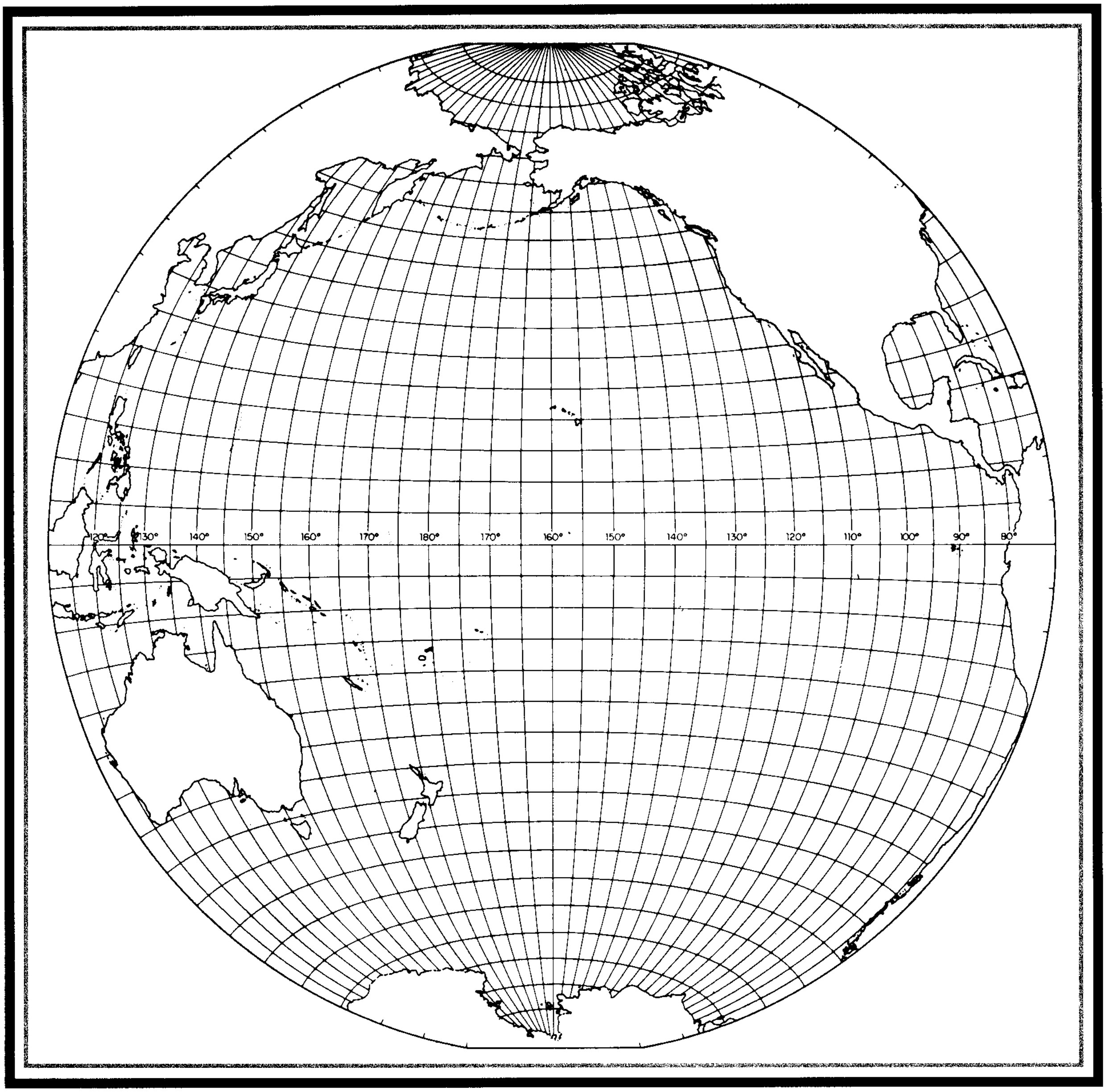

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

This year marks the fiftieth anniversary of the beginning of the seagoing operations and time series of sampling in the California Current that have become the hallmark of CalCOFI's research. In its five decades of collaborative work, CalCOFI has fielded over 300 coastal survey cruises, published over 6,000 documents and scholarly papers, spawned several new fields of research, and established benchmarks against which large-scale change may be evaluated. Methods of fishery and environmental research developed by CalCOFI scientists are used as standards worldwide. The marriage of federal, state, and university scientists in such a long-term endeavor is particularly successful for economically marshalling public resources.

This interagency approach to ocean measurement paid off in the ability to investigate the recent El Niño event. El Niño of 1998 (because it had been predicted) and the northward expansion of the growing population of California sardine stimulated increased temporal and spatial coverage of the California Current by CalCOFI cruises. In addition to the usual quarterly survey cruises in 1998, 48 extra ship days for 8 extra cruises were provided by UC ship funds; extra salaries for data collection and processing, and funds for supplies were made possible by a grant from the NOAA Office of Global Change. The data collected by the CalCOFI interagency consortium are summarized in Hayward et al. (this volume). Preliminary reports on the changes associated with the 1998 El Niño will be presented at the symposium of the 1999 CalCOFI Conference.

In 1999, CalCOFI returned to the less intense, quarterly sampling that has been its standard since 1985. However, studies of sardine spawning as far north as Monterey Bay have continued, with near-surface sampling of fish eggs and environmental properties. This sampling has given a much clearer picture than was previously available of the mesoscale spatial relations between spawning and the physical environment, and of differences between sardine and northern anchovy. The winter 1999 cruise was conducted on the Scripps Institution of Oceanography (SIO) RV *Roger Revelle*, whose large size and modern facilities permitted extensive participation by students conducting research independent of, but supported by, the CalCOFI time series of environmental data. Work performed by our Mexican colleagues, partly a consequence of mentoring and collaboration by CalCOFI investigators over several decades, has begun to help us understand how the Gulf of California stocks of Pacific sardine contribute to the Pacific coast population (cf. de Anda-Montañez and Seijo, Lluch-Cota et al., and de Anda-Montañez et al., this volume).

The Pacific sardine resource off California has now surpassed one million tons and is considered fully recovered for the first time since the mid-1940s. At an interagency Pacific sardine workshop held in 1983, it was agreed that the sardine population would be considered fully recovered when it reached a million tons, when it occupied its historic range (Mexico to Canada), and when all historic age classes were represented in the population. All of these criteria have now been met, representing a real success story for Pacific sardines and fishery managers. The most recent stock assessment, conducted jointly by the California Department of Fish and Game (CDFG) and the National Marine Fisheries Service (NMFS), estimated 1.07 million metric tons in the area off California's coast (Ensenada, Mexico, to San Francisco) and up to 1.6 million metric tons coastwide (Ensenada to British Columbia). Since the onset of the recovery, the sardine population is estimated to have increased by 20% to 30% per year in the presence of a steady fishery. Egg and larval data collected by the CalCOFI program have been a crucial tool in measuring the sardine's recovery.

The market squid (*Loligo opalescens*) has been the basis of an important fishery in California since the 1850s. In the last decade, increases in catch and price have combined to make market squid the most valuable fishery in the state. The squid fishery is the largest unregulated open access fishery on the West Coast. At the CalCOFI market squid symposium held in 1997, researchers from around the world identified critical biological data necessary to manage the fishery (cf. Butler et al., and Lowry and Carretta, this volume). Recent funding from the squid permit fees contained in Senate Bill 364 (Sher, D-Palo Alto), passed by the California legislature in 1997, has enabled the CDFG to begin addressing research and assessment needs by forming a Market Squid Investigations Unit. Collaborative research contracts have been let to

SIO/NMFS and UCLA. Port sampling and field research activities have been implemented and will continue over the next several years.

One of the first products of the research is a paper (Butler et al., this volume) describing the age and growth of market squid from daily increments in statoliths. This study indicates that both male and female market squid can mature as early as 6 months and that longevity is less than one year. The short life span of this species partly explains the high productivity of the stock and how it can recover rapidly from environmental fluctuations such as the recent El Niño. This study will provide the necessary life-history parameters for developing a management plan. A CDFG report will be submitted to the legislature in 2001 on the status of the fishery and will provide recommendations for such a squid conservation and management plan.

The Pacific Fishery Management Council approved draft Amendment 8 to the Northern Anchovy Fishery Management Plan and has submitted the plan to the U.S. Secretary of Commerce for review. This action changes the name of the plan to the Coastal Pelagic Species Fishery Management Plan, and includes northern anchovy, Pacific sardine, Pacific mackerel, market squid, and jack mackerel. The new plan is designed to allow more responsive council action and establishes two categories of species management: "actively managed" and "monitored only." Actively managed species will be managed under a harvest guideline or quota; monitored only species will not be managed under a harvest guideline or quota. At the outset of the plan, Pacific sardine and Pacific (chub) mackerel will be actively managed, and the other three species will be monitored only. The plan contains a limited entry program applying south of 39°N latitude for finfish species only (market squid is not included). The new plan identifies essential fish habitat and overfishing thresholds as required by the Sustainable Fisheries Act and implements new harvest control rules for Pacific sardine and Pacific (chub) mackerel that retain a portion of the biomass as forage and provide a stable fishery.

Governor Wilson signed Assembly Bill 1241 (Keeley), the Marine Life Management Act of 1998, and Senate Bill 1336 (Thompson), the Rockfish Research Conservation and Management Act. This action will result in fundamental changes in how the CDFG approaches the management of several currently important, and newly emerging, fisheries, including the white seabass and nearshore finfish fisheries. The thrust of AB 1241 is to empower the Fish and Game Commission to regulate specified and emerging commercial fisheries that have been managed in the past through laws enacted by the legislature. The bill establishes a policy of fishery management based on sustainable use and directs that management shall be through the development and implementation of fishery management plans (FMPs). The bill mandates that the CDFG do several things, including prepare a master plan by 1 September 2001 that describes the processes and resources required to prepare, adopt, and implement FMPs; prepare an FMP for the nearshore fishery, as defined in the bill, to be adopted by the commission on or before 1 January 2002; and bring FMPs established before 1 January 1999 into compliance with the provisions of the act on or before 1 January 2002. Governor Wilson's signing AB 1241 into law may prove to be historic in the management of California's marine resources.

The Marine Ecological Reserves Research Program (MERRP) study of production of planktonic fish eggs and larvae in nearshore waters continued in 1999 at the four southern California sites: Big Sycamore Canyon and Vandenberg Marine Ecological Reserves, and Anacapa and San Miguel Islands. In addition to the CUFES and bongo samplers used at these sites in 1998 (Watson et al., this volume), manta net sampling was added this year. The fortuitous timing of the study, which includes winter and summer surveys during the 1998 El Niño, a winter survey during the 1999 La Niña, and a scheduled summer 1999 survey, will allow comparison of nearshore ichthyoplankton production during these contrasting regimes. Preliminary examination of February 1999 samples suggests that compared with February 1998, planktonic shorefish egg abundance was lower at all sites except Vandenberg (where it was low in both years), but the abundance of rockfish (*Sebastes* spp.) larvae was much higher in 1999.

The rockfish genetics program has completed sequencing of the cytochrome *b* gene of almost all of the 70-plus species of rockfishes that occur along the west coast of North America. This has opened a new window of interesting research collaboration between the genetics group and the ichthyoplankton survey portion of the CalCOFI program. It is now possible to identify almost all of the rockfish larvae encountered in the CalCOFI survey. Recently William Watson brought in a common but unknown rockfish larva that turned out to be *Sebastes moseri*, a newly described species identified from a single adult specimen. The relatively common occurrence of these larvae in the CalCOFI collections indicates that the new species is abundant but not readily caught by traditional fishing gear. This discovery highlights the wealth of new information that can be obtained by the marriage of traditional and new methods of ocean observation within the context of the CalCOFI program.

In a related study, the genetics group has been examining population genetic structure in nearshore rockfishes. These studies are beginning to reveal significant intraspecific genetic differences between northern, central, and southern California. These differences are almost certainly due to oceanographic barriers to larval dispersal (e.g., coastal jets and eddies). We hope that these genetic studies can give insights into long-term circulation patterns along the California coast.

The Southwest Fisheries Science Center's Coastal Fisheries Resources Division, together with the CDFG, has completed a stock assessment of cowcod (*Sebastes levis*) for the Pacific Fisheries Management Council. This stock assessment incorporated catch per angler hour (CPUE) from logbooks of commercial passenger fishing vessels (CPFVs); larval abundance from CalCOFI plankton surveys; and juvenile abundance from Orange County and Los Angeles City Sanitation Districts otter trawl surveys. The population model was tuned to these three indices and indicated that the cowcod population was only 10%–15% of its virgin biomass. Thus, under the Magnuson-Stevens Fishery Management Act, the cowcod is an overfished stock and will require a rebuilding plan.

Principal investigators Paul E. Smith, John R. Hunter, and H. Geoffrey Moser secured extra ship time and additional money from NOAA's Office of Oceanic and Atmospheric Research to improve the time resolution of fish reproduction during the onset and decline of the recent El Niño–Southern Oscillation (ENSO) event, December 1997 to December 1998. The complete fish reports can be seen in Hayward et al. in this issue. Briefly, the ENSO event was severe in the Southern California Bight. Egg pump surveys of the California Current off central California showed the presence of tropical species spawning extensively off southern California. Sardine spawning was detected as far north as Vancouver Island, British Columbia, Canada, the first reported sardine spawning north of the Columbia River in recent decades. Off southern California, sardine spawning was higher than the 1951–98 average. Hake spawning was barely detectable off southern California, and presumably the population spawned farther north than the current CalCOFI survey area. The populations of sardine, anchovy, and hake will continue to be monitored so that the effect of this ENSO event on the abundance and biomass of these species in their respective fisheries can be evaluated.

The biological-oceanographic survey cruises of IMECOCAL (Investigaciones Mexicanas de la Corriente de California) continued during the past year. Six cruises have been completed, and much progress has been made in processing and analyzing samples and data. This spring Tim Baumgartner hosted a workshop at CICESE, Ensenada, Mexico, that brought together research partners from CICESE, CICIMAR, and CalCOFI to discuss progress of the program, methods and technology, collaborative projects, and funding. Martin Hernandez Rivas and coauthors from CICIMAR collaborated with William Watson, SWFSC, on a paper (in preparation) that describes the distribution and abundance of ichthyoplankton assemblages off Baja California based on initial IMECOCAL surveys.

Loren Haury, of SIO's Marine Life Research Group (MLRG), retired from the University of California after a 32-year career. Loren spent most of his career examining the interactions of biology and physics as they affect zooplankton. According to colleagues, Loren broke new ground in exploring one major, nearly untouched, section of the Stommel diagram: he led the biological oceanographic community toward an understanding of important oceanic ecological questions that can be addressed only through long-term, large-scale data sets. Loren plans to continue to pursue such interests less formally in a freshwater setting—the Colorado River and Grand Canyon.

After 33 years of service to CalCOFI and 20 years engaged in some aspect or other of the production of *CalCOFI Reports* and the hosting of the annual meeting, George Hemingway plans to hand over those functions at year's end. George was the first CalCOFI coordinator and managing editor after the sunset of the enabling law for the Marine Research Committee of the State of California, replacing Herb Frey of the CDFG. In 1979, beginning with *CalCOFI Reports* volume 20, he implemented a peer review policy and editorial criteria that have turned this journal into the twelfth most cited fishery science journal, and the second-highest-ranked regional fishery journal in the world, according to data published by the Institute for Scientific Information.

The seagoing personnel of CDFG's Marine Region, SIO's MLRG, and the Southwest Fisheries Science Center's Coastal Division contributed, through their dedication and diligence, to the success of CalCOFI's field work. Amy Hays of the SWFSC deserves special thanks for making every one of the cruises in 1998. The CalCOFI Committee thanks the officers and crews of the research vessels that have served us well as platforms for our observations during the past year: the CDFG RV *Mako*, the NOAA ship *David Starr Jordan*, the University of California RVs *New Horizon*, *Roger Revelle*, and *Robert Gordon Sproul*.

We gratefully acknowledge the work of Mary Yoklavich in organizing the symposium of the 1998 conference and for selecting reviewers and editing the papers. We also thank the reviewers of the symposium on marine reserves: Giacomo Bernardi, Louis Botsford, Mark Carr, Churchill Grimes, Dennis Hedgecock, Mark Helvey, Sam Herrick, Ralph Larson, Alec MacCall, Janet Mason, Deborah McArdle, Tory O'Connell, Richard Parrish, Pat Reilly, James Seger, Rick Starr, Cindy Thomson, David VenTresca, Patty Wolf, and Mary Yoklavich. We also thank the reviewers of the contributed papers in volume 40: Jon Brodziak, David Checkley, Loren Haury, Dennis Hedgecock, George Hemingway, John Hunter, George Jackson, Libby Loggerwell, Alec MacCall, Geoff Moser, Mike Mullin, Dick Parrish, Cindy Thomson, and H. J. Walker. Special thanks to our editor, Julie Olfe, for another fine volume in this long series of publications.

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John Hunter, NMFS
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REVIEW OF SOME CALIFORNIA FISHERIES FOR 1998: PACIFIC SARDINE, PACIFIC MACKEREL, PACIFIC HERRING, MARKET SQUID, SEA URCHIN, GROUNDFISHES, SWORDFISH, SHARKS, NEARSHORE FINFISHES, ABALONE, DUNGENESS CRAB, PRAWN, OCEAN SALMON, WHITE SEABASS, AND RECREATIONAL

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In 1998, commercial fisheries harvested an estimated 116,069 metric tons (t) of fishes and invertebrates from California waters, a 47% decrease from the 219,497 t harvested in 1997. Preliminary total commercial landings in California were 129,328 t, 42% lower than in 1997. The preliminary ex-vessel economic value of California commercial landings decreased by 37%, to $107 million. Statewide landings by recreational anglers aboard commercial passenger fishing vessels (CPFVs) decreased by 18%, to 3,155,995 individual fishes.

The El Niño event of 1997–98 continued to dramatically affect several important California fisheries, and was partly responsible for the significant decline in total landings and revenues. 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 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 continued high landings of Pacific sardine and mackerel. The El Niño event also had a devastating effect on the Pacific herring fishery, which had one of the poorest seasons since the early 1970s. Other commercial fisheries that declined for a variety of reasons (perhaps including El Niño) were sea urchin, chinook salmon, and numerous groundfish species.

In contrast to these declines, several fisheries increased in 1998. The Pacific sardine resource was declared fully recovered from a population decline which began in the 1940s. Fisheries with increased landings in 1998 included spot and ridgeback prawn, Dungeness crab, splitnose rockfish, white seabass (commercial), swordfish, thresher shark, and some fishes harvested by CPFVs (barracuda, albacore, bluefin tuna). Particularly notable was the continued growth of the fishery for live and premium fishes. Passage of the Marine Life Management Act (MLMA) will aid California Department of Fish and Game (CDFG) efforts to monitor and manage this complex nearshore fishery.

PACIFIC SARDINE

Rebuilding of the Pacific sardine (*Sardinops sagax*) fishery continued in 1998, with the year's total landings of 41,056 t ranking among the highest since the reopening of the directed fishery in 1986 (table 1, fig. 1). The 1998 fishery had an approximate ex-vessel value of $3.6 million, down from $3.9 million in 1997. Approximately 94% of the 1998 quota was landed, and the directed fishery remained open until year's end.

Fish and Game Code (§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. 2). Based on a 1 July 1997 biomass estimate of 420,934 t, the harvest formula generated an initial 1998 southern fishery quota of 29,030 t, and a northern fishery quota of 14,515 t (table 2). In October, the CDFG reallocated uncaught quota portions equally between north and south. The southern California fishery filled its portion of the reallocation in mid-December, but the CDFG did not recommend closing the southern fishery because only a few weeks remained in the year and several thousand tons were left in the northern allocation. Consequently, 2,489 t of the 1998 allocation was not taken.

The Pacific sardine resource off California has now surpassed one million tons and is considered fully recovered for the first time since the mid-1940s. The most recent stock assessment, conducted jointly by the CDFG and the National Marine Fisheries Service (NMFS), estimated 1.07 million t in the area of California's coast (Ensenada, Mexico, to San Francisco) and up to 1.6 million t coastwide (Ensenada to British Columbia).

Current regulations give the CDFG considerable latitude in setting annual sardine quotas. When biomass is estimated to be more than 18,144 t, Fish and Game Code requires that allowable catch must be consistent with resource rehabilitation. To calculate the 1999 quota, the CDFG used a harvest formula selected by the Pacific Fishery Management Council (PFMC) as the preferred option in the draft Coastal Pelagic Species Fishery

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

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
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	46,196	5,718	20,615	1,161	11,541	70,257	155,488
1998*	41,056	1,406	20,073	970	2,432	2,709	68,646

*Preliminary

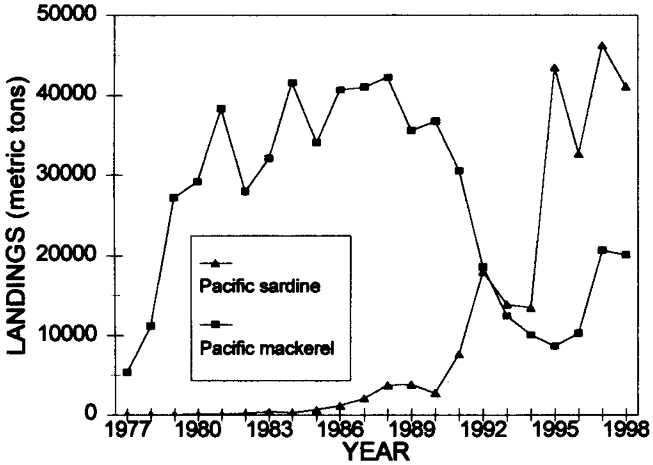

Figure 1. California commercial landings of Pacific sardine and Pacific mackerel, 1977–98.

Management Plan (Amendment 8). Based on the 1998 estimate of total biomass (age 1+), the 1999 sardine fishery opened on 1 January with a quota of 120,474 t for the California fishery. The 1999 quota was 177% higher than the 1998 allocation.

Prices paid to fishermen (ex-vessel price) for sardines remained relatively low in 1998, but were slightly higher than in 1997. Prices ranged from $66 to $110 per t, and averaged $89. 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 in 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: $564 per t for market squid and $600–$1,400 per t for tuna. During 1998, sardine landings varied by month because of availability, demand, and fleet participation in other fisheries.

TABLE 2
Pacific Sardine Quota Allocations (Metric Tons) in California for 1998

	Initial quota	Reallocated quota	Landings
North	14,515	10,220	9,081
South	29,030	10,220	31,975
Total	43,545	20,440	41,056

In 1998, most Pacific sardine landings in southern California were sold to market processors (78%) or to the canneries (22%). Currently, fish are processed for human consumption (fresh or canned), pet food, or export. Of the exported sardines, most are either sold for human consumption or used as feed in aquaculture facilities. About 15% of all sardines landed in California were canned domestically for human consumption. The only southern California cannery that packs fish for human consumption continued intermittent canning of sardines. In northern California, two canneries packed fish for human consumption.

Besides the wetfish fishery for sardine, there is a small bait fishery 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 1998, the ex-vessel value of the sardine live bait fishery was approximately equal in value to the directed fishery.

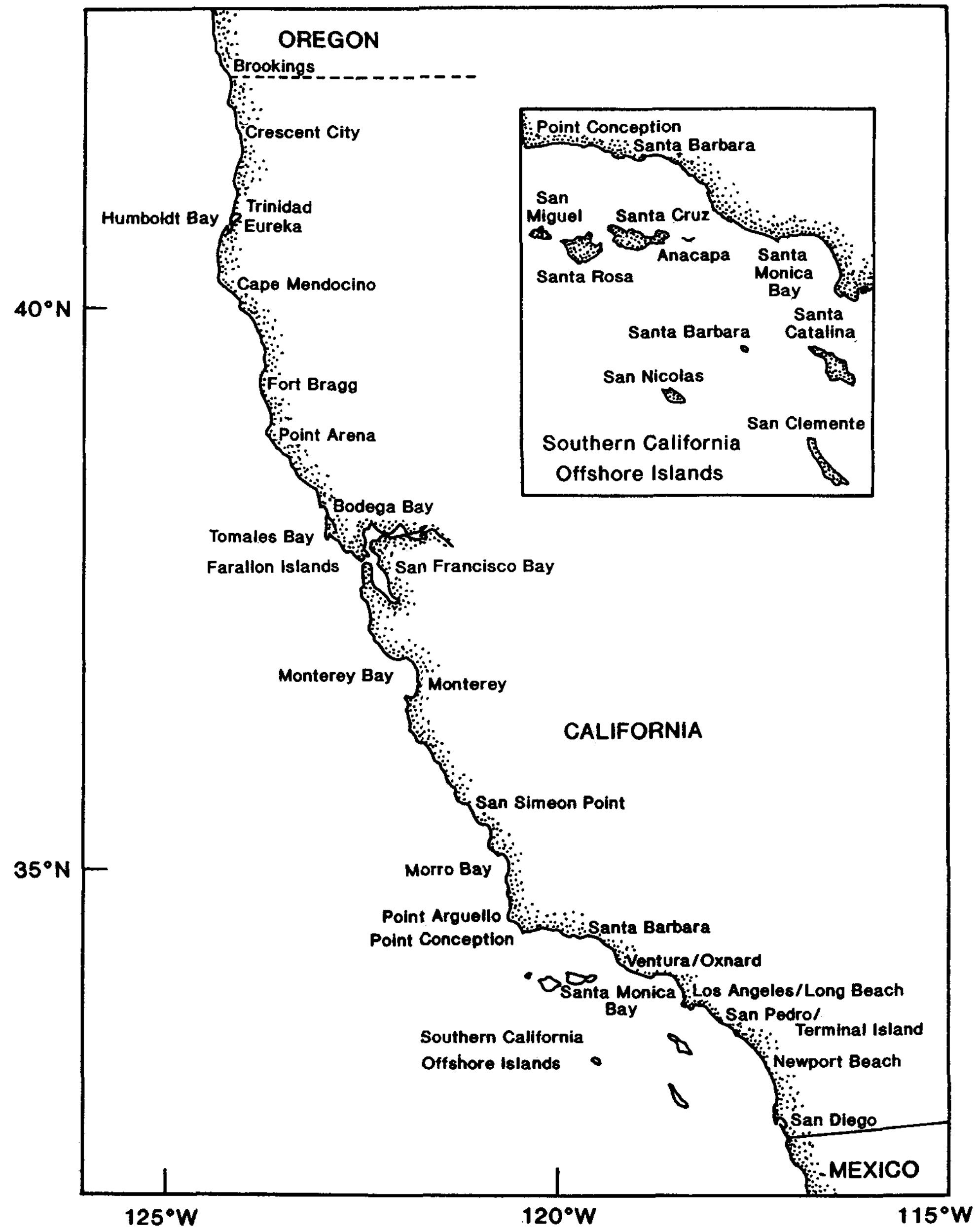

Figure 2. California ports and fishing areas.

Approximately 55% of California's sardine landings were exported in 1998, sold primarily (84%) as frozen blocks. In 1998, 22,397 t of sardines were exported, more than doubling the 1997 total of 10,977 t. Export revenues totaled $11.96 million at approximately $534 per t. The top importers of Pacific sardine were Australia (77%), Japan (9%), China (4%), Malaysia (2%), and Panama (2%). Australia imports sardines for fish food in aquaculture facilities, while Japan supplements its catch to meet consumer demand following the recent decline of its own sardine resource.

In September 1998, the PFMC approved the draft Coastal Pelagic Species Fishery Management Plan (Amendment 8 to the Northern Anchovy Fishery Management Plan) and submitted the plan to the U.S. Secretary of Commerce for review. At the outset of the plan, Pacific sardine will be actively managed. The plan implements new harvest control rules for Pacific sardine that retain a portion of the biomass as forage and provide a stable fishery.

PACIFIC MACKEREL

El Niño conditions continued to affect the Pacific mackerel (*Scomber japonicus*) fishery through the first half of 1998. The 1998 annual landings in California totaled 20,073 t, a 2.6% decrease from the 1997 total of 20,615 t (table 1, fig. 1). Effort was focused on traditional fishing grounds from Monterey south to the U.S./Mexican border. Ninety-three percent of the landings were made in southern California, primarily at San Pedro and

Terminal Island. Most northern California landings were made in the Monterey area. Persisting oceanic conditions favored a continued northward extension of the Pacific mackerel population up to British Columbia.

The Pacific mackerel fishing season is specified in the Fish and Game Code (§8410) as a 12-month period from 1 July through 30 June of the following calendar year. Based on an estimated biomass of 91,626 t on 1 July 1997, a 22,045 t quota was set for the 1997–98 season, a 2.5-fold increase from last season's quota of 8,709 t. When the total biomass is estimated by CDFG to be greater than 18,144 t but less than 136,078 t, allowable harvest is defined as 30% of the total biomass in excess of 18,144 t.

Unlike the 1996–97 quota, which was filled by the middle of March 1997, the 1997–98 quota remained open throughout the season. Monthly landings followed a pattern similar to the previous season, with most landings made in spring and fall. This pattern was driven not only by availability, but also by fishers' participation in other fisheries (sardine, market squid, and tuna), weather conditions, and market demands.

The 1998–99 fishing season quota was based on a biomass projection derived from a tuned virtual population analysis (VPA) model called ADEPT. On the basis of a projected biomass of 120,200 t for 1 July 1998, the commercial quota for 1998–99 was recommended and set at 30,572 t. The CDFG and NMFS continued to collect Pacific mackerel along with other fishery-dependent and fishery-independent data for the 1999 assessment. In 1998, approximately 2,350 Pacific mackerel were collected, and indices of length, weight, sex, maturity, and age were obtained for use in the biomass projection for 1 July 1999.

The ex-vessel price paid for Pacific mackerel (landings over one t) ranged from $22 to $441 per t, with an average of $132. The sale of the catch generated approximately $2.13 million paid to fishermen. Many landings (less than one t) were sold to small specialty markets and dealers and can inflate the price upward from $0.02 per kg to $0.91 per kg, with an average price of $0.25 per kg ($1,235 per t). Although these landings totaled only 84 t, they generated approximately $103,500.

PACIFIC HERRING

Pacific herring (*Clupea pallasi*) fisheries for 1998 clearly illustrated the devastating effects of the 1997–98 El Niño. Annual statewide landings declined to 2,432 t, down 79% from the previous year (table 1), and the 1997–98 sac roe season (December–March) produced only 1,825 t, an 83% drop from the previous season and arguably one of the poorest seasons since the fishery began in 1972–73. All sac roe fishery landings were significantly less than the allotted quotas: the San Francisco gill net fleet, composed of three platoons (385 permits), landed 280 t, 96% under the 7,007 t quota; and 25 round haul (purse seine and lampara) permits landed 1,523 t, 21% under the 1,932 t quota. For the first time during an open season, the Tomales Bay fishery did not land herring (the quota was 200 t); Crescent City permits landed 21 t, 22% less than the 27 t quota; and Humboldt Bay landings totaled approximately 1 t, 98% less than the 49 t quota. The fishery for herring as live or dead bait was nonexistent in 1998.

In addition to the decline from the 1996–97 season, herring collected from commercial catch and CDFG research nets manifested symptoms similar to herring sampled during the 1983–84 sac roe season. Mean weights per given lengths were as much as 25% lower than normal. Female herring appeared in San Francisco Bay with impaired gonadal development noted by roe technicians as "pencil roe" and lacking the typical golden coloration of ripe skeins, conditions related to a lack of food. Skeins containing opaque eggs or eggs in varying stages of resorption were observed with increased frequency in the latter part of the season and attributed to prolonged periods between spawning events.

Ex-vessel prices for herring with 10% roe recovery averaged about $441 per t for gill net landings and $276 per t for round haul fish during the 1997–98 season; an additional 10% of the base price per t was paid for each percentage point above 10%. The ex-vessel price per t was approximately 60% less per t than in the 1996–97 season, reflecting the downturn in the Japanese economy. Total ex-vessel value of the sac roe fishery was an estimated $600,000, down 96% from the 1996–97 season, and well below the average for the previous twelve seasons (approximately $11 million).

The San Francisco Bay herring eggs-on-kelp fishery landings totaled 30 t, 84% less than the 190 t quota. Record high landings of 173 t were made in the 1996–97 season. The total estimated value of the 1997–98 eggs-on-kelp harvest was $330,000, based on an average ex-vessel price of $5.00 per pound. El Niño–related effects plagued permittees: supplies of giant kelp (*Macrocystis pyrifera*) that met market criteria were very limited; low salinity in the bay severely reduced the time kelp could remain in suspension and yield a marketable product; and spawning events were inhibited by heavy rainfall and poor gonadal development related to a lack of food.

The CDFG conducted hydroacoustic and spawn deposition surveys to estimate herring spawning biomass in San Francisco Bay. Spawn deposition estimates were used to assess the Tomales Bay population. No surveys were conducted for Humboldt Bay or Crescent City Harbor. The 1997–98 herring spawning biomass estimate for the San Francisco Bay population was 18,182 t, the third lowest ever recorded. This represents an 80%

decline from the previous season, which was the third highest recorded. Given the large spawning biomass estimates for 1995–96 (90,000 t) and 1996–97 (81,454 t) and multiple consecutive years of successful recruitment (1992–95 year classes), far fewer fish returned to spawn than expected. El Niño conditions may have increased adult mortality, prevented herring from reaching reproductive condition, and driven herring farther than usual in a quest for favorable foraging conditions.

The Tomales Bay herring spawning biomass continued to fluctuate widely. The 1997–98 spawning biomass estimate was 533 t, a decline of 60% from the previous season and the fourth lowest recorded. This was the third consecutive season of decline. Age-structure analysis of the Tomales Bay commercial catch did not forecast large changes in abundance, but commercial gill net web size regulations allow escapement of smaller, younger fish and therefore do not indicate abundance of two- and three-year-old herring. Sample sizes from research gill nets were not robust enough to be conclusive. Spawns were probably inhibited by abnormally high rainfall, which lowered salinity and increased turbidity in Tomales Bay waters.

Northwesterly winds cooled the ocean waters off of central California considerably during the spring of 1998. Because of the degeneration of El Niño conditions, projections of a prevailing La Niña, and a return to normal ocean conditions, herring fisheries were expected to improve in the 1998–99 season. The 1998–99 December fishery in San Francisco Bay opened with good catches. The herring were in far better physical condition than in the previous season and had normal gonadal development. Ex-vessel prices, however, were expected to remain low because of uncertainty about the troubled Japanese economy.

MARKET SQUID

Statewide landings in the California market squid fishery plummeted in 1998. For the previous two years, market squid had ranked as the state's number one commercial marine resource in terms of volume and revenue. Distinguished by volatility, annual landings for the fishery totaled only 2,709 t, down from over 70,257 t in 1997 (table 1, fig. 3). This decrease was a consequence of the 1997–98 El Niño, resulting in warm water conditions inhospitable to squid.

The year was important with respect to management developments. Passage of the Sher Bill (SB364) in 1997 implemented a $2,500 permit fee for all fishery participants for the commercial season beginning 1 April 1998. As specified in Article 9.7 of the Fish and Game Code, fishers must hold a commercial market squid vessel permit in order to land more than two short tons of squid per day, and must hold a commercial squid light boat owner's permit in order to attract squid by light to seine vessels. In order to renew a permit, an applicant must have been issued a permit in the immediately preceding year. Before passage of the Sher Bill, the fishery had been open access and essentially unregulated.

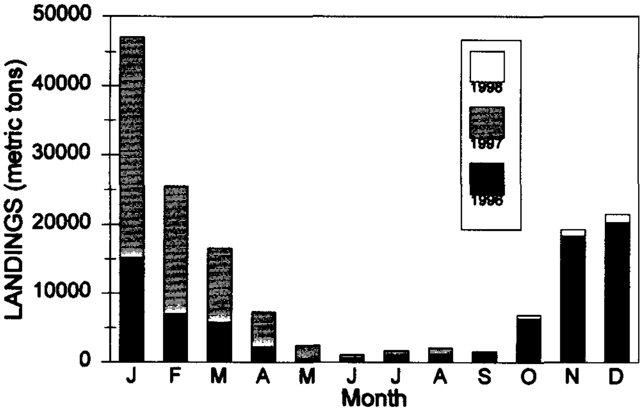

Figure 3. Monthly landings of California market squid, 1996–98.

By mid-1998, 240 market squid vessel permits and 41 light boat permits were issued for the 1998–99 season, generating nearly $750,000 in revenue. Of the 240 vessel permit holders, only 54 landed two tons or more in 1998. Many out-of-state vessels either did not participate or returned home early in the season to fish for groundfish or salmon because of poor prospects for squid for the remainder of the year. Other permits were purchased on speculation. Revenue generated from permit sales will be used by the CDFG to fund a 3-year pilot study to provide information for developing a squid conservation and management plan by April of 2001.

Northern and southern California have distinctly different fisheries for market squid, although the resource is harvested on the spawning grounds in both areas. In recent years, 90% of landings have been made in southern California, in sandy nearshore areas and around the Channel Islands in winter months during peak spawning activity. Conversely, squid in the northern California fishery, primarily centered in Monterey Bay, tend to aggregate and spawn during summer. In 1998, over 99% of the statewide total was taken in southern California, with most landings in Port Hueneme or Ventura. Less than 20 t of squid were landed in northern California, the lowest annual total for the area recorded since monitoring of the fishery began in 1930.

Because of low availability, the average price paid to fishermen was $564 per t, significantly higher than the $292 paid in 1997. Ex-vessel value of the fishery in 1998 is estimated at approximately $1.7 million, well below the $20.6 million generated in 1997. Revenues from sardine ($3.6 million) and Pacific mackerel ($2.13 million), often targeted by the same fleet, also exceeded squid revenues in 1998.

TABLE 3
Preliminary California Commercial Red Sea Urchin Landings (Metric Tons) for 1998

Port	Landings	Percentage of statewide catch	Value	Price per kg
Fort Bragg	734.1	15.6	$1,004,574	$1.37
Albion	194.8	4.1	$ 245,167	$1.26
Point Arena	344.3	7.3	$ 508,619	$1.48
Bodega Bay	233.0	4.9	$ 310,309	$1.33
Half Moon Bay	5.7	0.1	$ 7,943	$1.39
Other	21.0	0.4	$ 27,014	$1.29
N. Calif. subtotal	1,532.9	32.6	$2,103,626	$1.37
Santa Barbara	1,462.8	31.1	$2,659,150	$1.82
Oxnard/Ventura	1,024.4	21.8	$1,802,322	$1.76
Los Angeles	475.4	10.1	$ 810,818	$1.71
Orange	7.5	0.2	$ 11,842	$1.58
San Diego	200.8	4.3	$ 251,536	$1.25
Other	4.1	0.1	$ 5,951	$1.44
S. Calif. subtotal	3,175.1	67.4	$5,541,620	$1.75
Grand total	4,708.0		$7,645,246	

Despite the relatively high price paid for squid in 1998, international demand for California squid diminished significantly. Processors reported that the product was not being sought by foreign markets that had supported the fishery in the previous two years. In 1997, China purchased over 26,000 t of market squid, with statewide exports totaling approximately 48,000 t. Nearly $50 million was paid to California processors for these exports, mostly packaged in frozen blocks of 25 pounds, and representing approximately 71% of total California landings that year. In 1998, exports accounted for only 1,600 t and $2.4 million to processors. Leading export nations for the year included Mexico, the United Kingdom, and Japan, with China accounting for only a negligible portion of the total.

In an effort to provide information to the CDFG for squid research and development of the management plan, two advisory committees were established in 1998. The Squid Research and Scientific Committee and the Squid Fishery Advisory Committee were asked to recommend interim management measures for the fishery, and a series of statewide public hearings were held on the matter. Although no additional regulations were imposed in 1998, proposals for mandatory logbooks, time or area closures, limited entry, and gear restrictions were under consideration by the committees late in the year.

SEA URCHIN

Statewide landings of red sea urchin (*Strongylocentrotus franciscanus*) for 1998 totaled 4,708 t, continuing the downward trend since 1988 (table 3, fig. 4). Landings dramatically decreased by 42% from the 1997 total of 8,146 t. Northern California sea urchin landings declined by 26% from 1997, southern California by 48%. A combination of El Niño conditions and depressed Japanese market demand were responsible for lower prices. Most harvesters opted not to fish during most of the year because of decreased value and poor quality of product.

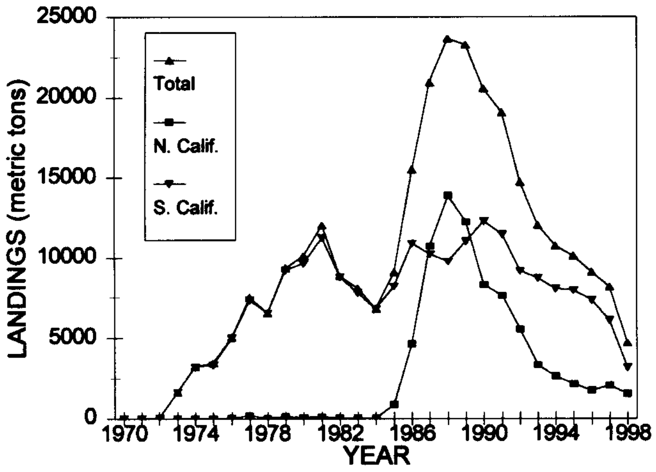

Figure 4. California sea urchin landings, 1970–98.

Santa Barbara and the Oxnard/Ventura areas were the most active ports for sea urchin landings in 1998, with a combined 53% of the statewide catch (table 3). Northern California urchin landings made up a larger portion of the statewide total—33%, compared to 25% in 1997. Fort Bragg was the third most active port for sea urchin landings; Los Angeles landings were only 10% of the total.

The overall value of the fishery in 1998 decreased by 49%, from $15 million in 1997 to $7.6 million (table 3). The unit price per kg decreased from $1.80 in 1997 to $1.62 in 1998. Northern California showed a larger decline in the unit price per kg, dropping from $1.82 to $1.37; southern California decreased slightly, from $1.79 to $1.75. The number of permits, 464, decreased by 9 from 1997. The return of cooler oceanic conditions toward the end of 1998 improved sea urchin quality, but depressed economic conditions in Japan kept unit prices low.

The expansion of sea otters into southern California may seriously affect sea urchins and other invertebrate species. In 1998 a significant number of sea otters (approximately 100) were observed and documented south of Point Conception for the first time. This southern expansion poses a direct threat to the sea urchin fishery in southern California.

GROUNDFISHES

The California commercial groundfish harvest for 1998 was 22,419 t (table 4), with an ex-vessel value of approximately $22 million. Total 1998 landings decreased by 23%, or 6,513 t, and ex-vessel revenues dropped 30%, or nearly $10 million, from 1997.

TABLE 4
California Groundfish Landings (Metric Tons) for 1998

Species	1997	1998	Percent change
Dover sole	5,282	3,556	−33
English sole	648	425	−34
Petrale sole	827	472	−43
Rex sole	453	289	−36
Other flatfishes	1,107	813	−27
Widow rockfish	1,336	928	−31
Bocaccio	286	141	−51
Splitnose rockfish	396	1,404	255
Other rockfish	5,271	4,426	−16
Thornyhead	2,754	1,909	−31
Lingcod	502	149	−70
Sablefish	2,888	1,435	−50
Pacific whiting	6,332	5,723	−10
Grenadier	632	500	−21
Other groundfish	218	249	14
Total	28,932	22,419	−23

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

	Swordfish	Common thresher shark	Shortfin mako shark
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	861	178	93
1998*	923	187	66

*Preliminary

Dover sole (*Microstomus pacificus*), thornyheads (*Sebastolobus* spp.), sablefish (*Anoplopoma fimbria*), rockfish (*Sebastes* spp.), and Pacific whiting (*Merluccius productus*) continue to dominate the harvest. The 1998 harvest of most species or species groups was off sharply from that of the previous three years, although landings of splitnose rockfish (*Sebastes diploproa*, "rosefish") increased dramatically. Many of the declines, particularly those for sablefish and lingcod, reflect increasingly restrictive PFMC landing limitations; other declines may be related to the strong 1997–98 El Niño event. Paradoxically, the large increase in splitnose rockfish landings, a species normally found on the continental slope, reflects their increased availability on the continental shelf during the northern propagation of a strong El Niño signal along the West Coast. The drop in sablefish landings was responsible for more than half of the decline in total groundfish ex-vessel revenues.

Most of the groundfish landed in California is taken by bottom and midwater trawl gear. In 1998, 88% of the groundfish landed was taken by those gears; a slight increase from 86% in 1997. Line gear accounted for the second largest percentage, 10%, a decrease from 12% in 1997, 15% in 1996, and a high of 18% in 1992. The gill and trammel net component is now stable at just under 1% after a steady decline from 5% in 1993. Traps account for approximately 1% of total groundfish landings.

For 1998, the PFMC maintained harvest guidelines (HG) for Dover sole, shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*Sebastolobus altivelis*), the *Sebastes* complex, widow rockfish (*Sebastes entomelas*), yellowtail rockfish (*Sebastes flavidus*), and canary rockfish (*Sebastes pinniger*). In addition, commercial harvest guidelines (CHG) were set for Pacific whiting, sablefish, bocaccio, and lingcod (*Ophiodon elongatus*). In the case of Pacific whiting and sablefish, CHG do not include that portion of the total allowable catch assigned to Washington treaty Indian tribes. For lingcod and bocaccio, CHG do not include the portion set aside for the recreational fishery. The PFMC again 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 in order to meet its objective of staying within the annual HG or CHG while providing a year-round fishery.

During 1998, stock assessments were prepared for sablefish, shortspine thornyhead, blackgill rockfish, chilipepper rockfish, and Pacific ocean perch by stock assessment teams and then reviewed by three stock assessment review (STAR) panels at public workshops. The Groundfish Management Team then developed recommendations based on the scientific information forwarded by the STAR panels. Assessments planned for 1999 include bocaccio, cowcod, canary rockfish, petrale sole, and southern lingcod.

In 1999, the PFMC will continue to investigate a program to reduce capacity in the groundfish industry, and the feasibility of a comprehensive observer program for groundfish. The PFMC will also reexamine rockfish harvest policies and adopt rebuilding plans for bocaccio rockfish and lingcod. Allocation of lingcod and rockfish within the limited entry fishery and between the commercial and recreational fisheries will continue to be evaluated.

SWORDFISH AND SHARKS

Swordfish (*Xiphias gladius*) landings totaled 923 t in 1998 (table 5), 7% higher than in 1997. During the past decade, the drift gill net fishery has accounted for the majority of the catch. In 1998, 59% of the catch was taken with drift gill nets, up slightly from 53% in 1997. Longline landings made up 32% of the catch. Fifteen vessels used longline gear outside the U.S. Exclusive Economic Zone (EEZ) and landed swordfish in south-

TABLE 6
Landings (Metric Tons) of Top Ten Nearshore Finfishes in California in 1998

	California		Northern California	Central California	Southern California
Market category	t	Value ($1,000's)	t	t	t
Cabezon	152	1,067	31	121	<1
Black rockfish	84	103	66	18	<1
Gopher rockfish group[a]	67	395	4	63	<1
Bolina rockfish group[b]	62	270	3	59	<1
California sheephead	56	341	<1	1	55
California scorpionfish	45	168	0	<1	45
Blue rockfish	41	56	21	20	<1
Grass rockfish	35	369	5	31	0
Lingcod[c]	29	79	8	22	<1
Copper rockfish	22	60	15	6	<1
Subtotal	593	2,908	153	342	101
Other fishes	77	341	22	38	13
Grand total	670	3,249	175	380	114

Source: Preliminary 1998 CDFG market receipt landing data.
[a] Includes market category gopher rockfish.
[b] Includes market category brown rockfish.
[c] Only live landings; January–July 1998.

ern California ports. Only three of these vessels, however, were based in California. Harpoon landings were down, constituting only 4% of the catch. Fifty-six percent of the swordfish catch was landed in southern California ports.

Gear type affected swordfish ex-vessel prices. Typically, fishermen landing swordfish caught with either drift gill nets or longlines received $1.50 to $5.00 per pound, although the average price for drift gill net fish ($2.99) was nearly $0.25 higher than for fish caught on longlines. Fishermen landing harpoon-caught swordfish received the highest average price—$5.85 per pound, with a range of $2.75 to $7.50 per pound.

Common thresher shark (*Alopias vulpinus*) landings totaled 187 t in 1998 (table 5), increasing 5% from 1998. Thresher shark were taken primarily with drift gill nets (78%), followed by set gill nets (18%) and other assorted gears (4%). Most landings (73%) were made in southern California. Typically, ex-vessel price varied from $0.40 to $2.75 per pound, with an average of $1.36.

Shortfin mako shark (*Isurus oxyrinchus*) landings in 1998 were 66 t (table 5). Although this is a decrease of nearly 30% from 1997, it shows a return to the pre–El Niño levels seen in 1995 and 1996. Most of the catch (74%) was landed in southern California ports, at ex-vessel prices between $0.50 and $2.25 per pound, with an average of $1.12. Mako sharks were also caught primarily by the drift gill net fishery (79%). The remainder of the catch was landed with set gill nets (9%), hook and line gear (4%), longline vessels operating outside the EEZ (4%), and as incidental catch from other gears (4%).

NEARSHORE FINFISHES

California commercial landings of nearshore live and premium marine finfishes were 670 t (417 t live) in 1998, with an ex-vessel value of approximately $3.2 million ($2.7 million live; table 6). Nearshore species were defined in the Nearshore Fisheries Management Act (NFMA) of the MLMA of 1998. The NFMA includes as nearshore finfishes: rockfish (genus *Sebastes*), California sheephead (*Semicossyphus pulcher*), greenlings (genus *Hexagrammos*), cabezon (*Scorpaenichthys marmoratus*), California scorpionfish (*Scorpaena guttata*), and other species found primarily in rocky reef or kelp habitat in nearshore waters.

The principal goal of this nontraditional fishery is to deliver fish live to the consumer in as timely a manner as possible. Trucks or vans equipped with aerated tanks are used to transport fish directly to buyers. Many fishers deliver and sell their own catch. All of these elements have complicated the required documentation of landings.

Ex-vessel prices for live and premium fish ranged from $0.20 to $12.00 per pound, with an average of $2.50 per pound. Prices vary with the condition and size of the fish. Many fish do not survive the rigors of capture and transport and are sold dead, sometimes at greatly reduced prices. Some buyers purchase only live fish. Dead fish may be sold to other buyers, taken home for personal use, or discarded. This fishery has increased substantially since 1988, and continues to supply California's Asian communities with live and premium quality fishes. Before 1988, the price per pound for line-caught rockfish ranged from $0.50 to $1.50. The impetus of this fishery is the unprecedented high price paid for live fish.

TABLE 7
Number of Fishers Landing Nearshore Finfishes in 1998

	Number of fishers[a]			
Total landings (kg)	California	Northern California	Central California	Southern California
<50	323	58	198	80
50 to 499	341	71	182	93
500 to 4,999	206	56	113	38
>5,000	31	8	19	4
Total	901	193	512	215

Source: Preliminary 1998 CDFG market receipt landing data.
[a]Some fishers operate in more than one area.

TABLE 8
Percentage of Annual Landings of Nearshore Finfishes by Gear Type in 1998

Gear type[a]	California	Northern California	Central California	Southern California
Line	72	97	80	34
Trap	22	<1	18	45
Net[b]	3	2	2	15
Dive	<1	0	0	5
Other	<1	<1	<1	1

Source: Preliminary 1998 CDFG market receipt landing data.
[a]Some fishers may use more than one gear type during a trip.
[b]Includes trawl and other net types.

Vessels of the nearshore fishery ranged in size from 8 ft (kayak) to 67 ft, with an average of 26 ft. Larger vessels may serve as mother ships for several smaller skiffs. Some fishers fish from shore. In 1998, 802 fishers made at least one landing of nearshore fishes, but the most active participants (landings of at least 500 kg during the year) numbered only 237 (table 7). These active fishers landed 90% of the total statewide landings.

Nearshore fishes were caught with a variety of gear types including line, trap, and net, as well as by divers. Line gear was the reported method of take for 72% of the statewide landings (table 8). Hook and line gear included rod and reel; horizontal and vertical set lines; pipes (sticks) consisting of short (4–8 ft) sections of PVC pipe (rebar or cable) with up to 15 (typically 5) hooked leaders attached; and groundfish troll lines. Fishers traveled farther from their home ports and explored more remote fishing grounds as the demand for live and premium fishes continued and the resources close to ports declined.

Fish landings are often recorded by market categories, not individual species. This is an important consideration when attempting to describe landings by species. Commercial landings are reported in market categories that include specific (e.g., cabezon) and nonspecific (e.g., small rockfish group) categories. Markets typically buy fish in groups based on value, not species. In 1998, CDFG sampling of market categories indicated that specific categories may contain from one to seven species, while nonspecific categories may contain from three to twelve species. For example, market sampling in Morro Bay found the species composition of market category cabezon to include cabezon, grass rockfish (*S. rastrelliger*), kelp greenling (*Hexagrammos decagrammus*), and copper rockfish (*S. caurinus*).

Approximately one hundred market categories of marine fishes were documented as landed live in 1998. Only twenty-nine categories are included in this review: eighteen rockfish, five targeted species, and six incidental categories. Four categories (red, unspecified, and small rockfish groups; as well as lingcod) included both nearshore and offshore catches. Only live fish were included from these four categories.

Landings of cabezon, black rockfish (*S. melanops*), gopher rockfish (*S. carnatus*) group, bolina rockfish group, California sheephead, and California scorpionfish categories dominated the harvest with 466 t (304 t live), 70% of statewide landings, with an ex-vessel value of $2.3 million ($2.0 million live; see also table 6).

Northern California (port complexes of Eureka and Fort Bragg) landings totaled 175 t (61 t live), 26% of statewide landings, with an ex-vessel value of $550,000 ($374,000 live). Landings were dominated by black rockfish, cabezon, blue rockfish (*S. mystinus*), copper rockfish, lingcod, China rockfish (*S. nebulosus*), and vermilion rockfish (*S. miniatus*) categories, which accounted for 82% of the area's landings. Line gear caught 97% of the landings.

Central California (port complexes of Bodega Bay, San Francisco, Monterey Bay, and Morro Bay) landings totaled 380 t (280 t live), 57% of statewide landings, with an ex-vessel value of $2.2 million ($1.9 million live). Central California landings were dominated by cabezon, gopher rockfish group, bolina rockfish group, grass rockfish, lingcod, and blue rockfish categories, which accounted for 83% of the area's landings (table 6). The port of Morro Bay was number one in both landings (131 t, 20%) and ex-vessel value ($973,000, 30%) statewide. Line gear caught 80% of the landings, followed by trap gear at 18%.

Southern California (port complexes of Santa Barbara, Los Angeles, and San Diego) landings totaled 114 t (75 t live), 17% of statewide landings, with an ex-vessel value of $548,000 ($423,000 live). Landings were dominated by California sheephead, California scorpionfish, kelp greenling, and leopard shark (*Triakis semifasciata*) categories, which accounted for 95% of the area's landings (table 6). Trap gear caught 45% of the landings, followed by line gear at 34% and net at 15%.

The MLMA of 1998 represents a fundamental and significant change in the way California's marine resources are to be managed. The act transfers management authority for nearshore fisheries from the legislature to the Fish and Game Commission, mandates the development of a nearshore fishery management plan by 1 September 2002, and authorizes the Fish and Game Commission to adopt regulations implementing the plan. The act also implements commercial size limits for ten nearshore species.

The MLMA requires all commercial fishing vessels to be commercially registered through the CDFG and requires the possession of a Nearshore Fishery Permit to take, possess, or land any of the ten species. Additionally, federal regulations require that groundfish species for which there is a size limit be sorted prior to weighing and the weight reported separately on the Fish and Game receipt. This is an important first step to help biologists more accurately estimate by species the number and pounds of fishes being removed from the nearshore ecosystem.

If these regulations are to be effective in protecting the nearshore fishes, it is essential that fishers and buyers be educated in (1) identification of species; (2) the importance of size limits and their purpose to allow more fish to reproduce before being harvested; (3) the basic biology of nearshore fishes, especially the rockfishes, which are slow-growing, long-lived, residential, and have irregular recruitment patterns. Other essential elements include rigorous enforcement of regulations and verification of species composition in market categories with market sampling. In all, the act will aid in the proper management and conservation of the complex nearshore ecosystem. In addition to state regulations, federal groundfish regulations apply to most of the species targeted in the nearshore fishery, except for California sheephead.

ABALONE

The commercial and recreational abalone fisheries were closed by the Fish and Game Commission in 1997. Subsequently, the California legislature established a moratorium on the fishery south of San Francisco, including the Farallon Islands. The recreational fishery in northern California was not included in this closure. The legislation (SB463) included a requirement that the CDFG develop a management plan for abalone by 2003. The legislation also established a $12 recreational abalone stamp with funds earmarked to a dedicated abalone account. Monies will be used to fund new biologist and wildlife protection positions, in addition to abalone research.

The northern California recreational fishery has not been closely monitored since 1994 because of a lack of personnel, but the legislation has resulted in new staff, so surveys and creel censuses will be resumed in 1999. In southern California, surveys have continued while the fishery is closed.

Black abalone have disappeared from southern California coastal areas. Central California still has small populations of older individuals. Juveniles have not been observed recently, probably because of higher seawater temperatures during El Niño. Withering syndrome has been found as far north as Carmel Bay, its spread probably influenced by increased seawater temperatures. Island populations have continued to decline as a result of withering syndrome and fishing pressure, and some sites are now totally without black abalone. Although the final testing of the pathogen is not completed, it appears that withering syndrome can be attributed to an undescribed rickettsial bacteria that interferes with food absorption.

Red abalone have virtually disappeared from the southern California coast. The only remaining adult aggregations occur off San Miguel Island, and a few are still found at Santa Rosa Island. Surveys at San Miguel Island indicate that only 5% of individuals are of commercial legal size (if the fishery were open). Withering syndrome has been found in populations of red abalone at San Miguel Island. Central coast populations of red abalone are generally small and restricted to crevices and protected areas, but they occur in large numbers at some locations. The central coast is within the range of the sea otter, and the fishery there is not expected to recover.

Pink abalone have disappeared from most southern California coastal areas, and population numbers are down at the Channel Islands. Surveys reveal that many of the remaining individuals are not sufficiently aggregated for effective reproduction. Populations were probably also affected by poor giant kelp productivity during the recent El Niño.

Green abalone have virtually disappeared from coastal areas, and populations are at very low levels at the Channel

Islands, where withering syndrome has had a severe impact. Because this species has narrow geographic and depth distributions (subtidal to about 8 m deep) there is concern about the continued existence of this species in southern California.

White abalone was listed as a candidate for consideration as threatened or endangered under the Endangered Species Act by NMFS. The status of white abalone is being reviewed. Recent surveys have found few individuals remaining in southern California, and those are solitary and reproductively ineffective.

During 1998, about 100 sea otters moved into southern California between Point Conception and Santa Barbara. These animals are mostly males, which range great distances. They will move back into their northern territory during the mating season, but will probably return to southern California again later. Persistent occupation and continued immigration into southern California could have serious ramifications for the recovery of the abalone resource and for other invertebrates as well. Several abalone species, including green, pink, and possibly white, are at such low densities that continued foraging by sea otters—in combination with the cumulative effects of predation, environment, and anthropogenic factors—could extirpate them.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1997–98 season totaled 5,136 t, an increase of 3,327 t from the previous season, and higher than the ten-year average of 4,339 t.

In northern California, the crab season opened on 1 December after a price settlement of $1.35 per pound. By mid-February the price peaked at $3.00 per pound. A fleet of 308 vessels landed approximately 3,518 t in northern California, including 1,489 t at Crescent City, 345 t at Trinidad, 1,188 t at Eureka, and 496 t at Fort Bragg.

The San Francisco–area Dungeness crab season opened on 15 November, but fishing was delayed until a price settlement of $2.00 per pound was reached on 17 November. Total crab landings increased by 801 t from the previous season, to 1,580 t. Crab fishers landed 644 t at Bodega Bay and Bolinas, and 936 t at ports in San Francisco Bay and Half Moon Bay. Monterey and Morro Bay fishers contributed 38 t to the statewide landings.

SPOT AND RIDGEBACK PRAWN

Preliminary 1998 ridgeback prawn (*Sicyonia ingentis*) landings totaled 185 t. This represented a 6% increase in landings from the 174 t landed in 1997 (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. Thirty-five trawl vessels landed ridgeback prawn in 1998. All of the landings were made in southern California ports, and over 98% of all ridgeback prawn were caught within the Santa Barbara Channel. The proportion of ridgeback prawn landed live has increased steadily since 1994. Live ridgeback prawn constituted 65% of total ridgeback landings in 1998, matching the proportion of live ridgeback prawn in the 1997 landings. The average ex-vessel price paid for all ridgeback prawn was $1.80 per pound. Live ridgeback prawn sold for an average of $2.00, dead ridgeback prawn for an average ex-vessel price of $1.50 per pound.

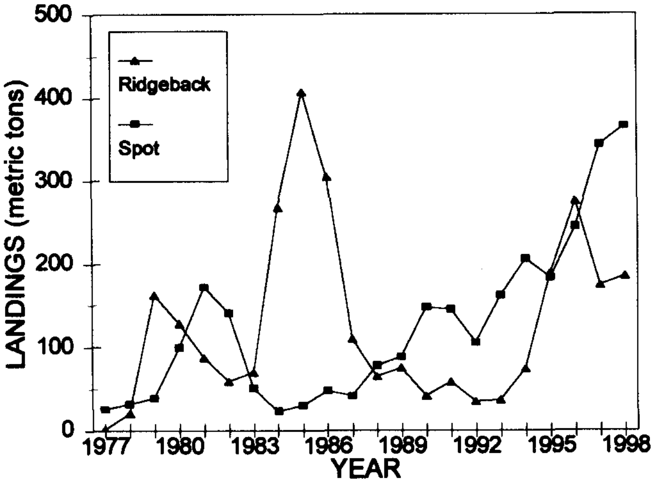

Figure 5. California ridgeback and spot prawn landings, 1977–98.

Preliminary 1998 spot prawn (*Pandalus platyceros*) landings were 365 t, a 6% increase over the 343 t landed in 1997 (table 9). Spot prawn landings have trended upward over the last ten years (fig. 5). Spot prawn are caught with both trap and trawl gear. A total of 102 vessels (57 trap and 45 trawl) made landings in 1998; table 9 shows types of gear and landings for spot prawn by port area. Note that some trap and trawl vessels fished in several different port areas during the year. Of the combined trap and trawl spot prawn landings in 1998, 57% were made in the Santa Barbara port area.

In the past, spot prawn were caught primarily with trap gear. More vessels have been using trawl gear since the mid-1970s, and their landings now dominate the fishery. In the last ten years the number of spot prawn trawlers has increased rapidly with an influx of vessels from other groundfish fisheries that have quota or seasonal restrictions. Approximately 257 t of spot prawn were harvested by trawl in 1998; 108 t were taken with trap gear (table 9).

Spot prawn are considerably larger than ridgeback prawn and command a much higher ex-vessel price, averaging $6.30 per pound. Live spot prawn had an average ex-vessel price of $7.50, and prices ranged as high

TABLE 9
1998 California Spot Prawn Landings (Metric Tons) by Port Area and Gear Types

Port areas	Number of fishing vessels by gear type: Trap	Number of fishing vessels by gear type: Trawl	Spot prawn landings: Trap	Spot prawn landings: Trawl	Spot prawn landings: Totals	Percentage of Total
Eureka	3	5	0.4	2.1	2.5	0.6
San Francisco	0	17	0.0	52.2	52.2	14.0
Monterey	10	12	26.7	17.2	43.9	12.1
Santa Barbara	11	36	22.9	184.0	206.9	57.0
Los Angeles	29	2	45.2	1.1	46.3	12.7
San Diego	14	0	13.0	0	13.0	3.6
Totals	67	72	108.2	256.6	364.8	100.0

as $9.00. Dead spot prawn sold for an average of $3.50 per pound. Approximately 72% of all spot prawn were sold as live product.

In 1998, the trap and trawl spot prawn permit fisheries in southern California (south of Point Arguello) operated under concurrent closures that ran between 1 November 1997 and 31 January 1998. Regulations were enacted in 1997 that changed the southern California trap and trawl seasonal closures to provide more protection for gravid female spot prawn. Previously, the trap closure in southern California ran between 15 January and 31 March, and the trawl closure ran between 1 November and 16 January.

OCEAN SALMON

In 1998, the PFMC again enacted restrictive commercial and recreational ocean salmon regulations in California to achieve (1) the escapement goal range for Sacramento River fall chinook salmon (*Oncorhyncus tshawytcha*) of 122,000 to 180,000 hatchery and natural adults combined; (2) a 9% exploitation rate on age-4 Klamath River fall chinook to accommodate inriver recreational and tribal subsistence and commercial fisheries, as well as a minimum adult natural spawning escapement of 35,000; (3) a 31% increase in escapement of Sacramento River winter chinook; and (4) a reduction in harvest impacts on depressed coho salmon (*Oncorhynchus kisutch*) stocks coastwide.

In 1998, 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 793 t (216,200 fish) of dressed chinook were landed by commercial trollers, who fished approximately 12,000 days (fig. 6). Ex-vessel prices for dressed salmon averaged $1.59 per pound, and the total ex-vessel value of the fishery exceeded $2.7 million.

Recreational fishing regulations in California were less restrictive than in 1997, with various time and area closures (14 February to 15 November). Statewide recreational landings decreased by almost 47% compared to the previous year (fig. 7), totaling 121,400 chinook during 149,900 angler trips (catch per unit angler = .81). 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 7 September between Point

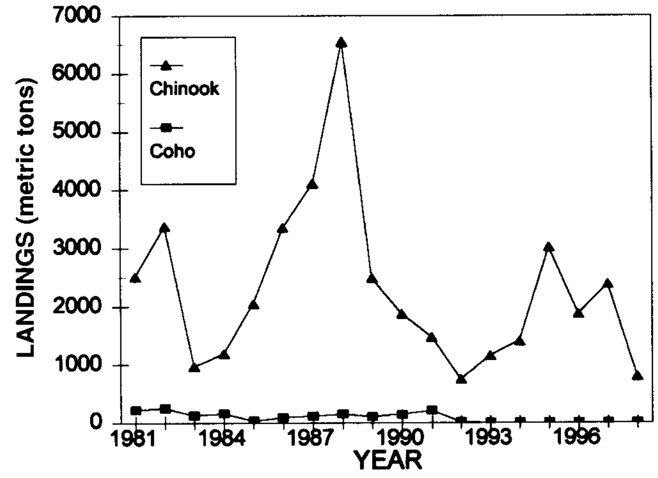

Figure 6. California commercial salmon landings, 1981–98.

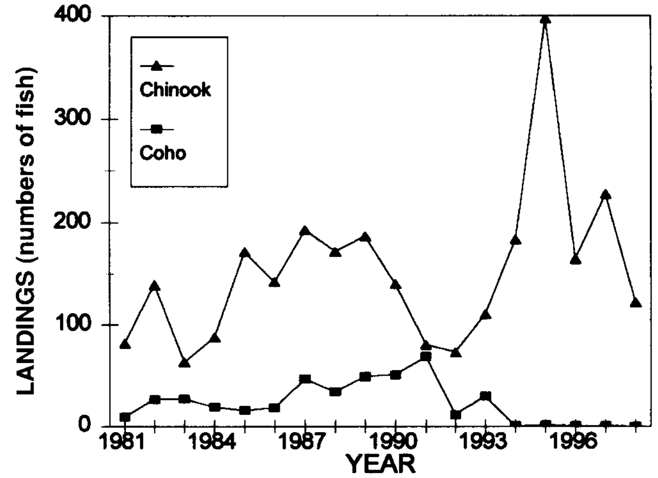

Figure 7. California recreational salmon landings, 1981–98.

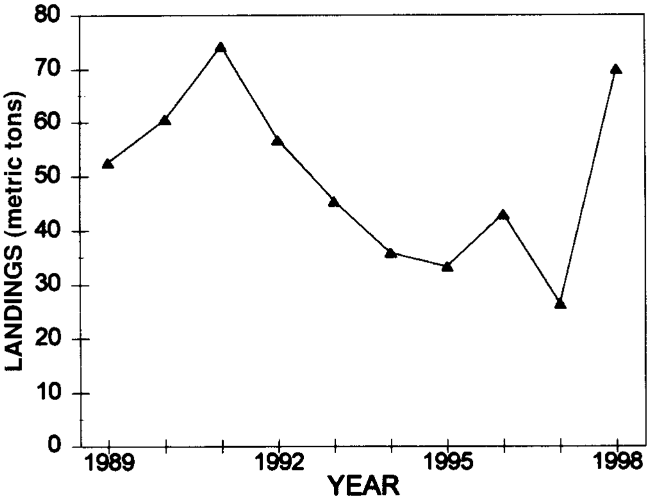

Figure 8. California commercial white seabass landings, 1989–98.

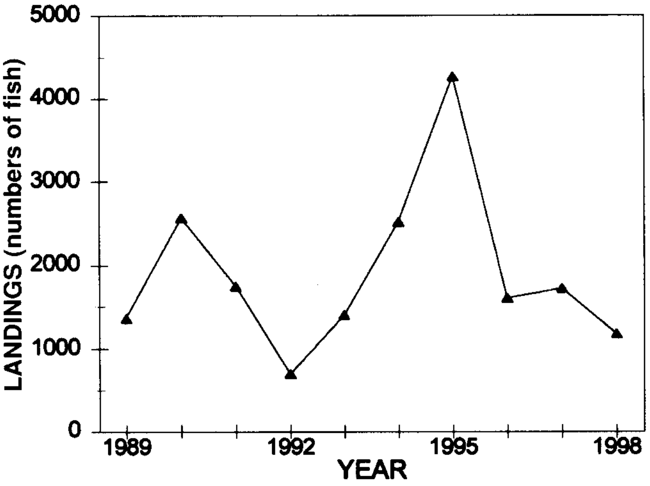

Figure 9. Landings of white seabass by California CPFVs, 1989–98.

Reyes and Pigeon Point, where anglers were required to keep the first two salmon regardless of size. Anglers fishing by any means other than trolling in the area between Point Conception and Horse Mountain were required to use only "circle" hooks.

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 Klamath fall chinook. In the KMZ, three separate seasons, open seven days a week, were enacted: 23 May to 10 June, 21 June to 5 July, and 11 August to 13 September. The bag limit was one salmon per day (all species except coho) with no more than 4 salmon in 7 consecutive days; there was a 20-inch TL limit north of Horse Mountain. In the California portion of the KMZ, anglers landed 2,900 chinook during 10,000 angler trips made primarily on private skiffs.

WHITE SEABASS

The commercial take of white seabass (*Atractoscion nobilis*) increased to 70 t in 1998 from 26 t in 1997 (fig. 8). Sixty-one percent of the catch was delivered to Terminal Island and San Pedro, 18% to Morro Bay and Port San Luis, 16% to Santa Barbara and Channel Islands Harbors, and 8% to ports in San Diego County. The 1997–98 El Niño event was probably responsible for the increased availability of white seabass to the commercial fishery.

Gill net gear was the reported method of take for 92% of the catch in 1998; hook and line gear was used to take 4%; trawl nets took 2%; and 2% was taken by miscellaneous gears. Data on catch location from gill net logs indicate that most of the effort occurred in the Huntington Flats area (56%) and in the closer islands (Anacapa, Santa Cruz, and Santa Rosa).

Commercial statutes prohibit taking white seabass in California water south of Point Conception between 15 March and 15 June. As in past years, much of the catch was landed soon after the fishery reopened in June. Fifty-two percent of the catch was landed after 15 June through the end of July.

The average ex-vessel price was $1.92 per pound (the 1997 value was $2.27). The threefold increase in landings from 1998 probably contributed to the overall decline in price.

Recreational catches reported on CPFV logs show 1,176 white seabass taken by anglers (fig. 9). This is a decrease of 547 fish from the reported catch of 1,723 in 1997. The ten-year average number of white seabass taken on CPFVs is 1,994. The scarcity of squid, a preferred bait for white seabass, and excellent fishing opportunities for yellowtail are probably why recreational anglers reported a lower catch of white seabass.

The Ocean Resources Enhancement and Hatchery Program (OREHP) released 32,000 fish in 1998 at eleven sites between San Diego and Santa Barbara, including Catalina. Since 1990, 281,000 hatchery-produced juvenile white seabass have been released. It takes four to five years for a white seabass to reach the legal size limit of 28 inches TL for the commercial and recreational fisheries. Staff of the CDFG and the Hubbs–Sea World Research Institute conducted a preliminary commercial market sampling program to detect if sampled white seabass contained a coded-wire tag (CWT) to indicate that the fish were a product of the OREHP hatchery in Carlsbad. In addition, several fishery technicians conducting a recreational fishing survey also checked for the presence of a hatchery CWT. No CWT was found in any of the 560 commercial fish or 7 recreational fish sampled. Eight white seabass taken during a broodstock collection effort in the fall of 1998 had CWT inserts. They

TABLE 10
Southern California CPFV Landings (Number of Fishes) in 1998 and 1997

Species/species group	1998 landings*		1997 landings		Percent change
	Number	Rank	Number	Rank	
California barracuda	442,465	1	334,626	5	+32
Barred sand bass	368,180	2	489,966	1	−25
Rockfishes, unspecified	350,315	3	397,387	3	−12
Yellowtail	232,680	4	398,345	2	−42
Kelp bass	224,251	5	335,126	4	−33
Albacore	143,684	6	71,503	11	+101
Pacific (chub) mackerel	120,954	7	224,721	6	−46
California scorpionfish	115,426	8	141,350	7	−18
Ocean whitefish	67,096	9	87,525	10	−23
Yellowfin tuna	64,473	10	89,080	9	−28
Pacific bonito	54,688	11	102,468	8	−47
Bluefin tuna	18,091	12	7,959	18	+127
California sheephead	17,753	13	25,782	14	−31
Skipjack tuna	11,663	14	19,156	15	−39
Halfmoon	7,833	15	51,092	12	−85
White croaker	6,212	16	9,332	17	−33
Dolphinfish (dolphin)	5,344	17	28,606	13	−81
California halibut	4,669	18	7,880	19	−41
Wahoo	4,131	19	3,844	23	+7
Lingcod	3,367	20	6,474	21	−48
Flatfishes, unspecified	3,243	21	9,752	16	−67
Jack mackerel	3,175	22	5,485	22	−42
White seabass	1,176	23	1,723	24	−32
Blacksmith	815	24	7,245	20	−89
Cabezon	740	25	1,468	25	−50
All others	9,590	—	26,992	—	—
Total number kept	2,282,014		2,884,887		−21
Number of anglers	546,875		635,803		−14
Reporting CPFVs	246		235		+5

*Preliminary

ranged in TL from 15 to 25 inches and had been released from 1996 through 1998. The fish will not be used as broodfish.

RECREATIONAL FISHERY

Southern California

Hook and line saltwater recreational fishing is conducted from private vessels, piers, shorelines, and CPFVs in southern California. Specific information about these recreational fisheries is collected through phone surveys and field samplers (Marine Recreational Fisheries Statistics Survey, NMFS). In addition, the CDFG collects and maintains a large database derived from mandatory logbook information supplied by CPFVs. Much of our knowledge of CPFV recreational fishing in southern California is based on these logbook 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 California 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. Conversely, La Niña conditions may cause an increased catch of colder-water species. Anglers are typically quick to exploit the fishing opportunities provided by these changing oceanographic conditions.

Throughout much of 1998, sea-surface temperatures (SSTs) in the coastal zone off southern California and Baja California remained above normal (e.g., SST anomalies for July 1998 exceeded 2.4°C in parts of the Southern California Bight). However, SSTs offshore and to the north and south of this area began to slowly decrease. As a consequence, landings continued to be high for subtropical species such as yellowfin tuna and yellowtail, but they also included substantial increases in California barracuda, albacore, and bluefin tuna (table 10).

In 1998, 546,875 anglers aboard CPFVs landed 2,282,014 fishes south of Point Conception (table 10). The number of reporting CPFVs was 246. The number of fishes landed represents 72% of the total landings by

CPFVs statewide (3,155,995 fishes). The number of fishes landed statewide was 18% lower than in 1997; landings in southern California decreased by 21%. The number of anglers using southern California CPFVs dropped by 14% from 1997, and represented 81% of anglers using CPFVs statewide.

In contrast to 1997, the 1998 landings of California barracuda in southern California exceeded those of all other species, increasing by 32% (table 10). Barred sand bass, which ranked first in 1997, dropped to the second rank. As in 1997, rockfishes ranked third in 1998, but landings decreased from the previous year. Yellowtail dropped from the second rank to the fourth, but compared to 1996, yellowtail landings remained high (232,680 in 1998 compared to 66,763 in 1996). Kelp bass ranked fifth, with landings down by 33%. Albacore moved from the eleventh rank to the sixth rank as landings substantially increased. Pacific mackerel landings reported by southern California CPFVs dropped for the second year in a row. California scorpionfish (ranked eighth) and ocean whitefish (ranked ninth) also showed decreases. Yellowfin tuna ranked tenth in 1998, with landings falling by 28%. Similarly, Pacific bonito landings (ranked eleventh) dropped by 47%. The greatest increase in 1998 landings (127%) was shown by bluefin tuna.

Although landings increased dramatically for several species, particularly bluefin tuna, albacore, and California barracuda, landings for most species in table 10 decreased. Blacksmith, halfmoon, and dolphinfish decreased the most, perhaps because CPFVs focused on California barracuda, yellowtail, and highly migratory species such as yellowfin tuna. There were more boat trips into Mexican waters in 1998, although the overall number of trips for southern California (including Mexico) dropped.

The decreases could also be a result of the changing oceanographic environment off of southern California. Landings of subtropical species like dolphinfish, yellowfin tuna, and yellowtail decreased, while landings of species more typical to the area (albacore, California barracuda) increased. Finally, it is possible that the lower numbers result from a reduction in the reporting of CPFV trips. The numbers in table 10 are preliminary and may change as this possibility is examined in more detail.

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, although recent occurrences

TABLE 11
Central and Northern California CPFV Landings (Number of Fishes) in 1998 and 1997

	1998 landings		1997 landings		
Species/species group	Number	Rank	Number	Rank	Percent change
Rockfishes	746,223	1	769,014	1	−3
Chinook (king) salmon	56,392	2	110,446	2	−49
Striped bass	18,679	3	7,365	7	154
Lingcod	16,024	4	29,744	3	−46
Pacific mackerel	8,783	5	16,249	5	−46
Albacore	8,019	6	16,567	4	−52
California halibut	7,233	7	7,964	6	−9
Jack mackerel	2,648	8	3,638	8	−27
Cabezon	1,818	9	1,665	10	9
Flatfishes, unspecified	1,058	10	3,475	9	−70
Sturgeon	649	11	465	13	40
White croaker	464	12	628	11	−26
Leopard shark	397	13	288	14	38
Shark, unspecified	222	14	407	12	−45
California barracuda	97	15	78	16	24
Bluefin tuna	92	16	15	18	513
Kelp bass	59	17	1	—	5900
Ocean whitefish	44	18	130	15	−66
Pacific bonito	31	19	45	20	−31
White seabass	21	20	7	19	200
Dungeness crab	12,733		7,148		78
Rock crab	3,321		3,939		−16
Jumbo squid	1,588		686		131
Other fishes			3,261		−100
Total number kept	871,420		972,438		−10
Number of anglers	130,578		164,356		−21
Reporting CPFVs	129		120		8

of warm water close to the coast have provided good striped bass fishing outside, as well as inside, San Francisco Bay. El Niño conditions in 1997, which caused warm oceanic waters to move near shore, continued into the first half of 1998, with warmer than normal temperatures along the central and northern California coastline. This warm water provided some unusual fishing opportunities.

In 1998, the top ten species or species groups by number of fishes in landings were rockfishes, chinook (king) salmon (*Oncorhynchus tshawytscha*), striped bass, lingcod, Pacific (chub) mackerel (*Scomber japonicus*), albacore, California halibut, jack mackerel (*Trachurus symmetricus*), cabezon, and unspecified flatfishes (table 11). These species or species groups were the same as in 1997, although the order of rank abundance changed. In 1998, 130,578 anglers caught 871,420 fishes, a 10% decrease from 1997, primarily due to decreased landings of chinook salmon, lingcod, Pacific mackerel, albacore, and flatfishes. While albacore landings were lower than in 1997, they were still considerably higher than in the previous eleven years. Landings increased for bluefin tuna (*Thunnus thynnus*), striped bass, sturgeon, and leopard sharks.

Changes in annual landings may reflect shifts in effort among preferred species, or changes in species availability (as for albacore, bluefin tuna, and Pacific mackerel) rather than changes in abundance. Data suggest that white sturgeon abundance in the Sacramento–San Joaquin Estuary during 1998 was the highest since the mid-1980s. There were no appreciable changes in reported catches of rockfishes and California halibut. Recreational anglers were not allowed to take coho (silver) salmon (*Oncorhynchus kisutch*) in 1998.

Warm oceanic water near the coast was responsible for the continued presence of several subtropical and southern California species in northern California, including Pacific bonito (*Sarda chiliensis*), skipjack tuna (*Katsuwonus pelamis*), yellowtail (*Seriola lalandi*), bluefin tuna, dolphinfish (*Coryphaena hippurus*), Pacific mackerel, albacore, white sea bass (*Atractoscion nobilis*), and jumbo squid (*Dosidicus gigas*). Bluefin tuna were one of the only warm-water species whose landings increased over the previous year. It is notable that reports of northward migrations of subtropical pelagic species during the 1982–83 El Niño do not include landings of bluefin tuna off central and northern California. It is possible that landings of bluefin tuna north of Point Conception during the recent El Niño are tied to the increased abundance of Pacific sardines. Most bluefin tuna and Pacific bonito landings were made in September by CPFV anglers fishing as far north as Bodega Bay.

Considerable landings of crab and squid were reported in 1998 (table 11). CPFV anglers caught and kept 12,733 Dungeness (*Cancer magister*) crabs and 3,321 rock crabs (*C. antennarius*) in conjunction with fishing for rockfishes, mainly from the port of Bodega Bay and north. Bodega Bay CPFVs continued to target giant squid while they were still abundant; 1,588 giant squid were reported landed.

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INDEX TO "REVIEW OF SOME CALIFORNIA FISHERIES," 1977–1998

For more than two decades, the California Department of Fish and Game has contributed its "Review of Some California Fisheries" to the annual *CalCOFI Reports*. Although the individual section titles (names of fishes and invertebrates) have not, until now, been included in the table of contents, they have been listed in the periodic general indexes covering all *CalCOFI Reports* (in volumes 24, 30, and 35). The following index, prepared by Antonella Preti (CDFG, La Jolla) lists all of the section titles from 1977 (volume 20) through 1998 (volume 39). This specialized index for the "Review of Some California Fisheries" is presented as a service to researchers studying past trends. The subjects will continue to be listed in the periodic general *CalCOFI Reports* indexes.

Each entry includes the year being reported, the *CalCOFI Reports* volume number, and page numbers.

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  - 1993, 35:7–8
  - 1994, 36:7–8
  - 1995, 37:7–9
  - 1996, 38:7–9
  - 1997, 39:9–11
- Seabass, white, *Atractoscion nobilis*
  - 1996, 38:18
  - 1997, 39:21–22
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  - 1993, 35:15–16
  - 1995, 37:15–16
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  - 1997, 39:14
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  - 1987, 29:16–17

BROWN SHRIMP FISHERY IN THE GULF OF CALIFORNIA

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There is a well-developed brown shrimp (*Penaeus californiensis*) fishery in the Gulf of California, Mexico, between Bahía Kino, Sonora, and Bahía Agiabampo, Sinaloa. The fishery operates on a single stock over its entire geographic range.

During 22 fishing seasons (from 1976–77 to 1997–98) the catch per unit of effort (CPUE) has fluctuated. Notable are two periods, the first from 1976–77 to 1990–91, during which the CPUE declined, and the second from 1991–92 to 1997–98, during which the CPUE increased (fig. 1). The lowest CPUE occurred during the 1990–91 season (0.04 t × 100).

Effort, principally number of vessels, has varied from about 300 to 500 vessels per season. The fleet declined from a high in 1979–80, and stabilized in 1984–85, with fluctuations between 300 and 350 vessels. This decrease in effort is due to an overcapitalization of the fishery and is regulating access to the fishery.

The fishing season has varied from September to April or from September to May. The difference in the fishing season corresponds to interannual variations in shrimp recruitment to the fishery, possibly related to strong year classes. These strong recruitments have been associated principally with anomalous temperatures such as those during El Niño events.

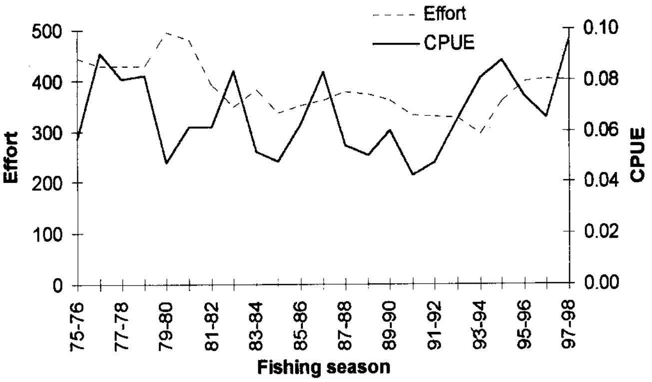

Figure 1. Effort and CPUE for brown shrimp in the Gulf of California, Mexico.

THE STATE OF THE CALIFORNIA CURRENT IN 1998–1999: TRANSITION TO COOL-WATER CONDITIONS

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ABSTRACT

This report reviews and provides a preliminary interpretation of recent observations made by CalCOFI (California Cooperative Oceanic Fisheries Investigations) and other programs sampling the coastal waters of the Californias. Since this is a continuation of a series of annual reports, the emphasis here is upon observations made during the past 18 months, but longer-term trends must also be considered. The major change in oceanographic structure in the past year was the transition from strong El Niño conditions in early 1998 to cool-water, La Niña conditions in early 1999. Ecosystem structure also showed large changes during this period. Phytoplankton abundance during 1998, as indicated by chlorophyll concentration, was typical of the values seen during the last decade, but it appeared to be increasing in early 1999 in association with the transition to cool-water conditions. Macrozooplankton biomass during 1998 continued the long-term trend of low values which have been seen since the mid-1970s regime shift, and El Niño–related changes were superimposed upon this trend. The 1999 macrozooplankton data are not yet available to assess whether biomass is increasing. Observations made at coastal shore stations, in southern California kelp forest communities, in central and northern California, and in Baja California, Mexico, are considered in order to place the CalCOFI observations in a larger regional context. Because this year marks the fiftieth anniversary of the CalCOFI program, we use the discussion to consider future directions for the time-series program and how the CalCOFI data can be put to greater use at the regional, state, and national level.

INTRODUCTION

This is a continuation in a series of reports (e.g., Hayward et al. 1996; Schwing et al. 1997; Lynn et al. 1998) which present and synthesize recent observations in the California Current system. The emphasis is upon data collected during 1998 and 1999. The 1998–99 period was marked by rapid and remarkable changes in physical and ecosystem structure in the study region. Winter and spring of 1998 was a period of strong El Niño conditions in physical and biological structure. The physical influence of El Niño declined during the summer and fall of 1998, and there was a transition to cool-water conditions during the winter of 1998 and the spring of 1999.

Oceanographic programs to the south—sampling off northern Baja California, Mexico—and to the north—sampling off Monterey and the central California coast—are making observations that help to put the CalCOFI time series in a larger regional context, and that allow the influence of El Niño to be examined on larger spatial scales. Observations made at coastal shore stations and in kelp forest communities are being related to CalCOFI time-series observations in order to determine

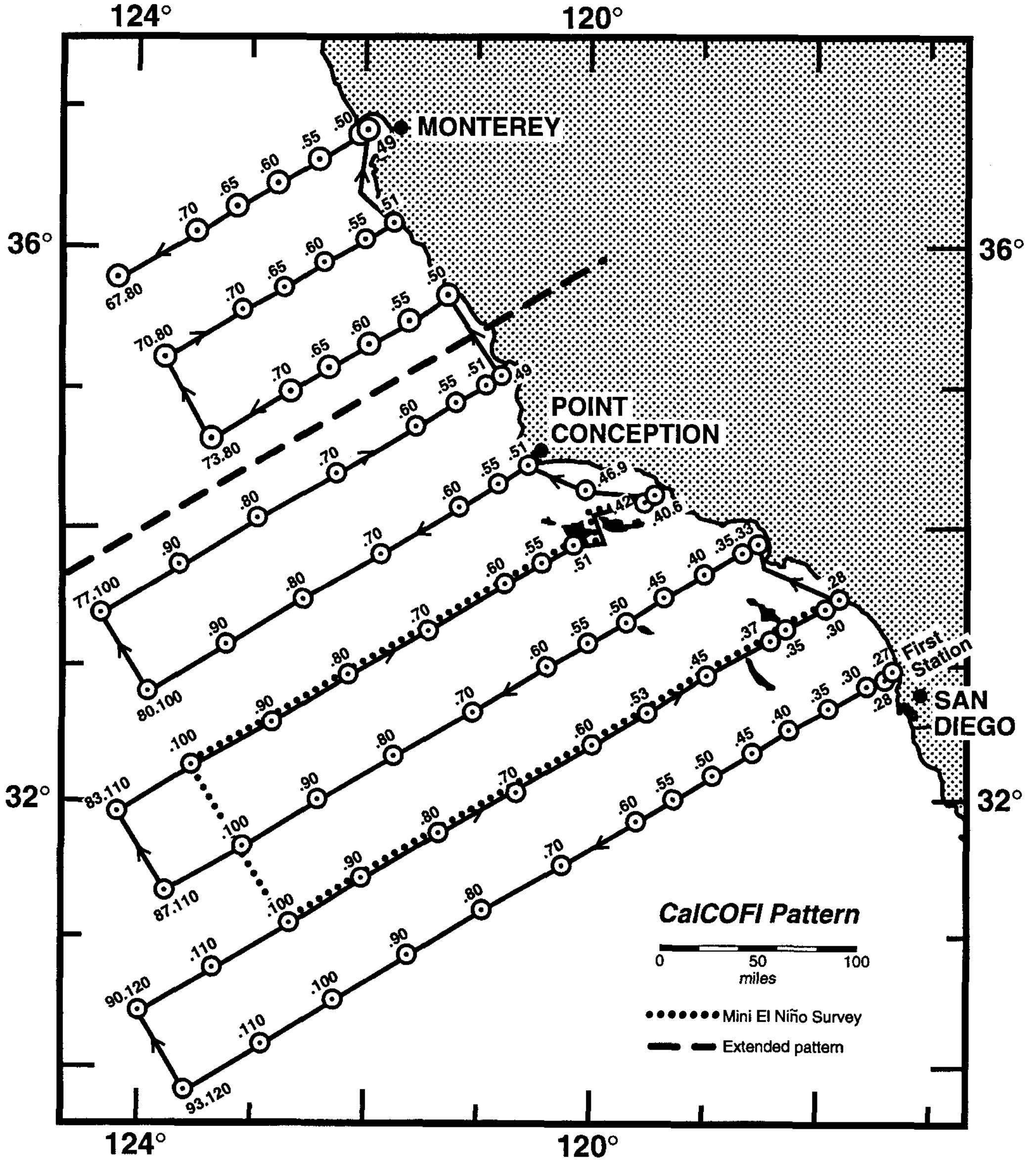


Figure 1. CalCOFI station patterns. The regular 66-station station pattern occupied by CalCOFI since 1985 (lines 77, 80, 83, 87, 90, and 93) is connected with a solid line. The stations for the mini El Niño cruises on lines 83 and 90 are shown with a dotted line. The area of additional underway sampling north of the regular pattern is above the dashed line (lines 67, 70, and 73).

if these regions respond in a similar way to changes in environmental structure and whether the higher-frequency, longer temporal coverage and greater spatial coverage of the coastal shore station data can be used to make inferences about structure in the offshore waters of the California Current.

As in past reports, we highlight the observations and findings of a few of the new types of techniques that are being evaluated in CalCOFI, and the results of some of the cooperative research programs. The 1998–99 period was also marked by the continuation of the process of implementing new observational approaches in the CalCOFI time series. Observations with CUFES (continuous underway fish egg sampler) provide greatly improved spatial resolution of the pattern of fish spawning during this period of rapid change. Implementation of the OPC (optical plankton counter) is providing the basis to determine whether the size spectrum and/or depth distribution of the plankton changes during this period of rapid environmental change.

DATA AND SAMPLING

The observations presented here were obtained from several sources. CalCOFI observations include data from the quarterly survey cruises and from the additional "mini El Niño" cruises which sampled lines 90 and 83 on RV *Robert Gordon Sproul* from December 1997 to January 1999 during months that did not include a normal time-series cruise (fig. 1). CalCOFI cruises are designated by year and month. CalCOFI stations are designated by line

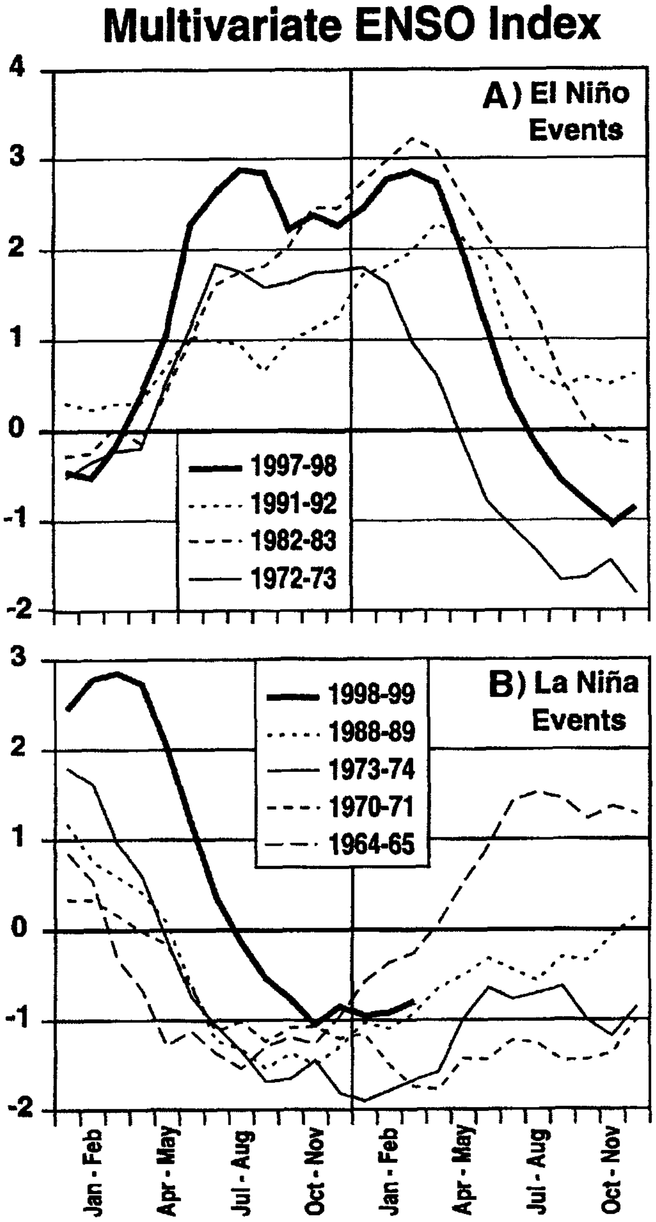


Figure 2. A monthly multivariate ENSO index, or MEI (Wolter and Timlin 1998). MEI indicates the intensity of (*A*) the 1997–98 El Niño relative to three recent strong El Niño events, and (*B*) the 1998–99 La Niña relative to four recent La Niña events.

and station number. Cruise patterns, methods, and data from the CalCOFI time-series cruises are published in data reports (Scripps Institution of Oceanography 1999), and this information is also available on the World Wide Web (*http://www-mlrg.ucsd.edu/calcofi.html*). Methods and data sources for data from other programs are briefly listed as the observations are presented.

OBSERVATIONS

Atmospheric Conditions

During 1998–99, many atmospheric and ocean fields in the equatorial and north Pacific, including sea-level pressure (SLP), wind stress, and sea-surface temperature (SST), typified classic El Niño and La Niña patterns (cf. Murphree and Reynolds 1995). In the tropical Pacific, 1998 was marked by a dramatic transition from one of the strongest El Niño events this century to a strong La Niña event. The multivariate ENSO index (MEI; Wolter and Timlin 1998) shows this change. The MEI dropped from an El Niño peak in spring 1998 to a minimum in late fall 1998 (fig. 2). This decline was unprecedented in the nearly 50-year history of the MEI (fig. 3).

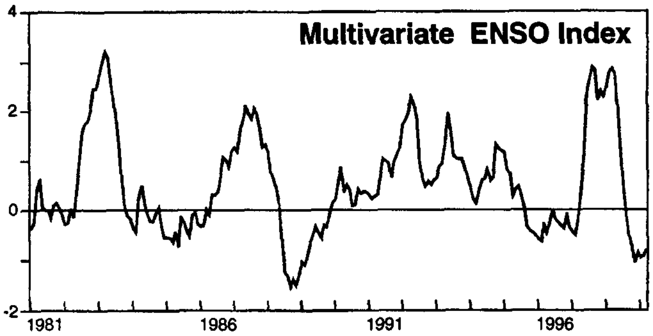


Figure 3. Monthly time series of the multivariate El Niño index, or MEI (Wolter and Timlin 1998), for 1981–98. The series highlights the rapid transition from El Niño to La Niña in 1998.

In early 1998, the 1997–98 El Niño reached a second peak in intensity (fig. 2A; the first having been in summer 1997). The event was clearly affecting the North Pacific Ocean at this time (Lynn et al. 1998). Beginning in March 1998, however, El Niño conditions in the equatorial Pacific weakened considerably (fig. 2B). Negative SST anomalies (SSTAs) developed in the central and eastern equatorial Pacific during May (NCEP 1998a). Anomalously cool subsurface (50–300 m) temperatures extended along the equator from the western Pacific well into the eastern Pacific (NCEP 1998a). This pattern resulted from the eastward expansion of a shoaling thermocline from the western Pacific beginning in July 1997 (NCEP 1997a). This suggested a clear transition toward La Niña conditions in the tropics. Anomalies of SLP (Kalnay et al. 1966) and SST (Reynolds and Smith 1995) for the Pacific illustrate the evolution of this event. SLP and Reynolds SST data were provided by the NOAA-CIRES Climate Diagnostics Center, Boulder Colo., from its Web site (*http://www.cdc.noaa.gov*).

SST anomalies were still characteristic of El Niño conditions during April–May 1998 (fig. 4B). Very warm SST anomalies (+2° to 4°C) extended west from South America along the equator. The North and South American coasts remained unseasonably warm (+1° to 2°), while the central north and south Pacific were unusually cool (−1° to −2°). Cool anomalies in the central north Pacific continued to shift east, as warm anomalies in the Kuroshio extension expanded east across the date line.

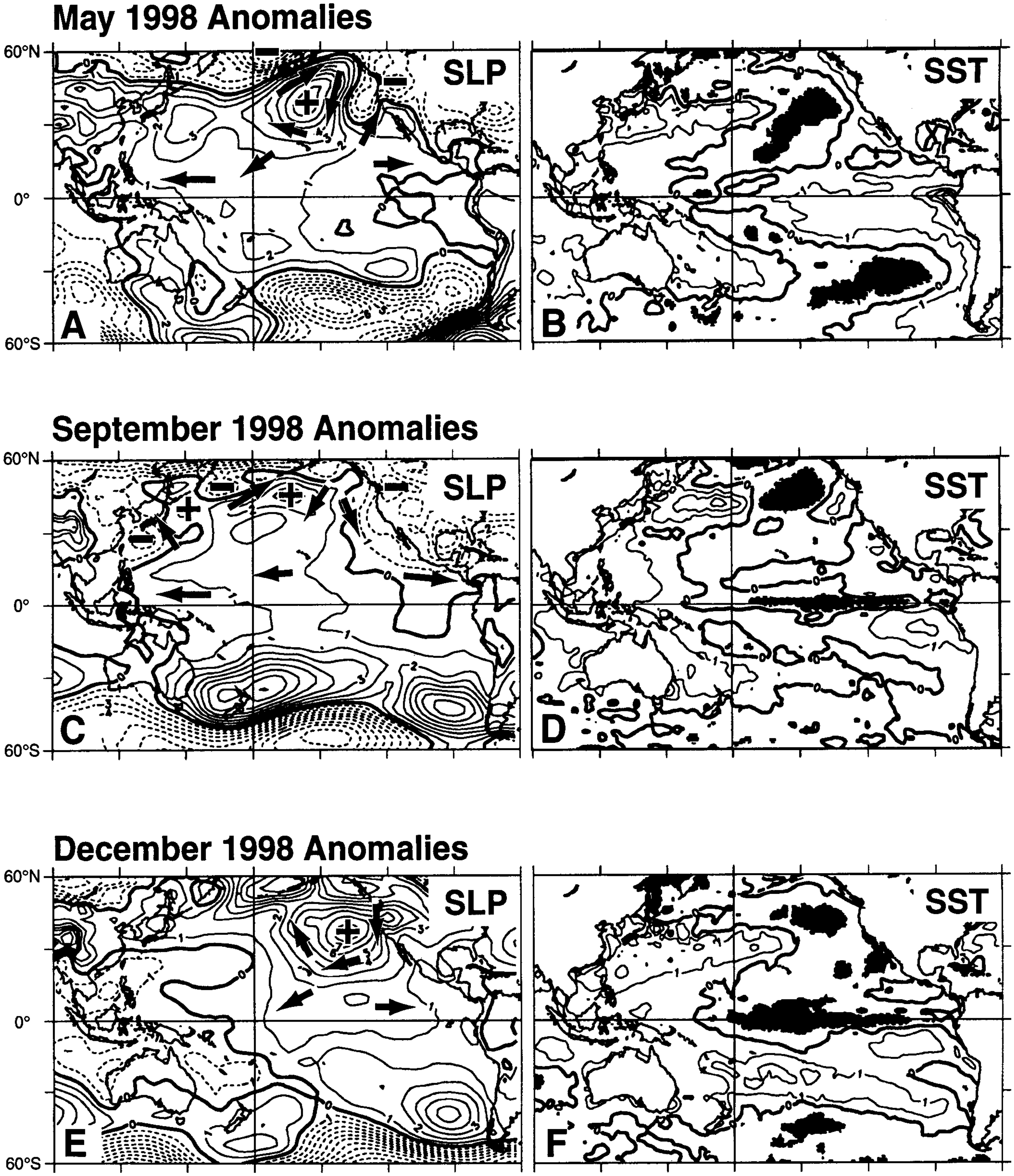


Figure 4. Anomalies over the Pacific Ocean for May, September, and December of 1998: *A*, *C*, and *E*, sea-level pressure (SLP) with anomalous surface wind; *B*, *D*, and *F*, sea-surface temperature (SST). Positive anomalies denote higher than normal atmospheric pressure and warmer than normal SST. Contour intervals are 1 mb and 1°C. Shading denotes SST anomalies greater than −1°. 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. Monthly data were obtained from the Climate Diagnostics Center. The SLP climatology period is 1968–96; the Reynolds SST climatology period is 1950–79.

The North Pacific High (NPH) pressure system is normally unseasonably weak (strong) during El Niño (La Niña) events. The NPH intensified east of the date line during April–May 1998, leading to a positive SLP anomaly in the northeast Pacific (fig. 4A). The resulting trade winds were stronger than usual, a precursor to the developing La Niña. Anomalously strong anticyclonic atmospheric circulation contributed to greater offshore surface Ekman transport near the U.S. west coast, which favored upwelling and cooler SSTs. This atmospheric pattern is likely to produce lower coastal sea level, a shallower thermocline, and increased equatorward flow in the California Current system (CCS). The opposite can be expected during El Niño events.

By early autumn 1998, coastal SSTAs along North and South America had diminished to near normal (fig. 4D). Negative SSTAs extended across the eastern tropical Pacific to near South America. Warm anomalies intensified from Japan to the date line. By October a shift to strong southward wind stress had produced cooler than normal SSTs in the CCS.

Anomalous atmospheric wave train activity emanating from east Asia displayed a pattern of alternating positive and negative centers that arced across the North Pacific (cf. Nitta 1987), as illustrated in figure 4C. This pattern is very reminiscent of a wave train seen in the developing phase of El Niño one year previously (Lynn et al. 1998; fig. 4C), but with the signs reversed. This late summer atmospheric teleconnection pattern in 1998 seems to be responsible for anomalous surface Ekman transports and a complex pattern of positive and negative SST anomalies over the north Pacific.

Trade winds continued to be stronger than normal at this time, a characteristic of La Niña events and counter to the pattern observed during El Niño events. Equatorial wind anomalies were divergent from the central tropical Pacific, again opposite those in the 1997–98 El Niño (Lynn et al. 1998). This divergence may have been partly responsible for the cool equatorial SST anomalies. An unusually shallow thermocline along the equator east of the date line, characteristic of La Niña events, produced negative subsurface temperature anomalies of 5° to 7°C at depths of 50–150 m (NCEP 1998b). A year earlier this region featured a deeper than normal thermocline and positive temperature anomalies of this magnitude.

By late 1998, atmosphere and ocean anomaly fields displayed a classic fully developed La Niña pattern (cf. Murphree and Reynolds 1995). Higher than normal SLP covered most of the north Pacific (fig. 4E). A well-developed North Pacific High, typically dominant only in spring and summer, produced strong anticyclonic winds over the northeast Pacific. This is related to the patterns of atmospheric convection, as reflected by anomalies in outgoing longwave radiation (OLRA). During the latter half of 1998, OLRAs in the central tropical Pacific and the CCS were positive (cf. NCEP 1998c), indicating low convection in these areas. Negative OLRAs and higher than normal convection were observed in the western tropical Pacific and over southeast Asia. The atmospheric flow into and out of these regions of unusual convection feeds into the upper tropospheric jets. The development and maintenance of pressure anomalies in the extratropics are teleconnected to tropical atmospheric anomalies through these jets (Murphree and Reynolds 1995).

Atmospheric flow anomalies are also responsible for redistributing heat and moisture. The unusual distribution of pressure during winter 1998–99 (fig. 4E) displaced the north Pacific jet stream northward. Winter storms favored a track over the northwest United States, bringing unseasonably heavy precipitation to Washington and Oregon, and leaving southern California relatively free of the intense storms experienced in early 1998.

Strong upwelling-favorable winds along the U.S. west coast associated with the strong NPH contributed to SSTs more than 1°C below normal (fig. 4F). SSTs up to 2° below normal stretched along much of the equator. Positive SSTAs covered the north Pacific west of the dateline.

A continuation of the La Niña patterns described above is shown in the most recent climate summaries, available for March 1999 (NCEP 1999). Equatorial and northeast Pacific SSTAs remained up to 1° to 2° below normal. High SLP over the northeast Pacific continued to generate strong upwelling-favorable wind stress along the U.S. west coast and feed into unusually intense trade winds. The MEI has remained level since late 1998 (fig. 2B). Historically, the MEI has stayed negative for many months following a La Niña event (e.g., 1970–71, 1988–89). However, conditions could shift back to El Niño as well (e.g., 1964–65). In recent months a deep thermocline in the western tropical Pacific has been developing and moving east (NCEP 1999). If this trend continues, El Niño conditions may develop later this year. Subsurface tropical temperature anomalies are reminiscent of those prior to the 1997–98 El Niño event (cf. NCEP 1997b).

Physical Structure and Ocean Circulation

Data taken at coastal shore stations and buoys have the advantages of a higher sampling frequency, greater alongshore geographic coverage, more rapid data distribution, and, in the case of the shore stations, longer periods of measurements. A challenge for CalCOFI is to improve our ability to use these data in order to make inferences about oceanographic and ecosystem structure in the offshore waters and improve our understanding of events on time scales shorter than can be resolved by

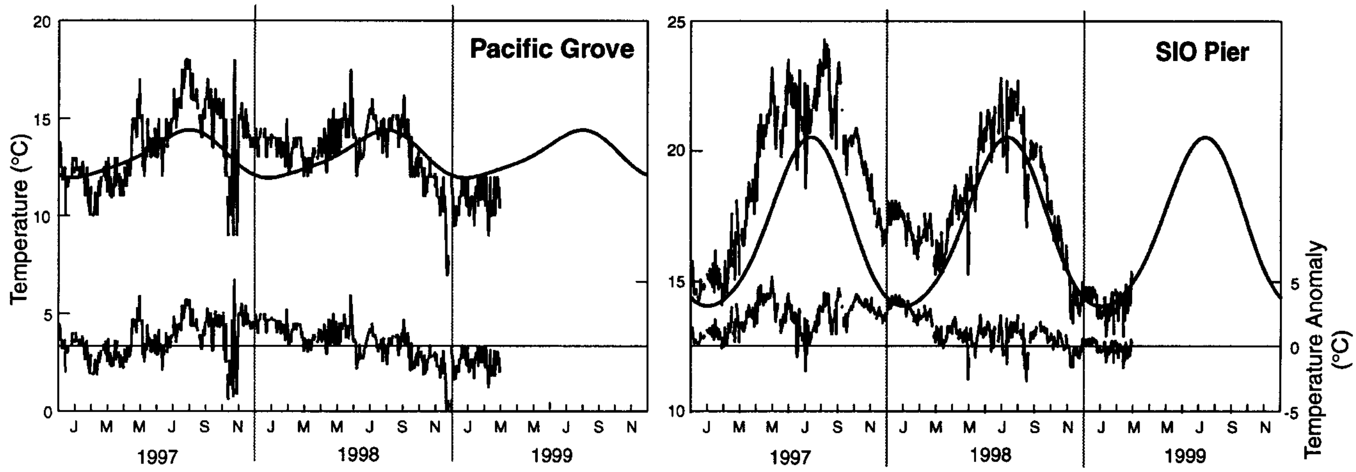


Figure 5. Sea-surface temperature at Pacific Grove and La Jolla (SIO Pier) for 1998 and 1999. Daily temperature and anomalies from the long-term harmonic mean (1919–93 for Pacific Grove and 1916–93 for La Jolla). The harmonic mean annual cycle in SST is also shown.

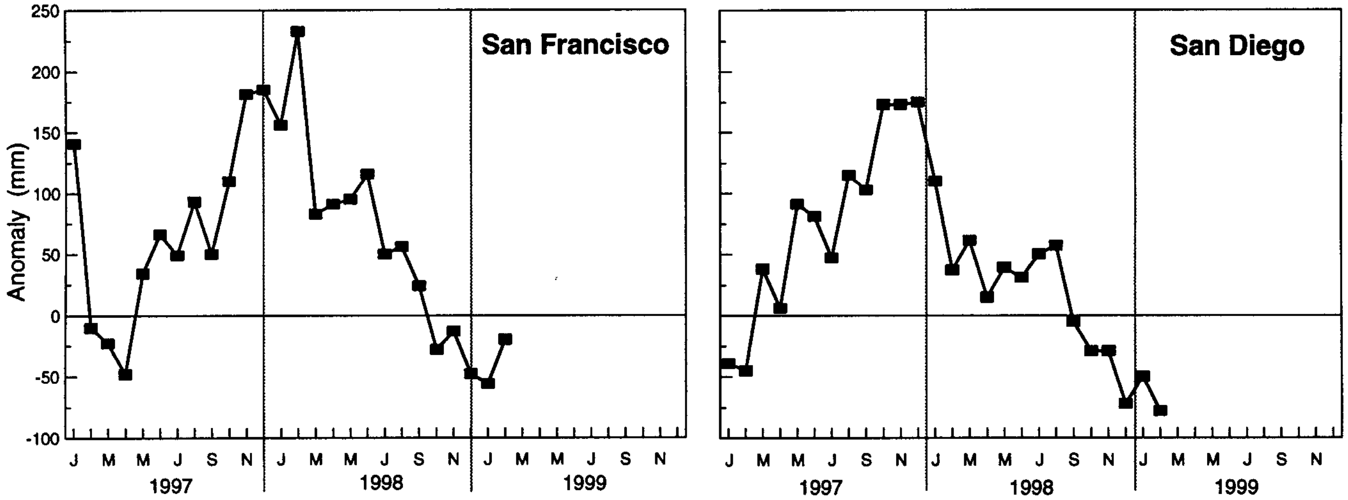


Figure 6. Monthly sea-level anomalies at San Francisco and San Diego for 1997, 1998, and 1999. The monthly anomalies are deviations from the 1975–95 period, corrected for atmospheric pressure.

the quarterly time-series cruises (McGowan et al. 1998). Since there has been a secular trend of warming and rising sea level since the mid-1970s (Roemmich 1992), it is important to consider the base period used to calculate the climatologies when comparing anomalies derived from different data sources. Coastal shore station temperature anomalies were calculated upon the base period of 1916–93 for La Jolla and 1919–93 for Pacific Grove (Walker et al. 1994). Sea-surface temperature at La Jolla was anomalously warm throughout 1997 and most of 1998, with only a few cool episodes of near-normal temperatures (fig. 5). Sea-surface temperature was normal to cool from the fall of 1998 through the early spring of 1999. Pacific Grove was cool to normal in the early part of 1997. Positive temperature anomalies were generally observed from August 1997 to September of 1998, although there were several episodes of below-normal temperatures. From October 1998 through the spring of 1999 temperatures were generally cooler than normal.

Sea-level anomalies (the difference between the mean sea level for the given month and the mean annual cycle for 1975 to 1995 corrected for the inverse barometer effect) provide another index of oceanographic structure that can be measured at coastal shore stations. San Diego and San Francisco showed quite similar temporal patterns from 1997 to early 1999 (fig. 6). Sea level began to rise to anomalously high values indicative of El Niño in May 1997, and remained anomalously high until September–October 1998. The highest values occurred from October 1997 to February 1998. Values in the fall and winter of 1998 and early 1999 were anomalously low. It may be that the similarity in the sea-level signal was due to the strong El Niño forcing standing out above the regional variability. The sea-level data were provided by the Joint Archive for Sea Level

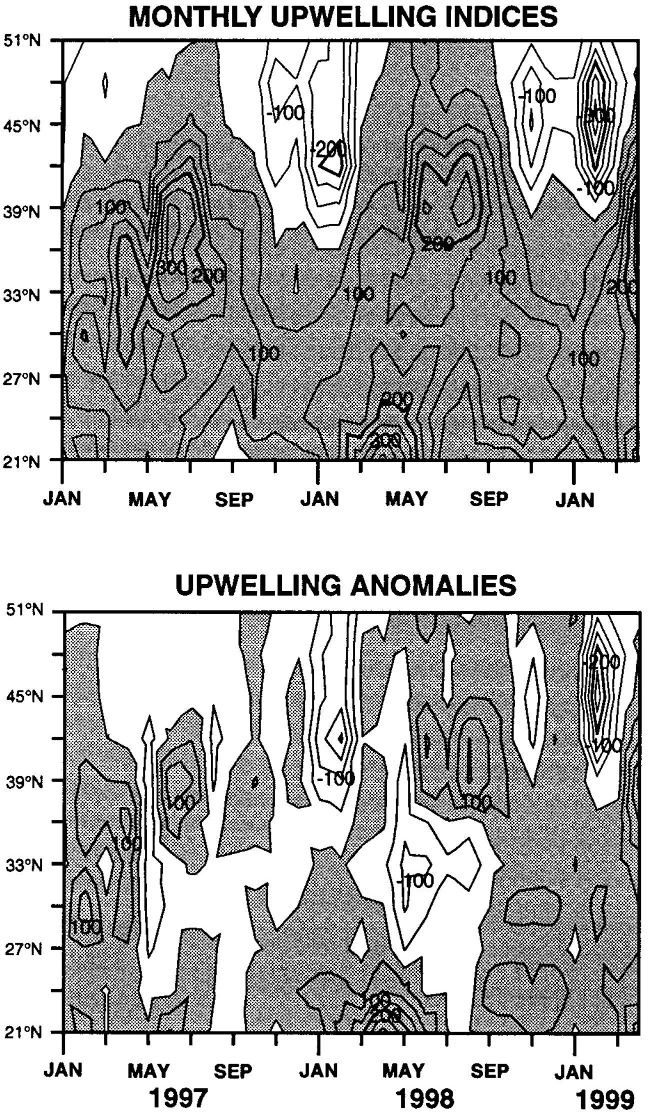


Figure 7. Monthly upwelling index and upwelling index anomaly for January 1997 to April 1999. Shaded areas denote positive (upwelling-favorable) values in the upper panel, and positive anomalies (greater than normal upwelling) in the lower panel. Anomalies are relative to the 1948–67 monthly means. Units are m^{-3} sec^{-1} per 100 km of coastline.

(JASL), a collaboration between the University of Hawaii Sea Level Center and the National Oceanographic Data Center *http://uhslc.soest.hawaii.edu/uhslc/jasl.html.*

Monthly coastal upwelling indices (Bakun 1973; Schwing et al. 1996) provide an index of atmospheric forcing of ocean circulation. The upwelling index during 1998 and early 1999 featured four periods of negative anomalies (fig. 7). Unusually strong downwelling extended north from Monterey in early 1998, and returned in November 1998 and February 1999. Weaker than normal upwelling occurred through late spring and summer 1998 from Monterey south to Baja California. Lower upwelling rates stretched along the entire west coast in May 1998. The remainder of 1998 and early 1999 featured higher than normal upwelling. Upwelling was particularly strong off northern California in late summer, and along the entire coast in April 1999. Upwelling anomalies along California in April 1999 (100–200 m^{-3} s^{-1} per 100 km of coastline) were among the largest in the over 50-year record of the upwelling index. They were comparable to anomalies in the early spring of other La Niña years (e.g., 1964, 1968). However, not all La Niña years featured anomalously strong coastal California upwelling in spring, and years of very strong upwelling were not necessarily linked to equatorial La Niña events. SSTAs in the CCS closely reflect these perturbations in coastal upwelling (fig. 4, also R. Mendelssohn, NOAA/PFEL, pers. comm.). The periods of high upwelling indices in the spring of 1999 were coincident with the decline in SST anomalies at the coastal shore stations to below normal values and the decline in sea level to below normal values. The changes in all of these indices are consistent with the transition to cool-water conditions.

Direct measurements of ocean temperature and winds at coastal buoys provide an additional source of information about physical processes that influence the California Current ecosystem. National Data Buoy Center winds at selected available locations along the U.S. west coast (fig. 8) display the short-term variability associated with synoptic atmospheric events which were superimposed on the annual climatological cycle of strong southward wind in summer and northward or weak southward wind in winter. Wind vectors align strongly with the local coastline (table 1). Returns of buoy data have been spotty over much of the past few years.

The 1997–98 winter featured numerous episodes of greater than normal northward buoy winds (more downwelling-favorable), and generally highly variable wind speeds. These were associated with heavy winter storm activity and copious precipitation for much of the Pacific Northwest. Winter winds were very strong and oscillated in direction even in the Southern California Bight, where winds are normally relatively weak and variable (cf. 1997). In late 1998, anomalous northward winds off northern California and Oregon were followed by a period of very strong southward winds. The upwelling index anomalies (fig. 4) correspond well with the tendencies of the buoy alongshore winds, with both indicating anomalous downwelling in early 1998, and greater than normal upwelling in the latter half of 1998.

From a peak in August–September 1997, when temperatures were as much as 6°C above average, buoy SSTs gradually cooled and returned to their climatological values by spring 1998 (fig. 9). SSTs remained near normal through most of 1998, fluctuating on synoptic (10–30 day) time scales in response to changing wind patterns. In late 1998, SSTs dropped to well below nor-

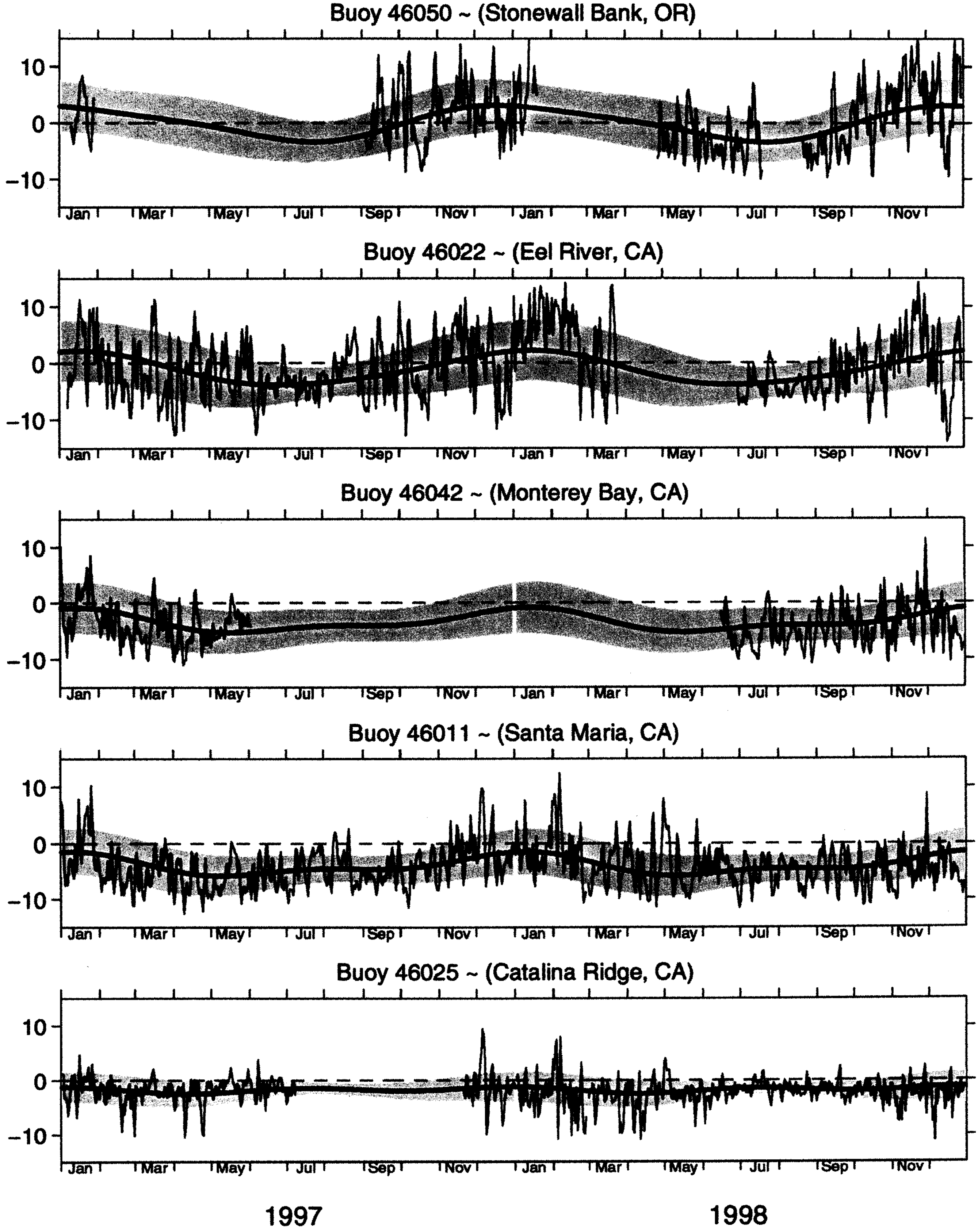


Figure 8. Time series of daily-averaged alongshore winds (knots) for 1997–98 at selected NDBC buoys. Bold lines are the harmonic mean annual cycle at each buoy. Shaded areas are the standard error for each Julian day. The period used for calculating the mean at each site and the alongshore angle are shown in table 1.

TABLE 1
Locations of SST and Alongshore Wind Time Series

Buoy	Name	Position	Base Period[a]	Alongshore angle (°N)[b]
46050	Stonewall Bank, Ore.	44.6°N 124.5°W	1991–98	0
46022	Eel River, Calif.	40.8°N 124.5°W	1982–98	354
46042	Monterey Bay, Calif.	36.7°N 122.4°W	1987–98	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.

mal in response to a period of very strong equatorward (upwelling-favorable) wind stress.

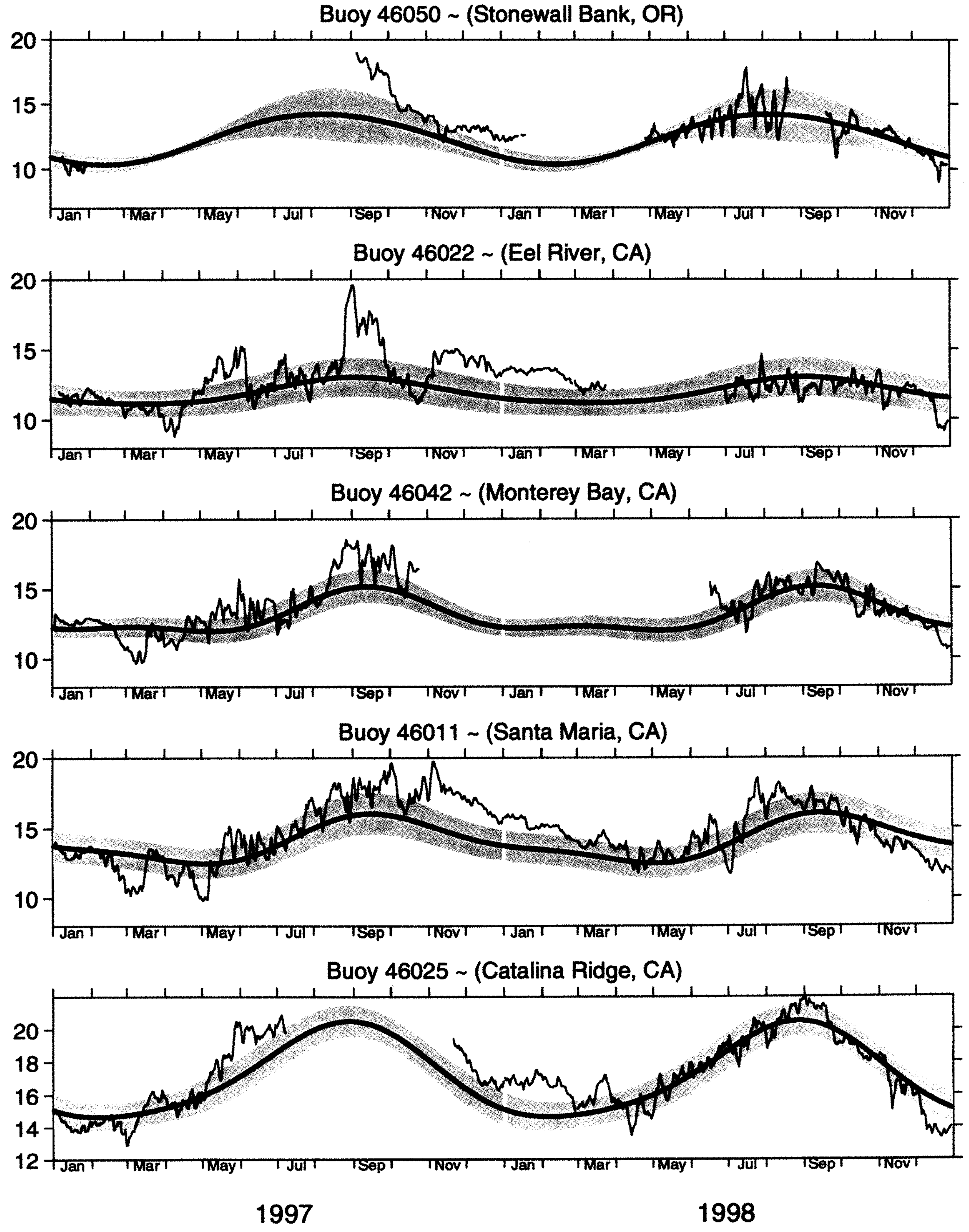
Atmospheric changes presumably contribute to variations in upper ocean temperature through changes in upwelling and downwelling rates, turbulent mixing and stratification, and air-sea heat exchange. However, not all wind events produce an obvious response in SST. Synoptic changes in SST were unusually light during November 1997–April 1998, despite vigorous wind variability on this scale. The steady decline in SST over this period suggests an unusually deep mixed layer. Even during episodes of strong equatorward wind, surface water may have been replaced by upwelled water of virtually the same temperature.

The oceanographic and biological data from the CalCOFI time-series cruises provide additional information about subsurface patterns and ecosystem structure. Patterns in these data can be considered in the context of the long-term mean circulation patterns (fig. 10). Since many studies have shown strong associations between ecosystem structure and circulation patterns in the California Current region (Hayward and Mantyla 1990; Strub et al. 1991; Haury et al. 1993; Hayward and Venrick 1998), the mean circulation pattern is a useful reference for physical structure. The location of the low-salinity jet which forms the core of the California Current, the continuity and strength of the coastal countercurrent, as well as the location and strength of mesoscale features including coastal filaments, eddies, and meanders of the California Current are associated with changes in plankton distributions and fish spawning.

Although cruise 9802 was reviewed in last year's report, we include it here because it sets the stage for the remarkable change in circulation and ecosystem structure which took place in early 1998. This cruise showed a circulation pattern consistent with strong El Niño conditions (fig. 11). There was a strong coastal countercurrent, and the low-salinity jet of the core of the California Current was unusually far offshore. Note the quite low salinity water (less than 33.0) in the core of the California Current jet in the central part of the pattern. The presence of this very low salinity water implies that there was both a strong coastal countercurrent and strong southward flow of the California Current jet at this time. Surface chlorophyll was relatively low throughout the pattern, as is typical of the January–February time period.

A remarkable change in the circulation pattern and chlorophyll distribution were evident by April in the data from cruise 9804 (fig. 12). The low-salinity jet of the California Current moved inshore, close to shore. Note that this cruise sampled three additional lines to Monterey north of the normal pattern in order to better resolve the range of sardine spawning. The strong coastal countercurrent seen in February was absent. The surface chlorophyll concentration was quite high in the coastal region bounded by the inshore edge of the low-salinity jet. This enrichment was likely caused by isopycnal shoaling (Hayward and Venrick 1998). The circulation changed from quite anomalous conditions in January to a pattern that looked more similar to the climatology in April. Hydrographic data from the March mini El Niño cruise (not shown) suggest that the replacement of the coastal countercurrent with strong southward flow and the increase in chlorophyll took place between the end of January and the middle of March.

There were again strong changes in the circulation pattern between April and July 1998. The strong coastal countercurrent had returned by cruise 9807 (fig. 13). There was also strong flow of the California Current in the middle of the grid. The pattern of flow was similar to the climatology, and it is interesting in that both the California Current and the countercurrent showed strong flow. The flow field is similar to that seen in previous strong El Niño summers in the southern California region. The water in the core of the California Current is again very low in salinity (less than 33.0) even off southern California. The strong eddy located south of Point Conception also shows up in the long-term mean circulation pattern (fig. 10). Chlorophyll was high (greater than 2 $\mu g\ l^{-1}$) in the Point Conception region and in a tongue located in the region of shear between the California Current and the countercurrent off southern California.



Buoy 46050 ~ (Stonewall Bank, OR)

Buoy 46022 ~ (Eel River, CA)

Buoy 46042 ~ (Monterey Bay, CA)

Buoy 46011 ~ (Santa Maria, CA)

Buoy 46025 ~ (Catalina Ridge, CA)

Figure 9. Time series of daily-averaged SST (°C) for 1997–98 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.

LONG-TERM MEAN CIRCULATION PATTERN

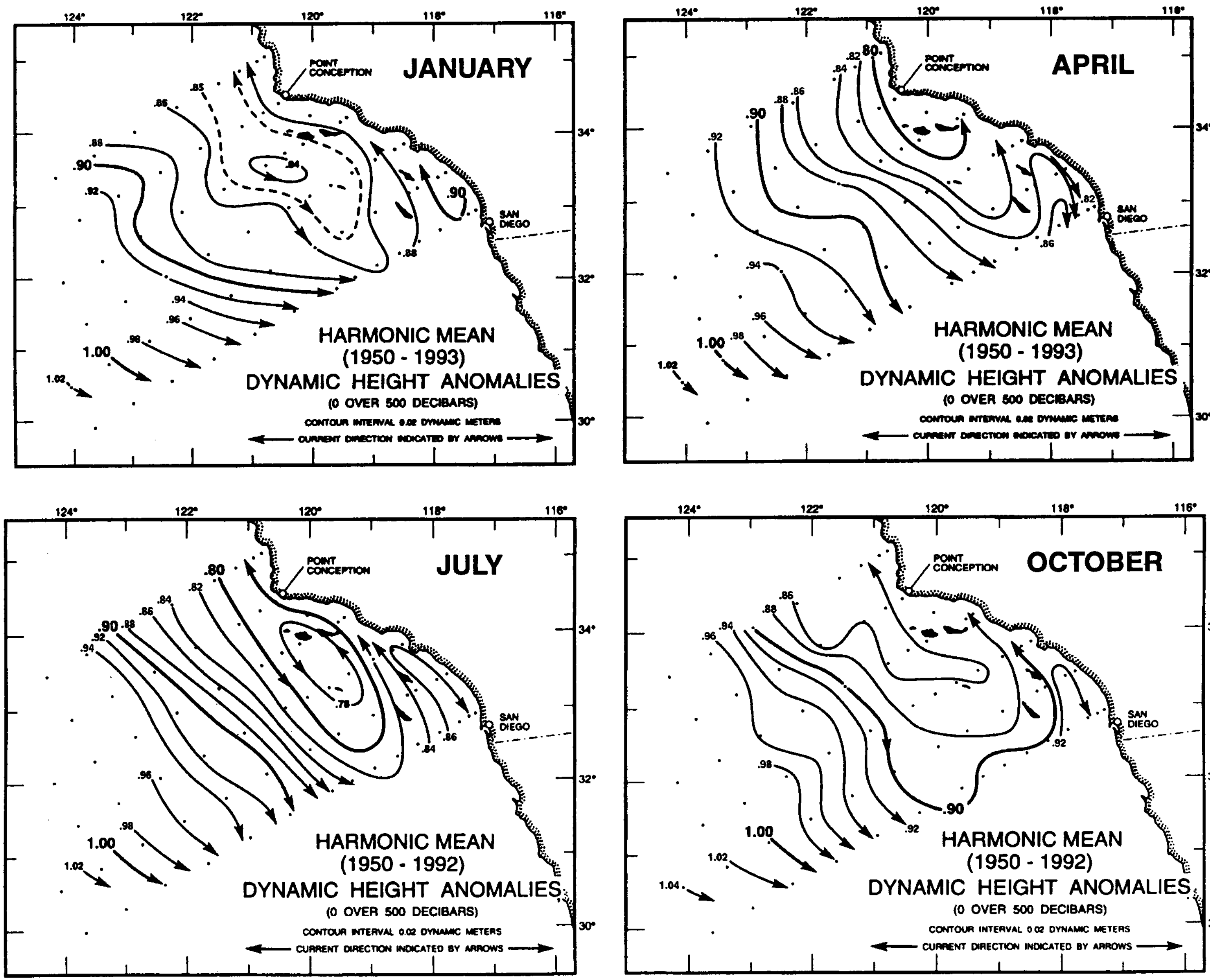


Figure 10. Long-term mean (1950–92) circulation patterns based upon 0 over 500 m dynamic height for the target months of the time-series cruises.

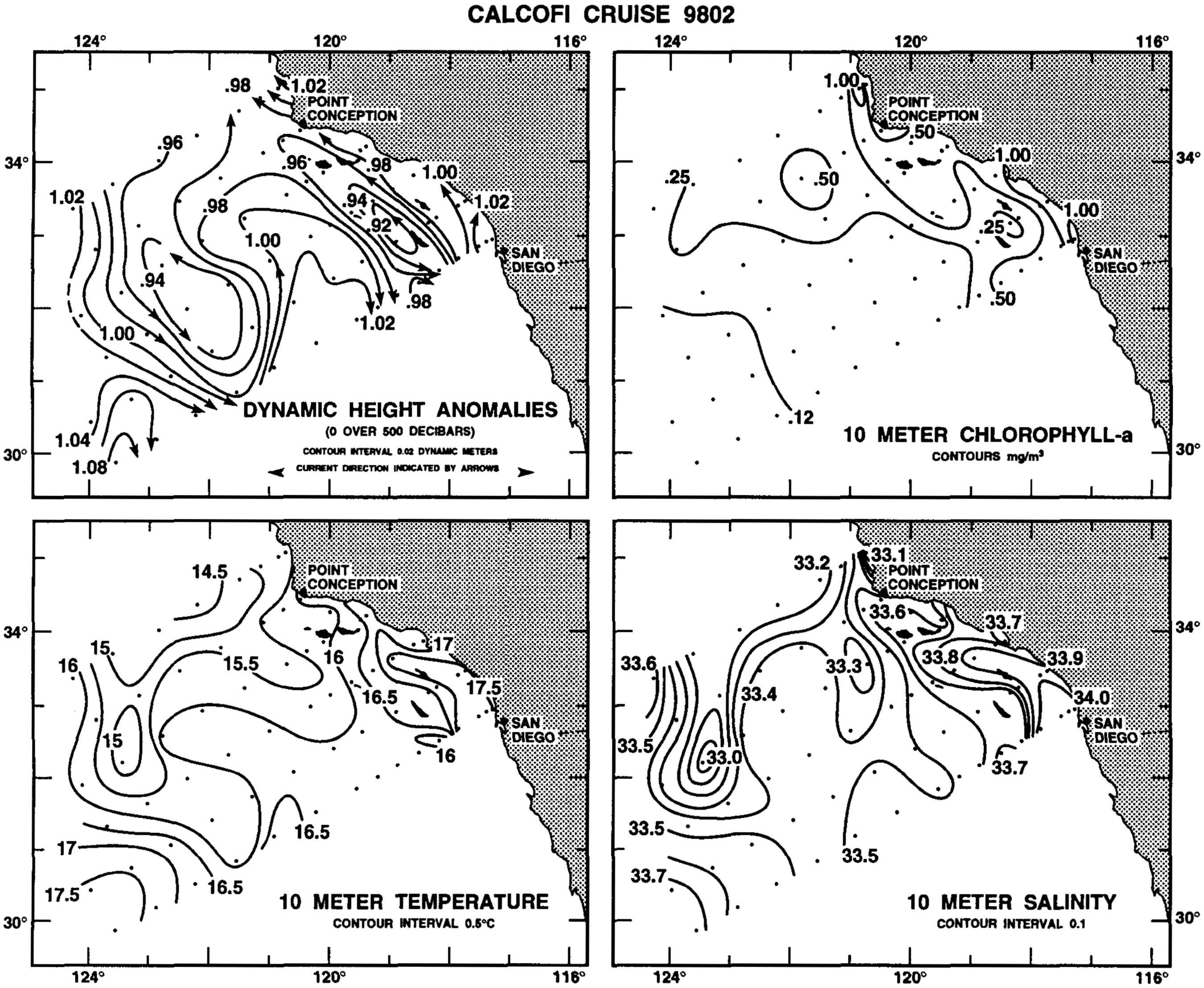


Figure 11. Spatial patterns for CalCOFI cruise 9802 (23 January–14 February 1998), including upper-ocean geostrophic flow estimated from 0 over 500 db dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

The circulation pattern on cruise 9809 (fig. 14) was again typical of the climatology, with the California Current flowing southward through the middle of the pattern, and weak northward flow along the coast. The salinity in the core of the California Current (33.1–33.2) was greater than in July. Chlorophyll was relatively low throughout the pattern, with the highest values along the coast, as is typical for fall.

The circulation pattern on cruise 9901 showed strong meandering flow of the California Current and a strong coastal countercurrent (fig. 15). The circulation pattern was strongly influenced by mesoscale structure. There were two strong mesoscale eddies and a sharp meander to the California Current. The mesoscale circulation pattern was reflected in the chlorophyll distribution. Chlorophyll was high on this cruise. Chlorophyll was elevated in an offshore tongue at the boundary between the southward flow of the California Current and the northward flow of the countercurrent, and also in coastal patches. This cruise was made on RV *Roger Revelle*, and the ship's greater capability, together with a few added days of station time, allowed an expanded group of cooperative research programs, including sampling with MOCNESS.

Cruise 9904 (preliminary data) was marked by a strong mesoscale circulation pattern (fig. 16). The California Current was well offshore, and the southward extent of the penetration of water below salinity of 33.0 is consistent with strong flow. Chlorophyll was high on this cruise. Again, the spatial pattern was strongly influenced by the circulation. High chlorophyll was found at the inner edge of the low-salinity jet of the core of the California Current (Hayward and Venrick 1998).

The data collected on the monthly *Robert Gordon Sproul* mini El Niño cruises provide additional infor-

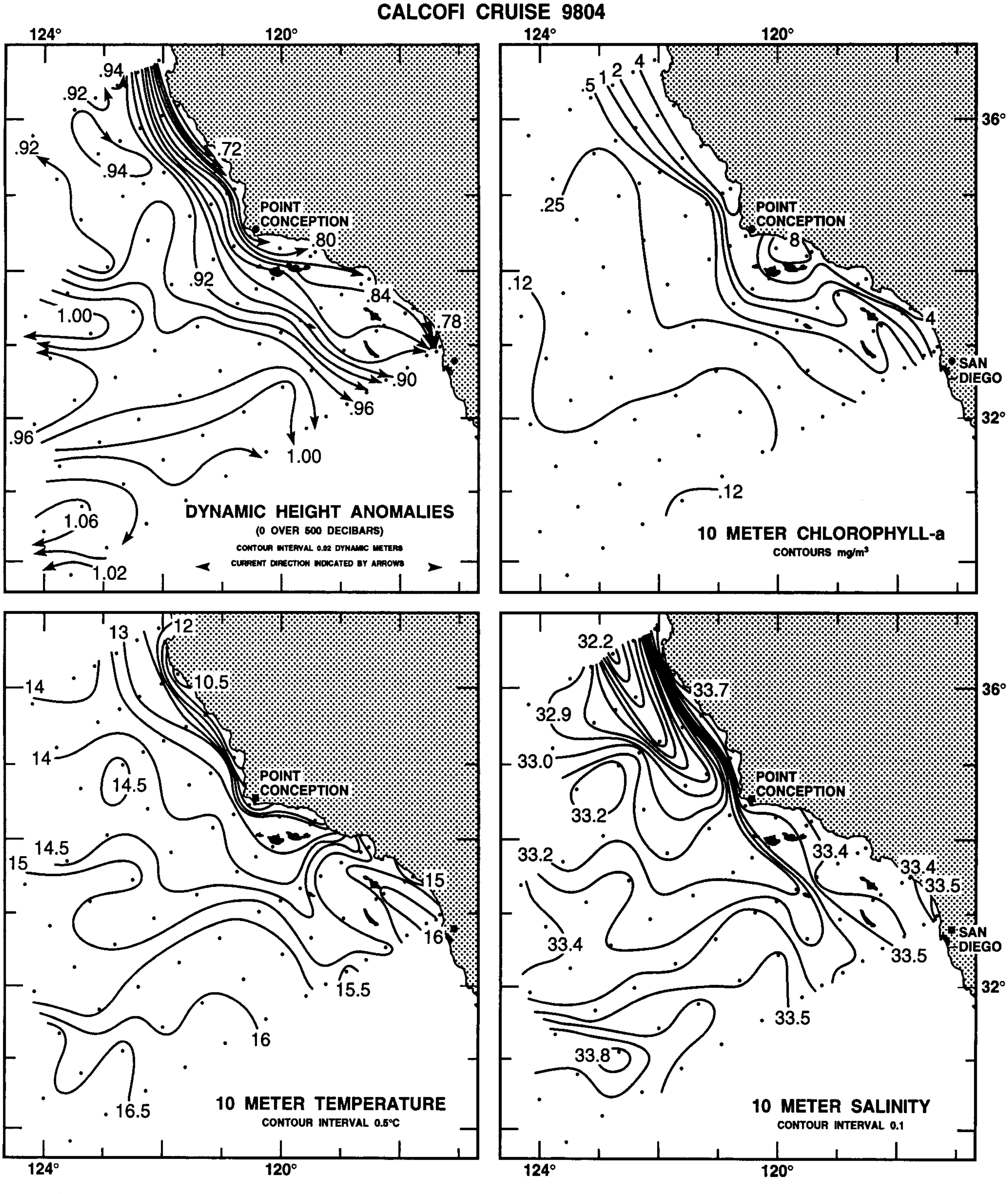


Figure 12. Spatial patterns for CalCOFI cruise 9804 (2–23 April 1998), including upper-ocean geostrophic flow estimated from 0 over 500 db dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

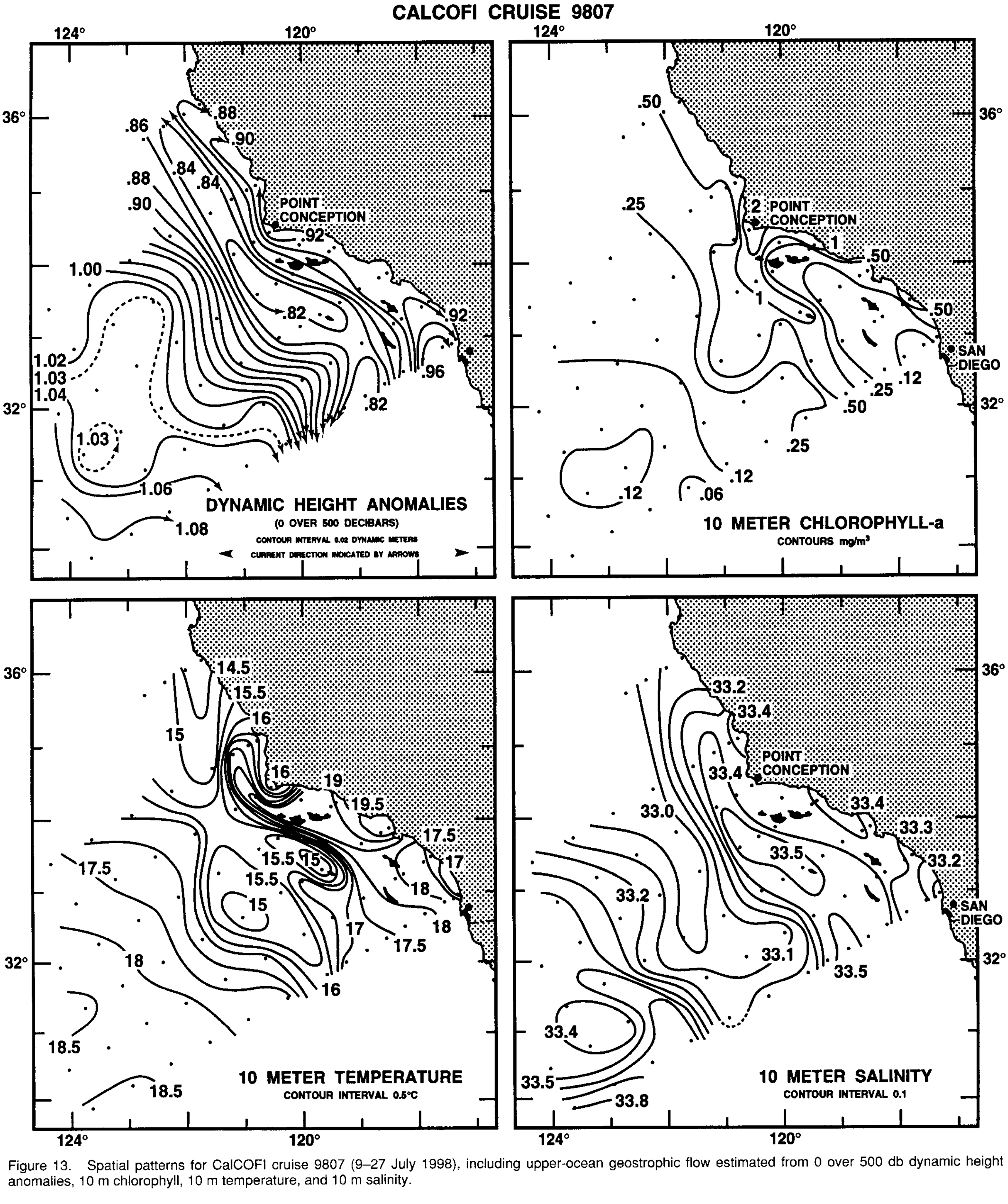


Figure 13. Spatial patterns for CalCOFI cruise 9807 (9–27 July 1998), including upper-ocean geostrophic flow estimated from 0 over 500 db dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

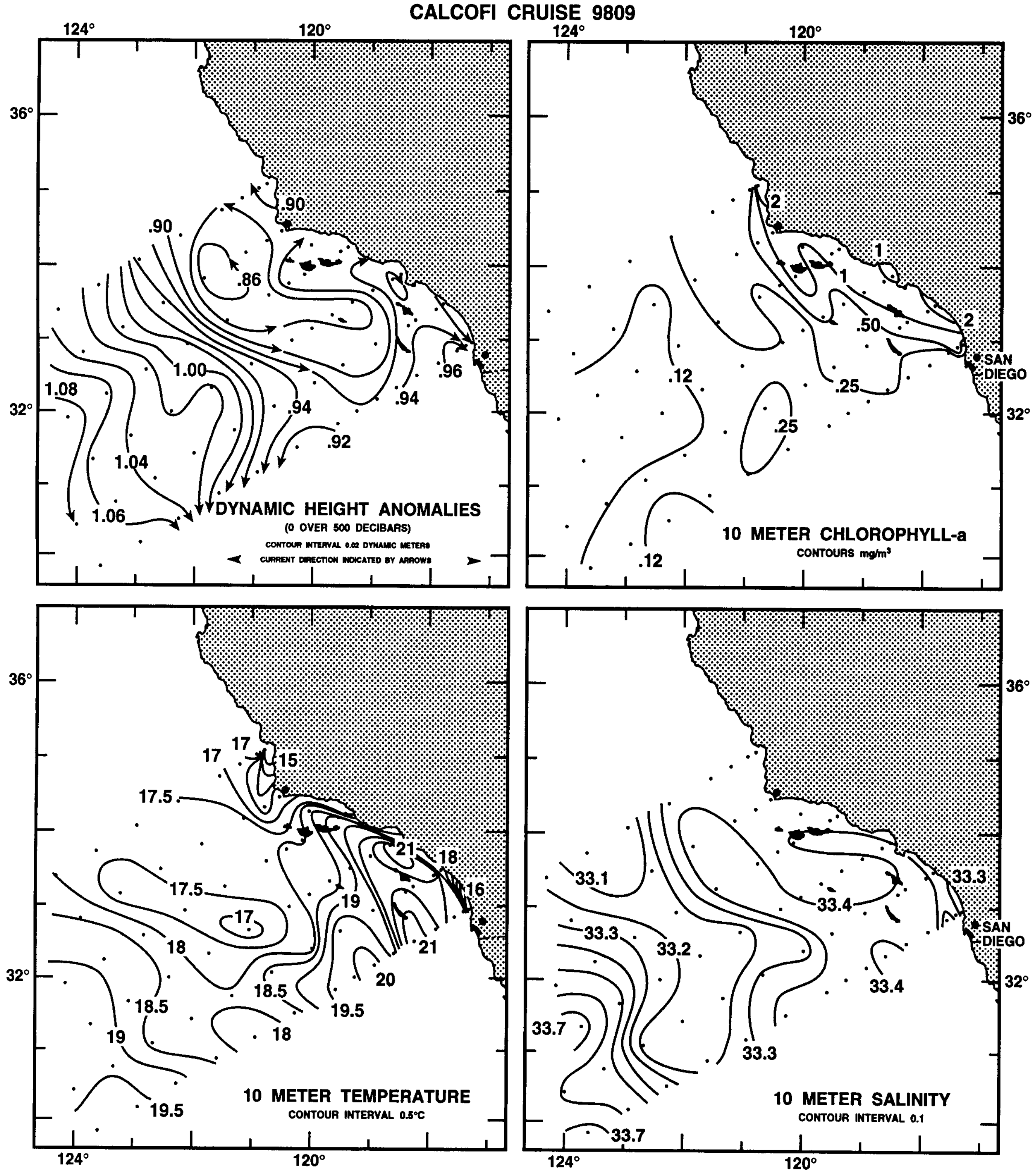


Figure 14. Spatial patterns for CalCOFI cruise 9809 (13 September–1 October 1998), including upper-ocean geostrophic flow estimated from 0 over 500 db dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

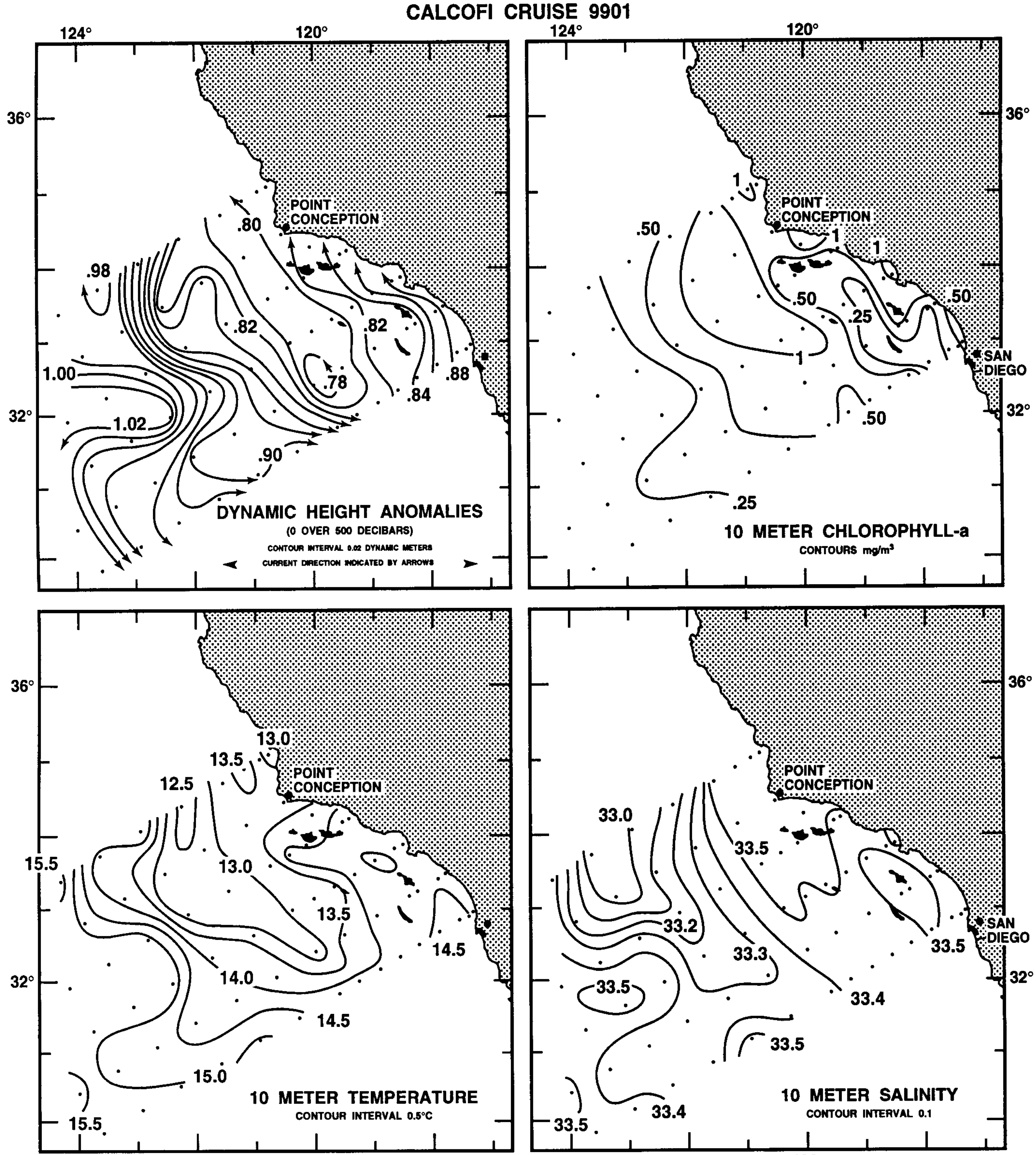


Figure 15. Spatial patterns for CalCOFI cruise 9901 (9–29 January 1999), including upper-ocean geostrophic flow estimated from 0 over 500 db dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

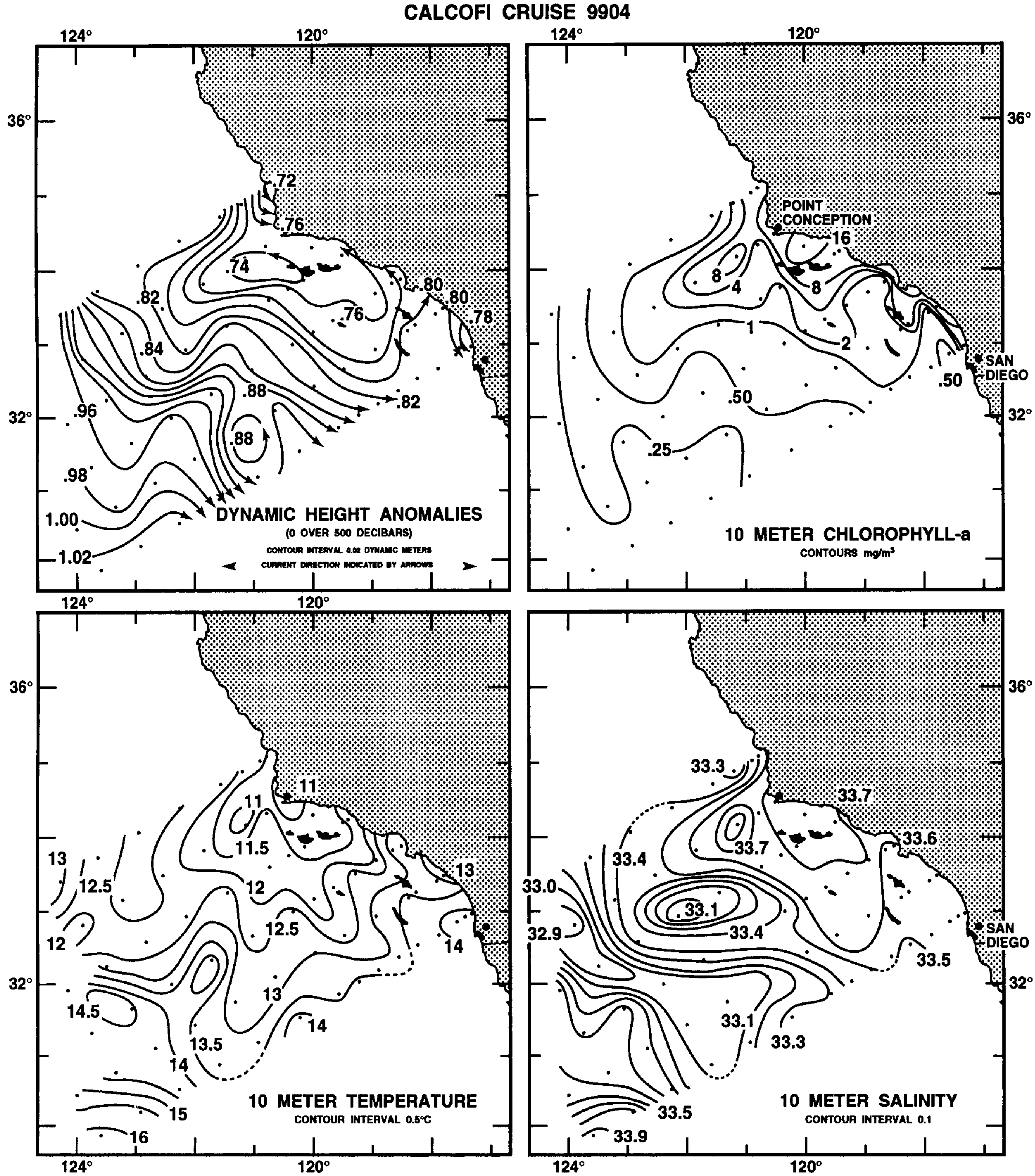


Figure 16. Spatial patterns for CalCOFI cruise 9904 (1–20 April 1999), including upper-ocean geostrophic flow estimated from 0 over 500 db dynamic height anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

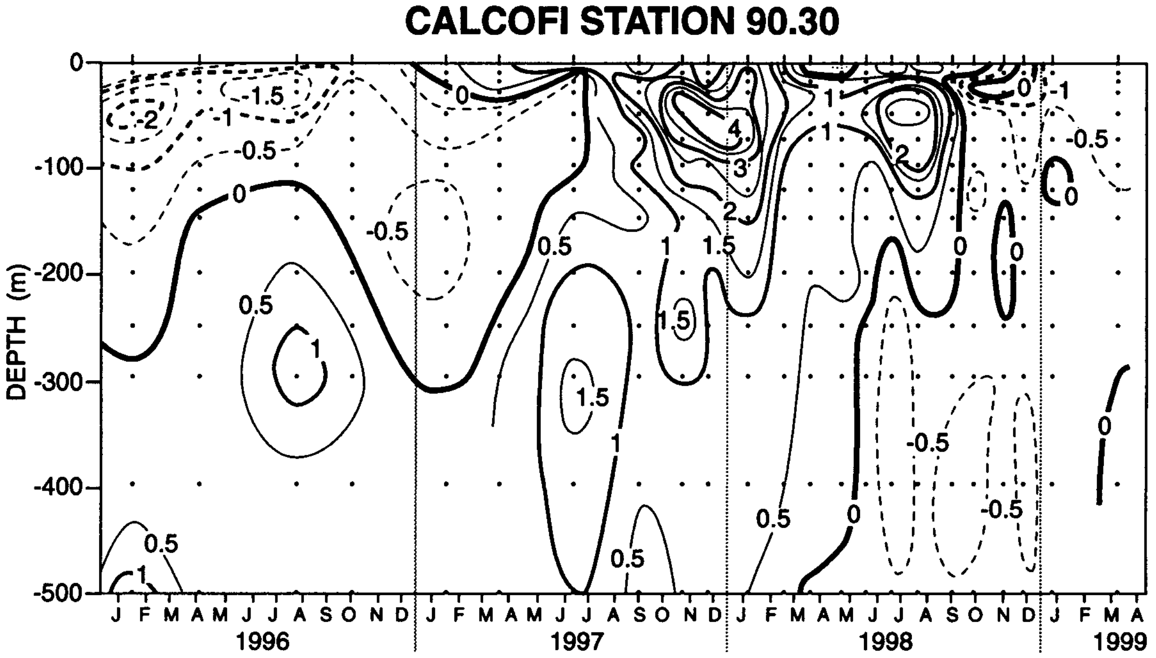


Figure 17. Anomalies in temperature (°C from the 1950–92 base period) versus depth and time for CalCOFI station 90.30.

mation about temporal changes in structure. The analysis here focuses on pattern in upper ocean thermal structure. Vertical sections of temperature anomalies versus time are shown from stations 90.30 and 90.60 (figs. 17 and 18). Station 90.30 is located in the coastal waters influenced by the countercurrent, and station 90.60 is farther offshore in a region which is often influenced by the low-salinity jet of the California Current (fig. 1). Both stations show similar patterns of anomalies in thermal structure. At station 90.30 the surface waters showed positive temperature anomalies of greater than 1°C in July of 1997 (fig. 17). However, the waters normally found in the thermocline (50–150 m) had nearly normal temperatures. The pattern of warming increased in the fall. There was an abrupt transition to strong El Niño conditions in November 1997. This can be seen from the pattern of large (greater than 4°) temperature anomalies in the upper thermocline. The surface waters were generally between 1° and 2° above normal throughout this period. The pattern of vertical maximum temperature anomalies in the thermocline is a characteristic structure during El Niño events in the California Current region (McGowan 1985; Lynn et al. 1995). The thermocline temperature anomalies decreased in magnitude during the spring of 1998, and there was another increase to values greater than 2.5° in July and August. The winter of 1998 and spring of 1999 were marked by cooler than normal temperatures in the upper layer. The patterns at 90.60 were quite similar to those at 90.30 (fig. 18). Again, surface temperature anomalies of greater than 1° were seen by July 1997, but temperatures in the thermocline were near normal. There was an abrupt shift to thermocline anomalies of greater than 6° in December 1997, and the strong thermocline anomalies persisted until September 1998. As at station 90.30, both the transition to warm and later cool temperature anomalies began at the surface and progressed downward in depth. The monthly measurements on the mini El Niño cruises show how rapidly physical structure can change in this region.

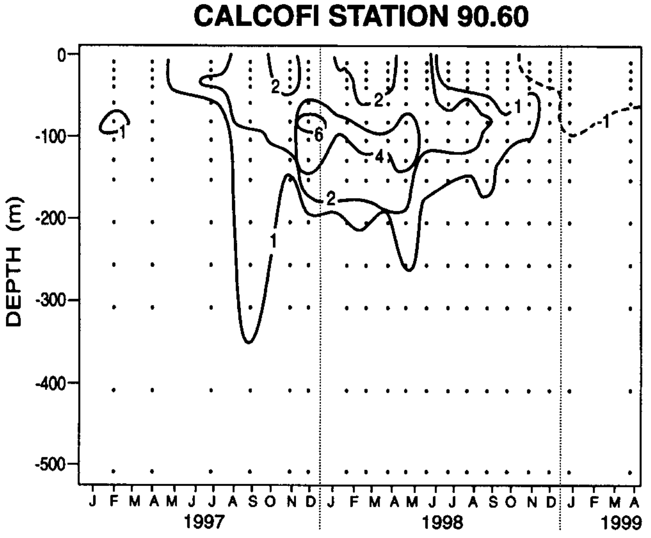


Figure 18. Anomalies in temperature (°C from the 1950–92 base period) versus depth and time for CalCOFI station 90.60.

The vertical sections of temperature anomalies versus time also show that the timing of events inferred from the thermocline signal differs from the surface signal. In November 1998 the surface waters were slightly cooler than normal, but the positive thermocline was much larger than that seen in July 1997. The patterns in anomalies derived from shore station temperature or sea level or from hydrographic data are all indices of a range of changes associated with El Niño. At any station the temperature anomalies will be influenced by both the heat content of the upper ocean and by the temperature-salinity structure. Temperature anomalies in the coastal waters will be influenced by whether cool and fresh California Current water or warm, saline water from the south is present. There is much more to be said about these data in the context of El Niño and the transition to La Niña conditions and also in the context of longer-term trends. But we have decided to not include an extensive discussion of these issues in this report because the data are still being processed and analyzed and because these events are the subject of the symposium at the 1999 CalCOFI conference. These issues will be separately presented in other publications.

Data collected to the south and north of the CalCOFI study area provide a valuable regional context. These data also will provide a basis for better defining how advection influences the abundance and species composition of the plankton. Sampling to the south was conducted by the IMECOCAL program. This program was initiated in October 1997 by seven Mexican institutions, and it has continued during 1998 and 1999. Three cruises were conducted in 1998 (January, July, and September–October; hereafter called IMECOCAL cruises 9801, 9807, and 9809) and another in January 1999 (9901). The cruises were planned to coincide closely with the timing of CalCOFI cruises off California. All cruises were made on the *Francisco de Ulloa*, and covered most of the station plan shown in figure 19. Core samples included CTD/rosette casts to 2,000 m with 5 l Nisken water samples from the surface to 150 m at standard depths. Water samples were analyzed for dissolved oxygen, inorganic nutrients, and chlorophyll. Continuous underway sampling of surface temperature and salinity, as well as continuous ADCP profiling was carried out. At each station, standard oblique bongo tows were made with 0.505 mm mesh, with one cod end dedicated to ichthyoplankton and the other to macrozooplankton. In situ productivity casts were carried out at selected stations. Cruise 9901 also included vertical CalVET tows to study fish larvae. Here we present some preliminary results based on CTD observations and dissolved oxygen measurements.

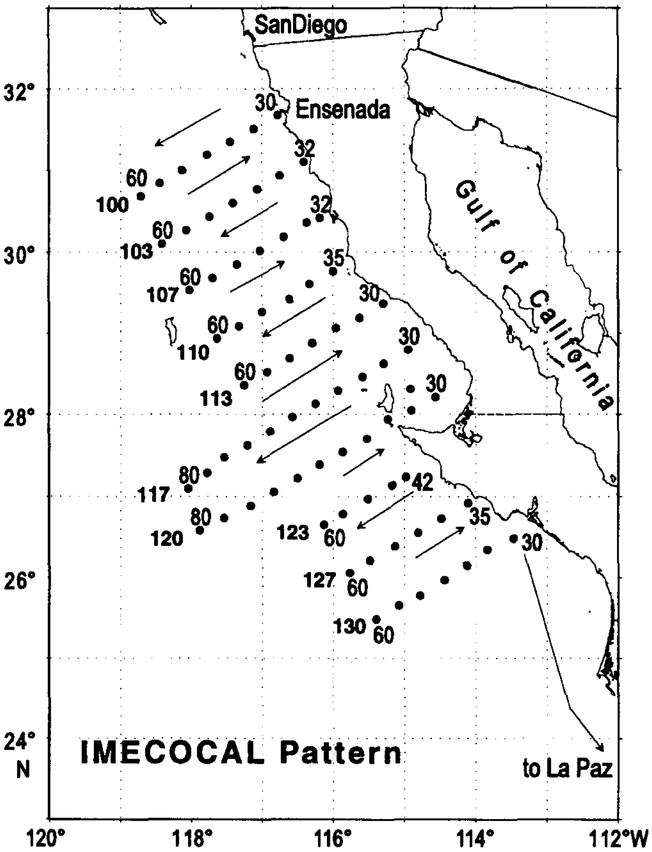


Figure 19. The IMECOCAL basic station plan.

IMECOCAL cruise 9801 showed relatively weak spatial patterns (fig. 20). There was a north-south gradient in salinity, with fresher water moving into the pattern in the northwest corner in a region of weak onshore flow. The weak horizontal gradients in dynamic height indicate a weak circulation pattern in the study region.

Property contours depict a meandering of the California Current in July 1998 on IMECOCAL cruise 9807 (fig. 21). The flow of the California Current and a series of eddies are more clearly defined in the pattern of dynamic height. In the north, about 300 km offshore, the California Current flows east of Guadalupe Island toward Vizcaíno Bay. The current turns to the southwest when close to the coast and goes around a clockwise eddy southeast of the island. Finally, the California Current bends again southeast and returns close to the coast at the southern edge of the survey area. Poleward flows at this depth are observed south of Ensenada where the California Current splits into two branches, one flowing to the southeast and the other to the north. A coastal poleward flow trapped into a cyclonic eddy southwest of Punta Eugenia apparently does not flow north of 28°N, but bends and leaves the survey area towards the southwest. The relatively low temperatures (<17°C) and low dissolved oxygen (<5.4 ml l^{-1}) in the region close to the coast, from 31° to 29°N, suggest the effect of coastal upwelling on this cruise.

A similar meandering flow of the California Current jet was seen on IMECOCAL cruise 9809 (fig. 22). The

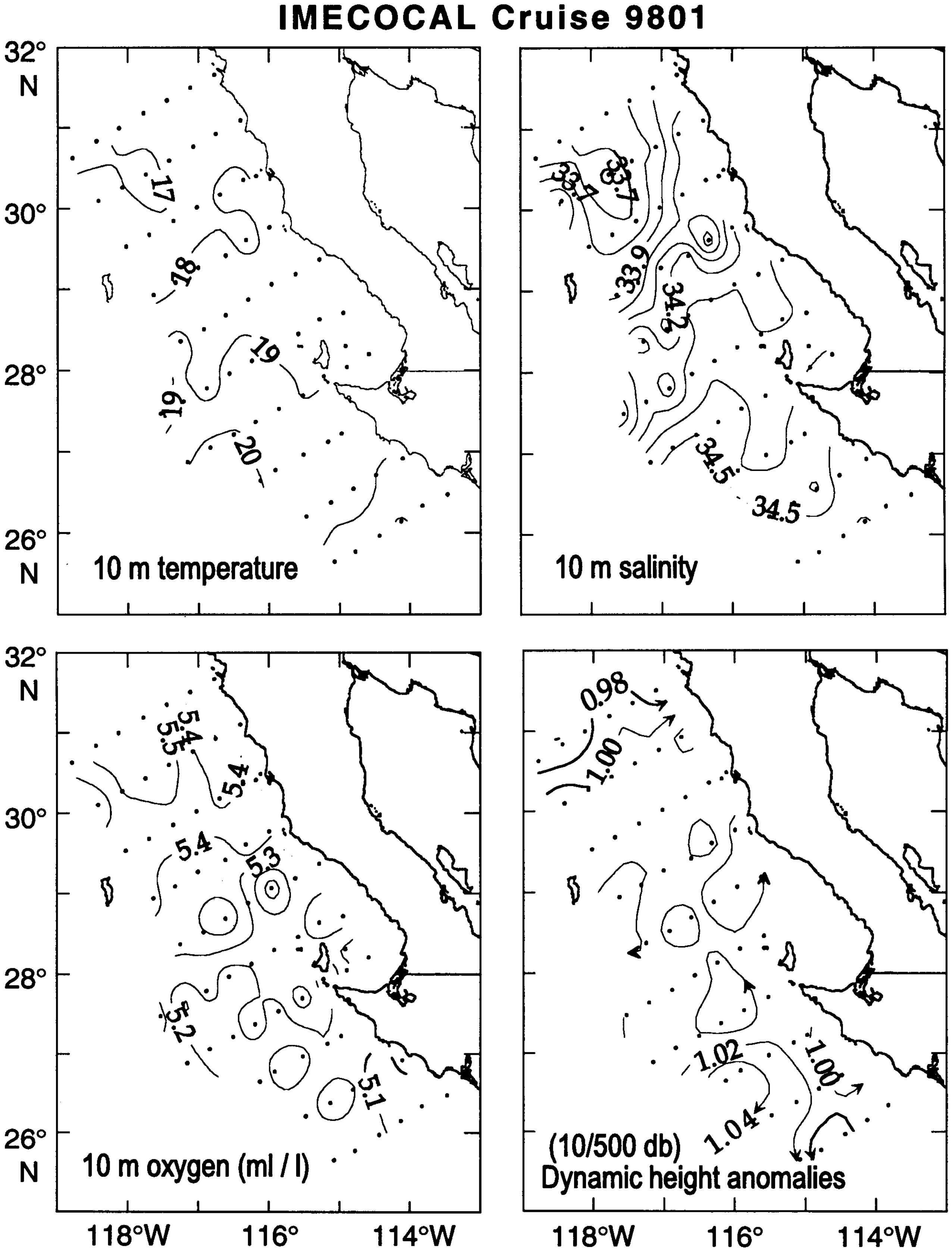


Figure 20. Spatial patterns for IMECOCAL cruise 9801 (25 January–12 February 1998) including temperature, salinity, and dissolved oxygen concentration at 10 m and geostrophic flow estimated from 0 over 500 db dynamic height anomalies.

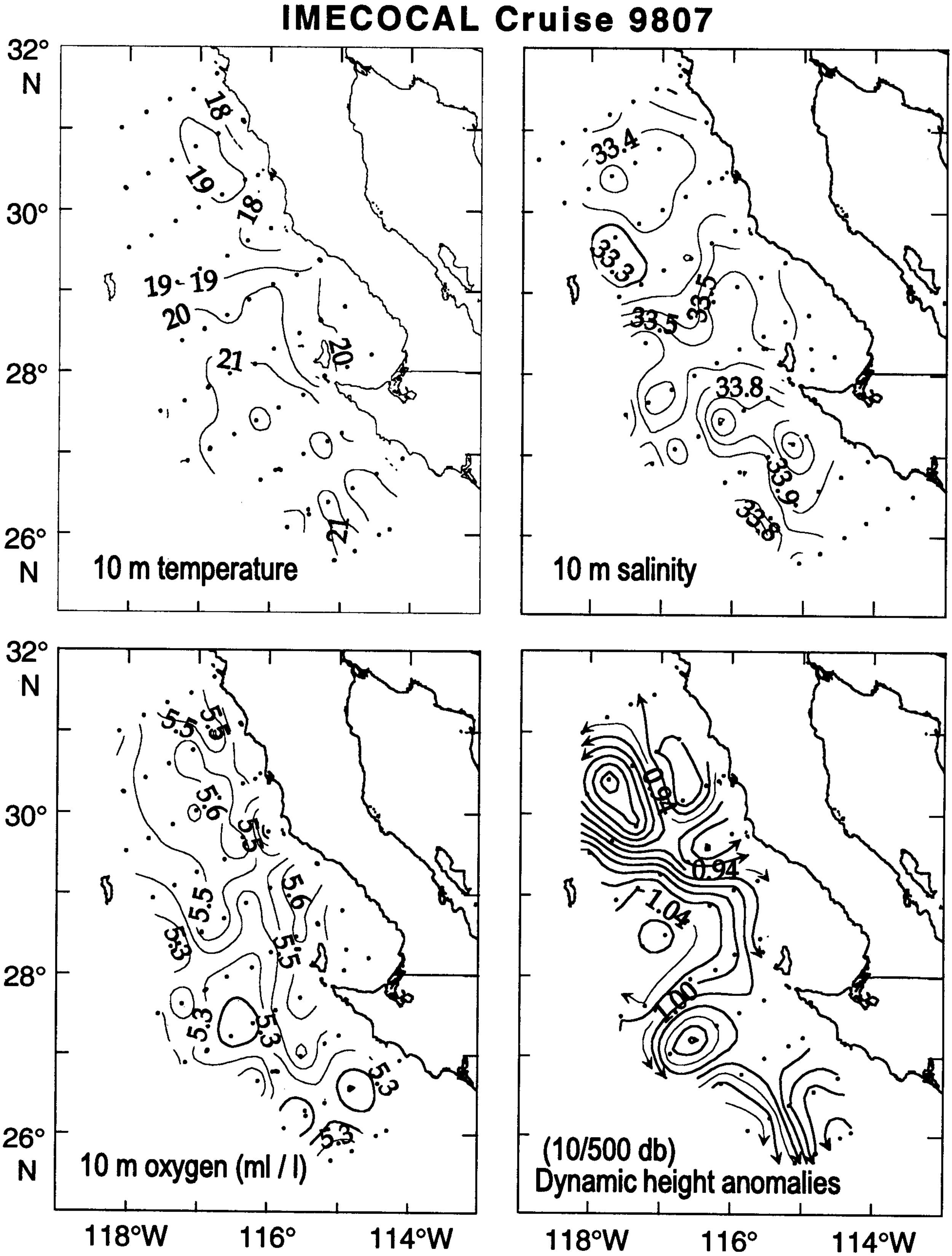


Figure 21. Spatial patterns for IMECOCAL cruise 9807 (15 July–3 August 1998) including temperature, salinity, and dissolved oxygen concentration at 10 m and geostrophic flow estimated from 0 over 500 db dynamic height anomalies.

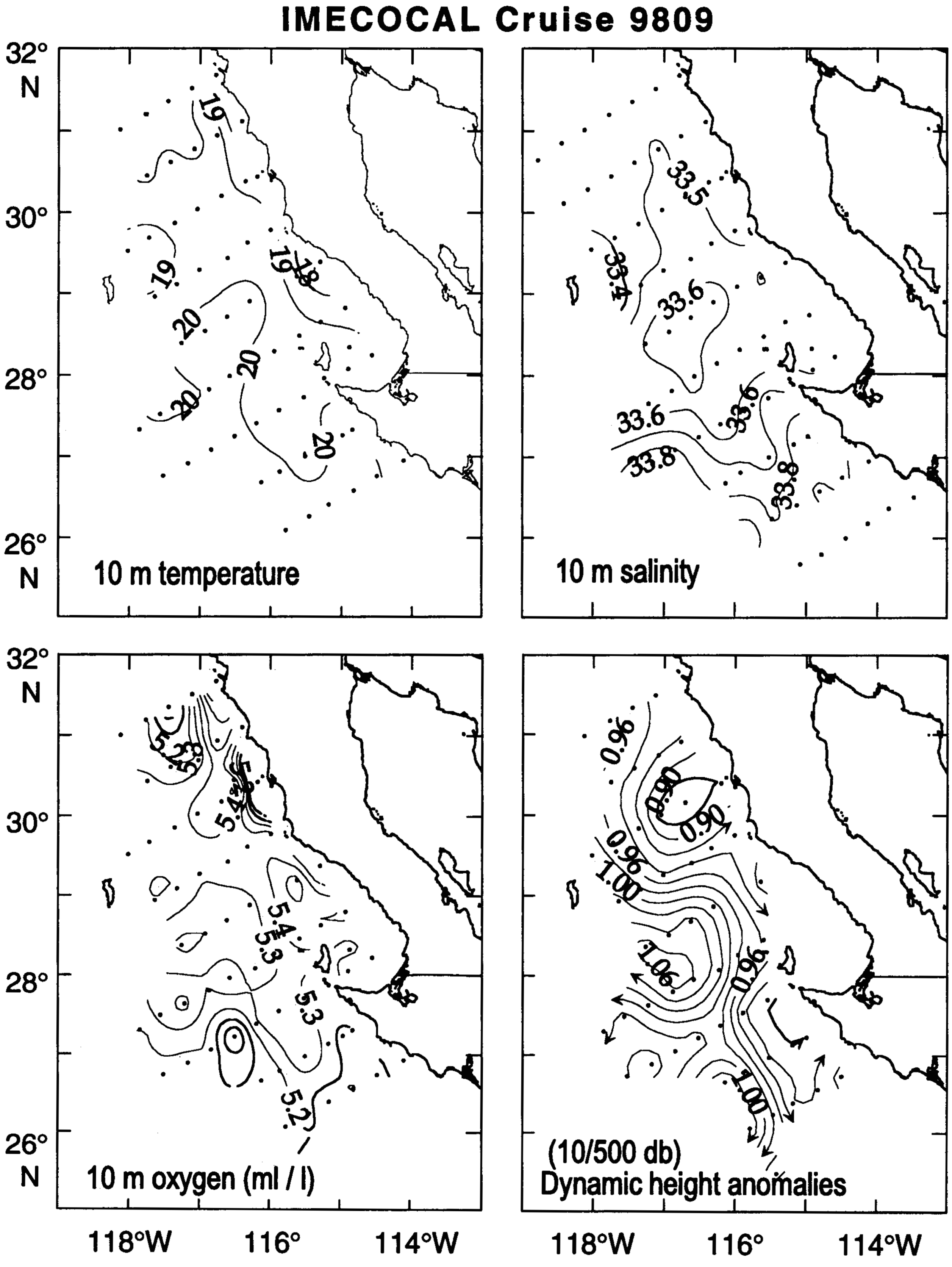


Figure 22. Spatial patterns for IMECOCAL cruise 9809 (29 September–1 October and 19 October–5 November 1998) including temperature, salinity, and dissolved oxygen concentration at 10 m and geostrophic flow estimated from 0 over 500 db dynamic height anomalies.

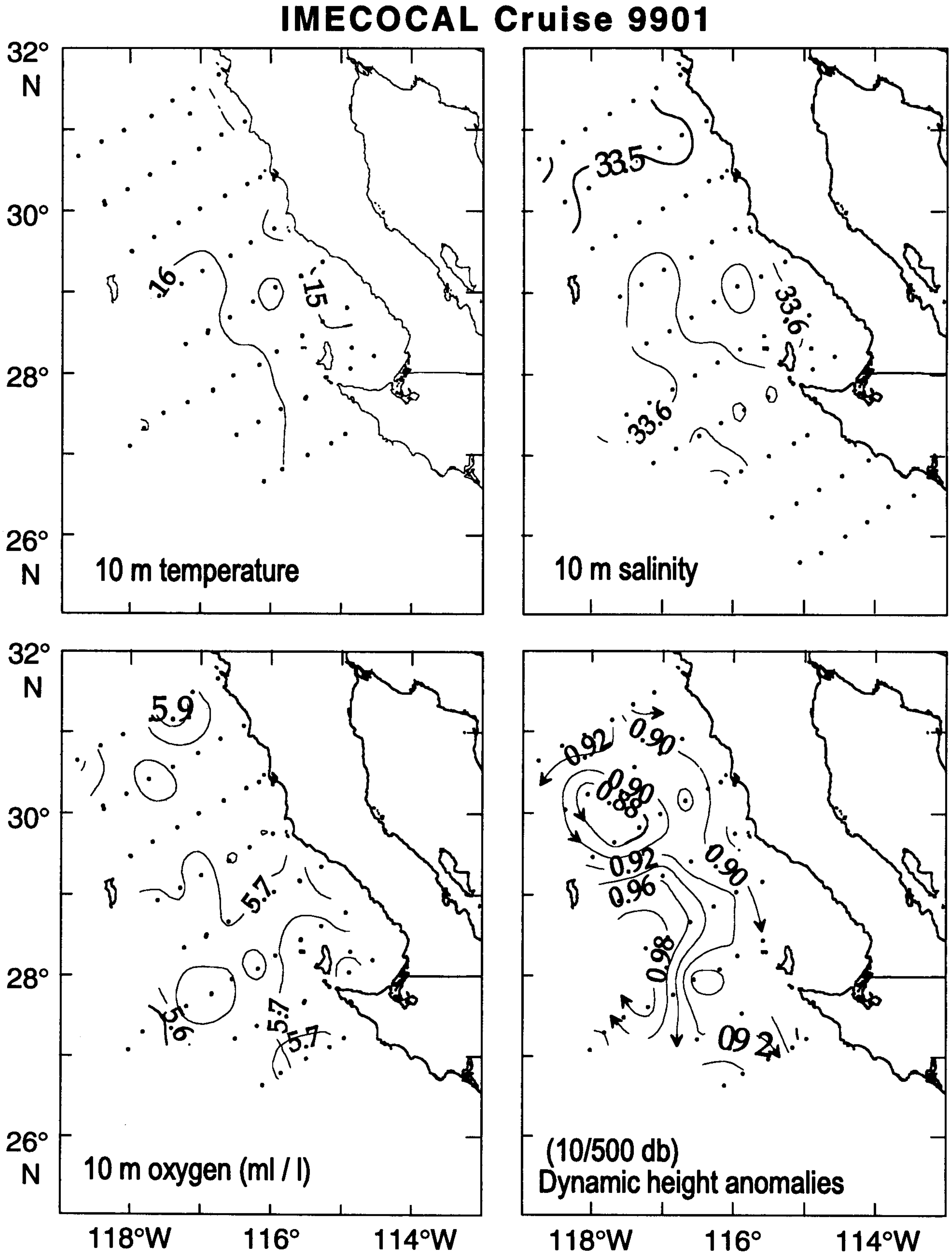


Figure 23. Spatial patterns for IMECOCAL cruise 9901 (16 January–4 February 1999) including temperature, salinity, and dissolved oxygen concentration at 10 m and geostrophic flow estimated from 0 over 500 db dynamic height anomalies.

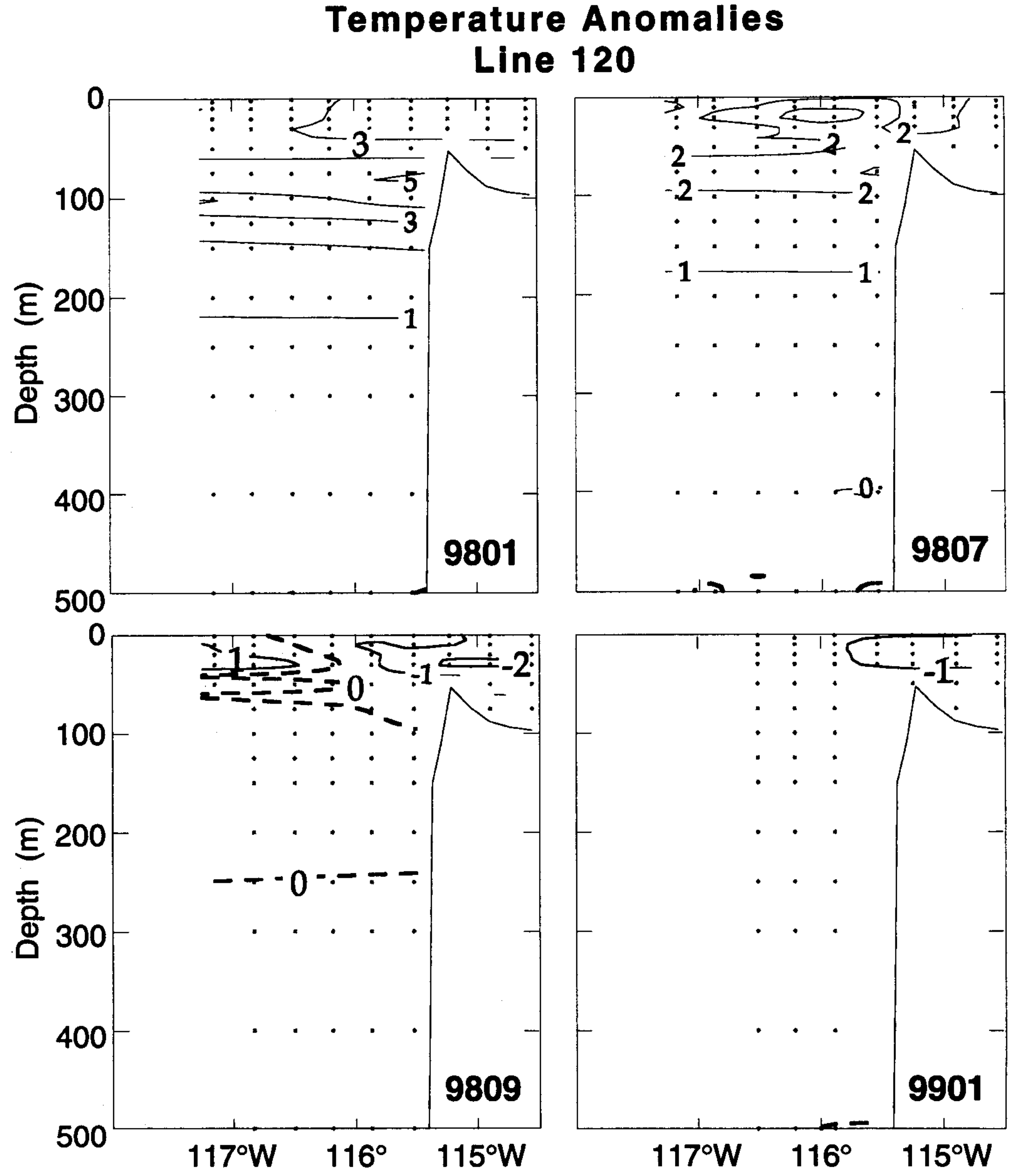


Figure 24. Temperature anomalies (°C) for line 120 from IMECOCAL cruises 9801, 9807, 9809, and 9901. Anomalies were calculated from mean values given by Lynn et al. (1982) for the period 1950–78.

California Current enters the region with a flow predominantly south, moves shoreward, and then southward around the clockwise meander near Guadalupe Island and leaves the area apparently in three branches—to the west, south, and shoreward. Coastal poleward flows are observed off San Quintín (30°N) and off Punta Eugenia (27°N). From 31° to 28°N, low temperatures nearshore (<18°) associated with low dissolved oxygen (<5 ml l^{-1}) indicate coastal upwelling.

There was a relatively homogeneous distribution of nearsurface properties on IMECOCAL cruise 9901 (fig. 23). Lower temperatures (<15°C) are found off capes and north of Vizcaíno Bay. During this cruise, strong and persistent northwesterly winds were observed. The California Current enters the survey area in the north and splits into two branches, one flowing west around a cyclonic eddy centered at ~200 km offshore, and the other flowing south as a coastal current. This coastal flow is also suggested by the salinity distribution. Near Guadalupe Island the California Current meanders and apparently merges with the coastal flow. There is no evidence for a coastal poleward flow at this depth. Temperatures and salinities were about 2° to 3°C and 0.2–0.4 lower than on IMECOCAL cruise 9801 (fig. 20), consistent with the transition to La Niña conditions.

Figures 24 and 25 show vertical distributions of temperature and salinity anomalies for IMECOCAL line 120 (off Vizcaíno Bay) for each cruise. The anomalies are

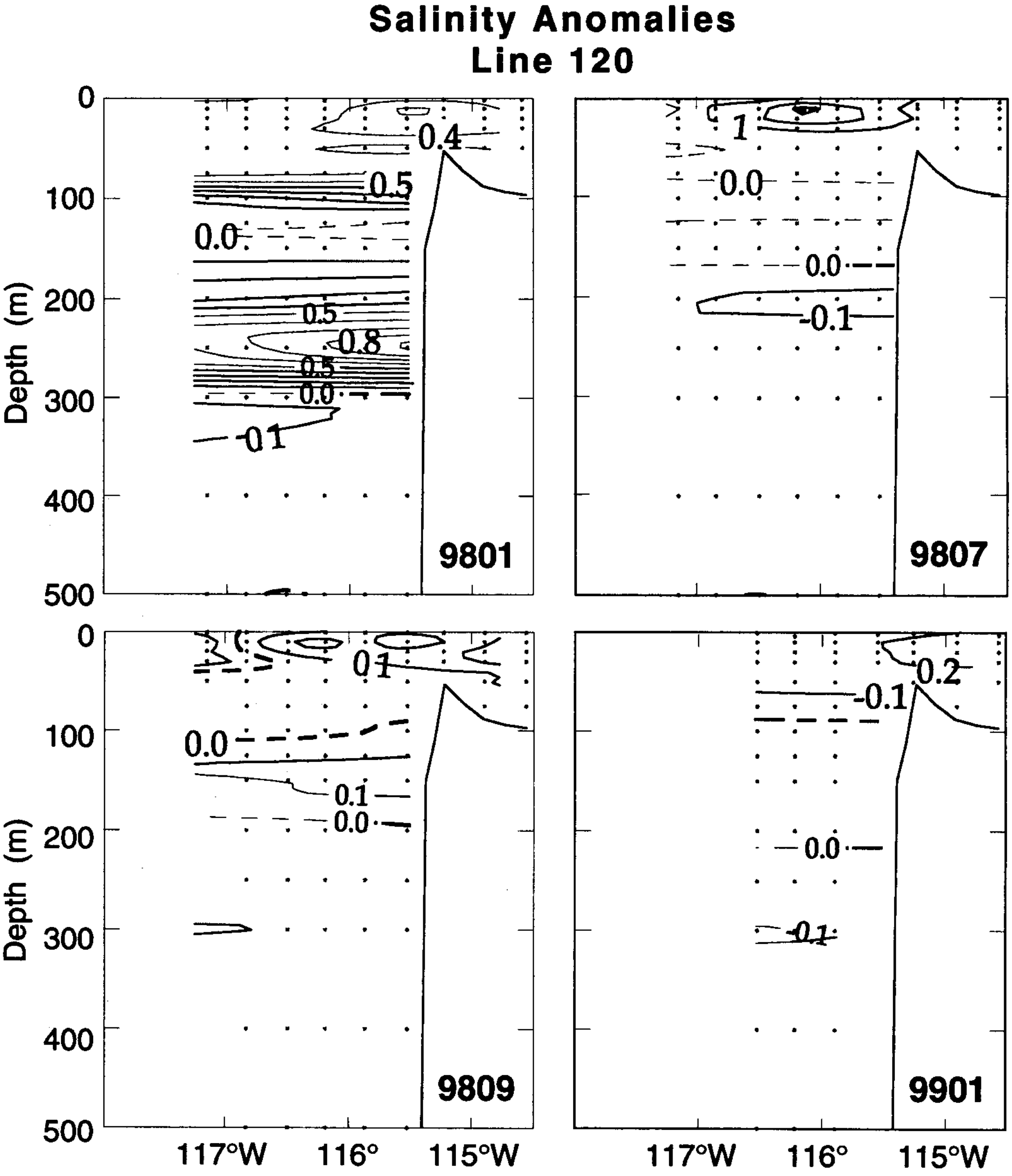


Figure 25. Salinity anomalies for line 120 from IMECOCAL cruises 9801, 9807, 9809, and 9901. Anomalies were calculated from mean values given by Lynn et al. (1982) for the period 1950–78.

based on climatological means for the period 1950–78 (Lynn et al. 1982) and may not be directly comparable in magnitude to the anomalies calculated for CalCOFI, which are based upon a longer reference period. In general, temperatures were above the norm on the January and July 1998 cruises, with maximum values of 5° over the shelf break at 100 m. July showed positive surface anomalies of up to 3°. Both 9809 and 9901 cruises showed 1° to 2° negative anomalies inside Vizcaíno Bay. Furthermore, cruise 9809 showed positive anomalies in the upper 50 m offshore. Salinity anomalies were relatively small on all of the cruises except for January 1998. Two maxima were observed, one at 100 m and another at 250 m, on cruise 9801. A similar pattern, but with smaller anomalies, was also observed in October 1997 (Lynn et al. 1998). The upper anomaly maximum (0.5) is at the same depth as the maximum temperature anomaly. The T-S plots (not shown here), suggest that this anomaly layer is found in the core of the California Current. The core is about 20–30 m thick and penetrates offshore as a gradually thickening subsurface lens. The dynamic topography for 100/500 dbar indicates that the California Current flows as an offshore clockwise loop, with southerly flow at this depth. The anomalous core at 250 m is located over the shelf break, and the anomalies reach values of 0.9. This core is associated with a poleward flow of subtropical subsurface water (Wyrtki 1967), with salinities

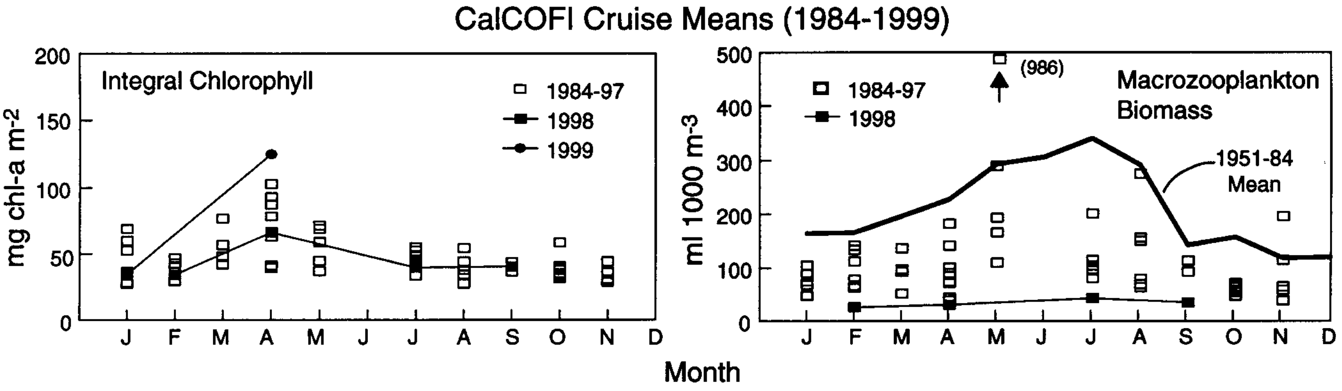


Figure 26. Cruise means of vertically integrated chlorophyll and macrozooplankton biomass plotted versus the month of CalCOFI cruises from 1984 to 1999. Each point represents the mean of all measurements on a cruise (normally 66). The open squares show the cruises that took place from 1984 to 1997. The solid symbols are cruises from 1998 and 1999; cruises from individual years are connected with lines. The bold line in macrozooplankton biomass indicates the monthly means for 1951–84.

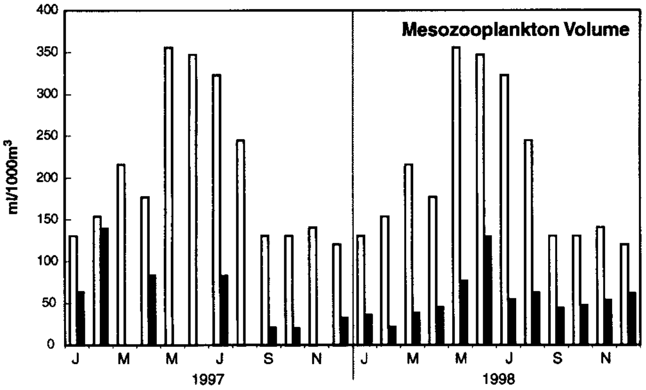


Figure 27. The time series of macrozooplankton volumes for 1997 and 1998. The clear bars represent long-term averages (including recent data) and are repeated for each year. The dark bars represent data for 1997 and 1998. The stations are the nearshore stations out to and including station 60 in the pattern occupied since 1985 between and including lines 77 and 93. Macrozooplankton volumes do not include the volumes of organisms whose individual volume is greater than approximately 5 ml.

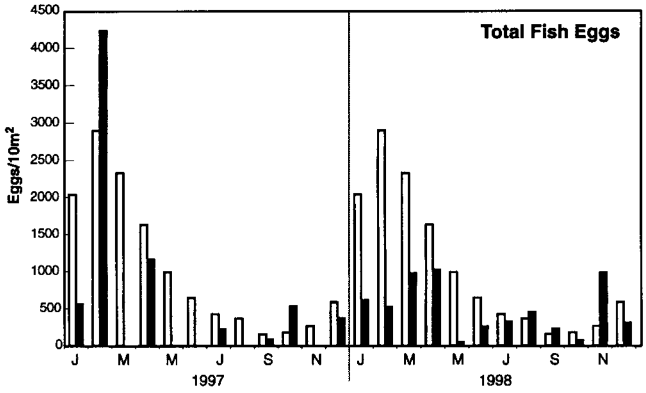


Figure 28. The time series of total fish eggs for 1997 and 1998. The clear bars represent long-term averages (including recent data) and are repeated for each year. The dark bars represent data for 1997 and 1998. The stations are the nearshore stations out to and including station 60 in the pattern occupied since 1985 between and including lines 77 and 93.

above 34.5 and temperatures in the range of 9° to 10°C, extending from 200 to 300 m in the vertical and about 120 km offshore.

Ecosystem Structure

The cruise mean plots for vertically integrated chlorophyll and macrozooplankton biomass (fig. 26) include the period of the strong influences of the 1997–98 El Niño and the transition to cool-water conditions (data for chlorophyll only). Chlorophyll followed the pattern of the last decade in that no long-term trend was evident. The vertically integrated values do not look anomalous in the context of data taken since 1984, when systematic time-series measurements of chlorophyll were started by CalCOFI. The April 1999 value was the highest observed since 1984, and this was coincident with the anomalously low temperatures and shallow nutricline seen throughout the study area. Macrozooplankton biomass also continued the long-term trend of decreasing values observed since the mid-1970s (Roemmich and McGowan 1995; McGowan et al. 1998). The values in 1998 were the lowest since 1984 for each of the cruises. The biomass values for 1999 were not available as this report was being prepared.

CalCOFI plankton samples are routinely sorted for the abundance of fish eggs and larvae in order to provide information about population dynamics of commercially important species. The abundances of macrozooplankton, total fish eggs, sardine eggs, anchovy eggs, and small larvae of hake from the CalCOFI survey cruises and the mini El Niño cruises are shown here (figs. 27–31). The standing crop of total fish eggs ranged from about 1/5 to 1/2 the long-term (1951–98) average from January 1998 to June 1998 (fig. 28). Since hatching time is faster in warm water, the decrease in production will not be as large as implied by the decline in standing stock. But this temperature dependence will, in principle, be small. We do not know the origin of this decline in production. It may be that less fecund fish species moved in from the equatorial side of the study area, or it may be

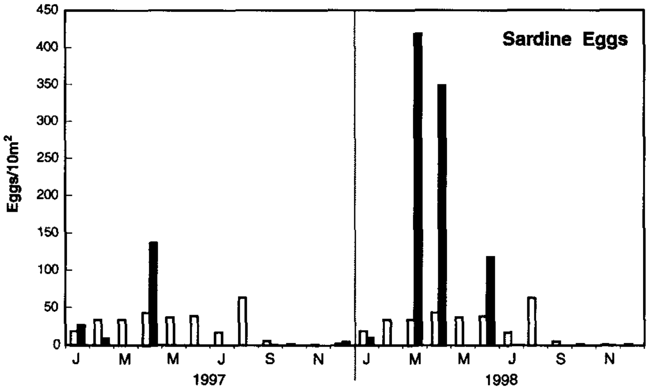


Figure 29. The time series of sardine eggs for 1997 and 1998. The clear bars represent long-term averages (including recent data) and are repeated for each year. The dark bars represent data for 1997 and 1998. The stations are the nearshore stations out to and including station 60 in the pattern occupied since 1985 between and including lines 77 and 93.

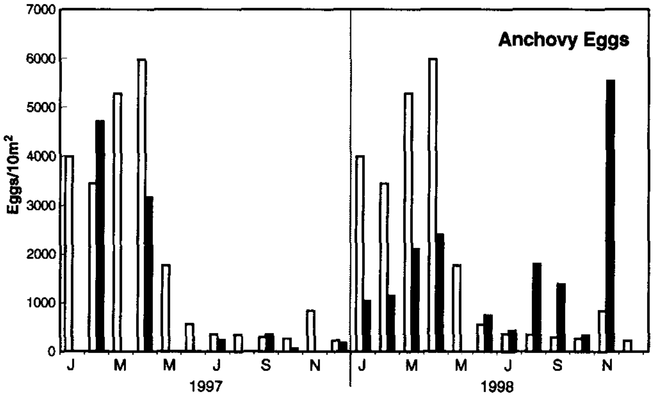


Figure 30. The time series of anchovy eggs for 1997 and 1998. The clear bars represent long-term averages (including recent data) and are repeated for each year. The dark bars represent data for 1997 and 1998. Extrusion of anchovy eggs has been adjusted for the years with 1 m ring nets with 30xxx gauze silk nets (1951–75) and the years with higher-speed bongo nets with 0.505 mm Nitex nylon netting (Loggerwell, pers. comm.). The stations are the nearshore stations out to and including station 60 in the pattern occupied since 1985 between and including lines 77 and 93.

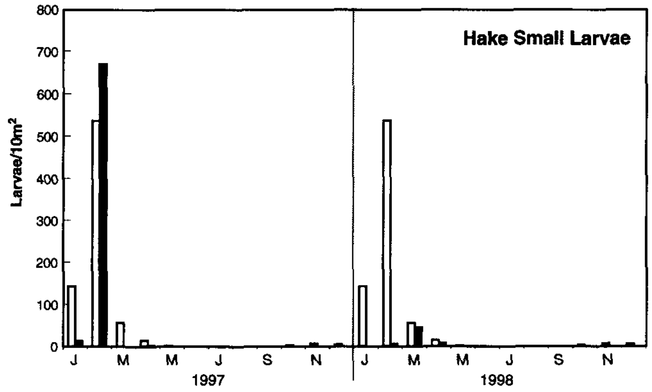


Figure 31. The time series of hake larvae for 1997 and 1998. The clear bars represent long-term averages (including recent data) and are repeated for each year. The dark bars represent data for 1997 and 1998. Extrusion of hake larvae (2 mm–3.75 mm) has been adjusted for the years with 1 m ring nets with 30xxx gauze silk nets (1951–75) and the years with higher-speed bongo nets with 0.505 mm Nitex nylon netting (Loggerwell, pers. comm.). The stations are the nearshore stations out to and including station 60 in the pattern occupied since 1985 between and including lines 77 and 93.

that local fishes produced less spawn. Another possibility is that with warm surface layers, fish normally found within the 0–210 m depths sampled by the bongo net spawned at greater depth, or their eggs sank or did not rise into the sampled layer.

Sardine eggs became more abundant in 1997 and 1998 (fig. 29). The sardine has been increasing in abundance and spawning area since the 1970s, and recent increases are probably more indicative of the long-term trend than a response to El Niño conditions. The low values at the onset of cooler conditions are correlated with the transition to La Niña conditions, but this too should not necessarily be interpreted in terms of a population response, because sardine spawning is normally at a low ebb in the autumn.

Conversely, the anchovy has been decreasing in spawning area in the last two decades, and the trend of low abundance, ranging from $^1/_5$ to $^1/_2$ normal, may be reflected in addition to a population response to El Niño conditions (fig. 30). The pattern of normally low anchovy egg abundance in autumn and the observed high rate during the fall of 1998 leads to a possibility that the anchovy population is increasing in concert with the transition to La Niña conditions.

The hake population has been remarkably stable in recent years, so the extremely low abundance of the spawn in 1998 is unusual (fig. 31). It is possible that hake spawning shifted to the north during the warm El Niño conditions, as it did during 1984. It is not likely that the low abundance of hake eggs is due to a lack of spawning biomass.

There is a clear need for additional information on the size and depth distribution of the zooplankton, ideally to include smaller sizes in order to better understand how plankton dynamics influence fish populations. To this end, the standard CalCOFI bongo net was augmented with an optical plankton counter (OPC; Herman 1988) beginning with cruise 9802. The OPC counts and estimates the size of particles of about 250 microns equivalent spherical diameter (ESD) and greater by measuring the light they occlude when passing through a fixed beam. The OPC in CalCOFI is mounted in the mouth of the starboard net of the standard bongo frame and is equipped with batteries, an integral flowmeter, and an internal data logger. Data include the number, size, and detection time of particles; flow rate; light attenuance; depth; and time. This new technological approach has the advantage that no additional station time is required to collect the information and that the electronic data can be processed and distributed quickly.

Here we present a representative set of preliminary data from deployments at stations on line 87 for cruises 9804, 9807, 9809, and 9901. The data have been binned over 10 sec intervals and within three size ranges corre-

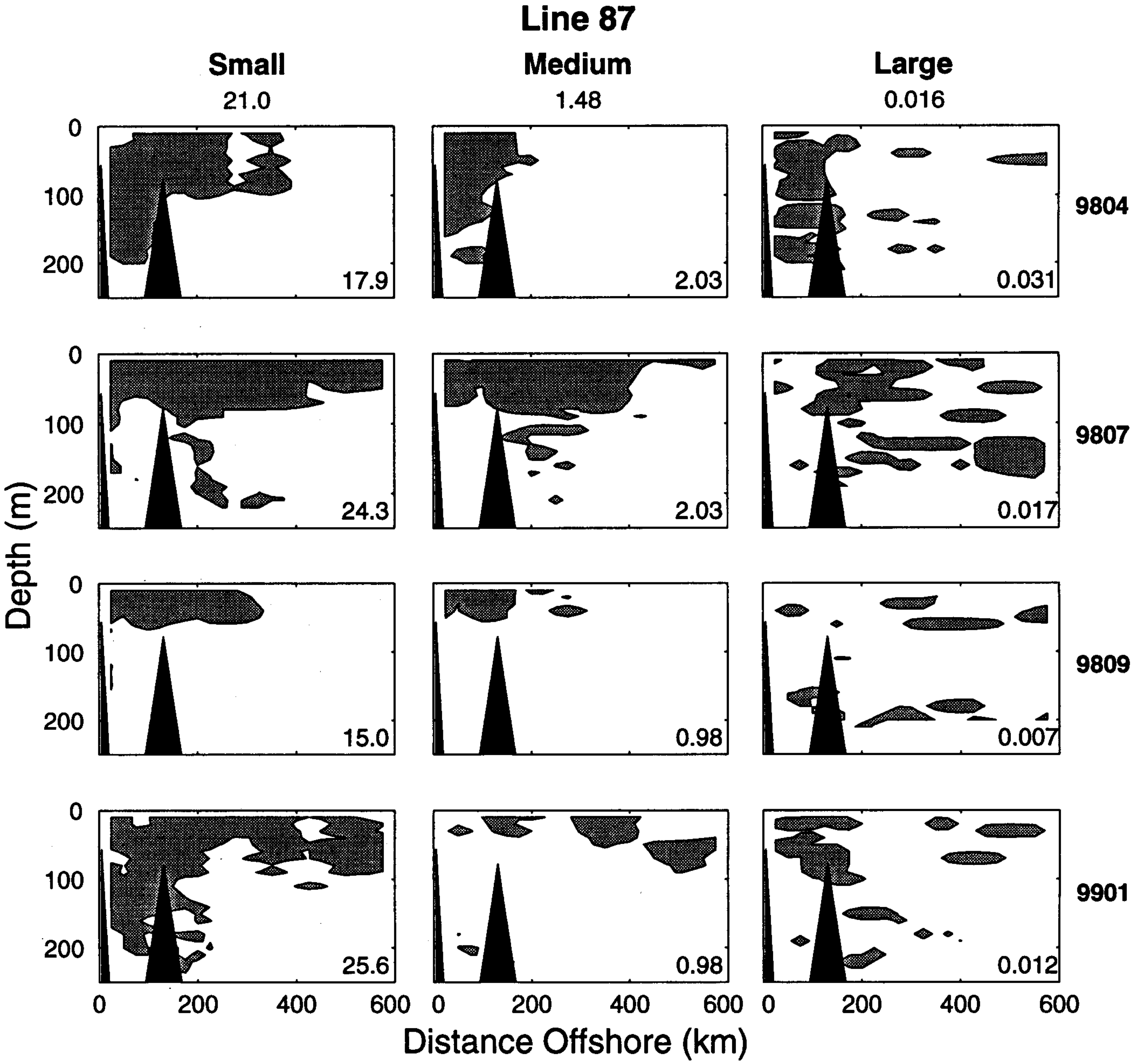


Figure 32. Optical plankton counter (OPC) data for line 87. Shown is particle concentration (particles liter^{-1}) for small (0.266–0.722 mm ESD, left panels), medium (0.722–2.38 mm ESD, center panels), and large (2.38–14.0 mm ESD, right panels) particles for four cruises (indicated at right). For each panel, particle concentration is shown in relation to distance offshore and depth. The number at the top of each column of panels is the mean particle concentration for all four cruises for the respective particle size class. The number in the lower right corner of each panel is the mean particle concentration within each cruise for the respective size class. The shaded regions in the panels represent particle concentrations greater than the mean concentration for all cruises for the respective size class.

sponding to (a) particles smaller than quantitatively retained by the CalCOFI 505 micron mesh bongo net (small: 0.266–0.722 mm ESD); (b) most copepods and smaller zooplankters quantitatively retained in the CalCOFI bongo net (medium: 0.722–2.38 mm ESD); and (c) large organisms, e.g., euphausiids (large: 2.38–14.0 mm ESD). The mean concentration (particles liter^{-1}) has been computed for each size class over all cruises and within each cruise (fig. 32). Regions within each cruise where particle concentration was greater than the average for all cruises are also shown in fig. 32 for each size class.

These data are too few to make inferences about interannual variability of the zooplankton in the California Current. But they do indicate the potential of the OPC for addressing this and the larger objective stated above. For example, the distribution and abundance of most (small and medium) particles show surface maxima. Table 2

TABLE 2
Optical Plankton Counter Data for Line 87

Cruise	Small:(medium+large)[a] Numbers	Biovolume
9804	8.68:1	0.304:1
9807	11.9:1	0.633:1
9809	15.2:1	0.845:1
9901	25.8:1	1.01:1
Combined cruises	14.0:1	0.599:1

[a] The ratios of small:(medium+large) particles are provided in terms of numbers and biovolume for four cruises separately and combined.

shows the ratio of small:(medium + large) particles sensed on line 87 in each cruise. Also shown are such data for estimated biovolume per liter; in this case, the biovolume of each particle was calculated from its ESD with the equation of Herman (1988). On average, there were 14.0 times more particles smaller than 0.722 mm ESD than particles larger than this, and the ratio varied between cruises (8.68 to 25.8). In terms of biovolume, however, the reverse obtained, with the medium size class containing the greatest biovolume, and on average there being 0.599 as much biovolume in the 0.266–0.722 mm ESD size class as in the 0.722–14.0 mm size class, with similar intercruise variation in this ratio (0.304–1.01). Thus, on average for the data considered here, the CalCOFI bongo net probably captured only a small fraction of the total number but most of the biovolume of particles sensed by the OPC. These preliminary data indicate significant spatial and temporal variation in the abundance and size of the zooplankton and demonstrate our ability to measure it, with potentially significant implications for our understanding of the California Current system and its change.

CalCOFI time-series cruises also provide a continuing opportunity for systematic surveys of the distribution and abundance of seabirds in relation to oceanographic conditions off southern California. Recent surveys during El Niño and the transition to La Niña conditions have facilitated the study of how seabirds respond to interannual oceanographic variability off our coast. Seabird communities off southern California have undergone persistent changes (Hayward et al. 1996; Veit et al. 1996; Hyrenbach and Veit 1999), which appear to be in response to long-term ocean warming and declining zooplankton biomass (Roemmich and McGowan 1995). In addition to these decadal trends, interannual changes in the location of water masses and current systems are known to influence seabird distribution and abundance in the eastern Pacific (Wahl et al. 1989; Ribic et al. 1992; Ainley et al. 1995).

Seabird populations off southern California responded to the recent onset of La Niña conditions during the fall of 1998 in two ways. First, the warm-water species prevalent during the preceding El Niño event were replaced by immigrating subarctic species. For instance, while the black-vented shearwater (*Puffinus opisthomelas*) made up over one-third of all birds recorded during the fall of 1997, its relative abundance dropped to less than 10% in 1998. Conversely, the pink-footed shearwater (*P. creatopus*) increased from 13% to 53% to become the most numerous bird during the fall of 1998 (fig. 33). Most notably, sooty shearwater (*P. griseus*) abundance increased six-fold

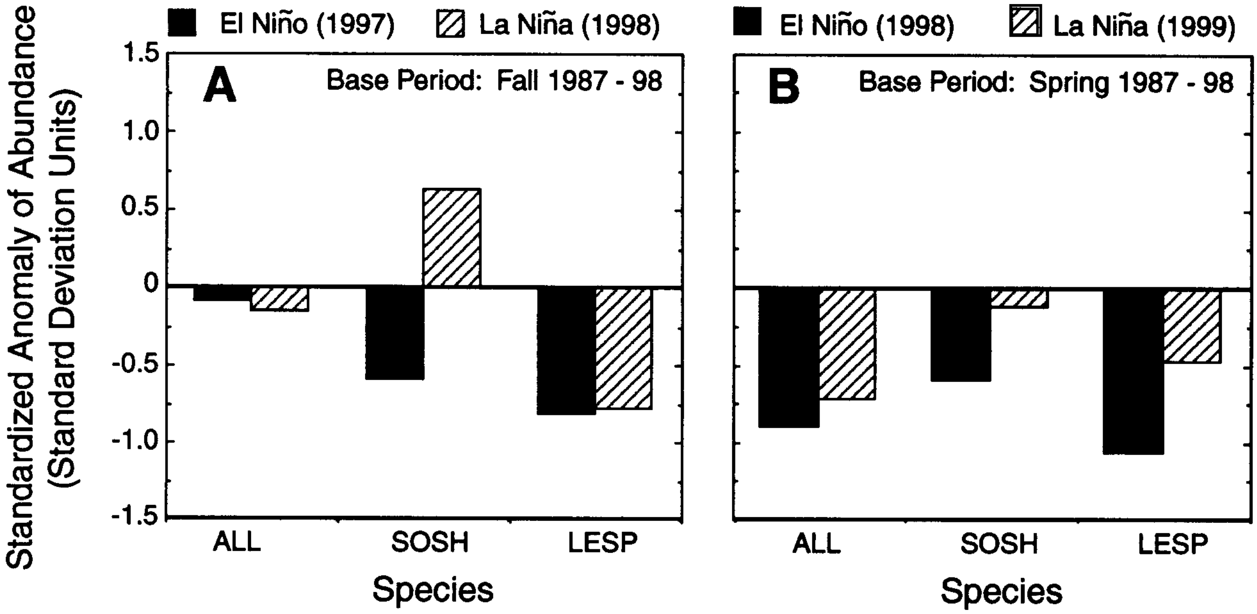


Figure 33. Changes in abundance for all bird species combined (ALL), and for the numerically dominant coastal (SOSH: sooty shearwater) and offshore (LESP: Leach's storm-petrel) seabirds during fall (*A*) and spring (*B*). Histograms depict deviations from the long-term seasonal means for cruises in September 1997–98 and April 1998–99.

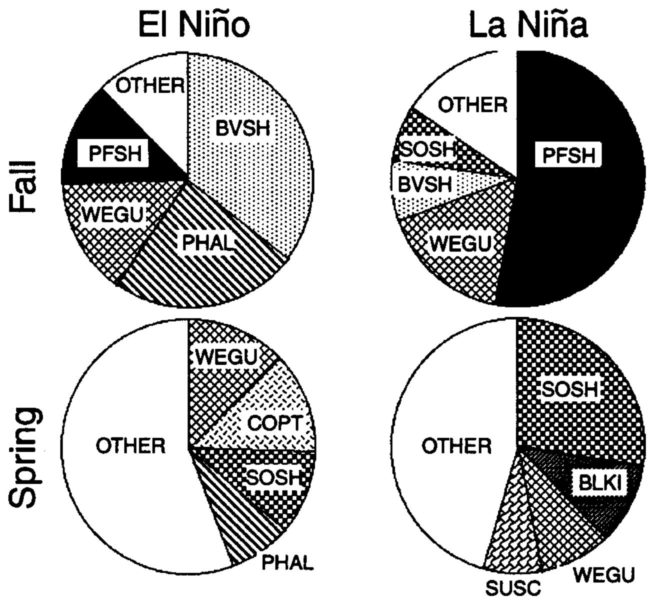


Figure 34. Relative abundance of the four most numerous bird species during El Niño (1997–98) and La Niña (1998–99) conditions. Relative abundance was computed by dividing the number of individuals of a given species by the total number of seabirds sighted during each cruise. BLKI: black-legged kittiwake; BVSH: black-vented shearwater; COPT: Cook's petrel; PFSH: pink-footed shearwater; PHAL: red and red-necked phalaropes; SOSH: sooty shearwater; SUSC: surf scoter; WEGU: western gull.

to soar beyond its long-term seasonal mean for the first time since 1992 (fig. 33). Similarly, the spring avifauna switched from one dominated by Cook's petrels (*Pterodroma cooki*) in 1998 to one dominated by sooty shearwaters and black-legged kittiwakes (*Rissa brevirostris*) in 1999. While the former is a subtropical seabird most abundant in central Pacific and transition zone waters (Wahl et al. 1989), the shearwater and kittiwake are subarctic species whose abundance off California peaks during years of cool ocean temperatures (Ainley 1976; Veit et al. 1996).

Additionally, surveys revealed that total bird abundance during 1998–99 consistently surpassed the levels observed during the 1997–98 El Niño (fig. 34). There were concomitant increases in the abundance of the dominant coastal and pelagic species in fall (fig. 33A) and spring (fig. 33B), though total seabird abundance increased only in spring. It is likely that the emigration of warm-water species in response to cooling conditions caused the decline in total bird abundance in the fall of 1998. This initial decline was offset by the arrival of far-ranging subarctic species during winter and spring.

A preliminary interpretation of these patterns is that shifts in water mass boundaries and large-scale productivity patterns driven by La Niña forcing probably affected seabird distributions off southern California (Ainley 1976; Veit et al. 1996). It is very likely that far-ranging subarctic species migrated into the CalCOFI region in response to cooling ocean temperatures and increased chlorophyll, while subtropical seabirds shifted their distributions to the south and west. It is unclear, however, whether the 1998–99 La Niña will affect long-term seabird abundance in the CalCOFI region. Years of high upwelling enhance the breeding success of resident seabird populations off central California (Ainley et al. 1995). Yet the demographic effects of these cold-water episodes on far-ranging visitors such as shearwaters and kittiwakes remain unknown. Moreover, data indicate that seabird abundance in the CalCOFI region has continued to decline in recent years, despite substantial variability in ocean conditions (Hayward et al. 1996; Lynn et al. 1998; Hyrenbach and Veit 1999). This observation suggests that the long-term association between seabirds and oceanographic variability off southern California overrides short-term fluctuations driven by interannual forcing.

The ecosystem observations in the CalCOFI study area can be related to biological changes in the region farther to the north. Since 1983, the NMFS/SWFSC Tiburon Laboratory has surveyed juvenile rockfish each spring off central California (36°30'–38°10') to develop a recruitment index. Present sampling includes ADCP, CTD, and chlorophyll. The catches of shortbelly rockfish and all rockfish juveniles from the May–June 1998 survey were the lowest in the history of the survey. Low abundances were apparent for other fish and invertebrate species as well, including normally abundant juvenile hake, squid, and euphausiids. Numbers of seabirds and marine mammals were the lowest since 1984. Juvenile sardines were an exception (Keith Sakuma, Tiburon Lab, pers. comm.). The upper water column was unusually warm (12°–15°C) and fresh (salinity of 32–33). Much of the region was dominated by a lack of upwelling and the onshore displacement of California Current water, while high freshwater discharge from the San Francisco Bay heavily influenced the Gulf of the Farallones. Chlorophyll levels were extremely low.

Few rockfish larvae were found in early 1999. The temperature was cool and the upper layer well mixed compared to previous years. Chlorophyll samples taken at the subsurface maximum layer were low (max = 1.9 $\mu g\ l^{-1}$). Generally, adult rockfish schools were smaller in comparison to historical data, which tends to corroborate the declining trend in the survival of juvenile shortbelly rockfish seen during the last decade. However, the stomachs of the fish that were collected were full of euphausiids, and they also had large volumes of mesenteric fat. This may lead to increased larval survival this year (David Woodbury, Tiburon Lab, pers. comm.).

The data from the offshore waters collected on CalCOFI cruises can also be related to events in southern California kelp forest communities. Forests of giant kelp (*Macrocystis pyrifera*) in southern California are highly

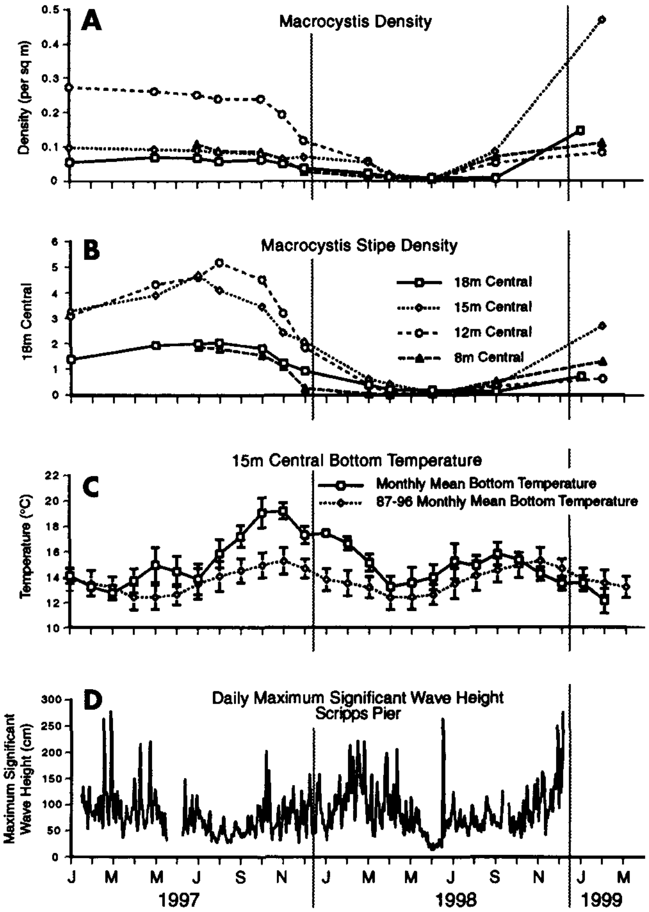


Figure 35. *A*, Changes in density of *Macrocystis* adults (defined as having four or more stipes), and *B*, stipe density from permanent sites at 18, 15, 12, and 8 m in the center of the Point Loma kelp forest, January 1997 through March 1999. See Tegner et al. 1997 for sampling details. *C*, In situ temperature at 15 m for 1997–99 and the mean for 1987–96; error bars represent one standard deviation. *D*, Daily maximum significant wave height from the SIO Pier. Gaps in the data are due to equipment failure (Coastal Data Information Program).

dynamic communities that track environmental variability associated with El Niño–Southern Oscillation events. Dependent on high levels of nutrients to maintain growth rates and standing biomass, *Macrocystis* populations are sensitive to interannual variability in sea-surface temperatures, measured as a surrogate for nitrate availability or stress (Tegner et al. 1996). Because these plants can only store up to a month's worth of nitrogen, there is little lag between ambient conditions and growth rates. Two major and interacting sources of mortality for giant kelp are storm waves and nutrient stress; the severity of the damage caused by storm waves is affected by the nutrient status of the plants (Dayton et al. 1992). *Macrocystis* mortality is also highly age dependent; two- to three-year-old plants have the highest survival rates at Point Loma (Dayton et al. 1984).

The timing of the very strong El Niño of 1997–98 in the Point Loma kelp forest near San Diego is illustrated by the temperature curve in figure 35. Positive temperature anomalies peaked in fall 1997 and winter 1998, and continued through the end of summer 1998. By winter 1999, there was evidence of cooler than normal, La Niña conditions. Strong El Niño winters in the Northern Hemisphere are often accompanied by extraordinary storm seasons in southern California. The winter of 1998 produced more than twice as many large wave events, including some with exceptionally long duration, than did the last strong El Niño in 1983 (Seymour 1998). The combination of the storms and warm water led to virtually complete mortality of *Macrocystis* at Point Loma (fig. 35A). There was recruitment of giant kelps in spring and summer 1998, but warm, nutrient-depleted water during the summer followed by another high-wave-energy winter led to poor growth and survival of young plants, especially at the shallower 12 and 8 m sites. Cold, nutrient-rich waters in winter and spring 1999 are supporting excellent growth of plants that survived the winter. Plant densities will remain low at the shallow sites for the lifetime of these cohorts because of the loss of so many juveniles; densities at the deeper sites will continue to increase as small plants grow to four stipes (analogous to the branches of land plants), our criterion for adulthood. Given the outstanding growth conditions, increased stipe density at the shallow sites has the potential to make up the loss of biomass from density reductions, because plant size is strongly related to temperature/nutrient availability (Tegner et al. 1996).

DISCUSSION

The fiftieth anniversary of the CalCOFI program is an appropriate time to consider the time-series observations in a larger context. A broad suite of new observational technologies is becoming available. Findings from prior observations are being analyzed and new insights being gained. This may lead to a reconsideration of the priorities for different types of measurements currently being made and new types of measurements that could be made. Here we place the CalCOFI time-series observations in a larger regional context and consider them over longer time scales. We consider the value of the CalCOFI time-series observations for purposes other than the fisheries oceanography focus of CalCOFI, such as their role in supporting policy making and management on both regional and global change space-time scales.

It is clear that CalCOFI needs to continue to consider how well the present sample scheme resolves temporal changes and whether the spatial scale of the sample grid is appropriate to support our basic mission. The present sample pattern (fig. 1) of quarterly cruises done every year was implemented in 1985. This represented a large change in space-time scales from the previous pattern of intensive sampling of a larger area extending from central Baja California, Mexico, to Point Arena;

the pattern was completed over one annual cycle every third year. This change in space-time scale of sampling was based upon the observation that the low-frequency signal is spatially coherent over large spatial scales (Chelton et al. 1982), and upon the need to better resolve seasonal and interannual variability. The suite of properties which were routinely measured was also increased in 1985 to include nutrients, chlorophyll, and primary production as "core" measurements. Additional properties have been added in recent years. This change in the scale of sampling has been successful in that the present pattern does a better job of resolving interannual and seasonal variability. But it can be seen from figures 17, 18, and 26 that the quarterly cruises still do not sufficiently resolve the annual cycle. Annual averages may be biased by hitting or missing what may be a sharp peak, especially during the period of rapid change in biological structure during spring and early summer. CalCOFI scientists are exploring approaches to additional cruises, possibly using continuous sampling technology, in order to better resolve the annual cycle.

CalCOFI researchers have observed (data not shown) that the spawning range of the sardine is expanding to the north. This expansion may be related to increases in the sardine population and changes in physical structure and circulation patterns related to El Niño. The need to sample, at least, the abundance of fish eggs in the region north of the present survey area led CalCOFI to consider the value of sampling three additional lines north of the normal pattern by using continuous sampling technology (CUFES, CUDLS—CalCOFI underway data logging system, and ADCP). This approach has the advantage of obtaining the most critical information at the least cost in ship and technician time. Its drawback is the lack of subsurface physical information, except ADCP, and CalCOFI researchers are exploring additional approaches to make up for this (e.g., seasoar or free-fall CTD systems, which can be deployed from a moving ship). The CalCOFI interest in sampling in the central California region coincides with renewed interest in ocean observing programs by U.S. GLOBEC and other large oceanographic programs.

The theme of applying new technological approaches to address longstanding questions is capturing increasing interest within CalCOFI as well as at the national and international levels. New technologies have the potential to provide new types of information (e.g., CUFES or OPC) or a more efficient way to gather the same type of information that is already being collected (e.g., replacement of Nansen bottle casts with CTD or seasoar profiles). When methodologies change, CalCOFI has generally been very conservative in its approach to implementing them in order to ensure the continuity of the time series. Detection of long-term trends requires that data sets be taken with comparable techniques. However, new technologies—especially those such as OPC, ADCP, and CUFES, which do not require additional station time—have great potential. CalCOFI researchers will continue to evaluate the design of the sample program to provide the best and most efficient approach to meeting information needs. The perception of the value of specific observations may also change as new understanding is gained. Such new understanding may also lead to changes in programmatic priorities. CalCOFI has encouraged participation by a wide range of cooperative research projects, thus providing a cost-effective opportunity for the development of new technologies and an opportunity to evaluate the operational value of new information.

In addition to supporting the basic programmatic objectives of CalCOFI, the observations gathered in the time-series program have great value for a broad range of other uses. Although meeting the core objectives of CalCOFI must take precedence in setting priorities for alternative sampling schemes, CalCOFI can share its time-series observations with other programs and would like to see such programs expand. There is renewed interest at the state, national, and international levels in ocean observing systems. The coastal ocean is highlighted as a region needing special attention. CalCOFI, due to its long historical record and the broad suite of properties which have been measured, will be an important component of an integrated observing system. The CalCOFI data have great potential value for supporting more broad policy and management objectives than the fisheries oceanography objectives that are central to CalCOFI. However, the use of the data may not reach its full potential because the data products developed in support of CalCOFI objectives may not be sufficiently focused to meet information needs in other policy and management areas. This is also an area in which CalCOFI would like to grow in the future.

Management and policy issues can be considered on at least two space-time scales. The first is the regional and local areas which are included within the CalCOFI survey area. CalCOFI is continuing to expand its collaboration with research programs focusing on kelp forest and "nearshore" ecosystems. One challenge here is for CalCOFI to make better use of the higher-frequency data collected at coastal buoy and shore station sites (e.g., figs. 5, 6, 8, 9, and 35), and, in turn, learning to what extent the findings of CalCOFI apply to these other ecosystems. The nature of the scientific and management issues differs to some extent in the nearcoastal region, and additional work will have to be done in order to directly apply CalCOFI observations to management and policy needs. There is more of an emphasis on ecosystem management and the processes occuring at the land-ocean interface than on fisheries oceanography issues. A large fraction of the observational effort is devoted to compliance monitoring (e.g., sampling around ocean discharges covered by a National Pollutant Discharge Elimination System permit to ensure compliance with the terms of the permit). Additional observations are made in support of basic research within this general region. Greater consideration of the results of the CalCOFI time-series observations would allow regional policy makers to place the results of local or point source compliance monitoring in a regional context. It may be necessary to develop additional types of data products which are more focused upon the needs of regional policy makers in order to increase the value of the CalCOFI data for such issues.

CalCOFI data will also be applied to studies of ecosystem change on global and climate change time-space scales. Here the CalCOFI observations will be considered as one component of a global monitoring system. Many of the changes in the California Current ecosystem documented by CalCOFI are correlated with climate-scale changes in the atmosphere and physical structure of the ocean (Chelton et al. 1982; Roemmich 1992; Roemmich and McGowan 1995; Veit et al. 1996; McGowan et al. 1998). CalCOFI observations will have great value in testing and developing new models linking climate change and physical structure. CalCOFI will benefit from the development of such models because the progress in predicting physical structure based upon observations or models is clearly proceeding more rapidly than predictive models of ecosystem structure. In particular, the CalCOFI region seems to be a natural region for the development and evaluation of assimilation models of ocean circulation. The ongoing time-series observations will be ideal as data inputs for such models and for testing the results. CalCOFI will benefit from an improved knowledge of the circulation, since the strong correlations between physical and biological structure in the region have been well established.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

Asilomar, California
4 November 1998

A CONTINUING DIALOG ON NO-TAKE RESERVES FOR RESOURCE MANAGEMENT

Interest is rapidly growing within state and federal agencies to reevaluate current practices of marine fishery management, and to consider alternatives that would more effectively maintain healthy coastal populations. This interest is largely motivated by the alarming long-term decline in abundance of several economically important fishery stocks, the increasing potential for significant habitat degradation from anthropogenic sources, and the heightened public awareness of challenges to marine ecosystems. Although the declines in abundance are probably due to a combination of overexploitation and the effects of natural environmental variability on spawning success and survival of young fish, it is clear that traditional management efforts alone have not successfully protected and sustained coastal resources.

Some aspects of spatial management, such as areas closed to fishing, are not new concepts in California. Various types of fishing gear have been excluded from specific areas of the coast for many years. For example, bottom trawls generally have been prohibited within three nautical miles of the coast, as has the use of gill nets for rockfishes. Fishing for abalone is completely banned in central and southern California, and limited to free diving in the north. Designated reserves (also known as harvest refugia, protected areas, and no-take zones), however, are a relatively new option being considered as a supplement to current management practices in California.

Marine reserves are being promoted to mitigate overfishing and the effects of fishing activities on seafloor habitats. Potentially, reserves can conserve and enhance fish populations by (1) increasing abundance, size, and age composition; (2) protecting critical spawning stocks; (3) providing multispecies protection; and (4) provid-

Figure 1. Participants in the 1998 Symposium of the CalCOFI Conference: A Continuing Dialog on No-Take Reserves for Resource Management. Top row, left to right, Ralph Larson, Richard Parrish, Mark Carr, Steve Murray, and Brian Baird; bottom row, Caroline Pomeroy, Cindy Thomson, Louis Botsford, Melissa Miller-Henson, Mary Yoklavich, and Bill Douros.

ing undisturbed, baseline areas against which fishery-induced changes may be evaluated. They also can help preserve and maintain the natural diversity of individual species, genotypes, and habitats. Although some of these attributes can be expected, reserve concepts largely remain untested, and their effectiveness in fisheries management is poorly understood.

Several recent activities have been initiated to examine the feasibility of using marine reserves to better manage fishery populations on the West Coast. At the workshop "Marine Harvest Refugia for West Coast Rockfish,"[1] there was consensus among scientists and resource managers that marine reserves exemplify a precautionary approach to the management and conservation of rockfish resources. The Pacific Fisheries Management Council appointed an ad hoc Marine Reserve Committee in November 1998 to advise the council on effectiveness, design criteria, and implementation of reserves. In addition, a cooperative process between state and federal management agencies is being developed to consider a system of marine reserves in the Channel Islands National Marine Sanctuary.

Examining issues critical to the establishment of marine reserves requires the balanced perspective and broad expertise of biologists, ecologists, social scientists, economists, resource managers, and policy makers. The 1998 CalCOFI symposium convened such a group to further the discussion of marine reserves for managing California's resources. Our objectives were to (1) identify processes and opportunities for implementing change in federal and state resource management; (2) consider costs, benefits, risks, and alternatives for establishing reserves; (3) examine biological aspects of reserve design; and (4) explore compliance and enforcement issues.

The efforts of several people contributed to the success of this symposium. I extend my appreciation to all participants for their verbal and written contributions to the symposium and proceedings. I thank a long list of scientists and resource managers for their reviews of the individual papers, and Julie Olfe for her technical advice and editorial services. The National Marine Fisheries Service, Pacific Fisheries Environmental Lab supported my efforts to convene this symposium and serve as editor of the proceedings. Thanks to George Hemingway for logistic support throughout the process, and to John Hunter for his perspective on the value of agency policy, planning, and procedures to these proceedings.

Mary Yoklavich

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[1] Yoklavich, M., ed. 1998. Marine harvest refugia for West Coast rockfish: a workshop. NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFSC-255, 159 pp.

ANALYZING CALIFORNIA'S MARINE MANAGED AREAS: EXISTING CLASSIFICATIONS AND OPTIONS FOR THE FUTURE

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ABSTRACT

California has a long history of establishing marine managed areas. Site designations have been made through various administrative, legislative, or voter initiative processes without the benefit of a statewide plan to ensure effectiveness or consistency among sites and designations. In recent years, the State of California has initiated a critical review of its marine management practices. The landmark report *California's Ocean Resources: An Agenda for the Future* called for a review of California's marine managed areas, which led to the establishment of the State Interagency Marine Managed Areas Workgroup, chaired by the Resources Agency.

The participants in this effort are working to identify and recommend a more effective and less complicated statewide classification system for marine managed areas, relying as much as possible on the expertise and knowledge of individuals with management responsibilities and interests in ocean and coastal managed areas. The final report will be a collaborative effort, the ultimate success of which will depend on a series of interactive workshops, meetings, and Internet discussions involving a wide variety of stakeholders. Final recommendations are likely to include a mix of administrative and legislative actions.

INTRODUCTION

> *The sardines cannot be treated as isolated organisms living in a vacuum. The investigation must be an integrated one in which proper weight is given not only to the currents and other aspects of the physical environment but also to the entire organic assemblage, including the plants and animals which form the food chain of the sardines, their competitors for the food supply, and the predators, including man.*
>
> —Roger Revelle *in 1947,*
> *as quoted by Harry Scheiber (1990)*

In a similar fashion, California's array of named, discrete marine managed areas (such as reserves, refuges, and natural reserves) should not be viewed as a single solution to the numerous and multifaceted problems related to ocean and coastal resource management. Marine managed areas (MMAs) are but one of many tools available to policymakers and managers and should be viewed within this context. We will describe the use of a collaborative approach between state agencies and constituencies in our investigation of the classification system for MMAs in California. The challenge presented by this task is great, because the current array of classifications to protect and manage marine resources is complex and often confusing. This effort can succeed only with the assistance, cooperation, and hard work of many people who care deeply about California's ocean and coastal resources.

BACKGROUND

The use of MMAs for protecting ocean and coastal resources has a long history in California, dating back to the early 1900s. Over the years numerous classifications have been established, evolving on a case-by-case basis through legislative and administrative actions and by public referendum. These designations have not conformed to any plan for establishing MMAs in the most effective way or in a manner that ensures that the most representative or unique areas of the ocean and coastal environment are included.

In addition, a number of state agencies have been given a role in the designation and management of marine areas, leading at times to duplicative or conflicting goals, rules, and regulations. A California Department of Fish and Game (CDFG) report released in 1989, *Marine Life Refuges and Reserves of California*, evaluated the different classifications managed by the department and found that "The net effect of these laws and regulations is that we now have only minor differences between the regulations governing the use of refuges and reserves established by the legislature and the Fish and Game Commission."

Shortly after the release of the CDFG report, the legislature passed the California Ocean Resources Management Act (AB 2000 as amended by AB 205 in 1991, Farr), which mandated several actions, two with major implications for the management of California's marine areas. First, all nonstatutory executive branch responsibilities for ocean resource management were transferred to the Secretary for Resources. Second, the act required the preparation of a document to lay out a vision for more coordinated, efficient, and effective approaches to a wide variety of issues dealing with ocean resource management.

In preparing the required document, the Resources Agency held six public workshops in 1993 and six more in 1995 along the California coast to discuss and take comment on issues relevant to ocean and coastal resource management in California. One such issue was what the public perceived as a complex and confusing array of marine "managed" areas along the coast. This issue surfaced in the early proceedings, but the public has become substantially more interested in it during the last two years.

The final document, *California's Ocean Resources: An Agenda for the Future* (Ocean Agenda; Resources Agency of California 1997), was released at the international conference "California and the World Ocean '97" held in San Diego in March 1997 (organized by the Resources Agency of California and the Coastal Zone Foundation). The Ocean Agenda is both a resource and a statewide strategy, identifying methods for improving the way we manage our economic and natural resources. The Ocean Agenda addresses four broad categories:

- California's ocean ecosystem and the relationship between land and sea
- Economic contributions of key ocean-dependent industries
- Research, education, and technology development
- Jurisdiction and ownership relating to ocean management.

MARINE MANAGED AREAS AND THE OCEAN AGENDA

The most familiar term for many people when referring to an area along the coast that is managed in some way to protect ocean and coastal resources is *marine protected area* (MPA). The term is typically used to describe areas of intertidal or subtidal terrain that are reserved by law or regulation to protect part or all of the resources within them.

The Ocean Agenda explicitly uses the term *marine managed area* rather than MPA for two reasons. First, the term *protected* often gives the misimpression that the area is under complete protection, and that no extraction of marine resources will be allowed. Because most of the existing classifications and designated sites do not provide this level of protection, the term *managed* has been used to provide a more accurate description. Second, how we manage our shoreline environment has a definite and measurable effect upon the intertidal and subtidal components of the ocean ecosystem. The Ocean Agenda uses the term *marine managed area* to identify discrete "named" areas that provide some level of management or protection to marine resources. While this is primarily intertidal and subtidal, terrestrial areas (such as coastal state parks) that are adjacent to marine waters are also included. Thus MPAs are a subset of MMAs in that all subtidal, intertidal, estuarine, and adjacent terrestrial areas are included in the definition of a marine managed area.

The Ocean Agenda found that California's array of ocean and coastal managed area classifications (approximately 20, including reserves, state reserves, ecological reserves, natural reserves, etc.) is complex and often confusing. Specifically, the Ocean Agenda identified uncertainty about the requirements of, restrictions within, and boundaries of the array of sites and classifications. For instance, reserves established by the Fish and Game Commission have no legally mandated mission or general regulations in the California Code of Regulations. As a result, there is confusion about the intent of reserve designations, and little consistency in limitations to the collection or harvest of species among reserve sites.

Maps in the Ocean Agenda show the general location of these areas, and accompanying charts explain the different classifications and their purposes. Questions have arisen about the effectiveness and enforceability of these designations meant to safeguard the state's ocean and coastal biodiversity and to promote public use and enjoyment of these resources (Murray et al. 1999). As a result, the Ocean Agenda recommended that the state evaluate this array of classifications to develop a more effective and less complicated statewide system of ocean and coastal managed areas. It further recommended developing a comprehensive program, with clear criteria for creating, administering, and enforcing management measures in these specially designated areas. To address these recommendations, the Resources Agency of California convened a State Interagency Marine Managed Areas Workgroup.

STATE INTERAGENCY MARINE MANAGED AREAS WORKGROUP

The State Interagency Marine Managed Areas Workgroup is charged with defining and evaluating the current array of state MMA classifications and recommending improvements. The initial approach is limited to state agencies and the classifications under their jurisdiction. Federal and local MMAs play an important role in California, but it was determined that the state agencies of jurisdiction in California needed to evaluate the purpose and design of a state system as a first step. The involvement and input of other interested parties in the evaluation of state designations is critical and will be discussed later.

The workgroup is chaired by the Resources Agency. Its members represent state entities with MMA responsibilities or interests. These include the California Coastal Commission, the Department of Fish and Game, the Department of Parks and Recreation, the San Francisco Bay Conservation and Development Commission, the State Lands Commission, the State Water Resources Control Board, and the University of California. Deborah McArdle, with the UC Sea Grant Cooperative Extension and author of *California Marine Protected Areas* (McArdle 1997), has been participating in an advisory capacity. The National Center for Ecological Analysis and Synthesis (NCEAS) has provided a postgraduate researcher to support the group's efforts.

Based upon the Ocean Agenda's recommendation and subsequent discussions, the workgroup identified its goal:

> *To develop a more effective and less complicated statewide classification system of ocean and coastal managed areas, relying as much as possible on the expertise and knowledge of state agencies with management interests in ocean and coastal managed areas. This goal should be met without hindering or slowing other work already taking place on marine managed areas.*

Note that this goal is related primarily to an organizational or "classification" analysis, as opposed to an analysis of the suitability or effectiveness of specific sites. While such a comprehensive site analysis is desirable, it would not be feasible before the classification analysis is completed.

Several points that the interagency workgroup addressed while conducting its analysis and preparing the draft report should be highlighted. First, it was important for the group to define MMAs and distinguish them from the more commonly known MPAs. For this project, the interagency workgroup defined MMAs:

> *Marine managed areas are named, discrete geographic marine, estuarine, and adjacent terrestrial areas along the California coast designated using legislative, administrative, or voter initiative processes intended to protect, conserve, or otherwise manage a variety of resources and uses. Adjacent terrestrial areas are included because they have a substantial effect on the protection, conservation, and management of California's ocean resources.*

Although the workgroup included adjacent terrestrial areas in its definition and analysis of state MMAs, it was decided that the recommendations specific to establishing and naming an integrated, organizational system should be limited to those marine areas seaward of the mean high tide line. This, in essence, includes the existing array of sites conventionally known as marine protected areas.

It is important to recognize that the above definition of MMAs does not include areas that are legislatively or administratively established for specific species or fishing gear (such as seasonal or geographic closures, size limits, etc.) in order to manage commercial or recreational fisheries. These areas tend to change over time (some are long-term, but many are not) and are difficult to analyze in conjunction with more permanent sites. This is not to imply that such areas are not important or significant in managing ocean and coastal resources, but simply that their analysis was beyond the scope of the workgroup's efforts. We believe such areas should be considered in conjunction with any future analysis of the designation or evaluation of specific MMA sites.

The workgroup has struggled with use of the term *system* to describe the existing array of MMA classifications and designated sites. In the case of California's MMAs, they were not developed as, nor do they function as a true system, which could be defined as a set or arrangement of things that are related to form a unity. The workgroup's efforts are centered around developing a relatively small set of classifications to represent the full spectrum of protective measures and management objectives that can reasonably be achieved through the use of MMAs, while minimizing duplicative classifications and confusing naming conventions.

WORKGROUP AND PUBLIC PROCESS

The first workgroup meeting was held on July 31, 1998; since then the group has met almost monthly in Sacramento. Much of the work has been completed between meetings through the use of a secure Web site and list server, both provided and maintained by NCEAS. Without these tools for rapid communication, the workgroup process would be much longer and more expensive. The group is summarizing background materials and making recommendations to be compiled into a draft report. So far, all of the group's decisions about agency roles and the classification analysis have been made by consensus.

After consulting with the participating agencies, and with the concurrence of the Secretary for Resources, the workgroup will present its draft report at a series of interactive public workshops to be held along the California coast. These workshops will be based on a collaborative process involving a wide variety of interests, and will be critical to the success of the effort. Public comments and recommendations will also be welcomed at a Web site, where the draft report will be posted and a discussion group will be available for people interested in establishing a dialog about the merits of the draft report and its recommendations.

Following the public process, the workgroup will amend the report and prepare a final set of findings and recommendations. The final recommendations are likely to include a mix of administrative and legislative actions.

The efforts of the interagency workgroup do not preclude progress on other efforts related to MMAs. The workgroup's findings and recommendations are being prepared in a way that will fit into an overall system of MMAs with multiple designating and managing entities.

FUTURE STEPS

Specific actions that will be necessary after the workgroup releases its final report to the governor and legislature will depend in large part on its final recommendations. However, a number of actions would seem apparent, regardless of the final recommendations.

No matter what design is recommended for a statewide system of marine managed areas, existing MMA sites and classifications will have to be incorporated into the new design. In addition, the workgroup is likely to recommend analyzing the effectiveness of MMAs in meeting statewide or regional management objectives. This will require establishing measurable goals, objectives, and evaluation criteria for each classification. Such an analysis could result in a recommendation to change the degree of protection for specific sites. Some level of monitoring to determine the relative long-term effectiveness of the system of MMAs will also be necessary.

The active involvement of stakeholders in helping to develop the final report through interactive workshops will be vital to the success of the process. The State of California cannot meaningfully approach MMAs without the involvement of commercial and sport fishermen, public interest groups, the scientific community, ocean industries, other government entities, and other interested parties in a cooperative relationship (see Pomeroy 1999). We are not the first to make this observation; the need for collaborative approaches was noted many years ago by Wilbert McLeod Chapman, the state's top fishery manager, who said in 1949 (as quoted by Harry Scheiber in 1991):

> *. . . these conditions involve biological, oceanographic, political, commercial, diplomatic, technological, marketing, academic, economic, and personal relations factors, many of which I do not understand. I've come to the conclusion that nobody else understands all these factors and the interrelations either. Therefore, at every opportunity I seek to thrust together people who have specialized knowledge of one or more of these factors, to the end that they jointly can produce decisions and conclusions bearing on this objective that are more sound and practical than those produced by any one individual . . .*

The challenges identified by Chapman are as true today as they were in 1949. In the coming year this process can either benefit from, or be stopped in its tracks by the diverse points of view that will be expressed about the protection and management of our marine environment. The formidable task before us is to build a system that will respond to these diverse needs as we enter the twenty-first century.

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MARINE PROTECTED AREAS AS A PRECAUTIONARY APPROACH TO MANAGEMENT

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ABSTRACT

Various sources of uncertainty have greatly impeded the effectiveness of traditional fisheries management to assure acceptable levels of sustainability of fisheries and species populations. Marine protected areas are receiving increasing consideration and show potential as a means of contributing to the sustainability of populations and guarding against fishery failures. Marine protected areas take advantage of the open population structure that characterizes most exploited benthic marine species by considering the pelagic dispersal of propagules and the patchy distribution of benthic habitat. Because protected areas have only recently been considered for west coast fisheries, because poorly designed reserves may be useless and possibly detrimental, and because optimal design criteria are not yet understood, incorporating the evaluation of empirically derived design criteria into the final implementation of protected area networks (i.e., adaptive management) is the only prudent approach.

INTRODUCTION

A number of recent articles review the potential value of marine protected areas (PDT 1990; Roberts and Polunin 1991; Rowley 1994; Agardy 1997; Bohnsack 1998; Murray et al., in press) and caveats regarding their design and evaluation (Carr and Reed 1993; Allison et al. 1998; Carr and Raimondi 1998). This paper is designed to (1) explain the ecological basis for the potential roles of marine protected areas (MPAs) as a mechanism contributing to sustainable fisheries; (2) describe how MPAs differ from the more traditional management strategy of stock assessment, quota forecasting, and catch adjustment; and (3) emphasize the importance of thoughtful design and evaluation. This paper complements the paper by Parrish (also in this symposium section) by summarizing reasons for the rapidly increasing interest in MPAs, along with some caveats regarding their limitations.

The increasing interest in marine protected areas as a complement to traditional management strategies stems from many growing concerns. First is the rapid increase in either fishery failures or dramatic declines in many fisheries globally as well as regionally along the west coast of North America. Examples from the west coast include the once very productive abalone fishery throughout southern California, the sea urchin fishery of northern California, and the dramatically declining stocks of lingcod and some rockfish.

Simultaneously, fisheries scientists have become keenly aware of the great difficulty in accomplishing, and uncertainty associated with, each of three components of traditional management: stock assessment, forecasting stock size, and catch adjustment. Accurate stock assessment is hindered both by the great and unpredictable natural variability in year class strength and stock size, which is characteristic of most exploited species, and by the logistical difficulties of estimating stock size, catch rates, and population parameters (Ludwig et al. 1993; Clark 1996; Botsford et al. 1997; Lauck et al. 1998). The problem is exacerbated by the usual paucity of resources (financial and human) to make such estimates and the statistical artifacts of fishery-dependent sampling (e.g., in most recreational finfish and most invertebrate fisheries).

Moreover, the environment continues to change in new and unpredictable ways. Natural long-term (e.g., decadal) shifts in oceanographic conditions have only recently been recognized by marine ecologists and fisheries biologists (Roemmich and McGowan 1995; Holbrook et al. 1997; Francis et al. 1998; McGowan et al. 1998; Steele 1998). In addition, anthropogenic effects develop or change unpredictably through time; they include new pollutants, global climate change, and new fisheries that can affect the sustainability of existing fisheries (e.g., multispecies fisheries, bycatch, and practices that alter critical habitat of existing fisheries).

Another component of uncertainty is the arbitrary or unpredictable behavior of the fishing industry, consumers, and the political arena of management decisions (e.g., the rapidly developed fishery for live fishes). The ability of managers to adjust catch rates promptly can be further jeopardized by the process of policy decisions that must encompass more than harvest recommendations from fisheries biologists.

Taken together, the natural, analytical, and social causes of uncertainty in projecting stock trends and adjusting fishery yields have prompted great concern and a more conservative approach to ensuring sustainability of marine resources (Parma et al. 1998; Shea et al. 1998).

LARVAL DISPERSAL AS A KEY TO SUSTAINABILITY

Fisheries ecologists have long recognized that life-history traits are key features for determining the potential sustainability of a fishery for any species (Clark 1991; Leaman 1991). The issue is complex because of the many life-history traits that influence a population's response to exploitation.

Historically, particular attention has been given to the intrinsic growth rate (r) of species populations, which can influence how rapidly a population recovers from exploitation (Pitcher and Hart 1982). Species with high intrinsic growth rates are typically characterized by short life spans, early age of reproduction, high per capita fecundity, and other traits that may contribute to high resiliency and the ability to rapidly rebound from exploitation. However, some populations characterized by high intrinsic growth rates have not sustained high rates of exploitation (e.g., sea palm, anchoveta, Pacific sardine, market squid).

Thus, other life-history traits must contribute to sustainability. Two critical traits are longevity and the difference between age of maturity and age of recruitment to the fishery (D_{MR}). The greater the longevity and D_{MR}, the greater the potential for a "storage effect" (sensu Warner and Chesson 1985). Most marine organisms are iteroparous, so adults can "store" opportunities for successful reproduction and recruitment from one favorable period to the next simply by surviving periods of unfavorable conditions. This is likely to be particularly important in temperate systems where episodic recruitment is common among species, presumably driven by variation in environmental conditions that contribute to the successful recruitment of a year class (Parrish et al. 1981; Leaman and Beamish 1984). The strength of the storage effect as a buffer against coincident periods of overexploitation and recruitment failure will depend (in part) on (1) lifespan, (2) D_{MR}, (3) the number of mature pre-exploitable individuals, (4) size-specific fecundity, and (5) degree of compensation (degree to which early mortality is density-dependent). For example, species with high fecundity and early age of maturity (high intrinsic growth rates) but very short life spans have little or no storage effect. Extreme cases are species that live only one or two years, mature, and become exploitable within the first or second year of life. Overexploitation of any year class in combination with poor recruitment conditions potentially depletes most adults and the reproductive potential of that population for many years into the future. Squid, anchovies, and pink salmon may be classic examples of species with high intrinsic growth rates but little storage effect. Thus, intrinsic growth rate is only one of several determinants of how a population will respond to exploitation.

Another critical life-history trait is the dispersal potential of reproductive propagules (spores, gametes, eggs, larvae) of a species. Many exploited marine species have life histories that include benthic juvenile and adult stages with very limited dispersal, but whose reproductive propagules can be dispersed great distances in the plankton. If juvenile and adult stages of a species move very little, increasing the dispersal potential of reproductive propagules dramatically influences the "openness" of a population. In general, offspring produced by a local adult population are dispersed from, and contribute little to replenishment of, that parental population. Rather, a parental population replenishes populations elsewhere, and its own replenishment depends on recruitment of larvae produced elsewhere. Such "open" populations are common among marine species, including almost all exploited coastal species. (Although some evidence for local retention of pelagically dispersed larvae exists for embayments and oceanic islands, there is little evidence of this for most commercially exploited species along the open coast.) The openness of a population depends on the spatial scale on which the population is defined. For a given dispersal potential, the smaller the spatial definition of a population, the more open that population (i.e., the more likely it is that larvae are dispersed from that population). At the other extreme, on the scale of the geographic range of a species, any population is closed. This suggests that a local open population can be harvested without reducing its replenishment rate, because replenishment is derived from larvae produced elsewhere. Likewise, local open populations protected from exploitation could export larvae to replenish exploited populations, acting as a buffer against overexploitation or possibly enhancing replenishment rates, relative to conditions in which all populations are exploited. However, the replenishment of the protected local population in this example depends on input from other, presumably unprotected, populations.

Taken together, intrinsic growth rate, longevity, and the dispersal potential of propagules contribute to our understanding of sustainability among representative west coast fisheries (table 1). We consider propagule duration as a proxy for dispersal potential of a species (Reed et al., in press). Species characterized by both low dispersal potential and low intrinsic growth rates are unlikely to sustain exploitation unless very carefully managed (probably best through traditional methods). Examples include most elasmobranchs, and the viviparous surfperches, which have relatively low fecundity, late maturity (elasmobranchs), and whose young recruit directly to local parental populations. Less extreme examples of low intrinsic growth rate and low dispersal potential include two commercially exploited gastropods that produce planktonic larvae: abalone and the turban snail,

TABLE 1
Life-History Characteristics of 14 Representative Taxa Exploited Commercially or Recreationally along the Coast of California

Taxa	Fecundity	Age at maturity (yr)	Longevity (yr)[a]	Relative "*r*"[b]	Propagule[c] duration (days)
Elasmobranchs	Low	Late (5–8)	Long (20)	Low	Short (0)
Surfperch	Low	Early (1)	Long (8–10)	Low	Short (0)
Sea palm	High	Early (<1)	Short (1)	High	Short (0)
Abalone	High	Late (5–7)	Long (20)	Low	Short (7)
Turban snail	High	Early (2–3)	Long (10)	Low (?)	Short (7)
Rockfishes	High	Late (7–8)	Long (20–120)	Moderate	Long (30– >100)
Lobster	High	Late (7)	Long (10–15)	Moderate	Long (270)
Cancer crabs	High	Early (2–3)	Long (8–10)	High	Long (130–150)
Bay scallops	High	Early (<1)	Long (12–25)	High	Long (20–40)
Red sea urchin	High	Early (2–3)	Long (20)	High	Long (37)
Anchovies	High	Early (1)	Short (5)	High	Long (50–60)
Sardines	High	Early (1)	Short (5)	High	Long (50–60)
Market squid	High	Early (<1)	Short (1–2)	High	Unknown
Pacific oysters	High	Early (1)	Long (25–30)	High	Long (28)

[a] Longevity is defined as the average life span of adults.
[b] "*r*" refers to intrinsic growth rate.
[c] Propagule refers to the life-history phase that is postfertilization and premetamorphic to adult form.

Lithopoma (= *Astraea*) (Tegner 1993; table 1). Fisheries for at least abalone have been difficult to sustain in the United States. In these species, high fecundity is offset by high larval and juvenile mortality.

In contrast, many exploited species characterized by relatively low or moderate intrinsic growth rates have high larval dispersal. Representative species include some rockfishes of the genus *Sebastes*, and lobster. Their low or moderate intrinsic growth rates are caused by a balance between late maturity and high fecundity. Though several rockfish populations are at historically low abundances, some species have sustained exploitation. Past sustainability may be the consequence of both high dispersal potential and great longevity (i.e., storage effect).

High intrinsic growth rate alone does not insure sustainability. Species with a potential for a high intrinsic growth rate but only limited dispersal have also suffered from heavy local exploitation. One example is the sea palm (*Postelsia palmata*), an intertidal alga with high fecundity and early maturity but extremely limited spore dispersal. *Postelsia* was exploited for only a short period before it became evident that the level and timing of harvest was having devastating effects on local populations (Dawson and Foster 1982).

Finally, there are species with both high intrinsic growth rate and high dispersal potential. Representatives include historically heavily exploited species such as sea urchins and some pelagic species such as anchovies and sardines. Though fisheries for these species have experienced great variability, including marked declines in the face of heavy exploitation, they have generally tolerated exploitation for several decades. The dramatic variability in the size of these exploited stocks over time, particularly in those with both high intrinsic growth and high potential for propagule dispersal, is believed to be caused by variation in the conditions for dispersal and survival of the early pelagic stages (Sinclair 1988). This observation reinforces the importance of the pelagic dispersive stage to the persistence of local populations and points to a need to manage adult populations so that recruitment failures do not necessarily lead to a long-term collapse of the fishery.

We suggest that the potential for larval dispersal is related to, and can contribute importantly to, the local sustainability of exploitation of a species—perhaps as importantly as the intrinsic growth rate of a species' population. Though traditional fisheries management strategies have indirectly taken advantage of larval dispersal, it has not been incorporated into the design of management approaches. In contrast, marine protected areas focus on this critical life-history trait, with the intention of using it as a means to insure against the uncertainties of exploitation and to contribute to the replenishment (sustainability) of exploited populations outside reserves.

THE SPATIAL STRUCTURE OF BENTHIC MARINE POPULATIONS

The recent surge in the theoretical and conceptual development of spatially structured population and community models in terrestrial ecology is thought to be one of the most important conceptual advances in population ecology and conservation biology since McArthur and Wilson's theory of island biogeography. Terrestrial ecologists have recently come to recognize how spatial structure and movement of individuals among local populations influences the persistence of both local and regional collections of local populations (i.e., source-sink and metapopulation models; Pulliam 1988; Gilpin and Hanski 1997). This development has had a tremendous influence on recent approaches to managing human effects on terrestrial species and environments.

The patchy distribution of reef habitats (usually along discrete isobaths) and current regimes contribute to a spatial structure with high connectivity among local populations. Though some traditional management strategies have explicitly considered this spatial structure, particularly at very large spatial scales (Sinclair 1988; Hilborn and Walters 1992, chap. 5), many continue to assume that stocks are largely homogeneously distributed, or that the scale of fishing regulations (zones) is appropriate to the spatial scale of reef-associated populations. These assumptions are partly evident from the way fisheries data are collected and stocks are assessed for fisheries in which catch records are based on arbitrarily defined "blocks." Such blocks encompass unknown numbers of local reef-based populations whose larval replenishment can be largely reliant on populations from other blocks. Differences in yield among local populations within a block are not distinguished, nor is the extent and effect of exploitation on these populations. In particular, many recreational and some commercial fisheries for nearshore reef-associated species continue to be managed this way, and stock assessments are based on port landings and fishing logs.

The conceptual basis of marine protected areas explicitly recognizes the spatial structure of populations and the critical role of larval dispersal among local populations. The decoupling of local adult fecundity from the replenishment of a parental population implies that exploitation of a local population may not reduce the rate at which that parental population is replenished (with the critical exception of species whose recruitment is increased by the presence of adults, such as the red sea urchin). Likewise, protecting a local population may not enhance its rate of replenishment, especially if recruitment is density-dependent, but can affect the replenishment of populations to which its larvae disperse. Thus a protected area sufficiently large to encompass larval dispersal, or a network of protected areas that replenish one another via larval dispersal, not only preserves populations within the protected area, but may also contribute to the replenishment of exploited populations outside the area. The realization that replenishment, and hence sustainability, of protected populations can be largely reliant on larvae produced outside the protected area is the rationale for a network of protected areas, and for continued management of the exploited populations to guarantee a level of larval production high enough to prime protected populations.

HOW MARINE PROTECTED AREAS MAY CONTRIBUTE TO MANAGEMENT

By emphasizing the critical role of dispersal potential and the spatial structure of marine populations, marine protected areas may contribute to the sustainability of a fishery in many ways. The most comprehensive reviews of the various ways that marine protected areas may contribute to fisheries management and create nonfishery benefits have been made by the Plan Development Team (PDT 1990) and Bohnsack (1998). Of a list of 21 benefits (PDT 1990), we present a handful to convey the breadth of possible benefits.

- Protection of spawning stocks enhances rates of replenishment of exploited populations, thereby countering the effects of recruitment overfishing.
- Emigration of older juveniles and adults from protected populations to exploited populations increases the average size of harvested individuals, thereby countering growth overfishing.
- The spawning potential of large numbers of adults in protected populations buffers regional populations from environmental variability, hastening the replenishment and recovery of populations after perturbations (especially the combined effects of exploitation and natural disturbances).
- Eliminating fishing activities and local sources of pollution preempts destruction of essential fish habitat and provides pristine habitat as a baseline for research and for assessing the effects of tourism and other nonconsumptive activities.
- The genotypes of protected populations are subjected to natural selective factors that maintain natural size and social structure, age at maturity, and genetic diversity. Because their larvae disperse to exploited populations, protected populations may counter the genetic effects of exploitation. Moreover, the decoupling of local reproduction and recruitment may prevent the deleterious effects of inbreeding (e.g., depression and genetic drift) which have plagued reserve efforts for terrestrial species with closed populations.

THE IMPORTANCE OF DESIGN AND EVALUATION

When possible, the degree to which any approach to fisheries management and conservation meets its intended objectives should be evaluated. The costs of any approach that fails to meet its objectives may be catastrophic, depending on how much managers rely on the success of that approach. Because of the many possible objectives identified for marine reserves and the early stages of development of this approach, the effectiveness of reserves in meeting each objective is not entirely clear. Moreover, reserves are vulnerable to external perturbations (e.g., pollution, invasive species, climate change) that might impair their effectiveness. Therefore, developing approaches to evaluate the effectiveness of a reserve (for a given objective) and an overall framework for responding to an evaluation must be developed.

Some aspects of the uncertainty that plagues traditional approaches to fisheries management also pertain to marine protected areas. For example, if the intention is to measure a fishery's response to the establishment of a protected area, using traditional assessment data will continue to be problematic. The statistical power to detect changes in the trajectory of stock size over time is often depressingly low. Examples for west coast groundfish come from recent assessments of two rockfishes—bocaccio (*Sebastes paucispinis*) and canary rockfish (*Sebastes pinniger*)—and the lingcod (*Ophiodon elongatus*; PFMC 1996; fig. 1). An analysis of statistical power (Lenth 1987) indicates that the year-to-year variability in abundance of these species requires a 50% increase in lingcod abundance, a 100% increase in canary rockfish, and an increase of 500,000 bocaccio (200%) from 1996 to 2000 to detect a significant increase with acceptable levels of error ($\alpha = 0.10$) and power ($1 - \beta = 0.80$). Thus, other methods for assessing the consequences of a protected area must be developed.

Likewise, detecting increases in rates of larval replenishment (recruitment to benthic populations rather than to the fishery) may be difficult because of the dilution of recruits over vast areas of larval dispersal (also difficult is identifying areas of recruitment).

Nonetheless, methods are available for determining whether areas closed to fishing are effective at protecting populations and assemblages within a protected area (i.e., detecting increases in density and average size). Recently developed approaches to detecting genetic signatures, the genetic structure of marine populations, and patterns of larval dispersal seem more promising than previously thought (Doherty et al. 1995; Herbinger et al. 1997; Shaklee and Bentzen 1998; Bilodeau et al. 1999; Davies et al. 1999). Also, the elemental microchemistry of otoliths of fish and statoliths of invertebrate larvae may prove valuable for tracing the dispersal of larvae, identifying areas of larval sources, and constructing patterns of connectivity among local populations (Swearer et al., in press). Such efforts to determine patterns of larval dispersal are fundamental to both the design and evaluation of marine protected areas. Taken together, these methods can provide evidence of increased spawning stocks within reserves and the export of larvae to exploited stocks beyond reserve boundaries.

Given some level of uncertainty in the performance or evaluation of protected areas, designing them in a way that makes it possible to evaluate differences in design criteria seems well worth consideration. For example, protected areas that differ in size, spacing, local oceanographic features, or methods of enforcement could be established and monitored to determine how such differences influence the sustainability of protected populations or assemblages. Such evaluation requires well-designed monitoring programs intended and funded for the many years necessary for effects of protection to be realized. Incorporating evaluation and the ability to respond to the result of such evaluation into reserve design (i.e., adaptive management) could foster the development of optimal designs for existing and future reserves.

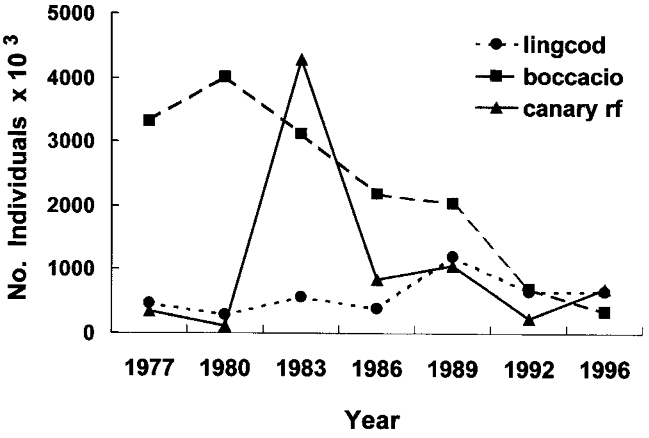

Figure 1. Estimated trends of abundance of three commercially exploited west coast groundfishes. Data are from fishery-independent triennial trawl surveys (PFMC 1996).

Such an approach would benefit from replication of design criteria, but establishing independent replicate reserves of each criteria level may be difficult, given the potential size of reserves and the spacing necessary to assure independence. One alternative analytical approach is the before-after-control-impact (BACI) design often used for point source environmental impact assessment (Schmitt and Osenberg 1996). Instead of spatial control-impact comparisons, the BACI design calls for comparisons between reserves differing in design criteria before and after establishment. However, such statistical approaches are designed to assess the effects of only one criterion. Another valuable approach would be to compare the response of exploited species with that of unexploited species (controls) to distinguish reserve effects from those caused by natural environmental variation over time. This approach may be problematic if the responses of unexploited and exploited species are not independent of one another. As Parma et al. (1998) state, "Experiments are not free, but neither is ignorance; some short-term sacrifices may be worthwhile if they can lead to better management in the future."

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MARINE RESERVES FOR FISHERIES MANAGEMENT: WHY NOT

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ABSTRACT

Marine reserves have recently become a politically correct way of viewing the management of marine resources. Much of the reason for this is due to the depressed state of many of the populations that have been the mainstay of both commercial and recreational marine fisheries. The apparent failure of past management has led to a headlong rush for a paradigm shift. Marine reserves that occupy no more than about 5% of the productive habitat can provide sites for research, for monitoring natural variability, and for preserving habitat and diversity for heritage purposes.

But the case for large marine reserves for fisheries management purposes has not yet been adequately made. The few available modeling studies suggest that for fisheries management purposes, marine reserves need to be on the order of 50% of the productive habitat. Analyses presented here suggest that, with reserves this large, current yields can be obtained only with a considerable increase in total fishing effort and a very large increase in the mortality rates in areas open to fishing. This implies a large increase in the trawling rate, and probably associated ecological damage, in the exploited area. Even if it were desirable to manage an individual species with large marine reserves, the concept breaks down when applied to the West Coast trawl fishery, which is based on many species, each with a different habitat. A marine reserve established for overexploited groundfish provides little real protection for migratory species such as Pacific hake, but may greatly increase the cost of fishing for these species.

INTRODUCTION

There is a sea change brewing in the way we manage our fishery resources in the California Current region, and it has its origin in the last several decades of decreasing yields and populations of many of the most important West Coast sport and commercial fisheries (Ralston 1998). It is not yet clear what changes will occur, because there are several competing strategies as to how we should alter current management. However, marine reserves are certain to play a much more important role than they have in the past, and a wide range of sizes has been suggested (Yoklavich 1998). Although no-take marine reserves have played a very minor role in the management of marine fisheries of the California Current region, areas have been extensively closed to specific commercial gear types (gill nets, purse seines, and trawl nets). For the purposes of this work I will define *marine reserves* as areas in which fish and shellfish cannot be legally taken by either commercial or recreational fishers, and *closed areas* as areas where specific fishing gear cannot be used.

The specifics of size and siting of marine reserves will be topics for research, confrontation, and political action in the coming years. For the purpose of this paper, I will use the classification developed by a working group at a recent workshop that suggested marine reserves could be classified into three design types based upon the motivations for establishing the reserves (Yoklavich 1998). These types are marine reserves as heritage sites and areas for fishery research, marine reserves as a buffer or insurance against overfishing, and marine reserves as an alternative strategy for sustainable fisheries. The working group suggested that the percentages of the total habitat, or range of an individual species, which was necessary to fulfill the goals of these types were <5%, 5%–20%, and 20%–50%, respectively.

The smallest reserves, those primarily intended for heritage and research purposes, are relatively uncontroversial. It is difficult to imagine that any resource users would be against the concept of reserves of this size, unless of course the reserves were in "their fishing hole." I will simply state that, in my opinion, reserves of this kind are long overdue, and managers should quickly proceed to develop them in all major habitat types.

The middle case, the use of reserves as a buffer or insurance against overfishing, will not be directly addressed in the analyses presented here. Analyses of this case should include multispecies effects and economic effects on fisheries, which are beyond the simple analyses presented here.

The largest reserve class—an alternative strategy for sustainable development—may be viewed as a form of adaptive management; i.e., a major alteration in management strategy followed by an evaluation of this alteration, rather than a gradual evolution of the management strategy. People favoring this size of reserve range from those who believe that incremental adjustments to the present management system cannot be expected to correct the present downward trends of many of our valuable marine resources, to those with a philosophical opposition to fishing and an acceptance of large reserves as a partial solution.

The purpose of this paper is to assess the population dynamics that would most likely result if adaptive management utilizing harvest refugia in 20%–50% of total habitat were enacted. In particular, I will compare the management potential of large marine reserves with the management strategy that has been followed by the Pacific Fisheries Management Council (PFMC).

BACKGROUND

One of the major difficulties confronting fishery research and management is in separating the effects of fishing from the effects of environmental variation at decadal or longer time scales. It is clear that at least parts of the California Current system have been very unproductive for an extended period, for both zooplankton (Brodeur and Ware 1992; McGowan et al. 1998) and fishes (Hollowed and Wooster 1992; Beamish and Bouillon 1993; Francis and Hare 1994). If marine reserves had been in place over the last several decades, it would be possible to determine whether the density of fishes within the reserves had declined, and, if so, how much in comparison to areas where exploitation has occurred. The use of marine reserves as controls to evaluate the effects of extensive and varied exploitation of living marine resources appears to be an essential tool in the research that will be necessary to tease out the complicated interactions between natural and human-induced alterations of these resources.

It should be noted that the analyses presented here are based on quite simple population dynamics; I have largely ignored multiyear to regime-scale environmental variation, which I believe is one of the most important factors in the current fisheries' situation.

Fish Behavior and Marine Reserves

One of the common arguments used by people favoring marine reserves is that they will provide areas where the marine fauna can recover to densities approaching those prior to exploitation. It is clear from population dynamics theory that marine reserves will foster conditions within the reserves that will result in increased fish density and diversity and a more natural age composition in comparison to that occurring at the present highly exploited state. But the state that is fostered will not be the same as that before exploitation. There will be fewer pelagic predators and small pelagic forage fishes, because of their exploitation outside the reserves, and there may possibly be more benthic and sedentary fishes. Because fishing effort will be displaced from areas that are included in reserves, the areas open to fishing should be expected to have exploitation rates considerably higher than the present ones. Marine reserves may increase recruitment to exploited areas for species with extensive pelagic larval stages, but species with little dispersal during the larval stage are unlikely to increase outside the reserves.

TABLE 1
Fish Behavior and Mobility in Relation to Residence Time within a Marine Reserve

1. Epipelagic and migratory species
Species that freely move in and out of reserves; they are often stocks with a large biomass. Their fisheries have minor bycatch, a minor effect on the substrate, and a high percentage of the catch may be taken in a relatively minor portion of their range:

Hake
Herring
Sardine
Salmon
Squid
Anchovy
Albacore
Mackerels
White seabass

Marine reserves will do little toward achieving optimum yield for these species. Annual quotas, closed seasons, or limitations on total and/or temporal effort will more likely be successful.

2. Benthopelagic, often schooling species
Species with moderate movement in and out of reserves and extensive larval dispersal:

Bocaccio
Chilipepper
Kelp bass
Widow rockfish
Sablefish
Lingcod
Pacific ocean perch
Shortbelly rockfish
Yellowtail rockfish

These are the most likely candidates for primary management by marine reserves or closed areas. Fisheries often have high bycatch rates and effects on the substrate.

3. Benthic, sedentary species
(particularly species such as abalone that have little larval dispersal); species that would have little movement out of reserves:

Many flatfishes
Many rockfishes
Abalones
Sea urchins
Many littoral species
Market crab

These are good candidates for achieving near virgin biomass levels in reserves but not likely candidates for improvement of fishery yields through reserve or closed-area management.

The success of marine reserves in maintaining near virgin densities will be highly dependent upon the behavior of the individual species (table 1). Species with highly pelagic or migratory behavior, such as Pacific sardine or Pacific hake, will be only partially, temporally protected by reserves, and their densities within the reserves should not be expected to differ greatly from those outside the reserves. Species with moderate mobility will be partially protected by reserves; depending on how much they move, their densities in the middle of large reserves could approach virgin densities. Near reserve boundaries, their densities will approach those outside the reserves. If, however, fishers respond to a reserve by concentrating their activity just outside the reserve, the net effect near the boundary may be densities that are considerably less than those deep in the reserve or even those at a considerable distance from a reserve.

Modeling studies suggest that marine reserves are most likely to positively affect fishery yields in species with moderate movements (Polacheck 1990; DeMartini 1993). This is particularly true when the reserve protects the younger fish that will move into the area open to fishing as they become larger. This was obviously realized by those who closed nearshore areas to trawling and have thus protected nursery grounds for more than four decades in California.

Benthic, sedentary species that move in and out of a reserve very little as adults are most likely to reach biomass densities and age structures near virgin levels. In theory, these species could attain even higher densities within marine reserves than before exploitation. This could happen if their populations are limited by predators or competitors that have highly or moderately mobile behavior, because these species would tend to be less dense than before exploitation. In contrast, modeling studies suggest that sedentary species are unlikely to increase with marine reserves (Polacheck 1990; DeMartini 1993). In fact, it is unlikely that a species could achieve near virgin biomass levels within a reserve and also increase fishery yields above levels that would occur with proper management without reserves. The exception to this is the special case where a large percentage of the recruitment of a stock consistently comes from a relatively small percentage of its habitat, and this same habitat is placed in a reserve. Species such as market squid and Pacific herring, which reproduce in restricted spawning grounds, are examples; in both cases, however, the species are highly mobile, and current fisheries are located primarily on their spawning grounds.

Growth versus Recruitment Overfishing

Fisheries biologists generally divide overfishing into two conceptual classes: growth overfishing and recruitment overfishing. The management techniques used to avoid these two classes of overfishing are quite different.

Growth overfishing is most likely to occur in species with low growth and natural mortality rates as well as delayed sexual maturity. It is therefore likely to occur in fisheries for rockfishes and other slow-growing groundfish species. Generally, the term refers to fishing a stock beyond the maximum yield per recruit, and this generally occurs when a species is exploited before the age that an individual cohort achieves its natural maximum biomass.

Growth overfishing is generally avoided by delaying, or at least reducing, fishing mortality on fish that have not yet reached the size or age of sexual maturity; this is often near the age that a year class reaches its maximum biomass. Typical management measures to avoid growth overfishing include size restrictions, mesh size restrictions, and area closures to prevent harvest in nearshore nursery grounds. These area closures have traditionally been limited to specific types of fishing gear (e.g., trawls or purse seines). No-take reserves have not been used to prevent growth overfishing in the California Current region.

Depending on the growth and behavior of individual species, reserves may or may not affect growth overfishing. Nonetheless, many of the beneficial effects of marine reserves observed in modeling studies are related to growth overfishing. The reserve models essentially protect fish at younger ages; then these fish move out of the reserve and are caught at a beneficial yield-per-recruit age and mortality rate. If reserves were concentrated in nearshore, nursery areas, they would have the same effect as the gear-specific closed areas mentioned above. In this case, the reserves will not fulfill the role of maintaining near virgin densities and population age structures because they will not protect adults. For sedentary fishes, where the areas open to fishing encompass the habitat of the whole age structure of the species (i.e., where there is no nursery grounds effect), regulations to prevent growth overfishing will have to be maintained.

Recruitment overfishing refers to fishing that reduces reproductive output to levels that markedly decrease recruitment. It is generally assumed that this does not occur at biomass levels less than 50% of the virgin level. Management techniques to avoid recruitment overfishing include setting annual quotas, fishing mortality, or fleet sizes at levels that will not reduce the adult biomass below some reference level. Unfortunately, this reference level is difficult to determine, and in practice it is seldom established until it has been exceeded.

Marine reserves of even modest size may help prevent recruitment overfishing of fishes that are sedentary, or have limited mobility and long pelagic larval stages. Very large marine reserves may protect enough of these fishes to prevent recruitment overfishing by providing a source of young fish even without any other regulations. In fact, several models suggest that reserves occupying up to 50% of a species' habitat may even increase yields (Polacheck 1990; DeMartini 1993). DeMartini (1993) showed that increased yields and protection of spawning biomass were highly dependent upon the behavior and growth rates of the species modeled; the best fishery and spawning enhancement occurred in species with moderate mobility and fast growth rates.

Spawner-Recruit Relationships

One convention often used in fisheries assessments is to assume that natural mortality and growth rates are not dependent on year or year class. Given these two assumptions, the shape of the spawner-recruit relationship becomes the primary factor in determining the stock's surplus production and thus the productivity of the stock. The spawner-recruit model most often used for California Current species is the Ricker model:

$$R = a\,S\,e^{-b\,S}$$

where R = recruit biomass or number
S = parent biomass, number, or reproductive output
a = the density-independent parameter
b = the density-dependent parameter

The potential productivity of a species with a Ricker spawner-recruit relation is described by the *a* coefficient, whereas the effect of stock size in reducing the potential productivity is determined by the *b* coefficient. Although it is not generally realized, the *b* coefficient also determines the percentage of the equilibrium stock size at which the maximum surplus production occurs. When biomass is expressed as a percentage of the equilibrium biomass, there is a unique *b* coefficient that defines any stock that has optimum production at a given percentage of equilibrium biomass (although it may be scaled by the assumed age at recruitment and the units that are used).

Ricker spawner-recruit models are usually fitted with a linear regression of the log of recruits/spawner on reproductive output or some proxy such as spawning biomass. A Ricker spawner-recruit relationship with maximum surplus production at 35% of the virgin biomass has a moderate dome shape (fig. 1); with maximum surplus production at 40%, the relationship has only a slight dome; and with 45%, recruitment continues to increase even beyond the virgin biomass level. In each case the potential productivity is dependent upon the *a* coefficient.

Source of Density-Dependence in Recruitment

The magnitude of compensatory density-dependence (the tendency for increased recruitment rates as the parent biomass decreases) is a measure of a stock's resiliency to exploitation and to temporary adverse environmental conditions. The source and degree of this density-dependence is not known for most, or perhaps any, of the exploited marine fishes in the California Current system. Knowledge of the source, or at least the life-history stage at which most of the density-dependence occurs, will be crucial in determining the relative merits of reserve versus traditional management.

Density-dependence in recruitment could occur during three life-history stages. The first stage includes processes affecting the production of eggs or larvae, and it would most likely be related to the availability of food for mature and maturing fish. Variations in food availability and quality would be expected to affect both the number and quality of eggs or larvae produced. This may be particularly important for live-bearers such as the rockfishes and for indeterminate spawners such as the California sardine.

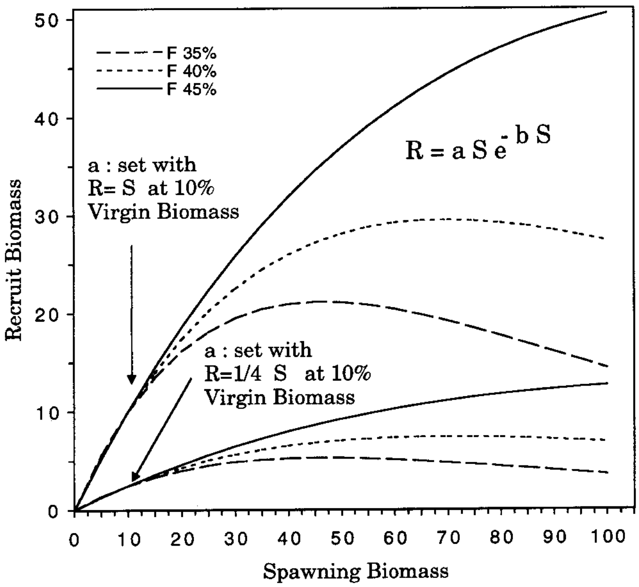

Figure 1. Ricker spawner-recruit curves. The upper set has an *a* coefficient four times as large as the lower set.

The second life-history stage—the pelagic larval phase—is quite extended in many California Current groundfish species. Most of these species have relatively small adult populations and therefore a very small biomass at the pelagic larval stage. Density-dependence at this stage is therefore unlikely because the larvae constitute a very minor portion of the zooplankton. Possible exceptions to this are Pacific hake and shortbelly rockfish, which have large populations; one could also argue that these species are not really groundfish but benthopelagic species.

The third life-history stage—postsettlement juvenile—is a likely candidate for density-dependence in many benthic fishes because their nursery grounds are often spatially restricted, so predation, competition, and cannibalism are potential sources of density-dependence in both juvenile growth and mortality. At this stage the density-dependence could be caused by the abundance of larvae or juveniles that are settling or by the abundance of older fish already present.

If a stock has an extensive larval-drift stage and if density-dependence occurs at the postsettlement stage, management with large reserves could be a real advantage for recruitment. For example, if the stock has maximum recruitment at 35% of the virgin biomass, well-placed large reserves would help maintain the stock near the level that produces the maximum recruitment even if the stock were depressed in areas open to fishing.

In contrast, if density-dependence occurs at the egg/larvae production stage (i.e., it is dependent upon the

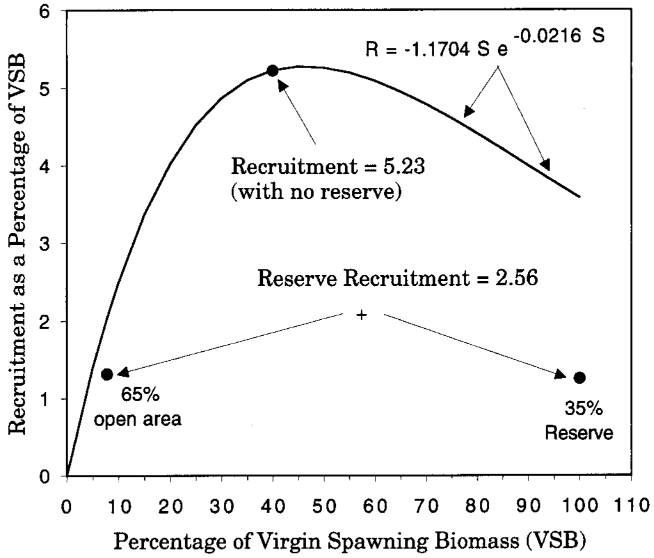

Figure 2. A comparison of recruitment under 35% reserve and no reserve management, when recruitment is density-dependent at the larval production stage.

condition of adults), management with 35% reserves could be counterproductive. To demonstrate this potential problem, I will use an example of a highly sedentary species with essentially no movement as adults between the reserve and exploited areas but with extensive dispersal during the pelagic larval stage. The stock has 40% of its virgin biomass—35% within reserves and 5% in open areas. The fish in the reserves would have a local density equal to the virgin state, and those in the open areas would have a local density of 5/65 virgin density. The stock-recruitment model is a typical Ricker spawner-recruit relation that produces a recruit biomass that is one-fourth of the spawning biomass at 10% of the virgin spawning biomass level, and maximum recruitment occurs at 35% of the virgin biomass. With reserve management, the total recruitment would be less than half of that which would occur without reserve management, and there would be more recruitment from the 5% of virgin biomass located outside the reserve than from the 35% within the reserve (fig. 2).

CASE HISTORIES

To evaluate the relative merits of reserve versus traditional fisheries management, one should first describe the state of traditional management. I will use one case that could be described as a failure (bocaccio, *Sebastes paucispinus*) and one that could be described as a success (widow rockfish, *Sebastes entomelas*).

The general harvest policy for most of the groundfish stocks regulated by the PFMC was an F35% policy (i.e., the stock should be harvested at a rate that produces a spawning potential per recruit equal to 35% of that which would occur if the stock were unexploited). Very recently, the PFMC has begun moving away from this policy—to F40% and F45% for several groundfish stocks, and it has enacted a management strategy for Pacific sardine, a very significant forage fish, that results in an average F65%.

Much of the analysis presented here will use the F35% base management strategy to compare traditional fisheries management as it has been practiced in the groundfish fisheries of the U.S. west coast, with reserve management using the management strategies that have been recently proposed to the fisheries management councils. Note that, by definition, an F35% policy will result in a steady state spawning biomass that is 35% of the virgin spawning biomass.

Given three assumptions—(1) a steady state environment, (2) a reserve system that protects 35% of the species' adult habitat, and (3) a highly sedentary species that is uniformly distributed over its habitat and highly dispersed during its pelagic larval stage—it would be expected that the reserve would prevent the reproductive output from falling below 35% of the virgin level even if the adult biomass in the area outside the reserve is reduced to trace levels. Thus in the worst case scenario a 35% reserve policy and no other fishery regulations could be considered the equivalent of a successful F35% exploitation policy with no reserves.

To assess the relative value of the historical fisheries management strategy versus reserve management, I will use the information available from stock-synthesis models for the two species: bocaccio (Ralston et al. 1996) and widow rockfish (Ralston and Pearson 1997). Bocaccio is a relatively productive species with a fast growth rate and a relatively early age of sexual maturity. It has been extensively exploited with a wide variety of gears for more than 80 years (Phillips 1939); its present biomass is in a very depressed state; and current management allows only a very small quota (Ralston et al. 1996). Widow rockfish is a less productive species, virtually unexploited by U.S. fisheries prior to 1977, when a fishery using midwater trawls rapidly developed. Landings increased quickly to a peak of nearly 28,995 MT in 1981; quotas were enacted in 1989; and the fishery has been managed with increasingly smaller quotas since 1989 (Ralston and Pearson 1997). Management was based on an F35% strategy, but this has recently been altered to F45% (PFMC 1998).

Ricker spawner-recruit curves were fitted for bocaccio and widow rockfish, and for comparison I have also shown two assumed spawner-recruit relationships. These assumed relations have an *a* coefficient that produces recruitment equal to 1/4 of the spawning when the spawning biomass is at 1/10 of the virgin level, and *b* coefficients that yield surplus production at 35% and 45% of the virgin biomass.

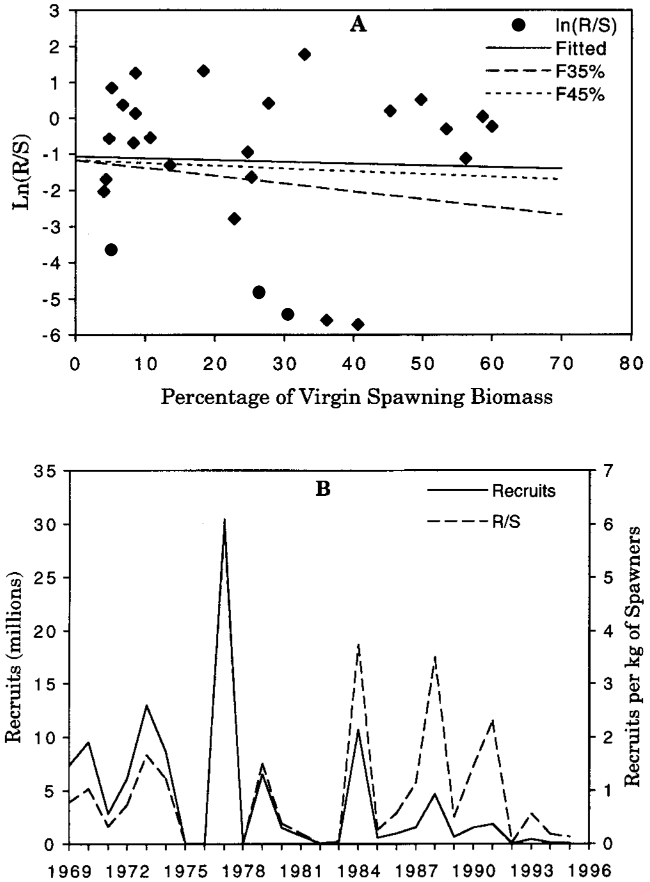

Figure 3. *A*, Bocaccio recruitment success, Ln(R/S), versus percentage of virgin spawning biomass. *B*, Bocaccio recruitment pattern 1969–95. (Data from Ralston et al. 1996.)

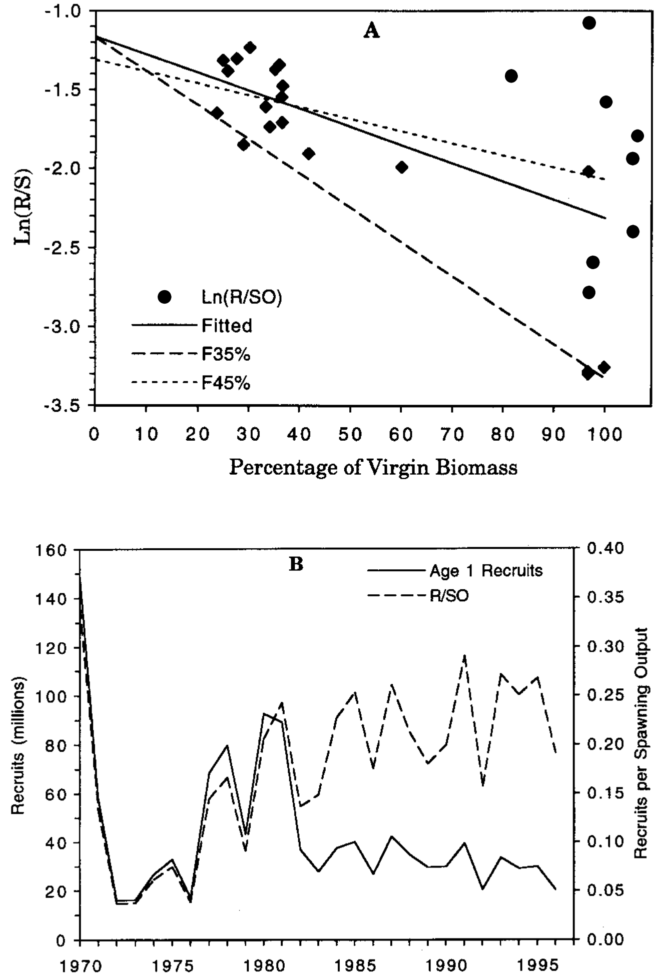

Figure 4. *A*, Widow rockfish Ln(recruits/spawning output). *B*, Widow rockfish recruitment pattern 1970–96. (Data from Ralston and Pearson 1997.)

The variation in reproductive success of the bocaccio stock is so large that it is difficult to determine if there is any density-dependence in the relationship. The fitted Ricker relation has a maximum surplus production at F47%; however, the relation accounted for only 0.2% of the variance and was obviously not statistically significant (fig. 3A). The F35% Ricker curve has essentially the same poor fit to the data as an F45% curve or the fitted curve. The time series of reproductive success and recruitment implies that the stock is maintained primarily by infrequent years of high reproductive success (fig. 3B). This pattern suggests that recruitment in bocaccio is environment-dependent, highly variable, and that no management strategy is likely to stabilize the population.

Widow rockfish have a much narrower range of reproductive success, and there is a marked density-dependence, with the number of recruits per spawning output increasing as the stock declines (fig. 4A). The fitted Ricker relation for widow rockfish results in an F40% surplus production, which accounts for 35.7% of the variance and is significant at the $P = 0.001$ level. The time series of reproductive success also clearly shows that recruits per reproductive output increased in recent years as the biomass declined, demonstrating that widow rockfish have considerable density-dependence in recruitment (fig. 4B).

The above spawner-recruit relationships suggest that recruitment is so variable that it cannot be determined which F strategy should be used for bocaccio, and that an F40%, not an F35%, strategy would be the minimum appropriate for widow rockfish. In 1997 an F40% management strategy for widow rockfish was proposed to the PFMC (Ralston and Pearson 1997) and in 1998 an F45% policy was enacted (PFMC 1998). It should be noted, however, that the previously mentioned and well documented climatic shift that occurred in 1976–77 could be responsible for the increase in the recruitment rate in widow rockfish as well as the lack of density-dependence in bocaccio.

Surplus Production

The potential productivity of the two species can be roughly estimated by calculating the surplus produc-

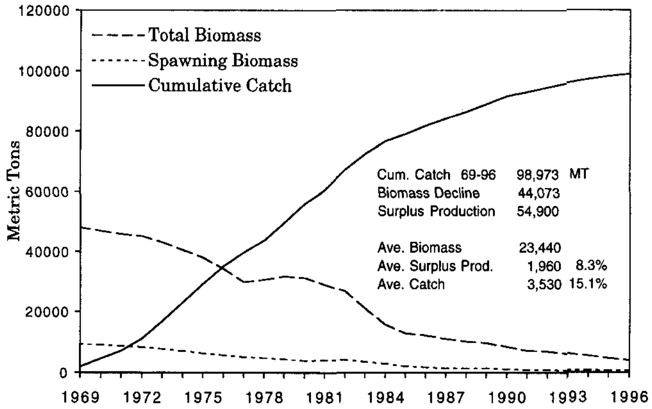

Figure 5. Bocaccio rockfish biomass, cumulative catch, and surplus production, 1969–96 (data from Ralston et al. 1996).

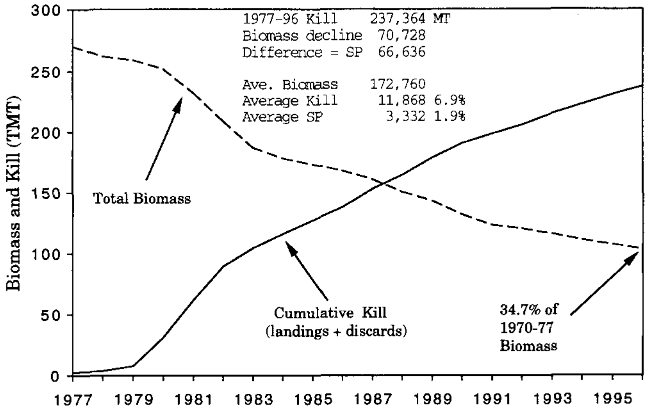

Figure 6. Widow rockfish biomass, cumulative kill, and production (data from Ralston and Pearson 1997).

tion during the period for which there is adequate information for each species. Of course, when estimated over a wide range of stock sizes, the estimate will be less than the maximum surplus production.

Although the bocaccio fishery extends back into the early part of the century, biomass estimates are available only since 1969, when the stock stood at 47,930 MT; by 1996 the stock had declined to 3,857 MT, and the cumulative catch (1969–96) was 98,973 MT (fig. 5). The 1969–96 biomass decline was 44,073 MT which, when subtracted from the cumulative catch, implies that the total surplus production over the 28-year period was 54,900 MT. Average catch over the period was 3,530 MT per year, and the average annual surplus production was only 1,960 MT. The bocaccio stock was therefore exploited at nearly twice the rate (E = 15.1%) of its average surplus production (E = 8.3%).

Widow rockfish presents a rather unusual case, because a data-based estimate of virgin biomass is available. This is because the behavior of the species made it unsusceptible to capture with traditional bottom trawls, and its deep distribution made it relatively unavailable to hook and line fisheries. The widow rockfish's average total biomass, just prior to the development of the fishery (1970–77), was 287,025 MT (Ralston and Pearson 1997). By 1997 total biomass had been fished down to 99,576 MT, 34.7% of the 1970–77 "virgin" biomass (fig. 6).

Because the stated objectives of the PFMC were to achieve an F35% management policy, the widow rockfish fishery could be termed "perfect management" in 1997, if the criterion was biomass. That is, the council would have met its target. Whether the target was right is another matter. The criterion of spawning output produces a different story. Average spawning output as calculated by Ralston and Pearson (1997) fell from an average of 442,484 (units not given) for the "virgin" population to 102,879 in 1997—23.2% of the virgin spawning output. On the basis of spawning output, it appears that the council's management strategy did not prevent the resource from declining below the stated goal.

In terms of surplus production, the widow rockfish stock had an average annual kill (landings + discards) of 11,868 MT, but an average annual surplus production of only 3,332 MT. Annual removals were 3.6 times the annual surplus production. It is expected that this ratio would be high because the data include the period when the biomass was near the virgin level; however, this is clearly the reason that the biomass dropped so quickly.

Comparison of F35% versus 35% Reserve Policies for Widow Rockfish

To directly compare the current F35% harvest policy with a management policy based primarily on reserves, I will use widow rockfish and a management situation with 35% of the species habitat being placed in reserves. According to Ralston and Pearson (1997) the 1999 catch (landings + discards) from an F35% widow rockfish fishery would be 5,689 MT with an exploitation rate of 12.6% of the summary (i.e., exploitable) biomass. Using this information, one can compare the exploitation, fishing mortality, and effort rates that would occur with the F35% management strategy versus a strategy in which marine reserves occupying 35% of the widow rockfish habitat were established.

For this comparison I will use the 1999 information to demonstrate the exploitation, trawling rates, and total effort that would be required to achieve the 1999 catch with current management versus that necessary if 35% of the widow rockfish habitat were in a marine reserve. If a reserve had been established at the beginning of the 1999 season, 65% of the exploitable biomass would have been in the area open to fishing (assuming a uniform distribution). However, as time progressed, a smaller and smaller proportion of the exploitable biomass would be outside the reserve area. Therefore, for a broader comparison I have included situations with the same 1999 bio-

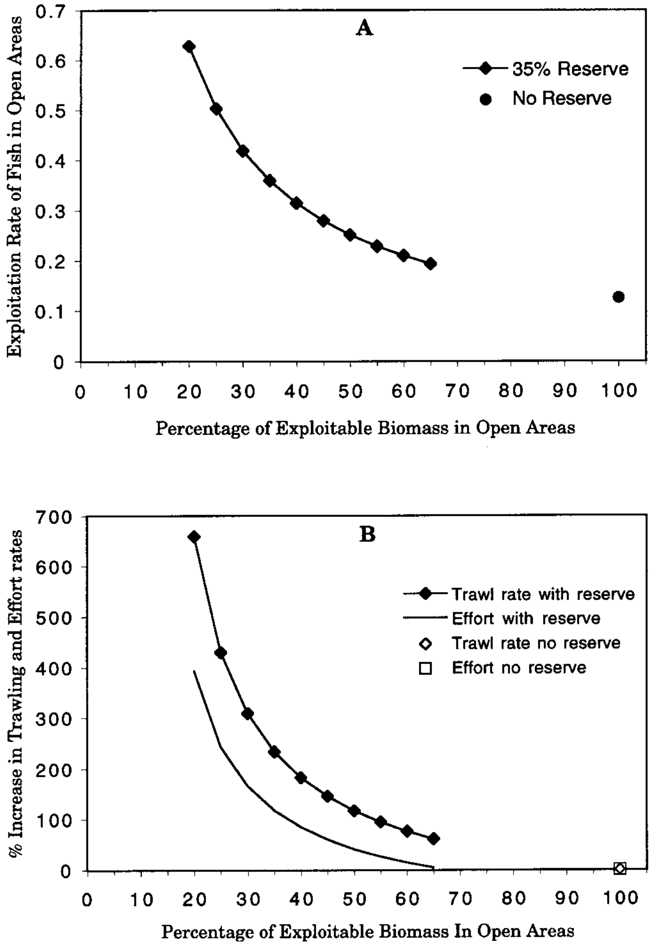

Figure 7. *A*, Exploitation rate of widow rockfish (outside of reserves) with a management of F35% and with 35% marine reserves. *B*, Widow rockfish trawling rate (in areas open to fishing) and total effort increases with F35% and with 35% marine reserves.

mass and catch, but with a varying percentage (20%–65%) of the exploitable biomass in the area open to fishing. Note that with a virgin density within the reserve and an exploitable biomass of 35% of virgin density, there would be 0% of the biomass in the area open to fishing.

In the situation where the local density of widow rockfish is the same in the reserve and in the open area, the exploitation rate of fish in the open area would increase from 12.6% to 19.3% (fig. 7A). There would be a 4% increase in total effort and a 60% increase in the trawling rate in the area open to fishing (fig. 7B). Where 50% of the biomass is in the area open to fishing, the exploitation rate is 25.1%, and the total effort and trawling rate increases are 41% and 116%. With 25% of the biomass in the open area, the values increase to 0.503%, 244%, and 429%.

An additional problem is that the increased exploitation rates on the exploited segment of the stock will reduce the age structure in the area open to fishing to just a few year classes, causing the fishery to become heavily dependent upon recruitment, which may be highly variable (figs. 3B, 4B).

The ecological damage caused by fishing (trawling or other gear) is a function of the fishing rates in an area (i.e., the instantaneous fishing mortality). Reserve management will greatly increase these rates in the area open to fishing, and decrease them to near zero within the reserve. The fishers' economic cost of harvesting is a function of the increased effort that will be required to catch the same volume of fish. The exploitation rate that the stock can support in the area open to fishing may, or may not, be higher than the current rate.

It is impossible, with this simple simulation, to determine if ecological factors (side effects of the increased trawling rate); fishery economics (the decreased catch per unit of effort); or population dynamics (increased exploitation rate) will be the limiting factor in reserve management of this type.

TRANSITION TO RESERVE MANAGEMENT

If very large marine reserves are established as an adaptive strategy for fishery management, one consideration will have to be the transition from the present state to a future state where there are near virgin levels within the reserves. At present some stocks are approaching or below 10% of their virgin levels (Ralston 1998). How long will this transition take, and what fishery yields can be taken from these depressed stocks during the transition?

In the California Current there have been three species (Pacific mackerel, Pacific sardine, and Pacific ocean perch) that were fished down to levels at which the directed fishery was closed long enough to expect a recovery of the population. The Pacific mackerel total biomass declined from a peak of 0.438 MMT in 1933 to 0.0001 MMT in 1968, and the commercial fishery was closed in 1970 (Parrish and MacCall 1978). By the late 1970s the population showed signs of a very strong recovery; in 1977 the fishery was reopened with modest quotas; by 1982, the population had surged to 1.18 MMT; and it has since declined again to 0.12 MMT in 1998 (Yaremko et al. 1999).

The Pacific sardine stock showed a similar pattern. Its total biomass was just under 4 MMT in 1934; it declined to 0.003 MMT in 1965; and the directed fishery was stopped in 1970 (Murphy 1966; MacCall 1979). Sardine biomass clearly increased during the 1980s and into the 1990s; total biomass reached 0.1 MMT in 1989 and 0.5 MMT in 1995 (Hill et al. 1998).

The Pacific ocean perch population was about 0.1 MMT before the foreign fishery developed in the mid-1960s; it declined to about 0.02 MMT in the mid-1970s and to about 0.01 MMT in 1995 (Ianelli and Zimmerman 1998). The fishery has been regulated at a lightly fished level (F = 0.05–0.10) from 1980 to the present.

Mackerel remained below 10% of the early peak biomass from 1966 to 1978. Sardine remained below 10% of the early peak biomass from 1951 to 1993. Pacific ocean perch continued to decline from about 25% of the early peak biomass in the mid-1970s to about 10% in 1995.

These examples indicate that quick-maturing, productive stocks such as the mackerel and sardine can be expected to show significant recovery in 1–3 decades when there is no directed fishery during early recovery. Slow-maturing, less productive stocks such as Pacific ocean perch may not recover in 3 decades, and may even decline further, when lightly exploited.

ALTERNATIVE STRATEGIES FOR MANAGEMENT

In recent years the management strategy used by the PFMC for rockfishes was based on the concept of a constant F35% harvest rate. This management strategy was not successful at stabilizing many of the rockfish stocks at or even near 35% of their virgin spawning biomass levels. There appear to be three major alternatives for change, and all three are currently being actively evaluated:

1. Incremental increases from F35% to F40% and higher; some of this change has already been made.
2. Establishment of marine reserves.
3. Adoption of recently proposed control rules that reduce the exploitation rate as biomass falls below some reference level. This change is also currently in progress.

As indicated by the preceding examples, catching the same quantity of fish while implementing reserve management will require an increase in total fishing effort and a large increase in fishing mortality rates within the exploited areas. Current management of widow rockfish is based on an F40% policy, and the fishing mortality required to achieve this policy without reserves is F = 0.153 (Ralston and Pearson 1997). To achieve the same landings with a reserve, the fishing mortality and fishing effort increase rapidly as the stock falls away from the virgin biomass. With a 35% reserve and a virgin stock, the fishing mortality rate required to achieve the F40% catch from the 65% open area is F = 0.2354. At a stock size 70% of the virgin biomass (i.e., with 35% in the reserve and 35% in the exploited area), it rises to F = 0.4371; at 45% it rises to more than 10 times the F = 0.153 (fig. 8). This estimate is based on the assumption that the reserve area remains at virgin biomass levels while the area outside the reserve is fished down (i.e., fish do not exchange between the reserve and open areas once they are old enough to be taken in the fishery). In addition, the entire increase in fishing effort will occur in the areas outside the reserve. If trawling does alter the nonexploited benthic fauna, the areas outside the reserves will be much more affected under reserve management than with the other two alternatives.

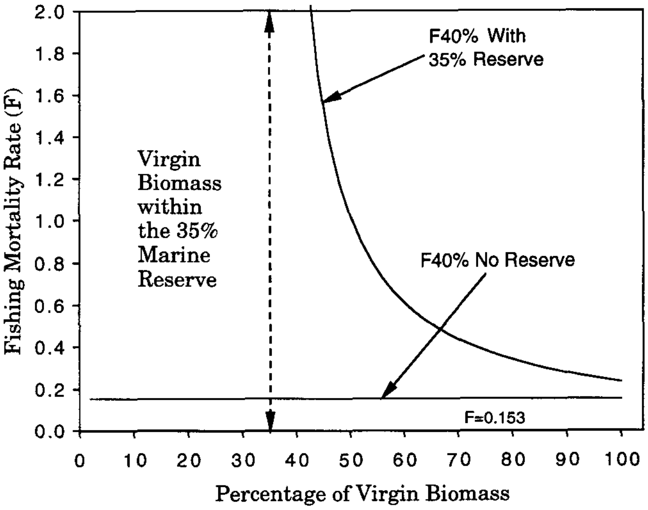

Figure 8. Widow rockfish fishing mortality rates in areas fished with and without a 35% reserve under a 40% harvest rate.

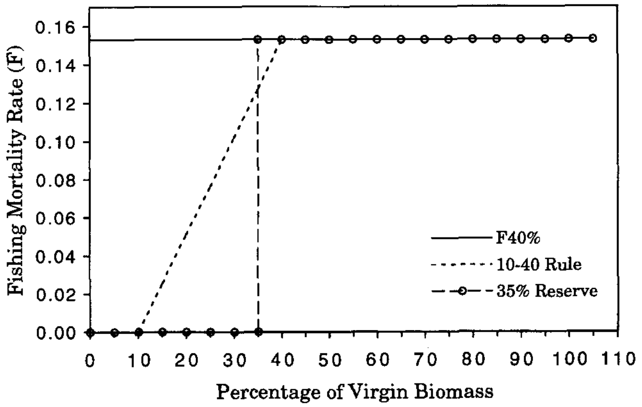

Figure 9. Widow rockfish instantaneous fishing mortality rates under different management strategies.

The third alternative for modification of the way the PFMC has been managing the Pacific Coast groundfish stocks is to base the exploitation rate on stock size and reduce the exploitation rate as the stock declines. An early example of this type of control was developed for the California Pacific mackerel fishery (Parrish and MacCall 1978). The PFMC has recently adopted such a rule for Pacific sardine, and in 1998 it adopted a new precautionary policy, the so-called 10-40 rule for groundfish management (PFMC 1998). This rule sets optimum yield at F_{MSY} when the stock biomass is above 40% of the virgin biomass, and the optimum yield declines linearly from F_{MSY} at 40% of the virgin biomass to zero at 10% of the virgin biomass (fig. 9).

The crisis in fishery management for groundfish and salmon in the region managed by the PFMC leads me to believe that all three alternatives will be employed during the next decade.

CONCLUSIONS

The admittedly "quick and dirty" fisheries analyses presented here suggest that considerable research should be carried out before very large reserves are considered as a viable alternative for managing the major fishery stocks of the California Current region. Concerns about management with large marine reserves include:

1. Considerable increases in fishing effort will be required to catch the same volume of fish, and the larger the reserves, the larger the increases will have to be.
2. Fishing mortality rates in the areas open to fishing are likely to increase well above present rates; if trawling causes ecological damage, reserves will extend this damage in the area open to fishing.
3. Reserves will have undesirable effects on the economics of fisheries for migratory species that are managed by annual quotas. These economic problems could be avoided by instituting closed areas for the fishing gear used to catch the species that need protection.
4. Depending upon the source of density-dependence in recruitment, reserves may result in considerable decreases in recruitment.
5. Increased exploitation rates in areas open to fishing will greatly reduce the age structure of the exploited portion of the population, concentrating most of the biomass in a very few year classes. Since many species (e.g., bocaccio) have highly variable recruitment, annual landings would also be expected to become more variable.
6. Some of the above concerns could be reduced if the total take were reduced by a percentage equivalent to the percentage of the habitat that is placed in reserves.

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MARINE RESERVES AND MANAGEMENT OF THE NORTHERN CALIFORNIA RED SEA URCHIN FISHERY

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ABSTRACT

Catch in the northern California red sea urchin fishery has declined from 14,000 metric tons in 1988 to less than 1,000 in recent years. Although the institution of marine reserves is not expected to restore catch to former levels, reserves at least have the potential to prevent further decline. The answer to the question of whether reserves would benefit this fishery depends on an essential uncertainty in recruitment, which we model as a parameter in a Beverton-Holt relationship between number of larvae produced and successfully settling juveniles. For high values of the slope of this function at the origin, recruitment is relatively impervious to fishing, and the addition of reserves diminishes catch. For low values of this slope, fishing decreases recruitment, and the addition of reserves increases catch by increasing recruitment. A decision analysis accounting for the distribution of possible values of this slope indicates a benefit in long-term equilibrium catch of 18% with one-sixth of the coast in reserves. However, accounting for short-term losses due to the initial implementation of the reserves by considering only catches over the first 50 years reduces this gain to 12%. This figure is sensitive to the relative value of short-term and long-term gains, and to the rate at which reserves are implemented.

INTRODUCTION

Marine reserves have been proposed as a possible remedy for the perceived problems associated with the decline in catch of the northern California red sea urchin fishery (fig. 1). It is generally believed that much of the decline was due to "fishing up" an unexploited stock (Botsford et al. 1999); thus reserves are not expected to restore the original catch levels. However, there is still concern that the population is in danger of further decline caused by a decrease in recruitment, and some believe that the institution of reserves could avert that decline. Here we attempt to answer the fundamental question: Given our current understanding of this fishery, will the institution of marine reserves lead to greater future catch than we would otherwise have?

Because the consequences of fishery management by marine reserves are complex and still poorly understood, we focus our answer to this question on a few essential mechanisms. We pose the question in terms of fishery management, and evaluate management only in terms of greater or lesser catch. We do not address other benefits of marine reserves, nor do we consider larval dispersal and the optimal spacing and configuration of the reserves. We also do not address other possible fishery management measures such as changes in fishing effort and size limits. All of these are unnecessary in answering the basic question posed, and each can be answered in other studies that make use of the results obtained here.

The cause of the decline in northern California is reasonably well understood, and enough is known about the life history of the red sea urchin to begin to evaluate the design of reserves. The red sea urchin fishery developed rapidly in the late 1980s as a result of a shift in the exchange rate of the Japanese yen and the ready availability of urchin divers from the southern California fishery (Kalvass and Hendricks 1997). Since that time catch has declined rapidly, as would be expected from the initial exploitation of an unfished population (Botsford et al. 1999).

Growth and both natural and fishing mortality rates are well known (Morgan 1997). Much is known about recruitment, such as the dependence of fecundity on size, and the influence of coastal circulation on settlement patterns (Morgan 1997). Some density-dependent mechanisms are known, such as the protection of juveniles under the spine canopy of adults (Tegner and Dayton 1977) and the decreasing efficiency of broadcast spawning (Levitan et al. 1992). However, survival through the larval stage, and the origin of recruits to each location are not known.

Marine reserves are currently of great interest because of their potential as a tool for combating overfishing and preserving declining marine biodiversity (e.g., Botsford et al. 1997; Murray et al., in press; and other papers in this symposium). But so far, reserves are poorly

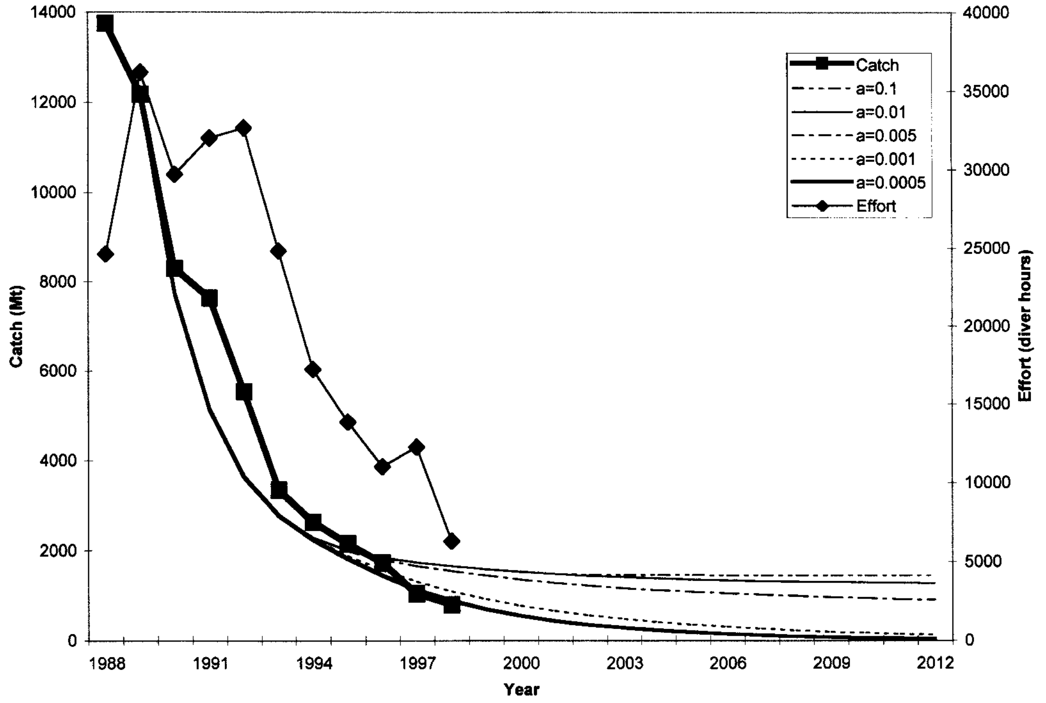

Figure 1. Catch in the northern California red sea urchin fishery from 1988 and catch from the red sea urchin model with constant fishing mortality rate and different values of *a*, the slope of the Beverton–Holt relationship between successfully settling juveniles and competent larvae at each location. The declining effort is also shown.

understood. With regard to fisheries management, they have been proposed for preventing overfishing in the presence of parameter uncertainty (Clark 1996; Botsford et al. 1997; Lauck et al. 1998); for providing greater fishery yields when effort is high (Quinn et al. 1994; Sladek-Nowlis and Roberts, in press); and for reducing variability in catch (Sladek-Nowlis and Yoklavich 1998; Sladek-Nowlis and Roberts, in press). Quantitative analyses of the effects of reserves in a fishery context have involved issues such as how reserves reduce uncertainty (Lauck et al. 1998); the effects on harvested cohorts of migration (Polacheck 1991; DeMartini 1993); and the performance of reserves in conjunction with standard fishery management (Quinn et al. 1994; Sladek-Nowlis and Yoklavich 1998; Sladek-Nowliss and Roberts, in press).

MODEL

To answer the question of whether reserves can lead to greater catch, we use a model that we have developed as a tool for answering the many questions associated with instituting reserves in the management of the northern California red sea urchin fishery. The model consists of 24 independent, size-structured subpopulations linked in the larval stage by a dispersal matrix representing all combinations of larval origins and destinations. We model each subpopulation by using von Bertalanffy growth with intrapopulation variability in L_∞. Parameter values for growth, natural mortality, and fishing mortality vary along the coast (Morgan 1997), but for our purposes here we use typical values. These values were estimated from data collected in the Bodega Marine Reserve: $L_\infty = 118$ mm; the standard deviation of $L_\infty = 10$ mm; the von Bertalanffy growth parameter $k = 0.22\ \mathrm{y}^{-1}$; and natural mortality rate $M = 0.08\ \mathrm{y}^{-1}$.

The nature of density-dependence in the recruitment process is critical to the question asked here. Density-dependence in fecundity occurs in sea urchins, but typically only at the densities of urchin barrens (Levitan 1989). Density-dependence in the larval stage is not known, but is not suspected to occur, since larval sea urchins would be a relatively unimportant consumer in the planktonic food web. It is likely that there is an upper limit on settlement density or early survival and that it is determined by the amount of available habitat. The essential limiting characteristic of the habitat would be the provision of structure for protection against predation. Similar mechanisms have been studied in benthic crustaceans (Caddy 1986; Wahle and Steneck 1991) and reef fishes. Those mechanisms may involve adults or other settled, older stages, but any specific habitat is typically suitable for only a narrow range of sizes. Hence it is doubtful that the density of adults influences postsettlement survival of red sea urchins other than through the spine canopy mechanism noted above.

Because of these considerations we use a Beverton-Holt relationship to describe the dependence of success-

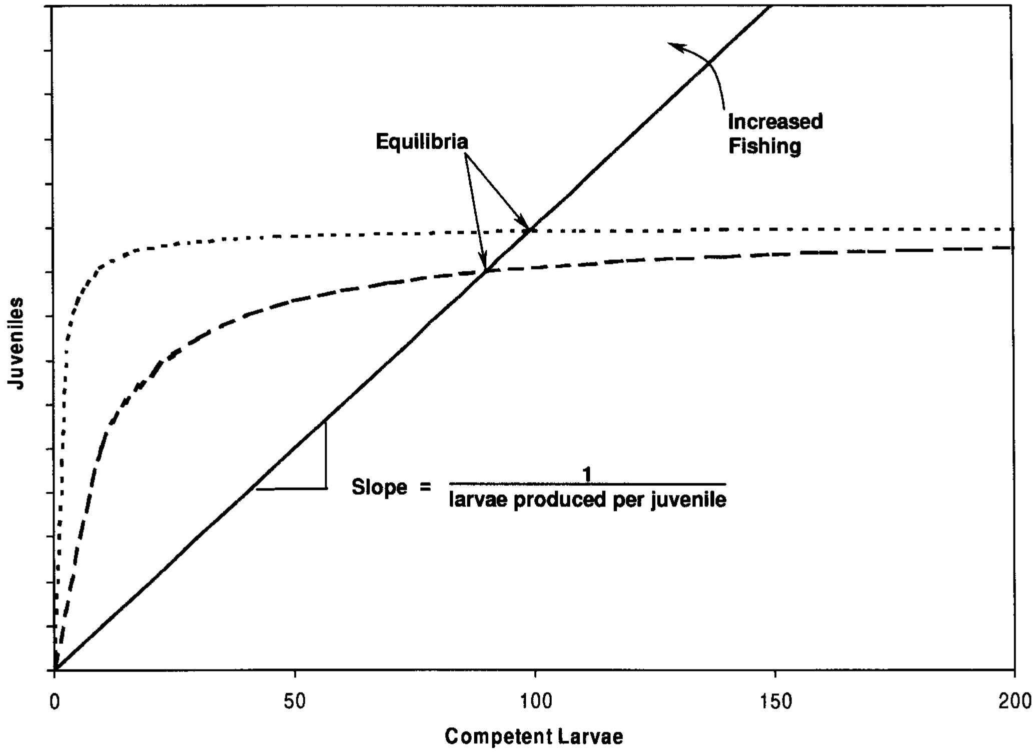

Figure 2. A schematic view of the model relationship between the number of juveniles successfully settling and surviving at a location, and the number of competent larvae attempting to do so, for two different values of the slope at the origin, *a*. The slope of the straight line is the inverse of the number of larvae produced in the lifetime of each settled juvenile, which increases as fishing mortality rate increases. The intersection of this line with the appropriate juvenile/larval line is the equilibrium rate of juvenile settlement.

ful settlement (S_t) on the number of larvae attempting to settle at each location (L_t):

$$S_t = \frac{L_t}{\frac{1}{a} + \frac{L_t}{C}} \qquad (1)$$

where *a* is the slope at the origin, and *C* is the maximum value or juvenile carrying capacity (fig. 2; Beverton and Holt 1957). The value of *C* was assumed to be the same for each of the 24 subpopulations, and was set to a value that yielded the observed total catch in this fishery. Because the value of *a* is unknown, we evaluated a range of values. For a fishery without reserves, equilibrium recruitment is the intersection of the Beverton-Holt curve describing the number of settling juveniles versus competent larvae, and a straight line whose slope is the inverse of the number of competent larvae produced in the lifetime of each successfully settling juvenile (fig. 2). As fishing mortality increases, larvae produced per juvenile decreases, and equilibrium recruitment declines (fig. 2). The equilibrium value of recruitment declines more rapidly for the juvenile/larval relationship with the smaller value of *a*.

The two other known density-dependent mechanisms involved in recruitment are included in this analysis only indirectly. The effect of adult spine canopy as a refuge from predation for juveniles (Tegner and Dayton 1977) is proportional to the number of adults, hence it would be a linear mechanism rather than a depensatory mechanism, and it is reflected approximately in the dependence of egg production on adult numbers, which directly influences the value of *a*. Our analysis of the proposed Allee effect associated with broadcast spawning (Levitan et al.1992; Lundquist and Botsford[1]) has shown that below a certain adult density, egg production becomes highly variable, but the shape of the dependence of mean recruitment on adult density does not exhibit a threshold; instead, it is approximately linear. Here we include that effect only as greater uncertainty in recruitment (as reflected in the value of *a*).

Our current understanding of how coastal circulation transports sea urchin larvae to their location of settlement indicates a specific spatial pattern of settlement each year, but the pattern is variable enough that we assume larvae are mixed and some settlement reaches all areas. Samples from settlement collectors and benthic size distributions indicate that red sea urchins tend to settle in greater abundance just to the north of major promontories (Morgan and Botsford 1998). This view is consis-

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[1] Lundquist, C. J., and L. W. Botsford. Stochastic Allee effects due to reduction in invertebrate density by a fishery. (manuscript)

tent with a mechanism for retention of invertebrate larvae in features associated with capes and points during active upwelling (Wing et al. 1998) and subsequent delivery of invertebrate larvae to settlement sites by poleward, onshore flow during upwelling relaxation (Wing, Botsford et al. 1995; Wing, Largier et al. 1995; Morgan and Botsford 1998). The effect of this spatial pattern on the fishable adult abundance has not yet been clearly demonstrated, and the amount of exogenous input of larvae carried by dominant currents from the north is unknown.

To maintain the focus of our analysis here on the simple question of whether reserves increase catch, we assume that all larvae produced by the 24 subpopulations are completely mixed and uniformly redistributed along the coast, and we set the dispersal matrix accordingly. Studies in which larval dispersal patterns and reserve configurations are explicitly included have indicated that this is a good approximation to a wide variety of situations (Botsford and Hastings[2]).

RESULTS

Under the model conditions described here, the efficacy of reserves depends critically on the value of the parameter *a*, the slope of the relationship between competent larvae and successfully settling juveniles (see equation 1 and fig. 2). As the amount of area placed in reserves increases from 1 of the 24 subpopulations, to 1 every 12 subpopulations, 1 every 8, 1 every 6, and 1 every 4 subpopulations, equilibrium catch either increases then decreases, or decreases monotonically (fig. 3). For high values of *a*, settlement will maintain a high, constant value regardless of how fishing affects total egg production and the number of larvae produced (fig. 2). In this case, reserves contribute nothing to future recruitment, and their only effect is to remove the reserve areas from access by the fishery. For low values of *a*, the equilibrium value of number of larvae successfully metamorphosing and settling without reserves is low, and placing parts of the coast in reserves increases total egg production and larval production. Catch increases to the point that adding more reserves no longer increases recruitment, then declines for the same reason it does with high values of *a*: areas are removed from access by the fishery.

This poses a problem that will be present in any analysis of the efficacy of reserves in this fishery, no matter how many other mechanisms and factors are considered; namely, that the advisability of reserves depends critically on the value of the parameter *a*, which is unknown. In many similar situations in fisheries (Hilborn and Walters 1992), conservation biology (Ralls and Starfield 1995), and resource management in general, similar decisions involving uncertainty are made by using formal decision analysis. In its simplest form, decision analysis involves (1) evaluating how the system of interest responds to various management options (e.g., fraction placed in reserves) under a variety of reasonable assumptions regarding the possible (but unknown) states of nature (e.g., values of *a*); and (2) comparing how well each decision performs across the range of possible states of nature. We accomplished the latter by computing the mean performance over the distribution of states of nature (e.g., the probability distribution of *a*). To do so, we first needed to assess how likely each value of *a* is, based on the information currently available.

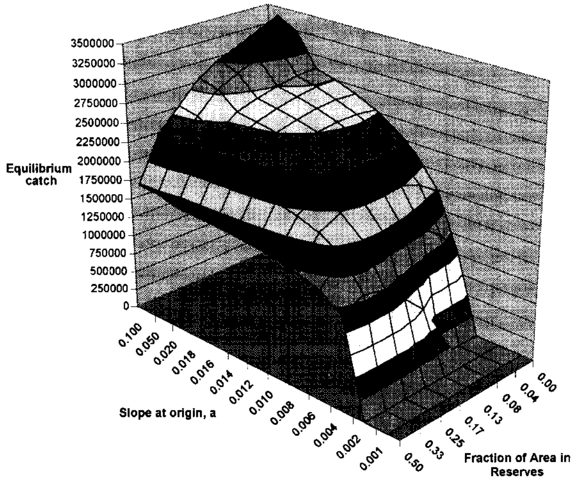

Figure 3. Equilibrium catch versus the fraction of coastline in reserves, for various values of *a*.

One source of information regarding the possible values of *a* is the catch record itself. Comparing actual catch with catch from the model with constant fishing mortality ($F = 0.5$) for various values of *a* indicates that the decline in model catch matches the actual decline quite well up to 1998, regardless of the value of *a* (fig. 1). However, after 1998 actual catch seems to decline more rapidly than model catch for any values of *a*. This could be due in part to a decline in fishing mortality rate caused by the general reduction in effort with the decline in abundance, but mortality rate need not decrease in proportion to abundance. Catch also would be influenced by market conditions; for example, it is known that the exchange rate between the Japanese yen and the dollar shifted by about 20% in 1997 and 1998. If we ignore the corresponding dip in catch in 1997, the slope of the actual catch trend from 1993 to 1996 most closely matches the lower model projections, indicating that the value of *a* could be as low as 0.001.

A second source of information on the value of *a* can be obtained by comparing the decline in fishable abundance, as reflected in CPUE, to the expected decline in fishable abundance due to the fishing up effect, as

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[2] Botsford, L. W., and A. Hastings. Sustainability of populations in marine reserves. (manuscript)

TABLE 1

The Expected Values of Improvements in Fishery Performance as the Area in Reserves Increases

No. of subpopulations (Percentage of coastline)	0 in 24 (0%)	1 in 24 (4.17%)	2 in 24 (8.33%)	3 in 24 (12.50%)	4 in 24 (16.67%)	6 in 24 (25%)	8 in 24 (33%)	12 in 24 (50%)
Equilibrium catch	1.00	1.08	1.11	1.17	1.18	1.14	1.06	0.85
50-yr catch	1.00	1.04	1.09	1.11	1.12	1.10	1.04	0.87
Discounted 50-yr catch	1.00	1.01	1.04	1.04	1.02	0.98	0.92	0.74

Note: The assumed distribution of *a* is probabilities of 0.1, 0.1, 0.2, 0.2, and 0.1 for $a = 0.001$, 0.002, 0.004, 0.006, and 0.008, respectively, and a probability of 0.05 for $a = 0.010$, 0.012, 0.014, 0.016, 0.018, and 0.020. The discount rate is 0.03 y^{-1}.

reflected in the size distribution of the catch (Botsford et al. 1999). For that analysis we computed the decline in CPUE that would be expected from the change in the size distribution assuming constant recruitment; we then compared that over the years 1988 to 1994 to the decline in CPUE at the four major ports in the northern California fishery. We found that in three of the ports CPUE declined faster than expected, but was statistically significant in only one port. This implies that there has been a decrease in recruitment since the advent of the fishery, at least at some points along the coast, which would indicate that the value of *a* for the population as a whole is near the value which would cause a long-term decrease in recruitment.

A third source of information on the value of *a* is values observed for fisheries in general. To minimize the chance of collapse due to overfishing, fishery biologists maintain the relative egg production per recruit above a certain level. The relative value of egg production per recruit is the ratio of egg production in the lifetime of an average female under current fishing to egg production without mortality due to fishing. Below a threshold level, which ranges from 0.20 to 0.35 and higher, a stock is declared overfished and steps are taken to reduce fishing mortality (Goodyear 1993; Mace and Sissenwine 1993; Rosenberg et al. 1994). In our model this parameter would be proportional to the value of *a*. The value of relative egg production per recruit for the northern California red sea urchin, assuming $F = 0.5$, is near 0.20, the lowest value of the overfishing threshold.

A decision analysis with a distribution of values of *a* based on these considerations suggests that the maximum expected equilibrium catch would be realized with 20% of the coast in reserves (table 1). For the distribution of *a*, we assumed that *a* was most likely to be near 0.004 or 0.006, but could be as high as 0.02. Specifically, we hypothesized that *a* was uniformly distributed between .01 and .02 inclusively; was twice as likely to have values of .008, .001, and .002; and was twice again as likely to have values of .004 or .006 (see table 1 note for probabilities). The gain in expected value of equilibrium catch with reserves was roughly 18% (table 1). Some of the possibilities used in computing the expected value of catch involved zero catch without reserves ($a = .004$), and no catch even with reserves ($a = .002$ and $a = .001$), i.e., indicating a collapsed population (fig. 3).

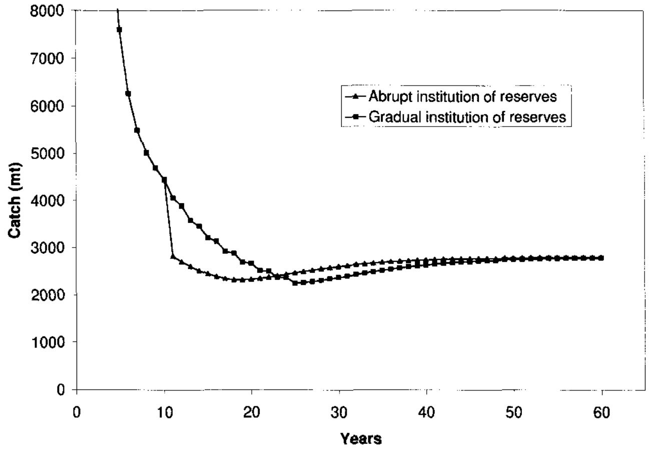

Figure 4. For a value $a = 0.008$, the abrupt decline in catch when one-third of the coast (eight reserves) is placed in reserves 10 years after a fishery is initiated (triangles), and the more gradual change in catch when the eight reserves are instituted gradually (squares).

This analysis omits an aspect of model behavior observed in the simulations that will be important for implementing reserves—namely, the immediate decline in catch in the years after the reserves are instituted. The performance in figure 3 is long-term equilibrium catch, which ignores the short-term economic effects of instituting reserves (fig. 4) and any differences in those effects between the various values of *a*. The dependence of these adjustment costs on the value of *a* is significant. In particular, even though the long-run catch may be greater at low values of *a*, catch recovers much more slowly after the institution of reserves. These short-term effects can be included in the decision analysis by computing catch over the first 50 years rather than eventual equilibrium catch (table 1). In that case fewer reserves are indicated as the best choice, and the expected value is close to the optimal over a broader range.

Another way of accounting for the relative value of near-term versus long-term catches is to discount future catches. With a discount rate of 0.03 y^{-1}, the optimal fraction in reserves shifts to fewer reserves; the optimal is even broader; and the gain through reserves is slight—4% as opposed to 12%. However, the large initial decline in catch can be reduced by phasing in reserves gradually (fig. 4).

DISCUSSION

The results described here illuminate the fundamental uncertainty that underlies the question of whether marine reserves can benefit management of the northern California red sea urchin fishery. That fundamental uncertainty is the same one that underlies the prevention of overfishing in fisheries throughout the world: as fishing increases, the number of larvae produced in the lifetime of a juvenile may eventually be reduced to the point that there is a decline in recruitment, but, because we have little or no data at low abundance (i.e., to the left in fig. 2), we do not know the value of the fishing mortality rate at which that will occur. Here we have outlined some of the difficulties involved in determining whether this population is recruitment overfished, but there is more information available for this population than for most others. For world fisheries in general, data are rarely available on the decline of a developing fishery or the size distribution as a fishery develops (Caddy and Mahon 1995).

The efficacy of reserves as a management tool depends on whether this population is currently overfished or is likely to become overfished in the near future. The several lines of evidence on this issue vary in strength. Comparison of the decline in catch to model runs under various assumed values of *a* provides compelling evidence, but suffers from the fact that we have no way of estimating how fishing mortality rate varies from year to year. We do not know whether the recent declines in catch are due to declining abundance at constant fishing mortality rate or declining fishing mortality rate. Effort has declined (fig. 1), but as abundance declines, the amount of effort required to remove a certain fraction of urchins from the smaller population will decline. Hence it is reasonable to expect a decline in effort even at the same fishing mortality rate. Changes in the exchange rate between the yen and the dollar also would be expected to influence catch. The comparison of the decline in CPUE expected from the change in the size distribution (Botsford et al. 1999) involves fewer assumptions, and thus provides stronger evidence of a decline. Placing the current value of relative egg production per recruit in the context of threshold values of that parameter in fisheries management on a global scale provides greater generality to this argument, but suffers from the fact that few of the species being considered in the assessment of safe targets were invertebrates.

While our results provide information on the dynamic interactions between parameter values and the consequences of reserves, they are not completely definitive, because we have not addressed all of the many issues relevant to this question. We have only indirectly included the effects of low density on broadcast spawning (Levitan et al. 1992). Recent research indicates that the combined effects of reduced density and aggregation on broadcast spawners produce specific stochastic as well as deterministic effects on recruitment (see footnote 1). The interaction of temporally and spatially varying dispersal patterns with reserve configuration is another area for further analyses.

We also have assumed no change in fishing mortality with the institution of reserves. This omits two important issues that deserve further consideration. First, if reserves are instituted, they will obviously affect the decisions of divers as to when, whether, and where to fish. Ongoing research on this issue will provide estimates of changes in effort patterns that will have to be considered in evaluating the efficacy of reserves. The second issue to be evaluated is how it would be best to change fishing mortality rate as reserves are instituted. Preliminary indications are that it is optimal to increase fishing mortality rates when reserves are instituted. Evaluation of this issue would include the necessary consideration of how well potential overfishing might be remedied by changing effort or size limits rather than by instituting reserves (Hastings and Botsford 1999; Parrish 1999). Another issue on which more information is needed is the possibility of predispersal density-dependence in reserves. Assessing such effects in the few, small, red sea urchin reserves that currently exist would be a valuable first step.

The decision of whether to institute reserves in this fishery will involve the response of managers to the uncertainty described here. There is no guarantee that reserves will increase catch; in fact, if reserves are instituted there will be no way to tell whether they increased catch over what it would have been. Recent global analyses of the causes of widespread overfishing have indicated that precautionary, more risk-averse strategies are needed (Ludwig et al. 1993; Botsford et al. 1997). The precautionary approach to fishery management involves a shift in the burden of proof, which in this case would indicate that reserves should be instituted unless it could conclusively be demonstrated that the fishery could persist without them.

The eventual decision of whether to institute reserves will depend on a broader range of considerations than addressed here. If one considers effects beyond the management of the fishery on this species, reserves can serve a more general function of preserving natural biodiversity in a more or less pristine state. Even within the context of fishery management, two benefits of reserves not usually considered are that (1) management by reserves involves fewer uncertain assumptions about the effects of fishing on population dynamics (e.g., Clark 1996), and (2) maintaining part of the fished species in an unfished state has value for informational purposes. As an example of the latter, in fisheries for which the ages of individuals cannot be determined, size-structured approaches to stock assessment require unfished stocks for estimation of natural mortality rate (Morgan 1997).

The results of our analysis can be viewed as the reserve concept passing a simple initial test. What remains is to assess other issues not considered here. These include (1) how other density-dependent recruitment mechanisms affect expected catches; (2) fishers' behavior in response to spatial management; (3) possible spatial configurations of reserves implied by dispersal patterns; and (4) the advisability of making other concurrent management changes, such as changing size limit in addition to adding reserves.

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SPATIAL AND TEMPORAL GENETIC PATCHINESS IN MARINE POPULATIONS AND THEIR IMPLICATIONS FOR FISHERIES MANAGEMENT

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ABSTRACT

A degree of genetic patchiness has been demonstrated in a variety of marine populations. When this "chaotic genetic patchiness" exists, populations a few kilometers apart may differ genetically by as much as those hundreds of km apart. Such genetic patchiness could be caused by any of several factors, including natural selection acting on a local level before or after settlement, and genetic drift before settlement. Hedgecock's "sweepstakes-chance matching hypothesis" addresses the latter explanation, and is based in part on the observation of reduced genetic variability in young-of-the-year, relative to adult populations. This reduced genetic variability among recruits suggests that surviving young-of-the-year are the products of spawning by only a small fraction of the adult population, which, according to Hedgecock's hypothesis, happened to produce their offspring at a place and time that was suitable for survival. The succession of such cohorts would then lead to the shifting genetic mosaic that is characteristic of marine populations displaying chaotic genetic patchiness. If generally true, this phenomenon has implications for all forms of fisheries management, including marine harvest refugia. To the extent that spawning success is spatially unpredictable, fisheries management should practice a degree of "spatial bet-hedging." That is, within a biogeographical region of potentially panmictic larval transport, spawning biomass should be conserved broadly, in an attempt to ensure that propagules are available when and where favorable conditions for survival happen to occur.

CHAOTIC GENETIC PATCHINESS AND ITS CAUSES

Hedgecock (1994a, b) has recently reviewed the phenomenon of "chaotic genetic patchiness" in marine populations, a term used by Johnson and Black (1982) to describe small-scale, unpatterned, genetic heterogeneity among local populations. In many cases, populations separated by less than 10–100 km can be as genetically different as populations separated by 100–1,000 km. In addition, genetic composition may vary as much over time at one place as it does over large distances. Instances of chaotic genetic patchiness have been described in populations from a variety of geographical areas and taxonomic groups, although most described cases are invertebrate animals (table 1). Additional cases that are consistent with Johnson and Black's description, but were not recognized as such, may exist (e.g., Lacson and Morizot 1991). Furthermore, David et al. (1997) noted that detection of such fine-scale genetic patchiness may require large sample sizes.

While other geographic patterns of genetic structure have been described—including genetic differentiation among retention areas (e.g., Bernatchez and Martin 1995), widespread uniformity with little obvious underlying structure (e.g., Shulman and Bermingham 1995), and limited genetic variation at any spatial scale (e.g., Richardson and Gold 1997)—chaotic genetic patchiness may have important implications for fisheries management. In this paper, we attempt to bring attention to the topic of chaotic genetic patchiness in the context of fisheries management. We provide an overview of the potential causes for this phenomenon, emphasizing Hedgecock's (1994a, b) "sweepstakes-chance matching" hypothesis, and we initiate discussion of the implications of Hedgecock's hypothesis for fisheries management and marine no-take areas.

Chaotic genetic patchiness has been attributed to natural selection or to chance acting before settlement, or to natural selection acting after settlement (Johnson and Black 1982, 1984; Watts et al. 1990; Hedgecock 1994a, b). Natural selection acting after settlement has been observed in populations of invertebrates (e.g., Johannesson et al. 1995), producing genetic heterogeneity on very small scales. In these situations, genetic composition often shows clines that parallel environmental gradients, and in the absence of disturbance the genetic composition at one site is likely to remain constant, reflecting the consistent, site-specific effects of selection. However, several studies have shown that the genetic composition of a local population can vary over time (indicating a lack of consistent selection), and that the genetic composition of recruits can vary over time, both indicating that these cases of chaotic genetic patchiness are caused by factors acting prior to settlement (Johnson and Black 1982, 1984; Watts et al. 1990; Hedgecock 1994a, b).

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TABLE 1
Some Examples of Chaotic Genetic Patchiness in Marine Populations

Organism and location	Reference
Limpet, *Western Australia*	Johnson and Black 1982, 1984
Crown-of-thorns starfish, *Great Barrier Reef*	Nash et al. 1988
Sea urchin, *Western Australia*	Watts et al. 1990
Bicolor damselfish, *Florida Keys*	Lacson and Morizot 1991
Queen conch, *Caribbean Sea*	Campton et al. 1992
Snail, *Western Australia*	Johnson et al. 1993
Balanus barnacles, *California*	Hedgecock 1994b
Northern anchovy, *California*	Hedgecock et al. 1994
Snail, *Sweden*	Johannesson et al. 1995
Purple sea urchin, *California*	Edmands et al. 1996
Clam, *France*	David et al. 1997

Variation in the genetic composition in recruits, which may produce genetic heterogeneity on a local level, can be produced by at least three processes. First, drift of larvae from different source populations, which themselves differ in genetic composition, may lead to variation in the genetic composition of recruits. Purcell et al. (1996) postulated that this might be responsible for temporal differences in the genetic composition of haddock on Georges Bank. Roberts (1997) also suggested that this process could have led to small-scale differences in the genetic composition of bicolor damselfish in the Florida Keys, as observed by Lacson and Morizot (1991). Shulman and Bermingham (1995) suggested that on a large scale, variation in currents can introduce novel genotypes into new areas, although they did not investigate particular episodes of larval transport leading to gene flow. Where there are large-scale differences in genetic composition, large-scale transport is always a means for generating temporal variation in genetic composition in local populations. However, in some presumed examples of this process—such as the Purcell et al. (1996) or Lacson and Morizot (1991) studies—other factors, as discussed below, could also have been important.

Another factor that could lead to genetic differences among recruits is natural selection acting on larvae prior to settlement. Johnson and Black (1984) suggested that this mechanism was responsible for temporal variation in recruits of a limpet off western Australia, citing in particular the genetic uniformity of the "cloud" of recruits arriving at their study areas at any one time, and correlations between weather conditions and the frequencies of particular alleles. Hedgecock et al. (1994) also thought that selection (among other factors) could have produced genetic heterogeneity in northern anchovy. David et al. (1997) discuss the difficulties of demonstrating selection during the larval phase, and Hedgecock (1994b) noted that selection explains clinal variation better than chaotic patterns.

Hedgecock (1994a, b) developed a third hypothesis for spatial and temporal genetic variation among recruits; this mechanism was also mentioned by David et al. (1997). Hedgecock proposed that genetic variation among recruits might be due to large variance in reproductive success among adults, so that a resulting year class is the result of spawning by only a small portion of the adult population. This "instantaneous (genetic) drift effect" (David et al. 1997, p. 1,321) would then lead to reduced genetic variation among recruits, to differences between the genetic composition of recruits and the adult population as a whole, and, to the extent that different portions of the adult population contribute successful progeny in different years, to differences in the genetic composition of recruits over time. This variation in recruits then produces the "genetic mosaic fluctuating in time" (David et al. 1997, p. 1,321) which is characteristic of populations that demonstrate chaotic genetic patchiness. Hedgecock (1994a, b) postulated that spatiotemporal variation in oceanographic conditions, producing limited windows for larval survival, is responsible for the variation in reproductive success among adults. This "sweepstakes-chance matching" of place and time of spawning, he proposed, leads to random variation in the portion of the adult population that produces surviving offspring, and therefore to the variation in genetic composition of recruits observed in chaotic genetic patchiness.

Hedgecock (1994a, b) described two testable predictions of this hypothesis. One prediction is that genetic drift in the population as a whole should be measurable over time, demonstrating that effective population size is much smaller than actual population size. His study of oyster populations in Dabob Bay, Washington, suggested that effective population sizes were about 400 individuals in actual populations that were several orders of magnitude larger (Hedgecock 1994a). The second prediction was that recruits should show a smaller degree of genetic variation than the adult population, as a result of the "instantaneous drift" experienced between spawning and the establishment of the year class. Li and Hedgecock (1998) found that the genetic composition of young oyster larvae in Dabob Bay varied over time, in a manner consistent with Hedgecock's hypothesis. Julian (1996) found reduced genetic variability in late pelagic juveniles of shortbelly rockfish relative to both adults and larvae off central California, also supporting Hedgecock's prediction. In addition, the lowest genetic variability among pelagic juveniles in Julian's study occurred in the most abundant patch of individuals, suggesting that selection, which would act to reduce numbers, was not the likely factor acting on the genetic composition of that population.

Therefore, in addition to evidence of microscale genetic heterogeneity and variation in the genetic composition of recruits, some genetic evidence exists to support Hedgecock's hypothesis as well. Clearly, as noted by Hedgecock (1994b), much more work would be required to establish the generality of "sweepstakes-chance matching." Some recent reviews of marine population genetics barely (if at all) address chaotic genetic patchiness, focusing instead on how larval drift affects population subdivision (e.g., Shulman 1998), or on how postsettlement selection affects small- and large-scale population structure (e.g., Hilbish 1996). Other studies that do address chaotic genetic patchiness may not even mention Hedgecock's hypothesis as a potential explanation for the pattern (e.g., Edmands et al. 1996), or dismiss the hypothesis (e.g., Purcell et al. 1996).

To establish the generality of sweepstakes-chance matching, it will be important to demonstrate spatial and temporal variation in the genetic composition of recruits, to demonstrate the reduction of genetic variation in recruits relative to the adult population, and to compare the genetic composition of recruits to the genetic composition of adults from different portions of the geographical range (to rule out the effect of drift of larvae from genetically different portions of the population). It will also be important to determine whether features of population structure such as the distribution of adults and the dispersal of larvae influence the likelihood of sweepstakes-chance matching. However, the apparent occurrence of this phenomenon both in Dabob Bay oysters with a localized population and a larval phase lasting weeks, and in shortbelly rockfish with a coastwide population and a pelagic stage lasting months suggests that the sweepstakes-chance matching could occur in a variety of species. Finally, it will be important, but difficult, to distinguish between the effect of chance events and selection as factors influencing the genetic composition of recruits prior to settlement.

MANAGEMENT IMPLICATIONS OF THE SWEEPSTAKES-CHANCE MATCHING HYPOTHESIS

Chaotic genetic patchiness in itself may not have major implications for fisheries management. Any effects of localized selection after settlement may be difficult to detect in the mobile animals that make up most fisheries, and mobile animals may be less subject to localized selection after settlement than are sessile animals, because of their greater ability to choose conditions for living. If selection after settlement did exist, it is difficult to see how this would have a major effect on fisheries management, unless a fishery were to concentrate in one habitat or location and as a result exert a disproportionate mortality on a certain portion of the gene pool. The factors affecting genetic composition of recruits prior to settlement may have greater consequences, depending on the mechanism that is responsible. The effects of natural selection on larvae are difficult to gauge, but might simply be considered a part of variability in recruitment. The effect of large-scale structure in populations and drift of larvae from different sources is an important consideration in fisheries management (Ryman and Utter 1987). This factor is also widely addressed in the context of marine harvest refugia (e.g., Carr and Reed 1993; Carr and Raimondi 1998; Morgan and Botsford 1998). In this paper, however, we wish to speculate primarily upon the effects of sweepstakes-chance matching on fisheries management and the establishment of harvest refugia.

The processes envisioned to produce sweepstakes-chance matching are not new ideas. Temporal variation in the survival of larvae within a season may be quite common, as indicated by the existence of temporal pulses of survivors (e.g., Methot 1983; Woodbury and Ralston 1991; Larson et al. 1994; Lenarz et al. 1995). Spatial variation in the survival of larvae is more difficult to demonstrate, but has been observed (e.g., Lasker 1978; Kiørboe and Johansen 1986; Frank 1988). Julian (1996) showed both a temporal and spatial component in the genetic composition and, presumably, survival of pelagic-stage shortbelly rockfish in 1994. As in many years with poor year-class strength in shortbelly rockfish (Lenarz et al. 1995), survival of larvae was greatest late in the 1994 season. In addition, the bulk of the surviving pelagic juveniles were strongly aggregated in two frontal areas, and one of these patches (the only one analyzed) was less diverse genetically than adults and newborn larvae, and its genetic composition differed significantly from the apparent spawning population (Julian 1996).

What is surprising in these results and in Hedgecock's general thesis is not that there is spatial and temporal variation in the survival of larvae, but that the pool of adults from which the survivors were drawn was so small as to affect the genetic diversity of the survivors. We think that the significance of this phenomenon for fisheries management lies primarily in the potential for stochastically varying, spatially restricted survival of larvae. Temporal variation in larval survival should not have a great effect on strategies for fisheries management unless different stocks spawn at different times or unless the fishery is for spawners. If the fishery is for spawners, and if periods of good larval survival cannot be predicted, then efforts might be taken to ensure that reasonable levels of escapement are allowed throughout the spawning season.

Stochastic spatial variation in the sources of successful larvae implies that, within a region that is panmictic and mainly self-replenishing in the long term, the particular sources of surviving recruits vary unpredictably over time. To the extent that this is true, we think that fisheries management should act to conserve the distribution as well as the total spawning potential of an exploited population. For example, management of most commercially exploited species of rockfish seeks to preserve a minimal "spawning biomass per recruit" (Pacific Fisheries Management Council 1996). But if much of the spawning potential for a population has become restricted to a small area, leaving the remainder of the range with less potential for spawning, the probability that good conditions for larval survival will coincide with areas of larval production may be reduced. This may reduce the chance for good year classes. This thesis may be most applicable to species with a wide spawning distribution, and less applicable to species that migrate to restricted spawning grounds.

At face value, the spatial stochasticity of successful spawning would also argue for a spatial dispersion of harvest refugia, if these harvest refugia were to be the basis for managing the exploitation of a population. However, as pointed out by Steve Ralston (NMFS, Tiburon Laboratory, pers. comm.), if a certain percentage of the range were set aside as reserves and the locations of successful spawning in any given year were random and pointlike, it would not matter whether the reserve areas were distributed as one large area or an equal area of smaller reserves. But if the locations of successful spawning, though still random, were larger and had some chance of intersecting smaller reserves, it might be better if the reserves were dispersed rather than congregated. Again, this dispersion of reserves would increase the chance that some spawners would release larvae into conditions favorable for survival.

This premise is predicated on data showing both reduced genetic variation in recruits relative to the adult population and temporal variation in the genetic composition of recruits themselves. Consistent genetic composition of recruits over time in any area would indicate a consistent source of recruits or a consistent system of retention. How the sweepstakes-chance matching concept fits with concepts of larval drift and population structure such as larval retention and source/sink areas (Carr and Reed 1993; Roberts 1997; Carr and Raimondi 1998; Morgan and Botsford 1998; and others) must still be resolved. If genetic variation in recruits indicates stochastic variation in the times and places of larval survival, how can this be reconciled with systems of larval supply or retention that are treated as essentially deterministic?

At one extreme, recurrent patterns of larval distribution and settlement (e.g., Wing et al. 1995; Caselle and Warner 1996) may represent typical patterns of recruitment, but the larvae contributing to such patterns may have been derived from different sources within that recruitment-retention system. At another extreme, a recurrent pattern may exist, but may constitute only one of several patterns of recruitment in an area. Another, more intermediate possibility is that the delivery of larvae to shore may follow a consistent pattern, but that the surviving larvae which enter such patterns may have come from a variety of areas, both within the geographical area of a local recruitment-retention system, and outside of that system. For example, the aggregations of pelagic juvenile shortbelly rockfish seen in 1994 are relatively common (associated with fronts related to upwelling), but the distinct genetic composition of fish in one such aggregation (Julian 1996) implies that there is no consistent source of shortbelly rockfish that come to exist in those aggregations. It would be very helpful to carry out fine-scale genetic analyses on some of the better-studied systems, because much of current thinking about the design of marine harvest refugia is based on defining regular patterns of larval sources, while the sweepstakes-chance matching hypothesis argues for greater stochasticity in larval sources.

The sweepstakes-chance matching hypothesis and its implications share some features with Cowen's (1985) study of recruitment off southern California and Baja California. He found that recruitment of the California sheephead was relatively consistent in the center of its range off central Baja California, and occurred to the north and south only during periods of unusual transport (what he termed "high-level" events). Pringle (1986) found a very similar pattern of larval distribution in spiny lobster. Cowen's findings contributed strongly to the notion of "sources and sinks" in marine populations (Ebeling and Hixon 1991), in that reproduction at the center of the range was seen as maintaining populations at the extremes of the range. However, another part of Cowen's thesis was that populations at the extremes of the range experience irregular recruitment because there are fewer sources of recruits than at the center of the range. The center of the range, in contrast, experiences more consistent recruitment in part because there are more places that could supply it with recruits, under a wider range of environmental conditions. In that respect, unless populations at the extremes of the range are sterile, they contribute to the consistency of recruitment at the center of the range and do not act entirely as sinks.

If larval survival varies stochastically in space as suggested by the sweepstakes-chance matching hypothesis, this aspect of Cowen's hypothesis may also act on a smaller spatial scale. That is, the consistency of recruitment at any point within a potentially panmictic region may depend on the number of different places within the region that can produce larvae, therefore increasing the chances that at least some larvae are produced in circumstances that permit their survival. This notion is similar to Cowen's idea that the effects of "low-level" variation in transport are influenced by the proximity of larval sources.

We conclude that the potential for both "high-level" (El Niño–scale) and "low-level" variation in transport, and the potential for spatial variation in the conditions favorable for larval survival, mean that recruitment patterns and the relation between production of larvae and settlement of recruits can be variable. The potential for such variation may be as important as the presumed average conditions in the design of successful marine harvest refugia.

Comparison of the sweepstakes-chance matching hypothesis with Cowen's (1985) discussion raises the issue of the spatial scale, in relation to the potential for dispersal, of various processes affecting the sources of larvae in a local population. The spatial component of variation in larval survival is the aspect of sweepstakes-chance matching that we consider to be most applicable to fisheries management, yet it is the aspect that is the least well documented, both genetically and ecologically. In addition, the spatial scale of processes involved in sweepstakes-chance matching are not well resolved at all. On large scales, variations in larval drift may influence both the demography (e.g., Cowen 1985; Pringle 1986) and the genetic composition (e.g., Shulman and Bermingham 1995) of local populations. The small-scale genetic variation seen in cases of chaotic genetic patchiness would suggest that factors may also act on a smaller scale. Therefore, if sweepstakes-chance matching is a process leading to chaotic genetic patchiness, we would suggest that it acts on a smaller scale. What that scale is, and how that scale is influenced by factors such as larval duration, remains to be determined. Once these features of spatial scale can be resolved, perhaps modeling studies can more critically evaluate the consequences of both small- and large-scale variation in recruitment on fisheries management and the design of marine no-take areas.

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HUMAN VISITATION AND THE FREQUENCY AND POTENTIAL EFFECTS OF COLLECTING ON ROCKY INTERTIDAL POPULATIONS IN SOUTHERN CALIFORNIA MARINE RESERVES

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ABSTRACT

Humans intensely use southern California rocky shores for recreational activities such as fishing, exploration, walking, enjoyment of the out-of-doors, and educational field trips. People also collect intertidal organisms for consumption, fish bait, home aquariums, and other purposes. In Orange County, visitors concentrate their activities on a few rocky headlands and reefs. Many of these shores have been designated as California Marine Life Refuges (CMLRs) or State Ecological Reserves (SERs), where the removal of most intertidal organisms, except for scientific purposes, has been unlawful for 30 years. In a yearlong study of eight Orange County shores, unlawful collecting of organisms was often observed. In addition, lifeguards have frequently observed unlawful collecting on these and other shores. The CMLR or SER designation did not deter collecting. Mussels, trochid snails, limpets, urchins, and octopuses were the most commonly collected organisms, primarily for food or fish bait. Several of the gastropod species targeted by human collectors had low population densities and population structures dominated by smaller and less fecund individuals, characteristics that often occur in populations exploited by humans. Most collected invertebrates were broadcast spawners that require high densities of fertile individuals to optimize reproduction. The cascading effects of collecting on community structure and the reproductive success of exploited populations are unknown. Except for state park rangers at one site, no state enforcement personnel were seen during 768 hours of low-tide observations throughout the year. Without effective enforcement, adequate signage, and educational programs to increase public awareness, CMLRs and SERs are not protecting rocky intertidal populations on heavily visited southern California shores. Improved management practices are needed if CMLRs and SERs are to protect rocky intertidal populations and to serve as benchmark sites where changes in populations due to regional climatic events or chronic human disturbances can be measured and evaluated in the absence of exploitation.

INTRODUCTION

The human population residing in the coastal zone is growing by more than 1% per year in the United States (Culliton et al. 1990). This growth has been particularly rapid in coastal southern California counties, where the population has increased by more than 50% over the past three decades (Anon. 1969, 1998). The disturbance produced by the activities of this expanding population is thought to have resulted in a widespread reduction in the biodiversity of southern California's rocky shores (e.g., Littler 1980; Littler et al. 1991; Murray and Bray 1994).

Previously, declines in rocky intertidal biodiversity have largely been ascribed to chronic, persistent disturbances including discharged sewage and industrial effluents (Dawson 1959, 1965; Widdowson 1971; Thom and Widdowson 1978; Littler 1980). But more episodic disturbances resulting from visitor foot traffic (Brosnan and Crumrine 1994; Keough and Quinn 1998); the collection of organisms for human consumption, fish bait, aquariums, and other purposes (Griffiths and Branch 1997); and the exploratory manipulation of rocks and specimens (Addessi 1995) can also significantly affect rocky intertidal populations and communities. Yet, little attention has been given to the effects of human visitation, despite the large numbers of people that use southern California rocky shores throughout the year for activities such as recreational fishing, food and specimen gathering, educational field trips, exploration, walking, and enjoyment of the out-of-doors.

Globally, marine protected areas (MPAs) are receiving increasing attention as management tools for protecting marine populations from human activities (Gubbay 1995; Ticco 1995; Agardy 1997). In the last fifteen years, the number of MPAs has grown from about 400 to more than 1,000 worldwide (Gubbay 1995). Along the heavily urbanized southern California mainland, California Marine Life Refuges (CMLRs), State Ecological Reserves (SERs), and Marine Resources Protection Act (MRPA) Ecological Reserves are the most common MPAs established to protect intertidal organisms from on-site visitor disturbance (McArdle 1997).

Although minor variations occur among sites, CMLRs and SERs prohibit the removal of almost all marine plants and invertebrates except with a scientific permit or special authorization by the California Department of Fish and Game (Smith and Johnson 1989; McArdle 1997). Exceptions generally include invertebrates of historical importance to recreational sport and commercial fishers, such as lobster (and in the past, abalone), which can be extracted lawfully from most CMLRs and SERs with an appropriate license or permit. The taking of most species of finfish with a sportfishing or commercial license is also allowed in most CMLRs and many SERs; only MRPA Ecological Reserves prohibit the extraction of all plants and invertebrates, and fishing for finfish without special authorization (McArdle 1997). Interestingly, none of these CMLRs, SERs, or MRPA Ecological Reserves include regulations that limit human access or restrict exploratory human activities.

Most of southern California's CMLRs and SERs were established between 1968 and 1973 (Smith and Johnson 1989; McArdle 1997), a period of heightened public interest in environmental issues. Unfortunately, like many other coastal conservation measures enacted at that time, the measures did not institute programs to evaluate the results of CMLR or SER establishment. Thus, a question of fundamental importance to the management and conservation of rocky intertidal populations and communities in southern California is: Have CMLRs and SERs been effective in protecting rocky intertidal invertebrate, plant, and finfish populations from the activities of an expanding human population during the last 30 years?

The purpose of this paper is to discuss how visitors can affect CMLRs, SERs, and unprotected rocky shores in urban southern California. On the basis of work performed on Orange County rocky shores, we describe and discuss (1) the magnitude of human visitation; (2) the collecting of intertidal invertebrates for food, fish bait, home aquariums, and other purposes; (3) the apparent decline of selected intertidal invertebrate populations; and (4) the effectiveness of CMLRs and SERs in protecting rocky intertidal populations and communities in urban southern California.

THE STUDY AREA AND HUMAN VISITATION

Orange County, located just south and east of the city of Los Angeles, has undergone extensive urbanization as its population has more than doubled during the past 30 years (Anon. 1969, 1998). The infrastructure created to support this urbanization includes major highways and roads that have made most of the county's shoreline easily accessible to visitors throughout the region. Because rocky headlands and low-lying bedrock reefs mostly occur along the Orange County coast between Little Corona Del Mar and Dana Point (fig. 1) and are separated by stretches of sandy beach, human visitors concentrate their activities on only a small portion (<20 km) of the county's shoreline. Most of this rocky intertidal habitat lies within the boundaries of seven CMLRs and the Heisler Park SER; these MPAs were established about 30 years ago. An additional section of the Orange County coastline was placed under CMLR protection with the implementation of SB-716 on January 1, 1994. This bill expanded the southern boundary of the Laguna Beach MLR to include the previously undesignated section of coastline between the Laguna Beach and South Laguna MLRs (fig. 1).

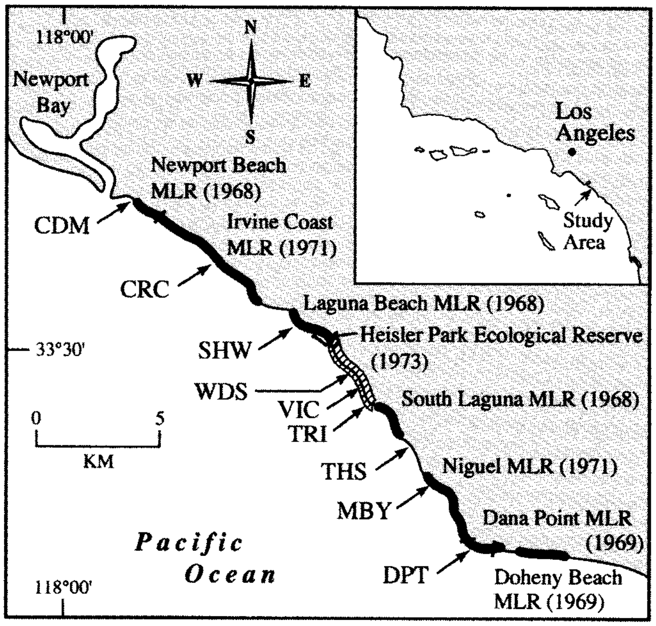

Figure 1. The south Orange County coastline, indicating California Marine Life Refuges (CMLRs) and State Ecological Reserves (SERs) and the dates of their establishment. Shaded areas indicate longstanding (ca. 30 years) CMLRs; the cross-hatched area depicts the January 1, 1994, extension of the Laguna Beach MLR. Arrows indicate the 8 sites assessed for human collecting: Crystal Cove (CRC), Shaw's Cove (SHW), Woods Cove (WDS), Victoria Beach (VIC), Treasure Island (TRI), Thousand Steps (THS), Monarch Bay (MBY), and Dana Point (DPT). The Little Corona Del Mar site (CDM) and the Heisler Park SER are also shown.

Rocky shores have long served as important recreational and educational resources for outdoor-oriented southern Californians (fig. 2). Although data on the number of visitors are not kept for most sites, partial records are available for selected locations where educational group activities take place. During 1996, for example, 7,690 people explored three to four rocky intertidal reefs at Crystal Cove State Park (M. Eaton, G. Scott, and W. Bonin, Calif. Park Service, pers. comm.) and 12,204 participated in organized field trips held within the Dana Point MLR (H. Helling and J. Goodson, Orange County Marine Inst., pers. comm.). In the same year, 12,000–15,000 persons made low-tide visits to a shoreline extending only about 125 meters at Little Corona Del Mar (fig. 1), a popular location for educational field trips in the Newport Beach MLR (T. Melum, City of Newport Beach, pers. comm.). At times, the number of shore visitors during a single afternoon low tide has reached levels as high as 1,443 persons in the Dana Point MLR (H. Helling, pers. comm.).

The activities of high concentrations of visitors, including their foot traffic, can significantly damage a wide

Figure 2. A large group of young people walks on organisms while participating in an educational field trip in the Dana Point MLR.

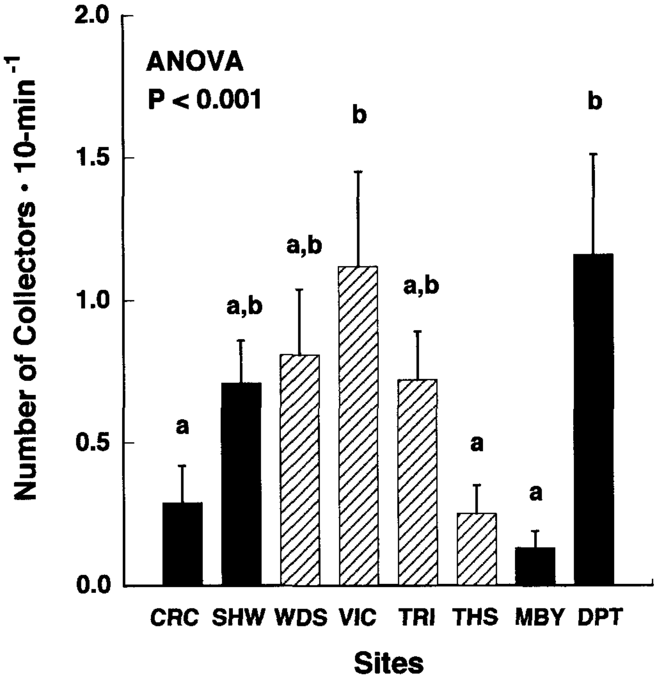

Figure 3. Human collecting activity at eight Orange County study sites (see fig. 1 for locations and abbreviations; after Murray 1998). Filled bars indicate longstanding, signed CMLRs; cross-hatched bars designate nonreserve sites (prior to 1994). Signs indicating CMLR status were not posted at nonreserve study sites given protection on January 1, 1994, until after all our data were collected. Plotted values represent the annual mean number of collectors (+1 SE) for each site calculated from the twelve monthly averages obtained between February 1995 and January 1996. Mean values designated by the same letter (a or b) belong to the same subset on the basis of the Student-Newman-Keuls (SNK) a posteriori multiple comparison test.

variety of rocky intertidal species (Keough and Quinn 1991, 1998; Brosnan and Crumrine 1994; Addessi 1995; Brown and Taylor 1999). Southern California intertidal populations susceptible to trampling include fleshy seaweeds, coralline algae, fragile tube-forming polychaetes, bivalves such as mussels, acorn barnacles, limpets, and grapsid crabs that seek refuge under loose rocks and seaweeds during low tide (Ghazanshahi et al. 1983; Murray 1998). Upper-shore fleshy seaweeds have been shown to be particularly susceptible to damage from human foot traffic throughout the world (Boalch et al. 1974; Beauchamp and Gowing 1982; Povey and Keough 1991; Brosnan and Crumrine 1994; Keough and Quinn 1998; Murray 1998; Schiel and Taylor 1999).

HUMAN COLLECTING ON ORANGE COUNTY ROCKY SHORES

Collecting Activity

A direct and potentially damaging effect of human visitation to the intertidal zone is the extraction of organisms. We quantified the frequency of human collecting of invertebrates and plants monthly for one year at eight rocky intertidal sites, four of which were within well-signed, longstanding CMLRs where collecting intertidal organisms without a scientific collector's permit was unlawful (Murray 1998). We visited the sites four times per month, twice during weekends and twice during weekdays between February 1995 and January 1996, to obtain monthly averages of collecting frequency. All site visits took place between sunrise and sunset; we did not sample on rainy days. Observations began one hour before and ended one hour after the predicted time of lower-low water. During each visit, the number of persons observed collecting was recorded for 10 minutes at the beginning of each 30-min period to produce five 10-min samples. We used these data to calculate the mean number of collectors observed per 10-min period for each site visit.

Our surveys indicate that collecting is frequent on Orange County rocky shores and does not appear to be deterred by CMLR designation in the absence of active education and enforcement. We estimated annual means of 0.1 to 1.1 collectors per 10-min observation period, indicating that at sites where collecting activity was most intense (i.e., Victoria Beach and Dana Point), an average of at least one person was engaged in collecting during every 10-min low-tide observation period throughout the year (fig. 3). No significant difference in the amount of collecting was detected between longstanding CMLRs and unprotected areas (one-tailed paired *t* test; $T = 1.007$; df = 11; $P = 0.17$; analysis based on comparisons of monthly averages of the number of collectors per 10-min period recorded for CMLR and nonreserve sites).

Collecting intensity, however, did vary significantly (ANOVA performed on square-root transformed data: df = 7; *MS* = 0.342; *F* = 4.162; $P < 0.001$) among the eight sites (fig. 3). Collecting was generally greatest on shores most easily accessible to visitors (e. g., Shaw's Cove, Woods Cove, Dana Point) and where recreational fishers were frequently seen removing organisms for fish bait (Shaw's Cove, Victoria Beach, Treasure Island).

Uniformed or other identifiable enforcement officials were never seen viewing the shore from overlooks, questioning people leaving the beach, or on the shoreline at our study sites during a total of 768 hrs of low-tide observations throughout the year. The only visible enforcement officials were state park rangers at our study site located inside Crystal Cove State Park, and lifeguards on duty during the summer and on holidays at sandy beaches adjacent to several of our study areas.

Records kept by Laguna Beach lifeguards also provide evidence that collecting is widespread and extensive along Orange County rocky shores, even in CMLRs and SERs (M. Klosterman, Marine Safety Chief, City of Laguna Beach, pers. comm.). For example, in 1997 and 1998, Laguna Beach lifeguards gave an annual average of 25,532 ecological advisements to persons collecting or engaged in ecologically damaging activities to intertidal populations and communities. Most advisements were given when tides were unfavorable for low-tide visitors, in the late morning and afternoon during the late spring and summer months when lifeguards were on duty. Lifeguards generally were not present in the fall and winter, when visitors most intensely use southern California rocky shores during favorable midday and afternoon lower low tides (Murray 1998). All advisements were given over a shoreline span (ca. 5 km) that extended from just north to just south of the historical limits of the Laguna Beach MLR and that included the Heisler Park SER (fig. 1). In summer (June–August) 1996, more than 40% of a total of 12,269 advisements were given at stations located either inside the Laguna Beach MLR or the Heisler Park SER. Heisler Park is a well-signed SER where all recreational and commercial extraction of marine plants, invertebrates, and finfish is prohibited without a scientific collector's permit or special authorization (McArdle 1997).

Species Collected

Slow-moving and sessile intertidal invertebrates are particularly vulnerable to collecting. Our surveys, and observations made during subsequent visits to our study sites, indicate that the organisms most commonly collected on southern California rocky shores are mussels, trochid snails, limpets, urchins, and octopuses.

Most collectors seemed to remove organisms for food or fish bait, although sometimes we found people taking animals for personal or commercial aquariums. Specimen collecting for scientific or educational purposes was seldom observed. Collectors often used iron bars, hammers, knives, or chisels to obtain mussels, and they frequently overturned rocks or damaged the rocky substrata while probing crevices and searching beneath larger boulders for octopuses. Flagrant collecting of large quantities of organisms occurred mostly when visitors took bags of mussels, presumably for food (fig. 4). Laguna Beach lifeguards also reported that the most extreme collecting incidents usually involved mussels (M. Klosterman, Marine Safety Chief, City of Laguna Beach, pers. comm.). On a few occasions, collectors took organisms for unusual purposes. For example, we saw a fisher leaving a signed CMLR with a bucket filled with kelp snails (*Norrisia norrisi* Sowerby) to be used the next day for fish bait in a nearby freshwater lake. We saw plants being collected only for scientific or educational purposes.

Figure 4. Collectors fill a bag with mussels in the Laguna Beach MLR.

We saw that recreational shore fishers fished at sites with steeply sloping rock platforms containing beds of mussels. Like recreational shore fishers in Australia (Kingsford et al. 1991), local fishers concentrated their bait-gathering adjacent to their preferred fishing spots, whether or not they were inside a CMLR or SER. Our observations indicate that mussels are by far the most commonly collected bait organism on southern California shores. Recreational fishers pull and cut mussels directly from the substratum; these practices also eventually dislodge other mussels by weakening their byssal attachment threads to each other and to rock surfaces. Recent surveys at our sites also revealed more gaps and less mussel cover within beds frequented by recreational fishers, probably as a result of bait removal.[1]

Effects of Collecting

The most direct effects of intense collecting are decreased abundances of exploited species and, because humans preferentially collect larger individuals, altered population size structures (Griffiths and Branch 1997). Decreased density and reduced size structures have been reported for exploited invertebrate populations in Chile (Moreno et al. 1984; Castilla and Durán 1985; Oliva and Castilla 1986); Costa Rica (Ortega 1987); South Africa (Branch 1975; McLachlan and Lombard 1981; Hockey and Bosman 1986; Lasiak and Dye 1989; Branch and Moreno 1994); Tanzania (Newton et al. 1993); and Australia (Catterall and Poiner 1987; Keough et al. 1993). In addition, reduced abundances of certain exploited invertebrates, including mussels (Siegfried et al. 1985; Hockey and Bosman 1986), oysters (Dye 1988), predatory gastropods (Moreno et al. 1986; Durán and Castilla 1989), and limpets (Hockey and Bosman 1986; Oliva and Castilla 1986; Lindberg et al. 1998) can lead to significant changes in community structure.

The status of several intertidal invertebrate populations on southern California shores may reflect recent human exploitation, even where CMLRs and SERs have made almost all extraction by humans unlawful for nearly 30 years. For example, recent qualitative observations made at longstanding CMLRs and SERs and at historically unprotected southern California sites revealed sparse populations of most species of mid- and large-sized snails (>30 mm in maximum shell dimension) and grapsid crabs, particularly on smaller rocky platforms (<75 m of shoreline) that receive high concentrations of human visitors. On some of these small rocky platforms, the densities of common mid-intertidal turban snails (*Tegula gallina* Forbes and *T. funebralis* A. Adams) were found to be extremely low (0 to <1 m^{-2}) despite the availability of suitable habitat (Sato and Murray, unpublished data). Also, Kido[2] found the mean shell sizes (26.2 to 35.2 mm maximum shell length) of populations of the relatively long-lived owl limpet (*Lottia gigantea* Sowerby) at our eight study sites to be comparable to sizes reported by Pombo and Escofet (1996) for sites in Mexico where human exploitation is common. Collecting of *L. gigantea* is known to drive populations toward low densities of small individuals and to have cascading effects on other intertidal populations (Lindberg et al. 1998).

Reduced density and altered size structures can also have profound repercussions on the reproductive success of intensely exploited populations (Branch 1975; Wells 1997). As discussed by Hockey and Branch (1994), this is particularly true for broadcast spawners, where the probability of fertilization is already low for individual gametes (Denny et al. 1992); decreased density can further reduce fertilization success (Levitan 1991; Tegner et al. 1996). Furthermore, the preferential exploitation of larger-sized individuals can significantly decrease reproductive output because the production of gonadal mass greatly increases with size in most marine invertebrates. For example, changes in size structure due to human exploitation led to more than an 80% reduction in the reproductive output of a South African limpet population (Branch 1975; Branch and Moreno 1994). For protandrous species like *Lottia gigantea*, whose individuals change from males to females with age, greater exploitation of larger and older animals may further diminish the reproductive output of local populations by reducing the availability of females. Allee effects on the reproductive success of southern California invertebrates that rely on external fertilization are unknown but may be significant where density and size structure have declined over broad regional scales.

CONCLUSIONS

Our observations raise serious questions about the effectiveness of CMLRs and SERs as they are currently being managed in urban southern California. Low-tide surveys made throughout the year at eight Orange County sites, together with records kept by Laguna Beach lifeguards, indicate that unlawful collecting of intertidal organisms is common on many southern California rocky shores. Moreover, sites that are easy for visitors to reach and that are preferred by fishers seem to have the highest frequency of collecting disturbance regardless of whether the sites have long histories of CMLR or SER designation and whether signs indicating their protected status are posted at entry points. Unfortunately, historical data on the abundances and sizes of recreationally exploited invertebrates are unavailable for most southern California shores, so it is difficult to measure population declines and to evaluate the current status of any population. However, our qualitative observations and recent studies suggest that several exploited intertidal invertebrates have densities and size structures characteristic of overexploited populations.

Compliance with regulations is listed as a key to MPA success (Causey 1995; Ticco 1995) but is often difficult to achieve (Proulx 1998). The almost complete absence of visible enforcement officials has clearly contributed to the high frequency of unlawful collecting in southern California CMLRs and SERs. Maintaining effective

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[1] Smith, J. R. 1999. The effects of bait collection and trampling on *Mytilus californianus* Conrad communities on southern California rocky shores. M.A. thesis, Calif. State Univ., Fullerton (in preparation).

[2] Kido, J. S. 1999. The status of *Lottia gigantea* Sowerby (owl limpet) populations among and within sites on southern California rocky shores. M.A. thesis, Calif. State Univ., Fullerton (in preparation).

enforcement is important especially for urban shores where visitors come from inland locations many kilometers away to exploit intertidal populations, and where coastal residents cannot depend on peer pressure or local educational efforts to achieve compliance with MPA regulations.

Clearly, the management of state MPAs in urban southern California has not received appropriate attention, and CMLRs and SERs do not seem to be effective in protecting intertidal populations from damaging activities. Improved and new management practices are needed, including the provision of effective enforcement, the use of volunteers or docents, the development of educational programs, and the initiation of scientific studies to evaluate MPA effectiveness. Only under these conditions can CMLRs and SERs protect rocky intertidal populations and communities, preserve coastal ecosystem functioning, and serve as benchmark sites in rapidly changing urban environments against which changes due to regional climatic events or the chronic inputs of anthropogenic pollutants can be scientifically evaluated in the absence of human exploitation.

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ECONOMIC AND MANAGEMENT IMPLICATIONS OF NO-TAKE RESERVES: AN APPLICATION TO *SEBASTES* ROCKFISH IN CALIFORNIA

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ABSTRACT

This paper presents some of the economic and management issues likely to arise if a no-take reserve is designed to protect and manage rockfish in California. These issues include equity matters associated with location of the reserve, implications for major sectors of the rockfish fishery, and possible external effects on fish stocks and fisheries outside the reserve area. These issues are described in the context of the current management regime and recent trends in the fishery. Particular attention is paid to two fishery sectors—groundfish trawlers and commercial passenger fishing vessels—whose logbook data provide detailed information about the area of harvest. Recommendations are made regarding the need to define objectives, address allocative issues and external effects, accommodate scientific uncertainties, and consider reserves in combination with more conventional management techniques.

INTRODUCTION

Permanent no-take marine reserves are being considered as a means of achieving a variety of resource management objectives, such as providing a hedge against collapse of fish stocks, or providing reference areas to facilitate the evaluation of natural versus human effects on fish populations (Bohnsack and Ault 1996). Economic benefits to fisheries outside a reserve may also arise: for instance, the stock enhancement that occurs within the reserve may eventually filter (via larval transport or export of adult fish) to outside areas (Rowley 1994). The extent to which such benefits are actually realized will vary, depending on the specifics of the particular reserve being considered.

This paper presents economic and management implications of reserves in the context of a specific hypothetical scenario—the establishment of a permanent no-take reserve to protect and manage rockfish (genus *Sebastes*) in California. Rockfish provide a plausible example for several reasons. As relatively sedentary stocks, they are considered amenable to enhancement by a reserve. Rockfish also have certain life-history characteristics (e.g., infrequent and variable recruitments) that lend considerable uncertainty to the stock assessments upon which management decisions are based (Ralston 1998). The current interest in rockfish reserves reflects an attempt to overcome the shortcomings of recent management in dealing with such uncertainty.

This paper provides information relevant to some of the fishery-related issues that are likely be raised with regard to rockfish reserves. This information is intended to be exploratory rather than conclusive and to encourage further discussion of real-world issues that must be addressed if reserves are to be considered as a rockfish management tool. Full development and evaluation of management options will require much more detailed iterations of the analysis provided here,[2] as well as extensive input from natural as well as social scientists, resource managers, enforcement and legal experts, the fishing industry, and the public at large.

ROCKFISH FISHERY MANAGEMENT

In 1982 the Pacific Fishery Management Council (PFMC) implemented a Fishery Management Plan (FMP) for the groundfish fishery in the Exclusive Economic Zone of California, Oregon, and Washington (PFMC 1982). The FMP covers a variety of finfishes, including 52 *Sebastes* stocks.

In 1994 the PFMC implemented a limited entry program (PFMC 1992) for the commercial fishery, and issued permits to vessels that met designated minimum groundfish landings requirements (MLRs) for trawl, longline, or fishpot gear. At the time of issuance, each permit was "endorsed" with the specific gear types for which the MLRs were met, with limited entry participation restricted to the gear types endorsed on the permit. Each permit, along with its particular gear endorsement(s), may be transferred to another vessel of similar or lesser length, and larger vessels may enter the fishery by consolidating permits held by smaller vessels. Other restrictions imposed on the limited entry fishery include quotas, limits on fish size, gear restrictions, and vessel landings limits.

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[2] A non–rockfish-specific but more comprehensive discussion of economic costs and benefits associated with reserves is provided in Thomson 1998.

The PFMC also manages an open access fishery, which is restricted to vessels that target non–PFMC-managed species (e.g., California halibut, sea cucumber) with trawl gear; vessels that land groundfish incidentally while participating in non-groundfish fisheries (e.g., shrimp trawlers); and vessels that use hook and line or fishpot gear without a limited entry permit to harvest small amounts of groundfish.

The PFMC annually establishes separate *Sebastes* quotas for the areas north and south of Cape Blanco, Oregon. The quota for the southern area (which includes California) is allocated 67% to the limited entry fishery and 33% to the open access fishery.

In 1997, 483 limited entry permit holders landed groundfish in California, Oregon, or Washington. Of these active permit holders, 234 landed groundfish in California, and 218 of those counted rockfish among their groundfish landings. Of the 218 rockfish harvesters, 83 possessed a longline endorsement, 130 had a trawl endorsement, and 5 had either a fishpot endorsement or multiple gear endorsements. Rockfish landings and revenue averaged 4.5 metric tons and $9,551 for the longliners, and 39.1 t and $29,563 for the trawlers, and accounted for about 10% of total landings and revenues from all species by both longliners and trawlers. Although the longliners make significant non-groundfish as well as groundfish landings and deliver most of their fish to California ports, the trawlers focus more exclusively on groundfish and are more likely to engage in interstate fishing (table 1).

TABLE 1

Average Landings (Metric Tons) and Ex-Vessel Revenue ($, Base Year = 1997) by Limited Entry Permit Holders Who Landed Rockfish in California in 1997, by Gear Type, Species Category, and State

	Longline		Trawl	
	t	$	t	$
California:				
Rockfish	4.5	9,551	39.1	29,563
Other groundfish	14.2	42,681	143.3	116,435
Non-groundfish species	25.5	26,130	42.9	56,430
Oregon/Washington:				
Rockfish	0.2	201	15.6	10,779
Other groundfish	1.3	6,311	179.3	43,465
Non-groundfish species	0.8	2,111	21.8	18,590
Total	46.5	86,985	442.0	275,262

Source: PacFIN data combined with limited entry permit information provided by Jim Hastie (NMFS, Alaska Fisheries Science Center, Seattle). In addition to 83 longliners and 120 trawlers, 5 permit holders with either a pot endorsement or endorsements for multiple gear types also landed rockfish in California. Mean landings and revenues for those five vessels are not reported here in order to protect data confidentiality.

In 1997, 1,111 vessels landed rockfish in California's open access fishery. Rockfish landings and revenues by these vessels averaged 1.6 t and $3,211. Four gear types accounted for 96% of these landings: hook and line, excluding troll (53%); troll (18%); trawl (14%); and non-trawl net (11%).

Although limited entry has been helpful in preventing the commercial groundfish fleet from expanding, the fishery remains significantly overcapitalized (pers. comm. between PFMC Chairman Jerry Mallet and U.S. Dep. Commerce Secretary William M. Daley, dated July 21, 1998). Growing concerns about the status of groundfish stocks have prompted the PFMC to reduce quotas and vessel landings limits (PFMC 1997). These decisions have been complicated by the need to minimize management-induced discards of fish and ensure that the conservation burden is equitably distributed among different segments of the fishery.

The 1996 Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA)[3] strengthened the responsibility of the PFMC and other regional councils to protect stocks from overfishing and rebuild overfished stocks. It also expanded the required scope of FMPs to include identification, conservation, and enhancement of essential fish habitat (NMFS 1996). Rockfish reserves, as well as other management measures, must be evaluated in the context of the new realities associated with the MSFCMA.

THE CALIFORNIA ROCKFISH FISHERY

The fishery for *Sebastes* rockfish in California includes both commercial and recreational components. Commercial landings declined from about 11,900 metric tons in 1988 to 7,400 t in 1997 (table 2). Ex-vessel revenues—corrected for inflation to 1997 dollars—also declined from $13.4 million in 1988 to $8.7 million in 1997 (table 3). The rockfish sport fishery includes anglers who fish from commercial passenger fishing vessels (CPFVs), private boats, and shore. According to logbook data submitted by CPFV operators to the California Department of Fish and Game (CDFG), CPFV rockfish harvest increased from 1.7 million fish in 1987 to over 2 million in the early 1990s, then declined to around 1 million by 1996 (table 4). Although these numbers are conservative estimates of CPFV activity (not all CPFV operators participate in the logbook program), they are believed to indicate general trends in the fishery. Time series data on harvests by private boat and shore anglers are not as complete, but also suggest a decline in rockfish landings.

Although landings may be affected by nonbiological factors (e.g., effort shifts resulting from changes in ex-vessel prices), the recent decline in rockfish landings is more likely attributable mainly to declines in stock abundance, as evidenced by downtrends in biomass, catch per

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[3] The Magnuson-Stevens Fishery Conservation and Management Act is the name given to the 1996 amendment to the 1976 Magnuson Fishery Conservation and Management Act, which established eight regional fishery management councils to manage fisheries in the Exclusive Economic Zone of the United States.

TABLE 2
Commercial Rockfish Landings in California by Gear Type, 1988–97 (Metric Tons)

Year	Trawl	Hook & line	Pot/trap	Nontrawl net	All else	Total
1988	6,104.4	1,893.0	39.2	2,420.2	1,485.5	11,942.3
1989	7,286.2	2,350.3	39.9	2,356.1	953.0	12,985.5
1990	7,836.0	2,731.3	31.8	2,288.4	1,046.6	13,934.1
1991	5,673.2	3,216.0	12.8	1,456.0	590.9	10,948.9
1992	4,057.8	4,140.9	17.3	1,464.4	524.8	10,205.2
1993	4,423.6	2,972.1	15.0	998.6	136.5	8,545.8
1994	4,236.8	2,135.4	18.2	582.5	531.7	7,504.8
1995	5,391.3	1,687.1	29.0	651.2	293.2	8,051.8
1996	5,457.4	1,599.2	23.2	240.2	224.5	7,544.5
1997	5,365.8	1,383.4	24.8	198.5	397.1	7,369.6
Avg.	5,583.3	2,410.9	25.1	1,265.6	618.4	9,903.2

Source: PacFIN database. "Trawl" pertains to the various types of groundfish trawl gear and "hook & line" to all hook and line gear except troll. "Nontrawl net" includes gill nets, trammel nets, dip nets, set nets, and seines. "All else" includes all gear types not covered elsewhere in the table (mainly troll and shrimp trawl).

TABLE 3
Ex-Vessel Value of Commercial Rockfish Landings in California by Gear Type, 1988–97 ($1,000s, Base Year = 1997)

Year	Trawl	Hook & line	Pot/trap	Nontrawl net	All else	Total
1988	5,352.3	3,535.0	49.2	2,933.9	1,502.6	13,372.6
1989	5,773.3	4,312.6	106.7	2,711.7	1,233.4	14,137.7
1990	6,019.1	4,714.3	44.3	2,770.4	1,262.3	14,810.4
1991	4,349.5	5,607.1	27.4	1,571.7	685.7	12,241.3
1992	3,087.5	6,450.2	42.7	1,579.3	630.4	11,790.0
1993	3,408.5	5,370.8	35.2	1,144.2	186.8	10,145.5
1994	3,554.0	4,351.5	66.4	681.5	652.9	9,306.3
1995	4,692.2	4,032.0	137.9	756.0	392.3	10,010.3
1996	4,403.8	3,946.9	101.3	314.4	285.4	9,051.8
1997	4,070.3	3,769.3	110.0	246.9	474.2	8,670.7
Avg.	4,471.0	4,609.0	72.1	1,471.0	730.5	11,353.7

Source: PacFIN database. Revenues corrected to 1997 dollars using GDP implicit price deflator. "Trawl" pertains to the various types of groundfish trawl gear and "hook & line" to all hook and line gear except troll. "Nontrawl net" includes gill nets, trammel nets, dip nets, set nets, and seines. "All else" includes all gear types not covered elsewhere in the table (mainly troll and shrimp trawl).

TABLE 4
Rockfish Landings by Commercial Passenger Fishing Vessels in California, in Numbers of Fish and as a Percentage of Total CPFV Landings in Each Area, 1987–96

	Southern California		Central California		Northern California		Total	
Year	No. fish	%	No. fish	%	No. fish	%	No. fish	%
1987	916,851	29%	744,348	81%	37,835	75%	1,699,034	41%
1988	1,053,906	32%	796,521	81%	41,850	79%	1,892,277	44%
1989	1,264,675	36%	853,021	83%	68,283	83%	2,185,979	48%
1990	1,265,471	35%	911,305	86%	98,880	90%	2,275,656	48%
1991	1,243,022	38%	759,554	90%	59,874	82%	2,062,450	49%
1992	1,110,692	36%	873,887	90%	66,997	96%	2,051,576	50%
1993	937,108	35%	721,038	87%	26,767	86%	1,684,913	47%
1994	812,361	33%	556,136	80%	26,795	89%	1,395,292	44%
1995	679,423	28%	460,624	74%	34,944	86%	1,174,991	38%
1996	645,802	24%	404,174	79%	26,134	84%	1,076,110	33%

Source: CPFV logbook summaries published by the California Department of Fish and Game. Estimates should be viewed as conservative, since not all CPFVs participate in the logbook program.

unit of effort (CPUE), and length frequency (Love et al. 1998; Ralston 1998; Mason, in press).

Over the past 10 years, the major commercial gears used to harvest rockfish in California have included trawl, hook and line (excluding troll), pot/trap and nontrawl net (including gill and trammel nets). Rockfish landings with nontrawl net gear have declined significantly—particularly since 1994, when California voters passed Proposition 132, which banned gill and trammel nets in state waters. Landings by trawl and hook and line gear have also fallen, though less dramatically, and pot/trap landings fluctuate from year to year while their absolute numbers remain modest (table 2). Although trawl gear accounted for 71% and hook and line gear for 20% of statewide rockfish landings in 1995–97, these gear types each account for a similar share of statewide rockfish revenue—49% for trawl and 44% for hook and line. The disproportionate contribution of hook and line landings to revenues is due to the higher average price of hook and line rockfish relative to trawl-caught rockfish. Rockfish harvested with pot gear commands an even higher price than hook and line rockfish.[4]

Depending on how rockfish landings are distributed across areas and fishery sectors, the location of a reserve can have a significant effect on which sectors are most likely to be displaced by the reserve. During 1995–97, trawl landings were concentrated in north/central areas, and nontrawl net landings in south/central areas of the state, while hook and line landings were more evenly distributed throughout the state (table 5); revenues fol-

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[4] Price differentials among gear types may be due to several factors, including differences in market quality associated with size or handling of the fish as well as differences among gear types in the composition of harvest between higher- and lower-priced rockfish species. Price is not necessarily a good indicator of economic value, since value is not determined by price but by the difference between price and harvesting cost.

TABLE 5
Average Annual Commercial Rockfish Landings in California, 1995–97, in Metric Tons and as a Percentage of Total Groundfish Landings Associated with Each Gear Type and Area

	Northern California		Central California		Southern California		Total	
Gear type	$	%	$	%	$	%	$	%
Trawl	2,462.1	17%	2,476.3	36%	466.5	18%	5,404.8	23%
Hook & line	402.3	47%	443.9	27%	710.3	72%	1,556.6	45%
Pot/trap	2.2	1%	3.8	13%	19.7	37%	25.7	8%
Nontrawl net	0.6	77%	191.3	82%	171.4	77%	363.3	80%
All else	49.1	49%	211.4	88%	44.4	49%	304.9	71%
Total	2,916.3	19%	3,326.8	36%	1,412.2	36%	7,655.3	27%

Source: PacFIN database.

TABLE 6
Average Annual Ex-Vessel Rockfish Revenue in California, 1995–97, in $1,000s (Base Year = 1997) and as a Percentage of Total Groundfish Revenue Associated with Each Gear Type and Area

	Northern California		Central California		Southern California		Total	
Gear type	$	%	$	%	$	%	$	%
Trawl	1,857.4	15%	2,118.1	30%	413.3	14%	4,388.8	19%
Hook & line	722.6	33%	949.8	28%	2,243.7	69%	3,916.0	44%
Pot/trap	3.9	1%	8.9	10%	103.6	30%	116.4	11%
Nontrawl net	0.7	65%	206.2	78%	232.2	79%	439.1	79%
All else	44.7	37%	242.3	86%	96.9	60%	384.0	68%
Total	2,629.4	17%	3,185.6	32%	3,089.5	44%	8,904.5	27%

Source: PacFIN database. Revenues corrected to 1997 dollars with GDP implicit price deflator.

lowed a similar pattern (table 6).[5] Although lack of complete data for the sport fishery makes it difficult to compare commercial and sport landings, rough extrapolations from available data[6] indicate that four fishery sectors account for most of the rockfish landed in recent years—trawlers 54%, hook and line vessels 16%, CPFVs 10%, and private boats 10%. The contributions of these sectors vary significantly by area (fig. 1), with landings in central/northern California skewed toward trawlers (64% trawl, 11% hook and line, 9% CPFV, 8% private boat), and landings in southern California somewhat more evenly distributed among sectors (32% hook and line, 21% trawl, 17% private boat, 13% CPFV).

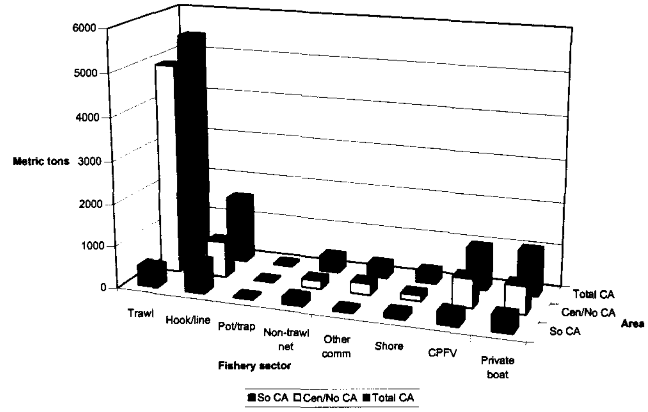

Figure 1. Recent annual rockfish landings in California, by fishery sector and area.

The discussion so far has focused on ports where the fish are landed rather than areas where the fishing occurs. Fishermen may base their choice of fishing areas on a variety of factors, including availability of target species, regulatory restrictions, distance from port, depth, and bottom terrain. To the extent that significant catches in an area reflect the presence of significant biomass or high-quality habitat, such an area may also be a good

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[5] Areas of landing are defined for purposes of this paper as southern California—San Diego, Orange, Los Angeles, Santa Barbara, Ventura, and San Luis Obispo counties; central California—Monterey, Santa Cruz, San Mateo, San Francisco, Marin, and Sonoma counties; northern California—Mendocino, Humboldt, and Del Norte counties.

[6] Commercial rockfish landings are represented by mean annual landings for each gear type and area during 1995–97, as estimated from the PacFIN database. Sport landings were estimated by combining results from the Marine Recreational Fishery Statistics Survey (MRFSS) with trends reflected in CPFV logbook data, as follows: on the basis of results from the MRFSS (NMFS 1992), the average annual number of Type A and Type B1 rockfish landed by marine anglers during 1987–89 was calculated by area (southern and central/northern California) and fishing mode (shore, CPFV, private boat). Type A estimates pertain to fish that were available in whole form for the researcher to identify; Type B1 pertains to dead fish that were not available in whole form for identification (e.g., fish used for bait, filleted, discarded dead). Given the high retention rates for rockfish (Wilson-Vandenberg et al. 1996) and the fact that filleting of rockfish at sea is a common practice in California, Type B1 harvest was assumed to consist largely of fish that were landed rather than discarded; thus A + B1 was assumed to provide a reasonable estimate of total rockfish landings. Because MRFSS interviewers routinely weigh fish landed whole, Type A landings estimates were available by weight as well as by numbers of fish, but the weight of the Type B1 harvest had to be inferred. Numbers of Type B1 rockfish were converted to metric tons by applying the mean weight of Type A rockfish associated with each area and fishing mode to the Type B1 rockfish caught in the same area and mode. The resulting average A + B1 tonnage estimates for 1987–89 were then scaled back to reflect recent fishery declines, as documented in CPFV logbooks. On the assumption of a similar decline in all fishing modes, the 1987–89 A + B1 tonnage estimates for each mode were scaled back by the ratio of average 1994–96 to average 1987–89 CPFV rockfish landings from table 7.

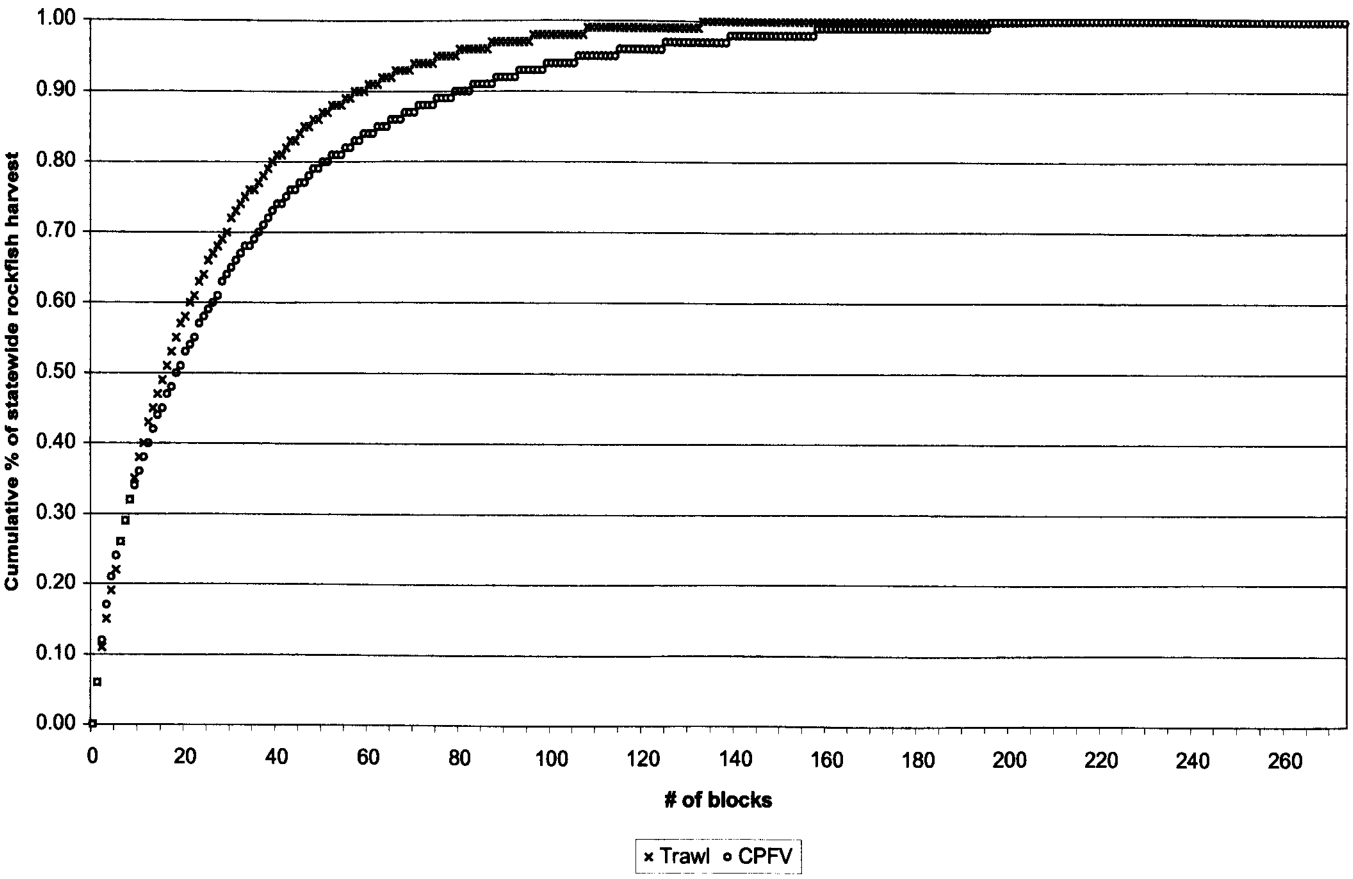

Figure 2. Extent of geographic concentration of trawl and CPFV rockfish harvest among blocks in California.

location for a reserve. The remainder of this section focuses on issues associated with placement of a no-take reserve in an area of high rockfish harvest.

Logbooks provided by trawlers and CPFVs include information on harvest by area fished. The fishing areas reported in these logbooks correspond to standardized 10 × 10 nmi blocks that have been mapped and numbered by the CDFG.[7] Because the representativeness of logbook data is uncertain (for instance, some fishermen are reluctant to disclose "hot" fishing spots), the data as used in this paper are intended to suggest rather than definitively identify areas of concentrated rockfish harvest.

For this discussion, the block areas reported in the 1994–96 trawl logbooks were sorted in descending order of average annual rockfish harvest, and—proceeding from the top to the bottom of the order—the cumulative number of blocks was plotted against the corresponding cumulative percentage of statewide rockfish harvest accounted for by those blocks. The same procedure was applied to 1995–97 CPFV logbook data to estimate the cumulative harvest distribution for CPFVs. The results (fig. 2) indicate a high degree of rockfish harvest concentration for both sectors of the fishery.

For figures 3, 4, and 5, I used the CDFG block maps for southern, central, and northern California to depict the geographic distribution of trawl and CPFV fishing activity. The filled and unfilled triangles denote major rockfish and non-rockfish areas for trawlers, while the filled and unfilled diamonds denote major rockfish and non-rockfish areas for CPFVs. Major trawl rockfish blocks are defined to include the 16 blocks that ranked highest in terms of average annual 1994–96 trawl rockfish harvest and that together accounted for 50% of statewide trawl rockfish harvest during 1994–96. Major CPFV rockfish blocks are similarly defined to include the 19 blocks that ranked highest in terms of average annual 1995–97 CPFV rockfish harvest and that together accounted for 50% of statewide CPFV rockfish harvest during 1995–97. I identified major non-rockfish blocks by applying a similar ranking procedure to the non-

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[7] Although, in recent years, fishing area information has been reported in the trawl logbooks on a finer scale (i.e., latitude-longitude coordinates), areas of trawl activity are reported here in terms of blocks, in order to be consistent with the block areas reported in the CPFV logbooks.

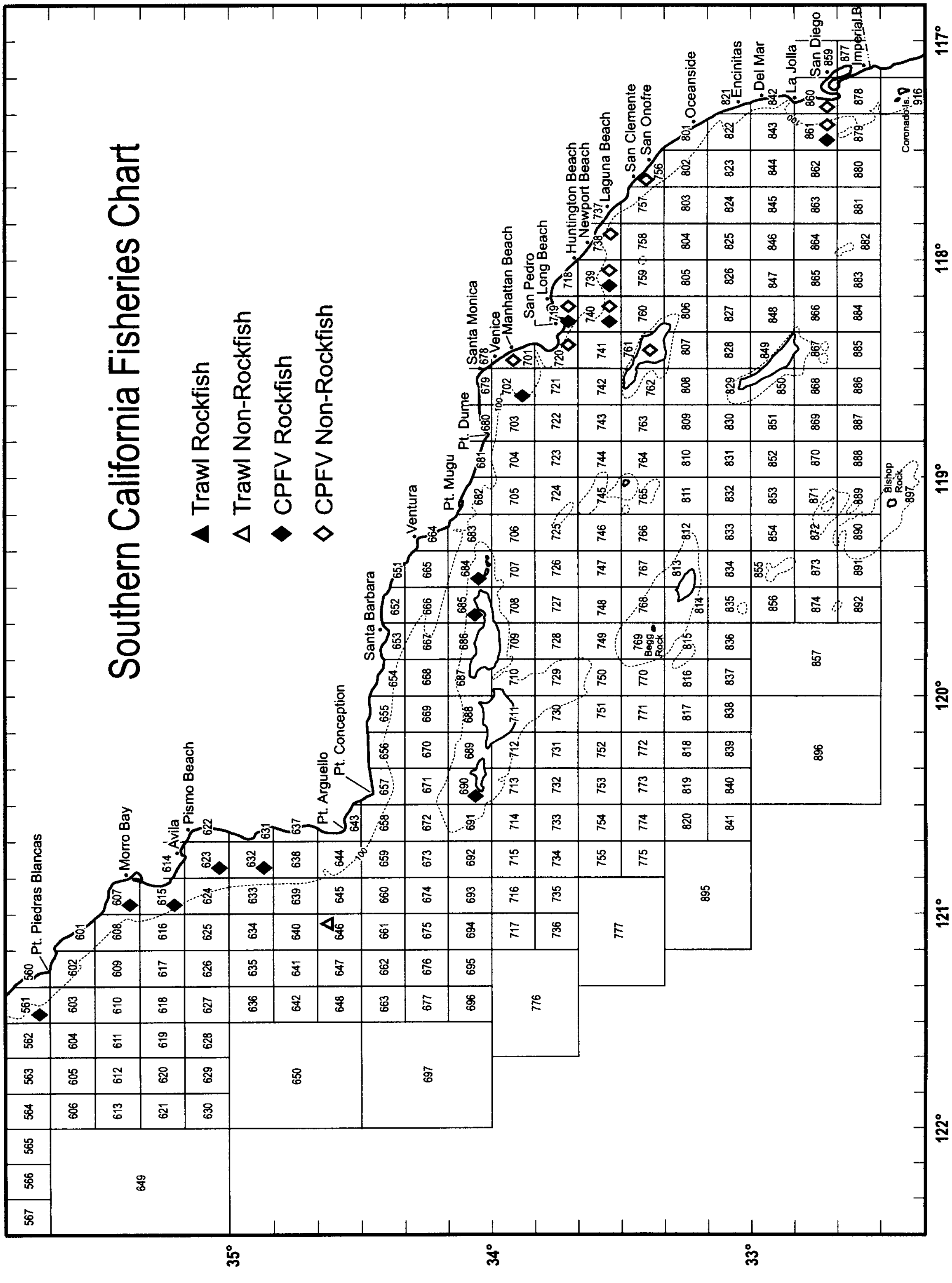

Figure 3. Distribution of major rockfish and non-rockfish blocks for trawlers and CPFVs in southern California.

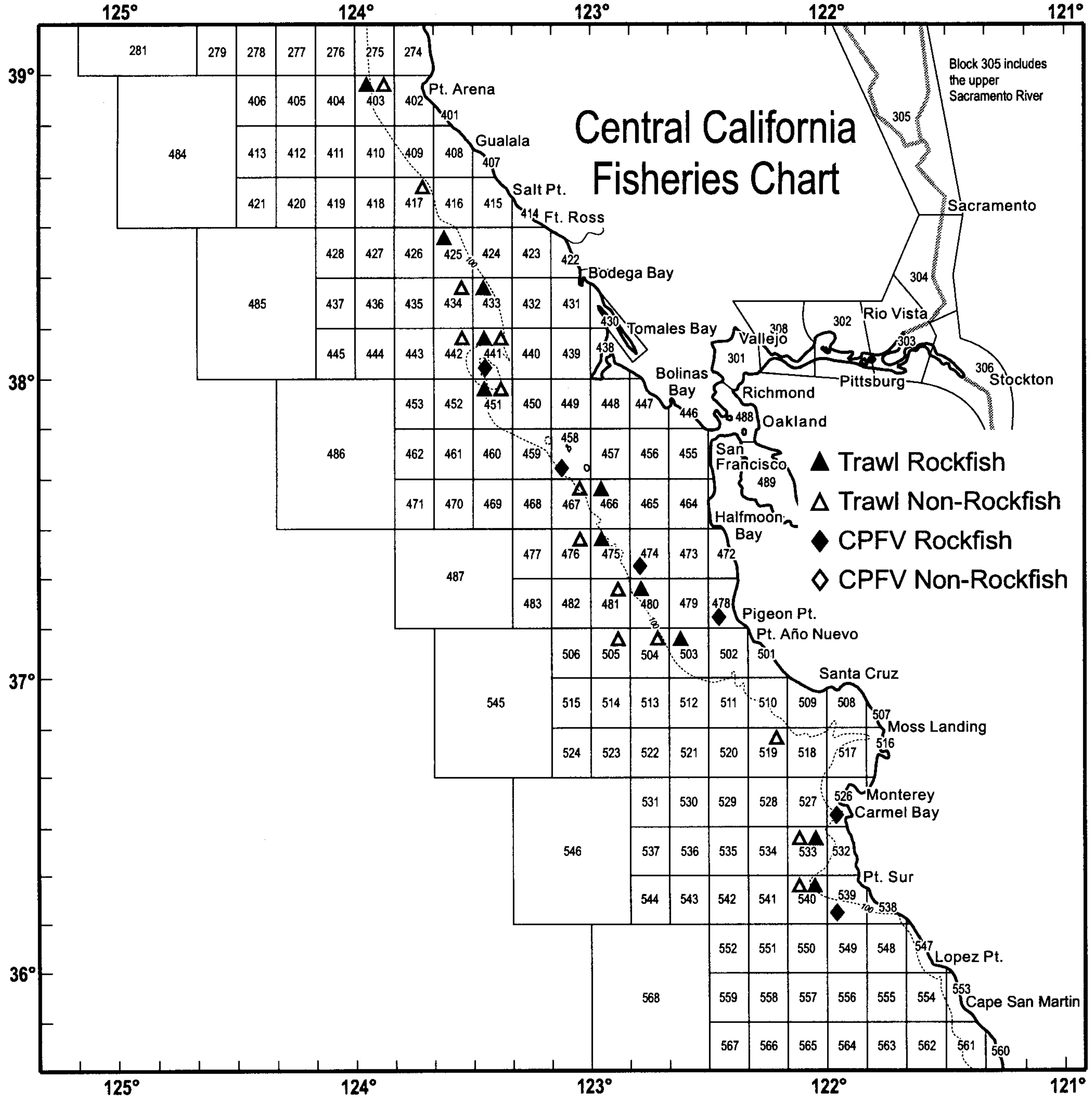

Figure 4. Distribution of major rockfish and non-rockfish blocks for trawlers and CPFVs in central California.

rockfish harvest data contained in the 1994–96 trawl logbooks and the 1995–97 CPFV logbooks.

Five of the 16 major trawl rockfish blocks are located in northern California (fig. 5) and 11 in central California (fig. 4). Of the 19 major CPFV rockfish blocks, 6 are located in central California (fig. 4) and 13 in southern California (fig. 3). Although there are some major trawl and CPFV rockfish blocks in central California, there are no major trawl blocks in southern California and no major CPFV blocks in northern California. Geographic differences such as these highlight the difficulty of ensuring that decisions about locating reserves are equitable.

In evaluating the effects of a reserve, it is important to consider how participants in both the commercial and recreational rockfish fisheries rely on non-rockfish species, the extent to which their non-rockfish as well as rockfish harvest would be directly precluded by closure of

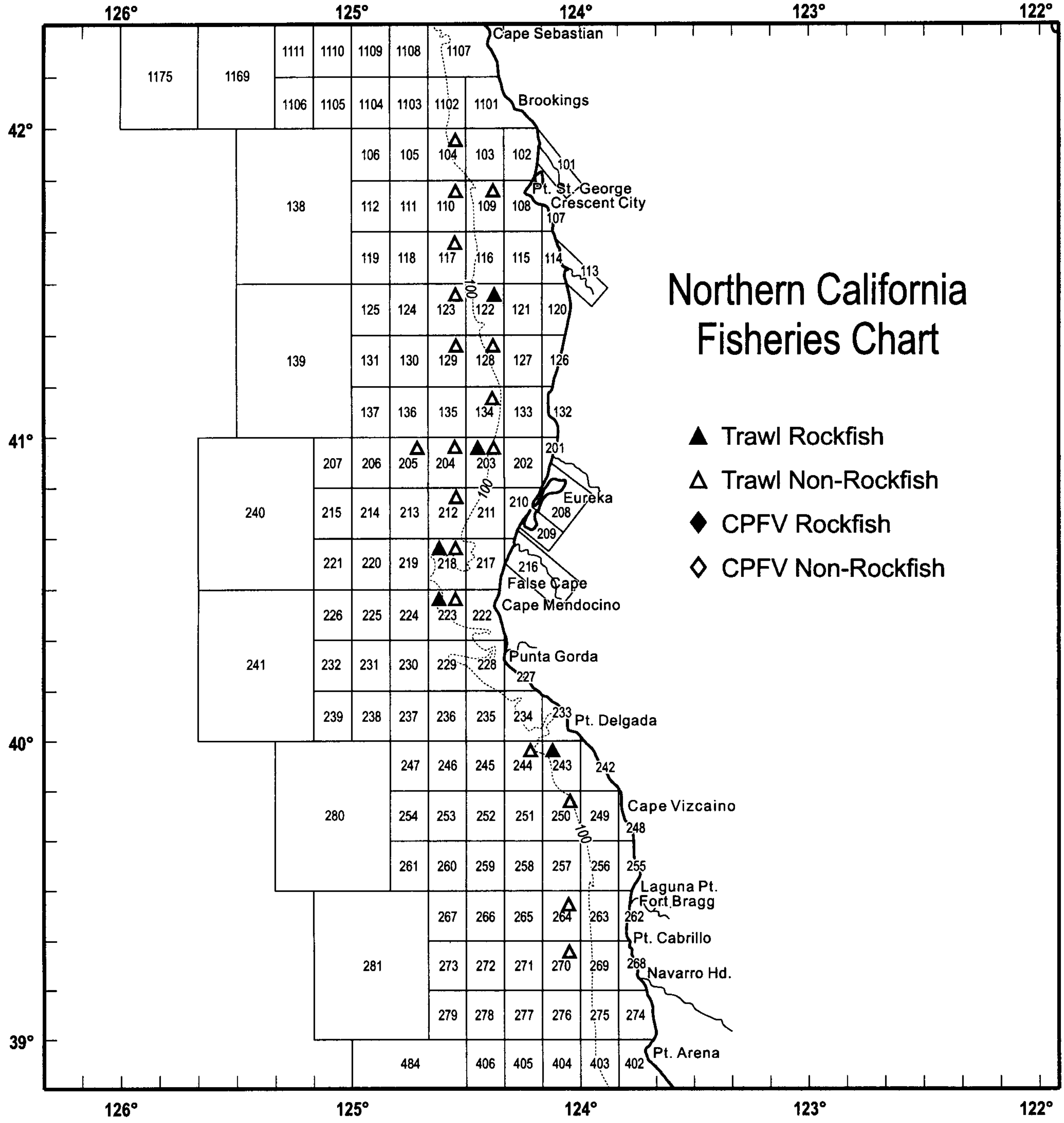

Figure 5. Distribution of major rockfish and non-rockfish blocks for trawlers and CPFVs in northern California.

the reserve area to all fishing, and the availability of rockfish and non-rockfish stocks outside the reserve.[8] Other fishing activities which customarily occur in the reserve area but are unrelated to rockfish—that is, which do not involve targeted or incidental harvest of rockfish—would also be displaced. Evaluating the effects on these latter types of fisheries, though beyond the scope of this paper, is also an important consideration for reserve design.

During 1995–97, the contribution of rockfish to total groundfish landings made by each commercial gear type varied significantly (8% for pot/trap, 23% for groundfish trawl, 45% for hook and line, and 80% for nontrawl

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[8] Included among the major non-rockfish species targeted by commercial rockfish fishermen in California are sablefish, Pacific whiting, Dover/English/petrale sole, thornyheads (a non-*Sebastes* rockfish), and Dungeness crab. Included among the major non-rockfish species targeted by sport fishermen are salmon, sturgeon, and striped bass in central/northern California, and sea basses, tunas, California halibut, and Pacific bonito in southern California.

net gear), and also varied across areas within each gear type (table 5). Revenues showed a fairly similar pattern (table 6). According to the 1994–96 trawl logbooks, 19% of statewide non-rockfish groundfish harvest by trawlers occurred in the 16 major trawl rockfish blocks, indicating the extent to which non-rockfish groundfish harvest would be directly precluded by including those blocks in a reserve. Eight of the 33 major non-rockfish groundfish blocks are also major rockfish blocks, and the other 25 (except for block 646 in southern California) generally occur near major rockfish blocks, though somewhat farther offshore and deeper (figs. 3–5).

According to CPFV logbooks, 32% of statewide CPFV non-rockfish harvest during 1995–97 occurred in the 19 major CPFV rockfish blocks, 3 of which are also major non-rockfish blocks. All 10 of the major non-rockfish blocks are located between Los Angeles and San Diego (figs. 3–5), reflecting the relatively high volume of CPFV fishing in southern California (table 7) and the tendency for CPUE to be higher for non-rockfish species taken in southern California (e.g., sea basses) than for those taken father north (e.g., salmon).

For CPFVs, evaluating dependence on rockfish and the effect of a rockfish reserve is complicated by several factors. In southern California, rockfish constitute 33% of total CPFV landings (table 7). According to the CPFV logbook data, 60% of southern California rockfish landings are made on the 10% of CPFV angler trips that are specifically targeted at rockfish. However, the majority of southern California angler trips (75%) are characterized simply as "coast" or "offshore" trips on which rockfish is one of several important components of catch; 31% of southern California rockfish landings are made on generic trips of this type. Thus the effects of a reserve will depend not only on the number of CPFV trips (rockfish and non-rockfish) customarily made in the reserve area but also on whether the species abundance and mix outside the reserve are sufficient to sustain the generic trips that constitute most CPFV activity in southern California.

In central and northern California, rockfish and salmon are the two major CPFV target species. Since CPUE is much higher for rockfish than for salmon, the rockfish share of harvest does not accurately reflect the proportion of angler trips attributable to rockfish. For instance, although rockfish make up 81% of total landings in central California (table 7), CPFV logbook data indicate that 24% of angler trips are targeted at rockfish and 52% at salmon. In northern California, where rockfish make up 80% of CPFV landings (table 7), the proportion of trips targeting rockfish and salmon is the same (43%). Closure of major rockfish areas in central/northern California would likely compound existing economic difficulties associated with recent declines in CPFV fishing activity (table 7) and with increasingly restrictive salmon regulations (PFMC 1998).

TABLE 7
Average Annual Rockfish Landings (Number of Fish), Total Landings (Number of Fish), Number of Angler Trips, and Number of Vessels in the CPFV Fishery in California, 1987–89 and 1994–96, by Area

	Southern California	Central California	Northern California	Total
1987–89 average:				
Rockfish landings	1,078,477	797,963	49,323	1,925,763
Total landings	3,297,546	979,361	61,850	4,338,757
Total angler trips	516,299	177,300	13,614	707,213
Total vessels	195	142	31	368
1994–96 average:				
Rockfish landings	712,529	473,645	29,291	1,215,464
Total landings	2,567,350	609,157	34,041	3,210,548
Total angler trips	481,609	126,812	5,894	614,314
Total vessels	203	96	12	311

Source: CPFV logbook summaries published by the California Department of Fish and Game. Estimates should be viewed as conservative, since not all CPFVs participate in the logbook program.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Given the nonuniform geographic distribution of rockfish landings by different sectors of the fishery, a system of reserves strategically distributed up and down the coast rather than concentrated in a single area would help ensure that short-term displacement costs associated with the reserve do not fall disproportionately on any particular sector. Given the importance of biological and enforcement considerations in the placement of the reserve, as well as equity, it will not be possible to achieve complete consensus about an acceptable distribution of reserves. Nevertheless, it is critical that allocative implications be recognized and addressed as much as possible. Ignoring this issue will not make it go away; it will merely appear in different guises as disputes over other, seemingly unrelated issues.

In recent years the California rockfish fishery has displayed a downward trend in abundance and landings of many stocks. Regardless of what combination of reserves and more conventional management measures might be used to rebuild these stocks, the short-term economic costs are likely to be significant and to have implications beyond the rockfish fishery. For instance, because of the multispecies nature of the groundfish fishery, rebuilding rockfish stocks via conventional management measures could involve reducing quotas for relatively healthy groundfish stocks that are caught concurrently with weak rockfish stocks; and non-groundfish fisheries that incidentally take rockfish might also have to be restricted. A no-take reserve would also involve direct restrictions on non-rockfish as well as rockfish fishing activities, though of a different type (i.e., displacement due to area closure). A reserve might affect an even broader range of non-rockfish fisheries than conventional management measures if fishing activities that have no bearing on rockfish are also displaced from the reserve.

Diverting fishing effort to areas outside a rockfish reserve might cause a variety of external effects, including higher exploitation rates for outside fish stocks and higher vessel operating costs and increased social conflict in outside areas. Management problems outside the reserve might be magnified if fisheries for outside stocks are already fully subscribed. Effects of this type are not unique to reserves and could also occur, for instance, if effort were diverted to other fisheries as a result of conventional management measures such as rockfish quota reductions or restrictions on the harvest of non-rockfish species caught with rockfish. But external effects might be broader in scope for reserves, depending on how much of fishing effort displaced from the reserve involved vessels that had targeted non-rockfish species in the reserve and whether the fishing subsequently undertaken by those vessels outside the reserve differed significantly from the activities undertaken by displaced rockfish vessels.

Good science is critical to the design of a reserve and the implementation of appropriate protocols for evaluating its long-term potential for enhancing fish stocks, fish habitat, and fisheries (Carr and Reed 1993). These are ambitious research goals. It is also important that science not be asked to provide more than it is capable of delivering. Just as questions are being raised about the desirability of basing rockfish quotas on highly uncertain stock assessments, it is also important to evaluate (1) the uncertainties associated with predicting and validating the biological benefits of reserves, (2) the extent to which such uncertainties could be reduced within a reasonable time frame and with reasonable funding, and (3) how management should proceed in the face of such uncertainties.

Reasonable predictions about the nature, extent, and timing of benefits to be generated from the reserve would be important not only for evaluating the reserve but for determining how to best regulate the rockfish fishery outside the reserve. Such predictions would also be of interest to the fishing industry, which would probably be concerned about its ability to absorb displacement costs while awaiting whatever fishery benefits might be generated by the reserve over the long term. Management, monitoring, and enforcement costs would be important considerations as well. It is important that reserves not be oversold as a panacea for the limitations and costs of current rockfish management. There are no easy fixes for rockfish.

Management objectives should be defined at the outset (Yoklavich 1998, p. 154). Objectives would provide guidance for the design of management options (e.g., size and location of the reserve) and the issues relevant to evaluating the options. The process of defining objectives might also be useful for clarifying the extent to which the reserve is intended as a species-specific management tool or as a tool for providing broader benefits—such as protection of essential fish habitat—more consistent with "ecologically based management units" (Davis 1989).

Since reserves are likely to supplement rather than replace more conventional management measures, it would be useful to explore whether and how the two approaches might be coordinated to achieve the desired objectives. This exploration should include a reevaluation of current regulations, including the groundfish limited entry program. Additional reductions in the limited entry fleet (perhaps via a vessel buyback program), combined with new restrictions on the open access fishery, might alleviate the economic costs associated with displacement from a reserve more immediately (and perhaps more definitively) than any fishery enhancement benefits that the reserve might provide over the long term. Capacity reduction might also alleviate the economic hardships associated with more conventional management measures such as vessel landings limits, which are becoming untenable as a way to maintain an extended fishing season in the face of declining quotas. Regardless of how reserves fare as a rockfish management tool, the current interest in them might provide a catalyst for looking "outside the box" to devise more effective ways to manage rockfish stocks.

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SOCIAL CONSIDERATIONS FOR MARINE RESOURCE MANAGEMENT: EVIDENCE FROM BIG CREEK ECOLOGICAL RESERVE

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ABSTRACT

Growing interest in no-take marine protected areas (MPAs) as a complement to traditional fishery management has led to increased attention to biophysical considerations for MPA design, implementation, management, and evaluation. Considerably less attention has been directed, however, toward social, cultural, and economic considerations for MPAs. Information on and understanding of the relationship between MPAs and local fisheries in social, cultural, and economic, as well as biophysical, terms is especially important. At the same time, there is growing interest in collaboration between fishers and scientists to provide more complete and accurate information on fisheries and marine ecosystems. Such collaboration is one element of cooperative (or co-) management of local fisheries, which is gaining recognition as potentially more effective, appropriate, and equitable than traditional, top-down resource management. These two themes—social considerations for MPAs and co-management of local fisheries—are central to a study being conducted at central California's Big Creek Ecological Reserve. This paper provides an overview of the local skiff fishery and the cooperative arrangement at Big Creek; discusses that arrangement as a form of co-management, and as it has played an integral role in the history of the marine reserve; and concludes with observations and emerging questions about the social aspects of establishing and maintaining no-take marine reserves in the context of local fisheries.

INTRODUCTION

Concerns about the shortcomings of traditional fishery management tools and approaches have prompted interest in two alternatives: no-take marine protected areas (MPAs; i.e., marine reserves) and cooperative (or co-) management of local fisheries. The interest in MPAs has led to increased attention to ecological considerations associated with the components of the MPA process, namely their design, implementation, management, and evaluation (see, e.g., Carr and Reed 1993). Much less attention has been directed, however, to social, cultural, and economic considerations for MPAs (Fiske 1992; Wolfenden et al. 1994; Suman 1998). Both sets of considerations are especially germane to the relationship between MPAs and local fisheries because of the diverse ways they affect one another, in sociocultural and economic as well as ecological terms. The interest in co-management has focused largely on its potential for fostering information gains, especially through fishing industry collaboration in the collection of scientific data. This is only one element of full-fledged co-management, however, in which government agencies and resource users share responsibility and authority for resource management (Jentoft 1989; Pinkerton 1989).

At California's Big Creek Ecological Reserve, a small group of local skiff fishers and the manager of the University of California, Santa Cruz (UCSC) Landels-Hill Big Creek (LHBC) Reserve established a cooperative arrangement with two key features: a no-take zone and a fishery-dependent data collection system, *before* the reserve's legal designation in 1994. The Big Creek case is an example of co-management in an MPA context that provides an opportunity for exploring the social, cultural, and economic aspects of these two alternatives or complements to traditional fishery management. This paper explores these themes, based on research the author has been conducting at Big Creek since 1996.[1]

The first two sections briefly discuss fisheries co-management and social considerations associated with MPAs. The third section focuses on the local fishery and the development of co-management at Big Creek. The final section presents emerging questions about the sociocultural and economic aspects of the Big Creek reserve and its co-management that are being pursued as the research continues. I conclude that these questions and considerations are critical not only to the Big Creek situation, but to MPAs and fishery management more generally.

FISHERIES CO-MANAGEMENT AND MPAS

Much of fishery management is based on the assumption that fisheries, as common pool resources

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[1] This research has included two studies: a demonstration project, sponsored by UCSC's Monterey Bay Regional Studies (MBRS) Program, conducted in 1996 to explore the cooperative arrangement; and a subsequent three-year (June 1997–May 2000) in-depth study, sponsored by the California Marine Ecological Reserves Research Program (MERRP, Grant no. R/BC-2). The goals of the latter study are to document the fishery adjacent to the reserve, analyze the cooperative arrangement between local fishers and the reserve manager, and evaluate their cooperative data collection system.

(CPRs), will inevitably come to ruin unless they are designated as private property or managed closely by the state (Gordon 1954; Olson 1965; Hardin 1968). However, evidence of cooperation among fishers to create and maintain local institutions—shared rules, norms, and strategies—to coordinate their use of CPRs challenges this assumption (Ostrom 1990). Such local CPR institutions may arise and operate independently, or they may be negotiated and coordinated (officially or unofficially) with government resource management, as cooperative (or co-) management. (See, e.g., Jentoft 1989; Pinkerton 1989; Jentoft and McCay 1995; and Sen and Nielsen 1996 for reviews of co-management case studies, including successes and failures.) Forms of co-management range from those in which government consults fishers but retains decision-making authority, to those in which fishers have initiated and participate in many aspects of management, including policy formulation, implementation, enforcement, and evaluation (Kearney 1989).

Fishery co-management is of growing interest to resource managers because it is often more effective in achieving management goals, more acceptable to fishers, and less costly than traditional (i.e., government-centered) management (Jentoft 1989; Pinkerton 1989). In making an explicit link between resource managers and resource users, co-management may overcome many of the limitations and pitfalls of centralized, top-down resource management, resulting in more effective, appropriate, and equitable resource management (McGoodwin 1990).

Among the potential advantages and benefits of co-management are its ability to foster meaningful communication in the decision-making process, improve the knowledge and databases of fisheries management, help reduce the political and equity problems that often arise in resource management, and increase the extent to which users see the management system as legitimate, and hence comply with the rules and regulations (McCay and Jentoft 1996; see also Pomeroy et al. 1995). As a result, government is likely to face reduced challenges to its authority and reduced management costs, while the likelihood of achieving management goals increases (Pinkerton 1989; McGoodwin 1990; McCay and Jentoft 1996).

Of particular interest is co-management's potential for affording information gains at low cost to government. These information gains accrue not only from fishing industry collaboration with researchers in the collection of scientific data, but also from the contribution of fishers' knowledge. This local or traditional ecological knowledge includes fishers' accumulated knowledge of local natural history based on their day-to-day experiences while fishing (Johannes 1989; Neis 1995). It can provide inexpensive and useful information that complements scientific data (Rettig et al. 1989). The integration of scientific and local ecological knowledge makes co-management stronger than either community-based or government management alone (Pomeroy and Berkes 1997). Information provided by user groups about the resource and its use may contribute to a more rational management process, because government agencies are unlikely to foresee all the consequences of regulatory measures (Jentoft and McCay 1995).

Yet the feasibility and success of co-management are contingent upon certain environmental, social, and political conditions.[2] The species and ecosystems involved, the number and heterogeneity of resource users, participants' attitudes toward management, and their ideas about the roles of government managers, scientists, and resource users are among the factors that matter. Co-management redefines the roles of managers, scientists, and resource users. It requires that government agencies and bureaucrats share authority with people they are accustomed to regulating, and that fishers share responsibility for fishery management, rather than continuing to depend on government to make and enforce the rules. Managers, scientists, and resource users alike must engage in "social learning," whereby they come to recognize, respect, and value each other's contributions to fishery management, and trust that each will hold up his end of the bargain (Kearney 1989). Co-management is likely to fail wherever such social learning does not occur.

Hanna (1996) notes that co-management must include effective representation of all stakeholders, and all stakeholders (resource users, managers, scientists, and others) must engage in the process in good faith. Otherwise, it is vulnerable to sabotage by excluded interests or corruption of the process by one or more interests (see also Leaman 1998). Groups involved in co-management may prefer to pressure government authorities rather than assuming responsibility for management functions (Jentoft 1989; Leaman 1998). It has been argued that when fishers participate in decisions that affect their welfare, they are more likely to buy in, and to strengthen the social institutions that encourage others to also abide by the rules (see, e.g., Pinkerton 1989; Fiske 1992). Yet fishers often are reluctant to serve as "informers" or otherwise enforce rules against their peers (Jentoft 1989).

SOCIAL AND ECONOMIC CONSIDERATIONS

Social and economic information is critical to effective fishery management in general (Orbach 1978; Clay and McGoodwin 1994; Buck 1995). Management de-

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[2] Ostrom (1990) has specified eight elements of design for local, self-governing CPR institutions: clearly defined boundaries, good-fitting rules, collective choice arrangements, monitoring and enforcement, graduated sanctions, conflict resolution mechanisms, minimal recognition of rights to organize, and nested enterprises. Pinkerton (1989) offers hypotheses on the preconditions favorable to co-management, conditions supportive of it, and the types of groups that are preadapted for effective co-management.

cisions that are informed by understanding of people's practices, values, and beliefs are more acceptable and successful, and less disruptive (Hanna and Smith 1994). It is essential to consider social, cultural, economic, and political factors, as well as biophysical factors, in the establishment and management of MPAs (Fiske 1992; Pomeroy et al. 1998; Suman 1998; Thomson 1998). These factors include peoples' values, attitudes, beliefs, and behaviors, both individually and collectively; the ways they value and use marine resources; and the social, economic, and political organization of resource use (Fiske 1992).

The permeability of MPA boundaries means that conditions (and changes) within a reserve will influence those outside its boundaries, and that activities and conditions outside an MPA will influence conditions (and outcomes) within it. It is therefore especially important to consider the social and economic impacts of, and peoples' perceptions, attitudes, expectations, and behavior regarding, MPAs in the context of local fisheries. Relevant questions to be asked include:

1. What is the nature and extent of fishing activity in and near the proposed MPA site?
2. Do fishers support or oppose the proposed MPA? Why, or why not?
3. What social and economic effects might be expected from establishing this MPA? How are these effects distributed? Are there alternative sites or designs that might lessen the negative effects or increase the positive effects on resource users?
4. How might the nature and extent of fishing activity change with MPA designation? Is there a concentration of fishing activity at the MPA perimeter? Is there crowding on the fishing grounds that remain open, and is this a source of conflict?
5. How would these changes affect resource conditions and outcomes—in ecological, social, and economic terms—within and outside the MPA?

Information on and understanding of these aspects of MPAs can be used to minimize their negative effects and maximize their positive effects. Failure to consider them can lead to the failure of MPAs to achieve their ecological, social, and economic goals (Fiske 1992; Pomeroy et al. 1998).

THE BIG CREEK CASE

The Setting

Big Creek is located on California's Big Sur coast about 85 km south of Monterey and 163 km north of Morro Bay (fig. 1). It is the site of both the 3,848 acre terrestrial Landels-Hill Big Creek (LHBC) Reserve managed by UCSC, and the 1,680 acre (6.86 km^2) Big Creek Ecological Reserve, co-managed by the California Department of Fish and Game (CDFG) and the LHBC reserve manager, a UCSC employee.

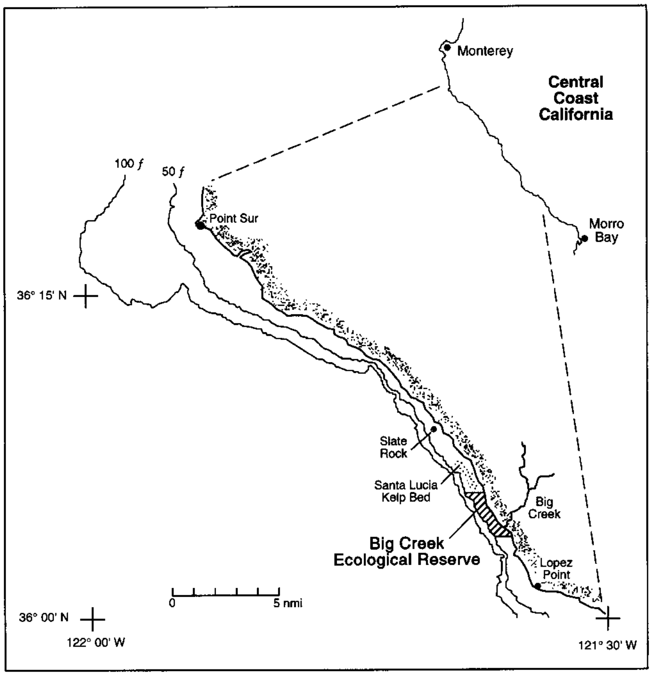

Figure 1. Big Creek MRPA Ecological Reserve and sites associated with the fishery and the Hook-and-Line Kelp Bed Survey.

The nearshore reefs and kelp beds at Big Creek and along the larger Big Sur coast provide important habitat for several commercially and recreationally valuable finfish species: *Sebastes* spp., e.g., vermilion (*S. miniatus*), kelp (*S. atrovirens*), black-and-yellow (*S. chrysomelas*), blue (*S. mystinus*), gopher (*S. carnatus*), copper (*S. caurinus*), olive (*S. serranoides*), and black (*S. melanops*) rockfish; cabezon (*Scorpaenithys marmoratus*); and lingcod (*Ophiodon elongatus*) (Paddack 1996). Although rough conditions and the limited number of safe launch sites along the Big Sur coast have tended to discourage fishing, Big Sur has been the site of a small, local, commercial hook-and-line fishery for these species since the late 1970s (Georgette 1981). Fishers launch 10–12-foot aluminum skiffs from the beach into the surf, and motor to shallow and midwater sites to fish. After a day of fishing, they land their catch and transport it to regional markets (e.g., Monterey, Morro Bay, Oakland).

A limited amount of commercial and recreational fishing activity originating in the Monterey and Morro Bay areas has also occurred in the area, despite Big Sur's remoteness from their established ports and fishery infrastructure (Mason 1995; see also CDFG 1993). Over the past two decades, commercial fishers have used a variety of net, trap, and line gears to target rockfish and other

TABLE 1
Gear Used by Commercial Fishers, and Target Species for the Big Sur Area

Gear	Target species
Round haul nets	California market squid
Pots	Dungeness crab, spot prawn
Trawls	Rockfish, lingcod, cabezon, spot prawn, English and petrale sole
Hook and line[a]	Rockfish, lingcod, cabezon
Gill and trammel nets[b]	Rockfish, lingcod, cabezon

[a] Since 1997, longlines used within one mile of the California coast from Point Conception to Point Mugu have been limited to a maximum of 150 hooks per boat, and 15 hooks per line.

[b] Since 1 January 1994, gill and trammel nets have been banned from California's nearshore waters.

species such as sardine, squid, dungeness crab, spot prawn, and various flatfishes (table 1). Table 2 shows the number of vessels, volume, and ex-vessel value of all 1981–98 landings reported to have been caught in this region, and in CDFG block 547, within which the Big Creek reserve lies. Commercial landings from the Big Sur region (CDFG blocks 526–613) have fluctuated widely, ranging from 43.7 million pounds with an ex-vessel value of $11.1 million in 1981 to 1.6 million pounds with an ex-vessel value of $376,000 in 1988 (based on Pacific Fisheries Information Network—PacFIN—data). Commercial landings reported from CDFG block 547 reached a brief (and anomalous) high of 124,000 pounds, with an ex-vessel value of $58,200 in 1988, but have generally been much lower, especially since the phasing out of nearshore gill nets in the early 1990s (PacFIN data).

The Final Environmental Impact Report for the Marine Resources Protection Act (MRPA) Ecological Reserves noted that "only a small amount of commercial fishing takes place within [block 547] because of its distance from major ports or landing sites. . . . Some trawl activity has been reported in the larger vicinity of Big Creek, but the reserve's rocky substrate has precluded such activity" (CDFG 1993). The report also notes little sport fishing in the vicinity of the reserve, largely because of the site's remoteness and rough conditions for fishing. Because of the already existing LHBC Reserve, there is no direct public land access. For 1988 through 1992, CDFG's Central California Sport Fish Survey and Analysis Unit reported no sport fishing activity within a 10-mile radius of Big Creek (CDFG 1993).

Several economic and regulatory changes are reflected in the commercial landings data, including the emergence of the live-fish market in 1993, the phasing out of gill and trammel nets starting in 1991 until they were banned in nearshore waters in 1994, and the establishment of the Big Creek Ecological Reserve the same year.

For the live-fish market, fishers use pots (or traps), sticks, and other hook-and-line gears to catch species such as grass, gopher, and black-and-yellow rockfish; cabezon; and lingcod in waters up to 15 fathoms deep. (Sticks are 4-foot PVC pipes with four to six hooks attached to a line tied along the length of the pipe. The stick is attached to a float by a length of rope, and is deployed in nearshore kelp beds and rocky reef areas.) Live rockfish bring a price 5 to 10 times that for dead fish ($.50 to $10 per pound; McKee-Lewis 1997), with relatively small in-

TABLE 2
Number of Vessels, Volume, and Value of Commercial Fishery Landings for CDFG Blocks 526–613 (Big Sur) and 547 (Which Includes Big Creek), 1981–98

	CDFG blocks 526–613			CDFG block 547		
Year	No. of vessels	Volume (1,000 lbs.)	Value ($1,000)	No. of vessels	Volume (1,000 lbs.)	Value ($1,000)
1981	1,150	43,673.9	11,124.3	15	41.6	18.5
1982	997	35,294.2	7,771.7	18	54.0	20.9
1983	820	17,633.7	5,627.6	14	25.1	12.2
1984	686	16,478.4	5,563.0	3	16.0	5.8
1985	711	17,925.5	7,547.9	7	33.5	9.0
1986	750	22,930.1	7,455.9	1	0.4	0.2
1987	551	14,535.1	3,791.1	3	59.6	26.2
1988	58	1,618.1	376.4	13	124.0	58.2
1989	67	3,291.7	558.0	5	16.7	7.9
1990	45	5,149.0	509.7	1	0.0	0.0
1991	132	2,561.1	710.1	2	0.1	0.2
1992	134	5,802.4	909.9	2	3.4	5.1
1993	162	5,830.5	1,247.3	11	3.2	3.4
1994	432	17,038.1	4,487.5	12	3.6	3.2
1995	536	15,417.0	4,736.2	12	4.9	6.0
1996	584	26,690.7	5,908.0	11	7.2	18.0
1997	539	25,347.3	6,955.0	27	16.3	45.1
1998	341	4,465.1	2,916.4	11	11.3	34.3

Source: PacFIN data.

vestments in additional equipment and effort to keep the fish alive between capture and market. Over the past five years, many Big Sur skiff fishers have shifted from traditional hook and line gear to sticks in order to fish for the live-fish market, especially as prices and demand for dead fish have remained stagnant or declined.

Big Creek Ecological Reserve

Big Creek Ecological Reserve is one of four no-take MPAs (marine reserves) established in 1994 pursuant to the 1990 MRPA. It stands out among the MRPA reserves not only for its high-quality rockfish habitat (Yoklavich et al. 1997), but also, importantly, for the support of local, small-scale commercial fishers, which facilitated its legal designation (Pomeroy and Beck, in press).

The fishers' support for the marine reserve grew out of a pre-existing cooperative arrangement between themselves and the manager of the LHBC Reserve. The primary elements of the arrangement were the establishment and monitoring of an informal no-take zone adjacent to the terrestrial reserve, and fishers' collection of extensive fishery-dependent data on their nearby fishery, in exchange for the opportunity to launch their skiffs from Big Creek. Both of these features emerged locally with little input from government authorities.

The origins of the arrangement date back to the early 1980s, when a small group of local skiff fishers first began to coordinate their fishing activities. They divided the area of the Big Sur coast that they fished into three sections, and agreed to rotate their effort, so that they fished each section for only four months, leaving it to "rest" during the remaining eight months of the year.[3] In October 1988, two of these fishers (on behalf of some eight individuals) asked the LHBC Reserve manager for permission to launch their boats from Big Creek in order to more easily reach preferred fishing spots to the north. The reserve manager consented in exchange for the agreement that those who launched from Big Creek would observe a no-take zone in the kelp beds adjacent to the terrestrial reserve out to 1,000 m (3,280 feet).

The following season (1989–90), the reserve manager, a CDFG biologist, and the two fishers discussed the possibility of research collaboration to sample rockfish inside and outside the no-take area. The idea of a research fishery appealed to the reserve manager, who sought to justify, but also to limit, fishers' launching from Big Creek. Following these discussions, the reserve manager designed the Big Sur Hook-and-Line Kelp Bed Survey (the HLS) in consultation with the Big Creek fishers. (CDFG's rockfish sampling program at Big Creek and at Mill Creek, located about 10 miles south of Big Creek, also resulted from these discussions, but the studies are independent of one another.)

TABLE 3
Design of the Big Sur Hook-and-Line Kelp Bed Survey

Two studies
  Twin Kelpbed (80 sortie limit)
  Slate Rock (40 sortie limit)

Procedure
  Sampling
    First 5 fish caught at experimental site within 30 minutes
    First 5 fish caught at preferred fishing site
  Data collection and recording
    Fisher name
    Date
    Location(s), depth fished, time to catch 5 fish
    Fishing conditions (cloud cover, precipitation, temperature, currents, sea state)
    Species, weight, length

The HLS includes the "Twin Kelpbed" and "Slate Rock" studies, each with a control and an experimental site (table 3).[4] On each "sortie" (launch) from Big Creek, fishers collect two five-fish samples, one from the control site and one from their preferred (i.e., experimental) site. After a day of fishing, they return to Big Creek to unload their catch, measure, and weigh their fish, and record the survey data at a recording station maintained by the reserve manager.

The passage of the MRPA in 1990 provided an opportunity to gain legal recognition and enduring and broader protection for the Big Creek no-take zone. Designation as an MRPA reserve would insure its continued and more institutionalized protection, but it also posed a potential threat to the cooperative arrangement, in part because it would prohibit passage through the reserve, unless permitted for research.[5] The reserve manager worked proactively with local fishers, landowners, and the state to promote the reserve's designation while insuring that some local control—including that associated with the Big Creek arrangement—was retained. He garnered broad local support for the reserve, beginning critically with that of the Big Creek fishers. An

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[3] The number of fishers involved in the arrangements referred to here and at Big Creek specifically has ranged from about 6 to 10, varying over time as individuals' interest in the fishery and other commitments have changed. Although these fishers tended to rotate their activities among the three areas (each associated with a particular Big Sur launch site) as noted, other fishers, both local and from more distant ports such as Monterey and Morro Bay, operate independently of this group of skiff fishers.

[4] The Twin Kelpbed study's control site is adjacent to the reserve and is characterized as "lightly fished," whereas the Slate Rock study's control site is farther from the reserve, and considered to be "medium fished." In both studies, fishers' preferred fishing sites constitute the experimental sites, and are assumed to be "heavily fished." This design allows comparison of fish species, lengths, and weights among sites where fishing pressure is assumed (by the design) to increase with distance from the reserve. The results of the experiment may be confounded, however, by the lack of control over other fishing activities near the reserve and the prior condition of the sites.

[5] In contrast to most of California's other MPAs (which number more than 100; McArdle 1997), these reserves protect all species within their boundaries, and use is "restricted to scientific research relating to the management and enhancement of marine resources" (California Fish and Game Code 630.5).

August 1991 letter from one of them on behalf of himself and the others states: "We offer our support not only in seeking the establishment of Big Creek Reserve as a Marine Ecological Refuge, but on a continuous basis, if in fact Big Creek Reserve wins the designation."

When it was established on 1 January 1994, the Big Creek Ecological Reserve retained the prior, informal no-take zone's northern and southern boundaries and extended its seaward boundary 179 m (586 feet; CDFG 1993). More important, it gave limited recognition to the existing institutional arrangement, and formalized co-management at Big Creek. Provisions in the California Fish and Game Code specify the LHBC Reserve manager's authority to approve research at Big Creek and recognize the priority of research initiated prior to legal designation—such as the HLS; 14 Sec. 630.5 Sec. (b)(2)(A); see also Sec. 630.5 (a)(2)—and a 1994 memorandum of understanding between CDFG and UCSC outlines the co-management arrangement for the Big Creek Ecological Reserve.

Analysis of these institutional developments at Big Creek led to three conclusions (Pomeroy and Beck, in press). First, the cooperative arrangement had been instrumental to the legal designation of the Big Creek reserve. Second, although the HLS holds promise as a source of fishery-dependent data that might be used (in combination with fishery-independent data) to monitor and evaluate the MPA, adjacent fisheries, and the relation between them, it has largely been ignored or dismissed by resource managers and scientists in the region, some of whom question the reliability and validity of the data. Third, the cooperative arrangement at Big Creek has not been adequately considered for its relevance to MPA management and broader resource management.

Although certain aspects of the situation—the fishery's small scale and relative isolation, the involvement of a small number of fishers whose fishing practices are relatively homogeneous, their history of cooperation and ongoing social ties, and the fact that they receive something of immediate value to them (access to the Big Creek launch site) in exchange for their observance of the no-take zone and data collection—may limit generalizations from any lessons learned at Big Creek. However, we have begun to identify other, similar arrangements already in place (Wright, pers. comm.), suggesting some opportunity for the Big Creek case to contribute to enhanced resource management.

QUESTIONS GUIDING FURTHER RESEARCH

Our findings led to a proposal to California's Marine Ecological Reserves Research Program (MERRP) to evaluate, optimize (as needed), and explore the replicability of the HLS and the larger Big Creek arrangement. We recently completed year one of the three-year MERRP study, during which we interviewed Big Creek fishers and others to develop a more complete understanding of the historical, sociocultural, and economic aspects of the local fishery and the cooperative arrangement; systematically observed boating and fishing activity along the Big Sur coast and HLS data collection; began to evaluate and analyze the HLS data; and began to analyze PacFIN data on rockfish landings in the region.

As the MERRP study progresses, we are seeking answers to several questions about co-management and the marine reserve at Big Creek. A first set of questions focuses on the Big Creek arrangement: Just how "cooperative" is it? Fishery co-management arrangements vary in terms of the activities that government and fishers are involved in, the nature and extent of communication among the people involved, and the types of information that they do and do not share. At Big Creek, co-management involves three sets of actors: the Big Creek fishers; the reserve manager; and state resource managers and scientists. At present, the reserve manager plays a central role as liaison between the other two groups, and direct interaction—and cooperation—between fishers and resource managers and scientists remains limited. This, in turn, has limited the opportunities for the social learning that is at once critical to and a benefit of co-management.

A second set of questions pertains to the HLS, and the reliability, validity, and utility of its data. What are the sources of bias in the HLS? What is the relation between markets (prices) and HLS practices and outcomes? How might these biases be addressed to make the HLS more useful? When multiple people collect data, evaluating and analyzing the data require understanding the different ways people interpret the research protocol and collect their data. Another source of bias stems from the fact that this is fishery-dependent data, and therefore reflects the species targeted, the locations fished, and the gear and techniques used by participating fishers. These are a function of, and change in response to, environmental, regulatory, and market conditions, as well as fishers' personal circumstances. For example, Big Creek fishers used to target larger fish, but market conditions (the live-fish market) have prompted a shift to targeting smaller (1–4-pound) fish, and a shift from filet fish (e.g., blue rockfish) to species valued by the live market (e.g., grass, gopher, and black-and-yellow rockfish; cabezon). Such conditions and changes within them must and can be accounted for in evaluating and interpreting the HLS data.

The third set of questions focuses on other aspects of the cooperative arrangement—such as fishers' local ecological knowledge—that might be useful to efforts to understand reserve-fishery interactions at Big Creek. Several of the Big Creek fishers have fished the Big Sur coast since the 1970s, and have observed changes in the availability and quality of different species, in biophysical conditions, and in the nature and extent of fishing activity in the region. This knowledge is not the product of scientifically structured sampling, but rather the result of frequent, year-round, spatially focused observation carried out over the long term. It is amenable to collection and analysis to afford qualitative, and in some cases quantitative, information that can be integrated with scientific data. Recognizing and bringing this knowledge to bear in reserve and fishery management would constitute an expansion of co-management at Big Creek, and would likely enhance understanding of the fishery, the reserve, and the interactions between them.

A fourth set of questions focuses on the spatial and temporal trends in fishing relative to the Big Creek reserve. What are fishers' perceptions, attitudes, and beliefs about MPAs in general, and the Big Creek reserve in particular? Does the existence of the reserve make a difference in their decisions about whether and where to fish along the Big Sur coast? Is fishing pressure at the reserve's perimeter greater than elsewhere? Has it increased, decreased, or remained the same over time?

McClanahan and Kaunda-Arara (1996) report that after the establishment of a no-take MPA in Kenyan waters, fishers redirected their effort, concentrating along the edge of the reserve. They cite this concentration of fishing activity at the MPA's perimeter as the cause of its failure to result in increases in mean sizes and ages of fish in the fished area despite the increases observed in the protected area. They attribute this redistribution of fishing effort to fishers' perceptions that fishing would be better along the MPA perimeter (although the coincident banning of set nets in the same area likely played a role as well).

For the Big Sur fishery, as elsewhere, the environmental, regulatory, and market conditions of fishing have changed in the five years since the reserve's designation. Moreover, fishers have had five years of conducting their fishing with the legal marine reserve in place. What changes, if any, did they make in their fishing in response to the reserve? What social and economic effects, positive and negative, have they experienced in connection with those changes and the reserve's formal establishment? What, if any, changes have they noticed in the resource and the fishery? How have fishers' attitudes, beliefs, and expectations of the reserve and the adjacent fishery changed over time? What factors have most influenced these changes?

CONCLUSION

The cooperative arrangement at Big Creek was instrumental to the legal designation of the Big Creek Ecological Reserve because it facilitated the incorporation of social and economic, as well as ecological, concerns into efforts to establish the reserve. But the co-management arrangement has potential value beyond the establishment of the reserve for its continued management and evaluation. This potential lies not only in the Hook-and-Line Survey through which fishers are contributing fishery-dependent data, but in the opportunity for eliciting and integrating their local ecological knowledge with scientific data, and engaging them more fully in the management process. The resulting communication, information, and understanding can help insure that social and economic considerations are aired and addressed throughout the MPA process, and thereby contribute to more effective use of MPAs as a management tool.

The questions raised about the reserve, the fishery, and the interaction between the two are sociocultural and economic, as well as biophysical, and have important implications for Big Creek Ecological Reserve and for the consideration of MPAs as a fishery management tool more generally. This is all the more significant as California proceeds to implement the 1998 Marine Life Management Act, which calls for greater collaboration among managers, scientists, and the fishing industry, and for fuller consideration of co-management for the state's fisheries. More generally, the Big Creek case may be instructive to those considering alternative approaches to fishery management, such as co-management and MPAs.

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Part III

SCIENTIFIC CONTRIBUTIONS

FINE-SCALE DISTRIBUTIONS OF PLANKTONIC FISH EGGS IN THE VICINITIES OF BIG SYCAMORE CANYON AND VANDENBERG ECOLOGICAL RESERVES, AND ANACAPA AND SAN MIGUEL ISLANDS, CALIFORNIA

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ABSTRACT

Nearshore ichthyoplankton surveys were conducted during late winter and early summer 1998, at four sites in southern California: Big Sycamore Canyon and Vandenberg Ecological Reserves, and Anacapa and San Miguel Islands. A continuous underway fish egg sampler (CUFES) was used to sample along each of three or four transect lines oriented alongshore and spaced at about 0.8 km or 1.6 km intervals offshore, and a bongo net was towed vertically through the water column at a series of stations spaced about 0.8 km or 1.6 km apart on each line.

A total of 41 fish egg taxa and an unidentified fish egg category were collected: 30 taxa in winter and 29 in summer. Winter fish egg collections were dominated by northern anchovy; California halibut, speckled sanddab, white croaker, and Pacific hake eggs also were common. Summer egg catches were more evenly distributed over several taxa, primarily senorita, California sheephead, California barracuda plus white seabass, and speckled sanddab, as well as unidentified eggs. Collections of eggs in early developmental stages suggested that many taxa spawned at night. Senorita spawned during the day, California sheephead probably spawned primarily during the day, and California halibut may have begun spawning during the afternoon and continued into the evening.

Both frequency of occurrence and abundance of eggs tended to be higher inshore and were much reduced on the most seaward line for the more common shorefish taxa. White croaker and California sheephead probably spawned primarily shoreward of about the 30 m isobath, and speckled sanddab and senorita shoreward of about the 60 m isobath. California halibut apparently spawned primarily between about the 40 and 60 m isobaths, and California barracuda and white seabass spawned over a broader depth range, about 45–90 m. Abundances of California halibut and white croaker eggs were highest at the Big Sycamore Canyon site, while the islands, especially Anacapa Island, were important sites for California sheephead, senorita, California barracuda, and white seabass spawning.

The CUFES proved to be an effective sampler for fine-scale distributions of planktonic fish eggs, but may inadequately sample taxa or developmental stages whose vertical distributions are centered above or below its intake depth. Use of another sampler that covers the entire vertical range of the taxa of interest is a necessary adjunct to CUFES sampling.

INTRODUCTION

Four marine ecological reserves were established along the California coast in 1994 as part of the California Marine Resources Protection Act of 1990. In February 1998, a study of the fine-scale distribution of planktonic fish eggs was initiated at two of these reserves on the southern California coast: Vandenberg Ecological Reserve, centered on Point Arguello, and Big Sycamore Canyon Ecological Reserve, just east of Point Mugu (fig. 1). The ultimate goal of this ongoing study is to measure the production of planktonic shorefish eggs from these reserves. Necessary first steps in reaching this goal are the identification of the eggs, and the determination of their temporal and spatial distributions in the vicinities of the reserves.

Among the many functions of a marine reserve (Agardy 1994; Rowley 1994), one of the potentially most important to coastal fisheries is the provision of a protected area for adult fishes whose eggs and larvae can "reseed" fished areas outside the reserve. However, owing to the difficulty of attributing planktonic eggs and larvae to a particular site of origin, the degree to which reserves might fulfill this role is largely unknown. Recently spawned eggs (or the recently released larvae of live-bearing fishes such as rockfishes) are least likely to have dispersed and to have been transported far from spawning sites, and thus are most likely to be attributable to a specific area of origin. Unfortunately, these stages often are among the most difficult to identify to species, and their usually highly aggregated distributions make them the most difficult and costly stages to sample with conventional towed nets.

To overcome this sampling problem, we tried a continuous underway pump system (CUFES: Checkley et al. 1997) as our primary plankton sampler. CUFES has been shown to be an effective tool for sampling large-scale planktonic fish egg distributions over deep coastal

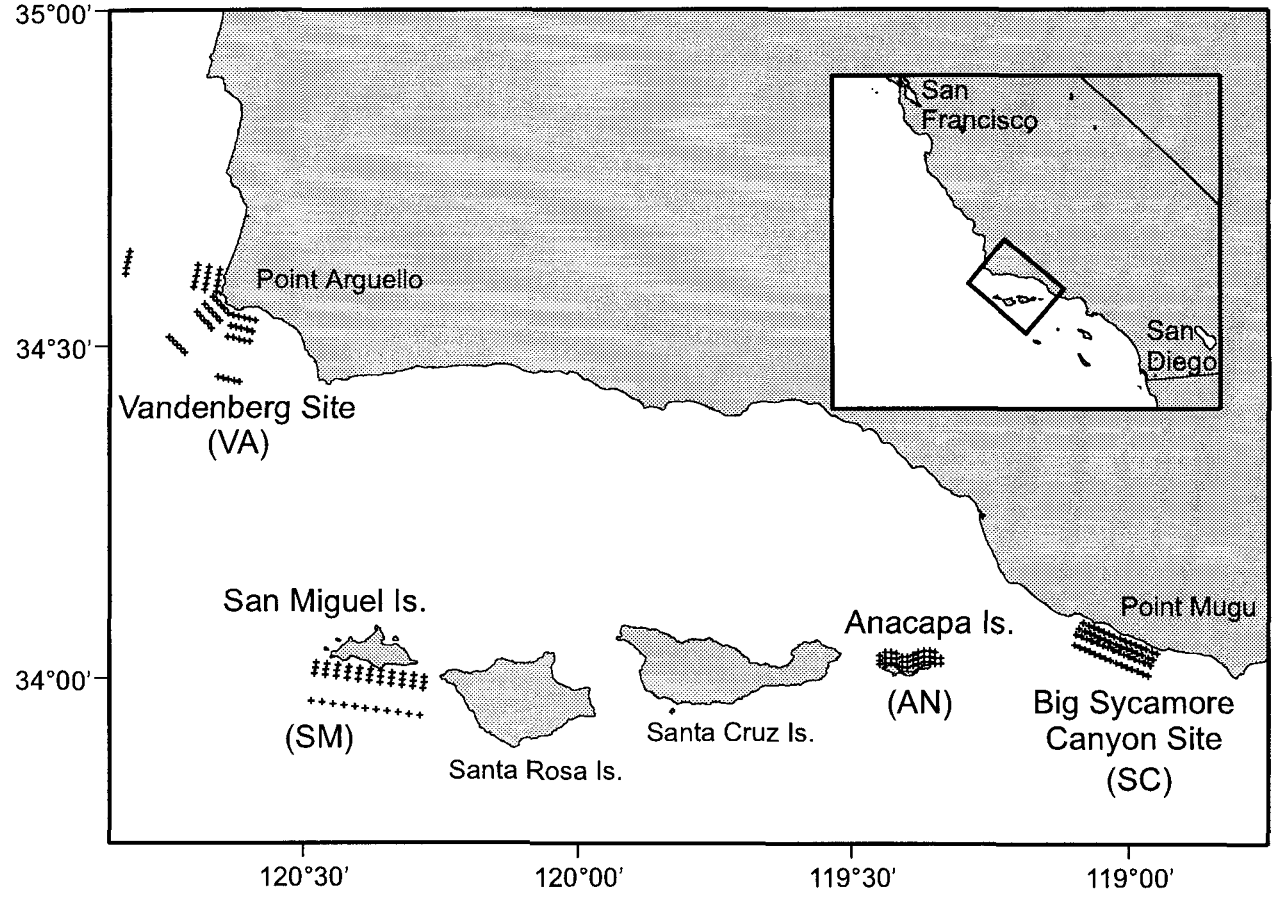

Figure 1. Location of the study sites.

and offshore waters (e.g., Checkley et al. 1997; Lynn et al. 1998), and this study is a first attempt to determine whether the methodology is also applicable to the measurement of fine-scale distributions in shallow, nearshore coastal waters.

Our objectives in this first year of the study were to (1) develop techniques to identify the planktonic eggs of the important—i.e., abundant or of value for commercial or sport fisheries—fish species in the area; (2) evaluate the usefulness of the CUFES system for measuring small-scale fish egg distributions in shallow waters; and (3) describe the temporal—primarily day-night—and fine-scale horizontal distributions of the eggs of the important taxa. The primary objective for the second year is to estimate site-specific (or habitat-specific) fish egg production (larval production of the live-bearing genus *Sebastes* will be estimated as well).

In this paper we show that the CUFES system is an effective sampler in shallow coastal water, and we describe the distributional patterns of the eggs of abundant and economically important shorefish taxa, as measured with the CUFES system. Patterns obtained with the CUFES are compared qualitatively with those obtained concurrently with a conventional bongo net.

METHODS

Two surveys were conducted in 1998: one during late winter (survey 9803JD: 19 February–4 March) and another in early summer (9806JD: 12–24 June). Four sites were sampled on each survey: Big Sycamore Canyon (SC) and Vandenberg (VA) Ecological Reserves, and Anacapa (AN) and San Miguel (SM) Islands (fig. 1). SC is a low-relief, soft-bottom site containing little hard-bottom and kelp habitat. VA likewise is predominantly a sandy bottom site, but with rocky headlands, some areas of hard bottom, and some patchy surf grass, but little kelp. Coastal currents flow primarily alongshore at both sites, predominantly southerly in spring and summer and northerly in autumn and winter (e.g., Hendershott and Winant 1996). The island sites are predominantly soft-bottom, but with more hard-bottom habitat than the mainland sites and, especially at SM, with more extensive kelp coverage. There has been a no-take reserve along the northeastern end at AN since 1978, in contrast to the recently established (1994) mainland reserves.

A station grid was established at each site (fig. 1). The most shoreward line of stations (line 1) was set approximately along the 20 m isobath, and the remaining three lines (two at AN) paralleled this line at fixed distances farther from shore without regard to bottom depth. Lines 2 and 3 were at 0.8 km (0.5 mi) intervals, corresponding very roughly to the 40 and 60 m isobaths, respectively. The most seaward line (line 4) was another 1.6 km (1 mi) farther offshore, or in the vicinity of the 200 m isobath. The reserve at SC extends offshore to the 37 m (20 fm) isobath, and line 1 thus passes through the reserve at this site. The AN and VA reserves extend offshore to approximately the 18 m (10 fm) isobath; concerns for vessel safety precluded sampling within these reserves. Stations were placed at 0.8 km (0.5 mi) intervals (1.6 km at SM) along each line. There were five stations, each corresponding to "downcoast," "reserve," and "upcoast" positions along each line, for a total of 60 stations each at the SC and VA sites. There were 44 stations at SM (11 per line), and 35 at AN (12 each on lines 1 and 2, 11 on line 3).

The CUFES sampling system included three principal components: a submerged pump installed in a box connected to a sea chest in the hull of the RV *David Starr Jordan*, a concentrator equipped with 0.333 mm mesh, and 0.333 mm mesh collectors (Checkley et al. 1997). The pump, with an 8 cm diameter orifice, drew water from 3 m depth at 640 l/min through a grating in the hull. The CUFES sampled continuously along each line as the vessel proceeded at about 2.6 m/s (5 kts), and the accumulating plankton was collected at 2–10 min intervals, depending on plankton volume (most of these samples were 10 min). A full pattern (all four lines) was sampled twice during the day and twice at night at each site, except during survey 9803JD, when two additional pattern occupancies were obtained at SM during a weather delay in other sampling, and two of the four pattern occupancies were curtailed at VA (line 4 not sampled) because of time limitations. A total of 740 CUFES transect samples was collected on survey 9803JD, and 581 samples on survey 9806JD.

A 71 cm bongo sampler was used to make a vertical plankton tow at each station. The bongo was equipped with 0.333 mm mesh nets and cod ends, and a General Oceanics flowmeter. The nets were attached to a 45 kg weight suspended just below the cod ends. At each station the bongo was lowered to 3 m above the bottom (to a maximum of 210 m at stations deeper than 213 m) and retrieved at 50 m/min. The bongo frame was oriented horizontally with the net mouths opening upward so that the nets did not sample on descent. An attempt was made to maintain a wire angle of ≤15°; this generally was the case on descent, but when the wind speed was ≥ca. 10 m/s during retrieval it was not uncommon for the angle to rise above 15° as the net neared the surface. A CUFES sample was collected at each station simultaneously with the bongo sample. Sampling was done without regard to day or night. A total of 199 bongo and CUFES sample pairs was collected during survey 9803JD; 191 pairs were collected during 9806JD (loss of the bongo precluded collection at VA stations 53–60).

Occasional surface tows were made with a manta net (0.333 mm mesh) to collect live eggs for rearing. Eggs from these samples were sorted into presumed monotypic categories, incubated at constant temperature in 1 l and 4 l beakers placed in Lauda water baths, and sampled at regular intervals through hatching (to yolk exhaustion in some cases). The primary purpose of this exercise was to confirm species identifications of the eggs.

Immediately after collection, each CUFES plankton sample usually was rinsed into a petri dish with seawater, scanned under a binocular dissecting microscope for a preliminary count of fish eggs, then preserved in 5% borate-buffered seawater formalin. Dense samples, and all bongo and CUFES station samples, were preserved directly without being scanned.

In the laboratory, all fish eggs were identified, staged according to the criteria of Moser and Ahlstrom (1985), and counted. All fish larvae were identified, staged as yolk sac, preflexion, flexion, or postflexion (Moser 1996), and counted (because this paper is concerned with fish eggs, larvae will not be discussed). Count data were converted to concentration (number per m^3 of water filtered), and the bongo data also were converted to abundance (number under 1 m^2 of sea surface) prior to analysis. For convenience in data analysis, egg stages were pooled into "early" (stages I–III), "middle" (stages IV–VII), and "late" (stages VIII–XI) categories.

RESULTS

Taxonomic Composition

A total of 41 fish egg taxa and an "unidentified egg" category were recognized in 1998: 30 taxa in winter and 29 in summer (tables 1–4). The "unidentified egg" category contained about 18 distinguishable egg types in winter and about 27 types in summer. Several taxa, primarily flatfishes, occurred in both surveys, but only speckled sanddab (*Citharichthys stigmaeus*) eggs were relatively common in both. Winter CUFES samples were dominated by eggs of the northern anchovy (*Engraulis mordax*) at all sites except SC, where California halibut (*Paralichthys californicus*) eggs were somewhat more common. Winter bongo samples likewise were dominated by northern anchovy eggs except at SM, where eggs of the Pacific hake (*Merluccius productus*) were most common. During summer, catches were more equitably distributed among several shorefish taxa in both CUFES and bongo samples, and the eggs of coastal pelagic, coastal demersal, and mesopelagic species were uncommon, except for Pacific argentine (*Argentina sialis*) eggs in the bongo samples.

The more commonly occurring taxa during each survey were essentially the same in both CUFES and bongo samples, but eggs of the Pacific hake and Pacific argentine were much more frequent in the bongo samples, reflecting their deeper vertical distributions. Only the two most commonly occurring taxa, northern anchovy and California halibut, were taken at all sites in winter CUFES samples; four additional taxa—Pacific hake, speckled sanddab, white croaker (*Genyonemus lineatus*), and California smoothtongue (*Leuroglossus stilbius*)—occurred at all sites in the bongo samples. Five taxa were collected at all sites in the June CUFES samples: senorita (*Oxyjulis californica*), California sheephead (*Semicossyphus pulcher*), speckled sanddab, C-O turbot (*Pleuronichthys coenosus*), and Perciformes—the indistinguishable early-stage eggs of white seabass (*Atractoscion nobilis*) and California barracuda (*Sphyraena argentea*). Only speckled sanddab eggs, however, were common to all sites in the bongo samples. The numbers of identifiable taxa collected with the CUFES at the mainland sites were higher in summer than in winter, but differed little between seasons at the island sites (although taxonomic composition differed considerably). More identifiable taxa were collected with the bongo during the winter than in summer at all sites.

Horizontal Distribution

Among the relatively common shorefish eggs (those occurring in ≥10% of the CUFES transect samples), patterns of declining concentration with increasing distance from shore were apparent at all sites (e.g., figs. 2–7), but not at every site for every taxon. The cross-shelf pattern most often took the form of generally similar concentrations along the inshore lines, and much reduced concentration on the most offshore line. Similar patterns were apparent in the bongo data, but less clearly so. In contrast, patterns of decreasing concentration as the bottom shoaled, or no pattern relative to distance from shore, depending on site, generally were apparent for the eggs of non-shorefish taxa; for example, the coastal pelagic species, northern anchovy (fig. 8).

Eggs of the California halibut were taken primarily at SC during survey 9803JD. They were rarest offshore and showed some evidence of declining concentration alongshore from generally higher values southeast of the reserve to lower values northwest of the reserve (fig. 2a). Concentrations were lower at the other sites than at SC, and cross-shelf patterns were visible primarily as reduced frequency of occurrence offshore. Alongshore patterns were not apparent at these sites, except at SM (fig. 2d, h) where the highest frequency of occurrence of eggs toward the eastern end of the island, and their virtual absence at the western end, may reflect the strong northwesterly wind (ca. 10–20 m/s) that blew during most of the transect sampling at this site.

Speckled sanddab (fig. 3) and white croaker (fig. 4) eggs showed essentially the same cross-shelf pattern as California halibut, but little evidence of alongshore pattern at SC. Like California halibut, speckled sanddab eggs occurred primarily off the eastern part of the island at SM. At VA, white croaker eggs were more concentrated in CUFES samples collected in a plume of slightly lower-salinity (ca. 32.6 ppt), green water north of Point Arguello than in the slightly saltier (ca. 32.8 ppt), blue water to the south (fig. 4b). No such pattern was apparent in VA bongo data (fig. 4d), suggesting that the "egg-rich" plume was a relatively thin, shallow layer.

During the June survey, senorita eggs were common on the shoreward two lines in CUFES samples at SC and SM, clearly less so farther seaward along line 3 at SC, and nearly absent from the most offshore line at both sites (fig. 5a, c). Alongshore patterns were not evident at either site. Both frequency of occurrence and concentration were highest at AN; here eggs were common on all lines, but the largest CUFES catches were along the most inshore line (fig. 5b). Bongo catches were much smaller at AN, with some indication of decreasing concentration offshore (fig. 5e).

California sheephead eggs were rare at the mainland sites but common at the islands, especially at AN, in June. Large collections were made with the CUFES on all three lines at AN (fig. 6a); at SM frequency of occurrence and numbers in CUFES samples were highest on the most inshore line, and eggs were nearly absent from the most offshore line (fig. 6b). Alongshore patterns were not apparent, except that concentration was lower off the west end of West Anacapa. Like senorita, California sheephead eggs were far less numerous in bongo samples than in CUFES collections; nevertheless, some indication of decreasing concentration offshore could be seen in the bongo data (fig. 6c, d).

White seabass eggs were collected only at the islands, mainly in CUFES samples at AN, at the beginning of the spawning season in late winter (tables 1 and 2), and they remained primarily at AN in summer (tables 3 and 4). During the summer survey, egg distributions were confounded with those of the California barracuda, whose eggs are nearly indistinguishable from white seabass eggs before mid-development (stage VI or VII), when conventional characters are used (e.g., Matarese and Sandknop 1984). Distributions and numbers of the older eggs of both species were similar, except that California barracuda eggs were more common than white seabass eggs at SC. White seabass plus California barracuda eggs (all stages pooled) were far more common at AN than elsewhere; moderate numbers were collected at SC, and

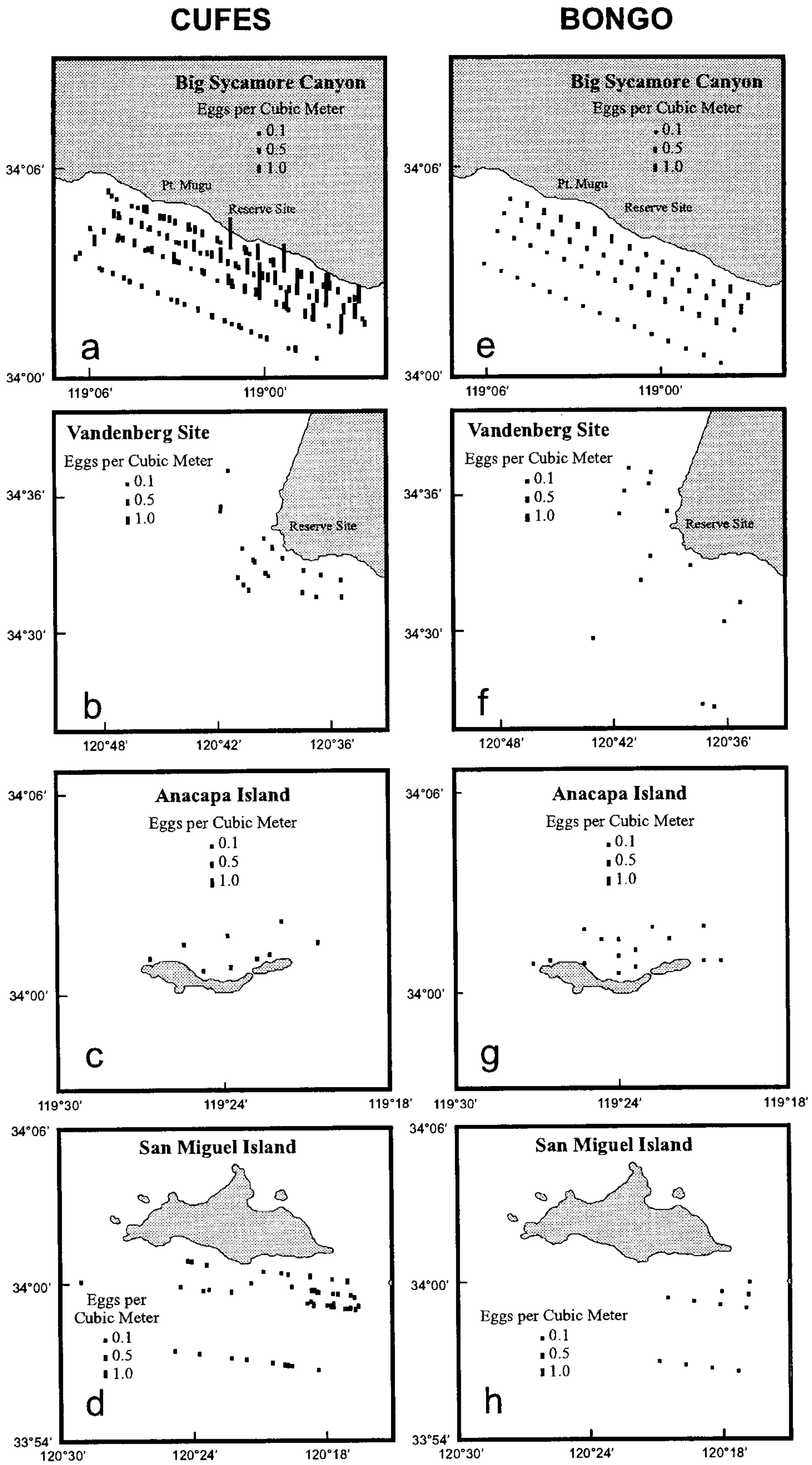

Figure 2. Distribution of California halibut (*Paralichthys californicus*) eggs at the four study sites during survey 9803JD, based on CUFES (*a–d*) and vertical bongo (*e–h*) sampling. All egg stages are included.

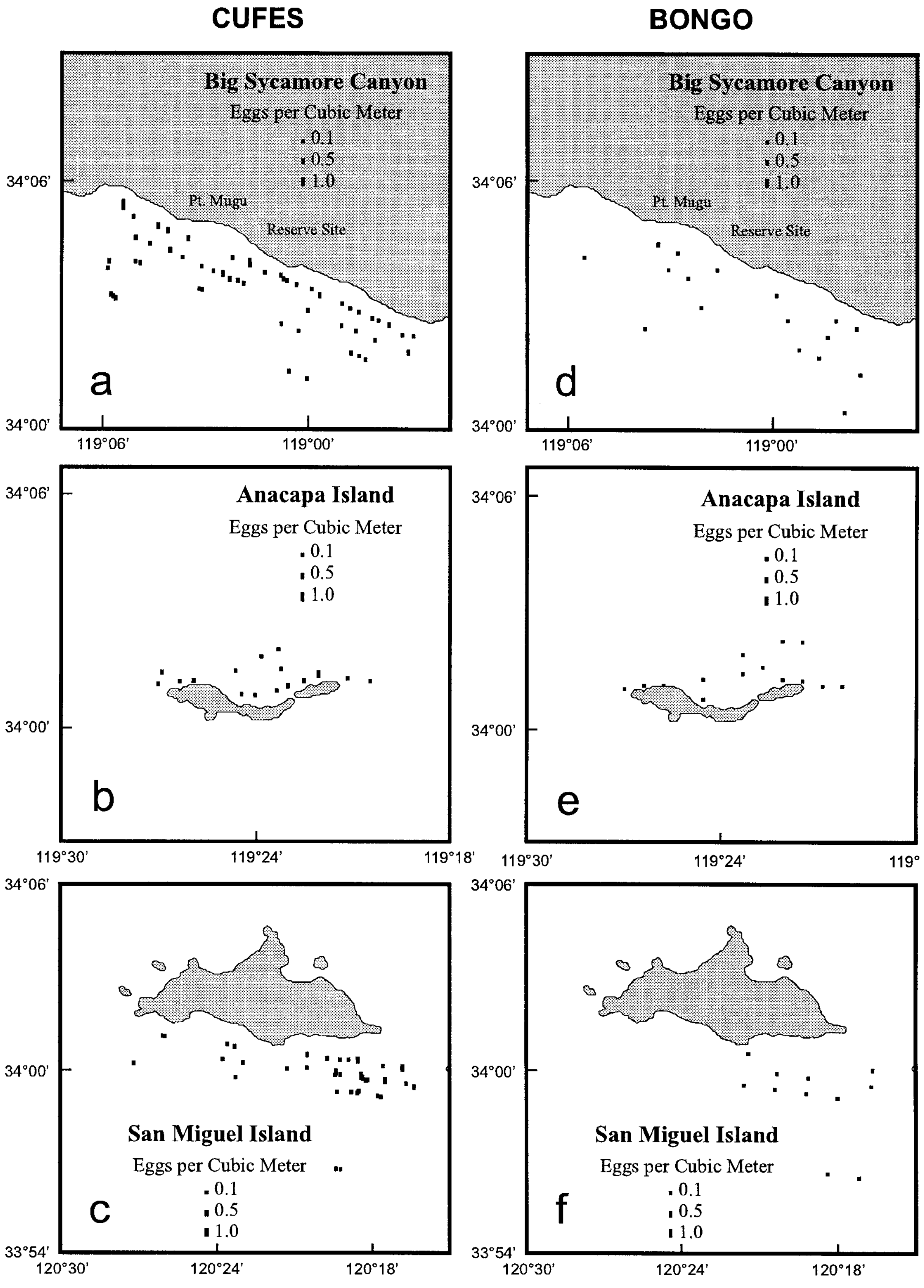

Figure 3. Distribution of speckled sanddab (*Citharichthys stigmaeus*) eggs at the SC, AN, and SM sites during survey 9803JD, based on CUFES (*a–c*) and vertical bongo (*d–f*) sampling. All egg stages are included.

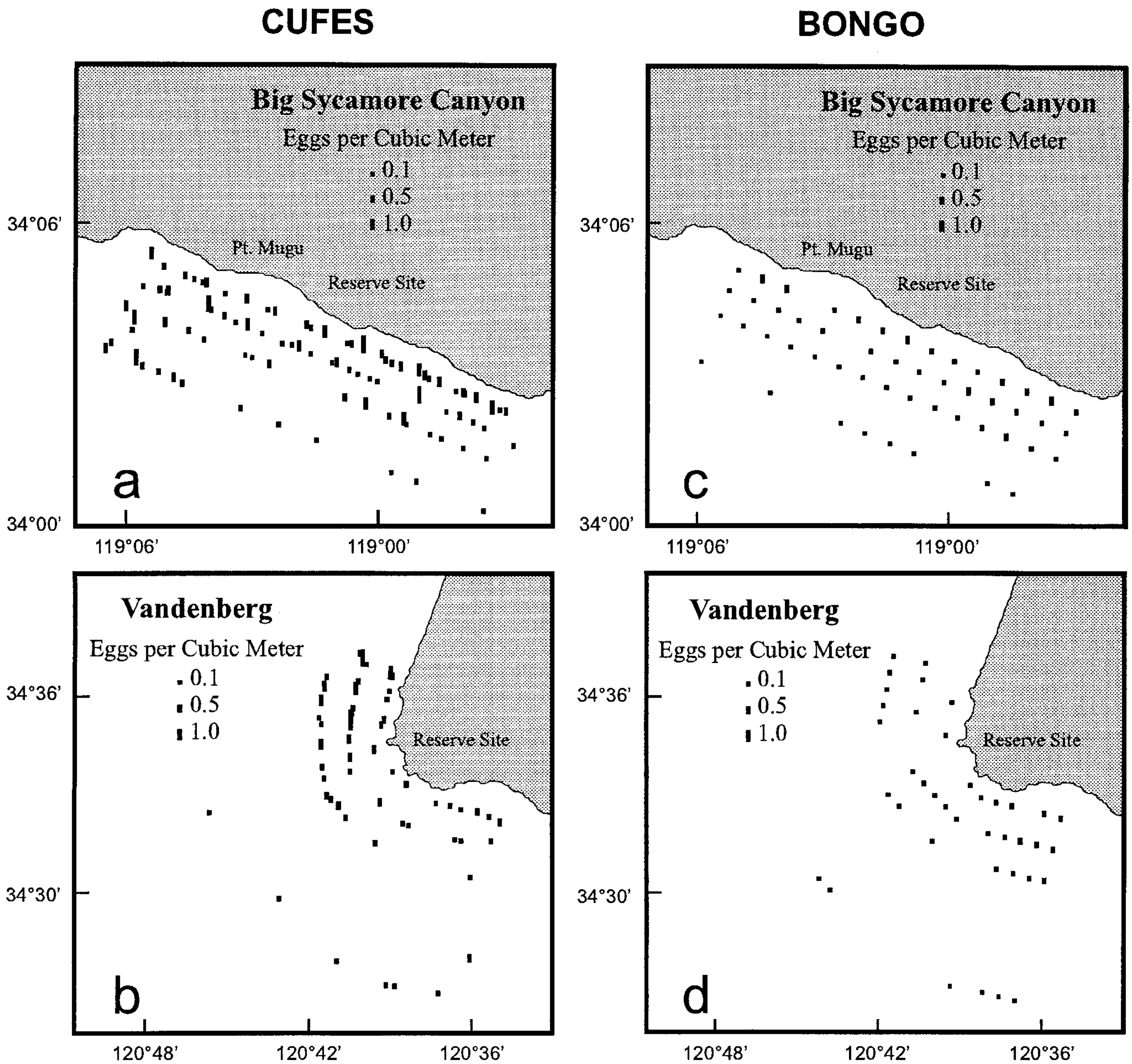

Figure 4. Distribution of white croaker (*Genyonemus lineatus*) eggs at the SC and VA sites during survey 9803JD, based on CUFES (*a, b*) and vertical bongo (*c, d*) sampling. All egg stages are included.

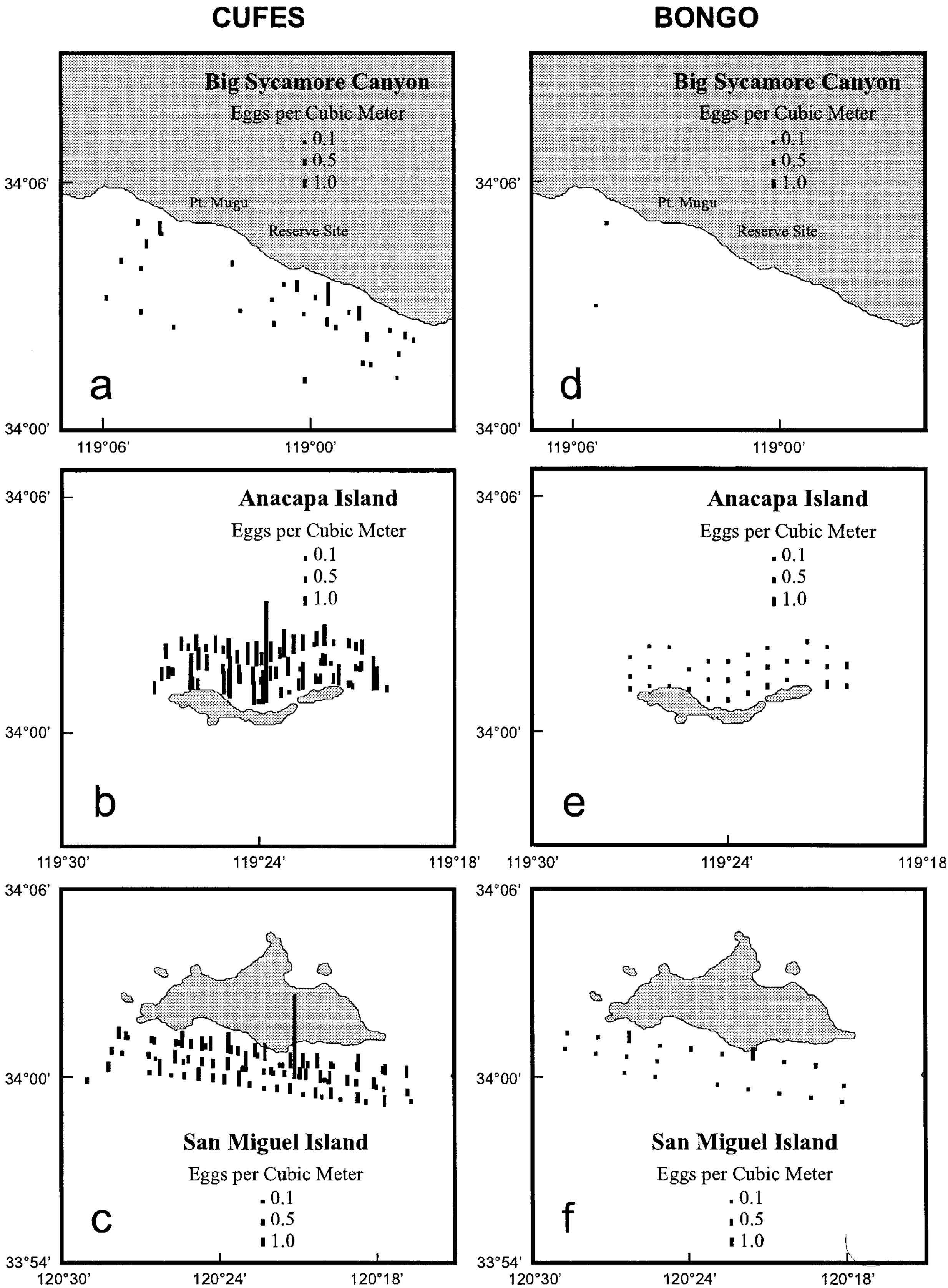

Figure 5. Distribution of senorita (*Oxyjulis californica*) eggs at the SC, AN, and SM sites during survey 9806JD, based on CUFES (*a–c*) and vertical bongo (*d–f*) sampling. All egg stages are included.

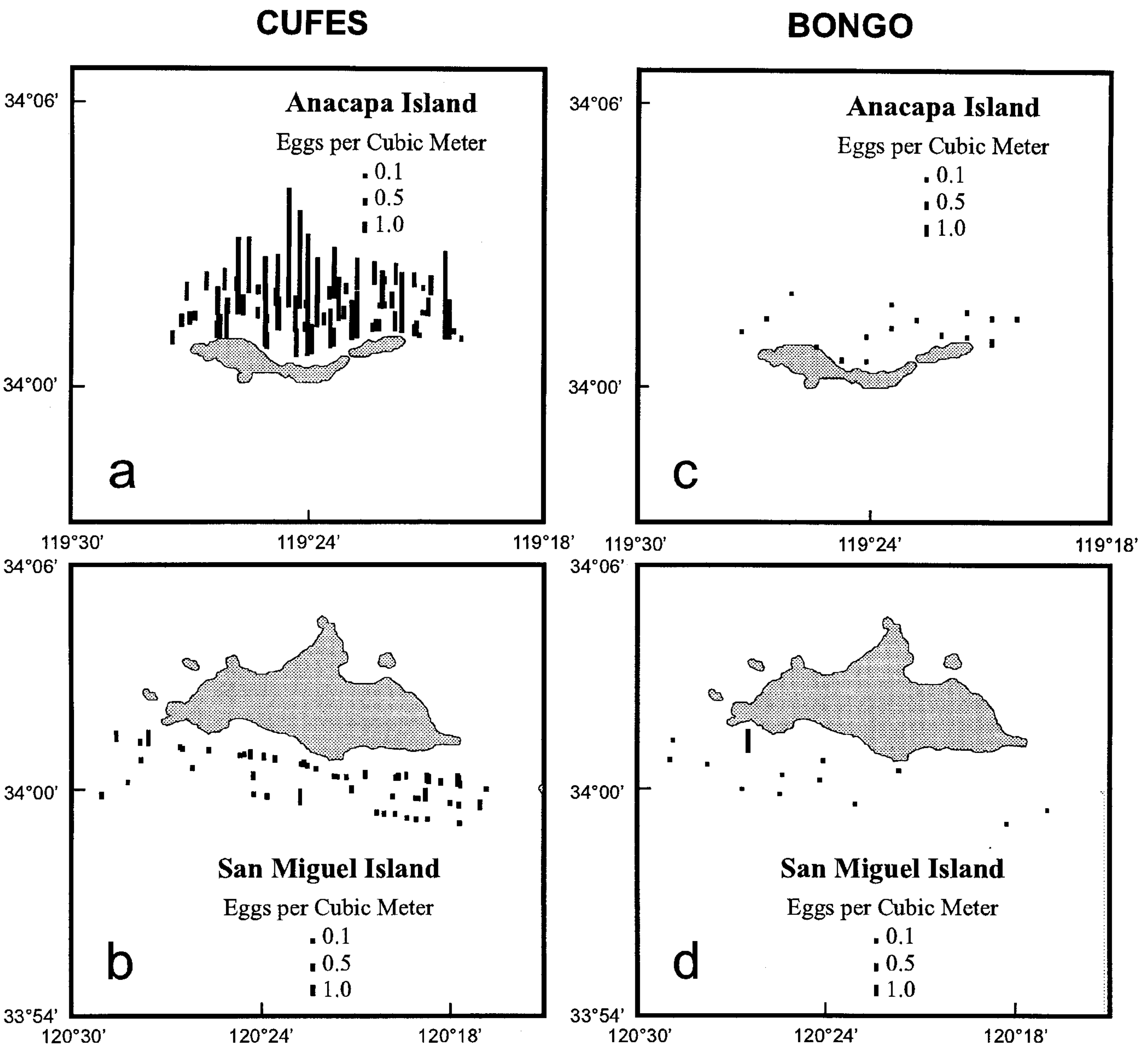

Figure 6. Distribution of California sheephead (*Semicossyphus pulcher*) eggs at the AN and SM sites during survey 9806JD, based on CUFES (*a, b*) and vertical bongo (*c, d*) sampling. All egg stages are included.

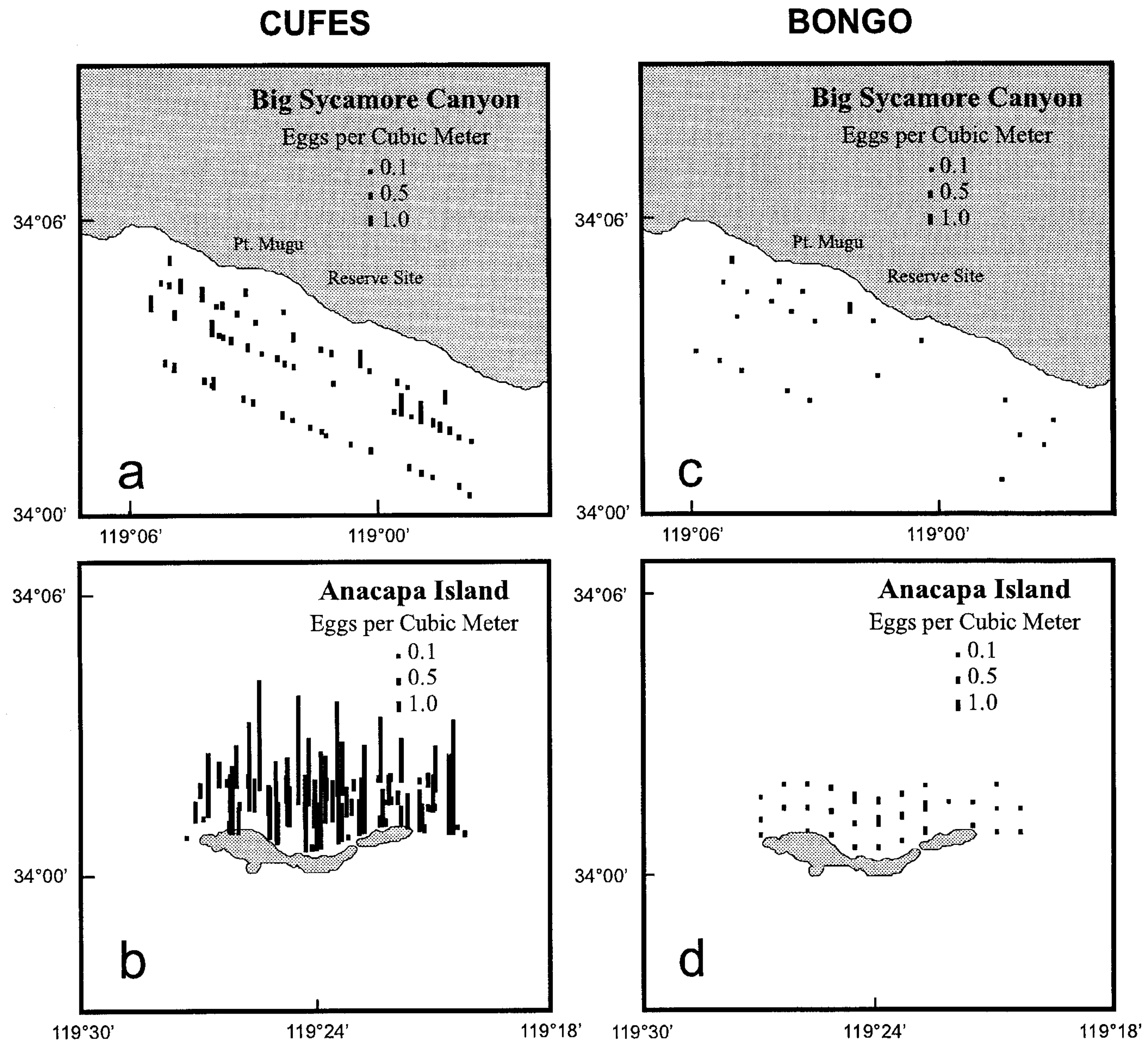

Figure 7. Distribution of white seabass (*Atractoscion nobilis*) plus California barracuda (*Sphyraena argentea*) eggs at the SC and AN sites during survey 9806JD, based on CUFES (*a*, *b*) and vertical bongo (*c*, *d*) sampling. All egg stages are included.

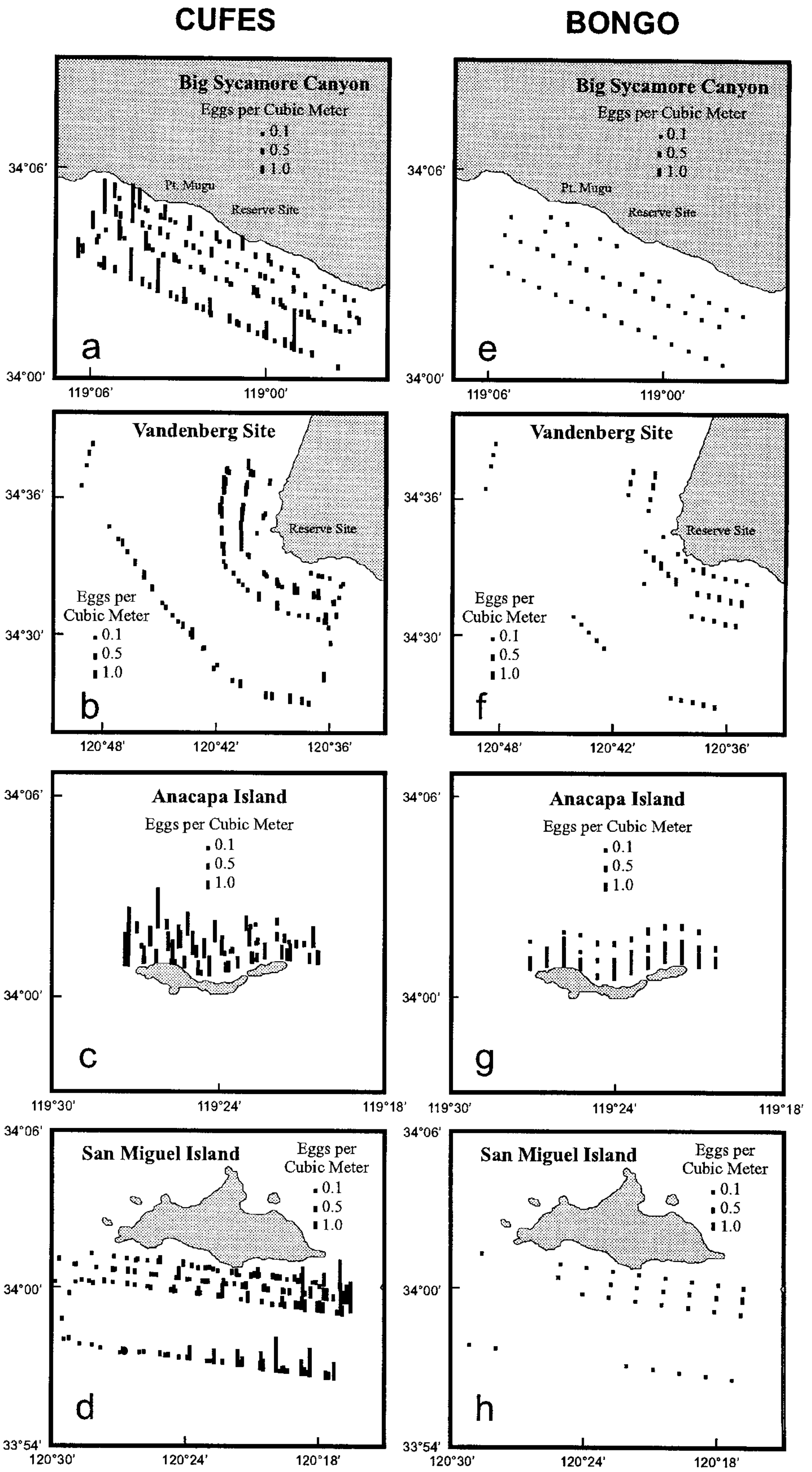

Figure 8. Distribution of northern anchovy (*Engraulis mordax*) eggs at all four study sites during survey 9803JD, based on CUFES (*a–d*) and vertical bongo (*e–h*) sampling. All egg stages are included.

TABLE 1
Percent Positive Collections of Fish Eggs in CUFES Transect Samples during Survey 9803JD, 19 February–4 March 1998

Taxon[a]	All sites	Big Sycamore Reserve	Vandenberg Reserve	Anacapa Island	San Miguel Island
Engraulis mordax	63.9	78.1	65.8	70.9	54.5
Paralichthys californicus	28.3	88.3	12.8	10.5	13.9
Genyonemus lineatus	20.6	56.9	35.6	9.3	
Citharichthys stigmaeus	14.4	35.0		17.4	11.2
Merluccius productus	8.6		5.4	3.5	15.5
Sardinops sagax	5.5			37.2	1.7
Atractoscion nobilis	3.9			25.6	1.3
Unidentified eggs	2.7	1.5	0.7	7.0	3.0
Pleuronichthys coenosus	1.9	0.7		5.8	2.3
Pleuronichthys verticalis	1.2	2.9	2.0	1.2	
Parophrys vetulus	0.7		3.4		
Pleuronichthys ritteri	0.7	2.9			0.3
Ophidiidae	0.6				1.3
Hypsopsetta guttulata	0.4			3.5	
Argentina sialis	0.3	0.7	0.7		
Citharichthys sp(p).	0.3	1.5			
Xystreurys liolepis	0.3	1.5			
Leuroglossus stilbius	0.1				0.3
Lyopsetta exilis	0.1			1.2	
Pleuronectidae	0.1		0.7		
Pleuronichthys decurrens	0.1			1.2	
Scomber japonicus	0.1		0.7		
Sebastolobus sp(p).	0.1				0.3

[a] Taxa are ordered from highest to lowest overall frequency of occurrence.

TABLE 2
Percent Positive Collections of Fish Eggs in Vertical Bongo Samples during Survey 9803JD, 19 February–4 March 1998

Taxon[a]	All sites	Big Sycamore Reserve	Vandenberg Reserve	Anacapa Island	San Miguel Island
Engraulis mordax	75.9	68.3	76.7	97.1	68.2
Merluccius productus	53.3	43.3	48.3	22.9	97.7
Genyonemus lineatus	50.3	85.0	66.7	22.9	2.3
Paralichthys californicus	50.3	98.3	23.3	42.9	27.3
Argentina sialis	23.1	40.0	25.0		15.9
Citharichthys stigmaeus	22.1	30.0	1.7	40.0	25.0
Leuroglossus stilbius	13.1	13.3	11.7	25.7	4.5
Pleuronichthys verticalis	11.6	26.7	5.0	11.4	
Unidentified eggs	11.6	6.7	18.3	20.0	2.3
Atractoscion nobilis	7.5		1.7	34.3	4.5
Pleuronichthys coenosus	7.5			31.4	9.1
Sardinops sagax	7.5		1.7	40.0	
Hippoglossina stomata	4.0	1.7		2.9	13.6
Parophrys vetulus	4.0	8.3	3.3	2.9	
Lyopsetta exilis	3.5	3.3	6.7		2.3
Citharichthys sp(p).	1.5		3.3	2.9	
Trachurus symmetricus	1.5	1.7	1.7		2.3
Embassichthys bathybius	1.0				4.5
Pleuronichthys ritteri	1.0	3.3			
Eopsetta jordani	0.5	1.7			
Glyptocephalus zachirus	0.5		1.7		
Ophidiidae	0.5		1.7		
Symphurus atricauda	0.5			2.9	
Tetragonurus cuvieri	0.5	1.7			

[a] Taxa are ordered from highest to lowest overall frequency of occurrence.

TABLE 3
Percent Positive Collections of Fish Eggs in CUFES Transect Samples during Survey 9806JD, 12–24 June 1998

Taxon[a]	All sites	Big Sycamore Reserve	Vandenberg Reserve	Anacapa Island	San Miguel Island
Oxyjulis californica	35.1	19.6	2.9	100.0	48.7
Citharichthys stigmaeus	27.8	49.0	14.0	61.0	8.6
Semicossyphus pulcher	23.6	1.3	1.8	93.6	29.9
Perciformes[b]	22.9	32.7	0.6	100.0	1.1
Unidentified eggs	20.7	35.3	7.6	40.2	12.3
Sphyraena argentea	7.9	6.5		43.9	0.5
Atractoscion nobilis	6.6	2.0		43.9	
Pleuronichthys coenosus	4.7	1.3	0.6	25.6	2.1
Citharichthys sp(p).	4.6	9.2	7.6		
Paralichthys californicus	3.0	7.8	2.9	1.2	
Ophidiidae	1.3	0.7	1.2	6.1	
Pleuronichthys verticalis	1.3		2.3	4.9	
Trachurus symmetricus	0.7		2.3		
Pleuronichthys decurrens	0.5		1.8		
Labridae	0.3			2.4	
Lyopsetta exilis	0.2		0.6		
Mugil cephalus	0.2	0.7			
Parophrys vetulus	0.2	0.7			
Peprilus simillimus	0.2				0.5
Pleuronectiformes	0.2	0.7			
Pleuronichthys ritteri	0.2	0.7			
Sardinops sagax	0.2				0.5
Sciaenidae	0.2	0.7			
Scomber japonicus	0.2		0.6		
Symphurus atricauda	0.2	0.7			

[a] Taxa are ordered from highest to lowest overall frequency of occurrence.

[b] Indistinguishable eggs of *Atractoscion nobilis* and *Sphyraena argentea*; almost all are stage I–VI eggs that have not yet developed diagnostic embryonic pigmentation.

TABLE 4
Percent Positive Collections of Fish Eggs in Vertical Bongo Samples during Survey 9806JD, 12–24 June 1998

Taxon[a]	All sites	Big Sycamore Reserve	Vandenberg Reserve	Anacapa Island	San Miguel Island
Oxyjulis californica	27.7	3.3		88.6	45.5
Perciformes[b]	22.0	21.7		82.9	
Citharichthys stigmaeus	18.8	31.7	17.3	17.1	4.5
Unidentified eggs	18.3	16.7	1.9	51.4	13.6
Paralichthys californicus	16.2	46.7	5.8		
Semicossyphus pulcher	15.2	1.7		45.7	27.3
Argentina sialis	9.4	13.3		20.0	6.8
Sphyraena argentea	9.4	18.3	1.9	17.1	
Trachurus symmetricus	5.8			31.4	
Pleuronichthys coenosus	4.2		3.8	14.3	2.3
Pleuronichthys verticalis	3.7	1.7	3.8	11.4	
Seriphus politus	2.6	8.3			
Citharichthys sp(p).	2.1	6.7			
Hippoglossina stomata	2.1	6.7			
Ophidiidae	2.1	3.3			4.5
Lyopsetta exilis	1.6	3.3			2.3
Atractoscion nobilis	1.0			5.7	
Peprilus simillimus	1.0			5.7	
Pleuronichthys decurrens	1.0		1.9	2.9	
Engraulis mordax	0.5		1.9		
Hypsopsetta guttulata	0.5	3.3			

[a] Taxa are ordered from highest to lowest overall frequency of occurrence.

[b] Indistinguishable eggs of *Atractoscion nobilis* and *Sphyraena argentea*; almost all are stage I–VI eggs that have not yet developed diagnostic embryonic pigmentation.

TABLE 5
Mean Concentrations of Early-Stage (I–III) Eggs of Selected Shorefish Taxa in Day and Night CUFES and Vertical Bongo Collections

Taxon	Survey	Day N	Day Mean	Day S.D.	Night N	Night Mean	Night S.D.
CUFES							
Genyonemus lineatus	9803	291	0.03	0.13	449	0.08	0.62
Atractoscion nobilis + *Sphyraena argentea*	9806	294	0.58	1.66	287	2.08	8.51
Oxyjulis californica	9806	294	1.23	7.87	287	0.22	0.82
Semicossyphus pulcher	9806	294	0.30	1.20	287	1.18	6.91
Citharichthys stigmaeus	9803	291	0.02	0.20	449	0.12	0.52
Paralichthys californicus	9803	291	0.09	0.39	449	0.15	0.52
Bongo							
Genyonemus lineatus	9803	87	0.01	0.06	112	0.04	0.11
Atractoscion nobilis + *Sphyraena argentea*	9806	133	0.02	0.06	58	0.03	0.12
Oxyjulis californica	9806	133	0.06	0.19	58	0.01	0.03
Semicossyphus pulcher	9806	133	0.03	0.25	58	0.001	0.005
Citharichthys stigmaeus	9803	87	0.01	0.02	112	0.01	0.03
Paralichthys californicus	9803	87	0.01	0.04	112	0.15	0.27

Concentrations (number/m^3) were averaged over all samples collected during the day, and all those collected at night, on survey 9803JD or 9806JD. Day was defined as 7 a.m. to 6 p.m. (sunrise to sunset) for survey 9803JD, and 5 a.m. to 8 p.m. for survey 9806JD. N = number of samples; S.D. = standard deviation.

few at the other sites. At SC, the highest concentrations of eggs were in CUFES samples at intermediate distance from shore (lines 2 and 3); there were fewer eggs along the most seaward line, and they were rare on the most shoreward line (fig. 7a). No alongshore pattern was apparent in the CUFES collections, and the smaller bongo catches showed neither cross-shelf nor alongshore patterns (fig. 7c). The large CUFES and small bongo catches at AN likewise showed no clear cross-shelf or alongshore patterns, except that perhaps there was some tendency for catches to be larger along Middle Anacapa and to decline off the west end of West Anacapa (fig. 7b, d). The later-stage eggs (stages VII–XI) of both species were absent from the west end of West Anacapa, and were present in somewhat lower concentration along line 3 than along the more shoreward lines.

Time and Cross-Shelf Location of Spawning

A preliminary comparison of mean concentrations of early-stage eggs in day and night (sunset to sunrise) samples (table 5) suggested that the majority of the common shorefish taxa may spawn at night. Senorita apparently spawned during the day, and California halibut may have begun spawning during the day and continued into the night. During the winter survey, CUFES and bongo catches of early-stage California halibut eggs suggested nocturnal spawning, with numbers increasing after sunset (especially in the bongo collections), peaking before midnight, and then declining concurrently with an increase in the number of middle-stage eggs (fig. 9). The concentration of middle-stage eggs peaked during the afternoon, was quite variable, and CUFES estimates tended to be higher than bongo estimates. Late-

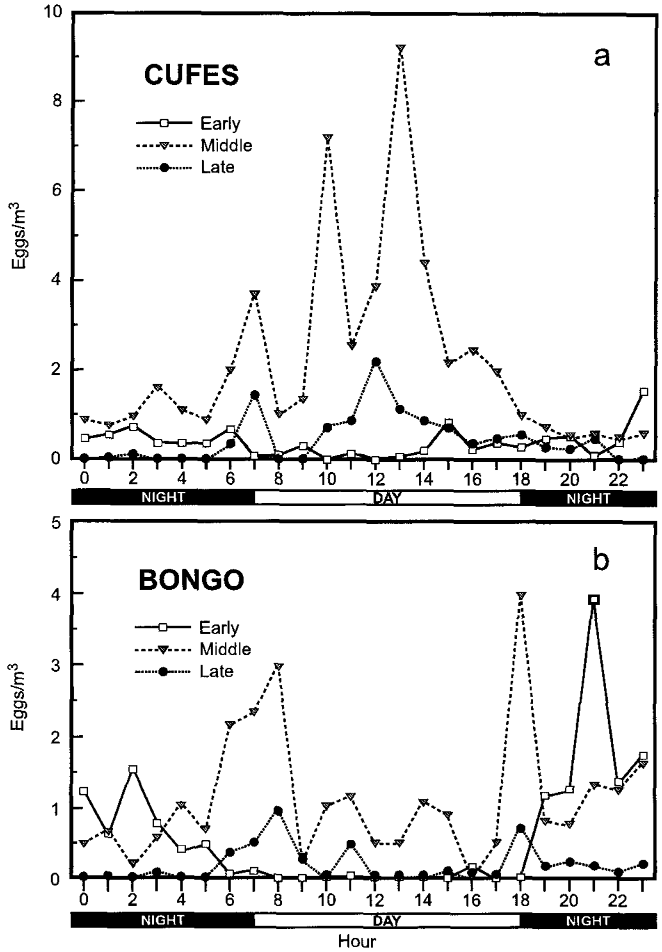

Figure 9. California halibut (*Paralichthys californicus*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9803JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

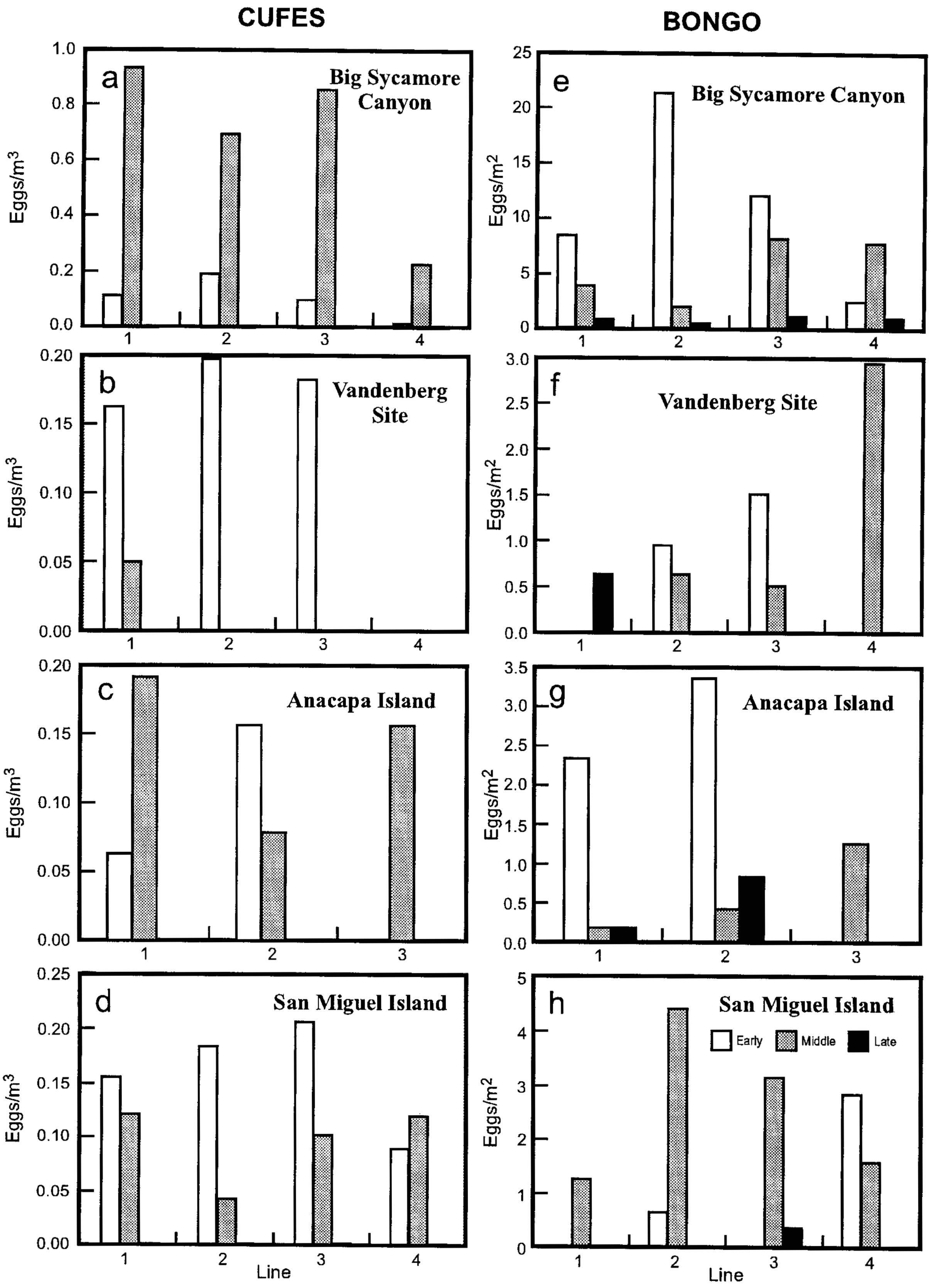

Figure 10. California halibut (*Paralichthys californicus*) eggs: concentration (*a–d*) and abundance (*e–h*) vs. distance from shore at the four study sites during survey 9803JD, using transect line as a proxy for distance. Data from CUFES (*a–d*) and vertical bongo (*e–h*) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

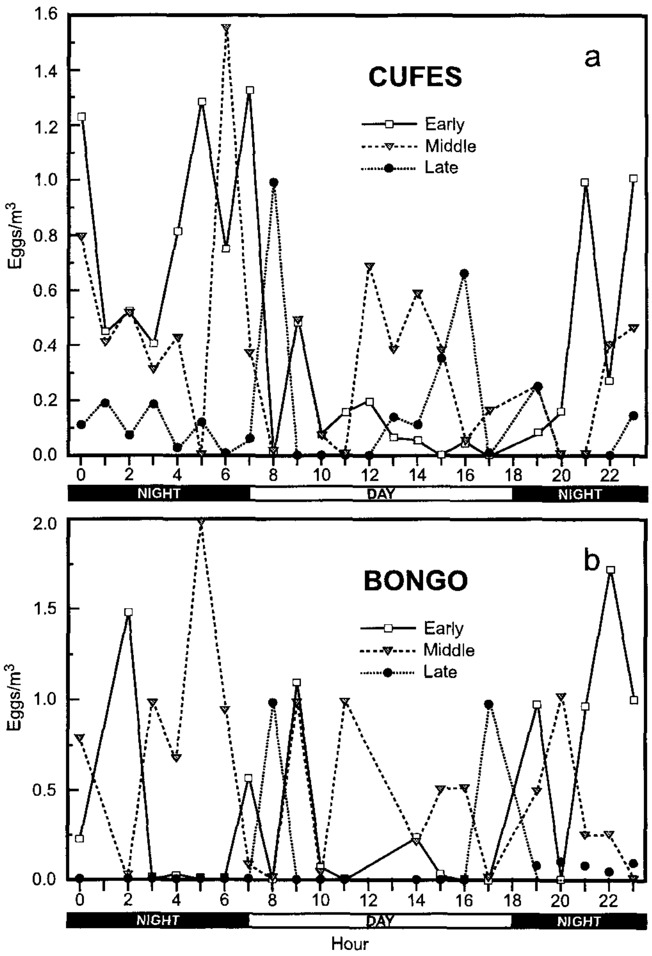

Figure 11. Speckled sanddab (*Citharichthys stigmaeus*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9803JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

stage eggs were rarer, and catches were variable with both samplers. Plots of cross-shelf concentrations and abundances of the composite stages suggested that spawning was centered primarily at intermediate distance from shore (fig. 10). At SC, where California halibut eggs were most common, early-stage eggs occurred in highest concentration (fig. 10a) and abundance (fig. 10e) on line 2 and decreased both shoreward and seaward.

Despite rather variable catches, early-stage speckled sanddab eggs showed some evidence of nocturnal spawning, probably beginning near sunset and perhaps continuing until near dawn, in the winter CUFES samples (fig. 11a). The largest bongo collections of early-stage eggs also were at night (fig. 11b), but because catches in the bongo samples were even more variable than in the CUFES samples, nighttime spawning was not clearly shown. Catches of middle- and late-stage eggs were quite variable with both samplers. Both concentration (fig. 12a–c) and abundance (fig. 12d–f) of early-stage eggs usually was highest toward shore, on line 1 or 2. In the CUFES samples, early stages were slightly more concentrated on line 2 than farther inshore; in the bongo samples they were most abundant on line 1, except at AN.

Nocturnal spawning of white croaker, probably beginning just after sunset, was suggested by catches with both samplers during the winter survey. The concentration of early-stage eggs measured with the CUFES rapidly increased beginning at about 8 p.m., peaked at about 11 p.m.–midnight, then declined to a generally low level by about dawn (fig. 13a). A similar pattern, with higher nighttime concentration but lacking the clear middle-of-the-night peak, was apparent in the bongo data (fig. 13b). Both CUFES and bongo provided more or less similar estimates of concentrations of middle-stage eggs, but for late-stage eggs bongo estimates tended to be slightly larger than CUFES estimates. Early-stage eggs were most concentrated on the inshore line at SC, and decreased monotonically with increasing distance from shore in both CUFES and bongo samples (e.g., fig. 14a), but abundance as indicated by the bongo samples was highest on line 2 (fig. 14c). At VA the few early-stage eggs collected with the bongo were taken primarily near shore on line 1, but the CUFES catches, dominated by the collections north of Point Arguello (fig. 4b), were slightly larger on line 2 than on the adjacent lines (fig. 14b).

In late winter, early-stage white seabass eggs usually were more numerous in the CUFES samples at night and early in the morning than later during the day, while in the bongo samples larger catches were made only at night (fig. 15a, b). At AN the concentration of early-stage eggs steadily increased with increasing distance from shore, based on the CUFES data (fig. 15c), while their abundance based on bongo data was slightly higher on line 2 than elsewhere (fig. 15d). During the summer survey, early-stage eggs of white seabass plus California barracuda peaked at night: before midnight in bongo samples and after midnight in CUFES samples (fig. 16). Concentration measured with the CUFES at SC was highest on line 3 (fig. 17a), although abundance based on the bongo samples was highest on line 4 (fig. 17c). At AN, where the eggs were far more common, both concentration (fig. 17b) and abundance (fig. 17d) were highest on the offshore line.

Early-stage eggs of California sheephead were most numerous at night, peaking near midnight and decreasing well before dawn, in summer CUFES samples (fig. 18a). Eggs were collected in bongo samples only between about 10 a.m. and 10 p.m. (fig. 18b), and concentrations of all stages except very recently spawned (stage I) eggs were lower on the basis of bongo samples than on the basis of CUFES samples. Nearly all of the stage I eggs collected were taken in the bongo samples—all during the day. At AN the highest concentrations of

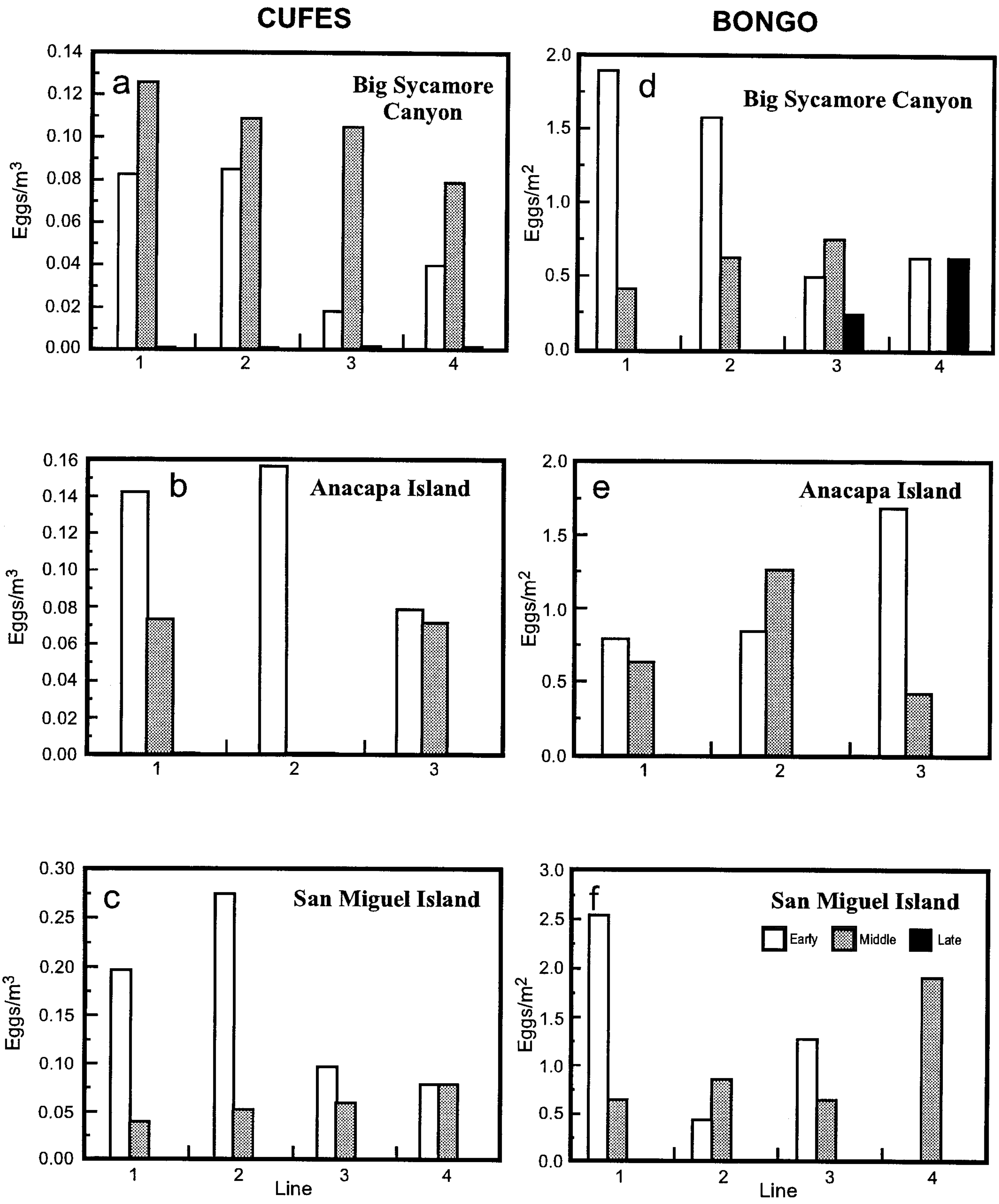

Figure 12. Speckled sanddab (*Citharichthys stigmaeus*) eggs: concentration (*a–c*) and abundance (*d–f*) vs. distance from shore at the SC, AN, and SM sites during survey 9803JD, using transect line as a proxy for distance. Data from CUFES (*a–c*) and vertical bongo (*d–f*) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

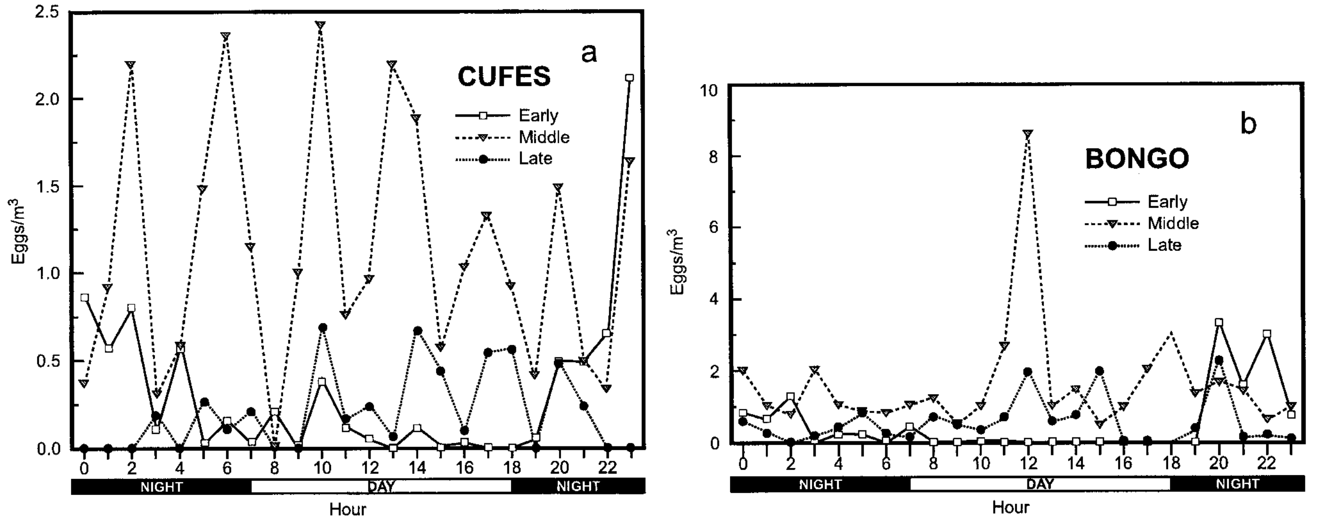

Figure 13. White croaker (*Genyonemus lineatus*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9803JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

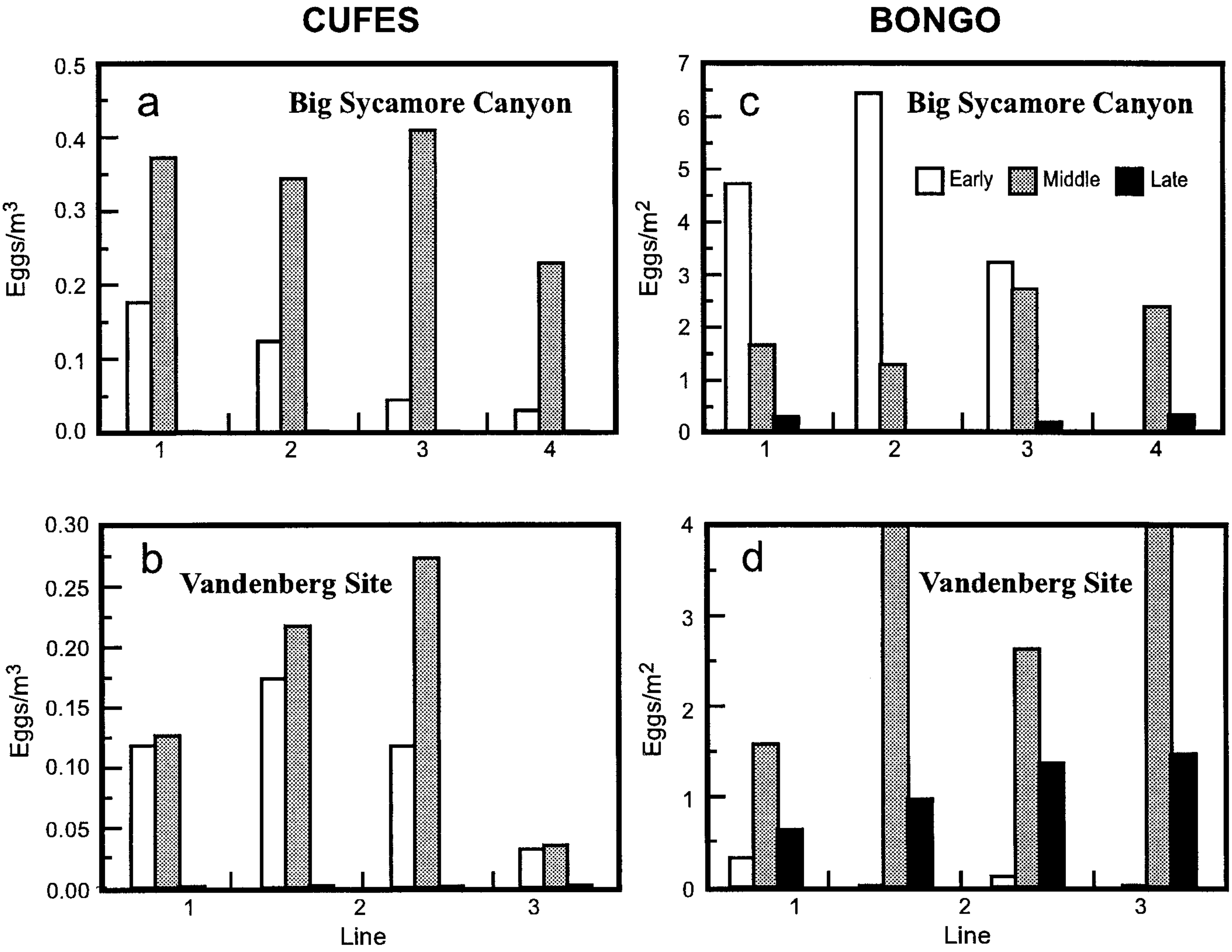

Figure 14. White croaker (*Genyonemus lineatus*) eggs: concentration (*a, b*) and abundance (*c, d*) vs. distance from shore at the SC and VA sites during survey 9803JD, using transect line as a proxy for distance. Data from CUFES (*a, b*) and vertical bongo (*c, d*) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

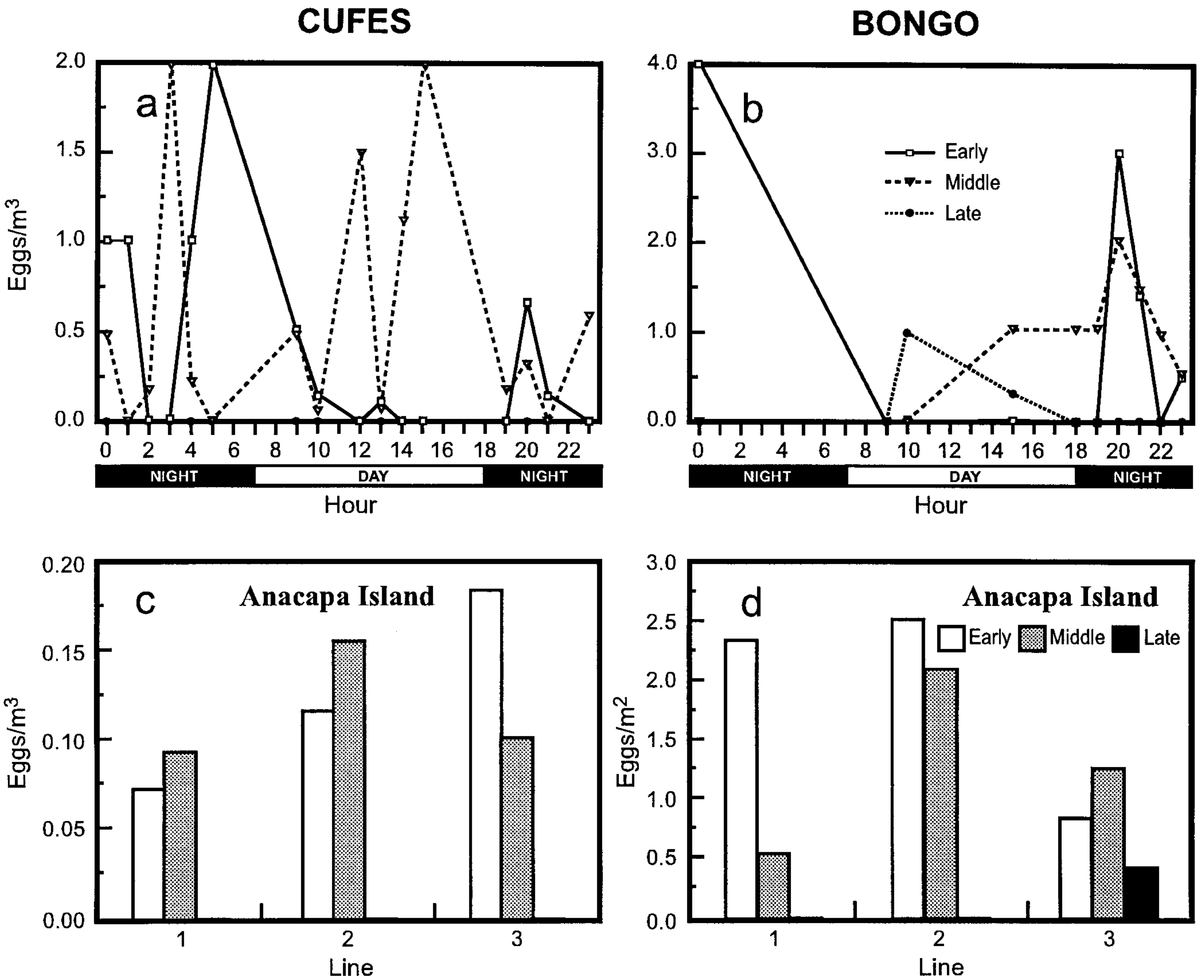

Figure 15. White seabass (*Atractoscion nobilis*) eggs: concentration vs. time of day (*a*, *b*), and concentration (*c*) and abundance (*d*) vs. distance from shore at the AN site, based on CUFES (*a*, *c*) and vertical bongo (*b*, *d*) sampling, during survey 9803JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

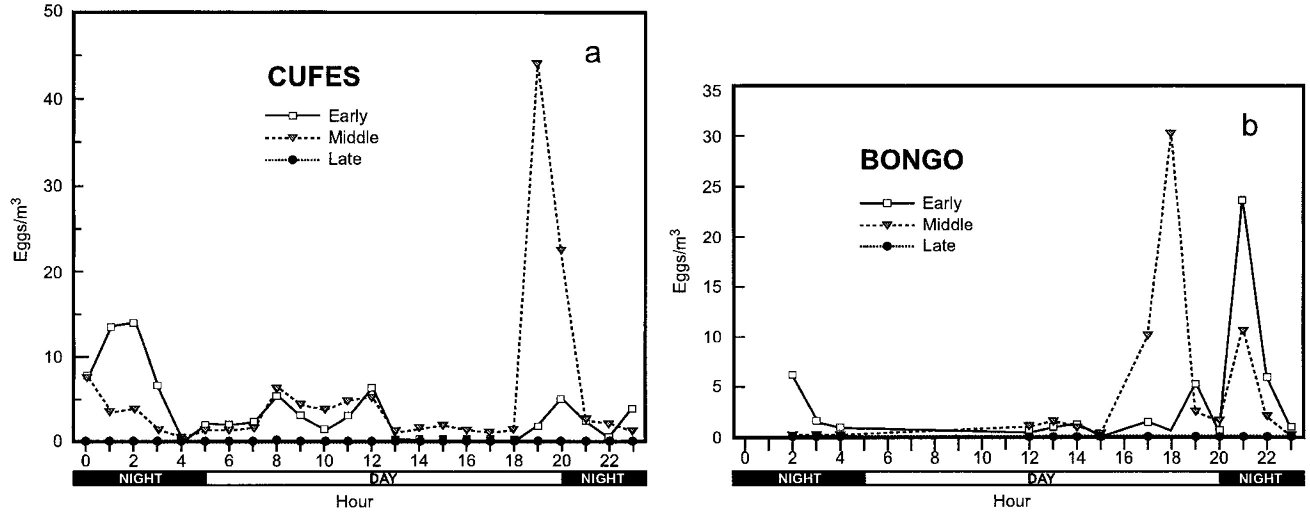

Figure 16. California barracuda (*Sphyraena argentea*) plus white seabass (*Atractoscion nobilis*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9806JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

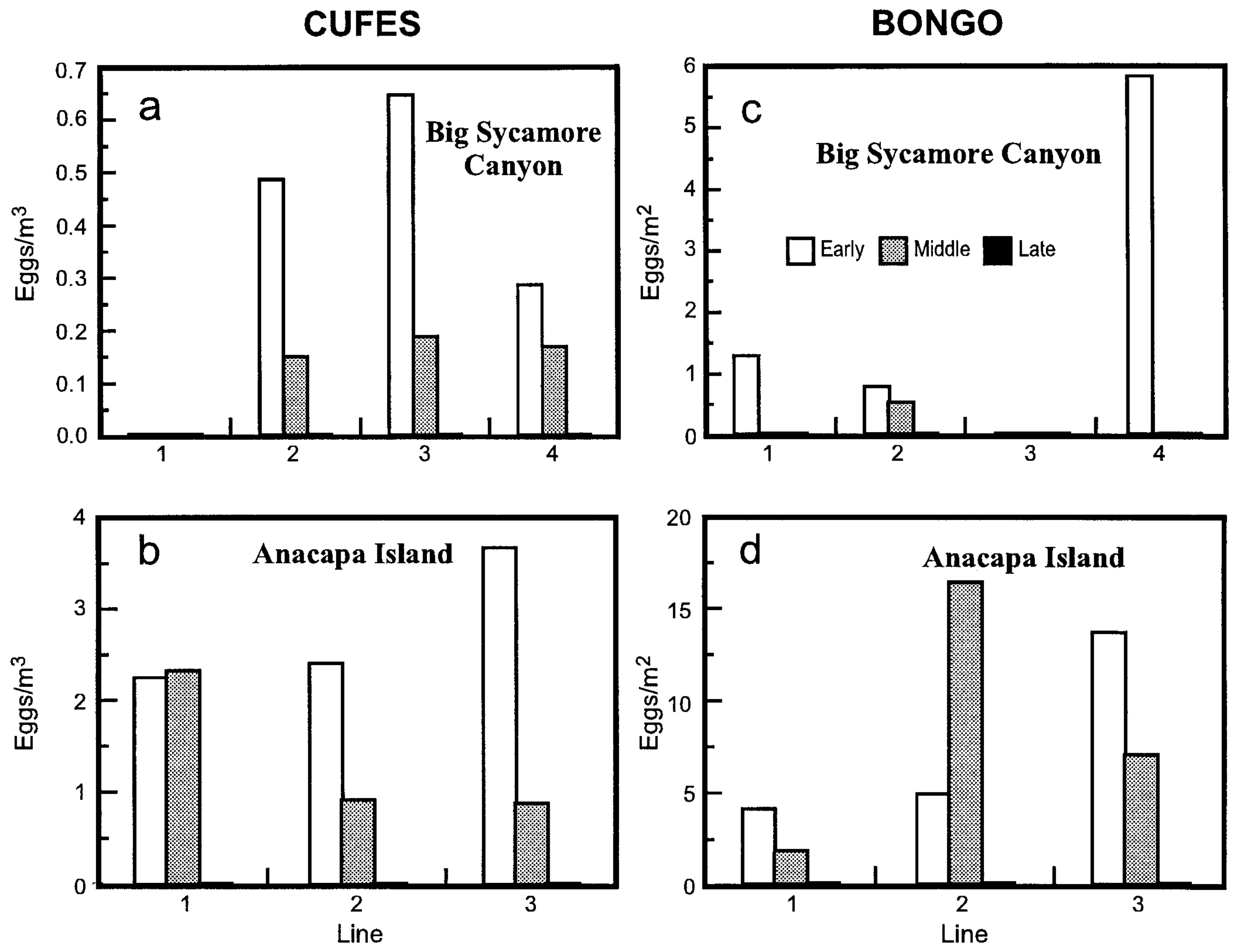

Figure 17. California barracuda (*Sphyraena argentea*) plus white seabass (*Atractoscion nobilis*) eggs: concentration (*a, b*) and abundance (*c, d*) vs. distance from shore at the SC and AN sites during survey 9806JD, using transect line as a proxy for distance. Data from CUFES (*a, b*) and vertical bongo (*c, d*) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

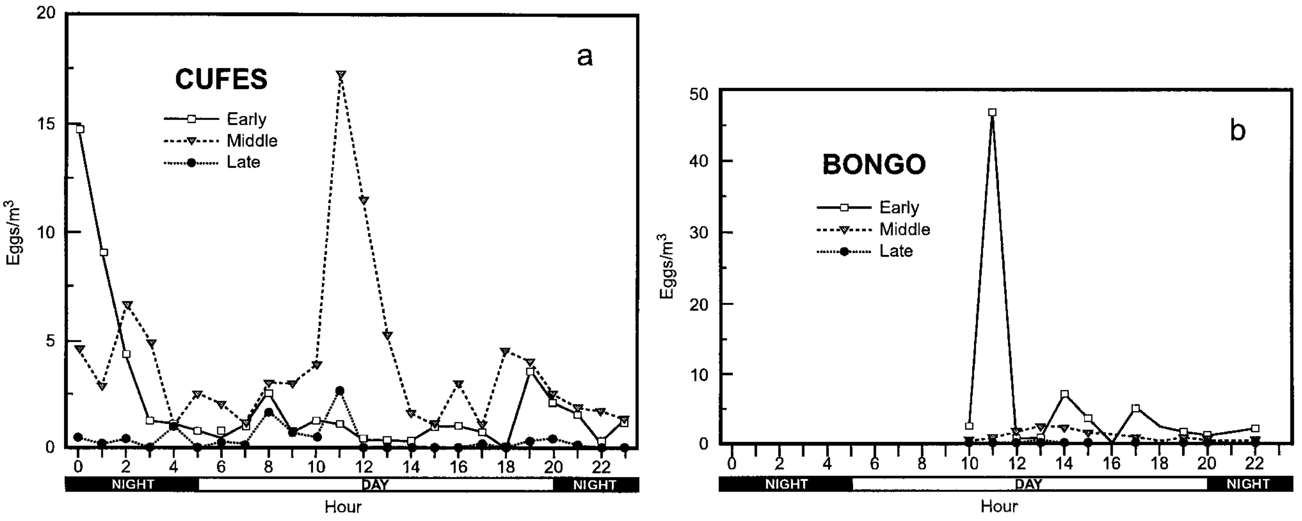

Figure 18. California sheephead (*Semicossyphus pulcher*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9806JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

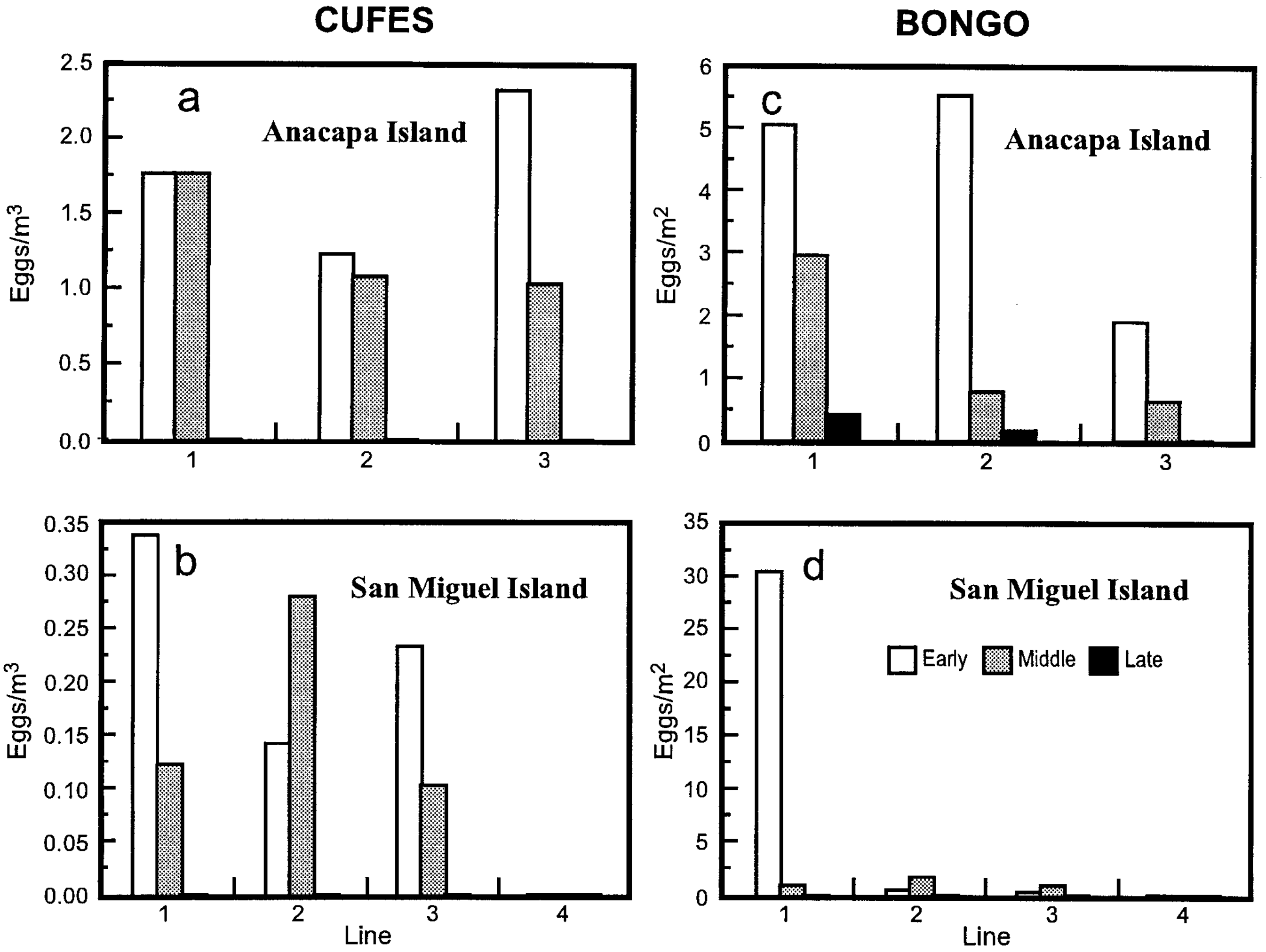

Figure 19. California sheephead (*Semicossyphus pulcher*) eggs: concentration (*a, b*) and abundance (*c, d*) vs. distance from shore at the AN and SM sites during survey 9806JD, using transect line as a proxy for distance. Data from CUFES (*a, b*) and vertical bongo (*c, d*) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

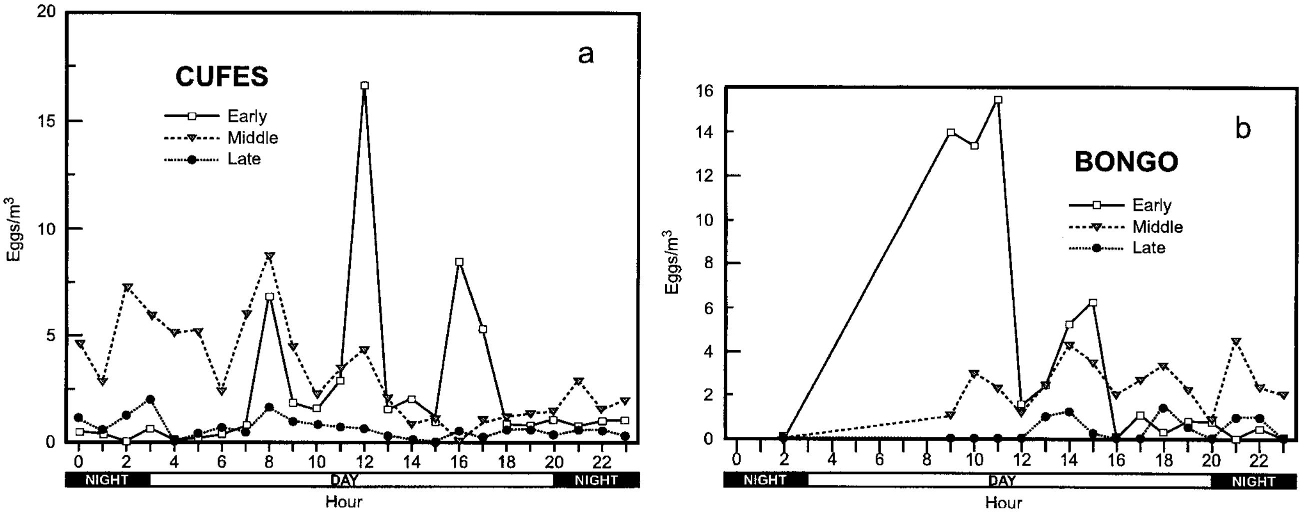

Figure 20. Senorita (*Oxyjulis californica*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9806JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

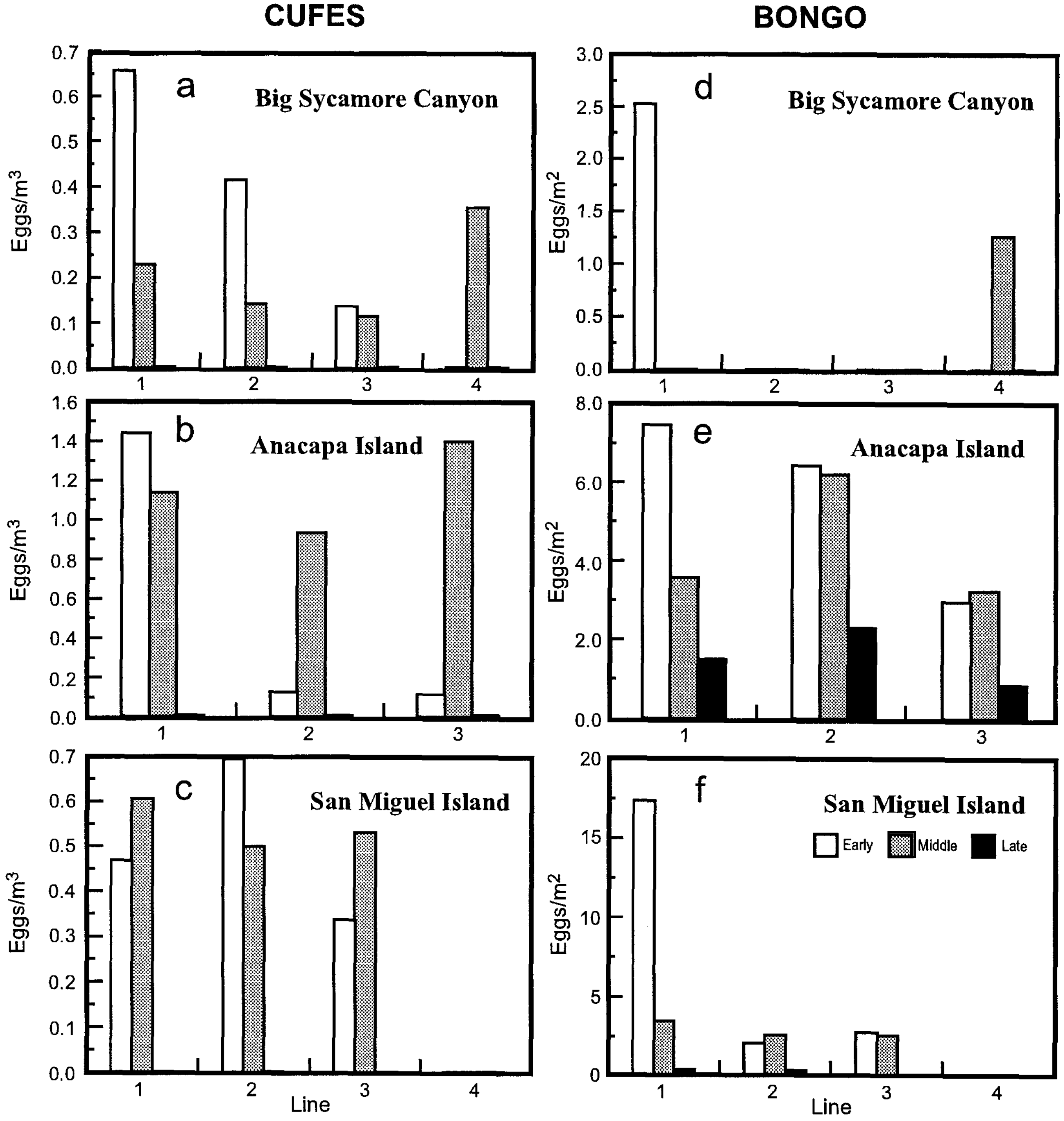

Figure 21. Senorita (*Oxyjulis californica*) eggs: concentration (*a–c*) and abundance (*d–f*) vs. distance from shore at the SC, AN, and SM sites during survey 9806JD, using transect line as a proxy for distance. Data from CUFES (*a–c*) and vertical bongo (*d–f*) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

early-stage eggs were offshore on line 3 as indicated by CUFES samples (fig. 19a) and inshore on line 1 as indicated by bongo samples, although abundance was highest on line 2 (fig. 19c). The high concentration offshore measured with the CUFES was attributable almost entirely (97%) to stage III eggs, while nearly 60% on line 1 were earlier (younger) stage II eggs. A few newly spawned eggs were collected at AN; most were taken on line 1. Both the concentration (fig. 19b) and abundance (fig. 19d) of early-stage eggs were highest on the most shoreward line at SM. Middle- and late-stage eggs tended to be more numerous toward shore at both sites.

Early-stage senorita eggs occurred primarily during the day in both CUFES and bongo samples (table 5), perhaps with morning, midday, and afternoon peaks (fig. 20). Concentrations measured with both samplers were more or less comparable for each of the composite egg stages. Concentrations of early-stage eggs were highest on line 1 or 2 (fig. 21a–c), and abundance was highest on line 1 (fig. 21d–f). No early-stage eggs were collected offshore, except at AN, where some were taken on line 3 with both samplers.

DISCUSSION

Most fish egg types collected in winter, but fewer in summer, were identifiable to some taxonomic level, usually to species. The taxonomic composition generally is consistent with results of other studies of nearshore ichthyoplankton (most were concerned primarily with fish larvae and gave little or no information on fish eggs) off southern California (e.g., Gruber et al. 1982; Lavenberg et al. 1986; Walker et al. 1987; McGowen 1993). For example, Walker et al. (1987) and McGowen (1993) identified winter-spring assemblages that included among their major components northern anchovy, white croaker, and California halibut—the three most common taxa in our winter survey. Summer-fall assemblages included queenfish (*Seriphus politus*) and the kelp and sand basses (*Paralabrax* spp.) among their major components, as well as labrids (including California sheephead and senorita), California barracuda, and white seabass. A few, mostly middle-stage, queenfish eggs were identified during our summer survey (table 4), but most early-stage queenfish eggs, as well as all stages of *Paralabrax* spp., were probably included in the "unidentified egg" category. Labrid, California barracuda, and white seabass eggs all were important components of our summer collections. Speckled sanddab eggs were common in the winter survey and present in lower numbers during summer; McGowen (1993) identified *Citharichthys* spp. eggs as part of a winter-spring assemblage, whereas Walker et al. (1987) characterized larval *Citharichthys* spp. as a primarily winter-spring taxon that remains moderately abundant throughout the remainder of the year.

Unidentified fish eggs were a minor component of our winter samples but an important part of the summer collections. At least four of the winter unidentified types might be mesopelagic ("stomiiform-like") taxa, and two might be shelf flatfishes. Many of the summer unidentified types might be shorefish species; however, nearly all were early- and middle-stage eggs that fell within the 0.7–1.0 mm size range, and had a single oil globule 0.1–0.2 mm in diameter—i.e., they were "typical" planktonic marine fish eggs (e.g., Ahlstrom and Moser 1980). It seems unlikely that most will be identifiable with conventional morphological characters (Ahlstrom and Moser 1980; Matarese and Sandknop 1984). Thus our first objective—identification of the planktonic fish eggs—was largely met in winter but less successfully met in summer.

Nocturnal spawning seems to be common among fishes with planktonic eggs (e.g., Johannes 1978) and may be common here as well: most of the shorefish taxa, with the notable exception of senorita, showed at least some indication of nighttime spawning, based on the occurrence of early-stage (stages I–III) eggs. Stage I eggs should provide the best estimate of spawning time, but for most taxa these very recently spawned eggs were collected only occasionally, or not at all. When stage I eggs were collected, estimated spawning times usually agreed reasonably well with those inferred from the broader "early-stage" category, except for California sheephead. The only taxon for which stage I eggs were collected with some regularity and in moderate abundance was the pooled taxon, California barracuda plus white seabass. Of the 35 stage I occurrences of this taxon, 30 were at night, between about 8 p.m. and 3 a.m. (about two-thirds of these between 8 p.m. and midnight), in accord with the nocturnal spawning inferred from the "early-stage" category. Two of the stage I collections were attributable with some degree of certainty to California barracuda (yolk segmentation, absent in white seabass and present in California barracuda—but often not visible in field-collected eggs—was visible in these eggs); both were collected between about 8 and 9 p.m. Thus California barracuda apparently spawns at night, probably beginning soon after sunset and continuing to about midnight or a little later. None of the stage I eggs was definitely attributable to white seabass during the summer survey, and none of their stage I or early stage II eggs were collected in the winter survey. Nevertheless, it seems likely that white seabass spawn at essentially the same time as California barracuda.

The single occurrence of a stage I speckled sanddab egg was just before midnight, and the few occurrences of first- and second-cleavage stage II white croaker eggs (stage I eggs were not collected) were at night before midnight. These are generally consistent with the nocturnal spawning times inferred for those species.

Concentrations of early-stage California halibut eggs were highest at night, peaking near midnight, with catches before the peak being predominantly stage II, shifting to predominantly stage III after the peak. Caddell et al. (1990) reported that California halibut cultured under natural light and water conditions spawn primarily during mid- to late afternoon early in the spawning season, shifting to evening spawning, or not, later in the season. Spawning beginning in the afternoon is not inconsistent with our results; indeed, occurrences of a few stage II eggs undergoing first blastomere cleavage in late afternoon samples suggested some afternoon spawning. However, a few first- and second-cleavage stage II eggs also were collected well into the evening, and all catches of stage I eggs were between 8 p.m. and 5 a.m. (three of the four occurrences were between 2 and 5 a.m.), suggesting that spawning may be protracted.

Eight of the ten occurrences of stage I California sheephead eggs were during daylight hours; six of these were between about 1:30 and 6:30 p.m., but the largest collection (94 eggs) was made just before noon. This clearly suggests spawning primarily during the day. The increasing numbers of stages II and III during the evening probably reflect both the rate of embryonic development and dispersal of the initially highly aggregated eggs following spawning.

Nine of the ten collections of stage I senorita eggs were in the morning; eight between 8 and 10 a.m. The remaining stage I egg was collected in midafternoon. Midday and late afternoon peaks of more advanced early-stage eggs probably reflect normal development and dispersal following morning spawning, although some spawning might have continued into the afternoon. Daytime spawning is well known in tropical labrids (e.g., Colin and Bell 1991) and appears to be the case for the local species as well.

Higher abundance and frequency of occurrence of some taxa at certain sites suggested that these sites are important spawning habitats for those taxa. For example, the low-relief, low wave energy, soft-bottom coastline of the Big Sycamore Canyon Ecological Reserve vicinity is a typical adult habitat for white croaker, California halibut, and speckled sanddab, and these species clearly favored it for spawning. All three species spawned primarily shoreward of the 60 m isobath. The highest abundance of early-stage California halibut eggs was on line 2, and the few stage I eggs collected were taken along line 2, between the 40 and 60 m isobaths (bottom depth ca. 45–57 m along most of this line). Allen (1990) noted that adult California halibut are most common inshore at depths ≤20–30 m, and Frey (1971) stated that they spawn near shore in about the 6–20 m depth range. Distributions of early-stage eggs in our study clearly suggest that spawning in the vicinity of Big Sycamore Canyon was centered farther from shore in deeper water in 1998. Abundances of early-stage eggs were highest, and most of the youngest (stage II) speckled sanddab eggs collected at this site were on lines 1 and 2 (ca. 20–60 m). Most of the youngest white croaker eggs (stage II) were collected on line 1 (ca. 20–30 m), although the abundance of the composite early-stage category was highest on line 2. During summer, white seabass and California barracuda spawned to some extent along the Big Sycamore Canyon coastline, where most of the youngest eggs (stage II, probably predominantly barracuda) were collected on lines 2 and 3 (ca. 45–90 m). Big Sycamore Canyon Ecological Reserve extends seaward to the 37 m isobath and thus probably includes a large part of the primary depth range for white croaker and speckled sanddab spawning, but it is possible that it includes little of the principal California halibut and California barracuda spawning habitat. Our surveys yielded no evidence of higher egg production at the reserve relative to nearby areas outside the reserve for any taxon. The only suggestions of alongshore patterns in the vicinity of the reserve were the tendencies for the concentration of California halibut eggs to decrease toward Mugu Submarine Canyon and for northern anchovy eggs to remain high on the shoreward lines in the vicinity of the canyon during the winter survey, and in summer for senorita eggs to occur more frequently, in slightly higher concentration on average, in samples east of the reserve, perhaps reflecting spawning near the small area of hard bottom and kelp habitat east of the reserve.

Like the Big Sycamore Canyon site, the Vandenberg area also is a mostly low-relief, soft-bottom site, but wave energy typically is much higher, and currents and upwelling are stronger than at SC. Vandenberg apparently was not particularly favored as a spawning site by any planktonic spawner during the 1998 surveys. The broad area of moderate white croaker egg abundance to the north of Point Arguello during the winter survey may have resulted from southwesterly advection in a shallow plume of eggs spawned inshore along the coast. During the summer survey, surface water temperature was quite low (13°–14°C) at the site, and temperature and salinity gradients north of Point Arguello suggested upwelling. These might account, at least in part, for the apparent low level of spawning in the area at that time. The reserve at the Vandenberg site extends seaward only to the 18 m isobath, and it may not encompass the principal spawning depth of any of the local planktonically spawning fish species.

The more extensive hard bottom and kelp coverage at the islands provide better labrid habitat than is available at the mainland sites, and the islands clearly were far more important than the mainland sites for California sheephead and senorita spawning in 1998. Lower concentration and frequency of occurrence of eggs at San Miguel Island suggests reduced spawning there relative to Anacapa Island, possibly associated with the lower water temperature (surface temperature ca. 13.5°–14.5°C vs. ca. 16°–18°) at San Miguel during the summer survey. The few newly spawned California sheephead eggs collected at Anacapa Island were mostly inshore, and the remainder were on the next line seaward. Most were taken off East Anacapa and the eastern half of Middle Anacapa. The very large collection of stage I eggs at San Miguel Island was made inshore, and two small collections there were farther seaward on line 3. Thus California sheephead appear to have spawned primarily, but perhaps not exclusively, inshore at the islands. There was a hint in the distribution of stage I eggs (but not in the distributions of stages II and III) that spawning at Anacapa Island might have been predominantly at the eastern half of the site. Stage I senorita eggs were collected mainly at San Miguel Island, with all but one occurrence on lines 1 and 2 (the majority on line 2). The single occurrence at Anacapa Island was on the inshore line at East Anacapa. Thus senorita also appear to have spawned primarily near shore, but perhaps over a broader depth range than California sheephead.

The northern Channel Islands are near the northern range limit of California sheephead, and recruitment there occurs only sporadically (Cowen 1985). During strong El Niño events recruitment to the northern islands should be especially good, and these events may largely account for recruitment north of Point Conception (Cowen 1985). If the high egg abundance at Anacapa and San Miguel Islands in June 1998, near the end of the 1997–98 El Niño, was typical of that event, then strong recruitment of California sheephead might be expected. However, zooplankton biomass was especially low through spring of 1998 (e.g., Lynn et al. 1998), and larval survival in 1997 might have been poor (very few larval California sheephead were collected during the 1997 CalCOFI cruises). Plankton volume generally was much higher in samples collected during survey 9806JD than during 9803JD, suggesting a return to higher zooplankton biomass; thus larval survival and subsequent recruitment of California sheephead to the northern Channel Islands, and perhaps north of Point Conception, might have been enhanced in 1998. The summer 1999 survey will allow a comparison of California sheephead spawning during the past El Niño and currently normal, or perhaps La Niña, conditions and afford an opportunity to determine whether spawning is enhanced in the northern part of the range during warming events.

Newly spawned eggs of California barracuda plus white seabass were collected almost exclusively at Anacapa Island. Stage I eggs were taken on all three lines, with slightly higher occurrences on the inshore line but with the larger catches mostly on the next two lines. The only other stage I occurrences were at San Miguel Island: one egg each on lines 2 and 3. Thus California barracuda and white seabass spawned over a broad depth range at the islands, shoreward of about the 100 m isobath but probably mainly seaward of about the 20 m isobath.

Fine-scale distributions detected with the CUFES system were generally concordant between sites for the more common taxa, and for the most part were consistent with what is known of the biology of those taxa, suggesting that the patterns were real. Similar patterns obtained with the vertical bongo sampling support this assessment of the CUFES data. Thus the CUFES system does appear to be suitable for measuring fine-scale distributions of planktonic fish eggs in shallow coastal waters, and the higher sampling intensity available with CUFES provides a clear advantage over conventional towed nets in this application.

On the other hand, the CUFES system has a potentially significant limitation in that it samples at a fixed depth. Eggs of some taxa were far more common in vertical bongo samples than in the CUFES samples—e.g., Pacific hake; hornyhead turbot (*Pleuronichthys verticalis*); bigmouth sole (*Hippoglossina stomata*)—suggesting that their distributions in the water column are centered well away from the CUFES intake depth. Comparisons of the CUFES and vertical bongo catches of early egg stages suggest that for some taxa (e.g., California sheephead, California halibut, white croaker) eggs are spawned below the CUFES intake depth and ascend during their first few hours of development, so that the youngest eggs are underrepresented in CUFES samples. For other taxa (e.g., senorita, California barracuda + white seabass) this may be less of a problem (although results of the shipboard rearing suggested that white seabass eggs may begin to sink shortly before hatching).

Estimates of the concentration of planktonic eggs collected with CUFES have been shown to be well correlated with abundance estimates based on vertically integrated net tows for some coastal pelagic fishes (e.g., Checkley et al. 1997), but it is unknown whether a similar relation holds for planktonic shorefish eggs. Linear regressions of concentration on abundance from our CUFES-bongo sample pairs generally yielded statistically nonsignificant results, with coefficients of determination ranging from -0.39 to 0.07 for the shorefish taxa. In contrast, the relationship (regression coefficient 0.028, $R^2 = 0.33$, $P << 0.01$) between samplers was significant for northern anchovy eggs during the winter survey, when they were far more abundant than any other taxon. Among the shorefish eggs, one of the "stronger" relationships was obtained for California halibut (regression coefficient 0.023, $R^2 = 0.03$, $P = 0.10$), one of the most common taxa in the winter survey.

These analyses suggest that CUFES may be inappropriate for obtaining abundance indices for planktonic shorefish eggs. Alternatively, they may indicate only that too few samples were available for analysis; reanalysis of the full two-year data set may clarify this. In any case, it is clear that the CUFES system cannot be relied upon as the sole sampler for all taxa; it must be calibrated against (and perhaps, for the less abundant taxa, always used in conjunction with) a sampler that includes the full vertical range of the taxa of interest.

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KEY SPECIES IN THE PELAGIC COPEPOD COMMUNITY STRUCTURE ON THE WEST COAST OF BAJA CALIFORNIA, MEXICO

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ABSTRACT

The community structure of pelagic copepods was obtained from 494 zooplankton samples collected on ten cruises made by CICIMAR in the northwest Mexican Pacific (31°N 118°W, 22°N 108°W) between 1984 and 1989. Of the 144 taxa identified, *Acartia danae* (temperate-tropical), *Calanus pacificus* (transitional), *Euchaeta marina* (tropical), and *Pleuromamma abdominalis* (tropical) were the most important species according to their frequency of occurrence, abundance, and contribution to total variance of the community. *C. pacificus* was dominant in almost every month sampled. The ratio of the abundance of this species to the other three decreased from north to south. The abundance of *A. danae*, *E. marina*, and *P. abdominalis* changed month by month and with latitude. The dominance of *C. pacificus* over the other species suggests resource partitioning favoring this species. The abundance of the two tropical species increased in summer and autumn, and that of the transitional species in winter and spring.

INTRODUCTION

Key species exploit a common resource in a similar way (Root 1967). Sometimes a single species is able to exploit most of the available resources. This means that the community structure depends on key species (Paine 1969) and that the dominant species controls the occurrence of other species. The number of species and their relative abundance is what community ecologists call species structure (McGowan and Miller 1980). An important aspect of a community species structure that seems highly variable is the constancy of the rank order of species abundance in time and space.

The rank order of plankton species changes dramatically from sample to sample, as McGowan and Miller (1980) showed in their paper on larval fish and zooplankton community structure in the California Current, as Hernández-Trujillo and Esquivel-Herrera (1997) showed for the copepod community along the west coast of Baja California, and as Palomares-García and Gómez-Gutiérrez (1996) showed for the copepod community at Bahía Magdalena on the southwest coast of Baja California Sur. Other studies of the abundance and species composition of zooplankton have shown that a few species dominate the whole community structure (Longhurst 1967, 1995; McGowan and Miller 1980; Weikert 1982; Palomares-García 1996). These small species groups become recurrent groups when they occur in the same sample more often than can be attributed to chance (Fager and McGowan 1963), which means there are common factors systematically influencing the occurrence of these groups.

The purpose of this paper is to identify the key species in the copepod community along the west coast of the Baja California peninsula between 1984 and 1989 by examining abundance, hierarchies, and the constancy of the frequency of occurrence of particular species.

METHODS

A total of 494 zooplankton samples was obtained on 10 oceanographic cruises made by the Centro Interdisciplinario de Ciencias Marinas (CICIMAR; fig. 1). The sampling protocol was taken from Smith and Richardson (1977): oblique tows of bongo nets equipped with digital flowmeters and mesh sizes of 333 and 505 μm were made. The adult copepods in the 505 μm net were sorted, identified, and counted with the method of Hernández-Trujillo (1991a). Sea-surface temperature (SST) data were collected at each station with an InterOcean CTD. Additional historical data were obtained from CD-ROM COAD (ORSTROM & NOAA). Cole and McLane (1989) divided the study area into three latitudinal blocks (21°–24°N, 24°–27°N, and 27°–30°N); I used their divisions.

I determined the key species by following three criteria: (1) occurrence in the cruises 100% of the time, (2) great abundance, and (3) contribution to total variance of the community according to principal components analysis (PCA). A two-way ANOVA was used to test for differences in the mean of key species abundance, phytoplankton abundance, SST variability among cruises and latitude, season, and latitude ($\alpha = 0.05$). The PCA

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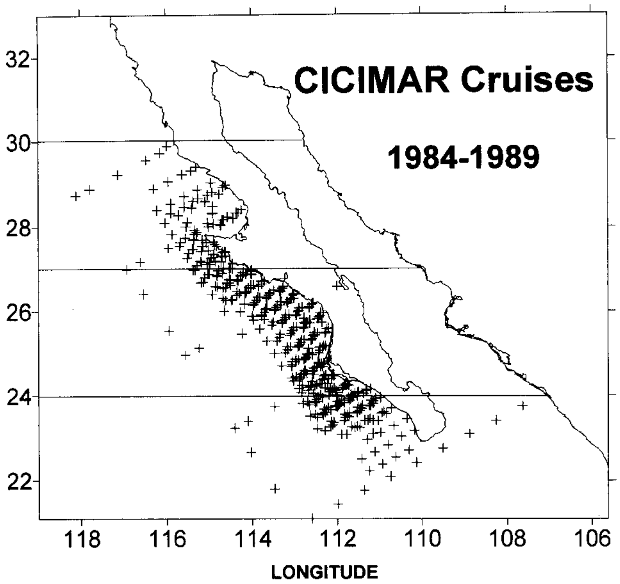

Figure 1. The CICIMAR station grid, 1984–89.

method was used to determine recurrent groups of the copepod species. I applied this analysis to a matrix with abundance values per sampling station after normalizing by log-transformation ($x + 1$).

Microphytoplankton (>20 µm, MF) and nannophytoplankton (5–20 µm, NF) data were from Hernández-Trujillo et al. (unpublished data). I analyzed the key species abundance with SST and phytoplankton (MF and NF) by season using regression of Pearson product-moment ($P < 0.05$) to indicate trends between variables and not to represent the functional forms of causal mechanisms (Mullin 1998).

RESULTS

A total of 144 copepod species was identified. From this assemblage 11 species (*Pleuromamma abdominalis*, *Euchaeta marina*, *Paracalanus parvus*, *Calanus pacificus*, *Pleuromamma gracilis*, *Rhincalanus nasutus*, *Labidocera acutifrons*, *Euchaeta longicornis*, *Acartia danae*, *Subeucalanus subcrassus*, and *Scolecithrix danae*) were found in every cruise. I found that 4 were dominant, and named them *key species*: *Acartia danae*, *Calanus pacificus*, *Euchaeta marina*, and *Pleuromamma abdominalis*. Their mean abundances by cruise are shown in table 1.

The relative abundance of *A. danae*, *C. pacificus*, *E. marina*, and *P. abdominalis* showed high variability during the period studied (table 2). Those changes can be seen in the changes of species rank within the community structure.

The ANOVA for *A. danae*, *E. marina*, and *P. abdominalis* shows significant differences by month ($P < 0.05$) but not for latitude factor ($P > 0.05$). The ANOVA for *C. pacificus* showed that H_0 was rejected for both month and latitude factor ($P < 0.05$; table 3).

Seasonally, the ANOVA (table 4) showed that *A. danae* abundance was not different by temporal and geographical factors ($P > 0.05$). The remaining key species showed

TABLE 1
Average Abundance (Org · 1,000 m^{-3}) of Copepod Key Species by Cruise on the West Coast of Baja California, 1984–89

Cruise number	8401	8405	8505	8508	8605	8611	8707	8710	8807	8906
Species (n_s)[a]	77	38	37	42	67	68	52	72	69	58
Acartia danae	705	9,719	1,420	118	503	48	4,954	474	279	252
Calanus pacificus	1,034	334,777	58,319	7,530	70,060	569	100,254	6,251	38,368	25,675
Euchaeta marina	1,325	1,402	324	825	354	1,023	345	1,786	757	339
Pleuromamma abdominalis	1,994	19,690	1,595	713	965	1,163	1,293	731	1,222	910

[a] n_s = number of species identified by cruise.

TABLE 2
Relative Abundance and Rank of Key Species in the Copepod Community by Cruise on the West Coast of Baja California, 1984–89

	Acartia danae		*Calanus pacificus*		*Euchaeta marina*		*Pleuromamma abdominalis*	
Cruise	Percentage	Rank	Percentage	Rank	Percentage	Rank	Percentage	Rank
8401	4.8	5	8.9	4	13.7	2	18.9	1
8405	1.4	5	85.8	1	<1.0	11	3.3	3
8505	1.7	5	81.5	1	<1.0	17	1.6	6
8508	<1.0	16	60.2	1	13.3	2	3.1	5
8605	<1.0	4	96.2	1	<1.0	7	<1.0	3
8611	<1.0	38	9.4	4	13.8	1	6.4	7
8707	3.3	2	92.7	1	<1.0	8	<1.0	5
8710	<1.0	25	36.2	1	8.7	3	2.5	8
8807	<1.0	11	84.5	1	1.2	4	2.0	3
8906	<1.0	15	88.2	1	<1.0	7	1.9	2

TABLE 3
Two-Way ANOVA of the Effect of Month and Latitude on the Variability of Key Species Abundance on the West Coast of Baja California, 1984–91

Source	*DF*	*MS*	*F*	*P*	H_0
Acartia danae					
Month	10	2.6E09	3.530	<0.05	Rejected
Latitude	2	1.6E07	0.225	>0.05	Accepted
Residual	194	75359057			
Total	206				
Calanus pacificus					
Month	10	5.6E11	8.007	<0.05	Rejected
Latitude	2	1.0E11	1.494	<0.05	Rejected
Residual	450	7.1E10			
Total	462				
Euchaeta marina					
Month	10	8359116	2.410	<0.05	Rejected
Latitude	2	41191	0.012	>0.05	Accepted
Residual	300	3468813			
Total	312				
Pleuromamma abdominalis					
Month	10	1.3E09	3.246	<0.05	Rejected
Latitude	2	3.8E08	0.949	>0.05	Accepted
Residual	287	4.4E08			
Total	299				

TABLE 4
Two-Way ANOVA of How Season and Latitude Affect the Variability of Key Species Abundance on the West Coast of Baja California, 1984–91

Source	*DF*	*MS*	*F*	*P*	H_0
Acartia danae					
Season	3	1.5E08	3.530	>0.05	Accepted
Latitude	2	9.4E06	0.225	>0.05	Accepted
Residual	201	83639810			
Total	206				
Calanus pacificus					
Season	3	6.0E11	7.760	<0.05	Rejected
Latitude	2	1.7E11	2.223	>0.05	Accepted
Residual	457	7.8E10			
Total	462				
Euchaeta marina					
Season	3	16012152	4.568	<0.05	Rejected
Latitude	2	173327	0.049	>0.05	Accepted
Residual	307	3505532			
Total	312				
Pleuromamma abdominalis					
Season	3	1.1E09	2.753	<0.05	Rejected
Latitude	2	4.6E08	1.076	>0.05	Accepted
Residual	294	4.3E08			
Total	299				

significant differences between season ($P < 0.05$) but not for latitude ($P > 0.05$).

The PCA shows the spatial representation of the abundance and the relation of copepod species with the first two principal components. For each cruise the variance of the two first components, obtained by the PCA applied to the matrix of copepod abundance, is shown in table 5.

The first component is identified with a set of variables that determines the differential abundance of each species; therefore all species have a positive correlation with this component. The groups are separated according to the density of the species that constitute them. The second component is identified with the SST, separating the species that have high abundance in warm or cold waters.

Figures 2 and 3 illustrate the dispersion diagram of the first two components for each cruise. The graphs have a point for each species, and the disposition of points spatially represents the relation between the abundance distributions of the species with respect to the first two components, which account for between 92% (August 1986) and 51% (November 1986) of the total variance.

The graphs show the key species position in bidimensional hyperspace according to their relative abundance and distribution. For almost all cruises, the key species position is separate from the other copepod species.

TABLE 5
Percent of Variance of First Two Principal Components (C1, C2), the Cumulative Percentage (Σ Variance), and Number of Samples by Cruise (*n*)

Cruise	C1	C2	Σ Variance	*n*
8401	47.02	9.75	56.78	47
8405	64.35	18.65	83.01	68
8505	74.13	7.98	82.11	38
8508	88.38	3.93	92.31	47
8605	87.16	4.67	91.83	61
8611	39.27	12.52	51.79	57
8707	86.26	5.61	91.87	39
8710	49.65	16.22	65.88	62
8807	44.55	23.39	67.94	37
8906	81.12	7.54	88.67	38

Figure 4 shows the seasonal relation between key species abundance and the SST for all 10 cruises over the 6 years. On the basis of linear regression, in winter, spring, and autumn (except for *E. marina*), the abundance of the key species was inversely related to SST. In autumn there was a positive relation of the key species and SST (table 6).

The abundance of copepod key species related to phytoplankton abundance (figs. 5 and 6) shows that in winter the greater abundance of key species was observed mainly in the microphytoplankton abundance range of 500 to 5,000 cell/L and for nannophytoplankton between 2,000 and 5,000 cell/L. In spring there was a wide range in copepod abundance (10 to 500,000 org/1,000 m^3) associated with microphytoplankton abundance between 100 and 25,000 cell/L. *Calanus pacificus* was clearly more abundant in comparison with the other key species. For nannophytoplankton, the highest copepod abundance was associated with 5,000 to 25,000 cell/L. Again, *C. pacificus* was more abundant than the other copepod species.

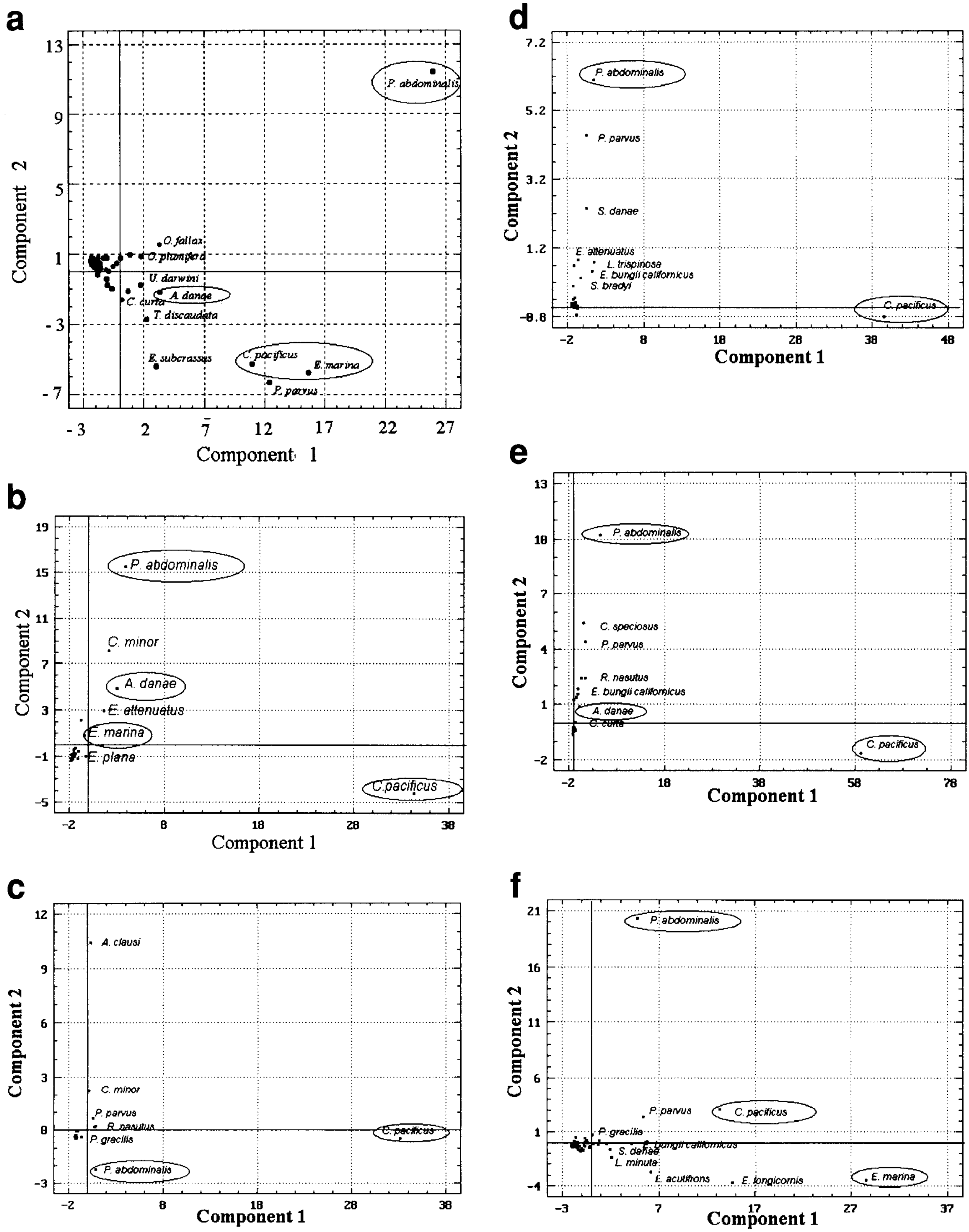

Figure 2. Dispersion diagrams of the two first principal components for cruises 8401 (*a*), 8405 (*b*), 8505 (*c*), 8508 (*d*), 8605 (*e*), and 8611 (*f*).

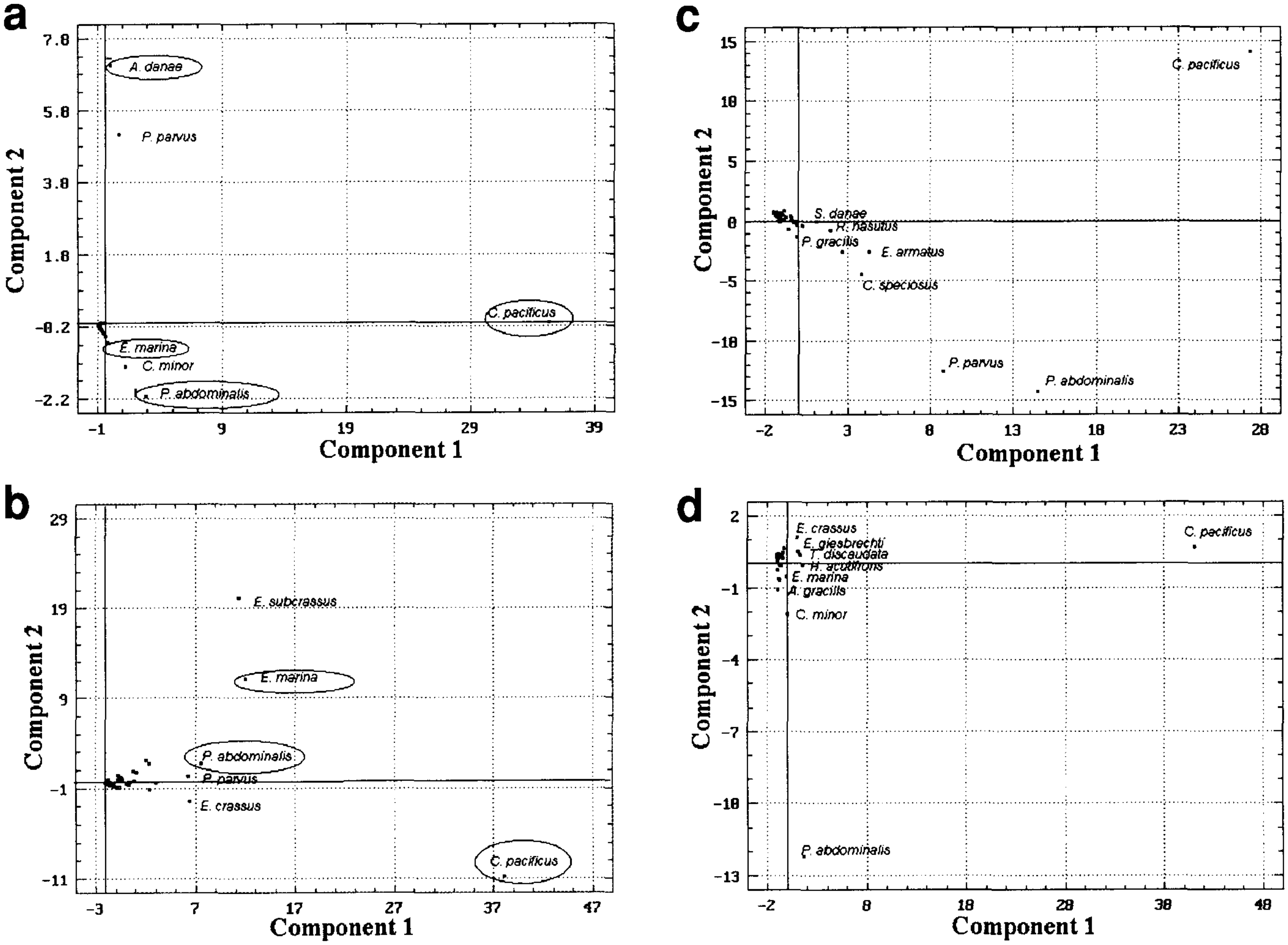

Figure 3. Dispersion diagram of the two first principal components for cruises 8707 (*a*), 8710 (*b*), 8807 (*c*), and 8906 (*d*).

In summer the key species abundance was similar to that in spring, and occurred with concentrations of microphytoplankton between 100 and $1 \cdot 10^6$ cell/L. For nannophytoplankton, abundance, as well as the key species, was similar to the microphytoplankton, but the main abundance of copepods occurred between 5,000 and 25,000 cell/L. For both phytoplankton size fractions, *C. pacificus* was the dominant species.

In autumn the abundance of copepods decreased to 10–25,000 org./1,000 m^3 and occurred at concentrations of microphytoplankton between 125 and 5,000 cell/L. For nannophytoplankton, the larger key species abundance was observed in the range of 5,000 and 60,000 cell/L. For both size fractions, the key species abundance was similar, without dominance of any one species.

The linear regression of the abundance of key species and MF showed an inverse relation for all species in winter, and a positive relation in the other seasons. For NF, a similar situation was observed for winter but not for the other seasons, in which there were negative correlations for *A. danae* in summer and autumn, and for *P. abdominalis* in autumn (tables 7 and 8).

TABLE 6
Product-Moment Correlation between Copepod Key Species and SST on the West Coast of Baja California, 1984–89

	Algebraic formula	*r*	r^2	*N*
Winter				
A. danae	$Y = 10.3 - 0.240x + eps$	**−0.25**	0.07	32
C. pacificus	$Y = 14.1 - 0.410x + eps$	**−0.44**	0.19	40
E. marina	$Y = 13.3 - 0.360x + eps$	**−0.32**	0.11	47
P. abdominalis	$Y = 14.5 - 0.430x + eps$	**−0.42**	0.18	42
Spring				
A. danae	$Y = 9.6 - 0.177x + eps$	−0.15	0.02	97
C. pacificus	$Y = 11.7 - 0.122x + eps$	−0.10	0.01	207
E. marina	$Y = 7.0 - 0.084x + eps$	−0.08	0	73
P. abdominalis	$Y = 8.6 - 0.105x + eps$	−0.09	0	126
Summer				
A. danae	$Y = 10.4 - 0.233x + eps$	**−0.38**	0.14	57
C. pacificus	$Y = 15.8 - 0.322x + eps$	**−0.43**	0.18	112
E. marina	$Y = 2.6 + 0.108x + eps$	0.20	0.04	77
P. abdominalis	$Y = 6.8 - 0.030x + eps$	−0.06	0	69
Autumn				
A. danae	$Y = 16.3 + 0.885x + eps$	**0.83**	0.69	17
C. pacificus	$Y = 1.9 + 0.20x + eps$	**0.25**	0.06	89
E. marina	$Y = 0.5 + 0.237x + eps$	**0.40**	0.16	98
P. abdominalis	$Y = 5.9 + 0.009x + eps$	0.01	0	56

Note: Bold type indicates significant ($P < 0.05$).

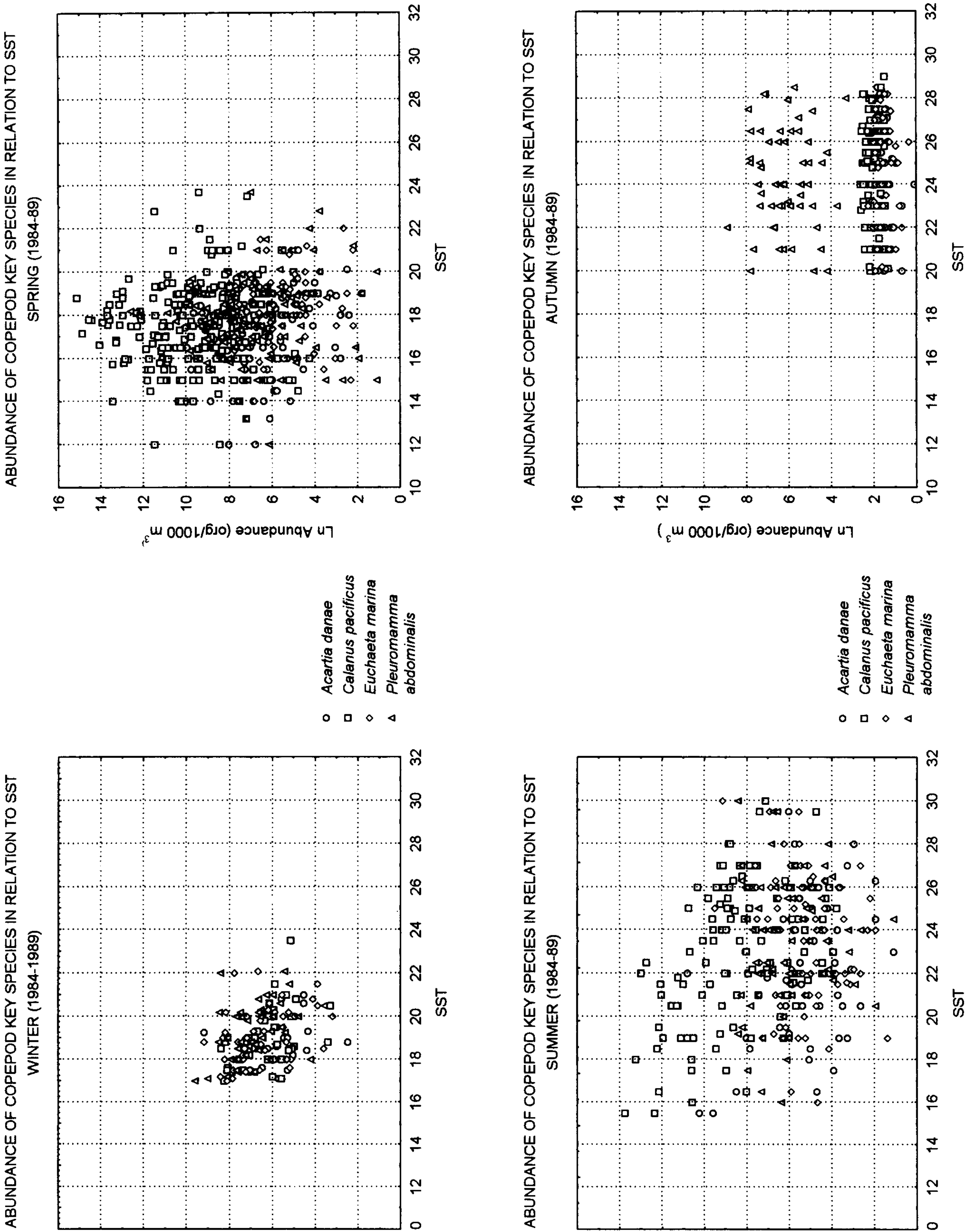

Figure 4. Seasonal relation between abundance of the copepod key species and the sea-surface temperature (SST).

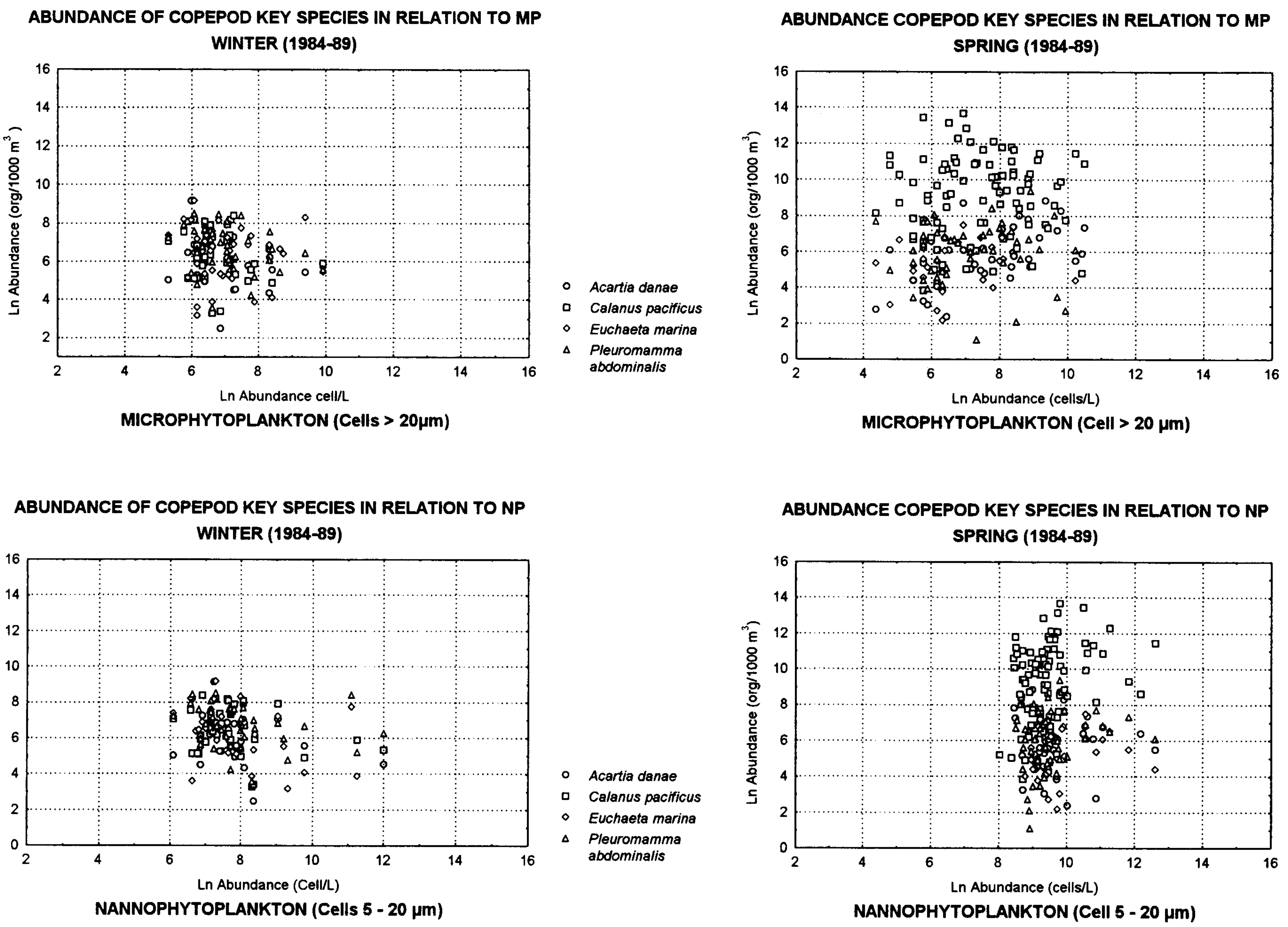

Figure 5. Winter and spring relation between abundance of the copepod key species and the abundance of micro- and nannophytoplankton.

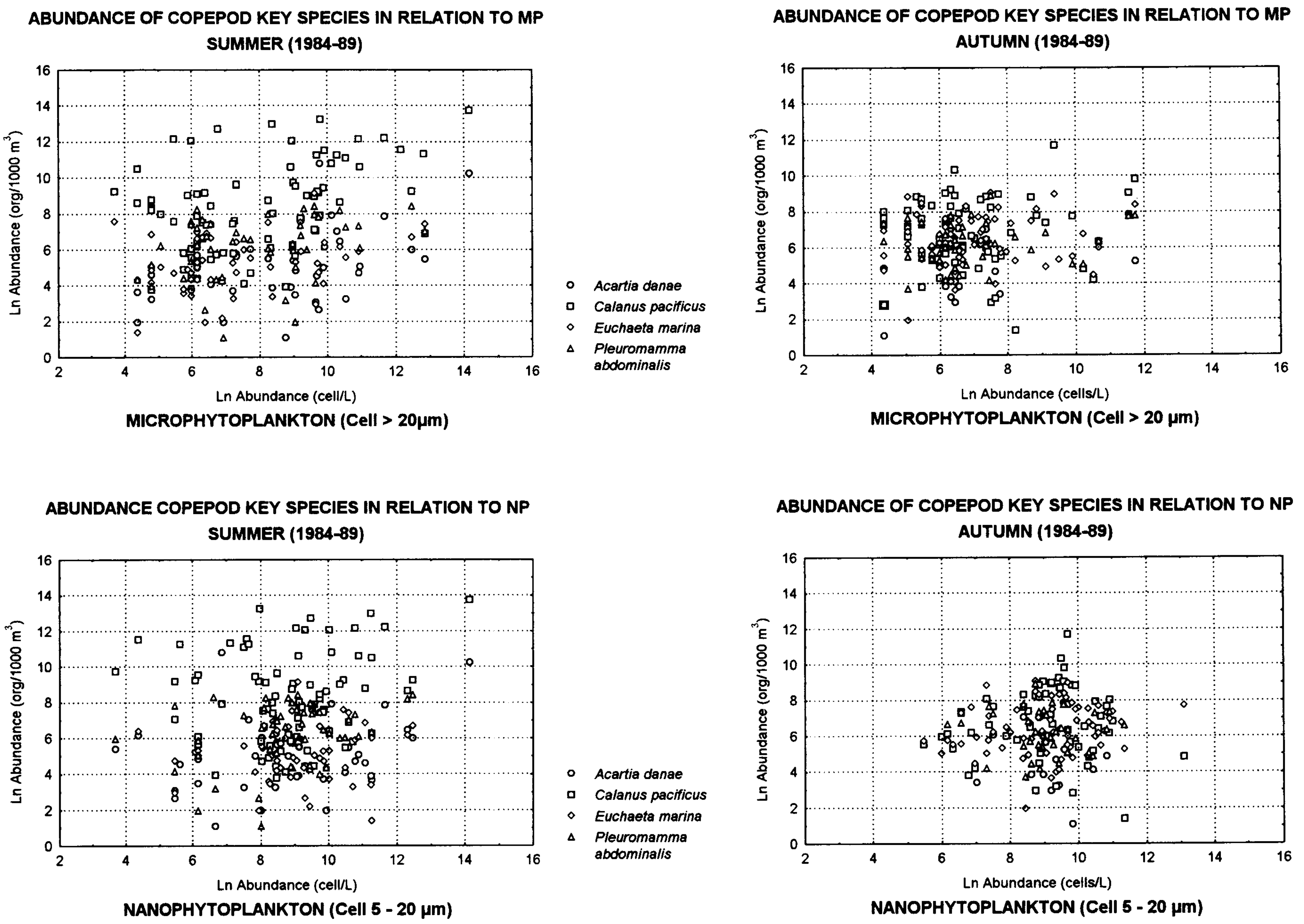

Figure 6. Summer and autumn relation between abundance of the copepod key species and the abundance of micro- and nannophytoplankton.

TABLE 7

Product-Moment Correlation between Copepod Key Species and Microphytoplankton on the West Coast of Baja California, 1984–89

	Algebraic formula	r	r^2	N
Winter				
A. danae	$Y = 7.1 - 0.179x + \mathit{eps}$	−0.15	0.02	30
C. pacificus	$Y = 7.9 - 0.224x + \mathit{eps}$	−0.15	0.02	35
E. marina	$Y = 6.6 - 0.054x + \mathit{eps}$	−0.03	0.01	42
P. abdominalis	$Y = 8.9 - 0.322x + \mathit{eps}$	−0.27	0.07	37
Spring				
A. danae	$Y = 1.7 + 0.538x + \mathit{eps}$	0.54	0.30	43
C. pacificus	$Y = 8.5 + 0.079x + \mathit{eps}$	0.05	0	88
E. marina	$Y = 4.1 + 0.143x + \mathit{eps}$	0.13	0.01	26
P. abdominalis	$Y = 5.8 + 0.006x + \mathit{eps}$	0	0	47
Summer				
A. danae	$Y = 1.9 + 0.367x + \mathit{eps}$	**0.42**	0.18	38
C. pacificus	$Y = 4.6 + 0.465x + \mathit{eps}$	**0.42**	0.17	77
E. marina	$Y = 3.5 + 0.227x + \mathit{eps}$	**0.31**	0.09	53
P. abdominalis	$Y = 4.4 + 0.222x + \mathit{eps}$	0.25	0.06	47
Autumn				
A. danae	$Y = 1.9 + 0.398x + \mathit{eps}$	0.46	0.21	15
C. pacificus	$Y = 6.1 + 0.094x + \mathit{eps}$	0.08	0	62
E. marina	$Y = 5.7 + 0.092x + \mathit{eps}$	0.10	0	72
P. abdominalis	$Y = 5.5 + 0.094x + \mathit{eps}$	0.14	0.02	40

Note: Bold type indicates significant ($P < 0.05$).

TABLE 8

Product-Moment Correlation between Copepod Key Species and Nannophytoplankton on the West Coast of Baja California, 1984–89

	Algebraic formula	r	r^2	N
Winter				
A. danae	$Y = 7.4 - 0.211x + \mathit{eps}$	−0.18	0.03	30
C. pacificus	$Y = 8.3 - 0.256x + \mathit{eps}$	−0.23	0.05	35
E. marina	$Y = 9.5 - 0.42x + \mathit{eps}$	**−0.32**	0.10	42
P. abdominalis	$Y = 8.3 - 0.204x + \mathit{eps}$	−0.22	0.05	37
Spring				
A. danae	$Y = 1.7 + 0.538x + \mathit{eps}$	−0.01	0	44
C. pacificus	$Y = 8.5 + 0.079x + \mathit{eps}$	**0.27**	0.07	88
E. marina	$Y = 4.1 + 0.143x + \mathit{eps}$	0.18	0.03	26
P. abdominalis	$Y = 5.8 + 0.006x + \mathit{eps}$	0.22	0.04	46
Summer				
A. danae	$Y = 3.0 + 0.234x + \mathit{eps}$	0.26	0.07	39
C. pacificus	$Y = 6.9 + 0.154x + \mathit{eps}$	0.10	0.01	79
E. marina	$Y = 4.6 + 0.062x + \mathit{eps}$	0.06	0	54
P. abdominalis	$Y = 3.6 + 0.296x + \mathit{eps}$	**0.29**	0.08	48
Autumn				
A. danae	$Y = 6.9 - 0.246x + \mathit{eps}$	−0.13	0.01	15
C. pacificus	$Y = 6.3 + 0.054x + \mathit{eps}$	0.04	0	62
E. marina	$Y = 4.8 + 0.167x + \mathit{eps}$	0.17	0.03	72
P. abdominalis	$Y = 6.3 - 0.017x + \mathit{eps}$	−0.01	0	40

Note: Bold type indicates significant ($P < 0.05$).

DISCUSSION

During the period studied in central and southern Baja California, a large proportion of the variability in the abundance of the copepod community was attributed to the 11 most frequent species, and more particularly to the named key species. These species never disappeared from the studied area; on the contrary, their abundance exhibited an important fraction of the total copepod community.

Calanus pacificus has been characterized as a transitional species of oceanic and subsurface distribution (Fleminger 1967). They occur, and are abundant, along the California and Baja California coasts. This holds true in the present study for the central and southern Baja California areas. The copepods *A. danae* (temperate-tropical species of wide north-south and inshore-offshore distribution), and *P. abdominalis* (tropical species, oceanic and epipelagic distribution) have been characterized as the most frequent species between central California and southern Baja California (Fleminger 1964; Bowman and Johnson 1973). The copepod *E. marina* (tropical-subtropical species, oceanic and subsurface distribution) has also been found in the study area, where it is less abundant than the other three copepod species.

In the study area *A. danae*, *E. marina*, and *P. abdominalis* predominated in the copepod community, had similar abundances, and showed changes of rank, month to month and by latitude. The latitudinal monthly abundance differences found for three key species mean that the change of the dominant species was affected by the season of sampling and not by the geographic position of the sampling stations.

The assemblage reflects the complexity of the copepod community in the area studied, as well as its structural dynamics. The three key species maintained their abundance below that of *C. pacificus* during the study period (except for summer) in each of the latitudinal blocks. For *C. pacificus*, I found spatial and temporal abundance heterogeneity in the study area. The dominance of *C. pacificus* over the remaining key species was shown in time and space. Its abundance was higher in the north, decreasing to the south. However, the seasonal pattern differed because *A. danae* abundance did not differ over time or space, and the remaining key species had temporal, but not geographic differences.

Temperature was found to be significant for all copepods. The type of correlation, either positive or negative, relies on the species' ecological habits: for tropical-subtropical species, maxima occurred during the warm period, and for the transitional species during cold periods. The PCA also suggests that the first component was temperature, influencing the variation of abundance and geographical distribution of the copepods. The abundance of key species related to the SST shows this effect. The habitat of the key species was another factor contributing to the species assemblages. Colebrook (1977) found similar results for the copepods in the California Current system in 1955–59.

The variance of the first factor obtained by PCA in each cruise shows that the variability of the abundance of copepod species in the Baja California peninsula area is linked to the structure of the environment, as Dessier and Donguy (1987) showed for epiplanktonic copepods in the eastern tropical Pacific. The greatest abundance of *C. pacificus* along the west coast of Baja California coincides with the strongest equatorward surface flow of the California Current, March through May, and their lowest abundance with an equally strong poleward flow, July through September (Lynn and Simpson 1987; Parés et al. 1997). The SST had an important effect on the seasonal spatial distribution and abundance of the key species, because in each season they were limited to waters in a specific temperature range.

The observed relations of micro- and nannophytoplankton with the fluctuations in copepod abundance probably reflect changes in the hydrological regime of the area. The abundance of micro- and nannophytoplankton showed a negative correlation with the abundance of all key species in winter; this could indicate that in the studied area the copepods showed some preference for food other than phytoplankton. For the remaining seasons the abundance of phytoplankton showed positive relations with almost all copepod abundances, especially for *C. pacificus.*

The importance of the seasonal phytoplankton abundance differed for each key species over the study period, especially for *C. pacificus*, whose abundance was higher than the other copepod species at low and high concentrations of cells (except in winter for both MF and NF fraction size). The relation between the abundance of the key species and the phytoplankton suggests that resource distributions and niches were slanted to *C. pacificus* to maintain high abundance levels for almost all concentrations of phytoplankton recorded, according to Hernández-Trujillo (1991b) and Mullin (1991, 1994, 1995).

Other oceanographic variables could be expected to influence the variability of abundance of the copepods in the study area. One is the warming and cooling by El Niño and La Niña episodes in the eastern Pacific, which affect the fauna and flora of the study area (Palomares-García and Gómez-Gutiérrez 1996; Hernández-Trujillo and Esquivel-Herrera 1997; Gárate-Lizárraga and Siqueiros-Beltrones 1998). In addition, more observations on the copepod community structure have to be made to demonstrate whether the key species extracted really represent the most important species.

To explore the functional relation between copepod species and environmental factors, we need a complete and continuous data set. The data indicated, at least during the period studied, that an important proportion of the variability of copepod abundance, represented by the 4 key species, can be associated with SST and phytoplankton abundance, both associated with the strength of the California Current.

CONCLUSIONS

Acartia danae, *Calanus pacificus*, *Euchaeta marina*, and *Pleuromamma abdominalis* were the key copepod species in the 1984–89 period. The dominance of *C. pacificus* in comparison to the other key species was the most important feature of the copepod community. The variability of the key species abundance was dependent on the SST and the phytoplankton abundance. The warm and cool episodes should be isolated to get the *normal* pattern of variation of the key species. The variability of distribution and abundance of *C. pacificus* suggests extensive resource partitioning along the west coast of the Baja California peninsula.

ACKNOWLEDGMENTS

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VARIATION IN FAT CONTENT OF NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) IN RELATION TO THE BAJA CALIFORNIA ENVIRONMENT

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ABSTRACT

Anchovy landings from Baja California were sampled from 1981 through 1988. Data on fat content are compared with annual series of sea-surface temperature, an upwelling index, and biomass and capture data. In the eight-year period an increasing trend in the fat content was observed, along with a minimum in 1983, possibly associated with El Niño. There is a seasonal pattern in fat content, with maximum values during summer months and minimum values in winter.

INTRODUCTION

Along the western coast of Baja California, a group of fishes known as small pelagics is commercially exploited. This group consists of two species of clupeids: the northern anchovy (*Engraulis mordax* Girard) and the Pacific sardine (*Sardinops sagax* Jenyns); one carangid: the jack mackerel (*Trachurus symmetricus* Ayres); and two scombrids: the Pacific mackerel (*Scomber japonicus* Houttuyn) and the Pacific bonito (*Sarda chiliensis* Cuvier). These species are captured near the coast (generally as far out as twenty nautical miles) by purse seine boats. Historically, the northern anchovy has been the most exploited species in Baja California. Pedrín-Osuna et al. (1992), García-Franco et al. (1995), and Vidal-Talamantes (1995) have described various aspects of the fishery, including exploitation rates, catch by species and by zones, virtual population analysis, fishing effort, and catch composition.

The mechanisms explaining how climate affects the populations of small pelagic fishes are based on the cyclic processes of warming and cooling of the seawater masses, which cause important changes in the distribution, abundance, and availability of these marine resources (Lluch-Belda et al. 1989).

The drastic changes experienced by these small pelagic fishes during the present century, such as the alternating dominance of the anchovy and sardine, undoubtedly have been caused by climate as well as fishing. Even so, there is no consensus on the impact or the influence of each of these two components (García-Franco et al. 1995).

Metabolic processes regulate the intake and outflow of materials and energy. Organisms use part of the energy obtained by feeding for basic functioning; another part is stored in the body in the form of fat and other compounds. The fat content of fish is an indicator of their degree of success in locating, ingesting, and assimilating food. The biochemical composition of fishes can vary with age, sex, and season of the year.

According to Cowey and Sargent (1979), fishes use lipids as a source of energy and for maintaining the structure of cell membranes. Unlike the fat of terrestrial animals, the oils of marine animals are rich in fat-soluble vitamins and unsaturated fatty acids. The presence of great quantities of oil in marine fishes means that lipids, instead of carbohydrates, are the main energy reserve of these organisms.

The dynamics of fat content and the condition of the fishes are related to the linear growth of the individual. The fat content may be used as an indicator of the condition of the organism. During the first stages in the development of fish, before maturity, the food resources incorporated in the organism are used mainly for growth. In the following stage of the life cycle, linear growth is less important, so most of the energetic resources are used for developing the gonads and accumulating reserve material to sustain metabolism during periods without feeding, such as during migration (Nikolsky 1963).

It is possible to predict changes in abundance from the accumulation of fat in marine organisms. Fat reserves constitute an energy source that determines the reproductive behavior of the population. This fat concentration means that the intensity and duration of spawning depends, to a certain degree, on the fat reserves of the population.

The objective of this study is to explore the association between the fat content determined in the anchovy

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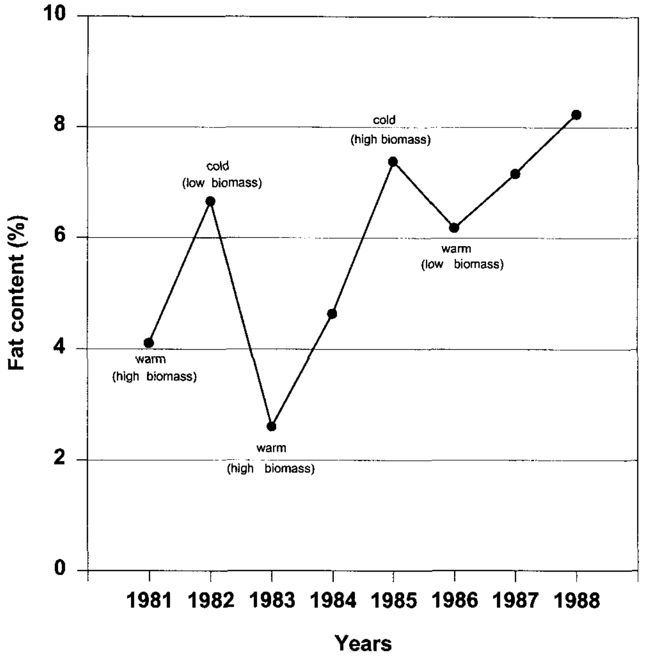

Figure 1. Annual variation of the fat content (%) of the northern anchovy in Baja California, 1981–88.

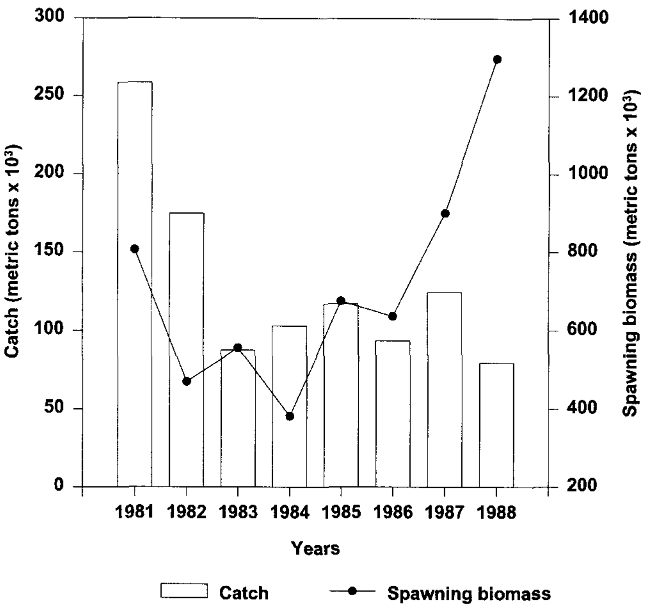

Figure 2. Annual variation of the catch (thousands of metric tons) and spawning biomass estimates (thousands of metric tons).

and other factors such as sea temperature, upwelling indexes, and anchovy biomass.

MATERIALS AND METHODS

The fat content of the anchovy was determined by extraction of the fatty compounds. We used methods 7.044 and 7.016 described in "The Official Methods of Analysis of the Association of the Official Analytical Chemist." We placed a dry sample in a cellulose cartridge by means of the Soxhlet extraction apparatus, which comprises a matrix, a refrigerant in reflux, a collector, and an electric heater. We added 100 ml of petroleum ether to the matrix to dissolve the fatty substances of the sample inside the cartridge and then heated it for 4 to 8 hours to evaporate the ether (Sidney 1984).

Subsequently, the matrix was disconnected from the equipment, and the ether was completely evaporated. We then heated the sample at 100°C until it attained a constant weight. We calculated the average weight by sample and related it to the daily catch. Finally, we calculated the monthly and annual averages.

The total sample consisted of 2,400 kg of adult anchovy, collected from 1981 to 1988. Each year we took random samples directly from holds of the commercial fleet—one kg daily from April to November (these were the months in which samples were in adequate condition on a regular basis).

Temperature data and upwelling indexes were obtained from the Northwest Biological Research Center (Centro de Investigaciones Biológicas del Noroeste S.C. CIBNOR) in La Paz, Baja California Sur.

We based our biomass evaluations on the stock synthesis model (Methot 1989; Jacobson and Lo 1990), which estimates the spawning biomass. This model is age-structured and parameterized so that the predicted values (relative abundance indexes and age composition of the catches) agree with the available data.

RESULTS

Interannual Variation

Figure 1 presents the annual variation of the fat content in wet weight of the anchovies captured in Baja California from 1981 to 1988. The general trend of the series is increasing. The maximum value was obtained in 1988 (8.24%), the minimum in 1983 (2.61%). Values greater than 5% were observed in 1982 and from 1985 to 1988.

The series of annual catch of anchovy in Baja California (fig. 2) shows a maximum value (258,000 t) in 1981 and notable drops in 1982 and 1983. From 1983 to 1988 the catch showed minor fluctuations around the 100,000 t value. The minimum catch (79,000 t) was made in 1988.

The series of spawning biomass for the anchovy in the California Current from 1981 to 1988 shows a downward trend from 1981 to 1984, but a rise from 1985 to 1988 (fig. 2). During 1981–86, relatively low values (less than 900,000 t) were estimated. In 1987 and 1988 the biomass rose to a maximum of 1,297,000 metric tons.

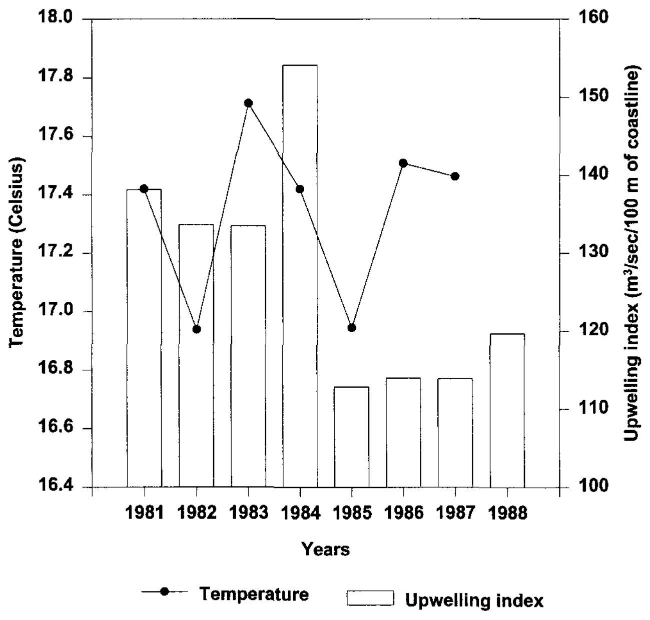

Figure 3. Annual variation of the sea-surface temperature and upwelling indexes (m^3/sec./100 m of coastline) along Baja California.

The sea-surface temperature off the west coast of Baja California (fig. 3) had an annual average value of 17.3°C. The maximum temperature in the series (17.7°C) occurred in 1983. In 1984 the temperature returned to a normal level (near 17.5°C), as it did in 1981, 1986, and 1987. The minimum values were obtained in 1982 (16.94°C) and 1985 (16.95°C).

The annual index of upwelling off Baja California (fig. 3) presented values near 135 m^3/sec./100 m of coastline during 1981–83. In 1984 it rose to a maximum of 154 m^3/sec./100 m; decreased the next year, and from 1985 to 1988 maintained a level between 110 and 120 m^3/sec./100 m.

Monthly Variation

The monthly values of fat content (fig. 4) displayed a bell-shaped pattern repeated annually, with maximums in the months from June to September. In 1981 and 1982 the maximum was observed in September. In 1983 the maximum occurred in August, although fat percentage did not increase from September to November, as it had in the two preceding years. Fat content increased in 1984 and 1985, when maximum values were reached in September and July. Relatively high values were observed from June to October during 1985–88. The maximum value for the complete series was reached in July 1988 (13.6%).

There was a regular and well-defined seasonal pattern in the monthly temperature series (fig. 4). As expected, high values were observed in summer and low values in winter. The highest values occurred in 1983 and 1984.

TABLE 1
Monthly Averages of Fat Content (%) in the Northern Anchovy, 1981–1988

Months	Average	SD	Max.	Min.	CV
April	2.26	0.86	4.20	1.40	0.38
May	3.34	1.56	5.90	1.60	0.46
June	6.63	2.94	11.00	2.50	0.44
July	8.09	3.41	13.60	3.00	0.42
August	7.81	2.19	10.60	4.70	0.28
September	7.60	2.41	11.00	3.00	0.32
October	6.31	2.49	9.90	2.10	0.39
November	4.85	2.27	8.60	1.90	0.47

TABLE 2
Monthly Average Values of Sea-Surface Temperature (Celsius) in Baja California, 1981–1988

Months	Average	SD	Max.	Min.	CV
January	15.75	0.64	16.43	14.85	0.04
February	15.60	0.42	16.15	15.04	0.03
March	15.50	0.51	16.20	14.43	0.03
April	15.89	0.42	16.55	15.31	0.03
May	16.16	0.21	16.47	15.81	0.01
June	16.93	0.57	17.71	15.95	0.03
July	18.27	0.52	18.80	17.06	0.03
August	19.43	0.73	20.77	18.23	0.04
September	20.09	0.68	21.28	19.44	0.03
October	19.34	0.61	20.39	18.56	0.03
November	18.08	0.48	18.80	17.39	0.03
December	16.81	0.49	17.36	16.06	0.03

Table 1 shows the monthly series of the average fat content from 1981 to 1988. Standard deviation, maximum and minimum values, and coefficients of variation are included for each month. Table 2 shows the monthly average temperature (1981–88) and the corresponding standard deviation.

DISCUSSION

The clupeid fish are seasonal feeders, storing great fat reserves for maintenance when food is scarce. Food consumption is the main factor determining fat reserves. The spring and autumn plankton peaks provide food, and their utilization by fish depend to a large extent on the condition of the gonads. Fish with well-developed gonads feed only lightly (Blaxter and Holliday 1963). These fishes have more fat in their tissues after the vernal plankton pulses than after spawning, the time of their leanest condition (Lagler et al. 1977). Lovern (1951) demonstrated that the fats stored in the herring are almost identical with those of their copepod prey.

The annual series of fat content for the anchovy during 1981–88 (fig.1) shows an ascending trend, similar to that of the biomass series (fig. 2). By contrast, the catch series trends downward.

Vidal-Talamantes (1995) and Pedrín-Osuna et al. (1992) have shown that anchovies caught by the com-

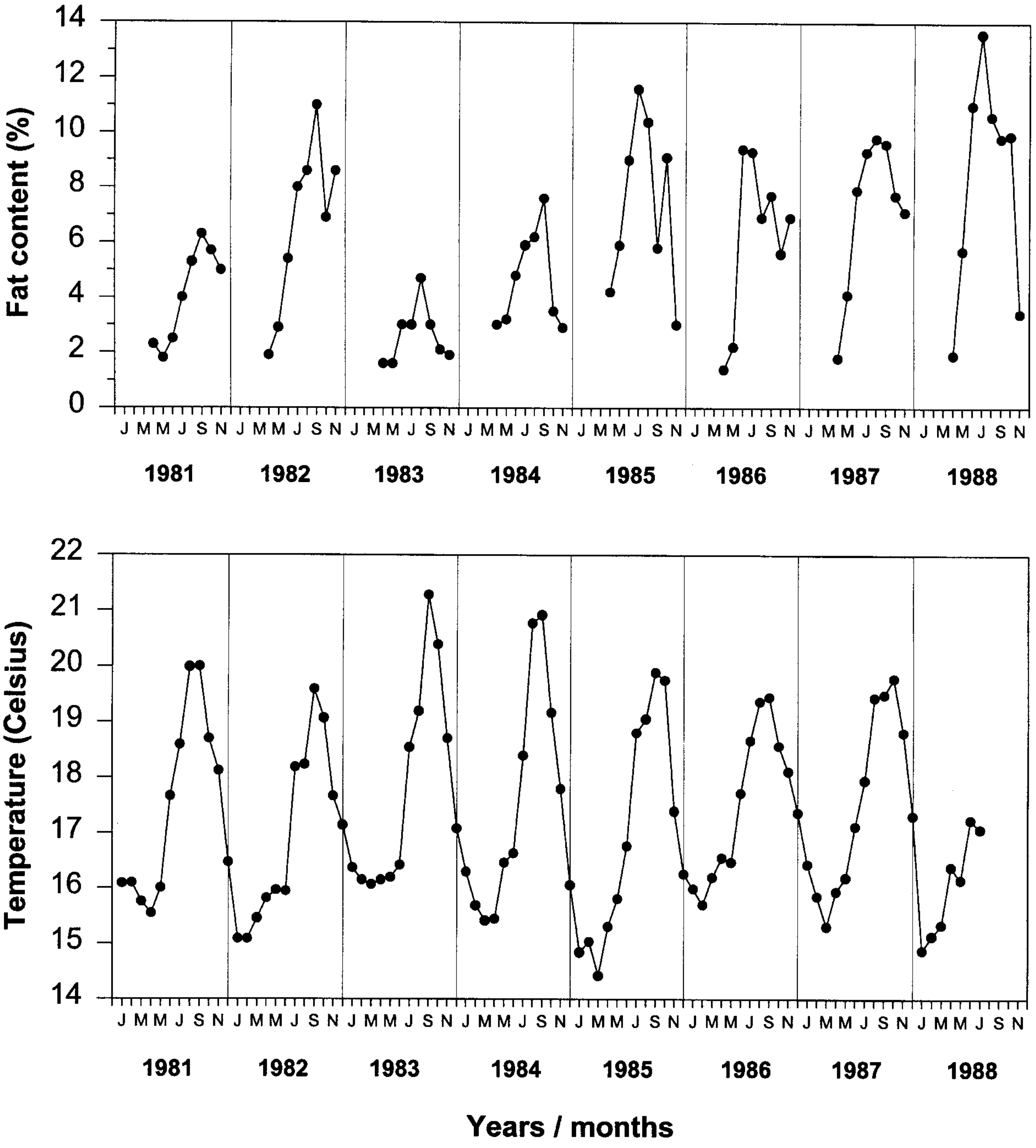

Figure 4. Monthly variations of fat percentage in the northern anchovy, and the sea-surface temperature.

mercial fleet during 1981 were mainly small-sized recruits of ages 0 and 1. The low fat content (4.2%) during 1981 (fig. 1) can be related to the small size of the individuals. The increased fat content in 1982 coincides with increased individual size (Vidal-Talamantes 1995).

There is a strong dependence between fat content and sea-surface temperature (figs. 1, 4, and 5): the warm months correspond to high fat content, cold months to low fat content. However, the yearly pattern is the opposite. The high temperatures in 1983 and 1984 (figs. 3 and 4) correspond with the 1982–84 El Niño, whose effects on the sea-surface temperature were evident in the region in 1983 (Fiedler et al. 1986). Thus the low values of fat content for 1983 may be related to the effects of El Niño. According to Vidal-Talamantes (1995), very small individuals were captured in 1983 and 1984.

The relation between biomass and temperature is not as consistent as that between fat content and sea-surface temperature. The maximum value of fat content (8.24%) was obtained in 1988, and this value coincides

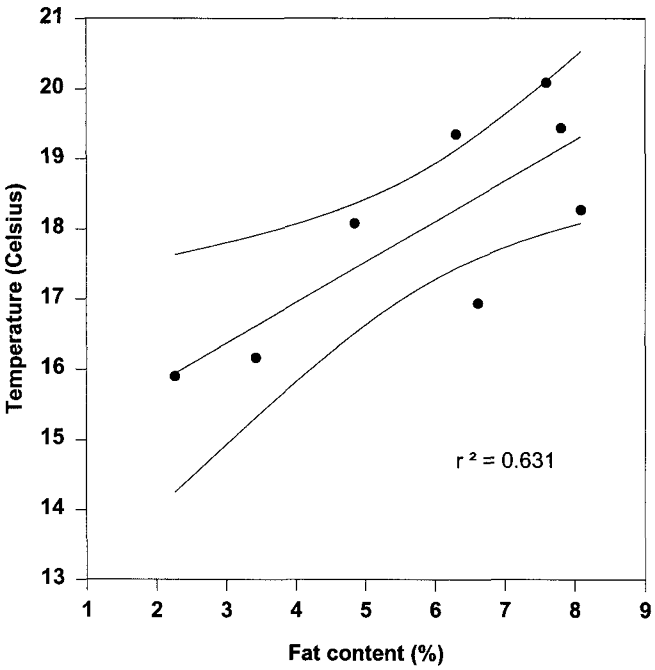

Figure 5. Relation between fat content (%) and sea-surface temperature. The points are averages for each of the eight months analyzed (April to November) for the 1981–88 period.

with the maximum biomass, the minimum catch, and a high percentage of recruits in the catch (Pedrín-Osuna et al. 1992). Perhaps the recruits did not have to compete with older individuals and thus were able to consume a greater quantity of food, accumulating more fat in their bodies. A high survival rate of the new annual class could increase the biomass of the population.

The monthly series of fat content showed a marked seasonal pattern, with higher values in the warmer months. It must be noted that the data available on fat content correspond only to eight months each year (April to November). From December to March the fat content may have been low, similar to that observed in April. The greater percentages of fat content during the warm months of summer (fig. 4 and table 1) coincide with the stronger upwelling—greater than 100 m^3/sec./100 m of coastline. Strong upwelling, producing high quantities of food for anchovy, may contribute to the accumulation of fat reserves.

When comparing the annual series of fat percentage with the biomass series (figs. 1 and 2) we note an interesting fact: A year with a low fat index was followed by a year in which the population showed a low level of abundance, as in 1981 and 1982. When the fat content was high, the biomass in the following year was high, as in 1982 and 1983. In 1983 the fat index was low, and the next year the population decreased. From 1985 to 1988 the fat content as well as the biomass were high. As in other animals, fat content in the northern anchovy represents stored energy for reproduction and survival. When fat content is low, reproductive capacity is drastically affected, because the available energy must be used mainly for survival.

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BIOECONOMICS OF THE PACIFIC SARDINE (*SARDINOPS SAGAX*) FISHERY IN THE GULF OF CALIFORNIA, MEXICO

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ABSTRACT

A bioeconomic model integrating biological and economic factors is developed for the Pacific sardine fishery in the Gulf of California. The model factors in the dynamics of the population structure and applies the basic concepts of the cohort-survival method. Seasonal recruitment was modeled with the distributed-delay method. The dynamics of the fleet were modeled by Smith's function with distributed delays to represent time lags in entry-exit processes. Performance variables such as biomass, fishery yield, effort, and net returns offered robust valuations of the behavior over time, showing a resource overexploited and a fishery fleet overcapitalized. The maximum economic yield and bioeconomic equilibrium of the fishery were also obtained. Of the alternative management strategies considered, minimum size of capture was most successful, offering important increases in the bioeconomic variables.

INTRODUCTION

The small pelagic fishery in the Gulf of California is one of the most important in terms of amount harvested and income generated. This fishery is based on a variety of different taxonomic groups, which include the Pacific sardine (*Sardinops sagax*, Jenyns, 1842; Parrish et al. 1989); the thread herring, including three species (*Opisthonema libertate*, *O. medirastre*, and *O. bulleri*); mackerel (*Scomber japonicus*); round herring (*Etrumeus teres*); "bocona" (*Cetengraulis mysticetus*); and northern anchovy (*Engraulis mordax*). Of these, the Pacific sardine catch is the largest. Its main landing port is Guaymas, Sonora, where Mexico's most important fish-processing plants are found. Fish meal constitutes 85% of the processing plants' production (Cisneros et al. 1988). Fish processing, as well as the fishery itself, is of major importance for the Mexican economy, as it provides work for a considerable number of people. In addition, the industry produces inexpensive food for large sections of the population.

The marine fisheries generally are characterized by overexploitation of the resource and an overcapitalization of the fishing industry. The management policy, known as open access, is characterized by (1) unrestricted access to the resource for all who have an interest in its use, and (2) adverse interactions among the users of the ecosystem. Overexploitation of a resource and the overcapitalization of the industry can cause important economic losses, especially in highly productive fisheries.

Regulating a fishery by considering only the maximum sustainable yield can be inadequate because it uses only biological criteria. To represent effort dynamics, one must consider additional criteria, such as the cost of fishing and the corresponding fleet benefits. It is appropriate to consider how different management strategies may affect capture, biomass, incomes of artisanal and industrial fishers, direct employment, and foreign exchange earnings. Dynamic bioeconomic modeling is a robust approximation for exploring a large number of management strategies of renewable marine resources (Seijo 1986; Seijo et al. 1997).

Until now, studies of the Pacific sardine have concentrated on biological factors, with no consideration of the economic aspects that determine its exploitation level over time. The purpose of this study is to analyze the Pacific sardine fishery with a dynamic stochastic and nonlinear model that integrates biological and economic factors. In addition, the bioeconomic effects of alternative management strategies are discussed.

METHODS

Bioeconomic Data Set

The biological, statistical, and behavioral data of the fishery were obtained from logbooks of the sardine fishing vessels, and from samples taken during off-loading in port. The required data were catch composition, fishing effort, and seasonal length-frequency distribution, all derived from commercial harvest for the period from 1972 to 1990. The information on costs and benefits of the fishing fleet was obtained by direct interview with fishermen and vessel owners.

The parameters used in the von Bertalanffy growth equation are those of natural fishing and fishing mortality, the population structure, the catchability coefficient, and the function that describes recruitment of individuals to the Pacific sardine population. Environmental variability effects on recruitment were incorporated by

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[Manuscript received 15 October 1997.]

using functions reported by De Anda et al. (1994). In addition, an analysis was made to estimate costs and benefits for the fishing fleet. All this information was incorporated into the simulation model.

Mathematical Model

The dynamics of the population structure of the Pacific sardine were modeled by applying basic concepts of the method of survival of cohorts (Gulland 1965; Pope 1972). This model is based on the dynamic accounting of the input and output of individuals to each cohort of the population. For a set of initial conditions $[N_K(0)]$, the structure of the population is estimated in a dynamic form by the expression

$$N_K(t + DT) = N_K(t) + \int_t^{t+DT}[S_{K-1}(t) \cdot N_{K-1}(t) - N_K(t)]dt \tag{1}$$

given N_K at time 0 and where

$N_K(t)$ = number of individuals of age K at time t;

$S_{K-1}(t) = 1- \{1\text{-exp} - [FM_K(t) + M]\}$; i.e., the survival rate of individuals of age K-1 in time t;

$FM_K(t)$ = mortality by fishing of age K at time t;

M = natural mortality coefficient;

DT = time increment.

Integrating equation 1 by the Euler method yields

$$N_K(t + DT) = N_K(t) + DT \cdot [S_{K-1}(t) \cdot N_{K-1}(t) - N_K(t)] \tag{2}$$

Subsequently, to obtain the biomass for age group B_K, the number of individuals of each age group (N_K) was multiplied by the average weight (W_K) of an individual of age K

$$B_K(t) = N_K(t) \cdot W_K$$

To estimate total biomass $[BT(t)]$ all ages were added up, resulting in

$$BT(t) = \sum_{K=1}^{MAGE} B_K(t)$$

where $MAGE$ = maximum age of species.

The number of individuals of the adult population (NA) is obtained from the expression

$$NA(t) = \sum_{K=s}^{MAGE} N_K(t)$$

where s = age at first maturity.

The feedback of expression 2 is given by $N_1(t) = R(t)$, where $R(t)$ is the recruitment estimated by the environmentally driven stock-recruitment function. The function incorporates biotic and abiotic factors that affect the recruitment of the Pacific sardine over time as follows:

$$R(t) = \{b_1 P(t) \cdot \exp^{-b_2 P(t)} \cdot \exp^{-b_3[VA(t)]}\} + X_1$$

Where $P(t)$ = spawning stock at time t;

b_1 = density-independent coefficient;

b_2 = density-dependent coefficient;

b_3 = coefficient that reflects the effects of environmental changes;

$VA(t)$ = environmental variable (upwelling index) over time;

X_1 = random variable with normal distribution, generated from the average and standard deviation observed for recruitment.

The incorporation of the above estimated number of recruits over time was modeled by using the distributed delay method (Manetsch 1976; Seijo 1986; Díaz de León and Seijo 1992; Seijo et al. 1997). The model is based on gamma probability density function, which is described as follows:

$$dr_1/dt = m/DEL(R(t) - r_1(t))$$

$$dr_2/dt = m/DEL(r_1(t) - r_2(t))$$

$$\begin{matrix} . & . & . & . \\ . & . & . & . \\ . & . & . & . \end{matrix}$$

$$dr_m/dt = m/DEL(r_{m-1}(t) - r_m(t))$$

where $R(t)$ = input to the delay process;

$r_m(t)$ = output from the delay process;

DEL = expected value of the transit time of an individual entity through the process;

m = order of the process of delay;

$r_1(t), r_2(t)..., r_{m-1}(t)$ are the intermediate rates of the delay process.

The parameter m specifies the member (distribution) of the gamma family of probability density function, which describes the transit time of entities through the recruitment process of delay.

In addition, we used a table look-up function known as TABLIM to numerically interpolate the values of the upwelling indexes.

The effort applied to the fishery was also modeled with the method of distributed delay to represent the gradual entry of vessels during the fishing season. The expression that represents the accumulated effort by type of vessel is

$$f_V(t+DT) = f_V(t) + \int_t^{t+DT}[VESS_V(t) \cdot TRIPS]dt \quad (3)$$

where $f_V(t)$ = the effort in number of vessels by category V;

$VESS_V(t)$ = the number of vessels in each category over time;

$TRIPS$ = fishing trips;

V = harvesting (storage) capacity where $V_1 < 120$ metric tons; $V_2 = 121–140$ t; and $V_3 > 141$ t.

The dynamics of the fishing fleet were modeled with the Smith function (1969), which assumes that the effort changes in proportion to profits; that is,

$$\frac{dVESS_V(t)}{dt} = k_V \P_V(t)$$

where k_V = fleet dynamics parameter, a positive constant ($K_V > 0$), and $\P_V(t)$ = profits in time t by vessel V.

The accumulated yield by type of vessel [$YIELD_V(t + DT)$] is calculated from the equation

$$YIELD_V(t + DT) = YIELD_V(t) + \int_t^{t+DT}[q_V(t) \cdot f_V(t) \cdot BT(t)]dt$$

where $q_V(t)$ = dynamic catchability coefficient of vessel type V, and $f_V(t)$ = number of vessels type V in time t.

By using the function of catchability (q) proposed by MacCall (1976) for pelagic species, which is

$$q_V = \alpha_V \cdot NA(t)^{-\beta_V},$$

in the interval $0.000124 < q_V < 0.0000476$ (Martínez-Aguilar et al. 1997), we estimate the $CPUE(t)$ according to type of vessel by applying the expression

$$CPUE_V(t) = \sum_{K=1}^{MAGE} W_K(t) \cdot N_K(t) \cdot q_V(t)$$

The accumulated net returns by type of vessel are obtained by the expression:

$$PROFIT_V(t + DT) = PROFIT_V(t) + \int_t^{t+DT}(((CPUE_V(t) \cdot PRICE_1) + (CATCHIN(t) \cdot PRICE_2) - COST_V) \cdot f_V(t))dt$$

where $PROFIT_V(t)$ = net returns by type of vessel in time t;

$PRICE_1$ = price of target species (US$/kg, constant);

$CATCHIN(t)$ = incidental harvest of species in time t;

$PRICE_2$ = price of the incidental species (US$/kg, constant);

$COST_V$ = unit cost of effort (US$/trip, constant) by type of vessel V.

A discount rate of 0% is assumed (i.e., net benefits should be given equal weight over time). The unit price was calculated as a weighted average of the packaged and processed prices, with the weights being the respective proportions of the harvest going to packaging and processing.

Finally, the trip costs by type of vessel are obtained from

$$TC_V(t) = FC_V(t) + OVC_V(t) + [OMEG(t) \cdot CPUE_V(t) \cdot PRICE_1 + CATCHIN(t) \cdot PRICE_2]$$

where $TC_V(t)$ = vessel's total costs (including fixed and variable costs) over time t;

$FC_V(t)$ = fixed costs (US$) by type of boat over time t;

$OVC_V(t)$ = other variable costs (US$/fishing trips) by type of vessel over time t;

$OMEG(t)$ = pay to fisherman as a percentage of the value of harvest (21%).

Stability Analysis

An appropriate value of the time increment (DT) was determined for stable numerical solutions of the differential equations in the distributed delays. The necessary condition of stability requires that DT be within the interval $2\ MIN\,[Dn] > DT > 0$, where $Dn = DEL/m$ and $[Dn]$ is the smallest delay constant of the model (Manetsch 1982 cited in Seijo 1986). In this case, the values were $DEL = 2$ and $m = 3$. Therefore, the upper limit for DT in this model is 1.33.

Given that the model contains feedback processes in estimating the population structure for stable simulations, one should be sure that $1/C > DT > 0$, where $C = 1/Dn$.

Thus the value of DT in this model must be within the interval given by $0.66 > DT > 0$. We used the value 0.05, because this value satisfies the conditions of stability, and errors of numeric integration are <5%.

Model Validation

The real values observed were compared with those generated by the model for the two important variables of the system: effort and capture by season. The Kolmogorov-Smirnov nonparametric test was used to validate the model.

Sensitivity Analysis

Natural mortality coefficient (M), the curvature parameter of the von Bertalanffy growth equation, age at first maturity, and unit cost of effort and price of species were varied. Each of these parameters was independently varied with increases and decreases of 10% and 20% of the initial conditions to observe changes in performance variables. The model was run in deterministic mode to prevent random variables from influencing the observed changes.

Simulation of Fishery Management Strategies

Different management strategies were simulated to determine the effect on relevant variables, recruits, biomass, effort, yield, and profits. These variables were compared with the value reached at the end of the simulation, run in deterministic mode with respect to the base run. The strategies were:

1. Restricting the entry of new vessels to the fishery (i.e., a license quota of 76 boats).
2. Instituting a minimum legal capture size of 150 mm standard length.
3. Increasing the fishing season from 10 to 12 months.
4. Reducing the fishing season from 10 to 9 months by starting the season in November.
5. Combining a minimum capture size with 12 months of fishing.

Each of these strategies was implemented for a time $t > 10$ (i.e., starting from the 1991–92 season and for a period of 40 years).

RESULTS

Model Validation

The historic data of effort, catch, and CPUE were compared with those generated by the models for a period of 10 years beginning with the 1981–82 season. In figure 1, the general performance of the model exhibits robust estimates of the output variables, showing—in the three cases (effort, catch, and CPUE)—congruent patterns with small deviations of the same sign.

We used the Kolmogorov-Smirnov nonparametric test to determine if the observed and modeled catch and effort distribution over time were equivalent. The effort variable had a significance of 99%; catch and CPUE were 76% significant.

The consistency of the model output with accepted theory is shown in figure 1c. At the beginning of the period, there are increases in effort, and subsequently increases in CPUE. Starting with the 1987–88 season, CPUE decreases even though effort continues to increase.

Sensitivity Analysis

In general, the model indicated moderate alterations, with nonlinear changes in the direction and magnitude theoretically expected from the cause-effect relations represented in the mathematical model.

Biomass and Recruitment

The results of modeling biomass and individuals age 1 and 3, over time (120 months, or 10 years, beginning in 1981–82) are presented in figure 2. Biomass shows two important periods, the first characterized by growth until the record season of 944,000 metric tons in 1986–87 (months 61–72). The second period was characterized by a decrease in biomass, possibly because of overexploitation of the resource. The levels of effort grew until the 1988–89 season (months 85–96), which began with a biomass of 526,000 t, when a record 4,133 trips were made. At the beginning of 1990–91 season (month 109), the biomass dropped to 326,000 t (fig. 2a).

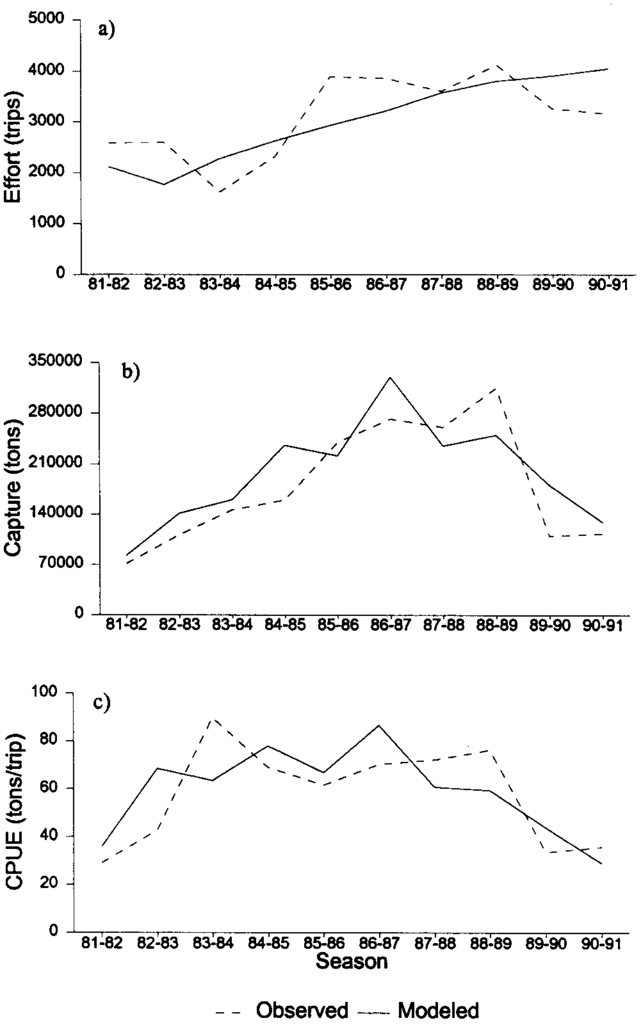

Figure 1. Validation of the model, comparing *a*, effort; *b*, captures; and *c*, CPUE for fishing seasons 1981–82 through 1990–91.

For the number of individuals of ages 1 and 3, alternating periods of good and moderately low levels of recruitment were observed. In the later years, the numbers decreased (fig. 2b, c).

Effort

The effort in number of modeled trips by category of vessel (V_1, V_2, and V_3 in equation 3) over time is illustrated in figure 3a. A positive trend is seen to a max-

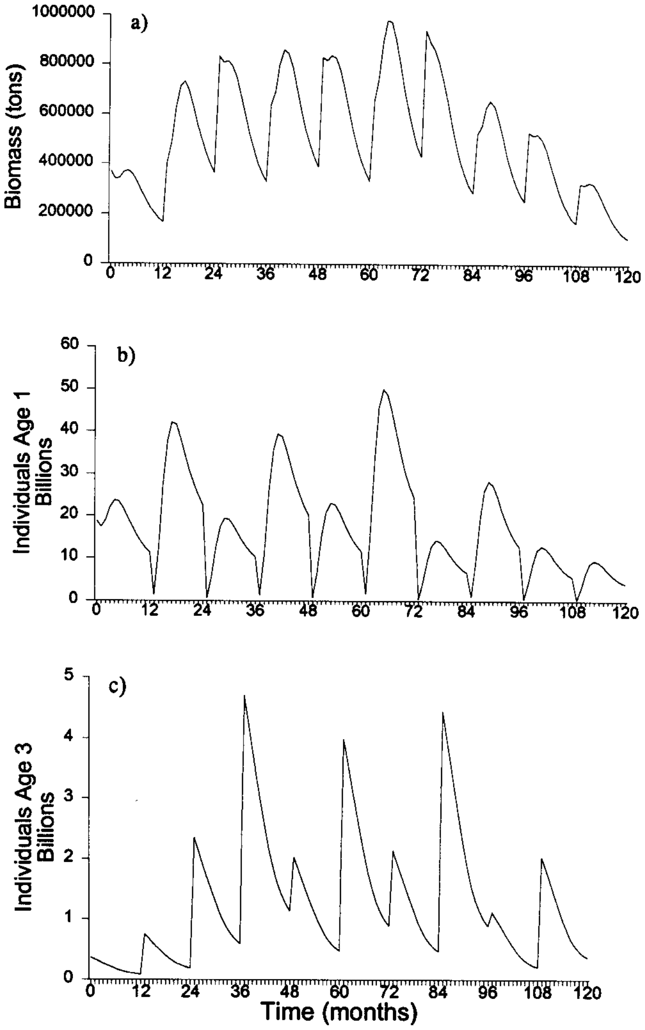

Figure 2. Model of dynamic behavior of the population of Pacific sardine over 120 months (10 years), beginning with the 1981–82 season: *a*, biomass; *b*, individuals age 1; and *c*, individuals age 3. Time (months) 1 = October 1981; 120 = September 1991.

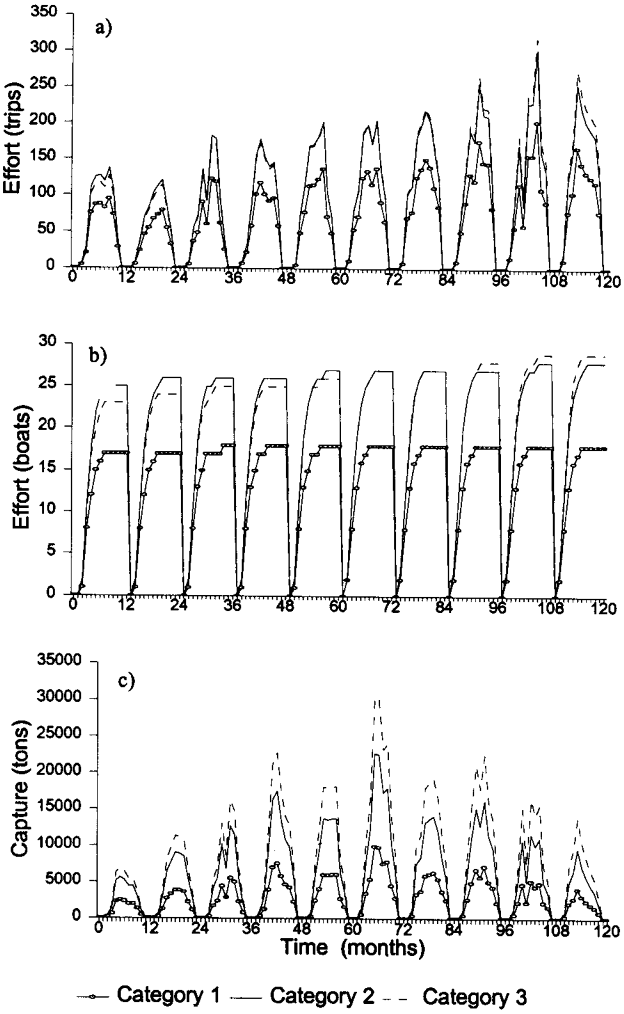

Figure 3. Model of dynamics of the short-term and long-term fishing effort by category of vessel in the Pacific sardine fishery, beginning with the 1981–82 season: *a*, effort in number of trips; *b*, effort in number of boats; and *c*, metric tons captured. Category 1, <120 t; category 2, 121–140 t; category 3, >141 t. Time 1 = October 1981; 120 = September 1991.

imum of 4,065 model fishing trips. Category 1 always shows a lower number of trips. This is reasonable, because when the season begins and the resource is farther away from the base port, smaller vessels take longer to reach the fishery. The same effect occurs at the end of the season, when the resource is again farther away. Category 1 vessels are the first to stop fishing because their cruising range is so limited.

At the end of each season, there are fewer trips, and fewer vessels in each category. Vessels in categories 2 and 3 show similar changes in distribution and number of trips per season.

Eight new vessels were added to the fleet from 1981–82 to 1991 (fig. 3b). Category 1 remains nearly constant during the 10 seasons, gaining only one new vessel. The total number of boats modeled for categories 2 (28) and 3 (29) correspond to the number in the real fishery. Category 3 added five new boats; category 2 added two. These results coincide with the net returns obtained for the three categories in the period modeled. The highest returns were from category 3 vessels, motivating the deployment of new vessels into the fishery.

Yield

The yield modeled by category of vessel is illustrated in figure 3c. Two important, well-defined periods were observed. The first increased until the 1986–87 season (months 61–72), with a maximum harvest of 340,000 t. The second period showed a decreasing harvest from the 1987–88 season (months 73–84) until the 1990–91 season (months 109–120); only 130,000 metric tons were captured. Category 3 and category 1 always had the highest and lowest captures. Because of this decrease during the second period, in spite of the increasing fishing effort, the CPUE by category of vessel remained the same (fig. 4a). The decrease produced a series of substantial economic losses for the fishing fleet.

Costs and Returns

The net returns by category of vessel modeled over time are illustrated in figure 4b. At first, in the 1980–81 season, small losses were observed for category 1. In this case, the total costs were more than the total returns. Later, the net returns for the three categories increased, the highest in category 3, until the record season of 1986–87 (61–72 months). After that, the net returns decreased, and the 1990–91 (109–120 months) season showed losses for category 1 and category 2. The average value of the CPUE for this season of losses was 18.6 and 28.6 metric tons for the first and second categories. At this level of CPUE, the average costs are higher than the average returns, causing vessels to leave the fishery or reduce the number of trips. The maximum economic yield is at $t = 6$ years (61–72 months; fig. 4b). Finally, the model predicted losses for the next two seasons for all three categories of the fishing fleet because of the low harvest.

Fishery Management Strategies

The effects of biomass, recruitment, effort in number of trips by category of vessel, and catch of the Pacific sardine, over time and under the different management strategies, are shown in table 1.

For biomass, the best results were produced with strategies 2 and 5. For recruits, strategies 2 and 5 yielded the best results. Strategy 2 (setting a legal minimum size) offered the best means of increasing biomass and recruits. This strategy is so important that even increasing the season to 12 months yields results similar to a 10-month season (closed in the summer).

Strategies 2 and 5 can sustain higher effort levels for category 1. These strategies' effects on category 2 were not as great, but still important. For category 3, strategy 1 caused a decrease of 47%, and strategy 5 an increase of only 16%. Strategy 3 had the least effect on the level of effort.

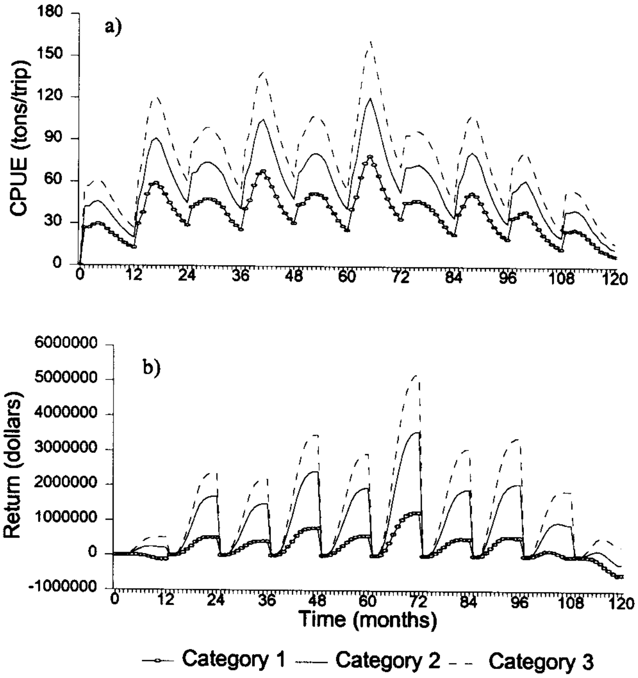

Figure 4. Model of dynamic behavior of CPUE (*a*) and the net returns (*b*) by category of vessel in the Pacific sardine fishery, beginning with the 1981–82 season. Category 1, <120 t; category 2, 121–140 t; category 3, >140 t. Time 1 = October 1981; 120 = September 1991.

All strategies except strategy 1 reduced the yield. Strategies 2 and 5 caused the catch to drop the most. Strategy 1 limits the entry of new vessels into the fishery, resulting in a 15% increase in catch, or 234,000 metric tons. This is about the same as the catch in the 1985–86 season, as well as in the two subsequent sea-

TABLE 1
Effects of Management Strategies,
Expressed as Absolute Values in Thousands, and as Percentages (in Parentheses)* of Baseline

		Management strategies									
Variables	Baseline	1		2		3		4		5	
Biomass (metric tons)	201	305	(52)	793	(295)	208	(4)	207	(3)	790	(294)
Recruits (number)	620,412	789,468	(27)	865,122	(39)	635,312	(2)	633,573	(2)	866,178	(40)
Yield (metric tons)	204	234	(15)	128	(−37)	200	(−2)	197	(−4)	129	(−37)
Effort (number of trips)											
Category 1	0.21	0.56	(169)	2.13	(912)	0.21	(0)	0.26	(23)	2.33	(1,008)
Category 2	1.27	2.37	(87)	3.40	(169)	1.28	(1)	1.51	(19)	3.73	(195)
Category 3	4.60	2.45	(−47)	4.82	(5)	4.43	(−4)	4.08	(−11)	5.32	(16)
Net returns (dollars)											
Category 1	−552	−161	(71)	11,988	(2,273)	−483	(12)	−564	(−2)	11,541	(2,192)
Category 2	−811	6,538	(907)	41,617	(5,234)	−245	(70)	−452	(44)	40,358	(5,079)
Category 3	4,917	13,917	(383)	88,166	(1,893)	6,410	(230)	5,042	(203)	86,139	(1,852)

*For instance, the biomass value (52) for strategy 1 means that biomass would be 52% higher than it would be for the baseline.

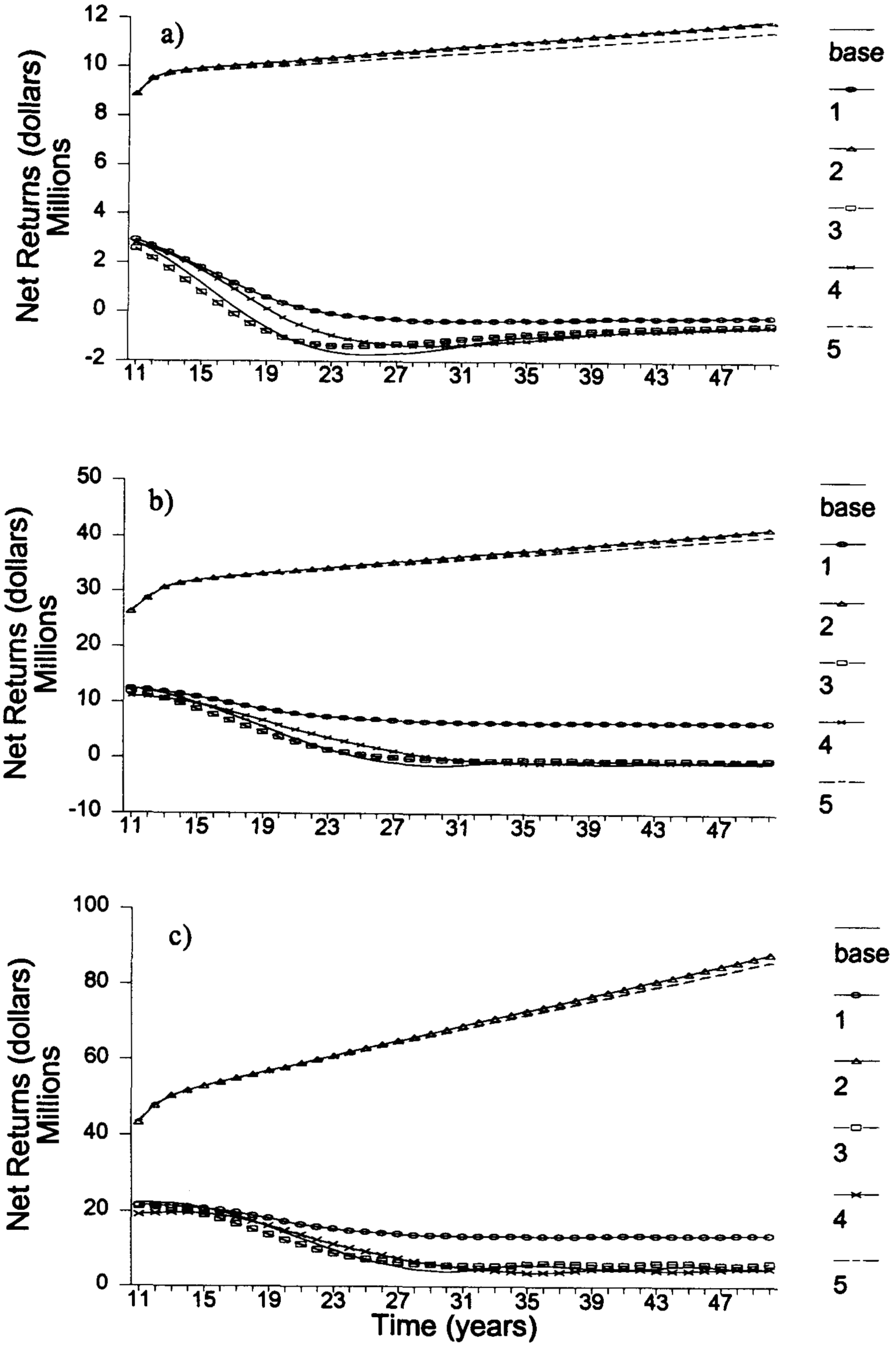

Figure 5. Effect on net returns by category of vessel with different modeled management strategies, deterministic manner: *a*, category 1 (<120 t); *b*, category 2 (121–140 t); and *c*, category 3 (>140 t). Time (years): 11 = 1991–92 season.

sons. Obviously, the decreasing catch, especially with strategies 2 and 5, affects the levels of recruitment and biomass in general, yielding substantial increases in biomass (fig. 1).

The changes in the net returns by category of vessel over time are illustrated in figure 5. For vessel category 1 (fig. 5a), the behavior of the base, run together with strategies 1, 3, and 4, shows a point of bioeconomic equilibrium at approximately 19 years. Later a negative economic yield is observed for category 1. The point of equilibrium for category 2 comes at approximately 25 years (fig. 5b) and for category 3 at about 29 years (fig.

5c). At these points, the average returns equal the average costs and consequently cause a lack of stimuli for entry into or exit from the fishery. Strategies 2 and 5 produce the best effects, with more economic yield for each of the three categories.

Of the five strategies analyzed, a minimum size at capture was the most important, offering considerable benefits from a biological and economic point of view.

DISCUSSION

Simulation Model

The bioeconomic model proposed for the fishery of the Pacific sardine in the Gulf of California satisfactorily represented the real system, considering the principal phenomena of the fishery. Holling (1978) mentions that a model is efficient if it leaves out everything except the essential part of the phenomenon.

The CPUE shows a behavior consistent with that accepted in the literature: after reaching a maximum, additional units of effort reduce the CPUE (Anderson 1977). This phenomenon has repercussions for total cost and total return. As the CPUE decreases, the cost increases and the return becomes smaller, until total cost surpasses the total return.

Possibly the most important parameters from the point of view of the sensitivity analysis were the natural mortality (*M*) and the curvature of the growth equation, which are difficult to estimate. An error in these parameters would affect all the performance variables used for the adequate management of the resource. Nevertheless, the results presented in this study, generated by systems simulation methodology, have produced a robust estimate, thus validating the model.

Modeling the principal variables in the system has produced a drastic decrease in the levels of biomass, recruitment, capture, and CPUE in the later seasons. The model simulates the overexploitation syndrome common to developed open access fisheries of the world. As a consequence of these low resource levels, the economic yield decreases until losses are observed in the 1990–91 season. These yields can be considered a measure of economic inefficiency caused by managing the resources with an open access regime.

The high catches of the 1987–88 and 1988–89 seasons and the coinciding high net returns did not result from an increased biomass of the Pacific sardine, but rather from high levels of effort in number of trips. Therefore, state intervention is imperative for preventing or mitigating the exhaustion of the Pacific sardine population in the Gulf of California. Clark (1976, 1985) and Anderson (1977) mention that the dynamics of a resource under open access exploitation will eventually lead to bioeconomic disaster for the fishery.

Simulation of Management Strategies

Of the five strategies analyzed, 2 and 5 offer highly desirable results for the main bioeconomic variables of the fishery, demonstrating the importance of restrictions on the minimum-capture size. Not capturing juveniles yields abundant biological and economic benefits, including—under strategy 5—a fishing regimen of 12 months.

In addition, we have shown how inefficient strategies 3 and 4 could be. From the biological point of view, the changes in biomass, recruitment, and yield would be nearly the same as the base run. But the poor performance of strategies 3 and 4 may result from the fact that they affect fishing activity only at end of the season and not during peak periods. Nevertheless, in the seasons when there was fishing in the summer, large numbers of Pacific sardine were captured, even in off-peak periods. Finally, strategy 1 offers positive and interesting results and an increase in all the biological and economic variables.

Establishing and enforcing a minimum size restriction is not an easy assignment for a fishery in which large volumes are captured with purse seines. But other mechanisms can help to prevent the capture of juveniles, such as establishing a closed season in the summer near Isla Angel de la Guarda on the west coast, where the juveniles are located, and where there have been sporadic closed seasons in the last decades. The closure would have to be permanent to substantially reduce the capture of juveniles.

Harvest quotas—another type of restriction that can be effective in purse-seine fisheries—were not considered in this study. As mentioned above, only strategies that we believe could be implemented and enforced were included in the simulation experiments for the Gulf of California Pacific sardine fishery. We did not include harvest quotas because of high enforcement costs and expected low levels of compliance.

Even if it were feasible to implement quotas, by themselves they would only maintain biomass at a desired level, forcing economic rent to be eliminated with the corresponding overcapitalization of the fishery. Catch quotas, to be bioeconomically efficient, require license quotas and other restrictions such as minimum size to enhance the resource over time. All management measures must be viable from an administrative, political, and practical point of view.

Although this type of holistic simulation model requires the estimation of more parameters than other, traditional fishery biology models, the dynamic structure of the model has allowed us to explore a large number of resource-management alternatives.

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LENGTH-BASED GROWTH ESTIMATES FOR PACIFIC SARDINE (*SARDINOPS SAGAX*) IN THE GULF OF CALIFORNIA, MEXICO

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ABSTRACT

Monthly length-frequency distributions for *Sardinops sagax* in the Gulf of California for fishing seasons 1972–73 to 1989–90 were used to estimate growth by the Shepherd length-composition analysis (SLCA). Data were organized into annual sets, and the parameters of the von Bertalanffy growth curve were computed. Estimates for K and L_∞ values were compared to others reported for the Gulf of California and derived from otoliths, scales, and other length-based methods. Otoliths and scales supported growth estimates with SLCA. On the assumption that variability observed in the values of growth parameters over 16 years represents individual variation, a maximum likelihood algorithm was used in the growth performance index, ϕ', to estimate confidence intervals (CI), for K and L_∞, as well as an average. Ranges for 90% CI were $0.34 < K$ year$^{-1} < 0.39$, $27.0 > L_\infty$ (TL) cm > 25.2; ranges for 75% CI were $0.33 < K$ year$^{-1} < 0.43$, $26.6 < L_\infty$ (TL) cm < 23.5. The best estimate was $L_\infty = 25.7$ cm, $K = 0.38$ year^{-1}, and $t_0 = -0.3$. This variability was interpreted as influences in the annual cohorts. These estimates were also compared with those from the Pacific coasts of Mexico, the United States, and Canada. Results suggest there are differences. In general terms, both K and L_∞ tend to be lower in the Gulf of California. This was interpreted to be a consequence of differences in the ecosystem dynamics.

INTRODUCTION

Structured stock-assessment models require growth estimations as part of the information used to estimate stock size and fishing mortality. For such studies, the von Bertalanffy growth equation (VBGE) is generally assumed to be valid. Currently, the information required by managers includes a good estimation of the growth coefficient (K) and the asymptotic length (L_∞). An important aspect emerges when relatively large series of length-frequency distributions are available and are used to estimate growth. These analyses can indicate variability of growth patterns and estimates of the biomass gain for a given fish per unit of time, with the obvious consequences on stock size, yield estimations, and accurate confidence intervals for biomass estimations. In this paper we deal with three major issues for the Monterrey sardine, *Sardinops sagax* (Jenyns 1842; Parrish et al. 1989) in the Gulf of California: (1) growth estimates from length-frequency distributions of commercial catch, (2) recognition of growth-pattern variability, and (3) growth validation.

MATERIALS AND METHODS

Catch-at-length data from landings at Guaymas, Sonora (fig. 1) for the fishing seasons of 1972–73 to 1989–90 were organized as monthly length-frequency distributions. Sample size in the period 1972 to 1983 was 60 kg, collected from 2 to 5 vessels daily. From 1984 to 1990, a minimum sample of 10 kg was collected from 2 to 5 vessels daily (Cisneros-Mata et al. 1995).

The length-weight relationship was used to expand samples to the whole catch for each period with a single transformation:

$$C(l) = \frac{w(l)s \cdot Wc}{Ws \cdot \bar{w}(l)}$$

where $C(l)$ = catch numbers at length; $w(l)s$ = sample total weight of the length class; Wc = total weight of the whole catch; Ws = sample total weight; and $\bar{w}(l)$ = average weight at length class.

Growth analysis was developed for annual periods: monthly length-frequency distributions were used to obtain a set of K and L_∞ values as an estimate of the average growth pattern and its variability. For this, we used the Shepherd length-composition analysis, SLCA (Shepherd 1987). The SLCA is based on an oscillatory test function $T(l)$ whose period is defined by the VBGE parameters, with the form

$$T(l) = \frac{\sin \pi(t_{\max} - t_{\min})}{\pi(t_{\max} - t_{\min})} \cos 2\pi\,(\bar{t} - t_s) \tag{1}$$

where $t_{\max}$ and $t_{\min}$ are the ages-at-length corresponding to the upper and lower bounds of a given length class (and computed from the VBGE); $\bar{t}$ is the average age; and t_s is the fraction of the year in which the sample was

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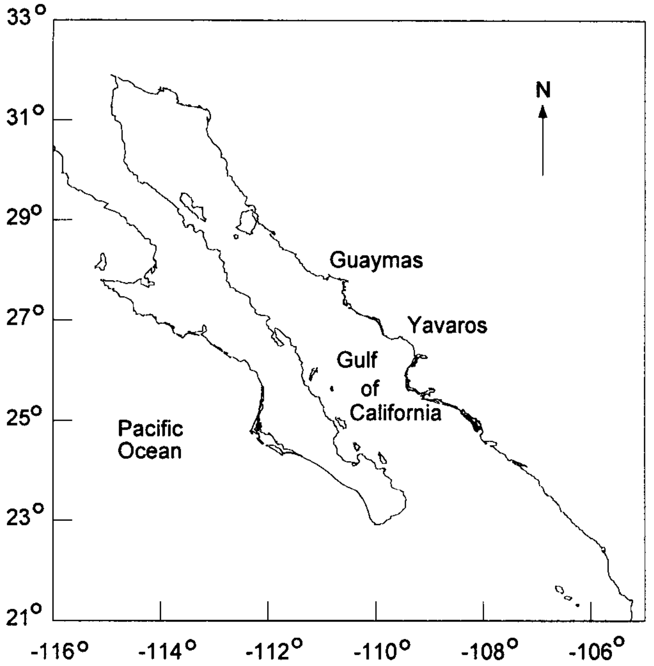

Figure 1. Area of study, showing landing ports in the Gulf of California.

taken. This test function varies between −1 and 1. Because this test function needs seed values for K and L_∞, the criterion for the appropriate K and L_∞ values is expressed by a Score function S with the form

$$S = \sum_{l=1}^{k} \sum_{i=1}^{n} N(l, i)^{0.5} \cdot T(l, i) \qquad (2)$$

where l indexes the length groups; i indexes the various distributions available; and N indexes the observed frequencies.

The test function (equation 1) is modulated by the parameters of the VBGE. When adequate values are given, larger positive values for $T(l)$ coincide with larger values for $N(l)$, giving higher values for S. When inadequate values for the growth parameters are used, negative values (or smaller than above) for $T(l)$ will coincide with larger values for $N(l)$, giving smaller values for S (as computed with equation 2). As Shepherd (1987) explains, the criterion for selecting K and L_∞ is to maximize the score function represented by equation 2.

We used the growth-pattern index suggested by Pauly and Munro (1984) to make interannual comparisons and to compare our results with those in the literature. The index is computed as $\phi' = \log_{10} K + 2 \cdot \log_{10} L_\infty$.

We validated growth in two ways: (1) by comparing our growth estimates with other estimates reported for the Gulf of California, including those based on hard parts (otoliths, scales), and (2) by comparing with estimates for *Sardinops sagax* from other regions.

RESULTS

Growth Estimates and Variability of Growth Patterns

Growth parameters of the VBGE estimated with SLCA are shown in table 1. Values for ϕ' involving all estimates for *S. sagax* (tables 1–3) ranged from 2.27 to 2.77, with an average of 2.399 and a coefficient of variation of 5.44%. Since longevity of *S. sagax* has been calculated to be 6 to 7 years, each single cohort will contribute information through the length distributions of several years. This means that yearly estimations do not represent variance in annual growth but rather variability of individual growth patterns. Thus the set of ϕ' values provides an estimate of mean and standard deviation, which we used to obtain confidence intervals for growth pattern from a single maximum likelihood algorithm using a normal distribution for the ϕ' values (Pauly and Munro 1984):

$$L\{\phi' \mid \mu,\sigma\} = \frac{1}{\sigma\sqrt{2\pi}} \exp(-(\phi'-\mu)^2/2\sigma^2) \qquad (3)$$

According to ϕ' values in tables 1–3 (involving K and L_∞), the 90% confidence interval provides ranges of $0.34 < K \text{ year}^{-1} < 0.39$, and $27.0 < L_\infty \text{ (TL) cm} < 25.2$.

TABLE 1

Growth Values for the von Bertalanffy Growth Curve for *Sardinops sagax* in the Gulf of California, after Application of SLCA

Fishing season	Growth coefficient K (year^{-1})	Asymptotic length, TL (cm)	t_0(year^{-1})	ϕ'[a]
1972–73	0.34	27.0	−0.69	2.39[b,c]
	0.32	26.0	−0.53	2.34
1973–74	0.38	25.7	−0.30	2.40[b,c]
1974–75	0.38	25.7	−0.38	2.40[b,c]
1977–78	0.36	25.3	−0.78	2.36[c]
1978–79	0.32	24.1	−0.65	2.27
	0.39	24.4	−0.32	2.36[c]
1979–80	0.31	26.3	−0.60	2.33
	0.37	23.4	−0.65	2.31
1983–84	0.39	25.2	−0.08	2.39[b,c]
1984–85	0.32	24.5	−0.87	2.28
	0.39	23.0	−0.10	2.32
1985–86	0.33	25.9	−0.19	2.35
1986–87	0.38	27.4	−0.96	2.45
	0.37	27.6	−0.93	2.45
1987–88	0.32	25.4	−0.97	2.32
	0.34	25.2	−0.11	2.33
1988–89	0.31	26.3	−0.72	2.33

Note: SLCA (Shepherd length-composition analysis) from Shepherd 1987.
[a] ϕ' Growth performance index according to Pauly and Munro 1984.
[b] Values within a 90% confidence interval, range $2.394 < \phi' < 2.399$.
[c] Values within a 75% confidence interval, range $2.363 < \phi' < 2.425$.

TABLE 2
Growth Parameters of the von Bertalanffy Growth Curve for *Sardinops sagax* in the Western Pacific as Reported in Fishbase 1996

Location[a]	Growth coefficient K (year^{-1})	Asymptotic length, length, TL (cm)	t_0(year^{-1})[b]	ϕ'	Method	Reference
BC	0.52	29.3		2.65		Pauly 1978
BC	0.52	30.0		2.67		Pauly 1978
BC	0.55	29.1		2.67		Pauly 1978
BC	0.57	25.1		2.56		Pauly 1978
BC	0.53	30.2		2.68	Nonlinear regression	Pauly 1979
Mexico	0.50	26.0		2.53		Granados-R. 1958
Mexico	0.34	23.4	−0.26	2.12		Cisneros-Mata et al. 1990
Mexico	0.60	27.0		2.48	ELEFAN I	Cisneros-Mata et al. 1990
USA	0.40	29.5	−2.10	2.54	Nonlinear regression	Pauly 1978
USA	0.40	30.5	−0.59	2.57	Nonlinear regression	Pauly 1978
USA	0.37	25.9		2.39		Erzini 1991
USA	0.46	31.0		2.65		Pauly 1978
USA	0.60	29.0		2.70		Pauly 1978
USA	0.70	27.0		2.71		Pauly 1978
USA	0.59	26.8		2.63		Pauly 1979
USA	0.56	26.9		2.61		Pauly 1979
USA	0.55	25.7		2.56		Pauly 1979
USA	0.54	26.0		2.56		Pauly 1979
USA	0.53	27.6		2.61		Pauly 1979
USA	0.52	26.1		2.55		Pauly 1979
USA	0.44	26.2		2.48		Erzini 1991
USA	0.45	29.3		2.59		Beverton 1963
USA	0.35	30.0		2.50	Nonlinear regression	Pauly 1980

[a] BC, British Columbia, Canada.
[b] Blank cells mean that authors did not provide value for this parameter.

TABLE 3
Growth Parameters of the von Bertalanffy Growth Curve for *Sardinops sagax* in the Gulf of California, Mexico

Growth coefficient K (year^{-1})	Asymptotic length, length, TL (cm)	t_0(year^{-1})	ϕ'	Method	Reference
0.43	31.0	−0.21	2.62	ELEFAN I	Estrada-G. et al. 1986
0.34	23.6	−0.26	2.28	Otoliths	Estrada-G. et al. 1986
1.22	20.3	−0.13	2.70	Lopez-Veiga	Félix-U. 1986
0.60	27.0	−0.15	2.64	ELEFAN I	Cisneros-Mata et al. 1990
0.43	30.0	−0.40	2.59	ELEFAN I	Cisneros-Mata et al. 1991
0.43	29.0	−0.40	2.56	ELEFAN I	Nevárez-M. et al. 1993
0.41	23.5	−0.13	2.36	Scales, Walford-Gulland	Gallardo-C. et al. 1991
0.43	23.5	−1.03	2.38	Scales, Beverton	Gallardo-C. et al. 1991
0.36	23.8	−1.63	2.31	Scales, Tomlinson-Abrahamson	Gallardo-C. et al. 1991
0.38	23.6	−1.42	2.33	Scales, Beverton	Gallardo-C. et al. 1991
0.33	23.9	−1.82	2.27	Scales, Allen	Gallardo-C. et al. 1991
0.35	23.9	−1.62	2.30	Scales, Beverton	Gallardo-C. et al. 1991
0.28	26.6	−0.60	2.30	Otoliths, Gulland & Holt	Jiménez-R. 1991
0.30	26.6		2.33	Otoliths, Ford-Walford	Jiménez-R. 1991
0.33	26.6	−1.66	2.37	Otoliths, von Bertalanffy	Jiménez-R. 1991
0.55	24.4	−0.74	2.51	Otoliths, nonlinear regression	Jiménez-R. 1991
0.27	26.6		2.28	Modal progression	Jiménez-R. 1991
0.45	30.0		2.61	ELEFAN I	Jiménez-R. 1991
0.40	25.8	−0.23	2.43	Gulland & Holt	Jiménez-R. 1991
0.45	25.8		2.48	Ford-Walford	Jiménez-R. 1991
0.59	25.8	−0.21	2.59	Von Bertalanffy	Jiménez-R. 1991
0.47	25.9	−0.82	2.50	Nonlinear regression	Jiménez-R. 1991
0.68	29.5		2.77	Modal progression	Jiménez-R. 1991
0.44	29.6		2.59	ELEFAN I	Jiménez-R. 1991

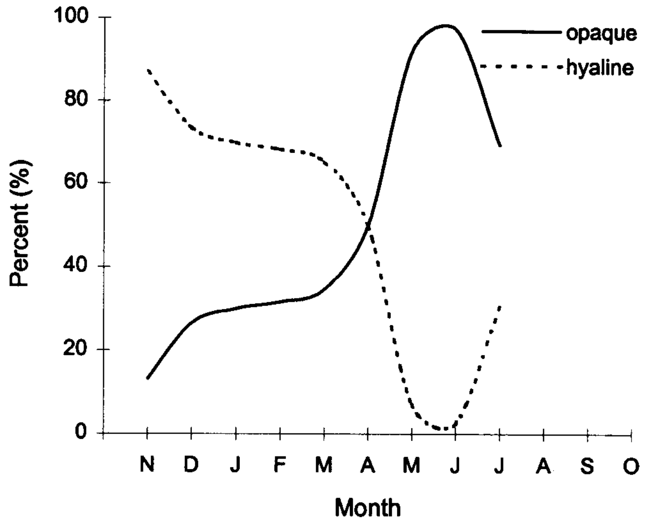

Figure 2. Monthly relative frequency in percentage of hyaline and opaque edge in otoliths of *Sardinops sagax* from the Gulf of California for the seasons 1988–89 and 1989–90 (from Jiménez-R. 1991).

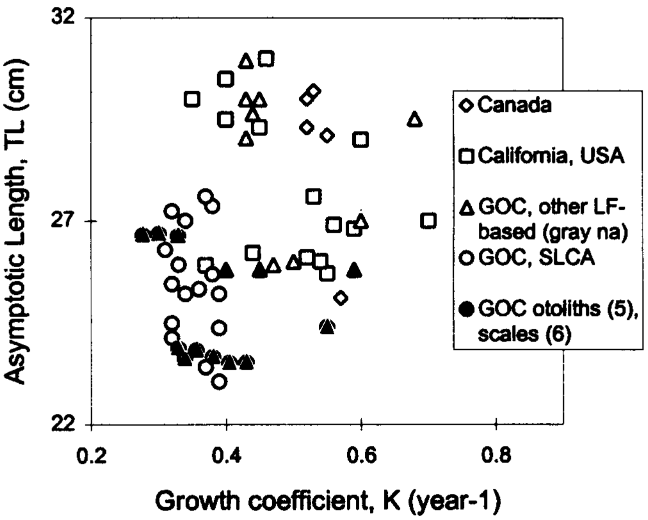

Figure 3. Estimates of growth parameters for *Sardinops sagax* from the Gulf of California (GOC), and the Pacific coasts of Mexico, the United States, and Canada (LF = length-frequency; na = not available).

Growth Validation

One of the main problems with growth estimates from length-frequency distributions is validation. Even when estimates are not directly validated with otoliths and scales, they can be compared with reports in the literature. Table 2 shows growth estimates for *S. sagax* reported in FishBase 1996. Table 3 lists other reports, particularly for the Gulf of California, in which estimates from otoliths and scales are emphasized. In general terms, and for both tables, estimates computed here correspond with those derived from otoliths, scales, and other procedures. In particular, otolith analysis validates annual ages (fig. 2).

DISCUSSION

Length-based growth estimates for *S. sagax* in the Gulf of California obtained with SLCA (table 1) seem reasonable when compared with age and growth estimates derived from otoliths and scales (table 3). We think that, for *S. sagax*, annual sets of length distributions provide a partial interannual variation of growth because in each year only one new cohort affects the growth pattern, whereas other ages contribute the same information over several years. Here, we suggest that the observed year-to-year variability in growth-parameter estimates reflects individual growth variability. According to this, and using a maximum likelihood function, the 90% confidence interval for ϕ' values provided values for the von Bertalanffy growth curve within a range of $0.34 < K\ \text{year}^{-1} < 0.39$ and $27.0 < L_\infty$ (TL) cm < 25.2.

Like many clupeoids, *S. sagax* has been characterized as a highly variable species strongly influenced by environmental variables. For this reason, we also computed a confidence interval of 75%, which yielded a range of values of $0.33 < K\ \text{year}^{-1} < 0.43$ and $26.6 < L_\infty$ (TL) cm < 23.5. Assuming these modal values for distribution of ϕ', we believe the best estimated values to be $L_\infty = 25.7$ cm, $K = 0.38\ \text{year}^{-1}$, and $t_0 = -0.3$.

Another aspect of interest is that growth performance for *S. sagax* in the Gulf of California appears to differ from that for the same species along the Pacific coast. This is shown in figure 3, where most estimates for the Gulf of California have lower K and L_∞ values than those from the Pacific coast of Mexico, the United States, and Canada. These estimates suggest that the metabolism of *S. sagax* within the Gulf of California is probably different. This observation agrees with those of some authors (Roden 1964; Wrash and Wrash 1971; Vandel Spoel 1984) who have noted that ecosystem dynamics within the Gulf of California differ from those in adjacent regions.

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VARIABILITY OF SARDINE CATCH AS RELATED TO ENRICHMENT, CONCENTRATION, AND RETENTION PROCESSES IN THE CENTRAL GULF OF CALIFORNIA

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ABSTRACT

The sardine (*Sardinops sagax*) fishery of the Gulf of California is among Mexico's most important fisheries, accounting for the largest catch and providing many productive jobs. During the early 1990s, this fishery collapsed to less than 3% of the production maximum. Surprisingly, after two years of very low catch the fishery recovered quickly. We propose that these large fluctuations may be explained mainly by physical processes (enrichment, retention, and concentration) governing the sardine spawning habitat. The spawning area may be influenced by processes such as tidal mixing, winter northwesterly winds, coastal upwelling, prevailing surface currents, and Ekman transport, but most of its variability is believed to be wind-forced. Therefore we attempted to relate spawning extension to wind variations. By fitting an equation that expresses spawning as a probability function of a wind-derived index, we have built a spawning-probability time series based on egg and larval survey data and then tested against an independent series of landings and biomass indices (number of recruits and adults). Results show coherent relations between the spawning-probability series and the biological and fisheries data, despite large fluctuations (collapse and recovery). Our results are encouraging and may provide a solid theoretical basis for future environment-monitoring systems for the sardine fishery in the gulf.

INTRODUCTION

Comparative studies of fish habitat climatology have provided key clues to understanding mechanisms linking physical environment to biological populations. Bakun (1996) noted that, for most cases, three major classes of physical processes (enrichment, concentration, and retention—the "fundamental triad") must co-occur to yield favorable reproductive habitats for many types of fish, including the small pelagics.

Optimal levels of wind stress drive optimal environmental conditions for reproductive activity. Cury and Roy (1989) have demonstrated that, in regions where Ekman type upwelling occurs, one physical variable (wind intensity) can result in a spectrum of conditions affecting the survival of small pelagic larvae. Three scenarios can be identified: (1) weak winds resulting in weak upwelling activity and thus in poor food levels, (2) strong winds producing strong upwelling activity but creating unfavorably high turbulence (see Lasker and MacCall 1983), and (3) moderate winds that produce enough upwelling and nutrient supplies while the water column remains stable. These scenarios, usually dome-shaped (named optimal environmental windows after Cury and Roy 1989), have proved to operate similarly in many small pelagic grounds (e.g., Ware and Thomson 1991; Cury et al. 1995).

Because weak winds result in nutrient depletion, and because strong winds may affect both retention and concentration, the optimal environmental window for reproductive success must properly combine the elements of the fundamental triad (cf. Bakun et al. 1998).

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Understanding regional triad systems should greatly benefit regional fishery management.

The Gulf of California Sardine

The history of the Gulf of California sardine (*Sardinops sagax*) fishery is mainly defined by fleet capacity and geographic distribution of landings (Lluch-Belda et al. 1986; Cisneros-Mata et al. 1995; table 1). Since the 1982–83 fishing season, it has been difficult to explain catch fluctuations solely in terms of changes in fishing capacity.

The last 14 years have seen the strongest and fastest changes in the fishery. From 1989 to 1990, a dramatic collapse caused severe economic displacement, including the loss of more than 3,000 direct jobs and about half of the fleet and processing plants. (Landings in 1991–92 were less than 3% of those in 1988–89.) Another strong change, a fast recovery, began in the 1993–94 fishing season, as shown by increasing landing levels (fig. 1).

An analysis of the fishery was done by Cisneros-Mata et al. (1995). They pointed out that a decreased recruitment index occurred several years before it became evident in the catch and catch per unit of effort (since 1986), indicating a decreased spawning biomass years before the collapse. They concluded that overfishing, in combination with climate, must have played an important role, given the high rates of exploitation during adverse environmental conditions.

TABLE 1
Periods in the Gulf of California Sardine Fishery History, with Average Annual Landings

Period	Definition	Average annual landings (t/year)
1960–70 to 1975–76	Exploration and establishment	25,354
1976–77 to 1981–82	Development and growth	51,502
1982–83 to 1988–89	Expansion and stabilization	212,377
1989–90 to 1992–93	Collapse	59,495
1993–94 to 1996–97	Recovery	175,450

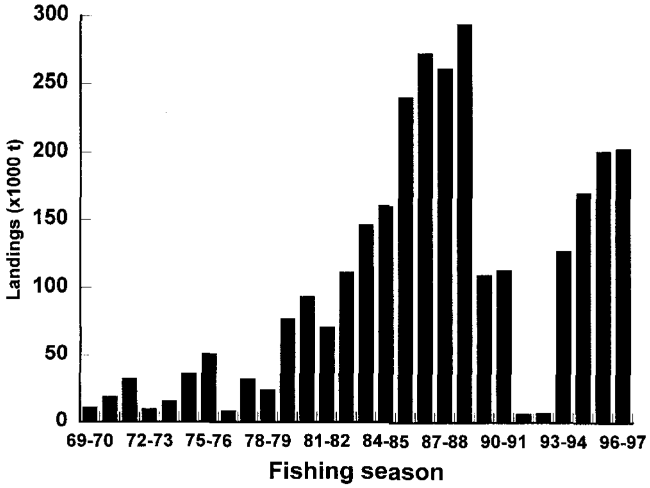

Figure 1. Gulf of California sardine landings, 1969 to 1997 (data provided by the Instituto Nacional de la Pesca, Centro Regional de Investigaciones Pesqueras CRIP-INP).

Although fishing mortality has been a major force driving the population collapse, analysis of sardine scale deposits in anaerobic sediments off the Guaymas Basin have shown large population fluctuations even in the absence of fishing activity (Holmgren-Urba and Baumgartner 1993), so natural variability must be considered. It is likely that management of the species depends on the ability to differentiate between natural variability and fishing mortality.

Previous studies of environmental forcing on the Gulf of California sardine population have been made by Sokolov (1974), Lluch-Belda et al. (1986), Nevárez-Martínez (1990), Hammann (1996), and Lluch-Cota et al. (1997).

Triad Physical Setting

Though few direct observations have been made in the Gulf of California, physical dynamics have been widely documented because the gulf combines two valuable properties: (1) It is often cloud-free, which makes it ideal for studies with satellite imagery (Badan-Dangon et al. 1985). (2) It constitutes a good-size basin for testing mesoscale and climate modeling (Ripa 1997).

Atmospheric forcing is characterized by weak summer winds blowing toward the northwest, and stronger winter winds toward the southeast (Roden 1964). Though this wind configuration is likely to produce Ekman-type upwelling along the continental margin during winter and along the peninsula during summer, only the first has been properly identified by satellite techniques (Lavín et al. 1997).

Ocean surface circulation has recently been described by Beier (1997), who used a two-layer linear model in which forcing agents (baroclinic waves, wind stress, surface heat flux) cause clockwise winter circulation and counterclockwise summer circulation. This general circulation scheme is supported by field observations (e.g., Lavín et al. 1997) and other model results (e.g., Ripa 1997).

Because both atmospheric and ocean circulation revert seasonally, strong intra-annual variability is present in almost every physical process in the gulf. An important mixing process takes place in the Canal de Ballenas area, where the bottom topography augments tidal currents year-round (Badan-Dangon et al. 1985).

We propose a theoretical model for the physical settings of the triad system in the Gulf of California (winter conditions) as a combination of six main components (fig. 2, panel 1): Strong tidal mixing (1) at the Canal de Ballenas results in an extremely dynamic water column

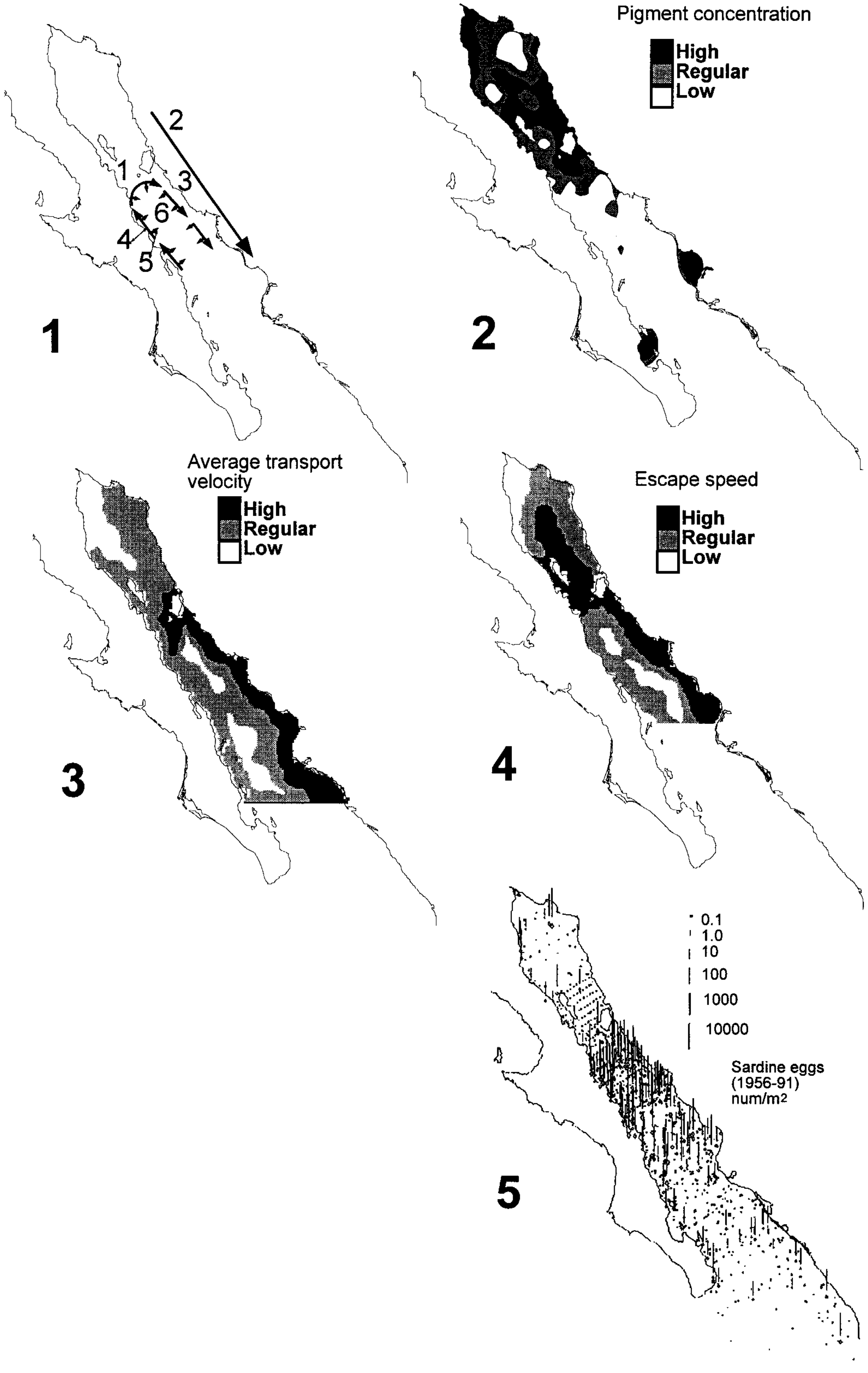

Figure 2. Hypothesis for the sardine triad system in the Gulf of California. All maps represent winter conditions. *Panel 1*, theoretical physical setting: 1, tidal mixing; 2, northwesterly winds; 3, wind-driven coastal upwelling; 4, predominant surface currents; 5, Ekman transport; and 6, weak dynamics area. *Panel 2*, satellite-derived winter-composite (October to March, 1978–86) of sea-surface pigment concentration (enrichment: data provided by Arias-Aréchiga, CIBNOR, S.C.). *Panel 3*, simulated ocean surface retention. *Panel 4*, surface circulation model results showing particle escape velocity (retention). *Panel 5*, historic abundance of sardine eggs in the Gulf of California (redrawn from Hammann et al. 1998).

inadequate for sardine reproduction (see Lasker and MacCall 1983). However, it exports nutrient-rich waters to nearby areas where more stable conditions prevail. During winter, when the wind blows south parallel to the coast (2), additional enrichment is associated with coastal upwelling along the continental margin (3). Rich water from both sources—tidal mixing and coastal upwelling—is carried along by the prevailing surface currents (4) and across the gulf by Ekman transport (5). Toward the middle area (6), the proper conditions for sardine reproduction result from high food concentration brought by surface currents and Ekman transport, as well as from water column stability and larval retention caused by weak dynamics.

METHODS

Sources and Preparation of Data

An area from the southern limit of Isla Tiburón south to Bahía Concepción and all across the gulf was selected as representative of the central gulf.

As an indirect indicator of the wind-forcing component relevant to the oceanographic processes in that area, we considered a monthly coastal upwelling index as derived from daily wind records at the Empalme (Sonora) Meteorological Station (Servicio Meteorológico Nacional). This index ($\mathrm{CUI}_{\mathrm{Empalme}}$), computed by Lluch-Cota (pers. comm.), represents the only long and continuous time series of wind-driven ocean processes inside the gulf.

We considered results from 24 sardine egg and larvae sampling cruises covering the central gulf (carried out by the Instituto Nacional de la Pesca from 1971 to 1987) as published by Nevárez-Martínez (1990). For each cruise, we evaluated the relation between the corresponding monthly value of the $\mathrm{CUI}_{\mathrm{Empalme}}$ and the estimated proportion of positive stations. Data are shown in table 2.

Spawning Probability Function

Attempts to express biological success as a function of one or a few easily measured environmental variables have been based on linear statistical methods, although nonlinearity is often recognized.

We have defined an equation to express spawning probability as a function of one measured variable (CUI) by combining simple ecological concepts with the hypothetical triad system dynamics in the Gulf of California:

1. Enrichment and stability limit spawning.
2. Nonlinearity in the relation between CUI and spawning success results from the interaction of two mutually exclusive processes: enrichment and stability.

TABLE 2
Base Data for the Spawning Probability Function

Cruise[a]	Total sampled stations	Positive stations	Proportion (positive/total)	Associated $\mathrm{CUI}_{\mathrm{Empalme}}$
AA7101	17	7	0.41	124.3
AA7204	24	12	0.5	57.3
AH7206	30	0	0	0.7
AA7302	25	4	0.16	8.8
AA7305	22	9	0.41	13
AA7308	16	3	0.19	−14.7
AA7402	12	7	0.58	97.9
AA7403	8	6	0.75	37.7
AA7405	9	9	1	56.9
AA7501	18	5	0.28	51.1
AA7503	13	6	0.46	99
AA7504	15	8	0.53	71.3
AA7601	18	7	0.39	57.9
AH7605	18	6	0.33	3.3
AA7605	17	0	0	3.3
AH7703	19	1	0.05	171.8
AA7708	16	5	0.31	−24.4
AA7802	24	10	0.42	8.8
AA7810	22	0	0	120.3
AA8103	18	15	0.83	89.7
PU8403	24	13	0.54	56.4
PU8611	135	58	0.43	153.4
AA8701	20	19	0.95	77.7
PU8711	22	19	0.86	138.2

Note: All data come from the central Gulf of California.
[a]Cruises as named by CRIP-INP.

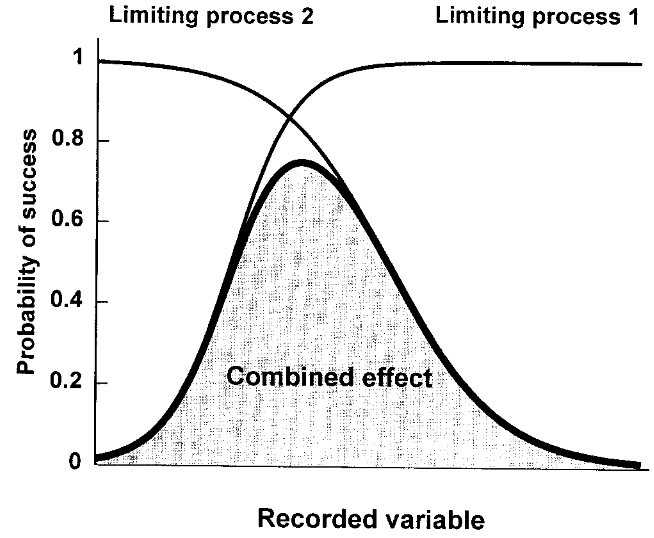

Figure 3. Theoretical approach for the spawning probability function.

Figure 3 shows the theoretical integration of these two concepts. We combined two sigmoid curves, each representing a limiting factor. These processes are mutually exclusive, inversely related, and controlled by the same external physical forcing (wind); thus one has a positive relation to the probability of success and the other a negative relation. Total probability is estimated by simply computing the arithmetic product. Because the response variable is given as a probability, the maximum possible value of individual curves (commonly called K) takes the value 1. This combination of curves is then expressed as

$$P_{spw} = [1/(1 + ae^{-b\cdot CUI})]\cdot[1/(1/(1 + ce^{d\cdot CUI})]$$

where P_{spw} is the final spawning probability; *CUI* is the associated upwelling index value; and *a* and *b* are the parameters for the first sigmoid curve, *c* and *d* for the second.

After fitting the model with our data (shown in table 2), we applied the resulting function to a winter $CUI_{Empalme}$ (built by averaging consecutive months of a typical sardine spawning season, October–March) and computed a spawning probability time series for the period 1978–96. We then filtered this series with a 3-year moving average to eliminate the highest frequency, and compared it with the number of recruits and adults (as published by Cisneros-Mata et al. 1995) and landings (as provided by the Instituto Nacional de la Pesca).

RESULTS

The curve representing spawning probability as a function of $CUI_{Empalme}$ is shown in figure 4, together with the original data (as presented in table 2). The spawning-probability time series was built by applying that function to the winter $CUI_{Empalme}$ data. The resulting series (fig. 5) shows a peak during the period 1981–82 through 1983–84 and then a persistent decline until the 1990–91 fishing season. Since then a fast upward trend can be seen. Published data series (number of recruits and number of adults) show peak values in 1985–86, and then downward trends (more recent data are not available). Landings peaked around the 1988–89 fishing season and dramatically declined through 1992–93. Since then, they have shown a persistent upward trend.

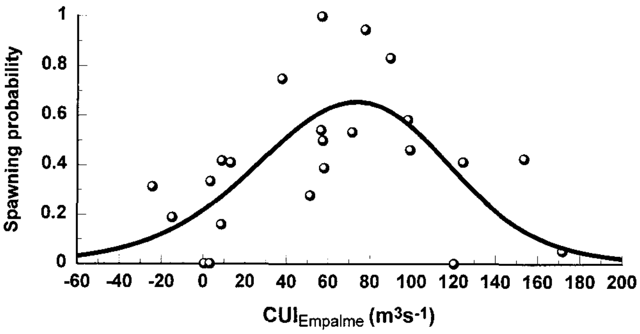

Figure 4. Spawning probability as a function of the $CIU_{Empalme}$ (circles) and fitted model (line).

DISCUSSION

Enrichment concentration and retention processes co-occur during a certain part of the year in the central Gulf of California. Panels 2 through 5 of figure 2 show

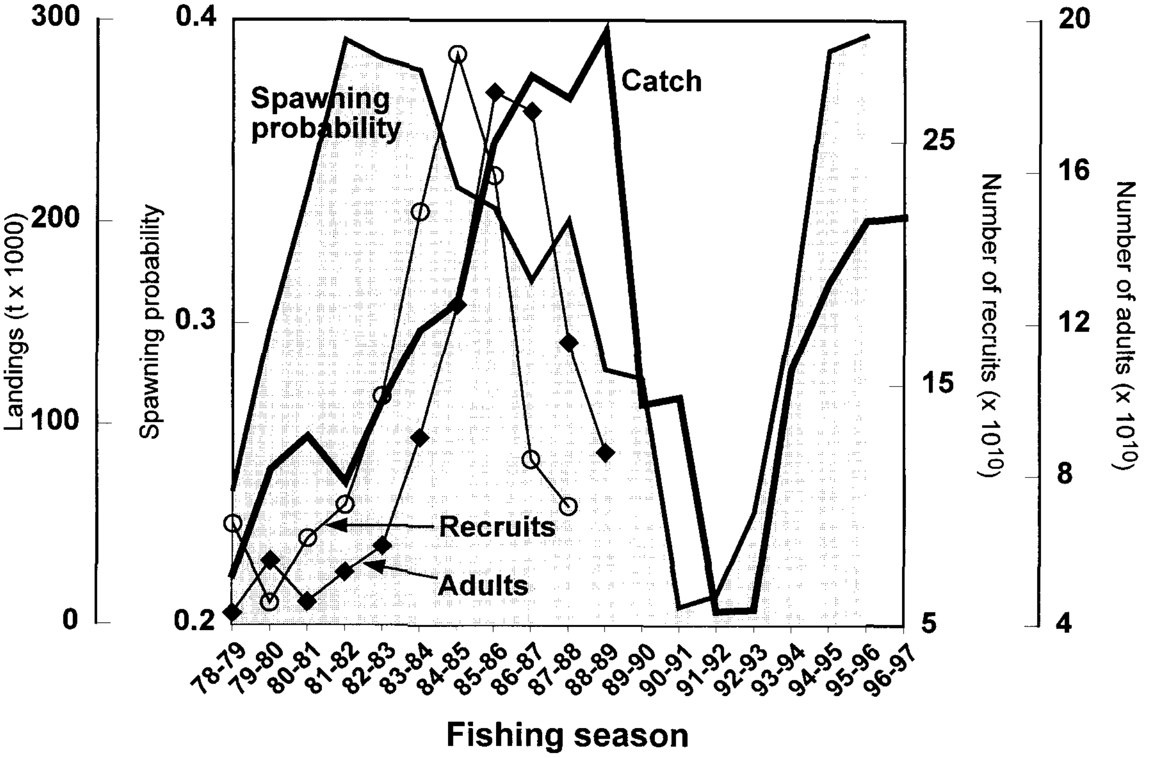

Figure 5. Time series of spawning probability as estimated from the spawning probability function (shaded curve), number of recruits (open circles), and number of adults (dark diamonds) digitalized from Cisneros-Mata et al. (1995). Landings of Gulf of California sardine (bold line) provided by CRIP-Guaymas-INP.

some real data and numerical model results. Enrichment is illustrated by a satellite-derived winter-composite pigment concentration (October–March; 1978–86). Retention and concentration are shown by outputs from a POM (Princeton ocean model; Blumberg and Mellor 1987) adapted to the gulf by Pares-Sierra and simulating surface ocean conditions after a month of winter winds and tidal forcing. Concentration is given as current residuals (i.e., transport without tidal influence). Retention is represented by a first escape index (the average residence time of a particle in a given). Finally, historically integrated sardine egg abundance (as modified from Hammann et al. 1998) demonstrates the importance of the central gulf as a spawning ground.

We believe the coherent, parallel behavior between the sardine series and the spawning probability series (i.e., an index of the extent of spawning as computed from wind data) strongly supports the existence of a wind-forced triad system governing the sardine spawning habitat and therefore large fluctuations of the population. If we look at the first part of the series (1978–86), coherent relations can be established between the probability series—based on egg and larval survey data—and the independent series of population dynamics. The environmentally favorable conditions, as reflected by the spawning probability estimated from the $\mathrm{CUI}_{\mathrm{Empalme}}$, are followed by the number of recruits with a delay of one year. The adult members and the landings series are also consistently delayed. Thereafter, from 1987 through 1996, spawning probability still led the sardine landing series, but the delay does not correspond to that observed during the previous period. Although we are not certain how the number of recruits and adults behaved during this second period, we can state that, at least to some extent, this difference is because the landings before the collapse consisted mainly of 2- to 3-year-old fish, whereas the recovery was based mainly on very young (1-year-old) fish (Nevárez-Martínez, pers. comm.). In any event, this second period is still more encouraging because it behaves coherently during a period of large, dramatic changes in the population (collapse and recovery). More important, the probability function was constructed only from data prior to this period, and thus the spawning probability series is predictive.

CAVEATS AND FURTHER RESEARCH

Though the physical setting of the model was formulated from observations and results from many authors, knowledge gaps must be filled and complete understanding reached by combining results from numerical models, retrospective analyses, and field observations. Besides testing the proposed hypothesis, we should improve our modeling capabilities. If it is true that the wind signal is a good predictor of tendencies in the fishery, it may also be true that more quantitative and valuable results could be obtained if we also consider other key environmental signals. Numerical modeling and field observations could indicate the concentration and retention processes in the spawning ground; the importance of coastal upwelling as a rich water source in relation to total food availability; changes in the size and quality of the spawning ground; and turbulence. Furthermore, quantification of the relative importance of temperature as a limiting factor, and its incorporation into the model should be relevant.

Implementing environmental monitoring systems for fishery forecasting represents a further step, and the main goal for this type of research. Such work requires high-quality data. Fortunately, remote sensing can now be combined with sophisticated field sensors to measure many physical properties of the ocean. However, a solid theoretical basis is needed before any advance can be made.

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AGE AND GROWTH OF MARKET SQUID (*LOLIGO OPALESCENS*) OFF CALIFORNIA DURING 1998

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ABSTRACT

Daily increments in statoliths indicate that both male and female market squid (*Loligo opalescens*) mature as early as 6 months after hatching. An analysis of 192 statolith pairs revealed maximum ages of 238 days for females and 243 days for males during 1998. These ages indicate that market squid may be a semiannual species and that spawning peaks may occur twice in a calendar year. Growth rate derived from size-at-age information was best described by a linear equation, with no difference between sexes.

INTRODUCTION

Market squid (*Loligo opalescens*) has been the basis of an important commercial fishery in California since the 1850s. The fishery takes place in northern California and southern California at different times of the year. The northern fishery season (mainly in Monterey Bay) traditionally occurs from April through November (fig. 1); the southern fishery (mostly in the Channel Islands vicinity) begins in October and generally lasts through March (fig. 2). Most squid are caught by fishers using lights to attract aggregations to the surface, where the squid are netted with brails, lamparas, and purse seines. The method of capture differs significantly from that for other loliginid fisheries worldwide (Hatfield et al. 1990; Augustyn et al. 1993), because fishing is done directly on spawning sites.

In the last decade, increases in catch and price have combined to make market squid the most valuable fishery in the state. Landings peaked in the 1996–97 season (1 April through 30 March; fig. 3), totaling over 113,000 metric tons valued at approximately $41 million. As a result of elevated sea-surface temperatures attributable to the 1997–98 El Niño event (Leos 1998), landings declined dramatically during the 1997–98 season to below

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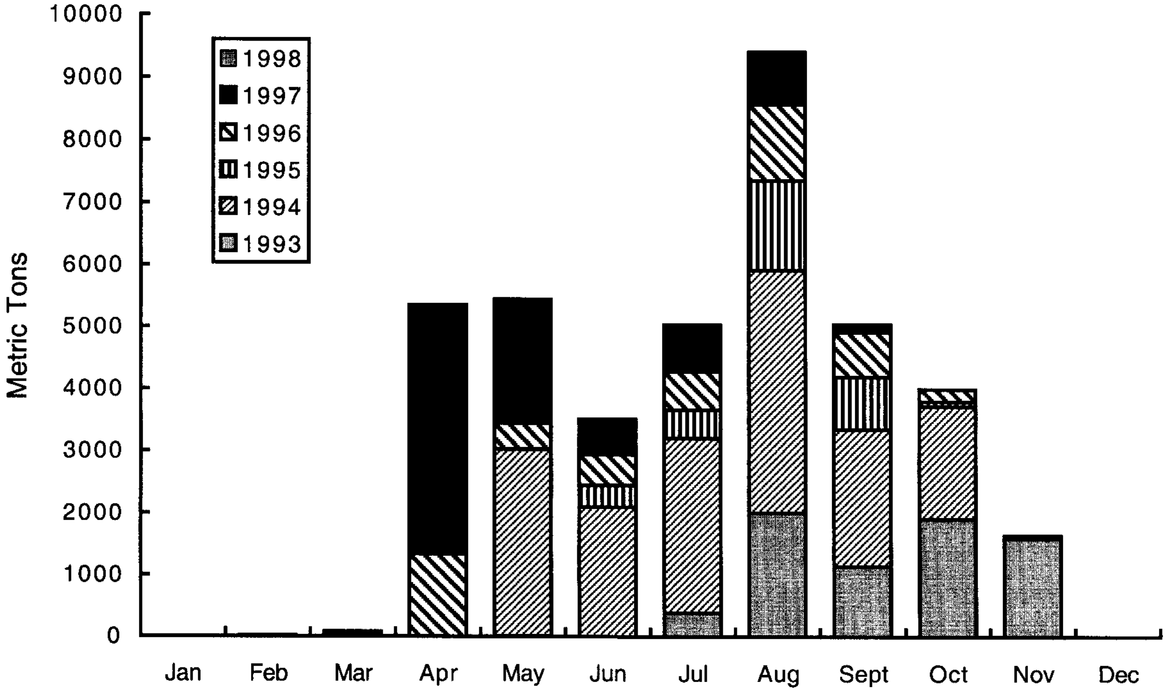

Figure 1. Monthly market squid landings in California north of Point Conception, 1993–98. Data for 1998 are preliminary.

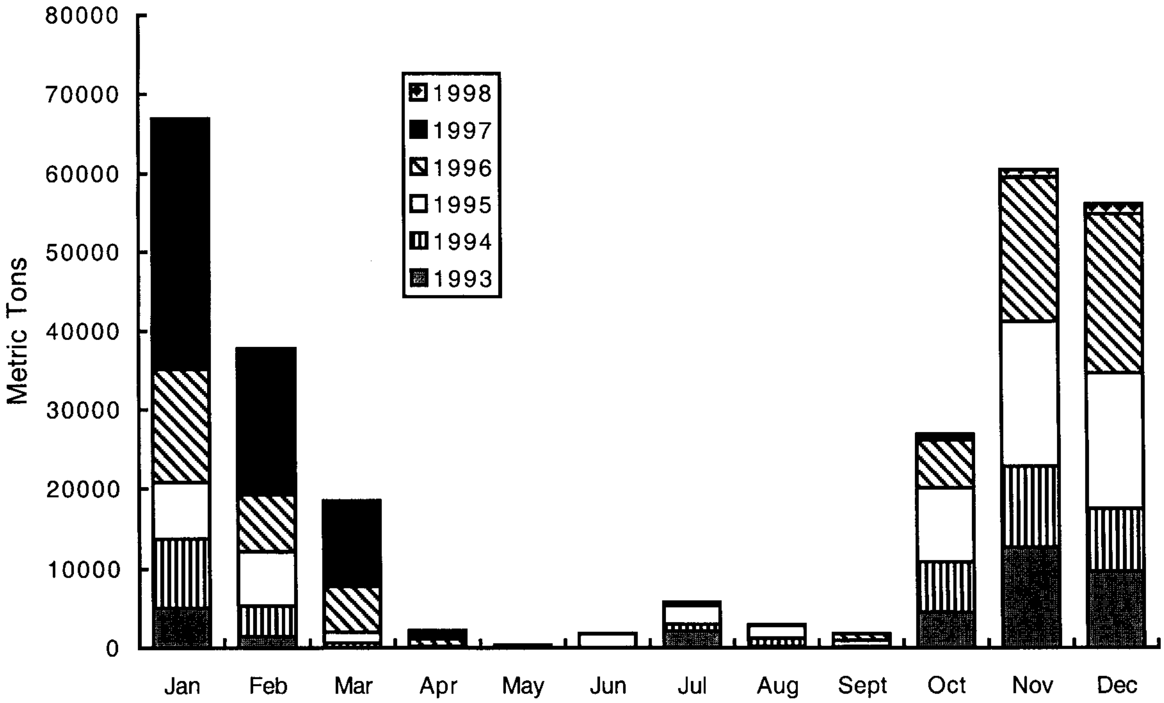

Figure 2. Monthly market squid landings in California south of Point Conception, 1993–98. Data for 1998 are preliminary.

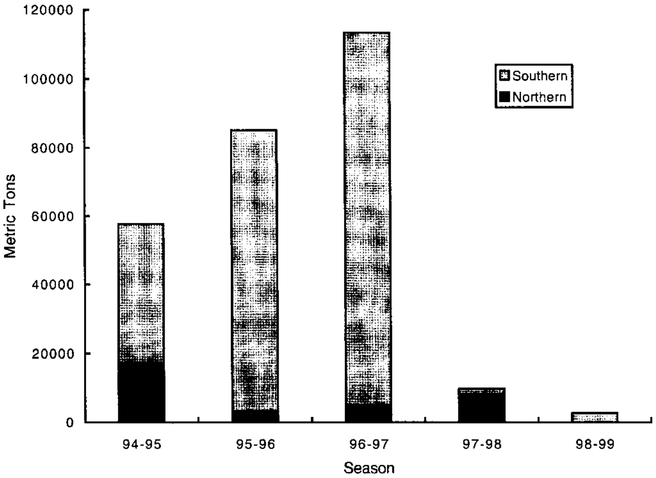

Figure 3. Seasonal (April through March) market squid landings in California, 1993–94 through 1998–99. Data for 1998–99 are preliminary.

10,000 t. In the first quarter of 1998, fewer than 40 t of squid were landed, compared with over 60,000 t landed for the same time period in the 1996–97 season.

Squid statoliths are calcareous structures analogous to fish otoliths (Rodhouse and Hatfield 1990a). Clarke (1966) first observed microincrements in squid statoliths and suggested that they might be useful for age determination. Although this observation predates Pannella's (1971) observation of microincrements in fish otoliths, the use of daily increments to age squid did not gain general acceptance until the mid-1980s (Hurley et al. 1985; Lipinski 1986; Jackson 1990a, b, 1994; Bettencourt et al. 1996; but see also Spratt 1978). Conversely, the application of daily increment analysis to fish otoliths was quickly accepted (Brothers et al. 1976; see also Campana and Neilson 1985, and Jones 1986 for reviews). The daily formation of microincrements has been validated in *Loligo opalescens* by Yang et al. (1980 and 1986). We adopted the daily ageing criteria of Yang et al. (1980 and 1986) and Jackson (1994) to age market squid.

Many aspects of the life history of market squid remain unknown. The California Department of Fish and Game and the National Marine Fisheries Service, recognizing the need for better scientific information on squid, held a meeting in August 1997 to identify priorities and develop a joint state and federal research protocol. Age and growth of squid ranked among the top objectives. This paper describes the age and growth of market squid and is the first contribution from the joint project. Although the data are preliminary and collection efforts spanned only one year (1998), knowledge of growth and longevity is crucial to management of the species.

MATERIALS AND METHODS

Market squid were collected with several gear types and at various times and locations throughout 1998 (table 1). We do not attempt to analyze variations in growth rate that may be attributable to these differences.

During a research cruise on the RV *David Starr Jordan* from 6 to16 January 1998, adult market squid were taken

TABLE 1
Squid Samples Collected in 1998 and Analyzed for Age and Maturity

Date	Number	Maturity	Gear type	Location
1/11/98	20	Juvenile	Midwater trawl	Off Santa Catalina Is.
1/12/98	111	Mature	Bottom trawl	Off Santa Cruz Is.
3/11/98	3	Juvenile	Commercial seine	Off Santa Catalina Is.
3/11/98	10	Mature	Commercial seine	Off Santa Catalina Is.
3/12/98	2	Juvenile	Commercial seine	Off Santa Catalina Is.
3/12/98	29	Mature	Commercial seine	Off Santa Catalina Is.
7/9/98	13	Juvenile	Midwater trawl	Off Purisima Pt.
7/10/98	7	Juvenile	Midwater trawl	Off Purisima Pt.

in bottom trawls at depths of 105, 225, and 440 m, at bottom temperatures of 8.3°–13.6°C. Juveniles were collected in one midwater trawl tow to depths of 95 m. In July 1998, squid were sampled with midwater trawls on the FV *Predator* at 34°31.02"N, 120°52.79"W. Additional samples were obtained from squid caught commercially by purse seine at Santa Catalina Island and landed in San Pedro on 12 and 16 March 1998. Light boats were used to aggregate the squid near the surface for those catches.

Daily growth increments in 192 statolith pairs were analyzed to back-calculate birth date. Statoliths were removed from all squid, stored dry in gelatin capsules, and later mounted on microscope slides with thermal plastic material. After polishing the statoliths, we enumerated daily increments by using Image Pro Plus software integrated with a spot CCD digital camera mounted atop a Leica DMLB compound microscope. The best images for analysis were obtained with a neutral-density light filter and no polarization.

Dorsal mantle length (mm) and weight information were taken from all specimens analyzed. Sex and state of maturity were observed in samples collected in the field, but we were unable to determine maturity in frozen samples. Females were considered to be mature if hydrated eggs were present in the ovary and oviduct; males were determined mature if spermatophores were present in the testes and spermatophoric sac.

RESULTS AND DISCUSSION

Catches

The onset of El Niño corresponds precisely with the decline in squid landings during 1997–98 (see Lynn et al. 1998 for complete documentation of El Niño conditions in the California Current). Additionally, El Niño conditions severely reduced squid catches during 1973, 1983–84, and 1992. Despite this, we believe the squid continued to reproduce during the 1997–98 El Niño, but avoided the warmer waters at the surface and traditional southern California spawning locations.

Market squid did not respond to commercial light boat efforts on traditional squid fishing locations near Santa Catalina Island, Santa Cruz Island, and Santa Rosa Island during January 1998, a month when peak fishing activity normally occurs in southern California. Similarly, during the January 1998 research cruise, no squid were seen at the surface under lights deployed to attract them. CTD profiles taken concurrently with the positive trawl efforts indicate that temperatures exceeded 17°C at depths shallower than 45 m, and exceeded 14° at depths shallower than 75 m (fig. 4). Squid were not taken in trawls at depths shallower than 95 m.

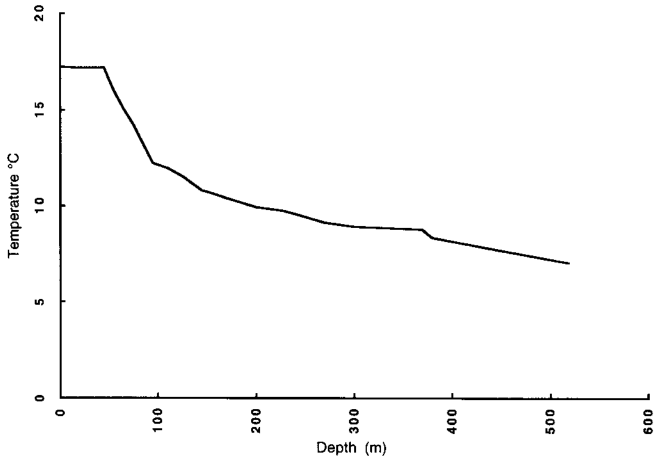

Figure 4. Temperature profile at CalCOFI station 90.37 on 14 January 1998.

Although adults collected at depths of 95 m and below were mature, no egg cases were collected concurrently in the trawls. However, commercial trawlers reported significant volumes of squid eggs in nets deployed at depths to 720 m off Carmel, California. These eggs were incubated and positively identified as market squid (Jerry Spratt, CDFG, pers. comm.). Thus it appears that squid were spawning in southern California but not at the normal depths of the traditional fishing grounds, probably because of warmer temperatures both at the surface and at depth. The extent of spawning compared to normal years is unknown.

Growth Rates

Size-at-age determined by statolith increment analysis indicates that market squid do not grow asymptoti-

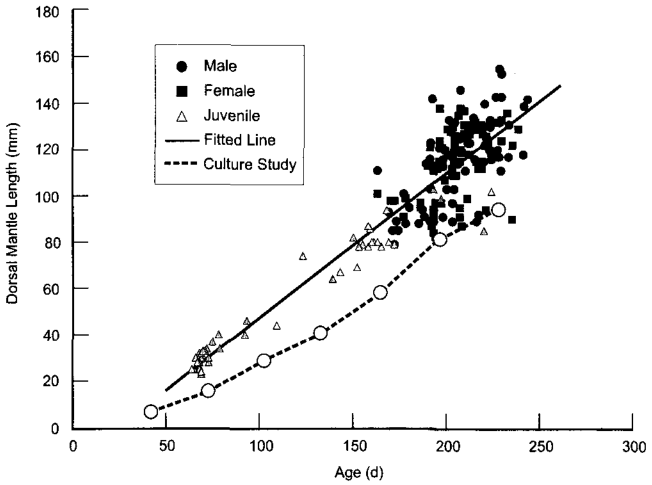

Figure 5. Size at age of male, female, and immature market squid (*Loligo opalescens*) taken in 1998. Solid line is DML = −14.7 + 0.627*Age. The dashed line is the trajectory of the reared specimens (Yang et al. 1986). R^2 value = 0.83.

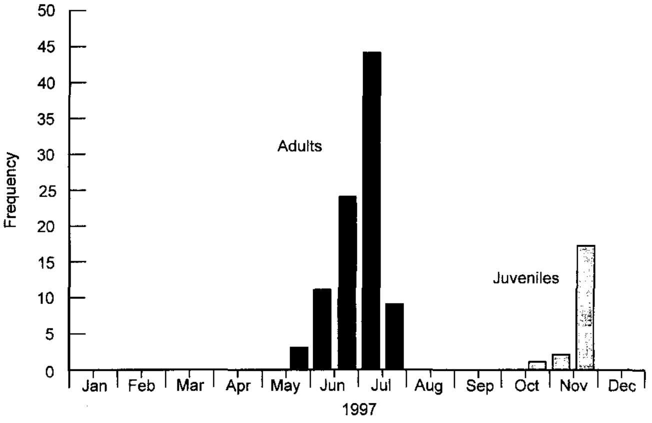

Figure 6. Distribution of hatching dates of market squid collected in 1998.

cally. Growth in length was best described with a linear equation (fig. 5), rather than an exponential or power function: DML = −14.7 + 0.627★Age, where DML is dorsal mantle length and Age is in days.

Growth averages about 0.6 mm DML per day. The youngest mature male and female aged were 163 days. The oldest female was 238 days, and the oldest male 243 days. There was no significant variation in growth rate between male, female, and indeterminate individuals.

The back-calculated birth dates of adult squid collected in January 1998 indicate that these squid hatched during May–July 1997 (fig. 6). Juvenile squid collected in January were born during November 1997. All of these squid were born during and survived El Niño conditions (Lynn et al. 1998), a period when little or no squid were landed, and no squid were observed on the shallow-water spawning grounds. We believe that our specimens were derived from eggs deposited at depth.

Growth rates reported here are similar to those determined for laboratory specimens (fig. 5). Jackson (1998) reviewed growth rates for market squid and concluded that early work by Fields (1965) and Spratt (1978) had underestimated growth and overestimated longevity, which had been determined at about 2 years. In more recent laboratory experiments (Yang et al. 1980, 1986) and supported by Jackson's (1994) 12 field specimens, squid demonstrated higher growth rates than previously reported, with maturation in less than 200 days and life spans of up to 300 days. Similarly, our study indicates maturation in less than 200 days, with life spans not exceeding 250 days.

Differences between our results and those of Jackson (1994) may be attributed to regional variation; his samples were collected from Monterey Bay and ours from southern California. Additionally, Jackson's (1994) samples were from a normal year in terms of water temperature, whereas ours were from an El Niño year. Seasonal variation may have affected our results as well; seasonal differences in growth rate have been reported for other loliginids, including the Patagonian squid (*Loligo gahi*; Rodhouse and Hatfield 1990b), long-finned squid (*Loligo pealei*; Brodziak and Macy 1996), and *Lolliguncula brevis* (Jackson et al. 1997).

The short life span and early maturation of market squid reported here are consistent with those reported for other species of *Loligo* (Collins et al. 1995; Bettencourt et al. 1996; Brodziak and Macy 1996). However, life spans of less than one year for California market squid would appear inconsistent with commercial fishery landings that show strong annual cycles.

Several scenarios could reconcile these inconsistencies. Strong seasonal landings trends may result from within-season cohorts who display different growth and survival rates. Brodziak (1998) and Brodziak and Macy (1996) have proposed this scenario for the long-finned squid in the northeast Atlantic.

However, the fact that the northern and southern California fisheries peak six months apart might suggest a second hypothesis: recruits from successful Monterey spawning activity may become the adults taken in the southern California fishery, and vice versa. The birth date distribution of adult squid spawning in southern California in January 1998 indicate that these individuals hatched from eggs deposited during the summer of 1997, which corresponds to the spawning period in northern California. This hypothesis is weakened somewhat by the fact that landings in northern California account for only about 12% of the statewide total. The northern California cohort would therefore probably exhibit a higher recruit-to-spawner ratio in order to perpetuate the population. At present there is no evidence to support a higher survival rate for eggs and larvae spawned in northern California.

A third hypothesis is that significant spawning activity may take place in southern California during the summer, but at depths which generally preclude commercial fishing with lights to attract squid to the surface. A research cruise aboard the RV *Mako* in August 1998 documented some summer egg-case deposition on southern California fishing grounds that in recent years have supported high-volume landings during winter. It is possible that additional spawning is occurring at greater depths.

The resolution of this paradox will require further study of the growth rates and life spans of cohorts from both northern and southern localities over several seasons as well as greater understanding of the depth distribution of squid spawning.

ACKNOWLEDGMENTS

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MARKET SQUID (*LOLIGO OPALESCENS*) IN THE DIET OF CALIFORNIA SEA LIONS (*ZALOPHUS CALIFORNIANUS*) IN SOUTHERN CALIFORNIA (1981–1995)

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ABSTRACT

California sea lion (*Zalophus californianus*) scat and spewing samples collected at three rookeries in southern California during 1981–95 were used to determine how sea lions utilized the market squid (*Loligo opalescens*) resource. The samples revealed that market squid is one of the most important prey of sea lions in southern California, occurring in 35% to 44% of scat samples from San Nicolas Island (SNI), San Clemente Island (SCI), and Santa Barbara Island (SBI). It is eaten by sea lions throughout the year, but most often during fall and winter, and patterns suggest periods of high and low consumption associated with prevailing oceanographic conditions and, possibly, with squid abundance and movements. Percent frequency of occurrence values for market squid in scat samples collected seasonally from SNI were positively correlated with those from SCI ($r = 0.78$), and samples collected during summer at SBI were positively correlated with summer samples from SCI ($r = 0.82$) and SNI ($r = 0.85$). Landings of market squid at ports in southern California and percent occurrence values of market squid in scat samples collected seasonally were positively correlated for SNI ($r = 0.66$) and SCI ($r = 0.74$), but not for summer samples from SBI ($r = 0.25$). Sea lions eat squid with dorsal mantle lengths from 10 to 235 mm (mean = 127 mm). Significant seasonal, annual, and interisland differences ($P < 0.001$) were found in the size of squid consumed by sea lions. Significant differences ($P < 0.001$) were found in size of squid between scats and spewings, and between individual samples.

INTRODUCTION

Market squid (*Loligo opalescens*) is one of the most common prey species for California sea lions (*Zalophus californianus*) in southern California (Antonelis et al. 1984; Lowry et al. 1990, 1991). Sea lions eat squid throughout the year, but predominantly during autumn and winter, and its presence in their diet varies from year to year (Lowry et al. 1990, 1991). A spring and summer study at San Miguel Island showed that sea lions eat squid with a dorsal mantle length of 62 to 185 mm (mean = 127 mm; Antonelis et al. 1984).

In 1995, the sea lion population along the U.S. Pacific coast was estimated at 167,000 to 188,000 individuals, with an average annual growth rate of 8.3% since 1983 (Barlow et al. 1997). Sea lions are also found in western Mexico from the U.S.–Mexico border to central Mexico, and in the Gulf of California (Le Boeuf et al. 1983), but there is no current abundance estimate for sea lions south of the U.S.–Mexico border.

Numbers of sea lions in southern California fluctuate during the year. More are present at rookeries (fig. 1) during the summer breeding season, and fewer during autumn and winter. Adult females generally remain in the area throughout the year to nurse their pups, and juveniles either remain near rookeries or travel north or south along the coast (Bartholomew 1967; Huber 1991). After the summer breeding season, subadult and adult males from U.S. rookeries migrate north (some as far as British Columbia, Canada) and those from western Baja California, Mexico, migrate into and through southern California (Bartholomew 1967; Bigg 1988).

Studies at San Miguel Island have shown that adult female sea lions forage between 10 and 100 km (mean = 54.2 km, SD = 32.4 km, $n = 9$) from the rookery (Antonelis et al. 1990), and dive to average depths of 31.1 to 98.2 m, with maximum dives between 196 and 274 m (Feldkamp et al. 1991). Laboratory studies indicated that sea lions travel at an estimated speed of 10.8 km/hr (Feldkamp 1985), and that one- and two-year-old sea lions have an initial defecation time averaging 4.2 hours (Helm 1984). Adult females spend 1.6–1.9 days on land and 1.7–4.7 days at sea (Heath et al. 1991). Feeding experiments on California sea lions that were fed market squid revealed that (1) 80% of squid beaks (i.e., mandibles) pass through the gastrointestinal tract within 48 hours and 95% within 96 hours; (2) squid remains may be spewed within 20 to 48 hours; and (3) all beaks are not regurgitated when squid remains are spewed—some pass through the gastrointestinal tract (Hawes 1983; Orr 1998). It is reasonable to assume, therefore, that scat and spewing samples collected at haul-outs represent a sample of feeding within 100 km of the haul-out site.

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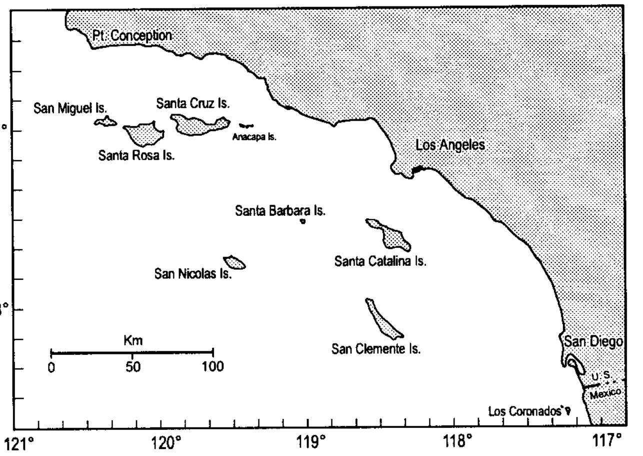


Figure 1. Map of Southern California Bight. California sea lion (*Zalophus californianus*) rookeries are located at Santa Barbara, San Clemente, San Miguel, and San Nicolas Islands.

Sea lions haul out of the water to rest, pup, and mate. While on shore, they eliminate waste in the form of scats (feces) and spewings (vomitus), which can be used to study their diet. Squid are identified from beaks, and fish from otoliths (earbones) recovered from scats and spewings collected at haul-out sites. Although fish otoliths are susceptible to erosion during digestion, chitinous beaks of squid are highly resistant to digestion (Hawes 1983).

Because market squid are one of the sea lion's most important prey items, it is apparent that the sea lion population and the squid fishery compete for the same resource. The California market squid fishery was the state's most valuable fishery in 1996, with ex-vessel revenues of $30 million (Yaremko 1997). Southern California fishermen accounted for 93% of 80,360 metric tons of market squid landed statewide in 1996, with most landings in autumn and winter.

Although sea lions consume a variety of fish and squid (Antonelis et al. 1984; Lowry et al. 1990, 1991), we will only report on market squid for three of four rookeries in southern California during 1981–95. Data on this and other prey species from San Clemente Island (SCI) and San Nicolas Island (SNI) during 1981–86 were published by Lowry et al. (1990, 1991). Long-term studies of sea lion diet provide information that may help to quantify how one of the top-level predators in the ecosystem affects the squid and fish resource. We investigate whether sea lion scat and spewing samples might be useful sources of information about trends in abundance or availability of market squid. We describe seasonal, annual, and interisland differences of market squid in sea lion scat samples, relationships with El Niño, and the size of market squid eaten by sea lions; we also compare the frequency of occurrence of market squid in scat samples to market squid landings (which may be a crude measure of abundance) by the southern California fishery.

METHODS

Sample Collection

Scat and spewing samples from sea lions were collected at Santa Barbara Island (SBI), SCI, and SNI during 1981–95 (fig. 1). As the population of sea lions increased during the study period, the number of haul-out sites at SBI and SCI remained the same, but in the late 1980s sea lions began to occupy additional sites along the southeastern shoreline of SNI. No samples were collected from new haul-out sites at SNI. Samples were collected from (1) the Southeast Rookery at SBI, (2) Mail Point and its vicinity along the western shoreline of SCI, and (3) three areas of coastline at SNI approximately 3.6–4.8 km, 5 km, and 6.5–7 km along the southern shoreline from Vizcaino Point (i.e., the westernmost point on the island). Samples from the 5 km site at SNI (added in 1992) were collected only in July, when subadult and adult males were separated from adult females. All other collecting sites were occupied year-round by adult females, but other age and sex classes were also present during various times of the year.

Samples were collected opportunistically at intervals ranging from two weeks to three months during 1981–87 at SCI and at intervals ranging from two weeks to nine months during 1981–90 at SNI. A quarterly sampling design was established in 1988 at SCI and in 1991 at SNI, and approximately fifty samples were collected (whenever possible) at each collection site during January, April, July, and October. Samples at SBI were collected only during summer (mostly in July). In 1981–82, samples at SBI were collected opportunistically; thereafter approximately fifty samples were collected each year.

Samples were grouped by season into winter (December–February), spring (March–May), summer (June–August), and autumn (September–November; table 1). Fresh and dry samples from monitored sites were collected at SCI in 1981–87 and at SNI in 1981–90, but thereafter only fresh samples were collected. At SBI, only fresh samples were collected. We estimated that fresh samples represented the diet within the last 3–4 days of the collection date, and dry samples represented the time since the last collection.

Sample Processing

Each sample was washed through a 2.8 mm^2 mesh sieve placed atop a 0.710 mm^2 mesh sieve (sometimes a 1.5 mm^2 mesh sieve was placed between the two sieves). Fish otoliths, cephalopod beaks, teeth from jawless and cartilaginous fishes, and crustacean exoskeletal remains were collected from all sieves and used to identify prey remains to the lowest possible taxonomic level. Market squid beaks were identified from museum voucher spec-

TABLE 1
Number of California Sea Lion (*Zalophus californianus*)
Scats and Spewings (in Parentheses) Collected at Sites in Southern California, 1981–95

	San Clemente Island				San Nicolas Island				Santa Barbara Island
Year	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Summer
1981				41			24(2)	18	76
1982	3	107	143	54(1)	12	15	68	13	50
1983	59(12)	110(1)	77	78	4	42	150	55(1)	31
1984	144(1)	101	89(1)	53	75	35	107	93(1)	50
1985	16	12	60	26	62	77(7)	64	63	44
1986		44	65	22	35	24	80	124	52
1987	6(2)	30	50	34(1)			25		57
1988	49(1)	57	43	12(2)	18	26	49		51
1989	25(43)	55	51(1)	68(11)	23	36	31		56
1990	37(33)	50	55	50		49			56
1991	51(8)	52	55	55	49(3)	52(1)	110	99(2)	51
1992	50(1)	51	52	50	102(3)	97	149	101	51
1993	50	50(2)	51	49(1)	102(9)	96(5)	152	99(2)	52
1994			49(1)	45(5)			98	99	50
1995	46(4)	51(5)	41(9)		99(1)	98(4)	147	102	49

imens and from a pictorial guide (Iverson and Pinkas 1971). Although several species of squid have been identified as prey of California sea lions (see Antonelis et al. 1984; Lowry et al. 1990, 1991), the distinctive shape and coloration of market squid beaks make them easy to distinguish from other species even when degraded by digestion.

Sample Analysis

Percent frequency of occurrence in scat samples was used as a seasonal index of consumption for each prey taxon, to rank prey, and to examine seasonal and annual changes. Percent frequency of occurrence is the percentage of samples containing either a prey taxon or unidentified fish otoliths, cephalopod beaks, teeth from jawless and cartilaginous fishes, or crustacean exoskeletal remains. We smoothed the time series of percent occurrence index values with a distance-weighted least squares (DWLS) smoother with the tension set at 0.25 (Systat 6.0 for Windows; Anonymous 1996a) to examine multiyear cycles of market squid in scat samples for the three rookeries. Percent frequency of occurrence index values for each season were arcsine-transformed.

We used correlation analysis to compare transformed index values among the three islands to test the hypothesis that market squid appears in the diet of sea lions from different islands in equal proportions. We also used correlation analysis to compare transformed index values from each island to seasonal market squid landings in southern California (landings data provided by Bill Jacobson, NMFS, Southwest Region, pers. comm., March 21, 1997) to test the hypothesis that squid in the diet of sea lions reflects abundance (assuming that landings are a crude measure of abundance).

Estimation of Squid Length

We estimated dorsal mantle length (DML) of market squid eaten by sea lions by measuring the rostral width of upper beaks recovered from scat and spewing samples. We used upper rostral width (URW) because it resists digestion better than other beak dimensions. Beaks were measured with a micrometer in the eyepiece of a dissecting microscope. Samples included beaks collected at SBI (1989–95), SNI (1987–95), and SCI (1981–95; table 2). We used the regression equation developed by Kashiwada et al. (1979) to estimate dorsal mantle length from each rostral width measurement. Measurements of URW were used for statistical analysis, and DML estimates from URW measurements were used for graphic presentations.

Analysis of Squid Size

A missing cells design means-model ANOVA (Systat 6.0 for Windows; Milliken and Johnson 1984; Anonymous 1996b) was used to compare URW measurements between islands, years, and seasons because not all seasons were sampled during 1981–95 (table 1) and because not all beaks found in samples were measured (table 2). We tested the null hypothesis that there was no difference (at $\alpha = 0.05$) in URW of market squid between season, year, and island for samples collected at SCI and SNI during 1988–95 (samples from SBI were not included because all seasons were not represented). We performed this analysis on URWs from beaks found in scats and, separately, scats and spewings combined. We also used the means-model ANOVA to compare URWs of beaks found in scats to those in spewings when both sample types were collected at SCI during 1988–95 and, separately, at SNI during 1991–95.

TABLE 2

Number of Beaks Measured from Scats and Spewings (in Parentheses) for Estimating Dorsal Mantle Length of Market Squid (*Loligo opalescens*) Consumed by California Sea Lions, 1981–95

	San Clemente Island				San Nicolas Island				Santa Barbara Island
Year	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Summer
1981				127					
1982		39	434	16					
1983	54(98)	3	70	40					
1984		1	1						
1985			47	4					
1986	74(22)	317	27						
1987		13	42	42			10		
1988	152	13	25	87	19	6	62		
1989	443	53	181	216	96	2	78		434
1990	442	167	23	159		250			335
1991	371	112	31	171	408	221(83)	748	995	163
1992	274(3)	10	10	91	627	11	120	1,332	10
1993	274	1(34)	51	235	718	133(4)	400	899	35
1994			56(38)	247			31	446	88
1995	736	145	154		1,048	671	702	556	95

TABLE 3

Frequency of Occurrence of Common Prey Found in California Sea Lion Scat Collected Seasonally at San Clemente (n = 2,543) and San Nicolas Islands (n = 2,980), and in Summer at Santa Barbara Island (n = 736), 1981–95

		San Clemente Island		San Nicolas Island		Santa Barbara Island	
Scientific name	Common name	n	%	n	%	n	%
Engraulis mordax	Northern anchovy	1,155	45.4	897	29.4	360	48.9
Loligo opalescens	Market squid	895	35.1	1,323	44.3	315	42.7
Merluccius productus	Pacific whiting	631	24.8	931	31.2	290	39.4
Trachurus symmetricus	Jack mackerel	631	24.8	659	22.1	147	19.9
Sebastes jordani	Shortbelly rockfish	328	12.8	423	14.1	100	13.5
Pleuroncodes planipes	Pelagic red crab	301	11.8	244	8.1	72	9.7
Scomber japonicus	Pacific mackerel	264	10.3	463	15.5	59	8.0
Sardinops sagax	Pacific sardine	122	4.7	371	12.4	73	9.9

We examined size of squid within individual scat and spewing samples to see if scat and spewing samples had beaks from similar-sized squid. We assigned a unique sample code number to each scat and spewing sample. There were insufficient spewing samples from most collections for this analysis (table 1), but seven collections had an adequate number of spewing samples: (1) winter 1989 at SCI, (2) autumn 1989 at SCI, (3) winter 1990 at SCI, (4) winter 1991 at SCI, (5) autumn 1994 at SCI, (6) summer 1995 at SCI, and (7) winter 1993 at SNI. We used a nested ANOVA for each collection to test the hypothesis that there was no difference (at $\alpha = 0.05$) in URW of squid found between sample types (i.e., scats and spewings) and individual samples (sample was nested within sample type). Graphic representations of these comparisons were chosen for two of the seven collections (autumn 1989 at SCI and winter 1990 at SCI).

RESULTS

Market Squid in the Diet of California Sea Lions

Market squid was found in 35.1% to 44.3% of scat samples, and represented the most common or second most common prey taxon found at three southern California rookeries during 1981–95 (table 3). Other common prey of sea lions were northern anchovy (*Engraulis mordax*); Pacific whiting (*Merluccius productus*); jack mackerel (*Trachurus symmetricus*); shortbelly rockfish (*Sebastes jordani*); Pacific mackerel (*Scomber japonicus*); Pacific sardine (*Sardinops sagax*); and pelagic red crab (*Pleuroncodes planipes*, consumed only during El Niño periods). Sea lions ate market squid year-round, but predominantly during autumn and winter (table 4).

Smoothed seasonal percent occurrence index data indicated fewer squid in sea lions' diet during and immediately after moderate and severe El Niño episodes (1983–84 and 1992–93) and more squid in 1989–90 and 1995 (fig. 2). The sharpest decline occurred in 1984 and the first half of 1985, during or just after the 1983–84 El Niño period in California. We found market squid in scat samples of sea lions from different rookeries in similar proportions. Percent frequency of occurrence values for market squid in scat samples from SCI were positively correlated with those from SNI (r = 0.78) and SBI (r = 0.82), and samples from SNI were positively correlated with samples from SBI (r = 0.85). Seasonal

TABLE 4
Seasonal Frequency of Occurrence Indices for Market Squid Found in California Sea Lion Scat, and Metric Tons of Market Squid Landed in Southern California Ports, 1981–95

		Percent frequency of occurrence[a]			
Year	Season	SBI	SCI	SNI	Landings (t)
1981	Summer	36.7	—	18.0	3.8
	Autumn	—	42.4	56.0	1,483.4
1982	Winter	—	66.6	92.0	7,737.1
	Spring	—	17.5	50.0	1,537.0
	Summer	40.4	26.4	12.0	337.0
	Autumn	—	19.6	53.8	2.3
1983	Winter	—	28.2	25.0	895.0
	Spring	—	8.4	14.3	9.0
	Summer	38.7	22.2	17.1	4.0
	Autumn	—	25.6	27.3	0.9
1984	Winter	—	5.5	7.1	0.5
	Spring	—	3.4	6.9	64.0
	Summer	0	1.1	13.5	11.0
	Autumn	—	0	7.4	0.1
1985	Winter	—	0	13.0	347.4
	Spring	—	0	4.5	800.1
	Summer	28.2	23.6	13.3	322.1
	Autumn	—	20.8	41.8	1,824.1
1986	Winter	—	—	19.4	6,475.2
	Spring	—	35.1	0	957.2
	Summer	31.2	23.4	17.8	349.7
	Autumn	—	0	58.6	5,640.4
1987	Winter	—	50.0	—	8,589.9
	Spring	—	63.3	—	2,437.7
	Summer	35.4	26.0	4.0	14.1
	Autumn	—	46.8	—	3,839.2
1988	Winter	—	35.4	60.0	9,651.2
	Spring	—	19.6	26.9	4,749.2
	Summer	58.3	36.8	45.6	1,836.4
	Autumn	—	72.7	—	11,540.9
1989	Winter	—	80.9	91.3	20,855.7
	Spring	—	50.9	11.4	3,101.3
	Summer	83.0	63.0	73.3	618.6
	Autumn	—	67.7	—	10,825.3
1990	Winter	—	94.5	—	10,212.4
	Spring	—	57.4	64.5	137.9
	Summer	69.2	47.2	—	1.4
	Autumn	—	71.1	—	9,275.7
1991	Winter	—	76.0	89.1	11,984.6
	Spring	—	38.0	51.0	19.8
	Summer	72.5	31.2	63.0	500.2
	Autumn	—	63.4	76.5	17,099.8
1992	Winter	—	70.8	69.4	9,292.7
	Spring	—	12.8	11.7	35.4
	Summer	20.4	12.2	23.0	0
	Autumn	—	50.0	65.9	751.4
1993	Winter	—	46.9	71.4	7,681.4
	Spring	—	6.1	40.7	86.2
	Summer	33.3	45.0	40.7	2,201.7
	Autumn	—	81.2	88.6	17,258.4
1994	Winter	—	—	—	22,187.8
	Spring	—	—	—	600.4
	Summer	29.1	34.1	25.9	1,193.8
	Autumn	—	53.6	55.2	16,283.7
1995	Winter	—	97.7	73.9	21,708.9
	Spring	—	70.7	75.5	1,808.3
	Summer	60.4	50.0	64.0	5,708.8
	Autumn	—	—	75.7	28,500.1

Note: No samples were collected where dashes appear.

[a] SBI = Santa Barbara Island; SCI = San Clemente Island; and SNI = San Nicolas Island.

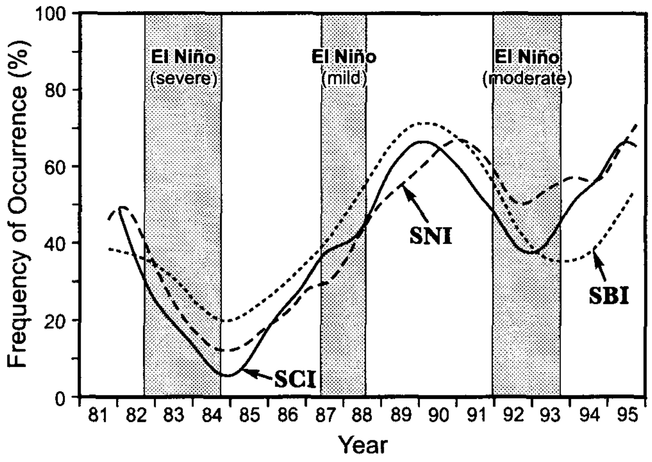


Figure 2. Distance-weighted least squares (DWLS) smoothed seasonal percent frequency of occurrence indices of market squid (*Loligo opalescens*) in California sea lion (*Zalophus californianus*) scat samples collected from Santa Barbara (SBI), San Clemente (SCI), and San Nicolas (SNI) Islands, California, 1981–95.

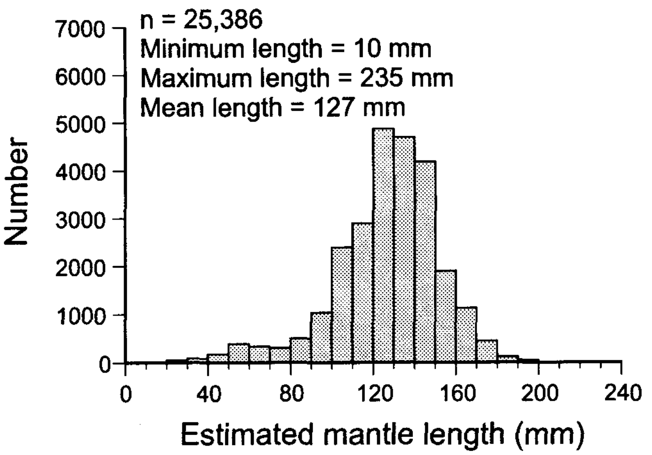


Figure 3. Size structure of all dorsal mantle length estimates of market squid (*Loligo opalescens*) derived from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples collected at Santa Barbara, San Clemente, and San Nicolas Islands, California, 1981–95.

landings of market squid in southern California ports correlated positively with seasonal frequency of occurrence values for SCI ($r = 0.74$) and SNI ($r = 0.66$), but did not correlate well with summer samples from SBI ($r = 0.25$).

Squid Length

Squid lengths from scats and spewings collected from 1981 through 1995 were combined into one data set to provide information on squid consumed by sea lions in the study area. Measurements of 25,386 squid beaks recovered from scats and spewings showed that sea lions ate market squid with a DML between 10 mm and 235 mm, with a mean length of 127 mm (fig. 3).

Seasonal, Annual, and Island Differences in Squid Length

The null hypothesis that there was no difference in size between seasons, years, and islands was rejected with the means model ANOVA ($P < 0.001$; table 5). The average size of squid (combining data from three rookeries) was 118 mm in spring, 109 mm in summer, 128 mm in autumn, and 137 mm in winter. Squid size was more variable between years in summer (fig. 4). Average squid size was 62–85 mm in El Niño summers and 109–128 mm in other summers (fig. 5). El Niño periods had smaller squid than non–El Niño periods (nested ANOVA: df $= 3$, $F = 1204.174$, $P < 0.001$). Sea lions at SCI ate larger squid than sea lions at SNI during winter (nested ANOVA: df $= 6$, $F = 139.190$, $P < 0.001$).

Size of Squid in Scats and Spewings

The mean upper rostral width of squid found in scats was significantly smaller than that in spewings at SCI (df $= 1$, $F = 82.182$, $P < 0.001$) and SNI (df $= 1$, $F = 5.406$, $P = 0.020$). Although squid represented in spewings were larger than squid in scats, overlapping distributions of seasonal samples indicated that no distinct size

TABLE 5

Means Model ANOVA for Upper Rostral Width Measurements of Market Squid Beaks Found in California Sea Lion Scat and Spewing Samples at San Clemente and San Nicolas Islands, 1988–95

	Scat samples			Scat and spewing samples		
Factor	df	*F*	*P*-value	df	*F*	*P*-value
Island	1	6.759	0.009	1	13.339	<0.001
Year	5	138.435	<0.001	5	184.812	<0.001
Season	4	418.133	<0.001	4	526.191	<0.001
Island*year	15	30.142	<0.001	15	37.950	<0.001
Island*season	16	44.389	<0.001	22	62.882	<0.001
Year*season	22	118.058	<0.001	22	185.164	<0.001

Note: Upper rostral width measurements were used to estimate dorsal mantle length.

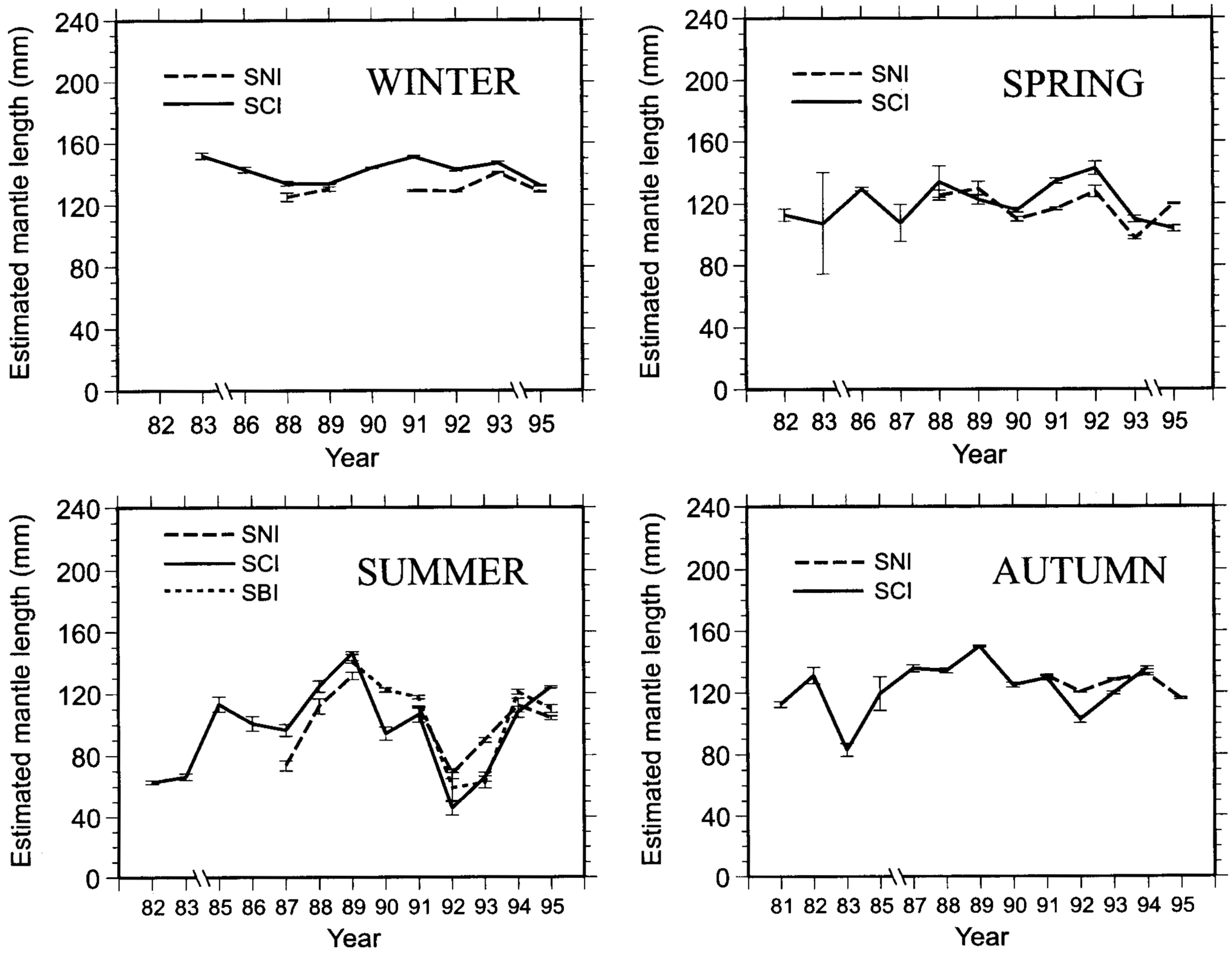
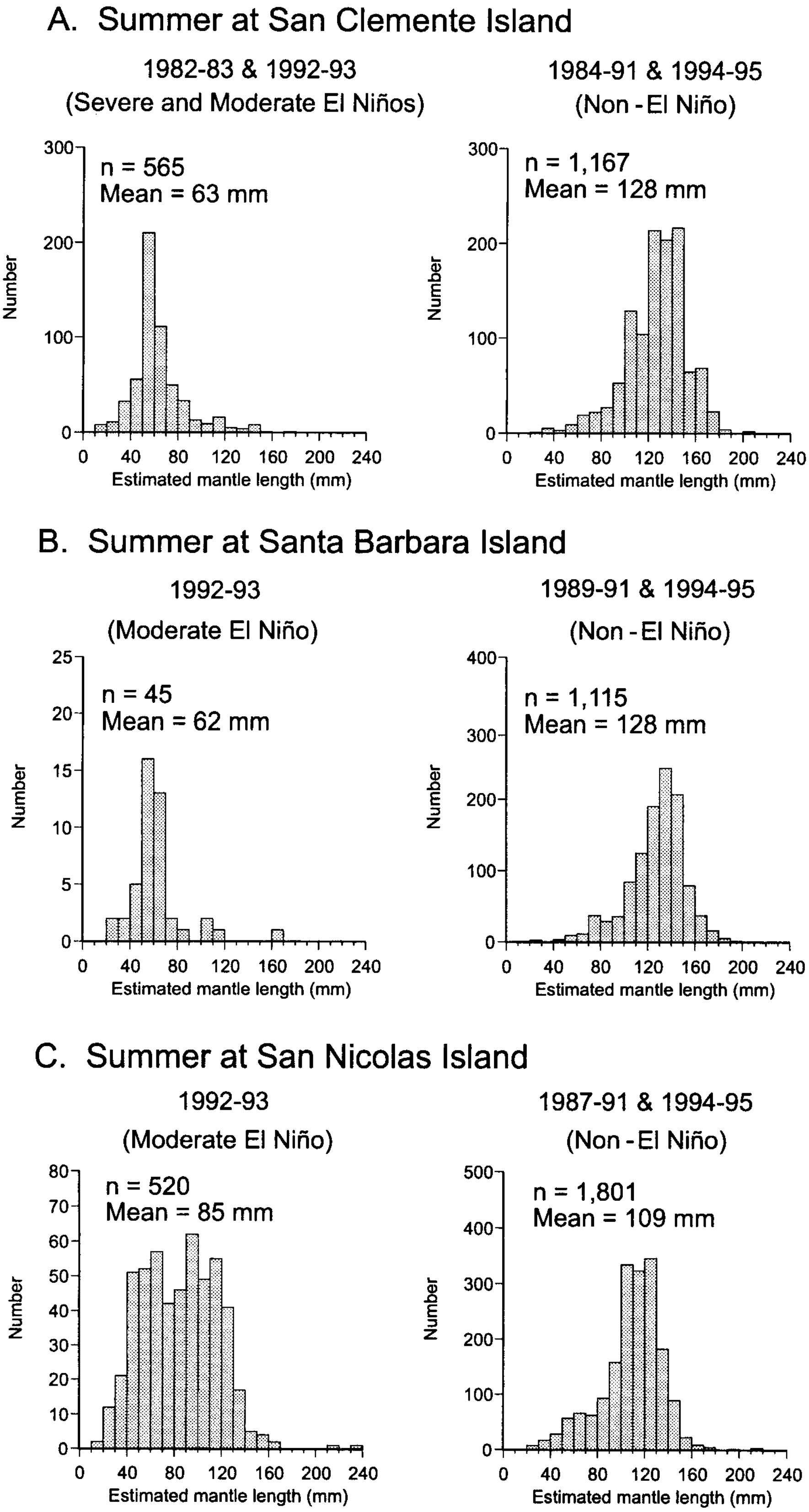


Figure 4. Annual estimated dorsal mantle length means of market squid (*Loligo opalescens*) derived from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples for each season at Santa Barbara (SBI), San Clemente (SCI), and San Nicolas (SNI) Islands, California, 1981–95. Bars indicate standard error of each mean.


A. Summer at San Clemente Island

B. Summer at Santa Barbara Island

C. Summer at San Nicolas Island

Figure 5. Comparison of size structure of dorsal mantle length estimates for market squid (*Loligo opalescens*) derived from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples collected during summer at (A) San Clemente Island, (B) Santa Barbara Island, and (C) San Nicolas Island during El Niño and non–El Niño years.

class was present in either sample type (figs. 6 and 7). Examination of individual collections (table 6) showed that squid size did not always differ ($P > 0.063$) between scat and spewing samples.

Size of Squid in Individual Samples

Size of squid in individual scat and spewing samples was significantly different for all seven collections examined (table 6). Although average size of squid varied, there was considerable overlap in distributions of size between samples (fig. 8).

DISCUSSION

Market squid is one of the most important prey of sea lions in southern California. Consumption of market squid by sea lions (inferred from the percent occurrence index) from three rookeries in southern California was synchronous; samples from the rookeries displayed similar seasonal and annual frequency of occurrence index values. Squid consumption was highly variable over shorter time periods: seasonal and annual data revealed periods when sea lions did not eat any market squid, and other periods when more than 90% of sea lions included it in their diet. The average size of squid consumed by sea lions had a DML of 127 mm, with a range from 10 mm to 235 mm. Although the average DML of squid in the Antonelis et al. (1984) study was similar to that in this study, the larger sample size of this study (25,386 vs. 76) showed that sea lions eat smaller and larger squid than previously reported.

Changes in oceanographic conditions within southern California, such as El Niño episodes, were reflected by dietary changes in sea lions (Lowry et al. 1990, 1991). During the 1981–95 period, oceanic waters off southern California were affected by three El Niño episodes of varying intensity: 1983–84 (severe), 1988 (mild), and 1992–93 (moderate). The sea lions ate fewer squid during moderate and severe El Niño episodes. These multiyear consumption cycles reflect the availability of market squid in southern California to sea lions, and may indicate the recovery rate of the squid population following moderate and severe El Niño episodes.

At San Clemente and Santa Barbara Islands, the average size of squid eaten during El Niño summers was half of that eaten during non–El Niño summers. This difference may be due to a lack of larger squid in the waters surrounding these two rookeries during El Niño summers, as evidenced by the paucity of larger squid in the samples. In contrast, at San Nicolas Island, both small and large size classes of squid were eaten during the 1992–93 El Niño summer, and the distribution of size classes is almost bimodal. The waters surrounding SNI

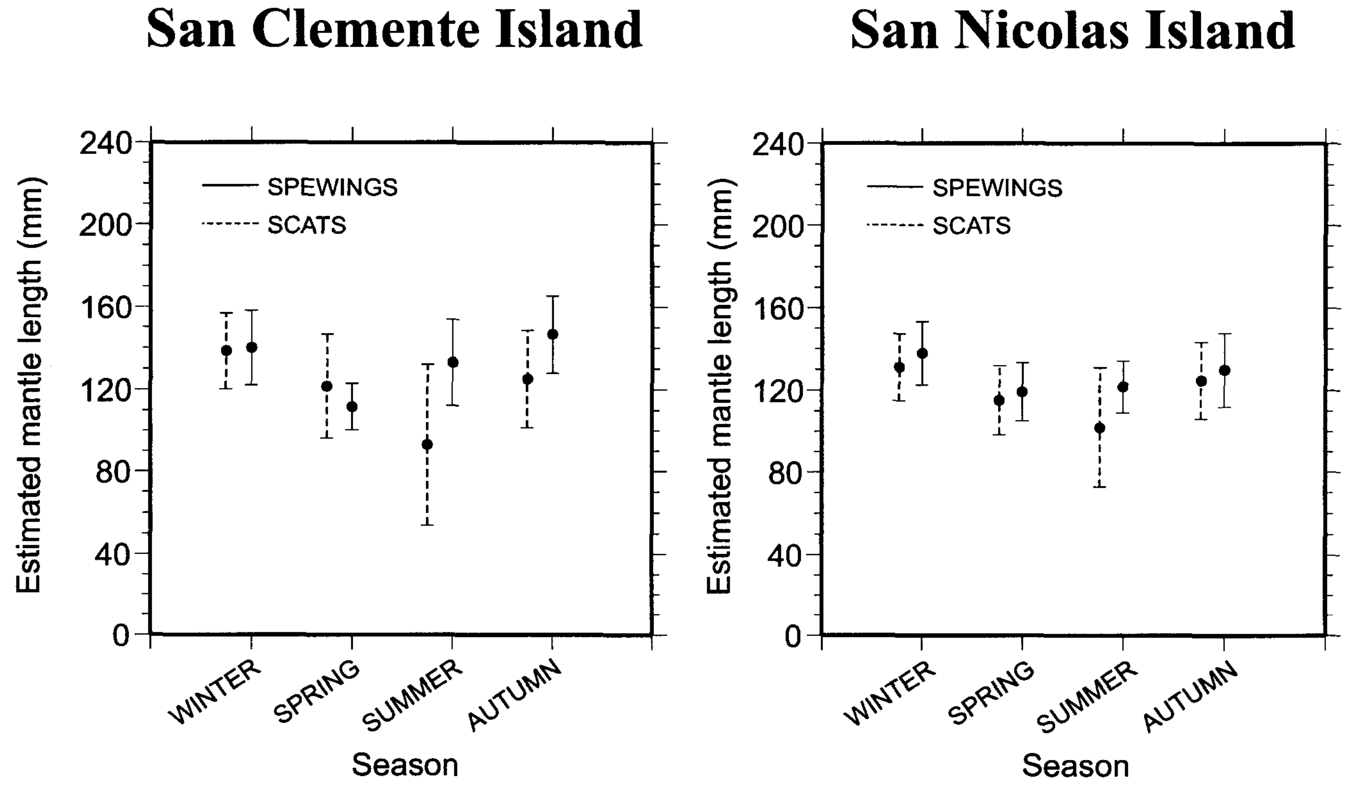


Figure 6. Mean dorsal mantle length of market squid (*Loligo opalescens*) estimated from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples collected seasonally at San Clemente and San Nicolas Islands, California. Bars indicate one standard deviation from each mean.

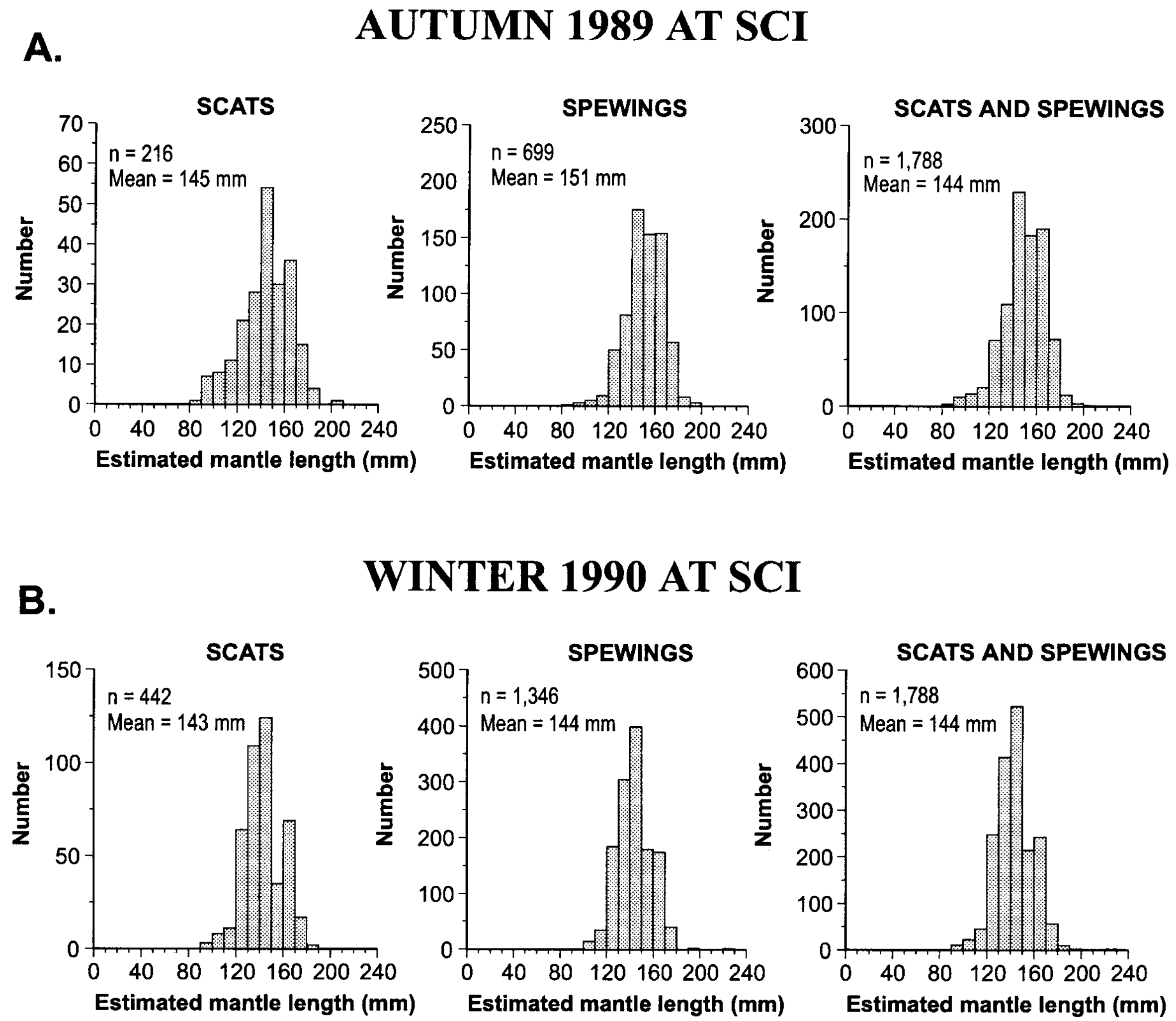


Figure 7. Size structure of dorsal mantle length estimates of market squid derived from beaks found in California sea lion (*Zalophus californianus*) scat and spewing samples collected at San Clemente Island, California, during (*A*) autumn 1989 and (*B*) winter 1990.

TABLE 6

Results of ANOVA Tests on Upper Rostral Width Measurements of Market Squid Beaks Recovered from Individual California Sea Lion Scat and Spewing Samples at San Clemente Island (SCI) and San Nicolas Island (SNI)

Source of variation	SS	df	MS	*F*-ratio	*P*-value
Winter 1989 at SCI					
Type[a]	0.631		0.631	23.908	<0.001
Sample[b] (type)	3.457	37	0.093	3.542	<0.001
Error	72.083	2,733	0.026		
Autumn 1989 at SCI					
Type	0.796		0.796	30.355	<0.001
Sample (type)	4.531	33	0.137	5.238	<0.001
Error	23.068	880	0.026		
Winter 1990 at SCI					
Type	0.028		0.028	1.108	0.293
Sample (type)	2.584	53	0.049	1.951	<0.001
Error	43.320	1,733	0.025		
Winter 1991 at SCI					
Type	0.003		0.003	0.080	0.777
Sample (type)	1.845	22	0.084	2.679	<0.001
Error	20.883	667	0.031		
Winter 1993 at SNI					
Type	0.139		0.139	5.262	0.022
Sample (type)	3.894	47	0.083	3.126	<0.001
Error	29.758	1,123	0.026		
Autumn 1994 at SCI					
Type	0.648		0.648	20.478	<0.001
Sample (type)	1.300	17	0.076	2.416	<0.001
Error	10.577	334	0.032		
Summer 1995 at SCI					
Type	0.082		0.082	3.464	0.063
Sample (type)	1.432	22	0.065	2.744	<0.001
Error	10.817	456	0.024		

[a] Scats and spewings.

[b] Individual samples (nested within scats and spewings).

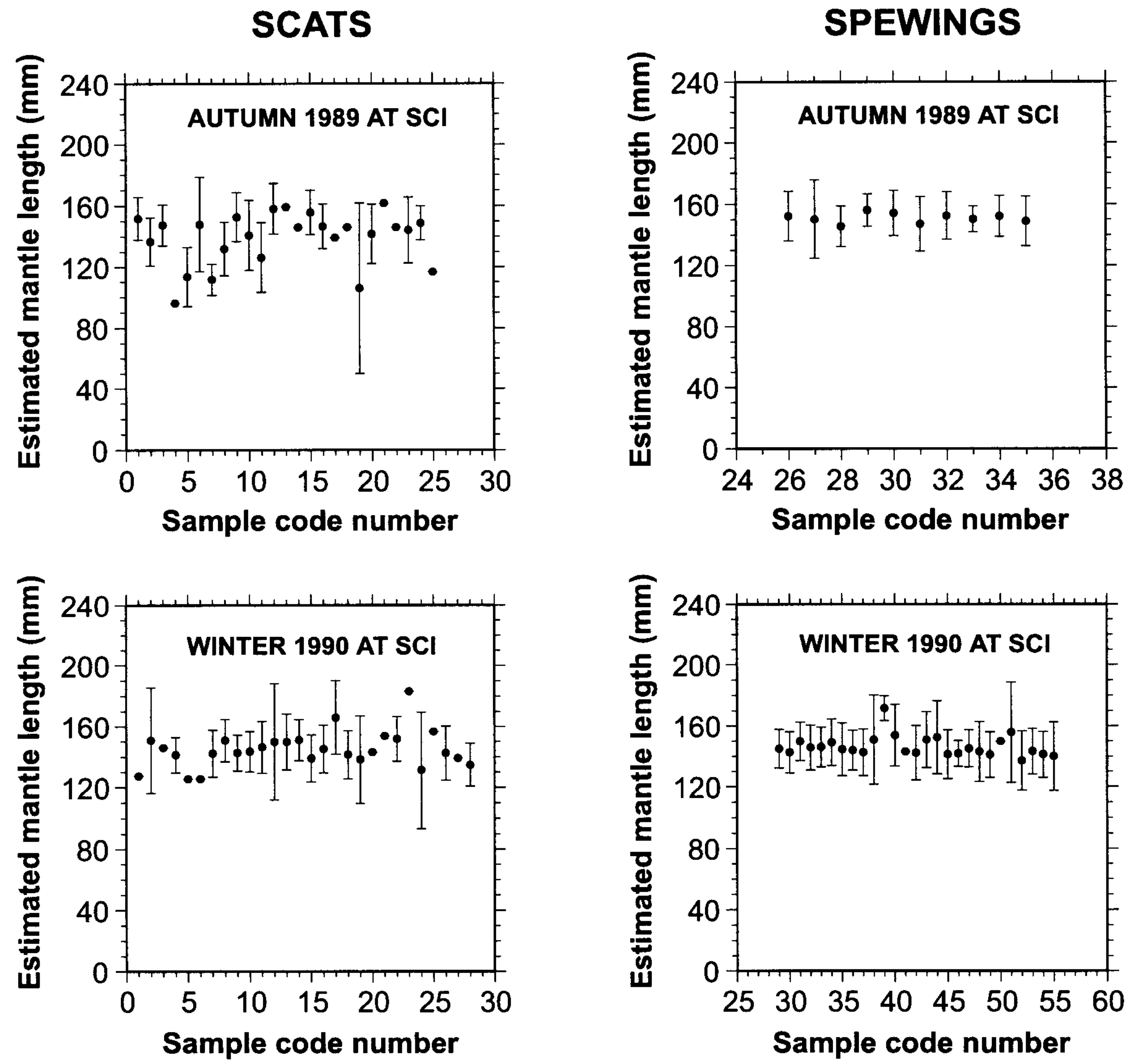


Figure 8. Mean dorsal mantle length of market squid (*Loligo opalescens*) estimated from beaks found in individual California sea lion (*Zalophus californianus*) scat and spewing samples collected at San Clemente Island (SCI), California, during autumn 1989 and winter 1990. Bars indicate one standard deviation from each mean.

were relatively cooler and more productive than the waters around SBI and SCI during summer 1992 and 1993 (Hayward et al. 1994), and it is possible that larger market squid moved to more productive waters in response to El Niño. Shifts in the distribution of pelagic forage species in response to El Niño episodes, and the negative effects of these prey shifts on sea lion populations have been well documented (Costa et al. 1991; DeLong et al. 1991; Feldkamp et al. 1991; Francis and Heath 1991).

The fact that small size classes were also consumed at San Nicolas Island during the 1992–93 El Niño may reflect a need for sea lions to augment their diet with smaller sizes of prey (and alternative species) that would be ignored during years of plentiful prey. Alternative hypotheses that may partially explain the smaller size classes of market squid eaten during El Niño summers are (1) oceanographic changes associated with El Niño result in a temporal shift (delay) in the spawning cycle of market squid; and (2) growth rates are slowed as a result of nutritional stress caused by declines in prey forage of market squid.

The percentage of scat samples with market squid yields the frequency of occurrence index which depicts sea lion consumption and the availability of squid to sea lions. The close correlation of this index to market squid landings in southern California (a crude measure of abundance) implies that the index may indicate market squid abundance. Spewings are not included in this index because the same animal may have deposited both sample types on the collection grounds. A better occurrence index might include lenses and squid pens (i.e., gladius) with beaks, because beaks are sometimes absent in scat samples (Bigg and Fawcett 1985).

Length-composition data showed significant differences between size of squid found in scats and in spewings. These differences were very small and were probably detected because of the large sample size and high statistical power. Differences in average size of squid found in these samples are likely to have little or no biological importance. Therefore, we derived the size structure of the market squid consumed by sea lions from beaks collected from both scats and spewings.

We have not attempted to estimate the biomass of market squid or other species eaten by California sea lions. Estimating biomass consumption by sea lions in southern California would be difficult for several reasons. (1) The population of sea lions fluctuates throughout the year. (2) The percentage of market squid in the diet of sea lions is highly variable through time. (3) Although timing, length, and distance of foraging trips are known for adult female sea lions (Feldkamp et al. 1989; Heath et al. 1991), they are not known for juveniles or subadult and adult males. (4) Consumption by age and sex is not documented. (5) Although beaks have been found to resist digestion (Hawes 1983), degradation rates of hard parts for other prey species must be determined. Once this information is known, models can be developed for estimating consumption of market squid and other species of commercial value that are preyed on by sea lions for a given region.

There are problems with using California sea lions to sample prey populations that commonly occur in their diet. First, presence-absence data (i.e., percent frequency of occurrence) is not a good index of abundance because it cannot go beyond 100% due to nonlinearity. Special modeling approaches to estimate population abundance, such as that used for sardine by Mangel and Smith (1990), would have to be developed for sea lion scat presence-absence data to index abundance of fish and squid. Second, scat and spewing samples have to be independent if they are to be used to predict size structure of squid and fish populations. There is no way to determine from scat and spewing samples if a sea lion, or a group of sea lions, fed on the same school of squid (or fish) or on multiple schools during a foraging trip, nor is it possible to determine where they foraged. The difference in sizes of squid in individual scat and spewing samples suggests that scat and spewing samples are independent. Also, time differences in deposition of samples and their location at the rookery may reflect sea lions' foraging on different schools.

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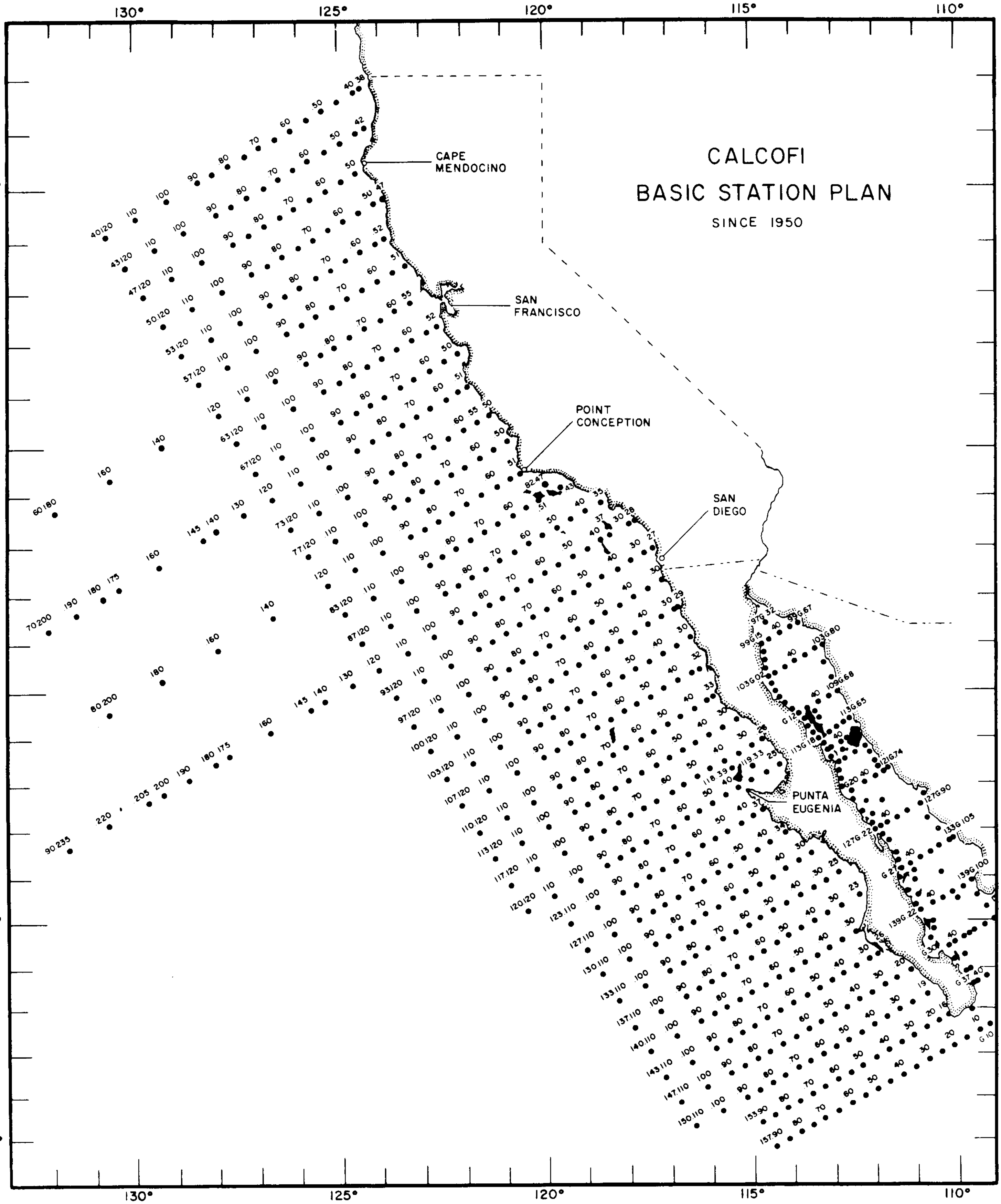

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