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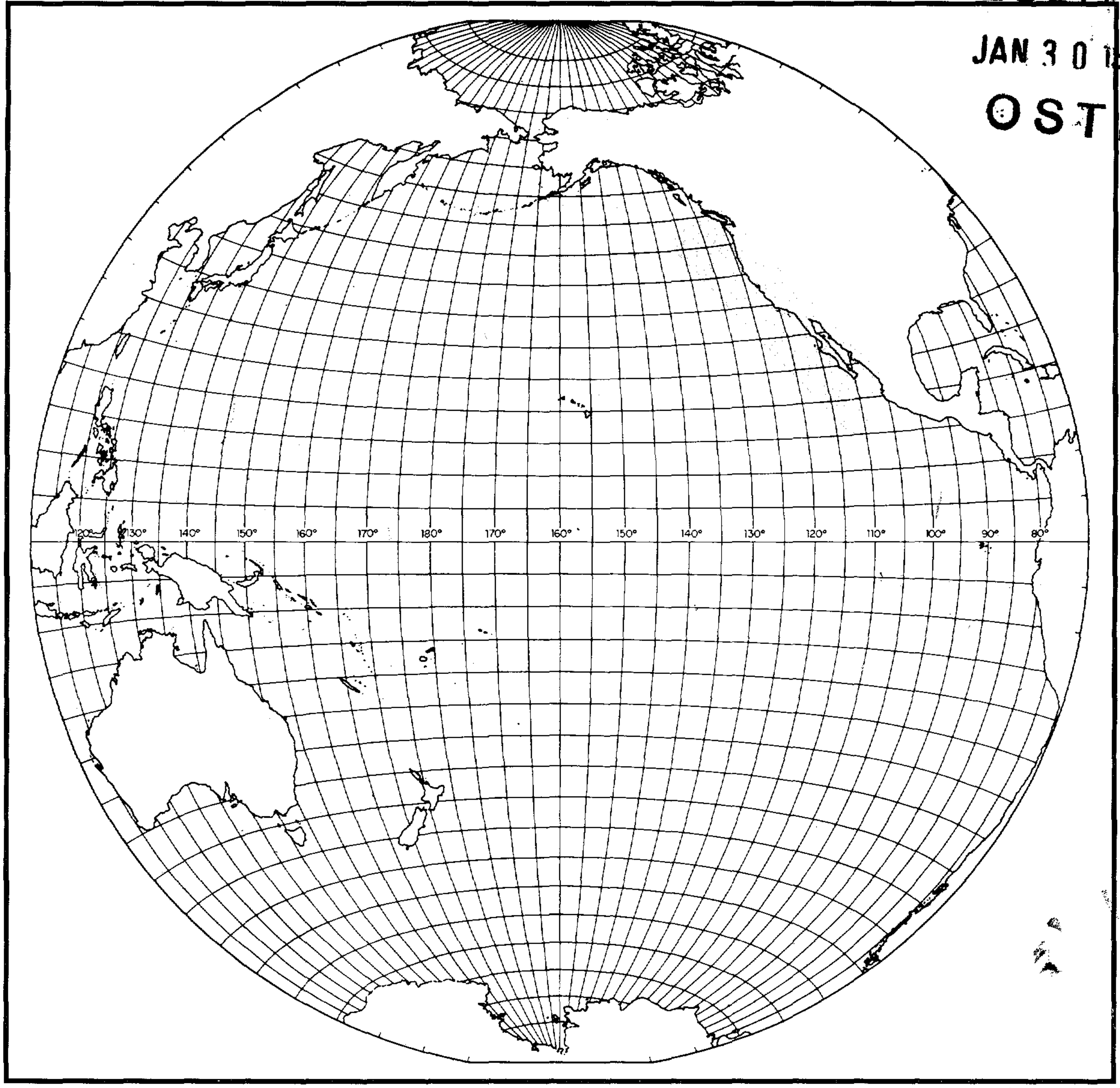

California Cooperative Oceanic Fisheries Investigations
Reports

VOLUME 36
OCTOBER 1995

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CALIFORNIA
COOPERATIVE
OCEANIC
FISHERIES
INVESTIGATIONS

Reports

VOLUME 36
January 1 to December 31, 1994

Cooperating Agencies:

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

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Published October 1995, La Jolla, California
ISSN 0575-3317

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

CalCOFI has now completed 45 years of sampling physical, chemical, and biological variables in the California Current. With each passing year the databases become larger, and conclusions that can be made about the environment and its inhabitants become more robust (cf. Mantyla et al. and Cisneros-Mata et al., this volume). At the same time, we learn more about sampling design and the importance of consistent and long-term sampling (cf. Ohman and Smith, this volume). More data and better understanding of the physics and chemistry of the California Current, and their effect on the food chain, make it possible to view current oceanographic and biological conditions in the context of the long term (cf. Sakuma and Ralston; Mullin; VenTresca et al., this volume).

Physical, chemical, and biological measurements taken during 1994 and early 1995 on CalCOFI cruises have indicated a return to "normal" conditions after anomalous conditions that dominated the two preceding years. Electronic gathering and evaluation of data have permitted increasingly prompt assessment of the state of the California Current system off southern California, relative to the long-term mean (cf. Hayward et al., this volume). Individual research projects, complementing long-term, standard measurements, have continued to provide additional understanding of the processes in the system, and new and useful time series have been developed (e.g., pelagic bird studies by R. Veit of the University of Washington).

Generating long time series of data, a science in which CalCOFI excels, requires not only persistence and continuity, but also the infusion of new ideas to maintain its vitality. We were fortunate to recruit into the Scripps Institution of Oceanography's team a group of five postdoctoral fellows; one is funded by the Mellon Foundation, another by the NOAA/SIO Joint Institute for Marine Observations, two by other extramural grants, and one from departmental funds of the Marine Life Research Group. California Department of Fish and Game reassigned four of its staff to La Jolla to form the California Stock Assessment and Fisheries Evaluation unit (CalSAFE) in collaboration with NMFS. These scientists are located at the Southwest Fisheries Science Center (NMFS, NOAA), adjacent to the facilities of the Scripps Institution of Oceanography at UC San Diego. CalSAFE biologists work cooperatively with NMFS fishery scientists and SIO researchers to investigate sport and commercial fish populations and other resources. CalSAFE makes the cooperative relationship between the two agencies, which has flourished for decades, more formal and more effective, and facilitates discussion and interaction with SIO personnel.

NMFS, CDFG, and Mexican governmental agencies collaborated in sardine surveys carried out in 1994. Using results from the survey, CalSAFE biologists estimated the biomass of the Pacific sardine to be approximately 350,000 MT. A harvest limit of 54,645 MT was recommended for U.S. fisheries, based on the estimated biomass. Scientific papers from the collaborative study will be presented at the 1995 CalCOFI Conference and published in the 1996 *CalCOFI Reports.*

The SWFSC has developed statistical models that evaluate how spawning biomass and environmental factors associated with warm sea-surface temperatures affect Pacific sardine recruitment. For decades it has been hypothesized that environmental conditions related to warmer water enhance sardine reproductive success, but that total recruitment also depends on the amount of spawning biomass. The work builds a bridge between the two primary hypotheses that originally attempted to account for the collapse of the sardine fishery.

The biomass of Pacific mackerel in the California Current has declined precipitously during recent years, to about 60,000 MT in 1994. Several sources of data, including U.S. and Mexican landing statistics, aerial observations, and ichthyoplankton surveys, indicate declining abundances compared to the early 1980s. Northern anchovy has also declined to about 130,000 MT.

The CalCOFI editorial board was pleased to publish, in late 1994, the second of two CalCOFI atlases that summarize the distribution and abundance of fish larvae collected on CalCOFI surveys from 1951 to 1984. These atlases (31 and 32) describe the seasonal, interannual, and areal distribution and abundance of all species of fish eggs and larvae identified in the CalCOFI time series. As the fruit of a joint project between the Minerals Management Service and NMFS, CalCOFI will publish, in 1995, *Atlas 33*, which will serve as a guide to the identification of the eggs and larvae of some 500 species of fishes from the California Current.

We were saddened to lose during 1994, in a sailing accident, Kenneth Plummer, who had served the Scripps Institution of Oceanography for many years as an analyst of CalCOFI data.

The Committee is very appreciative of the work of the reviewers for this volume: Larry Allen, Dan Anderson, Pablo Arenas, Kevin Bailey, Barney Balch, Tom Barnes, Patricio Bernal, George Boehlert, John Butler, Gregor Caillet, Dan Cayan, Martin Dorn, Richard Eppley, Walterio Garcia Franaco, Guillermo Gomez, Don Gunderson, Gregory Hammann, George Hemingway, Adriana Huyer, Larry Jacobson, Sharon Kramer, Ralph Larson, Michael Laurs, Bob Lavenberg, Bill Lenarz, Alec MacCall, Arnold Mantyla, Alan Mearns, Geoff Moser, Richard Parrish, Steve Ralston, Leslie Rosenfeld, Keith Sakuma, Paul Smith, Gail Theilacker, Al Tyler, Peter Wiebe, and Mary Yoklavich. The reviewers were conscientious in their work, contributing their time and energies wholeheartedly for the good of our profession. Editor Julie Olfe has once again shepherded the authors and manuscripts to produce a volume of excellent quality, within budget, and on time.

The officers and crews of the R/V *Mako*, NOAA Ship *David Starr Jordan*, and R/V *New Horizon* contributed greatly to the success of data collection at sea, for which we are deeply grateful.

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1994

CALIFORNIA DEPARTMENT OF FISH AND GAME
Marine Resources Division
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Total annual landings of fishes, crustaceans, echinoderms, and mollusks in California increased by 4% from 1993, to 149,596 metric tons (MT). The ex-vessel economic value of California's 1994 commercial landings rose 17% from the prior year's level, to $149.5 million.

Pelagic wetfish landings increased 12% from 1993, but the increase was mostly attributable to a 31% increase in market squid landings; Pacific sardine, Pacific mackerel, and Pacific herring, however, registered declines (table 1). The 1994 statewide market squid landings of 55,769 MT represent a new record for this species.

Groundfish landings continued an eleven-year decline with a 14% decrease from the previous year. California halibut landings also reflected this declining trend with a dramatic drop of 32% from the prior year's level.

The prevalence of soft-shell, postmolt Dungeness crabs delayed the start of the northern California season by four weeks and perhaps accounted for the reduced landings. Statewide sea urchin landings were 11% lower than in 1993 and declined 18% in northern California. Spot prawn catches increased by 25% in 1994, to 70 MT; ridgeback prawn catches increased by 89%, to 198 MT.

Swordfish landings decreased by 5%, and only 45% of the catch was taken in the drift gill net fishery. The contribution of longline gear to statewide landings increased 4.5 times, to 45% of the all-gears total. Twenty vessels used longline gear to fish outside U.S. waters and land swordfish in southern California. Statewide landings of live fish were estimated at 408 MT, an 88% increase over the previous year. Live-fish catches were primarily by hook and line gear, although over 73% of live California sheephead landings in southern California were made with trap gear.

PACIFIC SARDINE

In 1986, spawning biomass estimates of the Pacific sardine (*Sardinops sagax*) increased above the legally specified level for reestablishment of a commercial fishery in California. Each year since 1986, the California Department of Fish and Game (CDFG) has established a harvest quota based on an estimate of current spawning biomass. CDFG is required by law to include in the quota a directed fishery quota of at least 910 MT whenever the spawning biomass exceeds 18,200 MT.

At the fifth annual Pacific Sardine Resource Assessment and Management Workshop, scientists using the CANSAR (Catch at Age Analysis of Sardines) model estimated the 1993 sardine spawning biomass to be 71,700

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

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1974	6	73,810	60	11,362	2,348	13,111	100,697
1975	3	141,486	129	16,415	1,086	10,715	169,834
1976	24	111,503	293	19,882	2,151	9,211	143,064
1977	5	99,504	5,333	44,775	5,200	12,811	167,628
1978	4	11,253	11,193	30,755	4,401	17,145	74,751
1979	16	48,094	27,198	16,335	4,189	19,690	115,542
1980	34	42,255	29,139	20,019	7,932	15,385	114,764
1981	28	51,466	38,304	13,990	5,865	23,510	133,163
1982	129	41,385	27,916	25,984	10,106	16,308	121,828
1983	346	4,231	32,028	18,095	7,881	1,824	64,405
1984	231	2,908	41,543	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*	12,346	1,965	10,052	3,129	2,668	55,769	85,929

*Preliminary

TABLE 2
Pacific Sardine Quota Allocations (Metric Tons) for California, 1994

	Original allocations*			Revised allocations		
	Quota	Total landings	Unused	Quota	Total landings	Unused
Fisheries						
Directed						
Northern	3,327	1,832	1,495	868	463	405
Southern	6,652	7,677	—	990	1,256	—
Total	9,979	9,508	1,495	1,858	1,719	405
Dead bait						
Northern	56	0	56	56	0	56
Central	56	64	—	56	0	—
Southern	341	86	255	341	588	—
Total	454	150	311	454	588	56
Live bait	907	1,257	—	907	1,345	—
Incidental reserve	454	73	381	91	307	—
Grand total	10,886	9,732	2,187	2,403	2,614	461

*Original allocations were effective 1/1/94 to 9/30/94; revised allocations were effective 10/1/94 to 12/31/94.
**Live-bait quota is not included in the total allowable harvest.

MT, a decline from 116,200 MT in 1992. This decrease may have been caused by the displacement of sardines to the north of Point Conception, beyond the range of CDFG data collection efforts and consequently not included in the biomass estimate.

The total allowable harvest was set at 10,886 MT and allocated among three categories: (1) directed fishery—9,979 MT, (2) dead bait fishery—454 MT, and (3) incidental catch in the mackerel fishery—454 MT (table 2). A separate live-bait fishery allocation of 907 MT was not included in the overall total allowable harvest.

The directed fishery quota was divided geographically and opened on January 1, 1994 (table 2). The southern directed fishery quickly surpassed its quota and closed on May 6, 1994. After the closure, sardine landings remained low through October 1 in the dead bait fishery (86 MT) and as incidental catch (73 MT) in the mackerel fishery.

Recent installation in a northern California cannery of a new canning line which produces 155 g cans increased the utilization of smaller sardines prevalent in the area. Consequently, northern California landings increased greatly over previous years, and by October 1, 1994, over one-half (1,832 MT) of the northern California directed quota had been landed. On October 1, the remaining northern directed-fishery allocation (1,495 MT) was split 50:50 between the north and south (table 2). In addition, 363 MT of the incidental catch reserve was reallocated (one-third to the north, two-thirds to the south). Despite this reallocation, the northern directed fishery remained open through year's end, landing a total of 2,295 MT.

The southern directed fishery reopened on October 11, 1994, with an additional 990 MT. Approximately 1,256 MT were quickly captured, and the fishery closed on October 18. The central California dead bait fishery closed on April 1, 1994, with total landings of 64 MT, 8 tons over its 56 MT quota. The pace of the southern California dead bait fishery was slow, due to the small size of the fish, and the quota was not attained until December 5, 1994. Once again no landings occurred against the northern dead bait quota.

In September, the live bait fishery exceeded its allocation because many sportfishing vessels used small sardines because of a shortage of anchovies. The fishery was allowed to continue landing live bait because historically their landings decreased at year's end and it appeared that the northern directed fishery would not use all of its allocation.

In April 1994, the CDFG, the National Marine Fisheries Service (NMFS), and Mexico jointly conducted a cooperative daily egg production method (DEPM) cruise. The cruise ranged from San Francisco to Punta Abreojos, Baja California. Over 680 stations were occupied, and 74 were positive for sardine eggs. In addition, adult sardines were captured at 43 stations. In November 1994, the 1994 spawning biomass was estimated, by means of the CANSAR model, to be 330,495 MT. The large increase in biomass was due to the inclusion of DEPM cruise data from both northern California and Mexico, areas for which there had been no data for the previous two years.

PACIFIC MACKEREL

The California fishery for Pacific mackerel (*Scomber japonicus*) has declined precipitously since 1990, and statewide landings during 1994 totaled only 10,052 MT (table 1). The principal causes of the reduced 1994 catches were low biomass and poor availability on the traditional fishing grounds in southern California.

California-based round-haul vessels (commonly referred to as the wetfish fleet) account for nearly all the commercial fishing effort for Pacific mackerel in U.S. waters. The wetfish fleet also targets several other schooling species (e.g., Pacific sardine, jack mackerel, market squid, bonito, Pacific herring, and occasionally bluefin tuna and northern anchovy). Historically, Pacific mackerel landings have been concentrated in southern California, with most vessels operating from San Pedro/Terminal Island and a few others from Port Hueneme or Santa Barbara. A smaller fleet in Monterey catches a minor percentage of the state's total annual mackerel landings.

The fishing season for Pacific mackerel is defined by the California Department of Fish and Game as the 12-month period from July 1 of one calendar year through June 30 of the following calendar year. Pacific mackerel are fished during every month, as long as total landings remain below the harvest quota. Quota restrictions are set for the commercial fishery when the stock's total biomass is determined by the CDFG to be greater than 18,160 MT but less than 136,200 MT. Within that range, the harvest formula specifies that the quota shall be 30% of the biomass in excess of 18,160 MT. If the biomass is less than 18,160 MT, a moratorium on any directed catch is implemented; if the biomass is greater than 136,200 MT, there is no limitation on the total catch.

Total landings for the 1993/94 fishing season were 10,796 MT, well below the season quota of 23,154 MT. Poor mackerel availability continued during the last half of 1994, when the fishery operated with a 1994/95 season quota of 14,710 MT. Landings during July through December were only 3,973 MT, about 1,000 MT less than the same period for 1993, and 78% less than the average for 1988–1992.

Prices paid to fishermen for Pacific mackerel have declined since the early 1980s and are currently near the record low. During the 1993/94 season, fishermen received an average price of $105 per metric ton, with a total annual ex-vessel value of $1.4 million. The average ex-vessel mackerel price improved slightly in the latter half of 1994, to $109 per metric ton.

Several sources of information were available to scientists on the status of the Pacific mackerel stock. Landing statistics for both the U.S. and Mexican fisheries have shown similar declines during recent years. Data from aerial observations (spotter pilots employed to locate fish schools) and CalCOFI plankton surveys (mackerel larvae data) have also shown declines in abundance since the early 1980s. CDFG staff used a tuned virtual population analysis (VPA) model called ADEPT to estimate Pacific mackerel abundance during 1994. The model finds the best statistical fit (lowest sums of squares) between fishery-based, age-structured biomass estimates and other data from aerial observations and plankton surveys. Based on model output, the CDFG estimated that the Pacific mackerel biomass was 64,468 MT on July 1, 1994—the lowest estimate of biomass since the late 1970s.

Estimates of age-specific abundance suggested that the numbers of fish age three and older were currently at the lowest levels in many years, and that recruitment has been below average since 1989. Three of the four most recent year classes are the weakest ones to appear since the stock recovered from depressed levels in the late 1970s. Despite poor abundance for the 1993 and 1994 year classes, together they compose about 70% of the current biomass, because of the lack of older fish in the population.

A warm-water oceanic regime has dominated the California current region for about 15 years, and may have caused a northern emigration of Pacific mackerel, particularly the older ones. This may have been compounded during 1993, because of another strong El Niño influence on sea-surface temperatures. Such emigration would exacerbate availability problems to the southern California wetfish fleet. Model-derived estimates of age-specific fishing vulnerabilities support this hypothesis, with reduced vulnerability for each successive age beyond age two.

PACIFIC HERRING

Annual statewide landings for the Pacific herring (*Clupea pallasi*) roe fishery were 2,668 MT in 1994, a decrease of 39% from the previous year. Statewide landings for the 1993–94 season (November to March) totaled 2,380 MT. The three gill net platoons (352 permittees) in the San Francisco Bay fishery landed 1,618 MT, which was 23% over their 1,320 MT quota. Thirty-two round haul (purse seine and lampara) permittees fishing in San Francisco Bay landed 470 MT, four percent less than their 491 MT quota. Tomales Bay (figure 1) was open to commercial herring fishing for the second consecutive year since the 1988–89 season, and outer Bodega Bay remained closed to commercial herring fishing. Thirty-nine Tomales Bay permittees landed 199 MT, 27% under their 272 MT quota. The four Humboldt Bay permittees landed 57 MT, exceeding their 54 MT quota by 6%. Crescent City fishermen (three permittees) landed 30 MT, which was 9% over their 27 MT quota.

The price of roe herring rose from the previous season's level, when predictions of record Alaskan harvests depressed California roe herring prices. Ex-vessel prices for gill net–caught herring with 10% roe recovery ranged

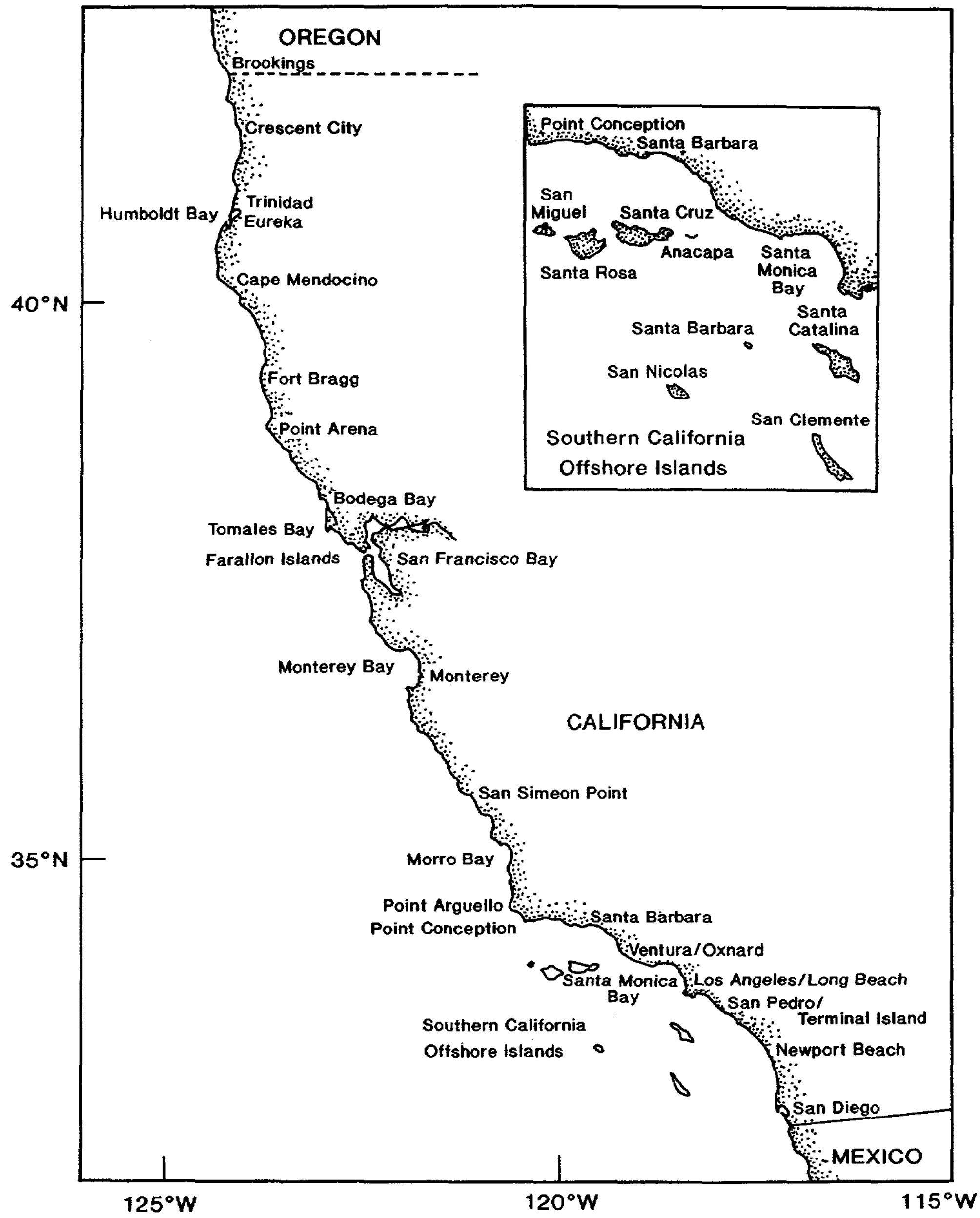

Figure 1. California ports and fishing areas.

from $700 to $800 per short ton during the 1993–94 season. The base ex-vessel price for round haul herring was $700 per short ton. The combination of a relatively low price-per-ton for roe herring and a lower quota than the previous season reduced the total ex-vessel value for California's 1993–94 roe fisheries to approximately $2.1 million. The ex-vessel value was 36% less than that of the 1992–93 season—well below the ten-year average of nearly $10 million.

Ten permittees in the San Francisco Bay herring roe-on-kelp fishery harvested slightly less than their aggregate 32 MT quota. The estimated ex-vessel value of the 1993–94 roe-on-kelp fishery was $910,000, at prices ranging from $8 to $16 per pound.

CDFG biologists estimated spawning biomass for San Francisco Bay and Tomales Bay populations, but not for the spawning populations in outer Bodega Bay, Humboldt Bay, or Crescent City Harbor. Hydroacoustic and spawn-deposition surveys were used to estimate spawning biomass in San Francisco Bay, and spawn-deposition surveys were used in Tomales Bay. After three consecutive years of decline, estimated spawning biomass of San Francisco Bay herring increased to 36,197 MT, 86% higher than the previous season's estimate of 19,500 MT.

However, the San Francisco Bay population remained below the long-term average of 49,900 MT. An apparent strong appearance of three-year-old herring from the 1991 year class accounted for most of the increase in biomass. Higher biomass levels might also be attributable to the return of fish temporarily displaced to the north by recent El Niño conditions.

The total spawning biomass estimate for Tomales Bay was 2,234 MT, a decrease of 40% from the 1992–93 estimate of 3,700 MT. This biomass decline followed four consecutive seasons of increase of the Tomales Bay population. The decline was anticipated because historical data indicated that biomass usually falls in years following El Niño conditions. The prior trend of increasing biomass and the population's age composition (indicating good recruitment) suggest that migration from Tomales Bay was the most likely cause of the current low biomass level.

GROUNDFISH

The California commercial groundfish harvest for 1994 was 24,156 MT, with an ex-vessel value of approximately $24 million. Total 1994 landings decreased approximately 14%, or 3,757 MT, from 1993. Dover sole (*Microstomus pacificus*), thornyheads (*Sebastolobus* spp.), sablefish (*Anoplopoma fimbria*), rockfish (*Sebastes* spp.), and Pacific whiting (*Merluccius productus*) continued to dominate the harvest. In 1994, as in 1993, significant decreases in harvest were noted for most categories (table 3). Reasons for the decline include a drop in production as stocks are fished down to optimum levels, and reduced market demand for some species. Pacific whiting and flatfish other than Dover sole showed increases in 1994.

The general distribution of 1994 landings for trawl and line gear showed the same trend evident during the past two years. The bottom and midwater trawl component rose to 82%, up from 78% in 1993 and 75% in 1992. The line portion of the catch dwindled from 18% in 1992 to 16% in 1993 then to 14% in 1994. The trap component was the same as in 1993 at 1%, but setnet groundfish landings dropped from 5% in 1993 to 3% in 1994.

TABLE 3
California 1994 Groundfish Landings (Metric Tons)

Species	1993	1994	Percent change
Dover sole	6,540	4,462	−32
English sole	470	432	−8
Petrale sole	457	524	13
Rex sole	456	548	17
Other flatfish	479	682	30
Widow rockfish	1,181	930	−21
Bocaccio	1,254	887	−29
Other rockfish	6,061	5,406	−11
Thornyhead	4,101	3,282	−20
Lingcod	686	546	−20
Sablefish	2,570	1,879	−27
Pacific whiting	3,144	3,662	14
Other groundfish	514	644	20
Total	27,913	24,156	−14

The Pacific Fishery Management Council (PFMC) implemented a license limitation program on January 1 within the Washington-Oregon-California (WOC) area. Annual harvest guidelines were allocated between a permitted limited entry (L.E.) fleet and nonpermitted "open access" (O.A.) fleet, and separate trip limits were established for each sector. The PFMC set harvest guidelines that affected the California fishery for Pacific whiting; Dover sole, thornyheads, and trawl-caught sablefish (the DTS complex); the *Sebastes* complex, widow rockfish (*Sebastes entomelas*); bocaccio rockfish (*S. paucispinis*); yellowtail rockfish (*S. flavidus*); and, for the first time, lingcod (*Ophiodon elongatus*). The PFMC continued to use cumulative landing limits as well as trip limits during 1994 in order to meet their objective of staying within the annual harvest guideline while providing a year-round groundfish fishery. However, cumulative landing limits were expanded by applying these limits to full calendar months and eliminating biweekly options.

No factory trawl vessels initially qualified for L.E. permits, but seven vessels eventually purchased and combined enough small-trawler permits to fish during the 1994 whiting season. By year's end, 109 of 390 original trawl permits had been combined, leaving a fleet of 291 trawlers (including 9 factory trawlers) permitted to take groundfish in the WOC area. The reduction was insufficient to significantly increase trawl trip limits. Each permitted factory trawler was entitled to only one catch limit for any species or species group, regardless of the number of permits purchased and combined. By year's end 204 vessels were permitted to use longline, and 31 vessels were permitted to use traps in the L.E. groundfish fishery. All other vessels targeting groundfish were delegated to the O.A. fishery with its more restrictive harvest guidelines and trip limits.

A 1994 WOC-area Pacific whiting harvest guideline of 260,000 MT was fully utilized by the domestic industry. As in 1992 and 1993, the resource was allocated between at-sea and shoreside processing sectors. The PFMC again restricted at-sea processing of whiting to waters north of California. Five midwater trawl vessels, fishing off the Eureka and Crescent City areas, landed virtually all of the California catch of 3,662 MT, a small increase from the 3,144 MT landed in 1993. A whiting fishery observation program, established in 1992 to monitor the bycatch of salmon and other species in the shoreside landings, continued through 1994. The California salmon-bycatch rate was 0.012 salmon per metric ton of Pacific whiting—a slight decrease from the previous season's 0.018 rate. All salmon observed were chinook (*Oncorhynchus tshawytscha*).

The monthly DTS-complex cumulative limit was initially set at 50,000 pounds, of which no more than 30,000 pounds could be thornyhead and no more than 12,000 pounds could be sablefish. Sablefish were further limited to 1,000 pounds or 25% of the DTS complex per trip (whichever was greater). High thornyhead prices attracted much greater effort than anticipated, and on July 1, the overall DTS limit was reduced to 30,000 pounds, of which no more than 8,000 pounds could be thornyheads and no more than 6,000 pounds could be trawl-caught sablefish. It became evident by October that the sablefish component of the DTS complex continued to be harvested at a high rate and that the harvest guideline would be exceeded by the end of the year. Consequently, the PFMC opted to prohibit the trawl-take of sablefish and limit Dover sole to 6,000 pounds cumulative catch per month and thornyheads to 1,500 pounds cumulative catch per month during December.

The coastwide 1994 catch of Dover sole was 9,340 MT, a decrease of 4,980 MT from 1993 landings and 4,260 MT lower than the 1994 harvest guideline. The decline in production was the result of both reduced market demand and a redirection of effort toward the more valuable sablefish and thornyheads. California 1994 landings of 4,462 MT were 48% of total WOC landings, compared with the previous year's 46% share.

Total coastwide thornyhead landings of 6,188 MT represent a decline from 1993 landings and were slightly less than the 1994 6,440 MT harvest guideline. California landed 3,282 MT, or 53% of the WOC thornyhead total, a near-identical proportion to 1993.

The WOC area trawl/nontrawl sablefish allocation remained at 58:42. The 7,000 MT harvest guideline (excludes INPFC Conception area) for 1994 remained unchanged from 1993. In addition, an acceptable biological catch (ABC) of 425 MT was established for the INPFC Conception area. After respective tribal and open-access allotments of 300 MT and 630 MT were granted, 6,070 MT remained for allocation between trawl (3,521 MT; 58%), and L.E. nontrawl (2,549 MT; 42%), fisheries. Total WOC-area landings of sablefish were 7,274 MT—4% over the harvest guideline. California accounted for 1,879 MT, or 26% of the total WOC sablefish catch.

WOC-area trawl sablefish landings were 3,581 MT, about 6% greater than the trawl harvest guideline, despite the landing prohibition in December. California trawl vessels landed 1,223 MT, or 34% of coastwide trawl sablefish landings.

In 1992 and 1993, the nontrawl unrestricted sablefish season lasted just 15 and 21 days, respectively. With the implementation of a limited entry system, managers and fishers expected a longer season because vessels without L.E. permits could not participate in the unrestricted season. But permitted vessel owners apparently purchased additional gear, because the 1994 season lasted only 20 days. Total L.E. nontrawl landings of 3,127 MT exceeded the 2,549 MT allocation by 19%. The O.A. fishery, limited to 250-pound or 350-pound trip limits, landed 256 MT of its 630 MT allocation. California fishers landed 656 MT, or 21%, of the total WOC-area nontrawl landings.

On January 1, the L.E. monthly cumulative limit for the *Sebastes* complex (including yellowtail and bocaccio rockfish) was set at 80,000 pounds coastwide, of which no more than 14,000 pounds could be yellowtail rockfish north of Cape Lookout, Oregon; no more than 30,000 pounds could be yellowtail rockfish south of Cape Lookout; and no more than 30,000 pounds could be bocaccio south of Cape Mendocino. The cumulative monthly limit was raised to 100,000 pounds south of Cape Mendocino on September 1. The O.A. cumulative limit was initially set at 40,000 pounds, with no more than 10,000 pounds per trip. The bocaccio and yellowtail rockfish limits were the same as L.E. limits. On May 1, the 10,000-pound-per-trip limit was removed for vessels using setnets.

PFMC manages the *Sebastes* complex with two harvest guidelines: *Sebastes* north and *Sebastes* south. The southern management area includes the Eureka, Monterey, and Conception INPFC statistical areas (California to Brookings, Oregon). For 1994 the *Sebastes* south harvest guideline of 13,000 MT allocated to limited entry (8,920 MT) and open access (4,520 MT) fisheries. The bocaccio component of 1,540 MT was allocated in the same proportion. California's *Sebastes*-complex landings dropped from 7,315 MT in 1993 to 6,293 MT in 1994. The 1994 bocaccio harvest included 887 MT of commercial catch and an estimated 200 MT from the recreational fishery. While all-fisheries *Sebastes* south landings were only 48% of the harvest guideline, the O.A. bocaccio landings of 442 MT approached the 450 MT harvest guideline.

The 1994 WOC-area widow rockfish harvest guideline of 6,500 MT was reduced from a 7,000 MT 1993 harvest guideline. The PFMC implemented a 30,000-pound cumulative catch limit until December 1 before imposing a 3,000-pound-per-trip limit. California landings constituted 15% (930 MT) of the WOC-area total of 6,183 MT.

In 1992 the PFMC examined the feasibility of individual transfer quotas (ITQs) and decided to proceed with developing an ITQ program for nontrawl sablefish. However, at its October 1994 meeting, the commission voted to postpone action indefinitely, largely in response to a congressional request for a delay while major policy issues are resolved at the national level.

The development of a coastwide mandatory onboard observer program for groundfish vessels was further delayed pending reauthorization of the federal Magnuson Fishery Conservation and Management Act.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1993–94 season were 2,752 MT, a decrease of 1,815 MT from the previous season, and well below the ten-year average of 3,662 MT.

The northern California season opened on December 1, 1993, but most fishers agreed not to fish because crab were in poor (soft-shell), postmolt condition. Oregon fishers from the port of Brookings violated the gentleman's agreement with California fishers to delay the season, and set gear in waters from the Oregon border to Point St. George. The conflict between Oregon and California crab fishers in California waters repeated a similar situation of the previous season. On December 27, northern California Dungeness crab marketing associations agreed to an ex-vessel price of $1.00 per pound, despite marginally acceptable crab condition, and fishing began in earnest.

A fleet of 424 vessels (30 fewer vessels than in 1992–93) landed approximately 2,371 MT at the northern California ports of Crescent City, Trinidad, Eureka, and Fort Bragg during the 1993–94 season. The port of Crescent City accounted for 1,568 MT of the total, followed by Eureka (510 MT), Trinidad (249 MT), and Fort Bragg (44 MT).

The San Francisco–area Dungeness crab season opened on November 10, 1993, with an ex-vessel price of $1.90 per pound. Total crab landings increased by 124 MT from the previous season, to a 1993–94 total of 245 MT. Crab fishers landed 79 MT at Bodega Bay, and 166 MT at ports in the San Francisco area. Monterey and Morro Bay contributed 136 MT to the season total.

Assembly Bill 3337 was signed into law by the governor in September 1994 chiefly to replace the current temporary moratorium on entry into the Dungeness crab fishery with a limited-entry program requiring permits on vessels, effective April 1, 1995. This bill also created a quality testing program, and empowered the CDFG director to delay the season, if necessary, on a recommendation from the California Seafood Council. Lastly, Assembly Bill 3337 prohibits a fishing vessel from taking crab for both commercial and sport use in the same day.

RIDGEBACK AND SPOT PRAWN

Ridgeback prawn (*Sicyonia ingentis*) are fished commercially with trawl nets. Ridgeback prawn may be trawled by permit from October 1 through May 31. An incidental catch of 50 pounds per trip is allowed during the closed season. Preliminary landings for 1994 totaled 70 MT, a catch total almost double that of 1993 (figure 2). Most of the 1994 catch came from the Santa Barbara Channel. A portion of the catch, approximately 6 MT, was sold live at ex-vessel prices ranging between $2.35 and $2.50 per pound. The ex-vessel price for fresh, dead ridgeback prawn ranged between $1.35 and $1.60 per pound. The average price paid in 1994 for ridgeback prawn, regardless of condition, was $1.50 per pound.

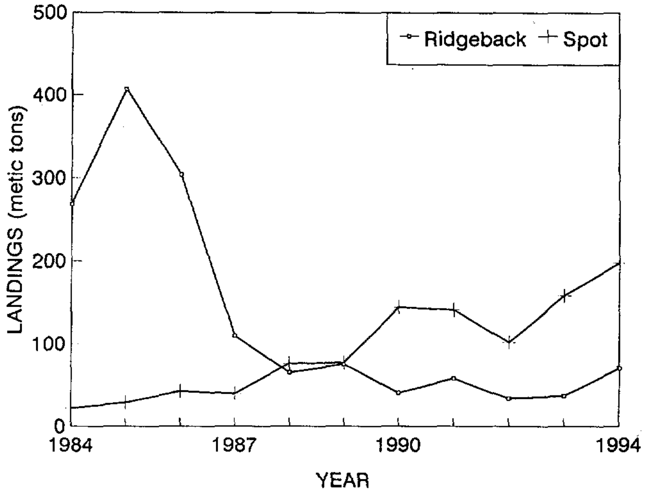

Figure 2. California ridgeback and spot prawn landings, 1984–94.

The spot prawn (*Pandalus platyceros*) is a large shrimp, and commands a higher price than the ridgeback. Spot prawn were caught with traps until the mid-1970s, when trawl nets became the primary capture gear. Because of an increasing demand for live product, traps have again become a significant method of harvest, and many trawl vessels have been retrofitted with live wells to keep their prawn catches alive. Preliminary 1994 spot prawn landings totaled 198 MT, a 25% increase over the 158 MT landed in 1993.

Approximately 132 MT of spot prawn were harvested by trawl, while 66 MT were taken with trap gear. Eighty-two percent of the combined trawl/trap spot prawn catch was landed and sold in live condition, thereby commanding significantly higher ex-vessel prices. Ex-vessel prices ranged from $2.50 to $3.50 per pound for dead spot prawn and from $4.50 to $9.00 per pound for live spot prawn. The average ex-vessel price for all spot prawn landed in 1994 was $5.80 per pound.

Spot prawn may be trawled by permit from February 1 through October 31. During the closed period, an incidental catch of 50 pounds per trip is allowed. Much of the 1994 trawl catch was taken in the Santa Barbara Channel, as in previous years, but Monterey Bay and the

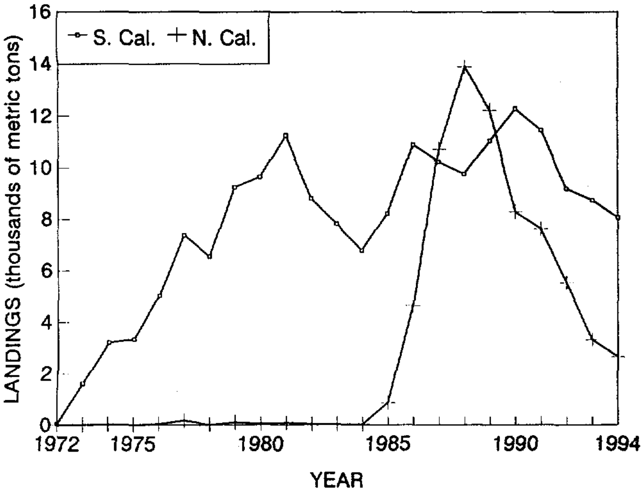

Figure 3. California sea urchin landings, 1972–94.

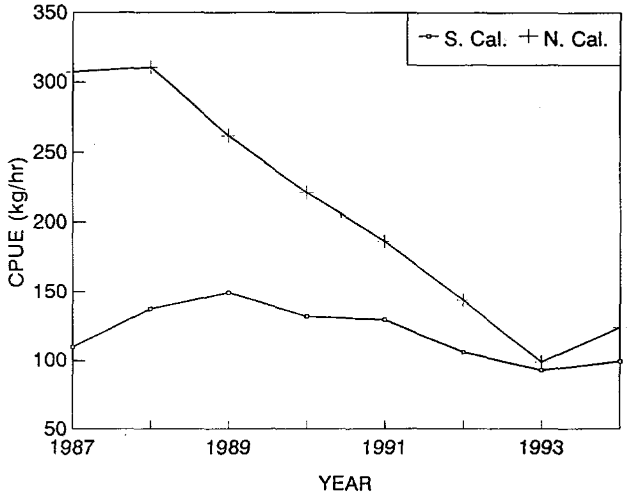

Figure 4. California sea urchin catch per unit of effort, 1987–94.

coastline between Point Piedras Blancas (San Luis Obispo County) and Point Arguello (Santa Barbara County) also contributed substantial trawl catches. Spot prawn may be harvested by trap year-round, except for a 50-fathom restriction from Point Conception south to the U.S./Mexico border. Santa Catalina, San Clemente, and San Nicolas Islands again proved to be productive prawn trapping sites.

SEA URCHIN

Statewide landings of red sea urchin (*Strongylocentrotus franciscanus*) in 1994 totaled 10,707 MT, a decrease of 11% from the 1993 total of 12,046 MT. Southern California landings decreased by 9% from the previous year, while northern California landings decreased by 18% (figure 3).

Catch per unit of effort (CPUE), in kilograms per diving hour, increased in both regions of the state. Northern California CPUE increased from 112 kg/hr in 1993 to 124 kg/hour in 1994, while southern California CPUE expanded from 93 kg/hr in 1993 to 99 kg/hr last year. The rise in CPUE was unusual because of the continued decrease in total landings (figure 4).

The number of sea urchin permits increased from 520 in 1993–94 to 525 for the 1994–95 season. The increase is credited to the termination of the sea urchin apprentice-diver program and the subsequent granting of full permit status to the holders of apprentice permits. The California Fish and Game Commission canceled the apprentice-diver program in March 1994 and will issue no additional sea urchin permits until the number falls below 300 permittees.

Statewide landings of purple sea urchin (*Strongylocentrotus purpuratus*) increased from 49 MT in 1993 to 63 MT in 1994. Although the market for purple urchins remained quite limited, interest in the fishery may grow as red sea urchin landings continue to decrease.

SWORDFISH AND SHARKS

Swordfish (*Xiphias gladius*) landings were 1,159 MT in 1994, 5% less than in 1993 (table 4). During the past decade the drift gill net fishery accounted for the majority of the catch. This year, however, only 45% of the catch was taken with drift gill nets. Harpoon landings constituted 9% of the catch, and longline landings increased 4.5 times from 1993, to 45% of the catch. Approximately 20 vessels (compared to only 6 in 1993) used longline gear outside the U.S. Exclusive Economic Zone (EEZ) and landed swordfish in southern California ports. Forty percent of the statewide swordfish catch was landed in Crescent City.

Gear type affected swordfish ex-vessel prices in 1994. Typically, fishers landing drift gill net–caught swordfish received $3.00 to $5.50 per pound, whereas longline-caught fish commanded only $2.00 to $5.00 per pound.

TABLE 4
Landings of Swordfish and Selected Shark Species (Metric Tons)

	Swordfish	Common thresher shark	Shortfin mako shark
1984	2,013	756	150
1985	2,362	700	103
1986	1,749	276	215
1987	1,246	239	274
1988	1,129	250	222
1989	1,296	295	177
1990	851	210	262
1991	711	344	151
1992	1,068	179	97
1993	1,218	162	84
1994*	1,159	190	87

*Preliminary

Fishers landing harpoon-caught swordfish received the highest prices: $4.00 to $6.50 per pound.

Landings of common thresher shark (*Alopias vulpinus*), caught almost exclusively by drift gill nets, increased to 190 MT in 1994—a slight improvement after a decade of decline (table 4). Forty-two percent of the catch was landed in the ports of Santa Barbara and Ventura. Ex-vessel prices varied from $0.90 to $2.00 per pound.

Shortfin mako shark (*Isurus oxyrinchus*) landings in 1994 increased slightly from the previous year's level, to 87 MT (table 4). Most (82%) of the catch was landed in southern California ports, at ex-vessel prices between $0.50 and $1.65 per pound. Mako sharks are caught primarily by the drift gill net fishery (63%), although hook-and-line gear accounted for approximately 21% of the mako catch, and 15% of the catch was landed by longline vessels operating outside the EEZ.

CALIFORNIA HALIBUT

The Marine Resource Protection Act of 1990 (Proposition 132), went into effect on January 1, 1994, restricting gill netting to outside of three miles in waters south of Point Arguello. Since nearshore gill netting has historically been the major method of take in southern California, the closure had a dramatic effect on California halibut (*Paralichthys californicus*) landings. In 1994, 232 MT of halibut were landed statewide (table 5), a 32% reduction from the 1993 catch (figure 5). Landings in southern California decreased by 54% (80 MT landed); landings in northern California decreased by only 14% (149 MT landed); illustrating the effect of Proposition 132 on the fishery in the south.

San Francisco accounted for 49% of the catch, followed by Santa Barbara (26%) and Morro Bay (7%). In Eureka there was a surprising 4.6-fold increase in halibut landings. Although the Eureka landings (2 MT) are a very small fraction of the statewide catch, they offer interesting anecdotal evidence of a possible shift in halibut population to the north. The halibut caught in Eureka were uniformly just over the minimum size limit (R. Warner, CDFG, pers. comm.), and may be a recruitment product of a recent El Niño.

TABLE 5
California Commercial Halibut Landings, 1994

Port	Catch (MT)	Percent of catch	Value
Unknown	2.81	2.81	$15,247
Eureka	1.73	0.75	$8,742
Bodega Bay	6.61	2.85	$38,334
San Francisco	111.23	47.98	$560,660
Monterey	13.72	5.92	$67,764
Morro Bay	15.66	6.76	$104,712
Santa Barbara	61.00	26.31	$438,456
Los Angeles	9.87	4.26	$68,828
San Diego	9.18	3.96	$33,815
Totals	231.82	100.00	$1,336,559

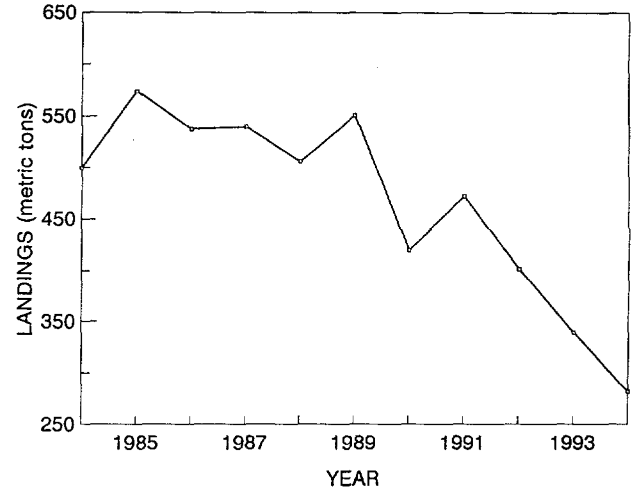

Figure 5. California landings of halibut, 1984–94.

Halibut landings peaked in the months of August (44 MT) and September (30 MT). The most productive fishing gear was the trawl (112 MT), followed by hook and line (52 MT). Gill nets landed 42 MT, a 65% decrease from 1993. Hook and line produced 38% more halibut than in 1993, a possible result of the growing live-fish market, which brings a higher price than the fresh, dead market.

The per pound ex-vessel price for halibut ranged from $0.27 to $9.50, with the highest prices paid for live fish. The average price of halibut was $3.00 per pound, and the total value of halibut landed in 1994 was $1.34 million.

OCEAN SALMON

In 1994, the Pacific Fishery Management Council enacted restrictive commercial and recreational ocean salmon regulations off California to (1) protect endangered chinook (*Oncorhyncus tshawytcha*) stocks—Sacramento River winter chinook and Snake River fall chinook; (2) ensure the fall chinook spawner escapement goals for Klamath, Sacramento, and Oregon coastal rivers; and (3) protect depressed coho (*Oncorhyncus ksutch*) stocks coastwide.

In California, commercial fishing for ocean salmon was allowed only south of Horse Mountain, in concert with various time and area closures during the May 1–September 30 season. A minimum size limit of 26 inches remained in effect. Commercial trollers, expending approximately 19,600 days of effort, landed almost 1.4 MT (»275,400 fish; figure 6) of dressed (eviscerated and cleaned at sea) chinook during 1994. Ex-vessel prices for dressed salmon averaged $2.06 per pound, and the total ex-vessel value of the fishery exceeded $5.9 million.

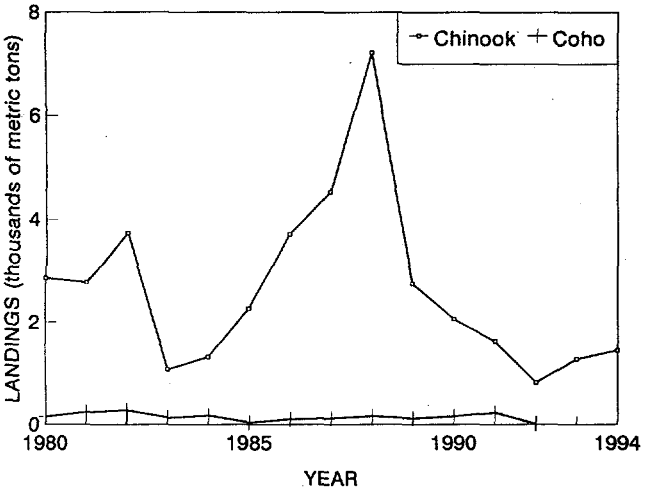

Figure 6. California commercial salmon landings, 1980–94.

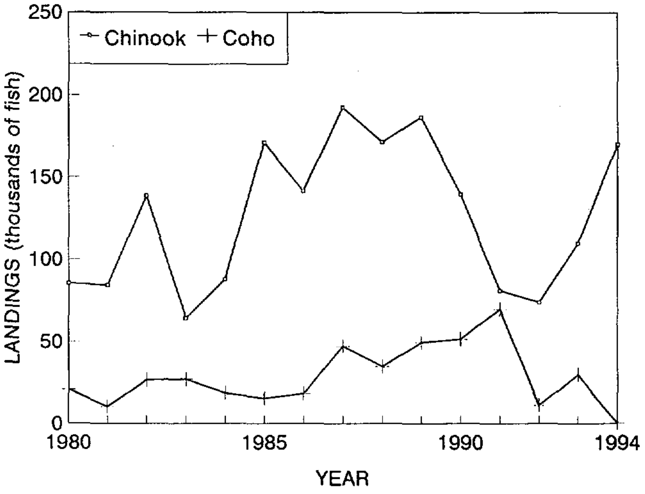

Figure 7. California recreational salmon landings, 1980–94.

Commercial fishing for coho salmon was not allowed during 1994.

In the Klamath Management Zone (KMZ; Horse Mountain, California, to Humbug Mountain, Oregon) quotas were used to manage the fisheries. The KMZ fishery opened on May 1 with a 10,300-fish quota (it closed on June 7), then reopened under a 500-fish quota from August 27 to 31. From September 1 to 5, there was an open, "no quota" fishery.

Recreational fishing regulations were similar to those of 1993, with various time and area closures enacted for the February 12–November 13 season. Anglers were allowed two salmon per day (no coho after May 1) with a minimum size limit of 20 inches. Statewide, recreational anglers landed 170,400 chinook (figure 7) during 169,000 angler trips, for an average of 1.0 fish per angler trip. This represented a 54% increase over 1993 landings of 110,000 chinook.

In the California portion of the KMZ, 1994 recreational landings of chinook exceeded the 1993 catch of 4,900 fish by 106%. Recreational anglers landed 10,100 chinook during 15,800 angler trips for an average of 0.6 fish per angler trip. Most fishing was done from private skiffs, although there was some charter boat activity.

No catch quotas were employed to manage the recreational fishery in waters south of Horse Mountain. Recreational anglers landed 160,300 chinook during 153,200 angler trips (average catch 1.1 chinook per angler trip) from both private skiffs and charter boats. This was a 52% increase over 1993 landings of 105,100 salmon. Approximately 80% of the recreationally caught salmon in this area were caught near the San Francisco port area.

LIVE-FISH FISHERY

The 1994 statewide landings for live fish were estimated at 408 MT, 88% more than in 1993 (table 6). This increase was attributable, at least in part, to the introduction in 1994 of new landing receipts that differentiate between live and dead fish. All such receipts were reviewed by CDFG biologists for completeness and accuracy. Knowledge of the port areas combined with pointed investigations of questionable data produced a more accurate estimate of reported landings for the live-fish fishery. Northern California live-fish landings may be underestimated by an unquantified amount because some fish buyers failed to properly code landings as live, not dead, fish.

The live-fish fishery began in 1988 to supply fish mainly to the California Asian community. For this market, fishes must be visually attractive and able to withstand rigors of capture and transportation. Optimum individual weights range between one and three pounds, a suitable single-entrée size at Asian restaurants. Ex-vessel prices ranged from $2.00 to $7.00 per pound. Larger fish were also sold live, but at a considerably reduced price. Prices fluctuated due to market demand, fish size, fish condition, and weather conditions. Hook and line gear was used to capture 59% of the live fish landed statewide; trap gear landed 22%.

Live-fish landings in southern California (Morro Bay

TABLE 6
Preliminary 1994 Landings (MT) of Live Fish (Data through September)

	Southern California	Northern California
Rockfishes	119	57
California sheephead	99	1
California halibut	36	7
Lingcod	23	13
All others	48	5
Total	325	83

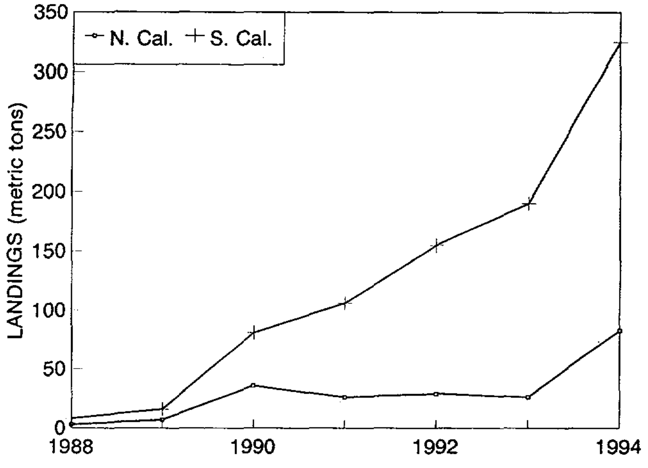

Figure 8. California live-fish landings, 1988–94.

southward) totaled 325 MT, 71% more than in 1993 (figure 8). Target species for all gear types included California sheephead (*Semicossyphus pulcher*); California halibut (*Paralichthys californicus*); California scorpionfish (*Scorpaena guttata*); cabezon (*Scorpaenichthys marmoratus*); lingcod (*Ophiodon elongatus*); and grass (*S. rastrelliger*), brown (*S. auriculatus*), and gopher (*S. carnatus*) rockfishes. Trapping accounted for 73% of all live California sheephead taken. Traps used for finfish were constructed like lobster traps, but variations abounded as this fishery continued to develop. Commercial fishery targeting on both the nearshore rockfish complex and California halibut was more intensive than prior landing data suggested. Live California halibut were caught with line, net, and trawl gear, primarily from the ports of Santa Barbara and Morro Bay. Halibut were kept alive to ensure optimum freshness, then bled, iced, and quickly shipped. This is a slight departure from the original market that displays live fish for entrée selection. Morro Bay reportedly has a rudimentary cabezon trap fishery.

Live-fish landings in northern California (north of Morro Bay) totaled 83 MT, 219% greater than in 1993 (figure 8). Landings were made primarily by hook and line vessels using vertical longlines, horizontal longlines, and troll longlines to harvest rockfish along nearshore rocky reefs and offshore banks. Finfish traps are not authorized for use in waters from Pigeon Point (San Mateo County) to the southern boundary of Mendocino County. Principal finfishes caught were gopher, brown, china (*S. nebulosus*), and copper (*S. caurinus*) rockfishes. Lingcod, halibut, and cabezon were specifically targeted for the first time in 1994.

In February, a state assembly bill was introduced to further regulate the live-fish trapping fishery. The bill proposed a limited-entry program, limitations on numbers of traps, requirements for trap construction, and incidental catch restrictions. General trap permit sales rose 10% in 1994, presumably fueled by fishermen's fears of exclusion in a future limited-entry program. However, the legislature defeated this bill in December 1994.

RECREATIONAL FISHERY

Statewide landings from commercial passenger fishing vessels (CPFV) for 1994 were not available at the time of publication because of a change in the logbook format. Although the new format was tested before being issued, a problem arose about how to interpret the number of fish landed. Because of this, all 1994 logs must be reviewed before final landing tables are released.

During 1994, CDFG personnel recorded the southern California CPFV catch as reported in the sports section of the *Los Angeles Times* newspaper. Each landing submitted a daily report of the catch to the *Los Angeles Times*, which published the reports the following day. All landings from San Diego to San Simeon (San Luis Obispo County) reported daily, but occasionally missed a day due to bad weather or the inability to meet the newspaper's deadline.

Because landing operators perceive the newspaper fish report as a marketing tool, they may overstate the number of fish caught by sport anglers. Because of this, comparisons of absolute numbers of fish in the newspaper reports with catches reported on CDFG logs are not appropriate. However, ranking (order of importance when ranked by number caught) comparisons between years or between the two reporting methods within a year are unaffected by potential overreporting. This review compares 1994 *Los Angeles Times* catches for southern California with reported CPFV logbook landings for 1993 (table 7).

Rockfishes (*Sebastes* spp.) as a group dominated the CPFV fishery during both years, primarily because there are a large number of species within the group and they are fished year-round. California barracuda (*Sphyraena argentea*) increased in importance, moving from fifth rank in 1993 to second rank in 1994. Kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) continued to rank third and fourth. Pacific mackerel (*Scomber japonicus*) slipped from second to fifth place, probably due to underreporting of this less-desirable species by CPFV landing operators to the newspaper. Pacific bonito (*Sarda chiliensis*) remained in sixth place. Ocean whitefish (*Caulolatilus princeps*) moved from ninth to seventh rank, reflecting a dramatic increase in catch due to the recruitment of a strong year class. Although landings of spotted scorpionfish (*Scorpaena guttata*) apparently doubled, they decreased in relative importance, dropping from seventh to eighth rank. Halfmoon (*Medialuna californiensis*) landings declined in rank, moving from eighth to ninth place. Yellowfin tuna (*Thunnus albacares*) remained

TABLE 7
Southern California Commercial Passenger Fishing Vessel Landings

	1994 L.A. *Times*		1993 CDFG logbook	
Species/species-group	Number of fishes	Rank	Number of fishes	Rank
Rockfishes	1,293,448	1	939,460	1
Barracuda	384,416	2	203,681	5
Kelp bass	384,084	3	355,077	3
Barred sand bass	382,966	4	313,390	4
Pacific mackerel	277,118	5	414,571	2
Pacific bonito	149,837	6	139,557	6
Whitefish	142,551	7	44,132	9
Spotted scorpionfish	124,273	8	69,527	7
Halfmoon	71,303	9	60,743	8
Yellowfin tuna	46,977	10	37,142	10
Sheephead	28,979	11	26,857	12
Skipjack	21,363	12	23,823	13
Lingcod	16,000	13	15,038	14
Yellowtail	10,518	14	35,681	11
California halibut	4,542	15	3,978	17
White seabass	3,821	16	1,401	18
Cabezon	1,382	17	1,500	19
Dolphin	689	18	8,952	16
Bluefin tuna	677	19	10,535	15

in tenth place, while skipjack (*Euthynnus pelamis*) moved from thirteenth to twelfth place. Among less frequently caught species, both California sheephead (*Semicossyphus pulcher*) and lingcod (*Ophiodon elongatus*) increased in importance by one rank. Two pelagic species, yellowtail (*Seriola lalandi*) and dolphin (*Coryphaena hippurus*) decreased in rank, dropping to fourteenth and eighteenth, respectively. California halibut (*Paralichthys californicus*), white seabass (*Atractoscion nobilis*), and cabezon (*Scorpaenichthys marmoratus*) each increased in importance by two ranks. While bluefin tuna (*T. thynnus*) dropped from fifteenth to nineteenth place, total landings decreased dramatically because of the absence of fish on the fishing grounds during the summer.

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THE STATE OF THE CALIFORNIA CURRENT IN 1994–1995: A PERIOD OF TRANSITION

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ABSTRACT

This report is a summary and preliminary analysis of recent observations of oceanographic and biological structure of the California Current region, with emphasis on atmospheric pressure and wind fields, ocean circulation pattern and hydrographic structure, and upper-ocean plankton distributions. There was a strong transition in atmospheric circulation and sea-surface temperature between the fall of 1994 and winter/spring 1995. A deep low pressure replaced high pressure over the eastern North Pacific, and this resulted in frequent and intense winter storms. During 1994, the California Current returned to a more typical circulation pattern, following El Niño conditions during 1992 and 1993. The cruise mean values of chlorophyll and primary production fit into the scatter of values observed during the prior decade, while macrozooplankton biomass continued its trend of being low both in terms of the last decade and the 45-year record. Winter and spring of 1995 were marked by an unusually strong red tide event in the coastal region of southern California, and high chlorophyll and primary production in the CalCOFI study region.

INTRODUCTION

Physical and biological structure in the California Current are variable on a broad range of space-time scales. Large interannual fluctuations, such as the changes associated with the 1992–93 El Niño event in the California Current (Hayward 1993; Hayward et al. 1994; Lynn et al. 1995), are superimposed upon the longer-term trend of increasing sea level (Roemmich 1992), warming of the upper layers, and decrease in macrozooplankton biomass (Roemmich and McGowan 1995). Regional patterns are also affected by the annual cycle and by the strong mesoscale structure of the California Current (Lynn and Simpson 1987), by storms, and by episodic events such as the dramatic red tide in southern California (described here). Understanding the causes of variability in the California Current region and wise management of its resources will require improvements in our knowledge of variability on a range of space-time scales. Management issues are further complicated by the need to make decisions based upon limited information, often before data sets can be fully analyzed. The latter problems underscore the need for a better understanding of how to interpret those data sets, such as coastal shore station data, which can be processed and distributed in a timely manner.

This is a continuation of an annual series of reports on the oceanographic state of the California Current. The emphasis here is upon the regional structure in the past two years, but some longer-term data are shown in order to place the more recent observations in a larger context. Emphasis is on the coastal shore station observations and on hydrographic data collected on CalCOFI time-series cruises and other process cruises conducted by NOAA and SIO.

DATA SETS AND ANALYTICAL TECHNIQUES

Coastal data include measurements of temperature and salinity made at a series of shore stations (Walker et al. 1994); data from La Jolla (SIO Pier) and Pacific Grove are shown here as temperature and daily anomalies from the long-term (1916–93 for La Jolla and 1919–93 for Pacific Grove) harmonic mean. Coastal sea-level data for San Diego and San Francisco are shown as monthly anomalies from the 1975–86 mean corrected for atmospheric pressure (data courtesy of G. T. Mitchum and K. Wyrtki and the IGOSS program).

Data from quarterly CalCOFI time-series survey cruises in 1994 and 1995 are shown. The CalCOFI monitoring program started in 1949; a brief history of the program is given in Hewitt 1988. The present program consists of quarterly (normally January, April, July, October) survey cruises which occupy a grid of 66 stations in the southern California region. Cruises are designated by the year and month; e.g., cruise 9501 sampled in January 1995. Station locations are designated by a line and station number; e.g., 90.60 represents station 60 on CalCOFI line 90. The station positions of the CalCOFI grid as well as the station plans for two survey cruises conducted off central California in the spring

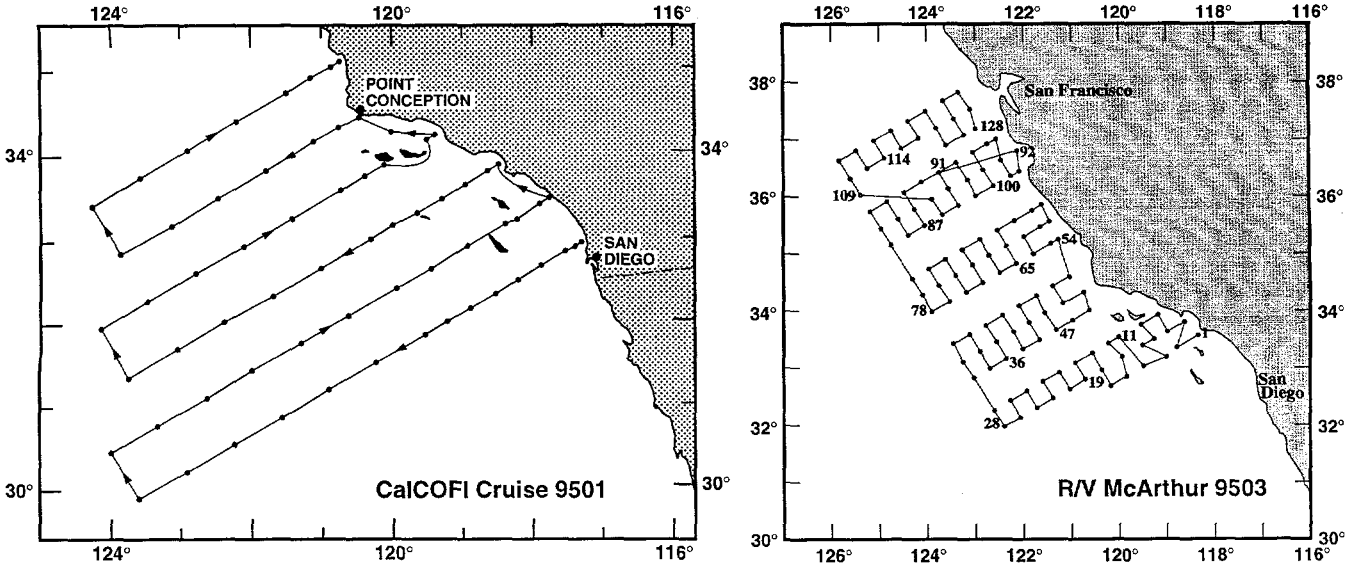


Figure 1. Current CalCOFI cruise pattern as illustrated by the cruise track for CalCOFI cruise 9501, and the cruise track for the hydrographic surveys conducted aboard R/V *McArthur* (9–27 March and 18 April–7 May 1995) as part of the hake biomass assessment program.

of 1995 are shown in figure 1. A two-ship survey using the CalCOFI station pattern was conducted 9–27 March 1995 by the Southwest Fisheries Science Center for surveying hake eggs and larvae and physical oceanography. A second survey, also with two ships, was conducted 18 April–7 May 1995 on the same basic pattern. Casts were made to 1000 m and included profiling of oxygen concentration, fluorescence, beam transmission, and, on the second survey, backscatterance. The hake egg and larval sampling (R/V *David Starr Jordan*) was conducted by a combination of bongo tows and MOCNESS tows on CalCOFI lines 87, 80, 73, 67, and, in the second survey only, 60.

The core time-series data set now collected at each station on the quarterly CalCOFI cruises includes a CTD/Rosette cast with sensors for pressure, temperature, salinity, dissolved oxygen, PAR (photosynthetically active radiation), fluorescence, and transmissivity. Water samples are collected with 10 l sample bottles at 20–24 depths in the upper 500 m for determination of salinity, dissolved oxygen, nutrients (NO_3, NO_2, PO_4, SiO_3), phytoplankton pigments (chlorophyll-a and phaeophytin), and primary production (^{14}C uptake at one station per day). Oblique and surface (neuston) net tows (0.505 mm mesh) are taken at each station. Continuous near-surface measurements of temperature, salinity, chlorophyll fluorescence, and dissolved oxygen are made from water pumped through the ship, and the data are logged at one-minute intervals. Acoustic Doppler current profiler (ADCP) data are also recorded continuously. The ADCP data provide a measure of zooplankton biomass based upon acoustic backscatter as well as a measure of upper-ocean currents. The most recent data presented here are preliminary, and some changes may be made after the final processing and quality control checks. The methods are described in more detail in the CalCOFI cruise data reports (Scripps Institution of Oceanography 1994). CalCOFI hydrographic data can be accessed via the Internet; telnet to **nemo@ucsd.edu** and login as **info.**

In addition to the above core measurements made by the CalCOFI program, a diverse group of measurements were made by cooperative research programs on recent cruises. These include pelagic seabird abundance (R. Veit, J. McGowan), bio-optical and phytoplankton measurements (G. Mitchell, M. Vernet, J. Collier, S. Bower, E. Venrick), copepod egg production (M. Mullin), phytoplankton pigment production (R. Goericke, M. Olaizola), optical particle counter (K. Osgood, D. Checkley), carbon dioxide (D. Keeling), chlorofluorocarbons (D. Min), methyl halides (B. Miller), and CO dynamics (O. Zafiriou). These observations will be discussed separately by the groups making them. Several students and volunteers have also been trained on recent cruises.

An index of monthly averaged coastal upwelling (Bakun 1973) was calculated. This index is based on six-hourly estimates of alongshore wind stress, which are derived from surface atmospheric pressure gradients using the geostrophic constraint. Time-series of the index were generated at coastal grid points every three degrees of latitude. Monthly anomalies, referenced to the mean for that calendar month for 1946–94, are contoured for the period January 1991 through April 1995.

EVOLUTION OF STRUCTURE

Sea-surface temperature (SST) at La Jolla was anomalously warm during most of 1994, and the positive

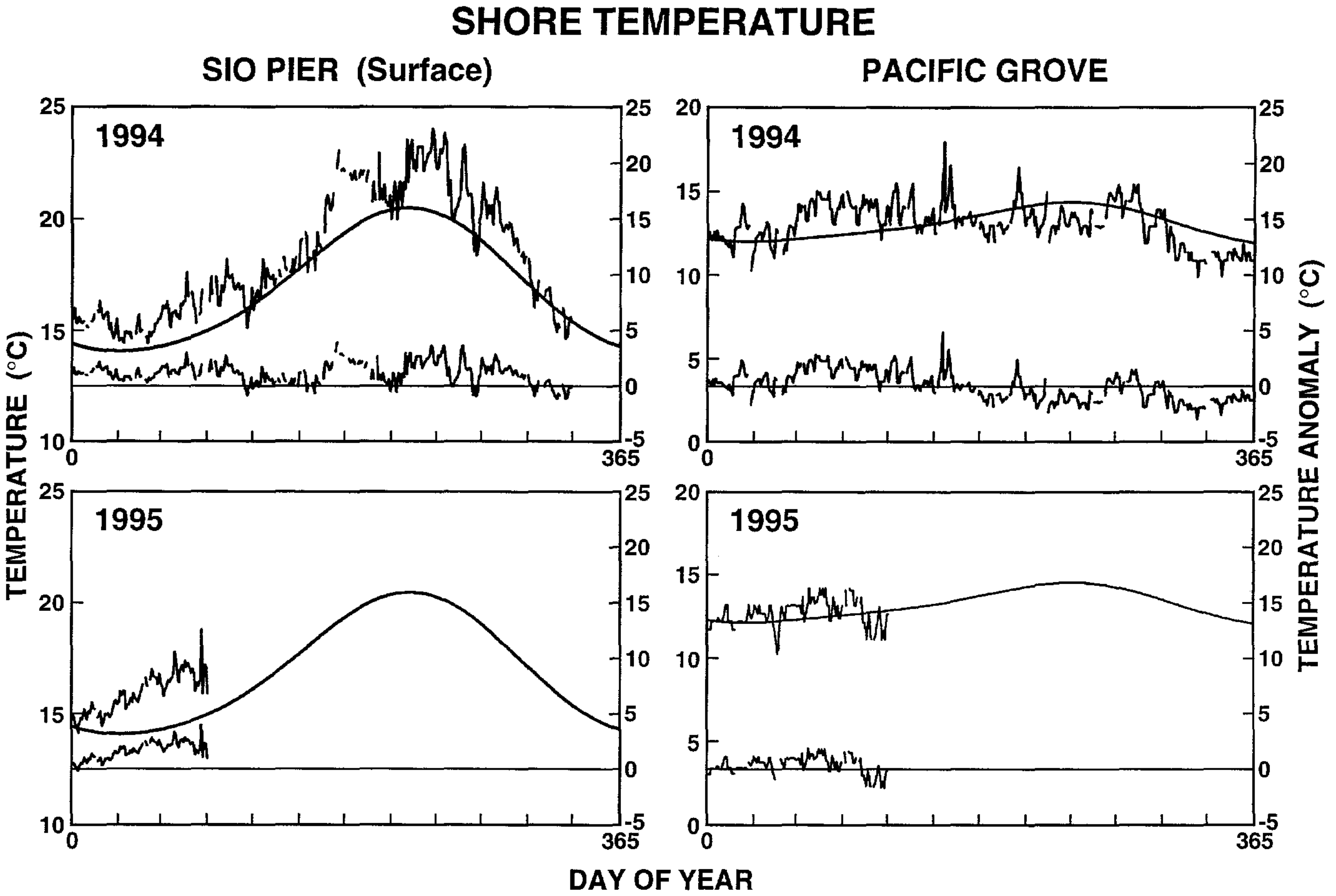


Figure 2. Sea-surface temperature at La Jolla (SIO Pier) and Pacific Grove for 1994 and 1995. Daily temperatures and daily anomalies from the long-term harmonic mean (1916–93 for La Jolla and 1919–93 for Pacific Grove). The *heavy line* shows the harmonic mean annual cycle in SST.

anomalies increased during the first few months of 1995 (figure 2). In contrast to the temperature signal, sea level at San Diego was near normal throughout 1994, with an increase becoming apparent in February and March 1995 (figure 3). Pacific Grove showed a somewhat different signal. SST was anomalously warm at Pacific Grove in the first half of 1994 and anomalously cool in the latter half of the year. Pacific Grove appeared to be fluctuating about normal conditions in early 1995. Sea level at San Francisco was anomalously low throughout 1994, but there was an abrupt increase to anomalously high values in January and February 1995. It is possible that the 1995 increase in sea level was associated with the runoff of large volumes of fresh water into San Francisco Bay, rather than being an indicator of the offshore hydrographic structure of the California Current.

Cruise mean values of vertically integrated chlorophyll, an index of phytoplankton abundance (and also primary production; Mantyla et al. 1995), and macrozooplankton biomass from the CalCOFI survey cruises provide an index of biological structure during this period. Cruise means of integral chlorophyll for 1993 and 1994 (figure 4) fit into the scatter of the cruise means observed during the prior decade. Chlorophyll tends to be low and stable from September to December, and there is a spring increase, with much interannual variability. The quarterly sampling scheme does not adequately resolve the annual pattern, and it is thus unclear whether the between-year differences are real or due to undersampling of the annual pattern. The January and, especially, April 1995 CalCOFI cruises showed high values of chlorophyll (see below). Macrozooplankton biomass showed a continuation of the long-term pattern described by Roemmich and McGowan (1995); the 1993 and 1994 cruise mean values were quite low when compared to both the preceding decade and the 1951–84 mean for the area. Anchovy spawning biomass has declined steadily since 1983–84 in the Southern California Bight, while sardine biomass continues to increase (see Smith 1995).

Atmospheric Forcing

There was a remarkable transition in the North Pacific atmospheric circulation and sea-surface temperature be-

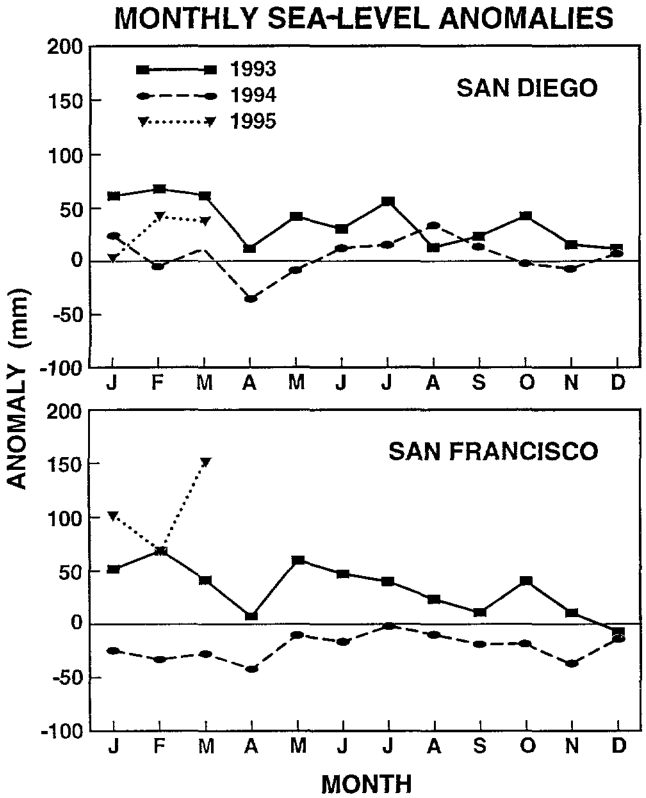


Figure 3. Monthly anomalies in sea level at San Diego and San Francisco for 1993, 1994, and 1995. The monthly anomalies are deviations from the 1975–86 period corrected for atmospheric pressure.

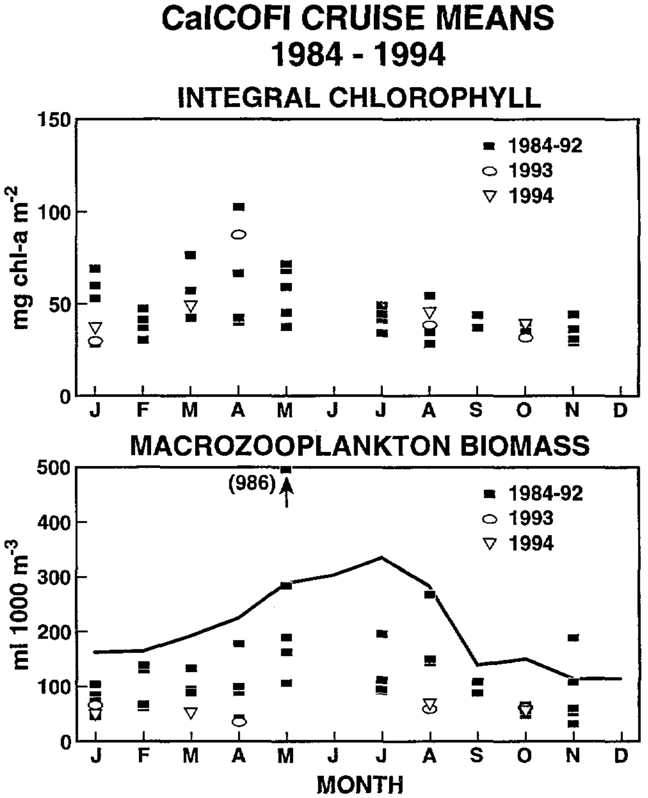
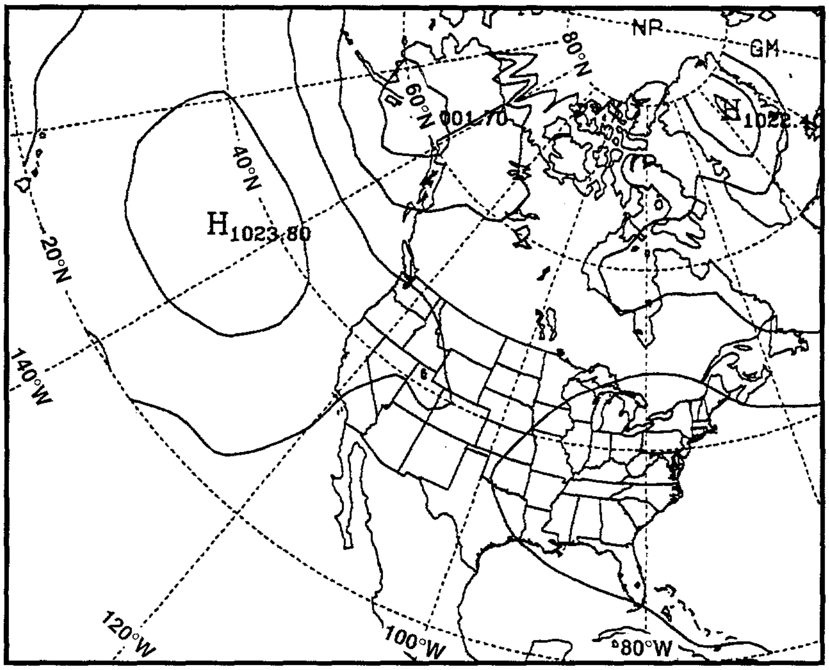


Figure 4. Cruise means of vertically integrated chlorophyll and macrozooplankton biomass plotted versus the month of each cruise. Each point represents the mean of all of the measurements made on a single cruise (normally 66). The *solid squares* show the cruises that took place from 1984 to 1992; the *open symbols* indicate data for 1993 and 1994. The monthly mean macrozooplankton biomass for the study area from 1951 to 1984 is shown as a *solid line*.

tween fall 1994 and winter/spring 1995. The fall was marked by higher-than-average atmospheric pressure and the anticyclonic (air) circulation over the eastern North Pacific, with enhanced northerly (equatorward) winds along the west coast of the United States (figure 5). Consistent with this flow pattern, fall 1994 had cooler-than-normal air temperatures over the western United States and cool SST along the west coast (figure 6). The atmospheric pattern reversed in winter, with the appearance of a deep low pressure (figure 7) and frequent storminess over the eastern North Pacific. The strong low which developed in December and prevailed during the early spring (figure 8) is a typical feature during winters with "mature" El Niño conditions such as those present during the 1994–95 winter. Offshore of northern California at about 40°N, 145°W the anomaly of the winter (December, January, February) mean sea-level pressure approached -9 mb, more than 2 standard deviations below its long-term mean. In response to the cyclonic flow around the deep low, enhanced westerly/northwesterly winds dominated the central North Pacific, and anomalous southerly/southwesterly winds occurred along the west coast of the United States. This would have promoted enhanced wind mixing and heat losses in the central North Pacific and diminished these effects along the eastern boundary. Evidence of these processes is provided by the marked cooling of the SST in the central North Pacific and a decided warming along the west coast, where the SST anomalies reversed from their cool state in the fall to positive values in March (figure 9).

The patterns in the coastal upwelling indices are consistent with the patterns in North Pacific atmospheric circulation and SST in 1994–95. The indices in fall 1994 were upwelling-favorable south of about 45°N. Anomalies, relative to 1946–94 means, were positive (greater-than-normal upwelling) along virtually the entire west coast. Anomalies in October and November 1994 were especially large, often more than 2 standard deviations above the long-term mean (figure 10). The situation changed dramatically in December. Indices were strongly downwelling north of 40°N; anomalies shifted to negative or near-zero from 27°–57°N. Anomalies were even more negative in January 1995 (< -100 m^3/s/100 m coastline), 2–6 standard deviations below the long-term mean over 36°–51°N, corresponding to downwelling indices of about -100 to -300 m^{-3} s^{-1} per 100 m

FALL 1994
SURFACE PRESSURE



PRESSURE ANOMALY

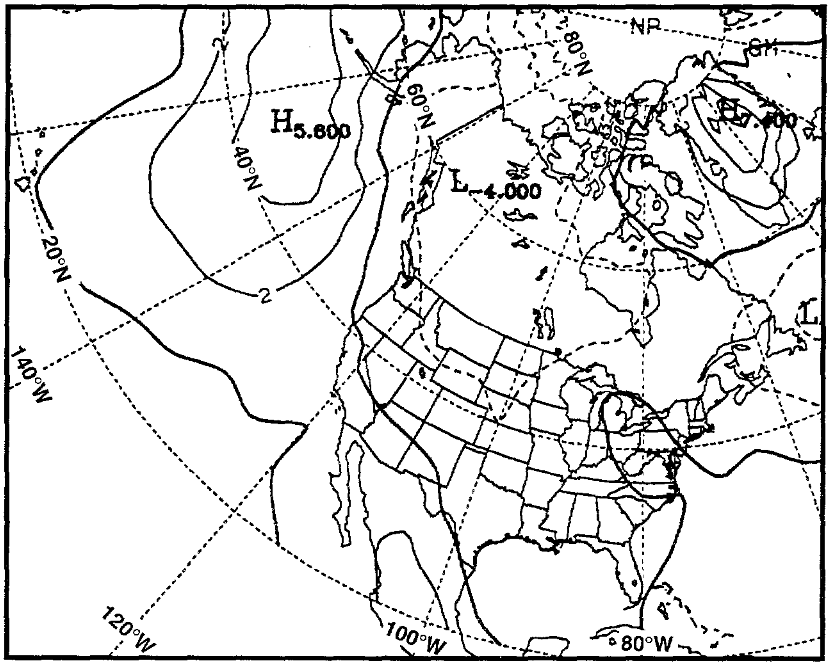


Figure 5. Surface atmospheric pressure (mb) and surface atmospheric pressure anomaly for fall (September–November) 1994.

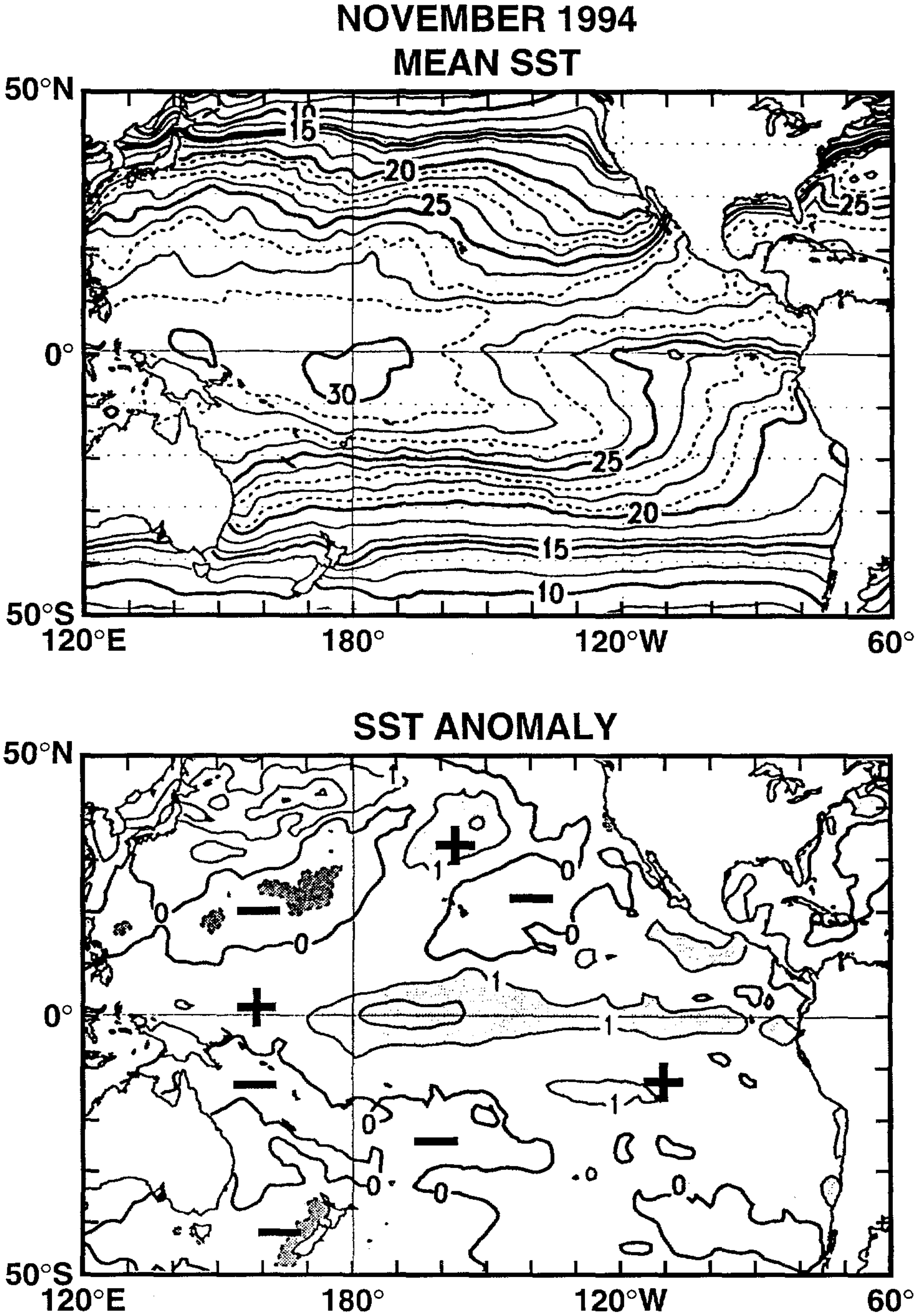
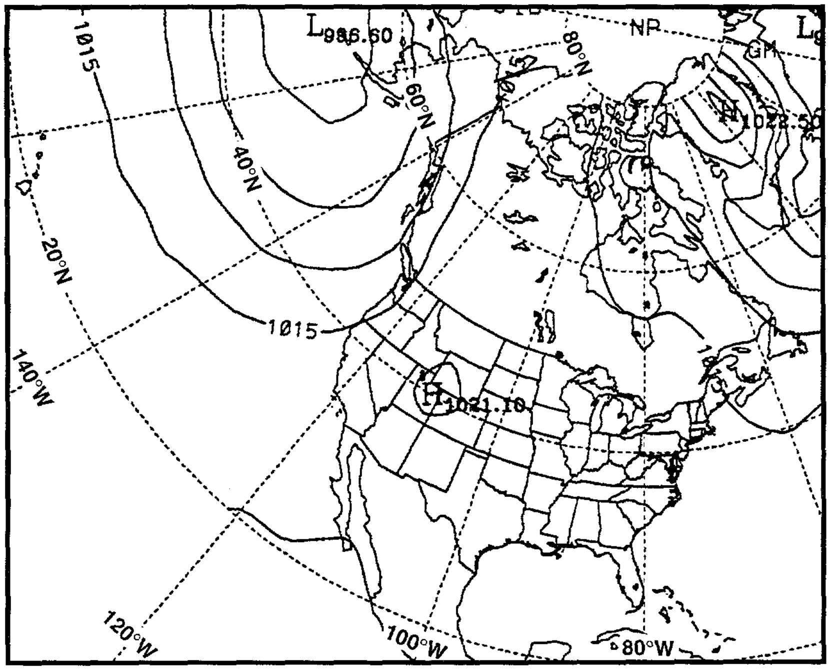


Figure 6. Mean and anomalous SST (°C) for November 1994.

coastline. Anomalies relaxed in February, but remained negative south of 40°N. The region of positive (upwelling) values coincided with this area of negative anomaly; i.e., weaker-than-usual downwelling north of 40°N, weaker-than-normal upwelling south of 40°N. While the sign of the index remained positive in March south of 40°N, negative anomalies (reduced upwelling) returned to virtually the entire California Current region. Thus the signature of upwelling conditions changed from positive anomalies and very strong upwelling in the fall of 1994, to very negative anomalies and strong downwelling in early 1995. This transition is presumably a reflection of the latest El Niño. It agrees with similar transitions in late 1991 and 1992, which also are associated with El Niño events, although the upwelling anomalies in early 1995 were significantly more negative than their 1992 and 1993 equivalents.

WINTER 1994
SURFACE PRESSURE



PRESSURE ANOMALY

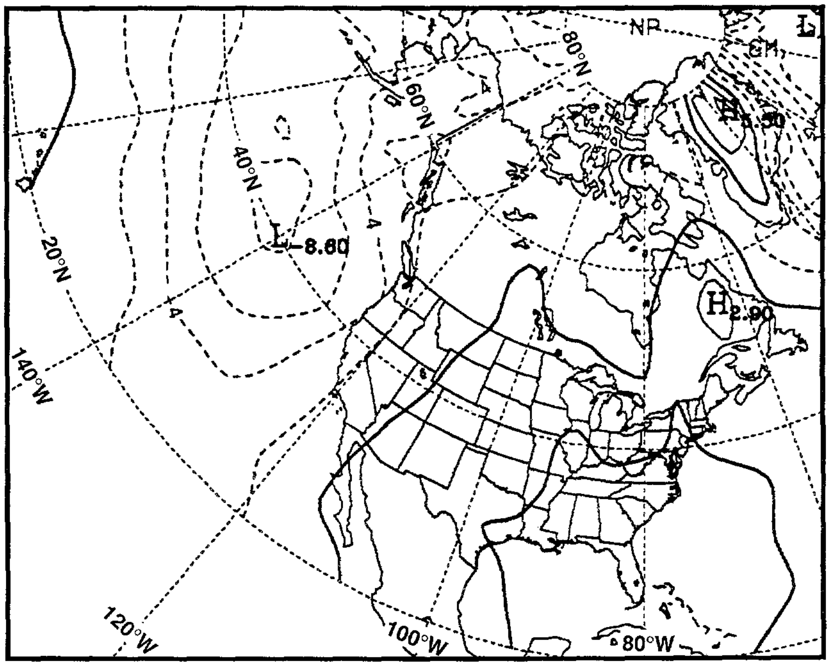
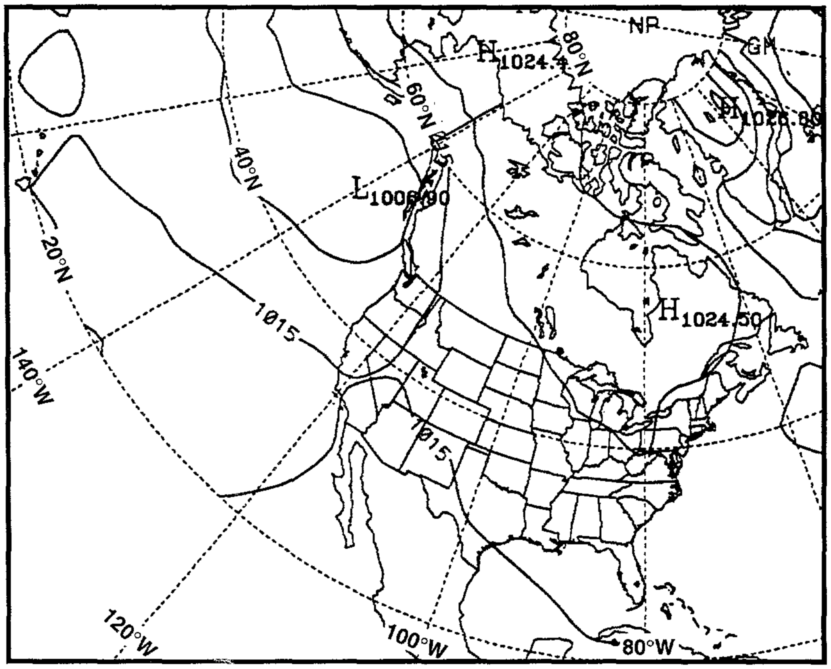


Figure 7. Surface atmospheric pressure (mb) and surface atmospheric pressure anomaly for winter 1995 (December 1994, January and February 1995).

MARCH 1995
SURFACE PRESSURE



PRESSURE ANOMALY

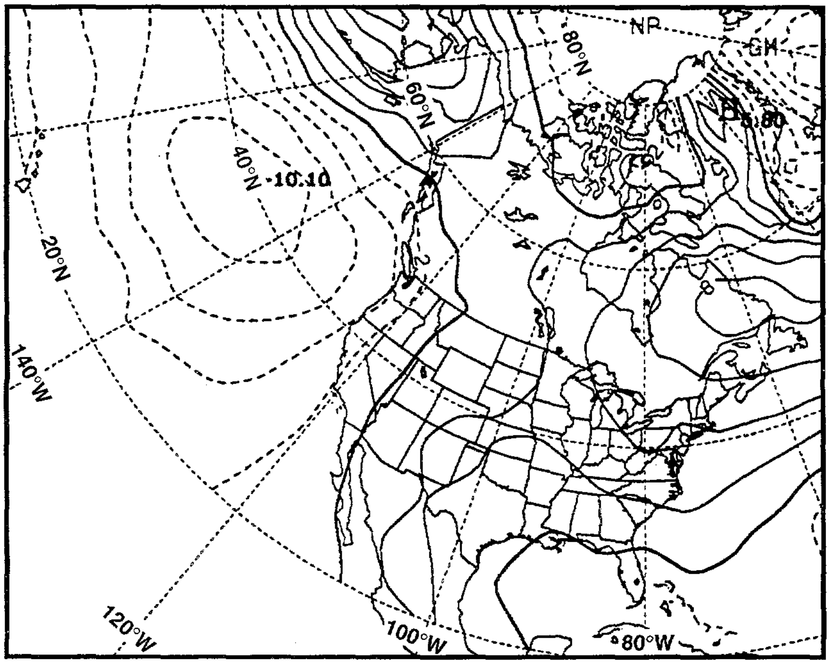
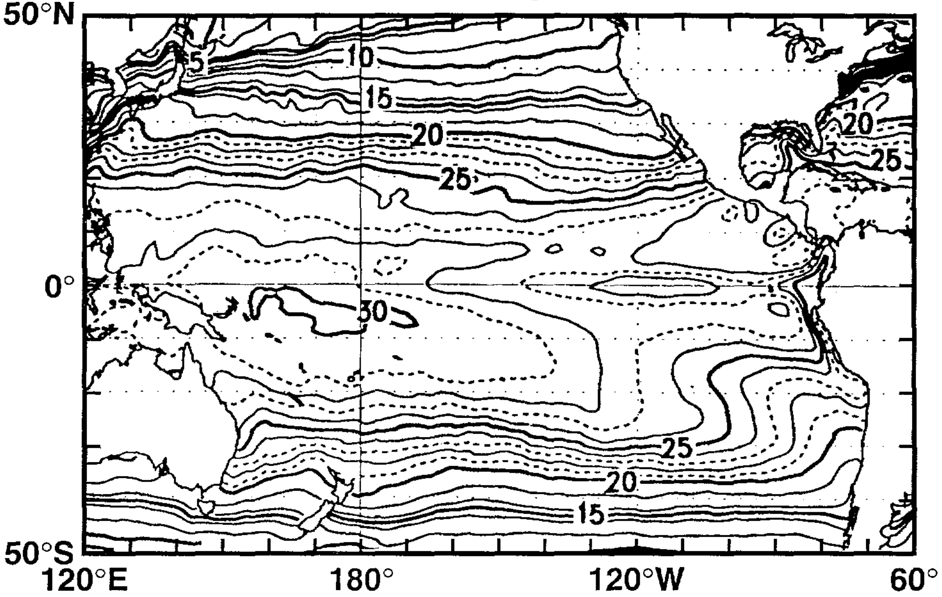


Figure 8. Surface atmospheric pressure (mb) and surface atmospheric pressure anomaly for March 1995.


MARCH 1995
MEAN SST

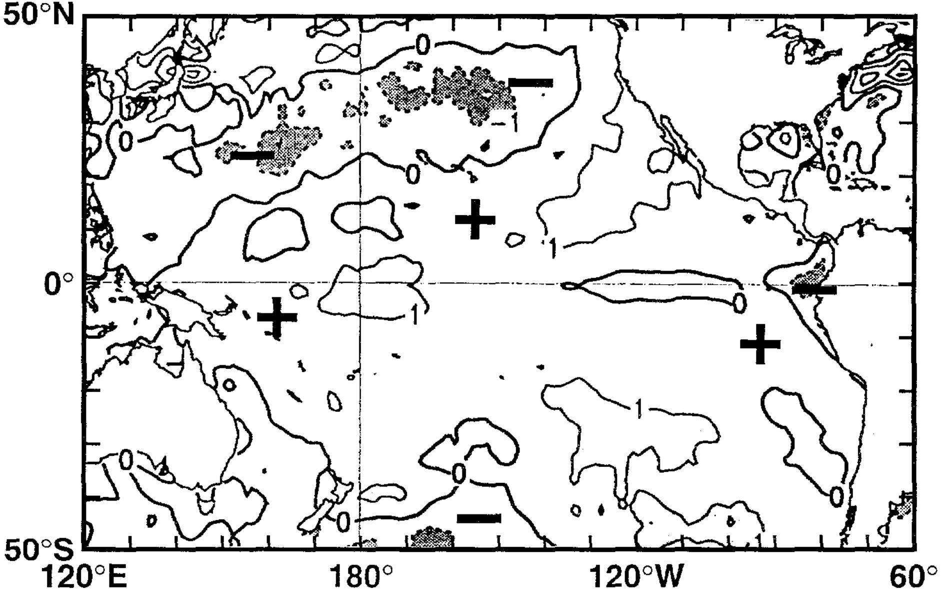

SST ANOMALY

Figure 9. Mean and anomalous SST (°C) for March 1995.

The 1995 Southern California Red Tide

The southern California coastal region was affected by a strong red tide event in spring 1995. Although no systematic study of this event was organized, a series of ad hoc observations including measurements from small boats and the SIO Pier, counts of phytoplankton samples collected on CalCOFI cruises, and observations from private planes and ships of opportunity allow a preliminary description of this phenomenon and its relation to the local weather. Discoloration of the coastal waters of southern California caused by massive accumulations of phytoplankton has been relatively common. Red tides have been recorded in the southern California region since 1901 (Torrey 1902), and they are usually created by the dinoflagellate species *Gonyaulax polyedra*, *Porocentrum micans*, *Gymnodinium sanguinium*, and—as "yellow tides"—*G. flavum*.

During the first four months of 1995, an exceptional

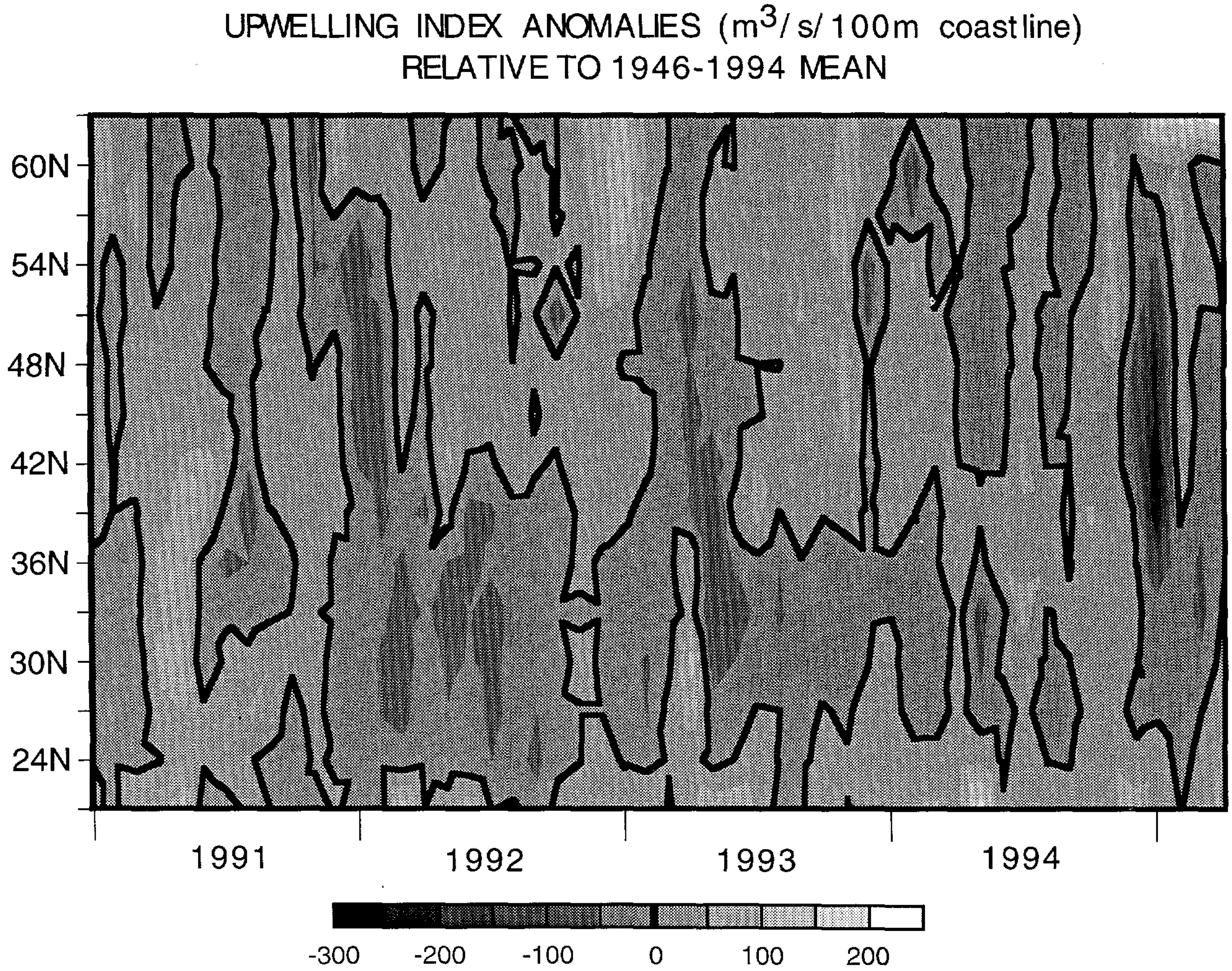


Figure 10. Contour plot of anomalies of monthly averaged coastal upwelling indices for January 1991 through April 1995 for 22°N to 60°N. Anomalies are referenced to the 1946–94 period. Positive values denote stronger-than-average upwelling, or weaker-than-normal downwelling. *Lighter shading* denotes higher (more upwelling) values. *Bold contours* denote zero anomaly (value equal to long-term monthly mean).

bloom of *Gonyaulax polyedra* Stein was recorded from Santa Barbara to San Diego, and as far offshore as San Clemente Island. This bloom reached concentrations of more than 2 million cells l^{-1}, with associated values of chlorophyll of 519 μg chl a l^{-1} at La Jolla. These were not the highest values recorded for this region; Holmes et al. (1967) measured similar chlorophyll values during a *Gymnodinium* bloom during May 1964. Not since the records of Torrey (1902), however, has a bloom been so dense or so widespread. While apparently nontoxic, this bloom was unusual in its timing, duration, and spatial extent.

January, February, and March 1995 were unusually wet in southern California, with some record warm temperatures during February. Approximately 17 inches of rain were recorded in San Diego, with about 10 inches falling in January alone (figure 11). Normal rainfall from July 1 to May 1 is about 9.7 inches. Extensive flooding occurred in northern California, while landslides, flooding, and great coastal runoff were recorded in many communities along the Southern California Bight.

Cell counts of samples taken from the SIO Pier on January 3, 1995, showed nearly 60,000 cells l^{-1} of *Gonyaulax polyedra*. This sample preceded the first major San Diego rainstorm by one day, indicating that there was a substantial population of *G. polyedra* in the water column before the heavy rains and runoff. Mixed-layer samples taken during the first 1995 CalCOFI cruise (9501) showed up to 80,000 cells l^{-1} in coastal waters of the Southern California Bight, with *G. polyedra* dominant in every coastal station (figure 12). The highest cell concentrations were associated with anomalously fresh water (salinity of 32.8) located between lines 90 and 87. Consistent with this, CTD/Rosette casts on CalCOFI cruise 9501 showed low surface salinity at a few coastal stations, and high nutrient concentrations in the low-salinity surface water.

The surface waters off Scripps Pier were freshened

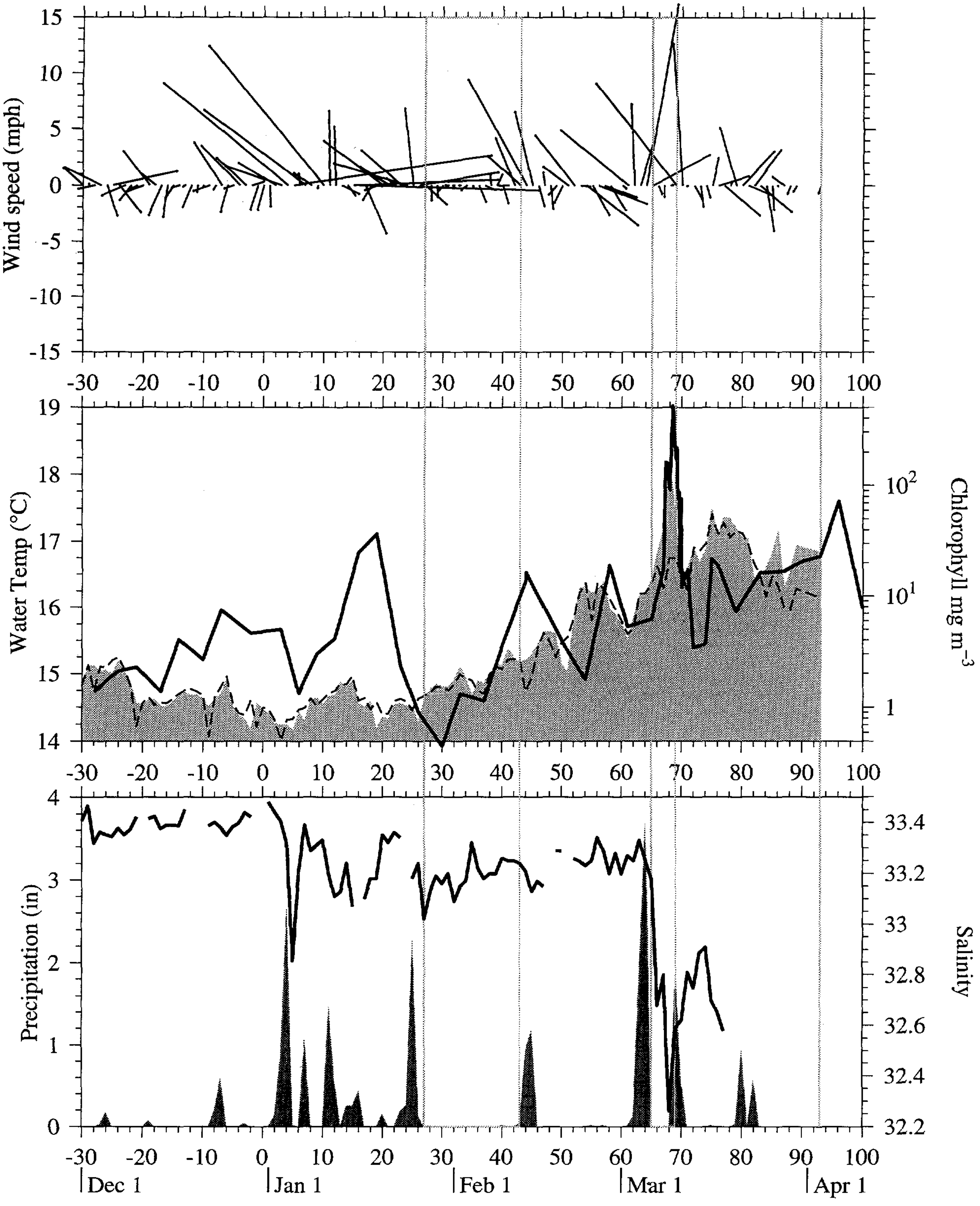


Figure 11. *Upper panel*, time series of wind speed and direction measured at the SIO Pier. Vector points in the direction toward which the wind was blowing. *Middle panel*, surface (*shaded area*) and bottom (*dashed line*) water temperatures measured at the SIO Pier. Temperatures are uncalibrated, but the trends are believed to be accurate. Chlorophyll concentration (*heavy solid line*) measured from surface samples taken at the SIO Pier. *Bottom panel*, precipitation (*shaded curve*) measured in San Diego, and surface salinity (*heavy line*) at SIO Pier. *Vertical gray lines* bracket the period of initial red patch observation and red tide growth (January 27 to February 12), peak red tide density and bioluminescence (March 6 to March 10), and peak *Noctiluca* concentrations (April 3).

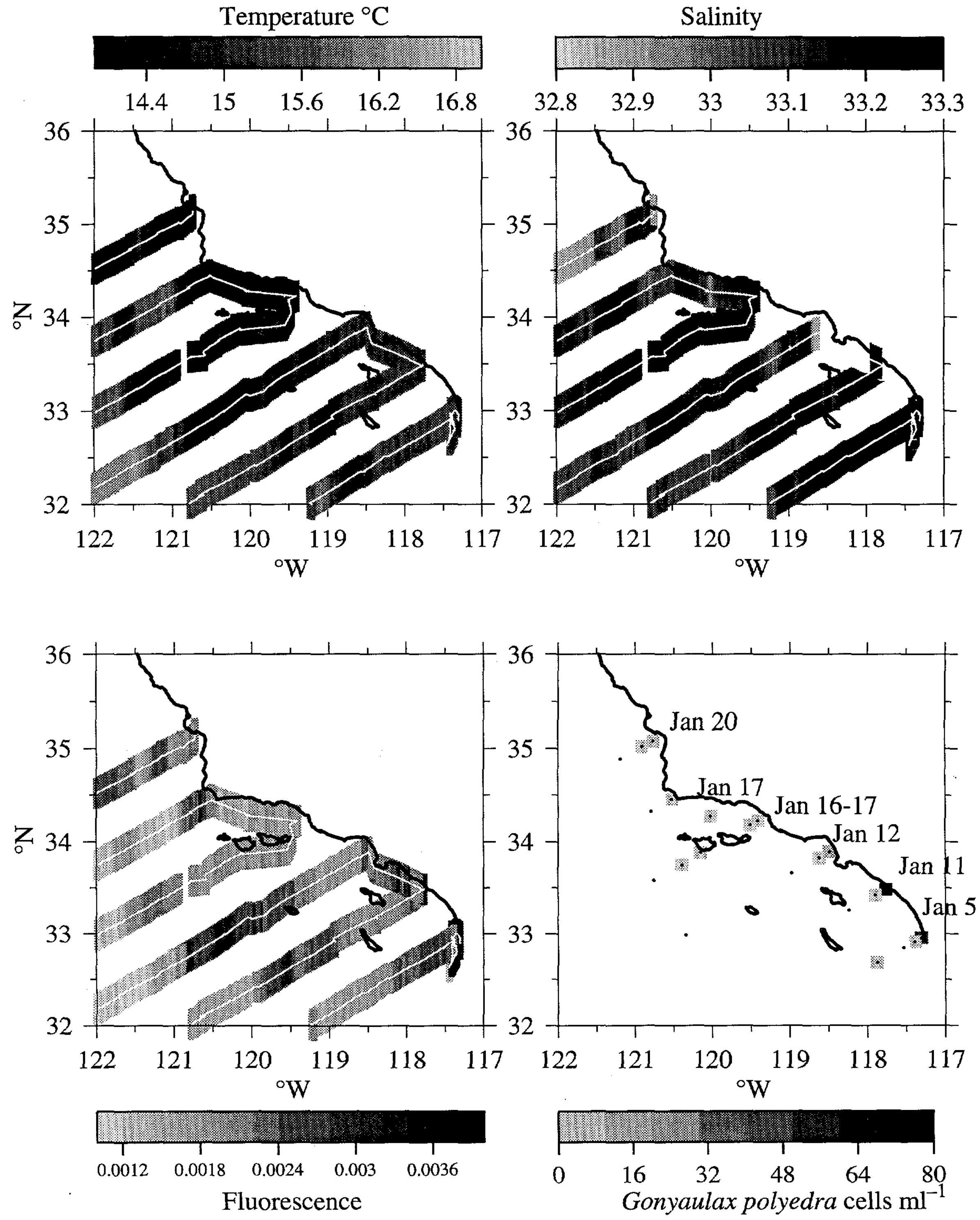


Figure 12. Temperature, salinity, fluorescence, and *Gonyaulax polyedra* cell concentration on CalCOFI cruise 9501. Data are from the continuous underway data logging system. *White line* gives the ship track. The salinity was below 30 (minimum value of about 22.5) in the area along the coast between the second and third lines (about 32.5° to 33°N) where no data are apparent. Dates on the *G. polyedra* panel indicate when the station was occupied.

dramatically after a major storm on January 4. By the middle of January chlorophyll values had climbed to nearly 40 $\mu g\ l^{-1}$, but they declined sharply during the latter part of the month. Around February 1, visible patches of red water were evident off the SIO Pier and in the waters off Point Loma. On February 7, red patches were observed off San Clemente Island. A calm, sunny period during the first two weeks of February led to warming of the surface waters and steadily increasing chlorophyll values at La Jolla. The phytoplankton community was dominated by *Gonyaulax polyedra*, which created almost a monoculture in coastal waters. By the first week of March, coastal waters were dark brown, with obvious stripes and patches created by the interaction of physical flows and dinoflagellate swimming behavior (e.g., Kamykowski 1974, 1981). Nocturnal bioluminescence was quite spectacular: the crests of breaking waves glowed with a strong blue light. The bioluminescence and chlorophyll peaked at SIO on March 10. Strong winds beginning on the night of March 10 temporarily dissipated the bloom.

The phytoplankton bloom recovered after the March 10 storm, but never to the levels recorded the previous week. About this time, high numbers of the heterotrophic dinoflagellate *Noctiluca miliaris* were recorded in the plankton, and the cells were filled with *Gonyaulax polyedra*. By the first week of April, the *Noctiluca* had reached such high concentrations that they created bright orange stripes in convergence zones along the coast. Observations from a small plane showed that these stripes were less than 100 m wide in their cross-shelf dimension, and as much as 40 km long, stretching from Point Loma to Solana Beach. The surface waters were a dense orange color, created by massive accumulations of floating *Noctiluca*. A storm during the weekend of April 8 effectively dissipated both the *Noctiluca* and *Gonyaulax* blooms.

The occurrence of such a dense *Gonyaulax polyedra* bloom in the winter months in the coastal waters of southern California had never previously been observed. Previous records show this dinoflagellate species to form red tides only during May–September (Torrey 1902; Allen 1938, 1946; Clendenning 1958; Holmes et al. 1967). The unusual timing of the formation of *G. polyedra* red tide is probably related to the unusual oceanographic conditions prevailing in the region during the winter of 1994–95 (see previous section).

Although there were substantial numbers of *Gonyaulax polyedra* present in the coastal waters before the high rainfall of January 1995, it is likely that the nutrients contained in the runoff contributed to the exceptionally high blooms seen during the following several weeks. In particular, the peak biomass and bioluminescence during the first week of March followed a very heavy rain and strong heating of the surface waters. The strong stratification that developed probably isolated the nutrients in the freshwater runoff to the surface layer, creating a well-lit, nutrient-rich stratum. Growth rates estimated from changes in chlorophyll concentration at the SIO Pier were very roughly 0.1 day^{-1}, a reasonable value for this dinoflagellate (e.g., Thomas and Gibson 1990). Peak growth rates may have been higher, but were still probably much lower than the maximal growth rate possible at that temperature (about 1.4 day^{-1} for diatoms at 14°C; Eppley 1972).

The decline of the *Gonyaulax polyedra* bloom was related both to grazing by *Noctiluca miliaris* and to storms. The highest concentrations of *Noctiluca* were found offshore of the maximum *Gonyaulax* numbers, in relatively clear waters (Secchi depths of 12–14 m versus 1–4 m in the *Gonyaulax* bloom). The clarity of the water probably resulted as grazing *Noctiluca* eliminated *Gonyaulax* from the water column. Both the *Gonyaulax* and *Noctiluca* blooms disappeared suddenly after a storm on April 8, which mixed the populations downward and washed them out to sea.

Pattern on CalCOFI Survey Cruises

9401. As suggested by the preliminary data shown previously (Hayward et al. 1994), the circulation pattern in January 1994 consisted of a meandering southward-flowing jet of low-salinity water (figure 13). The flow field was perturbed by a series of several strong mesoscale eddies. This flow field was anomalous with respect to the long-term January pattern derived from the harmonic mean dynamic height field in that the typical, well-developed inshore countercurrent was absent. This was in marked contrast to January of 1992 and 1993, when the coastal countercurrent was exceptionally strong and broad due to El Niño conditions (Hayward 1993; Hayward et al. 1994; Lynn et al. 1995). (The long-term harmonic mean dynamic height field for the period of time corresponding to each CalCOFI cruise is shown in Hayward et al. 1994.) Surface chlorophyll was generally low throughout the grid, except for a band of relatively high values (>1 $\mu g\ l^{-1}$) along the coast. Vertical sections along line 90 (shown in Scripps Institution of Oceanography 1994) show that shoaling of the pycnocline and nutricline at the inshore edge of the high-velocity southward flow features is associated with regions of elevated chlorophyll.

9403. The flow field on cruise 9403 was similar to the long-term mean pattern for March, with southward flow extending inshore to the coast and the normal seasonal absence of the Southern California Eddy (figure 14). These observations again show that pattern in the 100 m temperature field based upon preliminary data (shown in Hayward et al. 1994) was a good predictor of the dynamic height field. An eddy dipole was present in the

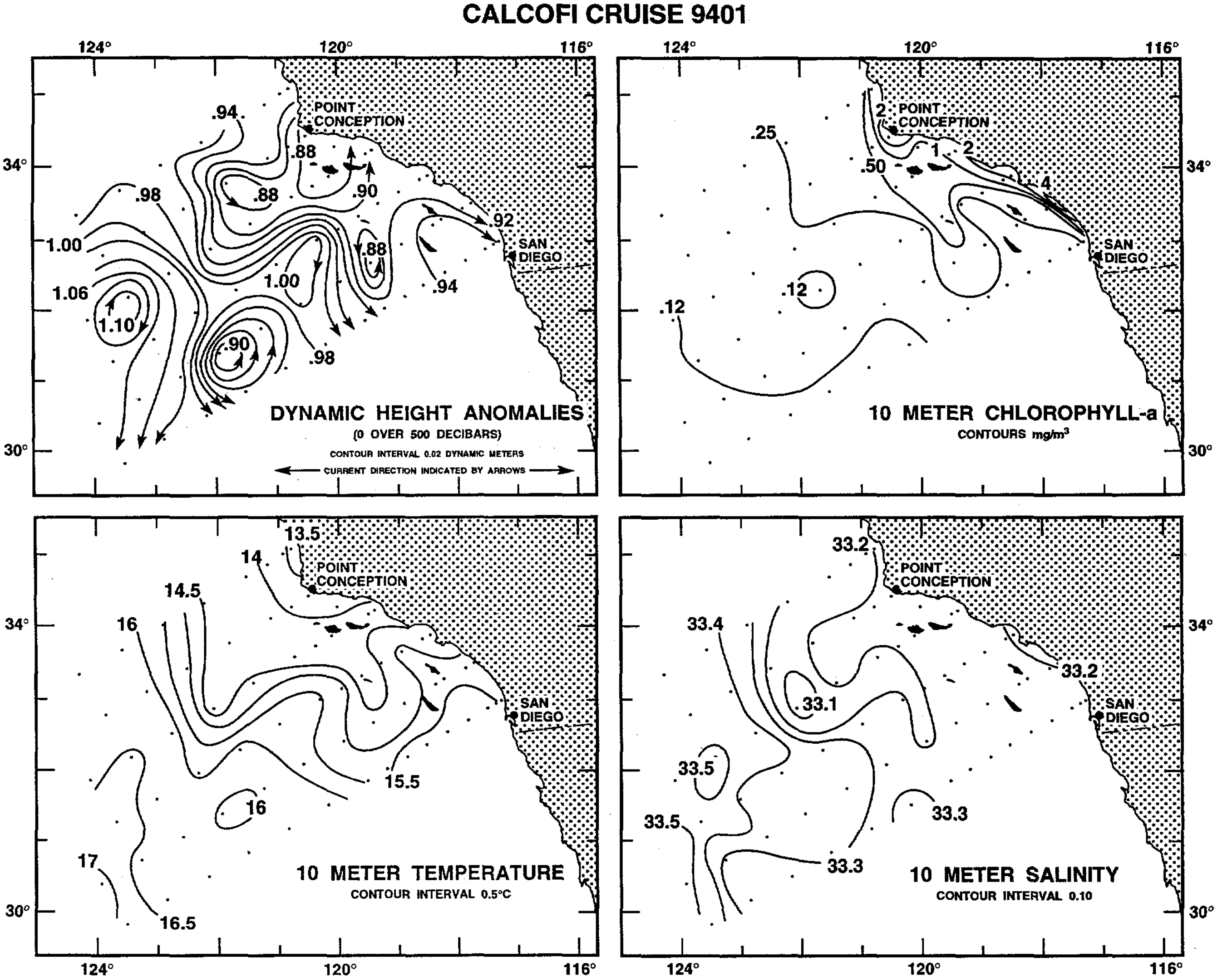


Figure 13. Spatial patterns for CalCOFI cruise 9401, 20 January–7 February 1994, including upper ocean flow field derived from 0 over 500 m dynamic anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

offshore part of the pattern. Chlorophyll increased to relatively high values (>4 µg l^{-1}) in the central coastal region, especially the Santa Barbara Channel. Vertical sections along line 90 show the sharp rise of the pycnocline and nutricline in the coastal region which is expected from the flow field, and that chlorophyll is elevated in the region where the nutricline has shoaled (figure 15).

9408. The circulation pattern in August 1994 continued to be typical of the long-term mean: the Southern California Eddy and a coastal countercurrent were well developed throughout the sample grid (figure 16). Broad southward flow of the low-salinity core of the California Current was evident offshore of the Southern California Eddy. No well-developed eddies were present in the sample grid. There was a sharp offshore bend to the California Current and associated east-west front between lines 90 and 93. Ten-meter chlorophyll was generally low throughout the grid, with the exception of the coastal region near Point Conception, where higher values were seen especially at inshore stations.

9410. The October 1994 current structure was also quite similar to the long-term mean pattern for October, with a broad coastal countercurrent extending along the shore to north of Point Conception, and southward flow of the low-salinity core of the California Current offshore (figure 17). Mesoscale structure had intensified from the weak structure of August, and several mesoscale eddies were now apparent within the sample grid. The sharp offshore bend of the California Current evident during the previous August was absent, indicating that it was not a persistent feature; this was in contrast to a sharp bend in the California Current in the same region, which persisted for at least six months during

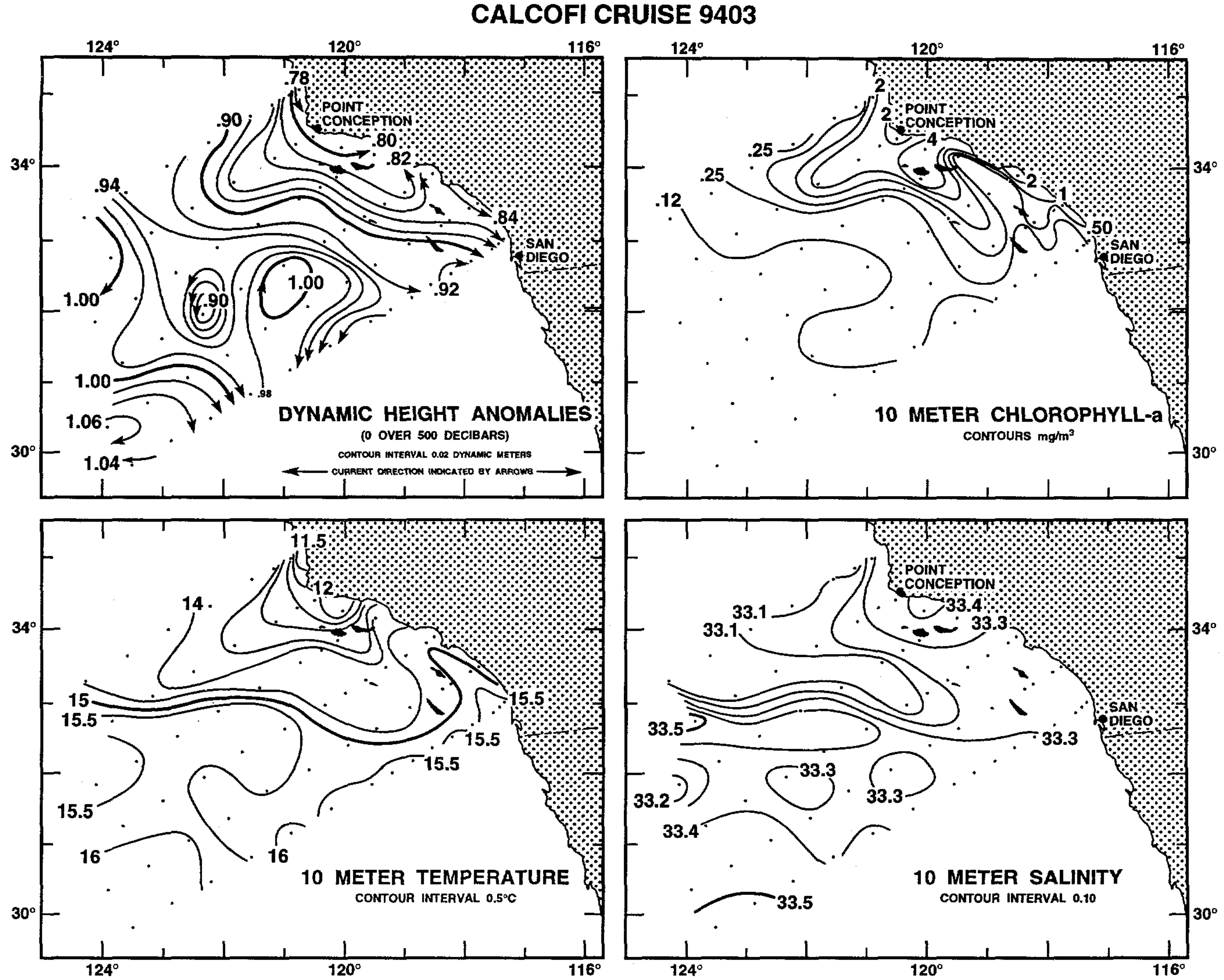


Figure 14. Spatial patterns for CalCOFI cruise 9403, 22 March–8 April 1994, including upper ocean flow field derived from 0 over 500 m dynamic anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

1993–94 (Hayward et al. 1994). Ten-meter chlorophyll continued to be low, except for the coastal region near Point Conception.

9501. The January 1995 dynamic height field indicated a confused circulation pattern with generally southerly flow in the offshore region of the California Current perturbed by a series of several strong mesoscale eddies (figure 18). There was strong onshore flow between lines 77 and 80. A coastal countercurrent was evident in southern California, and there was strong southward flow along the coast at Point Conception. The overall pattern was anomalous with respect to the long-term mean in that the northward flow along the coast did not extend around Point Conception. The January cruise sampled during a period of strong winter storms which also brought extremely heavy precipitation to California and much of the west coast. Some of the most inshore stations showed low surface salinity, high nutrient and high surface chlorophyll concentrations, presumably due to runoff and the developing red tide event. Chlorophyll exceeded 10 $\mu g\, l^{-1}$ at station 90.28. Ten-meter chlorophyll values were greater than in January of 1992 or 1993, with a pool with values of greater than 1 $\mu g\, l^{-1}$ offshore of southern California. Elevated values of chlorophyll were present in the coastal region near Point Conception as on several prior cruises.

9504. The April 1995 cruise sampled during what was perhaps the roughest weather observed at sea during a CalCOFI cruise in the last decade. In contrast to the large-scale patterns in atmospheric forcing, there were strong northerly winds and strong coastal upwelling for the duration of the cruise. This was also a cruise with some of the highest values of chlorophyll (and presumably primary production; e.g., Mantyla et al. 1995)

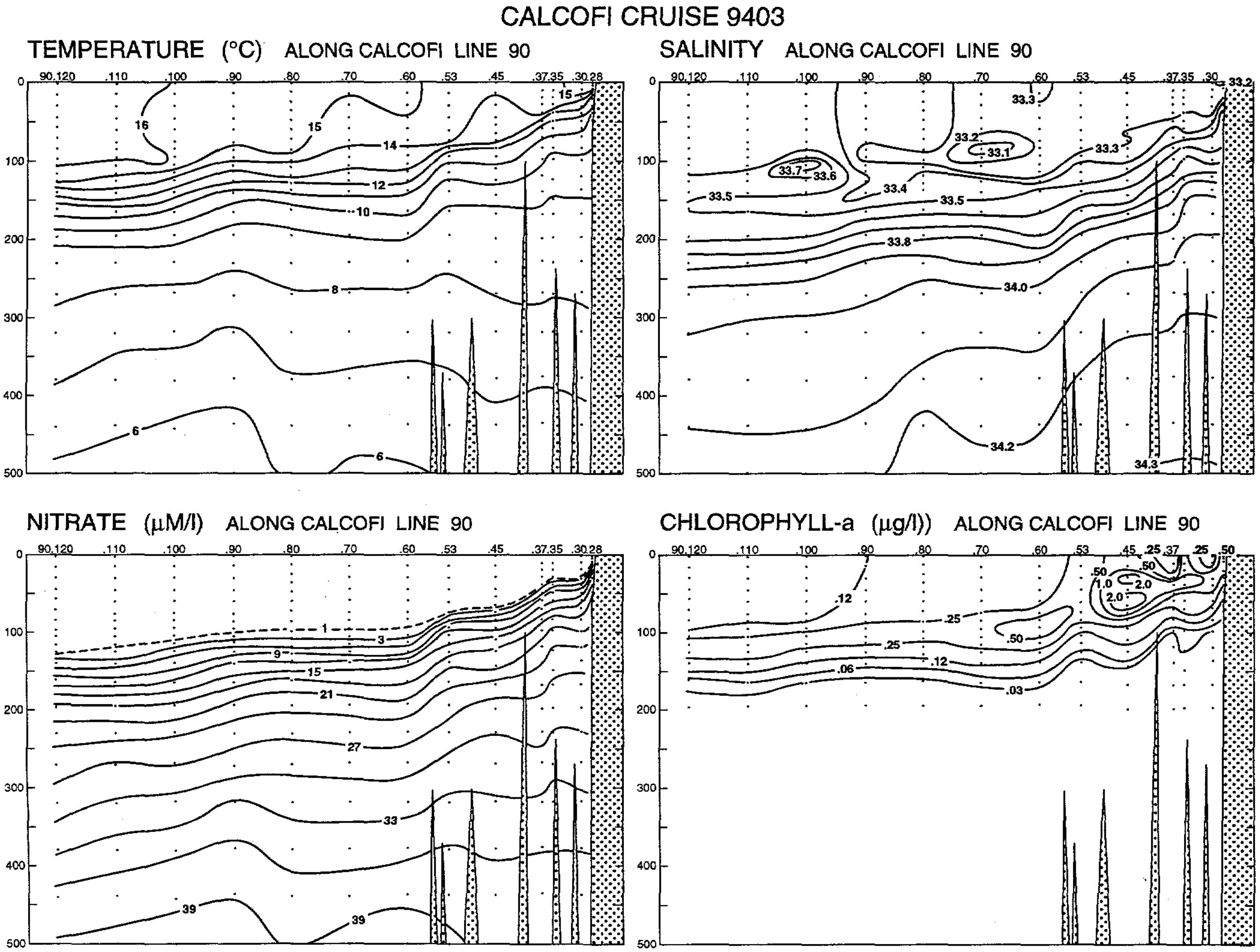


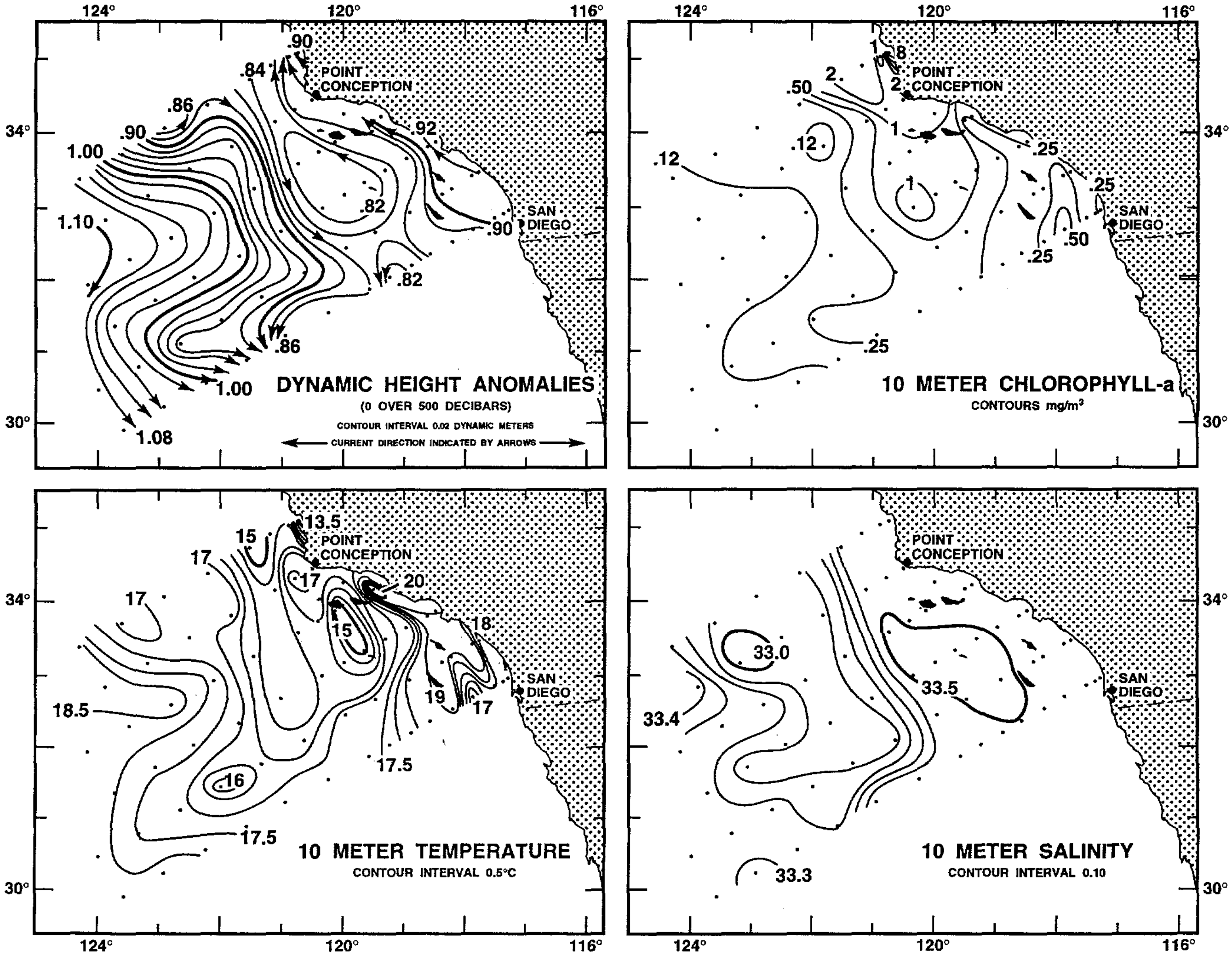
Figure 15. Vertical sections of temperature, salinity, nitrate, and chlorophyll along line 90 for cruise 9403.

during the past decade. The hydrographic data are preliminary. The current field inferred from the 100 m temperature shows generally southward flow with a strong eddy in the outer part of line 87 (figure 19). This looks very much like the long-term mean pattern of dynamic height. The coastal countercurrent appeared to be absent. In spite of the large positive SST anomalies at La Jolla, the circulation pattern is not consistent with El Niño conditions being present in the California Current. Ten-meter chlorophyll was very high throughout the coastal region. Values of greater than 20 µg l^{-1} were observed in the Santa Barbara Channel, and the area with values greater than 4 µg l^{-1} was quite extensive. This area was much more extensive than the area affected by the southern California red tide event. Examination of the phytoplankton samples showed that phytoplankton in the high chlorophyll regions was dominated by diatom species characteristic of the spring bloom, although red tide species were still present at some inshore stations in the Southern California Bight. Chlorophyll was much higher than in cruise 9304, probably due to sampling later in the year and a stronger bloom.

Central California Observations

The region off central California between Monterey Bay and Bodega Bay was surveyed once in March 1994 and three times in May–June 1994, as part of the SWFSC Tiburon Laboratory's annual surveys of pelagic young-of-the-year rockfish (data provided by William Lenarz and Stephen Ralston). At this time, the CTD data are available for interpretation; ADCP and biological data are currently being processed. The Tiburon Laboratory can supply further information on these data sets. In addition, the hake surveys in early 1995 extended north to this region.

The hydrographic and dynamic nature off central California during early 1994 suggests a return to more typical conditions following the 1992–93 El Niño period,



CALCOFI CRUISE 9408

Figure 16. Spatial patterns for CalCOFI cruise 9408, 5–20 August 1994, including upper ocean flow field derived from 0 over 500 m dynamic anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

consistent with the results of the CalCOFI surveys off southern California. The circulation in early March 1994, inferred from near-surface dynamic heights relative to 500 db, was generally southward and meandering, in stark contrast to the poleward flow noted at this time of year in 1992 (Lynn et al. 1995). The dynamic thickness of the upper ocean in 1994 was 5–10 dyn. cm lower than in early 1992 (Lynn et al. 1995) and 1993 (Sakuma et al. 1994), due to the post–El Niño return of more dense (cooler, more saline) water. The 1994 thickness values were more similar to early 1991, although the upper ocean was slightly warmer and fresher in 1994, suggesting a residual El Niño water type.

The dynamic topography in May–June 1994 off central California showed a continuation of the meandering southward flow typical of this time of year. Again the upper ocean was as much as 10 dyn. cm lower than during May–June 1992 (Lynn et al. 1995) and 1993 (Sakuma et al. 1994). Dynamic heights were very similar in magnitude and structure to 1991. Upper water-column temperatures and salinities were near typical values for this area, and cooler and more saline in comparison to 1992 and 1993. Slope water at 200 m depth in 1992 was cooler and fresher relative to 1992 and 1993, as well as relative to the long-term means. A possible explanation for this is a reduced undercurrent, or increased transport in the California Current. Alternatively, the California Current may have been displaced more onshore than normal at mid-depths.

Preliminary analysis of the CTD data collected during the hake egg and larvae surveys of March and April 1995 that were conducted off southern and central California (figure 1) were consistent with the circulation patterns observed on the CalCOFI cruises made

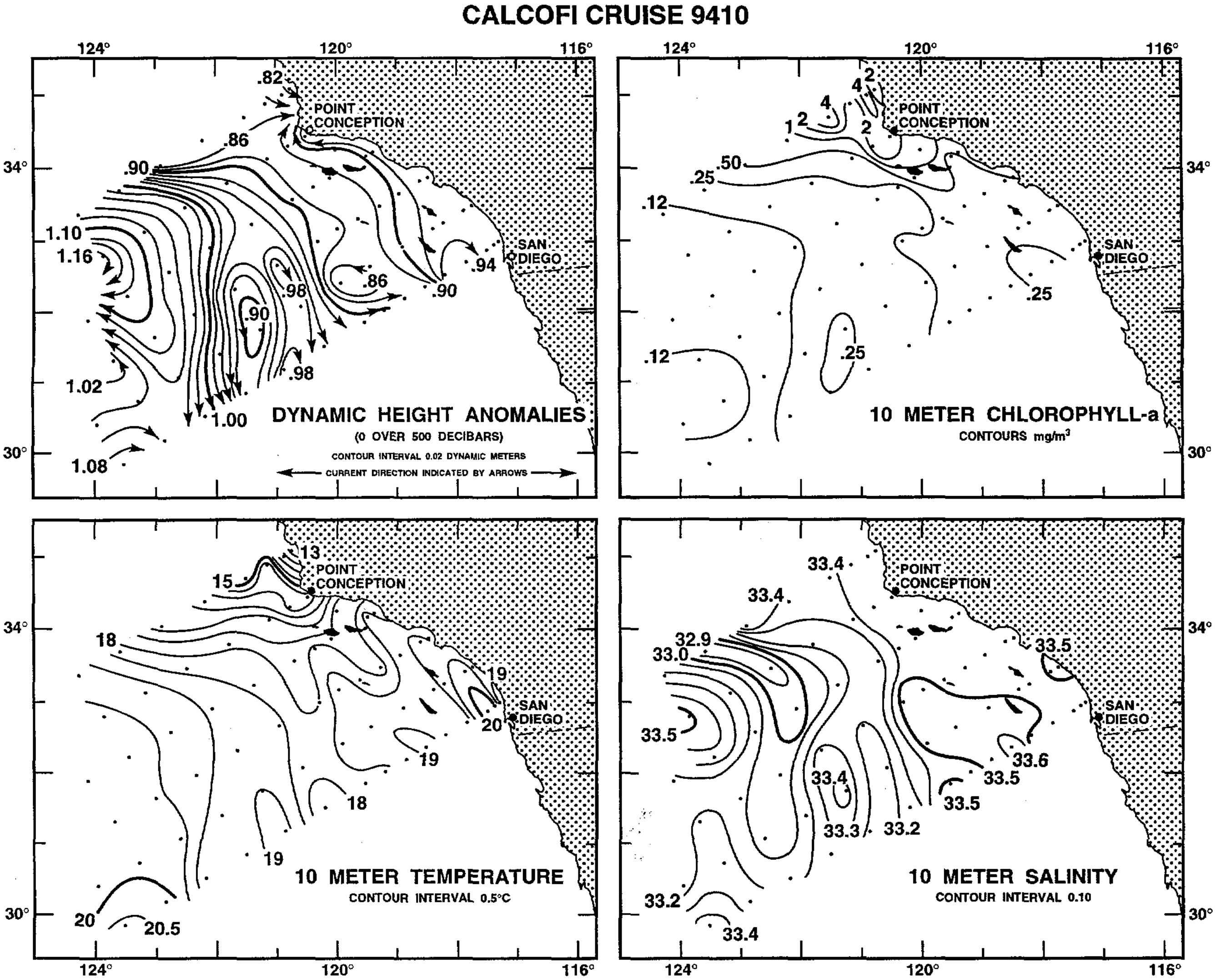


Figure 17. Spatial patterns for CalCOFI cruise 9410, 30 September–16 October 1994, including upper ocean flow field derived from 0 over 500 m dynamic anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

during the same period. The countercurrent was weak or absent, and the general southward flow was perturbed by a strong mesoscale eddy field.

DISCUSSION

The circulation pattern in the California Current during January 1994 was anomalous in the absence of a coastal countercurrent. By March, however, the circulation had returned to a pattern typical of the long-term mean, and this condition persisted into early 1995. The 1994–95 period followed El Niño conditions in the California Current during 1992–93, which were characterized by an anomalously strong and broad coastal countercurrent during winter months and a deeper than normal pycnocline and nutricline. Spatial pattern in dynamic height during most of 1994 and early 1995 was similar to the long-term harmonic mean, with a mesoscale eddy field superimposed upon it. In contrast to 1992–93 (Hayward et al. 1994), during 1994 the major features in the mesoscale structure, such as eddies and sharp meanders of the California Current, did not persist in a clearly recognizable pattern between cruises. The main mesoscale pattern of 1994–95 was a waxing and waning in the number and intensity of mesoscale eddies. Mesoscale structure declined to a low level in August 1994, when no strong eddies were apparent within the CalCOFI grid, and it then increased in the fall of 1994 and early 1995.

Winter and spring of 1995 was a period of transition in the atmospheric circulation pattern. The storms and reduced upwelling of early 1995 were associated with the formation of a strong and persistent atmospheric low off the U.S. west coast. Under this winter regime winds along the California coast were anomalously southerly,

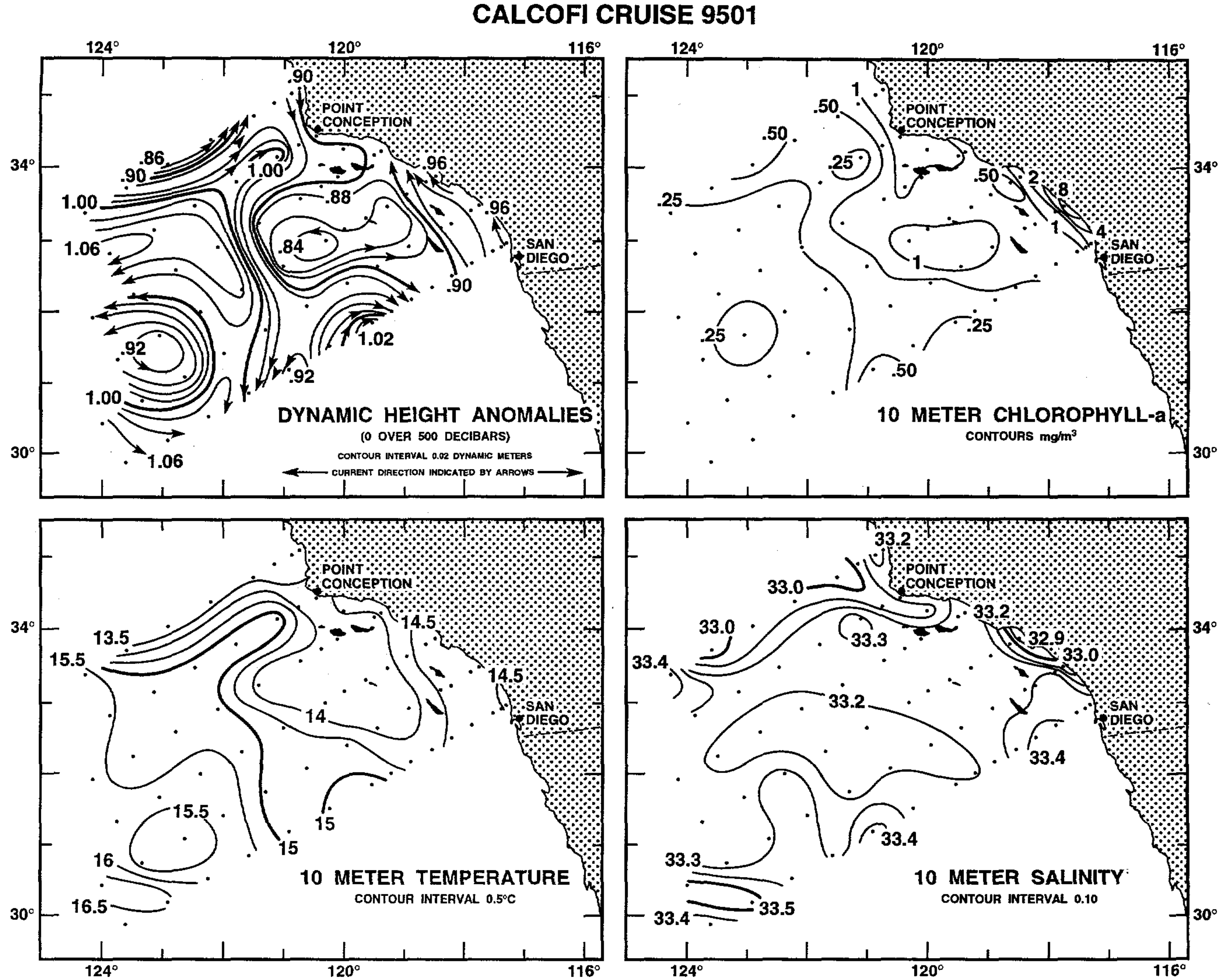


Figure 18. Spatial patterns for CalCOFI cruise 9501, 4–21 January 1995, including upper ocean flow field derived from 0 over 500 m dynamic anomalies, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

leading to reduced upwelling and warmer SSTs. But also note that the April 1995 CalCOFI cruise sampled during a period of strong upwelling and that there was an extensive phytoplankton bloom dominated by spring bloom species. Some combination of weather and oceanographic conditions during winter and early spring resulted in development of the extensive red tide in southern California. The causal factors may have included several strong storms and high runoff alternating with several days of calm and unusually warm weather in southern California and the strong slope of the pycnocline and nutricline associated with the southward flow of the California Current. Determination of what initiated the red tide will be an interesting area for further research.

The circulation pattern of the California Current during 1994 and early 1995 was not related to the coastal shore-station data in the expected manner. Predictions of a continuation or intensification of El Niño conditions in the California Current (e.g., enhanced poleward flow and a deepening of the thermocline and nutricline) based upon either the anomalously warm water at La Jolla during the second half of 1994 and early 1995 or the abrupt increase in sea level in January–March 1995 at San Francisco would have been incorrect. This shows that further research and modeling effort will be needed in order to predict the physical and biological structure of the California Current from the real-time data that are available.

Biological pattern during the study period showed a continuation of the long-term trends seen over the past few years. Chlorophyll and primary production in the CalCOFI region were typical of values observed during the prior decade. Macrozooplankton biomass continued

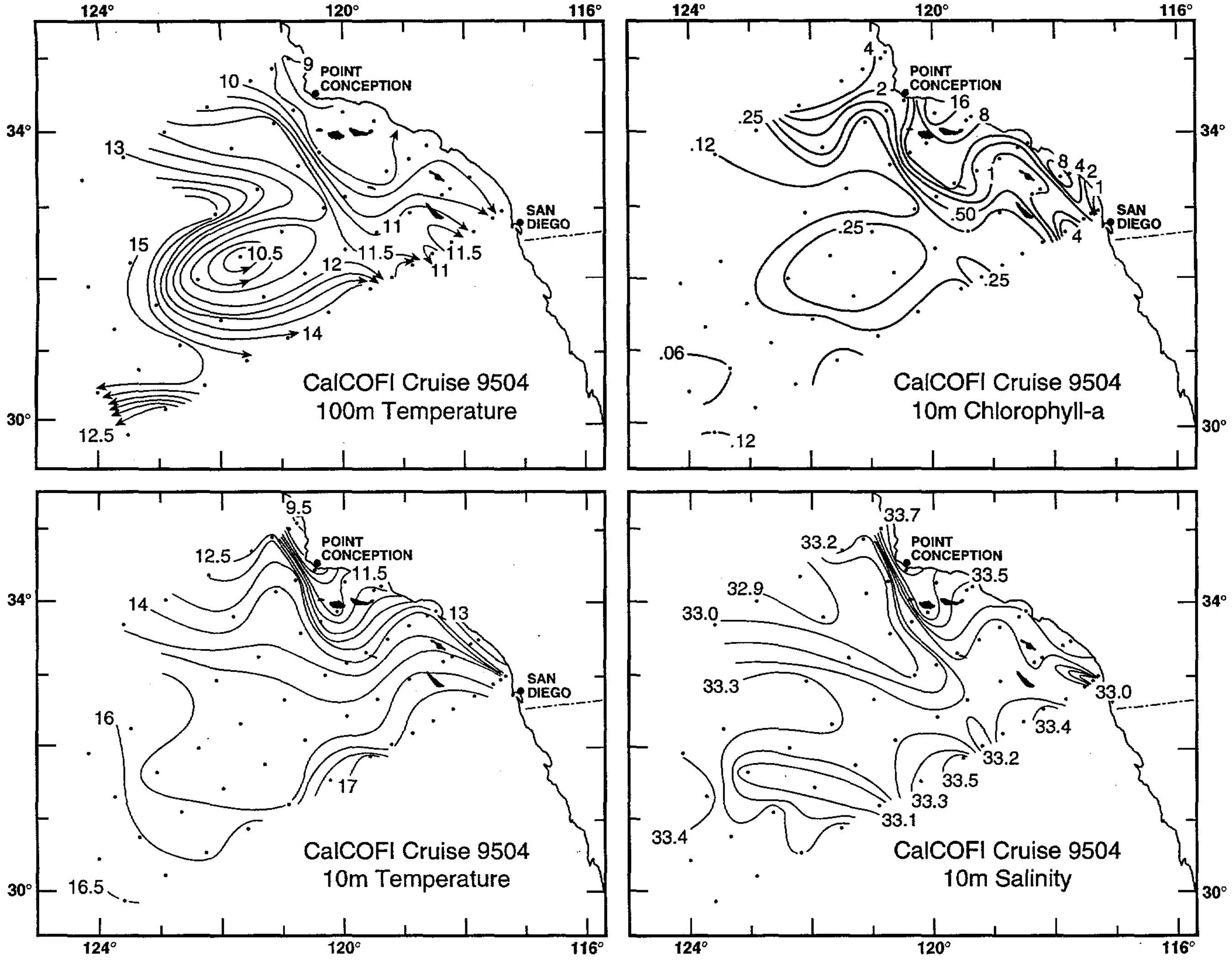


Figure 19. Spatial patterns for CalCOFI cruise 9504, 6–22 April 1995, including upper ocean flow field derived from the 100 m temperature field, 10 m chlorophyll, 10 m temperature, and 10 m salinity.

the long-term trend of anomalously low values, with the last two years low even in the context of the prior ten years. The winter 1995 red tide in southern California was notable because of its spatial extent (at least San Diego to Santa Barbara), its unusual timing, its density (greater than 500 μg chl a l^{-1}; 2×10^6 cells l^{-1}), its striking nocturnal bioluminescence, and its obvious discoloration of the coastal waters. Although the published reports have been inadequate, this was the first reported *Gonyaulax polyedra* red tide since 1966, and was the densest reported since 1958. Biweekly chlorophyll samples from the SIO Pier have a mean of 1.574 μg chl a l^{-1}, and a standard deviation of 2.159 μg chl a l^{-1} (1984–92). The peak value of 519 μg chl a l^{-1} recorded during the 1995 red tide was 240 standard deviations above the mean, underscoring the unusual nature of this event. It was geographically the largest red tide recorded in the last 95 years, and one of the densest and most persistent on record.

ACKNOWLEDGMENTS

We thank the many individuals in the technical groups at each of the participating agencies for their extraordinary efforts in collecting and processing the data shown here.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

Fallen Leaf Lake, California
October 25, 1994

THE 1991–92 EL NIÑO AND ITS IMPACT ON FISHERIES

In June 1958, Oscar Sette and John Isaacs assembled an eminent group of physical and biological scientists to describe and discuss "The Changing Pacific Ocean in 1957 and 1958." The list of participants includes names now recognized as the founders of modern climatology and of physical, biological, and fisheries oceanography. The symposium set a standard in terms of the multidisciplinary approach that must be used to address this complex subject. Its proceedings, published in *CalCOFI Reports*, volume VII (1960), is still one of the most comprehensive views of El Niño in the Pacific, and remains fascinating reading after nearly forty years.

Since the 1957 event, the California Current ecosystem has experienced several other El Niño–Southern Oscillation (ENSO) and El Niño–like episodes. With each new ENSO event, researchers have combined past experience with technological advancements to further our understanding of this phenomenon and its ramifications throughout the ecosystem. On the heels of the 1992–93 event, which occurred in conjunction with a particularly large number of ongoing fisheries research programs, the CalCOFI organizing committee felt it appropriate to reevaluate what is known about ENSO and its impact on the fisheries of the California Current. In the spirit of the 1958 meeting, we organized the 1994 CalCOFI Symposium, "The 1991–92 El Niño and Its Impact on Fisheries," as part of the 1994 CalCOFI Conference at the Stanford Alumni Association's Sierra Camp Conference Center. Although this was certainly not the only ENSO symposium to take place in recent years, its focus on fisheries-oceanography linkages during ENSO events make this conference and its proceedings unique.

The contributors describe the effects of the 1991–93 ENSO within different coastal regions of the northeast Pacific Ocean, from the Gulf of Alaska to Baja California, and compare them to previous ENSO events. In most cases the results are described in a multidisciplinary sense, relating the consequences of environmental perturbations to the fisheries ecosystem, with comparisons to "normal" years. The fisheries implications of La Niña ("cold" year) events are considered as well. A particular emphasis is the incorporation of results from all disciplines to create an integrated presentation that best represents our current understanding.

In addition to the authors listed in these papers, numerous other researchers contributed to the results and analyses described here and are recognized for their collaborative efforts. Finally, we gratefully acknowledge the experts who sent us timely reviews of the manuscripts, which added to the quality of these proceedings.

Franklin Schwing
Stephen Ralston

Participants in the Symposium of the CalCOFI Conference: The 1991–92 El Niño and Its Impact on Fisheries. *Left to right*: (*above*) Martin Dorn, Paul Smith, Bill Lenarz, David Ainley, Greg Hammann, Allen Macklin, Frank Schwing, Ron Lynn; (*below*) Tom Murphree, Steve Ralston.

EL NIÑO AND LA NIÑA EFFECTS ON THE NORTHEAST PACIFIC: THE 1991–1993 AND 1988–1989 EVENTS

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ABSTRACT

The 1991–93 El Niño and 1988–89 La Niña events had substantial effects throughout the tropical Pacific Ocean and atmosphere. These events also greatly affected the extratropics, especially the northeastern Pacific region. A mechanism which appears to have been important in producing these effects was tropical atmospheric forcing of the mid-latitude atmosphere. This process caused shifts in the mid-latitude storm track over the North Pacific. These shifts led to marked changes in the wind forcing of the ocean, which apparently caused substantial ocean anomalies. Evidence for an additional teleconnection mechanism involving ocean Kelvin waves was found in the equatorial Pacific.

1. INTRODUCTION

Many studies have linked El Niño conditions in the tropical Pacific to low-frequency variations in the northeast Pacific atmosphere and ocean (e.g., Bjerknes 1972; Horel and Wallace 1981; Haney et al. 1983; Emery and Hamilton 1985; Mysak 1986; Namias 1986; Simpson 1992). The northeast Pacific variations that have received the greatest attention are anomalous seasonal-to-interannual fluctuations in atmospheric pressures, winds, and precipitation; in oceanic near-surface temperatures, salinities, and currents; and in sea levels. Most attention has been directed to fluctuations that occurred during and soon after the mature phase of El Niño events (Rassmusson and Carpenter 1982). These fluctuations are also thought to have large effects on many marine organisms. Such effects have created a great deal of interest in unravelling the physical processes by which El Niño events affect the extratropical northeast Pacific atmosphere and ocean (e.g., Glantz et al. 1991).

We review in this paper some of the major large-scale ocean and atmosphere processes that occurred during the 1991–93 El Niño and 1988–89 La Niña events, including their apparent effects on the extratropical northeast Pacific region. La Niña events, sometimes called anti-El Niño or cold events, produce effects in the northeast Pacific that tend to be the reverse of those during El Niño events. Comparisons of the 1991–93 El Niño and 1988–89 La Niña events provide useful insights into how the tropical ocean and atmosphere may affect the northeast Pacific region. The major features of these two events and their extratropical effects are good examples of what is typically observed during El Niño and La Niña events.

In the following sections, the 1991–93 event is presented primarily in terms of oceanic and atmospheric phenomena from January to June 1992, because the events during this period were representative of the major features and effects throughout the event.

2. DATA AND METHODS

We have used a variety of data from several sources for this study. The main data and their sources are:

1. daily mean equatorial Pacific Ocean temperatures, currents, and surface winds from the Tropical Ocean-Global Atmosphere (TOGA) moored buoy array in the equatorial Pacific (McPhaden 1993);
2. weekly mean sea-surface temperature (SST) analyses from the Climate Analysis Center of the National Meteorological Center[1];
3. monthly mean outgoing longwave radiation analyses from the Climate Analysis Center of the National Meteorological Center; and
4. daily mean global atmospheric geopotential height and wind analyses from the European Centre for Medium-range Weather Forecasts (ECMWF).

The ocean temperatures from the TOGA buoys were missing for a number of days. Also, the temperatures were not recorded at the same depths at all longitudes across the Pacific. Thus, we did some averaging and linear interpolation to fill in data gaps and produce time series at common depths.

We used the outgoing longwave radiation (OLR) data to estimate the location and intensity of tropical convective storms, and the latent heat released in those storms. The relationship of OLR to convective storms and latent heating of the atmosphere is based on the following reasoning. OLR represents the infrared radiation emitted to outer space by Earth. Thus OLR depends very strongly on the temperature of the region of Earth from which the emission occurs (Hartmann 1994). Areas

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[1] Reynolds, R. W., and T. M. Smith. A high-resolution sea surface temperature climatology. MS submitted to J. Climate.

of strong tropical atmospheric convection (i.e., deep tropical storm systems) have tall clouds, with tops about 14–18 km above sea level. At these levels, cloud tops are quite cold, and OLR amounts from these convective systems are low.

Conversely, in tropical areas without strong convection, the levels that most effectively radiate to outer space are low lying and relatively warm (e.g., ocean, land, or low cloud tops). So the OLR from these surfaces is high. Since large amounts of latent heat are released in tropical convective systems, *low* OLR values indicate *high* latent heating of the tropical atmosphere, and vice versa. Latent heating in tropical convective systems is a very important process for driving the tropical and global atmosphere. So OLR is very useful for understanding the climate system and for diagnosing climate variations such as El Niño and La Niña events.

We used the geopotential height of the 200 mb surface to represent the atmosphere's dynamic topography near the top of the troposphere (8–18 km above sea level). Since horizontal variations in pressure force atmospheric motions, this topography can be used to infer upper-tropospheric winds.

Most of the data presented in this study are in the form of anomaly fields. We define an anomaly as the deviation of an individual time mean value from a multiyear mean value. For example, a wind anomaly for April 1992 is the mean wind for April 1992 minus the mean April wind of the past 14 years. The multiyear means used for the anomaly calculations varied with the data:

1. for SST, a blend of multiyear periods spanning 1950–93, with the exact period varying with the location and type of data[2]
2. for OLR, 1974–93
3. for geopotential heights and winds, 1980–93.

3. TROPICAL PROCESSES

a. El Niño and La Niña Events

El Niño and La Niña events are characterized by a complex set of anomalous physical conditions in the tropical Pacific Ocean and atmosphere. These anomalies occur on basinwide space scales and on seasonal to interannual time scales. Two anomalies of particular interest are those in tropical Pacific sea-surface temperature (SST) and OLR. These anomalies describe changes in the temporal and spatial distribution of thermal energy in the tropical ocean and atmosphere. These changes are important because the thermal energy of the tropics plays a major role in driving the climate system.

The thermal-energy disturbances that occur during El Niño and La Niña events are large, second only to normal seasonal changes (Peixoto and Oort 1992). Thus El Niño and La Niña thermal-energy changes may generate large disturbances around the globe. SST and OLR anomalies concisely represent these changes in the thermal energy of the tropical ocean and atmosphere. SST and OLR anomalies are also convenient to work with because there are extensive satellite observations from which SST and OLR can be readily calculated.

During El Niño events, the central and eastern tropical Pacific SST is higher than normal, and the OLR is lower than normal for several months or longer. During La Niña events, the SST and OLR anomaly patterns are similar but with opposite signs. Figure 1 shows representative examples of these anomalies during the 1991–93 El Niño and 1988–89 La Niña events. These anomalies are shown for the January-February-March (JFM) seasons of 1992 and 1989, when both the tropical anomalies and the extratropical responses to these anomalies tended to be largest. Note the general reversal between the El Niño and La Niña events of (a) the tropical Pacific SST and OLR anomalies, and (b) the extratropical North Pacific SST anomalies.

Good summaries of basic El Niño and La Niña processes and their relationship to other phenomena, such as the Southern Oscillation, are given by several authors (e.g., Philander 1990; Peixoto and Oort 1992).

b. Thermal Anomalies in the Tropical Ocean

SST anomalies (SSTAs) are an important and very commonly used indicator of anomalous ocean processes and air-sea heat exchange. But for processes and exchanges occurring on intraseasonal to interannual time scales, anomalies in the temperature or heat content of the upper ocean (i.e., the layer above the main thermocline) may be more useful. Both of these anomalies are based on information about the vertical distribution of temperature between the surface and the main thermocline. Unfortunately, this information is only occasionally available for most parts of the ocean. However, in the equatorial Pacific, there is an array of moored buoys designed to monitor upper-ocean and surface-atmosphere conditions (McPhaden 1993).

Upper-ocean temperatures from this array during the 1991–93 El Niño event are shown in figure 2. The subsurface temperatures from the buoy at 0°N, 155°W (figure 2a) had an especially distinct signal during October 1991–April 1992. At about 125–150 m (the approximate thermocline depth), the temperatures at this buoy underwent large fluctuations of 5°–10°C over periods of about 40–60 days. Note that the onset of these large fluctuations coincided with a large rise in SST during October–December 1991 (figure 2a). The period of large

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[2] Ibid.

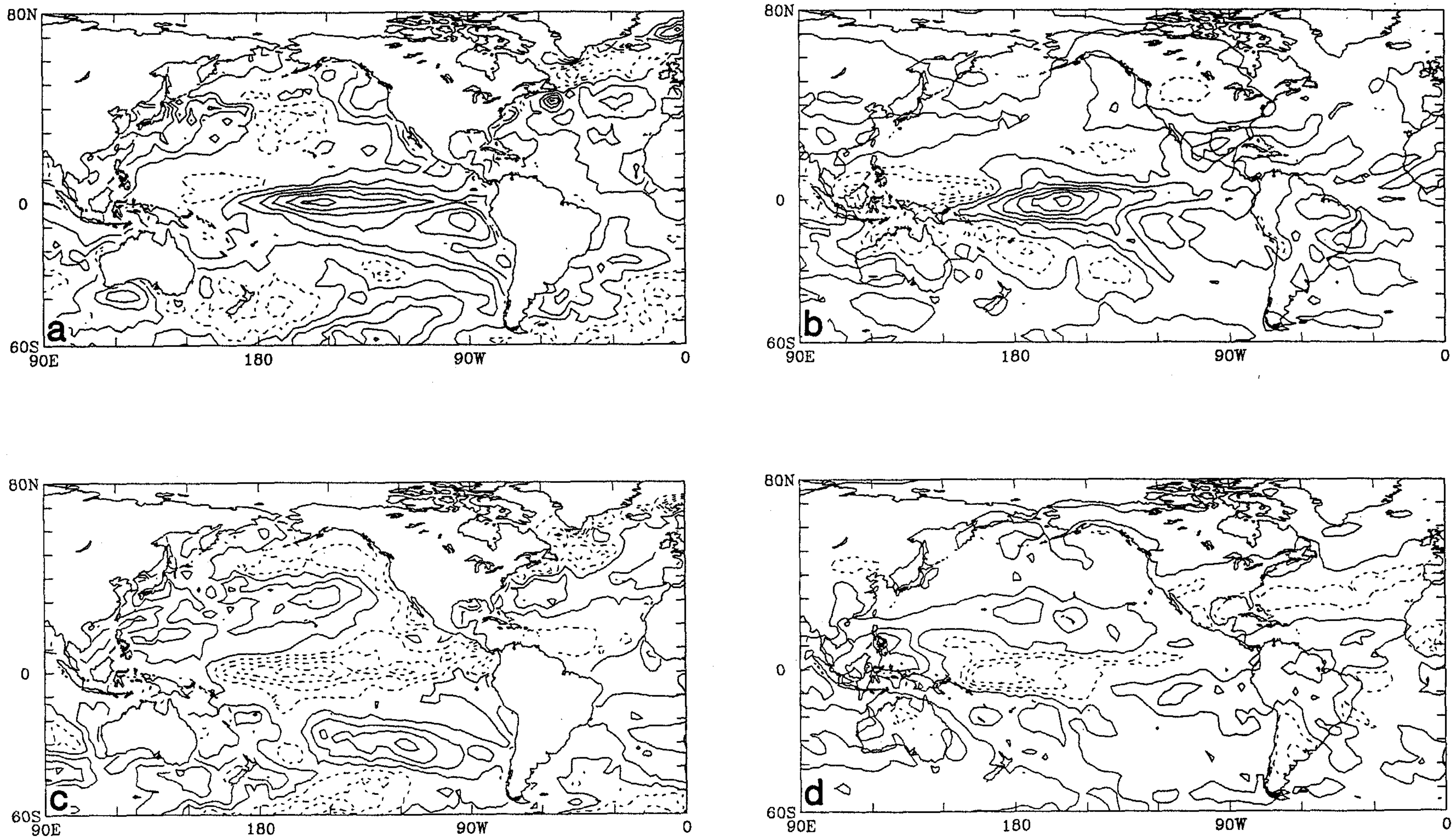

Figure 1. El Niño and La Niña sea-surface temperature anomalies (SSTAs) and outgoing longwave radiation anomalies (OLRAs) during the January-February-March (JFM) season. Negative (positive) OLRAs correspond to more-(less)-than-normal tropical convective storm activity, and more-(less)-than-normal latent heating of the tropical atmosphere. *a*, SSTA, JFM 1992; *b*, OLRA, JFM 1992; *c*, SSTA, JFM 1989; *d*, OLRA, JFM 1989. The SSTA contour interval is 0.5°C, with negative contours *dashed*. The OLRA contour interval is 10 Wm^{-2}, with positive contours *dashed*.

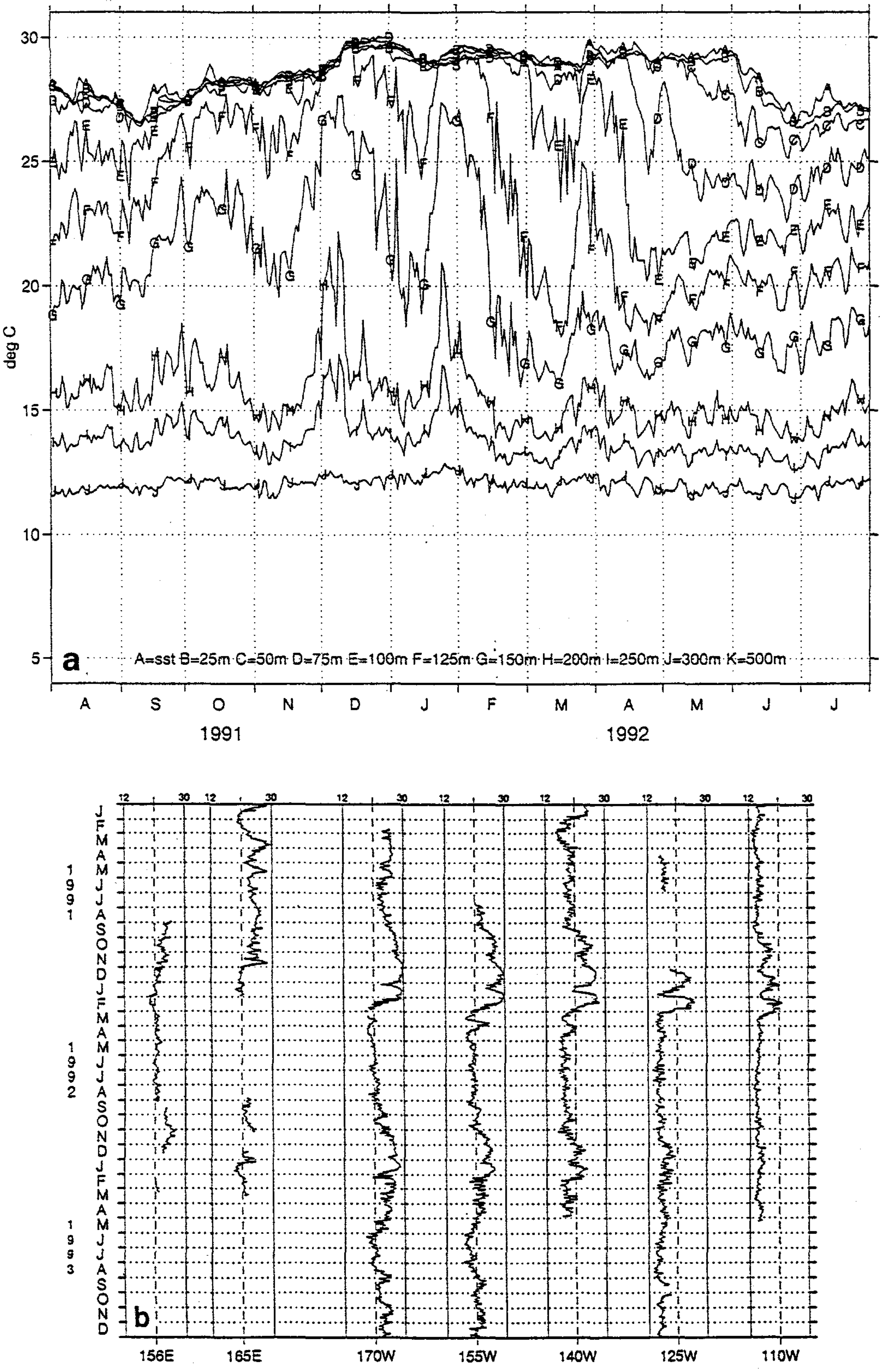

Figure 2. Ocean temperatures in the equatorial Pacific during the 1991–93 El Niño event. *a*, Temperatures at the equator and 155°W, 1 August 1991–31 July 1992, and from the surface to 500 m. Depths are indicated by the *letters* on the time series curves (key at the bottom of figure). *b*, Temperatures at 125 m along the equator at seven different longitudes, 1 January 1991–31 December 1993. For each longitude, the temperature scale range is 12°–30°C, marked by the *vertical lines* to the left and right of each time series.

subsurface fluctuations was also a time of warm SSTs (28°–30°C) and positive SSTAs (1°–2°C; figures 1a, 2a). Similar subsurface and surface temperature variations occurred at other central and eastern equatorial Pacific locations during October 1991–April 1992 and October 1992–April 1993 (figure 2b; McPhaden 1993).

The temporal and spatial patterns of these intraseasonal variations in upper-ocean temperature, along with current-velocity data (not shown), indicate internal equatorial ocean Kelvin waves (Kindle and Phoebus 1995; Murphree et al.[3]). Coriolis effects cause these waves to be confined within a few degrees of the equator and to propagate eastward along the equator (Gill 1982). The oscillatory motions within the waves produce horizontal convergence and divergence along the equator, which lead to downwelling and upwelling. The periods of especially warm subsurface temperatures in figure 2 indicate the passage of a downwelling Kelvin wave pulse. Note, as an example, the strong warming in the 125–200 m layer that occurred in late January–early February 1992 at 0°N, 155°W (figure 2a). The periods of especially cool subsurface temperatures represent the passage of upwelling pulses.

The eastward propagation of the 1991–93 Kelvin waves is indicated by the eastward shifts with time of the downwelling and upwelling phases, as shown in figure 2b. These shifts indicate eastward phase velocities of about 2.5 ms^{-1}, similar to those found in theoretical and modeling studies (e.g., Gill 1982; Geise and Harrison 1990; Kindle and Phoebus 1995). Correlations of the temperature time series in figure 2b with equatorial surface winds indicate that these Kelvin waves were initiated by eastward surface-wind anomalies, especially those associated with tropical cyclone winds, in the western Pacific.[4] Figure 2b shows that the major Kelvin wave activity occurred in October 1991–April 1992 and October 1992–April 1993. The SST and OLR anomalies were especially strong in the central and eastern tropical Pacific during these two periods (figure 1), indicating that these were the two mature phases of the 1991–93 El Niño event (Rassmusson and Carpenter 1982).

Ocean Kelvin waves are part of the process by which the tropical Pacific Ocean and atmosphere redistribute thermal energy and create anomalous SST and OLR patterns (Philander 1990). During El Niño events, equatorial ocean Kelvin waves play an important role in creating positive upper-ocean heat content anomalies in the central and eastern tropical Pacific (e.g., Graham and White 1988). These ocean anomalies, in turn, help create anomalies in tropical atmospheric convective activity—which may, in turn, enhance the ocean anomalies (e.g., Graham and White 1988; Philander 1992).

Equatorial ocean Kelvin waves may also play a role in producing some of the extratropical effects of El Niño and La Niña events. This may happen when the waves strike the coast of Ecuador and some of their energy propagates poleward, as coastal Kelvin waves, into the extratropics (Gill 1982). The changes in ocean temperature, salinity, flow, and sea level that occur during the passage of these waves may explain some of the anomalies observed in the extratropical northeast Pacific, especially very close to the west coast of North America (e.g., Enfield and Allen 1980; Chelton and Davis 1982; Clarke and Van Gorder 1994). This possibility is discussed further in section 7.

c. Thermal Anomalies in the Tropical Atmosphere

Thermal energy anomalies in the tropical atmosphere may be estimated from OLR anomalies (OLRAs). In JFM 1992, the central and eastern tropical Pacific OLRAs were negative and were located approximately over positive SSTAs (figures 1a, b). In JFM 1989, the OLRAs were positive and occurred over negative SSTAs (figure 1c, d). Persistent positive (negative) SSTAs during El Niño (La Niña) events tend to be associated with persistent positive (negative) tropospheric-heating anomalies. These associations occur because positive SSTAs tend to initiate and maintain atmospheric convection, whereas negative SSTAs suppress convection.

Tropospheric heating anomalies are thought to play a major role in producing the extratropical responses to El Niño and La Niña (Tribbia 1991). The anomalous tropical heating causes anomalies in the speed, direction, and convergence of lower-tropospheric tropical winds (e.g., the trade winds). These heating anomalies also cause anomalies in upward tropical convective winds and the divergence of upper-tropospheric tropical winds (Gill 1980). Anomalies in these tropical winds are linked to anomalies in extratropical winds through, in part, the anomalous advection of momentum and propagation of low-frequency atmospheric wave energy. This, in turn, leads to anomalies in the sea surface beneath these extratropical wind anomalies. These linkages are discussed further in sections 4 and 5.

4. EXTRATROPICAL EFFECTS

The extratropical effects of El Niño and La Niña events are generally easier to identify in the atmosphere than in the ocean. This is mainly because the atmosphere is much better observed and modeled than the ocean. Thus there is a *relatively* clear picture of how the extratropical atmosphere has responded in past events and might be expected to respond in future events.

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[3] Murphree, T., J. Kent, and R. Gelaro. Interactions of equatorial ocean Kelvin waves and tropical cyclones during the 1991–1993 El Niño event. MS submitted to J. Geophys. Res.

[4] Ibid.

a. Anomalies in the Extratropical Atmosphere

Some of the clearest and most immediate of these effects are in the mid-latitude upper troposphere, at about 9–14 km above the surface, where the major jets affecting mid-latitude weather occur. The atmospheric pressure in this region is roughly 200 mb. So a map of the 200 mb height gives a good indication of the dynamic topography of the upper troposphere, and, by inference, the upper-tropospheric winds. The heating from tropical Pacific convective regions is especially important to the dynamic topography and winds over the North Pacific–North America (NPNA) region. Thus the shifts in the tropical convective heating that occur during El Niño and La Niña events tend to have large effects in the NPNA region (cf. Tribbia 1991; Hartmann 1994).

These effects are most easily seen in maps of the anomalous height of the 200 mb surface. Figure 3 shows the 200 mb height anomalies and the corresponding wind anomalies during the JFM seasons of 1992 and 1989. The H and L symbols in the height panels indicate high and low height anomalies. In JFM 1992, there was a high anomaly over Hawaii, a low over the mid-latitude northeast Pacific, a high over Canada, and a low near the east coast of the United States (figure 3a). In JFM 1989, there was a low centered southeast of Hawaii, a high centered just south of the Aleutians, a low over most of Canada and southern Greenland, and a high centered over the eastern United States (figure 3b). In both years, there were four main height-anomaly centers in the NPNA region, in roughly similar locations but with the anomaly signs during the El Niño year opposite to those during the La Niña year.

During JFM of 1992 and 1989, the center of the main tropical Pacific OLRA (figure 1b, d) occurred about 3000 km to the southwest of the simultaneous high in the 200 mb height anomaly near Hawaii (figure 3a, b). This is a typical relationship during El Niño and La Niña events. This relationship—along with the typical coincidence of the tropical Pacific SSTAs and OLRAs (figure 1) and the typical four-centers pattern of the NPNA height anomalies (figure 3)—indicates the dependence of the extratropical upper-tropospheric height anomalies on tropical heating anomalies. El Niño and La Niña 200 mb height anomalies are often interpreted as parts of a single phenomenon—a Rossby wave train—that was initiated by the tropical heating anomalies (e.g., Lau and Lim 1984; Chelliah et al. 1988; Tribbia 1991). This wave train represents the propagation of low-frequency wave energy out of the tropics and into the extratropics. In this interpretation, the El Niño–La Niña reversal of the extratropical 200 mb height-anomaly signs is due to the reversal in the tropical Pacific forcing (e.g., the reversals indicated by figure 1).

Both El Niño and La Niña events vary in their extratropical influence. But certain regions show characteristic El Niño and La Niña effects (Horel and Wallace 1981). One of the regions with relatively consistent effects is the NPNA area; the height anomalies in figure 3 are good examples of these effects. The pattern of high-low-high-low anomaly centers in the Hawaii-northeast Pacific-Canada-western North Atlantic locations is typical during the mature phase of El Niño events. The pattern of NPNA highs and lows shown in figure 3a is similar to the Pacific-North American (PNA) teleconnection pattern described by Wallace and Gutzler (1981).

The wind anomalies associated with the height anomalies in figure 3 are shown schematically by the arrows in that figure. The climatologic flow at 200 mb over the northeast Pacific is generally eastward (Peixoto and Oort 1992). The wind anomalies in this region during JFM 1992 (figure 3a) reveal that this eastward flow was unusually weak at about 45°N-55°N and unusually strong at about 20°N-35°N. This corresponds to an anomalous southward shift of the eastward upper-tropospheric jets. The reverse was true during JFM 1989 (figure 3b).

Such anomalies in jet flow are dynamically linked to anomalies in mid-latitude storms and their associated winds. In particular, periods and locations with anomalously strong northeast Pacific jets indicate more or stronger surface wind events of the type associated with large-scale mid-latitude storms (e.g., the typical winter and spring storms of the western United States). The surface winds in these storms are cyclonic (i.e., counterclockwise in the Northern Hemisphere).

The jet anomalies shown in figure 3 imply that cyclonic wind events occurred farther south than normal during JFM 1992, and farther north than normal during JFM 1989. During JFM 1992, this led to surface wind anomalies that were cyclonic over almost all of the extratropical North Pacific (figure 4a). This pattern was especially clear in the northeast Pacific, where, along most of the west coast of North America, the alongshore component was poleward. In JFM 1989, the anomalous winds were anticyclonic (i.e., clockwise in the Northern Hemisphere) across most of the extratropical North Pacific (figure 4b). Along the west coast of North America, between about 30°N and 60°N, the alongshore component was equatorward. The northeast Pacific surface wind anomalies shown in figure 4 are typical during El Niño and La Niña events (cf. Horel and Wallace 1981). This means that the actual surface winds along most of the U.S. west coast tend to have a weaker (stronger) than normal equatorward component during El Niño (La Niña) winters.

Figure 4 also shows the equatorial western and central Pacific surface wind anomalies discussed in section 3. The eastward anomalies during JFM 1992 and the westward anomalies in JFM 1989 played key roles in the

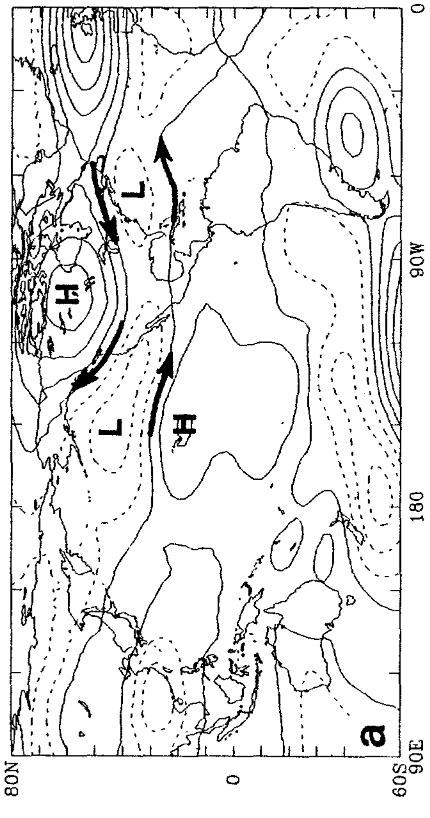

Figure 3. Atmospheric geopotential height and wind anomalies for the 200 mb surface during the January-February-March seasons of (*a*) 1992 and (*b*) 1989. Height anomaly contour interval is 30 geopotential meters, with negative contours *dashed*. Wind anomalies are shown schematically by *arrows* paralleling the height anomaly contours.

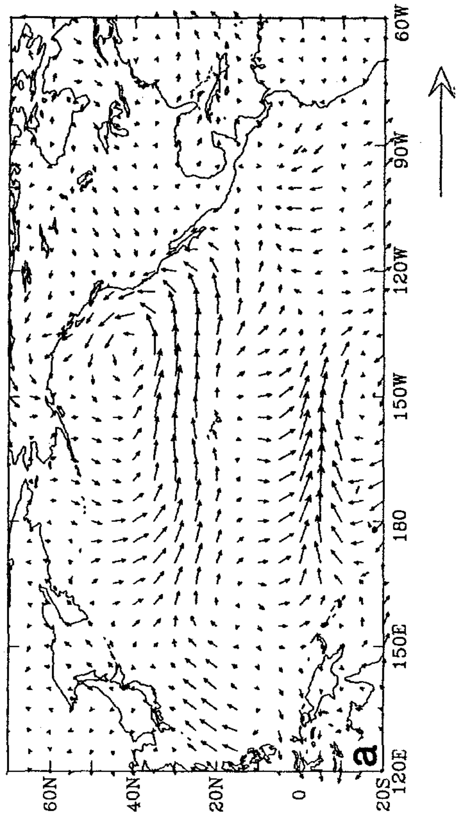

Figure 4. Surface wind anomalies during the January-February-March seasons of (*a*) 1992 and (*b*) 1989. Surface winds are represented by the *arrows* on the 1000 mb surface. The scale vector is shown at the bottom of panel *a* and represents 15 m s^{-1}.

development of the tropical SST and convective storm activity anomalies shown in figure 1.

b. Anomalies in the Extratropical Ocean

The extratropical surface wind anomaly patterns shown in figure 4 may have important effects on the extratropical ocean. Along the coast of California, the northward wind anomaly that is typical during an El Niño event has a poleward alongshore component that tends to produce anomalous decreases in offshore Ekman transport and upwelling. This produces anomalous increases in coastal sea level, SST, thermocline depth, and near-surface temperatures, plus anomalous decreases in equatorward flow. The long-term mean water-mass characteristics for the West Coast (Lynn et al. 1982) indicate that such coastal ocean circulation anomalies would also lead to anomalous decreases in salinities and increases in dissolved oxygen. These circulation, salinity, and oxygen anomalies, along with nutrient and biological anomalies, have been observed during past El Niño events (e.g., Wooster and Fluharty 1985; Mysak 1986; Breaker 1989; Simpson 1992; Lynn et al. 1995). For the 1991–93 event, Lynn et al. (1995) provide a detailed analysis of physical anomalies along the coast of California.

Ocean anomalies similar to those during El Niño events, but with opposite signs, tend to occur during La Niña events. For example, SST and sea-level anomalies along the west coast of North America have been observed to be positive (negative) during El Niño (La Niña) events (figure 1; Wyrtki 1989, 1992, 1993; Lynn et al. 1995). These ocean anomaly reversals are apparently linked to surface wind anomaly reversals such as those shown in figure 4.

5. VARIABILITY OF EXTRATROPICAL EFFECTS

A great deal of variability is embedded within the characteristic anomaly patterns described in sections 3 and 4. The duration and recurrence of El Niño and La Niña events shows some of this variability. Events tend to last about one year and recur at intervals of about three to seven years (Peixoto and Oort 1992). However, very different durations and intervals have been observed (e.g., Quinn et al. 1978; Diaz and Markgraf 1992). The 1991–93 event and its extratropical effects lasted about two years. Many tropical and extratropical aspects of the 1983–84 and 1988–89 La Niña events persisted into 1985 and 1990, respectively (e.g., Climate Analysis Center 1984, 1985; Kousky 1989, 1990; Bell and Halpert 1995).

The persistence of the 1991–93 event was somewhat unexpected, because the positive SSTAs and near-surface heat anomalies in the central and eastern equatorial Pacific had begun to decline by April 1992, and large areas of negative SSTAs occurred in that region throughout July–September 1992 (not shown). But in October 1992, the SSTAs there began to warm and continued to do so through about May 1993 (not shown).

Interseasonal variability during El Niño and La Niña events can be large. Such variability during the winter-to-spring transition can be especially important in the evolution of physical and biological anomalies in the northeast Pacific. Figure 5 shows the SST and surface wind anomalies for the April-May-June (AMJ) seasons of 1992 and 1989. A comparison of figure 1a with figure 5a shows that, from JFM to AMJ 1992, the negative SSTA in the central North Pacific and the positive SSTA along the west coast of North America intensified, except at about 45°N-50°N, where the positive SSTA weakened. Over the same period, the cyclonic surface wind anomaly in the northeast Pacific moved to the southwest, and the poleward wind anomalies along most of the west coast decreased (figures 4a and 5b).

The January–June 1989 changes over the North Pacific were dramatic. The positive SSTA in the western and central North Pacific weakened considerably, and the negative West Coast SSTA was replaced by a positive SSTA at about 20°N–60°N (figures 1c and 5c). The strong anticyclonic surface wind anomaly over southwest Alaska during JFM 1989 was drastically weakened and shifted eastward to the Gulf of Alaska (figures 4b and 5d).

The winter-to-spring changes in the SST and wind anomalies during 1991–93 and 1988–89 (figures 1, 4, 5) are representative of the wide range of interseasonal variability seen during individual El Niño and La Niña events. This range is similar to that seen at intraseasonal (e.g., month-to-month) scales (not shown).

6. PREDICTABILITY OF EXTRATROPICAL EFFECTS

Such variability from one event to the next and during an event makes predicting the extratropical effects difficult. Even small variations in key anomaly patterns may be significant. For example, relatively small changes in the location, orientation, and strength of the 200 mb height anomalies (section 4a) may lead to marked changes in the anomalies for the storm-track latitude, the speed of storms along the track, the angle between the track and the coast, the speed of the winds within the storms, and the location and amount of precipitation from the storms. These, in turn, may cause significant changes in mid-latitude air-sea interactions and ocean anomalies.

This sensitivity to small changes makes specific predictions of El Niño and La Niña events and their effects very problematic. For example, predictions of the location of the mid-latitude jet over the northeast Pacific for a particular week one month into the future are not reliable. This is due, in part, to the large internal variability of the mid-latitude atmosphere on such time scales.

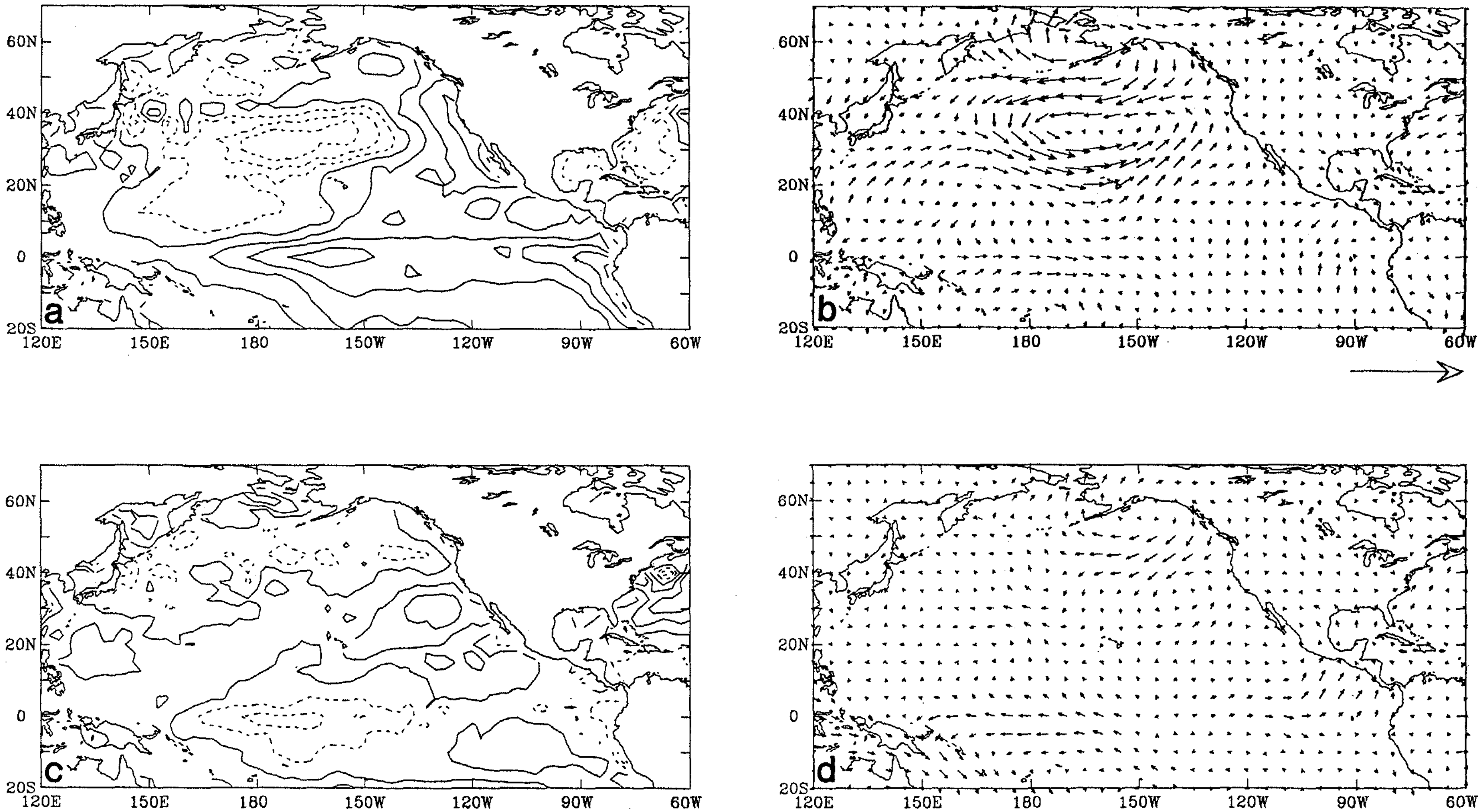

Figure 5. Sea-surface temperature anomaly (SSTA) and surface wind anomaly during the April-May-June (AMJ) seasons of 1992 and 1989. *a*, SSTA, AMJ 1992; *b*, wind anomaly, AMJ 1992; *c*, SSTA, AMJ 1989; *d*, wind anomaly, AMJ 1989. The SSTA contour interval is 0.5°C, with negative contours *dashed*. Surface winds are represented by the *arrows* on the 1000 mb surface. The scale vector is shown at the bottom of panel *b* and represents 15 m s^{-1}.

However, useful predictions may be made of the very large-scale and slowly varying anomalies related to El Niño and La Niña events (e.g., predictions of the broad-scale, seasonal 200 mb height-anomaly patterns, such as those shown in figure 3). Experimental predictions of El Niño and La Niña events and their effects are currently being made by several groups (e.g., Barnston 1994; Kumar and Hoerling 1995).

7. TELECONNECTION MECHANISMS

The El Niño and La Niña-driven interactions between the tropical Pacific and the extratropical northeast Pacific are examples of teleconnections, or interactions between widely separated parts of the environment. Most of the evidence for teleconnections forced by El Niño and La Niña events comes from observational time series correlation studies (e.g., Enfield and Allen 1980; Horel and Wallace 1981) and from modeling studies (e.g., Chelliah et al. 1988; Pares-Sierra and O'Brien 1989; Alexander 1992a, b; Clarke and Van Gorder 1994). The observational studies have established that there are a number of statistically significant teleconnections associated with El Niño and La Niña events. Both the observational and modeling studies have pointed toward two basic mechanisms that may explain how events in the tropics affect the extratropics. These mechanisms are, in essence:

1. the propagation of signals *through the atmosphere*, from the tropics into the extratropics, and then into the extratropical ocean
2. the propagation of signals *through the ocean*, from the tropics into the extratropics.

For both mechanisms, the primary propagating signal is the wave energy associated with large-scale, low-frequency waves—primarily Kelvin and Rossby waves (Gill 1982; Philander 1990). These waves play a key role in the adjustment of the ocean and atmosphere to El Niño and La Niña disturbances. As the thermal energy anomalies associated with El Niño and La Niña events evolve, the ocean and atmosphere adjust to the new distribution of thermal forcing by propagating wave energy away from the tropical Pacific disturbances.

Mechanism 1 involves the propagation of Rossby wave energy through the atmosphere (cf. section 4a). The observational and modeling evidence for this mechanism is, in general, good (e.g., Horel and Wallace 1981; Tribbia 1991). This is especially true for the broad-scale features of the atmospheric anomalies observed during El Niño or La Niña events. For example, the basic atmospheric anomaly patterns discussed in section 4a (e.g., the four upper-tropospheric height anomaly centers, the jet and storm-track shifts, the cyclonic and anticyclonic surface wind anomalies over the northeast Pacific) are explained by mechanism 1. This mechanism also explains the near-surface ocean anomalies that are driven by surface wind anomalies (see section 4).

But good support for this mechanism during *individual* El Niño or La Niña events has been more problematic (e.g., Chelliah et al. 1988). The primary reason is that Rossby waves are generated and affected by many processes other than El Niño or La Niña disturbances in the tropical Pacific. Thus, distinguishing the waves due to these other processes from those due to El Niño or La Niña effects is difficult. These other processes have also made it difficult to clearly identify the role of mechanism 1 in producing particular anomalies in an extratropical region.

However, as indicated in section 4, many regional anomalies are consistent with mechanism 1. The coastal sea-level and SST anomalies observed in the northeast Pacific are at least broadly consistent with the observed surface wind anomalies (section 4; Mysak 1986; Cayan 1992; Simpson 1992). These surface wind anomalies are linked to upper-tropospheric height anomalies that are consistent with a Rossby wave train emanating from a tropical Pacific heating anomaly (e.g., section 4a; Horel and Wallace 1981; Palmer and Mansfield 1986).

Mechanism 2 involves the propagation of ocean Kelvin waves eastward through the equatorial Pacific, and then poleward along the coasts of North America and South America (cf. section 3b). This mechanism also includes the possibility that westward-propagating ocean Rossby waves may be generated as the equatorial Kelvin waves strike the South American coast, and as the coastal Kelvin waves propagate along a coast with sharp changes in orientation (e.g., Gill 1982; White et al. 1989).

The equatorial Kelvin wave portion of mechanism 2 is well supported by observations, theory, and modeling (e.g., section 3b; Matsuno 1966; Gill 1980; Philander 1992). The poleward coastal Kelvin wave component of mechanism 2 is supported by some observations (especially coastal sea-level data; e.g., Enfield and Allen 1980; Chelton and Davis 1982) and by several modeling studies (e.g., Clarke and Van Gorder 1994; Jacobs et al. 1994). The TOGA array of moored buoys in the equatorial Pacific (McPhaden 1993) has provided much of the observational evidence for the equatorial part of mechanism 2. However, there is no comparable observation network for the eastern boundaries of the extratropical Pacific. That is, the relatively closely spaced (e.g., 2 degrees of latitude, 15 degrees of longitude) and frequent (e.g., hourly, daily) observations of the upper ocean and surface atmosphere that are available for the equatorial Pacific are missing for the coastal eastern Pacific. Thus the role of coastal Kelvin waves and associated Rossby waves in producing El Niño and La Niña teleconnections has been difficult to determine.

However, several aspects of the ocean anomalies discussed in section 4b are at least broadly consistent with mechanism 2. The northeast Pacific sea-level, current, and near-surface temperature anomalies associated with El Niño and La Niña events provide some evidence of poleward-propagating coastal Kelvin waves and westward-propagating Rossby waves (e.g., Enfield and Allen 1980; Chelton and Davis 1982; Jacobs et al. 1994; Norton and McClain 1994; Lynn et al. 1995).

Mechanisms 1 and 2 are not, of course, mutually exclusive. Both may be involved in producing the extratropical responses to El Niño and La Niña events, and the two mechanisms may interact with each other. For example, the extratropical surface wind anomalies that are part of mechanism 1 may well initiate coastal Kelvin waves and Rossby waves in the *extratropical* northeast Pacific (cf. Gill 1982). The extratropical near-surface ocean temperature anomalies that are part of mechanism 2 may influence the development of the overlying extratropical atmospheric pressures and winds that are part of mechanism 1.

8. DISCUSSION

We have examined the broad-scale features and effects of the 1991–93 El Niño and the 1988–89 La Niña events. These were relatively typical events in both their equatorial Pacific features and their extratropical effects (cf. Rassmusson and Carpenter 1982).

We have relied heavily in this study on monthly and seasonal anomalies. But such anomalies can be produced by several distinctly different series of events during the averaging period. For example, a number of mild storms off southern California during some March might cause a cyclonic surface wind anomaly for the month. But a couple of strong storms during a few days of the month, combined with otherwise weak winds could also cause such a cyclonic wind anomaly. Such differences in the *actual* wind events could, of course, lead to distinctly different monthly anomalies in ocean temperature, salinity, and flow—despite the similar monthly wind anomaly patterns.

Thus, although monthly and seasonal anomalies contain interesting patterns that reveal much about the workings of El Niño and La Niña events, they do not tell the whole story. In particular, they do not adequately address processes that occur at space and time scales that are smaller than those for which the monthly and seasonal anomalies were calculated. These unaddressed processes will be especially problematic in the study of ocean phenomena that have much smaller scales than the atmospheric anomalies. For example, attempting to interpret the variations of coastal eddies or comparably sized patches of marine organisms in terms of atmospheric anomalies may be very difficult because of scale mismatches.

These and other difficulties (see sections 6 and 7) would be well addressed by a more complete observational network (e.g., of moored buoys) in the northeast Pacific, especially along the eastern boundary. High-resolution satellite observations of SST, surface wind speeds, sea level, ocean color, and other ocean fields are available but have not been used much in exploring the effects of El Niño and La Niña on the northeast Pacific. The recent work by Strub and James (1995) gives an indication of how satellite-derived estimates of sea level might be used in concert with other satellite observations and on-site observations. Such satellite data should be very useful in resolving many of the present uncertainties about El Niño and La Niña effects.

ACKNOWLEDGMENTS

We wish to thank Ron Gelaro and Jeff Hawkins of the Naval Research Laboratory (NRL) in Monterey, California, for many helpful discussions and for their assistance in obtaining, displaying, and analyzing the ECMWF, SST, and OLR data. The Pacific Marine Environmental Laboratory provided the TOGA data. Grant Cooper, John Kent, and Todd Sitler—students at the Naval Postgraduate School—did much of the analysis of the TOGA data. The SST data were generously provided in a very accessible form by Dick Reynolds and Tom Smith at CAC. The OLR and ECMWF data were made available by CAC and ECMWF, by way of the National Center for Atmospheric Research. Leslie Rosenfeld of the Monterey Bay Aquarium Research Institute, Frank Schwing of the NOAA Pacific Fisheries Environmental Group, Dan Cayan of the Scripps Institution of Oceanography, and Patricia Phoebus of NRL provided very helpful suggestions for revisions of the original manuscript. This work was supported by NRL and the Office of Naval Research, Program Element 0601153N. Computing support was provided by the DoD High Performance Computing Program.

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THE EFFECT OF THE 1991–1993 ENSO ON THE CALIFORNIA CURRENT SYSTEM

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ABSTRACT

During 1992 and 1993 the coastal zone of the eastern North Pacific Ocean experienced widespread sea-surface warming (1°–2°C) and, for extended periods, higher-than-normal sea level (5–14 cm) and unseasonably strong poleward coastal currents. These are manifestations of an El Niño event as it affects the California Current system (CCS). The warm phase of the tropical El Niño–Southern Oscillation (ENSO) started in the fall of 1991 and, after the expected lag of several months, was evidenced in the CCS. Hayward (1993) and Hayward et al. (1994) give a preliminary look at the oceanographic effects of the 1991–92 event off California. We update these reports and present additional results from hydrographic surveys and coastal time series data. Comparisons are made with prevailing large-scale meteorological conditions. There is evidence that these El Niño conditions resulted from a combination of remote and local atmospheric forcing. Midyear reversals in anomalous coastal poleward currents and in corresponding high sea levels toward more typical conditions (equatorward flow, near zero sea-level anomalies) were followed by the renewal of positive anomalous sea level. The intra-annual pulsing of the current field and sea level observed during 1992 characterized the 1957–58 El Niño as well. This pattern also bears a strong resemblance to numerical model results, thus giving evidence for the development of a poleward-propagating coastal Kelvin wave and offshore-directed Rossby waves generated by El Niño.

INTRODUCTION

Like previous moderate-to-strong ENSO events, the 1991–93 ENSO had a substantial effect far beyond the equatorial zone. The physical impact of ENSO events upon the California Current system (CCS) and the Pacific Northwest have been described by many authors (e.g., Emery and Hamilton 1985; Mysak 1986; Simpson 1984, 1992; see also Wooster and Fluharty 1985). Typically, the oceanic effects in the CCS include widespread and intensive warming of the upper mixed layer, a depressed thermocline and nutricline, anomalously high sea level, an enhanced poleward countercurrent along the continental margin, and significant but varied effects on the marine biota. These effects were found along much of the west coast of North America during 1992 and 1993, and selected evidence is presented herein. The extensive and persistent nature of the sea-surface warming is illustrated in the *Climate Diagnostics Bulletin* series 1992 through June 1994. Hayward (1993) and Hayward et al. (1994) give a preliminary look at the oceanographic effects of the 1991–92 episode, including the sea-level anomalies. The purpose of this report is to describe the anomalous physical changes in the CCS during the 1991–93 ENSO event as indicated in hydrographic surveys and coastal time series data. We focus on the region's circulation, which is implied by dynamic height anomalies.

BACKGROUND

Enfield and Allen (1980) and Chelton and Davis (1982) show that sea-level fluctuations at ENSO frequencies propagate poleward along the west coast of the American continents. These observations have been used to support the concept that El Niño conditions off the U. S./Canadian west coast are linked to equatorial ENSO events by coastally trapped waves emanating from the eastern Pacific equatorial zone along the continental margin. But not all equatorial ENSO events have counterparts in the eastern subtropical Pacific, and vice versa. Simpson (1983) and Mysak (1986) provide strong arguments that large-scale anomalies in the winter barometric pressure field over the North Pacific and the resulting atmospheric circulation can better account for the occurrence of El Niño conditions off North America. Such anomalous atmospheric patterns have teleconnections to the Southern Oscillation (Horel and Wallace 1981) and match the spatial scale of SST anomalies. Theoreticians, however, continue to develop increasingly sophisticated wind-driven models that suggest the remote generation of energy and its propagation poleward along eastern ocean boundaries (e.g., Clarke and Van Gorder 1994; Jacobs et al. 1994).

Using a 34-year record of monthly mean temperature in the upper 300 meters of the eastern North Pacific (within 300 km of the coast), Norton and McLain (1994) proposed a method to distinguish between the dominance of local and remote forcing for El Niño events. Large, positive thermal anomalies that extend to 300 m correlate best to remote forcing (Southern Oscillation/coastally trapped wave propagation), whereas large anomalies limited to shallow depths correlate to local forcing (enhanced Aleutian low). The deeper-level warming along the coast is partially attributable to geostrophic adjustment to the increase in poleward flow, which is caused by the coastally trapped baroclinic Kelvin wave. Increased advection from the south may further contribute to the positive temperature anomaly of the water column. On the other hand, anomalous atmospheric forcing over the eastern North Pacific may significantly decrease upwelling-favorable wind stress (or increase downwelling-favorable wind stress) in the coastal regions. This condition causes unseasonably high surface-layer temperatures, but its effects below 100 m may be weaker than those caused by the remote forcing. Anomalies in the CCS are largest in those events in which both remote and local forcing are strong (e.g., 1940–41 and 1982–83).

Other large-scale processes may complicate the El Niño model. Latif and Barnett (1994) describe a cycle of large-scale sea-surface temperature (SST) patterns involving unstable air-sea interactions between the subtropical gyre circulation in the North Pacific and the Aleutian low-pressure system. In their model the SST in a large region of the central and western North Pacific (including the Kuroshio Extension) oscillates irregularly between positive and negative anomalies on a decadal time scale. The extensive warming of surface waters along the North American coast that occurs during strong El Niño events is part of this larger pattern that includes large-scale negative SST anomalies in the central North Pacific (Mysak 1986). In another study, Jacobs et al. (1994) used satellite altimeter observations to detect the northwestward progression over the last decade of a Rossby wave originally excited by the 1982–83 El Niño. Its impingement on the Kuroshio Extension during 1992–93 also has implications for the large-scale gyre circulation and the recent SST anomaly pattern. A simple model of the forcing of events in the eastern North Pacific may not be an appropriate approach.

Observations are inadequate for a clear understanding of the forcing of anomalous conditions along the North American coast. A modest number of hydrographic surveys conducted during 1992–93 describe conditions at various stages of development. The listing of cruises in table 1 was assembled from a general knowledge of ship activity and is not intended to be complete. Only a few of these surveys are treated in this report; however, the results are representative of seasonal patterns in the regional ENSO signal.

TABLE 1
1992–93 Surveys (CTD/ADCP) off California

Dates	Vessel	Spatial extent	Reference
1/28–2/13/92	*Jordan*	CalCOFI pattern	SIO 1992b
2/7–2/17/92	*Pt. Sur*	37.2–38°N, to 123.5°W	Jessen et al. 1992
2/23–3/6/92	*Jordan*	36.8–38.3°N, to 126°W	Sakuma et al. 1994a
3/14–4/2/92	*Jordan*	37–38.8°N, to 128.5°W	Lynn et al. (data rep., in prep.)
4/13–4/30/92	*Jordan*	CalCOFI pattern	SIO 1992b
5/11–5/19/92	*Jordan*	36.5–38.3°N, to 124.8°W	Sakuma et al. 1994a
5/19–5/26/92	*Jordan*	36.5–38.3°N, to 124°W	Sakuma et al. 1994a
6/4–6/16/92	*Jordan*	36.5–38.3°N, to 126°W	Sakuma et al. 1994a
7/24–8/9/92	*Jordan*	CalCOFI pattern	SIO 1992a
9/28–10/14/92	*N Horizon*	CalCOFI pattern	SIO 1992a
1/12–1/27/93	*Jordan*	CalCOFI pattern	SIO 1993
3/2–3/13/93	*Jordan*	36.5–38.5°N, to 127°W	Sakuma et al. 1994b
3/30–4/15/93	*Jordan*	CalCOFI pattern	SIO 1993
5/13–5/20/93	*Jordan*	36.5–38.3°N, to 124°W	Sakuma et al. 1994b
5/21–5/28/93	*Jordan*	36.5–38.3°N, to 124°W	Sakuma et al. 1994b
6/3–6/10/93	*Jordan*	36.5–38.3°N, to 124°W	Sakuma et al. 1994b
6/5–7/13/93	*Wecoma*	36.2–39.5°N, to 128.5°W	Kosro et al. (data rep., in prep.)
7/8–7/12/93	*Jordan*	37.8–38.5°N, to 124.5°W	Lynn et al. (data rep., in prep.)
8/11–8/27/93	*N Horizon*	CalCOFI pattern	SIO 1994
8/14–9/21/93	*Wecoma*	37–39°N, to 128°W	Kosro et al. (data rep., in prep.)
10/8–10/26/93	*N Horizon*	CalCOFI pattern	SIO 1994

OBSERVATIONS

Characteristically, El Niño warming in the eastern North Pacific occurs in the fall–winter following the summer–fall development of ENSO changes in the tropics. Early suggestions of a developing ENSO were noted in the July and August 1991 issues of *Climate Diagnostics Bulletin*. Tropical ENSO conditions ensued across the equatorial Pacific in the subsequent months. Despite this, the coastal zone waters of the eastern North Pacific (Vancouver Island to southern Baja California) were cooler than seasonal norms from the spring of 1991 through the remainder of the year (*Oceanographic Monthly Summary* series). Large coastal regions had anomalies of −1° to less than −2°C in June through September 1991. The magnitude of the cool anomalies diminished in late 1991. By February 1992, continued ocean warming produced significant widespread positive SST anomalies along the entire North American coastal zone, and offshore to distances greater than 1000 km.

Central California Hydrographic Surveys, 1992

The CTD/Rosette survey from 14 March through 2 April 1992 by R/V *David Starr Jordan* (table 1) reached 500 km offshore and fell within the early period of coastal warming associated with this ENSO event. The dynamic height of the surface with respect to 500 dbar (figure 1a) reveals a region of poleward coastal countercurrent extending 200 km offshore. The deeper flow, as shown by the dynamic height at 250 m with respect to 500 dbar (figure 1b), shows the same broad poleward flow at half the surface velocity. Northward components of acoustic Doppler current profiler (ADCP) velocity exceeded 20 cm/s near 30 m depth and 10 cm/s at 200 m depth (P. M. Kosro, pers. comm.).

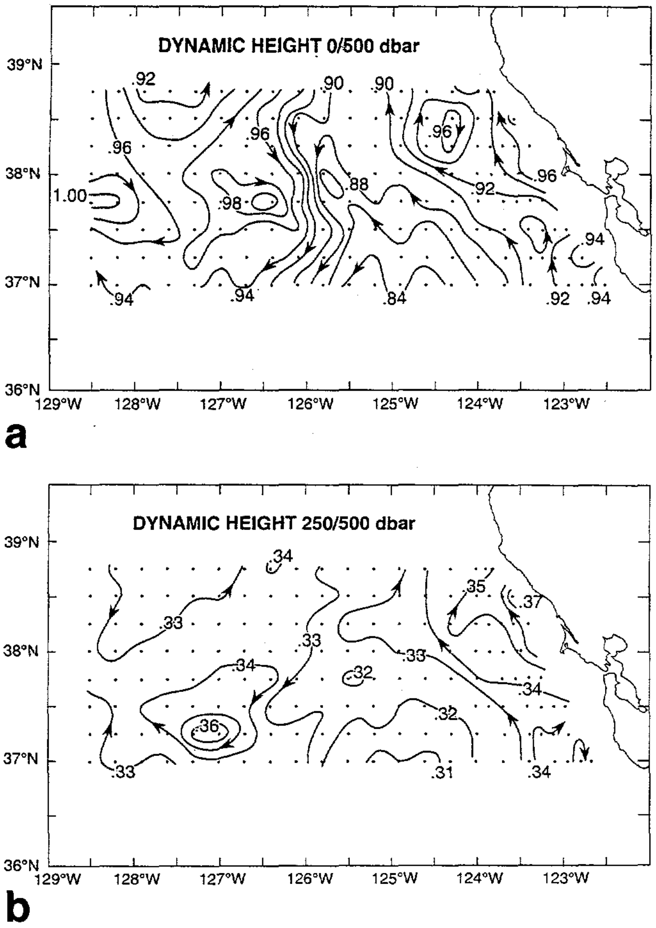


Figure 1. *a*, Dynamic height (dyn. m) of the surface with respect to 500 dbar for R/V *David Starr Jordan* survey, 14 March to 2 April 1992. Contour interval is .02 dyn. m. *Arrows* indicate direction of relative geostrophic flow. *b*, The same as a, except showing the 250 m level and with a contour interval of .01 dyn. m.

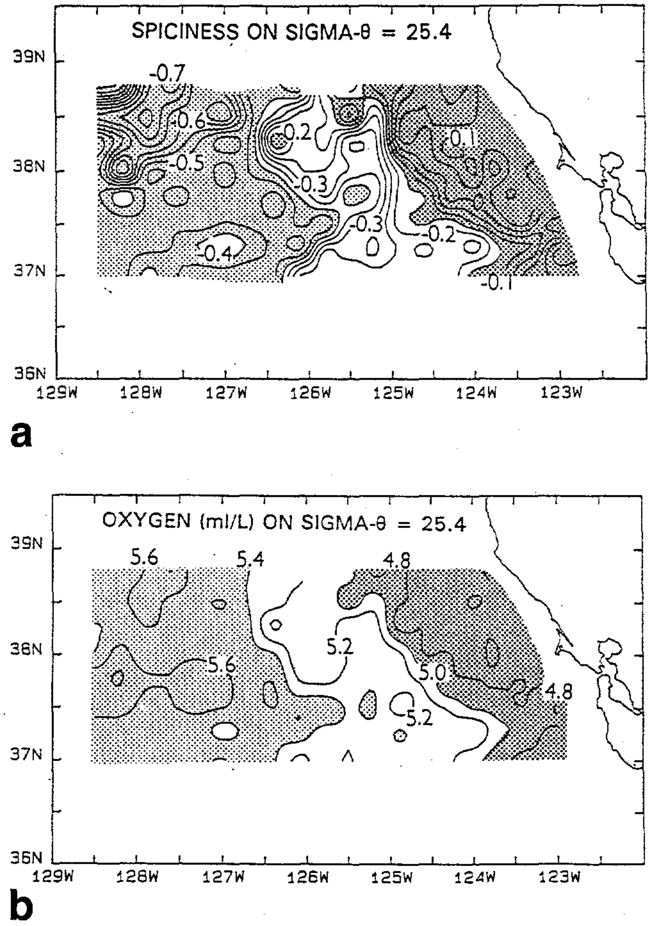


Figure 2. *a*, Spiciness on the surface where sigma-θ = 25.4 for survey shown in figure 1. Contour interval is 0.05. *b*, Same as *a*, except showing oxygen concentration (ml/l) and with a contour interval of 0.2.

Properties of the water mass have shown a high gradient in association with the jet of the California Current (Huyer et al. 1991; Strub et al. 1991). There is a high gradient in spiciness on the 25.4 sigma-θ surface in figure 2a that roughly aligns with the jet structure along the 126°W meridian (figure 1). Water to the west of the gradient has low spiciness (low temperature and low salinity) and is of northerly origin. A second gradient between 124° and 125°W (roughly parallel to the coastline) aligns with the outer portion of the strong poleward flow. Water shoreward of this gradient has the highest spiciness (highest temperature and highest salinity) on this density surface and is of southerly origin. A region of strong mixing is found between these two gradients. The distribution of oxygen concentration on this density surface shows a similar double gradient pattern (figure 2b), with lower oxygen concentrations associated with spicy, southern water (Lynn et al. 1982). Similar distribution patterns exist on other density surfaces; some have even stronger gradients (not shown). The vertical extent of this pattern is evidenced by the separation of envelopes about groupings of θ-S curves from stations in the coastal and offshore zones (figure 3). Except for the very-near-surface waters, these envelopes show little or no overlap for densities less than sigma-θ = 26.25 (nominally 370 m).

The survey described above was preceded by two surveys in the same region (table 1). In a survey aboard R/V *Pt. Sur* off the Gulf of the Farallones (7–17 February 1992) Ramp et al. (1992) found poleward near-surface ADCP velocities exceeding 40 cm/s. This contrasted with much weaker velocities and poleward flow limited to the slope (as opposed to the shelf) at the same location one year earlier. An ARGOS drifter drogued at 10 m and released in the gulf in February 1992 moved northward and onshore at speeds of 20–25 km/day (23–29 cm/sec) for about two weeks. In a more extensive survey (offshore to 126°W) conducted aboard the R/V *David Starr Jordan*, 24 February to 6 March, a flow pattern identical to the 14 March–2 April survey

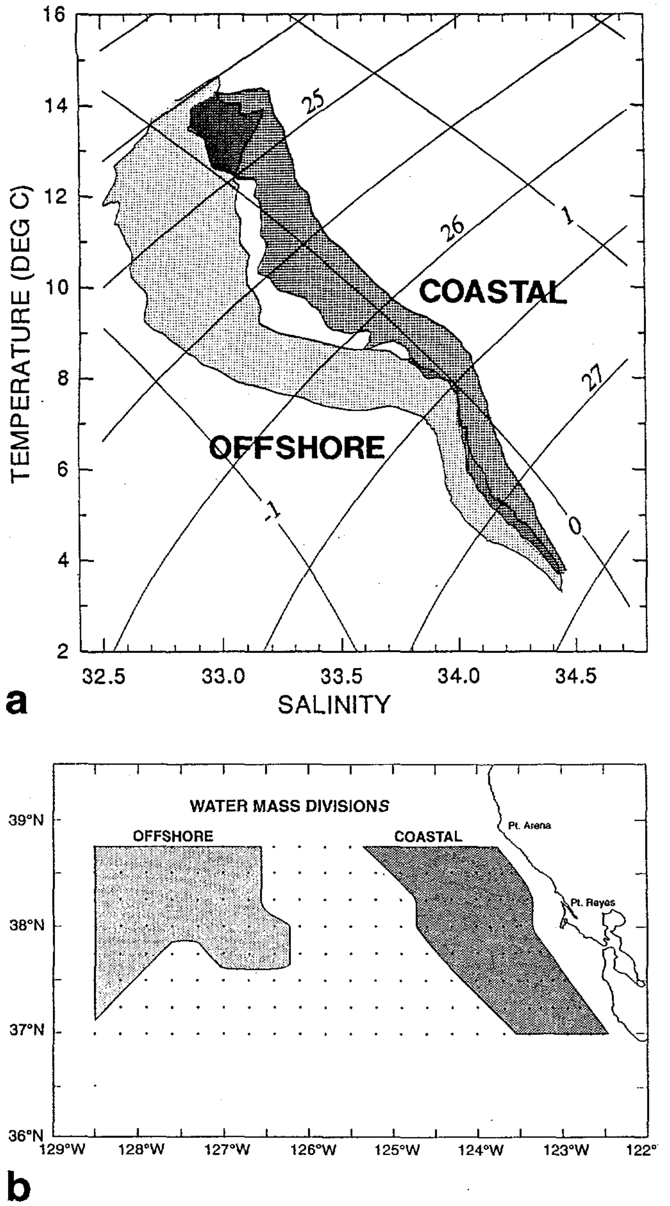


Figure 3. *a*, Envelopes about potential temperature-salinity (θ-S) curves (survey of figures 1 and 2) for coastal (*dark shading*) and offshore (*light shading*) waters. Curved lines slanting upward to the right are sigma-θ; lines slanting to the left are spiciness. *b*, Locations of coastal and offshore stations shown in *a*.

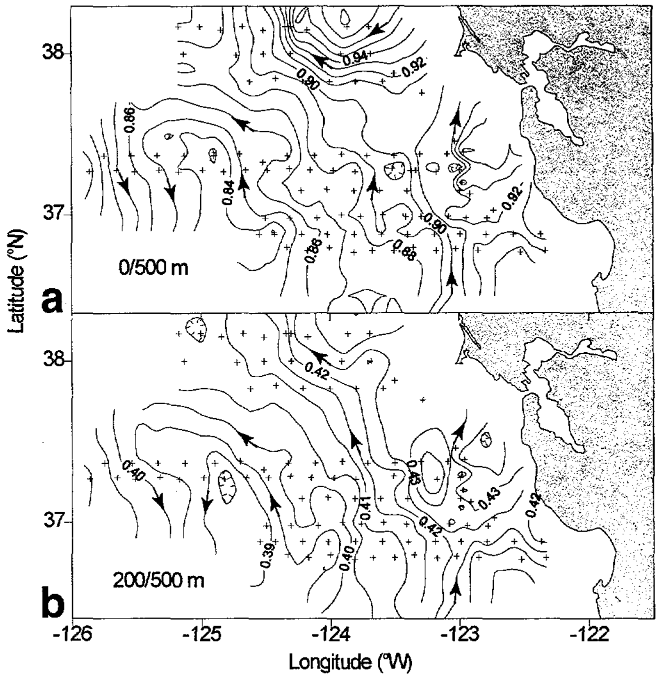


Figure 4. *a*, Dynamic height (dyn. m) of the surface with respect to 500 dbar for R/V *David Starr Jordan* survey, 23 February–March 6 1992. Contour interval is .01 dyn. m. *b*, Same as *a*, except showing the 200 m level and with a contour interval of 0.005 dyn. m.

(figure 1) was observed at the surface and at 200 m (figure 4); i. e., strong poleward flow along the coast and extending to 200 km offshore.

In the June 1992 R/V *David Starr Jordan* survey (table 1), portions of two CTD station lines taken in March (approximately 2.5 months earlier) were repeated, along with additional slope and shelf stations. No surface inshore countercurrent was found during the June period (figure 5a). The undercurrent at 500 m was confined to a narrow 50 km of the slope/shelf break (figure 5b). A comparison of water mass characteristics from late spring 1991 and 1992, represented by a station (37°N, 122.7°W) 37 km off Point Año Nuevo (figure 6), shows a warmer and less saline surface layer in 1992, and warmer and more saline waters on density surfaces in the pycnocline and deeper (to sigma-θ = 26.8; approximately 400 m). Although the May 1992 *Jordan* surveys did not cover as broad an offshore area (table 1), the circulation and water-mass distributions are very similar to those found in June.

Southern California (CalCOFI) Hydrographic Surveys, 1992

The dynamic heights of the surface with respect to 500 dbar for the February, April, July, and October 1992 CalCOFI surveys are given in figures 7–9; see also Hayward et al. (1994, 1995). The dynamic height for the 200 m level for February and April is also given in figures 7 and 8. The February 1992 pattern shows a strong and broad poleward countercurrent and undercurrent, which was highly anomalous when compared to Lynn and Simpson's (1987) long-term seasonal mean. By April 1992, surface currents were equatorward, in a pattern similar to the mean. The undercurrent at 200 m also disappeared by April and was replaced by a complex pattern of weak baroclinicity comparable to the mean. The July pattern of baroclinic flow was complicated by eddies, but did reveal a shoreward shift of a

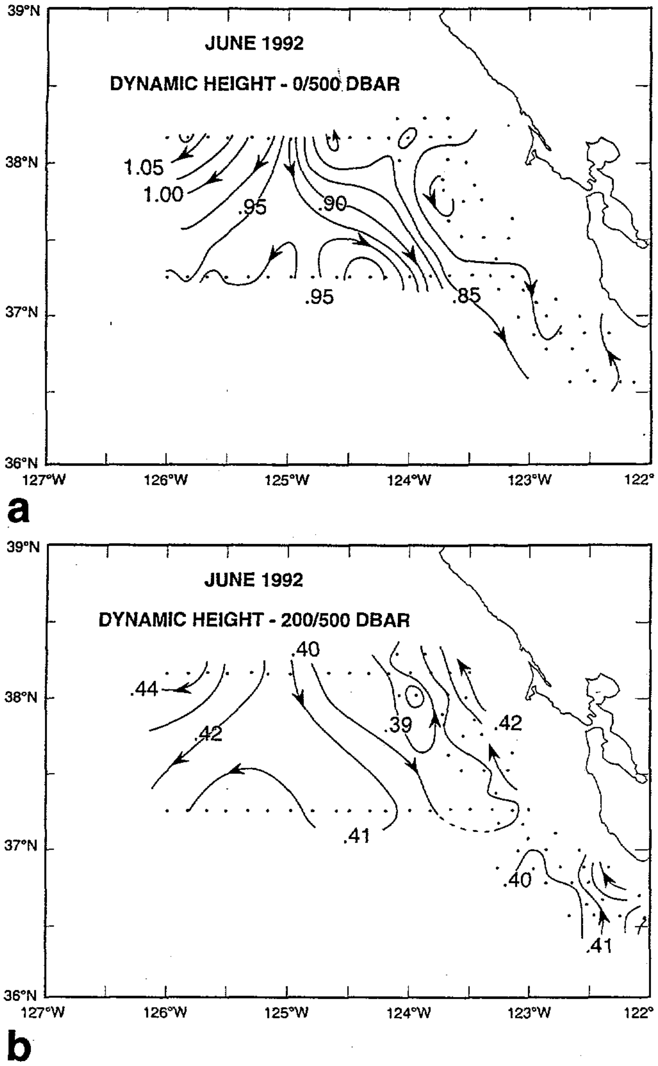


Figure 5. Dynamic height (dyn. m) of the surface with respect to 500 dbar for R/V *David Starr Jordan* survey of 4–10 June 1992. Contour interval is 0.025 dyn. m. *b*, Same as *a*, except showing the 200 m level and with a contour interval of 0.01 dyn. m.

strong portion of the California Current jet. A strong countercurrent was restored by October 1992.

The anomalous nature of these current patterns is better seen in the differences between the dynamic height and the long-term harmonic mean values for February and July 1992 (figure 10). Except for a small number of stations, these differences are positive, reflecting warmer (less dense) water that occupied the upper 500 m of the water column in 1992. The shading in figure 10 (>6 dynamic cm for February and >10 dynamic cm for July) emphasizes regions of relatively high values and shows that, whereas February had high coastal levels, the relative high in the differences existed as an offshore ridge by July. These differences demonstrate that the coastal countercurrent was stronger than its seasonal mean in February and weaker in July. The inshore poleward countercurrent was again stronger than its seasonal mean in October (not shown). One interpretation is that the anomalous buildup along the coast in February had migrated offshore by July and then been replaced along the coast by a second buildup in fall.

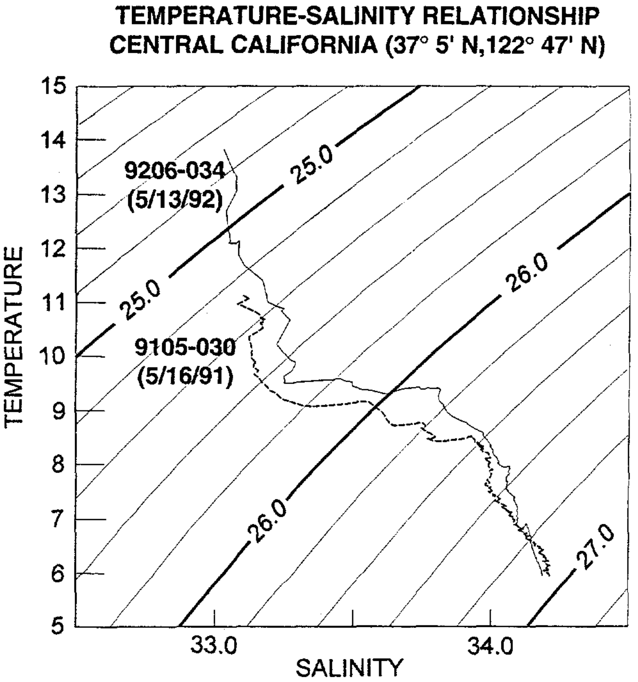


Figure 6. θ-S curves for the position 37° 05'N, 122° 47'W, 37 km off Point Año Nuevo, California. *Dashed line* is for 16 May 1991; *solid line* is for 13 May 1992.

Shore Station Time Series

With a few exceptions, the 1992 anomalies of sea level from the long-term monthly means were positive at San Francisco and San Diego (figure 11). The series confirm the idea that the quarterly CTD surveys sampled an event that cycled roughly over the period between February and October 1992. The largest positive monthly anomaly occurred in March; there was a midyear low and a secondary high in October–November. Coastal sea level has been shown to reflect the geostrophic adjustment of local baroclinic flow (Reid and Mantyla 1976), with high sea level associated with poleward flow. The sequence of monthly sea-level anomalies during 1993 has a more variable pattern, but its largest anomalies still occurred in midwinter (February). In contrast, sea-level anomalies were negative or near zero for much of 1991.

Surface temperatures measured at La Jolla (SIO Pier) and Pacific Grove for 1992 and 1993 were substantially higher than the long-term harmonic mean for much of both years (figure 12). The SST anomalies at La Jolla were near their mean or below it during June–July 1992,

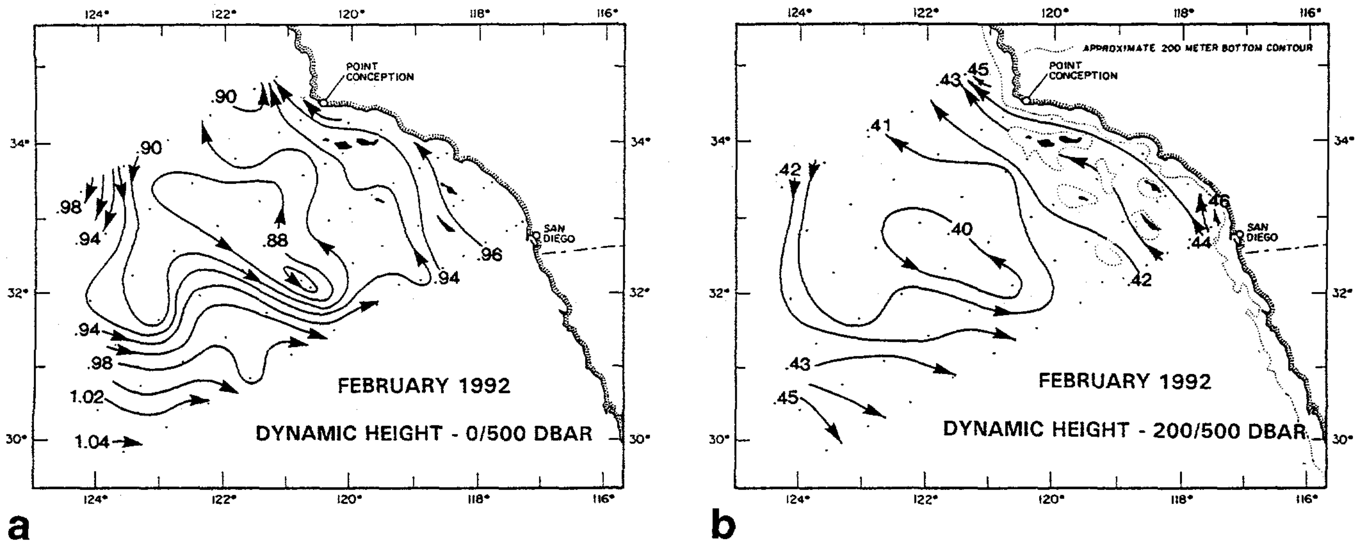


Figure 7. *a*, Dynamic height (dyn. m) of the surface with respect to 500 dbar for CalCOFI survey for 28 January–13 February 1992. Contour interval is .02 dyn. m. *b*, Same as *a*, except showing the 200 m level and with a contour interval of .01 dyn. m.

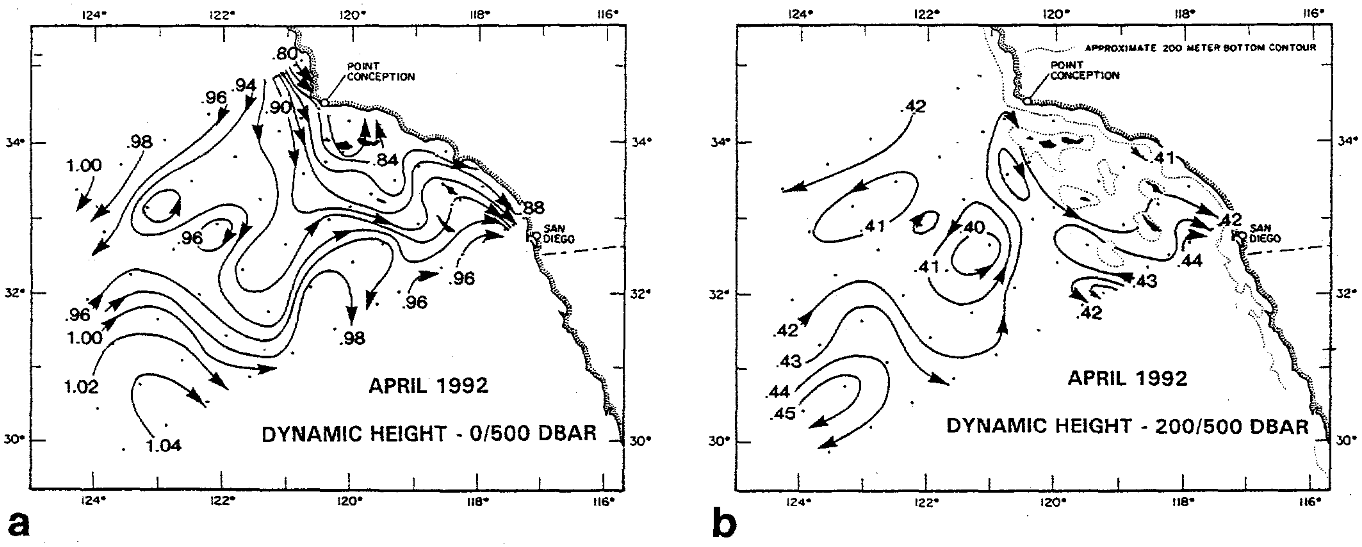


Figure 8. *a*, Dynamic height (dyn. m) of the surface with respect to 500 dbar for CalCOFI survey for 13–30 April 1992. Contour interval is .02 dyn. m. *b*, Same as *a*, except showing the 200 m level and with a contour interval of .01 dyn. m.

a period when San Diego sea-level anomalies were also near their mean. Pacific Grove SST approached near-zero anomalies in August–September 1992, coincident with the smallest San Francisco sea-level anomalies.

Upwelling Index

The time series of standardized anomalies of the Bakun upwelling index (Bakun 1973; Mason and Bakun 1986) between Vancouver Island and Punta Eugenia for 1990–93 (base period 1963–93) is presented in figure 13. Negative upwelling anomalies prevailed without significant interruption during 1992 and 1993 between Point Arena (39°N) and Punta Eugenia (27°N). These anomalies are interpreted as a persistent decrease in coastal upwelling or an increase in downwelling. These anomalies probably led to an increase in sea-surface temperatures above seasonal norms. Persistent alongshore winds that cause coastal upwelling are typical between March and October (figure 14). The anomalously low index values in March 1992 and 1993 indicate a delay in the typical onset of nutrient enrichment of near-surface waters by upwelling, and in the onset of spring plankton blooms. During both years the region between Point Arena and Vancouver Island (51°N) also shows negative upwelling anomalies during late winter and early spring (figure 13).

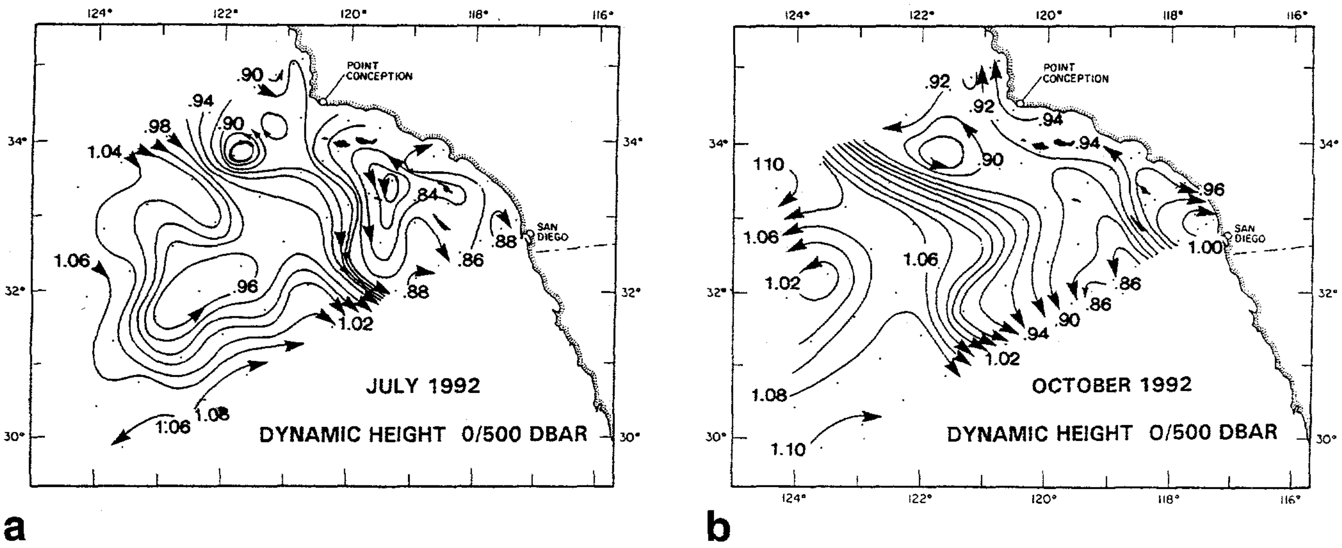


Figure 9. *a*, Dynamic height (dyn. m) of the surface with respect to 500 dbar for CalCOFI survey for 24 July–9 August 1992. Contour interval is .02 dyn. m. *b*, Same as *a*, except showing survey of 28 September–14 October 1992.

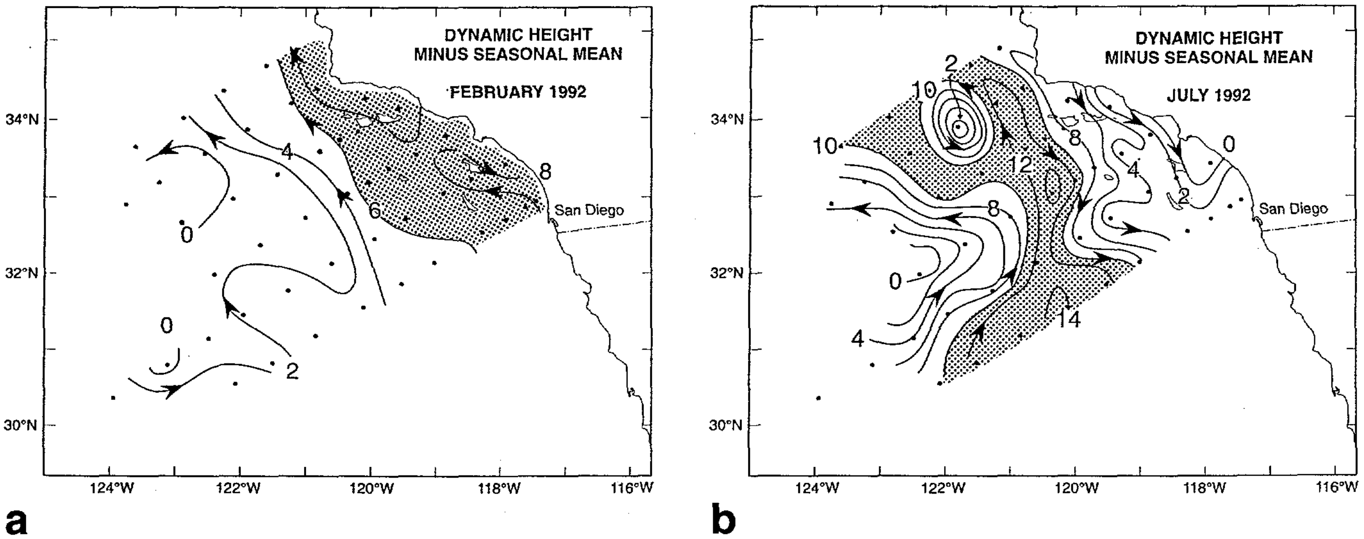


Figure 10. *a*, Dynamic height of figure 7a minus the long-term harmonic mean for February (base period: 1950–92). Contour interval is 2 dyn. cm, and values >6 dyn. cm. are *shaded*. *b*, The dynamic height of figure 9a minus the long-term harmonic mean for July. Values >10 dyn. cm. are *shaded*.

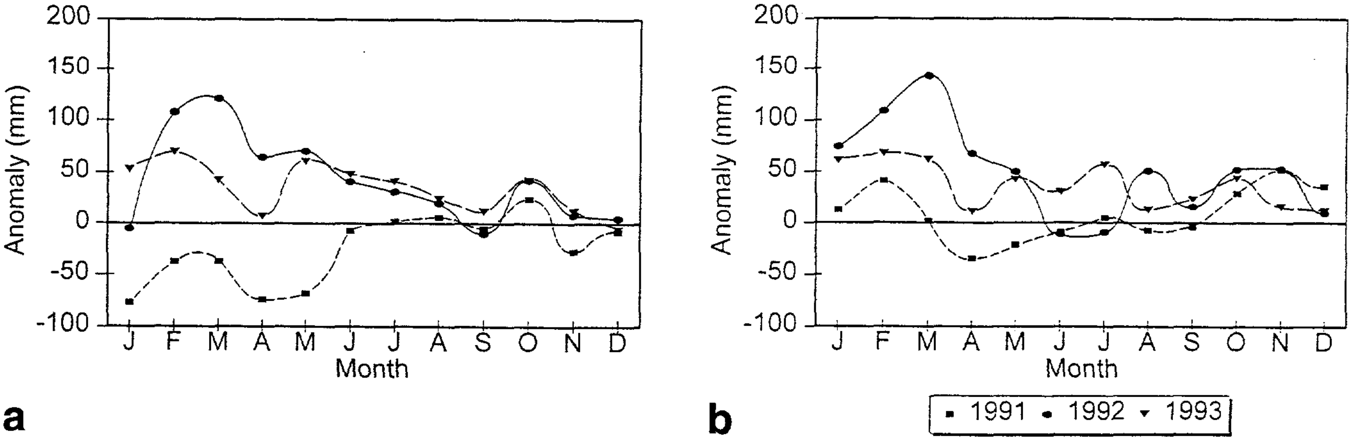


Figure 11. 1991, 1992, and 1993 sea-level anomalies (in mm corrected for atmospheric pressure) from their 1975–86 monthly means for (*a*) San Francisco and (*b*) San Diego. Data provided by the IGOSS program, courtesy of G. Mitchum and K. Wyrtki.

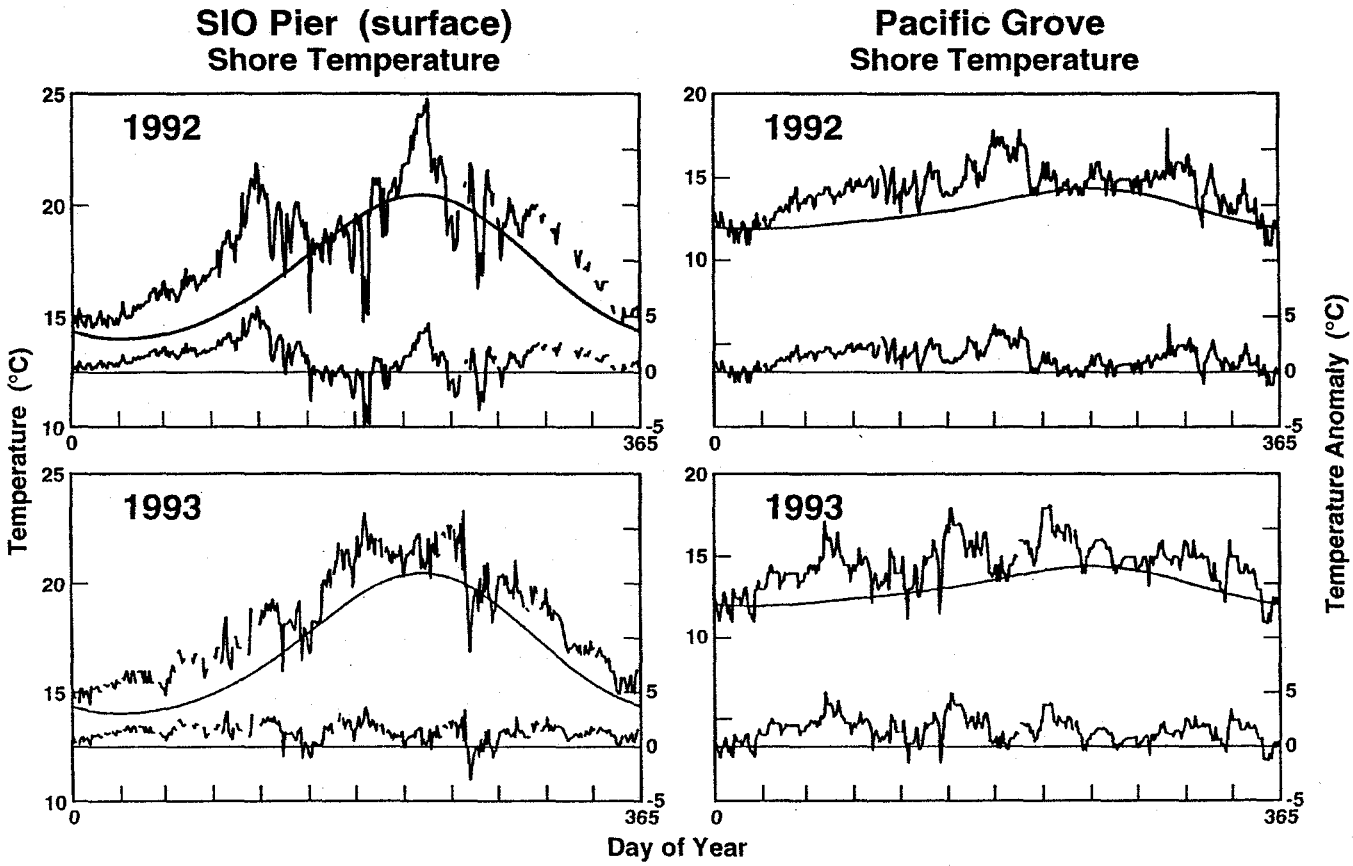


Figure 12. Sea-surface temperature (°C) and its long-term mean annual cycle (*upper curves*) and anomalies (*lower curves*) for the SIO Pier and Pacific Grove for 1992 and 1993 (from Hayward et al. 1994).

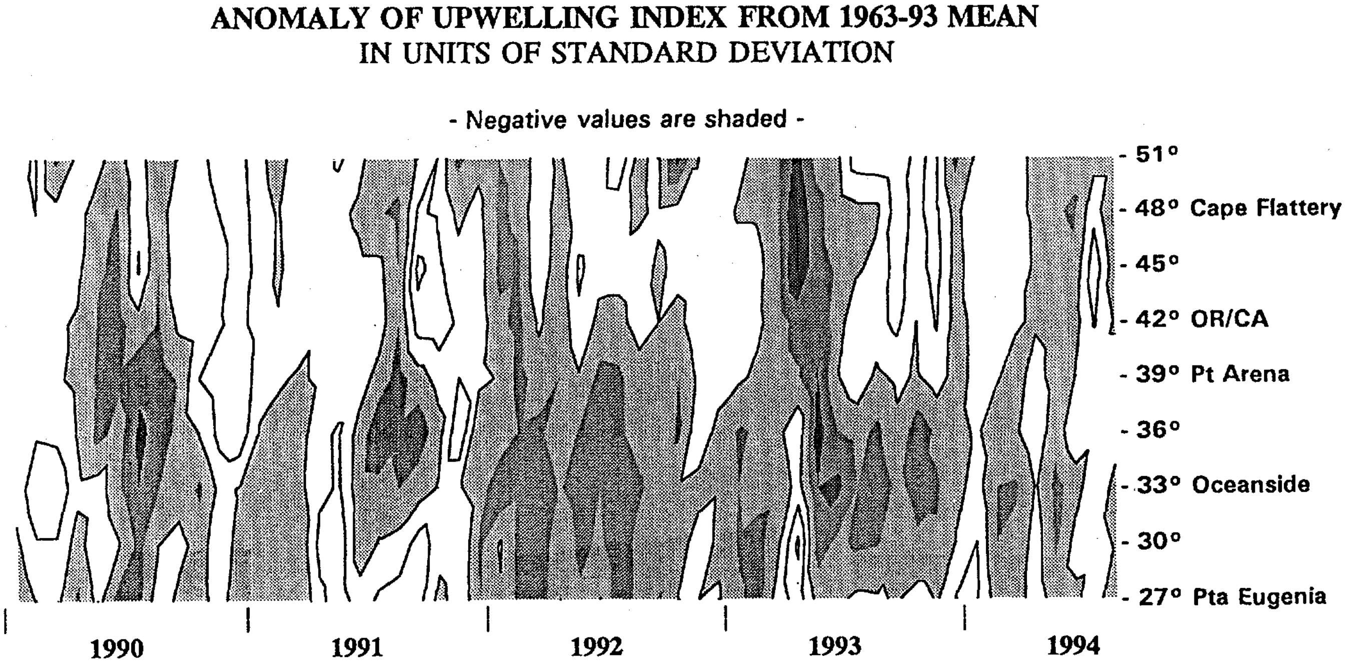


Figure 13. Anomalies of Bakun upwelling index (in standard deviations) from monthly means (base period: 1963–93) for 1990 through July 1994. Negative values (*shaded*) indicate below-normal upwelling or above-normal downwelling. Contour interval is 1 standard deviation.

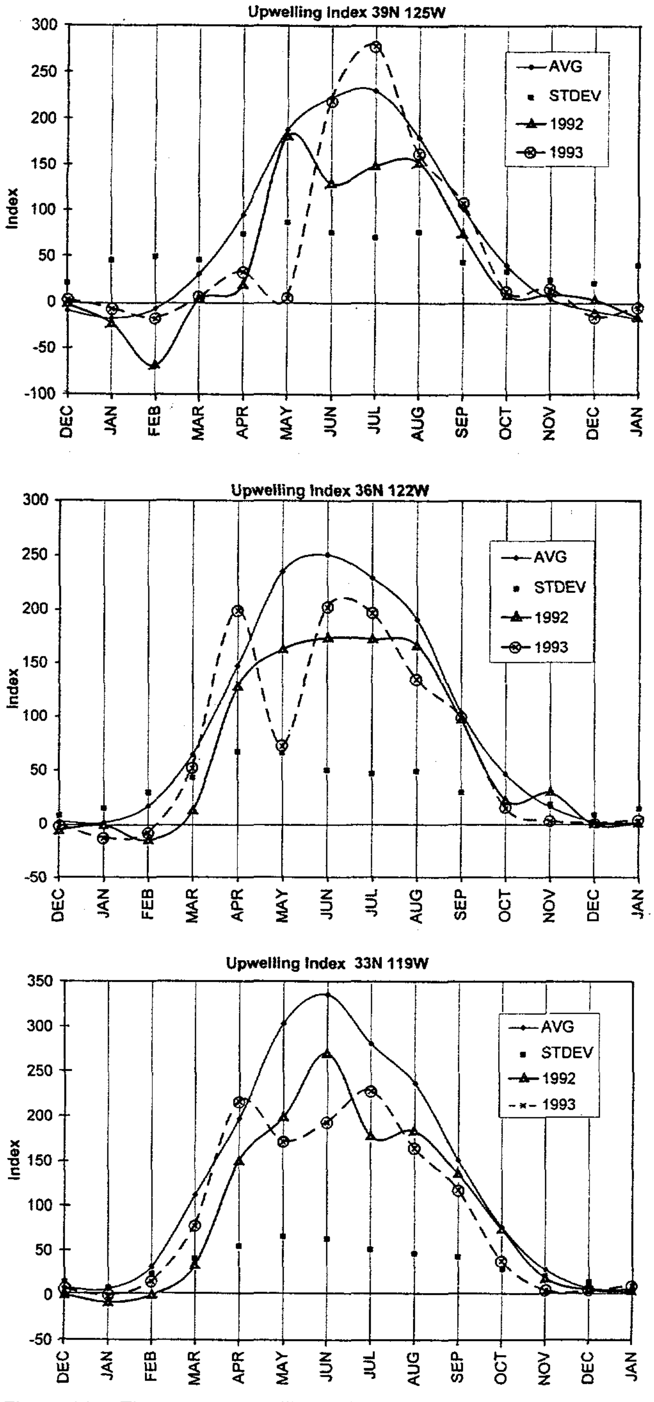


Figure 14. The annual upwelling index for three positions along the California coast as indicated in the key. Units are m^3/s/100 m of coastline.

Gradient Winds and Sea-Surface Temperature

This section provides only a cursory treatment of the large-scale meteorological conditions evident during 1991–93 over the North Pacific. A more thorough treatment of this topic is given by Murphree (1995). The March 1992 vector anomalies of 850 mb gradient winds (figure 15) were adapted from the *Climate Diagnostics Bulletin* series, and the SST anomalies from the *Oceanographic Monthly Summary* series. Reference is made to distributions for other months and years given in these publications but not reproduced here.

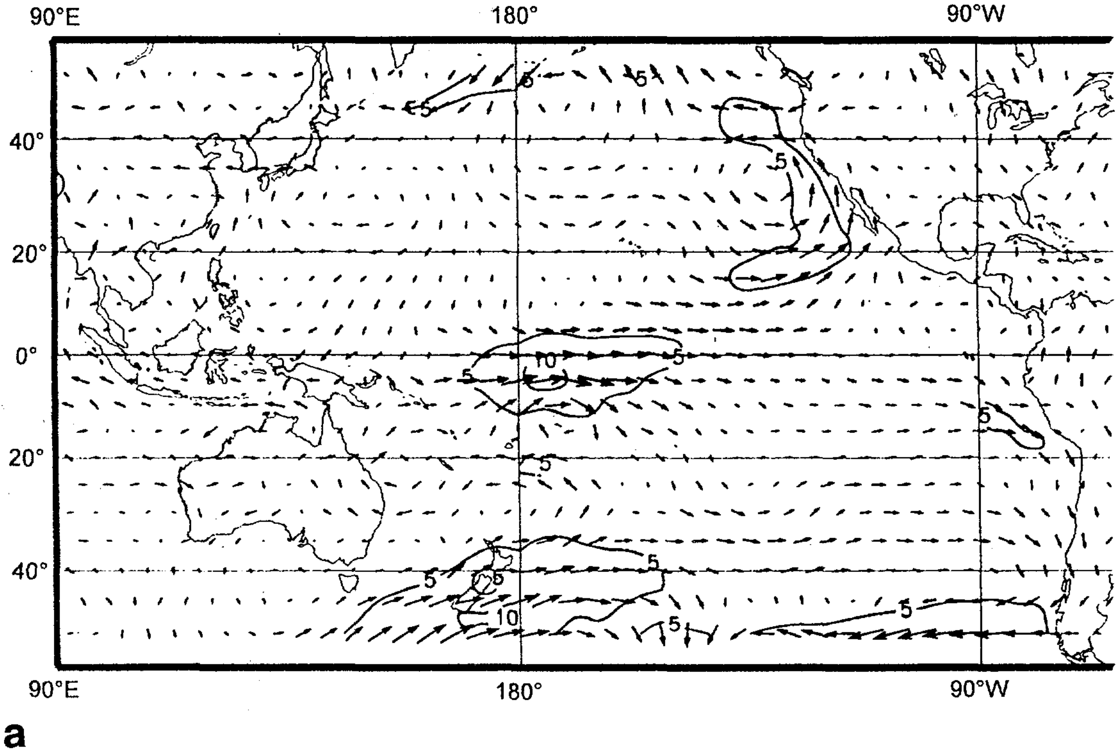
The seasonality of the winds over the eastern North Pacific is related to the oscillation between the dominance of the Aleutian low-pressure cell (winter) and the Subtropical high-pressure cell (spring and summer). Vector winds were calculated from the pressure distributions. Vector anomalies of 850 mb gradient winds (base period 1979–88) over the North Pacific and including the tropics for March 1992 show two major areas of high values (figure 15a). The eastward-directed vectors between 170°E and 140°W and 10°N and 20°S show that the easterly equatorial trade winds were weakened or reversed, a consequence of anomalous ENSO barometric pressure patterns. This change in the trades generates eastward-propagating equatorial Kelvin waves, decreased equatorial upwelling, and the resulting anomalous equatorial warming.

The other area of highly anomalous wind vectors was found in the eastern North Pacific, where a cusp-shaped contour surrounds anomalous vectors above 5 m/s. Vector anomalies over a large sector of the eastern North Pacific indicate a cyclonic anomaly component in atmospheric circulation. This component was downwelling-favorable along the North American coast. By June 1992, the wind anomalies had decreased, and approached normal seasonal values, but were qualitatively similar to the anomaly patterns in March. The pattern of wind anomalies for March 1993 and 1994 was very similar to March 1992 (although with slightly diminished magnitudes). An enhanced Aleutian low in late winter, followed by an underdeveloped subtropical high, produced similar wind-vector anomalies during winter and spring in 1992, 1993, and 1994.

The SST anomaly distribution for March 1992 (Figure 15b) forms a basinwide pattern. Positive values occurred in a broad sweep across the tropics, along a broad region off the North American continent, and down the Kamchatka Peninsula to Japan; a large body of the central North Pacific is negative. This general pattern of anomalous SST dominated most of 1992 and the first half of 1993. The equatorial SST anomalies returned to near zero and went negative after June 1993, but the large field of positive anomalies returned in the eastern North Pacific and persisted to June 1994.

DISCUSSION

The development of a strong and broad countercurrent/undercurrent during March and April 1992 (figure 1) contrasts sharply with the long-term average baroclinic flow for CalCOFI station line 60 (extending 240°T from Pt. Reyes; Lynn and Simpson 1987). Early spring



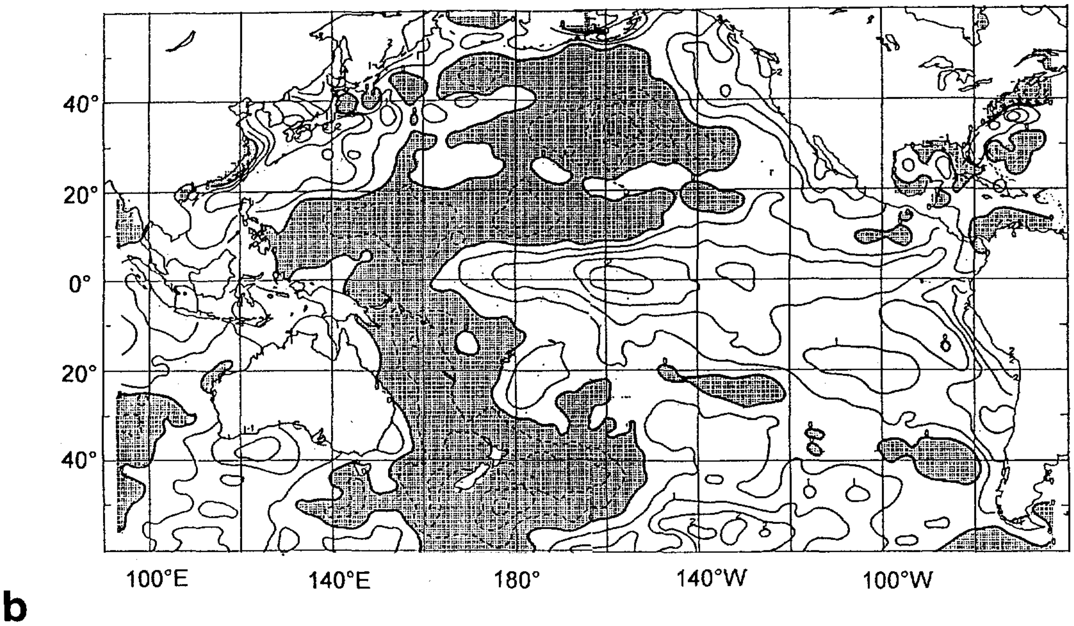


Figure 15. *a*, The vector anomalies of 850 mb winds for March 1992 (from *Climate Diagnostics Bulletin*). *b*, the SST anomalies for March 1992 (from *Oceanographic Monthly Summary*). Contour interval is 0.5°C. Negative anomalies are *shaded*.

is typically a period of no poleward flow, when the strongest equatorward flow occurs close to the coast (plate 1 of Lynn and Simpson 1987). As a basis for comparison, this suggests that the 1992 observations depart significantly from the norm. The water-mass distribution (figure 2) supports the findings in current dynamics. It has long been established that the California Undercurrent transports warm, saline, low-oxygen water poleward along the coastal margin (Lynn et al. 1982). The extensive offshore expanse of waters of southerly origin and the development of a strong double gradient in properties on density surfaces are a consequence of the greatly enhanced poleward flow in 1992. The earlier, February surveys show that this strong pattern existed for some period of time in late winter. The strong poleward flow is equated with high coastal values of dynamic height, matching the anomalously high sea level at San Francisco in that season (figure 11). The disappearance of the Inshore Countercurrent by June (figure 5) matches the decrease in sea-level anomaly.

The sequence of 1992 CalCOFI surveys shows the buildup of an anomalously strong countercurrent/undercurrent off southern California, its collapse, and its return within an eight-month period (figures 7–10). These CalCOFI surveys, like the surveys off central California, are generally descriptive of the major events found in local sea-level measurements. Although the surveys alone are not fully adequate for an unambiguous examination of an intra-annual cycle of events, the agreement between the intermittent measurements of anomalous coastal dynamic height and the continuous measurement of sea level suggests that the surveys are a good representation of the events. The record of sea-level anomaly reflects an exaggerated cycle of anomalous development of the Inshore Countercurrent and California Undercurrent.

The baroclinic adjustment to poleward flow requires a relative downsloping of nearshore density structure. Thus deeper levels generally have higher-than-average temperatures. In terms of the hypothesis of Norton and McLain (1994), an increase in deep (300 m) temperatures correlates with remote forcing, and thus is a consequence of a coastal baroclinic Kelvin wave. The cross-shore length scale of the poleward flow and its anomaly, however, is much broader than internal Kelvin wave theory implies (Mysak 1986). The development of a westward-propagating Rossby wave field (White and Saur 1983) may explain the offshore breadth of the enhanced poleward flow. A Rossby wave moving off the coastal margin would also produce the reversal in the anomalous coastal poleward flow between the February and the July CalCOFI surveys (figure 10). The maximum in dynamic height appears to move offshore over this period.

The large-scale distribution of SST anomalies in March 1992 (Figure 15b) is remarkably similar to that for March 1983 (Oceanographic Monthly Summary; see also Mysak 1986; figure 20); the 1982–83 El Niño was the strongest ever observed. Mysak (1986) and Simpson (1992), among others, conclude that the large-scale SST anomalies characteristic of El Niño and anti–El Niño events are caused by anomalous atmospheric forcing over the North Pacific. Large-scale anomalies in barometric pressure during winter are associated with the subsequent development of SST anomalies. The March 1992 wind-vector anomalies (and the barometric-pressure anomalies from which they were derived) had a length scale proportionate to that of the SST anomalies (figure 15). At their peak, positive SST anomalies extended 1500 km off the California coast.

The anomalous atmospheric circulation alters the wind-driven transport, increasing the poleward flow of the eastern limb of the Alaskan (cyclonic) gyre and decreasing the equatorward flow of the California Current. There is an eastward transport of surface waters toward the California coast (Simpson 1984) and increased vertical mixing in the central North Pacific (Mysak 1986). Anomalous poleward winds along the coast reduce upwelling and increase downwelling. Changes in the wind field could produce changes in Ekman divergence and upwelling over the North Pacific. The altered atmospheric and oceanic circulation and changes in air-sea exchanges result in the large-scale anomalies of SST. The persistence of the anomalous barometric patterns during winter–spring of 1992 and again in winter–spring of 1993 and 1994 provide ample argument that local atmospheric forcing was the dominant factor in the large-scale SST anomalies. But it is not clear that surface-forcing anomalies can account for deep-current and water-mass perturbations.

The cycle of the development of a relative coastal high in dynamic height, its offshore migration, and its reinstatement along the coast described here for 1992 was also observed in 1958 (Lynn and Reid 1975). In January 1958 there was a relative high in the difference of dynamic height from its long-term harmonic mean (figure 16); a trough was found offshore. The April 1958 distribution had a confused pattern, but by July 1958 the relative high appeared as a ridge off the coast. In October 1958 the relative high was again mostly coastal. This sequence of distributions in anomalous dynamic height describes a stronger-than-normal poleward flow in the coastal zone in January and October, and a stronger-than-normal equatorward flow in July. The SST anomalies were mainly positive during this El Niño event (figure 17); the major exception occurred in July, when anomalous equatorward flow predominated along the coast. The intra-annual cycle of coastal dynamic height revealed by this quartet of surveys is supported by the record of sea-level anomaly for 1958 off San Francisco and La Jolla (figure 18). For reference, the 1983 sea-level anomaly record is also given in figure 18.

Jacobs et al. (1994) applied a global ocean-circulation numerical model (GCM; Hurlburt et al. 1992) of sea-surface height (SSH) to the 1982–83 event. Their figure 2 is a sequence of three maps showing the progression of the simulated deviation of SSH from a 12-year mean for this event. Their results show the buildup of positive SSH anomalies at the equator in August 1982 as a result of the eastward-propagating Kelvin wave. In January 1983, the positive anomaly of SSH stretches northward along the coast to Alaska in response to a coastally trapped

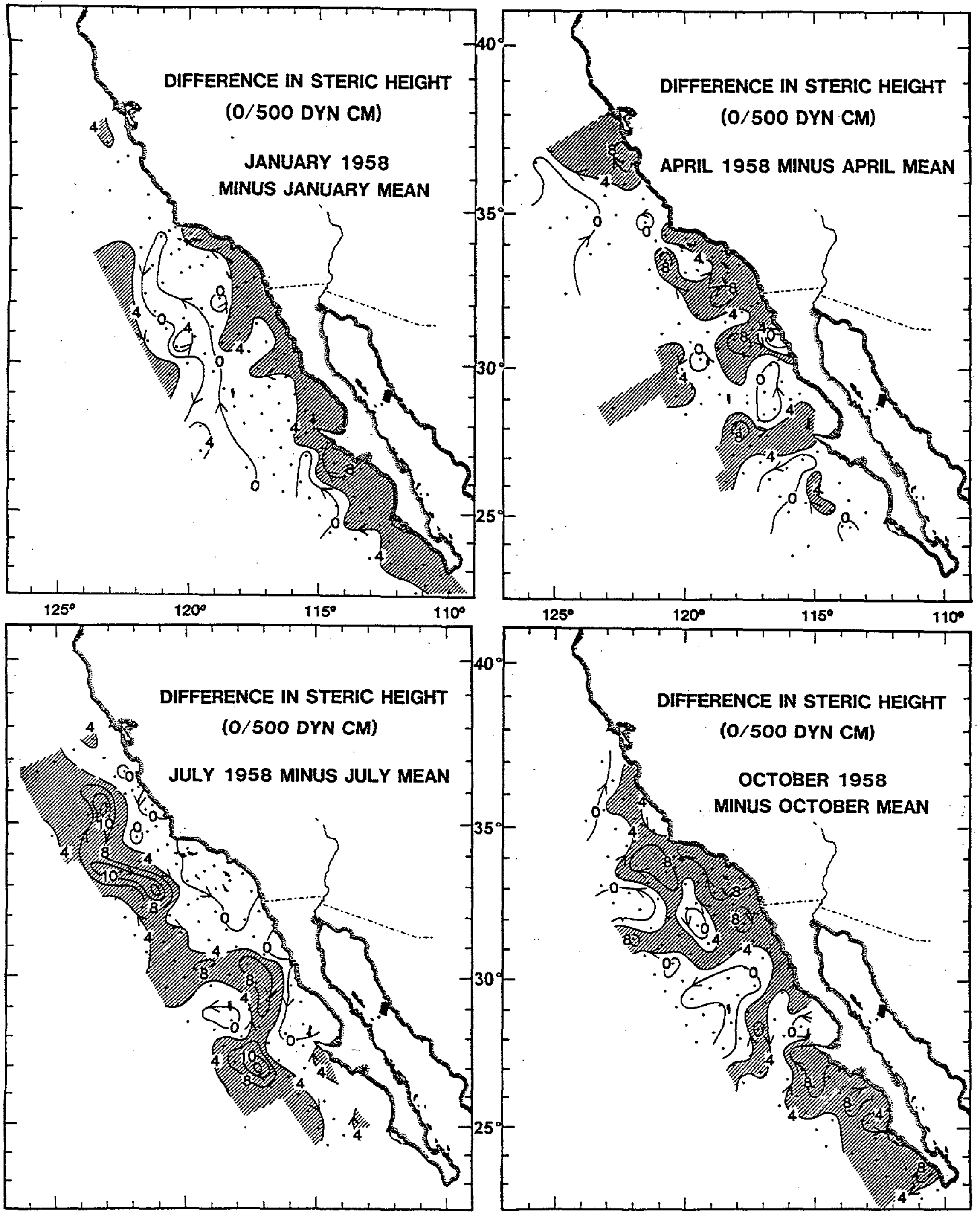


Figure 16. Steric height (same as dynamic height) for four CalCOFI surveys in 1958 minus the monthly harmonic mean steric height (base period: 1950–63). (From Lynn and Reid 1975.) Contour interval is 4 dyn. cm. Values >4 dyn. cm. are *hatched.*

Kelvin wave propagating poleward. Four months later, the signal is carried offshore of the North American continent as a westward-propagating Rossby wave; the positive SSH anomaly appears as an offshore ridge. These simulated distributions of SSH represent changes in circulation like those given by the observed differences of dynamic height from its long-term mean. The coastal high in model SSH anomalies for January would geostrophically balance an anomalous poleward flow. The ridge in SSH found for May 1983 would balance an anomalous equatorward flow on its shoreward side. The numerical model results closely resemble the

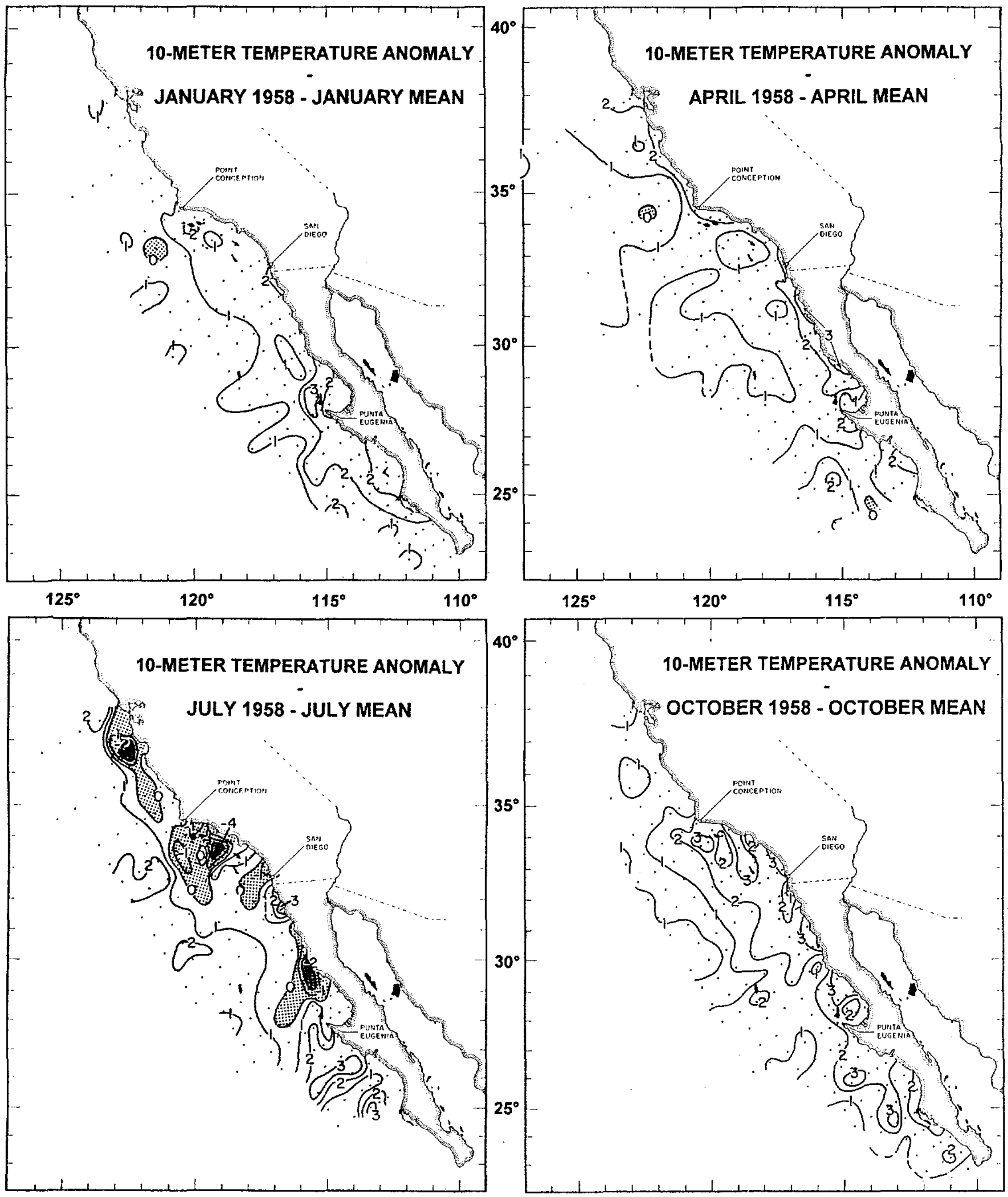


Figure 17. SST anomalies for the four surveys of figure 16 (from Lynn and Reid 1975). Negative values are *shaded.*

anomalous patterns of dynamic height found during 1958 (figure 16) and 1992 (figure 10) and thus provide an argument that some of the dynamical response of eastern North Pacific El Niño events is a consequence of modified Kelvin wave/Rossby wave forcing.

Researchers from the Los Alamos National Laboratory and the Naval Postgraduate School have simulated SSH and barotropic currents from January 1985 through June 1994, using a different GCM (Julie McClean, pers. comm.). Model SSH anomalies of about 20 cm and barotropic transport anomalies of 100 m^2/sec propagated poleward along the coast of North America from January through April 1992. The researchers conclude that the anomalously strong signal in 1992 is the poleward-propagating extension of equatorial Kelvin waves resulting from the 1991 El Niño event. They also note SSH anomalies propagating westward from the coastal region in April 1992, consistent with Rossby wave

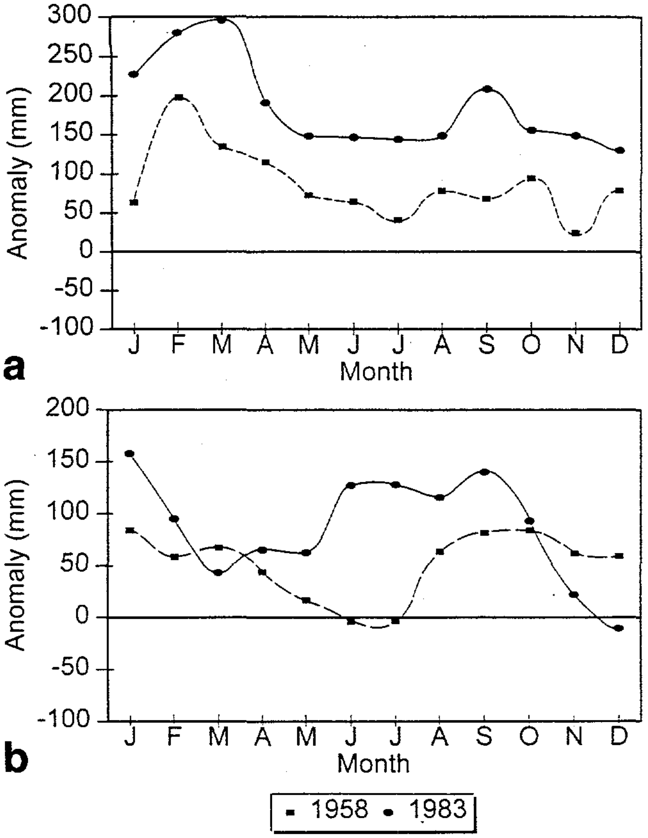


Figure 18. 1958 and 1983 sea-level anomalies (in mm) from the monthly means for (*a*) San Francisco (1900–92) and (*b*) La Jolla (1925–92). The secular trend has been removed from both sets.

development. We hope that the observations described in this report will stimulate further theoretical studies of the mechanism that produces oceanic anomalies off North America during El Niño events.

CONCLUSIONS

We speculate that the observed El Niño signal in the eastern North Pacific is some combination of anomalous local atmospheric forcing (which has its strongest influence in the upper ocean) and remotely generated oceanic perturbations (which likely propagate as coastally trapped waves and apparently are most evident at mid-depths within an internal Rossby radius of the coast). The dominant forcing that produces the enhanced and unseasonal Inshore Countercurrent remains unclear, although its occurrence in late winter during ENSO events is apparent. The suggestion is raised that the delay in spring transition to an upwelling regime, coupled with reduced upwelling (increased downwelling), large-scale onshore transport, and Kelvin wave dynamics may all play a part in the observed anomalous conditions in the California Current system. Comparative evidence with models suggests that the development of a Rossby wave may account for an offshore migration of a high ridge in anomalous sea-surface elevation, relating to a return to equatorward coastal circulation. The large-scale patterns of SST anomalies, however, are of such magnitude, extent, and persistence over this period that they are clearly attributed to anomalous atmospheric forcing.

An ENSO event began developing in the Pacific equatorial zone in mid-1994 and reached maturity by year's end (*Climate Diagnostics Bulletins* 1994). The large-scale SST pattern of the North Pacific for December 1994 is opposite to that often described as the typical El Niño north event (e.g., figure 15b). The central North Pacific has a large region of positive SST anomaly, and the North American coastal region is negative. However, the January 1995 *El Niño Watch Advisory* (issue 95-1, CoastWatch, SWFSC, La Jolla) shows recent coastal warming; the near-coastal waters as of mid-January were close to 1°C above their long-term mean. The ensuing degree of response of local waters will contribute to our understanding of the forcing mechanisms. A continuous monitoring system established at various positions along the coast within the water column would help to provide the unambiguous answer.

ACKNOWLEDGMENTS

We thank the scientific and technical staffs, both past and present, of the CalCOFI program; the personnel of the Southwest Fisheries Science Center involved in the FORAGE program at La Jolla (under the leadership of R. M. Laurs) and the Groundfish Analysis Investigations (under the leadership of W. H. Lenarz and S. Ralston); and other unnamed individuals involved in collecting the many sources of data that we have used. Processing and quality control of 1992–93 CTD data were handled by K. Bliss, A. Mantyla, and K. Sakuma. H. Parker provided the upwelling index data. We also thank Jane Huyer and an anonymous reviewer for very helpful suggestions that improved the manuscript.

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VARIATIONS IN MARINE BIRD COMMUNITIES OF THE CALIFORNIA CURRENT, 1986–1994

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ABSTRACT

Concurrent sampling (1986–94) off central and southern California revealed strongly concordant fluctuations in abundance of several of the California Current's most numerous seabirds. Pronounced anomalies of abundance occurred in 1986, 1988–89, and 1992–93. In 1986 and 1992–93, sea-surface temperatures were high; cold-water species were scarce; and warm-water species were abundant. In 1988–89 the reverse patterns held. These patterns exemplify bird populations' short-term response to large-scale change in oceanic conditions, particularly sea-surface temperature. In addition to these short-term responses, our surveys revealed long-term (7–8 year) declines of cold-water species and similarly long-term increases of warm-water species. The temporal contrast of these changes underlines the ecological importance of continuous, long-term records of animal abundance.

INTRODUCTION

Long-term data sets of variability in physical factors and of biological responses at the base of the food web are relatively common in marine systems (e.g., Peterson 1989). But long time series from upper trophic levels are rare. This is because of (1) the difficulty and expense in accumulating records, and (2) the effect of market conditions on the apparent prevalence of exploited resources. California Cooperative Oceanic Fisheries Investigations (CalCOFI) has done a remarkable job in maintaining a unique record of lower-ecosystem responses to marine climate variability (e.g., Brinton 1981; Chelton et al. 1982); recently, studies of upper trophic level organisms have been added to the program.

We report on variation in the abundance of upper trophic level predators (birds) as determined on CalCOFI cruises from 1987 to 1994, and compare that variation to patterns observed farther north, from 1986 to 1994. These are the longest such quantitative data sets on annual variation in at-sea marine bird abundance anywhere in the world. This long effort is born of necessity: given the extreme annual variation in marine climate found in eastern boundary currents, sampling for 5–10 years is the minimum required to characterize the variability inherent in the system and its avifauna. Previously, seasonal occurrence patterns of marine birds off California were reported by Ainley (1976) and Briggs et al. (1987). The former report also presented an analysis of interannual variability (1955–73) exceptional for its broad spatial and temporal coverage, and based on data collected in a semiquantitative fashion.

METHODS

We compared data sets gathered independently in the southern and central portions of the California Current (figure 1). Those from the southern area were collected in April and July 1987–94; those from the central area were collected in June 1986–94. The same vessel usually surveyed in both areas, and many of the same people conducted the work. Cruises covered waters from the coast to well beyond the continental shelf in the

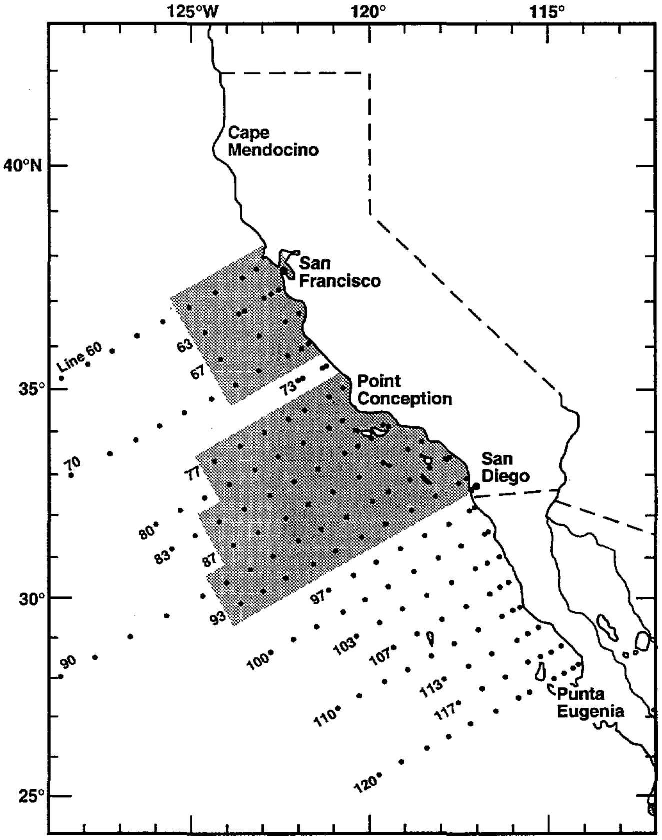

Figure 1. The CalCOFI study area, shaded to indicate the regions in which seabird studies were conducted.

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southern region, and to the deeper portion of the continental slope (e.g., 2000 m) in the central region.

One observer in the southern region and two in the central region counted birds continuously as they passed within a 300 m wide strip on one forequarter of the ship. Censuses continued whenever the ship was under way during daylight. In the south, birds that were attracted to the ship were counted when first detected but subsequently ignored. In the north, such birds were counted as 0.3 individuals if they approached the ship from the direction toward which censuses were being conducted; thereafter they were ignored like the rest of the ship followers. Censuses in the central region were corrected to account for bird flux, a function of the relative speed and direction of the ship and the birds (Spear et al. 1992). Thus, counts between the two regions are comparable on a relative but not absolute basis. In the central region, we did not include data gathered in waters <200 m deep between Point Reyes and Point San Pedro in an attempt to delete complications to overall patterns due to local birds associated with the huge breeding colonies at the Farallon Islands, midway between these two points.

Observations were converted to densities—i.e., number of birds per km^2 of ocean surveyed (a function of the distance the ship traveled during unit time multiplied by 300 m strip width). We report seasonal variation from the average density calculated for all spring or summer cruises. Differences were compared from year to year relative to average sea-surface temperature. The latter was assessed from data gathered from the ships' thermosalinographs, with a temperature reading made for each 1–3 km census segment along cruise tracks.

RESULTS

We include analyses for the numerically dominant species, and for less numerous species that showed clear-cut differences in annual abundance related to El Niño or to cooler periods. During the period of study, sea-surface temperatures were highest during 1992–93 (Sydeman and Ainley 1994; figure 2). Both that period and 1986 were considered El Niño periods (see other contributions in this volume for details).

In the central region, we separated species depending on whether they did or did not breed locally (figures 3 and 4). The dominant species was the sooty shearwater (see appendix for scientific names), a species that breeds on islands in the South Pacific. Like the black-footed albatross, it was more abundant early in the study period, especially 1988–89, than later (Veit et al., unpubl. data). Among the species that could be categorized as having affinity for cool water (Ainley 1976; Briggs et al. 1987), densities of sooty and pink-footed shearwaters and black-footed albatross were low during 1992–93; density of shearwaters was also low in 1986. The remaining species not breeding locally in central California (black-vented shearwater, black storm-petrel, brown pelican, Heermann's gull, and Xantus' murrelet) were all more abundant during 1992; black-vented shearwater was also more abundant in 1986 and 1993; and Heermann's gull was also more abundant in 1986. These species breed in areas of warmer water—on islands off Mexico. The occurrence pattern of the brown pelican was least consistent with the other members of this group.

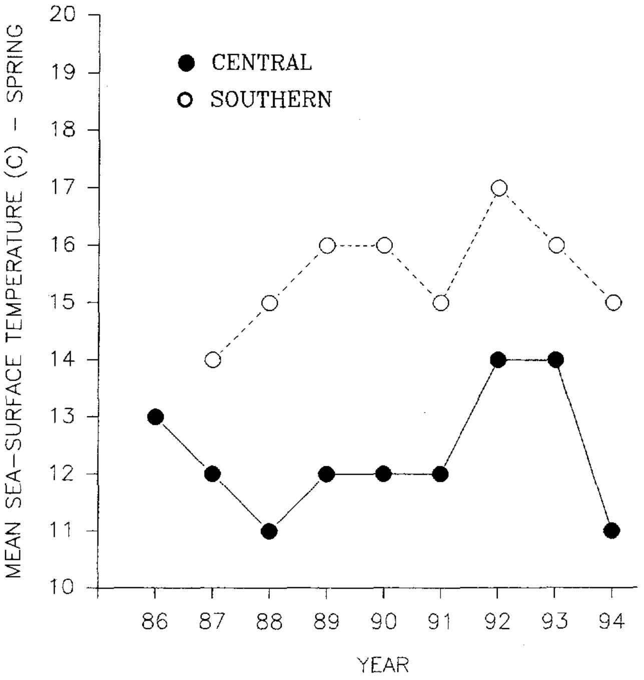

Figure 2. Average sea-surface temperatures (°C) based on measurements made during cruises from 1986 through 1994.

Among six prevalent species that breed and remain in central California for all or most of the year, Leach's storm-petrel, Brandt's cormorant, and common murre were more abundant during 1992–93 (figure 4). Cassin's auklet showed a large increase in 1986 and 1994; the western gull appears to have decreased in the second half of the study period; and the rhinoceros auklet demonstrated no clear pattern (rhinoceros auklets did change spatially, however; Allen 1994).

In the southern region, all species except sooty shearwater and least storm-petrel bred locally (figure 5). The gradually decreasing abundance of sooty shearwater and the gradually increasing abundance of Leach's storm-petrel were consistent with patterns in the central region. Also consistent with the central region were increases in density of black-vented shearwater and black storm-petrel in 1992. The least storm-petrel, a species that rarely occurs as far north as the central California Current region, also demonstrated this pattern. The remaining species showed no pattern that was consistent with the others.

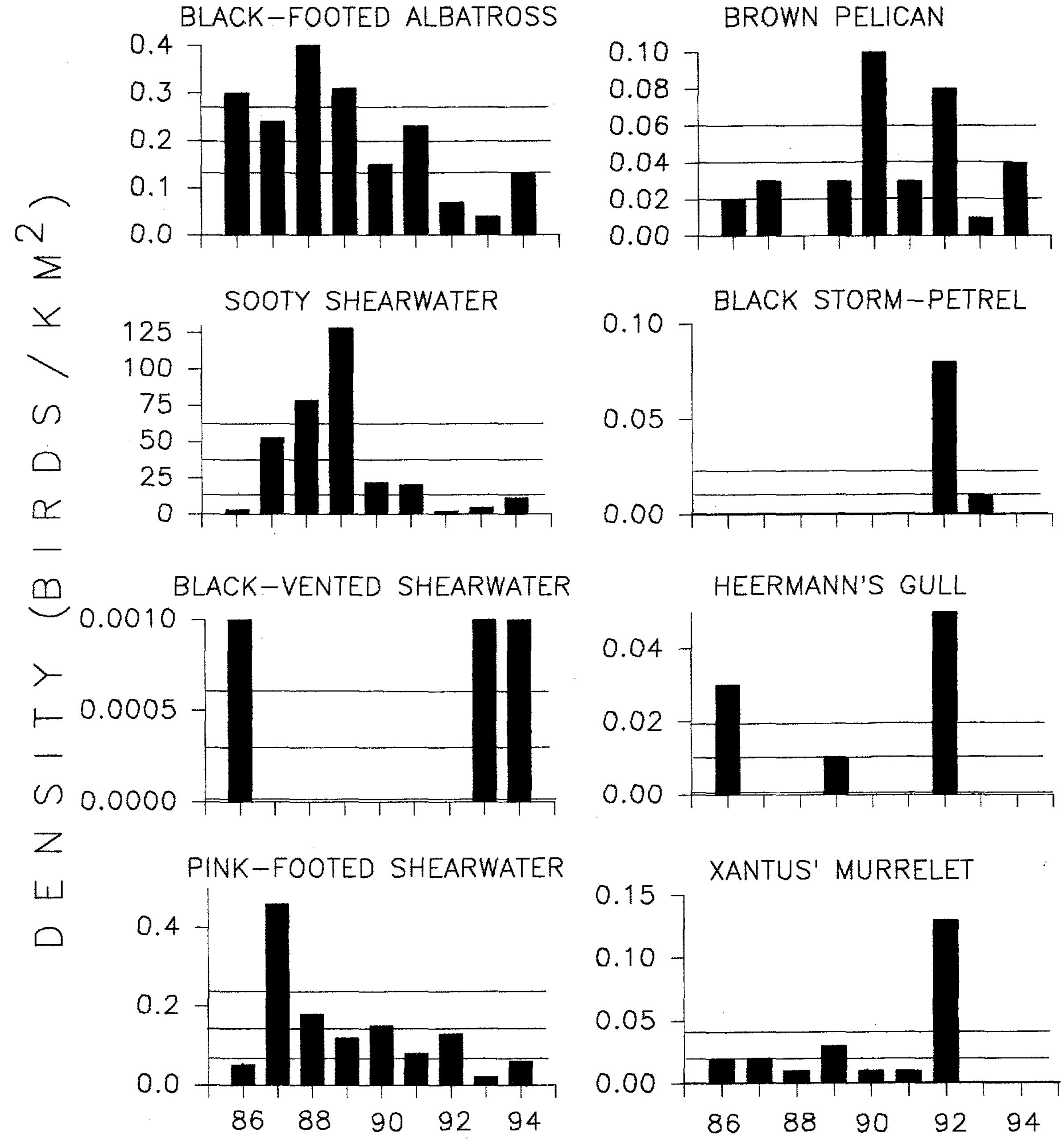

Figure 3. Mean densities (birds/km^2) of nonbreeding seabird species off central California, June 1986–94. *Horizontal lines* indicate the overall mean and plus or minus 95% confidence intervals.

DISCUSSION

When a large number of individuals of a single seabird species appear in a region such as central California, or if a species becomes uncommon for a time, one might consider that (1) reproduction or survivorship was especially good or poor, or (2) ocean conditions had changed to attract one species over another. The latter may be especially important in climatically variable eastern boundary currents such as the California Current (e.g., Glantz and Thompson 1981). Ainley (1976) showed convincingly that annual fluctuation in the prevalence of many seabird species in the nearshore California Current region reflected variation in marine climate, especially sea-surface temperature. Longer-term trends in abundance could be due to changed climate and to a change in food-web structure (e.g., Roemmich and McGowan 1995).

Accordingly, we observed increased numbers of most warm-water species in the southern and central portions of the California Current in 1986 and especially in

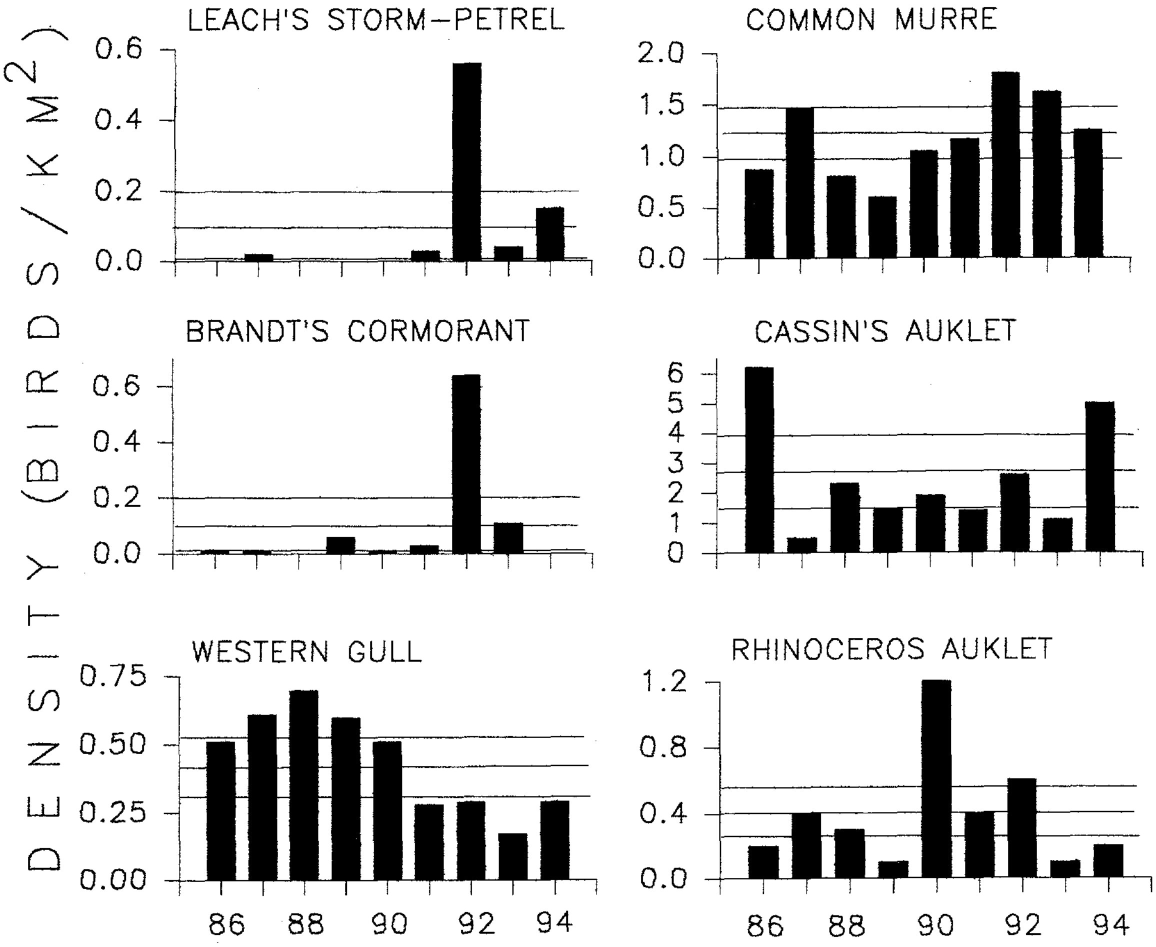

Figure 4. Mean densities (birds/km^2) of locally breeding species of seabirds off central California, June 1986–94. *Horizontal lines* indicate the overall mean and plus or minus 95% confidence intervals.

1992–93 (El Niño periods). Abundance of cool-water species decreased during these periods. Although some of the cool-water species were more abundant during the cooler period around 1988, regional and species concordance was less consistent. This may indicate that during this study cool-water periods in the California Current were well within the limits preferred by the region's avifauna. When water temperatures increased, however, the region was invaded by species from the south. In fact, considering also Ainley's 1976 data, the species that best indicated warm-water anomalies were black-vented shearwater, black storm-petrel, and least storm-petrel in a positive fashion (i.e., becoming more prevalent) and sooty shearwater in a negative way (becoming uncommon). Among the three warm-water species, increased abundance of the black-vented shearwater in central California ranks with invasions of the pelagic red crab (*Pleuroncodes planipes*) as a biological indicator of an especially strong California Countercurrent (Davidson Current); countercurrent strength is intensified during El Niño (McLain and Thomas 1983). Under normal conditions, only a few black-vented shearwaters reach central California during the Davidson Current season.

The brown pelican's inconsistent response to El Niño (increase in central California during 1992 but not 1986) was somewhat surprising, because a species often commensal with the brown pelican—Heermann's gull—showed a consistent response. The two species are among those that have large breeding populations in Mexico and that move in large numbers to the California Current during the nonbreeding season. Greatest numbers of pelicans occurred in 1990, not an El Niño year, but one in which their reproductive success was especially good (D. W. Anderson, pers. comm.). Thus the greater abundance that year could have resulted from large numbers of first-year birds that dispersed widely. During warm-water events, pelicans from the southern regions, and sometimes the Southern California Bight, appear in central and northern California much earlier in the year than otherwise (because they usually forego or lessen breeding in those years; D. W. Anderson, pers. comm.).

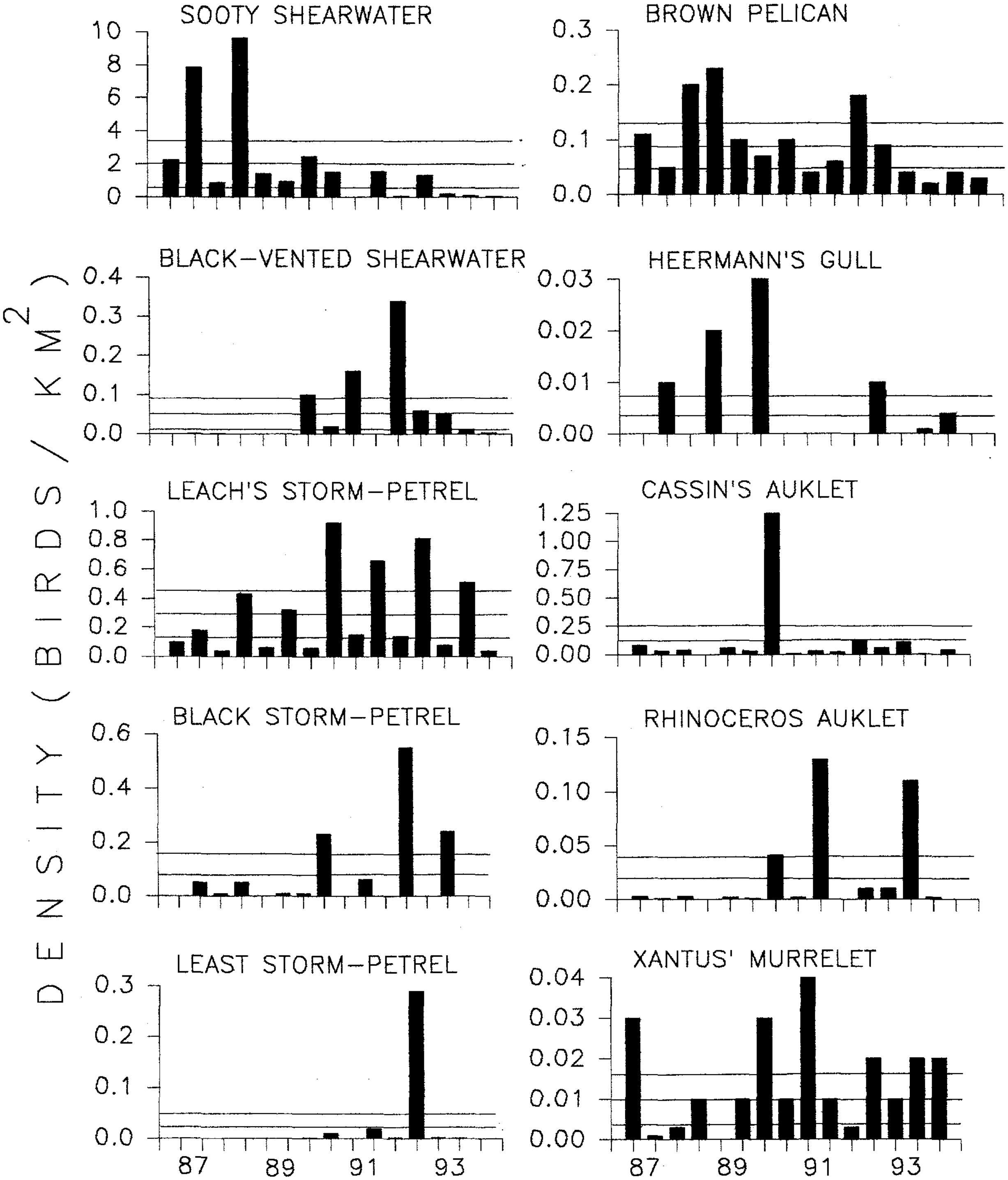

Figure 5. Mean densities (birds/km^2) of breeding and nonbreeding species of seabirds off southern California, April and June 1987–94. *Horizontal lines* indicate the overall mean and plus or minus 95% confidence intervals.

Such a within-year response is not evident in our analysis of the data, probably because of our inability to separate individuals from the local and the more distant breeding populations. In addition, Jacques (1995) has shown that pelicans move farther north than usual (to Oregon and Washington) during warm-water years, although not necessarily in larger numbers. Finally, the pelican and Heermann's gull are not as behaviorally linked in California as they are farther south, especially during spring (D. W. Anderson, pers. comm.), which also helps to explain these two southern species' inconsistent response to ocean conditions.

Species that breed locally (e.g., Brandt's cormorant, common murre, and Cassin's auklet) also responded to changed ocean conditions. Unlike the species that are good indicators of warm water, the locally breeding species did not seem to undertake long-distance movements. Rather, the apparent increases in density during El Niño were caused by their dispersing more widely within the region (see Allen 1994), as well as by greater numbers remaining at sea instead of spending considerable time at breeding sites. Indeed, it has become well established that El Niño and other warm-water events discourage breeding among seabirds in the California Current region (Ainley and Boekelheide 1990; Ainley et al. 1995). Conversely, these local species seemed less abundant during cool-water periods because they concentrated close to breeding colonies.

We are aware of no reports of a mass exodus of seabirds from the California Current or mass mortality during El Niño, as has often been observed in the Peru Current (cf. Murphy 1981; Ainley et al. 1986). California species show only slightly elevated mortality (Stenzel et al. 1988). The reason for the difference in the two current systems may stem from the birds' reliance on just one prey species in the Peru Current—the anchoveta (*Engraulis ringens*)—but reliance on a more diverse prey choice in California—e.g., anchovy (*E. mordax*), Pacific mackerel (*Scomber japonicus*), rockfish (*Sebastes* spp.), squid (*Loligo opalescens*), and euphausiids (Ainley and Boekelheide 1990).

ACKNOWLEDGMENTS

We thank the officers and crew of NOAA ship *David Starr Jordan* and the Scripps R/V *New Horizon* for logistical support. CalCOFI and the National Marine Fisheries Service, Tiburon Laboratory, made our participation possible. Our effort in the southern region was supported financially by NSF-OCE; work in the central region was supported by the Environmental Protection Agency, U.S. Fish and Wildlife Service, and the Gulf of the Farallones National Marine Sanctuary. Data analysis was funded, in part, by the state of California, Office of Oil Spill Prevention and Response. We also thank C. Alexander, J. Tweedy, R. Ferris, M. LaBarr, I. Gaffney, and D. Hardesty for help on cruises and G. Ballard for aid in data reduction. D. W. Anderson and A. D. MacCall made many helpful suggestions for improving the manuscript.

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APPENDIX

Common and scientific names of bird species discussed in the text.

Black-footed albatross *Diomedea nigripes*
Sooty shearwater *Puffinus griseus*
Pink-footed shearwater *Puffinus creatopus*
Black-vented shearwater *Puffinus opithomelas*
Black storm-petrel *Oceanodroma melania*
Leach's storm-petrel *Oceanodroma leucorhoa*
Least storm-petrel *Oceanodroma microsoma*
Brown pelican *Pelecanus occidentalis*
Brandt's cormorant *Phalcrocorax penicillatus*
Western gull *Larus occidentalis*
Heerman's gull *Larus heermanni*
Common murre *Uria aalge*
Xantus' murrelet *Synthliboramphus hypoleuca*
Rhinoceros auklet *Cerorhinca monocerata*
Cassin's auklet *Ptychoramphus aleuticus*

ENSO EVENTS IN THE NORTHERN GULF OF ALASKA, AND EFFECTS ON SELECTED MARINE FISHERIES

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ABSTRACT

The 1991–93 El Niño–Southern Oscillation (ENSO) event first appeared in the northern Gulf of Alaska in autumn 1991 with warm sea-surface temperatures. In winter 1992, there were pulses of increased sea level and anomalous circulation. El Niño conditions persisted at least through summer 1993. The effects of this ENSO event on major groundfish species and Pacific herring in the northern Gulf of Alaska were examined and compared with the effects of previous ENSO events. There is little evidence that the 1991–93 or 1982–83 ENSO events affected landings of walleye pollock, Pacific cod, Pacific halibut, or arrowtooth flounder. Some changes in distribution of groundfish species were observed in 1993, but the effect was similar to changes observed in non-ENSO warm years. In general, warm ocean conditions have a positive effect on recruitment of northern stocks, but ENSO events appear to have an inconsistent effect on year-class strength within species and among different species. For example, strong year classes of halibut and arrowtooth flounder sometimes, but not always, coincide with ENSO events; ENSO events are associated with moderate to weak year classes of cod and pollock. However, post-ENSO warm years often are associated with strong recruitment of many groundfish species. Major changes have occurred in the Gulf of Alaska ecosystem since 1977. The influence of the 1976 ENSO event in precipitating these changes and the role of the frequency or strength of subsequent El Niño events is presently unknown. Herring and other stocks of small pelagic fishes may be more affected by ENSO events. In particular, decreased catches, recruitment, and weight-at-age of herring are sometimes associated with ENSO events. Furthermore, a variety of seabirds which feed mostly on pelagic forage fishes or the pelagic juvenile stages of groundfish suffered widespread mortalities and breeding failures in the Gulf of Alaska during the ENSO years of 1983 and 1993. These effects on seabirds were also observed over a wider geographic range, from California to the western Bering Sea.

INTRODUCTION

El Niño–Southern Oscillation (ENSO) events along the west coast of North America are associated with oceanic conditions that can affect the distribution, growth, and abundance of fish populations (Wooster and Fluharty 1985). The poleward propagation of oceanic long waves along the coast or shelf break can result in deeper thermoclines, increased sea level, stronger poleward flow, and consequent redistribution of water properties with higher salinity and temperature (Simpson 1992). Atmospheric teleconnections that affect the northern Gulf of Alaska include the intensification of the Aleutian low-pressure system, changes in the wind field, increased storminess in the Gulf of Alaska, and relaxed coastal upwelling. Our objective in this paper is to document changes in the physical environment of the Gulf of Alaska that occurred in response to the 1991–93 ENSO event, compare them to previous events, and discuss how these changes may have affected marine fish populations.

There are many commercially important marine species in the Gulf of Alaska, as well as many ways to assess ENSO effects. Most commonly, range extensions or unusual occurrences of southerly species are documented. We focus our study on the impact of ENSO events on the most abundant or commercially important species, since variability in abundance of these key species will have repercussions throughout the ecosystem. We have chosen five key species for this analysis: walleye pollock, *Theragra chalcogramma*; Pacific cod, *Gadus macrocephalus*; arrowtooth flounder, *Atheresthes stomias*; Pacific halibut, *Hippoglossus stenolepis*; and Pacific herring, *Clupea pallasi*. For each of these species, we examine whether the 1991–93 ENSO had any observable immediate effects on fisheries through landings and distribution, or long-term effects on growth and recruitment. When data

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[Manuscript received November 2, 1994.]

are available, comparisons are made with prior ENSO events. The results of these observations are used to challenge two hypotheses about the effects of El Niño on northern marine communities: (1) that ENSO events have a beneficial effect on recruitment of northern fish populations, and (2) that pelagic communities are more strongly affected by ENSO events than demersal communities.

ATMOSPHERIC AND OCEANIC TELECONNECTIONS

As early as December 1989 (Janowiak 1990), the region of warm equatorial water in the tropical Pacific expanded and slowly shifted eastward. During the last half of 1990 and early 1991 other tropical conditions evolved toward an ENSO warm episode; the warm event was fully developed by fall 1991, when increased atmospheric convection in the region of positive sea-surface temperature anomalies demonstrated critical atmospheric-oceanic coupling (Janowiak 1990, 1993; Mo 1993). The mature phase persisted through spring 1992. During summer 1992, tropical conditions reverted abruptly toward normal, but anomalously warm water continued to be found along the equator just west of the International Date Line and at other sites (CAC 1992a). By December 1992 it was apparent that mature warm-episode conditions were continuing in the tropical Pacific (CAC 1992b, 1993a). The cooling of sea-surface temperatures and consequent reduced atmospheric convection over the eastern tropical Pacific Ocean during May and June 1993 (CAC 1993b, c) heralded the waning of the 3-year event. The 5-month running mean of the standardized Southern Oscillation Index (SOI; figure 1) summarizes the 1991–93 ENSO event and allows comparison with other warm episodes.

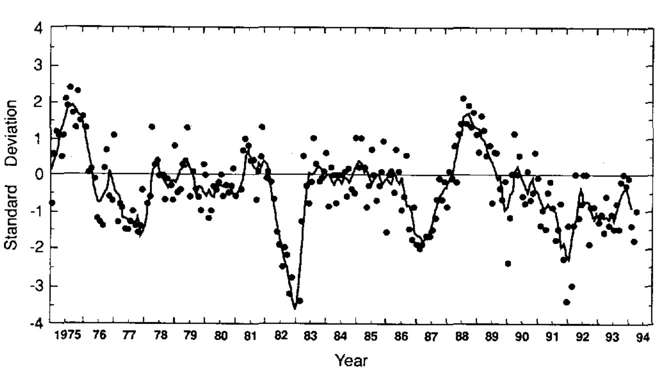

Figure 1. The Southern Oscillation Index: 5-month running mean of the difference between the standardized sea-level pressure anomalies at Tahiti and Darwin. Values are standardized by the 1951–80 mean annual standard deviation. *Circles* indicate individual monthly means. The *x-axis labels* are centered on the month of July.

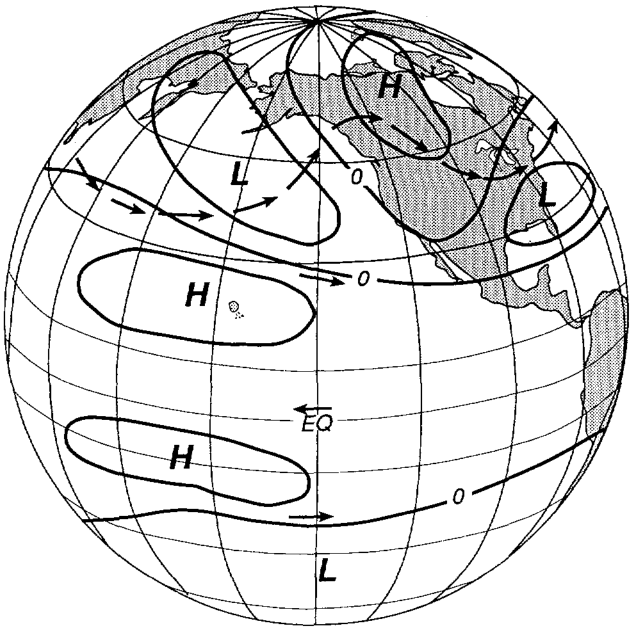

Figure 2. Schematic illustration of the hypothesized global pattern of middle- and upper-tropospheric geopotential height anomalies (*solid lines*) during a Northern Hemisphere winter that falls within an episode of warm sea-surface temperatures in the equatorial Pacific. The *single arrows* indicate strengthening of the subtropical jets in both hemispheres, along with stronger easterlies near the equator during warm episodes. The *path described by arrows* depicts a midtropospheric streamline as distorted by the anomaly pattern, with pronounced troughing over the central Pacific and ridging over western Canada (from Horel and Wallace 1981).

Teleconnections to the Northern Hemisphere

Horel and Wallace (1981) summarized theoretical studies suggesting that propagating Rossby waves provide a basis for understanding teleconnections to the Northern Hemisphere. Strong teleconnections to middle latitudes during warm episodes are possible only when westerly winds extend from the mid-latitudes into the equatorial troposphere above the region of warm water, a condition satisfied only during the Northern Hemisphere's winter. Negative midtropospheric geopotential height anomalies over the North Pacific Ocean bring about a deepening and southern displacement of the Aleutian low (figure 2). Teleconnections to the Northern Hemisphere are thought to be strongest during the second winter of a warm episode (Horel and Wallace 1981). Modified oceanic forcing due to the anomalous Aleutian low is a major reason for ENSO-related changes in the Gulf of Alaska (Emery and Hamilton 1985). Eastward-propagating equatorial oceanic Kelvin waves modify the ocean's mixed-layer characteristics and occasionally are strong enough to excite northward- and southward-propagating Kelvin waves along the west coast of the Americas (Wyrtki 1975; Enfield and Allen 1980) and Rossby waves that may rebound across the ocean (Jacobs et al. 1994).

The Pacific/North American (PNA) teleconnection index is a linear combination of normalized 500 mb geopotential height anomalies at four centers ranging from near Hawaii to the North Pacific Ocean, Alberta, and the Gulf Coast region of the United States (Wallace and Gutzler 1981). A deep Aleutian low characterizes positive values of PNA. Thus, sustained positive values of PNA during winter indicate the anomalous atmospheric pressure patterns responsible for modified forcing of the North Pacific Ocean. The Rossby wave train generated during an ENSO event is one mechanism that produces positive PNA anomalies.

The Northeastern Pacific Atmospheric Pressure Index (NEPPI) is another index of atmospheric circulation over the eastern North Pacific Ocean (Emery and Hamilton 1985). NEPPI measures the monthly mean sea-level pressure gradient between a point near Reno, Nevada, and a point in the North Pacific Ocean south of Amukta Pass in the Aleutian Islands. NEPPI tends to be strongly positive in winter, and low-valued to weakly negative in summer. Like PNA, NEPPI varies directly with the position and intensity of the Aleutian low, and positive winter excursions can result from ENSO-induced Rossby waves.

Northern Hemisphere Response

To estimate the strength and duration of the teleconnection to the North Pacific Ocean, we formed time series of PNA index anomalies (figure 3) and NEPPI anomalies (figure 4) based on 30-year and 48-year records, respectively, of indicial monthly means. In figure 3, a positive PNA trend occurred during the fall of 1991, when a distribution of negative height anomalies and above-normal height variability had developed over the eastern North Pacific. This distribution resembled the pattern associated with early stages of a developing ENSO episode (CAC 1991). The enhanced southerly winds associated with the negative height anomalies over the eastern North Pacific appeared to be related to above-normal sea-surface temperatures along the California coast during winter 1992. This pattern weakened during summer and fall of 1992. Between December 1992 and mid-January 1993, a major blocking high-pressure cell was observed over the eastern North Pacific, with persistent negative height anomalies over western North America. This anomaly pattern reflected the strong negative phase of the PNA teleconnection pattern (figure 3), and was associated with much above-normal storm activity and above-normal precipitation totals over the

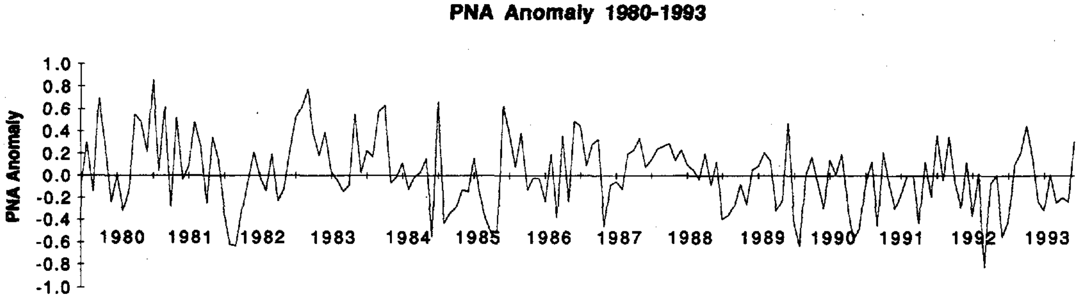

Figure 3. The Pacific/North American teleconnection index monthly anomaly, 1980–93, based on monthly means for the 30-year period from 1965 to 1994.

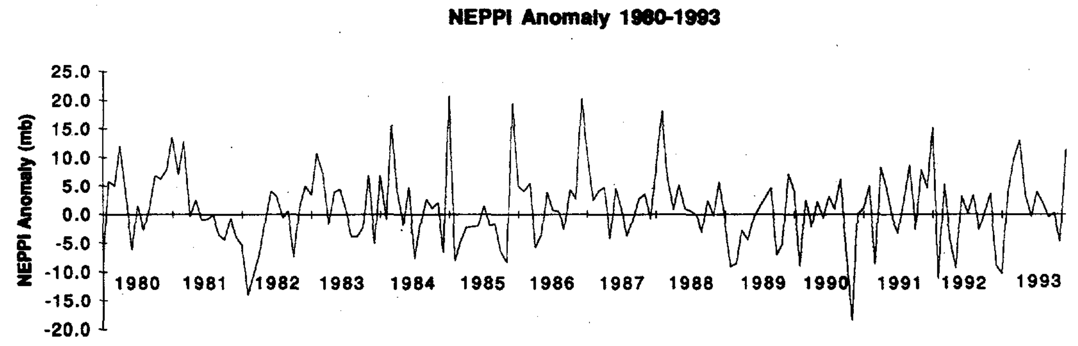

Figure 4. The Northeastern Pacific Pressure Index monthly anomaly, 1980–93, based on monthly means for the 48-year period from 1946 to 1993.

western contiguous United States (CAC 1993a). It is interesting that this well-defined PNA pattern occurred despite continued weak warm-episode conditions in the tropical central Pacific. The NEPPI anomaly series (figure 4) shows a similar relaxation of the northeastern Pacific sea-level pressure gradient during this time. In mid-January, this pattern reversed itself and persisted with well-above-normal temperatures over Alaska and the western United States until June, when a negative PNA pattern developed and lasted until December 1993.

The monthly PNA index showed positive anomalies that could be associated with an ENSO event during November 1991; January, March, and June 1992; and February, March, and April 1993 (figure 3). But only the April 1993 anomaly was larger than one standard deviation from the mean. The 1991–93 episode may be contrasted with the ENSO event of 1982–83, when PNA was anomalously positive during September and December 1982, and January through June 1983. January through April 1983 PNA anomalies were greater than one standard deviation from the long-term monthly means. The NEPPI anomaly series showed positive departures during September, November–December 1991; January, March, June, August, October–November 1992; and February–May 1993 (figure 4). Of these positive anomalies, September 1991, January and August 1992, and March–April 1993 were more than one standard deviation from their respective means. For 1982–83, NEPPI anomalies were positive during November–December 1982, January–March 1983, and May–June 1983. February, March, and June anomalies were greater than one standard deviation.

In summary, the ENSO atmospheric teleconnection to the Gulf of Alaska during 1991–93 did not appear to be as strong as during the 1982–83 warm episode, nor was the pattern as persistent. There were reversals of the PNA and NEPPI positive patterns during early 1992 and early 1993, and only the April 1993 positive anomaly was a significant departure from the 30-year PNA April mean. It is informative to note that PNA and NEPPI anomalies also occur in other years, caused by mechanisms other than ENSO events.

OCEANOGRAPHIC CONDITIONS

Sea-Level Anomalies

The upper ocean responds to climatic events in many ways, including changing sea level. One of the merits of using sea level as an index of change is that it integrates the effects of several oceanographic and atmospheric factors (e.g., local wind forcing, long-wave propagation, integrated water-column density, thermocline depth) and is often the most useful routinely measured quantity related to circulation and its variations. Sea level has been found to be a good indicator of El Niño events and their poleward propagation (e.g., Cannon et al. 1985; Huyer and Smith 1985).

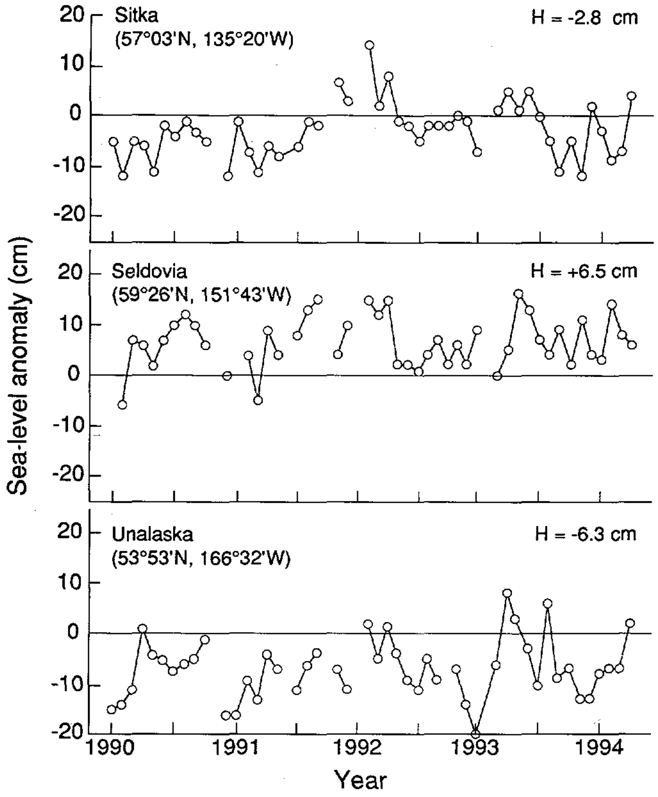

Figure 5. Sea-level anomalies from the mean monthly values (1975–86), corrected for atmospheric pressure variations, January 1990–April 1994 at Sitka, Seldovia, and Unalaska, Alaska. The mean anomalies (H) during this period are also shown. The gaps in the records resulted from missing maps in some issues of the *Climate Diagnostics Bulletin.*

We examined sea-level anomalies from January 1990 through April 1994 at three sites (Sitka, Seldovia, and Unalaska) in the Gulf of Alaska in relation to the 1991–93 El Niño event. The data used are the monthly sea-level anomalies, corrected for atmospheric pressure variations, from the mean monthly values for the period 1975–86 as taken from maps contained in the *Climate Diagnostics Bulletin* (U.S. Department of Commerce/NOAA 1990–94). The results are shown in figure 5; for comparison, see Reed and Schumacher (1981) for the long-term mean seasonal variation at these sites and an interpretation in terms of coastal circulation.

The anomalies in figure 5 show considerable variability at the three sites. The mean anomalies for this 52-month period were approximately −3 cm for Sitka, +6 cm for Seldovia, and −6 cm for Unalaska. These differences in mean sea level are not well correlated with variations in sea-surface temperature because the temperature anomalies were predominately positive during the 52-month period at all three sites (from *Oceanographic*

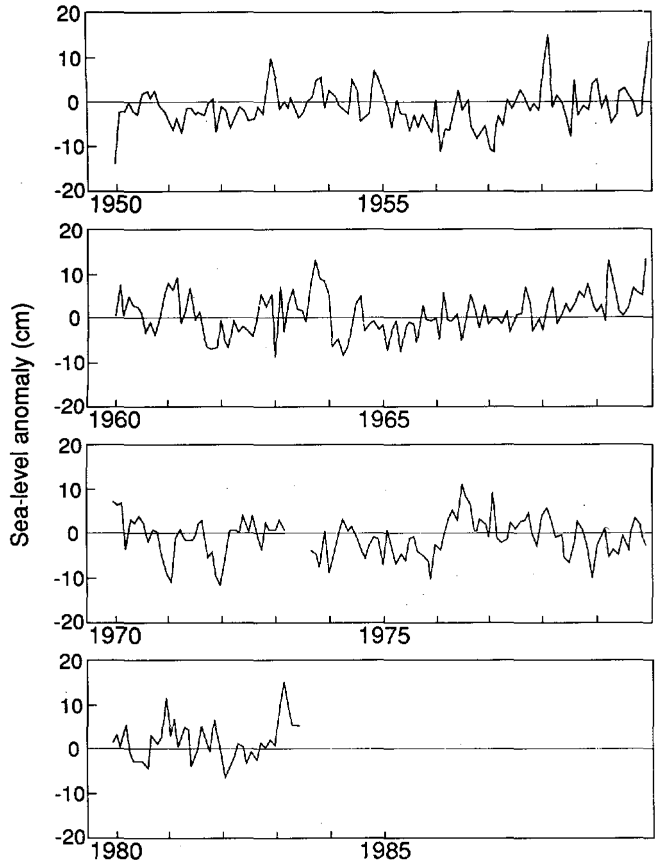

Figure 6. Sea-level anomalies from the mean monthly values (1938–83) at Sitka, Alaska, corrected for atmospheric pressure variations, 1950–83 (from data in Cannon et al. 1985).

Monthly Summary, U.S. Department of Commerce/NOAA 1990–94). There were clear increases in sea level at all sites in winter 1992 and spring 1993 in agreement with, but perhaps 2 months later than, peak temperature and sea-level anomalies at the equator off South America. The temperature-anomaly maps cited above strongly suggest rapid poleward propagation of the ENSO signal in the eastern Pacific in two separate pulses in early 1992 and early 1993. This behavior is believed to result from long waves, and it also occurred with the 1941, 1958, and 1982 El Niño events (Cannon et al. 1985). The maximum increase in sea level in figure 5 during the two events is about 15 cm. Thus there was a significant response in much of the Gulf of Alaska to the El Niño events of 1991–93. Winds probably enhanced the oceanic long-wave propagation. The near-surface wind anomalies (from the *Climate Diagnostics Bulletin*) were strongly northward during both pulses. Coastal sea levels in Alaska are also strongly affected by freshwater runoff (T. Royer, University of Alaska, Fairbanks, pers. comm.).

A longer time series of pressure-corrected sea-level anomalies, from 1950 to 1983, is shown for Sitka in figure 6. The 1958 and 1982 (early 1983) ENSO events are prominent and had anomalies of about 15 cm. Note, however, that the 1972 event, a major El Niño in the tropics, had little effect at Sitka. The anomalies at Sitka during all events appear to be only about one-half those off Oregon and northern California (Cannon et al. 1985; Huyer and Smith 1985). There are, however, large positive and negative anomalies that are not associated with El Niño events and that are sometimes related to large variations in wind-stress forcing (Chelton and Davis 1982). In summary, the 1991–93 event at Sitka was comparable in timing and magnitude to other large events (1941, 1958, and 1982); the strong tropical event of 1972 had little effect at Sitka; but the weak tropical event of 1976 did have an effect (Cannon et al. 1985). The 1972 event had little effect north of California, at least partly as a result of strong southward winds.

Gulf of Alaska Temperature Series

A time series of water-column temperatures dating back to 1970 is available from waters off Seward, Alaska, at 60°N, 149°W (see figure 7). Figure 8 shows sea-surface (SST) and 250 m temperatures off Seward. The coherence between both series is high ($r = 0.60$). The 1976, 1982, 1986, and 1992 ENSO events appear in this time series as positive anomalies about one year later, most obvious at the deeper depth. Royer and Xiong (1984) noted that the 1982–83 warming appeared at depth (150–200 m) several months prior to warming at the surface, and they thus concluded that warming in the Gulf of Alaska in 1982–83 was not caused locally, but rather was an advective event. During the winter of 1992 the anomaly was about +2°C at the surface and +0.5°C at 250 m, apparently similar to the 1982 ENSO event at the surface, but weaker at depth.

A longer time series exists for air temperatures at Sitka. In general, Sitka air temperatures correspond closely to the Seward water temperatures ($r = 0.41$ for SST, and 0.42 for 250 m temperature). From the longer air-temperature time series, there appear to be cyclic low-frequency trends. Royer (1989) has proposed that these trends are related to the 18.6-year lunar nodal cycle, which explains about 17% of the variance in Sitka air temperatures, whereas the SOI explains only about 5%. At the Seward temperature station the lunar nodal cycle explains 17% and 36% of the variability in SST and 250 m temperatures, respectively, whereas SOI events explain about 14% and 13% of the variance, respectively.

Upwelling Indices

Upwelling indices are derived from large-scale geostrophic wind-stress estimates (Bakun 1973). Generally, upwelling indices at Gulf of Alaska stations are strongly negative (downwelling) in winter; weakly positive

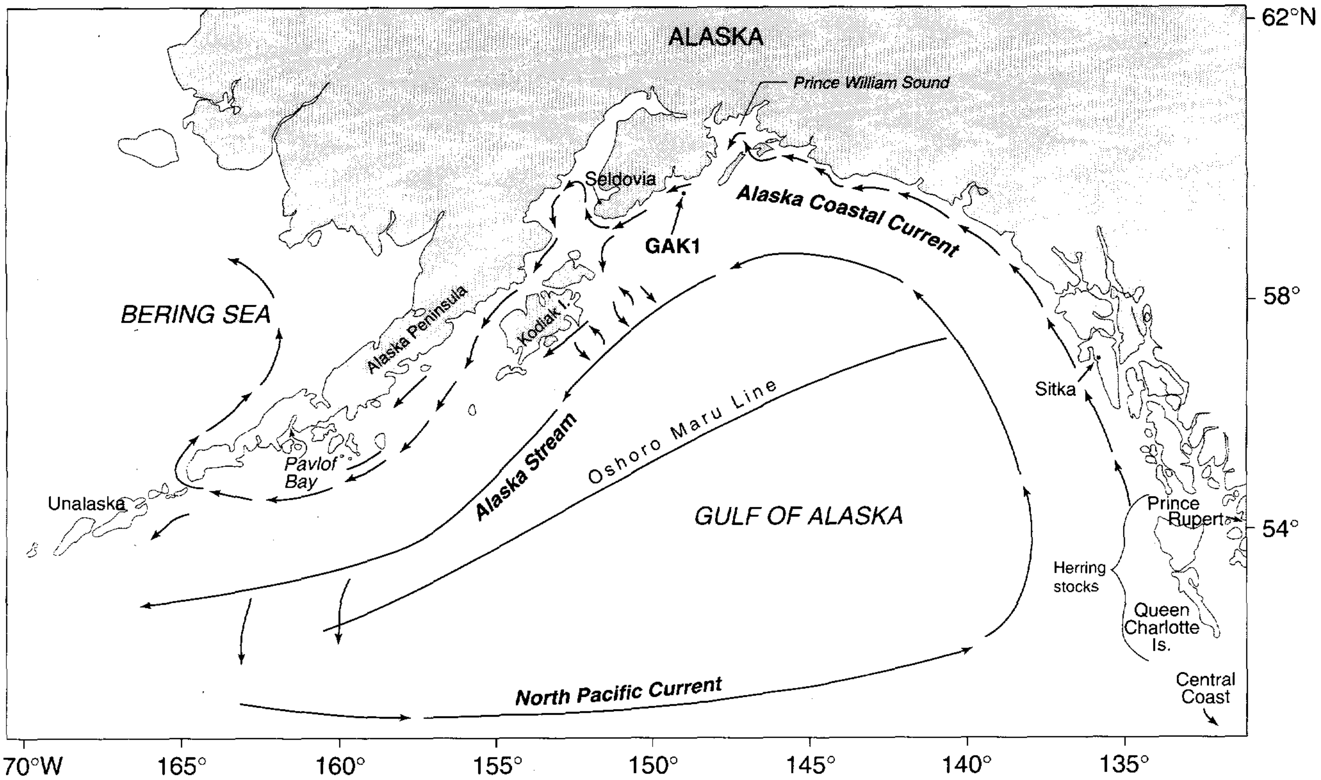

Figure 7. Gulf of Alaska, showing major current features and sites mentioned in the text. GAK1 is the water-column temperature station for Royer's (1989) series and the data shown in figure 8.

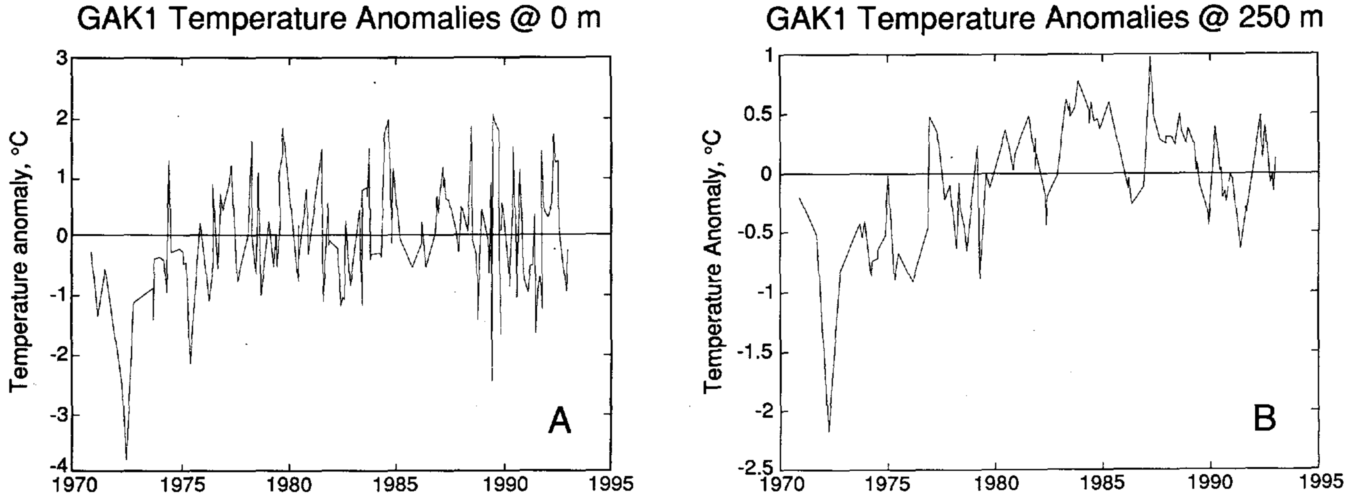

Figure 8. *A*, Sea-surface temperature anomalies at station GAK1, 1970–93. *B*, 250 m temperature anomalies at station GAK1 (from Royer, unpubl. data).

upwelling indices develop in June. Anomalies of winter (January–March) and spring (April–June) upwelling indices from 60°N, 146°W are shown in figure 9. El Niño events in the winters of 1952–53, 1957–58, 1965–66, 1982–83 were associated with strong downwelling anomalies. In some of these events, stronger downwelling anomalies appeared in the second winter, as noted above for atmospheric teleconnections. El Niño events in the winters of 1972–73, 1976–77, and 1991–93 were not associated with downwelling anomalies, and downwelling anomalies occurred in non-ENSO years such as 1950, 1974, and 1978–79. There was a springtime downwelling anomaly associated with the 1991–93 El Niño.

Circulation

Upper-ocean trajectories were simulated by the Ocean Surface Current Simulations (OSCURS; Ingraham and Miyahara 1989) model. This model combines a clima-

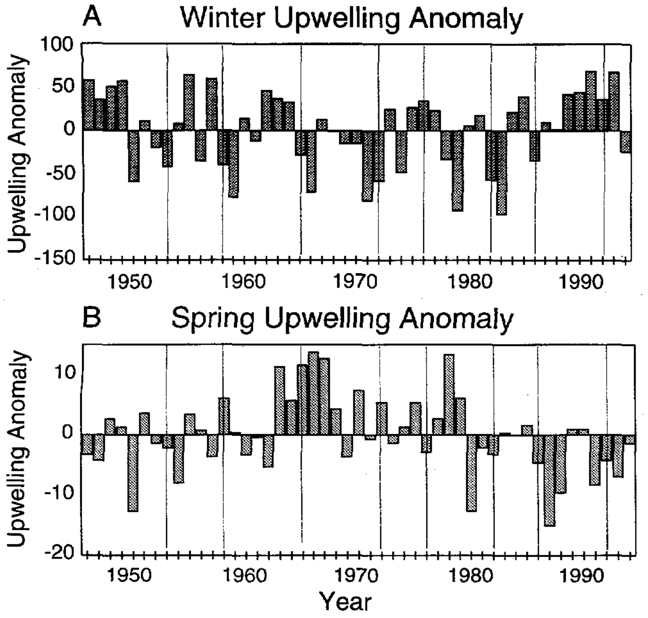

Figure 9. Upwelling index anomalies at 60°N, 146°W calculated as the deviation from the long-term mean for (*A*) winter (January–March) and (*B*) spring (April–June). Data provided by D. Husby.

tological mean density-driven (geostrophic) flow and empirically generated mixed-layer wind drift (Ingraham et al. 1991). The wind drift was derived from synoptic daily atmospheric pressure data (U.S. Navy, Fleet Numerical Oceanography Center). The wind-drift estimates were tuned to satellite-tracked drifter trajectories in the Gulf of Alaska reported by Reed (1980), and concurrent wind data. Trajectories were computed for December–March 1980–93. Most years show strong inflow toward the head of the Gulf of Alaska and southwestward outflow (as in 1989; figure 10). However, the winter of 1992–93 shows a strong anomaly, with very weak eastward flow in the central Gulf of Alaska and a strong westward flow near shore (figure 11). Flow characteristics in winter 1982–83 did not appear anomalous compared with other years.

EFFECTS ON MARINE FISHERIES

Landings

It is well recognized that landings reflect the influence of a number of factors, including fish distribution,

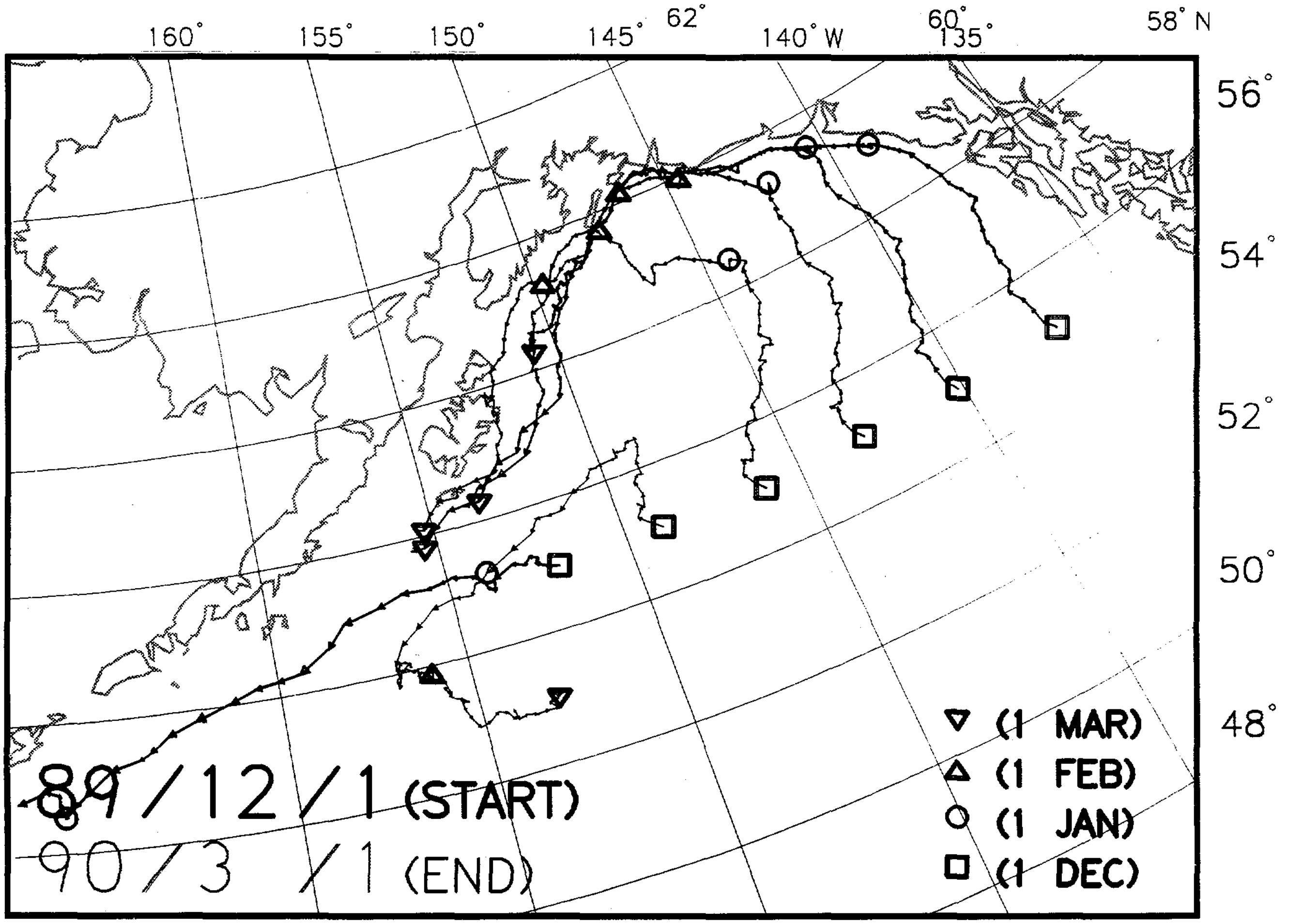

Figure 10. Computed trajectories of the upper ocean during a normal year (winter 1989–90). The symbols indicate positions on the first of the month for December, January, February, and March.

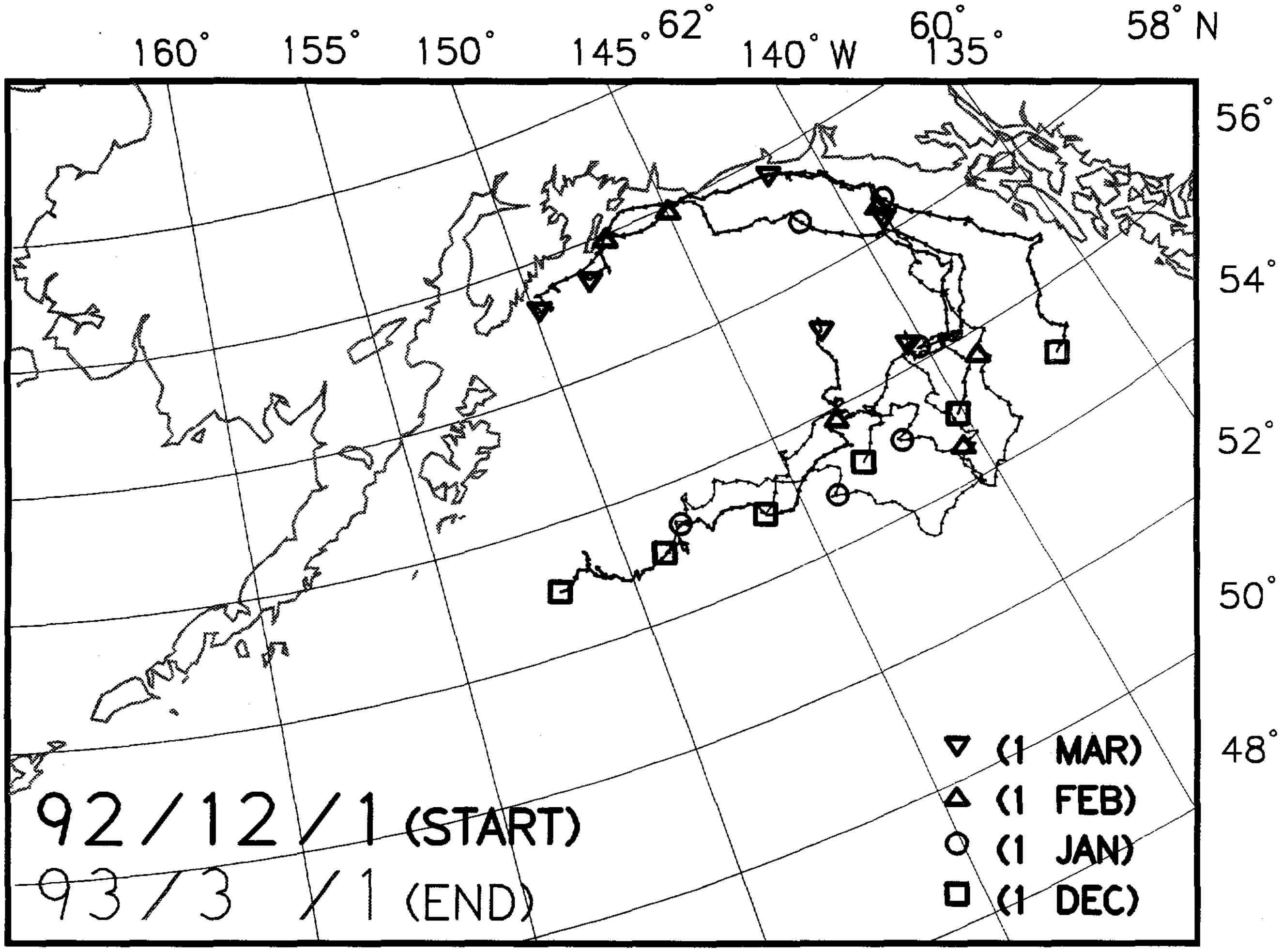

Figure 11. Computed trajectories of the upper ocean during the winter 1992–93 ENSO event. The symbols indicate positions on the first of the month for December, January, and February.

abundance, weather, economics, and management policies; but dramatic environmental events like ENSO are expected to affect catches. Landings of pollock, cod, arrowtooth flounder, halibut, and herring show marked changes over decadal time scales. However, the major ENSO events of 1957–58, 1982–83, and 1991–93 have no consistent obvious effect on landings above the longer-term trends, as reflected by the detrended time series (figures 12 and 13). Negative anomalies occurred in landings of cod and halibut in 1993, but similar decreases did not occur during much stronger El Niño events in 1958 and 1983 (the principal years when landings would have been affected). For herring, landings for three of four stocks (the three southernmost stocks) decreased in 1958. In 1983 the two northernmost stocks showed decreases in landings. However, herring landings were not anomalous in 1992–93, except in Prince William Sound, where a significant drop in landings in 1993 may have been due to a viral disease (F. Funk, Alaska Dept. Fish and Game, pers. comm.). These time series reveal little, if any, consistent short-term effect of ENSO events on fish landings.

Distribution

Distribution of fishes is one parameter expected to vary because of environmental changes. Our approach was to examine the distribution of groundfish in the Gulf of Alaska during summer 1993 and to compare the distribution with other non-El Niño warm years and with cooler years. The results are not presented in detail here, but are summarized. Data were available from the triennial National Marine Fisheries Service summer groundfish surveys in the Gulf of Alaska from 1984, 1987, 1990, and 1993. These surveys represented extensive coverage of the Gulf of Alaska. In general, the gear used was consistent for between-year comparisons (modified poly nor'eastern nets). Examination of surface-temperature maps from the triennial survey years of 1984 and 1993 showed anomalous warm surface temperatures in the northern gulf during the summer, whereas 1987 and

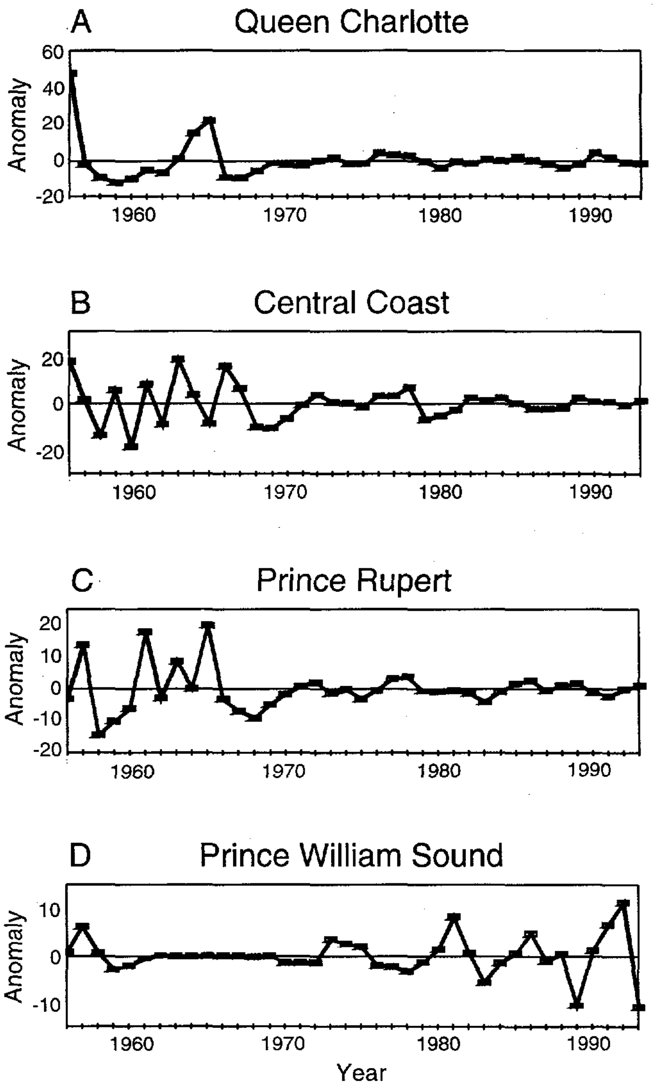

Figure 12. Anomalies of herring landings. Landings trend has been removed with a 6-year running mean.

1990 showed a mix of cool and warm surface waters. The Seward 250 m temperature series confirms that 1984 was anomalously warm and that 1990 was cooler than the other years, but 1987 and 1993 (by summer, the ENSO event may have passed) are not as clear. Examination of temperature records at gear depth from the bottom-trawl surveys confirmed that 1993 was warm and 1987 was cooler.

Several types of analysis were used to examine changes in the distribution of pollock, arrowtooth flounder, Pacific cod, and Pacific halibut. First, we visually compared maps of the distribution of catches for each species and year. The second analysis method tested the hypothesis that there was no difference in groundfish distribution between all possible pairs of years. We used a statistical hypothesis test based on the Cramér–von Mises nonparametric test for a difference between two univariate

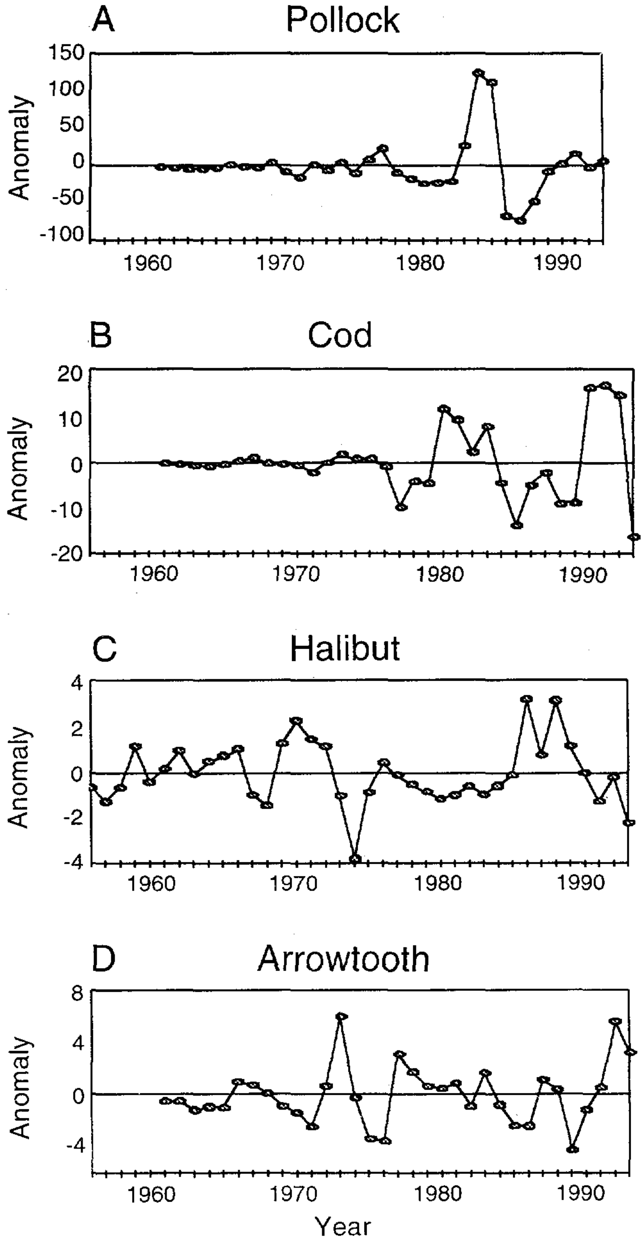

Figure 13. Anomalies of pollock, cod, halibut, and arrowtooth flounder landings. Landings trend has been removed with a 6-year running mean.

probability distribution functions, developed by S. Syrjala (pers. comm., National Marine Fisheries Service). The response variable was catch-per-unit-effort (CPUE) of the individual species at each sampling location. When significant differences did exist between years, we examined the areas of difference in more detail by drawing a line roughly through the middle of the sampling area from the southwest corner (near the Islands of Four Mountains) to the northeast corner (near Cape St. Elias). All station locations were projected onto the line, and the cumulative sum of the relative CPUEs was plotted against the projected longitude. The third method we

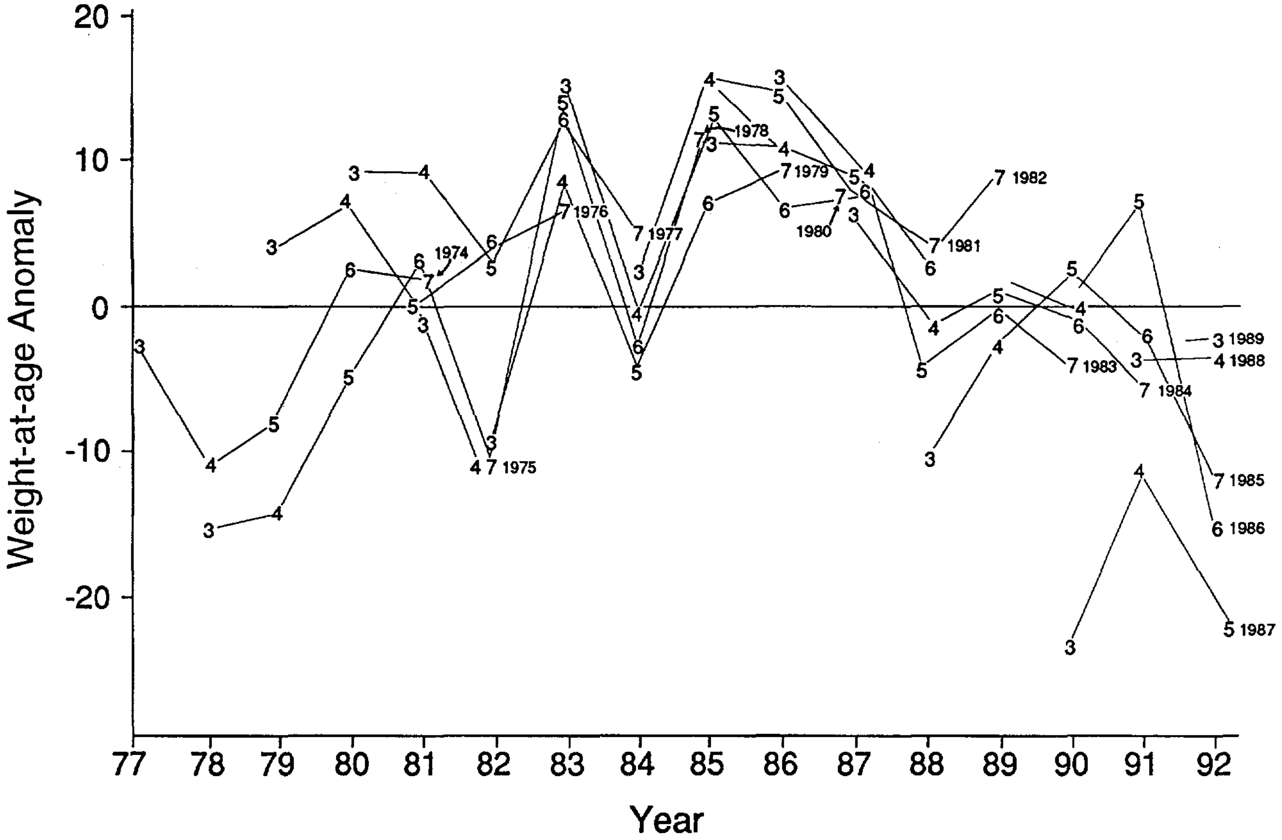

Figure 14. Anomalies of weight-at-age tracked by cohort-at-age in each year for Prince William Sound herring. Anomalies for each age grouping for each year were obtained by subtracting weight-at-age from the 1977–92 mean value for that age group. The year class is marked at the end age (usually age 7) for each cohort (data from Funk 1993).

used was a tree regression analysis on the survey data. We used the CPUE and presence/absence as the response variables, with depth and area strata as predictor variables. The Gulf of Alaska was divided into five depth strata (from 0 to 500 m) and four area strata (Shumagin, Chirikof, Kodiak, and Yakutat INPFC areas).

Visual comparison of the distribution maps did not reveal marked ENSO effects in 1993 for any of the four groundfish species. In the pairwise comparison, the distribution of pollock in 1993 was significantly different from both cool years (1987 and 1990), being more widespread, but was not different from the other warm year (1984). Arrowtooth flounder, Pacific halibut, and Pacific cod distributions did not show any differences that conformed consistently or unequivocally to ENSO, warm, or cool years. Likewise, the tree regression analysis produced no results consistent with an ENSO effect.

Distribution of groundfish species varies from year to year, and changes are difficult to detect, much less attribute to environmental factors. There may be year-class, age-class, and density effects. Furthermore, vertical distribution and activity levels may be influenced by environmental variability, thus affecting accessibility to trawl gear. Our data eventually should be subject to a thorough and stratified analysis, but the bulk approaches used here revealed no remarkable effects of the 1991–93 ENSO event on distribution of these groundfish species.

Weight-at-Age

Weight-at-age data for herring sampled from the fishery by the Alaska Department of Fish and Game are available from Prince William Sound. The weight-at-age anomalies of each cohort, calculated as the residual from the mean weight-at-age for each age group, were plotted by year (figure 14). A trend for a period of higher weight-at-age from 1980 to 1988 is observed, approximately corresponding to a warm ocean era (Hollowed and Wooster 1992). The 1982–83 ENSO event did not appear to have an effect on herring weight-at-age. Weight-at-age of herring caught in 1992 was anomalously low. Whether this was due to the viral infection mentioned above or ENSO conditions is unknown. In Kamishak Bay, near Kodiak Island, the results are somewhat different, with average to above-average mean weight-at-age in 1992, but below-average weight-at-age in 1993 (from data in Yuen et al. 1994). Trends can be removed from these data (and those following) by first-

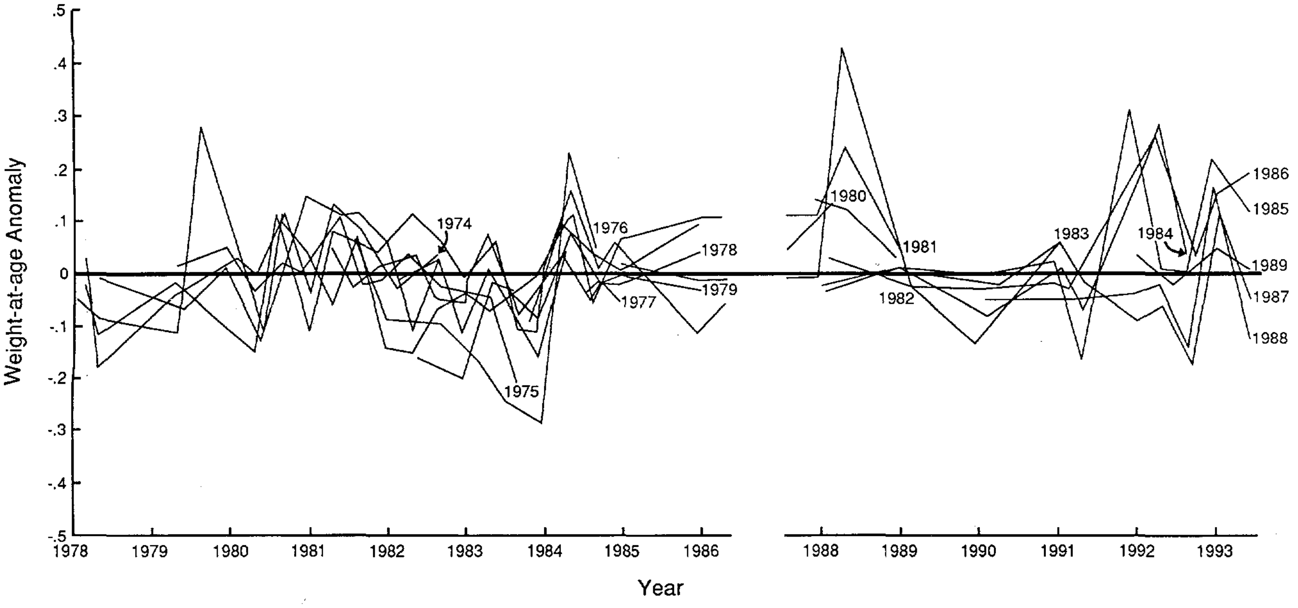

Figure 15. Anomalies of weight-at-age tracked by cohort-at-age in each year for Chirikof Island region male walleye pollock. Anomalies for each age grouping for each year were obtained by subtracting weight-at-age from the 1978–93 mean value for that age group. The year class is marked at the end age (usually age 8) for each cohort (Hollowed, unpubl. data).

order differencing, which is equivalent to analyzing growth increments; this result is easily visualized from the data presented and does not substantially influence our conclusions.

The mean weight-at-age of pollock sampled from the fishery is available from 1978 to 1993 (Hollowed, unpubl. data). For Hollowed's data, we plotted male pollock sampled from the Chirikof Island region. There are notable trends for every age group to show negative anomalies in the third trimester (autumn–winter) of 1983, and for every age group to show positive anomalies in the second trimester (summer) of 1984 and first trimester of 1993 (figure 15).

Recruitment

One problem in making quantitative observations about the 1991–93 ENSO effects on fishes is that many data are not presently available. For example, we will not know much about recruitment of most marine fish populations spawned during the last ENSO until 1996–97. Thus, we use data from earlier ENSO periods, such as 1957–59 and 1982–83, where year-class success and catches of marine fisheries are part of the historical record. The year classes of 1982–83 were relatively poor or unremarkable for herring stocks all over the Gulf of Alaska (figure 16). The post-ENSO years of either 1984 or 1985 were strong for all herring stocks examined. The 1958 ENSO had a positive effect on recruitment for the Prince Rupert stock, while recruitment was relatively poor for all other stocks. All herring stocks had strong year classes during one or more of the post-ENSO years from 1959 to 1961. Preliminary information indicates that herring stocks from the west coast of Vancouver Island will have a below-average to poor 1992 year class (Dan Ware, Pacific Biological Station, Nanaimo, B.C., pers. comm.).

Because halibut recruit to the fishery at age 8, data on recent ENSO effects are limited. Recruitment from the ENSO years 1941–42 and 1958 was relatively weak compared with surrounding years (unpubl. data for these early years). The 1983 year class of halibut in the northern gulf appears to be relatively strong compared with surrounding years (figure 17). This is similar to the situation for arrowtooth flounder. In fact, halibut and flounder both had relatively strong year classes in 1977 (1976–77 ENSO) and 1987 (1986–87 was a moderate ENSO). Given these similarities, it is interesting that the two species share early life-history characteristics of outer shelf/slope distributions, wintertime spawning, and relatively large larvae.

For pollock and cod—both mostly shelf-dwelling species—the 1983 year classes were relatively weak (figure 17). The 1976–77 year classes were strong for pollock, and other strong year classes appeared in the post-ENSO years 1978, 1984, and 1988. Cod showed strong year classes in 1977 and 1984. Preliminary data indicate that recruitment of the 1992–93 year classes of pollock will be average to below average (Anne Hollowed, pers. comm.), and there is some very preliminary information that the 1994 year class is strong (C. Wilson, pers. comm.). At this writing, no recent information was available for cod.

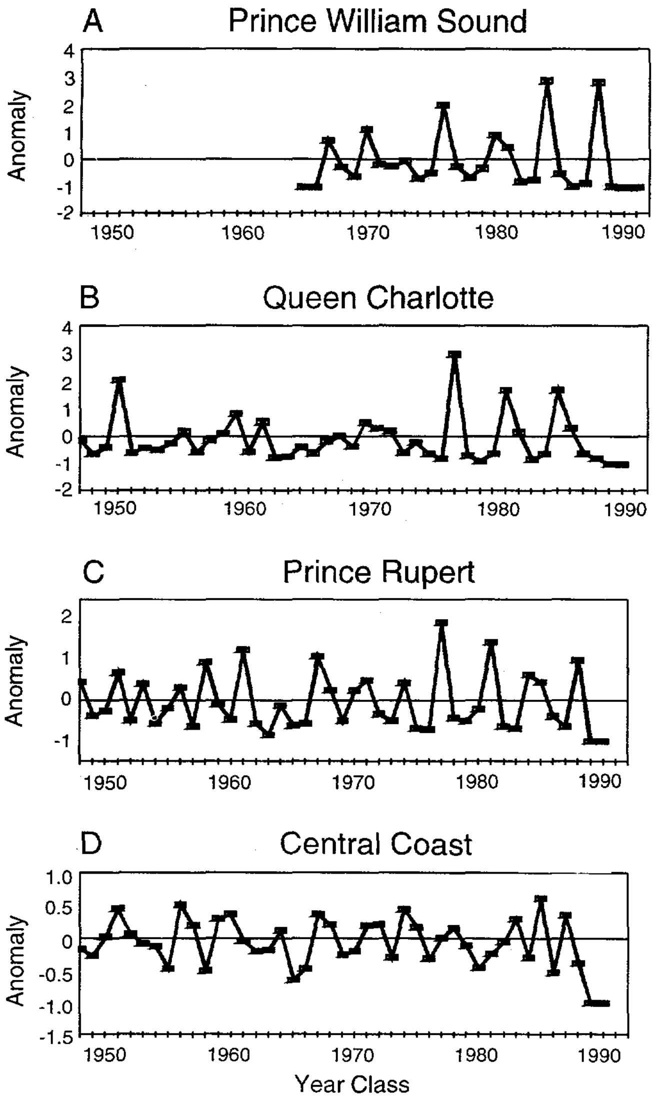

Figure 16. Recruitment anomalies for herring stocks, 1948–88, calculated as the deviation of recruitment from the 5-year running mean for each year class (data from Funk 1993; Schwiegert and Fort 1994).

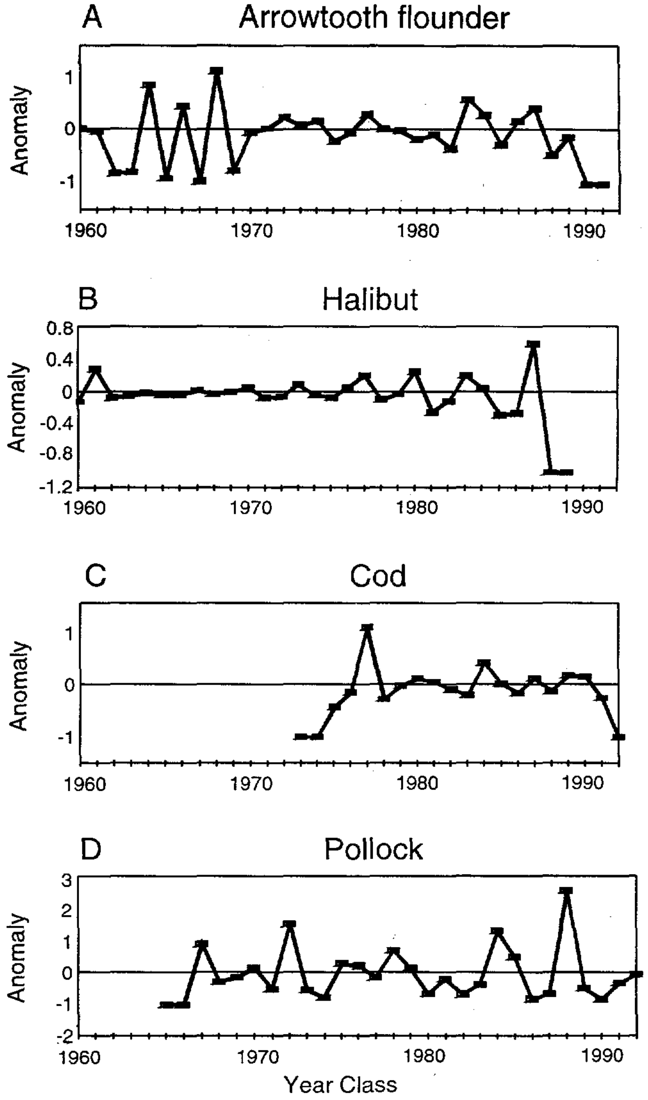

Figure 17. Recruitment anomalies for pollock, arrowtooth flounder, and cod, 1960–91, calculated as the deviation of recruitment from the 5-year running mean for each year class (data from A. Hollowed and T. Wilderbuer, Alaska Fisheries Science Center, pers. comm.). Recruitment anomalies for halibut were calculated from data provided by A. Parma (International Pacific Halibut Commission, pers. comm.) and from IPHC (1994). No single time series covering the historical and updated halibut data existed, therefore two time series of halibut recruit biomass were blended by means of regression where the two series overlapped; $R^2 = 0.88$, $P < 0.001$.

ECOSYSTEM EFFECTS

Pavlof Bay Community Time Series

A time series of trawl data from Pavlof Bay is available from Anderson (unpubl. data) and Piatt and Anderson (in press). Pavlof Bay is at the western part of the Gulf of Alaska (see figure 7) and has been sampled with shrimp bottom trawls every summer since 1972. Although Pavlof Bay is just one location on a very long coast, its long time series is the best available; there is consistency in the gear used and time of sampling; and the trends observed are long-lasting, apparently not just the result of short-term local variability. Where gulfwide data are available for comparison, the trends observed in Pavlof Bay are consistent. Most evident in the time series is a dramatic drop in the composition of shrimp and small pelagics beginning in 1977 (figure 18; these same trends appear when CPUE is plotted). This change was followed by increases in pleuronectids (mostly juveniles), including flathead sole, yellowfin sole, and arrowtooth flounder. However, pertinent to our analysis, there are no remarkable changes directly associated with the strong 1982–83 and 1991–93 ENSO events.

Zooplankton

Little detailed information on the dynamics of zooplankton species in the Gulf of Alaska during ENSO

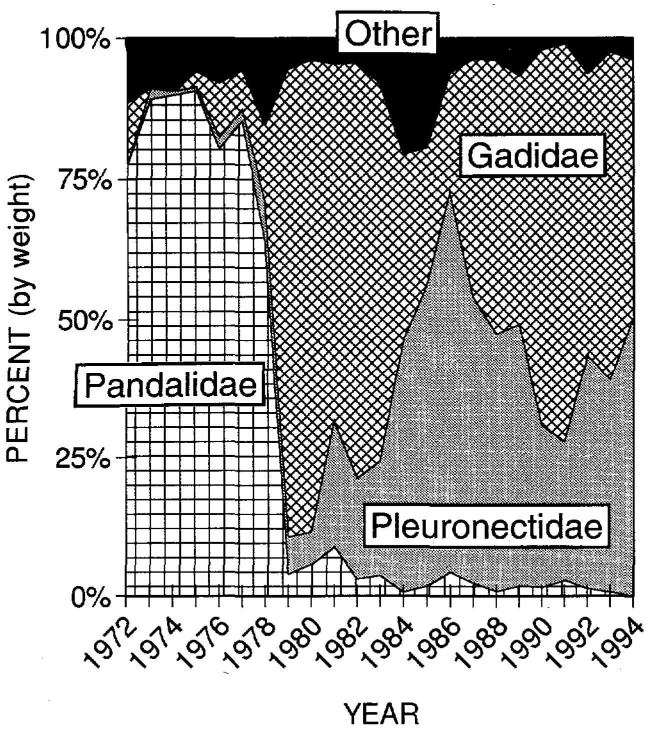

Figure 18. Change in the species composition by weight in "shrimp-trawl" catches in Pavlof Bay, Alaska, 1972–92 (P. Anderson, unpubl. data).

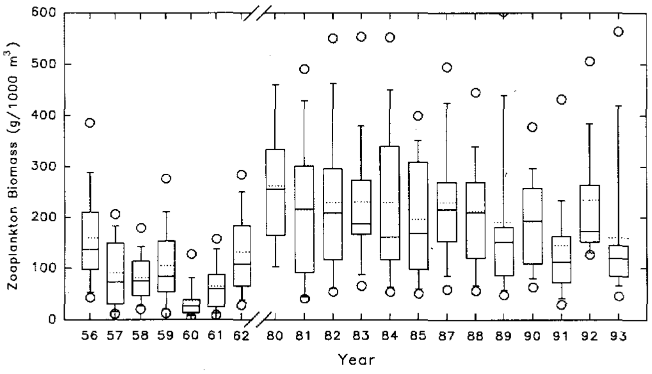

Figure 19. Box plot of annual zooplankton biomass across the *Oshoro Maru* line of stations, June 1956–93. Shown are means (*horizontal dotted lines*); 50% value (*horizontal solid lines*); 10% and 90% values (*vertical capped lines*); range (*circles*); and 25% and 75% values (*boxes*).

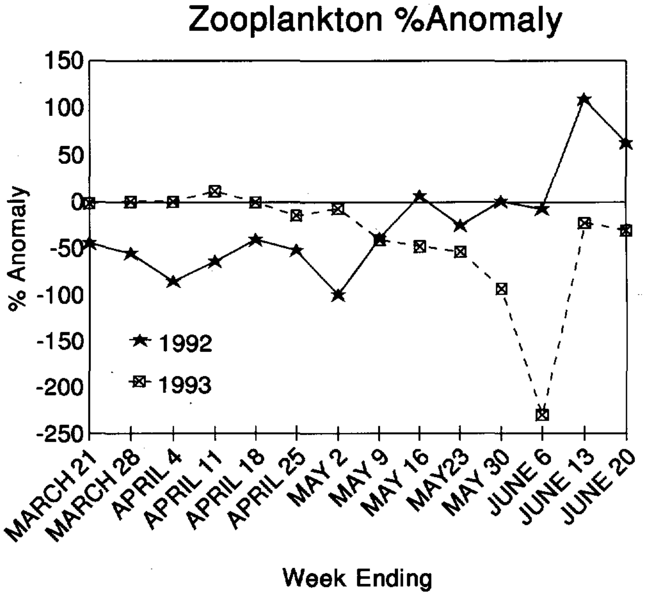

Figure 20. Weekly zooplankton volume anomalies in 1992 and 1993, calculated as the deviation from the long-term, 1986–93 mean value at Erlington Passage, Prince William Sound (data from Prince William Sound Aquaculture Institute).

events was available for this synthesis. Instead, several bulk parameters on zooplankton standing stocks were available. These may reflect changes in distribution, production, species composition, or predation mortality.

A long-term time series of zooplankton biomass (settled volumes) for the central Gulf of Alaska was available from data collected by scientists from Hokkaido University, sampling from the *Oshoro Maru*. Vertical hauls from 150 m to the surface were made with fine-mesh 330 μm mesh nets. These data were first summarized up to 1989 by Brodeur and Ware (1992), and the time series was extended for this analysis. Although a smaller number of stations were occupied since 1989 than previously, virtually identical transects were sampled during these later years (figure 7). In the central gulf, 1983 was unremarkable in zooplankton biomass compared with previous years. Zooplankton biomass was relatively high for 1992 and very low for 1993 (figure 19).

A coastal zooplankton-volume time series from 1986 to 1993 was available for Erlington Passage at the entrance to Prince William Sound (Prince William Sound Aquaculture Corp., unpubl. data). We examined anomalies by comparing the weekly zooplankton volume to the long-term weekly mean. Both 1992 and 1993 had long periods of anomalously low zooplankton abundance compared with the mean (figure 20).

Marine Bird Indicators

Seabirds may be more sensitive to ENSO events, or at least their response is more visible than that of large predatory fish. Aspects of seabird biology (e.g., reproductive success, diet, foraging effort) provide direct and indirect information on the availability of forage fish species. Abundant seabirds, such as common murres (*Uria aalge*), black-legged kittiwakes (*Rissa tridactyla*), and tufted puffins (*Fratercula cirrhata*) feed on a variety of pelagic fishes.

Evidence for exclusive effects of short-term ENSO events on seabird reproductive success in the gulf is equivocal because of high annual and geographic variability in breeding success of some species (Hatch 1987), a lack of time-series data on most seabird species, and the background effects of concurrent changes in forage-fish

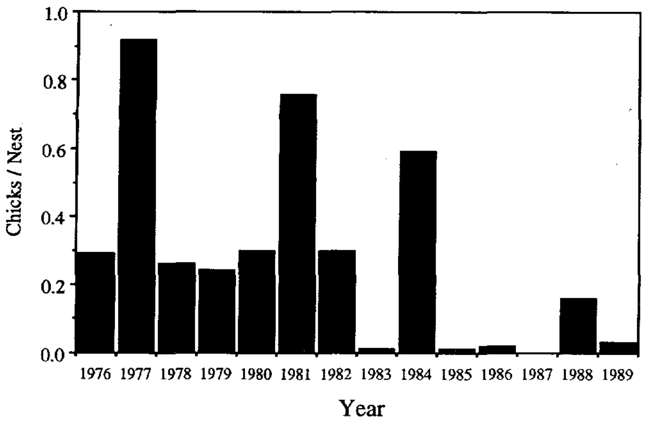

Figure 21. Productivity (number of chicks fledged per nest) of black-legged kittiwakes at selected colonies in the Gulf of Alaska from 1976 to 1989. Averaged data from Middleton, Barren, and Semidi Islands, and Chiniak Bay (data from Hatch et al. 1991).

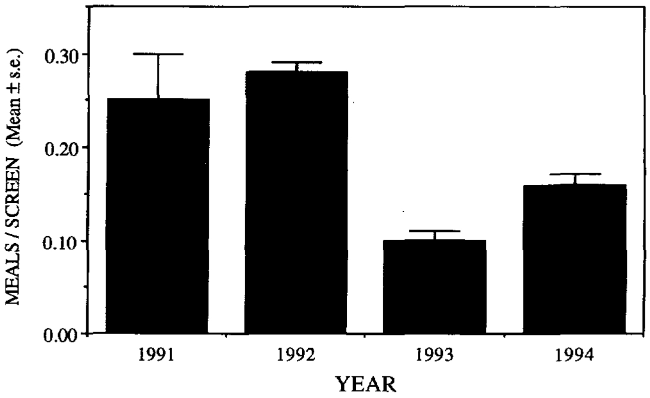

Figure 22. Foraging success of tufted puffins in 1991–94 at 16 colonies in the northwestern Gulf of Alaska as measured by the number of chick meal deliveries recovered per burrow entrance screened (analogous to CPUE, see text). From Piatt, unpubl. data.

populations and the marine environment (Piatt and Anderson, in press). For example, kittiwake breeding success in the Gulf of Alaska (figure 21) was extremely low in 1983 compared with previous years, but it was also low in subsequent years—perhaps in response to long-term changes in forage-fish populations. Some species (e.g., murres) are able to buffer against wide fluctuations in prey abundance by increasing the time spent foraging, thereby maintaining a relatively constant level of breeding success (Burger and Piatt 1990). Seabirds mature late (at 3–8 years) and are long-lived (average 8–15 years), so changes in population size generally reflect long-term processes. Short-term effects of ENSO events or other factors on recruitment or adult survival in any one year are difficult to detect from population surveys alone.

Large-scale mortality ("wrecks") of seabirds from starvation provides evidence for extreme changes in prey availability in response to ENSO events. Seabird wrecks occur periodically in Alaskan waters, and the largest wrecks in recent decades occurred during ENSO years. Following the 1982–83 ENSO event, widespread mortality and breeding failure of seabirds was observed from California to Japan and Russia (Lobkov 1986; Oka 1986; Hatch 1987; Ainley and Boekelheide 1990). In the Gulf of Alaska and western Bering Sea, thousands of dead, emaciated seabirds—mostly surface-feeding species such as kittiwakes and shearwaters—washed up on beaches. The 1992–93 ENSO event had similar far-reaching effects on seabirds. Breeding success and phenology of seabirds on the Farallon Islands in California was reduced, and unusual numbers of starved Cassin's auklets (*Ptychoramphus aleuticus*) were found on beach surveys in central California. In British Columbia, dead murres and rhinoceros auklets (*Cerorhinca monocerata*) were found in numbers 3–4 times higher than usual for winter beach surveys on Vancouver Island (Burger 1993). From Sitka to Kodiak in the northern Gulf of Alaska, an estimated 100,000 murres died of starvation in February–April 1993 (Piatt and van Pelt 1993). Breeding success of murres and kittiwakes at several locations in the gulf was also much reduced in summer 1993 (Piatt, unpubl. data; D. Roseneau, pers. comm.).

Detailed studies of tufted puffin feeding ecology in the northwestern Gulf of Alaska in 1991–94 (Piatt, unpubl. data) also suggest that forage fish were relatively unavailable to puffins in summer 1993. Preliminary analysis of these data suggest that "normal" puffin chick meal delivery rates observed in 1991 and 1992 declined by about one-half in 1993, and recovered somewhat in 1994 (figure 22). All-day observations of marked puffin burrows at three intensive study sites also revealed that maximum feeding rates declined from an average of about 6 meal deliveries per chick per day in 1992 to only about 2–3 meals/chick/day in 1993; the average returned to about 3–5 meals/chick/day in 1994. Puffin productivity was diminished in 1993, and large numbers of dead or emaciated puffin chicks were found in 1993. Juvenile pollock and cod, sand lance, and capelin made up most of the prey consumed in all years. Other than the fact that the proportion of pollock in diets peaked in 1992 at all sites, there were no consistent trends in diet composition between years and sites. This suggests that diminished puffin foraging success in 1993 was not due to problems in obtaining any one prey species, but rather to reduced availability of all forage-fish species.

DISCUSSION

How atmospheric and oceanic forcing affects the structure and dynamics of large marine ecosystems of the northeast Pacific over different time and space scales is a challenging problem facing fisheries oceanographers. Even with severe natural perturbations like El Niño, the

TABLE 1
Physical Characteristics of ENSO Events in the Gulf of Alaska

ENSO event	Subtropical classification	250 m Temperature anomaly	Winter SST	Sea-level peaks	SOI	PNA	NEPPI
1957–58	Strong		Very warm 1958–64	Strong winter 1958 1959 autumn	Moderate	Strong autumn 1957, winter–spring 1958	Moderate
1963	Weak		Very warm	1964 autumn	Weak	Moderate autumn 1963	Strong winter 1963–64
1965	Moderate		Moderate	None significant	Moderate	Weak	Weak
1969	Weak		Warm–1970	1969 winter 1970 winter	Weak	Strong spring/ autumn 1969, winter 1970	Strong winter 1969–70
1972–73	Strong	Cold	Cold 1971–76	None significant	Moderate but prolonged	Moderate	Weak
1976	Moderate	Warm winter/ spring 1977	Very warm 1977	1976 summer 1977 winter	Weak	Strong autumn 1976, winter 1977	Strong autumn autumn 1976, winter 1977
1982–83	Strong	Warm autumn 1982–spring 1985	Warm 1980–88	1983 strong winter	Strong	Strong winter 1983	Moderate winter 1983
1986		Warm autumn 1986–autumn 1988	Warm	1987 moderate winter	Moderate	Moderate winter 1986, 1987	Strong winter 1986, 1987
1991–92		Warm begins spring 1992	Warm 1992–94	1992 winter 1993 moderate winter/spring	Moderate but prolonged	Moderate winter 1992, winter/spring 1993	Moderate autumn/ winter 1992, winter/spring 1993

effects on high-latitude biological communities are hard to ascertain, partially because of the high degree of natural variability, complex interrelationships, poorly understood mechanisms controlling community structure, short time series, and statistical difficulties (Paine 1986). Furthermore, most fisheries information is collected for purposes of stock assessment and monitoring the fishery, not for studying environmental effects. Thus the space and time scales of data coverage are not always appropriate for alternate uses.

Although the 1991–93 ENSO event was a moderate one, in retrospect it manifested itself in the Gulf of Alaska as a clear signal in the physical environment, with anomalous atmospheric conditions, altered circulation patterns, increased sea level, and increased temperature. These conditions are compared with other ENSO events in table 1. Similar conditions, however, also occur in non-ENSO years in the Gulf of Alaska. Whether ENSO conditions in the northern Gulf of Alaska are due to local effects, remote forcing, or atmospheric teleconnections is not completely understood. Certainly anomalous warming and cooling patterns in the North Pacific result from complex interactions between atmospheric and oceanic processes in the tropics and extratropics. Norton and McClain (1994) conclude that warming episodes associated with equatorial forcing events are more likely to be detected at depth (>100 m), because of oceanic long waves, whereas warming associated with local forcing is more likely to be detected at the surface, and the most pervasive regional ocean warming effects during the fall–winter cooling season are associated with the equatorial atmosphere. Maximum warming (in the northern coastal California Current) occurs in the fall–winter season following the tropical El Niño initiated in the previous December through July. Trenberth and Hurrell (1994) point out the connection between tropical SST variations and atmospheric and SST variations in the North Pacific via the ENSO process and teleconnections through the North Pacific Oscillation (NPO, the oscillation from the winter Aleutian low pattern to summer North Pacific high pattern). Hamilton (1988) and Murphree et al. (1992) suggest that the teleconnection between the tropical and extratropical North Pacific may be more related to enhanced atmospheric heating in the far western equatorial Pacific due to high SST in the Western Pacific Warm Pool than to enhanced heating in the eastern or central equatorial Pacific. These studies point out that remote forcing, in terms of its sources and consequences, is complex. Indeed, a recent paper (Jacobs et al. 1994) suggests that ENSO events have long-term effects on the ocean and continental climate, lasting up to a decade or longer.

There are many documentations of ENSO effects on biota at lower latitudes, particularly within the California Current system, where the ENSO signal is more dramatic (e.g., see papers in Wooster and Fluharty 1985; also, Mysak 1986; Arntz et al. 1991). Mearns (1988) summarized unusual sightings and range extensions of fish species associated with historical ENSO events along the west coast of North America. However, Mearns noted that some years with many unusual fish observations could not be attributed to ENSO events or other obvious environmental anomalies.

For the Gulf of Alaska, there are also records of unusual sightings and range extensions of southern fishes during the 1982–83 ENSO (Karinen et al. 1985; Pearcy and Schoener 1987), but there is little knowledge of El Niño effects on groundfish production of key species. We use the data presented here to challenge two hypotheses about ENSO and biological communities: first, that El Niño events initiate strong year classes at the northern end of a species range through the beneficial effect of warming, and poor year classes at the southern end of a species range (Bailey and Incze 1985); second, that pelagic fish are more sensitive to ENSO events than demersal fish (adapted from Paine [1986], who proposed that pelagic communities were more sensitive than benthic communities).

Data presented here are not entirely consistent with the hypothesis that recruitment of northern stocks is favored by ENSO events (Arntz et al. 1991 and further data presented here for 1982–83 and 1991–93). In retrospect, it is overly simplistic to represent complex ecosystem interactions by a simple proxy like temperature (Wooster and Bailey 1989). The ENSO years 1958, 1983, and preliminary data for 1992–93 indicate that ENSO events do not have a consistent effect on recruitment for any species. The fact that 1983 was warm, but resulted in poor to average recruitment for many coastal species (cod, pollock, herring) in the Gulf of Alaska indicates that something other than warm temperatures was determining recruitment success in these circumstances. ENSO events may be unfavorable for recruitment because of decreased coastal upwelling (less nutrient input) and lessened zooplankton production (although possibly heightened upwelling in the central gulf gyre; Brodeur and Ware 1992); anomalous circulation patterns affecting distribution of organisms; or changes in food-web structure (Brodeur and Pearcy 1992). Strong year classes for many species occurred in the warm years of 1959–61, 1978, and 1984, all 1–3 years after ENSO events. If history repeats itself, one could speculate on strong recruitment years for many coastal species for the 1993–95 year classes.

However, for some of the outer shelf and slope species—arrowtooth flounder, Pacific halibut, and sablefish (off Canada; McFarlane and Beamish 1992)—strong year classes often coincide with ENSO events (winters of 1958–59, 1976–77, and 1986–87). Some aspects of this association are worth investigating further, including similarities in the life histories of these species, the effect of longwave propagation up the slope during strong ENSO events, the tendency for equatorial forcing to be felt more strongly at depth (Norton and McClain 1994), and transport of abundant large oceanic copepods shoreward (McFarlane and Beamish 1992).

Are pelagic species more affected by ENSO events than demersal species? The results presented here, and summaries of effects on salmonids (Mysak 1986; Pearcy and Schoener 1987; Arntz et al. 1991) are generally supportive. Since many pelagic species are active swimmers with high metabolic rates, one would expect that a 2° SST increase, coupled with decreased upwelling and consequent low zooplankton production (as observed in the coastal areas) would have a high cost. For demersal species that are often more sedentary, a 0.5° elevation in bottom temperatures would not appear significant. At more northern latitudes such as the Bering Sea, these species experience a higher degree of thermal variability (−2° to 3°) due to surface ice effects on bottom-water formation. Furthermore, since these species are higher-trophic-level predators, the complexity of the food web and time lags buffer these demersal species from variability in pelagic secondary production.

Although all the species examined here show long-term trends in abundance and landings, none of the groundfish species examined show obvious short-term perturbations directly attributable to ENSO events. The same conclusion holds for the distribution patterns of the major groundfish species; although some change in distribution is observed during ENSO events, the effect is similar to non-ENSO warm years. Many of the flatfish species appear to maintain their distributions independent of temperature variation; however, the roundfish species, like cod, are expected to vary their distribution in response to temperature (Perry et al. 1994). It may be that the distribution changes we observed were small relative to the large scale over which the groundfish data were examined, or that bottom-water temperature variations are relatively minor. The 1983 ENSO event appeared to be related to an anomalous low weight-at-age for pollock in the autumn, perhaps due to decreased upwelling and zooplankton production earlier in the year. However, pollock weight-at-age recovered for positive anomalies in the summer of 1984. In the moderate ENSO event of 1993, positive weight anomalies were noted for pollock in the winter season. These data point out the inconsistent and equivocal effect of different ENSO events on groundfish production.

Small pelagic fishes may be most vulnerable to ENSO-related changes in the environment. The weight-at-age of herring in Prince William Sound showed strong negative anomalies for most age classes in 1992, and in Kamishak Bay in 1993. However, strong positive anomalies were observed in Prince William Sound in 1983. Similar negative anomalies in weight were observed for herring in San Francisco Bay during the 1982 ENSO (Arntz et al. 1991). Although one would expect that this reflects poor condition and should result in poor reproductive success, the 1982 year class of herring in San Francisco Bay was relatively strong (Arntz et al. 1991).

The decreased seabird feeding levels, high mortalities, and reproductive failures observed in the gulf in 1983 and 1993 probably reflect changes in the abundance or distribution of small pelagic fish prey. Small fishes may have been distributed deeper or farther offshore, thus affecting their availability to seabirds and influencing foraging energetics. The mechanisms by which ENSO events can influence forage-fish availability are not well understood. The availability of forage-fish species near the sea surface may be strongly influenced by temperature and depth of the thermocline (Methven and Piatt 1991). Water temperatures may also affect spawning and schooling behavior of forage fish, thereby influencing the size and density of schools available to seabirds. The density of prey aggregations, rather than abundance, may be the most important factor influencing foraging success for diving species such as murres and puffins (Piatt 1990). Recruitment of pelagic fishes can also be influenced by ENSO events; recruitment of herring stocks has, for the most part, been below average or unremarkable during most major ENSO events.

Major changes have occurred in the Gulf of Alaska ecosystem beginning in the late 1970s. Hollowed and Wooster (1992) suggest that a climatic shift beginning in 1977 was initiated by the 1976 ENSO event. The shift in climate and oceanographic conditions occurring in 1977 is well documented (Royer 1989; Trenberth 1990; Trenberth and Hurrell 1994; Miller et al. 1994), as is its effect on marine production (Venrick et al. 1988; Brodeur and Ware 1992; Hollowed and Wooster 1992; Piatt and Anderson, in press). Although the 1976 ENSO event was described as moderate, the intensity of the Aleutian low was the strongest in 36 years, and warming of the West Coast was extensive in winter of 1977 (Mysak 1986).

Decadal changes in fish communities in the Gulf of Alaska observed by Piatt and Anderson (in press; figure 18) have apparently caused some notable changes in seabird ecology. While capelin populations crashed and pollock populations exploded in the late 1970s, the diets of five common seabirds in the Gulf of Alaska changed accordingly, as pollock and sand lance replaced capelin as the dominant prey. Breeding success and population size of several seabird species (murres, kittiwakes, murrelets) in some areas of the gulf have declined through the 1980s and remained low in the early 1990s (Hatch et al. 1991; Hatch and Piatt 1994; Piatt and Anderson, in press).

To summarize, the structure and dynamics of the Gulf of Alaska marine ecosystem are significantly affected by a complex series of atmosphere/ocean interactions occurring both remotely and locally, and at varying time scales. However, neither the linkage between oceanographic changes and the marine biota in terms of mechanisms, nor causes of the rapid and coherent shifts in this ecosystem are well understood. The phasing of atmospheric, ENSO, and tidal forcing may be important to the long-term physical and biological conditions in the Gulf of Alaska. An ENSO event during the nadir of the lunar tidal cycle might have a much different effect than if it arrived at the peak of the cycle. For example, the 1958 and 1976 ENSO events occurring as the tidal cycle produced warming appeared to trigger persistently warm climatic periods (1958–64 and 1977–84; see Hollowed and Wooster 1992).

The major ecosystem changes in the Gulf of Alaska are probably related to decadal-scale changes in the physical environment such as the warming episode commencing in 1977. Margalef (1986) speculated that the principal cause of biological fluctuations in marine ecosystems is change in the input of physical energy (sun, winds, currents). These inputs, or "kicks," are discontinuous and disrupt established ecological relationships within an ecosystem. It has been noted that for some fish species, strong recruitment years occur at the beginning of these ecosystem kicks (Saetersdal and Loeng 1984; McFarlane and Beamish 1992), perhaps because of disrupted community structure and an ecological release from predation and competition. For example, if pelagic fish populations are disrupted by an ENSO event, their effectiveness as competitors or predators on pelagic larvae of groundfishes may be diminished, allowing opportunistic recruitment success.

We conclude that ENSO events do appear to affect production processes of the major commercial groundfish fisheries in the Gulf of Alaska, but these effects are equivocal, sometimes minor, and inconsistent among different El Niño events. ENSO effects on the physical environment are diminished in the Gulf of Alaska compared with lower latitudes, and reverberations in the biological realm are also lessened. Relative to the major changes in the gulf ecosystem that occur over longer, decadal time scales, ENSO events are of relatively short duration. However, ENSO events, either by their frequency, atmospheric teleconnections, or phasing with other environmental factors, may be linked with these ecosystem shifts. ENSO effects on small pelagic fishes (including ichthyoplankton) are more likely to be consequential. In turn, fish-eating seabird populations can be strongly affected by ENSO events.

ACKNOWLEDGMENTS

We thank the following people for generously providing data and references: Charles Fort (Pacific Biological Station), Dave Husby (Pacific Fisheries Environmental

Group), Jeff Olson (Prince William Sound Aquaculture Corp.), Fritz Funk (Alaska Dept. Fish and Game), Anna Parma (International Pacific Halibut Commission), Alan Mearns (Hazmat, NOAA), and Tom Wilderbuer (REFM, Alaska Fisheries Science Center). We also thank Steve Syrjala for his original and labor-intensive statistical analysis, and Bill Pearcy, Art Kendall, Steve Ralston, and Gary Stauffer for reviews of the manuscript.

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THE EFFECTS OF AGE COMPOSITION AND OCEANOGRAPHIC CONDITIONS ON THE ANNUAL MIGRATION OF PACIFIC WHITING, *MERLUCCIUS PRODUCTUS*

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ABSTRACT

Adult Pacific whiting (also known as Pacific hake), *Merluccius productus*, migrate each year from spawning grounds off southern California to feeding grounds along the continental shelf break from central California to Vancouver Island. During spring and summer, there are large-scale commercial fisheries for this species in both U.S. and Canadian waters. The stock synthesis model, a flexible, age-structured, maximum-likelihood estimation model, was used to investigate the migratory behavior of Pacific whiting. In this implementation of the stock synthesis model, the U.S. and Canadian zones were defined as separate geographic areas, and the parameters of an age-specific migration function were estimated. Annual coefficients were estimated for the parameter specifying the asymptotic proportion of an age class migrating into the Canadian zone for years with coastwide acoustic surveys (1977, 1980, 1983, 1986, 1989, and 1992). Correlation analysis between these coefficients and a suite of environmental variables revealed that the March–April water temperature anomaly at a depth of 100 m from 30° to 42° N lat. had the highest correlations. High water temperatures were associated with an increased proportion of the Pacific whiting population in the Canadian zone, as occurred during the 1982–83 and 1991–92 El Niño events, whereas in 1989, low water temperatures were associated with a decreased proportion in the Canadian zone. This relationship was used in the stock synthesis model to estimate migration curves for years in which no surveys were made. The results of the stock synthesis models and the correlation analysis suggest that El Niño events promote the northward movement of Pacific whiting via intensified northward currents during the period of active migration. Although estimates of total population abundance are unaffected by modeling the interannual variation in migration, the results provide additional information on the transboundary distribution of the stock, which is important for forecasting how long-term climate change affects the Pacific whiting population.

INTRODUCTION

Marine species in the California Current ecosystem respond in a variety of ways to El Niño conditions. Changes in growth (Dorn 1992), condition (Schoener and Fluharty 1985), and reproductive effort (Ainley and Boekelheide 1990) have commonly been observed. Changes in spatial distribution are perhaps the most obvious response. Two primary mechanisms that change the distribution of marine species are (1) active movement to preferred habitat and (2) transport by altered currents. For planktonic species with limited ability for directed movement, distributional changes are related to transport by altered currents. For example, Bolin and Abbott (1963) found higher abundances of tropical and subtropical phytoplankton off the central California coast during years with elevated water temperatures. For nektonic species, active migration to altered habitat is a more likely mechanism, which apparently accounts for the increased abundance of highly migratory pelagic tunas such as albacore (*Thunnus alalunga*) off British Columbia and Washington during El Niño years (Smith 1985).

This paper describes research on Pacific whiting (*Merluccius productus*), also known as Pacific hake, a gadoid species that is an important component of the California Current ecosystem (Francis 1983). Adult Pacific whiting migrate north in spring to feed in the productive waters along the continental shelf and slope from northern California to Vancouver Island, British Columbia, during summer and fall (figure 1). There are large-scale commercial fisheries for Pacific whiting in both U.S. and Canadian waters during these months. In late autumn, Pacific whiting migrate south to spawning areas from Point Reyes, California, to Baja California (Bailey et al. 1982). Both active migration and transport by currents may change the latitudinal distribution of this species during El Niño years. The annual northward migration could be assisted or hindered by changes in current speed and direction. During El Niño events, upwelling in the California Current ecosystem is inhibited, and transport of subarctic Pacific water is reduced (McLain 1984). Since the thermocline is depressed during El Niño events, when upwelling occurs it brings nutrient-depleted water to the surface, further reducing productivity. The scarcity of food on the usual summer feeding grounds may induce Pacific whiting to forage farther north.

This paper is the first attempt to go beyond anecdotal reports of range changes of marine species during El Niño events to develop predictive quantitative models for changes in population distribution. Each summer,

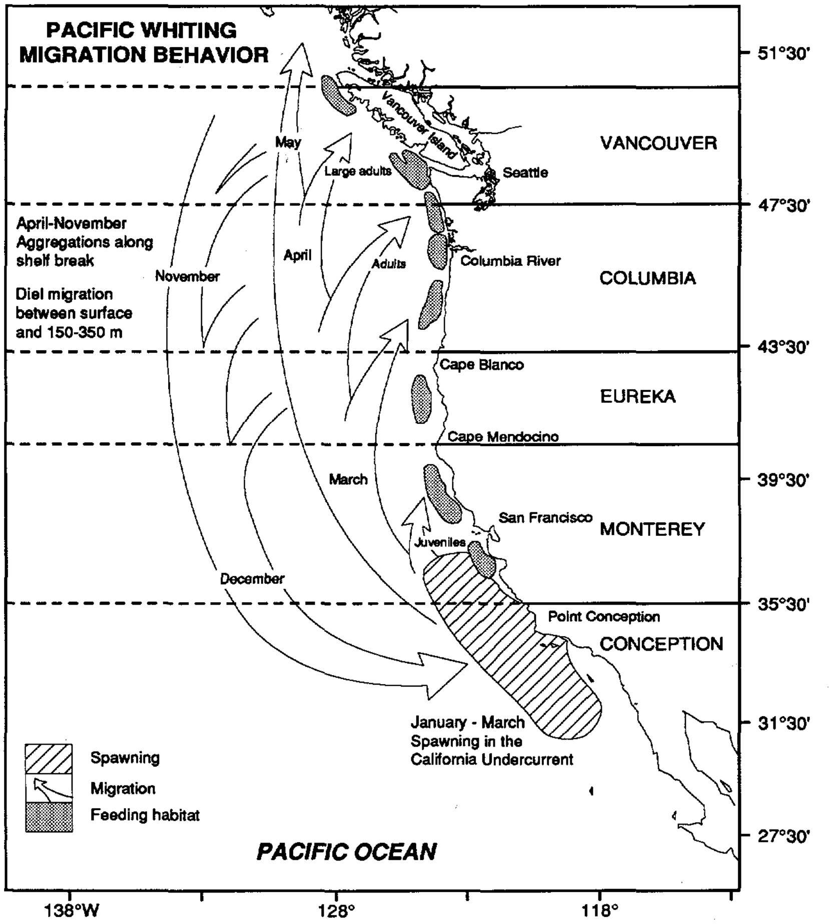

Figure 1. The general pattern of Pacific whiting migratory behavior (modified from Bailey et al. 1982).

some proportion of the Pacific whiting population migrates into Canadian waters. Using the stock synthesis model (Methot 1989), I develop a method for predicting the proportion that migrates. The method takes into account changes in the age structure and abundance of the population, and employs an environmental index that measures the strength of northward transport. I begin by discussing the key features of Pacific whiting natural history, focusing on average migration characteristics and annual migration timing. Next I briefly review El Niño effects on California Current oceanography that could influence Pacific whiting migration. Then I present the stock synthesis model with migration for Pacific whiting. I analyze the results of the model, and discuss the implications of these results in an environment characterized by decadal regime shifts and long-term climate change.

Pacific Whiting Migratory Behavior

Although the general features of Pacific whiting migratory behavior have been known for some time (Alverson and Larkins 1969), new fisheries and expanded surveys have increased our knowledge of Pacific whiting migration and summer distribution patterns. In 1991, a domestic fleet of factory trawlers and mother ships displaced the joint venture fishery for Pacific whiting in U.S. waters. The shore-based fleet, operating primarily out of Newport and Astoria, Oregon, has also expanded rapidly in recent years. These new domestic fisheries have operated outside the seasonal limits of the earlier joint venture and foreign fisheries for Pacific whiting and have provided additional details about the timing of the annual migration. Of course, deriving inferences about the distribution of fish from fisheries data is subject to the caveat that although the presence of fishing indicates the presence of fish, the absence of fishing does not indicate an absence of fish.

Since 1992, the at-sea fishery has opened on 15 April. During the first weeks (15–30 April), the fleet has fished as far north as the U.S.–Canada border (figure 2). This suggests that the population has moved considerably northward by this time. Although the shore-based fishery in Newport and Astoria has not started as early as the at-sea fishery, it has continued until late fall in several years. Earlier conjectures were that the southward

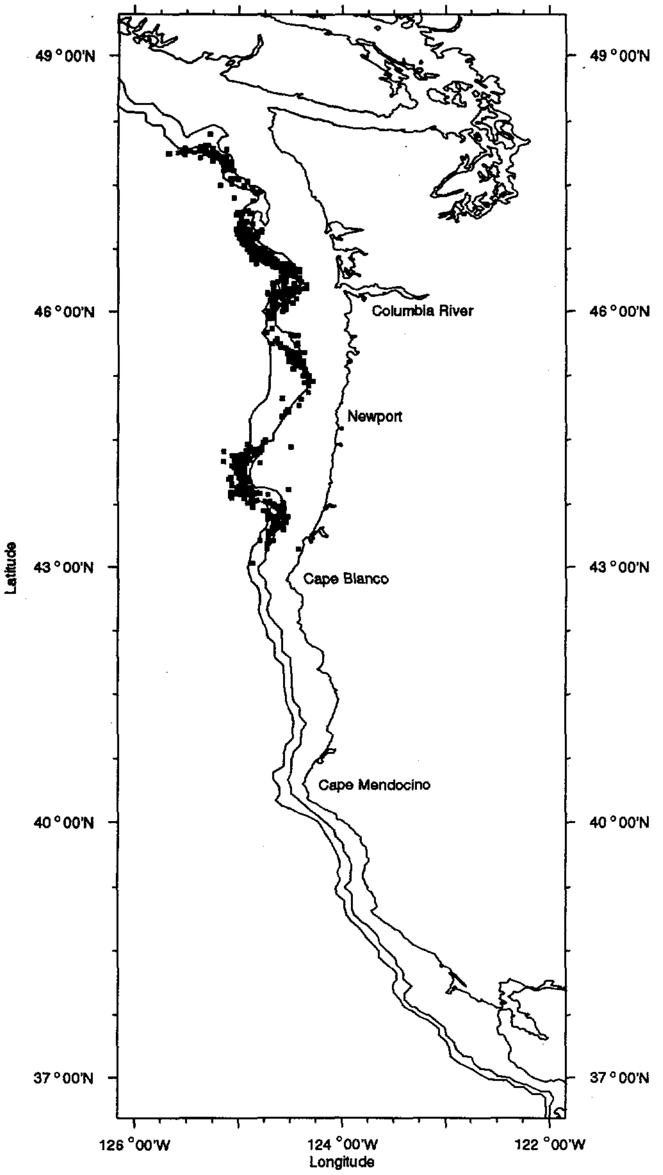

Figure 2. Haul locations during 15–30 April for the 1993 domestic Pacific whiting at-sea fishery. The 200 m and 500 m isobaths are also shown.

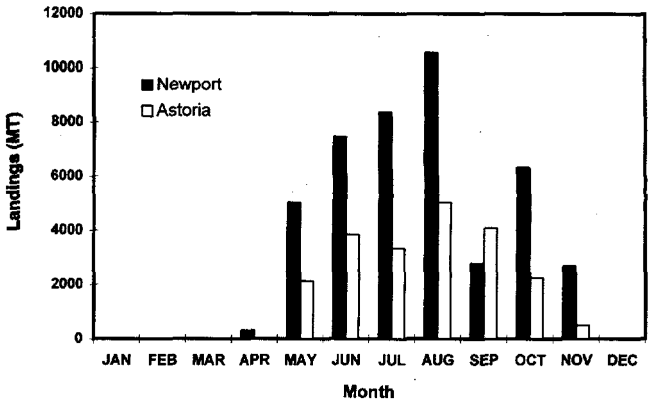

Figure 3. Pacific whiting monthly landings for 1994 in metric tons (MT) at Newport and Astoria, Oregon.

migration began in September (Stauffer 1985), although in the early years of foreign fishing (1967–76), catches in the Canadian zone were regularly reported in November (Beamish and McFarlane 1985). In 1994, the shore-based fishery ceased operations in mid-November (figure 3). Fishermen indicated that they had stopped fishing because of inclement weather and a decline in the availability of Pacific whiting (W. Barss, Ore. Dep. Fish and Wildlife, Marine Science Drive, Building 3, Newport, OR 97365, pers. comm., Dec. 1994). The availability of fish off Oregon in November suggests that the southward migration has not yet begun. From an analysis of early-stage larvae, Hollowed (1992) determined that February was usually the peak spawning month, with significant spawning also in January and March. This observation, in association with the seasonal pattern of fishing, suggests that the period of maximum northward movement is March and April, and that the southward return migration occurs primarily in November and December.

A coastwide acoustic survey of Pacific whiting was conducted by the National Marine Fisheries Service (NMFS) in summer 1992 (Dorn et al. 1994), and annual series of acoustic surveys of Pacific whiting were conducted by the Canada Department of Fisheries and Oceans (DFO) in 1990–93 (Cooke et al. 1992). These surveys had wider areal coverage than earlier surveys, both offshore of the shelf break and in the north, and produced population estimates considerably higher than those forecast by earlier surveys and models. These surveys reveal that in many years substantial aggregations of whiting are found north of the La Perouse area, where the Canadian fishery occurs. These aggregations extend along the west coast of Vancouver Island and into Queen Charlotte Sound. Pacific whiting density typically increases in a localized area offshore of Brooks Peninsula (50° N). In addition, it is apparent that significant midwater aggregations of Pacific whiting occur as far as 40 km offshore of the shelf break, over water up to 2,000 m deep. In 1992, these off-shelf aggregations were found from northern California to northern Vancouver Island (Dorn et al. 1994).

The migratory behavior of Pacific whiting is strongly age-dependent. It is possible to refine our ideas about the migratory behavior of Pacific whiting by introducing the concept of an annual migratory distance, defined as the distance between the spawning grounds and the northward limit of the annual migration of a particular fish. Figure 4 is a schematic of the age-structured migratory characteristics of Pacific whiting based on the assumption that all spawning occurs off Point Conception, and that the NMFS acoustic surveys in July–August

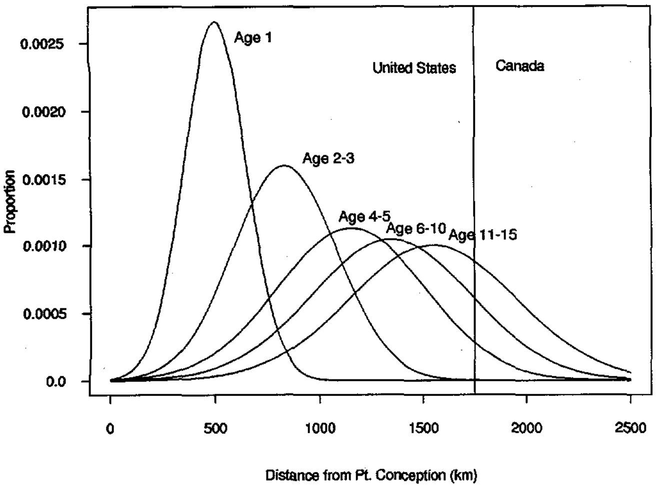

Figure 4. Schematic illustration of the distribution of annual maximum migration distances by age group for Pacific whiting. The *vertical line* at 1,750 km shows the approximate location of the boundary between the United States and Canadian zones.

observe the fish at the northern limit of their annual migration. The general characteristics of Pacific whiting migration evident in figure 4 are:

1. The mean migration distance of an age group increases with age.
2. The difference in mean migration distance between the consecutive age groups declines with age. For example, the mean distance migrated by the age-15 and age-14 fish is about the same.
3. Older age groups have a wider distribution than the younger age groups. In other words, the variance of the migratory distance increases with age.

These behavioral patterns are extremely resistant to change. For example, even in years when the population is found farther north, the older age groups are still farther north, on average, than the younger age groups.

The coastal Pacific whiting population is also remarkable for its extreme recruitment variability. The strong year classes (e.g., 1980 and 1984) can be two orders of magnitude larger than weak year classes (e.g., 1981, 1982, 1983, 1985). As a result of this variation in year-class strength, mean age in the population can change substantially as a strong year class passes through the population. For example, between 1983 and 1992, the mean age in the U.S. fishery increased by almost two years as the large 1980 and 1984 year classes became older and were not displaced by equally large incoming year classes. Since the extent of northward migration is related to age, the spatial distribution of the population will be affected by changes in the population age structure independent of any environmental factor.

Potential El Niño Effects on Pacific Whiting Migration

The link between El Niño events in the equatorial Pacific region and changes in oceanographic conditions in the North Pacific Ocean is a subject of active research and some controversy. The linking mechanism that offers the most supporting evidence is an atmospheric teleconnection between an El Niño and an intensification of the Aleutian low (Simpson 1992). The suggested sequence of events that would facilitate increased northward migration of Pacific whiting in the California Current system during El Niño events is the following:

1. Intensification of the Aleutian low through atmospheric teleconnection
2. Enhanced onshore transport of Pacific subarctic water, resulting in elevated sea-surface and subsurface water temperatures, a depressed thermocline, and elevated sea levels along the west coast of the United States and Canada
3. Intensification of poleward transport from the south via strengthened Davidson Current and California Undercurrent flow.

The a priori expectation, therefore, would be that enhanced northward migration of Pacific whiting would be positively correlated with anomalies of surface water temperature, subsurface temperature, and alongshore poleward transport. The potential for El Niño events to provide a boost for northward migrators during late winter and early spring is demonstrated by the path of satellite-tracked drifters. Emery et al. (1985) mapped the path of a satellite-tracked drifter drogued at 30 m during the onset of the 1982–83 El Niño. On 25 Jan. 1983 the drifter was slightly north of San Francisco at 39° N. On 27 Feb. 1983, 33 days later, the drifter was recovered off southern Vancouver Island.

During El Niño years, the normal summer upwelling regime off the West Coast is inhibited, and there is less transport of biomass-rich subarctic Pacific water from the Alaska gyre (Roesler and Chelton 1987). It is apparent, therefore, that northward transport is strong in years when it is advantageous for Pacific whiting to migrate farther north. Such an adaptive migratory pattern would not require complex behavioral adaptations and may indicate why this migratory pattern is so strongly developed in Pacific whiting.

METHODS

Stock Synthesis Modeling of Annual Migration

The stock synthesis model is now widely used to estimate abundance of exploited marine populations. The strength of the stock synthesis model lies in its flexibility in modeling how fisheries affect populations and how those populations are measured by resource surveys. I use a two-area (United States and Canada) version of the stock synthesis model similar to the model used for the stock assessment (Dorn et al. 1994). The intent here is to use the stock synthesis methodology to study the migratory characteristics of Pacific whiting. The results presented here are intended as a supplement to, not a replacement for, the more detailed annual stock assessments of the Pacific whiting resource (Dorn et al. 1994).

The stock synthesis model is a catch-age analysis that uses survey estimates of biomass and age composition as auxiliary information (Methot 1989). The synthesis model operates by simulating the dynamics of the population. Comparisons are made between the expected value of the observable characteristics of the simulated population and the actual observations of the population from surveys and fishery sampling programs. The goodness of fit to these observations is evaluated in term of log(likelihood). The total log(likelihood) is a weighted sum of the log(likelihood) components for each data type.

The data elements used in the stock synthesis model for Pacific whiting are as follows:

1. A time series of age composition and catch totals from the U.S. and Canadian fisheries for Pacific whiting (1977–93)
2. NMFS acoustic surveys (1977, 1980, 1983, 1986, 1989, 1992)
3. DFO acoustic surveys (Canadian zone only) 1990–93.

The NMFS survey biomass estimates for the Canadian zone were adjusted because of incomplete coverage, as described in Dorn et al. 1994.

I implemented a stock synthesis model with annual migration by assuming that migration occurs at the start of the year (before any fishing takes place) and that the population mixes at the end of the year. I used a three-parameter logistic curve to model the age-specific fraction (m_a, where a is age) of the population migrating into the Canadian zone:

$$m_a = \frac{p_3}{1 + e^{[-p_2(a-p_1)]}},$$

where p_1 is the inflection age, p_2 is the slope, and p_3 is the asymptotic proportion of an age-class migrating into the Canadian zone. Interannual variation in migration is obtained by estimating separate p_3 coefficients for each year. In this way a family of asymptotic curves can be obtained (figure 5). The procedure for incorporating oceanographic indices consisted of several steps. First, a preliminary model estimated the migration coefficients, p_{3i}, in NMFS survey years (i = 1977, 1980, 1983, 1986, 1989, and 1992).

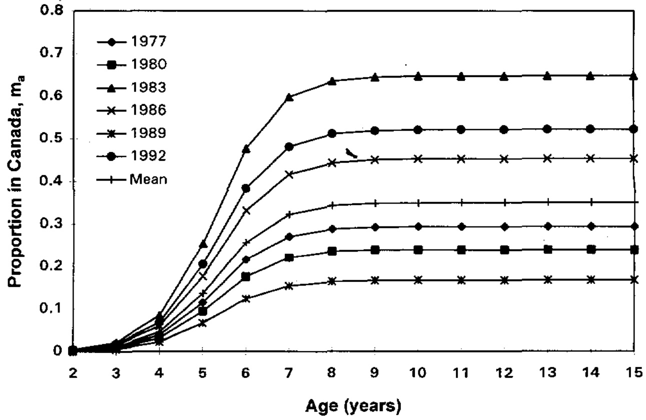

Figure 5. Annual age-specific migration curves estimated with the stock synthesis model. Separate curves are shown for years with a National Marine Fisheries Service acoustic survey (1977, 1980, 1983, 1986, 1989, 1992) and the mean for all years. The curves are the annual age-specific fraction of the population migrating into Canadian waters.

Next, I conducted a correlation analysis using these estimated migration coefficients and a suite of oceanographic indices. The oceanographic data consisted of monthly mean temperature at the surface, 100 m, and 200 m for 3-degree-latitude coastal blocks from ships of opportunity. The data were supplied by D. R. McLain (National Ocean Service, Monterey, CA 93942, pers. comm., July 1994). I obtained temperature anomalies for each 3-degree block by subtracting out the long-term mean. I obtained a "north" index by averaging the anomaly for the four blocks extending from 42° N to 54° N, and a "south" index by averaging the anomaly for the four blocks extending from 30° N to 42° N. I used the correlation analysis to select the oceanographic index that correlated best with the estimated migration coefficients during the survey years. I then used linear regression to obtain predicted migration coefficients for years in which no surveys were taken.

Finally, I used the predicted migration coefficients in a final stock synthesis model as part of an environmental likelihood component. This likelihood component had the form

$$l_p = -\sum_i (p_{3i} - \tilde{p}_{3i})^2,$$

where p_{3i} is the model-estimated migration coefficient for year i, and $\tilde{p}_{3i}$ is the predicted migration coefficient from the linear regression from the environmental index for year i. Only the years in which no surveys were made were included in the summation because in years with a coastwide acoustic survey the distribution of biomass is well established by the survey. A large emphasis on this likelihood component would force the model to return the predicted migration coefficients as the estimated

TABLE 1
Likelihood Components for Three Hierarchical Stock Synthesis Models for Pacific Whiting.

Likelihood components	Emphasis	Model 1: No interannual variability	Model 2: Interannual variability in survey years only	Model 3: Interannual variability in all years
U.S. fishery age composition	1.0	−300.4	−311.1	−312.0
Canadian fishery age composition	1.0	−388.6	−385.3	−387.2
NMFS survey, U.S. zone biomass	5.0	3.8	3.9	3.3
NMFS survey, U.S. zone age composition	1.0	−144.8	−143.4	−140.6
NMFS survey, Canada zone biomass	5.0	−2.4	7.2	7.3
NMFS survey, Canada zone age composition	1.0	−148.6	−148.5	−148.3
DFO survey, biomass	5.0	−47.8	−25.6	3.5
DFO survey, age composition	1.0	−141.3	−141.7	−141.5

values; a small emphasis would allow other data to determine their values. For the final model runs, I used an emphasis of 5000 for the environmental component. I selected this emphasis level so that the root mean square error of the fit to the DFO survey observations (0.195) was comparable to the root mean square error of the fit to the NMFS survey observations (0.152), and provided an appropriate trade-off between fitting the DFO survey observations and fitting the predicted migration coefficients.

RESULTS

The stock synthesis migration models were hierarchical, starting with a simple model with no interannual variability in transboundary migration, and progressing to models where the migration differed in each year. During the years of a coastwide NMFS acoustic survey, the spatial distribution of the population is well measured, and there is sufficient information for estimating the migration coefficients independently. In the other years, consistent patterns in the age composition of the U.S. and Canadian fisheries provide some information on the transboundary distribution of Pacific whiting. In trial runs, however, age-composition data alone were insufficient to estimate the migration coefficients. For 1990, 1991, and 1993, when only DFO conducted acoustic surveys of the Canadian zone, the biomass estimates can be matched exactly, since the migration coefficients can move simulated fish across the border without reducing the likelihood to other data sources. Because biomass estimates include statistical error, an exact model fit suggests that the model is overparameterized. Adding an environmental index increases the information in the model, and thus increases the precision of the estimated parameters. Model 1 in table 1 estimates a single migration curve for all years. Model 2 estimates migration coefficients for the years with an NMFS triennial survey, resulting in the set of migration curves shown in figure 5. The largest estimated asymptotic proportion in the Canadian zone was 0.65, which occurred in 1983 during the 1982–83 El Niño. In 1992, also an El Niño year, the estimated asymptotic proportion in the Canadian zone was 0.52, the second largest value. In 1989, the estimated asymptotic proportion in the Canadian zone was at its lowest value, 0.17.

The correlations between the migration coefficients and the sea-temperature anomalies for survey years were generally positive during the 12-month period prior to the survey (figure 6). Negative correlations occur only

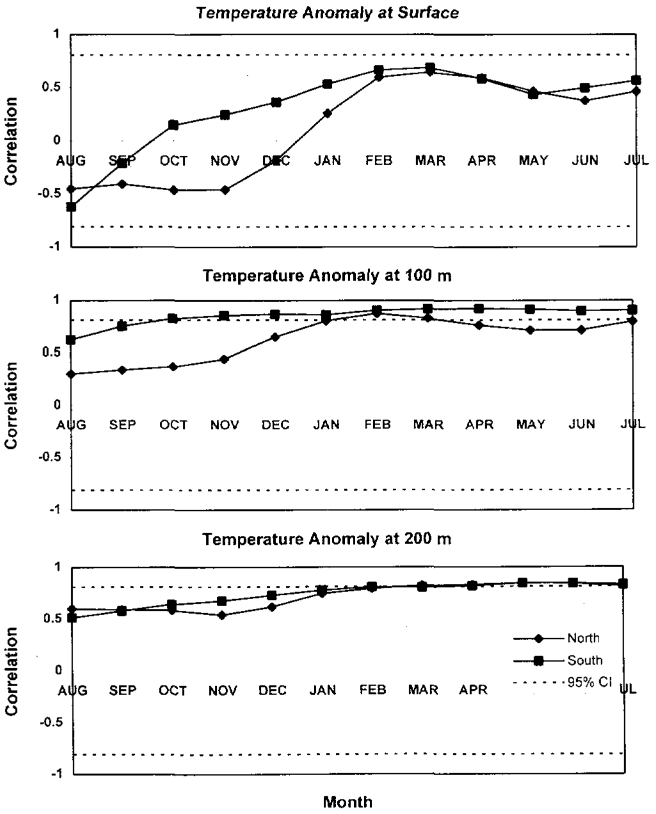

Figure 6. Correlation between estimated migration coefficients for survey years and sea-temperature anomalies (surface, 100 m, 200 m) for 12 months prior to the triennial survey. The "north" index is the mean anomaly for 42° N–54° N; the "south" index is the mean anomaly for 30° N–42° N.

for the surface temperature anomaly in the north. The 95% confidence intervals (Sokal and Rohlf 1981) for the observations under the null hypothesis (no correlation with temperature) show which correlations are the strongest, but should not be used to judge statistical significance, since many correlations were examined. The correlation with temperature anomalies at 100 and 200 m tended to be stronger than the correlation with the surface water temperature anomaly. The "south" index had higher correlations than the "north" index, suggesting that the environmental forcing of migration occurs in the south near the spawning ground rather than in the north on the feeding grounds. Higher correlations occurred during the semester (February–July) immediately before the survey, rather than the preceding semester (August–January). The tendency for high correlations to continue over a sequence of months is not surprising, because the monthly temperature anomalies themselves are highly correlated. Maximum correlations occurred during April–March at 100 m for the "south" index. I used this index in a regression analysis to predict the migration coefficient during the years without a survey.

The linear regression of the estimated migration coefficients on the temperature anomaly at 100 m was significant, $r^2 = 0.818$, d.f. = 4, $p = 0.013$. The temperature anomalies in 1983 (+1.29°C) and in 1989 (−0.42°C) are the largest and smallest temperature anomalies, respectively, and strongly influence the slope of the regression (figure 7). I used the regression equation ($p_3 = 0.28 + 0.30T$, where T is the temperature anomaly at 100 m) to predict the migration coefficients during years when there was no NMFS triennial survey. During 1977–93, none of the temperature anomalies for the years of no surveys were more extreme than the 1983 and 1989 anomalies.

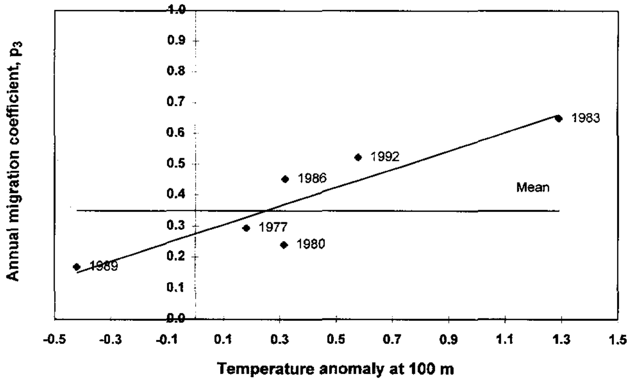

Figure 7. Regression of estimated migration coefficients p_3 for years with a National Marine Fisheries Service acoustic survey (1977, 1980, 1983, 1986, 1989, and 1992) on the March–April temperature anomaly at 100 m. The coefficients p_3 are the asymptotic proportion of the age group migrating into the Canadian zone.

TABLE 2
Estimated Coefficients for a U.S.–Canada Migration Function for Pacific Whiting

Parameter	Prediction based on sea temp. at 100 m	Stock synthesis estimate
p_1	—	5.297
p_2	—	1.478
p_{3i} (i = 1977, . . . , 1993)		
1977	—	0.294
1978	0.367	0.367
1979	0.316	0.314
1980	—	0.240
1981	0.336	0.335
1982	0.304	0.300
1983	—	0.649
1984	0.378	0.381
1985	0.300	0.303
1986	—	0.453
1987	0.371	0.371
1988	0.333	0.332
1989	—	0.169
1990	0.256	0.183
1991	0.202	0.249
1992	—	0.522
1993	0.405	0.397

The parameter p_1 is the inflection point of the logistic curve; p_2, the slope; and p_{3i}, the year-specific asymptotic proportion migrating into the Canadian zone. For years in which no surveys were made, two estimates are shown for p_{3i}: the prediction based on the sea temperature at 100 m, and the final stock synthesis estimate.

In the sequence of models 1–3, most of the improvement in fit—measured by increase in log(likelihood)—for the NMFS acoustic biomass estimate occurs when moving from model 1 to model 2 (table 1). The fit to the DFO surveys improves with each transition between models because the DFO surveys were made in years with an NMFS survey (1992) and also in years without an NMFS survey (1990, 1991, 1993). The substantial improvement in fit also indicates that the environmental index is consistent with the DFO acoustic time series. The model output included estimated coefficients for the migration function (table 2) and the predicted proportion of biomass in the Canadian zone that would have been measured by the NMFS acoustic surveys had they been made in all years (figure 8). This predicted proportion is obtained by filtering the age-specific population biomass through the survey selectivity curve. The mean proportion of biomass in the Canadian zone for all years (22.7%) corresponds reasonably well with the observed mean of the actual surveys (23.8%). Although the temperature anomaly is most positive in 1983, the maximum proportion of biomass in the Canadian zone occurred in 1992. This is due to two factors: a moderately positive temperature anomaly in 1992, and the population's relatively old mean age.

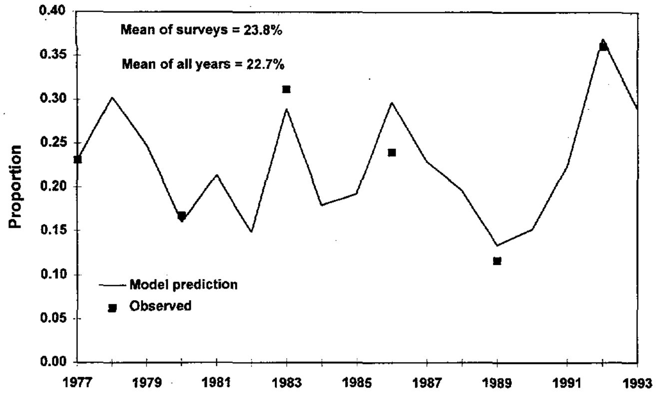

Figure 8. Predicted proportion of Pacific whiting biomass in the Canadian zone during 1977–93, based on a stock synthesis model with an environmental likelihood component. Observed proportion as measured by the National Marine Fisheries Service acoustic surveys in 1977, 1980, 1983, 1986, 1989, and 1992.

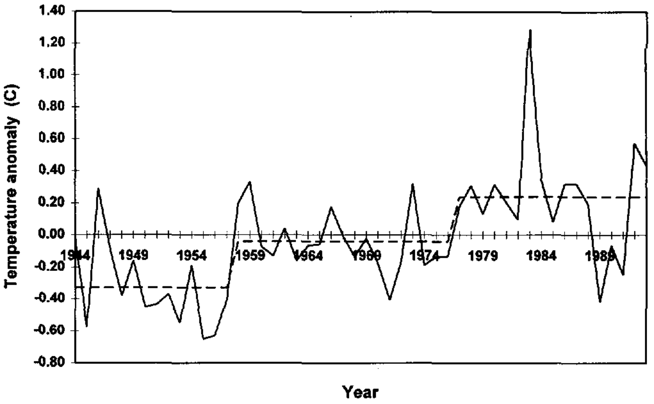

Figure 9. March–April temperature anomaly at 100 m, 30° N–42° N, 1944–93.

DISCUSSION

Correlation analysis and stock synthesis models show that the available data on the Pacific whiting population are consistent with a hypothesis that El Niño events promote the northward migration of Pacific whiting via intensified northward currents during the period of active migration. There are two primary benefits from the modeling approach used in this paper. First, a stronger assessment model results from using additional data. For example, the DFO surveys, which cover only the Canadian zone, provide little independent information on overall abundance. But when the environmental index is included in the model, the total population abundance and the value of the migration coefficients jointly determine the expected biomass in the Canadian zone. As a consequence, when a model is fit, the DFO biomass estimates provide additional inference on the total population abundance.

A second benefit of this approach is in predicting population response to climatic variation. During the NMFS acoustic survey years of 1977–92, the March–April 100 m temperature anomaly varied over most of the range of the anomaly for the past 50 years (figure 9). For temperature anomalies within this range, the potential response of Pacific whiting migration to climate change can be predicted. This 50-year period can be roughly divided into three parts: a "cold" period from 1944 to 1957, a "moderate" period from 1958 to 1976 initiated by the 1957–58 El Niño, and a "warm" period from 1977 to the present, punctuated by the spectacular 1982–83 El Niño and several years of negative anomalies in the late 1980s (figure 9). The NMFS acoustic surveys were all made during this warm period (only 1989 has a negative temperature anomaly). Although the mean distribution of biomass estimated from these surveys is probably close to the true mean for this warm period, it may significantly underestimate the long-term average proportion of biomass in the Canadian zone. A return to cooler conditions would be expected to reduce the biomass in the Canadian zone.

The stock synthesis model used in this paper is based on the assumption that spawning occurs in the same place each year. Maps of Pacific whiting larvae distributions (in Hollowed 1992) show clear interannual differences. In warm years, larval distribution usually shifts northward. The most extreme northward shifts in larval distribution usually occur a year or more after the onset of an El Niño, as in 1984 and 1994. It is unknown whether these changes are due to egg and larval transport or to changes in the location of spawning, or both. The spawning grounds of Pacific whiting are not known with any certainty. A model for Pacific whiting migration that includes changes in spawning location would be useful to develop, but the data are not available for estimating the parameters of such a model.

Ware and McFarlane (1995) show a correlation between a water-temperature time series from Amphitrite Point, a coastal station near La Perouse Bank, and a midwater trawl, volume-swept biomass estimate of Pacific whiting in the La Perouse region. Ware and McFarlane derive a regression equation to predict the biomass of Pacific whiting in the La Perouse region in August as a function of water temperature in the preceding June–July. Although the correlation is strong, it is useful to consider how Ware and McFarlane's relationship differs from that obtained in this paper. First, their correlation does not take into account the age structure of the population. Second, it does not take into account changes in the total biomass of Pacific whiting. Although the results in this paper are also based on patterns of correlation, they suggest that the significant oceanographic events affecting Pacific whiting migration into the Canadian zone occur earlier in the year, more than 500 km south of the La Perouse region. Of course, the Amphitrite Point temperature time series will be correlated with temperatures farther south, so the Ware-McFarlane correlation does not conflict with our results. However, to use a correlation between temperature and Pacific whiting biomass in an ecosystem model of the La Perouse region could potentially lead to incorrect conclusions regarding the trophic role of Pacific whiting. This is because any other ecological process in the model that was a function of water temperature would also be correlated with Pacific whiting biomass.

The primary management implications of this research concern the binational allocation of the Pacific whiting resource. No formal agreement has been reached on how to allocate Pacific whiting yields between U.S. and Canadian fisheries. Discussions have focused on an allocation based on the distribution of biomass between the two zones. However, agreement has not been reached, and since 1993 the United States has set its quota at 80% of the total available yield, and Canada has set its quota at a level that would be 30% of the combined quotas. From the perspective of this research, reaching an agreement that will be appropriate for the indefinite future may be difficult. An agreement based on current climatic conditions could be inappropriate in future conditions. The U.S. and Canadian fisheries have largely developed during a warm period, from 1966 to the present. Under some scenarios for climate change, global warming might result in persistent El Niño–like conditions on the west coast of North America, which could lead to high migration rates to the Canadian zone. Alternatively, a regime shift to cooler conditions is also possible in the near future, leading to decreased migration rates to Canada. The long-term performance of the Canadian fishery for Pacific whiting depends somewhat on climatic conditions. The U.S. fishery is less vulnerable, since it can fish over a much wider latitudinal range within the migration limits of the resource.

ACKNOWLEDGMENTS

I thank Jim Ingraham for his assistance in obtaining the temperature data used in this paper. Anne Hollowed, Paul Smith, and Alec MacCall read an earlier draft of the paper and gave valuable suggestions. Special thanks to Rick Methot for encouragement and many useful discussions.

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EXPLORATIONS OF EL NIÑO EVENTS AND ASSOCIATED BIOLOGICAL POPULATION DYNAMICS OFF CENTRAL CALIFORNIA

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ABSTRACT

During El Niño events off central California, temperatures were elevated, salinities were depressed, and there was evidence of poleward and onshore advection. El Niño conditions seemed to delay the annual phytoplankton bloom, affect the distribution and abundance of invertebrates, improve recruitment of southern fish species, cause recruitment failures of rockfish (*Sebastes* spp.), and cause poor growth and condition of adult rockfish. The 1992–93 El Niño off central California was less extreme than the 1982–83 event, but much stronger than the 1986–87 event. Water temperatures in 1992–93 were similar to the 1982–83 event, but poleward advection appeared to be weaker. Recruitment of southern species was higher in 1983 than in 1992; the condition of rockfish was better in the more recent event. Computer simulation indicated that fishery management practices can influence the intensity of El Niño effects on a fishery for rockfish. Possible causes of rockfish recruitment failures during El Niño events are discussed.

INTRODUCTION

Scientists familiar with waters off central California (figure 1) are aware that significant physical and biological changes are associated with El Niño events. However, little of the extensive scientific literature on El Niño events emphasizes central California. In this paper, we review some of the important papers dealing with El Niño characteristics in the northeastern Pacific Ocean, and then explore El Niño-related phenomena off central California, emphasizing the 1992–93 event, but also including the 1957–59, 1982–83, and 1986–87 events. We first examine physical oceanographic data, from shore stations and from oceanic surveys. We next present biological information for trophic levels ranging from primary production to planktivores. Finally, we show results of a computer simulation of El Niño effects on an exploited population of rockfish.

Most of the biological data come from research by the authors or close associates and have not been previously published in the peer-reviewed literature. Because of the review nature of this paper and the wide scope of the data, sources and descriptions of the data are provided in figure captions and the acknowledgments section rather than in a lengthy methods section.

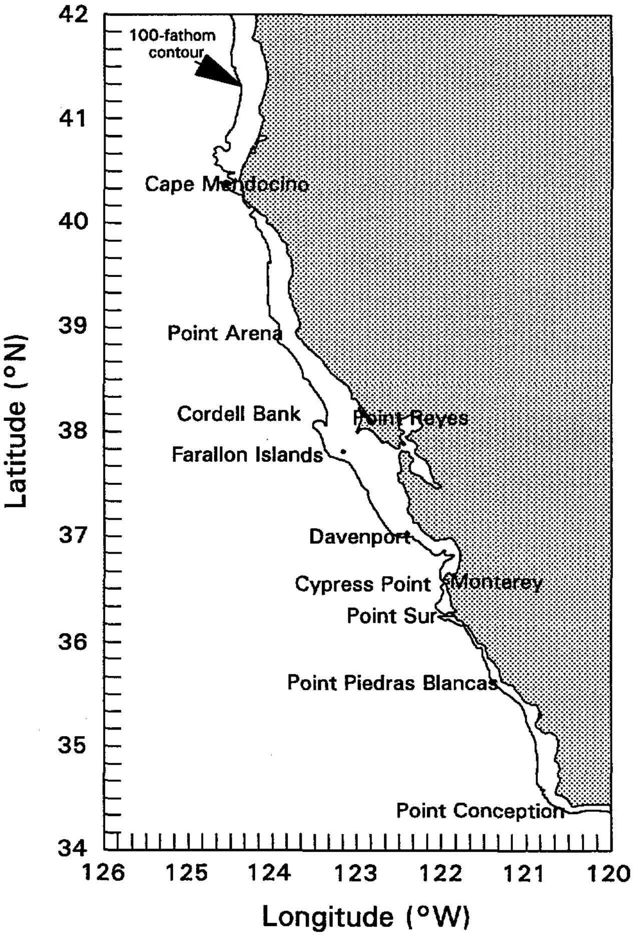

Figure 1. Map of central and northern California showing locations mentioned in text.

LITERATURE REVIEW

Researchers have documented numerous examples of physical and biological phenomena associated with El Niño events in the northeastern Pacific Ocean, including the very strong 1957–59 (*CalCOFI Reports*, vol. 7) and 1982–83 events (Wooster and Fluharty 1985). Mysak (1986) and Simpson (1992) presented extensive reviews of the physical dynamics of El Niño events, including proposed mechanisms that link events off the west coast of North America to events in the tropics. Although both of those papers addressed phenomena over much of the eastern Pacific Ocean, Mysak (1986) focused on British Columbia and Simpson (1992) on southern California. These authors concluded that El Niño events involve both onshore and poleward advection. They presented results indicating that onshore advection was forced by north Pacific atmospheric anomalies that appeared to be coupled with events at the equator. Poleward advection appeared to be caused by a combination of atmospheric anomalies and hydrodynamics related to the onshore movements. Both Mysak and Simpson expressed doubts about the importance of poleward advection being the result of forcing from tropical waters. Onshore advection appeared to cause nearshore salinities to be lower than normal. Both onshore and poleward advection could have caused elevated temperatures associated with El Niño events.

Both onshore and poleward advection during the 1982–83 El Niño were evident in the 1981–83 trajectory of a buoy drogued at 30 m, as reported by Emery et al. (1985). The buoy moved several hundred miles shoreward between December 1982 and late January 1983, approaching the coast at Point Arena. It then drifted rapidly northward, reaching Vancouver Island in late February 1983. Emery et al. (1985) presented evidence that North Pacific atmospheric anomalies caused the advection of surface waters and consequent movement of the drogue.

Although Mysak (1986) and Simpson (1992) question the importance of direct oceanic linkages of poleward advection with events at the equator, there is both theoretical and empirical work to indicate that direct oceanic linkages are plausible (e.g., Clarke and Van Gorder 1994). In addition, Norton and McLain (1994) correlated temperature data from the northeastern Pacific Ocean with atmospheric data from the tropics and the North Pacific. Although concluding that El Niño–related warming at depths below 100 m related to remote forcing through the ocean, they agreed with Mysak (1986) and Simpson (1992) that warming of surface waters involved North Pacific atmospheric anomalies.

Physical factors other than elevated temperatures, depressed salinities, and abnormal advection are associated with El Niño events off the West Coast. Hayward et al. (1994) associated reduced upwelling or increased downwelling, high sea level, thickened surface mixed layer, and depressed nutricline with the 1992–93 event.

Biological information related to El Niño events was reviewed by Radovich (1961). He noted many range extensions for fish along the West Coast associated with events of 1957–59 and earlier. Catch rates of some southern gamefish improved off southern California, and other species returned to areas of previous abundance. Although active swimming could explain most of the fish movements, Radovich hypothesized that several planktonic invertebrates had been advected northward. Several fish species appeared to reproduce successfully off southern California in areas north of their normal spawning region. Smith (1985) compared CalCOFI zooplankton catches off southern California during the 1957–59 event with adjacent years and found that effects varied among species, but overall zooplankton catch rates decreased dramatically during El Niño. Zooplankton volumes and chlorophyll concentrations were depressed off southern California during the 1982–83 (McGowan 1985) and 1992–93 El Niño events (Hayward et al. 1994). Pearcy et al. (1985) studied biological phenomena during the 1982–83 El Niño off Oregon and Washington. Surface chlorophyll levels were low during 1983 compared to 1982. Survival of salmon appeared to be poor, and their weights were low. Pearcy et al. also reported range extensions of several fish species, changes in the species composition of Oregon commercial landings, and shifts in species composition of fish and gelatinous zooplankton captured during a purse seine survey. Some of these biological effects of El Niño continued into the next year.

PHYSICAL CHARACTERISTICS ASSOCIATED WITH EL NIÑO

Surface Temperature

The first evidence of the 1992–93 event came from positive surface temperature anomalies at the Farallon Islands shore station early in 1992 after several years of generally cool conditions (figure 2). Temperatures declined during summer and early fall of that year and

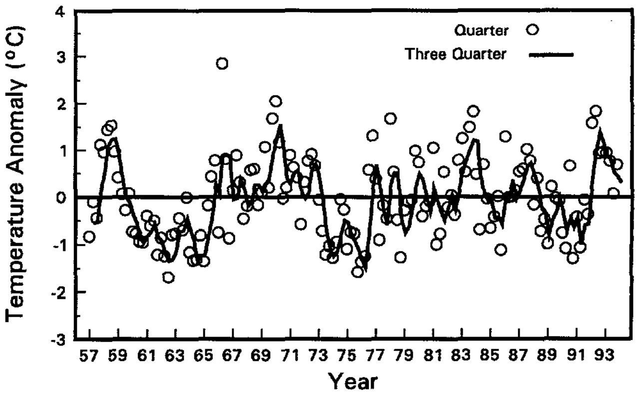

Figure 2. Quarter and three-quarter average temperature anomalies at the Farallon Islands shore station, 1957–93. Anomalies are deviations from monthly averages of 1957–93 data (Walker et al. 1992).

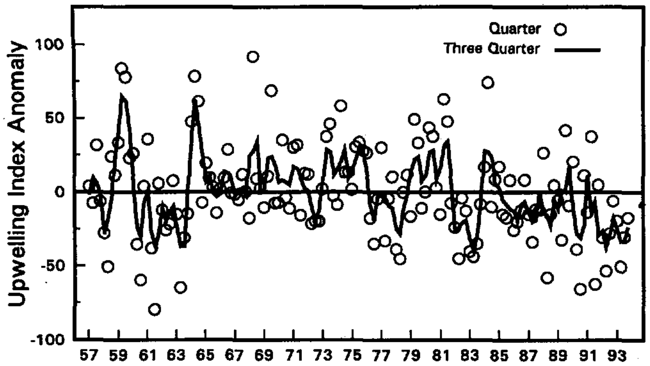

Figure 3. Quarter and three-quarter averages of the Bakun upwelling index anomalies $[\text{m}^3\text{s}^{-1}/(100 \text{ m of coastline})]$ at 36°N, 1957–93. Anomalies are deviations from monthly averages of 1957–93 data (Bakun 1973).

then increased again, a pattern also noted for southern California (Hayward 1993; Lynn et al. 1995). The 1992–93 temperature pattern essentially mirrored that of the 1982–83 event. Temperature anomalies during the 1992–93 event were similar to those of the 1957–59, 1969–70, and 1982–83 El Niño events (figure 2). Temperature anomalies were lower during the 1986–87 event, but still positive. The cool period that preceded the 1992–93 event was the coolest since 1973–76. There was also an extensive period of below-normal temperatures between 1960 and 1965.

Upwelling Indices and Sea Level

Anomalies in the upwelling index at 36°N (Bakun 1973) were negative during 1992–93 (figure 3), indicating weaker-than-normal upwelling or downwelling. The values were similar to those of the strong 1982–83 and 1957–59 El Niño events. The low values of 1992–93 continued a trend that started in 1975, as observed by Bakun (1990), and anomalies tended to be negative even during the cool period that preceded 1992.

Monthly sea-level anomalies at San Francisco were generally positive during 1992–93 (figure 4). The highest values were observed during early 1992 and were similar to the maximum values measured during the 1986–87 El Niño. Values in 1982–83 were considerably higher than those of 1992–93. High sea levels are associated with northward flow (Chelton et al. 1982) and also are consistent with downwelling or reduced upwelling.

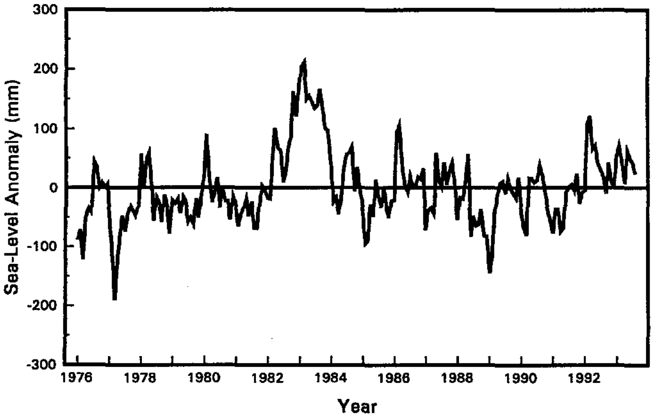

Figure 4. Monthly sea-level anomalies at San Francisco, 1976–93.

Vertical Temperature and Salinity Sections

Vertical temperature and salinity sections along a cross-shelf transect off Davenport in March and June during the 1992–93 event (figures 5–8) agree with the results of Simpson (1992) off southern California for the 1982–83 event. When compared to 1950–78 average conditions compiled by Lynn et al. (1982), temperatures were high and salinities low. The relatively high

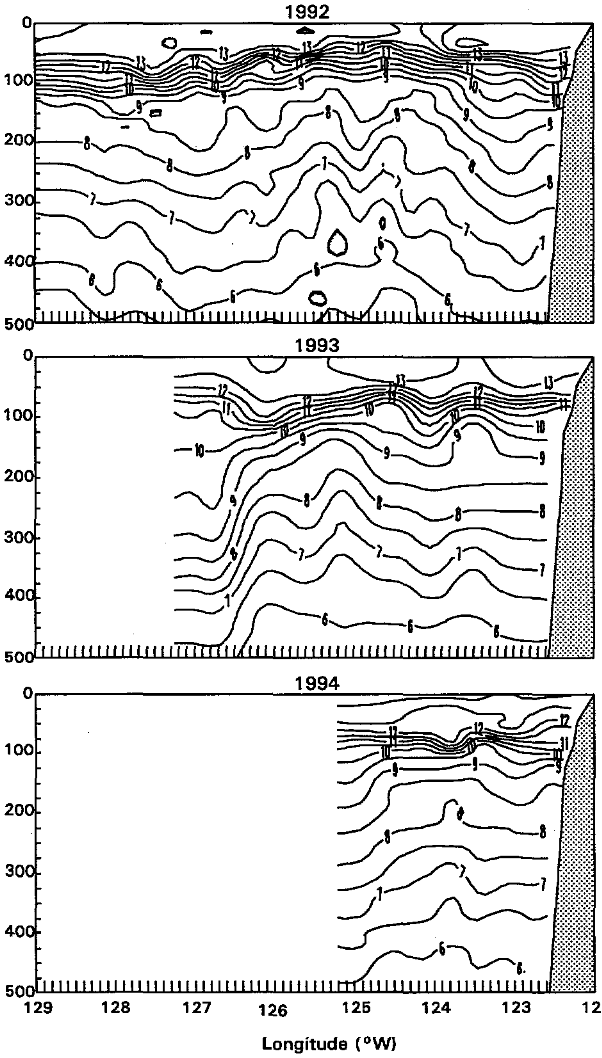

Figure 5. Vertical sections of temperature along a cross-shelf transect off Davenport (37°N), March 1992, 1993, and 1994. *Shaded areas* indicate the bottom. 1992 data were collected by a pre-FORAGE cruise. The 1993 and 1994 data were collected by the Tiburon Laboratory (Sakuma et al. 1994).

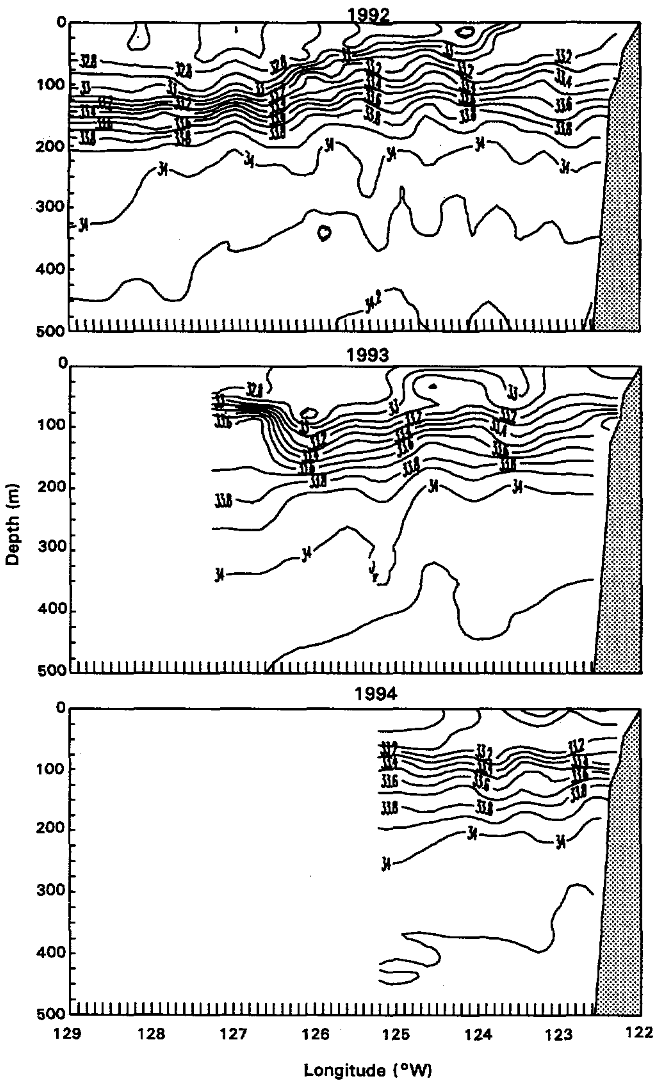

Figure 6. Vertical sections of salinity along a cross-shelf transect off Davenport (37°N), March 1992, 1993, and 1994. *Shaded areas* indicate the bottom. 1992 data were collected by a pre-FORAGE cruise. The 1993 and 1994 data were collected by the Tiburon Laboratory (Sakuma et al. 1994).

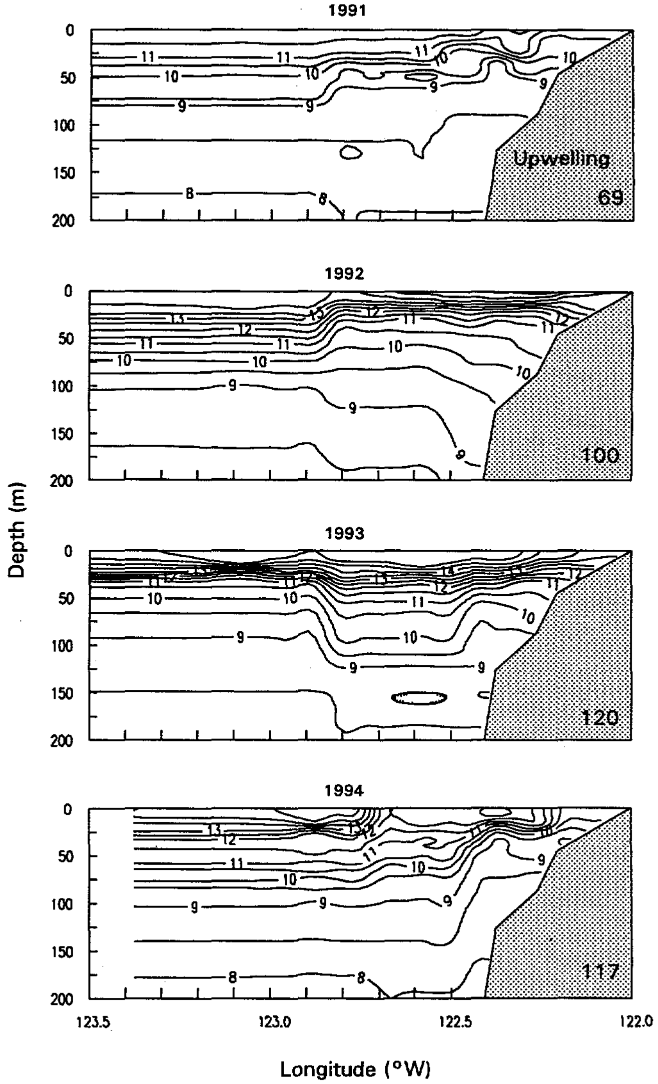

Figure 7. Vertical sections of temperature along a cross-shelf transect off Davenport (37°N), early June 1991–94. *Shaded areas* indicate the bottom. Five-day averages of the Bakun upwelling index [m^3s^{-1}/(100 m of coastline)] are shown in the *shaded areas*. Temperature data were collected by the Tiburon Laboratory (Sakuma et al. 1994).

temperatures combined with relatively low salinities suggest onshore advection, because climatological salinities decrease to the west and north and temperatures increase to the west and south (Lynn 1967; Lynn et al. 1982). Temperature and salinity fronts defining the eastern boundary of the California Current in June appear to be closer to shore than in March, and closer to shore relative to the climatology (Lynn 1967; Lynn et al. 1982), implying an onshore component of advection. In March 1992, temperatures on level surfaces down to 500 m tended to tilt down toward the coast inshore of 124°W (figure 5), which is contrary to typical conditions at that time of year. However, salinities tended to tilt up in an easterly direction, as is normal (figure 6).

Sakuma and Ralston (1995) calculated northward geostrophic flow to about 100 km off central California during March 1992. Direct shipboard acoustic Doppler current profiler measurements in late February support this (P. M. Kosro and R. J. Lynn, pers. comm.). By June 1992, the geostrophic flow was southward, except for a region of extremely strong subsurface poleward current over the continental slope (Lynn et al. 1995). The surface geostrophic circulation was southward during March 1993 as well (Sakuma and Ralston 1995). These observations indicate that both onshore and poleward advection occurred off central California during at least part of the 1992–93 period. The complete time history of these periods of anomalous advection is not known.

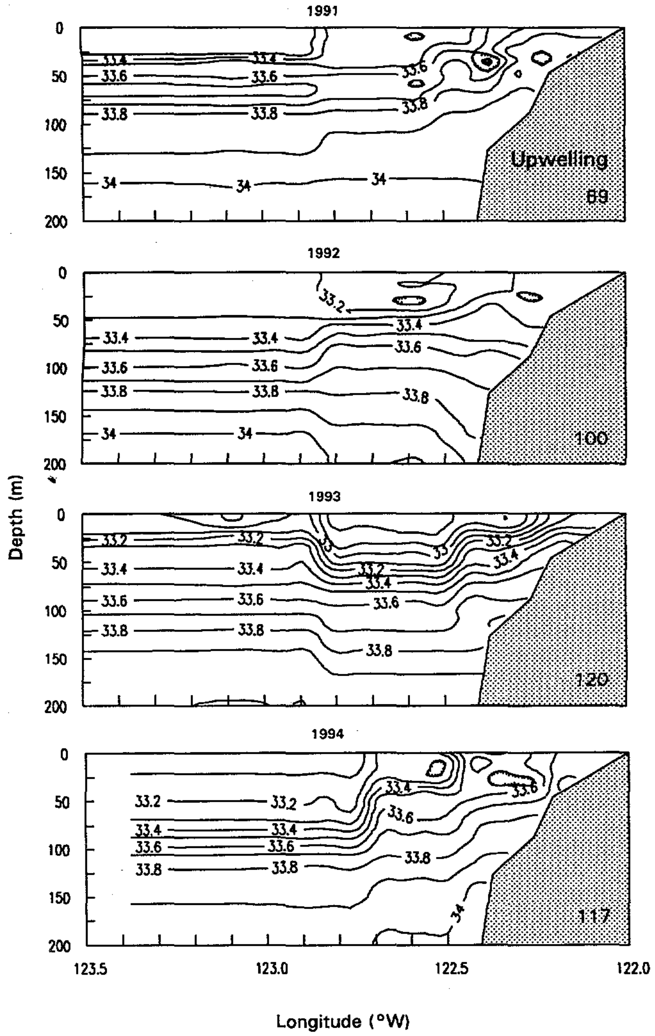

Figure 8. Vertical sections of salinity along a cross-shelf transect off Davenport (37°N), early June 1991–94. *Shaded areas* indicate the bottom. Five-day averages of the Bakun upwelling index [m^3s^{-1}/(100 m of coastline)] are shown in the *shaded areas.* Data were collected by the Tiburon Laboratory (Sakuma et al. 1994).

An upwelling center appears off Davenport in June during normal years and was evident in the temperature and salinity data during 1991, 1993, and 1994 (figures 7 and 8). There was little evidence of upwelling in the hydrographic data during 1992, even though the upwelling index for the five-day period immediately preceding the survey was similar to that of the other years. Large-scale poleward advection, possibly caused by remote forcing (Norton and McLain 1994), may have been strong enough to overwhelm evidence of local wind-induced upwelling during this time. In addition, short-term upwelling-favorable wind events, as defined by the upwelling index and direct wind measurements off central California, may not be sufficient to counter the seasonal effects of the anomalously weak equatorward stress observed throughout 1992.

Temperatures of the upper water column were slightly lower in March 1994 than during the preceding two years, but remained higher than normal (figure 5). Salinities remained low during March 1994 (figure 6). June 1994 nearshore temperatures dropped to 1991 levels, but temperatures remained warm offshore (figure 7). June 1994 nearshore salinities approached 1991 levels, but offshore salinities were similar to 1992 and 1993 levels (figure 8). This suggests that normal upwelling had recommenced in 1994, but a large anomalous water mass remained in the seaward portion of the survey region.

El Niño events are often associated with deeper-than-normal thermoclines (e.g., Norton and McLain 1994). It is difficult to characterize thermocline depth in our area because of the complex dynamics of upwelling and the California Current. The vertical sections off Davenport (figures 5 and 7) illustrate the difficulty in concluding that thermocline depth increases in our study area during El Niño events. However, the data indicate considerably more vertical thermal stratification during El Niño events than during other years (figures 5 and 7).

BIOLOGICAL CHARACTERISTICS ASSOCIATED WITH EL NIÑO

Primary Productivity

Primary productivity has been measured in Monterey Bay since 1989. Climatological primary production for the cool years of 1989–91 shows a peak in May–June at around 2.3 $gC/m^2/d$ (figure 9). In 1992 productivity was bimodal, with peaks in May and July–August of around 1.7 $gC/m^2/d$, about 25% lower than the 1989–91 average. However, and perhaps more important, the start of the productive season was delayed about two months compared to the 1989–91 climatology (figure 9). During the cool years, productivity began to increase from the winter low in late January. In 1992, productivity did not begin to increase until late March. The early months of the year are particularly important for members of the upper trophic level, as will be discussed below. When analyzing productivity effects during El Niño, it is obviously necessary to consider the change in the pattern as well as in the amplitude. The productive season was delayed only slightly in 1993; in contrast, the latter half of the year was substantially less productive than the 1989–91 climatology (figure 9). During 1993, the average productivity peaked in April at around 1.8 $gC/m^2/d$. Averaged over the year, primary production during 1992 was 28% lower than the 1989–91 climatology, and 1993 was 21% lower. Primary production did not return to pre-1992 levels in 1994.

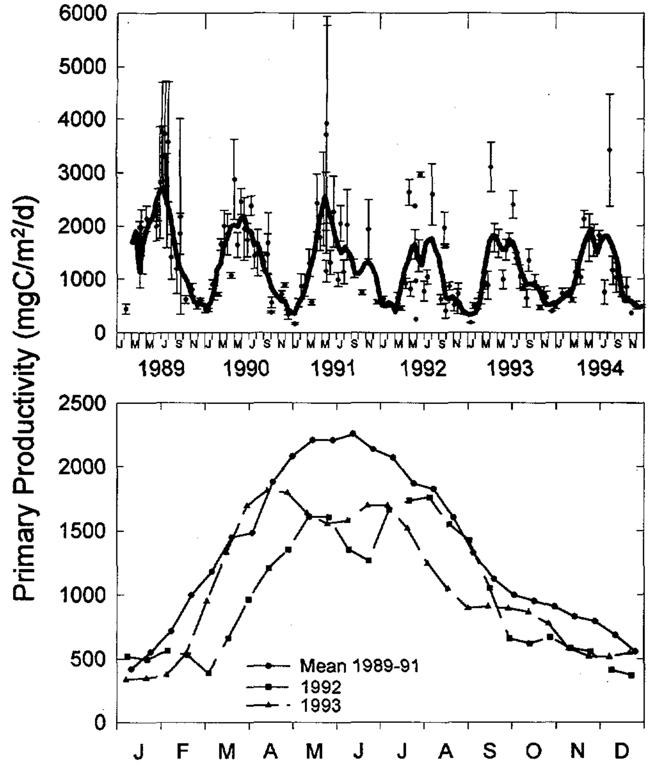

Figure 9. Time series of primary productivity for Monterey Bay for 1989–94 (*upper panel*). Primary productivity was measured by Francisco Chavez using incorporation of ^{14}C over 24 hr in simulated in situ incubations. Sampling was done at 2–5 stations and on intervals ranging from daily to monthly. Shown in the *upper panel* are the means and standard errors for stations occupied each day. The *solid line* represents a 4-point smooth of data that had been interpolated to biweekly intervals. The smoothed data were averaged for the period 1989 to 1991 and compared to the smoothed data from 1992 and 1993 (*lower panel*).

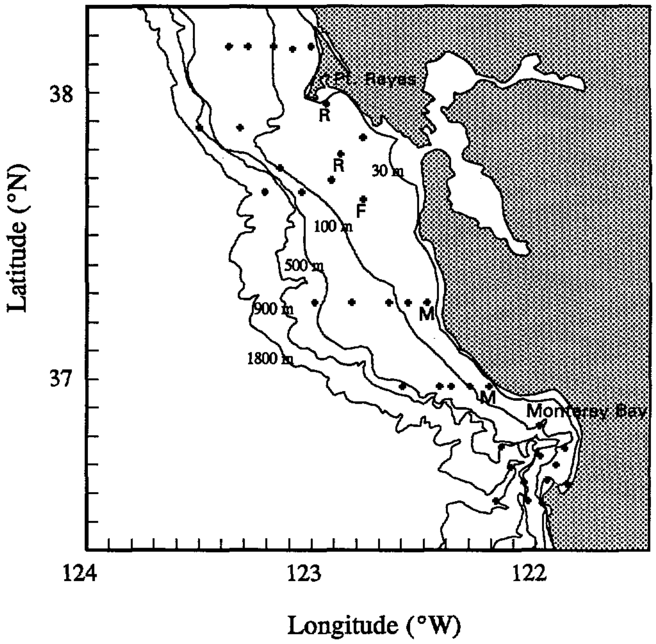

Figure 10. Locations of midwater trawl stations sampled annually during May–June since 1983 by the Tiburon Laboratory (Wyllie Echeverria et al. 1990). The Point Reyes area comprises the stations labeled *R*; the Gulf of the Farallons area contains the station labeled *F*; and the northern Monterey Bay area comprises stations labeled *M*.

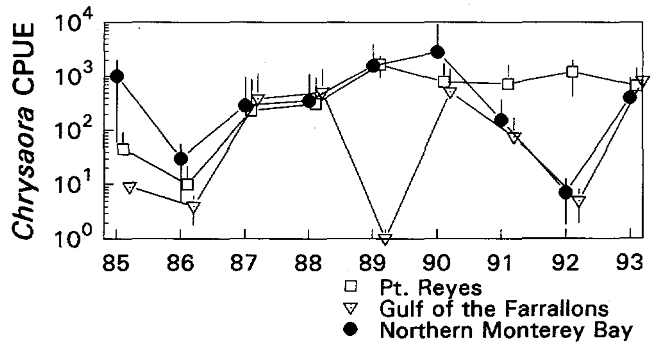

Figure 11. Average catch of *Chrysaora fuscescens* per trawl by the Tiburon midwater trawl survey at the nearshore areas shown in figure 10, 1985–93 (Graham 1994).

Invertebrates

Graham (1994) analyzed annual May–June midwater trawl survey (MWTS) catches of the scyphomedusa *Chrysaora fuscescens* between Cypress Point and Point Reyes since 1985. For the MWTS, the NMFS Tiburon Laboratory uses a square-mouthed trawl with 26.5 m sides and a 1 cm mesh cod end. The survey is conducted during the night at stations shown in figure 10. The MWTS is further described by Wyllie Echeverria et al. (1990). Three main localities (northern Monterey Bay, Gulf of the Farallons, and Point Reyes) usually accounted for most of the medusa biomass within the survey region.

There were two major low-abundance periods of *C. fuscescens* between 1985 and 1993 (figure 11). Except for the 1985–86 period, Point Reyes tended to have lesser year-to-year variation than the southern coastal sites. The 1986 and 1992 low abundances are consistent with the decline off Oregon in 1983 (Pearcy et al. 1985). Although the 1986 reduction in abundance off central California was evident over the breadth of the entire trawling region, Graham (1994) explained the 1992 reduction as a distributional shift of *C. fuscescens* towards the north. The distribution of the medusae towards the north is consistent with northward advection, but it should be noted that concentrations did not increase off Point Reyes during El Niño years. Lower concentrations in the southern regions may also be explained by weaker cross-shelf density gradients as a result of both weakened upwelling intensity and a warmer mixed layer. As previously mentioned, there was little evidence of upwelling off Davenport during 1992 (figure 7). However, there was some upwelling off Point Reyes during May–June 1992 (Sakuma et al. 1994).

Graham (1994) also documented changes in benthic juvenile crab distributions as a consequence of the 1992 event. Megalopae of the crab *Cancer gracilis* cling to the tentacles of *C. fuscescens*, where they molt to a juvenile stage and eventually fall to the seafloor. During normal upwelling years, when medusae are concentrated in convergences south of upwelling centers, these juveniles are concentrated at the front away from shore. But during 1992, when medusae were generally absent from Monterey Bay, these crabs were concentrated on the seafloor significantly closer to the coast. Graham (1994) attributes this shift to the distribution shift of the *C. fuscescens*.

Even though the MWTS was designed to sample pelagic young-of-the-year (YOY) rockfish, the (1.27 cm mesh cod end) trawl retains considerable quantities of euphausiids (mostly *Euphausia pacifica* and *Thysanoessa spinifera*). Catches of euphausiids were not quantified until 1990. Euphausiid abundance was considerably lower in 1992 than in 1991 or 1993, but catch rates were also low during the non-El Niño year of 1990.

Southern Fishes

Scuba divers have estimated the abundance of YOY blacksmith (*Chromis punctipinnis*), bluebanded goby (*Lythrypnus dalli*), and California sheephead (*Pimelometopon pulchrum*) near Monterey since 1981 (figure 12). These southern species were absent as YOY in most years, but were abundant in 1983, and some were common in 1992. Some also occurred in low numbers in 1993 and 1987. Adult bluebanded gobies are usually absent from the area. We believe that YOY bluebanded gobies were present in 1983 because of poleward advection. Adult blacksmith and California sheephead have occurred in the area and may have successfully reproduced only during the El Niño years.

Other evidence suggests that recruitment of California sheephead during El Niño years was the result of poleward advection. California sheephead were taken by recreational divers in spearfish meets along central California when they were available. Fish smaller than 356 mm (14 in.) did not qualify for competition but were occasionally speared. One large sheephead was landed in 1980; subsequently, none were landed until 1987, when two small fish were taken (figure 13). More than 60 fish were landed in 1988, followed by a declining catch through 1993. Average size slowly increased each year between 1987 and 1993, but did not reach the size of the one fish landed in 1980. The data suggest that sheephead were scarce or absent from the area between 1980 and 1983. As previously noted, YOY recruited to the area during the 1983 El Niño. The 1983 year class apparently had grown to sizes attractive to divers by 1987. The absence of catches in 1982 and 1983 suggests that large sheephead were not in the area and that recruitment in 1983 was the result of advection. If YOY that recruited to the area in 1992 survive and if their growth is similar to the 1983 year class, they should begin to recruit to the sport fishery in 1996. YOY sheephead abundance was not as high in 1992 in comparison with 1983.

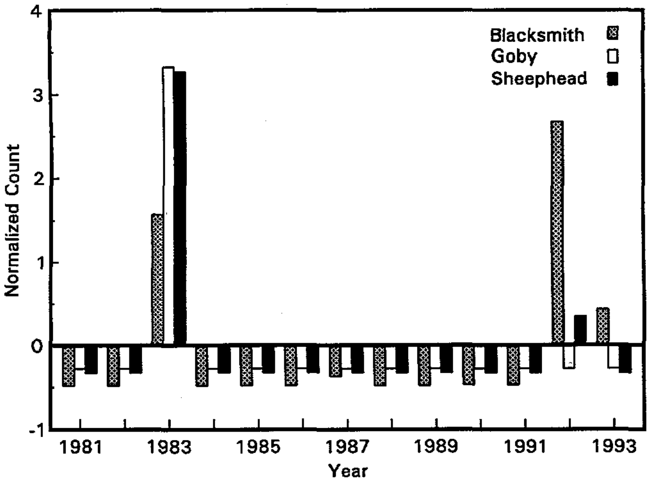

Figure 12. Standard deviates of diver counts of YOY blacksmith, bluebanded gobies, and California sheephead at the Monterey Jetty, 1981–93. Survey was made along standardized tracks (D. VenTresca, unpublished data).

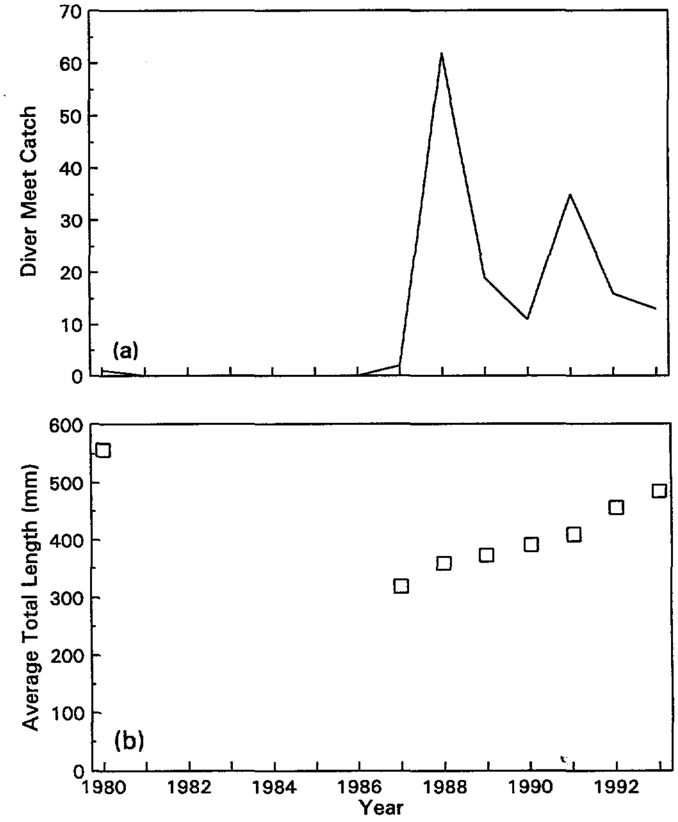

Figure 13. Catches (*a*) and average sizes (*b*) of California sheephead in recreational spearfish meets along the central California coast between Monterey and Piedras Blancas, 1980–93. Minimum size to qualify for the meets was 356 mm (14 in.), but smaller fish were occasionally taken. Data were collected by D. VenTresca.

Thus the 1992 year class is unlikely to affect the fishery as much as the 1983 year class.

Cowen (1985) presented evidence to support the argument that prevailing currents make Point Conception the northern boundary of the normal range of southern fish such as California sheephead. He proposed that recruitment does not occur in normal years because currents are southward and there are no sources of eggs and larvae to the north. He concluded that temperature is not the main factor because populations of these species are successful in cold-water upwelling areas off north-central Baja California.

Rockfish

The MWTS has followed a consistent sampling plan since 1986 (figure 10). Annual indices of abundance of YOY rockfish are estimated from the survey catches. The surveys are conducted at the end of the pelagic stage of juvenile rockfish, by which time we believe that year-class strength has been established. Ralston and Howard (in press) found that abundance indices calculated from MWTS results correlated well with diver estimates of settled YOY rockfish abundance between Cape Mendocino and thirty miles south of Point Arena. Thus the MWTS results appear to be representative of much of central California. The YOY rockfish abundance index was very low in 1986 and in 1992, as well as in 1990 (figure 14). A limited MWTS and diver counts indicate that it was also very low during 1983 (pers. comm., E. Hobson, NMFS, 3150 Paradise Dr., Tiburon, CA 94920).

Shortbelly rockfish (*Sebastes jordani*) usually constitute 70% or more of MWTS YOY rockfish catches, but the catches of two years differ markedly. The first half of 1991 was cold compared to other years since the survey began (figure 2), and shortbelly rockfish made up less than 50% of the catch in that year. Northern species of rockfish constituted a larger portion of the catch in 1991 than in other years, and for the first time, Puget Sound rockfish (*S. emphaeus*) were recorded south of Cape Mendocino. The other unusual catch composition occurred during the 1992–93 El Niño. The 1993 index of abundance was the fourth highest of the series (figure 14). However, shortbelly rockfish constituted less than 50% of the catch, and catches of brown rockfish (*S. auriculatus*) were much higher than in any previous year.

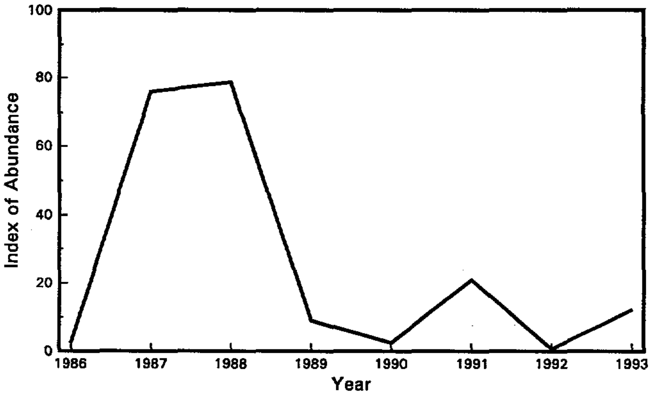

Figure 14. Index of abundance of pelagic YOY rockfish off central California, 1986–93. Index is calculated from catches by the Tiburon midwater trawl survey (Ralston 1994).

Brown rockfish belong to the nearshore demersal group. Adults of these species—kelp rockfish (*S. atrovirens*), brown rockfish, gopher rockfish (*S. carnatus*), copper rockfish (*S. caurinus*), black and yellow rockfish (*S. chrysomelas*), quillback rockfish (*S. maliger*), china rockfish (*S. nebulosus*), and grass rockfish (*S. rastrelliger*)—tend to be solitary individuals closely associated with the bottom in shallow water.

Another distinct group, structure schoolers, comprises widow rockfish (*S. entomelas*), yellowtail rockfish (*S. flavidus*), black rockfish (*S. melanops*), blue rockfish (*S. mystinus*), and olive rockfish (*S. serranoides*). Adults of these species often form midwater schools associated with structures such as pinnacles and kelp, and tend to occur in water deeper than the nearshore demersal group.

Pelagic YOY of the nearshore demersal group are relatively more abundant during El Niño years than during other years in comparison to structure schoolers (figure 15). In addition, fishes in the nearshore demersal group are captured higher in the water column than the structure schoolers (figure 16). The nearshore demersal group, therefore, may benefit from the onshore advection, or the reduced offshore advection, of surface

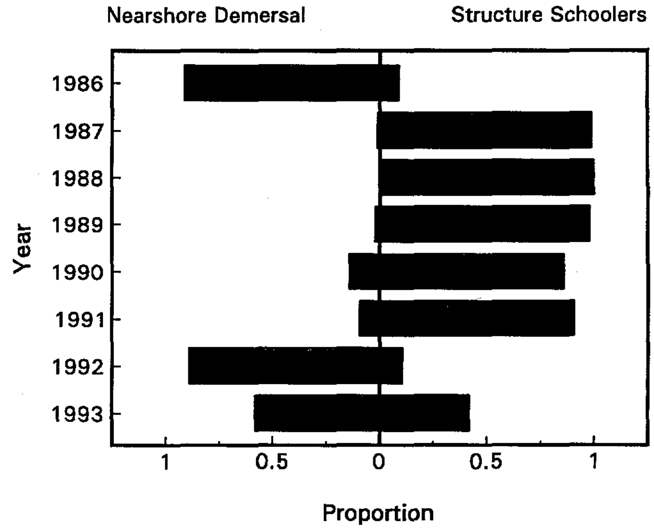

Figure 15. Relative proportions of nearshore demersal and structure schooler YOY rockfish captured by the Tiburon midwater trawl survey, 1986–93 (proportions calculated as fraction of combined catch of the two groups). See text for group definitions.

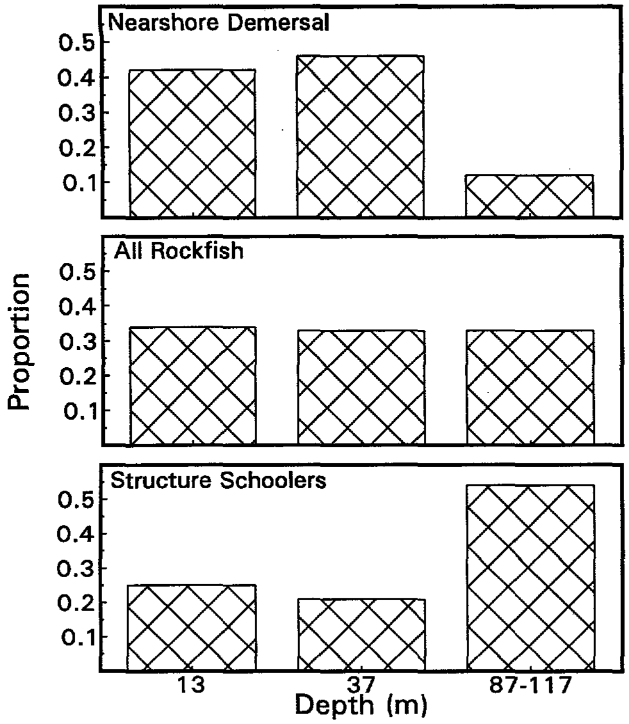

Figure 16. Unweighted average depth distributions of catches of YOY rockfish by the Tiburon midwater trawl survey, 1983–93. Depth-distribution estimation procedures were described by Lenarz et al. (1991).

waters that characterizes El Niño years. Conversely, the structure schoolers may benefit from onshore advection of deeper waters during non-El Niño years (Moser and Boehlert 1991).

The nearshore demersals and structure schoolers differ in another way that could affect their relative reproductive success during El Niño and non-El Niño years. Off central California, the peak parturition season for structure schoolers tends to be January and February, whereas that of the nearshore demersal group tends to be later. Peak parturition for blue rockfish occurs in January, and for black, widow, and yellowtail rockfish, in February (Wyllie Echeverria 1987). For the copper rockfish, parturition peaks in February (Wyllie Echeverria 1987), and for black and yellow rockfish, it peaks in March or possibly April (although little data are available for April; Zaitlin 1986). Parturition peaks in May for kelp rockfish (Romero 1988; figure 17), and June for brown rockfish (Wyllie Echeverria 1987).

Distributions of back-calculated birthdates of surviving YOY shortbelly rockfish and most other common species of rockfish captured by the MWTS varied considerably among years (figure 18 and Woodbury and Ralston 1991). However, adult samples and CalCOFI fish larvae surveys indicate that the parturition season varies much less than do back-calculated birthdate distributions of YOY that survive to the pelagic juvenile stage. MacGregor (1986) showed that there was little interannual variability in the seasonal distribution of shortbelly rockfish larvae caught by CalCOFI surveys. Wyllie Echeverria (1987) summarized data on gonad state of rockfish collected between 1981 and 1985 in routine samples of commercially landed rockfish. She found that peak months of parturition for widow rockfish ranged from January to February; peak months of chilipepper parturition varied from December to February; and peak months of bocaccio parturition varied from December to March. David Woodbury (pers. comm., NMFS, 3150 Paradise Dr., Tiburon, CA 94920) was concerned that

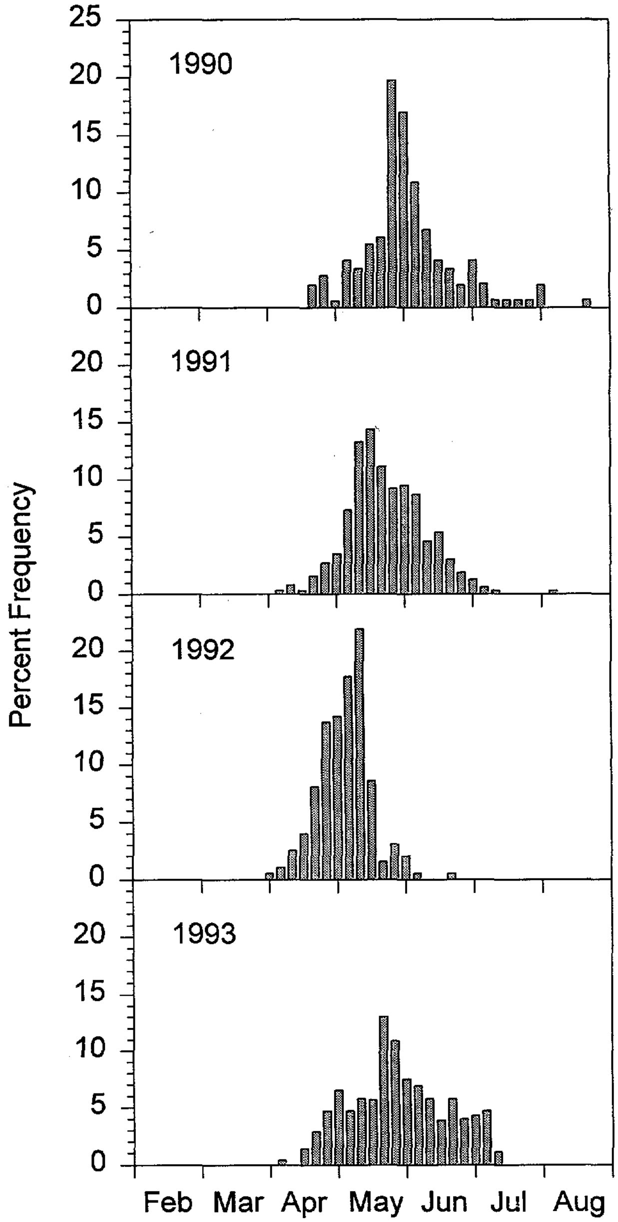

Figure 17. Back-calculated birthdate distribution of YOY kelp rockfish recruited to nearshore areas off central California, 1990–93. Fish were collected by D. VenTresca.

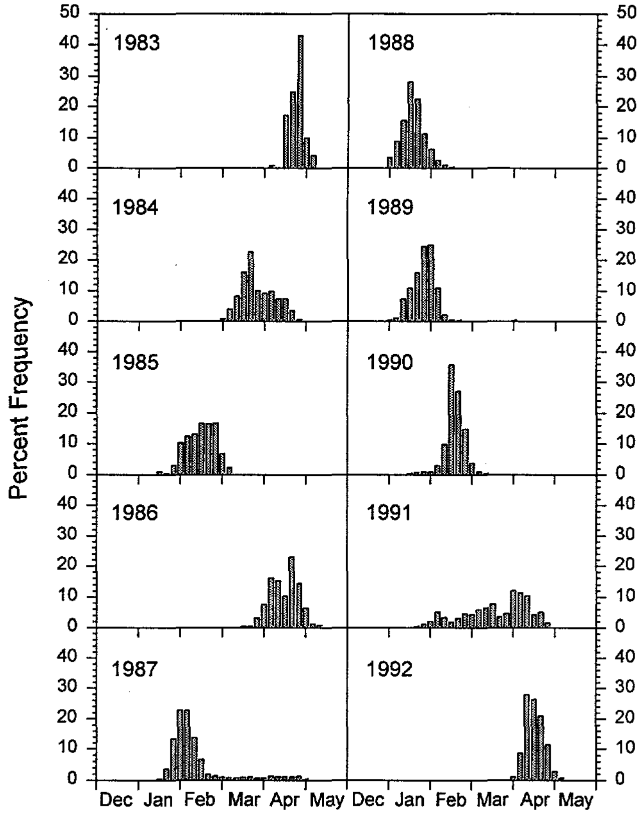

Figure 18. Back-calculated birthdate distribution of pelagic YOY shortbelly rockfish captured by the Tiburon midwater trawl survey.

sample size in the Wyllie Echeverria study was too small to adequately describe the parturition season and made a special effort to obtain chilipepper samples from commercial landings during 1990–92. He found that peak months of parturition were January and February in each of the three years. We believe that interannual variations in date-of-parturition-dependent survival rates are the primary cause of the variability in birthdate distributions shown in figure 18.

Back-calculated birthdate distributions of pelagic YOY of several important species of rockfish, including structure schoolers, covary with birthdate distributions of shortbelly rockfish (Woodbury and Ralston 1991); although these authors did not have data from the nearshore demersal group, the recent data for kelp rockfish (figure 17) indicate little interannual variability in back-calculated birthdate distributions, suggesting that the birthdate distributions of the nearshore demersal group do not covary with the structure schoolers. Survival of rockfish larvae released during January and February of 1983 and 1986 was poor (Woodbury and Ralston 1991). In those years and in 1992, most surviving shortbelly rockfish were larvae released during April (figure 18). In the other years, relatively few surviving shortbelly rockfish were released later than March.

Perhaps the seasonality of parturition is an important factor related to the interannual variation in relative reproductive success of the nearshore demersal and structure schooler groups. As previously shown, the annual primary productivity cycle started two months later than normal in Monterey Bay in 1992. Dominant prey of small larval rockfish are calanoid copepod nauplii (Sumida and Moser 1984) and calanoid copepod eggs (Bainbridge and McKay 1968). Mullin (1993) showed that food (phytoplankton) can limit egg production by calanoid copepods off California. Thus delayed phytoplankton blooms could indirectly cause failure of early-season rockfish parturition in El Niño years.

The low larval survival during the early season of El Niño years could also be related to onshore advection. There is some evidence that rockfish life-history stages are adapted to offshore waters. A summary of catches of rockfish larvae off central California by CalCOFI surveys taken during 1951–81 showed that the larvae were relatively abundant in offshore waters (Moser and Boehlert 1991). Pelagic juvenile YOY rockfish are often found off the continental shelf prior to settlement. Then they apparently undergo a behavioral change, sometimes supplemented by upwelling relaxations, that brings them onshore to settlement habitats (Larson et al. 1994). Ahlstrom (1959) found that rockfish larvae mainly occurred in the upper water column, which tends to be advected offshore in normal years.

The MWTS captured a gravid brown rockfish near the surface at a 55 m station during 1994 (pers. comm., David Woodbury). Until this capture, we had thought that adult brown rockfish were always associated with the bottom. The capture suggests that brown rockfish may swim into the upper water column to release reproductive products, as does another scorpaenid, the California scorpionfish (*Scorpaena guttata*). This species was thought to be closely associated with the bottom until Love et al. (1987) showed that it rose into the upper water column to spawn. While not conclusive, the evidence suggests that rockfish are adapted to an existence in offshore waters during their larval and pelagic juvenile phases.

Onshore advection and downwelling during El Niño events may bring young rockfish into nearshore waters that they are not adapted to, thus resulting in high mortality. Hobson and Howard (1989) found that a slightly more advanced life stage of shortbelly rockfish suffered high mortality in nearshore waters when southerly winds caused ocean currents that brought the fish inshore. The fish were apparently unable to avoid contact with the bottom. It is also possible that earlier life stages are not adapted to nearshore predators or prey.

Onshore advection is likely to be most severe during the early reproductive season, because average upwelling is weakest at that time (Bakun 1973). The high sea levels of early 1983, 1986, and 1992 (figure 4) are consistent with coastal downwelling and onshore advection.

El Niño events also appear to affect the growth and somatic condition of adult rockfish. The annual otolith growth increments in length (measured as the square root of surface area increments) of yellowtail and widow rockfish were 15%–20% lower in 1983 than in several adjacent years (pers. comm., Woodbury). Assuming that otolith growth increments are proportional to growth in body length, the decrease in annual otolith increment translates to about a 45% decrease in body-weight increment because of the cubic relationship between weight and length.

The condition of adult rockfish also deteriorated during El Niño events. We used length-specific weight as a condition measure for chilipepper, yellowtail, and blue rockfish, as did Winters and Wheeler (1994) for Atlantic herring. The specified lengths were common and sampled during each sampling period. We interpret condition as a measure of the well-being of a typical member of the species that is available to the sampling gear employed.

The condition of chilipepper was lowest during 1983 and early 1984 (about 5% below normal) and then recovered in late 1984 (figure 19). The other species were not measured for condition during 1983, although all three species had relatively low condition during 1992. Condition of yellowtail rockfish continued to be low in late 1993 through early 1994, but the condition of blue rockfish was high during the second half of 1993. Then the condition of blue rockfish deteriorated to about average levels during the first half of 1994. The condition of the three species was below average in late 1989 through early 1990, which was not during an El Niño. Condition was relatively high during 1988. Blue rockfish were not sampled until 1987. Condition for the other two species was about average during 1986, and tended to be above average for all three species during 1987. Thus the 1986–87 El Niño did not appear to adversely affect condition of the three species of rockfish. Lenarz and Wyllie Echeverria (1986) and VenTresca et al. (1995) also showed that condition of yellowtail and blue rockfish off central California deteriorated during El Niño events.

Simulated Effects of El Niño on Rockfish Population

We examined the combined effects of a severe El Niño and exploitation rates on a hypothetical population of chilipepper with a spreadsheet simulation model. We assumed that weight was reduced by 5% (as occurred in chilipepper during 1983) and that growth in weight was reduced by 45% (as occurred for widow and yellowtail rockfish in 1983). These factors were assumed to return to normal in the following year. Recruitment was assumed to be zero in the El Niño year and average in the other years. Growth, natural mortality, and the age-specific pattern of exploitation rates followed Rogers and Bence (1993). The simulation was run for three years because quotas are set at three-year intervals for some species of rockfish on the West Coast.

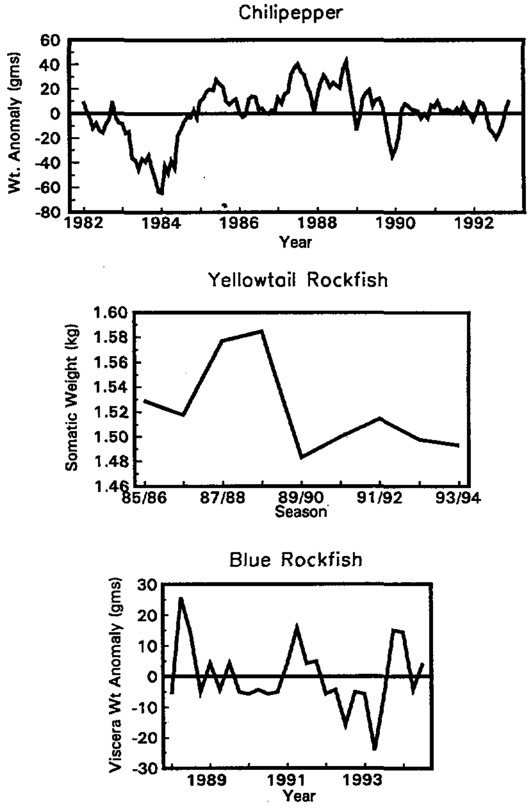

Figure 19. Weight at specified lengths for chilipepper, yellowtail rockfish, and blue rockfish. Chilipepper data are quarterly averages of monthly total weight anomalies of 400 mm fish sampled from commercial landings between San Francisco and Eureka, 1982–92. Expected weights were estimated using the methodology of Lenarz (1994). Yellowtail rockfish data are November–February averages of weight (with ovaries removed) of 400 mm female fish that were captured at Cordell Bank. Blue rockfish anomalies are deviations from quarterly averages of viscera weight without ovaries of 375 mm female fish captured in nearshore waters between Cape Mendocino and thirty miles south of Point Arena. Expected weights of blue and yellowtail rockfish were calculated by means of linear regression of log-transformed data. *Tic marks* on X-axes represent the beginning of the year.

The biomass of the stock dropped about 15% during the El Niño year (figure 20), recovered some in the next year, and then dropped as the failed year class did not replace losses due to natural and fishing mortality. Since the fishery still took the fixed quota from the reduced biomass, fishing mortality increased in the El Niño year and lowered the biomass more than would have occurred if the quota had been adjusted for El Niño conditions. Fishing mortality dropped in the following year and then increased slightly again because of the missing year class. The population was more strongly affected by

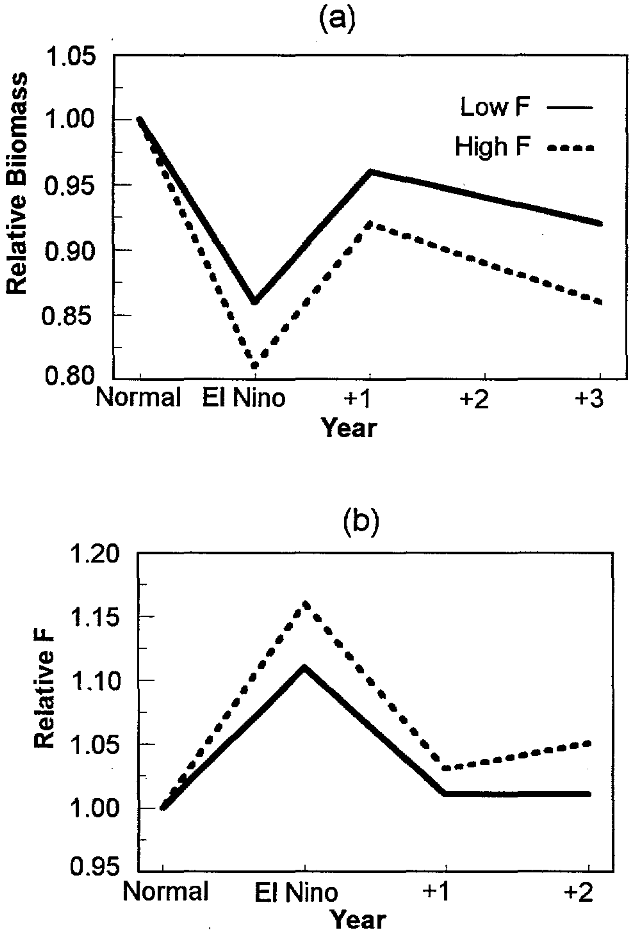

Figure 20. Results of computer simulation of how a severe El Niño would affect an exploited population of chilipepper rockfish: (*a*) relative biomass, and (*b*) relative fishing mortality (F).

El Niño when highly exploited than under low exploitation. The simulation demonstrated that fishery management practices can extend El Niño effects if harvest is not decreased in response to El Niño-related decrease in biomass.

GENERAL DISCUSSION

Physical phenomena associated with El Niño events were evident off central California during 1992–93. Temperatures were elevated, and salinities were depressed in 1992. The anomalies that appeared in 1992 remained to some degree in 1993 and 1994, with 1994 showing evidence of a return to more typical non-ENSO conditions. The observations also suggest that these anomalous conditions resulted from a combination of onshore and poleward advection, possibly combined with reduced upwelling. Although surface temperatures were equal to observations during the 1957–59 and 1982–83 events, coastal sea level was not as high during 1992–93 as during the 1982–83 event. Thus, poleward advection was probably not as strong off central California during the recent event as it was during the 1982–83 event. There was little physical evidence that the 1986–87 El Niño affected waters off central California. During this El Niño, temperature anomalies were less elevated than during the other El Niño events, and there was only a short period of high sea-level anomalies.

Physical aspects of El Niño events are better understood than biological repercussions off the West Coast; however, certain patterns are emerging. Primary productivity and zooplankton abundance appear to be reduced during El Niño events. There is considerable evidence of northward movement of southern species of fish, and some evidence of poleward advection of early life-history stages of some species. Reproductive success of most important species of rockfish tends to be poor off central California. The important early (January–February) parturition season seems to be particularly adversely affected. Condition of adult rockfish also appears to be poor off central California, similar to that of salmon off Oregon (Pearcy et al. 1985). Recruitment of southern fish was lower during the 1992–93 event than during 1982–83, and the condition of rockfish was higher during the more recent event. The 1986–87 event had little effect on either recruitment of southern fish or condition of rockfish.

Comparison of the three events indicates that the 1982–83 event was the strongest and the 1986–87 event was the weakest off central California. It appears that reproductive success of many species of rockfish off central California is very sensitive to El Niño conditions, because it was very poor during 1983, 1992, and 1986. Some El Niño physical attributes, such as elevated temperatures and depressed salinities, were still very evident off central California during the 1993 reproductive season, and rockfish reproduction was moderately successful (figure 14). Sea-level anomalies were considerably higher during the early parturition seasons of 1983, 1986, and 1992 than during 1993. Thus poleward advection or downwelling appear to be important factors in El Niño-associated rockfish reproductive failures off central California.

Just as some oceanic warm periods off the West Coast are not associated with tropical El Niño events, some of the biological characteristics observed during El Niño events off central California also occur during non-El Niño years. Rockfish condition was poor during late 1989 and early 1990. Rockfish reproduction was poor and euphausiid abundance was low during 1990. The 1989–90 event apparently also affected southern California waters. The condition of northern fur seals on San Miguel Island was relatively poor during 1990 (pers. comm., Robert DeLong, NMFS, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115).

Although oceanographers relate non-El Niño occurrences of El Niño-like physical phenomena to North Pacific atmospheric anomalies, we do not have a similar explanation for the biological events. Recognition of El Niño events and the wide geographical range of their effects has led to considerable progress toward understanding the dynamics of physical and biological ocean characteristics. The biological events of 1989–90 suggest that there may be another important oceanic regime awaiting discovery. Recognition of such a regime would give scientists another tool for understanding and perhaps predicting biological changes.

Longer time series are needed to ascertain that the El Niño–associated biological phenomena that we documented in this study are indeed common features of El Niño events off central California. The temporal sample size is small. Only a few events have been monitored. Considerably more work is required before we can do much more than speculate on the mechanisms that link the biological and physical phenomena. A better understanding of these mechanisms would reduce the variability that has hindered development of models relating fish reproduction success to adult population size and environmental factors. Much of the uncertainty in providing scientific advice on management of fisheries is due to a poor understanding of the recruitment process. Thus a better understanding of the mechanisms that link the biological and physical phenomena would have considerable pragmatic implications.

ACKNOWLEDGMENTS

We are thankful to many colleagues who were involved in the research programs that collected and compiled data used in this paper. We specifically mention some in order to document sources of data, but many more contributed. P. Walker (Scripps Institution of Oceanography, La Jolla, CA) provided Farallon Islands temperature data. H. Parker (Pacific Fisheries Environmental Group, Monterey, CA) provided upwelling index data. G. Mitchum (University of Hawaii, Honolulu, HI) provided sea-level data. R. Lynn (NMFS, La Jolla) provided CTD data collected by the pre-FORAGE cruise. K. Sakuma (NMFS, Tiburon, CA) provided the remaining CTD data and prepared the vertical section figures. D. Roberts (NMFS, Tiburon) provided the YOY rockfish catch data. D. Woodbury (NMFS, Tiburon) provided the YOY rockfish age data. M. Eldridge and E. Hobson (NMFS, Tiburon) provided data on condition of yellowtail and blue rockfish. We owe considerable thanks to S. Ralston (NMFS, Tiburon) for suggesting several references, acting as a sounding board, and reviewing the paper. We also thank M. Eldridge, E. Hobson, D. Woodbury, and three anonymous reviewers for their constructive reviews of the paper.

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A WARM DECADE IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

The year 1992 in the Southern California Bight is embedded in a 17-year warm anomaly which is the longest in the 1922–94 period. The length of the warm anomaly may make it more useful for studying the effects of global change on fish with generation times of 5 years than the usual ENSO event lasting 1–3 years. The trend since 1985 of zooplankton volume and anchovy spawning biomass has been downward, and that of sardine has been upward. Although the trends in the growth rates of fish populations can be observed, the causes result from the combined effects of the environment in the absence of a significant fishery. Directed, long-term, process-oriented research on the anchovy and the more subtropical sardine is needed to "explain" differences in population growth rates: incidental data from static monitoring and fish stock assessment are necessary but will not likely be sufficient to construct combined effects of temperature and zooplankton on population growth rates of sardine and anchovy.

INTRODUCTION

The Southern California Bight (SCB) is a partially isolated habitat within the California Current region. Topographically, the outer margin of the SCB is a ridge which extends southerly from Point Conception to Cortez Bank offshore of the Mexican border. Hydrographically, the California Current jet veers to the Mexican coastline west and south of the SCB. The interior of the SCB contains a semipermanent cyclonic gyre which flows among several islands and shoals and over several deeper, isolated basins. It is an important spawning habitat for both the central stock of the northern anchovy and the northern stock of the Pacific sardine (Ahlstrom 1967).

Temperature change can be expected to cause many biological changes (Fields et al. 1993) and to implicate other kinds of important change. For example, in 1992, during a warm spell, the Pacific sardine appeared in abundance for the first time in four decades off Vancouver Island, British Columbia (Hargreaves et al. 1994). Biologically, the SCB is a spawning and retention area for young fish, including sardines (MacCall 1990). During some El Niño/Southern Oscillation (ENSO) events, dominant plankton in the SCB react differently relative to the rest of the adjacent coastal waters (Colebrook 1977; Smith 1985; Jackson 1986).

Considerable monitoring activity at the urbanized coast of the SCB extends more than a century into the past (Hubbs and Roden 1964; Eppley et al. 1978; Smith and Eppley 1982; Dailey et al. 1993). Scripps Institution of Oceanography Pier (SIO Pier) temperature and salinity measurements have been conducted daily since 1916. Temperatures at the SIO Pier have been analyzed at hourly, weekly, and seasonal scales (List and Koh 1976; Piñeda 1991, 1994). Temperature changes at the SIO Pier are representative of coastwide temperatures at time scales longer than weeks. Interannual temperature anomalies at the SIO Pier represent anomalies over adjacent ocean areas in the northeast Pacific Ocean (Mooers et al. 1986; Latif and Barnett 1994). Biological oceanography surveys to find the cause of the collapse of the Pacific sardine in the California Current region began in the 1940s (Bernal 1981).

The purpose of this report is to describe the SCB in the last decade (1985–94) with comparison to the long-term record of the SIO Pier and to the 45-year record of CalCOFI measurements in the SCB.

SOURCES OF DATA

The sources of data are the SIO Pier measurements initiated in 1916 and the measurements of surface temperature and salinity and epipelagic zooplankton volume from the CalCOFI surveys that have been conducted in the SCB, among other areas, since 1951.

The monthly temperature anomalies for the recent period are referred to a 50-year series (1940–93) of monthly means of daily temperature measurements from the SIO Pier. The longer-term fluctuations are shown in a 24-month running mean.

The anomalies of CalCOFI survey station temperatures and salinities are assembled from incomplete time series because of the vagaries of ship scheduling, timing, policy, and availability of ship time. As opposed to the SIO Pier, where 30 measurements are taken per month with no direct spatial averaging, no CalCOFI station was sampled more than once a month, and the anomalies are assembled as a spatial average over a 16,000 sq. n. mi. region—Morro Bay (CalCOFI line 76.7) to San Diego (CalCOFI line 93.3) and offshore 120 n. mi. (CalCOFI station 70)—in which the SIO Pier is at the southeastern periphery. There have been no studies of how missing years, months, and stations affect the utility of these anomalies.

The biomass assessments of sardine and anchovy used for fisheries management are available only from 1985 to 1994 (Barnes et al. 1992; Jacobson et al. 1994; revisions and updates—L. D. Jacobson, SWFSC, pers. comm. July 6, 1994, and January 3, 1995). The more recent estimates are subject to annual revision based on new data from surveys and from the fisheries.

BIGHT WARMING

The SIO Pier recent period represents 17 years of positive anomaly which began in 1977 and reached a local minimum in 1987. From this assembly, it appears that the recent period is the longest warm anomaly in the 1922–94 period and exceeds the duration of the 15-year cold anomaly of 1942–57 (figure 1). Although the subject warm spell is marginally warmer than the 1957–59 and the 1982–83 warm periods, there was more contrast in the 1957–59 period, which emerged from the surrounding cold spell.

Annual averages from the CalCOFI surveys (figure 2) exhibit a 2-degree range. All annual averages since 1983 have been well above 15 degrees and approach the maximum 17 degrees in 1992 for the surveyed interval 1951–94. The mean temperature for the SCB CalCOFI surveys is 15.2 degrees, and the standard deviation is 2.2 degrees. Some differences with the SIO Pier anomalies can be noted in figure 3. Some of the difference can be explained by the years in which cruises were missing or quarterly rather than monthly from 1961 to the end of the record. Missing data are plotted as "zero" anomalies. The major features of the SIO Pier anomaly are reproduced in the CalCOFI surface-temperature data.

The plankton displacement volume determined by CalCOFI surveys has been noted to be inversely related to temperature (Reid et al. 1958; Reid 1962). The general effect can be seen in figure 4. Particularly notable are the low values in 1958–59 and the declining trend from 1972 through 1994, with the values of 1991–94 comparable to the low values of 1958–59. When the mean value of 221 ml per 1000 m^3 and standard deviation of 400 ml per 1000 m^3 are plotted as anomalies (figure 5) the inverse relationship to temperature is clear.

The long-term record of salinity anomalies from SIO Pier (figure 6) illustrates the unusual nature of the recent years. The low salinity of 1992 is materially lower

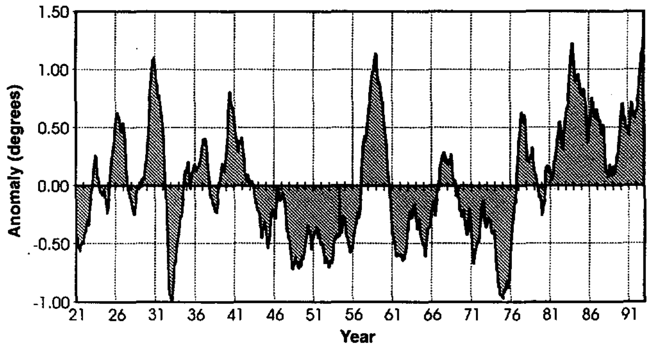

Figure 1. SIO Pier temperature anomaly, smoothed with a 24-month running average.

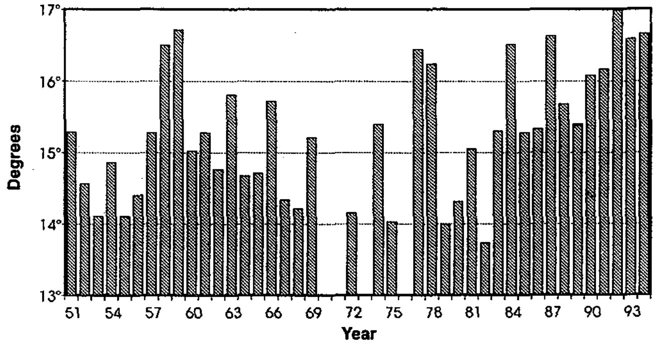

Figure 2. CalCOFI survey 10-meter temperatures.

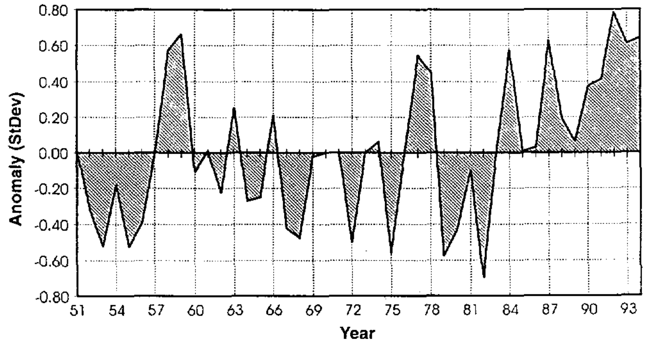

Figure 3. CalCOFI survey 10-meter anomalies: mean 15.2°C., standard deviation 2.2°C. Missing years shown as 0 anomaly.

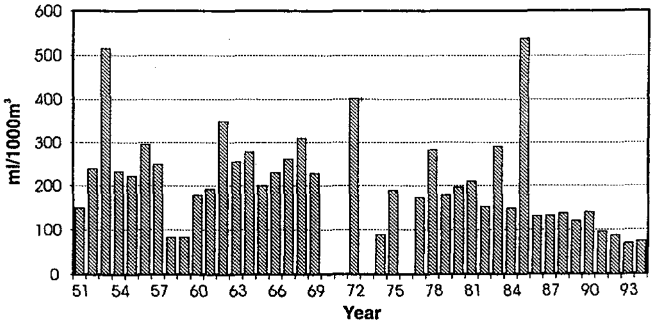

Figure 4. CalCOFI survey plankton volume in ml per 1000 cubic meters.

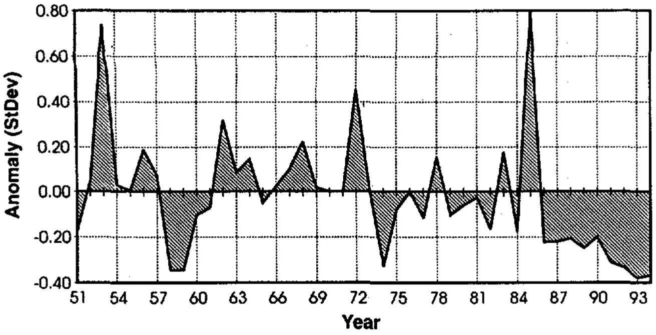

Figure 5. CalCOFI survey plankton volume anomalies: mean 221 ml, standard deviation, 400 ml. Missing years shown as 0 anomaly.

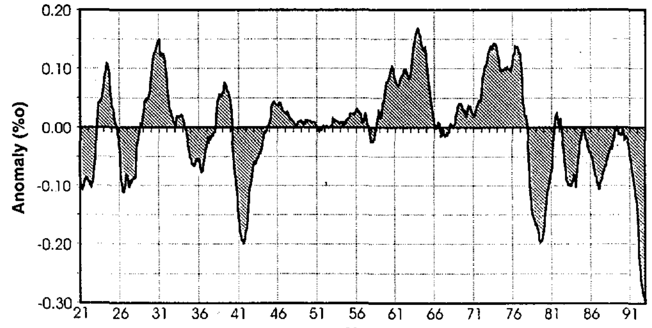

Figure 6. SIO Pier salinity anomaly, smoothed with a 24-month running average.

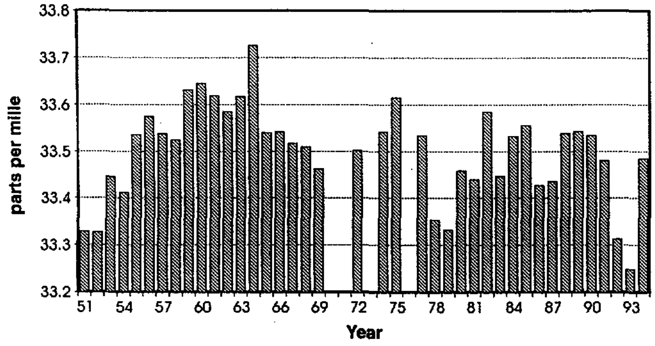

Figure 7. CalCOFI survey 10-meter salinities.

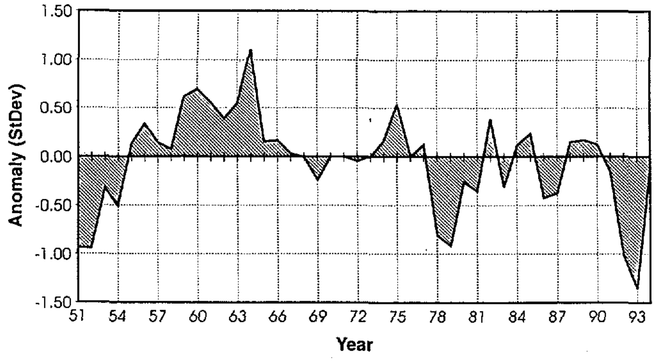

Figure 8. CalCOFI survey 10-meter salinity anomalies: mean 33.51 parts per thousand, standard deviation 0.19 parts per thousand. Missing years shown as 0 anomaly.

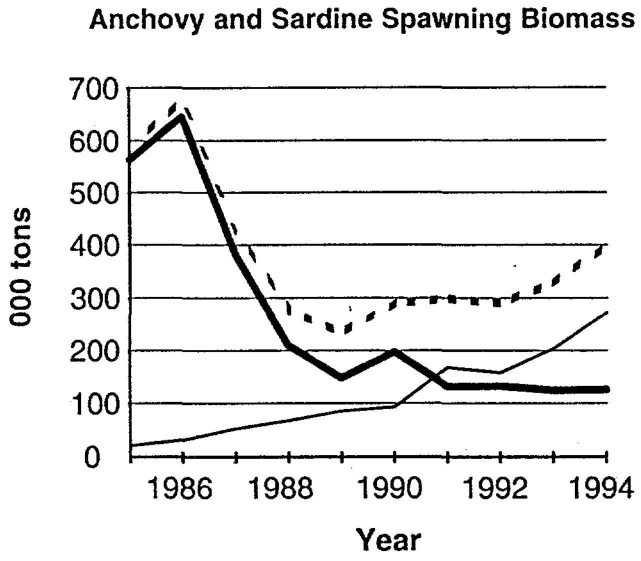

Figure 9. Trends in spawning biomass in thousands of metric tons of anchovy (*heavy solid line*), sardine (*light solid line*), and the two species combined (*dashed line*).

in this assembly than in any previously measured period. This trend is reversed only in 1994 from the CalCOFI survey record (figure 7) and anomalies (figure 8). The mean salinity for the SCB since 1951 is 33.51 ppt; the standard deviation is 0.19.

Between 1985 and 1991, northern anchovy spawning biomass decreased from 600,000 metric tons to about 125,000 metric tons, where it has remained through 1994 (figure 9). During the period of decline the rate was 0.8 (Lambda), which is well within population growth and decline rates originating in early life history, but not juvenile and adult parameters (Butler et al. 1993). Although measured with less precision, the standing crop of anchovy larvae diminished at a similar rate (figure 10). The fishing mortality during this interval ranged from 0 to .2 and averaged .1 (Jacobson et al. 1994).

The rate of population change in Pacific sardine has continued steadily from 1985 to 1994 from less than 20,000 metric tons to slightly less than 300,000 metric tons (figure 9). The standing crop of sardine larvae, although measured with very low precision, increased at a similar rate (figure 10). The population growth rate was 1.3, which is close to the theoretical maximum rate of change (Murphy 1967) of 1.5 (Lambda). This rate of change is well within the range examined by Butler et al. (1993) for early life-history population parameters.

The joint minimum of spawning biomass of anchovy and sardine populations was reached in 1989, after which the joint biomass increased at about 6 percent per year (Lambda = 1.06; figure 9). It is not certain that the individual estimates of spawning biomass are precise enough

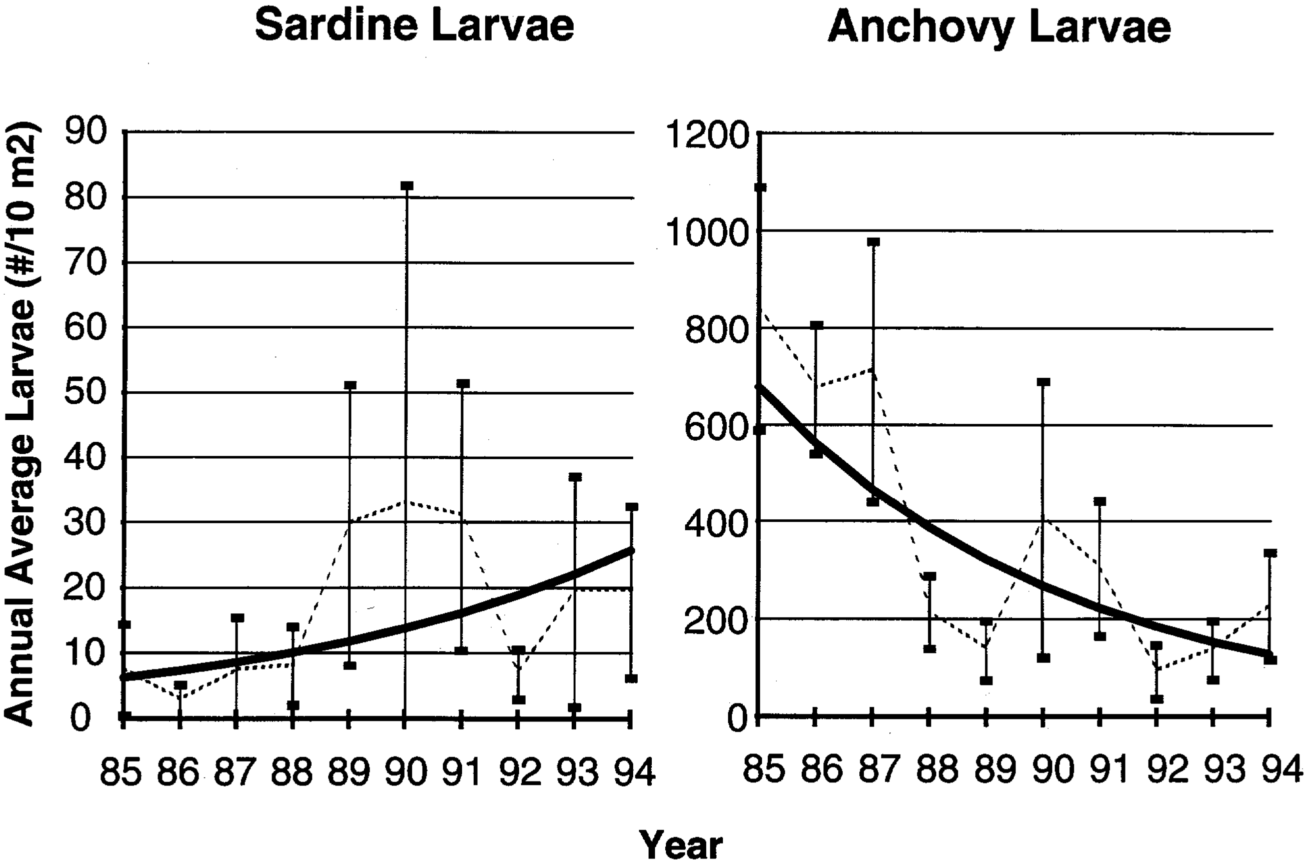

Figure 10. Trends in standing crop of sardine and anchovy larvae. The *dashed line* connects the means of successive years, and the *error bars* are plus or minus two standard errors. The *trend lines* are fitted to exponential models. The rate of increase of sardine larvae is 17 percent per year (Lambda = 1.17), while the adult spawning biomass increases at 31 percent per year over this period. The trend in anchovy larvae and spawning biomass is the same, decreasing at 17 percent per year.

to document an increase in the joint biomass density of these two planktivores inhabiting the SCB.

Annual change of surface temperature and zooplankton volume at the same sites evaluated for sardine and anchovy larvae are shown in figures 11 and 12. The temperature curve shows a linear and gradual increase in temperature, usually within the two standard error bands. The 1987 and 1992 values are more than 0.6 degree above the trend, and only 1989 is materially lower than the trend. The zooplankton shows a precipitous drop in 1985 followed by a gradual decline. Reid (1962) also noted the inverse trend in zooplankton and temperature.

DISCUSSION

If we assume that the warming of 1992 is one reason why the more subtropical fish—sardine—gained biomass in the last ten years and why the temperate fish—anchovy—lost biomass over the same period (figure 9), it is interesting to speculate on the many mechanisms that would involve temperature change. It is outside the scope of this report to completely analyze how temperature affects sardine and anchovy, but describing some direct and indirect effects may be sufficient. Current information would not support arguments for either competition or habitat replacement. In the competition scenario, limited food production at primary and secondary stages will support a trophically limited biomass of sardine, anchovy, and all the other herbivores and carnivores of planktonic forms. Under the habitat replacement argument, the anchovy and sardine occupy distinctive habitats which coexist variously in time and space within the SCB and adjacent areas.

It seems clear that sardine and anchovy populations are changing within the SCB and adjacent habitats. Although the SCB is open habitat, it is interesting to describe some direct and indirect mechanisms other than migration that could contribute to population change. Under direct effects I include incubation, maturation, gut evacuation, and viscosity (in increasing order of speculation). Under indirect effects I include primary production, expatriation, and exotic predators (all equally speculative).

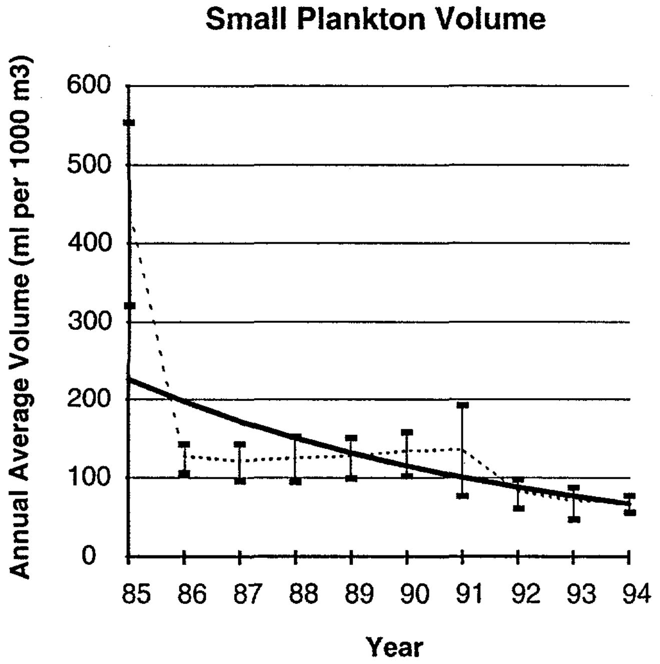

Figure 11. A linear trend in average annual surface temperature taken on the same CalCOFI cruises as the zooplankton and fish larvae are collected. The mean rate of temperature rise is about 0.17 degrees per year. The *error bars* represent plus or minus 2 standard errors of the mean.

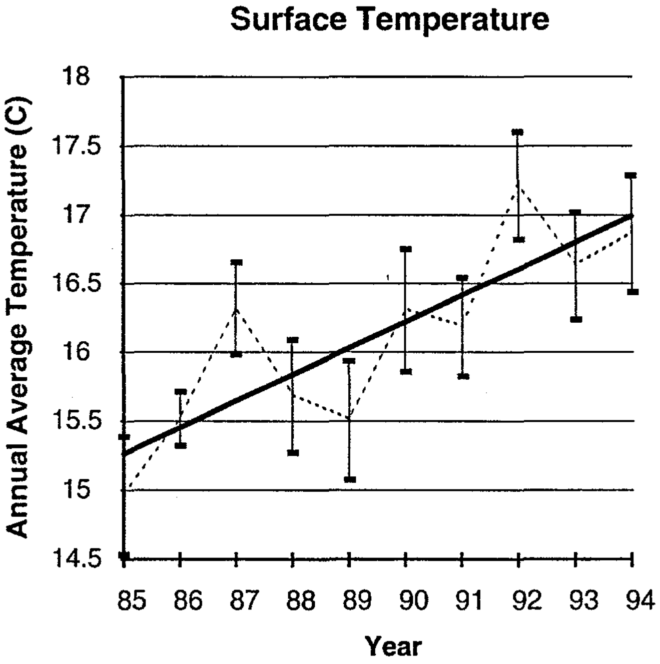

Figure 12. A decadal trend in zooplankton displacement volume. The smooth rate of exponential decline is about 13 percent per year (Lambda = 0.87).

Direct Effects

Incubation. The duration of the embryonic period of sardine and anchovy is directly and probably exclusively controlled by temperature (Zweifel and Lasker 1976). If all other parameters of the life cycle remain the same, a sardine population at equilibrium at a temperature of 15.5°C will increase at a rate of 10 percent per year at 16.4°C owing to the effects of more rapid hatching and proceeding to first feeding, which marks the end of the embryonic period (Butler et al. 1993). The positive effect in this case is shortening the time of high mortality as embryos and proceeding to the larval stages and beyond, where mortality is less. Similarly, anchovy at equilibrium at a temperature of 14.5°C will increase at a rate of 10 percent per year at 15.0°C owing to the effects of more rapid hatching and proceeding to first feeding (the end of the embryonic period). The equilibrium temperature for anchovy would cause, all other things being equal, a 10 percent annual decline in sardine numbers. These effects are at temperatures well above the sardine and anchovy embryo lethal limits of 13 and 12 degrees C, respectively.

Maturation. Methot (1989) used a temperature function to describe the maturation rate of young adult anchovy. Jacobson et al. (1994) have erected a simpler model which includes January–February SIO Pier temperatures as a proxy for the temperature at which juvenile anchovies develop. The fraction of 1-year-old anchovies mature declines in temperatures below 14.5°. Jacobson and MacCall (in press) find that sustained ("mean five-season") temperatures above 16.5° are required to sustain significant catches from Pacific sardine stocks available to California.

Gut evacuation. In the larval stage, the temperature effect on feeding and the rate of assimilation of food could be important. An individual larva must consume nearly its weight each day (Theilacker and Dorsey 1980). Because the larval anchovy is a visual feeder, feeding must be done in the daylight hours. For most anchovy larvae, spawned in winter, the feeding period may be materially less than 12 hours.

Viscous resistance. Temperature affects viscosity and the energy that early larvae exert in locomotion and subcutaneous exchange of respiratory and excretory products with the medium. I would expect the subcutaneous exchange with the medium to decrease rapidly as larvae differentiate specialized organs, and I would expect the locomotory resistance to gain in relative importance. The Reynolds number for resistance to searching for food and particularly avoiding predation is in transition (Weihs, pers. comm. 1994) from viscosity dominated at 4 mm to inertia dominated at 40 mm. Since the direct temperature effect is primarily mediated through viscosity, the temperature effects will diminish with the larvae's somatic growth and differentiation of specialized respiratory and excretory systems.

Indirect Effects

Primary production. Since rapid growth is a requirement for high survival and population growth in anchovy and sardine, the temperature influence on population growth would be substantial for these coastal fishes. Transport and vertical distribution of nutrients are the principal effects (Ware and Thomson 1991).

Expatriation. The transport of coastal larvae out of the habitat where they can survive may constitute the major drawback to increased new production as favoring population growth of anchovy and sardine. Thus, either increased transport from the subarctic or increased Ekman transport offshore could move larvae from coastal habitats to areas of the ocean where oceanic water is mixing (Roy et al. 1992). In the present warm spell, warming might indicate shallow upwelling (Roemmich and McGowan 1995a, b), low vertical mixing, low California Current transport (Roemmich 1992), or low offshore Ekman transport, each favoring additional retention of planktonic stages and the resultant population growth of sardines and anchovy and other residents of the SCB.

Exotic predators. As warming proceeds, some large, mobile, tropical predators may move northward along the coast of California and increase the mortality of anchovy to a greater degree than the mortality of larger sardine. For example, the subtropical yellowtail, Pacific mackerel, and bonito, and the tropical tunas—skipjack and yellowfin—could represent significant additional sources of mortality for juvenile and adult sardines and anchovy.

RECOMMENDATION

The warming of 1992 may itself be less important than the fact that it follows a sustained warm spell. Even more important to the productivity of the SCB, the warming was accompanied by low salinities, from which Roemmich and McGowan (1995a) infer a flow of nutrient-deficient water into the SCB. So in addition to recommending continued monitoring of the SIO Pier temperature, I suggest that the CalCOFI surveys continue to measure sections of temperature, salinity, nutrients, and zooplankton volume in order to interpret the more continuous records of temperature and salinity from the SIO Pier.

SUMMARY

Because of the diverse mechanisms influencing the population growth of stocks of anchovy and sardines that spawn in the SCB, it does not seem likely that surveys for stock assessment and static monitoring of the environment will permit definitive explanations for population change: directed process studies may be necessary to identify the mechanisms which alone and in combination effect population change in SCB fishes.

Although many of the biological effects of the warm spell of 1992 in the Southern California Bight cannot yet be analyzed, there is a major distinction between this period and the earlier warm spells: the zooplankton volume is no lower than the 1958–59 annual average values (figure 5), but the 1992–93 low plankton and high temperature values result from a decadal sustained increase in temperature (figure 11) and a similarly long decrease in plankton (figure 12).

The relatively brief episodes of ENSO warming in earlier decades may have had less effect on the longer-lived organisms than the current sustained period.

ACKNOWLEDGMENTS

I am much obliged to that long list of responsible technicians who have taken, over the past 45 years, the measurements used and cited in this study. I am particularly grateful to their current-day representatives—Connie Fey, Sherry Gripp, and Amy Hays—who provided me with up-to-date values of salinity, temperature, and zooplankton volume to complete this paper. I am also grateful to Geoff Moser, Loren Haury, Tom Powell, John McGowan, Frank Schwing, Dean Roemmich, Tom Hayward, and Ron Lynn for discussions on the topic of climatic change on the local and regional space scales at interannual to multidecadal time scales. I thank Frank Schwing and Steve Ralston for the invitation to speak at this CalCOFI symposium, and I thank John McGowan and Ron Lynn for editing the manuscript. I am also in debt to unnamed reviewers for improving the focus of this manuscript. The faults that remain are my own.

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THE EFFECTS OF THE 1992 EL NIÑO ON THE FISHERIES OF BAJA CALIFORNIA, MEXICO

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ABSTRACT

The 1992 El Niño affected the landings and distribution of several commercial and sport fisheries of Baja California, Mexico. Pacific mackerel, yellowtail, swordfish, and giant squid showed clear changes in seasonality (early fishing seasons). Increased landings of tropical roosterfish, dolphin, and marlin were reported in the recreational fisheries. Increased landings of northern anchovy and Pacific mackerel, and decreased landings of yellowtail and swordfish in Baja California waters may have been due to changes in availability under warm El Niño conditions.

INTRODUCTION

The state of Baja California is located in the northwestern part of Mexico (figure 1). Its fisheries exploit resources from the Pacific Ocean and the Gulf of California. In 1991, landings in Baja California were 231,319 MT, or 15.6% of the total Mexican production, and second only to the state of Sonora (25.4%; Anonymous 1992). The most important species in the total landings were yellowfin tuna (*Thunnus albacares*), skipjack tuna (*Euthynnus pelamis*), giant kelp (*Macrocystis pyrifera*), Pacific mackerel (*Scomber japonicus*), Pacific sardine (*Sardinops sagax caeruleus*), and red sea urchin (*Strongylocentrotus fransiscanus*). The tuna species, however, are mostly caught in waters south of state limits.

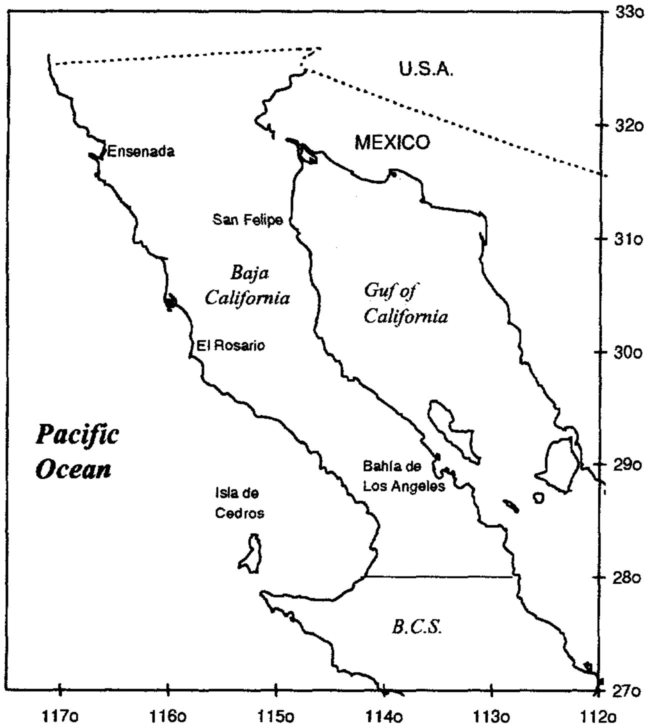

Figure 1. Map of Baja California, Mexico, showing the locations of the fishery offices for catch reporting.

The western coast of Baja California is part of the California Current system. In this system an association between the California Current and prevailing northerly winds produces upwelling along the U.S. Pacific coast, from the Canadian border to Baja California and beyond (Mann and Lazier 1991). Upwelling off the Pacific shore of the Baja California peninsula is strongest during spring and summer on the southern sides of land extensions (Hubbs and Roden 1964).

The fish fauna of the California Current changes dramatically under El Niño Southern Oscillation (ENSO) conditions (Hayward 1993). Pearcy and Schoener (1987) reported that the very strong 1982–83 El Niño was implicated in northern range extensions and shifts in population distributions of many species of marine organisms from Oregon to Alaska during 1983. Radovich (1960) discussed the redistribution of fishes during the 1957–58 El Niño event.

In the North Pacific basin as a whole, an ENSO episode has been associated with a counterclockwise range extension; many species have been reported farther north than usual on the west coast of North America, and farther south than usual on the coast of Japan (Mann and Lazier 1991). These changes in distribution, especially for the southern species typically found in warm waters, are presumably due to a combination of advection and a changed habitat structure (Hayward 1993).

For some fisheries, especially pelagic fisheries, El Niño can be catastrophic (Cushing 1982; Smith 1985). But warm periods benefit commercial and recreational fisheries for some species off southern California. During El Niño conditions, subtropical and tropical species such as yellowtail (*Seriola dorsalis*), California barracuda (*Sphyraena argentea*), Pacific bonito (*Sarda chiliensis*), skipjack tuna, yellowfin tuna, and dolphin (*Coryphaena* *hippurus*) become more available to northern fisheries (Radovich 1960; Squires 1987).

Although the 1983–84 El Niño event was characterized as the strongest of the century (Norton et al. 1985), the period from 1991 to 1993 was one of the longest continuously warm episodes recorded, and was only the third time during the 1900s that mature ENSO conditions were observed in consecutive winter and spring seasons; previous periods were 1911–13 and 1939–41 (Bell and Halpert 1995).

Earlier workers focused on El Niño effects on the distribution of fish in the California Current north of the U.S.–Mexico border. In this paper we review and summarize the monthly landings data reported from different fisheries in the state of Baja California, Mexico, from 1984 to 1993, and use changes in monthly and annual landings to qualitatively examine how the 1992 El Niño may have affected resource availability in time and space.

METHODS AND MATERIALS

Daily surface temperature data from Scripps Pier, La Jolla, Calif. (32°52.0'N, 117°15.5'W) were analyzed for 1980–93 to represent the development and relaxation of El Niño near the Baja California coast. Monthly means were calculated, and the monthly time series was adjusted for seasonality; a smoothed trend cycle was determined with a Henderson curve moving average (Statsoft 1994).

Monthly commercial landing records for Baja California during 1984 and 1993 were reviewed from logbooks, inspection sheets, and data files maintained at the Baja California Fisheries Delegation of the ex-Secretary of Fisheries (Ave. Lopez Mateus, Ensenada, Baja California). Monthly data for previous years were not available. Commercial vessels are required to keep a fishing log and inform the local fisheries office of their landings. Inspectors also collect information from small-boat operators who fish along the coast.

Official fisheries offices are at Tijuana (0.08% total state landings during 1984–93), Ensenada (94.58%), El Rosario (1.81%), and Isla de Cedros (2.27%) on the Pacific coast, and at Mexicali (0.12%), San Felipe (0.85%), and Bahía de Los Angeles (0.29%) in the Gulf of California (figure 1). We did not include data from Tijuana and Mexicali in our study because those reports include freshwater species and fish landed but not reported at the other offices; we do not expect this to produce a significant bias in the data.

We examined the database for inconsistencies in common names and in data reporting. For example, in some years, it was clear that certain sport species were not reported officially at all, but the sport fisheries logbooks did record catches. Our annual data are based on the sum of the corrected monthly data in our combined database, and may differ from the official reports in FAO and Mexican fisheries yearbooks because they may not have used the same criteria for data correction from monthly records, or the same common name–species name equivalencies. It was clear that errors due to changes in common name from one region to another increase when data summary is carried out far from the geographic region where fish are landed (for example, Mexico City or Rome). Furthermore, for yearbooks, landings are converted to live weight; in this paper we report landed weight.

Qualitative data from the sport fisheries at Ensenada were collected through interviews with four vessel operators and two seamen who move between the twelve vessels of the Ensenada sport fleet. Raw data sheets for commercial landings were reviewed to find tropical species that may have been specified as "others" in the data summary sheets and files.

We reviewed the monthly landings during 1984–93 to investigate the possibility of changes in seasonality. The monthly time series for several species had large gaps, which made seasonal analysis impossible. For 1992 no landings were reported for the California barracuda (*Sphyraena argentea*), and although an El Niño effect on this species has been reported in other works, analysis was not possible. Species regulated with strict fishing seasons were also not analyzed (e.g., lobsters, sea urchin, abalone).

Fishing effort data were not available, so we were unable to estimate catch per unit of effort as an index of relative abundance.

RESULTS AND DISCUSSION

Figure 2 shows the seasonally adjusted time series of monthly average SST at Scripps Pier, and the final Henderson curve trend cycle. Although SST off Baja and southern California did not warm as much as during the 1983–84 El Niño event, the 1992 El Niño was

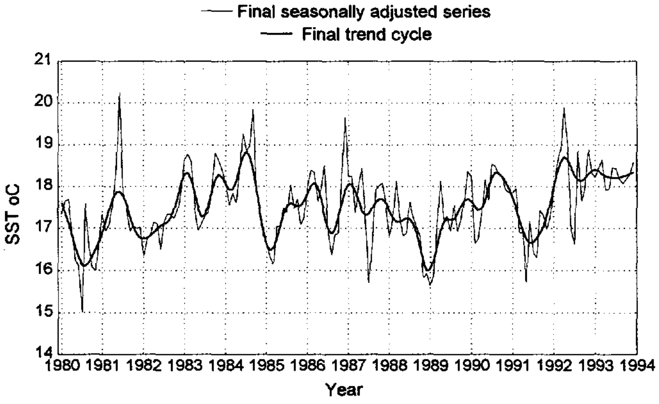

Figure 2. Mean monthly SST at Scripps Pier, La Jolla, Calif., adjusted for seasonality. The *heavy line* is the Henderson curve final trend cycle.

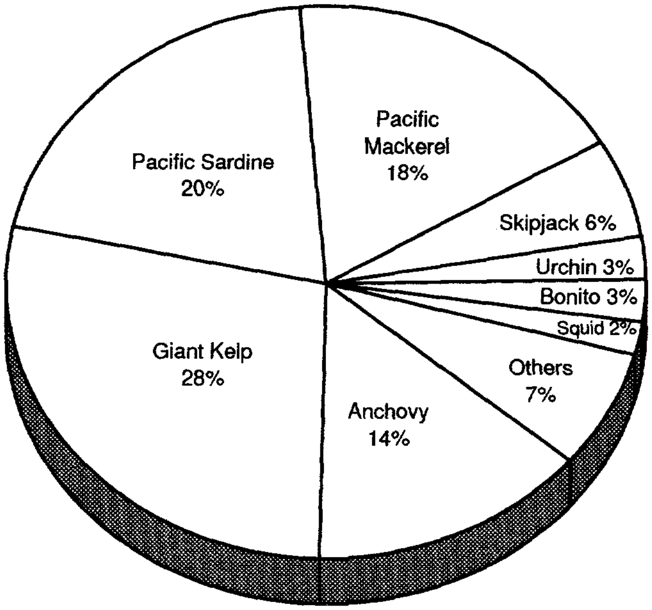

Figure 3. Species composition for the Baja California fisheries, 1989–93.

the strongest since then, with average monthly SST above 18°C, conditions which continued into 1994.

After combining all data sources, correcting for duplicated and synonymous species common names, and eliminating freshwater and newly cultured species, we had 99 marine species for analysis.

We determined the species composition for the five-year period (1989–93) to show the current status of the Baja California fisheries. We eliminated yellowfin tuna from the total because, although Ensenada has been an important port for tuna landings, fishing is done in waters south of the state boundary. Thus during 1989–93 giant kelp represented the greatest landed biomass (28%), followed by Pacific sardine (20%) and Pacific mackerel (18%). Northern anchovy, previously the most important fishery, decreased rapidly after 1989 and represented only 14% (figure 3).

During 1992, the landings of several species increased while others decreased, as occurs each year, and few patterns with El Niño were found. This may be partly due to the shortness of the time series relative to the occurrence of an El Niño event, and to the lack of effort data. Monthly data for previous years were not available. Table 1 shows the yearly landings from 1984 to 1993 for 13 selected species, in alphabetical order.

Species with Increased Landings

The landings of giant kelp ("sargazo"; *Macrosystis pyrifera*) surprisingly increased during 1992, although it is known that this cold-water species can be severely affected by El Niño (Dayton and Tegner 1990). Kelp landings decreased during 1984 and 1987, suggesting an El Niño effect not observed during 1992. We feel that this result is an artifact of a one-vessel fleet that cannot fully exploit the available kelp beds along the coast of Baja California. Unusual beaching of kelp (observed during 1983–84) was not reported during this period, and there is no evidence that survival was affected.

The northern anchovy ("anchoveta"; *Engraulis mordax*), almost nonexistent since 1989, increased from 340 MT in 1991 to 1785 MT in 1992. We included this species because the change in landings was remarkable. The northern anchovy is a temperate species that prefers cooler waters, so the observed increase in 1992 may be due to concentration in areas of local upwelling. Hammann and Cisneros-Mata (1989) suggested distribution changes due to the La Niña event of 1985 as a mechanism for the northern anchovy to expand its range into the Gulf of California.

Although the Pacific sardine ("sardina monterrey"; *Sardinops sagax caeruleus*) increased during 1992, the recent population recovery already described by several authors (Barnes et al. 1992; Lluch-Belda et al. 1992; Wolf 1992) is sufficient explanation. Landings also increased in California (CDFG 1994).

TABLE 1
Yearly Landings for Selected Marine Resources in Baja California, Mexico, 1984–1993 (Metric Tons)

Species	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
California sheepshead	31.35	4.64	6.55	11.29	18.05	9.19	14.18	12.36	33.06	19.49
Giant kelp	12,673.00	27,823.00	36,502.00	23,147.00	33,624.00	34,247.00	39,575.57	29,931.30	39,919.00	31,245.00
Giant squid	35.82	8.50	19.86	10.52	1,331.77	856.59	2,663.85	6,331.81	1,663.19	1.27
Marine snails	5.65	0.14	1.45	0.60	39.68	142.81	119.18	66.44	150.33	104.48
Northern anchovy	101,547.35	118,045.91	93,053.15	129,662.03	123,804.87	84,653.40	48.86	340.36	1,784.84	144.64
Pacific mackerel	2,106.31	7,355.39	9,114.33	3,295.37	8,946.99	16,134.64	39,502.80	18,690.05	24,529.28	10,639.48
Pacific sardine	1,521.10	8,747.47	3,273.00	5,121.13	2,563.00	7,546.24	13,248.65	30,077.14	34,866.35	38,917.91
Pismo clam	658.21	70.34	91.75	171.17	615.94	588.99	499.87	797.25	929.87	228.27
Red sea urchin	157.04	744.82	3,296.91	2,929.91	6,737.00	4,643.73	3,493.80	2,598.71	2,397.65	2,746.50
Sea bass	45.12	56.09	60.77	45.68	97.76	54.35	33.96	36.96	17.30	35.11
Striped mullet	204.17	238.77	159.39	172.38	367.84	251.21	72.02	94.68	35.73	92.87
Swordfish	37.44	2.15	286.76	425.46	633.76	406.84	632.68	829.69	554.26	384.64
Yellowtail	938.76	389.21	353.49	456.42	1,849.31	519.07	253.19	174.64	113.87	133.81

Pacific mackerel ("macarela"; *Scomber japonicus*) landings, after having fallen off during 1991, increased sharply during 1992 and decreased during 1993. Landings in California have decreased since 1990 (CDFG 1994), and the population biomass has decreased to less than 100,000 short tons since 1982 because of low recruitment (Jacobson et al. 1994). Increased landings in Mexico during 1992 may have been due to increased availability as a response to the warm El Niño conditions.

The Pismo clam ("almeja pismo"; *Tivela stultorum*), California sheepshead ("vieja"; *Semicossyphus pulcher*), and marine snails ("caracol panocha" and "caracol chino") increased in landings, with effort apparently similar to that of previous years. Limpets and snails are mostly used as bait for the lobster ("langosta") fishery. Although these increased landings were striking, it is difficult to attribute them to El Niño conditions with the information available.

In the 1992 recreational fishery, higher landings were found for roosterfish ("pez gallo"; *Nematistius pectoralis*), dolphin ("dorado"; *Coryphaena hippurus*), and (mostly striped) marlin ("marlin"; *Tetrapturus audax*). These species are not clearly documented in the database, but are reported in port interviews and private logs. The incidence of tropical, migratory, large pelagic species in temperate waters during an El Niño event has been previously documented (Radovich 1960; Squires 1987).

Species with Decreased Landings

Landings of the red sea urchin (*Strongylocentrotus franciscanus*) decreased during 1992. Landings also decreased during the 1984 and 1987 El Niño events, suggesting a connection with El Niño. Table 1 shows that kelp and sea urchin landings generally fluctuate together; sea urchin is one of the major grazers on giant kelp (Leighton 1971). It may be that the kelp was affected by El Niño, as suggested by the decrease in sea urchin landings, and that the one-vessel landing data for kelp do not reflect abundance.

Giant squid ("calamar gigante"; *Dosidicus gigas*) landings decreased during 1992, although during the previous two years large effort was carried out through an experimental fisheries program. This decrease is most likely due to permit problems, which closed the fisheries in late 1992. On the other hand, effort for yellowtail ("jurel"; *Seriola dorsalis*) appeared constant, and the decreased landings may be due to El Niño.

Swordfish ("pez espada"; *Xiphias gladius*) landings also decreased in 1992, and continued to do so during 1993. This relatively recent fishery suffered rapid increases in effort, and it is difficult to separate the effects of fishing effort from the environment. Nevertheless, decreased landings of this species have been reported during El Niño conditions as a result of loss to northern waters (Schoener and Fluharty 1985). Because of the closeness of the U.S.–Mexico border, this may be an important factor for Baja California fisheries. It is noteworthy that swordfish landings in California increased during 1992 and 1993 (CDFG 1994), suggesting that an El Niño effect on the fisheries cannot be eliminated as a contributing factor to decreased landings in Mexico.

Striped mullet ("lisa"; *Mugil cephalus*) and sea bass ("cabrilla"; *Paralabrax* spp.) landings all decreased during 1992 with no apparent changes in effort. No trends with other recent El Niño events are apparent, and in the case of striped mullet, landings have decreased since 1988, suggesting that the 1992 change for these species can be explained as normal interannual variation of exploited resources.

Seasonal Changes

From the entire database, we found a seasonal effect suggesting a relation to El Niño in only five species. Landings at ports other than Ensenada were too sporadic to allow monthly analysis, except for yellowtail.

During 1992, monthly Pacific sardine landings at Ensenada were much lower than usual until September (figure 4). Although the data suggest important changes in seasonality, large imports of low-priced fish meal from Chile caused significant reduction in fishing effort for sardine during this period. Thus the data can be explained by a market situation, and not by the El Niño event.

Figure 5 shows the monthly landings of Pacific mackerel at Ensenada during 1989–93. Normally, Pacific mackerel are caught off Baja California in summer; in

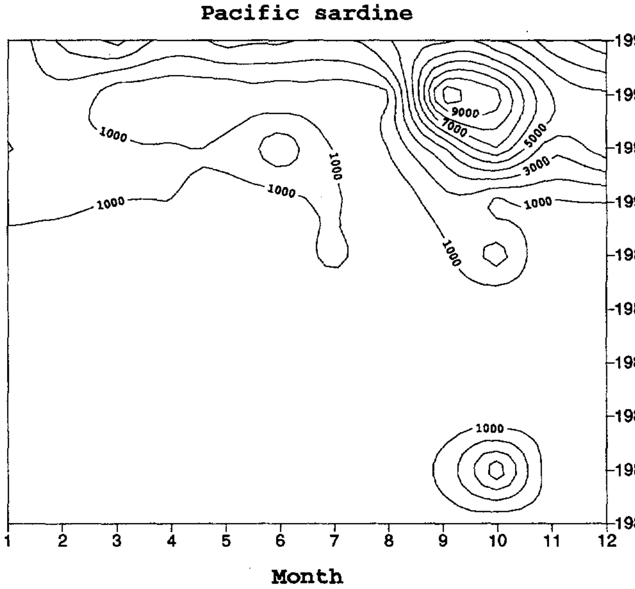
Pacific sardine

Figure 4. Plot of monthly landings (1000 MT contours) of Pacific sardine in Ensenada, Baja California, 1984–93.

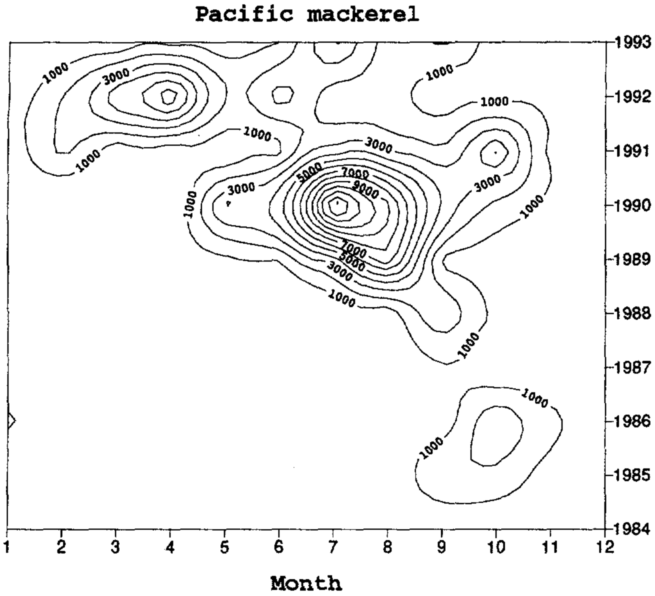

Figure 5. Plot of monthly landings (1000 MT contours) of Pacific mackerel in Ensenada, Baja California, 1984–93.

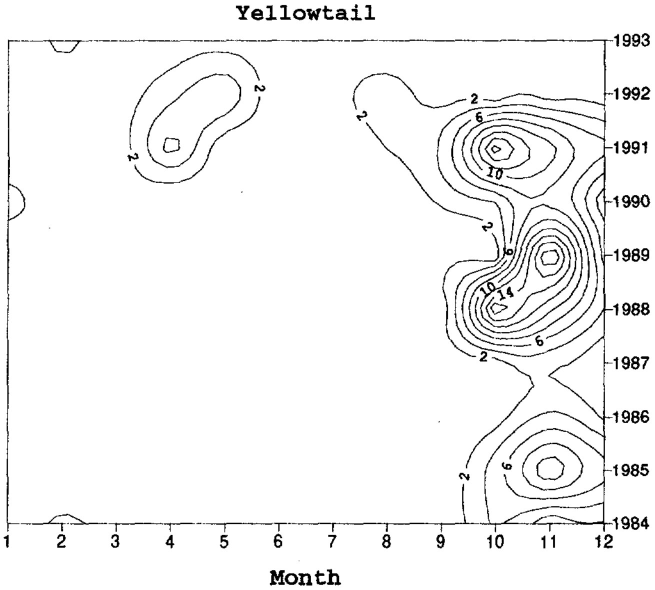

Figure 6. Plot of monthly landings (2 MT contours) of yellowtail in El Rosario, Baja California, 1984–93.

1992, however, catches were in spring. We suggest that both the higher yearly catch and early fishing season in 1992 were influenced by the warmer waters of the El Niño event.

We studied monthly landings of yellowtail in two different localities off the Pacific Baja California coast. Normally, yellowtail are caught in winter (Oct.–Dec.). For 1991–92 we found a clear change in seasonal pattern at El Rosario; landings were made in April and May (figure 6). In Ensenada, farther north, a change in seasonality was not apparent. This demonstrates a latitudinal effect of El Niño on yellowtail.

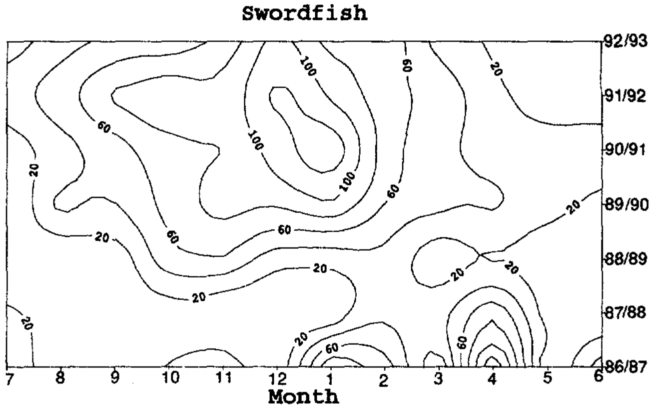

Figure 7. Plot of monthly landings (20 MT contours) of swordfish in Ensenada, Baja California, 1986/87–1992/93 fishing seasons.

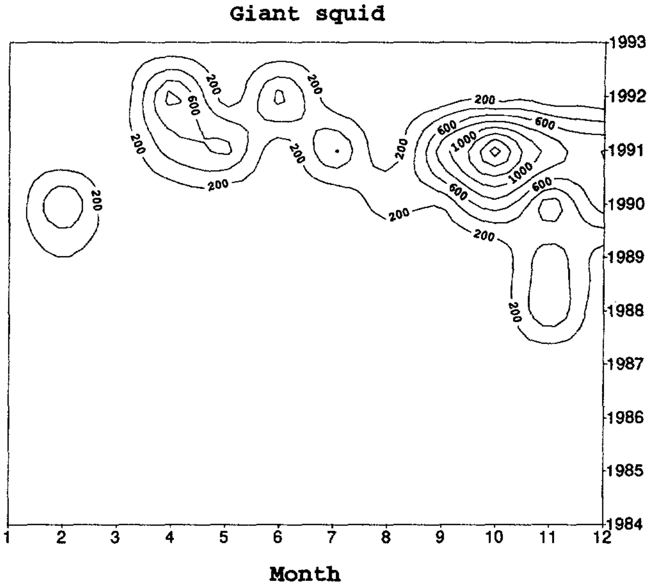

Figure 8. Plot of monthly landings (200 MT contours) of giant squid in Ensenada, Baja California, 1984–93.

Figure 7 shows monthly landings of swordfish. During 1986–88, catches were mostly in April, with lesser activity in January and February. During these years, the swordfish fleet was composed of longline vessels. Beginning in 1988, the fleet changed to drift gill net vessels, and December and January were the months of highest catches. The normal fishing season with this new fleet is October–March, but during 1991–92, catches were registered as early as August. This early fishing season further suggests the influence of El Niño on swordfish availability, and decreased landings because fish move to northern waters.

The early fishing season for giant squid in 1992 is clearly seen in figure 8. Peak landings usually are made

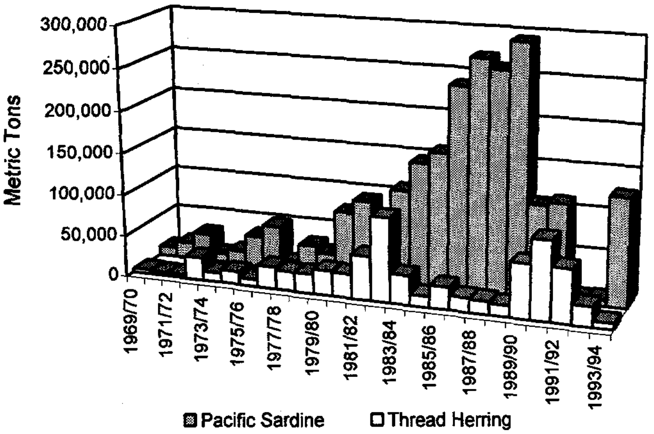

Figure 9. Landings of Pacific sardine and thread herring (MT) in the Gulf of California during the 1969/70–1993/94 fishing seasons.

in October (as in 1991), but in 1992, giant squid were caught from April to June. Ehrhardt et al. (1983) reported that giant squid are usually oceanic and move toward the shore and migrate northward during summer warming. Baja California is close to the northern distribution limit (Ehrhardt et al. 1986), and the normal fall fishing season off Baja California reflects the thermally related migration pattern. We suggest that the early warming under El Niño conditions increased spring availability of giant squid in 1992.

Gulf of California

The major fisheries of the Gulf of California are for the small pelagic species (sardine, anchovy, mackerel). Although we did not analyze the data from all other fisheries, the small pelagics show an interesting trend between the temperate Pacific sardine and the tropical thread herring (*Opisthonema* spp.). During cool periods, Pacific sardine have dominated the fisheries in the gulf, whereas during El Niño years, tropical thread herring are more available (figure 9); note especially the 1972–73, 1983–84, and 1991–92 events. Although data were not available, increased captures of yellowfin tuna were reported in the Gulf of California during the 1992 El Niño event.

CONCLUSIONS

In this paper we have provided a qualitative examination of trends in fisheries landings for the state of Baja California, Mexico, during the 1992 El Niño event. El Niño can affect fisheries by changing the short-term availability to the fleets, or by longer-term changes in recruitment; we have addressed only short-term availability in this paper. El Niño events can have profound economic effects, especially when changes in seasonal availability find the fleet unprepared, or when low catches correspond to periods of low market demand. Economic impact can be minimized by enhancing our knowledge of the relation between fish movements and ocean conditions; we hope that this paper contributes in that sense.

In order to better understand the relation between fish movement and behavior under El Niño conditions, more rigorous analysis is necessary in future studies. Yearly changes due to El Niño may be clear only after catch data are standardized with fishing effort, and after a much longer time series that includes several El Niño events is analyzed. Such data, unfortunately, are available for only a few species.

Recognizing that short-term fisheries management policies are also affected by an El Niño event, one must consider the importance of larger-scale analyses that treat El Niño as a normal part of an oscillating environment. Fisheries operational support in near real time, for example, with satellite imagery of sea-surface temperature, is an important tool, as is the capability to predict oceanographic events such as El Niño, to minimize error caused by not coupling fishing efforts to changes in resource availability or population production.

Additional complications arise when political and economic constraints are put upon the fisheries industry. For example, Pacific mackerel and swordfish move between Baja California and California, each of which has different management policies; the availability of both species appears to be affected by El Niño. Monthly and interannual fluctuations in interest rates and market conditions are also important realities that must be considered in a holistic analysis of medium- to long-term environmental change and its relation to fisheries, before final recommendations can be made.

ACKNOWLEDGMENTS

We thank the organizers of the 1994 CalCOFI symposium, Frank Schwing and Steve Ralston, for giving us the opportunity to speak about the fisheries in Baja California, Mexico. Teresa Fimbres assisted with raw data from the fisheries delegation, and Carmen Rodríguez Medrano helped with the database and sport fisheries survey. The comments of three anonymous reviewers greatly improved the manuscript. Frank Schwing's excellent editorial assistance is especially appreciated.

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Part III

SCIENTIFIC CONTRIBUTIONS

THE RISE AND FALL OF THE PACIFIC SARDINE, *SARDINOPS SAGAX CAERULEUS* GIRARD, IN THE GULF OF CALIFORNIA, MEXICO

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ABSTRACT

The Pacific sardine has been the most important species in the wetfish fishery in the Gulf of California, Mexico, for the past 20 years. In recent years, the sardine population has rapidly declined while the population of the northern anchovy, a newcomer to the gulf, has been increasing. The history of the sardine fishery, and population trends from 1969 to 1990 were examined with virtual population analysis (VPA) based on length frequencies converted to age. Schaefer's model was used to characterize catch and effort data from Guaymas, Sonora (Mexico). A time series of population biomass estimates was constructed from the results of the VPA and weight-at-age data. These results are discussed in light of the relative roles that fishing pressure and competition with the increasing population of northern anchovy may play in the observed changes of the sardine population.

INTRODUCTION

High interannual variability in populations of small pelagic fish (e.g., anchovy and sardines) is common (Csirke 1988). Beverton (1983) classified these species of fishes as highly unpredictable, vulnerable to exploitation, and difficult to manage. Classic examples can be found in the collapse of the Peruvian anchoveta (*Engraulis ringens*) in the early 1970s (Pauly et al. 1987); the collapse of the Pacific sardine (*Sardinops sagax caeruleus*) during the 1950s and the subsequent increase of northern anchovy (*Engraulis mordax*) in the California Current; and the collapse of the Japanese sardine (*Sardinops melanosticta*) population during the 1940s and its recovery during the 1970s (Kondo 1980).

With the discovery of sardine and anchovy scales preserved in anaerobic sediments off Santa Barbara, California (Soutar and Isaacs 1969; Baumgartner et al. 1992), it was possible to construct a long time series of fish abundance, from which it was evident that large interannual fluctuations in the population levels of both species occurred well before the fisheries began. Environmental factors such as food availability and competition (Lasker and MacCall 1983), predation (Butler 1991), and abiotic factors such as circulation patterns (Parrish et al. 1983) and temperature received increased emphasis in the study of the causes of population variability of these pelagic fishes, whereas a dominant role of the fisheries was questioned.

Nevertheless, fisheries exploitation cannot be discounted as a contributor to the collapses of pelagic fisheries around the world. Excess removal by fishing may provide available niche space for food competitors (MacCall 1986), and the fisheries may increase the amplitude of natural variations and drive a population to extremely low levels from which it may not recover (Lluch-Belda et al. 1989).

In this paper we analyze the early increase and later decline in the population and fishery of the Pacific sardine in the Gulf of California, Mexico, and we discuss the possible relationship to the recent arrival and population increase of the northern anchovy. Our objectives are to (1) show two decades of sardine population growth followed by the current decline, (2) demonstrate a density-dependent relationship between the adult sardine and offspring, and (3) propose an ecological mechanism to explain the sardine/anchovy relationship in the Gulf of California.

HISTORY OF THE FISHERIES

The sardine fishery in Mexico began during the fall of the sardine fishery in California, USA, during the 1940s. At that time, the fishery was between Ensenada and Cedros Island, but during the 1950s, fishing extended southward into Magdalena Bay (figure 1). During the late 1960s Pacific landings of sardine decreased, and fishmeal plants and canneries were installed in Guaymas in the Gulf of California, where the sardine resource was abundant. Since that time, Guaymas has been the major port for the sardine fisheries in Mexico (Lluch-Belda, et al. 1986; Cisneros-Mata et al. 1987).

Annual wetfish landings and Pacific sardine catch per unit of effort (CPUE) show four periods in the Gulf of California: (1) exploration and establishment, 1969/70–1975/76; (2) development and growth, 1976/77–1981/82; (3) expansion and stabilization, 1982/83–1988/89; and (4) decline, 1989/90–present (figure 2, table 1).

[Manuscript received September 6, 1994.]

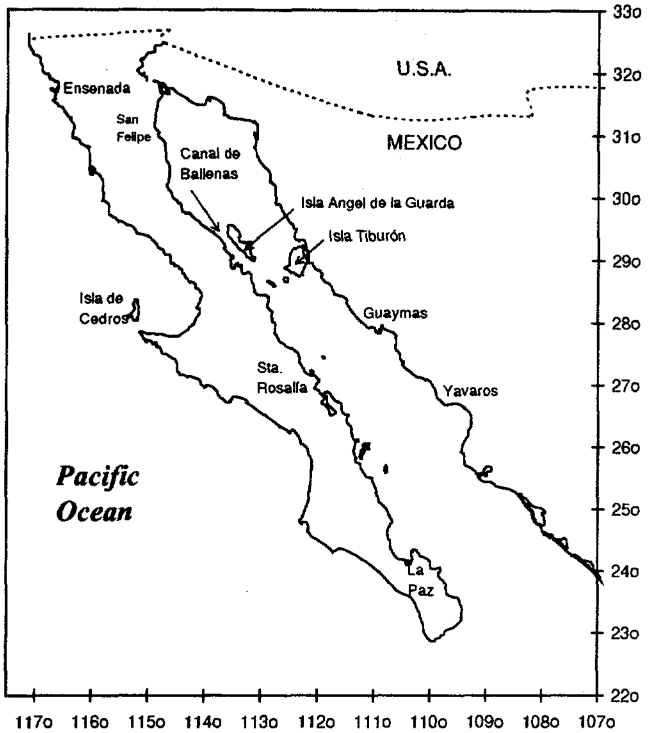

Figure 1. Map of Gulf of California, showing the principal ports for the sardine fishery.

Several important events occurred during these four periods. First, in 1970, the Pacific sardine fishery in Ensenada was closed and the vessels were moved to Guaymas. These boats were small (40–60 MT) and fished only from October to May ("winter fishing"). During the second period, in 1977, larger boats began to enter the fleet at Guaymas; first twenty-eight 120 MT ships were commissioned from Peru by the Mexican government after the fall of the Peruvian anchovy fishery. In 1979/80 the first landings during the June–September period were reported. During the early 1980s, as the newly installed processing plants increased the demand for sardine, the fishery expanded southward, and Yavaros, Sonora, began developing into an important sardine port (Estrada-Garcia et al. 1986; Cisneros-Mata et al. 1987). During this period, fishing effort was mostly characterized by short, one-day trips.

During the third period, in 1982/83, a regime of "summer fishing" was established, and the larger vessels began to operate farther from their home port of Guaymas, especially in the fertile "Canal de las Ballenas" (between the large islands and the western coast of the gulf) and in the area north of Tiburón Island. Pacific sardine CPUE increased directly with fishing power and with the increased experience of the fishermen. The fleet began using modern technology to locate schools, combining spotter planes with video sonars installed on the vessels. Trips during this period often lasted three days.

TABLE 1
Total Pacific Sardine and Northern Anchovy Catches; Standard Effort; and C/f for Pacific Sardine in the Gulf of California, 1969–1992

Fishing season	Std. effort (# trips)	Total catch (MT)	Pacific sardine catch (MT)	Anchovy catch (MT)	C/f sardine (MT/trip)
69/70	597.20	15,992	11,287	0	18.90
70/71	988.28	23,194	19,558	0	19.79
71/72	1,358.48	37,163	32,617	0	24.01
72/73	380.96	38,605	9,924	0	26.05
73/74	750.46	31,239	16,180	0	21.56
74/75	1,271.18	55,350	36,648	0	28.83
75/76	1,878.45	63,094	51,263	0	27.29
76/77	372.97	38,352	8,802	0	23.60
77/78	1,111.87	58,691	32,600	0	29.32
78/79	731.42	54,447	24,627	0	33.67
79/80	1,587.84	112,637	77,566	0	48.85
80/81	2,133.20	126,121	93,989	0	44.06
81/82	1,270.91	137,813	71,425	0	56.20
82/83	1,583.50	226,304	111,526	0	70.43
83/84	1,838.65	189,518	146,467	0	79.66
84/85	2,280.80	197,803	169,076	0	74.13
85/86	3,160.04	287,357	240,226	2,081	76.02
86/87	3,534.41	304,872	272,574	39	77.12
87/88	3,370.69	284,934	261,363	777	77.54
88/89	3,776.26	321,799	294,095	7,706	77.88
89/90	1,629.98	212,857	109,942	18,493	67.45
90/91	1,532.86	235,060	113,631	12,768	74.13
91/92	—	105,431	6,431	5,168	—

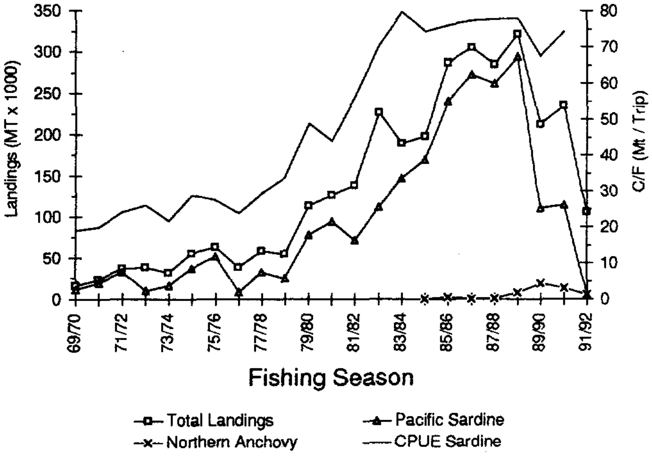

Figure 2. Total for small pelagics, Pacific sardine, and northern anchovy landings in metric tons (Guaymas and Yavaros combined), and total catch per unit of effort for Pacific sardine (metric tons/trip) in the Gulf of California, 1969–92.

In 1985, juvenile northern anchovy were discovered near Guaymas in the Gulf of California, and in 1986 they first appeared in commercial sardine landings (Cisneros-Mata et al. 1987; Hammann and Cisneros-Mata 1989). The Pacific sardine CPUE began to level off in 1984/85, and landings fell drastically after the 1988/89 fishing season.

In the following sections we analyze the time series (Instituto Nacional de la Pesca) of landings and fishing effort (number of trips) from the commercial sardine fleet of Guaymas, Sonora, Gulf of California, Mexico, from 1969 to 1990.

METHODS AND MATERIALS

Port sampling at Guaymas (Sonora, Mexico) has been carried out routinely since the 1972/73 sardine fishing season in the Gulf of California. From 1972 to 1983, 60 kg samples were collected from 2–4 vessels daily (depending on landings), and monthly length-frequency distributions were determined. Starting in 1984, a minimum sample size of 10 kg was determined for port sampling of length frequencies, and 2–5 vessels were sampled daily. The length-frequency distribution and weight-length relationship of the monthly samples were used to determine size composition and total numbers of the monthly landings reported in metric tons at the fisheries office. The monthly size compositions were combined to determine total numbers caught per size class per fishing season.

The Schaefer (1954) model (yield = $af-bf^2$) was employed to describe the relation between the catch and effort data during fishing seasons from 1969/70 to 1989/90 for the fleet operating in Guaymas. Effort data were not available from Yavaros. The number of trips was defined as the unit effort. The total yearly standard effort (f), in number of trips for each vessel size, was standardized to the fishing power of the most traditional vessel size (10–60 MT) by dividing the total yearly catch of each vessel size n by the CPUE of the standard vessel (Ricker 1975). The CPUE was calculated for Pacific sardine from total yearly catch and effort (number of trips) of each of eight size categories of vessels operating in the sardine fisheries in the gulf: net tonnages of (1) 10–60 MT, (2) 61–100 MT, (3) 101–120 MT, (4) 121–140 MT, (5) 141–160 MT, (6) 181–200 MT, (7) 201–220 MT, and (8) >221 MT. Thus the overall CPUE was calculated for each year in the time series as follows:

$$CPUE_{total} = \frac{CATCH_{total}}{\sum_{1}^{8}\left(\frac{CATCH_n}{CPUE_{(10\text{-}60t)}}\right)}$$

To estimate the annual number of organisms at age from the age structure observed in the commercial landings at Guaymas, the program ELEFAN III (VPA I; Gayanilo et al. 1989) was used to carry out a virtual population analysis (VPA; Jones 1984). Length-frequency distribution was transformed to age distribution with von Bertalanffy individual growth parameters and an age-length key. This procedure is used when age data are lacking over the entire time series (Clark 1991), with the assumption that growth parameters are constant over time, which is probably not the case. With the results from VPA, the Shepherd (1982) recruitment stock (P)$-$(R) function $R = \gamma P/(1+(P/k)^g$ was fit using the Marquardt nonlinear algorithm in the program FISH-PARM (Prager 1989).

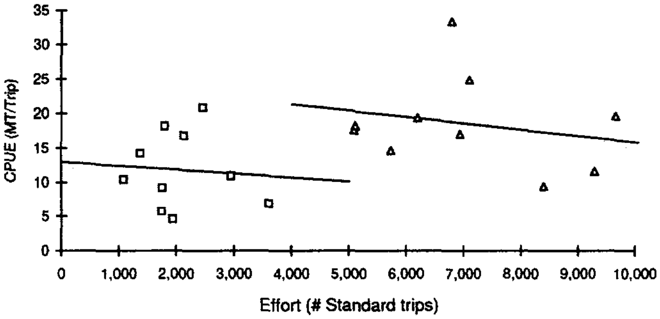

Figure 3. Relation between the catch per unit of effort and standard effort (trips) for the Pacific sardine fishery at Guaymas, Gulf of California, during two ten-year periods: 1969–79 and 1980–90 (*solid line* = Schaefer model).

During the 1988/89 and 1989/90 fishing seasons, age was determined from otoliths of 1283 Pacific sardines randomly sampled from 10 kg port samples. Data from both fishing seasons were combined to better represent the population, and the resulting individual growth parameters and the age-length key were used to transform length to age frequency over the entire time series. We recognize that we did not consider possible changes in growth rate over time, but otoliths were not collected in the early years of the fishery, so age was not routinely determined.

RESULTS

The relation between CPUE and standard effort shows a positive slope with increasing fishing effort, which in this case represents increased efficiency with acquired experience and new technology (sonar, spotter planes). Lines adjusted (Schaefer's model) for two ten-year periods (1969/79 and 1980/90), however, show decreasing trends, different only in the level of effort and CPUE (figure 3). Table 2 shows the calculated parameters and statistics for the lines describing the Schaefer model for the entire data set, and for each of the two ten-year periods.

The von Bertalanffy growth parameters describing the 1988/89–1989/90 fishery seasons are: L_∞ = 203.7

TABLE 2

Schaefer Model $Y = af + bf^2$ Parameters; Standard Deviations Are in Parentheses

Period	a	b
1969–90	10.8289 (6.6227)	0.00097 (0.00054)
1969–79	12.9567 (5.8705)	−0.000565 (0.0026)
1980–91	24.9174 (7.0474)	−0.00089 (0.00144)

TABLE 3
Age-Length Key in Percent for Pacific Sardine in the Gulf of California, Determined from Otoliths Sampled during the 1988/89 and 1989/90 Fishing Seasons

Size class	Age group								
SL mm	0	1	2	3	4	5	6	Total	*N*
<120	100.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	15
121–130	76.29	23.71	0.00	0.00	0.00	0.00	0.00	100.00	10
131–140	61.45	38.16	0.39	0.00	0.00	0.00	0.00	100.00	54
141–150	25.16	67.60	7.24	0.00	0.00	0.00	0.00	100.00	162
151–160	1.88	52.96	27.97	17.19	0.00	0.00	0.00	100.00	203
161–170	0.00	19.50	60.99	19.51	0.00	0.00	0.00	100.00	264
171–180	0.00	4.93	49.42	45.65	0.00	0.00	0.00	100.00	281
181–190	0.00	0.00	14.15	41.90	40.89	3.06	0.00	100.00	159
191–200	0.00	0.00	2.48	14.67	44.24	31.11	7.50	100.00	75
201–210	0.00	0.00	0.28	1.89	31.31	49.58	16.94	100.00	38
211–220	0.00	0.00	0.00	1.11	23.18	21.34	54.37	100.00	22
								Total	1283

TABLE 4
VPA Estimates of Recruits (Age Class 0), Spawners (Age Classes 1–6), and the Recruit/Parent Ratio

Fishing season	Recruits	Spawners	R/S
72/73	3,712,574,464	Incomplete	n/a
73/74	1,943,336,448	Incomplete	n/a
74/75	1,335,047,680	2,010,681,427	1.46
75/76	2,935,448,576	1,201,404,588	4.49
76/77	5,389,423,616	1,583,896,484	4.47
77/78	7,077,535,232	3,109,534,029	2.94
78/79	9,151,337,472	4,252,955,992	1.38
79/80	5,874,631,168	5,668,992,507	1.51
80/81	8,562,187,264	4,605,747,499	2.16
81/82	9,955,485,696	5,389,356,656	2.69
82/83	14,500,033,280	6,144,694,987	3.60
83/84	22,115,801,600	9,020,887,807	3.17
84/85	28,562,339,840	12,541,800,346	1.88
85/86	23,633,075,200	18,087,533,010	0.66
86/87	11,851,628,800	17,630,978,732	0.56
87/88	9,961,348,096	11,487,350,637	n/a
88/89	Incomplete	8,594,568,598	n/a
89/90	Incomplete	Incomplete	n/a

mm SL, $K = 0.8577\ y^{-1}$, $t_0 = -0.01394\ y$ ($r^2 = 0.99$, $N = 1283$); we used an age-length key to convert length to age (table 3). The extrapolated number at age of Pacific sardines landed per fishing season between 1972/73 and 1989/90 is given in appendix table A.

Using VPA, we determined the number of sardines per year class (appendix table B). The resulting time series shows that the number of spawners increased slowly until 1986, and later decreased; the number of recruits increased from 1975 to 1985 and then fell sharply during the following three years (figure 4). The tendencies for poor recruitment and, in particular, two rapid decreases in recruitment rate during 1977–79 and 1983–85 can be clearly observed in figure 5 and table 4 as decreases in the ratio between the parent stock (age classes 1–6) and the following year's recruitment (class 0).

The stock-recruitment relationship for Pacific sardine is best fit by a parabola ($r^2 = 0.77$, $N = 13$; figure 6). The slope at the origin ($\gamma = 2.697$) represents the maximum expected rate of adult recruitment that occurs when adult density and density-dependent mortality rates are low. The maximum P at the inflection point ($k = 1.471 \times 10^{10}$) is the limit above which density-dependent effects dominate over density-independent effects; below this point in figure 6, the population's vulnerability and thus the probability of a population crash increases. The compensation factor ($g = 6.499$) measures the force of density-dependence; values greater than 1.0 indicate strong overcompensation (Shepherd 1982). This

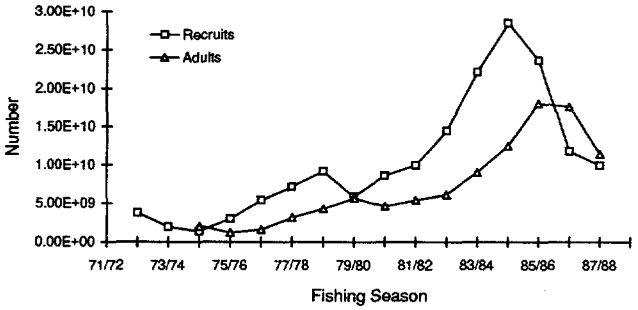

Figure 4. Numbers of recruits and adults for the Pacific sardine in the Gulf of California as determined by VPA on data from the fishery at Guaymas, Gulf of California.

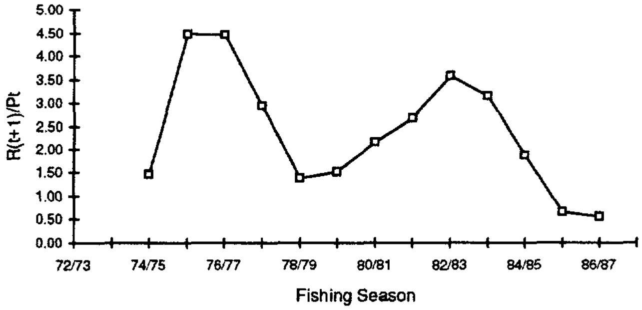

Figure 5. Recruitment rate for Pacific sardine in the Gulf of California $R_{(t+1)}/P_t$.

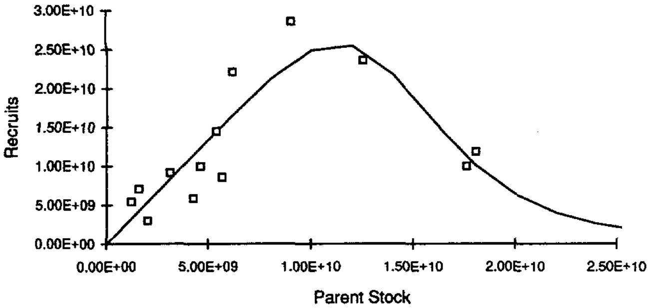

Figure 6. Shepherd stock-recruitment relationship for Pacific sardine fishery at Guaymas, Gulf of California. Numbers of recruits and parents were determined from VPA.

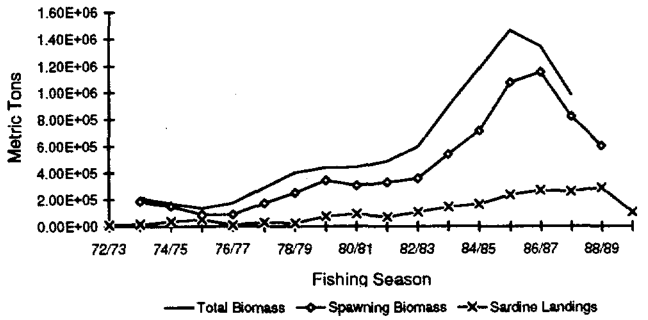

Figure 7. Total and spawning biomass of the Pacific sardine in the Gulf of California as determined by VPA and weight-at-age calculations. Pacific sardine landings are included for comparison.

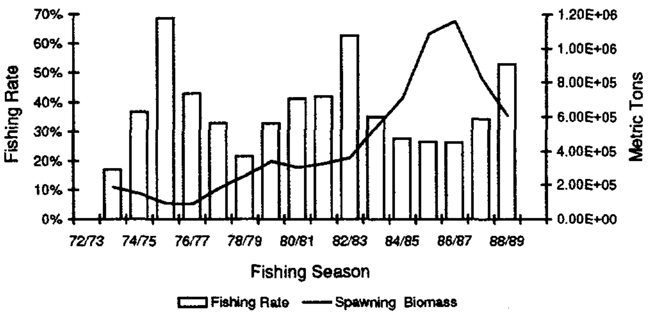

Figure 8. Fishing rate for the Pacific sardine in the Gulf of California expressed as the percentage of the Pacific sardine spawning biomass landed by the fisheries.

is the first evidence suggesting stock overcompensation for Pacific sardine in the Gulf of California as a population-stabilizing mechanism: the net rate of recruitment increases when population size is low, and decreases when it is high (Tyler and Gallucci 1980; Shepherd 1982).

We used results of VPA, in combination with weight-at-age data (the length-weight relationship was used to transform length-based von Bertalanffy parameters to weight-based parameters) to construct a time series of total and spawning biomass, which we compared to total Pacific sardine landings in the Gulf of California (figure 7). Maximum spawning biomass (1.159 million MT) occurred in the 1986/87 fishing season. In figure 8, the proportion of spawning biomass extracted by the fishery can be observed; in all but the earliest years, the rate of exploitation was above 20 percent of the spawning biomass.

DISCUSSION

In marine pelagic fish populations, the mechanisms of density-dependent regulation are reflected in the parent/progeny relation (Clark 1991), which can facilitate fishery management. But when catch-and-effort data from the commercial fleet are used, a warning of an imminent decline in population may come too late for effective regulatory actions to be initiated (Hampton and Majkowski 1986). An increasingly efficient fleet increases landings, even when recruitment is poor. A comparison of the time series of number of recruits and adults (figure 4) to that of landings and CPUE (figure 2) suggests that this may have been the case for the Pacific sardine fisheries in the Gulf of California. Maximum landings were reached in 1988/89, and CPUE did not fall off until 1990/91, even though several years earlier, in 1985/86, recruitment began to decrease.

The cyclic behavior in recruitment rate $(R_{(t+1)}/P_t)$ as shown in figure 5 demonstrates a large interannual variability and declining trend in early survival (egg[parent] to recruit); in 1976 and 1983, survival to recruitment reached a maximum and then dropped abruptly during the following three years. The decrease in recruitment rate in 1977/79 and 1984/86 (figure 5) could be due to environmental factors (these periods follow El Niño events); to interspecific relationships (e.g., competition for food, predation on eggs and larvae) with adult northern anchovy, which began to increase in the gulf in 1985 (Hammann and Cisneros-Mata 1989); or to a combination of both.

The El Niño events of 1976/77 and 1983/84, and the warming observed in 1989/90 may also have affected recruitment of Pacific sardine in the gulf. It has been argued that the invasion of warm waters during El Niño changed the geographic distribution of sardine captures (Lluch-Belda et al. 1986) and spawning (Hammann et al. 1988) in the gulf. Hammann et al. (1988) and Hammann (1991) suggested that density-dependent mortality of sardine eggs and larvae may occur when the warm-water intrusion of an El Niño event reduces habitat. Nevertheless, recruitment appeared to improve during such conditions. Hammann et al. (1991) described the increased availability and CPUE of sardine during warm summer conditions, which are enhanced during an El Niño event. During the warm periods of 1976/77, 1983/84, and 1989/90, over 50 percent of the spawning biomass was taken by the fishery (figure 8), and it is likely that the following poor recruitment results from the reduction of the spawning biomass during the previous year. This high overfishing of spawning stock was previously evidenced from length-based cohort analysis (Jones 1984; Cisneros-Mata et al. 1990).

The suggested overcompensation in the sardine population may be due to cannibalism or lack of food sufficient for adult maturity and growth (Harris 1975; Shepherd 1982). It is possible that competition between sardine and anchovy adults could have decreased the relative availability of food for sardine under the described population conditions (sardine decreasing, anchovy increasing). Studying the abundance of scales deposited and preserved in anoxic sediments off Santa Barbara in the California Current ecosystem, Lasker and MacCall (1983) proposed competition between these two species as a mechanism to explain the decline in the sardine population. On the other hand, Butler (1987) found little evidence for competition between these two species, and suggested predation on sardine eggs and larvae by northern anchovy adults as a plausible explanation.

The causes of interannual variability in recruitment of small pelagic fish species are still not understood. A combination of factors such as changes in the environment, intra- and interspecific relationships, and fishing may be responsible for the observed variability. Lluch-Belda et al. (1989) proposed that long-term environmental variations may give rise to "regimes" of anchovy or sardine. Nevertheless, a long-term change in the dominant population is the net result of many yearly changes in recruitment success. Cury and Roy (1989) described an "optimal environmental window" when all biotic and abiotic environmental conditions would permit successful recruitment. Cury (1988) combined population ecology and evolutionary biology to explain recruitment variability. According to Cury's hypothesis, when the population biomass is low, rapid changes can occur in the genome because of genetic drift (genetic revolution); the result would be organisms better adapted to compete advantageously with the dominant existing population and thereby increase their population.

Although the Pacific sardine is widely distributed in the Gulf of California (Cisneros-Mata et al. 1990, 1991) and does not restrict its spawning to the coastal areas (Nevárez-Martínez 1990; Hammann 1991), overfishing must also be considered to have played an important role, given the high rates of exploitation during environmental conditions such as El Niño, as shown in this paper.

ACKNOWLEDGMENTS

The authors would like to express their appreciation to R. Rosenblatt, J. R. Hunter, P. E. Smith, O. Sosa, L. Calderon, and three anonymous reviewers for their valuable comments on drafts of this manuscript. Partial funding for MGH was provided by CONACYT grants D112-904325 and T9201-1110. MACM was partially supported by CONACYT and the Center for Ecological Health Research (CEHR) at UC Davis.

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APPENDIX

TABLE A
Extrapolated Number at Age Landed for Pacific Sardine during the 1972/73–1989/90 Fishing Seasons

Fishing season	Age group						
	0	1	2	3	4	5	6
72/73	3,133,383	13,425,410	45,666,913	39,228,900	13,235,721	2,764,819	498,679
73/74	16,741,262	72,393,799	88,166,998	44,233,550	1,794,785	317,963	53,240
74/75	47,035,026	161,535,666	157,014,290	105,218,551	20,193,833	2,903,489	400,540
75/76	15,605,009	74,117,268	162,452,972	155,165,309	64,999,901	15,155,542	3,229,809
76/77	5,262,777	21,350,104	26,533,098	23,792,531	9,831,777	2,034,705	367,870
77/78	115,800,868	294,008,455	113,581,970	50,590,617	891,605	96,609	8,063
78/79	94,983,542	343,535,473	196,070,961	109,401,235	2,111,679	161,790	1,015
79/80	154,597,944	505,440,690	355,245,351	155,613,460	1,430,664	107,064	0
80/81	164,534,047	429,892,897	416,906,517	239,909,972	23,272,732	3,154,846	403,816
81/82	157,486,142	750,038,860	540,628,391	308,403,207	9,230,516	1,611,066	1,377,457
82/83	371,061,856	506,761,675	173,801,735	98,428,643	13,253,265	2,124,768	311,353
83/84	609,260,149	1,617,097,260	798,927,693	417,018,826	2,812,890	448,017	72,767
84/85	507,456,510	950,187,947	456,370,461	205,426,795	2,051,467	206,131	14,194
85/86	848,822,010	1,488,370,539	604,561,334	291,579,325	7,537,525	691,550	34,393
86/87	279,070,465	1,293,491,642	1,416,569,958	760,870,718	48,427,842	8,935,977	1,575,422
87/88	62,056,812	417,784,958	1,121,192,041	711,980,420	91,344,428	13,835,597	1,916,147
88/89	347,345,255	1,022,465,830	1,000,269,366	689,021,662	138,145,412	29,368,112	5,902,236
89/90	15,744,474	213,400,502	442,274,047	286,199,637	60,387,835	22,587,039	9,343,703

TABLE B
Virtual Population Analysis Estimates of Population Number at Age for Pacific Sardine during the 1972/73–1989/90 Fishing Seasons

Fishing season	Age group						
	0	1	2	3	4	5	6
72/73	3,712,574,464	1,828,364,416	554,549,696	131,834,272	21,167,092	—	—
73/74	1,943,336,448	1,682,751,232	866,306,176	221,926,896	34,953,600	1,763,075	—
74/75	1,335,047,680	870,927,104	716,326,080	335,851,360	72,291,528	14,690,023	595,332
75/76	2,935,448,576	575,088,128	291,269,760	224,440,736	85,838,456	19,966,972	4,800,536
76/77	5,389,423,616	1,321,900,800	212,964,784	34,095,716	11,985,341	2,403,069	546,774
77/78	7,077,535,232	2,442,326,528	585,899,840	79,448,232	1,728,014	119,430	11,985
78/79	9,151,337,472	3,135,966,464	917,703,424	192,859,248	6,184,875	240,472	1,509
79/80	5,874,631,168	4,090,689,280	1,264,491,904	290,707,232	21,627,746	1,476,345	0
80/81	8,562,187,264	2,682,035,712	1,528,759,168	348,017,472	37,453,108	8,881,838	600,201
81/82	9,955,485,696	3,949,766,656	987,031,424	428,444,320	18,876,978	3,189,933	2,047,345
82/83	14,500,033,280	4,615,188,480	1,377,709,568	130,532,976	17,896,864	2,904,328	462,771
83/84	22,115,801,600	6,626,971,520	1,851,060,735	537,761,664	4,378,843	606,890	108,155
84/85	28,562,339,840	10,078,614,400	2,081,420,000	367,508,992	13,872,996	362,861	21,097
85/86	23,633,075,200	13,203,678,720	4,145,572,480	686,666,960	46,353,188	5,217,757	43,905
86/87	11,851,628,800	10,637,752,320	5,270,338,560	1,564,715,840	139,168,690	16,988,524	2,014,798
87/88	9,961,348,096	5,432,792,320	4,184,076,160	1,572,530,020	260,840,720	34,652,868	2,458,549
88/89	—	4,682,058,752	2,297,138,720	1,250,579,600	292,648,420	64,594,770	7,548,336
89/90	—	—	1,547,267,072	450,866,520	163,179,200	51,179,030	11,949,601

DEVELOPMENT OF THE POPULATION BIOLOGY OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

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ABSTRACT

Pacific hake, *Merluccius productus*, population models have been assembled and manipulated to use in determining research strategies and priorities. Given the present preliminary estimates of life-table parameters, I estimate that the larval mortality rate is 0.135 instantaneous daily mortality, which means that there are an average of 87 survivors for each 100 larvae present the previous day. Ninety-five percent of the spawning takes place between December 19 and March 6 of each year. An equilibrium population requires 3.6 million eggs for each recruit at age 2, and that 217 late larvae become juveniles in mid-June of the same year. Exceptionally high cohorts would have 2173 juveniles, and poor cohorts would have 22 at this period.

The fact that we have not yet observed larger year classes in two adjacent years suggests that a highly successful year class may alter the narrow coastal brood habitat for ensuing cohorts. Mechanisms could include limited food, cannibalism on the new cohort, or population growth of other predators in the brood zone.

INTRODUCTION

The Pacific hake, *Merluccius productus*, in the northeast Pacific Ocean occupies three habitats in its life cycle (figure 1): a 30,000 km^2, narrow feeding habitat populated by adult hake for 6–8 months per year near the continental shelf break of California, Oregon, Washington, and British Columbia (Tillman 1968; Alverson and Larkins 1969; Bailey et al. 1982; Francis 1983; Methot and Dorn 1995); a 300,000 km^2, broad, open-sea area populated by spawning adults in winter, and the resultant embryos and larvae for 4–6 months each year offshore of California and Baja California (Ahlstrom and Counts 1955; Hollowed 1992); and a Baja California and California continental shelf juvenile brood habitat of unknown dimensions (Berry and Perkins 1965; Bailey et al. 1986; Woodbury et al. 1995). The spawning, juvenile nursery, and feeding habitats of the adult appear to be mutually exclusive in both time and space. The hake life cycle may involve a lengthy seasonal migration by the spawning adults (Alverson and Larkins 1969; Alheit and Pitcher 1995).

[Manuscript received March 8, 1995.]

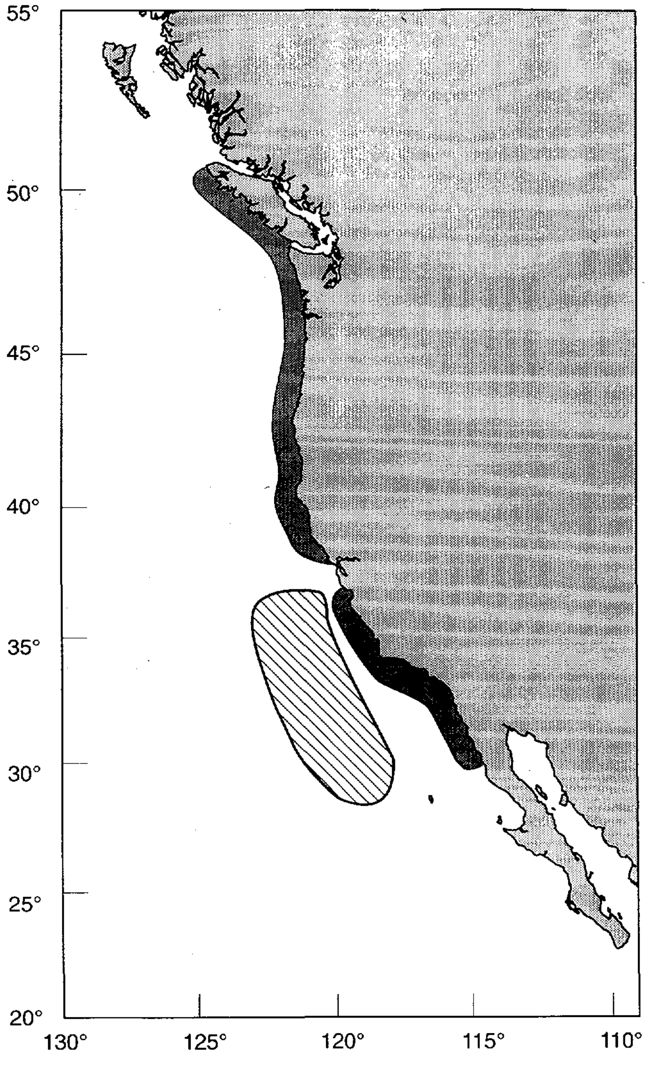

Figure 1. Three regions of the oceanic Pacific hake, *Merluccius productus*, life cycle. The *hatched region* off southern California and Baja California, Mexico, is defined by the 0.275 cm larvae, collected and measured from CalCOFI samples in 1951, and 1963–93. The *narrow strip* covering the upper continental slope, the shelf break, and the continental shelf off British Columbia, Washington, Oregon, and northern California is derived from maps of hake fishing effort (Dorn et al. 1993). The *shaded area* off central and southern California and northern Baja California is postulated to be the distribution of juveniles from the juvenile hake sampled in a general survey (Berry and Perkins 1965), from incidental catch of juvenile hake in anchovy surveys (Bailey et al. 1986), and from incidental catch of juvenile hake in rockfish surveys (Woodbury et al. 1995). The extent of the incidence of O-group hake is not yet defined by these incidental samples.

Estimated recruitment in Pacific hake varies more than two orders of magnitude (Dorn et al. 1993). The three largest cohorts to recruit came from the spawning years 1980, 1984, and 1977 and accounted for 75 percent (26 billion of the 35 billion recruits at age 2) of the recruitment for the 16-year period 1975–90. The three smallest cohorts to recruit came from the spawning years 1981, 1982, and 1985 and accounted for 0.75 percent of the recruitment for the same 16-year period. The smallest cohorts followed the largest by one or two years.

Most of the hundredfold interannual variability of per capita recruitment rate takes place in the first four months of life in the spawning area or adjacent juvenile nursery areas (Hollowed 1992). The actual mechanisms controlling recruitment are not known. Temperature of the spawning habitat might be directly or indirectly involved, as shown by the fact that five of the largest year classes in the 31 years between 1959 and 1989 (1961, 1970, 1977, 1980, and 1984) have been produced in 20 years classified as warm (>15 degrees off southern California), and no large year classes have resulted from the 11 cold years (Hollowed and Wooster 1992; Methot and Dorn 1995).

Batch fecundity, number of spawnings within season, fertilization rate, and embryonic survival of the Pacific hake are still poorly known. Estimates of standing stock of "advanced oocytes" of the oceanic stock of Pacific hake exist (MacGregor 1966), but the frequency of spawnings per year has not been described for most of the hakes with protracted spawning seasons (Pitcher and Alheit 1995). The possibility of multiple spawnings (Goldberg 1985) and the number of multiple spawnings in Pacific hake is raised by the observations of Alarcón and Arancibia (1993), who have defined the intraseasonal rate of egg batch production in the Chilean hake, *Merluccius gayi*, which is closely related to the Pacific hake (Ho 1989). The embryonic mortality rate (Hollowed 1992) should be reexamined, because it was derived, in part, from the standing stock of "advanced oocytes" of the Puget Sound stock of hake on the assumption of a single spawning (Mason 1986).

The spawning behavior of Pacific hake has not been observed: there are no estimates of the spatial scale of the pattern of spawning adults at the time of spawning. Eggs and larvae are at depths of 40–140 m (Ahlstrom 1959; Smith and Richardson 1977). To some degree, the intensity of aggregation at spawning can be inferred from the statistical distribution of eggs and larvae (Smith and Richardson 1977). Comparable data have been reported for other pelagic spawners such as sardine (Smith 1973), anchovy and jack mackerel (Hewitt 1981), Pacific mackerel and sardinella (Matsuura and Hewitt 1995), and the larvae of the demersal spawning herring (McGurk 1986). The pelagic spawners release eggs in intense patches, presumably to minimize the amount of sperm required for high rates of fertilization (Leong 1989; Mangel and Smith 1990). The importance of the scale and intensity of pattern for estimating abundance is that the sample survey must be adequate to estimate a precise mean. The biological importance of pattern is that the intensity and spatial scale of patchiness may control the rates of predator detection and prey mortality, and the larval pattern controls the feeding rates (McGurk 1986).

Near the time of spawning Pacific hake are distributed offshore of the continental shelf and slope off central and southern California, and northern Baja California, Mexico (figure 1). According to Methot and Dorn (1995), the fishery for adults is conducted far from the spawning area off British Columbia, Washington, Oregon, and northern California, centered on the shelf break. Berry and Perkins (1965), Bailey et al. (1986), and Woodbury et al. (1995) have described the location of juveniles in limited numbers or limited areas from samples in cruises designed for other objectives; the casual synthesis of these samples is represented in figure 1 as a southern image of the adult distribution inshore of the spawning distribution. *Merluccius productus* eggs and larvae are not prominent in the sample summaries of surveys taken off Washington and Oregon (Doyle 1992) and not mentioned in other surveys off the main fishing grounds for Pacific hake (Waldron 1972; Doyle et al. 1993).

Theory and a growing body of empirical studies confirm that population growth, as limited by population density, is focused on a single stage—the "critical stage"—of the life cycle (Charlesworth 1994). For Pacific hake the critical stage does not appear to be in the embryonic or early larval periods. For Pacific hake in an oceanic environment, density-independent controls on population growth rate could happen at every stage in the life cycle. For the purposes of predicting recruitment and projecting responses to environmental regime shifts, it will be necessary to consult more details about the carrying capacity of the habitat by life stage and to examine other environmental features that control survival and somatic growth in the late larval and juvenile stages.

This paper is intended for the use of those wishing to improve our understanding of the population biology of Pacific hake so that useful predictions of recruitment and responses to climate change can be made. This paper includes new and revised information on larval mortality rate and seasonality of spawning. I describe the standard life-table traits of age- and stage-specific rates of mortality and somatic growth, reproduction, and population growth.

METHODS

Several methods have been applied to existing hake data for use in this paper to (1) estimate larval mortality rate adjusted for day:night differences, (2) derive the seasonality of spawning from the incidence and abundance of early larvae, (3) construct a Leslie matrix with which to examine the consequences of multiple spawning behavior, and (4) erect a hypothetical Lefkovitch matrix (Crouse et al. 1987; Caswell 1989) emphasizing the age and size intervals when recruitment rate (critical stage) could be established.

Larval Mortality Rate

The estimates of mortality rate were reconstructed from samples taken from all months. The primary data source for mortality rate is the California Cooperative Oceanic Fisheries Investigations (CalCOFI) database of Pacific hake larvae by length, assembled and maintained by the Coastal Division of NOAA/NMFS Southwest Fisheries Science Center. All hake larvae taken from CalCOFI collections have been counted, but only those taken from 1951 and 1963–94 have been measured. Total data extend from 1951 to 1993. Although the original data are measured to 0.05 cm, I have grouped the sizes into 0.2 cm intervals. The midsize of each interval is 0.275, 0.475, . . . 1.875 cm. All samples were pooled without regard to year, season, or region. I assumed that the general form of the mortality is exponential (constant proportion per unit time), and fitted the equations by the Marquardt method without data transformation:

$$n_t = n_0(e^{-zt})$$

where n_t is the size-specific mean number of hake larvae at estimated age t;

t is the estimated age in days;

n_0 is the estimated number of hake larvae at time 0; and

z is the instantaneous mortality rate.

Ages and growth rates from Hollowed (1992) were used. Day:night differences in catch rate were assembled by a table of hour versus size group. Each hourly catch rate was divided by the mean of the 6 catch rates around midnight (3≤0≥3 hr). Each size was then corrected for day-night bias by dividing the mean abundance by the mean proportion for each hourly sample interval.

Seasonality of Length Groups

Seasonality of each length group was determined by cumulative number by month end starting with October 1. Each empirical cumulative curve was fitted to two models, the logistic and the Weibull. The results of the logistic are not reported here because the maximum time rate of increase is fixed at the midpoint. The Weibull fit can have the maximum rate of increase at any point in the cumulative curve. This is determined iteratively with the other parameters:

$$n_t = K[1-e^{-\left(\frac{t}{\sigma}\right)^{\tau}}]$$

where n_t is the cumulative number of hake larvae at time t;

t is the number of days after October 1, the nominal start of the spawning season;

K is the upper limit of cumulative number of hake larvae for the season;

σ is the time in days to the middle of the spawning season; and

τ is the shape parameter of the curve.

One estimate of growth rate is available from the comparison of adjacent size classes at the 50 percent point in the season. There are no obvious differences in seasonality among the regions by latitude or distance offshore (Moser et al. 1993). The incidence of hake larvae in the Los Angeles Bight appears to begin to increase before October 1, but this should have little influence on the fit because the major portion of the spawning season is in January–February.

Leslie Matrix Population Model

The Leslie matrix population model requires only information on annual survival and age-specific fecundity. Standing stock of "advanced oocytes" (MacGregor 1971) varies widely in individuals, from 38 to 556 eggs per gram of female. I chose the modal value from 50 females of 200 to avoid conveying a false sense of the precision. New information on number of batches in Chilean hake (Alarcón and Arancibia, 1993) was used in the "strawman" model. I arbitrarily set the number of batches at 10. The annual mortality of adults in the fishery was reported by Hollowed (1992) to be 0.2. Constant annual mortality is but one of three theoretical mortality assumptions. In another assumption—called the Laevastu-Cushing model by Francis (1983)—the mortality rate is a function of population density to a "critical age" (all females mature), and thereafter mortality rate increases with age, presumably due to the "stress" of spawning. A third approach—called the Peterson-Wroblewski mortality model (Peterson and Wroblewski 1984)—assumes that size-specific predation determines mortality rate; in this model the mortality rate of all fish at all stages is inversely proportional to size. In the Hollowed model the mortality stays the same after a brief prerecruit period of changing mortality rate. In the Peterson-Wroblewski model, natural mortality rate is a simple function of size. The Laevastu-Cushing model exhibits a sharply increasing mortality rate with each year of life after maturity.

TABLE 1
Catch Statistics for Oceanic Pacific Hake Larvae

A. Total catch

Length (cm)	Samples #	Average $(n/10m^2)$	Standard deviation $(n/10m^2)$	Maximum $(n/10m^2)$	Day:night bias (p)	Day:night adjusted $(n/10m^2)$	Fraction positive (p)	Average positive $(n/10m^2)$
0.275	4188	251.00	2471.00	116292	1.00	251.00	0.68	370.40
0.475	4188	81.70	655.20	22055	0.92	88.80	0.58	152.67
0.675	4188	21.10	244.20	10869	0.87	24.25	0.34	71.93
0.875	4188	6.91	96.20	4196	0.80	8.64	0.19	44.39
1.075	4188	2.27	32.16	1717	0.52	4.37	0.11	41.36
1.275	4188	1.29	18.23	839	0.51	2.53	0.07	36.75
1.475	4188	0.46	4.42	217	0.64	0.72	0.05	15.30
1.675	4188	0.15	1.73	60	0.45	0.33	0.01	28.68
1.875	4188	0.10	1.24	39	0.54	0.18	0.01	20.26
>1.975	4188	0.35	11.95	738	0.36	0.98	0.01	91.30

B. Exponential mortality curve

Age (d)	DN (data)	DN (fitted)	UDN (data)	UDN (fitted)	Positives (data)	Positives (fitted)	Std. dev. (data)	Std. dev. (fitted)
0		1110		1230		1090		11410
11	251.00	252	251.00	251	370.40	366	2471.00	2465
19	88.80	85	81.70	79	152.67	166	655.20	694
27	24.25	29	21.10	25	71.93	75	244.20	195
35	8.64	10	6.91	8	44.39	34	96.20	55
43	4.37	3	2.27	2	41.36	15	32.16	15

C. Parameters

Parameter		SE	CV	r^2	Parameter		SE	CV	r^2
Day:night corrected					Positives				
P_0	1112	58.57	0.05	0.99829	P_0	1085	145.4	0.13	0.97437
imr	−0.135	0.004	0.03		imr	−0.099	0.010	0.10	
Uncorrected for day:night difference					Standard deviation				
P_0	1234	54.87	0.04	0.99899	P_0	14080	1175	0.08	0.99716
imr	−0.145	0.004	0.03		imr	−0.158	0.007	0.04	

imr = instantaneous mortality rate;
P_0 = estimated production at time 0.
Positives—including only those observations with one or more larvae

Lefkovitch Population Model

The Lefkovitch matrix used for this study as a "strawman" model differs from the Leslie matrix in that variable length-stage durations (here in days) are used rather than a fixed interval (for example, 1 year) for a time step. Each stage has three parameters: duration, mortality, and maternity. From these, I calculated (1) the probability of surviving the time step given the daily mortality rate *z*; (2) the joint probability of surviving the time step and proceeding to the next stage given the daily mortality rate *z* and the stage duration *d*; and (3) the daily egg production characteristic of the stage. The values of the daily mortality and stage-duration parameters are the same as in Hollowed (1992) except for the embryonic parameter, which is estimated in this paper, and the tuning parameter (mortality–juvenile II), which is used to balance the matrix for stationarity of population size and constant stage composition. I also explored the consequences of multiple batches of eggs rather than a single spawning.

RESULTS

Larval Mortality Rate

The catch curve from raw data is shown in table 1 with the statistics of number of samples, average number per 10 m^2, standard deviation, and maximum number by .2 cm interval. In addition, table 1 shows values of the day:night bias, the catch curve adjusted for day:night bias, the fraction of samples positive for each size of larvae, and the average number of larvae per positive station.

The time rate of change in numbers assuming an exponential mortality curve is provided for the day:night corrected data, uncorrected data, average per positive station, and standard deviation for each length to 1.075 cm (table 1). For each series, the nonlinear least square fit is also provided.

The statistical table of parameter values, standard error of the values, and coefficients of variation and determination are in table 1. Daily instantaneous mortality rate

TABLE 2
Catch Statistics for Oceanic Pacific Hake Larvae

A. Weibull parameters

Length (mm)	*K*	Sigma	Tau	Mean	CorCoeff (r^2)
4.75	1.143E+2	1.439E+2	8.299E+0	7.654E+1	0.999

B. Date of birth

	Fraction	Days	Date
Age at 4.75 mm		13	
*K**0.025	2.86	92	19–Dec
*K**0.5	57.15	138	3–Feb
*K**0.975	111.44	168	5–Mar

over all years for early larvae from 0.275 cm to 1.075 cm long is −0.135: in other words, there are, on average, 874 survivors for each 1000 on the previous day (table 1). The assumptions underlying this estimate do not include a value for adult production of spawn, but the intercept of 1112 eggs per 10 square meters is an estimate of egg production, fertilization, and survival to the 0.275 cm stage. This is based on an assumption that survival rate of the embryos, not evaluated here, is the same as for the early larvae. At the end of the early larval period—43 days—the day catch is biased relative to the night catch by a factor of 2 (table 1). The instantaneous rate of decline in sample standard deviation, −0.158, is higher than the rate of decline of the mean per positive station, −0.099. From this difference I concluded that entire patches are disappearing rapidly. The effects of turbulent diffusion and other dispersive mechanisms must be slower.

Seasonality of Length Groups

Approximately 2 percent of the hake spawn is produced before December 19, according to the timing models (table 2; figure 2), and less than 2 percent is produced after March 6. As in the mortality rate tables, these back-calculations assume that fertilization and embryonic survival rates are about the same in all parts of the spawning season. These assumptions will have to be tested.

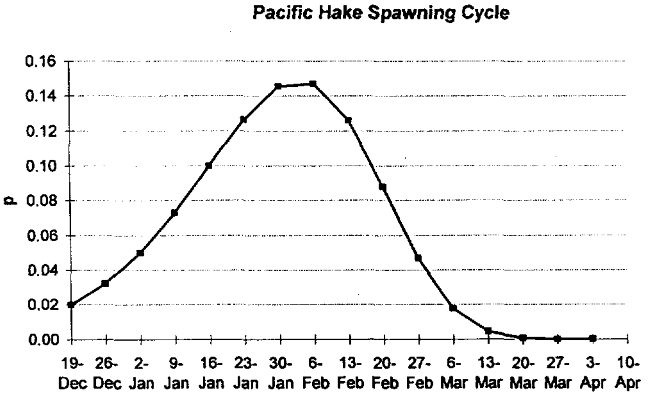

Figure 2. Modeled hake spawning cycle. The Weibull fit allows the shape of the curve to be determined by iteration. It is assumed that eggs are spawned 13 days before the 0.475 cm larvae appear and that the mortality rate from spawning to 0.475 cm larvae is essentially the same at all seasons. Limited hake egg data have been reported by Smith and Richardson (1977).

The importance of multiple batches of eggs depends heavily on the natural and fishing mortality rates as a function of age. When ten batches of eggs allow the life-table model to achieve equilibrium, nine batches—all other things being equal—will cause a Laevastu-Cushing model population to decline to 86.9 percent in 10 years. The Hollowed and Peterson-Wroblewski models decline to 90.9 percent and 90 percent in 10 years. Heavy fishing mortality would cause the population to respond more like the Laevastu-Cushing model. Table 3 presents three differing life-table models for Pacific hake.

For modelling recruitment variability, the Peterson-Wroblewski model maternity schedule is preferred (figure 3). The idea that mortality and trophic efficiency is a function of the actual size is reasonable, and the fecundity curve is very close to the empirically derived constant natural mortality of 0.2 (Hollowed 1992; Dorn 1992; Dorn et al. 1993; see also Francis 1983).

The estimates of mortality for the first two years of life (table 1) represent the stationary solution assuming a fixed population size with the value derived from the Leslie matrix with lambda = 1. Hake O-group mortality (tuned) is highest for the Hollowed model, and lowest for the Laevastu-Cushing model. At equilibrium, to get one recruit at age 2 in the Hollowed model one must start with 5.5 million eggs; the Laevastu-Cushing model requires 2.6 million eggs; and the Peterson-Wroblewski model requires 3.6 million eggs. With the range of recruitment rates of one-hundredfold, we may start with 0.1 the number of eggs in large recruitments and 10 times the number of eggs in poor recruitments.

To further localize the onset of big and poor recruitment, the Lefkovitch model (table 4) may be useful in finding the scope of changes in the first 128 days of life—embryo through late larval stages. With the egg production of the Peterson-Wroblewski model—3.6 million eggs for each recruit at age 2—there would be 217 late larvae moved to the 3.5 cm juvenile I stage in mid-June at equilibrium, 22 in a poor recruitment, and 2173 in a large recruitment.

DISCUSSION

It is important to develop population models of the Pacific hake oceanic population to enable predictions of recruitment and population responses to climatic change. Although the models themselves are probably sufficient as a framework for this round of improvement in our understanding of Pacific hake population dynamics, the parameters available for these models need much improvement. For example, the stock synthesis model

TABLE 3
Leslie Matrix Parameters for Pacific Hake

Age (yr)	Length (cm)	Weight (kg)	Mature (*p*)	Batches (/yr)	e/f/yr #	fe/f/yr #	Hollowed (*m*)	L-C (*m*)	P-W (*m*)
0			0	0	0	0	15.278	14.398	14.568
1	15.73	0.034	0	0	0	0	0.27	0.377	0.53
2	27.53	0.155	0.19	4	2.36E+4	1.18E+4	0.2	0.268	0.36
3	36.26	0.326	0.64	5	2.09E+5	1.04E+5	0.2	0.21	0.30
4	42.73	0.508	0.77	6	4.69E+5	2.35E+5	0.2	0.195	0.27
5	47.53	0.676	0.82	7	7.76E+5	3.88E+5	0.2	0.257	0.25
6	51.08	0.821	0.93	8	1.22E+6	6.11E+5	0.2	0.357	0.24
7	53.71	0.940	0.97	9	1.64E+6	8.21E+5	0.2	0.457	0.23
8	55.66	1.035	1	10	2.07E+6	1.03E+6	0.2	0.557	0.23
9	57.10	1.109	1	10	2.22E+6	1.11E+6	0.2	0.657	0.22
10	58.17	1.166	1	10	2.33E+6	1.17E+6	0.2	0.757	0.22
11	58.96	1.209	1	10	2.42E+6	1.21E+6	0.2	0.857	0.22
12	59.55	1.242	1	10	2.48E+6	1.24E+6	0.2	0.957	0.22
13	59.99	1.266	1	10	2.53E+6	1.27E+6	0.2	1.057	0.22
14	60.31	1.285	1	10	2.57E+6	1.28E+6	0.2	1.157	0.21
15	60.55	1.298	1	10	2.60E+6	1.30E+6	0.2	1.257	0.21
16	60.72	1.309	1	10	2.62E+6	1.31E+6	0.2	1.357	0.21
17	60.86	1.316	1	10	2.63E+6	1.32E+6	0.2	1.457	0.21
18	60.95	1.322	1	10	2.64E+6	1.32E+6	0.2	1.557	0.21
19	61.02	1.326	1	10	2.65E+6	1.33E+6	0.2	1.657	0.21

e/f/yr is eggs per female per year.
fe/f/yr is female eggs per female per year.
L-C is the Laevastu-Cushing life table (Francis 1983).
P-W is the Peterson-Wroblewski life table (Francis 1983).
p is the proportion of females mature (Dorn et al. 1993).
m is the instantaneous natural mortality rate (Hollowed 1992).

TABLE 4
Lefkovitch Estimated and Postulated Matrix Parameters for the Oceanic Stock of Pacific Hake

Stage	Length (cm)	Duration (d)	Mortality (per d)	Maternity (sfe/f/d)
Embryo	egg − 0.4	16	0.135	0
Early larva	0.4 to 1.0	23	0.135	0
Late larva	1.0 to 3.5	89	0.05	0
Juvenile I	3.5 to 6.0	64	0.0200	0
Juvenile II	6.0 to 11.0	128	0.0080	0
Juvenile III	11.0 to 13.5	64	0.0027	0
Juvenile IV	13.5 to 33.3	346	0.000548	0
Pre-recruit	33.3 to 50.0	730	0.000548	10.5
Adult	50.0 to L(inf)	5800	0.000548	199.2

sfe/f/d is surviving female embryos per day.

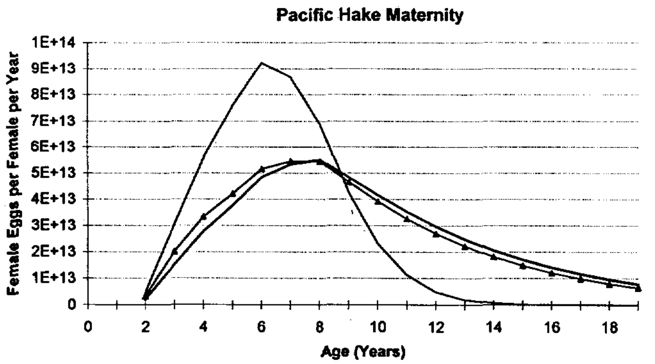

Figure 3. Postulated Pacific hake age-specific maternity function. The *lower solid line* represents the fisheries management life-history model (Hollowed 1992). The *higher solid line* is the Laevastu-Cushing model (Francis 1983) with a density-dependent onset of maturity reaching a maximum at age 6 and with an increase of adult mortality of 0.1 per year. The *line with solid triangles* is the Peterson-Wroblewski curve with the mortality rate a simple function of body length.

(Methot and Dorn 1995) appears to be sufficient for regulating fishing mortality. It is not expected that recruitment will be sensitive to stock size at the levels which have been maintained in the last three decades of fishing; rather, an environment:recruitment model will be necessary for prediction. Given an effective Leslie matrix and a tandem Lefkovitch matrix, one can examine the scope of change that can be detected. From this, the best mix of field studies can be designed to determine the earliest recruitment prediction for each cohort.

The hake life-history strategy differs radically from that of pelagic fishes shallower in the water column. Hake's principal similarity with northern anchovy and sardine life cycles is the intense pattern at time of spawning, which reflects a common need for aggregation before open-sea spawning to conserve sperm in the minutes between release and fertilization of the eggs. Principal differences of the deeper-spawning hake include the rates of mortality, intensity and persistence of patchiness, seasonality of spawning, vertical distribution of spawn, and temperature of the spawning habitat.

Egg and Larval Mortality

It would appear that pooling of all samples has achieved the goal of high precision of the mortality estimate. Of course this stratagem conceals the interannual and interregional differences so critical to understanding variations in mortality rate. It can be seen from the pooled results presented above that precise spatial and temporal egg and larval mortality rates may be attainable only by greatly increasing the sampling effort or by increasing the efficiency of sampling effort through allocation of additional samples in the patchiest areas and times. The uncorrected daily instantaneous rate is 0.145. In terms of the standard error of the fitted data (0.004), the expected ±1.96 S.E. limits of this mortality rate are 0.137 to 0.153, which overlaps broadly with the day:night corrected rate and also with the rate used by Hollowed for the 23-day early larval stage (Hollowed 1992). Since the standard deviation at time of spawning projected for this paper is an order of magnitude higher than the projected mean, it would appear that a few thousand positive samples would be necessary to estimate egg production per unit surface area with useful precision.

Seasonality

Two items of new information are available from the consideration of seasonality: the length of the season tends to support a hypothesis of in-migration, bouts of multiple spawning, and out-migration between October and April; the brevity of the season is an aid to mode-following applications for determining stage duration. If single spawning were the norm, early spawners might leave the feeding grounds late or return to the feeding grounds early; fishing success seems to point to coordinated departures and arrivals on the fishing ground (Dorn 1995). Approximately 35 percent of adults' growth in length is achieved in the spawning portion of the habitat and 65 percent in the feeding portion (Francis 1983). Given the energy expended in migration, aggregation, breeding behavior, investment of eggs with yolk, and formation of multiple batches, it seems likely that important amounts of adult feeding may still occur on the winter breeding grounds. Adult hake and their prey should be directly sampled to verify this.

Vertical Distribution

One of the more important distinctions between hake, which spawn at depth, and anchovy and jack mackerel, which spawn near the surface (Ahlstrom 1959; Moser and Smith 1993), is that the "subeuphotic" spawning habitat may be isolated from Ekman drift, other wind-driven transport, and mixed-layer turbulent diffusion. Similarly, sources of food may be fundamentally different than for the epipelagic larvae (Sumida and Moser 1980, 1984; Ware and McFarlane 1989).

Patchiness and Adequate Sampling

If measures of hake egg production are required, we may use the intercept of the size-specific standard deviation to estimate the number of samples required. For example, the intercept of the original data (table 1) is 1230 eggs per 10 m^2 of sea-surface area, and the intercept of the standard deviation is 14,080. If one required a standard error of 30 percent of the mean (370) by the central-limit theorem and assuming spatial and temporal independence of samples, the number of samples required is 1448; for a standard error of 20 percent of the mean (247) the number of samples required is 3255.

The matrix approach to population models is strategic rather than tactical in that actual projections from the set of parameters presented above (tables 3 and 4) would be valid for the mean population growth rate over many generations. The high variability of recruitment would negate the assumptions of stationarity and constant stage, age, or size distribution required for actually applying these models to practical problems (Bart 1995).

Most work on the early life history of fishes has been conducted on species whose larvae inhabit the upper mixed layer of the ocean. Pacific hake larvae occur somewhat deeper, therefore references to offshore transport of the larvae as described by Power (1986) may not be representative of the direction of transport below the mixed layer. Although much attention has been given to the population dynamics of the subarctic species *Euphausia pacifica* and *Thysonoessa spinifera*, the dominant adult hake food (Mullin and Conversi 1988), the most common euphausiid in the spawning area and depth range of the hake is the temperate species *Nematoscelis difficilis* (Brinton, pers. comm). Although it is clear that Pacific hake recruitment is not controlled by the contemporary changes in spawning biomass, it is not yet known which of the many biological populations and physical events—at many time and space scales—in its spawning and nursery habitats should be explored to understand cause-effect relationships of recruitment rate (Hollowed and Bailey 1989).

Pacific hake recruitment data show that the largest per capita recruitment rates preclude a large recruitment in the subsequent one or two years (Dorn et al. 1993). Is this a general trait in the gadoids? To answer this question, I extracted interannual recruitment standard deviation and lag-1 autocorrelation parameters from a Myers et al. (1990) study of recruitment time series for 50 stocks of North Atlantic gadoids (cod, haddock, pollack, saithe, hake, and the like). For comparison I plotted the same parameters for Pacific hake (Dorn et al. 1993) and Alaskan pollack (Hollowed and Megrey 1989). Figure 4 is a scatterplot of the variance of the natural logs of recruitment versus the autocorrelation (lag 1; ACF1) index. In this plot we find that the Pacific hake is unusual, not for its high variance, but for the combined high variance and negative autocorrelation function. The Alaskan pollack is nominally centered in the same scatterplot. It may be that the distributions from this collection of time series data may be partitioned by the ACF1. Since the environment tends to be autocorrelated, those stocks with ACF1 in the region 0.6–1 may be entrained to envi-

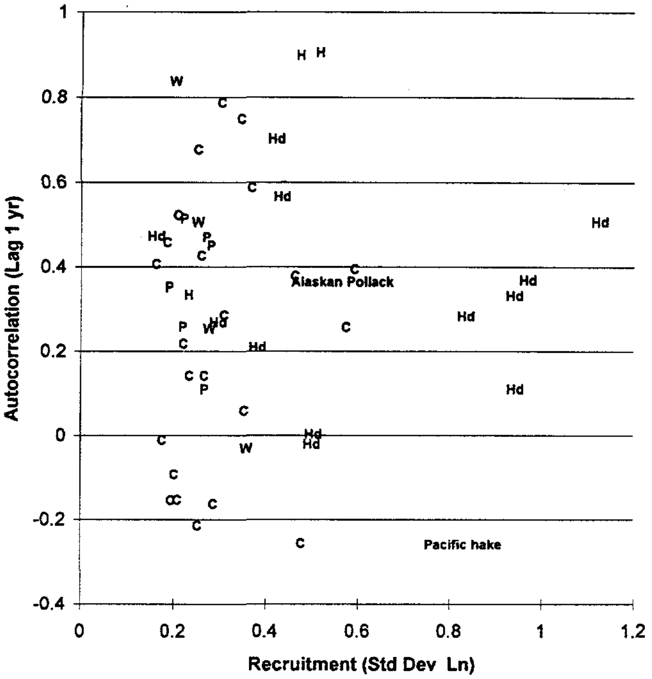

Figure 4. A scatterplot of interannual autocorrelation of the natural log of recruitment and standard deviation of ln recruitment for 49 stocks of gadoids—cod (C), haddock (Hd), pollack (P), hake (H), and whiting (W)) in the North Atlantic (Myers et al. 1990); Pacific hake (Dorn et al. 1993); and Alaskan pollack (Hollowed and Megrey 1989).

ronmentally induced autocorrelation. Those ACF1 in the range of .3–.6 may express only the continuity of large stocks tending to yield large recruitments and small stocks tending to yield small recruitments. The low positive ACF1 0–.3 may be moderate density-dependent lowering of sequential recruitments by way of within-cohort competition for food, slower growth, maturation at smaller sizes, and the like. The negative ACF1 area may be evidence for between-cohort cannibalism or some other more vigorous control on recruitment rate and, ultimately, population size.

What are some density-dependent controls on population growth? One usually refers to competition for food, given limits on production and thus carrying capacity. In addition, we could list aggregation and selectivity of predators, population growth of predators, shortened disease-transmission vectors, and, of course, combinations of these phenomena. Which life stage ("critical stage") would these affect? The compaction of the surviving larvae into the narrow juvenile brood zone is very appealing as a vulnerable stage for density-dependent control. What is the actual mechanism? The fact that we have not yet observed two adjacent larger year classes suggests that a highly successful year class populates a narrow coastal brood zone in sufficient density to influence the survival of the ensuing cohorts by consumption of limited food, by cannibalism on the new cohort, or by stimulating the population growth of the other predators in the brood zone.

ACKNOWLEDGMENTS

I acknowledge the editorial help and technical assistance of Anne Hollowed. One anonymous reviewer was particularly helpful in imposing a uniform organization of sections within the paper. Geoff Moser and John Hunter edited early drafts of this paper. Technical editing was by Julie Olfe. Most of the data assembly was accomplished by Rich Charter and Cindy Meyer. I especially acknowledge the massive amount of effort of the seagoing biological technicians who often work long hours under difficult conditions, and the laboratory technicians who carefully gather information through tedious bouts of sorting, counting, identifying, and measuring fish larvae. The service of the skippers and men of the many research vessels which have been the platforms for CalCOFI survey research over the past several decades is also credited here. The faults that remain are my own.

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A COMPARISON OF ZOOPLANKTON SAMPLING METHODS IN THE CALCOFI TIME SERIES

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ABSTRACT

We review changes in macrozooplankton sampling methods over the course of the CalCOFI time series (1949–present). After 1951, two major changes occurred: sampling depths were extended from 140 m to 210 m in 1969, and the 1.0-m-diameter bridled ring net was replaced with a 0.71-m-diameter bridleless bongo net in late 1977. We compare how these two changes affected the efficiency of collecting zooplankton biomass. We provide conversion factors between these sampling methods, supplemented by a description of the nonlinear relationship between wet and dry zooplankton biomass in the California Current system.

INTRODUCTION

Increased attention to long-term changes in world climate has renewed the scientific focus on measurement programs for detecting natural variations—and anthropogenic influences—over periods of decades or longer. The CalCOFI (California Cooperative Oceanic Fisheries Investigations) time series is among the very few oceanic measurement programs that permit such time scales of fluctuation to be discerned for biological properties. CalCOFI water-column measurements have illustrated the importance of large-scale interannual variations in the California Current system (Chelton et al. 1982; Roesler and Chelton 1987) and even longer-term, interdecadal variations in upper-ocean properties such as temperature, sea level, and zooplankton biomass (e.g., Roemmich 1992; Roemmich and McGowan 1995a, b). The sedimentary record has revealed natural, cyclical oscillations in pelagic populations of the Pacific sardine and northern anchovy (Baumgartner et al. 1992).

A cardinal concern for detecting and quantifying such long-term changes is the accuracy of sampling and analytical methods and the comparability of different methods that may be employed over time. A hallmark of the CalCOFI measurements is the attention given to calibration of biological, physical, and chemical methods, and the rigor with which different methodologies have been compared. The focus of this paper is on the principal methods used to sample the epipelagic macrozooplankton over the course of the CalCOFI time series. We analyze the efficiency of different sampling techniques for zooplankton biomass, in keeping with the tradition of careful attention to sampling methods.

What we now consider the CalCOFI time series began in 1949, although there were several ichthyoplankton surveys conducted from 1937 to 1941 (Hewitt 1988). Vertically stratified sampling on these early ichthyoplankton surveys showed that sardine eggs and larvae were distributed primarily in the upper 40 m of the water column, with none to be found below 70 m. Thus in the original standard tows that began in March 1949, 100 m of wire were paid out, for a nominal sampling depth of 70 m with a 45° wire angle (table 1). Beginning in 1951, the nets were deployed to depths of 140 m. Although it is not recorded why the depth was doubled at that time, the low diversity and abundance of zooplankton in the upper 70 m in daytime have been mentioned as factors by Edward Brinton and Joseph Reid (pers. comm.). The new depth was set at a nominal 140 m based on 200 m of wire out.

Subsequently there were two major changes in the methods used to sample macrozooplankton (table 1). (1) In 1969 the depth of hauls was increased to 210 m, and the net was changed from 0.55-mm-mesh silk to 0.505-mm-mesh nylon. The increase in sampling depth to 210 m (300 m of wire out) was made to encompass the vertical distribution of Pacific hake larvae. This increase was motivated by the onset of a large fishery on Pacific hake by the Soviet fishing fleet, amidst concerns about possible overfishing. The switch to an interlocking-monofilament nylon mesh was made because of the improved durability, lower cost, and improved filtration efficiency of the nylon mesh nets relative to silk. Although it was also determined that 0.333-mm mesh would retain an important fraction of anchovy eggs, the option to decrease the mesh size was not exercised because sorting fish larvae from the increased phytoplankton in finer mesh nets was much more costly. (2) In 1978 the standard sampling net was changed from a 1.0-m-diameter ring net to a 0.71-m-diameter bridleless bongo net because of the bongo net's improved collection of motile zooplankton (McGowan and Brown 1966). It is these two changes in methods that we wish to compare here. Although comparisons have been published of the catch efficiency of bongo and ring nets for individual eu-

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[Manuscript received February 27, 1995.]

TABLE 1
Standard CalCOFI Nets Used for Sampling Macrozooplankton

Cruises employed	Net mouth diameter (m)	Mesh size	Net type	Nominal depth (m)	Reference
4903–5009	1.0	0.55 mm[a] silk	Ring	70	Ahlstrom 1954
5101–6806	1.0	0.55 mm[a] silk[b]	Ring	140	Ahlstrom 1954; Smith 1971
6901–7712	1.0	0.505 mm nylon	Ring	210	Kramer et al. 1972
7712–present	0.71	0.505 mm nylon	Bongo	210	Smith and Richardson 1977

[a] Mesh opening after shrinkage (small posterior region of 0.25 mm mesh)
[b] Nylon substituted on some cruises in 1956–59 (Smith 1971)

phausiid species (Brinton and Townsend 1981) and for anchovy larvae (Hewitt 1980), there has been no such analysis for zooplankton biomass.

The reader should recall that in addition to the regular macrozooplankton time series, many other types of zooplankton samples have been and continue to be taken on CalCOFI cruises. These include the fine-mesh CalVet or Pairovet samples (Smith et al. 1985) taken in the upper 70 m of the water column on at least the first two of the quarterly cruises each year (the series with 0.150-mm mesh began in 1982). Neuston samples are taken by Manta net (Brown 1979, 0.505-mm mesh) on each cruise; this series began in 1977. Vertically stratified samples have been taken in conjunction with a variety of special studies. The above samples are available at the Planktonic Invertebrates Collection of the Scripps Institution of Oceanography, or the Southwest Fisheries Science Center of the U.S. National Marine Fisheries Service. However, this paper specifically addresses the methods employed in the long-term CalCOFI macrozooplankton sampling program.

METHODS

In all cases samples were taken by oblique hauls, with the hydrowire maintained at approximately 45° angles off the vertical on both descent and ascent. Further sampling details are furnished in Kramer et al. 1972 and the other references listed in table 1. Wet biomass of zooplankton was measured as displacement volume by standardized methods, following removal of animals >5 ml individual displacement volume (Kramer et al. 1972). This measure has the advantage that it is nondestructive and permits the entire sample to be used for other quantitative studies. Conversion from displacement volume to dry biomass is discussed below. Given the pairwise sampling designs, we used the Wilcoxon matched-pairs signed ranks test to test the null hypothesis of no difference between sampling methods.

Ring Net, 140 m vs. 210 m

The first comparison analyzed here is that of the ring net fished to 140 m (1.0-m-diameter, 0.55-mm silk mesh with small posterior region of 0.25-mm silk mesh), as deployed between 1951 and 1968, with a similar ring net of slightly different mesh size and composition (1.0-m-diameter, 0.505-mm nylon mesh throughout) fished to 210 m, as deployed from 1969 through 1977. The data reported here have been presented in tabular form with sampling details (Smith 1974). Briefly, samples were taken in randomized order between 2100 on 28 June and 0300 on 1 July 1968 at CalCOFI station 93.30 (32° 50.5'N, 117° 31.0'W), within 30–60 min. of each other. In one instance, an unusually high value of biomass was collected (838 ml 1000 m^{-3}; nylon mesh net sample at 1020), which was excluded from further analysis.

Ring Net vs. Bongo Net

This second analysis compares the characteristics of the 1.0-m (bridled) ring net (as deployed from 1969 through 1977) with a bridleless bongo net (as deployed from 1978 to the present; cf. McGowan and Brown 1966, but note that the bongo net is fished continuously open in CalCOFI sampling). The bongo nets used in this particular analysis had a mouth diameter of 0.60 m, though the standard CalCOFI bongo frame has a mouth diameter of 0.71 m. Both types of nets were of 0.505-mm-mesh nylon, and both were fished to 210 m, bottom depth permitting. Brinton and Townsend (1981) compared the catch efficiency of these two net designs for 12 species of euphausiids, each analyzed by length class. Their paper illustrates the two nets (note that the mesh size they reported should be corrected to 0.505 mm) and the sampling locations for the samples analyzed here. The data comparing total zooplankton biomass have not been previously published.

In this comparison, groups of samples were taken at three locations representing northerly, middle, and southerly sectors of the California Current system, on CalCOFI cruises 7501 and 7507. Net deployments were made while following a drogue. The stations occupied on cruise 7501 were 73.60 (12–13 Feb. 1975), 103.60 (21–22 Jan. 1975), and 137.50 (4–5 Feb. 1975); day samples were taken between 1000 and 1530 PST, night samples between 2000 and 0300. The stations on cruise 7507 were 70.60 (15–16 July 1975), 103.65 (28–29 June 1975), and 133.46 (12–13 July 1975); day samples were taken

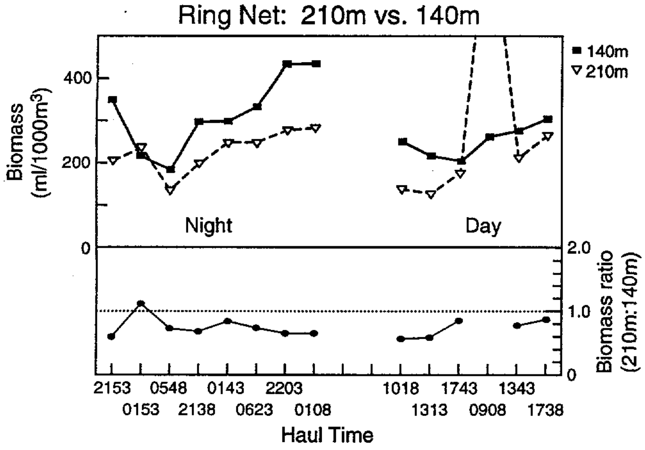

Figure 1. Comparison of zooplankton biomass collected by a 1.0-m-diameter ring net fished to either 140 m or 210 m. *Upper panel* indicates biomass; *lower panel* indicates the 210:140 biomass ratio; *dotted line* indicates a 1:1 ratio. One anomalously high daytime value was excluded from statistical analysis (data from Smith 1974).

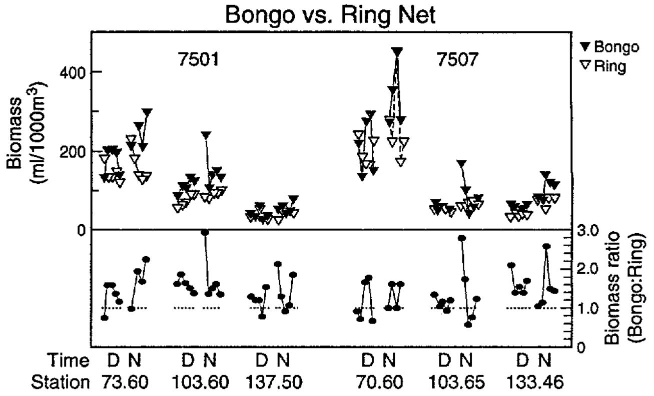

Figure 2. Comparison of zooplankton biomass collected by a 0.60-m-diameter bongo net with a 1.0-m ring net, both fished to 210 m. Comparisons were made on two cruises (CalCOFI 7501 and 7507), at three stations each, both day (*D*) and night (*N*). *Upper panel* illustrates biomass; *lower panel* indicates the 0.60-m bongo:ring net biomass ratio; *dotted line* indicates a 1:1 ratio.

between 1000 and 1615, night samples between 2200 and 0300. Samples were taken in groups of ten at each station, alternating regularly between bongo and ring net. Sample pairs were taken within 30–40 minutes.

The third comparison is also of a 1.0-m (bridled) ring net and a bridleless bongo net, both of 0.505-mm-mesh nylon. But in this comparison, the bongo net had a diameter of 0.71 m, the standard CalCOFI net used since cruise 7712. The data originate from five cruises (CalCOFI 7712, 7801, 7804, 7805, and 7807) with 11–22 pairs of samples from each cruise, usually taken within 30 minutes of each other. The lines sampled ranged from CalCOFI 60 to 130, the stations from 30 to 90. Euphausiid species comparisons, but not total zooplankton biomass, have been reported from some of these samples (Brinton and Townsend 1981). The biomass data are available from the senior author.

RESULTS

Ring Net, 140 m vs. 210 m

Comparisons of the zooplankton biomass per unit volume collected by a ring net fished to 140 m with a net fished to 210 m showed that in 12 out of 13 valid comparisons the biomass density was greater in the shallower samples (Wilcoxon signed rank test, 2-sided, $P <$ 0.01; figure 1). This result was previously reported in tabular form by Smith (1974). The ratio of biomass determined by the two methods (210 m:140 m) is 0.731 ± 0.091 ($\bar{x}$ ± 95%) and did not differ between day and night ($P >$ 0.50, t-test).

Ring Net vs. Bongo Net

The second comparison entailed contrasts between the 0.60-m bongo net and 1.0-m ring net, both sampling between 210 m and the surface (figure 2). There was a significant difference between biomass determined by the two nets (Wilcoxon, $P <$ 0.0001), with the bongo collection greater than the 1-m collection in 46/58 comparisons. For further statistical tests the biomass ratio (bongo:ring net) for each pair of samples was log$_e$-transformed, which resulted in homogeneity of variances (Bartlett's test = 19.29, P = 0.09) among the 12 groups of samples (i.e., day and night comparisons at each of six stations). There was no significant difference in bongo:ring net biomass ratio among these 12 groups (1-way ANOVA, $F_{11,46}$ = 0.998, $P >$ 0.40; see figure 2). Although the sampling design may appear appropriate for a nested analysis of variance, a nested ANOVA cannot be applied because subordinate-level groupings were fixed rather than free to vary randomly (Sokal and Rohlf 1981). There was no significant difference ($P >$ 0.10, t-test) between the day (1.320 ± 0.132, $\bar{x}$ ± 95%) and night (1.513 ± 0.228) ratio, resulting in an overall 0.60-m bongo:1.0-m ring net biomass ratio of 1.413 ± 0.128 (N = 58).

The third comparison was similar to the second, but employed the 0.71-m bongo (figure 3). The anomalously high biomass ratios of 4.9 and 9.7 were excluded from statistical analysis because they doubtless reflected patches of zooplankton and destabilized the variances. There was a significant difference between the biomass collected by the two nets (Wilcoxon, $P <$ 0.0001), with bongo collections greater than ring net collections in 101 of 138 comparisons. Following log$_e$ transformation (Bartlett's test = 9.06, $P >$ 0.40), 1-way ANOVA detected significant heterogeneity in the ratio of bongo:ring net biomass among trials ($F_{9,70}$ = 4.882, $P <$ 0.0001), where each of the ten trials is a series of day or night comparisons on a cruise. The trials that differed most consistently from others (by Tukey HSD multiple comparisons, $P <$ 0.05) were the day values on cruise 7801 and both

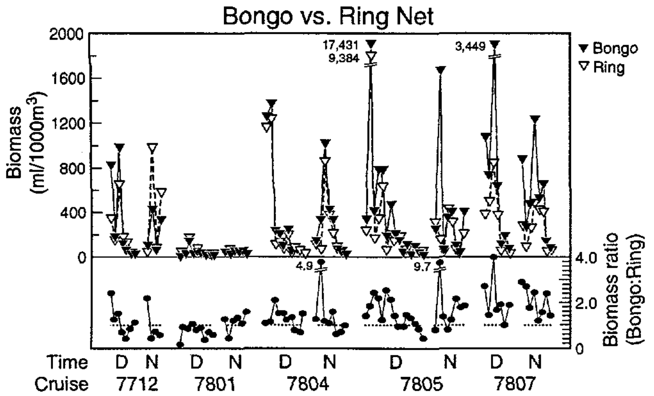

Figure 3. Comparison of zooplankton biomass collected by a 0.71-m-diameter bongo net with a 1.0-m ring net, both fished to 210 m. Comparisons were made on five cruises (CalCOFI 7712, 7801, 7804, 7805, 7807), both day (*D*) and night (*N*). Within a cruise and time of day, stations are ordered from inshore to offshore and then from north to south. *Upper panel* illustrates biomass; *lower panel* indicates the 0.71-m bongo:ring net biomass ratio; *dotted line* indicates a 1:1 ratio. Two anomalously high biomass ratios were excluded from statistical analysis.

day and night values on cruise 7807. In the absence of further information on the specific reasons for these departures on these particular cruises, we pooled ratios to obtain an estimator of the average biomass ratio. For the five cruises 7712 to 7807, the average daytime biomass ratio (1.341 ± 0.214; $\bar{x} \pm 95\%$, 0.71-m bongo:1.0-m ring) did not differ ($P > 0.50$, t-test, df = 78) from the night ratio (1.404 ± 0.238). The overall average ratio was 1.366 ± 0.156 (table 2).

The diameter of the bongo net (0.60 m or 0.71 m) had no detectable effect on the biomass ratio with the 1-m ring net ($t_s = 0.44$, $P > 0.50$).

DISCUSSION

These results illustrate that changes in zooplankton sampling methodologies over the course of the CalCOFI time series have resulted in quantifiable differences in zooplankton biomass. This result is not surprising, since the original motivation for introducing these changes was improving the effectiveness of sampling the epipelagic ichthyoplankton and holozooplankton.

Although the analysis of how changes in depth affect sampling would surely benefit from an increased number of samples for comparison, we see no reason to expect that the results obtained in the vicinity of station 93.30 should differ markedly from results in other regions of the California Current system (CCS). By analogy, the bongo:ring net comparison in this geographic region alone was quite comparable to that of the rest of the CCS. If we consider only those bongo:ring net comparisons made in this same region (lines 90 and 93, $N = 13$ comparisons), we obtain a biomass ratio of 1.393 ± 0.462 ($\bar{x} \pm 95\%$), which has a broader confidence interval, but similar mean value (1.366 ± 0.156, $N = 80$) to the biomass ratio obtained for the sequence of five cruises in several different geographical locations. Furthermore, the observation of decreasing biomass density (i.e., zooplankton displacement volume per unit volume of water filtered) upon extending sampling to a deeper segment of the water column (from 140 to 210 m) is sensible in terms of the general vertical distribution of zooplankton. The biomass of oceanic zooplankton has long been recognized to show a general decline with depth (e.g., Vinogradov 1970).

TABLE 2
Summary Conversion Factors

To convert:		Multiply (A) by:		
			($\bar{x} \pm 95\%$)	
From (A)	To (B)	Day	Night	Day-night average
1 m ring 0.550 mm silk 140 m	1 m ring 0.505 mm nylon 210 m	0.719 ± 0.185	0.738 ± 0.135	0.731 ± 0.091
1 m ring 0.505 mm nylon 210 m	0.71 m bongo 0.505 mm nylon 210 m	1.341 ± 0.214	1.404 ± 0.238	1.366 ± 0.156
1 m ring 0.550 mm silk 140 m	0.71 m bongo 0.505 mm nylon 210 m	0.964	1.036	0.998
Displacement volume ($\mu l\ m^{-3}$)	Ash-free dry mass ($mg\ m^{-3}$)	—	—	$AFDM = 0.0227\ DV^{1.2333}$
Total dry mass ($mg\ m^{-3}$)	Ash-free dry mass ($mg\ m^{-3}$)	—	—	0.854
>505 µm Ash-free dry mass ($mg\ m^{-3}$)	Total >202 µm Ash-free dry mass ($mg\ m^{-3}$)	1.538	1.391	1.433

The relations in the last three rows originate from Ohman and Wilkinson 1989.

The improved collection of biomass by the bridleless bongo nets relative to the 1.0-m bridled ring net is probably attributable to reduced net avoidance, although Brinton and Townsend (1981) pointed out that the difference in diameters of the nets to some extent confounds attribution to the presence or absence of a bridle alone. These authors also observed that the relation of catch efficiency of the two net designs varies by species and by developmental stage. For most of the euphausiid species analyzed by Brinton and Townsend, the bongo was a more effective collector of juveniles and adults, while the 1.0-m ring net was a better collector of young larval stages. Because euphausiid biomass is generally dominated by later stages, the bongo was generally a much preferred collector. Hewitt (1980) found that large anchovy larvae avoided the bongo net less than the 1.0-m net.

There is little doubt that the best approach to determining the effects of changes in sampling methods would be a taxon-by-taxon analysis in the manner conducted by Brinton and Townsend and by Hewitt. But this may not always be practicable because of the large number of taxa concerned. Where the integrated epipelagic zooplankton biomass is of interest, approximate corrections can be obtained from the information provided in table 2. The corrections applicable to the two major transitions in sampling methods (i.e., beginning in 1969, line 1; and beginning in 1978, line 2) can be multiplied to give an approximate correction to express the pre-1969 biomass values in terms of the post-1977 methods (table 2, line 3). Remarkably, the product of these two numbers is 0.998 (day-night average), suggesting that the pre-1969 and post-1977 mean biomass values are quite comparable, despite the differences in depths and net styles. However, in the intervening years (1969–1977) a correction is clearly necessary to render these biomass values comparable to those from preceding and following years. To obtain bongo-equivalent values between 1969 and 1977, the 1.0-m ring net values should be multiplied by 1.366 ± 0.156. Roemmich and McGowan (1995b, correcting for an error in Roemmich and McGowan 1995a) did not take into account this change, and therefore their time series needs to be corrected over this nine-year interval. Application of our correction factor to the results of Chelton et al. (1982) and Roesler and Chelton (1987) would slightly increase the long-term mean biomass and thus slightly alter the temporal pattern of anomalies from this mean.

Dry measures of biomass are related in a nonlinear way to wet biomass (Wiebe 1988; Ohman and Wilkinson 1989), and in some circumstances it may be useful to be able to convert between them. Accordingly, in figure 4A the relation between ash-free dry mass and displacement volume is described by a power function, based on 160 comparisons made on four CalCOFI cruises (Ohman and Wilkinson 1989). This regression applies to the macrozooplankton (>505 µm); see Ohman and Wilkinson for the relation applicable to zooplankton collected by 202-µm mesh nets.

For comparison with other data, the fit of a model

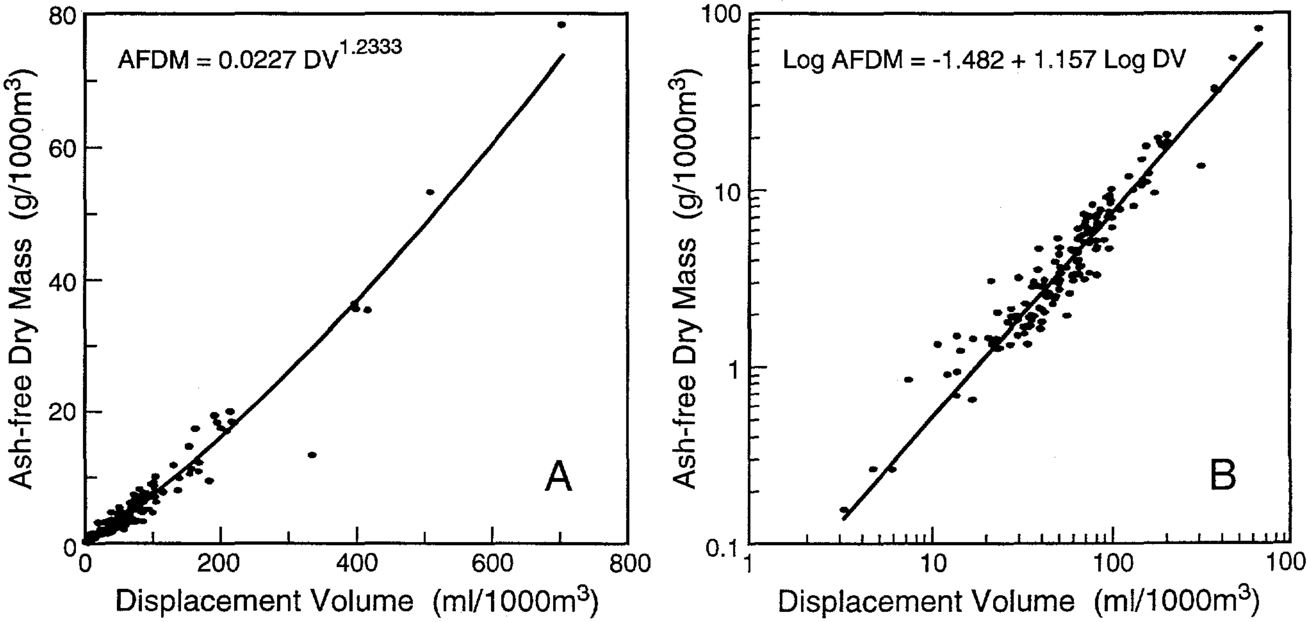

Figure 4. Relation between zooplankton biomass determined as ash-free dry mass and as wet displacement volume, based on samples collected on four CalCOFI cruises (8609, 8611, 8703, 8705; data from Ohman and Wilkinson 1989, >505 µm size fraction, $N = 160$). *A*, Nonlinear regression fitted by the Simplex method ($r^2 = 0.971$); *B*, geometric mean functional regression fitted to $\log_{10}$-transformed data ($r^2 = 0.917$).

II or functional regression to the $\log_{10}$-transformed values is shown in figure 4B, though the nonlinear fit in figure 4A is preferred because of the higher r^2 and lower serial correlation of residuals. The slope of the relation in figure 4B (1.157) is nearly identical to the slope of 1.156 obtained by Wiebe (1988, equation 4) when his equation is rearranged in the same manner as shown here and expressed in common units. The present intercept (-1.482) is lower than that for Wiebe's regression (-1.339), as expected, because we used ash-free dry mass whereas he used total dry mass. Converting the present data to total dry mass (=1.171 × AFDM; table 2, line 5) still produces a slightly lower intercept. The 15% difference between the two regressions may be attributed to the determination of dry mass from frozen samples in Wiebe's (1988) study and from Formalin-preserved samples in this study, or perhaps to a difference in faunistic composition of the two groups of samples. Another useful quantity is the relation between zooplankton biomass collected by the 505-μm net and the total zooplankton biomass greater than 202 μm (table 2, line 6). Although such expressions may be useful as general conversions, the temporal and spatial variability associated with them suggests that caution be exercised in their application.

In conclusion, we have verified that the two major methodological changes associated with the CalCOFI macrozooplankton time series have resulted in significant, but quantifiable, changes in measures of zooplankton biomass. Attention to these changes should facilitate rigorous analysis of long-term variations in zooplankton biomass—and of their underlying causes—in the California Current ecosystem.

ACKNOWLEDGMENTS

We thank Annie Townsend and Kevin Tinsley for helping to prepare data for analysis, and we express appreciation to the team of CalCOFI technicians for their sustained efforts. This work was supported in part by the Marine Life Research Group of SIO and by NSF OCE90-19639.

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PRIMARY PRODUCTION AND CHLOROPHYLL RELATIONSHIPS, DERIVED FROM TEN YEARS OF CALCOFI MEASUREMENTS

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ABSTRACT

On each CalCOFI cruise since 1984, primary production has been estimated at six depths on one station per day (the station occupied closest to noon). This is only 20% of the regularly occupied stations and leads to high variability in the estimate of mean production per cruise. We examine 500 stations occupied between 1984 (CalCOFI 8401) and 1994 (CalCOFI 9401) at which both production data and chlorophyll data were collected. A good relationship is found between the logarithm (base 10) of chlorophyll a integrated from the surface to 200 m (Chl) and integrated half-day primary production (*P*), standardized for potentially available half-day sunlight (L'):

$$P/L' = -617.3 + 495.3\ (\log_{10} \text{Chl})$$

where the light scaling factor, L', is approximated as

$$L' = 2.625 + 1.125\cos\left[\frac{360}{365}(\text{Julian day}-173)\right]$$

This regression is highly significant and explains 64% of the variability of the standardized production. Thus the chlorophyll data may be used as a proxy for primary production, providing a more detailed map of the spatial distribution of production and a better cruise mean estimate than is possible from the productivity stations alone. The success of this regression is examined for CalCOFI cruises 9403, 9408, and 9410.

INTRODUCTION

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has been surveying the California Current for more than forty years. In 1984 and 1985 there were major changes in spatial and temporal coverage of the cruises (Hewitt 1988). Since 1985, cruises have been conducted quarterly and have typically sampled 60–66 stations. It is important for our purposes that each cruise since January 1984 has included routine measurements of primary production and chlorophyll. Measurements made at each station now include temperature, salinity, oxygen, and nutrients above 500 m, and chlorophyll and macrozooplankton above 200 m. Estimates of primary production, however, are made at only one station per day, for a total of 14–16 estimates per cruise. Production measurements are not necessarily made on the same stations on each cruise.

High phytoplankton biomass and high production are usually restricted to a disproportionately small fraction of the survey area. Whether the complete grid of stations adequately samples this region is debatable. Almost certainly the restricted set of 16 noon stations does not.

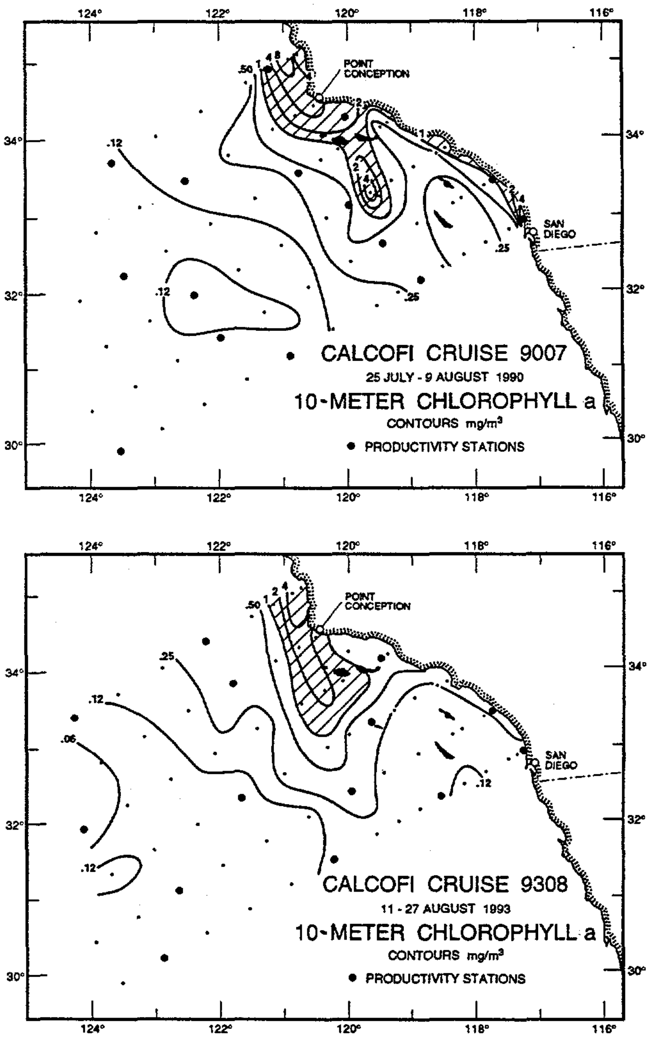

Figure 1. Locations of productivity stations on two summer cruises, and contours of chlorophyll concentration at 10 m. Contours are half or double the adjacent contour values. *Hatching* denotes chlorophyll ≥1 mg/m³.

[Manuscript received January 30, 1995.]

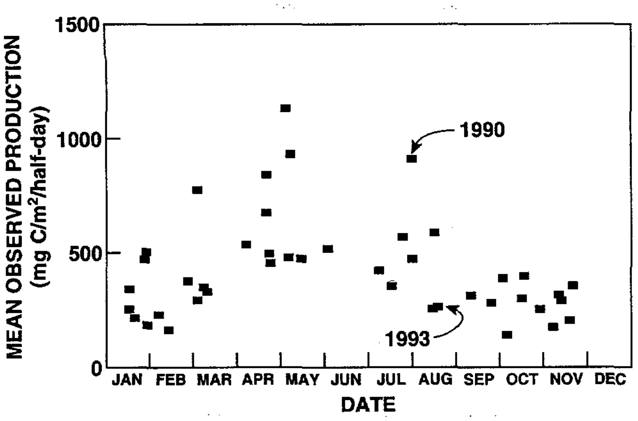

Figure 2. Seasonal cycle of measured production values, as cruise means, Jan. 1984–Jan. 1994, for data within the standard CalCOFI area, that region occupied by all cruises. Mean values for the summer cruises of 1990 and 1993 (figure 1) are indicated.

As a consequence, high sampling variability is associated with the mean production estimate on each cruise. This can be seen in a comparison of the summer cruises of 1990 and 1993 (figure 1). In both cruises, a tongue of elevated chlorophyll extended SE from Point Conception. In 1990, 3 of the 15 production stations were located in the region where near-surface chlorophyll exceeded 1 mg/m^3. The mean water-column production for that cruise is the highest observed in the months of July or August since measurements were started in 1984 (figure 2). In contrast, none of the production stations in 1993 were in the high-chlorophyll region. The mean production for 1993 is 29% of that measured in 1990 and is the second lowest observed in July or August.

The difference between these cruises seems due in large part to differences in the locations of the noon stations. This sampling variability might be reduced if a satisfactory relationship could be established between production and the measurements available for all stations. This relationship would allow more complete spatial coverage of production estimates, which would improve the mean estimates. The feasibility of this approach is suggested by an earlier study (Hayward and Venrick 1982), which established a linear relationship between production and chlorophyll on CalCOFI cruises 8105 J and 8105 NH. In this paper we develop an empirical relationship between total production, potential surface irradiance, and chlorophyll integrated through the upper 200 m. This algorithm appears to remove much of the variability between cruise mean production estimates.

METHODS

The Study Area

All of the observations come from within the region bounded by CalCOFI line 93 on the south, line 77 on the north, and stations XX.120 on the west (figure 3). This region roughly limits the two cruise patterns followed since 1985. However, a minor shift between patterns in 1986 (between cruises 8609 and 8611) introduced changes in spatial coverage that may increase the between-cruise variability of the data. In order to minimize this effect, several of the following analyses (e.g., figures 2 and 9 and table 1) include only data collected along lines 77, 80, 90, and 93 from the coast to station XX.100, and along lines 83 and 87 from the coast to station XX.70. Because this subset is common to both cruise patterns, it is referred to as the standard data set (figure 3), and the restricted region is referred to as the standard region. The spatial restriction of the data increases the calculated (unweighted) cruise mean by an average of 13%. No correction is made for stations missed because of weather or other unpredicted events.

To weight individual stations by area, the CalCOFI region is divided into 65 subregions, 47 in the standard region (figure 3). All data from within each subregion are pooled, and the resulting mean is weighted by the area of the subregion, indicated in figure 3 by the small numbers in the lower left corner of each region.

The Data

The chlorophyll data considered in this paper are those obtained from the standard hydrographic cast made at each station. Chlorophyll a concentrations are determined by the standard fluorometric method (Yentsch and Menzel 1963; Holm-Hansen et al. 1965). Before 1990, samples were filtered onto GF/C filters, which have a nominal retention size of 1.2 mμ. Thereafter, GF/F filters (0.7 mμ) were used. Comparison between the retention of the two filters, conducted in the central Pacific and in the CalCOFI study area on cruise 8105-J, indicated that GF/F filters retain about 15% more chlorophyll than GF/C filters at chlorophyll concentrations below 0.5 mg/m^3; at higher chlorophyll concentrations, this bias is negligible (Venrick and Hayward 1984). This filter change does not seem to influence the relationships discussed in this paper. The slopes of the regression lines before and after the filter change are not significantly different ($p >> 0.25$). The mean concentration of chlorophyll has decreased since 1990, but the effect of the filter change would be to increase recent values. Chlorophyll has been integrated to the deepest sample or 200 m, whichever is less, by means of the trapezoidal rule for numerical integration.

Primary production is estimated from the uptake of ^{14}C during half-day simulated in situ incubations (Scripps Institution of Oceanography 1994). Light penetration is estimated from the Secchi disk depth, assuming that the extinction coefficient is constant with depth and that the 1% light level is three times the Secchi depth. Samples for production estimates are collected with Niskin-type

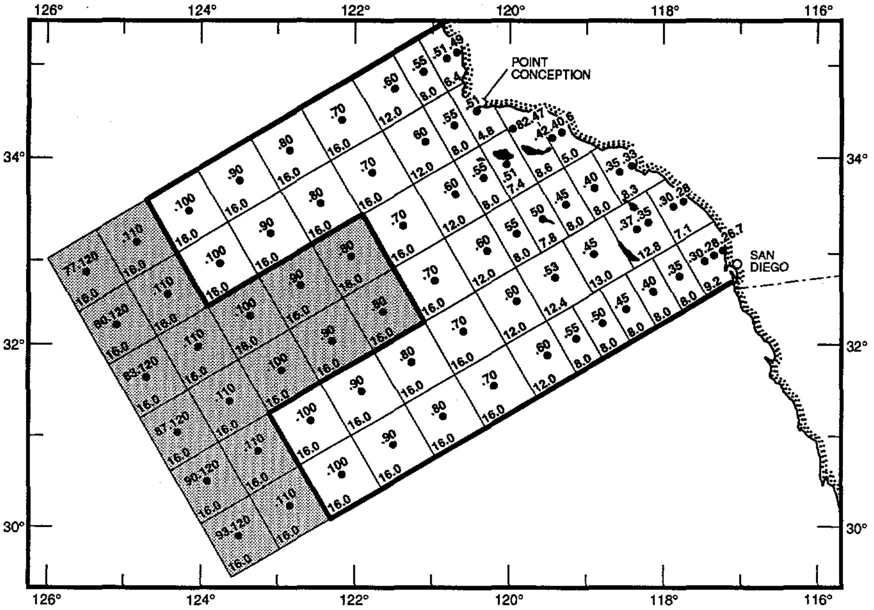

Figure 3. The general CalCOFI area since 1985, showing the 65 subregions used for weighting productivity data. Each subregion is centered around a station, indicated by the *dot* and station designation. All observations and estimates within each region are pooled and weighted by the spatial area, where the weighting factor (f) is indicated in the lower left corner of each box, and $f \times 10^2$ is the area in n.mi.^{2}. The *unshaded area* indicates the standard region, common to all cruise patterns; the *shaded area* indicates stations that were not occupied consistently.

bottles from six depths, the bottom depth being that reached by about 0.2%–0.5% of the surface irradiance (100–150 m in offshore waters). From each depth, samples are placed in two clear bottles and one dark (control) bottle. Each sample is inoculated with 10 µCi of ^{14}C as $NaHCO_3$. Incubations are carried out between local apparent noon and twilight in on-deck incubators cooled with surface seawater and equipped with neutral-density screens to simulate light intensities at the original depths of the samples. After incubation, samples are filtered through Millipore HA filters, acidified, and immersed in scintillation fluor until returned to SIO, where the radioactivity is determined with a scintillation counter. Uptake values are corrected for dark uptake and integrated to the deepest sample. Values are reported as carbon fixed per square meter per half-day. In the Southern California Bight, 24-hour production is approximately 1.8 times our half-day values (Eppley 1992).

Starting in August 1993, productivity casts have been merged with the standard hydrographic casts so that samples for productivity and chlorophyll come from the same bottles. Before that, the casts for productivity samples were separated from the standard hydrographic casts at the station by 0.5 to 3 hours.

Cloud cover is estimated as octas of sky cover at each daylight station. We have used the mean of cloud cover at the noon station and at the following station as an index of the sky conditions during incubation.

RESULTS

In the CalCOFI data, the most successful linear relation between integral chlorophyll and integral production is semilogarithmic. However, the parameters of the regressions vary seasonally (figure 4). Although the slopes of the regressions of spring and summer data are indistinguishable, as are those of fall and winter, the regression slopes of spring and summer are significantly greater than those of fall and winter ($p < 0.003$). This suggests an influence from seasonally varying parameters such as the light regime.

On CalCOFI cruises in 1969–72, direct measurements of daily incident radiation were made with an Eppley pyranometer (Owen and Sanchez 1974). Values from the study area are plotted in figure 5. There is considerable scatter in these measurements, presumably due to variable fog and cloud cover, but the maximum observed values approach those derived from the Smithsonian tabulated values for total daily solar radiation at 32.5°N corrected for 75% atmospheric transmission (List 1984, tables 132–135). A simple expression for potential irradiance is given by a cosine approximation to the Smithsonian values:

$$L(\text{cal} \times 10^{-6}/\text{m}^2/\text{day}) = 5.25 + 2.25\cos\left[\frac{360}{365}(\text{Julian day} - 173)\right]$$

where L is the potential daily irradiance. L is a function of both day length and sun elevation. We halve L to

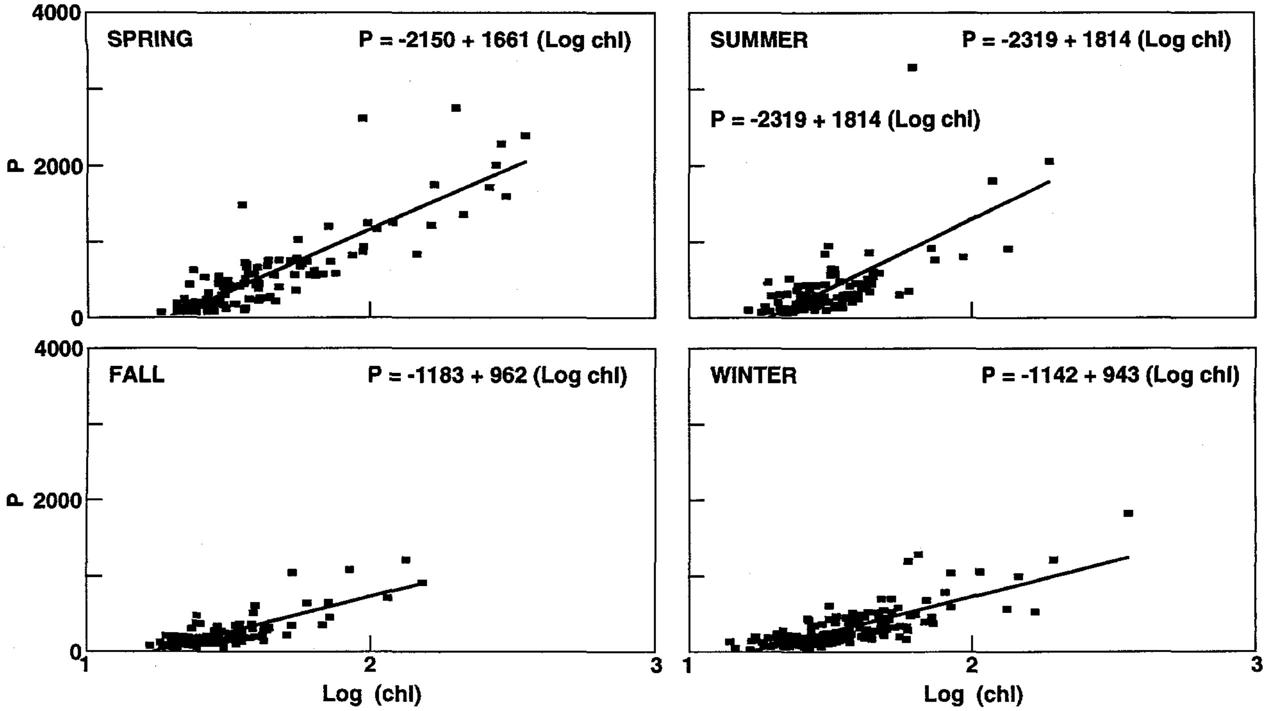

Figure 4. Regressions of observed integral production (P, mgC/m²/half-day) on log integral chlorophyll (Chl, mg/m²) for data divided into seasons: winter (Jan.–Mar.); spring (April–June); summer (July–Sept.); fall (Oct.–Dec.).

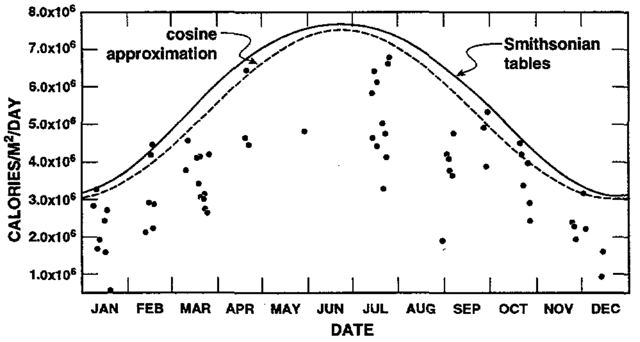

Figure 5. Measurements of total irradiance on CalCOFI cruises within the study area, 1969–72 (Owen and Sanchez 1974). The *dashed curve* indicates the Smithsonian tabulated values at 32.5°N adjusted for 75% atmospheric transmission (List 1984). The *solid curve* indicates the cosine function (L) used in this study to approximate the Smithsonian values.

make it comparable to our half-day production estimates:

$$L'(\text{cal} \times 10^{-6}/\text{m}^2/\text{half-day}) = 2.625 + 1.125\cos\left[\frac{360}{365}(\text{Julian day} - 173)\right] \quad (1)$$

Since L' is used only as a scaling factor, this half-day adjustment is not needed; but it may serve to avoid future confusion. At the equinox, L' changes by 12% of its annual range during a two-week period, the duration of a typical cruise. We have used daily values of L' in all of our calculations; close to the solstices it may be satisfactory to apply a constant value to the data from each cruise, using L' determined for the midpoint of that cruise.

When the observed rates of integral production (P, in mgC/m²/half-day) are standardized to potential irradiance by dividing by the cosine approximation for half-day irradiance (L', in cal × 10^{-6}/m²/half-day), the slopes of the seasonal regressions on log (base 10) chlorophyll (Chl, in mg/m²) become indistinguishable (slopes = 508, 536, 508, and 494 for spring, summer, fall, and winter, respectively; $p > 0.25$). Thus all the data can be combined into a single expression:

$$P/L'(\text{mg C/cal} \times 10^{-6}) = -617.3 + 495.3\ (\log_{10} \text{Chl}) \quad (2)$$

This regression accounts for 64% of the variability in standardized production and is highly significant (figure 6; $p < 0.001$). The regression will occasionally yield negative values of expected production. In the following applications, we have set such negative values to zero.

When this relationship is examined for the 43 individual cruises that make up the combined data set, a spectrum of fits is apparent. In some cases, regression 2 gives an excellent approximation of the relationship seen on a single cruise; in other cases the fit is poor. But in most instances in which the overall regression fails to describe the relationships within a cruise, all production stations were located in low-biomass regions, so there

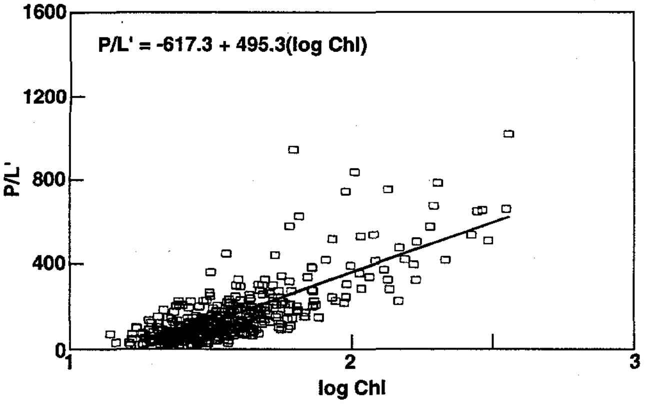

Figure 6. Regression 2: integral production (P, mgC/m^2/half-day), standardized to potential irradiance (L', cal. × 10^{-2}/half-day) on the logarithm of integral chlorophyll (Chl, mg/m^2) over all data; $n = 499$; $r^2 = 0.64$.

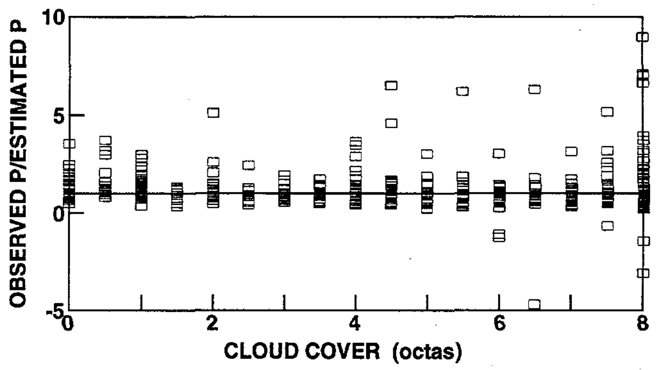

Figure 7. Relationship between local cloud cover (in mean octas, measured at the noon and the first afternoon stations) on the error about regression 2 (figure 6), where the error is expressed in relative terms as observed production/estimated production. A *horizontal line* at P/P' = 1.0 is provided for reference. A few points outside the range −5 to +10 are not shown.

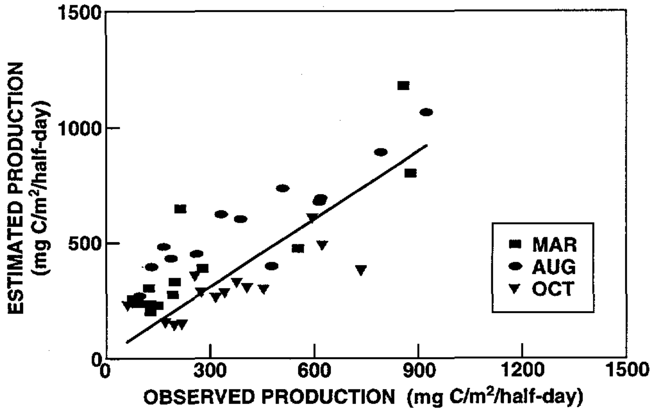

Figure 8. Performance of regression 2 on the three most recent CalCOFI cruises (9403, 9408, and 9410). The *solid line* indicates observed production = estimated production. These data were not used in the development of the regression.

are no observations of elevated production to define the relationship. To the extent that regions of elevated biomass and presumably production were present but not sampled at the noon stations, these cruises are precisely the ones for which this procedure is designed.

We have examined the residuals about regression 2 to see whether either nutrients or local cloud cover might explain some portion of the residual variability. There is a detectable positive influence of the surface nitrate concentration on production. Inclusion of surface nitrate (N, in μM/L) as an independent variable gives a regression:

$$P/L' = -572.9 + 462.2\ (\log_{10}\text{Chl}) + 11.7\ (N)$$

However, the coefficient of determination increases by less than 2% over that of regression 2. We do not believe that this level of fine-tuning is justified, and we have chosen not to include surface nitrate in our final regression. We have not explored the numerous other ways in which nutrient distributions might be incorporated into the regression.

Incorporation of local cloud cover is more of an intellectual exercise than a practical one, since local sky conditions are not available for stations occupied at night. Nevertheless, as figure 5 illustrates, the potential irradiance gives a poor estimation of actual incoming radiation, and much of the discrepancy is almost certainly due to local clouds and fog. However, neither the absolute nor relative magnitudes of the deviations of observed production from predicted production show any relationship with cloud cover other than a slight tendency for production to be overestimated (i.e., observed production depressed) when cloud cover is 100% (figure 7). This result is comparable to that reported by Eppley et al. (1985) from the Southern California Bight, where they found no relationship between production and incident radiation during 21 out of 22 cruises. The sole exception was a cruise during early March when several days were extremely foggy, and photosynthesis was correspondingly depressed.

To test the performance of regression 2, we apply it to data collected on cruises 9403, 9408, and 9410, which are not considered in the development of the regression equation. The production estimates derived from ^{14}C uptake experiments are compared with estimates of standardized production derived from chlorophyll measurements on the same station (i.e., regression 2), multiplied by the appropriate light factor (regression 1). For the data from March and August, the algorithm tends to overestimate the actual production (figure 8). In October, the reverse is true. Clearly, the estimate at any single station may be in error by a considerable amount, but as data are averaged, the overall agreement improves.

To illustrate the effect of our procedure on the spatial resolution of production, we apply regression 2 to the data from CalCOFI cruise 9308, a cruise in which

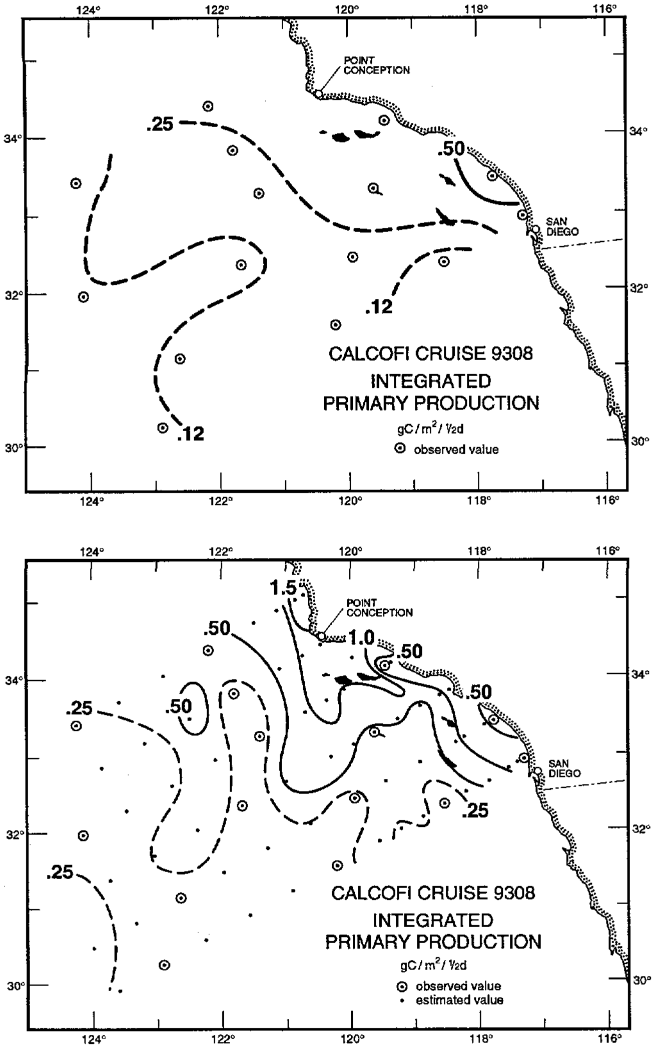

Figure 9. Spatial patterns of primary production on CalCOFI Cruise 9308 based on the 14 observed values of integral production (*top*) and on this set supplemented with 53 estimates derived from regression 2 (*bottom*).

there are no productivity measurements within the region of high chlorophyll extending south from Point Conception (figure 1, bottom). The 14 observed values of integral production are too widely spaced to properly contour, but they suggest nearly monotonic production values (figure 9, top). When these values are supplemented with the 53 estimates based upon integral chlorophyll and irradiance, a tongue of elevated production is indicated (figure 9, bottom), in agreement with the pattern of elevated near-surface chlorophyll. Although our procedure appears to perform as expected, we have no direct measure of the actual improvement in the estimate of cruise mean production.

A major motivation for this study is the reduction of error in our estimate of mean production per cruise, and hence a reduction in between-cruise variability. To examine how our procedure affects this variability, we apply our algorithm for standardized production to the past ten years of CalCOFI data. For those stations on which production was not directly determined, production (mgC/m^2/half-day) is estimated from chlorophyll and the appropriate light factor (L'). These estimates are combined with the observed data and weighted by area to reconstruct cruise mean values based upon all stations occupied within the study area (table 1).

TABLE 1

Cruise Mean Production (mgC/m2/half-day): Observed Data (*P*, Unweighted) Compared with Values Supplemented by Estimates Derived from Chlorophyll Data According to Regression 2 (*P*', Weighted by Area)

	All stations				Standard area			
	Observed		Supplemented		Observed		Supplemented	
Cruise	P	n	P'	n	P	n	P'	n
8401	307.0	18	167.2	62	336.7	15	174.5	56
8402–3	716.4	32	385.4	75	772.1	29	431.2	68
8404	762.0	18	695.6	62	839.4	16	751.3	56
8405	478.5	7	562.7	52	517.9	5	611.1	45
8407	338.4	17	403.1	59	356.8	15	442.3	53
8410	250.9	18	249.6	59	254.8	17	251.6	53
8502	346.8	10	295.8	52	374.1	9	328.6	47
8505	883.7	17	564.4	63	933.2	16	624.1	59
8508	224.8	13	237.6	65	252.4	11	273.8	56
8511	161.6	11	150.7	62	178.5	9	177.4	54
8602	152.1	12	169.2	56	161.2	11	187.6	52
8605	406.3	12	501.4	61	470.9	10	589.4	53
8609	244.4	12	282.7	65	284.2	10	335.4	55
8611	190.1	14	185.1	67	205.7	11	203.9	55
8703	305.0	13	306.2	70	346.5	10	349.1	59
8705	413.3	13	397.8	70	476.0	10	456.4	58
8709	267.5	13	284.1	69	318.7	10	336.5	57
8711	310.5	15	164.7	70	358.0	12	200.6	58
8801	427.3	12	352.2	65	469.0	9	381.5	53
8805	1076.2	11	676.6	59	1132.8	10	701.8	54
8808	495.8	15	465.3	69	589.3	12	563.1	57
8810	338.9	14	252.8	75	400.4	11	289.0	60
8901	425.7	14	316.5	67	499.1	11	358.4	54
8904	417.0	13	439.8	67	492.5	10	508.9	55
8907	477.9	15	501.2	65	570.0	12	561.0	55
8911	280.0	13	223.7	67	321.8	10	249.4	55
9003	314.1	13	478.0	65	327.7	12	505.0	58
9004	369.8	11	328.3	51	452.7	8	404.7	43
9007	774.1	15	488.0	65	911.7	12	556.7	53
9011	265.5	14	230.6	67	295.6	10	249.8	54
9101	236.2	14	264.6	63	250.1	12	279.8	54
9103	274.6	12	290.5	56	289.3	11	348.1	46
9108	420.3	14	393.6	69	475.2	11	445.6	56
9110	135.2	12	192.2	67	144.8	9	212.8	52
9202	225.2	13	177.8	64	225.2	10	197.5	52
9204	571.9	15	540.7	66	671.6	12	642.1	54
9207	366.3	14	410.5	66	422.9	11	451.6	54
9210	331.8	12	264.1	64	390.2	9	309.3	52
9301	189.9	13	144.9	66	209.0	10	169.1	54
9304	452.1	15	464.4	66	532.0	12	561.3	54
9308	235.5	15	376.2	66	265.8	12	425.2	54
9310	277.8	16	237.4	66	304.4	13	273.6	54
9401	170.8	16	179.3	66	182.6	13	201.2	54

When the reconstructed cruise means are plotted by season in a manner analogous to figure 2, much of the scatter about the emerging seasonal curve is removed (figure 10). The two cruises discussed earlier (9007 and

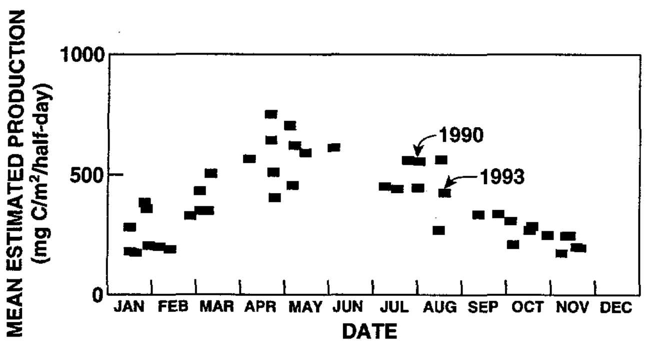

Figure 10. Seasonal cycle of supplemented production values, as cruise means, Jan. 1984–Jan. 1994, for data within the standard CalCOFI area (table 1). Mean values for the summer cruises of 1990 and 1993 are indicated for comparison with figure 2.

9308, figures 1 and 2) are no longer outliers. Thus we do accomplish a reduction of between-cruise variability, which is one indication of the success of our procedure for improving the spatial averages of production.

DISCUSSION

For nearly forty years, oceanographers have proposed algorithms relating primary production to pigments (e.g., Ryther and Yentsch 1957; Steele 1962). Many studies have one of two objectives. Some work toward developing a mechanistic, mathematical model relating photosynthesis to pigments and light, in the hopes that primary production can be determined directly from in situ measurements (Kiefer and Mitchell 1983; Bidigare et al. 1987; Smith et al. 1989). Such studies incorporate detailed information on the radiant energy field, pigment composition, and physiological parameters. Other studies are directed toward determining global production from satellites, and these studies emphasize parameters that can be remotely sensed, although many of the more successful of such studies also incorporate estimates of physiological parameters (but see the discussion of Occam's razor in Balch 1993). Balch et al. (1989, 1992) give a recent review of the development and performance of remote sensing algorithms. No previous study, however, is exactly comparable to the regression presented here because of differences in ultimate goals, parameters, or parameter formulations.

Most algorithms incorporate some measure of pigment and some measure of irradiance. Many, however, formulate the relationships in terms of production per unit pigment instead of production per unit light, as we have done. All combinations of linear and log-transformed relationships have been used. Other environmental parameters that have been useful in strictly empirical models such as ours include temperature or temperature anomaly (Smith and Eppley 1982; Eppley et al. 1985), mixed-layer depth (Collins et al. 1986; Eppley et al. 1987), and the diffuse attenuation coefficient (Smith and Baker 1978; Eppley et al. 1987). The success of a temperature function in empirical models has been attributed to temperature being a surrogate for nutrients. We have examined briefly, but directly, the influence of near-surface nitrate concentrations and have concluded that the effect is too slight to justify incorporation into our model, in agreement with the results of Banse and Yong (1990). We do not have measurements of recycled nitrogen, such as ammonium, but their influence on our regression would be interesting to examine.

A measure of diffuse attenuation is available to us through our Secchi disk depth determinations. But these are made only on daylight stations; so, like other daylight-dependent measurements, their usefulness to us is limited. We have not examined the mixed-layer depth.

In principle, the accuracy of the physiologically based bio-optical models is limited only by theoretical development and by our ability to determine the necessary parameters. Once developed, they should have broad generality and important advantages, since this approach is free of the contamination and containment effects that are thought to bias the conventional ^{14}C procedure; also, this approach may be amenable to long-term monitoring from moorings. We expect a bio-optical approach to be initiated on CalCOFI cruises in the near future.

In contrast, models that are primarily empirical seem to lack generality. The formulation and success of such models have varied both regionally and seasonally, and the more successful ones are calibrated to specific regional relationships (Eppley et al. 1985; Platt and Sathyendranath 1988; Morel and Berthon 1989; Balch et al. 1989). Coefficients of determination for relationships based primarily on shipboard measurements have ranged from less than 0.35 (e.g., Eppley et al. 1987; Balch et al. 1989; Banse and Yong 1990) to more than 0.80 (e.g., King 1986; Banse and Yong 1990). Except for studies based upon small data sets, which occasionally report very high coefficients (e.g., Hayward and Venrick 1982), most values of r^2 from studies in the CalCOFI region and the Southern California Bight are in the range of 0.55–0.62 (Smith and Eppley 1982; Smith et al. 1982; Eppley et al. 1985; Collins et al. 1986; Balch et al. 1989). Although the generality of our simple model remains to be examined in other environments, within the CalCOFI region it compares favorably with previous efforts.

ACKNOWLEDGMENTS

Without the CalCOFI program, these data would not exist. We particularly acknowledge the technicians, from both the Marine Life Research Group and the Southwest Fisheries Science Center, whose dedication and skill have insured the high quality of each measurement and calculation. In return for their contribution, we hereby offer them a party. R.S.V.P. by January 1, 1996.

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EL NIÑO EFFECTS ON THE SOMATIC AND REPRODUCTIVE CONDITION OF BLUE ROCKFISH, *SEBASTES MYSTINUS*

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ABSTRACT

The condition factors and gonadal indices of blue rockfish off central California declined during the 1982–83 and 1992–93 El Niño events. These periods were characterized by higher-than-normal spring sea-surface temperatures (SST), indicating weak upwelling of cold, nutrient-laden water into the nearshore euphotic zone. Resulting spring primary productivity was low. Blue rockfish, an important component of the central California sportfish catch, are primarily macrozooplankton feeders. Current literature suggests that they rely on plankton blooms during the spring upwelling period to build fat reservoirs in preparation for reproduction in the fall.

The condition factor of adult blue rockfish showed a general pattern of negative correlation with SST. The highest correlation was with fall SST ($R = -0.739$, $P = 0.0025$); however, correlations were also significant at the 5% level with annual and spring SST. Low monthly mean somatic condition factors of blue rockfish during El Niño years, compared to non-El Niño years, imply lower energy reserves for reproductive development. Mean female gonadal indices were also below long-term means in El Niño years.

INTRODUCTION

Fishery biologists have long scrutinized the relationship between fluctuations in the environment and the productivity of fish populations. Recent literature regarding the 1982–83 and 1992–93 El Niño events in the California Current region documented that these events were characterized by the reduced entrainment of cool, nutrient-enriched water into the euphotic zone, low surface chlorophyll concentration, and weak primary productivity (McLain and Thomas 1983; McGowan 1984; Norton et al. 1985; Hayward 1993; Lenarz et al. 1995). These anomalous conditions resulted in reduced productivity at higher trophic levels. For example, the paucity of large copepods (attributed to low phytoplankton levels) in waters off Oregon and Washington in 1983 was thought to have a detrimental effect on larval sablefish, *Anoplopoma fimbria* (Grover and Olla 1987). Lenarz and Wyllie Echeverria (1986) reported that low fat and ovary volumes in female yellowtail rockfish, *Sebastes flavidus*, may have resulted from poor feeding conditions during the 1982–84 El Niño period. Spratt (1987) found that weight-at-age and overall mean weight of herring, *Clupea harengus pallasi*, in the San Francisco Bay fishery was depressed in 1983. A significant decline in the growth increments of commercially caught young widow rockfish, *Sebastes entomelas*, along the Oregon coast was observed by Woodbury (Southwest Fisheries Science Center, Tiburon, pers. comm.), who suspected that the 1982–83 El Niño was the probable cause. Lenarz et al. (1995) also found that the 1982–83 and 1992–93 El Niño events affected the growth and somatic condition of adult rockfish off central California.

The Central California Marine Sport Fish Survey, a project of the California Department of Fish and Game, has collected life-history and stock-status information on nearshore rockfish off central California since 1950. Local sport fish populations are showing the effects of heavy utilization, highlighting the need for alternative management strategies to provide a high quality of sportfishing in the future (Reilly et al. 1993). The present objective of the sport fish survey is to determine the feasibility of establishing marine reserves as a management strategy to enhance nearshore rockfish populations. A crucial aspect of this objective is to examine the relationships among the somatic and reproductive condition of adults, oceanographic events, and the ultimate recruitment success of young-of-the-year (YOY) fishes.

The blue rockfish, *Sebastes mystinus*, a ubiquitous, schooling, nearshore rockfish, has been numerically the most important sport fish in central and northern California (Miller and Gotshall 1965; Miller et al. 1967; Reilly et al. 1993). Blue rockfish are primarily plankton feeders whose food consists mainly of jellyfish, crustaceans, and tunicates (Gotshall et al. 1965; Hobson and Chess 1988). Blue rockfish grow fastest during spring upwelling when these planktonic organisms are abundant (Miller and Geibel 1973). Guillemot et al. (1985) suggest that upwelling periods provide energy for simultaneous fat accumulation, somatic growth, and gametogenesis for some rockfish. Blue rockfish are viviparous (Boehlert and Yoklavich 1985). Insemination occurs from July through September, and females release larvae from December through January (Wyllie Echeverria 1987).

[Manuscript received February 1, 1995.]

Our objective in this paper is to examine how the somatic and reproductive condition of adult rockfishes relates to oceanographic events. We have chosen blue rockfish as an indicator of the annual variability in this relationship because this species' importance in sport and commercial fisheries has resulted in a long time series of length, weight, and high-quality reproductive information. Additionally, we suspect that blue rockfishes' food supply and ultimately their somatic and reproductive condition is influenced by spring upwelling.

METHODS

Study Area and Data Sources

From 1981 to 1994, blue rockfish were collected along the central California coast between Santa Cruz and Port San Luis (table 1). Specimens were collected in depths of 5 to 40 m throughout the year by hook-and-line fishing or by pole spear. Most specimens were processed the day of capture; a small number were refrigerated and processed the day after capture. Information recorded for each fish included standard and total length (mm), wet body weight (g), wet gonad weight (g), and stage of maturation (Lea et al., in press).

The two equations used to calculate the condition factor of individual fish were derived from length-weight relationships calculated by linear regressions of natural log transformations of the observed total length (TL) and wet weight of 4015 adult and 3129 young-of-the-year (YOY) blue rockfish. Condition factors were calculated as follows:

$$\text{Condition factor} = \text{observed total weight}/\text{expected total weight where:}$$
$$\text{Adult expected total weight} = 0.000008976\ TL^{3.1118}$$
$$\text{YOY expected total weight} = 0.000006482\ TL^{3.1679}$$

TABLE 1
Numbers of Male, Female, and Young-of-the-Year (YOY) Blue Rockfish Analyzed for Condition Factor (CF) and Gonadal Index (GI)

	Male		Female		YOY
Year	CF	GI	CF	GI	CF
1981	18	3	80	13	—
1982	13	4	56	11	—
1983	66	13	153	24	—
1984	55	15	149	30	—
1985	19	—	51	5	—
1986	23	—	70	17	—
1987	65	4	183	46	104
1988	29	4	150	12	427
1989	26	14	208	75	334
1990	41	6	214	62	805
1991	47	4	286	99	671
1992	106	23	712	126	41
1993	44	13	481	230	460
1994	69	7	184	31	287

We followed the methods suggested by Beauchamp and Olson (1973) to adjust the above regression coefficients for the biases introduced by log transformations. We found the calculated condition factors to have a strong seasonal cycle. Annual means of condition factors, which we used for comparisons with oceanographic factors, were therefore standardized by subtracting the respective monthly mean from each fish's condition factor. This correction was necessary to remove the bias that would have resulted from the different seasonal distribution of sampling which occurred in some years.

We used the gonadal index (GI) equation as an index of reproductive condition (DeVlaming et al. 1982). This index uses the gonad weight/fish length cubed relationship as an indicator of the reproductive state of the fish and is derived by the formula

$$\text{GI} = (GWT\ /\ TL^3) \times 10^5$$

where:

GWT = weight of gonad in grams
TL = total length of fish in millimeters
10^5 = value to bring index to unity

The time period we used to estimate the annual gonadal index differed for males (the breeding season, June–September) and females (the parturition season, November–January; Wyllie Echeverria 1987). We used only reproductively developing individuals (Lea et al., in press) to calculate the mean gonadal index for the month and year.

We calculated quarterly mean SST from monthly means of daily observations taken at the Granite Canyon Pollution Laboratory (GCPL), located 18 km south of Monterey, California.

Annual mean upwelling indices (UPIs) were calculated from monthly means at 36°N, 122°W; these means were obtained from the Pacific Fisheries Environmental Group, Monterey, California. The UPI is derived from atmospheric pressure fields and is an estimate of the offshore component of Ekman transport (Bakun 1973).

RESULTS

Sea-Surface Temperature

Elevated SST taken at the GCPL indicated the two major El Niño events (1982–83 and 1992–93) that occurred along the central coast from 1981 through 1994 (figure 1). Sea-surface temperatures during the first half of 1982 were only slightly above the mean, but from the second half of 1982 throughout 1983 they were well above the mean. Sea-surface temperatures were about average in 1984, slightly cooler in 1985, and warmer than average in 1986 and 1987. During the next 4 years (1988–91) annual SST averaged half a degree cooler than the mean. Although SSTs were not as high in 1992–93

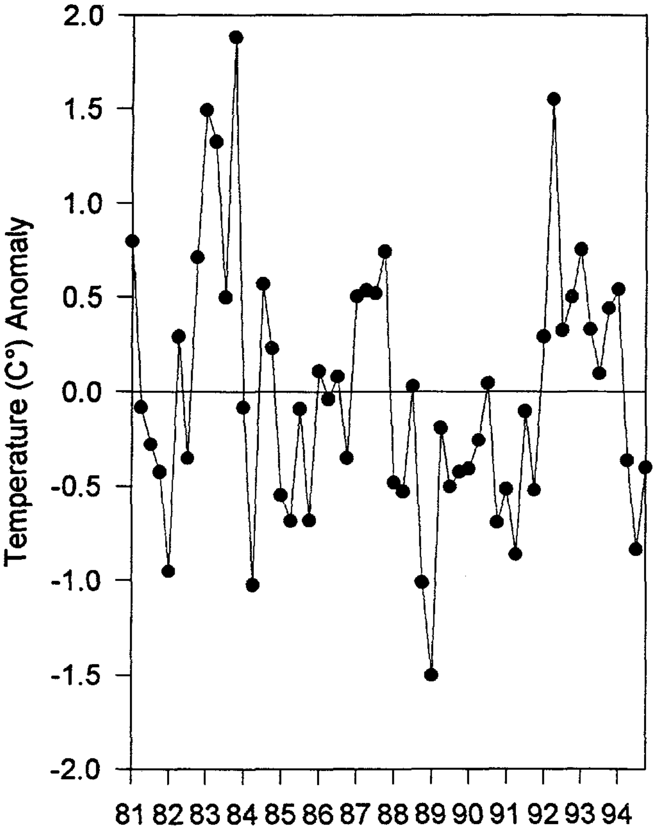

Figure 1. Quarterly sea-surface temperature anomalies derived from daily readings taken at Granite Canyon Pollution Laboratory, Monterey County, California.

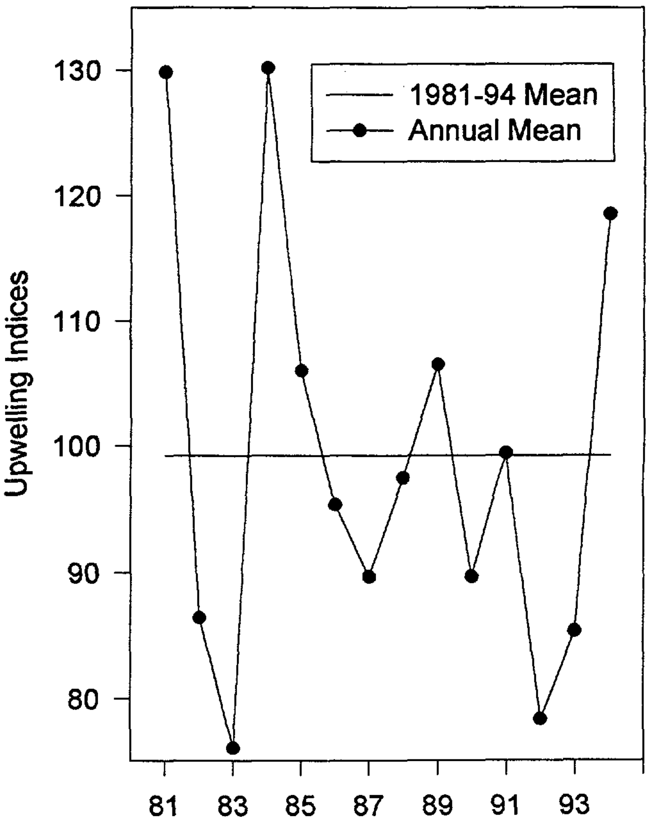

Figure 2. Annual upwelling indices calculated at 36°N, 122°W.

as in 1983, they were above the 14-year mean throughout most of both years. Sea-surface temperatures cooled in 1994 to half a degree below the 14-year mean.

Upwelling Indices

Annual mean UPIs at 36°N, 122°W were low during the 1982–83 and 1992–93 El Niño events (figure 2). Minimum UPIs in 1983 and 1992 correspond to maximum SST taken at the GCPL during those years. From 1981 through 1994 the highest UPIs occurred in 1981 and 1984. From 1985 through 1991 and in 1994 the annual UPI fluctuated only slightly from the 1981–94 mean.

BIOLOGICAL DATA

Condition Factor

Condition factors in male, female, and unsexed YOY blue rockfish have somewhat similar seasonal patterns (figure 3). Condition factor is at a minimum in the early spring and rises sharply to a maximum in early summer. In males, condition factor starts to drop in early fall; in females and unsexed YOY it does not decline until winter. The seasonal decline in the condition factor of males

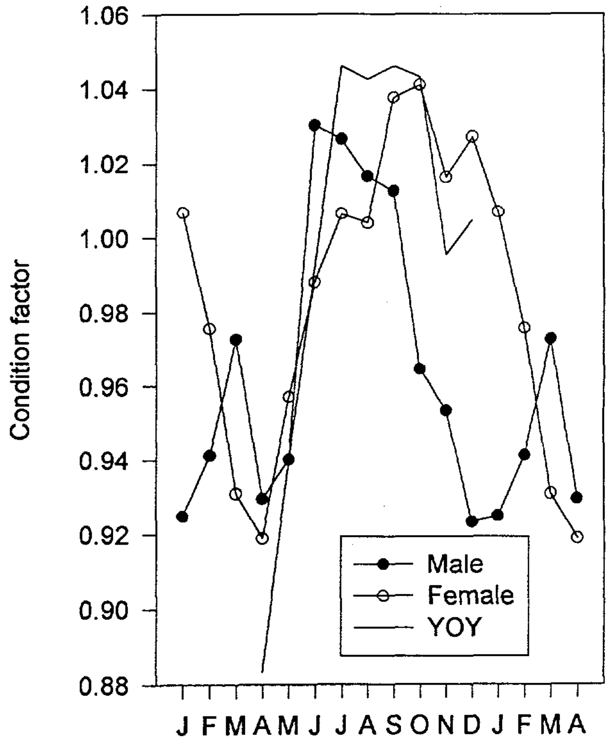

Figure 3. Seasonal condition factors of male, female, and young-of-the-year (YOY) blue rockfish, 1981–94.

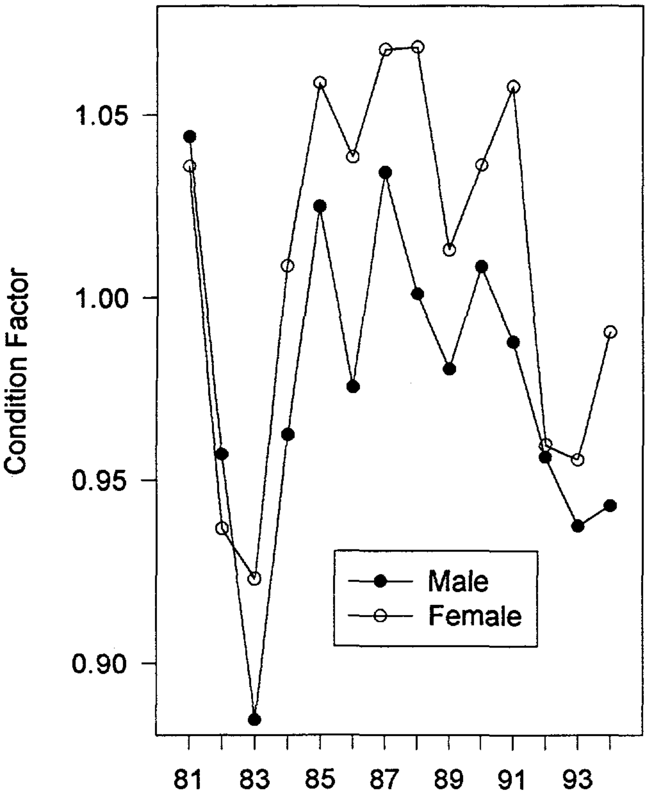

Figure 4. Corrected annual seasonal condition factors of male and female blue rockfish, 1981–94.

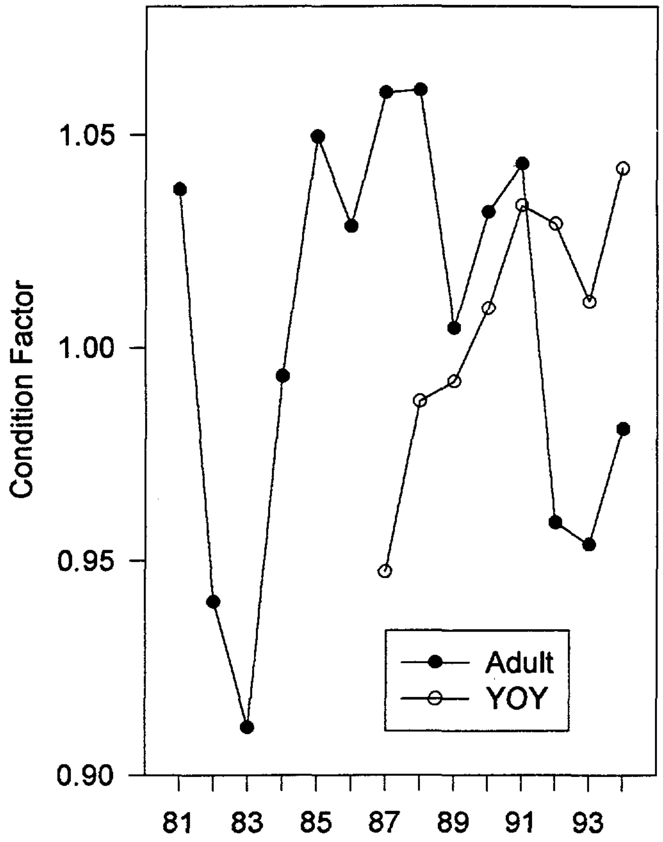

Figure 5. Corrected annual seasonal condition factors of sexually mature adult and young-of-the-year (YOY) blue rockfish, 1981–94.

corresponds to the end of the breeding season; the seasonal decline of females is associated with their parturition period (Lea et al., in press). Young-of-the-year recruit to the nearshore kelp forest in April. Their growth is rapid during the spring plankton blooms but levels off in late summer as suitable food sources diminish (VenTresca et al., in press).

Although condition factors in males and females exhibited slightly different seasonal cycles, seasonally adjusted interannual patterns were more congruent (figure 4). Seasonally adjusted female condition factors were "closest" to male values during and after El Niño periods (1982–84 and 1992–93), when both were at a minimum. From 1983 through 1994, female condition factors were generally higher than those of the males.

The condition factors of all sexually mature adults were lowest in 1982–83, and not until 1985—two years after El Niño—did adult condition factors recover to the 1981 level (figure 5). From 1985 to 1991 the condition factor of blue rockfish was relatively stable, although there were minor declines in adult condition factors in 1986 and 1989. A second major decline of adult condition factor occurred during the 1992–93 El Niño. Except for the first three years of sampling, the condition factors of YOY blue rockfish were similar to those of adults. Young-of-the-year condition factors rose in 1990 and 1991, declined in 1992 and 1993, and rose again in 1994 (figure 5).

As would be expected from the previous results, the seasonal condition factor cycles of males and females collected during the 1982–83 and 1992–93 El Niño events were lower and more variable than those collected during non-El Niño years (figures 6 and 7). Condition factors in males had essentially the same seasonal pattern in the non-El Niño years and in the 1992–93 El Niño, although the values were substantially lower during the 1982–83 El Niño. During the 1982–83 El Niño, males showed virtually no spring–summer increase in condition factor, and monthly values fluctuated considerably. In females the seasonal pattern that occurred in non-El Niño years (i.e., minimum in April, stable maximum from July through December, and decline from January to April) did not occur during the two El Niño periods. During the lesser El Niño of 1992–93, condition factors were considerably lower than during non-El Niño years in all months. A rapid spring increase did not occur, but rather condition factor peaked in September. During the major El Niño of 1982–83 the condition factor of females, like that of males, did not exhibit the "normal" spring–summer increase, and

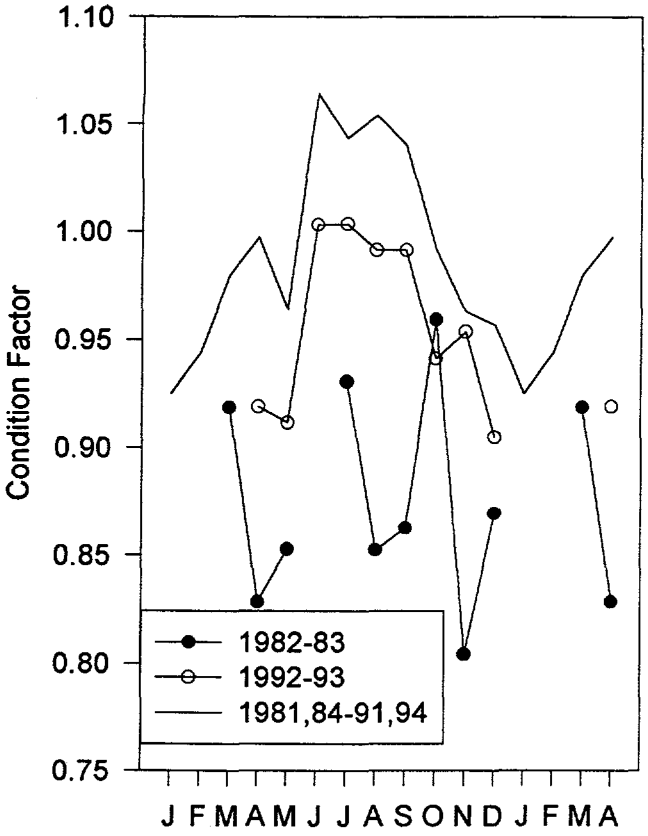

Figure 6. Seasonal condition factors of male rockfish during 1982–83; 1992–93; and 1981, 1984–91, and 1994.

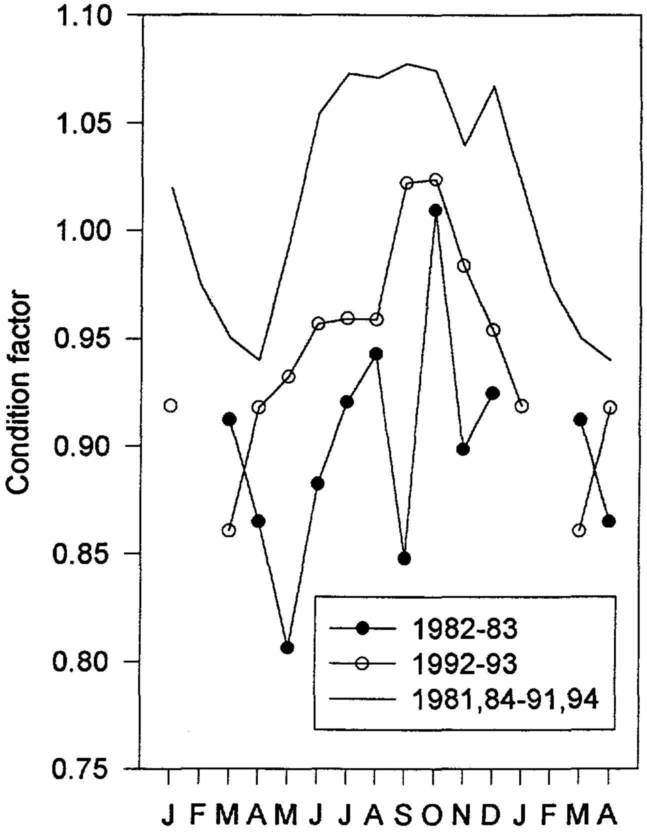

Figure 7. Seasonal condition factors of female rockfish during 1982–83; 1992–93; and 1981, 1984–91, and 1994.

monthly condition factor values were extremely variable. However, some of the monthly variations observed during the 1982–83 El Niño years, for both males and females, may be due to smaller sample size compared to the numbers of fish sampled during the 10 years grouped in the non-El Niño classification.

Gonadal Index

Male seasonal gonadal indices peaked in August; insemination occurred through October; and most testes were spent by January (figure 8). The August peak in male gonadal indices was preceded by two months (June and July) of maximum condition factor (figure 3). Female seasonal gonadal indices peaked in January, when most parturition occurred. Most ovaries were flaccid by March (figure 8). The January peak in female gonadal indices was preceded by four months (September through December) of maximum condition factor (figure 3).

The annual time series of male gonadal indices showed little interyear fluctuation. The minimum value occurred during the 1982–83 El Niño; however, male gonadal indices remained high during the 1992–93 El Niño (figure 9). Minima for females occurred during El Niño years, and high gonadal indices occurred during non-El

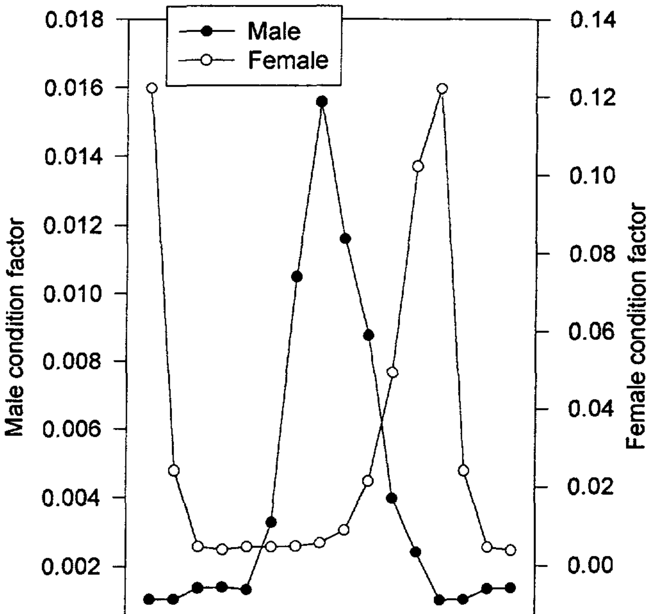

Figure 8. Seasonal gonadal indices of male (June–Sept.) and female (Nov.–Jan.) blue rockfish, 1981–94.

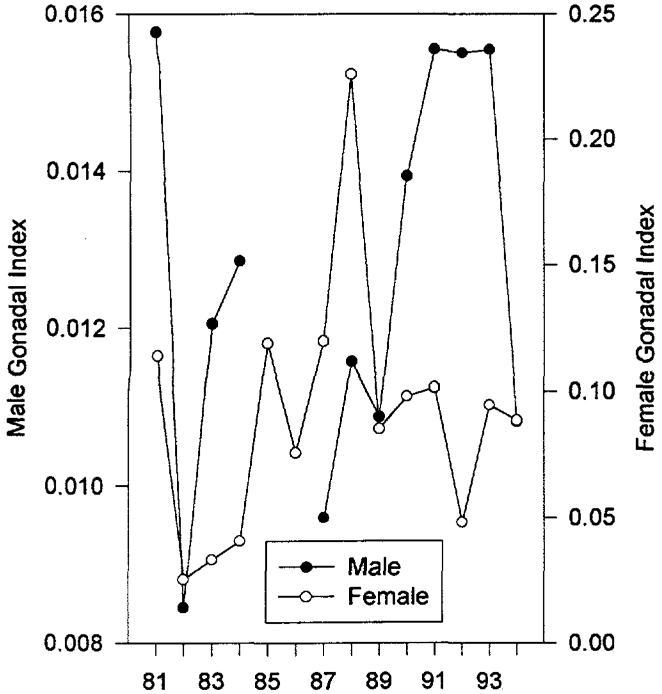

Figure 9. Annual gonadal indices of male and female blue rockfish, 1981–94.

Niño years. The maximum gonadal index in females occurred in association with the coldest period in the time series (figure 1). The recovery of female gonadal indices after the 1982 El Niño was slower than after the 1992 El Niño.

Statistical Relationships

To assess potential relationships with environmental factors, we performed standard Pearson correlation analyses comparing the time series of annual adult condition factors with annual and seasonal SST and UPI. As would be expected from the previously described pattern of lower condition factors during El Niño years, there was a general pattern of negative correlation with SST. The highest correlation was with fall SST ($R = -0.739$, $P = 0.0025$), but correlations with annual and spring SST were also significant at the 5% level (table 2). There were also significant (5%) positive correlations with spring and fall UPI. Correlations between condition factor and spring and fall environmental conditions were significant with both SST and UPI, whereas those with winter and summer SST and UPI were not significant.

Stepwise multiple regression analyses with annual condition factor as the dependent variable and the annual and seasonal environmental time series as independent variables resulted in a model (including fall and summer SST) which accounted for 73% of the variance in the condition factor time series.

Gonadal indices of male blue rockfish peaked in August (figure 6). Insemination occurred through October, and testes were spent by January. Female gonadal indices peaked in January (figure 7). By March, most parturition had occurred, and ovaries were flaccid. Because of these differences it was not surprising that male and female gonadal indices were not significantly correlated ($R = 0.059$, $P = 0.856$). Male gonadal indices were not significantly correlated with the adult condition factor or any environmental factors (table 2). Annual gonadal indices for females were strongly positively correlated with adult condition factors ($R = 0.736$, $P = 0.003$). The only environmental variable that they were significantly correlated with was fall SST, which also had the strongest correlation with adult condition factor (table 2).

TABLE 2
Correlation Coefficients among Condition Factor, Gonadal Index (GI), Sea-Surface Temperature (SST), and Upwelling Index (UPI)

	Adult condition factor	Female gonadal index	Male gonadal index
Female GI	0.736**	—	0.059
Male GI	0.122	0.059	—
Annual SST	−0.588*	−0.508	0.071
Winter SST	−0.330	−0.153	0.306
Spring SST	−0.583*	−0.395	0.001
Summer SST	−0.005	−0.129	0.178
Fall SST	−0.739**	−0.650*	−0.209
Annual UPI	0.376	0.156	0.074
Winter UPI	0.482	0.274	−0.322
Spring UPI	0.541*	0.206	0.351
Summer UPI	−0.158	−0.110	−0.139
Fall UPI	0.564*	0.338	−0.038

* significant at $P < 0.05$
** significant at $P < 0.01$
Winter = Dec.–Feb.; spring = Mar.–May; summer = June–Aug.; fall = Sept.–Nov.

DISCUSSION

Adult seasonal condition factors are at a minimum in early spring, following the summer insemination period for males and the winter parturition period for females and before the onset of upwelling. Condition factors quickly rise in the spring and remain high until the culmination of the reproductive periods. Adult annual condition factors are negatively correlated with SST in spring and fall, and positively correlated with UPI in spring and fall.

Female gonadal indices are significantly correlated with adult condition factors and SST in the fall. The high negative correlation of adult condition factors with SST in the fall may indicate the importance of this period for increasing body weight (fat reservoirs). Guillemot et al. (1985) suggest that upwelling periods may provide energy for the accumulation of fat reservoirs. Past literature (Gotshall et al. 1965; Miller and Geibel 1973; Hobson and Chess 1988) stresses the importance of spring upwelling in producing food for blue rockfish. It may be possible that female blue rockfish use the initial food production in spring for growth in length, and later in the year begin to store fat reservoirs for reproduction. The production of these fat reservoirs may be critical to increased gonadal production, as evidenced by the high correlation of gonadal indices with adult condition factor and fall SST.

Male gonadal indices seem unrelated to somatic condition factors or environmental variables (SST or UPI). Males develop gonadal tissues during the early spring (June and July), when upwelling is at an annual maximum (figure 2) and consequently food is most abundant. The males' highest condition factors also occur at this time. Therefore males may be developing gonadal tissues during the early spring when food is abundant rather than developing them from stored fat later in the year as do females. Also the amount of male gonadal tissue produced is small in comparison to total body weight—much smaller than in the females. It should also be noted that gonadal development in males and females appears to respond differently to El Niño events. Females show a strong negative correlation to SST and a pattern of lower gonadal indices during El Niño years, whereas males do not.

Although cold spring SST and increased upwelling were significantly correlated with increased annual condition factors, the "best" multiple regression model suggests that high SSTs in the summer and fall are more important determinants of both condition factor and female gonadal development.

To evaluate the effect that populations of sexually mature rockfishes within reserves have on recruitment, we must be able to determine these populations' annual variability in spawning potential. This study demonstrates that environmental perturbations are highly correlated with the somatic and reproductive condition of adult blue rockfish. This reproductive potential must now be correlated with recruitment success as well as with environmental events that occur during the planktonic stage of YOY blue rockfish.

ACKNOWLEDGMENTS

This project was partially supported by Federal Aid in Sport Fish Restoration Act Funds (California Project F-50-R). Without outside help, this project could not have been completed. We express our sincere gratitude to the following people for their generous assistance with data collection, advice, and editing of the manuscript: T. Abajian, D. Antonio, J. Harding, B. Hornady, P. Nelson, M. Paddack, and M. Tork, Pacific States Marine Fisheries Commission; J. Norton, Pacific Fisheries Environmental Group; J. Carroll, E. Danner, G. McCumber, B. Stephens, and M. Turpin, Tenera Environmental Services, Inc. (TES); W. Lenarz, Southwest Fisheries Science Center, Tiburon; C. Rawlinson of TES and Depth Perceptions Diving Services; D. Schroeder, University of California, Santa Barbara; J. Ames, B. Hardy, J. Goetzl, J. Hardwick, C. Haugen, M. Harris, G. Ichikawa, R. Lea, S. Owen, C. Pattison, P. Reilly, and J. Spratt, California Department of Fish and Game; and one anonymous reviewer.

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THE CALIFORNIAN EL NIÑO OF 1992 AND THE FALL OF *CALANUS*

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ABSTRACT

Although physical indications of the 1992 Californian El Niño were ambiguous off southern California in autumn 1991, chlorophyll and female *Calanus* were already anomalously scarce. Daily egg production in that autumn—calculated from the observed biomasses of chlorophyll, a fecundity-vs.-chlorophyll regression for autumn, and the observed abundances of female *Calanus*—was sufficiently reduced to explain the relative rarity of the next generation in winter 1992.

INTRODUCTION

The California Current system showed symptoms of an El Niño–like event during much of 1992, including anomalously high temperatures, deep mixed layers, deep nutriclines, elevated sea levels, and (for some of the year) reduced biomass of phytoplankton measured as chlorophyll (Hayward 1993). During similar past events, the biomass of zooplankton has been reduced (Chelton et al. 1982; McGowan 1985); in 1992 the reduction was superimposed on a longer-term depauperization associated with higher temperatures in the California Current system since the mid-1970s (Roemmich and McGowan 1995).

The temperature in the preceding autumn (1991), as reflected at the coast off La Jolla, California, was very near the long-term mean (the persistent positive anomaly did not begin until late December). However, sea level became anomalously high after September, and there was a strong, poleward countercurrent along the coast in October, which persisted through February 1992 (Hayward 1993). Thus some symptoms of the Californian El Niño were already present in autumn, even though some physical properties were normal.

Though the data series was too short to identify a genuine anomaly, females of the planktonic copepod *Calanus pacificus* were significantly less abundant off southern California during winter–spring of 1992 than during the comparable seasons of 1989–91. Per capita reproduction also was diminished in February 1992, in proportion to the depauperization of chlorophyll then, but the relative rarity of adult *Calanus* was much more striking than the change in fecundity (Mullin 1994). This rarity could have arisen from an excess of deaths during the ontogeny of the adults sampled in February, reduced net immigration from populations farther north as a result of altered advection, or rarity or reduced fecundity of the preceding (autumnal) generation.

I therefore examined data and samples from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) for the autumns (Oct.–Nov.) of 1988–91 to try to determine the antecedents of the biological anomalies observed in early 1992. Unfortunately, I did not measure reproduction in autumn 1991, so comparison of this demographic property with 1988 and 1989 (Mullin 1991) can be only indirect.

METHODS

The standard sampling methods used by CalCOFI, and the approaches I used for analyzing the data, have been described (Mullin 1994). Specifically, I present results for autumn 1991 as departures (anomalies) from the conditions averaged over the preceding three autumns, which for present purposes are defined as "normal."

It may be that, because of increased depth of diel vertical migration by *Calanus* in summer and autumn (e.g., Koslow and Ota 1981), the standard 200 m CalCOFI tow is less adequate in daytime as a sampler of the total population than it is in winter and spring. Further, if a larger fraction of the population lived deeper than 200 m during 1991 than during the preceding three autumns, so that underestimation of the real population was more serious in 1991 than previously, apparent negative anomalies of abundance for 1991 would be computed even if true abundances throughout the entire water column were unaltered. If the deep-living females were permanently inactive reproductively, the effect on the subsequent generation would be the same as if they were truly absent, and the negative anomalies would still be effectively real. If the deep-living females were active, they might also be migrating at night to depths shallower than 200 m, in which case negative anomalies would be calculated exclusively or primarily at those stations sampled during daylight hours.

To examine this possibility, I recalculated anomalies in abundance for (1) only those stations sampled nocturnally on Cruise 9110 and in at least two of the preceding three autumns, using only the nocturnal data, and (2) only those stations sampled diurnally on Cruise

[Manuscript received November 2, 1994.]

9110 and in at least two of the "normal" autumns, using only the diurnal data. These calculations revealed "nocturnal" and "diurnal" anomalies in abundance, and I then tested for difference in the medians. If a greater fraction of female *Calanus* migrated from below 200 m by day to shallower depths at night in autumn 1991 than in "normal" autumns, I should be able to reject the null hypothesis of equality of medians in favor of the 1-sided alternative that the median nocturnal anomaly was less than the median diurnal one.

I had measured the production of eggs by individual female *Calanus*, with and without supplemented food as cultured diatoms, in the autumns of 1988 and 1989 at a subset of the stations sampled during the CalCOFI cruises. These data, plus the concurrent CalCOFI measurements of chlorophyll biomass at those stations, resulted in regressions of per capita fecundity on chlorophyll (Mullin 1991). The mean regresssion was eggs·(female·day)$^{-1}$ = 0.37·(mg chlorophyll·m^{-2}), for chlorophyll $\leq$ 100 mg·m^{-2}.

For the present study, I used this equation, plus data on chlorophyll, to calculate per capita reproduction at all CalCOFI stations in the autumns of 1988, 1989, 1990, and 1991 (locations in figure 1). This expanded the set of stations for which reproduction could be calculated, but eliminated any variability not accounted for by the biomass of chlorophyll. I then multiplied the abundance of female *Calanus* at each station by the calculated per capita reproduction at that station to compute the population's reproduction during autumn 1991, and calculated average reproduction during the preceding three autumns similarly, in order to estimate the likely change in reproduction during 1991.

I also examined whether the mesoscale spatial distribution of *Calanus*, relative to that of chlorophyll, was any more advantageous in autumn 1991 than previously.

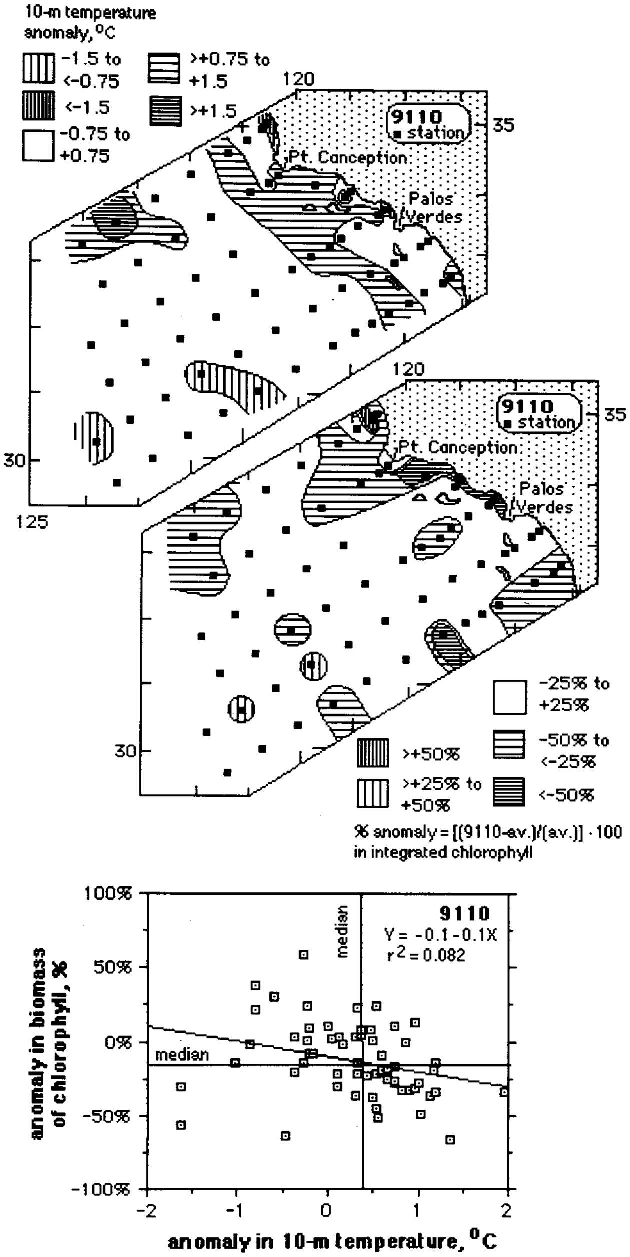

Figure 1. Anomalies in temperature at 10 m in °C (*upper*) and in biomass of chlorophyll to 100 m in percentages (*middle*) in October 1991 relative to conditions averaged (*av.*) in the previous three autumns; *horizontal striping* represents positive anomalies of temperature and negative anomalies of chlorophyll. *Bottom*, relation between the anomalies. The regression is significant ($p < 0.05$, 2-tailed).

RESULTS

The southern California sector of the California Current system in October of 1991 (Cruise 9110) already showed some symptoms of the El Niño that was present in February 1992. Although autumnal coastal temperature was normal relative to the long-term mean, the area sampled during Cruise 9110 was anomalously warm relative to the three earlier autumns (median anomaly +0.4°C, difference significant at $p < 0.01$ by sign test); the greatest positive anomalies were east of Point Conception in the Santa Barbara Channel and south-southeast along the Santa Rosa–Cortes Ridge (figure 1). The biomass of chlorophyll in much of the area was less than in the earlier autumns (median anomaly −16%, difference significant at $p = 0.01$ by sign test), and there was a negative relation between the two anomalies: the more anomalously warm a station was, the greater the negative anomaly of chlorophyll (figure 1).

The median abundance of female *Calanus* during Cruise 9110 was significantly less than that during "normal" autumn ($p < 0.01$ by sign test). The median anomaly was −67%, and was significantly ($p < 0.05$, 2-tailed) negatively related to 10 m temperature anomaly (figure 2): the more anomalously warm a station, the more anomalously rare was *Calanus*.

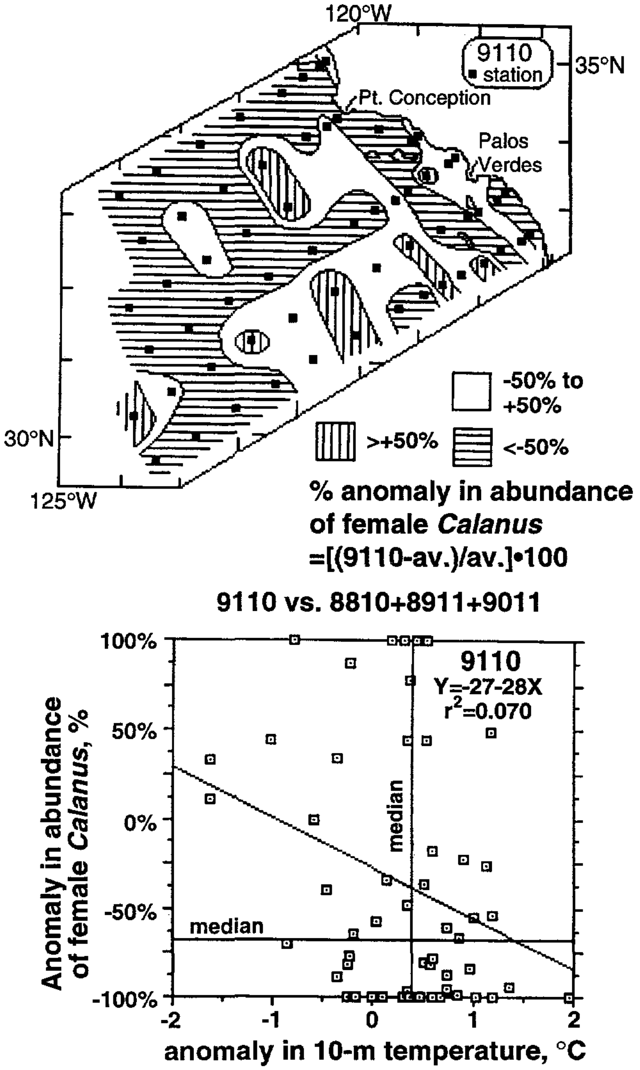

Figure 2. *Upper*, anomalies in abundance of female *Calanus*, as a percentage of the abundances averaged (*av.*) in the previous three autumns. *Lower*, relation of these anomalies to those of temperature. The regression is significant ($p < 0.05$, 2-tailed).

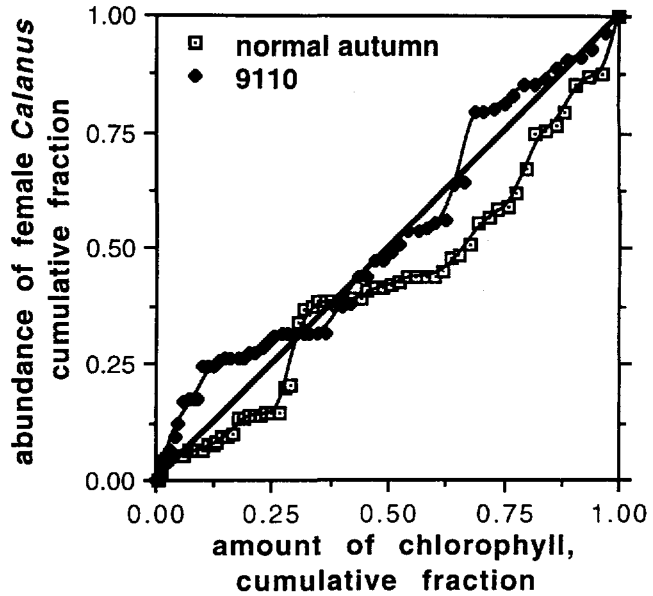

Figure 3. Relation between cumulative amount of chlorophyll and cumulative abundance of female *Calanus* in October 1991 and in the previous three, "normal," autumns. Pairs of data derived from each station (figures 1 and 2) were arranged in order of increasing biomass of chlorophyll before cumulative sums were calculated. Thus the most oligotrophic locations (with respect to chlorophyll) are to the left. The *diagonal* shows a "neutral" distribution for *Calanus* (see text).

By rank sum test, the median nocturnal and diurnal anomalies in abundance did not differ significantly ($p >$ 0.2, 1-tailed). This suggests that the negative anomalies shown in figure 2 were not due to increased undersampling of females during the day in autumn 1991, although it is still possible that, if the females were nonmigratory, such undersampling occurred both night and day. As noted earlier, it is not clear that the females living permanently below the depth of sampling would contribute to the population's reproductive output.

The biomass of chlorophyll in the water column can be used, with several important qualifications, as a surrogate for the biomass of food for *Calanus*. As shown in figure 1, the median biomass was significantly reduced in autumn 1991 relative to 1988–90, and thus (since egg production is generally food-limited in much of this region; Mullin 1991) decreased fecundity during autumn 1991 is to be expected. However, changes in the spatial distribution of *Calanus* relative to that of chlorophyll could ameliorate the general impoverishment if the female copepods became relatively more concentrated in those regions (stations or depths) where the biomasses of chlorophyll were relatively large. That is, *Calanus* could make better use of the available chlorophyll if the population's distribution changed appropriately.

To examine this question with respect to mesoscale horizontal distributions (since vertical distributions of *Calanus* were not determined), I arranged the pairs of data for amount of chlorophyll at each station (biomass times area represented by the station) and abundance of female *Calanus* in order of increasing amount of chlorophyll, then summed both and plotted the cumulative abundance of female *Calanus* against the cumulative amount of chlorophyll for autumn 1991 and for the "normal" situation represented by the three previous autumns (figure 3). Because of the way I had initially arranged the data, the diagonal on such a plot represents a distribution of *Calanus* that is nutritionally "neutral"; i.e., any given fraction of the total population of *Calanus* is spatially associated with the equivalent fraction of the available chlorophyll. Since the most oligotrophic stations with respect to chlorophyll biomass are towards the origin of the plot, points below the diagonal represent nutritionally "efficient" or "advantageous" distributions:

the fraction of *Calanus* associated with oligotrophic stations is less than the fraction of available chlorophyll these stations represent. Points above the diagonal are, by the analogous reasoning, nutritionally "inefficient" or "disadvantageous" (see Mullin 1994 for elaboration).

Figure 3 indicates that, in "normal" autumn, the horizontal distribution of female *Calanus* tended to be advantageous with respect to the food resources, whereas in autumn 1991 the distribution was essentially neutral. Thus there is no evidence of mesoscale distributional amelioration of heightened food limitation during autumn 1991.

As described in the Methods section, I estimated egg production for autumn 1991 from the biomasses of chlorophyll measured at each station and from the mean regression of individual daily egg production against biomass of chlorophyll for the autumns of 1988 and 1989 (Mullin 1991). I then multiplied these rates by the measured abundances of females and by the area represented by each station, and compared the egg production over the entire area in autumn 1991 to a similar calculation for the "normal" autumn, represented by the average of measurements in 1988–90.

I calculated that the *Calanus* population in autumn 1991 produced, over the entire area, $2.5 \cdot 10^{14} \cdot \text{eggs} \cdot \text{day}^{-1}$ [950 $\text{eggs} \cdot (\text{m}^{-2} \cdot \text{day})^{-1}$], which is $8 \cdot 10^{14}$ $\text{eggs} \cdot \text{day}^{-1}$ [3100 $\text{eggs} \cdot (\text{m}^{2} \cdot \text{day})^{-1}$] fewer than normal. By this calculation, the population's daily reproduction over the entire area was only 24% that in normal autumns, which is comparable to the finding that the abundance of female *Calanus* in the subsequent, El Niño, winter (1992) was 27% that of the preceding three winters (Mullin 1994).

DISCUSSION

Although the physical characteristics of El Niño off southern California that were clear in the winter of 1992 were ambiguous in the autumn of 1991, many of the biological symptoms were already detectable, relative to the three previous autumns. These symptoms (figures 1 and 2) included inversely correlated anomalies in 10 m temperature (significantly warm overall) and depth-integrated biomass of chlorophyll (significantly depleted), and similar anomalies in abundance of female *Calanus* (significantly rare).

The reduced median amount of food in autumn 1991, represented by negative anomalies in chlorophyll, implies a potential decrease in reproduction by the *Calanus* population. In principle, this could have been offset by an improved matching between the mesoscale distributions of female *Calanus* and chlorophyll, but such improved matching did not occur (figure 3).

The most important quantitative conclusion is that the reduction in daily egg production by the *Calanus* population calculated for autumn 1991 was sufficient to explain the relative rarity of the next generation of adult females in winter 1992. This does not mean that there were no changes in the balance of immigration and emigration (vertically or horizontally), or in the survivorship of juveniles, as the El Niño condition developed. However, these factors are not required to explain the status of the adult *Calanus* population in the full-blown Californian El Niño observed in early 1992.

ACKNOWLEDGMENTS

This study was supported by the Marine Life Research Group and by NOAA grant NA36GP0294-01. I thank Elizabeth McEvoy and Van Tang for counting the *Calanus*, and the seagoing technicians of the CalCOFI program for assistance and comradeship.

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DISTRIBUTIONAL PATTERNS OF LATE LARVAL GROUNDFISH OFF CENTRAL CALIFORNIA IN RELATION TO HYDROGRAPHIC FEATURES DURING 1992 AND 1993

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ABSTRACT

Late larval groundfish were collected off central California during late February and early March of 1992 and 1993. Hydrographic data obtained during these surveys showed that in both years ocean temperatures were relatively warm as a result of El Niño conditions. Contour plots of dynamic height topography at the surface indicated poleward flow in 1992, but equatorward flow in 1993. During 1992 large catches of shortbelly rockfish (*Sebastes jordani*), bocaccio (*S. paucispinis*), and other rockfishes (*Sebastes* spp.) were made on the shoreward side of a temperature front located 100–150 km off the continental shelf. Higher catches of Pacific and speckled sanddabs (*Citharichthys sordidus* and *C. stigmaeus*) were also associated with the front, but these species were found on both sides of the gradient. In contrast, Pacific whiting (*Merluccius productus*) were most abundant in the warm, nearshore waters of the southeastern portion of the survey area, which suggests that these fish had been advected northward by poleward flow during El Niño. Catches of all species were lower in 1993 than in 1992, and there were markedly fewer large (>20 mm SL) individuals. High catches of shortbelly rockfish and other rockfishes, and moderate abundances of bocaccio, Pacific and speckled sanddabs, and Pacific whiting were associated with an eddy feature detected in the salinity field off Monterey Bay; catches were also generally higher in nearshore waters, which were more saline. As in 1992, the largest catches of Pacific whiting in 1993 came from the warm nearshore waters of the southeastern portion of the survey area.

INTRODUCTION

Successful recruitment of marine organisms with planktonic eggs and larvae is often strongly affected by the hydrographic conditions prevailing during the early life history (Bailey and Francis 1985; Cowen 1985; Ebert and Russell 1988; Roughgarden et al. 1988; Sinclair 1988; Cury and Roy 1989; Hollowed 1992). The hydrographic regime off central California is driven by a complex mixture of geostrophic and wind-driven flow patterns (Parrish et al. 1981; Simpson 1987; Strub et al. 1987; Schwing et al. 1991). Geostrophic flow patterns are dominated by equatorward transport in the California Current (surface to 200 m) throughout the year, with a nearshore reversal to poleward flow during the winter months in association with the shoaling of the California Undercurrent (core at approximately 300 m; Parrish et al. 1981; Simpson 1987). Wind-driven flow patterns show strong high-frequency and seasonal variability (Largier et al. 1993). Southerly (i.e., northward-progressing) winds during winter storms typically lead to turbulent mixing, onshore transport, and downwelling. Following the spring transition to upwelling-favorable northwesterly winds, however, wind forcing leads to offshore transport in the upper mixed layer, nutrient enrichment, and increased primary productivity (Parrish et al. 1981; Simpson 1987; Strub et al. 1987).

Although the increased productivity during upwelling is generally viewed as beneficial, the offshore advection of planktonic larvae could adversely affect recruitment to nearshore settlement areas (Roughgarden et al. 1988). It has been hypothesized that, for many species off central California, spawning in the winter season, before spring transition, is a strategy for avoiding such advection offshore (Parrish et al. 1981).

The purpose of this study is to examine the distributional patterns of larval and late larval groundfish—in particular, rockfishes (*Sebastes* spp.), sanddabs (*Citharichthys* spp.), and Pacific whiting (*Merluccius productus*)—off central California during the period just before spring transition, and to relate observed patterns to the prevailing hydrography. Previous studies of distributional patterns have either used bongo nets to examine early larvae (Loeb et al. 1983; Moser et al. 1993) or midwater trawls to examine pelagic juveniles (Wyllie Echeverria et al. 1990; Larson et al. 1994). But there have been few studies on the distributional patterns of late larvae within the 10 to 20 mm size range, a stage during ontogeny that has been implicated as important in establishing year-class strength (Smith 1985).

MATERIALS AND METHODS

Late larval groundfish were collected with a 5 m^2 frame trawl fitted with a 2 mm mesh net and a 505 μm mesh codend (Methot 1986). A large Isaacs-Kidd depressor was used to stabilize the net at its targeted depth. Trawling was conducted in midwater aboard the National

[Manuscript received January 30, 1995.]

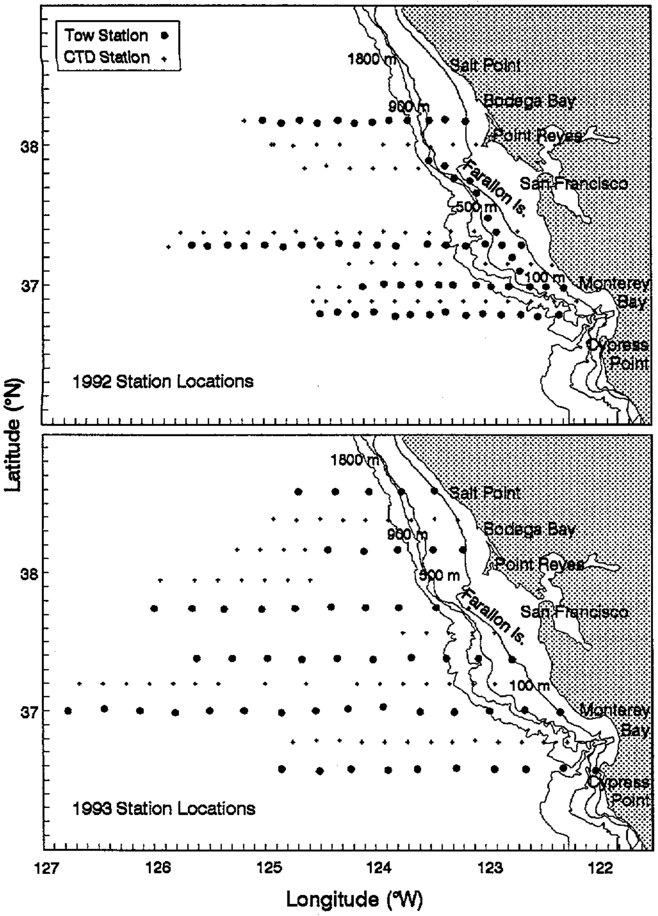

Figure 1. Map of the study area, showing the locations of trawl and CTD stations conducted during 1992 and 1993.

Oceanic and Atmospheric Administration (NOAA) R/V *David Starr Jordan* during the winters of 1992 (February 23–March 6) and 1993 (March 2–13). The survey area ranged from Bodega Bay to Monterey Bay in 1992 and from Salt Point to Cypress Point in 1993 (figure 1). Oblique tows were conducted at night for a duration of 20–30 minutes. The maximum depth fished by the net, determined from an attached time-depth recorder (TDR), was 70 m in 1992 and 80 m in 1993. At one station per night, an additional deep tow was conducted to a maximum depth of 135 m in 1992 and 149 m in 1993. Average tow speed was 1.2 m/second. A flowmeter affixed to the mouth of the net was used to determine the volume sampled.

In 1992 a conductivity-temperature-depth (CTD) cast was performed at each trawl station, with additional CTD stations sampled during the day (figure 1). In 1993 CTD casts were conducted at every other trawl station and at additional daytime stations (figure 1). Horizontal contour maps of temperature, salinity, and density (σ_t) at depths of 2, 10, 30, 100, 200, 300, and 500 m were created to chart the hydrography of the survey region. Contouring methods and plots are described and presented in Sakuma et al. (1994a, b). In addition, temperature and salinity at 60 m were contoured specifically for this study to characterize the hydrography within the lower depth range of the oblique tows. Likewise, dynamic height topography at the surface (0/500 m) and at depth (200/500 m) was contoured with the methods described in Sakuma et al. (1994a, b). To compare sea-surface temperature (SST) during the two survey years with data from previous years, we examined March SST data from 1973 to 1993 for the Farallon Islands shore station (37°41.8' N, 122°59.9' W) monitored by the Point Reyes Bird Observatory (PRBO; data obtained from Scripps Institution of Oceanography Marine Life Research Group). We also examined anomalous March sea levels from 1975 to 1993 obtained at the NOAA, National Ocean Service (NOS) San Francisco tide gauge station at Fort Point (37°48' N, 122°28' W; data obtained from the Joint Archive for Sea Level Data, University of Hawaii).

In 1992, larval fish were sorted at sea and placed in 95% EtOH. Two subsamples of the sorted remainder were saved from each tow to check the accuracy of the sorting conducted at sea. In the laboratory, larval shortbelly rockfish (*Sebastes jordani*), bocaccio (*S. paucispinis*), other rockfishes (*Sebastes* spp.), Pacific and speckled sanddabs (*Citharichthys sordidus* and *C. stigmaeus*), Pacific whiting (*Merluccius productus*), and "other" fish larvae were sorted and enumerated. In addition, standard length (SL) measurements were recorded for shortbelly rockfish, Pacific sanddab, and Pacific whiting, with large catches randomly subsampled and length measurements expanded to the whole catch.

In 1993, because of reduced catch rates, the seven taxa were sorted, identified, enumerated, and placed in 95% EtOH at sea. Subsamples of the sorted remainder were saved again and returned to the laboratory to check the accuracy of the shipboard sorts. Identifications of all taxa were reconfirmed in the laboratory. As in 1992, length measurements were recorded for shortbelly rockfish, Pacific sanddab, and Pacific whiting; large catches were subsampled; and the total length composition was estimated through expansion. Catch statistics for both years were adjusted with the flowmeter readings to numbers per 10,000 m^3 of water filtered.

We could not characterize the depth distributions of these species because of the vertical integration of abundance that occurs during an oblique tow. Therefore we excluded all deep trawls to standardize sampling to a specific depth range. We then calculated Spearman rank correlation coefficients to compare log-transformed abundance statistics ($\log_e[x+1]$) with hydrographic variables (i.e., temperature, salinity, and density) measured in situ (30 m depth). We selected this depth because prior

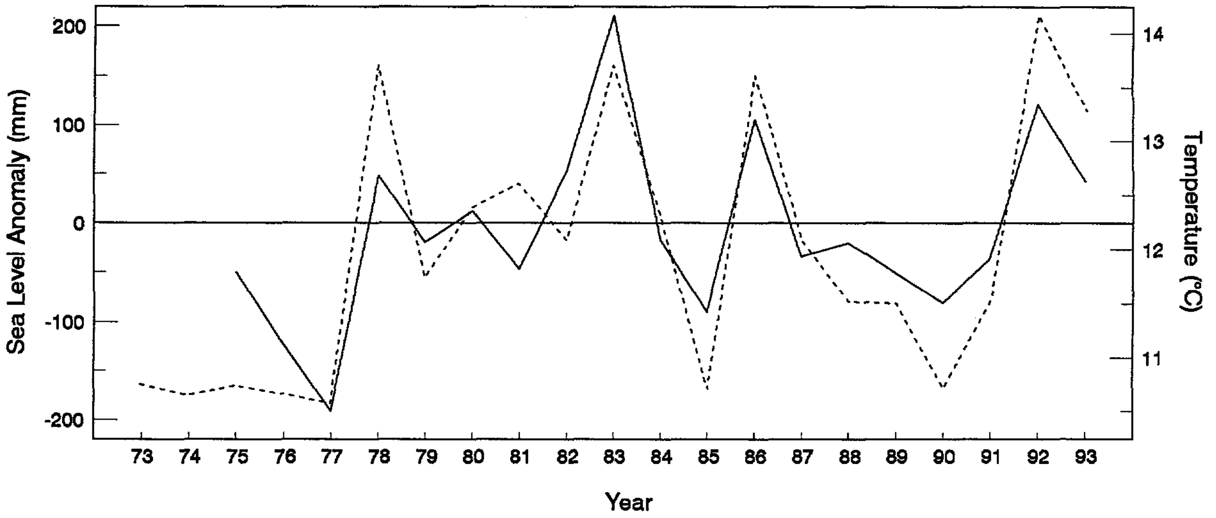

Figure 2. March sea-level anomaly at the NOAA, NOS San Francisco tide gauge station (*solid line*) from 1975 to 1993, and March sea-surface temperature at the Farallon Islands shore station (*dotted line*) from 1973 to 1993.

studies by Ahlstrom (1959) and Lenarz et al. (1991) indicated that larval and pelagic juvenile rockfish, sanddabs, and Pacific whiting are generally most abundant below 20 m. Likewise, additional data obtained during a 10 m^2 MOCNESS cruise conducted in March 1994 indicated that the vertical distribution of most of these fishes is broadly centered between 20 and 60 m (unpubl. data, National Marine Fisheries Service, Tiburon Laboratory, 3150 Paradise Drive, Tiburon, CA 94920). To increase sample sizes in 1993, we used gridded interpolations of the hydrographic variables when actual data were not available.

We superimposed total catches of shortbelly rockfish, bocaccio, other rockfishes, Pacific and speckled sanddabs, and Pacific whiting onto horizontal contour maps of temperature and salinity to examine spatial patterns of abundance in relation to the hydrographic regime. We then stratified catches of shortbelly rockfish, Pacific sanddab, and Pacific whiting into small (<10 mm SL), medium (10–19 mm SL), and large (>19 mm SL) size classes, and overlaid the data on hydrographic contours to examine differences in spatial distribution with size.

RESULTS

Increased sea levels were observed during March of 1992 and 1993 at the NOAA, NOS San Francisco tide gauge station (figure 2). In addition, data from the Farallon Islands shore station indicated that SSTs in March of 1992 and 1993 were anomalously warm (figure 2). Both the Farallon Islands shore station data and contours of CTD temperature at the surface indicated that SSTs were generally warmer in 1992 than in 1993 (figure 2). Sakuma et al. (1994a, b) reported that in both years the warmest SSTs were observed in the southern portion of the survey area off Monterey Bay. In addition, contours of temperature and salinity at the surface and at 30 m indicated that nearshore waters were generally warmer and more saline than offshore waters. A notable exception in 1993 was a high-salinity eddy feature offshore of Monterey Bay. This feature was most prominent at 30 m, but was present at the surface and down to 100 m (figure 3b; Sakuma et al. 1994b). A conspicuous hydrographic feature observed in 1992 was a strong alongshelf temperature gradient about 150 km from the coast; this feature was most prominent at 30 and 60 m (figure 3a; Sakuma et al. 1994a).

In 1992, plots of dynamic height topography, both at the surface and at 200 m, showed elevated values nearshore and progressively decreasing values offshore, indicating an overall pattern of poleward flow at distances up to ~140 km offshore (figure 4a). In contrast, the plot of 0/500 m dynamic height in 1993 showed elevated values well offshore and, to a lesser degree, over the continental slope, indicating a general pattern of equatorward flow, whereas the nearshore flow pattern was not readily discernable (figure 4b). At 200 m, dynamic heights were elevated both nearshore and well offshore, suggesting a general pattern of weak poleward flow nearshore and relatively strong equatorward flow offshore (figure 4b).

A total of 81 tows (including 14 deep tows) were made in 1992, and 65 tows (including 10 deep tows) in 1993. The preserved subsamples of the sorted remainders revealed substantial numbers of fish (i.e., more than 15% of the number originally sorted at sea) in 11 of the 81 tows in 1992, and 10 of the 65 tows in 1993. In these cases larval fish were enumerated from the subsamples, and their numbers were expanded to the total volume

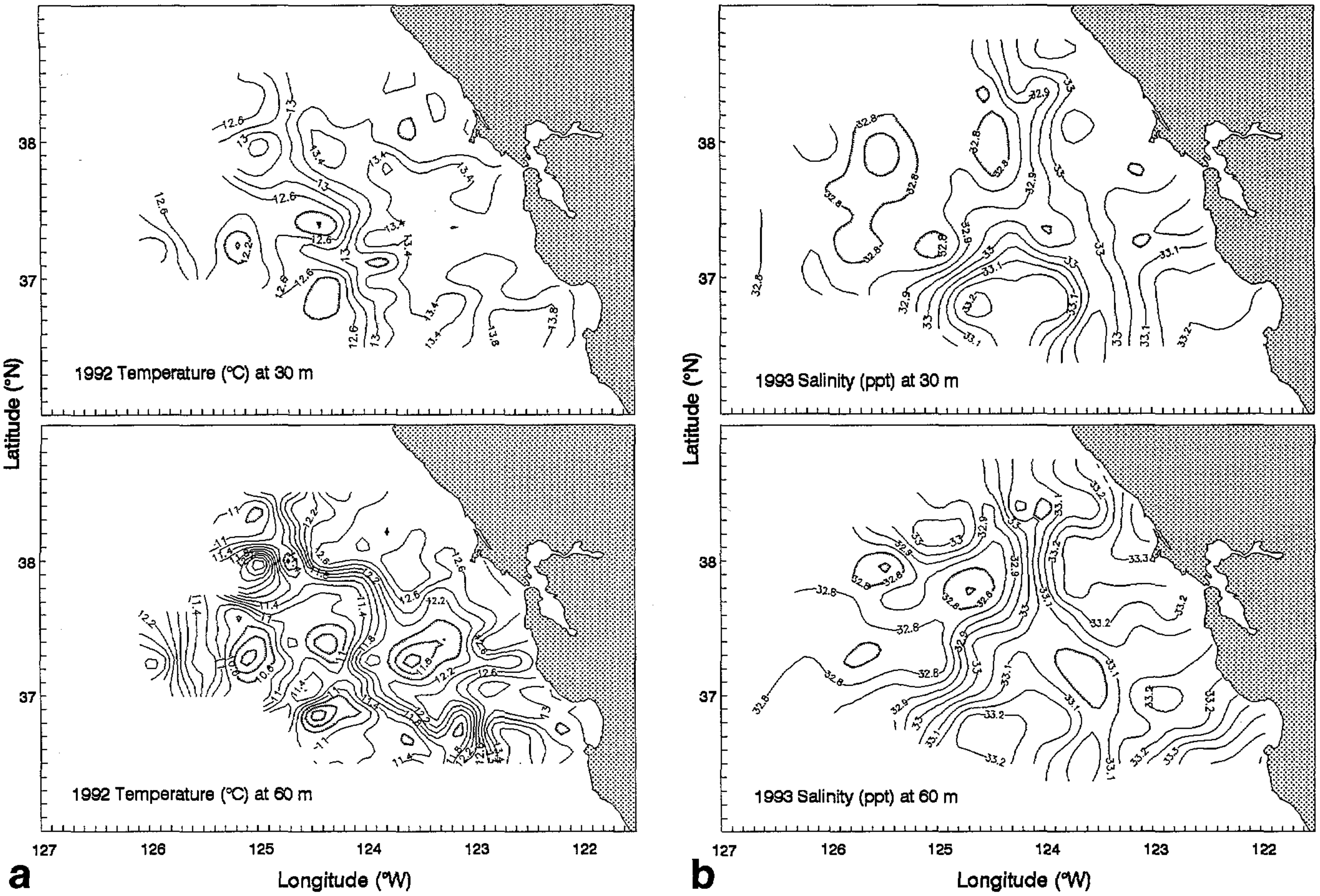

Figure 3. Contours of (*a*) temperature at 30 and 60 m in 1992 and (*b*) salinity at 30 and 60 m in 1993.

and added to the preliminary total. Catch rates of all taxa were higher in 1992 than in 1993 (figure 5). In addition, the length-frequency data revealed that fish collected in 1992 represented a wider size range than in 1993 (figure 6).

Catches of shortbelly rockfish, other rockfishes, and Pacific whiting were positively correlated with temperature in 1992 (table 1). Moreover, temperature correlations between other rockfishes and Pacific whiting were among the highest observed, indicating that temperature may have been an important influence on the distributions of these fishes in 1992 (table 1). In contrast, catches of Pacific and speckled sanddabs were negatively correlated with density and were uncorrelated with temperature (table 1). Catches of bocaccio were not significantly correlated with any variable, although there appeared to be a slight negative relationship with density (table 1).

In 1993, unlike the preceding year, only catches of shortbelly rockfish were correlated with temperature (table 2). Instead, all species showed strong positive correlations with salinity, indicating that this hydrographic variable most strongly affected the distributions of these fishes in 1993. In a reversal of trend, catches of Pacific and speckled sanddabs were positively correlated with density in 1993 (table 2). Likewise, catches of shortbelly rockfish, other rockfishes, and Pacific whiting were positively correlated with density (table 2).

Although symbols proportional in size to catch rate were superimposed onto contour maps of temperature and salinity, only temperature maps are presented for 1992, because the distributional patterns correlated best with temperature (table 1). Similarly, because salinity had the highest correlations in 1993 (table 2), we present only overlays of abundance on the salinity field for that year.

The overlays for 1992 showed that shortbelly rockfish, bocaccio, other rockfishes, Pacific and speckled sanddabs, and Pacific whiting were found offshore as well as nearshore (figure 7). However, large offshore catches of shortbelly rockfish and other rockfishes were made only on the warmer, nearshore side of the temperature front (figure 7a). Similarly, the largest catches of bocaccio came from the nearshore side of the gradient (figure 7a). In contrast, Pacific and speckled sanddabs were

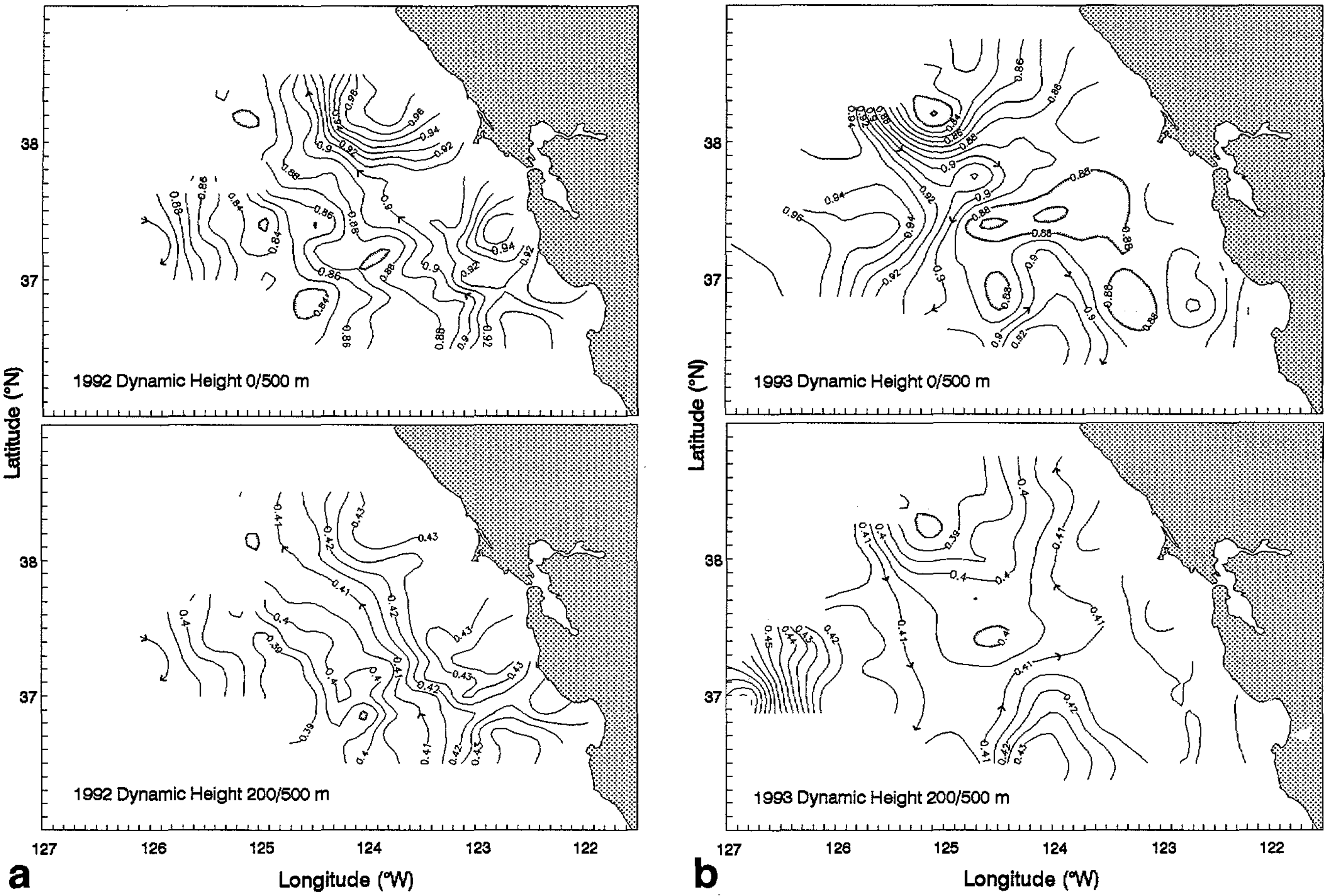

Figure 4. Contours of dynamic height topography at the surface (0/500 m) and at depth (200/500 m) in (*a*) 1992 and (*b*) 1993. *Arrows* indicate the flow direction of the 0.9 m contour interval at the surface and the 0.41 m contour interval at depth.

abundant on both the nearshore and offshore sides of the front (figure 7b). Large catches of Pacific and speckled sanddabs on the colder offshore side as well as the warmer nearshore side of this thermal feature could account for the lack of correlation with temperature (table 1, figure 7b). Large catches of Pacific whiting were made primarily in the southern portion of the survey area on the nearshore side of the frontal gradient in association with the warmest water temperatures, which accounts for the high correlation between temperature and whiting abundance (table 1, figure 7b).

In 1993 the largest catches of shortbelly rockfish, bocaccio, other rockfishes, Pacific and speckled sanddabs, and Pacific whiting were made in relatively saline nearshore waters or in association with the offshore eddy feature (figure 8). These results account for the significant correlations with salinity observed in 1993 (table 2).

The size-based overlays of shortbelly rockfish in 1992 indicated that small individuals were most abundant nearshore (figure 9). Medium-sized shortbelly rockfish were also relatively abundant nearshore, but the highest catches were made offshore. Large individuals were most abundant offshore (figure 9). In 1992 the highest catches of small Pacific sanddab were generally made nearshore, although very few specimens were collected in any one area (figure 10). In contrast, the highest catches of medium-sized and large Pacific sanddab were made offshore (figure 10). The 1992 size-based overlays of Pacific whiting showed no distinct differences in the distributions of small, medium, and large individuals (figure 11).

In contrast to the pattern observed in 1992 (figure 9), there were no distinct differences in distribution between small and medium-sized shortbelly rockfish in 1993 (figure 12). Small and medium-sized shortbelly rockfish were abundant nearshore and in association with the offshore eddy (figure 12). The spatial distribution of large shortbelly rockfish could not be discerned because only one specimen was collected (figures 6 and 12). Similarly, no size-based differences in distribution were observed for Pacific sanddab in 1993, because catches of small and large specimens were much reduced (figure 13). Although catches of Pacific whiting were much lower in 1993 compared with 1992, moderate numbers of small and medium-sized specimens were collected at several stations

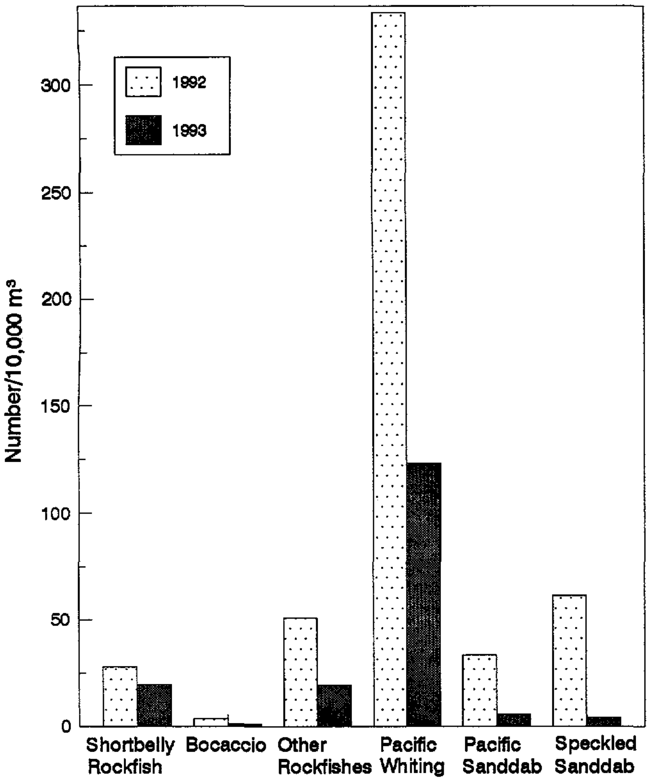

Figure 5. Abundances of larval groundfish (mean number/tow) collected in 1992 and 1993.

(figure 14). Small Pacific whiting were generally most abundant nearshore, whereas medium-sized individuals were abundant nearshore as well as offshore in association with the eddy (figure 14). Unfortunately, the largest single catch of Pacific whiting taken in 1993 (second station off Cypress Pt.; figure 8b) was discarded at sea, and no size data were recorded. However, the lack of size information for this nearshore station was not critical to describing differences in distribution with size, because all three size categories of Pacific whiting generally increased in abundance near shore (figure 14).

DISCUSSION

The relatively warm conditions in 1992 and 1993 were associated with a major El Niño event (see Symposium section; figure 2; Hayward 1993; Sakuma et al. 1994a, b). Along with increased temperature, other characteristics of El Niño along the California coast include a nearshore rise in sea level, enhanced poleward transport, increased onshore transport, reduced upwelling, and a depressed thermocline (Brodeur et al. 1985; Mysak 1986; Pearcy and Schoener 1987; Clarke and Van Gorder 1994). Anomalously high sea levels were observed in both survey years (figure 2). Enhanced poleward transport was clearly evident in our dynamic height data for 1992, but geostrophic flows at the surface apparently had

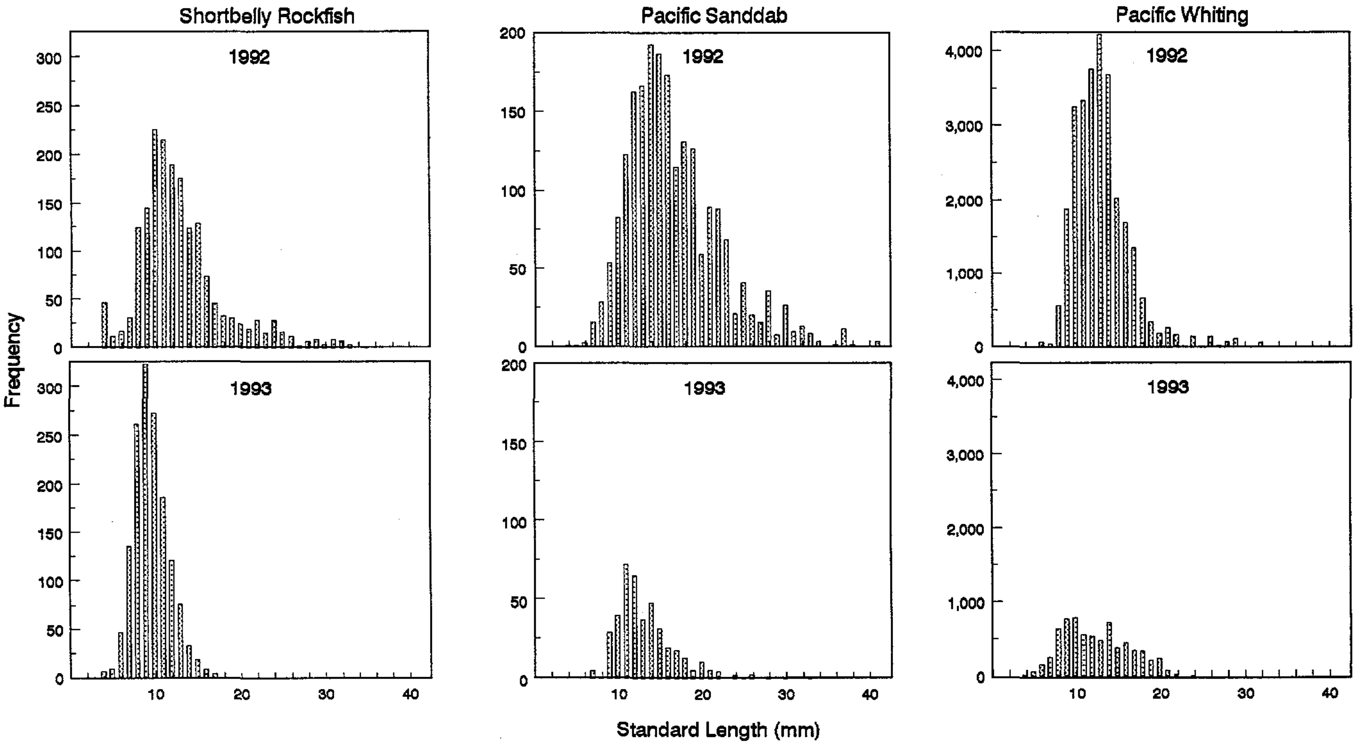

Figure 6. Length-frequency distributions of larval groundfish collected in 1992 and 1993.

TABLE 1
Spearman Rank Correlation Coefficients for 1992 (*n* = 66)

	Temperature (°C)	Salinity (ppt)	Density (kg/m^3)
Shortbelly rockfish	0.30 **0.0134**	0.35 **0.0044**	0.20 **0.1020**
Bocaccio	0.03 **0.8082**	−0.16 **0.2012**	−0.21 **0.0887**
Other rockfishes	0.42 **0.0005**	0.32 **0.0087**	0.11 **0.3815**
Pacific whiting	0.33 **0.0066**	0.09 **0.4565**	−0.11 **0.3942**
Pacific sanddab	0.05 **0.6777**	−0.23 **0.0655**	−0.30 **0.0145**
Speckled sanddab	0.12 **0.3463**	−0.13 **0.2890**	−0.28 **0.0234**

Significance probabilities for each correlation are given in boldface under the coefficients.

TABLE 2
Spearman Rank Correlation Coefficients for 1993 (*n* = 53)

	Temperature (°C)	Salinity (ppt)	Density (kg/m^3)
Shortbelly rockfish	0.30 **0.0292**	0.73 **0.0001**	0.58 **0.0001**
Bocaccio	0.24 **0.0851**	0.22 **0.1227**	0.10 **0.4863**
Other rockfishes	0.24 **0.0892**	0.49 **0.0002**	0.40 **0.0030**
Pacific whiting	0.20 **0.1338**	0.73 **0.0001**	0.61 **0.0001**
Pacific sanddab	0.05 **0.7246**	0.46 **0.0006**	0.49 **0.0003**
Speckled sanddab	−0.14 **0.3084**	0.27 **0.0530**	0.44 **0.0010**

Significance probabilities for each correlation are given in boldface under the coefficients.

reverted to the more typical condition of offshore equatorward transport in 1993 (figure 4). However, nearshore flow patterns at the surface in 1993 were not readily discernable (figure 4b). Therefore, because increased sea levels generally coincide with enhanced poleward transport (Mysak 1986), the timing of the 1993 survey may have coincided with a waning period in poleward transport rather than a total reversal of flow to equatorward transport (figures 2 and 4b). Because of unusual El Niño conditions, the distributional relationships we observed may not be indicative of spatial patterns prior to spring transition in other non–El Niño years.

Although ocean temperatures were warm in both 1992 and 1993 (figure 2; Sakuma et al. 1994a, b), there were distinct differences between these two years in the abundance patterns of the late larval fish we surveyed. In 1992 the best correlations of physical and biological data were between the various larval abundances and temperature (table 1). In contrast, salinity was more strongly correlated with abundance in 1993 (table 2). These interannual differences were probably representative of a more complex underlying relationship between the hydrographic regime and the distributional patterns of larval fish.

Between-year differences were also evident in our size-based analysis of shortbelly rockfish and Pacific sanddab. In 1992, these species were distributed progressively offshore with increasing size (figures 9 and 10); in 1993 all size categories of these species were found primarily in nearshore waters, or in association with the offshore eddy feature evident in the salinity field (figures 12–14). Whereas small shortbelly rockfish were found primarily nearshore in 1992, elevated numbers of small individuals occurred well offshore in association with the eddy feature in 1993, suggesting that in 1993 these early larvae were advected offshore (figure 12).

Larval catch rates during the winter of 1992 were high relative to 1993 (figure 5). However, this did not translate into greater year-class strength in 1992 than in 1993. To the contrary, midwater trawl surveys conducted in May and June indicated that catch rates of all pelagic juvenile rockfish species were very low in 1992, whereas abundances in May and June of 1993 were moderate (Eldridge 1994). This suggests that annual reproductive success, at least among the rockfishes, had not been established at the time our 1992 larval survey was conducted (early March), although the effect of advection or emigration of individuals out of the survey area cannot be discounted. Ralston and Howard (in press) have shown that rockfish year-class strength is set by May–June, even though cohort variability may increase later, upon settlement.

It is important to note that high catches of several species were made well offshore in both years (figures 7 and 8). One might presume that offshore-distributed late larvae of species like shortbelly rockfish, bocaccio, and Pacific and speckled sanddabs are effectively lost to adult populations, which inhabit the nearshore continental shelf and slope regions. Indeed, offshore Ekman transport due to equatorward wind stress has often been implicated as a contributing factor leading to poor recruitment in nearshore benthic species (Parrish et al. 1981; Bakun and Parrish 1982; Wild et al. 1983; Roughgarden et al. 1988; Ebert and Russell 1988).

It should be emphasized that even though both our surveys were conducted before the spring transition to

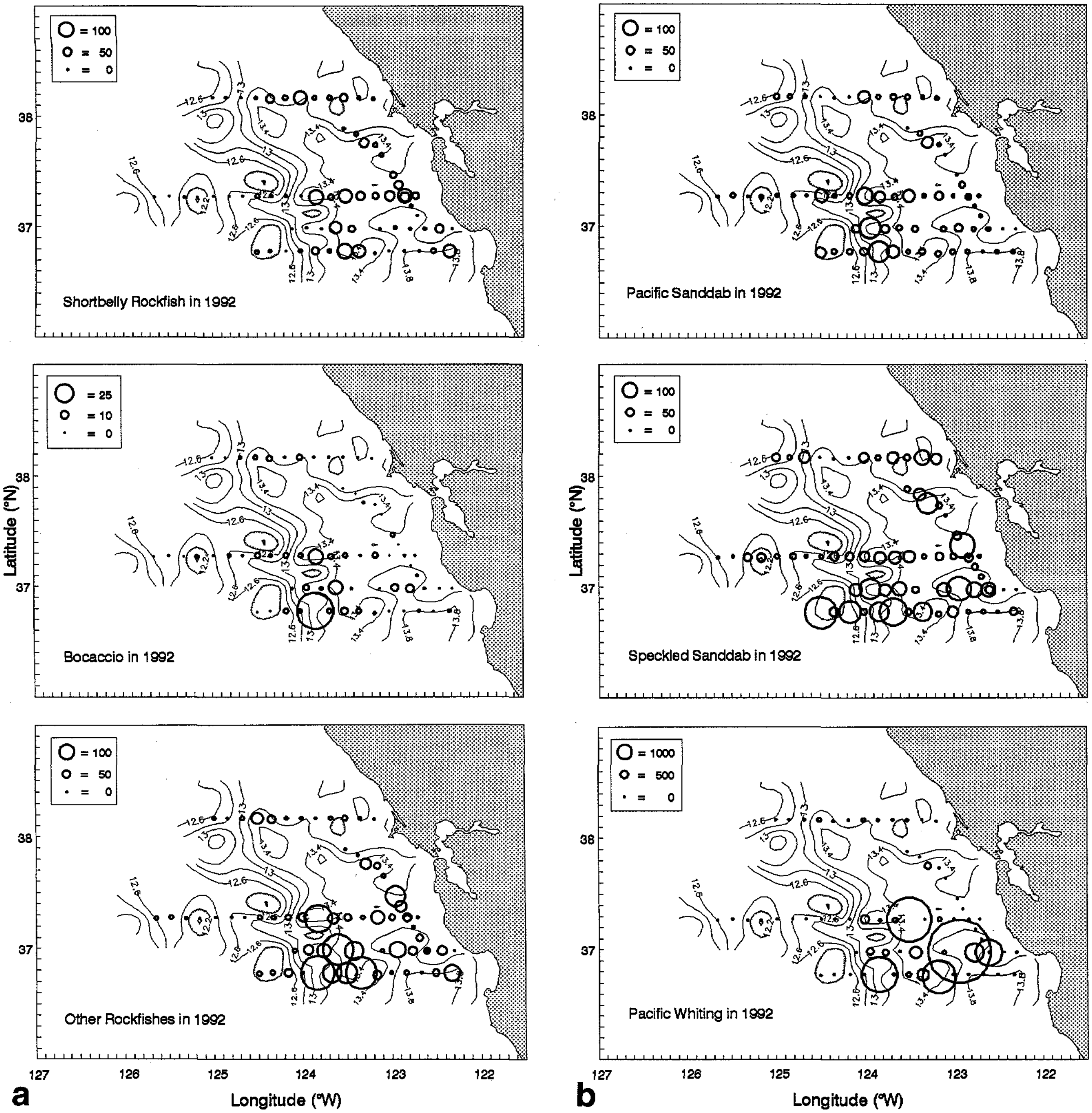

Figure 7. Temperature at 30 m in 1992 overlaid with total catches of (*a*) shortbelly rockfish, bocaccio, and other rockfishes; (*b*) Pacific and speckled sanddabs, and Pacific whiting.

the upwelling season, when offshore Ekman transport is greatest (Parrish et al. 1981; Strub et al. 1987; Largier et al. 1993), episodic cross-shelf transport to offshore waters does occur in winter. Results presented in Sakuma et al. (1994a, b) showed upwelling-favorable wind events during January of both years. We believe the offshore distribution of larvae may have been due to offshore Ekman transport stemming from episodic events of equatorward wind stress. In 1992 the offshore distribution of larvae may have been maintained by the poleward propagation of the warm-saline coastal water mass in association with the El Niño event (figure 4a; Clarke and Van Gorder 1994; Norton and McLain 1994). In 1993 the offshore distribution of larvae was probably maintained by the eddy feature evident in the salinity field (figure 3a).

The hypothesis that offshore larvae are vagrants gone

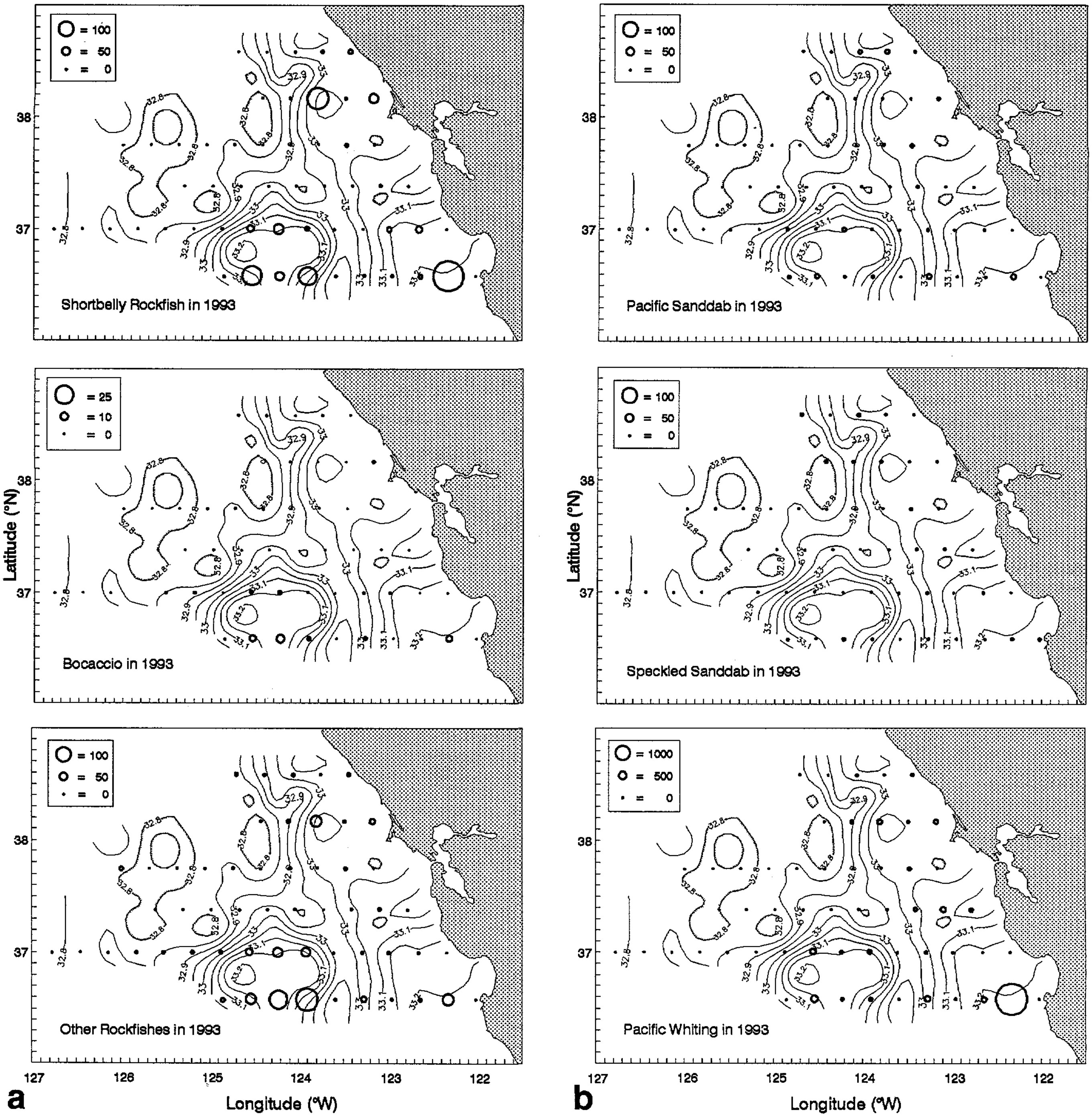

Figure 8. Salinity at 30 m in 1993 overlaid with total catches of (*a*) shortbelly rockfish, bocaccio, other rockfishes; (*b*) Pacific and speckled sanddabs, and Pacific whiting.

astray from retention areas (*sensu* Sinclair 1988) is consistent with additional data for young-of-the-year shortbelly rockfish and other rockfishes gathered in 1992. Midwater trawls conducted later in that year revealed that survival to the pelagic juvenile stage was very low (Eldridge 1994). It is not implausible to speculate that larvae distributed far offshore have little chance of reaching nearshore settlement areas. However, larvae within reasonable range of the continental shelf may reach nearshore settlement areas under the right set of conditions. Bakun and Parrish (1982) concluded that upwelling and offshore transport could be beneficial, depending on the timing and duration of the upwelling events relative to the life stage of the species being considered. In 1993 the survival of shortbelly rockfish and other rockfishes was moderate (Eldridge 1994), despite an

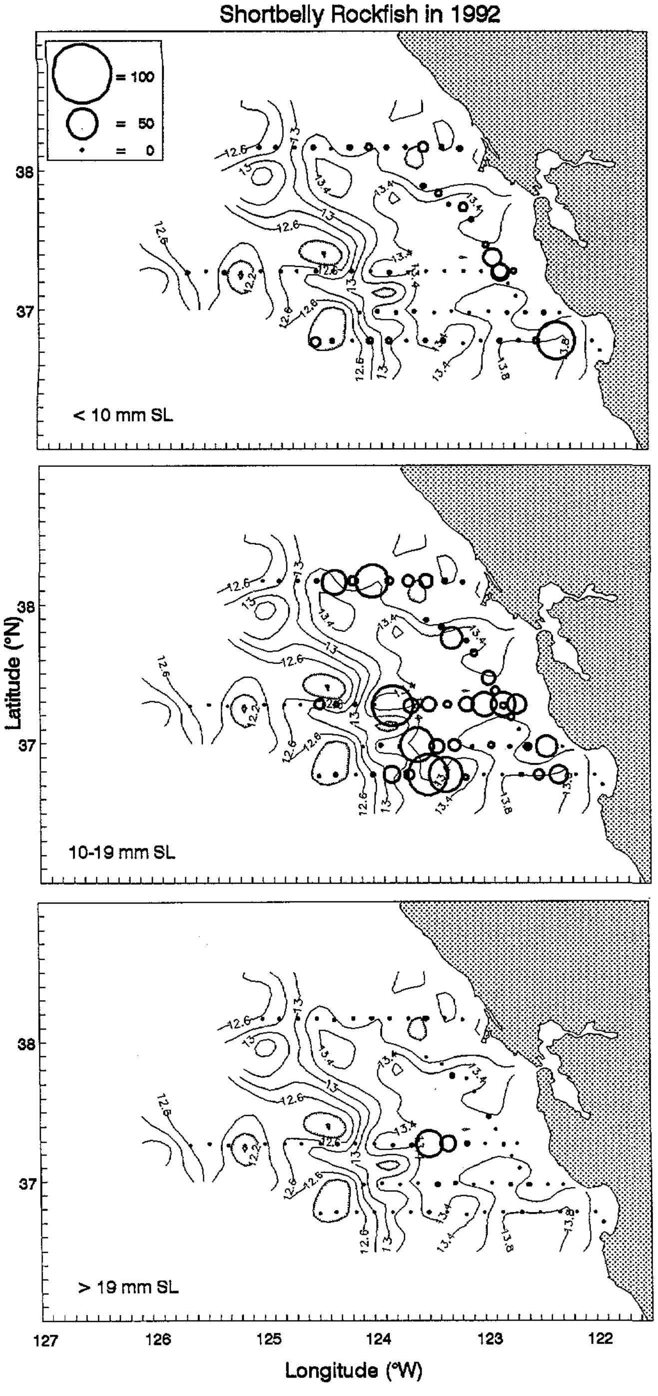

Figure 9. Temperature at 30 m in 1992 overlaid with total catches of small (<10 mm SL), medium-sized (10–19 mm SL), and large (>19 mm SL) shortbelly rockfish.

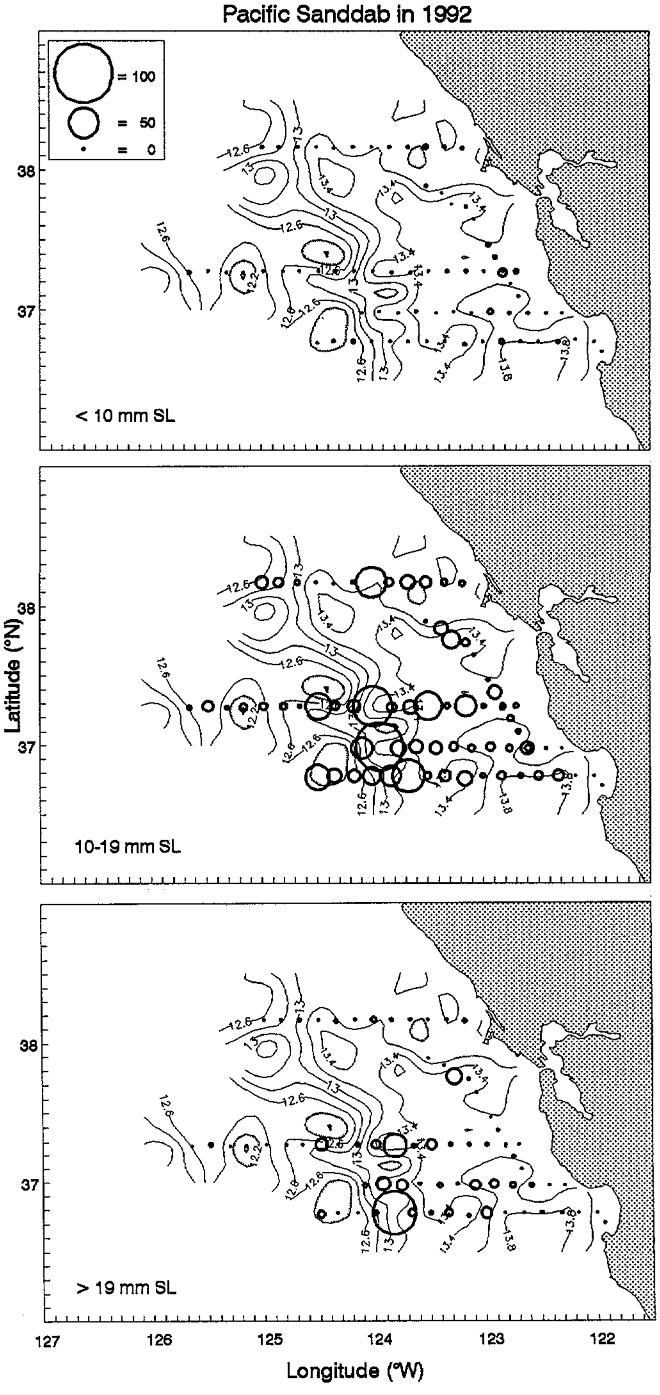

Figure 10. Temperature at 30 m in 1992 overlaid with total catches of small (<10 mm SL), medium-sized (10–19 mm SL), and large (>19 mm SL) Pacific sanddab.

extensive offshore distribution of late larvae (figure 8a). Even so, these offshore larvae were primarily distributed around an eddy feature (figure 8), which may have acted as a larval retention mechanism (Sinclair 1988). Schwing et al. (1991) have proposed that such mesoscale features can aggregate and maintain larvae near potential settlement areas (see also Lobel and Robinson 1986), despite the predominant equatorward flow of the California Current and offshore Ekman transport associated with upwelling. In addition, Hayward and Mantyla (1990) have reported that certain types of eddies can raise the nutricline into the photic zone, leading to increased primary production at the perimeter. The increased production in such areas would allow for better larval survival than

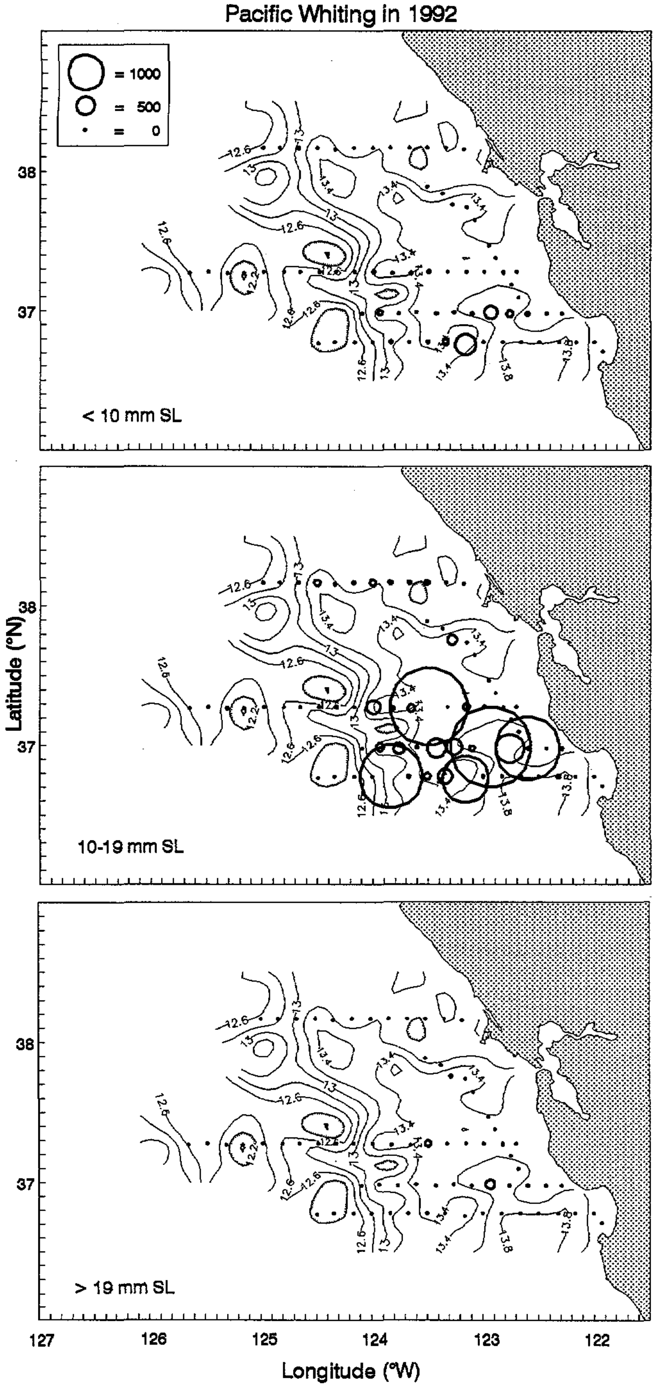

Figure 11. Temperature at 30 m in 1992 overlaid with total catches of small (<10 mm SL), medium-sized (10–19 mm SL), and large (>19 mm SL) Pacific whiting.

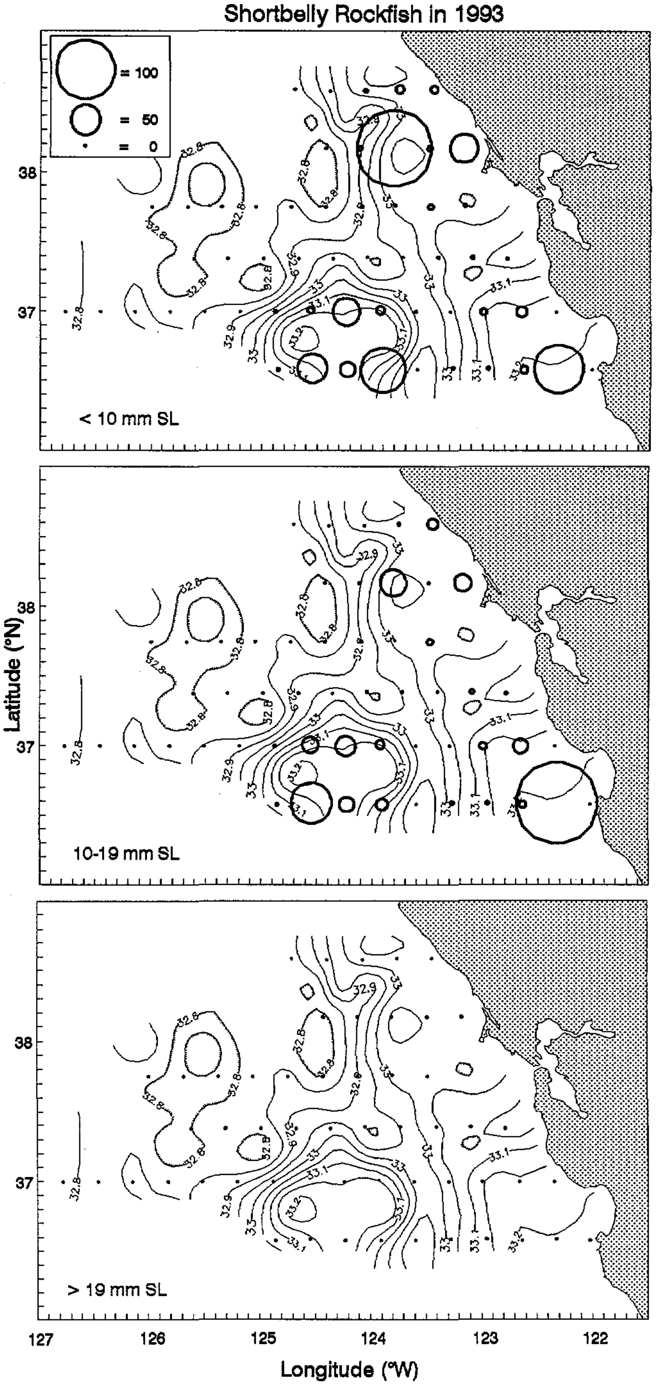

Figure 12. Salinity at 30 m in 1993 overlaid with total catches of small (<10 mm SL), medium-sized (10–19 mm SL), and large (>19 mm SL) shortbelly rockfish.

in the surrounding oligotrophic offshore waters. Therefore, within limits, an offshore distribution of larvae, in and of itself, may not be detrimental to survival.

Sakuma (1992) observed that early-stage metamorphic Pacific and speckled sanddabs were predominantly distributed farther offshore than late-stage individuals, which were distributed closer to shore. In this study, high catches of medium-sized and large Pacific sanddab, which correspond to the early-stage individuals in Sakuma 1992, were predominantly distributed offshore (figures 10 and 13). Larson et al. (1994) observed a similar trend in the pelagic juveniles of several species of rockfish, in which smaller individuals had a more offshore distribution, while larger ones were more often found nearshore. In this

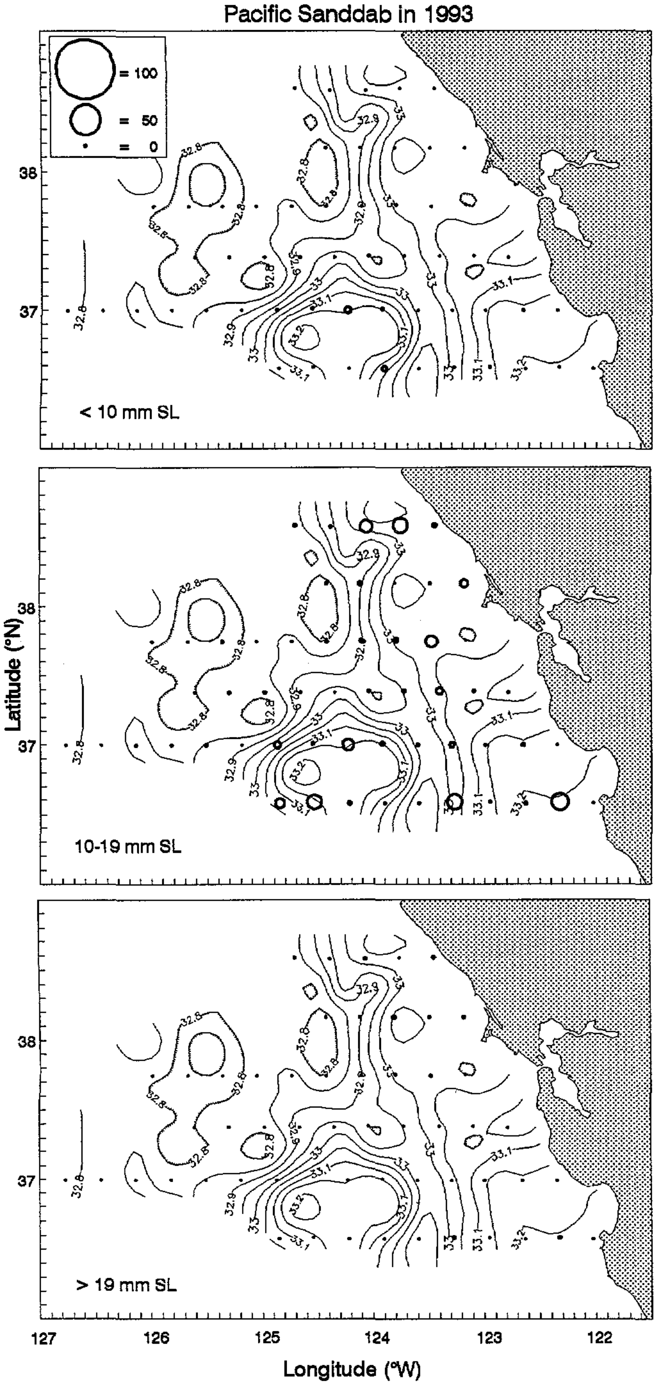

Figure 13. Salinity at 30 m in 1993 overlaid with total catches of small (<10 mm SL), medium-sized (10–19 mm SL), and large (>19 mm SL) Pacific sanddab.

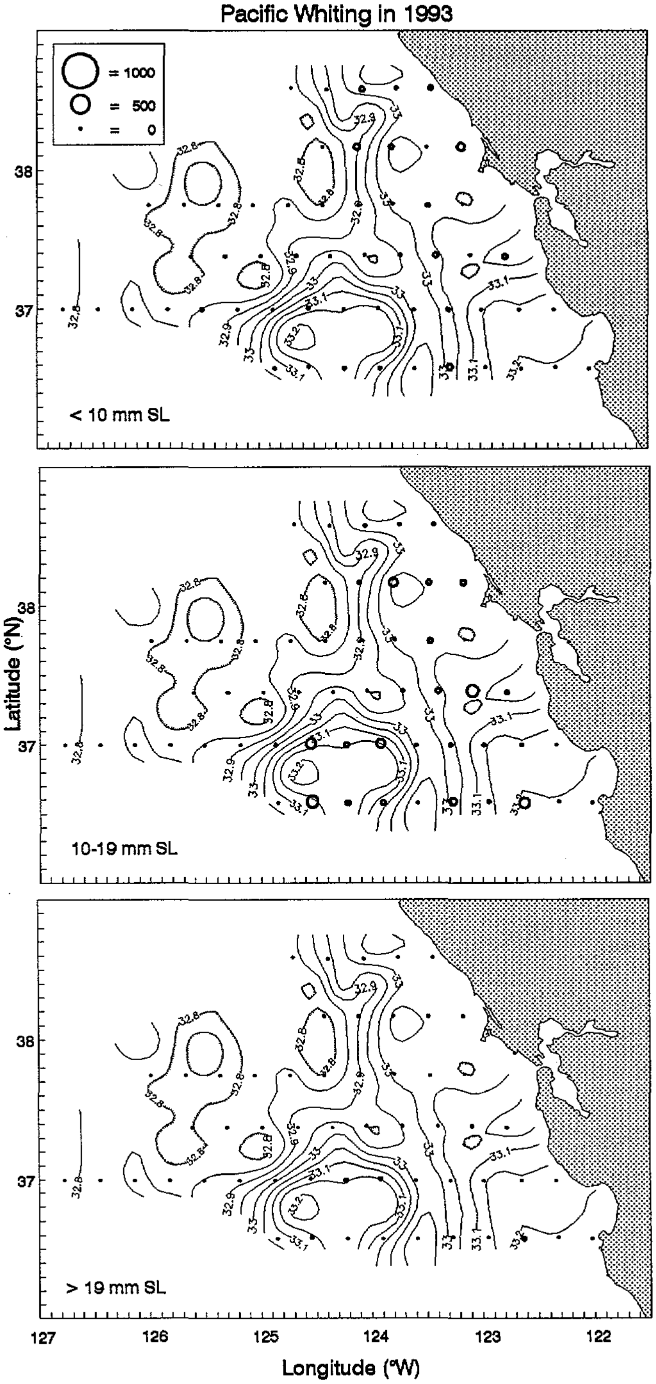

Figure 14. Salinity at 30 m in 1993 overlaid with total catches of small (<10 mm SL), medium-sized (10–19 mm SL), and large (>19 mm SL) Pacific whiting.

study, we observed high offshore catches of medium-sized and large shortbelly rockfish (figures 9 and 12), which corresponded to the small pelagic juveniles in Larson et al. (1994). Larson et al. (1994) and Sakuma (1992) both indicated that earlier larval stages were subject to transport offshore by prevailing current patterns, whereas later juvenile stages were able to reach nearshore settlement areas through some still-unknown set of mechanisms (Sakuma 1992; Larson et al. 1994). Given that juvenile rockfishes can remain pelagic for over 150 days (Woodbury and Ralston 1991), and that Pacific and speckled sanddabs can remain pelagic for over 270 days (E. B. Brothers, unpubl. data. EFS Consultants, 3 Sunset West, Ithaca, NY 14850; Kendall 1992), it is reasonable to postulate that larvae distributed offshore may be transported toward shore at some later period.

In contrast to the distributional patterns of sanddabs and rockfishes, the largest catches of Pacific whiting were made closer to shore in the southernmost portion of the survey area (figures 7b and 8b). This may have been due to northward transport of larvae spawned to the south, or a northward shift in spawning location during El Niño conditions (Bailey and Francis 1985; Hollowed 1992).

The difference in the horizontal distribution of Pacific whiting with respect to sanddabs and rockfishes could also be attributed to differences in their vertical distributions. Larval sanddabs and rockfishes are generally abundant between 20 and 60 m within the mixed layer (Ahlstrom 1959; unpubl. MOCNESS data), whereas Pacific whiting are generally most abundant below the mixed layer at depths greater than 50 m (Ahlstrom 1959; Bailey and Francis 1985). The deeper distribution of Pacific whiting larvae below the mixed layer would subject them to different current patterns and transport mechanisms than fish found within the mixed layer. Figure 3 indicates that, although the overall flow patterns observed at 30 m were similar to those at 60 m, there were smaller-scale differences in hydrography between the two depths. These smaller-scale differences over a period of time could account for the difference in the distribution of Pacific whiting compared with rockfishes and sanddabs in 1992 (figure 7).

In summary, the distributional patterns of these late larval groundfish prior to spring transition appear to depend on the prevailing hydrography. The hydrographic regime is subject to interannual variations in flow, and the various species groups are affected differently by these variations. Larvae appear to be subject to transport offshore away from the shelf and slope areas, but this does not preclude future recruitment to nearshore areas. In addition, at least for the rockfish species, reproductive success in 1992 had not been determined by early March, indicating that prevailing and future environmental conditions could dramatically affect recruitment.

ACKNOWLEDGMENTS

We wish to thank Tom Laidig, Bill Lenarz, Beth Norton, Don Pearson, Gareth Penn, Dale Roberts, and Dave Woodbury, who all participated as members of the scientific field party. We also thank the officers and crew of R/V *David Starr Jordan* for their able assistance. In addition, Glenn Almany, Tracy Hannigan, and Jennifer McCarthy helped process samples ashore. Special thanks to Ed Armstrong for providing the dynamic height calculations from the CTD data. The ideas we present evolved as a result of many discussions and careful manuscript critiques by Ralph Larson, Bill Lenarz, Dale Roberts, Frank Schwing, and Dave Woodbury.

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THE LIFE HISTORY OF THE SPOTTED SAND BASS (*PARALABRAX MACULATOFASCIATUS*) WITHIN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Spotted sand bass (*Paralabrax maculatofasciatus*) are under increasing angling pressure in the shallow waters off southern California. In southern California, spotted sand bass are largely restricted to shallow, warm-water areas such as bays, estuaries, and harbors, which appear to serve as warm-water refuges for this basically subtropical species. Rod-and-reel sampling from June 1991 to August 1993 yielded 639 individuals from seven locations. Specimens ranged from 51 to 400 mm SL, with only 8 fish below 150 mm SL and 10 above 330 mm SL. Analysis of otolith sections revealed that a single opaque zone was laid down each summer. The oldest fish was 14 years old; the vast majority of the large specimens were 6 to 10 years old. Growth rate was sharply asymptotic, with some fish reaching 200 mm SL in their first year. Because growth rates varied significantly among the four locations tested, the overall growth model was highly variable ($R^2 = 0.67$). Half of the female spotted sand bass matured very early (age class 0) and at a small size (155 mm SL). Males matured later (50% maturity at 1.4 years) and at a somewhat larger size (50% at 180 mm SL). Gonosomatic indices indicated that spawning occurred from June through August in southern California.

Spotted sand bass inhabiting the northern Gulf of California are believed to be protogynous hermaphrodites, and populations from San Diego Bay showed an age/sex composition pattern consistent with protogyny. However, populations from the six other southern California locations had roughly equal representation of the sexes throughout the age structure, and many of the oldest individuals were females. This pattern is more consistent with gonochorism or "partial" protogyny. Southern California spotted sand bass seem to have a complex reproductive strategy which may include flexible rates of female sex change among populations and sneaking males that mimic females within spawning aggregations.

Back-calculation of annual recruitment success from otolith data revealed that almost all of our fish came from two pulses during 1984–85 and 1989–90. These pulses occurred during post-El Niño years. Recruitment into southern California during El Niño years (1982–83, 1986–87, and 1992–93) appears to have been extremely low to nonexistent. However, summer sea-surface temperatures at the Scripps Pier peaked one to two years after these El Niño events, resulting in a highly significant correlation ($r = 0.723$, df = 13, $P = 0.002$) between recruitment (corrected for mortality) of spotted sand bass and mean summer sea-surface temperature off southern California over the past 15 years.

INTRODUCTION

Historically, spotted sand bass (*Paralabrax maculatofasciatus*) have ranged as far north as San Francisco Bay and south to Mazatlán, Mexico. Dense populations also occur in the northern portions of the Gulf of California (Sea of Cortez). Typically, spotted sand bass are rarely seen north of Santa Monica Bay. Early records of occurrence at more northern locations often came from El Niño and other warm-water periods. In southern California, spotted sand bass are restricted to shallow, warm-water areas such as bays, harbors, and quiet, protected areas of the coast that contain structure in the form of eelgrass, surfgrass, and rock relief (Fitch and Lavenberg 1975). These areas act as warm-water refuges for this generally subtropical species (Allen 1985).

While protected from commercial exploitation, spotted sand bass have come under increasing recreational angling pressure off southern California in recent years. Landings are greatest from private boats and rental skiffs fishing such prominent bay and estuarine habitats as Newport Bay, Mission Bay, and San Diego Bay (Love 1991; Ono 1992). The California Department of Fish and Game conducted a survey of skiff fishing and estimated that the annual catch of spotted sand bass in southern California waters ranged from 12,790 to 23,933 fish between 1976 and 1981. Subsequent estimates of sport catch, based on data from boat and shore fishing, indicated that between 53,000 and 170,000 spotted sand bass were taken per year from 1980 to 1989 (Ono 1992). Although the annual catch of spotted sand bass is considerably lower than the catches of its sympatric relatives the kelp bass (*Paralabrax clathratus*) and the barred sand bass (*P. nebulifer*), the fishing pressure on spotted sand bass must be considered significant because of their restricted habitat in southern California waters.

[Manuscript received January 30, 1995.]

Prior to the current investigation, very little was known about the biology of this important sport fish. The largest spotted sand bass on record measured 450 mm standard length (SL) and weighed 2.6 kg (Miller and Lea 1972), but specimens longer than 330 mm SL are very rare. Before this study, the only information available on age came from a single specimen, 380 mm total length (TL), aged at 5 years (Fitch and Lavenberg 1975). The larval and juvenile stages of spotted sand bass have been described from laboratory-reared specimens by Butler et al. (1982). In southern California, these fish appear to form spawning aggregations at the mouths of embayments during the late spring and summer. The eggs are pelagic and enter the plankton in coastal waters. Studies of the spotted sand bass population in the northern Gulf of California indicated that fish from that location appear to be sequential, protogynous hermaphrodites (Hastings 1989). According to Hastings, most fish mature first as females and later change into males, although primary males may also exist. In a recent paper, Oda et al. (1993) presented limited evidence that individuals from Mission Bay in southern California were also protogynous hermaphrodites.

The primary purpose of our study was to provide basic information on the life history and ecology of spotted sand bass from southern California. This paper summarizes information on (1) length frequency, (2) length-weight relationship, (3) age and growth, (4) food habits, (5) reproductive cycles, (6) age at first maturity, (7) sex composition with age, and (8) annual recruitment patterns of spotted sand bass within the Southern California Bight.

METHODS AND MATERIALS

Collection of Specimens

Spotted sand bass are structure-oriented, fairly sedentary fish that are virtually impossible to capture with standard scientific collecting methods (trawls, seines, and gill nets). Rod-and-reel (light tackle) sampling with artificial lures is the only efficient method for collecting large numbers of spotted sand bass. To this end, a professional fishing guide, Mike Gardner, was contracted to make twelve monthly sampling trips using rod and reel between March 1992 and February 1993. On these twelve trips we sampled spotted sand bass at the following locations within the bight (figure 1): Anaheim Bay, Long Beach Harbor, Marina del Rey, Newport Bay, and San Diego Bay. These collecting trips yielded about 40 spotted sand bass each month, except for January 1993, when no fish were caught following 13 straight days of rainfall. Additional collections were made with rod and reel from 6 m Boston whalers launched from the R/V *Yellowfin* operated by the Ocean Studies Institute of the California State University. These collections were taken at Catalina Harbor, Newport Bay, Mission Bay, and San Diego Bay from July 1991 through August 1993. National Marine Fisheries Service, Long Beach, provided five young-of-the-year spotted sand bass collected by beach seine from Mission Bay in April 1993. Finally, a number of large specimens were donated by local anglers in response to flyers distributed throughout southern California. Overall, 639 fish were included in this study.

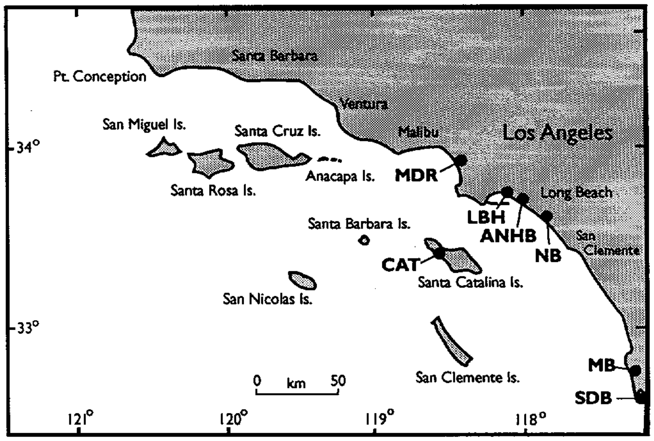

Figure 1. Mainland and Catalina Island locations where spotted sand bass were collected during 1991–93. *ANHB* = Anaheim Bay; *CAT* = Catalina Harbor; *LBH* = Long Beach Harbor; *MDR* = Marina del Rey; *MB* = Mission Bay; *NB* = Newport Bay; *SDB* = San Diego Bay.

Specimens were either returned to the research vessel or placed on ice and returned to the laboratory for workup. Donated fish were typically accepted in a frozen state and thawed before workup. Each fish was numbered, measured to the nearest mm (both SL and TL), and weighed to the nearest 0.1 g. Both sagittae were removed, cleaned, air-dried, and stored in labeled envelopes. Finally, the digestive tract and gonads were dissected out and preserved in 10% Formalin and seawater in individual zip-lock bags for later analysis.

All data were entered into Reflex 2.0 (Borland International Inc., Scotts Valley, CA) database form on an MS DOS desktop computer system for storage and subsequent analysis. Data summary and analyses were carried out with the Complete Statistical System (CSS; Statsoft Inc., Tulsa, OK).

Age and Growth

The left sagitta (in most cases) of each specimen ($N = 634$) was sectioned with a Buehler Isomet low-speed saw. Otoliths were attached to wood blocks with cyanoacrylate (Super glue). Each block with its sagitta was placed on the saw, and a dorsal–ventral, 0.5 mm section was cut through the otolith, with two diamond-edged blades separated by a stainless steel shim. Sections were placed in a black-bottomed watch glass filled with water and read under a dissecting scope at 50× magnification. Each otolith was read twice, by two different readers. When readings did not agree, the otolith was read again. The value of two concordant readings was accepted as the best estimate of age. Less than 0.1 percent of the otoliths had to be excluded from analysis because of difficulty in recognizing annuli.

Many fish lay down an opaque and a hyaline (translucent) band in their otoliths on a seasonal basis. We attempted to validate that these bands were formed annually by calculating the percentage of fish taken each month from April 1992 to February 1993 that had opaque and translucent margins (edges) on otoliths. It is reasonable to assume that band deposition was seasonal if the bands were present during only one portion of the year.

Lengths at age were estimated by taking the means of the standard lengths by age class as determined from direct reading of the otoliths. Growth was assumed to be described by the von Bertalanffy growth curve model using FISHPARM (Elsevier Scientific Publishers Co., Bronxville, NY):

$$L_t = L_\infty \, (1 - \exp - \mathrm{k}(t - t_0))$$

where

L_t = length at time t

L_∞ = theoretical maximum length

k = constant expressing the rate of approach to L_∞

t_0 = theoretical age at which $L_t = 0$.

First, a growth model was determined for all fishes collected from southern California. Secondly, due to the high variance of age-specific lengths of fish from different locations, individual growth models were also calculated for the four locations (Anaheim Bay, Catalina Harbor, Newport Bay, and San Diego Bay) where sample sizes were adequate to allow such a treatment. Growth rates at these four principal locations were compared by means of analysis of covariance (ANCOVA) of length-at-age data for individual fish. Thirdly, growth curves for males and females were calculated separately and also compared by means of ANCOVA.

Food Habits

The contents of 534 preserved spotted sand bass stomachs were examined. Artificial lures were used almost exclusively in the capture of specimens, thereby avoiding any bias introduced by the use of organic baits. Each item found was identified to the lowest taxon possible, counted, and weighed (wet weight) to the nearest gram. After data collection, items were grouped into higher-level taxonomic categories, and prey importance was represented using the Index of Relative Importance (modified from Pinkas et al. 1971):

$$\mathrm{IRI} = (N + W)\, F$$

where N = % numerical occurrence;

W = % wet weight;

F = % frequency of occurrence.

Timing of Maturation and Reproduction

To determine the duration of the spawning season, we calculated the gonosomatic index (gonad weight/total body weight × 100) for each specimen to quantify changes in gonad size over the months of the year.

We determined length and age at first maturity by classifying the gonads of 358 specimens collected during the peak breeding season (May–August) as immature or mature (male or female) based on the techniques of Bagenal and Braum (1971). The relationships between length and maturity and age and maturity were established with a transformation of

$$P_x = \frac{1}{1 + e^{ax+b}}$$

(Gunderson et al. 1980) to yield

$$ax + b = \ln\left(\frac{1}{P_x} - 1\right)$$

where P_x = the proportion mature at length or age x. We plotted x against

$$\ln\left(\frac{1}{P_x} - 1\right)$$

with stepwise linear regression (SPSS, version 2.1) to obtain values for a and b. We determined fifty percent maturity by calculating values for a and b and $P_x = 0.50$ to solve for x.

Sex Composition

Gonads were examined macroscopically. In cases where sex was uncertain, the gonads were teased apart under a dissecting microscope to verify sex class. Length frequencies of immature, male, and female fishes were plotted to examine relationship between length and sex for all southern California fish combined ($n = 634$).

Evidence of sexual strategies in this species was obtained by determining sex ratios over age classes for all southern California spotted sand bass, and for the two major populations studied (where $N > 100$) from Newport Bay and San Diego Bay. This technique should function as an indirect measure of sexual strategy.

Annual Recruitment Patterns

Annual recruitment patterns within the Southern California Bight were estimated from year-class strength as determined by the aging of individual fish. Year of birth was back-calculated for each fish that was successfully aged. The resultant year-class strength information for the last 15 years was presented graphically. The annual recruitment as measured by year-class strength was corrected for mortality with a general equation for mortality and survivorship (modified from Ricker 1975):

$$N_t = N_0 \left(\frac{1}{S}\right)^t$$

where

N_0 = number of fish in a year class at $t = 0$
N_t = estimated number of recruits at t years in past corrected for mortality
S = annual estimated survivorship (complement of mortality).

We estimated an annual mortality of 0.16 ($S = 0.83$) for spotted sand bass populations from southern California based on the frequency of fish in the 2 through 10 age classes. To err on the conservative side, we corrected annual recruitment by assuming a constant mortality rate and using the rounded-off value for annual survival, $S = 0.8$ ($M = 0.2$, $-Z = 0.2231$). To examine the possible relationship between annual recruitment success and sea temperature, we ran a Pearson's correlation analysis comparing the annual corrected recruitment with mean summer (June–September) sea-surface temperatures taken at the Scripps Pier for the years 1978 to 1992.

RESULTS

Length Frequency

The 639 specimens collected from 1991 through 1993 ranged from 51 to 400 mm SL; only 8 fish were smaller than 150 mm, and 10 were larger than 330 mm (figure 2). Overall, 72% of the fish ranged from 200 to 299 mm; the modal size class was 240–249 mm. The largest fish in our collection (400 mm SL) was donated by a local angler and stands as the current California state record fish.

Standard length (SL) was found to be about 80% of the total length (TL) across size classes; the two measures were related by the equation $TL = 1.233\ SL + 2.444$.

Length-Weight Relationship

We used 507 fish in the length-weight analysis. We included males and females with immature fish in this analysis since it made little sense to separate sexes in potentially hermaphroditic populations. The relationship between length and weight fit the relationship $W = aL^b$, where W = weight in grams, L = standard length in mm, and a and b are constants, with values determined by the nonlinear regression subroutine in CSS (figure 3). The length-weight function for this data set was $W = 0.000026L^{3.0187}$. Over 97% of the variance in the data was explained by the model ($R^2 = .9739$).

Age and Growth

Spotted sand bass appear to lay down opaque bands on a seasonal basis, beginning in spring and extending through the summer months (figure 4). We therefore judge the bands to represent annual rings. The focus of the average otolith was very wide; the first opaque ring did not form until the otolith was about 3 mm wide. Subsequent rings were typically closely packed and very readable. Initial readings by two independent readers were in 75% agreement. Reevaluation resolved all but a few cases.

The oldest fish encountered was a 14-year-old female from Newport Bay. The oldest male came from Anaheim Bay and was determined to be 13 years old. The vast majority of fish, however, were 10 years old or less

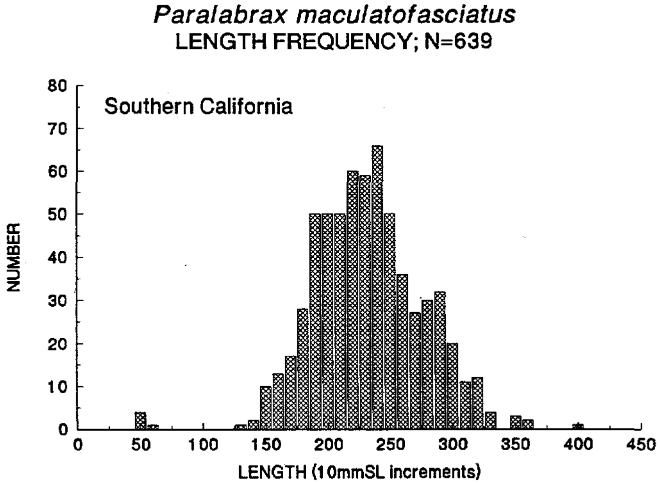

Figure 2. Length frequency of 639 spotted sand bass (*Paralabrax maculatofasciatus*) from all southern California locations combined, 1991–93, in length increments of 10 mm.

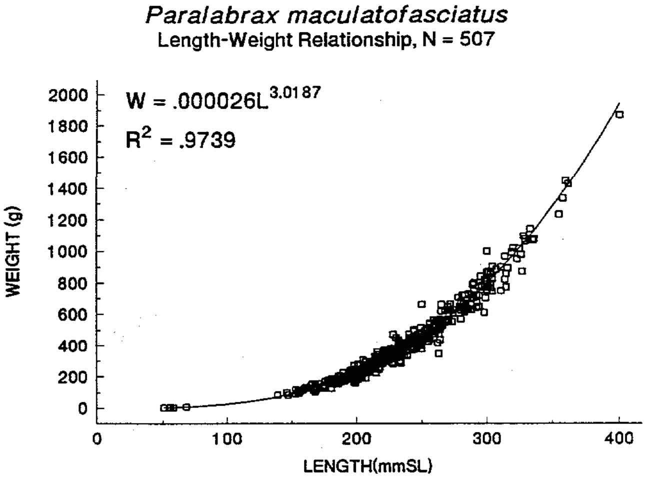

Figure 3. Length-weight relationship of 507 spotted sand bass (*Paralabrax maculatofasciatus*) collected from 1991 through 1993 from the Southern California Bight.

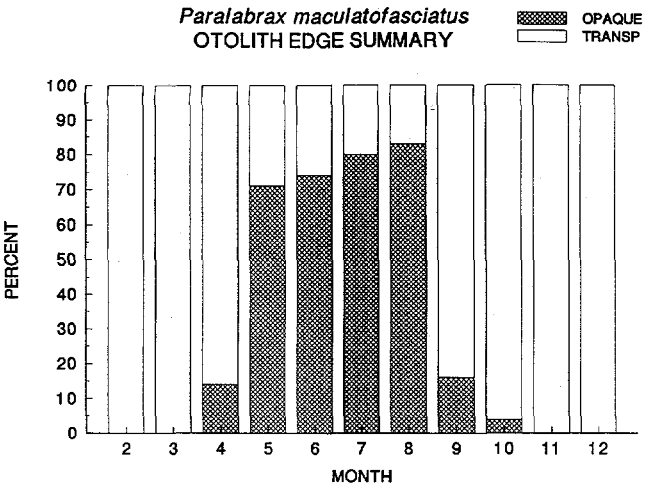

Figure 4. Otolith edge summary (opaque versus transparent ring at edge of otolith) of spotted sand bass (*Paralabrax maculatofasciatus*) captured each month from April 1992 through February 1993 from southern California. (No fish were taken in January 1993.)

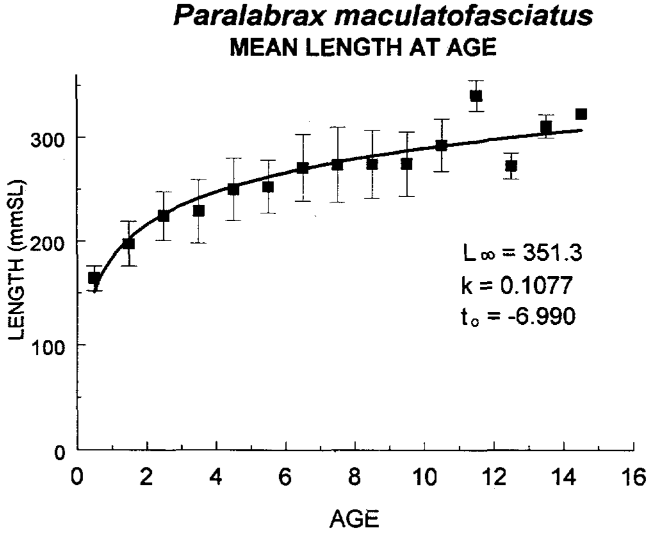

Figure 5. Mean length (mm SL) at age for spotted sand bass (*Paralabrax maculatofasciatus*) from southern California. *Error bars* represent 1 standard deviation. *Curve* was fitted using the von Bertalanffy growth equation. Von Bertalanffy parameters are listed on the right in the figure.

(figure 5); only eight individuals (1.3%) were 11 years or older.

Growth rate for all southern California fish combined was sharply asymptotic, with some fish reaching as much as 200 mm SL in their first year (figure 5). Fish in their first two years grew extremely fast, with the mean length of age-1 fish being 197 mm SL. The von Bertalanffy parameters for all fish were determined to be $L_\infty = 351.3$, $k = 0.1077$, and $t_0 = -6.990$. Growth rates of males and females were not significantly different (ANCOVA; df = 1, 517; $F = 2.79$; $P = 0.09$). But a slight trend toward very fast, early growth was evident in some males (figure 6).

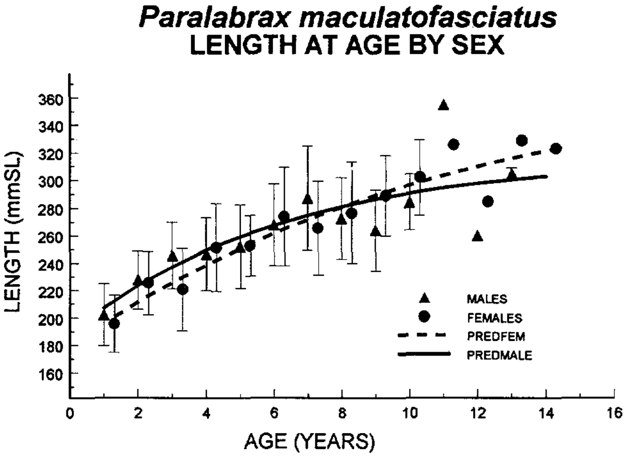

Figure 6. Mean length (mm SL) at age for female ($n = 367$) and male ($n = 218$) spotted sand bass (*Paralabrax maculatofasciatus*) from southern California. *Error bars* represent 1 standard deviation. *Curves* were fitted using the von Bertalanffy growth equation. *PREDFEM* = predicted curve for females; *PREDMALE* = predicted curve for males.

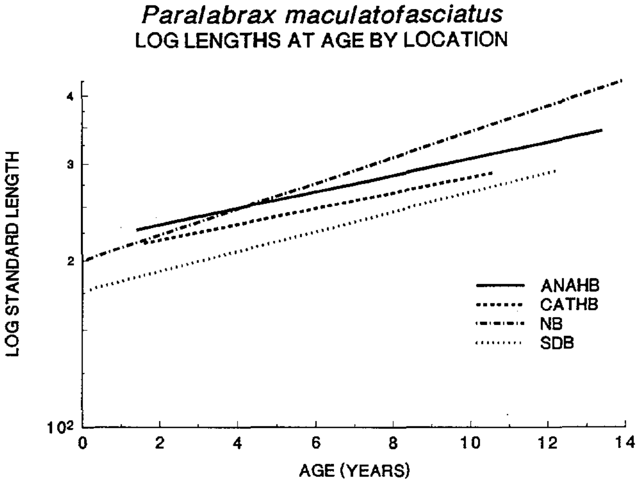

Figure 7. Growth rates (log-transformed) of spotted sand bass (*Paralabrax maculatofasciatus*) from four southern California locations. *ANAHB* = Anaheim Bay ($n = 96$); *CATHB* = Catalina Harbor ($n = 41$); *NB* = Newport Bay ($n = 264$), *SDB* = San Diego Bay ($n = 138$).

Variance in age-specific length data was high ($R^2 = 0.67$) when fish from all locations were considered together (figure 5). Log-transformed growth rates differed significantly (ANCOVA, df = 3, 541; $F = 134.03$; $P < 0.001$) among the four principal locations: Anaheim Bay, Catalina Harbor, Newport Bay, and San Diego Bay (figure 7). Of these, San Diego Bay fish exhibited the slowest overall growth rate; the Catalina Harbor, Anaheim Bay, and Newport Bay populations showed progressively faster growth rates.

Food Habits

Brachyuran crabs (IRI = 2020) and bivalve mollusks (IRI = 1326) were by far the most important food items

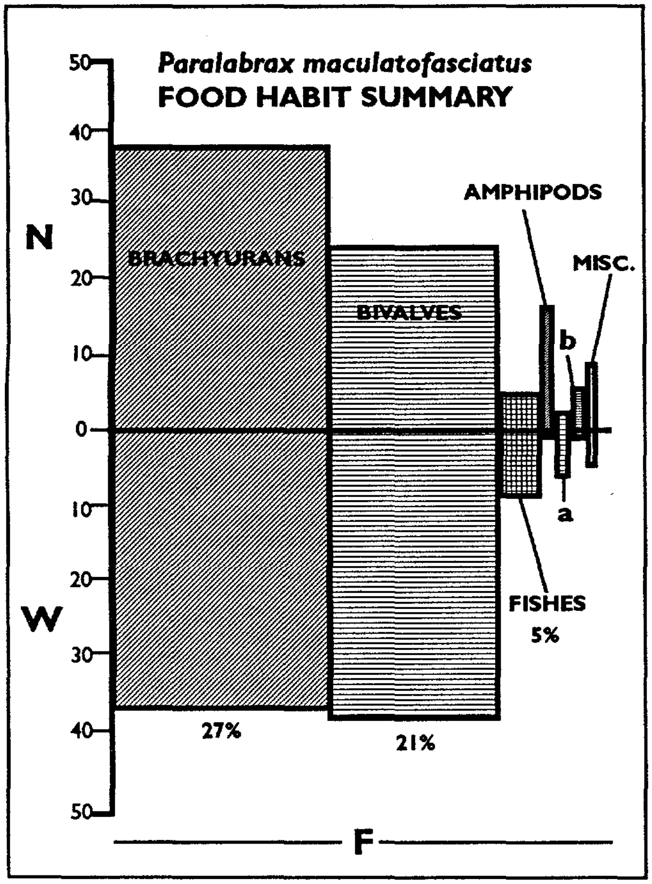

Figure 8. Relative importance of various food items found in the stomachs of 443 spotted sand bass (*Paralabrax maculatofasciatus*) from southern California. *N* = % number; *W* = % wet weight; *F* = % frequency of occurrence; *a* = Echiuroids; *b* = Gastropods (after Pinkas et al. 1971).

found in spotted sand bass (figure 8), followed much less commonly by bony fishes (IRI = 67) and amphipods (IRI = 28). In all, twelve taxonomic groups of mainly benthic organisms were identified from gut contents. Of the guts examined, 201 (38%) were found to be empty, probably because of the high incidence of regurgitation of gut contents during capture.

The prominent brachyuran crabs included the genera *Hemigrapsus*, *Pachygrapsus*, *Cancer*, and *Loxorhynchus*. The main bivalves were members of the genera *Tagelus* and *Laevicardium*. Identifiable fishes were mainly gobies (Gobiidae) and northern anchovies (*Engraulis mordax*).

Maturation and Reproduction

Female spotted sand bass matured very early and at a small size (figures 9 and 10); half matured before the end of their first year at a length of 155 mm SL. All females one year old or older were found to be mature. Males matured later (50% being mature in 1.4 years) and at a somewhat larger size (50% at 180 mm SL). The impact of potential sex change, if any, on these values is unknown.

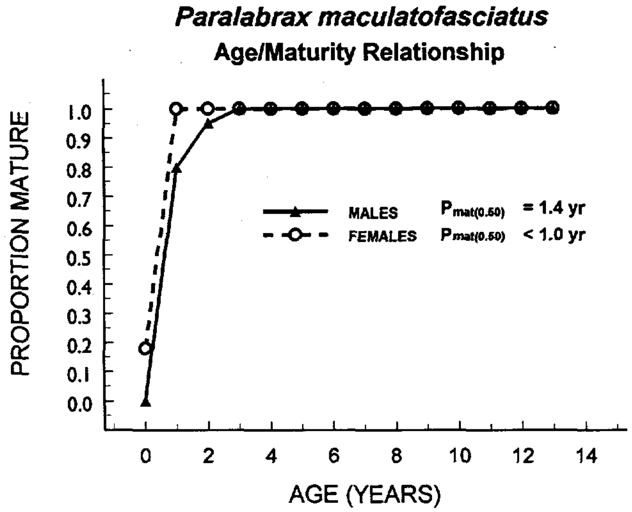

Figure 9. Age-maturity relationships for 585 male and female spotted sand bass (*Paralabrax maculatofasciatus*) from southern California, including the ages at which 50% of the males and females were mature.

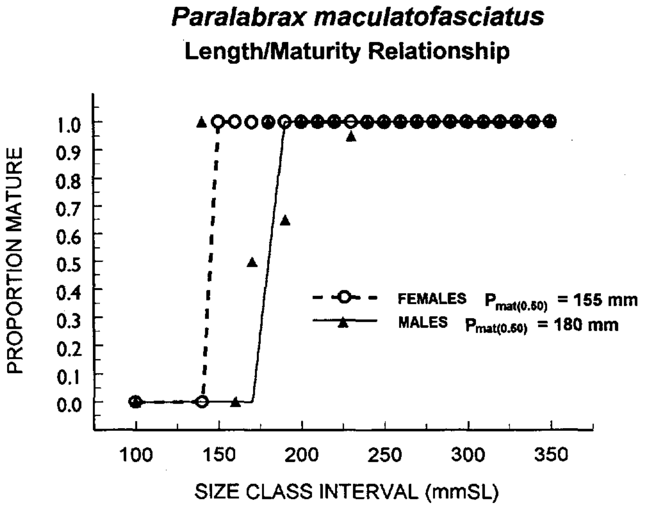

Figure 10. Length-maturity relationships for 585 male and female spotted sand bass (*Paralabrax maculatofasciatus*) from southern California, including the lengths (mm SL) at which 50% of the males and females were mature.

Analysis of gonosomatic indices throughout the year indicated that spotted sand bass spawn from June through August in southern California (figure 11). Female gonosomatic indices peaked in June (GSI = 6.2%) and decreased thereafter through August (2.9%). Male GSIs increased dramatically in June (3.6%), peaked in July (3.7%), and then declined through August (2.1%). Fall, winter, and early spring GSIs ranged from 0.1% to 0.4% body weight in males and 0.3% to 0.7% in females.

Sex Composition

The capture of breeding (ripe and running) spotted sand bass revealed the significance of the various color patterns in southern California populations. The large, high-contrast, black-and-white individuals with white

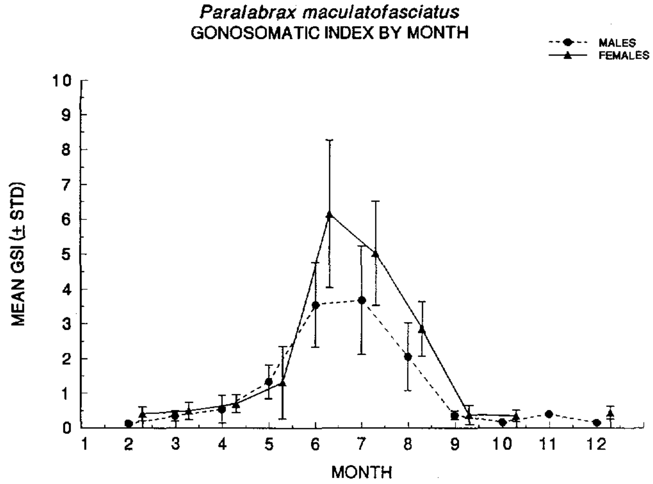

Figure 11. Gonosomatic indices for 168 male and 290 female spotted sand bass (*Paralabrax maculatofasciatus*) from southern California by month of capture from February 1992 to February 1993. Values are means ±1 s. (No fish were taken in January 1993.)

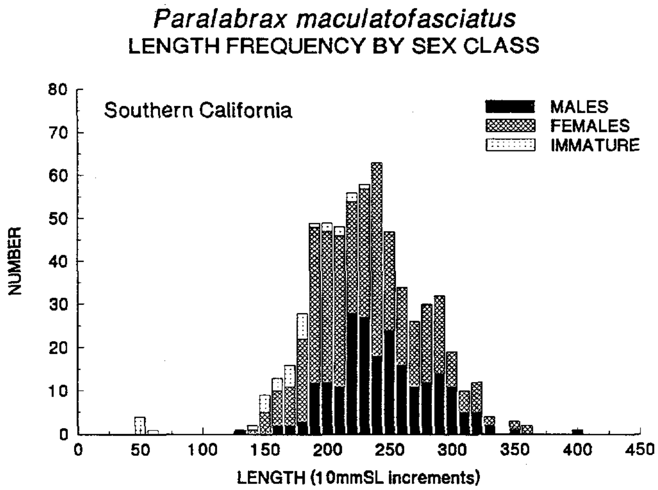

Figure 12. Length frequencies of all 639 spotted sand bass (*Paralabrax maculatofasciatus*) taken from southern California, classified by sex.

chins and jaws and prominent white spots below their dorsal fins are always males. Smaller fish with golden hues and yellow chins and jaws are usually females. However, some relatively large yellow fish turned out to be females, and small yellow fish were found to be males with extremely large testes. These observations suggest a complex mating system.

If southern California fish are functioning hermaphrodites practicing strict protogyny, all small fish should be either immature or females. As females grow, an ever greater number of them would change sex, making all large fish males. Length-frequency analysis by sex of a protogynous species should show a very large proportion of females in the smaller size classes, whereas males should dominate the larger size classes. However, both males and females were consistently represented throughout the size classes when all southern California fish were considered (figure 12). In fact, about half of the largest fishes in our samples turned out to be females. Immature fishes were represented into the 230 mm SL size class. Identifiable females appeared as far down as the 140 mm size class, and males as far down as the 130 mm class. A female bias in sex ratio was evident from 150 mm up through 240 mm. Thereafter, sex ratios appeared to be fairly equitable.

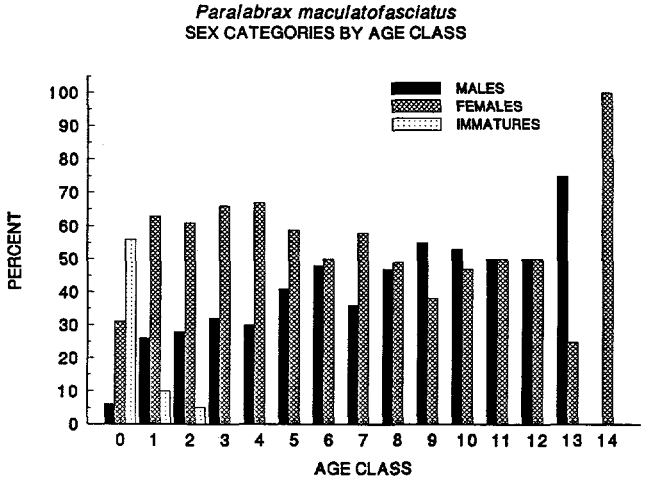

Figure 13. Percentage of 639 immature, female, and male spotted sand bass (*Paralabrax maculatofasciatus*) classified by age for all locations within southern California.

Sex composition by age class (figure 13) for all fish in the sample showed patterns similar to those for length. Females are well represented into the oldest age groups; the oldest fish aged (14 years) was female. Males were identified as early as age-0 (young-of-the-year, YOY) and were represented in all other age classes save the fourteenth. Thirty percent of the YOY fish were determined to be females; again, an early bias toward females is evident up to five or six years. Sex ratios appear to be about 50:50 throughout the older (7–10 year) age classes. Age classes 11, 12, and 14 were each represented by only one or two specimens. Immature fish were restricted to the first three year classes (0–2).

Preliminary examination of sex composition by age separately within Newport Bay and San Diego Bay indicated radically different patterns in the different populations. We believe that only two of the locations, Newport Bay and San Diego Bay, have been sampled sufficiently to warrant separate consideration at this time. A comparison between these two habitats is particularly instructive, since the Newport Bay fish were shown to be the fastest growing and the San Diego fish the slowest growing of all of the southern California populations considered.

In Newport Bay, female spotted sand bass are represented in all age classes present except 11 (figure 14).

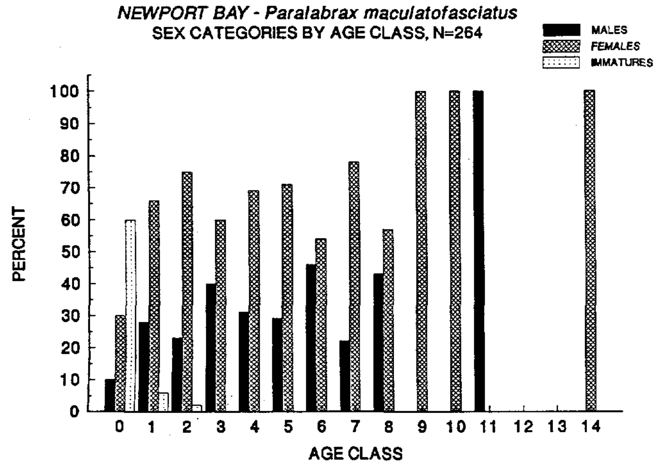

Figure 14. Percentage of 264 immature, female, and male spotted sand bass (*Paralabrax maculatofasciatus*) classifed by age, from Newport Bay only.

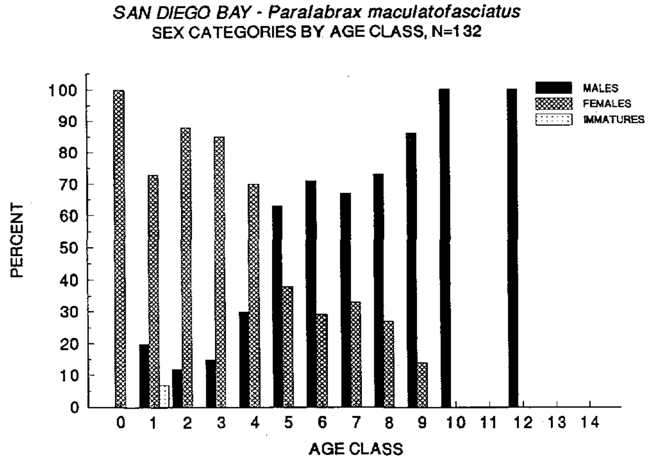

Figure 15. Percentage of 132 immature, female, and male spotted sand bass (*Paralabrax maculatofasciatus*) classified by age, from San Diego Bay only.

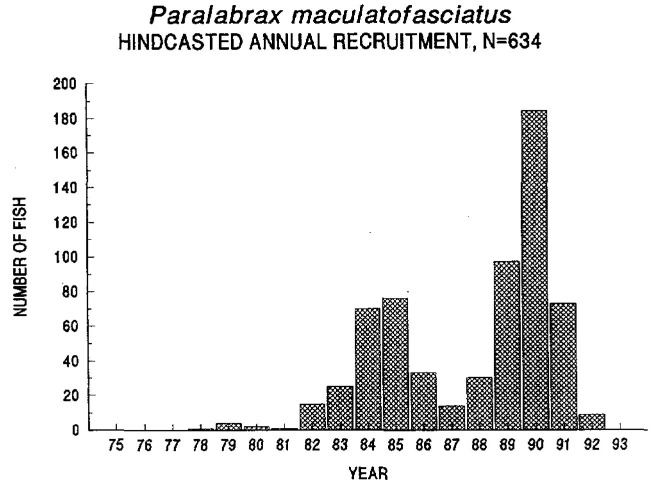

Figure 16. Annual recruitment of 634 spotted sand bass (*Paralabrax maculatofasciatus*) from southern California, 1975–93, as back-calculated from otolith age data not corrected for mortality.

Almost all of the 264 individual fish were eight years old or less. Males are represented in all age groups up to 8, but a pronounced bias toward females appears throughout the age structure. The overall sex composition of the Newport fish was 70% females versus 30% males.

On the other hand, the San Diego Bay population showed a strikingly different pattern of sexual composition over age classes (figure 15). In San Diego Bay, females dominate the younger age classes (0–4) and decline thereafter. In age classes 5 through 10, males dominate after constituting only a small proportion of the younger age groups.

Annual Recruitment Patterns

The 15-year pattern of annual recruitment for 634 fish, based on back-calculated year of birth (not corrected for mortality) was distinctly bimodal, with most of the fish coming from the very successful recruitment periods of 1984–85 and 1989–91 (figure 16). A small number of older fish (13–14 years) in the populations were recruited in 1979 and 1980. Notable depressions in recruitment appear to have occurred in 1981–82, 1987, and 1992–93.

Patterns of recruitment within five locations showed a similar pattern, with some notable exceptions (figure 17). The locations in figure 17 are shown in, roughly, north-to-south order, with Marina del Rey (MDR) being the northernmost site where fish were collected and San Diego Bay the southernmost. The recruitment peaks in 1984–85 and 1989–90 were evident in most locations, but recruitment seemed highly variable at this scale of resolution. Recruitment appeared to be highly successful in 1984–85 in Catalina Harbor (CAT), Anaheim Bay (ANB), and San Diego Bay (SDB), but not as evident in Marina del Rey and Newport Bay (NB). The 1989–90 recruitment appeared relatively strong at all locations except Catalina Harbor. Marina del Rey exhibited a relatively strong 1988 year class, while recruitment appeared to be very low in the other four locations. Finally, the San Diego Bay populations appeared to have experienced moderate recruitment in 1987, while all other populations did not, and San Diego Bay showed low recruitment in 1990 when Anaheim Bay, Newport Bay, and Marina del Rey had strong year classes.

For a closer examination of the variation in annual recruitment success and its relationship to sea temperature, we had to correct birth-year distributions for mortality, because fish recruited closer to the time of collection (young fish) have experienced lower mortality in their lifetime than older fish in the sample (figure 18). The pattern of annual recruitment corrected for mortality was distinctly trimodal. The years 1984 and 1985 were the best recruitment years for spotted sand bass since

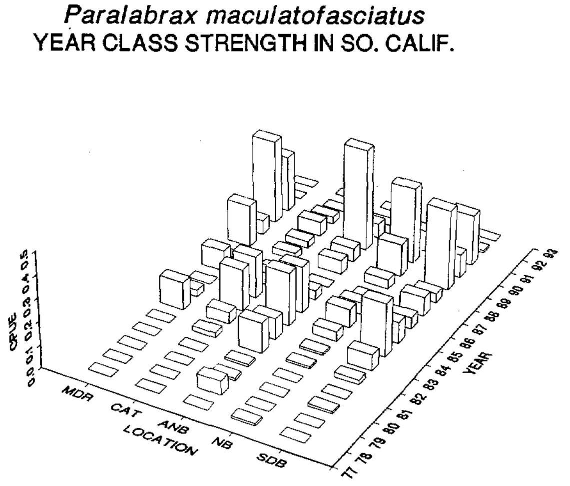

Figure 17. Estimated year-class strength (annual recruitment) for spotted sand bass (*Paralabrax maculatofasciatus*) from five locations in southern California, 1977–93. Catch-per-unit-effort was calculated by dividing the number of fish recruited (determined from back-calculating from otolith age data) by the number of angler hours spent at each location. Locations are ordered approximately north to south: *MDR* = Marina del Rey ($n = 36$); *CAT* = Catalina Harbor ($n = 41$); *ANB* = Anaheim Bay ($n = 97$); *NB* = Newport Bay ($n = 270$); and *SDB* = San Diego Bay ($n = 138$).

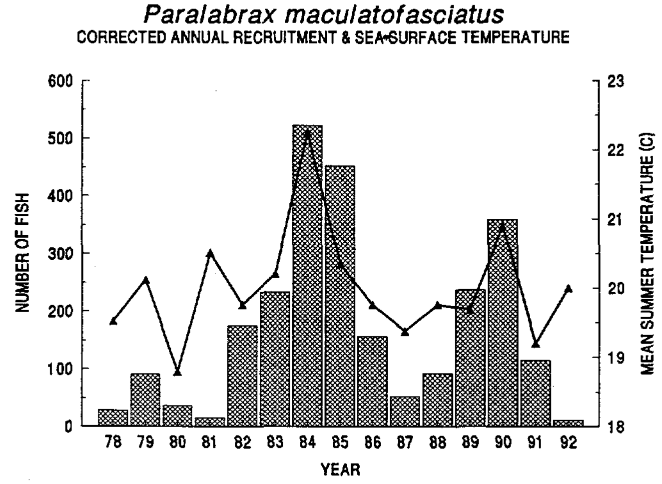

Figure 18. Annual recruitment (corrected for mortality) of 632 spotted sand bass (*Paralabrax maculatofasciatus*) from southern California compared to mean summer sea-surface temperature recorded at Scripps Pier, 1978–92.

1978, followed by 1989 and 1990. The third (smaller) peak, centered in 1979, is now more evident.

Mean summer sea-surface temperatures for the same 15-year period as measured at the Scripps Pier (figure 18) exhibit a similar pattern. In fact, corrected annual recruitment correlated significantly ($r = 0.723$; df = 13; $P < 0.002$) with mean summer sea-surface temperature.

DISCUSSION

Age and Growth

Spotted sand bass are fast-growing, short-lived fishes compared to their southern California close relatives, the kelp bass and barred sand bass. An average 1.5-year-old spotted sand bass (mean = 253 mm TL) was found to be about 1.6 times longer than the same-aged kelp bass (165 mm TL) or barred sand bass (166 mm TL; Love et al., in press). Maximum age for spotted sand bass (14 yr) in southern California is about 0.4 times that of kelp bass (33 yr) and 0.6 times that of barred sand bass (24 yr; Love et al., in press). The characteristics of fast growth and relatively short life span are usually associated with tropical fishes; in retrospect, it should not be surprising to have found these characteristics in what is basically a subtropical form living in a warm, temperate coastal zone.

The virtual absence of small (<150 mm SL) individuals in our samples was probably due more to very low recruitment of spotted sand bass in 1991 and 1992 than to sampling bias. The rapid growth in YOY and one-year-old fish plus the failed recruitment years largely explain the substantial gap in frequencies of small size classes that we observed. Spotted sand bass are aggressive carnivores which will bite lures at almost any size. We have caught hundreds of YOY and one-year-old fishes along both coasts of Baja California; if these small size classes had been available in southern California during our sampling, we would have collected them. Moreover, a beach seine study from 1989 to the present in San Diego Bay (Robert Hoffman, NMFS, unpublished data) yielded large numbers of YOY spotted sand bass in 1989–91 and none in 1992–93.

Although different growth rates in different populations of the same species are well documented in freshwater species (see Wooton 1990) and coral reef fishes (Jones 1986), this is the first example of this phenomenon in a coastal marine fish from California. The significant differences in growth rate discovered among the four principal populations of spotted sand bass may have a number of causes. Wooton (1990) listed a number of factors, both exogenous and endogenous, which have been shown to affect growth rates in fishes. These include (1) temperature; (2) food quantity, quality, and size spectrum; (3) dissolved oxygen; (4) salinity; (5) social interactions; and (6) genetics. Any one, or a number, of these factors may be operating to vary the growth rates of populations in the different locations. The different embayments vary dramatically in size, depth, temperature regimes, and—probably—population density. San Diego Bay is by far the largest and deepest of these habitats. Catalina Harbor is the smallest and the farthest offshore. The temperature regimes are probably cooler overall in these two embayments than in the moderately sized, shallow habitats of Anaheim Bay and Newport Bay. The slower growth rates of spotted sand bass in San Diego Bay and Catalina Harbor may be attributable to the reduced temperature regime alone. But many other variables such as food supply, population density, and pollution levels must also be considered.

Food Habits

The southern California members of the genus *Paralabrax* have all been characterized as important predators in nearshore coastal waters. Kelp bass are active predators around kelp beds and rocky reef habitats, and feed on a variety of motile organisms including fishes, squids, octopi, and benthic crustaceans (Love et al., in press). A large portion of their prey is taken from the water column. Barred sand bass are more benthic in orientation than kelp bass and feed on an array of fishes, crabs, shrimps, octopi, and other substrate-oriented invertebrates.

Ono (1992) listed small fishes, cephalopods, and crustaceans as the major prey items of spotted sand bass. This characterization of diet seems to be in error. Our study represents the most comprehensive sample ever taken of spotted sand bass from their normal habitats. The results clearly show that crabs and clams, particularly jackknife clams (*Tagelus* sp.), dominate the diet of spotted sand bass from southern California waters. How spotted sand bass actually capture jackknife clams remains a mystery, since most of the time these clams are buried 15–18 cm deep in the mud. Fishes form a relatively small component of the spotted sand bass diet, especially when compared to the two other species of *Paralabrax* in southern California.

Reproductive Strategies

Strict protogynous hermaphroditism is apparently not a general characteristic of all populations of spotted sand bass. Data from our extensive collections in the northern Gulf of California have, so far, supported Hastings's findings (1989). We have been able to age northern gulf fish, which Hastings was not able to do with his preserved specimens. Sexual composition over age groups in our fish from the northern Gulf of California are completely consistent with a protogynous strategy. Virtually all of the very young fish were females, and nearly all of the large, old fish have been males. These data, coupled with the detailed histological examination of gonads presented by Hastings (1989), make it highly probable that the northern Gulf of California fish are protogynous. Our San Diego Bay population exhibited an almost identical age-sex pattern to the fish in the northern Gulf of California.

As a group, the populations from all locations in southern California other than San Diego Bay exhibit a pattern of female bias in sex ratios in young age groups which gradually disappears over time. There appears to be a relatively high proportion of primary males in these populations, and large, old females are quite common. When we examined the populations separately, it was evident that spotted sand bass in Newport Bay maintained female bias throughout all age classes.

Conclusions on the actual reproductive strategies of these populations will have to await completion of our ongoing histological analysis.

Annual Recruitment Patterns

Variation in recruitment to individual embayments was expected, since recruitment success in fishes has been shown to be a highly variable process, particularly in broadcast spawners with pelagic larvae (cf. Doherty 1991). Because spotted sand bass have pelagic larvae, variable recruitment into their restricted habitats is to be expected. The sporadic recruitment to Catalina Harbor during the last 15 years is probably the best example of how habitat isolation influences recruitment. Almost all of the spotted sand bass collected from this offshore habitat were found to be 7- and 8-year-olds from the strong 1984–85 recruitment period. The interpretation of back-calculated recruitment data from individual locations in southern California is, however, complicated by variable fishing pressure. Fishing mortality may be a particular problem in Newport and San Diego Bays, which are heavily fished by recreational anglers. Therefore the data on annual recruitment presented here must be viewed and interpreted with caution.

The overall, bimodal pattern of recruitment was at first puzzling because it seemed to be almost anti-El Niño in nature, showing relatively small year classes in 1982–83, 1987–88, and 1992–93. This possibility seemed counterintuitive because one would predict a subtropical species to recruit well to southern California coastal waters during El Niño years. But in southern California, summer sea-surface temperatures (as measured at the Scripps Pier) actually peak one or even two years after a recognized El Niño event. These lagged peaks coincide closely with peaks in spotted sand bass recruitment (corrected for mortality) within the Southern California Bight as a whole. The highly significant correlation discovered between corrected recruitment and mean summer sea-surface temperature at Scripps Pier leads us to conclude that spotted sand bass recruit best during summers when the nearshore ocean temperatures off southern California are warmest.

ACKNOWLEDGMENTS

A study of this magnitude could not have been accomplished without the support of many people. We thank those who ably assisted in the demanding field work, especially Cheryl Baca, Andy Barbarena, Michael Franklin, Tom Grothues, Jo Korting, Loretta Roberson, Bob Scott, Greg Tranah, and Carrie Wolfe. The crew of the R/V *Yellowfin*—Jim Cvitanovich, Paul Irving, and Danny Warren—assisted greatly through their capable handling of vessels, sampling nets, and rods and reels. Andy Brooks (University of California, Santa Barbara) performed the age- and size-at-first-maturity analysis. The authors also wish to thank the following organizations for their donations of equipment to aid this research effort: Shimano American Corp., Eagle Claw, AA Worms, and Izorline International. Special thanks must go to Big Mike Gardner, our professional fishing guide, for his dedication to this project. Without Mike's skill and expertise, far, far fewer spotties would have been available for study. Angler Pat Gorman donated his record fish for study. Mary Yoklavich generously shared her insights on how to correct for mortality when back-calculating annual recruitment. We also gratefully acknowledge the assistance provided by Chuck Valle and Dave Parker of the California Department of Fish and Game in procuring funds, reviewing the manuscript, and scaling many administrative obstacles. This research was funded through contracts with the Bay, Estuarine, and Nearshore Ecosystem Studies (BENES) program of the California Department of Fish and Game which, in turn, is supported by the Federal Aid to Sport Fish Restoration Program (Wallop-Breaux).

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A TAGGING STUDY OF THE CALIFORNIA HALIBUT (*PARALICHTHYS CALIFORNICUS*)

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ABSTRACT

During a study that spanned forty years, the California Department of Fish and Game tagged 16,827 California halibut (*Paralichthys californicus*). A total of 858 tags were returned, for a return rate of 5.1 percent. Statistical analyses of the data indicated that this species remained in a localized area throughout its adult life. The mean distance traveled by California halibut during this study was 13.4 km. California halibut larger than 500 mm total length (TL) tended to travel markedly greater distances than halibut smaller than 500 mm TL.

INTRODUCTION

The California halibut (*Paralichthys californicus*) is important to both the recreational and commercial fishing industries of southern and central California. The California halibut ranges from Magdalena Bay, Baja California (Gilbert and Scofield 1898), to the Quillayute River in Washington (Pattie and Baker 1969), but is most common from Morro Bay south (Fitch and Lavenberg 1971). The movement of California halibut is of particular interest to fishery biologists, since this species occurs across a political border (Mexico/USA) and a biological border (Oregonian/San Diegan biogeographic provinces).

Researchers from the California Department of Fish and Game have been tagging California halibut since the 1950s. Young (1961) briefly summarized some of the early results of the tagging program, but the analysis was not rigorous. The subsequent accumulation of additional tag return data, and the recent publication of numerous papers on California halibut (see Haugen 1990), warranted a reexamination of the data.

MATERIALS AND METHODS

The California Department of Fish and Game tagged California halibut from 1955 through 1960, in 1965, and from 1989 through 1994. Tagging operations were conducted from Bahía Sebastián Viscaíno, Baja California, to Tomales Bay, California. Most halibut were tagged between Oceanside and Santa Barbara, California. Most halibut were captured with trawl gear, but many were also captured with gill nets and hook and line. The tagging method changed as the program evolved. A small percentage of the halibut were tagged with Peterson discs and silver pins; after these tags were found unacceptable, the fish were tagged with spaghetti tags. In recent years Floy T-bar anchor tags have been used.

Upon capture, each halibut was tagged below the dorsal fin just behind the head. Each fish was measured to the nearest mm total length and released at the site of capture. Tag returns came from the continued trawling efforts of the tagging program, commercial trawlers, commercial gill netters, and sport anglers. Size and location data were recorded for each recapture. Because California halibut are not sexually dimorphic, the sex of individual fish was recorded only when provided upon recapture.

Migration distances were plotted and recorded in nautical miles, the standard unit of measure on nautical charts, and later converted to kilometers (km). The direction of migration was also recorded. Migration distance was analyzed for relationships with the following: TL, sex, time at liberty, and direction of migration. Migration rate, defined as migration distance divided by time at liberty, was also analyzed with respect to the above variables, with the exception of time at liberty. Direction of migration was also examined with respect to TL. The variables of interest were tested for normality (Shapiro-Wilk W test), and nonparametric methods were used where appropriate.

The chi-square test of independence was used to determine if there were relationships between total length and migration distance/rate, time at liberty and migration distance, direction of migration and total length, direction of migration and migration distance/rate, and sex and migration distance/rate. Spearman rank correlation coefficients were also used to test for a relationship between time at liberty and migration distance/rate, and total length and migration distance/rate. All statistical analyses were performed with the Statistical Analysis System (SAS 1988).

The TL value used for all of the above tests was the length at time of tagging. This length was used rather than recovery lengths because of the unreliability of reported lengths from anglers and commercial fishers, the relative lack of data on recovery lengths, and preliminary results that showed no difference between length at tagging and length at recovery.

[Manuscript received January 23, 1995.]

RESULTS

During this study 16,827 halibut were tagged. The tagged fish ranged from 280 to 1005 mm TL (table 1), but the majority were less than 500 mm (figure 1). A total of 858 tags were recovered, resulting in a return rate of 5.1 percent. Of these returns, 839 included location of recovery; only 332 (39.6%) of these returns indicated that the fish had moved at least two km. Length of fish was indicated in 410 returns, and sex of the specimen in 87 returns.

Days at liberty for individual fish ranged from 1 to 1921, with a mean of 128 (table 1), but the majority were at liberty for fewer than 100 days (figure 2). Migration distances ranged from 0 to 365 km, with a mean of 13.4 km (table 1). Although some halibut rapidly migrated long distances, most returns showed no movement at all (figure 2). Time at liberty and migration distance were used to calculate a mean migration rate of 0.21 km/day (table 1).

From the data grouped by intervals of total length, average migration distance for every length group was 38 km or less (table 2). Halibut larger than 500 mm behaved differently from smaller halibut. The larger fish migrated farther and faster ($P < 0.001$ for both; tables 2–4). From the data grouped by time at liberty (table 5), halibut migrated farther when they were at liberty longer ($P < 0.001$, table 4). Spearman rank correlation coefficients also showed that these three trends were statistically significant: total length vs. migration distance ($r_s = 0.24$, $P < 0.001$); total length vs. migration rate ($r_s = 0.22$, $P < 0.001$); and time at liberty vs. migration distance ($r_s = 0.23$, $P < 0.001$).

However, sex vs. migration distance, and sex vs. migration rate were statistically not significant ($P = 0.20$

TABLE 1
Descriptive Statistics of 839 Tagged Halibut

	Mean value	Minimum value	Maximum value	Standard deviation
Migration distance (km)	13.4	0	364.8	39.8
Days at liberty	127.5	1	1921	198.3
Size (mm) when tagged	473.0	280	1005	108.8
Migration rate (km/day)	0.21	0	16.7	0.9

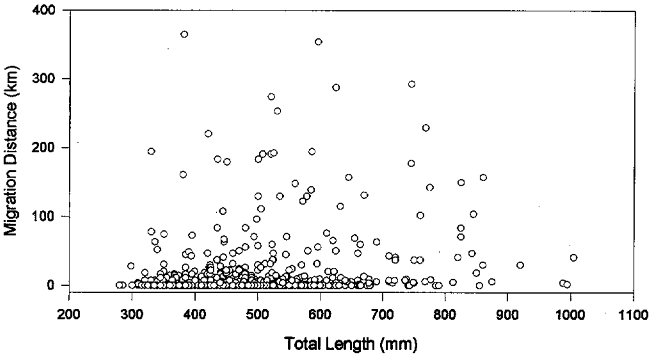

Figure 1. Migration distance (km) for 839 tagged halibut, versus total length (mm).

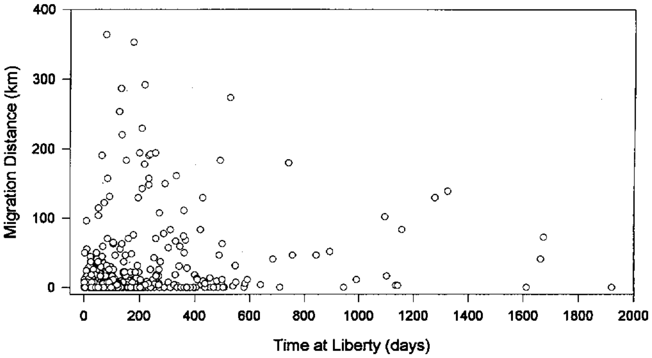

Figure 2. Migration distance (km) for 839 tagged halibut, versus days at liberty.

TABLE 2
Average Migration Distance (km) of Halibut, by Total Length (TL)

TL (mm)	*N*	Minimum	Maximum	Mean	SD
201–350	80	0	194	8.1	26.1
351–400	125	0	365	8.0	36.6
401–450	205	0	220	8.0	26.5
451–500	184	0	183	7.3	21.2
501–550	104	0	274	19.1	50.4
551–600	55	0	353	25.0	62.4
601–1200	86	0	292	37.8	62.3

TABLE 3
Average Migration Rate (km/day) of Halibut, by Total Length (TL)

TL (mm)	*N*	Minimum	Maximum	Mean	SD
201–350	80	0	7.41	0.15	0.84
351–400	125	0	4.62	0.12	0.49
401–450	205	0	1.85	0.14	0.36
451–500	184	0	10.7	0.12	0.80
501–550	104	0	2.93	0.22	0.48
551–600	55	0	16.67	0.59	2.36
601–1200	86	0	5.56	0.48	0.85

TABLE 4
Chi-Square Test Results

Relationships	*P*-value	*N*
Total length vs. migration distance	<0.001	839
Total length vs. migration rate	<0.001	839
Time at liberty vs. migration distance	<0.001	839
Direction of migration vs. total length	0.30	313
Direction of migration vs. migration distance	0.01	313
Direction of migration vs. migration rate	0.05	313
Sex vs. migration distance	0.20	87
Sex vs. migration rate	0.20	87

TABLE 5
Average Migration Distance (km) of Halibut, by Days at Liberty

Days at liberty	*N*	Minimum	Maximum	Mean	SD
1–50	357	0	96	3.9	9.7
51–100	184	0	365	10.9	37.2
101–150	94	0	287	14.9	46.3
151–200	65	0	354	19.4	56.7
201–400	88	0	293	37.4	63.3
401–600	31	0	274	29.6	61.5
601–2000	20	0	180	48.4	53.7

for both, table 4). Males and females did not exhibit different migratory patterns. The direction of migration vs. total length was statistically not significant ($P = 0.30$, table 4). Thus, size did not influence the direction of movement.

Because of the predominately north-to-south orientation of the California coast, all but three migrations were classified as north or south. Two of the three exceptions were east-west movements within large bays; the third was movement from the mainland coast to Catalina Island. Six fish moved from south of Point Conception to areas north of the point. No fish were reported moving from north to south of the point. The mean distance of northern migration was 47.1 km ($n = 157$); the mean distance of southern migration was 22.7 km ($n = 156$).

The difference between the number of halibut moving north and the number moving south, 157 vs. 156, was obviously not significant. The difference in migration distance with respect to direction (north vs. south) was statistically significant ($P = 0.01$, table 4). Of the fish moving north, 31 percent traveled more than 0.5 km/day; 19 percent of the fish moving south traveled more than 0.5 km/day. The difference in migration rate with respect to direction was statistically significant ($P = 0.05$, table 4). Thus halibut moving north tended to travel greater distances and at a faster rate.

DISCUSSION

Although some California halibut made distant, rapid migrations, clearly this behavior was unusual. The halibut tagged during this study tended to remain in a local area. This localized behavior may have important implications for the effective management of the species.

Young (1961) stated that "small halibut tend to move south (and) large fish north." This did not hold true during our analysis, and Young did not indicate how he reached his conclusion. However, we observed that halibut that moved northward moved significantly greater distances at a greater rate. There are no clear explanations for this phenomenon, which may be a result of biased reporting of tag recaptures. Most of our tagging effort was in southern California, and tagged fish that migrated large distances to the south may have ended up in Mexican waters. It is reasonable to assume that tagged halibut caught in Mexico have a much lower probability of being reported than tagged halibut caught in the United States, thereby biasing our results.

It is interesting to note that very few halibut tagged south of Point Conception were recovered north of Point Conception, and no fish migrated from north to south of the point. The relatively small number of halibut tagged north of Point Conception may explain the lack of recorded migrations from north to south, but a large number of halibut were tagged south of Point Conception (Ventura Flats). We do not feel confident in labeling Point Conception as a geographic barrier to halibut migration, but we believe the issue may warrant more research.

The short mean time at liberty may be due to a high incidence of tag shedding. California halibut do not have the dorsal spines or associated interneural bones that normally anchor T-bar tags. High rates of fishing mortality and natural mortality could also contribute to short times at liberty.

We speculate that the dramatic increase in average migration distance and rate for large halibut results from an important event in the life history of this species. Such events may be reproduction or shift in preferred prey. This topic needs further research. The large halibut, however, were estimated to represent a small percentage of the population (Domeier, data from biomass estimate).

California halibut use shallow-water embayments as nursery areas (Haaker 1975; Allen 1988; Kramer 1990); more detailed studies of migration from these nursery areas are needed. Migration of halibut from nursery areas to adult habitats may be the most significant migration of their life history, aside from larval dispersal. If juvenile migration is limited, an area that historically produces large numbers of halibut could become unproductive if the local nursery areas are destroyed.

Given the limited movement of adult halibut, future research should focus on recruitment pathways. It is not known whether local populations are self-recruiting or if larval dispersal occurs over a much larger area. If local populations are largely self-recruiting, then management becomes a localized problem, and different management practices may be justified in different areas. Electrophoretic work by Hedgecock and Bartley (1988) suggests the possibility of genetically distinct populations of California halibut even within the Southern California Bight. Further studies at the molecular level may provide valuable insight into the population structure and amount of gene flow between regions within this species' range.

ACKNOWLEDGMENTS

Many California Department of Fish and Game biologists worked on this project in the past four decades. Noteworthy contributions were made by J. Schott, R. Ally, and M. Vojkovich. The sport and commercial fishing industries of southern California were instrumental in supporting this program by returning tags that they recovered.

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The CalCOFI Editorial Board will consider for publication, in the section entitled Scientific Contributions, manuscripts not previously published elsewhere that bear some relationship to the following with respect to the Californias, the California Current, and the Gulf of California: marine organisms; marine chemistry, fertility, and food chains; marine fishery modeling, prediction, policy, and management; marine climatology, paleoclimatology, ecology, and paleoecology; marine pollution; physical, chemical, and biological oceanography; new marine instrumentation and methods.

Manuscript should be typed in a standard typewriter face (12-pt. Courier, and no dot-matrix printouts, please) **double-spaced** with wide, **ragged right margins**, and submitted complete with figures, figure captions, and tables, in triplicate to

CalCOFI Coordinator
University of California, San Diego
Marine Life Research Group
Scripps Institution of Oceanography
9500 Gilman Drive
La Jolla, CA 92093-0227

Manuscripts must be received by February 1 of the year in which publication is desired.

Sequence of the material should be TITLE PAGE, ABSTRACT, TEXT, LITERATURE CITED, APPENDIX (if any), FOOTNOTES (if any), TABLES, LIST OF FIGURES with entire captions, and FIGURES.

Title page should give:

a running head of no more than 60 letters and spaces
title of the article
author(s) name(s) and affiliation(s)
address(es), including zip code(s)

Abstract should not exceed one **double-spaced** page.

Text style will in general follow that of the U.S. Department of Commerce (NOAA) *Fishery Bulletin*. Contributors who are not familiar with this publication will do well to follow *The Chicago Manual of Style* (1993). Authors are strongly urged to compare their typewritten equations with similar expressions in the printed literature, with special attention to ambiguity of the symbols for "one" and for "el," before submitting. Whenever possible, write in the first person, and use active verbs.

Measurements must be given in metric units; other equivalent units may be given in parentheses.

Personal communications and *unpublished data* should not be included in the Literature Cited but may be cited in the text in parentheses. Use *footnotes* only when parentheses will not suffice. List footnotes on a separate sheet.

Literature cited should appear in the text as Smith (1972) or Smith and Jones (1972) or (Smith and Jones 1972; Jones and Smith 1973) or Smith et al. (1972); there should be no comma between author and date. All literature referred to in the text should be listed (**double-spaced**) alphabetically by the first author on a separate sheet under the heading Literature Cited. Only the authors' surnames and initials will be used. No reference should appear in the Literature Cited unless it is cited in the text, tables, or figure captions. Each citation must be complete according to the following:

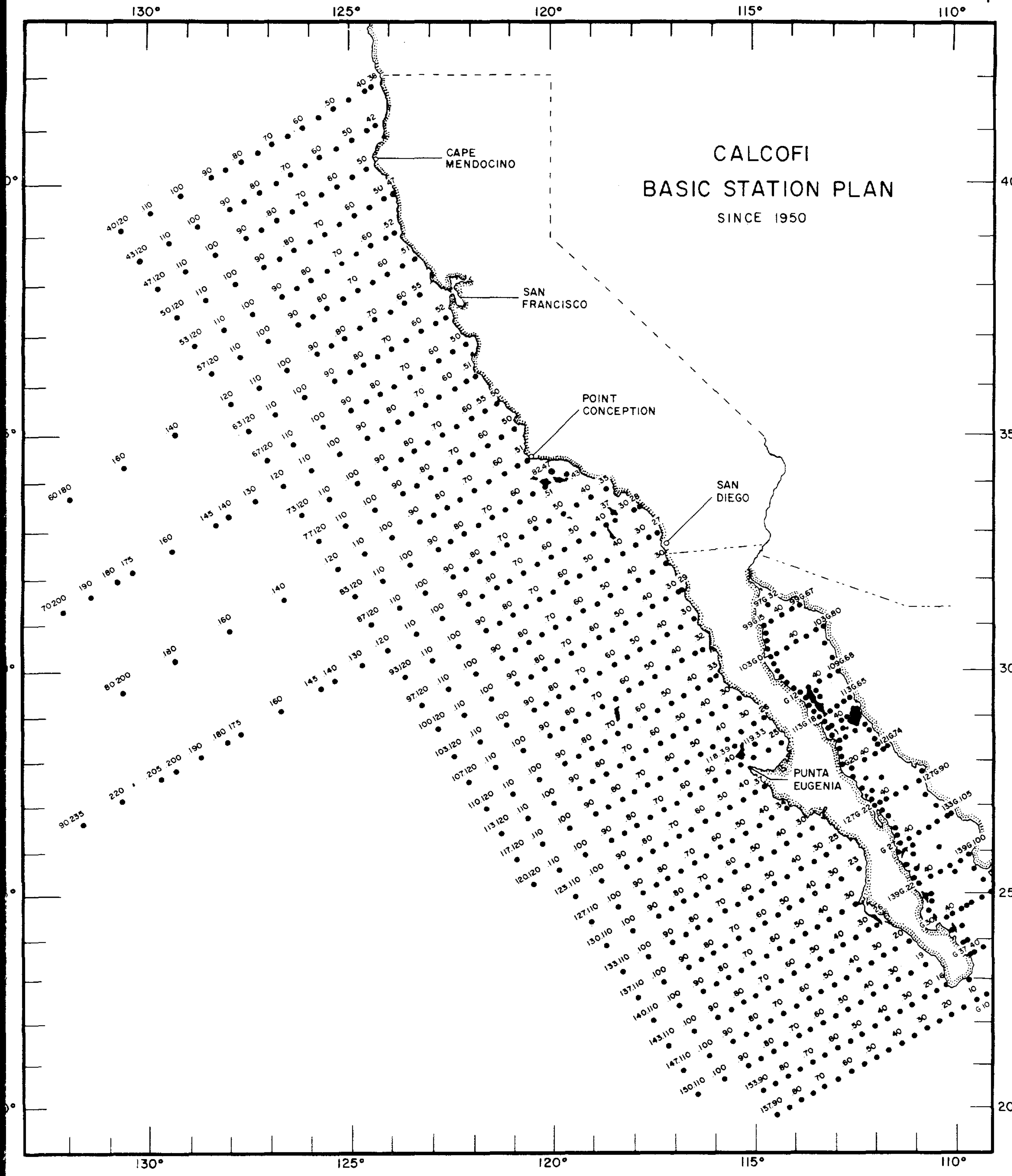
(article):
Barnes, J. T., L. D. Jacobson, A. D. MacCall, and P. Wolf. 1992. Recent population trends and abundance estimates for the Pacific sardine (*Sardinops sagax*). Calif. Coop. Oceanic Fish. Invest. Rep. 33:60–75.
(book):
Odum, E. P. 1959. Fundamentals of ecology. 2d ed. Philadelphia: Saunders, 546 pp.
(chapter):
Wooster, W. S., and J. L. Reid Jr. 1963. Eastern boundary currents. *In* The sea, M. N. Hill, ed. New York: Interscience Pub., pp. 253–280.

Tables (with arabic numbers) should be typed (**double-spaced**) separately from the text; each table should start on a separate page and must have a brief title. Explanatory material belongs in a note beneath the table, not in the title. Please avoid vertical rules and be consistent in format.

Figures, whether drawings or halftones, should be submitted in a format **not larger than 8½ × 11"**. Submit one set of camera-ready figures plus 2 sets of copies. Photographs should be printed on glossy paper. Drawings should be reduced photographically. A composite figure should be submitted as a single photostat or at least as a single careful paste-up. Figures will appear as either single-column (85-mm-width limit), or double-column (178-mm-width limit); or as full page. Special cases should be discussed with the editor before submittal. After reduction, no letter or number should be smaller than 1 mm. Special note should be taken of the disappearance of decimal points during reduction. If shading is used, make a trial reduction to ensure that the patterns do not merge at the required reductions. The determining factor for size should be the complexity of detail to be shown.

Each figure must have a *caption*; captions should be typed, **double-spaced,** in numbered sequence on a separate sheet. Illustrative materials submitted for publication are often first prepared for oral presentation in slide format. Authors should take special care that slide-format material submitted to *CalCOFI Reports* is appropriate to printed format with respect to economy, redundancy, and style.

Acknowledgments, if included, should be placed at the end of the text and may include funding source.



CALCOFI BASIC STATION PLAN

SINCE 1950

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Indexed in *Current Contents.* Abstracted in *Aquatic Sciences and Fisheries Abstracts* and *Oceanic Abstracts.*