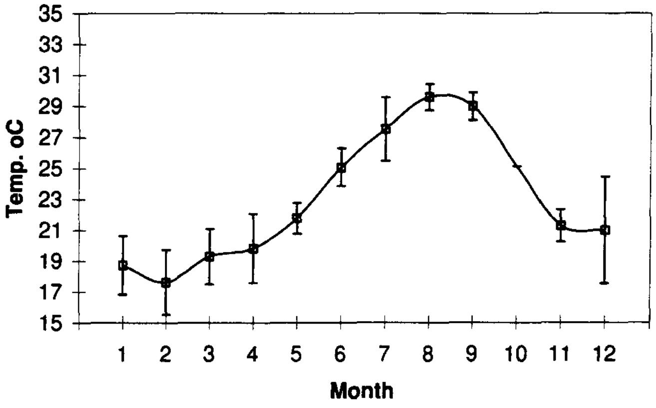

Figure 3. Average monthly sea-surface temperature in the Gulf of California from cruise data ±1 SD.

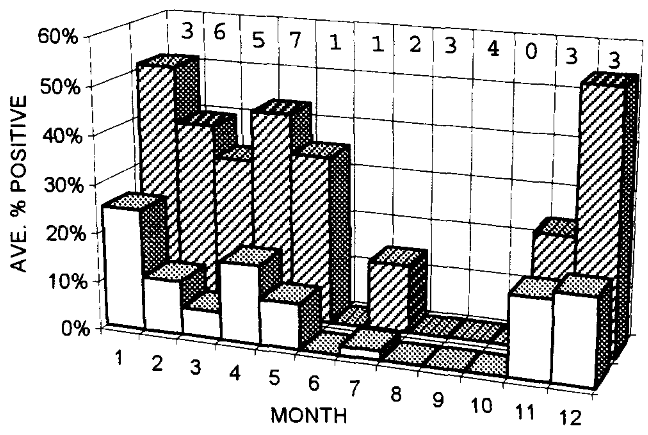

Figure 4. Monthly average percentage of positive stations for all egg stages (open bars) and larvae (hatched bars) of Pacific sardine in the Gulf of California, 1956–91. Numbers at top indicate the number of cruises per month.

TABLE 3
Percentages of Positive Stations for Pacific Sardine Eggs and Larvae in the Gulf of California

Cruise	Stations	Eggs	Larvae
CC5602	93	17.4	35.5
CC5604	129	16.7	35.8
CC5612	79	13.7	52.9
CC5702	70	29.2	42.4
CC5704	125	17.5	68.2
CC5706	132	0.0	0.0
CC5708	81	0.0	0.0
AA7101	50	30.0	32.0
AH7110	80	0.0	0.0
AA7204	77	10.4	40.3
AH7206	79	0.0	2.5
AA7302	71	5.1	36.7
AA7303	15	0.0	13.3
AA7305	73	9.3	34.7
AA7308	66	1.9	17.5
AA7402	40	11.3	51.9
AA7403	8	33.3	50.0
AA7405	16	31.6	89.5
AA7501	37	6.1	43.9
AA7503	50	10.0	36.0
AA7504	32	2.6	56.4
AA7601	39	16.9	33.8
AH7605	49	3.0	18.2
AA7605	39	1.7	10.3
AA7701	21	4.2	41.7
AH7703	48	3.4	0.0
AA7704	50	0.0	0.0
AA7708	48	8.3	18.7
AA7802	59	0.0	28.8
AA7810	59	1.7	0.0
AA8103	78	12.8	41.0
PU8403	87	0.0	35.6
PU8611	187	31.0	0.0
AA8701	56	51.8	75.0
PU8711	22	18.2	68.2
AL9002	110	4.0	35.0
BIP9008	38	0.0	0.05
PU9109	110	0.0	0.0

stations positive) were captured in more stations than eggs (5%–25%).

The central gulf is the most important area for spawning in the Gulf of California (fig. 5); spawning is not restricted to the coasts, but appears more related to the central gyre(s). Spawning was irregular in both the northern and southern gulf. More larvae than eggs were collected in the samples, and larvae were more widely distributed throughout the central gulf.

Monthly distribution maps for eggs and larvae are shown for November to May, when most spawning occurred (figs. 6 and 7). When spawning was most intense, higher concentrations appeared in the central gulf and became less dense and generally more coastal as spawning declined. Comparison of the distribution of eggs and larvae reveals little evidence for east–west transport, although transport of larvae to the south is suggested.

The SST interval within which eggs of stages I–III, IV–XI, and larvae were collected in the gulf clearly differed from that of the general gulf environment (fig. 8). Of the 1,209 stations sampled for eggs, only 59 were positive for stage I–III eggs. The average SST for those stations was 18.9° ± 1.9°. One standard deviation below and above the mean SST for these early-stage eggs is between 16.9° and 20.8°. A total of 213 stations were positive for eggs of any stage.

Older eggs (stages IV–XI) become dispersed over the SSTs found in this environment, and generally occur in warmer waters and within a wider SST interval than stage I–III eggs (Kolmogorov-Smirnov *t* test, $p < 0.07$). Larvae were found in significantly cooler water (19.0° ± 2.1°) than stage IV–XI eggs (Kolmogorov-Smirnov *t* test, $p < 0.008$), and no significant difference was found from the SST interval of stage I–III eggs. All egg stages and larvae were found in SSTs significantly cooler than

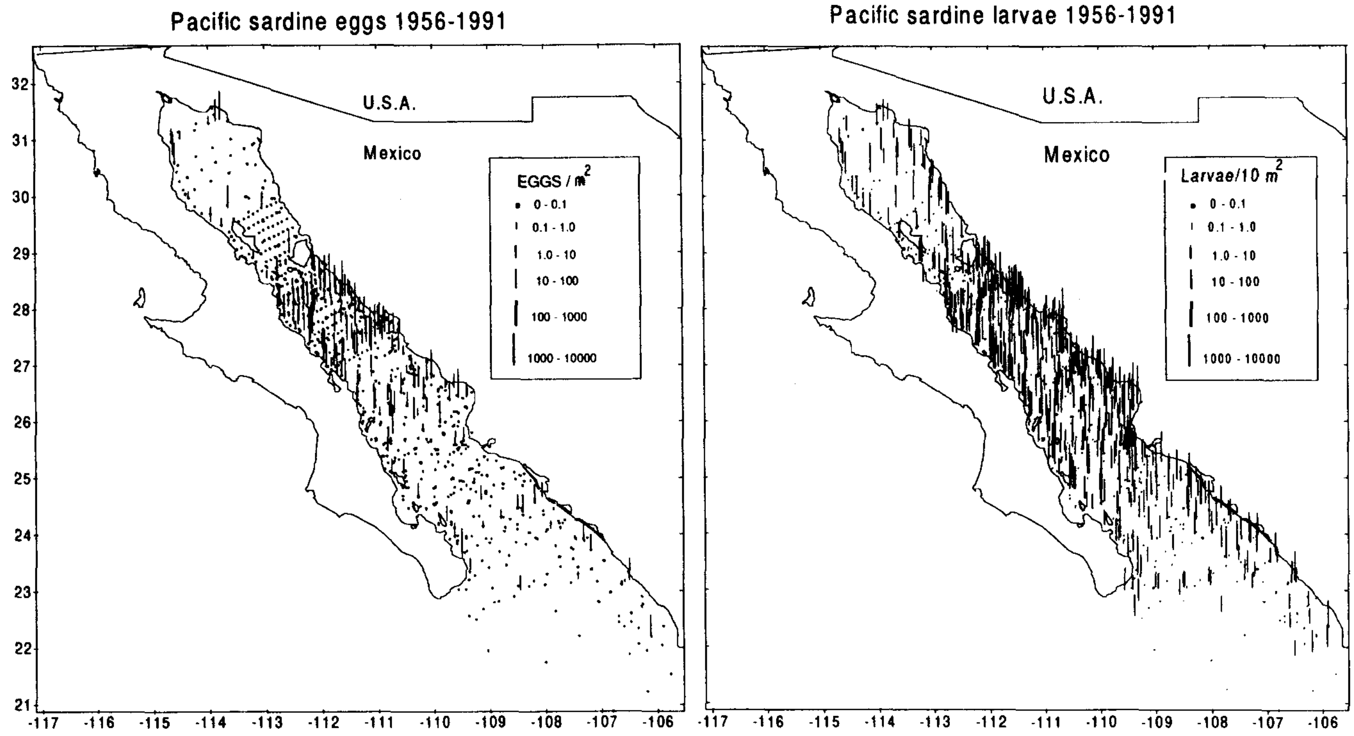

Figure 5. Distribution and abundance of Pacific sardine eggs and larvae collected on 38 cruises in the Gulf of California, 1956–57 and 1971–91.

the gulf's average SST of 22.3° ± 4.7° (Kolmogorov-Smirnov *t* test, $p < 0.001$).

The probability of collecting eggs at different SSTs available in the Gulf of California is truncated below 14°, and skewed toward higher SSTs (fig. 9). For eggs of any stage, 95% of positive stations are found between 15° and 23° SST. Dispersion of eggs into warmer, and possibly unfavorable, waters, as suggested by figure 8, is also shown here by the skewness of the curve; the wider SST interval is due to the inclusion of late-stage eggs.

DISCUSSION

This study incorporated historical data from 38 cruises of varying design; standard techniques were not always used, nor was the gulf equally represented in time and space. Recently, disparities between CalCOFI and INP egg staging showed that INP underestimated the numbers of early stages because many eggs were assumed to be damaged, and were not aged. For the purpose of the present paper, however, more emphasis was given to total eggs and their percentage of occurrence.

Because of these shortcomings in the database, interannual comparisons of distribution, abundance, and spawning biomass cannot be made. Nevertheless, by combining cruises and thus increasing sample size, it is possible to reach some conclusions about spawning habitat in relation to SST conditions of the gulf.

Dispersal of eggs and larvae is shown by the greater geographical area over which larvae were collected (see figs. 5–7), and by the increased SST range over which older eggs and larvae were found. Smith (1973) defined diffusion and transport as the only feasible causes of dispersal until larvae can swim well enough to determine their own distribution. Hewitt (1981) described a decrease in patchiness after spawning as eggs are dispersed passively; when larvae begin to form schools and swim, patchiness increases. The significant decrease in mean SST of stations positive for larvae compared to eggs, despite higher overall SST in the gulf, also suggests this pattern of dispersal and then schooling.

Optimal physical conditions for larval survival and growth occur where physical forces provide retention, concentration, and enrichment (Parrish et al. 1981; Lasker 1985; Cury and Roy 1989; Bakun et al. 1991; Hunter and Alheit 1995; Bakun 1996). The circulation in the Gulf of California provides an ideal combination of factors for larval survival, by aiding the retention of eggs and larvae in the highly productive central gulf region. Two major gyre systems have been described, one in the upper gulf, and the other in the central/southern region (Bray 1988; Marinone and Ripa 1988; Beier 1997; Marinone, unpubl. data). In the upper 100 m of the central gulf gyre, currents near the coast can be as strong as 60 km per day (70 cm s^{-1}), diminishing to almost zero about 30 km offshore (Beier 1997). During winter, flow is southward on the eastern coast and northward on the peninsular coast; during summer the flow reverses (Beier 1997). Both Beier (1997) and Marinone (unpubl.

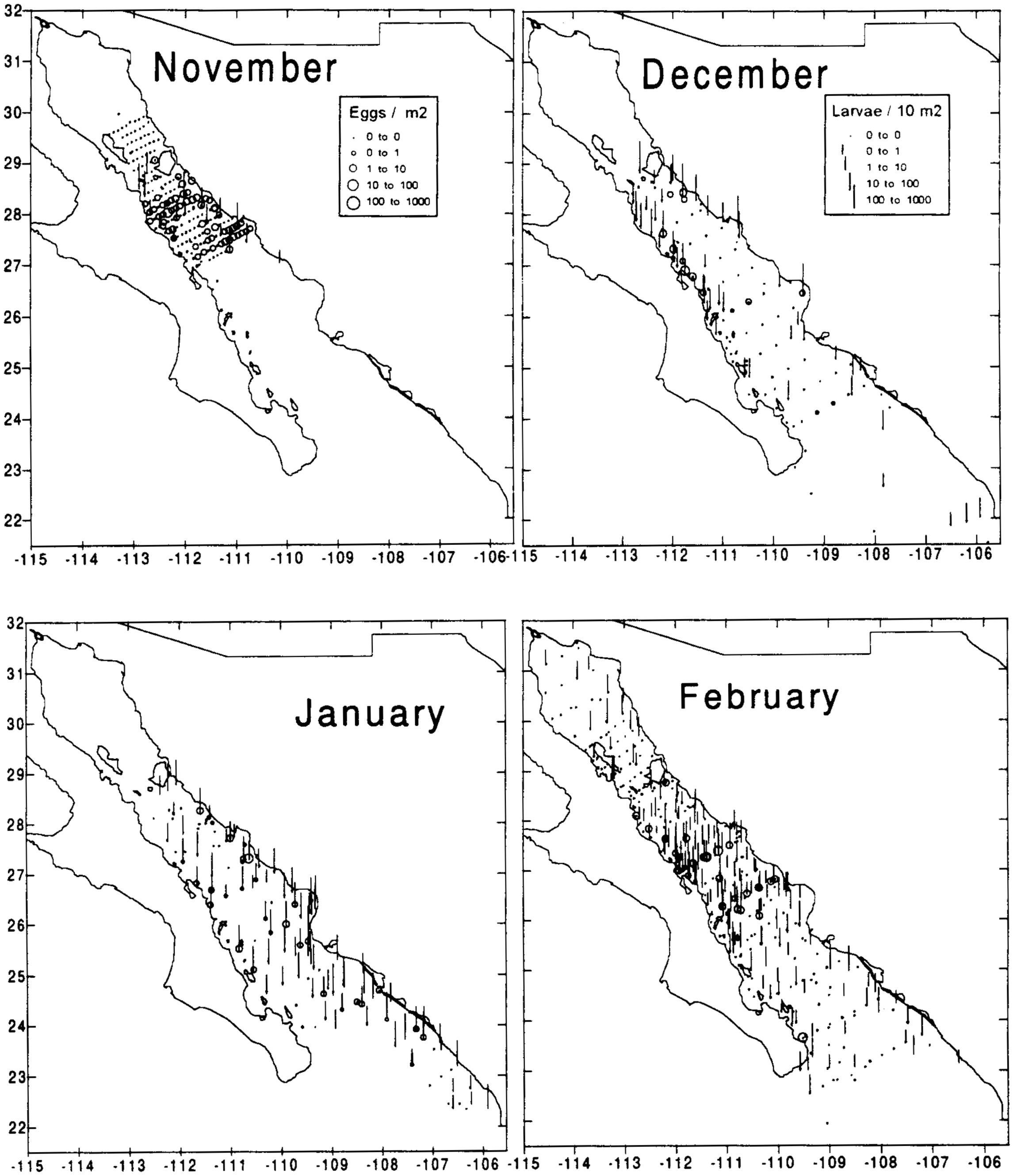

Figure 6. Monthly distribution combined for all years of Pacific sardine eggs (circles) and larvae (lines) in the Gulf of California, 1956–57 and 1971–91: November, December, January, February.

data) predicted weak east–west currents on the order of 1–2 km per day, which also change direction seasonally; flow is from east to west during winter. Mesoscale fronts and filaments in the central gulf were observed in satellite imagery and reported by Badan-Dangon et al. (1985) and Hammann et al. (1988). Similar filaments have been studied in the California Current and could represent flow velocities up to 50 km per day (Flament et al. 1985).

Pacific sardine eggs hatch in fewer than three days (Ahlstrom 1943), and 20 mm larvae are about 40 days old (Butler 1987). Although average east–west flow would cause only a net transport of about 40 km before larvae can swim and school, eggs and larvae near filaments could reach the western coast in a few days, where they would be entrained in the central gyral circulation. Some southern loss is evident, however, and could represent the eggs and larvae of adults that spawned too close to the east coast, where currents are fastest.

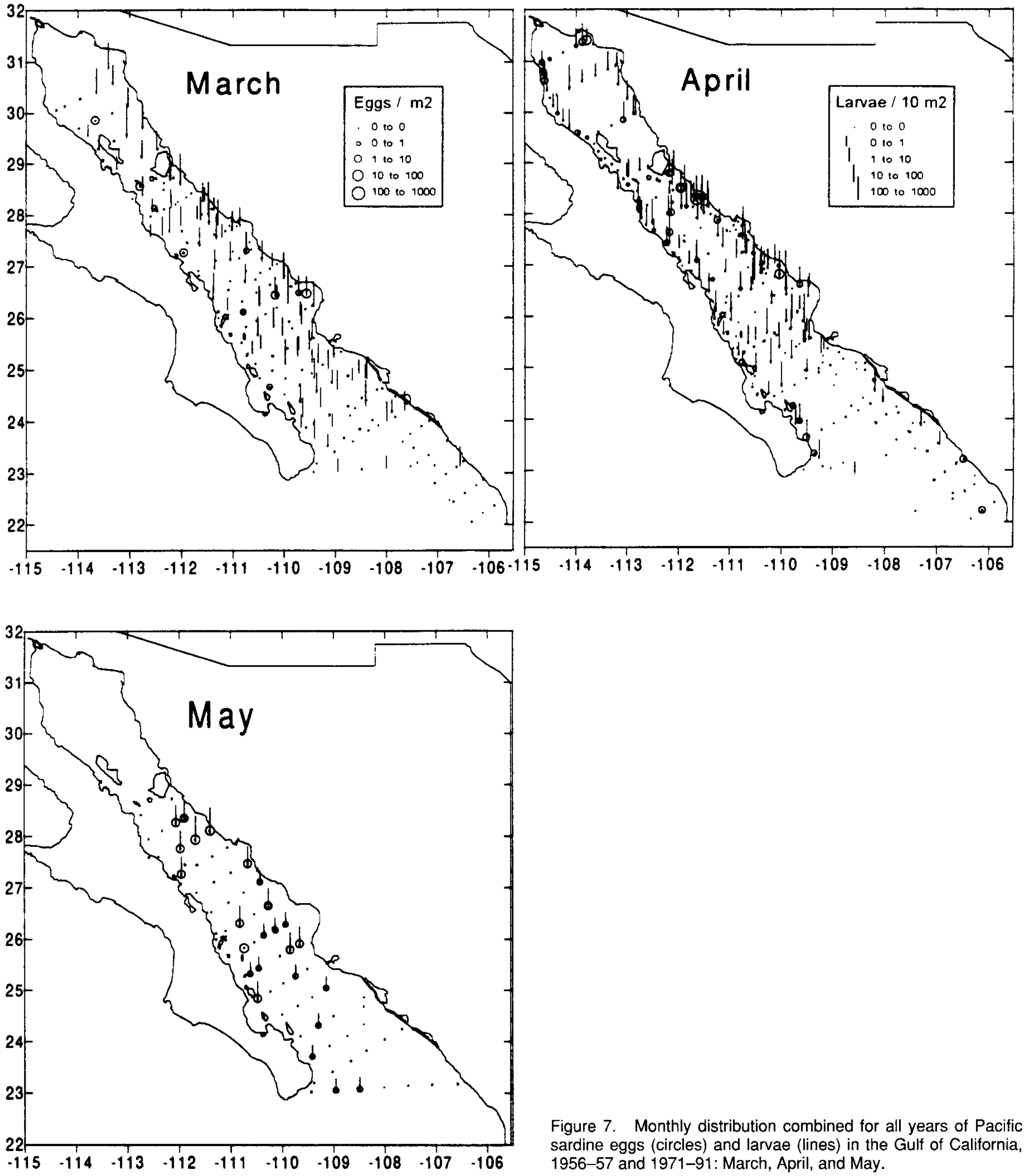

Figure 7. Monthly distribution combined for all years of Pacific sardine eggs (circles) and larvae (lines) in the Gulf of California, 1956–57 and 1971–91: March, April, and May.

Summer thermal conditions (SST) are accompanied by changes in the wind and circulation regime, and the central gyre reverses direction; larvae could be transported south toward unfavorable conditions. A similar mechanism for larval retention was described for haddock (*Melanogrammus aeglefinus*) in Georges Bank (Smith and Morse 1985). For the Southern California Bight, Parrish et al. (1981) related the spawning of several species of small pelagic fishes to weak offshore transport and coastal gyre circulation patterns. Nakata et al. (1989) found that eggs and larvae of *Sardinops melanosticta* were transported from offshore spawning grounds and concentrated in the frontal zone in Sagami Bay, Japan.

Our study shows that spawning was not restricted to the cool upwelled waters (<16°C) off the mainland coast but was more intense in the central gulf, within a range of 16.9° to 20.8° SST. Furthermore, the distribution of Pacific sardine eggs and larvae in the Gulf of California indicates retention near the spawning area in the central gulf. The difference observed in figure 8 between the temperature distribution of early- and late-stage eggs suggests spawning near fronts; at temperatures below 21°,

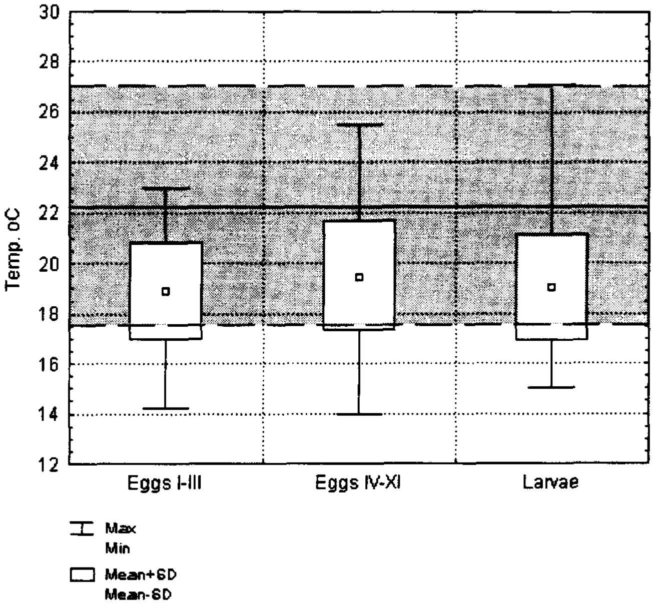

Figure 8. Sea-surface temperature for Pacific sardine egg stages I–III and IV–XI, and larvae collected in the Gulf of California on 38 cruises, 1956–57 and 1971–91. Mean overall environmental sea-surface temperature ±1 SD is shown in the shaded background.

stage I–III eggs mature in fewer than 13 hours. The model for the Pacific sardine life cycle in the Gulf of California proposed by Sokolov (1974) included winter spawning on the eastern coast, and transport of eggs and larvae toward the western coast. That study was based on fisheries and ichthyoplankton data collected during 1970–73, a period of low population size (Cisneros-Mata et al. 1995), which might explain the contrast with our study. Nevertheless, during those early years, the sardine fisheries operated only near the coast, and the ichthyoplankton surveys were concentrated in areas of known sardine abundance.

Although Pacific sardine biomass in the Gulf of California varied greatly from 1956 to 1991 (Moser et al. 1974; Cisneros-Mata et al. 1995), individual cruise reports show a similar distribution for eggs and larvae. A pattern of geographic habitat suitability related to population biomass, as suggested by MacCall's basin model (MacCall 1990), could bias a study of habitat usage. Nevertheless, in the Gulf of California, the seasonal variation in SST is much greater than the interannual variability, and thus should not greatly affect these results, especially when all years are combined. Furthermore, no trend was observed in percentage of stations positive for eggs during the study period (table 3). The relation between habitat availability and fluctuations in the sardine population will be explored in another paper.

The spawning season of Pacific sardine in the Gulf of California (November to May) can be related to the observed seasonality in SST and circulation, and matches the spawning seasonality reported in adult maturity studies by Torres-Villegas et al. (1986). Although small numbers of sardine eggs and larvae were reported during July, they could have been confused with *Opisthonema* spp. But as mentioned previously, it is not likely that the *Opisthonema* spp. eggs and larvae reported in summer months were in fact Pacific sardine; we merely suggest that there is a possibility of limited Pacific sardine spawning in localized areas during summer.

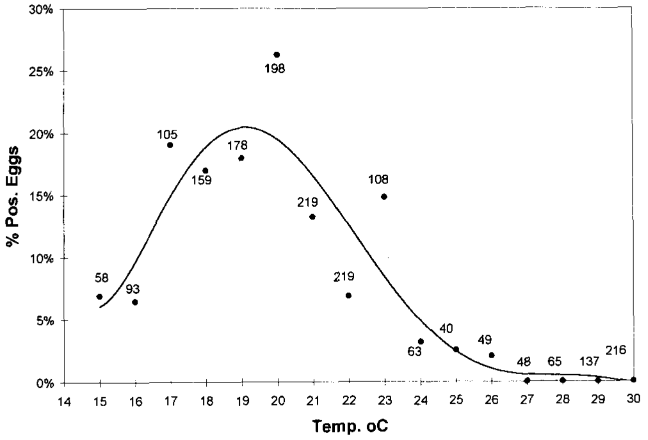

Figure 9. Probability of collecting Pacific sardine eggs of any stage at various sea-surface temperatures in the Gulf of California. Data are from the percentage of positive stations for all tows across all years at each temperature. The line represents the best fit with a polynomial model for the data from 38 cruises during 1956–57 and 1971–91.

Early southerly intrusion of warm water may affect recruitment by compressing the sardine's adult distribution northward, reducing available spawning habitat, and shortening the spawning season. There are few places in the world where populations of temperate sardines (*Sardinops, Sardina*) are as geographically limited as in the Gulf of California. North–south seasonal migration of the Pacific sardine has been described for the Gulf of California (Sokolov and Wong-Rios 1973) and the California Current (Clark and Janssen 1945). The land barriers to the north, west, and east, and the subtropical water to the south of the gulf, however, limit living space and the potential for population growth.

When habitats are compressed, cannibalism may increase (Hunter and Kimbrell 1980; Santander et al. 1983; Alheit 1987; Hammann et al. 1988), and increased food competition among juveniles may affect their mortality, growth rate, and future fecundity. Cisneros-Mata et al. (1996) demonstrated the importance of density-dependent and environmental factors for the population dynamics of Pacific sardine in the Gulf of California. Huato-Soberanis and Lluch-Belda (1987) suggested strong recruitment of Pacific sardine in the gulf after cool, anti-El Niño years, conditions which would represent an increase in available habitat. For adult Pacific sardines, Hammann et al. (1991) explained the three-fold summer

TABLE 4
Temperature Ranges for Peak Spawning of Sardine Species in Different Regions

Species	Region	Range (°C) for peak spawning	Reference
Sardinops sagax	Gulf of California	17–20.8 mean ±1SD	This paper
Sardinops sagax	Calif. Current	15–18	Tibby 1937
Sardinops sagax	Calif. Current	13–16	Ahlstrom 1959
Sardinops sagax	Calif. Current	15 and 23 (2 peaks)	Lluch-Belda et al. 1991
Sardinops sagax	Magdalena Bay, B.C.S.	16.1–25.6 (min/max)	Lluch-Belda et al. 1991
Sardinops neopilchardus	Australia	14–21 (min/max)	Whitehead 1985
Sardinops ocellatus	South Africa		Crawford et al. 1987
	23°S	12–16.5	
	20°S	16.5–22.8	

increase in the catch per unit of effort (CPUE, t/trip) in the large island region in the gulf by increased school density caused by habitat compression.

By comparing the SST intervals over which sardines have been found spawning or commercially captured around the world, one can see that as temperate species, all sardines live between 10° and 25°C and spawn mostly between 15° and 20° (table 4). The warmest peak spawning reported is in the Gulf of California and Bahía Magdalena, Mexico, and—late—in the California Current (Lluch-Belda et al. 1991). Warm-water spawning should benefit larval growth and mortality as long as there are sufficient food resources (Hunter and Alheit 1995). This combination may not be common in other areas of the world because warm temperatures do not often coincide with high food abundance. Finally, Lasker (1964) reported, from laboratory experiments on how temperature affects development rate, that few Pacific sardine eggs or larvae survive below 13°. The upper thermal limit, however, is unknown because the eggs survived the highest temperature tested (21°); field data presented here suggest the upper limit to be near 27° (fig. 9).

In this paper, the SST interval over which Pacific sardine spawn in the Gulf of California is defined, as is the probability of spawning at the temperatures available in the environment. Ninety-five percent of positive egg stations had SSTs between 15.1° and 22.7°, and there is less than a 5% probability of finding eggs in waters warmer than 24°. This information could be important for egg production cruises if real-time temperature data were available, for example from satellite imagery. Water temperatures lower than 14° are rare in the Gulf of California, and we suggest that Pacific sardine spawning is limited by habitat because of the summer intrusion of warm water. Furthermore, the relation of spawning to winter circulation patterns suggests that eggs and larvae are retained by the central anticyclonic gyre in the gulf, and that spawning close to the eastern coast could be detrimental.

In conclusion, Pacific sardine spawning is related to the strong seasonality in thermal and circulatory conditions in the Gulf of California, and the temperature relationship presented here could be useful for monitoring seasonal and interannual changes in thermal habitat for spawning.

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A SEVERE DECLINE IN THE COMMERCIAL PASSENGER FISHING VESSEL ROCKFISH (*SEBASTES* SPP.) CATCH IN THE SOUTHERN CALIFORNIA BIGHT, 1980–1996

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ABSTRACT

We analyzed data from the Marine Recreational Fishery Statistics Survey (MRFSS) to examine long-term trends in the Southern California Bight commercial passenger fishing vessel rockfish fishery. From 1980 to 1996 a total of 50 species were taken. There was a substantial decline in the overall catch per unit of effort (CPUE) during that time.

For individual species we observed four general temporal patterns: (1) a steady decline throughout the period; (2) high CPUE from 1983 to 1986; (3) variable catches throughout the 1980s but extremely low catches from 1993 to 1996; and (4) variable catches throughout the entire period. Among the several species with particularly large declines were bocaccio (98.7%), blue rockfish (95.2%), and olive rockfish (83.0%). Three species that were abundant in 1980 were absent by 1996 (chilipepper, swordspine, and yellowtail rockfishes). The number of species caught also decreased during the course of the survey.

We analyzed length frequencies for a subset of the species. On average, mean total length declined. This decline was due mainly to the removal of the larger size classes rather than to increased catches of juveniles. An extreme example was observed for vermilion rockfish: over the course of the survey, the fishery changed from one comprising primarily adults to almost entirely juveniles.

We conclude that the declines in rockfish catches in the Southern California Bight between 1980 and 1996 reflect reduced populations. These population declines probably result from poor long-term juvenile recruitment, caused by adverse oceanographic conditions, as well as from essentially unregulated overfishing of adults and subadults, perhaps leading to recruitment overfishing.

INTRODUCTION

Rockfishes (Scorpaenidae: genus *Sebastes*) dominate the fish communities of many California reefs (Lea 1992). Occupying a wide range of habitats and depths, this speciose group has been of major commercial and recreational importance for more than a hundred years (Lenarz 1986). In California, the value of these fisheries may have historically exceeded one billion dollars per year (Lenarz 1986).

Despite their importance, little is known about the condition of rockfish stocks in California (but see Ralston et al. 1996). Because most of the economically important species live over reefs in deeper waters, it has been difficult to determine population structure and size with the bottom trawl surveys used to assess many groundfish species. Tagging studies also present problems, because deeper-water rockfishes rarely survive being brought to the surface (O'Connell and Carlile 1994). In addition, it is not yet possible to identify all rockfish larvae to species, thus precluding estimates of spawning biomass from larval surveys.

Despite these limitations, in recent years there have been indications that at least some rockfish stocks in California are in jeopardy. Two studies of commercial passenger fishing vessel (CPFV) catches found both declining catch rates and declining mean lengths, as well as high takes of sexually immature fishes for a number of rockfish species (Reilly et al. 1993; Karpov et al. 1995). A study in Monterey Bay, central California, showed declines in the CPFV catches of a number of nearshore species, followed by a trend toward fishing for deeper-water species (Mason 1995). During the 1980s, trends in commercial rockfish landings and research trawl surveys implied some stress on stocks (Pearson and Ralston 1990; Dark and Wilkins 1994). Stocks of one species in particular, the bocaccio, are thought to be at historically low levels (Ralston et al. 1996). In addition, there is evidence of very poor survivorship of the pelagic juvenile stages of many species of rockfishes in central California (S. Ralston, pers. comm.).

All of these studies have been conducted in the central and northern part of California. Several factors indicate that the status of rockfish stocks in the Southern California Bight (SCB) may be similar to the status of stocks in the central and northern part of the state. Populations of many inshore fish species have declined markedly since the mid-1970s (Stephens et al. 1986, 1994; Holbrook and Schmitt 1996; Love et al. 1998). Much of this decline may be due to a decade-long oceanographic shift that has led to sharp declines in the juvenile recruitment of these species. Among inshore species, rockfishes appear to have been among the most

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affected. In much of the Southern California Bight, inshore rockfishes are no longer present, or their numbers are sharply reduced (Stephens et al. 1986, 1994; Love et al. 1998). This is probably due to a combination of poor juvenile recruitment and intense fishing pressure from both recreational and commercial fishermen. As in central California, survivorship of rockfish larvae and pelagic juveniles appears to be much reduced (M. Nishimoto, pers. comm.). This trend is not limited to inshore species. Stocks of deeper-water rockfishes are currently at very low levels (Love, unpubl. data). From 1995 to 1997, we used a research submersible to observe rockfish populations over deeper (50–300 m) reefs in the Southern California Bight. Most of the reefs we examined harbored few rockfishes longer than 20 cm total length, and many economically important species were absent.

There are, however, virtually no long-term published data on rockfish stocks in the Southern California Bight. In order to compare our direct observations of rockfish abundances in 1995–97 (Love, unpubl. data) we needed some assessment of rockfish stocks in the bight. In this paper we use information collected aboard CPFVs in the federally sponsored Marine Recreational Fishery Statistics Survey (MRFSS) to examine longer-term trends in Southern California Bight rockfish numbers.

METHODS

Data were taken by MRFSS observers from 1980 to 1989 and 1993 to 1996. The MRFSS program was suspended from 1990 through 1992. In addition, funding for the program was reduced in 1987–89, and monitoring activities were consequently reduced. Data during these years may not be completely comparable to other years. Observers rode aboard randomly selected CPFVs from all fishing ports in the Southern California Bight. The term CPFV includes charter boats and party boats fishing with hook and line gear only. Fishing trips selected were 1/2 and 3/4 day trips. Observers attempted to identify to species all fishes caught and to measure (mm fork and total length) as many fishes as possible. For details of the MRFSS program see U.S. Department of Commerce (1987) and Karpov et al. (1995).

Along the Pacific Coast, data from the MRFSS have been used to estimate the status of various fish stocks in central and northern California (Karpov et al. 1995). The MRFSS southern California data set targets only relatively short fishing trips (either 1/2 day or 3/4 day). During these trips, party vessels can travel only relatively short distances from port, almost entirely along the mainland; they do not have time to travel to more distant, and somewhat less fished, reefs.

A problem with this data might arise if, during the course of the survey, party vessels shifted away from fishing for rockfishes. This might happen if warm-water pelagic species such as yellowtail (*Seriola lalandi*) or Pacific bonito (*Sarda chiliensis*) were particularly abundant. In such a case, party vessels would fish in areas with few or no rockfishes, thus decreasing the rockfish CPUE even if there were no underlying decrease in rockfish populations. To counter this potential bias, we used catch data only from those CPFV trips that had caught at least one rockfish. This decreased any bias that might occur during years when fewer vessels fished for rockfishes.

We concentrated our analyses of CPUE on 21 species from the complete data set and calculated CPUE by dividing the total catch by the total cumulative fishing hours per year. The 21 target species had non-zero CPUE in at least 10 of the 14 years of data. We analyzed patterns of temporal abundance by plotting CPUE over time for each species. We present these plots in species groupings based on their patterns over time. We visually assessed similarities in the temporal patterns. Species fell into four general groupings: species that declined steadily from 1980 to 1996 (group A); species that increased from 1983 to 1986, some of which had a secondary peak in 1994 but generally were less abundant at the end of the 1990s than in the 1980s (group B); species that were extremely variable throughout the 1980s but were extremely low from 1993 to 1996 (group C); and species that were variable throughout the entire period (group D).

To summarize the CPUE patterns for these four species groups we standardized the data for each species by subtracting the mean CPUE for the entire period from each yearly value and dividing that by the standard deviation of the entire period. For each species, this gave a time series mean CPUE of 0 and a standard deviation of 1. We then fit simple linear regressions to the standardized CPUEs of each species against year, simply to summarize gross temporal trends in CPUE for each of the species groups. We present the slopes and variance explained (r^2) for each species as well as the average slope for each species group.

We also analyzed length-frequency data to determine differences among years. We performed this analysis for the 11 species with the highest CPUE in 1980. Length data for all other species were too sparse in the late 1990s to assess changes. We used length-frequency histograms to compare length frequencies graphically. We used total length in all analyses, and grouped lengths into 20 mm intervals. Small sample sizes, especially during the period 1987–89 (when sampling was reduced) and 1992–96 (when catches were greatly reduced), forced us to combine length-frequency data from some of these years. Whenever a yearly length sample contained fewer than 10 individuals, we combined that sample with the sample from the following year. We also compared mean lengths for each species by using either Student's *t*-tests (where variances were equal) and Welch ANOVAs (where variances were unequal). For these tests, we compared mean lengths for two time periods: 1980–89 (1980s) versus 1993–96 (1990s).

RESULTS

Catch per Unit of Effort

Over the course of the survey a total of 50 species were caught (table 1). Many of these species, however, were caught in only one year or in only a few years of the survey.

Between 1980 and 1996, the overall rockfish CPUE substantially declined (fig. 1). For the 21 target species, the total CPUE was 3,000 in 1980; decreased to 192 in 1995; and increased slightly to 345 in 1996.

The overall decline was largely reflected in the temporal patterns for the individual species. Over the sampling period, catch patterns varied among species (figs. 2 and 3). Four general patterns were observed. The first was a steady decline throughout the period (group A). Of the 6 species that made up this group (swordspine, blue, cow, flag, and olive rockfishes, and bocaccio), 3 (bocaccio and blue and olive rockfishes) had the first, second, and third highest CPUEs in 1980. The second general pattern was highest CPUE during 1983–86 (group B). These 6 species (greenspotted, starry, speckled, squarespot, bank, and rosy rockfishes) all had CPUEs in 1980 of about half the values during 1983–86. Some of these species had a secondary peak in 1994 but generally ended the 1990s lower than the 1980s. The third pattern, shown by 6 more species (group C), was characterized by variable catches throughout the 1980s but extremely low catches (or zero) from 1993 through 1996. The last pattern included 3 species which were variable throughout the entire period (group D).

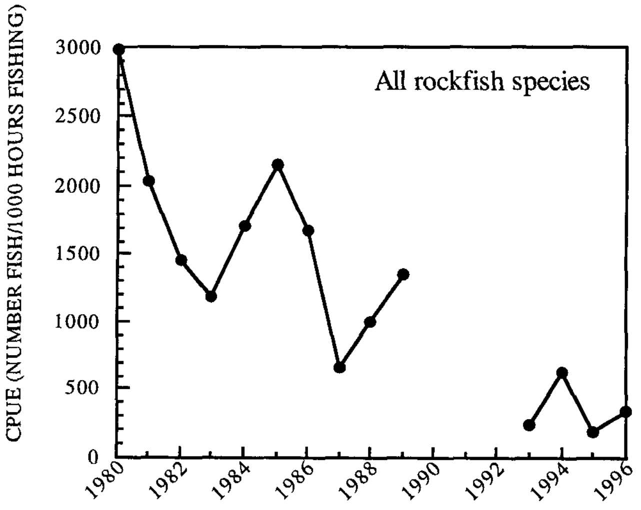


Figure 1. Catch per unit of effort for the 21 target species analyzed in this paper for 1980–96. No data are available for the period 1990–92.

We based our initial characterization of these groups on visual similarity of temporal patterns. However, we wanted to quantitatively assess the similarity of the patterns. To do this, we standardized CPUE, plotted each species group together, and fitted simple linear regressions to each species separately (fig. 4). We were not

TABLE 1
Sebastes **Species Caught during the MRFSS Survey, 1980–96, in Descending Order of Total CPUE**

Common name	Scientific name
Bocaccio*†	*S. paucispinis*
Chilipepper rockfish*†	*S. goodei*
Blue rockfish*†	*S. mystinus*
Bank rockfish*	*S. rufus*
Halfbanded rockfish	*S. semicinctus*
Greenspotted rockfish*†	*S. chlorostictus*
Squarespotted rockfish*	*S. hopkinsi*
Vermilion rockfish*†	*S. miniatus*
Yellowtail rockfish*†	*S. flavidus*
Olive rockfish*†	*S. serranoides*
Widow rockfish*†	*S. entomelas*
Speckled rockfish*	*S. ovalis*
Starry rockfish*†	*S. constellatus*
Rosy rockfish*	*S. rosaceus*
Gopher rockfish	*S. carnatus*
Copper rockfish*†	*S. caurinus*
Brown rockfish*	*S. auriculatus*
Honeycomb rockfish*	*S. umbrosus*
Greenstriped rockfish	*S. elongatus*
Rougheye rockfish	*S. aleutianus*
Flag rockfish*	*S. rubrivinctus*
Canary rockfish*	*S. pinniger*
Chameleon rockfish	*S. phillipsi*
Pink rockfish	*S. eos*
Swordspine rockfish*†	*S. ensifer*
Treefish*	*S. serriceps*
Greenblotched rockfish	*S. rosenblatti*
Calico rockfish	*S. dalli*
Kelp rockfish	*S. atrovirens*
Cow rockfish*	*S. levis*
Black rockfish	*S. melanops*
Blackgill rockfish	*S. melanostomus*
Bronzespotted rockfish	*S. gilli*
China rockfish	*S. nebulosus*
Grass rockfish	*S. rastrelliger*
Black and yellow rockfish	*S. chrysomelas*
Yelloweye rockfish	*S. ruberrimus*
Rosethorn rockfish	*S. helvomaculatus*
Mexican rockfish	*S. macdonaldi*
Redbanded rockfish	*S. babcocki*
Tiger rockfish	*S. nigrocinctus*
Stripetail rockfish	*S. saxicola*
Splitnose rockfish	*S. diploproa*
Shortbelly rockfish	*S. jordani*
Silvergray rockfish	*S. brevispinis*
Darkblotched rockfish	*S. crameri*
Redstripe rockfish	*S. proriger*
Sharpchin rockfish	*S. zacentrus*
Quillback rockfish	*S. maliger*

*Species for which CPUE data were analyzed. These species were caught in at least 10 of the 14 years of surveys.

†Species for which length frequencies were analyzed. These species had the highest CPUE values in 1980 and sufficient numbers in the late 1990s to make it possible to analyze patterns in time.

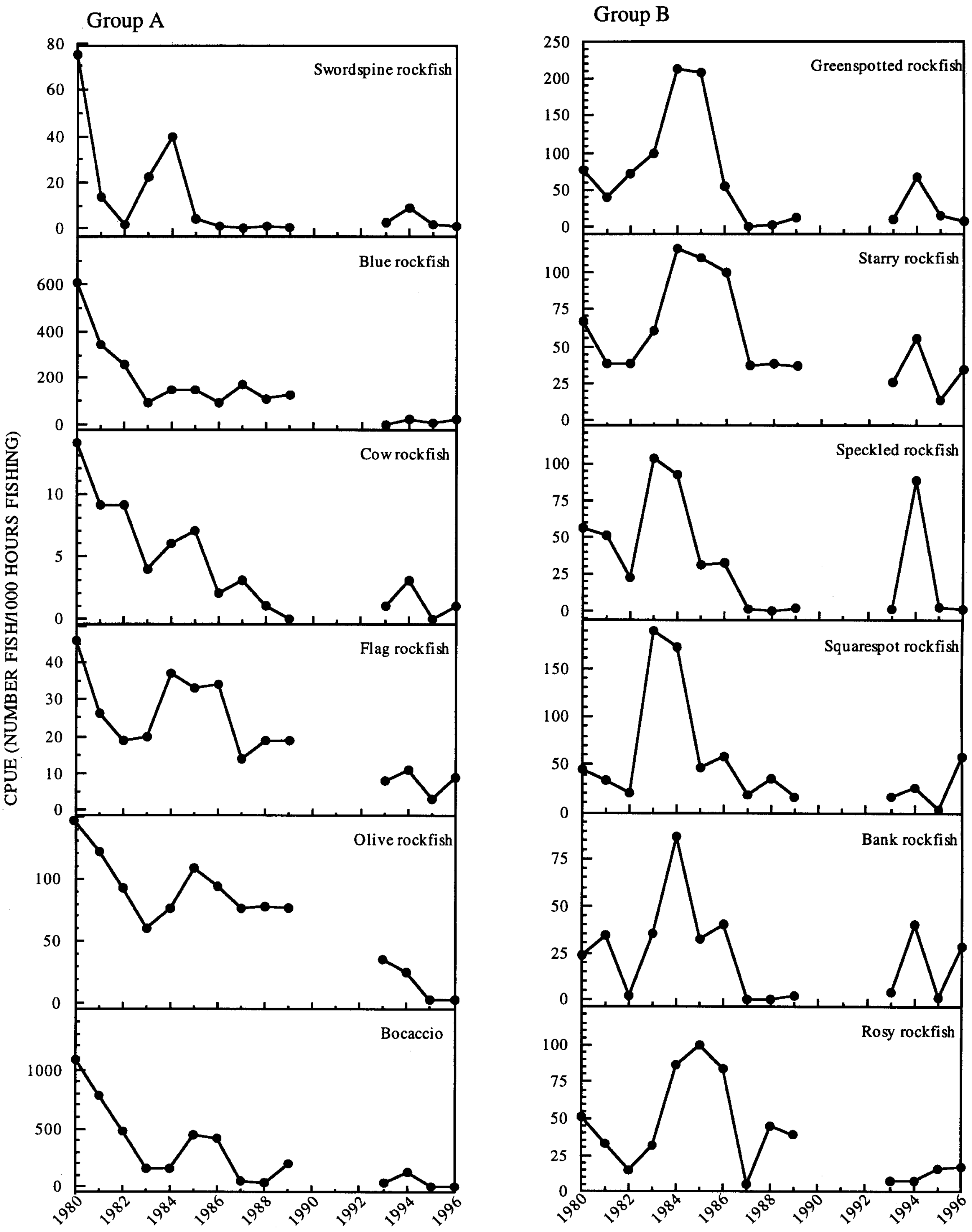


Figure 2. Catch per unit of effort versus year for each of the species in Groups A and B (see Methods).

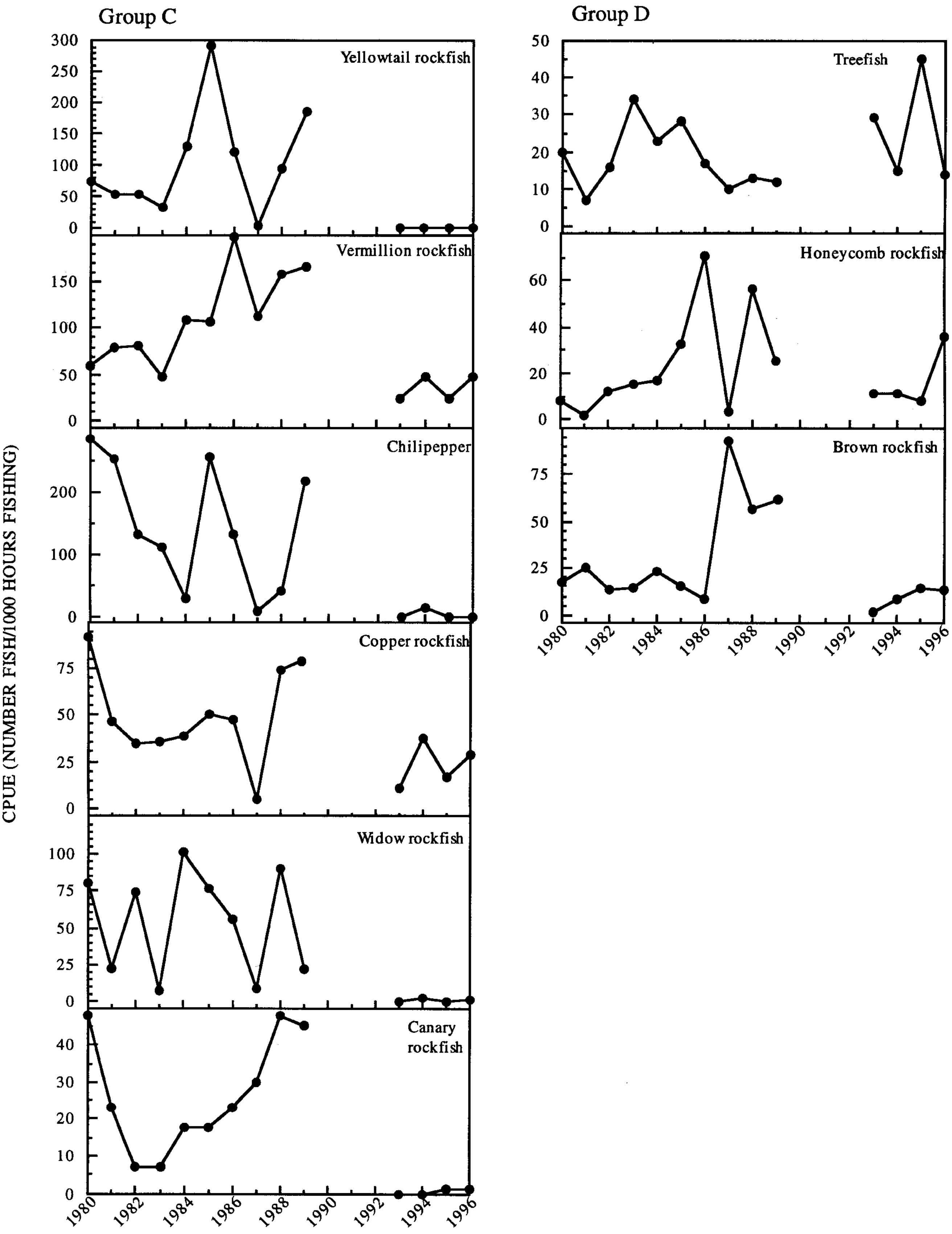
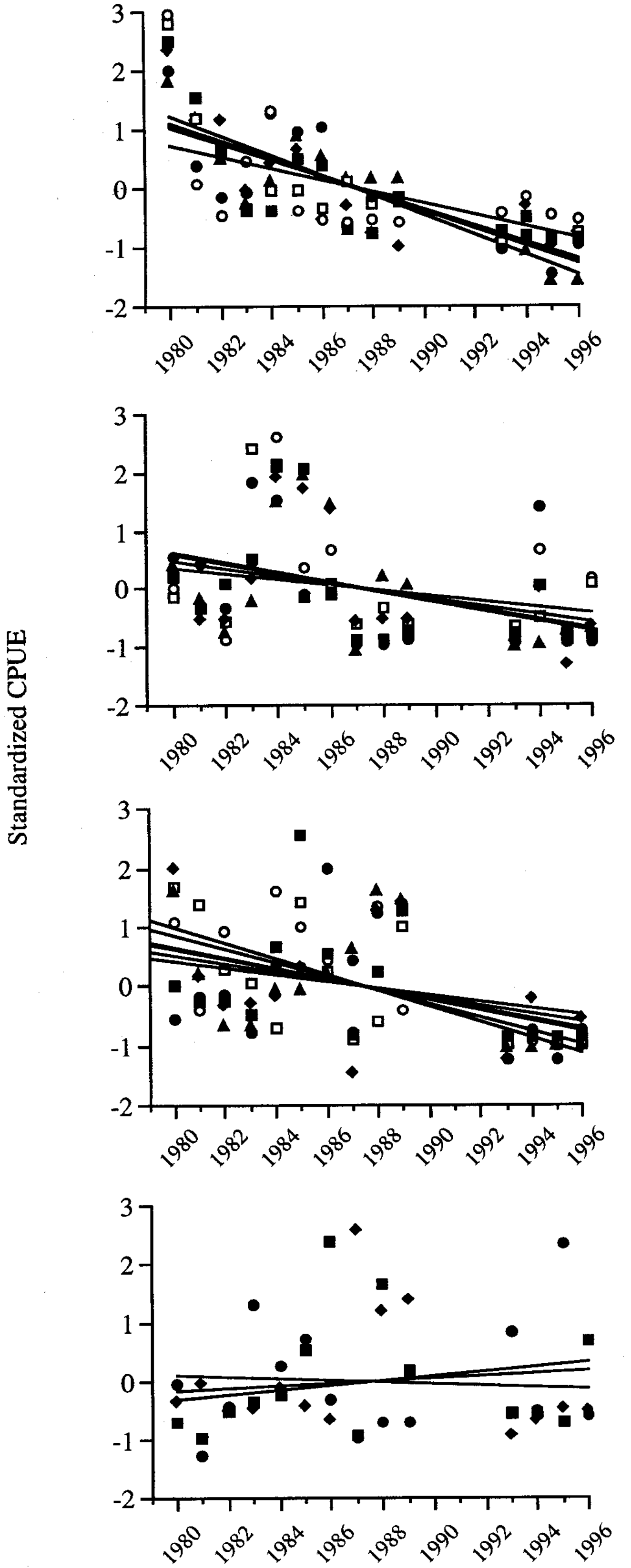


Figure 3. Catch per unit of effort versus year for each of the species in Groups C and D (see Methods).



Group A	Slope	r²
■ Bocaccio	-0.14	0.56
□ Blue rockfish	-0.15	0.60
● Flag rockfish	-0.15	0.62
▲ Olive rockfish	-0.17	0.82
◆ Cowcod	-0.15	0.63
○ Swordspine rockfish	-0.10	0.29

mean slope= -0.14

Group B		
■ Greenspotted rockfish	-0.08	0.20
□ Squarespot rockfish	-0.07	0.13
● Speckled rockfish	-0.08	0.18
▲ Rosy rockfish	-0.08	0.20
◆ Starry rockfish	-0.08	0.20
○ Bank rockfish	-0.05	0.07

mean slope= -0.08

Group C		
■ Yellowtail rockfish	-0.07	0.14
□ Chilipepper	-0.13	0.51
● Vermilion rockfish	-0.05	0.08
▲ Canary rockfish	-0.09	0.22
◆ Copper rockfish	-0.08	0.19
○ Widow rockfish	-0.11	0.36

mean slope= -0.08

Group D		
■ Honeycomb rockfish	0.02	0.01
◆ Brown rockfish	-0.02	0.01
● Treefish	0.04	0.05

mean slope= 0.01

Figure 4. Linear regression on standardized CPUE data for the four species groupings. Slope and r^2 are given for each species, as well as mean slope for the group. CPUE was standardized for each species by subtracting the mean CPUE for the entire period from each yearly CPUE value and dividing that by the standard deviation of the entire period.

interested in the predictive ability of the regression model; we simply wanted a means to compare the patterns. Group A (the steadily declining group) had a mean slope of −0.14, and 5 of the 6 species had an r^2 greater than 0.5. Groups B and C both had average slopes of −0.08, indicating a decline, but very low r^2s, which reflected the variability in the patterns. Group D, as expected, showed no relationship.

The general decline shown by the 21 target species reflects declines in the underlying catch rate for almost all previously abundant species (fig. 5). The species with highest CPUE in 1996 (squarespot rockfish) would have ranked only 12th in 1980. Of the 20 top species taken in 1980, about 15 were at or near historically low CPUE levels by 1996. Particularly large declines occurred in all of the 10 most commonly taken species in 1980. The first-ranked bocaccio declined by 98.7%, second-ranked blue rockfish by 95.2%, and fourth-ranked olive rockfish by 83%. The most extreme declines were those of chilipepper (third-ranked), swordspine rockfish (eighth-ranked), and yellowtail rockfish (ninth-ranked), all of which were absent in the 1996 catch. The smallest catch reduction among the top 15 species in 1980 was the starry rockfish, which declined by 20%.

Species Composition

Species composition also changed over the course of the survey. Comparing the catch rates of the top 10 species in 1980 with those of 1996, we found only 4 species (blue, olive, copper, and starry rockfishes) in common (table 2). Most striking has been the rise in importance of dwarf species, particularly squarespot and honeycomb rockfishes. Previously of only minor importance, these ranked first and third in 1996.

The number of species taken also decreased during the course of the survey (fig. 6). During 1980, 37 species were caught, compared to 31 in 1996. Species richness dropped to a low of 24 in 1995. Notably missing in 1996 were a number of primarily northern species (yellowtail, canary, yelloweye, China, black, silvergray, and redstripe rockfishes).

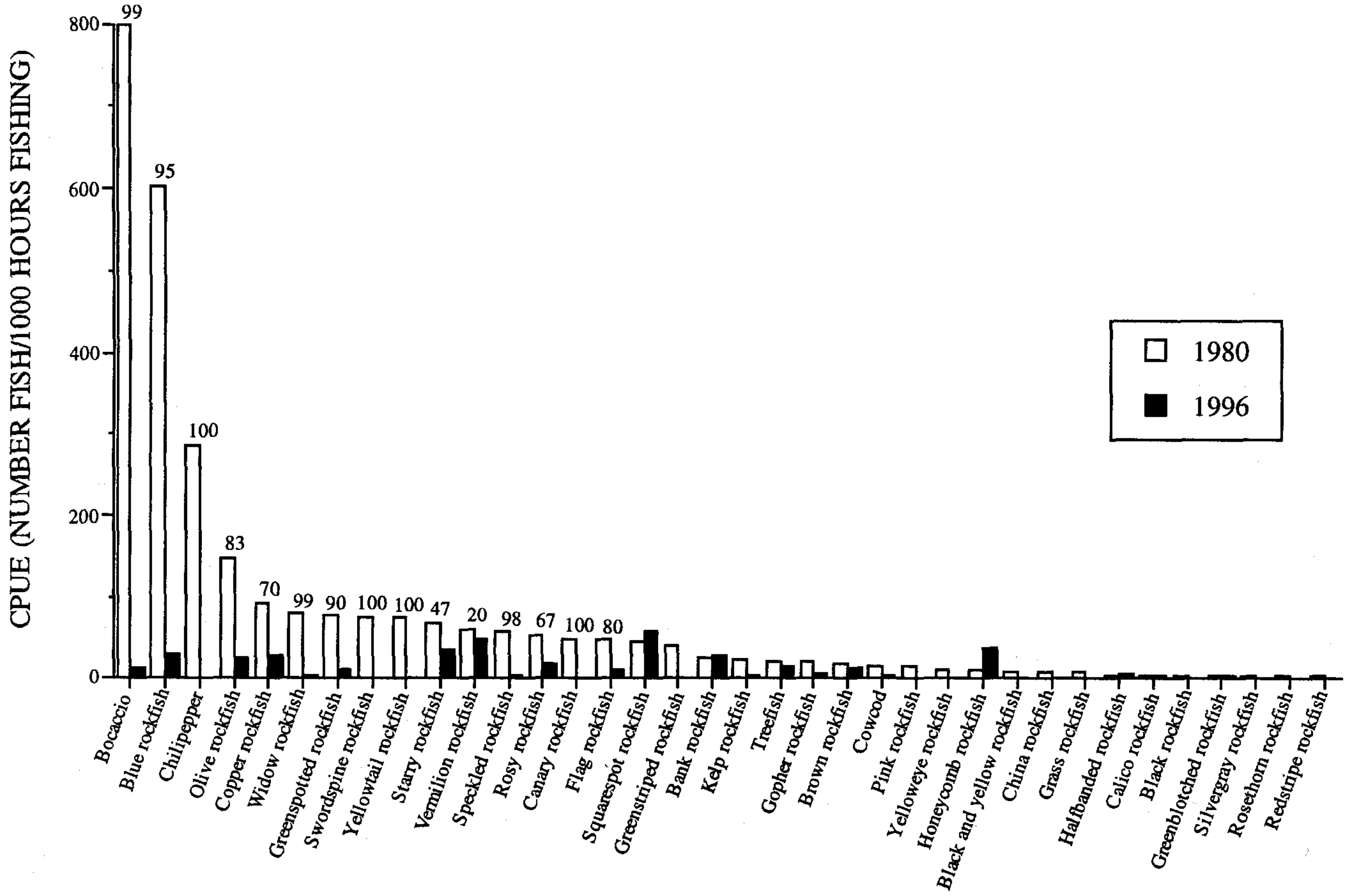


Figure 5. CPUE for 1980 (empty bars) and 1996 (filled bars) for all species in the MRFSS data set. Numbers above the bars are the percentage change from the period 1980 to 1996 for each of the top 15 species in 1980. Positive values indicate a decline over the period.

TABLE 2
Top Ten Species (on the Basis of CPUE) in 1980 and 1996

Top ten species caught in 1980	Ranking 1980	Ranking 1996	Top ten species caught in 1996	Ranking 1996	Ranking 1980
Bocaccio	1	12	Squarespot rockfish	1	16
Blue rockfish*	2	5	Vermilion rockfish	2	11
Chilipepper	3	30	Honeycomb rockfish	3	26
Olive rockfish*	4	8	Starry rockfish*	4	10
Copper rockfish*	5	7	Blue rockfish*	5	2
Widow rockfish	6	18.5	Copper rockfish*	6.5	5
Greenspotted rockfish	7	14	Bank rockfish	6.5	18
Swordspine rockfish	8.5	29	Olive rockfish*	8	4
Yellowtail rockfish	8.5	31	Rosy rockfish	9	13
Starry rockfish*	10	4	Treefish	10	20

*Species that were in the top ten during both years.

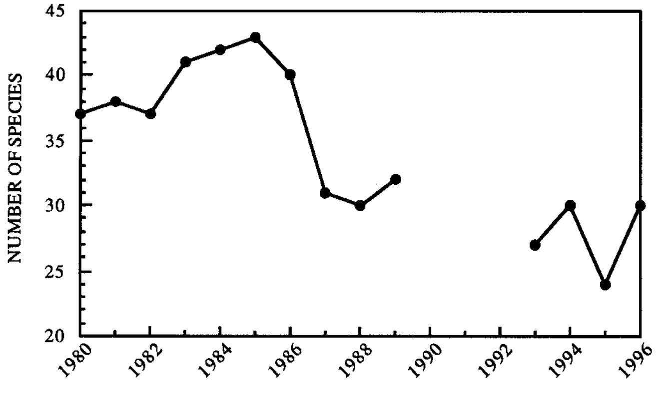


Figure 6. Number of species caught per year in the MRFSS data set.

Length-Frequency Analysis

Length-frequency histograms are presented for the top 11 species (figs. 7–12). Mean total lengths differed between the 1980s and the 1990s for 9 of 11 species (table 3). For 7 species, fishes averaged smaller in the 1990s. Decreases in mean lengths ranged from 1.1 to 5.6 cm, with the largest percentage drop for greenspotted rockfish (18%). Two species, blue rockfish and bocaccio, averaged larger in the 1990s, increasing 1.8 and 3.6 cm, respectively. For most of these species, decreased mean lengths reflected the removal of the larger size classes from the fishery rather than an increase in catches of smaller individuals. This was particularly evident for vermilion, widow, yellowtail, olive, greenspotted, and copper rockfishes and, to a certain extent, chilipepper.

Our data show that several of the fisheries always depended primarily on juveniles. This was particularly true for widow rockfish, but also for yellowtail and olive rockfishes. In the case of widow rockfish, the fishery targeted schools of 1- and 2-year-old fish during periods of good juvenile recruitment; adults were relatively rare in most years. By the 1990s, not only were few fishes of these species taken, but no more of the occasional adults that had been caught in previous years were evident.

By the 1990s, several other fisheries appeared to be dependent on juveniles. This was particularly so for vermilion rockfish, whose catch composition during the 1980s comprised primarily adult fish. By the mid-1980s, catches were an approximately even mixture of adult and immature fish. In the 1990s, however, catches, while still relatively robust compared to most other rockfish species, were composed almost entirely of juveniles.

The bocaccio fishery also appeared to have been at least partially linked to years with successful year classes, as mean sizes tended to increase over 4- or 5-year periods (1980–83, 1985–89) driven by years with good juvenile recruitment. This was most noticeable in 1984, when a number of very small individuals entered the fishery. This year class was fished until at least 1988 and probably longer. No such year class was evident in the 1990s.

DISCUSSION

There seems little doubt that the precipitous declines in rockfish catches in the Southern California Bight between 1980 and 1996 reflect much-reduced rockfish populations throughout southern California. This statement derives not only from this survey, but also from our direct observations from a research submersible. It is likely that these population declines result from both long-term, essentially unregulated, overfishing of adults and subadults, as well as from poor juvenile recruitment. The latter may be caused by adverse oceanographic conditions or recruitment overfishing.

While there have been large overall declines in catch rates of most rockfish species, the data show substantial year-to-year variability. In particular, we note two steep drops in CPUE during the periods 1981–83 and 1986–87 (fig. 1). These short-term fluctuations may result from the filter we used to qualify a CPFV trip for inclusion in the analyses. We included only vessels that had caught

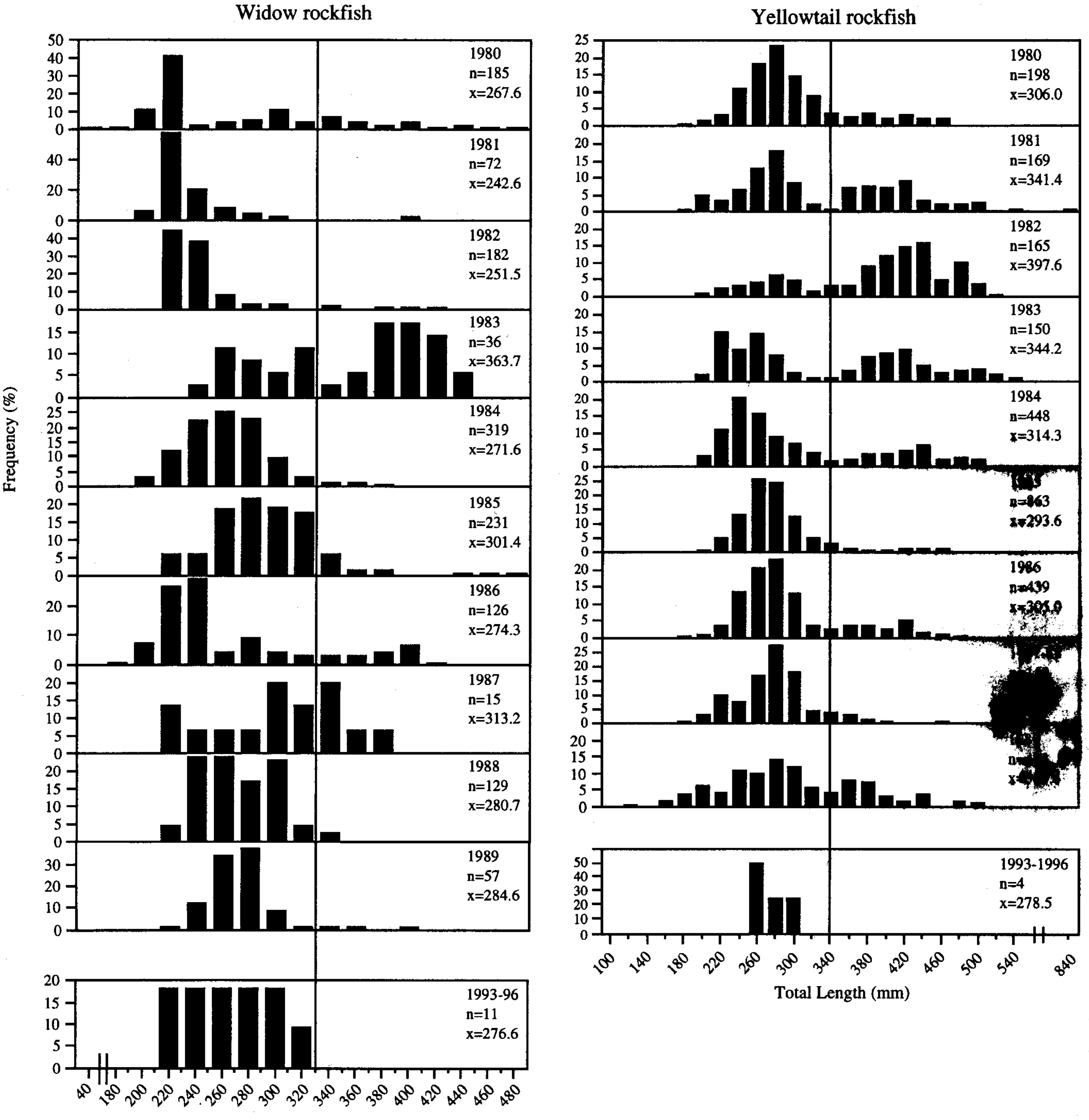


Figure 7. Length-frequency histograms for widow and yellowtail rockfishes. Lengths are total lengths divided into 20 mm bins. Sample size and mean length are given for each year. When sample size for a given year was less than 10, that sample was combined with the following year. Means in these cases are for the combined data. Vertical lines indicate the length at which 50% of the individuals are mature (values taken from Wyllie Echeverria 1987 and Love et al. 1990).

at least one rockfish. This cutoff may have been too lenient and may not have allowed us to detect vessels shifting effort away from rockfish. We chose this minimal filter because CPUE was so low by the 1990s that even vessels fishing over rockfish habitat were catching only a few rockfish. Nonetheless, these shorter-term fluctuations in CPUE do not detract from the overall longer-term decline.

There is considerable evidence that since the late 1970s and early 1980s rockfish juvenile recruitment has been generally poor in southern California. Waters in the Southern California Bight have warmed and upwelling

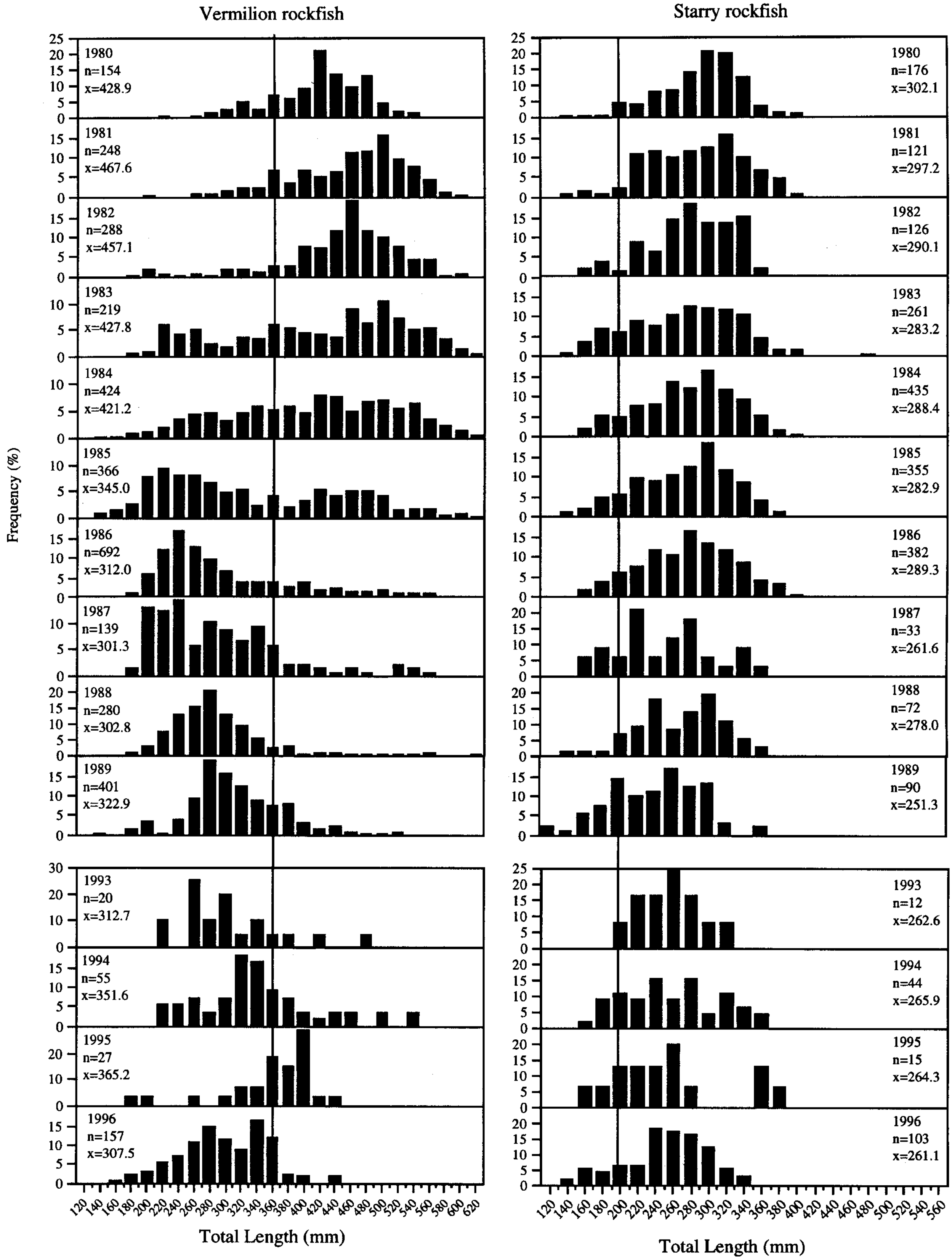


Figure 8. Length-frequency histograms for vermilion and starry rockfishes. Lengths are total lengths divided into 20 mm bins. Sample size and mean length are given for each year. When sample size for a given year was less than 10, that sample was combined with the following year. Means in these cases are for the combined data. Vertical lines indicate the length at which 50% of the individuals are mature (values taken from Wyllie Echeverria 1987 and Love et al. 1990).

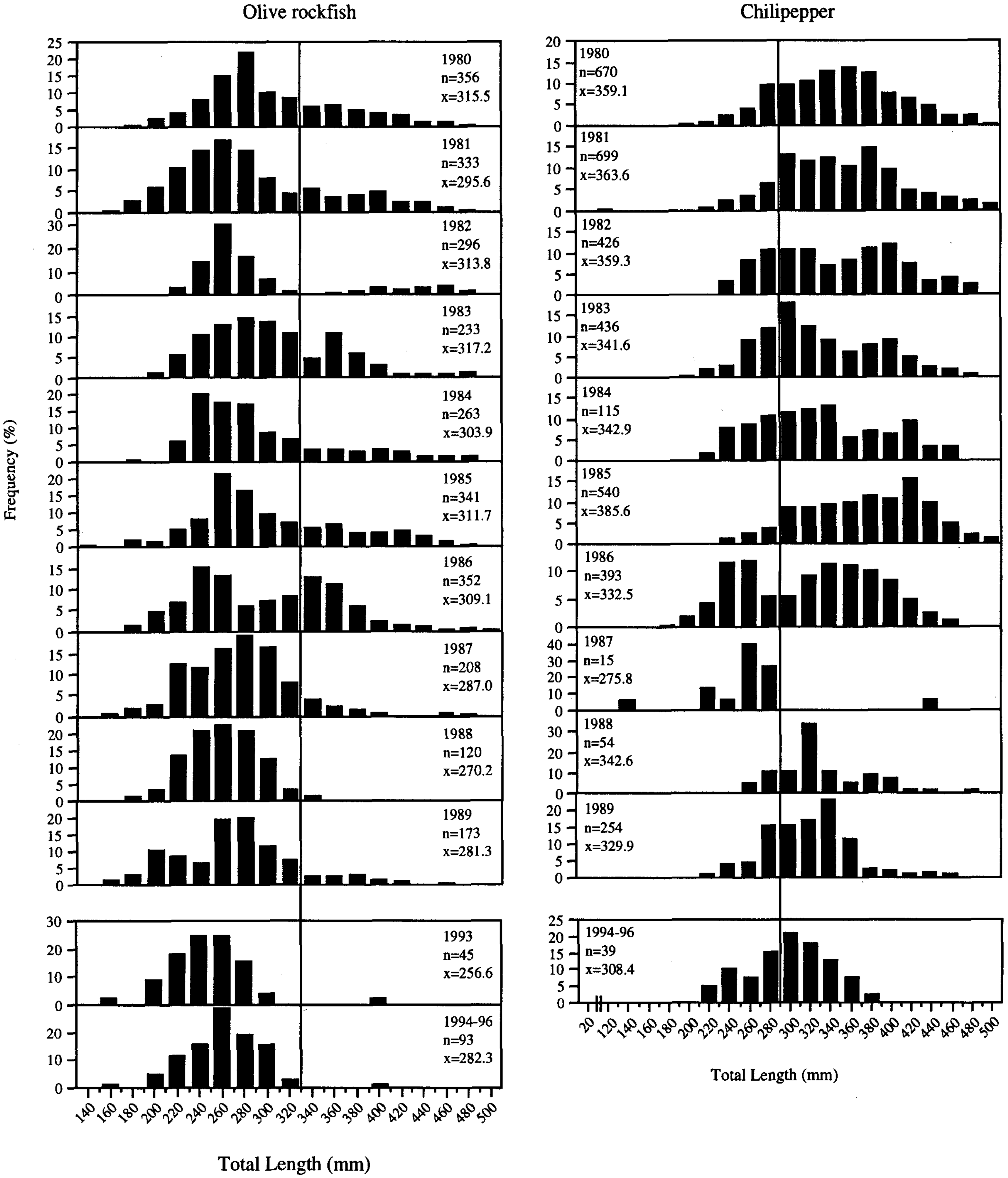


Figure 9. Length-frequency histograms for olive rockfish and chilipepper. Lengths are total lengths divided into 20 mm bins. Sample size and mean length are given for each year. When sample size for a given year was less than 10, that sample was combined with the following year. Means in these cases are for the combined data. Vertical lines indicate the length at which 50% of the individuals are mature (values taken from Love and Westphal 1981, Wyllie Echeverria 1987, and Love et al. 1990).

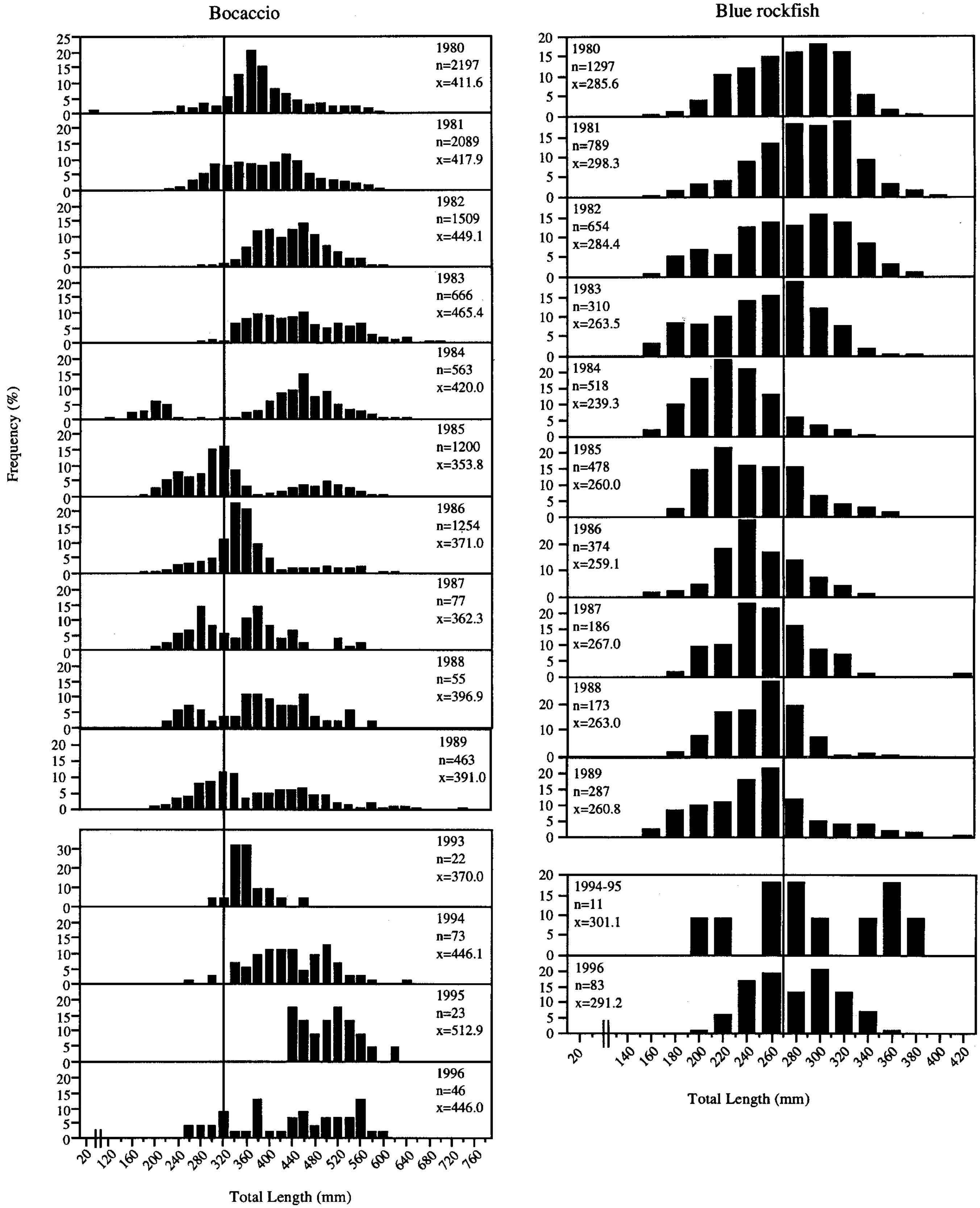


Figure 10. Length-frequency histograms for bocaccio and blue rockfish. Lengths are total lengths divided into 20 mm bins. Sample size and mean length are given for each year. When sample size for a given year was less than 10, that sample was combined with the following year. Means in these cases are for the combined data. Vertical lines indicate the length at which 50% of the individuals are mature (values taken from Wyllie Echeverria 1987 and Love et al. 1990).

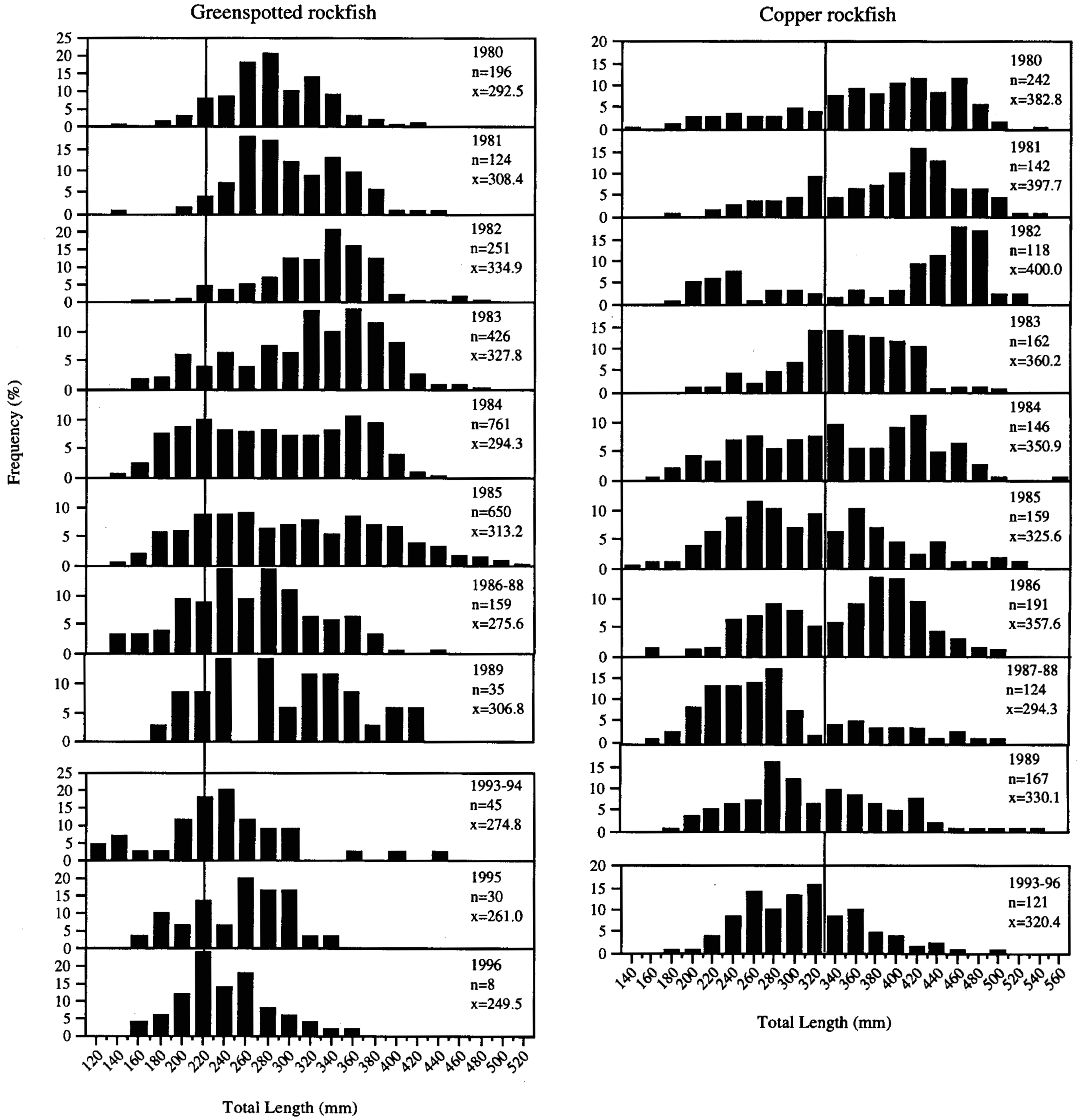


Figure 11. Length-frequency histograms for greenspotted and copper rockfishes. Lengths are total lengths divided into 20 mm bins. Sample size and mean length are given for each year. When sample size for a given year was less than 10, that sample was combined with the following year. Means in these cases are for the combined data. Vertical lines indicate the length at which 50% of the individuals are mature (values taken from Wyllie Echeverria 1987 and Love et al. 1990).

has declined, leading to reduced zooplankton production (Roemmich and McGowan 1995). In turn, larval and juvenile survival of many marine fishes has been reduced (Holbrook and Schmitt 1996). Studies of pelagic juvenile rockfishes have shown steep declines in central and northern California (S. Ralston, pers. comm.), and pelagic juveniles are relatively rare in southern California (M. Nishimoto, pers. comm.).

Additional evidence for poor recruitment comes from the sharp declines in catches of such species as widow and yellowtail rockfishes in this study. In southern California, most of the recreational fishery for these more

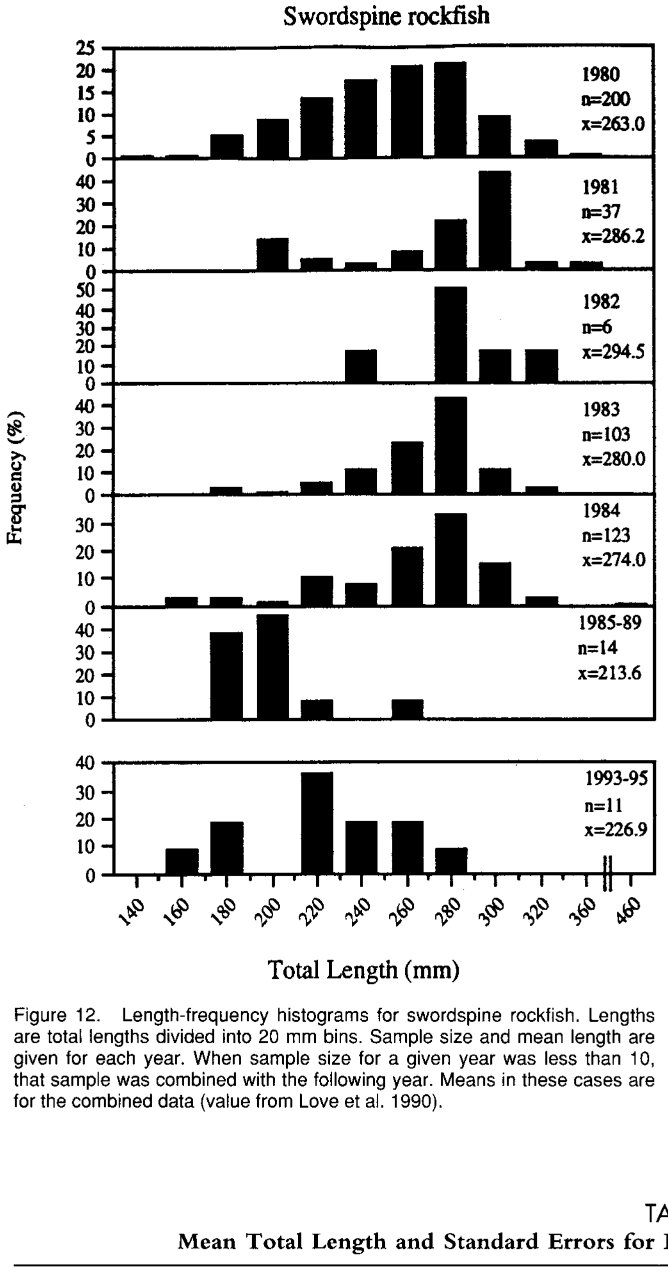


Figure 12. Length-frequency histograms for swordspine rockfish. Lengths are total lengths divided into 20 mm bins. Sample size and mean length are given for each year. When sample size for a given year was less than 10, that sample was combined with the following year. Means in these cases are for the combined data (value from Love et al. 1990).

northerly species targets young, often young-of-the-year, fishes. Successful fisheries for these species depend on relatively strong young-of-the-year cohorts, as was evident for widow rockfish in the early 1980s and perhaps again in 1986. That few widow and no yellowtail or canary rockfishes (another northern species that previously showed strong juvenile recruitment) were taken by 1996 strongly implies that there has been relatively little recruitment of these species. Our submersible surveys in central and southern California confirm the very low recruitment of these species in the Southern California Bight.

The MRFSS data also strongly imply that relatively cool-water rockfishes have declined in abundance in the Southern California Bight. In 1980 a number of primarily northern species such as yelloweye, China, black, silvergray, and redstripe rockfishes were at least occasionally taken in southern California. These species were absent in 1996. It is likely that these species had recruited during colder-water periods, and that little or no recruitment had taken place since. In addition, recruitment of even relatively warm-tolerant species, such as blue rockfish and olive rockfish, has vastly declined during this period, as reflected both in their catches and in a number of nearshore surveys (Stephens et al. 1984, 1986; Holbrook and Schmitt 1996).

Conversely, catches of a few rockfish species either increased or remained fairly constant, perhaps because of more successful juvenile recruitment. These species included either warmer-water or more cosmopolitan taxa such as treefish and honeycomb, vermilion, and brown rockfishes. The weakening influence of the California Current and a strengthening of poleward flow (Roemmich and McGowan 1995) may have caused their numbers to increase.

TABLE 3
Mean Total Length and Standard Errors for Eleven Species of Rockfish, 1980–89 and 1993–96

	1980–89			1993–96		
Species	Mean length (mm)	SE	*N*	Mean length (mm)	SE	*N*
Blue rockfish	274.1	0.6	5,066	292.4	4.8	94*
Bocaccio	409.2	0.9	10,073	445.2	6.5	164*
Chilipepper rockfish	355.8	1.0	3,602	308.4	6.5	39*
Copper rockfish	356.7	2.2	1,451	320.4	5.3	121*
Greenspotted rockfish	308.0	1.4	2,602	251.7	4.7	125*
Olive rockfish	304.0	1.2	2,675	273.9	3.1	138*
Starry rockfish	286.3	1.2	2,051	262.7	3.7	174*
Swordspine rockfish	270.2	1.8	483	226.9	9.6	11*
Vermilion rockfish	368.8	1.9	3,211	323.3	4.1	259*
Widow rockfish	277.7	1.3	1,352	276.6	10.1	11 ns
Yellowtail rockfish	311.9	1.3	2,986	278.5	10.6	4 ns

*$p < 0.001$

Means for the year groups were tested with Student's *t*-tests when variances were equal. When variances were unequal (chilipepper, copper rockfish, olive rockfish, and vermilion rockfish) a Welch ANOVA was used (see Methods).

Along with the large decreases in numbers taken, the sharp declines of adults in many of the fisheries are particularly disturbing. Some of the fisheries (e.g., widow and yellowtail rockfish) never depended on mature fishes and probably resulted from southerly transport of larvae from larger populations to the north. But the almost total absence of adult vermilion rockfish, a fishery formerly dependent on adults, is graphic evidence of overfishing.

Over time, relatively small species have assumed greater importance in the catches. To a certain extent, this is probably due to more successful juvenile recruitment of some small species, as mentioned above. But it also almost certainly reflects a major decrease in the availability of larger species. It is apparent from interviews with CPFV operators and from our own submersible observations that some reefs now contain essentially no larger rockfishes. An example of this is Lausen Knoll (also called the 14-Mile Bank), located about 22 miles south of Newport Beach. This reef area has been intensely fished for rockfishes by recreational and commercial anglers for many years. During 1996, we surveyed over 2 km of excellent rockfish habitat at Lausen Knoll and found only two rockfishes larger than 25 cm. At the same time, squarespot rockfish and other dwarf rockfishes were abundant. The rise in the importance of smaller species in the recreational catches, particularly of squarespot rockfish, may be a direct result of this intense harvesting. From our submersible surveys, we have noted that heavily fished reefs often have large numbers of small fishes, particularly squarespot and pygmy rockfishes (*S. wilsoni*). It is possible that removing most of the large, predatory rockfishes has increased the survival of these dwarf species.

Historically, rockfish populations have not quickly rebounded once management policies are set in place (Leaman and Stanley 1993). Thus once southern California rockfish populations have been depleted, it may prove difficult for them to rebuild. One factor is that many rockfish species appear to have highly variable juvenile recruitment (Archibald et al. 1983; Ralston et al. 1996), with strong cohorts occurring as rarely as every 10–15 years. Thus there may have to be a change in the present oceanographic regime off southern California, now characterized by warm temperatures and low productivity, before strong cohorts occur. Although it is unclear how long the present regime will last, some evidence points to a shift within the next 10 years (Ware 1995; MacCall 1996). It is more troubling, however, that in some cases, such as that of bocaccio, the absolute magnitude of stronger cohorts is diminishing (Ralston et al. 1996), implying recruitment overfishing.

In the Southern California Bight, there have been no quotas on the commercial rockfish harvest and, until recently, no limitations on commercial rockfish harvesting. Currently, the only commercial regulation is a ban on gill net fishing in waters within three miles of the mainland and one mile of the offshore islands. In the recreational fishery, there is a bag limit of 15 fish per day per angler. A problem in both industries is that except in very shallow water, fishes cannot be returned alive, making size limits ineffective.

It is probably necessary to lower overall fishing pressure to maintain those adult populations that still exist until oceanographic conditions are more favorable to successful juvenile recruitment. Only by reducing the rockfish catch of both recreational and commercial vessels can this be achieved. And while the commercial industry is certainly responsible for much of the population decline, additional responsibility must rest with CPFVs. This is true because, while commercial vessels often stop fishing an area when it is economically nonviable, recreational vessels do not. Because the quality of rockfish fishing has gradually eroded over many years, we have noted that many recreational anglers now expect fewer, smaller fish. This is exemplified by the importance of squarespot rockfish and other small species in the catch. On some trips most of the rockfish catch now comprises either dwarf or small species (such as squarespot, honeycomb, or rosy rockfishes) or juvenile rockfishes. Thus CPFVs tend to continue fishing reefs that harbor few, if any, larger rockfishes, thereby preventing a rebound in populations.

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REPRODUCTIVE MODALITY AND BATCH FECUNDITY OF THE EUROPEAN HAKE (*MERLUCCIUS MERLUCCIUS* L.) IN THE BAY OF BISCAY

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ABSTRACT

Appraisal of reproductive modality is necessary to quantify the reproductive potential of a fish species. We believe that European hake, *Merluccius merluccius* (L. 1758), may have an indeterminate fecundity modality because of (1) a continuum of oocyte sizes in the ovary of mature female hake during the whole reproductive season, i.e., no gap in the oocyte frequency distribution between immature and vitellogenic oocytes; (2) the maintenance of a similar diameter of vitellogenic oocytes throughout the spawning season; (3) a steady level of remnant total fecundity during the spawning cycle; and (4) the prevalence of atresia at the end of the spawning period.

Batch fecundity of hake in 1994 averaged 165 eggs g^{-1} (SE = 9.89) gutted female weight. Spawning frequency, based on the duration of different ovarian developmental stages, ranged from 0.052 to 0.189, which is equivalent to a batch interval of 19 to 5.3 days. Finally, a quantification of the per batch and annual reproductive output was made.

INTRODUCTION

The literature on European hake indicates that this species spawns several times in the reproductive season, and therefore is a fractional spawner (Andreu 1955; Pérez and Pereiro 1985; Sarano 1986).

Past reproductive studies on hake do not indicate if annual fecundity is determined at the onset of spawning or is variable, with the standing stock of yolked oocytes at the beginning of the spawning season being unrelated to annual fecundity. Potential annual fecundity is defined as the total number of advanced-yolked oocytes matured per year, uncorrected for atretic losses (Hunter et al. 1992). After correcting for atretic losses, the total number of eggs spawned per female in a year is called the realized annual fecundity. In fishes with determinate fecundity, the standing stock of yolked oocytes prior to the onset of spawning is considered to be equivalent to the potential annual fecundity. This decreases with each spawning because the standing stock of yolked oocytes is not replaced during the spawning season.

The term *indeterminate* refers to species in which potential annual fecundity is not fixed before the onset of spawning (Hunter et al. 1992). In such species, previtellogenic oocytes can develop and be recruited into the yolked oocyte stock at any time during the season (*de novo* vitellogenesis; Hunter and Goldberg 1980). Estimation of total fecundity in the ovary prior to the onset of spawning is meaningless if, during the spawning season, oocytes are recruited to that stock. In such species, the annual fecundity should be estimated from the number of oocytes released per spawning (batch fecundity), the percentage of females spawning per day (spawning frequency), and the duration of the spawning season (Hunter et al. 1985).

The objective of this study was to identify the fecundity modality of the European hake and to estimate its potential annual reproductive output. Four lines of evidence (Hunter et al. 1989; Greer Walker et al. 1994) were investigated to assess the fecundity modality of European hake:

1. Stage-specific variation of oocyte size-frequency distribution: A distinct hiatus separating the yolked-oocyte stock from the unyolked stock indicates that annual fecundity is determinate, whereas the lack of a hiatus may indicate that annual fecundity is indeterminate.
2. Seasonal decline in total fecundity: A decrease in the stock of vitellogenic oocytes during the spawning season supports evidence for determinate fecundity.
3. Seasonal increase in the mean diameter of the advanced vitellogenic oocytes: Fishes with determinate fecundity will show an increase in the average diameter of yolked oocytes because no new yolked oocytes are recruited to replace those that have been spawned during the season.
4. Incidence of atresia during the spawning season: Fishes with indeterminate fecundity show a generalized prevalence of atresia and resorption of mature oocytes at the end of the spawning season (West 1990).

MATERIALS AND METHODS

Mature hake were sampled aboard commercial fishing vessels working in the Bay of Biscay (fig. 1) in 1994 and 1995, during the main reproductive season of hake in the area (January to May; Martin 1991). No samples

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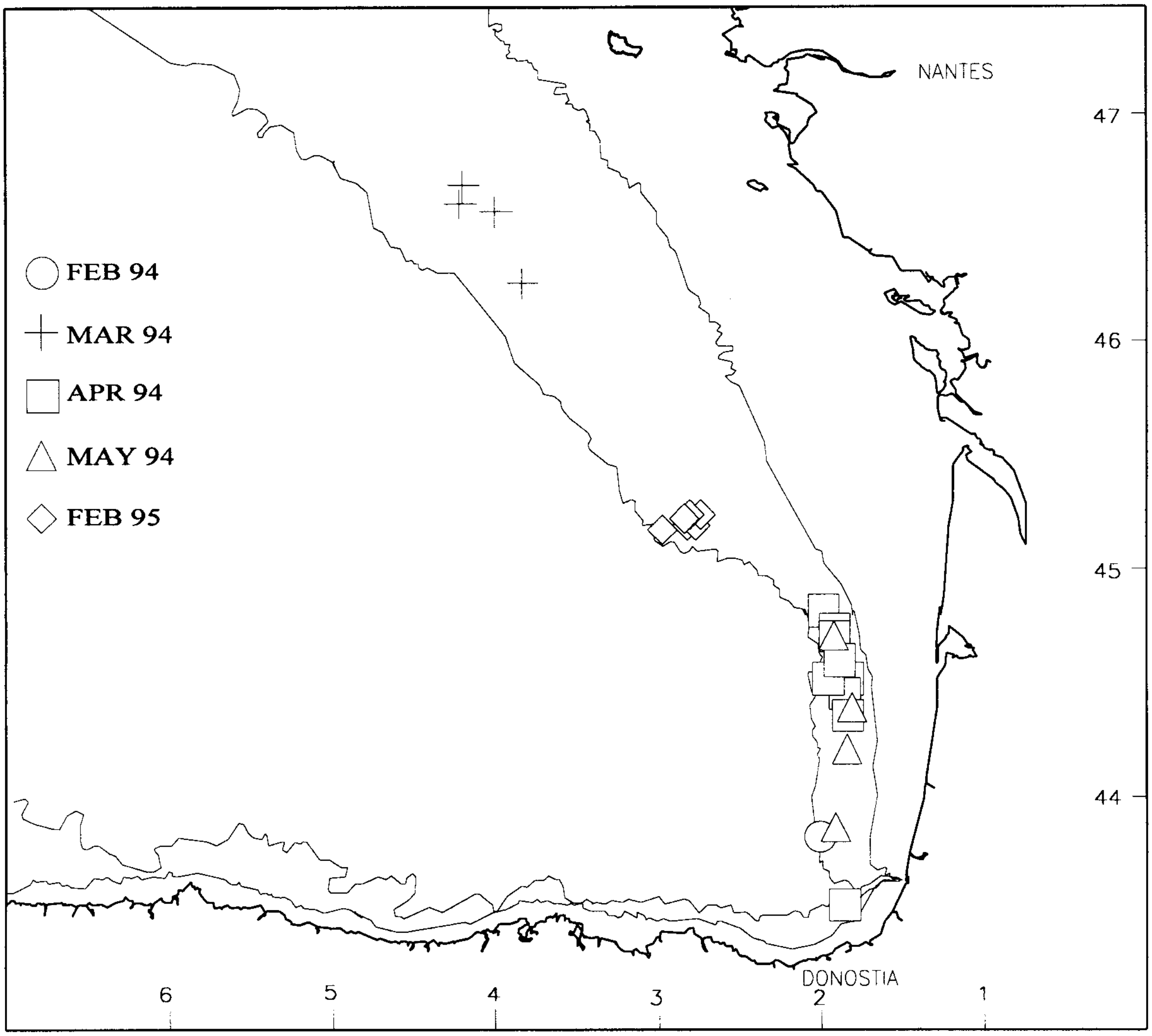

Figure 1. Location of fishing stations for gonad sampling in the Bay of Biscay. Samples were collected by longline (February 1994) or by pelagic trawl (March–May 1994 and February 1995).

were collected at the beginning (January) or at the end of the spawning season (June–July).

Mature females were selected at random from each trawl catch. All individuals were sexed, and total length was measured to the nearest 0.1 cm. Gonads were extracted and preserved in 4% buffered formaldehyde (Hunter 1985). The preserved ovaries provided material for histological descriptions (Hunter et al. 1985), oocyte size-frequency distributions, and estimates of fecundities. A total of 272 gonads of mature female hake were collected in 1994, and 79 gonads in 1995. Females ranged in total length from 40 to 102 cm in 1994 and from 41 to 82 cm in 1995.

We calculated total weight and gutted weight for each fish by using the length–total weight and total weight–gutted weight relationship given by Martin (1991).

Each ovary was classified histologically according to the most advanced oocyte stage present in the ovary. We followed Wallace and Selman's (1981) criteria for oocyte staging, with some modifications for hake ovarian structure. The diameter sizes for the different oocyte stages were measured only from oocytes that had been sectioned through the nucleus. The presence or absence of all the oocyte and postovulatory follicle stages was recorded.

Total fecundity (F_t) is defined as the total number of vitellogenic oocytes (>150 μm) in the ovary. In all of the 27 ovaries collected for total fecundity assessment, histological analysis identified postovulatory follicles, indicating that these females had already spawned. Consequently, our estimates of total fecundity should be regarded as estimates of the total remaining fecundity or remnant fecundity. These estimates were carried out with the gravimetric method (Hunter et al. 1989).

Batch fecundity (F_b) was determined by the gravimetric, hydrated-oocyte method (Hunter and Goldberg 1980; Hunter et al. 1985). When applying the gravimetric method, we did not evaluate the possible effect of spatial differences of oocyte density on the fecundity estimates.

The fraction of females spawning daily was assessed from the prevalence of the different spawning stages (Hunter and Goldberg 1980; Hunter and Macewicz 1985).

RESULTS

Stages of Oocyte Development

According to the classification by Wallace and Selman (1981), hake show "asynchronous ovaries" where oocytes of all stages are present without dominant populations. The different stages are a consequence of a continuous development process, since the cellular events of oocyte growth do not sequentially replace one another, but rather are initiated sequentially and remain active throughout oocyte development (Selman and Wallace 1989).

The criteria for spawning stages are described below. We found that oocytes smaller than 150 μm contained no yolk and may constitute a reserve fund for next year. Vitellogenesis starts at 150 μm and develops into the nuclear migratory stage (750 μm). The last stage of maturation—hydration (Fulton 1898)—is easily recognized by the translucent appearance of the oocytes (table 1).

Ovulation follows hydration and results in ruptured, empty postovulatory follicles and the release of the oocyte, which is now considered an egg. New postovulatory follicles are readily identifiable, but they degenerate afterwards (fig. 2). Four stages of postovulatory follicle (POF) deterioration were recorded: (1) The structure of the follicle is very well maintained with no signs of deterioration; the granulose and thecal nuclei are clearly distinguishable. (2) The first signs of vacuolation and nuclear pycnosis appear, but the follicle is still well recognizable. (3) The follicle is being resorbed; the granulose and thecal nuclei cannot be differentiated; the structure is disorganized; and vacuoles are abundant. (4) The follicle has shrunk substantially and become a very small structure, which will eventually disappear.

Reproductive Modality

Oocyte size distribution. The pattern of development of mature hake ovaries is shown in figure 3. Hake ovaries show a continuous distribution of oocyte sizes throughout the stages of mature gonad development. Several modes representing spawning batches appear. No hiatus can be observed between the unyolked (<150 μm diameter) and the vitellogenic oocytes. The only observable hiatus is between yolked oocytes and the mode of mature hydrated oocytes just before ovulation and is typical of partial or fractional spawners (Hunter and Goldberg 1980; West 1990).

The sequence of events in ovaries within the (partial) spawning cycle is the same from February until May.

TABLE 1
Development Stages of Oocytes

		Diameter (mm)	
Development stage	Characteristics	Oocyte	Nucleus
Chromatin nuclear	A large nucleus surrounded by a thin layer of cytoplasm. The nucleus contains a large nucleolus, and also a series of very small peripheral nucleoli. The oocyte is surrounded by a few squamous follicle cells.		<0.045
Perinucleolar	Bigger nucleus with several big peripheral nucleoli. Some vacuoles appear in the cytoplasm. The chorion precursor material begins to appear in patches.		0.045–0.07
Vitellogenic (yolked)			
Cortical alveoli formation	Small yolk vesicles start to appear in the cytoplasm. Oil droplets begin to accumulate in the cytoplasm. The chorion and follicle layers are apparent.	0.15–0.25	0.07–0.10
VIT 1	Oil droplets occupy more cytoplasmic area than yolk granules; yolk granule size of 0.003–0.075 mm.	0.25–0.45	0.10–0.12
VIT 2	Oil droplets occupy a similar cytoplasmic area to yolk granules; yolk granule size 0.075–0.125 mm.	0.45–0.55	0.12–0.15
VIT 3	Oil droplets occupy less cytoplasmic area than yolk granules; yolk granule size 0.125–0.20 mm.	0.55–0.65	0.15–0.20
Maturation			
Early migration	Oil droplets fuse into a unique oil globule, and the nucleus starts to migrate peripherally. Size of yolk granules: 0.20–0.25 mm.	0.65–0.75	0.20–0.25
Late migration	Nuclear migration continues; yolk granules fuse into plates starting in the center and extending centrifugally. Size of yolk granules: >0.25 mm.	0.75–0.95	
Hydration	Yolk has fused into a homogeneous mass. The nucleus has disintegrated. The cytoplasm and the cortical alveoli are restricted to a thin peripheral layer.	0.95–1.15	

Summary of oocyte developmental stages in European hake ovaries. The histological characteristics and the size ranges are given for each stage. Measures are made from histological sections.

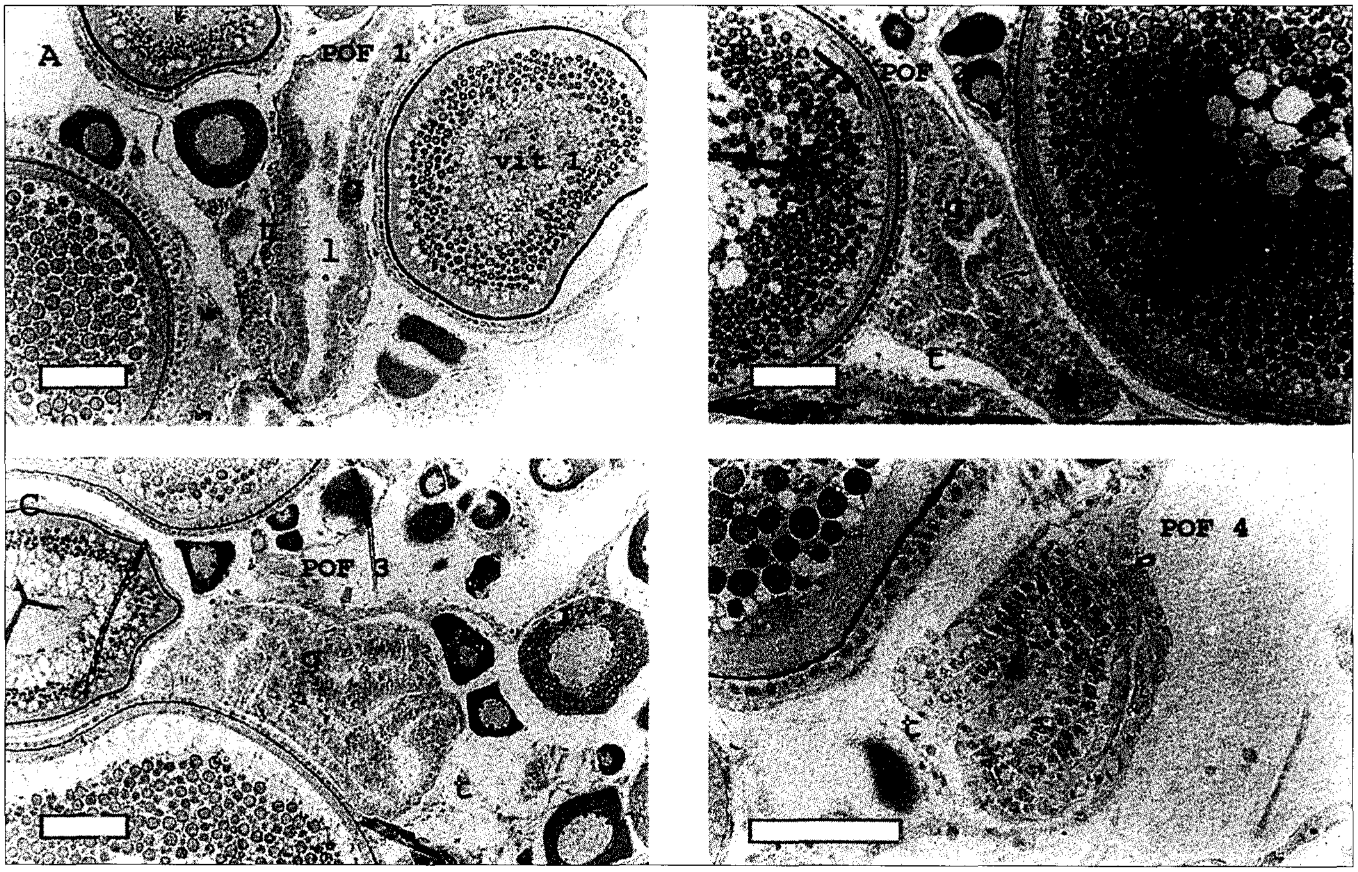

Figure 2. Postovulatory follicle stages: upper left, POF 1 (200×); upper right, POF 2 (200×); lower left, POF 3 (200×); lower right, POF 4 (400×). *t* = thecal connective cell layer; *g* = granulosa epithelial cell layer; *l* = lumen of follicle; bar = 0.1 mm.

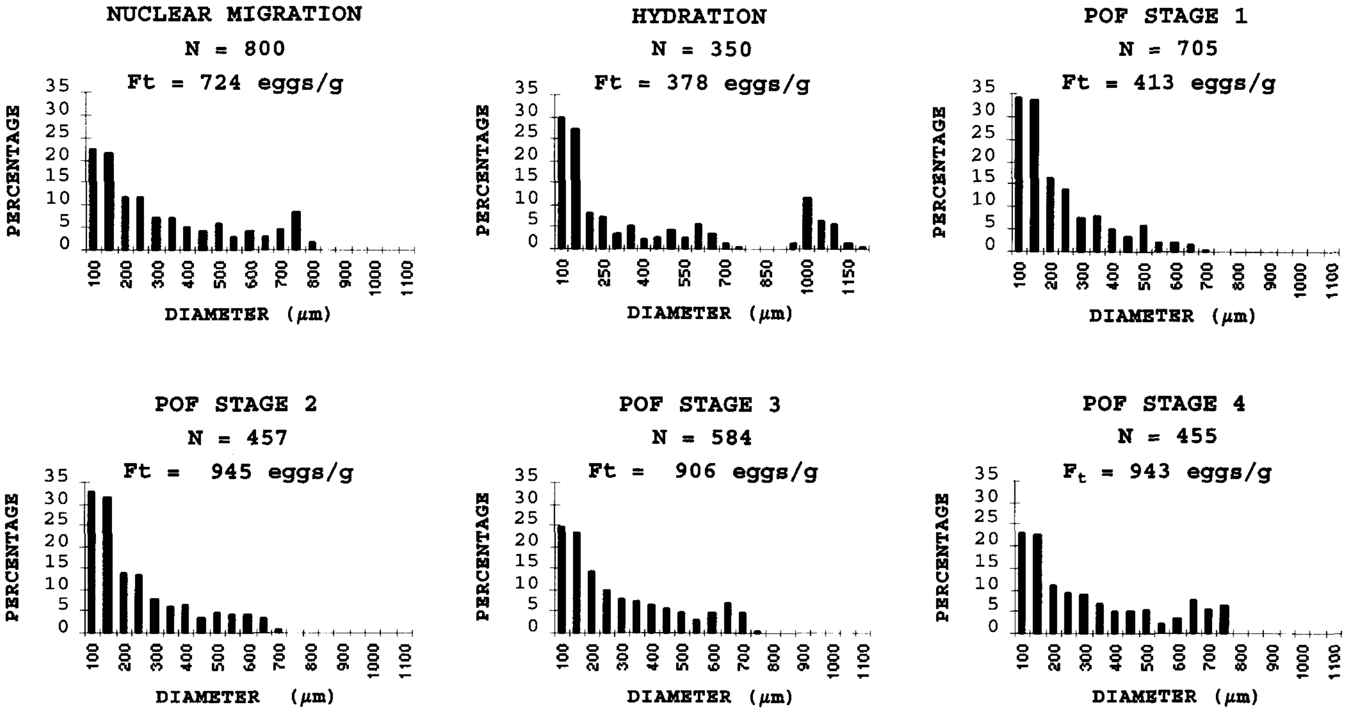

Figure 3. Evolution of oocyte size-frequency distribution (% abundance per 0.05 mm size class) through different spawning stages.

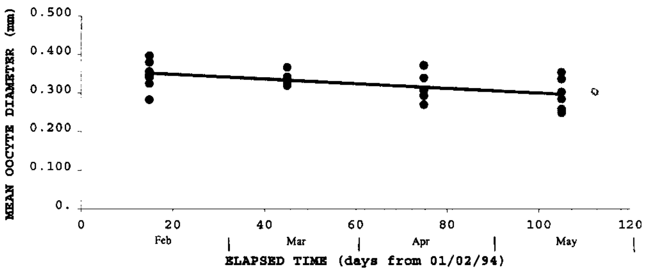

Figure 4. Relation between mean diameter (MD) of the advanced vitellogenic oocytes (excluding hydrated oocytes) and elapsed time, expressed as MD (mm) = 0.3609 − 0.0006 T (days); $R^2 = 0.2683$; $p = 0.004$; $N = 29$.

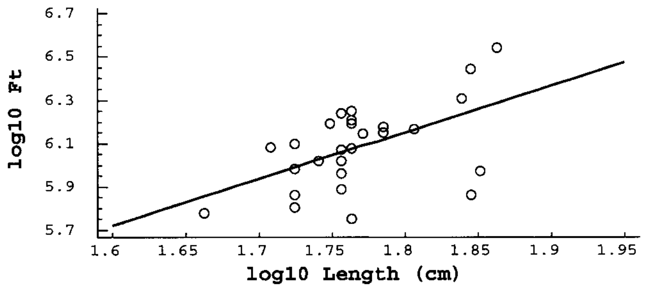

Figure 5. Relation between total (remnant) fecundity and total length for 27 active females collected in 1994.

Mean diameter. The mean diameter of the stock of yolked oocytes greater than 150 µm, but not including hydrated oocytes, decreased steadily from February to May (fig. 4). The points fit to a linear regression had a significant negative slope ($\alpha < 0.05$, $r^2 = 0.2683$). Certainly the mean diameter of the yolked oocytes did not increase during the reproductive season, one of the criteria used by Hunter et al. (1992) for determinate fecundity.

Total (remnant) fecundity. Twenty-seven females from 1994 were analyzed (fig. 5) for total fecundity. The total number of yolked oocytes (>150 µm) in the ovaries (F_t) of European hake in the main spawning season increased linearly with female length (L).

$$\log 10\ F_t = 2.292 + 2.144 \log 10\ L,\ n = 26,\ R^2 = 28.1\%$$

Total relative fecundity (number of vitellogenic oocytes per g gutted weight) ranged from 298 to 1,606 eggs g^{-1}, for an average of 957 eggs g^{-1} (CV = 34%).

A linear regression of fecundity on female weight for the elapsed time did not have a significant slope, indicating that total fecundity did not decrease substantially during the spawning season (fig. 6). An ANOVA on total fecundity using elapsed time as a main factor did not show any significant difference ($\alpha < 0.05$). Length was used as a covariant in this analysis to allow for the increasing relation between total fecundity and months ($p = 0.2517$).

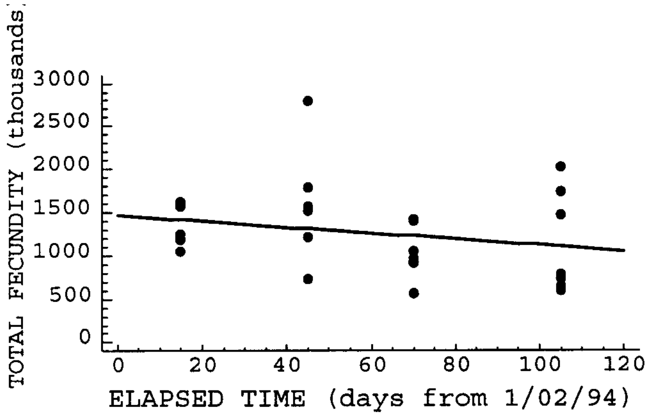

Figure 6. Relation between total fecundity and elapsed time expressed as $F_t = 1465.3 - 3.43\ T$ (days); $R^2 = 5.23$; $N = 27$.

Atresia. The incidence of atresia was low in the hake ovaries that we analyzed, perhaps because the females were sampled in peak spawning months. No ovaries were sampled at the end of the spawning period (June and July), when postspawning females with potentially highly atretic ovaries would be expected to be present. Sarano (1986) reported that the prevalence of atresia was low in ovaries with signs of recent spawning, whereas extensive atresia of yolked oocytes was prevalent in postspawning females taken at the end of April and May.

Batch Fecundity

Batch fecundity (F_b) relationships were established for 66 hydrated ovaries collected. The relation of batch fecundity to fish length (L) was best described by

$$F_b = -0.196L^{3.404} (N = 66,\ R^2 = 61.8\%)$$

A one-way ANOVA on batch fecundity did not show any significant difference between either years or months ($p = 0.344$, $p = 0.689$). We used fish weight in this analysis as a covariant to take into account the increasing relation between batch fecundity and fish weight.

We analyzed the relation between batch fecundity and fish gutted weight (W_g), and the resulting linear regressions presented better fits to the data. Batch fecundity increased with female gutted weight. The intercept of the regression line was not significantly different from 0 ($\alpha < 0.05$) and consequently the regressions were forced through the origin (fig. 7). The slope of this relationship provided a direct estimate of relative batch fecundity (number of eggs spawned per gram of female gutted weight).

The overall batch fecundity for 1994 was 165 eggs g^{-1} (gutted weight) (SE = 9.89), ranging from 67 to 379 eggs g^{-1}. When analyzing the evolution of batch fecundity during the season, we found small variations between months. Batch fecundity varied from 155 eggs

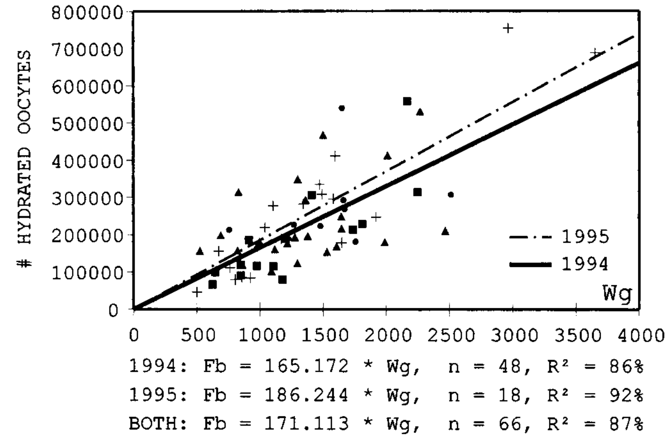

Figure 7. Batch fecundity (F_b) and gutted female weight (W_g) relationship for hydrated female hake sampled in 1994 and 1995. The linear regression fits for 1994 (heavy line) and 1995 (broken line) are shown. Symbols indicate month + year female was collected: diamond = Feb. 94; plus = Feb. 95; circle = March 94; triangle = April 94; and square = May 94.

g^{-1} in February, to 176 (SE = 26.79) in March, 170 (SE = 13.95) in April, and 145 (SE = 16.26) in May. In 1995 the mean batch fecundity reached 186 eggs g^{-1} (SE = 13.3).

Spawning Frequency

Because the duration of the spawning stages of hake ovaries are unknown, spawning frequency cannot be estimated. But spawning stages can be used to compare the relative rates of spawning during the season. The proportions of females with ovaries in different stages of development are shown in table 2.

If daily spawning were synchronous, oocyte stages would be observed at predictable times of day, but the diel timing of hake spawning is not known and the times of day that our samples were caught were too irregular for us to reach any conclusions. Thus we have neither adequate field sampling data by time of day nor laboratory data needed to assign the ages and duration to reproductive stages.

Hydrated females were much more prevalent than those in the migratory-nucleus stage, indicating that hydrated females may have been oversampled or that our catches were concentrated at times of day when hydrated females are more numerous and the migratory-nucleus stage is rare. The use of the migratory-nucleus stage to estimate spawning fraction requires that this stage would last less than one day.

Assuming a duration of less than 24 hours for the nuclear-migration stage implies a spawning fraction of 0.0525 (CV = 30%) and a batch interval of about 19 days in 1994. If hydrated females were not oversampled and the hydration stage lasted about 24 hours, then the spawning fraction would be 0.189 (CV = 17%) and the batch interval would be 5.25 days for 1994. As a reference point, we use the mean spawning frequency of these two stages—0.12 (batch interval = 8.3 days) in 1994.

Annual Fecundity

We computed different levels of realized annual fecundity, assuming that the spawning frequency was equivalent to the frequencies of migratory-nucleus stages (5.25%), hydrated stage (19%), and the mean of these stages (12%). The key assumptions here are that the stages last about 24 hours and that they are unbiased samples of the population (table 3).

To calculate annual fecundity one needs to know the duration of the spawning season. For an individual hake this is not known, but Sarano (1986) gave a duration for the stock of 3 months. Martin (1991) said that the period of reproduction of female hake at the population level lasted from January to April–May, but he stated that the limits of the reproductive period at the individual level are difficult to define.

By assuming a 3-month period from mid-January to mid-May and using the values of batch fecundity and of spawning fraction as stated above, we estimate that the realized annual fecundity of hake would be within the

TABLE 2
Percentage of Mature Females at Each Spawning Stage

			Spawning stages					
					POF classes[c]			
Month	Year	*N* mature females	NM[a]	H[b]	1	2	3+4	Other[d]
Feb.	94	21	4.8	4.8	19.1	19.1	52.2	0.0
Mar.	94	58	5.2	19.0	22.4	10.3	37.9	5.2
Apr.	94	141	7.1	26.8	9.2	8.5	38.0	10.4
May	94	52	3.9	25.0	9.6	7.7	38.4	15.4
Feb.	95	79	9.1	20.8	15.6	12.5	35.1	6.0

Collection of samples was by longline (Feb. 1994) or by pelagic trawl (March, April, May 1994 and Feb. 1995).
[a] Nuclear-migration-stage oocytes present.
[b] Hydrated oocytes present.
[c] See Results, Stages of Oocyte Development.
[d] Active ovaries, no signs of spawning, badly fixed ovaries, bad histological cuts, etc.

TABLE 3
Hypothetical Level of Realized Fecundity for an Individual Female Hake

			Nuclear-migration stage			Hydrated stage			Average spawning fraction		
Months	Duration (days)	F_b eggs/g	S[a] %	Number of spawnings	Number of eggs spawned/g	S[a] %	Number of spawnings	Number of eggs spawned/g	S[a] %	Number of spawnings	Number of eggs spawned/g
February	15	165	5	0.79	130	19	2.85	470	12	1.8	297
March	30	165	5	1.58	260	19	5.7	940	12	3.6	594
April	30	165	5	1.58	260	19	5.7	940	12	3.6	594
May	15	165	5	0.79	130	19	2.85	470	12	1.8	297
Total	90			4.74	780		17.1	2820		10.8	1782

Based on the findings of this work for 1994, assuming that the migratory-nuclear and hydrated stage lasts less than 1 day and that both stages are independent estimates of frequency.

[a] Spawning fraction values (S) are given according to the prevalence of the nuclear-migratory stage, hydrated stage, and average or mean spawning fraction value (0.12).

range from 780 eggs g^{-1} (female gutted weight) to 2,820 eggs g^{-1} (1,782 eggs g^{-1} for a spawning fraction of 0.12) for 1994. Thus a 60 cm hake with a corresponding gutted weight of about 1,332 g would spawn a total number of eggs ranging from 1,038,960 to 3,756,240 (2,373,624 eggs for a spawning frequency of 0.12). The total (remnant) fecundity we measured for a 60 cm fish averaged 1,265,774 eggs, which lies in the lower part of the annual fecundity estimate range.

DISCUSSION

The four lines of evidence pursued in this study do not support the conclusion that European hake have determinate fecundity or fixed annual fecundity. None of the evidence supports this hypothesis for hake, but negative evidence is not nearly as strong as positive. For example, failure of fecundity to decline with season could be due to not enough samples analyzed. Lack of a break in frequency distribution of oocytes is not strong evidence for indeterminate fecundity, whereas the presence of a substantial break is strong evidence for determinate fecundity. In addition, the negative slope in diameter could be considered either as evidence for determinate fecundity by the loss of advanced oocytes due to spawning without complete replacement, or as evidence for indeterminate fecundity by recruitment of new yolked oocytes into the yolk class. Even the lower end of the estimate of annual fecundity based on S, spawning frequency, and F_b, batch fecundity, are within the range for total fecundity.

Since the assumption of determinate fecundity, when it does not exist, can lead to a very large bias, we believe it is preferable to assume fecundity in European hake is indeterminate until there is strong evidence to the contrary. There is no risk in assuming indeterminate fecundity, because estimates of spawning biomass or annual fecundity will not be biased if the standard approaches for indeterminate fish are used (batch fecundity and spawning fraction).

Sampling in February 1994 was done from a longline boat. This can explain the unusually low prevalence of hydrated females in the samples. Hydrated females are unusual in longline catches, possibly because females may not feed in that condition. On the contrary, the unusually high incidence of postovulatory follicle stage 1 females sampled by longline might be a consequence of their rapid switch from spawning to feeding because of their lack of feeding during hydration. On the other hand, the longline may be an unbiased sampler indicating a population spawning ratio of 4.8 per day.

Estimates of total fecundity of European hake are available in the literature (table 4). Sarano (1986) and Pérez and Pereiro (1985) provided overall relations between total number of vitellogenic oocytes and fish length. Sarano's results differ substantially from ours. Sarano's results are half of the levels given by Pérez and Pereiro (1985), although the latter use a higher threshold for vitellogenic oocytes (250 vs. 150 μm). But when a similar oocyte size threshold is used, Pérez and Pereiro's results are comparable to our results. According to Pérez and Pereiro, a 60 cm fish would have around 800,000–900,000 vitellogenic oocytes, which would correspond to the total fecundity.

In our case, with a threshold of 150 μm for vitellogenic oocytes, we found that a 60 cm fish has a total (remnant) fecundity of around 1,266,000. This figure is more than an order of magnitude higher than the value given by Sarano (1986) but of the same magnitude as the figure provided by Pérez and Pereiro (1.39 times higher). Clearly, determining the size threshold of vitellogenic oocytes is a critical stage in the estimation of total fecundity. Since the numbers of oocytes present in these size classes are very high, the final counts will greatly depend on the location of this threshold.

At the same time, the level of batch fecundity for the same fish would be 216,471 hydrated oocytes, on average. This means that a mature ovary contains about six potential spawning batches of eggs greater than 150 μm.

TABLE 4
Total Fecundity (F_T)-Length (L) Relationships, where $F_T = AL^B$

Source	Size range[a]	B	A	Length (cm)	F_t number oocytes	F_t/g	F_t/cm
Sarano (1986)[b]	>160 μm	3.03	0.25	60	61,057	45	1,018
Pérez and Pereiro (1985)	>250 μm	3.27	0.144	60	908,803	682	15,147
This work	>150 μm	2.144	2.29	60	1,265,774	950	21,096
This work	>250 μm	2.23	1.93	60	785,737	590	13,096

Note: All equations based on regression of $\log_{10}$ = transformed data.
[a] The minimum diameter threshold for the standing stock of vitellogenic oocytes counted in the ovaries.
[b] The coefficients are taken from a potential relationship ($y = a{*}x^b$) given by Sarano (1986).

The number of batches spawned per year probably depends on the energy available for spawning, which could produce more than the six-batch standing stock, or less.

The relative batch fecundity (165 eggs g^{-1}) is very close to the estimates of 173 eggs g^{-1} gonad-free weight given for the Peruvian hake, *Merluccius gayi gayi* (Alheit 1986).

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THE BIOLOGICAL CHARACTERISTICS OF THE MONTEREY BAY SQUID CATCH AND THE EFFECT OF A TWO-DAY-PER-WEEK FISHING CLOSURE

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ABSTRACT

Biological data were obtained by sampling landings of market squid (*Loligo opalescens*) at ports in Monterey Bay, California, from 1989 to 1994. Weight, length, sex, and maturity data were recorded and summarized both annually and daily.

Results were compared with historical data, and squid were found to be significantly smaller now than in the 1950s, 1960s, and 1970s. Daily summaries were used to test the hypothesis that a two-day (weekend) closure produced significant changes in the daily biological characteristics of the catch. Analysis revealed that squid catches were highest on Mondays and that the percentage of spent squid in the catch was also highest on Mondays; there was a declining trend in daily catch and spent squid during the week.

It was concluded that a two-day closure is an effective resource management tool for the squid fishery because this is a terminal fishery on the spawning grounds. The higher proportion of spent squid on Mondays following the weekend closure indicated that squid could concentrate on the spawning grounds during the closure and spawn without being subjected to fishing pressure. These results suggest that the duration of the closure could be adjusted in response to the status of the resource.

INTRODUCTION

The market squid (*Loligo opalescens*) fishery is one of the largest, most important fisheries in the Monterey Bay area. Annual landings since 1943 have averaged approximately 5,863 tons, and after the major El Niño period of 1983–84, landings averaged 6,821 tons (fig. 1). From the late 1980s to the present the market squid fishery has ranked either first or second in annual total landings in the Monterey Bay area.

This important fishery has been studied in the past, but very little since the mid to late 1970s. Fields (1965) was the first to make an extensive study of the biology of market squid. He began sampling squid in the late 1940s and continued into the 1960s. Evans (1976) made morphometric comparisons of squid taken in 1974 from the Monterey Bay area and southern California. In 1973, the Department of Fish and Game and Moss Landing Marine Laboratories formed the Market Squid Research Program (Recksiek and Frey 1978) and conducted a series of studies on market squid including age and growth (Spratt 1978), morphometrics (Kashiwada and Recksiek 1978), and acoustic target strength and weight-length relationships (Vaughan 1978).

In 1989, the California Department of Fish and Game initiated a program to sample landings of market squid caught in the Monterey Bay area. This program covered the years 1989 to 1992, and 1994. Its purpose was to reestablish a database of biological information on locally caught market squid that would allow comparisons with data collected from other areas. In addition, data would provide answers to the following questions about the local squid resource: (1) What is the current size distribution of squid? (2) Has the size distribution changed over time? and (3) Are there differences in catch or biological characteristics of the catch that could be attributed to current regulations prohibiting squid fishing on weekends?

During the time of the study, the California squid fishery was essentially unregulated, with the exception of the Monterey Bay weekend closure. There were no regulations pertaining to seasons, quotas, boat or equipment size, limited entry, etc.

METHODS

Catchable quantities of market squid usually begin to appear on the traditional spawning grounds in the southern bight of Monterey Bay in April or May (fig. 2). The fishery continues until about the end of October,

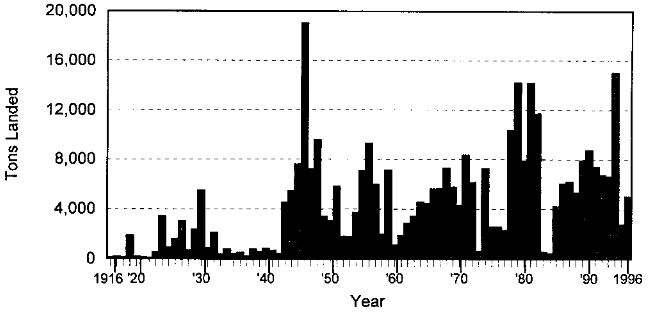

Figure 1. Monterey Bay area commercial market squid landings, 1916 to 1996.

[Manuscript received February 23, 1998.]

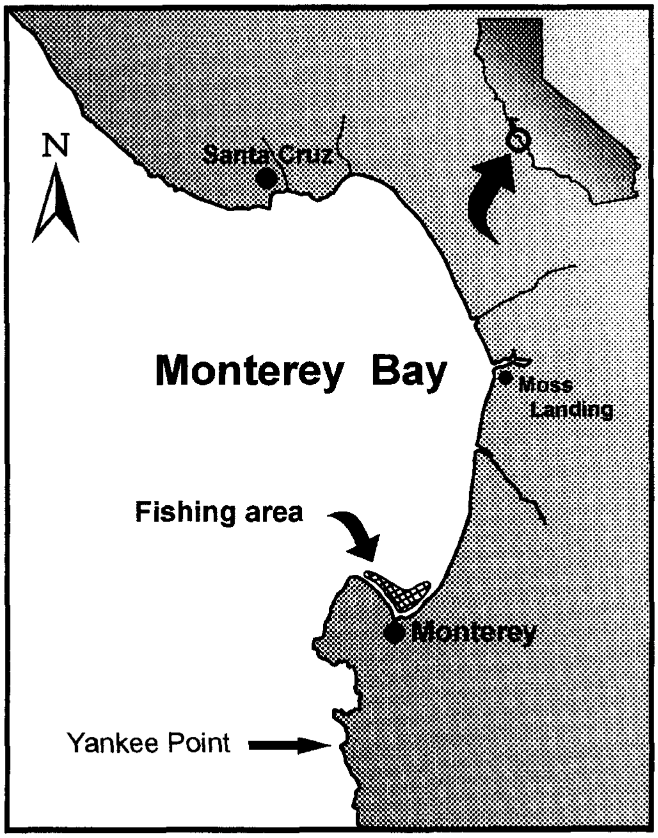

Figure 2. Traditional spawning and fishing area in the southern bight of Monterey Bay, California.

with occasional landings sometimes continuing into December. Occasionally some fishing is done just south of Yankee Point (Monterey County) and as far north as the Point Año Nuevo area (San Mateo County). Because boats frequently fish in several areas during a trip, there is no reliable way to separate or distinguish squid taken from a particular area. As a result, all squid sampled were considered caught in Monterey Bay, regardless of where they actually had been caught.

Sampling Procedures

Generally, one sample per day was taken. To ensure that samples were taken from as many different boats as possible, the three major Monterey Bay area dealers were put on a rotational sequence. The first boat unloading for the dealer at the top of the rotation was sampled on Monday morning. The next morning the next dealer in the sequence was visited, and its first boat was sampled, and so on throughout the week.

Sampling began when a single handful of squid from either the conveyor line or from a forklift bin was placed into a small plastic bucket. Squid were selected by reaching into the mass of squid and blindly grabbing a handful. This continued throughout the entire unloading procedure. I tried to regulate the timing and number of handfuls so that the first handful was taken at the beginning of the unloading and the last taken near the end, to increase the probability of selecting squid from the entire catch (frequently made up from multiple "sets" made on different schools). When the process was done correctly, the final handful topped off the bucket, resulting in a bucket sample weighing approximately 2,000 grams (g).

Processing the Sample

In the laboratory the bucket of squid was poured into a sink. A subsample of 25 squid was randomly picked, one at a time. Squid were selected by reaching into the mass and picking the first squid touched.

The 25 squid selected were allowed to drain further to allow any excess water in the mantle cavity to drain out as completely as possible—the method used by Fields (1965). Each squid was then weighed to the nearest 0.1 g, and its dorsal mantle length (DML) was measured in millimeters (mm). The DML was measured from the anteriormost point on the dorsal side to the posterior body tip. Sex and sexual maturity were determined visually. Though I did not measure internal structures, I used the general descriptive characteristics described by Kashiwada and Recksiek (1978), except that I combined their "immature" and "intermediate" levels and called them immature because of the difficulty in determining maturity levels in some male squid. Starr and McCrae (1984) also reported difficulty in distinguishing between maturity level 2 (intermediate) and maturity level 4 (spent) in males. Also, I followed Starr and McCrae's (1984) method of assigning females to the "spent" maturity category if more than two-thirds of a female's gonad was spent.

All squid were weighed and measured within one to two hours after removal from the boat. Samples were never frozen.

Data Analysis

The following statistical tests were used, with 0.05 as the level of significance: Student's *t* test to compare average weights and lengths and weight losses of males and females, and to compare average weights and lengths to historical data; chi-square to compare proportionate weight losses and sex ratio to previous studies, and to test the proportion of spent squid by the day of the week; analysis of variance (ANOVA) to test the significance of average monthly weight and length variations for males and females, and the significance of the number of landings per day, the total tons landed per day, and the catch per unit of effort per day; and Pearson correlation to compare the number of landings and the total tons landed per day, and to compare the number of landings and the average tons landed per trip.

In order to test for significant differences in the proportion of spent squid found in the daily samples, I stratified samples by day. All samples taken on Monday were grouped, as were Tuesday, Wednesday, Thursday, and Friday samples. I used chi-square to compare the proportion of spent squid from samples taken each day.

RESULTS

Average Weights and Lengths

A total of 248 samples (6,200 squid) was collected during the study period. A total of 3,230 male squid weighed an average of 44.4 g, and 2,970 female squid averaged 35.6 g (table 1; fig. 3).

Male squid had an average length of 129 mm DML, and ranged from 62 mm to 185 mm DML. Female squid had an average length of 125 mm DML, and ranged from 58 to 159 mm DML (table 1; fig. 4).

Comparison with Historical Weight and Length Data

In this study, both male and female squid weighed less and were smaller than those weighed and measured by Fields (1965) and Evans (1976; table 2). Student's *t* tests on the average weights for all males and females indicated that those of this study (males: $t = 85.48$, ∞ df, $P < 0.001$, females: $t = 79.3$, ∞ df, $P < 0.05$) were statistically significantly smaller than those weighed by Fields (1965). Because the means reported by Evans (1976) were nearly equal to the mean weights that Fields (1965)

TABLE 1
Average Weights and Lengths for Market Squid Measured in the Monterey Bay Area, 1989–92 and 1994 Combined

	Immature		Mature		Spent		Total	
	M	F	M	F	M	F	M	F
Number weighed/measured	264	112	2,304	2,532	662	326	3,230	2,970
Average weight (g)	22.6	20.6	47.4	37.2	43.0	28.5	44.4	35.6
Range	6.7–43.4	5.6–36.4	9.3–124.5	13.6–84.3	16.1–102.7	15.8–55.2	6.7–124.5	5.6–84.3
Standard deviation	5.7	5.5	16.4	9.3	15.5	7.3	17.0	9.9
Average length (mm, DML)	102.7	100.8	131.6	126.6	130.2	123.2	129	125
Range	62–130	58–124	71–185	89–159	93–174	95–147	62–185	58–159
Standard deviation	9.5	11.6	15.4	9.4	15.5	8.6	16.9	10.7

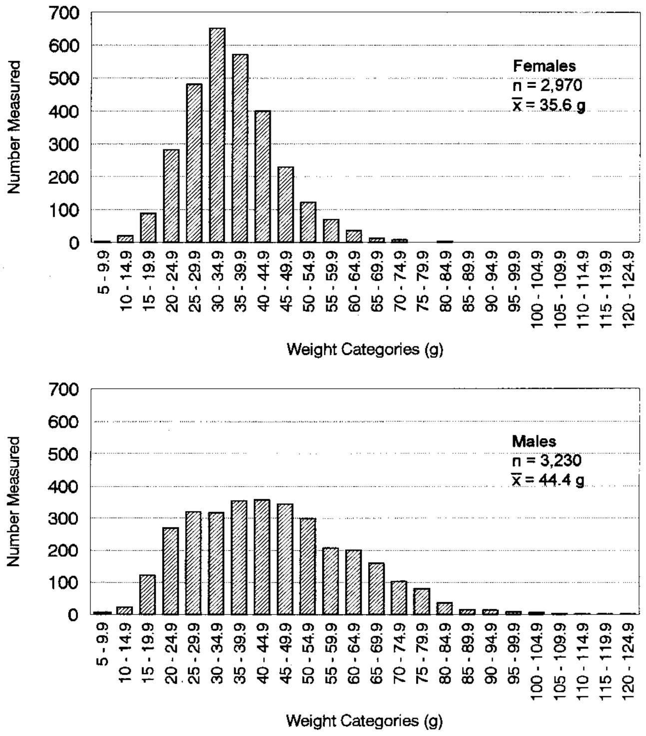

Figure 3. Weights of male and female squid grouped in 5-gram increments taken from the Monterey Bay fishery, 1989–92 and 1994 combined.

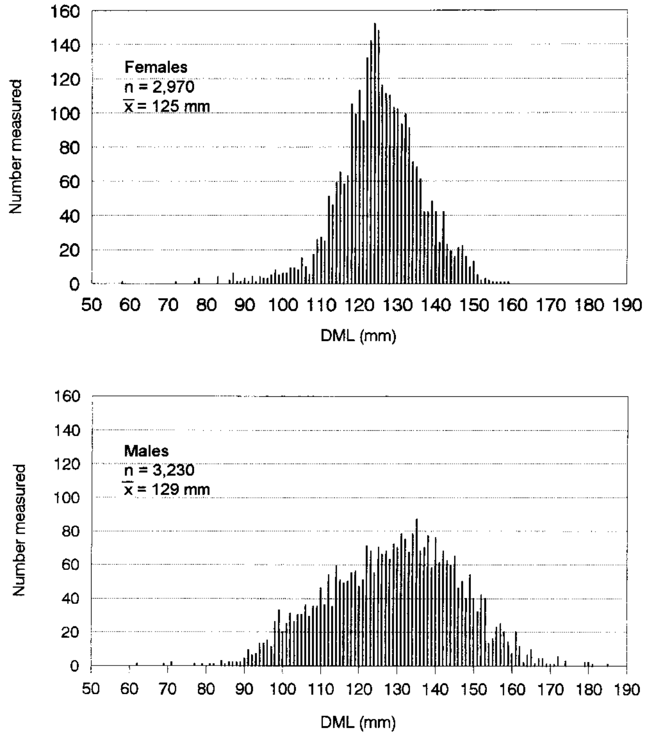

Figure 4. Dorsal mantle lengths (DML) of male and female squid taken from the Monterey Bay squid fishery, 1989–92 and 1994 combined.

TABLE 2
Historical Weight and Length Data of Monterey Bay Squid Compared with 1989–92 and 1994 Data Combined

	Fields (1965)	Evans (1976)	This study (1989–92 and 1994)
Males			
Average weight (g)	70	70.1	44.4
Standard deviation	n/a	22.4	17.0
Average length (mm, DML)	150	146.3	129
Standard deviation	n/a	13.9	16.9
Females			
Average weight (g)	50	49.3	35.6
Standard deviation	n/a	13.4	9.9
Average length (mm, DML)	140	133.9	125
Standard deviation	n/a	10.1	10.7

calculated for both sexes, I ran no comparison test using the means in Evans's study.

Evans (1976) reported average weight losses of 37% in male squid and 35% in females. A chi-square test on the proportions of weight loss for male and female squid in this study, using Evans's (1976) weight-loss proportions as the expected, showed significantly less weight loss ($X^2 = 33.5$, 1 df, $P < 0.001$) than for the squid weighed by Evans. No comparison data were available from Fields's 1965 study.

Student's *t* tests on male and female mean DML in this study compared to squid measured by Fields (1965) and Evans (1976) showed the mean DMLs for both sexes were significantly smaller (males: $t = 70.48$, ∞ df, $P < 0.001$, females: $t = 76.32$, ∞ df, $P < 0.001$) than those found by Fields, and significantly smaller (males: $t = 58.1$, ∞ df, $P < 0.001$, females: $t = 45.3$, ∞ df, $P < 0.001$) than those found by Evans.

Seasonality of Size Differences

The smallest squid were not the first to arrive on the spawning grounds, as had been anecdotally reported by the industry. Instead, squid that appeared in June and July averaged the smallest for both sexes (table 3; figs. 5 and 6).

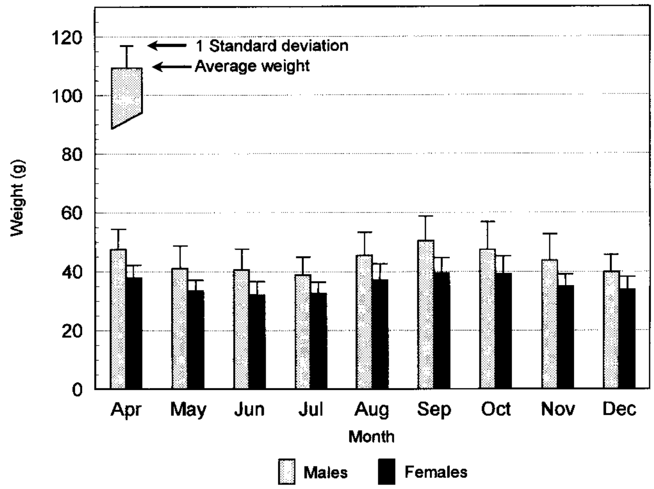

Figure 5. Monthly average weights of male and female squid taken from the Monterey Bay squid fishery, 1989–92 and 1994 combined.

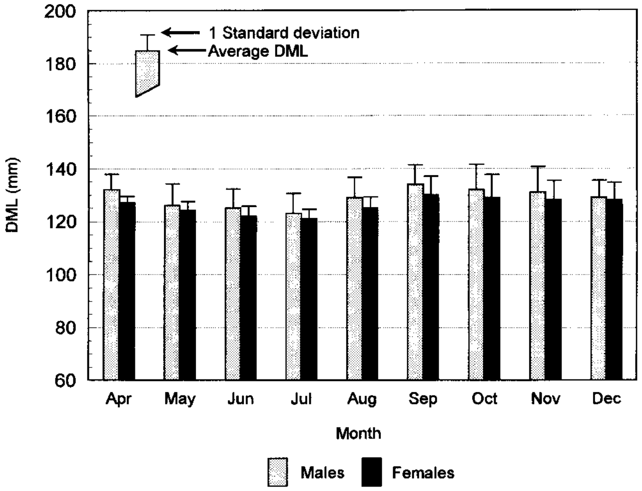

Figure 6. Monthly average lengths of male and female squid taken from the Monterey Bay squid fishery, 1989–92 and 1994 combined.

TABLE 3
Seasonality of Weight and Length Differences for Market Squid in the Monterey Bay Area, 1989–92 and 1994 Combined

	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Average weights (g)									
Males	47.4	41.0	40.5	38.8	45.4	50.3	47.3	43.6	39.8
(SD*)	14.5	15.4	14.7	13.7	17.2	17.2	19.3	18.1	12.4
Females	37.8	33.3	32.0	32.5	37.0	39.3	39.1	34.8	33.8
(SD)	8.4	7.4	8.0	7.4	8.7	10.7	13.2	9.1	8.8
Average lengths (DML, in mm)									
Males	132	126	125	123	129	134	132	131	129
(SD)	14.1	16.0	15.3	15.0	17.1	14.8	19.2	19.5	13.2
Females	127	124	122	121	125	130	129	128	128
(SD)	6.5	8.4	7.5	8.0	9.0	10.8	15.6	11.8	10.8

*Standard deviation

Single-factor ANOVA runs on the average monthly weights for male and female squid revealed no significant differences between months for males ($F = 1.94$, 8 df, $P = 0.1$), but a significant difference in the average weights between months for females ($F = 3.39$, 8 df, $P < 0.01$). A Student's *t* test run on the monthly average lengths indicated that there were no significant differences between the two sexes ($t = 1.51$, 16 df, $P = 0.15$). Single-factor ANOVA runs on the monthly average lengths for males and females indicated no significant difference between months for males ($F = 2.06$, 8 df, $P = 0.1$), but indicated a significant difference between months for females ($F = 3.15$, 8 df, $P = 0.01$).

Sex Ratio

A total of 3,230 male squid and 2,970 female squid were examined, yielding a male:female sex ratio of approximately 1.1:1. Wide variations in sex ratios were noted from sample to sample, week to week, and month to month, with males always accounting for slightly greater percentages on an annual basis (table 4). Single samples were frequently dominated by one sex. Monthly variations in sex ratio were also noted, but no discernible pattern was evident. A chi-square test run on the monthly variations, using 0.5 as the expected frequency, indicated no significant differences ($F = 41.4$, 32 df, $P < 0.05$).

Fields (1965) noted variations in sex ratios in his study, with an overall sex ratio of 1:1. Evans (1976) determined a male:female sex ratio of 1.51:1. I ran chi-square tests on the sex ratio of squid in this study using Fields's (1965) and Evans's ratios as the expected. No significant differences were found between the ratio of this study and Fields's (1965) ratio ($X^2 = 0.16$, 1 df, $P < 0.01$), or Evans's (1976) ratio ($X^2 = 2.67$, 1 df, $P < 0.001$).

TABLE 4
Monterey Bay Area Male:Female Squid Annual Percentages by Number, 1989–92 and 1994 Combined

	Males		Females	
Year	Percent	Number	Percent	Number
1989	51.1	753	48.9	722
1990	53.1	943	46.9	832
1991	50.8	495	49.2	480
1992	53.2	798	46.8	702
1994	50.7	241	49.3	234
Total		3,230		2,970

Kato and Hardwick (1975) commented that it was unfortunate that Fields had lumped several years of data and did not give sex ratios by seasons or smaller entities, implying that possibly seasonality in sex ratios may have been evident.

Ally et al. (1975) reported that squid attracted to lights, and caught by jigging, had a sex ratio of 7.68:1 males to females. They hypothesized that males were more attracted to lights than females. My study did not support that hypothesis. It is possible that the high ratio of males reported by Ally et al. (1975) was due to the aggressive behavior of males in their reaction to the jigs rather than their response to the lights. Squid in this study were caught only with purse seine nets and attracting lights.

Proportion of Spent Squid in Daily Landings

It would be expected that the majority of squid from commercial catches at any time of the season would be sexually mature. This study confirmed the assumption, with 78.0% of 4,836 squid identified as mature. There were 988 spent squid (15.9%) and 376 (6.1%) immature squid.

What is of interest, however, is the daily proportion of spent squid that appeared in the sampled landings. The proportion of spent squid in landings may be viewed as an indicator of spawning success. Spent squid were present in greater proportions on Mondays (18.1%), and generally decreased as the week progressed (table 5). A chi-square test run on the proportions of spent squid by day of the week showed that proportions of spent squid were highly significantly different ($X^2 = 14.25$, 4 df, $P < 0.01$).

Analysis of Daily Landings

To determine if there were patterns in daily landings, I totaled the number of landings per day for the years of the study. The total number of landings on Mondays (1,061) was greater than for other days of the week and decreased throughout the week; Friday's total (697) was lowest (table 6). A two-factor ANOVA test (using days

TABLE 5
Number and Percentage by Maturity of Squid Sampled per Day in Monterey Bay Area, 1989–92 and 1994 Combined

Condition	Monday		Tuesday		Wednesday		Thursday		Friday	
Immature	90	(5.9%)	80	(6.3%)	64	(5.4%)	46	(4.3%)	96	(8.3%)
Mature	1,159	(76.0%)	976	(76.5%)	941	(80.1%)	860	(80.0%)	900	(78.3%)
Spent	276	(18.1%)	219	(17.2%)	170	(14.5%)	169	(15.7%)	154	(13.4%)
Total	1,525		1,275		1,175		1,075		1,150	

as the randomized blocks) revealed a statistically significant difference among the days ($F = 13.19$, 4 df, $P < 0.001$). The total number of tons landed on Mondays was also greatest and decreased as the week progressed (table 6). Here too, a two-factor ANOVA test revealed a significant difference among the days ($F = 8.78$, 4 df, $P < 0.001$).

Daily Catch per Unit of Effort

I calculated the daily catch per unit of effort (CPUE) of squid boats, using the rationale that the unit of effort is a boat trip rather than actual effort on the fishing grounds (the number of sets or the hours fished). I used this method because there were no other effort data available from the squid fishery. Current Department of Fish and Game regulations do not require squid boat captains to document their effort or activity in any manner (e.g., logs). Therefore, a landing is equivalent to one boat trip. This follows the method described by Hardwick and Spratt (1979), except that I refined the CPUE estimate by dividing the combined total tons landed for each day of the week (for all years combined) by the number of trips per day of the week (all years combined) to arrive at a CPUE defined as the average catch (in tons) per trip per day of the week (table 6).

The CPUE was highest on Monday (11.58 tons/trip) and lowest on Thursday (10.23 tons/trip), with an overall average of 10.7 tons/trip. An ANOVA test run on CPUE with days and years as factors showed no statistically significant differences ($F = 0.7$, 4 df, $P = 0.06$).

Daily Changes in CPUE

A correlation coefficient analysis between the number of trips for each day of the week and the total tonnage of these landings indicated a positive relationship between the two variables ($r = 0.98$, 3 df, $P < 0.001$). This is to be expected, because more effort tends to result in greater landings (assuming that sufficient squid are on the fishing grounds).

A correlation coefficient analysis between the number of trips per day of the week and the average tons landed per trip resulted in no statistically significant relation between the two variables ($r = 0.65$, 3 df, $P = 0.80$). In other words, CPUE did not change from day to day.

TABLE 6
Catch per Unit of Effort, on a Daily Basis, for the Monterey Squid Fishery, 1989–92 and 1994 Combined

Day	Number of landings	Total tons landed	Total tons/ landing (CPUE)
Monday	1,061	12,283	11.58
Tuesday	928	9,625	10.37
Wednesday	824	8,590	10.42
Thursday	758	7,755	10.23
Friday	697	7,496	10.75
Total	4,268	45,749	
Average CPUE			10.72

DISCUSSION

Comparisons of Size Difference

The first of the two key questions that arise from the examination of these data is, Why were squid smaller in the 1989–94 catches than in the catches from the 1940s to 1970s? One reason may be that the ocean's primary productivity was greater during the times of the previous studies; water temperatures in the eastern Pacific were cooler (Reid 1988). From the early 1950s through the mid-1970s, zooplankton volumes were generally above average (Reid 1988), except during the 1957–58 El Niño period. Squid measured from catches during that time may have had more euphausiids (their main food) to feed on.

Squid measured during this study were taken during a period of relatively warmer water temperatures, linked to one of the strongest El Niño events (1982–83) recorded in this century. The period after the 1982–83 El Niño event was generally characterized by water temperatures at or just above normal in the Monterey Bay area. Another, less intense, El Niño event in 1992 continued the warm-water regime into the mid-1990s. The 1992 event certainly appears to have reduced primary productivity and zooplankton abundance in the central coast area (Lenarz et al. 1995). In fact, a warm-water period from 1990 to 1995, associated with an El Niño/Southern Oscillation event, is the longest event of its type in 130 recorded years (Trenberth and Hoar 1997). This entire warm-water period resulted in lower primary productivity (McGowan et al. 1996). The growth rate of squid may have been affected, reducing the overall size of squid caught from the late 1980s through the mid-1990s, compared to the sizes measured from catches in the late 1940s to the mid-1970s.

Seasonality of Size Differences

The fact that larger squid appeared on the spawning grounds during the first part of the season and then again later in the year suggests the possibility that spawning arises from two broods. This supposition has been addressed in the South African chokka squid (*Loligo vulgaris reynaudii*) fishery (Augustyn et al. 1992) and may be the case in the Monterey Bay area squid fishery.

Comparison of Weight Loss

One reason for a lesser weight loss when compared to Evans's (1976) study may be linked to the greater efficiency of today's purse seiners and the use of attracting lights mounted on the purse seiners and their associated light boats (Spratt and Ferry 1993). Rarely did we observe a completely spent male or female squid. Nearly all squid categorized as spent still had some spermatophores or eggs within the body cavity. Because squid show a strong positive phototaxis response, it was not necessary for the purse seine net to reach the bottom to capture the squid. Consequently, completely spent squid, near the bottom, apparently weakened by the spawning process and possibly not as reactive to the lights, may not have been as likely to be caught as the stronger squid. Thus, one result of the use of attracting lights may be that most, or at least a large percentage, of squid are caught before they complete their spawning (as some fishermen contend). The use of lights selects for stronger, more mobile squid that have yet to suffer the degenerative changes associated with spawning noted by Fields (1965).

Effect of a Weekend Closure

The second key question arising from this study is, Why were more spent squid in the Monday samples of the catch, with a decreasing trend as the week progressed? I speculate that this is directly associated with the weekend closure in the Monterey Bay area. If squid do regroup so that spawning increases during the 60-hour weekend closure (no squid fishing was allowed from noon Friday to midnight Sunday in CDFG districts 16 and 17), a greater number of spent squid would be present on the spawning grounds by the time fishing resumed at Sunday midnight. A greater percentage by number of spent squid was found on Monday (table 5). A chi-square test among proportions of spent squid by day of the week was significant ($P < 0.01$) among the days of the week.

Evidently, early in the week a greater proportion of the catch was made up of spent squid. This suggests and supports the possibility that the weekend closure allows squid to reschool and engage in increased, undisturbed spawning. The increased spawning is reflected in the resulting higher proportion of spent squid appearing in the samples taken from Monday. As fishing continued throughout the week, fewer spent squid were present on the spawning grounds, making a smaller proportion of the total catch.

Catch per Unit of Effort

The fairly consistent CPUE (table 6) may be a result of the processors' knowledge of the fishery and how to adjust the number of boats sent out in relation to the numbers of squid they feel are present on the fishing grounds. As the week progressed and squid became more difficult to catch because of lack of availability or scattering as a result of fishing pressure, processors sent out fewer boats; those that did fish had a better chance of reaching their trip limit or catching as much as possible. In effect, this affected the landings per day, CPUE, and the number of boats in the Monterey squid fishery and how much they ultimately caught. As a result, while the total daily tonnage that was landed decreased during the week and the number of landings decreased, CPUE remained relatively steady, especially from Tuesday to Friday (table 6).

Daily first-hand observations of the fishery confirmed this practice. I found that quite often toward the end of the week processors sent out only company boats or more successful boats. Smaller boats or those that had not been as successful during the beginning of the week were often ordered to stay in port. Frequently this order stayed in effect until reports came in that a new school of squid had arrived on the spawning grounds or until the uncaught, scattered squid were allowed to regroup. The scattered squid appeared to regroup during the weekend closure.

Hardwick and Spratt (1979) calculated CPUE by using the total annual landings divided by the number of "boat delivery days." They did not calculate CPUE on a daily basis. In both cases (Hardwick and Spratt 1979 and this study), CPUE so defined should be approached with a degree of caution. Boats that were unsuccessful for a given night's efforts are not factored in this definition of CPUE. This introduces a bias in CPUE as an indicator of relative availability in the squid fishery. Hardwick and Spratt (1979) point this out, stating that the average catch per delivery day is higher than it should be because these unsuccessful boats are not included. Also, CPUE as I calculated it did not and could not take into consideration boats placed on trip limits with possible smaller loads, yet another source of bias.

SUMMARY AND CONCLUSION

Squid measured during the 1989–92 and 1994 Monterey Bay area seasons were significantly ($P < 0.001$) smaller (mean weight and mean DML) than squid measured by Fields (1965) and Evans (1976). El Niño events during the 1980s and 1990s may have contributed to decreased productivity, resulting in less food for squid, with the end result that they were smaller.

Squid caught at the time of this study were attracted by powerful lights, and the amount of spawning may have been affected. Further studies should be conducted to test this hypothesis. Spent squid in this study did not lose as much weight as spent squid measured in previous studies. Again, this may have been an effect of the attracting lights. Further studies comparing squid caught by boats not using lights and those using lights may provide an answer.

The smallest squid did not appear on the spawning grounds at the beginning of the season, as had been previously reported. Instead larger squid appeared first, and then again later in the year. This gives rise to the possibility that the spawning population of Monterey Bay is composed of two broods.

Spent squid were present in significantly greater proportions early in the week, and the proportions declined until the last day of the fishing week. Increased spawning probably took place during the 60-hour weekend closure, resulting in the higher proportions early in the week.

Industry representatives reported that generally more squid were caught on Mondays and that the numbers decreased with each successive day of fishing. They feel the greater landings on Mondays are attributable to the weekend closure. Total landings were highest on Monday and decreased as the week progressed, although CPUE did not significantly change.

A weekend closure appears to be a cost-effective management tool that benefits the squid resource. I speculate that the weekend closure provides a respite period for squid, since this period of no fishing allows them to "regroup" after being subjected to five nights of fishing pressure. As a result, spawning increases and a higher proportion of spent squid appear in catches immediately after the closure. I recommend continuing a weekend closure of at least this duration. Further research may indicate that additional closure time may be necessary to allow increased spawning. Future research may also indicate that, as a management tool, a statewide weekend closure would be appropriate or necessary for the squid fishery.

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MANAGEMENT STRATEGY FOR THE GIANT SQUID (*DOSIDICUS GIGAS*) FISHERY IN THE GULF OF CALIFORNIA, MEXICO

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ABSTRACT

A single-cohort biomass model was developed for a management strategy using proportional escapement as a reference to control fishing effort for the giant squid (*Dosidicus gigas*) in the Gulf of California. Biological information (length and weight frequencies) and fishery statistics (catch and effort) from November 1995 to November 1996 for the commercial fleet were analyzed. The data showed the presence of one cohort of *D. gigas*, which recruited in May. This cohort supported the fishery throughout the year. Using a biomass estimate from a research cruise in the central area of the Gulf of California in October 1996, the model predicted the highest levels of abundance from October 1996 to January 1997. We suggest a proportional escapement, estimated from the point of maximum biomass, between 27% and 40%, with a remaining biomass of between 65,560 and 34,890 metric tons in May, a month in which a new recruitment can be expected in the fishery.

INTRODUCTION

Giant squid (*Dosidicus gigas*) landings during 1996 in the Gulf of California exceeded 100,000 metric tons (t) live weight. In this fishery, there are three fishing fleets: one from Baja California Sur, and two from Sonora, Mexico. Landings by these fleets vary seasonally according to the availability of squid. Off Baja California Sur, fishing is done during spring and summer; in Sonora, during fall and winter. Increased catch of giant squid during the last year has caused an increase in fishing effort, a situation that should be analyzed to avoid damaging the squid population.

The dynamics of a single cohort can be analyzed by interpreting the combined effects of changes in the natural mortality (*M*) and individual growth, given an initial recruitment (N_0; Alverson and Carney 1975). In previous studies on squids (Rosenberg et al. 1990; Morales-Bojórquez et al. 1997) the management strategy was to determine the number of recruits at the beginning of the fishing season, their exploitation rate, and the stock size at the end of the fishing season.

The strategy we propose is to determine a proportional escapement useful for controlling the fishing effort. Proportional escapement is defined as the number of spawners alive at the end of the fishing season as a proportion of those that would have been alive had there been no fishing (Beddington et al. 1990; Basson and Beddington 1993; Nevárez-Martínez and Morales-Bojórquez 1997). We simulate growth of a cohort and, from the point of maximum biomass, establish a management strategy that considers an increment of the fishing effort and the proportional escapement.

METHODS AND MATERIALS

Research Cruise

A biomass survey was done from the R/V *Lugo* from 9 to 29 October 1996 (LUGOCT). A total of 46 fishing operations covering 39 stations were made. The catch system consisted of an automatic device with jigs, and lighting. For each fishing operation, we recorded the initial and final position of the vessel, number of squid captured, fishing time, and time of illumination prior to the operation of the jigs. When the catch allowed it, 100 squid were measured, and 20 to 25 were selected at random for biological sampling; mantle length and weight, total weight, sex, and stage of maturity were recorded.

Abundance Estimation

We estimated the biomass of squid by the swept-area method, using total catch in weight (Pierce and Guerra 1994). To reduce the error of the estimate, we divided

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the study area into five strata (fig. 1).

The biomass estimate was obtained as follows (Pierce and Guerra 1994):

$$B_T = \sum_{i=1}^{n} \left(Y_i \star \frac{A_i}{a_i} \right)$$

with variance

$$\hat{V}(B_T) = \sum_{i=1}^{n} \left(\frac{A_i^2 \star n_i \star s_i^2}{a_i^2} \right)$$

where B_T = total biomass;
Y_i = total catch in the ith stratum;
A_i = total area of the ith stratum;
a_i = area swept in the ith stratum;
s_i^2 = variance of the catch of the ith stratum;
n_i = number of fishing operations of the ith stratum.

The swept area at each station was defined as the drift of the vessel (nautical miles) multiplied by the distance of influence of the jigs (established arbitrarily as 10 m from the ship's hull).

Biological Data and Fishery Information

Biological data were collected weekly in the port of Guaymas, Sonora, from November 1995 to November 1996. The information corresponded to commercial landings by the artisanal fleet (small boats with outboard motors, called *pangas*). We recorded length of the mantle (cm); weight of the mantle (kg); sex; and stages of maturity.

Weekly catch and effort statistics were obtained from the Subdelegación de Pesca of Guaymas. This information involved records of a fleet of shrimp trawlers adapted for squid fishing and an artisanal fleet of *pangas*.

Biological Parameters

We analyzed a mantle length (ML) frequency distribution considering biweekly periods, and used the Bhattacharya method, available in FISAT v.1.0 (Gayanilo et al. 1995), to separate cohorts. We then computed the parameters of the von Bertalanffy model for individual growth. The parameter values were optimized to get a best fit of the function $(Y_{Obs} - Y_{Est})^2$, where Y_{Obs} = observed length values and Y_{Est} = estimated length values (Hilborn and Walters 1992). The mantle length–mantle weight relation was also obtained. We used sample data to compute total numbers by interval of mantle length in the weekly landing at Guaymas (Sparre and Venema 1995).

The maturity stages were determined according to Lipinski (1995). Stages I (immature), II (in transition), and VI (end of spawn) were grouped as not active for reproduction, whereas stages III (maturing), IV (mature), and V (spawning) were considered active for reproduction (Hernández-Herrera et al. 1996).

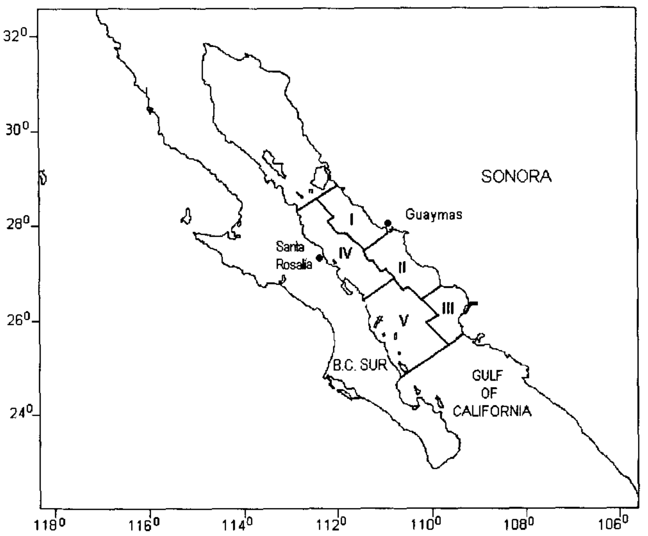

Figure 1. Study area divided into five strata according to the fishing grounds of the commercial fleets.

Yield Analysis and Simulation

We did a virtual population analysis (VPA) by fortnight considering all age groups present in the length-frequency distribution (Pope 1972), using a value of terminal fishing mortality (F) of 0.3, similar to the natural mortality value (M) estimated by Morales-Bojórquez et al. (1997; M = 0.202/fortnight), and using estimates of fishing mortality rate (F) and fishing effort (f) for two different periods (Silliman 1943, cited in Ricker 1975). The initial population size (N_0), corresponding to the size of the recruitment of *D. gigas* was thus determined.

We then used a modification of the model proposed by Alverson and Carney (1975) to explore growth and decay of a cohort. This model depends directly on the value on M, k, W_∞ and N_0. The expression is

$$P_t = N_0 \exp^{-M \star t} W_\infty (1 - \exp^{-k \star t})^{\beta}$$

where P_t = biomass of the population at time t; N_0 = initial recruitment; W_∞ = average individual weight at maximum length; and k = growth rate of the von Bertalanffy model. The modification considered incorporation of the fishing mortality (F) according to the following:

$$P_t = N_0 \exp^{-[(M+F) \star t]} W_\infty (1 - \exp^{-k \star t})^{\beta}.$$

In this expression, we optimized N_0 with the solver tool of Microsoft Excel v. 7.0, minimizing the difference between the direct estimate of population abundance and the population abundance calculated by the model for the corresponding fortnight. Because giant squid cannot live beyond two years, M was increased by 13% each fortnight for squid age 1 year and older. Otherwise it would appear that there is high abundance of squid larger than 80 cm mantle length in the Gulf of California, which is not the case. We optimized a biomass growth curve using an F value of 0.9 and used it as a reference to plot a family of curves for different F values, from $F = 1$ to $F = 1.5$, with increments of 0.1. For each biomass trajectory, we calculated a K value as $K = \text{exp}^{(-F)}$ (Rosenberg et al. 1990).

Thus the management strategy was to determine an escapement level that would be useful in the control of fishing effort. This control could be implemented in two ways: by limiting the number of licenses, and by limiting the length of the fishing season (Beddington et al. 1990; Basson and Beddington 1993).

With the theoretical values of F, and according to the expression

$$f_{Est} = \frac{F}{q},$$

we estimated the calculated effort (f_{Est}) in number of fishing nights for the adapted shrimp fleet by using $q = 0.000429$ (Morales-Bojórquez et al. 1997). For the artisanal fleet, we standardized effort (f_{Sta}) from f_{Est} by using a correction factor (Fc). This was estimated as $Fc = \overline{CPUE_{sr}} / \overline{CPUE_{af}}$, where $\overline{CPUE_{sr}}$ is the mean catch per unit of effort of the shrimp fleet, and $\overline{CPUE_{af}}$ is the mean catch per unit of effort for the artisanal fleet. Hence, $f_{Sta} = f_{Est} \star Fc$.

RESULTS

For the biomass survey, figure 1 shows the study area and five strata considered. The estimated total abundance of the population was 171,150 t (±21,200 t, 95% CI).

During the year of study, 1,934 individuals were sampled. Mantle lengths ranged between 24.3 and 86 cm, with an average of 58.6 cm. Analysis of the mantle length-frequency distribution showed one annual cohort (fig. 2), with a recruitment observed during May. Because the mantle lengths were measured biweekly, it was possible to estimate the age in years, every two weeks corresponding to 0.038 years. Thus squid recruited to the fishery at an estimated age of 6 months. The parameters of the von Bertalanffy growth model were: $k = 0.8$/year; $L_\infty = 87$ cm mantle length; and $W_\infty = 0.013$ t mantle

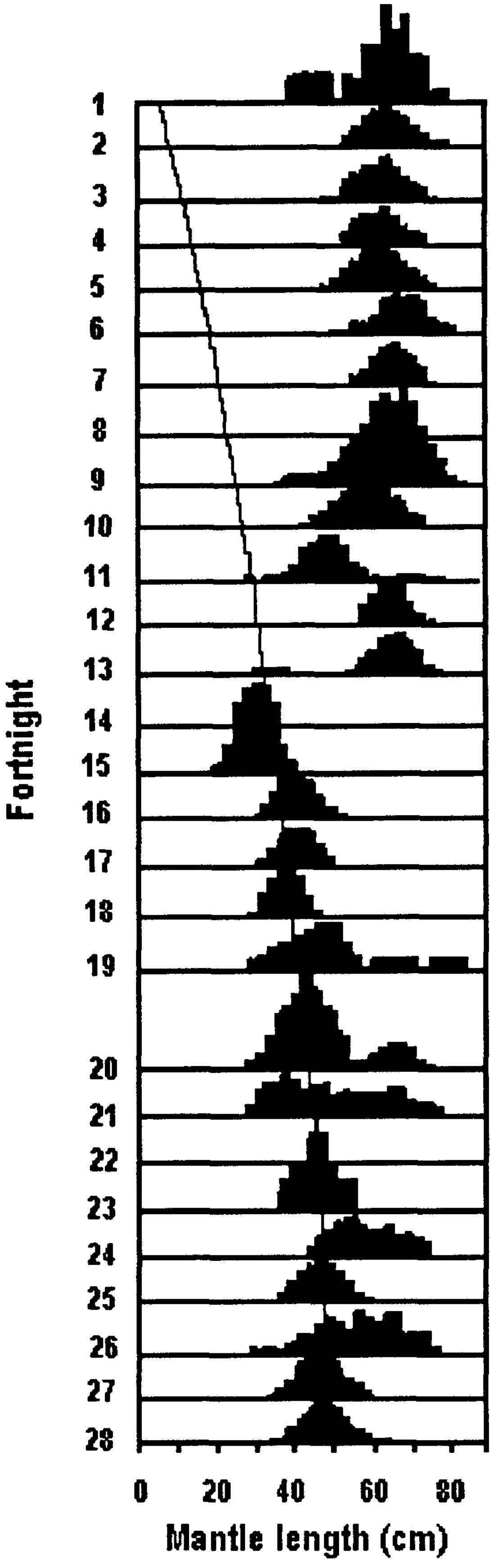

Figure 2. Progression modal analysis applied to mantle lengths (cm). Fortnight 1 is from 5 to 18 November 1995. Fortnight 28 is from 17 to 30 November 1996.

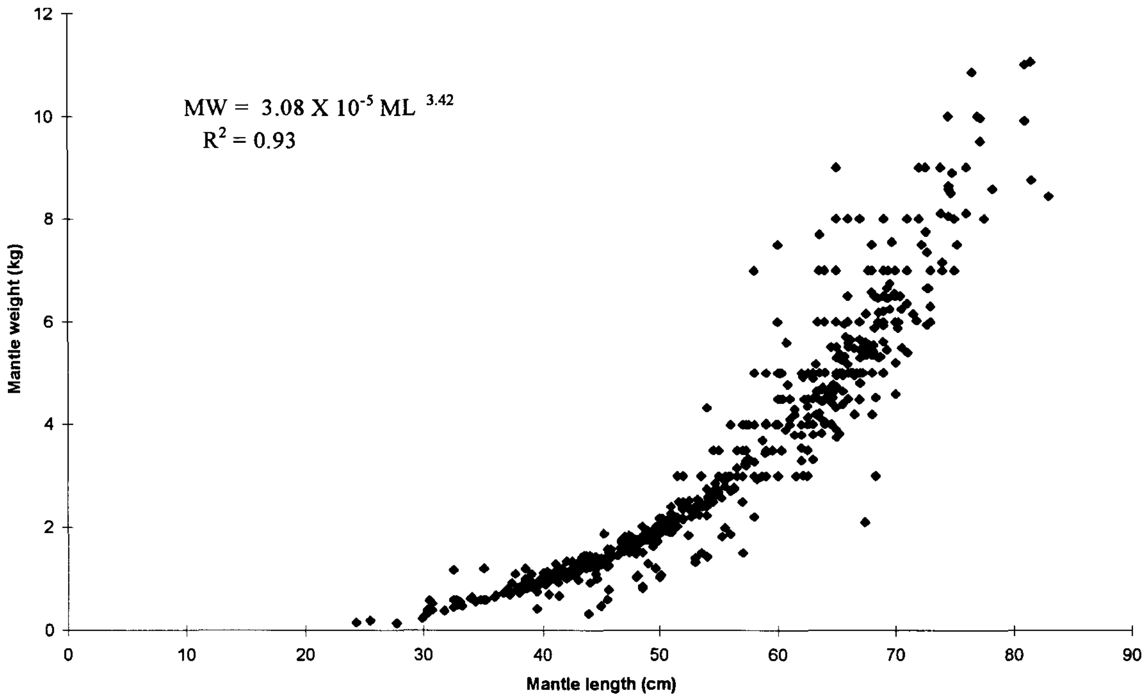

Figure 3. Mantle length (cm)–mantle weight (kg) relation for giant squid.

weight. Parameters of the length (L)–weight (W) relation for mantle were $\alpha = 3.08 \times 10^{-5}$ and $\beta = 3.42$ (fig. 3). The growth models in mantle length (ML) and mantle weight (MW) were

$$ML = 87 \times \{1 - \exp^{[-0.8*(t-0.115)]}\}$$

$$MW = 0.013 \times \{1 - \exp^{[-0.8*(t-0.115)]}\}^{3.42}$$

The stages of maturity showed that the spawning season lasts from February to May, with a relative frequency of active females greater than 90% during that period (fig. 4).

The estimate of N_0 from virtual population analysis was 386×10^6 individuals; the optimized value of N_0 with respect to the estimate of abundance of the survey was 303×10^6 individuals. The model to estimate biomass (t) is

$$P_t = 303 \times 10^6 \exp^{-[(0.202+F)*t]}\ 0.013(1 - \exp^{-0.8*t})^{3.42}$$

Figure 5 shows (a) the biomass curve with constant natural mortality ($M = 0.202$/fortnight), and (b) a biomass curve considering an increase in M from $t = 1.076$ years and older. According to model a, squid will live longer than two years, and the maximum yield will occur from fortnight 20 to fortnight 30. According to model b, maximum yield of approximately 190,000 t occurs from fortnight 12 to fortnight 18, whereas the remaining biomass for fortnight 27 was 65,560 t, when a new recruitment could be expected.

Figure 6 shows the trajectories of biomass with different levels of F. Table 1 shows the estimates of K, f_{Est}, f_{Sta}, and the remaining biomass for each value of theoretical F.

DISCUSSION

The annual mantle length-frequency analysis for the fishing grounds off Guaymas showed evidence of only one cohort with an annual recruitment. This recruitment was observed during May, when squid were 6 months old, corresponding to mantle lengths between 24 and 50 cm. During this period squid were actively reproducing off Guaymas, as described by Hernández-Herrera et al. (1996).

We assumed that recruitment observed in May was the most important, and that it sustains the squid fishery during the fishing season. This recruitment could be the result of a spawn at another time and in another area within or outside the Gulf of California. Ehrhardt et al. (1983) observed mature squid in December and January off the Pacific coast of the Baja California Peninsula, suggesting that this spawning event is of great importance because it generates the squid that recruit to the fishery from March to April and support the fishery from May to September, when fishing effort increases due to the presence of the shrimp fleet. Ehrhardt et al. (1983) also observed high percentages of mature females in May and June, which agrees with our observations

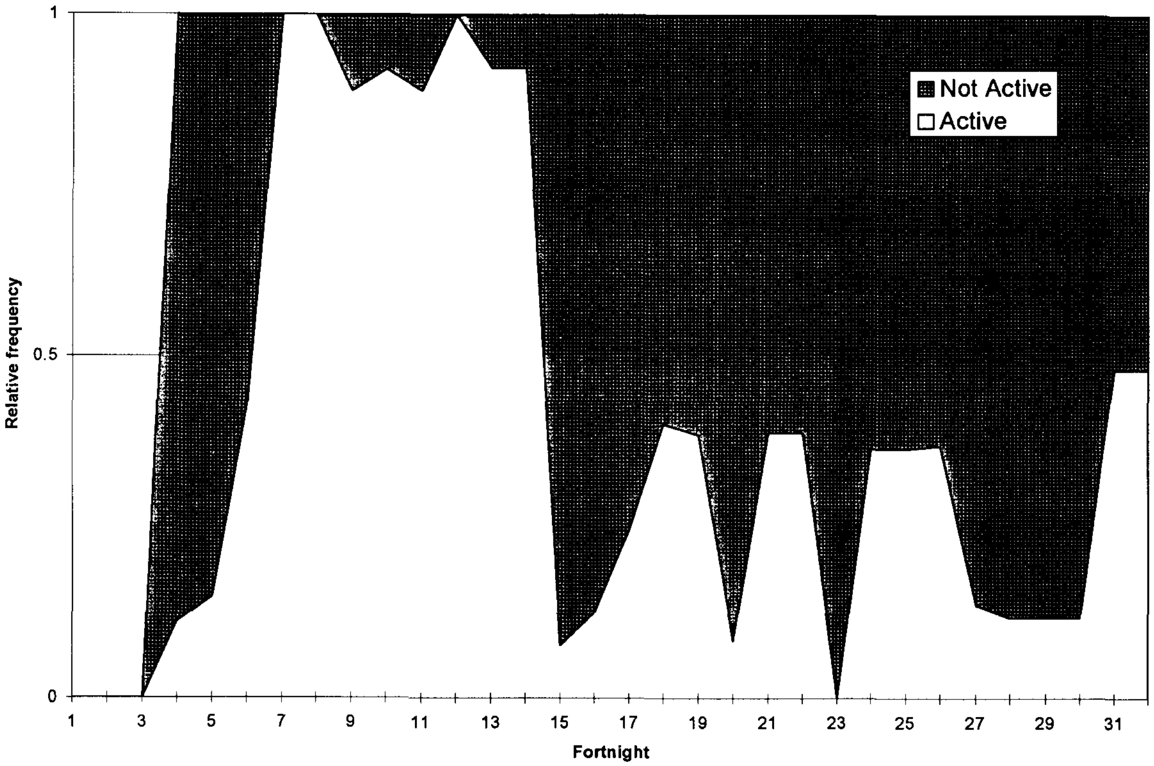

Figure 4. Proportion of females not active and active for reproduction. Not active were maturity stages immature (I), in transition (II), and final spawning (VI). Active stages were maturing (III), mature (IV), and spawning (V). Fortnight 1 is from 5 to 18 November 1995. Fortnight 32 is from 12 to 25 January 1997.

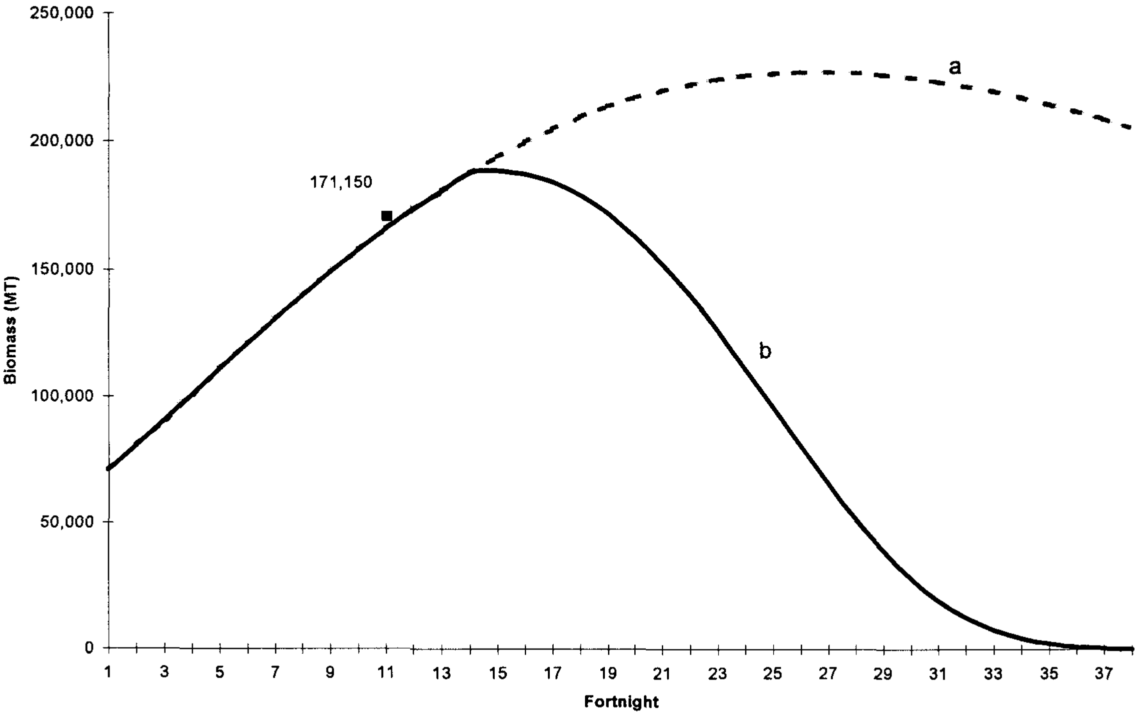

Figure 5. Biomass trend of giant squid: *a*, constant natural mortality; *b*, with an increment in natural mortality of 13% into each new instant of time *t* from *t* = 1.076 years. The value of 171,150 metric tons corresponded to the biomass estimation aboard the R/V *Lugo*. Fortnight 1 is from 19 May to 1 June 1996. Fortnight 38 is from 19 October to 1 November 1997.

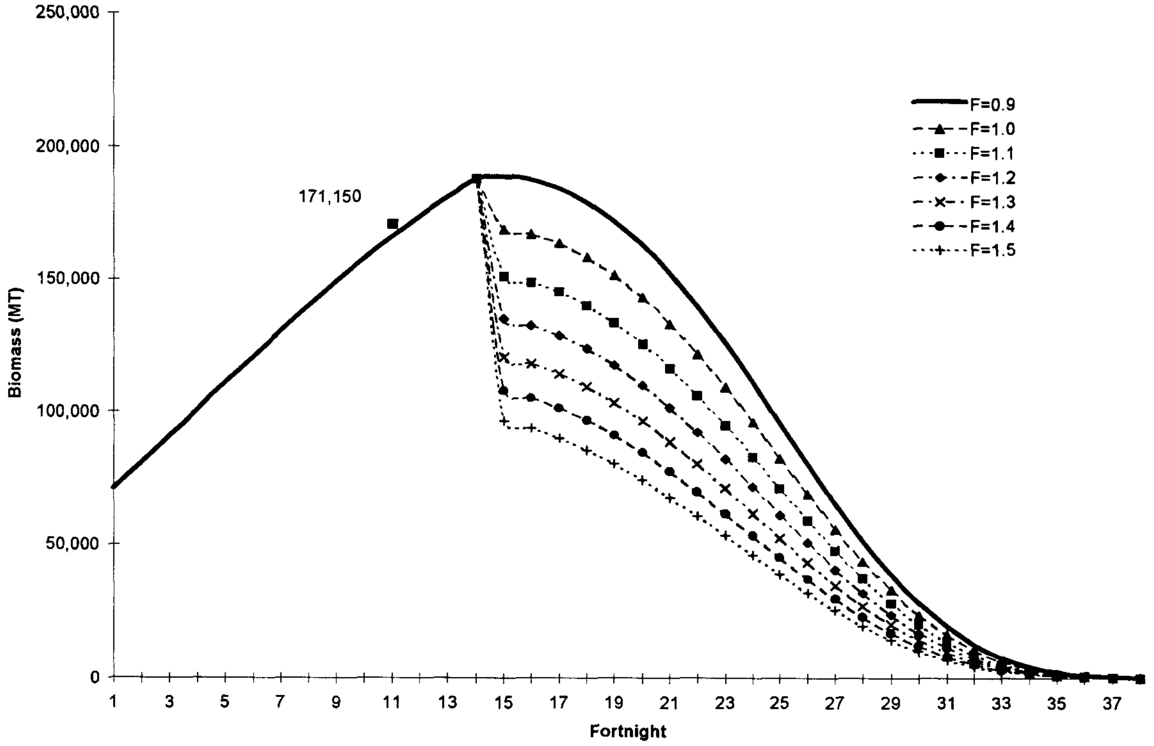

Figure 6. Biomass curves estimated with different levels of fishing mortality from 0.9 to 1.5. The value of 171,150 metric tons corresponded to the biomass estimation aboard the R/V *Lugo*. Fortnight 1 is from 19 May to 1 June 1996. Fortnight 38 is from 19 October to 1 November 1997.

TABLE 1
Management Scenarios at Different Levels of Fishing Mortality and Proportional Escapement

F	K	f_{Est}	f_{Sta}	Remaining biomass (t) at fortnight 27
0.9	0.407	2,096	4,192	65,560
1.0	0.368	2,329	4,658	56,000
1.1	0.333	2,562	5,124	47,830
1.2	0.301	2,795	5,590	40,850
1.3	0.273	3,028	6,056	34,890
1.4	0.247	3,261	6,522	29,800
1.5	0.223	3,494	6,988	25,450

near Guaymas during 1996. We therefore conclude that spring spawning generates individuals that eventually recruit to the fishery in September. But our observations off Guaymas do not support a second recruitment in autumn, although it is possible that this occurs in a different area. Another possibility is that in 1996 this recruitment was not successful.

Disregarding the possibility of a second recruitment to the fishery, the single-cohort model with a constant M (fig. 5a) assumed that squid live longer than two years, something that was not observed in the field. However, the single-cohort model with a variable M (fig. 5b) produced a maximum yield from fortnight 12 to fortnight 18; after that, the value of K was defined. Compared to the study of Rosenberg et al. (1990), in our study the proportional escapement was not estimated directly from the initial recruitment, but from the time when the maximum computed biomass was observed. The model allowed us to construct a family of curves that simulated the decay of the cohort from the maximum value of biomass estimate with variations of F (fig. 6) that also correspond to an increment in the fishing effort due to the end of the shrimp fishing season. The K values decreased from a value of 40% as F increased. This was then observed in the remaining adult biomass.

Our observations indicated that variations of K between 27% and 40% would allow an escapement of adult biomass between 34,890 and 65,560 t in May, when biomass could increase after a new recruitment. The choice of values of K was arbitrary because a stock-recruitment relation for giant squid is yet unknown (Beddington et al. 1990; Rosenberg et al. 1990). However, escapement and optimal effort levels were computed relative to maximum biomass, when fishing is directed to adults that possibly have already reproduced, and not at the moment of recruitment.

In the giant squid fishery, there are two risks in management decisions. The first includes fishing without a license, changes in catchability, selectivity, and accessibility to the fishing fleets. The second risk includes factors related to the biology of squid: changes in M due to migration (Ehrhardt et al. 1983; Klett 1996) and reproduction (Hernández-Herrera et al. 1996). Any change in these factors affects the estimation of K and consequently the size of the estimated recruitment for the next fishing season (Basson and Beddington 1993).

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EARLY STAGES OF THE BLOODY FROGFISH, *ANTENNARIUS SANGUINEUS* GILL 1863, AND THE BANDTAIL FROGFISH, *ANTENNATUS STRIGATUS* (GILL 1863) (PISCES: ANTENNARIIDAE)

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ABSTRACT

Antennarius sanguineus and *Antennatus strigatus* are benthic residents of coastal waters from the lower Gulf of California to northern Chile and Ecuador, respectively. Planktonic larvae of both species, collected primarily from the lower Gulf of California, are deep-bodied and compressed with large head, moderately long preanal length, and inflated skin. *Antennarius sanguineus* undergoes notochord flexion at 2.6–2.9 mm through 2.9–3.2 mm and settles from the plankton at about 8.0–8.5 mm; *Antennatus strigatus* completes flexion before 2.3 mm and settles at an unknown size <11 mm. Shortly before settlement small dermal spinules enclosed in small fleshy papillae begin to form in *Antennarius sanguineus*; larger, bare spinules are already present in the smallest available specimen (2.3 mm) of *Antennatus strigatus*. Caudal and dorsal fin rays are first to begin developing during the preflexion stage in *Antennarius sanguineus*, followed by anal, pectoral, and pelvic fin rays during the flexion stage. Neural and haemal arches and vertebral centra begin to ossify during the preflexion stage; addition of elements apparently is anterior to posterior. Ossification of the skull is already well under way in the smallest cleared and stained specimen of *A. sanguineus* (2.9 mm, preflexion stage).

Larval *A. sanguineus* are pigmented primarily on the mid- and hindbrain, on the opercle during the latter part of development, internally on the trunk, dorsally and laterally on the gut, and internally on the tail. Larval *Antennatus strigatus* are pigmented primarily on the lower jaw, laterally and ventrally on the cranium, on the opercular area, dorsally and laterally on the gut, and internally around the vertebral column of the trunk and much of the tail.

Larval *Antennarius avalonis*, *A. sanguineus*, and *Antennatus strigatus* can be distinguished by modal fin-ray counts and by pigment patterns. Diagnostic pigment includes (1) the internal dorsal melanophore series extending posteriorly from the nape, and in late larvae the external melanophores on the head and gut in *Antennarius avalonis*; (2) the mid-tail bar of melanophores in *A. sanguineus*; and (3) the jaw pigment and internal melanophores above and below the vertebral column in *Antennatus strigatus*. *Antennarius avalonis* has a specialized postflexion larval stage (the scutatus) that the others lack.

INTRODUCTION

Three frogfish species—*Antennarius avalonis*, *A. sanguineus*, and *Antennatus strigatus*—occur in the California Current vicinity (Pietsch and Grobecker 1987; Schneider and Lavenberg 1995). All three are benthic residents of coastal waters; *Antennarius sanguineus* and *Antennatus strigatus* are shallow-living (< ca. 40 m depth, most commonly < ca. 15 m), while *Antennarius avalonis* ranges deeper (to ca. 300 m, usually <100 m). Larvae of all three species have been collected primarily from the Gulf of California and Pacific coast of mainland Mexico and Central America; a few larval *A. avalonis* and two *A. sanguineus* were taken in CalCOFI collections off the Pacific coast of southern Baja California Sur.

Larval *A. avalonis* were described by Watson (1996), but early development stages of *A. sanguineus* and *Antennatus strigatus* have not been described. The purposes of this paper are to document the early development of *Antennarius sanguineus* and *Antennatus strigatus* from planktonic larval to early benthic juvenile stage, and to provide characters for distinguishing the larvae of all three species in plankton collections. Owing to the small number of specimens available, the description of *A. strigatus* is largely limited to illustrations and comparisons with the *Antennarius* species.

METHODS

Descriptions are based on 13 planktonic larvae and 35 benthic juveniles of *Antennarius sanguineus*, and 4 planktonic larvae and 6 benthic juveniles of *Antennatus strigatus* (Appendix). Eleven of the larval *Antennarius sanguineus* and three of the larval *Antennatus strigatus* were obtained from plankton collections taken with standard CalCOFI techniques (Kramer et al. 1972; Moser et al. 1974, 1994). The remaining two larval *Antennarius sanguineus* were obtained from plankton collections made during Scripps Institution of Oceanography (SIO) expedition Scot (SIO 1965), and one larval *Antennatus strigatus* was collected during Inter-American Tropical Tuna Commission (IATTC) survey 90048. All benthic juveniles were obtained from the SIO Marine Vertebrates Collection. Comparisons with *Antennarius avalonis* are

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based on Watson (1996) and on five additional postflexion specimens taken during CalCOFI and IATTC surveys (Appendix).

All specimens were used for the description of pigmentation (melanistic pigment only). Twenty-three of the *A. sanguineus* (all larvae and ten juveniles) were included in measurement series. Dimensions measured, including body length, preanal length, head length, snout length, eye diameter, head width, body depth, and lengths of the pectoral and pelvic fins, are defined by Moser (1996). Larval lengths always refer to body length. Head width includes the inflated skin; body depth was measured inclusive (BD) and exclusive (BDi) of the inflated skin. Measurements were made to the nearest 0.04 mm with a Wild M-5 binocular microscope equipped with an ocular micrometer. Illustrations were made with the same microscope equipped with a camera lucida.

Five larval *Antennarius sanguineus* (2.9–8.1 mm) and one larval *A. avalonis* (5.3 mm) were cleared and stained with alcian blue and alizarin red S following the method of Taylor and Van Dyke (1985) to help determine the sequence of fin formation and to make a cursory examination of skeletal development. Staining was not entirely successful, perhaps owing to the nearly 40 years (or more) of formalin storage of the larvae used (although the oldest specimen stained well—after 46 years of storage). Even when poorly stained, the bony structures could often be recognized by their hyaline appearance, and the cartilaginous structures by their reticulated appearance.

TABLE 1
Summary of Measurements of *Antennarius sanguineus*, Expressed as Percentage of Body Length (BL) or Head Length (HL); for Each Measurement the Range Is Given Above and the Mean Is Given Below

	Planktonic stage			Benthic juvenile stage
	Preflexion	Flexion	Postflexion	
Number of specimens	1	4	8	10
Size range (mm)	2.9	2.6–3.2	2.9–8.4	8.1–23.9
Proportions[a]				
Sn-A/BL	52	59–68	69–74	63–74
		64	71	71
BDi/BL	33	39–43	42–63	48–64
		41	54	57
BD/BL	37	43–54	50–72	49–66
		50	62	58
HL/BL	33	36–45	37–44	35–48
		41	41	41
P1L/BL	10	9–12	13–26	20–26
		11	21	23
P2L/BL	0	0–1	0–15	17–21
		1	9	18
HW/HL	94	56–72	79–134	82–112
		66	104	94
SnL/HL	19	12–21	12–20	14–20
		17	16	17
ED/HL	38	37–38	34–44	25–31
		37	38	28

[a] Measurements include preanal length (Sn-A), body depth inclusive (BD) and exclusive (BDi) of the inflated skin, head length (HL), pectoral fin length (P1L), pelvic fin length (P2L), head width (HW), snout length (SnL) and eye diameter (ED).

DESCRIPTION

Antennarius sanguineus Gill 1863 Bloody Frogfish

Morphology. *Antennarius sanguineus* is deep-bodied and somewhat compressed, with a large head, moderately long preanal length, and inflated skin throughout larval development (table 1; figs. 1 and 2). Relative head and snout lengths change little during development, whereas relative eye diameter remains stable through the larval period, then decreases after settlement (table 1). The other proportions gradually increase through the postflexion stage, then stabilize (preanal length), continue to increase (fin lengths), or decrease (body depth, head width). The decrease in relative body depth coincides with deflation of the skin at settlement; body depth exclusive of the inflated skin continues to increase relative to body length (table 1).

The only preflexion-stage specimen available (2.9 mm) has a thin, transparent, mildly inflated skin; short, tubular anterior nostrils; a moderately small, somewhat oblique mouth opening; a coiled gut; and developing rays in the dorsal and caudal fins (fig. 1a). No gas bladder is visible. Notochord flexion begins between ca. 2.6 and 2.9 mm and is completed between between ca. 2.9 and 3.6 mm (fig. 1b, c). Settlement and transformation to the benthic juvenile stage occurs between about 8.0 and 8.5 mm. During notochord flexion the skin tends to become more inflated, but it remains thin and translucent until midway through the postflexion stage, when it begins to thicken and become increasingly opaque (fig. 2a). Shortly before settlement a row of widely spaced, small, fleshy papillae forms anteriorly on the head and dorsolaterally along each side of the trunk. A small dermal spinule consisting of a horseshoe-shaped to ringlike base bearing two small spines is enclosed in each papilla. At settlement the skin nearly completely deflates and the papillae rapidly increase in number (fig. 2b), especially ventrally on the head at first, then spreading dorsad and caudad to densely cover the body and proximal parts of the fins by ca. 9.5 mm. The spinules are partially exposed by this size. The tubular anterior nostrils elongate and become prominent during the postflexion stage. The mouth opening remains oblique through early postflexion stage, then gradually rotates upward to become nearly vertical by settlement.

Fin and skeletal development. The sequence of initial fin-ray formation could not be determined except that the dorsal soft rays and caudal rays are first to begin forming: the anterior 8 dorsal rays and 7 (3+4) of the 9 caudal rays are forming in the preflexion specimen. Addition

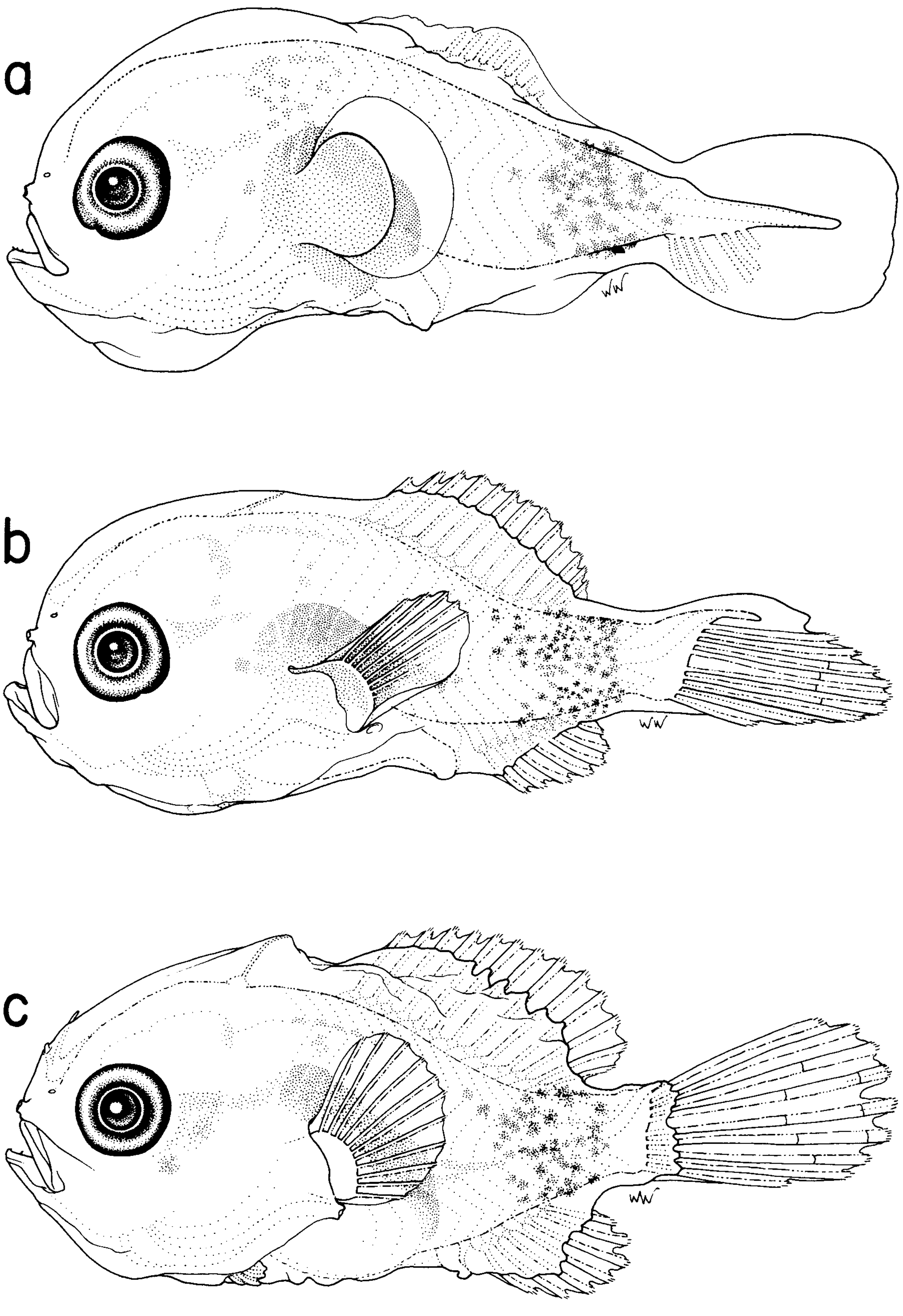

Figure 1. *Antennarius sanguineus*: *a*, preflexion, 2.9 mm (CalCOFI 5209, station 153G.32); *b*, flexion, 3.2 mm (CalCOFI 5612, station 173G.10); *c*, postflexion, 3.6 mm (CalCOFI 5706, station 153.20).

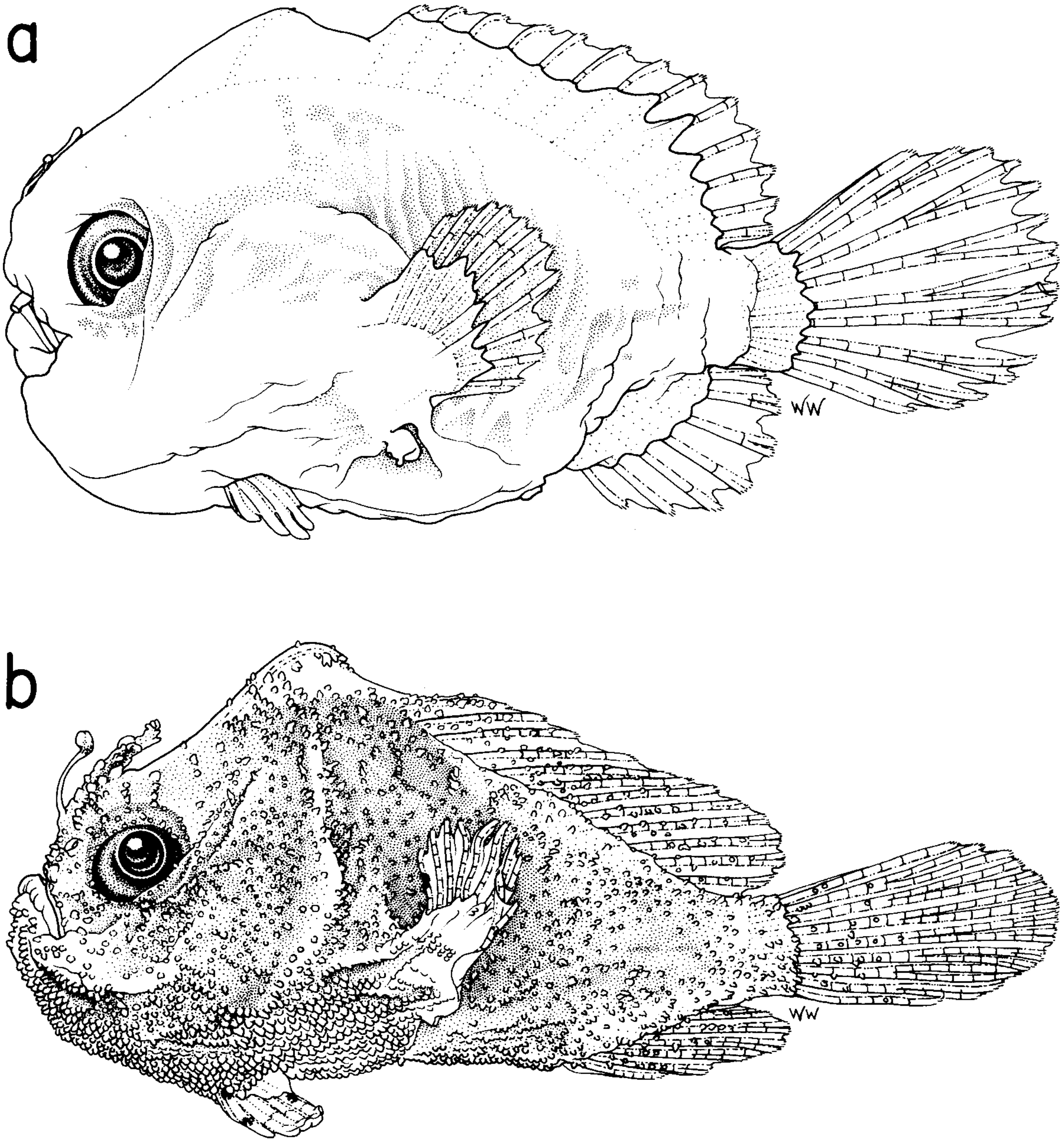

Figure 2. *Antennarius sanguineus*: *a*, late postflexion, 6.7 mm (CalCOFI 5612, station 163G.30); *b*, benthic juvenile, 8.6 mm (SIO 62-55).

of dorsal soft rays may be anterior to posterior. Full complements of soft dorsal (12–14), anal (6–8), and caudal (9) fin rays are present by midflexion. Most pectoral and pelvic fin rays also are present by midflexion, and full complements (10–12 and I,5, respectively) are completed during the postflexion stage. Addition of pectoral fin rays is ventrad. The spine is the last element to form in the pelvic fin. All three cephalic spines form during the flexion stage: the third spine forms first, followed by simultaneous development of the first two spines. The illicium (the first cephalic spine) remains unornamented until settlement, when it acquires a simple escal swelling (fig. 3). The first escal filaments form at ca. 13 mm, and by 20 mm the esca is approaching the typical adult form (fig. 3).

The state of dorsal- and anal-fin pterygiophore development in the preflexion stage could not be determined with certainty owing to the poor staining of the specimen: the cartilaginous pterygiophore of the third cephalic spine is forming; at least the anterior nine or ten dorsal soft-ray pterygiophores are present in cartilage; and no anal-fin pterygiophores are visible (fig. 4a).

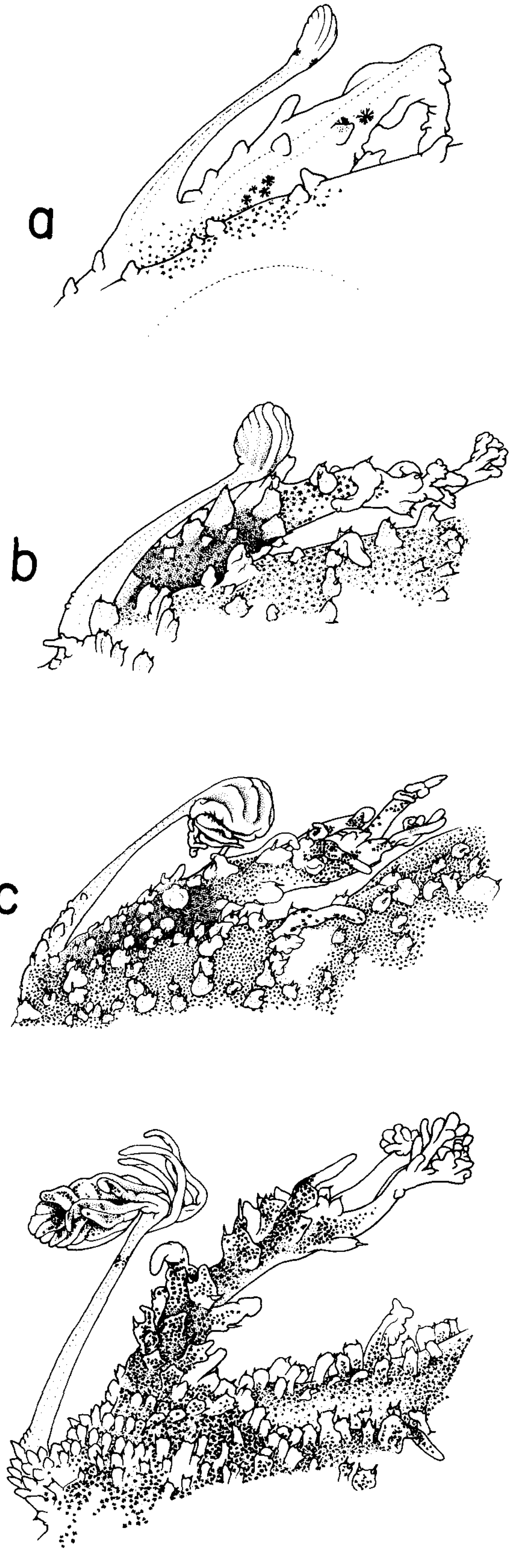

Figure 3. Development of the esca in benthic juveniles of *Antennarius sanguineus*: *a*, 8.1 mm (SIO 62-55); *b*, 9.5 mm (SIO 62-55); *c*, 12.6 mm (SIO 62-55); *d*, 19.8 mm (SIO 61-242).

All second dorsal- and anal-fin pterygiophores are present in cartilage in the 2.8 mm flexion-stage specimen. Although none of the pterygiophores clearly consists of separate proximal and distal radials at this stage, it appears that distal radials are beginning to detach from the ends of dorsal pterygiophores 4–11 in this specimen (fig. 4b). By early postflexion, dorsal rays 3–11 and anal rays 3–6 are clearly supported by separate cartilaginous distal radials (fig. 5a). The distal radial supporting dorsal ray 2 separates from the first pterygiophore a little later; the first proximal radial supports the first dorsal soft ray. The last pterygiophore, supporting the last dorsal ray, does not divide into proximal and distal radials. Likewise, the first and last anal-fin pterygiophores, supporting the first and last anal rays, do not separate into proximal and distal elements. The second anal ray articulates with the proximal radial of the second anal pterygiophore (fig. 5b). In the soft dorsal fin, pterygiophore ossification begins by early postflexion; each proximal radial may ossify initially at the middle of its anterior margin (as in the last two dorsal pterygiophores of the 3.6 mm specimen, fig. 5a). From this initial site, bone forms around the middle of each radial, then spreads along its length so that by late postflexion only the proximal tip and distal margin remain cartilaginous (fig. 5b). The central proximal radials may be the first to begin ossifying in the soft dorsal fin. Proximal radials of the anal-fin pterygiophores ossify at the same time, and each apparently ossifies in the same way, as the dorsal proximal radials. It is unclear whether the anal-fin pterygiophores ossify simultaneously or sequentially. Distal radials do not ossify during larval development in either fin.

The rodlike, cartilaginous pterygiophore of the third cephalic spine forms in the preflexion stage, and that of the first two spines forms during notochord flexion. All three spines are supported on somewhat compressed dorsal extensions of their pterygiophores. Each pterygiophore begins to ossify around the middle of its elongate shaft during the postflexion stage; the third spine probably begins to ossify first. Simultaneously with (or soon after) initial ossification of the shaft of the illicial pterygiophore, thin crescent-shaped ossifications form around the anterolateral margins of the spine supports below the illicium and second cephalic spine. These subsequently spread up the supports and by late postflexion form a thin flange pierced by a foramen below each spine. A pair of hooklike extensions from the base of each spine fits into its adjacent foramen. A similar flange and foramen supports the third cephalic spine, but it is unclear whether this ossification spreads forward from the pterygiophore shaft or originates independently.

In the preflexion specimen the first 16 neural arches are ossifying: the first six pairs of neurapophyses are ossified along their full length (or nearly so), the next

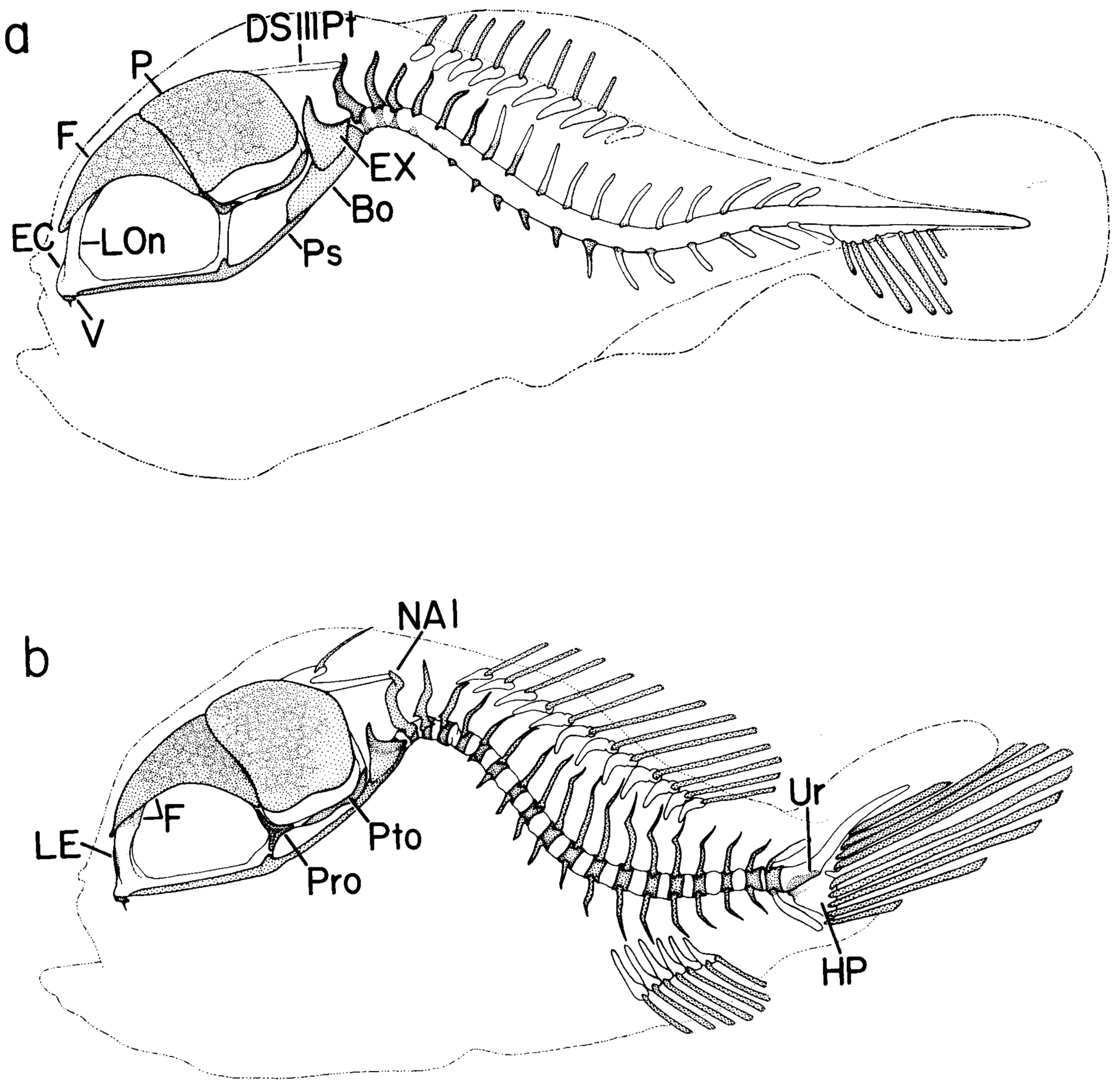

Figure 4. Development of the axial skeleton and skull of *Antennarius sanguineus*: *a*, preflexion, 2.9 mm (CalCOFI 5209, station 153G.32); *b*, flexion, 2.8 mm (CalCOFI 5708, station 151G.100). White = cartilage; stippled = ossifying. Abbreviations are Bo, basioccipital; DSIIIPt, pterygiophore of the third cephalic spine; EC, ethmoid cartilage; Ex, exoccipital; F, frontal; HP, hypural plate; LE, lateral ethmoid; LOn, lamina orbitonasalis; NA1, first neural arch; P, parietal; Pro, prootic; Ps, parasphenoid; Pto, pterotic; Ur, urostyle; V, vomer.

two pairs are ossifying on about the lower third, and the remainder are ossifying only at their bases (fig. 4a). The direction of ossification of each arch is thus proximal to distal. The first three neural arches are open distally (arches 2 and 3 are nearly closed) in the preflexion specimen. By late flexion all 3 are closed and all 18 neural arches are ossified, as are the neural spines on arches 2 and 7–17 (fig. 4b). Arches 1 and 3–5 lack neural spines, and the last neural spine is cartilaginous during the flexion stage. As the larvae grow the neural spines on arches 6–9 become spatulate and relatively shorter, barely interdigitating with the dorsal pterygiophores early in the postflexion stage (fig. 5a) and not interdigitating at all by late postflexion (fig. 5b). Neural arches 3–5 also

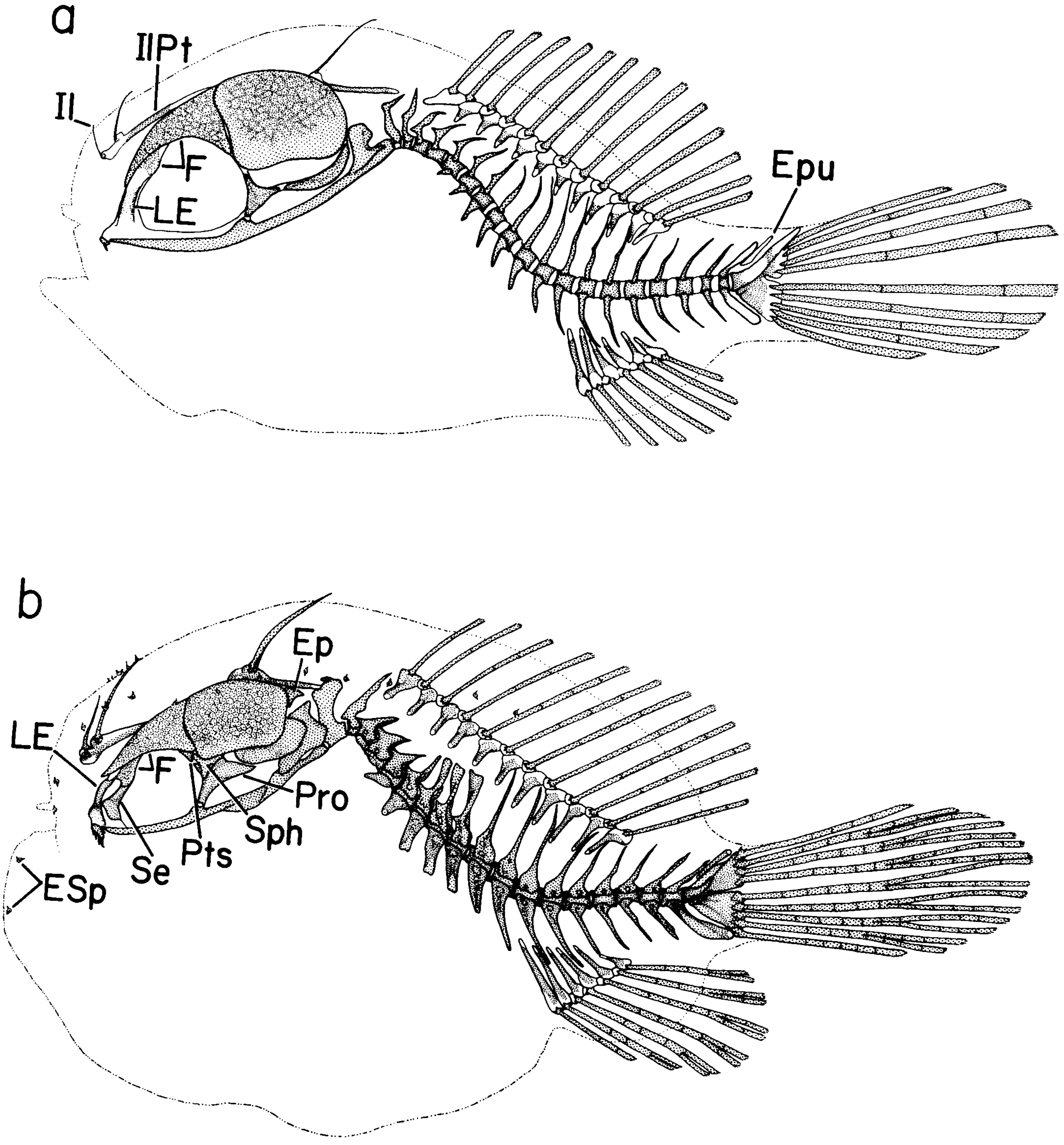

Figure 5. Development of the axial skeleton and skull of postflexion stage *Antennarius sanguineus*: *a*, 3.6 mm (CalCOFI 5706, station 153.20); *b*, 8.1 mm (TO 58-1, station 105). White = cartilage; stippled = ossifying. Abbreviations are Ep, epiotic; Epu, epural; ESp, epidermal spinule; Il, illicium; IlPt, illicial pterygiophore; Pts, pterosphenoid; Se, supraethmoid; sph, sphenotic. For other abbreviations see figure 4.

no longer interdigitate with the dorsal pterygiophores after early postflexion.

At least 12 pairs of haemapophyses and haemal arches are present in the preflexion specimen: the anterior five pairs of small haemapophyses appear to be mostly ossified, the sixth (at the site of the future first caudal vertebra) is ossifying on about its proximal third, the seventh through tenth at their bases only, and the last two are cartilaginous (fig. 4a). The direction of ossification of each haemal arch is thus distad from the base. By late flexion all haemal arches and spines are ossifying, except the posteriormost spine, which ossifies during the postflexion stage. This last haemal spine becomes broad and compressed by late postflexion and may partially support the lowermost caudal fin ray (fig. 5b).

It could not be determined with certainty whether any vertebral centra were ossifying in the preflexion specimen, but it appears that the first three abdominal centra might be present as thin rings around the notochord below the first three neural arches, and the fourth forming as a ventral ossification on the notochord opposite the fourth neural arch (fig. 4a). It is unclear whether a small ventral ossification corresponding to the fifth abdominal vertebra is the vertebra beginning to form, or the haemapophyses beginning to ossify, or both. In the 2.8 mm flexion-stage specimen, all the vertebrae are forming: the first 18 are present as ossifying rings around the notochord, and the urostyle is represented by a ventral ossification on the notochord adjacent to the anterior (= lower) section of the hypural plate (fig. 4b). The 3.6 mm postflexion specimen apparently has a second urostylar ossification site adjacent to the upper section of the hypural plate (fig. 5a), suggesting that the urostyle ossifies from both ends toward the middle (perhaps corresponding to ossification from an ancestral preural centrum 1 + ural centrum 1 proximally and ural centrum 2 distally?). There are 10–11 (nearly always 10) abdominal vertebrae and 9 caudal vertebrae, including the urostyle.

The hypural plate is a slender, triangular cartilage posteriorly below the notochord in the preflexion specimen, and has become a deeply notched, ossifying plate supporting all 9 caudal rays in the 2.8 mm flexion-stage specimen (fig. 4). Hypural ossification begins during notochord flexion, along the proximal margin of the anterior (= lower) section, and spreads both distad and along the hypural base onto the upper section by postflexion. The single epural cartilage forms early in the postflexion stage and ossifies except at its distal tip by late postflexion. A single pair of uroneurals ossifies along the dorsal margin of the urostyle and upper hypural plate in the postflexion stage (fig. 5b).

The pectoral girdle of the preflexion specimen consists of slender, ossified cleithra, postcleithra (only the ventral postcleithra form), and supracleithra (fig. 6a). A small coracoscapular cartilage is present. Owing to the poor staining of the specimen, it could not be determined whether the pectoral-fin base consists of a single cartilage pierced by a large foramen, or two cartilages, the lower larger than the upper. By late flexion the posttemporals have begun ossifying at the upper ends of the supracleithra; there definitely are separate upper and lower pectoral cartilages; and a foramen is present in the middle of the lower, larger cartilage. Ossification of the pectoral radials begins early in the postflexion stage around the middle of the upper cartilage and the middles of the two lower radials that are being defined by the elongating foramen in the lower cartilage (fig. 6b). By late postflexion the upper radial is completely ossified except at its tips, and the lower radials, which remain fused at both ends, are cartilaginous only at their proximal tip and in a band along their distal margin. Small, cartilaginous distal pectoral radials form along the margin of the lower proximal radials late in the postflexion stage; these support the pectoral fin rays (fig. 6c).

The elongate cartilaginous coracoid process regresses after the early part of the postflexion stage, and the scapula and coracoid ossify on the upper and lower half, respectively, of the coracoscapular cartilage late in the postflexion stage (fig. 6c). Cartilaginous basipterygia form during notochord flexion and ossify, beginning around the middle and spreading toward both ends, during the postflexion stage (fig. 6b). By late postflexion each basipterygium is ossified except at its proximal tip and distal margin (fig. 6c).

The neurocranium is already becoming well ossified in the 2.9 mm preflexion specimen (fig. 4a). Ossifying bones include the frontals, parietals, supraoccipital, prootics, pterotics, exoccipitals, basisphenoid, parasphenoid, and vomer. The frontals initially closely approach one another mesially, except for a small anterior mesial notch and groove, which subsequently widens and deepens. During the postflexion stage the supraethmoid ossifies on the ethmoid cartilage below this widening gap (fig. 5b). The groove receives the posterior section of the illicial pterygiophore. The parietals initially nearly touch one another mesially; the small, oval supraoccipital is located mesially at their posterior margins but barely separates them. However, as the supraoccipital grows anteriorly between the parietals during the postflexion stage, they become increasingly widely separated. Epiotics ossify behind the parietals during the postflexion stage, and together with the exoccipitals form most of the posterior part of the brain case. A shallow groove between the parietals (the supraoccipital is its floor) and extending between the epiotics receives the anterior part of the third cephalic spine pterygiophore. The prootic initially is a thin, V-shaped ossification on the cartilage forming

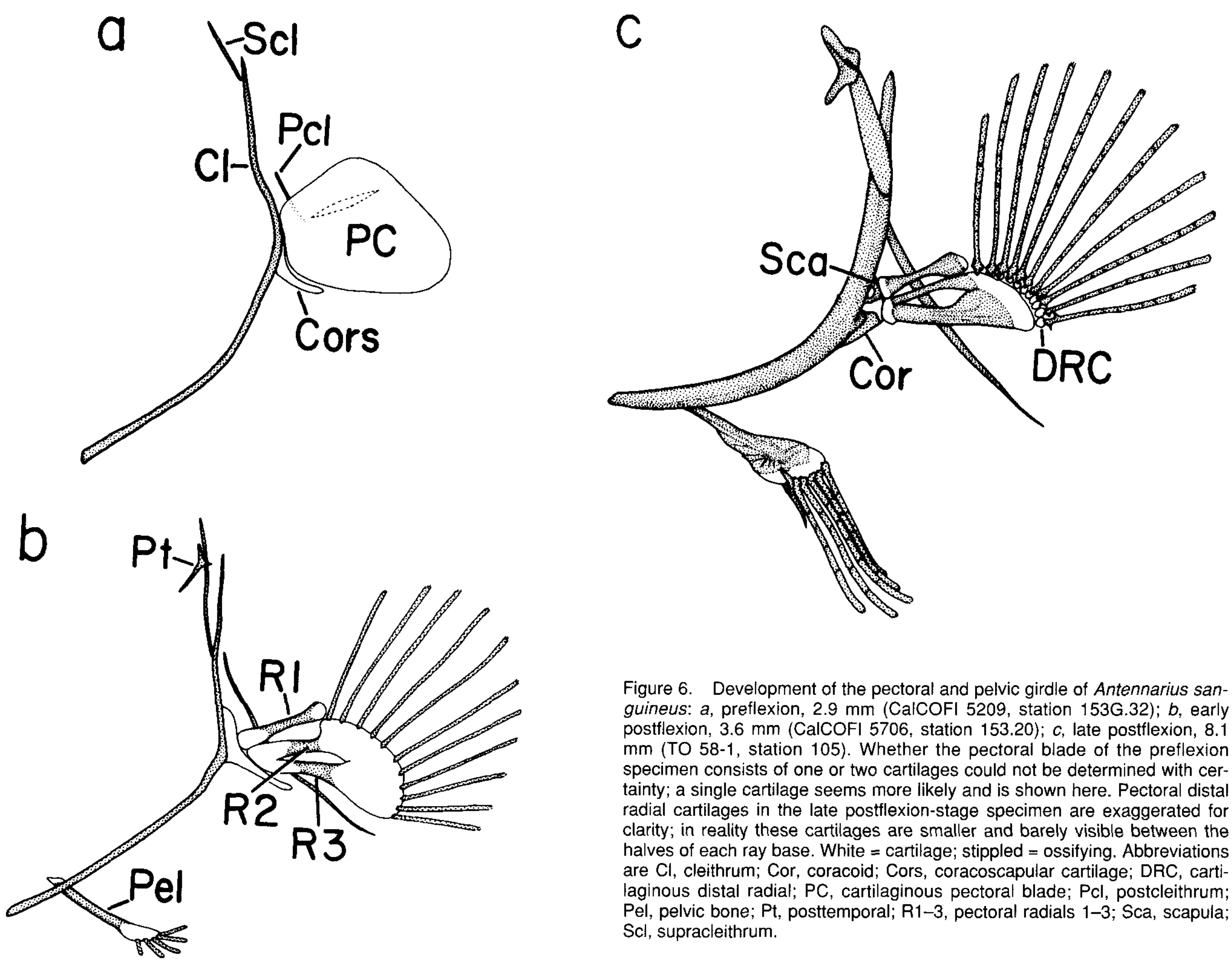

Figure 6. Development of the pectoral and pelvic girdle of *Antennarius sanguineus*: *a*, preflexion, 2.9 mm (CalCOFI 5209, station 153G.32); *b*, early postflexion, 3.6 mm (CalCOFI 5706, station 153.20); *c*, late postflexion, 8.1 mm (TO 58-1, station 105). Whether the pectoral blade of the preflexion specimen consists of one or two cartilages could not be determined with certainty; a single cartilage seems more likely and is shown here. Pectoral distal radial cartilages in the late postflexion-stage specimen are exaggerated for clarity; in reality these cartilages are smaller and barely visible between the halves of each ray base. White = cartilage; stippled = ossifying. Abbreviations are Cl, cleithrum; Cor, coracoid; Cors, coracoscapular cartilage; DRC, cartilaginous distal radial; PC, cartilaginous pectoral blade; Pcl, postcleithrum; Pel, pelvic bone; Pt, posttemporal; R1–3, pectoral radials 1–3; Sca, scapula; Scl, supracleithrum.

the anteroventral corner of the auditory capsule, while the pterotic is a thin, elongate oval ossification on much of the lower part of the capsule (fig. 4a). The prootic becomes Y-shaped during the flexion stage, with its lower arm extending mesially and ventrad toward the ascending arm of the parasphenoid (fig. 4b). During the postflexion stage the upper sections of the prootics expand to form much of the anteroventral part of the brain case. The foramen of the trigeminofascialis nerve complex is visible in each prootic, adjacent to the lower end of the sphenoid. The pterotics expand during postflexion to become large, roughly oval bones forming much of the ventrolateral part of the brain case. Each has an articular surface on its lower center that articulates with the pterotic process of the adjacent hyomandibula. During the postflexion stage the sphenotics ossify below the anteroventral corners of the parietals and lateral to the anterodorsal ends of the adjacent prootics (fig. 5b). Each roughly T-shaped sphenotic bone articulates with the sphenotic process of the adjacent hyomandibula. A small, triangular pterosphenotic bone ossifies between the posteroventral edge of each frontal and the adjacent prootic during the postflexion stage (fig. 5b).

The vomer is a small, crescent-shaped bone bearing a small tooth at each end, located ventrally on the ethmoid cartilage at the anterior end of the parasphenoid in the preflexion specimen (fig. 4a). The vomer lengthens and broadens with larval growth, and teeth are added sequentially toward the middle during postflexion. Thin, oval, lateral ethmoids begin to ossify on the slender lamina orbitonasalis cartilages during the flexion stage (fig. 4b). Ossification spreads along and around each cartilage during the postflexion stage, resulting in somewhat compressed, cylindrical lateral ethmoids that flare ventrally by late postflexion (fig. 5b).

The premaxillae, maxillae, dentaries (with four teeth), and articulars are ossifying in the 2.9 mm preflexion specimen, but the degree of development of these bones could not be determined with any certainty owing to the poor staining of the specimen. The premaxillae of the flexion-stage and early postflexion-stage specimens are slender bones, each of which tapers to a point distally, bears two or three small teeth proximally, and has a small, rounded, articular process posteriorly and a long, slender, ascending process dorsally at its proximal end (fig. 7a, b). The ascending processes gradually lengthen, extending into the groove anteriorly between the frontals. At the same time the articular processes greatly enlarge, and—during the latter part of the postflexion stage—a long, slender postmaxillary process extends posteromedially from the proximal end of each premaxilla (fig. 7c). The number of premaxillary teeth increases to 13 or 14 on each (all small, especially distally). Maxillae in the younger specimens are flat and moderately wide distally but taper and become quite slender along the proximal third, except that the proximal end is flared into a broad V shape, with the anterolaterally projecting wing overlapping the base of the premaxillary ascending process, and the anteromedially projecting wing nearly reaching the premaxillary articular process (fig. 7). The maxillae change little during subsequent larval development, except to become broader.

The dentaries are slender, Y-shaped bones (fig. 7) that abut at their proximal ends and bear a single row of a few teeth in the flexion-stage and early postflexion-stage specimens. During the postflexion stage the dentaries broaden, and the upper arm of the "Y" becomes longer than the lower. By late postflexion the number of teeth has increased to about 20 in the outer row on each dentary, and an inner row of smaller teeth is forming. The articular is a broad, T-shaped cartilage with its base extending forward between the arms of the dentary "Y," and ossifying on its base and lower arm in the flexion and early postflexion specimens (fig. 7). A notch on the posterior margin of the lower arm ossifies early and articulates with the quadrate (fig. 7a). The articular subsequently changes little in shape except to become broader and to acquire a posteroventral flange by late postflexion (fig. 7c). The angular is ossifying on the posteroventral margin of the articular cartilage in the flexion specimen, and by late postflexion it has become a roughly triangular bone that fits into a notch in the lower posterior articular margin (fig. 7).

The degree of development of the elements of the suspensorium is unclear in the preflexion specimen. Thin ossifications distally on the anterior and ventral arms of the palato-pterygoquadrate cartilages represent the palatines and quadrates, respectively, and the hyomandibulae are ossifying at least on their sphenotic, pterotic, and opercular processes, but whether any other bones of the suspensorium are ossifying cannot be determined. By the flexion stage the quadrate has ossified on the entire lower arm of each palato-pterygoquadrate cartilage; the palatine occupies about the anterior half of the anterior arm of each cartilage; the slender mesopterygoid is ossifying between the palatine and

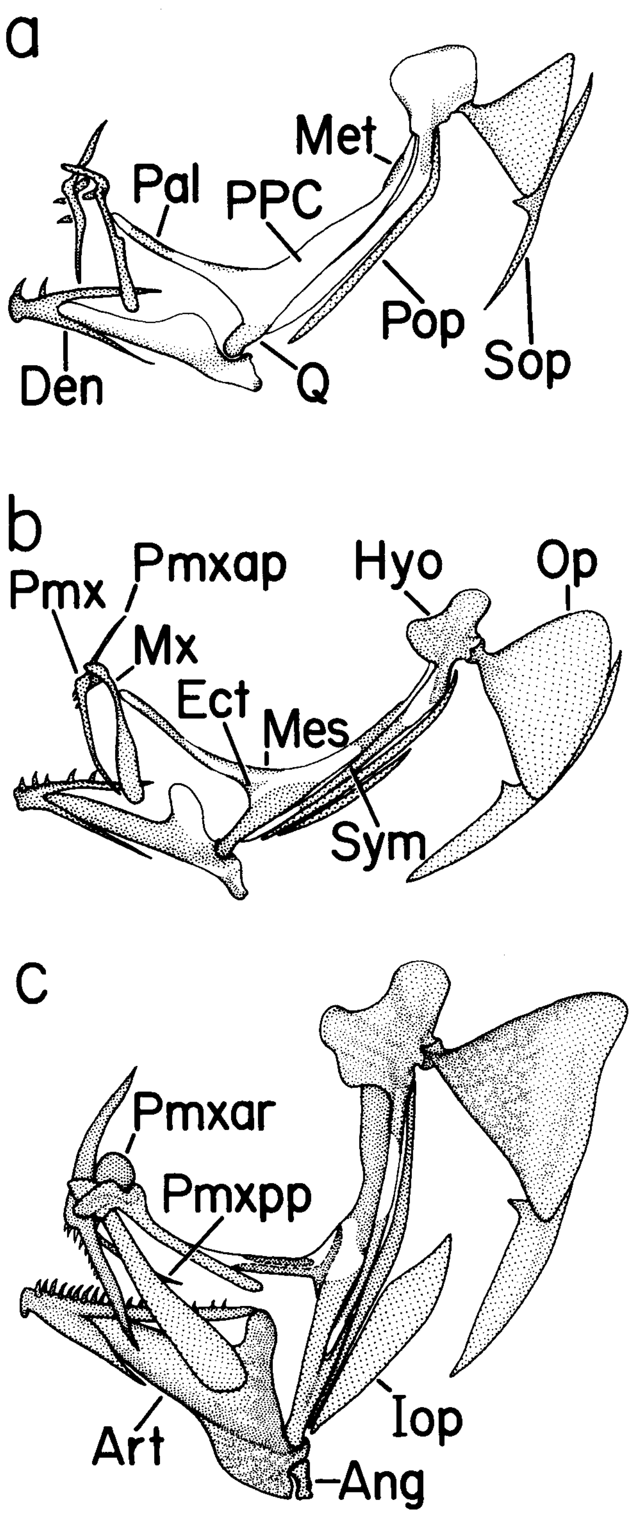

Figure 7. Development of the jaws, suspensorium, and opercular bones of *Antennarius sanguineus*: *a*, flexion, 2.8 mm (CalCOFI 5708, station 151G.100); *b*, early postflexion, 3.6 mm (CalCOFI 5706, station 153.20); *c*, late postflexion, 8.1 mm (TO 58-1, station 105). White = cartilage; stippled = ossifying. Abbreviations are Ang, angular; Art, articular; Den, dentary; Ect, ectopterygoid; Hyo, hyomandibula; Iop, interopercle; Mes, mesethmoid; Met, metethmoid; Mx, maxilla; Op, opercle; Pal, palatine; Pmx, premaxilla; Pmxap, ascending process of the premaxilla; Pmxar, articular process of the premaxilla; Pmxpp, postmaxillary process of the premaxilla; Pop, preopercle; PPC, palato-pterygoquadrate cartilage; Q, quadrate; Sop, subopercle; Sym, symplectic.

quadrate on the dorsal margin of the cartilage; and the metapterygoid is a small, slender distal ossification on the anterior margin of the upper arm of the cartilage (fig. 7a). During the postflexion stage the palatine develops a flattened anterolateral process that overlaps the upper end of the maxilla, and a flattened anteromedial process that lies adjacent to the lateral ethmoid. Palatine teeth form on the mesial surface along the middle of each palatine beginning late in larval development. The T-shaped ectopterygoid ossifies ventrally on the anterior arm of the palato-pterygoquadrate cartilage between the palatine and quadrate and below the mesopterygoid during the postflexion stage (fig. 7b, c). The symplectic ossifies on the lower part on the hyomandibulosymplectic cartilage during the postflexion stage.

Among the opercular series bones, only the opercles are clearly ossifying, at least in the vicinity of their articulations with the hyomandibulae, in the preflexion specimen, but whether any other opercular series bones are forming could not be determined. A broad, triangular opercle, together with the slender subopercle and the elongate, very slender preopercle are present on each side in the flexion-stage specimen, and the slender interopercle is added early in the postflexion stage (fig. 7). The proximal end of the opercle is more or less flattened where it meets the hyomandibula in the flexion stage, but by early postflexion this articular surface of the opercle has become a shallow cup which attaches in a ball-and-socket joint to the cartilaginous end of the opercular condyle of the hyomandibula (fig. 7). The subopercle elongates somewhat during the postflexion stage as its lower part simultaneously broadens. The interopercle likewise elongates a bit and broadens during postflexion. The preopercle is also a very long bone, but it remains quite slender.

Each hyoid arch of the preflexion specimen is largely cartilaginous, with thin ceratohyal, epihyal, and interhyal ossifications anteriorly and posteriorly around the cartilage (fig. 8a). It appears that there are small, thin, oval dorsal and ventral hypohyal ossifications at the anterior end of the hypohyal cartilage, as well. All six branchiostegal rays are ossified: the anterior two articulate with the ceratohyal, and the posterior four are supported by the broad hyoid cartilage. The ceratohyal ossification spreads posteriorly onto this broad section of the cartilage by early postflexion, so that all six branchiostegal rays are supported by the ceratohyal. The middle two branchiostegal rays curve downward distally to support the gill opening below the pectoral fin base. A small, triradiate urohyal bone forms early in the postflexion stage. One arm of the urohyal is directed dorsally and the other two are directed posteriorly, so that the urohyal appears to be more or less V-shaped in lateral and ventral views. A small, posteriorly directed, median urohyal flange begins to form during the latter part of the postflexion stage. The interhyal remains a simple cylindrical bone until late postflexion, when a short posterodorsal process forms on its upper lateral surface (fig. 8c). The posterior margin of the preopercle rides on the anterior face of this interhyal process.

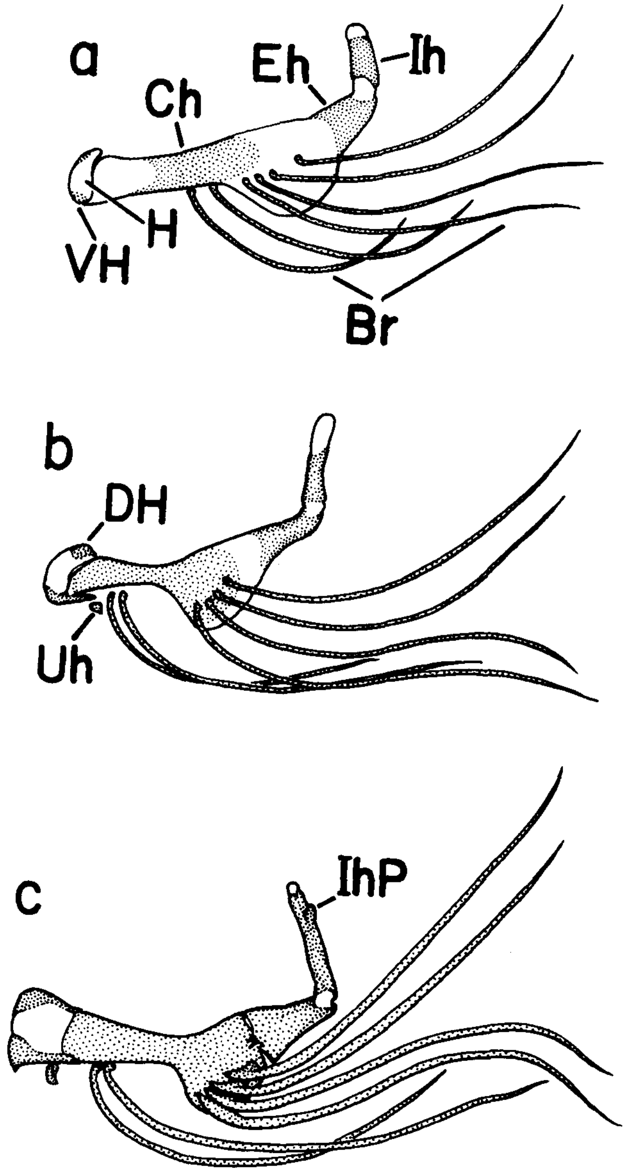

Figure 8. Development of the hyoid arch of *Antennarius sanguineus*: *a*, preflexion, 2.9 mm (CalCOFI 5209, station 153G.32); *b*, early postflexion, 3.6 mm (CalCOFI 5706, station 153.20); *c*, late postflexion, 8.1 mm (TO 58-1, station 105). White = cartilage; stippled = ossifying. Abbreviations are Br, branchiostegal rays; Ch, ceratohyal; DH, dorsal hypohyal; Eh, epihyal; H, hypohyal cartilage; Ih, interhyal; IhP, dorsolateral process of the interhyal; Uh, urohyal; VH, ventral hypohyal.

The basibranchial(s), gill arches, and second pharyngobranchial tooth plates (each with three teeth) are visible in the preflexion specimen, but apart from the tooth plates and ceratobranchials 1 and 2 ossifying on the middles of their respective arches, it could not be determined whether any other bones of the branchial arches were forming. In the flexion-stage specimen all three pharyngobranchials, four epibranchials, five ceratobranchials, and at least hypobranchials 1 and 2 and basibranchials 1 and 2 are ossifying. All are simple, flattened to cylindrical, rodlike bones. The second pharyngobranchials still bear three teeth each, and each of the fifth ceratobranchials has acquired a single dorsal tooth anteriorly. The number of teeth increases to four and two, respectively, by early postflexion; by late postflexion there are many teeth on the second pharyngobranchials and fifth ceratobranchials. Beginning early in the postflexion stage the second and third hypobranchials broaden proximally, and by late postflexion both have become Y-shaped. Late in the postflexion stage, epibranchial 1 begins to broaden distally; presumably it is beginning to acquire the triradiate adult shape described by Pietsch (1981).

Pigmentation. The inflated skin is unpigmented throughout the larval phase of development. "External" pigmentation described below refers to subdermal melanophores on the surface of the musculature; "internal" pigmentation refers to melanophores that are more deeply internal. The principal elements of the larval pigment pattern are melanophores dorsally on the head and nape; dorsally and laterally on the gut; internally, anteroventrally in the tail; and both internally and externally in a bar posteriorly on the tail. The preflexion specimen has melanophores on the posterior margin of the midbrain and dorsally on the hindbrain, a dense shield of melanophores over the upper 60%–70% of the gut, a large internal melanophore anteriorly on each side of the gut mesial to the cleithra at the level of the pectoral-fin origin, and a bar posteriorly on the tail (at ca. myomeres 14–16) consisting primarily of external, myoseptal melanophores (fig. 1a).

Pigmentation on the head subsequently increases: more melanophores are added on the mid- and hindbrain, and midway through the postflexion stage a few melanophores begin to form on the opercular area, increasing in number and spreading anteroventrally to below mid-eye by late postflexion, but still remaining somewhat sparse. Internal melanophores form in the nape area by the beginning of notochord flexion; these are primarily myoseptal, commonly continuous with the hindbrain pigment, and extend posteriorly to about the third myomere by the postflexion stage. During postflexion this pigment may extend ventrad to the level of the gut, or it may remain predominantly dorsal. External myoseptal melanophores form in the same area during the postflexion stage, spreading posteriorly sometimes as far as midtail by the end of the larval phase. This external pigmentation is light to moderate.

Gut pigmentation changes little during larval development: the shield covers a variable proportion of the gut (approximately the upper 25%–75%), and the terminal section of the hindgut always is unpigmented. Ventral gut pigment is also lacking, both in larvae and in benthic juveniles smaller than ca. 20 mm.

Internal melanophores form along the haemal arches beginning at about the last preanal myomere at the beginning of flexion, and slowly proliferate caudad below the vertebral column to about midtail by halfway through the postflexion stage. The tail bar gradually broadens, extending from myomeres 12–14 through 16–17 by the postflexion stage. External and internal pigmentation in the bar increase: external melanophores are predominantly myoseptal and on the horizontal septum, whereas internal melanophores are primarily above and below the vertebral column. The bar may extend onto the bases of the adjacent dorsal and anal fin rays by late flexion, and the external pigment usually extends forward ventrolaterally during the postflexion stage. In two of the larger postflexion-stage specimens, myoseptal melanophores are sparsely scattered along nearly the full length of the tail.

All of the larval pigmentation becomes increasingly obscure as the skin thickens and becomes opaque during the latter part of the postflexion stage, and it apparently decreases at settlement: the only such pigment consistently visible through the skin of recently settled individuals is on the horizontal septum of the tail and on the gut. Dissection reveals some additional small melanophores scattered dorsolaterally on the head, trunk, and tail.

Juvenile pigmentation first begins to appear as minute melanophores on the epidermis, initially mainly on the head and trunk, soon after settlement. These begin to resolve into the typical spotted adult pattern by ca. 20 mm. The spots are first discernable dorsally on the trunk and tail, and cover the body by ca. 30 mm.

The esca is lightly pigmented ventrally when it forms at settlement (fig. 3). A more or less even to irregularly striped pattern develops on the main body of the esca after the escal filaments begin to form. The first stripe forms on the illicium just below the esca at ca. 20 mm, and stripes are added toward the base of the illicium. The second cephalic spine begins to become pigmented at settlement.

Shortly after settlement (ca. 8.5 mm) melanophores form proximally on the first and last pelvic and pectoral fin rays (fig. 2b). By ca. 10 mm, bands are added distally on the pectoral, pelvic, and caudal fins, and the proximal pectoral and pelvic spots expand to small blotches. Another band is added on the pectoral and pelvic fins, and another one or two bands are added on the caudal fin by 13 mm. A large blotch forms proximally on the posterior part of the dorsal fin (ca. D10) by 13 mm, and additional smaller blotches form along the bases of some of the anterior dorsal fin rays and at the base of the last anal fin ray by ca. 16 mm. By ca. 20 mm several small blotches are scattered on the dorsal fin, and a distal stripe is present on the anal fin.

Antennatus strigatus (Gill 1863) Bandtail Frogfish

Morphology. Larvae generally resemble those of *Antennarius sanguineus* but are slightly more elongate, with a slightly larger head and smaller eye (table 2; figs. 9 and 10). The most striking morphological differences between the two species are the small larval size and the early development of dermal spinules in *Antennatus*. The smallest specimen of *A. strigatus*, 2.3 mm, already has completed notochord flexion, full complements of rays in all fins except the pelvic (4 rays forming), a fully formed illicium with slight escal thickening, and widely scattered, predominantly bifurcate, dermal spinules on the body (fig. 9a). Each spinule arises from a low, rounded, fleshy base. As the larvae grow, the number of spinules increases; the area covered by the spinules expands onto the skin covering the proximal parts of the dorsal and anal fins; and the individual spinules become smaller relative to body size (fig. 9b). By ca. 5 mm the lower part of each spinule is enclosed in a small, fleshy papilla (fig. 10a). In juveniles each papilla encloses most of its spinule; only the spinule tips are always exposed.

TABLE 2
Summary of Measurements of *Antennarius strigatus*, Expressed as Percentage of Body Length (BL) or Head Length (HL); for Each Measurement the Range Is Given Above and the Mean Is Given Below

	Planktonic postflexion stage	Benthic juvenile stage
Number of specimens	4	6
Size range (mm)	2.3–5.1	10.6–14.2
Proportions[a]		
Sn-A/BL	64–75	71–84
	72	76
BDi/BL	52–57	
	54	
BD/BL	65–68	53–72
	66	61
HL/BL	44–48	37–44
	46	41
P1L/BL	14–26	24–27
	20	25
P2L/BL	2–18	16–19
	10	17
HW/HL	87–104	100–120
	96	112
SnL/HL	14–20	15–20
	16	18
ED/HL	29–37	21–26
	33	24

[a] Measurements include preanal length (Sn-A), body depth inclusive (BD) and exclusive (BDi) of the inflated skin, head length (HL), pectoral fin length (P1L), pelvic fin length (P2L), head width (HW), snout length (SnL) and eye diameter (ED).

Pigmentation. Larval pigmentation is unlike that of *Antennarius sanguineus*. Principal elements of the *Antennatus strigatus* pattern are melanophores on the jaws, laterally and ventrally on the cranium, on the opercular area and below the eye, dorsally and dorsolaterally on the gut, and internally around the vertebral column and neural and haemal arches of the trunk and much of the tail (figs. 9 and 10).

In the smallest specimen the dentaries are nearly completely pigmented; a few melanophores are located on the posterior margin and ventrally on the posterior half of the midbrain; the upper ca. 60% of the gut is lightly pigmented; a large melanophore appears anteriorly on each side of the gut mesial to the cleithrum just below the level of the pectoral-fin origin; and the internal trunk and tail pigment extends from the next to last preanal myomere to the third postanal myomere (fig. 9a). Unlike the other three larvae, the 2.3 mm specimen has an external melanophore on each side over the proximal end of the urostyle.

The dentary pigmentation increases, spreading onto the lip and extending ventrad onto the anterior gular area by 3.4 mm. By this size the upper jaw also is pigmented, and the midbrain pigment has spread forward under the forebrain and dorsally onto the lower sides of the fore- and midbrain. The roof of the mouth and ethmoid cartilage are heavily pigmented as well, and a few melanophores have formed on the opercular area, extending to below mid-eye (fig. 9b). All of this pigment increases so that by 5.1 mm the head is nearly completely pigmented except on the dorsum (fig. 10a). Pigmentation on the gut becomes denser, but otherwise changes little. The internal trunk and tail pigment first spreads forward to nearly the full length of the trunk by 3.4 mm, then spreads dorsally to near the dorsal margin by 5.1 mm. The fins are unpigmented except that a few small melanophores form in the pectoral axil by 5.1 mm.

None of the larval pigmentation is visible externally, and dissection reveals that none remains in small benthic juveniles (11–12 mm). The opaque skin is lightly mottled and densely covered with unpigmented papillae; a pattern of irregular, large, light spots on a darker background begins to emerge by ca. 12 mm. The characteristic striped pattern is present on the fins by 11.6 mm (fig. 10b).

IDENTIFICATION OF LARVAE

Larvae of the three frogfish species that occur in the vicinity of the CalCOFI study area are generally similar in body form and proportions (tables 1 and 2; Watson 1996) and have similar numbers of myomeres (18–20) and fin rays (table 3). However, modal numbers of fin rays distinguish the species (table 3; Pietsch and Grobecker

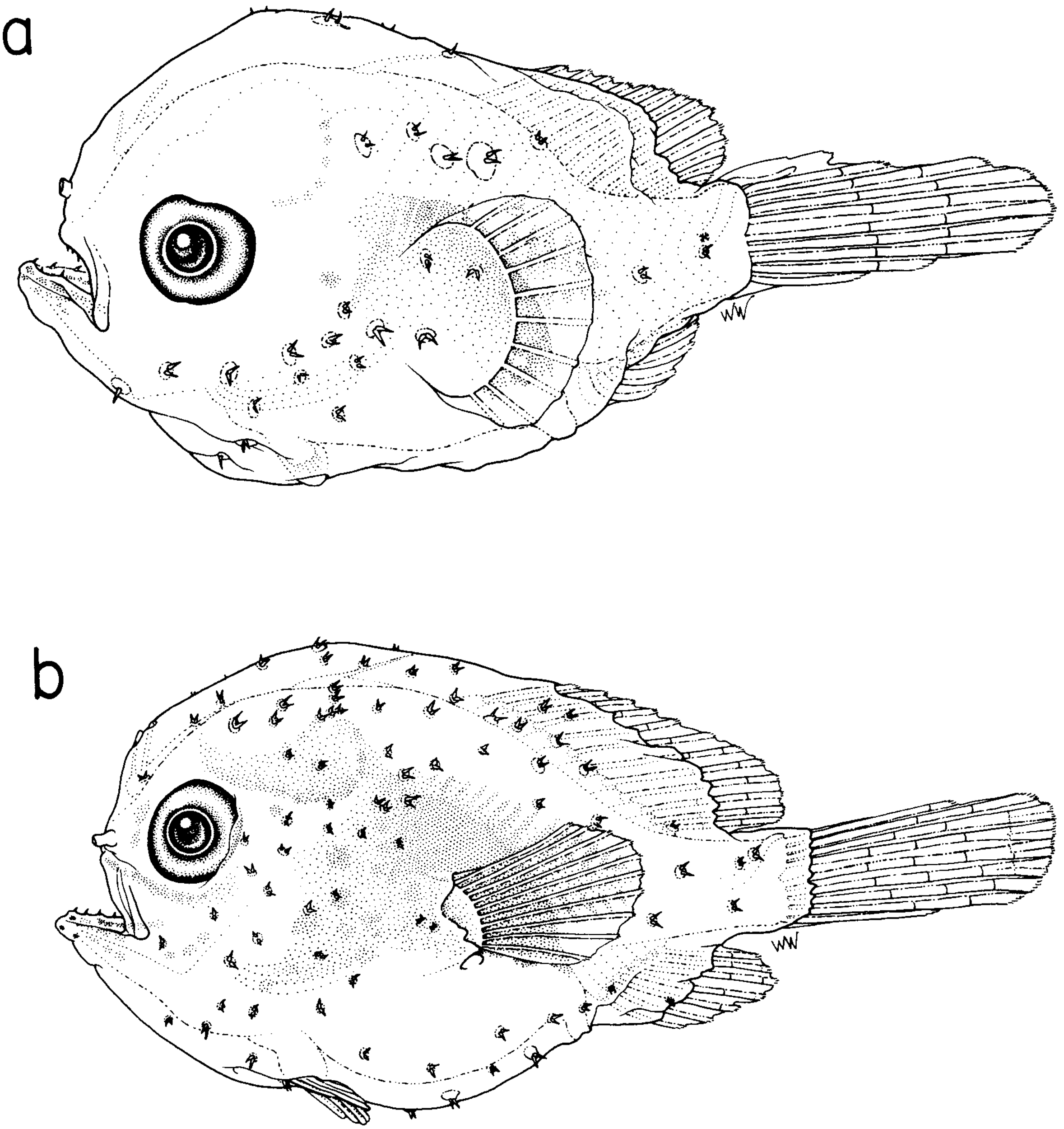

Figure 9. *Antennatus strigatus*: *a*, 2.3 mm (CalCOFI 5708, station 151G.100); *b*, 3.4 mm (CalCOFI 5708, station 145G.30).

1987), and all three differ in larval pigmentation (figs. 1, 2, 9, 10, 11; Watson 1996). Diagnostic elements of the pigmentation patterns include (1) the internal dorsal melanophore series extending from the nape (early preflexion) to mid-tail (by postflexion stage; Watson 1996) and the epidermal melanophores scattered over the head and gut (postflexion stage >ca. 5 mm: fig. 11a) in *Antennarius avalonis*; (2) the mid-tail bar of internal and external melanophores in *A. sanguineus* (all larval stages: figs. 1 and 2); and (3) the jaw pigment and internal melanophores above and below the vertebral column in *Antennatus strigatus* (figs. 9 and 10).

TABLE 3
Selected Fin-Ray Counts for the Antennariid Species of California and Baja California

Species	Dorsal rays	Anal rays	Pectoral rays
Antennarius avalonis	12–14	7–10	11–14
	13	8	13
Antennarius sanguineus	12–14	6–8	10–12
	13	7	11
Antennatus strigatus	11–13	6–8	9–11
	12	7	10

Segmented rays only. Ranges are given above, and modes are given below. Data are primarily from Pietsch and Grobecker 1987, supplemented with counts made during this study.

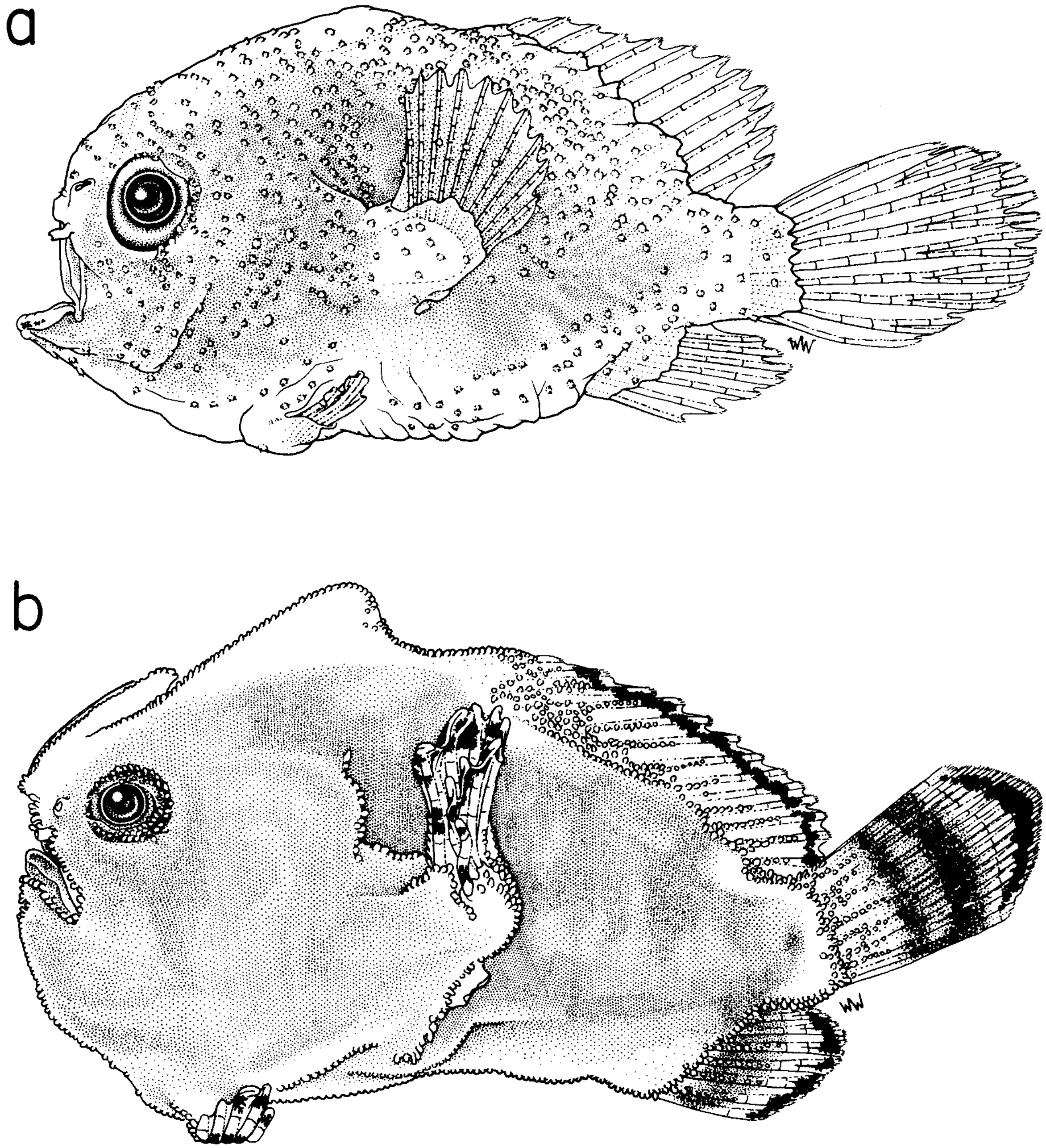

Figure 10. *Antennatus strigatus*: *a*, postflexion, 5.1 mm (IATTC 90048, station T-3); *b*, benthic juvenile, 11.6 mm (SIO 67-39). The benthic juvenile is densely covered with small, spinous papillae, but only those around the margins and on the fins are shown.

A. strigatus completes notochord flexion and fin-ray formation at a remarkably small size (<2.3 mm for all but the pelvic fin, which is nearly complete by 2.3 mm); the two *Antennarius* species have begun neither fin-ray development (at least *A. avalonis*, probably both species) nor notochord flexion at this size. *Antennatus strigatus* also begins developing the dermal spinules at a much smaller size than the two *Antennarius* species. The first spinules form by, or before, completion of notochord flexion in *Antennatus strigatus* but not until late in the postflexion stage in *Antennarius* (ca. 7 mm in *A. avalonis* and 8 mm in *A. sanguineus*). In both *Antennarius* species the spinules initially are completely enclosed (or nearly so) in small, fleshy papillae and become partially exposed after settlement, whereas in *Antennatus* the spinules initially are nearly fully exposed and gradually become enclosed in papillae, finally becoming mostly enclosed after settlement. *A. strigatus* may settle from the

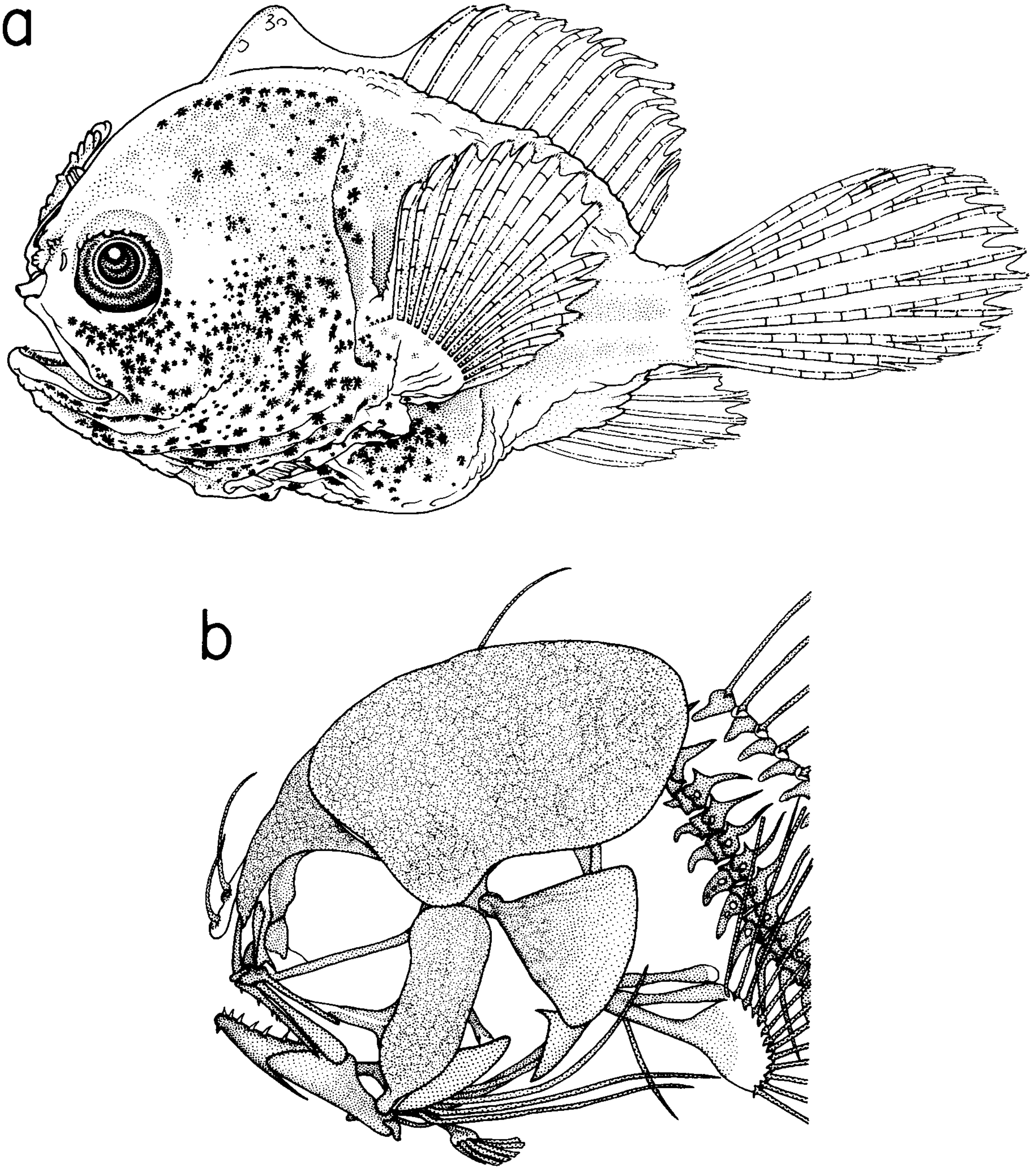

Figure 11. *Antennarius avalonis*: *a*, scutatus stage, 7.3 mm (IATTC 91005, station T-8); *b*, skull, pectoral-pelvic girdle, and anterior part of axial skeleton of scutatus stage, 5.3 mm (CalCOFI 5011, station 157.20). White = cartilage; stippled = ossifying.

plankton at a smaller size than the *Antennarius* species: although the *Antennatus* settlement size is unknown it certainly is <11 mm and probably near 5 mm. The *Antennarius* species settle at about 8 mm or a little larger.

A. avalonis has a specialized postflexion larval stage, the scutatus, that distinguishes it from the other two species. The scutatus is characterized by large, posterodorsal projections of the skull and a marked broadening of some bones of the suspensorium (fig. 11b; Pietsch 1984; Pietsch and Grobecker 1987). Watson (1996) erroneously stated that *A. sanguineus* also has a scutatus stage, based on the external appearance of the largest of the few larvae then available. Additional specimens found later did not share this scutatus-like appearance, and clearing and staining clearly demonstrated that *A. sanguineus* does not have a scutatus stage. In scutatus stage *A. avalonis* > ca. 5 mm the posterior margins of the cranial extensions are outlined with melanophores (fig. 11a).

The presence of the specialized scutatus larval stage in *A. avalonis* and *A. radiosus* (Schultz 1957; Hubbs 1958; Pietsch 1984)—both members of the *A. ocellatus* species group (Pietsch and Grobecker 1987)—and the absence of a scutatus in *A. sanguineus*—a member of the *A. nummifer* species group (Pietsch and Grobecker 1987)—supports separation of these groups and suggests that the scutatus stage may be a unique specialization of the *ocellatus* group. The similar development of the dermal spinules in the two *Antennarius* species, and their different timing and mode of development in *Antennatus strigatus*, suggests that the ontogeny of dermal spinules, when better known, may provide insight into the questions of *Antennarius* monophyly and the interrelationships of the antennariid genera, which currently are largely unknown (Pietsch and Grobecker 1987).

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APPENDIX. SPECIMENS USED FOR THE PREPARATION OF DESCRIPTIONS

Antennarius avalonis Jordan and Starks 1907

5 larvae: CalCOFI 5011, station 157.20 (1: 5.3 mm); IATTC 90037, station T-6 (1: 6.5 mm); IATTC 90043, station T-2 (1: 7.8 mm); IATTC 91001, station T-5 (1: 4.9 mm); IATTC 91005, station T-8 (1: 7.3 mm).

Antennarius sanguineus Gill 1863

13 larvae: CalCOFI 5209, station 152G.41 (1: 2.9 mm), station 153G.32 (1: 2.9 mm), station 157.20 (1: 5.1 mm); CalCOFI 5612, station 163G.30 (1: 6.7 mm), station 173G.10 (1: 3.2 mm); CalCOFI 5706, station 153.20 (1: 3.6 mm); CalCOFI 5708, station 106G.00 (1: 3.2 mm), station 145G.40 (1: 2.6 mm), station 151G.100 (1: 2.8 mm), station 157G.70 (2: 2.8, 8.4 mm); SIO Expedition Scot (TO 58-1), station 105 (1: 8.1 mm), station 137 (1: 8.1 mm).

35 juveniles: SIO 61-242 (6: 16.3–38.0 mm); SIO 62-55 (29: 8.1–29.0 mm).

Antennatus strigatus (Gill 1863)

4 larvae: CalCOFI 5708, station 145G.30 (1: 3.4 mm), station 145G.85 (1: 4.1 mm), station 151G.100 (1: 2.3 mm); IATTC 90048, station T-3 (1: 5.1 mm).

6 juveniles: SIO 59-225 (5: 10.9–14.2 mm); SIO 67-39 (1: 11.6 mm).

SEASONALITY AND ABUNDANCE OF BLUE WHALES OFF SOUTHERN CALIFORNIA

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ABSTRACT

We counted blue whales (*Balaenoptera musculus*) on transect surveys on 33 CalCOFI cruises between May 1987 and October 1995. Abundance of blue whales over this nine-year period was strongly seasonal: the numbers peaked in August–October, and no blue whales were recorded on winter cruises. We detected no increasing trend of abundance over the nine years. This finding contrasts with recent reports of pronounced increases in the size of blue whale aggregations feeding near the Channel Islands and elsewhere off southern California.

INTRODUCTION

Blue whales have a worldwide distribution that is usually divided into three different stocks: one each in the North Pacific and North Atlantic, and a third in the Southern Hemisphere (Leatherwood and Reeves 1983). North Pacific blue whales summer between the Gulf of Alaska and California, and winter in the temperate Pacific, south at least to 20°N. The Alaska and California whales may represent two separate stocks (J. Barlow, pers. comm.). North Atlantic blue whales summer from the Gulf of St. Lawrence to Iceland, and winter mainly in temperate latitudes, perhaps as far south as the tropics. Antarctic blue whales remain south of 40°S during the summer, and move north in winter to Brazil, Ecuador, and South Africa. There is perhaps a fourth population of "pygmy" blue whales, which is thought to be nonmigratory. It inhabits the Subantarctic Zone in the vicinity of Kerguelen, Crozet, and Heard Islands (Ichihara 1961; Ellis 1985). Accurate estimates of these populations have been notoriously difficult to make, but recent estimates of the eastern North Pacific population range as high as 6,000 (Rice 1974).

Blue whales feed on large zooplankton, especially euphausiids and small schooling fishes (Leatherwood and Reeves 1983). Off southern California they probably feed upon swarms of *Euphausia pacifica* or *Thysanoessa spinifera*, and anchovies or sardines.

Barlow (1994) compared whale surveys made off the west coast of the United States in 1979–80 and in 1991, and estimated 704 whales and 1,872 whales, respectively. Calambokidis et al. (1990), using mark-recapture estimates based on photographs, obtained estimates ranging from 1,989 to 2,315 blue whales for the period 1991–93. Barlow (1995) later increased his 1994 estimate for the 1991 cruise to 2,250 blue whales. Thus the blue whale population off the west coast of the United States appears to have increased from fewer than 1,000 in 1980 to over 2,000 in the early 1990s.

Estimates of blue whale populations off California have not included repeated systematic surveys with internally consistent methodology. The CalCOFI cruises provide an ideal opportunity for such a protocol. Veit and colleagues (Ainley et al. 1995; Veit et al. 1996, 1997) have been surveying seabird abundance on CalCOFI cruises since May 1987. All whales sighted during these seabird surveys have been recorded. Although counts of whales on CalCOFI cruises lack the precision required for estimating absolute abundance or population size, the methods were consistent over all 33 cruises, so we felt it would be worthwhile to analyze the counts of blue whales, and to use the counts as an index of relative abundance. As far as we are aware, this paper represents the first attempt to estimate seasonal and interannual variability in whale abundance on the basis of transects conducted from ships.

DATA COLLECTION

Whales were counted during a program designed to measure abundance and distribution of marine birds on CalCOFI cruises (Veit et al. 1996). Bird density is ordinarily low enough in the region sampled by CalCOFI to allow ample time for the person collecting data to scan for whales. Blue whales are especially easy to spot and identify because of their tall spouts, their distinctively tiny dorsal fins, and their habit of resting at the surface in groups. We acknowledge, however, the possibility that some other rorquals may have been misidentified as blue whales.

Because we did not record distance or bearing to each whale sighted, we were unable to convert our counts to estimates of density or population size (Barlow 1994). Nevertheless, our methods were consistent across all 33 cruises, and we feel that our counts faithfully reflect real changes in whale abundance over the nine-year period.

Our basic measurement of abundance was the number of blue whales recorded per nautical mile (nmi) of

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[Manuscript received March 16, 1998.]

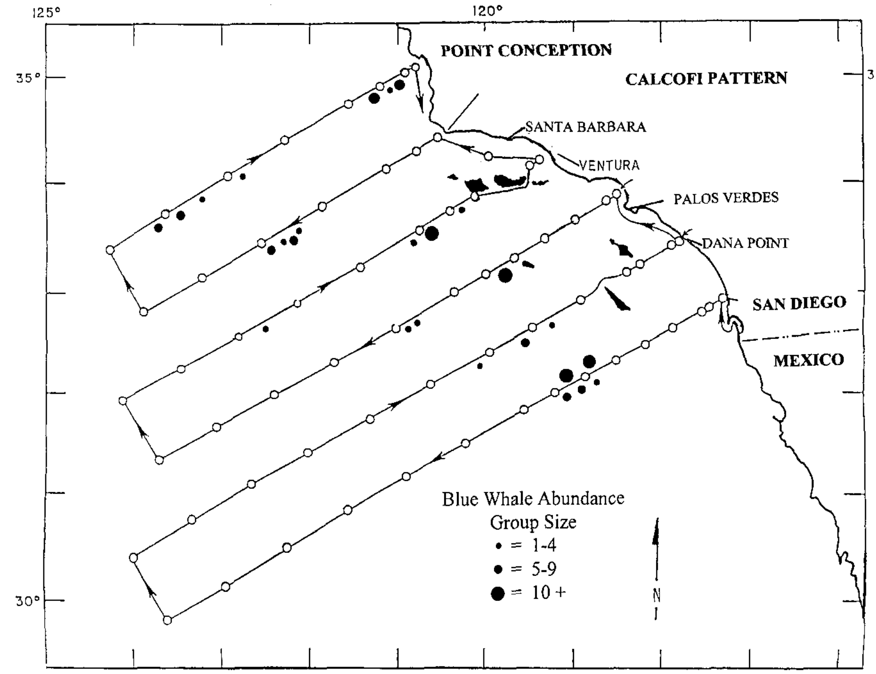


Figure 1. Spatial distribution of blue whales identified on CalCOFI cruises, 1987–95.

transect. An average of 864 nmi (1,600 km) of transect was surveyed during each cruise.

To take into consideration some misidentification of whales, we constructed two different time series. The first series consisted of whales identified as blue whales only, and the second series consisted of all large rorquals—blue, fin, sei, or unidentified whales.

RESULTS

The distribution of the 140 blue whales sighted on 33 CalCOFI cruises between May 1987 and October 1995 is shown in figure 1, and the time series of blue whale abundances and blue whale plus unidentified rorqual abundances are shown in figure 2. Blue whales were distinctly seasonal in their appearance in the region sampled by CalCOFI (fig. 3a). Blue whales were more abundant in the summer and fall over the nine-year period between 1987 and 1995 (one-way ANOVA, $F = 12.5$, $df = 3$, $P < 0.001$). Essentially the same held true for the abundance of large rorquals (fig. 3b).

We used linear regression to search for trends in blue whale abundance over the period 1987–96, and found no significant trend. We calculated the statistical power of this regression model as 0.88, using methods described by Zar (1996; pp. 343, 379; see also Gerodette 1987).

DISCUSSION

Blue whale abundance off the California coast was strongly seasonal between 1987 and 1996, and peaked in July–September. The three largest aggregations that

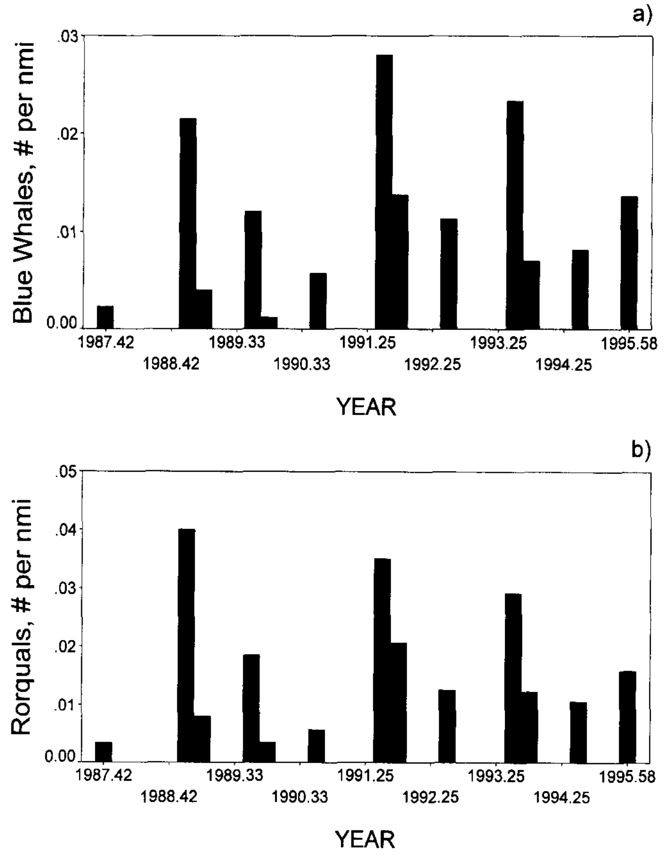
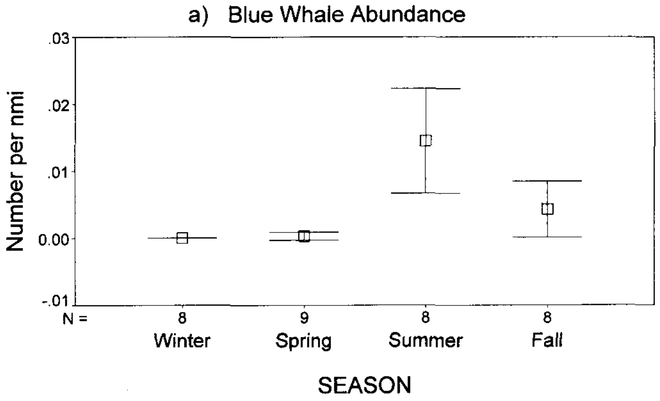
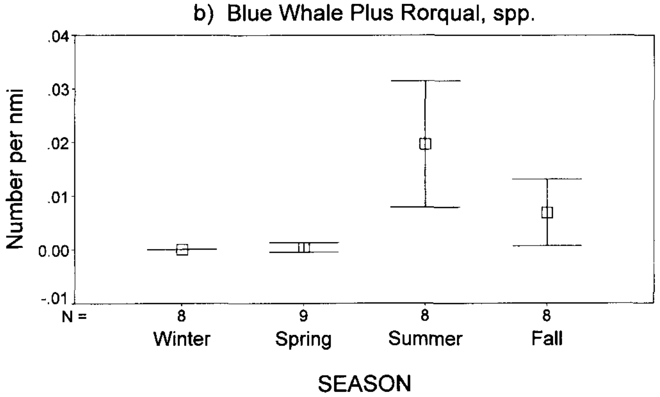


Figure 2. Whales (individuals per nmi) counted on 33 CalCOFI cruises, May 1987–July 1995: *a*, blue whales; *b*, blue whales plus unidentified rorquals. The x-axis is numbered in decimal years.



a) Blue Whale Abundance



b) Blue Whale Plus Rorqual, spp.

Figure 3. Seasonal distribution of whales sighted on CalCOFI cruises, 1987–95. Winter = December to February; spring = March to June; summer = July to September; fall = September to November. (One-way ANOVA $F = 12.5$, df = 3, $P < 0.001$). *a*, Blue whales; *b*, blue whales plus unidentified rorquals.

we saw were (1) off Avila Beach, 40 nmi north of Point Conception, (2) off San Miguel Island, and (3) in 1995, about 40 nmi southwest of the south end of San Clemente Island.

We did not detect any increasing trend in abundance of blue whales. This finding was surprising, and inconsistent with the findings of Barlow (1994) and Calambokidis et al. (1990) and with numerous recent sightings of especially large aggregations of blue whales feeding near the northern Channel Islands (P. E. Smith, pers. comm.). Our analysis is unique in that we have repeated very nearly the same survey pattern four times a year for nine years. For that reason alone, one would anticipate that we would have noticed an increase in abundance if such an increase had occurred. We freely admit that our techniques lack the precision of Barlow (1994, 1995) or Calambokidis et al. (1990). Nevertheless, our methods were consistent across all 33 cruises.

The CalCOFI pattern may not be ideally suited to surveying blue whales. For example, some of the largest aggregations that we have seen have been close to San Miguel Island, an area barely grazed by the regular transect line. Still, the disparity in results between our CalCOFI counts and the censuses reported by Barlow (1994) and Calambokidis et al. (1990) suggests that we need to determine the appropriate spatial scale for cetacean surveys.

The abundance of marine birds has declined dramatically from 1987 to 1995 (Veit et al. 1996, 1997). Because the most numerous marine birds of the Southern California Bight feed on the same zooplankton and small fish that are probable prey to blue whales, it seems paradoxical that especially large aggregations of blue whales should be more evident now.

There are at least two possible explanations for the disparity among recent estimates of blue whale numbers. First, it is possible that blue whales increased substantially up until about 1990, after which the growth slowed. Such a pattern would account for both Barlow's estimated increase and the apparent lack of increase in the CalCOFI data. Second, it is possible that food has become extremely aggregated in the vicinity of the Channel Islands, thus accounting for the especially large numbers of blue whales recorded there recently.

Detectability of whales varied with weather conditions, especially wind speed. Because the winter and spring CalCOFI cruises tended to be windier than the summer and fall cruises, part of the seasonal pattern we have described may be an artifact of the variability of detection. But the data suggest otherwise. In January 1995, for example, the weather was nearly flat calm for the entire cruise, and no blue whales were seen. Furthermore, we have often spotted blue whales in wind speeds over 30 knots; the whales' tall spouts and habit of resting near the surface make them conspicuous even in rough weather. Therefore, we believe that the patterns we describe are real.

Aircraft surveys conducted concurrently with CalCOFI surveys could help clarify the issue of scale of aggregation of blue whales, as well as how well suited the CalCOFI surveys are to monitoring their abundance.

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CalCOFI REPORTS—INSTRUCTIONS TO AUTHORS

CalCOFI Reports is a peer-reviewed journal. Papers that appear in the Scientific Contributions section have been read by two or more reviewers and by arbiters when necessary. Symposium papers have been invited by the convener of the symposium and are reviewed and edited at the convener's discretion. The Reports section contains newsworthy information on the status of stocks and environmental conditions; its papers are not peer reviewed. Unsolicited review papers will not be considered.

The CalCOFI Editorial Board will consider for publication, in the section entitled Scientific Contributions, manuscripts not previously published elsewhere that bear some relationship to the following with respect to the Californias, the California Current, and the Gulf of California: marine organisms; marine chemistry, fertility, and food chains; marine fishery modeling, prediction, policy, and management; marine climatology, paleoclimatology, ecology, and paleoecology; marine pollution; physical, chemical, and biological oceanography; new marine instrumentation and methods.

Manuscript should be typed in a standard typewriter face (12-pt. Courier) **double-spaced** with wide, **ragged right margins**, and submitted complete with figures, figure captions, and tables, in triplicate to

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

Manuscripts must be received by February 1 of the year in which publication is desired.

Sequence of the material should be TITLE PAGE, ABSTRACT, TEXT, LITERATURE CITED, APPENDIX (if any), FOOTNOTES (if any), TABLES, LIST OF FIGURES with entire captions, and FIGURES.

Title page should give:

- a running head of no more than 60 letters and spaces
- title of the article
- author(s) name(s) and affiliation(s)
- address(es), including zip code(s)
- e-mail address of principal author

Abstract should not exceed one **double-spaced** page.

Text style will in general follow that of the U.S. Department of Commerce (NOAA) *Fishery Bulletin*. Contributors who are not familiar with this publication will do well to follow *The Chicago Manual of Style* (1993). Authors are strongly urged to compare their typewritten equations with similar expressions in the printed literature, with special attention to ambiguity of the symbols for "one" and for "el," before submitting. Whenever possible, write in the first person, and use active verbs.

Measurements must be given in metric units; other equivalent units may be given in parentheses.

Personal communications and *unpublished data* should not be included in the Literature Cited but may be cited in the text in parentheses. Use *footnotes* only when parentheses will not suffice. List footnotes on a separate sheet.

Literature cited should appear in the text as Smith (1972) or Smith and Jones (1972) or (Smith and Jones 1972; Jones and Smith 1973) or Smith et al. (1972); there should be no comma between author and date. All literature referred to in the text should be listed (**double-spaced**) alphabetically by the first author on a separate sheet under the heading Literature Cited. Only the authors' surnames and initials will be used. No reference should appear in the Literature Cited unless it is cited in the text, tables, or figure captions. Each citation must be complete according to the following:

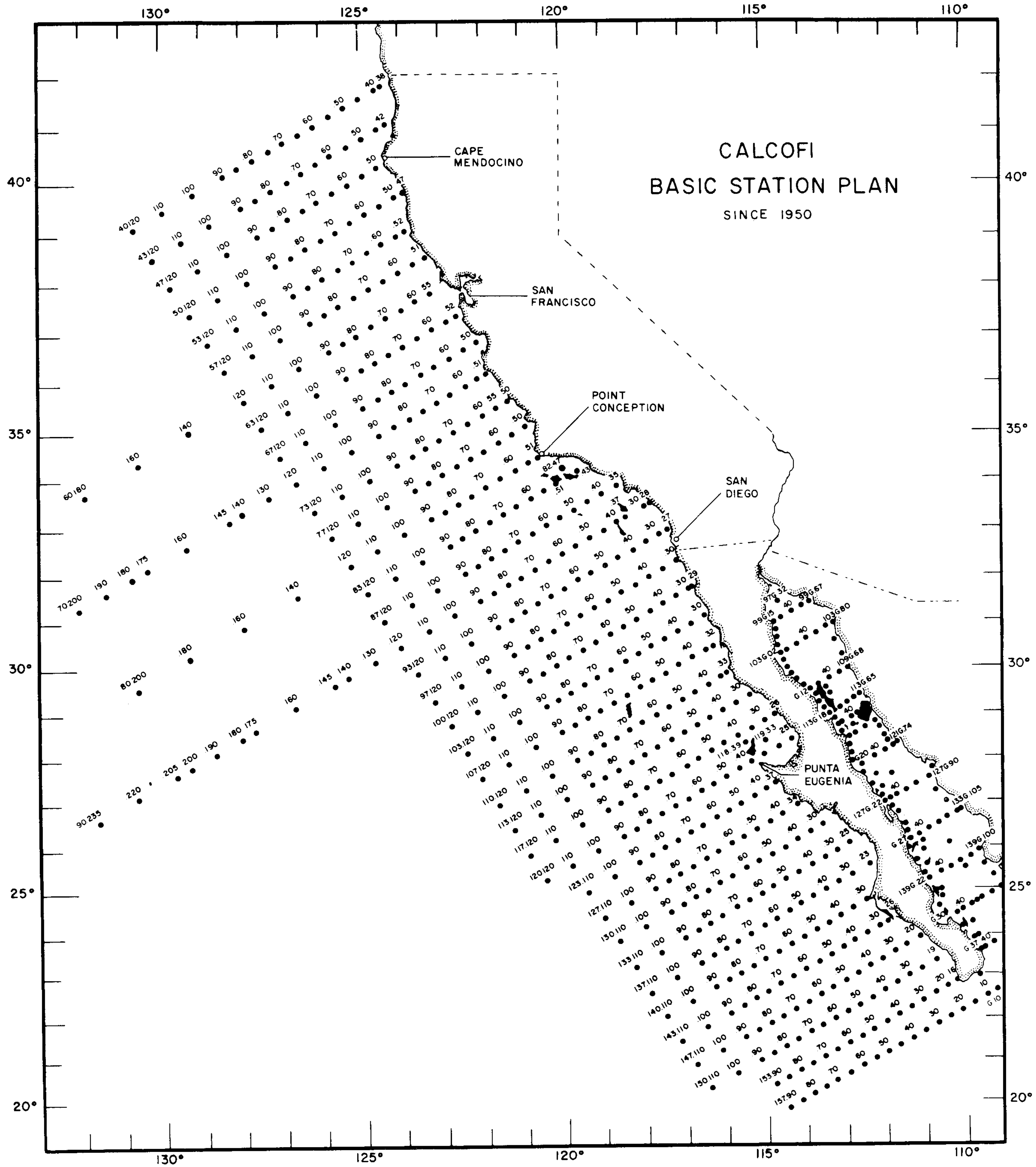
(article):
Barnes, J. T., L. D. Jacobson, A. D. MacCall, and P. Wolf. 1992. Recent population trends and abundance estimates for the Pacific sardine (*Sardinops sagax*). Calif. Coop. Oceanic Fish. Invest. Rep. 33:60–75.
(book):
Odum, E. P. 1959. Fundamentals of ecology. 2d ed. Philadelphia: Saunders, 546 pp.
(chapter):
Wooster, W. S., and J. L. Reid Jr. 1963. Eastern boundary currents. *In* The sea, M. N. Hill, ed. New York: Interscience Pub., pp. 253–280.

Tables (with arabic numbers) should be typed (**double-spaced**) separately from the text; each table should start on a separate page and must have a brief title. Explanatory material belongs in a note beneath the table, not in the title. Please avoid vertical rules and be consistent in format.

Figures, whether drawings or halftones, should be submitted in a format **not larger than 8½ × 11"**. Submit one set of camera-ready figures plus 2 sets of copies. Photographs should be printed on glossy paper. Drawings should be reduced photographically. A composite figure should be submitted as a single photostat or at least as a single careful paste-up. Figures will appear as either single-column (85-mm-width limit), or double-column (178-mm-width limit); or as full page. Special cases should be discussed with the editor before submittal. After reduction, no letter or number should be smaller than 1 mm. Special note should be taken of the disappearance of decimal points during reduction. If shading is used, make a trial reduction to ensure that the patterns do not merge at the required reductions. The determining factor for size should be the complexity of detail to be shown.

Each figure must have a *caption*; captions should be typed, **double-spaced**, in numbered sequence on a separate sheet. Illustrative materials submitted for publication are often first prepared for oral presentation in slide format. Authors should take special care that slide-format material submitted to *CalCOFI Reports* is appropriate to printed format with respect to economy, redundancy, and style.

Acknowledgments, if included, should be placed at the end of the text and may include funding source.



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