CALIFORNIA
COOPERATIVE
OCEANIC
FISHERIES
INVESTIGATIONS

Reports

VOLUME 45
January 1 to December 31, 2003

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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Printed and distributed August 2005, La Jolla, California
ISSN 0575-3317

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

PACOOS

Development of the Pacific Coast Ocean Observing System (PaCOOS), formerly called PaCOS, continues. The PaCOOS mission is to provide ocean information for the sustained use of the California Current large marine ecosystem under a changing climate. A science planning meeting was held in September 2003, followed in May 2004 by a Board of Governors meeting, during which a draft PaCOOS general science plan (initiated at the September meeting) was reviewed and the framework for a PaCOOS charter and memorandum of understanding was developed. The Board of Governors consists of one representative from each of twelve organizations, including two NOAA Fishery Centers, NOAA National Marine Sanctuary program, the three state conservation agencies, four universities, and two foundations. When implemented, CalCOFI shall become the southern component of a coastwide PaCOOS sentinel-species observing system. The geographic observational requirement of PaCOOS is the U.S. EEZ off the coasts of California, Oregon, and Washington, with links to comparable ecosystem observations of the California Current in México and Canada.

Data integration planning has also begun with initial funding from the National Marine Fisheries Service. Development of a Web-based searchable database that integrates physical and biological data is progressing. The software infrastructure to read both data sets is being developed for the region currently surveyed by CalCOFI. This will be expanded to incorporate data from partners along the coast such as from stations now occupied to the north by Monterey Bay Aquarium Research Institute (MBARI). We foresee the Web site's role broadening from a CalCOFI-specific information source to a portal for querying coastal relational databases and promoting ecosystem research. The Web address is http://calcofi-las.ucsd.edu

CALCOFI

Cruises

The CalCOFI program completed its fifty-fourth year, with four quarterly cruises during which were the usual seabird casts and plankton tows using the Bongo (oblique plankton tow fitted with an Optical Particle Counter), Manta (nueston), and Pairovet (vertical) nets. Measures of primary productivity, weather, sea birds, and marine mammals were also quantified. In spring 2003, the RV *Roger Revelle* completed its cruise of the 67 standard CalCOFI stations, and the RV *David Starr Jordan* completed an additional 42 stations, "boxing" the CalCOFI pattern in the south and then transitting north to San Francisco; this cruise included a one-day coastal survey off Imperial Beach with John Largier. In addition to the CalCOFI cruise station surveys, work continues on a number of ancillary research projects involving phytoplankton, HPLC, zooplankton, trace metals, seabirds, and marine mammals, as well as studies using the optical plankton counter, Continuous Underway Fish Egg Sampler, Acoustic Doppler Current Profiler, EK-500 scientific sounder, and bio-optics.

CalCOFI Web Site Overhaul

As the CalCOFI program synchronizes with other coastal observation programs, the interest in the CalCOFI Web site (www.calcofi.org) continues to grow rapidly. In the last 6 months, visitors from over 40 countries have accessed the site. Originally designed for general cruise information and as a hydrographic data archive, the Web site is expanding, offering new data products and oceanographic sampling and analysis information.

The 54-year data set is in a period of transition as vigorous efforts are being made to convert the data tables into a Web-based queriable relational database. Currently, the relational hydrographic database is available globally to users as a downloadable file, and a Web-based query interface is being developed.

This conversion of the tabulated data to relational database is the first step in facilitating the interlinking of related databases on the Internet. Our Live Access Server (LAS) project currently under development will dynamically link CalCOFI hydrographic data to biological databases and ancillary data products. Using a single Web-based query form, researchers will be able to extract and download interrelated data types from any of the linked databases.

Central California CalCOFI surveys

A collaboration between MBARI, the Naval Postgraduate School (NPS), the University of California, Santa Cruz (UCSC), and NOAA/NMFS has led to continued quarterly occupations of historical CalCOFI lines off central California. Line 67 was occupied quarterly from 1988 to 1991 and has been since 1997 in response to the 1997–98 El Niño. On the basis of discussions started with ACCEO and more recently with PaCOOS, it was decided to continue this important series. Continuous-mooring time series in the inner portion of line 67 (see http://www.mbari.org/oasis/) and more frequent ship surveys (once every three weeks or monthly; see http://www.mbari.org/bog/projects/centralcal/summary/tssummary.htm, and http://cimt.ucsc.edu/research.html), as well as AUV surveys, complement the larger scale but less frequent line 67 cruises.

During winter and spring, regular southern California CalCOFI surveys are extended into central California. Researchers from MBARI, NPS, and UCSC join the cruises for the lines north of line 77 and collect and analyze samples for chlorophyll and nutrients. Conductivity, temperature, and depth casts are extended to 1,000 m along line 67, and time-permitting station spacing is reduced to 10 nmi in the inshore portion of this line. In the summer and fall, dedicated 4–6-day cruises are carried out by MBARI, NPS, and UCSC scientists. To date these cruises have primarily occupied line 67, but in the future they are expected to occupy line 60 (off San Francisco) as well. These cruises include the typical CalCOFI measurements as well as other ancillary measurements (see http://www.mbari.org/bog/Projects/secret/default.htm for details). Measurements of the partial pressure of carbon dioxide in the atmosphere and the sea surface have recently been added to the regular and central California CalCOFI surveys. Funds from the Monterey Bay National Marine Sanctuary, Sanctuary Integrated Monitoring Network (SIMoN) have allowed the hiring of a postdoctoral researcher at MBARI. One of the tasks of this researcher will be to integrate the results of the central California surveys with those in southern California.

IMECOCAL

For highlights of the work in Baja California, Mexico, please visit IMECOCAL's Web site: http://imecocal.cicese.mx/.

SIO HIGHLIGHTS

PaCOOS's potential and three new research programs have brightened the outlook for CalCOFI at SIO this year in the aftermath of severe budget cuts two years ago. In a cooperative agreement that included continued interim support from NOAA (to replace operating funds lost in university budget cuts) SIO has agreed to begin coordinating and developing areas essential to the future of the PaCOOS program. These fall into two main categories: augmented development of an integrated data management system (presently being initiated by SWFSC and SIO personnel under the guidance of Dr. Christian Reiss at SWFSC); and initiation of technical training and cross-calibration of procedures, making use of the availability of RV *Roger Revelle* for the fall CalCOFI cruise. In a step toward achieving this goal, we are now posting our procedures on the SIO/CalCOFI Web site: www.calcofi.org/newhome/cruises/sample_analysis.htm.

SIO director Charles Kennel has offered office space and administrative infrastructure for the PaCOOS executive officer. This would facilitate interaction between PaCOOS and other large programs based at SIO (such as the Southern California Coastal Ocean Observing System, SCCOOS, and the Center for Biodiversity and Conservation) and allow access to a well-developed public-outreach program.

Three long-term research programs have received funding to use routine CalCOFI cruises as research platforms and provide new dimensions to our observations. SCCOOS will support an additional transect on each CalCOFI cruise. This will take place on the return leg; stations along this transect will be inshore of our shoreward routine stations and will consist of continuous measurements and CTD casts. In addition, SCCOOS will provide funds for the development of bio-optical approaches to measuring primary productivity.

Professor John Hildebrand has received funding from CNO-N45 and ONR to make quantitative visual and acoustic surveys of marine mammals on CalCOFI cruises 2004-2007. These surveys will supplement data he will collect through the deployment of long-term acoustic monitoring devices moored at six stations within the CalCOFI survey area.

Professor Mark Ohman, aided by several SIO scientists, has obtained funding from the Long-Term Ecological Research (LTER) Program of the National Science Foundation. These funds will allow the CalCOFI measurements to be routinely supplemented with measurements of iron concentration and particulate and dissolved organic material, as well as samples of the smaller size classes of plankton. (Many of these techniques have already been tried out on CalCOFI cruises.) LTER funds also provide for "special purpose" cruises to investigate hypotheses generated by the CalCOFI data. There will be a biophysical modeling component, a data management component, and an outreach program. The LTER funding begins in September 2004. It is awarded in 6-year increments, with the possibility of *n* renewals. In Ohman's words, "Here's hoping for a very large *n*."

CDFG HIGHLIGHTS

The Marine Protected Areas (MPAs) mandate focused primarily on implementing the Marine Life Protection Act (MLPA) and MPAs established in the Channel Islands National Marine Sanctuary in 2003. Though the MLPA working group process was informally halted for the calendar year, staff developed various scenarios for continuing implementation and reviewed the status of existing MPAs. The Channel Islands MPA network was implemented in April 2003, and staff focused efforts on developing a monitoring strategy and participating in ongoing monitoring efforts. Progress was made toward a long-term monitoring plan for the MPAs, and preliminary data from inside and outside these MPAs were collected.

CDFG has been collaborating with partner groups to assess fish and invertebrate populations in both shallow (< 20m) and deeper water rocky reef habitats in California. The team uses divers in shallow habitats and remotely operated vehicles (ROVs) in deeper water. Methodology studies have been the focus this year; the team is developing cost-effective methods for measuring the survey area using ROVs as well as determining the area and number of samples needed to measure changes in fish populations. Preliminary sampling focusing on the Channel Islands MPA has been conducted with The Nature Conservancy, the Channel Islands National Marine Sanctuary, and Marine Applied Research and Exploration.

The Squid Fishery Management Plan is being revised to include additional management options at the request of the Fish and Game Commission. Adoption is proposed for late 2004. The Pacific Fishery Management Council revised the reallocation of unharvested sardine in 2003. The new framework includes geographic boundary changes, the reallocation date in the year, the percentage of unharvested sardine to be reallocated, and coastwide allocation after 1 December.

In 2003, the Commission modified sea urchin fishery regulations, eliminating minimum landing requirements, adopting equal work days in northern and southern California, creating a preference system for experienced fishers in the permitting process, and allowing data collection on commercial vessels. Funding continued for studies of sea urchin recruitment. This was the second year of the experimental tanner crab fishery, which landed more than 90 metric tons. The fishery is male only, with a minimum legal size of 5 in. (carapace width), and occurs on the north coast in deep water (> 300 fathoms).

There was a northerly offshore shift in the salmon population in 2003 that contributed to a full season for the commercial fishery in Fort Bragg. The California recreational fishery survey program assumed the lead for sampling recreational ocean salmon. Samplers recorded numbers of fish and catch per angler information and collected adipose clip salmon heads for coded wire tag recovery. Coho salmon continue to be seen off California, but their origin is unknown (Oregon or California).

The Aquatic Nuisance Species component tracked emerging aquatic nuisance species statewide and began to develop a plan for minimizing the spread of the invasive brown seaweed, *Undaria pinnitifida*. Work that will involve research, surveillance, and outreach began under a $2.2 million grant from the State Water Resources Control Board for *Caulerpa* eradication.

The Shellfish Disease component continued to monitor the geographic distribution of the causative agent of withering syndrome and initiated an intertidal gastropod sampling effort to determine whether the South African sabellid polychaete has become established at any location statewide. Research continued on the development of an oral oxytetracycline-based treatment regimen for withering syndrome in cultured abalone, and on susceptibility of the federally endangered white abalone to the disease. The Fish Disease component continued certification of white sea bass for release from the hatchery to netpens and from netpens to the environment; it also conducted research on diseases at all life stages.

NOAA HIGHLIGHTS

The newest member of the CalCOFI Committee is Dr. Roger Hewitt, who recently assumed John Hunter's role as Director of the Fisheries Resources Division at the Southwest Fisheries Science Center and as the NMFS representative on the Committee. Roger came to the Center in the early 1970s and worked with Paul Smith and Ruben Lasker on interpretation of ichthyoplankton distribution patterns. For several years he was a regular at CalCOFI Conferences, publishing a dozen papers in *CalCOFI Reports* and in one of the *CalCOFI Atlases*. He was involved with the development of the egg production method and for several years coordinated production of the annual estimate of anchovy biomass using the technique. He also developed procedures for describing the mortality and dispersal of fish larvae; developed methods for using SONAR to map epi-pelagic fish schools and estimate their biomass; conducted field experiments to determine sources of mortality on young fish, acoustic properties of fish schools, and inshore fish production; developed models that described the influence of various processes on the survival of young fish; and studied the efficiency of ichthyoplankton sampling methods and recommended improvements. In the late 1980s he modeled the shipboard sampling regime for the U.S. Antarctic Marine Living Resources (U.S. AMLR) program after CalCOFI. He spent 16 field seasons in the Antarctic while working with the U.S. AMLR program, monitoring the krill-centric ecosystem, developing fishery management options, and providing advice to the U.S. delegation to the Convention for the Conservation of Antarctic Marine Living Resources. Roger reports that he is glad to return home to CalCOFI but also notes that he was never far away. We in the committee welcome him back and look forward to many years of working with him.

The winter and spring CalCOFI cruises took place this year in January–February and in April. In 2002 these cruises were extended northward to include line 60. SIO participates to line 77, and MBARI continues the oceanographic work on the five northern lines. During the April 2004 spring cruise the majority of sardine eggs found with the Continuous Underway Fish Egg Sampler were north of line 77 and were still being collected in large numbers on line 60. This egg distribution is quite different from previous cruises and indicates a northward shift of the sardine population.

Beginning in February 2004 the City of Los Angeles Department of Public Works resumed sampling (under contract to SWFSC) along four inshore survey lines that had been sampled by the Los Angeles County Museum during the Ichthyoplankton Coastal and Harbor Survey (ICHS) in the late 1970s to mid-1980s. Stations are located at the 8 m, 15 m, 22 m, 36 m, and 75 m isobaths on each line, following the ICHS design. An integrated, quantitative water-column sample is collected at each station with a CalCOFI bongo net, comparable to the sampling during ICHS and CalCOFI surveys. Sampling is quarterly, in conjunction with CalCOFI surveys. Sample analysis has not yet begun, but ichthyoplankton and squid paralarvae will be sorted from the samples, identified to the lowest practical taxon, counted, and quantitative abundance estimates generated. The survey currently is scheduled for six quarterly cruises.

KUDOS

The seagoing personnel of SIO's Integrative Oceanography Division, the SWFSC's Fisheries Research Division, and CDFG's Marine Region all contributed through their dedication, expertise, and diligence, making the CalCOFI program possible. The CalCOFI Committee thanks the officers and crew of the research vessels SIO RV *New Horizon*, SIO RV *Roger Revelle*, and the NOAA RV *David Starr Jordan*—they have served us well in 2003. We are indebted to them all, as we are to our sea-going crew, including Dimitry Abramenkoff, Ron Dodson, Dave Griffith, Amy Hays, Sue Manion, Sherry McCann, Fernando Raimirez, Jennifer Sheldon, Jim Wilkinson, and Dave Wolgast. Ralf Goericke has served again this year as the coordinator of the sea-going work, and the committee extends to him our gratitude.

The Committee would like to thank James Wilkinson this year again for his continued dedication as our Web master. Thanks to him, the CalCOFI Data Reports 0211 and 0302 are now online. The library of annual *CalCOFI Reports* is available online in a searchable PDF format thanks to Kevin Hill. The CalCOFI hydrographic data set is also available in Microsoft Access 2000 for 1949-2002. The database includes all hydrographic data published in the biannual Data Report.

The Committee would like to thank Robert N. Lea of CDFG, who served once again in 2003 on the editorial board of the *CalCOFI Reports*. We would also like to thank Maura Leos of CDFG, who served as CalCOFI conference registrar in 2003, for all her help and expertise coordinating the conference, running the audiovisual equipment, and attending to the needs of the conference participants.

The CalCOFI Committee:
Laura Rogers-Bennett, CalCOFI Coordinator
Roger Hewitt, NMFS
Elizabeth Venrick, UCSD

REVIEW OF SOME CALIFORNIA FISHERIES FOR 2003: MARKET SQUID, COASTAL PELAGIC FINFISH, DUNGENESS CRAB, SEA URCHIN, GROUNDFISH, OCEAN SALMON, TUNA, NEARSHORE LIVE-FISH, PACIFIC HERRING, AND ROCK CRAB

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SUMMARY

In 2003, commercial fisheries landed an estimated 121,010 metric tons (t) of fishes and invertebrates from California ocean waters (fig. 1). This represents a decrease in landings of over 32% from the 178,982 t landed in 2002 and a 52% decline from the 252,568 t landed in 2000. However, the preliminary ex-vessel economic value of commercial landings in 2003 was $127 million, a 21% increase from the $104 million in 2002 and an 8% decrease from the $137 million in 2000.

Market squid was once again the largest fishery in the state, by volume, at nearly 45,000 t, although the Dungeness crab fishery had the highest ex-vessel value at just over $34 million. The ex-vessel value of squid landings was over $24 million. Pacific sardine landings were second in volume at over 34,000 t and eighth in ex-vessel value at over $2.9 million. Other top five California landings included Dungeness crab at over 10,000 t, sea urchin at nearly 4,900 t, and Pacific mackerel at 4,400 t. Besides Dungeness crab and market squid, the top five California landings in terms of ex-vessel value included Chinook salmon at over $12 million, swordfish at $7.6 million, and sea urchin at $6.9 million. Notable changes in invertebrate landings for 2003 were the large (86%) increase in Dungeness crab landings compared with 2002, and the decrease in sea urchin landings, which were the lowest on record since 1975.

California's commercial groundfish harvest for 2003 was over 10,000 t, consisting mainly of Dover sole, rockfishes, Pacific whiting, sablefish, and thornyheads. Ex-vessel value of groundfish landings for 2003 was $14.9 million. Declines in groundfish landings reflect landing restrictions that went into effect in 2002 that were designed to reduce the harvest of depleted rockfish stocks. Depth-based fishery restrictions were implemented to reduce catch of impacted species.

Pacific herring landings for 2003 decreased by over 40% from 2002. Concerns over the status of the stocks led to an independent review of survey techniques and assessment models for the San Francisco Bay herring population. In contrast, declines in nearshore live-fish landings in 2003 were expected and reflect management measures set forth in the Nearshore Fisheries Management Plan adopted by the California Fish and Game Commission (Commission) in 2002.

In 2003, the Commission undertook 15 rule-making actions that addressed marine and anadromous species. In addition, the Commission voted to list the nocturnal seabird Xantus's murrelet as a threatened species, which may affect fisheries around the Channel Islands, where the majority of its nesting habitat is located. In addition, the California legislature gave the Commission authority to manage the commercial rock crab fishery.

During 2003, the Pacific Fishery Management Council (PFMC) revised the process for reallocating unharvested sardine, set a series of recreational and commercial salmon regulations to comply with both state and federal Endangered Species Act (ESA) biological opinions, and adopted the Highly Migratory Species Fishery Management Plan (HMSFMP). The PFMC also set 2003 optimal yields for a large number of groundfish species and species groups. The allowable harvest was reduced for nearly all groups in order to protect those species in rebuilding status, and emergency closures of selected recreational and commercial fisheries were implemented by both federal and state jurisdictions to reduce impacts. In the Pacific whiting fishery, an agreement between Canada and the United States set the coastwide allocation of landings at 26% to Canada and 74% to the United States.

MARKET SQUID

Market squid (*Loligo opalescens*) was the largest fishery in the state by volume and second in ex-vessel value in 2003. A total of 44,965 t were landed: 38% less than the 72,878 t landed in 2002, and 62% less than the record high set in 2000 (118,902 t) (fig. 2). High ex-vessel prices of $500 to $600 per ton for market squid were consistently paid throughout 2003. The 2003 ex-vessel value was approximately $24.1 million, second to Dungeness crab. This represents a 32% increase over the $18.2 million ex-vessel value of market squid recorded in 2002.

The fishing season for market squid runs from 1 April through 31 March of the following year. A northern fishery normally occurs during the spring and summer and is centered in Monterey Bay. A southern fishery

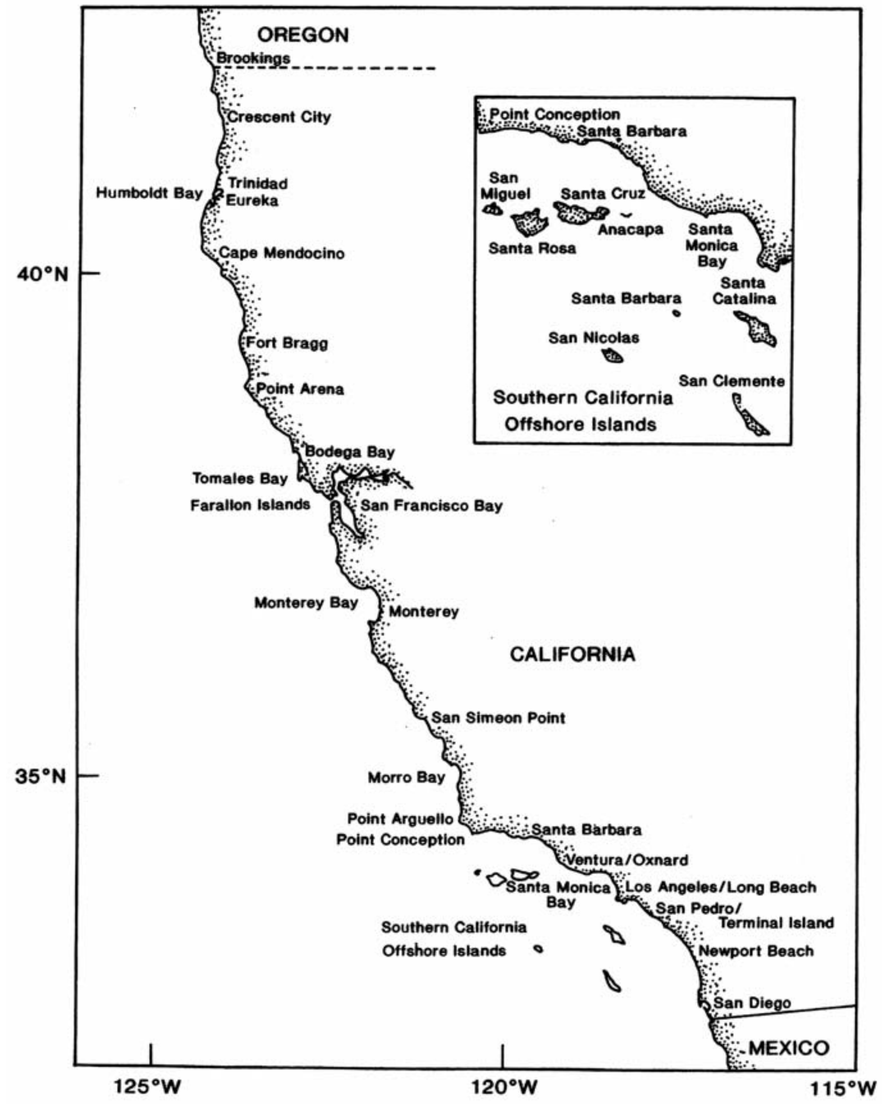


Figure 1. California ports and fishing areas.

normally occurs during the fall and winter off the Channel Islands and coastal southern California. Lingering effects of the moderate 2002 El Niño condition may have reduced the amount of squid available to the fishery. During the 2003-2004 season, 48,044 t were landed, 13% more than in the 2002–2003 season (42,596 t) (fig. 3).

The northern fishery experienced a significant decline in catch levels during the 2002–2003 season. A total of 17,377 t was landed (fig. 3), a 31% decrease from the total recorded in the 2002–2003 season. For the first time market squid were harvested in significant numbers from the Farallon Islands area. The length of harvest time was also unusually long. Landings began in mid-February and continued through November. There was also an increase in daytime fishing activity. During the day, squid were concentrated enough to allow for detection and capture by vessels using sonar. Daytime fishing also was reported to have reduced the number of interactions with sea lions.

The southern fishery surpassed the northern fishery in the 2003–2004 season (fig. 3), with 30,667 t landed (64% of the catch). Catches were made almost all year, even during the summer when historically squid are not available. Night fishing utilizing attracting lights is the predominant fishing mode in southern California.

California market squid has become an important international commodity. While some squid are used domestically for consumption and bait, most are packed and processed for export. In 2003, strong international demand for squid fueled high ex-vessel prices in California. Approximately 23,000 t of market squid were exported for a value of $27 million. Asian destinations are the main export market, with China and Japan taking about 68% of the trade.

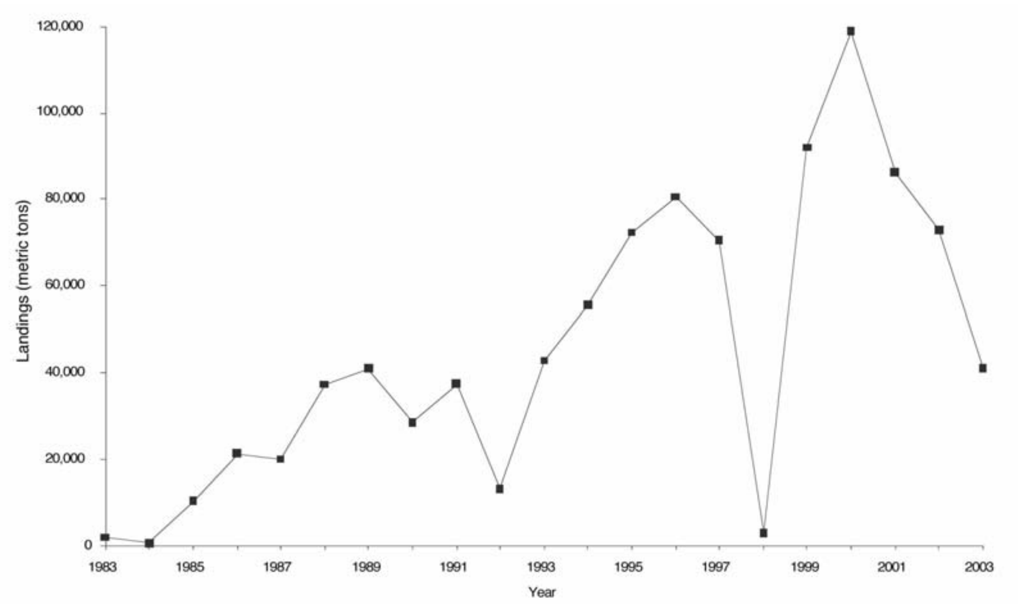


Figure 2. California commercial market squid landings, 1982–2003

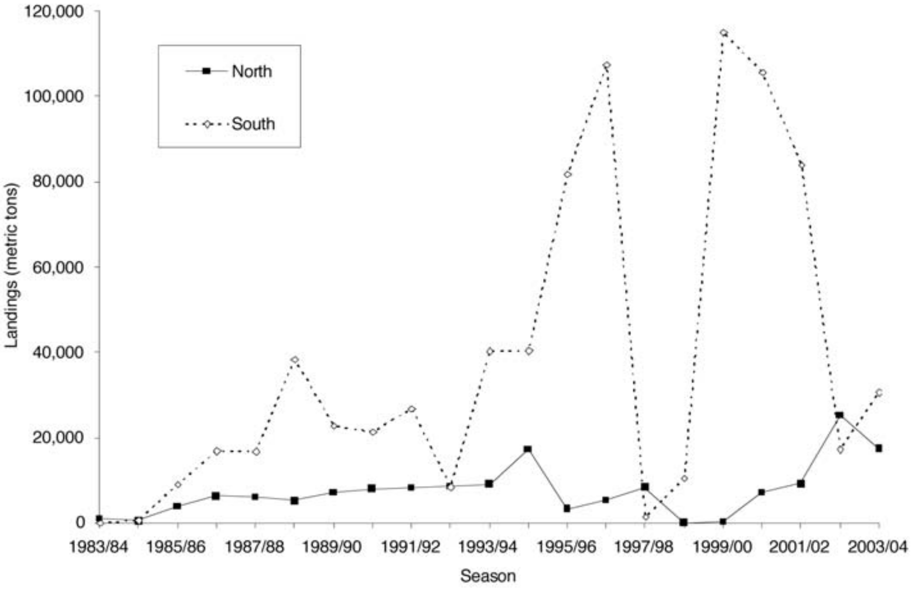


Figure 3. Comparison of market squid landings for northern and southern fisheries by fishing season (1 April to 31 March), from the 1982–83 season to the 2003–2004 season.

In May 2003, a revised draft of the Market Squid Fishery Management Plan (MSFMP) was released for public review and comment. Developed under guidelines set forth by the Marine Life Management Act of 1998, the MSFMP establishes a management program and procedures by which the Commission will manage the market squid resource. The goals of the MSFMP are to provide a framework and set of procedures to ensure sustainability of the resource and the marine life that depends on it, provide for an economically viable fishery, and to reduce the potential of overfishing. Key features of the MSFMP include (1) fishery control rules; (2) a restricted access program; (3) ecological considerations such as harvest replenishment and general habitat closures, as well as time and area closures to protect nesting seabirds; and (4) administrative items. Adoption by the Commission was postponed until mid-2004, with scheduled implementation for the 2005–2006 fishing season.

TABLE 1
Landings of Coastal Pelagic Species in California

	Landings (in metric tons)						
Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1977	5	99,504	5,333	44,775	5,200	12,811	167,628
1978	4	11,253	11,193	30,755	4,401	17,145	74,751
1979	16	48,094	27,198	16,335	4,189	19,690	115,522
1980	34	42,255	29,139	20,019	7,932	15,385	114,764
1981	28	51,466	38,304	13,990	5,865	23,510	133,163
1982	129	41,385	27,916	25,984	10,106	16,308	121,828
1983	346	4,231	32,028	18,095	7,881	1,824	64,405
1984	231	2,908	41,534	10,504	3,786	564	59,527
1985	583	1,600	34,053	9,210	7,856	10,275	63,577
1986	1,145	1,879	40,616	10,898	7,502	21,278	83,318
1987	2,061	1,424	40,961	11,653	8,264	19,984	84,347
1988	3,724	1,444	42,200	10,157	8,677	36,641	102,843
1989	3,845	2,410	35,548	19,477	9,046	40,893	111,219
1990	2,770	3,156	36,716	4,874	7,978	28,447	83,941
1991	7,625	4,184	30,459	1,667	7,345	37,388	88,668
1992	17,946	1,124	18,570	5,878	6,318	13,110	62,946
1993	13,843	1,954	12,391	1,614	3,882	42,708	76,392
1994	13,420	3,680	10,040	2,153	2,668	55,395	87,356
1995	43,450	1,881	8,667	2,640	4,475	70,278	131,391
1996	32,553	4,419	10,286	1,985	5,518	80,360	135,121
1997	46,196	5,718	20,615	1,161	11,541	70,257	155,488
1998	41,056	1,457	20,073	970	2,432	2,709	68,697
1999	56,747	5,179	9,527	963	2,207	90,322	164,945
2000	53,586	11,504	21,222	1,135	3,736	117,961	209,144
2001	51,811	19,187	6,924	3,615	2,715	85,828	170,080
2002	58,353	4,643	3,367	1,006	3,339	72,878	143,586
2003	34,300	1,547	3,999	155	1,975	44,965	86,941

TABLE 2
Northern and Southern California Commercial Landings and Ex-vessel Values of CPS Finfish for 2003

	Northern California		Southern California			
Species	Landings (metric t)	Ex-vessel value	Landings (metric t)	Ex-vessel value	Total landings (metric t)	Total ex-vessel value
Pacific sardine	7,321	$673,543	26,379	$2,265,831	33,700	$2,939,049
Pacific mackerel	1	$4,662	3,998	$628,002	3,999	$632,364
Jack mackerel	20	$2,478	135	$52,276	155	$54,754
Northern anchovy	706	$81,964	841	$178,340	1,547	$260,310
Totals	8,048	$762,647	31,353	$3,124,449	39,401	$3,887,096

COASTAL PELAGIC FINFISH

Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and northern anchovy (*Engraulis mordax*) are known as coastal pelagic species (CPS) finfishes. These species are jointly managed by the PFMC and NOAA Fisheries. During 2003, combined commercial landings of these four species totaled 39,401 t (tab. 1). Recent historical landings of these coastal species, as well as two managed by California, Pacific herring (*Clupea pallasii*) and market squid, are presented in Table 1.

Pacific Sardine

The Pacific sardine fishery extends from British Columbia, Canada, southward to Baja California, México; however, the bulk of the catch is landed in southern California and Ensenada, Baja California, México (BCM). The Pacific sardine harvest guideline (HG) for each calendar year is determined from the previous year's stock biomass estimate (≥ 1-year-old fish on 1 July). The 2003 Pacific sardine HG was set at 110,908 t using the 2002 stock biomass estimate of nearly 1.0 million t. Sixty-six percent (73,199 t) of this HG was allocated to the southern California fishery (south of Point Piedras Blancas, 35°40'00"N lat.) and the remaining 33% (36,600 t) was allocated to the northern California, Oregon, and Washington fisheries.

During 2003, the PFMC revised the process for reallocating unharvested sardine. The following allocation arrangement became effective on 4 September

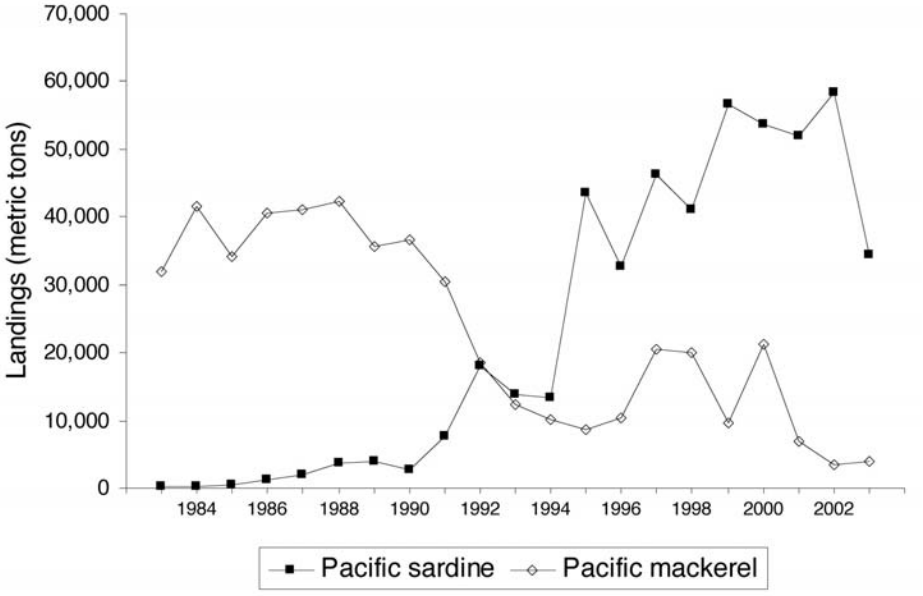


Figure 4. California commercial landings of Pacific sardine (*Sardinops sagax*) and Pacific mackerel (*Scomber japonicus*), 1983–2003.

2003: (1) The geographic boundary between the northern U.S. west coast fisheries (Subarea A) and the southern west coast fishery (Subarea B) was changed from 35°40'00"N latitude (Point Piedras Blancas) to 39°00'00"N latitude (Point Arena); (2) the date when unharvested Pacific sardine is reallocated to Subarea A and Subarea B was changed from 1 October to 1 September; (3) the percentage of the unharvested sardine that is reallocated to Subarea A and Subarea B was changed from 50% to both subareas to 20% to Subarea A and 80% to Subarea B; and (4) all unharvested sardine that remains on 1 December will be reallocated coastwide. This revised allocation framework will remain in place through the 2004 fishing season and may be used in 2005 if the 2005 harvest guideline is at least 90% of the 2003 harvest guideline.

In California, a total of 33,700 t of Pacific sardine was landed during 2003; a 41% decrease from the previous year (fig. 4). The 2003 ex-vessel value for Pacific sardine totaled just over $2.9 million dollars (tab. 2); a 50% decrease from 2002. Most of the catch (77%) was landed in southern California, and 71% was landed in Los Angeles County.

A total of 26,906 t of sardine, valued at $14.2 million, was exported from California ports during 2003. Of the 25 countries that imported sardine product from California, Australian (8,403 t) and Japanese (8,150 t) markets received 61% of the product.

Commercial landings of Pacific sardine increased in Oregon to 25,253 t in 2003 from 22,711 t in 2002, whereas Washington's 2003 landings decreased from 15,212 t in 2002 to 11,604 t in 2003. Like California and Washington, Ensenada, BCM, also experienced a decline in sardine landings during 2003. Approximately 30,537 t were landed in Ensenada in 2003; a 30% decline from 43,437 t in 2002.

Pacific Mackerel

Although Pacific mackerel are occasionally landed in Oregon and Washington, the majority of landings are made in southern California and Ensenada, BCM. California landings of Pacific mackerel have been steadily declining over the past 15 years (fig. 4); however, 19% more were landed in 2003 (3,999 t) than were landed in 2002 (3,367 t). Only one metric ton of Pacific mackerel was landed north of Point Piedras Blancas (tab. 2) in 2003. Most of the catch (99%) was landed in Los Angeles County, and of that, 69% (2,759 t) was landed in the port of San Pedro. The ex-vessel value of California's 2003 catch was $632,364. Ninety-three percent of Pacific mackerel were landed using purse seines. Export data on Pacific mackerel alone are not available; however, exports of all mackerel species for the year 2003 totaled 2,408 t, with an export value of $1.4 million.

The fishing season for Pacific mackerel runs from 1 July through 30 June of the following year. The HG for the 2002–2003 season was set at 12,456 t, based on a biomass estimate of 77,516 t. The HG for the 2003–2004 season was set at 10,652 t, based on a biomass estimate of 68,924 t. In accord with a 3 November 2003 federal ruling, 40% of Pacific mackerel in landings of any CPS will be allowed as incidental take in order to minimize bycatch of mackerel. This incidental allowance would become effective after 7,500 t of Pacific mackerel have

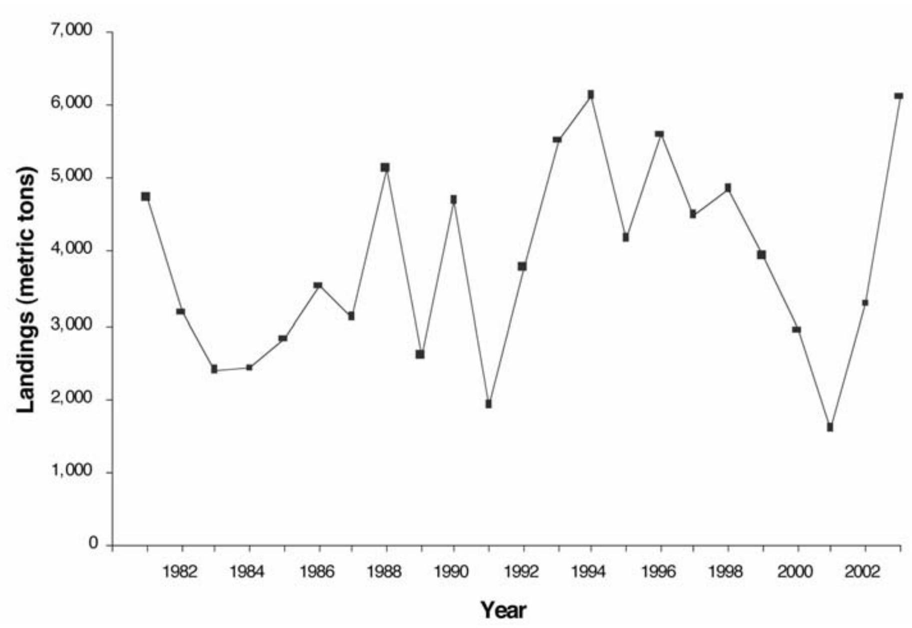


Figure 5. California commercial landings of Dungeness crab, 1981–2003.

been landed during the 2003–2004 season. Current landing trends suggest that the implementation of this allowance may not be necessary.

In Oregon, nearly 234 t of Pacific mackerel were landed in 2003, primarily as bycatch in the sardine fishery. Washington's commercial landings of Pacific mackerel totaled 51 t in 2003, and approximately 2,678 t were landed in Ensenada, BCM.

Jack Mackerel

Landings of jack mackerel in California decreased substantially in 2003 to 155 t (tab. 1), down from 1,006 t in 2002. This represents an 85% decline from 2002 landings and a 96% decline from 2001 landings (3,615 t). Ex-vessel revenues totaled $54,754, a 73% decline from $202,000 in 2002 (tab. 2). Eighty percent of the California catch was taken by purse seine vessels, and 87% of the catch was landed in southern California ports. There were no reported commercial landings of jack mackerel in Oregon or Ensenada, BCM, during 2003, and less than 2 t were landed in Washington.

Northern Anchovy

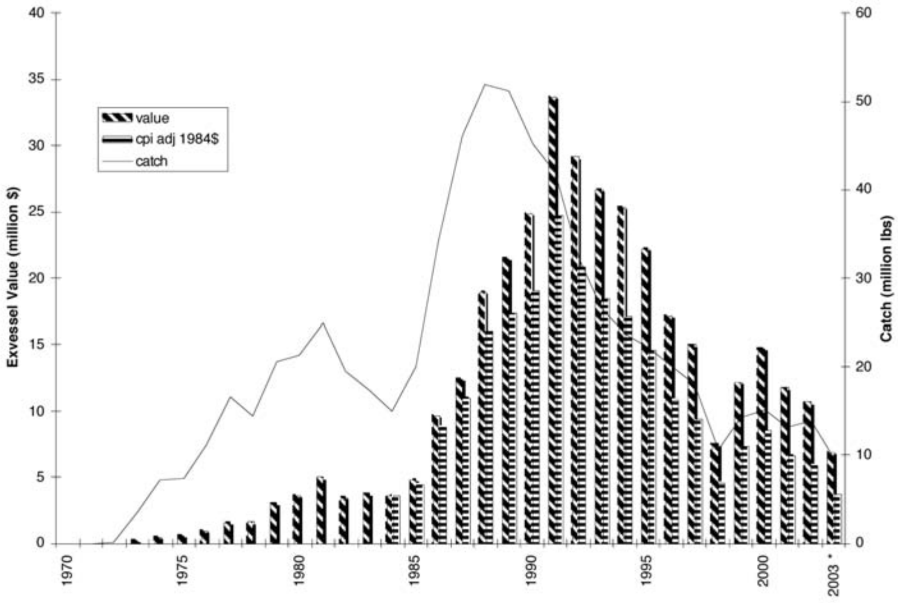
California's 2003 northern anchovy catch declined by two-thirds from 4,643 t in 2002, to 1,547 t (tab. 1). The ex-vessel value in 2003 was $260,304. Forty-six percent (706 t) of the catch was landed in Monterey County, and 54% (841 t) was landed in southern California. Most of the fish (66%) were taken using lampara nets and 17% using purse seines. During 2003, 52 t of preserved or salted anchovy product were exported from California ports at a value of $260,357. Approximately 1,287 t of northern anchovy were landed in Ensenada, BCM.

Domoic acid health advisories continued to plague California's CPS fisheries during 2003 as they had in 2002. The Monterey fishery was affected from 18 April to 24 June and again from 1 September to 31 October 2003. Likewise, health advisories were in effect in counties extending from San Luis Obispo to Los Angeles between 15 May and 2 July 2003. During these health advisories, fish could not be sold for human or pet consumption owing to high levels of domoic acid, a nerve toxin produced by marine diatoms belonging to the genus *Pseudo-nitzschia*.

DUNGENESS CRAB

Landings of Dungeness crab (*Cancer magister*) in 2003 were estimated at 6,112 t, an 86% increase in landings over 2002 (3,286 t) (fig. 5). This continues the trend of increased landings since 2001, which had the lowest landings in 25 years. Ex-vessel revenues for 2003 were $38.1 million, a 184% increase in value over 2002 ($13.4 million) and greatly above 2001 revenues ($9 million). The average price per pound decreased 4% from $1.84 in 2002 to $1.77 in 2003.

The Dungeness crab fishery in California is managed under a regimen of size, sex, and season. Only male Dungeness crabs are harvested commercially, and the minimum commercial harvest size is 6.25 in., measured by the shortest distance across the carapace immediately in front of the posterior lateral spines. The minimum size limit is designed to protect sexually mature crab from harvest for one or two seasons, and the timing of the



Source: CPI, US Bureau of Labor Statistics

2003* preliminary

Figure 6. California sea urchin catch and value, adjusted by consumer price index, 1970–2003.

season is designed to provide some measure of protection to crabs when molting is most prevalent. California implemented regulations prohibiting the sale of female Dungeness crabs in 1897. Minimum size regulations were first implemented by California in 1903 and have remained substantially unchanged since 1911. The commercial season runs from 1 December to 15 July from the Oregon border to the southern border of Mendocino County (northern area) and from 15 November to 30 June in the remainder of the state (central area). This basic management structure has been stable and very successful over time. Legislation to authorize a preseason soft-shell testing program was introduced during 1994, and industry-funded preseason testing began prior to the 1995–96 season. The testing is monitored by the Pacific States Marine Fisheries Commission, and a minimum crab meat recovery of 25% is required. The program is initiated each year around 1 November; if the crab meat recovery is less than 25%, another test is mandated. Two weeks later the second test is made, and if the pick-out is still below 25%, the season opening is delayed 15 days. This procedure can continue until 1 January, when no more tests can be made and the season must be opened on 15 January.

Summarizing 2002–2003 commercial season landings, rather than the annual totals presented above, results in lower landings, since 42% of the landings occurred in November and December, the start of the 2002–2003 season. Landings for the 2002–2003 season totaled 6,228 t, a 246% increase from the 2001–2002 season and the highest since the 1979–80 season. Landings in the northern area in the 2002–2003 season increased 372% over the 2001–2002 season and were 75% higher than the 2,316 t long-term 88-year average for this area. Central area landings increased by 135% and were 82% higher than the 999 t long-term 88-year average.

The average statewide price per pound for the 2002–2003 season was $1.90/lb, a decrease of $0.24/lb from the 2001–2002 season. The central area fishery began on the opening date of 15 November with a starting price of $2.22/lb. The northern area season opener was delayed because of a strike over the price, which was lowered due to the large volume of crab landed in the central area in November. The northern area season began 22 days after the 1 December official opening date with an agreed upon price per pound of $1.40. Price remained low throughout the remainder of the season, rising briefly at the end to over $3.50/lb. The 2002–2003 Dungeness crab season catch was worth $26.1 million, a 239% increase in value over the 2001–2002 season ($7.7 million). A total of 400 vessels made landings during the 2002–2003 season, up slightly from the 30-year low of 385 vessels in 2001–2002 season.

SEA URCHIN

In 2003, landings of sea urchin (*Strongylocentrotus franciscanus*) were the lowest on record since 1975. A total of 4,878 t were landed in 2003, with an ex-vessel value of $7.7 million. Northern California landings barely surpassed those of 1985, the year considered the onset of that fishery (fig. 6). This decline, at least in recent years, has been mostly market driven. Northern California

TABLE 3
2003 California Commercial Groundfish Landings (in metric tons)

	2003	2002	Change since 2002 (%)	1993	Change since 1993 (%)
Flatfishes	4,767	4,969	−4	8,490	−44
Dover sole	3,256	3,124	4	6,554	−50
English sole	131	373	−65	474	−72
Petrale sole	380	480	−21	464	−18
Rex sole	258	288	−10	457	−44
Sanddabs	605	564	8	351	72
Other flatfishes	137	140	−2	190	−28
Rockfishes	1,984	2,725	−27	12,727	−84
Thornyheads	1,281	1,581	−19	4,162	−69
Widow	5	49	−90	1,207	−99
Chilipepper	18	167	−89	2,317	−99
Bocaccio	1	22	−95	1,367	−100
Canary	1	11	−91	196	−99
Darkblotched	12	48	−75	287	−96
Splitnose	151	60	152	434	−65
Other rockfishes	515	787	−35	2,757	−81
Roundfishes	3,631	4,415	−18	6,803	−47
Lingcod	52	81	−36	699	−93
Sablefish	1,629	1,313	24	2,601	−37
Pacific whiting	1,741	2,773	−37	3,100	−44
Grenadier	163	189	−14	383	−58
Cabezon	40	50	−20	18	122
Other roundfishes	6	9	−33	2	200
Other groundfishes	182	147	24	101	80
Total	10,564	12,256	−14	28,121	−62

landings dropped by over 50% from 2002 levels, while CPUE (catch per diver) was virtually unchanged in Mendocino County ports and only down 16% in Bodega Bay.

A major contributing factor to California's declining landings is the dramatic slide in U.S. sea urchin exports during the past decade. In 1993, $110 million worth of sea urchins were exported to Japan from the states. By 2003, the value had declined to $50 million (about $36 million when adjusted for inflation compared to 1993 values). The increased domestic market for California sea urchin during the past 5 years has made up some of this shortfall.

Urchin diving is a rigorous occupation, and the increasing age of the commercial sea urchin diver pool has had a noticeable impact on fishery effort. The average age of permitted divers is now 48, with 25 of the 348 divers over 60 years of age. This trend will likely continue as entry into the fishery is limited to one new permit for every 10 retired.

Several changes to the commercial sea urchin regulations became effective in 2003. The most significant of these from a management perspective is the elimination of the once monthly, week long closures from May through September that have been a fixture of the fishery since 1992. The closures were intended to reduce effort during the period when fishery value was lowest and opportunity highest due to favorable weather conditions. The industry has long argued that the closures made it difficult to maintain a consistent market presence during the summer months, and that the overall effort decline has made the closures unnecessary. In addition to eliminating the weekly closures, the month of July was partially opened to fishing in northern California, providing for a uniform season statewide.

During June 2003, Humboldt State University contract divers partnered with CDFG divers to complete a total of 85, 30 m × 2 m transects at Point Arena Cove, Van Damme State Park, and Point Cabrillo Marine Reserve, Mendocino County. These sites serve a dual purpose as they are used for both abalone and sea urchin assessments. Van Damme had 1.4 red urchins per square meter, Point Arena had 0.76/m^2, and Point Cabrillo had 6.0/m^2. Point Cabrillo has been consistent since it was first surveyed in 1988 (it has been a reserve since 1975). Van Damme shallow water urchins (< 30 ft) have declined in number, while deep water urchins have increased since the 1990 survey (though fewer transects were surveyed in 1990). This was the first year for the Point Arena survey.

GROUNDFISH

California's commercial groundfish harvest for 2003 was 10,564 t (tab. 3). Total 2003 landings decreased 14%, from 12,256 t in 2002, and 62%, from 28,121 t in 1993. The ex-vessel value for all groundfish in 2003 was approximately $14.8 million, a decrease of 8% from 2002 revenues of $16.1 million.

In 2003, 85% of groundfish were landed using bottom and midwater trawl gear, a slight decrease from the 88% observed in 2002. Line gear accounted for the second largest amount at 11%, a slight increase from the 9% observed in 2002. The line gear contribution was at a recent high of 18% in 1992. Trap gear accounted for just over 2% of the total 2003 groundfish landings. The gill and trammel net component remained at just under 1% after a steady decline from 5% in 1993 to 1% in 1996.

The state's 2003 groundfish harvest was again dominated by Dover sole (*Microstomus pacificus*), rockfishes (*Sebastes* spp.), Pacific whiting (*Merluccius productus*), sablefish (*Anoplopoma fimbria*), and thornyheads (*Sebastolobus* spp.) (tab. 3). Landings of Dover sole, thornyheads, and sablefish (the DTS complex) experienced a slight increase (2%) from the 2002 total, owing mainly to a 24% increase in sablefish landings, despite a 19% decrease in thornyhead landings. Lingcod (*Ophiodon elongatus*), other flatfishes, and Pacific whiting all experienced declines from the 2002 totals. The declines reflected significant landing limitations, adopted by the PFMC in September 2002, designed to reduce the harvest of depleted rockfish stocks. These management measures were considered historic in scope considering the breadth of the restrictions and the large-scale economic impacts to the west coast fishing communities. A center piece of these measures was the adoption of depth-based restrictions that seasonally move fisheries that catch overfished stocks out of the depth zones they inhabit.

As in previous years, the PFMC continued to set 2003 optimal yields for a myriad of groundfish species and species groups. The allowable harvest was reduced for nearly all groups in order to protect those species in rebuilding status. Cumulative landing limits as well as trip limits were again used by the PFMC to meet their objective of staying within the small optimum yields while continuing to provide for a year-round fishery. Despite these efforts, emergency actions had to be implemented by both federal and state jurisdictions in the fall to shut down coastwide recreational fisheries and most commercial fisheries. This was due to an unexpectedly high take in the recreational sector during July and August.

A noteworthy event took place in 2003 in the Pacific whiting fishery. An agreement was reached between Canada and the United States to set the percentage of take so as not to exceed the allowable catch, which had been happening during the past few years. The percentages were set at approximately 74% for the United States and 26% for Canada. The allowable catch had been separately allocated each year at 80% for the United States and 30% for Canada. This agreement was reached, in part, because Pacific whiting was given an overfished designation in 2002 by the National Marine Fisheries Service. The formal implementation of this agreement, however, will not take place until 2005, but both countries will use it informally as early as 2004.

The Scientific and Statistical Committee recommended, and the PFMC adopted, new full stock assessments for use in 2004 management decision-making for Pacific ocean perch (*Sebastes alutus*), bocaccio (*S. paucispinis*), and widow (*S. entomelas*) and black (*S. melanops*) rockfishes, and assessment updates for cowcod (*S. levis*), and darkblotched (*S. crameri*) and yellowtail (*S. flavidus*) rockfishes. The PFMC also adopted new rebuilding analyses for Pacific Ocean perch, bocaccio, and widow and darkblotched rockfishes.

Additionally, the bocaccio assessment used a new estimate for natural mortality and validation of a strong 1999 year class. As a result, it is estimated the stock can rebuild in about 25–30 years, with higher levels of harvest during the rebuilding phase than what had previously been estimated. However, the new widow rockfish assessment is much more pessimistic than the one completed in 2001, with lower harvest levels under the new rebuilding analysis possibly having negative consequences for the Pacific whiting and other midwater trawl fisheries. Assessments for Pacific Ocean perch and darkblotched and yellowtail rockfishes have not significantly changed since their last assessments.

On the positive side, a new stock assessment of black rockfish for Oregon and California waters indicates that a portion of the stock is above the biomass that supports maximum sustainable yield. Also, the PFMC's nonretention measures and area closures to rebuild cowcod have been effective in constraining fishing mortality to prescribed levels.

Regulatory changes adopted by the Commission in December 2002 as interim management measures for 2003 affected the cabezon (*Scorpaenichthys marmoratus*) and the kelp (*Hexagrammos decagrammus*) and rock greenling (*H. superciliosus*) fisheries, as well as the California sheephead (*Semicossyphus pulcher*) fishery (CGS complex). Statewide cumulative trip limits were established for January and February, and a statewide closure was established for March and April. This action was done to align the fishing season for these species with the new federal seasons for nearshore rockfishes in most areas and to allow consistent fishing seasons for the CGS complex and nearshore rockfishes at the same time so as to minimize bycatch that might occur.

Management measures at both the federal and state level have evolved dramatically within the last few years. Some of those set in place, being developed, and under consideration as future management tools include groundfish management measures to be developed over the course of a two-meeting schedule for the PFMC,

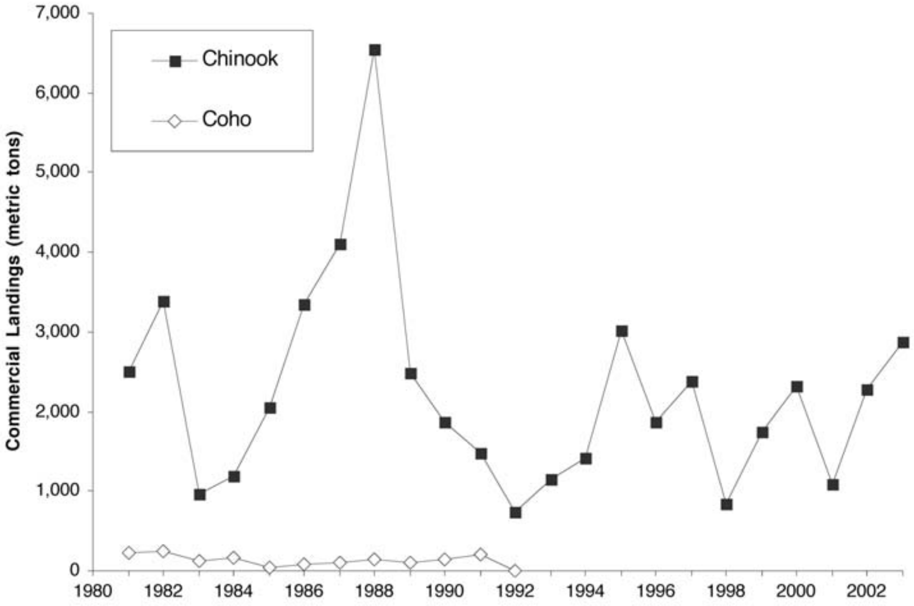


Figure 7. California commercial ocean salmon landings, 1981–2003.

conservative approach to area and season restrictions to facilitate rebuilding of stocks, depth-based restrictions, vessel monitoring systems (VMS), a multi-year management process, permit stacking, and moving from open-access to limited-entry fisheries to achieve capacity reduction, a buyback program, approval of the formation of an Ad Hoc Groundfish Habitat Technical Review Committee, and using exempted fishing permits (EFP) to test the ability of innovative fishing gears and strategies to more cleanly target healthy groundfish stocks while avoiding overfished stocks. Also, the Commission set aside 132 sq. nmi within the Channel Islands National Marine Sanctuary, creating a system of 12 separate no-take marine reserves. These marine reserves went into effect on 9 April 2003. And, finally, in response to concerns voiced by west coast industry and fishery managers, the recreational data system went through an overhaul. The nearly 25-year-old Marine Recreational Fisheries Statistics Survey (MRFSS) is to be phased out in California starting in January 2004. In its place a new program was developed that will be an all-inclusive recreational fisheries survey encompassing the salmon fishery and other marine fisheries. This new program is called the California Recreational Fisheries Survey (CRFS).

OCEAN SALMON

In 2003 the commercial troll fishery landed approximately 2,883 t (488,800 fish) of dressed Chinook (*Oncorhyncus tshawytscha*) (fig. 7) and fished approximately 15,600 boat days. Ex-vessel prices for dressed salmon averaged $1.90/lb, and the total ex-vessel value of the fishery exceeded $12.1 million.

Statewide recreational landings totaled 93,100 Chinook during 132,300 angler days (catch per angler day = 0.70) (fig. 8). Anglers were limited to two salmon a day (all species except coho, *Oncorhyncus kisutch*). South of Horse Mountain (near Cape Mendocino in Humboldt County) the minimum size limit was 24 in. total length (TL) through 30 April, and 20 in. TL thereafter. Anglers fishing with bait and by any means other than trolling in the area between Point Conception and Horse Mountain were required to use barbless "circle" hooks. In the Klamath Management Zone (KMZ: Horse Mountain, California, to Humbug Mountain, Oregon) the bag limit was two salmon a day and a minimum size limit of 20 in. TL. In the California portion of the KMZ, anglers landed 8,700 Chinook during 15,800 angler days.

In 2003, the PFMC enacted commercial and recreational ocean salmon regulations in California to meet the following objectives:

- The NOAA Fisheries Sacramento River winter Chinook 2002 Biological Opinion required that the duration and timing of the 2003 commercial and recreational fisheries south of Point Arena not change substantially relative to the 2000 and 2001 seasons.
- The Oregon coast natural (OCN) coho maximum allowable exploitation rate (marine and freshwater combined) of 15% under Amendment 13 of the Salmon Fishery Management Plan (FMP).
- Conservation and allocation objectives for Klamath River fall Chinook as follows: a spawner escapement to natural areas of 35,000 adults; a minimum adult natural spawner escapement rate of 33–34%; 50% of

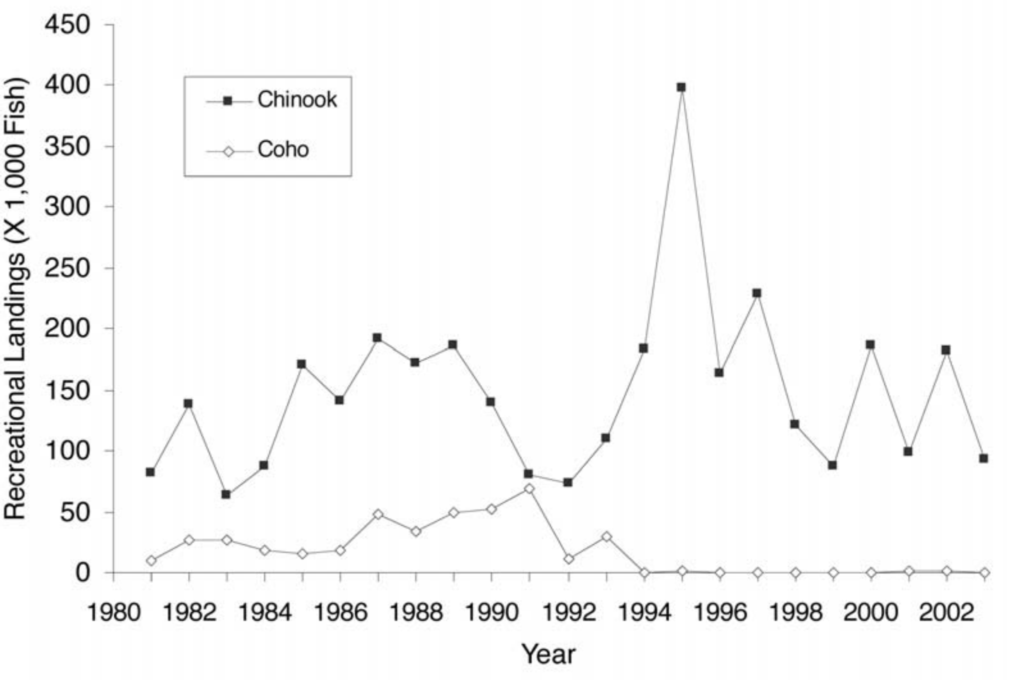


Figure 8. California recreational landings of ocean salmon, 1981–2003.

the allowable adult harvest for federally recognized tribal subsistence and commercial fisheries; 26.1% of the non-Indian harvest to the Klamath River recreational fishery; 14.8% of the ocean harvest to the KMZ recreational fishery.

- The California coastal Chinook consultation standard provided by NOAA Fisheries under the federal ESA of no greater than a 16% age-4 ocean harvest rate on Klamath River fall Chinook.
- The Sacramento River fall Chinook escapement goal range of 122,000 to 180,000 hatchery and natural adults.
- The prohibition of retention of coho in California as required under the NOAA Fisheries 1999 Biological Opinion for threatened central California coast coho.

Harvest impacts on northern California coastal Chinook are a primary management concern for commercial ocean fisheries from Pigeon Point, California, to Florence, Oregon, and for recreational fisheries in the KMZ. These regulations were expected to result in a 51%–49% California-Oregon sharing of Klamath River fall Chinook ocean troll harvest.

Commercial fishing opportunity in the Fort Bragg area (Horse Mountain to Point Arena) was increased, due to a moderate abundance of Klamath River fall Chinook and an increase in the exploitation rate on OCN coho over that permitted in 2002. In addition, recreational fishing opportunity was expanded in the KMZ and Fort Bragg areas.

For more complete information, see the PFMC's website, www.pcouncil.org, where you will find "Review of the 2003 Ocean Salmon Fisheries," compiled by the Salmon Technical Team and PFMC staff.

TUNA, INCLUDING ALBACORE

North Pacific albacore (*Thunnus alalunga*), eastern Pacific yellowfin tuna (*Thunnus albacares*), northern bluefin tuna (*Thunnus orientalis*), skipjack tuna (*Katsuwonus pelamis*), and bigeye tuna (*Thunnus obesus*) are managed under the PFMC's HMSFMP. The plan was first adopted in June 2003 and approved by NOAA Fisheries in March 2004.

There are several west coast commercial fisheries regulated by the HMSFMP that annually land tunas in California. The surface hook-and-line fishery, which accounts for almost all albacore landings on the west coast, consists mainly of trollers using trolling jigs or live bait. There is a small-mesh drift gill net fishery that incidentally lands and occasionally targets albacore, bluefin, yellowfin, and skipjack tunas. California prohibits pelagic longline gear inside of 200 mi, but longliners can fish outside of 200 mi and land their fish in California ports. California also has small coastal purse seiners (< 400 short tons, or 363 t carrying capacity) that primarily harvest coastal pelagic species. They also fish for northern bluefin and other tunas when these species enter west coast waters during May through October.

The recreational fisheries for tunas consist of commercial passenger fishing vessels (CPFVs) and private vessels using hook-and-line gear. Around 200 CPFVs annually provide recreational anglers with a platform to fish tuna. In southern California, there are an estimated 4,000–6,000 private boats fishing for tunas. Many of these boats fish in Mexican waters.

Under the HMSFMP, stock status is determined by estimating the abundance (biomass) of the stock throughout its range and comparing the estimate of abundance with the adopted acceptable level of abundance. Most stock assessments are conducted by the Inter-American Tropical Tuna Commission (IATTC), but the IATTC does not determine if a stock is overfished. Therefore, the criteria in the FMP will be used to determine stock status. West coast fisheries harvest a small fraction of the total catch taken by all nations in the North Pacific. The catch of all HMS by U.S. vessels based on the west coast, as a percentage of the total catch for the stock, ranges from less than 1% for bigeye tuna to about 16% for albacore. In most cases, effective conservation of tunas requires international action.

Albacore

Albacore is the leading species of tuna caught in both commercial and recreational fisheries in California. In 2003, both commercial and CPFV landings decreased. Commercial landings decreased by 34% from 2,602 t in 2002 to 1,710 t in 2003. Ex-vessel value decreased 31% from $3.76 million in 2002 to $2.59 million in 2003. The average price per ton paid to fishers for albacore increased 15% from $1,320 in 2002 to $1,516 in 2003. The decline in commercial harvest does not necessarily reflect a decline in the albacore population. Commercial landings for albacore have varied dramatically over the last decade, ranging from a high of 5,590 t in 1999 to a low of 818 t in 1995. These landings are still significantly lower than the peak decades of the 1950s and 1960s when commercial landings were routinely over 27,000 t. During the 1950s there were over 3,000 vessels in the commercial fleet; now there are fewer than 500. Also, during those early years the fleet used pole-and-line gear, trolling gear, longlines, purse seines, and drift gillnets. Since the 1980s trolling operations have dominated the fishery, taking 90% of the annual catch of albacore.

Beginning in the 1980s, the albacore fishery off California has typically operated within 900 mi of the U.S. Pacific coast. California commercial fishers concentrate on the North Pacific albacore stock during the summer and fall as the fish migrate through the northeastern Pacific Ocean. In recent years, during the winter months, some vessels have also targeted the western Pacific albacore stocks off the East Coast of New Zealand.

Preliminary landing figures derived from CPFV logbooks for 2003 indicate that the fleet landed 248,292 albacore, down 21% from the record high catch of 312,776 fish landed in 2002. In 2003, 172 CPFVs reported 3,687 trips in which at least one albacore was landed. A total of 62,536 anglers landed the 248,222 albacore, resulting in an increase in the catch-per-unit angler from 2.96 in 2002 to 3.97 in 2003.

In California there are no recreational size or bag limits on albacore, but California vessels fishing in Mexican waters must adhere to Mexican regulations. Mexican law permits the take of only 5 albacore, or any tuna, per day and no more than 10 fish per day of all species of tuna combined. According to CPFV logbooks, 78% of the 2003 catch of albacore was harvested from Mexican waters. Typically the majority of fish are landed in July and August when the bulk of the stock travels through the range of the southern California CPFV fleet. However, the arrival and departure times associated with albacore migration can vary from early spring arrivals to late winter departures.

Landing estimates of private boat anglers in California is provided by the Recreational Fisheries Information Network (RecFIN) through data collected by MRFSS. RecFIN offers a different view of recreational catches in that it only includes in its estimates fish taken in waters of the United States. In this case, private boat landings increased 79% (126,946 fish) from 2002 (70,897 fish). The average weight also increased 28% (10.19 kg) from 2002 (7.97 kg). RecFIN estimates that 1,181 t of albacore from U.S. waters were harvested by California private boaters in 2003. This is an 86% increase from 2002 (634 t).

Stock status of albacore is reviewed at 1–2-year intervals by the North Pacific Albacore Workshop (members: United States, Japan, Canada, and Taiwan). Presently, the stock is healthy and not being overfished. Stock and catches are increasing. No quotas are being contemplated, and no regional harvest guidelines are recommended.

Yellowfin Tuna

Commercial landings decreased by 15% from 544 t in 2002 to 465 t in 2003. Ex-vessel value decreased 24% from $588,676 in 2002 to $448,222 in 2003. The average price per metric ton paid to fishers for yellowfin dropped 11% from $1,082 in 2002 to $964 in 2003. Commercial landings of yellowfin tuna in California, while fluctuating, generally increased from 350,000 pounds in 1919 to 280 million pounds in 1976. Since 1976 yellowfin tuna landings declined steadily to 1 million pounds in 2003. The decline in commercial landings in California can be attributed to the relocation of cannery operations to American Samoa and Puerto Rico and the reflagging of U.S. vessels. Currently, there are no canneries operating in California. Purse seine and bait boat fisheries supply the bulk of the California commercial yellowfin tuna landings. Some commercial landings are also supplied by longline, troll, and gillnet fisheries. Almost all commercial landings of yellowfin are from waters south of the U.S. border.

In 2003, CPFVs logged 28,955 yellowfin, up 56% from the 18,594 fish caught in 2002. This increase was due to the availability of small yellowfin (< 40 in.) in coastal waters in the late summer and early fall. The catch was still significantly lower than the record high catch of 116,000 yellowfin landed in 1983. While CPFVs from San Pedro to San Diego recorded catches of yellowfin, 91% of the 2003 catch was harvested from Mexican waters. Currently, the majority of yellowfin landed by CPFVs are by the long-range boats operating out of San Diego. These boats specialize in multiday fishing excursions south of the U.S. border that land large yellowfin (> 40 in.) up to 140 kg.

RecFIN estimates private boats landed 6,774 yellowfin in 2003. The average weight was 5.18 kg. RecFIN has no estimates for 2002. Yellowfin may have been landed by private boaters in U.S. waters, but due to the random sampling protocol of MRFSS they may have been excluded.

The yellowfin stock appears to be below but near maximum sustainable yield (MSY), with fishing mortality higher than what is recommended by the FMP. The IATTC conducts stock assessments annually, and the recommended quota is usually between 250,000 and 300,000 t. In view of the small share (about 1%) of total eastern Pacific yellowfin catch made by west coast fishers, the productivity of the stock, and the apparent effectiveness of the IATTC management, no regional harvest guidelines are recommended.

Skipjack Tuna

Commercial landings increased by 48% from 236 t in 2002 to 349 t in 2003. Ex-vessel value also increased 25% from $128,245 in 2002 to $159,886 in 2003. The average price per metric ton paid to fishers for skipjack dropped 16% from $543 in 2002 to $458 in 2003. Commercial landings of skipjack tuna in California, while fluctuating, increased from 3 million pounds in 1918 to 174 million pounds in 1980. Since 1976, skipjack tuna landings have decreased steadily to the low of 125,000 pounds in 2001. The decline in commercial landings in California can be attributed to the relocation of cannery operations to American Samoa and Puerto Rico and the reflagging of U.S. vessels. Currently, there are no canneries operating in California. Purse seine and bait boat fisheries supply the bulk of the California commercial skipjack tuna landings. Some commercial landings are also supplied by longline, troll, and gillnet fisheries. Almost all commercial landings of skipjack are from waters south of the U.S. border.

In 2003 CPFVs had a substantial increase in landings of 968% (31,675 fish) over 2002 (2,967 fish). This increase was due to an abundance of skipjack schooling in coastal waters during the late summer and early fall. Skipjack were frequently caught by boats targeting albacore. In 2003, 68% of the skipjack landed by CPFVs was harvested in Mexican waters.

RecFIN estimates private boats landed 12,366 skipjack tuna in 2003. The average weight was 3.4 kg. RecFIN has no estimates for 2002. Skipjack may have been landed by private boaters in U.S. waters, but due to the nature of the random sampling protocols of MRFSS, skipjack may have been excluded.

The skipjack tuna stock of the eastern Pacific is assessed annually by the IATTC and appears to be very productive. No upper limit to the catch is evident, and no MSY has been established. In view of the small share (about 3%) of total catch made by west coast fishers, the productivity of the stock, and the apparent effectiveness of the IATTC management, no regional harvest guidelines are recommended.

Bluefin Tuna

Commercial landings increased dramatically by 272% from 9.6 t in 2002 to 35.7 t in 2003. Ex-vessel value also increased 131% from $31,937 in 2002 to $73,768 in 2003. The average price per metric ton paid to fishers for bluefin dropped 38% from $3,327 in 2002 to $2,066 in 2003. Commercial bluefin tuna landings in California peaked in the 1960s at nearly 40 million pounds. Bluefin are mostly taken by small purse seiners that primarily target coastal pelagic species. Small amounts of bluefin are caught off the California coast by drift gillnets and further offshore by longline vessels.

CPFV logbooks for 2003 showed the fleet landed 22,212 bluefin tuna, down 33% from 33,316 fish landed in 2002. In 2003 87% of the bluefin landed by CPFVs was harvested in Mexican waters. RecFIN has no estimates of bluefin catch for 2003. We are aware that private boaters in U.S. waters landed bluefin, but due to the nature of the random sampling protocols of MRFSS, they were not sampled. The RecFIN high estimate for private boaters was 1,605 bluefin in 1998.

The IATTC reviews the status of the northern bluefin tuna stock occasionally. Evidence of overfishing or persisting decline in the stock is lacking. West coast fishers account for about 10% of the total catch of the stock, harvesting mainly juveniles that migrate irregularly to the eastern Pacific. In view of the limited impact west coast fisheries have on the spawning stock and the lack of international agreement on the need to control fishing mortality, no regional harvest guidelines are recommended.

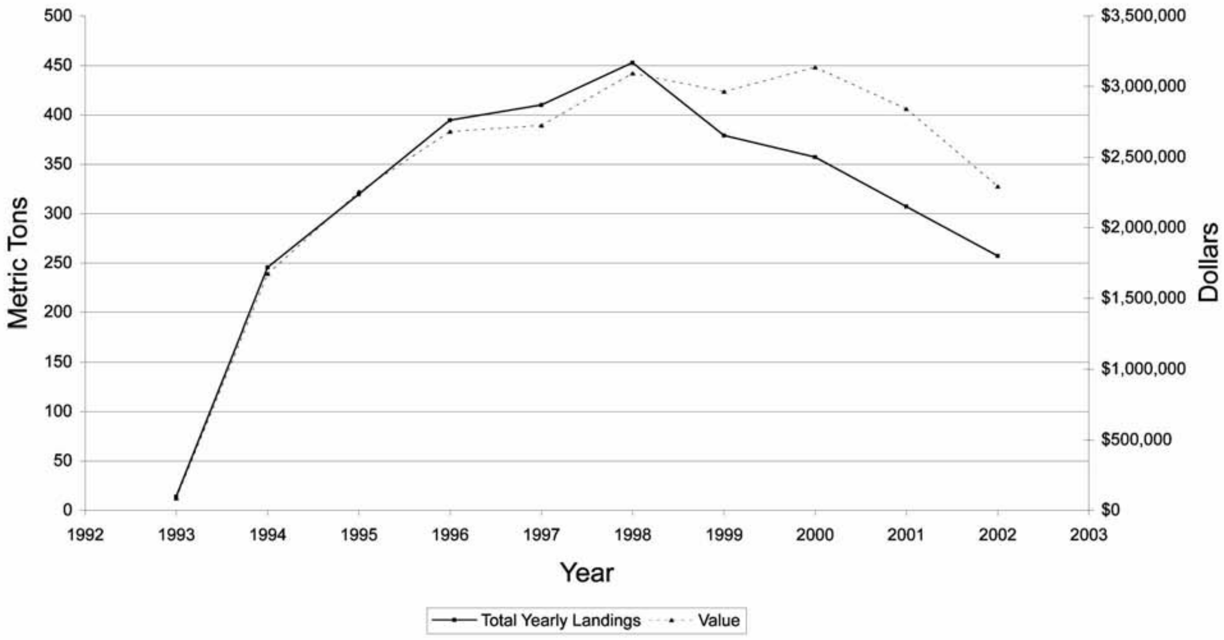


Figure 9. California nearshore live-fish landings and ex-vessel value, 1993–2002.

Bigeye Tuna

Commercial landings increased dramatically by 263% (34.1 t) from 2002 (9.4 t), and ex-vessel value also increased 200% ($262,765) from 2002 ($87,303). The average price per metric ton paid to fishers for bigeye dropped 17% from $9,287 in 2002 to $7,728 in 2003. Almost all the fish come from the offshore longline fishery.

In 2003, CPFVs landed 60 bigeye tuna, all from Mexican waters. RecFIN has no estimates of bigeye tuna catch for 2003. We are aware private boaters in U.S. waters may have landed bigeye, but due to the random sampling protocol of MRFSS they may have been excluded. The RecFIN high estimate for private boaters was 2,517 bigeye in 1982.

Bigeye tuna stocks appear to be at a level below MSY. The IATTC assesses the status of bigeye annually and has adopted both quotas and restrictions on floating object sets to control the catch of juvenile bigeye. In view of the small share (< 1%) of total bigeye catch made by west coast fishers, the productivity of the stock, and the apparent effectiveness of the IATTC management, no regional harvest guidelines are recommended.

NEARSHORE LIVE-FISH

Preliminary summaries of 2003 data indicated that commercial landings of California nearshore finfish totaled 231 t. Of that, 203 t were recorded as live landings and 28 t as dead landings. Preliminary ex-vessel value of total landings for 2003 was $2.0 million, of which $1.9 million was paid for live fish (fig. 9). Compared to 2002, this represents a 34% decrease in total nearshore landings and a 26% decrease in value.

Management of the Fishery

The nearshore fishery, as defined in the California Code of Regulations (Title 14, Section 1.9), includes a select group of finfish: cabezon (*Scorpaenichthys marmoratus*), California scorpionfish (*Scorpaena guttata*), California sheephead (*Semicossyphus pulcher*), kelp and rock greenlings (*Hexagrammos decagrammus* and *H. lagocephalus*), monkeyface eel (*Cebidichthys violaceus*), and the following rockfishes (*Sebastes* spp.): black (*S. melanops*), black-and-yellow (*S. chrysomelas*), blue (*S. mystinus*), brown (*S. auriculatus*), calico (*S. dallii*), China (*S. nebulosus*), copper (*S. caurinus*), gopher (*S. carnatus*), grass (*S. rastrelliger*), kelp (*S. atrovirens*), olive (*S. serranoides*), quillback (*S. maliger*), and treefish (*S. serriceps*). All except California sheephead, monkeyface prickleback, and rock greenling are designated as groundfish species under the PFMC's fishery management plan for Pacific coast groundfish. These 19 species represent the species most commonly captured in the nearshore live-fish fishery. They are primarily found in association with kelp beds or rocky reefs in waters less than 20 fathoms. They are territorial, slow-growing, and long-lived, which makes them vulnerable to overfishing even at low exploitation rates. This review focuses on the nearshore finfish species most commonly captured and sold live.

The Nearshore Fishery Management Plan (NFMP), adopted in 2002, is a framework plan that identifies a management strategy for many of the nearshore species targeted by the nearshore live-fish fishery. The five integrated management measures (fishery control rule, regional management, resource allocation, marine protected areas, and restricted access) together, over time, will meet the goals and objectives of the Marine Life Management Act (MLMA) and provide for sustainable nearshore stocks and fisheries.

History and Fishery Operations

The nearshore live-fish fishery began in the mid-1980s. Initially, the fishery supplied live fish for the California Asian community. The live-fish market has since expanded and now supplies markets nationally and, in some cases, internationally. Before the market for live fish developed, the wholesale value (ex-vessel value) for rockfishes, cabezon, California sheephead, and greenlings was low. An increase in consumer demand for premium live fish caused the value of the fishery to increase dramatically. For example, the average ex-vessel value of cabezon (landed dead) was less than $0.50 per pound in 1989. In 2003, the average price for live cabezon was $4.81 per pound (up from $4.02 in 2002). At any time, however, prices vary widely depending on port region, species, size, and marketability of fish. In 2003, ex-vessel prices for live landings of the 19 nearshore species ranged from $0.25 to $10.50 per pound.

Primary gear types used to capture nearshore fish include various hook-and-line methods and trap gear. Hook-and-line gear includes rod-and-reel, vertical longlines, horizontal longlines, and weighted "stick gear." Vessels using hook-and-line gear are limited to 150 hooks per vessel and 15 hooks per line. Vessels using fish traps along the mainland shore are limited to 50 traps per day. Most of the hook-and-line and trap vessels range from 20 to 40 ft in length and are capable of operating in shallow water close to shore. The fishery is generally short-range, taking day trips to deliver live fish to market or to dockside holding bins.

Nearshore Landings Information

Landing receipts, commonly called market or dealer receipts, are the primary CDFG information source for quantifying commercial fishing activity. By law, a fish buyer must complete a landing receipt at the time fish are delivered. Basic information such as species or market category, weight of the landing, price per pound, gear type, and condition (e.g., live) must be provided. Considerable effort is spent reviewing and editing landing receipts to ensure that critical information, such as market category and condition code, is accurately reported. When condition information is ambiguous, it can often be determined by examining the ex-vessel price: a substantially higher price usually indicates a live landing.

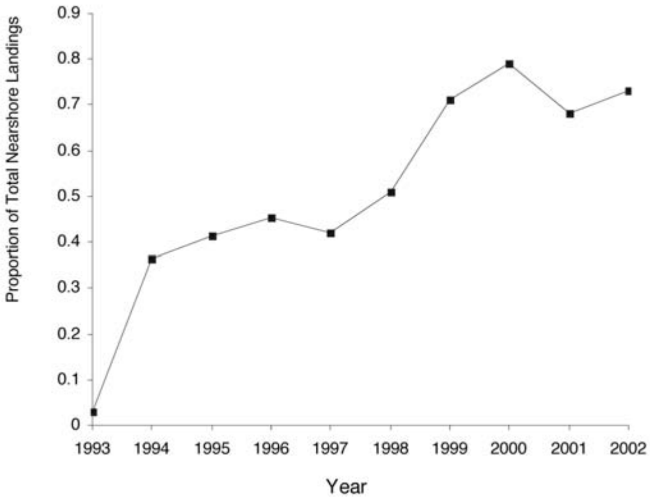


Figure 10. Proportion of fish landed live in the nearshore fishery, 1993–2002.

Landings information reported by market category provides very little information on the species composition of the catch. In recent years, regulations mandating dealers to record landing weights by species for the 19 nearshore finfishes has reduced the use of group market categories. Nevertheless, market categories on which this review is based likely contain several different species similar in appearance or market value. For example, the "group gopher" market category often includes gopher, brown, black-and-yellow, grass, kelp, copper, China, and quillback rockfishes. Information on the species composition of market categories provided by port sampling was not available for inclusion in this review.

Data used for this report are preliminary and live-fish landing weights provided in this review should be interpreted as low estimates of the actual live-fish landings in 2003. It should also be noted that condition (live or dead) of fish landed was not required on landing receipts until 1993; therefore, years prior were not considered in this review.

Statewide, 87% of nearshore fish were landed live in 2003 (fig. 10). This is the highest proportion of live nearshore catch recorded and is a reflection of the much higher value placed on the "live" condition.

Regional Landing

Prices and dominant landings varied by management region, ports within a region, and season. North Coast Region (Oregon border to Cape Mendocino; port complexes of Crescent City and Eureka) landings totaled 66 t, or 29% of nearshore fish landings statewide, with a preliminary ex-vessel value of $0.33 million. Of the total, 51 t were landed live and 15 t were landed dead. Approximately 25% of the state's live fish were landed in the North Coast Region for a value of $0.29 million.

Live landings were dominated by the black rockfish market category (42 t) followed by cabezon (2 t). These two categories accounted for 86% of the North Coast Region's landings of live fish. Hook-and-line gear was used for 100% of the live landings in the North Coast Region. There were no recorded landings of nearshore species made with trap gear.

North-Central Coast Region (Cape Mendocino to Point Año Nuevo; port complexes of Fort Bragg, Bodega Bay, and San Francisco) landings totaled 23 t or 10% of nearshore fish landings statewide, with an ex-vessel value of $0.21 million. Nineteen tons were landed live and 4 t were landed dead. Approximately 9% of the state's live fish were landed in the North-Central Coast Region for a value of $0.19 million. The largest market category landed was cabezon (6 t), followed by gopher (2 t), black-and-yellow (2 t), and black rockfish (approx. 2 t). These four market categories accounted for 64% of the North-Central Coast Region's landings of live fish. Hook-and-line gear accounted for approximately 75% of live landings, and traps for 25%. Finfish traps are not allowed in all areas of the North-Central Coast Region.

South-Central Coast Region (Point Año Nuevo to Point Conception; port complexes of Monterey and Morro Bay) landings totaled 78 t or 34% of nearshore fish landings statewide with an ex-vessel value of $0.88 million. Seventy-two tons were landed live and 6 t were landed dead. Approximately 36% of the state's live fish were landed in this region for a value of $0.86 million. Live landings were dominated by cabezon, brown, gopher, and grass rockfish market categories (62 t), accounting for 85% of the South-Central Coast Region's landings of live fish. Hook-and-line gear accounted for approximately 75% of live landings, and traps for 25% in the South-Central Coast Region.

South Coast Region (Point Conception to México border; port complexes of Santa Barbara, Los Angeles, and San Diego) landings totaled 64 t or 28% of nearshore fish landings statewide with an ex-vessel value of $0.57 million. Sixty-one tons were landed live and 3 t were landed dead. About 30% of the state's live fish were landed in the South Coast Region for a value of $0.56 million. In 2003, live landings were predominantly California sheephead (47 t), followed by cabezon (approx. 6 t), and California scorpionfish (4 t). All together, these categories accounted for 92% of the South Coast Region's landings of live fish. Trap gear was used to catch 63% of the live fish in the South Coast Region, and hook-and-line caught 30%; trawl gear (primarily for California scorpionfish) was also used.

Recent Trends in the Fishery

Preliminary data for 2003 showed a decline in landings for the fifth straight year, from a peak in 1998 (947 t landed). The 2003 total value of the fishery declined in proportion to landings (fig. 9), reflecting stable demand. The decline in landings can be attributed to management measures consistent with the Nearshore Fishery Management Plan. Current nearshore interim regulations (implemented in 2000) established an "allowable catch" of nearshore species equal to 50% of historical annual harvest levels. In addition, the Limited Entry/Restricted Access program reduced the number of permittees from a high of 1,127 in permit year 1999–2000, to 525 in 2002–2003, then to 207 in 2003–2004. (A permit year runs from 1 April through 31 March of the following year.) Size limits for certain nearshore species, a 2-month fishery closure, and gear restrictions were also used to achieve catch limitations set under interim regulations and to conform state regulations to the PFMC regulations for fishing in state waters.

CDFG and the Commission continue to develop regional total allowable catch limits (TACs), recreational and commercial sector allocation parameters, and cumulative trip limits. The initial phase of this work is being focused on cabezon, kelp and rock greenlings, and California sheephead.

PACIFIC HERRING

California's Pacific herring fisheries suffered a decline in landings in 2003. Statewide landings for the 2002–2003 sac roe season (December–March) totaled 1,975 t, a decline of 40.9% from last season's landings of 3,339 t. The San Francisco gill net fleet, composed of three platoons (332 permits fished, a decline of 17% from the 2001–2002 season) landed 1,902 t, 41% under the 3,211 t quota. The Tomales Bay fishery landed a total of 71 t, 15.6% of the 454 t quota. No permittees fished in Crescent City, which had a 27.2 t quota. Humboldt Bay landings totaled 1.8 t, 97% below the 54.4 t quota. Annual sac roe landings, January to December, fell from 3,290 t to 1,943.t, down 40.9% from the previous year (tab. 1).

Ex-vessel prices for herring with 10% roe recovery averaged an estimated $500 per short ton for gill net landings, with an additional $50 paid for each percentage point above 10%. The ex-vessel price per ton was lower than the previous season, reflecting continuing volatility of the Japanese economy. State wide ex-vessel value of the sac roe fishery was an estimated $1.6 million, an 11% decrease from last season and well below the average for the previous 17 seasons ($8.6 million).

The only bright spot in this otherwise disappointing season for California's herring fishery was the San Francisco Bay herring eggs-on-kelp fishery. Landings totaled 48.4 t, a 18% increase from last season's landings of 41.1 t, and 8% less than the 52.3 t quota. Total estimated value of the 2002–2003 eggs-on-kelp harvest was $745,934 based on an average ex-vessel price of $7.00 per pound. Price paid varies with product grade, with grade 1 receiving approximately $10 per pound, and grade 5 bringing $3–4 per pound.

Hydroacoustic and spawn deposition surveys were conducted by CDFG to estimate herring spawning biomass in San Francisco Bay. Spawn deposition estimates were used exclusively to assess the Tomales Bay and Humboldt Bay populations. Historically, the spawn deposition survey was used to set quotas from 1973 through 1989 for the San Francisco Bay fishery. From 1990 through 2003, the spawning biomass estimate was derived by integrating results of the spawn deposition survey and the hydroacoustic survey on a spawning-wave-by-spawning-wave basis. Over time, the two survey estimates have been diverging, and in recent years the population trends have differed. In 2003, results of the two surveys could not be resolved. Hydroacoustic survey results indicated the presence of large schools, while the spawn surveys did not find corroborating amounts of spawn. Concern regarding the status of the stock and survey results led to the establishment of an independent peer review panel to evaluate the use of a stock assessment model for the San Francisco Bay herring population as well as to evaluate the assessment surveys.

One of the panel's findings was that the method of combining the two surveys, often involving using the higher of the two estimates, has contributed to overexploitation by overestimating spawning biomass. The panel recommended continuing the spawn deposition survey annually as the primary index of abundance and as the spawning biomass estimate for use in setting the fishery quota. The panel also recommended continuing the hydroacoustic survey to support the location and timing of the spawn deposition survey, to better understand prespawning behavior of herring and to collect information on the age structure of the spawning population in San Francisco Bay. In addition to those recommendations, the peer review panel found that the San Francisco Bay herring population is presently at or near the lowest abundance observed since the 1970s and recommended that a rebuilding policy be implemented.

The moderate 2002 El Niño appeared to manifest its effects on San Francisco Bay herring. Weights of older fish, age 4 and above, were 5–10% lower than long-term averages, whereas 2- and 3-year-olds appeared to be 3% longer and heavier.

The Tomales Bay herring spawning biomass continued to demonstrate a tendency to fluctuate widely. The 2002-2003 spawning biomass estimate was 3,905 t, representing a 41% decline from the previous season's estimate (6,570 t). However, this season's biomass is the second highest since the 10,014 t El Niño season of 1982–83. For the third consecutive season, CDFG conducted spawning-ground surveys and monitoring of the herring gill net fishery in Humboldt Bay. An estimated 151 t of herring spawned in south and north Humboldt Bay. This is a decline of 73% from the previous season's estimate of 560 t. No surveys were conducted in Crescent City Harbor.

Neutral ocean conditions were forecast into the fall prior to the 2003–2004 season. The December fishery in San Francisco Bay opened to a slow start once again with limited fishing activity through mid-month. Kazunoko remains an integral part of traditional Japanese New Year's festivities. However, changes in Japanese culture and economy have also resulted in changes in the sac roe market. Demand for kazunoko is forecasted to wane by industry observers as younger Japanese become more westernized. Ex-vessel prices are expected to decline with concern for the Japanese economy, and herring buyers were offering similar prices to the those of the 2002–2003 season.

ROCK CRAB

Three species of crab are landed in the California commercial rock crab fishery: yellow rock crab (*Cancer anthonyi*), brown rock crab (*C. antennarius*), and red rock crab (*C. productus*). Rock crabs are fished along the entire coast of California, although the fishery is most active in southern California (from Morro Bay south), where 85–90% of the landings occur. The preliminary estimate of rock crab landings in 2003 is 412 t, a 26% decrease from 2002 (554 t) (fig. 11). This ends a 3-year trend of increasing landings that began in 1999, which had the lowest landings seen in the fishery in 28 years. Preliminary ex-vessel revenues for 2003 were $1.2 million, a 26% decrease in value from 2002 ($1.5 million). The average price per pound for rock crab has remained relatively stable in the last 5 years, ranging from $1.27 to $1.29/lb, with the average price since 1999 at $1.28.

Tracking historic landings of rock crab is complicated by the past use of generic CDFG market codes that lumped all crab landed in California, including Dungeness, into one category. All crab landed in the Monterey, San Francisco, and Eureka regions were assumed to be Dungeness crab, with all crab landed south of Monterey assumed to be rock crab. This practice was abandoned in 1950 when a separate market category was created for rock crab, which included red, brown, and yellow rock crabs. From 1950 to 1985, landings also include any rock crab claws that were landed separately. The crab claws were converted to whole crab weight using a 1:4 ratio (1 lb of crab claws equaled 4 lb of whole crab). In 1986 a new market category was created for crab claws; however, this category contains claw weight from both sheep crab and rock crab and is not included in more recent rock crab landing tables. In 1991 it became illegal

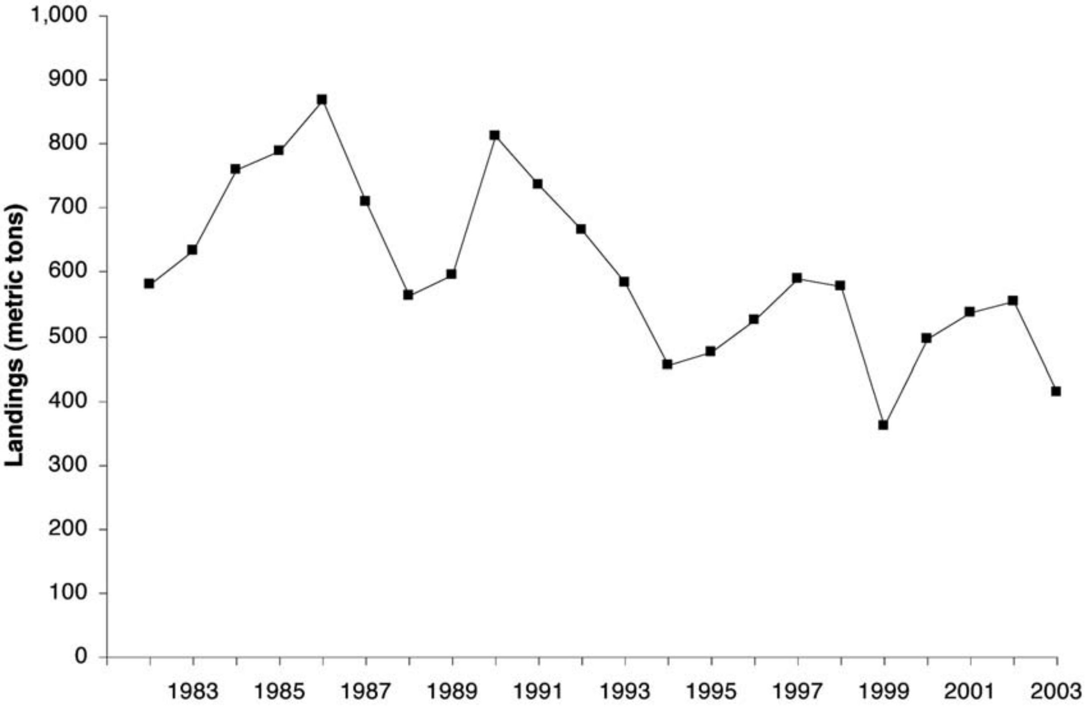


Figure 11. California commercial rock crab landings, 1982–2003.

to take rock crab claws, and the crab claw category became exclusively for sheep crab claws. Three additional, species-specific, market categories were created in 1994 for red, yellow, and brown rock crab. Landings for 1994–2003 are the sum of the combined rock crab market category and the three additional categories. Commercial rock crab landings in California appear to have steadily declined since the 1980s. However, due to the inconsistent methods of recording commercial landings in past years, it is difficult to determine if this is stock or sampling related. Individual rock crab species harvests are almost entirely recorded by fishers and processors in the general "rock crab" category instead of the species-specific categories. Efforts to assess the overall health of this fishery would be greatly enhanced by requiring fishers and processors to record the specific rock crab species being landed.

The majority of rock crabs commercially landed in California are captured by traps, with a small percentage caught as bycatch by vessels using trawl gear. It is unlawful to take or possess more than 500 lb of crabs on any boat on which any type of trawl or drag net is carried or operated. Commercial laws and regulations protect crabs that are below reproductive size. The law presently requires a minimum harvest size of 4.25 in. carapace width (widest part of the body shell), and each trap must include escape rings that measure 3.25 in. across. The minimum harvest size and escape ring size were chosen to accommodate the different characteristics of the three rock crab species. Growth studies conducted on yellow and brown rock crabs have shown that both species molt 10–12 times before reaching sexual maturity at about 3 in. carapace width.

A state law enacted in 2002 authorized the Commission to adopt regulations to manage the rock crab resource in a manner consistent with the MLMA. CDFG has proposed regulatory action that would create a northern and southern regional rock crab trap permit requirement beginning 1 April 2005, with the north/south boundary located at Lopez Point (latitude 36°N), Monterey County.

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THE STATE OF THE CALIFORNIA CURRENT, 2003–2004: A RARE "NORMAL" YEAR

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ABSTRACT

This report describes the state of the California Current System (CCS)—meteorological, physical, chemical, and biological—from January 2003 to the spring of 2004. The area covered in this report ranges from Oregon coastal waters to southern Baja California. Over the past year, most physical, chemical, and biological parameters were close to their climatological mean. Contributing to such "normal" conditions was the absence of a La Niña that had been expected after the previous year's El Niño. Noteworthy, however, are the cold and fresh anomalies in the upper 100–200 m that have been found over large areas of the CCS since 2002. Off Oregon these may have been responsible for increased productivity; off southern California these were associated with shallower nutriclines and subsurface chlorophyll maxima in the offshore areas. It is unclear if these anomalies are ephemeral or related to long-term changes in ocean climate. The effects of the hypothesized 1998 "regime shift" on the CCS are still difficult to discern, primarily because of other physical forcing varying on different time scales (e.g., El Niño/Southern Oscillation, ENSO, cycles; the "subarctic influence"; global warming). The resolution of many of these issues requires larger scale observations than are available now. Establishment of the Pacific Coast Ocean Observing System (PaCOOS) under the guidance of NOAA will be a crucial step toward achieving that goal.

INTRODUCTION

This is the eleventh in a series of annual reports summarizing the climatology, oceanography, and biology of the California Current System (CCS) between the springs of 2003 and 2004. This report is based on observations taken from Oregon to Baja California. The programs or institutions contributing to this report were the U.S. Global Ocean Ecosystem Dynamics Long-Term Observation Program (GLOBEC LTOP) working off Oregon, the Pacific Fisheries Environmental Laboratory (PFEL) providing basinwide and coastwide climatologies, the Point Reyes Bird Observatory (PRBO) working off central and southern California, the CalCOFI program working off southern California, and the Investigaciones Mexicanas de la Corriente de California program (IMECOCAL) working off Baja California.

Last year's "State of the California Current Report" (Venrick et al. 2003) described the development and demise of a minor El Niño event that peaked in the winter of 2002–2003. This event had only a small effect on the California Current. For example, off southern California phytoplankton biomass, primary production, and zooplankton displacement volumes were only slightly below their climatological averages (Venrick et al. 2003). A significant influence from the north during 2002–2003 was the intrusion of subarctic water into the CCS. These cold water and freshwater anomalies were evident all along the west coast of North America, from Vancouver

Island to San Diego. They were likely due to an intensification of the California Current flowing south and a weakening of the Davidson Current flowing north into the Gulf of Alaska (Freeland et al. 2003). Off Oregon, Wheeler et al. (2003) observed that higher nutrient concentrations, carried along by these "minty" water masses, stimulated primary production and increased standing stocks of phytoplankton biomass. Off southern California, few if any such patterns were observed, a likely effect of the El Niño (Bograd and Lynn 2003).

From 1999 until 2002, the CCS was dominated by cold sea-surface temperature (SST) anomalies, as reflected in negative values of the Pacific Decadal Oscillation index (PDO) (Mantua et al. 1997), which had been positive from the mid-1970s until 1998, the most recent warm period. During the recent cold period, dramatic changes in zooplankton community structure were observed in the California Current (Lavaniegos and Ohman 2003; Brinton and Townsend 2003; Peterson and Schwing 2003), suggesting that the CCS ecosystem had undergone a regime shift. However, it is questionable that this shift can be attributed to a phase shift of the PDO. Bond et al. (2003) have identified a new SST spatial pattern, now called the Victoria mode, that has replaced the dominance of the PDO since 1998 and contributed to the unusually cool state of the CCS during the recent cold period.

The expectations for the current year were the advent of a La Niña in the tropical Pacific, its manifestation in the CCS, and the return of the PDO to negative values. Instead, the last year was characterized by climatologically "normal" conditions on both basin and CCS scales, a rather unusual state since most climatological indexes have bimodal distributions. The one exception to "normality" is the continuation of cold and fresh anomalies associated with the CCS. This report describes the response of the CCS and its ecosystem to the larger scale physical forcing. We will use simple indicators of ecosystem state, such as concentrations of chlorophyll *a*, rates of primary production, and zooplankton displacement volume. Observations of avifauna community structure and production will be used as well; these integrate responses of the biological system to changing physical forcing (Veit et al. 1996; Hyrenbach and Veit 2003). It is hoped that this report will contribute to an understanding of the balance of forces responsible for the current state of the CCS.

DATA SETS AND METHODS

Large-scale anomalies for the North Pacific Ocean are summarized from the National Center for Environmental Prediction reanalysis fields (Kistler et al. 2001) from the NOAA-CIRES climate Diagnostics Center (http://www.cdc.noaa.gov/). The reanalysis fields are monthly gridded (approximately 2° x 2°) anomalies of SST and surface winds. The base period is 1968–96. Monthly upwelling indexes and their anomalies for the North American west coast (21–52°N) are calculated relative to 1948–67. The daily along-shore wind component and SST are from the NOAA National Data Buoy Center (NDBC). Values from six representative buoys from the CCS are plotted against the harmonic mean of each buoy.

The GLOBEC Long-Term Observation Program (LTOP) made interdisciplinary observations off Oregon five times a year along the Newport Hydrographic (NH) line at 44.65°N, and three times a year along a set of four or five zonal sections between 42°N and 45°N; limited sampling of the NH line is continuing on an opportunistic basis. The NH line had been occupied regularly from 1961 to 1971, and long-term seasonal averages have been calculated from these historical data (Smith et al. 2001). The LTOP sampling along the NH line extends offshore to NH-85, 157 km from shore.

Hydrography, nutrients, chlorophyll, and zooplankton are measured along the inner portions of the NH line biweekly in the spring, summer, and fall, and monthly in winter. This program began in 1996 and is supported by U.S. GLOBEC. Stations are 1, 3, 5, 10, and 15 nautical miles from shore, with depths ranging from 20 m to 95 m. Since 2001, sampling has been extended to 25 mi from shore (300 m water depth). Zooplankton are sampled with a 0.5 m net (0.2 mm mesh) towed vertically from the sea floor to the surface. Zooplankton are enumerated by species and developmental stage, and biomass is calculated by multiplying species abundance by individual carbon weight, then summing across stages and species. Total biomass of all copepod species is reported here.

This report covers observations made by the CalCOFI program between the summer of 2003 and the spring of 2004. Surveys, based on a fixed sampling grid (fig. 1), are conducted off southern California quarterly. The water column is routinely profiled to a depth of 500 m using conductivity, temperature, pressure, oxygen, fluorescence, and light transmission sensors. Water samples are retrieved from 12 to 20 depths, and salinity, dissolved oxygen, nutrients, and chlorophyll are determined. Standard (.505 mm mesh) oblique bongo tows are conducted to 210 m depth at each station. Sampling and analytical protocols followed are presented in data reports (e.g., SIO 2000) and on the CalCOFI website (http://www.calcofi.org). A census of avifauna is carried out during the daylight hours along the CalCOFI cruise track by personnel from the PRBO. The PRBO also assessed the reproductive performance of seabird populations at the Farallon Islands.

For each CalCOFI cruise, the average value of a prop-

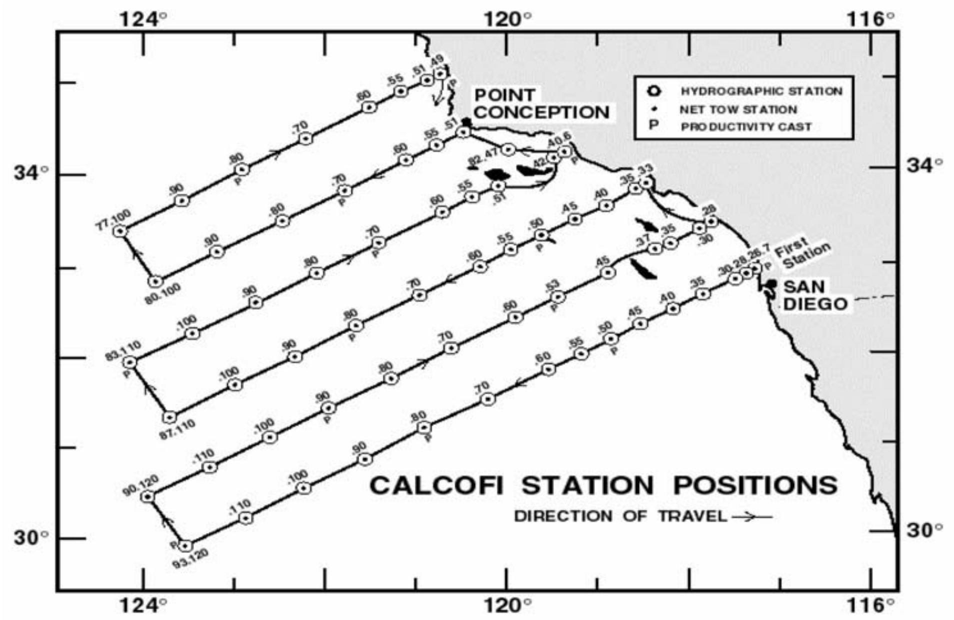

Figure 1. The standard CalCOFI station pattern. All 66 stations are occupied on most cruises. During the winter and spring cruises the pattern is extended north for observations of hydrographic properties and distributions of fish eggs.

erty was calculated, using data from all 66 standard CalCOFI stations (fig. 1); these are the CalCOFI region averages. A harmonic was fitted to the seasonal data from the last 20 years. Residuals from the harmonic are the anomalies of the parameter. The mixed-layer depth was assumed to be half way between those two depths where the temperature gradient reached values higher than 0.02 degrees per meter. For this analysis, the upper 12 m were excluded from the analysis to avoid including the diurnal thermocline in the analysis—that is, the slight or at times even large temperature increase in the upper 2–5 m that results from heating during the day and is typically eroded at night. This procedure will introduce a positive bias in calculation of the mixed-layer depth but will not affect the interpretation of the patterns, since the bias is consistent. A temperature-based mixed-layer depth was used for the analysis, since the density data were not yet available for all cruises at the time of analysis.

The data presented for the California Current off Baja California (IMECOCAL) were collected from April 2003 to February 2004 aboard of RV *Francisco de Ulloa* (fig. 2). The principal data collected at each IMECOCAL station include a CTD/Rosette cast to 1,000 m bottom, depth permitting, with sensors for pressure, temperature, salinity, and dissolved oxygen. Water samples for chlorophyll analyses were collected from CTD casts, using 5 l Niskin bottles. Macrozooplankton was sampled with bongo net tows from 200 m to the surface. Sampling methods and analyses are presented in greater detail in IMECOCAL data reports and on the web site (http://imecocal.cicese.mx).

BASINWIDE PATTERNS

While environmental conditions rarely appear as the climatological "average," recent atmosphere and ocean fields for the North Pacific closely resemble their long-term temporal means. Typically, spatially distinct regions display large anomalies of one sign associated with the ongoing climate event (e.g., El Niño, La Niña, or other climate regimes). A rapid reversal to an alternating anomaly pattern generally occurs as a new climate event develops. The resulting distribution of values for a variable is bimodal rather than normal; thus, the value at any location is rarely observed near its mean. It is even rarer to observe the greater North Pacific region at a near-neutral state.

Following the 2002–2003 tropical El Niño, SSTs in the equatorial Pacific have been near-average up to the present (spring of 2004) (NOAA CPC Climate Diagnostics Bulletin, http://www.cpc.ncep.noaa.gov). The equatorial ocean thermocline since early 2003 has been deeper than normal in the western Pacific and shallower than normal in the eastern Pacific, a pattern typically associated with La Niña. However, the atmospheric forcing and the indexes that represent it have been dominated by month-to-month variability associated with the intraseasonal Madden-Julian Oscillation (MJO). The relative strength of the MJO over the past year is due in part to the lack of any significant interannual ENSO development.

The Multivariate ENSO Index (MEI) is an index of El Niño and La Niña events, based on six tropical Pacific variables (Wolter and Timlin 1998). It became positive

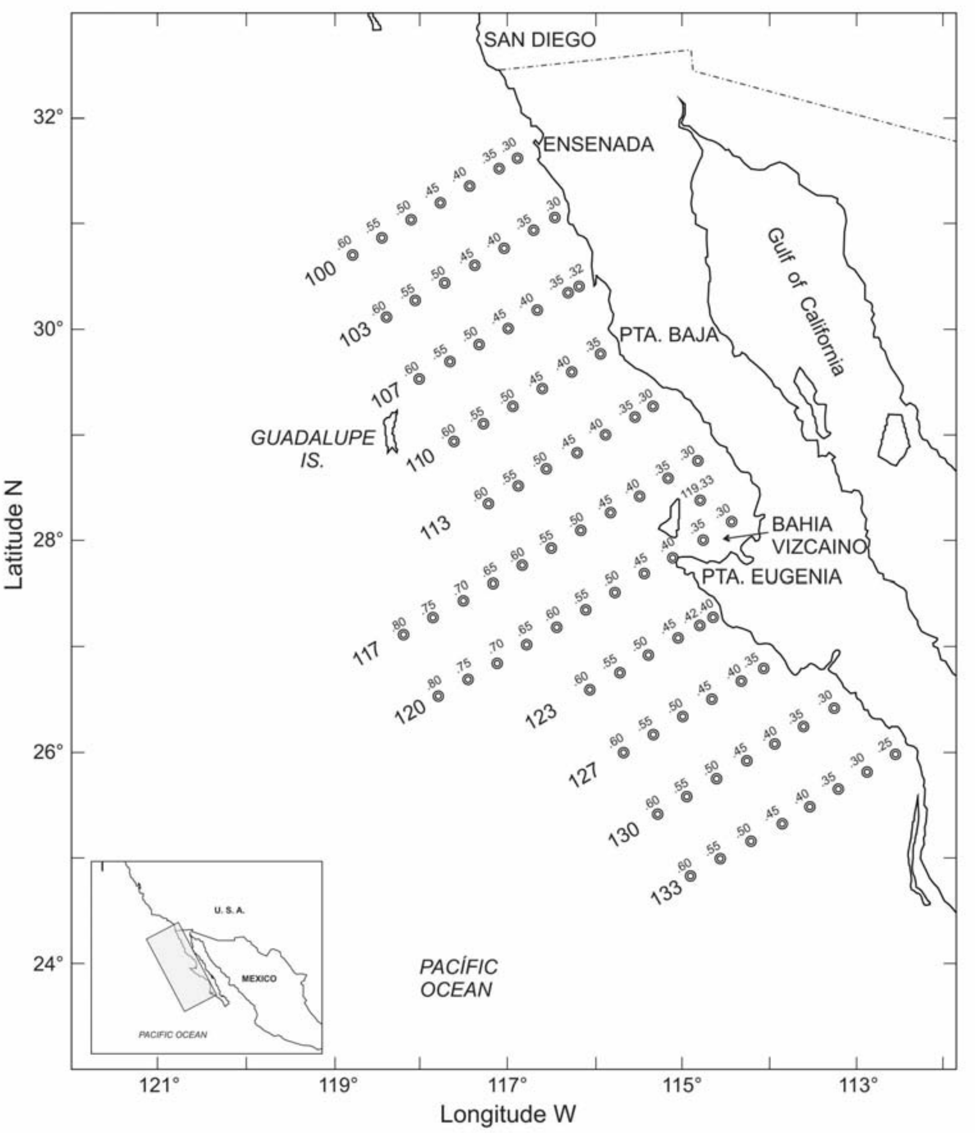

Figure 2. Standard IMECOCAL cruise pattern.

during the spring of 2002, indicating a weak-to-moderate El Niño, and has remained very slightly positive to the present. Enhanced intraseasonal variability has dominated the MEI during this time, and the spatial patterns of its individual components currently display a mixed signal with respect to ENSO. Current conditions in the tropical Pacific are similar to episodes during the late 1960s and late 1970s (http://www.cdc.noaa.gov/people/klaus.wolter/MEI/mei.html).

In the second half of 2002, a positive SST anomaly developed in the North Pacific, concurrent with the El Niño warming in the tropical Pacific. Overlaying this warm North Pacific feature was a region of unusual northward winds. By late 2002, cool anomalies along the west coast of the continental United States were replaced by northward wind anomalies and warm SSTs at the peak of the El Niño. This coastal warming lagged the development of positive SST anomalies in the greater Northeast Pacific by several months. These anomalies have weakened since early 2003, but remain generally warmer than normal.

Most recently (September 2003–April 2004), virtually the entire North Pacific has exhibited weakly warm anomalies. The PDO (Mantua and Hare 2002), which characterizes decadal-scale variability in the spatial patterns of North Pacific SST, defines a warmer than normal CCS during its positive phase (http://tao.atmos.washington.edu/pdo/). After a period of negative PDO values following the hypothesized "regime shift" in 1998, the PDO has been positive since August 2002 (20 consecutive months at present) but only weakly so since the 2002–2003 El Niño. As stated above, changes in the

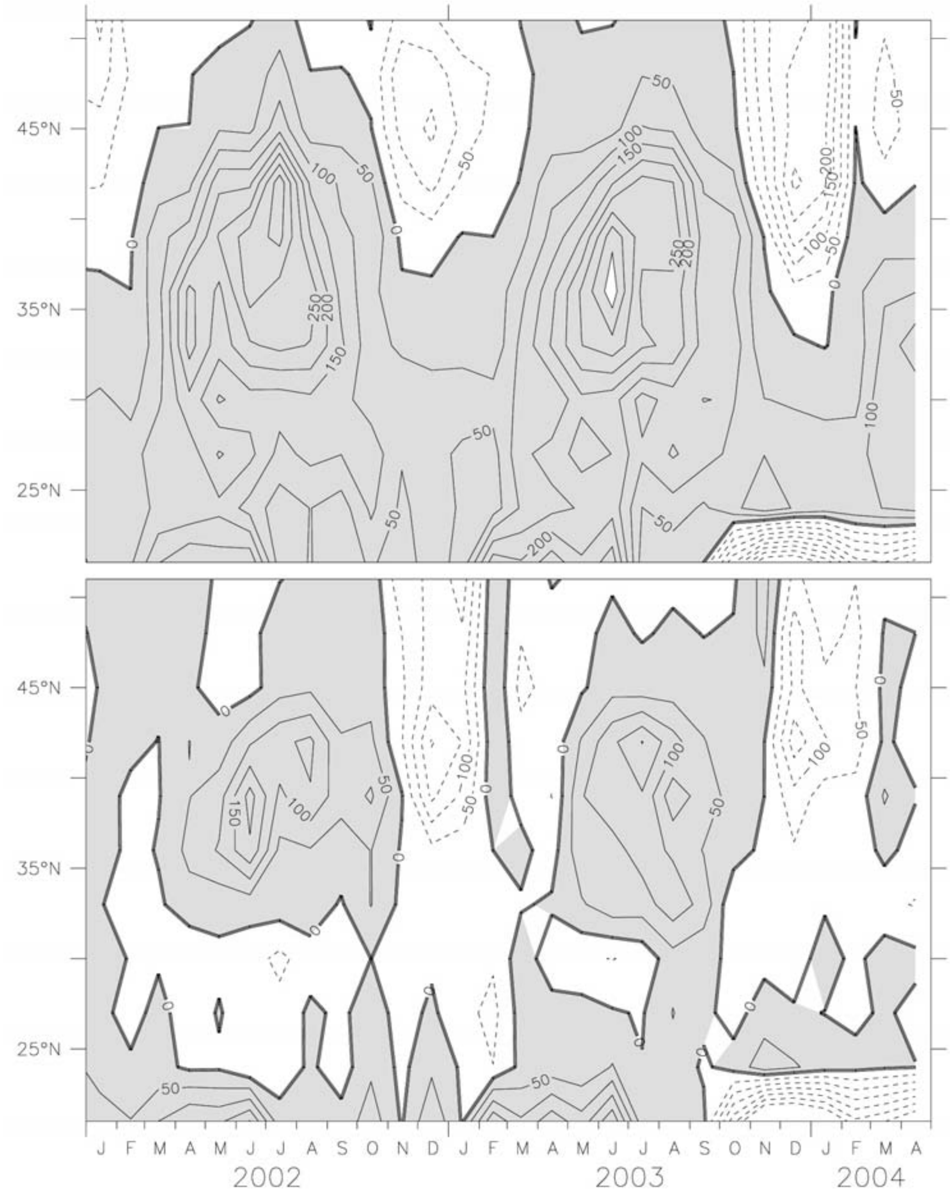

Figure 3. Monthly upwelling index (*upper panel*) and upwelling index anomaly (*lower panel*) for January 2002–April 2004. Shaded areas denote positive (upwelling-favorable) values in upper panel, and positive anomalies (generally greater than normal upwelling) in lower panel. Anomalies are relative to 1948–67 monthly means. Units are in m^3/s per 100 km of coastline.

PDO since 1998 may not represent a shift to a negative (cool) PDO phase but rather a shift into the Victoria mode (Bond et al. 2003). This may have contributed to the unusually cool state of the CCS during that period. To confound the issue further, the recent generally weak warm SST pattern over the greater North Pacific resembles neither the PDO nor the Victoria modes (J. Overland, pers. comm.).

Just as the ongoing tropical and North Pacific atmospheric and ocean conditions have been very close to the long-term mean, most models project ENSO-neutral conditions over the next several months. The models reflect great uncertainty beyond summer 2004. With the lack of any appreciable ENSO activity expected in the near future, the prospects for confirming the presence and continuation of the cool and biologically productive West Coast climate regime (Peterson and Schwing 2003) are good.

COASTWIDE CONDITIONS

Monthly coastal upwelling indexes (Bakun 1973; Schwing et al. 1996) have indicated generally stronger than normal summertime upwelling in the CCS since 1998 (Hayward et al. 1999; Bograd et al. 2000; Durazo

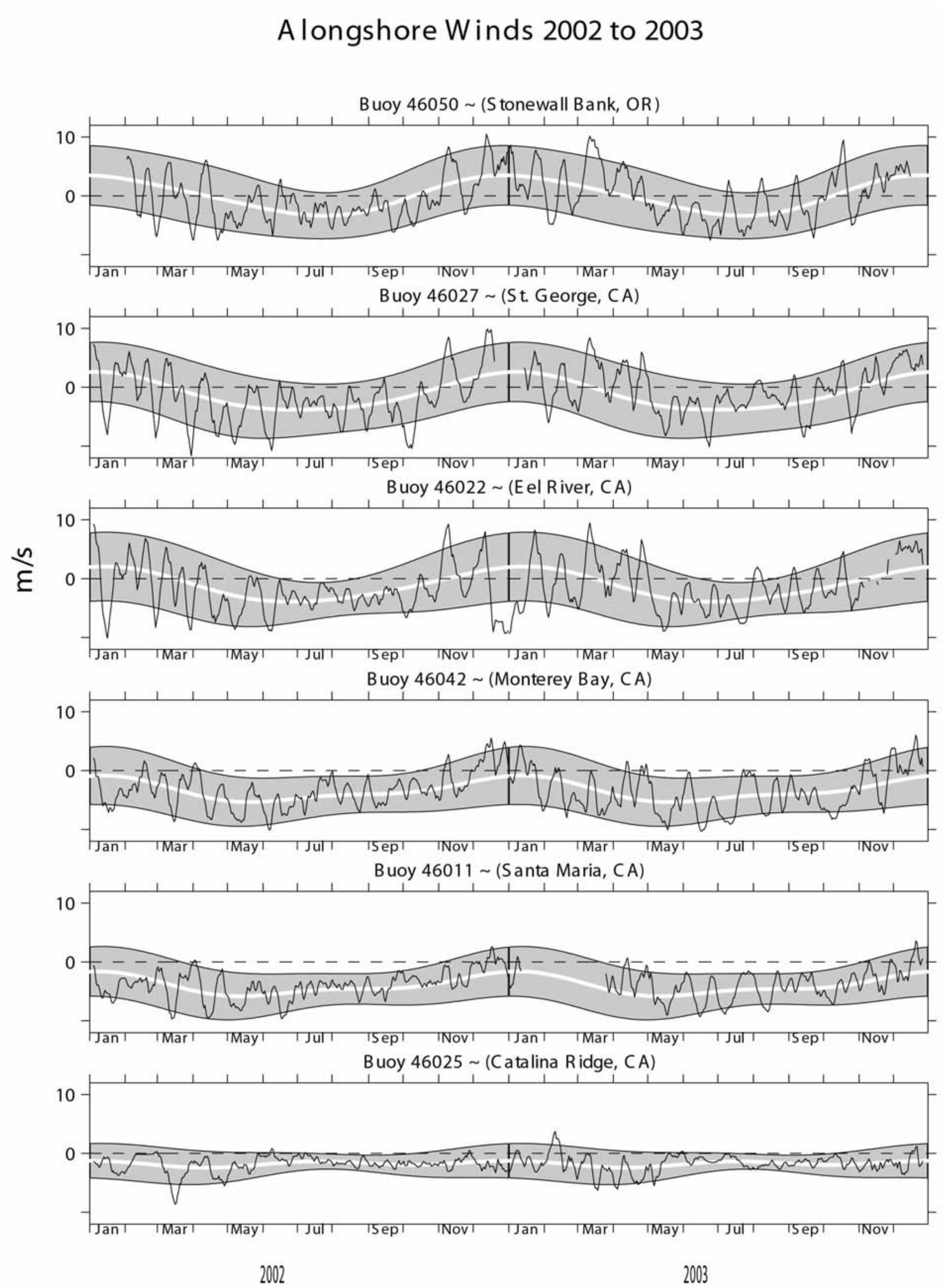

Figure 4. Time series of daily-averaged alongshore winds for January 2002–December 2003 at selected NOAA National Data Buoy Center coastal buoys. Bold lines are the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. Series have been smoothed with a 7-day running mean. Data provided by NOAA NDBC.

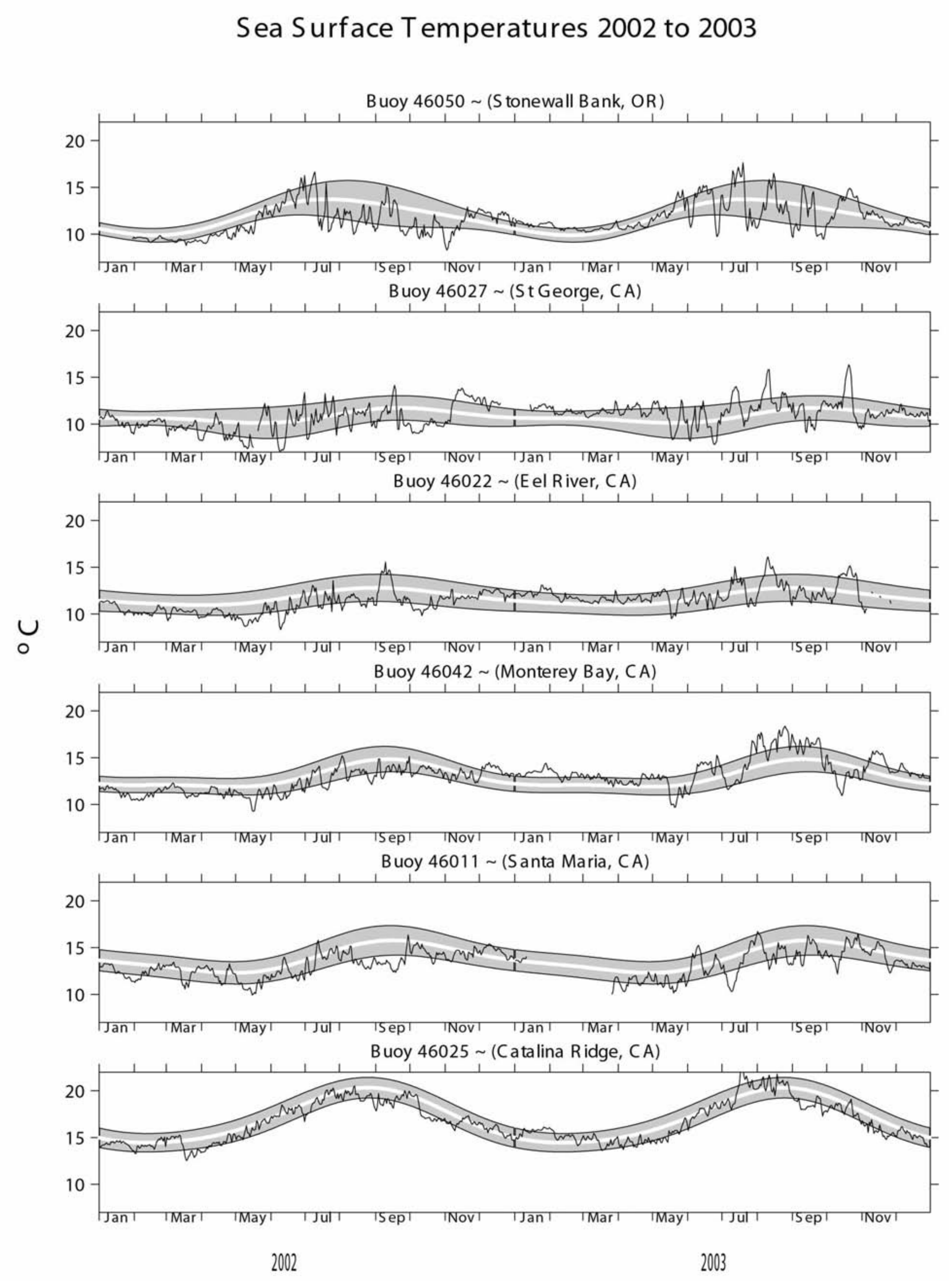

Figure 5. Time series of daily-averaged SST for January 2000–December 2001 at selected NDBC coastal buoys. Bold lines are the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. Data provided by NOAA NDBC.

et al. 2001; Schwing et al. 2002; Venrick et al. 2003). The normal cycle is for maximum upwelling in the summer, centered off California (shaded areas in upper panel of fig. 3), and downwelling in winter north of about 39°N. Winter 2002–2003 and 2003–2004 featured negative anomalies along the entire coast (white in lower panel of fig. 3), reflecting anomalously strong downwelling off northern California, Oregon, and Washington and very weak upwelling to the south. The 2002–2003 anomalies may have been influenced by the tropical El Niño event.

Summer upwelling was unusually strong throughout the CCS in 2003. The return to stronger than normal upwelling was particularly significant on the heels of the 2002–2003 El Niño, suggesting that this event had an ephemeral influence on conditions in the North Pacific and that the climate regime shift believed to have commenced in 1998 (Schwing and Moore 2000; Peterson and Schwing 2003) may be continuing. March 2004 upwelling anomalies were positive, but the most recent available indexes (April 2004) were slightly negative, reflecting the anomalies of the preceding winter. The strong summer upwelling of past years was not predicated by any clear signals in early spring, so we cannot speculate on the intensity of coastal upwelling in the next several months.

Winter 2002–2003 featured a very active intraseasonal pattern in the CCS, illustrated by a series of strong, approximately 30-day alongshore fluctuations in the NDBC coastal buoy winds (fig. 4). Winds were predominantly toward the north (positive) during winter and early spring of 2003 over most of the CCS. Summer 2003 winds were persistently to the south, indicating normal upwelling-favorable conditions in the northern CCS, but continued to be dominated by strong fluctuations or reversals in the alongshore winds on a roughly monthly scale. Note the greater amplitude of these monthly oscillations compared to summer 2002. This pattern is consistent with the intraseasonal variability in the tropical Pacific, which may have been affected by the MJO in recent months (March and April 2004).

The pattern of SSTs at the NDBC buoys (fig. 5) in the past several months reflects the pattern in alongshore winds. Regular intraseasonal fluctuations in SST exceeded 5°C (compared to the annual range of only 2–3°C). This pattern was particularly strong during the summer and fall of 2003 (again, compared to the previous summer). SSTs were unusually warm from November 2002 through April 2003, probably a response to the El Niño event. Unlike the winds, intraseasonal variability in CCS SST during the El Niño was relatively small, suggesting that the upper ocean was relatively well mixed. Seasonally averaged SSTs were close to the long-term mean in the northern portion of the CCS in 2003, but the southern CCS (buoys 46011 and 46025) was unseasonably cool since late spring. Preliminary data suggest that this pattern continued into early 2004.

Preliminary data from May 2004 revealed remarkably warm SSTs throughout much of the Northeast Pacific, with anomalies as high as 3–4°C in parts of the CCS. This represents a substantial increase from the previous few months. There is evidence to suggest, however, that these anomalies were confined to a relatively thin surface layer, perhaps driven by anomalous surface heat fluxes. Warm waters off the coast of Oregon were evident only within the upper few meters (Bill Peterson, pers. comm.).

REGIONAL STUDIES

Oregon Coast: GLOBEC LTOP Cruises

The long-term observation program (LTOP) of the U.S. GLOBEC Northeast Pacific Program that began seasonal sampling of the northern portion of the CCS in 1997 continued through most of 2003. During 2002, waters off central Oregon were subject to competing influences: a cooling influence from the subarctic Pacific and a warming influence from a weak or moderate El Niño in the equatorial Pacific (Venrick et al. 2003). Steric heights along the offshore portion of the NH line were above normal during much of 2003 (fig. 6); this may reflect influence from the 2002–2003 El Niño. Inshore steric heights were below normal in February 2003 when there was unusual winter coastal upwelling and above normal upwelling in early April after a month of very strong downwelling. Steric height values and anomalies (in dynamic centimeters) correspond directly to values and anomalies of sea surface elevation (in centimeters); offshore gradients of steric height are proportional to the alongshore component geostrophic surface current. Thus Figure 6 suggests the inshore current was more southward than normal in February and July but weaker than normal in early April.

NH line sections in 2003 (fig. 7) show the usual strong seasonal cycle in the upper 200 m of the ocean: in the winter, deep mixed layers and weak horizontal gradients, and in the summer, very strong stratification associated with the Columbia River plume. The strong summer tilt of the main pycnocline is also normal, with subsurface temperature decreasing and salinity increasing toward shore. The early April 2003 section clearly shows the influence of strong March downwelling, with very little stratification above 60 m offshore, and a lens of very fresh water (from local runoff) adjacent to the coast (fig. 7b).

Each NH line section contains positive temperature anomalies that differ from the seasonal average by more

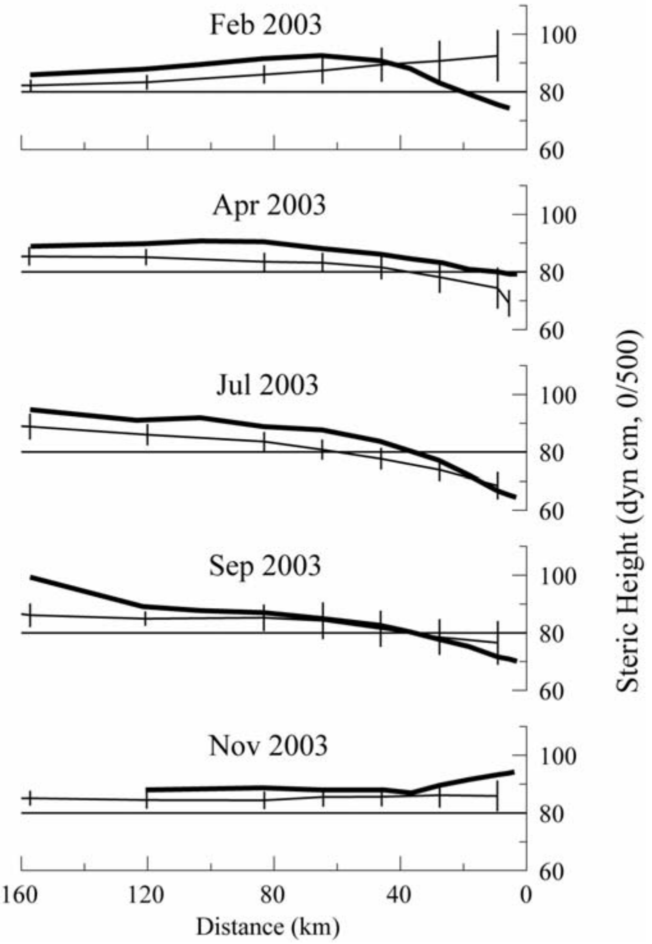

Figure 6. Steric height profiles of the sea surface relative to 500 dbar along the NH line at 44.65°N since April 2002 (heavy line) shown with the long-term (1961–71) seasonal or monthly average from Smith et al. (2001). Vertical bars indicate 1 standard deviation above and below the average. Values over the shelf and upper slope were calculated by the method of Reid and Mantyla (1976).

than 1 standard deviation (fig. 8); in the first half of the year these anomalies were strongest in the top 100 m. Each section (except in early April) also contains significant negative temperature anomalies at a depth of about 100 m, and within the permanent halocline (compare figs. 7b and 8). These negative anomalies suggest the 2002 subarctic intrusion (Freeland et al. 2003; Huyer 2003; Wheeler et al. 2003) lingered through 2003; temperature and salinity diagrams for the shelf-break station (NH-25) confirm this impression (fig. 9). In July 2003, the cool halocline anomaly was present along the entire section: in the salinity range of S = 33–33.8, temperatures were still about 0.5°C lower than they had been in July 2001, though not as low as in July 2002. Peak amplitudes in July 2003 occurred near 124.5°W over the outer shelf.

Regional surveys were made in April, July, and September 2003. As in recent years (Schwing et al. 2002; Venrick et al. 2003), surface temperatures were nearly homogeneous in April 2003 (fig. 10a), though there was equatorward flow near the coast (fig. 10b). A narrow wedge of low salinity water lay adjacent to the coast (fig. 10c), indicating recent downwelling and coastal trapping of local runoff. By July 2003, there were strong surface temperature gradients: inshore waters were 6–7°C colder than offshore waters (fig. 10a). Geostrophic flow at the surface, relative to 500 dbar, was equatorward except on the southeast flank of Heceta Bank (fig. 10b), and low-salinity Columbia River plume waters (S < 32.5) covered all but the inshore portion of the northern sections (fig. 10c). In late September, zonal gradients of surface temperature had weakened, the southward current had migrated offshore, and there seemed to be some eddies both north and south of Cape Blanco that were not resolved by our survey. Low-salinity Columbia River plume waters (S < 32.5) covered the offshore portion of each section. Winds had continued to be favorable for upwelling through most of September, and this continued upwelling is reflected in the cold, dense waters observed in the coastal strip at the end of September (fig. 10a,c).

Southern California Bight: CalCOFI Cruises

Overview. The CalCOFI program is based on quarterly surveys of the CCS off Southern California (CalCOFI region). Such quarterly observations can be biased. To determine such a bias we compared SST derived from AVHRR and MODIS for the 66 CalCOFI stations with mixed-layer temperatures measured at the 66 stations during the quarterly surveys. Patterns of temperature anomalies are very similar (fig. 11a,b), demonstrating that our quarterly surveys are sufficient to delineate effects of the major climatological events, such as ENSO cycles, on ocean climate. The cruise-based climatology (symbols in fig. 11C) shows only a little bias—such as the timing of the spring temperature minimum relative to the climatology based on the remotely sensed data (line in fig. 11C). The slight overall positive bias in the ship-based data, ~0.2°C, is surprising because one would expect ship-based mixed-layer data to be lower than satellite-derived SST, since ship-based observations include periods of cloud cover.

Mixed-layer temperature anomalies of the CalCOFI region (fig. 11B) have been close to zero over the last year. The difference between satellite-derived SST and ship-based mixed-layer temperature anomalies over the last year (fig. 11A versus 11B) is surprising, and the cause is unknown. As described previously (Venrick et al. 2003), the response of mixed-layer temperatures to the recent El Niño differed dramatically from the response to the 1997–98 event; during the peak of the recent El Niño, only weak positive anomalies were observed

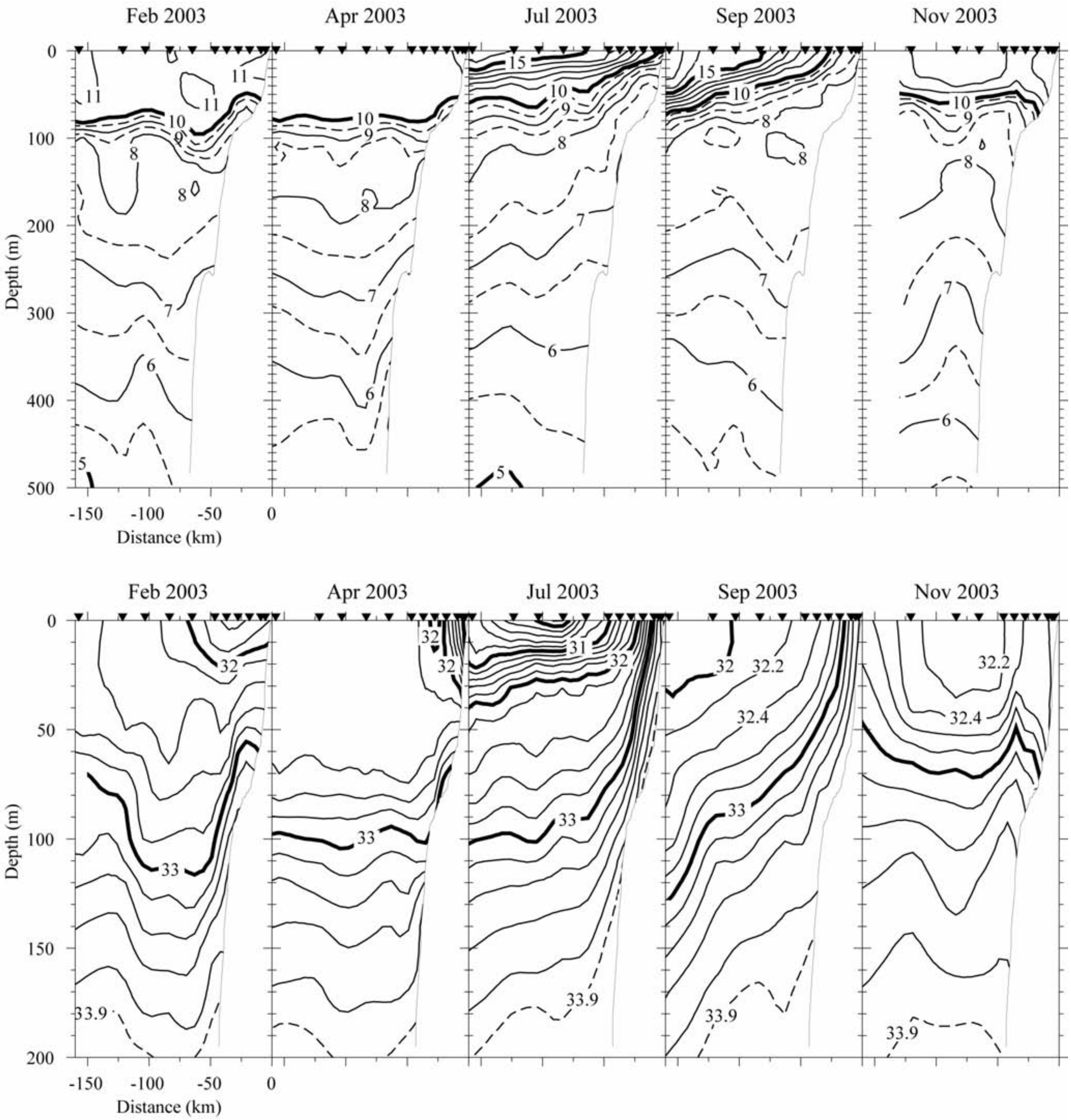

Figure 7. Temperature (*top*) and salinity (*bottom*) along the NH line at 44.65°N in 2003. Triangles on upper edges indicate the location of CTD stations.

(fig. 11B). Mixed-layer temperature anomalies have been close to zero since then; a La Niña did not develop.

Mixed-layer salinities have been dropping below long-term averages since the beginning of 2002, and this trend continued during 2003 (fig. 12). The average anomaly over the last year was −0.28. The salinity anomaly is found in most areas of the CalCOFI region (fig. 13). It is strongest at the edge of the Central Gyre (lines 90–93, stations 100–120, fig. 13A), slightly less in the region of the California Current (lines 83–90, stations 70–90, fig. 13B) and still noticeable in the coastal waters off Central California (lines 77–80, stations 60 and inshore, fig. 13C). In April 2004 the salinity anomaly was found between the surface and 100–150 m. The freshening of the CCS began in most regions in 2001 as a subsurface feature (Huyer 2003; Bograd and Lynn 2003) that has

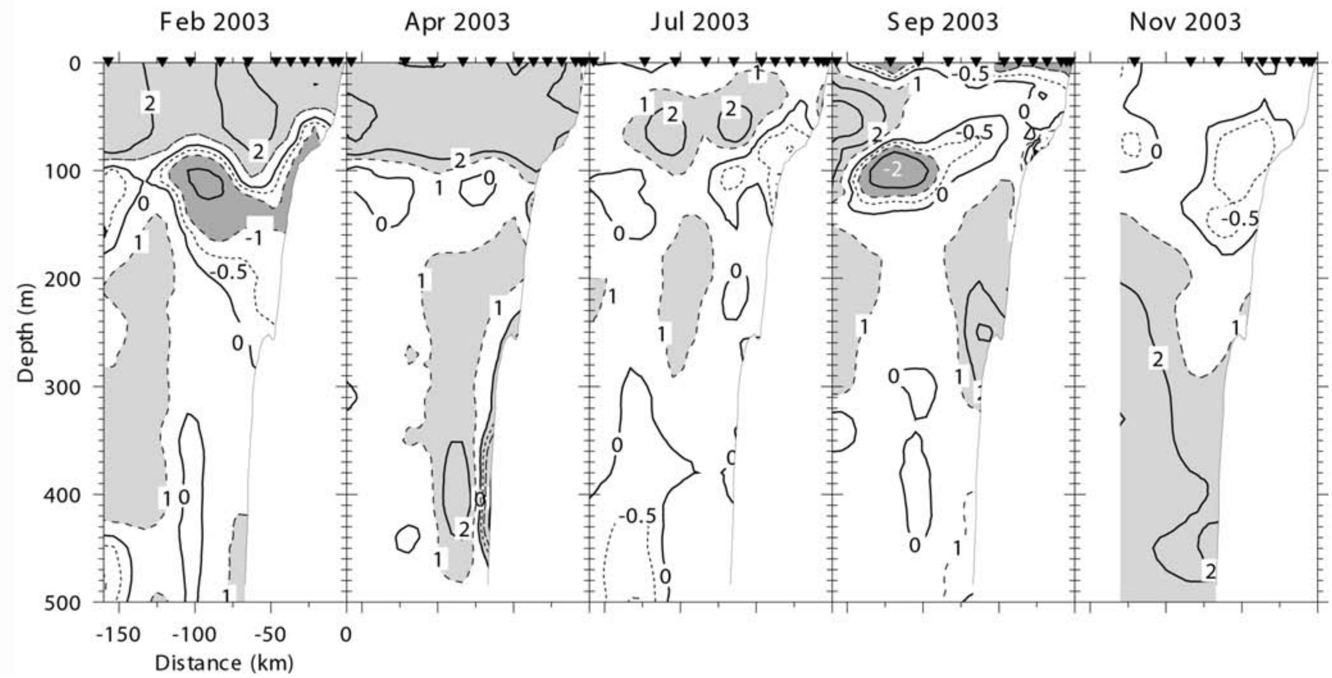

Figure 8. Normalized temperature anomalies for the NH line at 44.65°N. Positive (negative) anomalies indicate that present values are warmer (colder) than the historical (1961–71) seasonal or monthly averages. Values greater than 1 (2, 3) are significant at the 90% (95%, 99%) level.

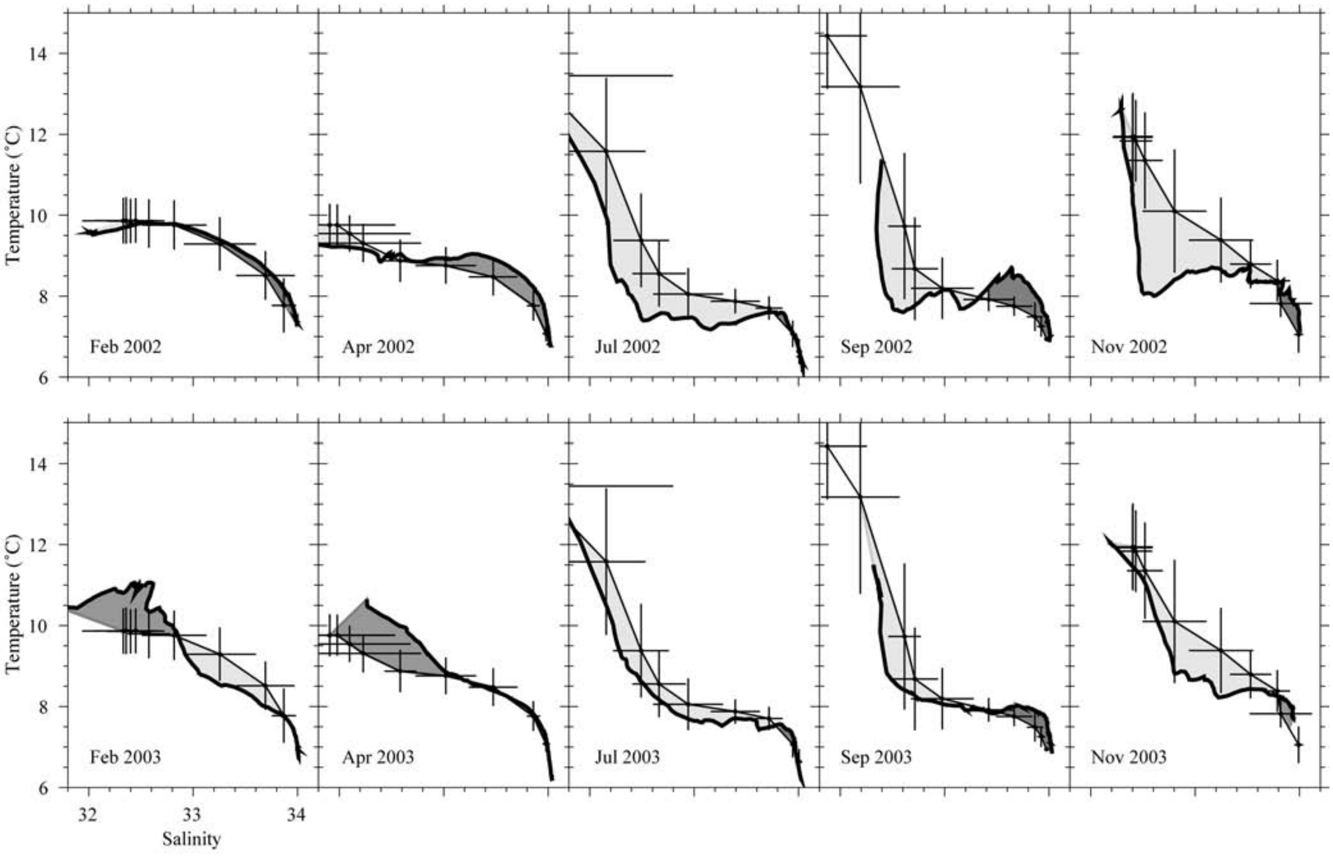

Figure 9. T-S diagrams for the shelf-break station (NH-25), comparing data from 2002 (*top row*) and 2003 (*bottom row*). Bold curves represent recent CTD casts; thin curves represent historical (1961–71) seasonal averages with cross-bars indicating plus and minus 1 standard deviation at standard sampling depths (Smith et al. 2001). Areas between the recent T-S curves (*bold*) and the historical-average T-S curves (*thin*) are shaded to emphasize the difference between warm, salty anomalies (*dark gray*) and cool, fresh anomalies (*light gray*).

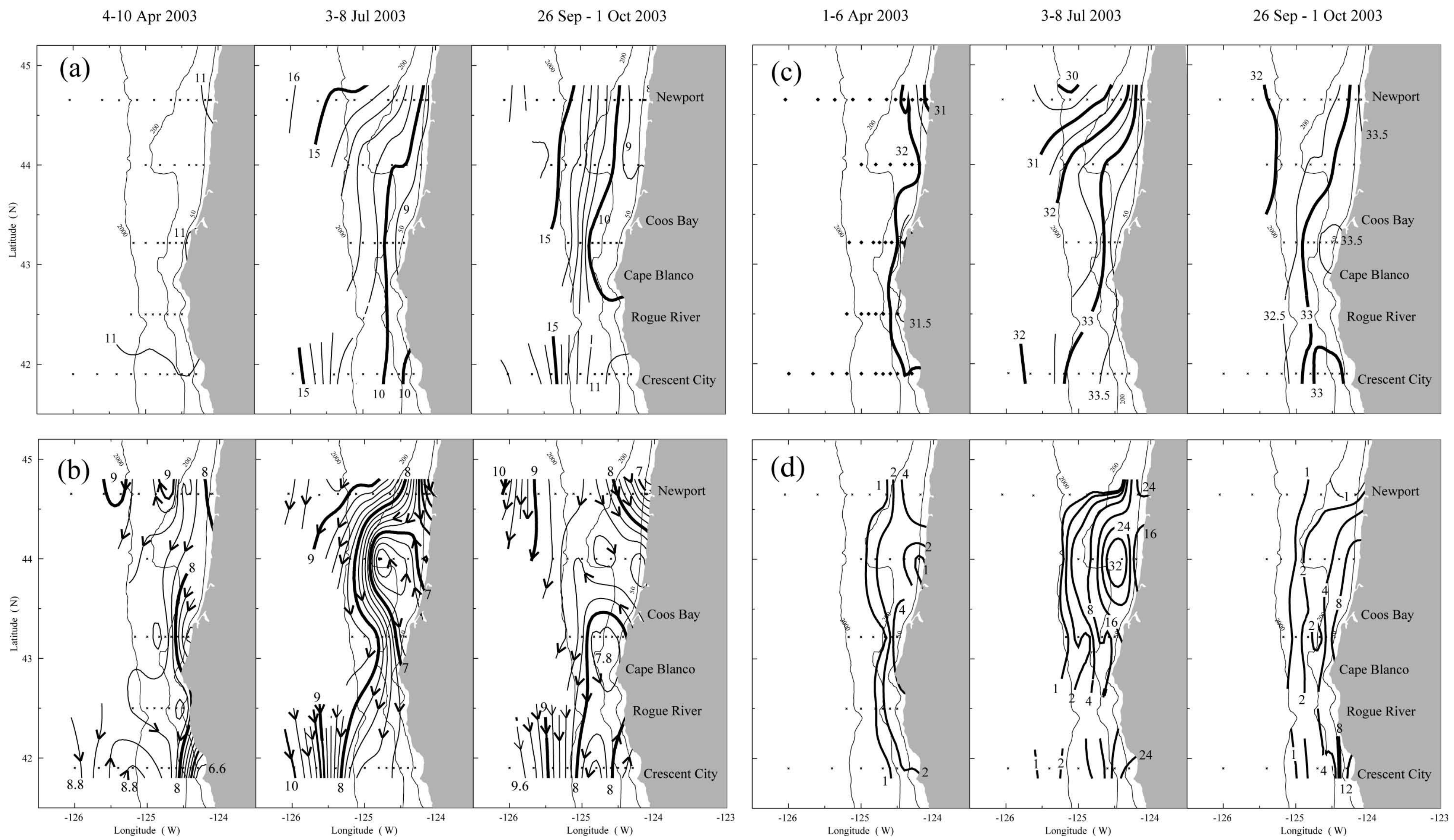

Figure 10. Spatial patterns for GLOBEC LTOP cruises: (*a*) 10 m temperature, (*b*) geopotential anomaly (J/kg) of the sea surface relative to 500 dbar, (*c*) 10 m salinity, and (*d*) 10 m chlorophyll (μg/L).

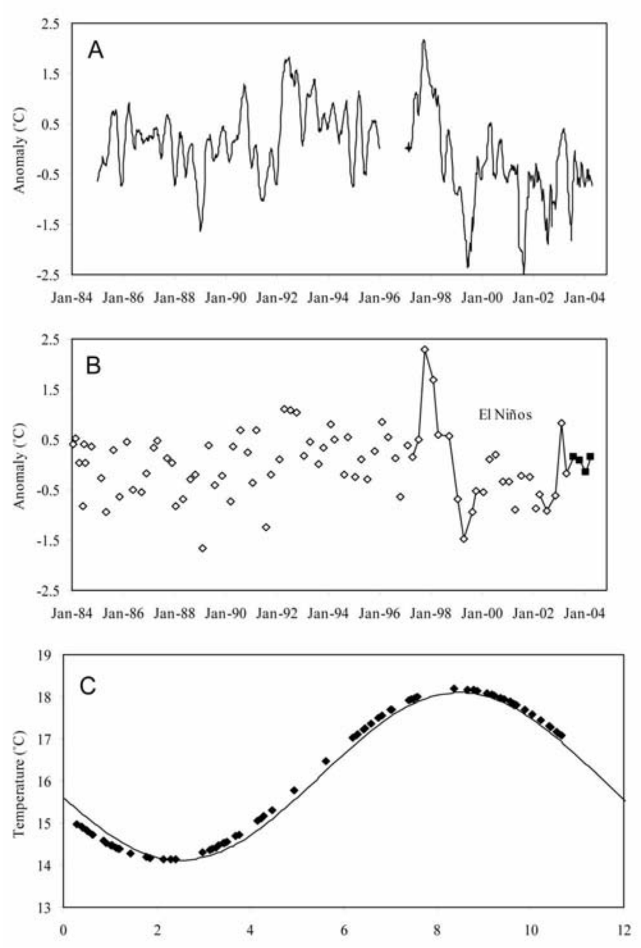

Figure 11. Average SST anomalies for the 66 standard CalCOFI stations calculated from (*A*) weekly AVHRR or MODIS data and (*B*) observation made on the quarterly CalCOFI cruises. Anomalies are calculated relative to the time period 1985–2004. Prominent in the time series are the effects of the 1997–98 El Niño and the subsequent La Niña. The 2002–2003 El Niño is only weakly expressed. (*C*) A comparison of harmonics calculated from CalCOFI cruise data (*symbols*) and weekly AVHRR or MODIS data (*line*).

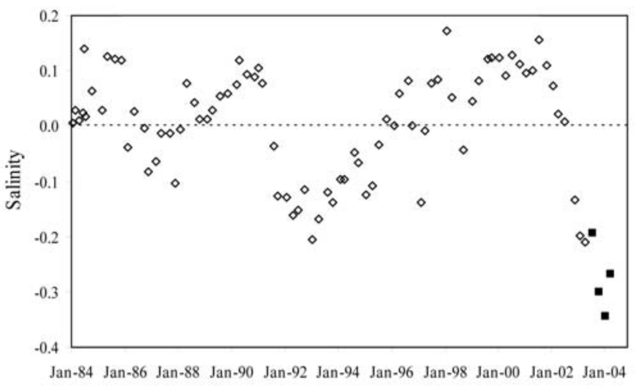

Figure 12. Cruise averages for mixed-layer salinity anomalies for the 66 standard CalCOFI stations. Solid symbols represent data from the last four cruises.

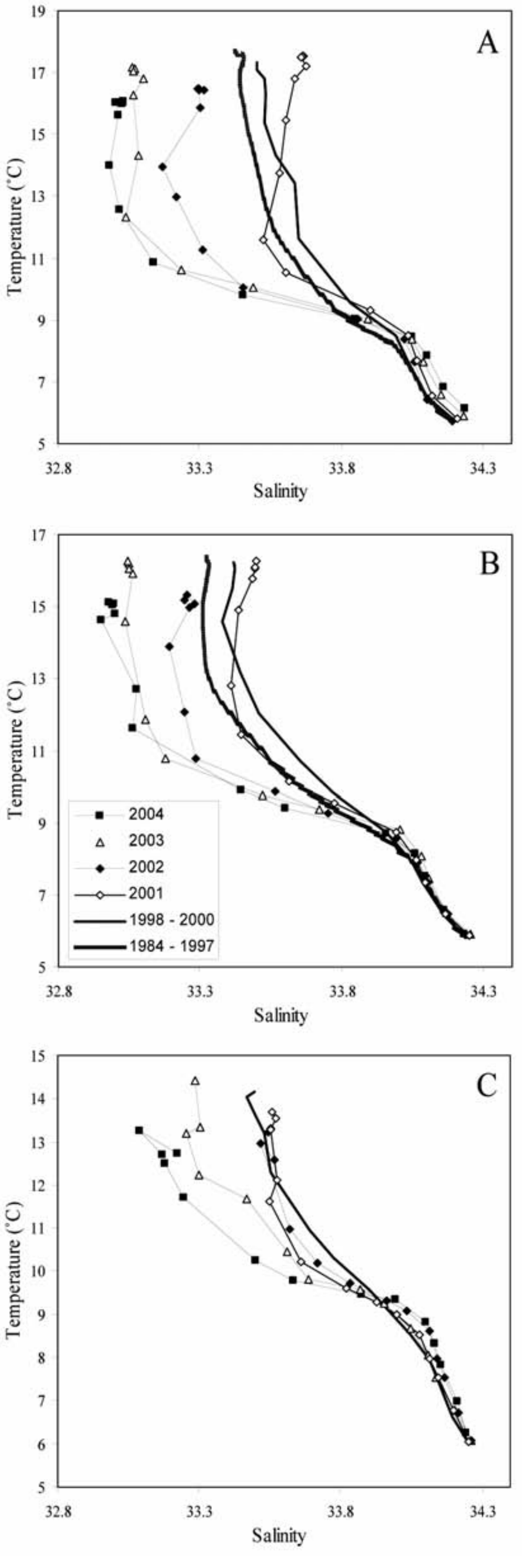

Figure 13. T-S lines for three representative areas of the CalCOFI region. (*A*) The edge of the central gyre (lines 90–93, stations 100–120), (*B*) the California Current region (lines 83–90, stations 70–90), and (*C*) the coastal areas in the north (lines 77–80, stations 60 and inshore). Each data point represents the average T-S characteristic of one standard depth level for the specified time period, such as the year 2002. Note that values for 2004 are based only on the winter and spring cruises.

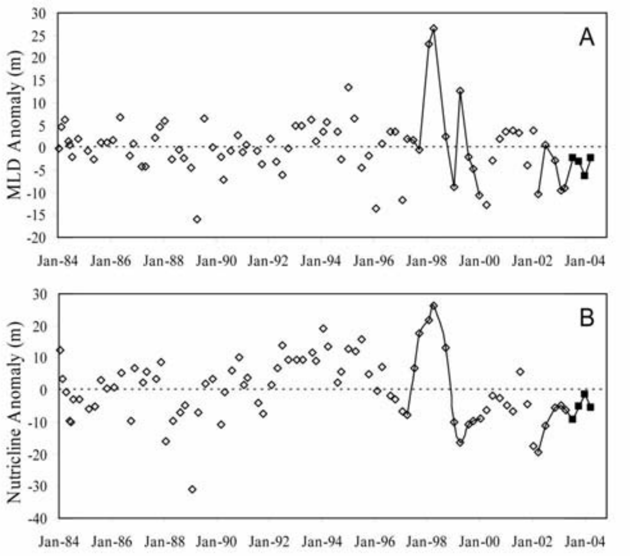

Figure 14. CalCOFI region anomalies for (*A*) mixed-layer depth and (*B*) nutricline depth. Data are derived from all 66 standard CalCOFI stations. Open symbols represent the period 1984 to the spring of 2003. Solid symbols represent data from the last four cruises. The two recent El Niño events are emphasized (*symbols connected with lines*) for a better comparison of the two events. Included in both events are data following the El Niño; for the 1997 event this represents the La Niña; for the 2002 event this represents the period of neutral anomalies.

intensified over the years and has been manifest at the surface for the last 2 years. Thermoclines are shallower in the California Current and, in particular, in regions west of the current

Mixed-layer depths during the last year were significantly below the long-term average (fig. 14A). Large excursions of mixed-layer depths, as were observed during the 1997–98 ENSO cycle, were not observed over the last 2 years. It is noteworthy that mixed-layer depths, so far, did not covary with the PDO cycle; mixed-layer depths for 1984–97 and 2000–2004 were, respectively, 34 ±11 m and 32 ±10 m. Nutricline depth (fig. 14B) over the last year showed a very similar pattern: values were smaller than long-term averages and were not noticeably affected by the recent ENSO cycle. Nutricline depth, however, reflects the PDO cycle, in contrast to mixed-layer depths.

CalCOFI Cruise 0307 (17–31 July 2003). This cruise did not occupy the usual outer-most stations on the four southern lines due to ship time constraints (fig. 15). However, the cruise did cross the main offshore California Current jet.

The surface currents showed features that are often seen during the summer: a strong southward California Current on the outer part of the region and a strong northward flow along the coast. This coastal surface countercurrent was not present on the spring cruise (0304). The currents appeared to be faster than usual. The cyclonic Southern California Eddy was present along the outer Channel Islands, and an anticyclonic loop and eddy was seen in the center of the region, between lines 83 and 90. This anticyclonic current loop persisted over the next 6 months and was more intense during the winter.

There was considerable variability in the near-surface temperature patterns due to the shallow seasonal thermocline with its strong near-surface temperature gradients and to the effects of the circulation in tilting the thermocline. The coolest water was found in the center of the Southern California Eddy, produced by the doming of the thermocline in the middle of the cyclonic eddy ("cold-core" eddy). A typical patch of warm surface water occurred between the coast and the Channel Islands, but there was much colder water immediately below. The northern edge of the anticyclonic current loop in the middle of the pattern carried warmer water eastward along lines 83 and 87.

The chlorophyll *a* patterns were similar to those seen on many previous summer cruises. The highest concentrations occurred in the Southern California Eddy, between the two opposing flows. The high chlorophylls were not an advective feature from the central California upwelling zones but occurred where the thermocline (and nutricline) was shallowest as a result of the geostrophic adjustment to the flow field. The depth of the chlorophyll maximum layer (not shown) showed a similar shoaling.

An anomalously high oxygen inversion (140% of normal) was seen at station 83.90, at a density of $\sigma_t = 26.375$ and a depth of 225 m. This feature was deeper than the usual near-surface oxygen maximum that commonly appears in summer and fall cruises and may not have been produced by local photosynthesis. A map of characteristics on this density surface shows this density at temperatures of 8.6–9.2°C and a salinity near 34.0—characteristics that are close to those of upwelling waters off the central California coast. Nitrate was also lower at the high oxygen anomaly station, suggesting a photosynthetic origin, most likely at the coastal upwelling areas. Upwelling is strongest there during spring to early summer, and the coastal upwelled water originates from as deep as 200 m where the initial oxygen levels are less than 2 ml/l and nitrate levels are around 30 µM. While dense upwelled water is in the photic zone, photosynthesis increases the oxygen concentration while reducing nutrient concentration. When upwelling winds subside, the inshore water may sink back down to its original density depth, but with altered chemical characteristics. The recently upwelled water may be subducted beneath lighter water offshore, embedded in either offshore "squirts" or eddies that drift away from the coast and southward into the California Current. The oxygen anomaly seen on this cruise was clearly in the main flow

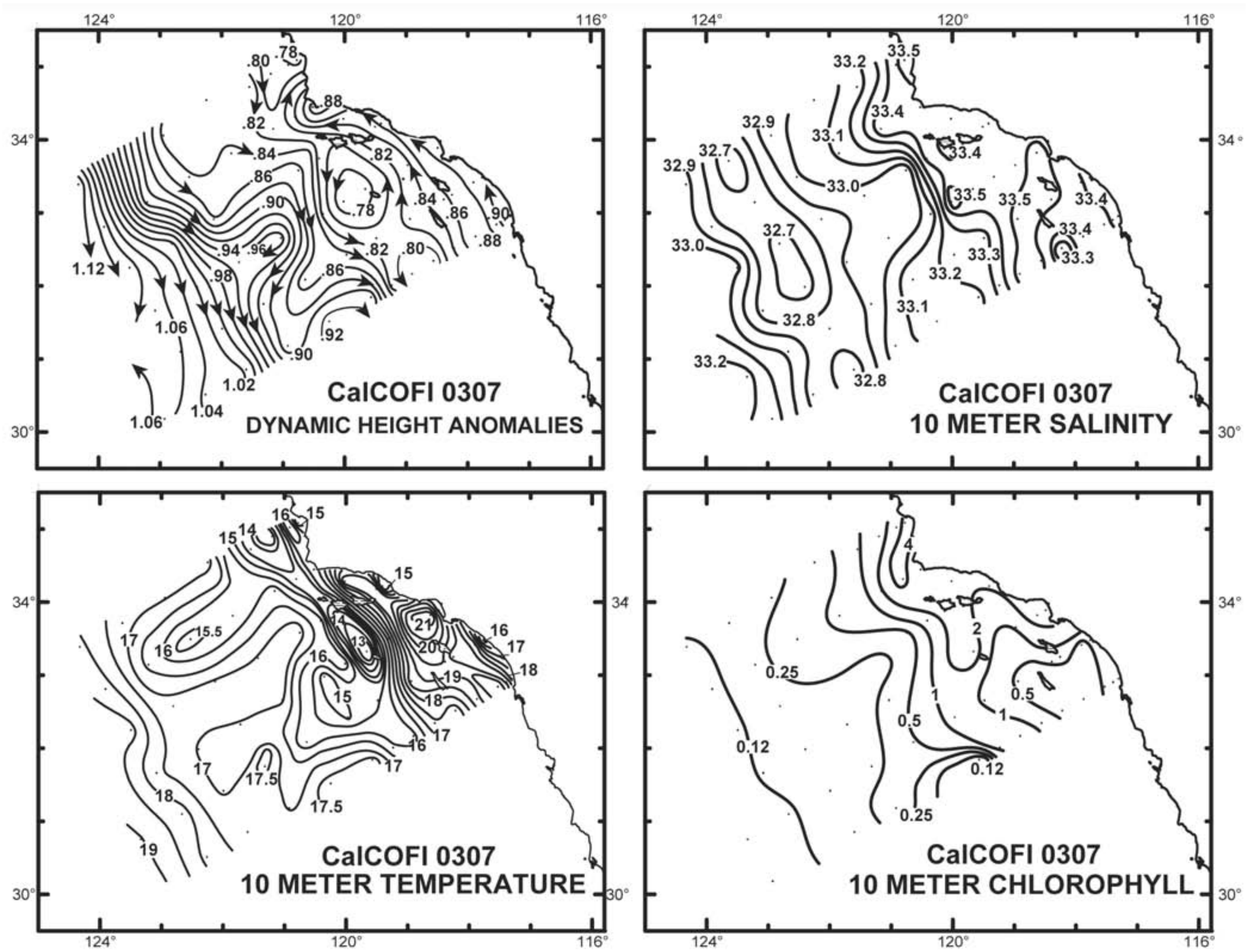

Figure 15. Spatial patterns for CalCOFI cruise 0307 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*.

of the California Current; a similar feature seen on CalCOFI cruise 8508 was in a cyclonic eddy.

CalCOFI Cruise 0310 (20 Oct.–4 Nov. 2003). The surface current map still shows some features that were seen during the summer (fig. 16). The onshore and offshore loop was still present, although shifted slightly further offshore. A cyclonic eddy had developed in the middle of lines 77 and 80. The Southern California Eddy was still present, with northward flow close to the coast. The cyclonic loop that was previously seen on lines 90 and 93, centered on stations 70 and 80, pinched off to form a cold core cyclonic eddy further offshore, centered on stations 100 and 110.

The cruise mean 10 m temperature anomaly was slightly warmer than normal, but there were also large areas down the middle of the pattern and around the Channel Islands that were cooler than normal. The 10 m salinities were all lower than normal, continuing a trend toward increasingly lower cruise mean 10 m salinities. The lowest salinities entered the pattern from the northwest corner, along with the California Current jet.

Surface chlorophylls were extremely high on the first station off Del Mar (93.26.7) as a result of a persistent red tide bloom (*Lingulodinium polyedra*) near the coast. The highest chlorophyll, > 60 μg/l, was measured at a depth of 3 m, and the dissolved oxygen was also extremely high: 11.1 ml/l, or 213% saturation. Elsewhere, the chlorophyll patterns appeared typical for a fall cruise, generally low, and with a deep chlorophyll maximum layer.

CalCOFI Cruise 0401 (5–20 Jan. 2004). The anticyclonic current loop that was present on the last two cruises intensified and penetrated farther toward the coast on this cruise (fig. 17). The cyclonic eddy that appeared at the middle of the northern two lines last fall was still strong and carried low salinity water from the northwest corner all the way around the eddy to just off of Point

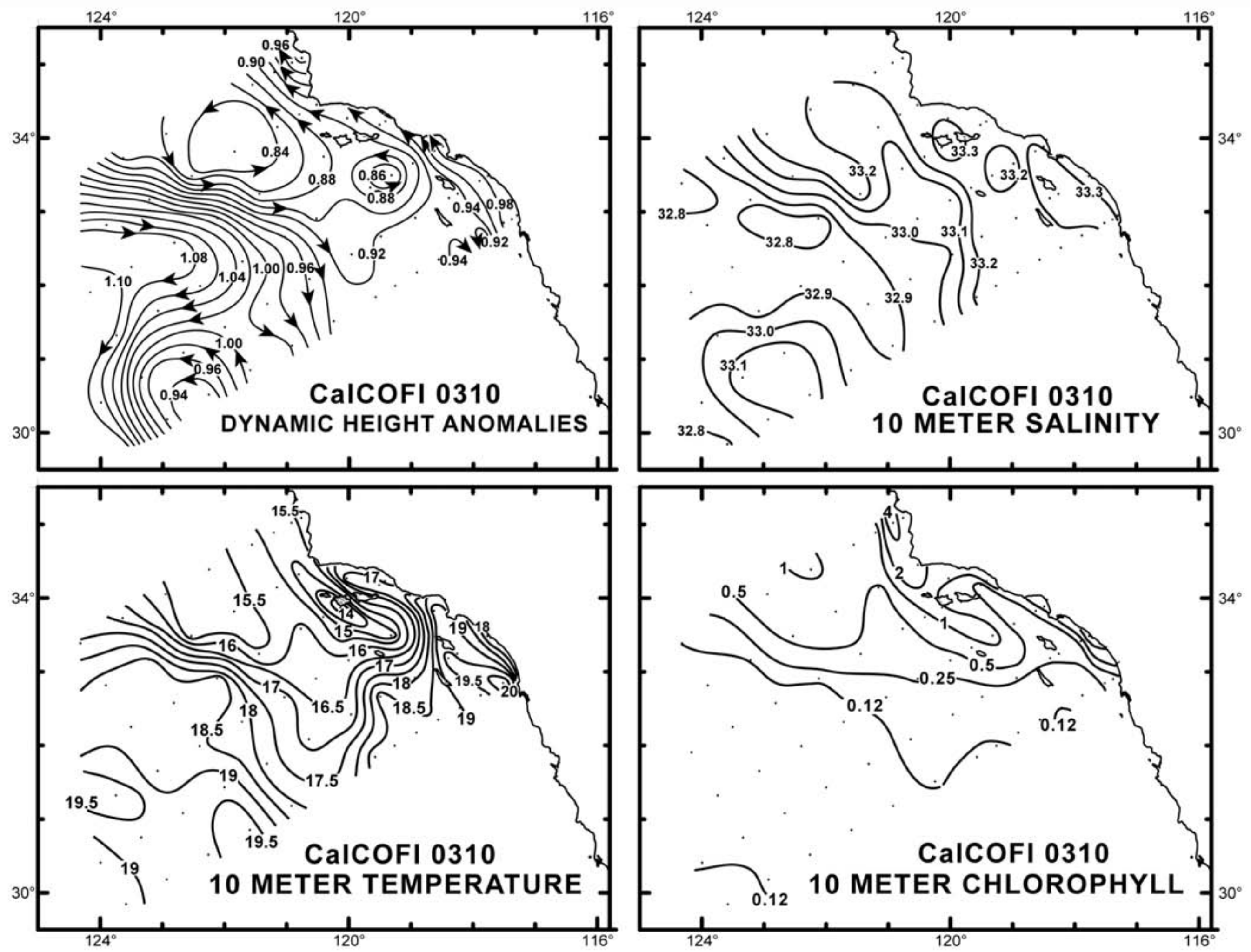

Figure 16. Spatial patterns for CalCOFI cruise 0310 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*.

Conception. The coastal surface countercurrent, strong in October, nearly disappeared in January.

The 10 m salinities continued the recent trend toward lower salinities. A comparison of the surface current and the salinity maps indicates that the salinity patterns were primarily due to advection. The 10 m temperatures remained slightly warmer than usual; warm water was seen in the warm-core clockwise current loop just to the south of the low-salinity water.

The 10 m chlorophyll *a* was highest in the Santa Barbara basin, somewhat higher than usually seen on winter cruises. Lower values were associated with the warm-water anticyclonic current loop.

CalCOFI Cruise 0404 (23 Mar.–8 Apr. 2004). The surface current patterns (fig. 18) were markedly different from those seen on the last cruise. The large northern cyclonic eddy was gone, as was the big loop that was present in the southern part of the pattern. The new pattern showed two bands of strong southward flow, quite similar to what was seen during the spring of 2003. The Southern California Eddy was present but centered around the northern Channel Islands.

The lowest 10 m salinities appeared in the northwest corner of the pattern, where the offshore California Current jet also entered the pattern. Highest salinities occurred in the cold newly upwelled water just north of Point Conception. Although the cruise-mean 10 m salinity anomaly was still below normal, the steady decrease in salinity seen over the last nine cruises was reversed slightly (fig. 12). The 10 m temperatures were cool in the upwelled water, as well as in the inshore edge of the current jet present around stations 55 and 70 on most of the lines. Warmer water was seen in the southeast corner of the pattern where there was a clockwise current loop. Cruise-mean temperature anomalies were slightly warmer than normal. High values for 10 m chlorophyll *a* were present in the cold-water regions; warm-water areas had low values.

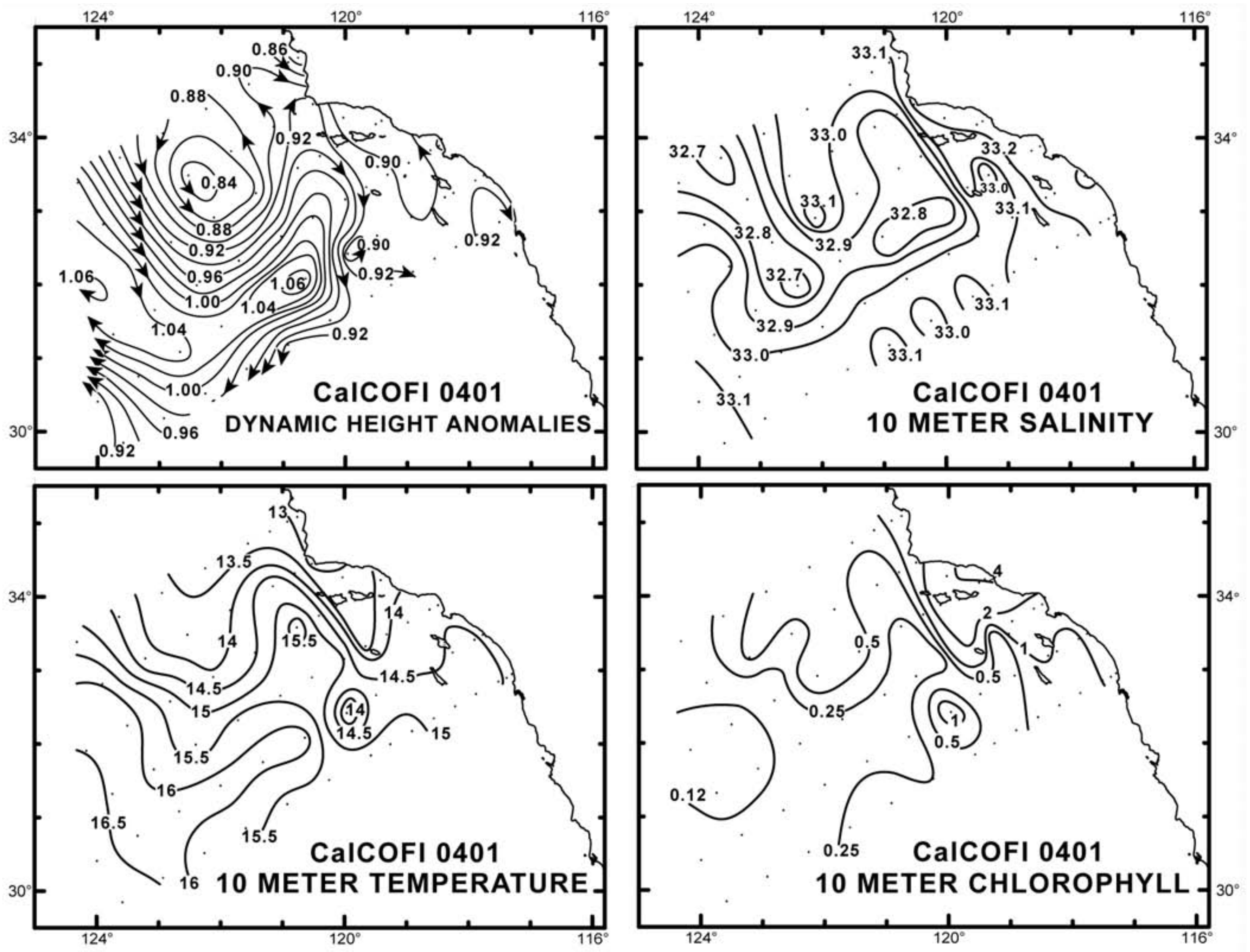

Figure 17. Spatial patterns for CalCOFI cruise 0401 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*. Data used for these plots are still preliminary.

IMECOCAL Cruises off Baja California

IMECOCAL Cruise 0304 (3–24 Apr. 2003). In April 2003, the typical spring pattern of strong southward flow of the California Current was observed (fig. 19). Isotherms parallel to the coast are consistent with this circulation pattern, showing the cool-water characteristic of coastal upwelling (fig. 20). The higher temperature was associated with the large anticyclonic eddy in the offshore central part of the area. A core of low salinity occupies almost the entire region (fig. 21). In the coastal region, the isohalines were parallel to the coast, and lightly saltier water was present, a pattern compatible with coastal upwelling. High inshore chlorophyll concentrations (> 4 mg m^{-3}) occurred at the upwelling centers, mainly off Punta Colonet (line 103), San Quintin (line 107), and Punta Canoas (line 113) (fig. 22). Chlorophyll values diminished immediately offshore to ~0.2 mg m^{-3}. Near-surface chlorophyll had a similar pattern but with values 50% lower than those reported for January 2003 (Venrick et al. 2003), when subarctic water was strongly affecting the region.

IMECOCAL Cruise 0307 (7–29 July 2003). The California Current was split into two jets during July 2003, one offshore and straight, and the other meandering between the coast and seaward (fig. 19). These meanders were apparently generating those eddies observed on lines 110 and 113. These eddies retained the cold and fresh water of the California Current (figs. 20 and 21). Saltier, warmer waters were found off Central Baja California. A strong thermal front was observed in the southeast edge of the area. The salinity in the upper few hundred meters of the region was anomalously low—reaching, for example, values of -0.3 near the surface along line 120 (fig. 23). However, negative temperature anomalies were not associated with these salinity anomalies. The spatial distribution of chlorophyll during the summer was similar to the spring pattern but with lower inshore concentrations in the northern IMECOCAL re-

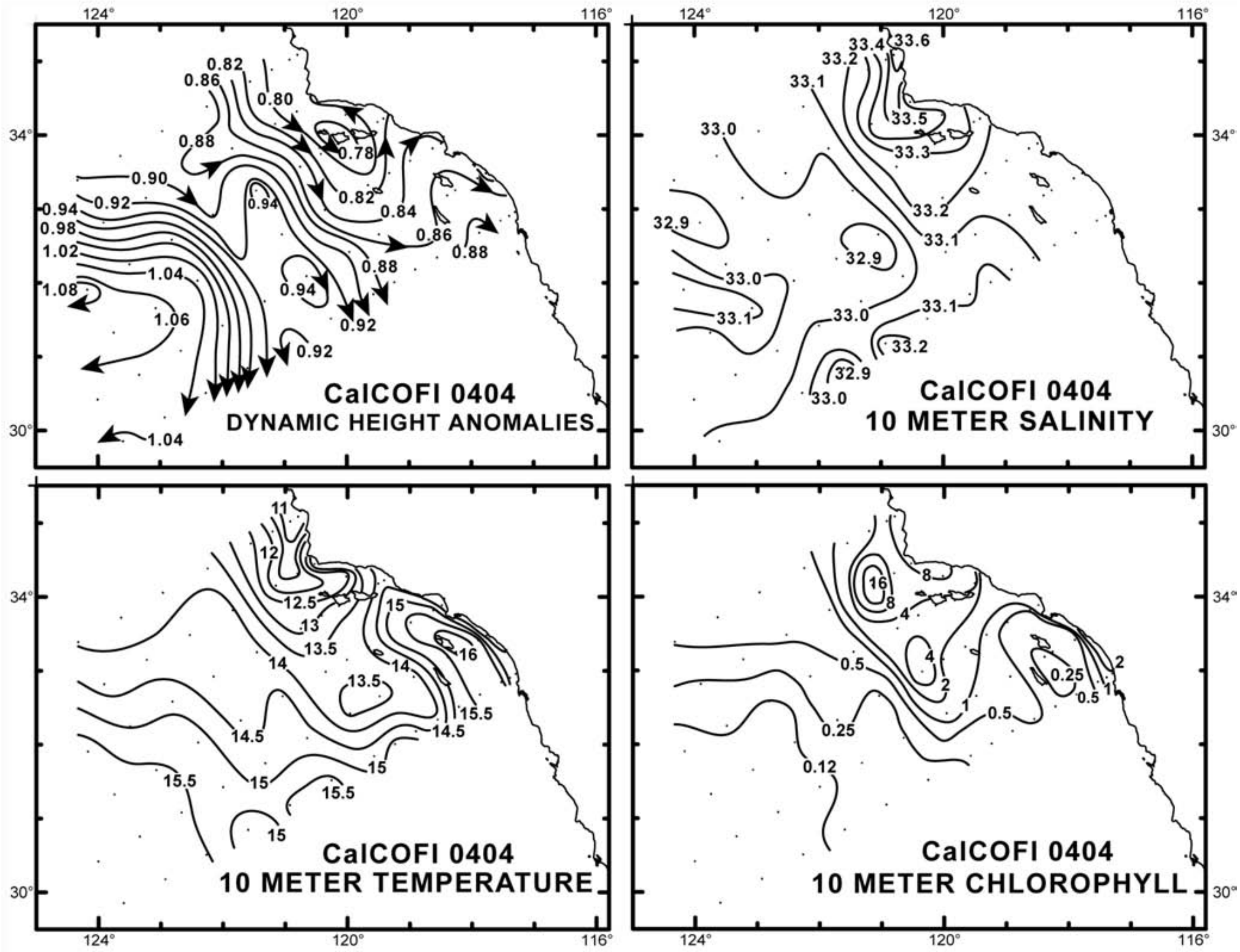

Figure 18. Spatial patterns for CalCOFI cruise 0404 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*. Data used for these plots are still preliminary.

gion (fig. 22). We detected only two inshore zones of high values, one between Ensenada and Punta Baja in the northern sampled lines, and one off Punta Abreojos (line 127) in the southern sampled lines, both areas where coastal upwelling occurs during the spring and summer. Some small areas of high chlorophyll, observed offshore, appear to be related to the meandering of the current.

IMECOCAL Cruise 0310 (10–31 Oct. 2003). In October 2003, a small cyclonic eddy off Ensenada (lines 100 and 103) altered the main flow of the California Current (fig. 19). From the northwest, a separate cool flow meanders toward the equator until line 127 (figs. 19 and 20), reversing impelled by the counterflow of warm and more saline water at the central offshore stations (fig. 21). South of Punta San Hipólito (27°N) the isotherms and isohalines were aligned in a strong gradient perpendicular to the coast. During autumn, the chlorophyll continued the decreasing trend, but the spatial patterns common to spring and summer remain unchanged (fig. 22). The higher levels (> 1.0 mg m^{-3}) at inshore locations follow the reinforcement of the equatorward circulation.

IMECOCAL Cruise 0401 (30 Jan.–20 Feb. 2004). In January 2004, the California Current was split into two jets off Ensenada. The California Current off Punta Baja (lines 110 and 113) was greatly distorted by a large seaward meander (fig. 19). Negative salinity anomalies were observed throughout the region; for example, salinity anomalies along line 120 reached values of up to -0.5 (fig. 23). These salinity anomalies did not correspond to negative temperature anomalies; these were only found along the coast out to station 120.60 (fig. 23), unusual for this time of the year. Subtropical water was compressed in the other half of the area, forming a thermohaline front affected by upwelling near the coast. Chlorophyll levels increased during winter along the coast (> 2.0 mg m^{-3}), maintaining the spatial pattern observed in the seasons described before (fig. 22).

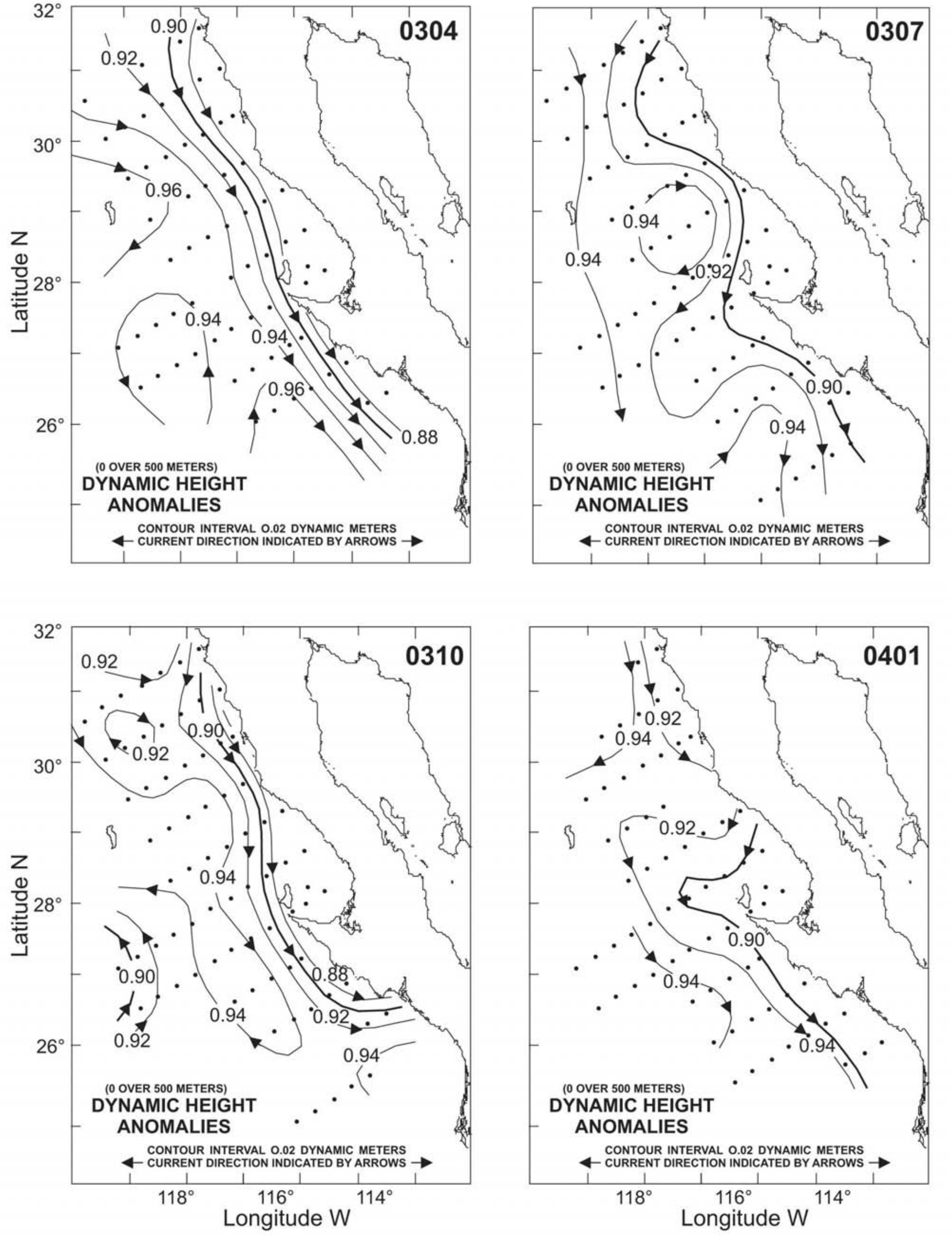

Figure 19. Spatial patterns of upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height anomalies for IMECOCAL cruises: 0304 (3–24 April 2003), 0307 (7–29 July 2003), 0310 (10–31 October 2003), and 0401 (30 January–20 February 2004).

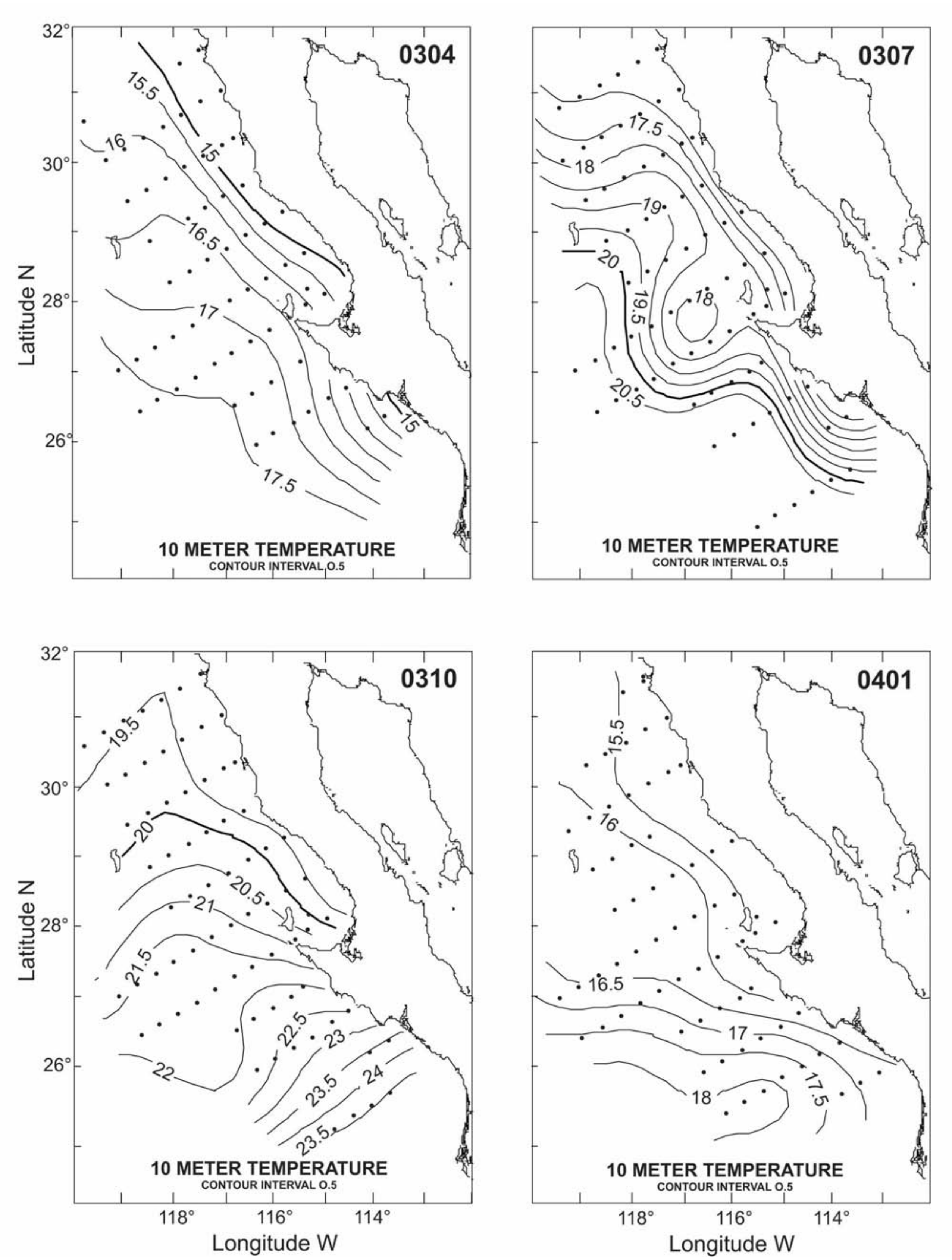

Figure 20. Spatial patterns of 10 m temperature (˚C) for IMECOCAL cruises: 0304 (3–24 April 2003), 0307 (7–29 July 2003), 0310 (10–31 October 2003), and 0401 (30 January–20 February 2004).

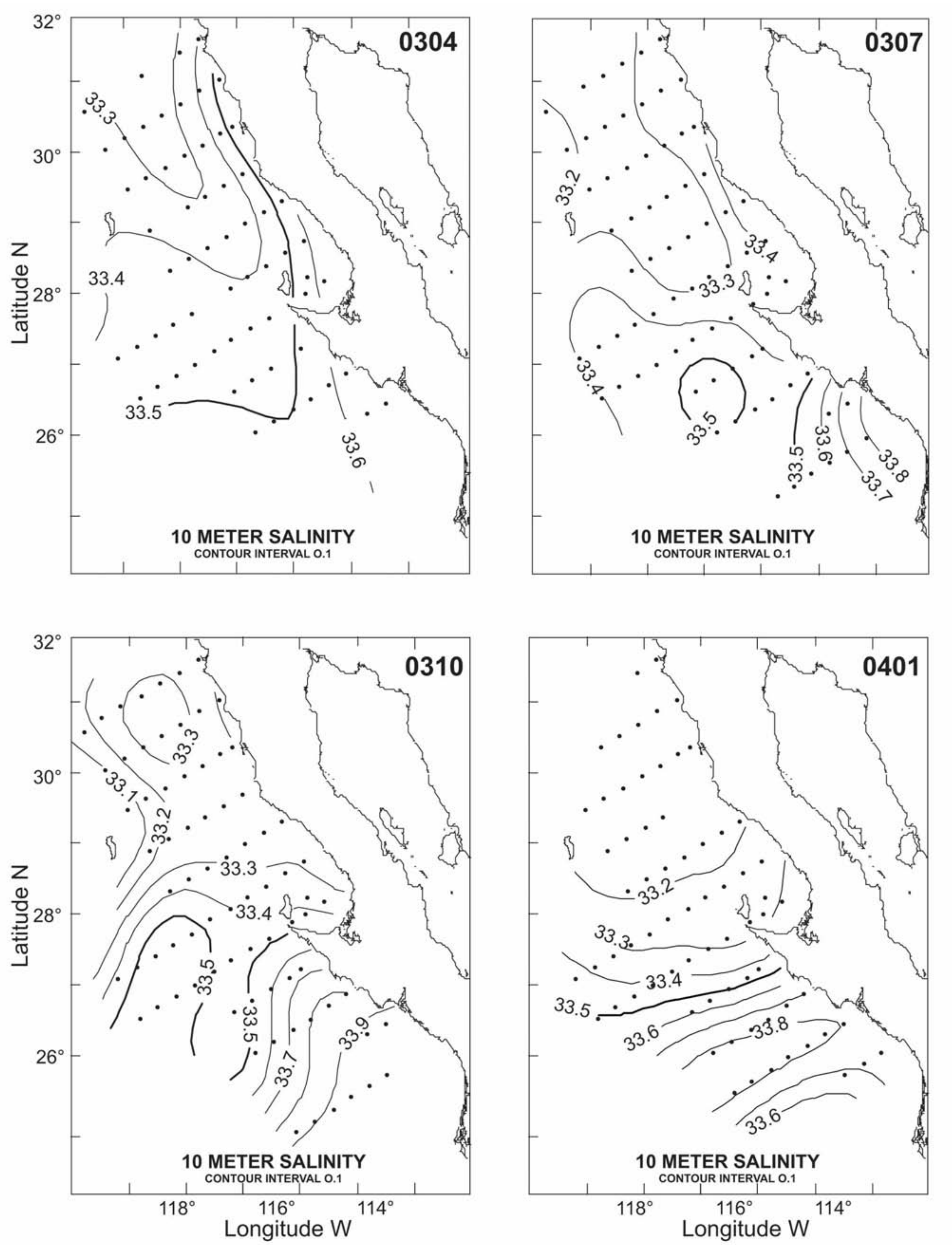

Figure 21. Spatial patterns of 10 m salinity for IMECOCAL cruises: 0304 (3–24 April 2003), 0307 (7–29 July 2003), 0310 (10–31 October 2003), and 0401 (30 January–20 February 2004).

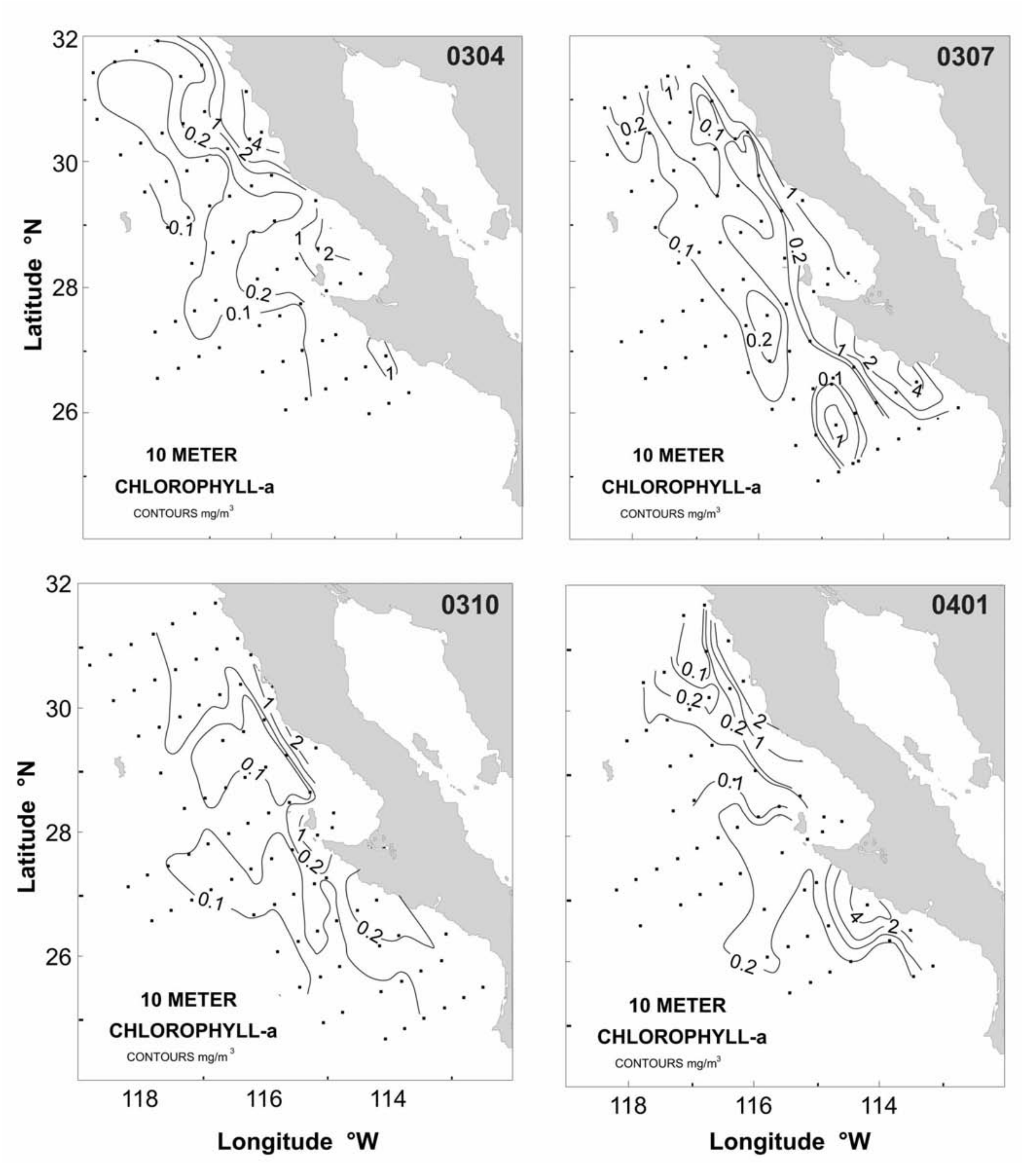

Figure 22. Spatial patterns of 10 m chlorophyll *a* for IMECOCAL cruises: 0304 (3–24 April 2003), 0307 (7–29 July 2003), 0310 (10–30 October 2003), and 0401 (30 January–20 February 2004).

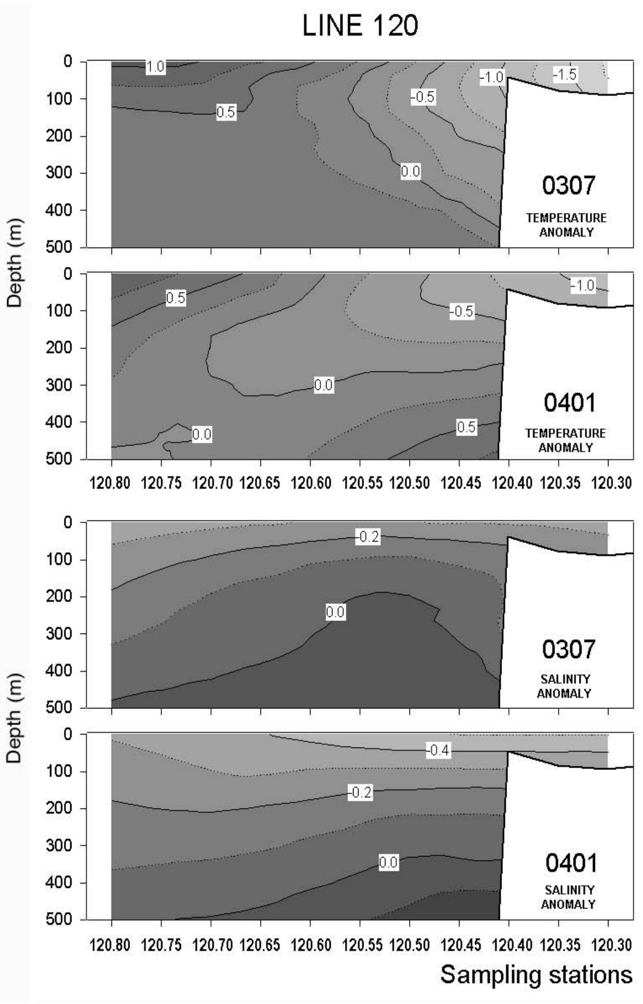

Figure 23. Temperature and salinity anomalies along line 120 for cruises 0307 and 0401. Anomalies were calculated relative to the 1950–78 time period (Lynn et al. 1982).

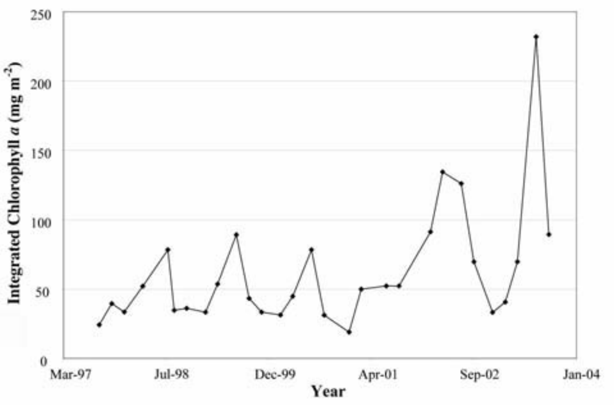

Figure 24. Time series of GLOBEC data showing mean integrated chlorophyll *a* averaged over all four lines (adapted from Wheeler et al. 2003).

BIOLOGICAL PATTERNS

Macronutrients, Chlorophyll *a*, and Primary Production

Oregon. Chlorophyll *a* concentrations in April 2003 (fig. 10d) were much lower than in April 2002, presumably because of the strong downwelling in March 2003 resulting from the persistent northward winds observed at Stonewall Bank and Point St. George (fig. 4). Chlorophyll concentrations in July 2003 were very high, exceeding 16 µg/l at one or more stations on each section. At the end of September, most of the inner shelf still had values > 4 µg/l. These high values for chlorophyll may reflect the persisting influence of subarctic waters (Wheeler et al. 2003); at densities corresponding to the permanent pycnocline and upper nutricline, subarctic waters have higher concentrations of phosphate (and other nutrients) than subtropic waters of the same density (Reid 1997). Time series of mean vertically integrated chlorophyll (fig. 24) suggest that summer phytoplankton biomass doubled from 2000 to 2003. Whether and to what extent these enriched conditions will persist through 2004 remains to be seen.

CalCOFI. Average concentrations of nitrate and phosphate in the mixed layer were close to their climatological averages during the observation period (fig. 25A,B). Mixed-layer concentrations of both macronutrients appear to be unaffected by the phase of the PDO. The shallow nutriclines observed off southern California since 2000 (fig. 14B) did not affect concentrations of the two macronutrients. Mixed-layer concentrations of both macronutrients were first negatively and then positively affected during the 1997–2000 ENSO cycle (solid lines in fig. 25A,B). In contrast, no significant response was observed for either macronutrient during the recent El Niño; concentrations remained close to their climatological means between the spring of 2002 and the present. Mixed-layer concentrations of silicate have been significantly below their climatological average since the beginning of 2003 (fig. 25C), a time period coinciding with the decline of mixed-layer salinities. This general trend would have masked an effect of the recent ENSO cycle on mixed-layer concentrations of silicate.

Mixed-layer concentrations of chlorophyll *a* were above the climatological mean throughout the last year (fig. 26A). Anomalies for mixed-layer chlorophyll *a* over the last two El Niños were surprisingly similar; anomalies were slightly below zero during both events (fig. 26A). However, it is not possible to unambiguously ascribe the patterns to the effects of the El Niño because of the large variability of mixed-layer chlorophyll *a* over the last two decades. Mixed-layer chlorophyll *a* differed significantly between periods of positive (1984–96) and negative (2000–2002) values for the PDO. Ascribing this difference to physical forcing associated with PDO phase changes is, again, difficult, not only because of the ap-

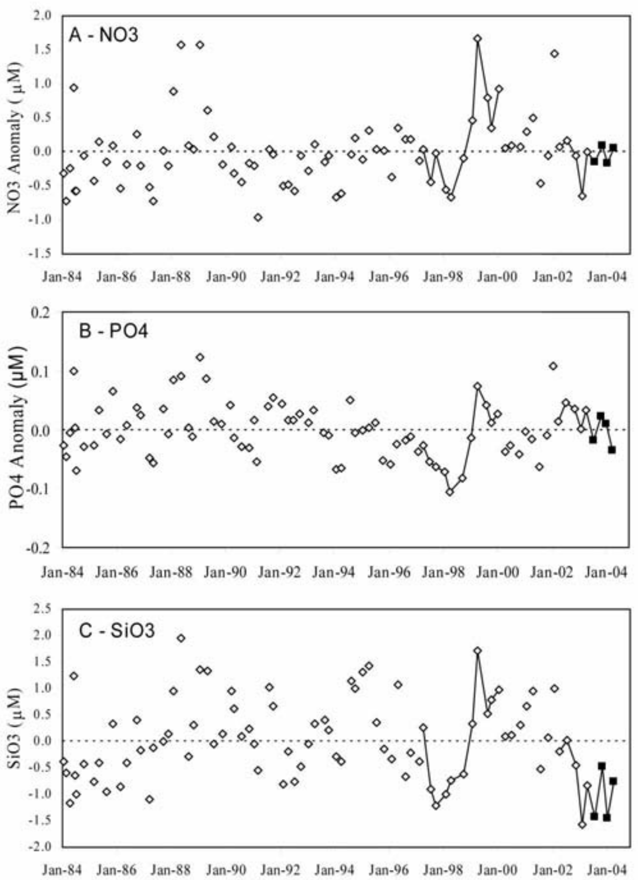

Figure 25. CalCOFI region anomalies for concentrations of (*A*) nitrate, (*B*) phosphate, and (*C*) silicate in the mixed layer. Data are derived from all 66 standard CalCOFI stations. Open symbols represent the period 1984 to spring 2003. Solid symbols represent data from the last four cruises.

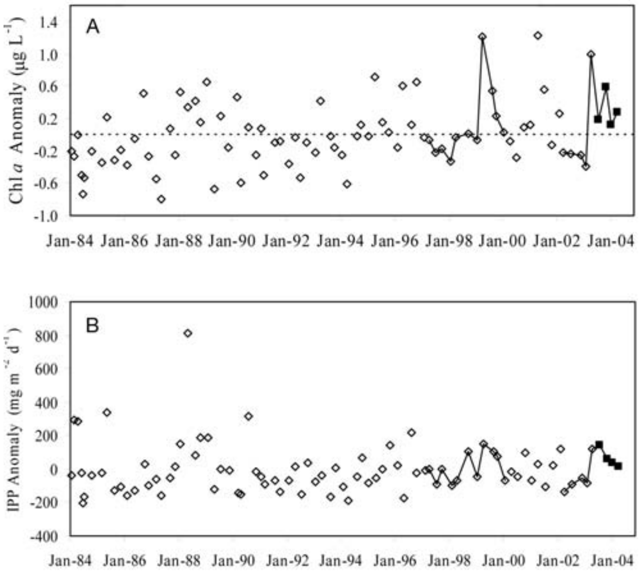

Figure 26. CalCOFI region anomalies for concentrations of (*A*) mixed-layer chlorophyll *a* concentrations and (*B*) integrated primary production (IPP). Open symbols represent the period 1984 to spring 2003. Solid symbols represent data from the last four cruises.

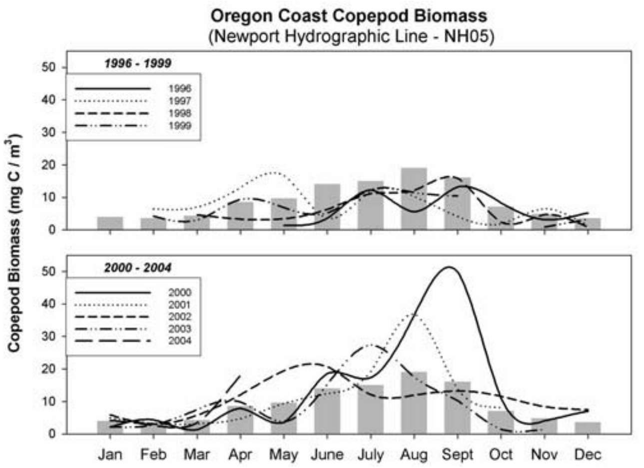

Figure 27. Seasonal and interannual patterns of copepod biomass at NH05 (60 m depth) of the NH line (45°N) compared to the 8-year climatological mean (*shaded bars*). The upper (lower) panel reveals data from 1996 to 1999 (2000 to 2004).

parent trend of increasing chlorophyll *a* over the time period 1984–96 but also because of the continuing positive chlorophyll a anomalies over the last year, even though the PDO is near neutral.

Depth-integrated rates of primary production (IPP) during the observation period (average 435 ±157 mg-C m^{-2} half-day^{-1}) were within the normal range (388 ±190 mg-C m^{-2} half-day^{-1}; fig. 26B). Patterns of IPP are too variable to detect patterns in response to interannual physical forcing.

Macrozooplankton

Oregon. Seasonal and interannual cycles of copepod biomass at NH-05 of the NH line off Oregon (44°40'N, water depth 60 m), together with an 8-year climatology, are shown in fig. 27. Seasonality is not strong, with winter and summer values differing on average by only a factor of four or so. There is no evidence for a spring peak in copepod biomass. Rather, peak values are often observed in August or September, near the end of the upwelling season. These observations are consistent with a loss of biomass to offshore waters during the active upwelling season (May–July) and that biomass in shelf waters does not begin to increase until upwelling weakens in late summer.

Copepod biomass was relatively constant for the first 4 years of the 8-year time series (fig. 27) but showed a dramatic increase (up to 200%) after the "regime shift" of 1998–99. Averaged over the May–September time period, biomass for the first 4 years of our sampling was approximately 10 mg carbon per cubic meter (8.8 m^3 in 1996, 10.3 m^3 in 1997, 10.5 m^3 in 1998, and 10.4 m^3 during the upwelling season of 1999). Although a climate shift seems to have occurred in 1999 (Peterson et al. 2002; Peterson and Schwing 2003), not until summer 2000 were significant changes in biomass observed. During 2000, copepod biomass averaged 25.5 mg carbon per cubic meter and remained high through 2001 (21.5 mg carbon per cubic meter).

During 1996 and 1997, and during the 1997–98 El Niño, copepod biomass was low, and species with southern and offshore affinities were unusually abundant in coastal waters (Mackas et al. 2005). This group includes *Mesocalanus tenuicornis*, *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus pergens*, *Clausocalnanus arcuicornis*, and *Clausocalanus parapergens*. This condition suggests that, at least during the 3-year period 1996–98, reduced coastal upwelling and low biomass characterized shelf waters of the northern California Current. However, following the onset of cool, La Niña-like conditions in 2000, copepod biomass doubled, and positive anomalies in the abundance of northern (cold-water) copepod species were observed off Newport (and off Vancouver Island; Mackas et al. 2001). The dominant members of this group include species that dominate the waters of the Bering Sea shelf, coastal Gulf of Alaska, British Columbia coastal waters, and the Washington-Oregon coastal upwelling zone—*Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae*. These indicators of "cold-water" conditions were common during the May-September upwelling seasons of 2000 and 2001, as well as the early part of 2002 (Mackas et al. 2005).

Similarly, euphausiid spawning intensity also increased. Prior to 1999, single spawning peaks were observed at the inner-shelf station. However, beginning in 1999, multiple spawning peaks were observed, and seasonally integrated egg densities were an order of magnitude higher than before (Feinberg and Peterson 2003). Marine survival of salmon stocks also showed a dramatic increase (Logerwell et al. 2003), contributing to near-record return rates of adult Chinook salmon not observed since the high-productivity years of the 1960s and 1970s.

Since 2002, however, trends in copepod biomass off the coast of Oregon suggest a high degree of variability that complicates a simple characterization based on interdecadal fluctuations of cool-water versus warm-water regimes. Greater-than-average copepod biomass was observed throughout the spring of 2002, only to be followed by a substantial decrease beginning in late June (fig. 27). This anomalous progression of events has been attributed to enhanced subarctic influence on shelf waters along the west coast (Huyer et al. 2003). The 2003 upwelling season was characterized by the onset of positive (warm) anomalies of PDO and MEI climate indexes, as well as greater-than-average biomass of southern/offshore copepod species. Although the seasonally integrated mean of total copepod biomass for 2003 was near the 8-year climatological mean (14.7 mg carbon per cubic meter), this was largely the result of an earlier-than-normal peak during mid-July, which had significantly declined by late August (fig. 27).

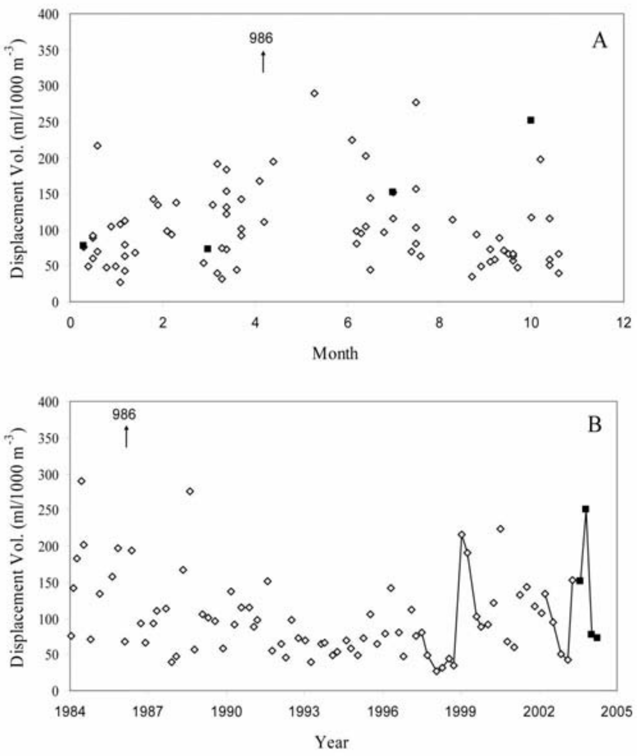

Figure 28. CalCOFI cruise mean macrozooplankton displacement volumes plotted against the month of the year (*A*) and the year (*B*). Open symbols represent the period 1984 to spring 2003. Solid symbols represent data from the last four cruises.

At the time of this writing (May 2004), the upwelling season of 2004 can be characterized by a high biomass of northern copepod species, but with continued high diversity (though low abundance) of offshore warm-water copepod species.

CalCOFI. Macrozooplankton displacement volumes during the observation period were close to the climatological mean, except for October 2003 (fig. 28A). Patterns of zooplankton displacement observed over the last ENSO cycle are surprisingly similar to the pattern observed during the previous cycle, 1997–2000 (fig. 28), including a post-El Niño bloom that is difficult to explain because the system did not enter a La Niña phase. Taken at face value, these patterns suggest that macrozooplankton biomass was affected by the recent ENSO event. This interpretation is tenuous since the recent change of the PDO phase coincided with the 1997–2000 ENSO event. It is similarly difficult to attribute the difference in zooplankton biomass between the pre- and the post-PDO phase change—for example, 1990–96 and 2000–2004—to the PDO phase change because the short period of positive PDO (1999–2004) includes not just an ENSO event; zooplankton biomass during the negative phase (1984–96) also had a significant downward

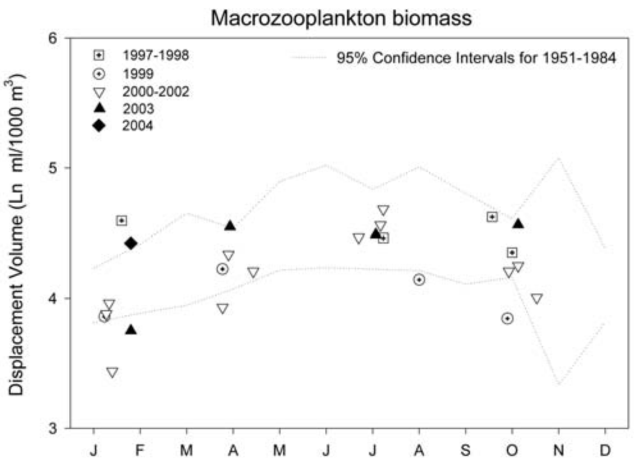

Figure 29. Mean macrozooplankton biomass for 25 IMECOCAL cruises from September 1997 to February 2004. Dotted lines indicate 95% confidence intervals for the historic mean of 1951–84 for the CalCOFI cruises in the region off Baja California. Data have been transformed to logarithms.

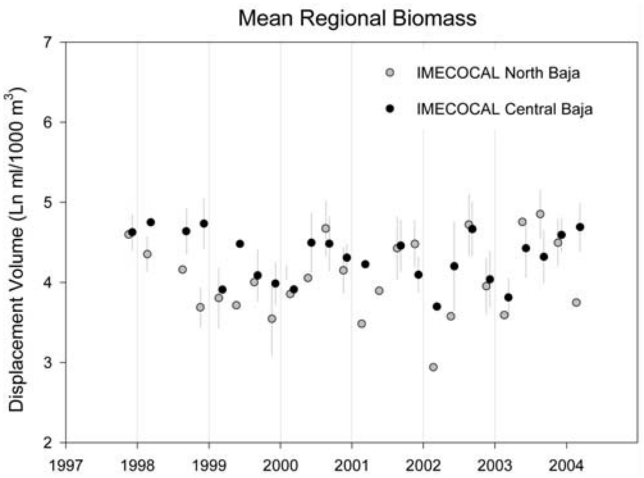

Figure 30. Mean macrozooplankton biomass in two regions of the California Current: northern Baja California (lines 100–110) and central Baja California (lines 113–133).

trend. This trend is driven by the extremely low zooplankton abundances during 1992–95. Thus, rather than looking for an effect of PDO phases on zooplankton displacement volume, one might want to ask why displacement volumes were so low during 1992–95. It is possible that these low displacement value are related to the consistently positive values of the MEI during the same period.

IMECOCAL. From April 2003 to February 2004 zooplankton biomass (i.e., displacement volumes) off Baja California was consistently high—a typical seasonal abundance cycle was not observed (fig. 29). The highest springtime values of biomass over the 1997–2004 time series were observed during the spring of 2003. Biomass during the summer of 2003 was typical for the season. Off Baja California, zooplankton biomass is usually highest during the summer and decreases in the fall. During 2003, in contrast, biomass in the region was high during the fall, similar to what was observed during the El Niño fall of 1997, despite the remarkable differences in hydrographic conditions (Lavaniegos et al. 2002). Winter is the season of lowest biomass in the region, and a sequence of extremely low values has been observed between 1999 and 2003. The winter of 2004 broke that sequence with a strong rebound, close to the mean biomass of the El Niño winter of 1998. Compared to CalCOFI data from that region collected from 1951 to 1984, the mean biomass of three of the analyzed cruises (0304, 0310, and 0401) fell in the upper limit of the 95% confidence interval (fig. 29).

Latitudinal variability in zooplankton biomass is high along the IMECOCAL area. The region from the U.S. border south to Punta Baja (lines 100–110) is characterized by low values during some periods, such as between October 1997 and April 1999, compared to the region covered by lines 113–133 (fig. 30). During other periods, however, such as July 1999 to October 2000, seasonal changes in biomass in both regions were coherent and similar to those observed in the CalCOFI region (fig. 28). Furthermore, two consecutive years (2001 and 2002) showed high regional variability in winter and spring. From October 2002 to October 2003 the three regions again showed similar trends, broken in winter 2004, with the biomass from southern California to northern Baja California being lower than off central Baja California.

Avifauna

Observations of marine bird populations provide information on the response of upper-trophic level predators to interannual and longer-term oceanographic variability. This perspective complements time series of physical variables (e.g., atmospheric pressure, upwelling indexes, thermocline depth) and lower trophic-level ecosystem constituents (e.g., phytoplankton, zooplankton, fish eggs, and larvae). CalCOFI cruises have provided the opportunity for systematic surveys of the distribution and abundance of marine birds and mammals in relation to oceanographic conditions off southern California since 1987.

The Point Reyes Bird Observatory (PRBO) Marine Ecology Division has monitored the reproductive performance and diet of seabird populations breeding at the Farallon Islands (37°N, 123°W) since the early 1970s. These time series have revealed that locally breeding bird populations are sensitive to shifts in ocean climate and prey availability over short (interannual) and long (decadal) temporal scales (Sydeman et al. 2001; Abraham and Sydeman 2004). In this report we compare at-sea and colony-based observations of marine bird populations collected during 2003–2004 with data from the CalCOFI and PRBO time series. Our objective is to quantify the interannual variability in marine bird community structure and productivity off the west coast of North America since the 1998–99 transition into a cold-water regime (Bograd et al. 2000; Durazo et al. 2001; Schwing et al. 2002; Peterson and Schwing 2003; Venrick et al. 2003).

We describe changes in seabird communities during spring and fall CalCOFI cruises after the winter of 1999. To place these observations in a broader context, we also include in this analysis observations from cruises during a period of warm-water (El Niño: fall 1997 and spring 1998) and cold-water (La Niña: fall 1998 and spring 1999) anomalies. During spring and fall, the avifauna is especially affected by incursions of warm-water and cold-water taxa. We focus, in particular, on four indicator species with different water-mass preferences and biogeographic affinities to illustrate short-term (interannual) fluctuations in the composition of marine bird communities. The subtropical black-vented shearwater (*Puffinus opisthomelas*) shifts its distribution northward into the CalCOFI study area during warm-water years. The Cook's petrel (*Pterodroma cooki*) is an offshore spring-summer visitor that moves shoreward during warm-water periods; its abundance increased significantly off southern California from 1987 to 1998. The numerically dominant cold-water species, the sooty shearwater (*Puffinus griseus*), is a spring–fall visitor whose abundance declined by about 74% from 1987 to 1998. Finally, the black-legged kittiwake (*Rissa tridactyla*) is a subarctic winter visitor from Alaska that becomes more numerous during cold-water years, particularly in spring (Lynn et al. 1998; Hayward et al. 1999; Hyrenbach and Veit 2003; Venrick et al. 2003).

During the fall cruise of 2003, the avifauna was dominated by phalaropes (Red, *Phalaropus fulicaria*, and Red-necked, *P. lobatus*) and western gulls (*Larus occidentalis*), which accounted for over 39% and 19%, respectively, of all birds sighted. No kittiwakes were observed within the study area, and the sooty shearwater contributed only 6% of all birds recorded. Similarly, the subtropical black-vented shearwater accounted for only 4% of all birds sighted, and few Cook's petrels were recorded within the CalCOFI survey grid at this time. Overall, the avifauna during the fall 2003 cruise consisted of a mixture of subtropical and subarctic taxa, without compelling evidence of incursions by warm-water or cold-water visitors. This mixed community structure was consistent with the concurrent pattern of simultaneous positive (+1.5°C) and negative (−1.5°C) SST anomalies off southern California at that time (El Niño Watch Advisory, October 2003, http://coastwatch.pfel.noaa.gov/cgi-bin/elNiño.cgi).

These intermediate oceanographic conditions, with low-amplitude temperature anomalies and a slightly positive MEI suggestive of weak El Niño conditions (http://www.cdc.noaa.gov/people/klaus.wolter/MEI/mei.html), prevailed from the summer of 2003 to the spring of 2004. By April 2004, the avifauna was dominated by endemic western and California (*L. californicus*) gulls, accounting for 28% and 11%, respectively, of all birds sighted. The kittiwakes were not recorded for a third consecutive year, and the sooty shearwaters, accounting for less than 1% of all the birds recorded, were also virtually absent. Though the black-vented shearwater and the Cook's petrel were present in very low numbers within the study area, there was evidence of northward shifts in range by other warm-water species. In particular, the black storm-petrel (*Oceanodroma melania*), a subtropical species known to expand its range into the CalCOFI region during El Niño events, occurred off southern California at this time (Lynn et al. 1998; Hyrenbach and Veit 2003).

To characterize the patterns observed during 2003–2004 in a broader context, we addressed interannual variability in seabird community structure after the 1998–99 regime shift. We considered all the species sighted during at-sea surveys and used cluster analysis to identify groups of years with similar community structure. We considered fall and spring cruises separately and included observations from an El Niño (fall 1997, spring 1998) and a la Niña (fall 1998, spring 1999) event as "outgroups" to better resolve the year-to-year variability.

The community structure of the avifauna observed during the fall of 2003 was similar to that documented during previous fall cruises after the 1998–1999 regime shift (fig. 31). The hierarchical clustering revealed only one cluster containing all cruises (1999–2003) except for the El Niño (1997) and the La Niña (1998) periods. Three of these years (1999, 2001, and 2003) were characterized by a mixed community structure with low levels (< 10% of all birds sighted) of warm-water and cold-water indicators. The two other years in this cluster (2000 and 2002) were characterized by a stronger subtropical influence, with substantial black-vented shearwater incursions (> 10% of all birds) and low sooty shearwater abundance (< 1% of all birds). These results underscore the mixed nature of CCS seabird communities in the last few years, without clear numerical dominance of warm-water or cold-water taxa (Venrick et al. 2003).

The hierarchical grouping revealed two distinct clusters of spring cruises (fig. 32). The first cluster, comprising 3 years (2002, 2003, and 2004), was characterized by intermediate community structure, with low levels of cold-water and warm-water indicators. In particular, it is noteworthy that the black-legged kittiwake, a subarctic species that accounted for over 10% of all birds sighted in spring 1999, has not been observed off southern California during the last three spring cruises.

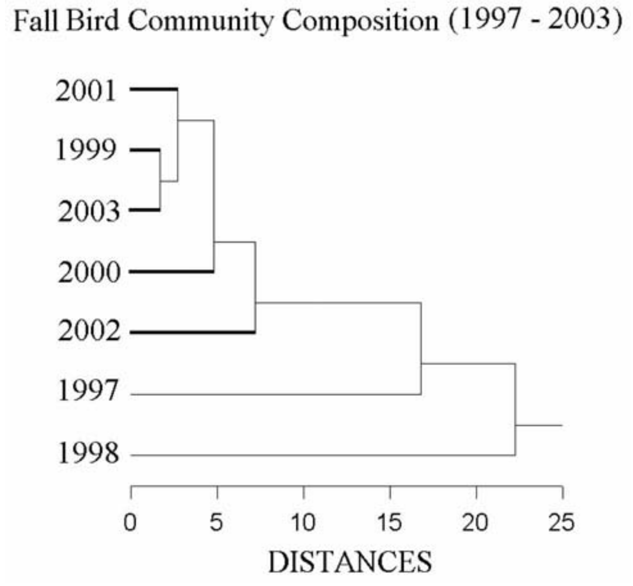

Figure 31. Cluster tree of marine bird community structure at-sea off southern California during fall CalCOFI cruises (1997–2003). The euclidean distances are based on the hierarchical clustering technique, with the median linkage algorithm. The thick lines identify years in the same cluster.

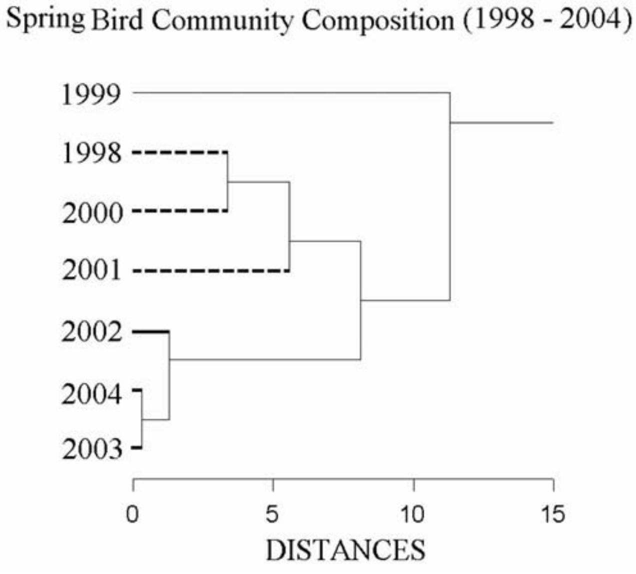

Figure 32. Cluster tree of marine bird community structure at-sea off southern California during spring CalCOFI cruises (1998–2004). The euclidean distances are based on the hierarchical clustering technique, with the median linkage algorithm. The dashed lines and the continuous thick lines identify years in the two different clusters.

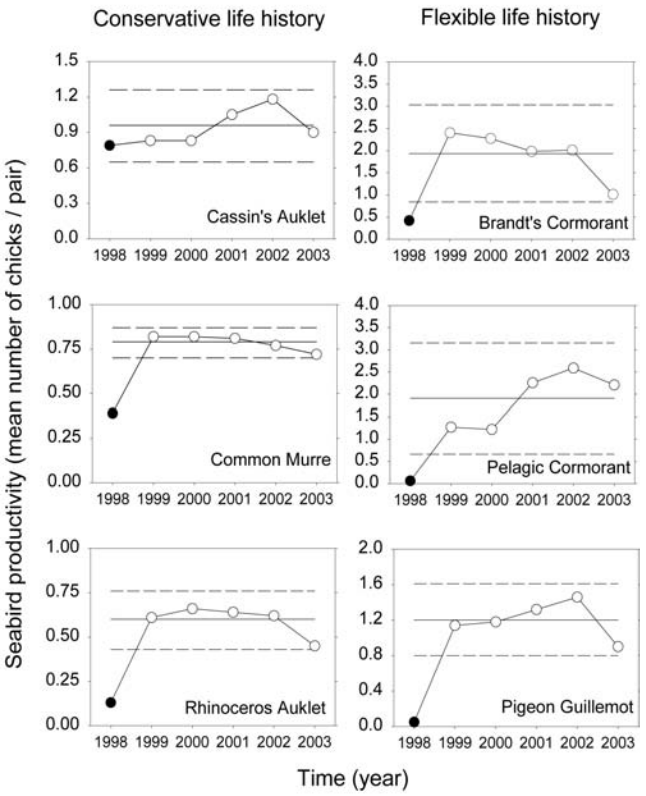

Figure 33. Anomalies of productivity for six seabird species breeding at Southeast Farallon Island (off central California). Solid horizontal lines indicate the long-term averages (1990–2002); hatched lines indicate the variability (mean ±2 SD). Solid circles highlight productivity values during the 1998 El Niño.

Similarly, the sooty shearwater has remained at low levels (< 1% of all birds) during the last three spring cruises (Venrick et al. 2003). The second cluster, comprising 3 years (1998, 2000, and 2001), was characterized by a slightly higher presence of sooty shearwaters (> 10% of all birds sighted) and intermediate levels of Cook's petrels. These results suggest that, in spite of transient incursions of warm-water species (2000 and 2001) similar to those during the 1998 El Niño event, springtime seabird communities off southern California from 1999 to 2004 have remained intermediate between a subtropical and a subarctic avifauna (Venrick et al. 2003).

Observations of marine bird populations breeding at the Farallon Islands, on the edge of the continental shelf west of San Francisco, revealed a widespread decrease in productivity during 2003, after record high reproductive performance during the previous year (Venrick et al. 2003). When we considered three species with conservative life histories (Cassin's auklet, *Ptychoramphus aleuticus*; common murre, *Uria aalge*; rhinoceros auklet; *Cerorhinca monocerata*) and three species with flexible ones (Brandt's cormorant, *Phalacrocorax penicillatus*; pigeon guillemot, *Cepphus columba*; pelagic cormorant, *P. pelagicus*), the mean number of chicks produced per breeding pair declined across the board in 2003 (tab. 1; fig. 33). Nevertheless, the mean species-specific productivity remained significantly higher after the hypothesized regime shift (1999–2003) than during the preceding warm-water period (1990–98) (Wilcoxon paired test, $Z = 2.201$, $n = 6$ species, $p = 0.028$).

TABLE 1
Productivity of Six Seabird Species Breeding at the Southeast Farallon Island (Central California), Before (1990–98) and After (1999–2003) the 1998–99 Regime Shift

	Productivity (chicks fledged per pair)		
Seabird species	Average, 1990-98 (mean +S.D.)	Average, 1999-2003 (mean +S.D.)	Proportional, 2002 vs. 2003 (% change)
Brandt's cormorant	1.38 ±0.93	1.93 ±0.55	−49.75
Cassin's auklet	0.62 ±0.24	0.96 ±0.15	−23.73
Common murre	0.66 ±0.27	0.79 ±0.04	−6.49
Pelagic cormorant	0.54 ±0.64	1.91 ±0.62	−14.67
Pigeon guillemot	0.54 ±0.38	1.20 ±0.20	−36.99
Rhinoceros auklet	0.48 ±0.16	0.60 ±0.08	−27.42

Note: The proportional change in seabird productivity from 2002 to 2003 is quantified as PC = 100% * [(2003 value) − (2002 value) / (2002 value)]. Positive and negative PC values indicate increasing and decreasing productivity, respectively.

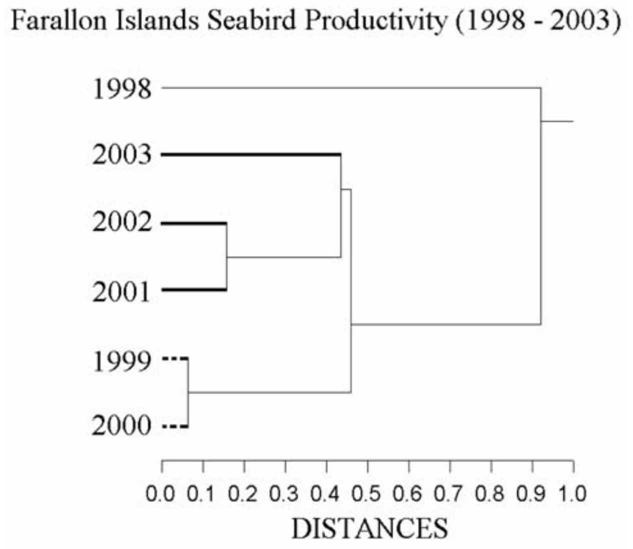

Figure 34. Cluster trees of marine bird productivity (mean number of chicks produced per breeding pair) for six species breeding at Southeast Farallon Island from 1998 to 2003. The euclidean distances are based on a hierarchical clustering technique, with the median linkage algorithm. The dashed lines and continuous thick lines identify years in the two different clusters.

Hierarchical clustering of the productivity data revealed two clusters of years after the 1998–99 regime shift: one containing two early years (1999 and 2000), and the other including the three subsequent years (2001, 2002, and 2003) (fig. 34). After the pervasive increase in reproductive performance during 1999 and 2000, the six monitored species behaved differently. A clear dichotomy was apparent in 2001. The reproductive success of three species (the planktivorous Cassin's auklet and the piscivorous pelagic cormorant and pigeon guillemot) soared, surpassing their long-term (1990–2002) average values by 1 standard deviation, and continued to increase in 2002. Conversely, the productivity of the three other piscivorous species (Brandt's cormorant, common murre, and rhinoceros auklet) declined in 2001 and leveled off or continued to decrease in 2002 (Venrick et al. 2003).

DISCUSSION

The state of the CCS over the last few years was potentially affected by three distinct factors: the change from a warm PDO phase over to the Victoria mode, the equatorial ENSO event, and the intrusion of subarctic waters into the system. Over the last year, the state of the system, when viewed from different perspectives, has been near neutral. This is also true for the whole North Pacific Basin.

ENSO Events

A La Niña phase of the recent ENSO event was undetectable in the equatorial Pacific. The climatological anomalies derived from observations made in the CCS, such as temperature, mixed-layer depth, and nutricline depth fields, have been near zero over the last year. Upwelling anomalies along the cost were little affected by the last El Niño (fig. 3). Anomalies of macronutrient concentrations in the CalCOFI region were either near zero (nitrate or phosphate) or displayed a pattern that was not affected by the ENSO event (silicate, fig. 25).

Temporal changes of the plankton and avifauna, relative to the recent ENSO event, differed greatly among different groups of organism and localities. Off Oregon, a large increase in phytoplankton biomass has been observed over the last 2–3 years, a signal clearly unrelated to the recent ENSO event and potentially masking its more subtle effects on the ecosystem. Zooplankton biomass off Oregon has been significantly larger over the last 4 years as well, when compared to the previous 4 years, with interannual variability masking effects that could be attributed to the recent ENSO event. Off southern California, temporal patterns of mixed-layer chlorophyll *a* and zooplankton biomass anomalies were very similar during the ENSO events of 1997 and 2002. The similarity of the patterns is disconcerting considering that the two ENSO events differed not only dramatically in strength, the latter having hardly any effect on the physical state of the CCS, but also in the development of a La Niña phase. Zooplankton biomass off Baja California covaried with zooplankton biomass off southern California only during the most recent ENSO event, not during the event beginning in 1997, suggesting that these patterns were not necessarily forced by the El Niño events.

The avifauna in the CalCOFI region was not affected substantially by the recent ENSO event. The spring seabird communities from 2002 to 2004 were virtually indistinguishable, that is, they were not affected by the recent ENSO cycle. The patterns observed during the fall are not that clear cut; however, the seabird communities of 2002 and 2003 were distinctly different from the ENSO-affected communities of 1997 and 1998. Despite a widespread decline in the productivity of seabird populations breeding off central California in 2003, annual reproductive success (number of chicks produced per breeding pair) at the Farallon Islands remained considerably higher than during the 1998 El Niño episode.

As has been concluded previously (Venrick et al. 2003), the data available for the CCS show that the recent El Niño had only a small to moderate effect on the CCS. Since a La Niña did not develop in the equatorial Pacific, La Niña-like conditions in the CCS were not expected. Thus, the similarity of some biological patterns off southern California with those observed during previous complete El Niño–La Niña cycles must be related to physical forcing other than ENSO.

Subarctic Influence on the CCS

There was enhanced subarctic influence on the California Current in 2002 (e.g., Freeland et al. 2003; Bograd and Lynn 2003). The CCS has strong subarctic characteristics: it is the only subtropical eastern boundary current in which salinity increases monotonically with depth. North of Point Conception, normal advection of cool, low-salinity, nutrient-rich subarctic waters enhances the productivity associated with coastal and offshore upwelling that is driven by the alongshore winds and by positive wind-stress curl, but this advective influence was stronger than usual in the late winter and spring of 2002 (Strub and James 2003; Barth 2003; Kosro 2003). This enhancement was apparently not related to either the MEI or the PDO but nevertheless resulted from anomalous winds over the northern North Pacific (Murphree et al. 2003). The anomalous wind field shows that both the Aleutian Low *and* the North Pacific High were stronger than normal in 2002. Bond et al. (2003) suggests that this pattern is orthogonal to the PDO. In any case, the oceanic effects of such a large-scale climatic anomaly are likely to persist for at least a year or two, since oceanic advection is so much slower than atmospheric advection. Thus, it is not surprising that anomalously cool, nutrient-enriched waters and high biomass were observed throughout the California Current region in 2003.

Off Oregon, cool, fresh, and likely nutrient-rich subarctic waters were observed intermittently over the last year, with anomalies strongest in the upper halocline. Anomalies observed in 2002 were stronger than those observed in 2003. Off southern California, the anomalies are now found in most areas of the CalCOFI region (fig. 13). These were first evident during 2001 and 2002 (Venrick et al. 2003) as subsurface anomalies at offshore stations but have since spread to the surface and to stations along the coast. The anomalies still tend to be strongest at the offshore stations, where conditions since 2003 have not changed much, but these have intensified over the last year at the inshore stations. Associated with the change in water masses, particularly at the offshore stations, was a shallowing of the seasonal thermocline and the nutricline. In contrast to the salinity data, which suggest a massive change in the upper 100-150 m of the system (fig. 13), climatologies of other water-column properties do not show such large anomalies over the last 2–3 years, with the exception of silicate. This contrast may not be that surprising when considering that properties such as salinity are strongly affected by advective forcing into the region, whereas properties such as SST are strongly affected by local atmospheric forcing. The expected effect of this subarctic influence on the ecosystem is an enrichment (Wheeler et al. 2003). The dramatic changes in phytoplankton biomass off Oregon over the last year are a likely consequence of this effect. Off southern California, much less dramatic domainwide changes in ecosystem properties were noticed over the last 2 years. However, a slight positive anomaly in mixed-layer chlorophyll *a* was observed, a likely consequence of this enhanced subarctic influence. More dramatic changes in ecosystem structure are evident in the offshore areas where the depth of the chlorophyll-maximum has changed over the last years from approximately 100 m to 80 m (data not shown). This ~20 m change corresponds to a 30 m change in the depth of the nutricline in that region. Negative temperature anomalies were found throughout the region off Baja California. However, these were not associated with negative temperature anomalies. These observations suggest that this region too has experienced an increased influence of subarctic waters (Lavaniegos et al. 2003; Durazo et al. submitted).

The State of the CCS after the 1998 Regime Shift

The state of the California Current system changed dramatically in 1998–99 (Chavez et al. 2003; Lavaniegos and Ohman 2003; Brinton and Townsend 2003; Peterson and Schwing 2003). It was hypothesized that this change represented a "regime shift" associated with a change in the sign of the PDO, and it was anticipated that the system would remain in this state for a long time. Recent studies, however, have shown that patterns of SST anomalies over the North Pacific since 1998 do not resemble those characteristic of a cool phase of the PDO (Bond et al. 2003). Rather, the North Pacific until 2003 was characterized by cool anomalies in the CCS but warmer conditions in the subarctic Pacific (Bond et al. 2003), a pattern called the Victoria mode. However, as stated above, conditions at present do not appear to be representative of either the PDO or Victoria modes. Indeed, the PDO has been slightly positive the last 2 years after a period of negative values since 1998.

Temperature anomalies in the CCS, which had responded dramatically to the 1998 climate shift, have been neutral over the last 2 years (e.g., fig. 11B). Off Oregon, dramatic changes in ecosystem structure have been observed since 1999, during which the recent trend for enhanced summer upwelling is associated with an overall increase in ocean production for this region, including primary production, and more plankton, small bait fish, and salmon in the Pacific Northwest. Off southern California mixed-layer concentrations of chlorophyll *a* have been significantly higher since 1998. However, ascribing these differences to physical forcing associated with a recent climate shift is not possible because of the possible trend of increasing mixed-layer chlorophyll *a* concentrations over the last two decades (fig. 26A). Anomalies of primary production off southern California were close to climatological means during either phase of the PDO. Zooplankton displacement volumes have been significantly higher during the last 5 years compared to the previous 5 years, 1992–97. Unfortunately, time series based on data collected off Baja California are too short, but compared to the CalCOFI data collected in the region from 1950 to 1978 they indicate a lag in the response to increased zooplankton biomass until 2000.

Surveys of marine bird communities at sea have failed to detect clear avifaunal signals suggestive of a transition into a persistent cold-water regime in the California Current since the winter of 1999. The "mixed" nature of the avifauna since the 1998–99 regime shift is underscored by the hierarchical clustering analyses of fall and spring cruise data (figs. 31 and 32). The seabird communities documented during recent fall cruises differ from the avifauna observed during 1997 and 1998 (Lynn et al. 1998; Hayward et al. 1999; Venrick et al. 2003). Similarly, in spite of episodic incursions of warm-water species (2000 and 2001), the springtime seabird community structure during the last 5 years (2000–2004) has remained intermediate between a subtropical and a subarctic avifauna (Lynn et al. 1998; Venrick et al. 2003). Thus, we conclude that the composition of seabird communities reflected the struggle for dominance by subarctic and subtropical influences in the CCS.

Because seabirds integrate the variability in oceanographic conditions and prey resources during the breeding season, we expected a strong response of the Farallon productivity indexes to recent year-to-year oceanographic variability (Ainley et al. 1995; Sydeman et al. 2001). Indeed, the diet and demography of seabirds are the population-level attributes most sensitive to fluctuations in the marine environment and prey availability (Montevecchi 1993). In spite of widespread declines in productivity across all six species monitored in 2003 (fig. 33), which we interpret as a response to El Niño conditions, the average values after the regime shift (1999–2003) remain much higher than those observed during 1990–98, when the ocean off central California was considerably warmer (tab. 1). This result suggests that breeding seabird populations continue to benefit from the transition into a cold-water regime of enhanced upwelling and prey availability. This has been reflected in the return of juvenile rockfish (*Sebastes* spp.) as a major prey item in the diet of the piscivorous species (Venrick et al. 2003; Mills et al., in press; Miller and Sydeman 2004); in the increase in the take of *Thysanoessa spinifera*, the larger bodied coastal euphausiid in this region, by planktivorous auklets (Abraham and Sydeman 2004); and in an offshore shift in the distribution of breeding common murre (May–June) in the Gulf of the Farallones from 1996–97 to 2001–2002, reversing an onshore trend previously described during the preceding warming period (1985–94) (Oedekoven et al. 2001; Yen et al. 2004).

CONCLUSION

Climatologically, the past year has been near neutral, both on basin and CCS scales. However, much of the data discussed here, particularly that collected off Oregon, support the hypothesis that the CCS is still in a state of higher ecological productivity that began in late 1998 (Peterson and Schwing 2003). It is unclear, however, if the observed changes were driven by changing physical forcing associated with the 1998 shift or by other factors. Increased phytoplankton biomass off Oregon, for example, may have been driven by the stronger subarctic influence. Indeed, this stronger subarctic influence is the most interesting phenomenon currently occurring in the CCS. Freeland et al. (2003) suggests that stronger subarctic influence is merely the result of a combination of stochastic processes—that is, coincidence, in which case it would be expected not to persist for longer periods of time. However, it is also possible that the enhanced southward transport of the California Current associated with the increased subarctic influence reflects a spin up of the entire Subtropical Gyre following the 1998 regime shift, in which case it can be expected to affect the CCS over a longer period.

The evolution of the current neutral oceanographic conditions in the tropical Pacific Ocean over the next months remains unclear as well, with forecasts ranging from neutral to full-fledged El Niño conditions beginning in the summer of 2004. Yet, because none of the forecasts indicate that a La Niña event will develop during 2004, we can anticipate neutral or warm-water conditions in the next 3–6 months (Climate Prediction Center ENSO Diagnostic Discussion, http://www.cpc.ncep.noaa.gov). On a longer time scale, the continued strengthening of the PDO index, which has remained slightly positive since August 2002, may indicate a developing shift back into a warm-water regime (http://jisao.washington.edu/pdo/PDO.latest). This uncertainty will set the stage for 2005.

The onset of an El Niño event would represent a great natural experiment to quantify the ecosystem response to a transient warm-water period, superimposed on a potentially longer-term cold-water regime. Additionally, a transition back into a warm-water regime would provide an excellent opportunity to contrast the behavior of the CCS during a warm-cold and a cold-warm transition. The ability to monitor and interpret these future fluctuations in the CCS depends on the existence of long-term time series of the physical, chemical, and biological ecosystem constituents (McGowan 1990).

ACKNOWLEDGMENTS

This report would not have been possible without the dedicated work of the ship crews and technician groups who collected the data, often under adverse conditions. We thank José M. Domínguez, Francisco J. Ponce, Xuemei Qiu, and Jim Wilkinson for help drafting the figures. The GLOBEC LTOP program in the northern California Current is supported by the National Science Foundation (OCE-0000733). The November 2003 sampling of the NH line sampling was supported by the National Oceanic and Atmospheric Administration. This is a contribution of the U. S. GLOBEC Program and was jointly funded by the National Science Foundation and the National Oceanic and Atmospheric Administration. We thank the officials and crew of the CICESE RV *Francisco de Ulloa*, as well as the students and technicians participating in the surveys. The IMECOCAL program was funded by G-35326-T CONACYT (Consejo Nacional de Ciencia y Tecnología-México) project and by CICESE (Centro de Investigación Científica y de Educación Superior de Ensenada) ship time support. Joaquin Garcia-Cordova and Gilberto Jeronimo helped in data processing. Carol Keiper and Cornelia Oedekoven (PRBO) conducted bird observations during 2003–2004 CalCOFI cruises. Pete Warzybok and Russell Bradley (PRBO) supervised collection of Farallon seabird data in 2003. Christine Abraham, Chris Rintoul, and Peggy Yen (PRBO) compiled the seabird data used in this report. The seabird data sets were collected with support of the U.S. Fish and Wildlife Service, the National Fish and Wildlife Foundation, the Packard Foundation, and the Friends of the Farallones. This is PRBO contribution no. 1196.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

Asilomar Conference Center
Pacific Grove, California
6 November 2003

ENVIRONMENTAL VARIABILITY AND ITS IMPACT ON INVERTEBRATE FISHERIES

The importance of oceanic conditions for the productivity of marine fisheries is increasingly being acknowledged. Environmental fluctuations on interannual and interdecadal time scales (Hare and Mantua 2000) complicate fishery science and management. Intense fishing pressure, more suited for highly productive conditions, can interact with poor environmental conditions and result in stock depletion. In the eastern Pacific it has long been recognized that populations of fish and the organisms they interact with respond to short-term El Niño Southern Oscillation (ENSO) events as well as to Pacific Decadal Oscillations (PDO), that is, interdecadal ocean "regimes" of warm or cool ocean conditions (Ebbesmeyer et al. 1991; Mantua et al. 1997). Sardine populations appear to have increased dramatically during the last interdecadal warm period (Jacobson and MacCall 1995), which suggests they are a "warm-water species," while rockfish (Love et al. 1998) and salmonid populations appear to have declined under these conditions (Mantua et al. 1997).

Less is known about the impacts of ocean conditions, both short- and long-term, on invertebrate populations and fisheries. Clearly, ocean conditions affect invertebrate fisheries, as is dramatically demonstrated by California's market squid (*Loligo opalescens*) fishery, which nearly collapses during El Niño events. One of the mysteries associated with this phenomenon is how squid populations rebound after warming events given their short life span (< 1 year). Long-lived invertebrates, such as red abalone (*Haliotis rufescens*) off southern California, are also affected by El Niño, exhibiting lower growth rates in warmer water (Haaker et al. 1998) and indirect effects from reductions in the quantity and quality of kelp food resources (Vilchis et al. 2004).

The increasing demand for marine invertebrate resources worldwide magnifies the importance of understanding the relationship between ocean conditions and invertebrate productivity. In California, invertebrate fisheries have surpassed finfish fisheries in both volume and ex-vessel price, making them among the most important fisheries in the state (Rogers-Bennett 2002), as is the case elsewhere (Caddy 1989). Fished marine invertebrates are a diverse group that exhibit a wide range of life-history strategies, from short-lived species that have mating behaviors (e.g., market squid) to long-lived, free-spawning species (e.g., sea urchins, *Strongylocentrotus franciscanus*) that have a variety of larval planktonic periods. However, little work has been done with invertebrate fisheries to weigh the potential benefits of fixed versus variable management and recovery strategies in response to variable environmental conditions (MacCall 2002). If we are to better manage this diverse group, we need to have a more mechanistic understanding of the relationship between environmental variability and marine invertebrate productivity so that these factors can be explicitly incorporated into population and fishery models.

The articles in this section are based on presentations given at CalCOFI's 2003 symposium "Environmental Variability and Its Impact on Invertebrate Fisheries."[1] Christian Reiss and his coauthors describe the dramatic effects of warm-water El Niño events on squid paralarvae during winter in the Southern California Bight and on adults during summer in the California Current. They show that temperature at hatching plays a significant role in the variability of mean growth rates of squid, and they present an age-based, temperature dependent population model for squid.

J. M. (Lobo) Orensanz and his coauthors describe a basinwide contraction in the geographic distribution of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea that started with the positive PDO warming phase three decades ago. Subsequent cooling in the 1990s,

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[1] Several presentations made at the symposium were not submitted for publication in *CalCOFI Reports.*

however, did not result in southern crab reoccupying its historical grounds, possibly as a consequence of the expansion of predatory cod or of impediments to larval dispersal. The authors propose an "environmental ratchet hypothesis" in which grounds lost during warm periods may not be reoccupied during cool periods, a feature that may be generally applicable to benthic invertebrate populations.

Juan Valero and his coauthors describe a steady decline in recruitment of geoduck clams (*Panopea abrupta*) from 1940 to 1970 followed by a post-1975 recovery that correlates with two environmental variables: sea surface temperature (positively) and river discharge (negatively). This recruitment pattern appears to be geographically coherent between British Columbia and Washington State and consistent with the hypothesis that large-scale climactic forcing drives these patterns.

Chris Harley and Laura Rogers-Bennett examine the potential combined effects of climate change and fishing on exploited intertidal invertebrate populations. Intertidal populations are particularly vulnerable to climate change since many species live at their physiological extremes and are exposed to both atmospheric and oceanic conditions. The authors use three case studies to demonstrate how species-specific life-history traits and fishing intensity influence the effects of climate on populations, as well as how there may be synergistic interactions between fishing and climate.

Laura Rogers-Bennett

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CONTRACTION OF THE GEOGRAPHIC RANGE OF DISTRIBUTION OF SNOW CRAB (*CHIONOECETES OPILIO*) IN THE EASTERN BERING SEA: AN ENVIRONMENTAL RATCHET?

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ABSTRACT

Over the last three decades the geographic range of distribution of snow crab (*Chionoecetes opilio*) from the eastern Bering Sea (EBS) has contracted dramatically to the north. An increase in near-bottom temperature (NBT) during 1975–1979 was accompanied by a northward contraction of the cold pool (bound by the 2°C NBT isotherm) that extends over the Middle Domain during the summer. Warming was tracked with a 6-year lag by a contraction to the north of the mature female's range. Snow crab settle and grow to maturity in the Middle Domain. Successful recruitment during cold regimes may result from the occurrence of spring blooms and the stenothermy of early benthic instars. However, recruitment to the mature female population did not expand back to the southern shelf after the mid-1990s, despite some years when NBT was low. Cross-correlation of year-to-year shifts in geographic distribution of cod (*Gadus macrocephalus*) and immature snow crab during the 1990s suggests that the northward expansions of cod controlled the southern boundary of snow crab's distribution range. Reestablishment of crab populations in the south may be hindered by cod predation. Also, because spawning females are now located "up-current," advection of larvae to the south is unlikely. Contraction to the north may not be followed by an expansion back to the south after a change in regime. We refer to this suggested asymmetry as the environmental ratchet hypothesis and discuss it in the context of other conceptual models of the EBS ecosystem.

INTRODUCTION

The geographical range of snow crab contracted to the north in the eastern Bering Sea (EBS) during the 1980s and 1990s (Zheng et al. 2001; Ernst et al. 2005). Estimated abundance and catch quotas declined, reaching historically low levels by 2000–2003 (Stevens et al. 2002). Since this is one of the largest crab fisheries in the world, the economic implications of the trend are significant; consequently, federal disaster relief funds have been directed toward studies of population dynamics and life history. It has been proposed that a possible cause of the contraction in range and reduction in abundance of snow crab is the regime shift that occurred in 1976–1977 (Adams and Bond 1999). During the ensuing period of intensification, seawater was generally warmer, and this could cause snow crab to concentrate in the colder northern shelf (Zheng et al. 2001). But the possible mechanisms linking climate to the contraction of the snow crab's range have not been considered.

This range contraction and abundance reduction is not an isolated phenomenon: during the same period other significant changes have been documented in the EBS ecosystem. Many economically significant stocks have fluctuated dramatically, and there has been much concern about disruptions of commercial fisheries (e.g., red king crab, *Paralithodes camtschaticus*; Loher 2001) and declining populations of some marine birds and mammals (Hunt et al. 2002). A growing understanding of the EBS pelagic ecosystem has led to the formulation of rich conceptual models and complex testable hypotheses, such as the oscillating control hypothesis (Hunt et al. 2002; Hunt and Stabeno 2002).

While changes in the pelagic subsystem have received considerable attention, changes in the benthic subsystem remain poorly understood. Unlike fish, benthic invertebrates are sedentary or move slowly, so their spatial response to environmental change has a different tempo. Because spatial structure is comparatively persistent in benthic populations (Orensanz and Jamieson 1998), a spatially explicit approach to investigating the system is necessary and can be revealing.

Crab stocks of the EBS have been surveyed with a consistent design during the last three decades (Zheng et al 2001; Stevens et al. 2002). Only recently has this rich data set been used to explore their spatial dynamics (Zheng et al 2001; Ernst et al. 2005). In this study we use that data set and several pieces of environmental information to investigate the dramatic contraction to the north of the snow crab population. We address possible

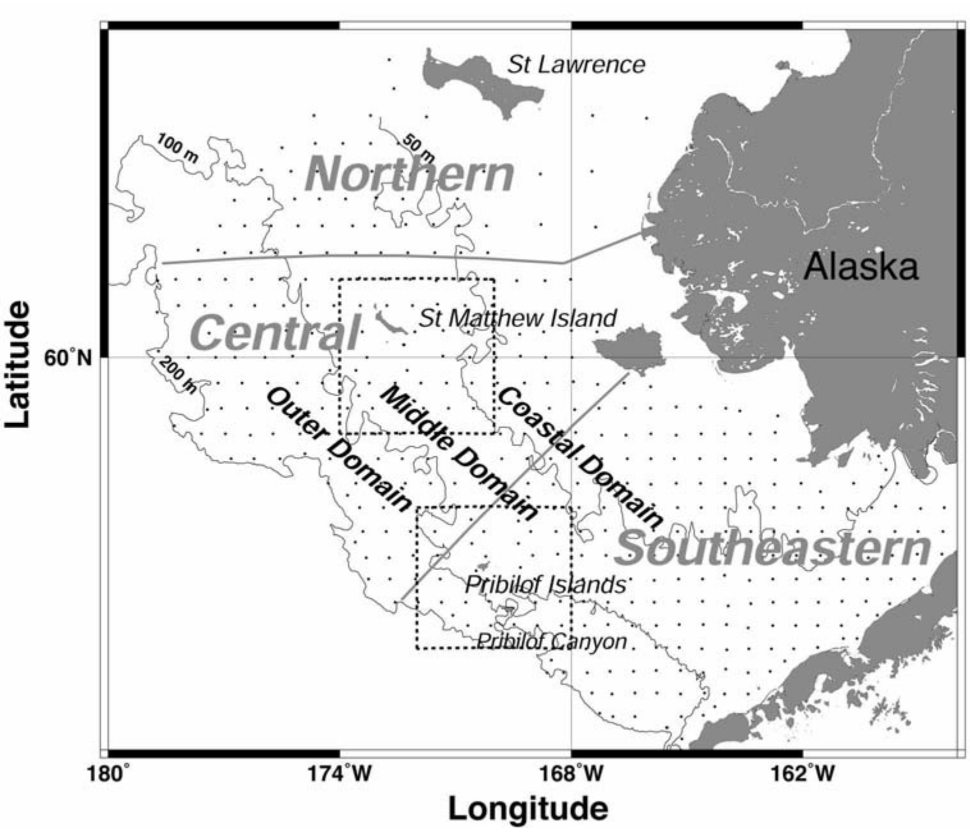

Figure 1. The eastern Bering Sea (EBS). Dots indicate NMFS survey stations where snow crab was observed at least once during surveys conducted between 1975 and 2001. Dashed rectangles around the Pribilof ("south") and St. Matthew ("north") Islands indicate windows that were defined to calculate time series of average near bottom temperature (NBT).

effects of the environment and predators on different life history stages and propose a composite hypothesis (the environmental ratchet hypothesis) to explain the contraction and to link the phenomenon to other oceanographic and ecological processes in the EBS.

BRIEF DESCRIPTION OF THE STUDY SYSTEM

The EBS Shelf

The extensive shelf of the EBS, more than 500 km wide, ends seaward in a shelf-break (generally coincidental with the 200 m isobath) that spreads northwest to southeast. The two main geographical features are St. Matthew Island and the Pribilof Islands (fig. 1). The shelf is conveniently partitioned in three sectors (Schumacher and Stabeno 1998, their fig. 27.1): northern, central, and southeastern. The central and southeastern sectors, the geographic setting of our study, extend from the Alaska Peninsula in the southeast to north of St. Matthew Island. Three zones or domains are usually recognized (Schumacher and Stabeno 1998): inner or coastal (shorewards from the 50 m isobath), middle (between the 50 and 100 m isobaths), and outer (between the 100 m isobath and the shelf-break). The Outer Domain is cut in two naturally discrete segments (southeast and northwest) by the Pribilof Canyon (fig. 1). Up to 75% of the EBS shelf water is covered by ice in late fall to early spring. The advance and retreat of ice averages about 1,700 km and is the most extensive process of this type in Arctic regions.

Circulation in the EBS (fig. 2) is dominated by the Alaskan Coastal Current, which enters from the Gulf of Alaska through Unimak Pass and other passes along the Aleutian Island chain (Reed and Stabeno 1999) and moves east onto the EBS shelf as a cyclonic gyre. Much of the Alaskan Coastal Current that enters through Unimak Pass flows to the northwest (Bering Slope Current); a second branch slowly flows counterclockwise within the Coastal Domain, first along the north side of the Alaskan Peninsula, then across the mouth of Bristol Bay, and finally to the north. Long-term average speeds are relatively fast within the Bering Slope Current (5–20 $\text{cm} \cdot \text{s}^{-1}$), slower nearshore along the peninsula (1–5 $\text{cm} \cdot \text{s}^{-1}$), and very weak within the Middle Domain (Kinder and Schumacher 1981), where there is virtually no net directional flow (Loher 2001). Oceanographic and satellite data have revealed an eastward flow (2–3 $\text{cm} \cdot \text{s}^{-1}$) across the shelf north of the

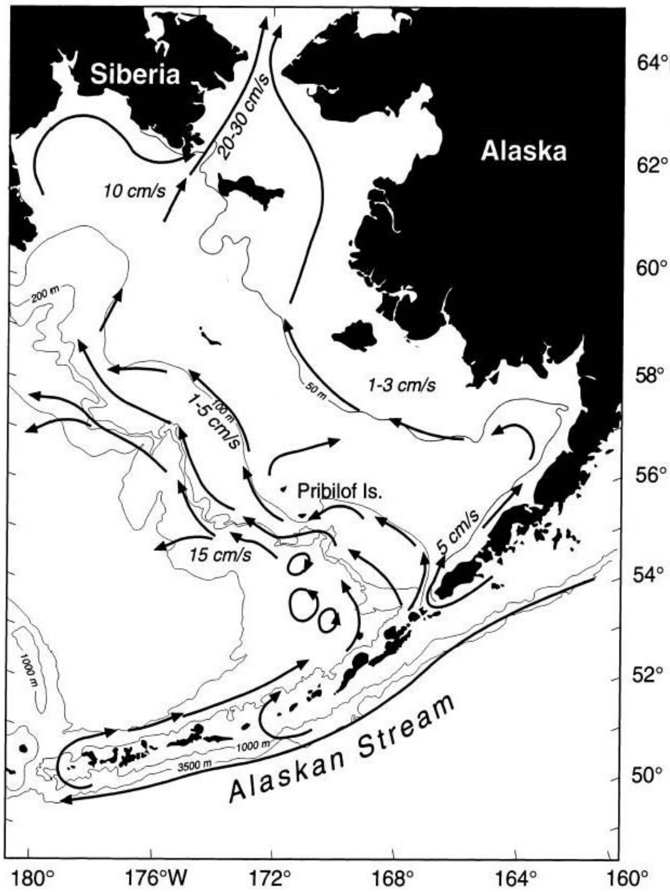

Figure 2. Schematic of mean circulation in the EBS shelf (modified from Stabeno et al. 2001).

Pribilof Islands (Schumacher and Stabeno 1998). Flow over the Outer Domain is moderate (4–8 cm · s^{-1}), following the 100 m isobath toward the northwest.

The southeastern sector of the shelf is divided by a series of three fronts into two interfrontal zones that correspond to the Middle and Outer Domains (Coachman 1986). Many biological phenomena can be conveniently conceptualized in this framework (Iverson et al. 1979), although the location and dynamics of the fronts are not clearly established for the central shelf (Schumacher and Stabeno 1998). As ice melts in spring, the less saline water "floats" over higher salinity marine water; this upper layer is heated, causing stratification of the water column. The stratified water column "traps" an extensive "cold pool" layer (water < 2°C) down to the seafloor over a large area of the EBS. In summer this cold pool averages 200 km north-south and 500 km east-west (Wyllie-Echeverria and Wooster 1998). The cold pool may persist over larger or smaller areas of the EBS for several consecutive years (Loher 2001), and the degree of spatial coverage influences the abundance and distribution of fishes and invertebrates.

Life History of Snow Crab in the EBS

Hatching and oviposition for the snow crab in the EBS start in March, peak in April, and are over in July (Somerton 1981, p. 32). Strong stratification of the water column in the Middle Domain during the summer (when larvae are in the plankton) provides a productive habitat for larval growth, which progresses through two zoeal and a megalops stage (Incze et al. 1987; Loher 2001). Immature females become vulnerable to the NMFS (National Marine Fisheries Services) survey gear when they reach a size range (30–60 mm carapace width) that is roughly equivalent to the three instars preceding the terminal (pubertal) molt to maturity. This pool of immature females is concentrated in the Middle Domain (Ernst et al. 2005). Female snow crab stop growing after the puberty molt, a transition recognizable in the relative width of the abdominal flap. Female age-at-maturity is unknown for the EBS; in eastern Canada it has been reported to range between 4.5 and 7.5 years after settlement (Alumno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998). To avoid confusion, we refer to all female crabs entering the mature pool during a given year as a "pseudocohort." Female recruits to the mature population (SCI-2, shell-condition index value; see "Sources of Information—NMFS Survey Data," below) are also concentrated in the Middle Domain of the central shelf but slightly displaced toward the Outer Domain by comparison to immature females. It is in the Middle Domain that the life-history events from the pelagic larval stage to maturity occur. Older females appear displaced toward the Outer Domain. Ernst et al. (2005) hypothesized that during their directed ontogenetic migration female snow crab track environmental gradients, such as depth and near-bottom temperature.

Males also experience a morphological transformation related to reproductive maturity: the propodus becomes proportionally larger (in relation to carapace width) at the terminal molt (Conan and Comeau 1986). Since allometric changes in the claws are generally associated with sexual maturity, males with proportionally large claws are usually known as "morphometrically mature" (as opposed to morphometrically immature). Maximum post-terminal molt lifespan is 6–7 years (Ernst et al. 2005). According to Ernst et al. (2005), the terminal molt of males is likely to take place in winter and early spring (February–May); they hypothesized that the pseudocohorts of morphologically mature males that are seen as recently molted (SCI-1) during the summer surveys are likely to migrate offshore, becoming available to the fishery in the Outer Domain during the next winter as "clean shell" crab.

Mating behavior and ecology of snow crab are very complex (Elner and Beninger 1995). Studies conducted in eastern Canada show that females can mate after the puberty molt while still in a soft-shell condition or (in subsequent years) while in hard-shell condition. The first are termed "primiparous," and the second "multiparous." Somerton (1982) proposed the "bipartite mating hypothesis" on the basis of field observations on tanner crab (*Chionoecetes bairdi*) in the Gulf of Alaska: primiparous females would mate with morphometrically immature, sexually mature males in shallow water, and multiparous females would mate with morphometrically mature males in deeper regions. Consistent with this hypothesis extensive experimental work conducted in eastern Canada has shown that morphometrically immature males are able to mate with primiparous females but not with multiparous ones, whereas morphometrically mature males can mate with both primi- and multiparous females (Conan et al. 1990).

INFORMATION SOURCES

NMFS Survey Data

Most of the information used in this study consists of time-series data collected during trawl surveys conducted by NMFS between 1975 and 2001 (Otto 1998; Stevens et al. 2002). Surveys follow a systematic sampling design in which stations are regularly spaced over a 20 nmi by 20 nmi grid and sampled every year. The 1975–1977 surveys were not included in the analyses because they covered only the southern end of the geographic range of interest. Systematic sampling surveys had a consistent spatial coverage after 1978 (fig. 1), with some variation north of 61°N; a cluster of northern stations was consistently occupied after 1988. The core temporal window of the surveys is June–July, but in some years work started in May (1975–1981, 1999–2000) or ended in August (1975–1976, 1978–1979, 1982–1986, 1988–1992). Information is collected on environmental variables and stocks of crab and groundfish. The environmental information used in this study consists of depth and near-bottom temperature (NBT), which has been regularly recorded since the initiation of the survey program.

Several observations are made on each individual crab caught in a haul or from a subsample when the catch is too large (for further information on the sampling protocol, see the "Manual of crab sampling methods for the trawl survey in the eastern Bering Sea"[1]). These observations include carapace width (CW, in millimeters), a shell condition index, sexual maturity (immature/mature, females only), color of the eggmass (if present), and height of the cheliped's propodus (males only, recorded only in recent years). After the terminal molt, shell condition changes as a result of wear and colonization by epibionts. Subjective "shell condition indexes" (SCIs) have been devised as a rough correlate of shell age. We used the SCI categories routinely recorded by NMFS and interpreted them following Ernst et al. (2005). Roughly, SCI-1:2 correspond to crab that molted very recently (during the survey's calendar year), SCI-3 to crab that molted during the preceding year, and SCI-4+ to individuals that molted two or more years earlier. In the case of females, SCI-2 and SCI-3 largely correspond to, respectively, primiparous recruits to the female pool and first-time multiparous breeders.

Catch per haul was used to estimate density using swept-area methods (Sparre and Venema 1998). Average density for each station was estimated as

$$D_t^S = \frac{1}{n_t^S} \sum_{i=1}^{n_t^S} \frac{d_{t,i}^S}{A_{t,i}^S} ,$$

where

D_t^S is density of station S in year t,

n_t^S is total number of hauls for station S in year t,

$A_{t,i}^S$ is swept area of haul i in station S in year t,

$d_{t,i}^S$ is number of specimens (crab or fish) of haul i in station S in year t.

We refer to this as "relative abundance," because no gear efficiency correction was used in the analysis.

The data were parsed and analyzed using scripts in AWK stream editor (Robbins 2001). Graphical analysis was conducted using GMT (Generic Mapping Tool) graphical software (Wessel and Smith 1998). Some graphs required surface plots, which implied the additional calculation of regular station grids over the entire distributional area. This was accomplished by using a near-neighbor algorithm (Wessel and Smith 1998). Centroids of density for a given category (species, sex, ontogenetic group) in a particular year were computed as weighted averages of latitudinal and longitudinal components, as described by Ernst et al. (2005). In the case of crab, the geographical location of pairs of centroids of consecutive life-history stages allowed us to estimate time series of mean migration distances and angles of migration for specified pairs of stages (e.g., mature females in SCI-2 in year i and SCI-3 in year i+1). We refer to Ernst et al. (2005) for details of the calculation.

We used temperature and depth records to calculate and map gradient (vector) fields as described by Ernst et al. (2005). The earliest surveys included in the NMFS database (1975–1977) were circumscribed to the southeastern part of the EBS. That period, however, is very

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[1] Available from NMFS, Alaska Fisheries Science Center, P.O. Box 1638, Kodiak, AK 99615-1638.

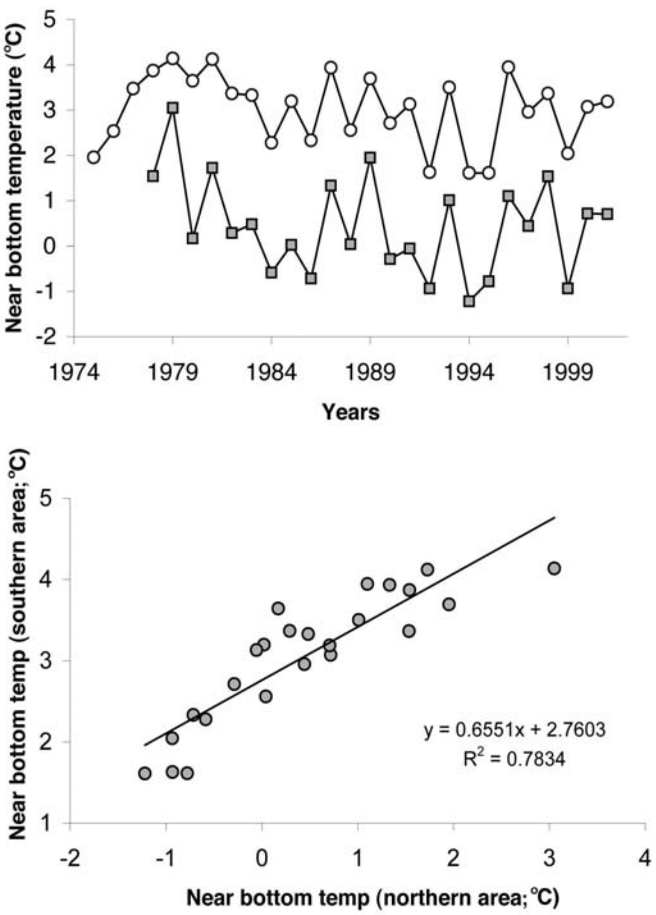

Figure 3. Upper panel shows time series of average NBT calculated for the northern (*rectangles*) and southern (*circles*) areas (see fig. 1); lower panel shows the correlation between the two time series.

significant for our study, so we explored NBT in two windows centered on St. Matthew Island (north; 59°–61°N, 186°–190°W) and the Pribilof Islands (south; 56°–58°N, 188°–192°W) (fig. 1). Trends are very similar in the two windows (fig. 3; cross-correlation coefficient is 0.78), so trends observed in the south window in 1975–1977 were most likely paralleled in the north window.

Fish Stomach Content Data

Data on cod predation and cod CPUE from the NMFS surveys were available for the period 1981–2000; for details we refer to Livingston (1989) and Livingston et al. (1993). Centroids of cod CPUE were computed as weighted averages. Predation centroids were computed from an index of predation, calculated as the proportion (in weight) of snow crab in the diet of cod at a particular site and time.

Crab Fishery Data

Fishery data were provided as a database ("Catch/effort by statistical area for the eastern Bering Sea snow crab from 1969 to 2002") by Gail Smith.[2] Centroids of the fishery were computed based on numeric abundance (not biomass) and as the weighted average of the landings by statistical area.

Ice-Edge Data

The National Ice Center, Anchorage, Alaska, made data on ice coverage in the EBS available. Ice concentration is recorded on a relative scale from 0 to 10 and reported on a spatial grid of 0.25 latitude degrees by 0.27 longitude degrees. Lines illustrated here (based on these data) correspond to maximum extension of ice coverage for specific dates and were constructed by including cells where concentration was ≥ 5/9.

RESULTS

The cold pool, as observed through the summer NMFS surveys, expands and contracts, tracking the extension of ice cover during the preceding winter. A comparison of consecutive "cold" (e.g., 1986) and "warm" (e.g., 1987) years makes this clear (fig. 4). In 1986, a typically "cold" year, the ice was spread along the outer border of the Middle Domain in the southeast and along the Outer Domain in the northwest (fig. 4c). During the summer, the outer boundary of the cold pool matched rather well the maximum reach of the ice edge during the preceding winter (fig. 4a). In 1987, a typically "warm" year, the maximum reach of the ice edge ran from east to west at 59°–60°N (fig. 4d), again matching the summer extension of the cold pool (fig. 4b). Year-to-year expansions and contractions of the cold pool are a Middle Domain phenomenon that takes place primarily between the 50 m and 100 m isobaths and along the northwest-southeast direction. There are two noticeable exceptions. First, the southeast outer fringe of the Middle Domain (MDf), ranging from ~59°N to the southeast and including the area around the Pribilof Islands, does not overlay the Cold Pool even during "cold" years (fig. 4a). Second, an expanse of the Coastal Domain located to the southwest of Nunivak Island (CDf) overlays the cold pool even in "warm" years (figs. 4b).

Recruitment to the mature snow crab population takes place over the Middle Domain. Little is known about distribution and abundance of early instars, which are too small to be captured in the NMFS survey gear. The only category of information available about the large-scale distribution of early snow crab instars is stomach content data from fish, primarily cod. Most of the snow crab sampled from cod stomachs are 6–35 mm CW (fig. 5) in size. The cumulative geographic distribution of snow crab sampled from cod stomachs gives

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[2] Groundfish/shellfish database coordinator, Alaska Department of Fish and Game, Juneau, AK; 907-465-6157; gail_smith@fishgame.state.ak.us.

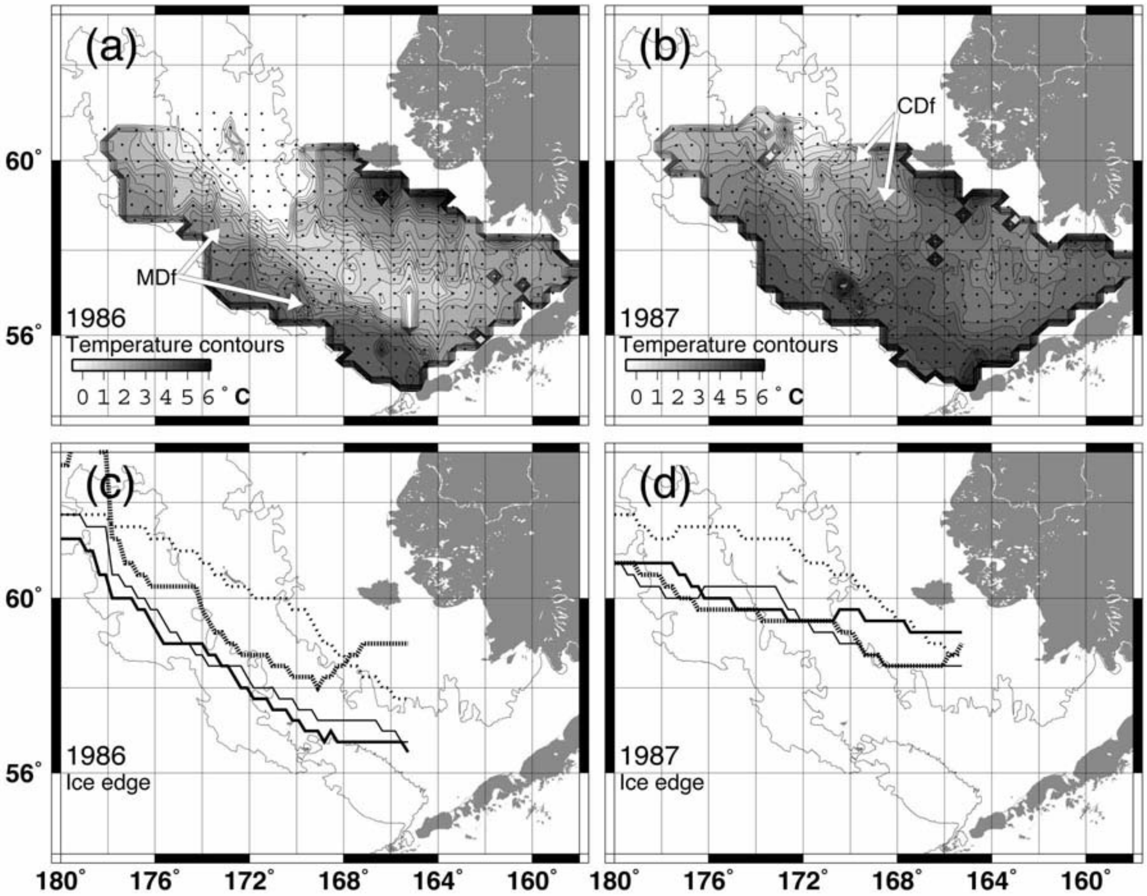

Figure 4. Extension of the cold pool during the summer (*a* and *b*) and position of the ice edge (*c* and *d*) in cold (*a* and *c*) and warm (*b* and *d*) consecutive years (1986 and 1987, respectively). In 1986, ice edge was calculated on 4 Feb. (c1), 25 Mar. (c2), 1 Apr. (c3), and 29 Apr. (c4); in 1987, on 3 Feb. (d1), 3 Mar. (d2), 31 Mar. (d3), and 21 Apr. (d4). CDf = Coastal Domain southwest of Nunivak Island; MDf = southwest fringe of Middle Domain.

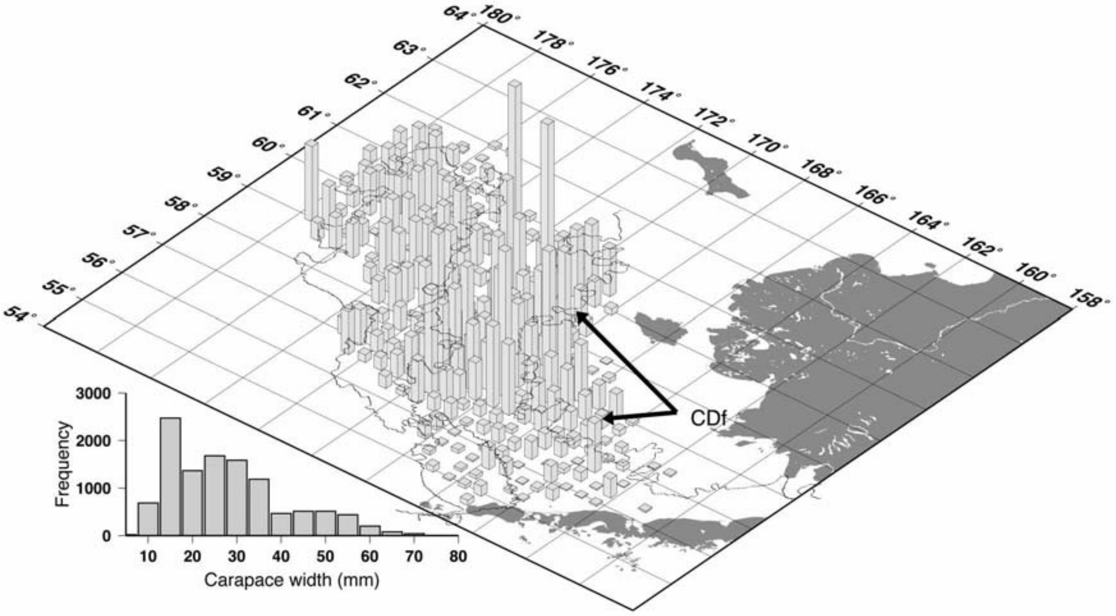

Figure 5. *Upper panel*, aggregated distribution (1981, 1984–1999) of cod predation on snow crab in the EBS; bar height is proportional to the count of individual cod with snow crab in their stomach that were sampled in each cell of the grid. *Lower panel*, size-frequency distribution of all snow crab sampled from cod stomachs.

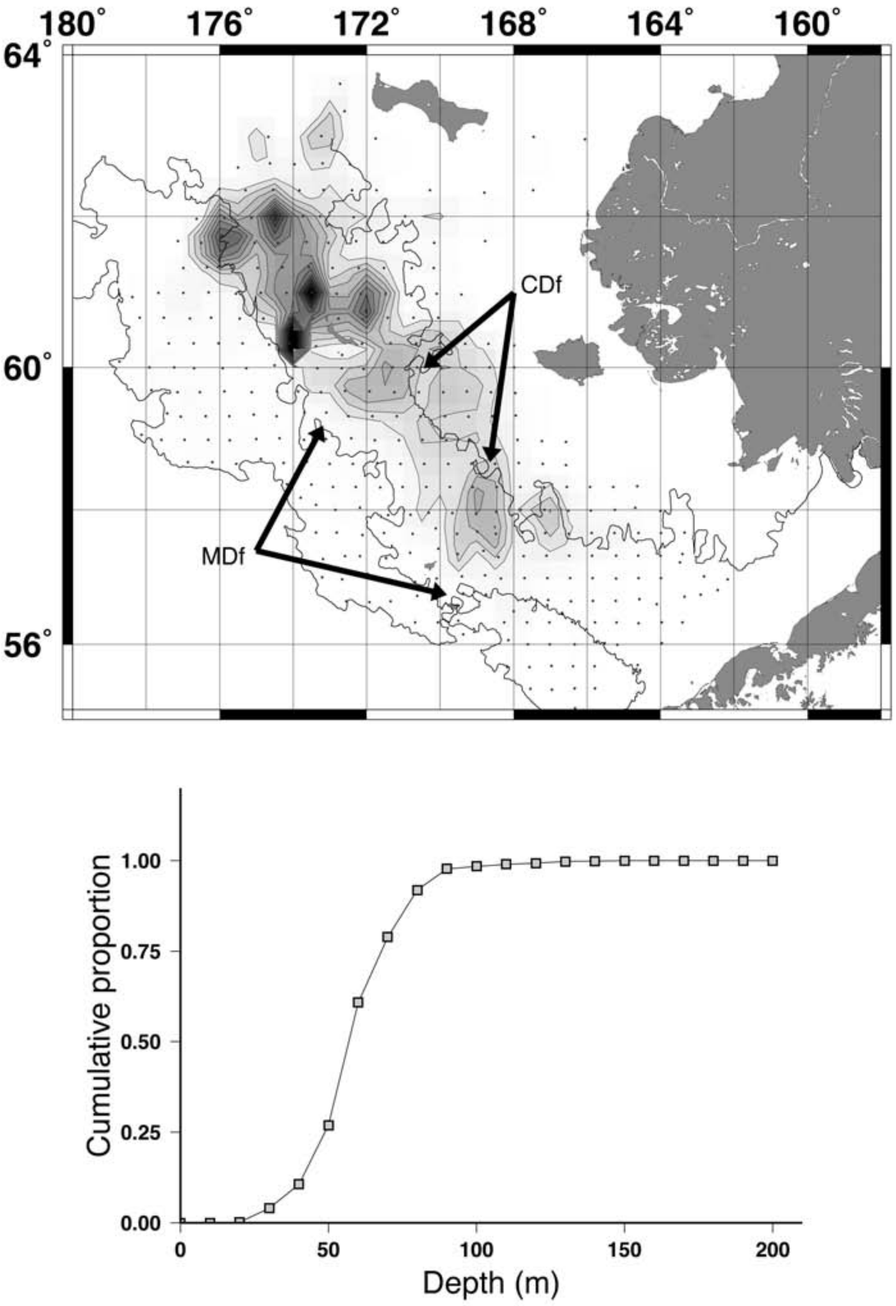

Figure 6. *Upper panel*, relative density (survey CPUE) of immature female snow crab integrated over time from 1978 to 2001. *Lower panel*, cumulative proportion of immature females (number sampled weighted by abundance) relative to depth (NMFS survey data).

at least a qualitative idea of the distribution of younger age classes (fig. 5). Juveniles are distributed primarily throughout the Middle Domain, spreading also eastward over the CDf (fig. 5) and (in smaller numbers) in areas of the Outer Domain west of 174°W and north of St. Matthew Island. This information must be considered qualitative because it is biased by cod behavior and geographic distribution. Immature females sampled during the summer NMFS surveys are 30–60 mm in size (intermediate between cod prey and mature females). The immature group is definable only for females because observers note the condition of the abdominal flap. In the case of males, it is not possible, with the data at hand, to separate morphologically mature and immature individuals in most of the survey data. Data pooled over all surveys shows that immature females are circumscribed to the Middle Domain (fig. 6, top), with the noticeable exception of the two fringe areas of the Coastal and Middle Domains described above (fig. 4a,b; fig. 6). In general, the region where immature females are found

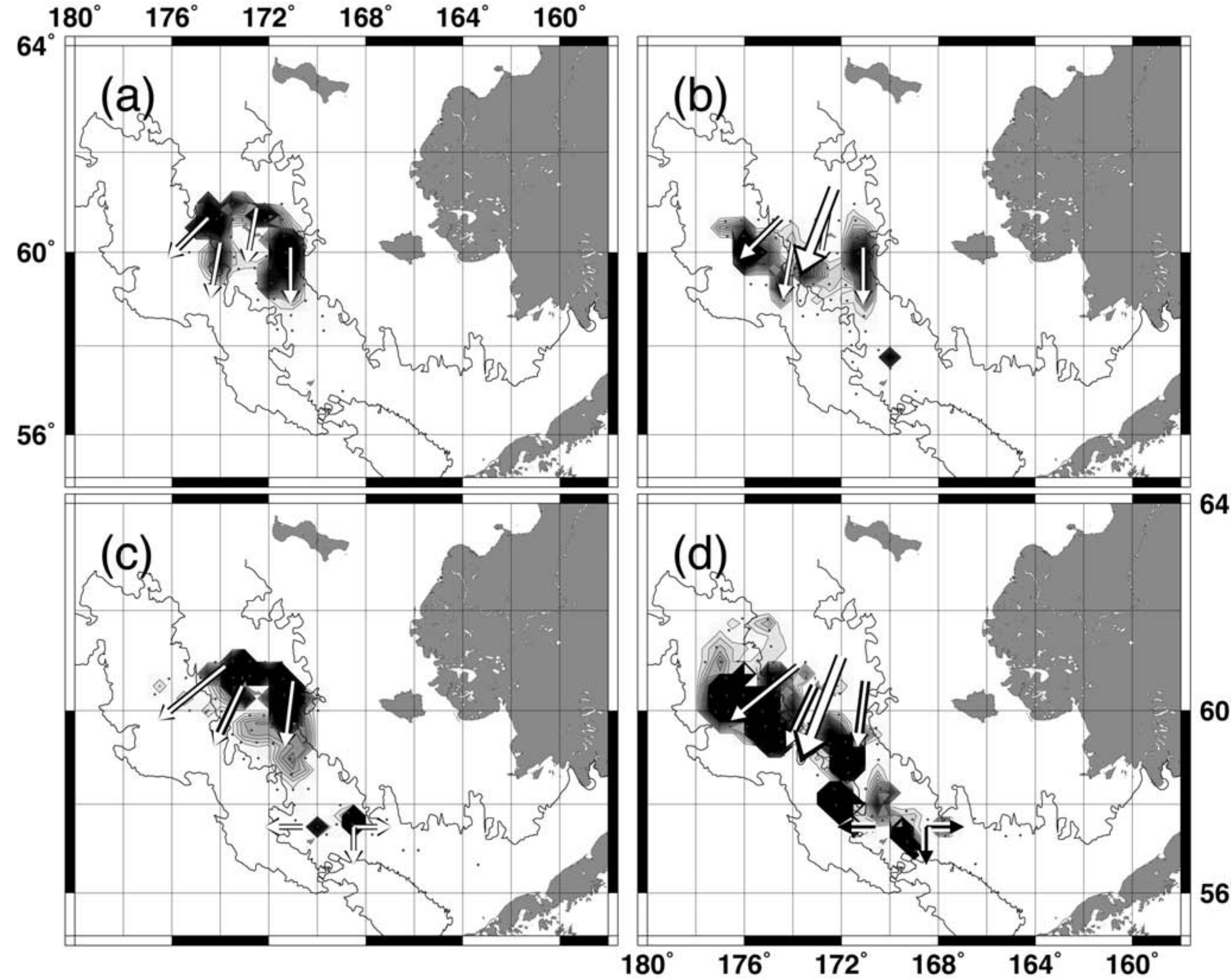

Figure 7. Relative abundance (survey CPUE) of mature females of two pseudocohorts. 1985 pseudochort: *a*, SCI-2 in 1985; *b*, SCI-3 in 1986. 1986 pseudocohort: *c*, SCI-2 in 1986; *d*, SCI-3 in 1987. Notice that 1986 and 1987 are the consecutive cold and warm years, respectively, shown in fig. 4. Large arrows in *b* and *d* indicate the azimuth of net large-scale migration; smaller arrows indicate apparent vectors of local, small-scale migration.

corresponds to the maximum extension of the NBT isotherm of 2°C, which bounds the Middle Domain. Over 25 years of surveys, more than 90% of the immature females sampled came from depths in the 50–100 m range that bathymetrically defines the Middle Domain (fig. 6, bottom).

Most females recruit to the mature population (that is, undergo their terminal molt) within the Middle Domain, then migrate to the south and to the west (for supporting evidence and details, see Ernst et al. 2005). The resultant direction (from northeast to southwest) is rather conservative, irrespective of whether years are "cold" or "warm" (fig. 7). The core of the ontogenetic migration takes place during the first year after the terminal molt, as females change from SCI-2 to SCI-3. This transition is often traceable at the level of large patches in the population, as Figure 7 shows for the 1985–1986 and 1986–1987 post-terminal molt ontogenetic migrations. Notice the similarities in distribution of the main pool of females in SCI-2 in 1985 and 1986, probably reflecting the fact that immature females in the source pool molt into maturity over more than 1 year.

While this general sequence of ontogenetic events appears to have persisted after 1981, the geographic range of the mature female population has contracted from southeast to northwest (fig. 8). During the 5-year period 1978–1982 the mature population was spread over the entire EBS shelf, with large concentrations in the southeast and northwest (roughly located in the region of, respectively, Pribilof Island and St. Matthew Island). In contrast, during the 5-year period 1998–2001, the southeast concentration had disappeared, and nearly all the mature population was concentrated north of 58°N (fig. 8). Between these two periods there were some

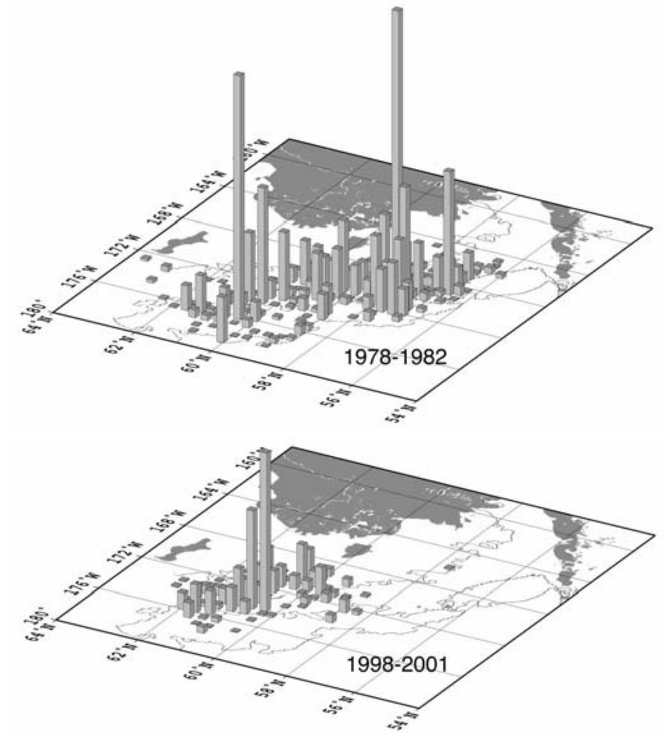

Figure 8. Aggregated abundance of mature females in SCI-2 at the beginning (*top*, 1978–1982) and toward the end (*bottom*, 1998–2001) of the study period. Bar height is proportional to abundance (survey CPUE) in each cell, aggregated for the period indicated.

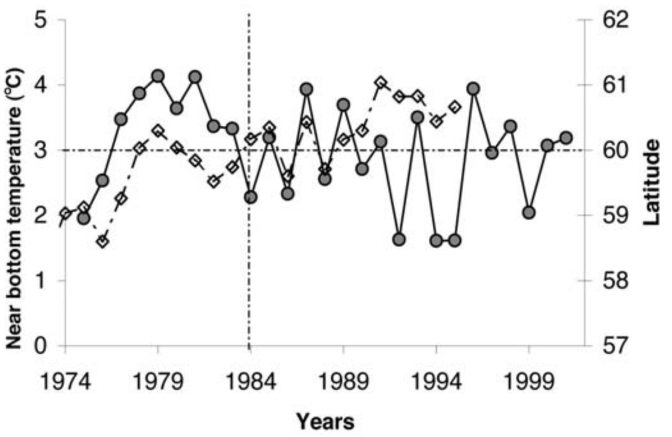

Figure 9. Time series of average near bottom temperature in the south window (*circles*; see fig. 1 for location) and latitudinal component of the centroid of distribution of primiparous (SCI-2) mature females (*diamonds*), the latter lagged by 6 years. The vertical line shows the change from an autocorrelated cycle of NBT to a period dominated by year-to-year variation.

transient expansions of the mature female stock, discussed below. Contraction to the north was accompanied by a long-term decline in abundance, punctuated by periodic pseudocohort recruitment (centered around 1980, 1987, 1994, and 2001).[3]

If temperature had an effect on settlement or recruitment, it is likely that the corresponding phenomenon relates to spawning, the pelagic larval phase, or early benthic instars, stages that are in the first calendar year of life. Age at female maturity has not been established for the EBS, but in eastern Canada it ranges from 4.5 to 7.5 years. Considering that life-history schedules are similar in the two regions (Ernst et al. 2005), 6 years is a reasonable guess for the EBS. Recruitment of female pseudocohorts is the most proximate estimate of year-class strength for snow crab in the EBS. Following these considerations, we compared the time series of average NBT and the latitudinal component of the centroids of distribution of females in SCI-2, the latter with a 6-year lag (fig. 9). Expansions and contractions of the cold pool, described above, are well captured by average NBT during the summers (NMFS survey data). The median NBT over that period is about 3°C (fig. 9). Figure 9 reveals a significant pattern : annual mean NBT during the summer rose continuously during the 5-year period 1975–1979. The summer of 1979 was the warmest for the study period, with the entire Coastal Domain experiencing NBT higher than 6°C and the cold pool not extending beyond the northern shelf. Once average NBT rose above the median, it stayed relatively warm (above 3°C) during the 7-year period 1977–1983. After 1980, change was dominated by year-to-year variation.

A displacement of the centroids of SCI-2 females toward the north during the 4-year period 1982–1985 matches the increase in average NBT 6 years earlier (fig. 9), even though the magnitude of the displacement is probably underestimated because between 1983 and 1986 the survey did not extend north of 60°N. The latitudinal position of lagged centroids tracked average NBT between 1976 and 1988 but afterward remained north of 60°N for 6 years. During the early 1990s, there were some short-lived expansions of the mature female population to the south. The centroids of 1992 and 1994 were well displaced to the south, tracking (as before with a 6-year lag) the cold years 1986 and 1988. This resulted in a transient expansion to the south of the mature female population that lasted until 1997, after which the 1992 and 1994 pseudocohorts vanished from the population. After 1988, the cold years 1992, 1994, and 1995 were not followed by a rebound of pseudocohort recruitment in 1998 and 2000, but they were followed by a small peak in the north in 2001. The latitudinal component of the lagged centroids did not track the year-to-year fluctuations of NBT that have been characteristic of the 1990s.

Tracking year classes or pseudochorts is more difficult for males than for females, in part because morphologically immature and mature males cannot be discriminated in the NMFS survey data. Ernst el al. (2005) hypothesized that large males (CW > 102 mm,

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[3] B. Ernst, D. A. Armstrong, and J. M. Orensanz, unpubl. results.

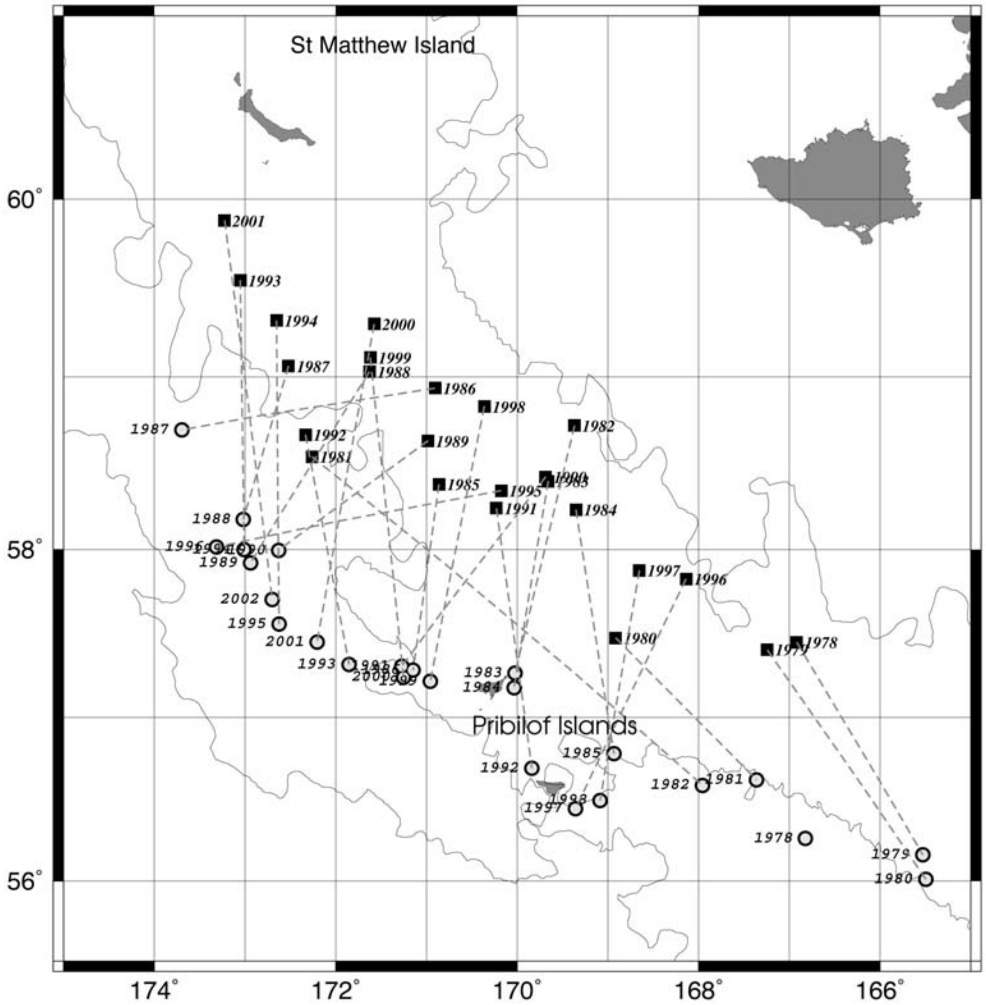

Figure 10. Centroids of large male abundance (CW > 102 mm) in SCI-1:2 (large new-shell crab, *squares*) and the fishery (*circles*). Dashed lines connect centroids for large new-shell crab observed during the summer surveys with centroids of the commercial catch during the following winter.

which corresponds to commercial size, virtually all morphologically mature) molting during the survey's calendar year (SC 1-2) correspond to the "clean crab" caught by the fishery in the Outer Domain during the subsequent winter fishing season. Winter fishery centroids are always located to the south of the large, recently molted crab centroids of the previous summer (fig. 10). This could be explained by two hypotheses: (1) male crab move offshore and southward (into the Outer Domain) after molting into maturity in the Middle Domain, or (2) males do not migrate, and the fishery is simply constrained by ice cover so that only the outer fringe of the large crab population is accessible to the fishery. Hypothesis (2) is falsified by two facts: first, during the early years of the series the fleet was not seasonally constrained by regulation, yet the observed pattern was the same, and, second, crabs molting to maturity are confined to the Middle Domain at the time of the summer survey.

If hypothesis (1) is correct (males move southward), then two predictions follow: first, the spatial allocation of fishing effort during the winter (captured by the location of the fishery centroids) should track the spatial distribution of large males reaching morphological maturity during the preceding calendar year (captured by centroids calculated with the NMFS spring/summer surveys), and, second, the fishery centroids should be located to the south of the centroids calculated with survey data. Both predictions hold remarkably well (fig. 11). Notice that the longitudinal separation of the centroids is relatively small compared to more obvious differences in latitudinal separation of these events, consistent with the notion of a southward migration to the fishing grounds after molting. As in the case of females, the centroids of males molting into maturity during the summer show a net northward displacement over the 25-year study period, from 57.5°N in 1978 to 60°N in 2001. While centroids of the survey and the fishery are well

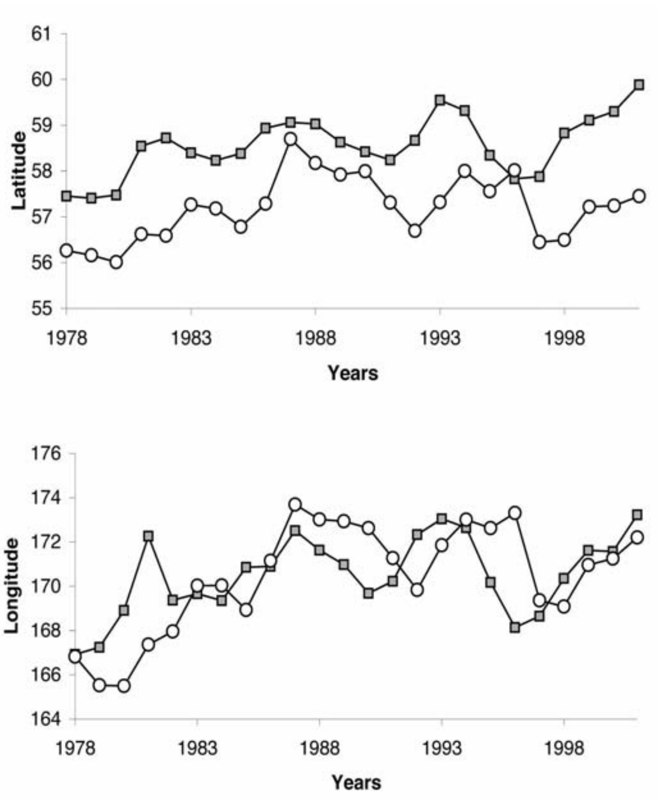

Figure 11. Latitudinal (*top*) and longitudinal (*bottom*) components of the summer centroids of large-male abundance (CW > 102 mm) in SCI-1:2 (new-shell large crab, *squares*) and the subsequent winter fishery (*circles*).

cross-correlated (with a 1-year lag), the fishery centroids moved northward between 1978 and 1987 (fig. 11, top) but fluctuated afterward between 56°N and 58°N. As a result, the shift between the summer centroids of stock abundance (survey data) and the fishery during the following winter has increased steadily over the 7-year period 1995–2001. This parallels a similar trend in SCI-2 females, which remained north of 60°N during the same period.

Cod predation is the main source of natural mortality of snow crab prerecruits so far identified in the EBS. The centroids of cod abundance (as indicated by CPUE observed in the NMFS surveys) showed a steady shift toward the north between 1979 and 1983. This closely paralleled (with a 4-year lag) the increase in average summer NBT observed between 1975 and 1979 and was 2 years ahead of a corresponding shift to the north of crab's range of distribution (indicated by the centroids of abundance of mature female pseudocohorts; figs. 8 and 9). After 1984 cod CPUE centroids fluctuated around 58°N (fig. 12, right), with no apparent relation to average NBT. Indexes of cod predation have been calculated for the period 1984–2000. During the 11-year period 1991–2001, the latitudinal component of the centroids of cod CPUE, abundance of immature females (the group sampled during the NMFS surveys that is closest to the size range of cod prey), and the index of cod predation (fig. 12, left)

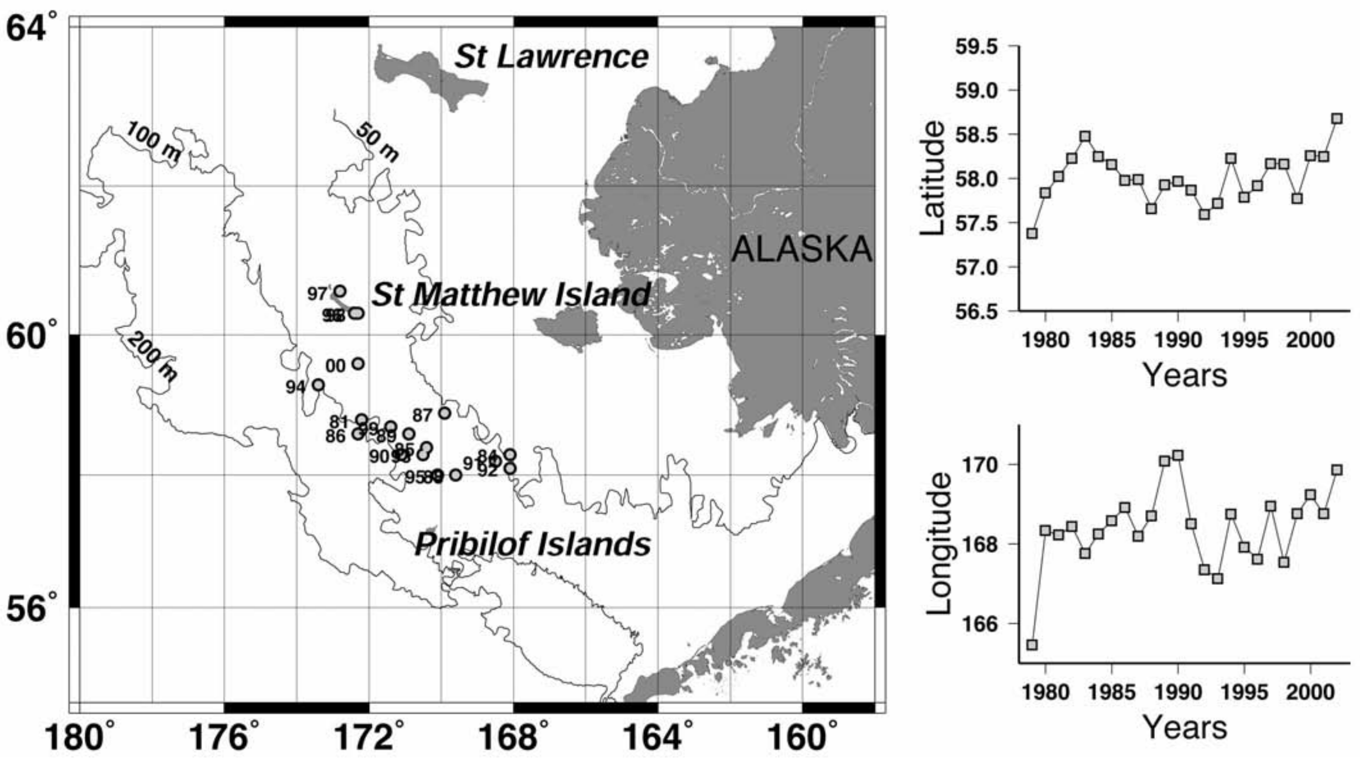

Figure 12. *Left*, centroids of cod predation calculated for 1981 and 1984–1999, weighted by cod CPUE. Right, time series of the latitudinal (*top*) and longitudinal (*bottom*) component of centroids of cod relative abundance distribution (survey CPUE).

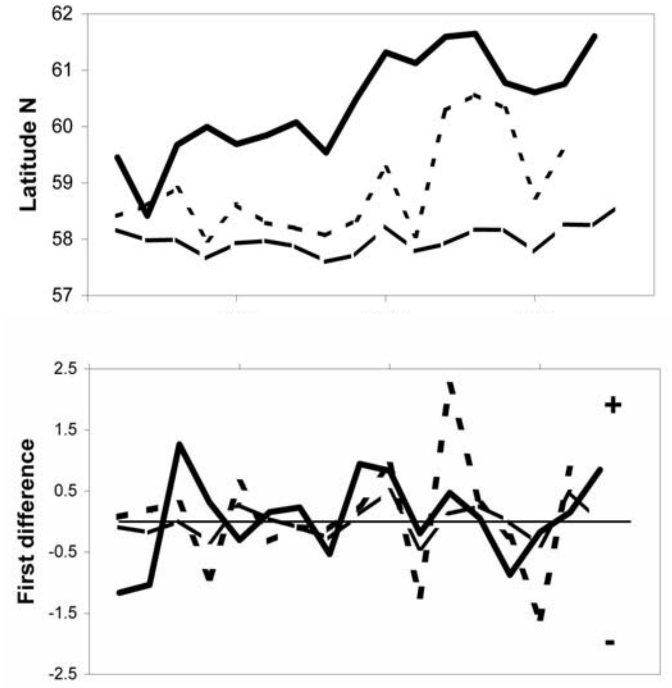

Figure 13. *Top*, time series of the latitudinal component of centroids of distribution (survey CPUE) of immature females (*solid line*), cod (*dashed line*), and predation index (*dotted line*). *Bottom*, first-order difference of the series shown in the top panel.

have fluctuated in a very consistent way: the first-order difference of the three series showed the same sign in every year (fig. 13). Cod CPUE centroids were located, on average, 1.5° latitude to the south of centroids of immature female abundance. This gap can be anticipated when Figures 6 (top) and 12 (left) are compared.

DISCUSSION

During the 24-year period 1978–2001, recruitment to the snow crab stock of the EBS (as indicated by the abundance of female pseudochorts) declined; the fishery reached historically low levels in 2002–2003 under the current rebuilding plan (Stevens et al. 2002). At the same time, the geographic range of the population (males and females) showed a significant long-term shift toward the north. Here, we suggest that these changes are, at least in part, related to climatic forcing, and we advance what we term the "environmental ratchet hypothesis." The elements of the hypothesis are as follows:

1. Snow crab settle and grow to maturity in the Middle Domain. Pelagic larvae find a favorable environment in the upper layer of the water column, strongly stratified during the summer between the middle and inner shelf fronts, foraging on phytoplankton blooms that develop in spring along the ice edge.
2. Larval retention in the Middle Domain is favored because of lack of a strong current pattern.
3. The area of seabed suitable for settlement is circumscribed by the 2°C NBT isotherm, that is, the cold pool, that expands over the Middle Domain to the southeast during cold years.
4. The lagged northward shift of female pseudochorts associated with warming during the 5-year period 1975–1979 indicates a corresponding northward shift in recruitment to the benthic population (settlement and early benthic survival). There are two reasons: Appropriate conditions for larval growth and survival are associated with spring blooms that develop under colder conditions, and early juvenile stages are stenothermic, requiring a NBT below 2°C.
5. Once the reproductive stock had contracted to the north, relaxation to the south tracking year-to-year fluctuations in NBT was made difficult by the current pattern: The reproductive stock had effectively contracted "up-current."
6. Females are not likely to repopulate depleted areas to the southeast of the Middle Domain, because routes of ontogenetic migration take them offshore toward the Outer Domain, whether years are cold or warm, reflecting the dominant direction of environmental gradients tracked during the migration (depth, NBT).
7. After contraction of the stock to the north, cod predation on juveniles controlled the southward expansion of the range of immature females.
8. Resurgence in the south based on the local reproductive stock is unlikely because of the small size of the stock and because of persistent cod predation on juvenile crab.

This composite hypothesis subsumes several single hypotheses on the dynamics of snow crab populations in the EBS. Each component hypothesis is supported by empirical evidence but can also be challenged on empirical grounds, making the composite hypothesis a useful framework for further inquiry. At the core of the hypothesis is the notion of an "environmental ratchet": given the nature of hydrographic features and the spatial behavior of crab and their predators, change in geographical range is asymmetrical. According to the hypothesis, contraction to the north during warm regimes is more likely than expansion back to the south during cold years.

Important elements of our hypothesis are based on a general oceanographic model of the EBS shelf, inferred largely from detailed long-term studies conducted over the southeastern shelf. Far less documented are the oceanographic processes for the central and northern parts of the shelf (Schumacher and Stabeno 1998), the main ambit of snow crab dynamics. Similarly, studies on snow crab larval ecology have been circumscribed to the southeastern part of its range (Incze et al. 1987). Further work focusing on the central and north portions of the shelf is needed to validate the rationales of the environmental ratchet hypothesis.

The 25-year study period (1976–2001) can be clearly partitioned in two segments in terms of the patterns of variation of average summer NBT, which, as noted earlier, is correlated with the extension of the cold pool. Following an extremely cold period (1974–1975; Azumaya and Ohtani 1995), NBT increased monotonically during 5 consecutive years; average summer NBT in this study's south window doubled from 2°C in 1976 to 4°C in 1979 (see also Loher et al. 2001, their fig. 9). Somerton (1981) hypothesized that successful larval development and settlement are related to spring blooms that develop near the ice-edge in early to mid-April, accompanying salinity changes during ice melting and subsequent stabilization of the water column. This could explain why the southern boundary of female snow crab distribution is approximately coincidental with the mean southern extent of sea ice in April. Hunt et al. (2002) proposed the oscillating control hypothesis as a conceptual model for the functioning of the pelagic ecosystem in the EBS. This hypothesis predicts alternation between primarily bottom-up control in cold regimes and primarily top-down control in warm regimes. According to the model, "the timing of spring primary production is determined predominantly by the time of ice retreat: late ice retreat (late March or later) leads to an early, ice-associated bloom in cold water, whereas no ice, or early retreat of ice before mid-March, leads to an open-water bloom in May or June." Coupling between holopelagic mesozooplankton and phytoplankton is probably weak in cold years, when primary production is dominated by spring blooms. In cold years the reproduction and growth of holoplankton (which are controlled by temperature) are retarded, the spring phytoplankton bloom is not controlled by zooplankton grazing (Napp et al. 2000), and phytoplanktonic production sinks ungrazed to the bottom. The case of meroplankton is different. Since the timing of larval hatching in snow crab is constrained by the reproductive cycle of benthic adults, which peaks in April, crab larvae are likely to thrive during cold years, consistent with Somerton's (1981) hypothesis. Interestingly, Comeau et al. (1991) and Starr et al. (1994) hypothesized that the trigger for snow crab eggs to release larvae in Bonne Bay (eastern Canada) is linked to the phytoplankton bloom and rain of organic particulate matter that follows.

Beyond pelagic larval life, association of recruitment with the cold pool could result from the stenothermy of early benthic stages. Experimental and field work by Dionne et al. (2003) in the Gulf of St. Lawrence (eastern Canada) showed that the preferendum for snow crab instars I–III is in the 0.0–1.5°C range, that this is the most stenothermic stage in snow crab life history, and that the most important factor constraining its distribution appears to be temperature. Because of narrow habitat requirements, they concluded, early juvenile instars could represent the weakest link in the snow crab's life cycle. Even if other factors influence trends in snow crab abundance and spatial distribution in the EBS, spread of the cold pool during the first year of life could easily determine the southern boundary of a cohort's range.

Somerton's (1981) hypothesis and juvenile stenothermy are consistent with the northward contraction of snow crab's range during the late 1970s and early 1980s, but they cannot explain why there was not a return to previous conditions during the 1990s. Fish predation, mostly by small Pacific cod (*Gadus macrocephalus*) on juvenile benthic stages, is the main source of snow crab natural mortality identified in the EBS (Livingston 1989). Three species of flatfish also prey on juvenile snow crab: yellowfin sole (*Pleuronectes asper*), rock sole (*P. bilineatus*), and flathead sole (*Hippoglossoides elassodon*). Livingston (1989) analyzed 3 years of cod stomach content data (1981, 1984, 1985) that suggest that the geographic distribution of young snow crab in cod stomach contents is related to the maximum extent of winter ice cover, which in turn is correlated with the extension of the cold pool during the following summer. This could not be explained by a link between changes in the geographic pattern of snow crab settlement and climate (e.g., Somerton's hypothesis, introduced earlier), because cod prey on snow crab of age 1+ and older (Livingston 1989, p. 821). Postsettlement migrations of juveniles tracking year-to-year changes in the geographic pattern of NBT can be ruled out, given the distances involved and what is known about snow crab migrations (Ernst et al. 2005).

Cod accounts for up to 64% of the aggregate total finfish predation on snow crab in the EBS; up to 84–95% of age 1+ snow crab can be consumed by Pacific cod (Livingston 1989; Livingston et al. 1993). Though tentative, these figures give an idea of the possible magnitude of predation based on what is known about cod and immature crab abundance and estimated cod consumption rate. During 1991–2001 (for which an index of cod predation is available), cross-correlated year-to-year variation in the location of the centroids of cod CPUE, cod predation index, and immature snow crab abundance strongly suggests that cod distribution controlled the spread of crab recruitment to the south in the Middle Domain of the central shelf. The index of predation indicates that when cod distribution shifts toward the north, the relative importance of snow crab as an item in cod diet also increases. We propose that expansions and contractions of the geographic range of cod results in "chopping off" the southern fringe of juvenile/immature snow crab. During warm years, the centroid of cod abundance moves northward, the amount of snow crab in cod diet is amplified as cod make a deeper dent into the snow crab's range, and the geographic range of juvenile/immature snow crab contracts accordingly, owing to predation. Bailey (1982) hypothesized that cod predation controls snow crab abundance in the Gulf of St. Lawrence (eastern Canada), but later studies failed to find consistency in population fluctuations of the two (Elner and Bailey 1986). Our results suggest that Bailey's hypothesis should be reexamined.

Resurgence of the mature female stock in the south requires at least one of three mechanisms: active displacement of females to the south, resurgence of the population in the south through retention of larvae produced locally by the residual stock, or southward transport of pelagic larvae produced in the north. Ernst et al. (2005) and results from this study indicate that females maturing in the Middle Domain of the central and northern shelves undergo an ontogenetic migration toward the Outer Domain, with a predominant northeast-southwest direction. This pattern has predominated in the postwarming years, starting with the 1981 female pseudocohort. However, some southward migration takes place within the Middle Domain in two regions: west of the CDf and to the northeast of the Pribilof Islands. The latter was significant during the late 1970s (1975–1979) and occurred occasionally afterward, whereas southward migration in the central shelf, near the Coastal Domain, occurs when patches of immature crab reach maturity to the east of the axis of the cold pool.[4] These alternative routes are insufficient for a significant southward migration originating in the northern shelf.

Southward transport of larvae produced in the central and northern parts of the shelf appears unlikely. Primiparous (SCI-2) females now spawn primarily in the Middle Domain north of 60°N, where flow is insignificant. There is no evidence of spawning in the Coastal Domain, and the larvae from multiparous females hatching in the Outer Domain are likely to be transported to the northwest, advected by a 1–5 $\mathrm{cm \cdot s^{-1}}$ flow along the 100 m isobath that becomes increasingly stronger toward the shelf edge, where it reaches 15 $\mathrm{cm \cdot s^{-1}}$. The implications of some local oceanographic phenomena for snow crab larval retention in the south are not understood, however. An eastward flowing current north of the Pribilof Islands could possibly advect larvae produced in the Outer Domain (otherwise likely to be flushed to the northwest) toward the Middle Domain. Clockwise circulation around the Pribilof Islands and Canyon (Kowalik and Stabeno 1999) may retain larvae produced in that region, as has been suggested before for blue king crab, *P. platypus* (Armstrong et al. 1985). Such phenomena could possibly create unforeseen favorable conditions for resurgence of the population in the southern part of the geographic range of distribution of snow crab in the EBS.

Many elements of the environmental ratchet hypothesis are based on phenomena (like the regime shift of 1976–1977) that have been observed only once. Future monitoring, as well as research in the less known parts of the EBS, will undoubtedly contribute to a better understanding of snow crab dynamics as well as the combined effects of fishing and climate. Increasingly integrated hypotheses on the functioning of this ecosystem are needed to frame further inquiry. The environmental ratchet hypothesis complements more comprehensive conceptual models, such as the oscillating control hypothesis (Hunt et al. 2002), by contributing a benthic perspective that emphasizes the spatial aspects of population structure and dynamics.

ACKNOWLEDGMENTS

This study was funded by NOAA grant NA16FN1275 through the Alaska Department of Fish and Game (ADFG). We thank Bob Otto, Lou Rugolo, and Gary Walters (NMFS) for making available NMFS trawl survey data; Jack Turnock (NMFS, Seattle) for feedback on database structure; Sigrid Salo for making ice-edge data available; and Geoffrey Lang (NMFS, Seattle) for assistance with data on fish predation. Doug Pengilly (ADFG) shared valuable insights on the system and effectively assisted throughout the project's development. Two reviewers helped improved the manuscript substantially; we appreciate their thorough reading and critique. Participation of L.O. was partially supported by a Pew Fellowship in Marine Conservation and CONICET (Argentina).

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GEODUCK (*PANOPEA ABRUPTA*) RECRUITMENT IN THE PACIFIC NORTHWEST: LONG-TERM CHANGES IN RELATION TO CLIMATE

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ABSTRACT

Investigation of climatic forcing on recruitment is often complicated by a scarcity of data at relevant spatial and time scales. Skeletal structures of long-lived sedentary animals can yield valuable long-term retrospective information, with fine spatial resolution. Geoducks are in that category: these gigantic and commercially valuable clams can reach an age of 168 years, and they aggregate in dense coastal beds from southeastern Alaska to Washington. Back-calculation of recruitment from age-frequency distributions compiled in 1979–83 in British Columbia and Washington shows a decades-long decline in recruitment over a vast geographical realm (British Columbia to Washington) that reached a minimum during the mid-1970s. Analysis of data collected between 1993 and 2002 confirms a large-scale pre-1970s decline and reveals a post-1975 rebound. Recruitment in British Columbia is correlated with coastal environmental indexes, such as river discharges (negatively) and coastal sea-surface temperature (positively).

INTRODUCTION

There has been a growing interest over the last decade to understand the effects of environmental variability on the dynamics of harvested marine populations (Hollowed and Wooster 1992; Clark et al. 1999; Zheng and Kruse 2000; Logerwell et al. 2003). Most of the search for connections between climate and recruitment (or year-class strength) has focused on oceanic ecosystems and mobile species (primarily finfish), and information has been aggregated at large geographical scales under assumptions of homogeneity. This emphasis reflects a scarcity of time-series data, both biological and environmental, that are informative at a spatial scale required to understand the complexity of processes in the intrinsically heterogeneous coastal ecosystems (Sinclair and Frank 1995). Evidence of climatic forcing, however, can be inferred from large-scale geographical coherence of year-class strength, even if the processes responsible for such effects are open to speculation (Orensanz et al. 1998).

Because of their life history and the distribution and spatial structure of their metapopulations, geoducks (*Panopea abrupta*) offer unique opportunities to investigate the effects of environmental factors on growth and recruitment along coastal ecosystems. They are among the longest-lived animals in the world (oldest recorded age is 168 years; Bureau et. al. 2002) and their shells contain a record of climate change (Strom 2002). They are also a convenient research material because of their size (largest infaunal bivalve, up to 5 kg in weight and 25 cm in shell length) and availability, as they support a very lucrative and widely spread commercial fishery. Back-calculation of relative recruitment based on age-frequency distributions compiled in 1979-83 indicates that by 1975 recruitment had been declining for decades over a large geographic range, from British Columbia to Washington (Orensanz et al. 2000). Suggestion of a rebound in recruitment during the 1980s and early 1990s, inferred from the post-harvest recovery of density in several tracts from Washington, could not be confirmed because no new age data became available for about 20 years.

New data became available in 2002 from an extensive ageing project conducted in British Columbia (Bureau et al. 2002). Preliminary analysis of these data revealed some significant features: recruitment was at a global minimum around 1975, and there was a post-1975 rebound in recruitment across all coastal zones of British Columbia (Orensanz et al. 2004). Geographical coherence in recruitment across British Columbia and Washington was observed both in the decline (pre-1975) and rebound (post-1975) phases. This large-scale spatial coherence suggests that coastwide climatic forcing may underlie the pattern. Several environmental variables have shown a major shift in the Pacific Northwest around 1975 (Ebbesmeyer et al. 1991). These changes have been referred collectively as regime shifts in the Pacific Northwest, and several studies have discussed their impact on the functioning at the ecosystem (Francis et al. 1998) and species level in the Pacific Northwest (Clark et al. 1999; Strom 2002). Prominent among the environmental variables capable of influencing the coastal zone at such large scales are coastal sea surface temperature (SST) and freshwater discharges by large rivers. Proximate effects aside, the latter integrates average climatic conditions on an annual basis. Here we explore the relationship between these two factors and geoduck recruitment from Washington to the Queen Charlotte Islands and discuss alternative hypotheses proposed to explain the decline in recruitment before 1975 and its subsequent rebound in the post-1975 era.

MATERIALS AND METHODS

Age-frequency distributions based on two large samples collected during the period 1979-82 in British Columbia (*n* = 2,276 specimens; Breen and Shields 1983) and Washington (*n* = 2,157 specimens; Goodwin and Shaul 1984), used by Orensanz et al. (2000) to back-calculate time series of an index of recruitment (here used as equivalent to year-class strength), were reexamined and compared to data that recently became available. The older samples are aggregates of small subsets of data (typically fewer than 200 specimens per site) spread over the entire Puget Sound Basin in Washington and the west coast of Vancouver Island and the Strait of Georgia in British Columbia.

Two ongoing ageing programs are yielding new age-frequency distributions after a period of almost 20 years during which little new data were gathered. Bureau et al. (2002) published a large data set based on biological samples collected from 34 sites throughout British Columbia between 1993 and 2000 (fig. 1). In order to avoid analytical difficulties resulting from pooling age distributions obtained during protracted periods, only samples collected between 1996 and 1998 (18 sites, 6,416 individuals aged) were used in the analyses. In Washington new data have been generated since 2000[1]; samples already processed and utilized in this study were collected in 2001 and 2003 from three nonharvested sites (*n* = 1,327 specimens; fig. 1). Harstene Island (*n* = 831, 47°40'N, 122°48'W, south Puget Sound) was sampled in 2001, and Quartermaster Harbor (*n* = 332, 47°22'N, 122°17'W, south Puget Sound) and Langley (*n* = 165, 48°03'N, 122°25'W, north Puget Sound) in 2003.

Age-frequency distributions were used to back-calculate time series of recruitment. Calculations of relative recruitment based on samples collected in 1979–82 followed Orensanz et al. (2000). In the case of the new samples from British Columbia (collected in 1996–98), calculations were based on (1) the age-frequency distributions compiled by Bureau et al. (2002), (2) estimates of virgin (unfished) biomass (B_0) reported by Canada's Department of Fish and Oceans (DFO; estimation is based on density of unfished beds, total area of known beds, and mean weight; for details see Hand and Bureau 2000), (3) annual catch data for each bed (made available by DFO), and (4) a constant natural mortality coefficient, $M = 0.02\ \text{yr}^{-1}$. The latter is close to the experimental estimate of Bradbury et al. (2000; $0.016\ \text{yr}^{-1}$) and to the value used by Washington Department of Fish and Wildlife (WDFW) ($0.0226\ \text{yr}^{-1}$). In order to combine age-frequency distributions with catch data and estimates of B_0 (both reported in metric tons), biomass figures were converted to numbers using average weights estimated from the surveys, assuming that the harvest is nonselective; this is justified by the fact that geoducks virtually stop growing in weight over the range of ages of interest (Bureau et al. 2002). The back-calculated indexes of recruitment were aggregated at the geographical scales of the entire coast of British Columbia and the regions of Georgia Strait and the North Coast (fig. 1). Data from sites within a region were weighted by the estimated size of the population they represented. In the case of data from Washington (samples collected in 2001–2003) the back-calculations involved only natural

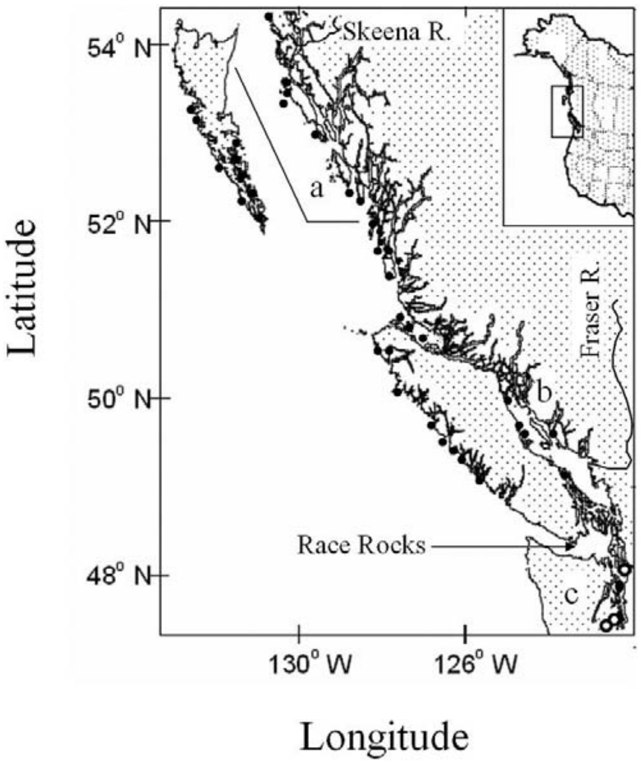

Figure 1. Geographic location of collections made during 1993–2003 in British Columbia (*black circles*) and Puget Sound, Washington (*white circles*). (*a*) North Coast, (*b*) Georgia Strait, (*c*) Puget Sound.

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[1] J. Valero, D. Armstrong, and R. Hilborn, unpubl. data.

mortality, because samples were taken from unharvested sites. Relative recruitment was calculated for the 1940–90 year-classes in British Columbia and for the 1940–95 year-classes in Washington. These windows were chosen in order to avoid biases caused by the under-representation of younger ages in the samples (geoducks are fully recruited at an age of 8–10 years; Harbo et al. 1983; Bradbury et al. 1998), and of older age-classes because of poor representation.

Time series of the recruitment index obtained with samples collected over the last decade in British Columbia and Washington were used to explore correspondence with environmental variables. Time series based on data collected in 1979–82 are informative when integrated at the large geographical scale of the entire sample (Puget Sound, British Columbia), but they are difficult to use when the analysis requires adjustment of the spatial scale. Physical variables investigated as indicative of environmental forcing are sea surface temperature (SST) and the annual discharge of the Fraser and Skeena rivers (fig. 1). Long time series of SST have been collected in British Columbia through a network of lighthouses (http://www-sci.pac.dfo-mpo.gc.ca/osap/data/lighthouse/bcsop.htm; Hollister 1972; Mueter et al. 2002). The series from Race Rocks (fig. 1), in the Juan de Fuca Strait, is the longest (1922 to present; Hollister 1972) and has been previously used in other studies of the relation between climate and bivalve populations from the Pacific Northwest (Orensanz 1989; Strom 2002). The Fraser and Skeena rivers were selected because they drain the largest basins in British Columbia. Total annual (December–January) flows for the Fraser (Hope Station: 49°22.83'N; 121°27.08'W) and the Skeena (Usk Station; 54°37'50"N, 128°25'55"W) are available from http://www.msc-smc.ec.gc.ca/wsc/hydat/H2O/.

The time series of recruitment, SST, and river discharge were scaled to a maximum of 1 in order to allow comparisons between indexes with different units and ranges. In time-series analysis we are often interested in determining autocorrelations at different time lags (e.g., the relationship between SST on a particular year and SST at lag *t*). Partial autocorrelation is the relationship between the current state of the variable and the state of the variable at lag *t* when we have controlled for the correlations between all of the successive time steps between the current step and step *t* (Crawley 2002). Partial autocorrelations can be extended to two time series to determine if the patterns of ups and downs of the series are cross-correlated at different time lags (Crawley 2002). As a first quantitative exploration of the data we performed partial autocorrelations between SST, river discharge, and recruitment indexes. A more detailed formal analysis of high-frequency variability with higher spatial resolution and more refined temporal windows (e.g., intra-annual information on SST and river discharge instead of annual means or totals) is beyond the scope of this study, though it is the subject of forthcoming contributions.

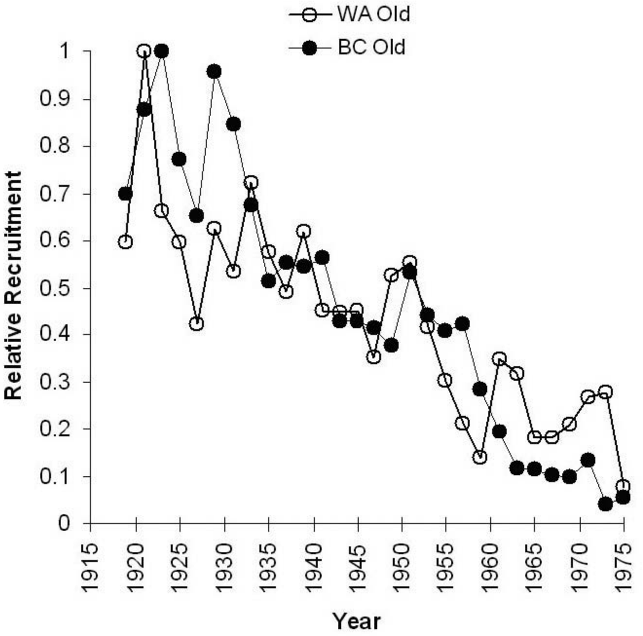

Figure 2. Trends in geoduck relative recruitment (1919–75) back-calculated from age-frequency distributions from British Columbia (data from Breen and Shields 1983) and Washington (data from Goodwin and Shaul 1984).

RESULTS

Time series of relative recruitment back-calculated from the old age-frequency distributions (1979–81) from Washington and south British Columbia (aggregated at the spatial scale of the two regions) show conspicuously similar patterns of decline during at least six decades (1920–75; fig. 2). The rate of decline of the indexes is comparable across these two large geographic domains, spanning nearly four degrees of latitude (47–51°N) of complex coastscapes. Relative recruitment calculated from age-frequency distributions of samples collected in British Columbia (54°N to 48°N) during the period 1996–98 shows a very similar pattern: a declining trend after 1940 and a minimum during the mid-1970s (fig. 3). The more recent data shows a consistent post-1975 rebound, reaching pre-decline levels during the early 1990s (fig. 3). In the case of Washington, new data are available from only three sites. Of these, Harstene Island is located in the southern part of Puget Sound (fig. 1), close to the Dougall site (*n* = 459, 47°19'N,122°50'W), sampled during the period 1979–82 (Goodwin and Shaul 1984). A comparison of the two series shows a similar pattern: while both show a distinct post-1940s decline, there is substantial high-frequency (year-to-year) variability (fig. 4). Both show,

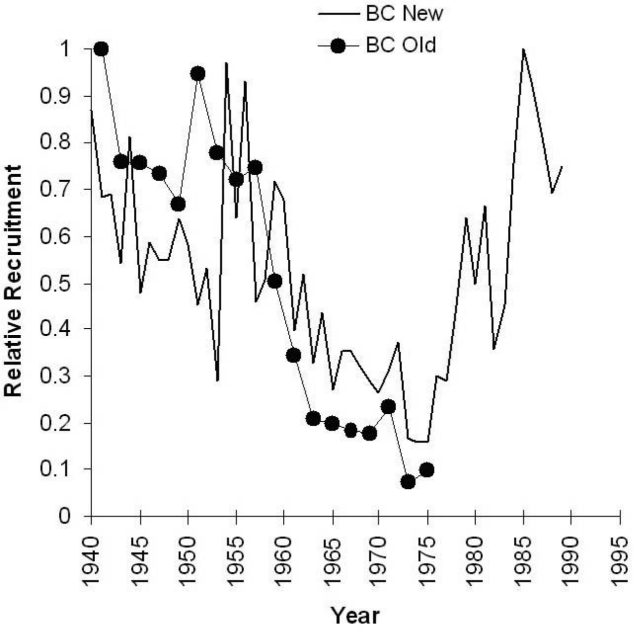

Figure 3. Trends in geoduck relative recruitment back-calculated from old (data from Breen and Shields 1983) and new (data from Bureau et al. 2002) age data from British Columbia.

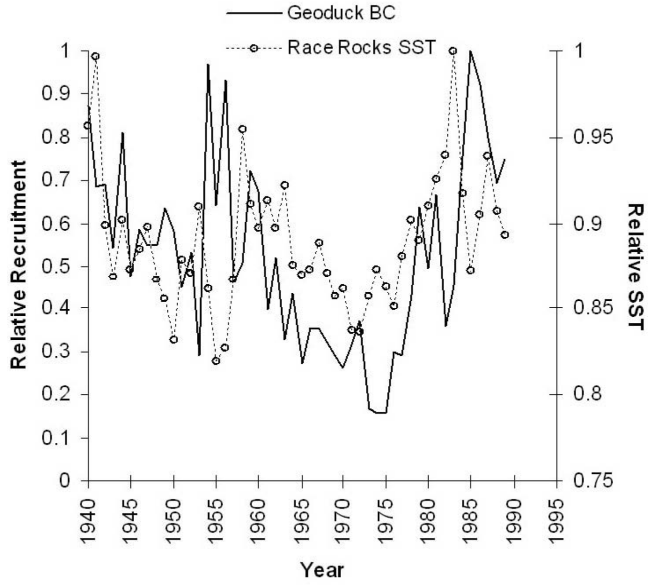

Figure 5. Time series of geoduck relative recruitment back-calculated from age-frequency distributions from British Columbia (data from Bureau et al. 2002) and relative sea surface temperature (SST) at the Race Rocks Station (data from Fisheries and Oceans Canada).

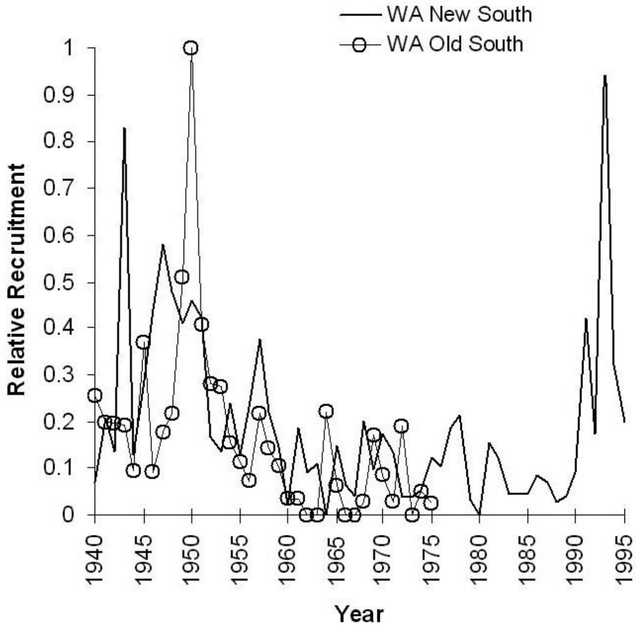

Figure 4. Trends in geoduck relative recruitment back-calculated from old (data from Goodwin and Shaul 1984) and new (data from this study) data collected from two closely located sites from Puget Sound: Dougall (sampled in 1979–81) and Harstene Island (sampled in 2001).

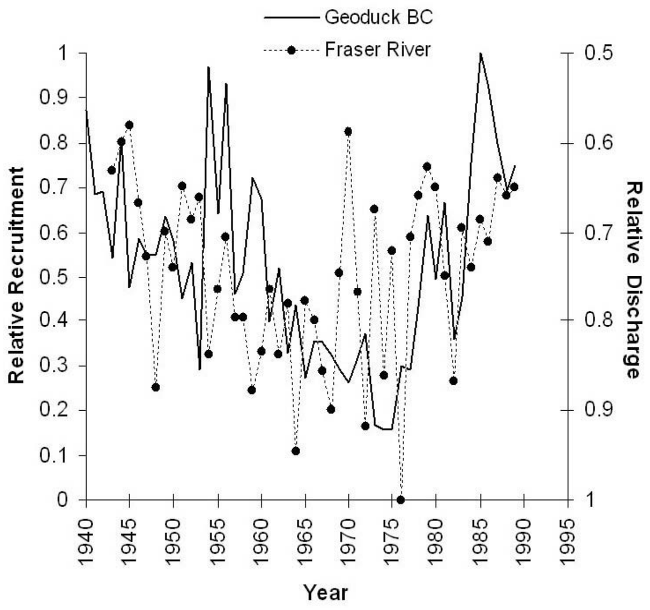

Figure 6. Time series of geoduck relative recruitment back-calculated from age-frequency distributions from British Columbia (data from Bureau et al. 2002) and relative Fraser River discharge at the Hope Station (data from Environment Canada).

on average, very weak year-classes during the 1960s and 1970s. The recent data shows a rebound of recruitment during the 1990s, reaching (as in British Columbia) pre-decline levels. Similar comparisons for the other two sites are precluded by the lack of comparable sampling sites in the earlier data series. Long-term trends of recruitment based on samples collected during 1996–98 in British Columbia are very consistent with long-term trends in SST recorded at Race Rock during the same period (fig. 5). Although there is considerable miss-match in year-to-year (high-frequency) fluctuations, there are significant positive cross-correlations at the 5% level at different lags.

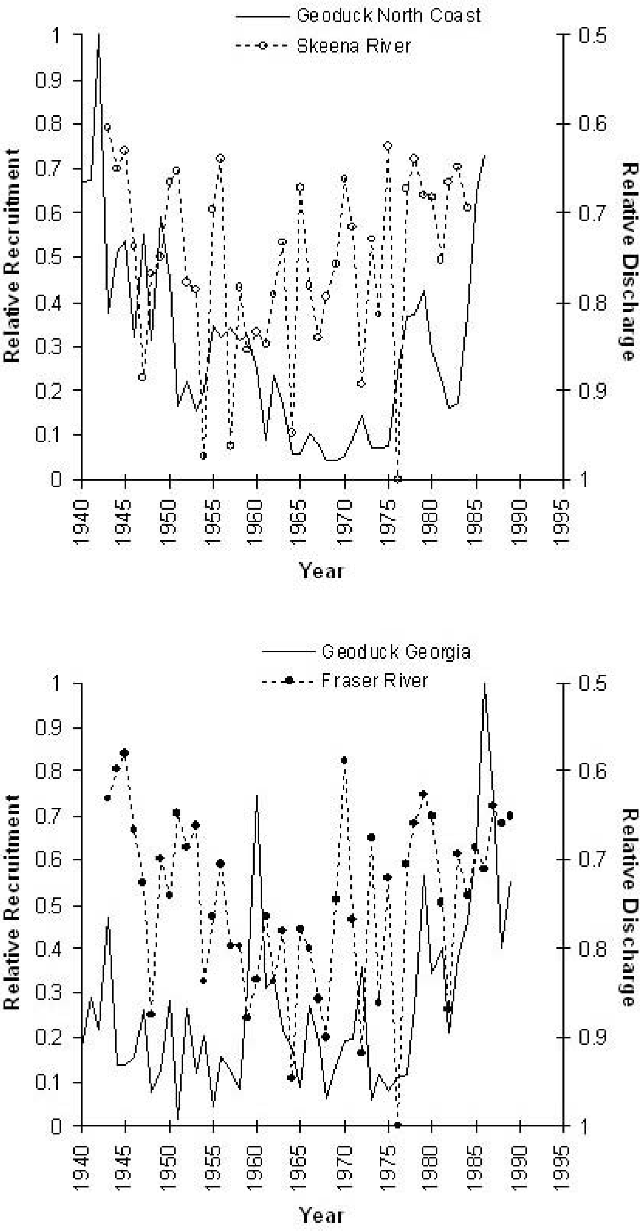

Figure 7. Time series of geoduck relative recruitment back-calculated from age-frequency distributions from the North Coast (*top panel, solid line*) and Georgia Strait (*bottom panel, solid line*; data from Bureau et al. 2002) and relative river discharge for the Skeena (*top panel, white circles*) and Fraser Rivers (*bottom panel, black circles*).

Discharge from the Fraser River showed an upward trend during the 1940s and 1950s. On average it remained relatively high during the 1960s and early 1970s (the maximum was reached in 1976), then during the 1980s it declined back to the level of the 1940s (fig. 6). In spite of strong year-to-year variability there is consistency between the long-term trends in flow discharge and geoduck recruitment (decreasing when river discharge increases, and vice versa). This is supported by significant negative cross-correlations at the 5% level at different lags.

The pattern seems to fade if the spatial resolution is increased to examine recruitment in the North Coast region in relation to annual discharge from the Skeena, and in the Strait of Georgia in relation to the annual discharge from the Fraser River (fig. 7). In spite of that, there are still significant negative cross-correlations at the 5% level. Year-to-year variation in the discharge from the Skeena River is very high, and the period of frequent high flows was more extended than in the Fraser, lasting from the mid-1950s to the mid-1970s. Recruitment in the North Coast region showed (as the aggregated British Columbia series did) a declining trend during the 1940s and 1950s and a rebound after 1975. By contrast, the period of low back-calculated recruitment is more protracted, extending over a decade (1964–75; fig. 7, *top*). Relative recruitment in the Strait of Georgia shows a post-1975 increase comparable to that observed in highly aggregated data, but there is no indication of a pre-1975 decline (fig. 7, *bottom*). In this region the back-calculation is based on two of the historically most heavily fished beds in British Columbia (Comox and Oyster rivers).

DISCUSSION

Orensanz et al. (2000, 2004) discussed a puzzling pattern in time series of year-class strength back-calculated for geoduck populations from the Pacific Northwest: a decades-long decline that reached a minimum during the mid-1970s, followed by a rebound to pre-decline levels during the 1980s and 1990s. Although subject to some regional variability, the general pattern appears very robust, showing up in data collected in various ways during 1979–82 and 1993–2001. While the pre-1975 decline (or at least a scarcity of young individuals in samples collected during the early 1980s) had been noticed in previous studies (Sloan and Robinson 1984; Bradbury et al. 1998), it was interpreted as an artifact created by patchiness (Breen and Shields 1983; Goodwin and Shaul 1984) or as the result of gear selectivity. The artifact of patchiness should disappear when data from many locations at a large geographical scale are pooled, but the pattern persists after pooling (Orensanz et al. 2000). With regard to gear selectivity, there is wide consensus that it can be assumed that geoducks are fully recruited by age 8–10 years (Harbo et al. 1983; Bradbury et al. 1998). It is interesting to notice that the only subset of the data in which the pre-1975 decline was not evident corresponds to the samples collected in 1996–98 from the Strait of Georgia. The two locations sampled correspond to the most intensely fished beds in British Columbia (the Comox and Oyster Rivers); this could cause errors in the back-calculation. Analysis of recent data (not included here) from an unharvested bed in the Strait of Georgia (South Round Island) may provide a valuable contrast.

Although the pattern appears robust, no attempts have been made to explain it. In the context of management it was noticed that the pre-1975 decline is not attributable to commercial harvesting (the decline started long before the onset of the fishery) or other anthropic influences (the decline was evident in pristine and in highly disturbed regions). Here we present evidence indicating that long-term trends in geoduck year-class strength in the Pacific Northwest parallel environmental indexes that indicate conditions prevailing in coastal environments at the regional scale. We show correspondence between time series of geoduck year-class strength, SST, and the discharge from the two largest rivers in British Columbia, the Skeena and the Fraser (no comparable rivers drain into the Puget Sound Basin). Trends in geoduck recruitment are coherent over a large geographic range, spanning approximately seven degrees of latitude (47–54°N; fig.1). River discharge integrates many environmental factors likely to have proximate local effects on a regional scale, including peripheral coastal zones (like Puget Sound) where there is no significant driver drainage. While many of the factors integrated are likely to influence the dynamics of populations of benthic sedentary organisms with pelagic larvae, the nature of the proximate operating mechanisms remains open to speculation.

The year-class strength minimum around the mid 1970s matches a period of low SST (the lowest in the post-1940 decades) and a high frequency of years with strong discharge from major rivers (figs. 5–7). Connections between environmental conditions and year-class strength in benthic organisms may involve temperature-related events in the reproductive calendar (e.g., Bonardelli et al. 1996), since sedentary organisms (unlike fish) cannot move to their preferred environment. Other sensitive processes are the advection/retention and survival of pelagic larvae. Delayed spawning during cold years or larval flushing off coastal environments during years of strong river discharge could possibly affect geoduck year-class strength. Extending the analysis to include additional variables such as wind, upwelling, and primary productivity should shed light on the processes responsible for the pattern described in this work.

Evidence of decadal climatic forcing of productivity in northeastern Pacific marine populations, ranging from plankton to marine mammals, has accumulated in recent years and has been widely discussed in the literature (Francis et al. 1998). One of the most conspicuous low frequency events of the last decades was a set of changes in environmental conditions that is referred to collectively as the 1976–77 regime shift (Ebbesmeyer et al. 1991; Francis et al. 1998; Hare and Mantua 2000). Phytoplankton and zooplankton productivity changed in response to the shift (Brodeur and Ware 1992; Polovina et al. 1995; Roemmich and McGowan 1995), with suggested cascading effects on survival of marine fish larvae (McFarlane and Beamish 1992). Year-class strength of groundfish (Hollowed and Wooster 1992; Clark et al. 1999) and salmon stocks (Hare and Francis 1995; Beamish et al. 1999) show coherence with environmental factors at decadal rather than annual scales. In the case of geoduck recruitment, long-term change appears to have been a gradual process that extended over decades.

Most studies of low frequency (decadal) forcing in marine systems have attended to mobile species in open oceanic ecosystems. Sedentary species from coastal ecosystems have attracted less attention, in part because of the difficulties posed by the spatial heterogeneity of such systems. Year-class strength of little neck clam (*Protothaca staminea*) in Garrison Bay (north Puget Sound, Washington) has been shown to be positively correlated with SST (Orensanz 1989) measured at Race Rocks, paralleling the pattern documented here for geoducks. There is indication of similar patterns in other bivalves of the Pacific Northwest, like butter and manila clams (A. Strom, pers. comm.). Previous work on climatic forcing on geoduck populations focused on patterns of growth rate, in which case the unit used to reconstruct a trend is an individual (Noakes and Campbell 1992; Strom 2002). In the case of year-class strength the detection of pattern is complicated by spatial heterogeneity. Strong year-classes should not be expected to be homogeneously distributed in space. Rather, a period of increasing year-class strength could consist of increasingly frequent but spatially localized pulses of settlement or recruitment, implying that series back-calculated for different locations can show little high-frequency spatial coherence. Interpretation of year-class strength data at different spatial scales requires aggregating the data at the appropriate scale.

The results presented here are exploratory. A detailed and formal analysis will require attention to (1) high-frequency (year-to-year) variability, (2) higher spatial resolution (analysis of the full data set with algorithms of hierarchical pooling) of both biological and environmental variables (e.g., Mueter et al. 2002), (3) more refined temporal windows (e.g., intra-annual information on SST and river discharge instead of annual means or totals), (4) potentially lagged responses, and (5) sequences of environmental events rather than events in isolation (e.g., Logerwell et al. 2003). These are beyond the scope of this study, but they are the subject of ongoing research by the authors.

Given geoducks' extreme longevity, the alleged stability of populations and the sustainability of the fisheries that they support could possibly be more apparent than real. Geoduck abundance changes slowly, the impact of recruitment variability being buffered by the large number of year-classes present in a population. Trends in abundance can be perceived only by examining long time series of data and understood only if placed in the context of long-term trends of climatic change.

ACKNOWLEDGMENTS

We thank Heather Honeycutt, Jessica Raaum, Michael Cooksey, and Elise Cronin for lab work in ageing samples from Washington. Bob Sizemore, Michael Ulrich, and Don Rothaus (WDFW) conducted most of the state-supported field sampling in Puget Sound. Mike McHugh (Tulalip Tribe) and David Winfrey (Puyallup Tribes) provided technical support and assistance with fieldwork. Lisa Veneroso and Alex Bradbury (WDFW) critiqued and supported the project. Are Strom (WDFW) and Dominique Bureau (Fisheries and Oceans Canada) provided geoduck biological data from, respectively, Washington and British Columbia. This work was partially funded by Washington Sea Grant and Washington Department of Natural Resources. Valero's work was supported by the Floyd E. Ellis Memorial Scholarship, the James and Joy Ellis Scholarship in Fisheries, and the Claire L. and Evelyn S. Egtvedt Fellowship of the School of Aquatic and Fishery Sciences, University of Washington. Three anonymous reviewers provided suggestions that helped to improve the manuscript.

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INVESTIGATING ENVIRONMENTAL EFFECTS ON POPULATION DYNAMICS OF *LOLIGO OPALESCENS* IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Using fishery-dependent and fishery-independent data on the distribution of paralarvae, juveniles, and adults, we assess the effects of the transition from the 1997–98 El Niño to the 1999 La Niña on the abundance, distribution, and production of market squid *Loligo opalescens* in southern California. Percentage occurrence of paralarvae within the CalCOFI survey of the Southern California Bight declined during El Niño, indicating that little production occurred during El Niño winters, and abundance from trawl surveys was low during the summer following the 1997–98 El Niño along the coast from Point Conception to Vancouver on the shelf and slope. Mean growth rates of *L. opalescens* declined with increasing temperature in the month of hatch, and hatch month temperature explained 67% of the variability in mean growth during the transition from El Niño to La Niña conditions (1998 and 1999). Using the observed temperature-dependent growth rates, we developed the first age-based, temperature-dependent population model for *L. opalescens*. Population dynamics were dramatically influenced by cumulative mortality, and the results predict that a bimodal recruitment period should be found with periods of 5 and 7 months and that the second peak should be narrower than the first peak.

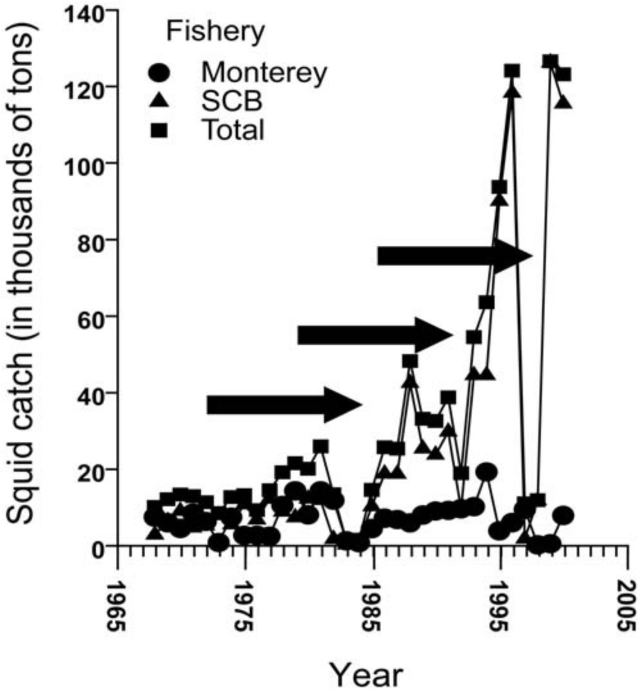

Figure 1. Plot of annual squid catch between 1965 and 2001 for Monterey (*circles*), Southern California Bight (*triangles*), and the total of both (*squares*). Arrows indicate fishery decline during El Niño periods followed by rapid recovery.

INTRODUCTION

The market squid *Loligo opalescens* supports one of the most valuable commercial fisheries in central and southern California with a value of more than $41 million a year (CDFG 2001). The total annual catch has increased exponentially since the 1970s (fig. 1; CDFG 2001). Most of the increased catch (80%) has occurred in the Southern California Bight (SCB), and there is uncertainty whether the increase is related to increasing abundance (Vojkovich 1998). Rapid declines in squid catch occur during El Niño years, and it has been suggested that the environment may be partially responsible by influencing the availability, population size, and recruitment success of this animal (McInnis and Broenkow 1978).

More remarkable than the near collapse of the fishery during El Niño periods is the rapid recovery of the catch to pre-El Niño levels within a year or two following (fig. 1; Maxwell et al., 2004). This is especially noteworthy given that *L. opalescens* is short lived (~ 6 months; Jackson 1994; Butler et al. 1999; although Spratt (1979) hypothesized that *L. opalescens* lived more than 18 months) and evidently semelparous (Knipe and Beeman 1978; Macewicz et al. 2004). The rapid changes in apparent abundance in the fishery have led to considerable speculation regarding the strategy of squid to ride out the presumably harsh El Niño conditions. Given the rapid recovery of squid, some investigators have argued that the population is displaced to the north or offshore during El Niño (CDFG 2001). If so, abundance of squid might increase with latitude during El Niño, or abundance or presence might increase offshore. Alternatively, during El Niño conditions squid may move to deeper waters where the environmental conditions necessary for proper development of eggs may be found, making the squid unavailable to the fishery and to those marine mammals that forage near shore (Lowry and

Carretta 1999; Roberts and Sauier 1994). Both hypotheses suggest that squid become unavailable to the fishery, thus allowing the population to rebound rapidly after an El Niño. They also suggest that harsh El Niño conditions are overcome by redistributing the population to more favorable refuge habitats, potentially maintaining production.

The observed patterns of fishing success during and following the El Niño may also reflect demographic processes occurring in the planktonic or juvenile stages, where the environment may change vital rates. Of the many environmental variables that may affect survival and recruitment of squid, temperature is thought to be one of the dominant mechanisms, because it can reflect different oceanographic regimes (Lynn et al. 1982; Waluda et al. 2001) and because temperature is related to physiological processes (Forsythe 1993). For example, growth rates are strongly influenced by temperature in many squid species including *Loligo* spp. (Hatfield et al 2001; Forsythe 1993). Using laboratory data, Forsythe (1993) showed that under conditions of *ad libitum* food, growth rates of squid increased with increasing temperatures. Jackson et al. (1997) used field data to show that growth rates increased in warmer conditions for a loliginid common to neritic waters of the northwest Gulf of Mexico. In contrast, Jackson and Domeier (2003) showed that age and size of *L. opalescens* declined with increasing water temperatures and increased with upwelling (an index of secondary production) in the SCB. Based on these data, Jackson and Domeier (2003) suggested that the size difference of squid observed in the diets of sea lions could be explained by variability in the temperature-dependent growth differences in the Southern California Bight. They did not examine the effects on population size and recovery.

Growth rate variability can potentially affect the synchrony of cohorts. Mixing of different cohorts on the spawning grounds may occur as a result of the strong temperature dependencies that cause fast growing cohorts to catch up to slow growing cohorts (Grist and de Clers 1998, 1999), and bimodality in recruitment pulses may result. Thus, the question remains whether the apparent rapid repopulation of *L. opalescens* is a function of environmental variability operating directly on the biological and physiological processes of the population or whether it is simply reflecting changes in availability.

In this study, we examine the hypotheses regarding the changes in abundance associated with El Niño conditions in an effort to determine whether squid "ride out" El Niño conditions by changing spatial distribution, or whether changes in demographic rates could be responsible for the observed changes and abundance in the fishery. To do this, we use (1) juvenile abundance and distribution data from the Northwest Fishery Science Center triennial summer trawl survey conducted between Point Conception, California, and Vancouver Island, Canada, to examine changes in distribution; (2) para-larval abundance data from winter and spring CalCOFI surveys conducted in the Southern California Bight to examine changes in productivity; and (3) growth rate data determined from mature adult squid collected from the SCB commercial fishery to examine the environmental control on recruitment to the fishery. After evaluating these hypotheses, we present an age-based temperature-dependent (TDGR) model of squid growth and develop a simple population dynamics model using TDGR to drive the population growth rates. We compare predictions derived from this model to the overall patterns of occurrence of squid in southern California as a starting point for directed studies on *L. opalescens*.

METHODS

Fishery Data

Loligo opalescens were sampled at biweekly intervals from the commercial catch landed at ports within the SCB between 15 November 1998 and 01 July 2000. On each date, mantle length (ML, in millimeters), gonad weight (GW, in grams), maturity stage (immature or mature), and sex (male or female) were obtained from a subsample of the catch. A further subsample of 15–60 animals each month provided statoliths for age and growth analysis. All samples from the SCB were pooled and given equal weight in all analyses.

Several studies have validated the daily deposition of rings in laboratory reared *L. opalescens* (Jackson 1994a; Butler et al. 1999). In the laboratory, statoliths were processed following Butler et al. (1999). Briefly, statoliths were mounted on microscope slides, ground on 400 µm paper until the primordium was visible. Under magnification (x100–400) daily rings were counted using transmitted light to determine the age of each squid. Hatch date was determined by subtracting the age at capture from the date of capture.

Preliminary analysis showed that most of the animals collected as part of this study were mature adults (98%; Maxwell et al. 2004), so we defined growth rate (GR) of mature animals in the fishery as

$$GR = \text{mantle length (mm)} \;/\; \text{age (d)} \qquad (1)$$

Thus, growth rate as estimated here was the average value over the entire life of the animal.

Many growth functions and growth models exist for squid (Jackson et al. 1997; Yang et al. 1986). We feel that the simple relationship we propose is adequate for this exploration for two reasons: (1) We are not predicting the size at any age during the paralarval or juvenile period when a more appropriate growth function would be necessary; and (2) under any contemporary model, faster (slower) growth rates would result in younger (older) animals recruiting to the fishery. We then correlated the mean growth rate of monthly cohorts, assigned using retrospective hatch-date distributions to examine the relationship between growth rate of survivors caught in the fishery and environmental variables, as indexed by hatch month sea surface temperature (SST) at Scripps Pier, La Jolla, California.

Fishery-independent Data

The relative occurrence and distribution of *L. opalescens* along the west coast of the United States was determined from summer (July–August) triennial groundfish trawl data collected by the Northwest Fisheries Science Center. Briefly, we used data from the 1995, 1998, and 2001 surveys from 512, 528, and 506 stations, respectively. The bottom trawl sampled at depths of between 50 and 300 m, corresponding roughly to 2–50 nmi offshore. The survey uses a high-opening Nor'eastern trawl, with 27.2 m headrope and a 37.4 m footrope. The survey is used to determine the abundance and distribution of principle groundfish species found on the shelf and slope. Given the pelagic and neritic nature of *L. opalescens*, the trawl is likely to be inefficient at capturing them. However, the survey should be consistent enough to provide an index of the spatial distribution and the relative occurrence during these different years, but it is not intended to provide an unbiased estimate of true abundance.

As part of the California Cooperative Fisheries Investigations (CalCOFI) plankton tows are made at each of 66 fixed stations in the SCB (Schwing et al. 2002) using a 1 m by 2 m surface Manta net equipped with 0.947 mm mesh and a General Oceanics, Inc. model 2030 flow meter to estimate the volume of water filtered. The Manta net is neustonic and samples the upper 0.5 m depth. The number of stations positive for paralarvae was counted for each winter (January–February) and spring (April–May) cruise and the average was used to estimate an annual index of productivity (percentage occurrence) for the period 1989 to 2003. Okutani and McGowan (1969) have shown that paralarvae are most abundant at depths of about 50 m, suggesting that the Manta nets may undersample paralarvae compared with bongo tows, which sample the water column. For data that overlap (1997–2003), bongo and manta tows were positively correlated ($r = 0.54$, $n = 7$, $p < 0.05$) and, more important, exhibited declines during the El Niño of 1997–98, suggesting that we can use manta tow data for describing the temporal pattern of production.

Physical Oceanographic Data

Sea Surface Temperature. Daily SST at Scripps Pier was extracted from the coastal temperature database at the University of California San Diego for the period January 1977 to July 2001 and averaged to derive a seasonal cycle (fig. 2). Missing values from this data set were replaced with climatological daily values of the missing days, using a nonlinear regression of the first two harmonics (annual and biannual) for all daily values (see Lynn et al. 1982). Monthly values were derived by averaging daily values, and these monthly values were used to examine temperature dependencies with growth rate.

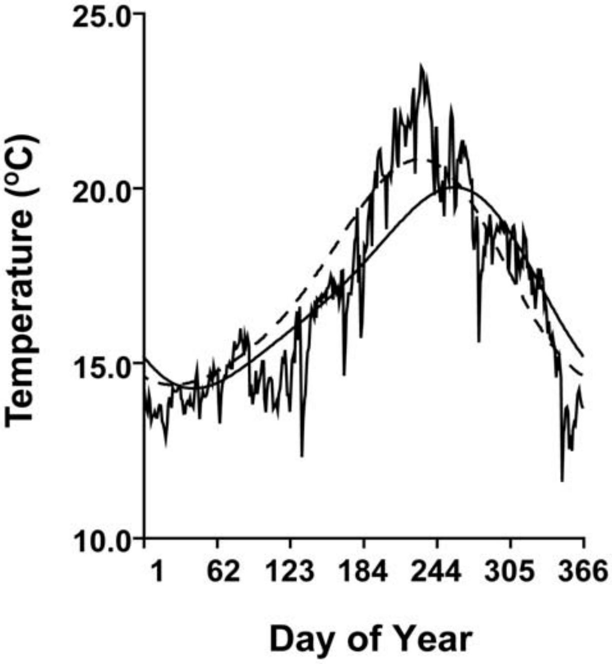

Figure 2. Seasonal daily temperature at Scripps Pier in 1999, as well as seasonal average daily temperature at Scripps Pier between 1977 and 2001 (*dashed curve*) and seasonal average temperature derived from harmonic constituents (Lynn et al. 1982) for station 90.30 in the Southern California Bight (*solid curve*).

Model Development. For use in the model, the annual climatic temperature cycle within the SCB was developed using published harmonics (Lynn et al. 1982) at CalCOFI station 90.30, located at 33.45°N and 117.43°W for the period 1977–99 (fig. 2).

Using TDGR we developed a first-order, age-based model of the population dynamics of *L. opalescens* to investigate the ability of this animal to respond to seasonal environmental forcing (fig. 3). In the first generation (the first year of the model), 53 weekly cohorts were released and hatched with a temperature-dependent growth rate that was determined by the climatic water temperature at hatching and subject to a uniformly distributed random error proportional to 1°C.

An appropriate mortality rate for the planktonic and juvenile period must be specified but is difficult to parameterize. Estimates of adult mortality range from 0.3 month^{-1}, suggesting a mortality rate of 0.01 d^{-1}; yet that mortality rate would mean that over a 200-day

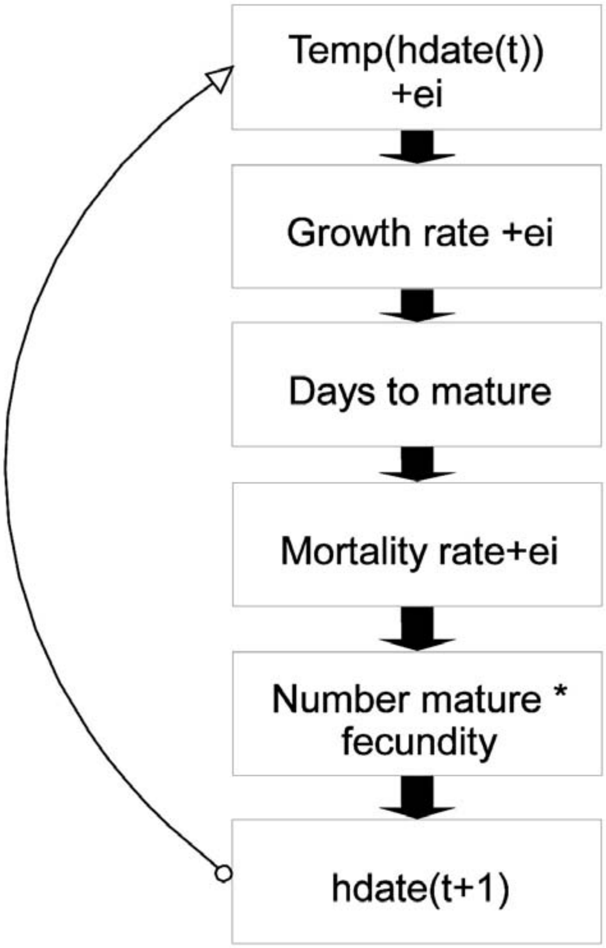

Figure 3. Diagram of temperature-dependent population model for *Loligo opalescens* in the Southern California Bight.

larval-juvenile period (Butler et al. 1999) 13% of eggs spawned would mature, suggesting that a higher planktonic mortality rate is necessary. A mortality rate of 0.035 means that over a 100- to 200-day larval-juvenile period, 3% to 0.01%, respectively, of the eggs would mature. Thus, we prescribed the mortality rate as fixed at 0.035 d^{-1} with a small amount of error (up to 0.005 d^{-1}) assigned using a uniformly distributed proportional error term. In the first generation, survivors from each of the 53 weekly cohorts produces 10^8 offspring to generate an initial population to spin up the model. In subsequent generations, we used the length-based total fecundity relationship described by Macewicz et al. (2004) where potential fecundity (F) was linearly related to mantle length (ML) as:

$$F = 29.8 \star ML \tag{2}$$

Macewicz et al. (2004) estimated that the average escapement prior to capture in the fishery is 36%, and the mean lifetime of animals on the spawning grounds is 1.67 days.

While there is some discussion in the literature regarding the effect of growth rate on size at maturity (Lipinski and Underhill 1995), we did not vary size at maturity. Instead, our model tracked the number of days required to reach a specified size at maturity (129 mm ML) and assumed that all animals that reached that size would spawn and would then be removed from the population through natural mortality or fishing. The hatch date of their offspring was calculated from the date of maturation of their parents and by adding 30 days to account for egg development time. No egg mortality was prescribed because there are no published data to provide a reference point. We calculated the monthly population size and the monthly number of weekly cohorts contributing to the population in each month of each year. The model was run for 25 years, roughly equivalent to 50 generations, in order to examine the long-term dynamics within the population.

RESULTS

Temperature

Sea surface temperature in the SCB showed a distinctive but skewed seasonal pattern with a minimum between January and April and a gradual heating between April and October before reaching a maximum and then a rapid decline (fig. 2). Little difference existed between the seasonal daily average temperature at Scripps pier and at station 90.30 in the SCB. The differences were principally related to the time of the mean maximum temperature that was shifted by about 30 days from the coast to the central SCB and exhibited a difference of about 2°C in mean maximum temperature.

Abundance and Distribution

Coastwide distributions of squid exhibited distinct patterns associated with the presence of El Niño conditions (fig. 4). Expanding-symbols plots of the numbers of *L. opalescens* collected in trawl surveys showed distinct spatiotemporal differences in the distribution of catch. Prior to the El Niño of 1997–98, squid were found all along the coast from Point Conception to Vancouver, British Columbia. During the summer 1998 El Niño squid abundance in trawl samples was very low with a considerable fraction of the stations containing no squid at all. No evidence for a shift in the abundance of squid to the more northern areas was observed, nor was there any apparent shift to slope waters from shelf waters. In 2001, squid were again abundant all along the west coast. The overall pattern of distribution strongly suggests that the decline of squid during El Niño is consistent along the coast, and its return is also a coastwide phenomenon.

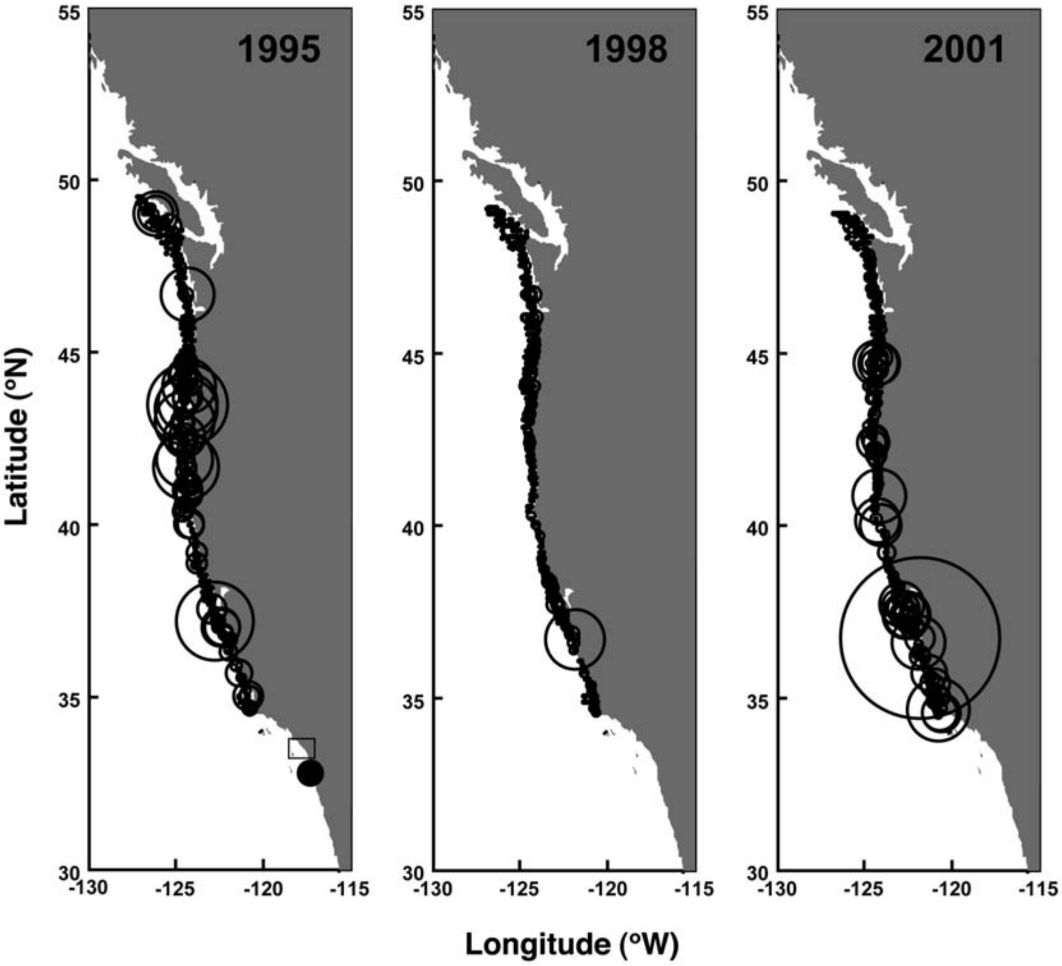

Figure 4. Expanding-symbol plots of *L. opalescens* collected as part of the by-catch in the summer triennial groundfish survey conducted by the NWFSC, between Vancouver Island, Canada, and Point Conception, California. Sample sizes were 512, 528, and 506 stations in 1995, 1998, and 2001, respectively. In the panel for 1995, the location of Scripps Pier is indicated by the filled circle, and the location of station 90.30 is indicated by the small rectangle.

Larval Production

Paralarval production (percentage occurrence) within the SCB also follows the pattern observed for juveniles and adults collected along the west coast as part of the trawl survey (fig. 5). Mean occurrence of paralarvae at CalCOFI stations between 1989 and 2002 was 14%. During El Niño years of 1992–93 and 1997–98, paralarval occurrence declined to less than 3% of stations. Immediately following the El Niño, mean percentage of occurrence increased from less than 3% to between 15% and 25% in a single year.

Size and Age

Market squid exhibit inter- and intra-annual variability in age and size at capture (fig. 6). A variety of patterns in size and age are evident when squid are plotted against hatch month (fig. 6). For example, after hatching during January and February of 1999, squid

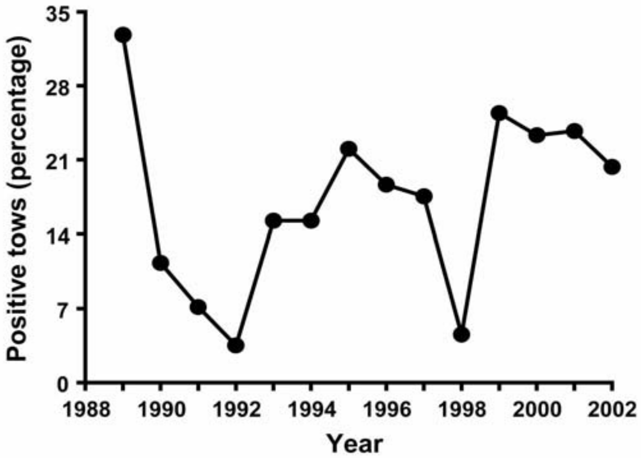

Figure 5. Percentage occurrence of *L. opalescens* paralarvae collected from manta tows conducted as part of the winter (January–February) and spring (March–April) CalCOFI surveys in the Southern California Bight between 1989 and 2003. The number of stations occupied in each cruise year ranged from 120 to 133.

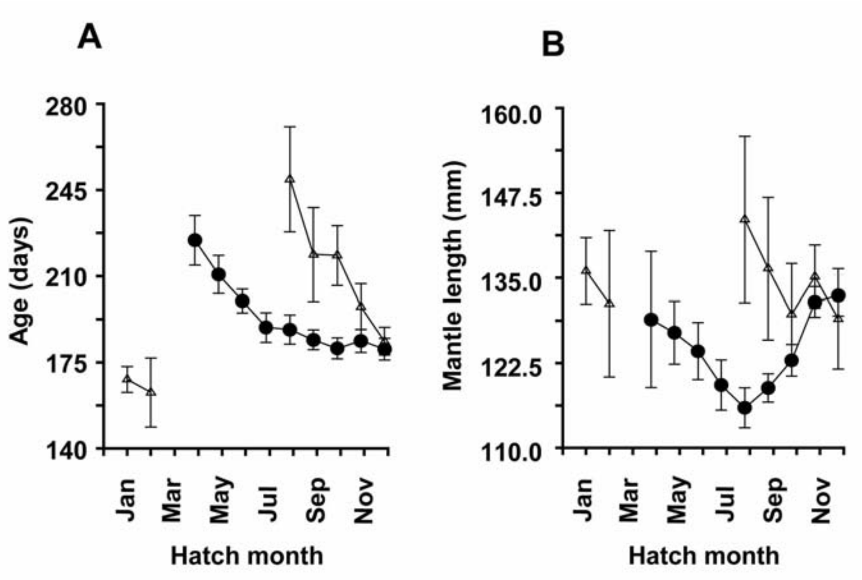

Figure 6. Age and mantle length of mature *L. opalescens* sampled from the Southern California Bight fishery in 1998 (*circles*) and 1999 (*triangles*) plotted by month of hatch.

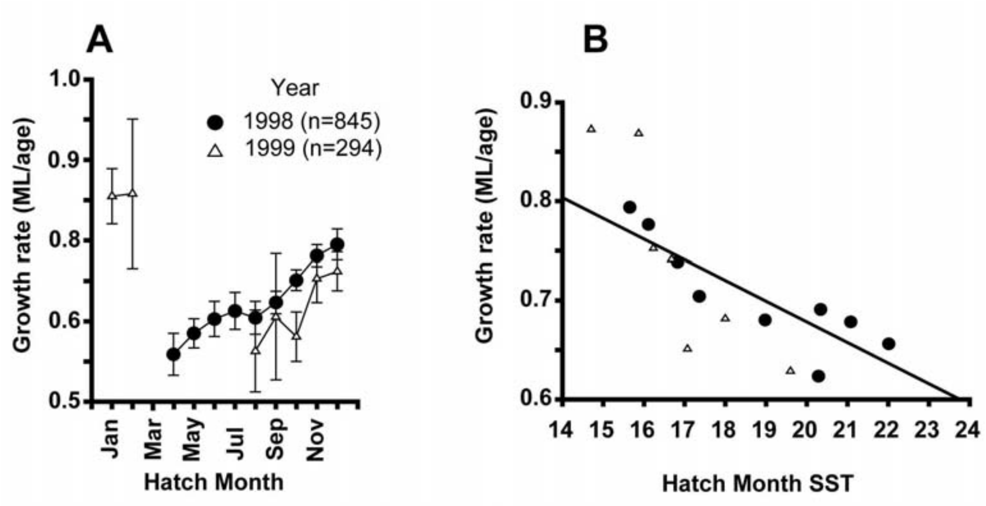

Figure 7. Mean growth rate (±1 SE) of mature *L. opalescens* from the Southern California Bight commercial fishery in 1998 and 1999 plotted by month of hatch (*A*), and means of growth rates in relation to hatch-month SST as calculated from the monthly mean temperature recorded at Scripps Pier (*B*).

grew large (130–135 mm) but were young (140–160 d) at capture. At other times, smaller (115 mm), older (~190 d) squid were captured. There were also large differences between years. For example, squid hatched in July 1999 were older (~240 d) and larger (140 mm) than squid hatched in July 1998. Furthermore, the change in mean age at capture for animals hatched from July to November in each year declined at different rates, while size increased in 1998, and declined over the same months in 1999. This interannual variability limits the usefulness of age or size data used independently in developing seasonal growth models.

Growth Rates and Temperature

Mean growth rates plotted as a function of the month of hatch show that growth rates of animals are more similar over seasons and between years than would be expected simply on the basis of age or size (fig. 7A). Growth rates were highest in January and February of 1999 (during La Niña), and were low during spring in both years, increasing from May to December. For periods where the data overlap (July to December of 1998 and 1999), mean growth rates were not significantly different ($p > 0.3$) between years in a two-way fixed factor ANOVA with year and hatch month as factors. Hatch-month growth rates did vary, with growth rates in July and August significantly different from those in October to December ($p < 0.01$). The slopes seem to be similar, yet the paucity of data (only 7 months) precludes formal testing. There is also a fair amount of variability in the first half of the year, but we have little data with which to examine that relationship further.

When growth rate is plotted against the mean temperature of the hatch month at Scripps Pier, growth rates for squid spawned during the two-year period decline with increasing temperature (fig. 7). Owing to the incomplete nature of our sampling, there were no animals sampled for age determination in mid- and late 1999 from which to estimate growth rates in March and April, yet the fishery operated successfully during that period. Overall, however, the mean growth rates for each year are the same, suggesting a similar temperature dependency for each year where the data overlap. A linear regression, fit to the combined data of growth rates versus mean monthly temperature during the hatch month and derived from monthly composite satellite data for the SCB, yielded a strong negative relationship between temperature and growth rate:

$$\mathrm{GR} = 1.18 - 0.0395 * \mathrm{T}$$
$$(R^2 = 0.67, \mathrm{df} = 14, p < 0.0001) \tag{3}$$

These results indicate that the timing of the seasonal warming and cooling cycles, which are different during El Niño and La Niña periods, can explain the variability in size and age differences when plotted against hatch month.

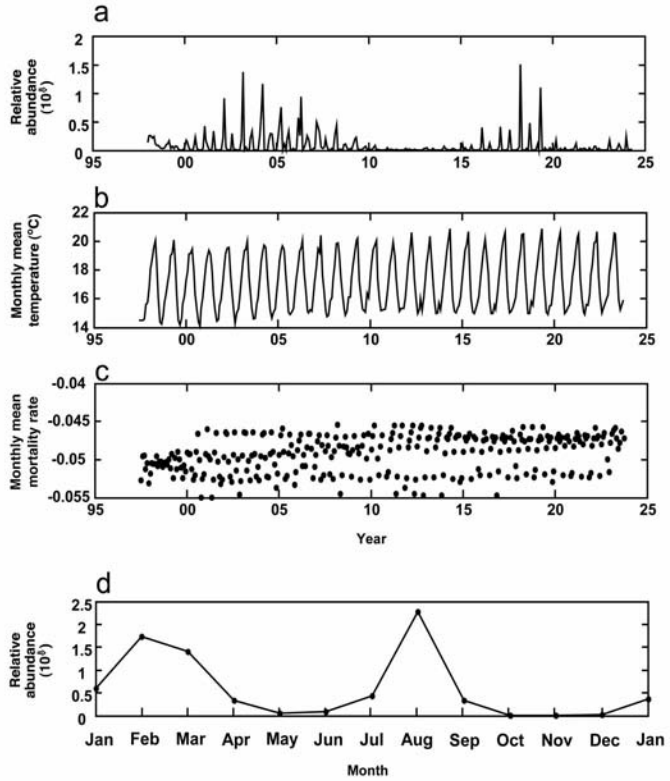

Figure 8. Twenty-five year population simulations of *L. opalescens* using an age-based temperature-dependent growth model. Time series of monthly population abundance (*a*), monthly average temperature (*b*), monthly mortality rates (*c*), and seasonal pattern of recruitment (*d*).

Model Runs

To shed light on the influence of the seasonal asymmetry in temperature on growth rates and recruitment, a baseline run of the model was made using the seasonal temperature-dependent growth rates and an initial (first year only) weekly egg production of 10^8 individuals, with a fixed ($0.035\ \mathrm{d}^{-1}$) mortality rate, and no stochastic variability. The resulting stable model showed that the seasonal temperature cycle produces an asymmetric recruitment pattern, with the first mode occurring in March and the second in August. In both recruitment peaks, most of the animals recruiting consisted of fast-growing animals, and recruitment occurred during early spring and summer.

The results of the stochastic model (variability in mortality rate and temperature dependent growth function) produced a variety of interesting patterns that reflected the balance between slight increases and decreases in mortality rate and growth variability. Figure 8 shows the results of one model run to illustrate the types of patterns produced by this simple model. The initial production of 10^8 individuals produced weekly during the first year is replaced by the fixed but length-specific fecundity beginning with the second generation. The population rapidly becomes bimodal after just a few generations (fig. 8a,b,c). In fact, in all model runs this bimodal pattern occurs and is a product of the ~6-month life cycle of this animal. Moreover, in all iterations this bimodal recruitment pattern was dominated by a broader peak in the spring and a narrower peak in the mid- to late summer period (fig. 8d). In model runs where the population remained fairly stationary the late winter recruitment was usually more than twice the summer recruitment. In some iterations and the one shown in Figure 8a, the population exhibited runs of successful recruitment and growth for periods of 10 to 15 years. In many instances, these periods of high abundance were followed by periods of rather low recruitment. During periods of rapid growth, the population was capable of increasing orders of magnitude in just a few generations, suggesting that the rapid increases observed in the fishery following an El Niño are well within the biological capacity of this species. Monthly mean temperature and mortality rates show that small differences in either factor create conditions sufficient to rapidly affect the population size.

DISCUSSION

The paucity of data regarding the life history of market squid complicates our ability to understand how this animal will respond to changing environmental conditions and fishing pressure. The lack of a reliable biomass time series obviates correlating environmental variables with catch. Instead, the exploration that we have pursued here should serve as a model to focus research questions in the near term, in order to elucidate the role of environmental forcing in the population dynamics of this species.

The results of this study indicate that, more likely than not, the collapse of the squid fishery in California is a result of a decline in the production of offspring during El Niño rather than a shift in habitat that lowers the availability of squid to the fishery. Our results also show that growth rate is negatively related to temperature and is generally predictable from the hatch month SST. This predictability provides a mechanism to model growth rate variability in years as environmentally diverse as the transition from El Niño (warmer-than-normal) and La Niña (cooler-than-normal) conditions.

The decline of the squid catch during El Niño periods has been attributed to a variety of behavioral responses to the environment that affect squid availability in the nearshore fishery because the increase in catch following an El Niño suggests a population growth rate that seems unnaturally high (CDFG 2001). Several studies have indirectly examined the availability hypothesis. For example, evidence from monitoring the scat of sea lions that eat squid suggests that the squid population collapses during El Niño years (Lowry and Carretta 1999). However, because the marine mammals studied forage nearshore, there is no way to quantify whether dietary changes result from changes in squid behavior or from population collapse (Lowry and Carretta 1999; but see Preti et al., this volume). Our data from fishery-independent surveys of juvenile and adult squid along the coast, coupled with data showing large declines in the occurrence of paralarvae in the SCB during El Niño, provide stronger evidence that the population declines to nonfishable levels all along the coast and that production resumes when conditions improve immediately following the El Niño. If squid simply moved offshore, or to depth to spawn, we would still expect to capture squid paralarvae in the CalCOFI surveys that extend much further offshore than the fishery. Likewise, offshore movement or northward migration of juveniles and adults would result in higher catches of squid in the trawl survey along the slope or in northern waters. Assuming that the bottom trawl surveys capture squid in sufficient quantity, their decline along the coast and throughout the survey area makes the possibility of their capture less likely.

Many researchers have fit length-based growth functions to squid (e.g., Mohamed and Rao 1997); however, it has become clear that plasticity in the growth function (generally attributed to temperature) and the short life span of most squids requires an age-based approach (Jackson 1994b). For example, Dawe and Beck (1992) showed that growth rates of *Illex* in the northwest Atlantic were substantially underestimated when length-based methods were used. Moreover, they showed that growth varied among individuals and with hatch date. These and other studies suggest that great care is needed to properly describe growth in all squids. Recent work (Butler et al. 1999; Jackson 1994a; Jackson and Domeier 2003) has validated the daily deposition of rings in *L. opalescens* and provided a solid foundation from which to assess growth variability. Our data provide another reason for using age to describe growth: it better quantifies environmental effects than either length or other measures of size alone do.

Generally, mantle length is either linearly or exponentially related to age (Bettencourt et al. 1996; Jackson and Domeier 2003), although logistic (Arkhipkin 1995; Brunetti et al. 1998) and two-stage (Yang et al. 1986) models have been used. No age-based growth model has, to our knowledge, explicitly incorporated temperature (but see Hatfield et al. 2001). Instead, most generate seasonally specific growth functions and acknowledge the effect of temperature (Collins et al. 1995; Jackson et al. 1996). In this study, we assumed that size and age at maturity could be combined to provide an index of the mean growth rate over the lifetime. Yet, even if growth rates are exponential—or two-stage, as has been suggested—our model has considerable utility because fast (slow) growth would result in younger (older) animals arriving on the spawning grounds in a manner predictable from the hatch-month temperature. Furthermore, this simple relationship will hold as long as we do not try to model intermediate sizes at age, when a better growth model would be needed. However, if the appropriate growth model for squid is more aptly described by a von Bertalanffy with a long asymptotic growth period, the use of our simple function would be less useful.

Given that a high level of variability in mean lifetime growth rate was explained by hatch-month temperature within and between years, we feel confident that hatch-month temperature is a proxy for the environmental conditions that may control growth of *L. opalescens* in the SCB. The exact function describing growth may well change when more data are included, so the exact parameter estimates here should be considered preliminary and subject to change. Moreover, there may be better measures of life-long temperature exposure prior to maturity (degree days or integral heat exposure) that would require a better growth model. However, to be useful, any other measure of environmental exposure during the larval and juvenile stages must have better predictive capacity, not only in terms of variability explained but also in predictions derived. Notwithstanding these considerations, given any hatch-date temperature and the mean lifetime growth function, it should be possible to predict the average arrival date on the spawning grounds.

Forsythe (1993) showed that under *ad libitum* conditions squid exhibit increased growth rates with increasing temperature. Jackson et al. (1997) were the first to show this response in the field for a Gulf of Mexico loligonid. In contrast to the predictions based on the temperature-growth model of Forsythe (1993), we found that growth rates in the SCB declined with increasing temperature. A negative relationship between age and temperature was also found by Jackson and Domeier (2003) for *L. opalescens*; and since they found a positive relationship between upwelling and size and age of squid in the SCB, they suggested that the negative relationship was a tradeoff between temperature and food. Such a possibility further emphasizes the preliminary nature of our relationships, and the importance of understanding the role of the environment on demographic characteristics of this species. Furthermore, the inconsistency between laboratory predictions and our observations suggests that generalizations from other congeners are unlikely to be supported unless the ecosystem (upwelling, boundary current, coastal temperate, and so on) is included.

We have developed the first age-based, temperature-dependent population model for any squid species. It differs in several ways from the two-stage, length-based and temperature-dependent growth model of Grist and des Clers (1998, 1999). In their model, they used temperature to modify seasonal growth, which allowed faster growing animals spawned later in the season to catch up with slower growing members hatched earlier. In this manner, they were able to develop a bimodal recruitment pattern of *Loligo* spp. based on the probability of reaching a given size. Our model explicitly assigns a growth rate based on an empirical relationship and tracks the time required to reach a prescribed size at maturity. By including a mortality term, the seasonality in our recruitment patterns is driven by differential levels of cumulative mortality in fast-growing and slow-growing cohorts rather than by differential growth producing synchronous recruitment through growth variability. It should be possible to test the predictions from either model by examining growth histories of mature animals collected in the commercial fishery.

Our simulations of the population dynamics of squid show that bimodal recruitment patterns can be generated from small changes in cumulative mortality arising from slightly lower or higher growth rates; they can produce the kinds of abundance fluctuations generally seen in the SCB fishery and are a consequence of squid's approximately 6-month life span. The model produced periods of relatively high abundance followed by periods of relatively low abundance, despite a climatic, seasonal temperature field. The model also produced periods where the population increased rapidly over a few generations, similar in magnitude to that observed in the SCB fishery following an El Niño. The model uses climatic seasonal temperatures and does not incorporate El Niño or La Niña conditions. The variability in population size over longer time periods is a consequence of the variability in the mortality rate and in the temperature-derived growth rate. Our model is not suitable for predicting recruitment trends since neither food nor density-dependent processes are included and the exact environmentally derived growth function is almost sure to change. For example, including food in this model through either upwelling indexes or some other measure will affect the dynamics of this population model by changing the empirically derived growth relationship. Specifically, it should shift the period of maximal growth rate from winter to late spring, when temperature is low and food is plentiful. And this should affect the size and persistence of annual recruitment peaks. Likewise density-dependent processes, although unknown, may effect recruitment by decreasing survival during the egg stage or by increasing cannibalism during the juvenile stage at high spawning biomass (O'Dor 1998). Several sources of mortality were not included in the model and should be considered when data are available. One important component is mortality during the egg stage, which in this model can be adjusted simply by decreasing fecundity. Yet, we have not varied it because it would also be a function of temperature given the temperature-dependent egg-development time. Field and laboratory studies on egg mortality are clearly needed. Moreover, because mortality rate is the only variable that can drive the population variability in this model, it is a truism that the population will be driven by mortality. On balance, however, this model provides a way forward that should be useful in defining effective research strategies.

We are encouraged by the present model because it provides hypotheses regarding the dynamics of the population that can be modeled or tested in the field. We anticipate that this model and its derivatives will begin to address such fishery questions as: Can fishing mortality over the last several days of life affect production more than a small change in the mortality or growth rates? To ensure future recruitment, is it necessary to protect the summer or winter recruitment pulse? Likewise, how different are the magnitudes of the abundance and duration of the summer and winter recruitment pulses? Yet it is clear that the preliminary nature of the model, and the fact that there are significant differences between seasonal catch patterns, means that this model cannot be used in any predictive sense.

The development of appropriate long-term management strategies for this species will likely require considerable modeling to understand the sensitivity and population dynamics of market squid to changes in fishing and the environment. Modeling will, in turn, require a large amount of high-quality demographic and biomass data. Future studies must investigate the effects of temperature and food on the growth rate of *Loligo*. Regionally, we know little about how growth rates in the Monterey fishery compared to those in the SCB. Are they similar, can they explain the shorter seasonal pattern in the fishery in Monterey Bay? Addressing these questions is crucial because recent data show that the fishery is beginning to be prosecuted during daytime and throughout the year in the SCB, potentially capturing mature squid prior to and during spawning (Forsythe et al. 2004). More generally, the role of the environment is critical in assessing the long-term productivity and persistence of this species. We see declines occurring during warm El Nino periods, yet the fishery has increased its catch during a warm phase of ocean temperature associated with general basin-scale ocean conditions (Hollowed et al. 2001). How different are populations likely to be during cooler periods? Was the population historically larger than it is now? Moreover, we know little about the relationship of growth rate and size at maturity of *L. opalescens*. Such details are critical to understanding energetic tradeoffs to future reproduction. The efficacy of retrospective growth determination using the statolith needs to be addressed by collecting multiple samples of cohorts during their pelagic period, an expensive but necessary task given the ecological role of squid in the California Current. The questions above suggest directions for future research that will provide the data necessary to support, modify, or refute the strawman we have built to understand the population dynamics of and environmental influences on squid.

ACKNOWLEDGMENTS

We acknowledge the many port samplers and biologists at the California Department of Fish and Game who not only collected the data used here but also processed the statoliths and spent many hours ageing them. Thanks also to Dale Sweetnam of CDFG for allowing us to use CDFG data for this modeling exercise. Kevin Piner of Southwest Fisheries Science Center reviewed an earlier version of this article. We also thank the three reviewers whose comments have made this a stronger manuscript.

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THE POTENTIAL SYNERGISTIC EFFECTS OF CLIMATE CHANGE AND FISHING PRESSURE ON EXPLOITED INVERTEBRATES ON ROCKY INTERTIDAL SHORES

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ABSTRACT

Climate change and fishing are both major determinants of the distribution and abundance of marine species. As the rates of climate change and exploitation accelerate, additive and synergistic interactions between them are becoming increasingly important to the dynamics of marine ecosystems and the sustainability of marine fisheries. We examine the impacts of climate change and fishing pressure on the stocks of three commonly exploited intertidal invertebrates on Northeast Pacific rocky shores. California sea mussels (*Mytilus californianus*) are not likely to experience dramatic population shifts in the face of climate change, and the current low levels of exploitation appear to be sustainable. Owl limpets (*Lottia gigantea*), which grow more slowly, exhibit higher temperature sensitivity, and are preferred targets of fishers, will likely experience considerable reductions in distribution and abundance if temperatures rise and exploitation continues. Black abalone (*Haliotis cracherodii*) have already experienced dramatic declines directly attributable to over-exploitation and indirectly to warming trends that have exacerbated the effects of a devastating disease. Two generalities emerge from these comparisons. First, differences in life history characteristics result in a wide range of climatic and anthropogenic effects among species. Second, the effects of fishing pressure may unexpectedly magnify the effects of climate change, and vice versa. Synergistic interactions between environmental change and exploitation on rocky shores and in other marine ecosystems present considerable challenges for fisheries managers. The key to successful management and restoration in marine systems lies in developing a mechanistic understanding of the interactions between climate change and fishing pressure and how they affect population and ecosystem dynamics.

INTRODUCTION

Climate change and fishing are expected to be dominant drivers of future trends at the population, community, and ecosystem level in marine systems, from tropical coral reefs to polar seas to the deep-sea benthos (McClanahan 2002; Clarke and Harris 2003; Glover and Smith 2003). Although relationships between marine ecosystem dynamics and both climate (Glantz 1992; Beamish 1995; Roemmich and McGowan 1995; Francis et al. 1998) and fishing (Dayton et al. 1998; Pauly et al. 2002; Jackson et al 2001; Botsford et al. 1997; Chavez et al. 2003) are well-known, rarely are fishing and climate change considered together. Indeed, climatic variability is not incorporated into most fisheries management schemes (but see Conser et al. 2001). While more is being learned about how climate change affects fished populations (Glantz 1992; Beamish 1995; Finney et al. 2000; Bjørnstad and Grenfell 2001; McGinn 2002), our understanding of the interactions between exploitation and changing environmental conditions remains poor.

Climate change and fishing can interact in ways that are additive or synergistic (fig. 1). Additive effects occur when environmental conditions and fishing each reduce stock abundance in ways that are independent of one another. When effects are additive, a 20% stock reduction due to environmental impacts and a 50% reduction due to fishing would result in a 70% reduction in stock size (fig. 1A). By comparison, synergistic interactions generate effects that are greater than the sum of their parts, such as when one forcing agent exacerbates the effect of another, or when the combined influence of both factors pushes a population past a threshold abundance level. In these cases, the 20% reduction due to climate and the 50% reduction due to exploitation result in a >70% reduction in stock size (fig. 1B). Although progress is being made (e.g., Jurado-Molina and Livingston 2002), we still know very little about how fishing interacting with climate change affects marine populations, particularly when interactions are synergistic. In most cases, we lack sufficient data to properly address these types of questions (but see Jacobson and MacCall 1995; Hobday and Tegner 2002; Jurado-Molina and Livingston 2002).

Rocky intertidal shores provide a model system for examining the effects of climate change, fishing, and their interactions. Climate change may have substantial direct impacts on intertidal species, many of which live close to their environmental tolerances (Tomanek and Helmuth 2002), and climatically forced changes in the distribution and abundance of intertidal species are well documented (Barry et al. 1995; Southward et al. 1995). Fishing pressure on rocky shores is high in most parts of

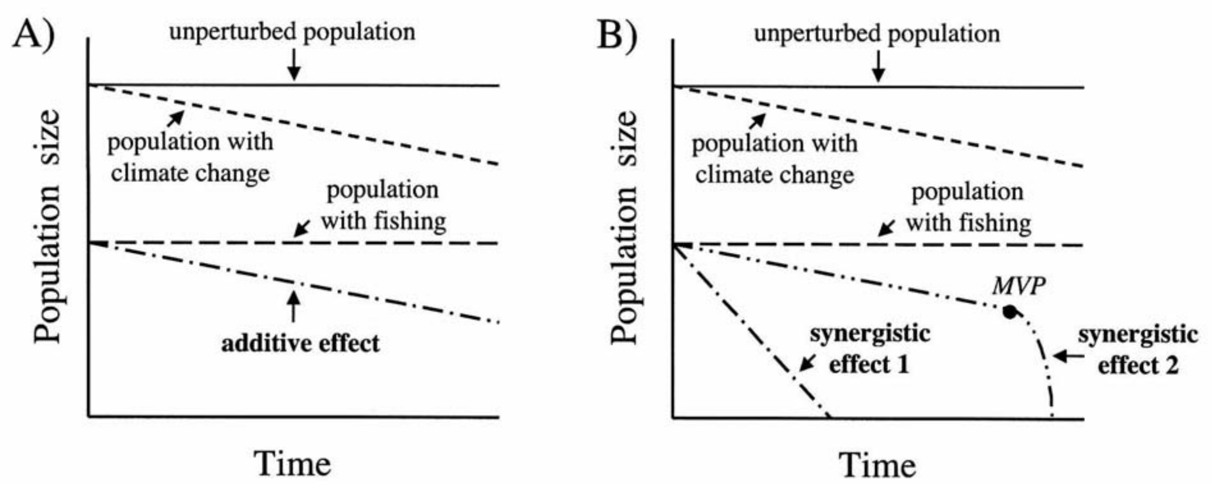

Figure 1. Additive versus synergistic effects of climate change and exploitation. *A*, The effect of fixed-quota fishing pressure (assuming constant environmental conditions) and monotonic climate change (assuming no fishing). Lower line represents additive effects, which are the sum of fishing and climatically induced reductions in population size. *B*, As in A, except the effects of fishing and climate change are nonadditive. Synergistic effect 1 can arise if fishing pressure increases the vulnerability of the population to climate change, or vice versa. Synergistic effect 2 can arise if the combined impacts of fishing and climate change push the stock below a threshold that would not be reached by climatic or fishing impacts acting in isolation. In the case illustrated here, the population declines below the minimum viable population size (*MVP*) and cannot recover.

the world, with important consequences for intertidal communities (for review, see Thompson et al. 2002). Anthropogenic climate change coupled with rapidly expanding coastal human populations has the potential to intensify both direct and indirect effects in the future and increases the probability of important synergisms between climatic variability and fishing.

In this article, we examine the relationships between environmental change and fishing on rocky shores in the Northeast Pacific, with specific reference to California (fig. 2). First, we summarize past and future climatic trends, as well as observed and predicted biological responses. Then, we examine the effects of climate change and fishing on three exploited intertidal invertebrates: the California sea mussel (*Mytilus californianus* Conrad), the owl limpet (*Lottia gigantea* Sowerby), and the black abalone (*Haliotis cracherodii* Leach). We use these case studies to demonstrate the general importance of climate-exploitation synergisms as well as the life-history characteristics that make an exploited species particularly vulnerable to synergistic effects. Finally, we discuss the importance of incorporating climatic variability into fisheries management strategies.

CLIMATE CHANGE AND INTERTIDAL ECOSYSTEMS

Environmental Change

A dramatic warming trend associated with greenhouse gas emissions is expected to be the dominant feature of environmental change over the next 100 years (IPCC 2001). Although this trend has already been detected, it is superimposed on natural environmental variability across a range of temporal scales. Natural environmental variation includes low-frequency 60–80 year oscillations (Ware and Thomson 2000), interdecadal oscillations (20–40 years) such as the Pacific Decadal Oscillation (Mantua et al. 1997), 18.6 year oscillations in the timing

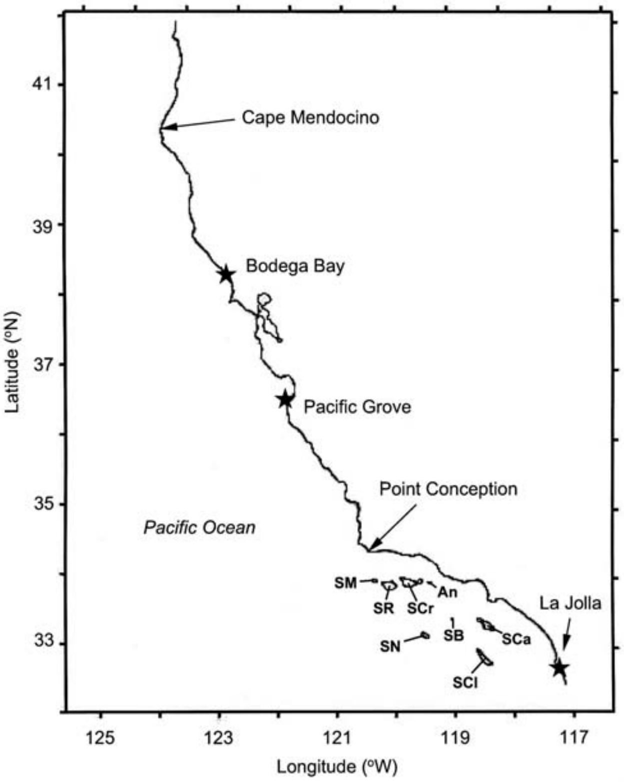

Figure 2. Map of the California coast. Stars indicate coastal sea-surface temperature recording stations. The Channel Islands, identified by letter codes, are San Miguel Island (SM), Santa Rosa Island (SR), Santa Cruz Island (SCr), Anacapa Island (An), San Nicolas Island (SN), Santa Barbara Island (SB), Santa Catalina Island (SCa), and San Clemente Island (SCl).

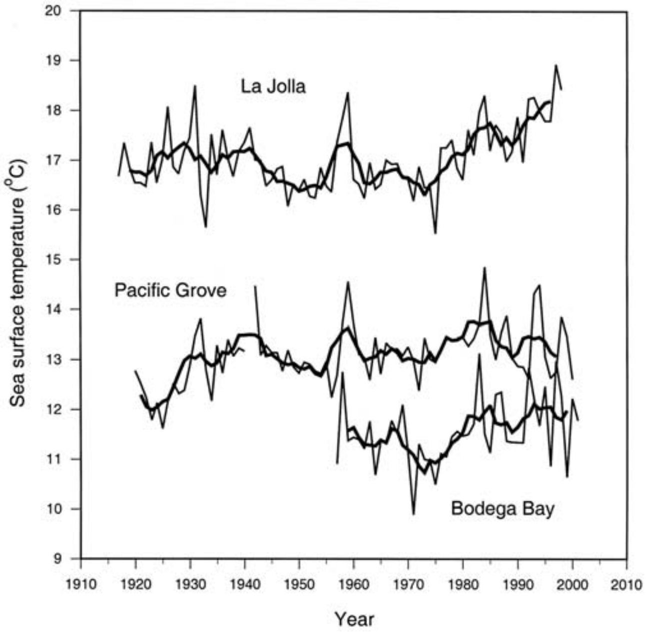

Figure 3. Nearshore sea-surface temperature records for three sites along the California coast: Scripps Institution of Oceanography, La Jolla; Hopkins Marine Station, Pacific Grove; and Bodega Marine Laboratory, Bodega Bay (see fig. 2 for map). Thin lines are annual means. Heavy lines are 5-year running means.

and duration of tidal emersion (Denny and Paine 1998; Helmuth et al. 2002), and high-frequency interannual oscillations such as El Niño Southern Oscillation events (Jones et al. 2001). These oscillations provide natural "experiments" that can serve as proxies for studying the impacts of long-term, nonoscillatory trends such as those predicted by anthropogenic warming scenarios (IPCC 2001).

Long-term changes have now been documented for many environmental variables in the Northeast Pacific. Instrumental sea-surface temperature records indicate both periodicity and general warming trends in California (fig. 3). Mean air temperatures near the northern California coast increased by more than 1.1°C in the past 50 years, although most of this trend is due to warmer temperatures at night (Nemani et al. 2001). An increase in El Niño frequency has been documented (Jones et al. 2001), as has an increase in winter storm frequency (Bromirski et al. 2003).

Climatologists provide several "high-confidence" predictions for future environmental trends (IPCC 2001). Sea level is predicted to rise approximately 30–50 cm over the next 100 years. Air and sea-surface temperatures will continue to increase at the global scale, although local trends along the coast will depend on additional factors such as upwelling and fog. Increased land-sea thermal gradients are expected to increase wind stress, which may in turn result in enhanced upwelling and increased storminess. Other aspects of oceanic circulation (e.g., California Current advection) and chemistry (e.g., pH) are likely to change in the future (IPCC 2001), but the nature and impacts of these trends are more difficult to forecast and will not be considered here.

Intertidal Responses to Climate Change

Rocky intertidal assemblages, by virtue of their straddling the interface between the marine and terrestrial realms, respond to changes in both oceanic and atmospheric conditions. Intertidal sampling in the 1930s and 1990s in Pacific Grove, California, revealed an increase in the abundance of southern invertebrate species and a concomitant decrease in the abundance of northern invertebrate species—a change attributed to increasing sea-surface temperature (Barry et al. 1995; for a British example, see Southward et al. 1995). Although intertidal populations are expected to keep pace with sea-level rise, warming air temperatures may compress vertical zonation patterns. A comparison of algal upper limits in the Gulf of Maine between 1928 and 1996 revealed that many species had shifted downwards on the shore while none had shifted upwards, which may have been a response to increasing air temperatures in the region (Mathieson et al. 1998). Compressed zonation may result in local extinctions if species are "squeezed out" in an ever-narrowing band of habitable shoreline. This squeeze effect is thought to set the local and regional distributional limits of a turf-forming algae in Washington (Harley 2003) and a barnacle in New England (Wethey 1983). Latitudinal range changes have been documented for intertidal species (e.g., Southward et al. 1995; Connolly and Roughgarden 1998), and many such range shifts are correlated with warming temperatures. Range shifts have also been documented for subtidal invertebrates in response to changes in temperature and/or larval transport (e.g., Zacherl et al. 2003; L. Rogers-Bennett, unpub. data). Poleward range shifts now appear to be a general response to warming at the global scale (Parmesan and Yohe 2003).

CLIMATE CHANGE AND EXPLOITED INVERTEBRATES

Case Study 1: Sea Mussels

Life History. The California sea mussel, *Mytilus californianus*, is a dominant rocky-shore species that forms extensive mid-intertidal and occasionally subtidal beds from Alaska to southern Baja California, Mexico (Suchanek 1985). Individuals grow rapidly and can attain sizes up to 15 cm in as little as 3 years. Sea mussels typically form a mosaic of mature, often multilayered beds interspersed with disturbance patches of various sizes, ages, and stages of recovery. The primary agents

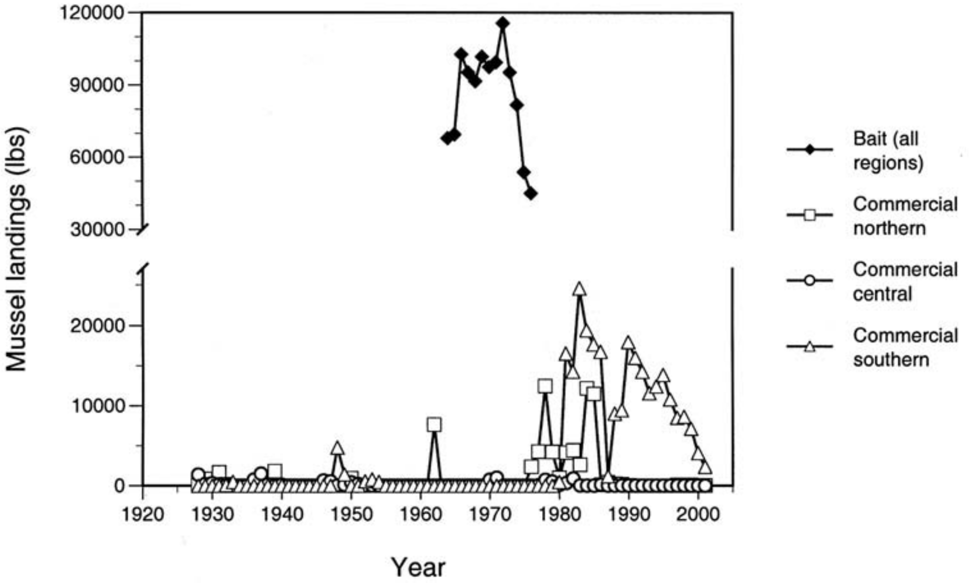

Figure 4. Mussel (*Mytilus* spp.) landings in California. Open symbols are commercial landings, divided into northern (Eureka and San Francisco), central (Monterey), and southern (Santa Barbara, Los Angeles, and San Diego) regions. Solid symbols are bait landings. Because 99.7% of the mussels in this category were landed at Los Angeles and San Diego, the data were not subdivided by region. Commercial landings data were obtained from the Pacific Fisheries Environmental Laboratory. Bait landings data were obtained from California Department of Fish and Game Fish Bulletins and were only available from 1964 to 1976. Note the change in *y*-axis scaling above the axis break.

of gap formation are hydrodynamic forces during storms and wave-born debris such as drift logs (Dayton 1971; Denny 1987). Rates of patch recovery are generally fastest in the low intertidal and at wave-exposed sites (Seed and Suchanek 1992). Depending on local conditions and larval supply, patch recovery may require a few years to several decades (Paine and Levin 1981; Seed and Suchanek 1992).

Sea mussels play an important role in structuring intertidal communities. Sea mussels are dominant competitors for space and can competitively exclude other large benthic organisms such as kelps and barnacles that require primary space for attachment (Paine 1966). However, mussel beds also provide biogenic habitat for several hundred species of algae and small-bodied invertebrates (Suchanek 1992). Finally, sea mussels provide an important trophic link in intertidal food webs; mussels are consumed by whelks, crabs, lobsters, sea stars, fish, shore birds, and sea otters (Seed and Suchanek 1992). The sea star *Pisaster ochraceus* is a particularly important mussel predator; *Pisaster* predation determines the position of the mussel bed's lower limit (Paine 1966).

Fishing History. Humans have exploited *Mytilus californianus* along the California coast for many thousands of years (Erlandson et al. 1999). In the early decades of the twentieth century, an average of 47,000 pounds of mussels (*Mytilus* spp.) were fished per year until 1927 when a major outbreak of paralytic shellfish poisoning occurred (Richards and Trevelyan 2001). After that, landings declined dramatically and remained low for several decades. Extensive commercial efforts resumed in the late 1970s but have declined recently (fig. 4). However, landings for bait, for the years in which data are available, far outweighed these commercial landings. Unfortunately, reliable landings data for *M. californianus* are lacking, as commercial records do not distinguish between *M. californianus*, *M. trossulus*, and *M. galloprovincialis*. Recreational landings of mussels, while probably substantial, are not required to be reported in California.

Today, both commercial and recreational mussel collection is legal outside of parks and reserves. Although *M. californianus* is currently of minor economic importance in California, it is still recreationally fished (10 lb bag limit) for bait and, less frequently, for human consumption (Richards and Trevelyan 2001). Unlike the congeneric *M. galloprovincialis*, *M. californianus* is not currently a target species for the California aquaculture industry (Richards and Trevelyan 2001). Commercial fishing of sea mussels occurs in Oregon, and a commercial fishery has been proposed in British Columbia. These more northerly fisheries and the markets they serve may increase the demand for commercially fished sea mussels from California.

Effects of Climate Change. Climate change may affect *Mytilus* populations through a variety of pathways. Individual growth rates in mytilid mussels are positively correlated with water temperature until some threshold is surpassed, at which point growth rates decline abruptly (Seed and Suchanek 1992). Thus, climate change may increase the growth and age-specific fecundity of this species at the local scale, provided that temperatures do not become extreme. Sublethal stress (Roberts et al. 1997) and even significant mortality (C. Harley, unpub. data) have been observed following spells of hot weather. However, increasing air temperatures may or may not lead to shifts in the vertical range of mussel beds. The upper limit of the mussel bed at one wave-exposed site (Tatoosh Island, Washington) is correlated with emersion time, not thermal stress (Harley and Helmuth 2003). Increasing winter storminess will likely increase rates of disturbance in sea mussel beds and may thus reduce overall population abundance. Finally, although larval recruitment patterns are heavily influenced by patterns of nearshore oceanography, future patterns of larval transport are difficult to forecast.

Climate change is also likely to impact mussel distributions indirectly through the effects of interacting species. The abundance and per capita consumption rate of the predatory sea star, *Pisaster ochraceus*, are both positively correlated with water temperature in short-term (2–6 week) experiments (Sanford 1999). Thus, warming sea-surface temperatures may compress the vertical zone occupied by mussels from below as a result of increased predation pressure. Pisaster do not appear to be negatively influenced by temporal trends in air temperature (Sanford 2002), suggesting that the vertical extent of *Pisaster* foraging will not be influenced by climatic warming. *M. californianus* is also affected by an array of diseases and parasites that can cause mortality or sterility (Bower 1992), but the role of temperature in influencing host-parasite relationships in sea mussels is largely unknown.

Implications for Mussel Populations. Increased frequency and severity of storms and thermal stress events are likely to become increasingly important sources of mussel mortality. If harvesters only remove mussels from the surface layer of the bed, the effects of harvest and hydrodynamic disturbance (which removes all mussels from a patch) are likely to be additive (i.e., neither factor will increase rates of mortality due to the other). Thermal stress typically only kills mussels in the surface layer of multilayered beds (C. Harley, unpub. data). Thus, thermal stress events or surface-layer harvesters operating in isolation will not result in the complete removal of a patch of mussels. However, if fishers remove the top layer of mussels, and the bottom layer is subsequently killed during a heat wave, no mussels will remain as a recruitment surface and nursery habitat for young conspecifics. Because gaps in the mussel bed take longer to recover than areas in which only the superficial layers have been removed, the effects of fishing and climate in this scenario are synergistic (see effect 1 in fig. 1B).

Indirect climatic effects mediated by other species may lead to substantial changes in mussel populations. Increasing water temperatures may increase sea star predation rates (Sanford 1999), thereby removing the largest, most fecund mussels along the lower limit of the bed. Furthermore, by raising the lower limit of the mussel bed, *Pisaster* would redirect fishing pressure to higher shore levels. Because higher shore levels take longer to recover from disturbance (Seed and Suchanek 1992), elevated *Pisaster* predation could magnify the impact of a fixed level of human exploitation. Conversely, climate change may indirectly enhance mussel populations by reducing the season during which mussels are fit for human consumption. In California, a ban on the recreational fishing of mussels is already imposed from May 1 to October 1 when mussels are most likely to ingest and concentrate toxins associated with harmful algal blooms (HABs). HABs tend to occur during warmer water conditions, and climate change has been suggested as the mechanism underlying recent observed increases in HABs (Mudie et al. 2002). Thus, the seasonal ban on mussel collecting may need to be extended if warm-water events begin to occur earlier in the spring and later in the fall, which would in turn reduce the impact of the fishery on mussel populations.

Although the scenarios outlined above may change the spatial and temporal availability of edible mussels, it would appear that sea mussel populations in general (and the bait fishery they support) are not in danger of decline. This conclusion, however, would need to be reevaluated if fishing pressure increased with, for example, the resumption of extensive commercial fishing operations. In the face of increasing fishing pressure, certain regulations should be instituted to ensure the sustainability of the resource, including hand-picking (as opposed to raking), leaving at least the bottom layer of mussels intact, and focusing collecting activities in the low intertidal and at exposed sites, which experience more rapid rates of recovery (Behrens Yamada and Peters 1988; Paine 1989).

Case Study 2: Owl Limpets

Life History. The owl limpet (*Lottia gigantea*) occupies exposed rocky shores from Crescent City, California, to Baja California, Mexico, although the species is most abundant south of San Francisco (P. Fenberg, pers. comm.). *L. gigantea* is the largest limpet on the west coast of North America, reaching lengths up to 10 cm and living for 15 years or more (Morris et al. 1980; Lindberg et al. 1998). Owl limpets are sequential protandric hermaphrodites, changing sex from male to female as they grow older and larger (Wright and Lindberg 1982). Female gonad mass, and presumably fecundity, increases exponentially with size (Kido and Murray 2003).

Owl limpets are territorial grazers, and can exclude many species of plants and animals through consumption, bulldozing, or harassment (Stimson 1970; Lindberg

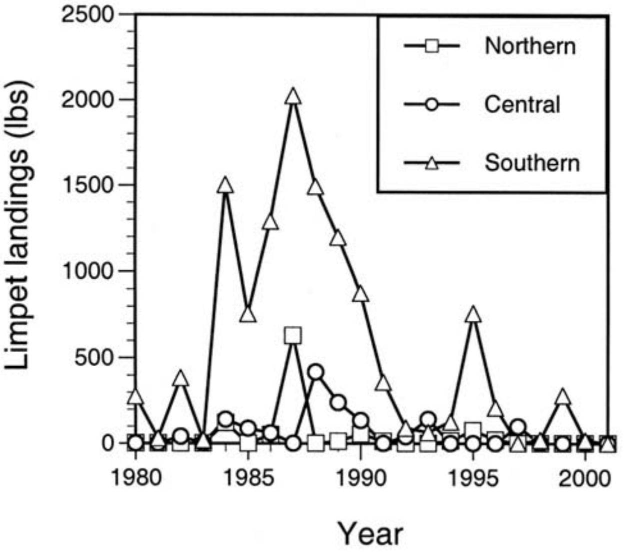

Figure 5. Commercial limpet landings (all species). Northern, central, and southern designations as in fig. 4. Data were obtained from the Pacific Fisheries Environmental Laboratory.

et al. 1998). Owl limpets "garden" their territories, maintaining a high biomass of microalgal biofilm relative to nongardened areas. The main predators of owl limpets are shorebirds and humans (Lindberg et al. 1987; Pombo and Escofet 1996; Lindberg et al. 1998; Kido and Murray 2003).

Fishing History. Limpets were historically fished by coastal Native Americans and have been fished recreationally and commercially in recent times. Commercial limpet fishing in California peaked in the mid to late 1980s, and has declined thereafter (fig. 5) due to a lack of market demand (I. Taniguchi, pers. comm.). Although the limpets, like mussels, were not identified to species in landing records, it is likely that the large individual size of owl limpets has made them the primary target of the limpet fishery. Owl limpets have been protected from commercial fishing in California since 1999. Sport fishing (35-limpet bag limit) is legal outside of state and national parks and other marine protected areas.

Artisanal fishing has reduced owl limpet population size and mean individual size along accessible shorelines in Mexico (Pombo and Escofet 1996). Recreational fishing (for food and occasionally for bait) is poorly documented in California, but indirect evidence suggests that it is substantial. Limpet shell lengths are negatively correlated with site accessibility and with the number of human collectors per unit shoreline in Orange County (Kido and Murray 2003). The mean size of adult owl limpets in southern California has declined significantly by approximately 6% over the past 150 years in all sampled areas except for a tightly regulated marine reserve, suggesting that human take has been influencing owl limpet populations for some time (Roy et al. 2003). Even reserves are vulnerable; poaching in central and southern California can remove hundreds of owl limpets in a single low tide (Lindberg et al. 1998).

Effect of Climate Change. Unlike sea mussels, owl limpets are likely to suffer severe stress in the face of increasing air temperatures. Owl limpet mortality has been observed following extended spells of hot, calm weather in Pacific Grove (C. Harley, per. observ.), and the upper distributional limit of owl limpets at this site is negatively correlated with temperature (Harley and Denny, unpub. data). Increasing air temperatures are therefore likely to force the upper limit of this species downwards through time. Thermal impacts may be most severe for small limpets, which have less visceral and extravisceral water available for evaporative cooling and higher rates of water loss due to a larger surface area to volume (and circumference to volume) ratio (Branch 1985). Increased storminess is unlikely to impact owl limpet populations, as hydrodynamic forces do not appear to be an important source of owl limpet mortality (Denny and Blanchette 2000).

Relationships with other species are likely to shift. Although changes in limpet food resources may occur, the precise nature of these changes is poorly understood. Perhaps more important will be the barrier to downshore migration represented by the mussel bed. Owl limpets require primary space to graze, and compete with mussels for this space (Stimson 1970). If the upper limit of the mussel bed is set by emersion time, it may remain relatively constant even as increasing thermal stress drives limpet distributions downshore. Because owl limpets are territorial and intraspecific competition is fierce, a reduction in habitable shoreline may lead to a reduction in owl limpet numbers. Declining densities and increased fragmentation of local populations could trigger further population declines by reducing fertilization success.

Owl limpet populations may be most severely impacted by climatic warming in the southern portions of their range, where thermal stress is already high. The degree to which declines of owl limpet populations at southern sites will be balanced by population increases at northern sites remains unknown. The northern range limit of owl limpets may be defined by patterns of larval transport, rather than temperature, as has been proposed for another high intertidal limpet (*Collisella scabra*) found along the California coast (Gilman 2003). If this scenario holds true for owl limpets, rising temperatures may result in both vertical and latitudinal range contractions.

Implications for Owl Limpet Populations. If fishing effort does not decrease in the coming decades, climate change will focus fishers on fewer and smaller local owl limpet populations, resulting in important additive effects.

However, it is likely that the effects of fishing will exacerbate the effects of climate change on *L. gigantea* in a synergistic fashion. Future increases in the frequency of high-temperature extremes may disproportionately affect smaller limpets, which have a limited capacity for evaporative cooling (Branch 1985). From the population perspective, this will increase the relative importance of reproductive output by large individuals that have reached a size refuge from brief temperature spikes. However, these large individuals will be the primary targets of human collectors. In addition to reducing population-level reproductive output, the removal of large individuals may further decrease the success of climatically impacted smaller size classes, which rely to some extent on raiding the gardened territories of larger limpets (Shanks 2003). Finally, by selecting larger individuals, fishers disproportionately reduce the number of females in local populations, which may further reduce population-level reproductive output.

Climatic warming, coupled with fishing pressure, is likely to reduce or eliminate local populations of owl limpets. Low individual growth rates suggest that the replacement of large, fecund individuals following a significant environmental or fishing-induced mortality event will require years. Depending on the magnitude of owl limpet declines, additional restrictions on take may need to be established if populations are to persist.

Case Study 3: Black Abalone

Life History. Black abalone, *Haliotis cracherodii*, occur in the rocky intertidal and shallow subtidal zones from Oregon to Baja California. Individuals grow slowly to lengths of 20 cm or more, and may live for over 25 years (Haaker et al. 1995). Small abalone graze benthic micro- and macro-algae, but larger individuals capture and eat drift kelp. In addition to humans, the predators of black abalone include sea stars, octopuses, cabezon, crabs, spiny lobsters, and sea otters (Tegner and Butler 1985; Shepherd and Breen 1992).

Baseline abundances prior to intensive commercial exploitation were estimated to be a minimum of 3.5 million black abalone in the 1960s (Rogers-Bennett et al. 2002). Black abalone occurred at extremely high densities (hundreds of thousands per hectare) in aggregations that were stacked several animals high. In the mid-1980s, black abalone began to suffer from withering syndrome (WS), a chronic wasting disease caused by a Rickettsiales-like prokaryote (Moore et al. 2001). Large numbers of dying abalone and empty shells were first observed in the central Channel Islands (Haaker et al. 1992). The disease spread throughout the islands (Lafferty and Kuris 1993; VanBlaricom et al. 1993) and along the southern California mainland (Steinbeck et al. 1992; Altstatt et al. 1996). Although the origins of the disease are still unknown, high abalone densities may have exacerbated the onset, virulence, and spread of WS (Moore et al. 2002).

It is unclear whether dense aggregations of black abalone occurred prior to the local extirpation of the southern sea otter, *Enhydra lutris*, in the nineteenth century (Davis et al 1992). Abalone in southern California have lived for hundreds of years without sea otters. In the late 1930s the remnant southern sea otter population near Point Sur began a range expansion moving north to Monterey and south to Point Piedras Blancas by 1956. This population has now expanded south of Point Conception into the Southern California Bight (Vogel 2000) and in the future they may move further south along the mainland or out to the Channel Islands. The impact on black abalone of sea otter reoccupation is likely to be at least as dramatic as it was for red abalone populations, which declined from 1,000 individuals per hectare to <100 individuals per hectare at Point Estero in 8 years (Wendell 1994).

Fishing History. Black abalone live higher in the intertidal than other species of abalone, making them particularly vulnerable to human foragers. Abalone fishing dates back to the late Pleistocene (*ca.* 10,500 years B.P.) in the Channel Islands (Erlandson et al. 1996). More recently, an extensive intertidal fishery was developed by Chinese immigrants in the 1800s, which largely collapsed due to overexploitation by 1900 (Rogers-Bennett et al. 2002). After 1968, when laws prohibiting the export of abalone were repealed, there was a rapid increase in black abalone landings. In 1973, landings from southern California and the Channel Islands peaked at 870 mt (fig. 6). Restrictions on black abalone fishing were implemented in 1974, including diver quotas of 240 abalone/day, an increase in the minimum legal size from 140 to 146 mm, and closure of certain areas (Parker et al 1992). However, in just 5 years, landings declined nearly 10-fold (Karpov et al. 2000). The commercial abalone catch declined on the Channel Islands closest to the mainland (e.g., Santa Cruz and Santa Catalina) first, and at more distant islands (e.g., San Miguel and San Nicolas) later (fig. 6), suggesting that human fishing played a major role in the collapse of the populations (see also Karpov et al 2000). After landings in the fishery declined (1979) and WS devastated remaining populations (mid- and late 1980s), the black abalone fishery was closed in 1993.

Effects of Climate Change. As with mussels and limpets, climate change may affect black abalone populations via several pathways. Although no information is available on the link between air temperature and black abalone performance, black abalone do possess behavioral adaptations that may facilitate evaporative cooling (Hines et al. 1982), which suggests that they occasion-

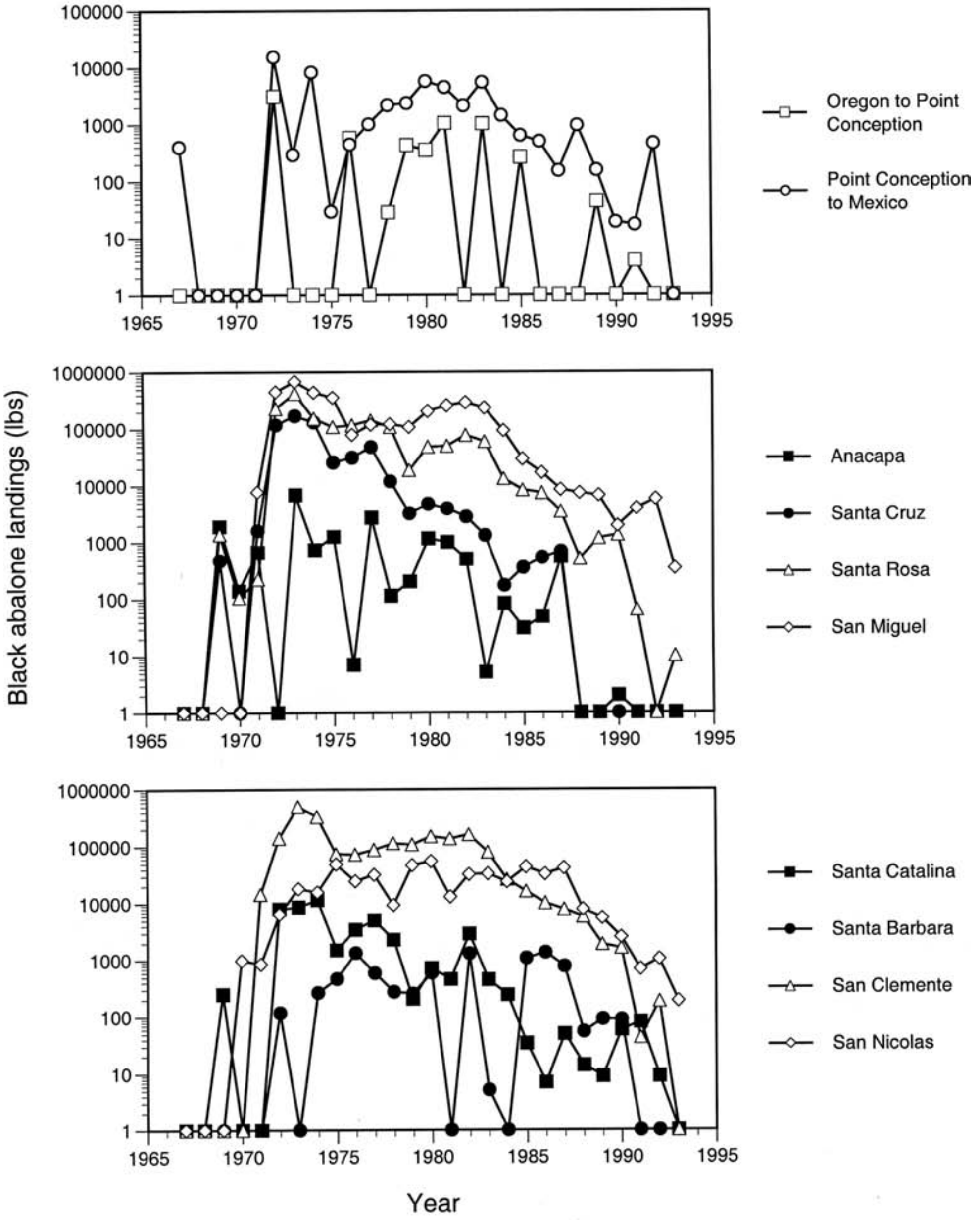

Figure 6. Commercial black abalone landings for mainland sites (top panel), the northern Channel Islands (middle panel), and the southern Channel Islands (bottom panel). The data (x+1 on the log scale) were obtained from the California Department of Fish and Game, using only those dive blocks adjacent to the coastline. Note that landings from nearshore islands (solid symbols) declined before landings from more distant islands (open symbols). See fig. 2 for map.

ally experience thermally stressful conditions. It is therefore conceivable that continued atmospheric warming will force black abalone into the very low intertidal and subtidal zones, where they will compete with other herbivores such as sea urchins. The direct effects of water temperature on black abalone are also largely unexplored (but see Haaker et al. 1995). However, elevated temperatures are associated with reduced growth, condition index, and reproduction in other abalone species (Haaker et al. 1998; Vilchis et al. 2005; Guzmán del Próo, pers. comm.).

Indirect effects of climate change will likely far outweigh the direct effects. Abalone growth is reduced during El Niño conditions (Haaker et al. 1998), and this is likely the result of a reduction in food quantity or quality (Vilchis et al. 2005). Increasing water temperatures, storm frequency, and El Niño frequency in the future could all serve to reduce the supply of drift algae food resources. More importantly, there is a positive relationship between water temperature and the expression of the fatal WS in black abalone in the lab (Friedman et al. 1997) and in the field (Tissot 1995). Mortality associated with WS during warm-water events has been slowly spreading north from Point Conception over the past 10 years (Raimondi et al. 2002). Warming trends in water temperatures are expected to allow the disease to continue its northward expansion and affect populations that are not currently symptomatic (Moore et al. 2002). This problem is particularly severe in light of the southern expansion of the sea otter population. Black abalone may be caught in a squeeze between the spreading of the disease from the south and the range expansion of otters from the north.

Implications for Abalone Populations. Climate-related disease outbreaks and overexploitation have already had tremendous impacts on black abalone populations, which have collapsed in the southern portion of their range. The recovery of black abalone populations is likely to be a slow process due to low growth rates and limited dispersal from potential source populations (Hamm and Burton 2000). The dramatic nature of the population crash and the uncertainties surrounding population recovery have prompted NOAA fisheries to convene workshops exploring the potential listing of black abalone as an endangered species (M. Neuman, pers. comm.). If they are listed, they would join their congener the white abalone, *H. sorenseni*, which was listed in 2001 (*Federal Register* 66 (103) 29046, 29 May 2001) as a result of overfishing.

The magnitude of exploitation and warming-related disease mortality make climate-exploitation synergisms particularly likely for black abalone. The combination of heavy fishing and disease may have reduced black abalone populations to such low levels that Allee effects will hinder natural recovery (see synergistic effect 2 in fig. 1B). Recovery from exploitation may be further slowed by reductions in food supply and warmer temperatures in the future, both of which have the potential to reduce growth and fecundity. Conversely, recent (post-1980s) overexploitation may have particularly tragic consequences for abalone populations in the face of WS if fishers removed individuals that had survived the disease by virtue of having some degree of genetic resistance (synergistic effect 1 in fig. 1B). The synergistic interactions between recent fishing and ongoing climate change may seriously delay or prevent the recovery of this species.

DISCUSSION

Climate Change, Exploitation, and Recovery

Climate change can enhance species' vulnerability to overexploitation, just as exploitation has made species particularly vulnerable to changes in climate. The combined influence of exploitation and adverse environmental change will tend to reduce and fragment exploited populations, making them more vulnerable to Allee effects. Fishing pressure may reduce population sizes sufficiently that additional stresses from rare environmental catastrophes (e.g., extreme high temperatures, winter storms) place populations at risk of local extinction. Increasing population fragmentation may also alter metapopulation dynamics, with potentially serious consequences for local and global populations of exploited species.

As demonstrated by the case studies presented here, the effects of climate change and fishing depend on the characteristics of exploited species, including resistance to various forms of disturbance (e.g., thermal extremes, storm-induced disturbance, and human collection) and resilience, or ability to recover following a disturbance. Species such as sea mussels, whose distribution appears to be largely independent of temperature, will be resistant to certain climatic trends and thus less susceptible to synergisms between climate and fishing. For owl limpets and black abalone, whose populations may be strongly linked directly and indirectly, respectively, to temperature, climatic warming may have large impacts and increase the likelihood of synergisms with exploitation.

The vital rates of exploited species will be a major factor in their resilience to climate- and fishing-induced reductions in population size. For organisms with low turn-over rates and slow growth (e.g., black abalone), exploitation and climatic fluctuations may reduce populations much more quickly than they naturally replenish. In these cases, the risk of multiplicative effects is high because populations may be pushed below abundance thresholds from which they may never recover. For species with more rapid growth and higher population recovery rates (e.g., sea mussels), the synergistic risks of climate change and fishing are reduced because population resilience is high and there is a greater likelihood of recovery between extreme events. In intermediate cases (e.g., owl limpets), the impacts of climate change and exploitation may be sustainable for years to decades, but risks are still substantial as rare climatic (or poaching) events could collapse entire populations.

Challenges of Uncertainty

Reducing Uncertainty. Several gaps in our current knowledge hamper our ability to understand, manage, and restore exploited populations in the face of climate change. First and foremost is the considerable uncertainty underlying the specifics of future climate (IPCC 2001). Although broad-scale trends, such as warming air and sea-surface temperatures, are virtually assured, cycles of warming and cooling complicate the picture. Furthermore, broad-scale global trends may not be representative of local or even regional-scale patterns. This is apparent in the patterns of sea-surface temperature variability at different sites in California (see, for example, fig. 3) and in the inverse production regimes in the California Current and the Gulf of Alaska (Hare et al. 1999). Even if environmental change were spatially uniform, biological responses may still be site specific. For example, the upper limit of intertidal barnacles is only influenced by temperature at a subset of sites in Washington (Harley and Helmuth 2003), suggesting that climate change may shift barnacle zonation patterns in some places but not in others. Finally, changes in many variables, such as current velocity, upwelling intensity, mass transport, and coastal fog are difficult to forecast given current information but are fundamentally important to coastal populations. Improvements in climatic forecasting at regional and local scales will be crucial if we hope to use environmental information to improve fisheries management strategies (Walters and Collie 1988).

Biological processes add an additional layer of uncertainty. Future species assemblages and community characteristics may not be easily inferred from present data or historical records since there may be no present or past analog (e.g., Overpeck et al. 1992). In order to predict potential ecological relationships under future environmental conditions, we must supplement correlative time-series information with novel approaches to research. Progress is being made through experimental manipulations during shorter-term natural fluctuations (e.g., Sanford 1999), monitoring of "nonscientific" manipulations such as localized sea-water warming near nuclear power stations (e.g., Steinbeck et al. 1992), and mathematical models of the relationships between organisms and the environment (Helmuth 1998; Hobday and Tegner 2002). A particularly important focus of future research will be the behavior of populations at low abundances and their ability to rebound under future climate scenarios. Such research will be of primary importance in predicting the prospects for restoration of depleted species and is seldom the focus of fisheries research.

Accepting and Incorporating Uncertainty. Although scientists are gradually reducing the uncertainties surrounding climate-fisheries interactions, management will always proceed in the absence of perfect knowledge. Management procedures with feedbacks from stocks to management may be one way to cope with uncertainty (Parma 2002). Model simulations have been used to examine whether fixed or variable fishing strategies are optimal under conditions of environmental fluctuations (Walters and Parma 1996; Spencer 1997). Fixed strategies performed well (within 15% of optimal) in situations with a Beverton-Holt stock recruitment relationship and relatively high productivity at low stock abundances (Walters and Parma 1996). In contrast, Spencer (1997) found that variable fishing policies outperformed fixed strategies in most cases incorporating depensation at low adult abundances. For species such as abalone, where depensatory effects become important at low population sizes (Shepherd and Brown 1993) and recruitment overfishing has been observed (Rogers-Bennett et al. 2004), recovery may be very slow or nonexistent during unfavorable environmental conditions.

For heavily exploited and overexploited populations, marine protected areas (MPAs) provide a conservative approach that may be vital to long-term population viability. Indeed, given the unavoidability of climate change, the only way to prevent synergistic effects between climate and fishing is to curtail fishing in some areas. MPAs, either explicit or de facto, will enhance the local abundance of many exploited species and increase the likelihood that at least some populations will survive the vagaries of environmental variability (Hughes et al. 2003). MPAs may also allow populations currently affected by both fishing and environmental change to recover, although recovery is by no means guaranteed (Tegner 1993). MPAs also provide opportunities for distinguishing between the effects of fishing and climate change as drivers of the dynamics of marine populations (Moser et al. 2000). However, MPAs are only effective if there is adequate enforcement (Daniels and Floren 1998), as is readily apparent from the effects of continued collection of owl limpets (Kido and Murray 2003) and remnant black abalone (I. Taniguchi, pers. comm.) in protected areas. Finally, MPAs are themselves vulnerable to climate change. An adaptive approach to siting new MPAs has been suggested as a way to optimize reserve-network performance as environmental conditions change (Soto 2002).

Conclusions and Recommendations

Human impacts on marine systems are increasing, both directly through fishing and indirectly through anthropogenic warming. The effects of either climate change or fishing alone are sufficient to dramatically alter marine populations and ecosystems and may drive heretofore abundant species to extinction (Roberts and Hawkins 1999; Dulvy et al. 2003). However, the synergistic effects of environmental change and exploitation may be more severe than the effects of either one in isolation. This is evident from our examples on rocky shores and may hold for other marine ecosystems. Managers need to be aware of these potential synergisms, which may lead to unwelcome surprises when anthropogenic impacts and global change interact (Paine et al. 1998). The intertidal examples highlighted here, along with a growing body of other evidence (e.g., Walters and Collie 1988; Walters and Parma 1996; McCall 2002), suggest that future management strategies must shift their emphasis from correlative data to a more mechanistic understanding of the effects of environmental variability and its interactions with fishing.

ACKNOWLEDGMENTS

We thank all those who participated in the CalCOFI Symposium "Environmental Variability and Its Impact on Invertebrate Fisheries," especially Lobo Orensanz, Juan Valero, Christian Reiss, Marc Mangel, Baldo Marinovic, and Lou Zeidberg. The University of California, Davis, climate change discussion group was an invaluable proving ground for many of our ideas. We thank the Marine Region of the California Department of Fish and Game for supporting this work, especially P. Wolf, M. Vojkovich, and E. Larson. William Bennett, Peter Haaker, Nature McGinn, Elizabeth Vu, and three anonymous reviewers helped improve the manuscript. The University of California Bodega Marine Laboratory provided logistic support. This research was supported in part by a Bodega Marine Laboratory post-doctoral fellowship (CH). This is contribution number 2202 of the Bodega Marine Laboratory, University of California, Davis.

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Part III

SCIENTIFIC CONTRIBUTIONS

UTILITY OF LARVAL PIGMENTATION TO IDENTIFY NEARSHORE ROCKFISHES OF THE *SEBASTES* SUBGENUS *PTEROPODUS* FROM SOUTHERN CALIFORNIA

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ABSTRACT

Unidentified larval rockfishes, *Sebastes* spp., were sorted from ichthyoplankton collected during the April 1999 CalCOFI cruise and categorized according to their similarity to the pigmentation typical of larval *Pteropodus*, a subgenus of nearshore rockfishes heavily targeted in the California live-fish fishery. The 62 larvae, ranging in size from 3.5 to 11.2 mm, were identified by molecular genetic methods to test the hypothesis that this pigment-based classification technique can reliably distinguish *Pteropodus* from all other *Sebastes* larvae. All larval *Pteropodus* were correctly classified, and only 5% of the non-*Pteropodus* were misclassified as *Pteropodus*, but there were so few *Pteropodus* in the CalCOFI plankton samples that the number of misclassified larvae was larger than the number of *Pteropodus* larvae. Larval *Pteropodus* may remain close to the shallow-water adult habitat shoreward and closer to islands than most CalCOFI stations. Ichthyoplankton sampling near shore (within the 200 m depth contour) would be required to examine this hypothesis, to provide the samples required for a better test of the pigment-based classification method, and, perhaps ultimately, to provide fishery-independent data on population trends in *Pteropodus.*

INTRODUCTION

A primary source of fishery-independent data used in current fisheries assessments is the ichthyoplankton collected during California Cooperative Oceanic Fisheries Investigations (CalCOFI) biological/oceanographic surveys off southern California. Larval rockfishes of the genus *Sebastes* are common and abundant in CalCOFI plankton collections (Moser et al. 2000). These larvae may represent more than 50 species in the Southern California Bight (SCB), most of which are targeted in commercial and sport fisheries (Miller and Lea 1972; Eschmeyer et al. 1983). However, only seven *Sebastes* species are unambiguously identifiable from CalCOFI samples by means of pigmentation and morphological criteria (Moser 1996; Moser et al 2000). Ichthyoplankton data for three of these—bocaccio (*Sebastes paucispinis*), cowcod (*S. levis*), and shortbelly rockfish (*S. jordani*)—have been used in recent assessments (Butler et al. 1999, 2003; MacCall et al. 1999; Ralston et al. 2003).

Attempts have been made to classify larval *Sebastes* into subgeneric or other categories based on larval pigmentation (e.g., Kendall and Lenarz 1987; Kendall 1991; Kendall and Gray 2001), but we have not found these classifications useful for routine analysis of ichthyoplankton samples. The CalCOFI collections potentially provide a rich source of data for constructing temporal abundance trends for the unidentified *Sebastes* species, but when larvae cannot be identified to species, their abundance trends are not available to use for indices of adult biomass.

We focus on nearshore rockfishes generally considered to belong to the *Sebastes* subgenus *Pteropodus*: grass (*Sebastes rastrelliger*), black-and-yellow (*S. chrysomelas*), gopher (*S. carnatus*), copper (*S. caurinus*), quillback (*S. maliger*; rare in southern California), China (*S. nebulosus*; rare in southern California), calico (*S. dallii*), brown (*S. auriculatus*), and kelp (*S. atrovirens*) rockfishes (Taylor 1998; Kendall 2000). This nearshore group is targeted by the live-finfish fishery that developed off California in the mid-1980s (Walters 2001). We chose this complex because reliable abundance estimates are lacking and because the larvae share pigmentation features that might be unique to the group. This could provide a means to reliably select these larvae for later molecular identification to species for use in fishery-independent abundance estimates. Alternatively, an abundance estimate may be developed for the subgenus as a whole.

We sorted possible *Pteropodus* larvae from other *Sebastes* species in CalCOFI collections on the basis of their pigmentation characters, and used molecular genetic methods to test the hypothesis that a pigment-based sorting technique can reliably distinguish *Pteropodus* from all other *Sebastes* larvae. Molecular genetic data, a constant at all life-history stages, provides a method by which we may assign species identifications to larvae by comparisons with known adult reference data.

[Manuscript received 2 February 2004.]

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MATERIALS AND METHODS

Oblique bongo net tows through the upper 212 m of the water column (from 15 m above the bottom in shallower water) are routinely collected according to standard protocols (Kramer et al. 1972; Ohman and Smith 1995) during quarterly CalCOFI cruises. The sample from one side of each bongo cast is fixed in 5% neutral buffered formalin and, beginning in 1997, the sample from the other net has been fixed and preserved in 5% tris-buffered ethanol, which is changed within 24 hours after fixation. For this study, we used samples collected during the April 1999 CalCOFI cruise (fig. 1), a time when larval *Sebastes* were abundant (Ambrose et al. 2001).

All fish larvae were sorted from the macrozooplankton in the laboratory and subsequently identified to the lowest possible taxon. For the ethanol-preserved samples, *Pteropodus*-like larvae were sorted from other unidentified *Sebastes* according to pigmentation characters. Other characters that may be helpful in conjunction with pigmentation include the relatively slender body and relatively large size at parturition (~ 4.5 to 5.5 mm) of the *Pteropodus* larvae (e.g., Watson and Robertson, 2004). In addition to the pigmentation of the head and gut through most or all of larval development that is common to most *Sebastes* species, larval *Pteropodus* share a common pigment pattern (fig. 2), the main elements of which are (1) a long melanophore row along the dorsal margin of the tail, commonly of about 5–30 melanophores between about myomeres 9–23, often extending forward onto the trunk; (2) a long melanophore row along the ventral margin of the tail, commonly of about 30–60 melanophores, usually originating at the last preanal or first postanal myomere and extending to myomere 23–25; and (3) little or no pigment on the pectoral fins (Watson and Robertson, 2004). For purposes of larval classification, this pattern is most useful for preflexion and flexion stages; pigmentation of postflexion-stage larvae converges progressively on a pattern shared with many other species (e.g., Watson and Robertson, 2004). Nevertheless, because ~ 90% of the *Sebastes* larvae collected in standard plankton tows off California are preflexion stage (Moser 1996), the method is potentially valuable.

In total, 298 unidentified *Sebastes* larvae were sorted from the samples; 121 of these were identified as possible *Pteropodus*. Details of pigment were noted for 62 of the 121 larvae that were in good condition, and they were placed into the following categories: (1) *Pteropodus*; (2) probable *Pteropodus*; (3) possible *Pteropodus*; and (4) probable non-*Pteropodus*. Larvae classified as *Pteropodus* displayed the exact *Pteropodus* pigment pattern; the other categories deviated progressively from that pattern. The 62 selected larvae ranged from 3.5 to 11.2 mm: 71% were preflexion stage (3.5 to 7.1 mm), 23% were flexion stage (6.8 to 8.3 mm), and 6% were postflexion stage (9.5 to 11.2 mm). The remaining 59 possible *Pteropodus* larvae (98% preflexion stage) generally were in poorer condition; they were not classified further, and details of their individual pigment patterns were not recorded. We focus here on the 62 larvae examined in detail.

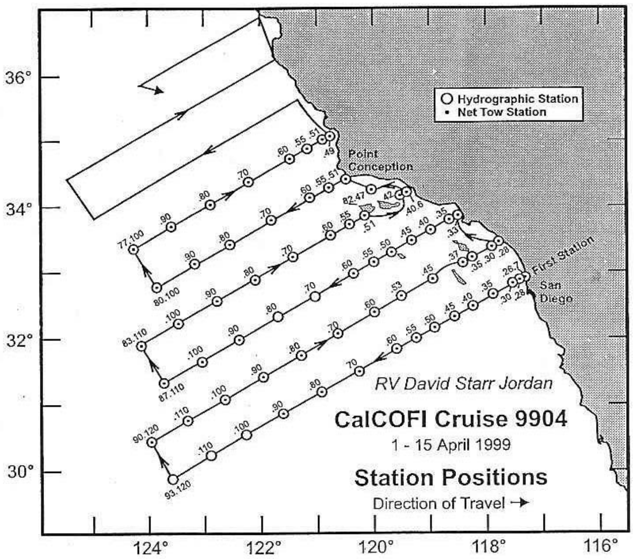

Figure 1. Cruise track and stations occupied during CalCOFI cruise 9904, 1–15 April 1999. Circles indicate standard CalCOFI stations; dots indicate net tow stations on cruise 9904 (from Ambrose et al. 2001).

Genomic DNA was extracted from tail or muscle tissue of larvae by means of a chelex extraction protocol (Walsh et al. 1991). We used PCR to amplify mtDNA in a 1× buffer containing 20 mM Tris HCl, 50 mM KCl, and 1.5 mM $MgCl_2$ with 0.3 μM of each primer. Primers included published (GluRF and CB3RF, Rocha-Olivares et al. 1999) and internal custom primers (CB306F 5’-TTACTACGGCTCVTACCT-3, Cb521R 5’-GTTG CATTGTCTACTGAG-3’, and CB364F, 5’-CTAGT TATAATAACTGCTTT-3’). We used Qiaquick kits (Qiagen, Inc.) to clean PCR products and cycle-sequenced them according to manufacturer protocols with an ABI 3100 automated sequencer. Chromatogram data for sequenced DNA were aligned by means of the biosequence analysis and editor program Sequencher (ver. 4.1.1, Gene Codes, Inc.).

Larval sequences were compared to DNA reference sequence data of identified adult *Sebastes* found in the Southern California Bight by means of an iterative approach within the software program Phylogenetic Analysis Using Parsimony (PAUP* 4b10; Swofford 2000), with the optimality criterion set to distance. Adult sequences in the PAUP file included only species known to be limited to the northeastern Pacific. We used nonparametric bootstrapping (100 replications, MAXTREES set to 1000) to cluster the unknown larval haplotype within a database of consensus haplotypes (consensus =

TABLE 1
Molecular Identification of the 62 *Sebastes* Larvae Classified as Potential *Pteropodus* Candidates

	Classification			
Identification	*Pteropodus*	Probable *Pteropodus*	Possible *Pteropodus*	Probable non-*Pteropodus*
S. carnatus	1			
S. caurinus	1			
S. hopkinsi	2	16	25	8
S. ovalis		1		2
S. rufus			1	
S. saxicola	1		3	
S. semicinctus		1		
Total	5	18	29	10

most common of intraspecific haplotypes available) from known adults for putative identification for 384 haplotypes representing 65 species of *Sebastes* found in the northeast Pacific (voucher specimens maintained at NOAA Fisheries, La Jolla Laboratory). If a larva clustered with a single reference haplotype with a bootstrap value ≥ 90%, this was accepted as the identification of the larva. If a larva clustered with a single haplotype with a bootstrap value < 90%, this was accepted as a first-pass identification, and a secondary analysis that included all available haplotypes of the three nearest (in uncorrected "p") species to the unknown larval haplotype was performed.

RESULTS

Among the 62 *Sebastes* larvae, only five (8%) displayed the full *Pteropodus* pigment pattern (tab. 1). Another 18 larvae (29%) classified as "probable *Pteropodus*" displayed pigmentation very much like the *Pteropodus* pattern, except that in all cases the melanophore series on the ventral margin of the tail originated at the second to fourth postanal myomere (commonly the second or third) rather than the first. The 29 "possible *Pteropodus*" (47%) all had the moderately long to long *Pteropodus*-like row of melanophores on the dorsal margin, but the ventral series on the tail originated at postanal myomere 3-7 (commonly 4-6). The ten (16%) "probable non-*Pteropodus*" had ventral pigmentation like the "possible *Pteropodus*," and either a shorter dorsal melanophore series or a predominantly double row of melanophores on the dorsum, in contrast to the long, predominantly single row typical of *Pteropodus* larvae.

Molecular identification revealed that among the 62 larvae, only two were *Pteropodus*: one each of *S. carnatus* and *S. caurinus*, both correctly classified (tab. 1). Two of the remaining three larvae classified as "*Pteropodus*" were *S. hopkinsi*, and the third was *S. saxicola*. Among the "probable *Pteropodus*," 16 (88%) were *S. hopkinsi*, and there was one each of *S. ovalis*, and *S. semicinctus*. The "possible *Pteropodus*" also were predominantly *S. hopkinsi* (25 larvae: 86%); three larvae (10%) were *S. saxicola* and one (3%) was *S. rufus*. The "probable non-*Pteropodus*" likewise were mostly *S. hopkinsi* (80%); two larvae (20%) were *S. ovalis*. Thus, among the 62 *Pteropodus* candidates, two (3%) actually were *Pteropodus* larvae, 51 (82%) were *S. hopkinsi*, four (6%) were *S. saxicola*, three (5%) were *S. ovalis*, and one each (2%) were *S. rufus* and *S. semicinctus*.

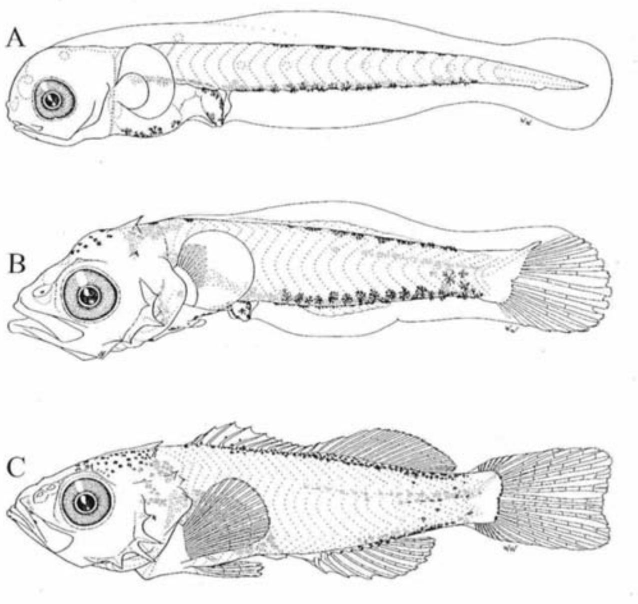

Figure 2. Larval *Sebastes atrovirens* showing an example of the typical *Pteropodus* larval pigment pattern. *A*, preflexion stage, 4.6 mm; *B*, flexion stage, 8.0 mm; *C*, postflexion stage, 14.6 mm (from Watson and Robertson, 2004).

DISCUSSION

This experiment demonstrates the value of molecular identification for validating identifications based on visual methods. The experiment also demonstrates that the characteristic *Pteropodus* pigmentation pattern should be strictly adhered to in attempting to classify larvae, because some other species (e.g., *S. hopkinsi*) have pigmentation patterns much like the *Pteropodus* pattern. These other species differ from the *Pteropodus* pattern primarily in lacking ventral pigment on the first 1–7 postanal myomeres, whereas larvae of most *Pteropodus* species typically have ventral pigment on those myomeres through at least flexion stage. For example, in laboratory-reared *S. atrovirens*, *S. caurinus*, *S. chrysomelas*, and *S. rastrelliger*, all larvae had ventral pigment at the first postanal myomere through flexion stage, although in laboratory-reared *S. auriculatus* only 26% had pigment on that myomere (ventral pigment originated at the second postanal myomere in the remaining 74%; Watson and Robertson, 2004). Thus strict adherence to the typical *Pteropodus* pattern in order to minimize misidentification of non-

Pteropodus larvae may result in some underestimation of the number of *Pteropodus* larvae.

Owing to the very small number of *Pteropodus* collected during the April 1999 CalCOFI cruise (the 59 potential *Pteropodus* not examined in detail also included two *Pteropodus*, both *S. atrovirens*; there were none among the 177 larvae not considered possible *Pteropodus*), it is difficult to evaluate the pigment-based classification. Nevertheless, one might argue that the classification was successful in that both *Pteropodus* larvae among the group of 62 were correctly identified, and only 5% of the non-*Pteropodus* were misclassified as *Pteropodus*. However, because so few *Pteropodus* were collected, the small number of misclassified larvae actually represents 60% of the total classified as *Pteropodus*. If this result is typical, the method clearly would not yield data useful for management purposes based on CalCOFI sampling. Molecular identification of additional *Pteropodus* larvae, or laboratory rearing of multiple broods, is needed to define the range in pigment variation for each species.

Parturition of larval *Pteropodus* is primarily in late winter-spring (e.g., Wyllie Echeverria 1987). If the *Sebastes* species composition in the April 1999 CalCOFI plankton samples is typical for the time of year in the SCB (the La Niña event at that time should not have adversely affected parturition), then larval *Pteropodus* must be rare off southern California as far seaward from adult habitat as the nearest CalCOFI stations. Observations on laboratory-reared *S. atrovirens*, *S. auriculatus*, *S. caurinus*, *S. chrysomelas*, and *S. rastrelliger* suggest that larval *Pteropodus* may prefer to remain near the edges of structures (in this case, primarily the edges of 500-1,700 L holding tanks and 5-19 L rearing containers), and most apparently are capable of doing so from birth even in modest currents (in contrast, laboratory-reared larvae of deepwater species such as *S. constellatus* show no affinity for the edges of the rearing containers) (pers. obs., W.W., July 1999). If this behavior also occurs in the field, most larval *Pteropodus* may not range far from adult habitat. Marliave (1986) showed that the larvae of several rocky intertidal fish species are able to maintain position inshore, near rocky habitat, from hatching through settlement. One of the two larval *Pteropodus* among the group of 62, a postflexion-stage *S. caurinus*, was collected inshore (CalCOFI station 93.28) near adult habitat; the other, a flexion-stage *S. carnatus*, was collected in deep water off Catalina Island (CalCOFI station 90.45). Both *S. atrovirens* in the group of 59 possible *Pteropodus* larvae were collected off Santa Rosa Island (CalCOFI station 83.55).

Morphological and more recent population genetic studies of *S. atrovirens*, a kelp forest associated species within *Pteropodus* suggest a clinal (Love and Larson 1978) or stepping-stone pattern of gene flow and an average dispersal distance of less than 20 km along the coast and at the northern Channel Islands.[2] Ichthyoplankton sampling near shore (within the 200 m depth contour), where the principal adult habitat is located, would be required to determine the absolute extent of pelagic dispersal for these species. If they are limited to the nearshore zone, nearshore sampling would be required to provide samples to adequately test the pigment-based classification method and perhaps, ultimately, to provide fishery-independent data on population trends in *Pteropodus*.

ACKNOWLEDGMENTS

Samples were obtained through CalCOFI in cooperation with the California Department of Fish and Game, the Scripps Institution of Oceanography, colleagues in NOAA Fisheries, and scientists and crew on the NOAA RV *David Starr Jordan*. We are especially indebted to R. Vetter and J. Hunter for their support of this work; to A. Hays, D. Griffith, and R. Charter, for their assistance in obtaining samples and data to support this work; and to J. Hyde for his valuable feedback in the laboratory. We acknowledge D. Ambrose, S. Charter, and H. G. Moser for their time and thoughtful comments on earlier drafts of this manuscript. We also wish to thank the Oceanids Foundation and the Frieda Daum Urey scholarship committee for their generous endowment to CAT. The genetic data collection was funded through NOAA Fisheries base funds and support was provided through the Biological Oceanography Fellowship at Scripps Institution of Oceanography.

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DIET DIFFERENCES IN THE THRESHER SHARK (*ALOPIAS VULPINUS*) DURING TRANSITION FROM A WARM-WATER REGIME TO A COOL-WATER REGIME OFF CALIFORNIA-OREGON, 1998–2000

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ABSTRACT

The diet of thresher shark (*Alopias vulpinus*) during a cool-water oceanographic regime, July 1999 through May 2000, was compared to the diet during the previous warm-water/transitional period, August 1998 through January 1999. Stomach samples were collected from the U.S. Pacific Coast drift and set gill net fisheries. Of the samples examined from the cool-water period, only 8 prey taxa were found, revealing a narrower trophic spectrum than found during the previous warm-water/transitional period, when 20 prey taxa were identified. As in the warm-water/transitional period, northern anchovy (*Engraulis mordax*) was the most important overall prey, even more dominant than in the previous period. Additionally, market squid (*Loligo opalescens*) was second in importance and dramatically more prevalent in the cool-water period than in the warm-water/transitional period. Other important diet items in the cool-water period, in descending order of importance, were "unidentified teleosts"; Pacific sardine (*Sardinops sagax*); Pacific hake (*Merluccius productus*); and Pacific or chub mackerel (*Scomber japonicus*): these were also among the top six items in the previous warm-water/transitional period. As expected, pelagic red crab (*Pleuroncodes planipes*), relatively common in the diet during the warmer period, was absent from the diet during the cool-water period. It is suggested that during cool-water periods the thresher shark subsists on a narrow range of food items (such as anchovy and squid), but the diet becomes more diversified and opportunistic during less-productive warm-water El Niño periods.

INTRODUCTION

The thresher shark (*Alopias vulpinus*) is currently the most important commercial shark in California and is also sought by recreational anglers, especially in southern California (Holts et al. 1998). It is to be managed under the Pacific Fisheries Management Council's new U.S. West Coast Highly Migratory Species Fishery Management Plan (PFMC 2003), to be implemented in 2004. Patterns of observed catches and tagging studies indicate that thresher sharks migrate seasonally along the Mexico-U.S. west coast from near Clarion Island, Mexico (18°32'N, 117°42'W), north to Johnstone Strait (50°15'N, 126°00'W), moving northward up the coast in summer, returning to waters off northern and central Mexico in winter (Hart 1973; Hanan et al. 1993; Smith et al. in press). Its greatest apparent abundance in the North Pacific is reportedly within 40 miles offshore (Strasburg 1958).

This species was heavily targeted by the West Coast drift gill net fishery in 1977–89, when the population was depleted to an estimated one-third of its virgin biomass (Hanan et al. 1993; PFMC 2003). Since the early 1990s, coastal states implemented various seasonal and area closures, and fishery effort was redirected toward swordfish. The closures and shift in effort appear to have helped protect the adult portion of the stock. A preliminary assessment suggests that the stock has rebounded to almost 60% of virgin biomass and is maintaining a modest amount of positive population growth (PFMC 2003, chap. 3).

In the early 1990s, Bedford (1992) suggested that off California this species had a highly specialized diet composed primarily of northern anchovy, but he did not present supporting data. More recently, Preti et al. (2001) found a far more varied diet composed of 20 prey taxa. Although northern anchovy (*Engraulis mordax*) was the most important species, Pacific hake (*Merluccius productus*), Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), market squid (*Loligo opalescens*), and pelagic red crab (*Pleuroncodes planipes*) were also important. The sampling was done while the California Current system was undergoing a change from warm-water El Niño conditions to cold-water La Niña conditions, with most samples collected during El Niño, before full transition into the cool-water period (Hayward et al. 1999). Preti et al. (2001) suspected that the oceanographic environment may have contributed to the great diversity of prey in the diet, but no comparative data were available.

Here we examine the results of new sampling during the following cool-water period to compare with the warm-water/transitional period. The purpose is to understand differences and flexibility in the diet of the thresher

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[Manuscript received 4 February 2004.]

shark in the California Current region under differing oceanographic regimes.

METHODS

Stomach samples were collected during a warm-water/transitional period (August 1998–January 1999) as described by Preti et al. (2001), and during a cool-water oceanic regime (July 1999–May 2000). Sample processing and analyses were similar for both periods. National Marine Fisheries Service (NMFS) fishery observers collected the samples aboard commercial drift gill-net (84 trips) and setnet vessels (4 trips) off the U.S. West Coast within the Exclusive Economic Zone.

Stomach content data were pooled and analyzed by prey taxa for relative measures of prey quantity (RMPQs) as follows: numeric occurrence percentage (%*N*), weight percentage (%*W*), and frequency-of-occurrence percentage (%*F*) of food items. The value %*N* is the number of individuals of one prey taxon divided by the total number of all prey individuals times 100; %*W* is the weight of one prey taxon divided by the total weight of all prey times 100; %*F* is the number of stomachs containing prey of one taxon divided by the total number of stomachs that contained any prey items time 100 (Preti et al. 2001).

Empty stomachs, slurry, and detritus were not used in calculating percentages or indexes. We examined the differences in degree of prey digestion (ranked 1–5, from 'fresh' to digested as in Preti et al. 2001) by tallying the frequencies of each digestive state in the two periods and testing them using a 2 × 5 contingency table.

Authors of fish dietary studies have long emphasized that each of the commonly used measures of prey quantity has its limitations, each biased toward different aspects of the diet (Hyslop 1980; Cortés 1997). We thus chose the geometric index of importance (GII) (Assis 1996; Mohan and Sankaran 1988; Fernández and Oyarzun 2001), and the index of relative importance (IRI) (Pinkas et al. 1971) to rank prey and to graphically represent the relative measures of prey quantity. In comparing the two indexes, we used each method to examine only the difference in ranking of the suite of prey types, because individual index values were not comparable.

The GII, in its simplified form, may be calculated

$$\mathrm{GII}_j = \frac{\left(\sum_{i=1}^{n} V_i\right)_j}{\sqrt{n}} \tag{1}$$

Where GII_j = geometric index of importance for the *j*th prey category; V_i = the magnitude of the vector for the *i*th RMPQ of the *j*th prey category; n = the number of RMPQs used in the analysis. In our study this can be expressed as

$$\mathrm{GII}_j = \frac{(\%N_j + \%W_j + \%F_j)}{\sqrt{3}} \tag{2}$$

Where $\%N_j$ is the percentage number; $\%W_j$ is the percentage weight; $\%F_j$ is the percentage frequency of occurrence for the jth prey category.

The IRI is calculated as

$$\mathrm{IRI} = (\%N + \%W) \times \%F$$

In the area north of 34°00'N, to determine if we could pool drift gill-net and setnet samples for the 1999–2000 sampling period (where we supplemented drift-net samples with setnet samples collected in Monterey), we used the Fisher Exact Test to determine statistical difference in diet between samples collected in the nearshore set gill-net fishery and samples collected in the offshore drift gill-net fishery over the same fishing season and same general area. If the diet was found not to differ significantly, we pooled the results.

We examined differences in diet between northern and southern fishing areas, in thresher sharks caught early and late in the fishing season, and by size of shark. We chose 34°00'N latitude as a boundary dividing the sampling area because the area north of that latitude (which crosses the Santa Barbara Channel Islands and includes the area between Point Conception and San Miguel and Santa Rosa islands) often has cooler water (generated by seasonal coastal upwelling) than areas south of that latitude. The data were pooled into subgroups, and 2 × 5 contingency table analyses were carried out to determine whether consumption of the five leading diet items varied significantly in number among the subgroups. Only the numerical measure was considered for this exercise, since it is the only statistically valid RMPQ that can be entered into the chi-square table. Weight was not tested because of the extensive range of the measurement values (in grams) and general dependence of this RMPQ on digestive state. Frequency of occurrence was not used because the row and column sums do not represent any real quantity, which violates the assumptions of the chi-square test (Crow 1982).

The following subgroups were considered:

1. Sharks collected north of 34°00'N, and sharks collected south of 34°00'N, all seasons combined for both periods.
2. Adult sharks (> 159 cm fork length) female and male first maturity (Smith et al., in press) and juvenile sharks (≤ 159 cm fork length), all latitudes combined, both periods.

Cool-water and warm-water/transitional period diet differences were compared with two-way 10-cell contingency table analyses of the major diet items of each sampling period. We tested only the top five major iden-

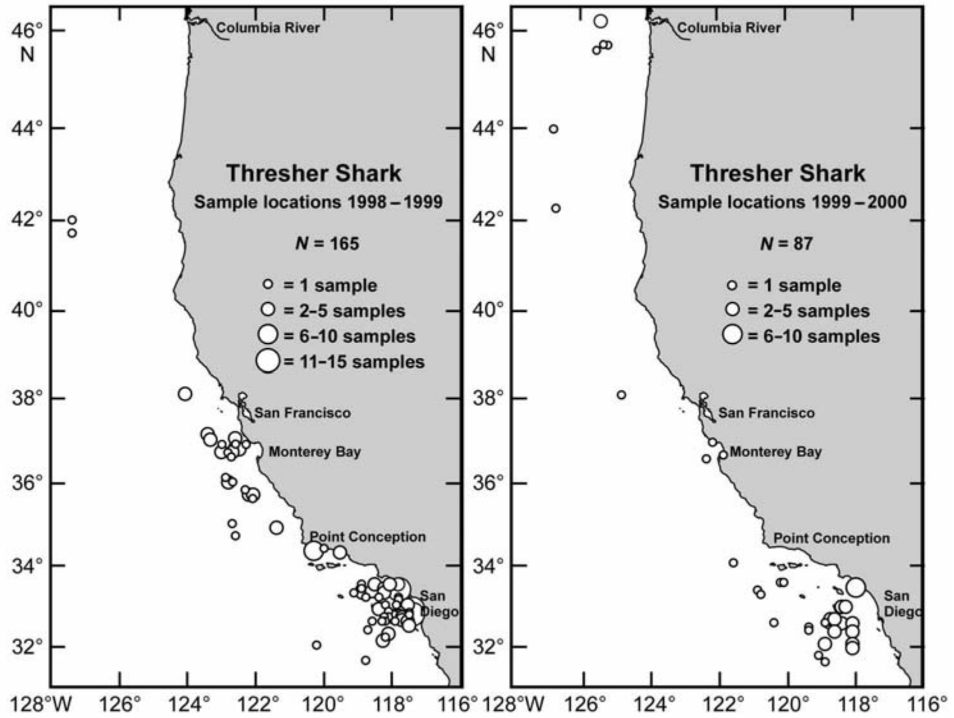

Figure 1. Collection locations for thresher shark (*Alopias vulpinus*) stomach samples, during warm-water/transitional period 1998-99 (*left*) and cool-water period 1999-2000 (*right*).

tifiable items in these analyses because the number values for others were too small to apply the test.

Randomized cumulative prey curves were constructed to examine trophic diversity and determine if sample sizes were sufficient to describe the full diet (Hurtubia 1973; Ferry et al. 1997; Gelsleichter et al. 1999; Yamaguchi and Taniuchi 2000). The order in which stomachs were analyzed was randomized 10 times, and the mean number of new prey types was cumulated consecutively in order of the stomachs obtained and plotted against the number of stomachs examined. In this type of sample-size analysis, the presence of an asymptotic relationship indicates that the number of stomachs analyzed is sufficient to represent the diet of a particular predator, and that the enlargement of the sample beyond the point of curve stabilization would cause little further increase in the measured trophic diversity (e.g., Gelsleichter et al. 1999).

The fork-length size composition of the samples in the two periods (data for 1998–99 from Preti et al. 2001) was compared by means of an unpaired Student's *t*-test to determine if the size composition was significantly different.

RESULTS

Vessel Operations and Sampling

Between 16 August 1998 and 24 January 1999, 165 stomach samples (107 with food) were collected aboard observed vessels on 48 trips operating from the California-Mexico border (31°37'36"N, 118°27'48"W) to the California-Oregon border (41°35'54"N, 127°13'48"W) over water depths from 27 to 2250 fm (49 to 4115 m). All vessels sampled during that period fished with drift gill nets (≥ 14-in. stretched mesh) set overnight and collected in the morning hours. Between 23 July 1999 and 17 May 2000, 87 stomach samples (67 with food) were collected aboard driftnet and set-net vessels on 40 observed trips operating from the California-Mexico border to southern Washington (46°25'30"N, 125°16'42"W) over water depths from 30 to 2,160 fm (55 to 3,950 m) (fig. 1). Most (94%) were collected during drift gill-net trips ($n = 36$) on overnight sets as before; five samples were collected from set gill-net vessels fishing in Monterey Bay ($n = 4$ trips; ≤ 12 in. stretched mesh), with average soak time of 26.4 hr (range: 21–45 hr), with net retrieval during morning hours.

Thresher sharks for both sampling periods were similar in size. The size compositions for the two periods were found not to be significantly different ($t = -1.37$, *d.f.* = 246, $p = 0.17$). Those collected during the warm-water/transitional period ranged from 79 cm to 237 cm fork length (FL) ($n = 163$) with 82.8% from 130 to 189 cm fork length (Preti et al. 2001). Those sampled during the cool-water period ranged from 70 cm to 262 cm fork length ($n = 85$) with 82.0 % from 130 cm to 189 cm fork length (fig 2).

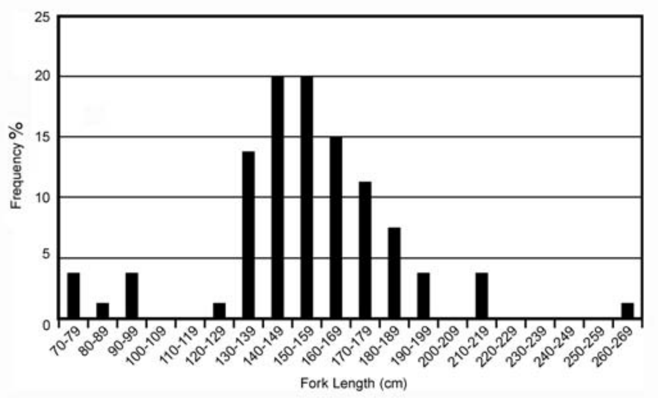

Figure 2. Length-frequency distribution of thresher sharks sampled during the July 1999–May 2000 cool-water period (n = 85 sharks). (For distribution during the August 1998–January 1999 warm-water/transitional period, see Preti et al. 2001.)

Analyses

Although range of values differed, ranking of prey items was the same with either GII or IRI (tab. 1, figs. 3 and 4). A two-way, 10-cell contingency table analysis of the five major identifiable diet items of fish captured during the two periods showed the diet to differ significantly for number ($\chi^2 = 219.4$, *d.f.* = 4, $\alpha < 0.05$). The variety of prey found during the cool-water period (only 8 taxa) was significantly less than that found during the previous warm-water/transitional period (20 taxa; Preti et al. 2001). During both fishing periods, northern anchovy was the most important identifiable prey. During the 1998–99 warm-water/transitional period, "unidentified teleost"[1] ranked first, but of identifiable taxa, northern anchovy had the highest indexes of importance (GII = 48.2, IRI = 1,332.1), followed by Pacific hake, Pacific mackerel, and Pacific sardine. Of invertebrate prey, pelagic red crab and market squid contributed to the diet in the warm-water/transitional period, the latter being of minor importance (GII and IRI = 2.0). Although northern anchovy was important overall during both periods, it was identified only in Southern California Bight samples, south of 34°00'N. During the warm-water/transitional period, Pacific hake was the most important food item north of 34°00'N, followed by unidentified teleosts and Teuthoidea. Rockfish (*Sebastes* spp.) and a variety of other species also contributed to the diet in the north, and occurred in the diet in both periods. Only two categories of rockfish were identified in our samples: *Sebastes jordani* and *Sebastes* spp. unidentified. The latter consisted of more highly digested (worn) otoliths that may have been *S. jordani*, but could not be identified beyond the generic level. During the cool-water period, all rockfish otoliths were identifiable to species as *S. jordani*. Of those examined during the warm

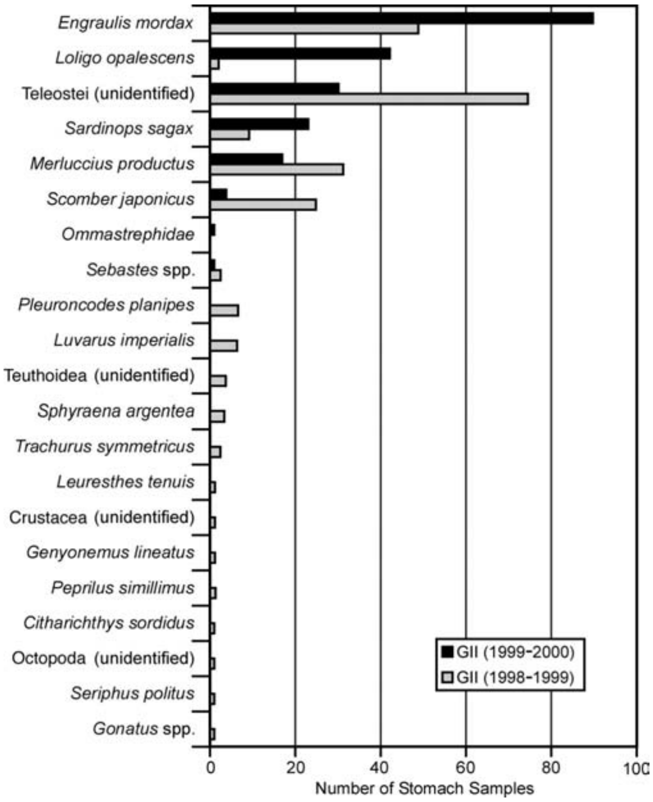

Figure 3. Geometric index of importance (GII) for prey taxa found in stomachs of thresher sharks during warm-water/transitional period 1998–99 and cool-water period 1999–2000. See also tab. 1.

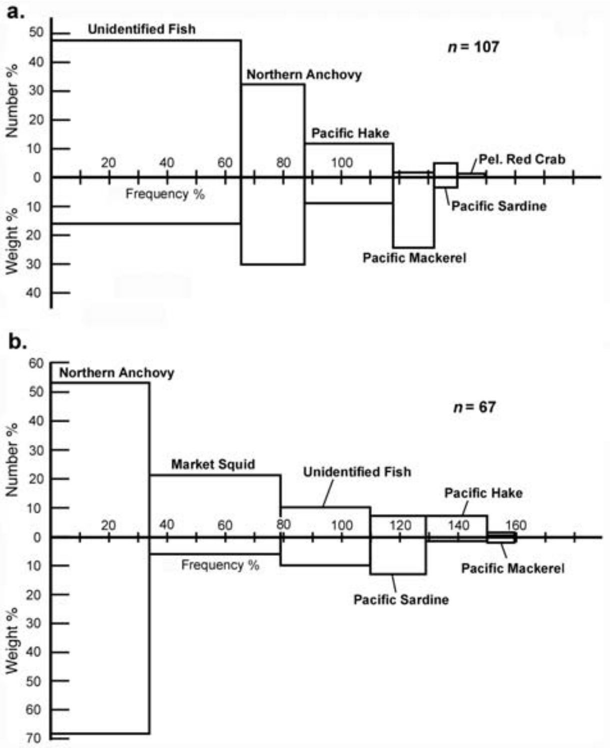

Figure 4. Graphical representation of index of relative importance (IRI) of major prey taxa found in stomachs of thresher sharks during (*a*) warm-water/transitional period 1998–99 and (*b*) cool-water period 1999–2000.

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[1] Bony fish remains that are highly digested or fragmented.

TABLE 1
Prey found in Stomachs of Thresher Shark (*Alopias vulpinus*) from the California-Oregon Coast

	1998–99 Warm-water/transitional period (n = 107 stomachs with food)[a]						1999–2000 Cool-water period (n = 67 stomachs with food)					
Prey species	%W	%N	%F	GII	IRI	Rank	%W	%N	%F	GII	IRI	Rank
Fishes												
Engraulis mordax (northern anchovy)	30.12	31.87	21.49	48.18	1,332.09	2	68.00	53.09	34.33	89.73	4,156.92	1
Teleostei (unidentified)	17.48	47.13	64.49	74.51	4,166.44	1	10.29	10.52	31.34	30.11	652.11	3
Sardinops sagax (Pacific sardine)	3.97	4.46	7.48	9.18	63.07	5	12.76	7.73	19.40	23.03	397.61	4
Merluccius productus (Pacific hake)	9.17	11.21	33.64	31.19	685.48	3	1.10	7.32	20.90	16.93	175.93	5
Scomber japonicus (Pacific mackerel)	24.73	1.42	16.82	24.81	439.86	4	1.79	0.31	4.48	3.80	9.4	6
Sebastes spp. (rockfishes)	0.01	0.54	3.74	2.46	2.06	11	<0.01	0.21	1.49	0.98	0.31	7[b]
Luvarus imperialis (louvar)	9.93	0.07	0.93	6.31	9.30	7	—	—	—	—	—	—
Sphyraena argentea (Calif. barracuda)	1.75	0.27	3.74	3.32	7.54	9	—	—	—	—	—	—
Trachurus symmetricus (jack mackerel)	2.17	0.14	1.87	2.41	4.30	10	—	—	—	—	—	—
Genyonemus lineatus (white croaker)	<0.01	0.14	1.87	1.16	0.26	13[b]	—	—	—	—	—	—
Leuresthes tenuis (Calif. grunion)	<0.01	0.14	1.87	1.16	0.25	13[b]	—	—	—	—	—	—
Peprilus simillimus (Pacific butterfish)	0.34	0.07	0.93	0.77	0.38	14	—	—	—	—	—	—
Seriphus politus (queenfish)	<0.01	0.07	0.93	0.58	0.06	15[b]	—	—	—	—	—	—
Citharichthys sordidus (Pacific sanddab)	<0.01	0.07	0.93	0.58	0.06	15[b]	—	—	—	—	—	—
Cephalopods												
Loligo opalescens (market squid)	0.12	0.61	2.80	2.04	2.03	12	6.06	20.62	46.27	42.12	1234.38	2
Ommastrephidae family	—	—	—	—	—	—	<0.01	0.21	1.49	0.98	0.31	7[b]
Teuthoidea (unidentified)	0.09	0.68	5.60	3.68	4.27	8	—	—	—	—	—	—
Gonatus sp.	<0.01	0.07	0.93	0.58	0.07	15[b]	—	—	—	—	—	—
Octopoda (unidentified)	<0.01	0.07	0.93	0.58	0.06	15[b]	—	—	—	—	—	—
Crustaceans							—	—	—	—	—	—
Pleuroncodes planipes (pelagic red crab)	0.13	0.95	10.28	6.55	11.01	6	—	—	—	—	—	—
Crustacea (unidentified)	<0.01	0.14	1.87	1.16	0.26	13[b]	—	—	—	—	—	—

Note: W = weight in grams; N = number; F = frequency of occurrence; GII = geometric index of importance; IRI = index of relative importance

[a] Preti et al. 2001.

[b] Tied ranks based on GII value.

period, 75% were *Sebastes* spp. unidentified; 25% were *S. jordani* (A. Preti, Southwest Fisheries Science Center, La Jolla, Calif., unpub. data).

Degrees of prey digestion were significantly different between the two periods. In the cool-water period prey items were less digested overall ($\chi^2 = 702$, *d.f.* = 4, $\alpha < 0.05$).

For the cool-water 1999–2000 period, the Fisher Exact Test showed that the diet of sharks sampled north of 34°00'N in the nearshore setnet fishery (*n* = 5) did not differ significantly from that of sharks collected from the offshore drift gill-net fishery (*n* = 10; *p* = 0.801), so we pooled these samples. Northern anchovy was the highest ranking in importance overall in the cool-water period (GII = 89.7; IRI = 4,156.9). Market squid, of minor importance in the warm-water/transitional period, advanced to second place (GII = 42.1, IRI = 1234.4), ranking first in frequency of occurrence. Other prey items in descending order of importance were unidentified teleosts, Pacific sardine, Pacific hake, Pacific mackerel, ommastrephid squids, and *Sebastes* spp. For the area north of 34°00'N, Pacific sardine was the most important identifiable food in the cool-water period, followed by market squid and Pacific hake, which were the only other identifiable prey.

Statistical differences in consumption of the top five diet items among the different groups were similar for both periods, even though diversity varied greatly. Numbers of the top five prey items consumed north (*n* = 9) versus south (*n* = 58) of 34°00'N during the cool-water period were significantly different ($\chi^2 = 92.4$, *d.f.* = 4, $\alpha < 0.05$), similar to results of the previous period (Preti et al. 2001). Diet differences (as measured by differences in numerical consumption of the top five items) were also significant between immature-sized thresher sharks (≤ 159 cm fork length, *n* = 39) and mature-sized sharks (> 159 cm fork length, *n* = 27) ($\chi^2 = 58.5$, *d.f.* = 4, $\alpha < 0.05$). During both periods, larger sharks ate greater numbers of prey.

Analyses of the randomized cumulative prey curves for both periods indicate that our sample sizes were large enough to adequately capture an accurate profile of at least the major diet items of *A. vulpinus*, as examined in various treatments (figs. 5 and 6). The prey curves for the cool-water period leveled off earlier and more dramatically than those constructed for diet samples observed in the warm-water/transitional period, reaching full asymptotic stabilization for small thresher sharks ≤ 159 cm FL (fig. 6). Large sharks and those sampled north of 34°00'N had the highest diversity and may need additional sampling to determine the full range of prey.

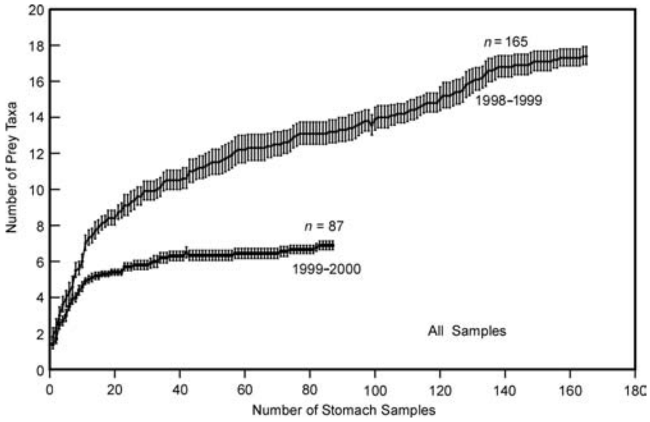

Figure 5. Randomized cumulative prey curve for thresher shark (*Alopias vulpinus*) diet samples. Mean values are plotted; error bars represent ±1 SE.

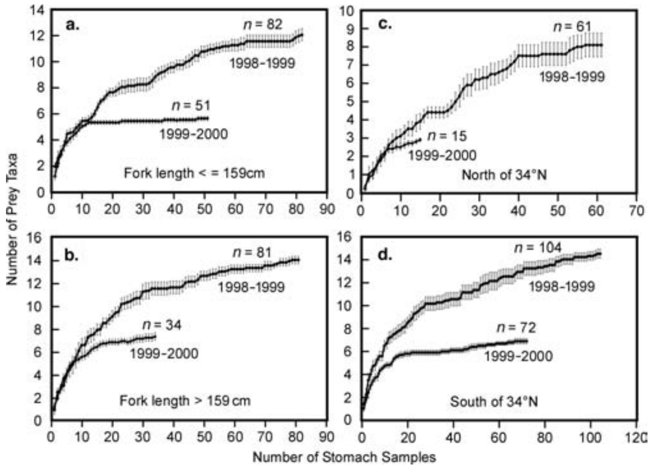

Figure 6. Randomized cumulative prey curves for thresher shark stomach samples for warm-water/transitional 1998–99 and cool-water 1999–2000 periods: (*a*) small sharks (≤ 159 cm fork length) and (*b*) adult sharks (> 159 cm fork length), (*c*) north of 34°00'N, and (*d*) south of 34°00'N. Mean values are plotted; error bars represent ±1 SE.

DISCUSSION

During the period spanned by this study, the California Current system made a full transition from warm El Niño to cool La Niña conditions (Hayward et al. 1999; Kahru and Mitchell 2000). A noticeable shift from El Niño conditions in 1997–98 to La Niña conditions is thought to have occurred around January 1999 after a period of intense El Niño conditions along the U.S. West Coast (Bograd and Lynn 2001; Chavez et al. 2003).

Our findings confirm the importance of northern anchovy in the diet of the thresher shark off southern California, where most juvenile and subadult thresher sharks in U.S. West Coast waters are found (PFMC 2003). Anchovy was the single most important prey during both periods, especially in the more recent cool-water period in the south. This small, schooling pelagic species tends to increase in abundance when cooler temperatures inhibit expansion of the sardine population along the U.S. West Coast, and has tended to decrease when the sardine population expands (Chavez et al. 2003).

The central stock of northern anchovy has its center of abundance in the Southern California Bight (PFMC

1998). Since 1980, sardine has greatly increased in abundance and expanded its range northward (Lluch-Belda et al. 1989). Anchovy was not identified in the diet north of Point Conception, where sardine was the most important identifiable prey in the cool period and hake the most important in the warmer period. Market squid changed from a minor diet item in the warm-water/transitional period to a major one in 1999–2000 (south of 34°00'N), mirroring its resurgence in fishery landings after a period of scarcity during the preceding El Niño regime (Rogers-Bennett 2001; Jackson and Domeier 2003).

In all, we found the trophic spectrum much narrower during the cool-water period, compared to the previous El Niño transition period. This is not likely due to differences in processing techniques or experience, because the same person processed both sets of stomach samples, and was probably more (rather than less) experienced in identifying stomach contents during examination of the 1999–2000 samples than in 1998–99, when there was a higher diversity of items. Mean digestive state was not higher for the cool-water period, which might have accounted for the low diversity of prey detected then (i.e., because so few diet items were identifiable). Analyses of the cumulative prey curves indicate that our sample sizes for both periods were sufficient to adequately capture an accurate profile of the major prey of *A. vulpinus* as examined, but more sampling may be needed for adult fish in northerly waters (north of 34°00'N). Although total sample prey diversity curves did not reach a complete asymptote in either sampling period, the leveling off was more pronounced and occurred at a smaller sample size in the cool-water period. Judging from the flat prey diversity curve of threshers ≤ 159 cm fork length, total prey diversity of small threshers might possibly have been captured by a sample size as small as 12 (Fig. 6). For prey items of primary and secondary importance, the statistical tests indicate a significant difference in individual number of the top five prey between the sampling periods.

Lower prey diversity during the cool-water period could have been partially due to the greater percentage of stomach samples collected south of 34°00'N (fig. 1), where northern anchovy dominated the diet in both periods. However, we believe that this low diversity, greater dominance of northern anchovy and squid and lack of the more tropical species in the diet were largely due to the biological oceanographic regime change that ushered in conditions more favorable for market squid and anchovy. These may be the two prey species most preferred by thresher sharks in this area (at least among subadults), but when conditions are less favorable, they may be forced to diversify their diet.

ACKNOWLEDGMENTS

We gratefully acknowledge the valuable help of three anonymous reviewers. We also wish to thank reviewers of earlier versions of the draft, such as David Au, Dave Holts, and Mark Lowry, NMFS Southwest Fisheries Science Center (NMFS/SWFSC). This work would not have been possible without the assistance and samples provided by the NMFS Southwest Region Drift Net Observer Program and the California-Oregon drift net and setnet fishermen. Mark Lowry, Kelly Robertson, and Suzanne Kohin (NMFS/SWFSC) helped identify specimens, and Roy Allen (NMFS/SWFSC) designed some of the figures. Gregor Cailliet (Moss Landing Marine Laboratories) offered valuable insight on the Pinkas IRI index; Michelle DeLaFuente (NMFS/SWFSC) helped with some technical editing and Debra Losey (NMFS/SWFSC) assisted with the library research. This project was funded by the National Marine Fisheries Service, Southwest Fisheries Science Center, Fisheries Resources Division, La Jolla, California.

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COMMUNITY STRUCTURE OF EUPHAUSIIDS IN THE SOUTHERN PART OF THE CALIFORNIA CURRENT DURING OCTOBER 1997 (EL NIÑO) AND OCTOBER 1999 (LA NIÑA)

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ABSTRACT

Zooplankton samples collected during October 1997 (El Niño) and October 1999 (La Niña) were used to study the effects of warm and cold events on the community structure of euphausiids from Punta Abreojos (26.7°N) to Punta Baja (30°N), Baja California, México. A total of 24 species (7 genera) were found. Total abundance was 16% higher during the warm event than during the cold conditions, mainly because of a higher contribution of larvae. The most abundant species in both periods was *Nyctiphanes simplex*. Other species showed low abundance, and their presence is presumed to be attributable to the particular oceanographic conditions associated with El Niño and La Niña. Differences in abundances of life stages indicated more intense reproductive activity in October 1997 or better larval-survival strategy than during the cold period. Species with tropical and equatorial affinity were more abundant in October 1997, whereas species with subarctic and temperate affinity were more abundant during October 1999.

INTRODUCTION

Marine ecosystems of the eastern Pacific are strongly affected by El Niño events (Barber and Chavez 1983; Chavez et al. 2002). The response of planktonic communities differs among taxa. The changes noticed are in biomass, abundance, specific distribution patterns, and recruitment rates of some planktonic larvae phases (Tegner and Dayton 1987; Connolly and Roughgarden 1999). Euphausiids, as with other planktonic invertebrates, are subject to environmental changes. These changes may occur seasonally or on longer temporal scales, such as during warmer and cooler years (Brinton 1960, 1962, 1981; Brodeur 1986; Brinton and Willie 1976; Brinton and Reid 1986; Gómez-Gutiérrez et al. 1995a; Marinovic et al. 2002). In the California Current, interannual events such as El Niño produce changes in the composition and distribution patterns of the euphausiid community, causing shifts in species assemblages and range extensions (Brinton 1960, 1981; Brodeur 1986; Brinton and Willie 1976; Brinton and Reid 1986; Gómez-Gutiérrez et al. 1995a).

The beginning of El Niño 1997–98 was marked by a warming of surface waters in the central tropical Pacific in March 1997. Although of shorter duration, this warming episode was comparable in magnitude to El Niño 1983–84. It is the strongest episode recorded in recent years (Webster and Palmer 1997; McPhaden 1999a,b) and has been referred as "the climate event of the century" (Webster and Palmer 1997; McPhaden 1999a,b). In April–July 1998, there was a dramatic transition from strong El Niño conditions to cool-water conditions in the central and eastern tropical Pacific. By late 1998, anticyclonic wind anomalies in the northeastern Pacific were associated with an intense center of high pressure. These anomalies contributed to stronger-than-usual trade winds in the eastern tropical Pacific that favored strong upwelling and colder-than-normal waters along the coast of the northeastern Pacific characteristic of La Niña conditions. This colder-than-usual state prevailed until early 2001 (Hayward et al. 1999; Schwing et al. 2002).

The California Current System (CCS), as an eastern boundary system, is known to be highly vulnerable to the changes in temperature, salinity, and circulation patterns associated with basinwide events (Simpson 1984; Lynn et al. 1998; Hayward et al. 1999). In the CCS, El Niño 1997–98 was recorded on July 1997 due to an expansion of the coastal countercurrent that transported warmer and saltier waters northward in the upper 100 m depth (Lynn et al. 1998). Off the west coast of Baja California (28°N), conditions were warmer (8.7°C) and saltier (0.8) than normal in the upper 600 m; there was also diminished mesoscale activity in the California Current during October 1997 (Durazo and Baumgartner 2002). Similar dynamics were observed to the north (32°N) (Lynn and Bograd 2002) and south (~20°N) (Filonov and Tereshchenko 2000) of this region, though temperature and salinity anomalies were smaller. The anomalous conditions in Baja California waters are attributable mainly to subtropical surface water fed from the southwest as a narrow, poleward flowing coastal jet. Other effects included a westward displacement of the core of the California Current (Lynn and Bograd 2002),

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[Manuscript received 23 February 2004.]

as well as a volume expansion of waters originating in the eastern tropical Pacific and forming the California Undercurrent. During late 1998 and 1999, the atmospheric pattern of La Niña in the CCS, particularly along the Baja California coast, caused a decrease in sea level, a rise in the thermocline, an increase of baroclinic instability, increased meandering and mesoscale activity, stronger upwelling, and a strengthening of the equatorward flow of the California Current (Hayward et al. 1999; Bograd et al. 2000; Durazo and Baumgartner 2002).

Within the CCS, most of the euphausiid-related studies have been conducted using data from the CalCOFI seasonal-monitoring program. In Mexican waters of the eastern Pacific, particularly along the Baja California peninsula, several investigations have focused on this group (Gómez-Gutiérrez 1995; Lavaniegos-Espejo 1993, 1994; Gómez-Gutiérrez and Robinson-Mendoza 1997; Gómez-Gutiérrez et al. 1995a, b, 1999). Since 1997, the IMECOCAL program (Investigaciones Mexicanas de la Corriente de California, designed to provide quantitative descriptions of the physical, chemical, and biological processes of the coastal waters in this region) has generated useful information to increase understanding of the pelagic ecosystem of the southern California Current. In this context, this study analyzes zooplankton data from IMECOCAL samples collected off Baja California, México, during two contrasting episodes. The goal of this work is to compare the euphausiid patterns of abundance, composition, and distribution from two major climatic events of the twentieth century, El Niño 1997–98 and La Niña 1999–2001. Comparative studies of the effects of warm and cold events on community structure of euphausiid in the southern part of the CCS are of special importance because in general the structure of zooplankton can be used as an indicator of the ecological state of the pelagic system.

METHODS

Zooplankton samples were collected onboard the research vessel *Francisco de Ulloa* during IMECOCAL cruises 9709/10 and 9910, between Punta Abreojos (26.7°N) and Punta Baja (30°N), Baja California, México, along 39 stations of the CalCOFI program (fig. 1).

Samples were obtained using a bongo net of 500 µm mesh, 61 cm diameter in October 1997 and 71 cm diameter in October 1999. Oblique tows were conducted from 200 m to the surface. Flowmeters were attached to each net entrance. Samples were preserved and stored in 4% formaldehyde in seawater and buffered with sodium borate. In the laboratory, euphausiid species and larval stages (calyptopes, furcilia, juvenile, and adult) were identified. Samples containing high densities of euphausiid ($n > 100$) were subsampled using a Folsom splitter. The number of each species was standardized to 1,000 m^3 of water.

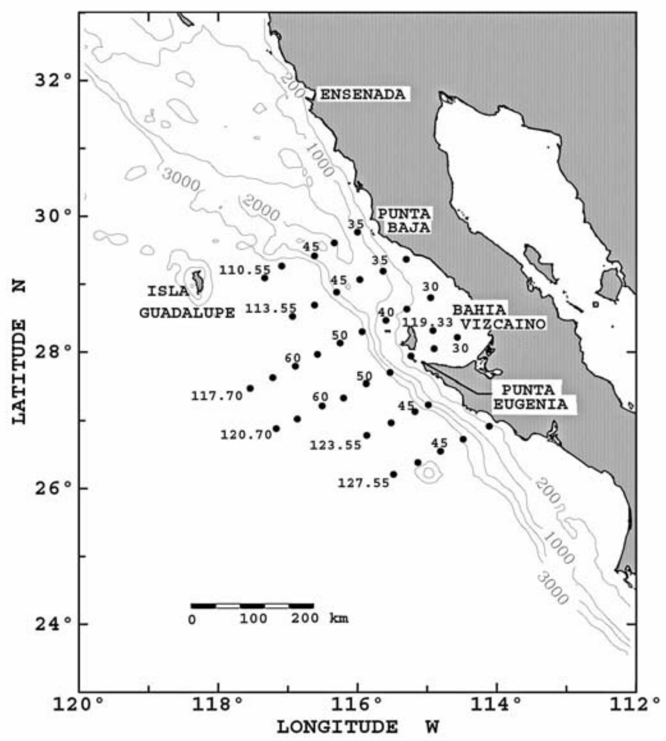

Figure 1. Study area indicating stations (*solid circles*) where zooplankton was sampled during October 1997 and October 1999. The system of numbering lines (110, 113, 117...) and stations (30, 35, 40 ...) follows the CalCOFI practice. Depth contours are given in meters.

Owing to their indistinctly differing morphologies and overlapping occurrences along the warm terminal part of the California Current, larval stages of *Euphausia diomedeae*, *E. eximia*, *E. mutica*, and *E. recurva* were grouped according to the identification key of Brinton (1975). Statistical analysis, particularly nonparametric Mann-Whitney U, were performed to test for significant differences between El Niño and La Niña conditions in total abundances, development stages of euphausiid, biogeographic groups, and the most common and abundant species.

RESULTS

Composition and Abundance

Taxonomic analysis of euphausiids for both periods yielded 24 species belonging to 7 genera. October 1997 samples contained 22 species; October 1999 samples had only 18 species. Table 1 shows the total abundance of each euphausiid species during each period according to its biogeographic affinity (Brinton 1996). The most abundant species during El Niño 1997 was *N. simplex* (83%), followed by *Euphausia eximia* (3%) and *Stylocheiron affine* (2%). The presence of tropical and subtropical species was notable during this period. During La Niña 1999, *N. simplex* was again the most abundant species (67%), while the abundance of *N. difficilis* increased sig-

TABLE 1
Total Abundances of Euphausiid Species Sampled During El Niño (October 1997) and La Niña (October 1999) Conditions (Individuals/1,000 m^3), Following Brinton 1996.

Biogeographic group as observed within study area	Species	Period Oct. 1997	 Oct. 1999
California Current (Baja California)	*Euphausia gibboides*	2,118	4,958
	E. pacifica	0	949
	Nematoscelis difficilis	1,008	34,066
	Nyctiphanes simplex	193,514	111,614
	Thysanoessa gregaria	1,218	5,687
Subtropical Oceanic	*E. eximia*	5,936	364
	E. hemigibba	279	176
	E. mutica	77	8
	E. recurva	1,013	438
	Nematobrachion flexipes	594	116
	N. tenella	290	238
	Stylocheiron longicorne	566	752
	S. maximum	90	85
	Thysanopoda astylata	149	270
	T. monocantha	6	0
	T. obtusifrons	8	87
	T. orientalis	0	7
Eastern Tropical Pacific (ETP)	*E. diomedeae*	396	8
	E. distinguenda	895	0
	E. lamelligera	20	0
	E. tenera	140	0
	N. gracilis	128	0
Subtropical + ETP	*S. affine*	5,663	4,268
	S. carinatum	15	0
	IA group[a]	17,790	3,481
Total		231,910	167,570

[a] Composed of *Euphausia diomedeae*, *E. eximia*, *E. mutica*, and *E. recurva* larvae (Brinton 1975).

nificantly (20%), followed by *Euphausia gibboides* (3%) and *Thysanoessa gregaria* (3%), species typically associated with oceanic waters of the California Current. The IA Group, consisting of species with tropical and subtropical affinity, was more abundant in October 1997 (8%) than in October 1999 (3%). The rest of the species showed low abundance in both periods, their presence in the region being indicative of the anomalous environmental conditions; examples are the warm-water species *Euphausia distinguenda*, *E. lamelligera*, *E. tenera*, *Nematoscelis gracilis*, and *Stylocheiron carinatum* observed only during October 1997; cold-water species, notably *E. pacifica*, were present only during La Niña.

Euphausiid abundances were 16% higher during the El Niño cruise than during the La Niña cruise, owing largely to the higher contribution of larvae—furciliae and calyptopes stages (fig. 2)—although no significant differences were detected between the periods (Mann-Whitney U test, $p = 0.42896$). The furciliae stages represented over half the euphausiid community during the warm-water conditions. There were significant differences in postlarval stages from 1997 to 1999 (Mann-Whitney U test, $p = 0.02198$), and juveniles of cold-water species were more abundant during October 1999 (fig. 2). Indeed, there were significant differences in juvenile abundances between the two periods (Mann-Whitney U test, $p = 0.017497$).

Due to its high abundance, *N. simplex* was excluded, and the developmental stages of the species—larval (calyptopes and furciliae) and postlarval (juveniles and adults)—were similarly grouped according to biogeographic affinity. Significant differences between El Niño and La Niña periods were found (fig. 3; tab. 2). Tropical

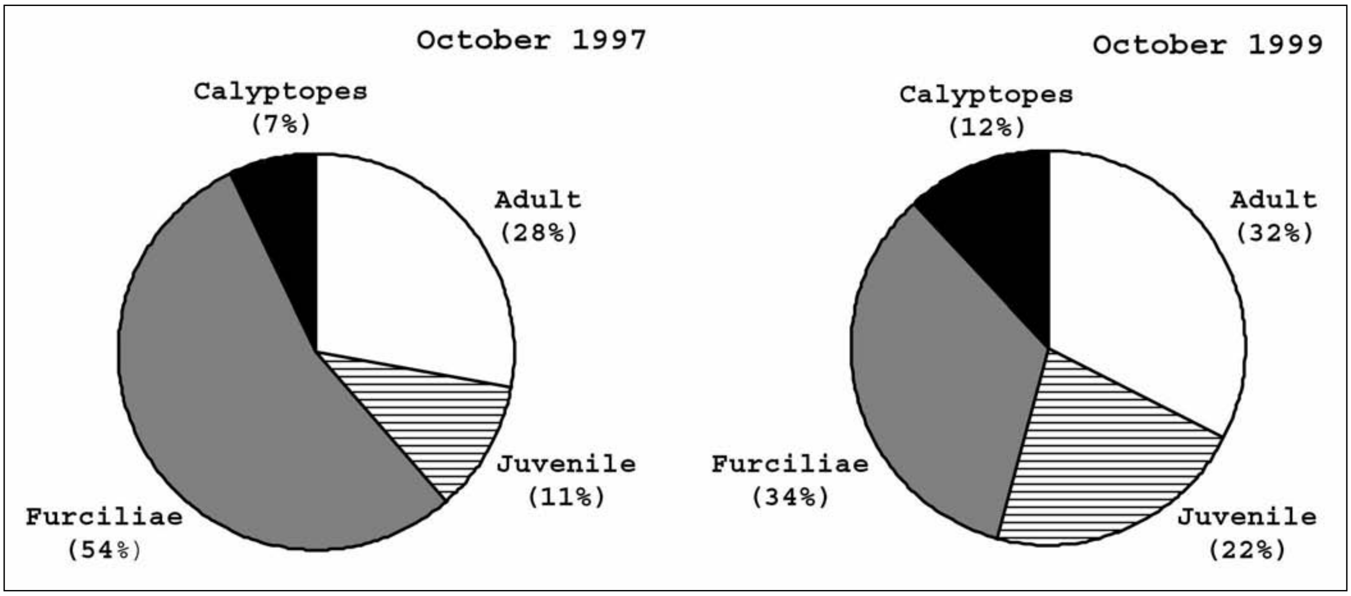

Figure 2. Developmental stages of euphausiids (calyptopes, furciliae, juveniles, and adults) recorded during October 1997 and October 1999.

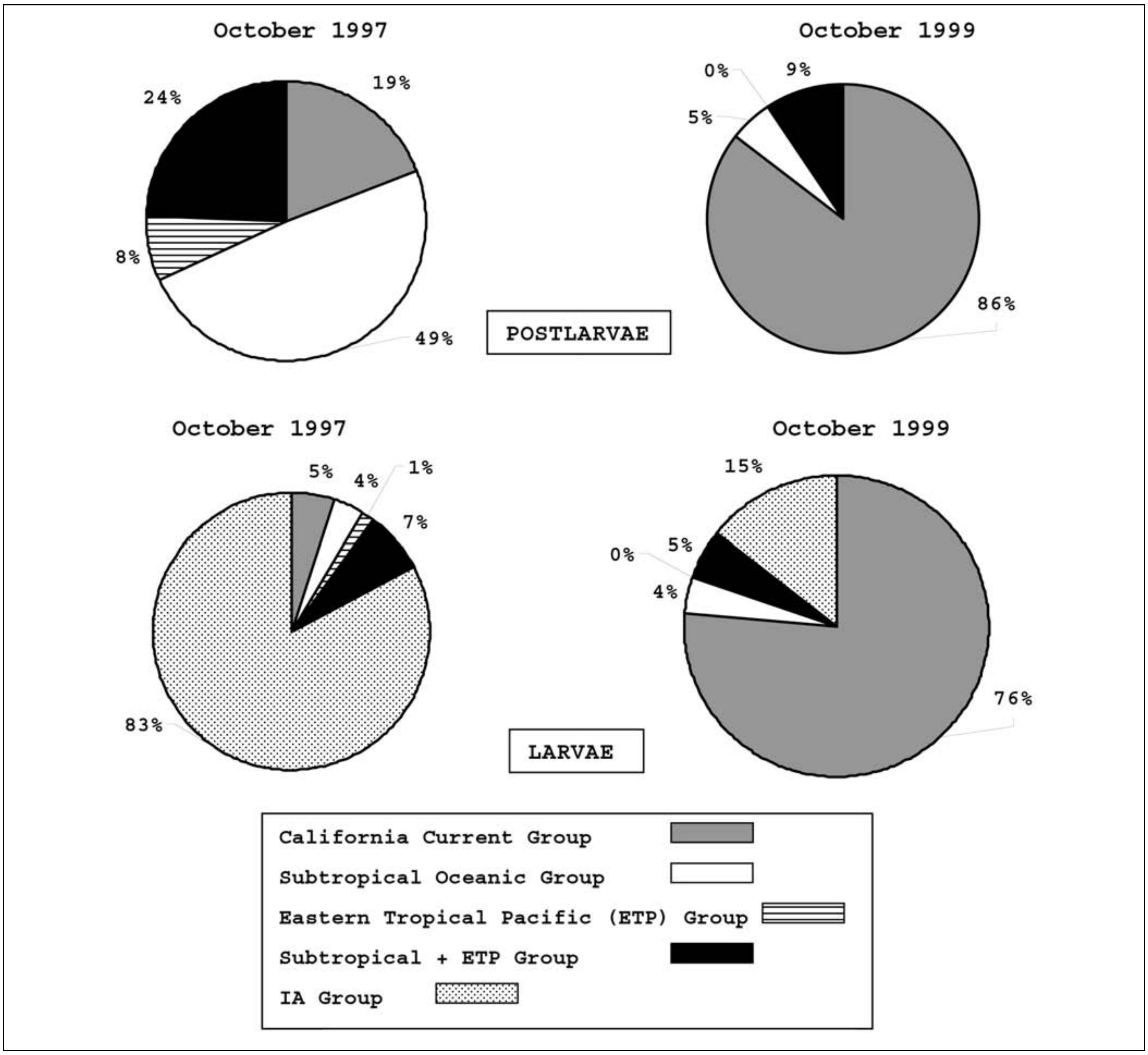

Figure 3. Euphausiids grouped according to biogeographic affinity described by Brinton (1996) during October 1997 and October 1999. Note that percentages exclude *Nyctiphanes simplex* abundance.

TABLE 2
Mann-Whitney U Tests Comparing Total Euphausiid Abundance Between October 1997 and October 1999. Species Grouped According to Their Biogeographic Affinity (Brinton 1996).

Biogeographic Group	Rank Sum Oct. 1997	Rank Sum Oct. 1999	U	*p*-level
California Current[a]	930	1,996	189	**0.0000**
Subtropical Oceanic	1,707	1,219	478	**0.0108**
Eastern Tropical Pacific (ETP)	2,005	922	181	**0.0000**
Subtropical +ETP	1,592	1,334	593	0.1830
IA group[b]	1,927	999	258	**0.0000**

Note: Boldface indicates significant tests ($p < 0.05$).
[a] *N. simplex* abundance was not considered.
[b] Composed of *E. diomedeae*, *E. eximia*, *E. mutica*, and *E. recurva* larvae (Brinton 1975).

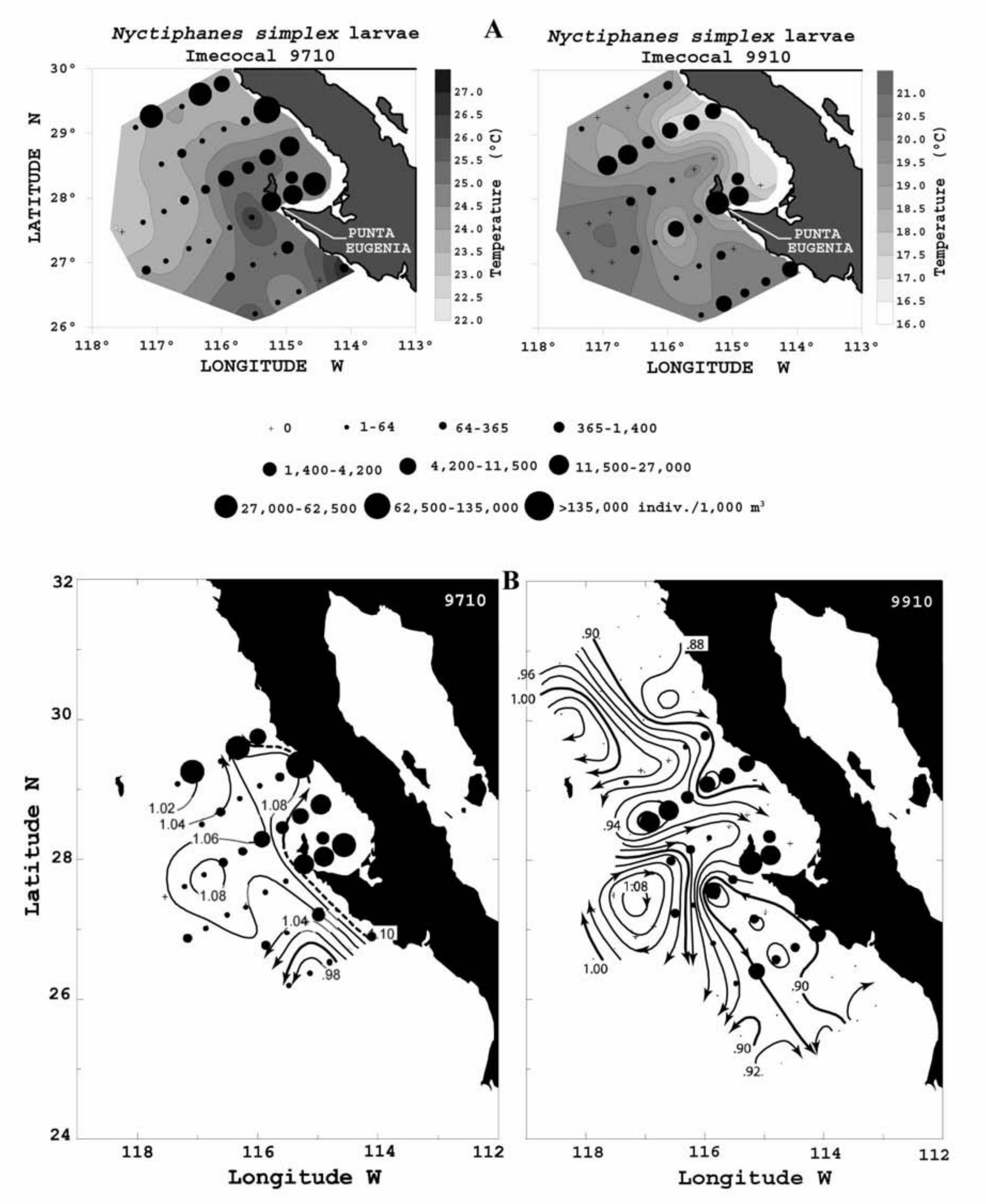

Figure 4. Distribution pattern of *Nyctiphanes simplex* larvae off southern Baja California during October 1997 (El Niño cruise) and October 1999 (La Niña cruise) related to (*A*) 10 m temperature and (*B*) dynamic height anomaly (dynamic meters, 0/500 db). Abundance values were classified in a metric scale log^2. Note that the two temperature scales in *A* are different.

and subtropical species were most abundant during El Niño, October 1997. For the larval stages, the IA Group of species was dominant. During the cold 1999 La Niña, California Current species were more abundant than during the warmer 1997 El Niño.

Spatial Distribution

To illustrate the spatial distribution during both periods, the larval stages of the most abundant species were chosen: *N. simplex*, *N. difficilis*, and IA Group species. The presence of these species during each period was

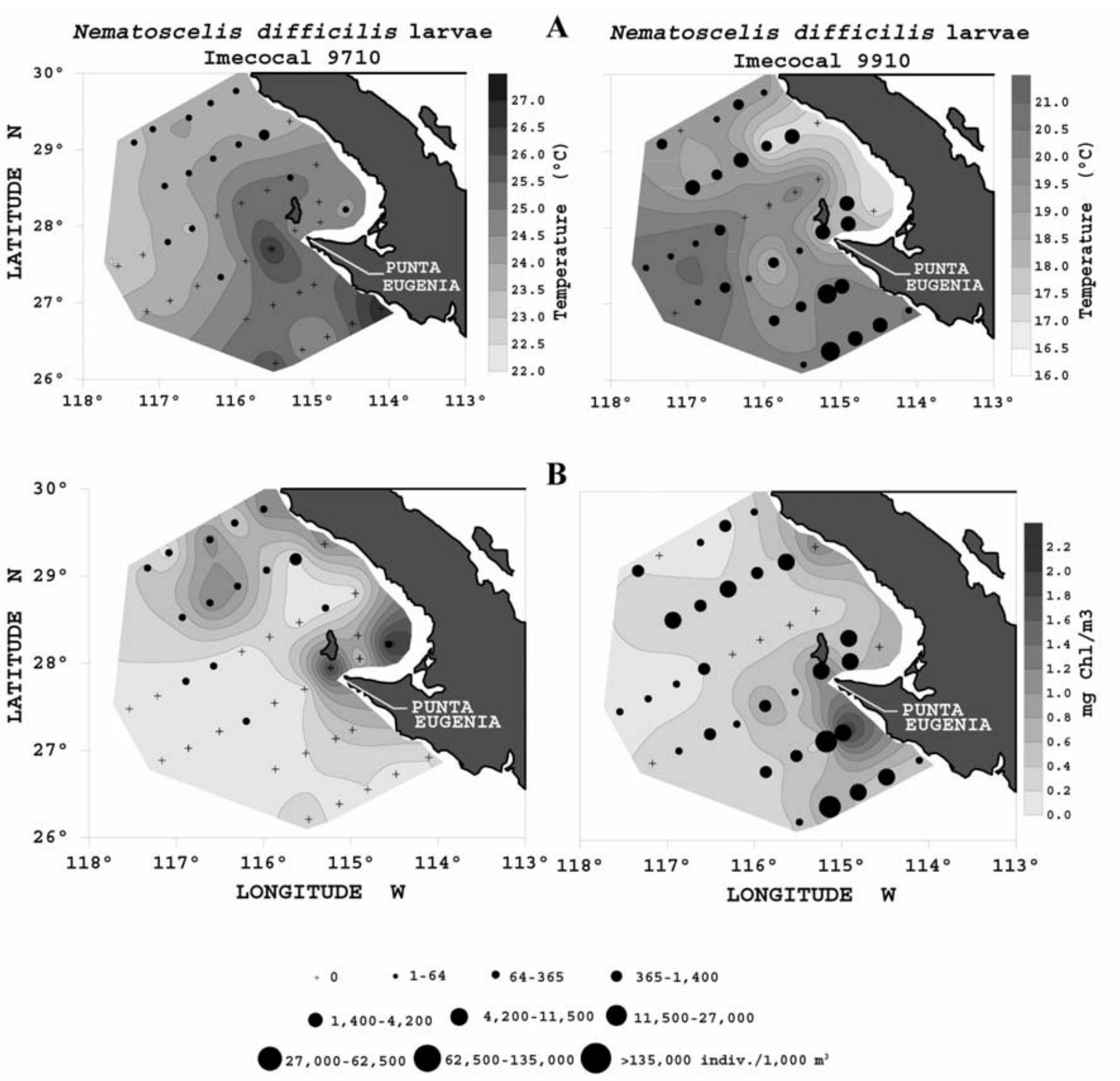

Figure 5. Distribution pattern of *Nematoscelis difficilis* larvae off southern Baja California during October 1997 (El Niño cruise) and October 1999 (La Niña cruise) related to (*A*) 10 m temperature and (*B*) surface chlorophyll *a*. Abundance values were classified in a metric scale $\log^2$. Note that the two temperature scales in *A* are different.

found to be associated with certain environmental parameters: temperature, chlorophyll *a*, and circulation. The most abundant species during the El Niño period, *N. simplex*, displayed striking differences in its larval distributions, though the differences were not significantly different between the two periods (Mann-Whitney U test, $p = 0.38783$). This is possibly associated with the circulation pattern and sea-surface temperature distribution in the study area (fig. 4). It is likely that *N. simplex* larvae were transported by northward (southward) flows to regions of relatively low temperatures during October 1997 (October 1999).

Contrasting patterns in the distribution of the temperate species *N. difficilis* are shown in Figure 5. Unlike *N. simplex*, the abundance and presence of *N. difficilis* during El Niño was relatively low and restricted to the northern part of the study area, while during La Niña large densities were recorded throughout the region. This pattern appears to be associated with low temperatures and food availability (chlorophyll-a). *N. difficilis* larval abundance were significantly different between two periods (Mann-Whitney U test, $p = 0.00000$).

The opposite trend was observed with the larvae of species with tropical-subtropical affinity (fig. 6). The IA Group was most abundant and frequent during the October 1997 cruise associated with the anomalous warm waters of El Niño. At this time, the group was uniformly distributed throughout the region, but during October 1999 the group was at a low level, particularly in coastal and cold regions.

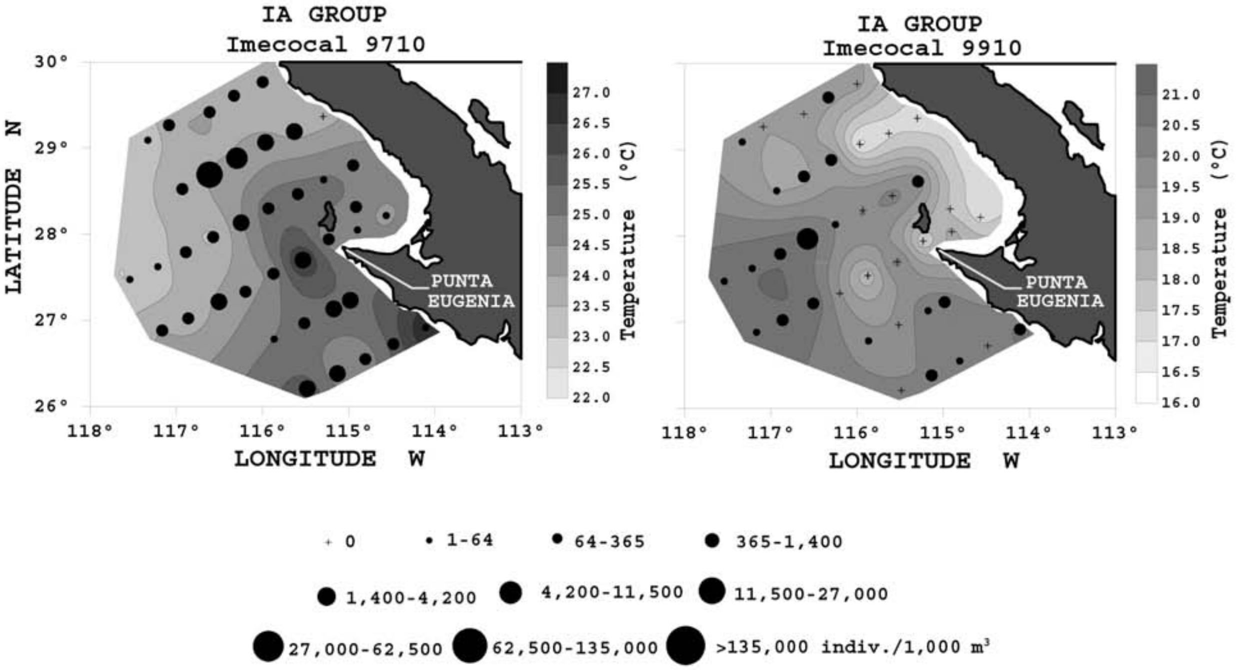

Figure 6. Distribution pattern of IA Group larvae off southern Baja California during October 1997 (El Niño cruise) and October 1999 (La Niña cruise) related to 10 m temperature. Abundance values were classified in a metric scale log^2. Note that the two temperature scales are different.

DISCUSSION

Most of the species identified in the current investigation have been previously reported in the study area by Brinton (1962), Gómez-Gutiérrez (1995), Lavaniegos-Espejo (1993, 1994), Gómez-Gutiérrez et al. (1995a, b, 1999), and Gómez-Gutiérrez and Robinson-Mendoza (1997). There were distinct differences between the species reported for "ordinary years" and those reported here in the Baja California region. Species present in October 1997 with tropical and subtropical affinities, such as *E. diomedeae*, *E. lamelligera*, *N. gracilis*, *S. carinatum*, *Thysanopoda monocantha*, and *T. obtusifrons*, have not all been reported for other periods, for example, October 1966 (Lavaniegos-Espejo 1993) and October 1994 (Gómez-Gutiérrez et al. 1999), years that can be considered normal or neither El Niño or La Niña periods. These previous works also recorded examples of species with subtropical (*Nematoscelis atlantica*, *Stylocheiron suhmii*, *S. elongatum*, *S. abbreviatum*) and temperate (*Thysanoessa spinifera*) affinities, species that were not recorded either in October 1997 or October 1999. Likewise, these oceanic species were not reported by Gómez-Gutiérrez et al. (1995a) in the same region during October 1987, a period characterized by weak El Niño conditions. However, Gómez-Gutiérrez et al. (1995a) recorded a subarctic affinity species, *E. pacifica*, typical of the California Current, found in the current investigation only during the La Niña cruise. This suggests that species' responses vary differentially, depending on environmental conditions modulated by interannual events that vary in strength and duration.

Euphausiid development stages varied in both periods (fig. 2). The large percentage of larvae during October 1997, mostly furciliae stages, was associated with the introduction of subtropical waters from the southwest to the coastal zone causing positive temperature anomalies of ~8.7°C (Durazo and Baumgartner 2002). While this water displaced California Current waters offshore, it is likely to have also displaced temperate species. However, the sampling region covered only the coastal zone (200 km), not enough area to discern whether these temperate species had indeed been displaced offshore or just remained off the study area. It is also possible that a transient development of an equatorial environment to the north enabled individuals to reproduce there and augment the larval stages of species that normally inhabit warmer, more southern waters. This is suggested by the high temperatures recorded in the region and the high proportion of developmental stages in the euphausiid community during October 1997. Brinton (1960) suggested this for during the warm period of 1957–58, when he found species with equatorial affinities, such as *E. distinguenda*, in the mid-Baja California region. The pattern was also recorded near Punta Eugenia (28°N) by Gómez-Gutiérrez et al. (1995a) during the weak El Niño of 1986–87, when the populations of tropical species, such as *E. distinguenda*, *E. lamelligera*, and *E. diomedeae*, contained adults in the reproductive phase. The significant differences in postlarval stage abundances between the two periods may be related to an increase in juveniles of temperate species during October 1999 (fig. 2), mainly *N. difficilis* and *E. pacifica*. This incremental difference in postlarval stages could be associated with an increased offshore advection of early developmental stages of euphausiid (calyptopes and furciliae), owing to stronger-than-usual upwelling recorded in the area during La Niña conditions (Hayward et al. 1999; Bograd et al. 2000; Durazo and Baumgartner 2002).

Composition and abundance of euphausiid, and consequently their spatial distribution pattern, appears to be strongly modulated during El Niño/La Niña, favoring the presence/absence and the increase/decrease of species according to the prevailing conditions. Differences found in the biogeographic groups between the two periods seem to be a consequence of advective processes that influenced the groups' abundances—that is, poleward flows during El Niño favored the transport of eastern tropical Pacific and subtropical oceanic species, whereas anomalously strong equatorward winds during La Niña favored the southward transport of cold-water species, characteristic of the California Current, toward the study area.

Advection appears to play an important role on the latitudinal limits of some species, even for those as abundant in these regions as *N. simplex*. A distinctive spatial distribution of larval stages of *N. simplex* was observed for both periods (fig. 4) and appears to be regulated by the circulation observed during 1997 and 1999, as Bograd et al. (2000) and Durazo and Baumgartner (2002) have described. Even though this warm-temperate, typically coastal species has a close association to the California Current, its maximum abundances were during the warm period (tab. 1), showing a distribution through most of the sampling grid. This distribution and nearshore abundance during El Niño could be associated with high concentrations of chlorophyll *a* north of Punta Eugenia (fig. 5b) as a consequence of an entrainment of California Current waters from offshore, as is suggested by the clockwise gyre in the dynamic height contours of Figure 4b. Therefore, the strong poleward flow during this period could be causing the larvae to be transported to the north, where cooler waters were recorded (fig. 4a). The effect of warm episodes on the abundance and distribution of *N. simplex* in the California Current along central and northern California waters has been reported for El Niño years. Northward extensions beyond its usual Baja California maximal distribution range were recorded during El Niño events in 1957–59, 1977–78, 1982–83, and 1997–98. Northern species, such as *E. pacifica* and *T. spinifera*, retracted northward, and *N. simplex* was abundant well into California waters (Brinton 1960, 1981; Broudeur 1986; Brinton and Willie 1976; Brinton and Reid 1986; Marinovic et al. 2002). Similar patterns were recorded during El Niño 1986–87 along the Baja California coast. The high-concentration centers of *N. simplex* were displaced progressively from Bahía Magdalena (24.5°N) to the north, attributable to a northward movement of the tropical countercurrent during July and October 1987 in response to seasonal variation of the CCS, possibly intensified during years of warming of the California Current (Gómez-Gutiérrez et al. 1995a).

During October 1999, the abundance and distribution of *N. simplex* larvae (fig. 4b) was closely associated with the circulation pattern and coastal upwelling regions. Isopicnal shoaling near the coast at sections 113 and 120 (not shown) brought to the surface cold, nutrient-rich waters that were trapped into offshore-displacing meanders and gyres. This dynamic promotes the formation of retention sites of nutrients and high densities of *N. simplex* larvae, as was observed off Punta Baja and Punta Eugenia. The proliferation of *N. simplex* in or adjacent to upwelling regions has been frequently recorded, apparently a general feature of the genus observed in other regions for *Nyctiphanes couchii* (Le Roux 1973) and *N. australis* (Bradford and Chapman 1988). The more offshore distribution of *N. simplex* recorded during La Niña period, in contrast to October 1997 (fig. 4), seems to be a consequence of increased westward advection (Ekman transport) related to a high upwelling index anomaly during September 1999 (70 m^3/s per 100 m coastline), a large value compared with -44 m^3/s per 100 m coastline computed in September 1997 for the region (www.pfeg.noaa.gov).

Nematoscelis difficilis inhabits a subarctic to subtropical transition zone of the California Current (Brinton 1960, 1962) and is a temperate species that displayed significant differences between the two periods described here. Its presence, restricted to the northernmost sections and significant low abundance during El Niño, was associated with the advection of warmer-than-normal waters from the southwest into the region, displacing the low-temperature and fresh waters of the California Current offshore (~275 km) (Durazo and Baumgartner 2002; Lynn and Bograd 2002). Thus, the centers of high chlorophyll *a* concentrations and smaller temperatures were located north of Punta Eugenia, where this species was largely present (fig. 5b). Low larval survival of *N. difficilis* at high temperatures (> 24°C) is closely tied to unfavorable tropical conditions, as has previously been reported in the zone by Gómez-Gutiérrez et al. (1995a).

A significantly different pattern in the larval distribution of *N. difficilis* was recorded during October 1999. Its high abundances appeared to be related to a more intense than normal California Current. During La Niña, the California Current core was shallow (~30–60 m) and closer to shore (~100–150 km). The salinity minimum depicting this core follows closely the 0.94–0.96 dynamic meter isolines, limiting the California Current meridionally (fig. 4b, 9910). The meandering equatorward flow favored local retention sites for nutrients, chlorophyll *a*, and species (fig. 5b, 9910). Thus, the highest abundances of *N. simplex* and *N. difficilis* were located eastward of the California Current core, which constrained productive, low-temperature upwelled waters, as well as an important portion of the euphausiid community, to a narrow region near the coast during the La Niña cruise. Similarly, Marinovic et al. (2002) found a high abundance of *N. difficilis* within Monterey Bay associated with the inshore intrusion of the California Current in central California waters during spring and summer of 1998. Seasonal changes in abundance of this species in the study zone have been noted (e.g., Brinton 1960, 1981; Gómez-Gutiérrez et al. 1995a) when the influence of the California Current was more intense.

Compared with the pattern of *N. difficilis* described above, the IA Group had significantly different changes in its abundance and distribution between periods (fig. 6 and tab. 2). It appears that the wide range of 10 m temperatures during the two cruises (22–27°C during 9710 and 16–21°C during 9910) was the main reason for the differences observed in their distribution. The latter is based in the tropical-subtropical affinity of the larvae. Indeed, the presence of warmer-than-usual waters during El Niño 1997 due to the intrusion of subtropical surface water (Durazo and Baumgartner 2002, their fig. 12) probably aided proliferation of this group once it entered the region. Moreover, during La Niña, a stronger-than-usual California Current limited the distribution range of this group to open ocean waters typical of the central Pacific. Bograd et al. (2000) described the development of a clockwise gyre off Punta Eugenia in October 1999, shown here in the dynamic height field in Figure 4b. The eddy brings central Pacific waters inshore and acts as a retention mechanism. This may be responsible for the high abundance spots of the IA Group at stations well off Punta Eugenia during La Niña cruise (fig. 6).

Although larvae in this group were not identified to species level, it is likely that *E. eximia* represented a large percentage of the population because of the high density of adults compared to other species in the group (tab. 1). *E. eximia* is known as an endemic species of eastern tropical Pacific waters and usually inhabits oceanic waters off southern Baja California (Brinton 1960; Gómez-Gutiérrez et al. 1999). Therefore, the large occurrence of the IA group during El Niño cruise could be favored because of a better survival of larval stages, mainly *E. eximia*.

El Niño/La Niña events play a substantial role in the circulation dynamics and ecosystem structure of the CCS. The results shown here largely reflect advective processes associated with variable flow of California Current waters and intrusion of water masses of different characteristics that modified the abundance and distribution patterns of euphausiid species between October 1997 and October 1999. This study shows that basinwide events, such as El Niño 1997–98 and La Niña 1999–2001, have strongly influenced the community structure of euphausiid in central Baja California waters.

ACKNOWLEDGMENTS

I greatly appreciate the work of numerous researches and technicians in the IMECOCAL program who obtained the zooplankton samples analyzed in this study. Thanks to the Zooplankton Laboratory at CICESE for the materials and space provided and thanks to G. Gaxiola for the chlorophyll *a* data. Margaret Knight and Annie Townsend at Scripps Institution of Oceanography provided valuable help in identifying euphausiid larvae. The comments and suggestions of R. Durazo to improve this manuscript are also appreciated. Thanks to the crew and officers of the B/O *Francisco de Ulloa* for their help at sea. Thanks to the two anonymous reviewers for their valuable comments and suggestions. This work was possible thanks to scholarships provided by OEA and by CONACYT under contract number G0041-T9607.

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LOCALLY AND REMOTELY FORCED ENVIRONMENTAL INFLUENCES ON CALIFORNIA COMMERCIAL FISH AND INVERTEBRATE LANDINGS

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ABSTRACT

This study extends the investigations of Norton and Mason (2003), who used empirical orthogonal function (EOF) analysis of the California commercial fish and invertebrate landings data (CACom database) to find two patterns of variability (EOF1 and EOF2) that describe major changes in species composition from 1930 through 2000. Temporal variations in EOF1 and EOF2 are closely correlated to climate-scale physical processes of the equatorial Pacific (remote) and the North Pacific (local) atmosphere and oceans, respectively. These findings suggest that changes in species composition of California landings begin as remote and local physical processes that are transmitted through the ecosystem to target species. Log$_e$-transformed sardine landings history is similar to the time variations in EOF1. As fish and invertebrate resources become fully utilized, variations in their landings become better indicators of environmental climate change off California; however, conservative resource management and fluctuating market demand may disrupt this close relationship. Consistent temporal associations of species groups with recurrent physical environmental conditions may allow timely detection of climate changes and thereby provide opportunities for proactive ecosystem management.

INTRODUCTION

Studies by Norton and Mason (2003) used empirical orthogonal functions (EOFs) to examine California commercial fish landings from 1930 through 2000. They found two modes of variability, EOF1 and EOF2, that explain more than 45% of the variance in composition of species making up more than 95% of the total landings. When time-varying coefficients or principal components of these EOFs, **C**1 and **C**2, were compared to indexes of physical change in the California fisher's harvest environment (CFHE) and to time series representing fishing effort and market factors, it was found that **C**1 and **C**2 are more closely correlated to the environmental indexes (correlation coefficient magnitude, $|r| > 0.8$) than to the effort and market indexes ($|r| < 0.6$). Variation in **C**1 and **C**2 show that the species composition of the landings changed continuously from 1930 to 2000, indicating that the California fishing industry adapted to profitable opportunities of changing CFHE conditions and expanding markets (Norton and Mason 2003). The purpose of this study is to extend investigations into how major changes in the species composition of California landings relate to the primary physical forcing of the CFHE.

The orthogonal property of EOF1 and EOF2 requires that changes in species composition will not be in phase throughout the 71-year series. If changes in the species composition of the California commercial landings, indicated by **C**1 and **C**2, are forced by the physical environment, then at least two modes of physical variability are likely. These modes may be related to combinations of (1) local atmospheric effects, such as wind forcing of the CFHE (Parrish et al. 1983; Norton and McLain 1994); (2) basin-scale forcing that causes variations in input of higher nutrient content, cooler water from the north (Chelton et al. 1982; Norton 1999; Parrish et al. 2000); and (3) locally and remotely forced changes in CFHE pycnocline and nutricline depth (Norton et al. 1985; Roemmich and McGowan 1995; McGowan et al. 1998). Norton and Mason (2003) found that the uncorrelated temporal patterns in **C**1 and **C**2 are uniquely correlated to indexes of southern California sea-surface temperature (SST, $r = 0.92$) and central California southward wind stress (SWS, $r = 0.85$), respectively. **C**1 species composition changes were also found to have significant correlation to the Pacific Decadal Oscillation (PDO; $r = 0.85$) index (Mantua et al. 1997). The dependence of the PDO index on both direct and indirect forcing from the equatorial ocean and atmosphere (Newman et al. 2003) suggests a connection of **C**1 to equatorial processes.

Temporal patterns in the California commercial landings shown by **C**1 and **C**2 correspond to patterns of variation in species not directly affected by California fisheries. Zooplankton biomass is affected by the same physical events in 1957–1962, 1973–1982, and 1998–2000 (McGowan et al. 1998) that are evident in **C**1 and **C**2. Reproductive success of central California seabirds (Ainley et al. 1995) also corresponds to **C**1 and

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[Manuscript received 2 February 2004.]

C2 variation. These examples suggest that EOF1 and EOF2 temporal patterns reflect variation of many noncommercial species of the California Current ecosystem and that EOF1 and EOF2 are not solely artifacts of directed harvest and fluctuating market demand (Norton and Mason 2003).

The California Current flows equatorward and extends up to 900 km seaward off the west coast of temperate North America. The offshore California Current environment, westward of 50–150 km, is separated from the coastal zone by an undulating transition band of maximum equatorward velocity. Shoreward of the transition zone, flow in the upper 500 m becomes increasingly poleward, except during frequent wind-forced upwelling events when surface currents in the upper 50–150 m flow equatorward over the poleward subsurface currents (Lynn and Simpson 1987; Strub et al. 1987). These three currents are the main components of the California Current system (CCS). The CFHE is that part of the CCS extending from the coast to 400–600 km offshore.

Remote forcing from the equatorial Pacific will affect the CCS by anomalous transmission of coastal long-waves, with wave length much greater than water depth, trapped by the eastern boundary (Shriver et al. 1991; Ramp et al. 1997) and by atmospheric teleconnections (Horel and Wallace 1981; Alexander 1992). As coastal-trapped waves propagate poleward through the CFHE, they lose energy to offshore propagating Rossby waves, which spread effects 300–400 km offshore (Fu and Qui 2002). In the case of downwelling long-waves, geostrophic adjustment depresses isotherms and isopycnals along the coast. This favors increased poleward transport, which leads to warming and increased sea level in the CFHE. Anomalous ocean-to-atmosphere heat transfer associated with SST anomalies in the equatorial Pacific Ocean teleconnect through the atmosphere to increase or decrease cyclogenesis over the northeastern Pacific Ocean (Alexander 1992). The teleconnection affects local North Pacific atmospheric forcing primarily during winter. Consequently, time series of surface oceanic and atmospheric variables from the North Pacific and from the equatorial Pacific may have considerable common variability.

Local large-scale forcing will have a different spatial pattern of effects than will remote forcing (Chelton et al. 1982; Enfield and Allen 1980; Parrish et al. 1983; Norton and McLain 1994; Miller et al. 1997; King et al. 1998; McGowan et al. 1998; Fu and Qui 2002), and it acts continuously and simultaneously on the entire northeastern Pacific Ocean. Variations in strength and duration of wind-field effects and the exchange of heat and mass between the North Pacific Ocean and atmosphere are the primary local forcing processes. Local atmospheric forcing thousands of kilometers distant may affect temperature and sea level in the CCS at lags of weeks to months. Because remote equatorial forcing of the North Pacific through the atmospheric teleconnection and local North Pacific forcing thousands of kilometers distant may lead to similar changes in the CCS, it is often difficult to distinguish remote from local forcing effects in CCS data sets. However, it appears from our analysis of the CACom data set of commercial fish landings that two forcing modes are detectable in our measures of CFHS biological variability.

METHODS

Time series of change in species composition over the 1930–2000 period are derived from the California commercial landings data by extracting the time-varying coefficients or principal components of the two empirical orthogonal functions (EOFs) explaining the most variance (**C**1, **C**2). These are compared to environmental climate indexes.

Commercial Landings

Summarized landings records were compiled from landing receipts by the California Department of Fish and Game. The Pacific Fisheries Environmental Laboratory of the Southwest Fisheries Science Center (Norton and Mason 2003; Mason 2004) has converted these summarized records to a computer-accessible database (CACom), available at http://www.pfeg.noaa.gov; it is the source of all landings data used in this report.

The effects of local biases in the landings data are reduced by the aggregation of the large number of landings transactions. By 1950, there were more than 100 locations where trip tickets had been completed and filed with the California Department of Fish and Game (tab. 1). During the 1930–2000 period, the number of boats reporting landings has varied from about 1,600 to 7,300 (Norton and Mason 2003). The large number of boats and the alternative markets for landing (selling) the catch have probably led to fewer systematic recording biases in averaged data.

EOF Analysis and Time-variable Coefficients

Let the data matrix [D'] consist of columns of market groups with annual catch for 1930-2000 in 71 rows (years). All columns are log-transformed,

$$\log_e [\mathbf{D}'] = [\mathbf{D}]. \qquad (1)$$

Then find correlation matrix **[R]** of **[D]** using matrix manipulations

$$[\mathbf{R}] = k[\mathbf{D}]^T[\mathbf{D}], \qquad (2)$$

where k depends on the dimensions of **[D]**, and $[\mathbf{D}]^T$ is the transpose of **[D]**.

TABLE 1

Number of Locations Reporting Landings in 1950 and Before

			Number reporting, by weight of landings		
CDFG statistical area	Northern limit	Southern limit	> 500 kg	> 5,000 kg	> 500,000 kg
Eureka	42.0°N (Del Norte County)	38.75°N (Mendocino County)	8	3	4
San Francisco	38.75°N (Sonoma County)	37.08°N (San Mateo County)	24	7	12
Monterey	37.08°N (Santa Cruz County)	35.78°N (Monterey County)	2	0	3
Santa Barbara	35.78°N (San Luis Obispo County)	34.03°N (Ventura County)	6	3	3
Los Angeles	34.03°N (Los Angeles County)	33.22°N (Orange County)	10	3	5
San Diego	33.22°N (San Diego County)	32.5°N (San Diego County)	7	0	2
Total			57	16	29

Source: From Scofield 1954.

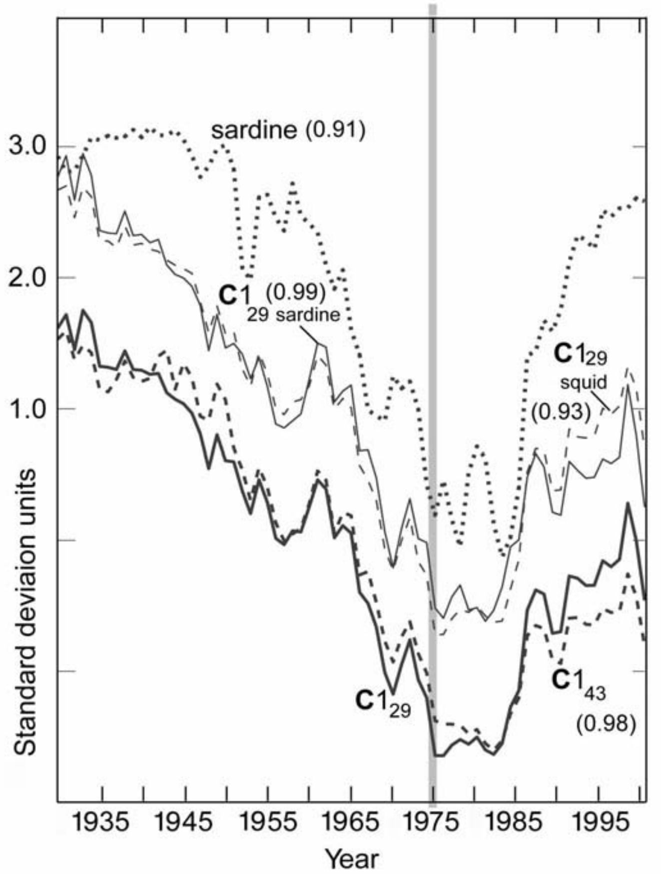

Figure 1. Time-varying coefficients, C1, for EOF1 computed from various landing data sets and $\log_e$-transformed sardine landings (*dotted line*). All series are standardized and offset in standard deviation increments for comparison. Bottom two lines show C1 computed from 29 ($C1_{29}$, *thick solid line*) and 43 ($C1_{43}$, *thick dashed line*) market groups. The middle series are $C1_{29}$, with either sardine (*thin solid line*) or squid (*thin dashed line*) landing series omitted from the 29 single-species market-group matrix. $EOF1_{29}$ and $EOF1_{43}$ explain 30% and 26% of the variance in their respective computation matrixes, $[D_{29}']$ and $[D_{43}']$. Correlation to $C1_{29}$ is given in parentheses. Log_e-transformed sardine series and $C1_{29}$ computed without sardines are the least similar ($r = 0.86$, $p < 0.05$) of these series. $C1_{29}$ is closely related to the sardine series ($r = 0.91$, $p < 0.01$).

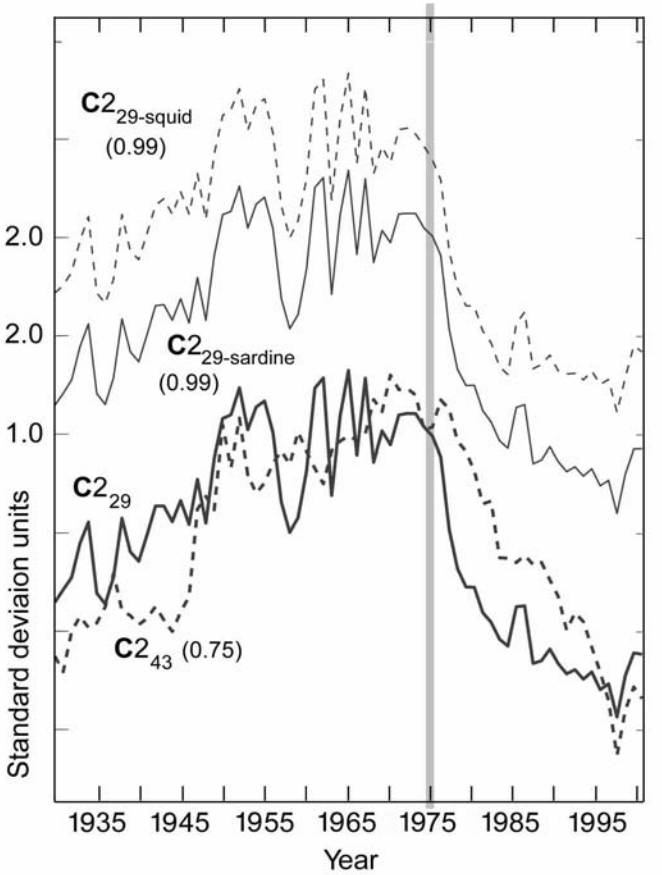

Figure 2. Time-varying coefficients, C2, for EOF2 computed from various landing data sets. All series are standardized and offset in standard deviation increments for comparison. Lower lines show C2 computed from 29 (D_{29}', *thick solid line*) and 43 (D_{43}', *thick dashed line*) market group computation matrixes. Upper series are C2 computed from the 29 single-species market-group ensembles, omitting sardine (*thin solid line*) and squid (*thin dashed line*) landing series. $EOF2_{29}$ and $EOF2_{43}$ explain 20% and 19% of the variance in their respective computation matrixes. Correlations with $C2_{29}$ are given in parentheses. $C2_{29}$ and $C2_{29}$ computed without the sardine series are correlated to the $C2_{43}$ series, with $r = 0.75$, $p < 0.10$. $C2_{43}$ series and $C2_{29}$ computed without the squid series are the least alike ($r = 0.68$) of the series shown.

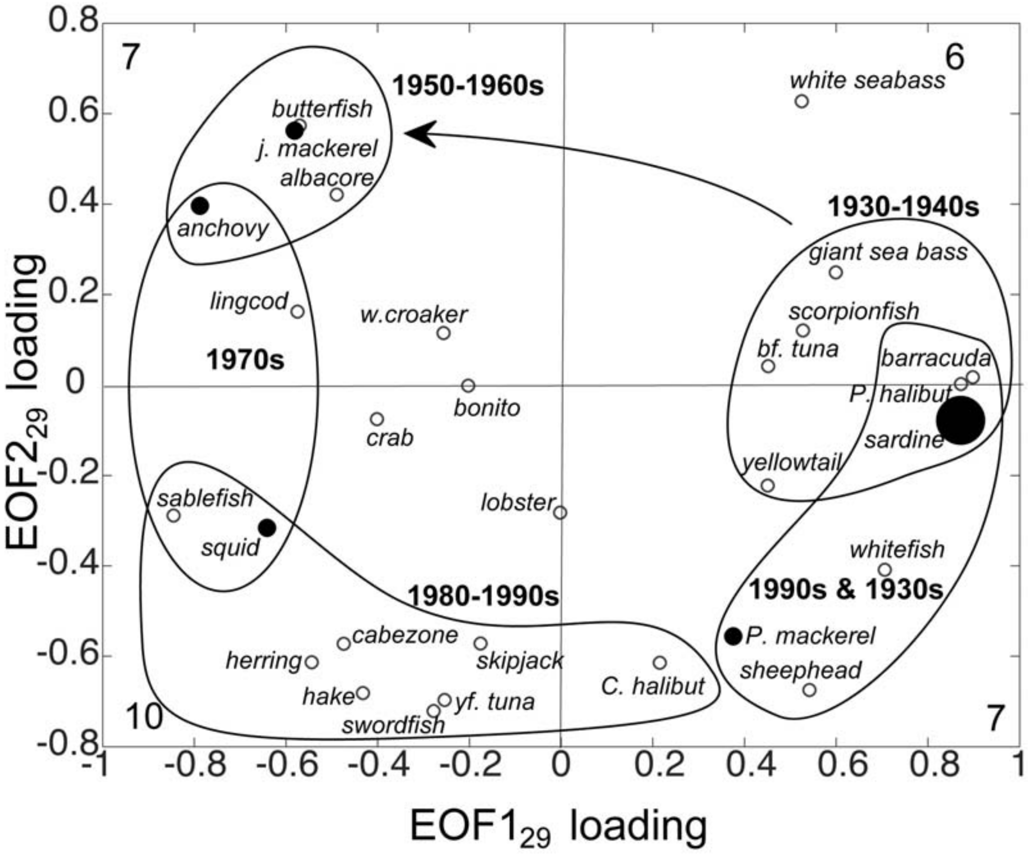

Figure 3. Species EOF loading values are plotted, with EOF1 on the horizontal and EOF2 on the vertical axes. The arrow and the enclosed species groups show the counterclockwise progression of species groups having landings maxima. Filled circles show species that have had total landings exceeding 10^9 metric tons; size of the filled circles indicates relative total catch among those species. Number of species in each quadrant is shown in the corners. Abbreviated common names for the 29 single-species market groups are albacore (*Thunnus alalunga*), anchovy (*Engraulis mordax*), barracuda (*Sphyraena argentea*), bluefin (bf.) tuna (*Thunnus thynnus*), bonito (*Sarda chiliensis*), butterfish (*Peprilus simillimus*), California (C.) halibut (*Paralicthys californicus*), cabezon (*Scorpaenichthys marmoratus*), crab (*Cancer magister*), croaker (*Genyonemus lineatus*), giant seabass (*Stereolepis gigas*), hake (*Merluccius productus*), herring (*Clupea pallasi*), jack (j.) mackerel (*Trachurus symmetricus*), lingcod (*Ophiodon elongatus*), lobster (*Panulirus interruptus*), Pacific (P.) halibut (*Hippoglossus stenolepis*), Pacific (P.) mackerel (*Scomber japonicus*), sablefish (*Anoplopoma fimbria*), sardine (*Sardinops sagax*), scorpionfish (*Scorpeaena guttata*), sheephead (*Semicossyphus pulcher*), skipjack (*Euthynnus pelamis*), squid (*Loligo opalescens*), swordfish (*Xiphias gladius*), white seabass (*Atractoscion noblis*), whitefish (*Caulolatilus princeps*), yellowtail (*Seriola dorsalis*), and yellowfin (yf.) tuna (*Thunnus albacares*).

Then the eigenvectors **[E]** and eigenvalues are derived from

$$[\mathbf{R}][\mathbf{E}] = [\mathbf{L}][\mathbf{E}]. \tag{3}$$

The diagonal elements of **[L]** are eigenvalues (l_n) that correspond to the column eigenvectors of **[E]**. EOF loadings (one value for each of n columns in **[D']**) are given by

$$\mathrm{EOF}n = (l_\mathrm{n})^{1/2}\, [\mathbf{E}_n], \tag{4}$$

where l_n gives the variance explained by EOFn. The first EOF, EOF1, has the largest l_n, EOF2 has the second largest l_n, and so forth. We use the method of North et al. (1982) to find that EOF1 and EOF2 are significant below the 0.05 probability level ($p < 0.05$). The time variation of EOFn over the sampling interval (time-varying coefficients) is given by

$$[\mathbf{Cn}] = [\mathbf{D}][\mathrm{EOFn}] \tag{5}$$

The following analyses focus on two data matrixes. The first data matrix, $[\mathbf{D}_{43}']$, has 43 columns corresponding to 43 market groups that are recorded consistently throughout the 71-year record. A market group may contain several species that have similar market characteristics. The 43-market-group matrix, $[\mathbf{D}_{43}']$, represents more than 85% of the total catch throughout the 71-year period, more than 90% of the catch during 65 years, less than 90% from 1980 through 1994, and more than 95% of the catch during 61 years. The second data matrix, $[\mathbf{D}_{29}']$, has 29 columns of annual landing totals for 29 single-species market groups (Norton and Mason

2003). Differences in the time-varying coefficients, C1 and C2, derived from $[D_{43}']$ and $[D_{29}']$ are shown in Figures 1 and 2. EOF1 and EOF2 loadings for $[D_{29}']$ are plotted as abscissa and ordinate, respectively, in Figure 3. EOF143, EOF243, EOF129, and EOF229 account for 26%, 20%, 30%, and 19% of the variance in $[D_{43}]$ and $[D_{29}]$, respectively. All loading values listed are from Norton and Mason (2003).

Physical Time Series

Because trends in the time variation of the EOFs persist over periods of 5-30 years, indexes showing persistence in physical processes were developed from available published data sets by accumulating anomalies from 1930 to 2000 or longer means.

Anomalies from means, **X**, were accumulated or integrated through time,

$$\mathbf{A}-\mathbf{X}(y) = \sum_{i=b}^{y} X(i) \tag{6}$$

where $\mathbf{A}-\mathbf{X}(y)$ is the accumulation of the anomaly time series **X**, *b* is the first year of the accumulation, and *y* is a year between *b* and 2001. This operation adds persistence (autocorrelation) to the physical series (Klyashtorin 2001; Hanley et al. 2002; Norton and Mason 2003).

The accumulated series may be interpreted in terms of processes that together cause negative or positive anomalies (Norton and Mason 2003). If a series trends or slopes in a positive (negative) direction, processes that led to positive (negative) anomalies dominate the interval. Seasonal and many interannual events are attenuated in the records, making accumulated series valuable for illustrating climate-scale (5–30 year) changes. These methods were used to derive the seven accumulated climate-index series described below.

Southward wind stress (SWS) was computed for an area off central California with consistently large numbers of observations through the sampling interval in the Comprehensive Ocean-Atmosphere Data Set (COADS). This area is bounded by the California coast and 39°N, 124°W; 37°N, 124°W; 37°N, 123°W; and 36°N, 123°N (Parrish et al. 2000; Norton and Mason 2003). By convention, greater SWS is indicated by larger negative values. A-SWS is the accumulated index.

Monthly mean sea-surface temperatures (SST) taken at the Scripps Institution of Oceanography Pier in La Jolla, California (32.9°N, 117.3°W), were developed into the La Jolla A-SST climate index. The monthly mean SST taken during August–October at Hopkins Marine Station in Pacific Grove, California (36.6°N, 121.9°W), was developed into the PG A-SST index. SST data are available at ftp://ccsweb1.ucsd.edu/pub/shore.

Sea-level atmospheric pressure (SLP) at Darwin, Australia (12.4°S, 130.9°E), is related to El Niño expression (Bjerknes 1969; Norton et al. 1985; Norton and McLain 1994). Darwin SLP is available from Kousky (2003) at http://www.cpc.ncep.noaa.gov. A-DSLP is the accumulated index.

Average equatorial SST (EqSST) from an area defined by 4°N to 4°S, 150°W to 90°W is also known as the JMA ENSO index (Hanley et al. 2002). EqSST is available at http://www.coaps.fsu.edu/~legler/jma_index1.shtml, and A-EqSST is the derived index.

August–October San Francisco, California (37.8°N, 122.4°W), mean sea level (SFSL) is available from NOAA/National Ocean Service Center for Operational Oceanographic Products and Services (CO-OPS), http://co-ops.nos.noaa/data-res.html. The only correction to SFSL was for a 1.2 mm per year increase (Roemmich 1992). The climate index is A-SFSL.

The Pacific circulation index (PCI), available at http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/climate/clm_indx.htm, is a temporal accumulation (eq. 6) of atmospheric flow anomalies over the North Pacific Ocean (King et al. 1998). Positive PCI-values suggest increased northward atmospheric flow along the coasts of the northern United States, Canada, and Alaska. (Note that the signs of La Jolla A-SST, PG A-SST, A-SFSL, and the PCI are reversed in fig. 5).

Significance levels for all correlations were adjusted for effective degrees of freedom, which were determined by the long-lag (20–30%) correlation method (Chelton 1983). In general, correlation coefficient magnitudes larger than 0.8 ($|r| > 0.8$) are likely to occur by chance at a rate of less than 1 in 20 trials ($p < 0.05$).

RESULTS

Norton and Mason (2003) showed that there is considerable agreement in the time-varying coefficients representing landings variation in species composition, **C**1 and **C**2, when they are computed from either 43 market-group or 29 single-species market-group matrixes, $[D_{43}']$ or $[D_{29}']$. In the following section we explore the dependence of **C**1 and **C**2 on dominant species in [D'] and illustrate how species associations develop in the landings through time. The linkages of **C**1 to remote equatorial and **C**2 to local North Pacific physical forcing regions are also examined.

Stability in EOF Calculations

Four input data matrixes, [D'], were compared to examine the effects of removing dominant species and species groups from the EOF computations. Time-varying coefficients, **C**1 and **C**2, were computed from $[D_{29}']$ and $[D_{43}']$ and from $[D_{29}']$ with either the sardine or squid landings series deleted. **C**1 patterns are more similar ($r \geq 0.93$, $p < 0.01$) than the **C**2 patterns ($r \geq 0.74$, $p < 0.10$) among the four alternatives (figs. 1

and 2). The largest differences in the computed **C**1 and **C**2 curves are in the last half of the record (figs. 1 and 2). We selected **[D_{29}']** to develop further because this matrix excludes noise introduced by combined-species market groups. The individual species of combined-species market groups may react differently to ocean climate changes.

Sardine made up 80–90% of total landings from 1930 to 1944 and 15–30% of landings from 1995 to 2000. Squid catch grew from 10% to 20% of the total landings in the mid-1970s to about 50% of landings from 1999 through 2000. When either squid or sardine are omitted from **[D_{29}']**, the **C**1-values are generally similar ($r \geq 0.93$, $p < 0.01$), with the largest differences in **C**1 in the 1990–2000 interval (fig. 1). Sardine landing patterns through 1930–2000 appear, in Figure 1, to be similar to **C**1_{29} ($r = 0.91$, $p < 0.01$). Even though sardine is a dominant species in terms of percentage of landings before 1950 and after 1995, it does not greatly influence the results of the C1 computation when it is deleted from the input matrix (fig. 1). **C**2-values were nearly identical ($r = 0.99$, $p < 0.01$) when either sardine or squid were omitted from the calculations (fig. 2). The **C**1 and **C**2 temporal patterns are apparently important in the life histories of many of the 29 species and are not solely characteristics of the species contributing the highest percentages to total landings.

Temporal Change in Species Groups

Each of the 29 species in **[D_{29}']** has had five-year or longer periods when its recorded landings were near maximum. The temporal distribution of these species-maxima show species characteristic intervals within the 1930–2000 period. The progression of species maxima through the 71 years is presented in Figure 3, where EOF1_{29} loading values for each species are plotted on a horizontal axis and EOF2_{29} loading values are plotted on the vertical axis. In the 1930s and 1940s (fig. 3, center right) sardines, scorpionfish, barracuda, and yellowtail were at or near their individual maximum landings. In the 1950s and 1960s (fig. 3, upper left) jack mackerel and albacore were near their maximum landings. During the 1970s (fig. 3, center left), anchovy and sablefish were near their maximum abundance in the landings. Skipjack, yellowfin tuna, swordfish, hake, and herring were common in the landings during the 1980s and 1990s (fig. 3, lower left and center). A cycle appears to be completing in the 1990s (fig. 3, lower right), with Pacific mackerel and sardine increasing in the landings. The progression of species-maxima may indicate integrated changes in the flow of productivity (renewable food energy) through California Current ecosystems.

Some species, such as butterfish, have always contributed less than 1% to the total landings, while increases or declines of other species, such as the mackerels and anchovy, cause large changes in the fishery, as described by MacCall (1996) and Chavez et al. (2003). The general implications of Figure 3 are consistent with these previous studies (MacCall 1996; Chavez et al. 2003) and they extend the conclusions of these previous studies to include a larger number of commercial fish and invertebrates.

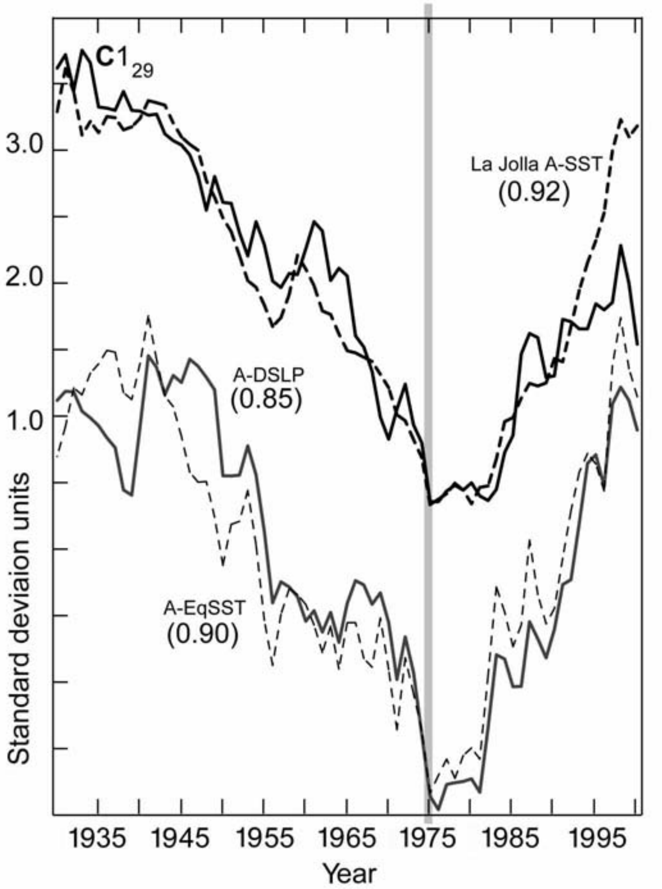

Figure 4. Comparison of C1 computed from 29 single-species market groups, C1_{29} (*upper solid line*), to environmental indexes formed by accumulation of anomalies. All series are standardized and offset in standard deviation increments for comparison. The index derived from sea-surface temperature (SST) at La Jolla, California (La Jolla A-SST), is the upper dashed line. The lower solid line is the Darwin SLP index (A-DSLP), and the lower dashed line is the equatorial SST index (A-EqSST). Correlation of C1_{29} with the physical indexes is in parentheses. Correlation of La Jolla A-SST to A-DSLP is $r = 0.93$ and to A-EqSST is $r = 0.95$ ($p < 0.015$).

Large-scale Environmental Forcing

Changes in landings composition shown by **C**1_{29} over the 1930–2000 period are closely related to persisting anomalous conditions in the CFHE as indicated by anomalies in SST measured at La Jolla, California (Norton and Mason 2003). The integrated anomaly index for southern California, La Jolla A-SST, and **C**1_{29} are also closely related to equatorial atmosphere-ocean processes indexed by A-DSLP and A-EqSST (fig. 4). All series shown in Figure 4 are well correlated ($r \geq 0.85$, $p > 0.05$).

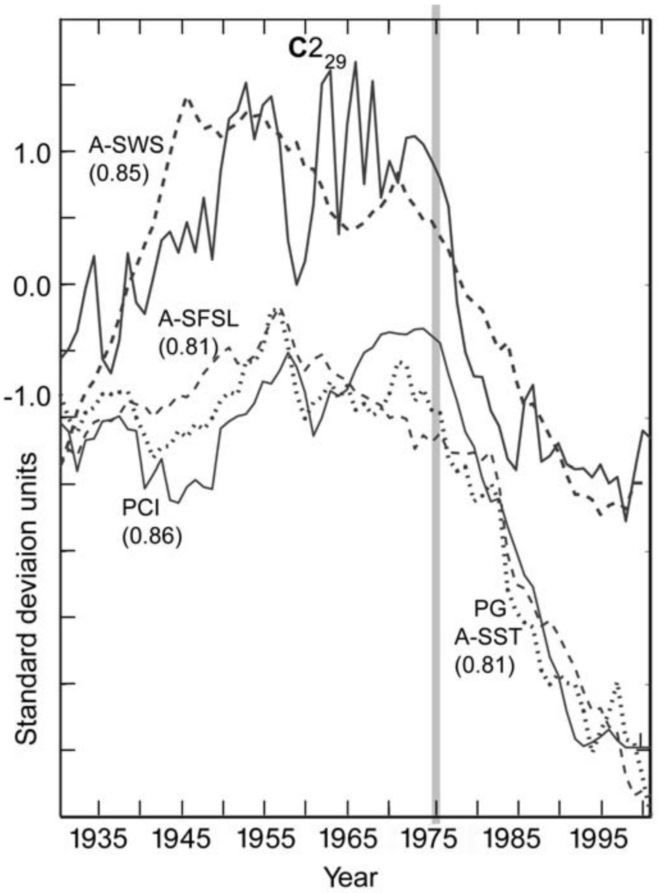

Figure 5. Comparison of C2 computed from 29 single-species market groups, $C2_{29}$ (*upper solid line*), to environmental indexes formed by accumulation of anomalies. All series are standardized and offset in standard deviation increments for comparison. The index of central California southward windstress (A-SWS) is the upper dashed line. The lower dashed line is the sign-reversed August–October San Francisco sea-level index (A-SFSL). The lower dotted line is the sign-reversed August–October Pacific Grove sea-surface temperature index (PG A-SST). The lower solid line is the sign-reversed Pacific circulation index (PCI). Correlation of $C2_{29}$ with the physical indexes is in parentheses.

These physical indexes are more similar to each other than any of them are to $C1_{29}$ because of the lower slope in $C1_{29}$ after 1990. The implication of causal connection among variables is supported by the progression of multiyear events that occur earlier in the equatorial indexes than in La Jolla A-SST and $C1_{29}$ (fig. 4).

Of several events that show progression from equatorial to California Current indexes, the best example may be the well known 1955–1960 warming event (Sette and Isaacs 1960; Parrish et al. 2000). After three to four years of negative anomaly, this event is shown by positive excursions that first appear during 1955–1956 in the equatorial regions. It continues in 1956–1958 in the La Jolla A-SST and was evident during 1958–1960 in the California fish landings, $C1_{29}$ (fig. 4).

Landings changes indicated by $C2_{29}$ are closely related to changes in southward wind stress (SWS), August–October A-SFSL and PG A-SST, and the Pacific circulation index (PCI) (fig. 5). The relationship to the PCI suggests that forcing of $C2_{29}$ is related to large-scale atmospheric processes occurring over the northeastern Pacific Ocean (King et al. 1998; Chelton et al. 1982; Parrish et al. 2000) rather than to unique California Current processes. The $C2_{29}$ temporal pattern also corresponds to variation in the concentration of fish larvae and other zooplankton over the 1954–1998 period (McGowan et al. 1998; Norton and Mason 2003).

The PCI is a large-scale atmospheric indicator for the North Pacific (King et al. 1998), but the large-scale North Pacific Ocean indicator that covers the 1930–2000 period has not yet been identified. Instead, we present the A-SWS, A-SFSL, and PG A-SST indexes because these are derived from the only available published data that is continuous for 1930–2000.

Association of Species and Environmental Indexes

Observations that species-groups at their maximum landings abundance change through time may be quantified and modeled in terms of physical indexes (figs. 3–5). The horizontal axis (EOF1) in Figure 3 corresponds to La Jolla A-SST. Positive trend in La Jolla A-SST (fig. 4) corresponds to species groups on the right side of Figure 3 and shows persistence of remote warming influence. Similar scales might be developed for the remote climate influence of A-DSLP and A-EqSST. EOF2 is associated with southward wind stress (SWS). By convention, increased SWS has anomalously high-magnitude negative values. Therefore, persisting anomalously strong SWS, indicated by negative slope in A-SWS, will be associated with species in the lower two quadrants of Figure 3. A-SFSL, PG A-SST, and PCI indexes are negatively correlated to EOF2; a quantitative scale for indexes would be the reverse sign to the ordinate shown in Figure 3. The potential availability of any species might be modeled as functions of species association and environmental indexes. This modeling approach will be pursued as additional landings data become available.

DISCUSSION

The California commercial finfish and invertebrate landings data (CACom) are not a rigorously select scientific sample, but our results are reasonably clear and indicate low noise levels. Several conditions contribute to this result. First, thousands of fishers and scores of fish dealers have been in compliance, or at least proportional compliance, with state regulations requiring recording of the weight of commercial landings by market category (tab. 1). Minimum estimated recording has been 5,000–35,000 landings records per year (assuming five commercial landings per boat each year; Norton and Mason 2003). Second, California Department of Fish and Game statisticians have been precise and consistent in keeping landings records over the 1930–2000 period. Third, intensive utilization of California fisheries resources contributes to close correlation between species composition of the landings, as indexed by **C**1 and **C**2, and physical environmental indexes.

Intensive utilization of CFHE fish and invertebrate resources occurred as the result of increasing consumption of fish and fish products and exploitation of world markets by California fish dealers (Dietz et al. 2003). From 1930 to 2000 the human population of California increased sixfold, but the overall weight of fish landed in California ports in the 1990s was half that of the 1930s and 1940s. From 1930 to 2000, per capita annual consumption of edible fish in the United States grew from 4.5 kg in 1930 to 7.1 kg in 2000. In addition, the U.S. population has more than doubled from 1930 to 2000, leading to a 340% increase in U.S. fish consumption.

The fact that almost half of the total fish and invertebrate products consumed in the United States is imported (O'Bannon 2001) suggests that demand exceeds supply for most U.S. fisheries. Products receiving labor-intensive preparation and species not available to U.S. fishers are obtained from foreign sources at a lower cost and therefore do not increase demand on CFHE resources. These exceptions, however, do not hinder the tentative conclusion that many California fisheries have become fully utilized during the 1930–2000 period.

During 1930–2000, the three-fold increase in the world's human population and the extension of foreign markets have created continuing utilization incentives for California commercial fishers (Dietz et al. 2003). For example, there is a major market in Japan for urchins and another in China for squid. The sea urchin (*Strongylocentrotus* sp.) fishery is the only major California fishery not included in the present analyses, because there was no commercial fishery for urchins before 1970. Much of the recent sardine catch has been exported to Australia (Leet at al. 2001). Because these species constitute large percentages of total California landings (Mason 2004), their sales destinations illustrate the influence of foreign markets on CFHE resources. The statistics reviewed above and the reasonably clear results of this report lead to the proposition that because of full and intensive resource utilization, the CACom landings records yield reasonable indications of relative changes in CFHE commercial fish stocks.

Sardine Availability and Physical Processes

Total catch of sardines over the 1930–2000 period exceeded 8 million metric tons (t), with most of the landings occurring between 1930 and 1950. Total landings of sardine were five times greater than landings of either Pacific mackerel or anchovy, which were second and third, respectively, in total landings (fig. 3). The largest catch of sardines was in 1941, when 572,550 t were reported. Landings declined to fewer than 100 t in the 1970s (fig. 1). The population rebounded in the 1980s and 1990s when average annual landings totaled 13,400 t and 30,400 t, respectively (Wolf et al. 2001). Since the total catch of sardines has been nearly equivalent to the total catch of all other species during 1930–2000, it might be expected that the sardine landing pattern would dominate **C**1 and **C**2 calculations but this is not the case. **C**1 and **C**2 patterns remain when the sardine landings series is excluded from the calculations (fig. 1).

Sardine management regulations followed catch declines from 1940 to 1973 and preceded increases in landings after 1985. Before 1967 the state did not limit total sardine landings, but in 1967 incidental catch was set at 15%, and landings for bait were limited to 250 t. In 1974 a moratorium was placed on all directed sardine fisheries, but 15% bycatch was allowed. Following initial rebound of sardine stocks, directed fisheries resumed in 1986 with a quota of 1,000 t. After 1991, quotas were increased until 1999, when 51,476 t were landed (Wolf et al. 2001; Mason 2004). Market demand and responsive regulation have allowed landings to follow sardine availability (fig. 1).

The sardine time series is closely correlated to the same physical indexes that are closely related to **C**1_{29}: La Jolla A-SST, $r = 0.90$; A-DSLP, $r = 0.87$; and A-EqSST, $r = 0.86$ ($p \leq 0.05$), suggesting a strong relationship between sardine availability and climate processes forced from the equatorial ocean. Figure 1 shows that the sardine series and **C**1_{29} without sardine are closely related ($r = 0.86$, $p < 0.05$), indicating that many of the other 28 species used in calculating the **C**1_{29}-pattern are affected by the same environmental factors that affect sardine abundance. Many other species throughout California Current ecosystems probably follow similar patterns of abundance in response to the environmental effects of remote climate forcing.

Climate Forcing

It is not within the scope of this report to attempt a detailed account of California Current processes that have changed on climate scales during the 1983–2000 rebound of the sardine fishery or during other changes in landings composition (figs. 1–3), but there are some generalities worth noting. Local North Pacific forcing affects large areas of the North Pacific Ocean, including the California Current, on a continuing basis. The remote signal comes partially along the eastern ocean margin and spreads westward to become a dominant environmental influence in the CFHE (Fu and Qui 2002). Atmospheric components of remote forcing are also important, particularly during the northern winter (Alexander 1992).

The PCI index represents large-scale aspects of local North Pacific forcing. Southward wind stress off central California (A-SWS) and San Francisco sea-level variation indexed by A-SFSL show the large-scale local signal in the California Current system and within the CFHE. The Darwin sea-level pressure indexed by A-DSLP and the equatorial SST indexed by A-EqSST are unambiguous representations of equatorial climate signals. The remote climate signal is clearly represented within the CFHE by the La Jolla A-SST.

CONCLUSIONS

The species composition of the California finfish and invertebrate commercial fishery has followed two dominant patterns of climate-scale variation that are related to remote equatorial Pacific and local North Pacific large-scale oceanic and atmospheric processes. In addition, there are five related results. First, the empirical orthogonal functions (EOFs) explain more than 45% of the variance in landings data constituting more than 85% of the total landings. The low noise levels in the data, summarized landings indicated by the large percentage of variance explained by EOF1 and EOF2, suggest that consistent landings of more than 25 species during the 71-year study period and the demand-responsive fishery contribute to the utility of the CACom data. Second, the progression of species maxima in the landings is tied to environmental conditions that appear to be completing a cycle and returning in the 1990s to physical and biological conditions similar to those of the 1930s and 1940s. Third, landings patterns (EOFs) are robust to changes in species groups and to the removal of dominant species from the input data matrixes. This indicates that the characteristics of the EOFs and their temporal variability (**C**1 and **C**2) are shared by many of the commercially landed species and possibly by other major components of California Current ecosystems. Fourth, remote and local modes of atmosphere-ocean forcing correspond to time variation in EOF1 and EOF2, respectively. This association, together with the grouping of species, presents predictive possibilities that will provide opportunities for proactive ecosystem management. Fifth, the history of sardine landings is similar to the time variation in EOF1 (**C**1). Sardine landings appear to be closely related to climate events occurring first in the equatorial atmosphere-ocean system and propagating into the California Current from the south. This relationship implies that fluctuations in sardine abundance within the 1930-2000 interval were environmentally dependent and not caused primarily by the directed fishery or its management.

ACKNOWLEDGMENTS

We thank Michael Laurs, director of the Pacific Fisheries Environmental Laboratory (PFEL) of the Southwest Fisheries Science Center, for his help and encouragement in this study. Thanks are also due to Richard Parrish, Frank Schwing, and George Watters (PFEL), Gary Sharp (Center for Climate/Ocean Resources Study), and the editor and reviewers of *CalCOFI Reports*, who have given valuable guidance.

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ON THE EXISTENCE OF PACIFIC SARDINE GROUPS OFF THE WEST COAST OF BAJA CALIFORNIA AND SOUTHERN CALIFORNIA

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ABSTRACT

Three possible Pacific sardine groups were detected using monthly catch and sea surface temperature (SST) data from landing ports of Magdalena Bay, Cedros Island, and Ensenada in México, and San Pedro in the United States. With the use of temperature-at-catch criteria, the groups were clearly defined by monthly periods when maximum catches were observed and at specific intervals of SST: one at temperatures above 22°C, one between 17° and 22°C, and a third below 17°C. Assuming that the observed patterns are indicative of sardine stock structure, this method also serves as a practical approach to partitioning and attributing the catch data of each fishing zone to each sardine group, thus improving estimates of population abundance from stock-assessment models. A conceptual model of time-space distribution is proposed to describe the occurrence of Pacific sardine along the west coast of Baja California and southern California. This model mainly explains the seasons of higher abundance of the resource in the different fishing areas.

INTRODUCTION

Pacific sardine (*Sardinops sagax*) is distributed in the northeastern Pacific Ocean, from southeastern Alaska to the southern tip of Baja California and into the Gulf of California (Kramer and Smith 1971; Parrish et al. 1989). Pacific sardine has a wide range of distribution, and it is important to know whether this population consists of one or several stocks and if multiple stocks do exist to define their corresponding distributions.

Some studies suggest that prior to the collapse in 1952 of the Pacific sardine fishery in California, the population consisted of several subpopulations. Radovich (1982) revised several publications (Felin 1954; Sprague and Vrooman 1962; Radovich 1962; Vrooman 1964) and identified four sardine subpopulations along Pacific sardine's distribution range as well as defined the area occupied by each one. However, Hedgecock et al. (1989) found low genetic variability among broadly distributed samples of sardine, contradicting the hypothesis of different latitudinal subpopulations of Pacific sardine. Lluch-Belda et al. (1991) proposed a hypothetical model to explain fluctuations of abundance in the Pacific sardine population. They proposed that during cold periods the population withdraws toward the south, subsequently reducing its area for successful spawning. Conversely, during warm periods sardine expands its spawning, residence, and feeding habitats. Rodríguez-Sánchez et al. (2001) supported this hypothesis using data from the catch of juvenile sardines by tuna baitboats during 1931–1979. Félix-Uraga et al. (1996) described migratory movements of Pacific sardine along the western coast of Baja California; they proposed the existence of three stocks in this region, noting that in Magdalena Bay two sardine stocks are present, one during winter and another during summer.

Along the west coast of Baja California and southern California (fig. 1), the fishery for Pacific sardine has experienced a sustained increase in capture since 1984, when at least 3,650 t were landed; in 2002, 148,100 t

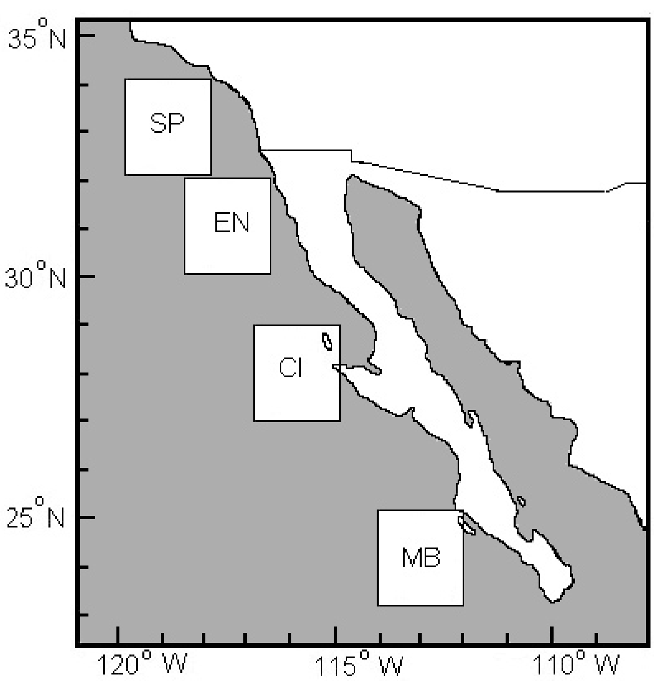

Figure 1. Landing ports of Pacific sardine on the west coast of Baja California and southern California. Magdalena Bay (MB), Cedros Island (CI), Ensenada (EN, and San Pedro (SP).

were landed. We proposed that, on the basis of catch and temperature information recorded during 1981–2002 for Magdalena Bay, Cedros Island, and Ensenada in Mexico and San Pedro in the United States, there are three possible Pacific sardine groups along the west coast of Baja California and southern California.

MATERIAL AND METHODS

Monthly catch data from Magdalena Bay, Cedros Island, and Ensenada were obtained from cannery records by Centro Interdisciplinario de Ciencias Marinas (CICIMAR) and Centro Regional de Investigaciones Pesqueras de Ensenada (CRIP) personnel from 1981 to 2002. Catch data from San Pedro were provided by Kevin Hill, Southwest Fisheries Science Center. Monthly mean of sea surface temperature (SST) data from these regions (2° latitude by 2° longitude square) were obtained from the Hadley Centre for Climate Prediction and Research (HadISST) for the same period. The selected squares were 23–25°N by 112–114°W for Magdalena Bay, 27–29°N by 115–117°W for Cedros Island, 30–32°N by 117–119°W for Ensenada, and 32-34°N by 118–120°W for San Pedro (fig. 1).

The time series of the monthly mean catch was plotted for each fishing zone for the period 1981–2002. The monthly catch information was grouped in matrixes and added by intervals of 1°C (i.e., 17°C = 16.5–17.4°C) of SST for each year and fishing zone during this period and plotted using contour graphs. Another three matrixes were made to integrate the catch for each month from 1981 to 2002, previously grouped by 1°C intervals, for Magdalena Bay, Ensenada, and San Pedro. The matrixes were plotted on a contour graph for comparative purposes for Magdalena Bay and Ensenada together, and for Magdalena Bay and San Pedro. The data from Cedros Island were scarce, so its was not included in this analysis.

The total monthly catch by degree of SST was plotted for 1981–2002 for each fishing zone and for all the zones combined. The monthly mean of SST was plotted for each fishing zone for the whole period. On this basis of this information, we propose a simple conceptual model to describe the time and space variation of several Pacific sardine groups along the west coast of Baja California and Southern California.

RESULTS

Landings by Area and Season

The bulk of monthly sardine landings in Magdalena Bay occur midyear, but a lower second peak occurs at the end of the year (fig. 2); in this zone, the catch increased to more than 50,000 t during 2002. The Cedros Island catch peaks during the spring and fall months. In 1987 the maximum catch was 2,856 t. Fishing activities for sardine in this area were ended in 1995, when the unique cannery closed because of economic constraints. For Ensenada, the bulk of the catch occurs around the beginning and end of each year, though the catch is higher at the end of the year. At San Pedro the maximum catch occurs in March, and a lower second peak occurs in October; the minimum catch is in June. Overall, the monthly mean catch in Magdalena Bay varied inversely with that of Cedros Island, Ensenada, and San Pedro. In all the fishing zones, two catch peaks were observed in the Pacific sardine catch in different seasons of the year (fig. 2).

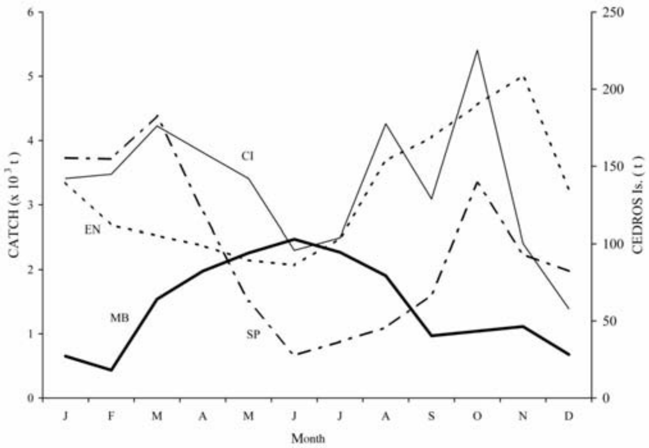

Figure 2. Monthly mean catch from Magdalena Bay (MB), Cedros Island (CI), Ensenada (EN), and San Pedro (SP).

Landings by Area and SST

The contour plot of catch by temperature and year for Magdalena Bay indicates (eye-balling) that two groups of sardine were present in most years: the first at SSTs of 17–22°C; the second at SSTs higher than 22°C. At Cedros Island, only one group was observed, at SSTs of 17–22°C. The data from Ensenada and San Pedro indicate two groups: the first at 17–22°C, and the second at 13–17°C (fig. 3).

On the basis of SST range, we identified (by eyeballing) three Pacific sardine groups in the combined contour plots of catch by temperature and month for Magdalena Bay versus Ensenada and Magdalena Bay versus San Pedro (fig. 4). The group present in Magdalena Bay at SSTs above 22°C was captured mainly from July to December. The second group, present in Magdalena Bay at SSTs of 17–22°C, was captured primarily from February to June. This 17–22°C group is probably the same as that observed from July to November off Ensenada and San Pedro. A third group was present in Ensenada and San Pedro at SSTs of 13–17°C and was caught mainly from December to May (fig. 4).

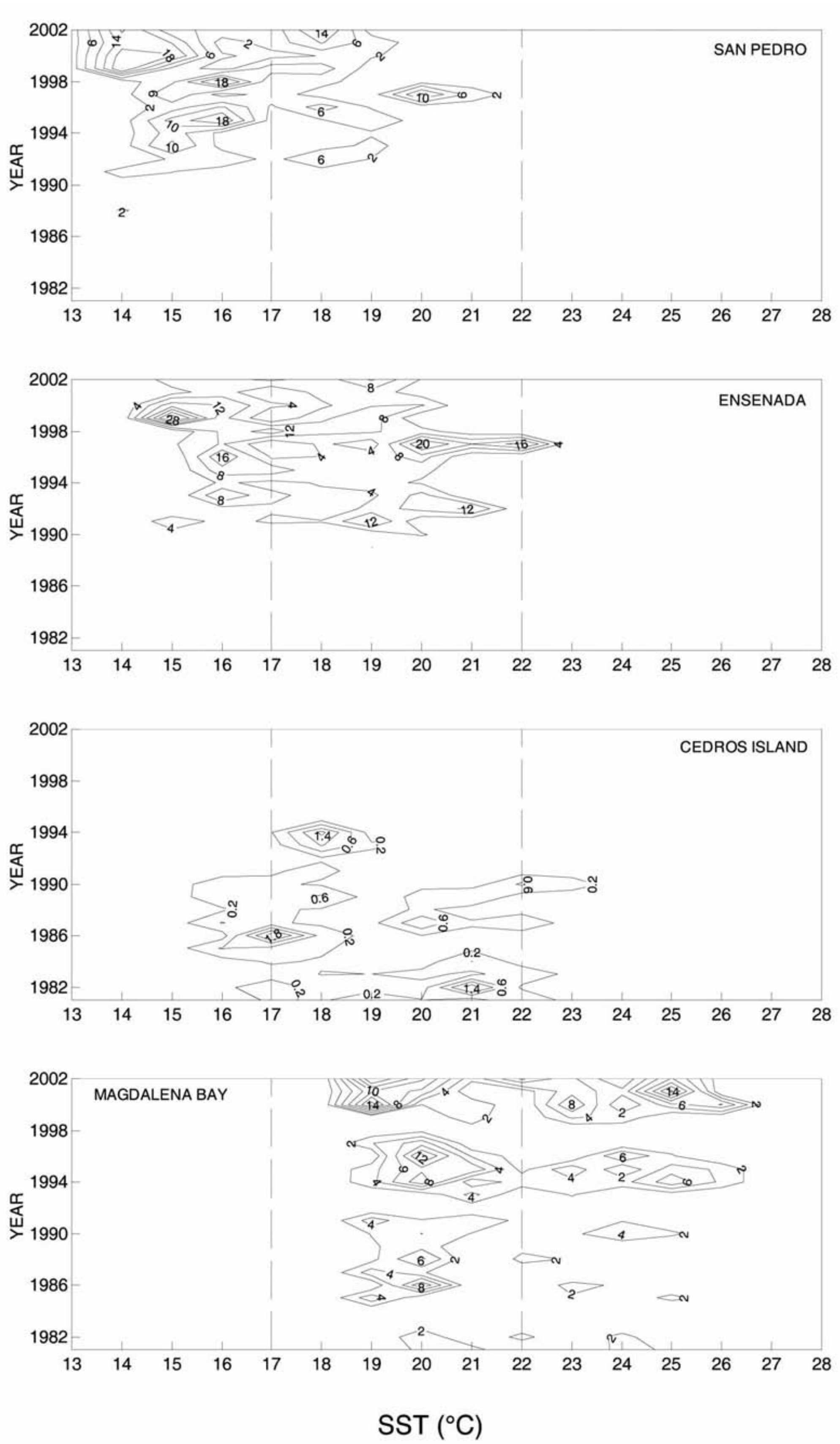

Figure 3. Catch isolines (thousands of tons), added by 1˚C intervals of SST at San Pedro, Ensenada, Cedros Island, and Magdalena Bay.

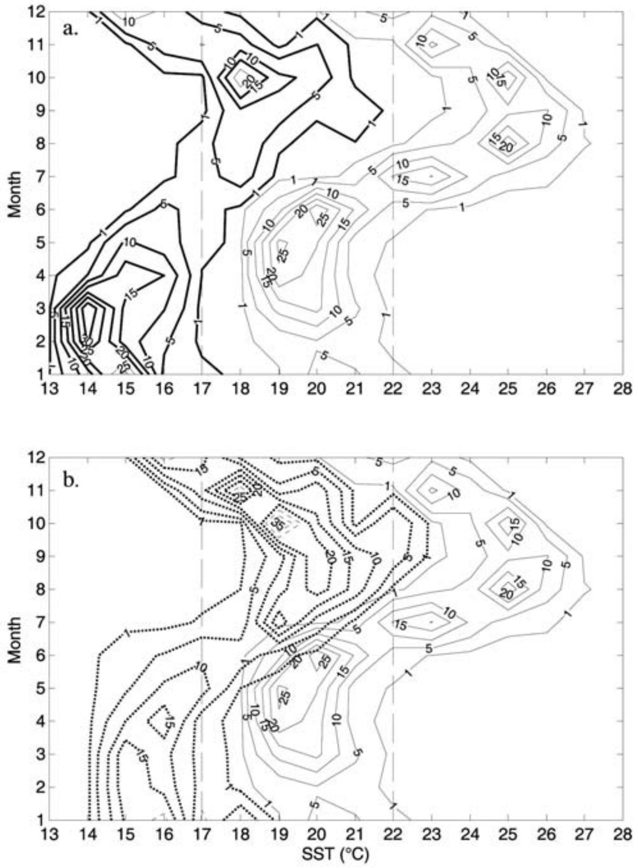

Figure 4. Catch isolines (thousands of tons) by SST and month during 1981–2002 for (*a*) San Pedro (*thick line*) and Magdalena Bay (*thin line*) and (*b*) Ensenada (*dotted line*) and Magdalena Bay (*thin line*).

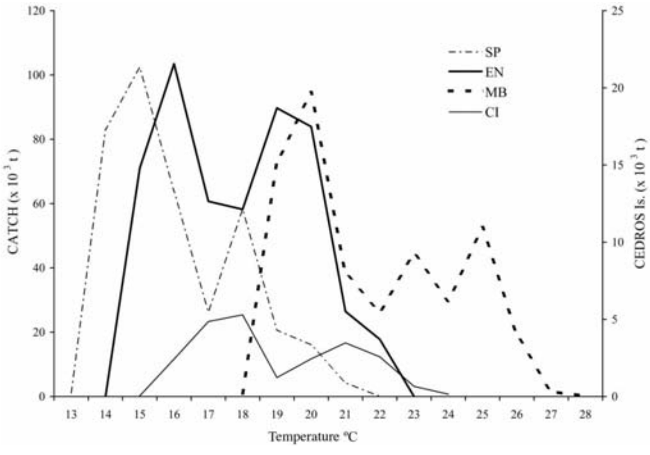

Figure 5. Pacific sardine catches added by 1°C intervals of SST at landing ports: San Pedro (SP), Ensenada (EN), Cedros Island (CI), and Magdalena Bay (MB).

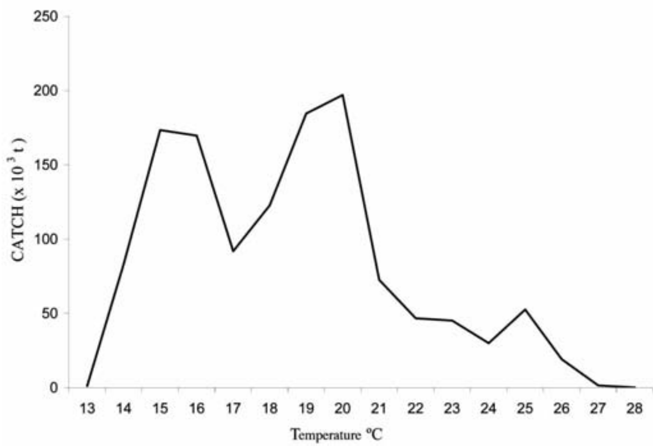

Figure 6. Pacific sardine total catches added by 1°C intervals for the four landing ports during 1981–2002.

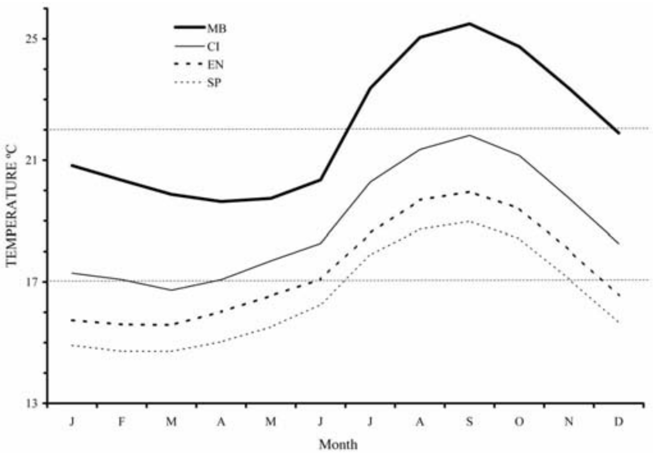

Figure 7. Monthly mean of SST at landing ports: San Pedro (SP), Ensenada (EN), Cedros Island (CI), and Magdalena Bay (MB).

In summary, the total catch integrated by SST, landed in Magdalena Bay, Ensenada, and San Pedro, showed two peaks in each fishing zone at different temperature ranges. The two peaks at Cedros Island correspond to the same temperature range (fig. 5). Plots of total landings for all fishing zones, from Magdalena Bay to San Pedro, at 1°C intervals of SST, clearly showed three peaks of catch (fig. 6). We assume that each peak corresponds to a different group of Pacific sardine.

The monthly mean SST showed that in Magdalena Bay SSTs were higher than 22°C from July to December and were 17–22°C from January to June. Off Cedros Island, SSTs were 17–22°C for nearly the entire year. At Ensenada, SSTs were 17–22°C from June to December and were below 17°C from January to May. At San Pedro, SSTs below 17°C occur from December to June, and those above 17°C from July to November (fig. 7).

DISCUSSION

As is well known, catch data is a crude measure of abundance (Lluch-Belda et al. 1989). However, we considered catch data to be a good index of the availability of Pacific sardine at Magdalena Bay, Cedros Island, Ensenada, and San Pedro. The pronounced seasonality of the catch among the four zones (fig. 2) indicates changes in availability and probably means latitudinal movements among these locations. The ability of the Pacific sardine to realize rapid, large-scale migrations was demonstrated by Clark and Janssen (1945).

Changes in sardine availability are quite evident in Figure 2; the catch in Magdalena Bay was inversely related to the catch in Cedros Island, Ensenada, and San Pedro. In Magdalena Bay, higher catches occurred from March to August, and lower catches from September to February; at Cedros Island, Ensenada, and San Pedro, higher catches occurred from September to March. This observed seasonality in the catch from Ensenada and San Pedro is similar to that reported for southern California (Clark and Janssen 1945; Clark 1952).

Several researchers have been indicated that oceanic environmental conditions affect the distribution of Pacific sardine (Radovich 1982; Lluch-Belda et al. 1989; Lluch-Belda et al. 1991; McFarlane 1999). In the contour plots of catch by temperature and year, it is clear that there are two catch groupsin each fishing zone (fig. 3); these could represent two groups of Pacific sardine adapted to different temperature intervals.

Despite a low level of genetic variation, Hedgecock et al. (1989) found that the current Pacific sardine population shows a north-south cline in size-at-age that is as large as that observed in the historical, precollapse population. Felin (1954) noted that a significant difference in sardine growth rates may represent a phenotypic response of a plastic genotype to varying hydrographic conditions and that it could be useful as an indicator to separate homogeneous populations of certain fishing areas without implying significant genetic differences. Similarly, we propose that it is possible to separate Pacific sardine groups according to the temperature-at-catch criteria, because Pacific sardine seems to be adapted to different temperature ranges.

Figures 4, 5, and 6 identify three different groups of sardine along the west coast of Baja California and southern California, each one adapted to a different temperature interval. The warmer group, adapted to temperatures ranging from 22° to 27°C, was present in Magdalena Bay from July to December, when higher SSTs are recorded at this latitude. This group may be coming from the Gulf of California, as suggested by Ahlstrom (1954, 1957; cited by Hedgecock et al. 1989), particularly during cold years.

The temperate group, adapted to temperatures ranging from 17° to 22°C, was present at all four fishing zones but at different seasons of the year. This group was captured in Magdalena Bay mainly from March to June, in the lower SST recorded in the area. At Cedros Island it was the only group observed during two seasons of the year. Off Ensenada and San Pedro it was caught mainly from August to December, when higher SSTs are present.

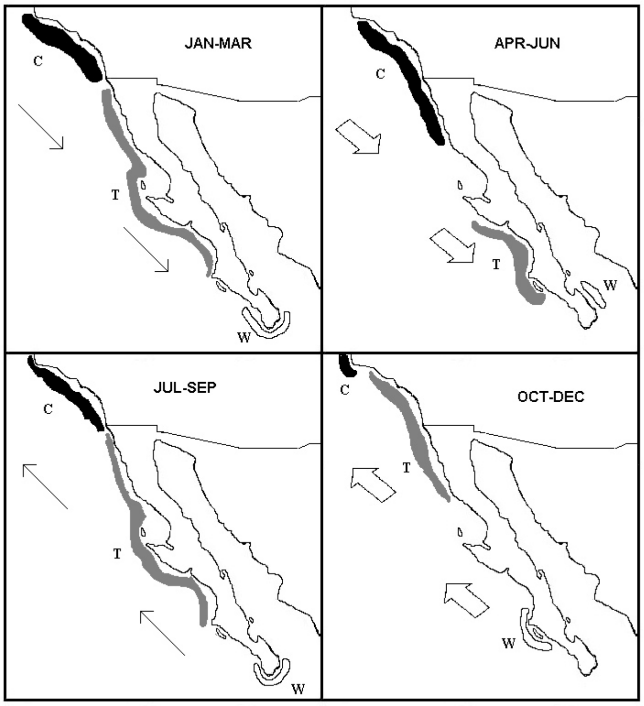

Figure 8. Time-space model of Pacific sardine displacements to explain the presence of three possible stocks on the basis of monthly periods of maximum landings and observed SST. C = cold group, T = temperate group, and W = warm group.

The colder group, adapted to SSTsranging from 13° to 17°C, was caught off Ensenada and San Pedro mainly from January to April, when lower SSTs were present. Using data from IMECOCAL (Investigaciones Mexicanas de la Corriente de California) surveys, two groups of sardine eggs were identified (van der Lingen and Castro 2004; fig. 2), the first in temperatures above 17.5°C, which could have been spawned by the temperate sardine group (17–22°C), and the other below 17.5°C, which would have come from the colder group (13–17°C).

The intermediate group (17–22°C) seems to be the most important for its contribution to the catch along the west coast of Baja California, and perhaps has an important impact on southern California catches. We believe that the colder group (13–17°C) contributes more to the San Pedro catch than to the Ensenada catch (figs. 2, 4, and 5).

The thermal subdivision of the sardine population was used to build a conceptual distribution model in space-time for the three sardine groups (fig.8). The model shows that the southward movement of the three groups begins in winter with the strengthening of flow of the California Current. In spring, with the full influence of the California Current, all the groups reach their southernmost distribution. In summer, the northward movement of the three groups begins with the onset of the equatorial countercurrent flow. In fall, all groups reach their northernmost latitudinal distribution. A tagging study for Pacific sardine is strongly recommended to probe this model.

Our proposed model is similar to that reported by Radovich (1982). Our model also agrees with the perspective presented by Sprague and Vrooman (1962), Vrooman (1964), and Mais (1972): that the different sardine groups do not generally distribute in the same space and at the same time, even though the distribution areas are shown as overlapping, since all stocks move toward the north or the south simultaneously, with little exchange among the three groups.

Finally, if our proposal is true, that each sardine temperature group is adapted to a specific temperature interval, it represents a practical approach to separating and attributing the monthly catch data (catch-at-age) from each fishing zone by sardine group. Thus, it is possible to better evaluate the stock-specific population abundance using virtual population analysis and compare this with previous estimates of sardine abundance (Barnes et al. 1992; Barnes et al. 1996; Deriso 1993; Deriso et al. 1996) using information from fishing zones rather than just stock assessments.

ACKNOWLEDGMENTS

Financial support was provided by Coordinación General de Estudios de Posgrado e Investigación del Instituto Politécnico Nacional. We thank Kevin Hill (National Marine Fisheries Service, Southwest Fisheries Science Center, NOAA) and Tim Baumgartner (Inter-American Institute for Global Change Research) for the support that we received in our participation in the Trinational Sardine Forums carried out in San Pedro, California. Roberto Félix-Uraga, Víctor M. Gómez-Muñoz, Casimiro Quiñónez-Velázquez, and Felipe Neri Melo-Barrera are scholarship holders of Comision de Operacion y Fomento de Actividades (COFAA) and Estimulos al Desempleño de los Investigadores (EDI).

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RETENTION OF LARVAL ROCKFISHES, *SEBASTES*, NEAR NATAL HABITAT IN THE SOUTHERN CALIFORNIA BIGHT, AS INDICATED BY MOLECULAR IDENTIFICATION METHODS

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ABSTRACT

Larval (<16 mm SL) *Sebastes* spp. that could not be identified visually were identified with molecular genetic methods from plankton samples collected during a California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruise in April 1999. Our goals were to characterize natal habitat and to determine the abundances of individual rockfish species in CalCOFI ichthyoplankton samples. This is the first time the entire complex of *Sebastes* larvae collected during a CalCOFI cruise has been identified to species. For three abundant species, we found a significant association between abundance and stations within the Southern California Eddy (SCE), and a significant relationship between the distribution of 1-d-old larvae and potential adult habitat for the most narrowly distributed of the three species. These results suggest that the interplay of natal spawning habitat overlaid by the persistent SCE contributes to larval retention in this region. We also found low abundance and number of occurrences for larvae of the nearshore subgenus *Pteropodus*, suggesting that CalCOFI stations are too far offshore to evaluate distributions of this group.

INTRODUCTION

Early life history stages of fishes collected during California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys are a primary source of fishery-independent information used to track abundances of marine fishes off southern California and to examine hypotheses about pelagic dispersal. Because net tows are easier and cheaper than sampling benthic or patchily distributed adults, surveys of planktonic larvae can be an efficient means to assess populations of marine fishes (Lasker 1985). Larval rockfishes (*Sebastes*) are common and abundant in CalCOFI plankton collections (Moser et al. 2000); more than 50 species occur in the Southern California Bight (SCB), and the majority are taken in commercial and sport fisheries (Miller and Lea 1972; Eschmeyer et al. 1983). Adult rockfishes commonly are benthic and often show high fidelity to a single site (Love 1979; Love et al. 1990).

The CalCOFI collections are a rich data source for constructing temporal abundance trends in many species; however, larvae of only seven northeastern Pacific *Sebastes* species can currently be positively identified by means of pigmentation and morphological criteria (Moser et al. 1977; Moser 1996). The remainder, grouped as unidentified *Sebastes* spp., ranked fourth in abundance and second in frequency of occurrence over the history of CalCOFI sampling from 1951 through 1998 (Moser et al. 2001).

Molecular genetic data, a constant at all life stages, provide a method to assign species identifications to unidentified larvae by comparison to reference data of known adults. This study is the first in which the entire complex of *Sebastes* larvae collected during any cruise has been identified to species through a combination of visual and molecular methods. We present species-specific larval distributions mapped onto the velocity flow field during the April 1999 CalCOFI cruise to examine patterns over the course of the early (<40 days) pelagic period, and to examine the hypothesis that larvae are equally distributed inside and outside of the Southern California Eddy (SCE), a persistent feature with a low velocity center in the spring in the SCB. We further examined distributions of 1-d-old larvae for the

[Manuscript received 8 April 2004]

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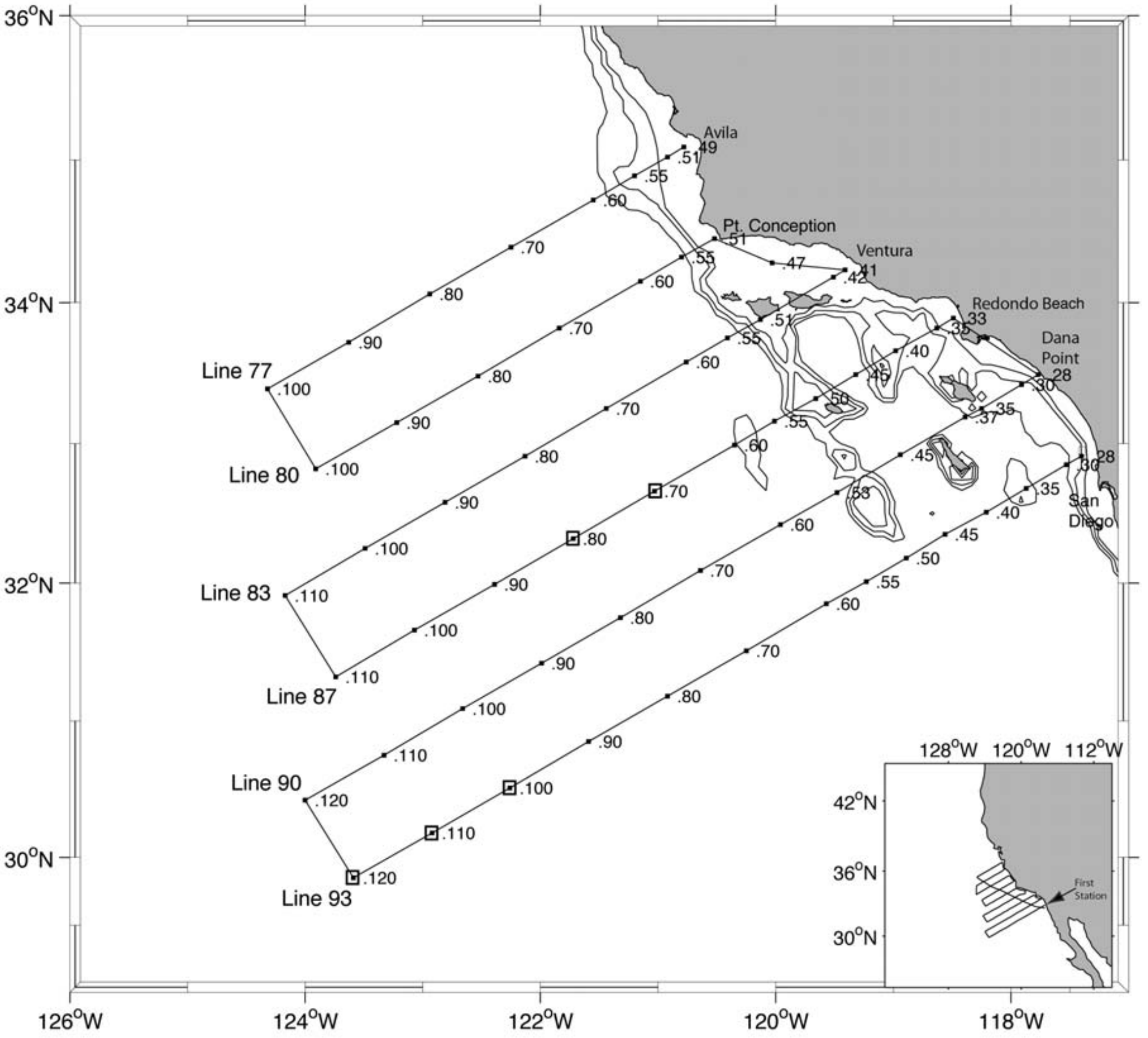

Figure 1. Standard CalCOFI stations. Squares indicate stations that were not sampled during the April 1999 cruise (from Ambrose et al. 2001). Ethanol-fixed samples were collected seaward to station 80 on all lines. Isobaths are 300, 500, and 700 m. Underway acoustic measurements were made up to Monterey (*inset*). The first station occupancy was 1 April 1999 at station 93.30 off San Diego.

most abundant species relative to adult depth ranges, which we define as potential adult habitat (PAH), to evaluate the association of larval occurrence with PAH. These data are useful for identifying the natal habitat of target species—critical information for fisheries management, including the siting of marine protected areas.

MATERIALS AND METHODS

Sample Collection

Parturition in *Sebastes* takes place during winter and spring for most species (e.g., Moser et al. 2000); the April 1999 CalCOFI cruise was selected for analysis because larval *Sebastes* were relatively abundant at that time (Ambrose et al. 2001). Oblique bongo net tows were made following standard CalCOFI protocols (Kramer et al. 1972; Ohman and Smith 1995) from 1 to 15 April 1999 aboard the *RV David Starr Jordan*. Briefly, a tow was made through the upper 212 m (or from 15 m above the bottom in shallower water) using a flowmetered 71 cm bongo net with 0.505 mm mesh and towed at a ship speed of about 1 m s^{-1} at each of 61 standard stations from Avila Beach to San Diego (fig. 1). The sample from one side of the bongo net was fixed in 5% sodium-borate-buffered formalin at all stations. At stations shoreward from station 80, the other sample was fixed and preserved in 95% tris-buffered ethanol that was changed within 24 hours after fixation. Ethanol-preserved samples were collected seaward to station 80; nearly all *Sebastes* larvae occur shoreward of station 80 (e.g., Moser et al. 2001).

Fish larvae were sorted from the macrozooplankton in the laboratory, identified to the lowest possible taxon, and enumerated. The counts were converted to abundance (number of larvae under 10 m^2 sea surface) by multiplying the larval count by the standard haul factor

(SHF = [10 • (tow depth/volume of water filtered)]) for each tow (Kramer et al. 1972; Smith and Richardson 1977; Moser et al. 1993). An "OPC adjustment" was made to account for the effect of an optical plankton counter that partially obstructed the opening of the net used for ethanol-fixed samples. This adjustment was calculated by use of a least squares regression between counts of *Sebastes* larvae in the obstructed side of the bongo and counts from the unobstructed side ($R^2 = 0.90$, [formalin = (ethanol * 1.51) + 1.86]). Morphologically identifiable *Sebastes* larvae (*S. aurora, S. diploproa, S. goodei, S. jordani, S. levis, S. moseri,* and *S. paucispinis*) were presorted from the ethanol-fixed samples, and all the remaining *Sebastes* spp. were identified using molecular methods. Larvae that were positively identified to species based on pigmentation and morphology were not reidentified with molecular methods. Larvae from the formalin-fixed side of the bongo were visually identified to the lowest possible taxon.

DNA Extraction and Data Collection

Genomic DNA was extracted from caudal fin or muscle tissue of larvae using a chelex extraction protocol (Walsh et al. 1991). PCR was used to amplify 782 bp of the mtDNA cytochrome *b* gene in a 1× buffer containing 20 mM Tris HCl, 50 mM KCl, and 1.5 mM $MgCl_2$ with 0.3μM of each primer. Primers included previously published GluRF and CB3RF (Rocha-Olivares et al. 1999) and internal custom primers (CB306F 5'-TTACTACGGCTCVTACCT-3, Cb521R 5'-GTTGCATTGTCTACTGAG-3', and CB364F, 5'-CTAGTTATAATAACTGCTTT-3'). The protocol: Hotstart at 90°C for 2:00 min, followed by 36 cycles with denaturing at 92°C for 0:45 min, annealing at 50°C for 1:00 min, and elongation at 72°C for 1:30 min. PCR products were cleaned with Qiaquick kits (Qiagen, Inc.) and cycle-sequenced according to manufacturer protocols with an ABI 3100 automated sequencer. Chromatogram data for sequenced DNA were aligned by means of the biosequence analysis and editor program Sequencher (ver. 4.1.1 Gene Codes, Inc.).

Larval sequences were compared to DNA reference sequence data of 374 independent haplotypes representing 67 species of identified adult *Sebastes* with an iterative approach within the software program Phylogenetic Analysis Using Parsimony (PAUP* 4b10; Swofford 2000) with the optimality criterion set to distance (number of bp differences divided by total bp sequenced). Species included in the PAUP reference file are listed in the appendix.

Nonparametric bootstrapping was used (100 replications, MAXTREES set to 1000) to cluster each unknown larval haplotype within a database of consensus haplotypes (consensus = most common haplotype from a database of up to 17 known adults, see appendix) from known adults for putative identification. If a larva clustered with the single haplotype of a reference species with a bootstrap value ≥ 90%, this was accepted as the identification of the larva. Distance between reference haplotypes and the unknown was examined to confirm that the unknown fell within the expected intraspecific diversity based on the reference data. If a larva clustered with a single haplotype of a species with a bootstrap < 90%, this was accepted as a first-pass identification; a secondary analysis was performed that included all available haplotypes of at least the three nearest (in distance) species to the unknown larval haplotype, and the haplotype was identified by direct comparison to the reference species. Intraspecific diversity for reference species in the NE Pacific has a mean distance 0.002 with a minimum of 0 (e.g., *S. jordani*) and a maximum of 0.01 (in *S. aleutianus*).

ADCP and Circulation

Upper ocean currents were measured continuously along the ship track from a hull-mounted RD Instruments 150 kHz narrowband acoustic Doppler current profiler (ADCP). The ADCP was configured to transmit an 8 m pulse every second along 4 beams directed downwards at 30 degrees from vertical, and equally spaced in azimuth. The recorded data were 3-min vector-averages. The estimates were binned vertically every 8 m. The shallowest depth with good data was 24 m, and the maximum depth range of the profiler was about 350 m. Velocities were calibrated for transducer misalignment and in situ temperature (Pollard and Read 1989) and converted from ship-relative to absolute currents by means of GPS measurements. The absolute currents were then averaged over hourly intervals, reducing errors due to position uncertainty to about 2 cm s^{-1}. Additional errors arise from the aliasing of unresolved short-period motions such as tides and near-inertial waves. The barotropic tide was estimated with the OSU global tide model TPXO6.2 (Egbert et al. 1994) and subtracted from collocated ADCP current observations. The barotropic tide predicted by the model was a fairly small signal, 1–3 cm s^{-1}. Near-inertial motions typically have high vertical wavenumber and are largest near the surface. To reduce noise from these motions, we averaged the currents vertically from 25 m to 75 m. This layer was below the mixed layer in the SCB during April 1999 (SIO 2000) and corresponded to the upper part of the bongo tow depth where *Sebastes* larvae are often most abundant (e.g., Ahlstrom 1959; Moser and Pommeranz 1998). We used a quasi-geostrophic streamfunction objective analysis (Chereskin and Trunnell 1996) to map the averaged and de-tided ADCP velocities. The smoothing and nondivergence enforced by the mapping further reduces errors in the large-scale velocity field.

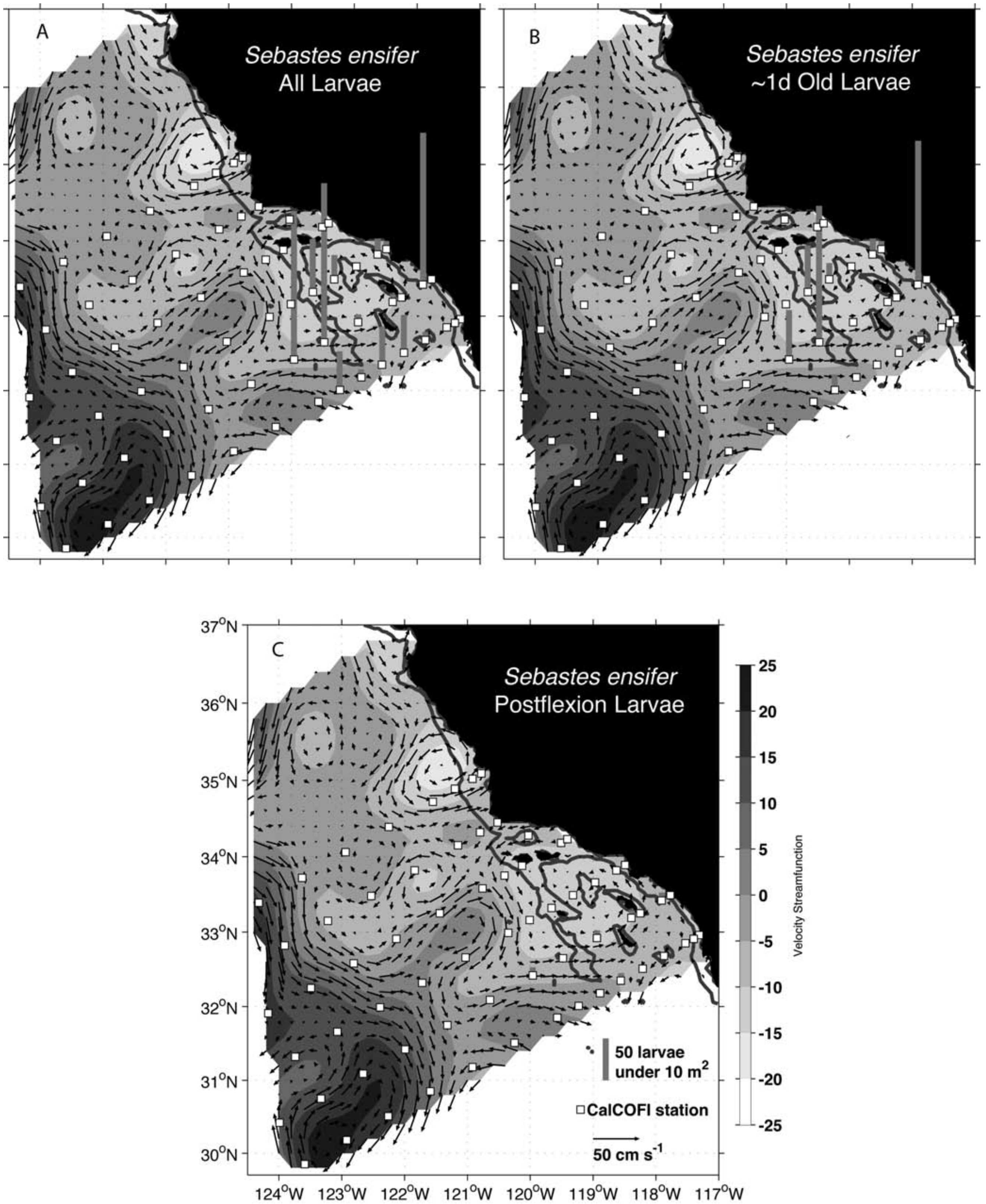

Figure 2. Distributions of larval *Sebastes ensifer* off southern California in April 1999. (*A*), all larvae; (*B*), larvae estimated to be ≤ 1-d-old; (*C*), postflexion-stage larvae. The 500 m isobath, indicating potential adult habitat, is shown as a dashed line. The ADCP-derived velocity stream-function data are shown with shading, and current vectors are shown as arrows.

TABLE 1
Rockfish Species with Fewer than Two Occurrences During the April 1999 CalCOFI Cruise

Sebastes spp.	Observed station(s)	Abundance(per 10 m^2)	Length (mm)	Flexion
S. constellatus	87.50, 83.55	23.67,16.35	3.0–3.8	Preflexion
S. elongatus	90.53, 87.35	18.09, 9.20	2.9–4.2	Preflexion
S. semicinctus	90.45, 87.35	9.32, 9.20	4.0 and 17.4	Pre- and postflexion
S. chlorosticutus	87.35	18.39	3.5 and 3.6	Preflexion
S. rosaceus	90.60, 87.50	9.86, 7.89	3.2 and 4.6	Preflexion
S. atrovirens	83.55	16.34	3.4 and 4.1	Preflexion
S. goodei	90.35	10.4	7.3	Flexion
S. rufinanus	90.60	9.86	4.5	Preflexion
S. carnatus	90.45	9.32	7.5	Flexion
S. rosenblatti	93.55	9.15	5.4	Preflexion
S. levis	90.53	9.05	4.2	Preflexion
S. caurinus	93.28	8.73	9.5	Postflexion
S. diploproa	87.50	7.89	4.2	Preflexion

Eddy and Potential Adult Habitat Association

We used an analysis of variance (ANOVA) to examine the null hypothesis that each species is distributed equally inside and outside of eddies within the SCB. We used the map of the ADCP data to categorize stations as inside or outside the SCE. We used the high-frequency array of surface currents collected in April 1999 and used CODAR (available from the Institute for Computational Earth System Science research at the University of California, Santa Barbara) to identify a gyre within the Santa Barbara Channel (www.icess.ucsb.edu/iog/codar_realtime.htm). The 15 eddy-positive stations included line 90, stations 28–53; line 86, stations 33–55; line 83, stations 51–55; and line 82, station 47 (e.g., fig. 2). All abundance data (A) were converted to ln(A+1) for the analyses, which could be performed only on the most abundant species (*S. hopkinsi, S. ensifer, S. rufus,* and *S. jordani*). Distributions of species with more than three occurrences were mapped (and examined) relative to the ADCP (and CODAR) data. Observations for species with fewer occurrences are listed in Table 1 as are corresponding data on locality, abundance, and size.

We also used ANOVA to examine the null hypothesis that 1-d-old larvae are randomly distributed and no more likely to be found in the vicinity of PAH (potential adult habitat) than non-PAH. Stations were categorized as within 20 km of being vertically over PAH, or beyond 20 km (non-PAH). Generally we refer to any habitat deeper than 501 m as "basin." We defined 1-d-old larvae by otolith-based aging (*S. hopkinsi*),[2] or by using length (mm) as a proxy for age (*S. ensifer* and *S. rufus*), where otolith ages were not available. We used published average length at parturition for *S. ensifer* (4.2 mm) and *S. rufus* (4.5 mm), and mapped distributions for larvae within 0.5 mm of this size.

RESULTS

Five *Sebastes* species were identified in the formalin-fixed samples (tab. 2), with 94% of the total *Sebastes* larvae classified as "*Sebastes* spp." In the ethanol-fixed samples an additional 18 species were identified through molecular methods; only 0.64% of the total *Sebastes* larvae remained unidentified (tab. 3). For the few ethanol-preserved larvae in the *Sebastes* spp. category, PCR amplification was unsuccessful and identification was not possible; we suspect poor DNA quality, perhaps because the larvae were from an earlier haul that was incompletely washed down, delaying fixation.

Molecular identification resulted in unambiguous identifications for 20 of the 23 species. *Sebastes hopkinsi* occurred in highest abundance and most frequently, followed by *S. ensifer*, *S. rufus*, and *S. jordani* (tab. 2). For *S. "wilsoni"* it was possible only to narrow the identification to three (*S. variegatus*, *S. wilsoni*, and *S. zacentrus*); for *S. carnatus*," to two species (*S. carnatus* and *S. chrysomelas*). For cytochrome *b*, there is incomplete lineage sorting among some closely related *Sebastes* sister species. *Sebastes variegatus* does not occur off southern California, and although *S. zacentrus* does, it is much less common than *S. wilsoni* (Love et al. 2002; J. Butler, pers. comm.). Thus, *S. wilsoni* is the most likely identification among the three, but we use quotations to indicate the ambiguity. For the *S. "carnatus,"* although the haplotype was most closely related to an adult *S. carnatus* haplotype, both *S. carnatus* and *S. chrysomelas* are common in the SCB, and either species is a likely identification for this larva.

Most larvae identified visually as *S. "moseri"* were presorted from the ethanol-fixed samples and not sequenced. There was one exception: a larva that was missed in the presort was subsequently identified as *S. rufinanus*. In an earlier study of larval *S. moseri* based on other ethanol-preserved CalCOFI samples, while most matched the putative *S. moseri* haplotype, 22% had a haplotype that differed by 2% from the *S. moseri* reference. These were

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[2] Taylor, C. A., W. W. Watson, T. Chereskin, A. Henry, and R. D. Vetter. Age-specific dispersal patterns of larval (1–42-d-old) squarespot rockfish, *Sebastes hopkinsi*, in the Southern California Bight identified using molecular methods (manuscript).

TABLE 2
Rockfish Species from the April 1999 CalCOFI Cruise

				Mean abundance	
Sebastes spp.	Total abundance	Positive stations	Larval counts	All tows	Positive tows
S. hopkinsi	979.74	22	116	21.07	44.07
S. ensifer	843.06	14	91	18.33	60.22
S. rufus	140.91	9	15	3.06	15.66
S. jordani	204.92	9	23	4.45	22.77
S. melanostomus	103.59	5	11	2.25	20.72
S. "wilsoni"	92.76	7	11	2.02	13.25
S. "moseri"	89.67	8	18	1.94	11.21
S. ovalis	68.22	3	8	1.48	22.74
S. jordani[a]	64.84	3	13	1.41	21.62
S. aurora[a]	62.56	5	12	1.36	12.51
S. "moseri"[a]	57.80	6	8	1.26	9.63
S. paucispinis[a]	52.37	5	12	1.14	10.47
S. saxicola	45.63	3	5	0.99	15.21
S. constellatus	40.02	2	5	0.87	20.01
S. simulator	28.59	3	3	0.62	9.53
S. elongatus	27.29	2	3	0.59	13.64
S. semicinctus	18.51	2	2	0.40	9.25
S. chlorosticutus	18.39	2	2	0.40	18.39
Sebastes spp.	26.14	3	2	0.57	8.71
S. rosaceus	17.75	2	3	0.39	8.87
S. atrovirens	16.35	1	2	0.36	2.38
S. goodei	10.40	1	1	0.23	10.39
S. rufinanus	9.86	1	1	0.21	9.86
S. "carnatus"	9.32	1	1	0.20	9.31
S. rosenblatti	9.15	1	1	0.20	9.15
S. levis	9.05	1	1	0.20	9.05
S. caurinus	8.73	1	1	0.19	8.73
S. diploproa	7.89	1	1	0.17	7.89
S. levis[a]	4.58	1	1	0.10	4.58

Note: Species in quotation marks are the most likely of two possible identifications.
[a]Species from the formalin-fixed side of the bongo net.

TABLE 3
Comparison of the Ethanol-fixed Versus the Formalin-fixed Sides of the Bongo Net for CalCOFI Cruise 9904

Side of bongo net	Species identified	Total abundance	Positive tows	Larval counts
Formalin-fixed	5 + 94% in *Sebastes* spp.	2,521.16	28	577
Ethanol-fixed	23 + 0.64% in *Sebastes* spp.	2,916.03	26	327

Note: An OPC adjustment based on larval counts was used to make formalin- and ethanol-fixed sides of the bongo net comparable.

later found to match the *S. rufinanus* haplotype. Thus, both species are likely to be included in the presorted group listed here as *S. "moseri"* (tab. 2), although the larvae are probably predominantly *S. moseri*. Observations from submersibles suggest that *S. moseri* is more abundant than *S. rufinanus* off southern California (J. Butler, pers. comm.).

The California Current appears in objective maps of velocity and velocity streamfunction at 50 m depth as a meander offshore of station 80, seaward of the continental shelf break (e.g., fig. 2). Velocity streamfunction is analogous to dynamic height, with positive streamfunction corresponding to dynamic highs and negative streamfunction corresponding to dynamic lows. The California Current flows south as a core of high velocity at the boundary between dynamically lower coastal waters and the offshore high of the North Pacific subtropical gyre. The change in streamfunction across the core of about 25 m km^{-1} over roughly 100 km corresponds to currents of magnitude 25 cm s^{-1} that flow parallel to the mapped streamlines. Between the California Current core and the coast there are numerous mesoscale eddies and meanders, with cyclonic circulation corresponding to cold anomalies and anticyclonic circulation corresponding to warm anomalies. These eddies are nonlinear, with amplitudes on the same order as the total height increase across the California Current, and thus they have the potential to transport anomalies (and potentially larvae) offshore (Chereskin et al. 2000; Cornuelle et al. 2000). In April 1999 there were 3 cyclonic and 2 anticyclonic eddies in the SCB. A cyclone/anticyclone pair occurred between lines 80 and 87 near station 70. A second anticyclone was located near line 93, station 120. A second cyclone was off Avila, and a third was consistent with the SCE, a persistent feature in the SCB northwest of San Clemente Island (fig. 2). The SCE is weakest in spring; it strengthens with the seasonal appearance of the Inshore Countercurrent and shoaling of the California Undercurrent in summer and fall (Lynn and Simpson 1987; Chereskin and Trunnell 1996). Thus, some of the weakest currents observed during April 1999 were within the SCB, and the area of highest potential larval retention was over PAH.

Sebastes hopkinsi larvae were the most abundant of the rockfish larvae. Adults have been reported to 150 m depth (Love et al. 2002) but have been observed on ROV transects to 200 m (J. Wagner, pers. comm.). This currently is the most commonly taken rockfish in the southern California recreational fishery, primarily because of the declining abundances of larger species (Love et al. 2002). We mapped distributions of the 1–42-day-old larvae relative to the 200 m depth contour.[3] Age-specific larval distributions allowed "tracking" of larvae through the early pelagic period, assuming constant larval input. The data suggested that although larvae were quickly swept away from the immediate vicinity of PAH, the youngest larvae and total larvae were retained in the proximity of the SCE in significantly higher abundance (mean[A] = 0.16 larvae under 10 m^2) than outside (mean[A] = 0.02) (F_1= 26.13, p = 0.0001). All 1-d-old larvae were near PAH, with no observations farther than 20 km away.

Sebastes ensifer, a small species sold primarily in the Asian fish market, is only a moderate part of the recreational catch, probably because of its small size (Love et al. 2002). It ranges deeper (to 433 m) than *S. hopkinsi*, more like other species in the survey. Larval distributions were mapped relative to a 500 m PAH (fig. 2). Total larval abundance was significantly higher at eddy stations (mean[A] = 1.868) than at non-eddy stations (mean[A] = 0.691; F_1 = 4.977, p = 0.031). Although a statistically significant association of 1-d-old larvae with PAH was not detected (F_1 = 1.302, p = 0.26), mean abundance over PAH was more than twice that at stations away from PAH (mean[A] = 0.415).

Sebastes rufus is often seen in ROV surveys off southern California (J. Butler, pers. comm.) and frequently is caught by recreational fishers (Love et al. 2002). It ranges to a maximum reported depth of 454 m. We mapped larval distributions over a 500 m PAH (fig. 3) and found that larval occurrence was not concordant with the SCE (F_1 = 0.23, p = 0.64), and 1-d-old larvae were not more abundant over PAH (F_1 = 0.493, p = 0.49).

Sebastes jordani has been thought to have the highest biomass of any rockfish off California (e.g., Ralston et al. 2003), but it has little direct commercial or recreational fishery value (Love et al. 2002). It ranges to 491 m, and we mapped larval distributions relative to a 500 m PAH (fig. 4). Total larvae were significantly more abundant within eddies (mean[A] = 1.15) than outside eddies (mean[A] = 0.243; F_1 = 7.03, p = 0.01). This was the only *Sebastes* species found in the Santa Barbara Channel. *Sebastes jordani* offered an opportunity to compare catches between the ethanol- and formalin-fixed sides of the bongo net (fig. 4A,B). The highest abundances were concordant between nets and near adult habitat. However, some positive stations in the ethanol-fixed samples lacked matching occurrences in the formalin-fixed samples. The majority of these (4 of 6 stations) reflect a lack of *S. jordani* in the formalin-preserved samples; at one of the remaining two stations, two larvae identified as *Sebastes* spp. were similar to *S. jordani* and might represent a previously unrecognized pigment polymorphism. In the ethanol-fixed samples, 56% of the *S. jordani* larvae were too damaged or distorted to be positively identified by sight as *S. jordani* but could be positively identified with molecular methods.

Sebastes melanostomus, one of the deeper-dwelling species, with a reported maximum depth of 768 m, is important in Asian fish markets of southern California and is occasionally landed in the recreational fishery (Love et al. 2002). The larval distribution was largely concordant with PAH, and most occurrences were within the SCE, with the highest abundances within the gyre (fig. 5A).

Sebastes wilsoni ranges to 383 m depth, and we mapped the larval distribution of *S. "wilsoni"* relative to a 500 m PAH. There was no clear association of preflexion larvae with either PAH or the SCE (fig. 5B).

Sebastes ovalis is a part of the commercial catch off southern California. Adults range to 366 m (Love et al. 2002), and larval distributions were mapped relative to a 500 m PAH. Abundances were concordant with both PAH and the SCE (fig. 5C).

Sebastes aurora has been important in artisanal fisheries off Newport Beach, California, and is landed recreationally off southern California. It ranges to 768 m (Love et al. 2002) and we mapped larval distributions relative to a 1,000 m PAH. Larval abundance was concordant with PAH, the SCE, and with a coastal eddy off Avila (fig. 5D).

Sebastes paucispinis is an important sport and commercial fishery species currently considered depleted and subject to a stock rebuilding plan (MacCall et al. 1999). Adults range to 478 m (Love et al. 2002, and the larval distribution was mapped relative to a 500 m PAH (Love et al. 2002). With the exception of nearshore stations off San Diego and Dana Point, collections were concordant with the SCE (fig. 6A). All larval occurrences were concordant with PAH.

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[3] Taylor et al., Age-specific dispersal patterns (manuscript).

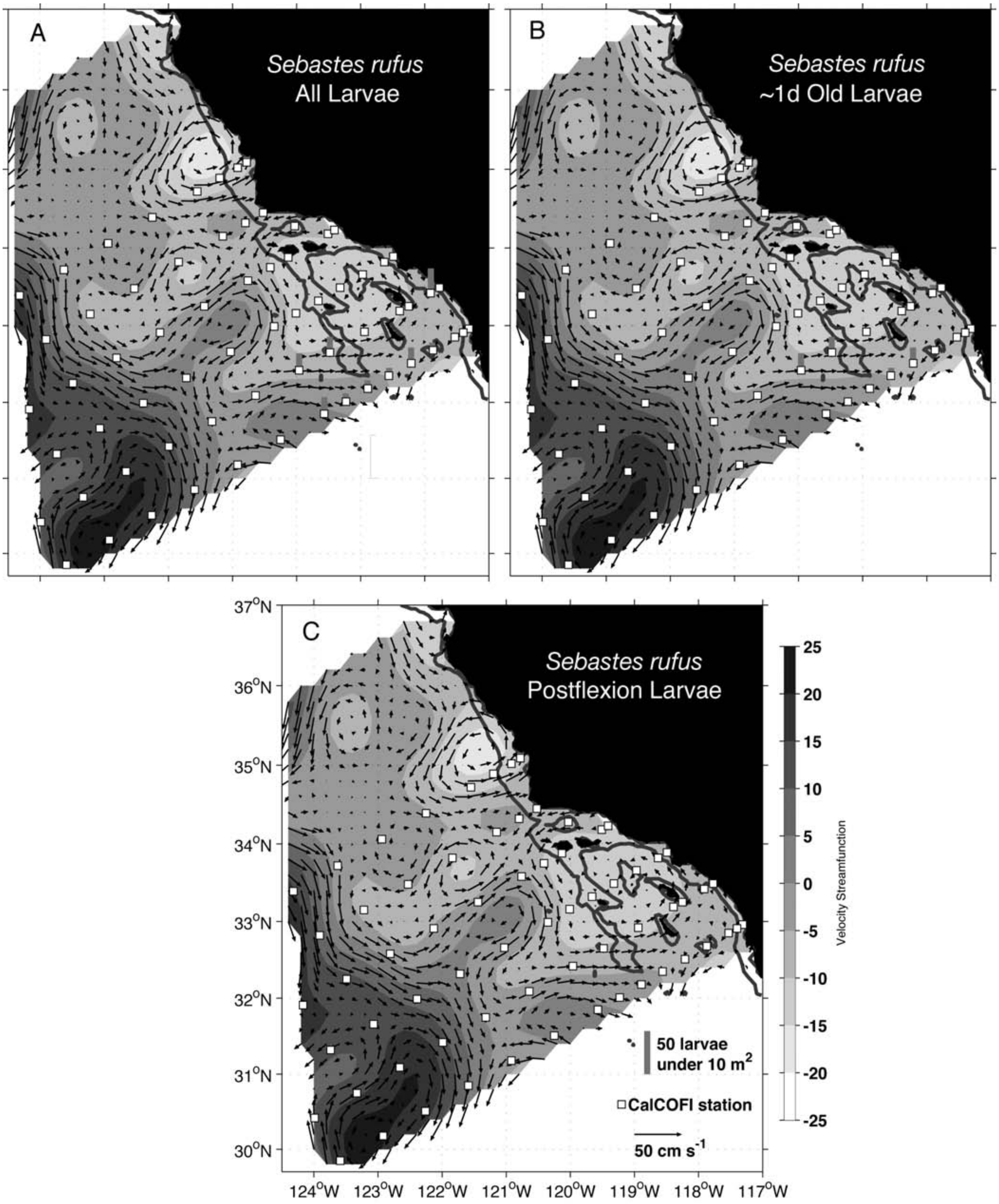

Figure 3. Distributions of larval *Sebastes rufus* off southern California in April 1999. (*A*), all larvae; (*B*), larvae estimated to be ≤ 1-d-old ; (*C*), postflexion-stage larvae. The 500 m isobath, indicating potential adult habitat, is shown as a dashed line. The ADCP-derived velocity stream-function data are shown with shading, and current vectors are shown as arrows.

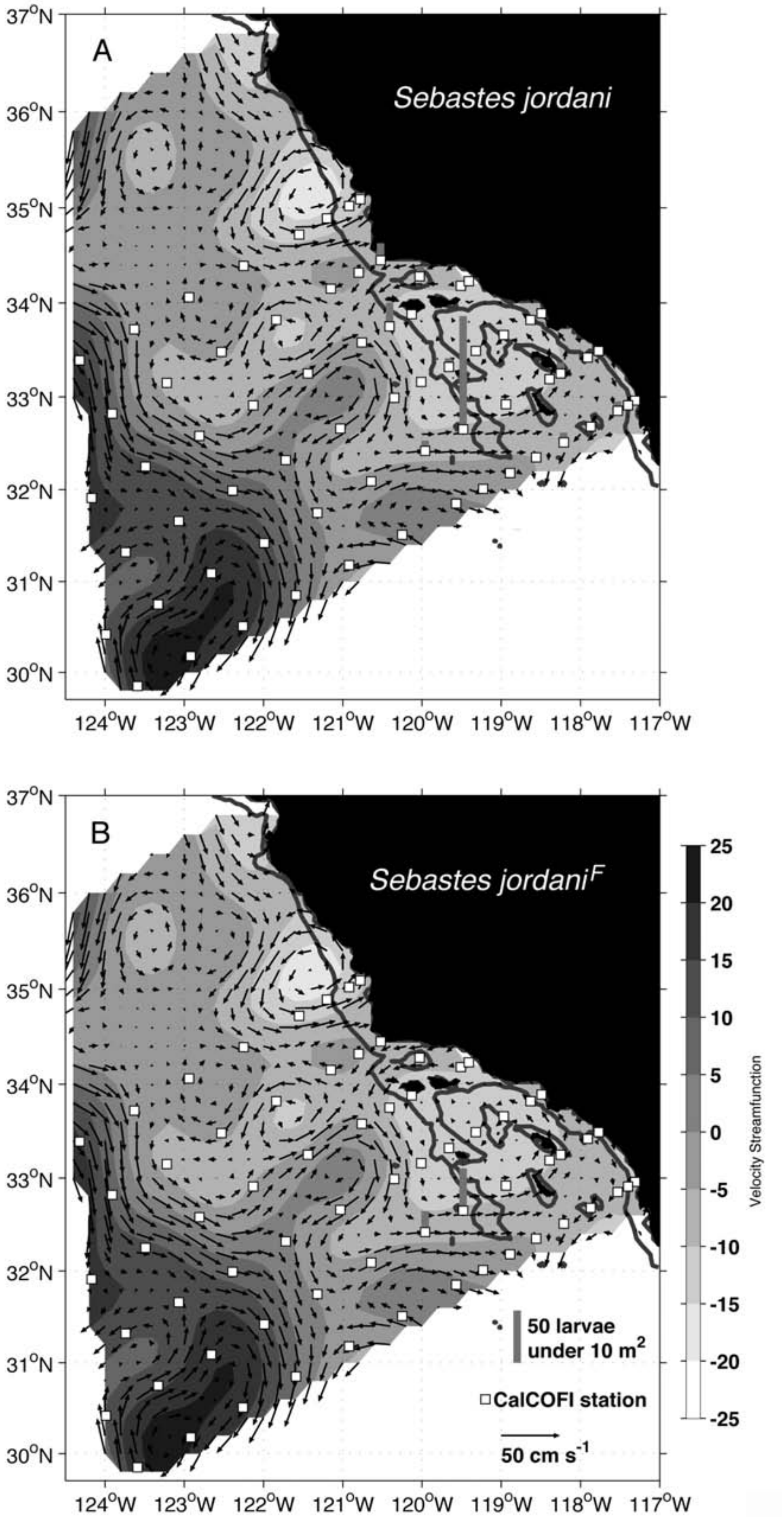

Figure 4. Distributions of larval *Sebastes jordani* off southern California in April 1999. (*A*) all larvae from ethanol-preserved samples; (*B*) all larvae from formalin-preserved samples. The 500 m isobath, indicating potential adult habitat, is shown as a dashed line. The ADCP-derived velocity stream-function data are shown with shading, and current vectors are shown as arrows.

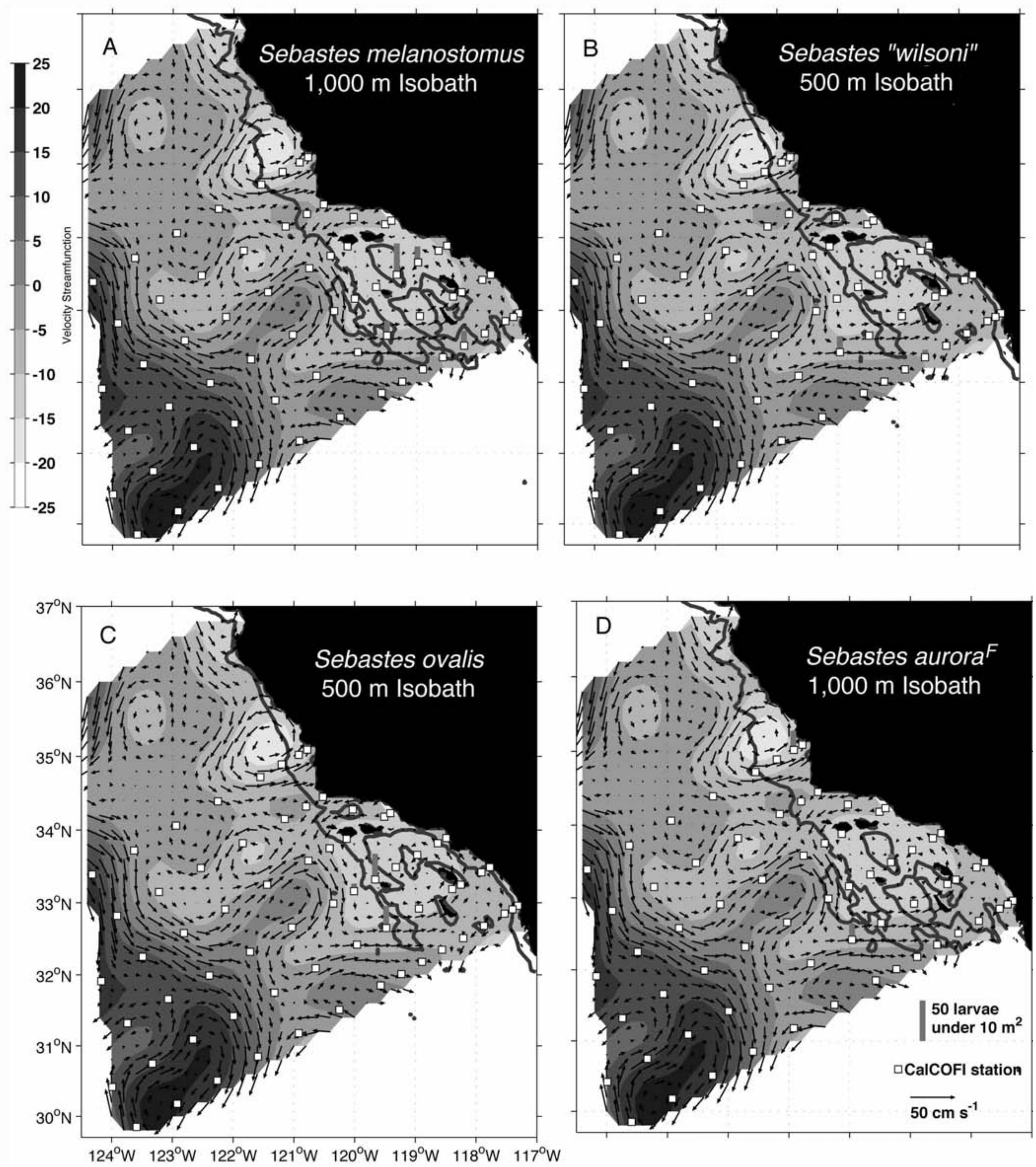

Figure 5. Distributions of larval *Sebastes* off southern California in April 1999. (*A*) *S. melanostomus*, all larvae; (*B*) *S. "wilsoni,"* all larvae; (*C*) *S. ovalis*, all larvae; (*D*) *S. aurora*, all larvae from formalin-preserved samples. Potential adult habitat is denoted by the 500 m (*B*, *C*) or 1,000 m (*A*, *D*) isobaths, shown as a dashed line. The ADCP-derived velocity stream-function data are shown with shading, and current vectors are shown as arrows.

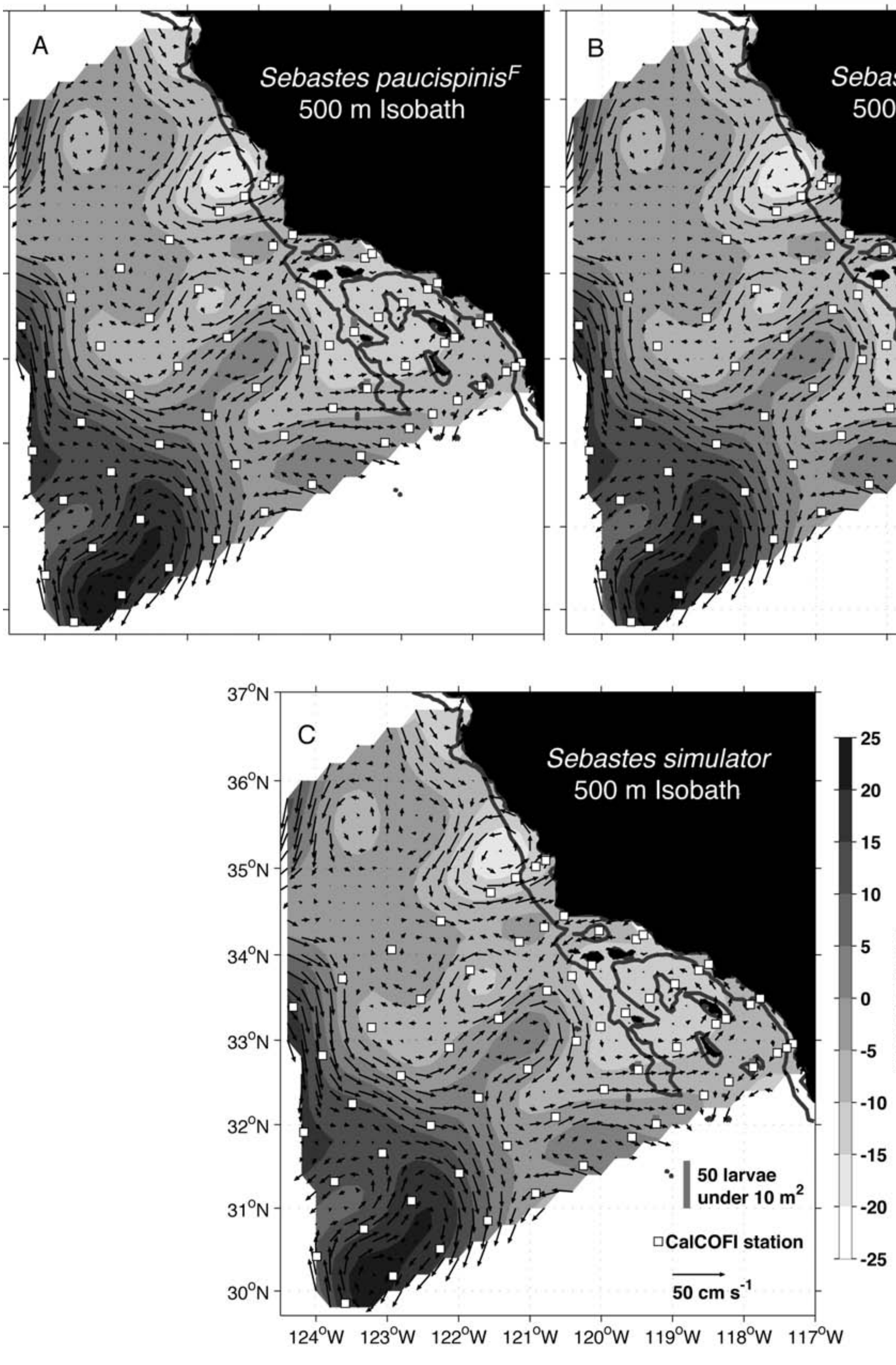

Figure 6. Distributions of larval *Sebastes* off southern California in April 1999. (*A*) *S. paucispinis*, all larvae in formalin-preserved samples; (*B*) *S. saxicola*, all larvae; (*C*) *S. simulator*, all larvae. The 500 m isobath, indicating potential adult habitat, is shown as a dashed line. The ADCP-derived velocity stream-function data are shown with shading, and current vectors are shown as arrows.

Sebastes saxicola is a small species not used in sport or commercial fisheries (Love et al. 2002). It can be found to 547 m, and we mapped the larval distribution relative to a 500 m PAH. Postflexion larvae were found at a nearshore station (93.30); the preflexion larvae were found in association with the SCE, near adult habitat, and at a station too close to the edge of the CalCOFI pattern to determine the closest adult habitat (fig. 6B).

Little is known about *Sebastes simulator*, but it is thought to occur at depths to 265 m. We used a 500 m PAH and found the larvae to be near PAH but well outside the SCE (fig. 6C).

DISCUSSION

This is the first time that the entire complex of *Sebastes* larvae collected during a CalCOFI cruise has been identified to species; this was made possible by the use of a combination of visual and molecular methods. In doing so, we confirmed seasonal spawning incidence of 22 species and identified the extent of their larval dispersal pattern in the SCB during April 1999. We also present the first attempt at reconciling larval *Sebastes* distributions with concurrent ADCP data.

Identifying larval vertical distributions is important when attempting to understand the degree to which larvae might be vulnerable to Ekman transport and resulting onshore-offshore advection, and when putting larval distributions into the context of physical oceanography at depth. Larval *Sebastes* might show species-specific vertical distributions (Ahlstrom 1959; Sakuma et al. 1999; Nishimoto 2000), and some undergo an ontogenetic shift in vertical distribution during the pelagic period (Tully and Oceidigh 1989; Doyle 1992). Early larvae typically occur above the thermocline (Ahlstrom 1959; Boehlert et al. 1985; Moser and Boehlert 1991), but not as shallow as the neuston (Tully and Oceidigh 1989; Doyle 1992). Later-stage larvae and juveniles are rarely found deeper than 100 m in depth-stratified samples in the SCB (Nishimoto 2000; Watson and Taylor, unpub. data). Thus 25–75 m was a reasonable depth interval over which to integrate velocity data in this study. We also observed consistent patterns of flow weakly sheared flow) to 100 m depth at positive stations. Larvae would have gained little additional horizontal transport from vertically migrating at this time of year.

By mapping ADCP data and treating it as a synoptic view of the velocity field experienced by the larvae, we demonstrated concordance of the two most abundant species with the SCE. Our data suggest that the SCE is a retention mechanism, overlaying some PAH for species in the study. Unlike planktonic spawners that are pelagic as adults (e.g., Pacific sardine, Logerwell and Smith 2001), rockfishes typically release their larvae from demersal locations. Distributions of 1-d-old larvae probably give the best estimate of rockfish natal habitat. For species with natal habitat overlaid by the SCE during the April 1999 cruise (e.g., *S. hopkinsi*, not shown, and *S. ensifer*, fig. 2B), total larval abundance was significantly associated with the SCE. We surmise that those larvae are retained in the vicinity of their natal habitat.

Some other species did not fit this pattern, however. For example *S. rufus* (fig. 3A) occurred largely outside the SCE, and presumed 1-d-old larvae (fig. 3B) were not concordant with expected PAH. It could be that *S. rufus* has a deeper than reported distribution, or that this species, often observed in schools (Love et al. 2002; J. Butler, pers. comm.), might release larvae away from expected PAH. We suggest that if larvae are not released within the SCE, they cannot be retained there, although they might later return as pelagic juveniles.

For demersal species with habitat fidelity and live-born larvae, the interplay of two key but independent features—PAH overlain by a persistent SCE in the season of parturition—might contribute retention in these species off southern California. The degree to which behavioral factors, including swimming ability, might contribute to larval retention is unknown; these factors probably become important only as larvae develop into the postflexion stage. Observations of postflexion larvae for *S. hopkinsi* (not shown), *S. ensifer* (fig. 2C) and *S. rufus* (fig. 3C) show close proximity to PAH, but we did not statistically test the significance of this association, because of the high effect of mortality on these abundance data. The relatively brief sampling of this survey limits our ability to generalize, but the hypothesis of SCE retention might be explored by examining ADCP data and larval distributions from additional cruises when the SCE is weaker or absent.

Both the CalCOFI grid and our definition of PAH are coarse. Reported *Sebastes* depth data are largely from fishers and may be adjusted in the future with ROV and submersible surveys when we can observe rockfishes in their natural habitat. Our plan in this study was to resolve mesoscale features of the natal habitat for individual rockfish species. This information would make it possible to prioritize areas of species habitat as targets for marine reserves and more focused sampling (e.g., the Cowcod Closure Area off southern California is currently the subject of high-resolution ichthyoplankton surveys). This information would also facilitate characterizing relative production from various regions in order to prioritize real estate in the marine environment. Collecting these data over time during the principal *Sebastes* parturition season (winter–spring) will bring us closer to these goals, but data based on the current CalCOFI grid apparently will be useful primarily for offshore species (e.g., abundant species identified here) and not for species with more restricted nearshore distributions.

At the outset of the study we expected to find larvae of the subgenus *Sebastes Pteropodus*, a complex of nearshore species heavily targeted by the live-fish fishery (Walters 2001). This group includes the grass (*Sebastes rastrelliger*), black-and-yellow (*S. chrysomelas*), gopher (*S. carnatus*), copper (*S. caurinus*), quillback (*S. maliger*), China (*S. nebulosus*), calico (*S. dallii*), brown (*S. auriculatus*), and kelp (*S. atrovirens*) rockfish (Taylor 1998). Few larvae of this subgenus were collected, and only at nearshore stations (tab. 1). The most likely explanation is that CalCOFI stations are too far offshore to assess these kelp forest and nearshore species. Nearshore, long-term monitoring projects, like those conducted by the Channel Islands National Park, and nearshore ichthyoplankton surveys, such as those proposed as part of the Southern California Coastal Ocean Observing System (SCCOOS), are better suited for identifying natal habitat and characterizing abundance trends for nearshore species.

Molecular methods are useful for identifying both previously unidentifiable species and damaged or distorted specimens of the visually identifiable species that previously would not have been included in counts. For example, *S. jordani* on cruise 9904 might have been under-reported by >50% without molecular identification (fig. 4), and a specimen of *S. levis* identified by molecular methods was not visually identifiable in the presort of ethanol-fixed samples because of severe distortion of the pectoral fins, a key diagnostic character (tab. 1).

In the past decade, molecular identification methods have become easier to use, and costs have decreased enough to allow quick sequencing of many individuals. As the number of genetic markers and information on intraspecific polymorphism increases, apparently fixed differences between species in the form of single nucleotide polymorphisms will be useful for designating some species and species complexes within *Sebastes*. A reasonable outcome from this is the development of microarrays and microbeads multiplex assays that will allow automated reading of fluorescent-labeled probes after a series of species-specific enzyme-ligation steps. These methods have sufficiently high throughput and are rapid enough to be promising for collection of real-time data aboard ship.

ACKNOWLEDGMENTS

Samples were obtained through CalCOFI in cooperation with the California Department of Fish and Game, the Scripps Institution of Oceanography, NOAA Fisheries and scientists and crew on the NOAA ship RV *David Starr Jordan*. We are especially indebted to A. Hays, D. Griffith, and R. Charter for their help in obtaining samples, and A. Brooks and H. Timms for their assistance in the laboratory. We also thank the Oceanids Foundation, the Frieda Daum Urey Scholarship Committee, and the Biological Oceanography Fellowship Committee. TKC was supported through NSF grant OCE-0324360. The genetic data collection was funded by NOAA Fisheries, the California Department of Fish and Game, California Sea Grant, and the Marine Ecological Research Reserves Program 4-M-N.

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APPENDIX

Locations of Adults Used for Reference to Identify Larvae

Sebastes spp.	Location	Latitude, longitude	Total haplotypes
S. aleutianus	Point Reyes, Calif.	37.93°N, 123.46°W	3
S. alutus	Cape Mendocino, Calif.	40.92°N, 124.42°W	2
S. atrovirens	La Jolla, Calif.	32.83°N, 117.25°W	9
S. auriculatus	Monterey Bay, Calif.	36.98°N, 122.20°W	6
S. aurora	Monterey Bay, Calif.	36.79°N, 122.13°W	7
S. babcocki	San Francisco, Calif.	37.24°N, 122.72°W	2
S. borealis	Trinidad Head, Calif.	41.23°N, 124.42°W	2
S. brevispinis	Alaska	49.20°N, 126.74°W	4
S. capensis	Off South Africa	N/A	9
S. carnatus	San Luis Obispo Bay, Calif.	35.14°N, 120.72°W	6
S. caurinus	Punta Baja, Baja California, Mex.	29.89°N, 115.82°W	6
S. chlorostictus	Richardson Rock, Calif.	34.12°N, 120.55°W	11
S. chrysomelas	Monterey Bay, Calif.	36.75°N, 122.00°W	1
S. ciliatus	S. Baranof Island, Alaska	56.08°N, 134.92°W	6
S. constellatus	Cordell Bank, Calif.	38.00°N, 123.04°W	11
S. crameri	San Francisco, Calif.	37.58°N, 122.05°W	5
S. dallii	San Luis Obispo, Calif.	35.14°N, 120.72°W	5
S. diploproa	Monterey Bay, Calif.	36.77°N, 122.20°W	7
S. elongatus	S. San Clemente Island, Calif.	32.74°N, 118.41°W	6
S. emphaeus	Seattle Aquarium, Hood Canal, Wash.	47.92°N, 122.58°W	1
S. ensifer	60-mile Bank, Calif.	32.08°N, 118.25°W	7
S. entomelas	Ascension Canyon, Calif.	36.98°N, 122.58°W	7
S. eos	Palos Verdes, Calif.	33.70°N, 118.36°W	16
S. exsul	N. Gulf of Calif., Mex.	28.59°N, 113.43°W	5
S. flavidus	Ascension Canyon, Calif.	36.98°N, 122.58°W	6
S. gilli	Cortes Bank, Calif.	32.57°N, 119.25°W	2
S. goodei	S. San Francisco, Calif.	37.25°N, 122.85°W	6
S. helvomaculatus	N. San Francisco, Calif.	38.26°N, 123.49°W	9
S. hopkinsi	Offshore of Hood Canal, Wash.	32.57°N, 119.25°W	17
S. jordani	Ascension Canyon, Calif.	36.98°N, 122.58°W	11
S. lentiginosus	La Jolla, Calif.	32.83°N, 117.25°W	2
S. levis	60-mile Bank, Calif.	32.08°N, 118.25°W	5
S. macdonaldi	Bahia de Los Angeles, Mex.	28.98°N, 113.43°W	9
S. maliger	San Francisco Fish Market	N/A	6
S. melanostomus	Offshore of San Diego, Calif.	32.75°N, 117.75°W	5
S. melanops	Davenport port sample	37.02°N, 122.17°W	8
S. melanosema	San Pablo Point, Baja California, Mex.	N/A	1
S. miniatus	San Clemente Island, Calif.	37.74°N, 118.41°W	6
S. moseri	San Clemente Isle, Calif.	32.63°N, 117.96°W	1
S. mystinus	Point Sur, Calif.	36.28°N, 121.97°W	8
S. nebulosus	San Francisco Fish Market	N/A	6
S. nigrocinctus	Fairweather Grounds, O'Connell, Alaska	58.25°N, 139.00°W	3
S. notius	Uncle Sam Bank, Mex.	25.59°N, 113.37°W	2
S. ovalis	S. San Clemente Island, Calif.	32.74°N, 118.40°W	8
S. paucispinis	S. of Monterey, Calif.	36.82°N, 122.10°W	2
S. phillipsi	Seattle, Wash.	N/A	4
S. pinniger	Humboldt, Calif.	41.75°N, 124.08°W	5
S. polyspinis	Off Kodiak Isle, Alaska	58.40°N, 153.65°W	5
S. proriger	Cape Mendocino, Calif.	40.56°N, 124.50°W	4
S. rastrelliger	Bodega Bay, Calif.	38.30°N, 123.10°W	5
S. reedi	Point Arena, Calif.	38.64°N, 123.74°W	1
S. rosaceous	Ascension Canyon, Calif.	36.98°N, 122.58°W	7
S. rosenblatti	Monterey Bay, Calif.	36.83°N, 122.16°W	12
S. ruberrimus	Off Inverness, Marin County, Calif.	38.56°N, 123.62°W	5
S. rubrivinctus	San Clemente Island, Calif.	32.74°N, 118.41°W	5
S. rufinanus	San Clemente Island, Calif.	32.79°N, 118.33°W	1
S. rufus	Lincoln City, Ore.	45.74°N, 124.69°W	4
S. saxicola	Point Sur, Calif.	36.83°N, 122.16°W	1
S. semicinctus	Santa Cruz, Calif.	37.41°N, 122.91°W	6
S. serranoides	Richardson Rock, Calif.	34.12°N, 120.55°W	6
S. serriceps	Santa Catalina Island, Calif.	33.28°N, 118.34°W	5
S. simulator	Baja California Norte, Mex.	32.87°N, 117.87°W	10
S. spinorbis	Bahia de Los Angeles, Mex.	28.98°N, 113.43°W	3
S. umbrosus	Between Cortes and 60-mile Bank	32.43°N, 119.11°W	6
S. variegatus	Alaska fisheries	N/A	2
S. wilsoni	Santa Cruz, Calif.	37.24°N, 122.77°W	5
S. zacentrus	Santa Cruz, Calif.	37.25°N, 122.85°W	2

Note: GenBank accession numbers available on request.

COMPARISON OF RECREATIONAL FISH CATCH TRENDS TO ENVIRONMENT-SPECIES RELATIONSHIPS AND FISHERY-INDEPENDENT DATA IN THE SOUTHERN CALIFORNIA BIGHT, 1980–2000

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ABSTRACT

Although southern California recreational fish catches have changed in recent years, their relationship to environmental change is not well described. This study describes the relationship of recreational fish catch trends (all modes, 1980–2000) to environment-species interactions and fishery-independent population data. We used oceanic temperature and upwelling data as indicators of environmental trends, and power-generating-station data on fish impingement as indicators of fishery-independent population trends. Twenty-one dominant species showed significant changes in average catch from the 1980s to 1990s, with three species (shore-caught grass rockfish, *Sebastes rastrelliger*; boat-caught Pacific bonito, *Sarda chiliensis*, and olive rockfish, *Sebastes serranoides*) decreasing significantly both for landings and catch per unit of effort. These declines generally corresponded to a strong negative population response to temperature or a strong positive response to upwelling in southern California, with temperature being more important. Overall, 61% of 44 species examined had catch or population trends significantly correlated with environmental variables. Fishery-dependent and fishery-independent data trends were similar, with the former lagging the latter by one or more years. Cross-correlation analysis at lags of 0–7 years between the two data sets revealed significant correlations for two croakers and five rockfishes. The results in this study provide a basis for forecasting fish species responses to natural environmental change and thus may facilitate more adaptive management of recreational fisheries.

INTRODUCTION

Recreational fishing contributes millions of dollars in revenue to southern California (Weber and Heneman 2000) and provides enjoyment to many anglers. However, declines in catches of many recreational fishes in recent years have been severe, forcing fisheries managers to close several important recreational fisheries, including cowcod (*Sebastes levis*), yelloweye rockfish (*Sebastes ruberrimus*), and canary rockfish (*Sebastes pinniger*). Rebuilding plans for some species estimate several generations of no fishing pressure before populations reach prefishing levels (Butler et al. 2003). As a result, much research has been conducted in the last decade to clarify the causes of the observed declines and more successfully conserve the recreational fishery. The scientific community has become increasingly aware that multidecadal changes in oceanographic conditions have affected fished and nonfished populations (Hollowed et al. 1995; Mantua et al. 1997; Klyashtorin 1998; Hollowed et al. 2001; Brooks et al. 2002; Chavez et al. 2003). While it is evident that increased and sustained fishing pressure have severely affected several fisheries in southern California (e.g., rockfishes and abalone) (Davis et al. 1992; Love et al. 1998; Mason 1998; Schroeder and Love 2002; Butler et al. 2003), the influence of natural oceanic change on recreational fish populations in this area has not been well described. Further understanding of natural environmental influence on recreational catch trends may help to conserve our southern California recreational fisheries.

In a recent report (Allen et al. 2003), we described trends for over 100 nearshore fishes in southern California relative to atmospheric-oceanic influences. The study made use of fish abundance data from a variety of sources, including both fishery-independent and fishery-dependent data. Thus, species relationships were described in a broad context without focus on important recreational fishes. Here, we highlight the environmental responses of important recreational fishes in southern California and compare them with recreational landings data to determine the degree to which observed declines (or increases) in landings may be explained by natural variation in the environment. Because environmental variables influence fishes to varying degrees, it is of interest to relate how well landings data correspond to the species' responses we observed. Furthermore, identification of fish species with trends that deviate from natural oceanic trends may stimulate additional research addressing the extent of anthropogenic influence, such as fishing and habitat alteration, on local fish populations.

[Manuscript received 2 February 2004.]

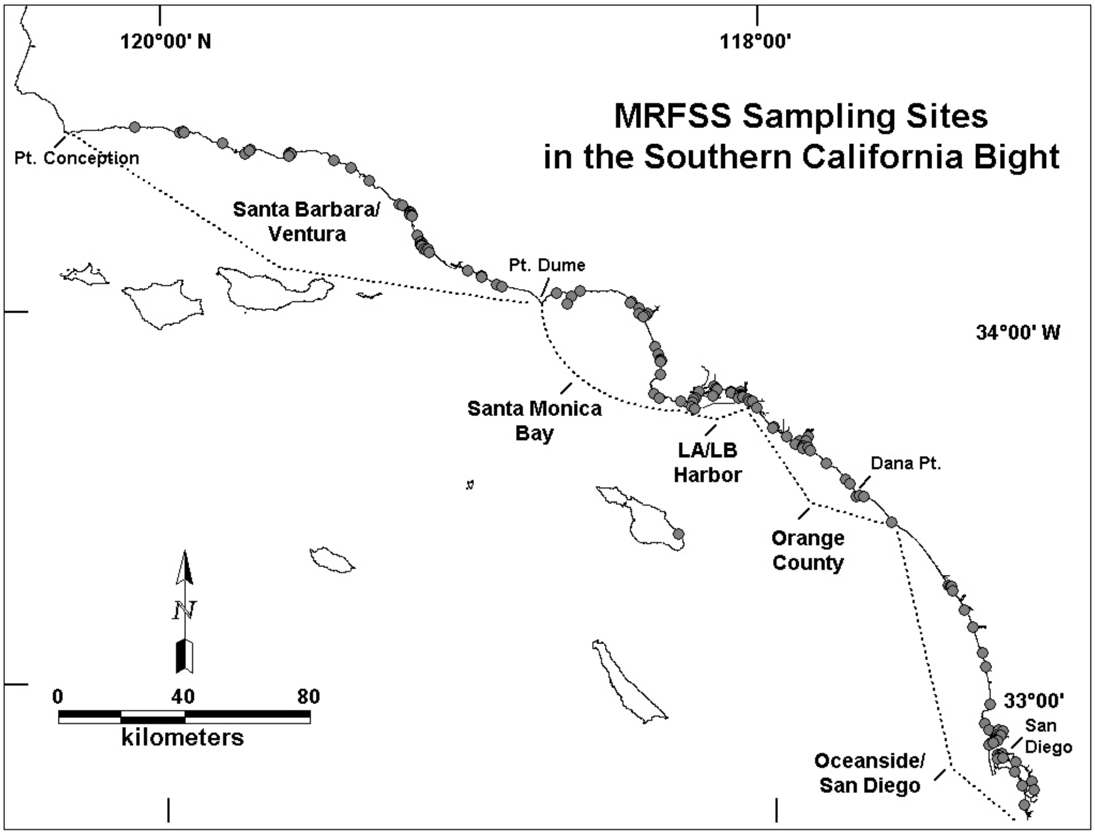

Figure 1. Location of recreational angler interview and sample sites of the Marine Recreational Fisheries Statistics Survey (MRFSS; LA/LB = Los Angeles/Long Beach Harbor), 1980–2000, within five southern California geographic regions.

Factors influencing fishery-dependent data, such as changes in fishing regulations and postings of contaminated fish advisories, make it difficult to discern whether observed changes in recreational catch data represent actual changes in the overall population. Therefore, we also compare trends in recreational catch data with those of fishery-independent data (impingement data). In cases where the two data sets are significantly correlated and an environment-species relationship exists, the extent of oceanographic influence on observed declines may be validated.

The objective of this study is to describe the relationships among catch trends for important southern California recreational fish species, our established environment-species interactions, and fishery-independent population data, with emphasis on dominant species that exhibit significant changes in landings and catch per unit of effort (CPUE) from 1980 to 2000. An understanding of these relationships may be useful in forecasting fish landings in the future (Parrish and Tegner 2001) and implementing fisheries regulations or management actions to complement observed trends in the oceanographic environment.

METHODS

Data Sources

Trends in recreational fish catch. We selected 44 southern California recreational species from Leet et al. (2001) on the basis of the fishery's geographic location and history (i.e., relative value to sport fishery). We chose fishes that were highly targeted, caught in large numbers, restricted to the recreational fishery, or showed declining catch in recent years. We used two types of recreational fish-catch data (total yearly estimates of recreational fish and sample data) reported by the Marine Recreational Fisheries Statistics Survey (MRFSS).[1] These were obtained from the Recreational Fisheries Information Network (RecFIN) Web site (http://www.psmfc.org/recfin) for the years 1980 to 2000 (with a hiatus from 1990 to 1992 due to interrupted funding).

The MRFSS landings data are estimates of fish landed (in thousands of fish) in southern California, calculated from MRFSS samples and a telephone survey of house-

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[1] As of 2004, the MRFSS in California has been replaced by the California Recreational Fisheries Survey (CRFS).

holds in coastal counties to estimate trips (PSMFC, http://www.psmfc.org/recfin). We used MRFSS sample data (catch rates) for fish species caught from shore and by boat (on the ocean within 4.8 km [3 mi] from shore), with all fishing gear types, from Point Conception, California, to the United States-Mexico International Border (fig. 1). Shore fishing access sites consisted of piers, docks, breakwaters, beaches, banks, bridges, and breachways; boats included privately chartered boats, commercial passenger fishing vessels (CPFVs), rental boats, and privately owned boats. We selected data representing fish kept by the angler and available for identification and species counts by the interviewer. In addition, we used only sites with the longest time-series of data to obtain more complete temporal and spatial coverage. Catch rates were estimated for missing species data,[2] and all catch rates were converted to number of fish per 10,000 hr. Fish catches were divided by the total number of hours fished in a year; therefore, CPUE reflects a measure of relative abundance or availability among species (Stull et al. 1987).

Independent and dependent variables for environment-species analysis. For the environment-species analysis we used three sources of CPUE values (dependent variables): (1) MRFSS sample data described above; (2) fish impingement data[3] for five southern California power-generating stations (1972–1999 for Ormond Beach, El Segundo, Redondo Beach, and Huntington Beach combined; 1983–2000 for San Onofre) obtained from Southern California Edison Company; and (3) demersal fish trawl data (1973–1999) obtained from County Sanitation Districts of Los Angeles County (CSDLAC) (nonoutfall stations).

The environmental variables (independent variables) were developed from a variety of data sources by means of principal component analysis (PCA). The environmental data trends selected for this study and defined by the PCA were (1) shoreline sea-surface temperature (fig. 2a) (reported by the Marine Life Research Group, Scripps Institution of Oceanography) used to construct a dummy plot of the Pacific Decadal Oscillation (PDO) without El Niño effects (fig. 2b); (2) offshore sea-surface temperature from California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruise data (fig. 2c); (3) multivariate El Niño-Southern Oscillation (ENSO) indexes obtained from the National Oceanic and Atmospheric Administration (NOAA)-Cooperative Institute for Research in Environmental Sciences (CIRES) Climate Diagnostics Center (fig. 2d); and (4) coastal upwelling indexes (downwelling events are not included) obtained from the Pacific Fisheries Environmental Laboratory (fig. 2e–g).

Annual fish and environmental data were converted to *z*-scores (number of standard deviations above or below the mean) to standardize the data for direct comparison between species trends and environmental responses. Data were Loess smoothed to diminish short-term variability (Grosse 1989; Venables and Ripley 2002).

Data Analysis

Recreational fish catch trends. We identified catch dominants in the overall shore and boat fishing modes by using the MRFSS landings data. Dominant fish species were those comprising 75% of the total catch for both fishing modes (shore and boat). Because some species are not caught in high numbers throughout southern California, and because landings data were not available by county, we identified additional catch dominants from the MRFSS sample data as the top 10 species from five regions within the Southern California Bight (SCB): Santa Barbara/Ventura, Santa Monica Bay, Los Angeles/Long Beach Harbor, Orange County, and Oceanside/San Diego (fig. 1). Regional catches were standardized by effort.

We identified catch dominants exhibiting significant changes throughout the study period by calculating decadal differences in average bightwide landings and CPUE for each species and fishing mode from 1980 to 2000. Annual data were normalized by log-transformation and grouped by decade to calculate a mean catch (landings) and CPUE for the 1980s (1980–1989) and 1990s (1993–2000).[4] Significant differences in mean catch and CPUE between the 1980s and 1990s for each species were tested using the student's *t*-test ($\alpha = 0.05$). Mean values were then back-transformed. The back-transformed values for each decade were used to quantify the proportional change in average annual catch and CPUE between the two decades for each species as PC = [(1980s–1990s)/1980s]*100.

Relationship to environmental variables. Fish population responses to the atmospheric/oceanographic (temperature) and upwelling variables (independent variables) were measured with stepwise multiple-regression analysis, using two steps of analysis. We first considered the large-scale atmospheric/oceanic variables, described by temperature, and second, the more regional variables

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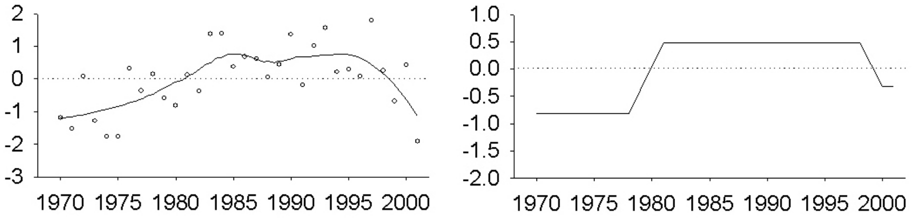
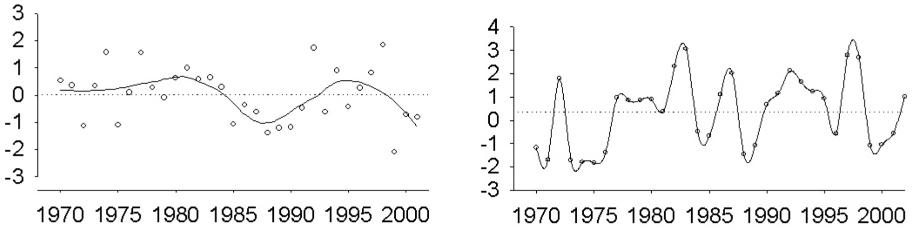
[2] Missing species data for a given site and wave (2-month period) were estimated by multiplying the average deviation in catch rate for that "fish year" (November–October) by the average catch rate of all other years for the same site and wave.

[3] Impingement data incorporate both normal operation and heat-treatment fish collection. All data were standardized to flow. We applied a heat-treatment factor to heat-treatment abundance for normalizing against an average number of fish collected during a 24-hour normal operation. Heat-treatment data were summed with normal operation data (daily fish abundance in fish/million gallons) for a yearly impingement rate per species.

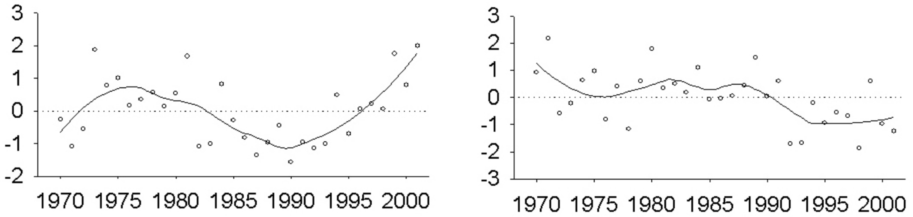
[4] Shore landings were available only from 1981 to 2000.



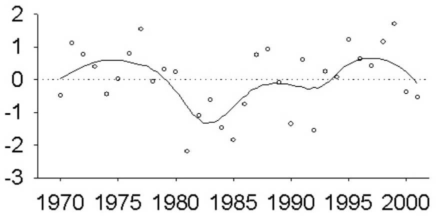
(a) Shoreline sea-surface temperature (b) Long-term PDO with lag effect



(c) OffShore sea-surface temperature (d) El Niño Southern Oscillation (ENSO)



(e) Upwelling north of SCB (f) Upwelling in SCB



(g) Upwelling south of SCB

Figure 2. Smoothed temperature and upwelling plots (from Allen et al. 2003), 1970–2002. PDO = Pacific Decadal Oscillation; SCB = Southern California Bight.

(upwelling). Thus, temperature variables were used as the independent variables and species CPUE values as the dependent variables in the initial analysis. In the second analysis, temperature effects were removed and the fish residual plots were used as the dependent variables and the upwelling trends as the independent variables.

The multiple-regression analysis output included standardized partial-regression coefficients (or the measure of correlation, r), R^2 values, and p values associated with tests of the null hypotheses for the overall regression of each fish species and independent variable. The standardized partial regression coefficients are directly comparable, since the dependent and independent variables were standardized to z-scores. At each stage of the regression analyses of all species, regression models were computed for all combinations of lags of 0, 1, and 2 years for each of the independent variables, except that the PDO variable was already built with a gradual 4-yr lag. The regression model with the lowest p value associated with the overall regression was chosen for inclusion in the results as the basis for the next level of analysis.

Because some methods of fish sampling are better estimators of actual fish population trends, significant environmental responses for a particular species were selected only from the most relevant (appropriate) fish database. The most relevant for each fish species was selected on the basis of species frequency of occurrence (>50% of years relative to a 30-yr database) and, in case of ties,

TABLE 1
Estimated Number of Recreational Fish Landings Ranked by Total Percentage of Catch in the Recreational Fishery in Southern California, 1980–2000

			Bightwide landings (×1,000)				
Scientific name	Common name	Region[a]	Shore	Boat	Total[b]	% of catch	Cum. %[c]
Scomber japonicus	**Pacific chub mackerel**	**B**	**13,905**	**51,517**	65,421	25.4	25.4
Paralabrax clathratus	**Kelp bass**	**B**	**1,019**	**28,312**	29,330	11.4	36.7
Genyonemus lineatus	**White croaker**	**B**	**5,160**	**13,790**	18,951	7.3	44.1
Paralabrax nebulifer	**Barred sand bass**	**B**	408	**18,187**	18,595	7.2	51.3
Sarda chiliensis	**Pacific bonito**	**B**	**1,125**	**12,562**	13,686	5.3	56.6
Sphyraena argentea	**Pacific barracuda**	**B**	100	**12,412**	12,512	4.8	61.4
Paralichthys californicus	**California halibut**	**B**	**1,737**	**6,963**	8,700	3.4	64.8
Amphistichus argenteus	**Barred surfperch**	**B**	**5,352**	80	5,432	2.1	66.9
Scorpaena guttata	**California scorpionfish**	**B**	140	**4,773**	4,913	1.9	68.8
Sebastes mystinus	**Blue rockfish**	**B**	12	**4,531**	4,543	1.8	70.6
Sebastes spp.	Rockfish, unidentified	—	106	4,349	4,455	1.7	72.3
Sebastes paucispinis	**Bocaccio**	**B**	**1,533**	**2,694**	4,227	1.6	73.9
Seriphus politus	**Queenfish**	**B**	**3,370**	577	3,947	1.5	75.5
Atherinopsis californiensis	**Jacksmelt**	**B**	**3,570**	349	3,919	1.5	77.0
Sebastes carnatus	Gopher rockfish	—	23	1,945	1,967	0.8	77.8
Embiotocidae, unidentified	Surfperches, unidentified	—	1,889	—	1,889	0.7	78.5
Sebastes miniatus	**Vermilion rockfish**	**S**	147	**1,682**	1,829	0.7	79.2
Caulolatilus princeps	**Ocean whitefish**	**D**	3	**1,777**	1,779	0.7	79.9
Hyperprosopon argenteum	**Walleye surfperch**	**B**	**1,687**	50	1,737	0.7	80.6
Sebastes serranoides	**Olive rockfish**	**S**	20	**1,697**	1,717	0.7	81.2
Seriola lalandi	**Yellowtail jack**	**D**	4	**1,656**	1,660	0.6	81.9
Semicossyphus pulcher	**California sheephead**	**L**	47	**1,207**	1,254	0.5	82.3
Umbrina roncador	**Yellowfin croaker**	**O**	**948**	**300**	1,247	0.5	82.8
Sebastes caurinus	**Copper rockfish**	**S**	1	**1,201**	1,201	0.5	83.3
Paralabrax maculatofasciatus	Spotted sand bass	—	99	952	1,051	0.4	83.7
Citharichthys sordidus	**Pacific sanddab**	**S**	28	**979**	1,006	0.4	84.1
Sebastes auriculatus	Brown rockfish	—	32	930	962	0.4	84.5
Ophiodon elongatus	Lingcod	—	38	777	815	0.3	84.8
Atractoscion nobilis	White seabass	—	92	714	807	0.3	85.1
Sebastes rosaceus	Rosy rockfish	—	2	796	797	0.3	85.4
Sebastes goodei	Chilipepper	—	0	601	601	0.2	85.6
Menticirrhus undulatus	**California corbina**	**O**	**563**	38	601	0.2	85.9
Scorpaenichthys marmoratus	Cabezon	—	141	390	531	0.2	86.1
Sebastes rastrelliger	**Grass rockfish**	**S**	**140**	321	461	0.2	86.3
Sebastes umbrosus	Honeycomb rockfish	—	—	387	387	0.2	86.4
Rhacochilus toxotes	Rubberlip seaperch	—	90	81	171	0.1	86.5
Rhacochilus vacca	**Pile perch**	**L**	**101**	56	157	0.1	86.5
Roncador stearnsii	**Spotfin croaker**	**D**	**116**	28	144	0.1	86.6
Sebastes dallii	calico rockfish	—	12	114	126	0.0	86.6
Prionace glauca	Blue shark	—	3	109	112	0.0	86.7
Sebastes rufus	Bank rockfish	—	5	102	107	0.0	86.7
Sebastes levis	Cowcod	—	—	42	42	0.0	86.7
Alopias vulpinus	Thresher shark	—	2	30	33	0.0	86.8
Isurus oxyrinchus	Shortfin mako	—	—	32	32	0.0	86.8
Coryphaena hippurus	Dolphinfish	—	—	23	23	0.0	86.8
Sebastes melanostomus	Blackgill rockfish	—	—	1	1	0.0	86.8

Source for landings data: Marine Recreational Fisheries Statistics Survey (MRFSS); no data available 1990–1992.

Note: Species in boldface represent bightwide or regional dominants by mode; remaining species are other important recreational fishes selected from Leet et al. 2001. Common names used are those of Nelson et al. 2004.

[a] Region: B = Southern California Bight (SCB), S = Santa Barbara/Ventura, D = Oceanside/San Diego, L = Los Angeles/Long Beach Harbor, O = Orange County.

[b] Total estimated landings (×1,000) in the SCB from 1980 to 2000 = 258,001.

[c] Cumulative.

highest percentage of catch. Further, we focused only on "strong" significant species correlations. Species considered to be strongly correlated with an independent variable were those with regression coefficients greater than +0.50 and less than −0.50. In a few instances, species were strongly correlated with more than one independent variable. Here, we focus on the environmental variable with the regression coefficient of greatest magnitude.

Relationship to fishery-independent data. We compared trends in recreational catch rate with trends in impingement rate where applicable. For instance, we did not examine trends of highly migratory species because of the assumed inefficiency of sampling these species from nearshore intake conduits. Upon initial investigation, visual comparisons of the species plots between the two data sets appeared to show recreational catch data lagging impingement data, suggesting that smaller individuals in a population were sampled in the impingement catch and later captured in the recreational fishery as larger individuals. Although length-frequency data are necessary to track cohorts of species through time from one database to the other, we were not able to obtain these because of time constraints.

Alternatively, we tested lag periods between the two data sets. Species plots visually identified as having similar trends in both data sets were further analyzed using product-moment correlation analysis. Cross-correlation coefficients were plotted at yearly MRFSS data lags from 0 to 7 yr. To meet the stationarity requirement for correlation analysis of autocorrelated data, the yearly catch rates from both data sets were first converted to z-scores (mean = 0, standard deviation = 1). To account for any within-series autocorrelation present in the fish data sets, we tested correlation coefficients derived from the correlation analysis against an adjusted r_{crit} value based on "effective" degrees of freedom ($N*$) at N/5 lags (Chelton et al. 1982; Brooks et al. 2002).

RESULTS

Trends in Recreational Fish Catch

We identified 26 dominant recreational fish species from the MRFSS estimated landings data and regional sample data from 1980 to 2000. Fourteen species made up 75% of either the bightwide shore catch or boat catch, and 12 species were identified as regional shore or boat dominants (tab. 1). Unidentified surfperch (Embiotocidae) and unidentified rockfish (*Sebastes* sp.) could not be distinguished by individual species, so they were not included in the rest of the analyses. The total cumulative bightwide catch of all 44 species was 87%, with catch dominants constituting 81% (tab. 1). In general, significant declines in landings for several recreational fish dominants were higher in frequency and magnitude than increases in both shore and boat fishing analyses. Also, the overall numbers of species showing either increases or decreases in CPUE were more evenly distributed than the numbers in the landings analysis, possibly indicating consequential shifts in target species as more desirable fishes became less abundant (available).[5]

In the shore fishery, 10 of the 15 dominant species showed significant proportional change in average annual catch (landings) between the 1980s and 1990s (fig. 3). Landings of barred surfperch (*Amphistichus argenteus*) and walleye surfperch (*Hyperprosopon argenteum*) declined the most (almost 100% fewer landings in the 1990s). Landings of queenfish (*Seriphus politus*), jacksmelt (*Atherinopsis californiensis*), pile perch (*Rhacochilis vacca*), and grass rockfish (*Sebastes rastrelliger*) declined by more than 75%. Landings of bocaccio (*Sebastes paucispinis*) also declined by more than 75%, but the decline was not significant. These declines may have influenced the significant increase in shore landings of kelp bass (*Paralabrax clathratus*) and California halibut (*Paralichthys californicus*) because similar increases in kelp bass and California halibut landings were not observed in the boat fishery (fig. 4) (shore CPUE did not also significantly increase). An increase in Pacific chub mackerel (*Scomber japonicus*) abundance and a decrease in grass rockfish abundance in the 1990s are evidenced by the significant changes in both landings and CPUE in the shore fishery. However, for three species showing significant decreases in landings (pile perch; queenfish; and Pacific bonito, *Sarda chiliensis*), CPUE also decreased (>50%), though not significantly (fig. 3).

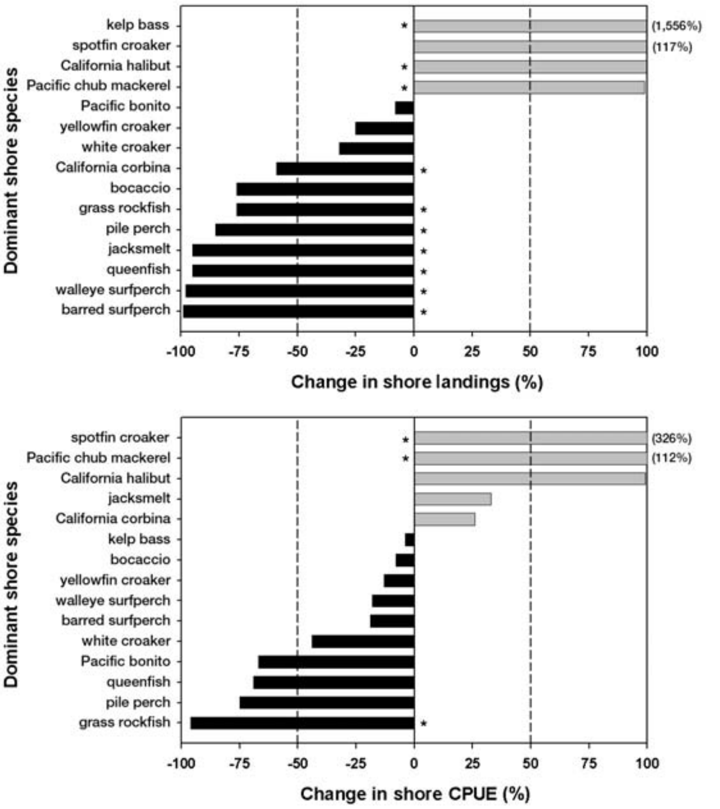


Figure 3. Percentage change in average landings (*top*) and catch per unit of effort (CPUE) (*bottom*), 1980s–1990s, of dominant fish species in the southern California recreational shore fishery. *Significant at $p < 0.05$.

Of the 18 regional dominant boat species, landings for 7 significantly decreased in the 1990s, while landings for 2 increased (fig. 4). Blue rockfish (*Sebastes mystinus*), Pacific bonito, olive rockfish (*Sebastes serranoides*), and white croaker (*Genyonemus lineatus*) declined the most (>75%), while landings of yellowfin croaker (*Umbrina roncador*) and ocean whitefish (*Caulolatilus prin-*

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[5] Because CPUE here reflects a measure of relative availability among species, significant decadal differences in landings for a species are not always matched by significant decadal differences in CPUE.

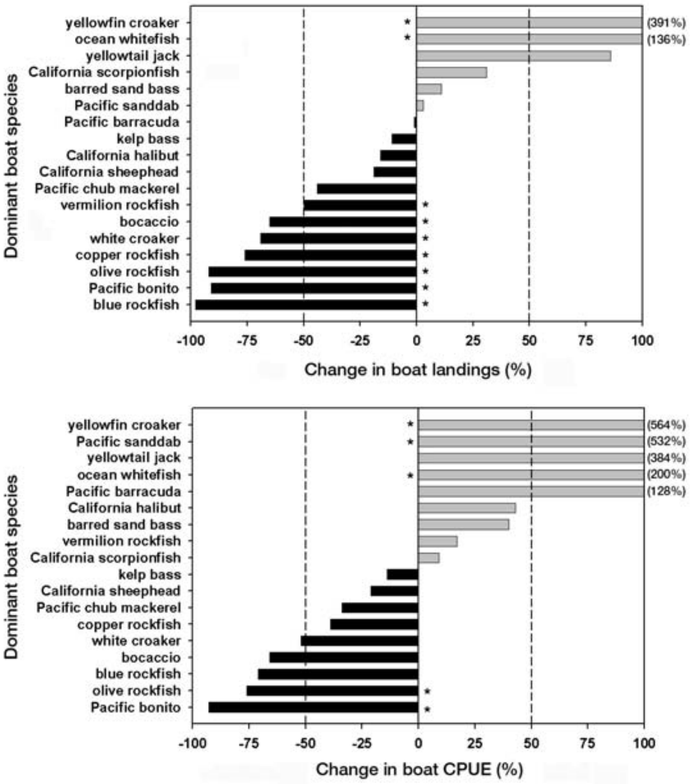


Figure 4. Percentage change in average landings (*top*) and CPUE (*bottom*), 1980s–1990s, of dominant fish species in the southern California recreational boat fishery. *Significant at $p < 0.05$.

ceps) increased by 391% and 136%, respectively. Although landings of Pacific bonito did not significantly decrease in the shore fishery, Pacific bonito landings and CPUE declined greatly in the boat fishery (>75%). Landings and CPUE for olive rockfish similarly decreased. Again, for several species in the boat fishery, it appears that either species availability or fishing effort increased in the 1990s in response to decreased availability of more desirable fishes (e.g., rockfishes). Yellowfin croaker, Pacific sanddab (*Citharichthys sordidus*), and ocean whitefish average CPUE increased by at least a factor of two in the 1990s. Although not statistically significant, yellowtail jack (*Seriola lalandi*) CPUE increased by 384%, and Pacific barracuda (*Sphyraena argentea*) CPUE increased by 128%, respectively.

Environmental Variables

Of the 45 recreational species selected in this study, 36 species correlations (representing 27 species) were identified (tab. 2). Of these 27 species, 10 were dominant species exhibiting significant changes in landings or CPUE. Overall, the highest percentage of species correlations (33%) was with the PDO, followed by upwelling in the bight (25%), upwelling in the south (20%), offshore sea-surface temperature (11%), upwelling in the north (8%), and El Niño (3%).

Of the 12 PDO correlations, 10 were negative responses (as sea-surface temperature increased throughout the 1980s and 1990s, fish population trends decreased) (tab. 2). The greatest negative responses were with ocean whitefish, rosy rockfish (*Sebastes rosaceus*), barred surfperch, gopher rockfish (*Sebastes carnatus*), and bocaccio. The PDO explained 99.9% of the variability within the barred surfperch shore data, 71% within the olive rockfish impingement data, and 77% within the bocaccio impingement data. All three species were catch dominants exhibiting declines in either shore or boat landings by more than 50%; however, the significant increase in ocean whitefish landings and CPUE is contrary to its negative response to the PDO. White seabass (*Atractoscion nobilis*) and shortfin mako (*Isurus oxyrinchus*) were the only species exhibiting positive correlations with the PDO (higher catch in the 1980s and 1990s).

All of the species trends that correlated with upwelling in the SCB were positive responses (tab. 2), indicating that residuals of the fish trends showed higher abundance (or catch) in the 1980s (relative to the 1990s) when upwelling in the SCB was greatest. Most of these species were rockfishes (chilipepper, *Sebastes goodei*; blue rockfish; bank rockfish, *Sebastes rufus*; and copper rockfish, *Sebastes caurinus*), with chilipepper showing the greatest positive correlation (0.81, 2-yr lag). Five species trends (barred sand bass, *Paralabrax nebulifer*; Pacific barracuda; Pacific sanddab; Pacific chub mackerel; and blue shark, *Prionace glauca*) were correlated with upwelling south of the SCB (tab. 2). Of these, barred sand bass (2-yr lag) and Pacific barracuda (1-yr lag) were negatively correlated, while the other three species were positively correlated. A negative correlation with upwelling south of the SCB implied higher residual abundance (or catch) in the 1980s (relative to the 1990s). Only brown rockfish (*Sebastes auriculatus*) was correlated with upwelling north of the SCB (0.58, 2-yr lag; tab. 2). Of the dominants exhibiting significant changes in landings, upwelling in the SCB explained 36% of the variability in the residuals for copper rockfish, 51% for blue rockfish (both MRFSS boat data), and 45% for spotfin croaker (*Roncador stearnsii*) (San Onofre Nuclear Generating Station impingement data). Southern upwelling explained 34% of the variability in the residuals for the Pacific sanddab CSDLAC trawl data and 56% for Pacific chub mackerel shore data.

Two species trends were correlated with offshore sea-surface temperature (tab. 2). California corbina (*Menticirrhus undulatus*) was positively correlated (0.56, 2-yr lag), while honeycomb rockfish (*Sebastes umbrosus*) was negatively correlated (−0.66, no lag) (tab. 2). Offshore sea surface temperature accounted for 33% of the variability in the residuals of the impingement data for California corbina, whose landings significantly decreased in the 1990s.

TABLE 2
Positive and Negative Partial Regression Coefficients (Species-Correlations) by Recreational Fish Species and Environmental Variable (PDO, El Niño, Offshore Sea-surface Temperature, and Upwelling Relative to the Southern California Bight), Ranked by Magnitude

	Temperature			Upwelling				
Common name	PDO	El Niño	Offshore	North	Bight	South	R^2	Relevant Database[a]
Ocean whitefish[b]	**−1.84**	—	—	—	−1.10	−0.61	35	recfin_b
Rosy rockfish	**−1.46**	—	—	—	—	—	82	recfin_b
Barred surfperch[c]	**−1.42**	—	—	—	—	—	99	recfin_s
Gopher rockfish	**−1.21**	—	—	0.69	0.76	0.63	91	recfin_b
Bocaccio[b]	**−0.98**	—	—	—	—	—	77	imp_ns
Olive rockfish[c]	**−0.94**	—	—	—	—	—	99	imp_ns
Spotted sand bass	**−0.93**	—	—	—	—	—	45	imp_ns
Calico rockfish	**−0.90**	—	—	—	—	—	53	laco
Rubberlip seaperch	**−0.68**	—	—	—	—	—	82	imp_ns
Cabezon	**−0.55**	—	—	—	**0.61**	—	54	imp_ns
White seabass	**0.51**	—	—	—	—	—	30	imp_ns
Shortfin mako	**1.36**	—	—	—	—	—	39	recfin_b
Lingcod	—	—	—	—	**0.56**	—	50	recfin_b
Bank rockfish	—	—	0.52	0.53	**0.59**	—	45	recfin_b
Copper rockfish[c]	—	—	—	—	**0.59**	—	36	recfin_b
Blue rockfish[c]	—	—	0.63	—	**0.64**	—	51	recfin_b
Spotfin croaker[c]	—	—	—	—	**0.65**	—	45	imp_23
Chilipepper	—	—	—	—	**0.81**	—	45	recfin_b
Barred sand bass	—	—	—	—	—	**−0.57**	43	imp_ns
Pacific barracuda	—	—	—	—	—	**−0.51**	71	imp_ns
Pacific sanddab[c]	—	—	—	—	—	**0.51**	34	laco
Pacific chub mackerel[c]	—	—	—	—	—	**0.54**	56	recfin_s
Blue shark	—	—	—	—	—	**0.70**	33	recfin_b
Honeycomb rockfish	—	—	**−0.66**	—	—	—	23	recfin_b
California corbina[c]	—	—	**0.56**	—	—	—	33	imp_ns
Brown rockfish	—	—	—	**0.58**	—	—	47	imp_ns
Cowcod	—	**−0.53**	—	—	—	—	23	laco
Albacore	—	—	—	—	—	—	—	N/A[b]
Blackgill rockfish	—	—	—	—	—	—	—	recfin_b
California halibut[c]	—	—	—	—	—	—	—	imp_ns
California scorpionfish	—	—	—	—	—	—	—	laco
California sheephead	—	—	—	—	—	—	—	recfin_b
Dolphinfish	—	—	—	—	—	—	—	N/A[b]
Grass rockfish[c]	—	—	—	—	—	—	—	imp_ns
Jacksmelt[c]	—	—	—	—	—	—	—	imp_ns
Kelp bass[c]	—	—	—	—	—	—	—	imp_ns
Pacific bonito[c]	—	—	—	—	—	—	—	recfin_b
Pile perch[c]	—	—	—	—	—	—	—	imp_ns
Queenfish[c]	—	—	—	—	—	—	—	imp_ns
Thresher shark	—	—	—	—	—	—	—	recfin_b
Vermilion rockfish	—	—	—	—	—	—	—	laco
Walleye surfperch[c]	—	—	—	—	—	—	—	imp_ns
White croaker[c]	—	—	—	—	—	—	—	laco
Yellowfin croaker[c]	—	—	—	—	—	—	—	imp_ns
Yellowtail jack	—	—	—	—	—	—	—	recfin_b
Total species correlations	12	1	4	3	9	7		

Note: Boldfaced values are the species-correlation of greatest magnitude for each species. Common names used are those of Nelson et al. 2004.

[a] recfin_b = recreational boat catch data, recfin_s = recreational shore catch data, imp_ns = non-SONGS (San Onofre Nuclear Generating Station) power-generating-station impingement data, laco = County Sanitation Districts of Los Angeles County trawl data, imp_23 = SONGS 2 and 3 power-generating-station impingement data.

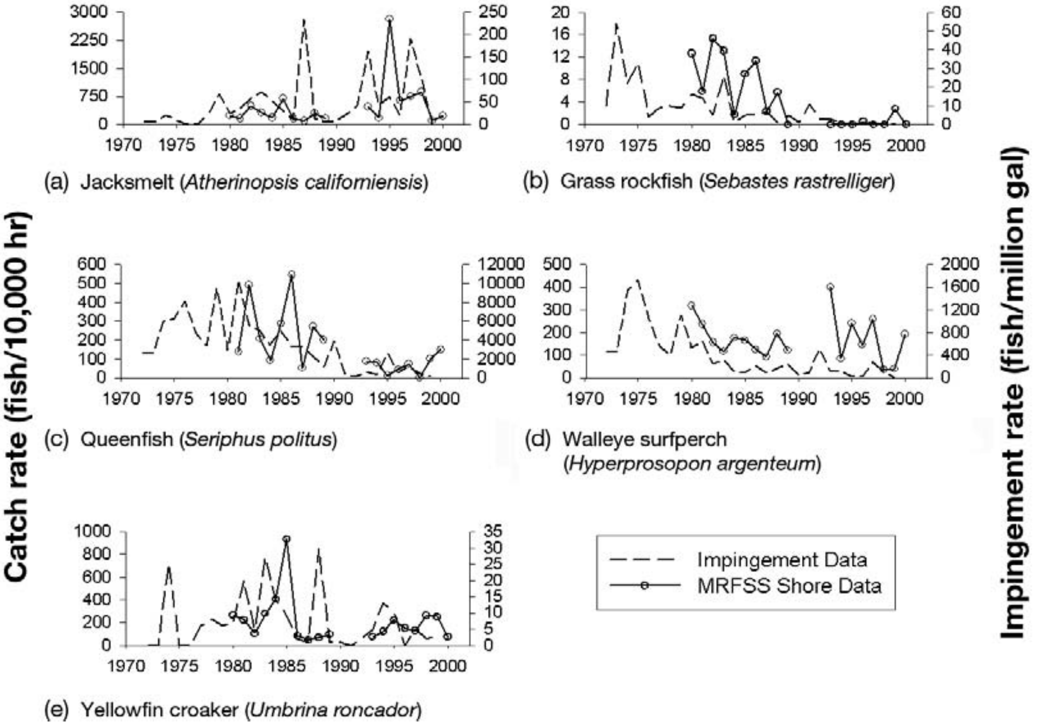
[b] N/A = not enough data for analysis.

[c] Species exhibiting significant differences in catch or CPUE between the 1980s and 1990s.

Cowcod trawl data showed a strong negative correlation (tab. 2) with El Niño at a lag of zero. As cowcod in the trawl data are typically small, the lag suggests there may be reduced recruitment of young-of-the-year from the water column to the bottom during El Niño years; larger juveniles may move to greater depths not sampled in the trawl surveys.

Relationship to Fishery-independent Data

Thirty-five recreational species trends (MRFSS sample data) were investigated for similarities to impingement data (fishery-independent data). When catch rates were plotted together on the same graph, recreational shore data trends for five species of fish (fig. 5), and boat data trends for six species (fig. 6), appeared similar to the



(a) Jacksmelt (*Atherinopsis californiensis*)

(b) Grass rockfish (*Sebastes rastrelliger*)

(c) Queenfish (*Seriphus politus*)

(d) Walleye surfperch (*Hyperprosopon argenteum*)

(e) Yellowfin croaker (*Umbrina roncador*)

Figure 5. Comparison of MRFSS shore data trends (all modes, 1980–2000) and power-generating-station impingement data trends in southern California (1972–1999). No MRFSS data for 1990–1993.

impingement data trends, with MRFSS data lagging impingement data. Of these species, shore trends for grass rockfish, queenfish, yellowfin croaker, and walleye surfperch showed declining catch rates in both data sets over time, with jacksmelt increasing (fig. 5). Boat trends for white croaker, brown rockfish, bocaccio, blue rockfish, and olive rockfish also showed declining catch rates in both data sets over time (fig. 6). Barred sand bass remained stable.

Cross-correlation analysis of the MRFSS data and impingement data revealed only six species trends with significant correlations to the impingement data trends. Two correlations (grass rockfish and yellowfin croaker) were found with shore data and four (white croaker, blue rockfish, brown rockfish, and olive rockfish) with boat data (fig. 7). Significant correlations found between the two data sets indicate a similar forcing of declines. However, environment-species relationships were found only for brown rockfish, blue rockfish, and olive rockfish (tab. 2).

Only two significant species correlations occurred at a specific lag (white croaker, boat data, 1 yr; yellowfin croaker, shore data, 1 yr) (fig. 7a,b). Cross-correlation coefficients for blue rockfish, olive rockfish, grass rockfish, and brown rockfish were significant at nearly all lags (fig. 7c–f), possibly because the MRFSS sampled several year classes of rockfish. In this case, the lag with the highest cross-correlation coefficient (strongest correlation) most likely represents a dominant year-class present in the MRFSS data. The strongest cross-correlation coefficient ($r = 0.80$, $r_{\mathrm{crit}} = 0.45$) of all species occurred with blue rockfish boat data at a lag of five years (fig. 7c).

DISCUSSION

Nearly half of the important recreational fishes analyzed in this study showed mostly negative population responses to temperature or positive population responses to upwelling in the SCB to varying degrees, the most influential environmental variable being the PDO. These species-specific environmental responses corresponded with significant changes in landings or CPUE between the 1980s and 1990s, thus strengthening the validity of the identified responses. And, although we found few significant relationships between fishery-dependent (recreational catch) and fishery-independent (impingement) data to further validate the extent of an environmental influence, the relationships that were identified indicate another potential tool for forecasting recreational fish catches.

Most of the species negatively correlated with the PDO were rockfishes. This negative relationship with warm temperatures is consistent with widespread recruitment in 1999 (a cold year following the warm regime) of young-of-the-year (YOY) rockfishes at all of the oil platforms surveyed in the Santa Barbara Channel

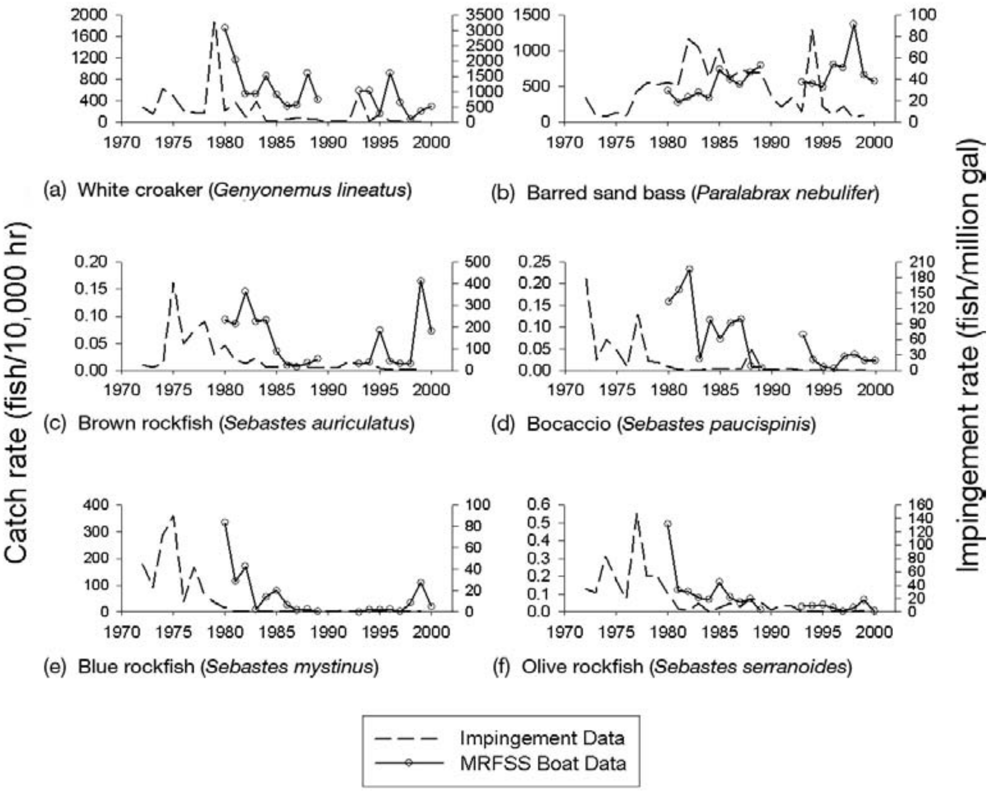


Figure 6. Comparison of MRFSS boat data trends (all modes, 1980–000) and power-generating-station impingement data trends in southern California (1972–1999). No MRFSS data for 1990–1993.

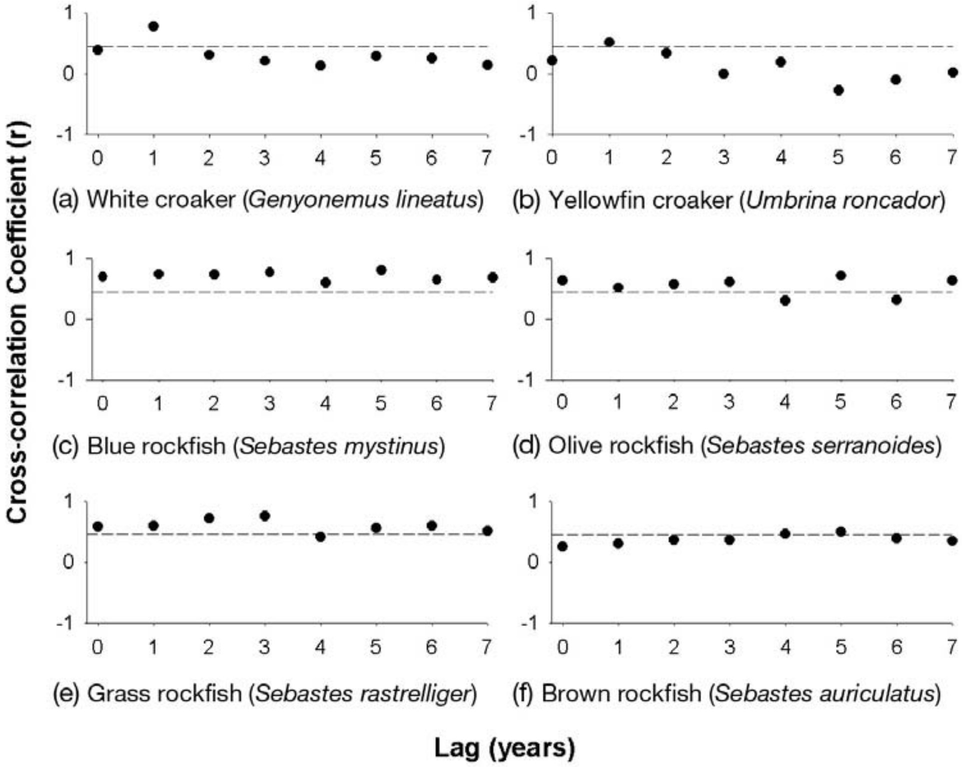


Figure 7. Cross-correlation coefficients at lags 0–7 yr. Dashed lines indicate the r_{crit} significance level at $p < 0.05$; the point falling above this line defines the lag at which MRFSS data significantly correlated with impingement data.

and Santa Maria Basin (Love et al. 2003). In addition, the 2003 stock assessment for bocaccio also indicated a strong 1999 year-class and increased abundance since 1999.[6] With the PDO accounting for 30–99% of the variability within the species plots, significant catch declines of barred surfperch, bocaccio, and olive rockfish are likely explained in part by a negative PDO response. One might expect only cold-temperate or temperate species to respond negatively to warming ocean conditions. However, many of the negative PDO responses were in warm-temperate species (ocean whitefish; spotted sand bass, *Paralabrax maculatofasciatus*; barred surfperch; rubberlip seaperch, *Rhacochilus toxotes*; calico rockfish, *Sebastes dallii*; gopher rockfish). We concluded in our earlier report that environmental variable responses appeared to be species-specific and did not show definite patterns by life-history categories,[7] but with respect to recreational fishes, other factors discussed below may have driven these results.

Although the species responses to temperature do not appear to be easily generalized, temperature responses of commercial species reported by Norton and Mason (2003) are consistent with results in this study. Norton and Mason report a significant positive correlation with white seabass commercial landings data and temperature over the last 70 years along the California coast, in addition to a negative correlation for cabezon (*Scorpaenichthys marmoratus*). Multiple-regression analysis used in this study also shows a positive relationship with temperature for white seabass and a negative correlation with cabezon (tab. 2). Norton and Mason (2003) report temperature correlations with Pacific barracuda (strong positive), Pacific chub mackerel (weak positive), and lingcod (*Ophiodon elongatus*; strong negative), where we identified only upwelling associations. The most representative database for these species in this study was the 20-yr MRFSS boat database. Many of the upwelling correlations were found in 20-yr MRFSS databases, suggesting that if these data had extended for 30 yr (to better capture the last PDO cycle), we may also have found temperature correlations with these species. Indeed, Stull et al. (1987) report higher catches at Palos Verdes Peninsula of Pacific chub mackerel and Pacific barracuda coincident with the El Niño events of 1966, 1976–1978, and 1982–1983. They also report lingcod catches highest from 1973 to 1980 (cold years) in the Palos Verdes area, but numbers were few in comparison to other local fish species.

Upwelling was also an important predictor of species trends, but it accounted for less of the variability, suggesting that over the long term changes in upwelling influence recreational fishes less than changes in temperature. Nevertheless, upwelling in and south of the SCB corresponded to a higher number of declines and increases in catch of dominant species than did the PDO. Upwelling responses reported in this study may be an artifact of fishing locality, which may in turn reflect higher fish abundance in upwelling sites with high seasonal food availability. But population trends positively correlated with upwelling were also observed with fishery-independent data for several other species (barred sand bass, Pacific barracuda, Pacific sanddab, and spotfin croaker).

Although only one El Niño correlation (cowcod) was identified, biological effects of El Niño in southern California have been studied extensively over the last two decades. Increased abundances or range extensions for many fish species, including several species in our study (e.g., Pacific chub mackerel; Pacific bonito; Pacific barracuda; and dolphinfish, *Coryphaena hippurus*) have been reported during El Niño events (Mearns 1988; Karpov et al. 1995; Lea and Rosenblatt 2000). Fish population responses to El Niño may be better characterized in combination with data on larvae and recruitment. Recent research in central California found that high juvenile recruitment of several species of rockfish occurred during either El Niño or La Niña, coinciding with relaxation and upwelling events, respectively.[8]

Many recreationally fished species that did not show responses to environmental trends are valued more highly than those that did. Some of the most targeted sport fishes are Pacific bonito, California halibut, kelp bass, yellowtail jack, albacore (*Thunnus alalunga*), dolphinfish, and thresher shark (*Alopias vulpinus*). Albacore, dolphinfish, and thresher shark are seasonal migrants (Leet et al. 2001) and did not occur in greater than 50% of the years in their most relevant database; trends for these species were most likely too incomplete to show good correlations. This was also the case for blackgill rockfish (*Sebastes melanostomus*), which is primarily commercially fished (Love and Butler 2001), bank rockfish (*Sebastes rufus*), chilipepper, and blue shark. Of species occurring in more than 50% of the years in our data, commercial catch data show weak correlations with temperature over the last 70 years for Pacific bonito (negative), California halibut (positive), and white croaker (negative) (Norton and Mason 2003), coincident with reduced catches in the 1990s of white croaker and Pacific bonito, and increased catches of California halibut found in our study. Norton and Mason (2003) also found moderately strong temperature correlations with albacore (negative), yellowtail

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[6] MacCall, A. 2003. Status of bocaccio off California in 2003. Pacific Fishery Management Council, Portland, OR.

[7] See n. 1.

[8] Stephens, T. 2003. New studies reveal connections between oceanographic processes and rockfish populations. *In* UC Santa Cruz Currents Online, 17 February 2003, http://www.ucsc.edu/currents/02-03/02-17/rockfish.html.

jack (positive), California sheephead (*Semicossyphus pulcher*) (positive), and California scorpionfish (*Scorpaena guttata*) (positive). Still, no environmental relationships were identified in this study for seven important species (walleye surfperch, pile perch, grass rockfish, queenfish, jacksmelt, kelp bass, and yellowfin croaker) for which data appeared relevant and in sufficient frequency.

Recent recreational catch trends described by Dotson and Charter (2003) report that as the relative availability of rockfishes declined, the availability of California scorpionfish, ocean whitefish, and Pacific sanddab increased. Pacific sanddab CPFV catch reports in 1998 rose by 12,200% of the long-term mean in only four years. These trends are also evident in our reports of the significant positive proportional change in CPUE for these species (figs. 3 and 4). The increase in Pacific sanddab catch has been a heightened topic of interest over the last several years. Fish biologists and fisheries managers speculated whether the higher catch indicated an actual increase in availability or if anglers switched target species in response to rockfish regulations. While it is now agreed that the recreational catch increases represent a shift in exploitation from the rockfish fishery, data from CSDLAC time-series (fishery-independent data) also show much larger trawl catches of Pacific sanddab beginning in 1995. Although not easily explained, our environment-species data suggest that this increase in trawl catch may be partly due to increased upwelling off southern Baja California (tab. 2), which can be interpreted as upwelling relaxation in southern California in the 1990s (fig. 2).

Comparisons of the MRFSS recreational fish catch data and the fishery-independent impingement data reveal that for a few nearshore species, MRFSS sample data trends correlate with impingement data trends. Still, it is difficult to assess whether similar temporal changes reflect fishery effects or natural population dynamics. The timing of the regime shift in the SCB coincides with the expansion of several fisheries, but mainly rockfishes (Moser et al. 2000). However, environment-driven trends are indicated by negative PDO responses that we also found with nonexploited rockfishes.[9] For yellowfin croaker, the correlation between the two data sets seems even less fishery-driven. The population appears relatively stable compared with many rockfish populations, and our results (MRFSS data lag at 1 yr) correspond well with those of another report,[10] which shows that yellowfin croaker CPFV catch trends peaked a year after impingement data. The authors reasoned that impingement cohorts would probably not enter the CPFV fishery until a year or so later. If more connections such as this can be identified, impingement data (in combination with oceanographic data) may prove very useful for forecasting changes in recreational fish catches. The efficacy of using these data sources together would be strengthened with additional studies determining age-class relationships between fishery-dependent and fishery-independent data.

As mentioned above, other factors may have influenced some of our unexpected results. First, lag data suggest that our environment-species correlations may apply only to a specific life-history stage. For example, impingement data may be primarily sampling YOY of certain fish species, and, therefore, environment-species correlations may not apply to the adult population. In the case of cowcod, where El Niño was found to reduce catch, the average length sampled in the CSDLAC trawls was 15 cm—the average size of juveniles approximately two years of age (Love et al. 2002). On the other hand, CPFV catches of adult cowcod do not show marked decreases in catch during El Niño years compared with other years (Dotson and Charter 2003). Second, for species such as spotted sand bass and ocean whitefish, whose adult populations in southern California are highly dependent on sporadic recruitment events related to El Niño and upwelling (Allen et al. 1995; Rosales-Casián and Gonzalez-Camacho 2003), our results may represent fishing effects. Because of the highly variable timing and success of these recruitment pulses, our data sources for these species likely include relatively few year classes. Fishing pressure on these small populations in the SCB may be the driving force in the spotted sand bass impingement and ocean whitefish boat catch trends and consequently, in our observed negative PDO responses (L. G. Allen, CSUN, pers. comm.). Lastly, while we attempted to diminish the effects of sampling bias, it is also possible in a few instances that environment-species results may be an artifact of smoothing the data or of chance.

The extent of environmental influence on the variability of the species plots and residual species plots with respect to temperature and upwelling ranged from 30% to 91% (tab. 2). This indicates that fish populations are influenced by environmental variables to varying degrees. Therefore, the results discussed here are not meant to suggest that environmental effects are more influential on fish populations than are such factors as fishing, habitat alteration, disease, or pollution. Our findings merely emphasize the complexity of the relationships and point out where we need future work. With the continuation of long time-series of fishery-dependent, fishery-independent, and oceanographic data, we have

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[9] See n. 1.

[10] Herbinson, K. T., M. J. Allen, and S. L. Moore. 2001. Historical trends in nearshore croaker (family Sciaenidae) populations in southern California from 1977 through 1998. *In* Southern California Coastal Water Research Project Annual Report 1999–2000, S. B. Weisberg, ed. Westminster, Calif.: S. Calif. Coastal Water Res. Proj., pp. 253–264.

the opportunity to refine our knowledge of the relationship between natural environmental change, human influence, and fish populations.

ACKNOWLEDGMENTS

A portion of this article was developed from our larger report (see n. 1), which was funded in part by the Santa Monica Bay Restoration Commission and the California State Coastal Conservancy (CSCC Proposition 12 Grant Program, SMBRP grant agreement no. 01-088). Jim Allen (Southern California Coastal Water Research Project; SCCWRP) provided insight, comments, and editorial review. Robert Smith conducted the multiple-regression analyses that were the basis of the environment-species relationships described in this study. We thank Kevin Herbinson (Southern California Edison) who provided southern California power-generating station fish impingement data; Valerie Raco-Rands (SCCWRP) for a huge contribution to database development; Brock Bernstein for input on oceanic studies; Kerry Ritter and Ananda Ranasinghe (both of SCCWRP), for statistical advice; Michele Horezcko and Tom Mason (Pacific States Marine Fisheries Commission) for spatial information and interpretation of the MRFSS data; and Larry Allen (CSUN) and one anonymous reviewer for their insightful comments on the manuscript.

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HISTORICAL PATTERNS FROM 74 YEARS OF COMMERCIAL LANDINGS FROM CALIFORNIA WATERS

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ABSTRACT

California's commercial fisheries harvested many different species of finfish and invertebrates from 1928 to 2001. A time series of the landings from waters off California was created to examine changes in the species composition, weight, and value of the landings. Small coastal pelagic fishes dominated the landings weight until the late 1980s, when landings of invertebrates increased. Tunas, groundfish, salmon, crabs, sea urchins, and squid have all contributed significantly to the value of the landings. Value and landings were affected by domestic and international market conditions. The availability of certain species, especially coastal pelagics, has varied in response to decadal-scale changes in environmental conditions, and tunas, herring, and squid varied with interyear environmental warming from California El Niño events. The depletion and subsequent regulation of many of the stocks, including several rockfish, have contributed to declines in their landings over time. Invertebrates became more important in both the weight and value of landings in the 1990s. The declining trend in the total value of landings, despite increased total landings, raises concern for the future of the fishing economy.

INTRODUCTION

California's fisheries have experienced wide changes in abundance of targeted species, leading to the collapse of some fisheries, including Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), and certain groundfish species. Many fisheries have maintained high landings for only ten to twenty years, and new fisheries have been developed to replace those that have declined. Changes in the size and type of fish landed on the U.S. Pacific Coast were described for four periods from 1888 to 1976 by Deimling and Liss (1994). In this article, a continuous series of California landings from 1928 to 2001 will be examined.

At the beginning of the twentieth century, California's fisheries were generally assumed to be inexhaustible. Among the first fisheries to be regulated were those that had been heavily exploited in the rivers and estuaries, such as salmon (*Oncorhynchus* spp.)(Fry 1949) and sturgeon (*Acipenser* spp.)(Nelson 1949). California barracuda (*Sphyraena argentea*) was among the early marine species to be regulated, beginning in 1915 (Ally and Miller 2001). The notion that our fisheries are inexhaustible was proven untrue by the collapse of the Pacific sardine population and fishery in 1952. Sardines staged a slight recovery in the late 1950s but then continued to decline until a moratorium was placed on their sale in 1974. Heavy fishing pressure on spawning stocks (Murphy 1966) and ocean environmental conditions (Chavez et al. 2003) contributed to the changes in sardine availability.

The groundfish fishery expanded after the collapse of the sardine fishery, when many vessels converted from the sardine fleet to the groundfish fleet. Groundfish landings reached a peak in the 1980s but then decreased as more regulations were created to slow the harvest and protect certain species from overfishing. In 1996, the goal of sustainability was incorporated into federal management strategies in the revision of the Magnuson-Stevens Fishery Conservation Act, and quotas and trip limits were placed on many species to order to achieve that goal. Recent estimates of rockfish productivity were lower than previously modeled, and some species became overfished despite intensive management (PFMC 1998b). To protect certain overfished rockfishes, the Pacific Fisheries Management Council closed about half the bottom-fishing grounds on the continental shelf of the West Coast in 2002.

How sustainable have California fisheries been? The duration of fisheries and changes between fisheries will be examined for the last 74 years from records of California commercial landings published by the California Department of Fish and Game (CDFG). Landings are not an unbiased representation of the abundance or availability of species in the area, but they do indicate changes in the fisheries, which were also affected by market demand and fishing regulations. To better indicate the market's effects on the fisheries, the value of the landings will also be examined.

[Manuscript received 23 February 2004.]

METHODS

The weight and value of the catch brought to shore for sale (the landings) are recorded by fish buyers, markets, and canneries and compiled by CDFG. The monthly commercial landings of fish and invertebrates are taken from summary tables published in CDFG's *Fish Bulletin* series for 1928-1976 (numbers 44, 49, 57, 58, 59, 63, 67, 74, 80, 86, 89, 95, 102, 105, 108, 111, 117, 121, 125, 129, 132, 135, 138, 144, 149, 153, 154, 159, 161, 163, 166, 168, 170). The published tables include California landings of fishes caught either north or south of California's borders; the majority of these landings were tropical tunas. In order to track the variability of species from California waters, this data set includes only the landings recorded as caught off California. The initial year for our data set was 1928, the first year that monthly landings from southern waters were distinguished from those caught off California.

Published landings after 1976 in *Fish Bulletin* 173 did not indicate catch from north or south of California nor monthly values, so the 1977–1980 data were taken from unpublished reports of monthly landings produced by the Statistics Branch of CDFG. Beginning in 1981, the monthly landings were obtained in a digital file from PacFIN (Pacific Fisheries Information Network) with data supplied by CDFG. The extract of the PacFIN data was limited to waters off California and was standardized to dressed weights (rather than round weights) for all species, to be consistent with CDFG tables before 1981. The landings data can be accessed through the live-access server on the Web page www.pfeg.noaa.gov.

Landings are recorded by market categories; many of them contain a single species, but some contain several species caught and sold together. Over time, the number of categories used each year has increased from 67 to over 300. Most of this increase stems from the subdivision of existing categories, such as unspecified sole (Pleuronectidae), into separate species categories, but some is from the harvest of formerly unexploited groups, such as red sea urchins (*Strongylocentrus franciscanus*). Pacific mackerel and jack mackerel (*Trachurus symmetricus*) were landed together as unspecified mackerel from 1977 to 1990; the CalCOFI table of landings of pelagic wetfishes was used to separate landings of those two species for those years (CDFG Marine Region 1998). For this analysis, market categories were combined into major groups plotted as stacked-column time series of total landings. The composition of each major group is also broken down in a separate plot to show more detail, but only seven species or groups with significant shares of the landings can be clearly displayed in each figure.

The value of the landings paid to fishers (ex-vessel value) for market groups was also recorded in CDFG's *Fish Bulletins* beginning in 1939. This was put into a second data set. To remove the value of the landings caught north or south of California's borders, the value of those landings was calculated for each market group, using that group's average price per pound for that year and subtracted from the value of the landings. PacFIN data were used to extend the series from 1981 through 2000, and tables from the United States Bureau of Fisheries (1928–1938) were used to extend the series of values back from 1938 to 1928. To remove the effects of inflation, all values were then standardized to year 2000 dollars with the Consumer Price Index (Bureau of Labor Statistics 2002).

The time series of commercial landings does not necessarily reflect the relative abundance or availability of different species in the ocean off California. Instead, it is a composite of abundance, availability, market demand (which sets price and maximum trip weight), and each fisher's preference (based largely on economics, experience, gear, and type of vessel) for catching one species or group over another. Fishing regulations, such as catch quotas, also play a part in limiting some fisheries, particularly since the 1980s. Thus the relative increase or decrease of a species in the landings may reflect more than just a change in abundance.

RESULTS

Most of California's landings come from four categories: groundfishes, coastal pelagic fishes, tunas, and invertebrates. A few other significant fisheries that do not fit into these categories are grouped here as "other fishes." Within each fishery, the dominant species landed has changed over time. Different kinds of vessels and equipment are used in each of these fisheries, and this limits the opportunity to change from one fishery to another.

Groundfishes comprise several different types of fish caught on or near the bottom, including flatfish (Pleuronectidae and Bothidae), rockfish (*Sebastes* spp.), thornyheads (*Sebastolobus* spp.), sablefish (*Anoplopoma fimbria*), and Pacific hake (*Merluccius productus*). Most groundfishes are caught with otter trawls towed from boats 50 feet or longer; some are caught in midwater, particularly widow (*Sebastes entomelas*) and yellowtail rockfish (*S. flavidus*) and hake. Some sablefish are caught with traps, some sablefish and thornyheads are caught on longlines, and since the 1990s a small percentage of rockfishes have been caught on hooks in shallow water for the live-fish market. Gill nets were also used for rockfishes and California halibut (*Paralychthys californicus*) in the 1980s and earlier, but gill nets were restricted to progressively deeper water in the 1990s to prevent bycatch of diving birds and mammals.

There were two periods of rapid growth for total groundfish landings, one in the mid-1940s and the other in the 1970s; and there was a period of steady decline in

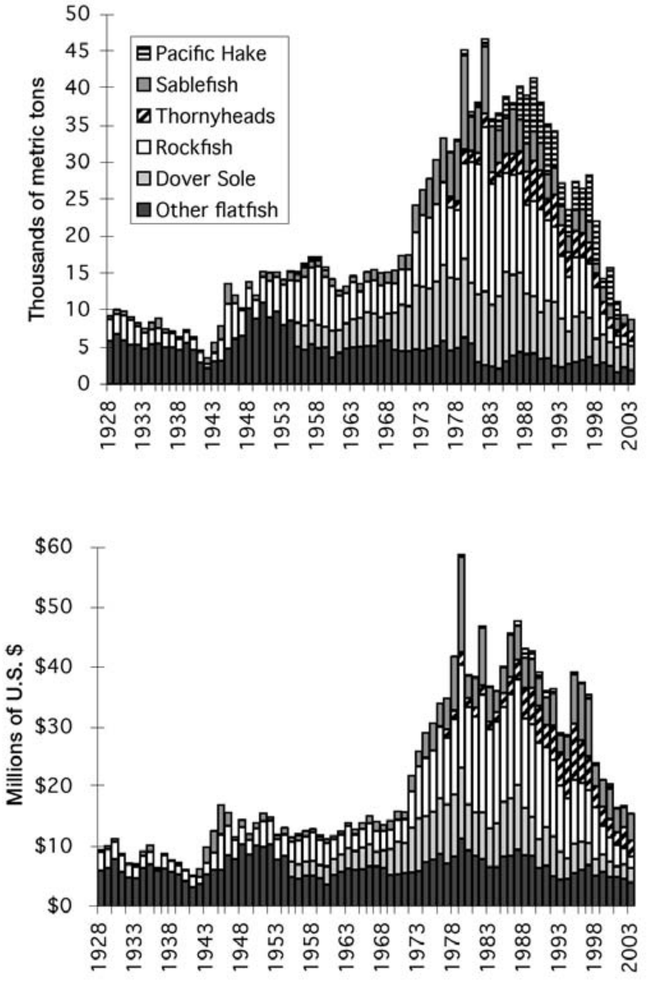

Figure 1. Landings of groundfishes, by weight (*top*) and value (*bottom*). Stacked columns represent cumulative total of species groups.

the 1990s (fig. 1a). Groundfish landings increased in the late 1940s because of improved technology with the development of the balloon trawl, and because of increased markets for frozen fillets of rockfishes and flatfishes to the U.S. military during World War II (Phillips 1949; Lenarz 1987). Dover sole (*Microstomus pacificus*) landings were part of the 1940s increase and reached 8 million pounds by 1948 (Henry et. al 2001); however, flatfishes were not separated by individual species in the published tables (nor are they in fig. 1) until 1955. Dover sole continued to increase until the mid-1970s, stabilized for a decade, and then declined after the mid-1980s, dropping to 34% of the 1980s average by 2000. The "other flatfishes" category includes all species of soles (except Dover sole after 1955), flounders, turbots, and halibuts; their combined landings were steady from 1955 to 1980 but declined in the late 1990s as restrictions were placed on the harvest of certain associated rockfishes.

The increase in groundfish landings from 1972 to 1982 came primarily from increased landings of Dover sole, rockfishes, especially widow rockfish (Pearson and Ralston 1990), and sablefish. Rockfishes were the largest component of groundfish in the 1980s but declined in weight in the 1990s, and by 2000 had dropped to only 12% of their 1980s average. Sablefish landings grew to a maximum in 1979 as an export market in Japan was developed and traps were used, but their landings declined after 1982, when regulations limiting their harvest were imposed. Thornyheads, deepwater relatives of the rockfishes, increased in landings in the late 1980s as fishing expanded into deeper water and as a market developed in Japan. In recent years, total groundfish landings declined as sablefish, thornyheads, and certain rockfish species became increasingly regulated to prevent overfishing and to rebuild certain depressed stocks. Pacific hake (Pacific whiting) is a perishable fish that did not have a large U.S. market through the 1970s. From 1966 to 1976, Pacific hake was fished by foreign fleets off California and by joint-venture fisheries with U.S. vessels delivering landings to foreign-processing vessels at sea (Quirollo et al. 2001), but those catches were not landed in California and do not appear in this data set. Shoreside processing in northern California developed in the late 1980s, and all landings have been domestic since 1991; only domestic landings are included in Figure 1a.

Total groundfish value (fig. 1b) followed the same general trends as the landings. However, certain species of the "other flatfishes" category, especially California halibut and petrale sole (*Eopsetta jordani*), commanded a higher price (adjusted to year 2000 dollars), and therefore "other flatfishes" contributed a higher proportion to the groundfish value. The average price per pound of rockfish doubled between 1998 and 2001 as live and premium-quality rockfish became a higher proportion of the landings. Thornyheads and sablefish brought a high price for export to Japan in the 1990s. The price for hake was relatively low, so it contributed only a small percentage of groundfish value despite the high landings. The main cause of the drop in total value of groundfish has been the decline in their landings from 1989 to 2001.

The coastal pelagic fishes include Pacific sardine, northern anchovy (*Engraulis mordax*), Pacific mackerel, and jack mackerel—all schooling species caught by setting seine nets around the schools, generally within a few miles of shore. The fish were mostly canned or reduced to fish meal and fish oil through the 1970s, and frozen by the 1990s. Dominant species of coastal pelagics and their total landings changed after the first 20 years of the series. In 1928 (fig. 2a), the sardine fishery was already well underway, having grown tenfold during World War I, and another threefold by 1928 (Scofield 1936). Sardines dominated the statewide landings until

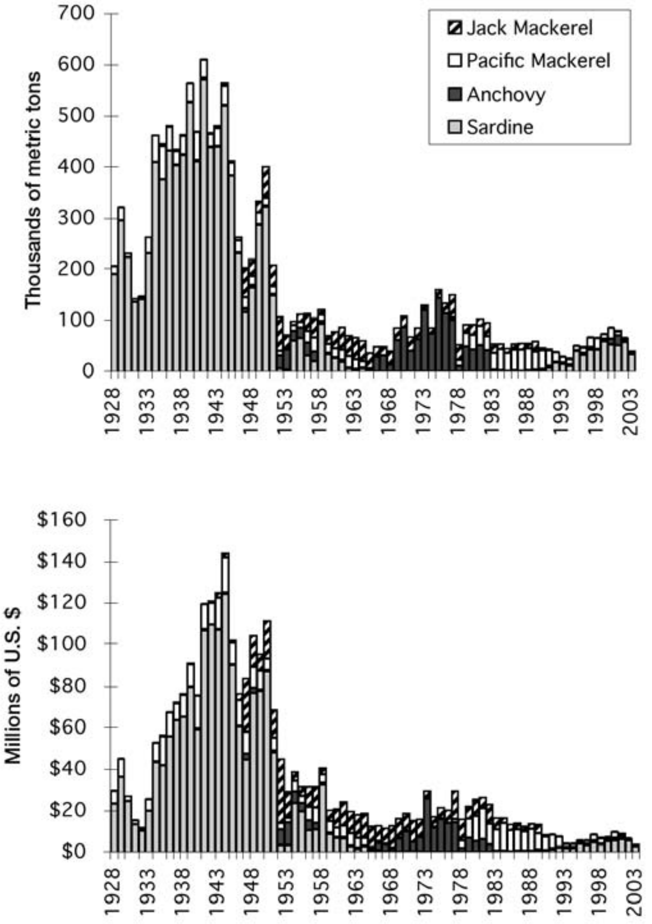

Figure 2. Landings of coastal pelagic species, by weight (*top*) and value (*bottom*).

the collapse of the fishery in 1952. No other species has come close to the magnitude of the 1940s sardine landings. Coastal pelagic fisheries were relatively steady in total landings after 1952, but their species composition changed markedly over time. Landings of Pacific mackerel, which were the second highest landings in the 1940s, declined along with sardine landings in the 1950s. Jack mackerel became the leading coastal pelagic species in the early 1960s. Northern anchovy appeared in the 1950s landings but did not dominate until after 1965, when reduction of anchovy without associated canning was permitted (Bergen and Jacobson 2001). The viability of the anchovy fishery was closely related to the production and price of fish meal worldwide. A 40% decline in the price of fish meal in the worldwide market from the winter of 1981 to the summer of 1982 (Durand 1998), along with a gradual decline in anchovy abundance, led to the virtual end of anchovy reduction in California by 1983. The harvest of coastal pelagics then shifted to Pacific mackerel as its population recovered in the 1980s, and then to sardine in the 1990s as Pacific mackerel became less available and the sardine population recovered enough to allow fishing within quotas. In all, there have been five periods in the landings of coastal pelagics dominated by different species: sardine until 1951, an increasing proportion of jack mackerel until 1965, anchovy until 1977, increasing Pacific mackerel until 1990, and sardine through 2002.

The value of the coastal pelagics generally followed the pattern of their landings (fig. 2b), but mackerels brought a slightly higher price per ton than sardine and anchovy. The overall value of coastal pelagic fishes has declined since the 1980s, despite steady total landings, as the dominant species shifted from mackerels to sardine. The fishery for anchovy as live bait is not included in the landings data set, but it may well exceed the value of the landed catch after 1983 (Bergen and Jacobson 2001).

Tunas are migratory species caught as they pass seasonally through waters off California. They move through different parts of the North Pacific depending on species, age, and ocean conditions, so California landings represent their occurrence in waters off California rather than their total abundance. The total landings of tuna caught in waters off California varied less than the landings of small coastal pelagics, but changes in tuna species are apparent (fig. 3a). Three different fisheries caught most of the tunas: trolling, purse seine, and live-bait. Bluefin tuna (*Thunnus thynnus*) were caught by purse seine, and their landings were highest in the 1930s, dropped in the late 1940s, then increased during and immediately after the 1957 El Niño. Albacore (*Thunnus alalunga*) were caught on hooks with live bait in the early years, but after 1980 they were caught almost exclusively by trolling (Crone 2001). Albacore landings grew from the 1940s to their peak in 1963, and from 1948 to 1981 landings of albacore were greater than those of bluefin or any other tuna species. Bonito (*Sarda chiliensis*) are included in Figure 3, although they cannot be marketed as tunas and were not as valuable as the tunas. Bonito, caught with purse seines, increased in landings in the late 1960s and early 1970s but dropped in the 1990s. Yellowfin (*Thunnus albacares*) and skipjack (*Euthynnus pelamis*) tunas were caught by bait boats before the 1960s and by purse seines more recently. Yellowfin and skipjack tunas increased in landings from California waters in the early 1980s, especially in 1983 and 1984, during and after El Niño. As albacore landings disappeared in the late 1980s, yellowfin and skipjack tunas maintained the quantity of tuna landings until 1997 but then declined, leaving albacore as the principal tuna species. The large tuna purse seine fleet based in southern California from the 1950s through the 1970s caught yellowfin and skipjack tunas in the tropical Pacific; therefore, their landings are not included here. All the tuna canneries except one closed in southern California as the tropical tuna fleet shifted

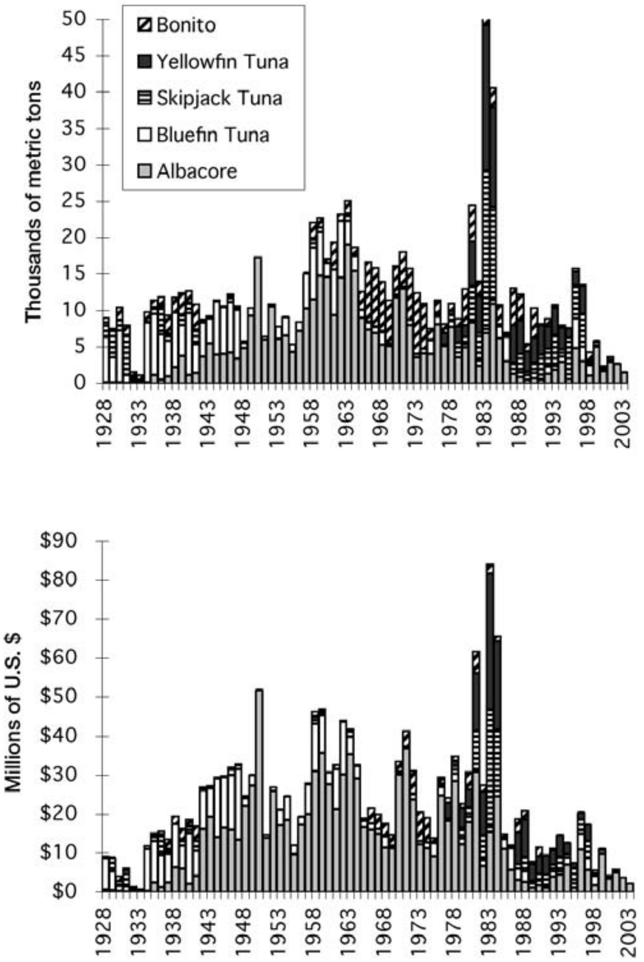

Figure 3. Landings of tuna, by weight (*top*) and value (*bottom*).

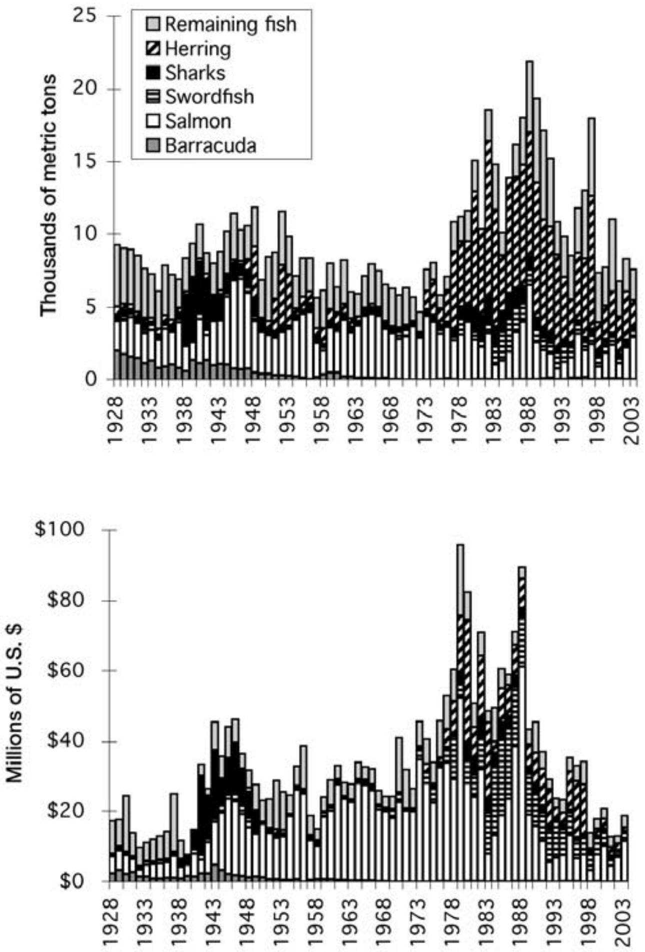

Figure 4. Landings of other species, by weight (*top*) and value (*bottom*).

operations to other ocean areas and other ports in the 1980s and 1990s.

Tuna values (fig. 3b) have generally followed the pattern of their landings. Albacore commanded the highest market price, followed by bluefin, yellowfin, and skipjack tunas, and bonito. Highest total tuna ex-vessel values occurred in 1981 through 1984 because of the unusual availability of skipjack and yellowfin tunas off California. Total tuna value was lower in the 1990s and beyond, reflecting the lower landings.

In addition to tunas, coastal pelagics, and groundfish, many other fish species have contributed smaller amounts to the total landings. The most important of these were salmon, Pacific herring (*Clupea pallasii*), swordfish (*Xiphias gladius*), and sharks (Squaliformes and Lamniformes), as shown in Figure 4a. Most of the salmon were taken by trolling in the ocean, but salmon were also fished in rivers and bays with gill nets until 1956, and during World War II this method caught nearly half of the salmon landed (Fry 1949). Salmon contributed the most in landings and value among these "other fish" from the 1950s through the 1970s. Salmon landings are quite variable from year to year but have gradually declined since 1956 except for record high landings in 1988. Salmon's contribution to total value declined in the mid-1990s (fig. 4b) as imported farmed salmon undercut the price of locally caught salmon, but both landings and price per pound increased in 2003.

Among these "other fish," Pacific herring contributed the most landings in the 1980s. There was an early herring fishery (1947–1954) for canning when sardine became unavailable, but canned herring was not as profitable, and this fishery soon ended. A second herring fishery, for herring roe exported to Japan, was more valuable. It was conducted primarily in San Francisco Bay by purse seines and gill nets from 1973 to 1998 and then with gill nets alone. Herring landings were lower during and after the El Niño events of 1984, 1994, and 1998. Herring landings since the 1980s have probably been closely tied to abundance, since quotas were based on biomass assessments (Watters et al. 2001), but lower catches in earlier years reflected the limited demand.

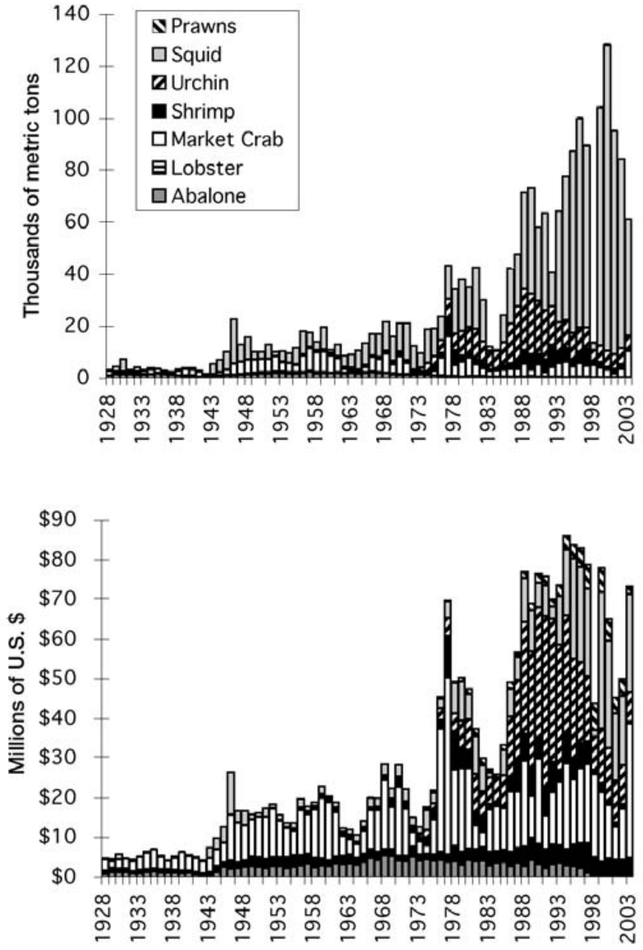

Figure 5. Landings of invertebrates, by weight (*top*) and value (*bottom*).

Swordfish were caught with hand-thrown harpoons until the late 1970s: demand fell in 1971–1972 as a result of public concern over high levels of mercury detected in some swordfish. Swordfish grew in importance in the late 1970s with the development of the drift gill net fishery on thresher sharks and swordfish and reached a maximum in 1985 before implementation of a series of regulations to reduce effort, landings of sharks, and marine mammal bycatch (Hanan et al. 1993; Holts 2001). Landings continued to decline as seasonal area closures were imposed in 2001 on the drift gill net fishery to reduce the bycatch of protected leatherback turtles (PFMC 2002). Catches of swordfish outside the 200 nmi U.S. Exclusive Economic Zone (not included in data set) rose in 1999–2001 as longline boats were displaced from Hawaiian waters by regulations to prevent turtle bycatch around the Hawaiian Islands. Although the drift net fishery was originally developed to target thresher sharks (Alopiidae), swordfish carries a substantially higher value, and concern about depleting shark populations has led to a redirection of this fishery toward swordfish.

Highest landings of sharks occurred in the 1940s, when soupfin sharks (*Galeorhinus galeus*), caught with gill nets, supported a valuable fishery for vitamin A from their livers. Shark catch was even higher than reported because sometimes only livers and not whole sharks were landed in the 1940s (Roedel and Ripley 1950).

In addition to the fish groups described above, many different kinds of invertebrates, taken with different gear, have been important in the commercial landings. The dominant species in weight landed has been market squid (*Loligo opalescens*), which increased dramatically from the 1980s to 1999 but declined from 2000 to 2003 (fig. 5a). Squid was harvested with purse seines, and in recent years bright lights have been used to attract squid to the boats. Dungeness crab (*Cancer magister*), California spiny lobster (*Panulirus interruptus*), and some of the spot prawns (such as *Pandalus platyceros*) were caught with traps. The remainder of the spot prawns, ridgeback prawns (*Sicyonia ingentis*), and all ocean shrimp (*Pandalus jordani*) were harvested by trawling. Dungeness crab landings were highly variable through the time series but were second only to squid in invertebrate landings through the 1960s. The ocean shrimp fishery started in the early 1950s and has varied, with maximum landings in 1992. Landings of red sea urchin, harvested by divers, grew from the early 1970s to a maximum in 1989 but then declined.

The value of invertebrate species (fig. 5b) is quite different from their landings because of the great price differences between species. Dungeness crab was the most important invertebrate in total value until it was surpassed by red sea urchin from 1988 to 1997; crab landings and their total value were very high in 2003. Market squid dominated invertebrate landings after 1966, but because of its low price did not surpass urchin in value until 1996. Abalone (*Haliotis* spp.), spiny lobster, and prawns were barely visible in the plot of landings (fig. 5a) but contributed to invertebrate value for decades because of their high price. Shrimp value was highest in 1977–1978 and in the early 1990s but dropped in both weight and value in the late 1990s and beyond as competition from shrimp from other areas reduced the market value (van Zile 2003).

The five major groups are displayed in the total California landings of Figure 6a. Over 90% of landings came from coastal pelagic fishes, mostly sardines, until the 1950s. Other coastal pelagic fishes continued to contribute over half the landings until the late 1970s. Groundfish increased to 31% of the landings by 1985 but dropped to 9% by 2003. Exceptional landings of yellowfin and skipjack tunas in 1983 and 1984 brought tunas up to 28% of total landings in 1983. Invertebrates continued to increase in importance to 50% of the landings by 2003 and were dominated by squid, which

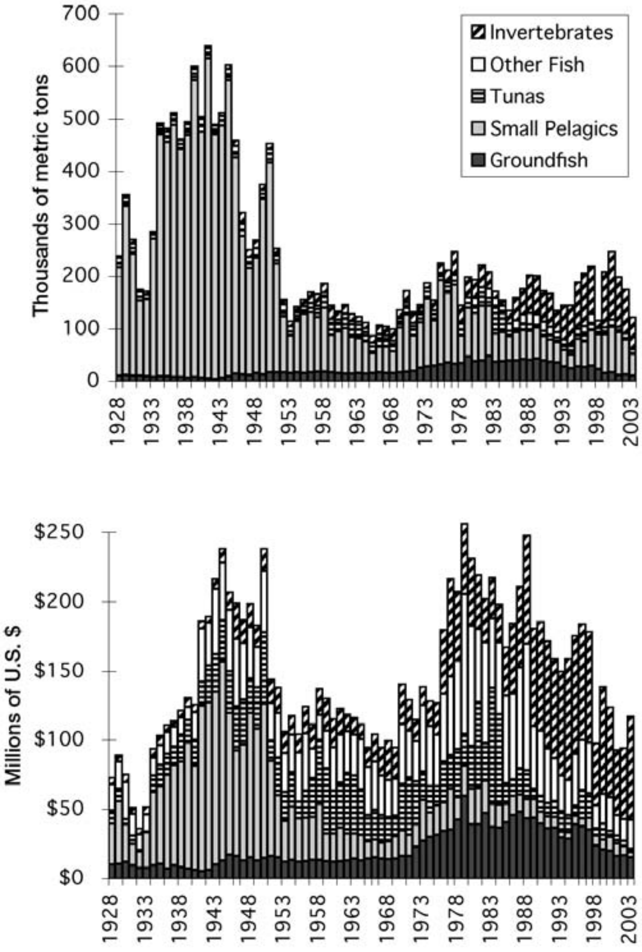

Figure 6. Total California landings, by weight (*top*) and value (*bottom*).

contributed 48% of total landings in 2000 but dropped to 37% by 2003.

The total landings were highest in the 1930s and 1940s, with over 600,000 metric tons. Landings were much lower after 1951, varying from a low of 87,000 metric tons in 1965 to a high of 246,800 metric tons in 1977. The series dips then climbs back from 1993 to reach 246,000 metric tons in 2000, but it drops to 122,000 metric tons by 2003.

The value of landings presents a contrasting view of the relative importance of these fisheries (fig. 6b). There has been a shift over time from coastal pelagics to tunas, other fishes, groundfish, and finally invertebrates. Total value appears high in the 1940s, when total landings of coastal pelagic sardines were highest, but even when they provided 90% of the landings, they contributed only 54% of the value. Total value dropped along with the sardine landings from 1951 to 1968 and remained low despite increased weight from anchovy in the 1970s. But from 1968 the value climbed 61% to a second peak in 1979 while landings increased only 50%. The value grew from increases in landings of tunas (especially albacore in the 1950s) and in value of "other fish": salmon in the 1960s and 1970s, herring in the late 1970s, and swordfish in the 1980s. In the 1970s and 1980s, groundfish landings and value grew, and they retained a fairly constant share of value (about 20%) as their landings declined through the 1990s but fell to 13% in 2003. Tuna values dropped sharply after 1984, along with their landings. The group of high-value "other fishes" averaged only 6% of the landings in the 1970s and 1980s but contributed 30% of the value; by the 1990s, however, these "other fishes" declined to 20% of the total value, and to 13% by 2003. Only invertebrates increased in relative value, from 20% in the 1980s to 48% of the total in the 1990s, to 60% in 2003. Dungeness crab had exceptionally high landings in 2003, contributing 29% of the total value. Among the invertebrates, sea urchin rose to 25% of the total value in 1991 but then declined to 6% by 2003, and squid grew to 21% of the total value by 2003, a year with lower squid landings but a remarkably high price per ton.

Although the total landings have remained high and even increased in the 1990s from increased sardine and squid, the value of the landings has been falling since 1988, the year of highest salmon and sea urchin landings and also high groundfish landings. The declines in the amount of salmon, herring, and swordfish, and the price of salmon contributed to the declining value of "other fish" in the late 1990s. The value of groundfish dropped as landings of valuable sablefish, thornyheads, rockfish, and Dover sole were restricted. Groundfish contributed only 9% of the landings and 13% of the value in 2003. The value of invertebrates fell as the proportion of urchin and crab dropped relative to squid until 2002.

DISCUSSION

The advantage of examining California landings as a long time series is the broad picture it provides of the dynamic nature of California's fisheries. It emphasizes the changes over time between different fisheries, both in weight of landings and in their value. Three major factors contributing to changes in landings over time are: (1) market demand, (2) ocean variability on multidecadal and interyear scales, and (3) prolonged exploitation.

Changes in demand for a species affect how much markets will pay for it and how much they will buy. The total value of soupfin sharks is an example of change in demand and a redirection of fishing effort to profit from that demand in an unregulated fishery. In 1938, when soupfin shark livers were discovered to contain high levels of vitamin A, in short supply during World War II, landings of shark increased eightfold and value increased tenfold (Roedel and Ripley 1950). Value peaked in 1942 at 130 times the 1937 total value and remained above 50 times the 1937 value until 1947. Demand ended abruptly in 1950 with the development of synthetic vitamin A, and landings and value returned to pre-1938 levels.

Demand for several California species has been increased by the development of international markets, especially in Japan in the 1980s. These markets brought higher prices for herring roe, sablefish, thornyheads, and sea urchin gonads. These high-value export fisheries compensated in part for lower total landings and contributed to maintaining the total value through the 1980s, but the amount of compensation dropped in the late 1990s as landings increased for lower-priced squid and sardine (also primarily exported), and the higher-valued fisheries declined.

Two scales of ocean variability, multidecadal and interyear, are noticeable in California's fishery landings over time. Long-term trends in California landings were examined by Norton and Mason (2003), who found relationships of landings to multidecadal environmental signals in ocean temperature and southward wind stress. The changing coastal pelagic fish populations and possible environmental connections have been the focus of CalCOFI research and discussions for the last 50 years. MacCall (1996) showed the same sequential pattern of coastal pelagic species in California landings and populations shown in Figure 2a. Wide fluctuations in biomass of coastal pelagic fishes and the replacement of one species with another in the fisheries are characteristics of other eastern boundary current-upwelling areas, such as Peru, where fisheries shifted with availability from one species to another, and total landings varied widely over time (Lluch-Belda et al. 1992; Schwartzlose et al. 1992). A similar sequence of replacement species has been noted in the Japanese fishery (MacCall 1996; Schwartzlose et al. 1999). These fluctuations have been linked at least in part to decadal changes in gyre-scale ocean circulation and resulting changes in ocean temperature and stratification (Lluch-Belda et al. 1992; Schwartzlose et al. 1999; Parrish et al. 2000). Similar fluctuations in populations of coastal pelagic species occurred in prefishery times in California, as recorded in sediments from the Santa Barbara Basin (Baumgartner et al. 1992). Environmental conditions, however, were not the only factors contributing to the decline of sardine in the 1950s. The extremely heavy fishing pressure for this valuable species reduced its resiliency to interyear environmental variability. Comparing the harvest rates (catch divided by adult biomass) of the fishery as it declined in the 1950s (MacCall 1979) to the maximum sustainable yield calculated in the 1998 fishery management plan (PFMC 1998a) indicates that the fishing pressure on sardine exceeded the maximum sustainable yield every year from 1953 to 1965 as the population continued to decline.

In addition to these decadal environmental patterns, interyear variability of ocean conditions during El Niño events that produced strong warming off California apparently affected availability of some species, although not equally in all years. Availability of migratory, warm-water, yellowfin tuna and skipjack tuna increased dramatically during the warm 1983–1984 El Niño (fig. 3a). Landings of some other warm-water species—barracuda (fig. 4a) and yellowtail (*Seriola dorsalis*), in decline from the 1930s through the 1950s-increased during the 1957–1959 El Niño (Radovich 1961). In contrast, landings of salmon declined during the El Niño events of 1957–1959, 1983–1984, and 1998, and landings of both herring (fig. 4a) and squid (fig. 5a) declined sharply in 1983–1984 and 1998. Interyear variability may have affected the reproductive success of various species (Radovich 1961; Smith 1985), but the delay of years between reproduction and recruitment to the fishery makes this difficult to detect in the landings data.

In addition to market changes and ocean variability, 70 years of heavy exploitation of marine resources reduced landings for many of California's fisheries. By 1955, barracuda, yellowtail (Crooke 2001), white seabass (*Atractoscion noblis*) (Vojkovitch and Crooke 2001), and giant seabass (*Steriolepsis gigas*) (Domier 2001) landings had each been reduced to less than 5% of the 1930 California levels, although they continued to be harvested off Mexico. These warm-water species may also have been affected by the cooler waters of the 1950s and 1960s, but their landings have not recovered as sardine did in the warmer 1990s. Combined landings of cooler-water rockfish have declined since their peak in the 1980s. Different species have been landed in different periods: canary rockfish (*Sebastes pinniger*) in the 1970s, bocaccio rockfish (*S. paucispinis*) in the 1970s and early 1980s, widow rockfish (*S. entomelas*) in the early 1980s, black rockfish (*S. melanops*) in the late 1980s (MacCall 2002; Pearson and Ralston 1990), and bank rockfish (*S. rufus*) in the mid-1980s (Love and Waters 2001). The large initial catches of long-lived species reflect the harvest of existing biomass as the fishery moves into new areas or depths—referred to as "fishing up" by Ricker (1975)—are followed by lower landings of a species as the fishery becomes dependent on annual recruitment. The groundfish fishery compensated in the 1970s and 1980s by shifting into new areas to find other unexploited species. Invertebrate fisheries harvested by divers have also changed targeted species, first among abalone species as the shallow-water species were depleted and the fishery shifted to deeper water (Karpov et al. 2000), then from abalone to sea urchin as abalone availability declined and a lucrative Japanese market for red sea urchin gonads developed. The original sea urchin biomass present in the 1980s was "fished up" first in the Channel Islands and then in northern California, and catch per diver hour continued to decline in the 1980s and 1990s (Kalvass and Hendrix 1997).

Changes in the degree and type of management of fisheries over time have affected the landings. In the early years, most species were limited only by economics, not regulations. For example, the unregulated soupfin shark fishery severely reduced the local population during World War II before alternative sources of vitamin A reduced the fishery's profitability and led to the fishery's demise (Roedel and Ripley 1950; Ebert 2001). Some fisheries were managed by restricting gear, such as round haul nets for yellowtail in 1933 (Greenhood 1949) and for white seabass in 1940 (Fitch 1949). Other fisheries were managed by area closures and mesh-size requirements (for bottom trawling). Rockfish landings doubled in the early 1970s as that fishery expanded, and doubled again in the early 1980s when large midwater aggregations of widow rockfish (*Sebastes entomelas*) were discovered. After 1982, when widow rockfish harvests were limited to slow their exploitation, the fishery extended to other species including those in deeper water (Pearson and Ralston 1990). In the 1980s, groundfish were managed with quotas to try to prevent overfishing of heavily targeted species, but nonselective multispecies fisheries made it difficult to protect all species, and in the late 1990s rebuilding plans were required for several depressed stocks, further reducing rockfish landings. The difficulty of predicting a sustainable level of harvest for stocks of rockfishes with intermittent recruitment dependent on occasional favorable ocean conditions has left several rockfish stocks at such low levels that many years will be required to rebuild them to sustainable levels (MacCall 2002).

Some single-species fisheries have provided significant landings for many years; these include Chinook salmon, herring, and crab. The Chinook salmon fishery has been more stable than most California fisheries, generally maintaining annual landings of over 2 million pounds, despite year-to-year variability (fig. 4a). In recent years, however, wild stocks have declined and much of the production has come from hatcheries (PFMC 1996; Yoshiyama et al 1998). Salmon was relatively valuable, with a high price per pound until the 1990s, when the price of ocean-caught salmon fell because of competition with low-priced farmed salmon (fig. 4b).

The herring roe fishery has remained productive for more than 20 years under close management. Active management with quotas based on annual biomass estimates produced a healthy sustained fishery despite interyear variability until the 1998 El Niño warming (Watters et al. 2001). Annual monitoring of the biomass and condition of herring as they enter shallow bays for spawning allowed annual adjustment of quotas and a reduced fishery since the 1998 El Niño. The high value of herring roe exported to Japan drives the fishery.

Dungeness crab maintained a strong fishery for 74 years despite high interyear variability (fig. 5a). The fishery in the San Francisco area collapsed in the late 1950s, but northern areas remained productive. The crab fishery harvests a relatively short-lived species managed with seasonal closures, size limits with good survival of undersized released animals, and protection of all female crabs. The herring and crab fisheries are single-species fisheries that are not generally complicated with bycatch of other restricted species, as are the groundfish trawl fisheries.

Prospects are not favorable for the return of California's fisheries to the high value of landings before 1998. Although total landings have remained relatively stable for the last three decades, with a slight increase from 1993 to 2000, the total value has declined. Total value in 2001 was down 63% from 1988 and down 50% from 1997 but increased slightly in 2003 because of the high value of crab and squid. The fisheries have historically maintained the value of landings by switching effort from declining species to those not yet fully exploited, but this is no longer possible: we are running out of marketable unexploited species.

A second strategy for maintaining value has been to switch to more valuable species; however, lower catches since the mid-1990s of more valuable swordfish, salmon, herring, and ocean shrimp, combined with lower world market prices, competition from fisheries in other areas, and lower exchange rates (van Zile 2003), reduced their total value. The more valuable species are now less available, and the bulk of the landings are coming from lower-value squid and sardines, contributing to a severe decline in the value of landings. The relative value of finfish in the landings has dropped along with their weight, down from a high of $205 million (80% of landings value) in 1979, to $98 million (55%) in 1997, to $46 million (50%) in 2001. The value of invertebrates dropped from a high of $88 million in 1994 to only $67 million in 2000 ($48 million in 2001), despite increased landings through 2000, as landings of valuable urchin, shrimp, and crab have declined.

A third strategy for improving the value of some species has been through special handling. The live rockfish fishery commands several dollars per pound for fish that would sell for less than one dollar per pound if dead. However, the fishery can use only shallow-water species, and management to protect them has reduced their landings since 1998 (Osario and Leos 2003). The sea urchin and herring roe fisheries have also maximized the value of their landings by careful handling for export markets (Kalvass and Hendrix 1997). Maximizing value and seeking optimal markets will remain important to the economic survival of California's fisheries.

The period of expansion of fisheries to relatively unexploited species in California appears to be coming to an end. The fisheries have already expanded to cover the whole length of the state and have fished all reasonable depths. There are very few unexploited species of finfish left. In addition, it is difficult to switch to an existing fishery because of limited entry programs or reduced quotas for most of the remaining fisheries. California may continue to receive bonuses of tunas or swordfish passing through when ocean conditions are favorable but will not be able to control the availability of these highly migratory species. California's fishers will now have to live with the annual production of local resources and management restrictions that prevent overharvesting.

In the last decade, the contrast between the dominance of low-value species in weight and high-value species in total value suggests that the economic recovery of the fisheries will depend on higher-value species or value-added fisheries such as those for live fish. Increased landings of low-value species will not be enough for the fisheries to attain the economic values they had in the 1980s.

CONCLUSIONS

Invertebrates had greater increases than finfish in both landings and value in the 1990s, and they have contributed more than half the total value of landings from California waters since 1999. Decadal-scale environmental ocean variation affects the recruitment of coastal pelagic species. Interyear ocean variability affects the local availability of migratory warm-water species such as tunas and yellowtail, as well as local squid, ocean shrimp, and herring. The strategy of "fishing up" an unexploited population and then switching to an alternate species is limited by management regulations to protect reduced populations.

Higher-value fisheries appear to be the best hope for the economic survival of California's fisheries. Harvesting smaller quantities of higher-value species and processing landings from lower-value, high-volume fisheries to enhance their value may be two ways to compensate for decreased landings. Many high-value species are sold overseas and will be subject to fluctuations in world economics and competition from fisheries in other countries. We must be cautious in developing new high-value fisheries so that we do not reduce the productivity of their populations before bringing them under appropriate management.

ACKNOWLEDGMENTS

Thanks to Gerry Kobylinski for providing PacFIN data, Jerry Norton for helping develop the value database and investigating decadal trends, Lynn DeWitt for developing Web site access to the landings data, Richard Parrish for review and guidance, and the comments of three anonymous reviewers.

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