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Reports

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

Fifty years of collaborative research in CalCOFI were celebrated at the annual CalCOFI meeting held at the Scripps Institution of Oceanography in La Jolla. The meeting included introductory comments by Charles Kennel, director of the Scripps Institution of Oceanography (SIO); Robert Hight, director of the California Department of Fish and Game (CDFG); and Rod McInnis, acting regional director, National Marine Fisheries Service (NMFS) Southwest Region. There was a special presentation of formal commendation from the California assembly. In celebration of the anniversary, the director of SIO hosted a reception at the Birch Aquarium. The conference attracted a record attendance for recent years.

At the conference, the CalCOFI Committee gratefully acknowledged the long-time service of Coordinator George Hemingway, who has retired from the position. George served CalCOFI in various capacities for 33 years, and was engaged in aspects of producing *CalCOFI Reports* and hosting the annual meeting for 20 years. He 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 CDFG. The CalCOFI Committee has appointed Kevin Hill of CDFG as the new coordinator. Thank you, George, for your many years of dedicated service!

The quarterly CalCOFI sampling program continued as planned in 2000. Additional northern stations, crucial for annual Pacific sardine assessments, were sampled during R/V *Jordan* cruise 0004. Much was accomplished in 1999 and 2000 with respect to processing and distributing CalCOFI data. Dissemination of CalCOFI products was enhanced by the completion of a CD-ROM containing data, information, and software. The CD-ROM presents the Web site's content in browsable (offline) form. CalCOFI data, hydrographic and productivity reports, as well as general and personnel information are included. The IEH data archives are retrievable by any application, especially software designed specifically for IEH processing. Software (Windows9x/NT) developed for extracting data, developing a database, and calculating climatological anomalies from IEH data are included.

The arduous task of identifying the backlog of CalCOFI ichthyoplankton samples was completed, and the database was revised in collaboration with Richard Charter (NMFS) and his staff. Ichthyoplankton and station data for 14 annual surveys (1985–98) were published as an NMFS Technical Memorandum series, authored by NMFS scientists David Ambrose, Sharon Charter, Elaine Sandknop, William Watson, and others. Ichthyoplankton data reports are now available for all cruises from 1951 to 1998.

Identification of larvae from selected rockfish species archived in the CalCOFI ichthyoplankton collection was also completed. Continuous time series were constructed for four species (*Sebastes paucispinis, S. levis, S. jordani,* and *S. aurora*), and partial time series were completed for two species (*S. diploproa* and *S. goodei*). The study was presented by Geoffrey Moser at the annual CalCOFI Conference in November 1999 and is published in this volume. The newly available time series for *S. levis,* the cowcod, has already proved valuable for population assessment and management of that species. Cowcod has been overfished, and a plan for rebuilding the stock is being formulated. Data on *S. paucispinis* (bocaccio) larvae from CalCOFI surveys will be an important component of future assessments and management strategies for this overexploited species.

Significant progress has been made toward producing CalCOFI Atlas number 34. Similar in design to Atlas 31, Atlas 34 will summarize the distribution and abundance of CalCOFI fish larvae for the entire time series from 1951 to 1998. The area covered is the Southern California Bight, the area bounded by the current sampling pattern. Geoffrey Moser, Richard Charter, and coauthors will complete work on this project in 2000.

CalCOFI oceanographic and ichthyoplankton data have been used to characterize larval fish survivors' habitat. Paul Smith and Elizabeth Logerwell have separated the embryonic and larval phases of the life cycle of anchovy, sardine, and hake into two categories. In the first category, the distribution pattern is a residual of the spawning adult pattern as modified by dispersal and survival. In the second category, the distribution pattern is one of survival as modified by larval swimming behavior and the onset of schooling or other aggregation.

Following a survey of the measured larvae of all three species, Logerwell has continued studies of sardine larvae which show that disproportionate numbers of large larvae are offshore of the main spawning areas. Until now this has been interpreted as expatriation of the planktonic stage. It may well be that the offshore habitat is important to the occasional augmented recruitment we find in sardine, rather than a disadvantage.

Through the Pacific Fisheries Management Council (PFMC), the CDFG and NMFS were extensively involved in managing West Coast fisheries, including salmon, groundfish, and coastal pelagics (Pacific sardine, Pacific mackerel, jack mackerel, northern anchovy, and market squid). The Coastal Pelagic Species Fishery Management Plan (CPS FMP) Amendment 8 was approved and implemented in January 2000. Harvest guidelines were established for Pacific sardines (186,000 metric tons) and Pacific mackerel (20,740 t). Several items in the plan were disapproved by NMFS, and PFMC teams are amending it to address (1) provisions to better describe bycatch in the CPS fishery; (2) maximum sustainable yield and acceptable biological catch for market squid; (3) capacity goals and permit transfer rules for the limited entry fishery; and (4) tribal fishing rights. CalCOFI egg and larval sampling continue to play a critical role in the monitoring and managing of coastal pelagic species.

The CDFG continued research on market squid and began developing an FMP. To support this work, three research cruises were conducted with a remotely operated vehicle and scuba divers. The research focused on egg-case deposition transects to identify spawning areas and enumerate density. In addition, a midwater trawl survey conducted aboard R/V *Mako* in February 2000 continued a relative-abundance time series for squid that was initiated during CDFG's sea surveys in the 1960s. The data will be incorporated with early life history, ageing, and fecundity studies to develop management scenarios for presentation to the state legislature by 1 April 2001.

During 1999, CDFG began implementing the Marine Life Management Act, the flagship of change in California management of marine resources. The legislation directed CDFG to begin preparing FMPs for all fisheries under state authority, and specified the order of preparation. The legislation also requires CDFG to enhance the procedure for involving constituents in the process, and moves management authority from the legislature to the California Fish and Game Commission. The commission has five members appointed by the governor and confirmed by the state senate. The first plans in preparation are for nearshore fisheries and white seabass.

The NMFS Marine Ecological Reserves Research Program (MERRP) study of planktonic fish egg and larvae production in nearshore waters has continued in 2000. The four southern California reserve sites include Big Sycamore Canyon and Vandenberg Marine Ecological Reserves, administered by the state of California, and Anacapa and San Miguel Islands, which are part of the Channel Islands National Marine Sanctuary. The fortuitous timing of the study included winter and summer surveys during the 1998 El Niño and the 1999 La Niña. Year 2000 is devoted to analyzing the ichthyoplankton data and completing side-scan habitat mapping of the four study sites.

Fieldwork for the final year of the MERRP program was completed during two cruises in 1999. Intensive fine-scale ichthyoplankton sampling was carried out at the four research sites. A total of 1,849 samples were taken with the continuous underway fish egg sampler (CUFES) during the two cruises. Vertical bongo tows were taken for the purpose of calibrating the CUFES samples and to capture fish larvae. Manta net and MOCNESS samples were taken on each cruise to provide information on the density of fish eggs and larvae at the surface and in the water column. The cruises also included a diving program to measure habitat variables and collect adult and juvenile rockfishes. Results from the first year of the MERRP ichthyoplankton program were published in *CalCOFI Reports*, volume 40 (Watson et al.).

The rockfish genetics program has completed sequencing the cytochrome b gene of almost all of the more than 70 species of rockfishes that occur along the west coast of North America. This study 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 surveys. Currently, NMFS is examining the occurrence of previously unidentifiable nearshore rockfish larvae in CalCOFI's standard bongo survey samples. For the past several years CalCOFI material collected in the second net of the bongo has been preserved in ethanol, making it suitable for DNA analysis. If suitable visual characters can be determined for unknown but genetically identified material, it may be possible to reconstruct historical trends in the abundance of species or subgenera and estimate historical abundance of these presently nearshore species.

The NMFS genetics group has also 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). It is hoped that these genetic studies can give insights into long-term dispersal patterns along the California coast.

Within the Marine Life Research Group (MLRG), and in SIO at large, efforts to establish a CalCOFI-like collaboration between university, federal, and state agencies, as well as other entities interested in California's coastal zone, have increased considerably. Although many of the tools of investigation, and the scientific and resource management questions addressed, will differ from those of CalCOFI, the purpose is to establish a framework to emulate the remarkable success of CalCOFI as a continuing collaboration. Such a framework would serve as an important nucleus for establishing a still larger coastal observing system.

The seagoing personnel of SIO's MLRG, the SWFSC's Coastal Division, and CDFG's Marine Region all contributed, through their dedication and diligence, to the success of CalCOFI's quarterly fieldwork. 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 NOAA Ship *David Starr Jordan*; the University of California R/Vs *New Horizon*, *Roger Revelle*, and *Robert Gordon Sproul*; and the CDFG R/V *Mako*.

We also thank the reviewers of contributed papers in volume 41: Jim Allen, Darrin Bergen, Steven Bograd, Mark Brzezinski, Gregor Cailliet, Ted Durbin, Donald Gunderson, Annette Henry, Larry Jacobson, Robert Lea, Elizabeth Logerwell, Ronald Lynn, Beverly Macewicz, Geoffrey Moser, Bruce Phillips, Jeffrey Polovina, Antonella Preti, Ginger Rebstock, Louise Savard, Steven Schroeter, Elizabeth Venrick, William Watson, and Marci Yaremko. Special thanks go to Dick Schwartzlose for compiling the subject and author index and to our editor, Julie Olfe, for another fine volume in this long series of publications.

Kevin Hill, CalCOFI Coordinator
Doyle Hanan, CDFG
John Hunter, NMFS
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REVIEW OF SOME CALIFORNIA FISHERIES FOR 1999:
MARKET SQUID, DUNGENESS CRAB, SEA URCHIN, PRAWN, ABALONE, GROUNDFISH, SWORDFISH AND SHARK, OCEAN SALMON, NEARSHORE FINFISH, PACIFIC SARDINE, PACIFIC HERRING, PACIFIC MACKEREL, REDUCTION, WHITE SEABASS, AND RECREATIONAL

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In 1999 commercial fisheries landed an estimated 214,229 metric tons (t) of fishes and invertebrates from California ocean waters (fig. 1), an increase of 66% from the 128,885 t (updated estimate) landed in 1998. The preliminary ex-vessel economic value of California commercial landings in 1999 was $145 million, an increase of 36% from the $107 million of 1998.

The commercial invertebrate fisheries in California had a greater combined ex-vessel value ($79 million) than the combined finfish fisheries value ($66 million) in 1999. The top three fisheries in millions of dollars ex-vessel value were market squid ($35 million), groundfish ($18 million), and Dungeness crab ($17 million). Market squid increased dramatically to a new record high in 1999. Sea urchin landings increased slightly from their ten-year low in 1998, although landings in northern California continued to decline in 1999. Ridgeback prawn increased 320% in 1999, while spot prawn decreased 25%. In 1999 Dungeness crab landings were slightly above their ten-year average, and a high percentage (28%) of meat was recovered from the crabs. The commercial abalone fishery remained closed statewide, while 40,000 fishers participated in the recreational-only red abalone fishery in northern California.

Ocean conditions along the California coast were dominated by cold La Niña conditions following the dramatic El Niño of 1997–98. Pacific sardine landings were at their highest level in decades, while Pacific mackerel landings dropped to less than half of the 1998 levels. Other pelagic species such as Pacific herring recovered from El Niño with a 45% increase in landings during the 1998–99 sac roe season, although the San Francisco Bay herring eggs-on-kelp fishery landed the second lowest tonnage on record. Commercial chinook salmon landings in the ocean nearly doubled in 1999 compared with 1998. Swordfish landings increased more than 50% in 1999, while shark landings continued to decline. Commercial white seabass landings reached their highest level in 17 years.

In spite of the cold-water La Niña conditions, landings in several fisheries continued to decline in 1999,

most notably groundfish. Commercial groundfish landings decreased 37% from 1998 levels and 51% from 1997. Landings of rockfish such as bocaccio, widow rockfish, and chilipepper decreased from 1998 levels. The National Marine Fisheries Service listed lingcod, bocaccio, and Pacific ocean perch as overfished. As a result, more restrictive limitations have been put in place for these species. Landings for some flatfishes, such as sablefish, sanddabs, and petrale sole, increased in 1999. The drop in revenues from the groundfish fisheries was slightly moderated by increased landings of high-value sablefish and increased value of rockfish in the live-fish fishery. The live-fish fishery in California continued its exponential growth with a tenfold increase in the number of vessels from 1989 to 1999. Prices paid for live rockfish reached $10 per pound.

Statewide landings by recreational fishers aboard commercial passenger fishing vessels (CPFVs) increased by 8%, to 3,395,471 individual fishes. Fishers in southern California brought in 75% of the statewide landings reported from CPFVs in 1999. Recreational landings of ocean salmon decreased to 87,600 chinook salmon; no coho salmon were permitted to be taken. Recreational landings of white seabass increased eightfold in 1999.

The Marine Life Management Act continues to direct California Department of Fish and Game (CDFG) efforts to sustainably manage marine resources. As part of this effort, the CDFG is moving toward an ecosystem-based management approach. The CDFG also continues to strengthen ties with other groups in an effort to co-manage marine resources within the state. Finally, many of the data presented in this report are generated from the CDFG's new, Oracle-based data system, called the Commercial Fisheries Information System.

INVERTEBRATE FISHERIES

Market Squid

Market squid (*Loligo opalescens*) landings reached a record high of 90,322 t during La Niña conditions in 1999, surpassing the previous high of 80,402 t in 1996
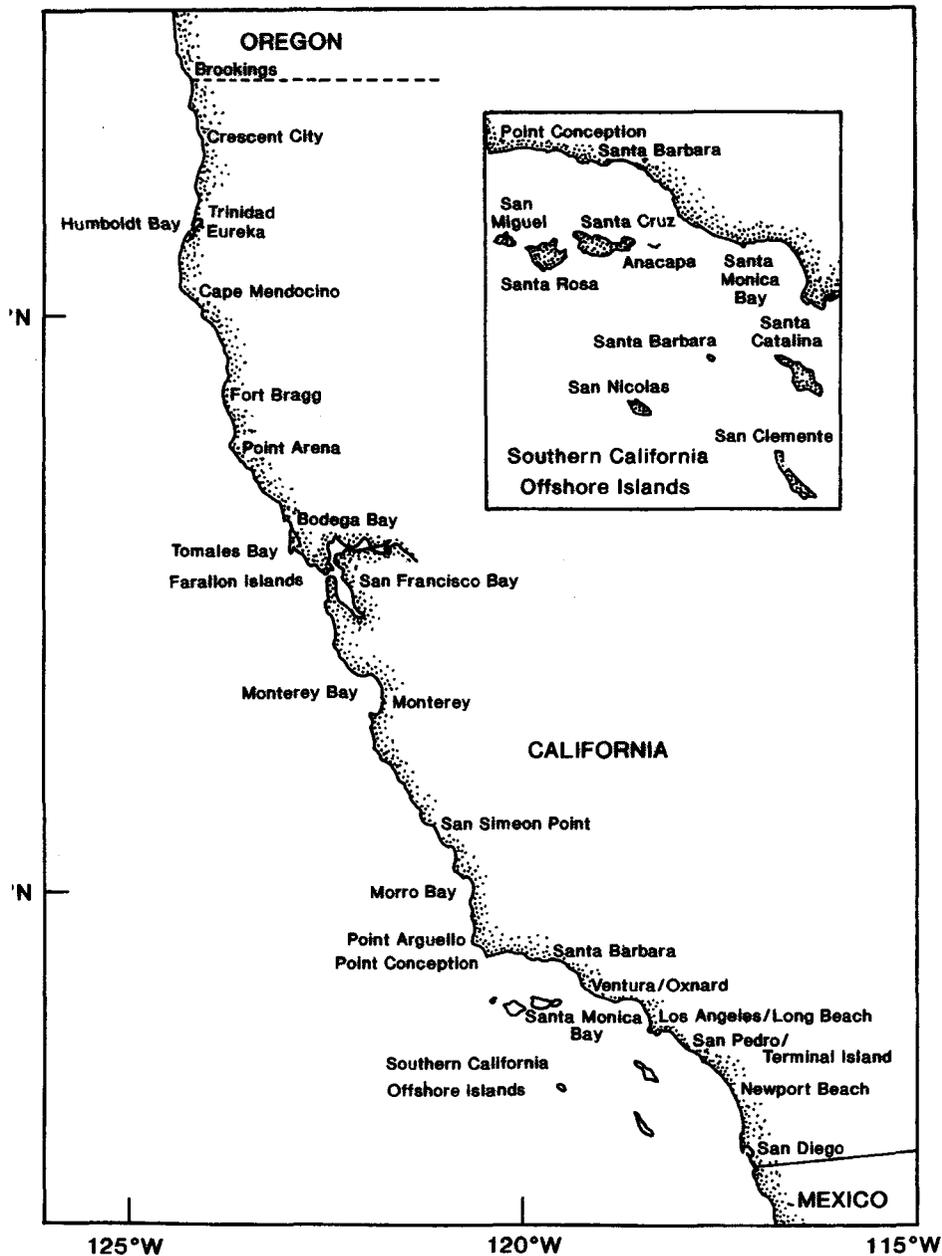
Figure 1. California ports and fishing areas.

(table 1, fig. 2). This was more than a 30-fold increase over the previous year (2,894 t), when the fishery was hampered by the 1997–98 El Niño. Landings reached new highs five times in the 1990s, reflecting the continued expansion of the southern California fishery and increased export demand.

Market squid is one of the most important fisheries in the state, in terms of both volume and revenue. In 1999, ex-vessel revenues generated from market squid were approximately $35 million, ranking this fishery first among California commercial fisheries. Average ex-vessel price paid to fishers was $388.32 per t. Nearly 38% of landings were exported; market squid ranked sixth by volume and sixteenth in value among U.S. exports of

edible fishery products. The primary country of export was China, which received 10,295 t, an increase over the 46 t exported to China in 1998, but less than the 26,000 t in 1997. More than 70% of squid exports went to China and five additional importers: Spain (5,470 t), Japan (3,626 t), the Philippines (2,995 t), Italy (2,230 t), and Hong Kong (1,920 t). Processors reported that the Patagonian squid fishery did not noticeably affect their 1999 exports. Domestically, market squid was sold throughout the country, primarily to restaurants, Asian fresh fish markets, and as frozen bait. Processors grossed approximately $36 million from exports in 1999.

The California market squid fishery is separated at Point Conception into northern and southern fisheries.

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	1,457	20,073	970	2,432	2,709	68,646
1999	56,747	5,179	9,527	963	2,207	90,322	164,945
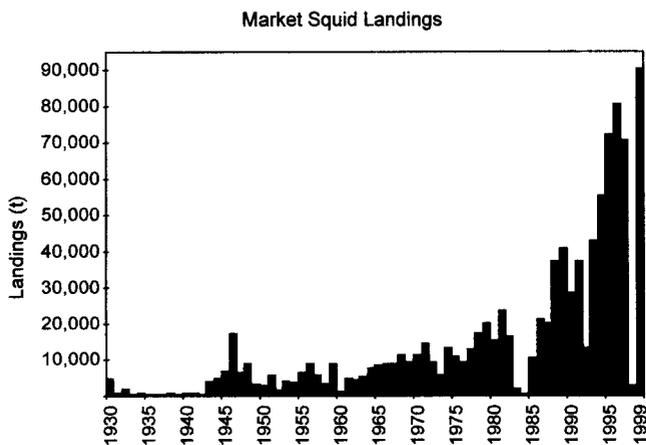
Figure 2. California market squid landings from 1930 to 1999.

Historically, the northern fishery accounted for the greater portion of the catch. Since the early 1980s, however, the southern fishery has repeatedly increased its landings and has dominated the fishery. Typically, the northern fishery is active during the summer months and the southern fishery in the winter. In 1999, the northern fishery was essentially inactive, accounting for less than 0.5% of statewide landings for the second year in a row. Landings in the north (348.2 t) were considerably below their annual average (1,750 t average for 1981–98).

In 1999 the southern fishery, near the Channel Islands, continued for nearly the entire year, with record-high monthly totals in April, May, and June. The southern fishery comprises 170 vessels that landed 89,973.9 t.

Although fishers and processors alike acknowledge that squid was readily available most of the year in southern California, catch levels were generally dictated by market conditions that expressed only moderate demand for the product. During most of the year, vessels fished on market-imposed limits of 30 short tons per trip.

The market squid fishery was an unregulated, open access fishery until 1 April 1998, when new legislation placed a three-year moratorium on the number of vessels in order to assure sustainability of the fishery. This legislation requires fishers to purchase a $2,500 permit each year either to land more than 2 short tons per trip or to attract squid by light for purposes of commercial harvest, and participants must have purchased a permit the previous year. For the 1999–2000 squid fishing season (1 April to 31 March), 218 market squid vessel permits and 52 light-boat permits were sold, down from 248 vessel permits and 54 light-boat permits the previous season. The sale of permits provides funds for biological assessments of the resource and development of recommendations for a market squid conservation and management plan due 1 April 2001.

The same legislation provides for the Squid Fishery Advisory Committee and the Squid Research and Scientific Committee, established in 1998. Management measures recommended by the committees and approved by the Fish and Game Commission during 1999 include mandatory logbooks for squid vessels and light boats, and statewide weekend closures.

In 1999, the National Park Service reported to the CDFG and the two committees that there was an appar-
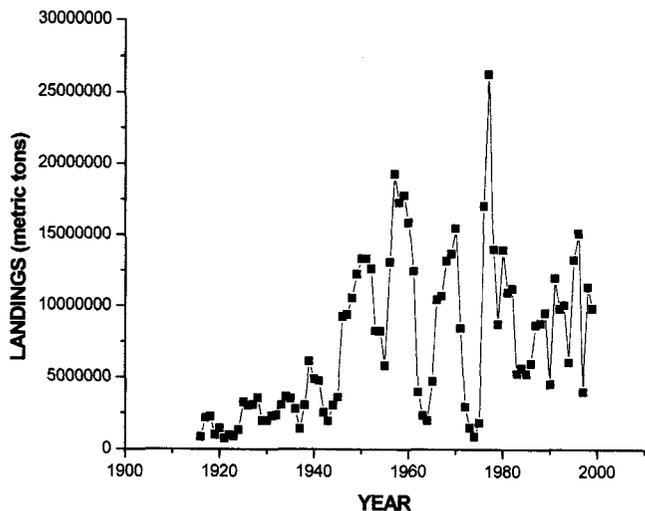
Figure 3. California landings of Dungeness crab, 1916–99.

Figure 4. California landings of red sea urchin, 1971–99.

ent increase in nest abandonment and chick predation among shorebirds at the Channel Islands. The Park Service questioned whether the abundance of vessels lighting for squid near these islands during the nesting season could have been responsible. In answer to the concerns, the Squid Fishery Advisory Committee recommended reduced lighting (maximum 30 kilowatts per vessel) and shielding lights as interim management measures.

Market squid research objectives for the CDFG include (1) collecting fishery data by port sampling, (2) conducting fishery-independent squid surveys with a remotely operated vehicle to describe spawning habitats and measure egg density, as well as conducting midwater trawl surveys to estimate relative abundance, (3) culturing eggs and paralarvae to determine the lowest viable temperature, in order to resolve spawning range constraints, and (4) analyzing satellite data to track growth of the market squid fishery since 1992. Preliminary port sample data indicate that the average squid taken in the commercial fishery weighs 45 g, is 133 mm long, and is approximately 185 days old.

Dungeness Crab

California Dungeness crab (*Cancer magister*) landings during the 1998–99 season totaled 4,458 t, a decrease of 678 t from the previous season, and only slightly higher than the ten-year average of 4,352 t (fig. 3). The Dungeness crab fishery had an ex-vessel value of $16.9 million.

In northern California the season opened on 1 December after preseason testing showed that the crab were in exceptionally fine condition, allowing a 28% meat recovery. Price started at $1.25 per pound but by 22 December rose to $1.95 and peaked in February at $3.50 per pound. The fleet landed approximately 3,876 t in northern California, including 2,193 t in Crescent City, 330 t at Trinidad, 1,119 t at Eureka, and 234 t at
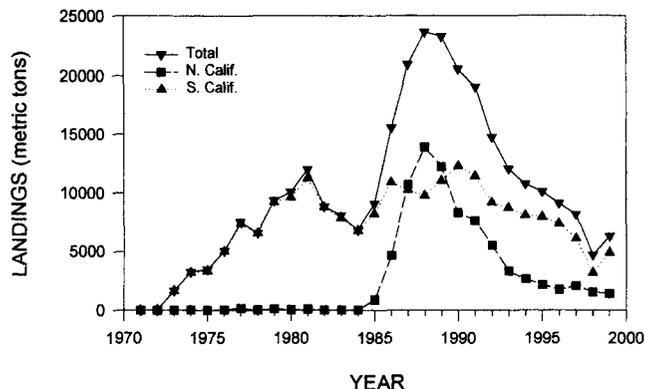
Fort Bragg (fig. 1).

The central California Dungeness crab season opened on 15 November. Total landings decreased by 1,036 t from the previous season, to 582 t. Crab fishers landed 247 t at Bodega Bay and Bolinas, and 318 t at ports in San Francisco and Half Moon Bay. Monterey and Morro Bay contributed only 17 t to the statewide totals.

Sea Urchin

Red sea urchin (*Strongylocentrotus franciscanus*) fishery landings in 1999 increased from the record 20-year low in 1998. Statewide landings in 1999 totaled 6,283 t, up 25% from the 1998 total of 4,708 t. The rebound is attributed to the rise in southern California landings, which increased by 35% from 1998 (fig. 4). Northern California landings continued to decline, dropping 9% from 1998. The cooler seawater temperatures of La Niña provided good growth conditions for kelp and thus improved gonad quality in sea urchins, which was reflected in the increased landings.

Along with the increased landings, overall value of the fishery increased by 42%, from $8 million in 1998 to $13 million. The price per kg climbed from $1.62 in 1998 to $2.12. Southern California experienced a greater increase in price per kg (from $1.82 to $2.25) than northern California (from $1.37 to $1.65). The San Diego area experienced the largest increase in unit price ($0.49) between 1998 and 1999. Fishery permits cost $330, and sales dropped by 9% to 421 in 1999, still well above the permit target set at 300 in 1992.

Santa Barbara and the Oxnard/Ventura areas continued to be the most active ports for sea urchin landings, with a combined 55% of the statewide catch in 1999 (table 2). Los Angeles was the third most active port, with 18% of the total catch, while Fort Bragg in northern California was fourth. Landings in all other northern California ports either declined or remained the same.

The return of cooler sea temperatures helped boost the sea urchin fishery from its 20-year record low in

TABLE 2
Preliminary California Commercial Red Sea Urchin Landings (Metric Tons) for 1999

Port	Landings	Percentage of statewide catch	Value	Price per kg
Fort Bragg	650.3	10.4	$ 1,099,835	$1.69
Albion	191.0	3.0	$ 307,265	$1.61
Point Arena	332.4	5.3	$ 548,461	$1.65
Bodega Bay	195.0	3.1	$ 324,696	$1.67
Half Moon Bay	6.5	0.1	$ 9,222	$1.41
Other N. Calif.	18.8	0.3	$ 24,365	$1.30
N. Calif. subtotal	1,394.1	22.2	$ 2,302,976	$1.65
Santa Barbara	2,063.3	32.8	$ 4,708,447	$2.28
Oxnard/Ventura	1,402.5	22.3	$ 3,367,150	$2.40
Los Angeles	1,150.4	18.3	$ 2,353,948	$2.05
Orange	7.3	0.1	$ 12,572	$1.73
San Diego	262.2	4.2	$ 455,873	$1.74
Other S. Calif.	3.0	0.0	$ 8,920	$2.98
S. Calif. subtotal	4,888.7	77.8	$10,983,335	$2.25
Grand total	6,282.7		$13,286,311	

1998. The continued decline of the northern California fishery in the face of this recovery and the fact that 1999 statewide landings were 27% of the historical peak fishery levels raises questions about the sustainability of the fishery. To help address these concerns, a workshop was held in the summer of 1999 to discuss the status of the fishery and the future direction of management. The workshop was funded by the CDFG's Sea Urchin Advisory Committee and the California Sea Grant College System. Workshop participants included CDFG biologists and managers, academic researchers, fishery representatives, and invited guest speakers from other states and Canada. The information presented at this workshop will serve as a basis for formulating a sea urchin management plan with the goal of managing the fishery sustainably in the near future.

Spot and Ridgeback Prawn

Spot prawn. Preliminary 1999 spot prawn (*Pandalus platyceros*) landings were 279 t, a 25% decrease from the

372 t landed in 1998. Approximately 187 t of spot prawn were harvested by trawl in 1999, while 92 t were taken with trap gear (table 3). This reversed a ten-year trend of increasing landings (fig. 5). The largest decline occurred in the Santa Barbara area trawl catch, where spot prawn landings dropped 62 t from the previous year's total.

Spot prawn are caught with both trap and trawl gear. A total of 95 vessels (46 trap and 49 trawl) made landings in 1999; table 3 shows types of gear and landings for spot prawn by port area. Some trap and trawl vessels fished in several different port areas during the year. Over half of the combined trap and trawl spot prawn landings in 1999 were made in the Santa Barbara port area. In the past, boats using trap gear were the major contributors to the fishery. However, since the mid-1970s boats using trawl gear have increased in number, and their landings now dominate the fishery. In the last ten years the number of spot prawn trawlers has increased even more rapidly, with an influx of vessels from other groundfish fisheries that have been subjected to increasingly restrictive quotas or seasons.

Spot prawns are large and command high prices. In 1999 the ex-vessel value of the spot prawn fishery was approximately $4.3 million. The median ex-vessel price for all spot prawns was $7.50 per pound. Live spot prawn had a median ex-vessel price of $7.50 per pound, and prices for live prawn ranged from $3.50 to $10.60. Fresh dead spot prawn sold for a median ex-vessel price of $3.50 per pound, with a range of $1.50 to $5.00. Approximately 80% of all spot prawn were sold live.

During 1999, the trap and trawl spot prawn permit fisheries in southern California (south of Point Arguello) were operating under concurrent closures running between 1 November and 31 January. Up to 50 pounds of incidentally trawled spot prawns could be retained during the closure. This southern California trap and trawl closure was enacted in 1997 to protect gravid female spot prawns. North of Point Arguello the spot prawn season was open all year.

In 1999 a CDFG ad hoc advisory committee was

TABLE 3
1999 California Spot Prawn Landings (Metric Tons) by Port Area and Gear Types

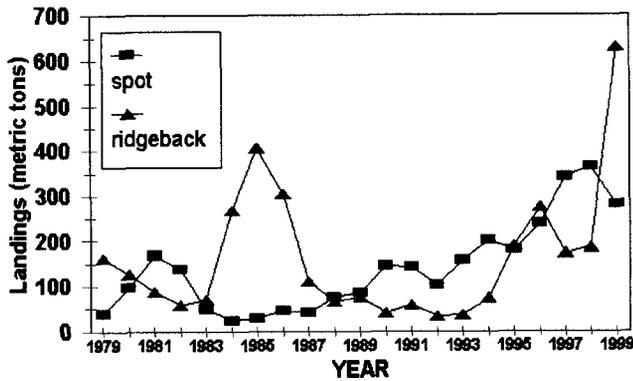| Port areas	Number of fishing vessels by gear type		Spot prawn landings (metric tons)			
	Trap	Trawl	Trap	Trawl	Totals	Percentage of total
Eureka	0	4	0.0	3.4	3.4	1.2
San Francisco	7	21	2.9	40.4	43.3	15.5
Monterey	10	14	9.7	14.3	24.0	8.6
Santa Barbara	16	41	28.1	121.8	149.9	53.8
Los Angeles	18	6	34.5	7.7	42.2	15.1
San Diego	16	0	16.0	0.0	16.0	5.8
Totals	67	86	91.2	187.6	278.8	100.0

Figure 5.   California landings of spot and ridgeback prawn, 1979–99.

formed in response to concerns about the fishery expressed by some spot prawn harvesters. The advisory committee's mandates were to determine the sustainability of current spot prawn harvest levels, and to document the magnitude and composition of the fishery's bycatch of finfish and invertebrate species. The advisory committee's findings will be used to develop new regulatory strategies, including possible additional trawl gear restrictions or modifications, requirements for excluder devices, seasonal harvest restrictions, or area closures.
Ridgeback prawn.   Preliminary 1999 ridgeback prawn (*Sicyonia ingentis*) landings totaled 631 t, a 320% increase from the 197 t landed in 1998 (fig. 5) and the highest total since 1985. The availability of ridgeback prawn on the trawl grounds, coupled with a growing market demand for both dead and live ridgeback prawns, accounted for the large increase in landings. In 1999 the ex-vessel value of the ridgeback prawn fishery in California was approximately $1.7 million. In 1999 five ridgeback prawn dealers purchased 100,000 or more pounds; only one dealer purchased that much in 1998.

Ridgeback prawn are smaller than spot prawn and are taken exclusively by trawl nets. From 31 May through 1 October the season is closed, although an incidental catch of 50 pounds is allowed. Thirty-five trawl vessels made ridgeback prawn landings in 1999, about the same number as in 1998. All of the landings were made at southern California ports, between Los Angeles and Santa Barbara, and almost all ridgeback prawn were caught within the Santa Barbara Channel.

Live ridgeback prawn composed 28% of total ridgeback prawn landings in 1999, a major decrease from 1998, when over 50% of the catch was landed live. The median ex-vessel price paid for all ridgeback prawn was $1.30 per pound. Live ridgeback prawn sold for a median price of $2.00 per pound, with a range from $1.00 to $4.00, while dead ridgeback prawn sold for a median ex-vessel price of $1.00 per pound, with a range from $0.20 to $3.35.

Abalone

The southern and central California commercial and recreational abalone fishery moratorium, established by the Fish and Game Commission and the legislature in 1997, continues. A state legislature–mandated Abalone Recovery and Management Plan is currently being prepared for all seven California species, and will focus primarily on the traditional commercial and recreational species: red, pink, green, black, and white abalone. The magnitude of the declines in these species in southern California offers little hope for recovery of the resource over the next decade.

In contrast, red abalone stocks north of San Francisco continue to provide recreational divers and shore pickers a vigorous fishery involving 32,000–40,000 fishers annually. This recreational-only fishery continues to be sustainable. Restrictions include size limits, daily limits, season closures, and participation by skin divers and shore pickers only. The prohibition of scuba creates a de facto refuge for abalone at depths greater than 9 m. New regulations placed on the fishery will include an annual limit of 100 red abalone per fisher, with the date, location, and number taken recorded on a punch card. Enforcement of abalone fishing regulations and closures in California remain a priority. Several poaching cases were made in 1999, involving large numbers of legally harvested recreational abalone from northern California being illegally sold to commercial markets.

While the abalone fisheries are closed throughout most of California, abalone remains one of the top species of concern, particularly—but not exclusively—in northern California. Fishery-independent measures of red abalone abundance were made in northern California at fished and reserve sites in 1999 and compared with similar studies in 1986. Preliminary data indicate that even at fished sites, adult abalone densities are comparable to 1986 levels. During timed swim surveys, 100 red abalone per hour were observed at some sites. Size-frequency data collected during these surveys indicate, however, that there are few juvenile and sublegal red abalone at the sites. Creel surveys of abalone taken by shorepickers and divers in northern California at ten major sportfishing areas were conducted in the spring of 1999 for the twenty-fifth consecutive year. These surveys reveal that the average size of abalone taken in 1999 has not declined. More studies are being conducted to examine recruitment and reproduction in red abalone in northern California. Evaluation of red, pink, green, black, and white abalone in southern California continues.

The discovery of withering syndrome (WS) in northern California red abalone stocks has caused serious concern. Although the abalone merely carried the WS bacteria and showed no symptoms, a north coast–wide evaluation was made to determine the extent of the

pathogen. The WS pathogen may have entered natural populations through the introduction of infected abalone into nearshore areas from aquaculture facilities or through out-planting infected animals. While the presence of the WS pathogen in north coast red abalone populations has not caused symptoms of the disease, its presence is significant. If environmental conditions (e.g., warm, ENSO-influenced sea temperatures) that stress abalone populations increase, the disease could become symptomatic, spread, and become lethal throughout the north coast.

Scientists in the CDFG shellfish laboratory have identified the pathogen responsible for WS as a rickettsia-like bacteria, and developed a prophylactic treatment for abalone held in culture, but this treatment is not practical for treating natural populations. Researchers in the laboratory are currently studying the red abalone WS problem in northern California and developing nonlethal methods to evaluate the presence of WS in seawater.

White abalone was designated a candidate species for listing under the Endangered Species Act by the National Marine Fisheries Service (NMFS). A consortium of public and private agencies, including the CDFG, the NMFS, the National Park Service, the University of California (Scripps Institution of Oceanography and Santa Barbara), the U.S. Geological Service, Proteus Sea Farms, and the Marine Conservation Biology Institute, are working on the recovery of this abalone. A cruise, supported by a Saltonstall-Kennedy grant and the NMFS Southwest Fishery Science Center, used the *Delta* research submersible to survey and evaluate white abalone populations at the southern Channel Islands and offshore banks. A total of 157 white abalone were located, and extensive data about the ecology of the species were collected. Unfortunately, only about 25% of the abalone were found in groups, which facilitate reproduction. White abalone will be collected for culture research and grow-out studies.

Black abalone population levels are very low throughout southern California. This abalone has also been designated a candidate species by the NMFS. Research centers on WS, and the development of resistant black abalone strains. Some recent recruitment has been observed in central California, and gametes from these individuals are being used for study. Little recovery has been observed in Channel Islands locations, where black abalone once dominated the intertidal community.

FINFISH FISHERIES

Groundfish

The California commercial groundfish harvest for 1999 was 14,206 t (table 4). Total 1999 landings decreased 37%, or 8,312 t, from 1998 and 51%, or 14,726 t, from 1997. The ex-vessel value for 1999 was approximately $18.8

TABLE 4
California Groundfish Landings (Metric Tons) for 1999

	1998	1999	Percent change
Flatfish			
Dover sole	3,572	3,745	5
English sole	427	375	−12
Petrale sole	473	529	12
Rex sole	289	282	−2
Sanddabs	644	925	44
Other flatfish	173	141	−19
Rockfish			
Widow rockfish	906	574	−37
Chilipepper	1,417	885	−38
Bocaccio	148	70	−52
Splitnose rockfish	1,435	138	−90
Thornyheads	1,919	1,467	−24
Other rockfish	3,052	1,152	−62
Roundfish			
Lingcod	150	153	2
Sablefish	1,442	1,905	32
Pacific whiting	5,723	1,308	−77
Grenadier	503	312	−38
Cabezon	163	144	12
Other	82	101	23
Total	22,518	14,206	−37

million, a drop of 13% from 1998 revenues of $21.7 million and of nearly 41% from 1997 values.

In 1999, 86% of the groundfish landed were taken by bottom and midwater trawl gear, a slight decrease from the 88% in 1998. Line gear accounted for the second largest amount at 12%, a slight increase from the 10% in 1998 and similar to that of 1997. The line gear contribution reached a recent high of 18% in 1992. Gill and trammel nets landed just under 1%, after a steady decline from 5% in 1993 to 1% in 1996. Traps accounted for approximately 1% of total 1999 groundfish landings.

Dover sole (*Microstomus pacificus*), thornyheads (*Sebastolobus* spp.), sablefish (*Anoplopoma fimbria*), Pacific whiting (*Merluccius productus*), and rockfish continue to dominate landings, although the 1999 harvest of Pacific whiting and rockfish was off sharply from the previous year. Landings of some flatfish species and sablefish were higher in 1999. The sharp decline in Pacific whiting landings reflects their reduced availability to the Eureka area shoreside fishery during the 1999 season and not a drop in overall coastwide abundance. The redistribution appears to be associated with the onset of La Niña conditions. Many of the rockfish declines reflect increasingly restrictive Pacific Fishery Management Council (PFMC) landing limitations, although the decline in splitnose rockfish (*Sebastes diploproa*) landings is also associated with the transition to La Niña conditions after the weakening of the strong 1997–98 El Niño. The drop, therefore, most likely reflects a return to their more normal distribution on the slope, where fishing is minimal.

The drop in overall ex-vessel revenues when compared to total landings was moderated by an increase in high-value sablefish landings and the increasing value of rockfish in the live-fish fishery. And even though Pacific whiting landings were down sharply, the effect on total groundfish revenues was relatively small because Pacific whiting is a high-volume, low-value fish.

For 1999 the PFMC maintained optimal yields (OYs) for Dover sole, shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*Sebastolobus altivelis*), sablefish, Pacific whiting, lingcod (*Ophiodon elongatus*), widow rockfish (*Sebastes entomelas*), yellowtail rockfish (*Sebastes flavidus*), canary rockfish (*Sebastes pinniger*), bocaccio (*Sebastes paucispinis*), and Pacific ocean perch (*Sebastes alutus*). Also for the first time, OYs were set for both splitnose and chilipepper rockfish (*Sebastes goodei*) south of Cape Mendocino. The PFMC again used cumulative landing limits as well as trip limits to meet the objective of staying within the annual OYs while providing for a year-round fishery.

Stock assessment teams prepared assessments for Pacific whiting, southern lingcod (California), petrale sole (*Eopsetta jordani*), bocaccio, canary rockfish, and cowcod (*Sebastes levis*). These assessments were reviewed by stock assessment review (STAR) panels, whose recommendations were forwarded to the Groundfish Management Team (GMT). While developing management measures for the year 2000, the GMT addressed the STAR panel recommendations as well as the NMFS notice that lingcod, bocaccio, and Pacific ocean perch were overfished and that the PFMC needed to implement rebuilding plans. Incorporating the yields recommended in the draft rebuilding plans for overfished species necessitated management strategies that will greatly reduce landings of the overfished species as well as species normally associated with them.

In 2000, the PFMC will continue to investigate a capacity-reduction program for the groundfish industry, and the feasibility of a comprehensive groundfish observer program. Planned stock assessments include bank rockfish (*Sebastes rufus*), darkblotched rockfish (*Sebastes crameri*), coastwide lingcod, widow rockfish, yellowtail rockfish, Pacific ocean perch, and Pacific whiting. Results from the 1999 cowcod and canary rockfish assessments indicate that these species are also overfished and will require the PFMC to develop rebuilding plans for implementation in 2001.

Swordfish and Shark

Swordfish and shark fisheries in California are located primarily in the southern part of the state. Although swordfish (*Xiphias gladius*) and common thresher shark (*Alopias vulpinus*) are caught in directed fisheries, shortfin mako shark (*Isurus oxyrinchus*) is more often landed

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

	Swordfish	Common thresher shark	Shortfin mako shark
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	859	175	64
1999*	1,356	148	42

*Preliminary

incidentally in these and other fisheries. Fluctuations in landings for all three species are attributed partially to changes in marketability and demand, although oceanic conditions have also played a major role.

Preliminary swordfish landings totaled 1,356 t in 1999 (table 5), 58% more than 1998. Drift gill nets accounted for only 30% of the catch, down significantly from the 59% of 1998. High-seas longline landings showed a corresponding increase from 32% in 1998, to 64%. This pattern has not been seen since 1994, when the high-seas longline fleet was most active. Twenty-six vessels using longline gear outside the U.S. Exclusive Economic Zone (EEZ) landed swordfish in southern California ports. Though several of these vessels made only one landing in 1999, the average landing increased from around 4 t in 1997 and 1998 to nearly 8 t. The majority of vessels fishing outside the EEZ were Hawaii-based; only two California-based vessels made landings. Harpoon landings constituted 4% of the catch, the same as in 1998 but down from highs of around 8% in 1994–97. Eighty-three percent of the swordfish catch was landed in southern California ports.

As expected, gear type affected swordfish ex-vessel prices. Typically, fishers landing either drift gill net- or longline-caught swordfish received $1.25 to $4.50 per pound. The drift gill net catch, however, tended to claim a higher price (mode = $3.00) than longline (mode = $1.75). This is probably due to the fact that the longline fishery is conducted outside the EEZ, so fish are held onboard for longer periods. The swordfish fishery had an ex-vessel value of $8.2 million in 1999. Fishers landing harpoon-caught swordfish received the highest ex-vessel prices, with a range of $3.00 to $7.50 per pound.

Preliminary landings of common thresher shark totaled 148 t in 1999 (table 5), decreasing 15% from 1998. Thresher shark were taken primarily with drift gill nets (60%), followed by set gill nets (34%), and assorted other gears (6%). Most (90%) landings continued to be made
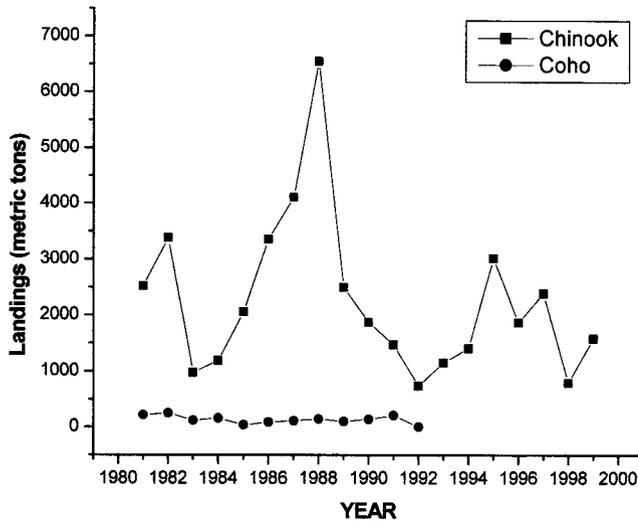
Figure 6. California commercial landings of ocean salmon, 1980–99.

Figure 7. California recreational landings of ocean salmon, 1980–99.

in southern California. The thresher shark fishery had a $462,000 ex-vessel value in 1999. Typically, ex-vessel price varied from $0.50 to $3.25 per pound.

Shortfin mako shark preliminary landings totaled 42 t in 1999 (table 5), a decrease of 34% from 1998 and the lowest total since 1980. The decreasing catch over the past two years could be indicative of the cold-water regime shift noted for California waters. The ex-vessel value of the mako shark fishery in 1999 was $115,000. Most of the catch (84%) was landed in southern California ports, at ex-vessel prices typically ranging between $0.50 and $2.50 per pound. Like thresher sharks, mako sharks were caught primarily by the drift gill net fishery (72%). The remainder of the catch was landed by set gill nets (12%), longline vessels operating outside the EEZ (8%), hook-and-line gear (3%), and incidentally by other gears (5%).

Ocean Salmon

In 1999, the PFMC again enacted restrictive commercial and recreational ocean salmon regulations in California to achieve (1) the escapement goal for Sacramento River fall chinook salmon (*Oncorhynchus tshawytscha*) of 122,000 to 180,000 hatchery and natural adults combined; (2) a 12.3% exploitation rate on age-4 Klamath River fall chinook salmon 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 the adult spawner replacement rate for endangered Sacramento River winter chinook salmon relative to the observed 1989–93 mean rate; and (4) a reduction in harvest impacts on depressed coho salmon (*Oncorhynchus kisutch*) stocks coastwide.

In 1999, commercial fishing for ocean salmon (all species except coho salmon) in California was allowed
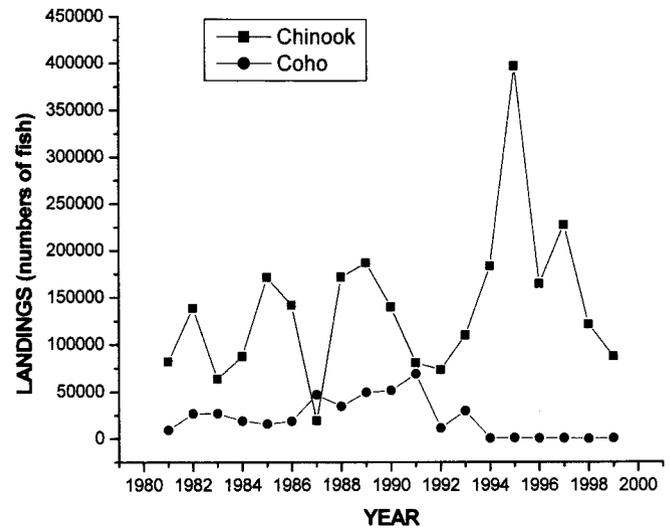
coastwide from 14 April to 30 September, with various time and area closures. The minimum size limit was 26 inches total length (TL), 27 inches after June 30 to help reduce retention of the generally smaller Sacramento River winter chinook salmon; however, the 1998 Bodega Bay test fishery was conducted in July, and maintained a minimum size limit of 26 inches. Approximately 1,583 t (264,500 fish) of dressed chinook salmon were landed by commercial trollers, who fished approximately 14,000 days (fig. 6). Ex-vessel prices for dressed salmon averaged $1.89 per pound, and the total ex-vessel value of the fishery exceeded $6.6 million.

Recreational fishing regulations in California were less restrictive than in 1997, with various time and area closures (14 February–15 November). Statewide recreational landings decreased by almost 28% compared to the previous year (fig. 7), totaling 87,600 chinook salmon during 148,000 angler trips (catch per unit angler = 0.59). Anglers were limited to two salmon per day (all species except coho salmon) with a minimum size limit of 24 inches TL, except from 1 July to 7 September between Point 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 more fishing days because of increased Klamath fall chinook salmon. In the KMZ, two separate seasons were enacted: 29 May–4 July, and 29 July–14 September, open all days a week. 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 size limit north of Horse Mountain. In the California portion of

TABLE 6
Top 20 Fish Species and Market Category Groups Landed (Metric Tons)
in California's Live/Premium Fish Fishery in 1999

Market category	1999 Live	1999 Dead	1999 Value ($1,000's)	1998 Live	1998 Dead	1998 Value ($1,000's)	Live rank
Cabezon	137.9	6.9	906	157.4	11.5	1,020	1
California sheephead	54.6	4.0	373	102.5	16.0	607	2
Gopher/group gopher rockfish	47.6	6.8	274	55.8	16.0	337	3
Group bolina/brown rockfish	39.0	20.4	264	36.5	26.1	179	5
Lingcod	36.7	114.4	91	31.7	118.4	79	6
California scorpionfish	29.6	8.3	146	29.9	21.1	100	7
Grass rockfish	26.0	0.4	190	39.2	2.5	319	4
Unspecified rockfish	19.4	270.3	123	21.0	1,348.0	114	8
Kelp greenling	13.2	1.4	77	5.8	0.9	38	11
Group red rockfish	12.5	95.7	60	4.9	316.4	20	14
Black and yellow rockfish	10.3	0.4	81	0.4	0.5	3	26
Blackgill rockfish	8.5	26.7	23	0.6	152.0	0.9	24
Copper rockfish	8.3	7.5	42	4.2	25.8	19	17
White croaker	6.5	85.6	19	1.3	63.3	2	21
Black rockfish	6.0	52.6	14	4.9	80.6	9	15
Quillback rockfish	5.4	2.6	53	5.0	6.9	22	13
China rockfish	5.2	1.1	33	5.7	4.2	42	12
Blue rockfish	4.7	8.7	8	3.8	38.0	8	18
Ocean whitefish	3.7	1.3	19	4.7	6.1	18	16
Vermilion rockfish	3.4	7.1	13	1.1	9.1	3	22
Subtotal	478.5	722.2	2,809	516.4	2,263.4	244	
Other fishes	25.5	2,202.8	114	17.3	4,524.9	57	
Grand total	504	2,925	2,923	533.7	6,788.3	301	

the KMZ, anglers landed 6,200 chinook salmon during 17,800 angler trips made primarily on private skiffs.

Nearshore Finfish

Preliminary 1999 California commercial landings of nearshore finfishes totaled 504 t of live fish and 2,925 t of dead fish, for a combined total of 3,429 t, yielding an ex-vessel value of approximately $5.9 million, of which $2.9 million was paid for live fish. This compares to a total of 534 t of live fish and 6,788 t of dead fish landed in 1998 (table 6). Finfish landed dead in 1999 decreased by more than 50% from 1998, while landings of live fish dropped slightly. The top 20 species landed live in 1999 are compared to landings for 1998 in table 6. Fishers traveled farther from their home ports and explored more remote fishing grounds as the demand for live and premium-quality fish continued and the resources close to ports declined.

The principal goal of the fishery is to deliver the fish live to the ultimate consumer in as timely a manner as possible. The fishery ranges from the intertidal zone to about 30 m over rocky habitat. Fish are transported by trucks or vans equipped with aerated tanks, directly to fish markets, restaurants, or individuals. Many fishers deliver and sell their own catch. All of these elements have complicated the accuracy of reported landings, which may be substantially higher.

The commercial fishery for nearshore live and pre-

mium fish began in California in the mid-1980s; in the last decade the number of vessels in the fishery has increased tenfold. In 1989, 76 vessels made at least one landing of nearshore fishes; by 1999 the number of vessels had increased to 819. The most active vessels—those landing at least 500 pounds during the year—numbered only 304 in 1999 and brought in 94% of the total statewide landings. Vessels in the nearshore fishery ranged in size from 3 m (kayak) to 33 m, with an average size of 9 m. Larger vessels may serve as mother ships for several smaller skiffs. Some fishers fish from shore.

The Nearshore Fisheries Management Act of the Marine Life Management Act of 1998 defines nearshore finfishes as rockfish (genus *Sebastes*), California sheephead (*Semicossyphus pulcher*), greenlings (genus *Hexagrammos*), cabezon (*Scopaenichthys marmoratus*), California scorpionfish (*Scorpaena guttata*), and other species found primarily in rocky reef or kelp habitat in nearshore waters. Historically, the commercial use of the nearshore resources was minimal, but with potentially high profits and low overhead costs. Before 1988, the price per pound for line-caught rockfish ranged from $0.50 to $1.50. In 1999, ex-vessel prices for live and premium fish ranged from $0.20 to $10.00 per pound, with an average price of $2.82. Prices vary depending on species, physical condition, and size of the fish. Many fish do not survive the rigors of capture and transport and are sold dead, often at greatly reduced prices.

Nearshore fishes were caught with a variety of gear types, including lines, traps, nets, and diving. Line gear was the reported gear type used for 70% of the statewide landings. Hook and line gear included rod and reel; horizontal and vertical set lines; pipes (stick gear), which consist of short (4- to 8-foot) sections of PVC pipe (rebar or cable) with up to 15 (typically 5) hooked leaders attached; and groundfish troll lines. Net gear was used for 23% of the statewide landings; trap gear accounted for 7%. Diving gear was also used but accounted for less than 1% of the statewide landings.

Approximately 50 market categories of marine fishes were documented as landed live in 1999. Commercial landing weights are reported on landing receipts as 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. Market sampling in Morro Bay found the species composition of market category cabezon to comprise cabezon, grass rockfish (*S. rastrelliger*), kelp greenling (*Hexagrammos decagrammus*), and copper rockfish (*S. caurinus*).

Sablefish, thornyheads, and California halibut have also been landed live in recent years. Preliminary landings from 1999 totaled 136 t for live fish and 3,642 t for dead. These landings are projected to increase as new regulations with low quotas are enacted to protect species targeted in the fishery for nearshore premium and live fish.

Northern California (port complexes of Eureka and Fort Bragg) landings totaled 1,430 t dead and 105 t live fish. Together, these landings (1,535 t) make up 45% of the statewide landings for live and premium fish, with a total ex-vessel value of $1.8 million, of which $0.5 million was paid for live fish. In 1999, live landings were dominated (over 10,000 pounds landed) by cabezon, lingcod, kelp greenling, and copper and china rockfish categories, which accounted for 74% of the area's landings of live fish. Line gear was used to catch 99% of the live fish.

Central California (port complexes of Bodega Bay, San Francisco, Monterey Bay, and Morro Bay) landings of finfish totaled 1,352 t of dead and 238 t live fish. Together these landings (1,590 t) make up 46% of statewide landings for live and premium fish, with a total ex-vessel value of $2.8 million, of which $1.3 million was paid for live fish. Central California landings were dominated by cabezon, bolina, and gopher rockfish groups, grass rockfish, lingcod, and black and yellow rockfish categories, accounting for 85% of the area's landings of live fish. Line gear caught 88% of the land-
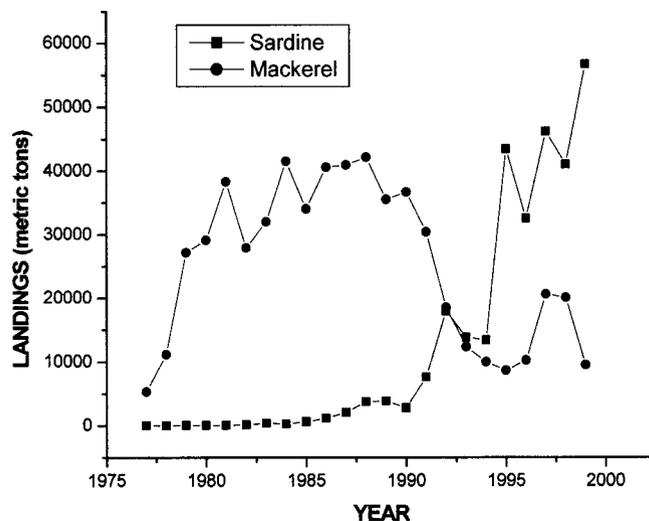

Figure 8. California commercial landings of Pacific sardine and Pacific mackerel, 1977–99.

ings of live fish, followed by trap gear (11%) and net gear (1%).

Southern California (port complexes of Santa Barbara, Los Angeles, and San Diego) landings of live fish totaled 143 t of dead and 161 t of live fish. Together these landings make up 9% of statewide landings for live and premium fish, with an ex-vessel value of $1.3 million, of which $1.1 million was paid for live fish. Live landings were dominated by California sheephead, California scorpionfish, cabezon, and unspecified rockfish categories, which accounted for 82% of the area's landings of live fish. Line gear caught 51% of the live fish, followed by trap gear (28%), net gear (20%), and diving (<1%).

Pacific Sardine

Rebuilding of the Pacific sardine (*Sardinops sagax*) fishery continued in 1999, with the year's total landings of 56,747 t being the highest since the reopening of the directed fishery in 1986 (table 1, fig. 8). The 1999 fishery had an approximate ex-vessel value of $5.0 million, up from $3.6 million in 1998. Approximately 47% of the 1999 CDFG quota was landed, and the directed fishery remained open until year's end.

Fish and Game Code (§8150.8) stated that annual sardine quotas were to be allocated two-thirds to southern California (south of San Simeon Point, San Luis Obispo County) and one-third to northern California (fig. 1). Based on a 1 July 1998 biomass estimate of 1,073,091 t, the harvest formula generated an initial 1999 southern fishery quota of 80,286 t, and a northern quota of 40,188 t (table 7). In October, the CDFG reallocated uncaught quota portions equally between north and south. The revised quotas were 72,183 t for the southern fishery, and 48,291 t for the northern fishery. Neither of these allocations were approached during the 1999 season.

TABLE 7
Pacific Sardine Quota Allocations (Metric Tons) in California for 1999

	Initial quota	Reallocated quota	Landings
North	40,188	48,291	13,884
South	80,286	72,183	42,449
Total	120,474	120,474	56,333

The most recent stock assessment, conducted jointly by the CDFG and the 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).

Management authority for all coastal pelagic species was transferred to NMFS through the PFMC on 1 January 2000. Regulations prior to 2000 gave the CDFG considerable latitude in setting annual sardine quotas. When biomass was estimated to be more than 18,144 t, Fish and Game code required that allowable catch be consistent with resource rehabilitation. To calculate the 2000 harvest guideline, a harvest formula selected by the PFMC as the preferred option in the draft Coastal Pelagic Species Fishery Management Plan (Amendment 8) was used. Based on the 1999 estimate of total biomass (age 1+), the 2000 sardine fishery opened on 1 January with a harvest guideline of 186,791 t for the California fishery, 65% higher than the 1999 CDFG quota.

Ex-vessel prices paid to fishers for sardines remained relatively low in 1999, and were similar to those in 1998, ranging from $66 to $110 per t, and averaging $89 per t. Other important target species for the southern California wetfish fleet include Pacific mackerel (*Scomber japonicus*) and market squid (*Loligo opalescens*) in winter, and tunas in 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: $388 per t for market squid and $600–$1,400 per t for tuna. During 1999, sardine landings varied by month because of availability, demand, and fleet participation in other fisheries.

In 1999, most Pacific sardine landings in southern California were sold to market processors (78%) or to 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, one cannery packed fish for human consumption.

Aside from 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 1999, the ex-vessel value of the sardine live bait fishery was about equal in value to the directed fishery.

Approximately 61% of California's sardine landings were exported in 1999, primarily (85%) as frozen blocks. For the year, 36,089 t of sardines were exported, up from the 1998 total of 22,397 t. Export revenues totaled $17.13 million at approximately $475 per t. Australia is the major importer of 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.

Pacific Herring

Pacific herring (*Clupea pallasi*) fisheries for 1999 recovered from the devastating effects of the 1997–98 El Niño. Statewide landings for the 1998–99 sac roe season (December–March) totaled 2,637 t, a 45% increase from the previous season. Annual sac roe landings declined from 2,432 t to 2,207 t, down 9.2% from the previous year (table 1). Success of the sac roe fisheries was mixed. The San Francisco gill net fleet, composed of three platoons (434 permits) landed 2,571 t, 2.7% over the 2,501 t quota. The Tomales Bay fishery landed a total of 49 t, well below the 390 t quota following the 1997–98 season, when no landings were made. A total of 53 pounds were landed in Crescent City from the 27 t quota, and Humboldt Bay landings totaled 19 t, 39% of the 49 t quota.

Herring collected from CDFG research nets and the gill net fishery appeared to have physically recovered from the weakened state attributed to El Niño conditions during the 1997–98 season. Mean weights per given lengths were within normal ranges; female herring did not display evidence of abnormal gonadal development (as seen during El Niño); and eggs were the typical golden roe that technicians are accustomed to seeing. Higher ratios of female to male herring in samples were reflected in higher than average roe counts for all three gill net platoons, and a higher frequency of unripe male and ripe female herring was noted throughout the season.

Ex-vessel prices for herring with 10% roe recovery averaged about $600 per short ton for gill net landings, with an additional 10% of the base price per ton paid for each percentage point above 10%. The ex-vessel price per ton was approximately 50% more than in the previous season, reflecting improvement in the Japanese economy. Total ex-vessel value of the sac roe fishery was an estimated $2.3 million, nearly a fourfold increase from

the previous season, partly because of higher roe recoveries and improved fish condition. This increased value, however, was well below the average for the previous twelve seasons (approximately $11 million).

The San Francisco Bay herring eggs-on-kelp fishery landings totaled 28.8 t, 42% less than the 49.5 t quota, and the second lowest total on record. Total estimated value of the 1998–99 eggs-on-kelp harvest was $317,000, based on an average ex-vessel price of $5.00 per pound. Product quality varied considerably during the 1998–99 season. Lower-quality product was discarded because of the low price and because the higher processing costs made it economically infeasible to land marginal product. During the 1998–99 season, permittees reported that giant kelp (*Macrocystis pyrifera*) lasted longer while suspended due to higher salinities in the bay. These higher salinities probably resulted from the lack of early winter storms.

The CDFG conducted hydroacoustic and spawn deposition surveys to estimate herring spawning biomass in San Francisco Bay. Spawn deposition estimates were used exclusively to assess the Tomales Bay population. No surveys were conducted for Humboldt Bay or Crescent City Harbor. The 1998–99 herring spawning biomass estimate for the San Francisco Bay population was 35,909 t, nearly double that of the previous season. The stock's recuperation is associated with the abatement of El Niño and the return of favorable ocean conditions, resulting in improved recruitment of 2- and 3-year-old fish.

The Tomales Bay herring spawning biomass continued to fluctuate widely. The 1998–99 spawning biomass estimate was 3,699 t, almost a sevenfold increase from the previous season's estimate of 533 t. This was the highest annual increase since the fishery reopened after the 1992–93 season, and was close to the 25-year average of 4,123 t. This increased biomass followed three consecutive seasons of decline. Age-structure analysis showed that younger and smaller fish, unavailable to commercial gear, made up the bulk of the spawning biomass during the 1998–99 season, but fish age five and older were poorly represented.

Northwesterly winds cooled the ocean waters off central California considerably beginning in spring 1998. Favorable ocean conditions have continued with the prevailing La Niña, and herring fisheries were expected to improve in the 1999–2000 season. The December fishery in San Francisco Bay, however, opened with limited success. High salinities in the bay may have precluded mass spawning, although sampled herring were in good physical condition with normal gonadal development.

Kazunoko remains an integral part of traditional Japanese New Year's festivities. However, changes in the Japanese culture and economy have also resulted in changes in the sac roe market. Industry observers predict that demand for kazunoko will wane as younger Japanese become more Westernized. Ex-vessel prices are expected to improve somewhat with the stabilization of the Japanese economy, but herring buyers were proceeding cautiously and offering only slightly higher prices than in the 1997–98 season.

Pacific Mackerel

The 1999 annual landings of Pacific mackerel (*Scomber japonicus*) in California totaled 9,527 t, a 53% decrease from the 1998 total of 20,073 t (table 1, fig. 8). Effort was focused on traditional fishing grounds from Monterey south to the U.S./Mexican border. Ninety-nine percent of the landings were made in southern California, primarily at San Pedro and Terminal Island. Monterey landings typically range from 1,000 to 3,000 t per year, but were negligible in 1999. Cold oceanic conditions decreased mackerel availability to the northern California fishery in 1999, although Pacific mackerel were caught incidentally in the Canadian whiting fishery.

Management authority for Pacific mackerel was transferred from the CDFG to the NMFS through the PFMC as of 1 January 2000. Under the management of the CDFG, the Pacific mackerel fishing season was specified in the Fish and Game Code (§8410) as a 12-month period from 1 July through 30 June of the following calendar year. The 1999–2000 fishing season harvest guideline was based on a biomass projection derived from a tuned virtual population analysis (VPA) model called ADEPT. When the total biomass was estimated by CDFG to be greater than 18,144 t but less than 136,078 t, the allowable harvest was defined as 30% of the total biomass in excess of 18,144 t. On the basis of an estimated biomass of 230,446 t on 1 July 1999, the CDFG did not establish a quota for the first half of the 1999–2000 season. After the transfer of authority, the PFMC used the CDFG biomass estimate to set a harvest guideline of 46,428 t for the second half of the 1999–2000 fishing season. Landings made between 1 July 1999 and 31 December 1999 will be subtracted from the harvest guideline.

Unlike the 1997–98 season, when the quota was exceeded by 931 t (4%), the 1998–99 season closed with 7,155 t (23%) of the quota remaining. Availability of Pacific mackerel to the wetfish fleet remained low throughout the season, and processors had standing orders that were not filled. Monthly landings varied, from a high of 6,157 t in September 1998, to a low of 2.3 t landed in June 1999. 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 ex-vessel price paid for Pacific mackerel (landings over one t) ranged from $40 to $160 per t. The sale of the catch generated approximately $1.09 million for fishers.

Reduction

The reduction fishery targets species with the intent of landing whole fish for processing into protein products. Reduction products such as fish meal, oil, flour, or fertilizer are sold as supplements for animal feeds. (Fish scraps are also reduced, but they are not part of the reduction fishery.)

During the last several decades California's reduction fishery has targeted northern anchovy (*Engraulis mordax*). Northern anchovy landings for reduction peaked in 1975, when 141,586 t were processed. In 1976, landings in the reduction fishery began a general decline, reaching a low of 63 t in 1990. In 1991, a small fishery landed an annual total of 1,037 t. From 1992 to 1995 no northern anchovy landings were reduced. From 1996 to 1998 the fishery was limited to a few landings totaling approximately 3,900 t for the three years.

In 1999, the California anchovy domestic reduction harvest was low, less than 50% of the 16,000 t domestic allowable harvest quota set by the NMFS in its Northern Anchovy Fishery Management Plan. The NMFS used the 1995 spawning biomass estimate for the central subpopulation of northern anchovy to set interim harvest limits (which ultimately became the final limits) for the 1999–2000 fishing year because no new assessment of the northern anchovy resource had been made. The NMFS had also used the 1995 spawning biomass estimate to establish harvest limits for the 1995–96 through 1998–99 fishing years. Also in 1999, the PFMC recommended that 3,000 t be set as a harvest limit for two vessels participating in an experimental fishery in the Farallon Islands Closed Area off San Francisco. Nearly all northern anchovy landed for reduction in California were taken in Subarea A, the northern portion of the Pacific anchovy fishing area (between Point Reyes in the north and Point Buchon in the south), and were processed by one company.

Poor market conditions influenced the 1999 anchovy reduction fishery, with ex-vessel prices averaging about $40 per short ton, continuing a trend that has dominated the market since the early 1980s. Industry representatives have commented that because of the low price structure, reducing anchovy is, at best, a break-even exercise. As a result, only a few orders were placed, with very few boats participating in the northern anchovy reduction fishery in 1999.

In recent years, many in the industry have expressed an interest in the possibility of a reduction fishery for Pacific sardine (*Sardinops sagax*). Prior to 1999 no permits were issued allowing processors to engage in a re-
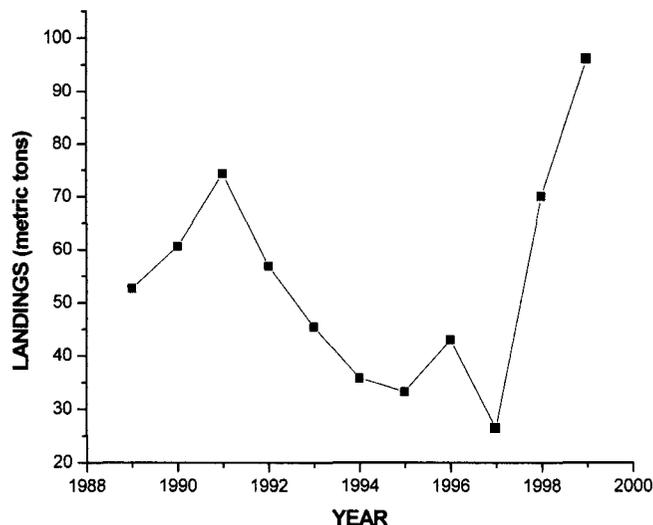

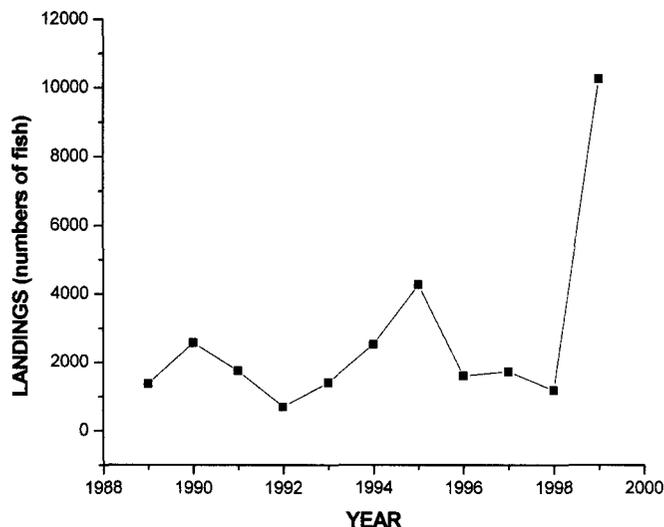Figure 9.   California commercial landings of white seabass, 1989–99.

Figure 10.   California CPFV landings of white seabass, 1989–99.

duction fishery for Pacific sardine. In 1999 one central California processor applied for, and received, a permit to reduce Pacific sardine. This occurred several months after the CDFG declared that the Pacific sardine resource was officially recovered. Even though this processor obtained a permit to reduce Pacific sardine, no landings of whole sardine were actually reduced. Instead, Pacific sardine reduction was limited to the processing of scraps left over from canning.

White Seabass

White seabass (*Atractoscion nobilis*) is the largest member of the Sciaenid family harvested from California's nearshore waters and islands. Both the commercial and recreational components of this fishery reported relatively high yields in 1999 (figs. 9 and 10). In 1999, commercial white seabass landings rose to 96 t, the largest value

TABLE 8
Recovery of Coded-Wire Tagged OREHP-Produced White Seabass in 1999

Location		Size (mm)		Days at liberty	Distance traveled (nmi)
Release	Capture	Release	Capture		
Channel Is. Harbor	Malibu Point	216	724	1,679	25
Mission Bay	Long Beach Harbor	203	762	1,752	85
Mission Bay	Mission Bay	279	737	730	n/a
Newport Harbor	Platform Gina	221	770	1,789	77

Data provided by Hubbs–Sea World Research Institute

in 17 years (fig. 9). This value represents a 27% increase from 1998, and a 73% increase from the historical low of 26 t reported in 1997. Commercial market data for 1999 indicated that most landings by weight (65%) were made at fish markets in Los Angeles Harbor. Other landings were made in Santa Barbara and Channel Islands Harbors (24%), Port San Luis and Morro Bay (6%), San Diego County (3%), and Monterey County (2%).

The ex-vessel price paid to the fishers by markets ranged from $0.50 to $6.00 per pound. The average price per pound was $1.91, down $0.36 from 1997, when commercial white seabass landings were at a historic low. The relatively low average price in 1999 is likely a function of supply and demand.

White seabass were harvested primarily by gill net gear: 55% by set gill net and 35% by drift gill net. Additional gears used to harvest white seabass included hook and line (5%), miscellaneous (4%), and trawl (1%). Catch data indicate that most of these fish were taken between Orange and Los Angeles Counties, while a small number of fish were taken from Ventura County, and north of Point Conception.

Two regulatory events over the past 20 years have negatively affected the number of commercial white seabass reported landed in California. Before 1982, most of the white seabass landed in California were harvested in Mexican waters. In 1982, the Mexican government prohibited U.S. commercial fishing vessels from exploiting its sovereign waters, and landings of white seabass in California plummeted. In 1990, California voters approved Proposition 132, which prohibited the use of gill and trammel nets in southern California's newly created Marine Resources Protection Zone (MRPZ). The MRPZ extends three nautical miles offshore of the mainland coast, between Point Arguello and the Mexican border. The MRPZ was completely closed to gill netting on 1 January 1994, and annual reported landings of white seabass dropped once again.

Recreational anglers landed 10,260 white seabass while fishing aboard commercial passenger fishing vessels (CPFVs) in 1999, a more than eightfold increase from 1998 (fig. 10). The CPFV industry has not made landings of this magnitude since the mid-1960s. Before 1999, annual reported landings from 1980 through 1998 os-

cillated between 600 and 5,000 fish, averaging 1,640 fish over a 19-year period.

In the early 1980s, the white seabass population in California appeared to be in decline. In 1983, the California legislature created the Ocean Resources Enhancement and Hatchery Program (OREHP) to perform basic and applied research on the artificial propagation, rearing, stocking, and distribution of adversely affected marine fish species that are important to sport or commercial fishing in California waters south of Point Arguello. Since 1989, white seabass has been OREHP's primary focus of research. Approximately 306,073 OREHP-produced juvenile white seabass were released into the ocean from 1990 through 1999; 25,115 fish were released in 1999. Each OREHP-produced fish was coded-wire tagged (CWT) at the hatchery before being transported to a predetermined grow-out site. There are twelve grow-out sites in bays and marinas from San Diego to Santa Barbara, including Catalina Island. The fish are raised by volunteers until they reach 200 mm, and then released at the grow-out site or nearby.

In 1999, four CWT white seabass that had recruited into the recreational fishery were the first to be recovered by either the recreational or commercial fishery (table 8). The recaptured fish had been at liberty between two and five years, and had traveled up to 85 nautical miles from their release site. The minimum size at release was 203 mm, and the maximum size at recapture was 770 mm. One of the recaptured fish had grown 458 mm in two years. This fish was released and recaptured in Mission Bay.

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 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

TABLE 9
Southern California CPFV Landings (Number of Fishes) in 1999 and 1998

Species/species group	1999 landings Number	Rank	1998 landings* Number	Rank	Percent change
Rockfishes, unspecified	495,873	1	358,722	3	+38
Barred sand bass	435,777	2	377,853	2	+15
California barracuda	386,315	3	455,776	1	−15
Albacore	239,554	4	147,436	6	+62
California scorpionfish	225,726	5	119,620	8	+89
Ocean whitefish	139,281	6	69,222	10	+101
Kelp bass	129,475	7	233,591	5	−45
Pacific mackerel	82,802	8	127,596	7	−35
Yellowtail	78,466	9	250,587	4	−69
Bluefin tuna	36,362	10	18,891	12	+92
Flatfishes, unspecified	35,301	11	3,318	22	+964
Halfmoon	25,500	12	7,951	15	+221
California sheephead	23,084	13	18,354	13	+26
Yellowfin tuna	21,215	14	75,367	9	−72
White seabass	11,512	15	1,344	23	+755
White croaker	10,039	16	6,449	17	+56
California halibut	9,285	17	4,834	18	+92
Wahoo	5,151	18	4,348	19	+18
Jack mackerel	4,690	19	3,544	20	+32
Dolphinfish (dolphin)	3,633	20	6,470	16	−44
Lingcod	3,579	21	3,539	21	+1
Pacific bonito	2,810	22	57,630	11	−95
Skipjack tuna	2,707	23	13,734	14	−80
Blacksmith	1,253	24	888	24	+41
Queenfish	1,100	25	88	27	+1,150
Cabezon	687	26	745	25	−8
Shark, unspecified	532	27	283	26	+88
Jumbo squid	104,549	—	1,590	—	+6,475
Total number kept	2,538,251		2,376,944		+7
Number of anglers	543,626		580,730		−6
Reporting CPFVs	254		198		+22

*These 1998 landings have been revised. The numbers presented here are the final 1998 commercial passenger fishing vessel landings.

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 availability in southern California waters of species normally found off Mexico. Conversely, La Niña conditions increase the numbers of colder-water species. CPFVs are typically quick to exploit the fishing opportunities provided by these changing oceanographic conditions.

The top ten species or species groups in 1999 in southern California (by number of fishes in landings) were rock-fishes, barred sand bass, California barracuda, albacore tuna, California scorpionfish, ocean whitefish, kelp bass, Pacific mackerel, yellowtail, and bluefin tuna (table 9). These top ten species or species groups include nine of the top ten groups from 1998. The exception, bluefin tuna, jumped in 1999 from the twelfth rank to the tenth, while yellowfin tuna dropped from ninth to fourteenth. The order of abundance also changed for nine of the top ten species or species groups, except for barred sand bass (second rank).

In 1999, 543,626 anglers aboard 254 reporting CPFVs landed 2,538,251 fishes south of Point Conception (table 9). These southern California landings represented 75% of the total landings by CPFVs statewide (3,395,471 fishes). The number of fishes landed statewide was 3% more than in 1998, with landings in southern California increasing by 7%. The number of anglers using southern California CPFVs dropped by 4% in 1999, and represented 80% of anglers using CPFVs statewide.

Decreased landings were reported in 1999 for Pacific bonito, skipjack tuna, yellowfin tuna, yellowtail, dolphinfish, kelp bass, Pacific mackerel, California barracuda, and cabezon (table 9). Decreases in some of the more southerly species or species groups (e.g., skipjack tuna,

TABLE 10
Central and Northern California CPFV Landings (Number of Fishes) in 1999 and 1998

Species/species group	1999 landings		1998 landings*		Percent change
	Number	Rank	Number	Rank	
Rockfishes, unspecified	758,364	1	791,070	1	−4
Chinook (king) salmon	35,465	2	57,459	2	−38
Lingcod	23,268	3	16,847	4	+38
Albacore	15,429	4	8,549	6	+80
Striped bass	10,774	5	19,720	3	−45
California halibut	5,054	6	7,357	7	−31
Cabezon	2,218	7	1,834	9	+21
Flatfishes, unspecified	1,693	8	1,122	10	+51
Pacific mackerel	832	9	9,018	5	−91
White croaker	705	10	468	12	+51
Leopard shark	610	11	444	13	+37
Jack mackerel	475	12	2,060	8	−77
Sturgeon	354	13	686	11	−48
Shark, unspecified	117	14	241	14	−51
Bluefin tuna	28	15	94	15	−70
Dungeness crab	26,544		13,787		+93
Rock crab	1,914		3,321		−43
Jumbo squid	0		1,588		−100
Total number kept	857,220		919,059		−7
Number of anglers	131,791		137,506		−4
Reporting CPFVs	120		112		+7

*These 1998 landings have been revised. The numbers presented in this table are the final 1998 commercial passenger fishing vessel landings.

yellowfin tuna, yellowtail, dolphinfish) can be primarily attributed to decreased availability. Cooler oceanic waters moved onshore along the California coast in 1999, causing some species to shift southward. Decreased landings of Pacific mackerel and Pacific bonito also may have been related to decreased availability, but reduced biomass may also have been a factor.

In response to the decreased availability of southerly species, the southern California CPFVs shifted their effort to other species or species groups, including albacore, bluefin tuna, and a number of nearshore species. Albacore landings increased 62% and bluefin landings 92%. The increase in albacore landings was due in part to increased effort. The number of trips that landed albacore in 1999 increased 29% over the previous year. Increased landings were also reported for a number of nearshore species including unspecified flatfishes, white seabass, halfmoon, ocean whitefish, California halibut, California scorpionfish, white croaker, rockfishes, California sheephead, and barred sand bass (table 9). White seabass landings increased from 1,344 fish in 1998 to 11,512 in 1999. The last year that white seabass landings exceeded 10,000 individuals was in 1964, when 14,901 fish were landed. The substantial increase in landings of unspecified flatfishes was partly due to an increase in CPFV trips out of the Seal Beach/Long Beach/San Pedro port group that targeted sanddabs.

Tremendous landings of jumbo squid were also recorded in 1999 by CPFVs operating in the Los Angeles area and south. The 1999 landings jumped 6,475%, from 1,590 squid in 1998 to 104,549 in 1999. This is

in contrast to the central and northern California area, where 1,588 squid were landed in 1998, compared to zero in 1999. The increase in jumbo squid landings in southern California is probably a result of both increased availability as squid shifted south in response to cooler nearshore waters, and more CPFV trips targeting this species.

Central and Northern California

Along the California coast north of Point Conception, CPFV anglers traditionally 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. In addition, more southerly species such as bluefin tuna (*Thunnus thynnus*), white seabass (*Atractoscion nobilis*), skipjack tuna (*Katsuwonus pelamis*), and yellowtail (*Seriola lalandi*) may be targeted in warmwater years. Within San Francisco Bay, CPFV anglers target California halibut (*Paralichthys californicus*), striped bass (*Morone saxatilus*), sturgeon (*Acipenser* spp.), rockfishes, and leopard shark (*Triakis semifasciata*).

The top ten species or species groups taken in 1999 by northern and central California CPFVs (by number of fishes in landings) were rockfishes, chinook (king) salmon (*Oncorhynchus tshawytscha*), lingcod, albacore, striped bass, California halibut, cabezon, unspecified flatfishes, Pacific (chub) mackerel (*Scomber japonicus*), and white croaker (*Genyonemus lineatus*; table 10). These ten species or species groups included nine of the top ten from 1998. The exception, white croaker, rose in 1999

from the twelfth rank to the tenth, while jack mackerel dropped from eighth to twelfth. Also, the order of rank abundance changed for eight of the top ten species or species groups. Only rockfishes (first) and chinook salmon (second) ranked the same in 1998 and 1999.

In 1999, 131,791 anglers caught 857,220 fishes, a 7% decrease in landings from 1998. Decreases in chinook salmon, California halibut, striped bass, sturgeon, Pacific mackerel, jack mackerel, bluefin tuna, and unspecified sharks contributed to this overall decrease (table 10). In addition, fewer than ten individuals of California barracuda (*Sphyraena argentea*), white seabass, and ocean whitefish; and no yellowtail, Pacific bonito (*Sarda chiliensis*), skipjack tuna, or dolphinfish (*Coryphaena hippurus*) were landed in central and northern California ports in 1999. Decreases in some of the more southerly species or species groups (e.g., California barracuda, white seabass, yellowtail, skipjack tuna, dolphinfish) can be attributed to a return to colder water conditions along the California coast in 1999. Lower landings of species such as Pacific mackerel, jack mackerel, and Pacific bonito may be due to a decrease in availability as well as a reduction in biomass. Decreased landings of striped bass may be due to several factors, including the presence of colder water outside San Francisco Bay, which reduced the availability of these fish to CPFVs in the area; increased bait availability and thus reduced catch rates; and a shift in effort to other species, such as albacore.

Albacore landings in 1999 increased to 15,429, slightly lower than the 16,567 albacore landed in 1997 but 80% higher than the 1998 landings. Increased landings also were reported for lingcod, cabezon, unspecified flatfishes, white croaker, and leopard shark (table 10). The increases in albacore landings can be attributed partly to an increase in effort. Although the number of reporting vessels that landed albacore between 1998 and 1999 stayed the same (42), the number of trips that landed albacore increased by 11%. Lingcod landings increased from 16,847 fish in 1998 to 23,268 fish despite a change in bag limit from 3 to 2 fish starting on 1 January 1999.

Landings of crab and squid changed considerably between 1998 and 1999. Dungeness crabs increased by 93%, while rock crabs (*Cancer antennarius*) decreased by 43%. No jumbo squid were taken by CPFV anglers in this region in 1999, probably because the jumbo squid population shifted south as colder water returned to the area (see section describing the southern California CPFV landings).

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THE STATE OF THE CALIFORNIA CURRENT, 1999–2000: FORWARD TO A NEW REGIME?

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ABSTRACT

This report is the latest in an ongoing series that describes oceanographic conditions in the coastal waters of the Californias. The emphasis here is on observations made by CalCOFI (California Cooperative Oceanic Fisheries Investigations) and other programs during the 1999–2000 period. The physical environment off southern California shifted dramatically between 1997 and 1999 from El Niño (warm anomalies, low productivity) to La Niña (cool anomalies, high productivity) conditions. The tropical ocean has remained in the La Niña state through 1999 and into spring 2000, while the region off southern California has been characterized by a vigorous, offshore-displaced California Current, and near-surface temperatures close to the climatological mean. Primary and secondary production in the California Current system have rebounded since the biological drought of the 1997–98 El Niño. In light of the dramatic variability observed in the CalCOFI region over the past few years, we discuss the physical and biological future of the southern California Current system within the context of a potential large-scale climatic regime shift.

INTRODUCTION

This is the seventh in an annual series of reports (Hayward et al. 1994, 1995, 1996, 1999; Schwing et al. 1997; Lynn et al. 1998) that present and synthesize recent observations of the physical and biological structure of the southern California Current system (CCS). The emphasis in this report is on observations made over the past year (April 1999 to April 2000), primarily from the quarterly CalCOFI surveys. We also present data from observational programs which sample other portions of the CCS, and which place the CalCOFI observations in a larger regional context.

The past few years constitute one of the most remarkable periods in the 50-year history of CalCOFI. One of the strongest El Niño events on record, and by far the most thoroughly monitored, affected the region during 1997–98, generating anomalously warm waters and low productivity (Lynn et al. 1998). CalCOFI responded to this event by augmenting its traditional sampling plan with monthly mini cruises between the quarterly surveys, yielding a high-resolution time series of the physical and biological response to a strong El Niño (e.g., Hayward 2000). Following this event, there was a dramatic transition to cool-water, more highly productive conditions, associated with both a strong La Niña event (Hayward et al. 1999) and anomalous upwelling-favorable wind forcing along the West Coast (Schwing et al. 2000). The tropical ocean has remained in the La Niña state through 1999 and into spring 2000. Consequently, the period 1999–2000 has been characterized by a continuation of relatively cool water conditions in the southern CCS, but with a more vigorous, offshore-displaced California Current than is expected from the CalCOFI hydrographic climatology. Primary
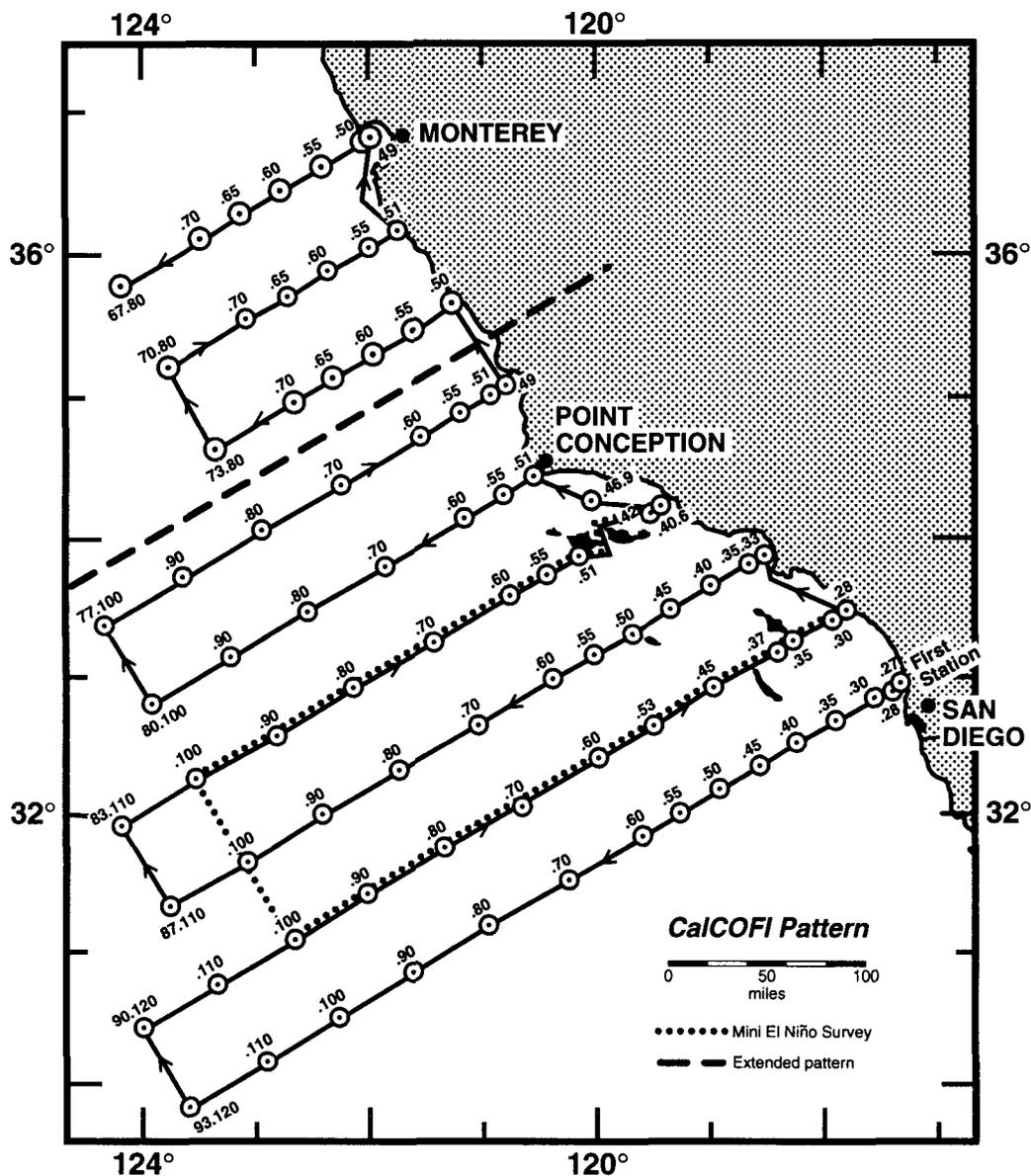
Figure 1. The standard CalCOFI sampling grid. The regular 66-station pattern occupied by CalCOFI since 1985 (lines 77, 80, 83, 87, 90, and 93) is shown by a solid line. The stations for the 1997–98 mini El Niño cruises on lines 83 and 90 are shown by a dotted line. The area of additional underway sampling north of the regular pattern is above the dashed line (lines 67, 70, and 73).

and secondary production have rebounded following the biological drought of the 1997–98 El Niño.

We begin our report with a summary of the large-scale atmospheric and oceanic conditions that have affected the CCS during 1999–2000. We then describe general patterns of ocean circulation and water properties in the CCS as revealed by survey cruises off southern California (CalCOFI) and Baja California (IMECOCAL). The corresponding biological patterns are then summarized, focusing on the near-surface chlorophyll a patterns, cruise-mean macrozooplankton biomass, and seabird communities in the CCS. The biological response to the recent environmental variabil-

ity is further explored by comparing satellite-derived and in situ chlorophyll estimates from the CalCOFI region. Finally, we conclude the report by speculating on the future of the California Current in the context of an anticipated large-scale climatic regime shift.

DATA SETS AND METHODS

The CalCOFI program maintains quarterly (normally January, April, July, and October) survey cruises that occupy a geographically fixed grid of 66 stations off southern California (fig. 1). This grid has been expanded in recent years to include three northern lines in winter and spring, where underway measurements are made,
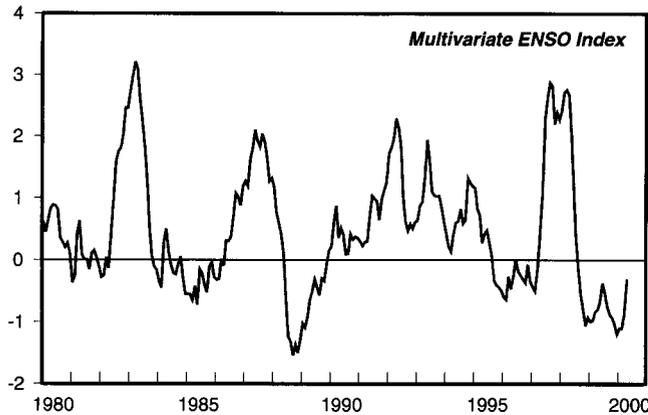
Figure 2. Monthly time series of the multivariate ENSO index, or MEI (Wolter and Timlin 1998), for January 1980–April 2000. The series highlights the rapid transition from El Niño to La Niña in 1998, and the extended negative phase of MEI associated with the 1998–2000 La Niña.
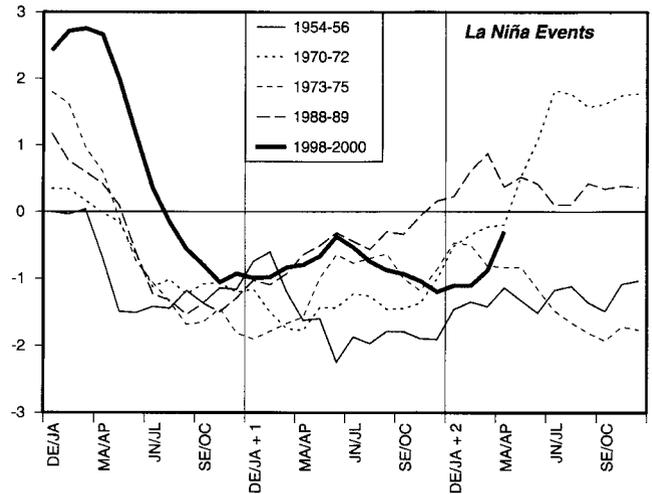

Figure 3. Monthly multivariate ENSO index, or MEI (Wolter and Timlin 1998), comparing the intensity and duration of the 1998–2000 La Niña to four previous strong La Niña events. Multiyear La Niña events are not uncommon.

and the additional occupations of lines 83 and 90 during the 1997–98 El Niño event. Standard station sampling includes a CTD/rosette cast, with water samples collected at 20–24 depths in the upper 500 m to determine salinity, dissolved oxygen, inorganic nutrients, phytoplankton pigments (chlorophyll a and phaeophytin), and primary production (^{14}C uptake at one station per day). Continuous underway sampling of surface temperature and salinity is carried out, and high-resolution measurements of upper ocean currents are made with an acoustic Doppler current profiler (ADCP). The continuous underway fish egg sampler (CUFES; Checkley et al. 1997) is used to track fish eggs and larvae along the transects. Oblique and surface (neuston) net tows (0.505 mm mesh) are taken at each station.

We also present data from a Mexican sampling program, Investigaciones Mexicanas de la Corriente de California (IMECOCAL), which has occupied historical CalCOFI lines off Baja California since 1997. These cruises are planned to coincide closely with the timing of the CalCOFI cruises, and use complementary sampling methods. Additional data sets presented here include seabird observations conducted on the CalCOFI surveys, and ocean color from the OCTS (ocean color and temperature scanner) and SeaWiFS (sea-viewing wide field-of-view sensor) satellites. Details of sampling methods and data sources are briefly described as these observations are presented.

OBSERVATIONS

Large-Scale Atmospheric and Oceanic Patterns

After a dramatic transition in 1998 from one of the strongest El Niño events of this century to a strong La Niña event, 1999 and early 2000 were marked by a continuation of La Niña conditions in the tropical Pacific.

The multivariate ENSO index (MEI; Wolter and Timlin 1998) dropped from an El Niño peak in spring 1998 to a minimum in late fall 1998 (fig. 2), the most dramatic decline in the 50-year history of the MEI (http://www.cdc.noaa.gov/~kew/MEI/mei.html). The MEI has remained moderately to strongly negative since late 1998 (figs. 2 and 3).

The MEI can remain negative for many months, suggesting a multiyear La Niña event (e.g., 1954–56, 1970–72; fig. 3). However, conditions can also shift quickly back to El Niño (e.g., 1972). As of April 2000, the MEI had remained negative for 21 consecutive months, the longest continuous negative period since the 1976–77 climate regime shift. The MEI does indicate, however, that La Niña conditions weakened considerably in April 2000, signaling a possible end to the 1998–2000 La Niña. A similar decline in the MEI occurred in April 1999, but was followed by a regrowth of La Niña. May is often a pivotal month in the development of climate anomalies such as El Niño; this La Niña could reintensify as it did in 1999, or return to a positive MEI and El Niño conditions as in 1972.

Surface anomalies throughout the Pacific during 1999 and early 2000 (fig. 4) remained in a pattern typical of La Niña (Murphree and Reynolds 1995). Strong clockwise wind anomalies in the northeast Pacific were associated with a very strong North Pacific High (fig. 4). These anomalies contributed to enhanced trade winds in the western tropical Pacific, and unusually robust upwelling-favorable winds along the North American west coast. Upper-level winds were affected by the unusual sea-level pressure patterns. For much of the previous several months, the North Pacific jet stream flowed over western Canada, well north of its usual path; however, a more zonal, southerly-positioned jet stream redevel-

July 1999 SST and 1000 MB Vector Wind Anomalies

September 1999 SST and 1000 MB Vector Wind Anomalies

January 2000 SST and 1000 MB Vector Wind Anomalies

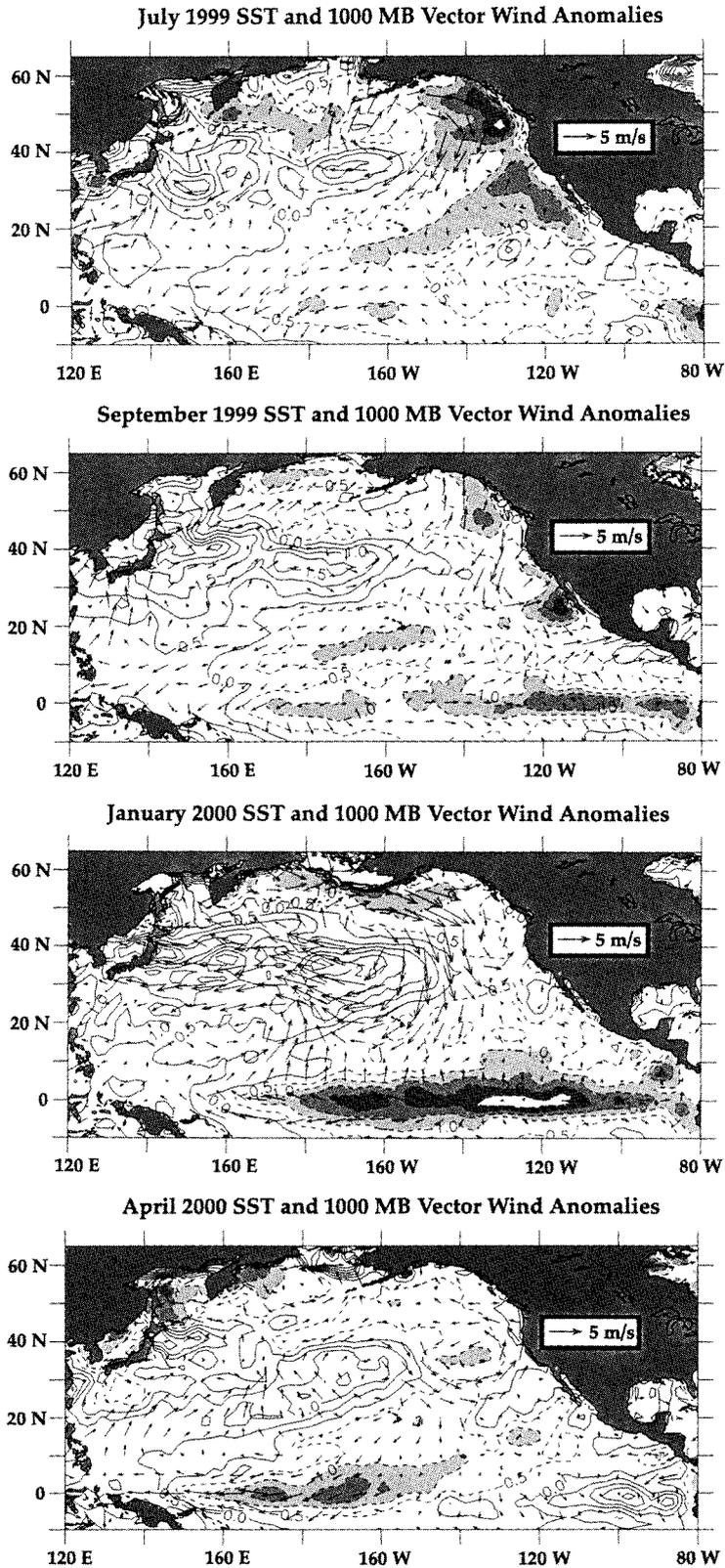## April 2000 SST and 1000 MB Vector Wind Anomalies

Figure 4.   Anomalies in the North Pacific Ocean. Anomalies of surface wind velocity and sea-surface temperature (SST) for July 1999, September 1999, January 2000, and April 2000. Arrows denote magnitude and direction of wind anomaly. Contours denote SST anomaly. Contour interval is 0.5°C. Negative SST anomalies (dashed contours) less than −1.0°C are shaded. Wind climatology period is 1968–96. SST climatology period is 1950–79. Monthly data obtained from the NOAA-CIRES Climate Diagnostics Center Web site (*http://www.cdc.noaa.gov*).

October 1999 200 MB Vector Wind Anomalies

January 2000 200 MB Vector Wind Anomalies
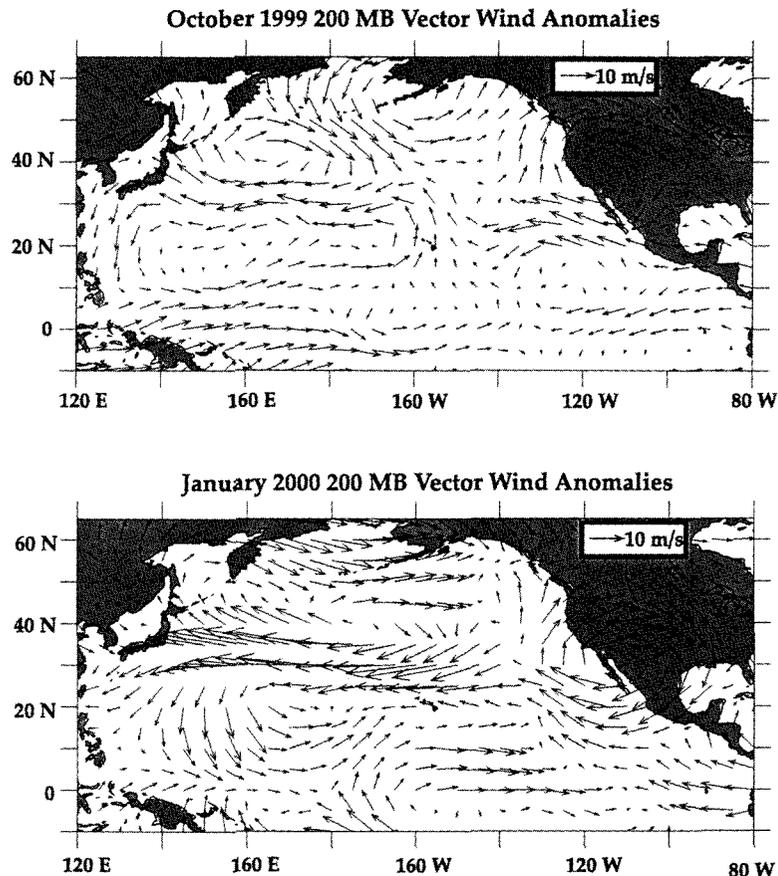
Figure 5. Anomalies of wind velocity at 200 mb for October 1999 and January 2000. Arrows indicate the direction and magnitude of the wind anomalies. Scale vector is 10 m/s. Winds at this level show position and strength of the jet stream, and general storm track. Monthly data obtained from NOAA-CIRES Climate Diagnostics Center. Wind climatology period is 1968–96.

oped in early 2000 (fig. 5). This provided a steady supply of moist, subtropical air from the southwest from mid-January through February, bringing heavy precipitation to northern and central California and producing normal annual precipitation totals in an otherwise relatively dry winter.

Since late 1998 a horseshoe-shaped region of cooler than normal sea-surface temperatures (SSTs) has stretched roughly along the axis of the North Pacific trade winds from the western equatorial Pacific to Baja California, and along the North American west coast into the Gulf of Alaska (fig. 4). Cool anomalies also spanned the equator east of the date line. These negative SST anomalies were particularly large in the CCS. The most extreme stage of this pattern was in spring–summer 1999 (fig. 4), when strong southward wind stress produced record levels of coastal upwelling for most of California (Schwing et al. 2000). Positive SST anomalies were maintained in the western tropical Pacific and from the western North Pacific to Hawaii.

The thermocline in the eastern tropical Pacific has remained unusually shallow since mid-1998, while an anomalously deep thermocline has continued in the western tropical Pacific (fig. 6). This condition typifies La Niña events. A switch toward El Niño conditions will probably occur if the associated warm subsurface anomalies move eastward along the equator, which eventually happens as La Niña wanes. Surface tropical temperature anomalies continue to display a general La Niña pattern (fig. 4). Positive SST anomalies developed in late March 2000 in the eastern equatorial Pacific (NCEP 2000b), but still were underlaid by an anomalously shallow thermocline and cooler than normal subsurface temperatures (fig. 6).

Coastal Conditions

Monthly coastal upwelling indices (Bakun 1973; Schwing et al. 1996) indicate that 1999 was a period of generally stronger than normal upwelling in the CCS (fig. 7). After an interval of weaker than normal upwelling through late spring and summer 1998 south of San Francisco, upwelling was slightly above normal in late 1998 (Hayward et al. 1999). Anomalies remained positive through 1999. Upwelling was particularly strong

ANOMALOUS DEPTH OF 20°C ISOTHERM
Equatorial Pacific
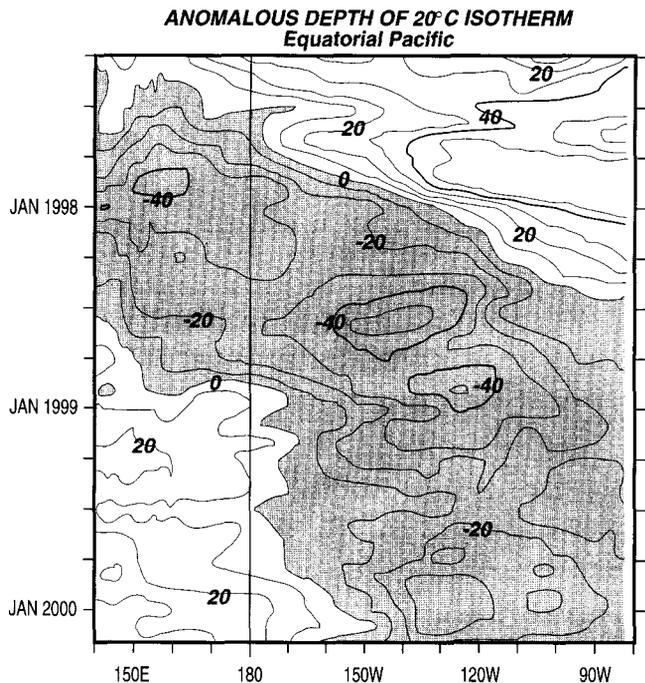
Figure 6. Anomalous depth (m) of 20°C isotherm for 5°N–5°S in the Pacific Ocean. Contour interval is 10 m. Negative anomalies (anomalously shallow thermocline) are shaded. Reference period is 1983–92. Adapted from NCEP 2000a.
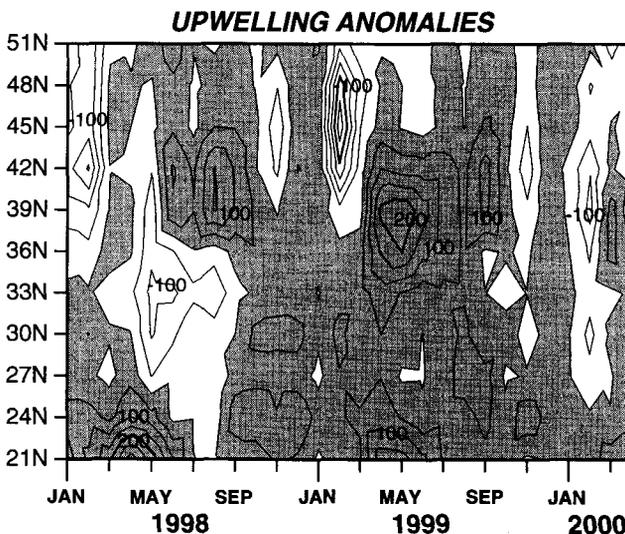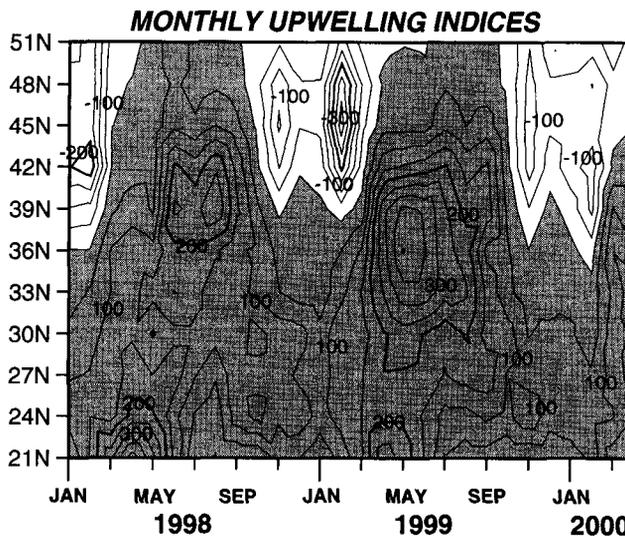
MONTHLY UPWELLING INDICES

UPWELLING ANOMALIES

Figure 7. Monthly upwelling index and upwelling index anomaly for January 1998–April 2000. Shaded areas denote positive (upwelling-favorable) values in upper panel, and positive anomalies (generally greater than normal upwelling) in lower panel. Anomalies are relative to 1948–67 monthly means. Units are m³/s per 100 km of coastline.

along the California coast in spring and summer 1999. Upwelling anomalies off central California during the 1999 upwelling season were the greatest in the 54-year record of the upwelling index (Schwing et al. 2000). Negative upwelling anomalies throughout the CCS in early 2000 were associated with downwelling-favorable winds and a persistent northeastward upper-level flow across the region.

In the California Current region, NDBC coastal buoy winds (fig. 8) display the short-term variability associated with synoptic atmospheric events, superimposed on the annual climatological cycle of strong southward wind in summer and northward or weak southward wind in winter. Winds are typically strongest off northern California and weakest within the Southern California Bight (SCB). Wind vectors align strongly with the local coastline (table 1).

Coastal alongshore winds through the latter half of 1998 and much of 1999 were dominated by stronger than normal southward winds (i.e., more upwelling-favorable; fig. 8). A number of very robust wind events were observed coastwide during the first half of 1999. Particularly strong events occurred in late March, early May, and June–early July. The region was under the influence of northward winds in November 1999 associated with a north-south trough of low pressure that also forced the storm track well north of California (fig. 5). Winds during early 2000 were northward (fig. 8), also

in association with a northward jet stream (fig. 5) and the passage of winter cyclones.

In less than two years, SSTs in this region dropped from the warmest on record—during the height of El Niño—to low temperatures not seen in decades. West Coast buoy SSTs began to drop in late 1998 following the mature phase of El Niño (fig. 9). A series of unseasonably strong upwelling-favorable wind events during this time (fig. 8) contributed to the dramatic cooling. SSTs continued to decline through the first half of 1999 (fig. 9). The very strong southward wind events in spring and summer 1999 led to enhanced coastal upwelling and contributed directly to this rapid cooling (Schwing et al. 2000). Coastal sea level was also well below normal during this period (Schwing et al. 2000).
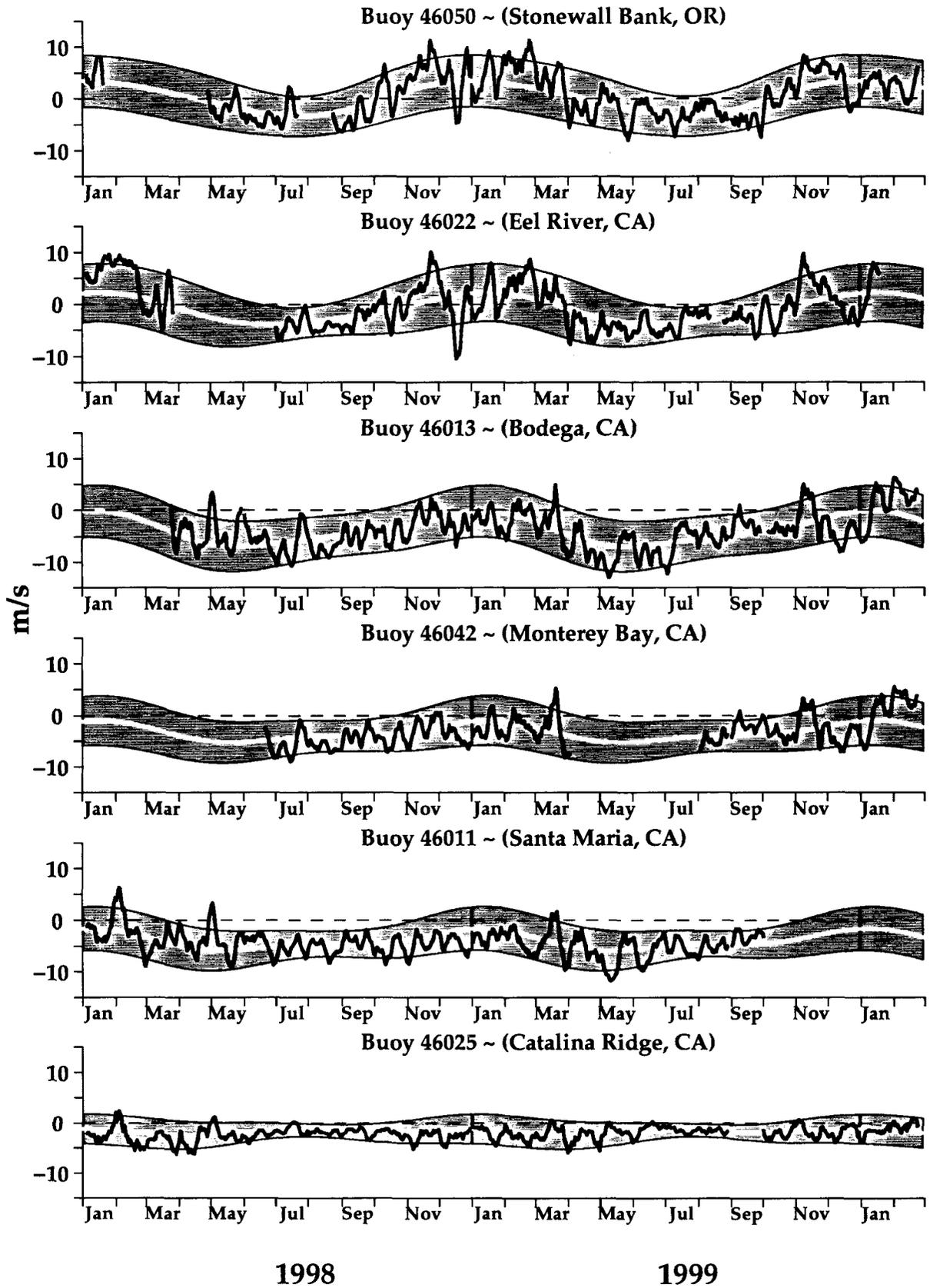
Figure 8.   Time series of daily averaged alongshore winds for January 1998–February 2000 at selected NDBC coastal buoys. Bold lines indicate the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard error for each Julian day. Series have been smoothed with a 7-day running mean. The periods used for calculating the climatology at each site and the alongshore angle are shown in table 1.
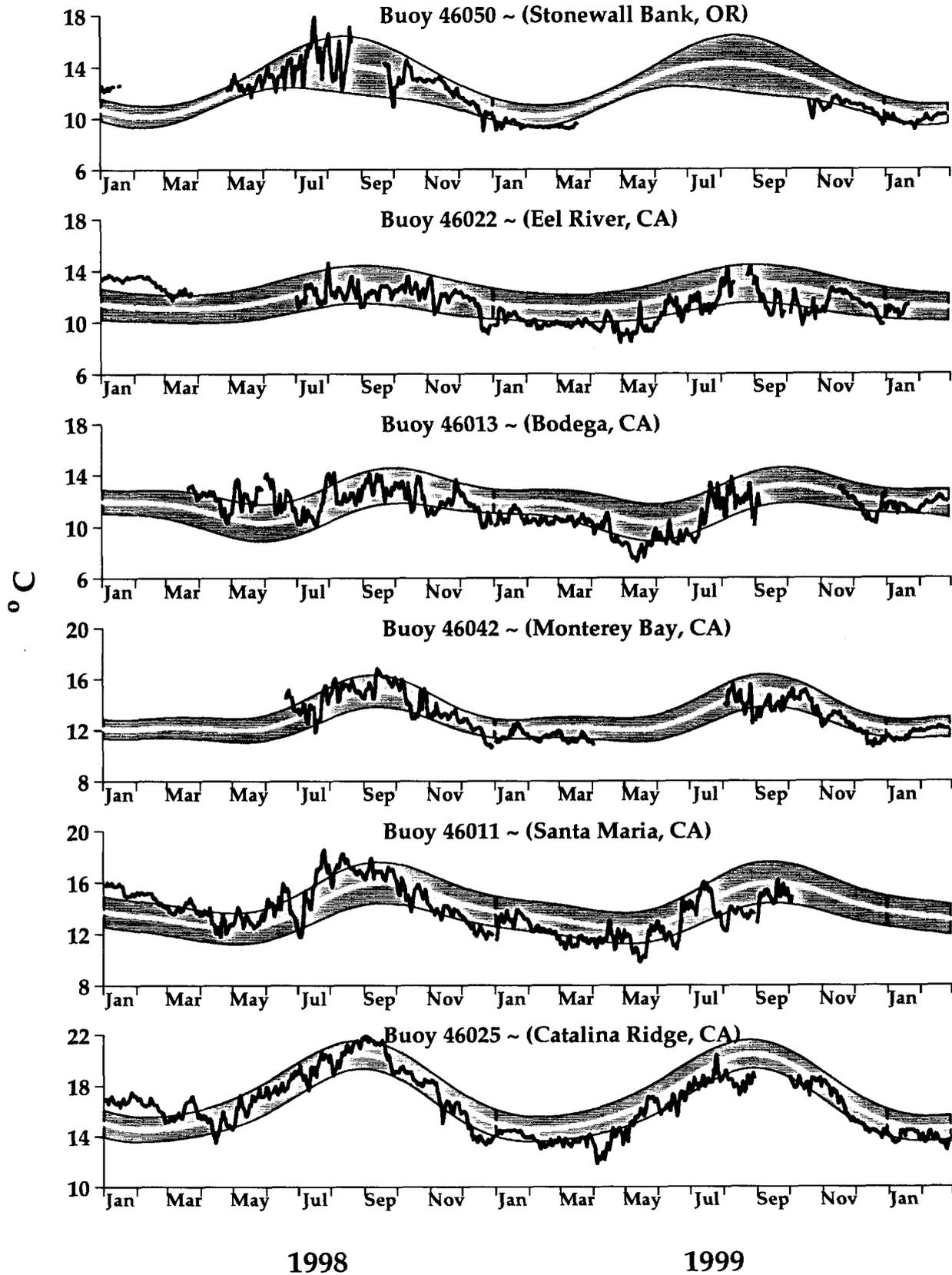
Figure 9. Time series of daily averaged SST for January 1998–February 2000 at selected NDBC coastal buoys. Bold lines show the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard error for each Julian day. The periods used for calculating the climatology at each site are 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	1991–99	359
46022	Eel River, Calif.	40.8°N 124.5°W	1982–99	354
46013	Bodega, Calif.	38.2°N 123.3°W	1981–99	312
46042	Monterey Bay, Calif.	36.7°N 122.4°W	1987–99	328
46011	Santa Maria, Calif.	34.9°N 120.9°W	1980–99	325
46025	Catalina Ridge, Calif.	33.7°N 119.1°W	1982–99	295

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

Surface anomalies were as much as $3°-4°C$ below normal during the 1999 upwelling season, with a drop at some locations of nearly $10°$ in less than one year (fig. 9). Bodega buoy SST, for example, was $\sim7.5°$ for several days in May 1999. With few exceptions, SST anomalies remained negative throughout the CCS from fall 1999 into early 2000. Individual southward wind events throughout this period are reflected as significant drops in the buoy SST time series. However, SST at several locations appeared to be returning to seasonal means in January–February 2000 under northward winds.

CalCOFI Survey Cruises

We summarize a portion of the data obtained on each of the five quarterly CalCOFI cruises conducted since the preparation of last year's report. Here we focus on the near-surface physical and biological parameters. The reader is encouraged to refer to the cruise data reports (e.g., Scripps Institution of Oceanography 1999) or the CalCOFI Web page (http://www-mlrg.ucsd.edu/calcofi.html) for a complete presentation of the data sets. A CD-ROM containing the first 50 years of CalCOFI data (1949–99), as well as software tools for navigating and extracting data segments, is also available.

The long-term seasonal mean circulation in the CalCOFI region provides a useful reference for the patterns seen in 1999–2000 (fig. 10). The southward-flowing core of the California Current is seen as the offshore region of high gradient in the 0/500 dbar dynamic height field. It is strongest in spring and summer, and tends to be closer inshore in spring. The seasonally modulated Inshore Countercurrent is the poleward-flowing near-surface feature near the coast (Lynn and Simpson 1987). The subsurface (200–300 m) California Undercurrent transports relatively warm and saline (spicy) slope waters into the region from the south, particularly in summer and autumn (Lynn and Simpson 1990). The quasi-permanent Southern California Eddy (SCE; Lynn and Simpson 1987) often occupies much of the Southern California Bight, and is evident in each season of this climatology. Numerous studies have shown a strong association between circulation patterns and ecosystem

structure within the CCS (e.g., Hayward and Mantyla 1990; Haury et al. 1993; Hayward and Venrick 1998; Bograd et al., in press).

9904 (1–20 April 1999). Preliminary data from this cruise were included in last year's report (Hayward et al. 1999). This cruise marked the peak of the dramatic shift from El Niño to La Niña conditions in the southern CCS, and is included here for reference. This was also the period of unusually strong coastal upwelling along the California coast, including the region around Point Conception (Schwing et al. 2000). The 0/500 dbar dynamic height field reveals a strong California Current meandering through the offshore side of the grid, with its characteristic low-salinity core (fig. 11). The SCE is evident south of Point Conception, while another eddy appears on line 90. The strong coastal upwelling kept inshore near-surface waters anomalously cool, particularly near Point Conception, while weak poleward flow (the Inshore Countercurrent) between stations 93.30 and 93.45 transported relatively warm and saline waters into the region from the south. The most dramatic pattern observed on this cruise is that of near-surface chlorophyll-a, with elevated values extending well offshore over the entire grid (fig. 11). The mesoscale structure of the 10 m chlorophyll-a pattern closely resembles that of the near-surface dynamic height field.

9908 (6–29 August 1999). The near-surface circulation pattern in August was similar to that observed in April (fig. 12). The California Current was vigorous, but located considerably farther offshore than in the climatological mean (fig. 10). Significant mesoscale eddy activity was again evident, with a strong cyclonic eddy in the southwest portion of the grid forcing a large meander in the California Current. The Southern California Bight was characterized by a recirculation south of the SCE, with poleward flow north of line 87. Strong coastal upwelling continued in parts of the SCB through the summer of 1999 (Schwing et al. 2000), keeping near-surface waters anomalously cool (fig. 12). The 10 m temperature near Point Conception was nearly $4°C$ cooler than the long-term mean. Near-surface temperatures farther south, on the other hand, were warmer than

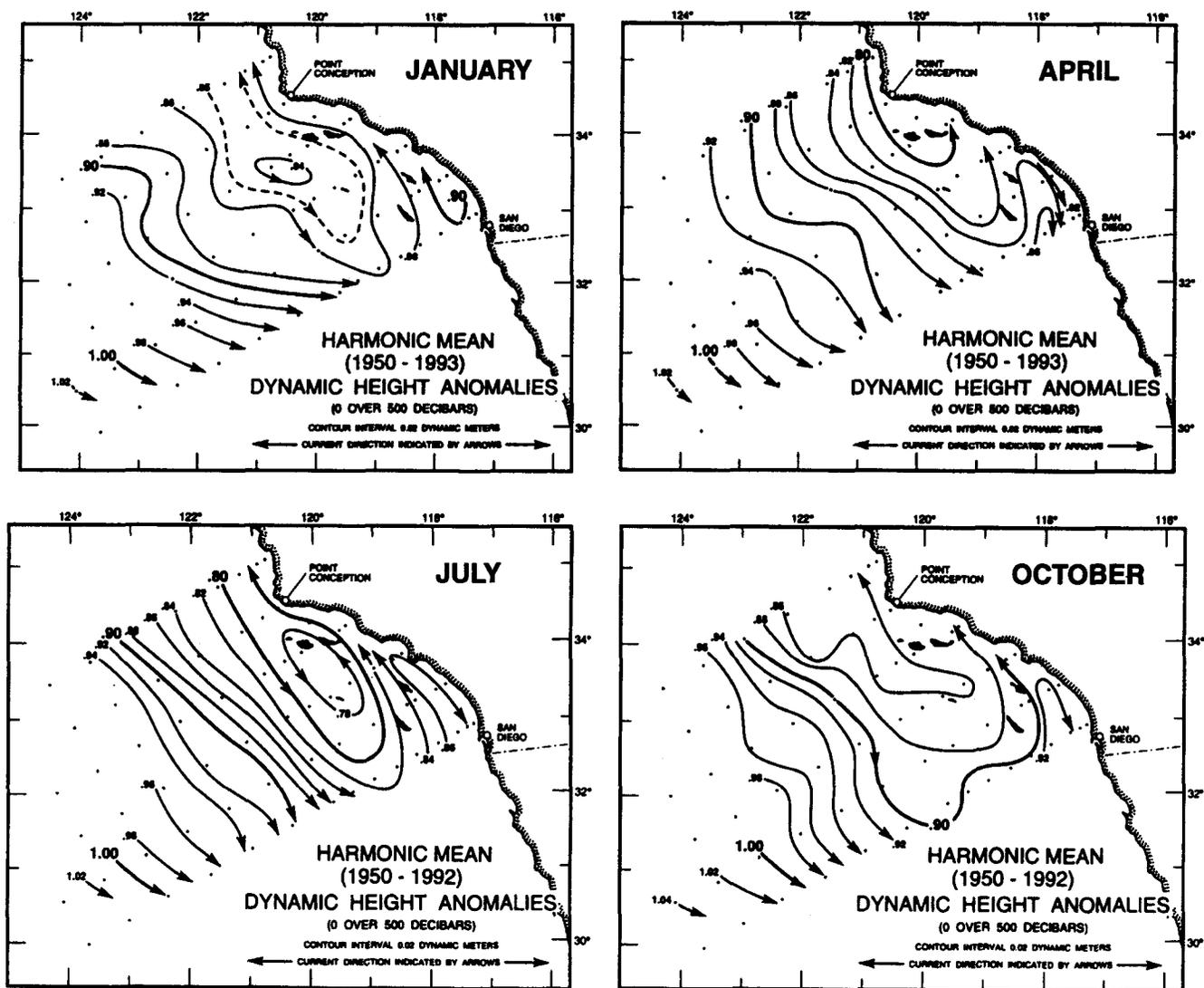# LONG-TERM MEAN CIRCULATION PATTERN

Figure 10.   Long-term mean (1950–92) circulation patterns based upon 0/500 dbar dynamic height for the target months of the CalCOFI quarterly surveys.

usual. The 10 m salinity field (fig. 12) clearly shows the low-salinity core of the California Current on lines 77, 80, and 83, and has little gradient within the bight. Chlorophyll-a levels continued high (fig. 12), but with most of the productivity confined to the region of up-welled water in the inner bight.

9910 (3–21 October 1999).   The California Current was again (or perhaps still) located well offshore in October, and considerably stronger than the usual October pattern (fig. 13), while flow in the SCB was weak and variable. There was an incursion of Subtropical Gyre water into the southwest corner of the grid. The 10 m temperature and salinity fields (fig. 13) resemble those from the previous cruise, with an offshore low-salinity core and cool inshore temperatures on the three northern

lines (anomalies near Point Conception of about 3°C). As in the previous cruise, there appeared to be a transport of warmer water from the south into the southeast corner of the grid. The highest chlorophyll-a values were again at the Point Conception upwelling region and the Santa Barbara Channel (fig. 13), but were lower than those measured in August.

0001 (7–27 January 2000).   The near-surface dynamic height field for January 2000 reveals two southward-flowing jets, one near the center of the grid and another at the southwest corner (fig. 14). This may represent two distinct branches of the California Current, as has been observed in past hydrographic surveys (Hickey 1979). The SCE was well developed at this time, with the Inshore Countercurrent composing its eastern limb and

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CALCOFI CRUISE 9904
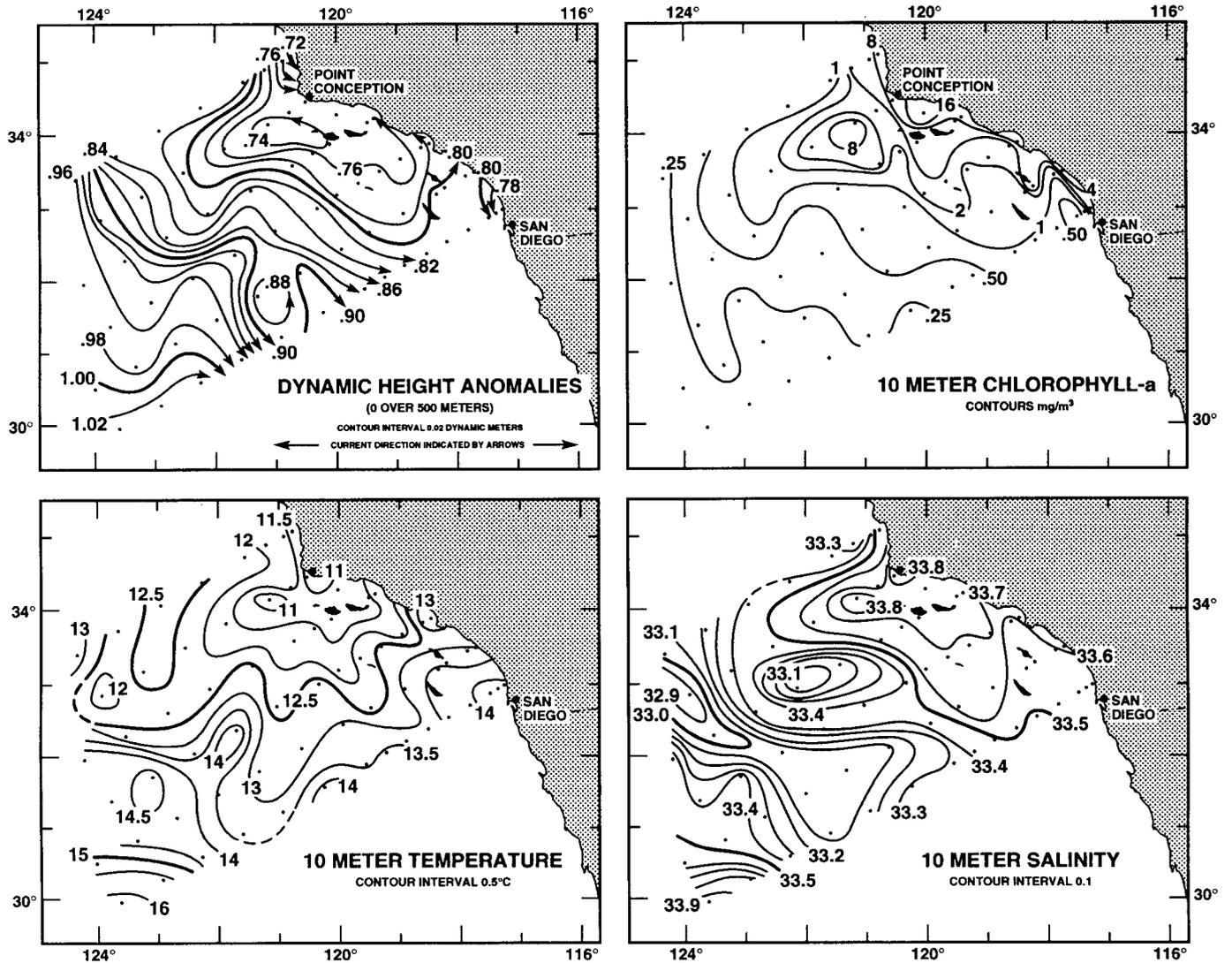
Figure 11.   Spatial patterns for CalCOFI cruise 9904 (1–20 April 1999), including upper ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m chlorophyll-a, 10 m temperature, and 10 m salinity.
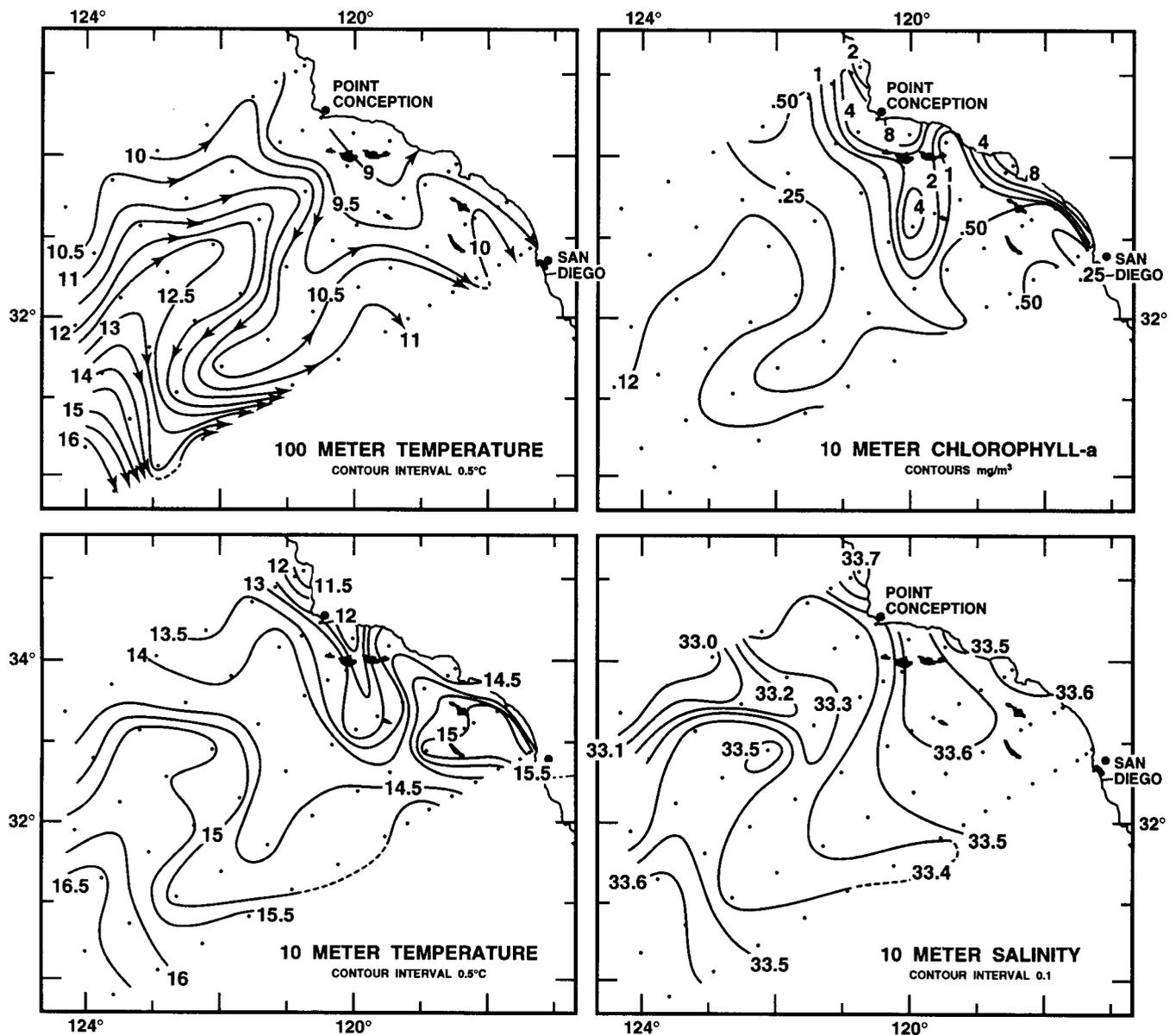
CALCOFI CRUISE 9908
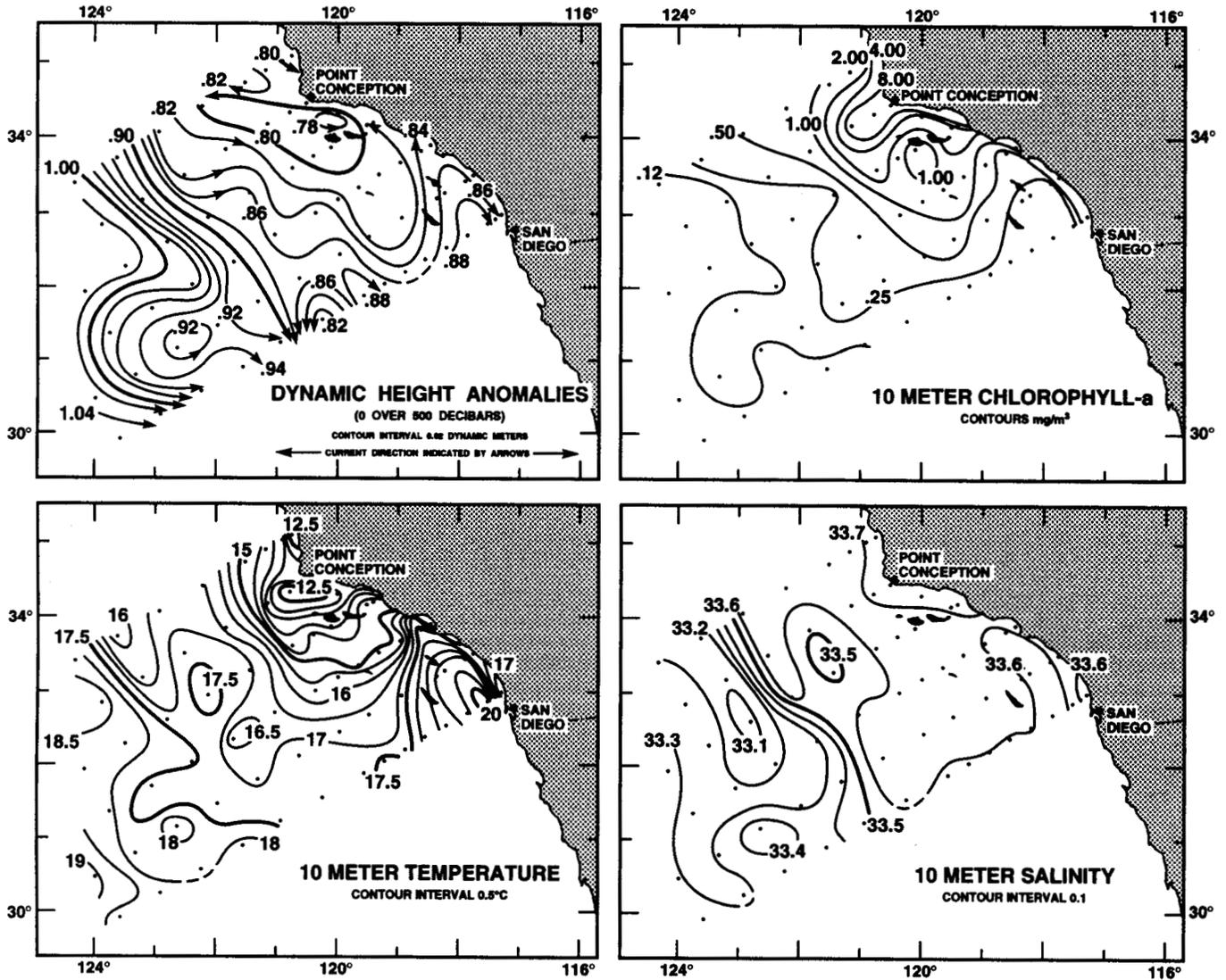
Figure 12.   Spatial patterns for CalCOFI cruise 9908 (6–29 August 1999), including upper ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m chlorophyll-a, 10 m temperature, and 10 m salinity.

CALCOFI CRUISE 9910
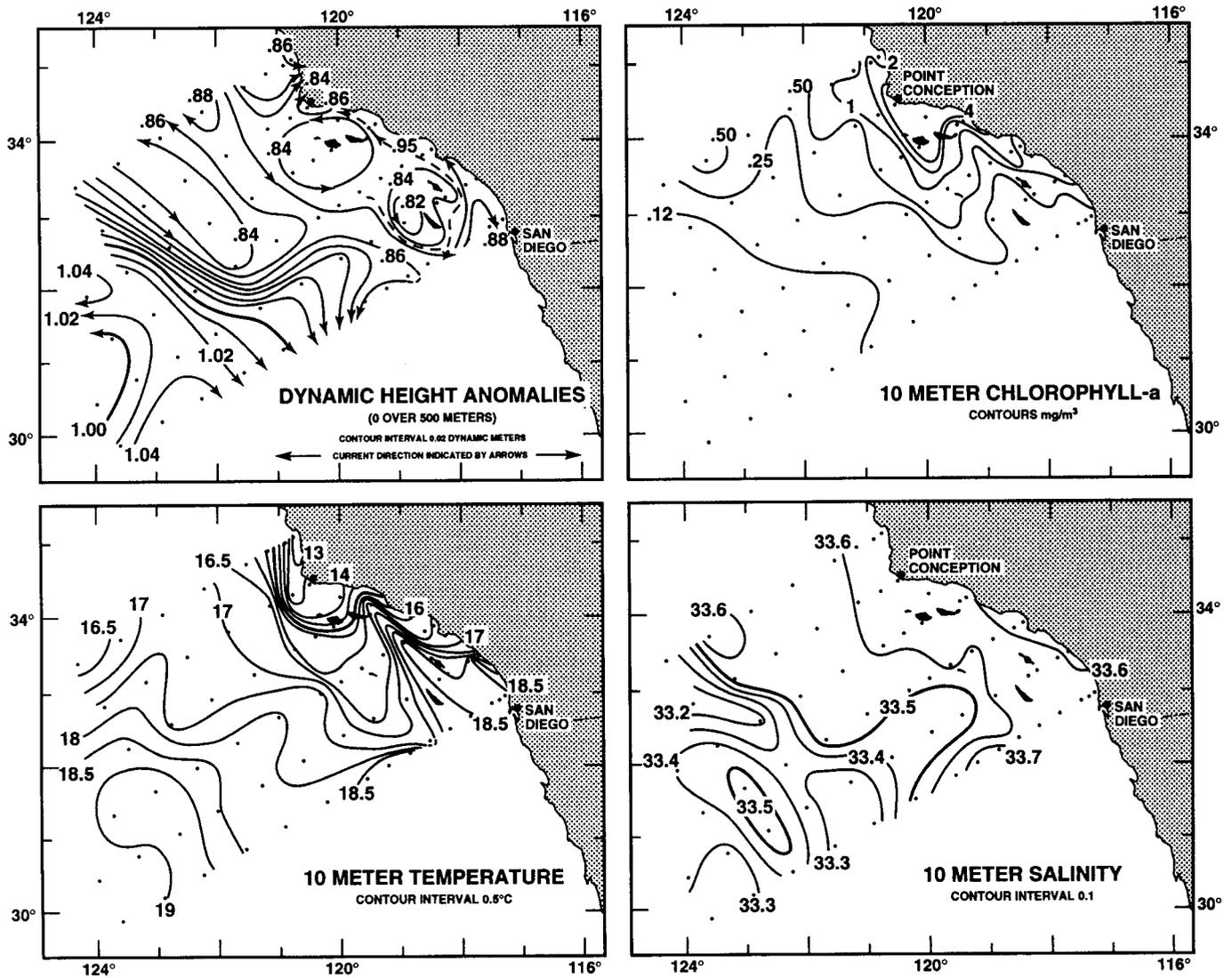
Figure 13.   Spatial patterns for CalCOFI cruise 9910 (3–21 October 1999), including upper ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m chlorophyll-a, 10 m temperature, and 10 m salinity.

CALCOFI CRUISE 0001

DYNAMIC HEIGHT ANOMALIES
(0 OVER 500 DECIBARS)
CONTOUR INTERVAL 0.02 DYNAMIC METERS
CURRENT DIRECTION INDICATED BY ARROWS

10 METER CHLOROPHYLL-a
CONTOURS mg/m³

10 METER TEMPERATURE
CONTOUR INTERVAL 0.5°C

10 METER SALINITY
CONTOUR INTERVAL 0.1
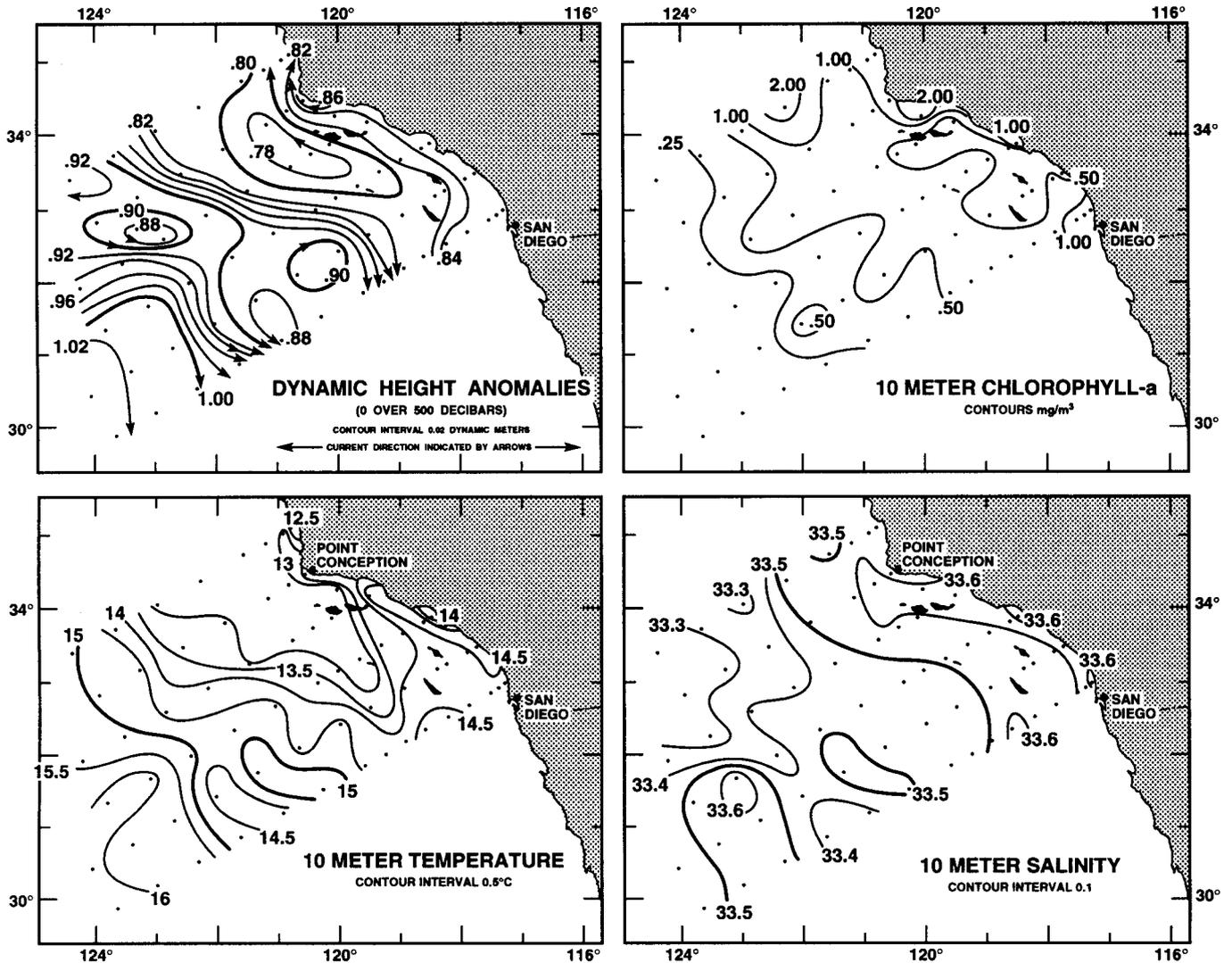
Figure 14.   Spatial patterns for CalCOFI cruise 0001 (7–27 January 2000), including upper ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m chlorophyll-a, 10 m temperature, and 10 m salinity.

CALCOFI CRUISE 0004

Figure 15. Spatial patterns for CalCOFI cruise 0004 (4–28 April 2000), including 100 m temperature (proxy for upper ocean geostrophic flow), 10 m chlorophyll-a, 10 m temperature, and 10 m salinity.

transporting relatively warm, saline water poleward along the extent of the coast (fig. 14). There was again considerable eddy activity throughout the region. Near-surface temperatures and salinities were very near their climatological means, except for a pool of relatively cool water just south of Point Conception. Chlorophyll-a was low at this time (fig. 14), but its mesoscale pattern again appeared to be correlated with the flow field.

0004 (6–29 April 2000). We include preliminary data from the April 2000 cruise, which had just returned as this report was being compiled (fig. 15). This cruise surveyed farther north than usual, to Cape Mendocino, using the CUFES system to track sardine and anchovy

eggs. The 100 m temperature field, a reliable proxy for near-surface flow (A. Mantyla, pers. comm.), reveals unusual dynamics on the CalCOFI grid. There was a great deal of zonal (inshore/offshore) flow, which may reflect the early stages of large eddy development. The California Current can be recognized from the low-salinity core meandering through the center of the grid. The inshore region was composed of strong southward-flowing currents from Point Conception to San Diego, which brought relatively cool water into the near-coastal region from the north. The tilting of isopycnals near the coast, evident by the cool, saline waters, yielded a surface oxygen saturation of 144% at station 90.28 (A.
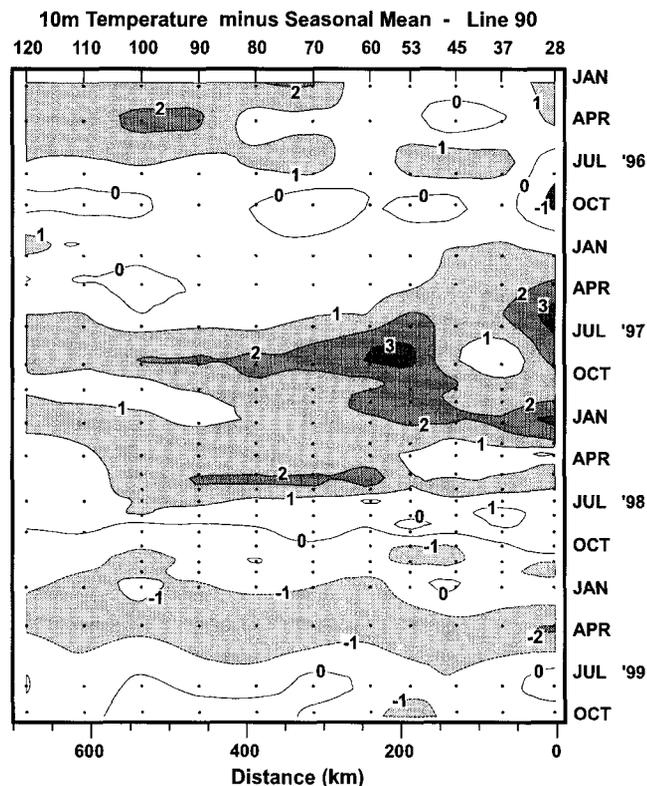
Figure 16. Ten-meter temperature anomalies from January 1996 through October 1999 for line 90 stations. Anomalies are based upon the 1950–98 harmonic means.
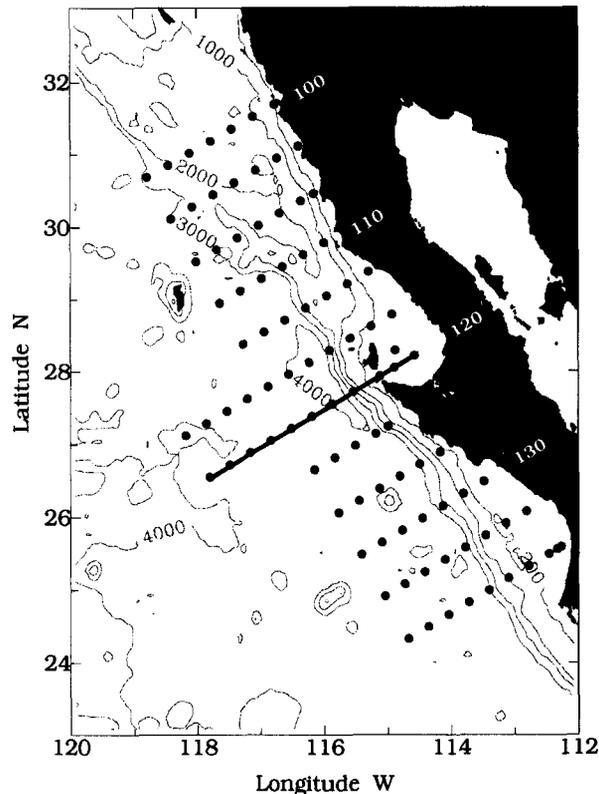

Figure 17. IMECOCAL station map. Lines 100 and 103 were extended offshore to station 60, and lines 133 and 137 were added to the grid. Depth contours in meters. Solid line indicates line 120, which is analyzed in detail.

Mantyla, pers. comm.). This is much higher than is normally observed in the SCB. Chlorophyll-a values were correspondingly high all along the coast, and within the tongue of cool water extending south from Point Conception. There appears to be a close relation between the chlorophyll-a pattern and the flow field, with the shallowest (deepest) chlorophyll-a maximum in the cyclonic (anticyclonic) loops (not shown). The dynamics of mesoscale physical-biological coupling is an important area of research, and one for which CalCOFI continues to be an ideal platform.

A tremendous transition in the physical environment of the CalCOFI region has taken place over the past few years. The 10-meter temperature anomaly time series at stations along line 90 summarizes the strong pattern of nonseasonal temperature variations over the period from January 1996 through October 1999 (fig. 16). The pattern of warm offshore and cool inshore temperatures that prevailed at the beginning of 1996 evolved into a near-neutral pattern by midyear. Strong surface warming started in mid-1997. Because atmospheric teleconnections between the tropics and temperate zone are weak in summer months, the warming has been ascribed to regional wind anomalies rather than to the develop-

ing equatorial Pacific El Niño (Lynn et al. 1998). Strub and James (2000) have shown, however, that a direct effect of the equatorial El Niño progressed poleward along the continental margins in May–July 1997 as transient events of sea-surface height anomalies and geostrophic transport. The warming spread to offshore waters by September 1997.

The effects of the large-scale atmospheric conditions and ocean dynamics of the equatorial El Niño on the surface waters were clearly evident in the fall and winter months of 1997–98. The greatest warming occurred in the coastal area, where there was also variation probably associated with local upwelling events. High SST anomalies began to lessen after July 1998 while La Niña conditions began to develop in the equatorial Pacific. Below-seasonal temperature developed in fall across the entire line. Cool conditions that developed in late 1998 and into 1999 have been attributed to strong coastal upwelling (Schwing et al. 2000). Although the central and northern California coast experienced sustained strong upwelling and seasonally low SST through much of 1999, this was not the case for much of southern California. Near-surface temperatures were very close to their long-term seasonal means by August 1999, at least over the southern portion of the CalCOFI grid.
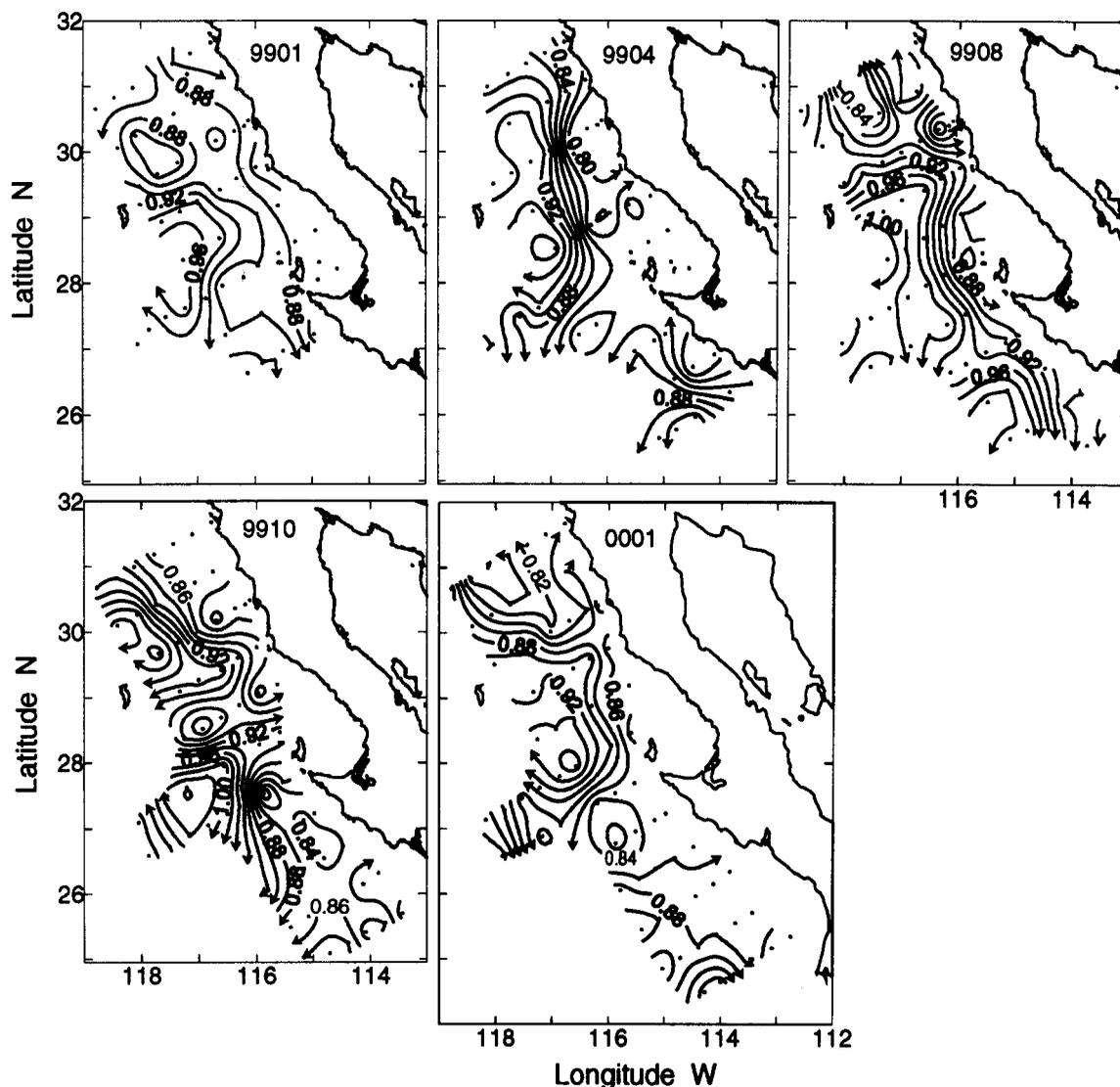
Figure 18.   Dynamic heights (10/500 dbar) for the five IMECOCAL cruises from January 1999 to January 2000. Note that cruises 9910 and 0001 have more stations to the south of the sampling region.

IMECOCAL Survey Cruises

The IMECOCAL program continued sampling the southern California Current system in waters off Baja California. The sampling program carried out since 1997 was modified in order to accommodate more stations and to fully cover the station grid on each cruise. Vertical CTD casts were shortened to 1000 m, with the exception of the six deepest stations, which were sampled to 10–50 m above the bottom for purposes of conductivity calibration. Reducing the maximum depth of CTD casts made it possible to include stations 55 and 60 where needed, and to add lines 133 and 137 to the south of the grid (fig. 17).

From January 1999 to January 2000, five quarterly cruises were conducted: 9901, 9904, 9908, 9910, and 0001. Cruise 9908 was made on the B.O. *El Puma*, the rest on the B.O. *Francisco de Ulloa*. The methodology used was the same as during previous cruises (Lynn et al. 1998; Hayward et al. 1999) and follows standard CalCOFI procedures. The CUFES system has been used since April 1999, but the results are not presented here.

Dynamic height contours (10/500 db) for the five cruises depict the state of the CCS off Baja California (fig. 18). During 9901, the southward flow was restricted to distances 50–100 km from the coast, while offshore the flow was characterized by a diffuse meandering around two mesoscale eddies (a cyclonic eddy at ~30°N and an anticyclonic eddy at 28°N). April 1999 (9904) dynamic heights show the southward flow moving from the coast near 31°N and flowing around an anticyclonic eddy centered at 28°N. Part of the southward flow returned to the coast as part of a coastal cyclonic

TEMPERATURE ANOMALIES LINE 120
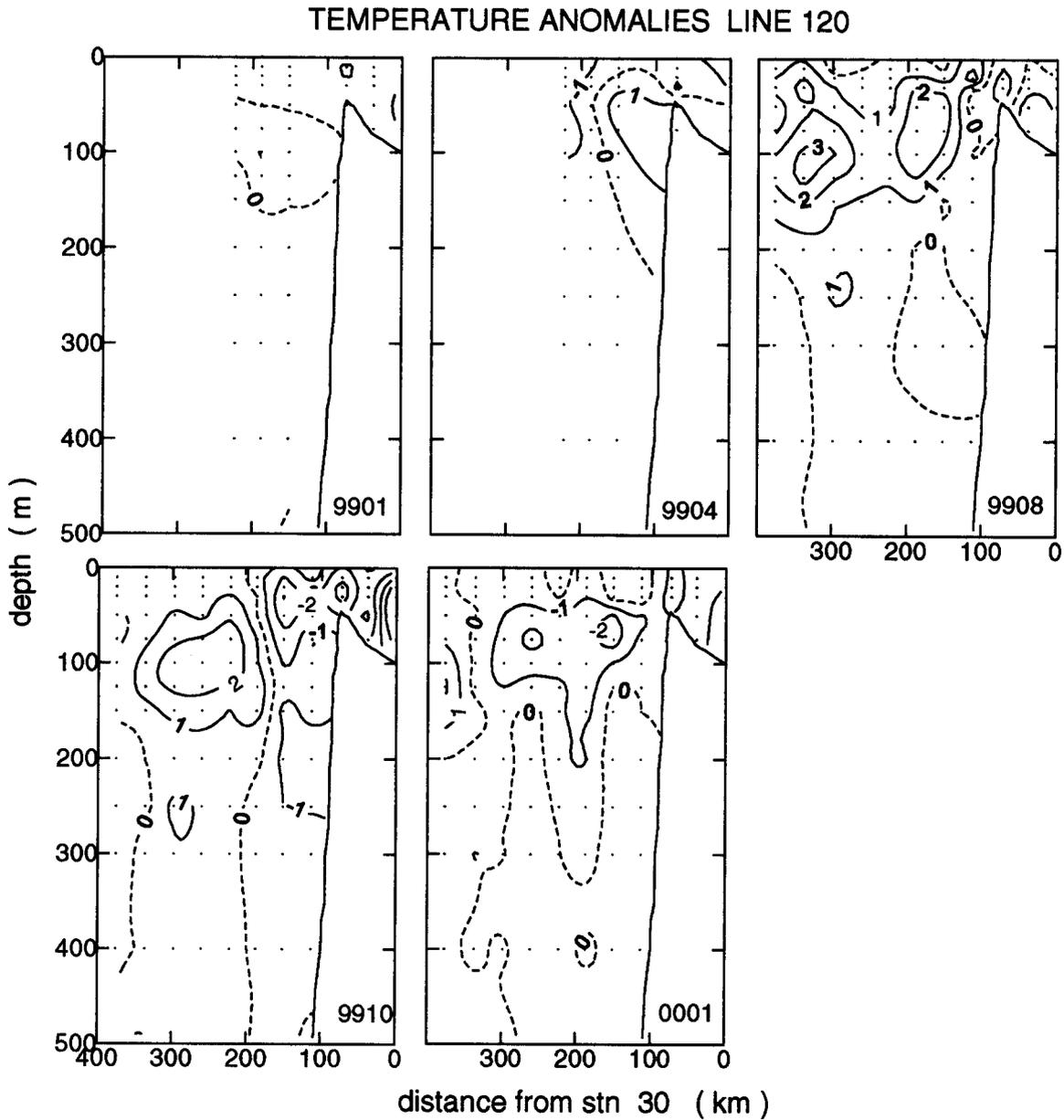
Figure 19.   Temperature anomalies °(C) for line 120. Numbers in the lower right denote year and month.

eddy. South of Punta Eugenia (PE), the dynamic height field indicates northward flow which appears to merge offshore with the equatorward current. Cruise 9908 clearly depicts the southern limit of the Southern California Eddy, where the currents flow east and impinge over the coast at 30°N to separate into two branches, one flowing north and another south. The southern branch continues a more or less straight path parallel to the coast. West of the southern branch, the quasi-permanent anticyclonic eddy is discernible. October dynamic heights (9910) depict a diffuse southward current, flowing equatorward around several small-scale (20–40 km) to mesoscale (~100 km) eddies, the most

conspicuous being the clockwise gyre off PE. South of PE, diffuse northward currents are also evident from the dynamic height field. The circulation charted on the January 2000 cruise, which extended as far south as line 137, greatly resembles the circulation observed on cruise 9908, with the southern limb of the SCE impinging on the coast and a southward current flowing around the large-scale, quasi-permanent eddy southeast of Isla Guadalupe.

Figures 19 and 20 show vertical distributions of temperature and salinity anomalies for line 120 (off PE) for each cruise. The anomalies are based on climatological means for the period 1950–78 (Lynn et al. 1982), and

SALINITY ANOMALIES LINE 120
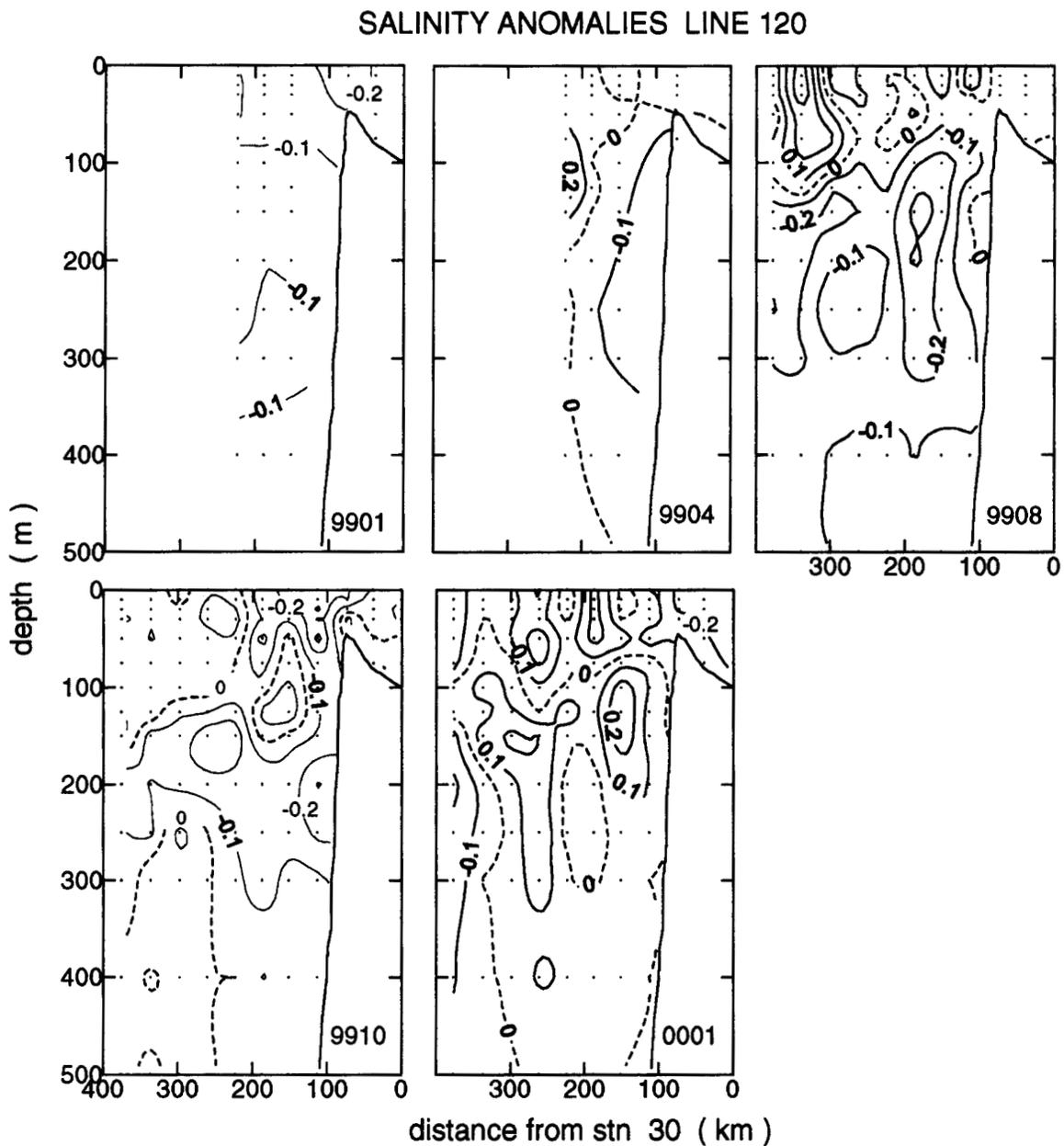
Figure 20.   Salinity anomalies for line 120. Numbers in lower right denote year and month.

may differ from anomalies calculated for CalCOFI, which are based on a longer reference period. After relatively high temperature and salinity anomalies (~8°C and 0.8) during 1997–98 (Lynn et al. 1998; Hayward et al. 1999), anomalies during the latest five cruises were relatively small. Cruise 9901 showed normal temperatures and slightly lower than normal salinities (−0.1) throughout the water column. Cruise 9904 showed warmer and fresher than normal waters (1°C and −0.1) over the shelf break, but slightly cooler and saltier than normal (−1°C and 0.2) offshore. As suggested by the dynamic height field (fig. 18), positive (negative) temperature (salinity) anomalies near the coast were associated with a pole-

ward flow south of Punta Eugenia. West and north of PE the flow was southward.

By August 1999 (9908), temperature and salinity anomalies indicate warmer (2°−3°C) and saltier (0.1−0.3) than normal conditions in the upper 100–120 m. Below 150 m, temperatures were within the climatological mean values, but fresher waters (~−0.2) were present. In close relation to the cyclonic-anticyclonic eddy pair observed west of PE, temperature anomalies near the coast (150 km) were negative throughout the water column, with maximum values at 40–50 m. Offshore water temperature anomalies were positive, with the peak (2°) at a depth of about 100 m. Salinities were

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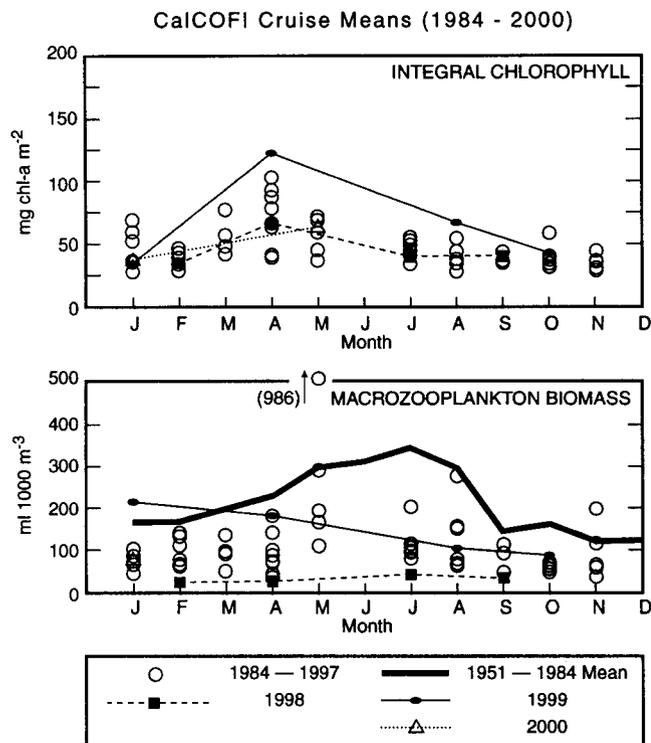
Figure 21. Cruise means of vertically-integrated chlorophyll and macrozooplankton biomass plotted versus the month of CalCOFI cruises from 1984 to April 2000. Each point represents the mean of all measurements on a cruise (usually 66). The open circles show the cruises that took place from 1984 to 1997. 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 22. Macrozooplankton biomass for northern (upper panel) and central (lower panel) Baja California. Biomass from 1984 to 1998 (squares) and 1999 (open circles) is shown.

fresher, with maximum values nearshore at the surface and at 250 m over the shelf break.

Finally, cruise 0001 showed cooler and fresher waters in the upper 100–150 m, with maximum anomalies near the center of the section corresponding to the core of the California Current (fig. 18). Below 150 m, normal temperatures and higher than normal salinities were observed. Relatively low spiciness was observed at the center of the section throughout most of the water column, with higher values near the coast and offshore.

BIOLOGICAL PATTERNS

Chlorophyll and Macrozooplankton

Cruise-mean values of vertically-integrated chlorophyll-a and macrozooplankton biomass for 1999–2000 are given in the context of the historical CalCOFI time series (fig. 21). The dramatic transition in the physical environment between El Niño (1997–98) and La Niña (1998–2000) periods is apparent in the biological patterns as well. After the lowest macrozooplankton biomass in the long-term (1951 to present) CalCOFI database through 1998 (Lynn et al. 1998), macrozooplankton rebounded greatly in January and April 1999,

to values near the 1951–84 long-term mean. This rebound continued in the latter half of 1999 and into January 2000, although these values are below the long-term mean. The ecosystem in the CalCOFI region is undoubtedly still responding to residual effects of the recent El Niño and La Niña events, and may continue to do so for years. It is presently unclear whether the trend of declining macrozooplankton biomass in the region (Roemmich and McGowan 1995) has been affected by these events.

Chlorophyll-a production also rebounded after the El Niño period (fig. 21). The April and August 1999 means were the highest spring and summer values recorded. In fact, the April 1999 value of 123 mg chl a m^{-2} is the highest since regular measurements began on CalCOFI cruises in 1984, and occurred during the period of vigorous coastal upwelling (Schwing et al. 2000) and a very shallow nitricline (not shown). The values measured in January and April 2000, however, are not particularly high relative to the past 16 years. The effects of the 1997–98 El Niño on primary production in the CCS are further discussed in the following section.

Zooplankton was also sampled by Centro Interdisciplinario de Ciencias Marinas (CICIMAR) over the period 1983–91. Figure 22 puts the historical observations of CalCOFI and CICIMAR in perspective, as well as recent observations carried out by the IMECOCAL program. The data have been divided spatially into two regions, one north of 30°N, and including volumes sampled along lines 97 to 110, and a central region comprising lines 113 to 133. The northern region appears to have a secular decline similar to that observed for southern California (Roemmich and McGowan 1995),
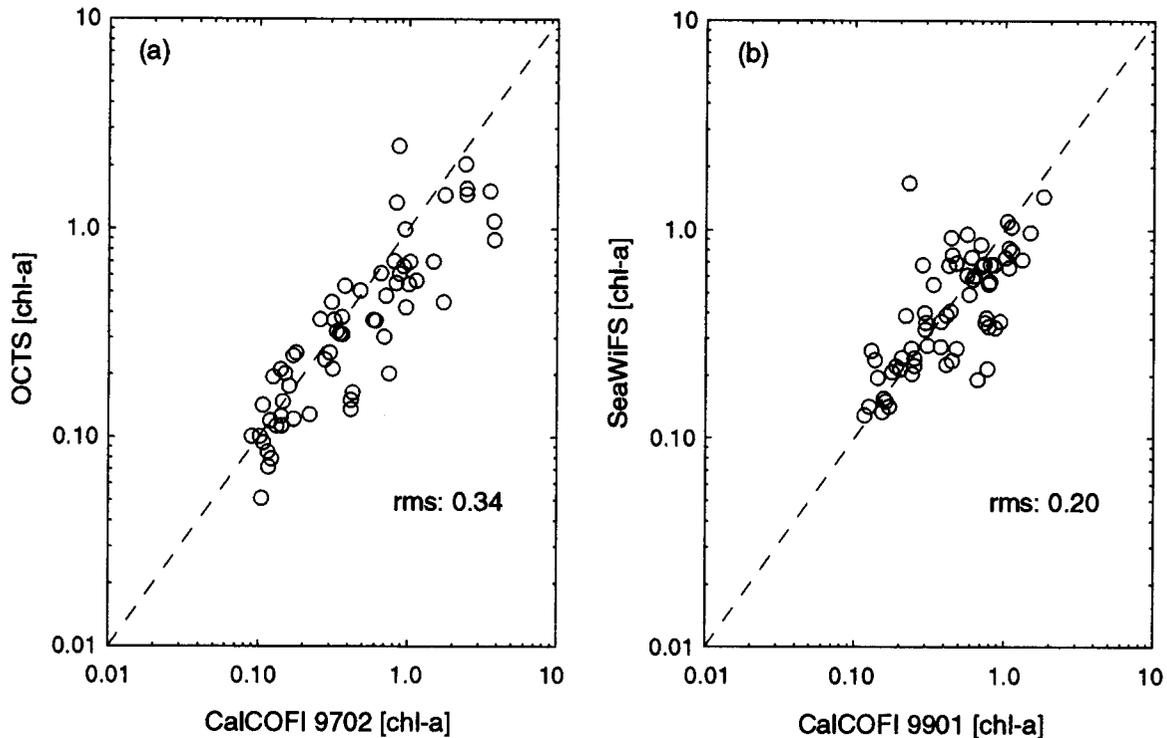
Figure 23. Comparison of in situ and satellite chlorophyll-a values, for coverage that overlaps within one week. a, CalCOFI cruise 9702 data (lines 77 to 93; 0–30 m station mean) versus weekly averaged OCTS data (version 4, level-3). b, CalCOFI cruise 9901 data (lines 77 to 93; 0–30 m station mean) versus weekly-averaged SeaWiFS data (version 2, level-3). Depth bins of 0–30 m were used to encompass at least one attenuation length.

because the 1951–84 macrozooplankton volume mean is higher than recent observations. The 1999 volumes are, however, comparable to values observed after 1984. For central Baja California, zooplankton biomass in 1984–98 is scattered around the historical mean. The region thus appears to be less rich in zooplankton than northern regions of the CCS, with means rarely exceeding 300 ml/1000 m³. The low volumes observed during August and October of 1999 were unexpected. These were lower than the historical mean, and lower than observations during the 1997–98 El Niño.

Ship vs. Satellite-Derived Chlorophyll Patterns

Following an extended absence, the reintroduction of ocean color sensors to space in the mid- to late 1990s provided an invaluable opportunity for evaluating the biological effects of the 1997–99 El Niño/La Niña events in the California Current system. DiGiacomo (1999) used OCTS (1996–97) and SeaWiFS (1997–98) chlorophyll-a data, complemented by other satellite and field measurements, to describe how a combination of atmospheric and oceanic forcing led to large reductions in CCS phytoplankton biomass during the 1997–98 El Niño relative to the preceding year. Because the accuracy of ocean color data is always of concern, particularly in coastal zones, OCTS/SeaWiFS data were compared to CalCOFI cruise data from October 1996

through April 1999 to examine their overall correspondence, as well as to identify relevant trends (figs. 23–25).

Generally speaking, satellite-derived chlorophyll-a values were comparable to data from ship stations (e.g., fig. 23). For the CalCOFI time series in question, rms errors ranged from 0.20 to 1.16, with most values under 0.5. The largest rms errors were observed during early periods of strong upwelling (e.g., April 1997, 1999), associated with higher chlorophyll-a values. The good overall correspondence between ship and satellite-derived chlorophyll-a values can also be seen in both the relative trends and mean absolute values for inshore (fig. 24) and offshore (fig. 25) waters over this same time period. Where differences exist in these values, it is usually a case of the satellite data underestimating the ship data. Kahru and Mitchell (1999) indicated that the SeaWiFS OC2-v2 algorithm could underestimate intermediate chlorophyll-a values (1 to 10 mg m^{-3}); this seems to be the case with the OCTS algorithm as well. This also appears to explain why the chlorophyll-a differences are more pronounced inshore (fig. 24) than offshore (fig. 25), where chlorophyll-a values are generally less than 1 mg m^{-3}.

Interannual comparisons of chlorophyll-a, temperature, and nitrate data from corresponding seasonal cruises (e.g., 9610 vs. 9709) revealed a number of important trends. CalCOFI cruises 9709 and 9802, during the peak
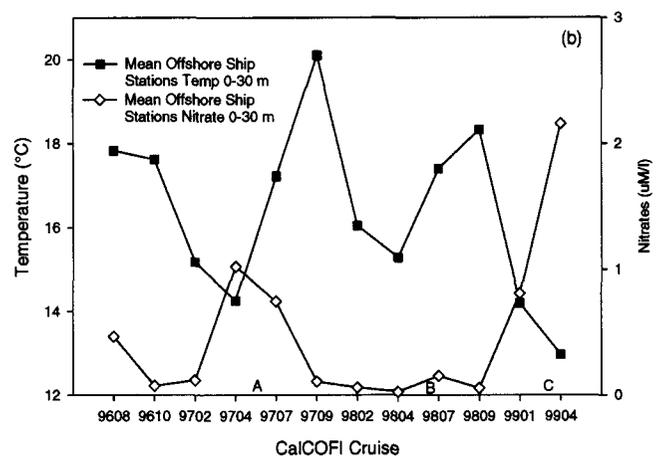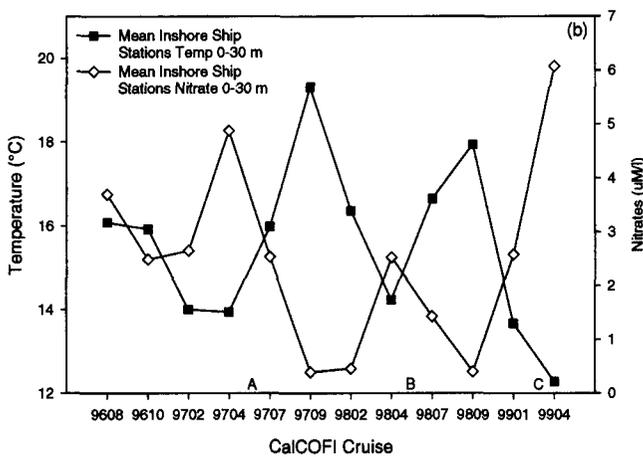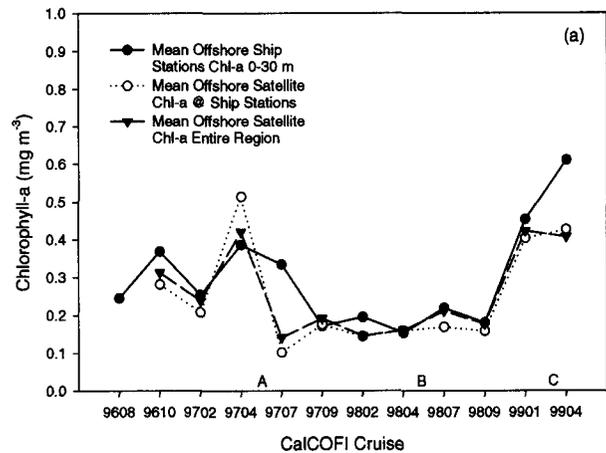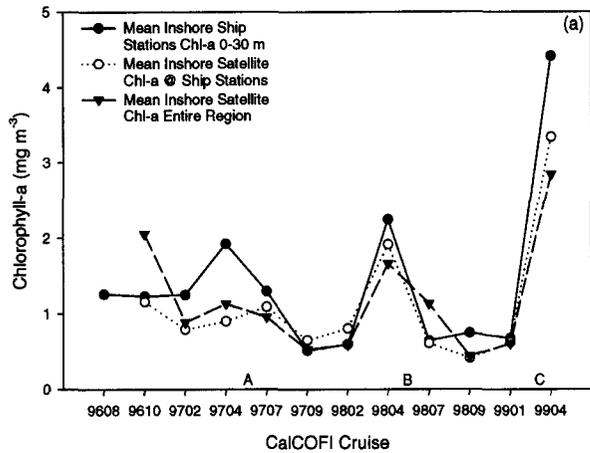
Figure 24. a, Comparison of mean inshore and in situ chlorophyll-a values, for coverage that overlaps within two weeks. Satellite data were extracted at corresponding CalCOFI stations and for the entire region that encompassed those stations. The "inshore" designation refers to CalCOFI stations (on lines 77 to 93) that are less than about 130 km offshore. Weekly averaged OCTS data (version 4, level-3) used for CalCOFI cruises 9610 to 9707; weekly averaged SeaWiFS data (version 2, level-3) used for CalCOFI cruises 9709 to 9904. b, Mean inshore temperature and nitrate from CalCOFI station data (0–30 m mean). At bottom of each graph, A indicates the approximate start of the 1997–98 El Niño; B indicates its approximate end; C indicates the approximate start of La Niña.

Figure 25. a, Comparison of mean offshore and in situ chlorophyll-a values, for coverage that overlaps within two weeks. Satellite data were extracted at corresponding CalCOFI stations and for the entire region that encompassed those stations. The "offshore" designation refers to CalCOFI stations (on lines 77 to 93) that are more than approximately 130 km offshore. Weekly averaged OCTS data (version 4, level-3) used for CalCOFI cruises 9610 to 9707; weekly averaged SeaWiFS data (version 2, level-3) used for CalCOFI cruises 9709 to 9904. b, Mean offshore temperature and nitrate from CalCOFI station data (0–30 m mean). At bottom of each graph, A indicates the approximate start of the 1997–98 El Niño; B indicates its approximate end; C indicates the approximate start of La Niña.

of El Niño, had lower mean chlorophyll-a and nitrates and higher mean temperature than the 9610 and 9702 cruises, both inshore (fig. 24) and offshore (fig. 25). Conversely, during cruise 9904, when La Niña conditions prevailed, mean chlorophyll-a and nitrate values were higher, and the mean temperature was lower relative to the two preceding spring cruises (9804 and 9704; figs. 24 and 25). Also of interest in the April 1997–99 series is the reduction observed in mean offshore chlorophyll-a (and nitrate) values during April 1998, presumably at least partly because of reduced coastal upwelling.

Avifauna

CalCOFI cruises have provided the opportunity for systematic surveys of the distribution and abundance of seabirds in relation to oceanographic conditions off south-

ern California. Data collected between 1987 and 1998 have revealed that seabird populations fluctuate in response to interannual and longer-term variability in the properties of the California Current (Veit et al. 1996; Lynn et al. 1998; Hayward et al. 1999; Hyrenbach and Veit 1999). However, surveys during 1999–2000 have failed to detect avifaunal changes in concordance with the notion of a transition into a regime of enhanced upwelling and production in the California Current. A preliminary analysis of the available data suggests, on the other hand, that the changes in seabird abundance and community composition observed during 1998–99 were transient fluctuations apparently in response to La Niña.

Seabird communities responded to the onset of La Niña conditions during the fall of 1998 with a concomitant increase of cold-water taxa and a decline in the

importance of warm-water species: subtropical seabirds prevalent during the preceding El Niño event (1997–98) were replaced by immigrating subarctic species such as the black-legged kittiwake (*Rissa brevirostris*) and the sooty shearwater (*Puffinus griseus*; Hayward et al. 1999). Additional surveys during 1999–2000 revealed that the changes in avifauna observed during the fall of 1998 persisted into the fall of 1999. During the spring and fall of 1999, the cold-water taxa (e.g., black-legged kittiwake and sooty shearwater) continued to be numerically dominant. Conversely, the southern and central Pacific species that had dominated the community in 1998 declined in 1999. Cool ocean temperatures during the fall of 1999 inhibited the immigration of southern species (e.g., black-vented shearwater, *P. opisthomelas*) and central Pacific species (Cook's petrel, *Pterodroma cookii*) into the CalCOFI grid (fig. 26a). Conversely, these conditions attracted subarctic seabirds that regularly do not occur during fall. For instance, it is noteworthy that the black-legged kittiwake, which was not sighted in the CalCOFI grid during the fall of 1997 and 1998, was observed off southern California in October 1999.

Additional surveys during the spring of 2000 revealed that the shift in community composition observed during the previous year was a transient fluctuation in response to a prolonged cold-water period (fig. 26b). After seventeen months (October 1999–February 2000) of negative temperature anomalies and enhanced upwelling, conditions reversed in the early spring of 2000. The intensity of the upwelling-favorable winds dropped to "normal" levels during March, and anomalous warm-water temperatures became apparent along the coast in April (El Niño Coastwatch Advisories, September 1998–April 2000). Seabirds responded rapidly to the changes in oceanographic conditions, and by April 2000, the avifauna included a mixture of the warm- and cold-water assemblages prevalent during the preceding El Niño (1997–98) and La Niña (1998–99) episodes.

In addition to documenting interannual variability, the CalCOFI program is particularly suited to detect changes in the physical forcing and ecosystem structure indicative of long-term shifts in ocean climate (McGowan 1990; Roemmich 1992; Roemmich and McGowan 1995). Similarly, the time series of seabird observations collected since 1987 provides a baseline for interpreting unusually large avifaunal fluctuations. Additionally, the response of seabird communities to ocean warming off southern California makes it possible to predict the probable consequences of the hypothesized transition into a cold-water regime. Thus the onset of a prolonged period of cool ocean temperatures in the fall of 1998 would likely be followed by increased numbers of sooty shearwater and overall seabird abundance after a lag of three CalCOFI cruises (Veit et al. 1996). Specifically, we would
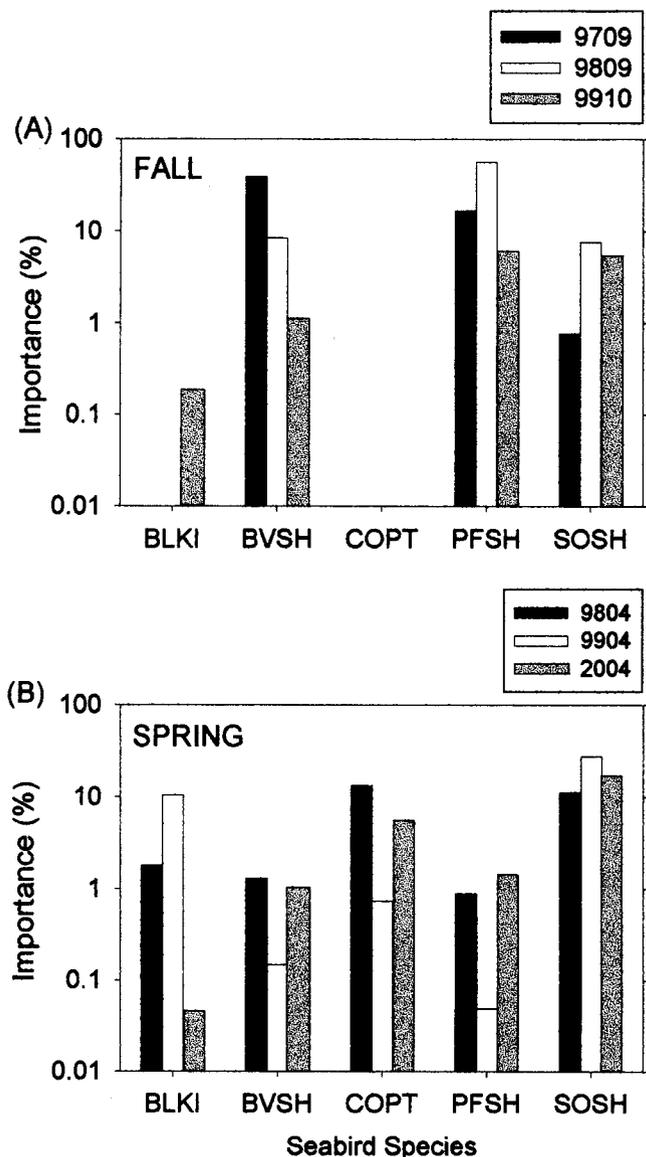

Figure 26. Relative fall (*A*) and spring (*B*) abundance of the five indicator seabirds with an affinity for different water temperatures and biogeographic domains. Importance was computed by dividing the number of individuals of a given species by the total number of seabirds sighted during each cruise. Subtropical/warm-water taxa are BVSH (black-vented shearwater); PFSH (pink-footed shearwater); and COPT (Cook's petrel). Subarctic/cold-water taxa are SOSH (sooty shearwater) and BLKI (black-legged kittiwake).

expect the response of the avifauna to be particularly strong during the boreal summer (July), when far-ranging shearwaters migrate into the California Current from the Southern Hemisphere (Briggs et al. 1987; Tyler et al. 1993). In spite of the prolonged period of cold-water conditions, surveys during the summer of 1999 revealed that overall bird abundance and sooty shearwater numbers remained below the levels recorded off southern California during the late 1970s (1975–77; Tyler et al. 1993) and the late 1980s (1988–90; Veit et al. 1996; fig. 27).
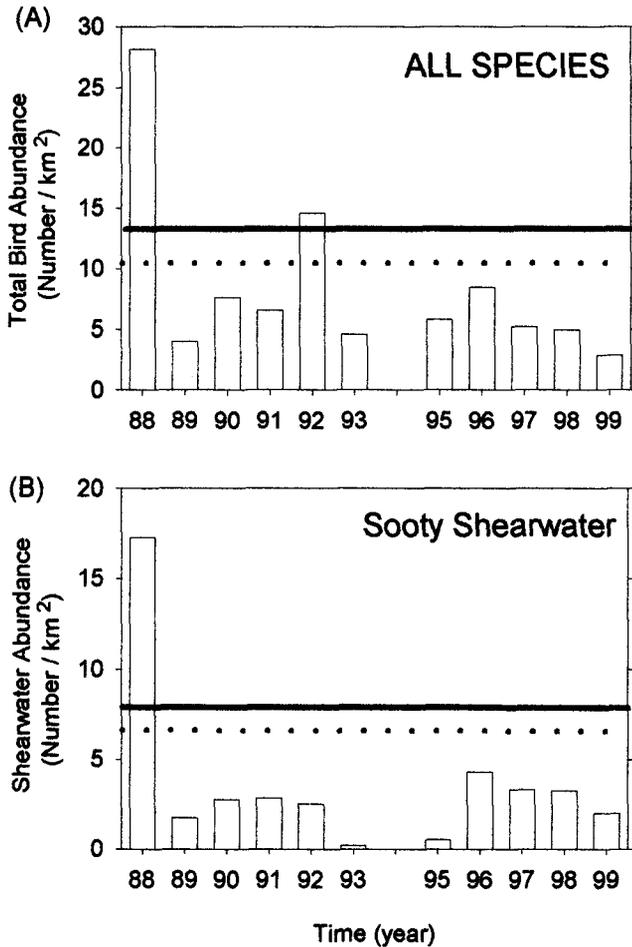
Figure 27. Changes in (A) overall bird abundance (all species combined) and (B) the density of the once numerically dominant sooty shearwater during summer CalCOFI cruises. The solid line shows the mean abundance during the early part of the CalCOFI time series (1988–90); the dotted line depicts average summer densities off southern California during the late 1970s (1975–77) from Tyler et al. 1993. No data are available for 1994.

Seabird communities off southern California have undergone persistent changes during the last decade (Veit et al. 1996; Hyrenbach and Veit 1999). Veit et al. reported a 40% decline in overall seabird abundance between the late 1980s (1987–88) and the early 1990s (1993–94), largely due to a 91% decline in the abundance of the dominant cold-water species—the far-ranging sooty shearwater. Continued surveys in recent years have revealed consistently low shearwater densities within the CalCOFI region, during periods of normal circulation (Hayward et al. 1996), El Niño (Lynn et al. 1998), and La Niña (Hayward et al. 1999). Although sooty shearwaters have increased slightly during the late 1990s, they remain well below the historical densities observed in the late 1980s. Overall, they have declined by 71% between the beginning (1987–90) and the end (1995–98) of the CalCOFI time series (Hyrenbach and Veit 1999).

Surveys in recent years have also revealed the con-

tinued presence of warm-water taxa (e.g., Cook's petrels, pink-footed and black-vented shearwaters) off our coast, despite the prolonged period of cool ocean temperatures. These observations suggest that the increase of warm-water species recorded off southern California since 1987 represents a permanent shift in the range of subtropical and southern taxa (Fields et al. 1993; Veit et al. 1996). These increases have been particularly striking for several far-ranging *Pterodroma* and *Procellaria* petrels (Cook's, Parkinson's, and dark-rumped), which have been regularly sighted in the California Current during the 1990s (Pyle et al. 1993; Schwing et al. 1997; Hyrenbach and Veit 1999).

Seabird populations are ideal indicators of changes in ocean productivity and ecosystem structure because they are sensitive to fluctuations in pelagic food webs (Sydeman and Ainley 1994; Ainley et al. 1995). The Point Reyes Bird Observatory Marine Science Program has monitored the diet and the reproductive performance of seabird populations breeding at the Farallon Islands (central California) since the early 1970s. Surveys in 1999 revealed a concomitant increase in the reproductive performance of three of the four regularly monitored pelagic species, apparently in response to the cool-water conditions since the fall of 1998. Moreover, in 1999, three species had positive anomalies over their long-term mean productivity levels. These results contrast with data from the previous year, when only the Cassin's auklet (*Ptychoramphus aleuticus*) showed a positive anomaly in productivity (fig. 28).

It is likely that seabirds' response to environmental variability is not a linear function. Moreover, it is conceivable that different processes which seem to affect the environment in a similar way (e.g., cool conditions as a result of La Niña or a regime shift) may elicit distinct ecosystem responses of varying lag and magnitude. This is particularly pertinent when dealing with a regime shift, which, by definition, entails a change in the dynamics and the mechanisms regulating a complicated system. Thus, additional surveys will be necessary to determine whether the avifauna within the CalCOFI region changed in response to a possible transition into a new oceanographic regime during 1999–2000. This uncertainty underscores the value of long-term time series to interpret changes in large-scale marine ecosystems (McGowan 1990).

DISCUSSION

Perhaps the most striking result to come out of the recent CalCOFI observations is the speed at which the physical environment varied, and at which the ecosystem apparently responded to that variation. In a period of less than one year, for instance, macrozooplankton in the CalCOFI region went from the lowest (through
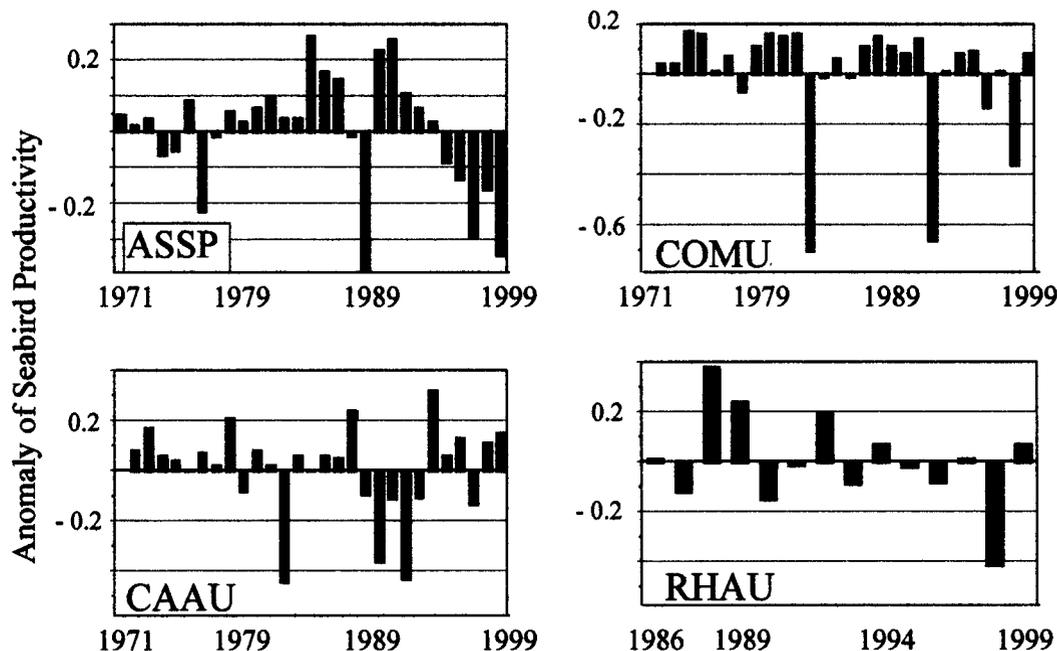
Figure 28. Interannual variability in the productivity of pelagic seabirds (ASSP: ashy storm petrel; COMU: common murre; CAAU: Cassin's auklet; RHAU: rhinoceros auklet) breeding at the Farallon Islands, central California.

1998) to the highest (winter and spring 1999) abundances observed over nearly the past two decades (fig. 21). What processes determine zooplankton biomass in the California Current? Has the trend of declining zooplankton biomass (Roemmich and McGowan 1995) been stalled or reversed, and if so, what will the effects be on higher trophic levels? These are critical questions for CalCOFI to address, even though the answers are not readily forthcoming.

Large-scale changes in zooplankton abundance and fish stocks in the North Pacific have been linked to decadal-scale climate shifts ("regime shifts"), the most notable of which occurred around 1977 (Francis and Hare 1994; Miller et al. 1994; Trenberth and Hurrell 1994; Mantua et al. 1997). Mantua et al., for example, defined a Pacific Decadal Oscillation (PDO), a measure of the leading North Pacific SST pattern, which has reversed polarity three times in the past century (1925, 1947, and 1977). They found a remarkable correlation between the PDO and the abundances of many populations of Pacific salmon, with northern (Alaska) stocks varying out of phase with southern (Oregon, California) stocks. A similar out-of-phase relationship has been found for zooplankton populations in the North Pacific (Chelton et al. 1982; Brodeur and Ware 1992; Roemmich and McGowan 1995).

Recent studies (e.g., Gargett 1997; Parrish et al., in press) have taken a mechanistic approach to understanding the relation between large-scale climate variability and fish stocks. Gargett (1997) took as a starting point three of the principal observations to come out of the correl-

ative studies: (1) there is a link between the size of North Pacific salmon stocks and the strength of the Aleutian low-pressure system in the Subarctic Gyre; (2) northern and southern stocks vary out of phase; and (3) the major ocean influence on salmon survival occurs in early life stages, i.e., within coastal waters. Her proposed mechanism for explaining these observations is coastal water-column stability: northern and southern phytoplankton populations occupy opposite ends of an "optimal stability window," with northern (southern) populations, which are more limited by light (nutrients), experiencing amplified (reduced) growth as water-column stability increases. Gargett further proposed that coastal water-column stability, in turn, varies in phase along the entire eastern Pacific coastal margin, and depends directly on the strength of the wintertime Aleutian low. It is reasonable to assume, as Gargett (1997) did, that fluctuations in primary production directly affect production at higher trophic levels. The findings of Parrish et al. (in press) also indicate that regime shifts in coastal ecosystems are triggered by rapid shifts in large-scale extratropical atmospheric forcing.

Might we be in a transitional period to a new regime? Minobe (1999) has identified synchronized phase reversals between pentadecadal (30–80 year) and bidecadal (10–30 year) variations in the strength of the winter- and springtime Aleutian low as likely candidates for forcing the observed North Pacific regime shifts over the past century. If this synchronization were to continue, Minobe (1999) predicts a new regime shift to occur as early as 1999–2000, and most likely within the

next several years. The present state of the California Current, in fact, is similar to that observed in the years prior to the 1977 regime shift, as well as to conditions following the strong El Niño events of 1957–58 and 1982–83 (Schwing et al. 2000).

In the event of a regime shift, we might expect a prolonged period during which the Aleutian low (subtropical high) is relatively weak (strong), and transports in the California Current are anomalously high. According to Gargett's (1997) hypothesis, this situation would lead to increased coastal upwelling, decreased coastal water-column stability, and higher productivity off California. A higher California Current transport, in fact, may be sufficient to increase zooplankton biomass in the CCS (Chelton et al. 1982), and may partly explain the higher zooplankton abundance seen on recent CalCOFI cruises. Decreased stratification may also provide a deeper source for upwelled waters and enhanced nutrient input into the euphotic zone (Roemmich and McGowan 1995), thus contributing to heightened productivity in the region.

We must consider short-term climate fluctuations such as El Niño and La Niña within the context of lower-frequency variability, which may include natural variability on decadal time scales (including regime shifts) or anthropogenically forced global warming. Indeed, resonance of variability on different time scales may be a necessary trigger for climate shifts (Minobe 1999). Furthermore, Parrish et al. (in press) point out that the climate does not necessarily oscillate between two extremes (regimes), but may enter a new state that differs from any recent previous regime. North Pacific climate and coastal ecosystems are complicated, nonlinear systems, and may vary in unpredictable ways.

Whither the California Current? At the risk of disappointing eager readers, the question asked in the title of this paper must go unanswered for now. Over the next year CalCOFI surveys will provide a comprehensive suite of physical and biological data from the CCS, and may take us closer to an answer. It should be recognized, however, that the unusual nature of the recent observations could not have been fully appreciated without reference to the historical CalCOFI time series. There is an obvious need for continuing the CalCOFI monitoring, as well as for augmenting the program with process-oriented field studies and continued modeling efforts (e.g., Miller et al. 2000) in order to more fully understand, and eventually predict, the relation between environmental variability and ecosystem structure.

ACKNOWLEDGMENTS

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Part II

FIFTIETH ANNIVERSARY SYMPOSIUM
OF THE CALCOFI CONFERENCE

La Jolla, California
26 October 1999

THE ECOLOGICAL EFFECTS OF THE 1998 EL NIÑO IN EASTERN BOUNDARY CURRENTS

One of the major achievements of the 50-year CalCOFI program has been the identification and description of major El Niño events in the California Current system (CCS), emphasizing their ecological consequences. Even this achievement could, in retrospect, have been improved: at the time of the 1982–83 El Niño, CalCOFI was sampling extensively only every third year (1981 was a year of sampling), and only modest monitoring of this intense event was achieved, after considerable effort. This mismatch between nature and fiscal planning, plus evidence that the southern California sector of the CCS is representative of other areas on interannual time scales, led to the reduction of spatial coverage and enhancement of temporal coverage of monitoring (quarterly, every year)—the pattern currently followed.

The 1997–98 El Niño was predicted from events in the equatorial Pacific, resulting in enhanced spatial and temporal monitoring of this event by CalCOFI, supported by supplemental funding from the University of California and NOAA. Other research entities mounted analogous efforts. Accurate description of important, interrelated, properties of the environment, and detection of the timing of significant changes in them, are important steps toward understanding; although the *post hoc ergo propter hoc* logical fallacy must be avoided, an effect should follow its putative cause. Therefore, the purpose of the CalCOFI fiftieth anniversary symposium was to present results—necessarily preliminary in some cases—describing this event, in the context of longer time series defining "normal" conditions (including physical/biological modeling). Speakers were invited to present topics covering several regions of the eastern Pacific, and several trophic levels. The papers that follow are based on these presentations (with the exception of a summary of studies on marine mammals that Robert DeLong of NOAA presented at the meeting but which is not reproduced here). The papers were edited by Michael Mullin and Julie Olfe, but not refereed externally.

Michael Mullin

THE 1997–98 EL NIÑO: THE VIEW FROM LINE-P

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ABSTRACT

Though the earliest observations at Ocean Station Papa began in 1949, the useful oceanographic data along Line-P begin with 1956. Nevertheless, we do have 45 years of high-quality data describing the physical, chemical, and some aspects of the biological signals in the Gulf of Alaska. This note reviews the history of observations along Line-P, but focuses on the way the 1997–98 El Niño event manifested itself there. We were fortunate in being able to find the resources to mount an aggressive El Niño Watch program built around the long time series of Line-P and the La Pérouse project. This has allowed a thorough description of the evolution of El Niño as it progressed past the coast of British Columbia.

INTRODUCTION

As I began developing this presentation I became increasingly aware of the incredible value of the long time series, as exemplified by CalCOFI and by its northern colleague, Line-P. Both of these programs make it easy to compute and present plots of, for example, temperature anomaly fields. But we tend to forget that behind each of the anomaly fields is a mean field with 50 years of history behind it.

First, we must deal with some nomenclature. Ocean Station Papa, or Station P, is at 50°N, 145°W. The time series of observations at Station P is longer than the time series along "Line-P," which is the line of stations extending from the mouth of the Juan de Fuca Strait to Station P (fig. 1).

On 18 December 1949 the site subsequently known as Ocean Station Papa was occupied for the first time by a weather ship owned by the U.S. Weather Bureau, and the first oceanographic observations began with mechanical bathythermographs run once a day.

In December 1950 the U.S. ship was replaced by a Canadian weather ship, which did not immediately begin oceanographic observations. In July 1952, twice-daily mechanical bathythermograph observations began.

In July 1956, hydrographic stations were started. They usually sampled only to 1200 dbars, but occasionally they sampled to the bottom. This development represents the start of the really useful oceanographic program.

In April 1959 the Line-P program began, as hydrographic casts were started at five stations along a line
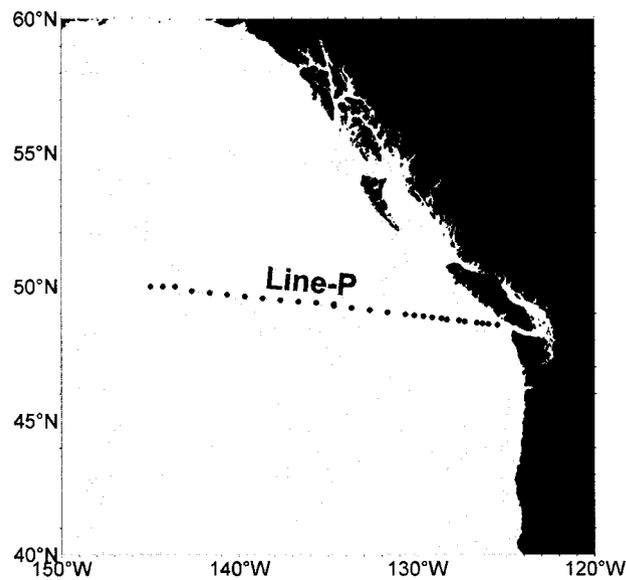
Figure 1. The location of Line-P in the Gulf of Alaska. Each dot represents a station.

leading to Station Papa. At various times improvements were made, and, in subsequent years, the number of stations constituting Line-P gradually expanded to 13.

In April 1969 a Bissett-Berman STD was used for the first time. In August 1974 a Guildline CTD was used for the first time.

In August 1981 the Canadian weather ship program was terminated. The value of the oceanographic program was well recognized, so the Line-P oceanographic program was maintained purely as a research program, with vessels operated by the Institute of Ocean Sciences. At that time the number of stations constituting Line-P was increased to 26, and a little later to 27, where it rests today.

Now we usually manage three surveys per year along Line-P, in February, May, and September. This timing is aimed at observing the conditions following the winter nutrient injection period, the peak of spring production, and the consequences of spring and summer production. In August 1998 NOAA/PMEL deployed an optical/climate mooring at Station P.

Figure 1 shows the locations of the 27 stations that currently make up Line-P. The line runs roughly along the boundary between the Alaska Gyre and the California
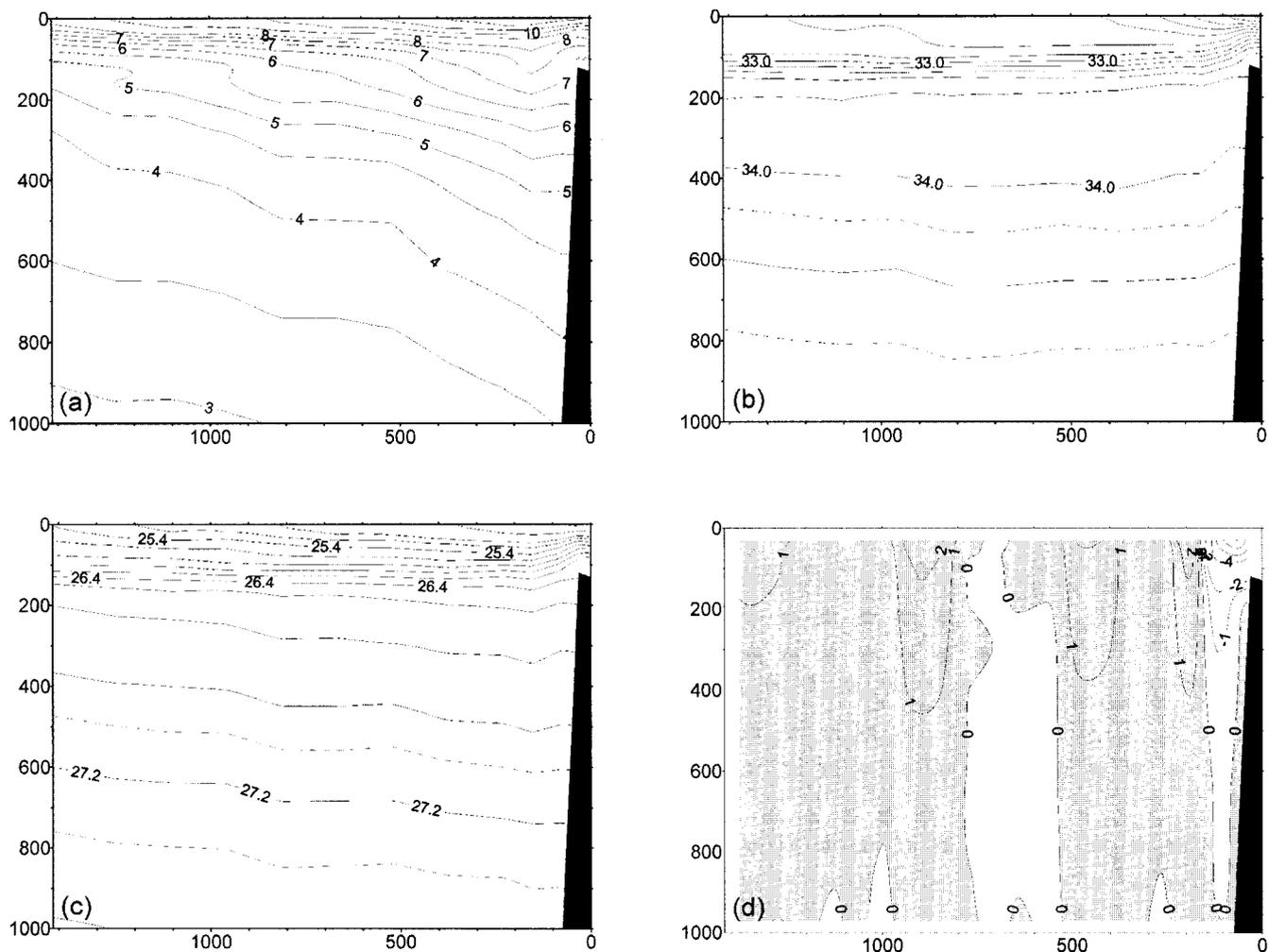
Figure 2. The mean state for June conditions along Line-P in (a) temperature, (b) salinity, (c) sigma-t, and (d) geostrophic velocity computed relative to 1000 dbars. In d, northward flows are shaded.

Current system. It is frequently argued that Station Papa is in the wrong place, that it might be better to monitor either the California Current system or the center of the Alaska Gyre. There may be some merit to this view, but an alternative view is that the right place for it is where it has always been, emphasizing the continual nature of the monitoring program. I concur with the latter view.

The continual nature of the sampling allows for the definition of mean fields. The diagrams in figure 2 show plots of the mean state for June conditions along Line-P, computed on the basic 13 stations. In comparing panels a, b, and c, we see that the dominant stratification in near-surface waters is supplied by salinity rather than temperature. As will be seen later, however, the contributions from temperature cannot be ignored. Below 200 dbar, temperature decreases monotonically with increasing distance offshore, whereas salinity shows little variation along Line-P.

Geostrophic velocities were estimated with the methods outlined by Reid and Mantyla (1976). As expected, the velocity field shows somewhat variable mean flows across Line-P in the offshore regions. Near the continental slope we see southward flow at the shelf edge. The mean state for other months shows northward flow at the shelf edge during the winter months and southward flow during summer. This transition is well known and described, for example, by Freeland et al. 1984. I find it slightly surprising that we see little evidence in figure 2 for the California Undercurrent. It should be present, but may have been missed by the relatively coarse sampling along Line-P.

THE 1982–83 EL NIÑO EVENT

Line-P is not the only monitoring program in the coastal regions of British Columbia. At 14 lighthouses around our coast, lighthouse keepers sample sea-surface temperature and salinity every day. The oldest stations
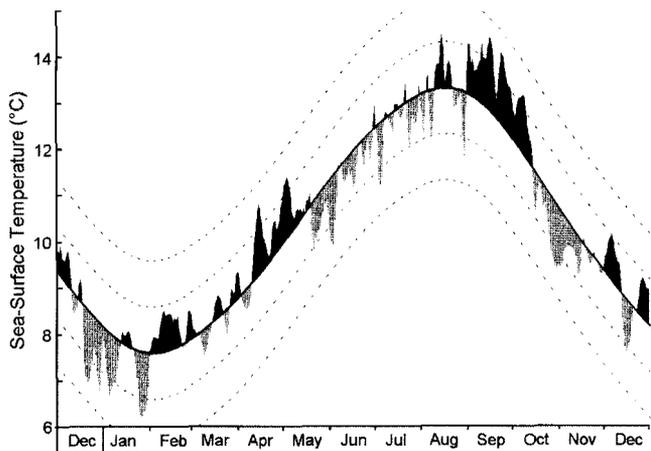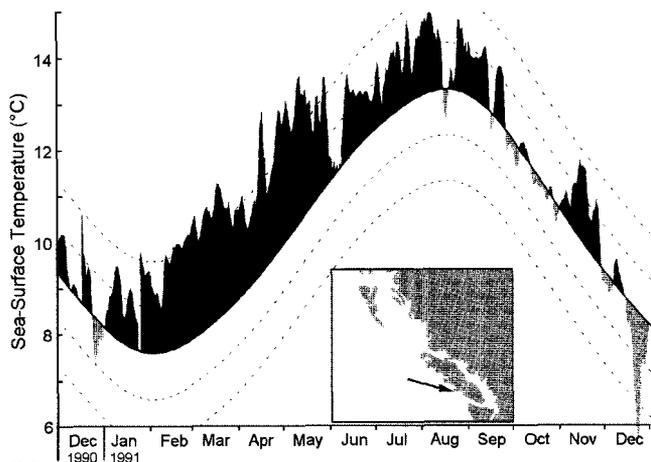
Figure 3.   Sea-surface temperatures observed at Amphitrite Point, on the west coast of Vancouver Island (*inset*): a, December 1990–91; b, December 1982–83. Areas above the line show temperatures above normal; areas below the line, temperatures below normal.
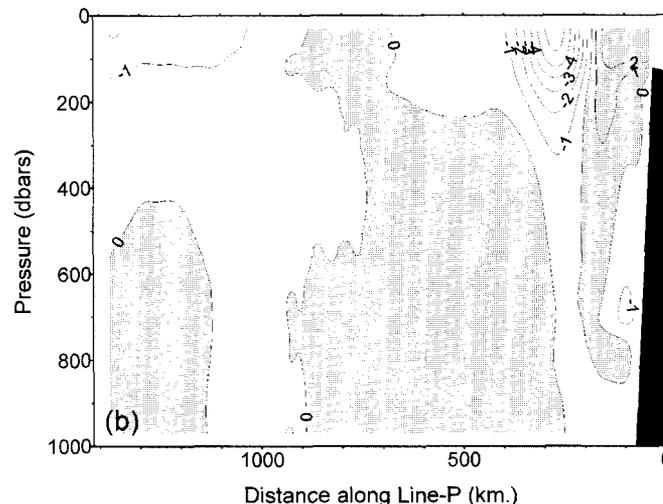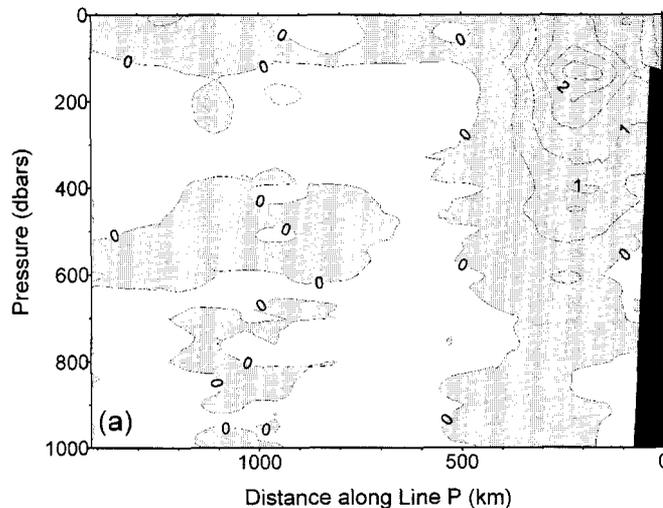
Figure 4.   Temperature anomaly field (a) and velocity anomaly field (b) observed along Line-P during March 1983.

are poorly exposed to the open ocean but have data from 1914 to the present.

Figure 3a shows a plot of the temperature observations at Amphitrite Point for December 1990 to December 1991, a relatively "normal" year with nothing much going on. Figure 3b shows a plot for December 1982 to December 1983, indicating the response to the 1982–83 El Niño. The contrast is obvious: temperatures were considerably above normal for an extended period during 1983.

Figure 4 shows section plots of the temperature and geostrophic velocity anomalies along Line-P. The positive temperature anomalies and northward flows are shaded. It is striking how deep the maximum anomaly was in 1983, and we will be comparing this diagram with data from March 1998.

The velocity anomaly diagram is, however, baffling. Again this was computed with the methods recom-

mended by Reid and Mantyla (1976) but produces an unusual picture. The contour of zero velocity anomaly separates a strong northward flow from a strong southward flow and coincides precisely with the maximum temperature anomaly. One might reasonably expect that the temperature anomaly feature should have an advective origin. In that case we might expect a bulls-eye pattern in the velocity anomaly, coincident with the temperature anomaly. To check the plausibility of the velocity anomaly field, we used the dynamic height estimates to compute the implied surface height anomaly at station P1; the implied height anomaly is about 4 cm.

The actual evolution of sea-surface height is shown in figure 5, which indicates actual height anomalies of more like 30 cm in March 1983. Clearly, our geostrophic velocity estimates are missing a large part of the actual signal, presumably a barotropic field.
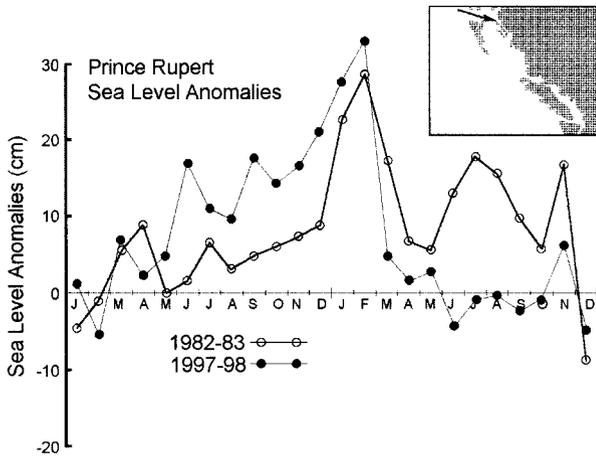
Figure 5. The evolution of monthly mean sea levels observed at Prince Rupert, B.C. (*inset*), for January 1982–December 1983 and January 1997–December 1998.

THE 1997–98 EL NIÑO EVENT

Figure 5 also shows the plot of sea-level anomalies for 1997–98, in comparison to those for the earlier event. The 1997–98 plot shows all the well-known and well-reported features of this El Niño event: the early start, the great intensity, and the abrupt collapse in March 1998. By this measure it is clear that the 1997–98 El Niño was the largest event of the century, at least in the response off the coast of British Columbia.

The Topex-Poseidon data set has been reanalyzed by Foreman, Crawford, and Cherniawsky (pers. comm.). Their analysis shows weak sea-level anomalies offshore from Vancouver Island immediately before the El Niño event, and eventually a very intense response, with maximum sea-level perturbations at the coast decaying monotonically offshore. Superficially, the distribution of sea level suggests Kelvin wave dynamics, but this has not been verified.

The six panels of figure 6 summarize the evolution of the large anomalies that dominated the northeast Pacific Ocean from spring 1997 into late 1999. In February 1997 (not shown here) the anomaly fields indicated very small perturbations throughout the northeast Pacific, or along Line-P. In the top pair of panels we see that by September 1997 the Gulf of Alaska was dominated by a major warm event. But the section plot shows that the warming was extremely superficial and confined to about the top 50 meters of the water column.

The middle pair of panels in figure 6, for March 1998, paints a dramatically different picture. The surface distribution suggests that a significant retreat of the warm waters of the Gulf of Alaska has taken place, but the section plot shows very large temperature anomalies concentrated below 150 dbars. This plot is remarkably similar to the plot in figure 4 showing the same anomalies for the 1983 event.

The final pair of diagrams in figure 6 shows the transition to the 1999 La Niña conditions. In this case the surface of the Gulf of Alaska is dominated by low temperature anomalies, and the right-hand panel indicates that the cooling is very superficial. However, we also see an intrusion of warm water in the offshore half of Line-P. At the present time it is not possible to speculate on the origin of this water mass.

Thus the development of the large anomalies of 1997–99 shows several distinct phases:

1. A superficial warming of the entire Gulf of Alaska between the onset of El Niño and the winter of 1997–98.
2. During the winter of 1997–98 and early spring of 1998 the Gulf of Alaska remained under the influence of warm anomalies, but much weaker ones at the surface. The largest anomalies appeared near the continental slope, perhaps in the coastal waveguide, though not necessarily as a Kelvin wave.
3. Finally, a rapid transition from warm-water anomalies to cold anomalies began in 1998 and intensified in 1999. As in phase 1, the anomalies were confined to the near-surface layers.

The velocity anomalies associated with the temperature and salinity anomaly fields of March 1998 can be estimated much more exactly than was possible in 1983, because of the availability of altimetry data from the Topex-Poseidon satellite. We computed the dynamic height fields for March 1998 and for the March mean, in both cases referenced to the surface, and computed the anomaly field of zero-referenced dynamic heights. We then adjusted this anomaly field to create an estimate of the absolute velocity field by using a surface height anomaly field determined to be the difference in Topex heights seen along Line-P in March 1998 and the distribution in February 1997, before the El Niño signal arrived.

Figure 7 shows the resultant velocity field, which is considerably more satisfactory than that estimated for the data gathered in March 1983 in that it does suggest that the temperature anomaly field is an advective feature. We can multiply the velocity anomaly field of figure 7a into the temperature anomaly field of figure 6 to map the heat-flux anomaly field shown in figure 7b. In this case the negative anomalies are all extremely weak. The only significant feature is the large northward heat flux over the continental shelf and slope. The total heat flux suggested by this calculation is too small to be the dominant warming influence in the Gulf of Alaska, but is large enough to be a major contributor to the El Niño heat budget.

Finally, we must ask how the 1997–98 El Niño affected the northeast Pacific ecosystem. This question can only be answered in the context of the systematic trends
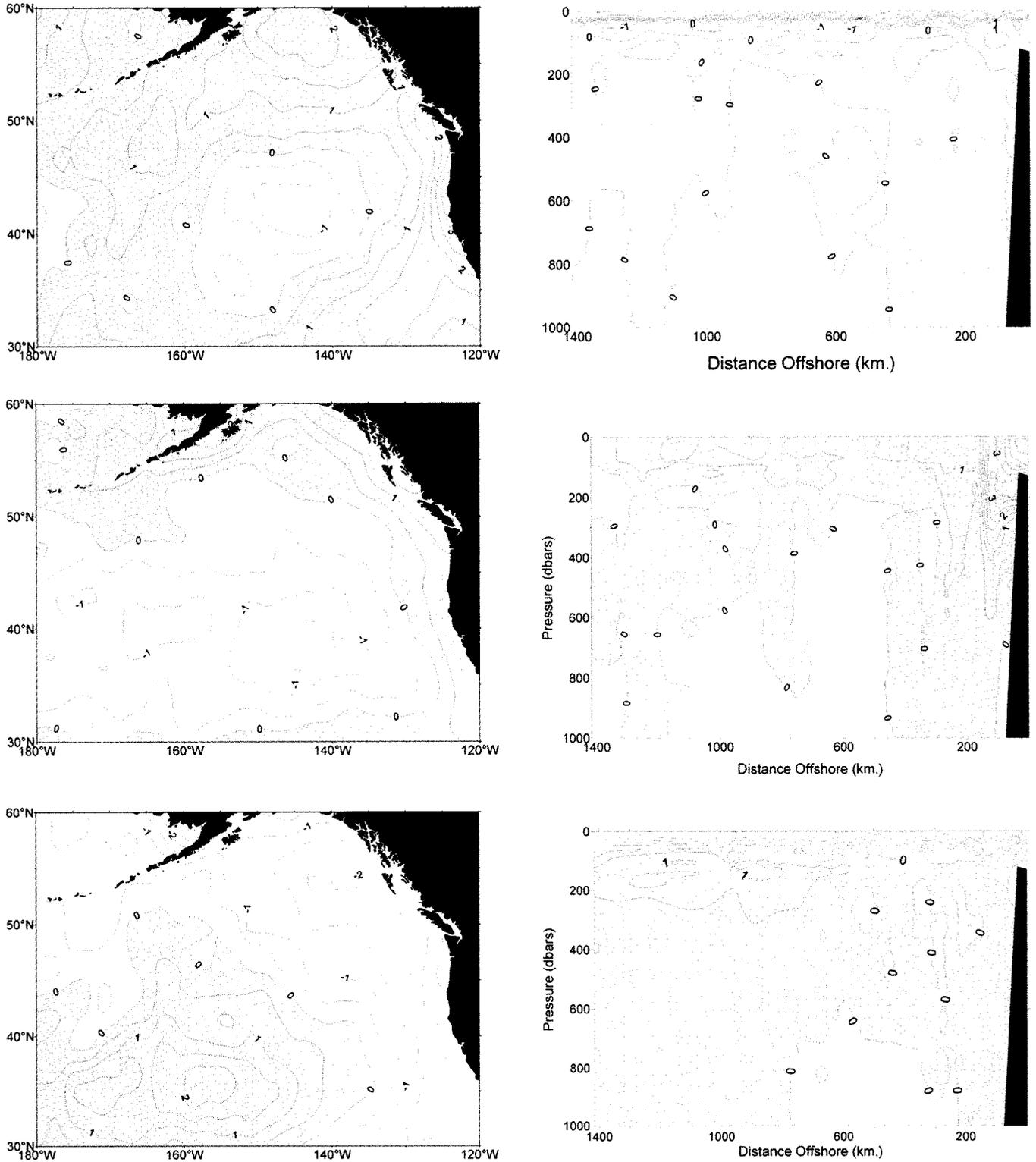
Figure 6. *Left*, a sequence of sea-surface temperature anomaly maps showing the context for section temperature anomaly plots (*right*). The three rows show distributions for September 1997, March 1998, and June 1999. Positive anomalies are shaded.

being seen along Line-P. A paper by Freeland et al. (1997) reported the shallowing mixed layer at Ocean Station Papa, attributed to a decrease in the salinity of the upper layer in the northeast Pacific.

Figure 8 shows the shallowing trend in midwinter mixed layer depth at Station Papa. The shallowest depth recorded in the history of observations at Station Papa is marked "B" on the plot. It occurred in the winter of

Distance along Line-P (km.)

Distance along Line-P (km.)
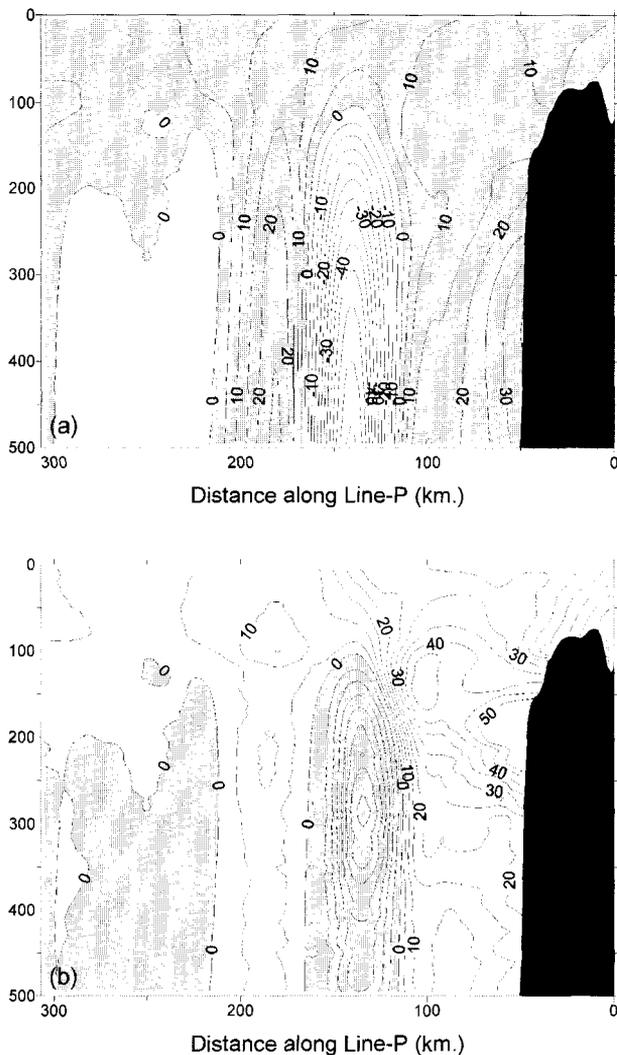
Figure 7. *a*, Velocity anomaly field estimated from Line-P hydrography and Topex-Poseidon observations; *b*, heat-flux anomaly field. Positive velocities and negative heat-flux anomalies are shaded.

Figure 8. Midwinter mixed layer depth at Station Papa, updated through the winter of 1998–99. The value labeled A immediately followed the 1982–83 El Niño event. Value B indicates the shallowest depth recorded in the history of observations at Station Papa. Value C indicates the deeper mixed layer in winter 1998–99.

1997–98 and presumably resulted from the extreme warm conditions that prevailed at that time. By the end of 1998 the surface of the northeast Pacific was substantially cooler than normal, and this resulted in a decreased stratification and therefore a deeper mixed layer in the winter of 1998–99, labeled "C" in figure 8. The value labeled "A" immediately followed the 1982–83 El Niño event.

The shallow mixed layer of winter 1997–98 restricted the supply of nutrients to the upper ocean. This allowed normal spring primary production to reduce the nitrate in near-surface waters to undetectable levels by April 1998. By the summer of 1998 it was evident that the entire Gulf of Alaska was under the influence of a major nitrate depletion event. Observations along Line-P sug-

gest that primary production was reduced by at least 50%, and Mackas (pers. comm.) indicates that zooplankton were also depleted in coastal waters. This was a major anomaly in the food supply of the Gulf of Alaska.

At the same time reports were arriving from fishers that salmon were "in poor condition." Other reports indicated that salmon migrating to the Fraser River were migrating up the wrong rivers, in some cases rivers on the west coast of Vancouver Island.

In summary, for the period January 1997 through fall of 1998 we witnessed:

- Record surface temperature anomalies in the northeast Pacific Ocean
- Record deep temperature anomalies
- Record sea-level anomalies
- Record low midwinter mixed layer depths
- Record low supply of nitrate to the near-surface layers
- Very low primary production
- Probably, low secondary production
- Record perturbations to the salmon fisheries.

We have to conclude that these perturbations are all related.

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THE 1997–98 EL NIÑO AND ITS EFFECTS
ON THE COASTAL MARINE ECOSYSTEM OFF PERU

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ABSTRACT

We summarize the important effects of the extraordinary El Niño 1997–98 on the Peruvian marine ecosystem, and we compare these with what was observed during the extraordinary El Niño 1982–83. The SST anomalies at coastal stations, as well as data from marine explorations carried out during 1996–98, show, among other things, that the preceding cold period ended in January–February 1997; that El Niño 1997–98 was clearly defined along all the Peruvian coast in March–May 1997 (earlier in the north) and ended between April and June 1998, beginning from the south; and that El Niño was followed by a moderately cold period, evident since August 1998 (winter in the Southern Hemisphere). The most dramatic alterations in chemical characteristics were observed in December 1997 and February 1998, when low concentrations of nitrate (0.15–1.1 µg-at/L) extended south from Callao. Apparently, chemical conditions were more extreme in the water column in 1997–98 than in 1982–83, because the oxycline and nutricline were located at greater depths.

Anomalously small volumes of plankton were observed, and abundant dinoflagellates and copepods typical of warm waters entered the coastal waters with the equatorial surface waters (ESW) and subtropical surface waters (SSW), similar to what occurred during El Niño 1982–83. Anchovy were found near the coast in the first phase; in the second phase they shifted toward the south and into deeper water, while sardine increased in the first phase, and then migrated to the south. Hake widened their distributional range to the south and also vertically, because this species inhabits the zone influenced by the southern extension of the Cromwell Current (SECC). On the other hand, subtropical, equatorial, and even tropical species widened their distribution, being observed off the Peruvian coast. Of special relevance was the samasa, because its abundance and distribution reached 18°S, which made it an important resource for the Peruvian fishery during El Niño 1997–98.

INTRODUCTION

Peruvian coastal waters have a great variety of biological resources and constitute an important fishery region of the southwestern Pacific; the main species are the anchovy among the pelagics and the hake among the demersals. Two typical phenomena regulate the spatiotemporal distribution and the abundance of these resources: coastal upwelling and El Niño.

Coastal upwelling is mainly responsible for the great biological production that feeds the different trophic levels of the coastal environment. This process takes place along the Peruvian coastline, particularly around 5° and 15°S (Zuta et al. 1978), and it is associated with the SE trade winds that are commonly weak in summer and more intense in winter in the Southern Hemisphere.

The El Niño phenomenon arises from interannual variability in macroscale interaction between the ocean and the atmosphere. Its main scenario is the equatorial zone of the Pacific, and its manifestation is spectacular off the Peruvian coast, with variable features and distinct peculiarities. Its impact on fisheries resources depends on the type of event: weak El Niño, moderate El Niño, intense El Niño, and extraordinary El Niño.

This paper will present the biological responses in the main stages of the extraordinary El Niño of 1997–98, which, according to the anomalies of surface temperature, had a moderate peak in its initial development phase and a second, great peak in its second phase of development that ended with a rapid decline in autumn 1998.

We also make a brief comparison with El Niño 1982–83, which was one of the most intense in the decade of the eighties, and about which Halpern (1996) has made interesting reflections that we should always keep in mind.

METHODS

The material used for this study was obtained from sea operations carried out by the Instituto del Mar del Perú (IMARPE) in monitoring El Niño 1997–98, mainly from evaluation cruises of pelagic and demersal resources as well as some oceanographic cruises. We also used information on sea-surface temperature (SST) at fixed stations from the coastal laboratories of IMARPE and reports from the Dirección de Hidrografía y Navegación de la Marina (DHNM).

For hydrographic profiles, Niskin bottles and CTD

were used to obtain samples at standard depths to 300 m. Salinity was determined with a Plessey 6230 salinometer. The nutrient analyses were done according to Strickland and Parsons (1972), and the oxygen analyses by Winkler method, modified by Carrit and Carpenter (1966).

The phytoplankton samples were taken with standard nets of 75 μm mesh size, in horizontal tows of 5 minutes at velocities of 3 knots. Surface plankton volumes were obtained by centrifugation at 2400 rpm for 5 minutes, expressing results in ml per m^3 of seawater filtered. Samples were analyzed qualitatively, considering the main groups of phytoplankton and zooplankton, giving conventional values for the abundances of the more representative organisms. Zooplankton samples were collected with Hensen nets of 300 μm mesh size in tows from 50 m to the surface, and were preserved in a 2% formaldehyde solution. These samples were analyzed qualitatively, and the ichthyoplankton were analyzed qualitatively and quantitatively, with results expressed in number of eggs or larvae per m^2.

The distribution and abundance of the pelagic resources were monitored with an echosounding digital system and echointegration (SIMRAD EY-500 and EK-500). Information on landings of the main fish resources was obtained from the Plan of Monitoring of Pelagic and Demersal Fisheries of the Peruvian coast. The reproductive states of the anchovy and sardine were estimated from macroscopic observation and from the histological state of the gonads. Information about marine birds and mammals was obtained by sighting and recording their geographic position during sea operations.

PHYSICAL FEATURES

We present the main features at the sea surface for the period September 1996–October 1998, using selected data published in many papers by DHNM in 1997 and IMARPE in 1997 and 1998, for coastal stations and research cruises. According to maps of SST in the Climate Diagnostics Bulletin (NOAA 1997, 1998), there was a great development of a warm coastal tongue to the Peruvian-Chilean border from February to April 1997, with a great equatorial transgression in February. During the rest of the year, the warm western tongue and the warm eastern tongue remained together, creating a band of temperatures greater than 28°C, which apparently favored the start of a new equatorial transgression. This new transgression intensified in January–March 1998 and persisted until June 1998, when the equatorial cold tongue could not be completely reestablished.

The preceding, 1995–96 moderately cold period (Zuta and Otininano 1998) ended in January–April 1997, with a delayed southward displacement: in January to Paita, in February to Chicama and Chimbote, in March to Callao, and in April to Ilo.

The warm period with SST anomalies greater than 1°C lasted much longer in the north than in the south: 16 months (March 1997 to June 1998) in Talara and Paita; 15 months (April 1997 to May 1998) in Chicama-Callao; and 13 months (May 1997 to May 1998) in Ilo (fig. 1). Figure 2, from *Humboldt* cruises 9704, 9706-07, and 9709-10, shows the distribution of SST anomalies in the first phase, including values higher than 6°C north of Pimentel (7°S) and between 10° and 17°S during June–July 1997.

The positive SST anomalies of coastal stations showed two peaks (fig. 3a). The first was moderate and took place around August 1997; the second was more intense (January 1998). In between, the main decline was in October 1997 along the whole coastal band (fig. 3b). During the first phase of this warming period, the positive anomalies were as high as 6°C; during the second phase the anomalies were up to 9°. The coastal area between 7° and 12°S was much more affected by the warming period.

Cruise 9702-03 (Vásquez 1997) and cruise 9704 (Morón and Marquina 1997) recorded a strong southern intrusion of equatorial surface waters (ESW) and tropical surface waters (TSW) to 12°S and an intrusion of subtropical surface waters (SSW) south of 15°S (San Juan) during the first phase of the warm period.

Cruises 9711-12 and 9803-05 (figs. 4 and 5) showed that during the second phase of the warm period there was another intrusion of ESW between 81° and 84°W, and southward displacement up to 12°S, with salinities of 32–34.8 ppt and temperatures of 25°–29°, at the time when SSW were in the coastal band south of 8°S (Salaverry), with salinities of 35.1–35.6 ppt and temperatures of 19°–25°. In fact, the SSW was much more permanent than was the ESW.

The decline of the positive SST anomalies and consequently the end of El Niño 1997–98 started in March 1998 at Ilo and in June 1998 at Paita. Around August–September 1998 a negative SST anomaly appeared, and then the post–El Niño conditions started. They were characterized by a moderate cold period that remains evident. Between June and July 1998, there was evidence of normalization of the coastal zone from Huarmey northward, in both temperature and salinity. The SSW off Paita had temperatures from 19° to 21°.

The extraordinary El Niño event of 1997–98 was not expected to reappear sooner than 100 years after the extraordinary El Niño event of 1982–83.

CHEMICAL FEATURES

The presence of warm equatorial and subtropical water masses along the Peruvian coast was well defined at the beginning of El Niño in April (cruise 9704), June–July (9706-07), November–December (9711-12),
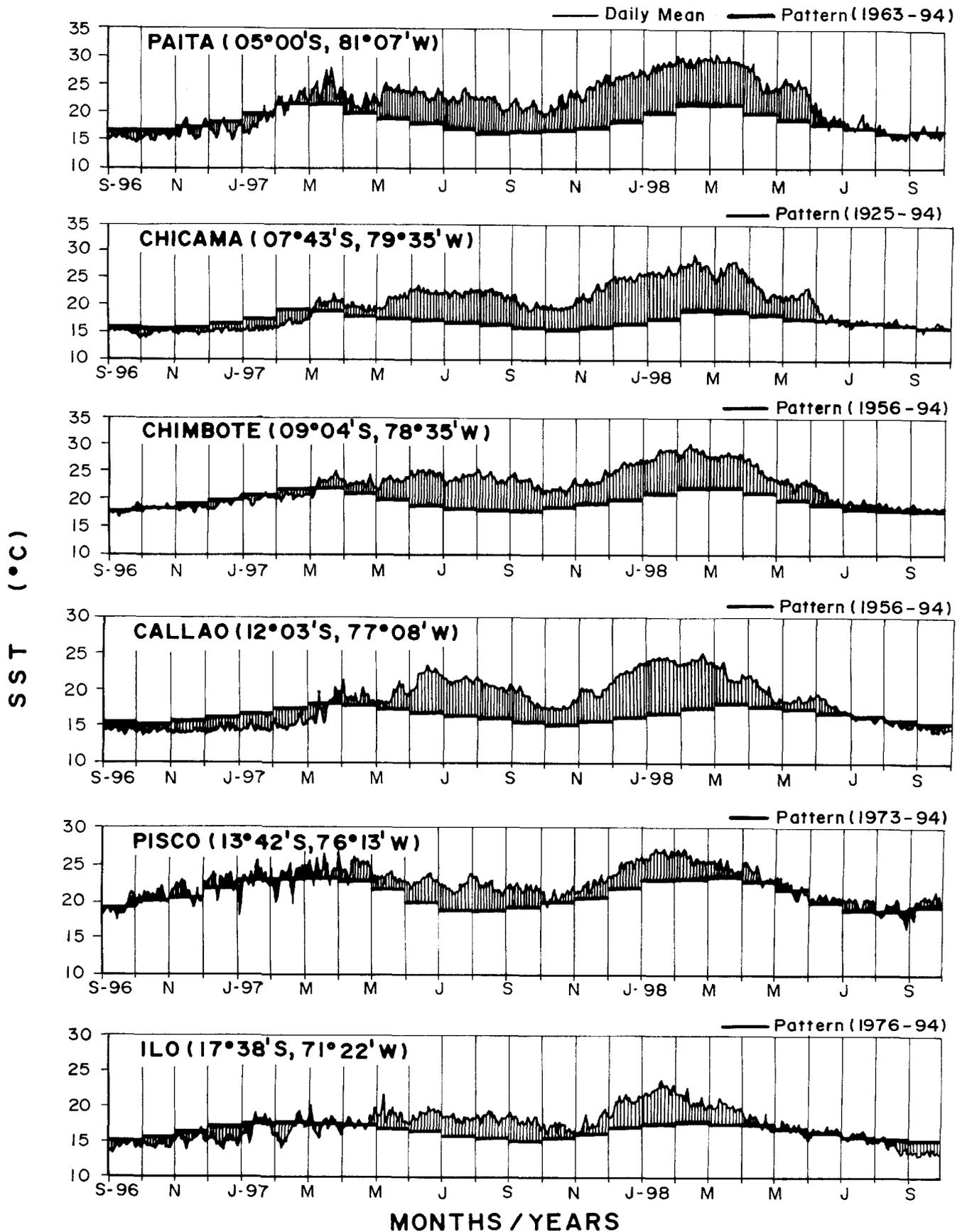
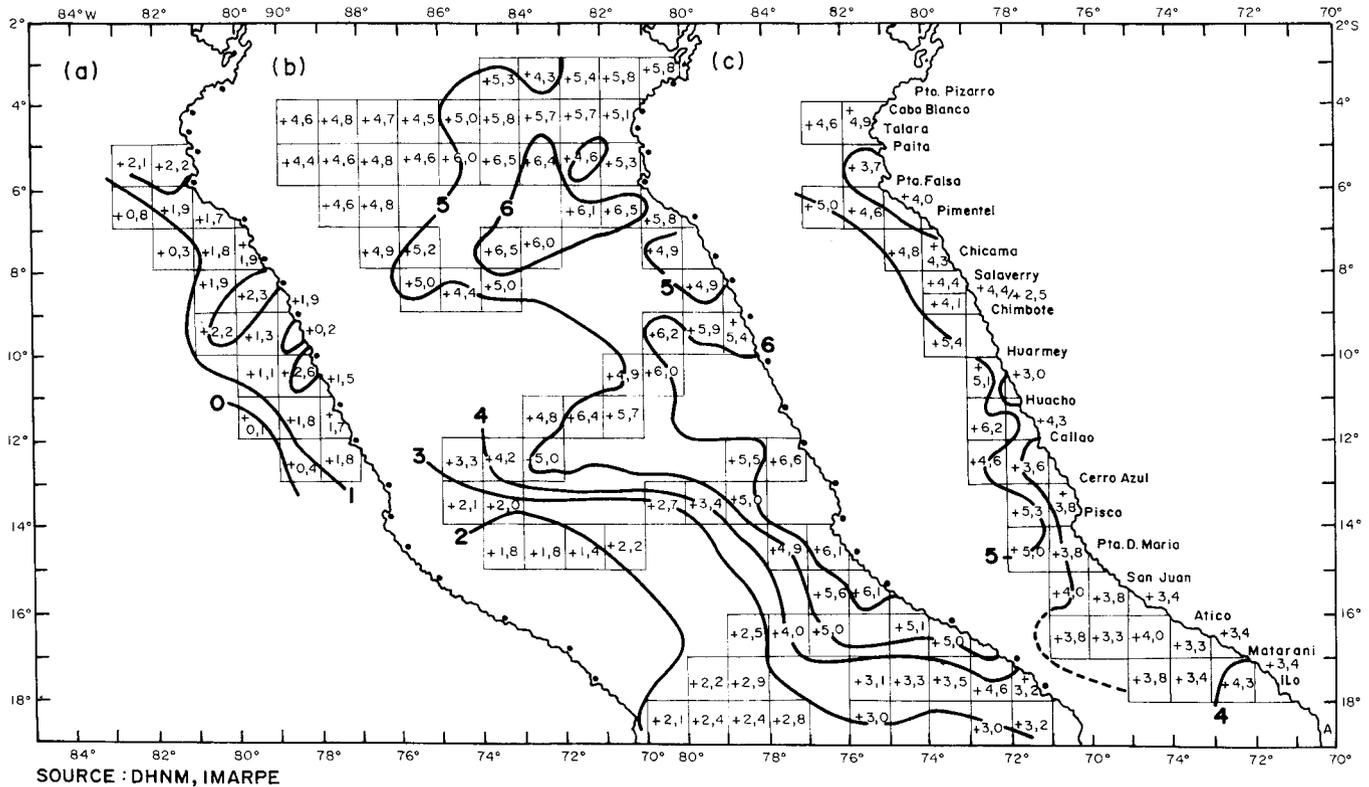Figure 1.   Time series of daily mean SST (thin line); the thicker line represents the long-term monthly mean.

Figure 2. Maps of monthly mean SST anomalies for research cruises of autumn (a, b), and winter (c) of 1997. Adapted from Morón and Marquina 1997, and Gutierrez et al. 1998.
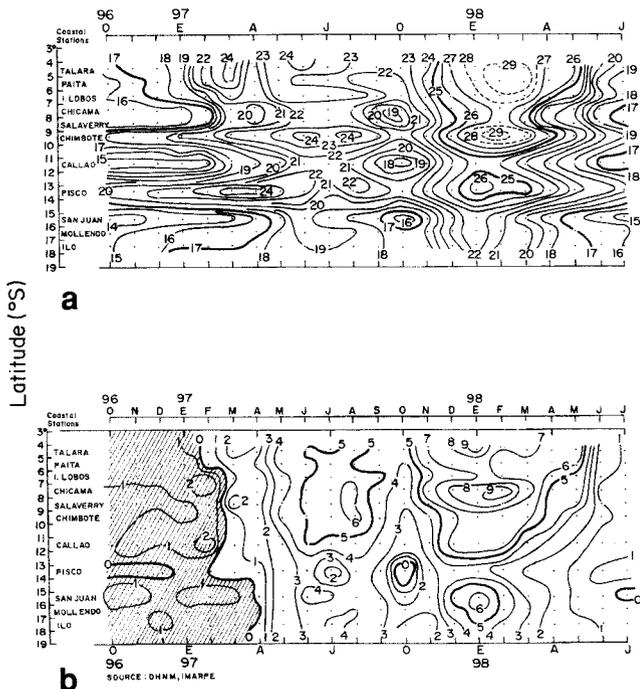

Figure 3. Composite structure of the monthly mean SST (a) and SST anomalies (b) for the stations along the entire Peruvian coast (October 1996–July 1998).

and February–March (9802-03) by thermohaline features (Gutierrez 1997; Pizarro 1997a, b; Garcia 1998). The distribution of oxygen and nutrients at the sea surface also characterized these periods. Among the nutrients, nitrate was selected as an indicator of anomalous distribution for comparison with preceding events, since it was reported by other authors.

Seasonal Variation of Oxygen and Nutrients

Figures 6 and 7 describe the seasonal sequence of changes in dissolved oxygen and nutrients in the sea surface, providing indicators for monitoring the warm event.

At the beginning of autumn 1997 in the Southern Hemisphere, *Humboldt* cruise 9704 detected the first hydrochemical alterations of El Niño in the initial movement of equatorial waters, which mixed with coastal waters to produce an irregular distribution of dissolved oxygen with high values between 5 and 7 ml/L. The nitrate concentrations were lower than 5 µg-at/L beyond 20 nmi, and changes were not observed in the coastal band.

At the end of autumn and beginning of winter 1997 (9706-07) the dissolved oxygen had a different distribution than in April, being more homogeneous, where values <5 ml/L (4.8–4.9 ml/L) corresponded in general to the equatorial surface waters (ESW; <34.8 ppt), which
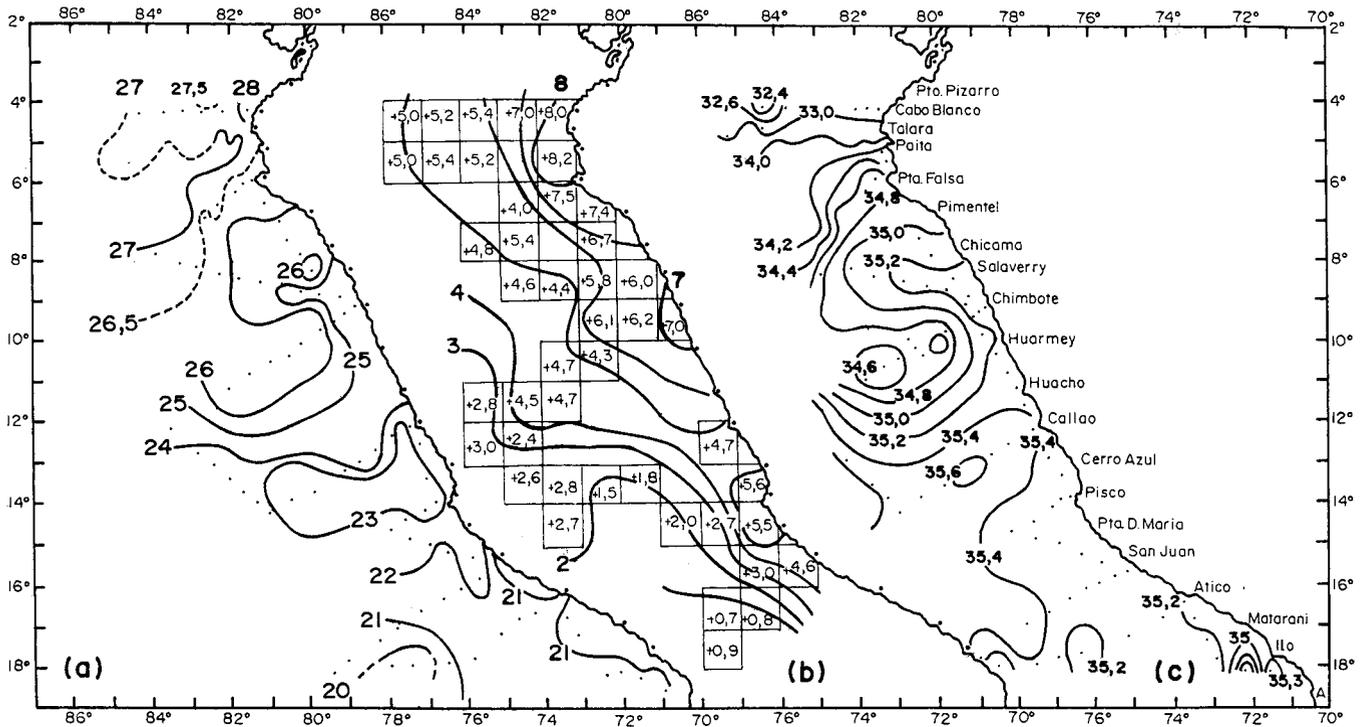
Figure 4.   Maps of SST (a), SST anomalies (b), and salinity (c) for BAP *Carrasco* cruise 9711-12 (spring). Adapted from Pizarro 1997.
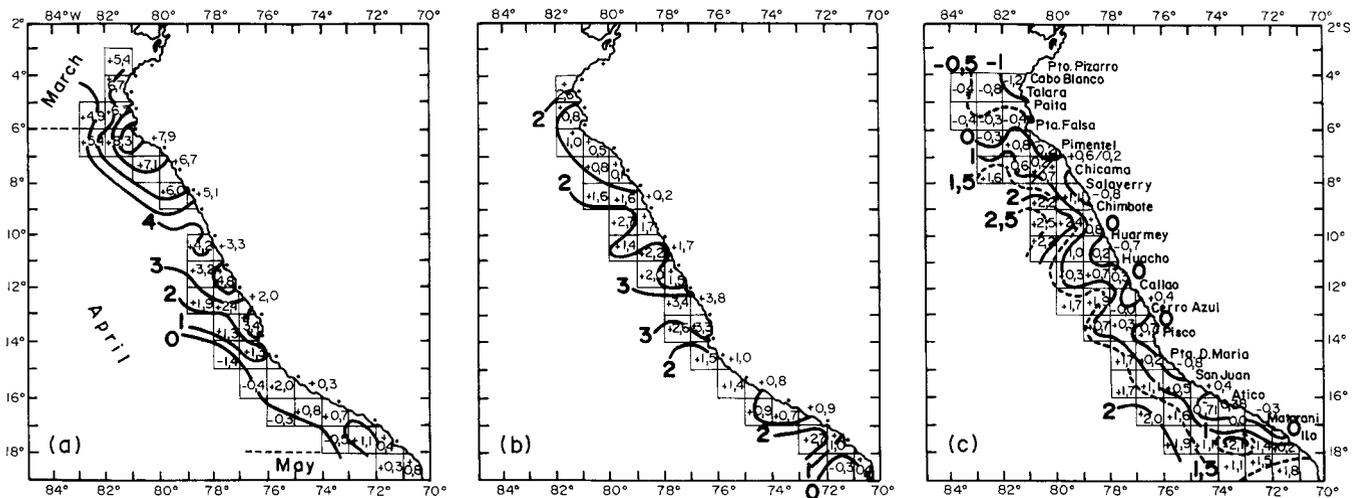
Figure 5.   Maps of monthly means of SST anomalies: a, cruise 9803-05 (20 March–7 May, 1998); b, cruise 9805-06 (20 May–25 June 1998); c, cruise 9808-09 (20 August–18 September 1998). Adapted from Vasquez and Tello 1998; Morón 1998; and Morón et al. 1998.

extended past 12°S, and concentrations >5 ml/L belonged to subtropical surface waters (SSW; >35.1 ppt) south of Callao; this relation was not quite accurate in defining the limit between these waters. Both water masses had nitrate concentrations <3 µg-at/L, except for a small coastal band. The 5 µg-at/L isopleth of nitrate that usually surrounds the cold coastal waters in normal conditions for more than 150 nmi in autumn (Calienes and Guillen 1981; Calienes et al. 1985) was discontinuous in this anomalous period.

At the end of winter (9709-10) the attenuation of the warm conditions on the Peruvian coast was reflected in a limited recovery of the normal oxygen and nutrients. The oxygen range indicated coastal waters mixed with predominant subtropical waters (Gutierrez et al. 1998), especially to the south of 6°S, while equatorial waters were north of Paita. Values of 5 ml/L of oxygen were related to the salinity of 35.2 ppt, and concentrations <4 ml/L that delimited the areas of upwelling occurred with high concentrations of nitrate (10–15
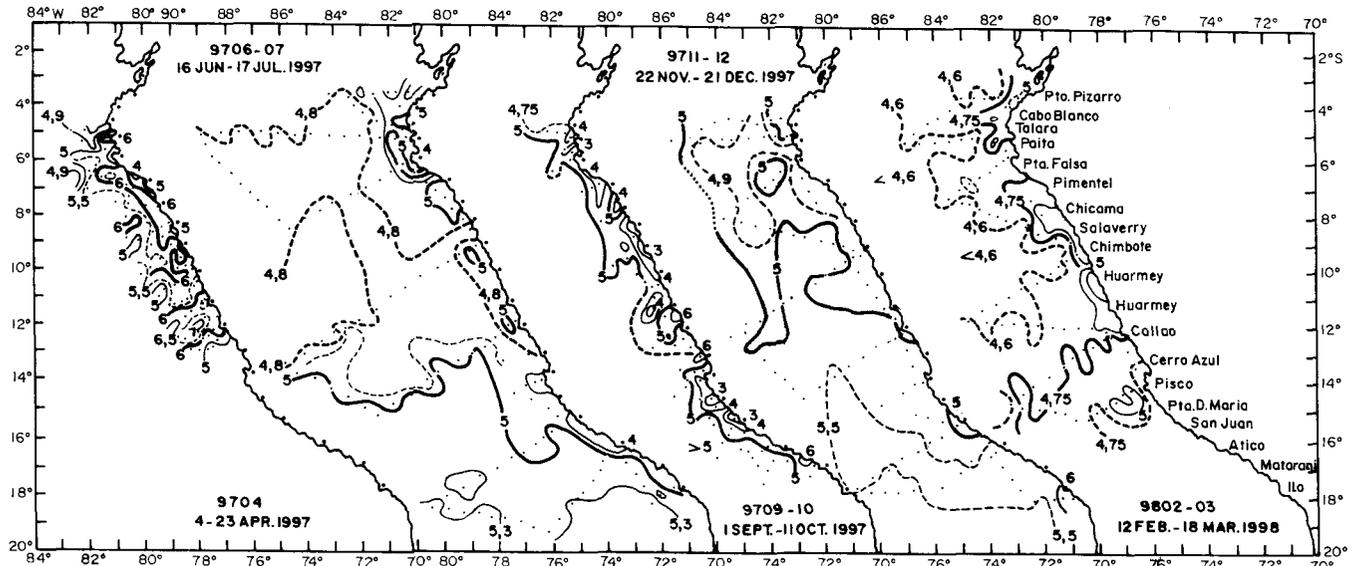
Figure 6. Seasonal distribution of oxygen (ml/L) at the sea surface along the Peruvian coast (April 1997–March 1998). Small dots indicate cruise track.
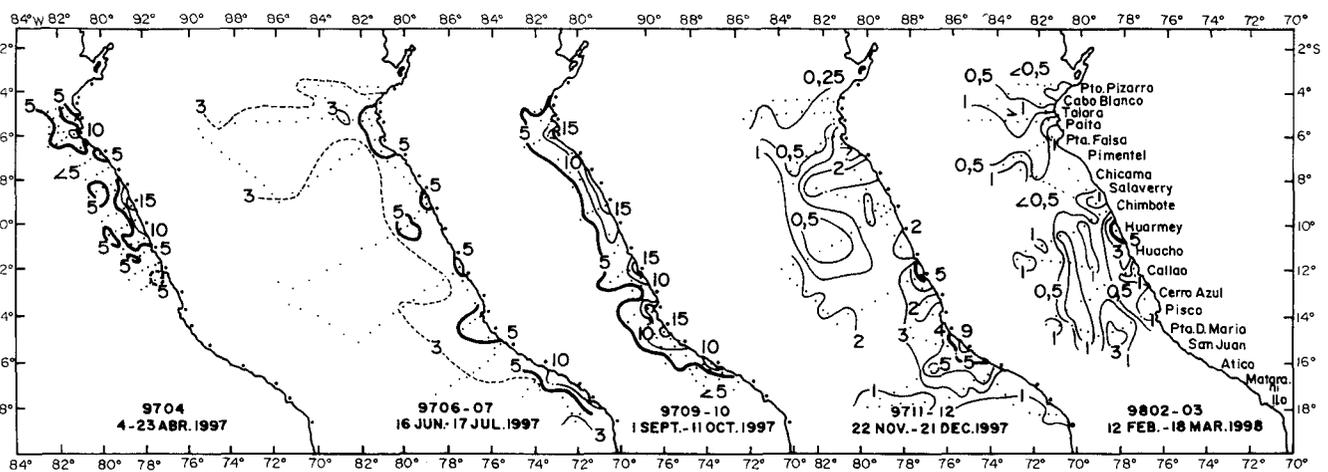
Figure 7. Seasonal distribution of nitrate (μg-at/L) at the sea surface along the Peruvian coast (April 1997–March 1998).

μg-at/L), which broadened its distribution in relation to autumn, especially in Salaverry-Huarmey and Pisco-San Juan.

The evolution of the chemical features of the warm event in spring 1997 (cruise 9711-12) showed a new advance of equatorial waters toward the Peruvian coast to 12°S, with the axis of the warm tongue far from the coast. These waters had concentrations of 4.4–4.8 ml/L of oxygen and contrasted with SSW, which had values >5 ml/L. The surface distribution of nutrients was interrupted once again, and very low concentrations were found by the cruises during 1997, with 0.15–1.1 μg-at/L nitrate in the equatorial waters north of Callao. These values were possibly lower in January (a period for which we do not have information).

For the physical features described in the first part of

this review, the monthly averages of temperatures and surface anomalies of the coastal stations were higher in the second peak, between 7° and 9°S from December 1997 to January 1998. For the chemical features, the most drastic alterations in water surface were observed in December 1997–February 1998, when lower concentrations of nitrate moved south of Callao (9802-03). In this final month the oxygen distribution had values lower than 5 ml/L in most of the studied area (3°30'–15°S), not only in equatorial waters, but also in subtropical waters, which formed a front between Salaverry and Chimbote (8°–10°S).

Changes in Vertical Patterns

The oxycline associated with the thermocline was found at greater depths than usual due to the circulation
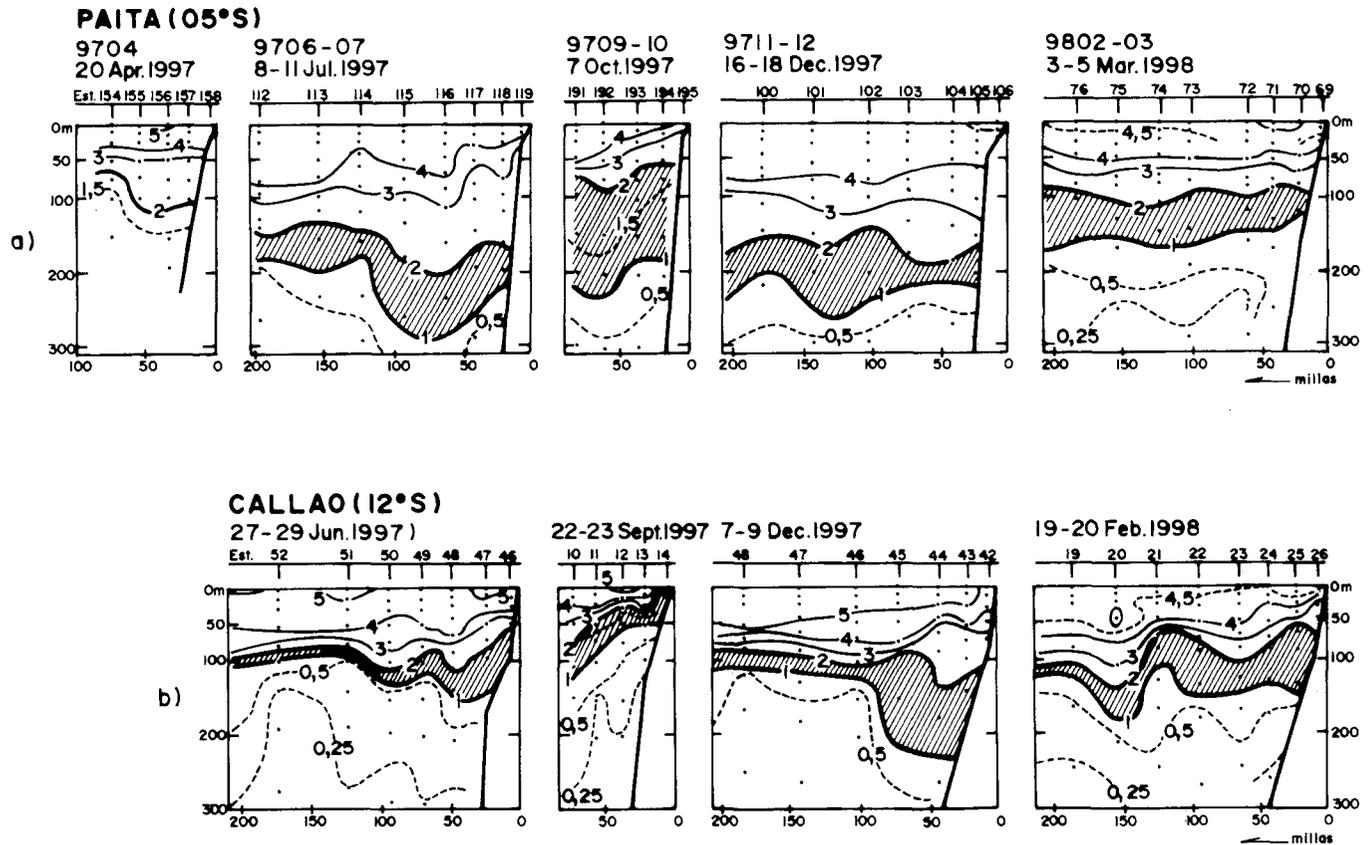
Figure 8.   Profiles of dissolved oxygen (ml/L) at Paita (5°S) and Callao (12°S; April 1997–March 1998).

changes, including the intense effect of the coastal current of the SECC, which had seasonal variations.

The location and features of the oxycline in the water column in the area of Paita during the phenomenon (fig. 8a) indicate a greater deepening in winter 1997, during the development of El Niño (9706-07), and in spring (9711-12), during the second peak, when concentrations of 1 ml/L of oxygen were found deeper, north of Callao. In February 1998 (9802-03), this feature was weaker. At the same time the effect was less intense in the area of Callao, except for December 1997 (fig. 8b).

The nutricline was at 50 m when the alterations started in April 1997, increasing in depth in June–July to 100 m. In winter (9709-10) the nutrient-poor layer shoaled again to 50 m in Paita and to 80 m in Chimbote. In the period of main intensity (December 1997), nitrate concentrations <5 µg-at/L were found to 100 m along almost all the Peruvian coast except at the southern extreme (fig. 9).

The trend toward normalization in the hydrochemical conditions began in autumn 1998 in small coastal nuclei (Chimbote-Huarmey, Pta. Doña María-San Juan and Atico-Mollendo), being more remarkable in the southern area (Flores, Cordova et al. 1998; Flores, Ledesma,

and Solís 1998). Afterwards, normalization widened, with the slow retreat of warm waters and the progressive recovery of the upwelling areas along the coast, with characteristic oxygen values and nutrient concentrations.

VARIATIONS IN TROPHIC LEVELS

The warm event affected the distributions and abundances of many species that constitute important resources of the Peruvian ecosystem. The initial alteration was the presence of the ESW in April 1997, when the anchovy Engraulis ringens was found near the coast, especially north of Callao. This distribution continued during September and October along the coast, when there were still acceptable conditions for the species. In November 1997 the anchovy schools began to be displaced southward, and could be found in higher concentrations between Cerro Azul (13°S) and Ilo (18°S). In 1998, coinciding with the normalization of the environment, anchovy maintained a coastal distribution in low abundance.

Plankton

During summer 1996, plankton volumes fluctuated from 0.04 to 10.2 ml/m³, with upwelling diatoms and several species of Chaetoceros being common. In winter
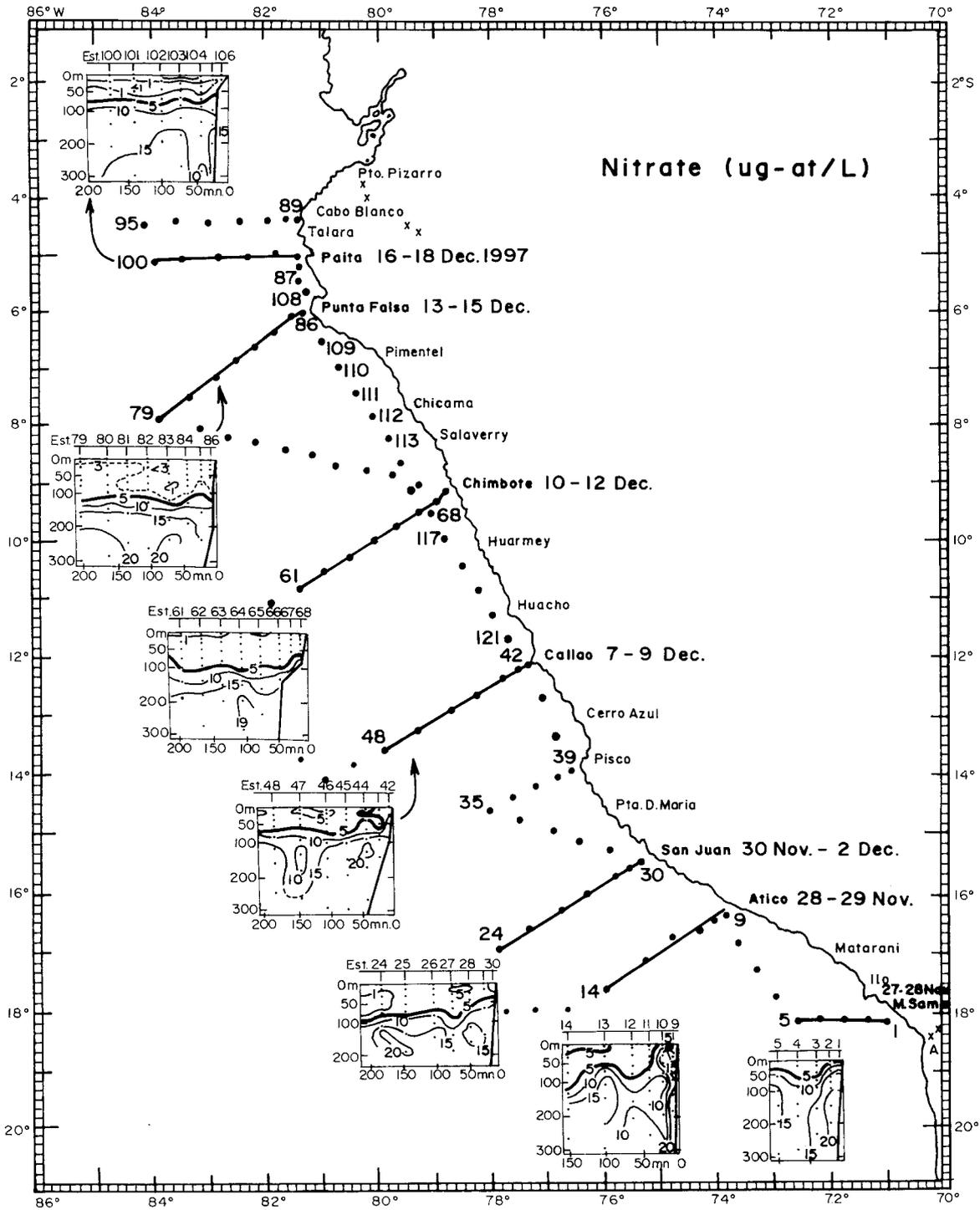
Figure 9.   Nitrate (µg-at/L) profiles at seven areas off the Peruvian coast from 27 November to 18 December 1997 (cruise 9711-12).

of the same year, the dominance of diatoms typical of upwellings, such as *Chaetoceros debilis*, *Ch. socialis*, and *Skeletonema costatum* continued, indicating normal distribution patterns for water masses in that period of the year (Ayón et al. 1996).

In 1997, at the end of summer and the beginning of

autumn (9702-03, 9704), when the warm event took place along the Peruvian coast, the volumes of plankton varied between 0.1 and 6.0 ml/m³, with the highest mean values of 2 ml/m³ within 30 nmi of the coast (fig. 10a). These values were lower than those obtained for the same period during the two previous years. This
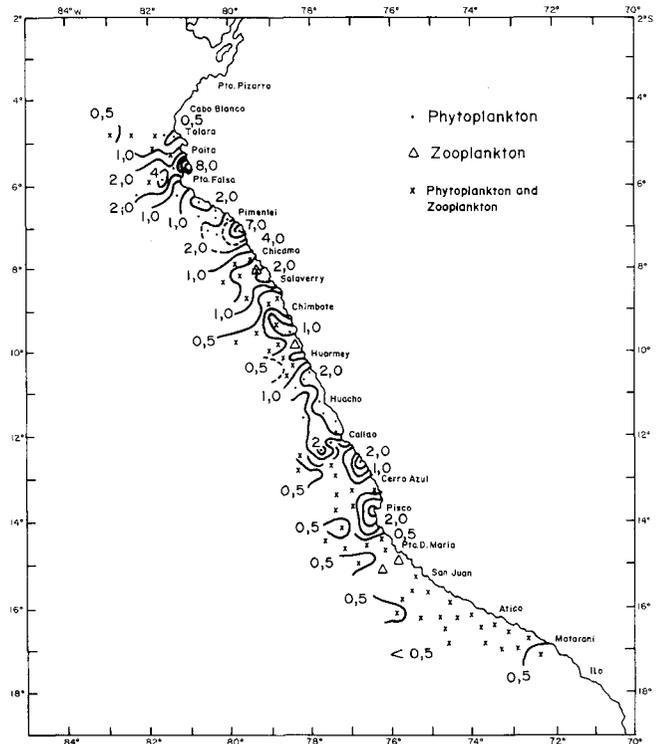
Figure 11.   Map of plankton volume for R/V *Humboldt* cruise 9709-10 (1 September–11 October 1997). Adapted from Delgado and Villanueva 1998a.

Figure 10.   Maps of plankton volume (ml/m³): *a*, R/V *SNP-I* cruise 9702-03 (13 February–13 March 1997) and R/V *Humboldt* 9704 (4–23 April 1997) and *b*, R/V *Humboldt* cruise 9706-07 (16 June–17 July 1997). Adapted from Chang et al. 1997; Sánchez et al. 1997.

phenomenon is related to the cooling process. The greatest concentrations were found at 5°, 8°, and 18°S inside 30 nmi (Sanchez et al. 1997). Species considered as indicators of equatorial water masses were *Ceratium breve* and *Ornithocercus steinii* and, within the zooplankton, *Centropages furcatus* and *Sagitta regularis*.

In June and July 1997 (9706-07), near the first peak of the warm event, there were very small volumes of plankton all along the coast (fig. 10b). Around the end of winter 1997 (9709-10), the peak decayed, and phytoplankton volumes increased, with values fluctuating

between <0.5 and 8.0 ml/m³ (average of 3.5 ml/m³) associated with a temperature range of 17.7°–24.7°C and salinities lower than 35.2 ppt (fig. 11). According to Delgado and Villanueva (1998a), diatoms characteristic of coastal upwelling were present within 30 nmi. Warm-water species were found between Pta. Falsa and Paita, in addition to species of zooplankton indicating warm waters. The common zooplankton species were *Acartia danae*, *A. negligens*, and *Calocalanus pavo* between 5° and 17°S and *Rhincalanus nasutus* and *Centropages furcatus* between Paita and Chicama and from Chimbote to Pisco. Also, chaetognaths such as *Sagitta enflata*, *S. regularis*, and *S. pacifica* remained in mixed waters during the temporal decline of the warm event (Girón 1998).

Thereafter, in the spring season (9711-12), between Pto. Pizarro and Callao, the volume declined markedly (reaching a value of 0.44 ml/m³). In the southern region between San Juan and Atico two small nuclei appeared, with values greater than 1 ml/m³, related to temperatures that fluctuated between 21.0° and 28.0°C, with salinities of 35.0 to 35.4 ppt. The volumes of plankton during summer (February–March 1998) varied between 0.12 and 5.9 ml/m³, with maximum values north of Pta. Falsa and Pto. Pizarro in the coastal region (fig. 12a).

At the end of summer and beginning of autumn 1998 (9803-05), in the decline of the second peak of thermal anomalies, the average volumes of phytoplankton
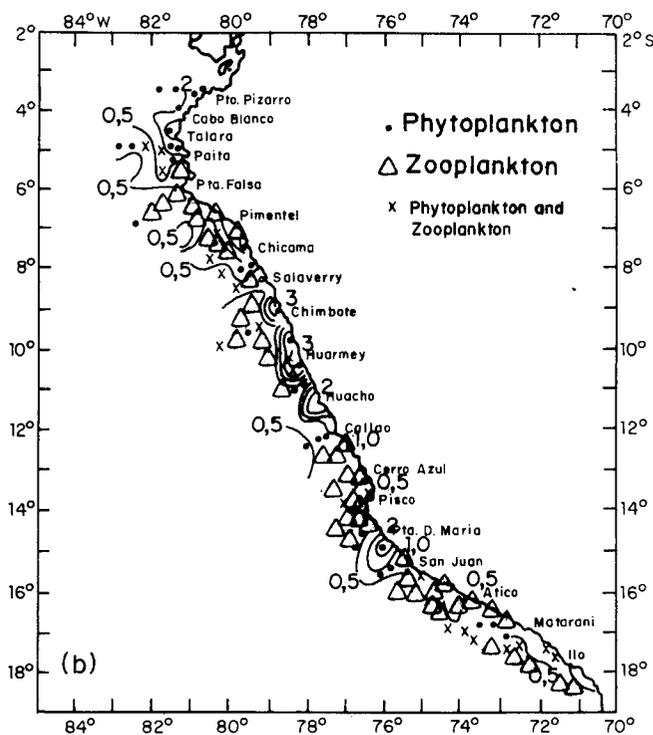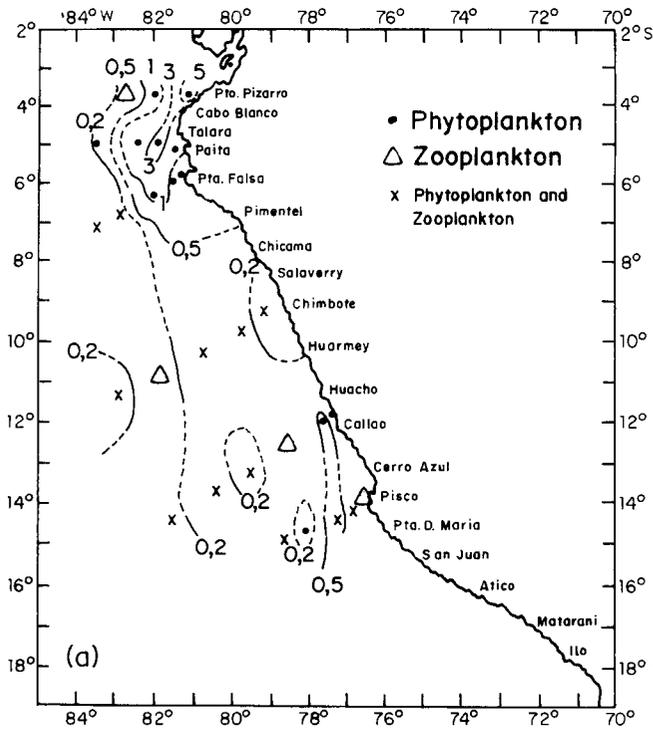
Figure 12. Maps of plankton volume: *a*, BAP *Carrasco* cruise 9802-03 (18 February–12 March 1998); *b*, R/V *Humboldt* 9803-05 (20 March–7 May 1998). Adapted from Delgado and Fernandez 1998; Delgado and Villanueva 1998b.

were still low (0.5–3.0 ml/m^3, means 0.64 ml/m^3 overall, and 2.6 ml/m^3 within 30 nmi; fig. 12b). The greater values belong to isolated coastal patches (>1 ml/m^3) between Mancora-Paita, Chimbote, Huarmey, and Pta. Doña María, with species typical of upwelling, indicating a recovery of the environment (Delgado and Villanueva 1998b).

During the beginning of winter (9808-09), the planktonic community recovered, with volumes that varied between 0.01 and 23.3 ml/m^3 (mean 1.16 ml/m^3). This increase in plankton volumes indicated that the normal conditions had intensified along the Peruvian coastline, with temperatures fluctuating between 15° and 17°C and salinities of 35.1 ppt, except for the area in front of Pta. Falsa (17°–18°C and 35.4 ppt).

In winter, during the start of the post–El Niño period, neritic species such as the diatoms *Coscinodiscus perforatus, C. wailesii, C. centralis, Chaetoceros* spp., *Lithodesmium undulatum, Thalassiosira subtilis,* and *Skeletonema costatum* were present. Thermophyllic dinoflagellates were found at distances greater than 30 nmi (Villanueva et al. 1998).

It is very unfortunate that during the 1997–98 event no information on chlorophyll and primary productivity was collected to permit evaluation of the mechanisms of interaction between nutrients and primary production, and to compare with the data reported by Barber and Chavez (1986). Nor were plankters smaller than 75 μm sampled. However, the larger plankton reflected the sequence of ecological effects produced during the different phases of El Niño 1997–98.

Fish Eggs and Larvae

Ichthyoplankton plays an important role in the marine community life cycle and indicates the reducing or broadening of the distributions and concentrations of some species.

Engraulis ringens, **anchovy.** In normal conditions, this species spawns in summer (February–March) along the entire coast from Paita to Ilo, with a second important spawning in August–September. The spawning relates closely to environmental conditions, and normally takes place within 60 nmi of shore, the principal spawning area being from Pimentel (6°50'S) to Chimbote (9°S).

In the summer of 1997, anchovy spawned all along the coast, widening the area to 80 nmi. The greatest intensity of spawning occurred between Chimbote and Pisco (fig. 13a). Larvae of this species were found in almost the same areas as the eggs (Ayón and Girón 1997). The greatest concentration of larvae was offshore of Huacho (>1000 larvae/m^2; fig. 13b). Larvae were absent in the northern zone from Salaverry to Chimbote, where the ESW were close to the coast (Morón and Marquina 1997; Vásquez 1997). Eggs and larvae of anchovy were associated with temperatures <22°C and
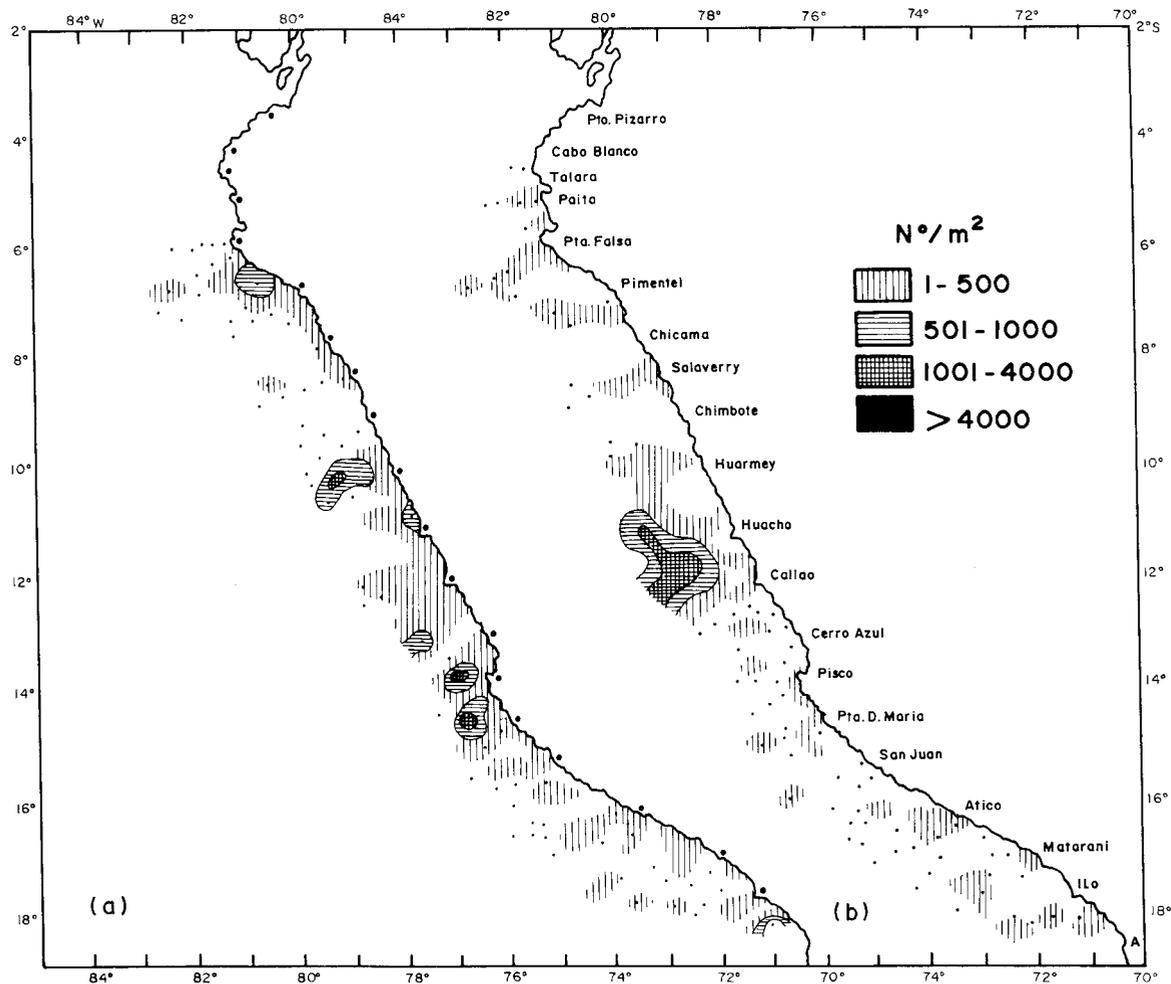
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Figure 13. Distribution of anchovy eggs (a) and larvae (b), R/V *SNP-1* cruise 9702-03 (13 February–13 March 1997) and R/V *Humboldt* 9704 (4–23 April 1997). Adapted from Ayón and Giron 1997.

salinities between 34.9 and 35.0 ppt, which differs from the ranges described by Ayón and Girón (1997).

At the end of winter and beginning of spring 1997 (9709-10), in a period of momentary cooling of waters, we found eggs of anchovy all along the coast, up to 30 nmi offshore, with rare patches of high concentration. The larvae had a wider distribution, reaching 70 nmi (5°–17°S), with abundances <4000 larvae/m²; larger patches had been found in 1996. A patch (<4000 larvae/m²) was located near Supe at 10 nmi from the coast, and there were minor patches of fewer than 1000 larvae/m² at Callao and Pimentel at 30 and 20 nmi, respectively. The distributions of anchovy eggs and larvae were clearly related to the distribution of adult anchovy, which was near the coast, generally within 18 nmi (Girón 1998; Gutierrez et al. 1998).

In March–May 1998, at the end of summer and beginning of autumn, (9803-05), anchovy spawning was poor; however, there were two patches with concentrations of >1000 eggs/m² south of Huacho and Atico, and <500 eggs/m² distributed from Salaverry to south of Ilo,

generally within 10–20 nmi of the coast (fig. 14a). The larvae had a similar distribution between Pta. Falsa and the southern boundary.

Relatively few anchovy eggs were also found at the end of autumn 1998 (9805-06), between 3 and 2150 eggs/m² (fig. 14b), when the subtropical tongue (20°–22°C, 35.2–35.3 ppt) was close to the coast. Eggs were found most frequently between Huacho and Pisco; the maximum concentration was found at the southern extreme of the coast, due to the warm, high-salinity tongue which produced a shift to that area, where the environmental conditions had recovered. In general, when compared with the distribution during the previous warm event, this distribution was restricted to within 10 nmi, and in May and June extended to 35 nmi (Ayón and Quesquén 1998). Also, the start of anchovy spawning was delayed.

Sardinops sagax sagax, **sardine.** Normally the distribution center for eggs and larvae of this species is north of Huacho (11°S), generally with abundance <500 eggs/m² and related to SSW. In anomalous conditions,
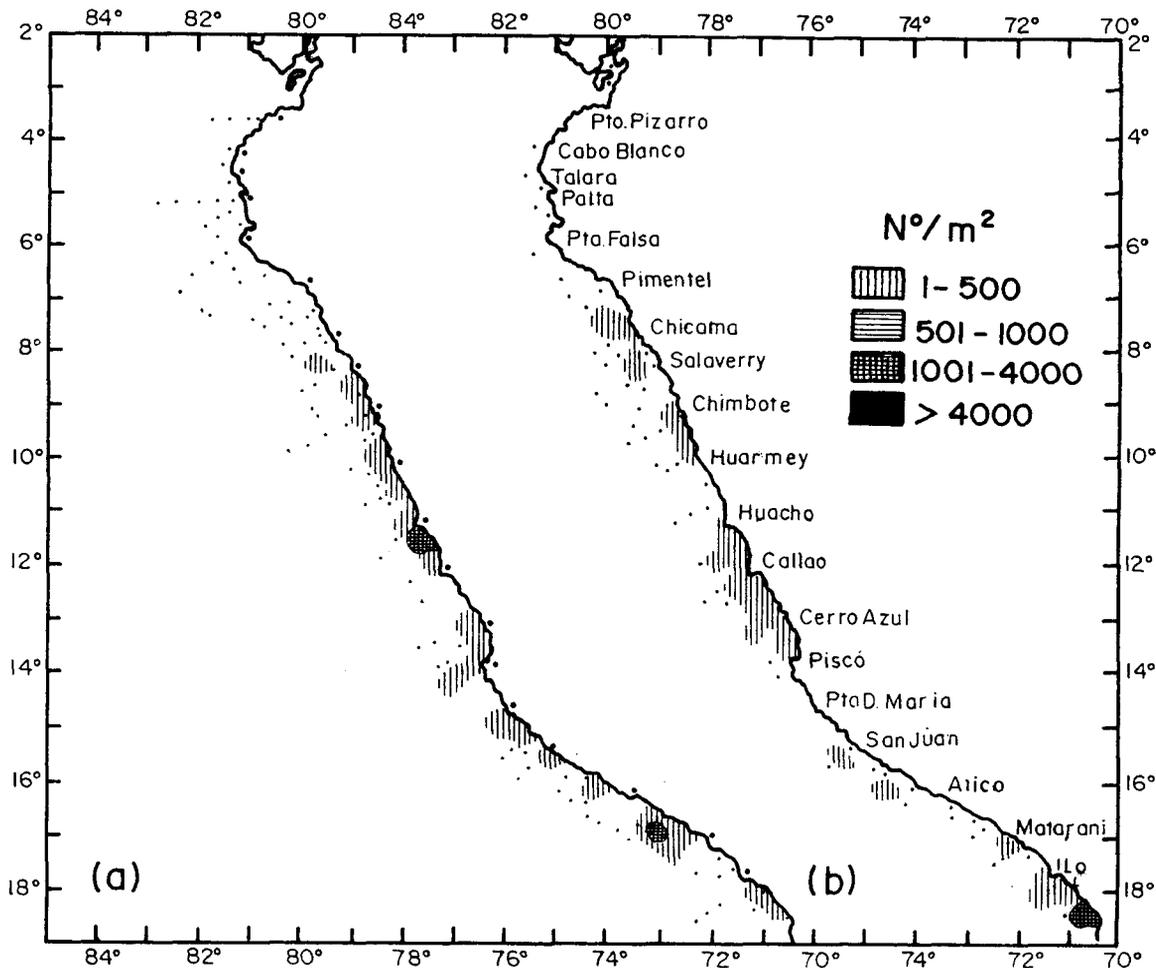
Figure 14. Distribution of anchovy eggs: a, R/V *Humboldt* cruise 9803-05 (20 March–7 May 1998); b, R/V *Humboldt* 9805-06 (20 May–25 June 1998). Adapted from Ayón et al. 1998; Ayón and Quesquén 1998.

at the end of summer and beginning of autumn 1997 (fig. 15), eggs were found within 40 nmi of the coast between Paita (5°S) and Callao (12°S). The larvae were found within 80 nmi between Paita (5°S) and Supe (11°S; Ayón and Girón 1997). In winter 1997 (9706-07), sardine eggs were distributed between Pto. Pizarro and Chimbote (Girón and Quesquén 1997).

In the following months of the warm event (9709-10) sardine larvae were more widely distributed than during 1996 and the first months of 1997, extending from Punta Aguja to Cerro Azul, associated with SSW. Eggs and larvae of sardine were very scarce: <500 eggs/ m^2 from Paita to Pisco and 500–1000 larvae/m^2 from Paita to Callao. From March to May of 1998 (9803-05) the eggs and larvae had concentrations <500/m^2 in SSW (salinities up to 35.6 ppt).

In the autumn of 1998 (9805-06) sardine eggs were distributed between Pimentel and Callao, with abundance reaching >5000 eggs/m^2. The larvae extended less far and had a smaller concentration (fig. 16; Ayón and Quesquén 1998).

During winter 1998 (9808-09), sardine larvae were located all along the coast, generally outside 30 nmi, extending to more than 100 nmi from the coast (Guzmán et al. 1998). Both eggs and larvae extended far from the coast between Pimentel and Callao, influenced by SSW. **Scomber japonicus, mackerel.** In September and October 1997, mackerel larvae were found along much of the coast from Paita to Punta Doña María (5°–14°40'S) and mainly within 40 nmi of shore. This differs from the distribution in 1996, when they were limited to the central zone and farther than 70 nmi from the coast. Later, around the end of May through June 1998, mackerel eggs were found at two stations near Chicama and Pisco (fig. 17a).

Merluccius gayi peruanus, hake. In autumn of 1997 (9705-06), at the beginning of the warm event, we found larvae of this species between Salaverry (8°S) and Callao in very low concentrations (1–4 larvae/m^2; Ayón and Aronés 1997), in general agreement with the distribution of adults in the same area. At the end of the warm event, autumn 1998 (9805-06), hake eggs were found
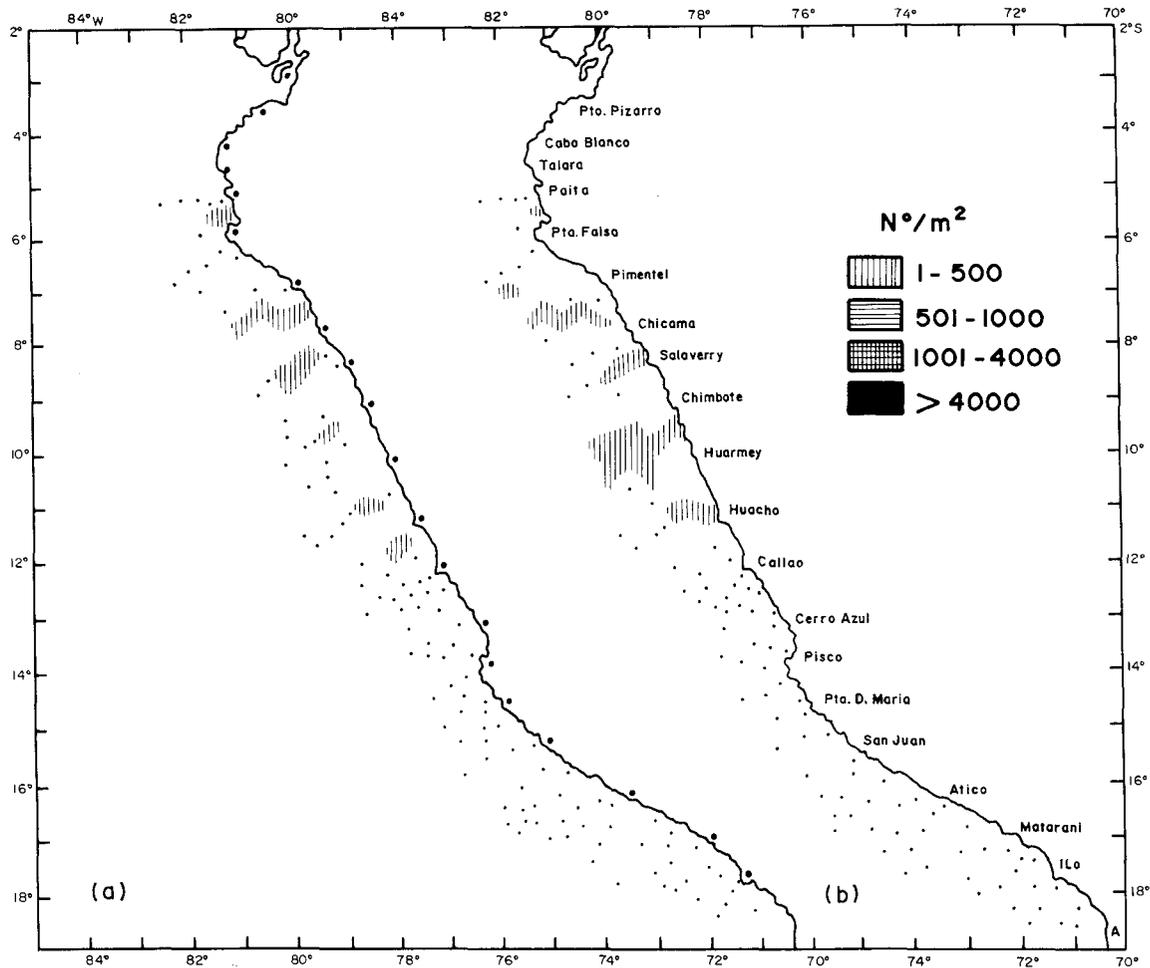
Figure 15. Abundance and distribution of sardine eggs (a) and larvae (b). R/V *SNP-I* 9702-03 (13 February–13 March 1997) and R/V *Humboldt* 9704 (4–23 April 1997). Adapted from Ayón and Giron 1997.

30 nmi from the coast at Chimbote, with abundance >3 eggs/m²; the larvae had a wider distribution, between Paita and Supe with abundances of 3–9 larvae/m² (fig. 17b; Ayón and Quesquén 1998).

Anchoa nasus, anchoa; samasa. In the winter of 1997 (September–October) eggs and larvae of this species, which normally is distributed to the north, were very abundant along the Peruvian coast at temperatures of 19°–22°C, occupying the space left by the anchovy (Gutierrez 1998). In the next year, from May to June 1998 (fig. 17c), the distribution broadened; larvae were present to the southern boundary of Peru, and north to Callao (Pimentel-Salaverry).

Mictophydae family, lanternfishes. The fishes of this family (*Diogenichthys laternatus, Lampanyctus parvicuda, Benthosema panamense,* and *Triphoturus nigrescens*) generally are distributed offshore of the Peruvian coast (>100 nmi). With the intrusion of warm waters, most of these species widened their distribution, and diversity reached 20 species at the beginning of autumn 1998 (Ayón and Quesquén 1998). These species were distributed all along

the Peruvian coast, except for *B. panamense*, which was found only to 7°40'S.

In winter 1998, the larvae of *Diogenichthys laternatus* were distributed widely all along the coast (fig. 18a), at 44% of the analyzed stations, and were more abundant than in autumn of that year (Ayón and Quesquén 1998; Guzmán et al. 1998).

Bregmaceros bathymaster, unicorn cod. Other species with wider distributions of eggs and larvae included this endemic species of the Panamanian province of ATS, which widened its distribution because of warm waters. It appeared during May and June of 1997 (Ayón and Aronés 1997) and increased to 43% of sampled stations in March and May of 1998, with a remarkable presence north to Callao and extending to the south (Atico and Matarani) when the TSW were found north of 7°S (Ayón et al. 1998). On the other hand, its frequency decreased in June 1997 (fig. 18b), decaying strongly in winter 1998 (9808-09), when it was found at only 6.8% of the total stations (Guzmán et al. 1998), related to high-salinity waters (up to 35.6 ppt).
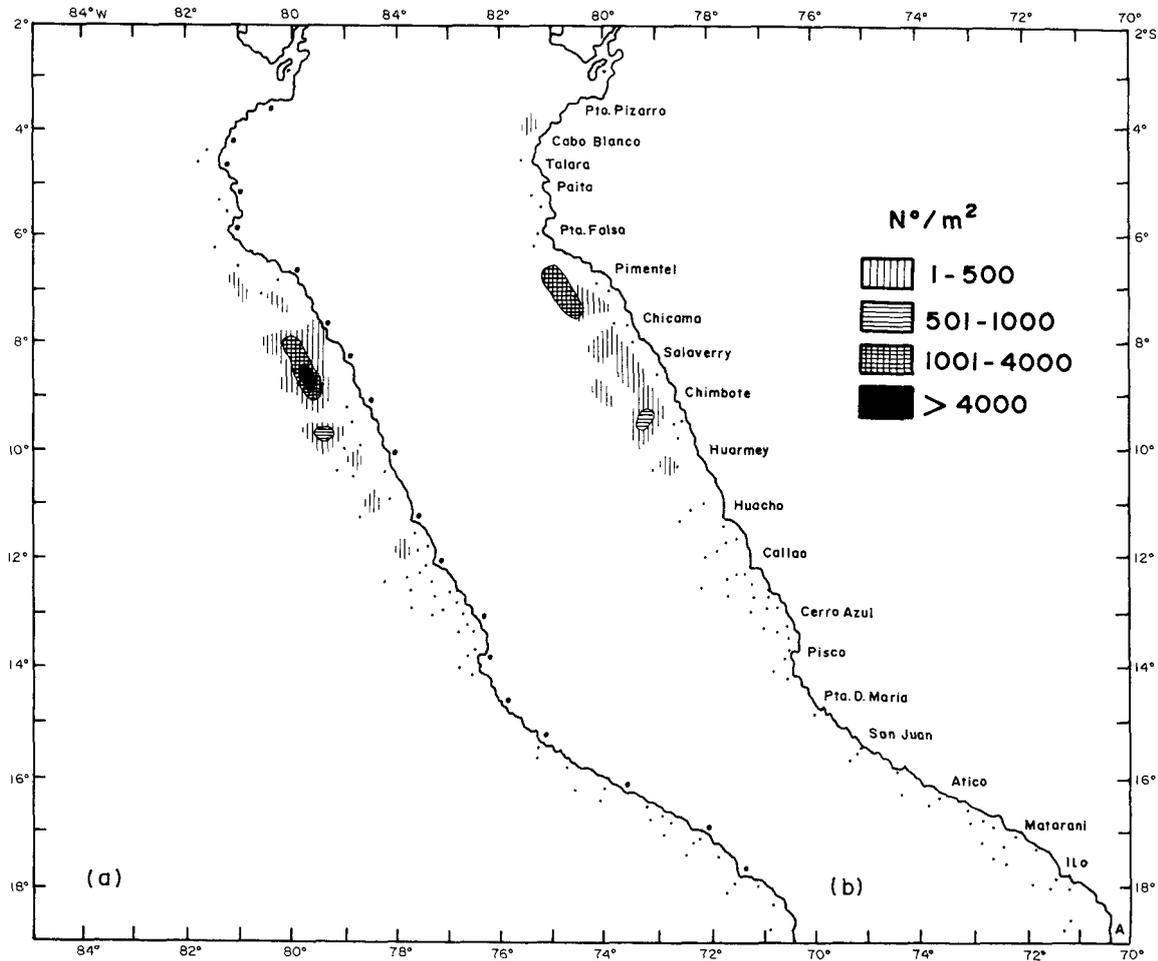
Figure 16. Abundance and distribution of sardine eggs (a) and larvae (b). R/V *Humboldt* cruise 9805-06 (20 May–25 June 1998). Adapted from Ayón and Quesquén 1998.

***Prionotus stephanophrys*, gurnads.** Normally the larvae of this species are not found on the Peruvian coast (8°S), but in summer 1997 they were found between Paita and Callao, out to 80 nmi. They were more frequent in autumn of the same year (in 56% of samples; fig. 18c; Ayón and Aronés 1997), and began to decrease in September (9.4% of samples), reaching less than 1% of the total samples in the autumn of 1998.

Pelagic and Demersal Resources

***Engraulis ringens*, anchovy.** From 1991 to 1994 (which included an El Niño event) biomasses of anchovy increased. During the cold years of 1995 and 1996 anchovy decreased, but after the negative anomalies, again started a recovery that was interrupted by the warm El Niño 1997–98 (fig. 19).

At the beginning of the warm event and during February and April 1997 (9702-03, 9704) anchovy were found near the coast between Paita and Callao in very dense concentrations, especially between 7°–8°S and 9°–12°S (fig. 20a). The strong intrusion of ESW in the

north and SSW in the south considerably reduced the distribution of the resource, with a biomass (estimated by virtual population analysis) of 9.5 million metric tons (t; ERFEN 1998).

As of July 1997, positive temperature anomalies increased, mainly along the Peruvian north coast, but the distribution of anchovy was unchanged. During September and October 1997 (9709-10), anchovy remained very close to the coast from south of 5° to 17°S (fig. 20b) due to the width of the SSW. These data were obtained after the first spawning peak; apparently there was little negative effect on the adult population and very little effect on the juveniles. The biomass was 5.8 million t (Gutierrez et al. 1998).

From November 1997, when the anomalies in the north exceeded 6°C, the schools of anchovy were displaced to the central zone, especially in December, when the anomalies at Salaverry exceeded 7.9°. Large concentrations of schools were found between Cerro Azul (13°S) and the coastal band (10 nmi) to the south of Atico and Ilo (18°S). Only in Ilo did the
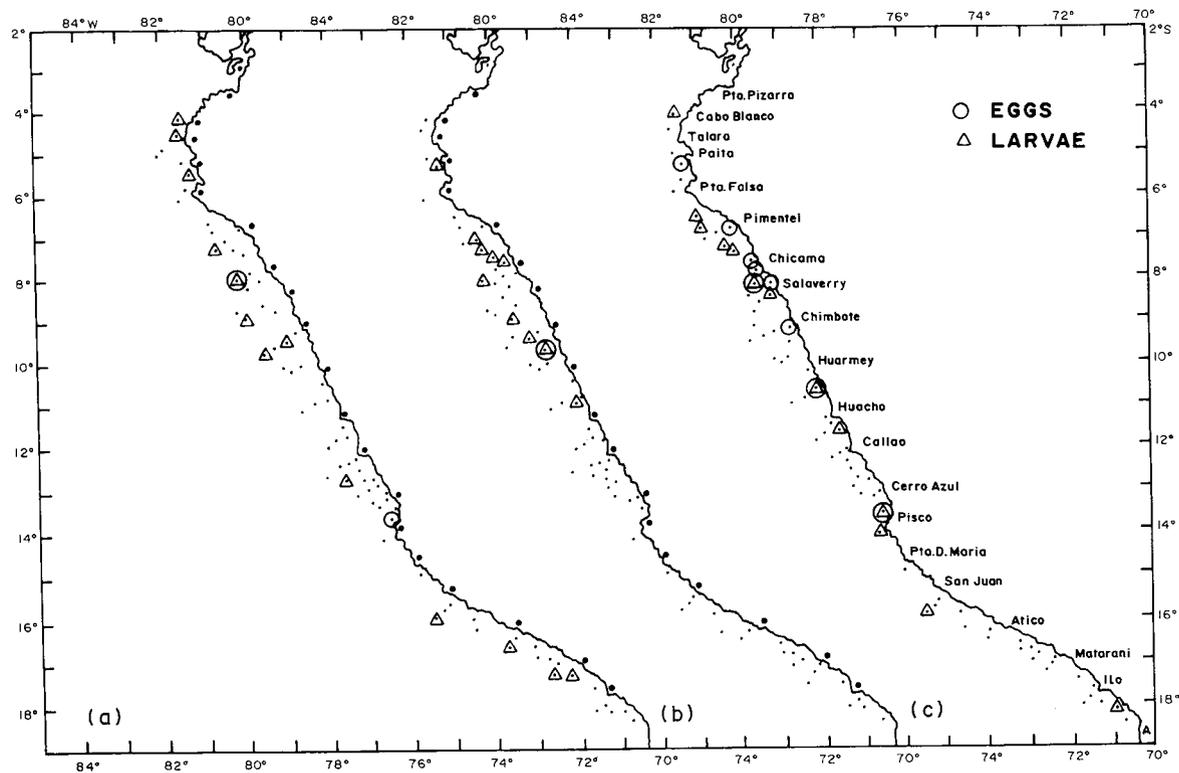
Figure 17.   Distribution of eggs and larvae of mackerel (*a*), hake (*b*), and anchoa (*c*). R/V *J. Olaya* cruise 9805-06 (20 May–25 June 1998). Adapted from Ayón and Quesquén 1998.
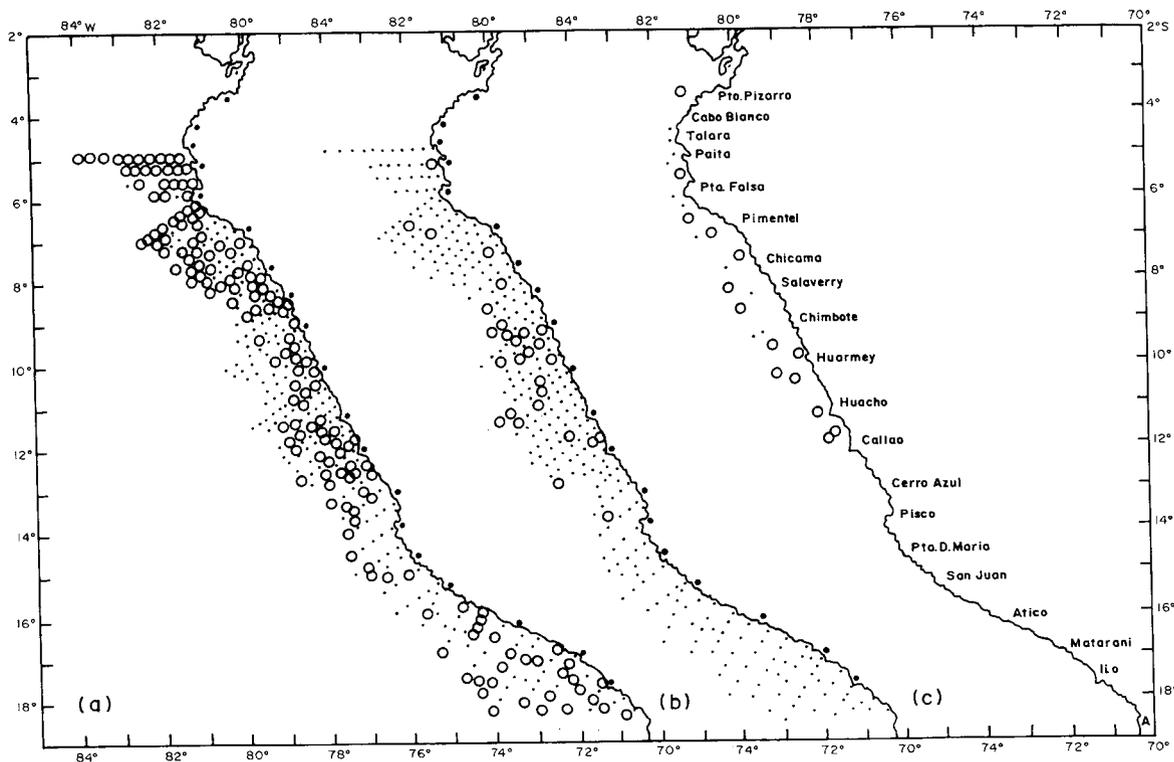

Figure 18.   Distribution of larvae: *a, Diogenichthys laternatus,* and *b, Bregmaceros bathymaster.* Cruise R/V *J. Olaya,* R/V *Humboldt* 9808-09 (18 August–17 September 1998). *c, Prionotus stephanophry,* R/V *Humboldt* cruise 9705-06 (15 May–8 June 1997). Adapted from Ayón and Arones 1997; Guzmán et al. 1998.
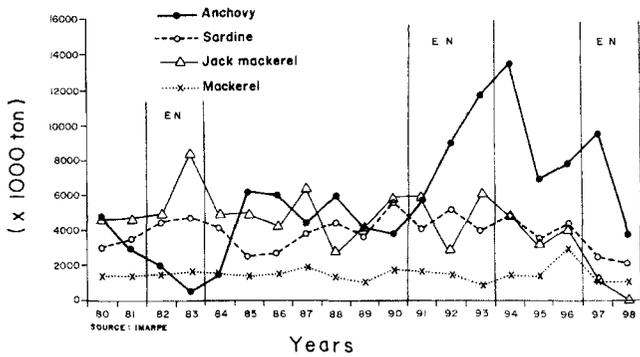
Figure 19. Biomass of the main pelagic resources, 1980–98.

distribution of anchovy reach 30 nmi (Gutierrez et al. 1998).

The pelagic resources evaluation made between March and May of 1998 (9803-05) found anchovy in coastal areas with a discontinuous distribution, including 14°S and 18°S (fig. 20c). The distribution depth ranged from 4 to 100 m, but was generally near the surface, especially at night.

From May to June 1998 (9805-06) anchovy were detected near the coast, distributed in isolated areas south of Salaverry, with the greatest concentrations between Pisco and Chorrillos. In the north, anchovy were found from the surface to 58 m depth. In the second half of 1998 (9808-09), anchovy were located between Huarmey-Huacho and Callao-San Juan in dispersed concentrations, between 3 and 20 m in depth, at a biomass of 1.2 million t (Castillo et al. 1998; fig. 19).

The reproductive cycle of the anchovy during the first months of 1997 was normal in relation to the summer spawning, with high values in the gonodosomatic index (GI). The main (but less than normal) spawning of winter and spring took place at the same time as the relaxation, which produced a change in time relative to normal. From January 1998, the GI of anchovy increased. Values higher than the historic standard of spawning were observed all along the coast (fig. 21). The spawning peaked in September, a post–El Niño period. These variations in the reproductive process reduced the population of anchovy (Mori et al. 1999).

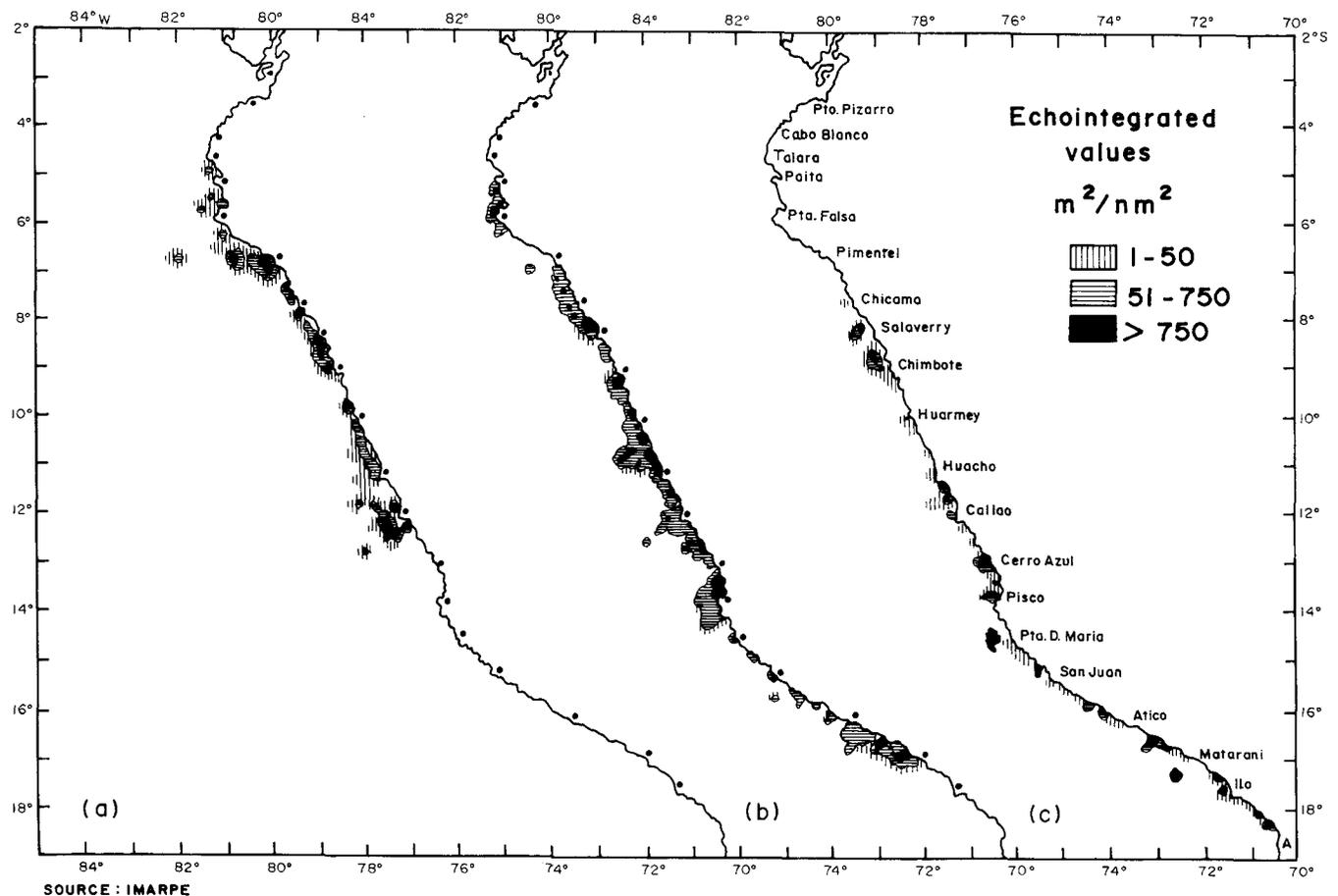*Sardinops sagax sagax,* **sardine.** In March and April

Figure 20. Distribution of anchovy, *Engraulis ringens*: *a*, R/V *Humboldt* cruise 9704 (4–23 April 1997); *b*, R/V *Humboldt* 9709-10 (1 September–11 October 1997); *c*, R/V *Humboldt* 9803-05 (20 March–7 May 1998).
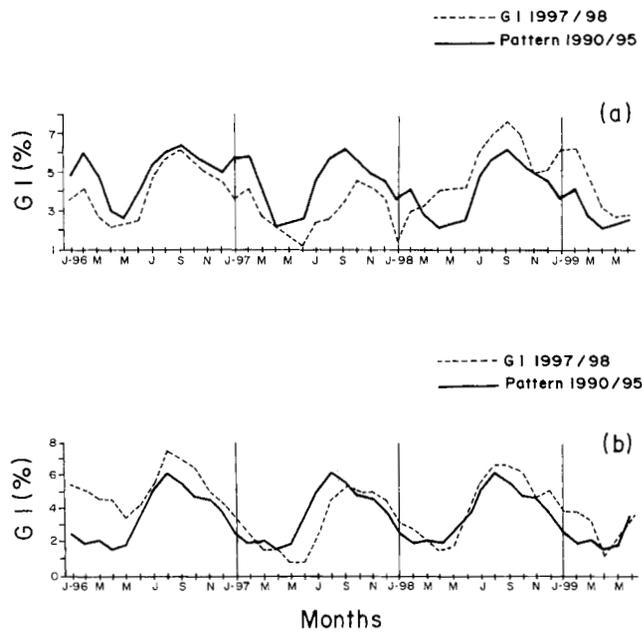
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Figure 21. Gonadosomatic index (GI) of anchovy: a, north and central Peruvian region (3°24'–15°59'S); b, south Peruvian region (16°–18°21'S). Adapted from Mori et al. 1999.

1997, sardine were distributed between Pimentel and Huacho; the greatest concentrations were north of 10°S, associated with ESW, which were close to the coast off Salaverry (fig. 22a). The estimated biomass was 2.5 million t (fig. 19). Vertically, sardine reached 60 m depth. This species was very scarce in September and October 1997 (9709-10), but was detected between 6° and 12°S at 5–100 m depth, associated with the SSW, <35.2 ppt (fig. 22b). Biomass at this time was 1.1 million t (Niquén et al. 1998).

In March to May 1998 (9803-05), sardine were detected near the coast, with a discontinuous distribution between Salaverry and Matarani (17°40'S) in subtropical waters very close to the coast (35.7 ppt) and off Chimbote-Salaverry at depths from 4 to 60 m (fig. 22c). Biomass was 2.1 million t (Castillo et al. 1998). Sardine remained present along the coast from May to June 1998 between Cerro Azul and Callao; the lowest concentration was found between Salaverry-Chimbote and the Pimentel area, associated with the high-salinity waters >35.2 ppt moving away from the coast (>21°C).

In the next assessment of the sardine resource (9805-06), with the normalization of oceanographic condi-
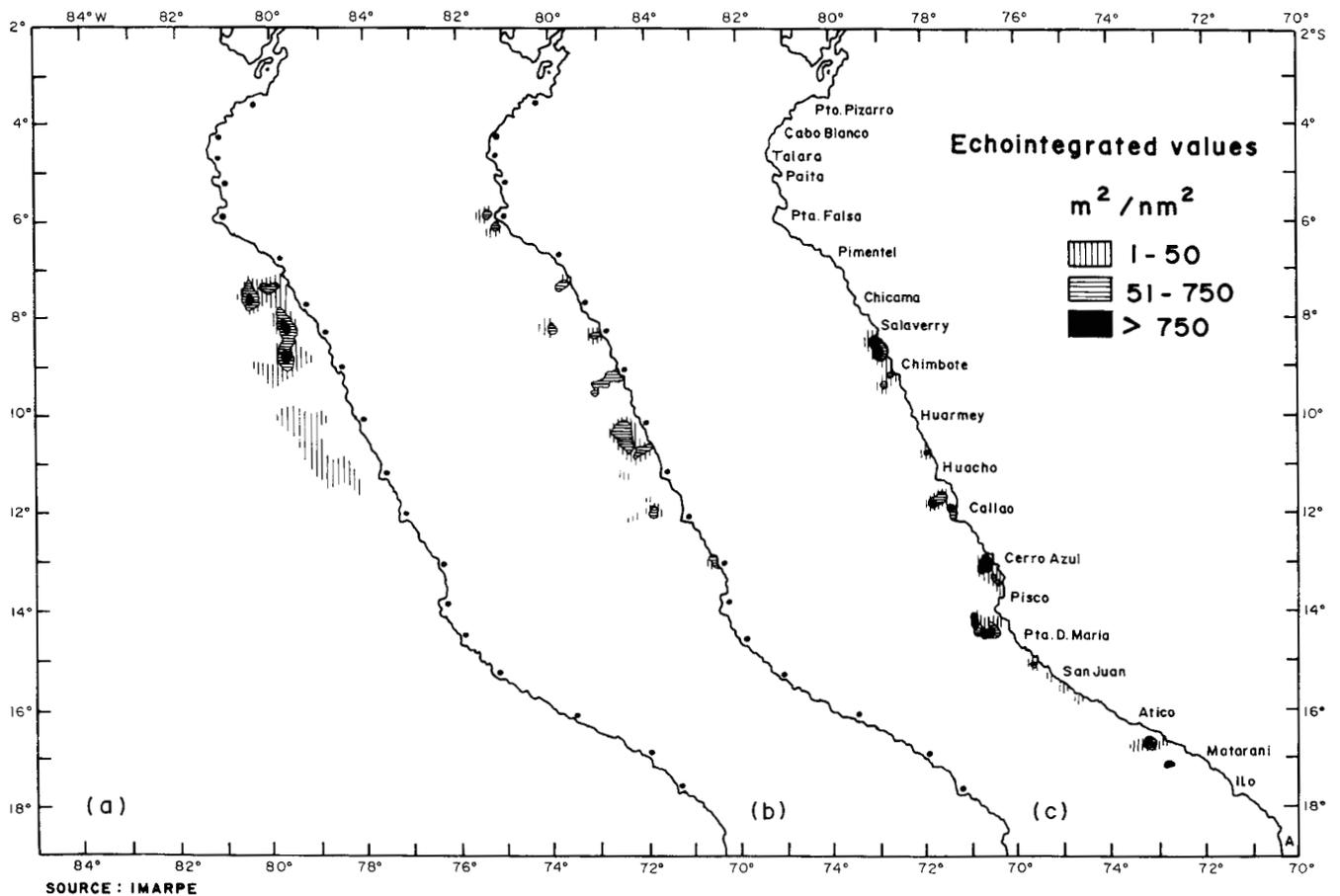

Figure 22. Distribution of sardine, Sardinops sagax sagax: a, R/V Humboldt cruise 9704 (4–23 April 1997); b, R/V Humboldt 9709-10 (1 September–11 October 1997); c, R/V Humboldt 9803-05 (20 March–7 May 1998).
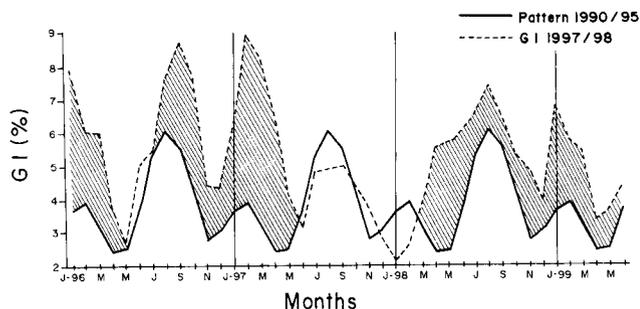
Figure 23. Gonadosomatic index (GI) of sardine 1995–99. Adapted from Mori et al. 1999.

tions, the biomass was very similar to that of autumm 1998, but with a retreat to the north (13°S).

Summer spawning in 1997 was more successful than normal, and the process was quite prolonged. In autumn, the gonads had immature and maturing stages. During winter 1997, a high percentage of sardine captured on the central coast were spawning or partially spawned. This species continued spawning in winter 1998 (cold, post–El Niño conditions), as shown by high gonadosomatic indexes (fig. 23).

Trachurus picturatus murphyi, southern jack mackerel. In September–October 1997 (9709-10) jack mackerel were distributed between Salaverry and Callao, at temperatures <23° (fig. 24a), with the greater concentrations in the central zone between Huarmey and Callao. Dispersed concentrations were found between Pisco and San Juan, with colder waters (around 19°C). In the north and especially near Paita, jack mackerel were found jointly with hake in depths of 150 to 250 m, associated with the waters of SECC, which started moving southward when El Niño began. The biomass was 1.2 million t in April, and 1.9 million t in October 1997 (Gutierrez 1997; Gutierrez et al. 1998).

During autumn 1998 (9803-05) jack mackerel showed a disjunct distribution north of 7°S (17°–21°C and 34.8–35.0 ppt) near the coast (associated with ESW), and also in the south between San Juan and Ilo (SSW; 20°C, 35.2 ppt), and the biomass was smaller (Castillo
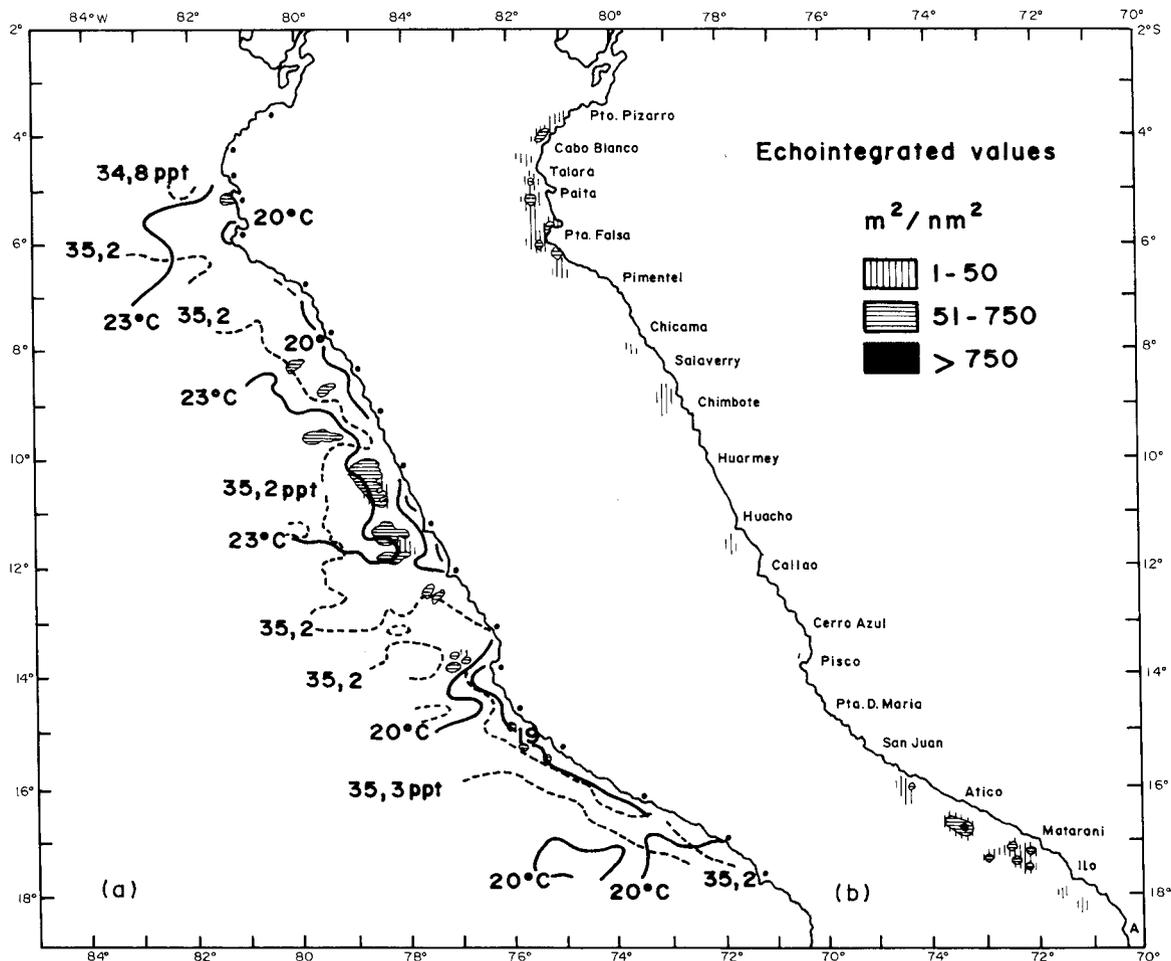

Figure 24. Distribution of jack mackerel, Trachurus picturatus murphyi: a, R/V Humboldt cruise 9709-10 (1 September–11 October 1997); b, R/V Humboldt 9803-05 (27 March–1 May 1998). Adapted from Gutierrez et al. 1998.

Figure 25.   Distribution of chub mackerel, *Scomber japonicus: a,* R/V *Humboldt* cruise 9709-10 (1 September–11 October 1997); *b,* R/V *Humboldt* 9803-05 (27 March–1 May 1998). Adapted from Gutierrez et al. 1998.
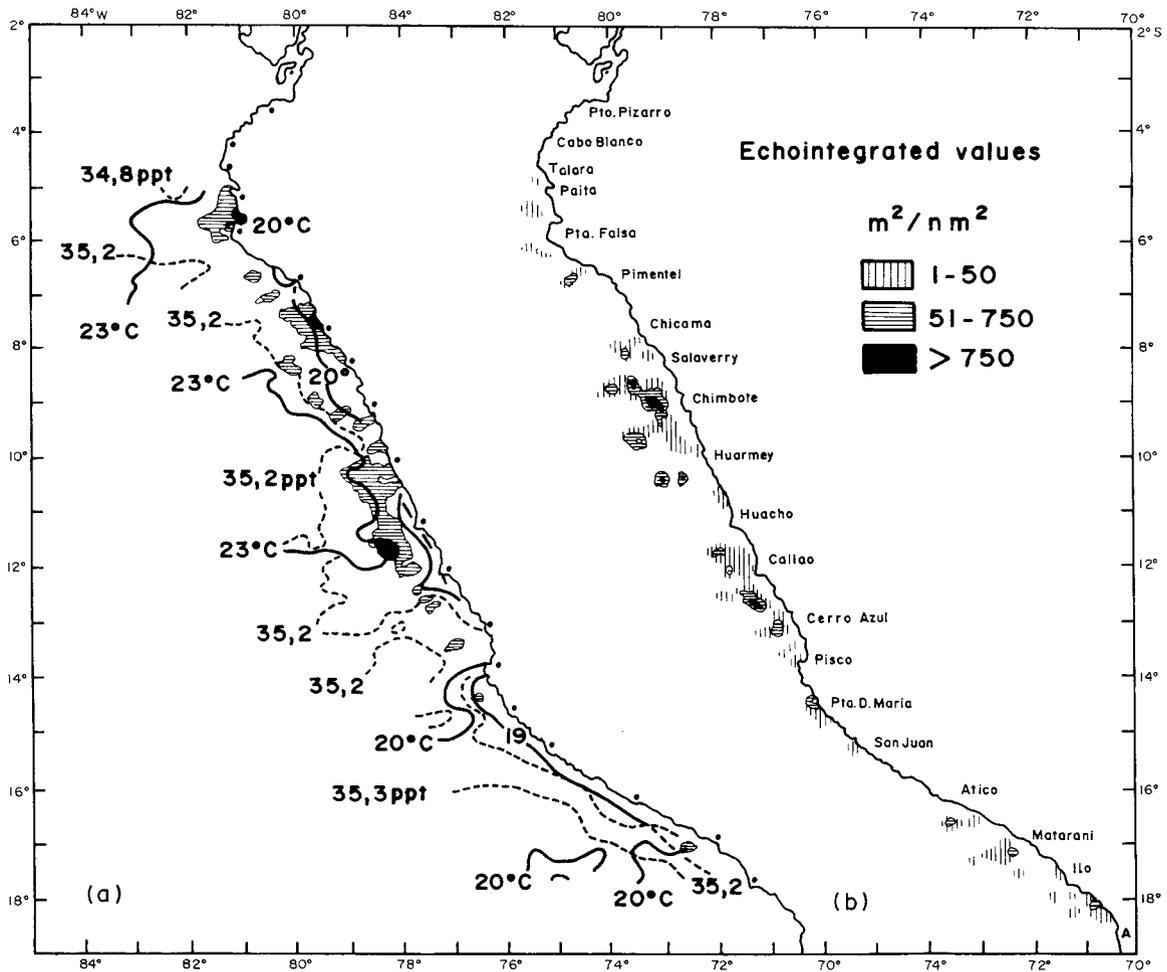
et al. 1998). This distribution of jack mackerel remained equally poor in winter (fig. 24b).

Scomber japonicus, chub mackerel.   The response of chub mackerel to El Niño was similar to that of sardine and jack mackerel, shifting to the south (Ñiquén et al. 1998). The biomass of this species varied from 1.1 to 2.5 million t from April to October 1997 (9704, 9709-10), corresponding to the beginning and development of El Niño.

In September–October (9709-10) the chub mackerel was distributed from Paita to Pucusana (12°28'S), but with greater indices of abundance on the central coast of Peru, associated with SSW (fig. 25a). Vertically, this species was found between 5 and 110 m. Between summer and autumn 1998 (9803-05), as ESW retreated, the chub mackerel was found all along the Peruvian coast, but very scarcely (fig. 25b); its distribution was mainly between Pacasmayo (7°24'S) and Cerro Azul (13°S), with the greatest concentration between Salaverry and Chimbote in SSW.

Merluccius gayi peruanus, **hake.**   Hake extended their range to 12°S, which allowed the blackfin gurnad to move northward with good results, especially between Cabo Blanco and Paita.

In summer 1997, hake were strongly concentrated north of 6°S, due to a strong retraction of the SECC, which significantly reduced the distribution area of this species (Espino 1999), as in the cold year of 1995. During the first peak of El Niño (9705-06) this demersal species widened its area of distribution, together with the displacement of the SECC to the south, and even had a pelagic behavior extending to Callao (fig. 26a) during May and June 1997 (Castillo et al. 1997).

During May–June 1997 the main areas of higher concentration were in Callao-Huarmey, Salaverry-Chimbote, Paita-Pimentel, and north of 4°S, mainly along the border of the shelf, where the axis of the SECC, with temperatures of 13°–20°C and 34.9–35.0 ppt of salinity, was apparently located (Vásquez 1997).

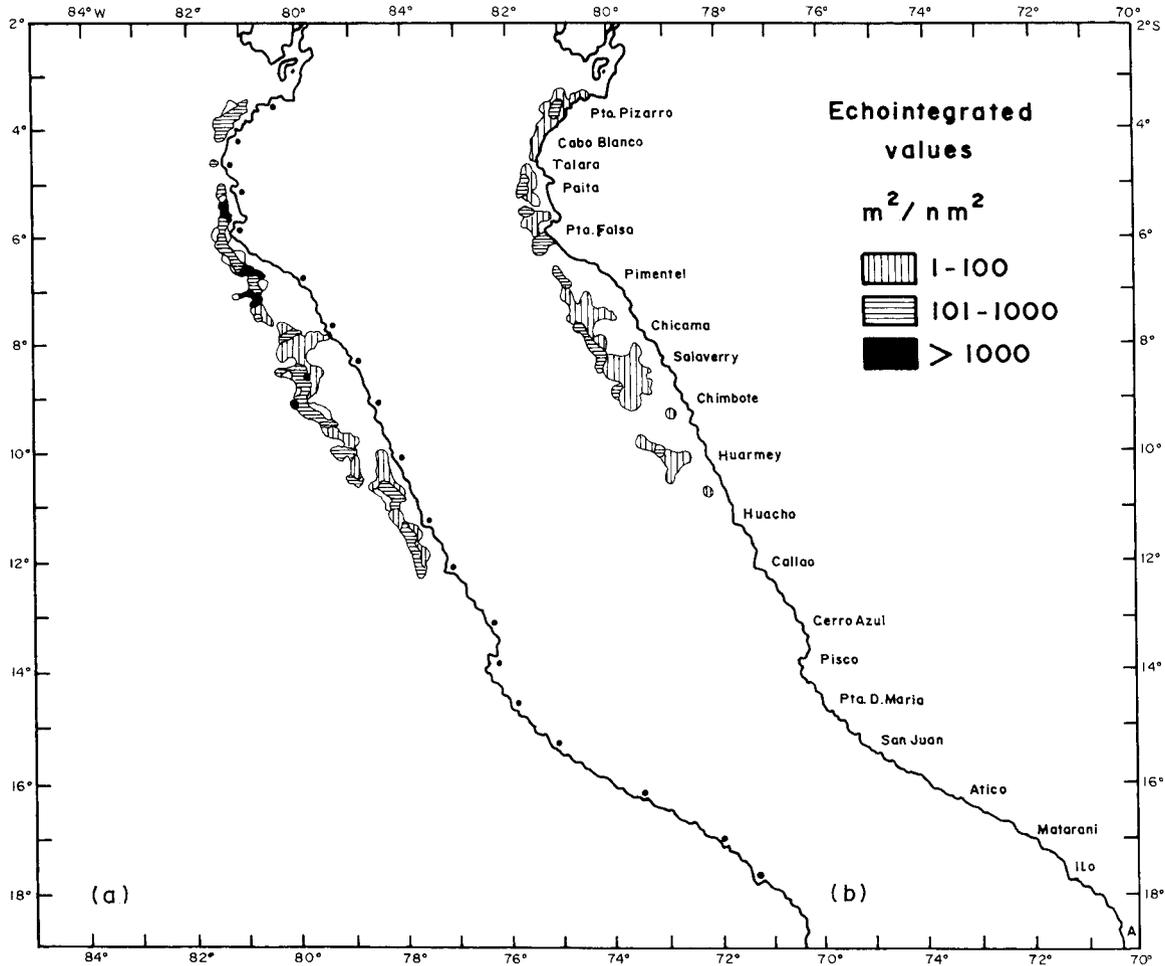After January 1998, this species started to repopulate

Figure 26. Distribution of hake, *Merluccius gayi peruanus:* a, R/V *Humboldt* cruise 9705-06 (15 May–8 June 1997); b, R/V *J. Olaya* cruise 9806-07 (27 June–13 July 1998). Adapted from Castillo et al. 1997; Samamé and Fernandez (1998).

its usual areas of distribution, and in June there was more density between 6° and 8°S (fig. 26b) and between 100 and 200 fathoms, while south from 9°S, trawls were poor or negative (Samamé and Fernandez 1998).

Other Fish

Anchoa nasus, **samasa.** During El Niño this species was abundant in winter 1997, with a biomass of 1.5 million t (Gutierrez et al. 1998), sharing its vertical distribution with the anchovy between 3 and 50 m and in mixed coastal and subtropical waters (fig. 27a). In the first half of 1998 (fig. 27b) it was found near the coast from Máncora to the south of Ilo (Castillo et al. 1998), with a greater presence between Pimentel and Pisco and denser concentrations off Salaverry; it was also observed on cruise 9803-05, when its greatest concentration was in the northern region (7°–9°S), with a calculated biomass of 2.09 million t (Gutierrez 1998).

From June to September 1998 there was a greater availability of samasa, but only in the north zone of the

Peruvian coast, as the resource retreated to its natural habitat associated with the ESW.

***Myctophidae*, lanternfishes, and others** Diversity of this group of oceanic fishes was remarkable during El Niño 1997–98, and included many fishes typical of the Panamanian province. The most conspicuous was *Diogenichthys laternatus*, which was found along the Peruvian coast from the beginning of the sea warming, and which, together with other species, became more frequent as the thermal anomalies intensified.

***Bregmaceros bathymaster*, unicorn cod.** This species is normally restricted to the Gulf of Panama. During El Niño 1982–83 it was recorded with the incursion of TSW along the Peruvian coast, constituting an important diet item for pelagic resources such as chub mackerel and jack mackerel and for demersals such as hake (Sánchez et al. 1985). According to the ERFEN report (1998) this species was present since autumm 1998, together with other pelagic resources of the SSW, including bullet tuna, *Auxis rochei*; yellowfin tuna, *Thunnus albacares*;
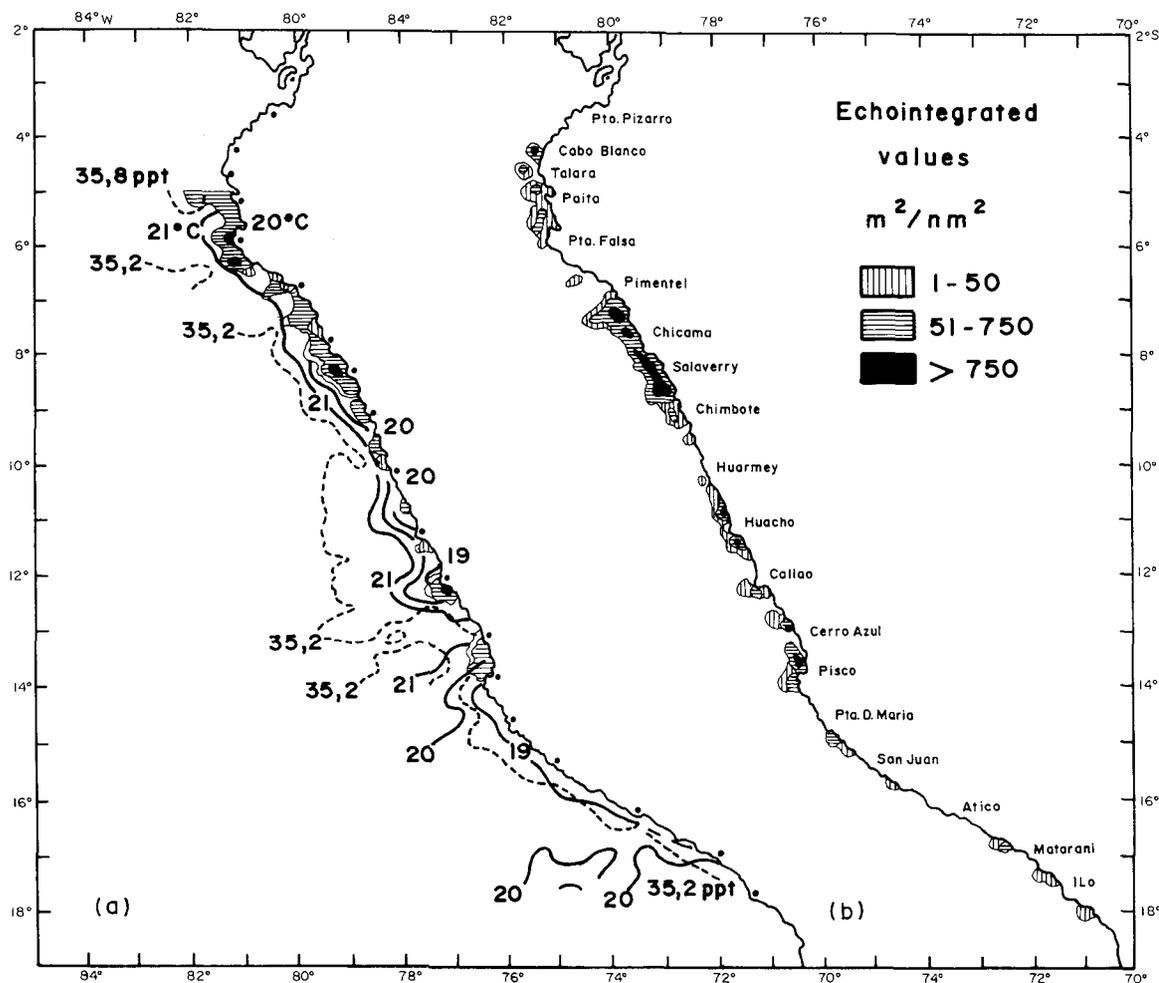
Figure 27. Distribution of the samasa, *Anchoa nasus: a*, R/V *Humboldt* cruise 9709-10 (1 September–11 October 1997); *b*, R/V *J. Olaya* cruise 9803-05 (20 March–7 May 1998). Adapted from Castillo et al. 1998; Gutierrez et al. 1998.

mahi mahi, *Coryphaena hippurus*; blue shark, *Prionace glauca*; sierra, *Scomberomorus maculatus*; and cutlassfish, *Trachiurus nitens*. During El Niño these species were constantly present in the northern and central regions.

Marine Mammals

During ENSO, cetaceans (whales and dolphins) migrated southward in search of cold waters and food to fulfill their energetic needs (Arntz and Fahrbach 1996; Bello et al. 1998). In October 1997 *Tursiops truncatus, Delphinus capensis, Lagenorhynchus obscurus, Globicephala* sp., *Megaptera novaeangliae, Balaenaptera* sp., and *Delphinus delphis* were reported.

Between March and May 1998, dolphins like *Tursiops truncatus* and the common dolphin, *Delphinus delphis*, were seen frequently along the Peruvian coastline. The tropical dolphin *Stenella* sp. was also observed. The higher concentrations of minor cetaceans were found near Salaverry, between Huacho and Callao and between Mollendo and Ilo. Dolphins appeared at a wide range of temperatures, tending toward the south, in relation

to the distribution of anchovy and sardine (Sánchez et al. 1998).

Seabirds

As has been reported for previous El Niño events, El Niño 1997–98 brought a reduced abundance and a redistribution of piscivorous bird species typical of the Peruvian marine ecosystem—mainly guanay, boobies, and pelicans—that were forced to modify their distribution according to the availability of anchovy.

Observations of marine birds carried out during cruises 9803-05 and 9808-09 showed differences in relative abundance. In the first cruise the camanay, *Sula nebouxii*; the pardelas, *Puffinus* spp.; and the albatross of Galápagos, *Diomedea irrorata*, were abundant. Also observed were tropical species such as *S. nebouxii* and *S. leucogoster*, which was recorded for the first time at 6°S, the most austral record of that species. The guano birds were more abundant during the second cruise (Jahnke et al. 1998), when oceanographic conditions were normalized.

LANDINGS OF THE MAIN FISH RESOURCES

El Niño decreased landings of the main pelagic species by 74%, mainly because of a reduced anchovy catch (ERFEN 1998; fig. 28).

In summer 1998, the anchovy in the central and southern regions were mainly adults. In winter 1998, the main modal size of anchovy was 5.5 to 6 cm total length, with a secondary mode of recruits between 8 and 8.5 cm. The smallest specimens, aged 4 to 6 months, came from spawnings in autumn of 1998. The estimates of recruits for 1998 were very positive, in that they reached a high percentage of the total biomass; thus a quick recovery of the stock for the biological year 1998–99 is expected (Ñiquén et al. 1998).

Sardine catches increased slightly at the end of November 1997, with daily capacity of 20,000 t. The ports of Chicama and Chimbote were the most important. Nevertheless, in December a decrease was observed in association with thermal anomalies in the northern zone. The total length range of sardine at the end of the first peak of El Niño, in winter 1997, was from 2 to 30 cm, with modes at 4, 10, 12, and 27 cm (9709-10).

The sardine population at the end of El Niño 1997–98 (9808-09) comprised predominantly juveniles (3–23 cm total length, with a main mode at 6 cm and a secondary mode at 21 cm) of approximately 2 years of age, from the spawning period between winter and spring 1996 (Ñiquén et al. 1998).

Jack mackerel landings increased from January to October 1997, stabilizing in the last two months at over 50,000 t per month. At the end of winter 1997, jack mackerel had three groups of modes of prerecruit sizes between 6 and 14 cm and recruits smaller than 26 cm. The group of smaller sizes was found within 20 nmi of the coast. In summer 1998, jack mackerel (as expected) had a distribution of larger sizes on the north coast to 6°S, while to the south, the size structure had modes from 21 to 36 cm.

Mackerel landings were not impressive between January and July 1997. Nevertheless, between August and September they increased significantly, from 36,000 to 49,000 t. In relation to 1996, landings increased more than 300%. At the end of summer 1998 this species presented a structure of bimodal sizes from 12 to 33 cm long (to the tail fork; Chipollini et al. 1998). In autumn and winter its size structure encompassed juveniles and adults between 5 and 33 cm; the juvenile specimens were distributed nearer the coast than usual.

Hake landings from January to the first week of September 1998 were 62,000 t—less than in the same period of 1997 (108,000 t). In the second semester of 1998 the landings increased progressively, with a high percentage of juveniles. This increase was due to an increased number of trawling boats in the area of Paita and to the availability of the resource (fig. 29).
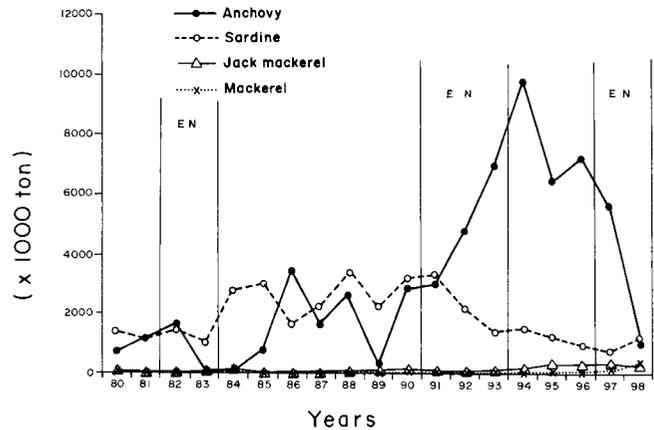

Figure 28. Landings of the main pelagic resources, 1980–98. Adapted from Bouchon and Ñiquén 1999.
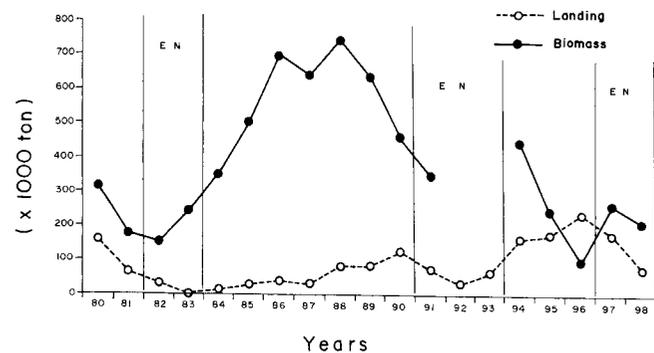

Figure 29. Landings and biomass of Peruvian hake, 1980–98.

At the beginning of 1998, in the second peak of El Niño, there was a recruitment mode at 25 cm, as recruits entered the fishery. In the second semester of 1998, with the reestablishment of normal environmental conditions, the mode increased (43 cm) in the zone of Paita. Smaller sizes (juveniles of 25 cm) were found south of this area.

DISCUSSION

In the three last decades the El Niño events of highest impact in Peru were in 1972–73, 1982–83, and 1997–98. The last is considered exceptional and was better observed than the two others (Hansen 1989; Halpern 1996; Leetma 1999) because it was prognosticated. Many countries were able to take mitigation measures (even though the forecast was not quite accurate for the first phase). As noted earlier, however, we have little information about primary production off Peru.

El Niño 1997–98 was preceded by a period of moderate cold (1995–96) and followed by a cold, post–El Niño period that started in 1998. The cooling trend continued in 1999 with an atypical distribution of the anchovy *Engraulis ringens*, while the sardine's distribution was restricted to the northern region.

During the evolution of the extraordinary 1997–98 event, there were two peaks in the SST anomalies: the first in July 1997 (anomalies of 6°C) and the second around January 1998 (anomalies of 9°). Defined by anomalies higher than 1°, it can be said that the event lasted 13 or 16 months, fewer in the south than in the north, with a period of relaxation in October 1997. Associated with the thermal anomalies of the first peak, very poor volumes of plankton and an abundance of dinoflagellates and small copepods endemic to warm waters were observed. This situation was also present during El Niño 1982–83, when the diatoms were not present (Chavez 1987) and warm-water dinoflagellates appeared in the coastal environment. Those species, endemic to warm waters, had an indicator value at the beginning of the anomalies in the Peruvian coast, but afterwards their presence did not represent a clear response to the environmental conditions.

The patterns of nitrate observed during 1997–98 were most altered from normal in December 1997, when the deepening of the oxycline and nutricline was notably intensified (1 ml/L iso-oxygen depths greater than 250 m, and concentrations of 5 µg-at/L of nitrate at 100 m). The chemical conditions in the sea surface in 1997–98 were similar to those of El Niño 1982–83, but the nutricline and oxycline were deeper in that year (Chavez et al. 1983). All nutrients showed similar patterns of distribution, except in summer 1998 (9802-03), when the silicate concentrations near the coast were high north of Paita (5–20 µg-at/L) due to continental influence, because rains intensified the river discharge. A higher local photosynthetic activity was detected in the volumes of plankton recorded by Delgado and Fernandez (1998) for that cruise. This situation was similar to that found in February of 1972 and 1983 by Guillén and Calienes (1981), and by Guillén (1985) in the same area.

During the first phase of the advance of low-salinity equatorial waters, the anchovy were near the coast. The decrease in biomass from 9.5 million t in January 1997 to 1.2 million t after El Niño 1997–98 was similar to the depression caused by environmental perturbations of the 1982–83 ENSO (Jordan 1983).

The distribution of sardine in the first months of the event was associated with the ESW and SSW. The same situation occurred in El Niño 1982–83, when the sardine were more highly concentrated in the coastal zone due to the position of SSW, as well as having come from the equator with the advance of ESW (Tsukayama and Santander 1987). Like the anchovy, this species also migrated to the south, as was observed during El Niño 1982–83 (ERFEN 1984). In the intermediate phase of thermal relaxation, sardine were very scarce and associated with SSW south of 12°S.

On the other hand, the success of the endemic species'

spawning in the upwelling zone was affected by the perturbation of the environment. Anchovy during El Niño 1997–98 had, according to the gonadosomatic indexes, a low intensity and change in time of spawning. In the second peak (summer 1998) spawning was above normal, and reached a peak in September of that year (cold, post–El Niño period). These variations in the reproductive process were reflected in a decreased population, and had consequences in recruitment, but the strategy used by some species was to stay near the coast, as during El Niño 1982–83 (Barber and Chavez 1986), and also to move to the depths and to migrate southward. Adequate management of the resource allowed the anchovy population to recover promptly.

The gonadosomatic indexes of sardine indicated the effect of the cold year (1996), and spawning was good in the summer of 1997. In the second peak of the warming of El Niño 1997–98, a phase shift in time was observed, but spawning was good in the post–El Niño phase, and sardine recruitment improved during 1998 and even 1999.

The habitat of jack mackerel and chub mackerel, which are more oceanic species, is in SSW, so the two species are found far from the coast. With the coastward penetration of these waters (SSW, ESW), the distributions were near the coast in El Niño 1997–98, and in the north zone they deepened with the SECC. This pattern was present in the events of 1972–73 (Chavez 1987) and in 1982–83 (Tsukayama and Santander 1987).

Another species which significantly increased its distribution and biomass was the samasa, or anchoa, the greatest biomass being around 2.09 million t during September–October 1997, diminishing substantially to 214,000 t in the post–El Niño period (cruise 9808-09; Castillo et al. 1998). The catch of samasa was very significant during the event, although this species in normal years occurs only on the north coast, typical of the Panamanian province.

Guillén et al. (1985) showed that the layer of 2–1 ml/L O_2 was between 100 and 150 m deep off Callao in February 1983. That layer was between 100 and 250 m in December 1997 in the same area, and deeper in Paita—between 150 and 280 m in July and December. In average conditions (1981) this layer is found at 30–50 m. This anomaly has great importance when related to the demersal species, especially hake. Hake shifted to 12°S during the first phase of the event (Castillo et al. 1997); probably in the second peak of the event, when the low oxygen layer was deepest, the species migrated to great depths with more favorable environmental conditions.

The developmental details of El Niño 1997–98 off the Peruvian coast were not forecast adequately to allow an environmental evaluation during the main warming peak of the event, so it is not possible to precisely describe its

effects on the different resources of the Peruvian marine ecosytem. However, during the event the main fishery resources were intensively evaluated in order to determine such factors as vertical and latitudinal distributions, abundance variations, and reproductive behavior.

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MODELING CALCOFI OBSERVATIONS DURING EL NIÑO:
FITTING PHYSICS AND BIOLOGY

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ABSTRACT
Surveys of temperature, salinity, and velocity from CalCOFI, altimetric measurements of sea level, and drifter observations of temperature and velocity during the 1997–98 El Niño are now being fit with an eddy-resolving ocean model of the Southern California Bight region to obtain dynamically consistent estimates of eddy variability. Skill is evaluated by the model-data mismatch (rms error) during the fitting interval and eventually by forecasting independent data. Preliminary results of fitting July 1997 physical fields are discussed. The physical fields are used to drive a three-dimensional NPZD-type model to be fit to subsurface chlorophyll a (chl a), nitrate, and bulk zooplankton from CalCOFI surveys, and surface chl a from SeaWiFS. Preliminary results of testing the ecosystem model in one-dimensional and three-dimensional form are discussed.

INTRODUCTION
The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has sampled the oceanographic conditions of the Southern California Bight (SCB) for 50 years, providing an unprecedented time series of physical and biological data (e.g., Roemmich and McGowan 1995). However, our understanding of the physical processes controlling the large-scale and mesoscale variations in these properties is incomplete (e.g., Bograd et al., in press). In particular, the nonsynopticity and relatively coarse spatial sampling (70 km) of the hydrographic grid do not resolve the mesoscale eddy field (fig. 1a). Moreover, these physical variations exert a dominant influence on the evolution of the ecosystem (e.g., Hayward and Venrick 1998).

In recent years, additional data sets that partially sample the SCB have become available. Acoustic Doppler current profiler (ADCP) measurements now sample upper-ocean velocity between stations (fig. 1b) and give a more complete picture of the mesoscale (Chereskin and Trunnell 1996). Observations of sea level along TOPEX tracks (fig. 1c) give another partial view of the mesoscale, well-sampled along each track but coarsely sampled temporally and between tracks. Surface drifters occasionally pass through the region (fig. 1d). SeaWiFS

provides estimates of upper-ocean chlorophyll a (chl a), usually giving nearly complete coverage after weeklong intervals (depending on cloud coverage).

In order to better interpret the dynamical balances of the physical and biological fields, we are attempting to use an ocean model to fuse together the various data types and develop a complete four-dimensional picture of the evolving flow field and its biology during a particular three-week cruise. This model-testing procedure is often called a fit. If the fit is successful, the model run can be used to assess the balances that control the evolving phenomena. If not, the model must be corrected or discarded. The final test of the model's quality is to determine if forecasting skill is present by running the model beyond the fitting time interval into the forecast time interval (independent data).

Assuming that unstable mesoscale eddies dominate the physical balances, one anticipates that model fitting and/or forecasting skill is achievable to at least the eddy turnaround time scale, which is roughly one to three months. If atmospheric forcing dominates the flow variability, such as in the surface mixed layer, then the fitting time scale is infinite (quantitatively limited only by the model's physics), and the forecasting time scale is the roughly weeklong time scale of atmospheric forecasting skill.

Unfortunately, these fitting and forecasting time scales are probably overestimated, because limited oceanographic data cannot yield unique solutions for the fits or unambiguous verifications for forecasts (e.g., Miller and Cornuelle 1999). However, the 1997–98 El Niño and the 1999–2000 La Niña time periods were sampled particularly well in the SCB, giving us a unique opportunity to test fitting and forecasting skill and to assess dynamic and ecosystem balances during these strongly anomalous warm and cold time periods.

The fundamental scientific issues to be ultimately addressed by this research are the relative importance of mesoscale instabilities, topographic control, remote oceanic forcing, and wind forcing in the evolution of eddies in the CalCOFI region; the relative predictive time scales of deep ocean versus surface processes versus shelf-slope processes; and the ecosystem balances.
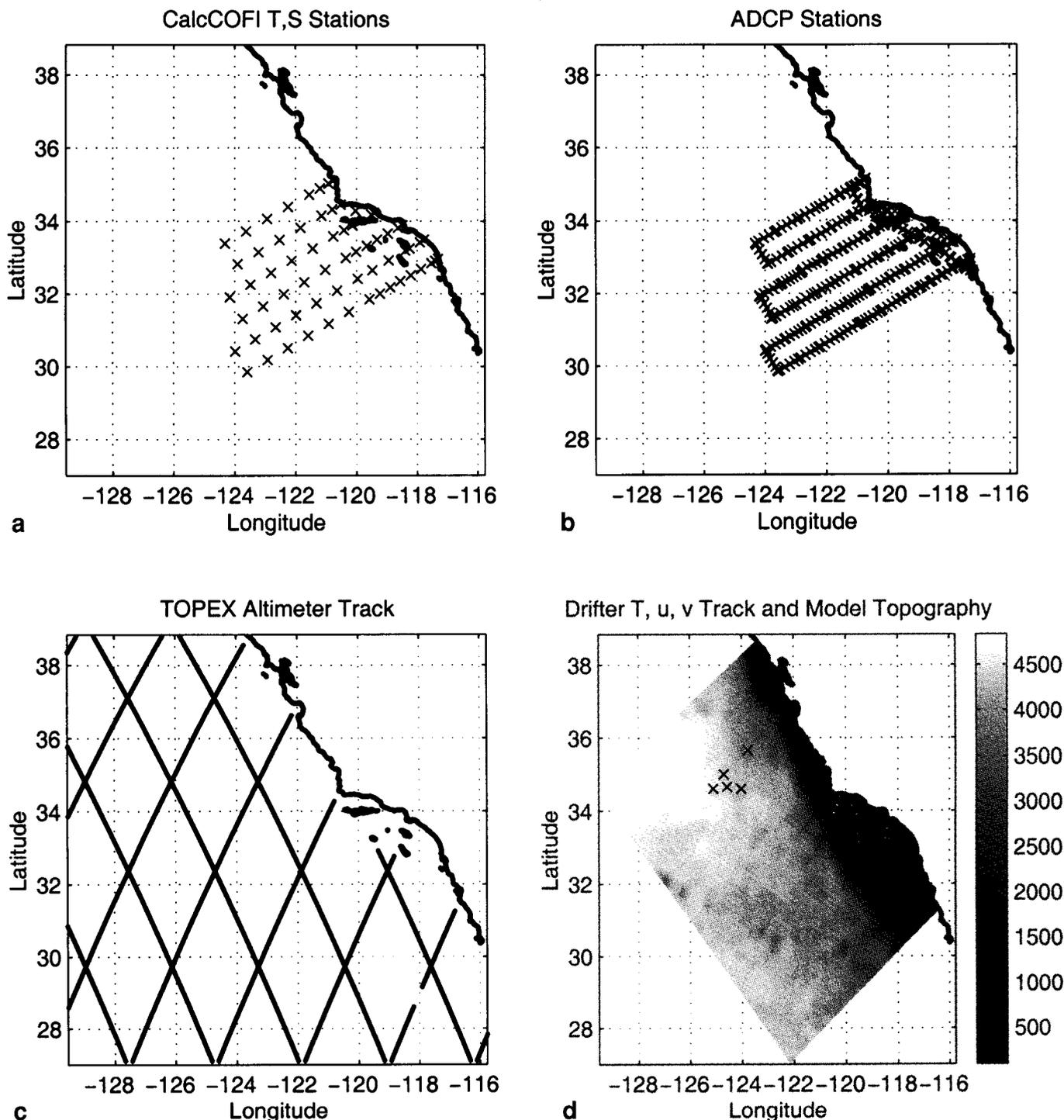
Figure 1. Distribution in space of the data types to be fit by the inverse method in the model domain for July 1997: a, CalCOFI hydrographic stations of temperature, salinity, nitrate, chl a, and bulk zooplankton; b, ADCP upper-ocean currents; c, sea level from TOPEX representing 9-day time differences; and d, drifter observations of 15 m velocity and SST, and bathymetry used in the model (m).

We report here our progress in fitting July 1997 hydrography, tuning one-dimensional ecosystem parameters based on historical CalCOFI data, and initializing three-dimensional ecosystem structure from data during February 1998.

DATA SOURCES

CalCOFI hydrographic data (*http://www-mlrg.ucsd.edu/ calcofi.html*) from 1949 through 1999 were used for comparing against model results, and for creating first-guess initial and key background nudging conditions. The data

used herein for various purposes include temperature, salinity, density, oxygen, nitrate, chl a, and primary production rates.

Climatological profiles of the data were created by binning the offshore and coastal stations. Profiles of the coastal temperature, salinity, and nutrient climatologies show a marked seasonal 50 m doming of the isopleths with a maximum vertical shoaling in May, coincident with the seasonal maximum of California Current velocities. Offshore climatologies show little variability except in May and December, when the profiles show the presence of colder, nutrient-rich water. This variability has been attributed to sampling biases resulting from a change in the CalCOFI sampling schedule. In the last 15 years CalCOFI has not sampled in the months of May and December.

Further analysis of the CalCOFI data includes objective analysis (OA) to create maps of the data fields at model levels for first-guess initial conditions. These techniques are discussed in more detail in subsequent sections. Raw hydrographic observations are also used for quantifying fitting skill. ADCP velocity estimates are used as one-hour averages, which provide roughly five samples between CalCOFI hydrographic stations. TOPEX altimetric measurements of sea level are used as differences between nine-day repeat track times in order to remove geoid effects. Drifters provide daily surface velocity and temperature estimates. Atmospheric forcing is derived from COADS and NCEP/NCAR reanalysis fields.

Daily satellite-derived estimates of surface chl a were obtained from the NASA SeaWiFS data archive. We use the global gridded L3m data set, which has 9 km resolution. The satellite began collecting data in September 1997, so we presently have close to 2.5 years of images. The daily images are unfortunately incomplete in the CalCOFI region due to the frequent cloud cover offshore. Therefore, 5-day composite images have been created for use in developing initial conditions and quantitative model-data comparisons.

PHYSICAL AND ECOSYSTEM MODELS

We use an eddy-resolving primitive equation (PE) generalized sigma-coordinate ocean circulation model called the Regional Ocean Modeling System (ROMS), which is a descendant of SCRUM (Song and Haidvogel 1994). The 9 km model grid is curvilinear and extends about 1,200 km along the coast from northern Baja California to north of the San Francisco Bay area, with roughly 700 km offshore extent normal to the coast (fig. 1d). The northern, southern, and western boundaries are open, and are treated by using a modified version of the Orlanski radiation scheme or with nudging to specified time-dependent temperature and salinity

values. We use ETOPO-5 for the bathymetry (fig. 1d) and the coastal masking along the eastern boundary. In the vertical, 20 layers reach from the free surface to the bottom of the ocean. The sigma layers are such that they have increased resolution in the surface and bottom boundary layers. In the shallow coastal region, the top layer can be as thin as 2 meters.

We initially tested the physical model with simple parameterizations of the external forcing and bathymetry, in order to verify its ability to capture the basic physics of the region. Integration with smooth climatological forcing (COADS data) showed that the statistics of the model are comparable with observations. Some of these features include a meandering current flowing from north to south, a poleward undercurrent on the continental slope, and a recirculation gyre in the SCB. In a qualitative analysis of the model results, we found the horizontal eddy length and time scales to be comparable with the observed eddies. A more quantitive measure of the model's skill is assessed by the fitting procedure described below.

The physical model drives a seven-component ecosystem model (either uncoupled or coupled via the light-absorption feedback) which includes nitrate, phytoplankton, ammonium, zooplankton, chl a, and two (large and small) detritus pools. The present model is similar in structure to the coupled ocean circulation ecosystem model developed and applied to the California coastal transition zone by Moisan et al. (1996). The simulated flow fields from the three-dimensional physical model are used to advect and diffuse the ecosystem's model constituents. The biological quantities are solved in the model as tracers with the addition of a nonlinear source/sink term that regulates the exchange between one biological variable and the other (e.g., Fasham et al. 1990).

The biological portion of the model, therefore, is a system of seven coupled partial differential equations that govern the spatial and temporal distribution of a nonconservative quantity, which is of the form

$$\frac{\partial B}{\partial t} = \nabla \cdot K \nabla B - (\vec{v} + \vec{v}_{\text{biology}}) \cdot \nabla B$$
$$+ S - r_{\text{nudge}}(B - B_{\text{clim}})$$

where ∇ is the 3D gradient, B is a nonconservative quantity (one of the seven components in the biological model), $\vec{v}$ is the vertical and horizontal velocity of the fluid, and $\vec{v}_{\text{biology}}$ is the vertical sinking rate of the biological components. The velocity, $\vec{v}$, and the kinematic eddy diffusivity, K, were obtained as described below. The source or sink term, S, for the biological component is defined by the sum of the individual forcing terms associated with the ecosystem model, and r_{nudge} is the

rate at which the biological component is nudged back to the climatological mean of the biological component, B_{clim}. In this study, the climatological fields will be used to relax only the deep-water values over a long time scale so that climate drift of the deep-water nutrient fields can be avoided.

INVERSE METHOD FITTING TECHNIQUE

Many techniques exist for combining data with models (e.g., reviews by Ghil and Malanotte-Rizzoli 1991; Bennett 1992; Wunsch 1996). Least-squares methods are widely used for fitting both steady and unsteady models to data, and can be implemented sequentially as the Kalman smoother, or globally by solving the Euler-Lagrange equations to find the minimum of an objective function (Le Dimet and Talagrand 1986; Wunsch 1988; Thacker 1989; Tziperman and Thacker 1989; Bennett and Thorburn 1992). The objective function is a sum of quadratic terms penalizing misfit between the observations and the data produced by the model, and also penalizing corrections to the assumed model parameters, including forcing, initial conditions, and boundary conditions. The weighting of the penalty terms may include smoothness criteria, and the forcing errors may include errors in the model equations at every point in space and time (Bennett and Thorburn 1992). A global inverse method similar to the "Green's function method" (Wunsch 1996) was used to fit the regional PE model to the hydrographic data of a CalCOFI survey covering about 3 weeks by adjusting the initial state of the model. Because the model forcing and boundary conditions were not adjusted, the model evolution depended only on the initial conditions.

The starting guess for the model's initial conditions came from a time-independent, three-dimensional objective analysis of the CalCOFI observations, treated as if they were simultaneous at the start of the survey. The model was run from this poorly resolved initialization, and the modeled data were compared to the raw observations throughout the duration of the CalCOFI survey (fig. 2).

The misfits between the model and the observation were corrected by adjusting the initial conditions based on Green's functions that relate changes in the model's initial conditions to changes in the model's estimates of the observations. The model's initial state was adjusted to minimize the sum of the squared, normalized misfits between the observations and the temperatures and salinities predicted by the model at all the data points over the time range, while also minimizing the sum of squares of the normalized changes to the model's initial conditions. The changes to the initial conditions are expanded in sinusoids in the horizontal and smooth functions (EOFs) in the vertical, so the minimization procedure
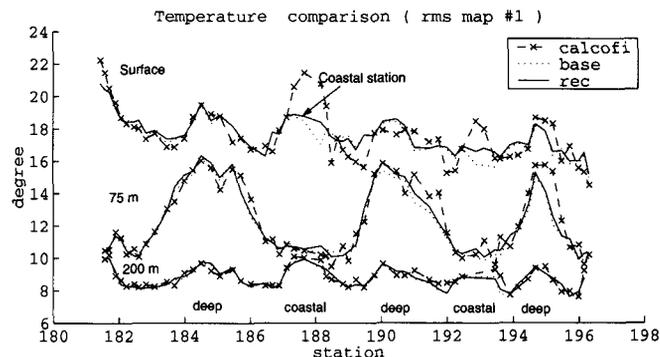

Figure 2. Observed (—x—) and modeled temperature at 0, 75, and 200 m plotted along-track as a function of station for the July 1997 CalCOFI cruise. The base model run (dotted line) is initialized from an objective analysis of the CalCOFI hydrographic data. The model run using the correction to initial conditions provided by the inverse solution (solid line) shows reduced misfit mainly in the shallow near-coastal stations.

includes smoothness constraints by penalizing short length scales more than long scales. The assimilation retains the form of objective mapping as a least-squares fit (Davis 1985), with the data covariance matrix derived from the time-dependent Green's functions and the model parameter covariance. Setting the model's covariance controls the smoothing constraints, and the data error covariance governs the fit to the data.

Errors in fitting to the data were assumed to come both from errors in the observations and from model errors due to the linearization, the limited set of initial perturbations, and the limited horizontal and vertical resolution. The assumed data error bars were checked against the final misfits ("residuals") after the fit, to assure that the assumptions had not been violated, and that no single datum exerted significant influence on the estimate. Because advection is important in this example, the linear Green's functions depend on the initial state, so the estimation procedure must be iterated. Miller and Cornuelle (1999) provide further details of our fitting procedure in the context of a different oceanographic region.

TESTS OF THE DYNAMICAL FITS

The fitting procedure was tested for the July 1997 CalCOFI survey (cruise 9707) when El Niño conditions prevailed in the tropical Pacific. At this time, the initial signal of El Niño in California waters was observed as an increase in the coastal undercurrent, which transported unusually warm waters northward at depths below 100 m (Lynn et al. 1998). Local changes in the wind forcing due to the atmospheric teleconnections with El Niño followed only in November 1997.

The general view of the physical structure from CalCOFI hydrography at this time shows the core of the California Current system (CCS) to be displaced slightly farther west than usual (Lynn et al. 1998).

A well-defined inshore countercurrent, evident in both temperature and salinity, with greater-than-average velocity was observed. A vertical section along CalCOFI line 93 shows a plug of water with salinity exceeding 34.4 at the 200 m depth level that was not found during the previous cruise. The ADCP velocities confirm a strong and continuous poleward California Undercurrent through the SCB and around Point Conception that advects highly saline and warm waters from the southern boundary. This pattern is thought to be related to the coastally trapped Kelvin-like waves excited by the strong El Niño event in the tropics.

Initialization Procedure and Forcing

In order to commence the model fitting procedure, an initial ocean state must be constructed to be as close as possible to the (unknown) observed one. Observations for the nonsynoptic three-dimensional temperature and salinity fields are available only in the small "CalCOFI subdomain," for which we use the cruise data for temperature and salinity as a time-independent picture of the ocean. Further data (Leetmaa Pacific Ocean Analysis provided by the Climate Diagnostics Center *http://www. cdc.noaa.gov/cdc/data.leetmaa.html*) are used to fill in the ocean's initial state outside this region in a smooth way.

Before merging the two data sets, we confirmed that the vertical structure of the Leetmaa data compared well with the CalCOFI data for July 97. We merged the two data sets by making an objective map over the entire model domain of the anomalous temperature and salinity fields defined as Leetmaa minus CalCOFI. Merging data sets during other cruise periods is not always practicable in this way, and further treatment of the data is required. For example, for the February 1998 cruise the vertical analysis revealed some discrepancy in the profiles at depth in both temperature and salinity around the perimeter of the CalCOFI subdomain. This is due to the smoothing implicit in the Leetmaa data, which is an assimilation of data with an ocean model. The salinity data used in the assimilation are inadequate to properly resolve the vertical structure in the proximity of the coast. The horizontal gradients in density produced by these discrepancies generate strong adjustment currents at depth, which are artificially induced by the matching. We therefore computed a mean vertical profile anomaly for temperature and salinity in the CalCOFI subdomain and subtracted this anomaly from all Leetmaa data. We then defined a horizontal anomaly as CalCOFI data minus Leetmaa at each depth. Before objectively mapping the anomalies on the entire model grid, we also fit a smooth plane to account for horizontal large-scale background gradients in temperature and salinity. This initial guess will subsequently be corrected by the inverse solution.

The initial velocity field for the model is also critical in that it should be nearly geostrophically balanced with the horizontal density gradients. We initially computed geostrophic currents from the density fields. We assumed a level of no motion at around 1,000 m, since we know that the core of the CCS can easily extend down to 500 m with velocities on the order of 0.2 cm/sec (Chereskin and Trunnell 1996). The problem with this calculation is that the initial kinetic energy state of the model is not in equilibrium, and integration over time shows a sharp spin-up of the velocity field during the first day. In order to compute sensitivity to initial conditions with the inverse method, it is not useful to allow this spin-up process. Therefore we have computed the initial velocity field by integrating the model forward in time for half a day, keeping the density constant and with no forcing. This second approach insures a more balanced energetic state in the initial condition. We eventually will correct this first-guess initial velocity state by using the inverse method.

For the forcing fields we use Levitus climatology for heat fluxes and COADS monthly wind stress. The time span of the cruise is about three weeks. In later experiments we plan to investigate the sensitivity to higher frequency in the forcing and how this affects our fitting and forecasting time scales.

Basis Functions for Assessing Sensitivity

As described in the section "Inverse Method Fitting Technique," we project the error field between model and observed initial conditions onto a reduced space. The optimal basis to be chosen for this projection is not known, so we arbitrarily picked the Fourier basis sets of sines and cosines for horizontal structures as a first try. In the vertical, we used empirical orthogonal functions (EOFs) of the difference between CalCOFI observations and model-derived temperature and salinity profiles from the base run from first-guess initial conditions. These vertical modes tend to show maximum variability at roughly 100 m, with about 70% of the variance explained by the first EOF and 20% by the second.

Initial tests of the model runs' sensitivity to slight changes in the initial conditions when we used these basis functions showed strong nonlinearity in the upper ocean. That is, a large-scale, small-amplitude perturbation in temperature or salinity resulted in a time-dependent perturbation from the base run that had large amplitudes at the grid scale after only a few days. We traced this nonlinearity to the model KPP mixed-layer parameterization (Large et al. 1994), which gives a time- and space-dependent vertical diffusion coefficient based on a number of criteria. Since this strong nonlinearity would complicate the linear fitting procedure, we set the vertical diffusion to be a constant chosen to yield

reasonable mean and eddy variance states. When surface-forced mixed-layer processes are addressed in future work, we plan to reexamine the KPP framework in the context of the linear inverse.

Results of the Inverse

We ran a total of 500 perturbation runs for temperature and salinity, resolving up to six wavenumbers in each horizontal direction and three vertical modes. Each model run is sampled in time as the CalCOFI cruise sampled the real ocean. Each perturbation run is the model's forecast for the cruise from a slightly different initial state.

In the application of the inverse, we also need to assign rms fitting error to each datum. The error includes both observational error and representational error, which comes from the inability of the model to reproduce all the physical processes seen in the data (e.g., internal waves). Our first fitting attempt used a constant rms-error-bound for each observation. However, the results (fig. 2) tended to place more emphasis on fitting the coastal station data where the mismatch is highest. Since we anticipate that slow open-ocean eddies will be better resolved by model physics than fast shallow-water coastal eddies, we next attempted to allow a larger fitting error in the coastal region than offshore.

In order to better minimize the misfit in the deep ocean, we redefined an rms-error-bound map based on the spatial distribution of the station, with larger error for coastal than offshore stations. Since the inverse is a linear method, we also took into account the level of nonlinearity of each individual station in the rms-error-bound map. A test of the nonlinearity can be obtained by rerunning many of the perturbation runs with the opposite sign of the perturbation amplitude. The difference in the response to the positive and negative perturbations is an estimate of the nonlinearity in the response. If we map this variance horizontally we see that nonlinearities are stronger in the coastal region, as we would expect. An error variance reduction of 68% was obtained with this new rms-error-bound map definition, and a better fit of the offshore eddies was achieved, as can be seen in figure 3.

Figure 4 shows the time-dependent map of 50 m temperature from the model run from the corrected initial state for the CalCOFI cruise in July 1997. The slow evolution of the larger mesoscale eddies offshore and the more rapid evolution of the smaller eddies nearshore suggests that we have a much better chance of skillfully fitting the offshore thermocline eddies than the near-coastal squirts and jets with the available data. More highly resolved observations in space and time will be needed for near-coastal fits. Likewise, processes in the
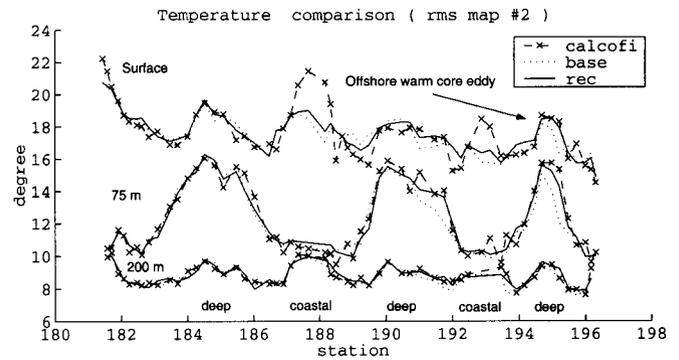

Figure 3. Same as figure 2 but for inverse solution using observational rms-error-bounds that are larger for near-coastal data than for deep-ocean data.

surface mixed layer are not skillfully modeled here because time-dependent surface forcing is not included and because of the limited oceanographic data.

TESTS OF THE BIOLOGICAL MODEL

The biological fields are strongly influenced by the physical variations. Therefore, once a physics fit is complete, it can be used to drive the biological model as a first test. The first SeaWiFS images were collected in September 1997, so our tests of the July 1997 physical field fits are not suitable for testing the ecosystem model. The best-sampled CalCOFI period after SeaWiFS began is February 1998 (cruise 9802), so we began testing the 4D biological model for that period. We first want to understand how sensitive the biological model is to the various terms that influence it.

We created an initial chl a field for the CalCOFI domain from daily 9 km SeaWiFS imagery collected during the cruise 9802 period. A 5-day running average was applied to the resulting 19-day, 2D chl a time series to insure minimal pixel dropout. Remaining holes in the images were removed by iteratively averaging from the hole edges into the hole centers. Finally, the 2D time series was interpolated to the ROMS West Coast model grid. For the purpose of initializing the 3D chl a field, we selected the first 2D field in the averaged time series, corresponding to the 5-day average centered around day 3 of the 9802 cruise, and calculated the subsurface chl a distribution. Following Morel and Berthon (1989), this calculation produces a Gaussian distribution of chl a between the surface and the light penetration depth as defined by the SeaWiFS chl a concentration (fig. 5a). We set the chl a concentration to zero for all depths greater than the penetration depth. Vertical integration of the 3D model field reproduces the horizontal distribution as seen by SeaWiFS (fig. 5b). The 3D chl a field was added to the physical model as a passive tracer, and 30-day model runs were made with and without diffusion.
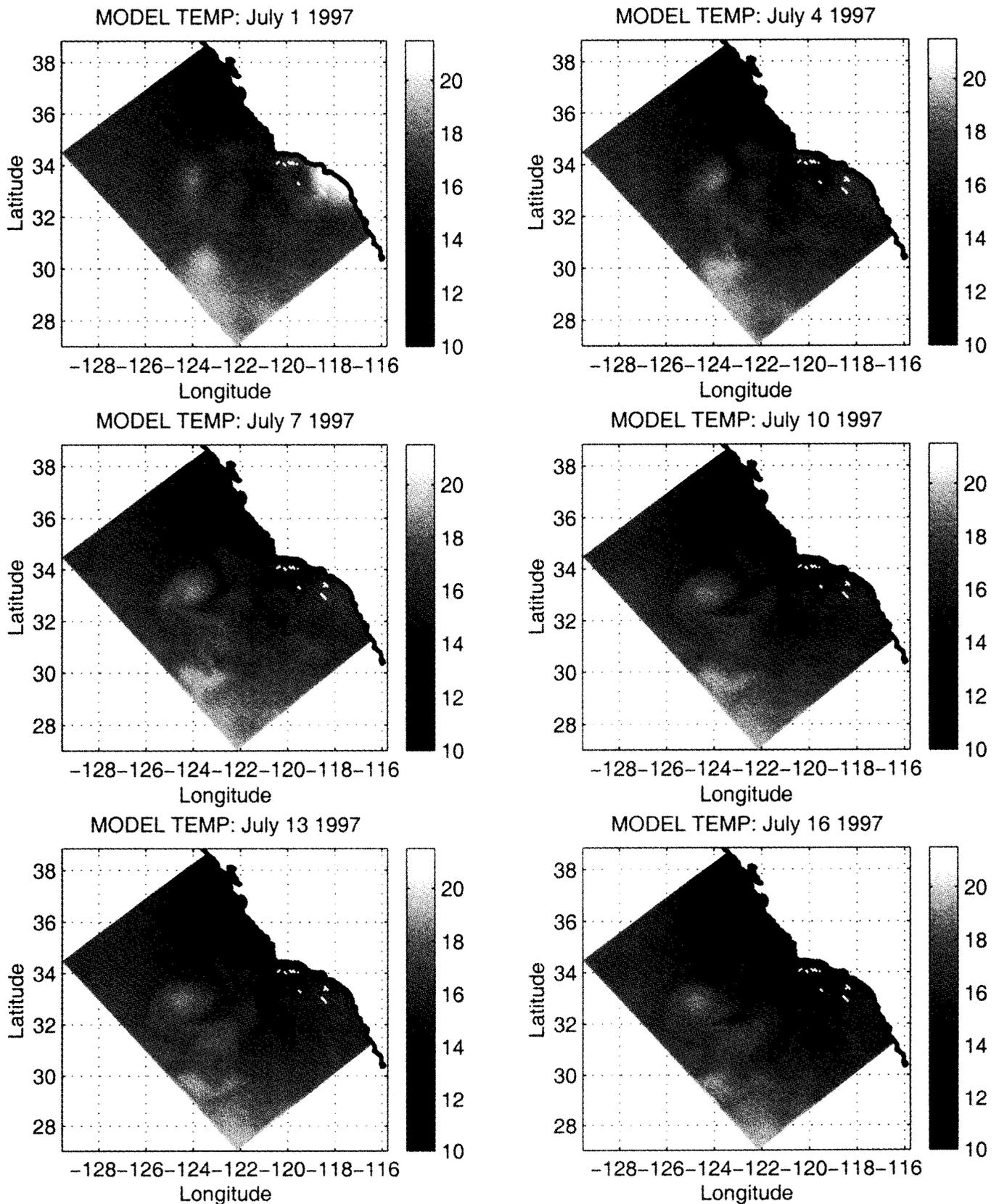
Figure 4. Time sequence of model temperature at 50 m depth from the case where the model's initial conditions have been corrected by the inverse method with rms-error-bounds larger in the near-coastal region.
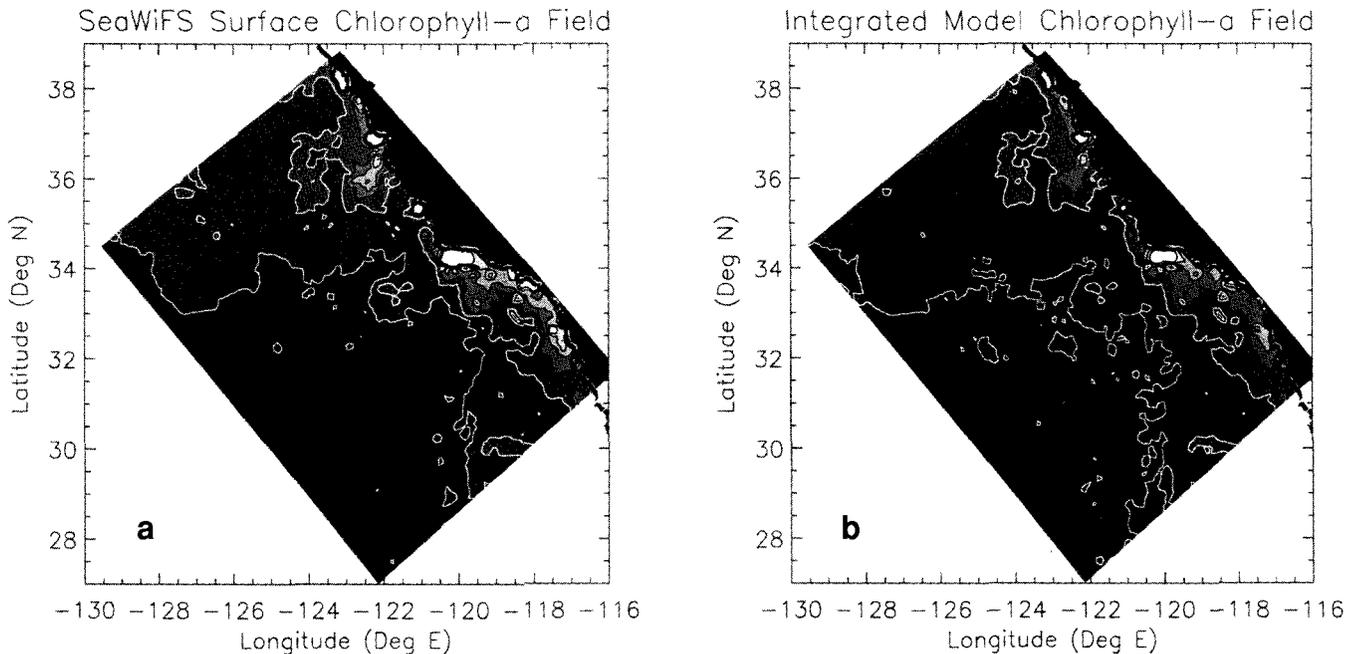
Figure 5.   Comparison between a, raw 5-day average SeaWiFS image of chl a (integrated from the surface to one optical depth) and b, SeaWiFS-derived model initial condition of chl a (integrated from surface to ocean bottom) for the beginning of 9802 CalCOFI survey. SeaWiFS image contours range from 0.01 in the open ocean to peak values near 0.4 in the shallow-water regions. Model image contours are proportional to SeaWiFS by an unspecified factor.

3D Ecosystem Model Evolution

Examination of the SeaWiFS record for the 9802 period reveals a persistent chl a signature in the coastal waters. In animations of both the SeaWiFS imagery and model output, this coastal chl a is generally moved north or south along the coast with agreement between the two data sets as to direction. As would be expected, without replacement of the chl a via production, the modeled chl a tracer is quickly lost from the coastal waters and transported either offshore or to deeper depths. The pattern of movement is different depending on whether vertical or horizontal diffusion is present in the physics, but the end result, without active biological production, is still a general loss of chl a from the coastal surface waters.

We are now investigating how various pathways in the 7-component model affect the spatial distribution of chl a in the model. Starting at the simplest: chl a and phytoplankton with uptake of nitrate and parameterized loss, we intend to add components and pathways incrementally until we have the full 7-component model running over the CalCOFI domain. Although the full model has already been run successfully, this approach will allow us to examine the biological response of the model while comparing the results to both the CalCOFI 9802 data set and associated SeaWiFS imagery. The incremental approach will also allow us to rigorously determine many of the rate and flux parameters associated with the model.

1D Ecosystem Model Performance

Because many of the parameters in the ecosystem model are poorly known, we have investigated the model's sensitivity over a wide range of parameters. Our approach has been to use a one-dimensional mixed-layer model that has been coupled to the ecosystem model. We have tested this model at two extrema in the CalCOFI domain, the coastal and the offshore regions. The model is initialized with climatological profiles of temperature, salinity, and nitrate that were obtained from each of the two regions. The climatological profiles are also used as nudging fields for the temperature, salinity, and nitrate profiles. The nudging time scale is set to a constant 5 years. All other model variables are set to a constant value and are not nudged. In order to further diagnose the model's results, we added an oxygen component to the model to track the effects of the remineralization process. The oxygen value is set to the saturation value at the surface for the given SST. The simulations are carried out for 10 years, which is enough time to allow the model to develop a steady seasonal cycle.

By reducing the ecosystem model testing to a 1D problem, we are able to examine many cases by using different parameter sets. The model's results are compared against the climatological profiles of temperature, density, nitrate, chl a, and oxygen that were obtained from the CalCOFI data set. An example of one such comparison (fig. 6) demonstrates that the model is capable of resolving several of the observed features. The
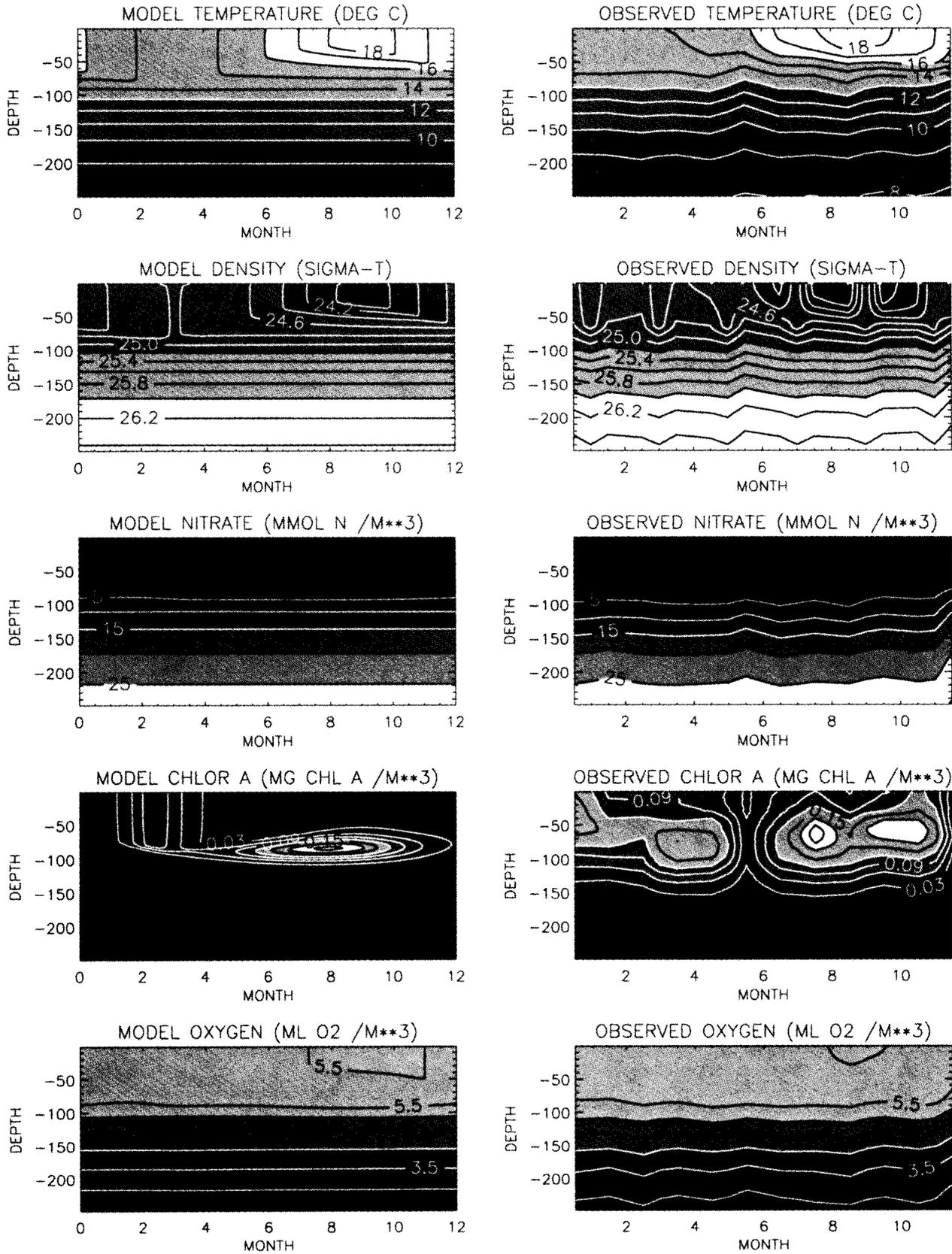
Figure 6.   Comparison between 1950–99 mean seasonal cycle CalCOFI offshore profiles (*right*) and 1D mixed-layer/ecosystem model simulation with seasonal cycle climatological forcing (*left*). Plotted are (*top to bottom*) temperature, density, nitrate, chl a, and oxygen profiles from 0 to 250 m and from January to December.

mixed-layer model is capable of resolving the seasonally varying SST and mixed-layer depths. The nitracline is well established at about 100–150 m, with very low concentrations at the surface. Surface chl a is highest in the winter, with an established chl a maximum at about 80–90 m. Unfortunately, the chl a climatologies had to be averaged over 2 months in order to achieve a smoothly varying chl a field. One issue that has yet to be resolved is why the model creates such a thin chl a maximum at depth while the data suggest a wider feature. Part of this discrepancy may be due to the averaging of many profiles to obtain the climatologies of the data set. The oxygen profile from the model compares well with the climatologies and shows a gradual decline in oxygen levels with depth and a sub-mixed-layer oxygen maximum during the summer.

We are now configuring the 1D model to the coastal CalCOFI climatologies. After we have achieved good agreement between both offshore and coastal locations, we will compare the resulting parameter sets to try to resolve the differences between regions. The parameter sets which result from the 1D simulations will be used as a starting point for the full 3D data assimilation of both the circulation and ecosystem models.

SUMMARY AND OUTLOOK

Our initial test of the fitting procedure successfully reduced the error variance of the model-data misfit in temperature and salinity by nearly 70% during the July 1997 CalCOFI cruise. These encouraging results suggest that we should eventually be able to reduce the misfits even further by including adjustments to horizontal velocity and sea level. We are presently preparing the TOPEX, ADCP, and drifter data to additionally constrain the fit.

Our success so far is geared toward deep-ocean thermocline eddies, which evolve slowly and geostrophically. Progress in fitting the shelf-slope eddies will be hindered by limitations in the volume of data needed to constrain these faster and smaller-scale features. Progress in fitting the upper-ocean mixed-layer variations will depend on the quality of surface-forcing data from atmospheric analyses or direct observations, because these oceanic features are strongly influenced by direct atmospheric forcing rather than by intrinsic oceanic instabilities.

Fits of the ecosystem variations are likewise limited by the small amount of subsurface data available and the great uncertainties in coupling parameters between the biological variables. Nonetheless, since the physical variations control the biological variations to a large degree, we expect to successfully match the available data to within error bars.

Once the fits are complete for a given survey, we will break down the dynamical and ecosystem balances that hold in the model and assess their consistency with other modeling studies. The true test for the model and the inverse technique is to forecast independent data in subsequent CalCOFI hydrographic and ADCP surveys, TOPEX data sets, and SeaWiFS observations. Since there was monthly sampling (albeit limited spatial sampling) during the 1997–98 El Niño, we expect to be able eventually to quantify predictive time scales for this region.

ACKNOWLEDGMENTS

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EL NIÑO 1997–98 IN THE COASTAL WATERS OF SOUTHERN CALIFORNIA:
A TIMELINE OF EVENTS

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ABSTRACT

Timely detection of changes in the tropical Pacific and subsequent predictions that the west coast of North America would be impacted by a strong El Niño event in 1997 enabled CalCOFI to augment its time-series sampling to provide monthly coverage of a subset of the sample grid. The 1997–98 El Niño event in California waters is described here in terms of a preliminary timeline of events. This improved description of the timing of changes in the CalCOFI region provides new insights into the types of changes that might be expected during future events, and it also constitutes a natural experiment which can be used to test hypotheses about the cause-and-effect mechanisms linking changing physical structure with ecosystem impacts. Although some effects attributed to El Niño were evident in the summer and fall of 1997, the strongest occurred in winter 1997–98 and spring 1998. Advection and changes in ranges of mobile populations were consistent with the northward extension of the range of southern warm-water species of migratory game fish and plankton. However, the timeline observations were not consistent with predictions based upon a simple model of bottom-up trophic processes (changes in physical structure, nutrients, phytoplankton, zooplankton, upper trophic levels) as the mechanism linking changing physical and ecosystem structure. While not surprising, since few simple models have much skill in predicting structure in natural ecosystems, this suggests that ecosystem managers will have to await a better understanding of cause-and-effect linkages before improved skill in observing and predicting the physical effects of El Niño upon California waters can be directly translated into improved skill in predicting ecosystem effects.

INTRODUCTION

Observations of increases in upper ocean temperature and mixed layer depth derived from satellites and the buoy array in the tropical Pacific led to the successful prediction that the west coast of North America would be affected by strong El Niño conditions starting sometime in 1997 (e.g., NCEP 1997). Several research groups responded to these predictions by enhancing their ocean observation programs. CalCOFI increased the frequency of the time-series sampling program. Two lines of the time-series sample grid were sampled at monthly intervals from December 1997 to January 1999, in addition to the normal quarterly sampling done during each year.

The added sampling greatly improved our knowledge of how changes in physical properties and ecosystem structure are related to each other during a strong El Niño event. In particular, the sequence of events that occurred during the onset of El Niño conditions within the CalCOFI study area was much better defined than has been possible in the past. A more detailed picture of the timing of events is interesting, if for no other reason than that it provides a better idea of the changes that might be expected during future events. However, a more important goal is to go beyond simply describing effects and attributing them to El Niño, to developing an improved understanding of cause-and-effect relations that will ultimately lead to improved predictions and models. The recent success in observing El Niño's physical conditions and predicting that they would strongly impact the west coast leads to the question of determining to what extent this new skill can be translated into ecological information that is directly useful to managers and policymakers. The existence of a better-resolved timeline constitutes a natural experiment that can be used to test hypotheses of the cause-and-effect relations linking changes in physical structure and ecosystem structure.

Here I describe the changes in structure in the CalCOFI study region during the 1997–98 El Niño. This description is organized as an overview of the timeline of events. These events are then interpreted in the context of how this new information may be useful to managers and policymakers. This description is preliminary and incomplete, in that most research groups are still working on processing and analyzing their data, and only preliminary highlights are available. It is also premature to attempt to address the larger regional issues. Sampling of other regions along the west coast of North America and studies of additional aspects of physical and biological structure by other programs will eventually be synthesized in a much more comprehensive picture
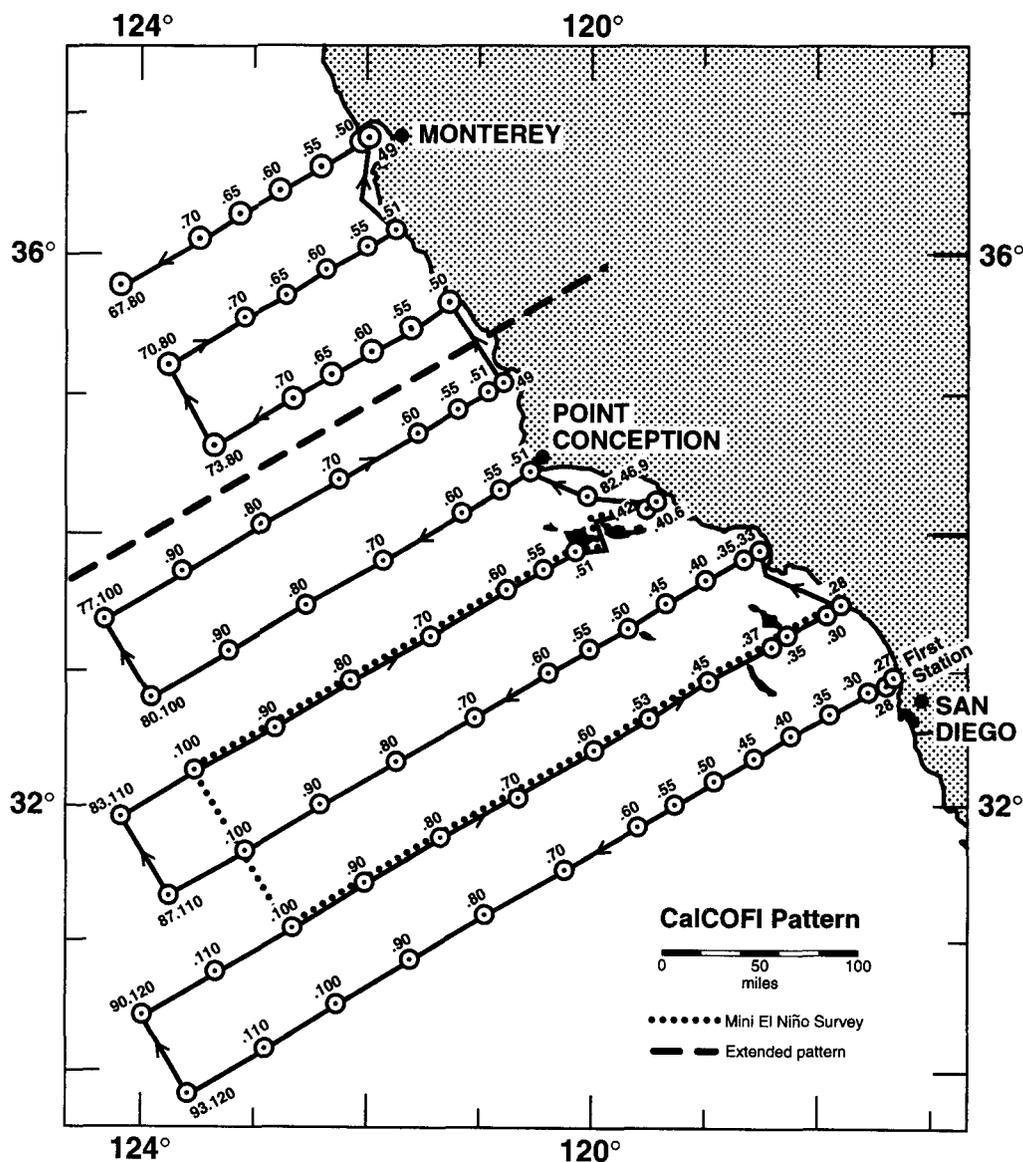
Figure 1.   Sample plan for CalCOFI time-series cruises and mini El Niño cruises. The mini El Niño cruises covered lines 90 and 83 out to station 100, and are illustrated by a dotted line. On some cruises the pattern has also been extended to the north with continuous mapping to cover lines 67–73.

of this event. Some studies are summarized in other con-
tributions to this symposium.

DATA AND METHODS

The analysis emphasizes CalCOFI hydrographic data
and the high-frequency (e.g., coastal shore station) data
that are widely distributed and routinely available in a
timely manner. These are the types of data that will be
used by managers in assessing future events. Additional
information on the sources of these data, such as repre-
sentative Web sites, are also listed as the data are presented.

The station plan for the quarterly CalCOFI time-
series cruises and for the additional "mini" El Niño
cruises added during 1997–98 is shown in figure 1.

CalCOFI hydrographic data, as well as the methods and
some preliminary interpretation are available in pub-
lished data reports (e.g., Scripps Institution of Ocean-
ography 1999) and at the CalCOFI Web site (http://
www-mlrg.ucsd.edu/calcofi.html).

One commonly used tool to detect and quantify the
effects of El Niño in a time-series data set is calculation
of anomalies from the long-term mean annual cycle (the
climatology). This approach can be applied only when
the historical data set is sufficient to calculate a repre-
sentative long-term mean. The few long time series of
oceanographic observations that exist have great value
in this regard. The harmonic mean annual cycle (Lynn
et al. 1982) was used to calculate the climatology for

CalCOFI hydrographic data and the shore station temperature data.

An additional issue becomes important when using these anomalies to interpret El Niño effects and, especially, when comparing data sets from different regions or different properties. If the base period used to calculate the climatologies differs and if there is a long-term trend in the data, the magnitude and even the sign of anomalies may differ, even from observations which are basically the same. Long-term trends have been observed for sea level (Roemmich 1992); temperature and macrozooplankton biomass (Roemmich and McGowan 1995a, b; McGowan et al. 1998); and the upwelling index (Bakun 1973, 1990). The existence of such long-term trends complicates comparison of time series of these properties made in different regions or from different data sources (e.g., temperature from shipboard measurements, shore stations, buoys, or remote sensing) where the base periods often differ greatly. It would be ideal if all climatologies were calculated with the same base period. However, the data needed to do this do not exist. The approach here is to use the timing of strong trends in a data set to define the onset and decline of El Niño conditions, rather than the time at which an anomaly time series crosses a zero line. I have also tried to avoid comparing the magnitude of anomalies based upon differing base periods. The base period used for calculating climatologies is indicated as the data are presented.

There are also constraints upon the analysis imposed by the interaction of the availability of data and the annual cycle in a given property. For example, if a fishery, such as market squid, takes place only during winter months, fishery data provide no direct information about whether the system was affected by El Niño conditions during summer.

RESULTS

1. Physical Structure

Pattern in the tropical Pacific Ocean is considered first, so that the timing of changes in California waters can be compared to the timing of the events that were used to predict these changes. Conditions in the tropical Pacific are summarized by the multivariate ENSO index (Wolter and Timlin 1998: updates were taken from the NOAA Office of Global Programs Web site http://www.ogp.noaa.gov/enso/). Strong positive values of the multivariate index indicate El Niño conditions, and strong negative values indicate La Niña conditions. There was a sharp transition to El Niño conditions in the first part of 1997, with strong El Niño conditions evident by April–May and near maximum values by July–August (fig. 2). These very strong El Niño conditions persisted in the tropical Pacific until April–May 1998, when there
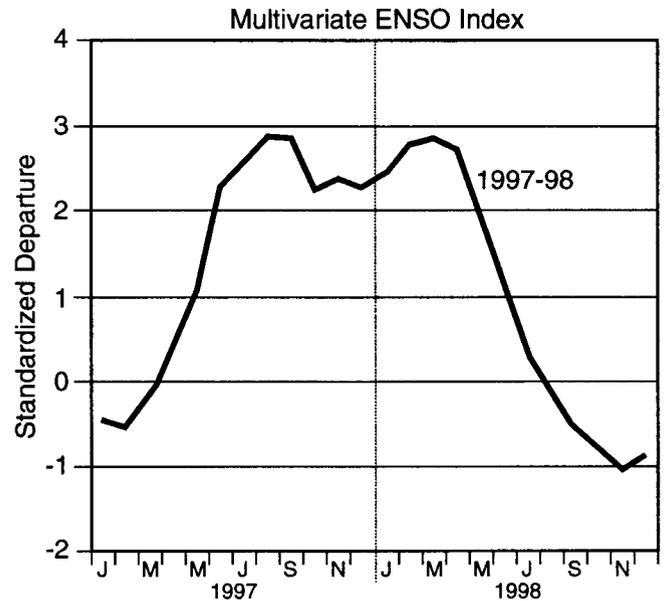

Figure 2. Multivariate ENSO index for 1997–98.

was a rapid decline and transition to La Niña conditions. The multivariate index showed negative values by July–August 1998. The period of very strong El Niño conditions in the tropical Pacific Ocean, as indicated by the multivariate ENSO index, lasted from June 1997 to April 1998.

Several indices have been used to detect El Niño–caused changes in the physical structure of the coastal waters of California. Sea-surface temperature and sea level are measured at coastal shore stations. Anomalously warm water is consistent with El Niño conditions. The pattern in SST anomalies is illustrated with data from San Diego (SIO Pier) and Pacific Grove (These data are from the SIO shore station program, Walker et al. 1994; http://www-mlrg.ucsd.edu/shoresta/index.html). The base period for calculating the climatologies was 1916–93 for San Diego and 1919–93 for Pacific Grove. The surface water at San Diego was anomalously warm from March 1997 to March 1998, and episodic warm pulses were seen for the remainder of 1998 (fig. 3). Early 1999 was near normal at San Diego. Pacific Grove was anomalously warm from July 1997 to March 1998, and it was cool from September 1998 into early 1999. The winter of 1997–98 was anomalously warm at both sites.

A more clear El Niño trend was evident in the pattern of sea-level anomalies (data from the University of Hawaii Sea Level Center: http://uhslc.soest.hawaii.edu/). The base period for calculating these climatologies was 1975–95. Coastal sea level tends to be elevated during El Niño events due to the existence of a warmer and deeper mixed layer than normal and an increase in the strength of the coastal countercurrent. Anomalies in sea
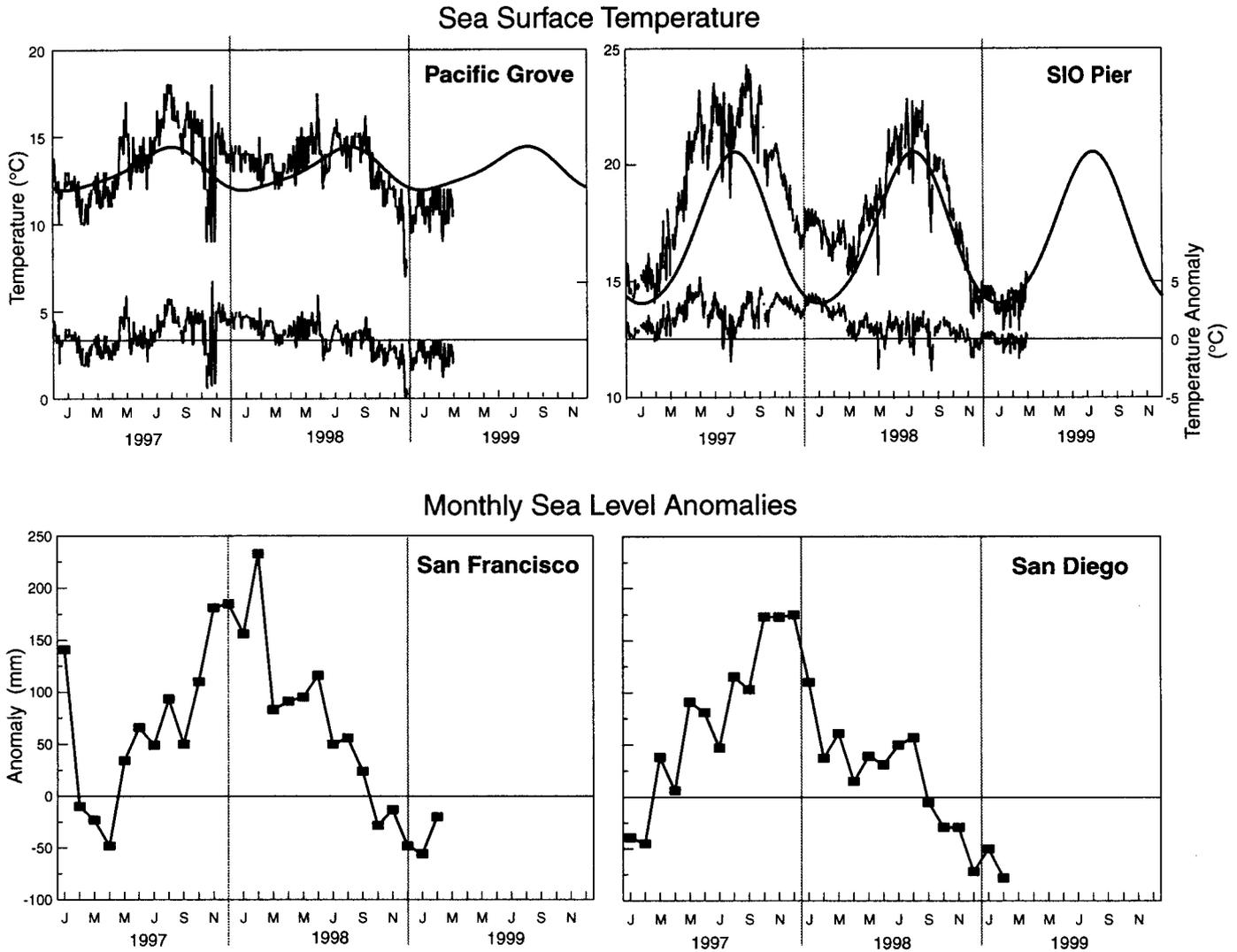
Sea Surface Temperature

Monthly Sea Level Anomalies

Figure 3. *Upper panel:* SST and SST anomalies at Pacific Grove and SIO Pier. *Lower panel:* Sea-level anomalies at San Francisco and San Diego.

level measured at coastal tide gauge stations have been shown to be related to both the seasonal cycle in coastal currents and nonseasonal anomalies (Reid and Mantyla 1976). Sea level was elevated at both sites from June 1997 to August 1998 (fig. 3). San Diego and San Francisco showed very similar patterns in sea-level anomalies.

The upwelling index is also commonly used as an indicator of El Niño conditions in California coastal waters. Anomalously low values of the index (negative anomalies) are presumed to be consistent with El Niño conditions. The upwelling index and anomalies for 33°N (the Southern California Bight) are illustrated here. (Data were provided by the Pacific Fisheries Environmental Laboratory: http://www.pfeg.noaa.gov/index.html). The base period for calculating the climatologies was 1948–67. Pattern in the anomalies should be considered in the context of the annual cycle in the upwelling index. In the Southern California Bight, the index is normally

very low in winter, and it peaks in late spring. Spring and summer of 1997 showed a variable pattern of positive and negative anomalies. The upwelling index was near normal to slightly below normal in the winter of 1997–98, the season when the index is normally low (fig. 4). The winter of 1997–98 showed values near the climatology. The large anomalies in the upwelling index were seen in the summer of 1998, when it was much lower than normal, and in 1999, when it was higher than normal.

The hydrographic data collected on CalCOFI cruises provides additional information about the circulation pattern in the coastal waters and the temperature-salinity structure below the surface layer. Past studies have shown that El Niño conditions are characterized by a stronger and broader coastal countercurrent, and by a warmer and deeper-than-normal mixed layer (McGowan 1985; Simpson 1992; Lynn et al. 1995). Detection of El Niño
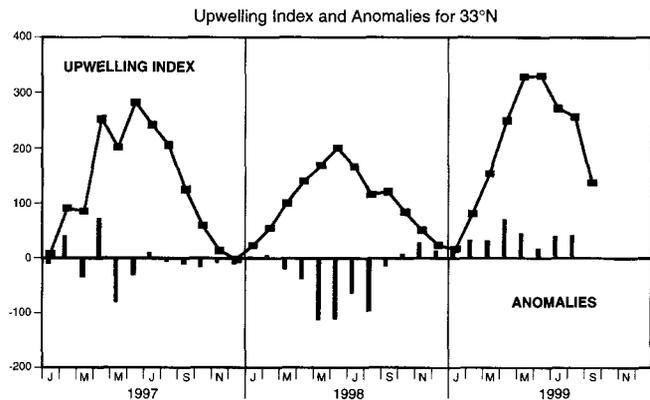
Figure 4. The upwelling index and anomalies in the upwelling index for 33°N. Units are in m³ s⁻¹ per 100 km of coastline.

effects upon the circulation pattern by comparing an observed pattern with the climatological mean is a more subjective process than for temperature or sea level because there is no single index which reflects the circulation pattern. The circulation patterns measured on the CalCOFI cruises during 1997–99 are illustrated in the annual State of the California Current reports (Lynn et al. 1998; Hayward et al. 1999), and only the highlights as they relate to El Niño conditions are illustrated here.

The first cruise in which changes in the circulation pattern were attributed to El Niño was made in July 1997 (cruise 9707). The upper ocean circulation was similar to the climatology (calculated from the 1950–92 base period). However, the anomalously strong northward flow of relatively warm and saline water in the undercurrent at middepths (300–400 m) along the coast was attributed to El Niño (Lynn et al. 1998; fig. 5). The circulation on the next cruise (October 1997) was relatively similar to the climatology (data not shown here but see Lynn et al. 1998). The February 1998 pattern showed very strong northward flow, now in the upper layers in the countercurrent along the coast, and this strong northward flow continued around Point Conception (fig. 6a). The strong advection from the south is reflected in the quite high salinities along the coast. The southward-flowing, low-salinity jet that forms the core of the California Current was also located farther offshore than normal. These patterns are characteristic of prior El Niño events (Lynn et al. 1995). Interpretation of these patterns is subjective, but the differences in circulation during 1997–98 do not necessarily appear to be as pronounced as those seen in 1992 during the 1992–93 event (fig. 6b). The northward flow extended farther offshore in February 1992, making the change in circulation pattern more conspicuous, but the coastal gradient in dynamic height was stronger in February 1998 than in February 1992, indicating greater northward transport in 1998.

The more frequent hydrographic sampling during the 1997–98 event provided a good example of how rapidly the circulation pattern and related biological structure can change during an El Niño event. By April 1998, the circulation had changed from the pattern seen in February (relatively strong and broad northward-flowing countercurrent along the coast) to strong southward flow of the low-salinity core of the California Current along the coast (Hayward et al. 1999; fig. 6a). Sampling along CalCOFI line 83 during the March 1998 mini El Niño cruise showed that the change in circulation took place relatively rapidly between February and March 1998. There was a strong increase in chlorophyll along the coast, related to the change in circulation pattern (Hayward et al. 1999). A similar pattern was observed during the 1992–93 El Niño event, when the circulation pattern reversed in a similar manner and chlorophyll concentration increased rapidly from low values in January to normal spring levels in April (Hayward 1993). In each case the increase in chlorophyll was attributed to the dramatic shoaling of the pycnocline and nutricline, associated with the change in circulation. The circulation patterns on the July and September 1998 cruises were relatively similar to the long-term mean (Hayward et al. 1999).

Additional insights from the hydrographic data can be gained by plotting data from individual stations over time. Although spatial information is lost, this provides better temporal resolution of structure, since the data from the mini El Niño cruises can be included. T-S plots from station 90.30 show the evolution of water-mass structure in the coastal waters (fig. 7). The individual cruise data are compared with the 1950–92 climatology. The first strong El Niño signal is again seen in July 1997. The anomalously warm, saline water associated with the strong northward flow in the undercurrent is clearly evident in the T-S plot. However, note that the T-S structure in the upper layers is similar to the climatology (as was the circulation).

The data in December (cruise 9712) show the first strong El Niño signal in T-S structure that affected the full water column. The T-S plots show that the entire water column is warmer and more saline than normal. The February to April 1998 structure continued the trends from December, and the anomalies increased in magnitude. By May 1998 the surface layer was slightly cooler and fresher than normal, but the thermocline continued to be anomalously warm and saline, and this pattern continued in June. By July 1998 the surface layers were much fresher than the climatology and near normal in temperature, and the T-S structure in the lower layers was similar to the climatology.

The hydrographic data are also illustrated by plotting the vertical structure of temperature anomalies (again
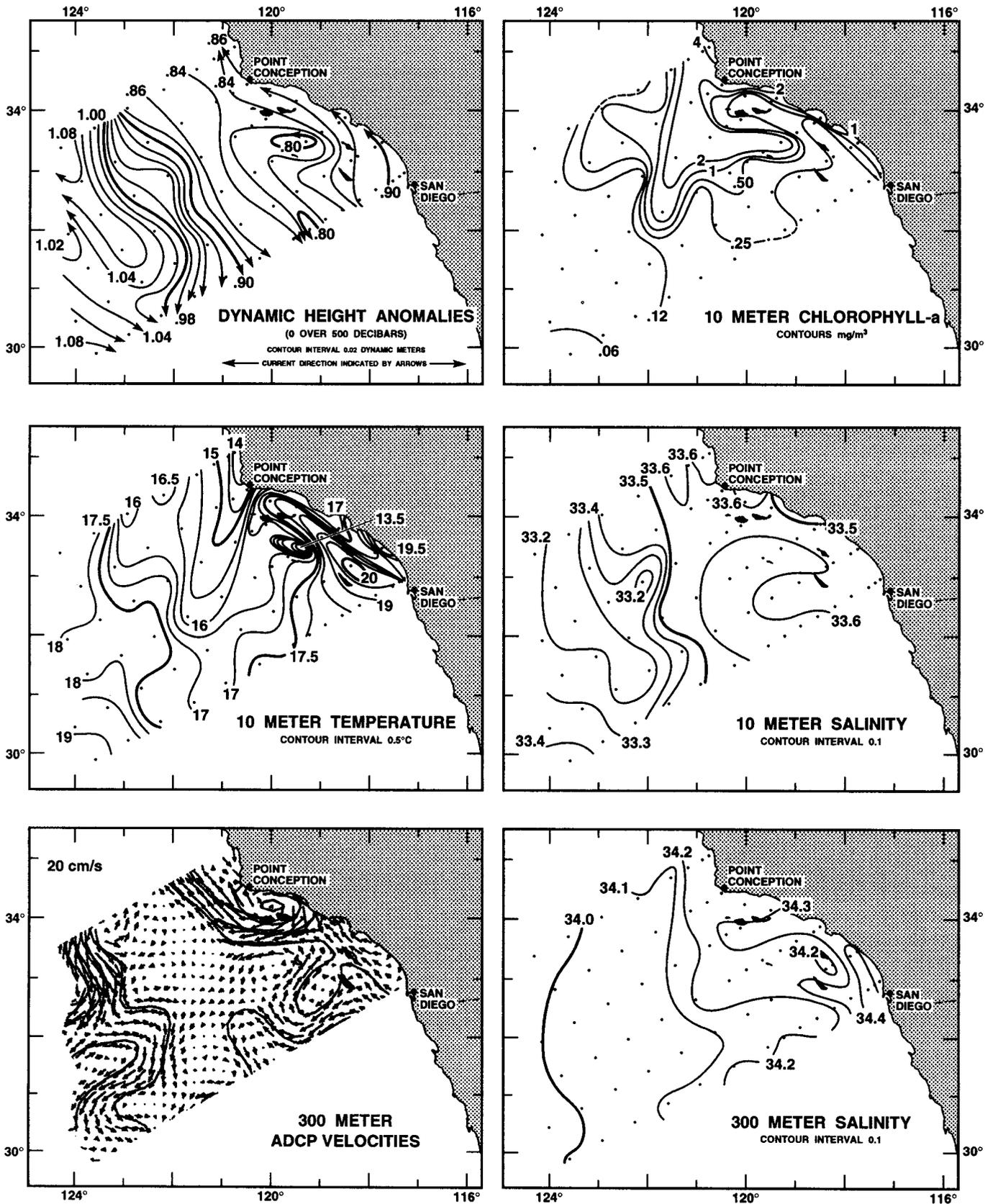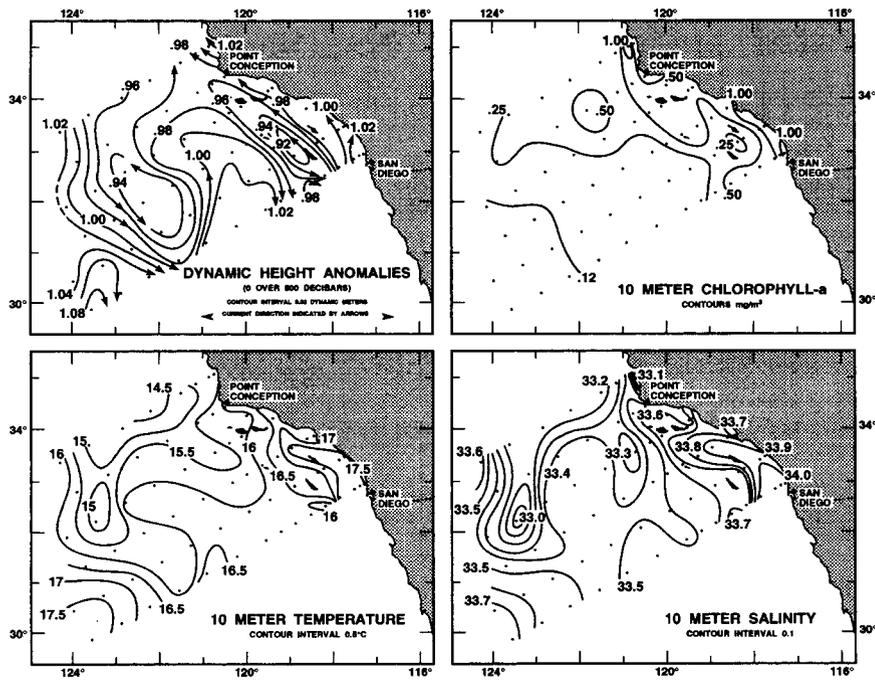
CALCOFI CRUISE 9707

Figure 5. Spatial distribution of properties on CalCOFI cruise 9707.
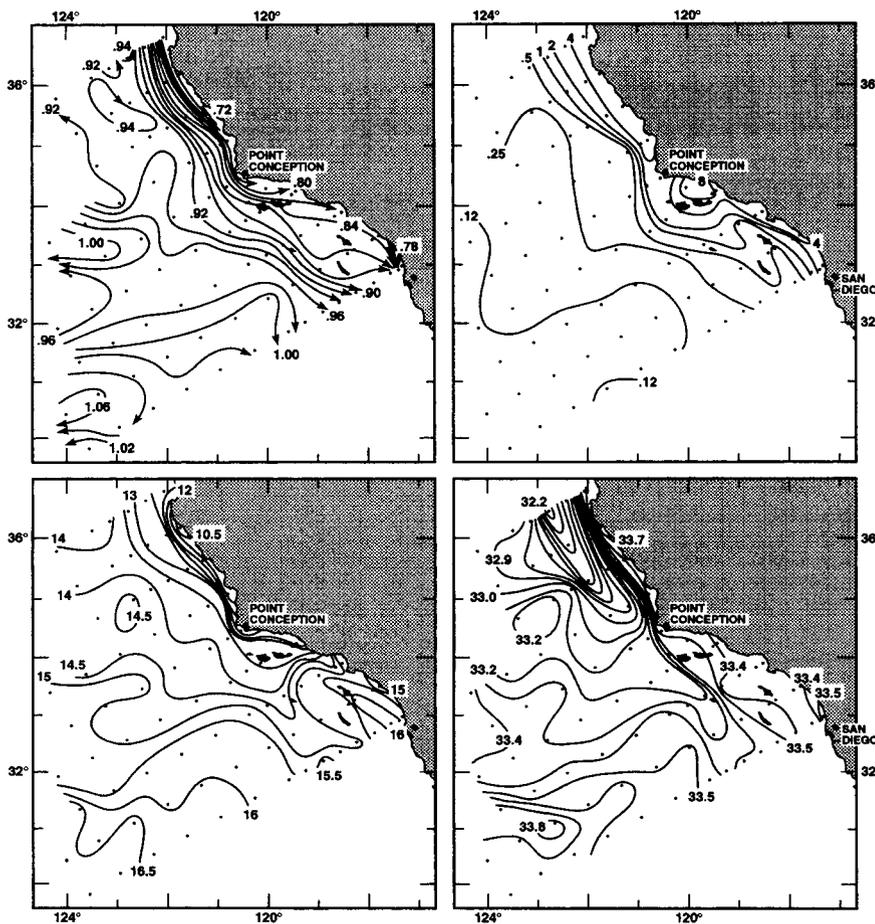
CALCOFI CRUISE 9802

CALCOFI CRUISE 9804

Figure 6a. Spatial distributions of dynamic height, salinity, temperature, and chlorophyll on CalCOFI cruises 9802 and 9804.
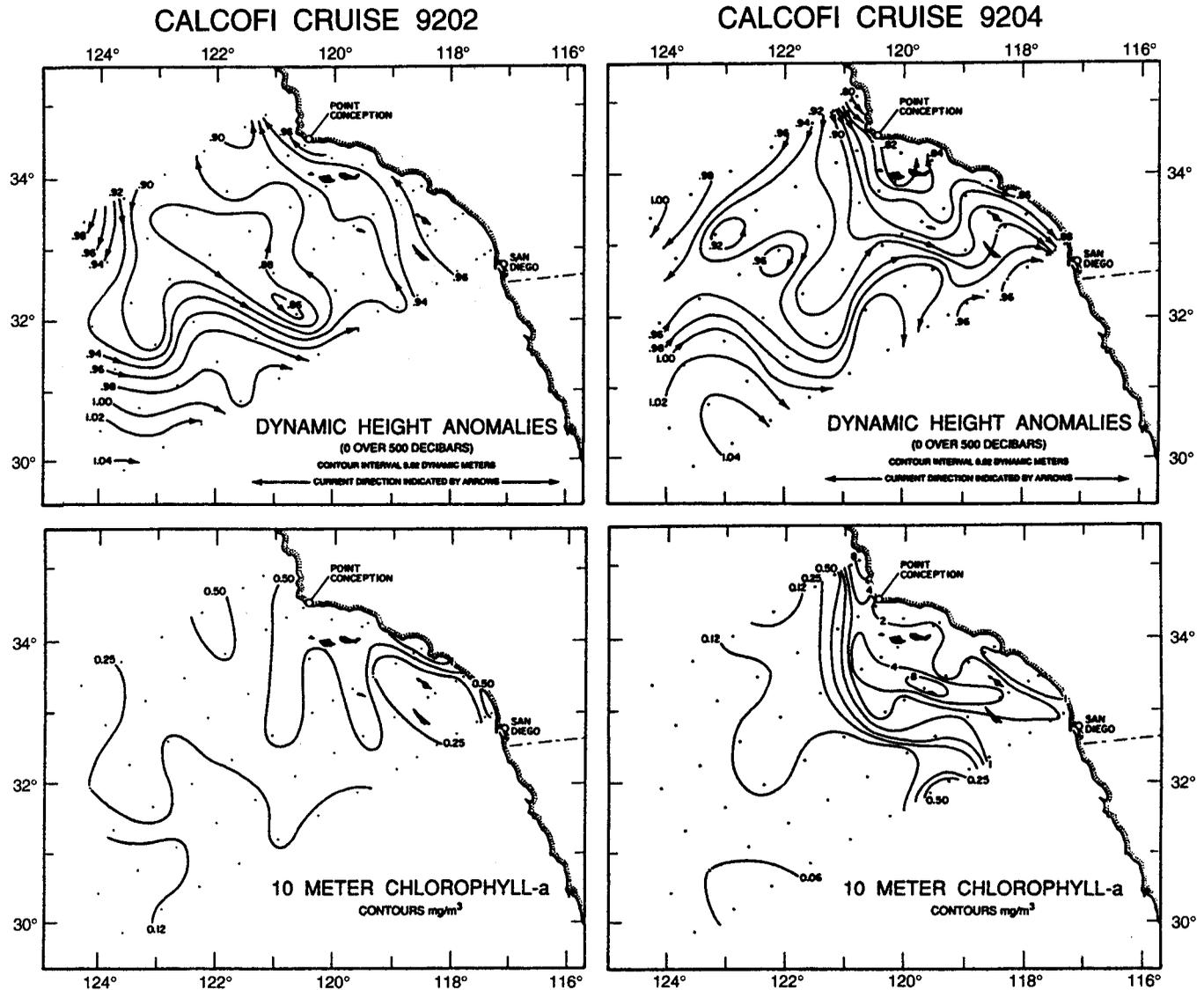
Figure 6b. Spatial distributions of dynamic height and chlorophyll on CalCOFI cruises 9202 and 9204.

based upon comparison with the 1950–92 climatology) over time. This illustrates the warming of the upper layers and the deepening of the thermocline. The deepening of the thermocline associated with El Niño can be seen in the characteristic subsurface maxima in temperature anomalies (McGowan 1985; Lynn et al. 1995). Stations 90.30 and 96.60 showed similar patterns (fig. 8). Warming of the surface layer was evident at both stations in the spring and summer of 1997, but note that the waters in the thermocline were normal to cool during this period. The absence of a subsurface maximum in temperature anomalies shows that the thermocline was not shallower than normal in the summer of 1997. The thermocline deepened dramatically in December 1997 at both stations, and positive temperature anomalies of greater than 4°–6°C were seen in the thermocline. These thermocline temperature anomalies are quite

large by historical standards. Thermocline anomalies of greater than 4°C that were seen in January and March 1983, during the 1982–83 El Niño event, were 9 standard deviations from the long-term mean calculated at that time (Simpson 1983). Anomalies greater than 2° were seen in January 1993, during the 1992–93 event (Hayward et al. 1994). The strong El Niño signal in thermocline temperature anomalies persisted until about September 1998, when there was a rapid transition to negative temperature anomalies in the upper layers and thermocline. It is interesting to observe that during both the onset of El Niño conditions and the transition to La Niña conditions, the change in temperature anomalies first took place in the mixed layer and then penetrated downward into the thermocline. At the onset of El Niño the thermocline was normal to cool while positive temperature anomalies developed in the mixed layer, and
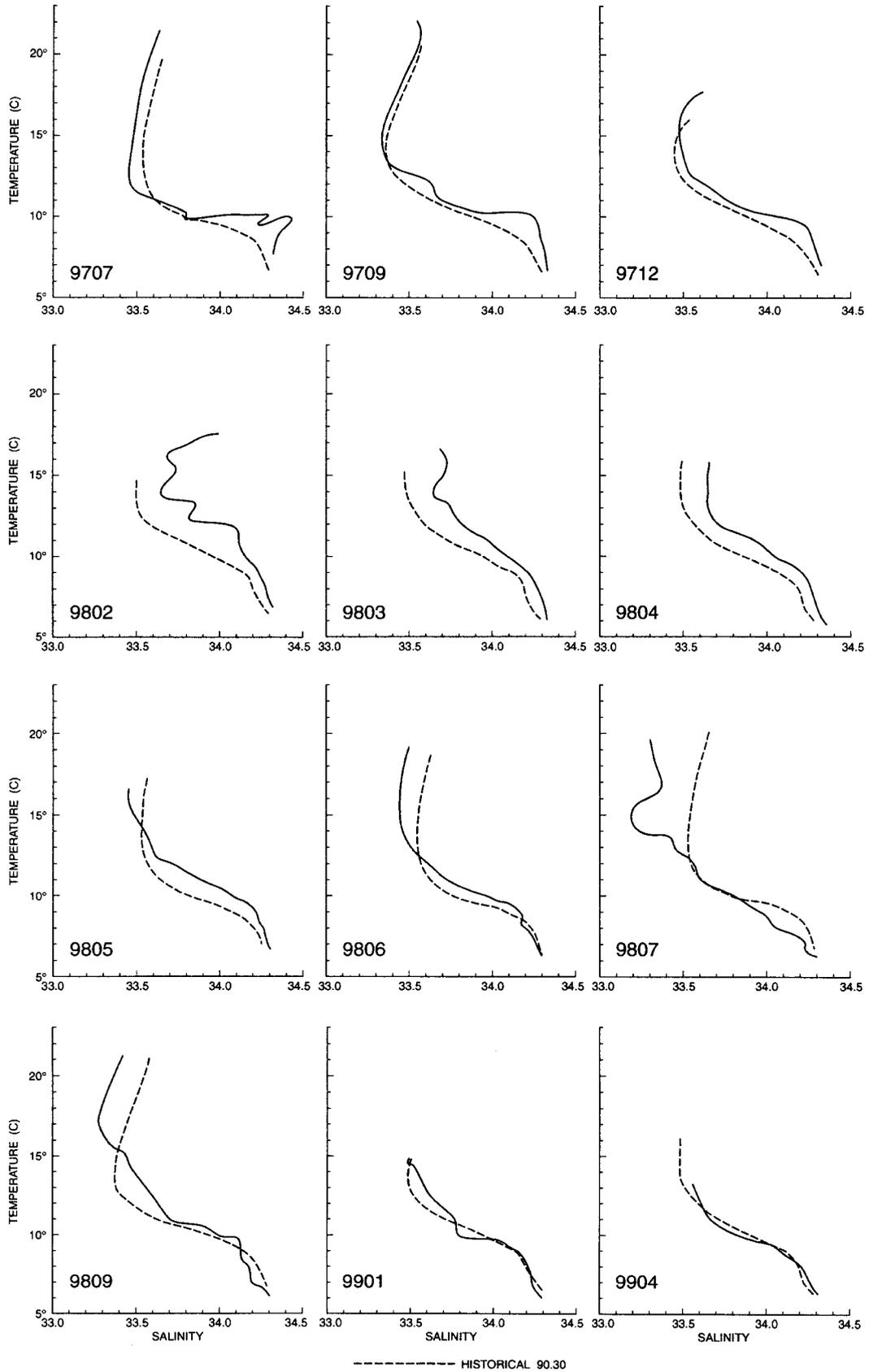
Figure 7. T-S plots for CalCOFI station 90.30. The historical mean T-S structure for each month is also shown (dashed line).
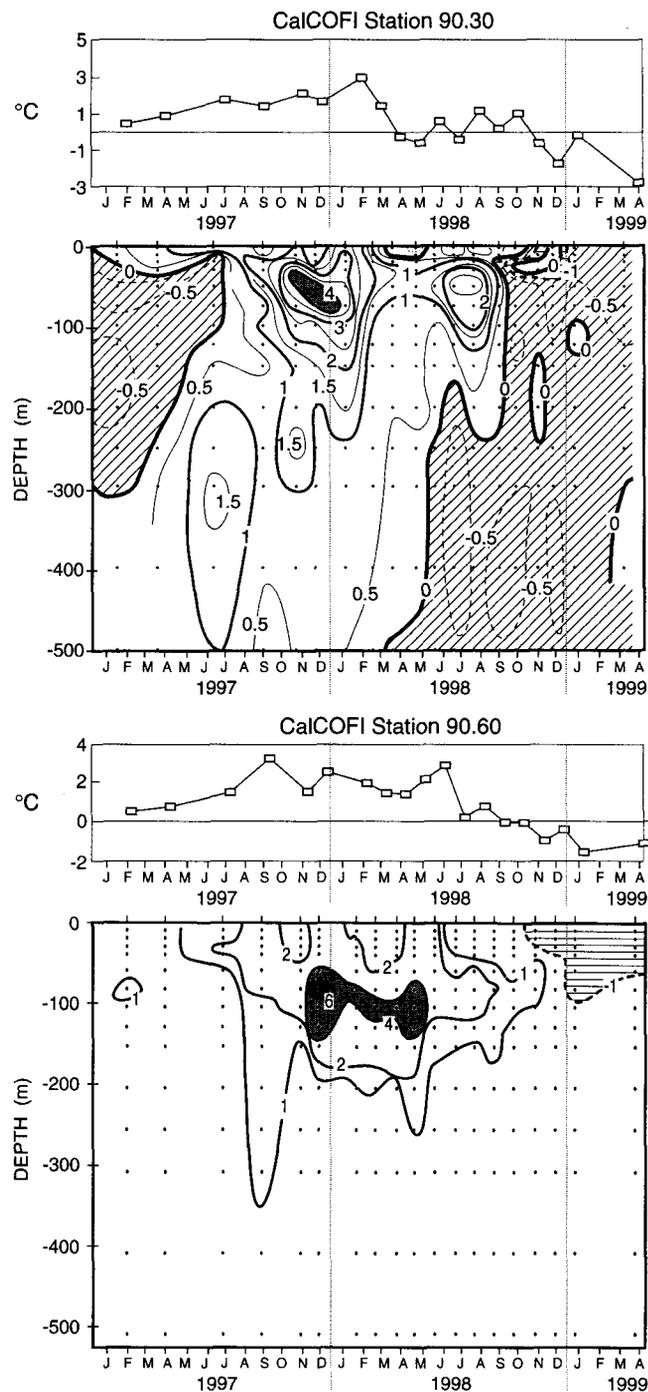
Figure 8. Vertical sections of temperature anomalies versus time for CalCOFI stations 90.30 and 90.60. SST anomalies are also illustrated above each section.

the converse was true during the transition to La Niña. In contrast to the impression that might be gained from surface data, the thermocline temperature anomalies were much larger in July 1998 than they were in July 1997. The surface (mixed layer) signal will give a different impression of the timing of events than the thermocline signal.

Much additional analysis remains to be done on the hydrographic data. The reader should be aware that there are some inconsistencies in the preliminary interpretation presented here. In particular, the abrupt change in the circulation in April 1998 when cool, fresh water appeared along the coast (fig. 6a) does not appear to be reflected in the sections of temperature anomalies over time (fig. 8) or in the time series of T-S plots (fig. 7). Plotting vertical sections and making temperature anomaly sections and T/S time series at additional stations will help to reveal the spatial pattern of changes in hydrographic structure associated with El Niño.

2. Ecosystem Structure

This analysis of changes over time in ecosystem structure begins with a summary of the trends in chlorophyll concentration. El Niño effects on chlorophyll are more difficult to quantify than the trends in physical properties because the long-term data set is limited. CalCOFI has made routine measurements of chlorophyll concentration only since 1984, although measurements were made on some individual cruises prior to this.

Perhaps the most interesting and surprising aspect of the chlorophyll data is that the measurements made during the 1997–98 El Niño event do not appear to be anomalous when considered in the context of the 1984–99 period. Since this finding is unexpected and it bears upon the mechanisms by which El Niño affects other aspects of ecosystem structure, I illustrate this in several ways. First, the cruise mean values for vertically integrated chlorophyll (typically based upon sampling 14 depths at each station and averaging 66 stations per cruise) for 1997 and 1998 do not stand out in the scatter of the cruise means for the 1984–99 period (fig. 9). These data are from the quarterly sampling cruises covering the full CalCOFI grid. Including data from the mini El Niño cruises provides better temporal resolution during 1997–98 along line 90. Here I illustrate the average vertically integrated chlorophyll on the 7 stations from the coast to station 90.60 for 1996 to 1999 (fig. 10). The 1997–98 period does not differ from 1996. Indeed, the unusual aspect in this period is the quite high chlorophyll seen in December 1998 and April 1999 (during the transition to La Niña conditions; Hayward et al. 1999). These figures illustrate the spatial average of vertically integrated chlorophyll.

El Niño may also affect the vertical distribution and spatial pattern of chlorophyll (McGowan 1985). Vertical structure and spatial pattern in these chlorophyll data are still being analyzed, but the first analysis again does not show any obvious trends during the 1997–98 period. This is illustrated by comparing the spatial pattern of 10 m chlorophyll on the spring CalCOFI time-series cruises from 1996, 1997, 1998, and 1999 (fig. 11). The spatial
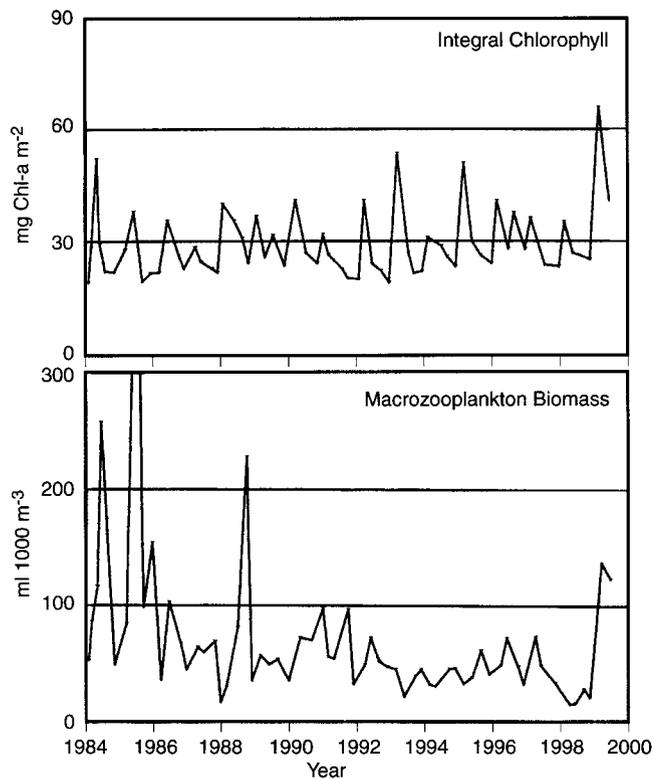
Figure 9. Cruise means of vertically integrated chlorophyll and macrozooplankton biomass for CalCOFI cruises from 1984 to 1999, for the cruise grid covering lines 77 to 93 (fig. 1).

Figure 10. Averages of vertically integrated chlorophyll for the six stations along line 90 from the shore to station 90.60.

pattern and concentration of near-surface chlorophyll during the springs of 1997 and 1998 do not look unusual when compared to springs of the other years.

An additional aspect of pattern in the distribution of chlorophyll during the 1997–98 El Niño is worth emphasizing. Chlorophyll increased rapidly from January to April 1998 (fig. 6a). This is surprising in light of the strong thermocline temperature anomalies which were observed at this time (fig. 8). However, a rapid transition in hydrographic structure also took place between February and April 1998 (Hayward et al. 1999). The California Current moved inshore along the coast, resulting in a strong upward tilt to the thermocline, and this nutrient input appeared to fuel the increase in chlorophyll. This is a common event during spring, but it is interesting to observe that it can still take place and result in a normal increase in chlorophyll even during strong El Niño conditions when the thermocline and nutricline are unusually deep. It is possible that a normal cycle in the circulation pattern and a strong spring increase in chlorophyll related to the changing circulation is a normal event, even during El Niño conditions. This same general pattern was also observed during the 1992 El Niño event, and in each case chlorophyll concentrations were elevated along the coast (fig. 6b).
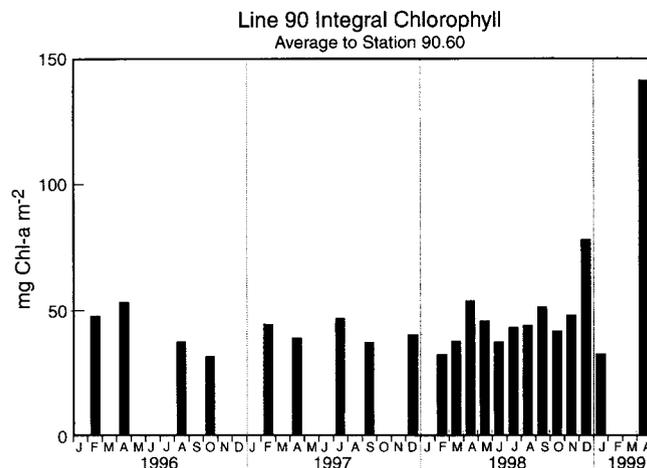
The apparent lack of a trend in chlorophyll during the 1997–98 El Niño event differs from the common dogma, and it is worth asking why. There are few direct observations of chlorophyll during prior events, and there are even fewer long-term data sets to compare these observations to. McGowan (1984, 1985) summarized the shipboard observations made by CalCOFI during the 1982–83 El Niño event. He reported a large decrease in surface chlorophyll, and concluded that there was a redistribution of the vertical structure in chlorophyll. The chlorophyll maximum became deeper in association with a deepening of the nutricline. Fiedler (1984) compared a CZCS image of near-surface chlorophyll made during the 1982–83 El Niño (15 March 1983) with an image made on 19 April 1982. He concluded that near-surface chlorophyll during El Niño was reduced to less than half of the 1982 values.

The question of whether chlorophyll concentration changed or its vertical or spatial distribution changed during the 1997–98 El Niño event remains open. Analysis of the vertical and spatial distributions is continuing. It will be important to resolve this to the extent possible given the available data, because El Niño–caused changes in the nutrient distribution, chlorophyll, and primary production are presumed to be one of the main ways in which changing physical structure impacts the ecosystem. Given the range of interannual variability, only relatively large effects can be detected. Comparison of the 1997–98 El Niño period with only the immediately preceding and following periods may give a misleading impression. The quarterly CalCOFI time-series cruise in October 1996 was quite unusual in that high chlorophyll was observed. Fall is generally a time of low chlorophyll, and the chlorophyll measured on this cruise was the highest measured in the 1984–96 period (Schwing et al. 1997). Very high chlorophyll was also measured in
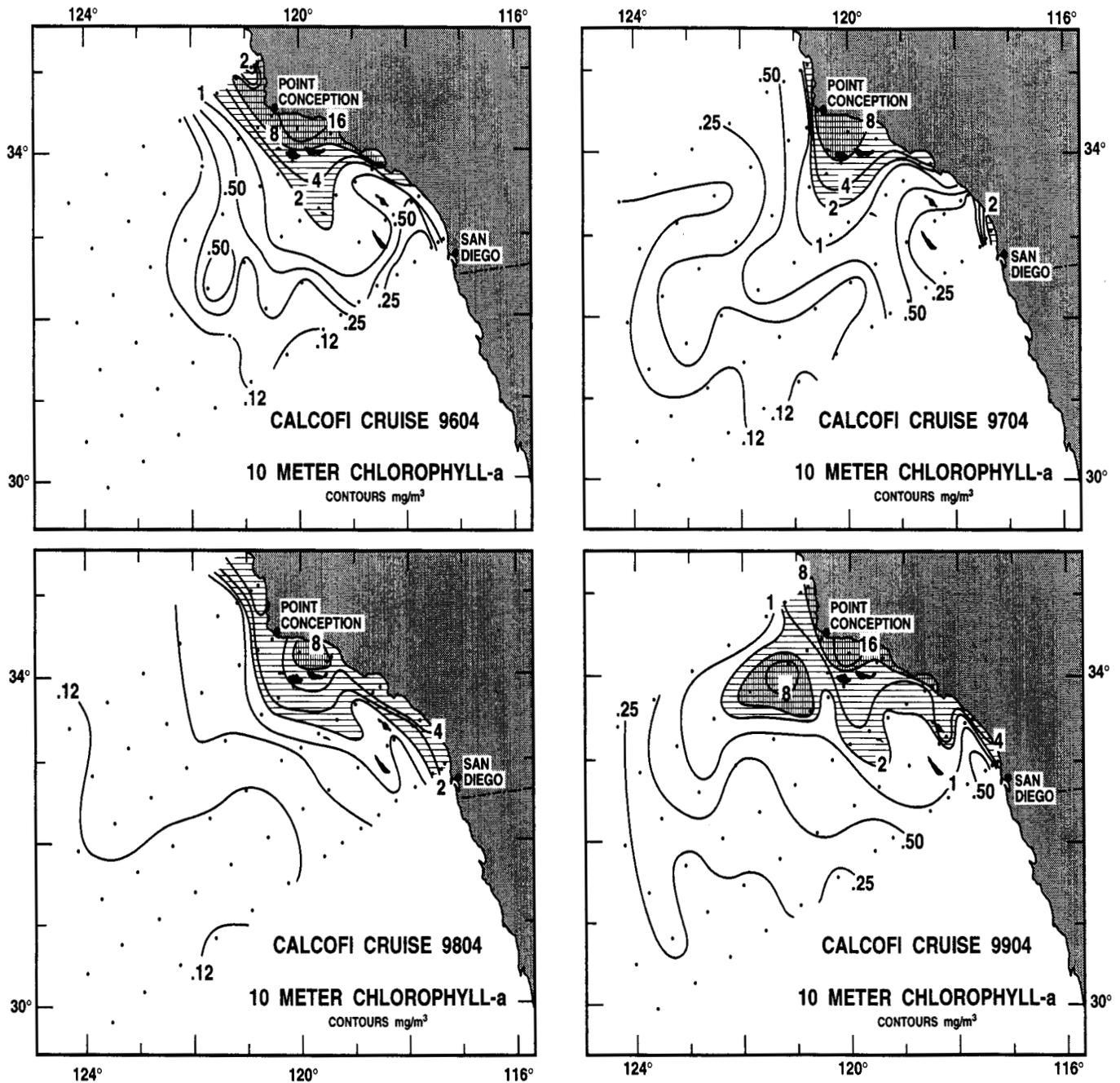
Figure 11.   Spatial pattern of 10 m chlorophyll for spring CalCOFI cruises in 1996, 1997, 1998, and 1999.

the spring of 1999 in association with the transition to La Niña conditions (Hayward et al. 1999). Hence comparison of chlorophyll concentrations in the 1997–98 El Niño period with the periods immediately preceding and following it might lead to the impression that chlorophyll declined during the El Niño event, whereas analysis of the 15-year data set leads to the impression that the real anomalies were in the preceding and following years. Shipboard and remote sensing data will have to be carefully compared in order to answer the question

of whether observed changes are due to changes in vertically integrated chlorophyll or a redistribution of vertical structure.

Zooplankton is the most thoroughly sampled biological property in the CalCOFI data set, having essentially the same spatial and temporal coverage as the hydrographic data. During past events, macrozooplankton biomass has shown a strong El Niño signal. Very large declines in macrozooplankton biomass during prior strong El Niño events (particularly 1958–59 and 1982–83) have
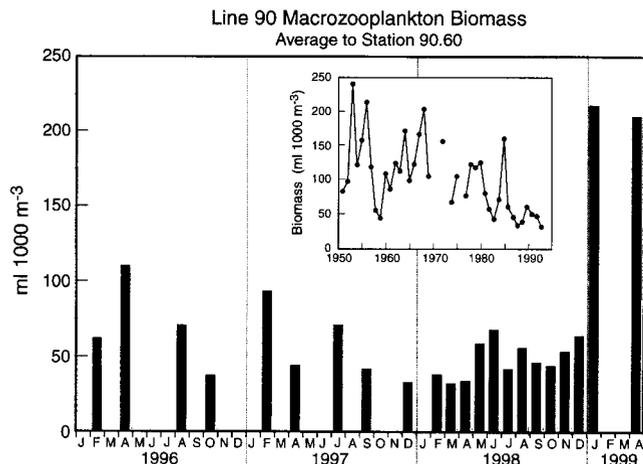
Figure 12. Averages of macrozooplankton biomass for the six stations along line 90 from the shore to station 90.60; *inset,* the long-term trend in macrozooplankton biomass.

TABLE 1
Preliminary Summary of El Niño Effects on Euphausiid Populations in the CalCOFI Study Area

Year	Abundance
Euphausia pacifica (an abundant cool-water species)	
1996	High
1997	Decline from high 1996 values to typical values
1998	Very low—lowest in the record
1999	Strong increases from 1998 levels
Nyctiphanes simplex (a southern species)	
1997	Not abundant in CalCOFI sample region
1998	Average in winter—high in spring
1999	Average to low

Note: Data from winter (January–February) and spring (March–April) cruises only. Thanks to Ed Brinton, Marine Life Research Group, Scripps Institution of Oceanography.

been described (Roemmich and McGowan 1995a, b; McGowan et al. 1998). The 1997–98 event also affected macrozooplankton biomass. The cruise means of macrozooplankton biomass during 1998 were all the lowest in the 1951–98 record (Hayward et al. 1999; figs. 9 and 12). However, calculation of anomalies from the long-term (50-year) mean may in some senses overstate the impact of this event. There has been a strong (70%) long-term trend of declining values of macrozooplankton biomass (Roemmich and McGowan 1995a, b) . The relative effect of El Niño upon macrozooplankton biomass can be illustrated by comparing El Niño periods with the preceding and following years. (In contrast to the situation with chlorophyll, the El Niño signal in macrozooplankton biomass is very clear in the long-term record. The comparison with adjacent years is not intended to ask whether an El Niño signal can be detected over the variability on other space-time scales, but rather, given that such a signal has already been detected: What is the short-term impact of each event?) The 1958–59 and 1982–83 El Niño events reduced macrozooplankton biomass to about 20%–30% of the preceding and following years (fig. 12). These were very strong events by this measure. The relative decline in macrozooplankton biomass during 1997–98 (about a 50% decline in comparison to 1994–96 period) is smaller than during the prior strong events (fig. 9). It is hard to say when an El Niño–related decline in macrozooplankton biomass began, because the signal is superimposed upon significant interannual variability and patchiness. The large increases in 1999 in association with the transition to La Niña conditions are also evident.

In addition to changes in biomass, zooplankton species composition in the CalCOFI study area may also be affected by El Niño. Due to a combination of advection

and changes in habitat structure, southern "warm-water" species tend to become more abundant and northern "cool-water" species less abundant during El Niño events (Brinton and Reid 1986). Without data from the entire range of a population, it is difficult to separate local changes in population size (due to changes in the distribution of a species) from trends in the overall abundance of the species. Some preliminary information on the El Niño effect on the distributions of individual euphausiid species during 1997 and 1998 is also available (thanks to Ed Brinton, SIO). Data are presently available only for winter and spring cruises during this period (table 1). The California Current dominant cool-water species *Euphausia pacifica* was extremely abundant in the winter and spring of 1996. This species then declined in abundance in 1997 to nearly normal values, and the decline continued in 1998 to the lowest values on record. The winter and spring of 1999 showed strong increases from the low values of 1998. For *E. pacifica,* 1998 was certainly a year of unusually low abundance, but it is hard to know whether to attribute the 1997 data to El Niño forcing or to a decline from the unusually high 1996 density. Shifts in springtime abundances of *E. pacifica* from highest to lowest recorded extremes followed by abrupt (one-year) recoveries were previously associated only with the 1957–59 and 1980–84 periods, which were also El Niño events. *Nyctiphanes simplex,* a southern, warm-water species, was not abundant in the CalCOFI study region in 1997, but it was quite abundant in 1998, and it returned to normal to low abundances by 1999. The euphausiid data thus generally show the expected declines in the northern, cool-water species and increases in the southern, warm-water species in winter and spring of 1998 and a reversal in 1999. But the 1997 data are ambiguous as to whether there was an early El Niño signal in the euphausiid distribution.

Pinnipeds in the northern Channel Islands were strongly affected by El Niño conditions in both 1997

TABLE 2
Preliminary Summary of El Niño Effects on Pinniped Populations in the Channel Islands

1997
Northern fur seals and California sea lions: Pup mortality increased dramatically; few pups born during 1997 survived.

1998
Northern fur seals: Pup production low; increased mortality in adult females. California sea lions: Few pups born; pup mortality high.

1999
Improved conditions for pinnipeds.

Note: The pupping and breeding season is from June to September. Thanks to Robert DeLong et al. (National Marine Mammal Laboratory, AFSC, NMFS, Seattle).

TABLE 3
Preliminary Summary of El Niño Effects on Seabirds in Southern and Central California

Southern California
1997
Brown pelican and double-crested cormorant: Near normal nesting effort, but significant chick mortality (brown pelican) and nest abandonment (double-crested cormorant).

Greater than 50% reduction in productivity (chicks/pair) for double-crested cormorant.

No signal in productivity for Cassin's auklet, Xantu's murrelet, or western gull.

1998
Greater than 50% reduction in breeding populations of brown pelican, double-crested cormorant, Brandt's cormorant, pelagic cormorant, and Cassin's auklet; but no signal in Xantu's murrelet.

50% reduction in productivity (chicks/pair) for brown pelican but no signal in productivity for Cassin's auklet, Xantu's murrelet, or western gull.

Central California
1997
No apparent signal.

1998
Reduction in nesting effort; significant delay in breeding; reduction in productivity.

Amplitude of response is species dependent.

Thanks to Bill Sydeman, Point Reyes Bird Observatory, and collaborators: Point Reyes Bird Observatory, University of Washington, Channel Islands National Park, UC Davis, San Francisco Bay National Wildlife Refuge.

and 1998. (Robert DeLong, pers. comm.) The breeding and pupping season runs from June to September (table 2). This is the part of the annual cycle for which information is available, but changes seen during the pupping season presumably reflect an integration of the population response to environmental conditions over some longer period of time. The poor survival of northern fur seal and California sea lion pups born in June and July 1997 (most were dead by October) means that pinniped populations experienced a dramatically different environment in California waters in the summer of 1997. The poor conditions for pinnipeds continued into 1998. Pup production was low; pup mortality was high; and there was increased mortality in adult females of northern fur seals. The onset of the El Niño effect on pinnipeds appeared to precede the onset of the effect on thermocline and nutricline depth by several months. Conditions improved for pinnipeds in 1999. The El Niño signal must also be interpreted in the context of the long-term trend of population increases in pinnipeds.

Observations made at seabird colonies provide information on trends in abundance and physiological state. (Thanks to Bill Sydeman, Point Reyes Bird Observatory, and collaborating projects; table 3). Some effects on seabirds nesting in the Channel Islands during the summer of 1997 were attributed to El Niño. These included nest abandonment and a greater than 50% reduction in productivity (chicks/pair) in double-crested cormorants, and significant chick mortality in brown pelicans. The effects were even greater during the summer of 1998, and central and southern California were affected.

El Niño effects on seabird populations are also being studied by examining long-term patterns of seabird distribution and abundance at sea (Ainley et al. 1995; Veit et al. 1996; Hyrenbach and Veit 1999). Routine surveys made on CalCOFI cruises during 1997–98 revealed that overall seabird abundance between July 1997 and April 1998 remained consistently low when compared to long-term seasonal means (Lynn et al. 1998; Hayward et al. 1999). Additionally, the seasonal cycle of seabird abun-

dance was disrupted during 1997–98. Instead of the usual summertime maximum, overall seabird abundance peaked in the fall of 1997 in response to the transient immigration of southern warm-water species (i.e., black-vented shearwater and black and least storm petrels; Lynn et al. 1998; Hayward et al. 1999). These fluctuations in seabird community composition resemble similar changes observed during the 1992–93 El Niño (Ainley et al. 1995; Veit et al. 1996). However, it is difficult to separate a clear El Niño signal during 1997–98 from the long-term trend of declining seabird abundance (fig. 13; Veit et al. 1996; Hayward et al. 1999; Hyrenbach and Veit 1999).

Squid populations also respond to El Niño events, and understanding the effects is an important management issue. Market squid was the most economically valuable fishery in the state of California in 1996 (California Department of Fish and Game 1997, 1998). The market squid data (thanks to Marci Yaremko, California Department of Fish and Game) can be best considered in the context of a five-year record of landings. The fishery in the northern Channel Islands normally occurs during winter (November–March), and the data are thus shown for the winter periods spanning two years (fig. 14). There has been a steady increase in the fishery since at least the mid-1990s, to the
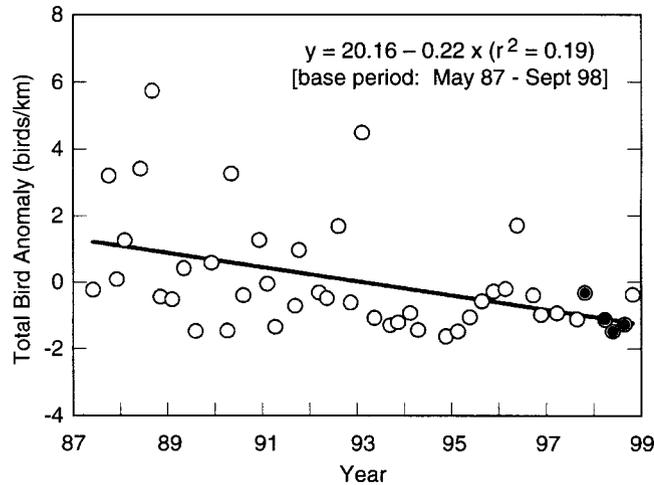
Figure 13. Seasonal anomalies in overall seabird abundance obtained by subtracting the average abundance from each cruise from the long-term (1987–98) seasonal mean. Values for cruises between July 1997 and April 1998 are depicted by filled circles.
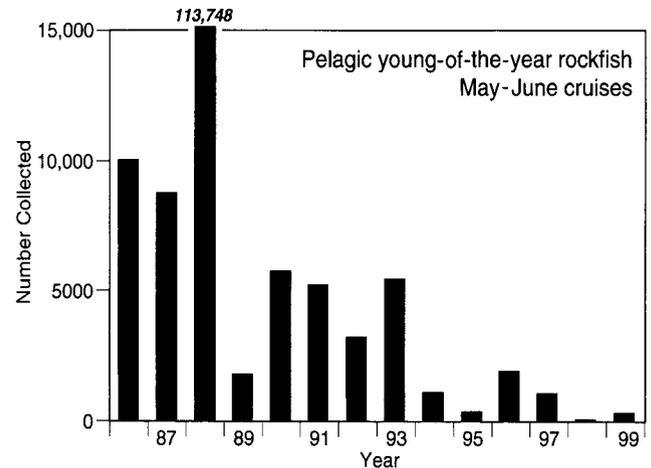

Figure 14. Monthly landings of market squid in the southern California region, 1994–99.

Figure 15. Abundance of pelagic young-of-the-year rockfish collected by midwater trawl in the Monterey region during spring, 1986–99.
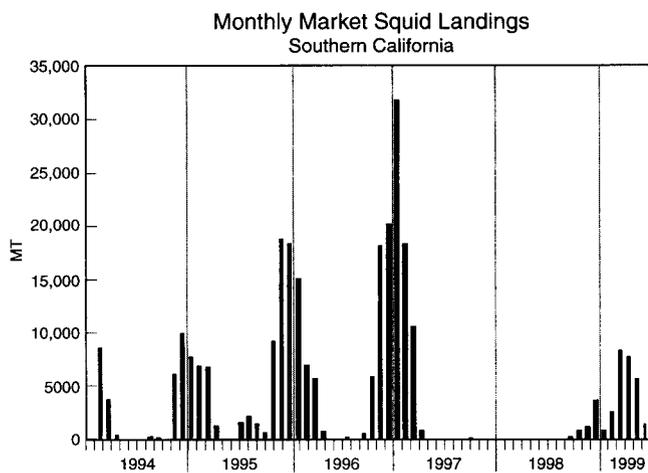
considered in the context of the longer-term trend of a strong decline over the last decade. Abundance was low in the years 1997, 1998, and 1999, but it is not necessarily clear that an El Niño signal can be detected over the longer-term trend of declining values (fig. 15).

Long-term studies have shown that kelp forest communities tend to be affected by changes in physical structure associated with El Niño events (Tegner et al. 1996). The cause-and-effect relations linking changes in physical structure and kelp forests may be better understood than is the case with pelagic populations. Kelp forests respond to changes in nutrient inputs, which are correlated with trends in coastal temperature anomalies. Kelp forests are also affected by disruptions caused by El Niño storm events. Time-series observations in the Point Loma kelp forest (thanks to Mia Tegner, SIO) show that kelp density and the stipe index (an index of physiological state, Tegner et al. 1996) were both strongly affected from the fall of 1997 through calendar year 1998 (fig. 16; Hayward et al. 1999). The decline in abundance was attributed to direct impacts by storm events and indirectly by reduced growth rates due to nutrient stress during warm-water conditions.

DISCUSSION

Managers and policymakers are concerned with better understanding how and why the ecosystem in our local waters changes during El Niño events. With respect to physical impacts, it is important to have an objective way to determine when physical structure changed, how strong the impacts were, and when they ended. Improved understanding of the ecological consequences, including determining which observed ecosystem changes should be attributed to El Niño as opposed to something else, and better determining the specific physical causes of ecosystem effects are impor-
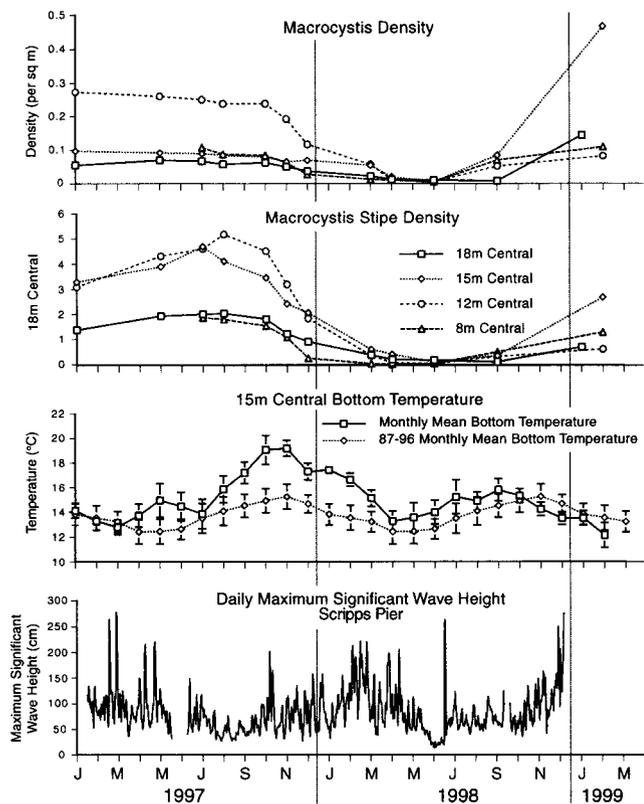
quite high landings of the winter of 1996–97. There were virtually no landings from the Channel Islands fishery in the winter of 1997–98. Landings were low in the winter of 1998–99, but there was an unusually significant catch in the spring of 1999. The squid data are consistent with strong El Niño effects in the winter and spring of 1997–98 and a recovery in the winter and spring of 1998–99.

Pelagic young-of-the-year rockfish are another group with important implications for fishery management and for which there are time-series data that can be used to look for an El Niño signal and its relation to longer-term trends. Recent data on rockfish (thanks to David Woodbury, NOAA-NMFS Santa Cruz/Tiburon Laboratory, http://www.pfeg.noaa.gov/tib/index.htm) must be

Figure 16. *A*. Changes in density of *Macrocystis* adults (defined as 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 Scripps Institution of Oceanography Pier. Gaps in the data are due to equipment failure (Coastal Data Information Program).

tant scientific goals that support management and policy objectives.

The 1997–98 El Niño event affected different aspects of structure at different times. Hence, the question of when El Niño conditions started to affect California waters, and, specifically, the question of whether the system was affected by El Niño forcing during the summer and fall of 1997, depends upon which aspects of structure are considered. Elevations in sea-surface temperature and sea level, and the intensification of the undercurrent and related changes in T-S structure showed that some effects on physical structure were detectable by the summer of 1997. There was thus a short time lag for these aspects of the system to respond to (or at least be associated with) the dramatic changes which took place in the tropical Pacific that summer (fig. 2). However, the timing of changes in other aspects of local structure, particularly thermocline depth, T-S structure in the upper layers, and the upwelling index, showed that the full suite of physical effects of El Niño did not occur in California waters until the winter of 1997–98.

Managers considering how to respond to future El Niño events will generally have the easiest access to such widely and rapidly distributed physical data as SST anomalies and sea-level anomalies. The question is how such information is related to the overall trends in physical structure. The timeline showed that the El Niño impact upon these indices preceded the impact upon thermocline structure by a period of several months. The difference in timing of surface versus thermocline signals is particularly evident in the vertical section of temperature anomalies versus time (fig. 8). The onset and decline of temperature anomalies in the thermocline lags the surface layer by about six months. The upper thermocline (e.g., 50 to 150 m depth) was normal to cool in the summer of 1997, well after positive SST anomalies were evident. The converse was also true during the transition to La Niña conditions. Relatively large positive anomalies persisted in the thermocline during spring and summer 1998 as the surface layer became anomalously cool. Generally, however, the suite of physical indices examined here was in better agreement about the timing of the decline of El Niño conditions and that there was a relatively rapid transition to La Niña conditions in the summer of 1998.

Advection associated with the enhanced flow in the undercurrent in summer 1997 may be the explanation for the unusual northward range extension of southern warm-water species that summer. The strongest impacts upon upper ocean physical structure started during the winter of 1997–98. The deepening of the thermocline that started in November 1997 is probably the physical change which is most directly related to the nutrient distribution and primary production. The upper ocean physical structure suggests that primary production and related aspects of biological structure should have been most strongly affected during spring 1998 rather than summer 1997.

As with physical structure, there is ambiguity in the extent to which El Niño conditions affected ecosystem structure in California waters during the summer of 1997. Effects on pinnipeds and seabirds and northward extensions of the range of warm-water species in the summer of 1997 were attributed to El Niño forcing. However, El Niño effects during spring and summer 1998 were more pronounced in that more ecosystem properties were affected and the impacts were greater.

The observation that a few aspects of both physical and ecosystem structure were affected by El Niño conditions in the summer of 1997, while others were not affected until winter and spring of 1998 makes it difficult to develop a multivariate "California El Niño" index that could be used to define the timing of the onset or the intensity of El Niño conditions in California waters for a broad range of management and policy decisions.

It is not clear what criteria should be used to select the physical aspects of structure used to define El Niño conditions for the index. For many purposes those physical aspects which most strongly affect ecosystem structure would make good components of such an index. However, it is not clear what these are. There is a clear chicken-and-the-egg problem in defining cause-and-effect linkages between physical and biological trends by correlating timelines. If an aspect of ecosystem response is first used to define physical aspects of El Niño forcing, one cannot then turn around and use a timeline of that physical property in an El Niño index to detect the ecosystem response by correlation. Ambiguity in defining indices of physical forcing and ecosystem response should not necessarily be surprising, since attributing cause-and-effect relations to observed ecosystem changes is one of the great challenges in ecology and fisheries oceanography.

The timeline can be used to further study cause-and-effect linkages by examining whether the observed temporal patterns are consistent with those expected from theory. A range of mechanisms which link changing physical and ecosystem structure has been proposed (table 4). In each of these mechanisms changes in physical structure are expected to affect ecosystem structure following some time lag. The theories are better developed for some mechanisms than for others, and the time lags are generally not well defined. Testing these theories is also complicated because they are not mutually exclusive and more than one may affect a given population. Different mechanisms may also affect different populations. In spite of these complications, it is still useful to examine the timeline and determine the predictive skill that can be attributed to a basic approach a manager might use to implement these theories. Even when the expected time lags are not well known, an effect should follow its cause.

Changes in range due to advection of plankton and migration of mobile species have been invoked to explain the popular reports of northward extensions of the range of southern, warm-water plankton and game fish species. This general explanation has also been invoked to explain shifts in the local abundance of planktonic species, such as euphausiids, with northern and southern affinities. However, the timing and nature of the trends in circulation pattern are not necessarily consistent with this explanation. The strong northward flow in the summer of 1997 occurred at middepths. There was quite strong northward flow along the coast in February 1998, and the high salinity was consistent with strong advection from the south. The role of physical forcing in changing the range of mobile species will be hard to deal with until more is known about the specific aspects of physical structure to which these species

TABLE 4
Summary of Mechanisms by Which El Niño Conditions May Affect Ecosystem Structure, and Expected Effects

Bottom-up Forcing

Physics → nutrient inputs → phytoplankton–primary production → zooplankton grazers → higher trophic levels.

Expect effects to occur in sequence (e.g., with time lags) following the physical change of an increase in mixed-layer (thermocline/nutricline) depth.

Advection

Changes in spatial distribution (especially plankton) due to changes in ocean circulation pattern.

Expect changes to occur at the same time and be correlated with changes in circulation pattern and water mass (T/S) structure.

Changes in Range and Location of Preferred Habitat

Changes in physical environment (temperature and salinity) cause mobile species to migrate and change their range. This will be seen as a change in abundance as species move in and out of the study area.

Expect changes in abundance of mobile species within the study area correlated with changes in habitat structure. This is best studied by looking at a larger area and documenting changes in range.

Top-down Forcing and Changes in Community Structure

Advection, migration, and changes in the range of top predators lead to changes in abundance of prey and competitor species (changes in community structure).

These mechanisms will be difficult to evaluate until the roles of predation and competition in structuring the pelagic community are better understood.

Internal Changes in Habitat Structure

Changes in other aspects of habitat structure such as changes in the vertical distributions of phytoplankton (e.g., depth and intensity of chlorophyll maximum layer) and zooplankton, changes in the size distribution or taxonomic composition of phytoplankton or zooplankton, or changes in horizontal distributions and intensity of patchiness on a range of scales could all affect abundance and pelagic community structure.

The impact of El Niño upon these mechanisms will also be difficult to evaluate until the processes influencing pelagic community structure are better understood.

Direct Thermal Effects

Changes in abundance or limits in range due to direct thermal effects.

Such changes will occur where the biogeographic boundary (or limit of the range of a species) is directly associated with temperature, and El Niño changes make the temperature of the habitat unsuitable for a species.

Examples include coral reef bleaching and direct temperature effects on kelp forests in the southern part of the range off Baja California, Mexico.

respond. It is also difficult to separate trends in local abundance due to trends in overall population size from trends in local abundance caused by changes in range, although a regional synthesis will help with this. Planktonic populations, such as the euphausiids, also show long-term trends in abundance whose causes are not well understood. Even when, as in 1998, it appears that there was an El Niño effect, it is difficult to determine the precise timing or magnitude of El Niño changes and separate them from trends due to processes on other time scales. Additional research is needed in several areas. It would be helpful to have a quantitative index of upper ocean transport (an advection index) which could be

used for comparison with population trends. A synthesis of the data from regional programs along the west coast of North America will help in showing whether changes in local abundance are due to changes in range or changes in overall population size. Development of a time series which reflects the preferred habitat structure of mobile species for comparison with population trends would be helpful, as would the development of additional time series of ecosystem structure.

Bottom-up trophic forcing is probably the most commonly cited cause-and-effect mechanism linking in situ changes in physical properties with ecosystem structure. In this mechanism, El Niño is hypothesized to affect the system by deepening the thermocline (and nutricline) and thus reducing the nutrient input, primary production, and phytoplankton abundance. This, in turn, is presumed to reduce the abundance of grazers upon the phytoplankton and their predators in the food chain above them. The link between physics and nutrients, at least, is clear. In the CalCOFI study region, there is a strong correlation between temperature and nitrate (Hayward and Venrick 1998). Changes in thermocline depth are thus a very good indicator of changes in nutricline depth. In the most simple implementation of the bottom-up theory, the strong impacts of El Niño on nutricline depth should be indicated by anomalies in thermocline depth as indicated by thermocline temperature anomalies. Warm water in the thermocline (e.g., 100–150 m) indicates that the nutricline is deeper than normal, and cooler water indicates that it is shallower than normal. Waters in the thermocline were normal to cool in July 1997, and the strong positive thermocline temperature anomalies did not develop until November–December 1997 (fig. 8). These warm thermocline anomalies persisted into summer 1998, and the greatest negative effect on production should have been during the time of the 1998 spring phytoplankton bloom.

The timeline observations are inconsistent with the expectations of a simple model of bottom-up trophic forcing in several ways. The effects on pinnipeds and seabirds in summer 1997 preceded the deepening of the nutricline. Further, the lack of a decrease in chlorophyll (and thus primary production, since the two are strongly correlated in the CalCOFI study region; Mantyla et al. 1995) in 1998, coupled with a decrease in macrozooplankton biomass, presents an ambiguous picture of whether even the first link in this presumed sequence of events following a deepening of the nutricline can be documented. Recall also the remarkable change in circulation in the spring of 1998, when the California Current swept shoreward along the coast, and shoaling of isopycnals and the nutricline resulted in a sharp increase in chlorophyll to what appear to be normal spring levels (fig. 6a). The facts that some of the presumed responses to bottom-up forcing preceded the forcing and that the first change in the presumed sequence of responses cannot be detected, indicate that this very basic implementation of a bottom-up model may have little skill in predicting the types of changes in ecosystem structure that managers and policymakers need to understand.

The above is clearly not a sufficient test of the bottom-up hypothesis; nor is it intended to be. The intent is to illustrate the level of predictive skill about ecosystem structure associated with the most simple implementation of a bottom-up model based upon observed trends in physical structure. Given that physical trends now can be predicted, this is the approach that would be used as a first step in the absence of other information. The theory may be correct, but a more complicated implementation may be required. El Niño may change phytoplankton taxonomic composition, size, or distribution in a way that affects food quality or availability to grazers but which is not reflected in the simple phytoplankton index used here (vertically integrated chlorophyll). However, Mullin (this volume) shows that large phytoplankton were anomalously abundant since the depression of the nutricline. It may also be that the grazer community changes in some way, such as taxonomic composition or vertical distribution, that affects the higher trophic levels that feed upon them but which is not correlated with the nutrient distribution or chlorophyll concentration (Mullin 1995, 1997). Preliminary evidence from the seabirds and pinnipeds suggests that nutrition is an issue. El Niño–induced changes in the food chain remain a likely candidate for linking changes in physical structure and the ecosystem. However, simple implementations of the bottom-up model appear to have little predictive value usable by managers or policymakers.

Although much more analysis of these data remains to be done, this is an appropriate place to end this analysis. The mechanisms listed in table 4, other than bottom-up control, would probably be difficult to test because the theories for these mechanisms are generally not developed to the point that predictions can reasonably be tested with existing data. Theoretical development, ecosystem modeling, and new types of observations will all be required. Future work will also include a more detailed analysis of the timeline, particularly to address the aspects of the data which appear to be inconsistent. The timeline presented here is just one way to consider the new data that were collected during this event. Development of a coastwide synthesis and consideration of how these new findings contribute to understanding individual populations and aspects of structure will be exciting next steps.

ACKNOWLEDGMENTS

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OBSERVATIONS ON FISHES ASSOCIATED WITH THE
1997–98 EL NIÑO OFF CALIFORNIA

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ABSTRACT

From mid-1997 through 1998, anomalously warm water occurred off the California coast as part of the more global El Niño phenomenon of 1997–98. Warm-water periods of comparable magnitude were observed in 1957–59 and 1982–84; this most recent event may in fact be the strongest of the three. Biological evidence supporting the impact of this phenomenon was noted in a northern latitudinal shift in the range of a number of eastern tropical Pacific fishes into the warm-temperate waters of southern California. Families of fishes represented include Carcharhinidae, Sphyrnidae, Elopidae, Albulidae, Ophichthidae, Clupeidae, Synodontidae, Fistulariidae, Scorpaenidae, Triglidae, Serranidae, Apogonidae, Carangidae, Lobotidae, Mullidae, Chaetodontidae, Pomacanthidae, Pomacentridae, Sphyraenidae, Polynemidae, Labridae, Scaridae, Blenniidae, Callionymidae, Gobiidae, Trichiuridae, Bothidae, Tetraodontidae, and Diodontidae. Of particular significance are the following new California records of Panamic species: *Fistularia corneta*, deepwater cornetfish; *Diplectrum maximum*, greater sand perch; *Apogon pacificus*, pink cardinalfish; *Caranx vinctus*, cocinero; *Sphyraena ensis*, Mexican barracuda; *Decodon melasma*, blackspot wrasse; *Nicholsina denticulata*, loosetooth parrotfish; *Plagiotremus azaleus*, sabertooth blenny; *Synchiropus atrilabiatus*, blacklip dragonet; and *Engyophrys sanctilaurentii*, speckled-tail flounder. Several species taken had not been reported since the Pacific Railroad Survey of the 1850s or the early 1900s (e.g., threebanded butterflyfish and longtail goby). Additionally, several species heretofore known from single or a few records were taken on multiple occasions and in some numbers. Differences between the 1997–98 and previous El Niño events and a measure of the intensity of this event are discussed. Changes in the ichthyofauna of California during the most recent El Niño were perhaps the most dramatic of the twentieth century.

INTRODUCTION

Periods of warm water off California have been observed by a number of ichthyologists since the early 1900s. Thompson (1918) noted the appearance of more southern fishes off southern California in 1918, but did not mention temperature as a causative factor. Hubbs and Schultz (1929) reported on the occurrence of southern forms of marine life along the Pacific coast in 1926, and Walford (1931) reported more specifically on the northward occurrence of southern fishes off San Pedro in 1931. Hubbs (1948), in a seminal paper, discussed changes in the fish fauna of the eastern North Pacific correlated with changes in ocean temperature. At the seventh meeting of CalCOFI in Carlsbad, California, Radovich (1960) described the redistribution of fishes in the eastern Pacific Ocean during 1957 and 1958. He followed with a more detailed account further describing eastern Pacific tropical fishes and other organisms off California during the warm-water event of 1957–58 (Radovich 1961).

The next major warm-water period, which manifested itself off California in early 1983 and is now referred to as El Niño of 1982–84, was discussed generally by McGowan (1984) and Wooster and Fluharty (1985) and in specific articles by Swift (1986), Brooks (1987), Jones et al. (1988), Lea et al. (1989), Lea and Rosenblatt (1992), and others. Mearns (1988), in an overview, reviewed unusual occurrences of marine organisms as indicators of changing ocean conditions.

Sea-surface temperatures taken by the Scripps Institution of Oceanography and known as Scripps Pier temperatures represent a continuous data series from 1917 and serve as an indicator of general marine temperature conditions for southern California (fig. 1). This data set represents one of the longest series of ocean temperatures for the eastern North Pacific, and is the primary ocean temperature information considered in this report. We note that from 1992 to 1997 sea-surface temperatures were well above the long-term mean of approximately 17°C. Beginning in mid-1997 sea-surface temperatures rose dramatically and continued at a high level through 1998. In 1999, sea-surface temperatures cooled considerably, introducing a La Niña oceanographic condition.

In this paper we discuss a number of northward occurrences of eastern tropical Pacific (Panamic) fishes
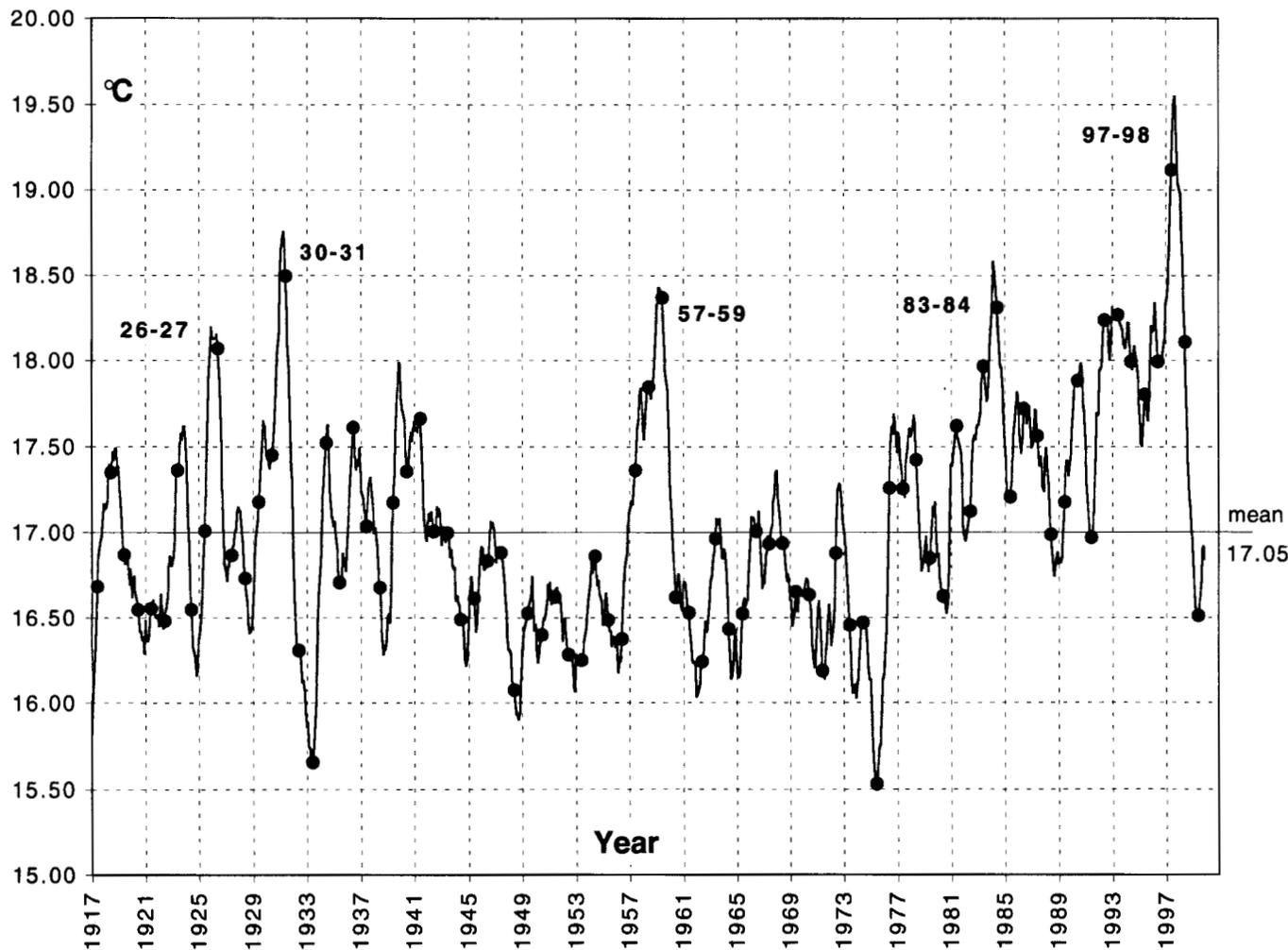
Figure 1. Sea-surface temperature at Scripps Pier, 1917–99. Line indicates 12-month moving mean; circles indicate annual means. Major warm-water periods are indicated. Compiled by Jerrold Norton, NOAA-NMFS, Pacific Grove.

that came to our attention during the 1997–98 El Niño and which we believe were a consequence of the oceanographic conditions relating to this event. We are aware that some of these observations may have been associated with the warm-water conditions persisting from 1992 to 1997. However, the majority of the records presented herein directly relate to the 1997–98 El Niño event.

DATA AND METHODS

The observations presented herein were obtained from a myriad of sources. Specimens came to our attention through the generosity of commercial and recreational fishers, state and federal research and assessment programs, environmental monitoring programs such as the Southern California Water Resources Project (SCWRP) and the City of San Diego, public aquaria, academic researchers, underwater photographers, and persons with simply a general interest in the marine environ-

ment. In most cases the relevant specimens have been accessioned into the ichthyological collections at the Scripps Institution of Oceanography, the Los Angeles County Museum of Natural History, and the California Academy of Sciences. In several instances we were given a photograph of a fish but not the specimen itself. As media coverage of El Niño became an almost daily topic in 1998, we received many anecdotal reports of unusual fishes as well as other organisms. We have not included these unless there was additional convincing and corroborative evidence as to the identity of the organism.

Our observations and discussion are presented in a phylogenetic sequence, listed by family. We follow (with minor exceptions) the arrangement presented by American Fisheries Society Special Publication 20, *Common and Scientific Names of Fishes from the United States and Canada* (Robins et al. 1991). Twenty-nine families of fishes are discussed; the majority are considered tropical in their zoogeographic affinities, and many exhibit

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TABLE 1

Panamic Species New to California Collected during 1997–98 El Niño, in Chronological Order

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Species	Common name	Family	Location	Date[a]
Caranx vinctus	Cocinero	Carangidae	San Diego Bay	12 Aug. 1997
Sphyraena ensis	Mexican barracuda	Sphyraenidae	Oceanside	20 Oct. 1997
Fistularia corneta	Deepwater cornetfish	Fistulariidae	Huntington Beach	7 May 1998
Apogon pacificus	Pink cardinalfish	Apogonidae	La Jolla	12 May 1998
Decodon melasma	Blackspot wrasse	Labridae	Dana Point	2 June 1998
Plagiotremus azaleus	Sabertooth blenny	Blenniidae	King Harbor	18 Aug. 1998
Engyophrys sanctilaurentii	Speckled-tail flounder	Bothidae	San Diego	6 Sept. 1998
Diplectrum maximum	Greater sand perch[b]	Serranidae	Newport Beach	30 Nov. 1998
Synchiropus atrilabiatus	Blacklip dragonet[c]	Callionymidae	Santa Catalina Island	19 Jan. 1999
Nicholsina denticulata	Loosetooth parrotfish[c]	Scaridae	Santa Catalina Island	22 May 1999

[a]Date of collection of specimen, except for the loosetooth parrotfish, which was photographed; we identify the species without question.
[b]Proposed common name.
[c]Not collected or observed until 1999. However, we attribute the arrival of the species off California as occurring during the 1997–98 El Niño.

circumtropical distributions. Ten of the included species are reported from California for the first time (table 1).

RESULTS

Carcharhinidae

Requieum sharks of the genus *Carcharhinus* are represented primarily from warm seas by a large number of species from throughout the world (Rosenblatt and Baldwin 1958). On 14 July 1998, a dusky shark, *Carcharhinus obscurus*, was taken off Huntington Beach during a California Department of Fish and Game shark tagging cruise. The specimen was retained for documentation but inadvertently lost because of a freezer failure. However, a photograph of the specimen allows us to confirm the identification as a dusky shark.

Fitch and Schultz (1978) stated, regarding *C. obscurus*, "Californian records based upon actual specimens are extremely rare, although the species was at one time reported as being common in San Diego Bay." Starks (1917) reported on a specimen of this species (as *C. lamiella*) taken at Santa Catalina Island that measured twelve feet in length. Carcharhinid sharks are notoriously difficult to distinguish, and the validity of this early record cannot be confirmed.

Sphyrnidae

Three species of hammerhead sharks are known from California waters; all are considered rare in our area. Starks (1917) first reported the smooth hammerhead, *Sphyrna zygaena*, as occasionally being taken off the southern California coast. Fusaro and Anderson (1980) reported on the scalloped hammerhead, *Sphyrna lewini*, from an adult specimen, 262 cm TL, taken west of Santa Barbara. Seigel (1985) reported on three additional scalloped hammerheads, including a juvenile (545 mm TL), taken off Pacific Palisades, Los Angeles County, during El Niño 1982–84.

Between April 1997 and mid-January 1998, at least 10 juvenile scalloped hammerheads were taken in San Diego Bay. All specimens were less than 1 m, which we consider to be neonates; no umbilical scars were noted on any of the specimens examined. The number of scalloped hammerhead taken during the 1997–98 El Niño, as well as their relative small size suggests that during extreme warm-water conditions San Diego Bay may serve as a nursery area for this species.

Elopidae

The elopids, tenpounders, are a group of five to six species, occurring worldwide in tropical and subtropical waters. The machete, *Elops affinis*, is a rare species in southern California waters (Fitch and Schultz 1978). On 30 December 1997, a machete measuring 458 mm SL was captured in south San Diego Bay.

Albulidae

Bonefish, *Albula vulpes*, are known historically from California (Starks 1918), but their occurrence has been sporadic; the family is considered circumtropical in distribution (Fitch and Lavenberg 1971). The taxonomy of the genus *Albula* is unresolved, and although we apply the name *Albula vulpes* herein, we realize that the eastern Pacific population undoubtedly represents a species separate from *A. vulpes* and in time will take on a different name.

From January 1998 throughout most of the year, bonefish were reported from bays and estuaries from San Diego County to Venice Canal, Los Angeles County. Leptocephalus larvae were collected in some locations, including San Diego Bay; transforming leptocephali and juveniles were taken more broadly. A juvenile bonefish was also taken in Morro Bay, San Luis Obispo County, in August 1998 (Robert Hardy, pers. comm.). The year 1998 appears to represent a unique recruitment event for bonefish off southern California.

Ophichthidae

Snake eels of the family Ophichthidae from the eastern Pacific constitute a rich and diverse assemblage of tropical species (McCosker and Rosenblatt 1998); four species have been recorded from California waters: *Myrichthys tigrinus*, tiger snake eel; *Myrophis vafer*, Pacific worm eel; *Ophichthus triserialis*, Pacific snake eel; and *O. zophochir*, yellow snake eel. Of these, two species were taken during the 1997–98 El Niño and are relevant to this discussion.

***Ophichthus zophochir*, yellow snake eel.** The genus *Ophichthus* was first reported from California by Hubbs in 1916, from a specimen taken off Long Beach. Since then, there have been a number of reports of the two species from California (Clark 1937; Hopkirk 1965; Quirollo and Dinnel 1975; McCosker and Rosenblatt 1998; and others). These snake eels have all been adults and most have been exceptionally large individuals (McCosker and Rosenblatt 1998).

Ophichthus have been collected in warm-water as well as cold-water years, and it is difficult to correlate captures with El Niño events. Because ophichthids are generally fossorial and difficult to collect, it is possible they may live for extended periods before being discovered. During 1997–98 a large *Ophichthus zophochir* was collected in April 1998 inside Newport Bay. When this fish arrived in California is not possible to determine, but warm oceanographic conditions have persisted since 1992. Of greater importance was the collection of a leptocephalus-stage *O. zophochir* from San Francisco Bay in January 1999. We believe this specimen most likely arrived sometime during the 1997–98 period. This example would seem to explain the mechanism of transport for tropical ophichthids to higher-latitude waters. It may be that ophichthid leptocephali arrive off our coast during conditions of northerly flow of ocean currents correlated with warm-water events, settle out, and then live an expatriated existence. Charter (1996) reported that *Ophichthus* larvae are unknown in the CalCOFI area north of the Cabo San Lucas region of Baja California.

***Myrophis vafer*, Pacific worm eel.** This eel was first reported from California as a new species of echelid eel, *Hesperomyrus fryi*, being taken under a night-light near the San Pedro breakwater in August 1930 (Myers and Storey 1939). It was later recognized that *H. fryi* was a junior synonym of *M. vafer* (Rosenblatt and McCosker 1970). We are aware of but one other collection of this species from California prior to the 1997–98 El Niño, a 455 mm SL specimen taken at the Los Angeles Harbor breakwater in July 1966.

In July and October 1998, two Pacific worm eels were collected from Batiquitos Lagoon, San Diego County. In January–February 1999, during La Niña conditions, four other Pacific worm eels were collected from Mission Bay and Batiquitos Lagoon. We attribute these post–El Niño records as carryovers of worm eels that had arrived and settled out in southern California during the warmer-water period.

Clupeidae

Species of the genus *Opisthonema*, thread herring, are commercially important coastal pelagic fishes in the waters from Mexico to northern Peru. Three species are known from the eastern Pacific; two have been recorded from California: *Opisthonema libertate*, deepbody thread herring, and *O. medirastre*, middling thread herring. The species of thread herring are extremely difficult to distinguish morphologically, and the surest method requires the enumeration of ceratobranchial gill rakers, a tedious technique at best (Berry and Barrett 1963).

Three thread herring were taken by gill net set off Carlsbad in August 1997. From September through November 1997, thread herring were caught by anglers at Port Hueneme, Belmont Shore, and Balboa piers (Ventura, Los Angeles, and Orange counties). We have examined several of these fishes, and all have been attributable to *Opisthonema libertate*. It is impossible to say whether *Opisthonema medirastre*, the second species known from California, was a component of the thread herring occurring off southern California during this period.

Synodontidae

Lizardfishes occur worldwide, primarily in tropical seas. The California lizardfish, *Synodus lucioceps*, is a normal element of the southern California ichthyofauna. It is uncommonly taken north of Point Conception; however, during the 1982–84 El Niño California lizardfish were recorded as far north as Puget Sound, Washington (Gonyea and Burton 1985).

On 9 October 1998 a "calico lizardfish," *Synodus lacertinus*, was collected off the United States–Mexico boundary by the City of San Diego Ocean Monitoring Program. The site of capture is approximately 6 kilometers south of California waters. The 145 mm SL specimen was taken by trawl on sand bottom at 27 m. This record is included because of its proximity to California and its occurrence in warm-temperate waters. We propose the common name calico lizardfish for this species in reference to its reddish-mottled color pattern. Most *Synodus* species are rather drab in color; this is an exceptionally beautiful member within the genus. Prior to the above record, the northernmost locality of this Panamic species of which we are aware was Islas San Benito, off the outer coast of central Baja California.

Fistulariidae

The cornetfishes are a small family of gasterosteiform fishes comprising four species and exhibiting a circum-

tropical distribution. Two cornetfishes occur in the eastern Pacific: *Fistulatia commersonii*, reef cornetfish, and *Fistularia corneta*, deepwater cornetfish (Fritzsche 1976). These highly specialized fishes are stalking predators most often associated with reef habitat.

In May 1998 two deepwater cornetfish, *F. corneta*, were collected at the Huntington Beach Generating Station, Orange County (Mike Curtis, pers. comm.). The deepwater cornetfish is a Panamic species previously known to Bahía San Hippolito, on the outer coast of Baja California (Thomson et al. 1987). This represents the first capture of the species and family in California.

Scorpaenidae

The rainbow scorpionfish, *Scorpaenodes xyris*, is a Panamic species with a known range from Santa Catalina Island, California, to Peru and the Galápagos Islands. This scorpionfish was first reported from California by Strachan et al. (1968) from a specimen collected at San Clemente Island, at 18 m by ichthyocide, in May 1966 (several other specimens were observed but not collected). A second rainbow scorpionfish was collected at Isthmus Reef, Santa Catalina Island, at 24 m, in March 1967.

We list four reports of rainbow scorpionfish that relate to the 1997–98 El Niño and are significant, two in 1998 and two in 1999. A rainbow scorpionfish was collected at Santa Catalina Island in June 1998 by Jeff Landesman of the Cabrillo Marine Aquarium. Additional sightings were made at Santa Catalina in October 1998 (Joe Wible, pers. comm.) and September 1999 (Paul Reilly and Chuck Kopezak, pers. comms.). All of the Santa Catalina reports were from Blue Cavern Point or Bird Rock.

Triglidae

The lumptail searobin, *Prionotus stephanophrys*, was originally described by William Lockington in 1881 from a San Francisco market specimen trawled off Point Reyes. Fitch and Lavenberg (1971) noted "... the species was not reported again until 1945, and even today fewer than two dozen individuals have been caught north of Mexico." Since Fitch and Lavenberg's account, additional specimens have been taken off California, including several during the 1982–84 El Niño. The species has also been reported as far north as the Columbia River, Oregon.

We comment on four captures relative to the 1997–98 El Niño. In October 1997 a lumptail searobin was taken by a commercial trawler off Humboldt County, California. In April 1998 an individual was trawled off Coos Bay, Oregon (Mike Hosie, pers. comm.), and in October 1998 and August 1999 lumptail searobins were taken in Monterey Bay.

Serranidae

Twelve species of serranid fishes are known from California (Robins et al. 1991). However, only three species would be considered as common: *Paralabrax clathratus*, kelp bass; *Paralabrax maculofasciatus*, spotted sand bass; and *Paralabrax nebulifer*, barred sand bass. Three species of serranids, one new and two rare for California, were taken during the 1997–98 El Niño.

A sport-caught *Diplectrum maximum*, a sand perch, was caught off Newport Beach and turned over to Stephen Crooke of the California Department of Fish and Game by an angler who initially thought he had an unusually colored barred sand bass. The 335 mm SL specimen was taken over sand bottom on 30 November 1998. The genus *Diplectrum* exhibits an Amphi-American distribution in primarily tropical waters. Rosenblatt and Johnson (1974) reviewed Pacific species, and the genus was revised by Bortone (1977). Eight species of *Diplectrum* are known from Baja California, the majority from Magdalena Bay and southward (nine species are known from the eastern Pacific). Of these, *D. maximum* is the largest species of the genus and perhaps the least common member. Only juveniles are known from off Baja California.

To our knowledge, the Newport Beach specimen is the first adult *D. maximum* collected north of Peru, the type locality. Our determination was based on the size of the specimen and the morphology of the preopercular spur. The specimen is deposited in the Los Angeles County Museum of Natural History, LACM 53932-1, and represents the first California record for the species. We apply the common name "greater sand perch" to *D. maximum* in reference to its size relative to other members of the genus, which are referred to as sand perches.

Epinephelus is primarily a tropical genus, although several species previously have been taken off California: *E. acanthistius*, gulf coney; *E. analogus*, spotted cabrilla; *E. dermatolepis*, leather bass; and *E. niphobles*, star-studded grouper (Lea and Fukuhara 1991). The spotted cabrilla is considered rare in California, and we are aware of but one California record prior to the 1997–98 El Niño. A photograph appeared in *Western Outdoor News* (20 Feb. 1998 issue) of a sport-caught, "14-pound," spotted cabrilla, taken off Port Hueneme, Ventura County, on 9 January 1998. The species is quite distinctive, and we are confident of the identification.

A juvenile *Serranus aequedens*, measuring 59 mm SL, was collected off San Diego in April 1998 by the City of San Diego Ocean Monitoring Program. The specimen was taken by trawl at 100 m on sand bottom. The first record of the species from California is of two specimens collected in April 1990 off Whites Point, Los Angeles County (Pondella 1999). The San Diego *Serranus* is the second record (third specimen) of the species from
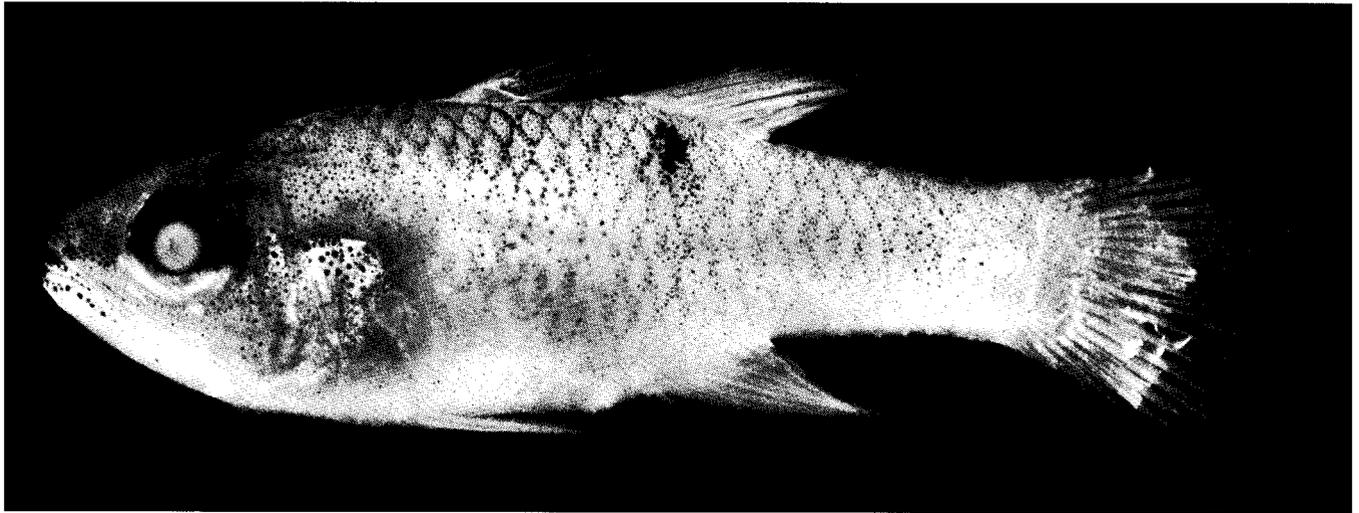
Figure 2. Pink cardinalfish, *Apogon pacificus*. Specimen from San Diego–La Jolla Ecological Reserve, 12 May 1998, 49.5 mm SL, SIO 98-49. Note bar under second dorsal fin.

California. The size of the fish would indicate relatively recent recruitment, likely within a year, to our area.

Apogonidae

The Apogonidae are a family of small tropical fishes with six species known from the eastern Pacific. The Guadalupe cardinalfish, *Apogon guadalupensis*, was first observed in California at San Clemente Island in November 1967 (Hobson 1969b). Specimens were later collected from this location to confirm their specific identification. Since the original observation, occasional sightings and collections have been made at San Clemente Island, mainly at the southern end in the vicinity of Pyramid Head.

During 1998 we received a number of reports of Guadalupe cardinalfish, with sightings not only at San Clemente Island, but also Santa Catalina Island, Santa Barbara Island, Anacapa Island, and La Jolla Cove. In late 1998 oral brooding by male cardinalfish was observed at San Clemente Island (Joe Wible, pers. comm.). This observation would indicate that water temperatures were warm enough for successful reproduction for the species at the southern Channel Islands.

On 25 April 1998 several cardinalfish with a distinctive bar under the second dorsal fin were observed in La Jolla Canyon by Robert Snodgrass and Hugh Khim. This color pattern is characteristic of the pink cardinalfish, *Apogon pacificus*; the Guadalupe cardinalfish is a uniformly colored species. Several weeks later, on 12 May, six pink cardinalfish, measuring 27 to 50 mm SL, were collected from this locality, at 12 m, by Ronald McConnaughey and Philip Zerofski (fig. 2). The above observation and collection represent the first California record for the species.

In September 1998, both species of cardinalfish were photographed at San Clemente Island. The pink cardinalfish was originally described as *Mionorus pacificus* from the Galápagos Islands (Herre 1936). The closest known locality for *A. pacificus* is Islas San Benito, off central Baja California.

Carangidae

The Carangidae, jacks, are a large family of primarily tropical fishes. Fourteen species have been attributed to the California ichthyofauna, of which only two species are considered temperate in distribution (Lea and Walker 1995). During the 1997–98 El Niño, four species of jacks of particular interest were taken off California: Pacific crevalle jack, *Caranx caninus*; bigeye trevally, *Caranx sexfasciatus*; cocinero, *Caranx vinctus*; and Mexican lookdown, *Selene brevoortii*.

A Pacific crevalle jack was collected in San Diego Bay on 21 January 1998. This is the fourth record of the species from California. All four were from south San Diego Bay; the last previous Pacific crevalle jack was taken in 1984.

The bigeye trevally was first reported from California on the basis of three specimens taken during November 1990 in San Diego Bay. On 3 January 1998 a bigeye trevally was taken by Mike Irey while fishing for mullet and corvina in south San Diego Bay.

The cocinero, also referred to as barred jack, is a small jack that has not previously been reported from California. On 12 August 1997 a specimen measuring 245 mm FL was collected in south San Diego Bay by Mike Irey while commercial fishing with seine for mullet and corvina. The addition of this species now brings to 15 the known number of carangids from California, 13 of which have a tropical affinity.

The fourth jack, the Mexican lookdown, was previously known from a single specimen collected in February 1993 (Lea and Walker 1995). During the period from December 1997 through April 1998, several dozen Mexican lookdown were caught in south San Diego Bay, again by Mike Irey. Approximately 10 Mexican lookdown collected during this period were donated to the Scripps Aquarium by Mr. Irey; some were still on display in October 1999 (at the time of the CalCOFI conference).

Lobotidae

Lobotes pacificus, Pacific tripletail, was first reported from California (as *Lobotes surinamensis*) from a single specimen taken off the Cabrillo Breakwater, Los Angeles Harbor, on 5 April 1992 (Rounds and Feeney 1993). The tripletail was caught by a recreational angler and measured 533 mm TL. In the intervening period to the 1997–98 El Niño we are aware of no other captures of this species.

During the 1997–98 El Niño event, at least six Pacific tripletail were taken off southern California. On 23 August 1997 a Pacific tripletail was caught 22 km south of Dana Point, Orange County. The fish measured 384 mm TL and was caught by an angler fishing on drift kelp at the surface. On 2 September 1997 a tripletail was caught off Balboa Pier, Orange County, and on 6 September 1997 a third tripletail, measuring 461 mm TL, was caught from the beach at Belmont Shore, Los Angeles County. Additionally, three specimens were captured from south San Diego Bay between 5 November 1997 and 1 January 1998 by Mike Irey, a commercial fisherman targeting mullet and corvina.

All of the tripletail captured were relatively large adults ranging in size from 384 to approximately 700 mm TL. Tripletail are known to associate with flotsam such as floating debris, trees and logs, and floating kelp. We assume this to be the mechanism of transport for those individuals reaching southern California waters. Larvae of *Lobotes* have not been identified from the CalCOFI sampling area (Watson 1996).

Mullidae

Goatfish were first reported from California in March 1919 based on "several specimens of a rare and beautiful fish hitherto unknown in southern California waters. . . ." (Higgins 1919). The species was ascribed to *Upeneus dentatus*, now placed in the genus *Mulloidichthys* and known as the Mexican goatfish. No other goatfish were reported from California until a small specimen, 173 mm SL, was collected at San Onofre Nuclear Generating Station in San Diego County in February 1979. This specimen was identified as *Pseudupeneus grandisquamis*, bigscale goatfish, and represented the first record for the species from California (Fitch 1980).

During the 1997–98 El Niño at least four bigscale goatfish were collected off southern California. On 15 July 1998 a specimen was collected by trawl in San Diego Bay, and on 24 August 1998 three specimens were collected in kelp beds off Carlsbad in northern San Diego County. Additionally, a bigscale goatfish was reportedly taken (but not saved) at San Onofre Nuclear Generating Station during the summer of 1998 (Robert Moore, pers. comm.). In 1999 we are aware of one collection and several reports of sport-caught bigscale goatfish from San Diego Bay. We believe these goatfish to have arrived during 1997–98 and successfully settled at that time. Bigscale goatfish commonly associate with flotsam, especially floating logs but also drifting kelp, and this may have been the mechanism of transport to California from more southerly waters.

In reviewing the recent collections and reports of goatfishes from California, including Higgins's (1919) brief note of *Mulloidichthys dentatus* in which he described his specimens as "covered with large scales, and brilliantly marked with crimson and yellow bands," we questioned that identification. The coloration described by Higgins is more typical of *Pseudupeneus grandisquamis* than of *Mulloidichthys dentatus*. At the California Academy of Sciences RNL located three specimens that are undoubtedly the basis for Higgins's first records of goatfish from California. The three specimens, in one jar, are CAS 125625 (originally at Stanford University—SU 25625). Two included labels state: "Large specimen Haul 238—Off Coronado (San Diego)" and "2 Small Specimens Haul 149 Off Cardiff & Encinitas 21 fm. 1½ mi. offshore." There is no collection date on the jar labels or in the museum catalog. However, a notation giving a date of identification as "Aug 19, 1922 O. E. Sette" places the specimens in the correct time frame. Although there are some discrepancies in Higgins's published record (off Long Beach) and the museum register (off Coronado) we feel this is a matter of how the specimens and collection data were transferred from the California Department of Fish and Game Laboratory to Stanford University. The three specimens are all *Pseudupeneus grandisquamis*, based on general morphology and low interdorsal scale counts (3 in all specimens). We therefore conclude that *Pseudupeneus grandisquamis* is the only mullid verifiable from California and that the numerous listings and citations of the Mexican goatfish, *Mulloidichthys dentatus*, from California have been a perpetuation of Higgins's report of 1919.

Chaetodontidae

The threebanded butterflyfish, *Chaetodon humeralis*, is considered the "commonest butterflyfish in the tropical eastern Pacific" (Thomson et al. 1987). Prior to the 1997–98 El Niño only one occurrence of the species
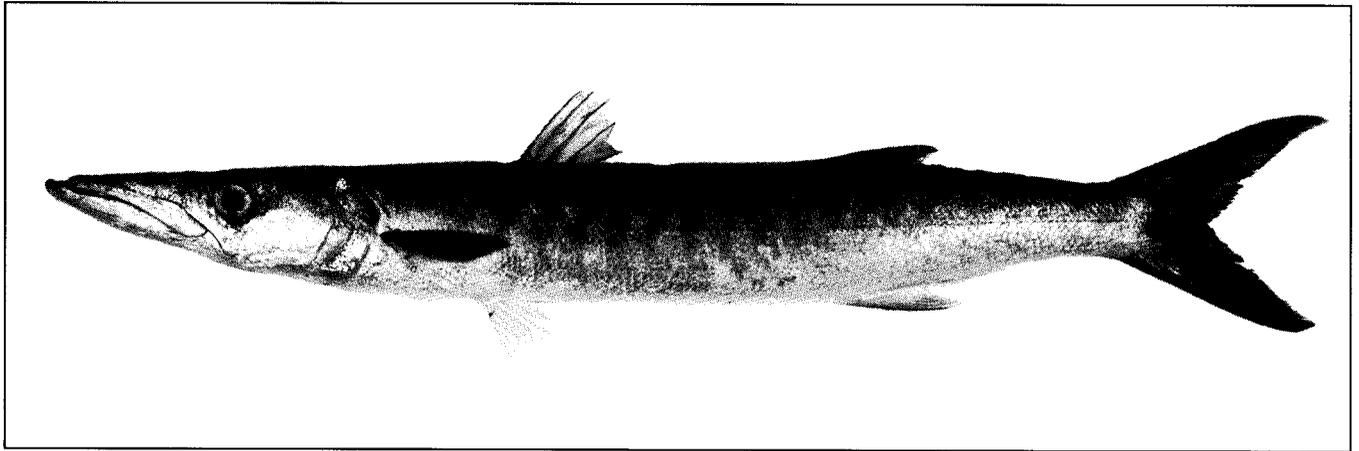
Figure 3.   Mexican barracuda, *Sphyraena ensis*. Specimen from off Bird Rock, La Jolla, 11 January 1998, 452 mm SL, SIO 98-35. Note chevrons on side of body.

was known for California: two specimens collected from San Diego Bay during the Pacific Railroad Survey of the 1850s.

On 1 November 1997 a juvenile threebanded butter-flyfish was observed in the San Diego–La Jolla Ecological Reserve by Hugh Khim. The butterflyfish was video-taped three weeks later at the same location by the late Robert Snodgrass. On 12 December another three-banded butterflyfish, a juvenile measuring 38.6 mm SL, was collected at King Harbor, Redondo Beach (Pondella et al. 1998). This specimen is deposited at Scripps Insti-tution of Oceanography: SIO 98-23. The reoccurrence of this Panamic species off southern California after a period of almost 150 years is one of the outstanding find-ings from the 1997–98 El Niño.

Pomacanthidae

A single species of the angelfish family is known from California waters; the family is primarily tropical in distribution. Three Cortez angelfish, *Pomacanthus zonipectus*, were observed or collected between Imperial Beach, San Diego County, and the Los Angeles break-water between March 1984 and October 1986 (Lea et al. 1989). It was felt that these fishes had most likely been transported to California during the 1982–84 El Niño and not discovered until the end of or after that warm-water event.

On 7 September 1998 an adult Cortez angelfish, 304 mm TL, was collected at the Redondo Generating Station, which takes in water from Santa Monica Bay.

Pomacentridae

The damselfishes are a large family of primarily trop-ical fishes occurring in all warm seas, with a few species found in temperate waters. Four species are known from California, two of which are common: blacksmith, *Chromis punctipinnis*, and garibaldi, *Hypsypops rubicundus*; and two

of which are rare: Panamic sergeant major, *Abudufduf troschelii*, and swallow damselfish, *Azurina hirundo*. The Panamic sergeant major was added to the Califonia ichthyofauna in August 1996 on the basis of specimens collected and observed at King Harbor, Redondo Beach (Pondella 1997). *Azurina hirundo* was first observed in California at Santa Catalina Island in 1991 and docu-mented photographically the following year at San Clemente Island (Lea and McAlary 1994).

During the 1997–98 El Niño several sightings of swallow damselfish were reported to us: Santa Catalina Island, December 1997 and October 1998; Anacapa Island, August 1998; and San Clemente Island, September 1998. Whether these are fishes that arrived in 1997 or are carryovers from earlier in the 1990s cannot be de-termined. However, it appears that the species has ex-panded its range farther to the north.

Sphyraenidae

The barracudas are a small family of about 20 species that are primarily tropical in distribution. The Pacific barracuda, *Sphyraena argentea*, is the only species previ-ously known from California. It is an important recre-ational and commercial species in the southern part of the state, particularly during the warmer seasons and es-pecially in warm-water years. It is rarely taken north of Point Conception but has been recorded as far north as Kodiak Island, Alaska.

In October 1997 a Mexican barracuda, *Sphyraena ensis*, measuring 463 mm SL, was captured by gill net in a kelp bed off Oceanside. In January 1998 a sport-caught Mexican barracuda, 452 mm SL, was taken at Bird Rock, off La Jolla (fig. 3). At the time of capture the Mexican barracuda was schooling with Pacific barracuda. These two specimens are deposited at the Scripps Institution of Oceanography as SIO 98-36 (Oceanside) and SIO 98-35 (La Jolla). Mexican barracuda were reportedly

caught by recreational anglers off San Diego County in 1998 (Mike Shane, pers. comm.). The species has chevrons on the side of the body that distinguish it from the more uniformly colored Pacific barracuda. The Mexican barracuda can be distinguished from a third Pacific species of barracuda, *S. lucasana*, which has vertical bars (as opposed to chevrons) and a more posterior position of the pelvic fins. These distinctions are subtle and might easily be missed unless one is aware of them. The above two specimens represent the first records for Mexican barracuda from California waters.

Polynemidae

Polynemids, known as threadfins, are a small family of tropical and subtropical marine and brackish-water fishes. Two species are known from the eastern Pacific, and both have been reported from California: the blue bobo, *Polydactylus approximans*, and yellow bobo, *Polydactylus opercularis*. Both species are considered rare north of southern Baja California. Blue bobo were first reported from San Diego, California, in the early 1900s (Jordan and Evermann 1902). Follett (1948) reported on seven *P. approximans* taken during 1940–41, one as far north as Monterey Bay. Radovich (1961) noted an additional specimen taken off Seal Beach, Orange County, during the 1957–59 warm-water period and estimated that perhaps 15 or 20 blue bobo had been taken off California up to that point.

In December 1997 a blue bobo of approximately 200 mm TL was collected in San Diego Bay. Six more blue bobo were taken in January 1998 and four more from February through April, all from San Diego Bay. On 4 August 1998 an additional specimen, approximately 200 mm TL, was taken at Marina Del Rey, Los Angeles County. Juvenile bobo are pelagic, often occurring far offshore. This life-history characteristic may have allowed northward transport of the species during or prior to the 1997–98 El Niño.

We are aware of only three records of the yellow bobo from southern California. To our knowledge, none was taken during the 1997–98 El Niño event.

Labridae

Labrids, or wrasses, are a large family of primarily tropical fishes occurring in the three major oceans. Three species of wrasses are common members of the southern California ichthyofauna: California sheephead, *Semicossyphus pulcher*; rock wrasse, *Halichoeres semicinctus*; and señorita, *Oxyjulis californica*.

In June 1998, two blackspot wrasse, *Decodon melasma*, were taken by trawl, on separate occasions, off Dana Point in 60 m (M. James Allen, pers. comm.). A third blackspot wrasse, measuring 57 mm SL, was taken off San Diego at 100 m in April 1999 by the City of San

Diego Ocean Monitoring Program. This specimen is deposited at the Scripps Institution of Oceanography, SIO 99-100. All three *Decodon* are juveniles. The above collections represent the first records for the species from California.

Scaridae

The Scaridae, parrotfishes, are circumtropical, with six species known to occur in the eastern tropical Pacific (Rosenblatt and Hobson 1969; Thomson et al. 1987). In May 1999 a parrotfish was observed by Erik Erikson at Lovers Cove Reserve, Santa Catalina Island. Several months later the species was documented by photography and videotape at the same location. The fish was identified from the photograph by RNL as *Nicholsina denticulata*, the loosetooth parrotfish; it represents the first record of the family and species from California. Although the sightings were made following the 1997–98 El Niño event and during the colder La Niña period, we feel the occurrence of this parrotfish off Santa Catalina is best explained by arrival sometime in 1998.

The species was observed at Islas San Benito, off central Baja California, in August 1995 and again in August 1998 by RNL. At both San Benito and Catalina it was often observed in association with the brown alga *Eisenia*. Within the Gulf of California it commonly associates with the algae *Sargassum* and *Padina*. Prior to the Islas San Benito observations the range of the loosetooth parrotfish was listed as "from Puerto Peñasco throughout the Gulf and from Bahía Magdalena south to Peru and the Islas Galápagos" (Thomson et al. 1987).

Blenniidae

The Blenniidae, combtooth blennies, are a large family of primarily tropical and subtropical marine fishes. Three species of combtooth blennies are common in southern California waters, all in the genus *Hypsoblennius* (Stephens et al. 1970). On 8 January 1998, two sabertooth blenny, *Plagiotremus azaleus*, were observed in King Harbor, Redondo Beach, at approximately 1.5 m depth (Daniel J. Pondella II, pers. comm.). *Plagiotremus azaleus* is characterized as being "widespread in the tropical eastern Pacific" (Hobson 1969a). Between 8 January and 15 December 1998, four other sightings of sabertooth blenny were made at King Harbor. On 18 August an individual sabertooth blenny, measuring 59.8 mm SL, was collected and is deposited at the Scripps Institution of Oceanography (SIO 98-263). We find it of interest that no Cortez rainbow wrasse, *Thalassoma lucasanum*, were observed during the period of sabertooth blenny sightings. *Plagiotremus* is commonly associated with the Cortez rainbow wrasse, which is by far the more abundant of the two species (Hobson 1969a). D. J. Pondella II and M. T. Craig will present the details of these

observations in a future publication. The above observations and collection of *Plagiotremus azaleus* represent the first record of the species from California.

Callionymidae

Dragonets are perciform fishes occurring in tropical marine waters, primarily in the Indo-West Pacific. A single species is known from the eastern Pacific: *Synchiropus atrilabiatus*, blacklip dragonet (Fricke 1981). In July 1998 a blacklip dragonet was collected by bottom trawl off Santa Catalina Island (M. James Allen, pers. comm.). On 19 January 1999 the City of San Diego Ocean Monitoring Program trawled a second blacklip dragonet off Ocean Beach. This fish, measuring 83 mm SL, was collected by bottom trawl at 100 m on sand bottom and is deposited at the Scripps Institution of Oceanography, SIO 99-1.

The above captures represent the first records of the family and species from California. To our knowledge, these are the first dragonets recorded north of Magdalena Bay, Baja California. The occurrence of this benthonic Panamic species outside its normal range can best be explained by transport of larval or early juvenile fishes.

Gobiidae

There is but a single record of *Ctenogobius sagittula*, longtail goby, from California. Starks and Morris (1907) reported on several specimens taken in San Diego Bay, near Old Town, a locality which most likely has long since disappeared. To our knowledge, the species has not been taken since. The taxonomy of this goby has undergone several changes in nomenclature over the years and has been recorded from California as *Gobionellus sagittula*, *Gobionellus longicaudus*, and most recently as *Ctenogobius sagittula*. The species is a common estuarine and lagoon fish from mainland Mexico to northern Peru.

In May 1998 we began to receive reports of captures of the longtail goby from San Diego Bay. During the ensuing months, longtail goby were collected from Mission Bay, Santa Margarita River lagoon, Newport Bay, Long Beach Harbor, and Marina Del Rey. The 1997–98 El Niño appears to have been an extraordinary period of recruitment off southern California for this species.

Trichiuridae

Cutlassfishes are characterized as primarily tropical in distribution. Records of cutlassfishes from California date from 1921 (Higgins 1921). Occurrence of the species has been sporadic off California. Fitch and Lavenberg (1971) noted that during the early 1930s a small commercial fishery for cutlassfish existed in the Los Angeles Harbor area, but after 1934 the species was "rarely seen and then only a few individuals at a time."

Beginning in March 1998 and extending throughout the year, Pacific cutlassfish, *Trichiurus nitens*, were taken during most months, at several southern California localities, and by various means. Pacific cutlassfish were collected during March and May from fish screens at the San Onofre Nuclear Generating Station, San Diego County, at times in large numbers (Mike Shane, pers. comm.). During the latter half of August 1998 schools of cutlassfish were observed in Long Beach Harbor, and for a short period a minor sport fishery developed. During September 1998 we received reports of cutlassfish being caught by bait boats off Ventura County. On 1 October 1998 a specimen measuring 512 mm TL was collected by the bait boat *Traveler* fishing off Oxnard in 5 fathoms. This represented a slight northern extension of the range, the previous limit being San Pedro (Hubbs and Hubbs 1941). In late October, Pacific cutlassfish were caught in Dana Harbor, Orange County, by recreational anglers; water temperature at the time was reported as 19.4°C.

The most noteworthy captures of the species were from San Francisco Bay in January 1999, where two cutlassfish were caught by commercial herring boats within a three-week period. The first of these was taken on 6 January in south San Francisco Bay and measured approximately 700 mm TL. The second was caught on 27 January in north San Francisco Bay and measured 681 mm TL. These records are significant, as they set a new northern limit for the species. San Francisco Bay is within the Oregonian biogeographic province of the eastern North Pacific, a region of cold temperate water.

Bothidae

Bothids are left-eyed flatfishes primarily restricted to tropical marine waters on soft bottoms. California flatfishes previously placed in the Bothidae are now assigned to Paralichthyidae fide Chapleau (1993). On 6 September 1998 a speckled-tail flounder, *Engyophrys sanctilaurentii*, was collected off San Diego at 60 m by the City of San Diego Ocean Monitoring Program (M. James Allen, pers. comm.). This represents the first record of the family as well as species from California waters. The species has a broad Panamic distribution and occurs not uncommonly as far north as Magdalena Bay, on the outer coast of Baja California.

Tetraodontidae

Two species of puffers of the genus *Sphoeroides* have been reported from California waters: *Sphoeroides annulatus*, bullseye puffer, and *Sphoeroides lobatus*, longnose puffer.

Sphoeroides annulatus is reported as ranging from San Diego to the Galápagos Islands and northern Peru, but it is extremely rare north of about Magdalena Bay, Baja California (Fitch and Lavenberg 1975). The first California record for the species dates from 1857.

Sphoeroides lobatus was first reported from California at Redondo Pier, in December 1972 (Fitch 1973) and is equally rare. During the 1982–84 El Niño five puffers, all reported to be longnose puffer, were caught again at Redondo Pier, and all were taken in late September and October 1984.

We are aware of five puffers either observed or collected in southern California during the 1997–98 El Niño; all were taken in 1998. A longnose puffer was photographed off La Jolla on 24 January (Constance Gramlich, pers. comm.). Eleven days later, on 4 February, a juvenile longnose puffer, 62 mm SL, was found as a beach cast along La Jolla Shores and brought to the Scripps Institution of Oceanography for identification and subsequent deposit in the Marine Vertebrates Collection: SIO 98-2. It is possible, but unlikely, these two records may represent the same fish. In February a bullseye puffer was observed at Santa Catalina Island (Joe Welsh, pers. comm.). On 19 February and 7 April bullseye puffers were collected at the El Segundo Power Station and Scattergood Power Station, respectively. Both of these power stations are in Los Angeles County and receive water from Santa Monica Bay. They are within close proximity to Redondo Pier, the site of the 1972 and 1982–84 captures.

Diodontidae

The porcupinefishes are a small family of highly specialized fishes with a circumtropical distribution. Some ichthyologists have combined them with the Tetraodontidae. Three diodontids have been recorded from California waters, where all are rare: *Chilomycterus reticulatus*, spotfin burrfish; *Diodon holocanthus*, balloonfish; and *Diodon hystrix*, porcupinefish. In September 1997 a spotfin burrfish was collected from Los Angeles Harbor and displayed for a short period at Cabrillo Marine Aquarium, San Pedro (Lea 1998). In October 1997 a balloonfish was observed at Santa Catalina Island during a shallow-water dive by the research submersible *DELTA*. In March 1998 divers from the Catalina Island Marine Institute snorkeling in Fourth of July Cove, Santa Catalina Island, observed a diodontid estimated to be 750 mm long (Joe Welsh, pers. comm.). The fish is assumed to be *Diodon hystrix*, because of its large size.

SUMMARY AND CONCLUSIONS

We document the occurrence of Panamic fishes from off California during the El Niño event of 1997–98. During this period members of 29 families of Panamic fishes were recorded from California waters. Ten species are reported as new for the state, of which most are first records from the warm-temperate or San Diegan biogeographical region of the eastern North Pacific. Included are two species, blacklip dragonet and loose-tooth parrotfish, which were collected or observed during the La Niña period of 1999, immediately following El Niño. We regard these post–El Niño records as most likely representing arrival at some point during the 1997–98 period.

In considering fishes at the family level, four circumtropical taxa are new to California. The remarkable number of Panamic species represented can only be attributed to the magnitude and intensity of this most recent El Niño, which surpasses the warm-water event of 1957–59 and El Niño of 1983–84. Reports of Panamic species became relatively frequent during midsummer of 1997 and continued to the end of 1998.

During El Niño conditions, poleward transport of larvae and early-stage juvenile fishes is an extremely important mechanism in the redistribution of Panamic fishes. In some cases, however, species apparently are transferred as advanced juveniles or adults, and explanation by larval transport is not logical. Species within the families of jacks, goatfishes, threadfins, and tripletails are all known to associate with flotsam, and that has most likely facilitated their redistribution to higher latitudinal waters. Free-swimming fishes such as sharks, herrings, jacks, barracudas, and cutlassfishes most likely move freely within water masses of suitable temperature. Hence, the method of arrival of the various species of Panamic fishes corresponds to the adaptation that best allows for transport and movement into the higher-latitude waters of California.

The appearance of families such as the Fistulariidae, Lobotidae, Pomacanthidae, Polynemidae, Scaridae, Callionymidae, and Bothidae in California waters is extraordinary. At the species level, an amazing array of Panamic fishes appeared off California (threebanded butterflyfish, pink cardinalfish, sabertooth blenny, longtail goby, etc.). The number of tropical families and Panamic species noted off California during the 1997–98 El Niño event, including several post–El Niño records, exemplifies the magnitude and intensity of this most recent warm-water phenomenon. The local recruitment of bonefish and longtail goby during the 1997–98 El Niño, which as far as we can determine is unprecedented, is suggestive of future events. We hypothesize that if warming ocean conditions in the eastern North Pacific continue in the future, an increasing number of Panamic fishes will reach the coast of California; some of them may become established, with a resultant change in the composition of the California ichthyofauna. The 1997–98 El Niño appears to have been the strongest warm-water event off California during the twentieth century.

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Part III

SCIENTIFIC CONTRIBUTIONS

ABUNDANCE AND DISTRIBUTION OF ROCKFISH (*SEBASTES*) LARVAE IN THE SOUTHERN CALIFORNIA BIGHT IN RELATION TO ENVIRONMENTAL CONDITIONS AND FISHERY EXPLOITATION

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ABSTRACT

In this study we describe seasonal, interannual, and long-term changes in the larval abundance of six rockfish (*Sebastes*) taxa in relation to spawning biomass and to variability in the ocean environment. We used rockfish larvae from a total of 11,472 CalCOFI plankton tows taken in the Southern California Bight from 1951 to 1998. Species included in the study were bocaccio (*S. paucispinis*), cowcod (*S. levis*), shortbelly rockfish (*S. jordani*), aurora rockfish (*S. aurora*), and splitnose rockfish (*S. diploproa*). Interannual trends in occurrence and abundance are described for each species in relation to biomass trends of adults and to changes in the ocean environment caused by ENSO events and by the cool and warm regimes of the Pacific Decadal Oscillation (PDO). Larval abundance of *S. paucispinis* and *S. levis* declined abruptly during the shift to a warm regime and continued to decline, as did the adult biomass. Abundance of *S. jordani* larvae declined during the regime shift but increased after the 1982–83 El Niño, reaching the peak value for the time series in 1991. Within each regime, minor declines in larval occurrence and abundance were associated with ENSO episodes. The tightly grouped series of three La Niña events in 1970–76 immediately preceded the shift from the cool to the warm regime late in 1976 and may have contributed to the marked decline in larval occurrence and abundance that, for most species, continued through the 1982–83 El Niño. The decline in larval rockfish abundance during the regime shift may be a consequence of the decline in rockfish populations caused by the expanding rockfish fishery; however, the ocean environment may be a causal factor, because larvae of *S. jordani*, an unexploited species, underwent declines similar to those of fishery target species during that period.

INTRODUCTION

Sebastes, with over 65 species, is the most speciose genus of fishes of the west coast of North America, from Cabo San Lucas, Baja California Sur, Mexico, to the Bering Sea. The genus is well represented in the north-

western Pacific, with at least 25 species in addition to the several (e.g., *S. aleutianus*, *S. alutus*, *S. borealis*) that occur on both Asian and North American coasts (Masuda et al. 1984). Numbers of species decrease to the south of California, and only one, *S. macdonaldi*, continues into the Gulf of California from the Pacific coast. Six other species are restricted to the gulf, and at least two species are found off the temperate coasts of Chile, Argentina, and South Africa (Chen 1971, 1975, 1986; Rocha Olivares 1999a, b). Similarly depauperate is the North Atlantic, with only four species representing the genus (Eschmeyer 1998). The Southern California Bight (SCB), with its continental borderland, offers prime habitat for more than 50 rockfish species (Miller and Lea 1972; Eschmeyer et al. 1983). Found here are southern representatives of rockfish species whose distributions are primarily to the north; northern representatives of more southern species; and a large number of species whose distributions are centered off southern California.

In addition to a large species complement and extraordinary diversity of size, form, and color, *Sebastes* is characterized by viviparous reproduction (Boehlert and Yoklavich 1984), relatively slow growth rates for most species (Phillips 1964; Love et al. 1990; Lea et al. 1996), and variable recruitment with occasional dominant year-classes (Ralston 1998). The type of viviparity found in rockfishes ensures a high reproductive potential. Fecundity is relatively high (e.g., >2 million young per brood in large species); some species produce more than one brood per year; and the young are nurtured within the ovarian cavity of the mother. The brood is released at the first-feeding larva stage, thus avoiding the mortality associated with the egg and yolk-sac larva stages of oviparous fishes (Moser 1967a, b; Boehlert and Yoklavich 1984; Wyllie Echeverria 1987; Moser and Boehlert 1991; Wourms 1991).

On the west coast of the United States, rockfishes have supported commercial and recreational fisheries since the latter half of the nineteenth century and have continued as a mainstay of fresh fish markets since that time (Lenarz 1987). Total rockfish landings in California were approximately 7,000 metric tons (t) per year from 1950 to the mid 1970s, when they increased sharply,
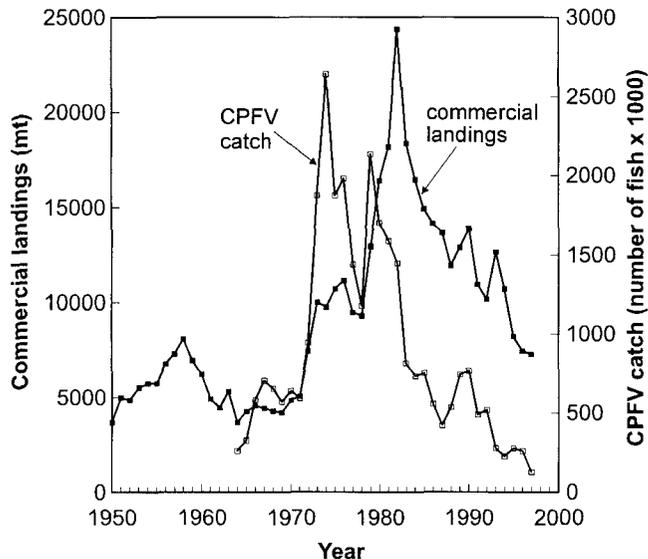
Figure 1. Total California rockfish landings by the commercial fleet in California and total commercial passenger fishing vessel (CPFV) catch for southern California. Data for commercial landings are from Thomas Barnes, California Department of Fish and Game (pers. comm.); data for CPFV catch are from California Department of Fish and Game CPFV logbooks (see Hill and Barnes 1998). CPFV catch is approximately one-half of the total recreational catch.

peaking at >24,000 t in 1982, and subsequently declined at a steady rate to the present (fig. 1). A similar trend was evident in rockfish catches of the commercial passenger fishing vessel (CPFV) fleet off southern California (fig. 1). Often an occasional highly successful year-class becomes the primary component of the fishery for that species for many years, as illustrated by the 1970 year-class of widow rockfish (S. entomelas; Lenarz and Gunderson 1987; Ralston and Pearson 1997) and the 1977 year-class of S. paucispinis (MacCall et al. 1999).

Rockfish typically are the third or fourth most abundant category of fish larvae taken on annual CalCOFI plankton surveys (Moser et al. 1993). Identification of Sebastes larvae to species is difficult because of the large number of species and the relatively few unique characters available for distinguishing the larvae (Matarese et al. 1989; Moser 1996). We routinely identify larvae of seven Sebastes species in CalCOFI plankton tows and now have assembled complete time series for four of these: bocaccio (S. paucispinis), cowcod (S. levis), aurora rockfish (S. aurora), and shortbelly rockfish (S. jordani). The time series are for the SCB region (present survey pattern) from 1951 to 1998.

Despite the high reproductive potential, decreasing catches indicate that stocks of most rockfish species have declined markedly over the past three decades. The decline is so severe for some species (e.g., S. paucispinis, S. levis) that extensive stock rebuilding measures are required (MacCall et al. 1999; Butler et al. 1999). The generally poor condition of rockfish stocks, documented

by assessments of individual species, points to a crucial need for comprehensive management of eastern Pacific rockfishes (Ralston 1998). In addition to overfishing, poor reproduction and recruitment have been suggested as causal factors in this decline.

The role that ocean environment may play in the decline of rockfish stocks has only recently been investigated (Lenarz et al. 1995; Ralston and Howard 1995; Yoklavich et al. 1996; Love et al. 1998) but may be important when considering future management options. Environmental change is the hallmark of the eastern Pacific, which is well known for its distinct high-frequency and low-frequency oscillations in ocean temperature. The El Niño–Southern Oscillation (ENSO) produces a series of alternating warm (El Niño) and cold (La Niña) episodes in the equatorial Pacific with durations of two to seven years. When these equatorial events are particularly intense and persistent they may affect temperature and other aspects of the ocean environment as far north as the Bering Sea. Hollowed et al. (1998) coined the term "Niño North" for El Niño events that result in maximum warming at higher latitudes, and identified five of these (1957–58, 1963, 1982–83, 1993, and 1997) in the last half-century. Although there have been almost as many La Niña as El Niño events in the past 50 years, fewer of these have affected higher latitudes of the northeastern Pacific. Particularly important is the 1954–56 event, which produced cold ocean conditions throughout the northeast Pacific, and the tightly grouped series of La Niña events between May 1970 and March 1976, which caused prolonged cold ocean temperatures north of the tropics for a half-decade. A moderate La Niña occurred in 1988–89 and a stronger one began in mid-1998. Its effects in the California Current region remained through 1999.

The low-frequency oscillation in the North Pacific known as the Pacific Decadal Oscillation, or PDO, is related to basin-scale changes in atmospheric pressure and particularly to the intensification and position of the Aleutian Low Pressure System (Mantua et al. 1997). The result is a 20–30-year cycle of alternating cool and warm ocean regimes. The northeastern Pacific was anomalously cool in 1900–1924, warm in 1925–1946, cool in 1947–1976, and warm from 1977 to 1999. Among the apparent biological consequences of these regime shifts are basinwide changes in primary and secondary production and in the abundance of eastern Pacific fish stocks. Plankton production in the central Pacific and in the Gulf of Alaska increased dramatically after the regime shift of 1977, while the opposite was true for west coast waters from northern Baja California to Washington (Venrick et al. 1987; Brodeur and Ware 1992; Polovina et al. 1995; Roemmich and McGowan 1995a, b; Ware 1995; Hayward 1997; McGowan et al.

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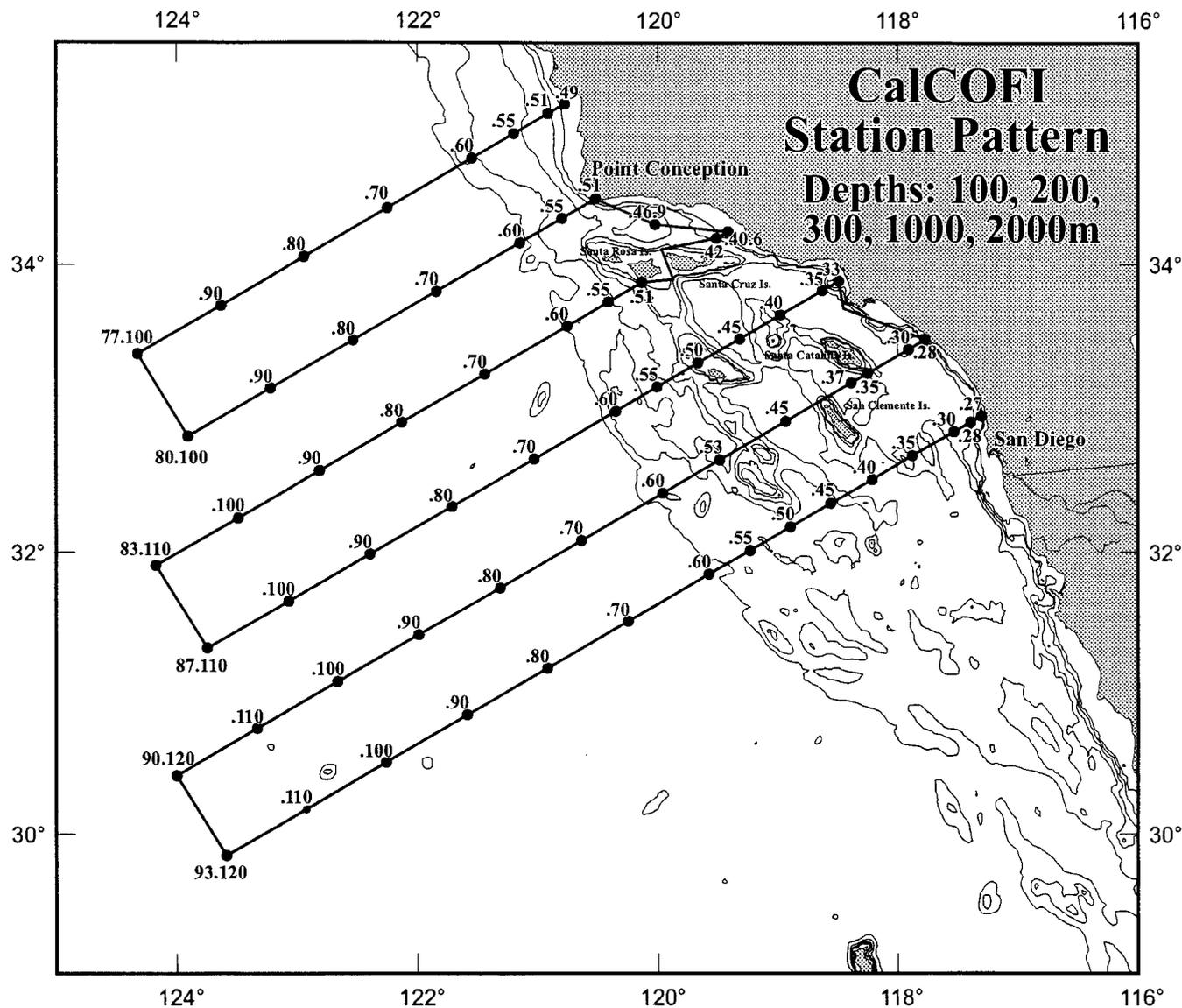
Figure 2. Station pattern for CalCOFI survey cruises from 1985 to the present, and bathymetry of the survey region. Isobaths are 100, 200, 500, 1000, and 2000 m.

1998). Groundfish and salmon stocks increased markedly in the Gulf of Alaska and neighboring Bering Sea, whereas these stocks generally declined markedly in west coast waters (Francis and Hare 1994; Mantua et al. 1997; Francis et al. 1998; Hollowed et al. 1998).

In this study we describe seasonal, interannual, and long-term changes in the larval abundance of six rockfish taxa in relation to adult biomass trends and to variability in the ocean environment, and we present information on the role that these factors may play in the dynamics of rockfish populations.

METHODS

We used larval rockfish counts from a total of 11,472 CalCOFI plankton tows taken in the area of the present CalCOFI survey pattern, which is essentially the SCB (fig. 2). This included all standard survey tows taken since 1985, when occupancy of the present pattern was initiated on a quarterly basis. Tows used prior to 1985 are a subset from wider-ranging surveys, conducted on a monthly or quarterly basis, typically from central California to southern Baja California (Hewitt 1988; Moser et al. 1993, 1994). Ichthyoplankton and station data for all cruises are summarized in a series of data reports (see Charter et al. 1999 and previous reports in the series). Hydrographic data from these surveys are published by the Scripps Institution of Oceanography (see Univ. of Calif., SIO 1999 and previous reports in the series).

Standard oblique tows from 1951 through 1968 employed a 1 m ring net towed to a depth of 140 m. Begin-

ning in 1969 the nominal tow depth was increased to 210 m, and the 71 cm bongo net (McGowan and Brown 1966) replaced the ring net from the last cruise in 1977 to the present. Silk mesh (0.55 mm opening), used from 1951 to 1968, was replaced by nylon mesh (0.505 mm opening) in 1969. Detailed descriptions of gear and methods are given by Kramer et al. (1972) and Smith and Richardson (1977). Ohman and Smith (1995) summarized historical CalCOFI zooplankton methods and calibration factors for the various gear types.

Samples were preserved in 5% formalin aboard ship and returned to the laboratory, where zooplankton displacement volumes (expressed as ml per 1000 m³) were determined, and the fish eggs and larvae were removed (Kramer et al. 1972). Rockfish larvae were identified as a composite taxon from 1951 to 1969. Beginning in 1972 larvae of *S. aurora*, *S. jordani*, *S. levis*, *S. macdonaldi*, and *S. paucispinis* were identified; identification of *S. diploproa* began in 1987. Archived CalCOFI samples for the years 1951–68 were reexamined in 1997 and 1998 in order to obtain complete time series for these species. Only those stations represented in the current survey pattern were examined for these years, and *S. goodei* was added to the list of identified larvae. Thus, complete time series for 1951–98 are available for *S. aurora*, *S. jordani*, *S. levis*, *S. macdonaldi*, and *S. paucispinis*. There is a gap in the series for *S. diploproa* from 1972 through 1986, and data on *S. goodei* larvae are available only for the years 1951–69. Methods used for identifying the species in this study are documented in Moser 1996 and Sakuma and Laidig 1995.

Larval abundance is expressed as the number of larvae per 10 m² of surface area determined by multiplying the larval count by the standard haul factor (SHF = [(tow depth/volume of water filtered) · 10]) determined for each tow. Larval occurrence is expressed as the proportion of positive tows for a given species. All 11,472 tows were used to calculate the proportion of positive tows or mean abundance if larvae of a given taxon occurred over the entire present survey pattern and during all months. A subset of the total tows was used when a taxon's distribution was limited to a portion of the survey pattern or was seasonally limited. Temperatures used in this study (surface bucket temperature or 10 m temperature, depending on which was available) were those associated with each of the net tow stations. Temperatures were available for 70% of the stations in the study, and plankton volumes were available for all stations.

RESULTS

Areal Distribution

The inner third of the current CalCOFI survey pattern overlies the continental borderland off southern California, a region of complex topography that includes the mainland continental shelf and slope, approximately 13 deep-water basins, and numerous islands and banks (submerged islands) and their shelves and slopes (fig. 2). This region offers a wealth of habitats for rockfish species, as reflected in the abundance of larvae at these stations (figs. 3 and 4). The ocean overlying the continental borderland is higher in surface nutrients and chlorophyll in comparison to the offshore region and is physically and biologically complex (Hayward and Venrick 1998). The distinct mesoscale oceanographic features of the region and the complex topography with which they interact form a uniquely dynamic and productive habitat.

Sebastes paucispinis larvae had relatively high average abundances in the Point Conception and Channel Islands areas on lines 77 to 90 out to station 60, the margin of the continental borderland (fig. 3A). Low average numbers of larvae were present on all lines seaward of station 60, out to station 90, and larvae occurred as far seaward as station 83.110 (~200 nmi from the borderland slope margin). Approximately 76% of the occurrences and 88% of the total larvae were in an area bounded by station 60 on lines 77 to 90. Station 83.55, southwest of Santa Rosa Island, had the highest average count (11.3 larvae per 10 m²) for the time series, followed by relatively high counts at station 87.50, northeast of San Nicholas Island, and 80.55, southwest of Point Conception.

Sebastes levis larvae, the rarest species in this study, had a somewhat more restricted distribution than *S. paucispinis*, with highest average numbers at a cluster of stations in the northern Channel Islands area (fig. 3B). Approximately 68% of the occurrences and 76% of the larvae were in an area bounded by lines 80 and 87, seaward to station 55. The peak average abundance (0.29 larvae per 10 m²) was at station 83.42 in the Santa Barbara Channel; however, four other Channel Islands stations (82.46.9, 83.55, 87.40, and 87.50) had average values nearly as high. There were only four positive tows seaward of the borderland margin. After the regime shift, larvae occurred at only three stations in the Santa Barbara Channel (station 82.46.9) and Point Conception area (80.51 and 80.55).

Highest average larval abundances of *S. aurora* larvae were found at a group of stations (stations 51–70 on line 77, stations 55 and 60 on line 80, and station 83.60) in the Point Conception area, with the highest average value on station 77.55 (fig. 3C). On lines south of line 83, larvae were relatively evenly distributed at stations seaward to station 60, although average values were low on shelf stations nearest the coast. The distribution of *S. diploproa* larvae was similar to that of *S. aurora*, with highest average values in a cluster of stations in the Point Conception area and a relatively even distribution over the remainder of the survey pattern out to station 60
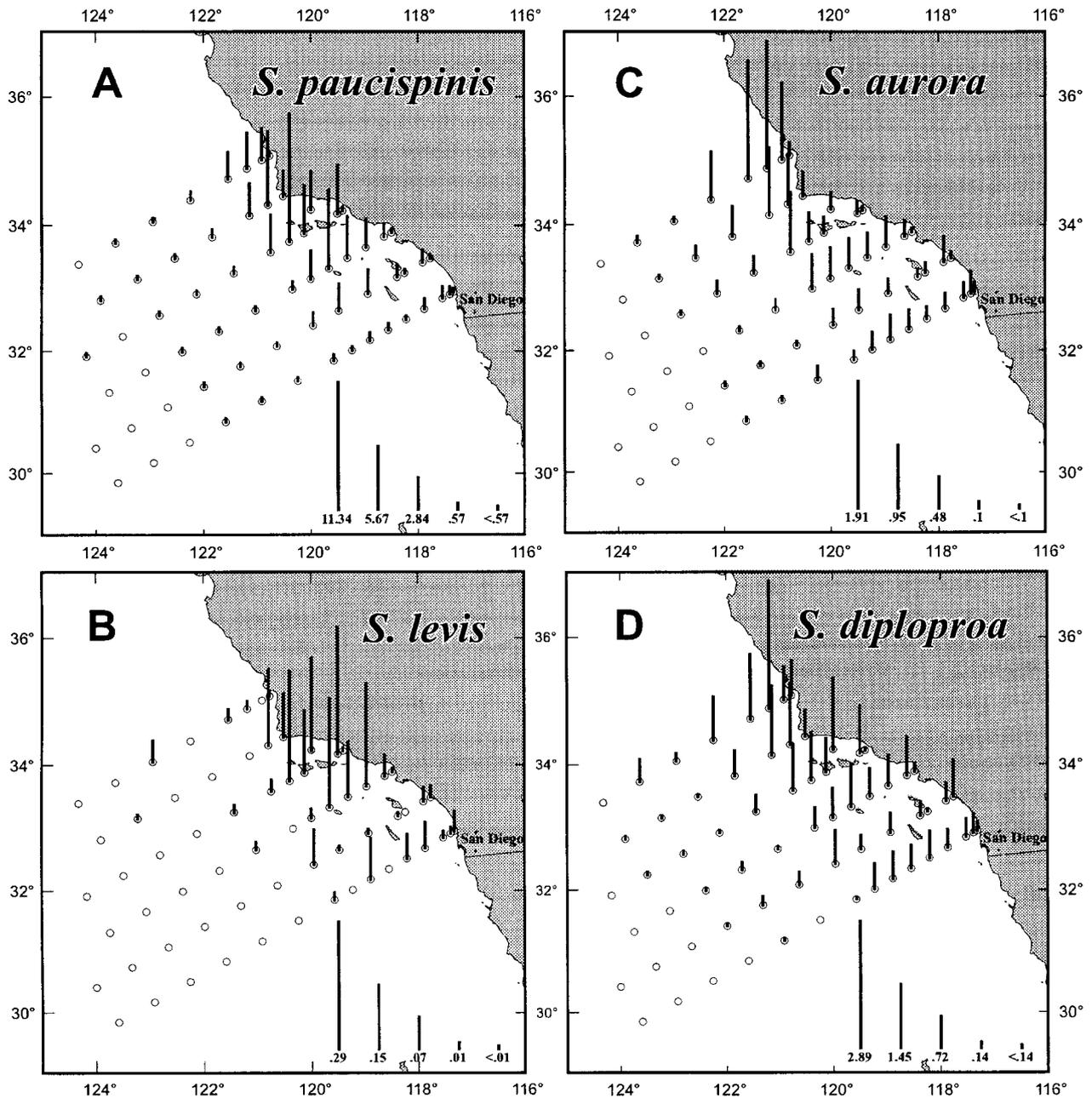
Figure 3. Average abundance of *Sebastes* larvae at nominal CalCOFI stations from 1951 to 1998. *A, S. paucispinis,* bocaccio; *B, S. levis,* cowcod; *C, S. aurora,* aurora rockfish; *D, S. diploproa,* splitnose rockfish. Length of vertical bars indicates average larvae per 10 m² scaled proportionally from the station with the highest value.

(fig. 3D). As for *S. aurora,* larvae extended relatively farther seaward (at least to station 70 on lines 77–83) in the region of the Point Conception plume. Larval *S. diploproa,* in contrast to *S. aurora,* had relatively higher average values at stations nearest the mainland coast.

S. jordani larvae, the most abundant species in this study, were concentrated closer to the coast compared to other species (fig. 4A). Peak abundance was at station

77.51 north of Point Conception; other stations with relatively high average abundance were proximal to, or shoreward of, the Channel Islands. Occurrences, with low average abundance, were recorded at most stations seaward to station 90.

Larvae of *Sebastes* spp. (unidentified *Sebastes* larvae in aggregate, constituting 76% of total rockfish larvae in the samples) occurred at nearly all stations in the survey
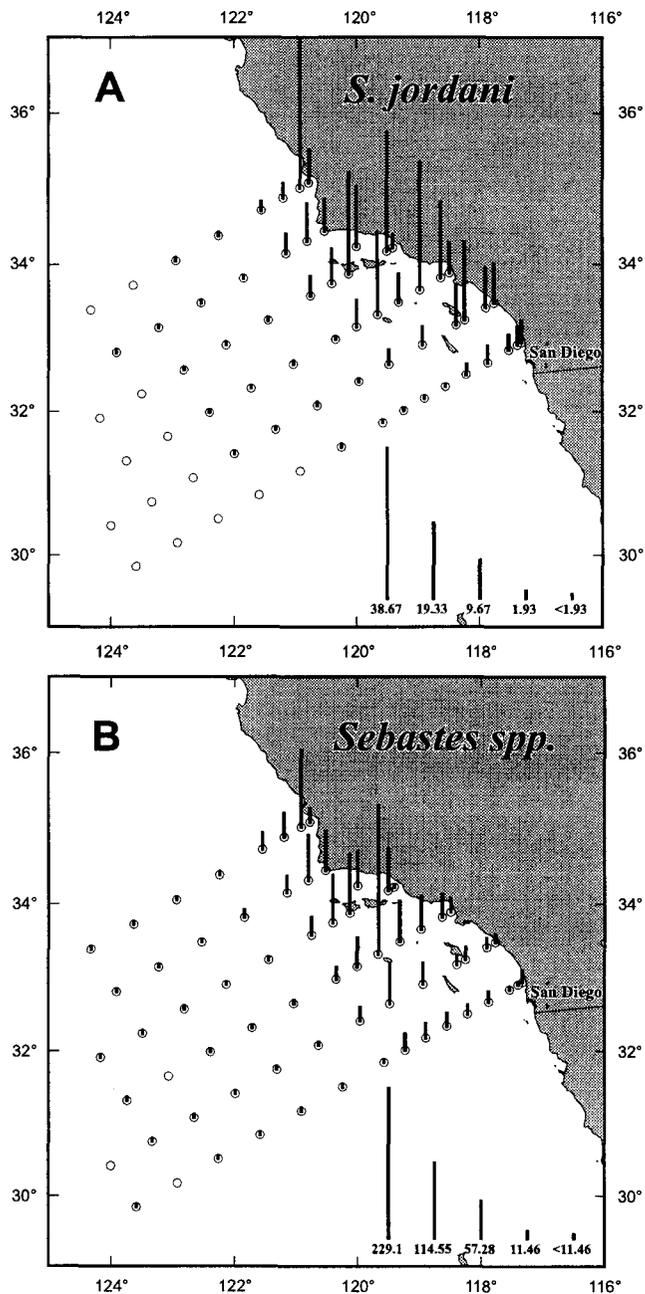
Figure 4. Average abundance of *Sebastes* larvae at nominal CalCOFI stations from 1951 to 1998: *A, S. jordani*, shortbelly rockfish; *B, Sebastes* spp., unidentified rockfish larvae. Length of vertical bars indicates average larvae per 10 m² scaled proportionally from the station with the highest value.

pattern, but the highest average abundances were at stations in the Point Conception and northern Channel Islands area (fig. 4B). Approximately 79% of the total *Sebastes* spp. larvae were in the region bounded by station 55 on lines 77–90, although only 40% of the total occurrences were in this region. Station 87.50, just northwest of San Nicholas Island, had the highest average abundance (229.1 larvae per 10 m²).

Seasonal Larval Occurrence and Abundance

Most of the rockfish larvae taken in CalCOFI oblique net samples are early-stage larvae; in a sample of 11,633 larvae, more than 90% were smaller than 7 mm (Moser and Butler 1987). Thus, larval abundance provides information on reproductive seasonality and could be used as an index of larval production.

Most rockfish species give birth to their broods of larvae during winter and spring (fig. 5A). After a period of low larval production during the summer, average larval abundance begins to increase in November and December, reaches a peak in January–March, and then declines during spring months. Larvae of *S. paucispinis* are essentially absent from summer and early fall samples but begin to appear in November and increase to peak abundance in January, after which their abundance declines steadily (fig. 5B). Larvae of *S. levis* have a similar seasonal pattern: some larvae appear in late fall, and there is a distinct peak in January–March, followed by a sharp decline through spring and early summer (fig. 5C). The parturition season for *S. jordani* off southern California begins in January, with larval abundance peaking sharply in February, and then declining rapidly through March and April (fig. 5D).

Sebastes aurora and *S. diploproa* have different seasonal patterns than most other rockfish species (figs. 5E, F). Larvae of *S. aurora* are infrequent in late summer and essentially absent during early fall. Numbers begin to increase in late fall and through the winter, reaching a peak in May–June (fig. 5E). Larvae of *S. diploproa* are present during the entire year, with lowest average abundance in March, after which there is a steady increase to a peak in October, then a sharp decline in November and a more gradual decline through February (fig. 5F).

Temperature and Zooplankton Volume

Average annual temperatures for the stations included in this study clearly show the well-documented cool regime prior to 1976 and the warm regime in effect since 1977 (fig. 6). Within the survey area the average temperature for 4,428 stations during 1951–76 was 15.4°C vs 16.4° for 3,523 stations from 1977 to 1998. Average winter (January–March) and summer (July–September) temperatures for the cool regime were 14.1° and 17.2°. Average winter and summer temperatures for the warm regime were 14.9° and 18.1°. The prominent contiguous La Niña and El Niño events of the mid-1950s were evident in the data from this study. Average annual temperature decreased in 1954 and further in 1956, then increased abruptly in 1957 to a peak in 1959 (fig. 6). A moderate average decrease in 1960–62 was followed by a sharp increase in 1963 in response to the short-lived 1963 El Niño. Although this El Niño lasted
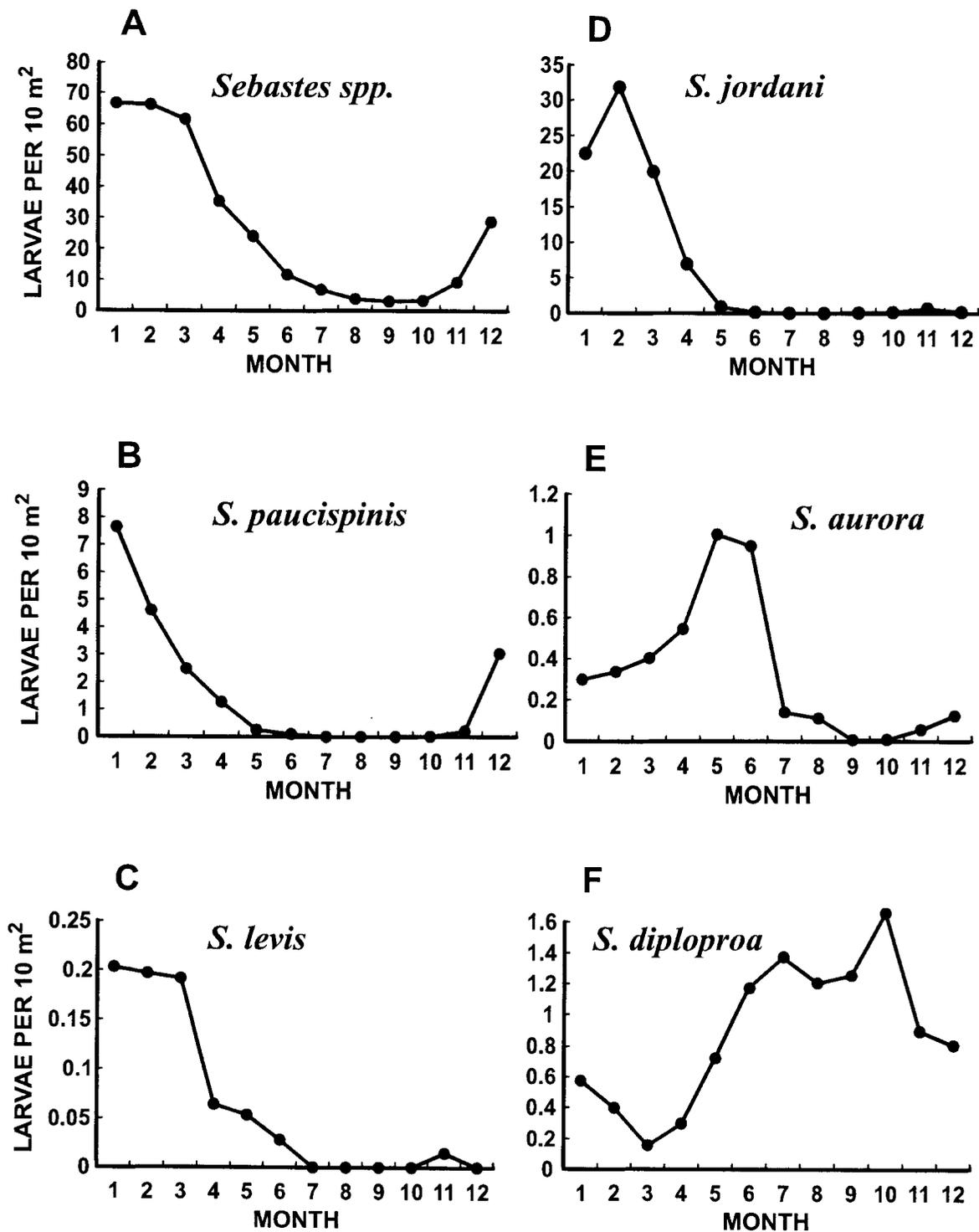
Figure 5.   Seasonal abundance (average number per 10 m²) of larvae of six *Sebastes* taxa from the CalCOFI time series. *A, Sebastes* spp., unidentified rockfish larvae; *B, S. paucispinis,* bocaccio; *C, S. levis,* cowcod; *D, S. jordani,* shortbelly rockfish; *E, S. aurora,* aurora rockfish; *F, S. diploproa,* splitnose rockfish.

less than a year, it produced sustained anomalous warm conditions in the Gulf of Alaska (Hollowed et al. 1998). A series of closely grouped La Niña events from May 1970 to March 1975 resulted in anomalously cold conditions in the study area. The CalCOFI record is incomplete because the surveys were triennial during this

period, but the low average temperatures for surveys in 1972 and 1975 clearly demonstrate the generally cold conditions for these years (fig. 6).

The shift to a warm regime in late 1976 was not documented by CalCOFI because of the cruise hiatus during 1976–77; however, the regime shift is clearly ap-

Figure 6. Average annual temperatures (*upper panel*) and zooplankton volumes (*lower panel*) for CalCOFI stations included in this study. Cool and warm regimes of the Pacific Decadal Oscillation (PDO) are indicated above each graph, and Southern Oscillation (ENSO) events are indicated by vertical bars (El Niño, shading; La Niña, hatching; the wide hatched bar represents a series of three consecutive La Nina events between May 1970 and March 1976). Dashed line indicates the period of triennial CalCOFI surveys.

Figure 7. Plot of average annual temperature versus average annual zooplankton volume for CalCOFI surveys from 1951 to 1998. Equation for the regression line: $y = -67.545x + 1245.8$; $R^2 = 0.319$.

Average plankton volumes for the warm regime were 90.0 in winter and 130.0 in summer. A peak in average plankton volume of almost 500 ml per 1000 m³ preceded La Niña of 1954–56 (fig. 6). The effect of the 1957–59 El Niño is clearly evident in the low average volumes during 1958–59. The next high value was in 1972, and after the regime shift average values declined steadily, except for a spike in 1985 (fig. 6). The inverse relationship between temperature and plankton volume for the stations included in this study is apparent when average values for each year are plotted (fig. 7).

Annual and Interannual Changes in Larval Occurrence and Abundance

Sebastes paucispinis. The proportion of net tows positive for *S. paucispinis* larvae declined about 60% from the cool to the warm regime (table 1). During the cool regime the proportion of positive tows peaked in 1954, the beginning of a La Niña event, and then declined in 1955–56, the remaining years of La Niña (fig. 8). An increase in 1957, a transition year to El Niño, was followed by a sharp decline during 1958–59, the remaining years of El Niño. Then followed a general increase to relatively high values from 1966 to 1972. The decline between 1975 and 1978 was abrupt, and generally low values were typical of warm regime years, except for the relatively high average value during the 1988–89 La Niña.

Average larval abundance declined 52% from the cool to the warm regime (table 1), with annual trends (fig. 8) similar to trends in the proportion of positive tows. Values were unusually high in 1969–75, then decreased precipitously in 1978 after the regime shift. The unusually high average value for 1981 is the result of a single large sample of 622 larvae from station 87.50 on cruise 8101. Without that station, average abundance for 1981 would

parent in the abrupt increase in average temperature in 1978 and the consistently high temperatures in the years immediately following, including the major El Niño of 1982–83 (fig. 6). A short-lived La Niña in 1988–89 was evident in the low average temperature for 1989, and this was followed by El Niño events in 1992–93 and 1997.

Historically, in the California Current region plankton volume has been higher during cold ocean conditions than during warm conditions, and the decline in zooplankton volume in the recent warm regime is well documented (Roemmich and McGowan 1995a, b; McGowan et al. 1998). In this study, average plankton volume for 6,809 stations in the cool regime was 228.2 ml per 1000 m³ vs 123.8 ml per 1000 m³ for 4,663 stations during the warm regime, an overall reduction of 46%. Average winter and summer plankton volumes for the cool regime were 186.8 ml per 1000 m³ (January–March) and 287.4 ml per 1000 m³ (July–September).

TABLE 1
Average Occurrence (Proportion of Positive Tows) and Abundance (Larvae per 10 m²) for Larvae of
Six *Sebastes* Taxa during Cool (1951–76) and Warm (1977–98) Regimes in the Southern California Bight Region

|	Proportion of positive tows			Average larvae per 10 m²		
Taxon	Cool regime	Warm regime	Percentage change	Cool regime	Warm regime	Percentage change
Sebastes spp.	0.56	0.43	−23.2	27.65	30.79	+11.4
S. paucispinis	0.31	0.12	−61.3	4.69	2.24	−52.2
S. levis	0.04	0.002	−95.0	0.18	0.03	−83.3
S. jordani	0.39	0.22	−43.6	17.41	13.77	−20.9
S. aurora	0.09	0.03	−66.7	0.50	0.36	−28.0
S. diploproa	0.14	0.05	−64.3	0.99	0.55	−44.4
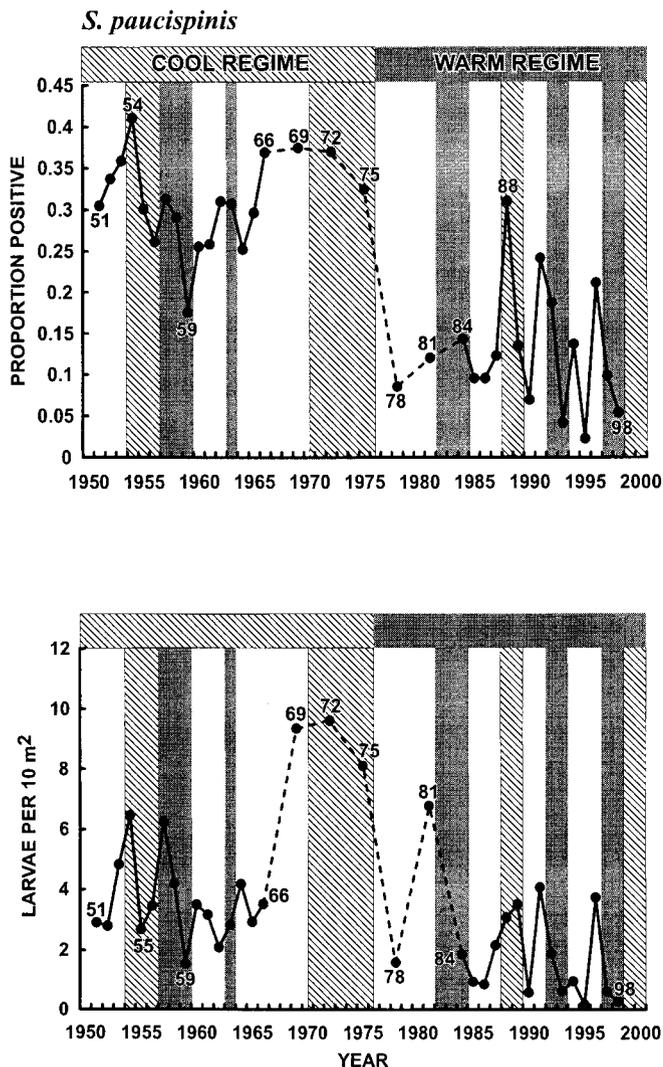
Figure 8. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes paucispinis*, bocaccio, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². Cool and warm regimes of the Pacific Decadal Oscillation (PDO) are indicated above each graph, and Southern Oscillation (ENSO) events are indicated by vertical bars (El Niño, shading; La Niña, hatching; the wide hatched bar represents a series of three consecutive La Nina events between May 1970 and March 1976). Dashed line indicates the period of triennial CalCOFI surveys.

follow a trend similar to the trend for average occurrence. Sharp declines were associated with El Niño events during both regimes, and the value for 1998 is 6% of the average abundance during the cool regime.

Sebastes levis. In CalCOFI samples *S. levis* larvae were relatively rare: a total of 117 positive tows produced 550 larvae. The trends in occurrence and abundance for *S. levis* larvae were similar to those for *S. paucispinis*, with a 95% decline in proportion of positive tows and an 83% decline in abundance from the cool to the warm regime (table 1; fig. 9). The peak in 1969 was followed by abrupt decline in 1972 and 1975 for both occurrence and abundance. Except for a few larvae taken in the early 1990s, *S. levis* larvae were absent from CalCOFI tows during the warm regime.

Sebastes jordani. In this study *S. jordani* larvae were the most abundant of the identifiable rockfish larvae. During peak years, they accounted for about 15% of the total rockfish larvae and occurred on about half of the total stations in the study area. Their average occurrence declined 44%, and their average abundance declined 21% from the cool to the warm regime (table 1). The difference between the mean abundances for the two regimes is not significant statistically ($p = >0.05$), and variability in larval abundance was greater than for the other species in this study. There was a slight decline associated with La Niña years 1955–56 and an abrupt decline during the subsequent El Niño (fig. 10). The decline just before the regime shift was sustained after the shift to a low point in 1984. Average proportion of positive tows declined from 0.4 in 1972 to 0.014 in 1984, and average abundance declined from 28.4 larvae per 10 m² in 1969 to 0.2 larvae per 10 m² in 1984. Equally remarkable was the increase in occurrence and abundance that followed the low values in 1984. The proportion of positive tows increased steadily to 0.43 in 1992, and average abundance peaked at 63 larvae per 10 m² in 1991, when there were five tows with >400 larvae per 10 m². The increase in proportion of positive tows was almost linear, whereas the increase in abundance was interrupted by a decline during and imme-

S. levis

S. jordani
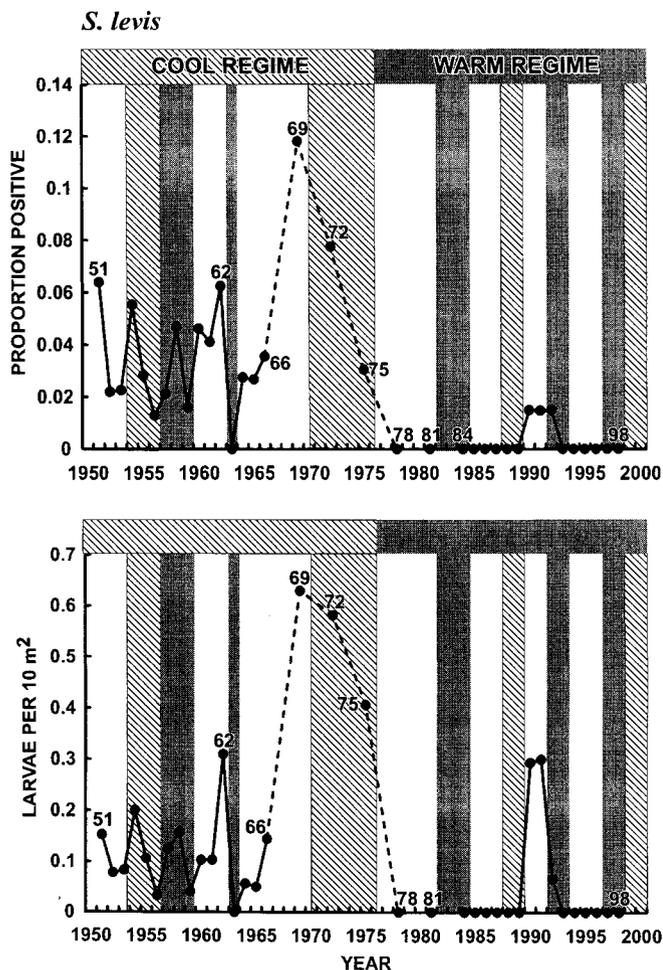
Figure 9. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes levis*, cowcod, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.
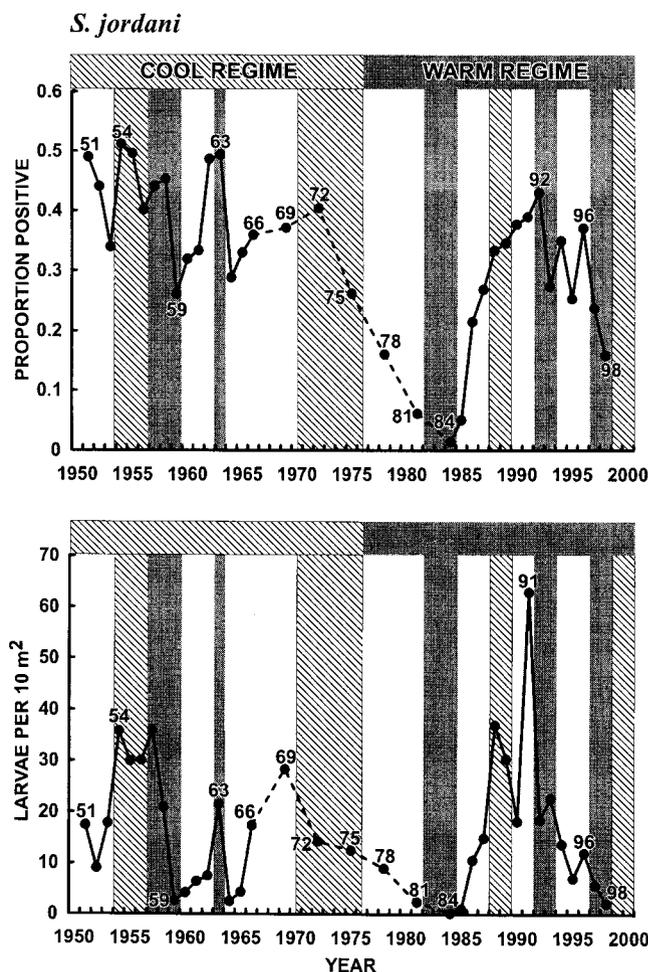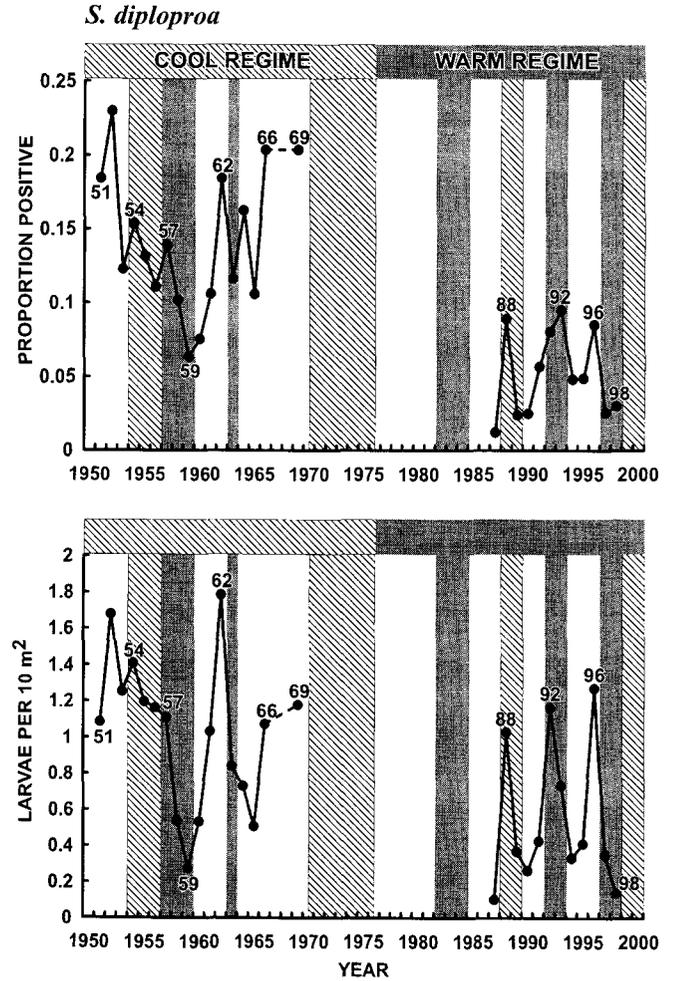
Figure 10. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes jordani*, shortbelly rockfish, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.

diately following the 1988–89 La Niña. Both occurrence and abundance declined sharply during the 1992–93 El Niño, beginning a downward trend that continued through 1998.

Sebastes aurora. From the cool to the warm regime *S. aurora* larvae declined 67% in proportion of positive tows and 28% in abundance (table 1). There was a decline in occurrence in 1956, the last year of a La Niña event, and a more pronounced decline associated with the 1957–59 El Niño (fig. 11). The proportion of positive tows generally increased after 1961 to high values in 1966–69. Occurrence declined markedly in 1972 and 1975, increased slightly in 1978, and then declined to zero in 1985. Following this low point, occurrence generally increased to a peak in 1991, dropped sharply during the 1992–93 El Niño, then increased slightly up to 1995, after which it decreased. The increase between 1985 and 1991 was interrupted by a decline in 1989, the last year of the 1988–89 La Niña. Trends in abun-

dance were similar to those of occurrence, except that 1966 was the peak year in the cool regime, and the average number of larvae was high in 1978.

Sebastes diploproa. Trends in occurrence and abundance of *S. diploproa* larvae were similar to those for *S. aurora* (fig. 12). There was a general decline associated with the contiguous ENSO events of the 1950s, followed by an increase during the 1960s. We lack data for the period from 1972 to 1986, but average occurrence declined 64% and abundance declined 44% from the cool regime to the warm regime (table 1). During the warm regime, declines in occurrence and abundance were associated with the 1988–89 La Niña and the subsequent two El Niño events.

Sebastes spp. The proportion of positive tows for unidentified rockfish larvae declined 23% from the cool to the warm regime; however, average abundance increased 11% (table 1). In the cool regime, there was a general decline in proportion of positive tows during
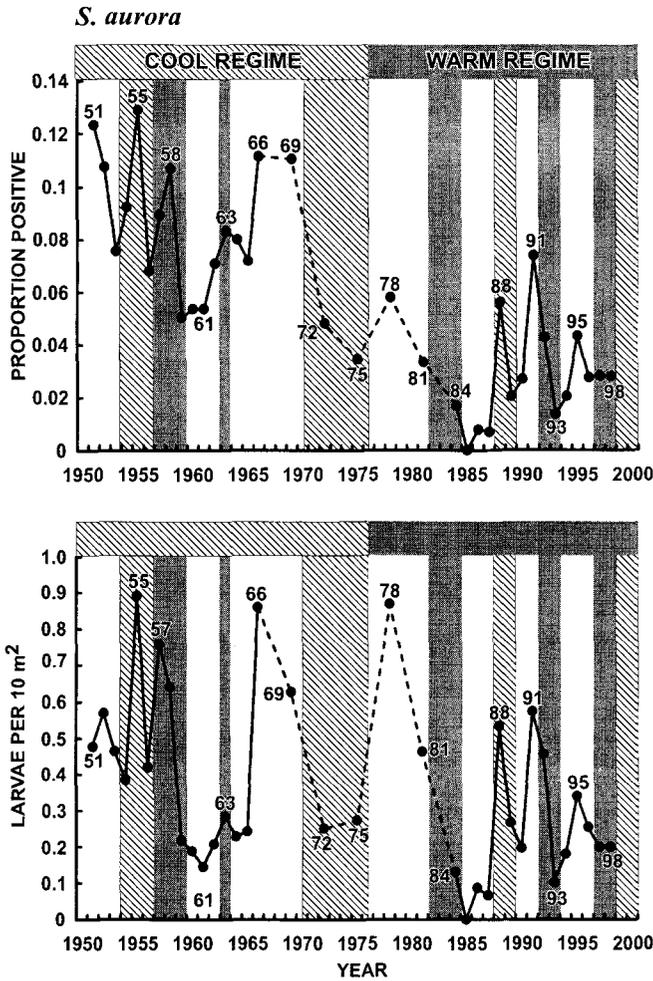
S. aurora

Figure 11. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes aurora*, aurora rockfish, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.

S. diploproa

Figure 12. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes diploproa*, splitnose rockfish, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.

the contiguous ENSO events of the 1950s, followed by a general increase to a peak in 1972 (fig. 13). Following this was a gradual downward trend in proportion of positive tows to a low in 1998. Abundance trends were less gradual, declining in association with the ENSO events of the 1950s, followed by gradual increases up to 1966, and then abrupt increases in 1969 and 1972. The trend of abruptly declining abundance to a low value in 1984 was interrupted by an unusually high value in 1981. Abundance increased again during the late 1980s, and declined during the 1990s.

DISCUSSION

Fishery Trends

Interpretation of trends in occurrence and abundance of larval rockfishes in the CalCOFI time series depends on knowledge of adult biomass trends and larval pro-

duction for these species over the same time span. Despite the history of severely declining catches for most species over the past several decades, comprehensive stock assessments have been produced for relatively few rockfish species (Ralston 1998; Pacific Fishery Management Council 1999). Most of these assessments have revealed a history of overfishing and, for some species, a dire need for stock rebuilding. Estimates of total biomass are available for only two species in this study: *S. paucispinis* and *S. levis* (MacCall et al. 1999; Butler et al. 1999). For the other three species, catch data give limited insight into the status of the populations.

Historically, *S. paucispinis* has been one of the most important species in trawl, setnet, and hook-and-line fisheries off California and has received much attention from fishery biologists and managers (Bence and Hightower 1990; Bence and Rogers 1992; Ralston et al. 1996; MacCall et al. 1999). Annual landings in
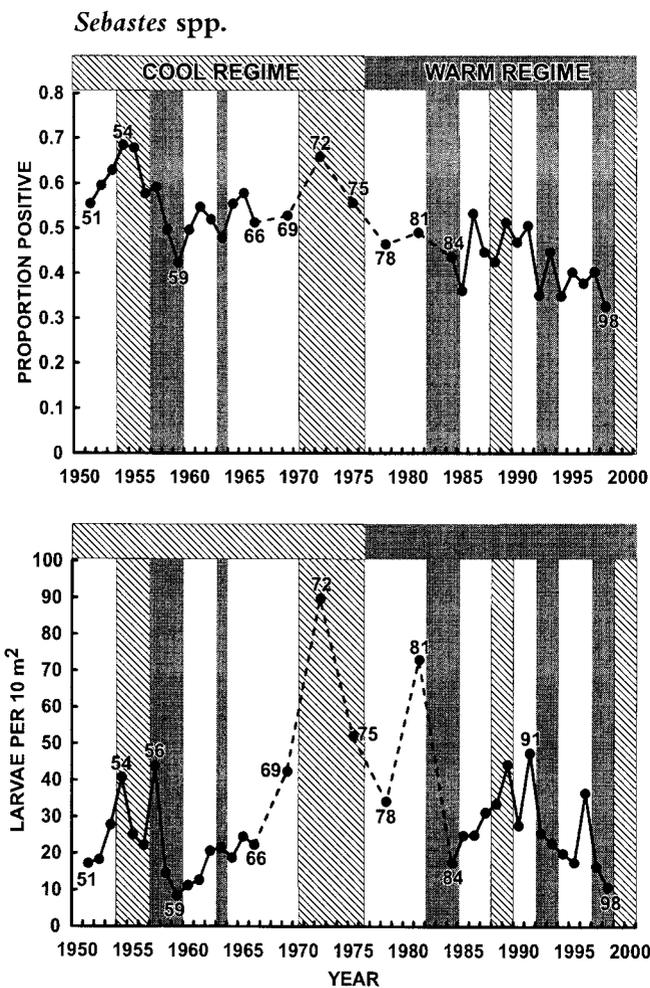
Sebastes spp.

Figure 13. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes* spp., unidentified rockfish larvae, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.

Figure 14. Estimated biomass of *Sebastes paucispinis*, bocaccio (from MacCall et al. 1999) and of *S. levis*, cowcod (from Butler et al. 1999).

California averaged ~2,500 t during the 1960s, increased sharply in the early 1970s, varied between ~4,000 and 7,000 t from 1973 to 1983, and then dropped abruptly from the mid 1980s to the present (MacCall et al. 1999). MacCall et al. (1999) estimated a steady reduction of biomass from about 70,000 t in the early 1970s to about 1,200 t in 1999, <7% of the unfished biomass (fig. 14).

Sebastes levis is a large, predatory species with a distribution centered in the SCB. Historically, it has supported a substantial commercial fishery, and has been a prize species in recreational fisheries. Trends in catch are similar to those of *S. paucispinis*. Total annual catch averaged ~76 t in the 1960s and increased to ~140 t in the 1970s, peaking at 194 t in 1976. The catch began to decline in the 1980s, precipitously so after 1989, to a low of 19 t in 1997 (Butler et al. 1999). Butler et al. (1999) estimated a decline in total biomass from ~2,700

t in the 1970s to ~238 t in 1998, <5% of the virgin biomass (fig. 14).

Sebastes jordani is a relatively small species whose biomass may approach 500,000 t and is essentially unexploited commercially (Pearson et al. 1991). Annual catches since 1980 usually were <10 t; exceeded 20 t only in 1985, 1996, and 1997; and fell far short of the present allowable biological catch of 13,900 t (fig. 15). Nearly all of the historical catch has been off central California (Pacific Fishery Management Council 1999). The lack of fishery interest in this species, despite its huge biomass, relates primarily to the relatively small size of adults and associated problems in processing and marketing. *Sebastes jordani* is important ecologically; it is a major prey species for piscivorous fishes, including other rockfishes, marine mammals, and seabirds, and it occupies an important part of the food web of coastal California and northern Baja California.

Sebastes aurora live on and around deep reefs, are rarely encountered by recreational anglers, and prior to the 1980s were taken incidentally with other rockfish in the commercial fishery. Catches of *S. aurora* (fig. 15) increased during the early 1980s, in association with the rapidly expanding set-line and setnet fishery for blackgill rockfish (*S. melanostomus*), reaching a peak of slightly more than 100 t in 1990 (Butler et al. 1998). The catch then declined steadily to ~20 t in 1998. In the 1970s and 1980s the catch was predominantly from northern and central California, but after 1992 the fishery shifted to southern California.

Sebastes diploproa is a moderately important trawl species along the entire west coast, and catches off California remained relatively stable—between 200 and
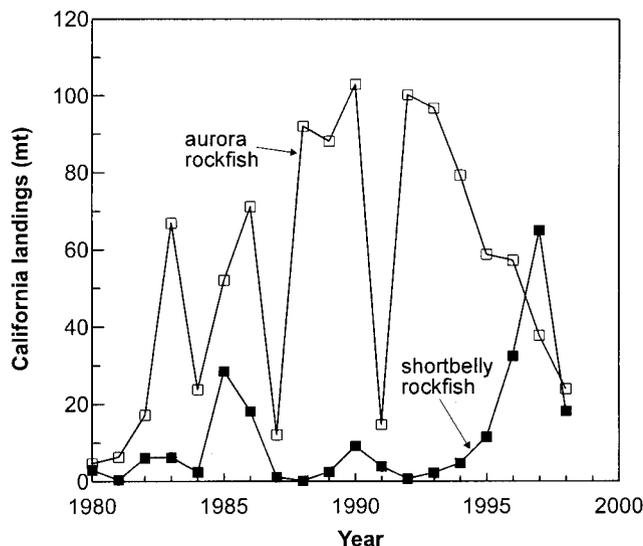
Figure 15.   Total California landings for *Sebastes jordani*, shortbelly rock-fish, and *S. aurora*, aurora rockfish, during 1980–98. Data from CALCOM database (see Pearson and Erwin 1997).
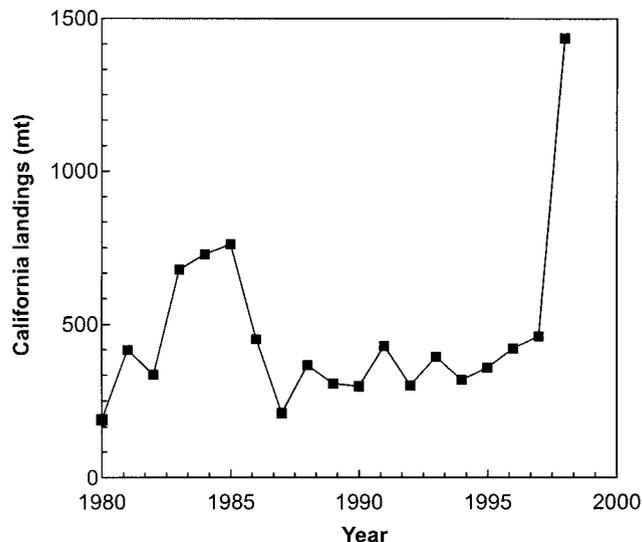
Figure 16.   Total California landings for *Sebastes diploproa*, splitnose rockfish, during 1980–98. Data from CALCOM database (see Pearson and Erwin 1997).

800 t—from 1980 to 1997 (fig. 16). It, like *S. aurora*, has been managed as part of the *Sebastes* complex and has not had a formal stock assessment. The catch increased to 1,400 t in 1998 as a result of increased effort directed to "large aggregations of splitnose [rockfish] suddenly becoming available to the fishery," primarily off central California (Pacific Fishery Management Council 1999). This resulted in separate management recommendations for this species.

Larval Trends

Comparison of trends in biomass for *S. paucispinis* and *S. levis* with interannual trends in their larvae suggest that spawner biomass and biomass-specific reproductive effort are the major factors determining the level of larval abundance. There is roughly an order of magnitude difference between the abundance of *S. jordani* and *S. paucispinis* larvae, and another order of magnitude difference between *S. paucispinis* and *S. levis*. Estimates of peak spawner biomass for these species (500,000, 70,000, and 2,700 t) also differ by roughly an order of magnitude. Since most of the rockfish larvae captured in plankton nets are small, recently-born individuals, their incidence and abundance are primarily measures of the reproductive effort of the stock. The most important factors affecting larval production are biomass of the adult stock and the reproductive effort for the year. The latter is closely tied to the amount of energy that is available for reproduction during egg maturation and gestation of the young. Declines in larval abundance most likely reflect declines in adult abundance due to fishery harvest or previous recruitment failures. Short-term fluctuations are most likely related to episodes of high or

low reproductive output, since rapid biomass changes would not be expected.

Larval abundance of *S. paucispinis*, *S. levis*, *S. jordani*, and *Sebastes* spp. (unidentified rockfish larvae) increased markedly during the late 1960s, reaching peak values just before or during the extended period of unusually cold ocean conditions that marked the end of the cool regime. Larval abundance of these taxa declined during the cold period and continued to decline through the regime shift. Assigning some role in this decline to environmental conditions during this period of major ocean change is confounded by the fact that this was precisely the time when the fishery was expanding in the study area. Gear and technical improvements in the fishery, particularly the use of gill nets, increased both harvest efficiency and the number of species harvested. Arguing for the role of ocean climate as a contributing factor in rockfish larval decline during this period is the fact that the larvae of *S. jordani*, an essentially unexploited species, underwent a decline similar to those of fishery target species during the period of the regime shift. If fishery removals were the principal factor in rockfish larval decline, one would not expect *S. jordani* larval abundance to decline in relation to the regime shift in a manner similar to the exploited species.

The wide variability in larval *S. jordani* abundance, and the remarkable recovery of the larval population during the warm regime suggest that something besides the regime shift (or fishery) has a strong influence on their abundance. The steep rise in larval abundance during the late 1980s may reflect an abrupt increase in biomass due to an unusually successful recruitment during the early 1980s. Such intermittent large year-classes are

typical of rockfishes, and the early age of maturity—50% at age two and 100% by age four (Pearson et al. 1991)—would favor a rapid population response. A similar increase in biomass of one or more small, nonexploited species could account for the average increase of 11% in larval abundance of *Sebastes* spp. from the cool to the warm regime and for the abrupt increase in *Sebastes* spp. abundance during the late 1980s. The rapid decline in larval abundance of *S. aurora* during the series of cold episodes prior to the regime shift and the marked increase in abundance in 1978 after the regime shift may be related to the fact that the reproductive peak for this species comes in late spring, when water temperatures are increasing. A similar response in larval abundance could be expected of *S. diploproa*, a species with a summer-fall spawning peak, but larval data are not available for the period from 1972 to 1986.

How might changes in ocean condition alter larval rockfish production? Lenarz and Wyllie Echeverria (1986) showed that visceral fat volume in yellowtail rockfish (*Sebastes flavidus*) was significantly lower during 1983, an El Niño year, compared to 1980, a non–El Niño year; this correlated, to some extent, with differences in gonad volumes for the two years. Also, Lenarz et al. (1995) showed that condition factors for adults of chilipepper (*S. goodei*), blue rockfish (*S. mystinus*), and *S. flavidus* were lower during the 1982–83 and 1992–93 El Niño events than during associated non–El Niño years, and VenTresca et al. (1995) showed that adult condition and gonad indices in *S. mystinus* were depressed during these two El Niño events. Recently, Woodbury (1999) has shown that growth rates of adult *S. entomelas* (widow rockfish) and *S. flavidus* were depressed during El Niño conditions in 1983 compared to other years between 1980 and 1987.

These studies suggest that reduced ocean productivity during El Niño events and the associated effects on female rockfish condition could lower larval production. Likewise, the prolonged decline in ocean productivity associated with the recent warm regime may have caused a prolonged depression in larval rockfish production. This does not explain why larval abundance declined during La Niña conditions, when presumably primary and secondary production and trophic conditions were generally enhanced. Clarification of the relation between ocean conditions and rockfish reproduction will require a thorough study of maternal condition and larval production in a variety of rockfish species in relation to ocean climate.

Is survival of early-stage rockfish larvae a significant factor in the decline in larval abundance associated with the regime shift and with ENSO episodes? Because rockfish are viviparous, the condition of the pregnant female affects fetal-maternal exchange and particularly brood

nutrition. The relatively poor condition of female rockfishes during El Niño episodes could be reflected in the condition of intraovarian young and could result in poor survival immediately after birth. The well-documented decline in ocean productivity associated with El Niño events may play an important role in the survival of first-feeding larvae and in subsequent larval stages. If declines in larval rockfish abundance were due to starvation, early larvae should show histological evidence of starvation as demonstrated for larvae of jack mackerel (Theilacker 1986) and northern anchovy (O'Connell 1980). Such a study has yet to be conducted for rockfish larvae.

Yoklavich et al. (1996) presented evidence contradicting the notion that starvation during El Niño conditions reduces survival of rockfish larvae. They found no evidence of starvation in rockfish larvae collected during the 1992–93 El Niño, and growth rates in *S. jordani* larvae from their samples were similar to growth rates of *S. jordani* larvae from non–El Niño years in the same region (Laidig et al. 1991; Ralston et al. 1996). Yoklavich et al. (1996) concluded that reduced survival of larval rockfish in their samples taken during the 1992–93 El Niño was due to predation following transport of the larvae to near-coastal waters, where chaetognath populations were extremely high. Their suggestion that upwelling conditions led to offshore transport of rockfish larvae and enhanced larval survival contradicts Parrish et al. (1981), who hypothesized that offshore transport of the larvae of demersal fishes in the California Current region is generally detrimental to larval survival.

It is obvious that much more research is needed to provide a basis for a thorough evaluation of the survival of larval rockfish in relation to environmental variation, especially if Ralston and Howard (1995) are correct in concluding that year-class strength in rockfishes is determined largely during the larval period.

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RECORD COASTAL UPWELLING IN THE CALIFORNIA CURRENT IN 1999

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ABSTRACT

An extremely unusual level of coastal upwelling in the spring and summer of 1999 over much of the California Current system (CCS) is described, based on direct and indirect observations. Wind and ocean anomalies in 1999, a period characterized by an equatorial La Niña, are compared to climate trends for the previous several years, and specifically contrasted with the extremes associated with the 1997–98 El Niño event. Conditions in the CCS during the spring and summer of 1999 were consistent with extremely high levels of sustained coastal upwelling. The Pacific Fisheries Environmental Laboratory (PFEL) upwelling indices reached record highs for a series extending back to 1946. Strong, sustained upwelling-favorable winds were measured at coastal buoys through late 1998 and much of 1999. Coastal sea-surface temperatures (SSTs) were 3°–4°C below their seasonal mean in spring 1999, and about 10° cooler than the region experienced in late 1997. Hydrographic surveys off central California suggest upwelling of water by 100 m or more relative to the long-term spring average. Coastal sea-level (CSL) anomalies in the northern CCS were the lowest in at least 65 years. Greater than usual southward transport by the California Current is implied. A number of population and ecological changes observed during this period may be linked to the unusual ocean conditions and the striking transition from El Niño to La Niña. Physical conditions in the CCS can change swiftly and dramatically, and its marine populations appear to respond nearly as rapidly. The large physical and biological changes that occurred in 1999 may signify the initiation of a new climate regime for the CCS.

INTRODUCTION

In less than two years sea-surface temperatures (SSTs) over much of the California Current system (CCS) dropped from the warmest on record during the height of El Niño in late 1997 (as much as 6°C above the seasonal mean; Lynn et al. 1998) to low temperatures in 1999 not seen in decades (more than 3° below normal). This rapid cooling is unprecedented, particularly in the

context of the very warm regional ocean temperatures of the past decade, and is especially impressive given that the annual range of SST is about 3°C off central California, and its interannual variance is only 1°C.

Coastal upwelling is arguably the dominant process affecting the physical and ecological structure of the CCS and other eastern boundary current ecosystems. Upwelling in spring and summer significantly affects regional and local ocean circulation, thermohaline structure and stability, and water-mass exchange between the coastal and deep ocean. It drives the biological productivity and energetics of the system through the vertical transport of nutrients into the photic zone and the lateral advection of nutrients, primary and secondary producers, and larvae of higher predators. This process also contributes to the generation of ocean fronts, where organisms and material often aggregate.

Interannual variability in coastal upwelling is reflected in the physical, biochemical, and ecological nature of the CCS (Chelton et al. 1982). Much of the variability on this time scale is attributed to El Niño and La Niña; another major contribution is from longer-term climate change (Mantua et al. 1997; Schwing and Mendelssohn 1997; Schwing et al. 1997). Yet it is not always clear whether unseasonable levels of upwelling are locally or remotely forced. It is also noted that interannual fluctuations in CCS transport or biological character (e.g., population distribution or recruitment) do not always have a corresponding shift in coastal upwelling.

The goal of this paper is to describe the extremely unusual level of coastal upwelling that occurred in the spring and summer of 1999 over much of the CCS, based on direct and indirect observations. Anomalies of coastal winds, ocean temperature, structure, circulation, and coastal sea level are compared to coastal California climate trends for the previous several years, and specifically contrasted with the extremes associated with the 1997–98 El Niño event. We speculate on the impact of the resulting anomalous conditions on coastal marine populations. We also look at the possible role of 1999 in predicting future conditions. This paper complements the article on the status of the California Current in this volume (Bograd et al. 2000).

May 1999 SST and April-May 1999 Vector Wind Anomalies
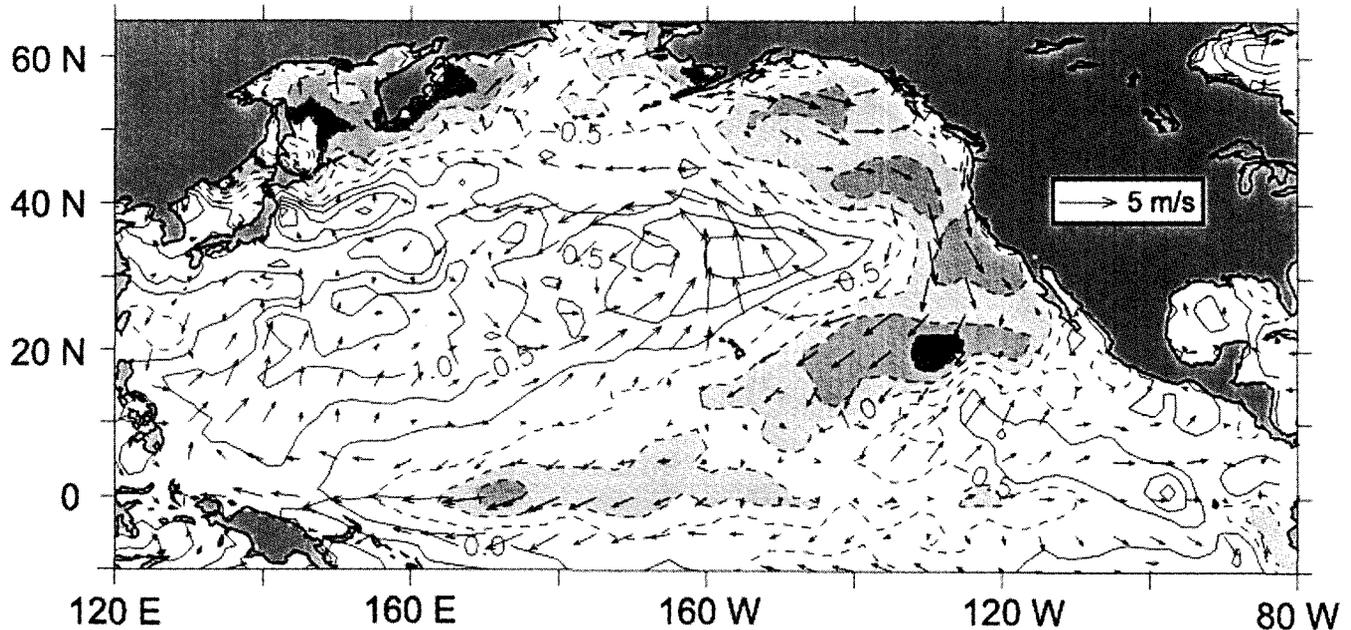
Figure 1. May 1999 SST anomalies and April–May 1999 wind anomalies for the North Pacific. Arrows denote magnitude and direction of wind anomaly. Contours denote SST anomaly. Contour interval is 0.5°C. Negative SST anomalies (dashed contours) less than −1.0°C are shaded. Anomalies computed on NOAA-CIRES/Climate Diagnostics Center Web site (http://www.cdc.noaa.gov).

LARGE-SCALE CONDITIONS AFFECTING THE NORTHEAST PACIFIC

The latter half of 1998 was marked by the rapid decay of one of the strongest El Niño events of this century and the equally sudden onset and intensification of La Niña conditions. The multivariate ENSO index (MEI; Wolter and Timlin 1998) dropped from an El Niño peak in spring 1998 to a minimum in late fall 1998 (http://www.cdc.noaa.gov/~kew/MEI/mei.html). This decline was unprecedented in the 50-year history of the MEI. The intensity of the 1998–99 La Niña, as indicated by the MEI, remained moderately strong from October 1998 through 1999 (Bograd et al. 2000).

Through much of the 1999 upwelling season, unusually high atmospheric pressure in the North Pacific High (35°N, 130°W) led to vigorous anticyclonic wind stress, including anomalously strong alongshore upwelling-favorable winds along the North American west coast. This pattern was at its strongest in early spring 1999 (fig. 1). This also contributed to stronger than normal trade winds, a typical feature of the La Niña phase of ENSO. The anomalous winds in 1999 were similar to those during the several years prior to the 1976 climate regime shift (Parrish et al., in press).

The pattern of North Pacific sea-surface temperature (SST) anomalies during spring–summer 1999 (fig. 1) was similar to that seen during many past La Niña events. It also was similar to patterns of surface anomalies seen

before the 1976 regime shift (Parrish et al., in press) and more generally during the negative phase of the Pacific Decadal Oscillation (Mantua et al. 1997). Positive anomalies extended from the western North Pacific to north of Hawaii. A region of cooler than normal SST stretched roughly along the axis of the North Pacific trade winds from the western equatorial Pacific to Baja California, and along the North American west coast into the Gulf of Alaska. This horseshoe-shaped region of negative SST anomaly developed in late 1998 and intensified in spring 1999, particularly in the CCS. At the same time, the anomalous anticyclonic atmospheric circulation over the northeast Pacific, and the associated southward wind stress along the west coast strengthened (fig. 1). The wind stress curl over this region of cool anomalies was higher than normal, reinforcing cool upper ocean temperatures via enhanced Ekman pumping (open-ocean upwelling). The implication is that regional wind anomalies led to the extreme SST anomalies in the CCS and northeast Pacific through Ekman processes in the upper ocean. No clear links between the wind or SST anomalies in the northeast Pacific and the equatorial Pacific are apparent for this period.

WEST COAST ANOMALIES 1998–99
Coastal Upwelling

The PFEL upwelling index (Bakun 1990; Schwing et al. 1996) estimates the intensity of large-scale, wind-
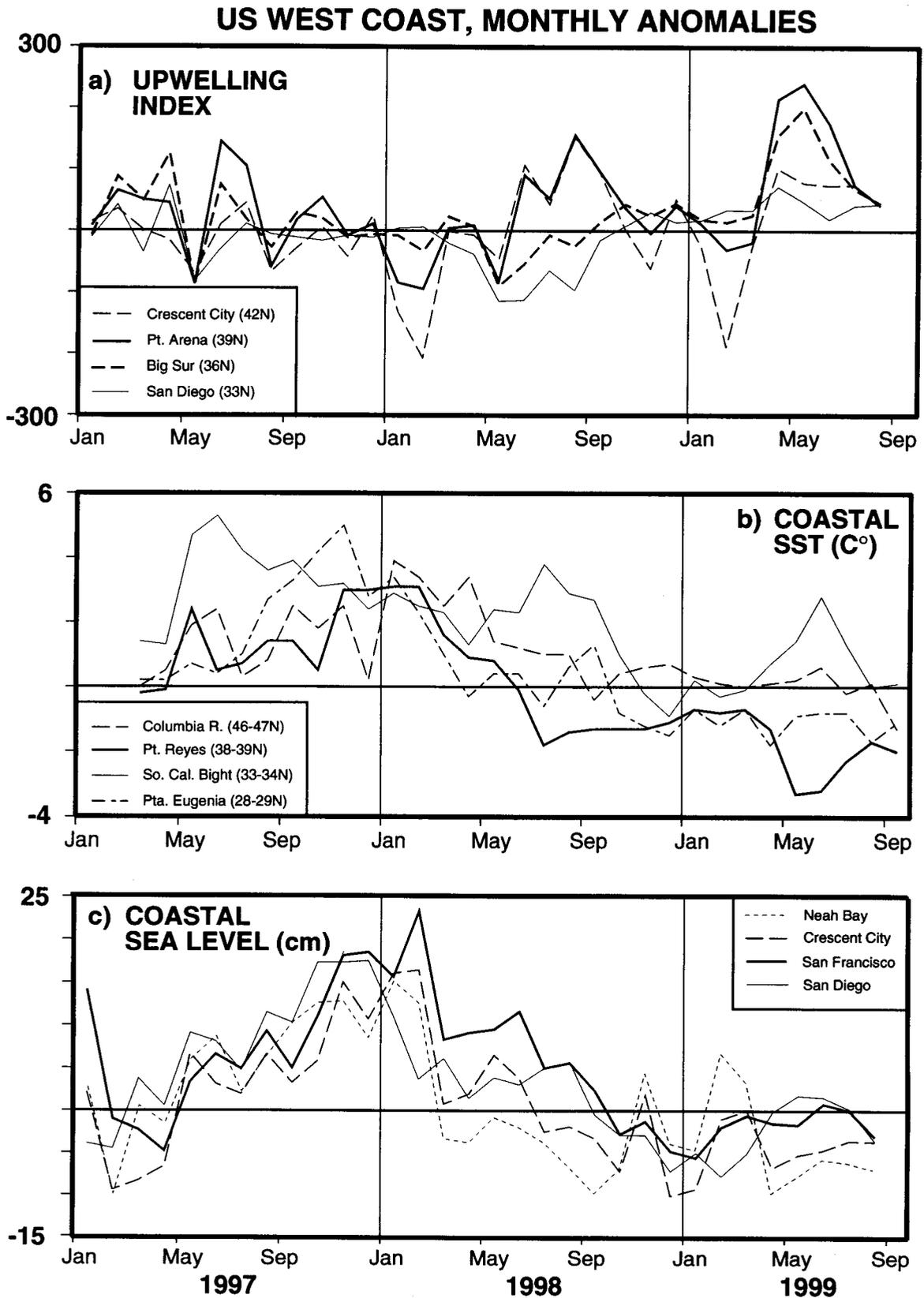
Figure 2. Monthly anomalies of (a) upwelling (m³/s along each 100 m of coastline; anomaly reference period, 1948–67); (b) SST (one-degree summaries of surface reports, ship reports, and buoy observations; anomalies calculated by using the climatology from the UWM/COADS analysis); and (c) coastal sea level (anomaly reference period 1975–95) at selected locations along the North American west coast, 1997–99.

**COASTAL UPWELLING INDEX, CALIFORNIA CURRENT
APRIL-JULY MEAN ANOMALIES, (normalized to 1948-67)**
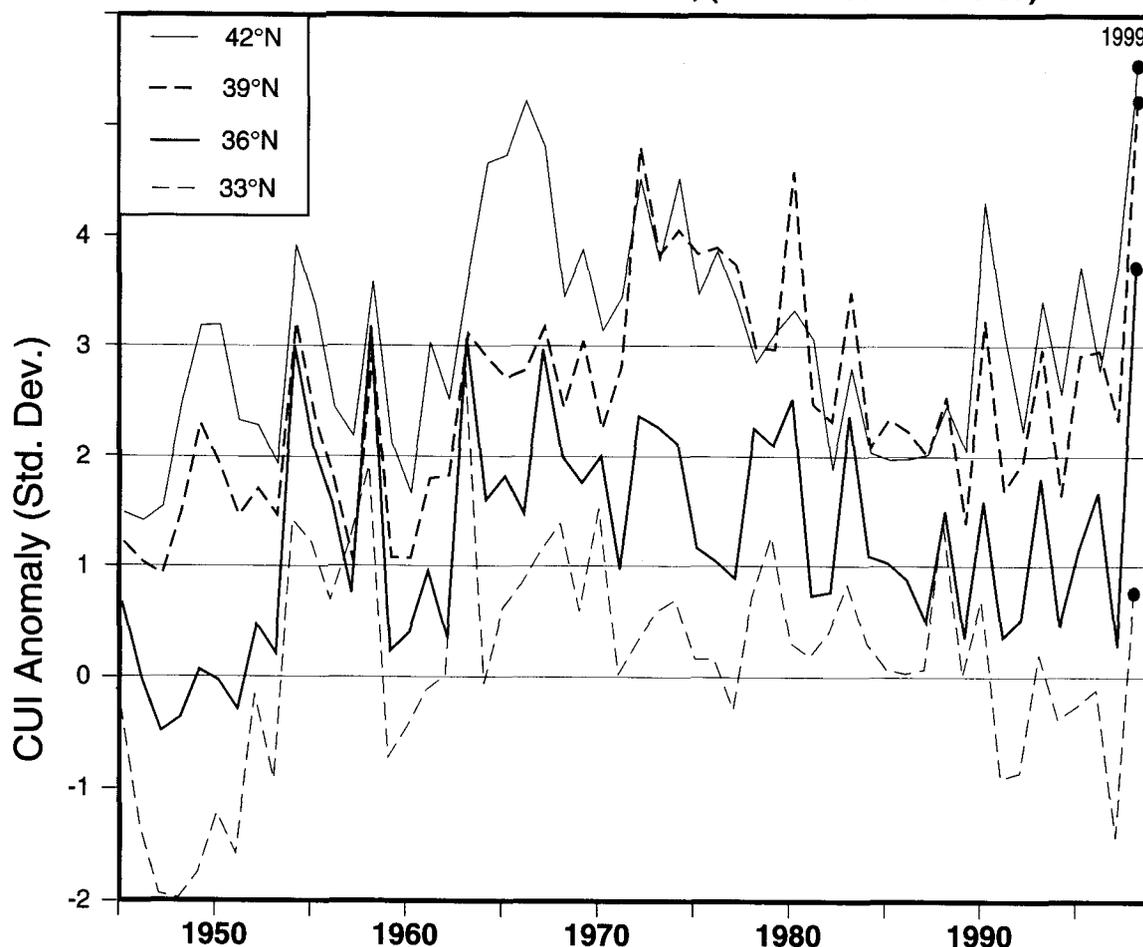
Figure 3. Anomalies of coastal upwelling index during the upwelling season (April–July), 1946–99 at four west coast locations. Each series normalized to 1948–67 period. Series from 36°N, 39°N, and 42°N offset by 1, 2, and 3 standard units. Horizontal lines denote mean of each series. Solid circles denote 1999 values.

induced coastal upwelling along the North American west coast. After a period of generally weaker than normal upwelling through late spring and summer 1998 from San Francisco to southern Baja California, the positive index anomaly indicates slightly above normal upwelling in late 1998 and early 1999 (Hayward et al. 1999). Extremely strong upwelling, centered near Point Arena and extending the length of the California coast, developed in April 1999 (fig. 2a). At the same time, upwelling anomalies were negative off Oregon and Washington. Upwelling off northern California during April–July 1999 (the peak of the upwelling season) was the strongest in the 54-year record of this index, 2.5–3.5 standard deviations above normal (fig. 3). Anomalies remained positive into the fall of 1999.

Large positive upwelling anomalies have been observed in the spring of other La Niña years (e.g., 1965, 1971, 1974). Conversely, weaker than normal upwelling followed the strong 1997–98 El Niño, a relationship seen

in 1983 and 1992 as well. However, not all La Niña years feature anomalously strong coastal California upwelling (e.g., 1951, 1963), and some years of very strong upwelling (e.g., 1973) are not linked to equatorial La Niña events. Although there is a clear connection between tropical and extratropical variability on the interannual scale, anomalous conditions in mid-latitude regions such as the CCS cannot always be explained by an anomalous equatorial state.

Coastal Winds

Coastal winds off the western United States are linked to the Pacific basin-scale wind patterns. Winds measured at west coast NOAA National Data Buoy Center (NDBC) buoys are highly coherent over large alongshore distances (Dorman and Winant 1995), yet most of the buoy records from recent years feature large data gaps. Composite time series of available wind and SST observations for three geographical regions of the CCS

Wind

California Current – North

(a)

California Current – Central

(b)

California Current – South

(c)
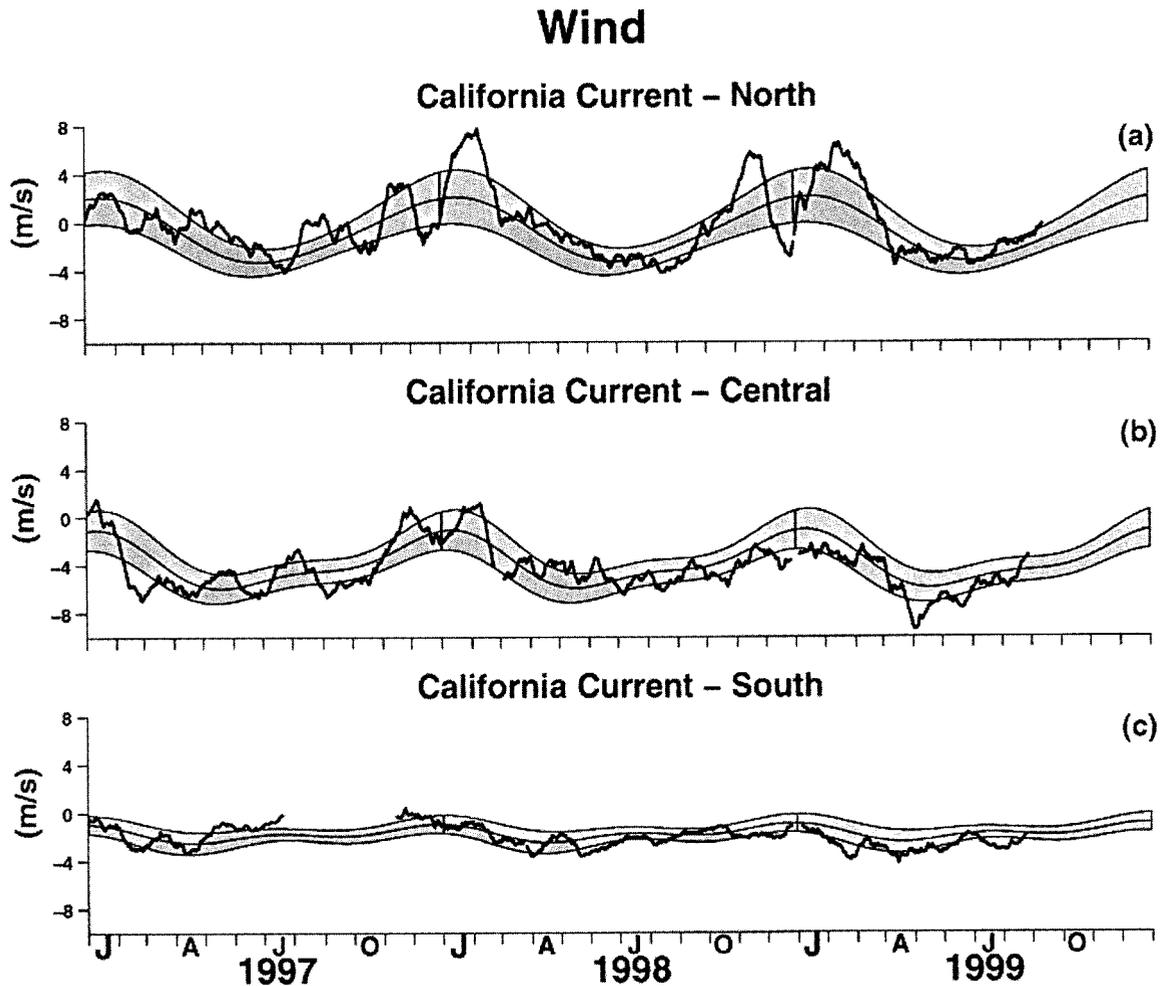
Figure 4.   Regional composite series (1997–99) of NDBC buoy alongshore winds superimposed on long-term (1981–99) composite annual biharmonic mean and standard error envelope. Northern region is north of Cape Mendocino, southern region is south of Point Conception. Buoys used for each composite are listed in table 1.

are presented in figures 4 and 5, respectively. These represent the regions' patterns over the past three years. The buoys used in the creation of these composite series are listed in table 1.

Alongshore winds in the central and southern CCS were dominated by stronger than normal northerly (more upwelling-favorable) winds through the latter half of 1998 and much of 1999 (fig. 4b, c). A number of stronger than normal northerly wind events were observed coastwide during this period. Two particularly strong events occurred in February and April 1999 off southern California (fig. 4c) and in early May and June 1999 off central California (fig. 4b). Strong equatorward wind stress leads to low coastal sea level (CSL) and cool ocean temperatures due to offshore surface Ekman transport and subsequent coastal upwelling. North of 40°N, winds in late 1998 and again in early 1999 were unusually strong from the south (fig. 4a), an artifact of winter storms moving through the Pacific Northwest. Unlike the CCS

regions to the south, this area did not experience unusually strong upwelling-favorable winds during the 1999 upwelling season. Buoy winds throughout the CCS weakened considerably in the late summer of 1999.

Coastal SST

SST anomalies in the CCS reflect perturbations in local coastal upwelling, complicated by the effects of large-scale atmospheric forcing and regional anomalies in ocean circulation. After an extended period of above-normal coastal ocean temperature, west coast SST summaries show a steady, long-term decline in late 1998 following the mature phase of El Niño (figs. 2b, 5). SST anomalies became negative off California in early fall 1998. A series of strong northerly wind events affecting the central and southern CCS during late 1998 contributed to these dramatic drops in SST. A strong correlation between increased upwelling and lower SSTs existed after June 1998 (fig. 6). The most notable of

SST

California Current – North

(a)

California Current – Central

(b)

California Current – South

(c)

1997   1998   1999
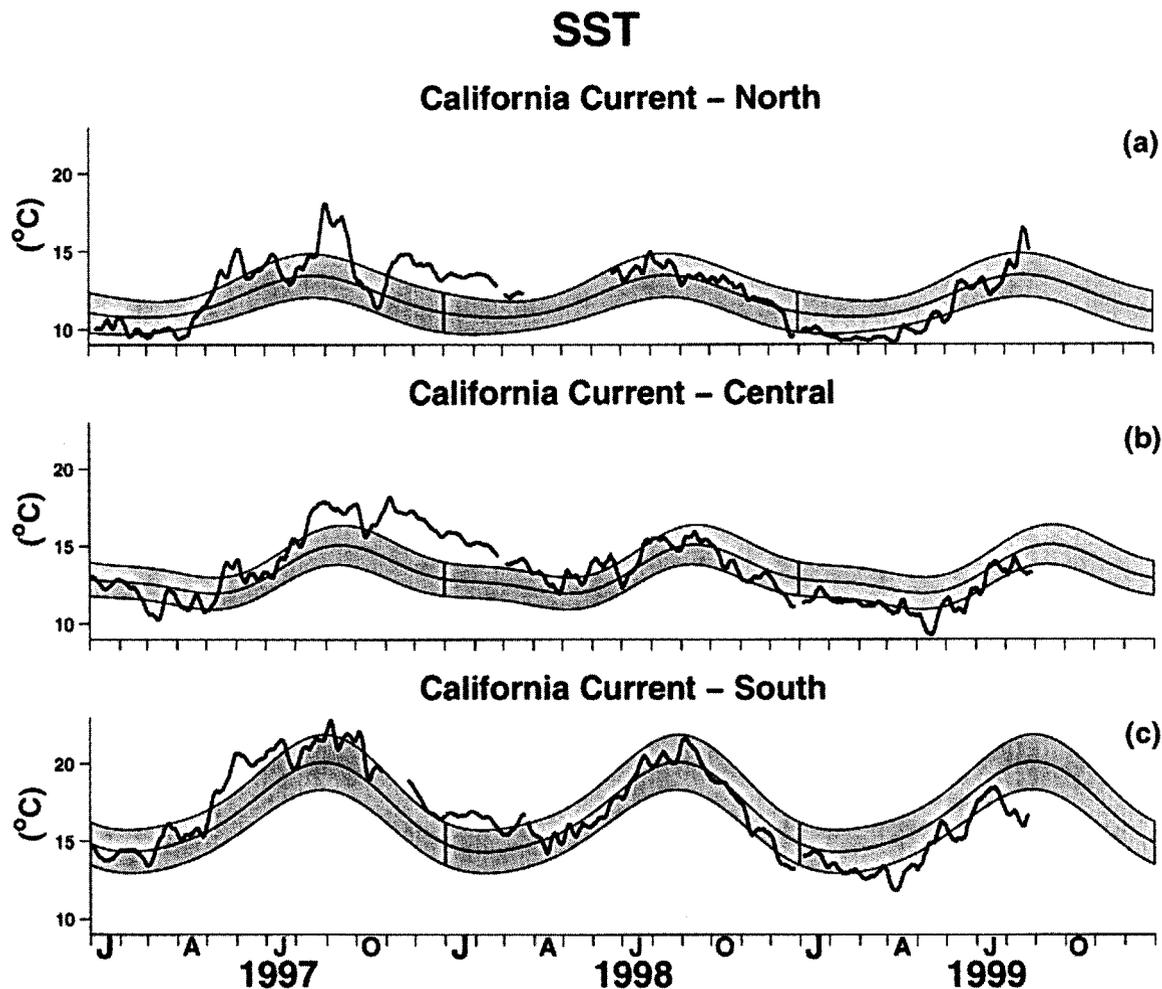
Figure 5.   Regional composite series (1997–99) of NDBC buoy SST superimposed on long-term (1981–99) composite annual biharmonic mean and standard error envelope. Northern region is north of Cape Mendocino, southern region is south of Point Conception. Buoys used for each composite are listed in table 1.

these events were in early November and December. A similar cooling occurred at buoys in the northern CCS, despite the concurrent strong southerly winds during this period.

Unseasonably cool coastal SSTs dropped even further in April and May 1999 from Point Conception to the California-Oregon border, corresponding to the time and region of greatly enhanced upwelling (figs. 2a, 4). This led to very cool SSTs through the 1999 upwelling season. SST anomalies were as much as 3°–4°C below normal during this time. The coolest SSTs during May–July 1999 followed the strongest upwelling rates (lower right corner of fig. 6). Near Point Reyes, SSTs were about 7.5° during much of May.

Localized warm areas were seen during the summer of 1999 in the Southern California Bight (inshore of the Channel Islands) and along the Oregon coast (fig. 2b). Warm SSTs in the Pacific Northwest were associated with weaker than normal northerly winds and negative

upwelling anomalies. Southern California shore temperatures were actually warmer than normal during much of this time (Bograd et al. 2000). Positive anomalies in the inner Southern California Bight may have been due to a combination of reduced upwelling, a lack of ocean mixing, and transport of warm water from the south.

A major difference in the atmospheric forcing of upper ocean temperature in the past three years is that the very cool conditions in 1999 developed in situ adjacent to the coast, and can be attributed directly to strong coastal upwelling. Positive SST anomalies during the 1997–98 El Niño were a product of large-scale atmospheric conditions (e.g., open-ocean upwelling in the outer CCS) and ocean transport in addition to reduced local upwelling at the coast. This is especially clear during fall 1997 along central California (fig. 5b). This distinction is illustrated by the relationship of SST with upwelling off Point Reyes (fig. 6). During the 1998–99 La Niña there was a strong negative correlation between monthly

TABLE 1
National Data Buoy Center (NDBC) Buoys in the
California Current Used to Calculate Composite
Climatologies for Figures 4 and 5

Region	Location	NDBC buoy no.	Lat./lon. (°N/°W)
North	Columbia River Bar	46029	46.2/124.2
	Eel River, CA	46022	40.8/124.5
Central	Bodega, CA	46013	38.2/123.3
	San Francisco, CA	46026	37.8/122.8
	Santa Cruz, CA	46012	37.4/122.7
	Monterey, CA	46042	36.8/122.4
	Cape San Martin, CA	46028	35.8/121.9
	Santa Maria, CA	46011	34.9/120.9
	Point Conception, CA	46023	34.3/120.8
South	Santa Barbara, CA	46053	34.2/119.8
	Long Beach, CA	46045	33.8/118.4
	Catalina Ridge, CA	46025	33.7/119.1

anomalies in local upwelling and coastal SST (fig. 6, solid squares); no relation was seen during the 1997–98 El Niño (open squares). However, both regressions have a non-zero intercept, suggesting that monthly variations in SST due to upwelling occurred on a warmer than normal background during El Niño and on a cooler than normal background during La Niña.

Coastal Sea Level

Consistent with strong coastal upwelling, coastal sea level (CSL) was uncharacteristically low along the west coast during the 1999 upwelling season (fig. 7). Detrended CSL means for this season at Crescent City and Neah Bay were the lowest since at least 1934, and the third lowest at San Francisco since 1975 (http://uhslc.soest.hawaii.edu/). Although San Diego CSL anomalies were negative in 1999 as well, they were not highly unusual in the context of the past few decades. The observed drop in CSL during 1999 is consistent with theoretical estimates for the magnitude of the observed wind and upwelling index anomaly (Brink et al. 1987).

As the 1997–98 El Niño developed and dissipated, CSL rose and fell uniformly (fig. 2c). West coast anomalies became negative in the latter half of 1998, approximately at the time that the northerly winds strengthened. They remained near or below their seasonal means into late 1999. The greatest negative anomalies in CSL developed north of San Francisco in spring 1999, at the time of very strong upwelling. San Francisco and San Diego levels were less responsive to the positive upwelling anomalies. In spring and summer 1999, CSL sloped downward toward the north, reversing the southward sea-level slope of late winter. The coastwide low in winter is not clearly related to unusual coastal winds or upwelling. It is possibly linked to the concurrent anomalous clockwise atmospheric circulation over the North Pacific,
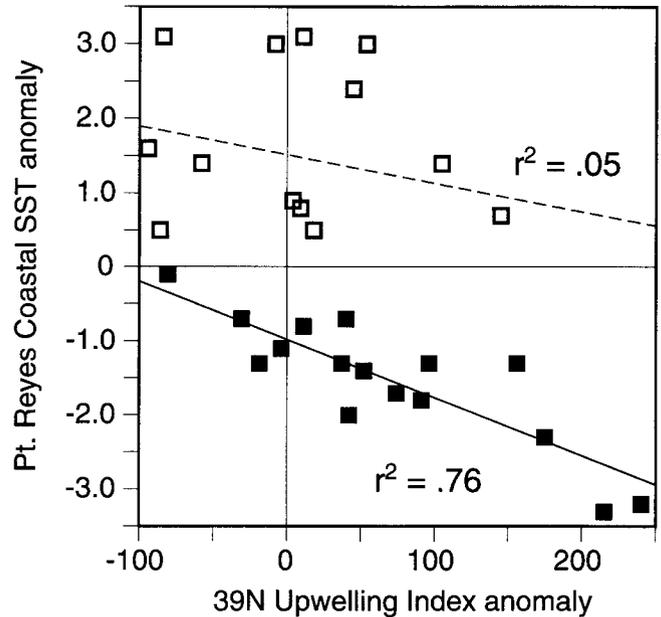
Figure 6. PFEL monthly upwelling index anomaly at 39°N plotted against monthly SST anomalies off Point Reyes (38°–39°N, 123°–124°W). SST lags upwelling index by one month. Both series were detrended to remove long-term climate variability. Open squares denote monthly anomalies during El Niño (May 1997–May 1998). Solid squares denote monthly anomalies during La Niña (June 1998–September 1999). Periods based on Southern Oscillation Index. Dashed line is regression for El Niño; solid line is regression for La Niña.

which may not be displayed by the nearshore winds, or to a steric response to the rapid cooling shown by SST.

The rise in CSL during the 1997–98 El Niño was probably a reflection of steric expansion of the water column and increased poleward transport of the California Current. Anomalous coastal upwelling (fig. 2a) was probably not the major factor in the high CSLs during 1997. Large positive west coast CSL anomalies generally follow El Niño events (e.g., 1983, 1993, 1998; fig. 7). But previous low extremes in summer CSL anomalies (e.g., 1977, 1991, 1994) were not associated with equatorial La Niña events.

An example of the long-term relation between CSL and coastal upwelling is shown in figure 8. Lower sea level generally accompanies years of higher upwelling, with 1999 being the most extreme case in the past 54 years. The highest CSL anomalies occur during strong El Niño years, but are not necessarily related to unusually weak upwelling. This finding supports the contention that large-scale and remote processes contribute substantially to variability in the CCS during El Niño events. Also noteworthy is that the best statistical relationship for Crescent City CSL is not with local upwelling, but with upwelling south of Crescent City. This is true for San Francisco and Neah Bay as well.

The spatial coherence of CSL is much more extensive than for SST, suggesting that sea level is less affected

US WEST COAST SEA LEVEL
APRIL-JULY MEAN , ANOMALIES (detrended)
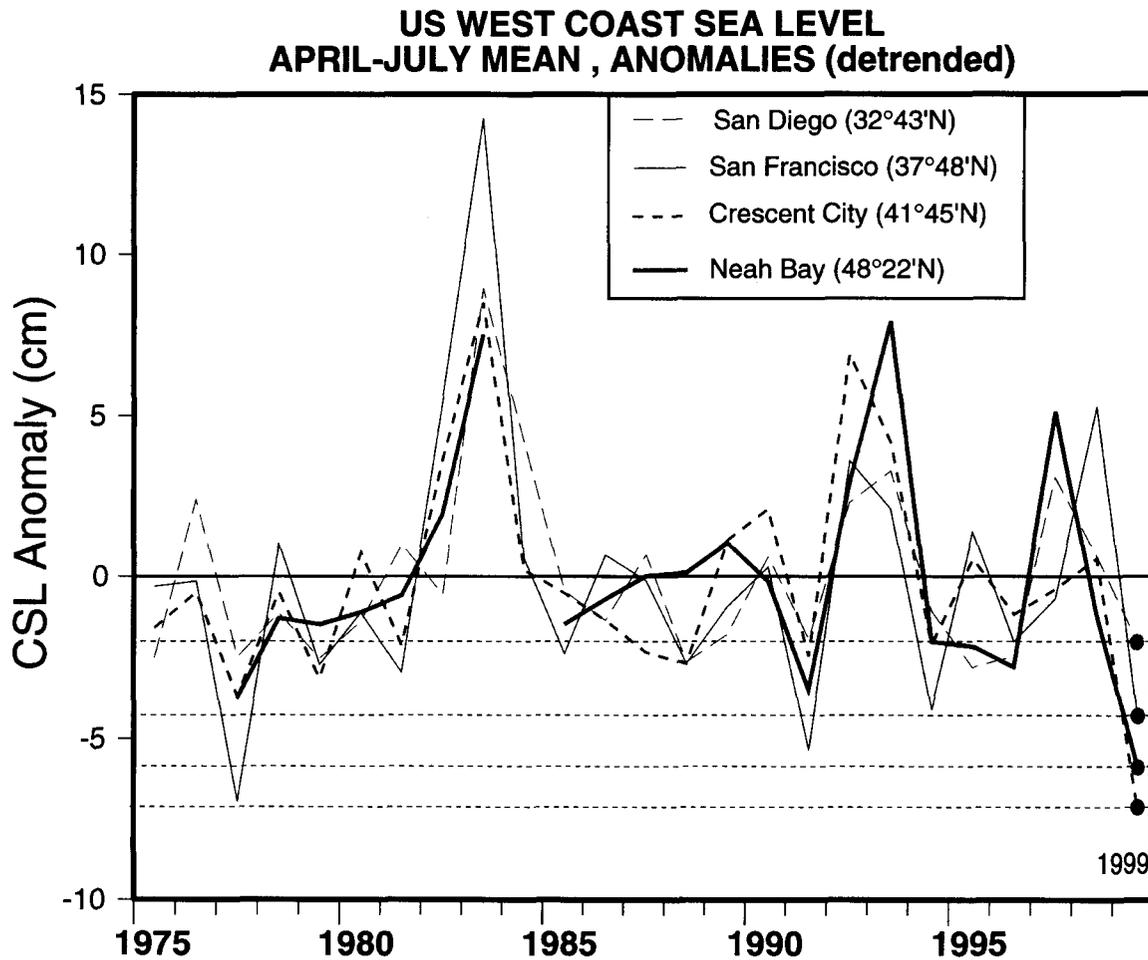
Figure 7.   Coastal sea-level anomalies, annual April–July means. Series were detrended to remove long-term climate variability. Solid circles and horizontal dashed lines denote 1999 anomalies.

by local and regional differences in seasonal forcing (fig. 2). It also implies that CSL integrates the west coast climate signal, including El Niño and La Niña, to a greater degree than other ocean variables.

Subsurface Temperature and Salinity

Thus far the description of strong upwelling in 1999 has been based on surface observations. Perturbations in subsurface conditions confirm the significant impact of anomalous coastal upwelling on ocean conditions. Stronger upwelling is reflected in an uplifting of isotherms and isohalines toward the coast, identified by cooler temperatures and higher salinities at a given depth. The discussion here will focus on central California. The coverage of southern California by the CalCOFI surveys is detailed in Bograd et al. 2000.

In May 1999 the Tiburon Laboratory (NMFS-SWFSC) examined ocean structure off central California as part of the annual pelagic juvenile rockfish surveys. Strong upwelling was indicated at that time by very low tem-

peratures and high salinities throughout the upper water column (figs. 9 and 10). The Point Reyes upwelling filament was the coldest observed in the 17-year history of the Tiburon spring surveys. Mixed layer (upper 50 m) measurements were 1–2 s.d. ($1°$–$2°$C cooler and S = 0.2–0.4 higher) outside the long-term (1987–96) means for this area (Baltz 1997). Vertical sections off Point Reyes show robust coastal upwelling and very cool, saline water on the shelf (fig. 10). Temperature and salinity values observed in the upper 50 m indicated an upwelling of water on the order of 100–150 m in response to the unusual coastal upwelling of 1999, relative to typical spring ocean conditions. This corresponds dynamically to a 10–15 cm drop in CSL, as noted in figure 2c. Upwelled isohalines that normally outcrop near the coast surfaced 50 km offshore. This helped produce a strong ocean front at the surface convergence of offshore-flowing upwelled water with the warmer California Current.

Robust and sustained upwelling in 1999 led to stronger net offshore Ekman transport, particularly with respect
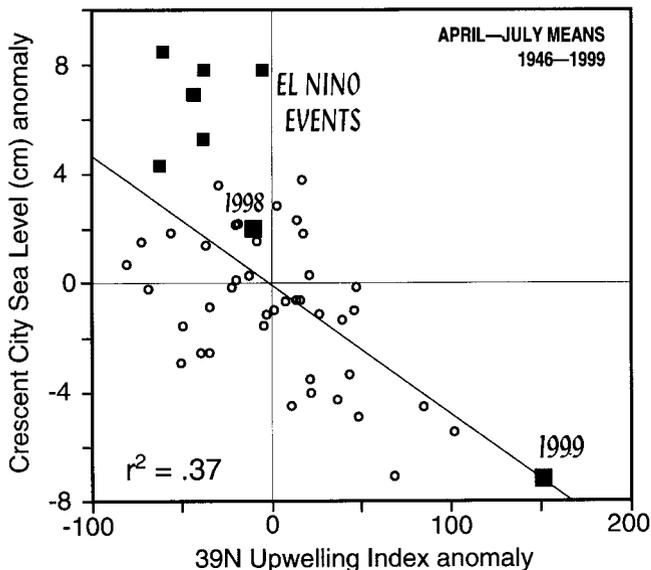
Figure 8. Annual April–July anomalies of PFEL monthly upwelling index (39°N, 125°W) versus Crescent City coastal sea level, 1946–99. El Niño years denoted by gray squares. Regression shows effect of very strong upwelling on sea level in 1999 (labeled). Sea level is higher than expected during El Niño because of thermal expansion of water column and higher northward transport of California Current.

to the upwelling jet at Point Reyes and elsewhere. This resulted in an unusual offshore displacement of the upwelling front and the maximum of chlorophyll (fig. 11). It also contributed to an unusually strong southward geostrophic surface flow in association with the upwelling front, and a reduction and even reversal of the poleward California Undercurrent at 200 m off central California. The low dynamic thickness of the upper 200 m in 1999, 5–10 dyn. cm lower than in 1998, indicates anomalously dense water in the upper ocean. This would be true in the case of strong coastal upwelling. It also implies a strong southward flow (Ramp et al. 1995). Anomalous southward transport in the CCS is consistent with the very low CSLs at this time. The relative alongshore CSL gradient between Crescent City and San Francisco (fig. 2c) is equivalent to an approximately 10 cm/s greater southward geostrophic current.

BIOLOGICAL CONSEQUENCES OF STRONG UPWELLING

Although the mechanisms linking climate change to biological variability are not fully understood, a number of correlations between interannual and longer physical changes and marine organisms have been identified (cf. Chelton et al. 1982; Hollowed and Wooster 1992). In general, swings in population growth, abundance, distribution, and ecosystem structure accompany shifts in climate patterns. For example, the collapse of the California sardine fishery in the 1940s is now believed to have been at least partly due to a shift to cooler ocean

conditions, whereas a revival in this species has accompanied ocean warming since 1976. A five-fold drop in macrozooplankton off southern California over the past 50 years has been attributed to long-term warming (Roemmich and McGowan 1995). Interannual variability, such as El Niño and La Niña, is linked to changes in the species assemblage of phytoplankton, and to latitudinal shifts in the distribution of zooplankton such as euphasiids and copepods.

Interannual fluctuations in coastal upwelling can affect marine populations in three major ways. First, organisms are metabolically sensitive to thermal extremes and may migrate into or out of a region if it becomes too cool. Development, growth, and feeding rates are influenced by temperature as well. Second, the ecosystem is nutritionally enhanced by higher upwelling. Primary production increases, providing grazers and ultimately higher consumers with more food. Third, upwelling-related advective processes transport zooplankton and pelagic larval stages. Many species are adapted to use upwelling circulation patterns for recruitment. Upwelling jets also represent a transport of nutrients, prey, and larvae out of the coastal zone into the deep ocean.

The speed at which the Pacific transitioned from a very strong El Niño state to a moderately strong La Niña is illustrated by indices such as the multivariate ENSO index (Wolter and Timlin 1998). The sudden transition from one climate extreme to the opposite is evidenced by the dramatic changes seen in the northeast Pacific as well. Climate models currently forecast a continuation of La Niña well into 2000. Thus the present coastal anomalies may be sustained into the 2000 upwelling season. If this is the case, a transition to a different marine ecosystem structure than seen for most of the 1990s is likely.

Of relevance to the physical changes in the CCS in 1999 are a number of biological observations that appear to go against recent and long-term ecosystem patterns. Most of these latest observations are consistent with those historically identified with a cooler regional ocean climate.

Chlorophyll concentrations off central California were greatest nearly 50 km offshore in May 1999, in association with the position of the upwelling front (fig. 11). Typically, the highest chlorophyll levels are immediately next to the coast. However, synoptic variability within a season is too high to allow an interannual difference to be determined. Chlorophyll, as indicated by SeaWiFS, increased significantly off coastal California, with 1999 concentrations much higher than typical (Bograd et al. 2000).

The zooplankton communities off Oregon (W. Peterson, pers. comm.) and British Columbia (D. Mackas, pers. comm.) shifted from a structure dominated by a
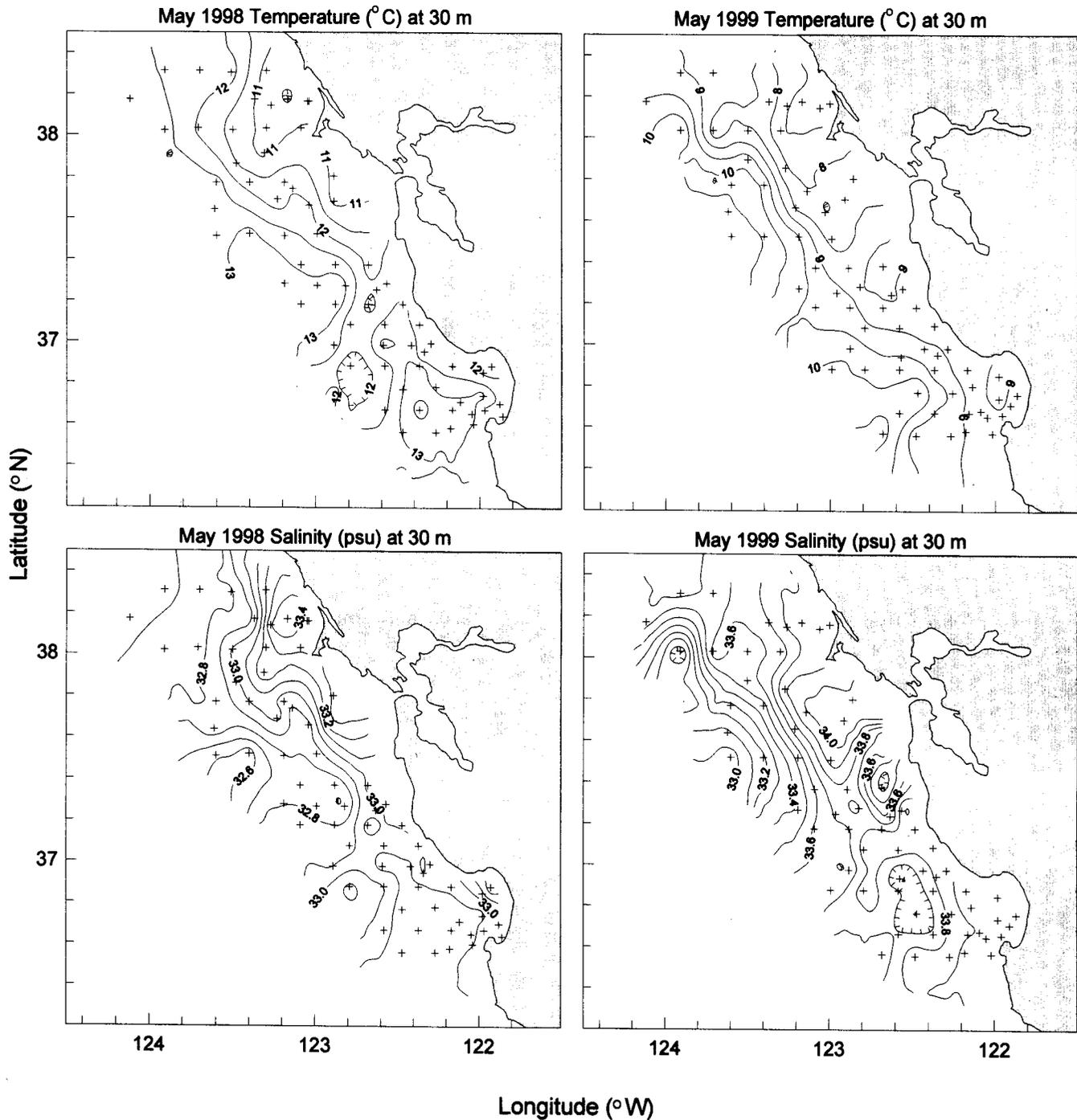
Figure 9.   Temperature and salinity at 30 m depth off central California during early May of 1998 and 1999. Crosses show CTD stations.

mixture of warm water and oceanic species to one comprising exclusively subarctic species. Macrozooplankton biomass levels off southern California in early 1999 were very high relative to the past 15 years (S. Bograd, pers. comm.). The January 1999 biomass was the highest in this period, representing a potential change in the long-term decline described by Roemmich and McGowan (1995). The lowest biomass levels in the past 15 years

were observed in 1998. The zooplankton displacement volume, estimated from acoustic returns, was much higher than usual in April 1999 off southern and central California (R. Lynn, pers. comm.).

Strong and sustained upwelling may have had a negative effect on recruitment of benthic nearshore species (e.g., urchins, barnacles, crabs) that rely on "relaxations" in upwelling to transport larvae onshore for settlement.
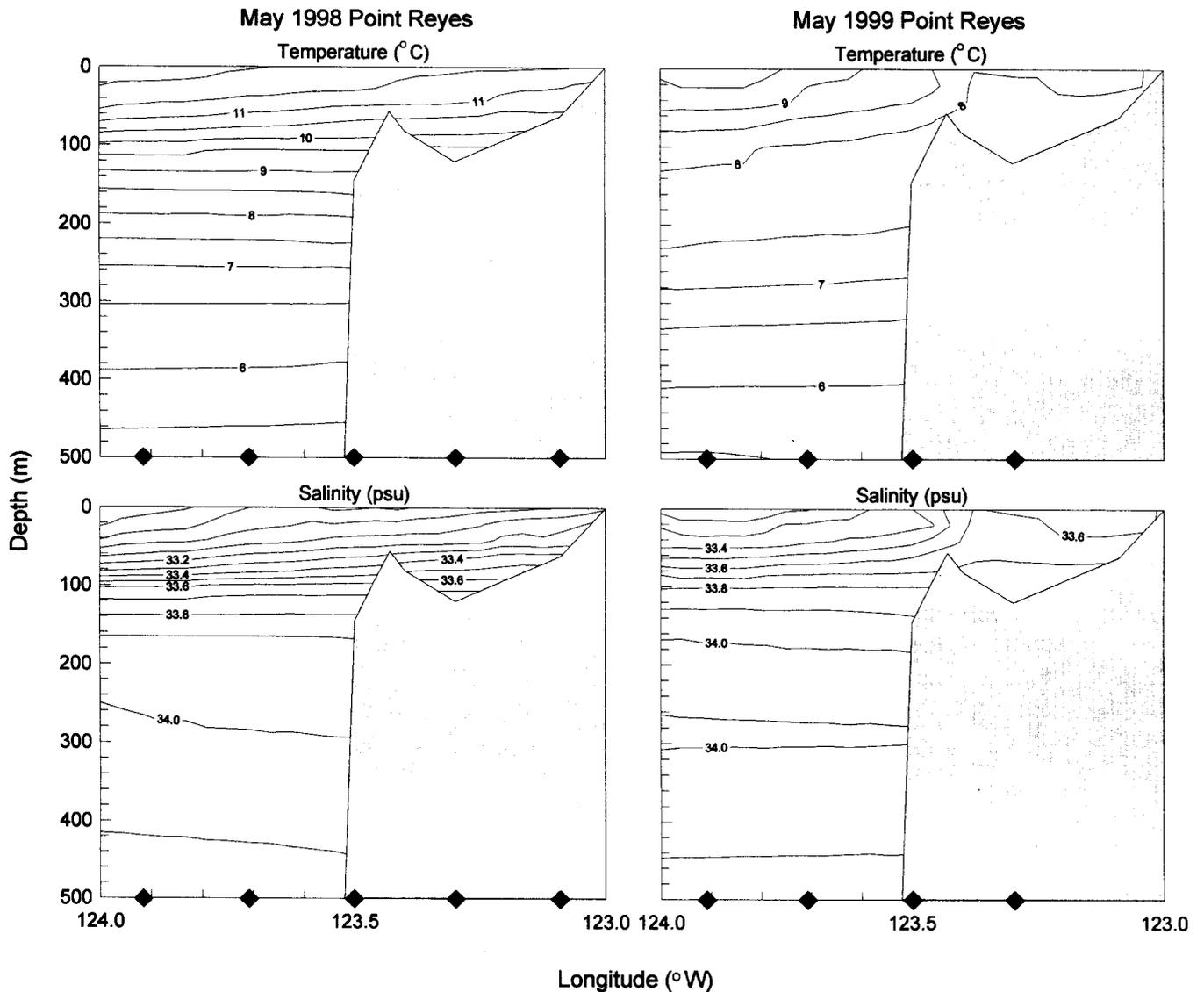
Figure 10.   Vertical sections of temperature and salinity off Point Reyes, Calif. (38°10'N) during early May of 1998 and 1999. Diamonds show CTD stations.

Returns of northern and central California populations were very low in 1999 (C. Lundquist, pers. comm.). This may be due to the unusual offshore extent of the upwelling front, combined with the relative lack of onshore transport events.

Sardine eggs off southern California, an indicator of the spawning biomass of sardines and the likely recruitment to the future population, occurred in higher densities in 1999 and were dispersed farther offshore (R. Lynn, pers. comm.). Pelagic juvenile rockfish off central California continued a decade-long trend of low abundance over the continental shelf and slope. However, juveniles were found farther offshore than in the past, probably because of the very high and sustained offshore Ekman transport.

Adult bocaccio rockfish, normally a northerly distributed species in the CCS, were caught in unusually high numbers south of Point Conception. Adult rockfish off central California were full of euphasiids and had high levels of stored fat (Hayward et al. 1999). In 1999, six times as many juvenile coho salmon were caught in NMFS surveys off Washington/Oregon as in 1998 (W. Peterson, pers. comm.).

A switch in marine bird populations was noted in 1999 (Hayward et al. 1999). Total abundance was up over 1998, and the community shifted from a prevalence of subtropical to subarctic species. Hayward et al. (1999) reported higher *Macrocystis* growth in 1999, relative to the previous year, a result of higher upwelling (Tegner et al. 1997).
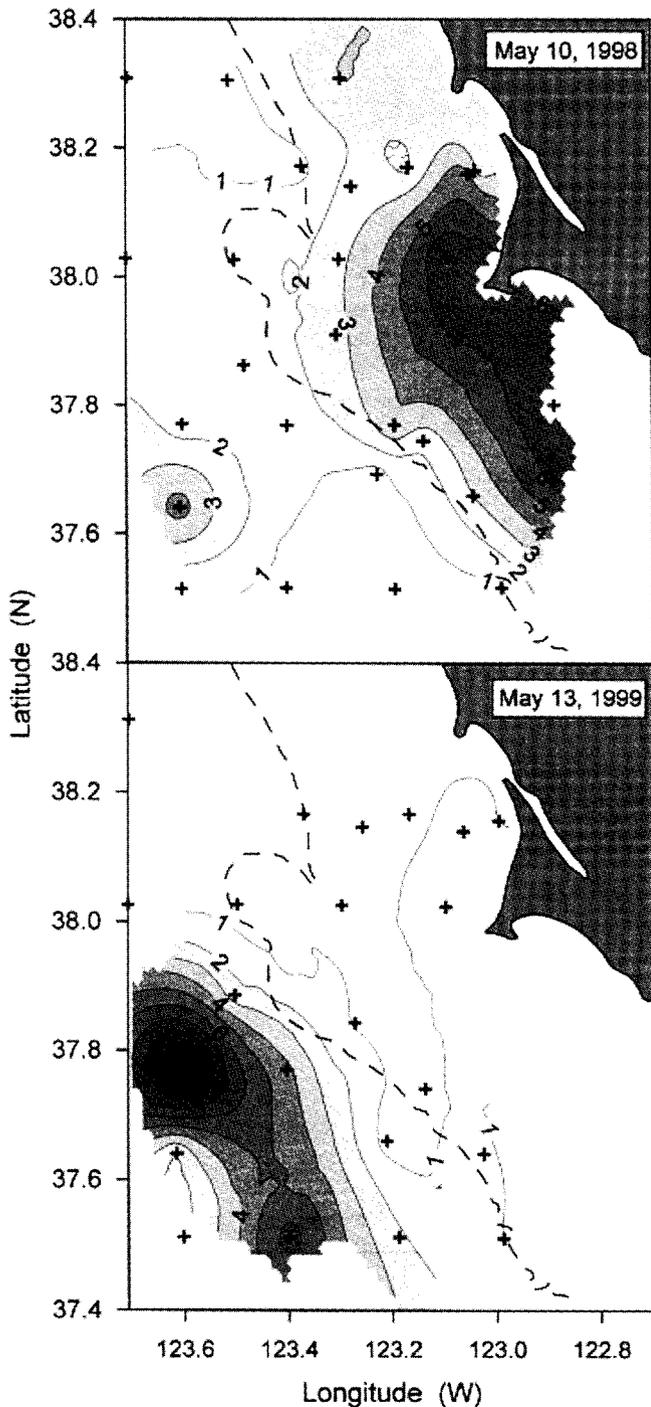
Figure 11. Chlorophyll concentrations (mg /m³) at 10 m depth near Point Reyes, Calif., in early May of 1998 and near Point Reyes in May of 1999. Crosses denote sampling locations.

CONCLUSIONS

Conditions in the CCS during the spring and summer of 1999, a period characterized by an equatorial La Niña, were consistent with extremely high levels of sustained coastal upwelling. The PFEL upwelling indices were record highs for a series extending back to 1946.

Strong, sustained upwelling-favorable winds were measured at coastal buoys through late 1998 and much of 1999. Coastal SSTs were 3°–4°C below their seasonal mean in spring 1999, and about 10° cooler than the region experienced in late 1997. Hydrographic surveys off central California suggest upwelling of water by 100 m or more relative to the long-term spring average. Coastal sea level in the northern CCS was the lowest in at least 65 years. Direct and indirect current measurements indicate greater than usual southward transport by the California Current.

The anomalous ocean conditions typically observed along the North American west coast during El Niño events (warm SST, high CSL) are the combined result of local and remote atmospheric and oceanic processes. In previous years, and specifically during the 1997–98 El Niño, ocean temperature anomalies were linked to regional and large-scale processes, and were less affected by local wind forcing. The upwelling season of 1999, however, shows a close relation between local wind and SST anomalies, indicating that local upwelling processes controlled coastal ocean conditions.

For much of California, the summer of 1999 was one of the coolest on record. From February through late 1999, sustained cool air temperatures along the central coast of California set numerous records (R. Renard, pers. comm.). The mean temperature at Monterey for March–July 1999 was 1.4°C cooler than the long-term average for these months. March and May tied and set 48-year records for their respective low mean and minimum average temperatures.

The relatively cool waters of the Pacific exert a strong maritime influence on the western United States. Unusually cool ocean conditions contribute to cooler than normal land temperatures. The west coast's weather is colored considerably through the development of a daily sea breeze and frequent coastal stratus and fog. Even the track and intensity of winter storms, as well as the amount of moisture they carry over the continental United States, are affected by upper ocean conditions.

It is too early to say for certain, but the unusual physical and biological conditions of 1999 may be the first signs of a shift in climate. Decadal-scale climate shifts, often referred to as regime shifts in the literature, have been described in a number of articles (cf. Mantua et al. 1997; Parrish et al., in press). The most familiar shift in the North Pacific occurred about 1977. Increasing recent evidence suggests that another significant climate shift occurred around 1990. Minobe (1999) has identified interdecadal oscillations in the Aleutian Low as a possible mechanism for climate shifts, and suggests that a phase reversal could occur as early as 1999–2000. The recent situation off California is reminiscent of the climatic and ecological patterns common in the years prior

to 1977. Conditions in 1999 also appear to be an extreme case of the relatively cool state of the CCS for several years after the strong El Niño events of 1957–58 and 1982–83. Perhaps the Pacific climate has undergone a new, analogous transition, returning to a former environmental and ecological state. Or the unusual physical and biological conditions of 1999 may be merely a brief reaction to a strong, extended La Niña, a hiatus in the recent trend toward a warmer climate. In either case, recent months have revealed that the CCS can change swiftly and dramatically, and that its marine populations appear to respond nearly as rapidly.

ACKNOWLEDGMENTS

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LARGE-CELLED PHYTOPLANKTON, THE NITRICLINE, AND GRAZING DURING THE CALIFORNIA 1997–98 EL NIÑO

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ABSTRACT

During autumn 1997 and winter and spring 1998, nitriclines were deep and macrozooplankton sparse in the California Current system. However, general relations between absolute and relative biomasses of ≥ 8 μm cells and nitricline depths and grazing pressure from macrozooplankton, derived from non–El Niño years, remained valid for all but a small group of nearshore stations in winter.

INTRODUCTION

Biomass of phytoplankton is routinely measured by proxy as chlorophyll retained on a filter of 1–2 μm porosity. However, because many planktonic herbivores graze selectively on different sizes of particles, categorizing phytoplankton by size may refine the estimation of the food supply for zooplankton (e.g., Durbin and Durbin 1989). Spatial/temporal variations in the physical forces in the ocean may affect secondary production through the food web by altering total phytoplanktonic biomass, size distribution, or both.

Mullin (1998) confirmed earlier findings by Malone (1971, incorrectly cited by Mullin as Hopkins 1971) that, in the California Current system, the relative importance of large cells was greatest where and when total phytoplanktonic biomass was augmented, and that the large-cell biomass was the more responsive to physically caused variations in supply of nutrients. Malone (1971) also argued that small cells were grazed primarily by protozoans and other microzooplankton, which respond quickly to changes in food supply, while the time lags inherent in population change for macrozooplankton permit greater variability in the biomass of their large-celled food. Mullin (1998) found evidence that the residual variability of biomass of ≥ 8 μm cells (i.e., variability not related to variability in depth of the nitricline) could be related to the grazing pressure by macrozooplankton.

The vertical distributions of many properties change dramatically during a California El Niño (i.e., the manifestation of El Niño–Southern Oscillation [ENSO] in the California Current system). Generally, the nitricline

occurs deeper in the water column, but the strength of this anomaly may vary spatially, and its biological effect depends partly on whether (or where) the ratio between the depths of the nitricline and the euphotic zone is changed. The purpose of the research reported here was to determine whether the relations between biomass of large phytoplankton cells, the nitricline, and macrozooplankton were similar during the 1997–98 El Niño to those of earlier, non–El Niño years.

As in the earlier study, I will draw inferences concerning processes (acting instantaneously) from biomasses (resulting from integration of processes over time). Therefore, time lags between the acting of a process and its detectable effect on a biomass potentially confound these inferences.

The oceanographic and ecological properties of the region sampled, and relations relative to long-term mean conditions and to events in the equatorial Pacific, are reported in Lynn et al. 1998 and Hayward et al. 1999. In brief, though equatorial signs of ENSO were strong by June 1997, and southern California coastal waters were anomalously warm through much of 1997, the latter phenomenon was attributed to regional anomalies in winds during spring and summer rather than to ENSO directly. I therefore considered the California El Niño to be present in autumn 1997, though I did not use data from the spring and summer of that year to represent non–El Niño conditions.

Upwelling-favorable winds in the area studied were anomalously weak in April–June 1998, and the thermocline was anomalously deep for about one year, but the biomass of phytoplankton in the water column (as integrated chlorophyll) was normal through 1997 and 1998. However, the macrozooplankton biomasses in February and April 1998 were the smallest recorded in 50 years, and continued to be small through the year. Coastal surface waters had returned to temperatures only slightly above normal by May 1998, though positive anomalies at 50–100 m persisted until autumn.

METHODS

The biomass of large-celled phytoplankton is defined here as the chlorophyll retained on an 8 μm-porosity
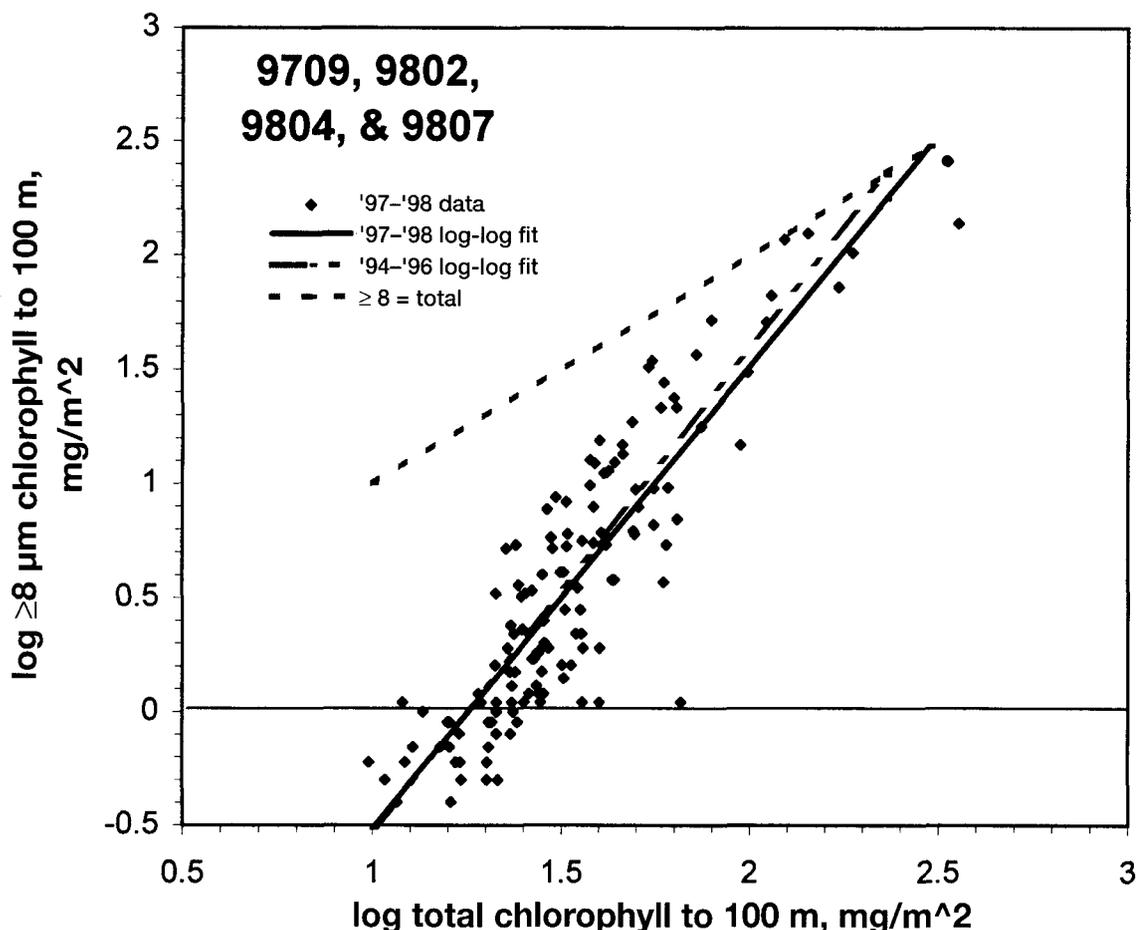
Figure 1.   Log-log relation between depth-integrated biomasses of ≥8 µm chlorophyll and total chlorophyll during the 1977–98 El Niño: September 1997 (cruise 9709) and February, April, and July 1998 (cruises 9802, 9804, and 9807). Also shown is the linear best fit for the same relation in non–El Niño years, 1994–96, and the line representing ≥8 µm chlorophyll = total chlorophyll.

membrane filter from water taken at ten depths through the upper 100 m (as in Mullin 1998, where the other methods used, and locations sampled, are also given). This measure could, of course, include firmly bound aggregations of small cells. The results of the quarterly cruises in the three years (1994–96) reported in that publication are used in the present study as non–El Niño baselines. As previously, I have used negative exponential best-fit curves to describe or idealize many data sets, but a causal linkage of this mathematical form between the variables is not necessarily implied.

RESULTS

Although no stations in the present study had chlorophyll biomasses >500 mg · m^{-2}, the relation between ≥8 µm chlorophyll and total chlorophyll was similar to that found in previous years (fig. 1), the large cells becoming more important as total biomass increased. The linear fit to log-transformed data implies that ≥8 µm chlorophyll was ≈16% of the total at 50 mg · m^{-2} and ≈100% of the total at 300 mg · m^{-2}.

At the subset of CalCOFI stations considered in the present study (see Mullin 1998, fig. 1), nitricline depths tended to be deeper by September 1997 than in the autumns of 1994–96, the modal decameter being displaced 20 m (fig. 2). As expected for an El Niño condition, this deepening continued in February 1998; in springs, although the frequency distributions of both 1994–96 and 1998 had several modes, arguably the 1998 nitriclines tended to be the deeper. This difference was not evident in summer (cruise 9807), and other symptoms of El Niño had waned by this time (see Introduction).

As in earlier years, there was considerable variation in the relation between the biomass of ≥8 µm cells (either as a fraction of the total biomass or in absolute terms) and the depth of the nitricline (fig. 3). In autumn (9709), spring (9804), and summer (9807), the general pattern can be approximated by a negative exponential curve, as in the earlier years, though when the nitricline was shallower than about 50 m in autumn and spring, the ≥8 µm biomasses were greater than those expected from 1994–96 relations (the solid curves in fig. 3). Table 1
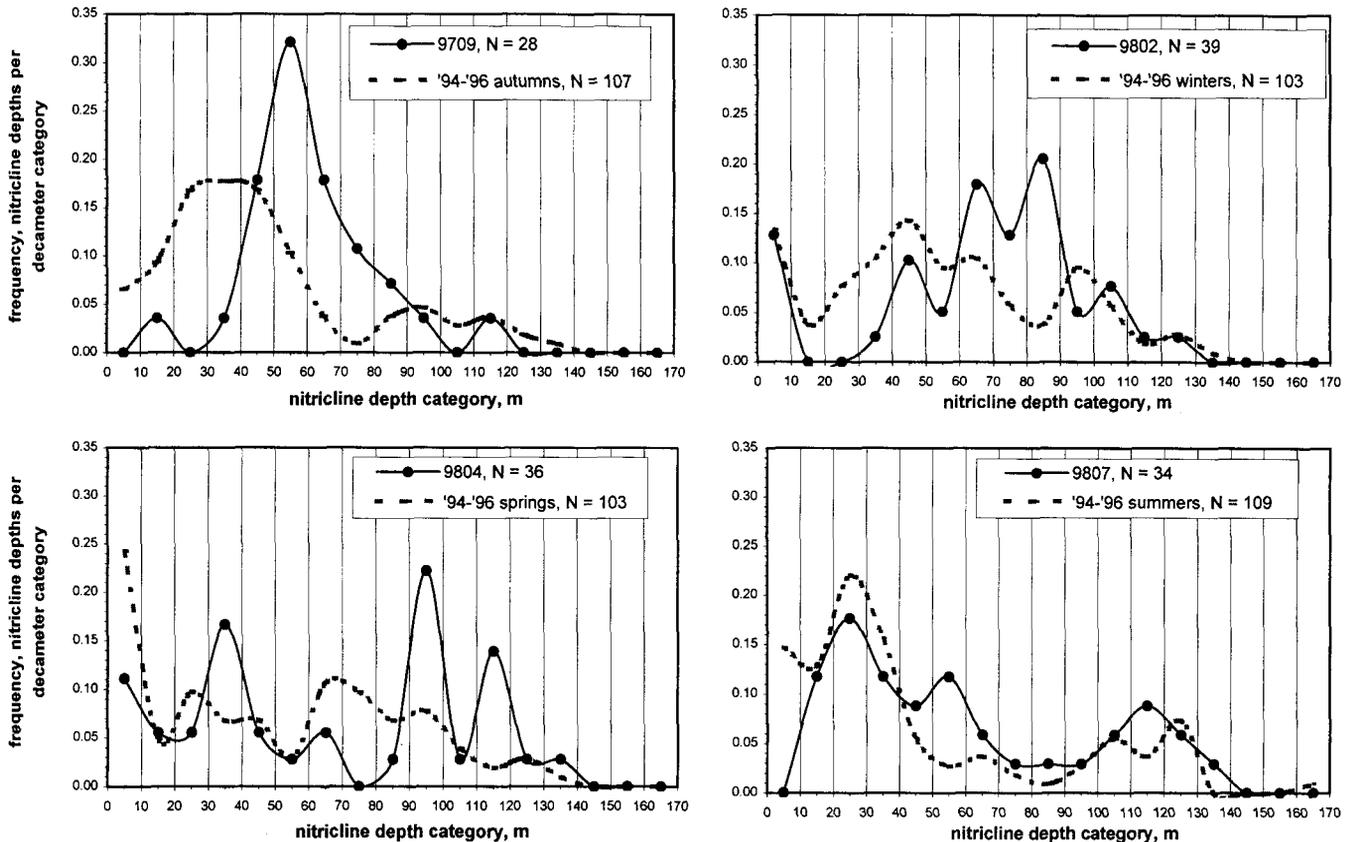
Figure 2. Frequency distributions of nitricline depths in September 1997 (cruise 9709) and February, April, and July 1998 (9802, 9804, and 9807), relative to the comparable seasons in 1994–96. Depths are categorized by decameter intervals.

illustrates this, and the normalcy of summer, by comparing the solutions for cruises 9709, 9804, and 9807 best-fit negative exponentials at three standard nitricline depths with the 1994–96 best fits for autumn, spring, and summer, respectively.

Winter 1998 (9802; fig. 3, upper right) was unusual in that there was little ≥8 µm chlorophyll at all five stations where the nitricline was at the surface, and a negative exponential fit is not reasonable. The five stations with unexpectedly sparse ≥8 µm biomass were contiguous at Point Conception and the Santa Barbara Channel. During summer (9807; fig. 3, lower right), the relations were similar to those of the previous years (see also table 1).

In 1994–96, some of the variation around the trend relating biomass of ≥8 µm cells to the depth of the nitricline was related to the biomass-specific grazing pressure by macrozooplankton on these large cells (Mullin 1998, fig. 6). It is thus reasonable to ask three questions about figure 3: (1) Is the variability around the negative exponential relation to nitricline depth related to grazing pressure within each cruise (9709, 9804, and 9807)? (2) Is the greater-than-expected ≥8 µm biomass in 9709 (relative to 1994–96 autumns) and in 9804 (relative to 1994–96 springs; table 1) related to low grazing pres-

sure? (3) Is the unexpectedly sparse ≥8 µm biomass where the nitricline was at the surface in February 1998 (fig. 3, upper right) due to unusually heavy grazing pressure?

An answer to question 1 is given in figure 4 (upper). The large positive residuals or anomalies (i.e., more ≥8 µm chlorophyll at a station than predicted from the overall relation to nitricline depth for that cruise) were dominantly at stations where the proxy for biomass-specific grazing pressure was relatively low. This is particularly evident for cruise 9804 (which also had one station with a large negative anomaly), but also true for the other two cruises. This result is similar to that for 1994–96 (Mullin 1998, fig. 6, where anomalies in both space and time were considered).

Question 2 is similarly answered in figure 4 (lower), which shows that during September 1997 (9709) and particularly April 1998 (9804), the largest excesses of observed biomasses of ≥8 µm cells from the biomasses expected from the biomass–nitricline-depth relations for autumns and springs of 1994–96 (fig. 3, table 1) were found where the biomass-specific grazing pressure was small. By this standard, question 2 is answered affirmatively.

While changes in the biomasses of macrozooplankton could plausibly be expected to signal a change in grazing pressure on all phytoplankton, it is less obvious
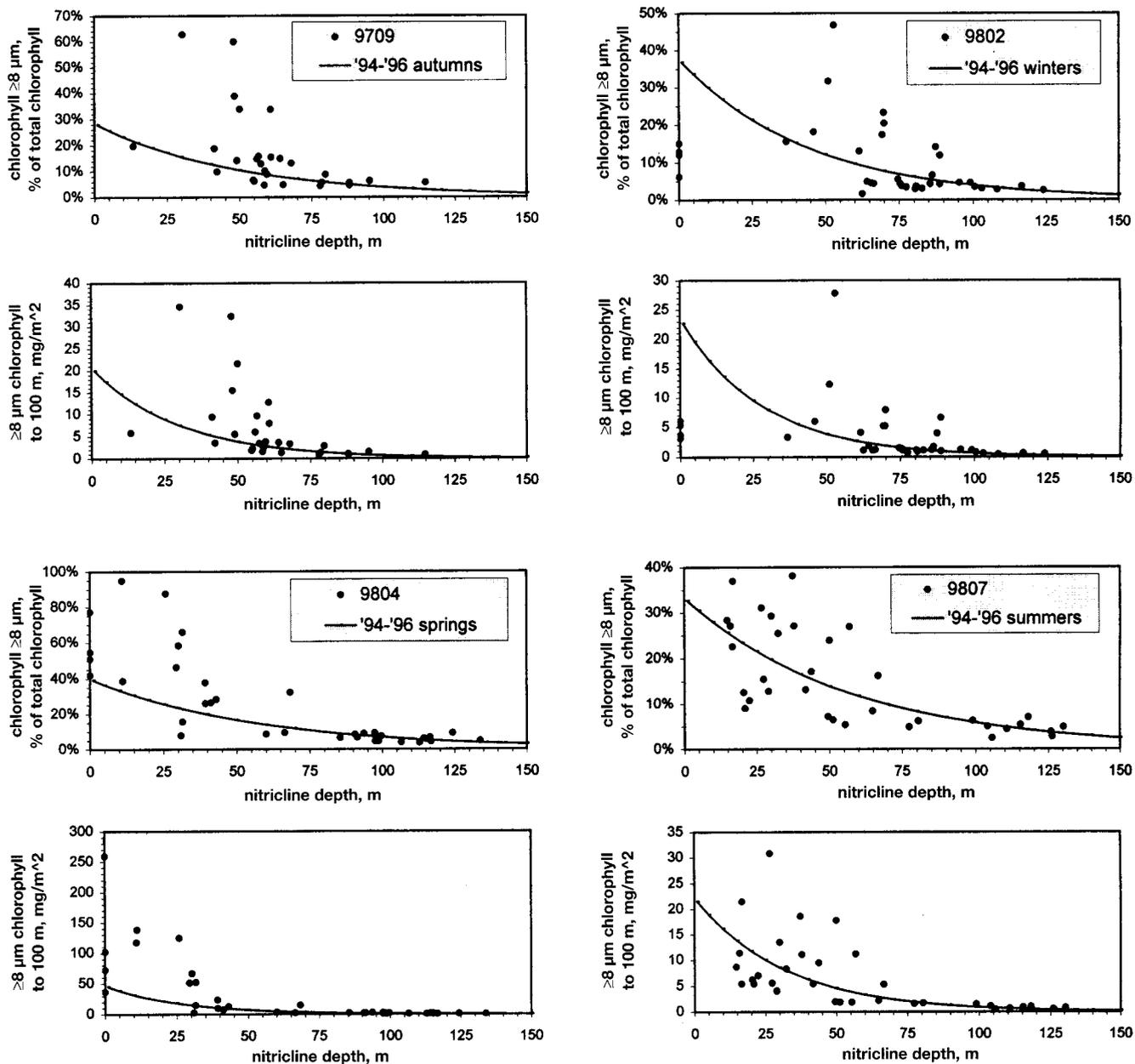
Figure 3.   Chlorophyll ≥8 μm, as a fraction of total chlorophyll (upper of each pair) or biomass per m² (lower of each pair), vs. depth of nitricline for September 1997 (cruise 9709), and February, April, and July 1998 (9802, 9804, and 9807). Also shown on each plot are the best-fit negative exponential relations for data from the appropriate season from 1994–96 (see Mullin 1998).

(though still plausible) that such changes would alter the size composition of the phytoplankton. If changes in grazing pressure were equally distributed over all size categories of phytoplankton, the fraction of total phytoplankton contributed by large cells should be predictable solely from depth of the nitricline, and not related to grazing. However, the anomalies in the fraction of total chlorophyll which was ≥8 μm, relative to the seasonal mean relations to nitricline depth for the 1994–96 period, were also related to the surrogate for biomass-specific grazing pressure by macrozooplankton

(fig. 5). This finding, in turn, supports the use of the ratio macrozooplankton biomass · (biomass of ≥8 μm chlorophyll)$^{-1}$ as a surrogate for biomass-specific grazing on the larger cells.

Finally, there is the issue of the unexpectedly small biomasses of ≥8 μm cells at all five stations in February 1998, where the nitricline was at the surface (fig. 3, upper right). At one of these stations, data for macrozooplanktonic biomass were not taken, but at the other four stations, the biomass-specific grazing pressures (as in the abscissae in fig. 4) were not particularly great.

TABLE 1
Comparisons of Best-Fit Negative Exponential Relations, as Functions of Nitricline Depth, of the Relative
and Absolute Biomasses of Chlorophyll ≥8 μm Three Standard Depths, in 1997–98 and in the Reference Years, 1994–96

Nitricline depth (m)	% ≥8 μm		mg/m² ≥8 μm	
	Cruise 9709	94–96 aut.	Cruise 9709	94–96 aut.
10	41%	23%	25	15
25	28%	17%	14	9
50	16%	10%	6	4
	Cruise 9804	94–96 spr.	Cruise 9804	94–96 spr.
10	50%	33%	66	32
25	36%	26%	34	18
50	21%	17%	12	7
	Cruise 9807	94–96 sum.	Cruise 9807	94–96 sum.
10	25%	28%	14	16
25	20%	22%	9	10
50	13%	14%	5	5

Note: The negative-exponential fit should not imply a causal mechanism, and in any case was not appropriate for February 1998 (9802).
aut. = autumns; spr. = springs; sum. = summers.
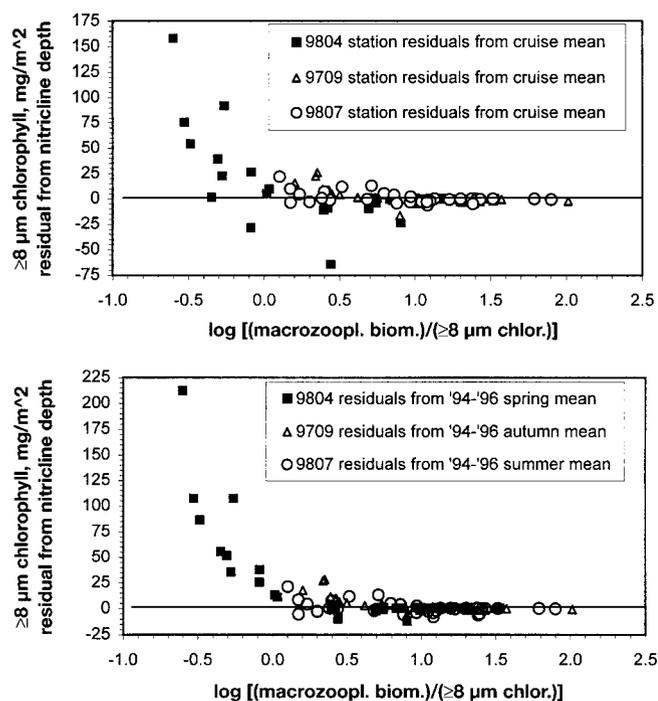
Figure 4. Anomalies in biomass of ≥8 μm cells, relative to a proxy for grazing pressure per unit ≥8 μm biomass. The horizontal line at 0 represents the ≥8 μm biomass predicted from an overall relation between biomass and nitricline depth; positive values indicate "excess" biomass. *Upper panel* shows anomalies for stations within each cruise relative to the overall relation for that same cruise. *Lower panel* shows anomalies for each station relative to the appropriate seasonal mean from 1994 to 1996 (cf. fig. 3, solid lines in lower panel of each pair).

Therefore, some other factor must account for the paucity of large cells, and the proximity of the stations to Point Conception–Santa Barbara suggests a topographically related cause. Very recent upwelling of subnitricline water, causing the nitricline to shoal, to which biomass of large cells had not yet responded, is plausible. This should be indicated by a pronounced negative anomaly in temperature and positive anomaly in salinity at these particular stations, relative to other locations, but the 10 m temperature and salinity maps given in Lynn et al. 1998 provide little support for this explanation. However, the concentration of dissolved oxygen in the upper 10 m at these five stations (and at only one other on the entire cruise) was <99% of saturation, which is consistent with recent upwelling to which the phytoplankton have yet to respond with increased productivity.

DISCUSSION

The results of this study confirm the general relations between biomass of large phytoplankton, both in absolute and relative terms, and the depth of the nitricline (an indicator of supply of new NO^3 to the euphotic zone) during the 1997–98 California El Niño, except for a small cluster of nearshore stations in winter. In this sense, the basic relations between the size composition of phytoplankton and the nutritional environment are the same during El Niño years as during other years, even though that nutritional environment changed. The implication is that the regional-scale change in the nutrient(s) or physical process(es) affecting the distribution of sizes of phytoplanktonic cells, if not NO^3 itself, closely paralleled the change in depth of the nitricline.

Indeed, the biomass of large cells was greater than expected where the nitricline was shallow in autumn and spring of the El Niño year (cruises 9709 and 9804 in table 1). This was related to (and possibly caused by) unusually slight grazing pressure from macrozooplankton, relative to 1994–96, especially in spring (fig. 4, lower). Slight grazing pressure also meant that large cells contributed more to the total biomass of phytoplankton than would have been predicted from the relation to depths of the nitricline in 1994–96 (fig. 5). Slight grazing pres-
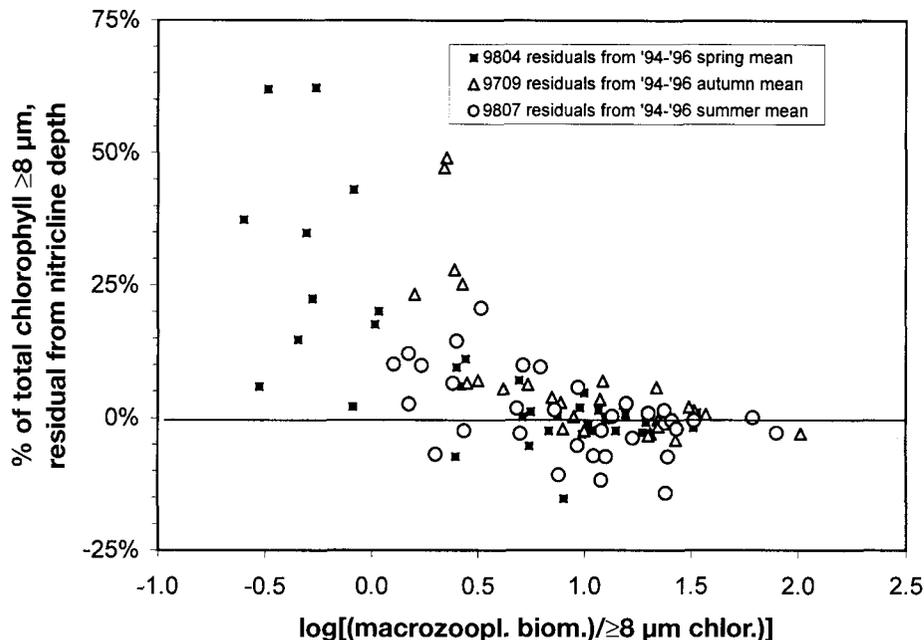
Figure 5.   Anomalies in contribution of ≥8 μm cells to total chlorophyll, relative to a proxy for grazing pressure per unit ≥8 μm biomass. The horizontal line at 0 represents the percentage of total chlorophyll which is ≥8 μm, predicted from an overall relation between this contribution and nitricline depth for springs, autumns, and summers of 1994–96 (cf. fig. 3, solid lines in upper panel of each pair); positive values indicate "excess" contribution to the total.

sure, relative to other locations on the same cruise, was also related to unusually large biomasses of large cells, compared to the overall relation to nitricline depth for that cruise (fig. 4, upper).

There remain circumstances, such as the anomalously low biomass of large cells at stations in February (fig. 3, 9802), which are not explained by the proxy variables available. In this example, spatial proximity of the anomalous stations suggests a common cause for the paucity of large cells, and some (but not all) of the evidence suggests the cause is upwelling to which the phytoplankton have not had time to respond with increased productivity and biomass.

The size distribution of phytoplankton can potentially influence sedimentation of organic matter and the structure of pelagic food webs. The results of the present study indicate that empirical relations or models developed for non–El Niño conditions in the California Current system will be useful, at least on a regional scale, during a California El Niño.

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EFFECTS OF EL NIÑO AND LA NIÑA ON LOCAL INVERTEBRATE SETTLEMENT IN NORTHERN CALIFORNIA

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ABSTRACT

During the spring and summer upwelling season (April–August) of the years 1997–99, we monitored settlement of juvenile crabs and sea urchins in northern California. Oceanographic conditions during these three years included El Niño in 1997–98, and La Niña in 1999. Prior data had shown strong annual settlement in years during which an intra-annual upwelling/relaxation mechanism was dominant. During active upwelling, invertebrate and fish larvae were retained south of Point Reyes. When winds relaxed, larvae could be transported northward and onshore in warm, less saline water, and settle on our collectors at the Bodega Marine Laboratory. During years in which this upwelling/relaxation mechanism dominated and salinity was inversely correlated with temperature, higher temperatures, which represented relaxation flow, were associated with cancrid crab settlement. The settlement response in 1997 and 1998 was similar to that of earlier years, but 1999 was quite different. In 1997, the lack of an inverse correlation between temperature and salinity indicated that wind-driven upwelling/relaxation was not dominant, and cancrid crab settlement was not correlated with temperature. In 1998, temperature and salinity were inversely correlated, but wind and temperature were not as highly correlated as in years prior to 1997. Settlement appeared to be driven by relaxation, but the relationship was not as strong as in previous years. Although they appeared to settle during relaxation events, neither sea urchins nor non-cancrid crabs settled in relation to temperature in 1997–99, nor in most earlier years. In 1999, strong, constant upwelling winds resulted in no relaxation events, and settlement was an order of magnitude lower than in any previous year. On interannual scales, data from 1997–99 were consistent with previous data for cancrid crabs, showing a negative correlation with wind stress,
but 1999 was not consistent with previous findings of a negative correlation between temperature and settlement of non-cancrid crabs.

INTRODUCTION

The dramatic changes in physical oceanographic conditions and biological productivity in the California Current system (CCS) during El Niño events are well documented (Chelton et al. 1982; Tegner and Dayton 1987; Glynn 1988). The general biological effect of El Niño–Southern Oscillation (ENSO) events on marine animals in the CCS is reduced productivity at all trophic levels. Reduced chlorophyll levels indicate lower primary productivity (Lenarz et al. 1995). A negative correlation between zooplankton biomass in California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys (Chelton et al. 1982) and lower abundance in more northern waters (Brodeur et al. 1992) indicate lower secondary productivity. Effects at higher trophic levels include smaller size and lower catches of salmon (Johnson 1988; Kope and Botsford 1992; Pearcy 1992), reduced survival of Pacific mackerel (Sinclair et al. 1985), reduced recruitment in rockfish species (Ralston and Howard 1995; Yoklavich 1996), and decreased reproductive success of seabird colonies (Ainley et al. 1995).

While ENSO-related effects on productivity have received much attention, the effect of ENSO events (both anomalously warm El Niño and cold La Niña events) on settlement of planktonic larvae has rarely been documented. A few relatively short time series for settlement of benthic invertebrates in the CCS provide some insight into how individual species respond to oceanographic conditions, including ENSO events. Sea urchins exhibit patchy and episodic settlement (Ebert et al. 1994) and recruitment (Pearse and Hines 1987; Sloan et al. 1987). During El Niño years, sea urchins have recruited or settled at lower levels in southern California (Tegner and Dayton 1987; Ebert et al. 1994), but at higher levels

in northern California compared to prior, non-ENSO years (Ebert et al. 1994). Larval rockfish have shown low abundances during both strong El Niño and La Niña events, and appear to have highest survival in years of intermediate temperature (Ralston and Howard 1995; Yoklavich 1996).

Upwelling winds in the CCS are generally higher during non-ENSO years. Moreover, the time series of upwelling index, ocean temperature, and sea level in central California can be represented by a single time series of its first principal component (empirical orthogonal function), which represents ENSO/non-ENSO conditions (approximately equal loading of positive temperature, negative upwelling, and positive sea level; Kope and Botsford 1992). However, a relation between the intra-annual, weekly time-scale wind patterns of interest here, and ENSO conditions has not been identified. On annual time scales, successful nearshore settlement of larvae of benthic and intertidal invertebrates is generally greater during periods of lower upwelling winds (Roughgarden et al. 1988; Ebert et al. 1994; Connolly and Roughgarden 1999). However, the sampling in these studies covers short time periods, although one study did encompass both ENSO and non-ENSO conditions over 3.5 years (Ebert et al. 1994).

Here we compare settlement of marine invertebrates at Bodega Marine Laboratory (BML) during the 1997–99 period with results from sampling in 1992–96, described in Wing et al. 2000.[1] This comparison can be naturally phrased in terms of ENSO effects on settlement at this location because a strong El Niño occurred during 1997 and 1998, and there was a strong La Niña in 1999. In the earlier sampling of invertebrate settlement, we identified a mechanism by which larvae were retained in the lee (south) of Point Reyes (fig. 1) during active upwelling (Wing et al. 1998) and were transported poleward and settled onshore during occasional relaxations or reversals of upwelling winds (Send et al. 1987; Wing, Botsford et al. 1995; Wing, Largier et al. 1995). Examination of interannual variability in this mechanism during the years 1992–96 revealed that this mechanism did not operate consistently each year (see footnote 1).

Although intra-annual patterns in upwelling winds were not the same each year, daily temperature at BML covaried significantly with daily wind stress in each year. However, covariability between local temperature and salinity did not always indicate an upwelling/relaxation pattern; correlations were significantly negative only in 1992, 1993, 1995, and 1996. During these years, settlement of cancrid crabs was higher during periods of
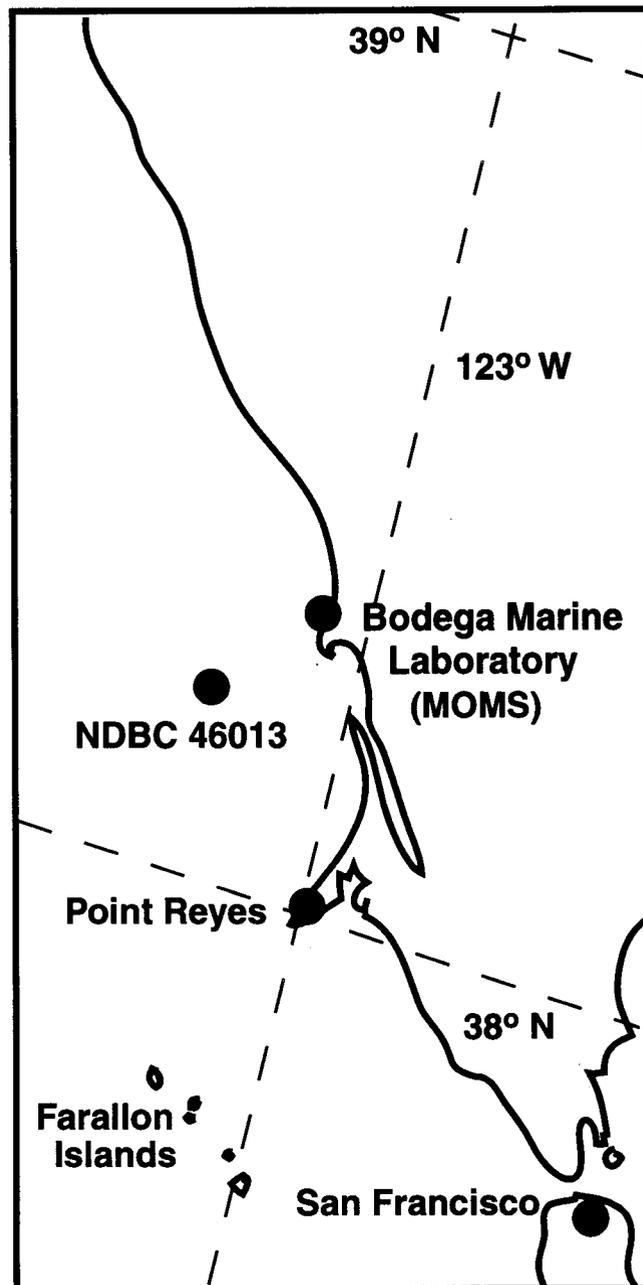
Figure 1. Map detailing location of study site at Bodega Bay, California. Meteorological observations were taken from the Bodega Marine Laboratory's Meteorological and Oceanographic Monitoring Station (MOMS) and NOAA/National Data Buoy Center (NDBC) buoy 46013.

higher BML temperature, reflecting relaxation flow, than during periods of strong upwelling winds. There was a significant correlation between weekly cancrid crab settlement and temperature, except in 1995, when samples may not have been frequent enough to identify this relation. Interannual variability in total annual settlement of cancrid crabs was negatively correlated with upwelling and alongshore wind stress. Weekly settlement of noncancrid crabs and sea urchins was not correlated with

fluctuations in local temperature, in part because their
settlement seasons are much shorter, and there were fewer
opportunities to observe settlement. Interannual vari-
ability in total annual settlement of non-cancrid crabs
was positively correlated with La Niña conditions; 1992
through 1994 were moderate ENSO years, and 1995
through early 1997 were moderate La Niña years.

Here we present observations of crab and sea urchin
species during the anomalous 1997–99 period and ex-
amine (1) intra-annual variability in settlement due to
local wind forcing and the wind relaxation mechanism
as proposed by Wing, Botsford et al. (1995), Wing, Largier
et al. (1995), and Wing et al. (1998); and (2) interannual
variability and the effect of anomalous oceanic condi-
tions on invertebrate settlement.

MATERIALS AND METHODS

Oceanographic Data

Oceanographic data used in this study were collected
from multiple sources. Time series of wind velocities,
temperature, and salinity were obtained from Bodega
Marine Laboratory's Meteorological and Oceanographic
Monitoring Station (MOMS), located offshore of BML
(38°19'N, 123°04'W; fig. 1). Data from MOMS are col-
lected as 20-minute averages for sea-surface temperature
and conductivity sensors, and as 10-minute averages for
wind-velocity data. Temperature time series for 1999
were obtained from NOAA buoy NDBC 46013
(38°14'N, 123°18'W), because temperature data were
not continuously available from MOMS over the 1999
sampling period.

MOMS temperatures and buoy temperatures were
highly correlated over periods when both data sources
were available ($r = 0.899$). No salinity data were avail-
able near Bodega Bay in 1999. For each settlement sea-
son (April 30–August 13, day 120–day 225) we calculated
daily averages of wind velocities, temperature, and salin-
ity. Alongshore wind stress (317°) was calculated from
wind velocities (Pond and Pickard 1983), according to

$$\tau = \rho_a C_N V^2$$

where τ = magnitude of wind stress at 317°
ρ_a = density of air = 1.3 kg/m^3
C_N = drag coefficient
V = magnitude of wind velocity at 317° (m/s).

C_N was calculated per Trenberth et al. (1990) as a step
function where

$$
\begin{aligned}
10^3 C_N &= 0.49 + 0.065V & &\text{for } V > 10 \text{ m/s} \\
&= 1.14 & &\text{for } 3 \le V \le 10 \text{ m/s} \\
&= 0.62 + 1.56/V & &\text{for } V \le 3 \text{ m/s}
\end{aligned}
$$

To reflect the variability in wind that is associated
with relaxation events, we also present an index of re-

laxation strength that uses a nonlinear transformation of
the alongshore wind stress values. Relaxations occur
when winds cease or reverse direction from the typical
alongshore (317°) direction during upwelling periods,
and these events are recognizable in the wind stress time
series as periods of low or negative values. Researchers
have postulated that several days of wind relaxation are
necessary for larvae to be transported from upwelling
retention zones south of Point Reyes to the sampling
location at Bodega Head (fig. 1; Send et al. 1987; Wing,
Botsford et al. 1995; Wing, Largier et al. 1995). To re-
flect this multiday relaxation period, we calculated a 4-
day running average of $\log_{10}$ (wind stress+1) as an
indicator of relaxation flow reaching the BML site as in
Wing et al. 2000 (see footnote 1). We calculated corre-
lations among all oceanographic variables by using a stan-
dardized linear correlation statistic (Zar 1984). We
calculated 95% confidence limits based on sample size
during the primary settlement period (30 April–13
August, day 120–225; $n = 106$).

To put the influence of local oceanographic condi-
tions on settlement in the context of anomalous ENSO
events, we compared annual settlement to ocean basin-
scale and other large-scale indices of ENSO and up-
welling. Daily Bakun upwelling indices were obtained
from the National Oceanic and Atmospheric Adminis-
tration (NOAA) for latitude 36°N. Monthly standard-
ized Southern Oscillation Indices (SOI) were obtained
from the NOAA Climate Prediction Center. The SOI
is the standardized monthly mean pressure difference be-
tween Darwin, Australia, and Tahiti, French Polynesia.
Negative values correspond to warm, El Niño events;
positive values correspond to cold, La Niña events. An
extratropical analog to the SOI has recently been cre-
ated to more accurately describe the strength of ENSO
events in midlatitude Northern Hemisphere regions.[2]
Data for this alternative index, the Northern Oscillation
Index (NOIx), were obtained from the NOAA Pacific
Fisheries Environmental Laboratory. The NOIx is the
standardized monthly mean pressure difference between
the North Pacific High (35°N, 135°W) and Darwin,
Australia.

Invertebrate Settlement Data

In spring and summer of 1997–99 at the Bodega
Marine Laboratory (38.19°N, 123.04°W; fig. 1) we sam-
pled settlement of crabs and sea urchins approximately
weekly. The general characteristics of our collection site
include an exposed coastline and a rocky substrate. Each
year we placed an array of three collector moorings at
10–12 m depth separated by approximately 100 m.

[2]Schwing, F. B., T. Murphree, and P. M. Green. 2000. A climate index for the
northeast Pacific. (manuscript)
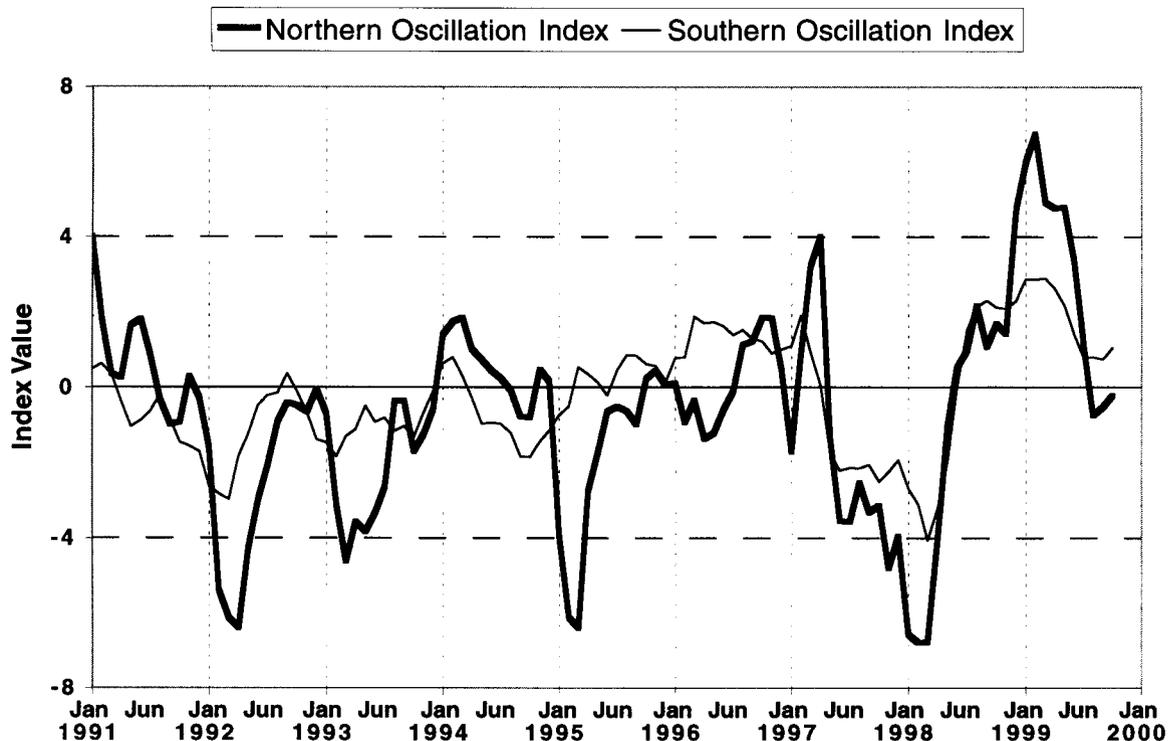
Figure 2. Time series of monthly extratropical Northern Oscillation Index (NOIx) and Southern Oscillation Index (SOI). Positive values indicate La Niña conditions; negative values indicate El Niño conditions. Time series are presented as 3-month running averages.

Collections generally were made weekly, but several were delayed because of inclement weather, and periods between samples were sometimes two weeks; one period in 1999 was one month. Because of this, some important variability on weekly (or shorter) time scales may have been unresolved for some time periods.

We sampled juvenile invertebrates with two types of settlement collectors. "Brush" collectors consisted of four, 7-inch-long, wood-backed scrub brushes with polypropylene bristles, based on methods of Ebert and colleagues (Ebert and Russell 1988; Ebert et al. 1994). "Bag" collectors were constructed from half-inch Nytex plastic mesh, forming a 75 cm-long bag with a 30 cm-wide opening that contained a 1 m by 5 m section of #30 3/4 inch nylon mesh trawl netting, based on methods of Wing et al. 2000 (see footnote 1). Each collector was moored by a polypropylene line with net floats for buoyancy, anchored to the bottom with a 25 kg cement anchor. One brush and one bag collector were attached to each mooring line so that the collectors floated approximately 0.5 to 1 m above the bottom. After weekly exchange, we rinsed the collectors in fresh water, and fixed the resulting material in ethanol for later enumeration and identification of newly settled crabs and sea urchins.

We used a dissecting microscope to identify crab and sea urchin species to the lowest taxon possible. Sea urchin

species included the red sea urchin (*Strongylocentrotus franciscanus*) and the purple sea urchin (*S. purpuratus*). Cancrid crab species included larval and juvenile crabs of primarily *Cancer antennarius* and *C. productus*, but also some individuals of *C. magister* and *C. gracilis*. Other crab species included primarily porcellanid crab megalopae and juveniles (*Petrolisthes* spp.) and also various majid (*Pugettia producta*, *Loxorhynchus crispatus*), pagurid (*Pagurus* spp.), and grapsid (*Hemigrapsus nudus*) species.

To analyze patterns, we considered settlement of all sea urchin species combined, and settlement of cancrid crabs and settlement of non-cancrid crabs separately. We reported cancrid and non-cancrid (primarily porcellanid) crab species separately because of their different larval periods (cancrid crabs: 3–6 months, porcellanid species: 4–6 weeks) and different times of larval release (cancrid crabs: winter, before spring transition; porcellanid crabs: near the spring transition; Strathmann 1987), which may cause these different larvae to be transported in different water masses and subject to different local conditions for transport and settlement.

Settlement rates were calculated as the average number of settlers per brush collector per day of the collection period for each taxon. Bag collector data were not used in the average calculation so that we could make comparisons to prior years of settlement data at BML (Wing, Botsford et al. 1995; Wing, Largier et al. 1995;

Wing et al. 2000[3]). Average daily settlement rates were calculated for each collection period from 30 April to 13 August (day 120–225) each year.

Intra-annual Correlations of Settlement with Physical Variables

To determine correlations between oceanographic variables and invertebrate settlement, we calculated average values of temperature, salinity, alongshore wind stress, $\log_{10}$ (wind stress+1), and upwelling over each sampling period. We calculated correlations between these oceanographic values and average settlement on brush collectors of sea urchins, cancrid crabs, and non-cancrid crabs during each sampling period at Bodega Head by using a standard linear correlation statistic (Zar 1984). We calculated 95% confidence intervals based on sample size (number of sampling periods) for each year.

Interannual Correlations of Settlement with Physical Variables

Annual settlement rates for cancrid crabs, non-cancrid crabs, and sea urchins were calculated for each year (1997–99) of settlement collection. We calculated these as the average settlement rate over the period 30 April–13 August (days 120–225) of each year. Annual values of oceanographic variables—temperature, salinity, wind stress, $\log_{10}$(wind stress+1), and upwelling index—were calculated as the mean value of daily time series over the period from day 120 to day 225. We calculated annual values of the NOIx and SOI as the mean value of the monthly time series from April to August.

RESULTS

Intra-annual Variability in Settlement and Oceanographic Conditions

The years 1997–99 included more extreme values of basin-scale indicators of ENSO conditions than the 1991–96 time series. Time series of NOIx and SOI indicate that 1997–99 were anomalous years with extremely low values in late 1997 and early 1998, representing strong El Niño conditions of much longer duration than El Niño events in 1992 and 1995, and extremely high values in 1999, representing strong La Niña conditions (fig. 2). During previous settlement monitoring at BML, 1992 and 1993 appear as mild El Niño years in both indices, whereas 1994 represents a transitional year of moderate conditions for both indices. The NOIx shows early 1995 to be an El Niño event of similar magnitude to that of 1992–93, but the SOI gives no implication of anomalous conditions. A mild La Niña event is apparent in both indices from 1996 through early 1997.
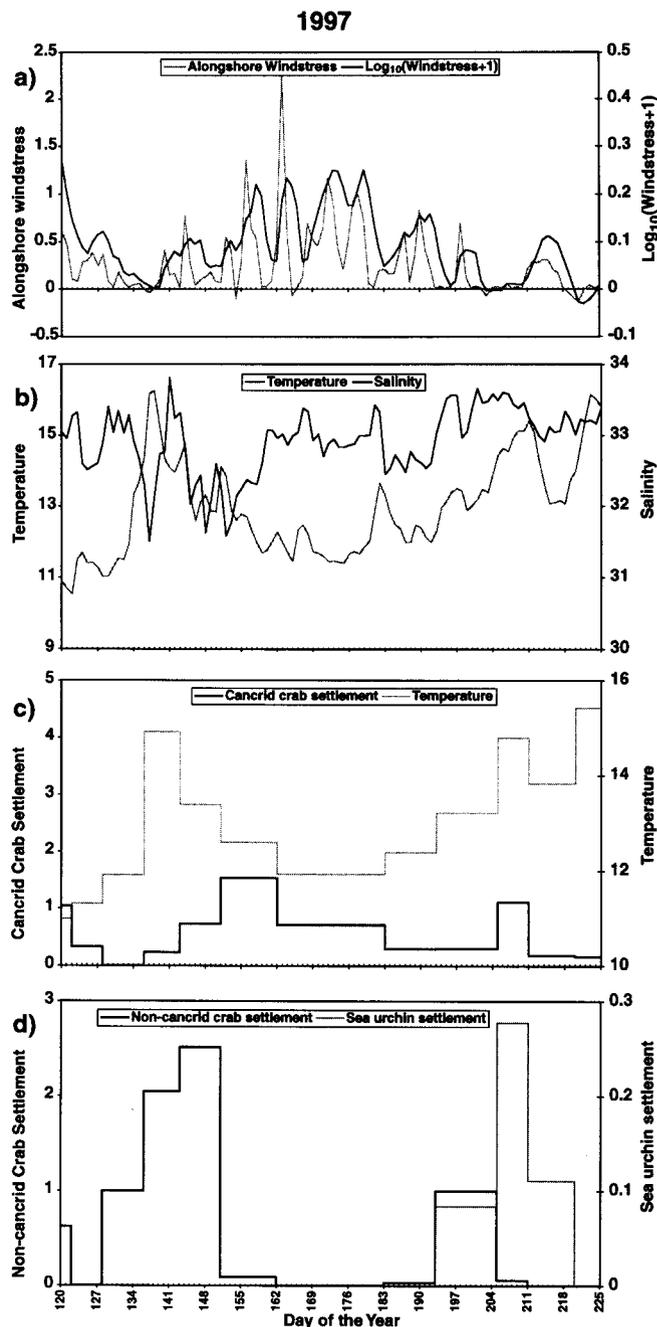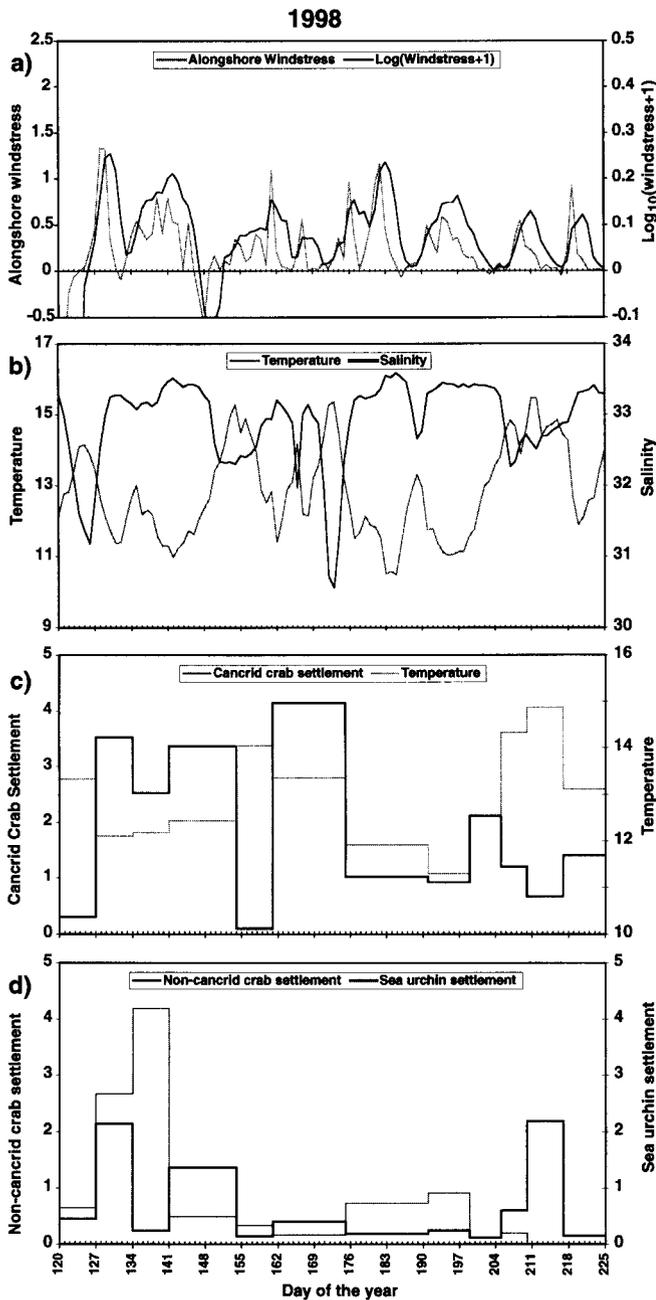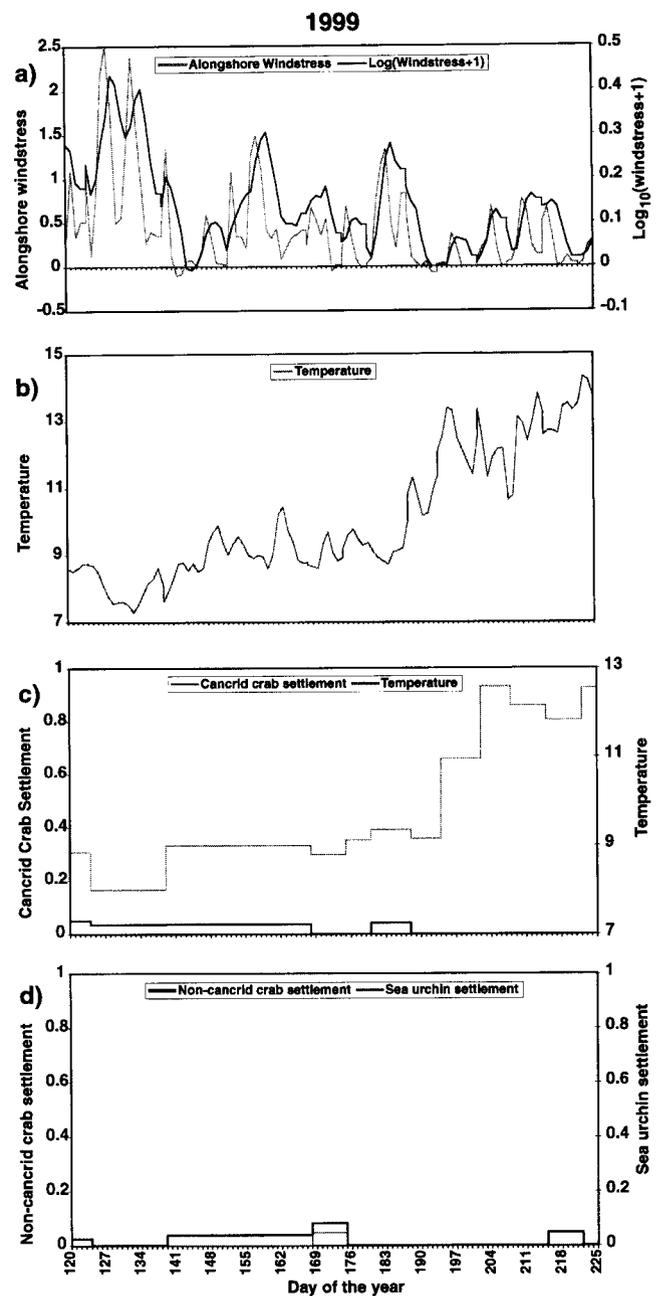
Figure 3. 1997 time series at Bodega Head of a, alongshore wind stress (dynes/cm², pale line) and $\log_{10}$(wind stress+1; bold line); b, temperature (°C, pale line) and salinity (ppt, bold line); c, settlement per brush-collector-day of cancrid crabs (bold line) and average temperature per sampling period (pale line); d, settlement per brush-collector-day of non-cancrid crabs (bold line) and sea urchins (pale line). In c and d, lines extend over the entire settlement period, but this does not imply constant settlement.

1997. During the early settlement period of 1997 (day 120 to approximately day 150), covariability among oceanographic variables—temperature, salinity, alongshore wind stress, and $\log_{10}$(wind stress+1)—showed conditions typical of the upwelling/relaxation season at this location (fig. 3a, b). High wind stress values were

TABLE 1
**Intra-annual Correlations between Daily Values for
Oceanographic Variables (30 April to 13 August)**

Year	Wind stress vs. temperature	Log_{10}(wind stress+1) vs. temperature	Temperature vs. salinity
1997	−0.354	−0.733	0.087
1998	−0.217	−0.334	−0.737
1999	−0.377	−0.584	NA

Significant correlations ($p < 0.05$) are in bold.

TABLE 2
**Intra-annual Correlations between Invertebrate
Settlement Rates and Temperature Averaged over
Each Settlement Collection Period, 1997–99**

Year[a]	Taxon	Temperature
1997	Cancrid crab	−0.178
($n = 12$)	Non-cancrid crab	0.151
	Sea urchin	0.431
1998	Cancrid crab	−0.302
($n = 12$)	Non-cancrid crab	−0.084
	Sea urchin	−0.298
1999	Cancrid crab	**−0.586**
($n = 12$)	Non-cancrid crab	−0.229
	Sea urchin	−0.261

Significant correlations ($p < 0.05$) are in bold.
[a]n refers to the total number of collection periods.

associated with low temperatures and high salinities, due to Ekman transport of warm surface water layers offshore, and replacement by cold, upwelled water. When the winds relaxed, however, as on days 135–140, oceanographic conditions reversed, resulting in a rapid rise in temperature and a decrease in salinity that has been associated with alongshore transport during wind relaxation periods (Send et al. 1987; Wing, Botsford et al. 1995; Wing, Largier et al. 1995). Water transported from south of Point Reyes is fresher and warmer than upwelled water (Schwing et al. 1991; Wing et al. 1998).

High winds from day 150 to day 180 led to constant low temperature and high salinity. After day 180, there appeared to be a shift from a system dominated by upwelling and relaxation to one in which wind relaxation events raised temperature, but temperature appeared to be positively correlated with salinity on a daily scale (days 180, 195, 200). The remainder of the settlement period of 1997 was marked by increasing temperature and salinity, and decreasing alongshore wind stress, atypical of conditions in the upwelling season in northern California, but more common of late summer and early fall in this region—the relaxation season described by Largier et al. (1993).

Wind stress was negatively correlated with temperature, as expected in this system, where upwelling conditions are generated by strong wind forcing (table 1). A stronger correlation was seen between temperature and the smoothed log of wind stress, which is also expected, because this index reflects the degree of relaxation. Salinity, however, was not correlated with temperature, indicating that there was no wind-forced upwelling/relaxation variability in 1997, particularly later in the season (table 1).

In 1997, there were no significant correlations between any of the three taxa (cancrid crabs, non-cancrid crabs, and sea urchins) and temperature during the settlement period (table 2). This was consistent with earlier years (e.g., 1994) in which the upwelling/relaxation mechanism was not dominant.[4] Cancrid crabs settled after a prolonged relaxation event early in the season (approximately day 140) and once during a wind relax-

ation late in the season (day 205; fig. 3c). Non-cancrid crabs settled during the early, prolonged relaxation event and once later in the season (fig. 3d). Sea urchins showed a small settlement pulse during the relaxation event at day 195 (fig. 3d).

1998. Although 1998 began under strong El Niño conditions, basin-scale indicators (NOIx, SOI) show a return to non–El Niño conditions in May–June, shortly after our sampling period began (fig. 2). Although temperatures were 2°–3°C above normal, the typical pattern of upwelling periods punctuated by wind relaxation events occurred in 1998 (fig. 4a). All events in 1998 were associated with temperature increase and salinity decrease, although the magnitude of the change in temperature and salinity was usually related to the length of the wind relaxation period (fig. 4b). Temperature was significantly negatively correlated with both wind stress and log_{10}(wind stress+1) in 1998 (table 1), although the low correlations (lowest of the 1992–99 time series) indicated that local wind forcing was not a strong driver of local relaxation. Temperature and salinity were significantly inversely correlated (table 1).

Cancrid crabs appeared to settle during relaxations (fig. 4c), but this response was not reliable enough to produce a significant negative correlation between temperature and settlement (table 2). Three periods of low settlement at high temperature (days 120–127, 155–161, and 210–217) appear to make the correlation between settlement and temperature negative. Although it could be argued that in each of these periods temperature is high while settlement is low because the sampling period includes the end of a relaxation event, the temperature/settlement relation is not as strong as in previous years (1992–96). The deviation from the upwelling/relaxation mechanism during 1998 is in part due to the lack of sampling resolution.

Non-cancrid crabs showed highest settlement during wind relaxation periods, at approximately day 132 and day 150 early in the season, and during a later

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[4]See footnote 1 on p. 168.

1998

Figure 4.   1998 time series at Bodega Head of *a*, alongshore wind stress (dynes/cm², pale line) and log₁₀(wind stress+1; bold line); *b*, temperature (°C, pale line) and salinity (ppt, bold line); *c*, settlement per brush-collector-day of cancrid crabs (bold line) and average temperature per sampling period (pale line); *d*, settlement per brush-collector-day of non-cancrid crabs (bold line) and sea urchins (pale line). In *c* and *d*, lines extend over the entire settlement period, but this does not imply constant settlement.

1999

Figure 5.   1999 time series at Bodega Head of *a*, alongshore wind stress (dynes/cm², pale line) and log₁₀(wind stress+1; bold line); *b*, temperature (°C, pale line) and salinity (ppt, bold line); *c*, settlement per brush-collector-day of cancrid crabs (bold line) and average temperature per sampling period (pale line); *d*, settlement per brush-collector-day of non-cancrid crabs (bold line) and sea urchins (pale line). In *c* and *d*, lines extend over the entire settlement period, but this does not imply constant settlement.

relaxation at about day 215 (fig. 4d). Sea urchins settled unusually early in the season at high levels, overlapping a wind relaxation event at day 135, and continuing to settle the following week (fig. 4d). A smaller settlement pulse of sea urchins later in the season followed the day 175 and day 195 relaxation events. Sea urchin settlement

rates were an order of magnitude higher in 1998 than in 1997.

1999.   Basin-scale indicators (NOIx, SOI) indicate strong La Niña conditions at the beginning of our sampling period, but these conditions had declined to moderate levels by the end of the period (fig. 2). The early
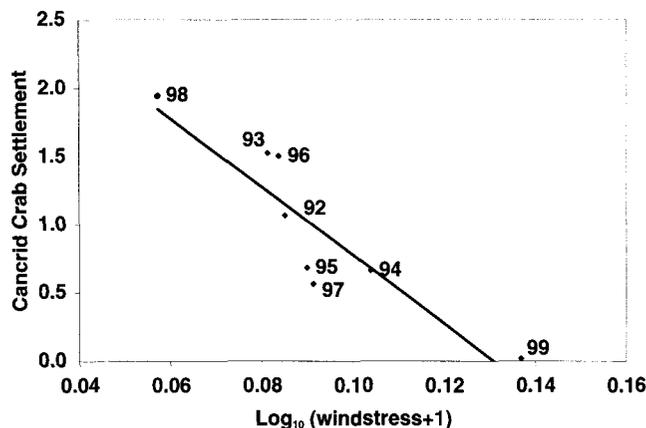
Figure 6.   Linear regression of seasonal (30 April–13 August) cancrid crab settlement on brush collectors during 1992–99 at Bodega Head with seasonal average of $\log_{10}$(wind stress+1) ($y = -24.37x + 3.18$, $R^2 = 0.8376$) collected at BML MOMS.

Figure 7.   Nonlinear regression of seasonal (30 April–13 August) non-cancrid (porcellanid, grapsid, pagurid, and majid) crab settlement on brush collectors during 1992–99 at Bodega Head with seasonal average of the temperature ($y = -0.3824x^2 + 8.7761x - 49.116$, $R^2 = 0.6483$) collected at BML MOMS.

TABLE 3
Interannual Correlations between Settlement and Oceanographic Variables

	Cancrid crabs	Non-cancrid crabs	Sea urchins
Salinity	0.277	0.591	0.018
Temperature	0.476	0.044	0.395
Wind stress	**-0.777**	-0.140	-0.339
$\log_{10}$(wind stress+1)	**-0.900**	-0.217	-0.539
Upwelling	-0.645	-0.120	-0.423
NOIx	-0.027	0.028	0.256
SOI	0.199	-0.318	0.128

All variables are based on the years 1992–99, except for salinity (1992–98). All values are calculated as the average during the settlement period of days 120 to 225 (30 April–13 August). Significant correlations ($p < 0.05$) are in bold.

part of the settlement season was dominated by strong alongshore upwelling winds, resulting in prolonged periods of lower temperatures than usual (fig. 5a, b). Low daily variability in temperature, combined with the strong alongshore winds, resulted in no clear evidence of relaxation in the temperature time series. Two atypical wind relaxation events did occur during the season, at days 145 and 190, but neither event was associated with a temperature increase of the magnitude observed during similar events in 1997 and 1998 (fig. 5b). The second relaxation event came near the beginning of a general increase in temperature that continued through the remainder of the settlement season. However, the lack of decrease in temperature as winds began after this event makes it unlikely that the temperature increase was related to wind relaxation events (fig. 5a). Correlations between daily values of temperature and wind stress and temperature and $\log_{10}$(wind stress+1) were significant, showing evidence of wind-forced upwelling (table 1).

In 1999, settlement of all taxa was very low, with background levels at least an order of magnitude less than

those seen in 1998 (fig. 5c, d). Settlement of cancrid crabs showed a significant negative correlation with temperature (table 2), which was probably spurious and due to the low rate of settlement occurring only during the early, colder portion of the settlement season, rather than reflecting settlement in relation to any upwelling/relaxation pattern. Settlement of non-cancrid crabs and sea urchins showed no significant correlations with temperature (table 2).

Interannual Variability in Settlement and Oceanographic Conditions

Cancrid crabs had lower settlement in years with high seasonal alongshore wind stress, $\log_{10}$(wind stress+1), and upwelling values (fig. 6, table 3). Although the previously observed negative correlation between non-cancrid crab settlement and temperature was evident for 1997 and 1998, adding 1999 to the time series resulted in no significant linear correlation, and a dome-shaped relation between settlement and temperature (fig. 7, table 3). A similar dome-shaped relation was observed between non-cancrid settlement and upwelling. Sea urchin settlement was not significantly correlated with any oceanographic variables. Sporadic settlement of sea urchins, with five of the eight years having little or no settlement, provides few data points for study, though the analysis showed relatively high negative correlations with wind stress, $\log_{10}$(wind stress+1), and upwelling (table 3).

DISCUSSION

In general, settlement in 1997 and 1998 was similar to that in previous years, but 1999 was unusual because of the extremely strong upwelling winds. In 1997, the lack of inverse correlation between temperature and salinity indicated that wind-driven upwelling/relaxation was not dominant, and cancrid crab settlement was not

correlated with temperature. In 1998, temperature and salinity were inversely correlated, and settlement appeared to be driven by relaxation, with some exceptions. In 1999 strong, constant upwelling winds resulted in no relaxation events and settlement an order of magnitude lower than in any previous year.

It is somewhat surprising that our 1998 data did not show the expected positive correlations between temperature and settlement of cancrid crab and sea urchin species. This is partly due to the gaps in sampling because weather and other factors limited our ability to sample frequently. At several times in the season, sample collection was delayed, and two weeks elapsed between samples, diminishing our ability to detect responses to rapid changes in temperature. Examination of the oceanographic and settlement data on a fine scale (fig. 4) does indicate settlement following wind relaxation events; but because collection periods generally averaged over both upwelling and relaxation conditions, we cannot detect the correlation between settlement and relaxation normally evident in good settlement years. Longer collection periods also make our settlement collections more susceptible to the influence of postsettlement survival, which may bias longer-term collections. However, our 1998 (and 1999) data emphasize the necessity of examining settlement processes at the relevant temporal scale. Because settlement seems to occur over the first few days of a relaxation event (Wing, Botsford et al. 1995), weekly or even daily monitoring is much more useful for evaluating the settlement responses to local oceanographic conditions.

Settlement in 1999 was unusually low. High upwelling and only a few weak, ineffective relaxation events caused a lack of noticeable levels of settlement of any taxa. It may be that the constant, extreme upwelling winds of the early part of the season resulted in stronger alongshore and offshore transport of the warm surface layer, so that a longer relaxation event was required for nearshore temperatures to rise and for planktonic cancrid crabs from south of Point Reyes to reach BML on the coast. Another equally likely hypothesis for the lack of settlement is that larvae were transported out of the retention zone into the stronger than normal alongshore flow of the coastal jet (Hayward et al. 1999), and thus lost from the local system.

Settlement of non-cancrid crabs varied intra-annually in response to wind relaxation events, though correlations in oceanographic variables over the season do not show the same strong negative correlations between wind values and settlement. The short settlement period of non-cancrid (primarily porcellanid) crabs, with large pulses primarily early in the spring settlement season (Strathmann 1987), makes it difficult to describe direct associations of settlement with oceanographic variables

over the entire season, as noted in Wing et al. 2000.[5] Previous observations have shown the highest settlement in years with low temperatures, strong upwelling, and low salinity. The highest years of settlement were 1994 and 1996, years with the highest non-ENSO index values for the NOIx. Our 1999 findings modified this simple linear response between La Niña conditions and non-cancrid crab settlement to a nonlinear, dome-shaped response of settlement to both temperature and upwelling conditions (table 3). This implied that non-cancrid crabs generally settle most strongly in years of high upwelling (and presumably high CCS productivity); however, extremely high upwelling restricts settlement of these coastal crabs, possibly by transporting them offshore or southward in the coastal jet. It has also been suggested that the lack of settlement in April–August of 1999 could be explained by temperature-related disruptions in reproductive timing, because gravid porcellanid crabs were not observed until late summer (Robert Toonen, pers. comm.).

Sea urchin settlement continued to be sporadic in these years, and reasons for the exact timing and magnitude of settlement are still unknown. Other researchers have documented similar episodic settlement of sea urchin species via direct observations of settlement (Ebert et al. 1994) and indirect observations through adult size-frequency distributions (Tegner and Dayton 1981, 1987; Pearse and Hines 1987; Ebert and Russell 1988). Researchers have also documented sea urchin settlement during winter and early spring (Ebert et al. 1994), a period for which we are subject to logistical constraints (weather). Settlement of sea urchins in response to wind relaxation events has also been observed (Miller and Emlet 1997). In spite of the sporadic temporal nature of sea urchin settlement, its spatial pattern indicates that sea urchins respond to the alongshore transport in the upwelling/relaxation mechanism near headlands (Wing, Botsford et al. 1995). The pattern of recent recruitment in size distributions of the red sea urchin indicates higher settlement just north of Point Reyes and Point Arena than elsewhere (Morgan et al. 2000; cf. Ebert and Russell 1988).

The findings described here represent local settlement at BML, a single point on the coast that does not necessarily reflect the coastwide settlement strength of the species we described. Settlement at BML could be influenced by two separate mechanisms: one that determines general annual strength of the year class in plankton all along the coast, and another that determines how much of that year class settles at this specific location as determined by local winds and associated circulation.

Our ability to draw any of these conclusions about ENSO-related settlement effects depends critically on the long-term monitoring program in place at BML. Though the data set is, in itself, rather short (only 8 years), shorter time series often lack baseline settlement data, making it difficult to draw conclusions about the effect of relatively rare ENSO events (of the 1997–98 magnitude). There is a dire need for more long time series, to put these anomalous events in context. Although we will never know past settlement data, long-term monitoring projects will allow us to document how future anomalous events, including ENSOs and global warming, affect invertebrate settlement.

ACKNOWLEDGMENTS

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INTERANNUAL CHANGES IN THE CALANOID COPEPOD COMMUNITY
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ABSTRACT

The calanoid copepod community was studied from zooplankton samples collected along transect 570 (off Bahía Magdalena) of the CICIMAR sampling grid during four spring cruises carried out during 1983–86. The null hypothesis postulating no interannual differences of the copepod community was tested. Calanoids represented between 84% and 96% of the total copepod numbers. Interannual variability of abundance was high: the overall abundance was lowest in 1985 and highest in 1984. A characteristic pattern of calanoid species abundance occurred each year; each arrangement could be considered as the result of local resource partitioning in which the abundance of a given species is in some way equivalent to the portion of niche space it occupies. In 1983 three species showed high abundance but a reduced distribution: *Subeucalanus subcrassus*, *Euchaeta rimana*, and *Pleuromamma abdominalis*. Between 1984 and 1986, *Calanus pacificus* was the most abundant and widely distributed, and was considered to be the representative species of the Copepoda during this period. Results of this study allowed rejection of the null hypothesis: interannual changes in oceanographic conditions are reflected in the copepod community, which shifted from a low-diversity, high-dominance stage during non–El Niño conditions to a more tropical, diverse community during the 1983 El Niño event. The southern boundary of the California Current system off Baja California varies, with changes identifiable through analysis of the structure of the calanoid copepod community.

INTRODUCTION

Calanoid copepods are among the most representative taxa of the pelagic mesozooplankton, and are both highly diverse and abundant (Angel 1994). The copepods of the California Current area have been surveyed for decades (Esterly 1924; Brodsky 1950; Fleminger 1964, 1967; Bowman and Johnson 1973), and only some dynamic aspects have been described (Longhurst 1967; McGowan and Miller 1980).

However, relatively little is known about the behavior of the pelagic Copepoda along middle and southern

Baja California, part of the southernmost boundaries of the California Current's area of influence. Taxonomic knowledge of the calanoid copepod fauna in the oceanic waters off the western coast of Baja California has been summarized by Hernández-Trujillo (1998) and Palomares et al. (1998).

The oceanic environment off Bahía Magdalena, on the western coast of Baja California, occupies a biogeographically interesting zone, the temperate-tropical transitional area. The limits of this area are not stable and have a wide range of interannual variation (Roden 1991). Transect 570 of the basic Centro Interdisciplinario de Ciencias Marinas (CICIMAR) sampling grid is located precisely in this key transitional area, off Bahía Magdalena. This transect was sampled by 37 cruises between 1982 and 1998. However, we determined that May was the only month during which four consecutive annual zooplankton samplings were performed. In fact, this month is particularly relevant because it is in May that the oceanographic conditions of the California Current reach their southernmost limits and have a detectable influence in the area. The May samples also include zooplankton from El Niño and non–El Niño years. So we used this material to estimate the extent of the interannual persistence or change of the community structure of calanoid copepods along transect 570 off the Baja California Peninsula. These data are intended to contribute to the understanding of interannual dynamics affecting the zooplankton distribution in this transitional area of the Pacific Ocean.

METHODS

Zooplankton samples were obtained with a bongo-type net in all the localities along transect 570 of the CICIMAR sampling grid in the Baja California Peninsula (BC). The transect is perpendicular to the coastline (fig. 1) and was sampled during May of four consecutive years: 1983–86. Stations 80 (112.45°W, 24.05°N, tow 250–0 m); 60 (112.25°W, 24.25°N, tow 250–0 m); and 45 (112.05°W, 24.45°N, tow 175–0 m) are separated from each other by about 20 nautical miles. The sampling methods, including fixation and preservation of the material, estimation of zooplankton biovolumes, and quantification of calanoid copepods is standard for all
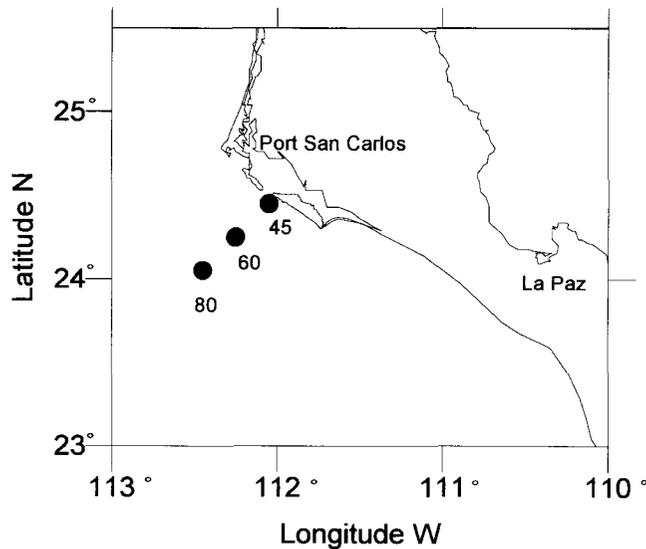
Figure 1.   Locations of CICIMAR transect 570 on the western coast of southern Baja California.

TABLE 1
Number of Copepod Species in
Transect 570 during May 1983–86

Year	Number of copepod species	Number of calanoid species	Percentage of calanoids
1983	27	26	96
1984	20	17	85
1985	11	10	91
1986	32	27	84
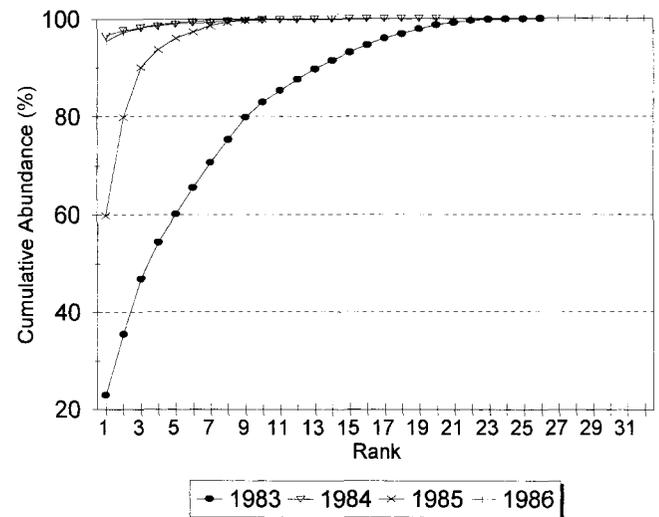
Figure 2.   Rank abundance of calanoid copepod species along transect 570 (1983–86).

CICIMAR zooplankton collections, and has been described in detail by Hernández-Trujillo (1998).

After the calanoid copepods from the samples were identified and counted, a rank abundance was plotted to present species abundance data (Magurran 1988) and to provide a direct comparison between communities of calanoid copepods with different numbers of species during the period of the study. Hence, the interannual variation of the calanoid copepod abundance was determined, considering the dominant species and the most frequent forms.

Surface temperature data were obtained at each station with an InterOcean CTD; a decadal time series of the sea-surface temperature (SST) for May 1980–90 was built by integrating data from Cole and McLain (1989) and from the CD-ROM COADS of NOAA. Temperature anomalies were estimated as well.

RESULTS

The taxonomic analysis of the total copepod fauna in the studied samples yielded 50 species. The numbers of copepod species and calanoid species during each year surveyed are presented in tables 1 and 2. There were differences in calanoid communities between 1983 and 1986 (fig. 2). The upper curves represent the least diverse community, dominated by one species; the lower curves were the most diverse. In comparison to 1983, the overall species richness decreased 26% in 1984 and 59% in 1985. This situation was reversed in 1986, when the species number increased 18.5% from the 1983 figure. The species of Calanoida followed the same general trend, but not for their relative density within the community structure. Calanoid copepods represented, in all cases, between 80% and 96% of the species richness.

Considering the biogeographic affinities of the 50 species recorded, 62% are tropical, 16% subtropical, 14% equatorial, and 8% transitional forms. Interannual variation of the biogeographic composition showed that the tropical component of the community was consistently the most relevant (55%–67%) during the four years considered (fig. 3).

The interannual average abundance of calanoid copepods along transect 570 showed a wide range of variation: its maximum value occurred in 1984, with 112,832 individuals·1000 m^{-3} (fig. 4), its minimum value in 1985 (259 ind·1000 m^{-3}). The general trend of the local calanoid copepod community showed a decreased abundance toward the coastal areas (fig. 5).

The interannual analysis of the community structure showed that during 1983 three calanoid species were the most representative in terms of density: *Pleuromamma abdominalis*, *Euchaeta rimana*, and *Subeucalanus subcrassus*; despite this, their distribution was relatively reduced. In contrast, the most important in 1984 were *Calanus pacificus*, *Calanus minor*, and *Pleuromamma gracilis*. In both 1985 and 1986, *C. pacificus*, *P. abdominalis*, and *Rhincalanus nasutus* were clearly dominant and most widely distrib-

TABLE 2
Copepod Species Recorded during May (1983–86) at CICIMAR Transect 570

Species	Affinity	May 1983	May 1984	May 1985	May 1986
Calanus pacificus	Transitional	▨	▨	▨	▨
Candacia bipinnata	Transitional			▨	
Eucalanus californicus	Transitional	▨			▨
Rhincalanus nasutus	Transitional	▨		▨	▨
Acartia clausi	Subtropical	▨			▨
Calanus minor	Subtropical		▨		▨
Candacia pachydactyla	Subtropical				▨
Corycaeus typicus	Subtropical			▨	
Gaetanus secundus	Subtropical				
Lophothrix frontalis	Subtropical				▨
Pleuromamma quadrungulata	Subtropical	▨			
Scolecithricella vittata	Subtropical		▨	▨	
Acartia danae	Tropical	▨			▨
Acrocalanus gracilis	Tropical				▨
Aetideus armatus	Tropical	▨			▨
Caligus sp.	Tropical			▨	
Candacia pectinata	Tropical			▨	
Copilia quadrata	Tropical				▨
Corycaeus lautus	Tropical		▨		
Corycaeus speciosus	Tropical				▨
Eucalanus crassus	Tropical	▨			
Euchaeta rimana	Tropical				▨
Euchaeta media	Tropical	▨			▨
Euchirella amoena	Tropical				▨
Haloptilus mucronatus	Tropical	▨			
Haloptilus ornatus	Tropical	▨			▨
Labidocera acutifrons	Tropical	▨			▨
Oithona plumifera	Tropical	▨		▨	▨
Oncaea venusta	Tropical				▨
Paracalanus parvus	Tropical	▨			▨
Phaenna spinifera	Tropical		▨		
Pleuromamma gracilis	Tropical		▨		
Pleuromamma abdominalis	Tropical		▨		▨
Pontellopsis perspicax	Tropical	▨			
Pontellopsis sp.	Tropical		▨		
Pontellopsis villosa	Tropical				▨
Sapphirina gastrica	Tropical				▨
Scolecithricella bradyi	Tropical	▨			
Scolecithricella sp.	Tropical	▨			
Scolecithrix danae	Tropical			▨	▨
Scottocalanus sp.	Tropical				▨
Temora discaudata	Tropical	▨			▨
Aetideus giesbrechti	Equatorial				▨
Candacia catula	Equatorial		▨		
Candacia curta	Equatorial			▨	▨
Candacia truncata	Equatorial	▨			▨
Eucalanus attenuatus	Equatorial	▨	▨		▨
Subeucalanus subcrassus	Equatorial		▨		
Undinula darwini	Equatorial	▨	▨		

Shaded columns indicate that the species was present.

COPEPOD FAUNA VARIATION

May 1983

Equatorial (14.81%)
Transitional (11.11%)
Subtropical (7.41%)
Tropical (66.67%)

May 1984

Equatorial (20.00%)
Transitional (5.00%)
Subtropical (15.00%)
Tropical (60.00%)

May 1985

Equatorial (18.18%)
Transitional (27.27%)
Tropical (54.55%)

May 1986

Equatorial (12.50%)
Transitional (9.38%)
Subtropical (15.63%)
Tropical (62.50%)
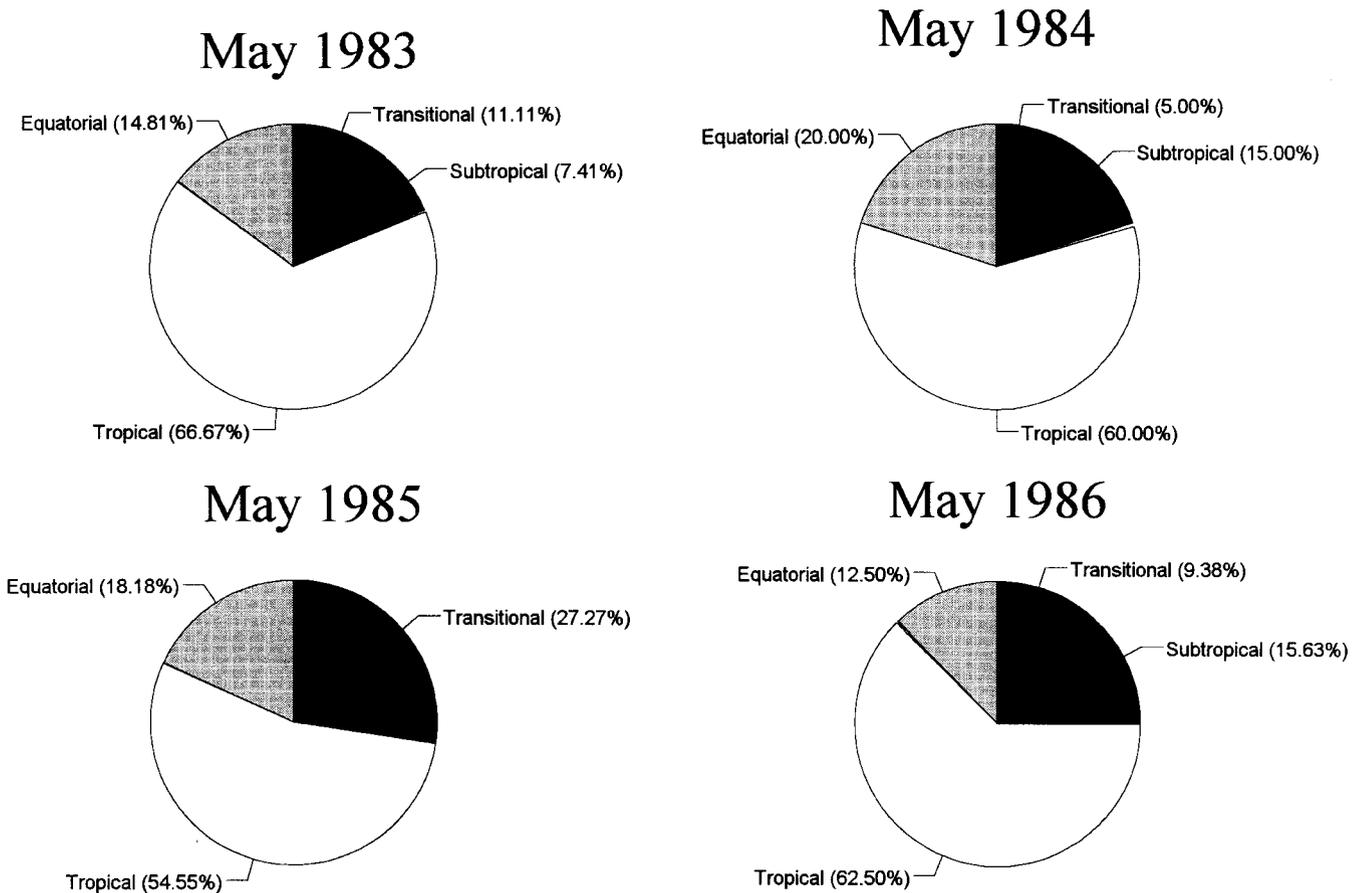
Figure 3.   Variation of the biogeographic structure of the copepod fauna during May 1983–86.

Total abundance of calanoid copepods along line 570

Ln Abundance

Line 570 Station Numbers

■ 1983 ▨ 1984 ■ 1985 ■ 1986

CALANOID COPEPODS 1983-1986

Ln Copepod Abundance

±Std. Dev.
±Std. Err.
□ Mean

LINE 570 STATION NUMBER
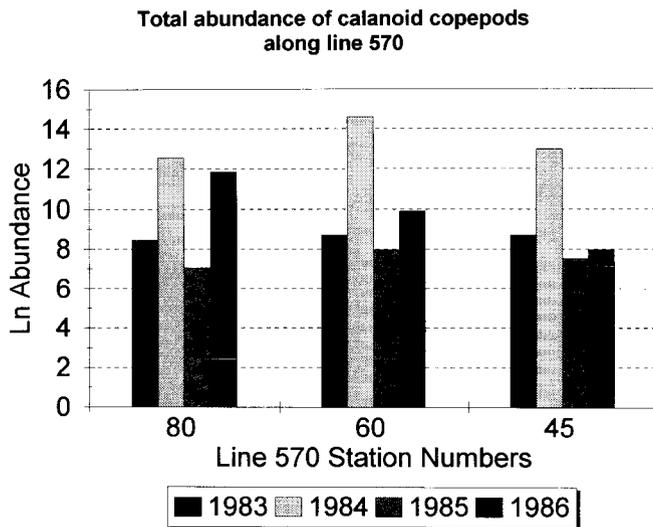
Figure 4.   Total abundance of calanoid copepods along transect 570 (1983–86).
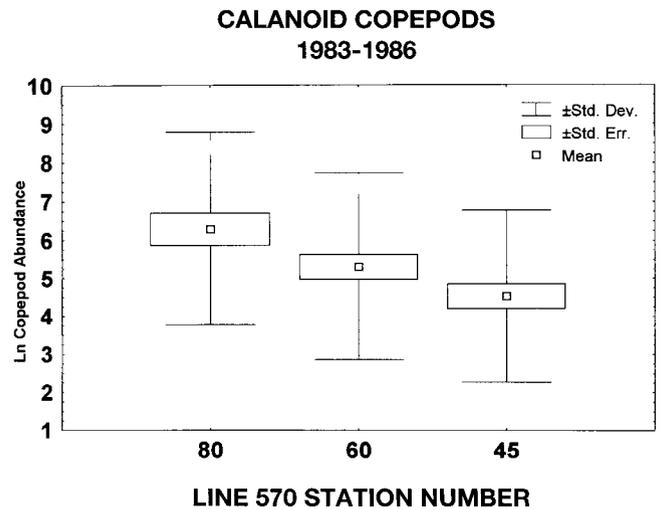
Figure 5.   Ocean-coast distribution of calanoid copepods during May 1983–86.

uted (figs. 6 and 7). Due to this dominance, except for 1983, the interannual abundance of *C. pacificus* is representative of that shown by the calanoid copepods together (fig. 8a).

Changes in zooplankton biovolume values were evident among the different years considered. The highest value (>500 ml·1000 m^{-3}) was recorded in 1983; the lowest in 1985 (<25 ml·1000 m^{-3}; fig. 8b).

The SST showed a maximum average value in 1983 (19.9°C); the lowest value was recorded in 1985 (15.1°; fig. 8c). The SST showed a definite trend in terms of the coast-ocean gradient, with lower values toward the coast during the four years studied. The mesoscale interannual analysis of decadal SST (1980–90) and the corresponding anomaly in the area between 22° and 24°N varied widely during May (fig. 9). The highest temperature of the decade (22.8°) was recorded in May 1983. Lowest values within the same 10-year period were recorded in 1988 (19.4°) and 1989 (20.1°). The

anomaly analysis showed that seawater stayed longer during the 1980–90 period (fig. 9).

DISCUSSION

According to Lynn and Simpson (1987), the coastal surface waters of the California Current flow southward along BC (32° to 25°N) between March and May; this is part of a highly variable seasonal pattern in the region. Near the BC coasts, SST increases southward from 15° to 20° in winter, and from 20° to 25° in summer (Badán 1997). Considering the topography of the 20°C isotherm as a reference for the advancement or retreat of the California Current, figure 10 shows that in 1984 and 1985 waters with temperatures over 20° were distributed south of transect 570; in 1985, they reached as far south as Cabo San Lucas. In contrast, in 1983 and 1986, SST values over 20° were distributed north of Bahía Magdalena.

This strong SST variability had different effects on the structure of the local calanoid copepod community.
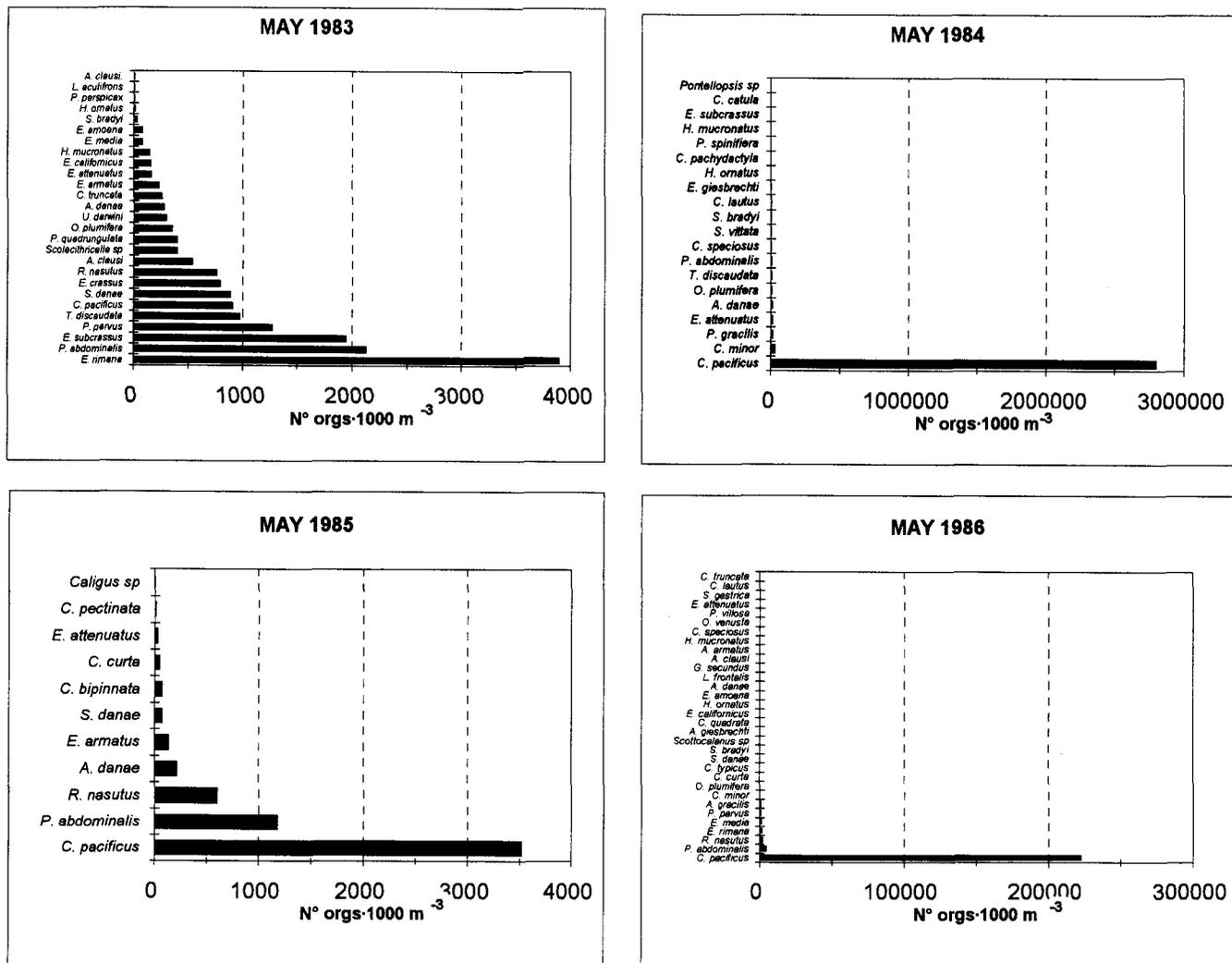
Figure 6.   Abundance-diversity of the pelagic Copepoda in May 1983–86.
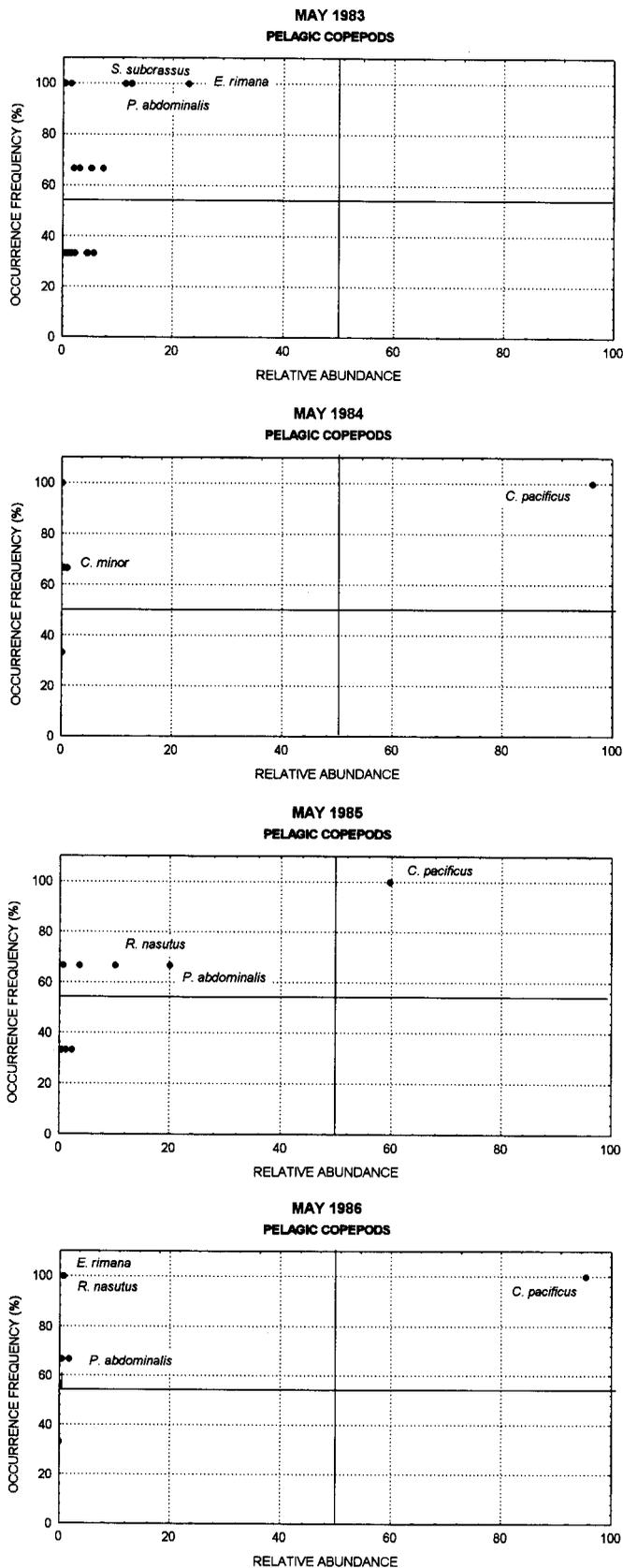
Figure 7. Frequency–relative abundance of the calanoid copepods in May 1983–86.
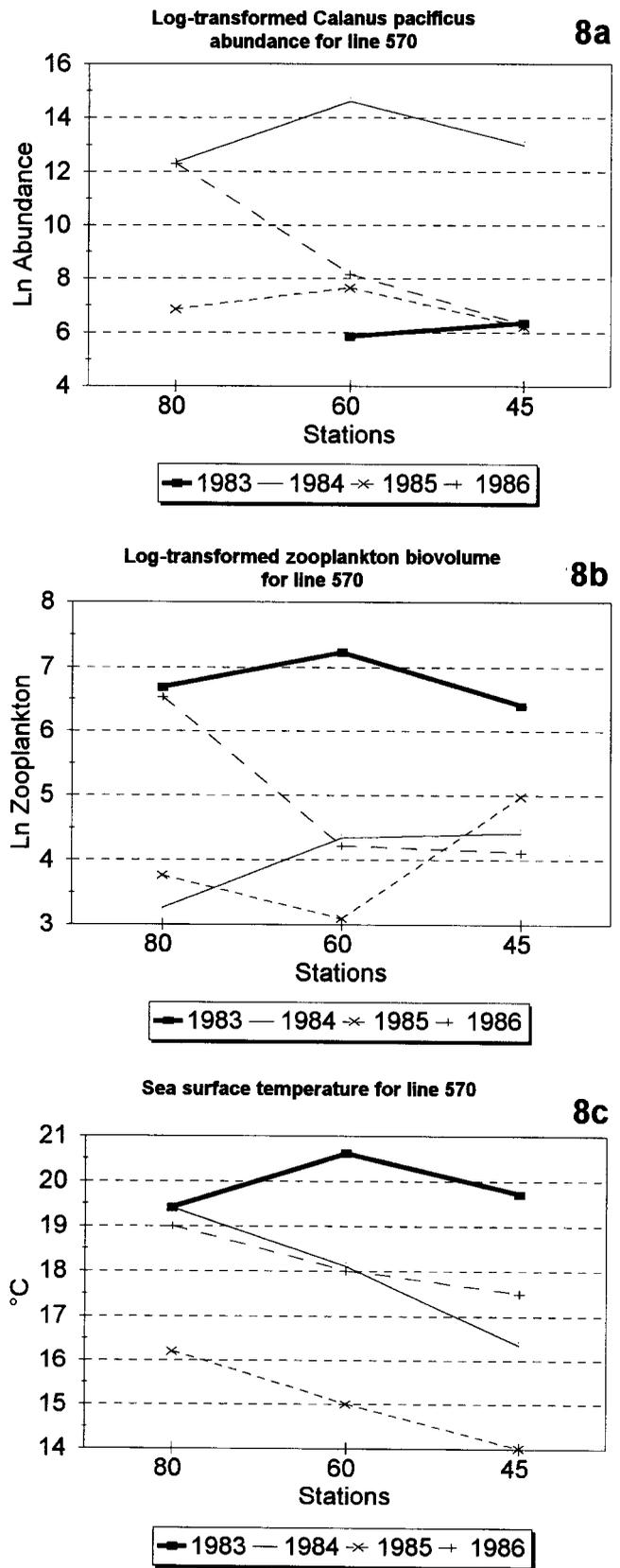
Figure 8. Ocean-coast distribution of (a) the abundance of Calanus pacificus, (b) zooplankton biomass, and (c) sea-surface temperature along transect 570 during May 1983–86.

**Time series of the SST for May
22-24°N**
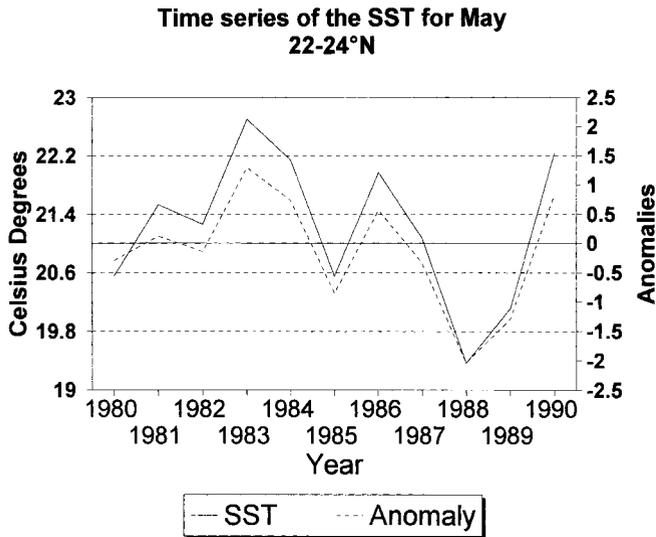
Figure 9. Time series of SST data and anomalies between 22° and 24°N (1980–90).

One of the most relevant was the induction of a stage featured by low species dominance, higher diversity, and a relatively complex community structure during the onset of anomalous warm conditions such as those related to El Niño 1983. Another consequence was to promote, with relative consistency, the persistence of a simplified structure, with a high dominance of a single species, and a reduced diversity in relatively colder conditions related to the influence of the California Current (Wolter 1987; Wolter and Timlin 1993; Hernández-Trujillo 1998).

The species richness recorded in the surveyed area represented between 9% and 26% of the faunal diversity previously known in the area off southern Baja California (Hernández-Trujillo 1998; Palomares et al. 1998), thus only a few species periodically become the dominant forms of the calanoid copepod community in the area. The changes in this community were followed through successive modifications of its structure, which showed different stages of complexity.

The sharpest changes were evident in 1983, when the abundance and frequency of the calanoid copepods did not center on a particular species, contrasting to the profile observed in the other years. The extreme dominance of *C. pacificus* during 1984–86 simplified the community structure. As has been shown by Hernández-Trujillo (1998), temperature and salinity conditions modify the structure of the pelagic copepods off the western coast of southern Baja California.

It is clear from figure 3 that the temperature increase is related to the invasion of warmer waters of tropical origin and to a higher proportion and abundance of tropical species. During these conditions, the distribu-

tion of resources is more homogeneous because of the decreased population of *C. pacificus*.

Interannual changes in the calanoid density values, and particularly for *C. pacificus*, seem to be only weakly related to food availability. Photosynthetic pigment concentrations reported by Zuria-Jordán et al. (1995) off Bahía Magdalena in May 1983–86 were 3.5, 3.5, <1, and 8 $mg \cdot m^{-3}$, respectively. These concentrations were associated, in the same sequence, to phytoplankton densities varying from 960 to $4 \cdot 10^{-3}$; $2 \cdot 10^{-3}$ to $47 \cdot 10^{-3}$; $2 \cdot 10^{-3}$ to $490 \cdot 10^{-3}$; and $240 \cdot 10^{-3}$ to $328 \cdot 10^{-3}$ $cel \cdot l^{-1}$; nannophytoplankton was dominant in all cases (Martínez-López 1993).

Most of the dominant species, including *C. pacificus*, are herbivorous forms, enhanced by a phytoplankton-rich environment (Zuria-Jordán et al. 1995). In 1985, when conditions were different, the pigment concentration was lowest, the SST was 1°C below the average, and the overall abundance and species richness of copepods decreased. However, these apparently adverse conditions did not affect the community structure of copepods. Despite the reduced abundance and species richness in 1985, the dominant and codominant species were mostly the same and in a similar relative proportion.

The analysis of the time series of pigments obtained by Zuria-Jordán et al. (1995) showed that the anomalies detected between 1983 and 1985 were always negative during May off Bahía Magdalena; the anomaly was positive only in 1986. This is an inverse situation with respect to the SST anomalies, suggesting that phytoplankton values dropped as a consequence of the warming produced by El Niño 1982–83 in the surveyed area (Martínez-López 1993). The event showed detectable residual effects in the zooplankton until 1984 (Hernández-Trujillo and Esquivel-Herrera 1997); for copepods, the effect was a reconstitution of structure, from a complex stage to a simpler one.

El Niño 1982–83 had important effects in the BC area, including the reduced hydrologic rate of mixing of surface and subsurface waters (Wooster and Fluharty 1985) and the decrease of both zooplankton and phytoplankton abundance. Our results show that part of the strong oceanographic influence of El Niño 1983 persisted for years after the event, even in the southern BC area. This is reflected in the calanoid copepod community structure, with the shift from the dominance of one species to a shared dominance of several others, the high rate of specific renewal, and 60% of tropical species.

An ecological explanation for differing behavior of calanoid copepods under similar conditions of SST (see fig. 10) could be food availability, which favors only a few species. This idea is supported by the results of Hernández-Trujillo (1999a), who found that the highest densities of calanoid copepods, including *C. pacificus*,
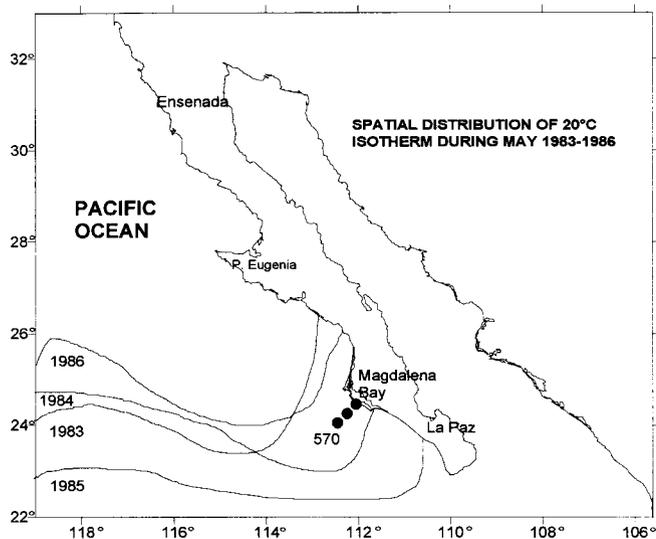
Figure 10. Spatial distribution of the 20°C surface isotherm off the west coast of southern Baja California.

were related to nannophytoplankton concentrations between 5,000 and 25,000 cel/l^{-1} and SST between 16° and 22°C.

The conditions related to transect 570 represent an adequate situation for surveying interannual changes in the structure of the copepod community and its relation to El Niño and non–El Niño years. Our work is intended to provide insights into the effects of the acyclic onset of new conditions to which the general zooplankton community, and particularly that of the pelagic copepods, must adapt (Funes et al. 1995; Palomares-García and Gómez-Gutiérrez 1996; Hernández-Trujillo 1999a, b). It is expected that these interannual variations are comparable to or stronger than the seasonal ones (Chelton et al. 1982). In fact, the seasonal data of Hernández-Trujillo (1998) for the copepod community in the same area supports this idea. This information is particularly relevant for a transitional area such as BC, where knowledge about these aspects is still limited, thus providing complementary data about the behavior of zooplankton toward the southern boundaries of the California Current system.

CONCLUSIONS

Interannual variation of the calanoid copepod community in the surveyed area was high. A single species was dominant during three consecutive years, but the codominant ones were not the same each year, and they did not occupy the same niche. The persistent characteristic of the community was the stability of *C. pacificus* and *Pleuromamma abdominalis*, representative of non–El Niño years.

The expected tropical conditions associated with El Niño 1983 were clearly reflected in the local cope-

pod structure as an apparent evenness in the use of the available resources and an increased complexity. During 1984–86, the wide dominance of a single species suggests an asymmetric distribution of the resources and represents a reduced stage of complexity.

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RESPONSE OF SILICEOUS MICROPLANKTON FROM THE SANTA BARBARA BASIN TO THE 1997-98 EL NIÑO EVENT

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ABSTRACT

We report on fluxes of siliceous microorganisms (diatoms, radiolarians, and silicoflagellates), organic carbon, calcium carbonate, biogenic silica, and lithogenic particles in the Santa Barbara Basin (SBB; 34°4'N, 120°02'W), offshore of California, in a sediment trap set 540 m deep. We describe changes in particle fluxes, emphasizing the period from 1996 to early 1998, and compare flux values and species composition for non–El Niño (1996) and El Niño (1997–98) conditions. The California coastal waters were strongly influenced by El Niño conditions beginning late in the summer of 1997. Terrigenous input to our sampling site, as measured by the lithogenic flux, was significantly higher during the El Niño period, presumably reflecting higher rainfall and runoff into the basin. Samples from December 1997 to February 1998 contained large amounts of detritus, Chrysophyte cysts, benthic diatoms, and estuarine benthic foraminifers, indicating that considerable material was flushed from the river mouths during large storms. Both opal and organic carbon fluxes mirrored the productivity cycle, with high fluxes during the spring-summer upwelling period and low fluxes during fall and winter. However, for the winter of 1998 organic carbon fluxes were unusually high, and coincided with a February peak in the carbonate flux and high abundance of arenaceous tintinnids. Opal fluxes decreased, and major changes in the contribution of siliceous microplankton assemblages to the biogenic opal flux were observed during El Niño conditions: (1) Diatom fluxes were an order of magnitude lower, and species richness was higher than in the 1996 non–El Niño period. (2) The flux of radiolarians was 20% lower in late 1997–early 1998 when compared to the 1993–96 period. (3) The fall-winter peak in silicoflagellate fluxes, seen annually from 1993 to 1996, was missing in 1997. In addition, major changes in species composition were observed, including a significant increase in the proportion of warm-water flora and fauna, and a decrease in the relative contribution of the siliceous microorganisms indicative of spring upwelling conditions in the SBB.

INTRODUCTION

The onset and decay of El Niño events have been difficult to predict locally, so data on the response of microorganisms to these phenomena are rare. We were fortunate to have a sediment trap mooring already deployed in the center of the Santa Barbara Basin (SBB), southern California (fig. 1), beginning in August 1993 (table 1; Lange et al. 1997; Thunell 1998), which allowed us to study the changes in the flux of particles associated with the 1997–98 El Niño event, considered to be the strongest El Niño of this century (Davey and Anderson 1998; Wolter and Timlin 1998).

Many of the physical observations in the California Current region during late 1996 and early 1997 were fairly close to the seasonal norms. El Niño conditions developed very rapidly in March 1997 in the western and central equatorial Pacific (Chavez et al. 1999), becoming the dominant forcing process in the summer of 1997 in the eastern Pacific (Lynn et al. 1998; Chavez et al. 1999) and reaching peak strength in January–March 1998 (fig. 2). In the SBB, temperatures of the upper water column were unusually high at the end of summer 1997 and remained elevated throughout the fall and winter (fig. 3A; Thunell et al. 1999). A dramatic return to non–El Niño conditions in the equatorial Pacific occurred in May 1998 (fig. 2; Chavez et al. 1999; Takayabu et al. 1999), and by early autumn 1998 a shift to strong southward wind stress had produced cooler than normal sea-surface temperatures (SST) in the California Current system (Hayward et al. 1999).

It is our intent to describe temporal changes in the particle fluxes of organic carbon, calcium carbonate, biogenic silica, and the lithogenic fraction, and to compare flux values as well as the species composition of planktonic siliceous microorganisms for non–El Niño (1996 through mid-1997) and El Niño (mid-1997 through spring 1998) conditions in the SBB. Previous studies have already reported on particle fluxes and calcareous and siliceous components for the period 1993–96 (Thunell et al. 1995; Lange et al. 1997; Thunell 1998; Kincaid et al. 2000). These studies demonstrated that the flux patterns of the various components of the plankton are a response to changes in upper ocean conditions in the SBB, and that the shifts in species composition
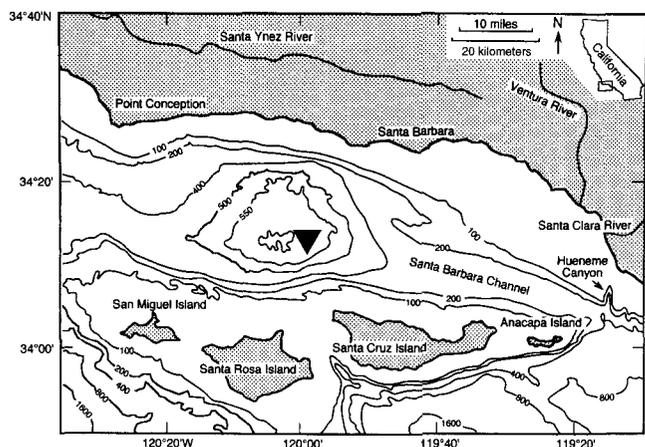
Figure 1. Bathymetry (in meters) of Santa Barbara Basin, and location of sediment trap mooring (black triangle).

Figure 2. Southern Oscillation Index (SOI) anomaly from January 1996 through August 1998 (modified from Thunell et al. 1999). This index is based on atmospheric pressure difference between Tahiti and Darwin, Australia. Positive values indicate non–El Niño conditions, and negative values represent El Niño conditions. The 1997–98 El Niño began in March 1997 in the western and central equatorial Pacific and ended abruptly in mid-May 1998; a cold La Niña condition began in mid-1998 (e.g., Chavez et al. 1999). Data provided by the National Oceanic and Atmospheric Administration (NOAA).

do indeed reflect the circulation patterns in the area (Hendershott and Winant 1996). In addition, benthic diatoms advected from the shelf trace the influence of rainfall and river runoff.

This work is a continuation of the original plan to monitor biweekly changes in the flux of planktonic microorganisms over an exceptionally long time span in the SBB. The goal of this ongoing trapping program (being carried out by the University of South Carolina) is to monitor seasonal changes in sediment fluxes, to evaluate seasonal and interannual variability in response to El Niño (La Niña) events, and to appraise sediment formation and accumulation in the SBB. Results from sediment trap studies, in conjunction with measurements of climatic conditions, are relevant for identifying and calibrating climate proxies that can be applied to the sediment record in order to reconstruct and interpret climate signals contained in the well-preserved laminated sediments of the SBB (e.g., Soutar and Crill 1977; Kennett et al. 1995; Schimmelmann and Lange 1996).

MATERIALS AND METHODS

The SBB is at the northern end of the Southern California Bight. A description of the study area and general hydrology of the SBB and the adjacent California Current can be found in Hendershott and Winant 1996, Lange et al. 1997, and Thunell 1998. The location of the sediment trap (34°14'N, 120°02'W; fig.1) as well as the type of trap used (cone-shaped with 13 cups; 0.5 m² collection area) has not changed over the five years of the experiment (August 1993–April 1998; Lange et al. 1997; Thunell 1998). The mooring was deployed at 590 m water depth, and the trap was positioned about 50 m off the bottom. Each trap sample represents a two-week period of collection except for the interval 22 May to 25 June 1997, when sampling resolution increased to 7

days (table 1). Samples were collected continuously and poisoned with $HgCl_2$.

Analysis of the siliceous microplankton, including diatoms, silicoflagellates, and radiolarians, was carried out on 1/64 splits of the total material in the original sample. The split was first washed with distilled water to remove salt and preservative and then acid-cleaned and prepared according to the method described in Wigley 1984. Samples were passed through a sieve so that all counts refer to cells ≥ 45μm. Thus the abundance of small diatoms such as Chaetoceros vegetative cells and resting spores (which range in size between 5 and 30 μm) is somewhat underestimated. This underestimation may not be that great because of the formation of sticky transparent exopolymer particles by Chaetoceros (Passow et al. 1994), which are very hard to disaggregate during the cleaning procedure, and are therefore retained in the sieve.

Two types of permanent slides were made: (1) Naphrax mounts for diatoms and silicoflagellates, which were analyzed quantitatively with an Olympus Provis AX 70 microscope with phase contrast illumination usually at 250× magnification and at 650× for resting spores and other small valves; and (2) Canada Balsam mounts for radiolarians, which were counted with a Zeiss Photomicroscope 1 at 100× magnification. The organisms were identified to the lowest taxonomic level possible.

Daily fluxes in each sample were estimated for the three taxonomic groups surveyed as well as for individual species, and are expressed in numbers $m^{-2} d^{-1}$ (Sancetta and Calvert 1988). Relative contributions of selected diatom and radiolarian species, which represent upwelling conditions, warm oceanic waters, or littoral influence advected from the upper shelf (see Lange et al. 1997; Weinheimer and Cayan 1997, for definition of species groups) are given as percentages of total assemblages.

TABLE 1
Fluxes of Siliceous Microorganisms in Santa Barbara Basin, August 1993 to April 1998

Sample #	Date cup opened	Days after 1 Jan 1993	Collection days	Flux diatoms	Flux silicoflag.	Flux radiolaria
1	12 Aug 93	224	14	2.92E+04	0	5.40E+03
2	26 Aug	238	14	1.19E+05	2.56E+02	6.31E+03
3	09 Sep	252	14	7.31E+04	2.01E+02	5.93E+03
4	23 Sep	266	14	7.06E+04	4.94E+02	7.93E+03
5	07 Oct	280	14	1.06E+05	8.23E+02	1.21E+04
6	21 Oct	294	14	7.08E+04	6.95E+02	1.44E+04
7	04 Nov	308	14	1.18E+05	1.54E+03	1.65E+04
8	18 Nov	322	14	7.99E+04	3.20E+03	9.00E+03
9	09 Dec	343	14	2.72E+04	1.66E+03	5.08E+03
10	16 Dec	350	14	3.42E+04	1.05E+04	5.34E+03
11	30 Dec	364	14	4.79E+04	8.06E+03	5.36E+03
12	13 Jan 94	378	14	4.10E+04	2.27E+03	4.22E+03
13	27 Jan	392	14	3.90E+04	6.77E+02	6.97E+03
14	11 Feb	407	14	1.03E+06	5.49E+02	1.05E+04
15	25 Feb	421	14	3.21E+04	1.65E+02	8.86E+03
16	11 Mar	435	14	2.06E+04	1.10E+02	4.77E+03
17	25 Mar	449	14	3.33E+04	8.23E+01	3.87E+03
18	08 Apr	463	14	6.74E+05	0	4.99E+03
19	22 Apr	477	14	6.81E+06	3.66E+01	5.19E+03
20	06 May	491	14	2.90E+05	1.65E+02	5.80E+03
21	20 May	505	14	7.30E+04	2.74E+02	4.00E+03
22	03 Jun	519	14	7.79E+04	7.31E+01	2.58E+03
23	17 Jun	533	14	7.42E+05	1.83E+02	5.12E+03
24	01 Jul	547	14	2.32E+05	2.56E+02	4.83E+03
25	15 Jul	561	14	1.91E+05	4.57E+02	5.96E+03
26	29 Jul	575	13	2.42E+05	1.38E+02	6.18E+03
27	23 Aug	600	14	1.20E+05	1.04E+03	5.32E+03
28	06 Sep	614	14	1.61E+05	1.37E+03	6.80E+03
29	20 Sep	628	14	8.51E+04	8.78E+02	1.09E+04
30	04 Oct	642	14	8.92E+04	7.09E+03	1.03E+04
31	18 Oct	656	13	5.90E+05	2.76E+03	8.68E+03
32	21 Feb 95	782	14	1.24E+04	3.40E+03	1.61E+04
33	07 Mar	796	14	6.47E+03	7.31E+02	1.30E+04
34	21 Mar	810	14	7.57E+03	2.30E+03	1.35E+04
35	04 Apr	824	14	1.38E+05	1.57E+03	1.59E+04
36	18 Apr	838	14	2.86E+05	6.22E+02	1.09E+04
37	02 May	852	14	1.62E+06	7.31E+01	1.48E+04
38	26 Aug	968	14	1.77E+05	4.61E+03	1.32E+04
39	09 Sep	982	14	4.42E+05	1.82E+04	1.19E+04
40	23 Sep	996	14	3.23E+05	1.06E+05	1.58E+04
41	07 Oct	1010	14	7.95E+04	2.43E+04	1.57E+04
42	21 Oct	1024	14	1.93E+05	2.36E+04	1.40E+04
43	04 Nov	1038	14	2.06E+05	9.51E+03	2.44E+04
44	18 Nov	1052	14	6.69E+04	7.02E+03	9.36E+03
45	02 Dec	1066	14	3.88E+04	1.35E+04	8.48E+03
46	16 Dec	1080	14	1.27E+05	2.34E+04	1.44E+04
47	30 Dec	1094	14	1.27E+05	5.08E+04	9.51E+03
48	13 Jan 96	1108	14	1.17E+04	2.56E+03	4.17E+03
49	27 Jan	1122	14	1.68E+05	1.17E+03	1.45E+04
50	10 Feb	1136	13	2.77E+05	8.78E+02	1.17E+04
51	26 Mar	1181	14	2.77E+05	7.31E+01	1.13E+04
52	09 Apr	1195	14	1.97E+06	0	9.03E+03
53	23 Apr	1209	14	1.02E+06	1.46E+02	1.27E+04
54	07 May	1223	14	1.37E+06	5.12E+02	1.42E+04
55	21 May	1237	14	1.30E+05	3.66E+01	5.38E+03
56	04 Jun	1251	14	4.20E+05	2.93E+02	7.53E+03
57	18 Jun	1265	14	2.19E+04	0	1.03E+04
58	02 Jul	1279	14	8.91E+04	4.39E+02	9.62E+03
59	16 Jul	1293	14	1.19E+05	6.58E+02	8.70E+03
60	30 Jul	1307	14	2.09E+05	1.10E+03	1.52E+04
61	13 Aug	1321	14	1.41E+05	5.49E+02	1.25E+04
62	27 Aug	1335	14	3.05E+05	4.02E+02	8.70E+03
63	24 Sep	1363	14	4.91E+05	6.36E+03	1.29E+04
64	08 Oct	1377	14	1.97E+05	1.53E+04	1.66E+04
65	22 Oct	1391	14	5.74E+05	1.48E+04	1.87E+04
66	05 Nov	1405	14	2.70E+06	6.36E+03	8.89E+03

TABLE 1 (continued)
Fluxes of Siliceous Microorganisms in Santa Barbara Basin, August 1993 to April 1998

Sample #	Date cup opened	Days after 1 Jan 1993	Collection days	Flux diatoms	Flux silicoflag.	Flux radiolaria
67	19 Nov	1419	14	3.08E+06	3.88E+03	1.37E+04
68	03 Dec	1433	14	1.79E+05	3.99E+03	1.43E+04
69	17 Dec	1447	14	2.89E+05	1.13E+04	2.50E+04
70	31 Dec	1461	14	5.30E+04	3.66E+02	7.86E+03
71	14 Jan 97	1475	14	4.45E+05	6.58E+02	8.81E+03
72	28 Jan	1489	14	1.54E+05	1.83E+02	1.09E+04
73	11 Feb	1503	14	1.26E+05	1.10E+02	9.51E+03
74	25 Feb	1517	14	2.17E+05	3.66E+02	1.96E+04
75	11 Mar	1531	13	8.45E+05	8.78E+02	1.77E+04
76	22 May	1603	7	4.65E+05	2.49E+03	2.93E+04
77	29 May	1610	7	2.72E+05	3.95E+03	1.74E+04
78	05 Jun	1617	7	1.18E+04	4.02E+02	no data
79	12 Jun	1624	7	7.38E+04	3.29E+02	no data
80	19 Jun	1631	7	5.22E+04	2.19E+02	no data
81	26 Jun	1638	14	4.79E+04	2.82E+03	no data
82	10 Jul	1652	14	3.17E+05	3.07E+03	no data
83	24 Jul	1666	14	5.15E+04	1.68E+03	no data
84	07 Aug	1680	14	4.27E+04	1.28E+03	no data
85	21 Aug	1694	14	2.18E+04	5.49E+02	no data
86	04 Sep	1708	14	3.42E+04	8.05E+02	no data
87	18 Sep	1722	14	5.51E+04	1.32E+03	no data
88	02 Oct	1736	14	3.32E+04	2.56E+02	no data
89	17 Oct	1751	14	1.13E+04	9.87E+02	4.53E+03
90	31 Oct	1765	14	1.18E+04	3.29E+02	2.89E+03
91	14 Nov	1779	14	8.67E+03	7.31E+01	3.22E+03
92	28 Nov	1793	14	2.72E+04	6.58E+02	6.18E+03
93	12 Dec	1807	14	3.04E+04	1.46E+02	1.12E+04
94	26 Dec	1821	14	4.15E+04	4.39E+02	5.45E+03
95	09 Jan 98	1835	14	2.52E+04	1.17E+03	5.49E+03
96	23 Jan	1849	14	6.40E+03	1.32E+03	3.22E+03
97	06 Feb	1863	14	2.60E+03	7.31E+01	5.05E+03
98	20 Feb	1877	14	4.46E+03	1.43E+03	3.11E+03
99	06 Mar	1891	14	3.75E+04	2.45E+03	3.33E+03
100	20 Mar	1905	14	8.01E+04	1.83E+03	3.44E+03
101	03 Apr	1919	19	6.08E+04	0	3.10E+03

RESULTS

Temperature

Upper ocean temperatures at the sediment trap location were derived from conductivity-temperature-density (CTD) casts conducted between 1 July 1993 and 22 July 1998. These data are used to evaluate overall changes in the thermal structure of the upper 100 m during the study period. Data from the CTD casts were transformed into a 15-day by 2-meter matrix which underwent two smoothing passes and was then contoured. Figure 3A is a visual representation of the temperature profile for the study period presented here, January 1996 to April 1998. Daily SSTs are shown in figure 4 (top panel).

Throughout 1996, which is considered to be a normal non–El Niño period, SSTs in the SBB ranged from a low of ~10.5°C in April at the onset of upwelling to a high of ~17.5° in September and October (fig. 4). The most noticeable change in response to El Niño occurred in late summer 1997, when SSTs reached almost 20°, which is nearly 3° warmer than for the same period the previous year (fig. 4); temperatures did not drop in late

fall when cooling typically begins. In fact, temperatures remained elevated throughout fall and winter, and thermocline depth reached a maximum between December and January (fig. 3A). In winter 1998, temperatures in the SBB were 1°–2° higher than during the two previous winters (figs. 3A and 4).

Chlorophyll Concentrations

Chlorophyll a concentrations for CalCOFI station 82.47 (see inside back cover for basic station plan) of cruises 9602, 9604, 9608, 9610, 9702, 9704, 9707, 9709, 9802, and 9804 were used to construct figure 3B. Routine CalCOFI procedures include measurements at discrete depths of 0, 1 or 2, 10, 20, 30, 40, 50, 60, 70, 75, 85, 99, 100, 118 or 119, 125, 138 or 139, and 150 m. The original data can be found at www-mlrg.ucsd.edu/calcofi.html. We generated a 45-day by 5-meter data matrix from the original CalCOFI data set by using a linear interpolation algorithm that was chosen to preserve the true data points. The resulting unsmoothed matrix was then contoured, representing the seasonal cycle (fig. 3B).

Temperature (°C)

Chlorophyll (mg m⁻³)
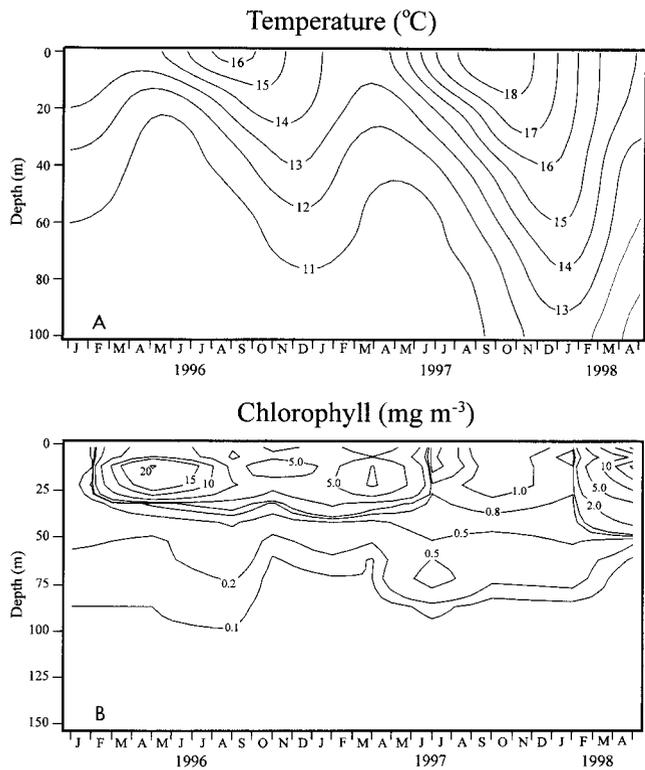
Figure 3. January 1996 to April 1998. A, Upper ocean (0–100 m) temperature at sediment trap location generated from conductivity-temperature-density (CTD) casts. The data set from the CTD casts was then reduced by averaging depth bins of 2 meters and transformed into a 15-day by 2-meter data matrix. The resulting matrix underwent two smoothing passes and was then contoured. B, Time/depth plot of chlorophyll a concentration (measured quarterly) at CalCOFI station 82.47 in Santa Barbara Basin. A 45-day by 5-meter data matrix was generated from the original CalCOFI data set with a linear interpolation algorithm, and the resulting unsmoothed matrix was then contoured.

Chlorophyll a concentrations typically indicate the seasonal cycle in the SBB, with high values in spring and early summer (strong winds-upwelling-high productivity) and low concentrations in fall and winter (weak winds-diminished upwelling-decreased productivity). This general pattern was also observed during the study period (1996–98) except for fall 1996, when chlorophyll a concentrations were particularly high in the basin (fig. 3B) and in the coastal region near Point Conception (Schwing et al. 1997). These high levels may have been related to a pattern of relatively high mesoscale activity in the California Current, and elevated upwelling north of Point Conception in October (Schwing et al. 1997). Despite the strong 1997–98 El Niño, the concentration and spatial distribution of chlorophyll in spring 1998 was similar to that observed in previous springs (fig. 3B; Venrick 1998).

Bulk-Sediment Flux

Bulk-sediment flux data at the SBB mooring are summarized in figure 4, and include daily fluxes of organic
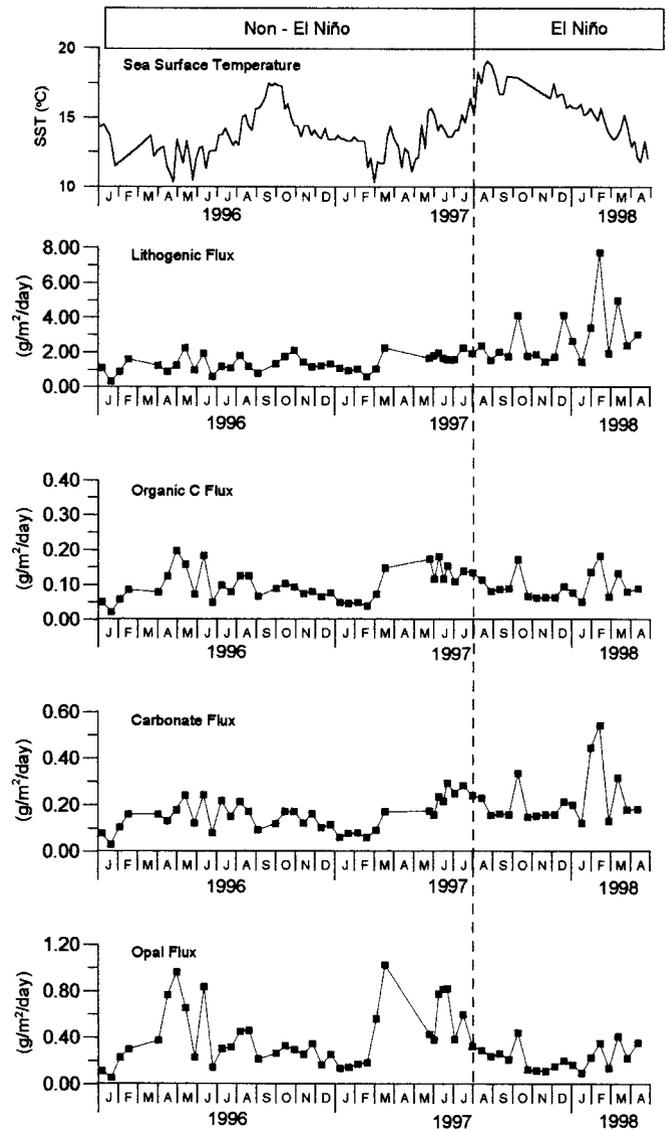
Figure 4. Daily sea-surface temperature records from a NOAA buoy (U.S. marine buoy #46054) located close to the sediment trap mooring, and fluxes of lithogenic particles, organic carbon, carbonate and biogenic silica (opal) measured in two-week-long samples from Santa Barbara Basin, from January 1996 to April 1998, emphasizing non–El Niño (1996 through mid-1997) and El Niño (mid-1997 through spring 1998) conditions. All fluxes are in g/m²/day.

carbon, calcium carbonate, biogenic silica, and lithogenic particles, as determined by the methods of Thunell et al. (1995). Lithogenic material is the single largest contributor to the total mass flux, typically accounting for 50%–80% of the total. Terrigenous input to our sampling site, as measured by the lithogenic flux, was much higher during the El Niño period (up to 8 g m⁻² d⁻¹ vs. 1–2 g m⁻² d⁻¹ for the non–El Niño period), presumably reflecting higher rainfall, runoff, and downslope transport into the SBB (fig. 4). In fact, December 1997 to February 1998 was a period of exceptionally

intense winter storm activity along the West Coast, especially during February (Lynn et al. 1998). Samples from this period contained large amounts of detritus, clay minerals, pollen grains, plant debris, Chrysophyte cysts, littoral shelf diatoms, and estuarine benthic foraminifers, indicating that a considerable amount of terrigenous material was flushed into the SBB during large storms.

Both biogenic opal and organic carbon fluxes (fig. 4) mirror the normal productivity cycle in that fluxes are high during the spring-summer upwelling period and low during fall and winter. Opaline silica is by far the dominant biogenic sediment produced in SBB, periodically accounting for up to 35% of the total flux (Thunell 1998). Interestingly, when comparing the magnitudes of the opal fluxes measured during the spring upwelling periods, we observe similar values for 1996 and 1997 (> 0.8 g m^{-2} d^{-1}) and lower values for 1998 (< 0.4 g m^{-2} d^{-1}). This would suggest reduced export of silica-bearing organisms as a response to El Niño conditions, as is also evidenced in the fluxes of radiolarians, diatoms, and—to a lesser extent, silicoflagellates (see below; fig. 5).

Organic carbon fluxes almost always account for less than 5% of the total flux (Thunell 1998). However, in the winter of 1998 organic carbon fluxes were unusually high for that time of year (up to 0.15 g m^{-2} d^{-1} compared to values of 0.05 g m^{-2} d^{-1} for the previous winters) and coincided with a February peak in the carbonate flux (mainly derived from foraminifers and coccolithophores) and high abundances of tintinnids of the genus Stenosemella.

Siliceous Microfossil Flux

We observed definite changes in the timing and magnitude of total flux for each siliceous microplankton group, as well as shifts in species composition of the assemblages (figs. 5 and 6). Changes include (1) a 20% drop in the flux of radiolarians for the period late 1997–early 1998 with respect to the 1993–96 average; (2) a substantial drop of an order of magnitude in the flux of diatoms (from ≥10^5 valves m^{-2} d^{-1} in 1996–early 1997 to ca. 10^4 valves m^{-2} d^{-1} in 1998) and an increase in species richness (from 5.4 to 6.5, Margalef [1958] Index) during El Niño conditions; and (3) a lack of the fall-winter peak in silicoflagellate fluxes seen annually from 1993 to 1996 (Lange et al. 1997; Kincaid et al. 2000). Instead, silicoflagellates peaked very briefly in late spring 1997 and then again in January 1998 (with Dictyocha fibula dominating the assemblage).

Diatom and radiolarian species groups associated with El Niño show unusually high percentages of warm-water taxa in coincidence with maximum temperatures in the water column (figs. 3A and 6). The average percentage of warm-water radiolarians was 2.5 times higher during
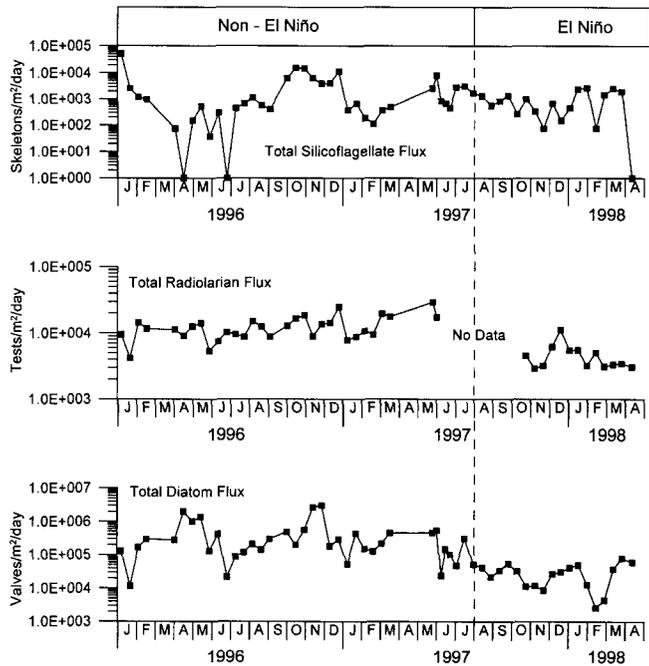
Figure 5. Fluxes of silicoflagellates, radiolarians, and diatoms (in numbers of individuals/m²/day) from January 1996 to April 1998, emphasizing non–El Niño (1996 through mid-1997) and El Niño (mid-1997 through spring 1998) conditions.

this period when compared to 1996. Additionally, there was an unusually high contribution (>20%) in late summer and fall 1997 of diatom taxa representative of warm offshore waters (e.g., Asterolampra marylandica, Bacteriastrum comosum, Hemiaulus hauckii) and an atypical presence during fall 1997 and winter 1998 of warm-water radiolarian species Pterocorys hertwigii, Didymocyrtis tetrathalamus, and Dictyocoryne truncatum. This further reflects the effects of the 1997–98 El Niño on the coastal ecosystem of the SBB (fig. 6).

In contrast to the increase in warm-water indicators, there was nearly a 50% drop in the relative contribution of the siliceous microorganisms indicative of spring upwelling conditions in the SBB (Lange et al. 1997); for example, the diatom Chaetoceros radicans (resting spores and vegetative cells) and the radiolarians Lithomelissa setosa and Spongopyle osculosa (fig. 6).

Finally, the contribution of littoral, non-planktonic diatoms such as Amphitetras antediluviana, Aulacodiscus kittonii, and Biddulphia biddulphiana increased dramatically in November 1997 and February 1998 (fig. 6), probably reflecting the intense storm activity, high precipitation, runoff, and lateral advection into the central basin during the El Niño period.

DISCUSSION AND CONCLUSIONS

The complicated hydrography of the SBB and the seasonal changes that occur as a result of the strong
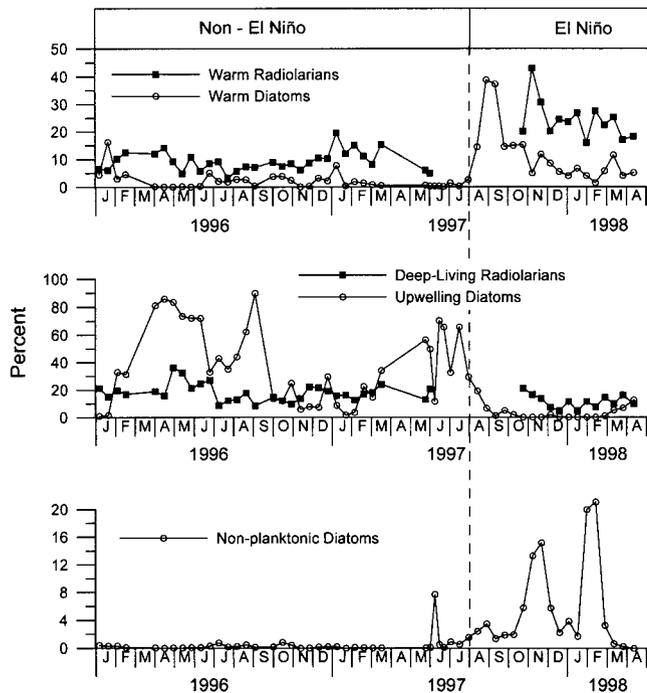
Figure 6.   Relative contribution (in percentage of total assemblage) of selected diatom and radiolarian species representative of upwelling conditions, warm oceanic waters, and littoral influence advected from the shelf, from January 1996 to April 1998, emphasizing non–El Niño and El Niño conditions.

spring–early summer winds and the weak, variable winter winds make it a region of high climatic variability. The production and flux of biogenic material, and the diverse species composition of the microplankton reflect this seasonal variability, which has been studied in a few time-series experiments (Thunell et al. 1995; Lange et al. 1997; Thunell 1998; Kincaid et al. 2000). Added to this is the rainfall regime of the southern California coast, which accounts for terrigenous components carried by river runoff in the winter months and subsequent downslope movement and transport at depth of detrital material to the center of the basin. Overlying this repeatable seasonal pattern, the intermittent El Niño condition, which occurs at intervals of 3 to 7 years, disrupts the annual cycle. In 1997 a major El Niño developed in the western and central Pacific (see Chavez et al. 1999, and references therein), and by summer 1997 the coastal waters of California were strongly influenced by El Niño conditions (Lynn et al. 1998). The year 1998 was marked by a dramatic transition from El Niño conditions in early 1998 to cool-water La Niña conditions by late 1998 (e.g., Chavez et al. 1999; Hayward et al. 1999).

Since 1993 we have been carrying out a sediment-trapping experiment in the Santa Barbara Basin, offshore of California, which enabled us to document the dramatic biogeochemical perturbations associated with the 1997–98 El Niño event. Lange et al. (1997) showed that

fluxes of diatoms, radiolarians, and silicoflagellates in the SBB exhibit a distinct seasonal pattern, with marked production maxima at different times of the year reflecting a succession of these microplankton groups: radiolarians in late summer and fall, silicoflagellates in winter, and diatoms in spring (table 1). This "normal" scenario was altered during the 1997–98 El Niño event. In the nearly 5 years of sediment trap data, from August 1993 to April 1998, the lowest diatom fluxes ever measured (2.6 and 4.5 x 10^3 valves m^{-2} d^{-1}) occurred at the height of El Niño in February 1998 (table 1). The flux of radiolarians dropped by 20% compared to the 1993–96 mean, and overall biogenic silica fluxes of non–El Niño conditions in 1996 and early 1997 (average = 0.42 g m^{-2} d^{-1}) were much reduced compared to El Niño conditions of late 1997–early 1998 (average = 0.23 g m^{-2} d^{-1}).

In addition to lowered total group fluxes (fig. 5), major changes in species composition coincided with the El Niño event (fig. 6). There was an increase in the relative abundance of eastern tropical Pacific and central gyre species, and a decrease in the deep-living radiolarians and in diatoms representative of upwelling conditions (Lange 1988; Lange et al. 1997; Weinheimer and Cayan 1997). These changes reflect warm-water incursions into the SBB and diminished upwelling associated with El Niño conditions. The excessive runoff from heavy rains brought high terrestrial discharges (Shipe et al. 2000) and unusually high abundances of benthic diatoms into the basin (fig. 6). Although these diatoms are a normal component of the trapped winter assemblage, their relative contribution never exceeded 7% in previous years (Lange et al. 1997).

The presence of the tintinnid *Stenosemella* sp. in high numbers in February 1998 is noteworthy. It has been demonstrated that members of the genus *Stenosemella* produce arenaceous loricae composed principally of mineral particles of nonbiological origin (with quartz as the principal grain type; Gold and Morales 1976). Our findings can be compared with a similar occurrence in February 1983 during an El Niño period (Reid and Stewart 1989). This was noted within 2–3 km of the coast in the San Diego area. Water temperature in 1983 was also higher than normal, and there was a decrease in total phytoplankton and a higher abundance of warm-water species along the coast. Precipitation was unusually high, and continental runoff, with associated sediment load, increased. It was suggested that this situation enhanced the availability of lithogenic silica particles necessary for the lorica building of these neritic tintinnids (Reid and Stewart 1989). This could also have been the situation in our case, with *Stenosemella* using particles resulting from terrestrial runoff.

Our findings point to reduced biogenic opal export production in the region and increased siliceous

microplankton diversity consistent with the prevailing El Niño conditions, as suggested earlier by Lange et al. (1987, 1990) and Weinheimer and Cayan (1997) after studying the sedimentary imprint of previous El Niño events in the SBB. This reduced export production may be a consequence of lowered biogenic opal productivity in the upper waters. Previous observations on the biological consequences of the 1958 and 1983 El Niño events in the California Current region included substantial declines in phyto- and zooplankton biomass (McGowan et al. 1998), as well as anomalous occurrences of tropical species in the Southern California Bight (see articles in Eppley 1986).

ACKNOWLEDGMENTS

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THE FEEDING HABITS OF SPOTTED SAND BASS (*PARALABRAX MACULATOFASCIATUS*) IN PUNTA BANDA ESTUARY, ENSENADA, BAJA CALIFORNIA, MEXICO

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ABSTRACT

The feeding habits of spotted sand bass (*Paralabrax maculatofasciatus*) and their seasonal changes are described for the Punta Banda Estuary, Baja California (B.C.). Samples were collected monthly from April 1992 to March 1993, yielding 92 specimens ranging from 80 to 330 mm standard length. In the entire survey, decapods, fish, and mollusks were the major food items of spotted sand bass, with total indexes of relative importance (IRI) of 37.2% (1,828), 32.0% (1,572), and 13.4% (658), respectively. Prey groups with high numeric importance were eggs of topsmelt (*Atherinops affinis*) and gammarids. In summer, the decapods had the highest IRI value (6,234), representing 58.4% of total IRI; followed by gammarids (2,255), 21.1% of total; and mollusks (1,234), 11.5% of total. In winter, fishes were the most important item, with 42.3% (1,964) of total IRI, followed by decapods (910), 21.9% of total. Other seasonal changes were the variation in the numeric importance of gammarids (major in summer, minor in winter) and topsmelt eggs (absent in summer, high in winter). The difference in spotted sand bass diet and its seasonal changes probably reflect differences in available prey and the trophic flexibility of the species. The diet of spotted sand bass indicates foraging close to the substrate, frequently in seagrass beds, as indicated by the high occurrence of eelgrass (*Zostera marina*) fragments in gut contents.

INTRODUCTION

In the last decade, spotted sand bass (*Paralabrax maculatofasciatus*) and other serranids have acquired a high economic importance in nearshore and recreational fisheries of Ensenada, B.C., Mexico (Hammann and Rosales-Casián 1990; Rodriguez-Medrano 1993). These fishes live in areas such as bays, estuaries, and harbors (Allen et al. 1995) and, like other fish species, play a significant role in the energetic balance and the structural progression of the marine environment. Therefore, the study of their ecology is important for improving resource management. Studies of spotted sand bass diet help determine trophic relations with other economically im-

portant species, interpret the dynamics of the estuarine environment, and indicate how this species uses the resources of its habitat.

Most studies of spotted sand bass feeding habits have been done along the southern California coast (Feder et al. 1974; Ono 1992; Allen et al. 1995). Only two studies have been made along the Baja California coast, one in Los Angeles Bay (Ferry et al. 1997) and another in Punta Banda Estuary (Navarro-Mendoza 1985). The latter study, which used a small number of stomachs (53), yielded useful but limited information; its data were not analyzed quantitatively. In addition to expanding the information of Navarro-Mendoza and emphasizing quantitative aspects, the study reported here considers seasonal variations in diet.

METHODS

Study Area

The Punta Banda Estuary is located in the North Pacific, off the Baja California Peninsula, in the southern part of Todos Santos Bay, Ensenada, B.C., Mexico (fig. 1). This lagoon covers an area of 21 km^2, has a median depth of 5 m, is characterized by salt marshes (Ibarra-Obando and Poumian-Tapia 1992), and has both muddy and sandy bottoms. During most of the year, evaporation exceeds precipitation, yielding hypersaline conditions; tides are the main avenue of water exchange. The estuary meets true estuarine conditions only during intense winter rains (Acosta-Ruiz and Alvarez-Borrego 1974; Celis-Ceseña and Alvarez-Borrego 1975).

Sampling Methods

The sampling period started in April 1992 and ended in March 1993. Samples were collected with a beam trawl (with a mouth 0.36 m high and 1.70 m wide, and of 3 mm mesh) and an otter trawl (with a mouth 2.5 m high and 7.5 m wide; 19 mm mesh in body and 5 mm in bag end). Five-minute tows were made along the 5 m depth contour at approximately 0.75–1.0 m/sec (1.5–2.0 knots). Four replicate samples were collected each month with each trawl. Once per month, a variable mesh monofilament gill net (50 m long and 2.5 m
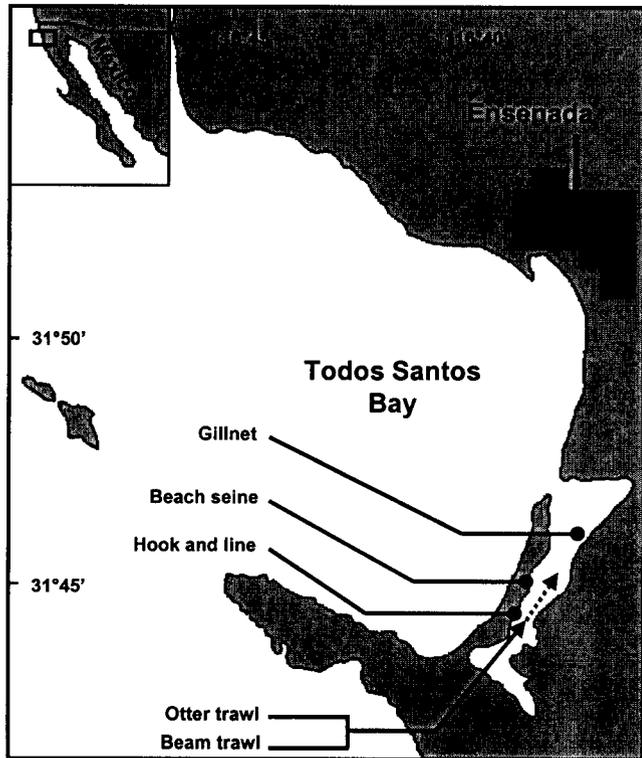
Figure 1. Punta Banda Estuary in Todos Santos Bay, with locations and methods used for collecting spotted sand bass during 1992–93.

high) was fished for 12–14 hours at night (<6 m depth). Hook and line sampling with cut bait or lures was also done after the gill net was recovered. From September to March 1993 only, four replicate samples were collected with a 3 cm mesh beach seine net (33 m long and 3 m high) from depths less than 3 m.

After each monthly sampling, spotted sand bass were identified from the Miller and Lea (1972) key. Each fish was measured (standard and total length) to the nearest millimeter, and weighed (total and somatic weight) to the nearest gram. The stomachs were extracted by cutting the anterior side of the esophagus and pylorus; they were fixed in 10% formaldehyde neutralized with sodium borate.

Seasonal Classification

Spotted sand bass were classified into two seasonal groups based on differences in monthly surface temperature (measured with a bucket thermometer) to test for possible variation in diet. We poststratified the data into two seasonal periods: summer (April–October), with warm temperatures; and winter (November–March), with cold temperatures. We used the analysis of variance (ANOVA) test (Zar 1984) to test for statistical differences between monthly temperatures of the two periods and for differences in average standard lengths of fish between the two seasons.

Stomach Content Analysis

The contents of 92 (34 summer, 58 winter) spotted sand bass stomachs were examined. Each item found was identified to the lowest possible taxon, counted, and weighed (wet weight) to the nearest 0.001 g. After data collection, items were grouped into higher-level taxonomic categories. To determine if the number of stomachs was sufficient to describe the spotted sand bass diet, we determined minimum sample size by plotting the cumulative stomach number (x axis) against the cumulative number of prey groups (y axis). The point at which the curve becomes level is considered the minimum sample size (Smith 1976; Roberts et al. 1984). Relative importance of each type of prey was represented with the index of relative importance (modified from Pinkas et al. 1971):

$$IRI = (\%N + \%W) \star \%F$$

where N = numerical abundance of each prey type
W = wet weight of each prey type
F = frequency of occurrence of each prey type.

Diet difference in prey abundance between seasons (summer, winter) was tested with the G statistic (Crow 1981; Sokal and Rohlf 1981). We estimated feeding intensity index in summer and winter by dividing the total wet weight of food by the somatic weight expressed in percentage. We used a Mann-Whitney ANOVA (Zar 1984) to test for statistical differences.

RESULTS

The mean surface temperature throughout the year was 18.84°C (±2.01 SD). The maximum monthly temperature was 22.07° (±0.38 SD) in September, corresponding to summer (April to October), and the minimum monthly temperature was 15.90° (±0.10 SD) in December, corresponding to winter (November to March). The mean surface temperature during summer was 19.91° (±1.38 SD), and 16.63° (±1.09 SD) in winter (fig. 2). Seasonal monthly temperatures were statistically different (ANOVA, $p < 0.05$).

The mean standard length (SL) of all spotted sand bass collected was 249.47 mm (±51.04 SD). The mean standard length was 262.20 mm (±34.31 SD) in summer and 244.61 mm (±55.49 SD) in winter (fig. 3). Seasonal means were significantly different (ANOVA, $p < 0.05$). Fish smaller than 200 mm SL were not collected in winter.

The cumulative prey curves constructed from annual, summer, and winter data indicated that sufficient numbers of stomachs were examined to describe the spotted sand bass diet in the Punta Banda Estuary (fig. 4).

Fourteen major taxonomic prey groups were identified in the stomachs: eelgrass fragments (*Zostera marina*);
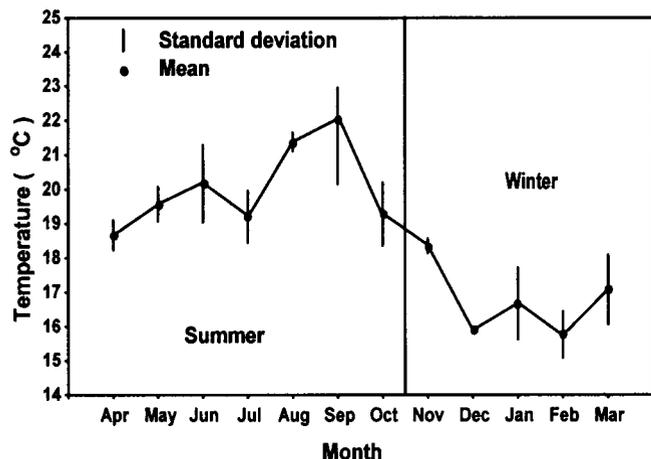
Figure 2. Monthly surface temperature variation during study period (April 1992–March 1993).

Figure 4. Cumulative numbers of prey taxa with increasing numbers of spotted sand bass stomachs. Arrows indicate the minimum number of stomachs.

Figure 3. Length-frequency distribution of spotted sand bass (*Paralabrax maculatofasciatus*) from Punta Banda Estuary.

sponges; hydrozoans; nemerteans; polychaetes; mollusks; decapods; gammarids; caprellids; isopods; echinoderms; ascidians; fishes; and topsmelt (*Aterinops affinis*) eggs.

Decapods and fishes were the most important food items in the annual diet of spotted sand bass, and had the highest values: 37.2% of total IRI (IRI = 1,828) for decapods, and 32.0% (IRI = 1,572) for fishes. Mollusks ranked third, with 13.4% of IRI (IRI = 658; fig. 5).

The highest percentage by weight was attributed to fishes, with 40.7% of annual diet values. The eggs of topsmelt dominated by percentage of numbers (67.5%), followed by gammarids, with 16.7%. The most frequently occurring items were the decapods (51.9%), fragments of eelgrass (45.4%), and mollusks (44.1%).

The principal species of decapods were yellow shore crab (*Hemigrapsus oregonensis*); arched swimming crab (*Callinectes arcuatus*); and tuberculate pear crab (*Pyromaia tuberculata*). Principal food fishes were topsmelt (*Atherinops*

affinis); silversides (atherinidae); and gobies (gobiidae). Important species of mollusks were California jacknife (*Tagelus californicus*); rosy jacknife (*Solen rosaceus*); and California bubble (*Bulla gouldiana*; see Appendix).

In the summer season, decapods were the dominant food item (IRI = 6,234), representing 58.4% of total IRI. Gammarids were second, with an IRI of 2,255, representing 21.1% of the total. Mollusks placed third, with an IRI of 1,234 (11.5%), and fishes ranked fourth, with an IRI of 439 (4.1%; fig 5). Decapods represented the highest percentage of weight (64.0%) and frequency of occurrence (84.2%). Gammarids constituted the highest numeric percentage (70.7%). Mollusks and fragments of eelgrass occurred in almost 52.6% and 47.3% of all stomachs. The most important decapods were the tuberculate pear crab and the yellow shore crab. *Corophium acherusicum* was the most important species of gammarid (Appendix).

In winter, fishes dominated the diet of spotted sand bass, with 47.31% of total IRI (IRI = 1,964). Decapods and mollusks ranked second and third, with IRIs of 910 (16.5%) and 494 (11.9%; fig 5). In numbers, fishes contributed a low percentage (2.4%), but were the highest in percentage of weight (51.8%). The main species contributing to the weight were topsmelt and silversides (Appendix). Topsmelt eggs dominated the numerical percentage (86.5%). The most important decapod species were the yellow shore crab and the arched swimming crab. The California bubble and the bivalve Pacific eggcockle (*Laevicardium substriatum*) were the most important prey species in the mollusk category.

In summary, decapods and fishes were the most important groups in the annual diet of the spotted sand bass. The main seasonal differences were the dominance of decapods in summer, and of fishes in winter. In summer, the gammarids occupied the highest numerical
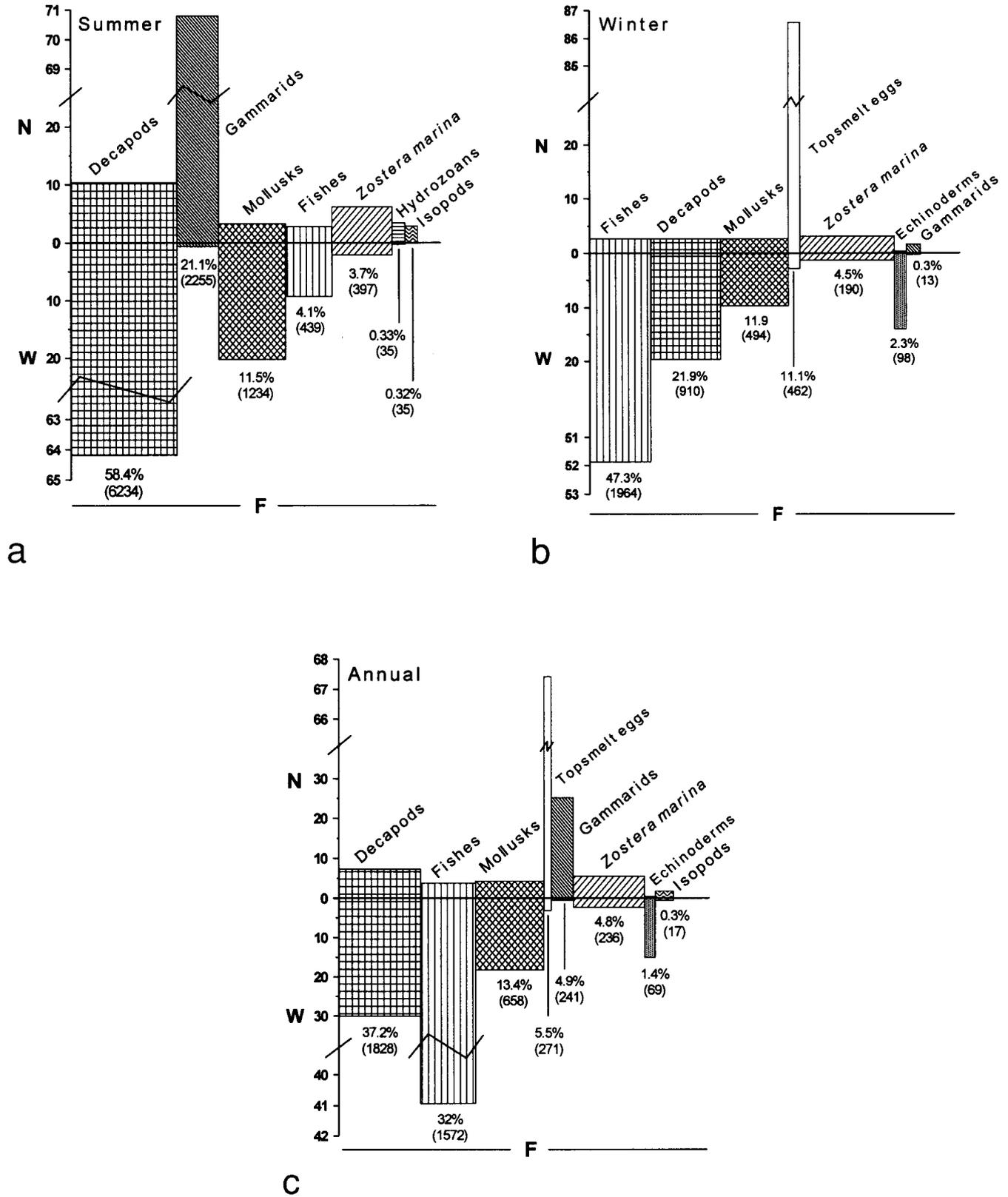
Figure 5. Relative importance by percent number (*N*), percent weight (*W*), and percent frequency of occurrence (*F*) of principal prey of spotted sand bass (*Paralabrax maculatofasciatus*) from Punta Banda Estuary during the 1992–93 annual survey (*a*), the summer survey (*b*), and the winter survey (*c*). Below bars: IRI percentage and IRI value (parentheses).

percentage, but were replaced by topsmelt eggs in winter. The frequency of occurrence of eelgrass fragments in the stomach contents was high in the annual survey; by season, it increased from summer to winter. Significant differences in the diet were determined in the total numerical abundance of groups between winter and summer (X^2, $p < 0.05$). The difference can be attributed to the high variation in abundance of topsmelt eggs between seasons. Other groups that contributed to the seasonal difference were gammarids, decapods, and caprellids.

The mean feeding intensity of spotted sand bass was lower in summer (1.07% ± 1.0 SD) than in winter (1.28% ± 2.42 SD). No significant differences in seasonal feeding intensity were observed. There were more empty stomachs in summer (20.8%) than in winter (7.9%).

DISCUSSION

Decapods and fishes dominated the diet of spotted sand bass for the entire survey, with medium-high occurrence and a high weight contribution. Other important foods were mollusks, topsmelt eggs, gammarids, and fragments of eelgrass; there were eight more groups of minor relative importance.

Ono (1992) noted small fishes as the highest-ranked food item, followed by cephalopods and crustaceans. Ferry et al. (1997) listed fishes, crustaceans, echinoderms, and mollusks as the main food items for spotted sand bass from Los Angeles Bay in the Gulf of California. Our results show that fish was an important food for spotted sand bass in Punta Banda Estuary only during winter, with high weight contribution but low occurrence.

On the other hand, Allen et al. (1995) mentioned that Ono's characterization of spotted sand bass diet seemed to be in error, since they found that brachyurans, crabs, and clams dominated the diet. Feder et al. (1974) listed possible food items for spotted sand bass, citing crabs and small fishes as important prey. In Punta Banda Estuary, another study (Navarro-Mendoza 1985) indicated that spotted sand bass fed basically on fishes, crustaceans, and mollusks; his findings were similar to those of the study reported here.

Included among the items eaten by spotted sand bass were the siphons and whole bodies of jacknife clams. Allen et al. (1995) posed the question of how spotted sand bass managed to capture these clams, since most of the time they are buried 15–18 cm in the mud. It may be that sometimes during the day (possibly at daybreak) the clam is close to the sediment surface, so it can be pulled out of sediment when the fish bites the siphon. The fact that our samples were obtained during morning supports this assertion.

Spotted sand bass food items differed between seasons. In summer, decapods, gammarids, and mollusks were important; in winter the most important prey were fish, decapods, and topsmelt eggs. Seasonal changes in feeding have been observed in the kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*), which have a feeding morphology similar to that of spotted sand bass (Quast 1968; Love and Ebeling 1978; Mendoza-Carranza 1995).

The different characterizations of spotted sand bass diet, and seasonal changes in it probably reflect differences in available prey over time and space, as well as the trophic flexibility of the species. Spotted sand bass are opportunistic predators, capable of feeding on a wide variety of prey (more than 60 species). Physical and chemical conditions influence the abundance and availability of prey, in this case the general temperature increase attributed to ENSO (El Niño–Southern Oscillation) by Hayward (1993). On the other hand, eelgrass fragments in the stomach contents indicate this species' close relation to eelgrass habitat. Eelgrass beds contain large quantities of small and medium size invertebrates that are eaten by many fishes, and in this case probably explain the large number of prey species.

Although prey is diverse, the main items in the diet of spotted sand bass in Punta Banda Estuary are associated with the benthos and suprabenthos. Muddy, muddy-sandy, and sandy bottoms as well as eelgrass beds are important components of this habitat, where spotted sand bass can feed on a great diversity of prey.

ACKNOWLEDGMENTS

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APPENDIX
Importance of Annual and Seasonal Prey Species in the Diet of Spotted Sand Bass in Punta Banda Estuary, Ensenada, B.C., Mexico

Taxon	Prey	Annual				Summer				Winter			
		%Nᵃ	%Wᵇ	%Fᶜ	%IRIᵈ	%N	%W	%F	%IRI	%N	%W	%F	%IRI
Plantae	Zostera marina	3.77	1.50	45.46	4.8018	6.2	2.18	47.36	3.71	3.08	1.15	44.83	4.56
Porifera	Porifera UIᵉ	0.03	0.01	1.3	0.0012	—	—	—	—	0.04	0.01	1.72	0.002
Hydrozoa		0.14	0.99	5.19	0.1144	0.32	3.03	10.52	0.33	0.09	0.21	3.45	0.02
	Obelia sp.	0.04	0.003	1.3	0.004	0.16	0.01	5.26	0.04	—	—	—	—
	Sertularella turgida	0.11	0.99	3.9	0.34	0.16	3.02	5.26	0.78	0.09	0.21	3.45	0.07
Nemertea	Anopla	0.21	0.22	6.49	0.05	—	—	—	—	0.27	0.27	8.62	0.11
Mollusca		2.61	12.3	44.15	13.4	3.35	20.11	52.63	11.56	2.42	9.54	41.37	11.91
Gastropoda	Prosobranchia UI	0.12	0.05	1.3	0.02	0.64	0.17	5.26	0.2	—	—	—	—
	Opisthobranchia UI	0.04	0.03	1.3	0.01	0.16	0.11	5.26	0.07	—	—	—	—
	Nudibranchia UI	0.51	0.55	3.89	0.34	—	—	—	—	0.71	0.60	5.17	0.51
	Bulla gouldiana	0.32	4.29	12.48	4.83	0.64	6.39	10.53	3.43	0.31	3.40	12.07	3.22
	Aplysia californica	0.03	0.32	1.3	0.04	—	—	—	—	0.04	0.31	1.72	0.05
	Lacunidae UI	0.07	0.03	2.6	0.02	—	—	—	—	0.09	0.04	3.45	0.03
	Crepidula sp.	0.03	0.02	1.3	0.00	—	—	—	—	0.04	0.02	1.72	0.01
	Astraea undosa	0.03	0.03	1.3	0.01	—	—	—	—	0.04	0.04	1.72	0.01
Bivalvia	Pectenidae UI	0.04	0.03	1.3	0.01	0.16	0.11	5.26	0.07	0.04	1.12	1.72	0.15
	Tagelus californicus	0.1	1.58	3.89	0.58	0.32	3	10.53	1.62	0.04	1.12	1.72	0.15
	Solen rosaceus	0.11	1.43	3.90	0.48	0.16	3.46	5.26	0.88	0.09	0.52	3.45	0.17
	Lasaea sp.	0.04	0.16	1.3	0.02	0.16	0.57	5.26	0.18	—	—	—	—
	Laevicardium substriatum	0.62	2.02	9.09	1.99	—	—	—	—	0.80	2.2	12.07	2.99
	Bivalve remains	0.35	1.52	11.69	2.18	1.11	6.3	26.32	9.04	0.22	0.17	6.90	0.24
Polychaeta	Sabellariidae UI	0.03	0.06	1.3	0.002	—	—	—	—	0.04	0.07	1.72	0.004
Decapoda		4.08	31.11	51.94	37.24	10.01	64.02	84.21	58.41	2.41	19.59	41.37	21.92
Caridea	Crustacea caridea	0.07	0.82	2.6	0.15	0.32	2.43	10.53	1.34	—	—	—	—
	Hippolite californiensis	0.14	0.23	5.19	0.09	0.48	0.19	15.79	0.49	0.04	0.04	1.72	0.01
	Palaemonella holmesi	0.04	0.20	1.3	0.01	0.32	0.18	5.26	0.12	—	—	—	—
	Alpheus sp.	0.14	0.54	3.89	0.17	—	—	—	—	0.18	0.50	5.17	0.25
Thalassinidea	Callianasa sp.	0.03	0.17	1.3	0.005	—	—	—	—	0.04	0.02	1.72	0.01
	C. californiensis	0.10	0.93	2.6	0.18	—	—	—	—	0.13	1.00	3.45	0.27
Anomura	Isocheles pilosus	0.04	0.59	1.3	0.05	0.16	1.61	5.26	0.43	—	—	—	—
	Pagurus sp.	0.07	0.53	1.3	0.05	—	—	—	—	0.09	0.48	1.72	0.07
	Pagurus granosimanus	0.03	0.30	1.3	0.02	—	—	—	—	0.04	0.20	1.72	0.03

APPENDIX (continued)
Importance of Annual and Seasonal Prey Species in the Diet of Spotted Sand Bass in Punta Banda Estuary, Ensenada, B.C., Mexico

Taxon	Prey	Annual				Summer				Winter			
		%N[a]	%W[b]	%F[c]	%IRI[d]	%N	%W	%F	%IRI	%N	%W	%F	%IRI
Decapoda (continued)													
Brachyura	Portunus xantusii	0.04	1.37	1.3	0.13	0.32	4.46	5.26	1.17	—	—	—	—
	Callinectes arcuatus	0.18	6.26	5.19	2.59	0.32	5.46	5.26	1.41	0.18	5.89	5.17	2.20
	Pyromaia tuberculata	0.34	2.48	7.79	1.66	1.43	8.4	26.32	12	0.04	0.04	1.72	0.01
	Pugettia sp.	0.04	0.20	1.3	0.01	0.16	0.17	5.26	0.08	—	—	—	—
	Pachigrapsus crassipes	0.20	3.13	2.59	0.66	0.79	10.04	5.26	2.64	0.04	0.30	1.72	0.04
	Hemigrapsus oregonensis	0.90	1.83	16.88	3.47	0.95	5.3	15.79	4.58	0.89	7.55	17.24	10.21
	H. nudus	0.07	0.62	2.6	0.11	—	—	—	—	0.09	0.60	3.45	0.17
	Lophopanopeus sp.	0.07	0.26	1.3	0.02	0.32	0.4	5.26	0.18	—	—	—	—
	L. bellus bellus	0.11	1.24	3.9	0.37	0.48	3.99	15.79	3.27	—	—	—	—
	L. leucomanus leucomanus	0.04	0.28	1.3	0.02	0.16	0.46	5.26	0.15	—	—	—	—
	L. leucomanus heathi	0.07	0.43	1.3	0.04	0.32	1.03	5.26	0.33	—	—	—	—
	Cancer sp.	0.24	1.32	6.49	0.73	0.64	2.96	10.53	1.76	0.13	0.46	5.17	0.22
	C. antennarius	0.03	0.51	1.3	0.04	—	—	—	—	0.04	0.46	1.72	0.06
	C. gracilis	0.03	0.78	1.3	0.07	—	—	—	—	0.04	0.80	1.72	0.10
	C. anthonyi	0.07	0.46	1.3	0.05	—	—	—	—	0.09	0.48	1.72	0.07
	Pinnixia barnharti	0.04	0.53	1.3	0.04	0.16	1.42	5.26	0.39	—	—	—	—
	Brachyuran remains	0.97	5.10	9.09	4.18	2.68	15.52	10.53	9.14	0.35	0.76	8.62	0.65
Gammaridea		16.71	0.19	14.28	4.92	70.75	0.67	31.57	21.13	1.52	0.03	8.62	0.32
	Gammaridea sp. 1	0.56	0.02	7.79	0.36	0.95	0.11	21.05	1.03	0.45	0.01	3.45	0.11
	Gammaridea sp. 2	0.49	0.01	3.9	0.15	0.48	0.04	5.26	0.12	0.49	0.01	3.45	0.12
	Gammaridea sp. 3	0.04	0.0003	1.3	0.004	0.16	0.001	5.26	0.04	—	—	—	—
	Gammaridea sp. 4	0.07	0.001	1.3	0.01	0.32	0.002	5.26	0.08	—	—	—	—
	Corophium sp.	0.17	0.003	1.3	0.02	0.79	0.01	5.26	0.2	—	—	—	—
	C. acherusicum	14.89	0.15	7.79	9.33	67.41	0.5	5.26	16.57	0.13	0.003	1.72	0.02
	Erichtonius sp.	0.04	0.001	1.3	0.004	0.16	0.002	5.26	0.04	—	—	—	—
	Hyalidae UI	0.04	0.0003	1.3	0.004	0.16	0.001	5.26	0.04	—	—	—	—
	Hyale sp.	0.07	0.001	1.3	0.007	0.32	0.002	5.26	0.08	—	—	—	—
	Gammaridean remains	0.35	0.01	1.3	0.04	—	—	—	—	0.45	0.01	1.72	0.06
Caprellidea	Caprella sp.	0.94	0.09	6.49	0.13	3.65	0.24	10.53	0.38	0.18	0.03	5.17	0.02
Isopoda		1.26	0.25	11.68	0.35	2.86	0.48	10.53	0.32	0.80	0.16	12.06	0.28
	Paracerceis cordata	0.49	0.10	7.79	0.37	—	—	—	—	0.62	0.14	10.34	0.55
	Cirolana harfordi	0.77	0.15	3.89	0.28	2.86	0.48	10.53	1.63	0.18	0.02	1.72	0.02
Echinodermata		0.21	10.96	6.49	1.39	0.16	0.03	5.26	0.01	0.22	13.98	6.89	2.35
Ophuiroidea	Amphiodia sp.	0.07	0.02	2.59	0.02	0.16	0.03	5.26	0.05	0.04	0.02	1.72	0.01
Holothuroidea	Holothuroidea UI	0.14	10.93	3.89	3.43	—	—	—	—	0.18	13.96	5.17	5.13
Ascidiacea	Ascidiacea UI	0.03	0.21	1.30	0.006	—	—	—	—	0.04	0.26	1.72	0.01
Actinopterygii		2.5	43.31	36.36	32.06	2.71	9.22	36.84	4.11	2.41	51.84	36.2	47.31
	Syngnathidae UI	0.04	0.02	1.3	0.005	0.16	0.06	5.26	0.05	—	—	—	—
	Sciaenidae UI	0.04	0.003	1.3	0.004	0.16	0.01	5.26	0.04	—	—	—	—
	Labridae UI	0.04	0.003	1.3	0.004	0.16	0.01	5.26	0.04	—	—	—	—
	Gobiidae UI	0.38	0.76	6.49	0.59	1.43	1.38	15.79	2.06	0.09	0.48	3.45	0.14
	Atherinidae UI	0.17	6.79	3.89	2.15	—	—	—	—	0.22	8.67	5.17	3.22
	Atherinops affinis	0.17	28.88	3.89	8.99	—	—	—	—	0.22	36.89	5.17	13.46
	Paralabrax nebulifer	0.04	1.23	1.3	0.13	0.16	4.49	5.26	1.13	—	—	—	—
	Fundulus parvipinnis	0.07	1.17	2.59	0.26	0.16	3.26	5.26	0.83	0.04	0.36	1.72	0.05
	Ilypnus gilberti	0.17	0.19	6.49	0.18	—	—	—	—	0.22	0.24	8.62	0.28
	Hypsoblennius sp.	0.03	0.60	1.3	0.06	—	—	—	—	0.04	0.76	1.72	0.10
	Fish remains	1.32	3.47	16.88	6.44	0.48	0.01	5.26	0.12	1.58	4.44	20.69	8.70
	Atherinops affinis eggs	67.56	2.23	3.89	21.60	—	—	—	—	86.46	2.85	5.17	11.12

[a] %N = numeric percentage
[b] %W = weight percentage
[c] %F = frequency of occurrence percentage
[d] %IRI = percentage of index of relative importance
[e] UI = unidentified species

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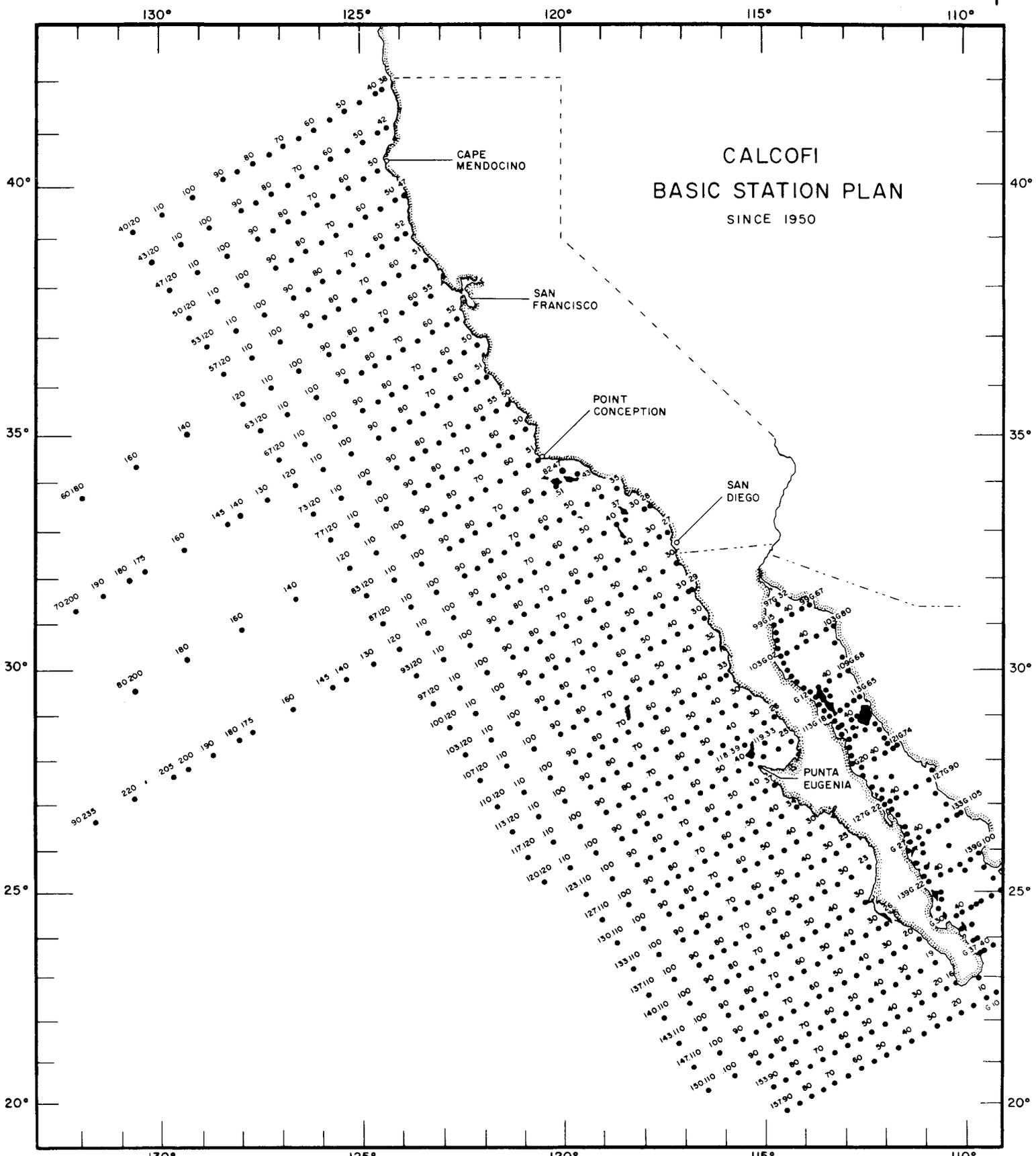
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