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UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY
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CONTENTS

In Memoriam

I. Reports, Review, and Publications

II. Symposium of the CalCOFI Conference, 2001

III. Scientific Contributions

Indexed in *Current Contents*. Abstracted in *Aquatic Sciences and Fisheries Abstracts* and *Oceanic Abstracts*.

IN MEMORIAM

MIA JEAN TEGNER

1947–2001

On 7 January 2001 Mia Jean Tegner died in a scuba-diving accident while working in the kelp forests off San Diego, California. She died at the height of her career, doing what she loved best. We lost not only a good friend and colleague but also a powerful champion for marine conservation.

Mia had a genuine, abiding passion for marine ecology, so it may come as a surprise that she received her Ph.D. in molecular biology. She traded a postdoc in molecular biology for another one to study sea urchin ecology with Paul Dayton. It was, like so much of what she did, a gutsy move. Lucky for us she did change fields and was so very good at marine ecology. Her scientific excellence was apparent early in her career when she published in such prestigious journals as *Nature* and *Science*.

Mia Tegner, 1975.

Mia's research focused on abalone, sea urchins, and the kelp forest communities off southern California. She examined the role of environmental variability on fisheries and kelp forest productivity. Through her creativity and scientific rigor, she was able to detect the impacts of interdecadal shifts in ocean climate. She helped to convince us all of the importance of episodic El Niño events on the structure of kelp communities. Mia did not distinguish between basic and applied research. She studied what she thought was important and made sure it met the most rigorous scientific standards. Her research highlighted the importance of the health of nearshore kelp forests. During her 30 years at Scripps Institution of Oceanography, Mia developed a strong research program, publishing more than 70 papers, symposia contributions, and book chapters. Her work helped us change our perspective on the marine environment; what we once thought of as a vast, boundless ocean has now become recognized as a fragile ecosystem in need of conservation.

Mia's work gave us a framework for restoring populations and ecosystems. It is an exceptionally difficult task to determine just how many lobsters the kelp forest once harbored. Mia, in collaboration with Paul, produced seminal work in historical ecology, quantifying how baseline abundances have changed over time. She then took the first steps toward abalone restoration when she co-authored the federal status review of white abalone. As a result of these efforts, white abalone became the first marine invertebrate to be listed as an endangered species. Her work earned her fellowships in the American Association for the Advancement of Science and the prestigious Pew Marine Conservation Program. The fact that she was in the middle of her Pew research examining the impacts of ocean conditions on abalone productivity when she died is one of the many reasons we have taken her death so hard.

Mia was an academic, though no one considered her meek or cloistered away in an ivory tower. She worked closely with natural resource managers and policymakers to sustain California's marine resources and was often quoted by the press. She had a grittiness to her core, and a fierce determination that served her well when dealing with controversial issues such as San Diego wastewater treatment, abalone conservation, and marine reserves. With over 4,000 hours of bottom time she was

Baja Wreck, 1976. Photo by Eric Hanauer.

an exceptional diver, some might say (I would say) a macho diver. Perhaps as a consequence of her extensive first-hand experience underwater, her abilities as a scientist, and her love of people, she could converse with anyone interested in the ocean, whether scientist, politician, or fisher. Mia's passion for her work was contagious, and often whatever Mia thought was important became the central topic of the panel discussions she participated in. Her work gained her worldwide attention, and her love of travel meant that she and her husband Eric were frequently invited to wonderful and exotic places. Such a blend of passion, courage, scientific excellence, honesty, and integrity is extremely rare and will be sorely missed.

Over the years Mia and I became friends. We first met in 1986 when I was a graduate student. I had read all her papers and we began to correspond about our overlapping interests in sea urchins, abalone, diving, and marine conservation. Over the years I would stop in on her whenever I was in La Jolla, asking her advice, dropping off copies of my latest papers, or inviting her to give seminars. I spent a week with Mia in South Africa, listening to abalone talks during the day and eating and talking with friends in the evenings. What could be better? We visited the diverse intertidal zone where the Indian and Atlantic Oceans meet. We had a standing invitation to dive each others' sites: hers in the Point Loma kelp beds and mine in the Bodega Marine Life Refuge. But in the end we never got the chance. I know that when I do finally get to dive with her, she will have figured out all the best dive spots and will reveal the secrets of the kelp beds. I only hope that in the meantime, we will be wise enough to take Mia's advice and protect our ocean's treasures.

Laura Rogers-Bennett

The Abalone Song

The poet George Sterling and his wife, Carrie Sterling, wrote *The Abalone Song* in the early 1900s while they were living in the artist colony of Carmel. The Sterlings, with the likes of Jack London and Jimmy Hopper, feasted on California's prime delicacy around a roaring fire on the beach at Point Lobos or at the Café Ernest at the foot of Fisherman's Wharf. Adding verses to the abalone song, sung to the tune of "Yankee Doodle Dandy," has become a tradition among the family of researchers who ply abalone symposia around the world. There are few rules to the tradition save these two: verses may be composed only when in high spirits and good company, and all verses must end in the word *abalone*.

OH! Some folks boast of quail on toast
Because they think its tony
But I'm content to owe my rent
And live on abalone!

OH! Mission point's a friendly joint
Where every crab's a crony
And true and kind you'll ever find
The clinging abalone.

He wanders free beneath the sea
Where 'ere the coast is stony
He flaps his wings and madly sings
The plaintive abalone.

On Carmel Bay the people say
We feed the Lazzaroni
On Boston beans and fresh sardines
And tender abalone.

Some live on hope and some on dope
And some on alimony
But my tomcat, he lives on fat
and tender abalone.

OH! Some drink rain and some champagne
Or brandy by the pony
But I will try a little rye
With a dash of abalone.

OH! Some like ham and some like jam
And some like macaroni
But bring me in a pail of gin
And a tub of abalone.

He hides in caves beneath the waves
His ancient patrimony
And so 'tis shown that faith alone
Reveals the abalone.

The more we take the more they make
In deep sea matrimony
Race suicide cannot abide
The fertile abalone.

I telegraph my better half
By Morse or by Marconi
But if the need arises for speed
I send an abalone.

They came to hear from far and near
To meat in Californee
Scoresby, David, Martin, and Kit
To save the abalone.

We came to Canada to meet
Nanaimo was so homely
Where DFO, First Nations tried
To save the abalone.

To Africa in Capetown clear
Where Mia broke her bony
Came eighteen nations' scientists
To talk of abalone.

Oh Sweijd and Peter were belayed
By calls from China to Omani
To help their native perlemon [par-la-mon]
another abalone.

Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

THREE CALCOFI ICONS BID FAREWELL

Dr. Geoffrey Moser, a world leader in the field of larval fish ecology and taxonomy, retired on 14 June 2002, after nearly 40 years of service with the Bureau of Commercial Fisheries and its successor agency the National Marine Fisheries Service (NMFS). Thanks to his pioneering work and leadership and to the excellence of his research team, it is possible to identify the larvae of most fishes in the California Current by visual means. The 1,517-page monograph *The Early Life Stages of Fishes in the California Current* (CalCOFI Atlas 33), one of the finest scholarly achievements ever produced by NMFS, contains descriptions of 586 species and 2,500 illustrations. It is widely used throughout the world as an identification guide and frequently copied in regional guides. Moser's work has been central to CalCOFI and continues to this day. In CalCOFI's early years most of the larvae taken in cruises were not identified, but today most of them are; over 500 species are routinely identified each year. He and his staff identified the larvae of many previously unidentified species; they also went back through earlier collections, identifying larvae using the new characters and thereby making a new time series for each species starting from CalCOFI's inception. They accomplished this huge task in spite of a large backlog of unidentified specimens. Upcoming CalCOFI atlases and publications will document this work. The bottom line is that the CalCOFI ichthyoplankton time series is, and continues to be, up to date; the data are available for stock assessments from the current year back to 1951. Over the years, Moser has published many outstanding papers on larval ecology, and recently he has begun studying assemblages of species as a measure of ecosystem state. Our hope is that his ideas about ecosystem functioning that evolved through his work with CalCOFI are just the beginning of a new understanding of ecosystems that will be carried onward by others. We expect a continuation of the fine tradition Moser established, of making the collection of ichthyoplankton data a practical and timely undertaking for resource agencies. Moser is undeniably one of the best minds in the field and an unparalleled source of knowledge on the early life history and ecology of larval fishes. Those of us at the Southwest Fisheries Science Center (SWFSC) and in the CalCOFI family wish him well in his new endeavors.

Dr. Thomas Hayward retired from the University of California in November 2001. Hayward was a strong proponent of the CalCOFI program for his entire career. Since 1993, he served as academic administrator in charge of the SIO-CalCOFI seagoing operations and data processing and distribution. He expanded and improved CalCOFI measurements and guided the development of the CalCOFI Web site and procedures for online data-dissemination. His efforts significantly expanded the number of ancillary programs participating on CalCOFI cruises. He obtained external funding to support monthly "mini-CalCOFI" cruises during the 1997–98 El Niño. He introduced the "State of the California Current" section into the *CalCOFI Reports* and authored many of them himself. We are pleased to report that Dr. Ralf Goericke has agreed to replace Hayward in the role of academic administrator. We are confident Goericke will bring the same combination of resourcefulness and innovation to the job.

In the spring of 1982, Julie Olfe first met with Reuben Lasker and took on the editorship of *CalCOFI Reports*. Since that time, Olfe has been responsible for editing and co-producing 20 volumes of *CalCOFI Reports*, beginning with Vol. 23 (1982) and ending with Vol. 42 (2001). Much to the disappointment of the Committee, Olfe announced her retirement from *CalCOFI Reports* in the fall of 2001. Through her diligence and attention to detail, Olfe has helped make *CalCOFI Reports* the outstanding journal it is today, and she will truly be missed. We are pleased to announce the hiring of Joni Harlan (with strong recommendations from Olfe) as our new editor. Harlan makes her debut with this volume.

ALLIANCE FOR CALIFORNIA CURRENT ECOSYSTEM OBSERVATION (ACCEO)

Participants in the 2001 CalCOFI Conference recommended the development of a new vision of monitoring the pelagic ecosystem of the California Current built upon the solid base of CalCOFI and other survey programs but expanded to observe the entire California Current pelagic ecosystem. Such an integrated monitoring program would require building a new coastwide monitoring consortium and generating information that would benefit communities from British Columbia to

Baja California. A comprehensive California Current observation system is needed because the dynamics of current flow, marine populations, and ecosystems cannot be accurately interpreted from regional monitoring programs without considering the dynamics of the larger system of which any given region is a part. In addition, resource management should be based on the dynamics of populations, not pieces of them, yet no population of any California Current species is contained within the boundaries of any present California Current survey.

Subsequent to the 2001 CalCOFI Conference, John Hunter, NMFS, held planning meetings at Monterey and Seattle, where representatives of the marine scientific community expressed keen interest in the proposed alliance. The recommended partnership would have a new name, broader mission, and different structure from CalCOFI, but would preserve the most successful features of CalCOFI. These include (1) sustaining a flexible alliance of academic and resource organizations, (2) supporting a blend of applied and long-range science goals, (3) a commitment to understanding the dynamics of the California Current and of the populations it contains, and (4) dedication to maintaining the physical and biological time series needed for this understanding. A central research theme of such an alliance would be understanding and predicting how decadal to interannual shifts in the climate of the California Current affect the dynamics of marine populations. Another planning meeting was held in September 2002 in Portland, Oregon.

CALCOFI ATLAS 35

CalCOFI Atlas 35, entitled *Distributional atlas of fish larvae and eggs from Manta (surface) samples collected on CalCOFI surveys from 1977 to 2000*, was published in May 2002. Authors included Geoffrey Moser, Richard Charter, Paul Smith, David Ambrose, William Watson, Sharon Charter, and Elaine Sandknop. This atlas summarizes the spatial and temporal distribution and abundance of 93 ichthyoplankton taxa collected in manta net tows on CalCOFI biological-oceanographic survey cruises. Manta net tows, included in CalCOFI station protocol since December 1977, provide a quantitative sample of planktonic organisms that live, either permanently or facultatively, in the upper 15 cm of the water column. This time series contains data on commercially and ecologically important species of fish larvae (e.g., cabezon, lingcod, greenlings) that are not sampled adequately by oblique tows. The station, tow, and ichthyoplankton data that form the basis for Atlas 35 have been published in a series of 19 reports in the NOAA Technical Memorandum NMFS series; principal authors of individual reports are David Ambrose, Sharon Charter, Geoffrey Moser, Elaine Sandknop, and William Watson. Atlas 35 is the fourth CalCOFI atlas on the ichthyoplankton time series. CalCOFI Atlases 31 and 32 presented distributional summaries for all taxa taken in oblique tows on surveys that covered the greater CalCOFI sampling area extending from northern California to Cabo San Lucas, Mexico, during 1951–84. CalCOFI Atlas 34 summarized distribution and abundance of fish eggs and larvae taken in oblique tows from 1951 to 1998 in the area defined by the present survey pattern. Atlas 35 and the Manta data reports were distributed during 2002 and are available on request.

CALCOFI ROCKFISH LARVAE

Russell Vetter and staff at the SWFSC have made it a priority to develop molecular methods for identifying previously unidentifiable ichthyoplankton from CalCOFI bongo tows. The focus is on *Sebastes* (rockfish) because of the large number of unidentified species, the lack of species-specific visual characters, and the importance of rockfish to resource management. Cynthia Taylor (Scripps Institution of Oceanography, SIO) is working with William Watson (SWFSC) to identify all of the *Sebastes* larvae from the 1999 CalCOFI cruises. The population genetics of the adults of some nearshore rockfish species such as the brown rockfish, *S. auriculatus*, show evidence of limited dispersal (e.g., genetic differences north and south of Point Conception). Other species, however, such as the bocaccio rockfish, *S. paucispinus*, do not show genetic differences. Retention and limited dispersal would correlate with the high level of genetic structure.

A manuscript entitled “Biology and population dynamics of cowcod (*Sebastes levis*) in the Southern California Bight from 1918 to 1997,” by John Butler, Larry Jacobson, Thomas Barnes, and Geoffrey Moser, has been submitted to *Fishery Bulletin*. The paper was based in part on the long time series of cowcod larvae in the CalCOFI collection. Since the larval time series closely tracks the cowcod population and provides a link to historical biomass levels, an ichthyoplankton survey is one tool being used in a baseline study of the recently created Cowcod Conservation Area (CCA). Closely spaced plankton samples in the CCA are embedded within the CalCOFI survey area. The first cruise to monitor the CCA took place in February 2002 using standard CalCOFI protocols.

MOCNESS SURVEY FOR JUVENILE ROCKFISHES

A second micronekton survey of the Southern California Bight was conducted with a 10 m^2 multiple opening/closing net and environmental sensing system (MOCNESS) in June–July 2001, to continue the investigation that began in 2000 on the spatial distributions of late larval and pelagic juvenile rockfishes. Because young stages of many rockfish species cannot be reliably identified below the family level using visual characters, molecular techniques will be used to identify the rockfishes collected. In addition to the rockfishes, late larvae and pelagic juveniles of many other fishes and several cephalopod species were collected during the 2000–2001 micronekton surveys. These often are poorly sampled with standard plankton nets and trawls, which typically target smaller and larger size classes, respectively. All survey data have been entered into the CalCOFI ichthyoplankton database.

MARINE ECOLOGICAL RESERVES RESEARCH PROGRAM (MERRP)

The NMFS study of the distributions of planktonic fish eggs and larvae in nearshore waters in the vicinities of Big Sycamore Canyon and Vandenberg Marine Ecological Reserves and Anacapa and San Miguel Islands in the Channel Islands National Marine Sanctuary was completed, and the resulting data have been incorporated into the CalCOFI database. Eggs and larvae of fishes that reside in hard-bottom and kelp habitats were most abundant at the islands, which have much more of those habitats than the mainland reserve sites. Eggs and larvae of soft-bottom fishes were more abundant at the Big Sycamore site, which is almost entirely soft-bottom habitat. It appears that no significant production of planktonic fish eggs and larvae occurred in the immediate vicinity of Vandenberg Marine Ecological Reserve. The University of California Sea Grant College Program, La Jolla, published the results of the MERRP study on CD-ROM this year. Highlights from two MERRP projects are published by Watson et al. and Yoklavich et al., in this volume.

ACOUSTIC DOPPLER CURRENT PROFILER (ADCP)

The acoustic backscatter from the Acoustic Doppler Current Profiler (ADCP) provides an alternate method to the bongo-tow volumetric measure of zooplankton. Ronald Lynn (SWFSC) has a manuscript in press that relates the distribution of strong backscatter to spring sardine spawning, as determined by the continuous underway fish egg sampler (CUFES), and to the development of the California Current jet. Backscatter, as a measure of zooplankton, has important advantages over net tows because it provides continuous along-track recording (an ensemble reading every 1.5 km at 10 knots) and vertical structure. However, target strength is highly variable between zooplankton species, and returns are dependent upon instrument frequency. The 150 kHz unit aboard the *David Starr Jordan* is best for macrozooplankton. In spite of any caveats, the pattern of results from four spring surveys reveals a strong relationship to the current patterns and large response to the extreme annual changes caused by the El Niño/La Niña cycle. In the four spring surveys studied (1996–99) there is a large drop-off in acoustic backscatter at the offshore limit of sardine eggs; this suggests that presence of adequate forage is an important factor in the spawning habitat. A level of forage may be needed for spawning energetics and/or as an element of spawning strategy for the survival of larvae.

SIO HIGHLIGHTS

This past year brought extensive internal reevaluation of the Scripps/CalCOFI program and of its relationship with the rest of SIO. In preparation for a presentation to the Director's Academic Council, statistics were compiled on the number of ancillary programs participating in CalCOFI. The numbers are impressive. In the past 10 years, 23 graduate students have used either CalCOFI data or samples as a major portion of their doctoral research, or have "piggy-backed" on CalCOFI cruises to collect their data. There were 50 graduate-student-trips on CalCOFI cruises. There were 8 participating post-docs (24 post-doc trips), and 40 visitor trips with 10 countries represented. During the past year alone, five externally funded programs used CalCOFI as a platform.

Each of these ancillary programs enriches our knowledge of the California Current system at very little cost to CalCOFI. We are encouraging others at SIO (and elsewhere) to make use of CalCOFI resources in their research. Two proposals are currently under discussion: one would contribute a modeling component to the program, the other would develop a shipboard technique for rapidly identifying phytoplankton, microzooplankton, and larval fish by genetic analyses. Our goal is to obtain external funding to support these and other ancillary activities. Two proposals were recently submitted to the U.S.-Mexus Program to enhance our collaboration with the IMECOCAL (Investigaciones Mexicanas de la Corriente de California) program. If funded, one proposal would establish a coordinated program of phytoplankton pigment analysis using high-performance liquid chromatography. The other would implement a joint database to facilitate the exchange of information and stimulate collaborations between CalCOFI and IMECOCAL.

CALIFORNIA'S LIVING MARINE RESOURCES: A STATUS REPORT

California Department of Fish and Game (CDFG) and the University of California Sea Grant Extension Program proudly announced publication of *California's Living Marine Resources: A Status Report*, edited by William Leet, Christopher Dewees, Richard Klingbeil, and Eric Larson. This 592-page report examines the current status of the state's commercial and recreational fisheries and discusses the natural history of many of the plants and animals of California's marine environment. The report involved dozens of California's and the nation's best marine scientists in its preparation and review, and it provides readers with photos and population and biological information on the current state of more than 150 marine species. It includes the writings and contributions of more than 125 scientists affiliated with well-known natural resource organizations, including scientists from CDFG, University of California and California State University, NMFS, National Oceanic and Atmospheric Administration, and numerous private organizations. The status report was mandated under landmark legislation known as the Marine Life Management Act of 1998. To download a free copy of the report or to print individual chapters of species, see the CDFG's Web site at <www.dfg.ca.gov/mrd/status>.

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 and diligence, to the success of CalCOFI's quarterly fieldwork. The CalCOFI Committee thanks the officers and crews of the research vessels that have served us well as platforms for our observations during the past year: the NOAA Ship *R/V David Starr Jordan*, the University of California *R/V New Horizon*, and CDFG's *R/V Mako*.

We also thank the reviewers of contributed papers in Volume 43: Jim Allen, Todd Anderson, Tom Barnes, Darrin Bergen, Steven Bograd, Jim Bohnsack, Susan Bower, Ray Conser, Paul Crone, Don DeAngeles, Chris Ehrler, Carolyn Friedman, Marty Golden, Pete Haaker, Annette Henry, John Hunter, Larry Jacobson, Mati Kahru, Raphael Kudela, Dave Kusner, Ralph Larson, Nancy Lo, Milton Love, Bev Macewicz, Mark Ohman, Bill Peterson, Steve Ralston, Laura Rogers-Bennett, Niklas Schneider, Paul Smith, Dale Sweetnam, and Paul Waterstrat. We are especially grateful to Joni Harlan for her professional style in editing this volume of *CalCOFI Reports*.

Finally, we would like to thank Marisela Vargas (IOD-SIO), Brad Neuschwanger (CDFG), and Diane Foster (SWFSC) for providing invaluable assistance to the CalCOFI Committee throughout the year.

The CalCOFI Committee:
Kevin Hill, CalCOFI Coordinator
John Hunter, NMFS
Laura Rogers-Bennett, CDFG
Elizabeth Venrick, UCSD

REVIEW OF SOME CALIFORNIA FISHERIES FOR 2001: MARKET SQUID, SEA URCHIN, DUNGENESS CRAB, LOBSTER, PRAWN, ABALONE, GROUNDFISH, SWORDFISH AND SHARK, COASTAL PELAGIC FINFISH, OCEAN SALMON, NEARSHORE LIVE-FISH, PACIFIC HERRING, WHITE SEABASS, AND KELP

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SUMMARY

In 2001, commercial fisheries landed an estimated 200,996 metric tons (t) of fishes and invertebrates from California ocean waters (fig. 1), a decrease of nearly 19% from the 247,122 t landed in 2000. The preliminary ex-vessel economic value of California commercial landings in 2001 was $104 million, a decrease of 22% from $133 million in 2000.

Two of the top three grossing fisheries in the state were invertebrate fisheries, as was the case in 2000. The top three fisheries for 2001 (excluding kelp) in ex-vessel value were market squid ($17.5 million), groundfish ($16 million), and red sea urchin ($11.5 million). These fisheries all decreased in value in 2001 compared with 2000: squid declined 35%, groundfish declined 20%, and sea urchin declined 11.5%, continuing its downward trend since its historic high in 1988. The Dungeness crab fishery, with landings significantly lower than the ten-year mean, fell from the list of the top three fisheries and was valued at $8.9 million in 2000. The swordfish fishery, worth $8.6 million in 2001, was the fifth most valuable fishery in the state, recovering slightly from the low in 1998. Ridgeback prawn decreased 76% in 2001 from its 20-year high in 2000, and spot prawn continued its downward trend from the high set in 1998. White abalone was listed as endangered under the federal Endangered Species Act (ESA) in May 2001, making it the first marine invertebrate to be listed. A recovery plan is currently being drafted. Revenue generated from kelp harvesting in 2001 was worth an estimated $19 million, after production, to the major harvester and producer of algin products, ISP Alginates; revenue was down from the $40 million reported in 2000 due to the weakening in the U.S. economy in 2001, intense competition from foreign algin producers, and ISP's decision to shift production to its facility in Scotland.

Management authority over coastal pelagic species (Pacific sardine, Pacific mackerel, northern anchovy, and jack mackerel) was transferred from state agencies in California, Oregon, and Washington to the Pacific Fishery Management Council (PFMC) by the National Marine Fisheries Service (NMFS) in January 2000. Landings of Pacific sardine remained high in 2001, with an increase in ex-vessel value per metric ton. Only 56% of the sardine harvest guideline was caught in 2001. Pacific mackerel landings fell to 7,000 t in 2001, as did landings in Baja California, Mexico. The fishery was closed in March when the harvest guideline was met. Anchovy landings increased substantially in 2001 to 19,000 t, up 37% from 2000.

Landings in the commercial groundfish fishery were less than 12,000 t in 2001, a 67% decrease compared with ten years ago and a 28% decrease compared with last year. The groundfish harvest was again dominated by the Dover sole, thornyhead, sablefish (DTS) complex, which declined substantially compared with 2000. Stock assessments prepared for the DTS complex show a lack of sablefish recruitment over the past decade. Rockfish landings were also down in 2001; 2,401 t were landed in 2001 compared with 3,238 t in 2000, a decline of 26%, and a decline of 83% compared with 1991. As a result of stock assessments in 2000, widow rockfish and darkblotched rockfish were added to the list of groundfishes declared "overfished"; already on the list are lingcod, bocaccio, Pacific ocean perch, and some rockfishes.

The nearshore finfish fishery landed 447 t statewide in 2001, well below the 1997 peak in the fishery of 947 t. The live-fish landings component was 307 t, 69% of the overall nearshore catch. In 2001, the ex-vessel value for live-fish landings was approximately $2.8 million, about 17.5% of the value of the groundfish fishery (nearshore and offshore) and a greater proportion of the fishery's value than in the previous year. 2001 was the second consecutive year PFMC implemented two-month fishery closures for all nearshore rockfishes (winter closure south of Monterey and spring closure north of Monterey; no closure north of Cape Mendocino). During the rockfish closures, fishing effort for the live-fish market shifted to other species in some areas, such as surfperch in the San Francisco area.

Recreational finfish landings increased by 5%, to 3,073,793 individual fish caught by 682,019 anglers aboard commercial passenger fishing vessels (CPFVs) in 2001. Southern California CPFV landings comprised 83% of the statewide total, the same as in 2000. Commercial salmon fishers landed more than 1,012 t of

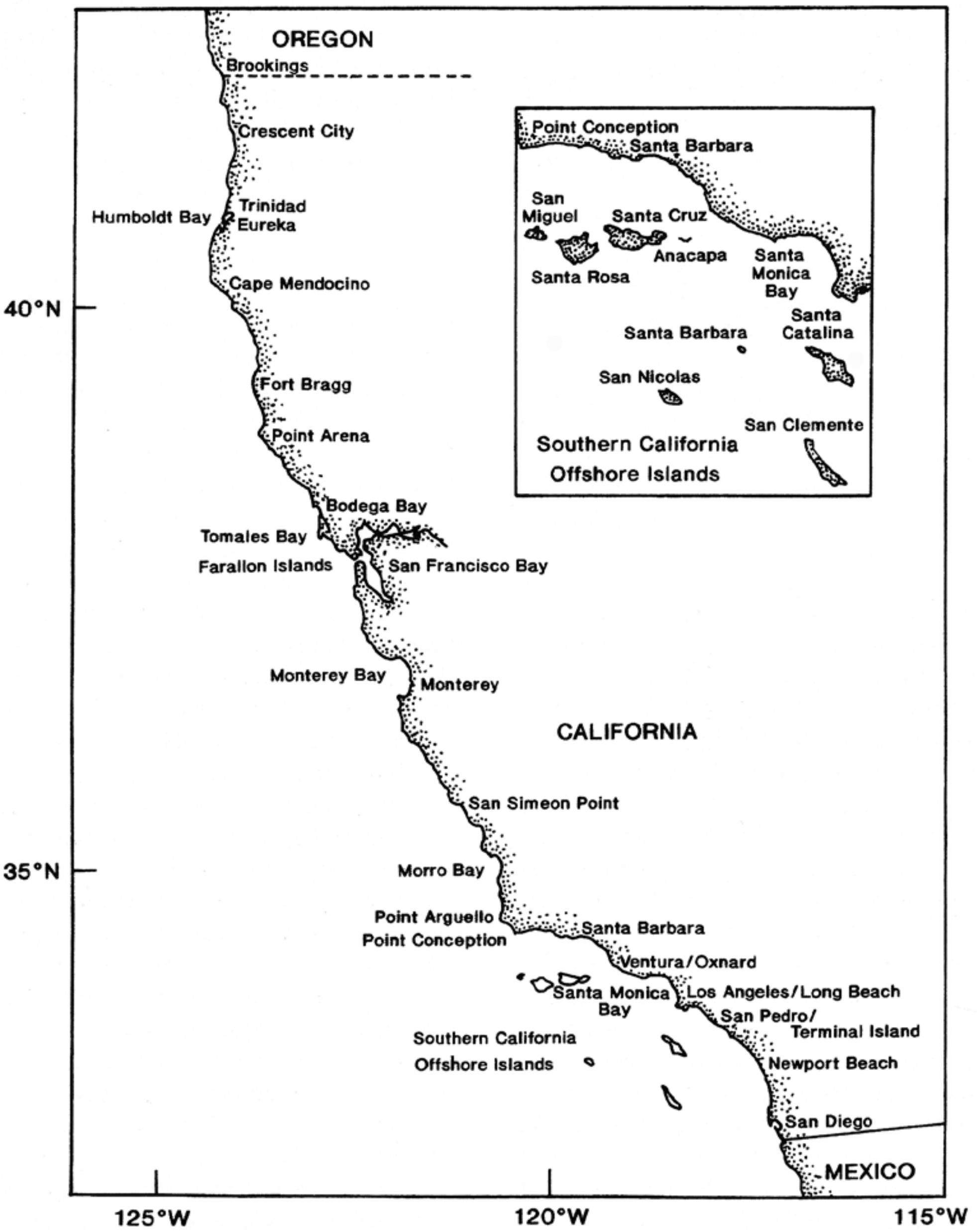

Figure 1. California ports and fishing areas.

chinook salmon, a six-fold decrease from the 20-year high set in 1988. Recreational anglers landed 97,000 chinook salmon from the ocean in 2001, a decline of 48% from the previous year. The coho salmon fishery remained closed. Commercial and recreational landings of white seabass reached an all-time high in 2001: commercial fishers landed more than 120 t, and recreational anglers landed more than 38,000 fish.

The Marine Life Management Act provides that fishery management plans (FMPs) shall form the basis for managing California's marine fisheries. A major component of the California Department of Fish and Game (CDFG) Marine Region's work in 2001 was to draft these plans as well as to amend existing plans, such as the Coastal Pelagic Species FMP (finfishes only), which set a capacity goal for the limited-entry fleet. The California Fish and Game Commission is expected to adopt three more FMPs in 2002—for nearshore fishes, abalone, and squid. As part of the FMP drafting process, CDFG held numerous workshops to facilitate constituent input into the process. Furthermore, CDFG has partnered with PFMC and others to develop the preliminary FMP for West Coast highly migratory species.

In 2001 the California Fish and Game Commission undertook 25 rule-making actions that address marine and anadromous species. In May 2001 the emergency closure of the gill-net fishery in shallow waters (<60 fathoms deep) off the central California coast was upheld, continuing the prohibition established in September 2000 to protect the common murre and the southern sea otter. In addition to the regulatory actions, the commission also received extensive oral and written testimony from the public. In response to comments received regarding Initial Draft Concepts for Marine Protected Areas within California state waters in July 2001, a new process was launched late in the year. This new process established Regional Working Groups composed of representatives from a broad range of constituencies to discuss issues related to the Marine Life Protection Act. In 2001 CDFG and the California Sea Grant Program published an update of "California's Living Marine Resources: A Status Report," which details the status of 150 marine species in the state. (To view this publication online, go to CDFG Marine Region's Web site, <www.dfg.ca.gov/mrd/index.html>).

INVERTEBRATE FISHERIES

Market Squid

Market squid (*Loligo opalescens*) is the largest fishery in the state by volume and ex-vessel value. In 2001, 85,828 t of market squid were landed, 27.2% less than the record high of 117,961 t set in 2000. The 2001 ex-vessel value was approximately $16.9 million; the average ex-vessel price was $197/t, a 10.5% decrease from 2000. The fishery remained strong, but landings were lower due to slumping market conditions.

Eighty-two percent of the market squid catch was sold internationally, with a total export value of $49 million. China, the top export destination, bought 26,313 t of product, worth $17.5 million. Domestically, the product was sold throughout the country to restaurants and Asian markets, was frozen for sale as bait, or was kept in cold storage for future sale.

The California market squid fishery targets large aggregations of spawning adults over a sandy substrate. Two vessels are used in the process: one, a vessel that uses intense lighting to attract the squid to the surface, and another, a seine vessel, that surrounds the aggregation with a seine net and captures the squid.

Most fishing takes place near the Channel Islands of southern California (the southern fishery) and in the Monterey Bay region of central California (the northern fishery). The southern fishery season occurs during the fall and winter. The northern fishery season typically runs from spring through fall. In the past 20 years landings have increased dramatically (fig. 2, tab. 1) in response to increased international demand for squid. In 2001 the southern fishery landed 78,059 t (90.9% of the catch) and the northern fishery landed 7,769 t (9.1% of the catch). As in the past, market demand regulated catch levels most of the year.

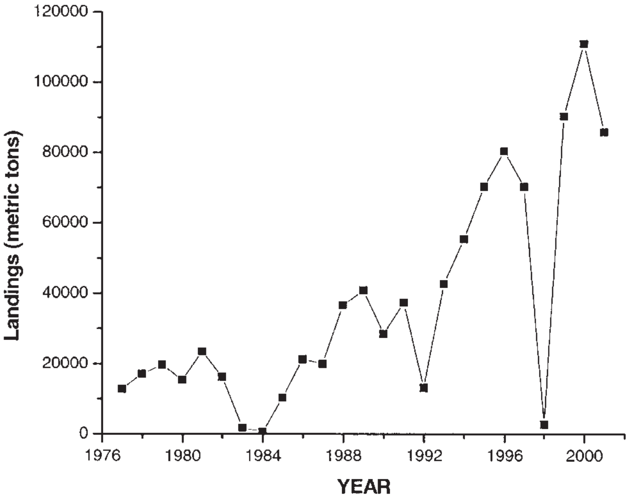

Figure 2. Northern and southern California landings of market squid, 1977–2001.

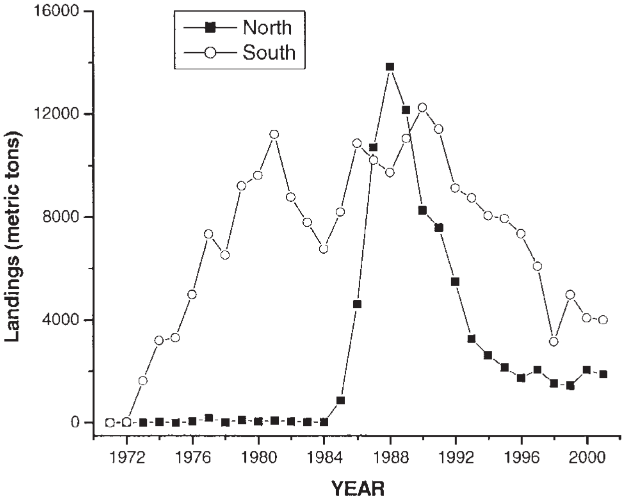

Figure 3. Northern and southern California landings of red sea urchin, 1971–2001.

In 1997 the California legislature approved Senate Bill (SB) 364 to establish a moratorium on new permits and launch a 3-year study of the fishery, which began on 1 April 1998. The bill also gave interim management authority during the study period to the California Fish and Game Commission. The commission adopted several interim regulatory measures during this period, including a weekend closure, mandatory logbooks, lighting restrictions, and a seasonal harvest limit of 113,400 t.

A report on the history of the fishery and a summary of scientific research, titled "Status of the Market Squid Fishery with Recommendations for a Conservation and Management Plan," was completed and submitted to the California legislature in May 2001. The report also outlines information and recommendations on restricting

TABLE 1
Landings of Coastal Pelagic Species in California (metric tons)

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1977	5	99,504	5,333	44,775	5,200	12,811	167,628
1978	4	11,253	11,193	30,755	4,401	17,145	74,751
1979	16	48,094	27,198	16,335	4,189	19,690	115,542
1980	34	42,255	29,139	20,019	7,932	15,385	114,764
1981	28	51,466	38,304	13,990	5,865	23,510	133,163
1982	129	41,385	27,916	25,984	10,106	16,308	121,828
1983	346	4,231	32,028	18,095	7,881	1,824	64,405
1984	231	2,908	41,534	10,504	3,786	564	59,527
1985	583	1,600	34,053	9,210	7,856	10,275	63,577
1986	1,145	1,879	40,616	10,898	7,502	21,278	83,318
1987	2,061	1,424	40,961	11,653	8,264	19,984	84,347
1988	3,724	1,444	42,200	10,157	8,677	36,641	102,843
1989	3,845	2,410	35,548	19,477	9,046	40,893	111,219
1990	2,770	3,156	36,716	4,874	7,978	28,447	83,941
1991	7,625	4,184	30,459	1,667	7,345	37,388	88,668
1992	17,946	1,124	18,570	5,878	6,318	13,110	62,946
1993	13,843	1,954	12,391	1,614	3,882	42,708	76,392
1994	13,420	3,680	10,040	2,153	2,668	55,395	85,929
1995	43,450	1,881	8,667	2,640	4,475	70,278	131,391
1996	32,553	4,419	10,286	1,985	5,518	80,360	135,121
1997	46,196	5,718	20,615	1,161	11,541	70,257	155,488
1998	41,056	1,457	20,073	970	2,432	2,709	68,646
1999	56,747	5,179	9,527	963	2,207	90,322	164,945
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

access to the fishery, number of days a week the fishery should be open, harvest replenishment areas (areas closed to fishing), a research and monitoring program, regulation of light vessels, catch limits, coordination with the federal Coastal Pelagic Species FMP, modifying fishing gear, advisory committee structure, and management authority.

In September 2001 the California legislature approved SB 209, which transferred management authority for the fishery from the legislature to the California Fish and Game Commission. CDFG must submit a Market Squid FMP to the commission on or before 31 December 2002; the FMP will describe alternatives to the recommendations presented in the report to the legislature, and the commission will select one of these alternatives for each management measure in the FMP.

Sea Urchin

Red sea urchin (*Strongylocentrotus franciscanus*) landings statewide in 2001 were estimated to be 5,880 t, with an ex-vessel value of $11.53 million, a 3% decrease compared with 2000, when 6,049 t, worth $13.1 million, were landed (fig. 3).

In southern California, the red sea urchin fishery landed less than 4,536 t for two consecutive years, a level not seen since 1975, during the early days of the fishery. In the early 1990s annual landings averaged close to 9,000 t. The northern Channel Islands have supplied most of the catch over the years, but beginning in 1992 catches began to decline as effort and landings increased at San Nicolas and San Clemente Islands, signaling a shift away from the northern islands. This shift has been exacerbated by poor kelp production in the northern Channel Islands since the last El Niño event in the late 1990s. Though it appears that the kelp has made a comeback in these islands recently, sea urchin production remains depressed.

The northern California fishery has been characterized by rapid growth; landings peaked in 1988 at 13,600 t and then declined by the late 1990s, to about 1,350–1,800 t. The 2001 catch in the north is estimated at 1,874 t. The sea urchin resource is fully exploited in California, and evidence from a variety of sources points to an overfished condition in northern and portions of southern California. Additional management measures may be needed to address this condition. The number of sea urchin permits issued has slowly declined during the last decade, dropping to 385 in 2001. The target number of permits remains at 300 for this limited-entry fishery; however, no formal fleet capacity goals have been set.

Legislation reauthorizing the Director's Sea Urchin Advisory Committee (DSUAC) became effective in 2002; committee members have been incorporated into the restructured Sea Urchin Fishery Advisory Committee. CDFG and the California Wildlife Federation are drafting an agreement to allow the transfer of sea urchin enhancement funds, collected from an industry-imposed

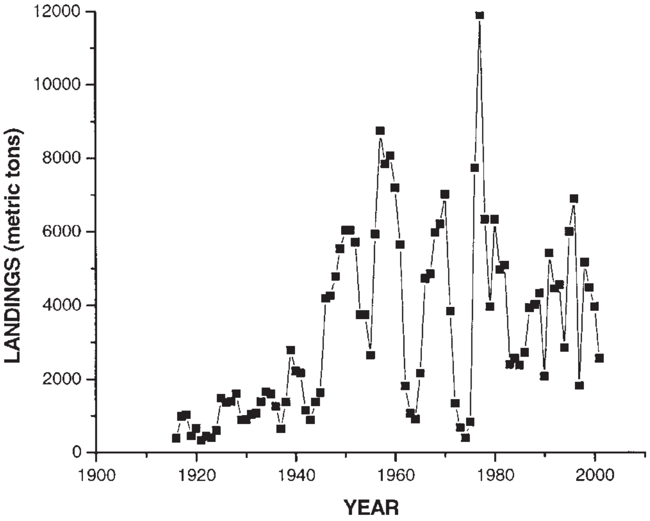

Figure 4. California landings of Dungeness crab, 1916–2001.

sea urchin landing fee, to the nonprofit California Wildlife Federation. Although the landing fee expired in 2001, the industry account has over $300,000 remaining. Divers and processors are planning to spend the funds on data collection and other activities that will support and augment CDFG's efforts to enhance and manage the resource and associated fishery. CDFG Marine Region's invertebrate team, in conjunction with industry, will begin working on research goals and protocols for fishery-independent sea urchin data collection at the beginning of 2003. This will be done in conjunction with other preparatory actions in anticipation of the drafting of a sea urchin FMP. Sea urchins received a high ranking in CDFG's Master Plan, which the department will use to prioritize species for new FMPs. In the meantime, the industry and CDFG are working on interim regulatory changes that could be brought before the commission by the end of 2002.

Dungeness Crab

Commercial Dungeness crab (*Cancer magister*) landings for the 2000–2001 season in California totaled 2,559 t, a 36% decrease from the previous season and a significant decline from the ten-year average of 4,279.5 t (fig. 4). These were the second lowest landings on record in 26 years. Statewide landings through January 2002 were 1,252 t, a 42% decrease from the very poor season of 2000–2001 and a 64% decrease from the 1999–2000 season. Southern Oregon has also reported low crab landings; this is in contrast to northern Oregon and Washington, which are reporting their best catches in years.

The crab fishery was worth $12.6 million in 2000–2001, a decrease of 29% from the $17.8 million produced in 1999–2000. The average price per pound for the season was $2.23, the highest in ten years. The fleet was composed of 424 vessels, the fewest in ten years and a 45% decline from the 769 that fished in 1991–92. A restricted-access program has been in place since the 1995–96 season.

The Dungeness crab season south of Mendocino County opened on 15 November, with the industry agreeing on a price of $2.50/lb. Fishers in the San Francisco Bay area landed a total of 735.1 t, an increase of 78% from the 1999–2000 season, when 412.9 t were landed. Crab fishers from the Monterey Bay area south landed 15.5 t, a 10% increase from the previous season.

The season in northern California from Fort Bragg to Crescent City opened on 1 December, but fishing did not start for another week because of price negotiations, which were finally settled at $1.60/lb. The price reached a high of $4.65/lb in May and fell to $2.50/lb in July. This followed the general price trend, which is highest in the middle of the season on declining volume and falls toward the end of the season as crabs approach the molt and quality becomes more variable. The catch in northern California totaled 1,808.5 t, a 49% decrease from the previous season.

The crab fishery in California is managed using size, sex, and season limits. Only male crabs are fished commercially, and the minimum commercial legal 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 crabs from being harvested for a season or two; season limits protect crabs when molting is most prevalent. The sale of female Dungeness crabs has been prohibited in California since 1897. Minimum-size regulations were first implemented in California in 1903 and have remained essentially unchanged since 1911. This management structure has been stable and very successful. Landings appear to cycle over time; a record high of 11,915 t were landed in the 1976–77 season.

Legislation authorizing a pre-season soft-shell crab testing program in California was introduced in 1994, and the industry-funded testing began prior to the 1995–96 season. The testing program, monitored by the Pacific States Marine Fishery Commission, is initiated each year around 1 November. A minimum meat recovery of 25% is required for the season to open. If meat recovery is less than 25%, the fishery remains closed until a second test is conducted two weeks later; if the pick-out is still below 25%, the season opening is delayed 15 days. This schedule may continue until 1 January, after which no more tests are conducted, and the season must be opened by 15 January. The first test of the 2000–2001 season produced a 25.2% pick-out.

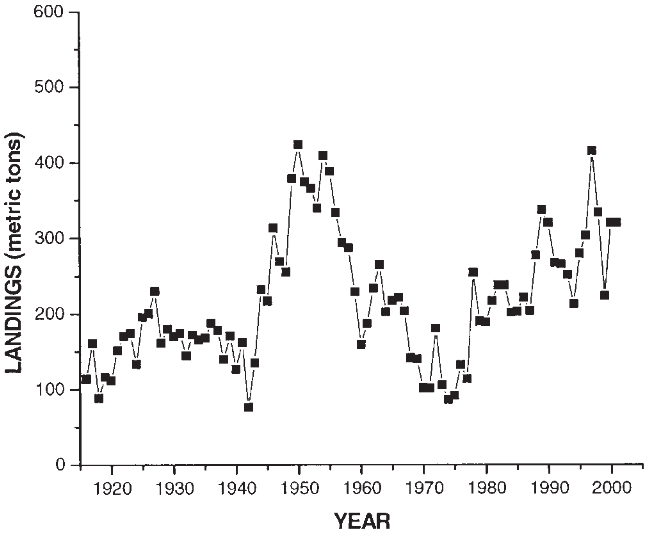

Figure 5. California landings of spiny lobster, 1916–2001.

California Spiny Lobster

Landings in 2001 for California spiny lobster (*Panulirus interruptus*) totaled 320 t, the same as in 2000 (fig. 5). Landings were split equally among three ports: Santa Barbara (36%), San Diego (34%), and Los Angeles/Orange Counties (30%). Landings in previous seasons were centered in the San Diego area—in the 1995-96 season, 40% of the landings were in the San Diego area, suggesting a northern shift in landings.

The lobster fishery was valued at $4.49 million in 2001, down from $6.88 million in 1997. In southern California ex-vessel prices for spiny lobster rank among the highest compared with other fisheries, and prices ranged from $6.00 to $8.00/lb. Over the last three years, however, the average price per pound has fallen from $7.30 in 1999, to $6.90 in 2000, and down to $6.65 in 2001.

In southern California, there has been a commercial fishery for California spiny lobster since the late 1800s, and commercial landings have been recorded since 1916 (fig. 5). The commercial fishery uses baited traps to capture live lobster for wholesalers and markets. There is also a recreational fishery, and both scuba and free diving are allowed, although only bare hands or hoop nets can be used to capture lobster. These fisheries operate in shallow coastal rocky areas from Point Conception south to the Mexican border and at offshore banks and islands. The season runs from early October through mid-March, and the majority of the landings occur in the first few months of the season.

Since the 1950s, there have been several major regulation changes to better manage the fishery. In 1955 a minimum-size limit of 3.25 in. carapace length was established. This regulation is still in effect today for both recreational and commercial fishers. Since 1976, commercial fishers have been required to use rectangular escape ports (2.375 × 11.5 in.) on traps to decrease the retention of undersized lobster. This management tool, along with warming ocean conditions following the regime shift in 1977, may have helped reverse the long downward trend in landings from the 1950s to the 1970s (fig. 5). In 1997 access restrictions were placed on the commercial fishery to limit the number of participants. In 2001 CDFG issued 246 lobster operator permits, down from 298 in 1996.

A logbook for the commercial fishery has been required since 1973. The logbook contains catch and effort information, such as the number of legal-sized lobster taken, the number of small lobsters released, the number, depths, and locations of traps used, and the number of nights the traps were fished. During the 1999–2000 season, more than 800,000 traps were fished for over 41,000 nights; nearly 340,000 legal-sized lobsters were taken, and over 805,000 under-sized lobsters were caught and released. This is down from a peak in the 1997–98 season, when over 600,000 legal-sized lobsters were taken. However, the proportion of undersized lobster caught and released increased from 60% to 70% in the same time period, suggesting good recruitment to the fishery. Analysis of logbook compliance shows that prior to the 1995–96 season, reporting was nearly 50%, increased to 80% for the 1995–96 fishing season, and reached 95% for the 1999–2000 season.

Currently, there are no set quotas on the amount of lobster commercial fishers can land nor on the number of traps they can use. Some fishers have been reported to set 500 or more traps at the beginning of the season, though 100–300 traps is more typical. The bag limit for recreational fishers is seven lobsters a day, down from ten a day in 1971. There are no in-season limits or reporting requirements, such as punch cards, to track the recreational take of spiny lobster.

Spot and Ridgeback Prawn

Preliminary 2001 spot prawn (*Pandalus platyceros*) landings were 188 t, a 6% decrease from the 199 t landed in 2000. This was the third consecutive year spot prawn landings decreased (fig. 6). The sharpest decline occurred in the Santa Barbara and Morro Bay port area trawl catches, where spot prawn landings dropped 31% from the previous year's total.

Spot prawn are caught with both trap and trawl gear. A total of 70 vessels (36 trap and 34 trawl) made landings in 2001. Over 40% of the combined trap and trawl spot prawn landings in 2001 were made in the Santa Barbara port area. Since the mid-1970s, the number of spot prawn trawlers has increased, particularly so in the last ten years because of an influx of vessels from other

TABLE 2
Landings of California Spot Prawn by Port Area and Gear Type, 2001

	No. of fishing vessels		Landings (metric tons)			
Port Area	Trap	Trawl	Trap	Trawl	Total	% of total
Eureka	1	4	1	5	6	3
San Francisco	0	9	0	28	28	15
Monterey	5	6	17	5	22	12
Morro Bay	1	14	2	33	35	19
Santa Barbara	7	20	28	20	48	25
Los Angeles	15	4	27	1	28	15
San Diego	10	0	21	0	21	11
Total			96	92	188	100

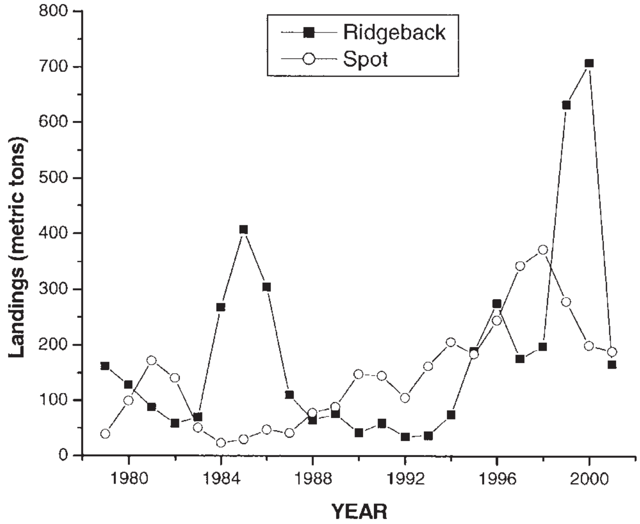

Figure 6. California landings of spot and ridgeback prawn, 1979–2001.

groundfish fisheries that have been subjected to restrictive quotas or seasonal closures.

Trawlers harvested approximately 92 t of spot prawn in 2001, and trappers took 96 t (tab. 2). The median ex-vessel price paid for all spot prawns was $9.25/lb. Approximately 80% of all spot prawn were sold live. Ex-vessel prices for live spot prawn ranged from $5.00 to $13.00/lb, with a median ex-vessel price of $9.25/lb. The ex-vessel price for fresh dead spot prawn ranged from $1.50 to $5.00/lb, with a median price of $3.50/lb.

During 2001, the trap and trawl spot prawn permit fisheries in southern California (south of Point Arguello) and the trawl spot prawn fishery in northern California were closed from 1 November to 31 January. Up to 50 lb of incidentally trawled spot prawn could be retained during the closure. This southern California trap and trawl closure was instituted in 1997 to protect gravid females. North of Point Arguello, the spot prawn trap season was closed 1 May to 31 July.

In 1999 trap fishers and environmental representatives expressed concern at a California Fish and Game Commission meeting about the level of bycatch in the spot prawn trawl fishery. The commission directed CDFG to study the type and relative magnitude of bycatch in the spot prawn trap and trawl fisheries. Beginning in the fall of 2000 and continuing for approximately one year, CDFG on-board observers were sent out on spot prawn trawl and trap vessels to monitor the bycatch. The samplers obtained passage on 9 trawl and 17 trap vessels and observed a total of 86 trawl tows and 262 trap strings.

Primary bycatch species of fishes by weight observed in trawl tows from vessels originating north of Point Conception were Pacific hake, Dover sole, sablefish, English sole, and splitnose rockfish. For trawl vessels fishing from ports south of Point Conception, the primary bycatch fish species were Pacific sanddab, Pacific hake, slender sole, shortbelly rockfish, and Dover sole. For northern and southern trawl vessels, rockfishes comprised 25% and 9%, respectively, by weight of the total fish bycatch. Primary bycatch fish species by weight observed in trap strings from vessels originating north of Point Conception were sablefish, rosethorn rockfish, greenblotched rockfish group, spotted cusk eel, and filetail catshark. For trap vessels fishing from ports south of Point Conception, the primary bycatch fish species were lingcod, greenblotched rockfish group, threadfin sculpin, sablefish, and swell shark. Most sablefish, lingcod, and sharks, many sculpin, and some cusk eels taken by prawn trap were able to survive after being returned to the water. For northern and southern trap vessels, rockfishes comprised 25% and 32%, respectively, of the bycatch by weight. In general, the weight ratio of bycatch to spot prawns, particularly finfish bycatch, was substantially lower in the trap fishery than in the trawl fishery. A final report is being drafted for submission to the California Fish and Game Commission.

In 1999 a spot prawn ad hoc advisory committee, consisting of trap and trawl fishery representatives and a nonfishery representative from the Marine Science Institute in Santa Barbara, was formed to help CDFG develop new regulatory strategies, such as trawl gear restrictions or modifications, excluder device requirements, seasonal harvest limits, area closures, and restricted access to harvest permits. In 2000 the California Fish and Game Commission adopted a package of regulatory changes that included establishing a control date to qualify for restricted-access spot prawn fisheries. In 2001 the commission adopted a two-tiered restricted-access program for the spot prawn trap fishery; the program was implemented in April 2002.

Preliminary 2001 ridgeback prawn (*Sicyonia ingentis*) landings totaled 165 t, a 77% decrease in landings from the 707 t landed in 2000 (fig. 6) and the lowest recorded in the fishery since 1994. Two major factors affected landings: the scarcity of ridgeback prawn on the trawl grounds and diminished market demand for ridgeback prawn.

Ridgeback prawn are taken exclusively by trawl nets. The season is closed from 31 May to 1 October, but an incidental catch of 50 lb is allowed. Thirty-one trawl vessels landed ridgeback prawn in 2001, 13 fewer vessels than in 2000. All landings were made at southern California ports from Santa Barbara to Los Angeles, and almost all ridgeback prawn were caught within the Santa Barbara Channel.

The median ex-vessel price paid for live ridgeback prawn was $1.50/lb, and for dead ridgeback prawn, $.93/lb. Approximately 67% of the landings were live ridgeback prawn, similar to the proportion landed live in 2000. Most of the dead ridgeback prawn were frozen whole and delivered to domestic and overseas markets

Until 1998, ridgeback prawn landings were limited by market demand and the few dealers who could buy and process large quantities of prawn. By 1999, however, 45 dealers were purchasing ridgeback prawn. The fishery reached a peak in 2000, but in 2001 ridgeback prawn landings fell to pre-1998 levels as a consequence of both La Niña–driven oceanic cooling and economic market factors. These relatively rapid and substantial changes in the ridgeback prawn fishery warrant periodic monitoring surveys to assess whether the ridgeback prawn fishery is sustainable under existing harvest levels.

Abalone

The recreational red abalone (*Haliotis rufescens*) fishery along the coast north of San Francisco is the only abalone fishery open in the state. The use of scuba or surface-supplied air is prohibited in this fishery. This regulation effectively restricts abalone fishers to intertidal and shallow depths. Abalone in deeper water are protected in "de facto" deepwater reserves along the coast. Also, a number of intertidal and shallow areas are protected because they are difficult for abalone divers to access. No abalone less than 178 mm (7 in.) may be taken, which prohibits the take of smaller pinto abalone (*H. kamtschatkana kamtschatkana*) and flat abalone (*H. walallensis*).

Landings in the recreational fishery have been estimated from measures of fishing pressure. Two methods are used for harvesting abalone: shore picking (wading) and free diving (breath-holding), and there is a continuum between the methods. In 1960 an estimated 11,000 diver-days were expended to take 53 t (118,000 lb) of red and black abalone; in 1972 29,000 diver-days were expended to take 87 t (192,000 lb). Since the 1960s the number of free divers fishing for abalone, including those using boats, has increased faster than the number of shore pickers. The estimated number of participants in the fishery in 1985–89 is 33,000. Estimated red abalone landings for the same period in northern and central California (divers and shore pickers combined) range from a high of 1,700 t (3.4 million lb) in 1986 to a low of 580 t (1.1 million lb) in 1989. In 1998 an abalone stamp was issued to generate revenues for fishery assessments and enforcement. In 2001, 40,790 abalone punchcards were sold, and in 2000, 39,297 were sold, showing that effort levels are slightly higher now than estimated for the 1985–89 period.

Many data sources, including fishery-dependent and -independent data, are used to assess the status of the recreational red abalone fishery on the northern California coast. Fishery-independent data suggest that red abalone populations at three heavily fished sites in northern California have higher densities of adults or not significantly different densities than observed in a survey conducted in 1986. Despite this finding, the population structure at five key sites suggests that no strong recruitment event has occurred in the past five years, as evidenced by the lack of red abalone with shell diameters smaller than 100 mm. Evidence also suggests that red abalone stocks are depressed north of the sea otter range in central California and at the Farallon Islands. Few abalone were found at the Farallon Islands during extensive CDFG remote-operated-vehicle surveys in 2000 or in the Half Moon Bay area during diver surveys in 1993. Other sources of information have raised concerns about the status of the red abalone fishery—for example, there has been a concentration of fishing effort in Sonoma and Mendocino Counties during the past decade, deepwater stocks at some sites have declined, the number of recreational abalone fishers has increased, and organized poaching has increased. To address these concerns, the California Fish and Game Commission implemented precautionary regulatory changes in 2001 reducing the daily limit from 4 to 3 abalone per fisher and the annual limit from 100 to 24 abalone per fisher.

In southern California, stocks on the northern Channel Islands show little evidence of recovery. In the most recent CDFG cruise (2001), red abalone abundance (measured as the number of abalone encountered by one diver in an hour) was very low. For example, at

TABLE 3
California Commercial Groundfish Landings (metric tons)

	2001	2002	% change since 2000	1991	% change since 1991
Flatfishes	4,559	5,259	−13	10,766	−58
Dover sole	2,399	3,267	−27	7,721	−69
English sole	419	299	40	812	−48
Petrale sole	555	628	−12	734	−24
Rex sole	235	223	5	621	−62
Sanddabs	788	727	8	559	41
Other flatfish	163	115	42	319	−49
Rockfishes	2,401	3,238	−26	13,830	−83
Thornyheads	847	1,240	−32	2,871	−71
Widow rockfish	332	705	−53	1,304	−75
Chillipepper	343	444	−23	3,116	−89
Bocaccio	23	27	−15	1,314	−98
Canary	9	13	−31	271	−97
Darkblotched	71	99	−28	341	−79
Splitnose rockfish	95	78	22	488	−80
Other rockfish	681	632	8	4,125	−84
Roundfishes	4,198	7,232	−42	11,111	−62
Lingcod	62	54	15	787	−92
Sablefish	1,547	1,859	−17	3,353	−54
Pacific whiting	2,306	4,986	−54	6,893	−67
Grenadier	211	221	−5	71	197
Cabezon	72	112	−36	7	929
Other groundfishes	704	633	11	128	450
Total	11,862	16,362	−28	35,835	−67

Santa Rosa and Santa Cruz Islands, abundance from timed swims ranged from approximately zero to eight abalone encountered in an hour at Santa Rosa Island and from zero to one abalone an hour at Santa Cruz Island; this is compared with 70 red abalone encountered in an hour at a site in northern California in 2000. San Miguel Island is the only location thought to have a minimum viable population size (of approximately 2,000 abalone per hectare) based on CDFG surveys in 1997.

Population levels of white, black, pink, and green abalone continue to be low, and there is concern about the continued viability of these species at such levels. White abalone was listed as endangered under the federal ESA in May 2001. A recovery team has been named by the National Marine Fisheries Service and this team will aid in the drafting of a recovery plan for the species. Several hundred thousand small white abalone are being raised at the Channel Islands Marine Research Institute for potential stocking to assist in population enhancement and recovery. Black abalone—virtually extirpated off the coast of southern California because of both withering syndrome and overfishing—is now a candidate species for listing under the federal ESA. CDFG surveys in 2001 found few pink or green abalones at the Channel Islands; average abundances from timed swims in March 2001 were 5.0 pink abalone an hour and 0.5 green abalone an hour.

CDFG is currently developing an Abalone Recovery and Management Plan (ARMP) mandated by Fish and Game Code (FGC §5522). The plan will be submitted to the California Fish and Game Commission on or before 1 January 2003. This plan will outline the strategy for restoring depleted abalone stocks in central and southern California and describe the management approach for fishable abalone stocks in northern California. The plan will also describe a data-collection strategy to enable an adaptive management approach. A peer review committee was convened twice in 2001 to review and comment on elements of the plan. The committee is composed of representatives from the recreational and former commercial fisheries, nonprofit organizations, and scientists from major universities and the federal government. The timeline for the plan includes a period for public comment and formal peer review.

In 2001 the abalone aquaculture industry produced over 94 t (208,300 lb) of red abalone statewide, worth $3 million. The causative agent of the disease withering syndrome has been identified in cultured animals, and this may impact production, particularly during warm water conditions.

FINFISH FISHERIES

Groundfish

The California commercial groundfish harvest for 2001 was 11,862 t (tab. 3). Total 2001 landings decreased 28%, or 4,500 t, from 2000; compared with 1991, landings decreased 67%, or 23,973 t. If Pacific whiting (*Merluccius productus*) landings are not included in the

1991, 2000, and 2001 total groundfish landings, then the total groundfish harvest shows a 16% decline from 2000 and a 59% decline from 1991. The ex-vessel value for all groundfishes in 2001, including Pacific whiting, was approximately $16.2 million, a decrease of $4.0 million, or 20%, from 2000 revenues.

In 2001, 86% of the groundfishes landed were taken by bottom and midwater trawl gear, a slight decrease from the 89% observed in 2000. Line gear accounted for the second largest amount at 11%, a slight increase from the 9% observed in 2000. The line gear contribution was at a recent high of 18% in 1992. The gill and trammel net component remained at just under 1% after a steady decline from 5% in 1993 to 1% in 1996. Trap gear rose to nearly 2% of total 2000 groundfish landings.

California's 2001 groundfish harvest was again dominated by Dover sole (*Microstomus pacificus*), thornyheads (*Sebastolobus* spp.), sablefish (*Anoplopoma fimbria*), rockfish (*Sebastes* spp.), and Pacific whiting. Landings of Dover sole, thornyheads, and sablefish (the DTS complex) and of most rockfishes were substantially lower in 2001 than in 2000; landings of lingcod and other flatfish were relatively stable. The declines reflect landing limits adopted by the PFMC in November 2000 that were designed to reduce the harvest of depleted rockfish stocks. Shoreside landings of Pacific whiting declined because of reduced availability in the Eureka–Crescent City area during spring and early summer, normally the period of peak availability.

For 2001, the PFMC continued to set optimal yields for a myriad of groundfish species and species groups. The allowable harvest was reduced for nearly all groups to protect those species in rebuilding status. Cumulative landing and trip limits were again used by PFMC to meet their optimal-yield objectives while continuing to provide for a year-round fishery.

Stock assessments prepared in 2000 by PFMC showed that widow rockfish (*Sebastes entomelas*) and darkblotched rockfish (*S. crameri*) are "overfished"; a rebuilding plan developed in 2001 will be adopted in 2002. The 2001 fishery for darkblotched rockfish was constrained by a separate optimal yield for the first time; because of the "overfished" status of darkblotched rockfish and widow rockfish, optimal yields for both were greatly reduced.

PFMC prepared stock assessments in 2001 for sablefish, Dover sole, and shortspine thornyhead. Stock Assessment Review Panels reviewed the assessments, and recommendations were forwarded to the Groundfish Management Team for development of 2002 management measures. The sablefish assessment indicated that a lack of recruitment in the last ten years has significantly decreased spawning biomass and that stocks are at risk for becoming "overfished." The PFMC addressed these concerns by adopting a reduced optimal yield for sablefish in its 2002 management measures. Dover sole appears to be undergoing a similar though less severe recruitment decline, and PFMC imposed a precautionary harvest reduction for 2002. The shortspine thornyhead assessment indicated that biomass is increasing, so the optimal yield was set slightly higher for 2002. Assessment plans for 2002 include assessing bocaccio (*S. paucispinis*) and canary rockfish (*S. pinniger*) and updating the sablefish assessment to incorporate new recruitment information.

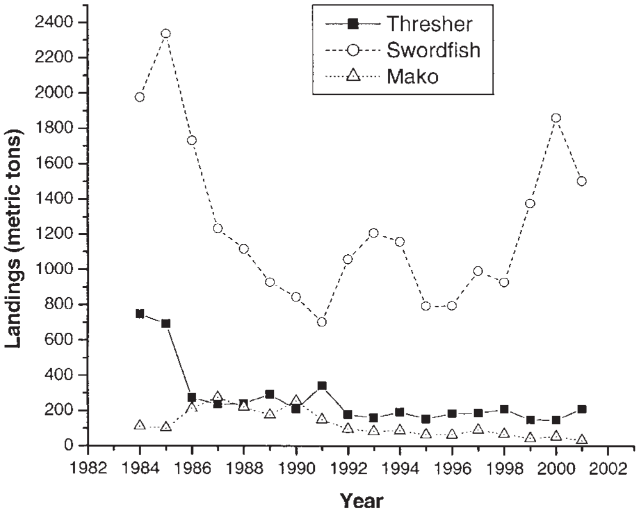

Figure 7. California commercial landings of swordfish, thresher, and mako sharks.

Swordfish and Shark

Commercial swordfish (*Xiphias gladius*) landings for 2001 totaled 1,502 t (fig. 7), a decrease of 19% from the 2000 total of 1,861 t. Swordfish are primarily targeted by the drift gill-net fishery, a small harpoon fishery operating within the Southern California Bight, and by a California-based longline fishery that fishes beyond the U.S. exclusive economic zone (EEZ). In 2001, 16% of the catch was taken with drift gill nets, down from 23% in 2000. Harpoon landings were also down, constituting only 2% of the catch. Longline landings, however, were up from 70% of the catch in 2000 to approximately 80% in 2001. Thirty-seven vessels used longline gear outside the U.S. EEZ and landed swordfish in southern California ports; only eight of these vessels were based in California. Approximately 98% of the swordfish catch was landed in southern California.

The total ex-vessel value for swordfish landings for 2001 was approximately $8.7 million. As expected, gear type, size, and quality affected swordfish ex-vessel prices. Fishers landing swordfish caught in gill nets received $.40–7.00/lb, or an average of $3.25/lb. Longline fishers received $.50–4.50/lb, or an average of $2.18/lb; and

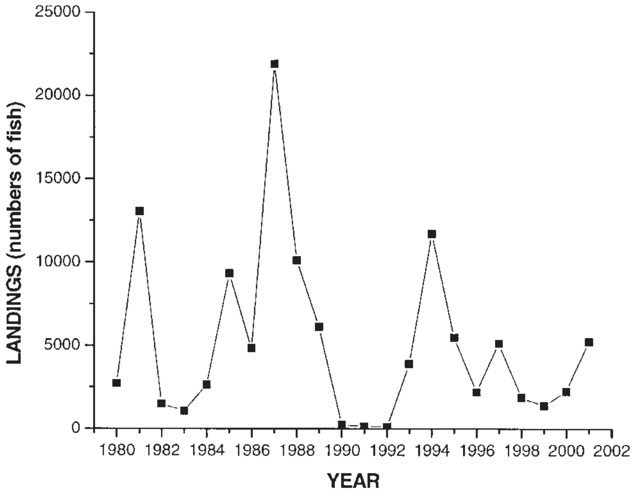

Figure 8. California recreational landings of shortfin mako shark, 1980–2001.
Note: Recreational landings for 1990–93 are CPFV logbook data only; all other years include CPFV data and MRFSS total landed estimates (catch type A + B1, private boats).

fishers landing harpoon-caught swordfish received the highest average price, $6.39/lb; the range was $1.00–8.25/lb.

The common thresher shark (*Alopias vulpinus*) was the leading commercial shark taken in California in 2001; preliminary landings totaled 210 t (fig. 7). This was the highest yearly landing since 1991 and an increase of 44% from 2000. Thresher sharks were taken primarily with drift gill nets (76%), followed by set gill nets (20%) and other types of gear (4%). Most (82%) of the thresher shark catch was landed in southern California. Ex-vessel prices varied from $.25 to $2.50/lb, with an average of $1.38/lb. The total ex-vessel value was approximately $600,000.

In 2001 the shortfin mako shark (*Isurus oxyrinchus*) was the second most important commercial shark in California. Shortfin mako landings totaled 32 t, a 41% decrease from the 2000 total of 54 t (fig. 7). The catch was primarily taken by drift gill nets (56%) targeting swordfish. The rest of the catch was landed by set gill net (15%), hook-and-line gear (11%), and longline vessels operating outside the U.S. EEZ (14%). Ninety-seven percent of the catch was landed in southern California ports. Ex-vessel prices varied from $.50 to $2.25/lb, with an average of $1.11/lb. The total ex-vessel value was approximately $76,000.

Shortfin mako shark was the primary shark target species for recreational anglers in 2001. Recreational anglers landed approximately 5,235 mako sharks, up 132% from 2000 (fig. 8). Ninety-nine percent of the catch were caught within the Southern California Bight, and the remaining 1% were caught in Mexican waters. The shortfin mako shark does not occur regularly in the recreational catch north of Point Conception.

PFMC is currently developing an FMP for West Coast highly migratory species fisheries; the plan will include swordfish, shortfin mako shark, and common thresher shark, among others. After receiving public comment and advice from the Highly Migratory Species Advisory Subpanel, the PFMC will consider final adoption of the FMP at its November 2002 meeting in San Mateo County, California. Once adopted, the plan will be submitted to NMFS for review and approval. Upon approval, NMFS will publish the proposed regulations, request public comment, and publish the final regulations.

Coastal Pelagic Finfish

In January 2000, management authority over coastal pelagic finfishes—Pacific sardine, Pacific mackerel, northern anchovy, and jack mackerel—was transferred from state agencies in California, Oregon, and Washington to the PFMC by NMFS. These fishes have been among the traditional targets of California's "wetfish" fleet and are frequently found nearshore in mixed schools. The sardine fishery extends from Baja California to British Columbia.

The federal Coastal Pelagic Species FMP has placed Pacific sardine and Pacific mackerel under an active management status that requires annual stock assessments, which are conducted jointly by CDFG and NMFS, and seasonal harvest guidelines. Northern anchovy and jack mackerel will continue to be monitored until landings increase to a threshold level of 25,000 t for anchovy and 31,000 t for jack mackerel for two consecutive years. Exploitation of northern anchovy is generally constrained by market forces, where availability is high but ex-vessel prices are low. Jack mackerel is desirable for human consumption, but because larger fish do not tend to school, the life history of the jack mackerel tends to prevent the fishery's expansion.

Some limited amounts of these coastal pelagic finfishes are used domestically as dead bait, pet food, and products for human consumption. The primary use of Pacific sardine is for aquaculture feed in Australian tuna farms; in Japan large fish are sold in specialty markets both for human consumption and for long-line bait. Northern anchovy has been substituted in the Australian markets in the absence of sardine. Almost the entire Pacific mackerel catch in 2001 was exported frozen to South Korea, Australia, and the Philippines.

In addition to the directed fishery for sardine, the live-bait industry in California supplies sardine and anchovy to CPFVs, the albacore fleet, and recreational anglers. Live bait is a low-volume, high-value fishery not subject to quotas; it consists of fewer than two dozen vessels and has taken an annual reported average of 2,700 t of sardine and anchovy combined in the last decade. As with the directed fishery, live-bait vessels typically participate in more than one fishery throughout the year, dependent on seasons and availability of target species.

In December, the Australian government began investigating reports of viral hemorrhagic septicemia (VHS) in Pacific sardine and Pacific mackerel from California waters. It is likely that import restrictions will severely affect the coastal pelagic species fisheries in California in the future.

Pacific Sardine. California landings of Pacific sardine (*Sardinops sagax*) in 2001 totaled 52,000 t, nearly matching the 2000 catch of 54,000 t (tab. 1, fig. 9). The approximate ex-vessel value was $6.3 million, up from $5.5 million in 2000. Combined landings from California, Oregon, and Washington totaled roughly 76,000 t (about 56% of the 2001 harvest guideline), and ex-vessel revenues totaled over $9.1 million. The Ensenada fishery in Baja California, Mexico, landed 22,000 t in 2001, down from 51,000 t in 2000, and Canada had a small fishery, which landed about 1,600 t.

Pacific sardine biomass is estimated using a modified version of the integrated stock-assessment model Catch-at-Age Analysis for Sardine-Two Area Model (CANSAR-TAM). CANSAR-TAM is a forward-casting, age-structured analysis using fishery-dependent and fishery-independent data to estimate annual sardine abundance, year-class strength, and age-specific fishing mortality for 1983 through 2001. The modification of CANSAR was developed to account for the expansion of the Pacific sardine stock northward to include waters off the northwest Pacific coast. Based on a biomass estimate of nearly 1.2 million t, two-thirds of the coastwide harvest guideline of 134,737 t for the 2001 season was allocated to southern California (south of San Simeon Point, San Luis Obispo County), and one-third was allocated to northern California, Oregon, and Washington. The initial allocation was 89,825 t to the southern fishery and 44,912 t to the northern fishery. In October 2001, NMFS reallocated the uncaught portions equally between the two fisheries at 36,153 t each. Although both fisheries remained open through the entire 2001 season, 44% of the harvest guideline remained unmet. Most of the sardine catch was from southern California ports, where summer fishing was affected by a bycatch limit on Pacific mackerel following a closure of that fishery. Landings in the Monterey fishery were low in the first semester of the season but increased in September as the availability of market squid declined. The 2002 season opened with a harvest guideline of 118,442 t, based on a biomass estimate of about 1.06 million t coastwide.

In October 2001, the California Department of Health Services issued a warning concerning elevated levels of domoic acid in the internal organs of sardines and anchovies along the Santa Barbara coast; this was in addition to an existing warning about sardines in Monterey. Monitoring of coastal pelagic species and shellfish continues in California because domoic acid has been found in other species in other areas.

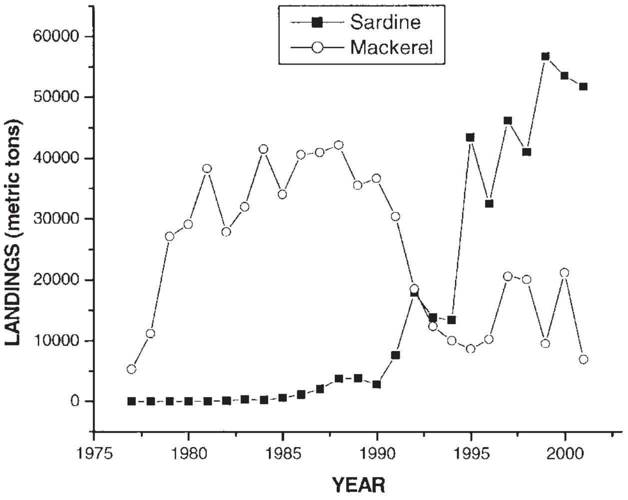

Figure 9. California commercial landings of Pacific sardine and Pacific mackerel, 1977–2001.

Pacific Mackerel. Landings of Pacific mackerel (*Scomber japonicus*) in California totaled nearly 7,000 t in 2001, significantly down from the 21,000 t catch in 2000 (tab. 1, fig. 9). The ex-vessel price averaged $154/t in 2001 and generated $1.1 million in total revenues. The average price per metric ton in 2000 was $132, for an annual total of $2.9 million. No significant fisheries for Pacific mackerel exist in Oregon or Washington; landings at Ensenada, Baja California, Mexico, totaled 4,000 t in 2001, down from 7,000 t in 2000.

The fishing season for Pacific mackerel is July to June. In the 2000–2001 season, a harvest guideline of 20,740 t was met in March 2001 and the fishery was closed. The harvest guideline for the 2001–2002 season, based on a biomass projection derived from ADEPT, a tuned virtual population analysis model, was 13,837 t. This guideline was allocated to take advantage of high availability and demand in the first semester of the season, with a portion set aside to allow incidental catch in the sardine fishery without exceeding the seasonal guideline. The directed fishery was closed when the initial allocation of 6,000 t was met and was reopened on 1 April 2002 to fill the remainder of the guideline.

Northern Anchovy. California landings of northern anchovy (*Engraulis mordax*) increased substantially to 19,000 t in 2001, up from 12,000 t in 2000 (tab. 1) and the highest level since 1982. Ex-vessel revenues for each of these years generated about $1.4 million, with an average price per metric ton of $66 in 2001 and $110 in 2000. Oregon and Washington had no reported landings of anchovy in 2001; landings at Ensenada, Baja California, Mexico, dropped to only 76 t, from 1,500 t in 2000.

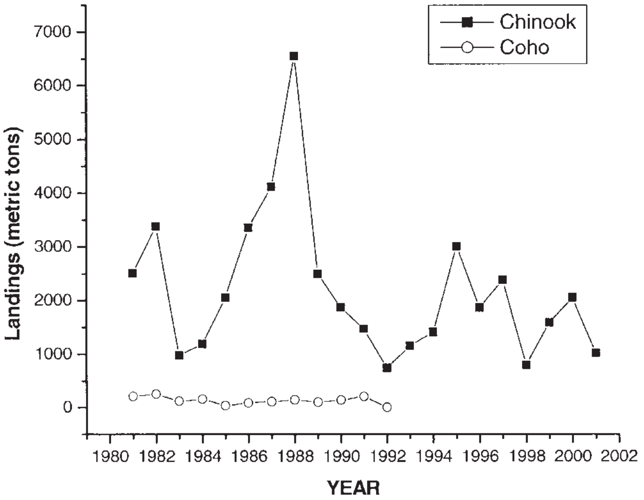

Figure 10. California commercial landings of ocean salmon, 1981–2001.

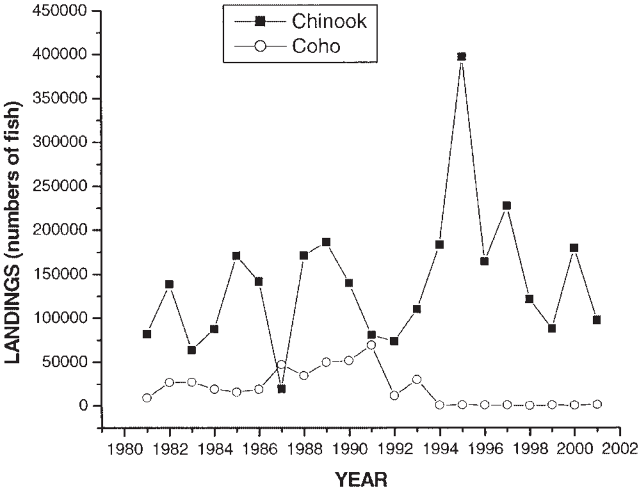

Figure 11. California recreational landings of ocean salmon, 1981–2000.

Jack Mackerel. Landings of jack mackerel (*Trachurus symmetricus*) in California totaled 3,600 t in 2001, up from 1,300 t in 2000 (tab. 1). Revenue totaled $560,000 in 2001, an increase from $260,000 in 2000. Oregon reported only 183 t in 2001 and 161 t in 2000, and no landings were reported by Washington or Ensenada for either year.

Ocean Salmon

Commercial ocean salmon landings for chinook salmon (*Oncorhyncus tshawytcha*) were greatly reduced in California in 2001, reflecting a northern shift in populations that boosted landings 400% higher than average in Oregon. Approximately 1,012 t (179,600 fish) of dressed chinook salmon, less than half the landings made in 2000, were landed by commercial trollers. Commercial trollers fished approximately 12,600 days in 2001, down from 17,700 fishing days in 2000 (fig. 10). In 2001, commercial fishing for ocean salmon (all species except coho salmon) in California was allowed coastwide from 1 May to 12 October, with various time and area closures. The minimum size limit was 26 in. total length, 27 in. total length after 30 June to help reduce retention of the generally smaller Sacramento River winter chinook salmon. Ex-vessel prices for dressed salmon averaged $1.95/lb; the total ex-vessel value of the fishery exceeded $4.3 million.

Recreational fishing regulations in California were less restrictive than in 2000, with various time and area closures enacted (the fishery was open 17 Feb.–18 Nov.). Despite fewer fishing restrictions, recreational landings statewide decreased by almost 48% compared with 2000 (fig. 11), and a total of 97,200 chinook salmon were taken during 163,000 angler trips (catch per unit angler = 0.6). Landings were well below the ten-year mean of 164,000 chinook salmon. Anglers were limited to two salmon a day (all species except coho salmon) and a minimum size of 20 in. total length, except prior to June 1, when the minimum size was 24 in. total length. Anglers fishing by any means other than trolling in the area between Point Conception and Horse Mountain were required to use only "circle" hooks.

In 2001, the PFMC enacted commercial and recreational ocean salmon regulations in California to achieve (1) the escapement goal range for Sacramento River fall chinook salmon of 122,000–180,000 hatchery and natural adults combined; (2) a 17% exploitation rate on age-4 Klamath River fall chinook salmon to accommodate in-river recreational and tribal subsistence and commercial fisheries, as well as a minimum adult natural spawning escapement of 35,000; (3) a 31% increase in the adult spawner replacement rate for endangered Sacramento River winter chinook salmon relative to the observed 1989–93 mean rate; and (4) a reduction in harvest impacts on depressed coho salmon (*O. kisutch*) stocks coastwide.

The Klamath ocean harvest model was reworked to incorporate the fishing power of the fleet and more recent data to forecast future catches. In the Klamath Management Zone (Horse Mountain, California, to Humbug Mountain, Oregon) season management, rather than quotas, continued with more fishing days because of increased Klamath River fall chinook salmon. In the Klamath Management Zone, two separate seasons were enacted: (1) 17 May–8 July and 24 July–3 September, both open every day. The bag limit during the first season was two salmon a day and no more than four salmon in seven consecutive days (all species except coho salmon); during the second season, the limit was two salmon a day and no more than six salmon in seven consecutive days; north of Horse Mountain there was a minimum-size limit of 20 in. total length. In the California portion of the Klamath Management Zone, anglers landed 12,700 chinook salmon during 24,300 angler-trips made primarily on private skiffs.

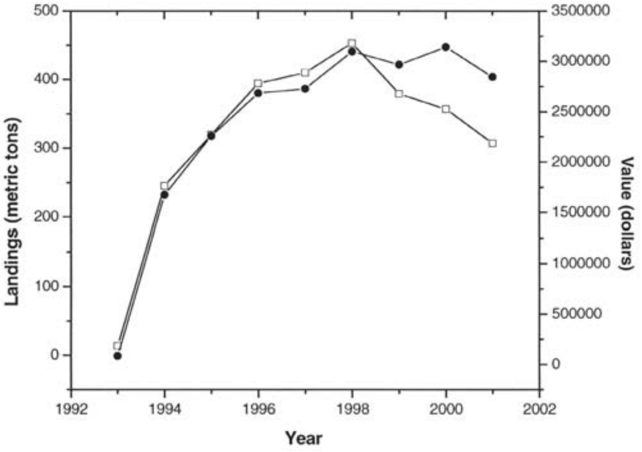

Figure 12. California landings of nearshore live-fish, 1993–2001.

Nearshore Live-fish

Current Fishery. Preliminary landings summaries for the nearshore live-fish fishery in 2001 indicate that statewide landings of nearshore species totaled 447 t. These landings are less than half of the recent peak in 1997 (947 t). This decline may be partly attributed to the continued interim closures and two-month cumulative limits as well as the size restrictions and permit requirements for the fishery. The live component of the landings decreased to 307 t in 2001, down 32% from the peak of 452 t in 1998. Although live-fish landings accounted for 69% of the overall nearshore catch, this proportion represents the second time since 1993 that the amount of nearshore catch landed live has declined (fig. 12).

Although the landing weight of live nearshore finfishes declined slightly from the previous year, live landings in 2001 remained substantially higher than levels in the early 1990s when the fishery began. In 1999-2000, the total value of the nearshore live-fish fishery increased slightly despite a decrease in landings due to increases in the price per pound. In 2001, however, the total value of the nearshore live-fish fishery declined; this trend did not continue and value declined roughly in proportion to landings (fig. 12). Live-fish continued to command higher ex-vessel values than dead fish as overall landings decreased due to environmental factors, depleted stocks, and regulatory changes. Given this scenario, it is likely that a relatively high proportion of nearshore finfishes will be marketed live.

From 1990 through 2000, most nearshore vessels made fewer than 25 landings a year and landed less than 0.45 t (1,000 lb) of nearshore fish each. Presumably, the smaller landings were primarily live-fish. The overall number of hook-and-line vessels landing nearshore species peaked in the early 1990s (1,138 vessels in 1990) and has declined approximately 43% since. The number of permit holders has declined steadily since nearshore fishery permits were instituted in 1999: 1,127 permits were issued for 1999, 1,007 for 2000, and 752 for 2001. In 2001, 439 permittees landed nearshore fish.

2001 was the second consecutive year PFMC authorized two-month closures in selected areas for nearshore rockfishes. The take of nearshore rockfishes was prohibited south of Lopez Point (Monterey County) during January and February and between Lopez Point and Cape Mendocino (Humboldt County) during March and April. There was no closed season north of Cape Mendocino. During months open to fishing, there were two-month cumulative landings limits applied to the fishery; these limits differed according to the type of permit held and the area fished.

CDFG observations have shown that during the rockfish fishery closures fishing effort in some areas shifted toward other species that can be marketed live. For example, in the San Francisco port area fishing effort shifted to surfperch (family Embiotocidae). Although commercial surfperch landings have been common in this area for the past several years, only recently have they been marketed live, coincident with the PFMC's two-month closures of the rockfish fishery. Presumably, fishers and dealers sold the surfperch live (at premium prices) to make up for revenue losses associated with the closures.

History of the Fishery. The nearshore fishery, as defined in the California Code of Regulations (Title 14) concerns a select group of finfish found within 3 mi of shore and in waters less than 20 fathoms deep. These nearshore species occur primarily in association with kelp beds or rocky reefs. This review focuses on the nearshore finfish species most commonly captured and sold live.

Many of the nearshore species targeted by the premium live-fish fishery are territorial, slow-growing, and long-lived, which makes them vulnerable to overfishing even at low exploitation rates. The Nearshore FMP, prepared in accordance with the Marine Life Management Act of 1998, will include 19 species of finfish that CDFG has identified as needing immediate management attention; these are cabezon, California scorpionfish, California sheephead, kelp and rock greenlings, monkeyface prickleback, and the following rockfishes: black, black-and-yellow, blue, brown, calico, China, copper, gopher, grass, kelp, olive, quillback, and treefish. These species represent the most common species captured in the nearshore live-fish fishery. All but three (California sheephead, monkeyface prickleback, and rock greenling) are designated as groundfish species under the PFMC's Pacific Coast Groundfish FMP.

Under the Nearshore Fishery Management Act (NFMA) size limits were implemented in 1999 for commercial fishers for the following nearshore species: black-and-yellow rockfish, cabezon, California sheephead, China rockfish, gopher rockfish, grass rockfish, greenlings, kelp rockfish, and California scorpionfish. Also implemented under the NFMA was a permit requirement for the take, possession, or landing of any of the ten covered species. Comprehensive interim management regulations for the fishery began in 2001. The Nearshore FMP, adopted by the California Fish and Game Commission on 6 September 2002, will move the management of the fishery beyond interim status. The Nearshore FMP integrates five management measures (fishery control rule, regional management, resource allocation, marine protected areas, and restricted access) that together meet the goals and objectives of the Marine Life Management Act and provide for sustainable nearshore stocks and fisheries.

The nearshore live-fish fishery began in the mid-1980s in southern California. Starting in 1993, condition codes (live or dead) were required on market receipts. Prior to 1993 an estimated 0.024 t of nearshore live-fish, worth an estimated $146,000, were landed in 1989. Initially, the fishery supplied live-fish for the Asian community in California; it now supplies markets in other states and other countries. The primary fishing gear is various hook-and-line methods and traps. Hook-and-line gear includes rod and reel, vertical longlines, horizontal longlines, and weighted "stick gear." Most of the hook-and-line and trap vessels are 20–39 ft in length.

Before market demand for live-fish increased, the price paid to fishers (ex-vessel value) for rockfishes, cabezon, California sheephead, and greenlings was low, especially when compared with prices paid for salmon and California halibut. Increasing consumer demand for premium, live-fish and its continued recognition as a specialty product have increased its value dramatically; for example, the average ex-vessel value of cabezon was less than $.50/lb in 1989 but was $4.25/lb in 2001. Target species, fishing methods, and locations fished are determined by the demand for high-quality, fresh live-fish. In 2001, the ex-vessel value for live-fish landings was approximately $2.8 million (fig. 12).

Landing receipts, commonly called market receipts, are the primary data source for quantifying commercial fishing activity and characterizing the fishery. By law, a fish buyer must complete a landing receipt when fish are delivered. The buyer must provide the weight of the fish landed, price paid to the fishers, and the condition of the fish (live or dead). Most often, fish are separated into market categories and recorded by group rather than by species. This means that a particular market category (e.g., "group gopher") likely contains several different species. Also, in the nearshore fishery, fish that have been landed live are not always recorded as live on the landing receipt (this condition information can sometimes be inferred by examining the price paid per pound: a higher price may indicate a live fish). Because of this incongruity, landing weights discussed here should be taken as conservative estimates of the actual live-fish landing weights. Also, the condition (live or dead) of fish being landed was not required on landing receipts prior to 1993; therefore, data used here refer to the period 1993–2001.

Regional differences exist in the nearshore live-fish landings. This is because several of the 19 nearshore species have different geographic ranges. South of Point Conception, California sheephead and California scorpionfish were the primary species landed live. In central California, from Point Conception to Cape Mendocino, the species composition of the live-fish landings was more diverse. Cabezon was by far the most common market category landed live in central California, and the more inclusive market categories "group gopher" and "group bolina" ranked second and third, respectively. These groups include gopher, brown, black-and-yellow, grass, kelp, copper, China, and quillback rockfishes.

Future of the Fishery. The implementation of the Nearshore FMP represents a plan to address the dynamics of this unique fishery. The plan's fishery control rule will establish the total allowable catch based on three sequential stages of fishery information, and limits will be imposed regionally to allow for localized fishery planning, policy, and management. Consequently, there is a clear need to accurately determine fishing patterns and indexes of abundance on both temporal and spatial scales. A fair and equitable distribution of allowable catch will be sought between recreational and commercial fishing sectors. To meet the goals and objectives of the Marine Life Management Act CDFG will seek to establish Marine Protected Areas in the nearshore ecosystem to help sustain marine resources during times of environmental fluctuations. Furthermore, fishing effort may need to be adjusted to match available resources in fished areas.

Pacific Herring

California's Pacific herring (*Clupea pallasi*) fisheries for 2001, though improved since the 1997–98 El Niño, remain below average levels. Statewide landings for the 2000–2001 sac roe season (Dec.–Mar.) totaled 3,049 t, a 1.6% decline from last season's landings of 3,098 t. Annual (Jan.–Dec. 2001) sac roe landings declined from 3,736 t in 1999–2000 to 2,715 t in 2000–2001, a 27.3% decrease (tab. 1). Success of the sac roe fisheries continues to be mixed. The San Francisco gill-net fleet, composed of three platoons (428 permits), landed 2,713 t, 18.7% over the 2,285 t quota. The Tomales Bay fishery landed a total of 270 t of the 363 t quota, a record high for the area. A total of 9.5 t was landed in Crescent City from the 27 t quota, and Humboldt Bay landings totaled 55.5 t, 2% above the 54.4 t quota.

Ex-vessel prices for herring with 10% roe recovery averaged about $700/short t for gill-net landings; an additional $60 was paid for each percentage point above 10%. The ex-vessel price per ton was lower than the previous season, reflecting the continuing volatility of the Japanese economy. Statewide ex-vessel value of the sac roe fishery was an estimated $3.0 million, a 21.1% decline from last season; however, this was well below the average for the previous 16 seasons ($9.1 million).

For the fourth consecutive season, the San Francisco Bay herring eggs-on-kelp fishery landings were well below average. Landings totaled 24.7 t, 44.8% less than the 44.7 t quota, and the second lowest total in the past 16 seasons. Total estimated value of the 2000–2001 eggs-on-kelp harvest was $380,000, based on an estimated average ex-vessel price of $7.00/lb. Price paid varies with product grade; grade 1 received approximately $10.00/lb, and grade 5 $3.00-4.00/lb. Permittees reported that giant kelp (*Macrocystis pyrifera*) lasted longer while suspended because of higher salinities in the bay. Higher salinities were likely caused by the lack of early winter storms.

CDFG conducted hydroacoustic and spawn deposition surveys to estimate herring spawning biomass in San Francisco Bay. Spawn deposition estimates were used exclusively to assess the Tomales Bay and Humboldt Bay populations. The 2000–2001 (Nov.–Mar.) herring spawning biomass estimate for the San Francisco Bay population was 33,838 t, an increase of 36.1% from the previous season. Although oceanic conditions were favorable, and returning herring were in good physical condition, an apparent displacement or loss of older-year-class fish, 5 year olds and older, continued this season. Younger herring, 1-, 2-, 3-, and 4-year-old fish comprised 97% of the spawning biomass for the 2000-2001 season. Of note, 1-year-old herring from the 2000 year class appeared in the spawning population in the highest numbers in 28 seasons.

The Tomales Bay herring spawning biomass continued to demonstrate a tendency to fluctuate widely. The 2000–2001 spawning biomass estimate was 3,807 t, which represents an increase of 98% from the previous season's estimate (1,786 t). This season's biomass is slightly below the 26-year long-term average of 4,653 t. For the first time since the 1991–92 season, CDFG conducted spawning ground surveys to monitor the herring gill-net fishery in Humboldt Bay. Because of the patchy distribution of eelgrass in northern Humboldt Bay, current data on vegetation density, essential to spawn escapement calculations, are not available. However, eelgrass density data were applied from a 1979 study in Humboldt Bay to spawning ground surveys conducted this season. An estimated 349 t of herring spawned in north Humboldt Bay. No surveys were conducted in Crescent City Harbor.

Favorable ocean conditions have continued with the prevailing La Niña, and herring fisheries were expected to improve in the 2001–2002 season; however, the December fishery in San Francisco Bay opened with limited success. High salinities and cold water temperatures in the bay may have influenced spawning activity, although sampled herring were in good physical condition and exhibited normal gonadal development.

Kazunoko kumbo (herring roe on kelp) remains an integral part of traditional Japanese New Year's festivities; however, changes in Japanese culture and economy have affected the market. Industry observers expect demand for kazunoko sac roe to wane as younger Japanese become more Westernized. Ex-vessel prices are expected to decline as continued concern for the Japanese economy has herring buyers proceeding cautiously and offering lower prices than were offered in the 2000–2001 season.

White Seabass

The white seabass (*Atractoscion nobilis*) is the largest member of the Sciaenid family in California waters. This species is targeted by commercial and recreational fisheries, which since 1997 have experienced increases in annual landings of up to 78% and 80%, respectively. The commercial white seabass fishery landed 121 t in 2001 (fig. 13), a 19% increase over the previous year. The recreational fishery landed 38,119 white seabass in 2001 (fig. 14), according to CPFV logbooks and Pacific States Marine Fishery Commission RecFIN data. Using RecFIN data for average weight estimates by fishing mode, recreational landings in 2001 were an estimated 307 t. The estimated combined commercial and recreational catch for 2001 was 428 t.

Although most (62%) of the commercial white seabass catch was landed in southern California ports in 2001, landings in northern California have increased since 1997. Over the past 20 years, the proportion of the com-

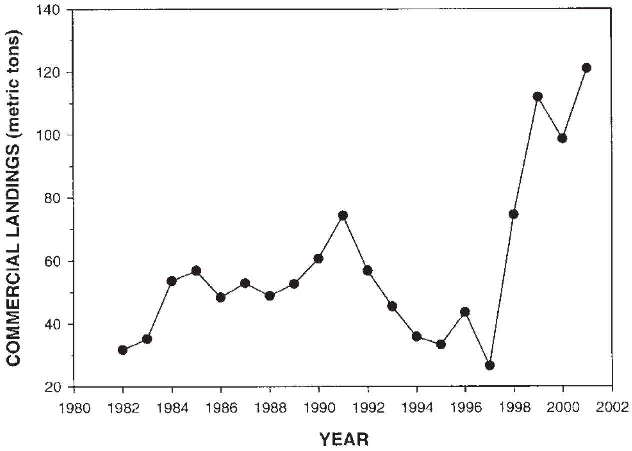

Figure 13. California commercial landings of white seabass, 1982–2001.

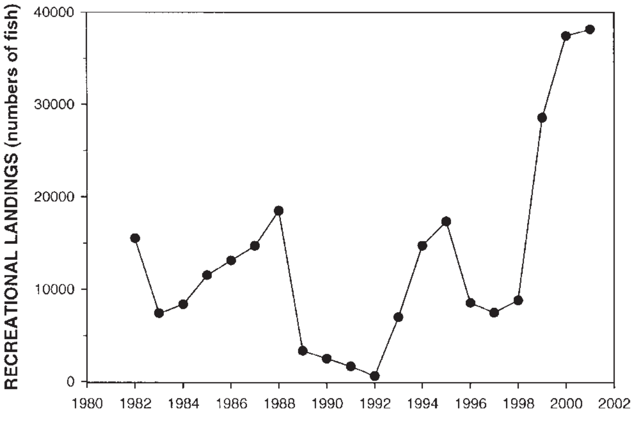

Figure 14. California recreational CPFV and RecFIN landings of white seabass, 1982–2001.
Note: RecFIN data were unavailable during 1990–92; data from those years do not include catch estimates from private/rental boats and shore-fishing modes.

TABLE 4
Commercial Landings of White Seabass by Port Area, 2001

Port area	Landings (metric tons)	% of total
North of Point Conception		
Bodega Bay–San Francisco	2.5	2
Monterey	27.4	23
Morro Bay	15.7	13
Total	45.6	38
South of Point Conception		
Santa Barbara	32.7	27
Los Angeles	39.8	33
San Diego	2.9	2
Total	75.4	62

mercial white seabass catch landed in ports north of Point Conception has ranged from 2% to 19%. During 2001, however, the proportion was 38%, with most fish being landed in Monterey (tab. 4). In 2001, fish dealers paid from $.25 to $7.75/lb for white seabass. The average price per pound was $2.28, for an estimated total exvessel price of $607,935, approximately 30% higher than the previous year's total.

Historically, most of the commercial white seabass catch has been taken with set and drift gill nets. The proportion of drift gill nets used to catch white seabass increased until January 1994, when the use of gill and trammel nets within three nautical miles of the mainland from Point Arguello to the Mexican border was prohibited (FGC §8610.3). Probably in response to this regulation, the proportion of white seabass landed commercially with hook-and-line gear has increased since 1995. In 2001, 55.6% of the commercial catch was taken with set gill nets, and 24.5% was taken with hook-and-line gear.

The commercial fishery for white seabass is closed between Point Conception and the Mexican border from 15 March to 15 June (FGC §8383). Just over half (62 t) of the total commercial catch in 2001 was landed during June and July, and 88% was landed from June through November.

A survey of 2001 CPFV logbooks and Pacific States Marine Fishery Commission RecFIN data indicated that an estimated 29,205 white seabass were taken on private or rental boats, 8,342 were taken on CPFVs, and 572 were taken from shore (e.g., from piers and jetties). Eighty percent of the white seabass taken by CPFV anglers came from waters around southern California's Channel Islands, and the remaining 20% were taken along the mainland from Trinidad, in northern California, to San Diego, or from offshore waters. Most (85%) white seabass caught on CPFVs were taken during May through September, with 60% taken during May and June.

In 1983, the California legislature authorized the creation of the Ocean Resources Enhancement and Hatchery Program (OREHP). Managed by CDFG, the program performs basic and applied research on the artificial propagation, rearing, stocking, and distribution of adversely affected marine fish species important to commercial or recreational fishing in California waters south of Point Arguello. Since 1989, white seabass has been OREHP's primary species for research. Juvenile white seabass are produced at the OREHP hatchery facility in Carlsbad, grown to 50–75 mm, and then placed in a grow-out facility. Currently there are 14 grow-out facilities located in bays and marinas from San Diego to Santa Barbara, including Santa Catalina Island. The fish are raised by volunteers until they reach 200 mm and then released at or near the grow-out site. This program had its best year of production in 2001, when approximately 131,000 hatchery-reared juvenile white seabass were placed in grow-out facilities and 100,318 were ultimately released into the open ocean. Since 1986, 503,000 white seabass, each marked with a coded wire tag, have been released from OREHP hatchery and grow-out facilities.

OREHP gill-net surveys are designed to capture 1- to 4-year-old juvenile white seabass at 19 sites from Santa Barbara to San Diego Bay, including six embayments and Santa Catalina Island, to help evaluate the success of releasing hatchery-raised white seabass. These surveys have been conducted since 1995 and have provided recruitment data on white seabass based on catch per unit effort (CPUE). The data show that the recruitment of white seabass in the areas sampled can be highly variable; however, the overall trend showed an increase in CPUE since 1995. In addition, 111 coded wire tagged white seabass released by OREHP were recovered during fiscal year 2000–2001, the most ever recovered.

In 1996, the California Fish and Game Commission adopted an initial FMP for the state's white seabass fishery. But legislation to fully implement the plan was never

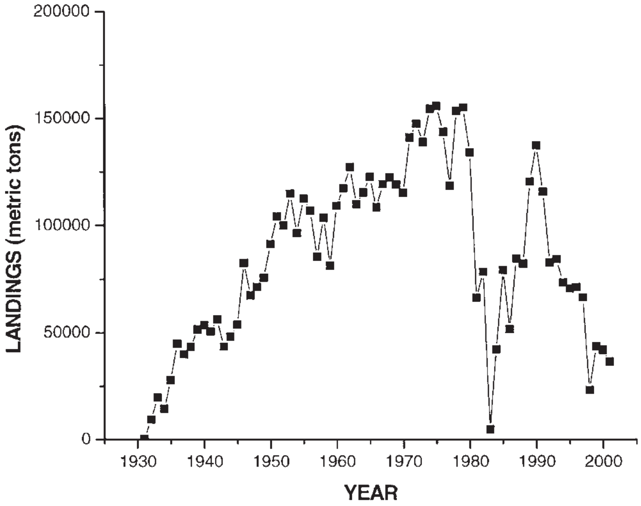

Figure 15. California harvest of giant kelp, 1931–2001.

introduced. In 1998, the legislature enacted the Marine Life Management Act, which granted broader authority to the Commission, and declared that the white seabass FMP would remain in effect until amended and brought into compliance with the Marine Life Management Act. CDFG revised the FMP in accordance with the Marine Life Management Act and submitted it to the commission, which adopted it unanimously on 4 April 2002.

KELP

The commercial harvest of giant kelp (*Macrocystis pyrifera*) in 2001 totaled 36,390 t, a decline of approximately 5% from 2000 (fig. 15). Kelp harvesting for algin was worth an estimated $40 million in products to the major harvester, ISP Alginates. The value of kelp landings was comparable to 2000. One firm, ISP Alginates, harvested 92% of the total for use in its production of alginates, though 16 firms/individuals purchased commercial licenses to harvest kelp in 2001. Favorable oceanographic conditions in 2001 supported high productivity from kelp beds, especially those in southern California; this allowed ISP Alginates to conduct most of its harvesting operations from beds it leases off San Diego County. The second largest use of kelp, after the production of alginates, is to feed cultured abalone. Six abalone aquaculturists actively harvested kelp in 2001, and their combined harvest accounted for approximately 7% of the total statewide landings; most of this kelp is harvested from leased beds in central California using small mechanized harvesters. One aquaculturist, based in northern California, uses a skiff to harvest bull kelp (*Nereocystis luetkeana*). The remaining 1% of kelp landings were harvested by the herring-roe-on-kelp fishery, Pacific Gas and Electric Co., edible seaweed distributors, basket makers, and various research organizations. Edible seaweed harvesting reported by two harvesters in northern California decreased in 2001 from 9.7 t in 2000 to 5.5 t in 2001. Kelp is also harvested for recreational use; however, with a current bag limit of 4.5 kg/day and a low amount of effort, the total amount taken by this group is probably negligible when compared with the commercial fishery. Recreational harvesters generally collect drift kelp that has been cast ashore.

Oceanographic conditions were favorable for kelp growth during 2000 and 2001; relatively cool summer sea surface temperatures were followed by mild, dry winters with relatively few large swell events. These conditions provided for strong recruitment and a general increase in canopy area for many beds, particularly those in southern California; however, the total amount of area occupied by kelp canopy is still far below levels documented in the early twentieth century. This long-term decline can be attributed both to natural disturbances, such as warm-water stress and intense storms associated with El Niño, and to human-induced disturbances, such as increased turbidity and siltation associated with coastal development, pollution, and commercial and recreational fishing activities. Fishing activities remove animals such as California sheephead and California spiny lobster, which help sustain kelp forests through trophic interactions.

In 2002 CDFG will conduct a statewide aerial survey using multispectral imagery to document the abundance and distribution of kelp during the late summer when most beds have reached their maximum canopy potential. Survey images will be entered into a GIS database, which will be used to map and monitor the health of this economically and ecologically important resource. CDFG intends to conduct at least one statewide kelp survey a year in the future.

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THE STATE OF THE CALIFORNIA CURRENT, 2001–2002: WILL THE CALIFORNIA CURRENT SYSTEM KEEP ITS COOL, OR IS EL NIÑO LOOMING?

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ABSTRACT

This report summarizes physical and biological conditions in the California Current System (CCS), from Oregon to Baja California, in 2001 and 2002. The principal sources of the observations described here are the CalCOFI (California Cooperative Oceanic Fisheries Investigations), IMECOCAL (Investigaciones Mexicanas de la Corriente de California), and U.S. GLOBEC-LTOP (Global Ecosystems Long-term Observation Program) programs. Large-scale atmospheric and oceanic conditions in the Pacific point to a fourth consecutive La Niña-like year. This has contributed to generally stronger than normal upwelling and uncharacteristically cool waters in much of the CCS, a pattern that has persisted since late 1998. Biological productivity has been generally higher as well, particularly off Oregon. Within the observed interannual fluctuations of recent years, these conditions suggest a generally elevated production off California and Oregon, but cool conditions have led to lower than normal zooplankton biomass off Baja California. Although the tropical Pacific has exhibited some indications of a developing El Niño, it is not likely to impact the CCS during the productive upwelling season of 2002. These observations are continuing evidence that a regime shift may have occurred in 1998, resulting in substantial change in ecosystem structure in the CCS. Continued monitoring and analysis of the state of the CCS in this context is needed. We outline a plan for an integrated monitoring program for the entire region, through the creation of ACCEO (Alliance for California Current Ecosystem Observation).

INTRODUCTION

In 1994 a small group of scientists began an annual *CalCOFI Reports* tradition, preparing the first summary of recent physical and biological conditions in the California Current System (CCS) (Hayward et al. 1994). This concept has continued and has been expanded to include information from ongoing surveys off Baja California, Mexico, central California, and Oregon, and assessments of the large-scale conditions that affect the CCS region (Hayward et al. 1995, 1996, 1999; Lynn et al. 1998; Schwing et al. 1997; Bograd et al. 2000; Durazo et al. 2001).

Over this time period, these "State of the California Current" reports have documented the evolution of one of the strongest El Niño events on record in 1997–98 and the subsequent development of an extended period of unseasonably cool conditions in the CCS initiated by a strong La Niña in 1997. The recurrence of a cool, La Niña-type state over the past 4 years (1998–2002) at the time of this writing, along with major changes in a number of CCS populations, has led some scientists to suggest that the CCS and the north Pacific have undergone a fundamental climate shift, on the scale and significance of those documented in the early 1920s, mid-1940s, and mid-1970s (cf. Mantua et al. 1997; Hare and Mantua 2000). Others argue that this recent period has been a sequence of isolated La Niña events. To complicate matters further, the signals of a developing El Niño in the tropical Pacific are now being detected. The degree to which these interannual and longer-term climate phenomena evolve, interact, and compete for control of the CCS in the coming months will reveal a great deal about how climate variability influences the physics and biology of the CCS.

In this report, we summarize conditions in the CCS from about 24° to 45°N between January 2001 and April 2002, based on ship surveys and related at-sea sampling, monitoring from coastal buoys, and large-scale analyzed fields of atmospheric and oceanic variables. We focus on evidence for a possible climate regime shift in 1998 and speculate on early indicators of a developing El Niño in the tropical Pacific. This is not meant to be a complete description of all scientific activities in the CCS during the past 12 to 18 months but to characterize recent conditions based on representative physical and biological data and to highlight selected research programs in the region. This report demonstrates the value of continued monitoring of marine ecosystems such as the CCS and of integrating physical and biological factors from complementary regional field programs.

DATA SETS AND METHODS

Large-scale anomalies for the Pacific Ocean region are summarized from NCEP (National Center for Environmental Prediction) reanalysis fields (Kalnay et al. 1996) from the NOAA-CIRES Climate Diagnostics Center, <http://www.cdc.noaa.gov/>. The reanalysis fields are monthly gridded (roughly 2° × 2°) anomalies of sea surface temperature (SST) and surface wind. The base period is 1968–96. Ocean temperature anomalies at 100 m depth were computed from the Global Temperature-Salinity Profile Program (GTSPP) database, monthly averaged on a 1° spatial grid. Anomalies were computed by subtracting the 1° monthly climatologies (base period 1945–96) of the World Ocean Database 1998 (Levitus et al. 1998) from the gridded observations. The anomalies were then averaged into 5° × 5° spatial boxes.

Monthly upwelling indices and their anomalies, relative to 1948–67, for the North American west coast (21°–51°N) are presented. Time series of the daily alongshore wind component and SST from six representative buoys throughout the California Current region (data courtesy NOAA National Data Buoy Center) are plotted against the harmonic mean of each record; the location and base period of each buoy are given in Table 1.

Ocean conditions in the CCS off southern California are described from quarterly CalCOFI surveys in 2001 and early 2002. The CalCOFI monitoring program began in 1949; a brief history of the program is given in Hewitt (1988). The present program consists of quarterly (normally Jan., Apr., July, and Oct.) cruises that occupy a grid of 66 stations off Southern California (fig. 1). The core time-series data set now collected at each station includes a conductivity-temperature-depth (CTD)/Rosette cast to 500 m depth, with sensors for pressure, temperature, salinity, dissolved oxygen, photosynthetically active radiation, fluorescence, and transmissivity. Water samples are collected at 20–24 depths to determine salinity, dissolved oxygen, nutrients (NO_3, NO_2, PO_4, SiO_3), phytoplankton pigments (chlorophyll *a* and phaeopigments), and primary production (^{14}C uptake at one station per day). Oblique and surface (neuston) net tows (0.505 mm mesh) are taken at each station. Continuous

TABLE 1
Locations of Sea Surface Temperature and Alongshore Wind Time Series

Buoy	Name	Position	Base period[a]	Alongshore angle (°N)[b]
46050	Stonewall Bank, Ore.	44.6N 124.5W	(1991–99)	359
46027	St. George, Calif.	41.8N 124.4W	(1983–99)	341
46022	Eel River, Calif.	40.8N 124.5W	(1982–99)	354
46042	Monterey Bay, Calif.	36.7N 122.4W	(1987–99)	328
46011	Santa Maria, Calif.	34.9N 120.9W	(1980–99)	325
46025	Catalina Ridge, Calif.	33.7N 119.1W	(1982–99)	295

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

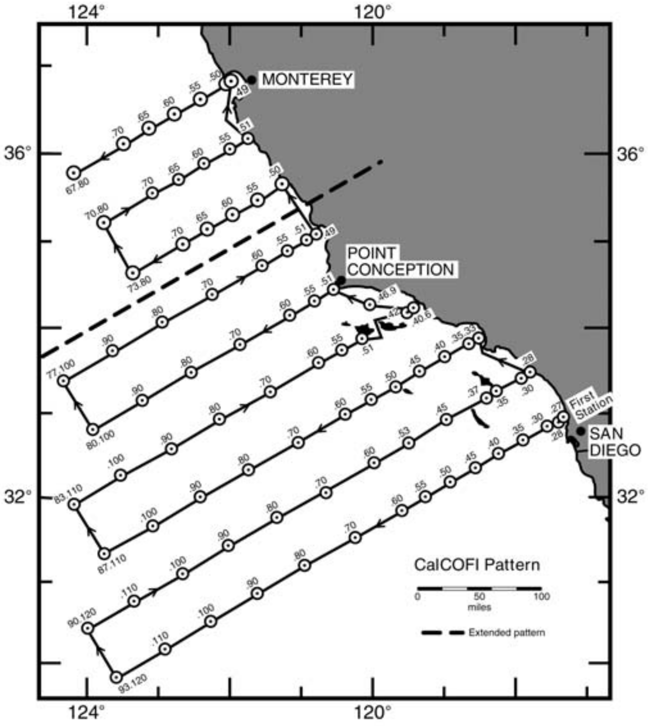

Figure 1. The standard CalCOFI sampling grid. The regular 66-station pattern occupied by CalCOFI since 1985 (lines 77, 80, 83, 87, 90, and 93) is shown by a solid line. The dashed line demarks the area of additional sampling north of the regular pattern (lines 67, 70, and 73).

near-surface measurements of temperature, salinity, and chlorophyll fluorescence are made from water pumped through the ship. Acoustic Doppler current profiler data are also recorded continuously, providing a measure of upper ocean currents as well as an estimate of zooplankton biomass based upon acoustic backscatter. During the winter and spring cruises, the continuous underway fish egg sampler (CUFES; Checkley et al. 1997) is used. More details on the methods, information about recent activities, and CalCOFI hydrographic data can be accessed online at <http://www.calcofi.org>. In addition, CalCOFI line 67, off Monterey, California, has been surveyed periodically by the Monterey Bay Aquarium Research Institute and Naval Postgraduate School.

Systematic surveys of the distribution and abundance of marine birds have been taken on CalCOFI cruises since 1987. Vessel-based observations have revealed that the overall abundance and composition of seabird communities fluctuate in response to interannual and longer-term variability in the physical and biological properties of the CCS (Veit et al. 1996; Hyrenbach and Veit, in press). Colony-based observations by the Point Reyes Bird Observatory Marine Science Program have monitored the reproductive performance of seabird populations breeding at the Farallon Islands (central California) since the early 1970s. These locally breeding populations are sensitive to fluctuations in ocean productivity and prey availability over interannual and decadal scales (Ainley et al. 1995; Sydeman et al. 2001). Our objective is to compare marine bird demography and community structure during 2000–2001 to the 1997–98 El Niño and the subsequent La Niña event, and to quantify the response of marine bird populations to the hypothesized 1998 regime shift.

The IMECOCAL program continued sampling the southern portion of the CCS, off Baja California, on a reduced CalCOFI grid of 93 stations (fig. 2). The data presented here were collected from April 2001 to January 2002. All the quarterly IMECOCAL cruises reported here were done aboard the CICESE (Centro de Investigación Científica y de Educación Superior de Ensenada) RV *Francisco de Ulloa*. Sampling includes CTD casts to 1,000 m, bottom depth permitting, as well as water samples from the upper 200 m to determine dissolved oxygen, nutrients, chlorophyll *a*, and primary production (one ^{14}C in situ incubation per day). Standard (0.505 mm mesh) oblique bongo tows are conducted, with one cod end dedicated to ichthyoplankton and the other to macrozooplankton. Continuous underway measurements of temperature, salinity, and fluorescence are also made. The Acoustic Doppler Current Profiler (ADCP) was used for continuous underway current profiling. Starting in January 2000, a CUFES system has been incorporated into the sampling. For more information about data collection, analysis, databases, and cruises schedules, refer to the IMECOCAL Web page, <http://imecocal.cicese.mx>.

TABLE 2
Dates of GLOBEC LTOP Cruises in the Northern California Current, 2001–2002

Cruise name	Dates	Sections (latitude)
W0101B	27–28 Jan. 2001	NH (44.65°N)
W0103A	15–18 Mar. 2001	FM(43.2), RR (42.5)
W0103B	20–24 Mar. 2001	NH (44.65°N), FM(43.2), RR (42.5), CR (41.9)
W0107A	6–8 July 2001	NH (44.65°N)
W0109A	4–10 Sept. 2001	NH (44.65°N), HH (44.0), FM(43.2), RR (42.5), CR (41.9)
W0111B	27–29 Dec. 2001	Inshore portion of NH (44.65ºN)
W0202A	19–21 Feb. 2002	NH (44.65°N)
W0204A	4–10 Apr. 2002	NH (44.65°N), HH (44.0), FM(43.2), RR (42.5), CR (41.9)

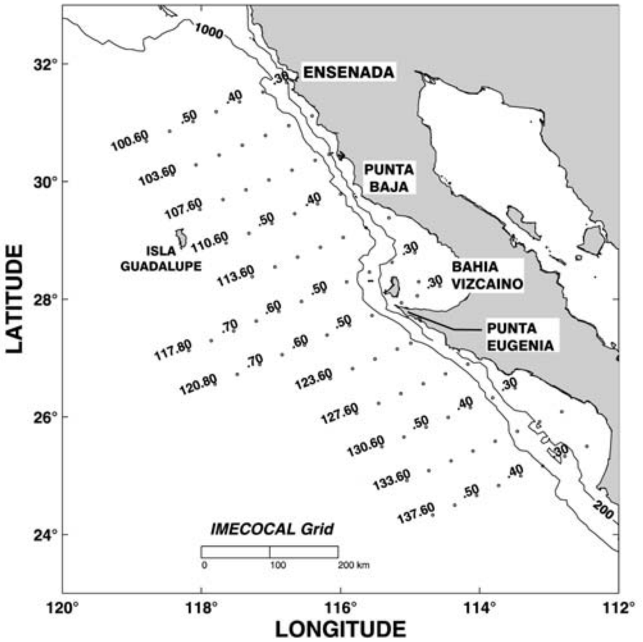

Figure 2. The standard IMECOCAL sampling grid. Solid dots represent the regular 93-station pattern (lines 100 to 137). Depth contours are in meters.

The U.S. GLOBEC Northeast Pacific Program began a series of seasonal cruises in the northern California Current in July 1997, as part of its long-term observation program (LTOP). Observations are made five times a year along the Newport Hydrographic (NH) Line at 44.65°N, and three times a year along a set of 4 or 5 zonal sections between 42°N and 45°N (Smith et al. 2001; Huyer et al. 2002). The NH line was occupied regularly from 1961 to 1971; Smith et al. (2001) have calculated long-term averages using data from this earlier decade for winter (1 Jan.–29 Feb.), summer (22 June–31 Aug.), and fall (1 Nov.–21 Dec.), and for each month in spring, late summer, and early fall. Dates for the 2001–2002 GLOBEC LTOP cruises are shown in Table 2.

Hydrography, nutrients, chlorophyll, and zooplankton are measured along the inner portions of the NH Line biweekly in 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 mi from shore, with water depths ranging from 20 m to 95 m. Zooplankton is 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 their carbon weight and then summing over all species. Copepod biomass data are presented here.

LARGE-SCALE OCEANIC AND ATMOSPHERIC CONDITIONS

Basin-scale anomalies in the Pacific during the past year reflect a continuation of the patterns that developed during the 1998–99 La Niña (Hayward et al. 1999; Bograd et al. 2000; Schwing and Moore 2000; Schwing et al. 2000; Durazo et al. 2001; Schwing et al. 2002b). Large-scale winds over the northeast Pacific displayed a generally anomalous clockwise flow, consistent with a stronger than normal North Pacific High and, at times, an unusually weak Aleutian Low (fig. 3a). For the CCS, this pattern means greater equatorward winds. During spring and summer, this translated into unseasonably strong coastal upwelling north of Point Conception. Much of Baja California experienced anomalously weak upwelling (poleward anomaly) winds.

The SST anomaly pattern seen since late 1998 also has persisted into 2002. The dominant feature in the north Pacific continues to be a horseshoe-shaped region of cooler than normal upper ocean water that covers much of the CCS and extends north into the Gulf of Alaska and to the southwest past Hawaii. This is a characteristic anomaly pattern associated with La Niña on interannual time scales (Schwing et al. 2002a,b) and the negative phase of the Pacific Decadal Oscillation (PDO) on longer scales (Mantua et al. 1997). The spring and summer 2001 SSTs (fig. 3a) in the northern CCS were unusually cool, where anomalous upwelling winds were observed. Weaker than normal winds corresponded with slightly above normal SSTs off southern California and Baja California.

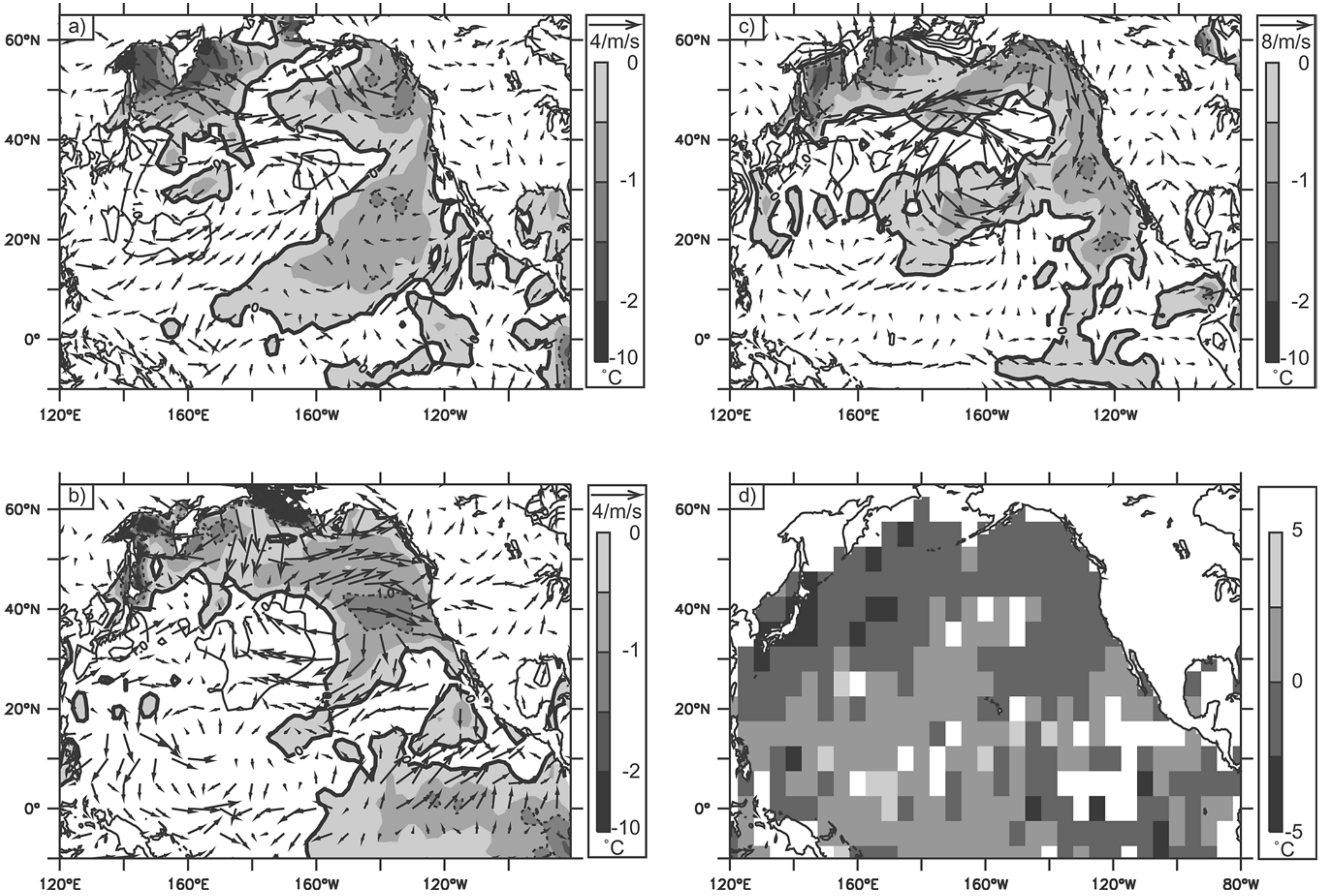

Figure 3. Anomalies of surface wind velocity and sea surface temperature (SST) in the north Pacific Ocean, for (*a*) May–July 2001, (*b*) Dec. 2001–Jan. 2002, and (*c*) Apr. 2002. Arrows denote magnitude and direction of wind anomaly. Contours denote SST anomaly. Contour interval is 1.0°C. Negative (cool) SST anomalies are shaded. Wind climatology period is 1968–96. SST climatology period is 1950–79. Monthly data obtained from the NOAA-CIRES Climate Diagnostics Center. (*d*) Anomalies of ocean temperature at 100 m depth for Feb.–Apr. 2002, based on the Global Temperature-Salinity Profile Program database, for a base period 1945–96. Shading interval is 2.5°C; lighter shades denote positive (warm) anomalies. White areas denote no data for the period shown.

The summer wind and SST anomaly patterns continued into winter 2001–2002 (fig. 3b), although shifted more toward the northeast, and the maximum anomalies were centered off the West Coast to about 140°W. These anomalies show clear indication of being maintained into the 2002 upwelling season, based on the latest available data (Apr. 2002, fig. 3c). Stronger than normal upwelling-favorable winds along the West Coast were again part of clockwise wind anomalies, due to a premature decay of the Aleutian Low combined with a high-pressure center compressed near the West Coast.

Temperature anomalies at 100 m depth over the Pacific basin show these conditions are not limited to the surface. The upper ocean has featured a thermal anomaly pattern similar to that of SST (fig. 3d), indicating that the processes responsible for ongoing surface anomalies have affected temperatures in the thermocline of much of the north Pacific as well. Sea level height anomalies support this idea (Durazo et al. 2001). In summary, the upper 100–200 m of the CCS continues to be unusually cool, a pattern that began in late 1997. These temperature anomalies are associated with persistent stronger than normal equatorward winds throughout much of the CCS, suggesting that coastal upwelling and Ekman processes are a strong contributor to these ocean anomalies.

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). As indicated by negative MEI values, the winter of 2001–2002 marked the fourth consecutive year of weak to moderate La Niña conditions (fig. 4). The April 2002 MEI value shows a big increase toward El Niño conditions. This is the first time since June 1998 (45 months) that the MEI has attained weak El Niño status. Negative MEI values historically have persisted for periods of 20–35 months (e.g., 1995–97 La Niña), suggesting that multiyear La Niña events are common (Schwing et al. 2002a). However, this is the second longest non–El Niño stretch since before 1950, surpassed only by the April 1959–July 1963 period.

The Northern Oscillation Index (NOI) is another ENSO index, one that highlights the intensity of interannual climate events in the northeast Pacific (Schwing et al. 2002a). Positive NOI values, which indicate La Niña–like conditions, have prevailed since mid-1998 (fig. 4), further supporting the idea that the period following the 1997–98 El Niño has been unusually cool in the CCS region. A third commonly used climate index, the Pacific Decadal Oscillation or PDO (Mantua et al. 1997) identifies multi-decadal periods of variability in the Pacific; positive PDO values are associated with warmer than normal SST in the CCS. Summer-means of the PDO have been negative for the past 4 years; a negative PDO of more than 1-year duration has not been observed since the early 1970s.[1] The recent negative tendency of the PDO is consistent with the MEI and NOI in characterizing the northeast Pacific as being unusually cool since 1998. It also suggests that the transition from the 1997–98 El Niño could signal the shift to a new climate regime analogous to those seen in the early 1920s, mid-1940s, and mid-1970s (cf. Mantua et al. 1997; Hare and Mantua 2000).

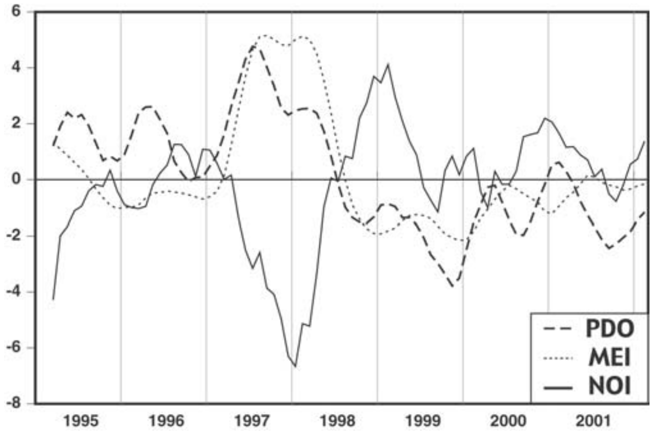

Figure 4. Monthly time series of the Pacific Decadal Oscillation (PDO), Multivariate ENSO Index (MEI), and Northern Oscillation Index (NOI), Jan. 1995–Apr. 2002. Series have been smoothed with a 5-month running mean.

Interannual differences in the CCS are connected to tropical Pacific Ocean anomalies, via atmospheric and oceanic teleconnections (Schwing et al. 2002b). Temperature anomalies at 100 m depth along the equator reflect the evolution of recent El Niño and La Niña events (fig. 5). Warm/cool anomalies at this depth are generally due to a deepening/shoaling of the thermocline. The west to east shift of positive (warm) anomalies in 1997 is part of the 1997–98 El Niño. The 1998–99 La Niña that followed can be identified by the eastward movement of negative (cool) anomalies. Subsequent years have seen this same shoaling thermocline pattern, which has intensified each summer during the seasonal westward expansion of cool water along the equator (Philander 1990).

During the past two winters, positive upper ocean temperature anomalies have developed east of the dateline along the equator (fig. 5). This has been interpreted by some as a sign of an impending El Niño. In early 2002, ocean temperature anomalies have moved east along the equator (NCEP 2002), deepening the thermocline and warming temperatures at 100 m (fig. 5). Coastal SSTs off Ecuador and Peru became unseasonably warm. March 2002 SSTs remained as much as 2–3°C above normal. The subsurface temperature at 60 m off

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[1] Peterson, W. T., and F. B. Schwing. Recent changes in climate and carrying capacity in the California Current: a positive sign for recovery of salmon. (manuscript)

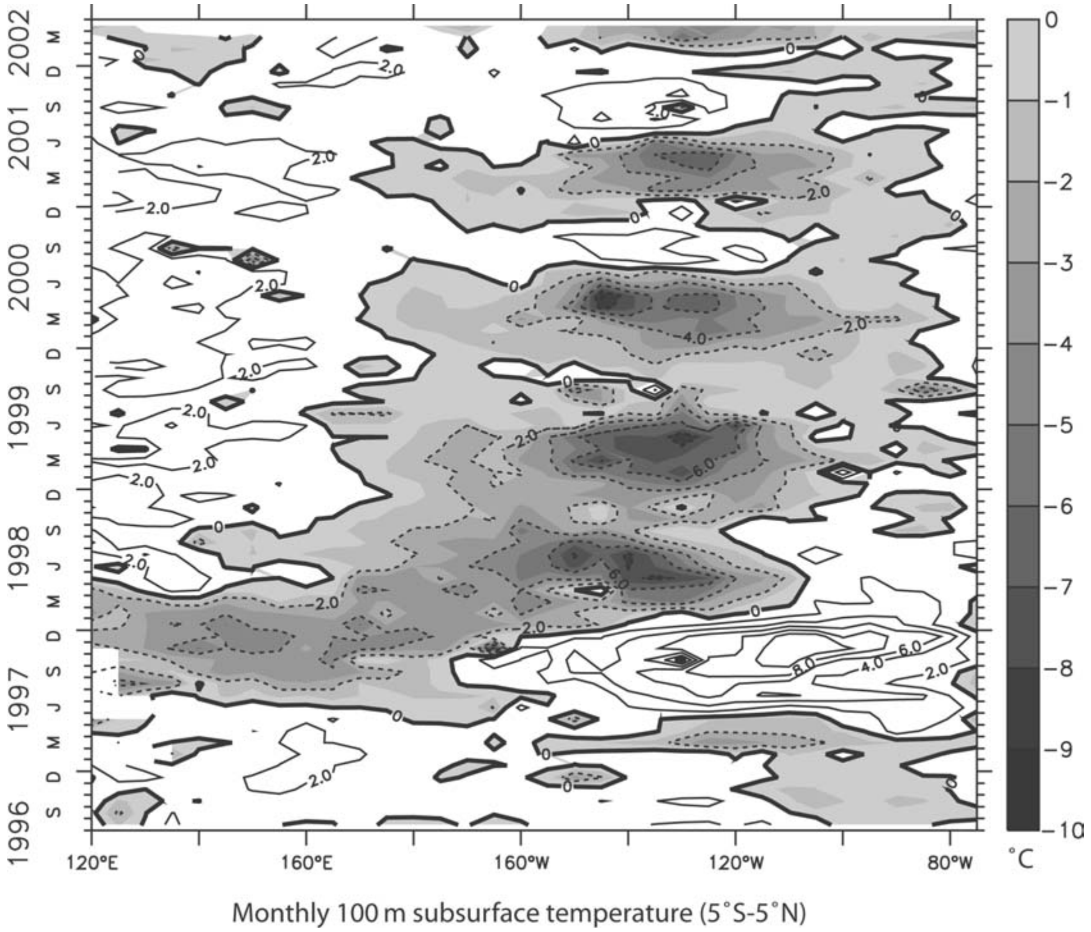

Figure 5. Monthly anomalies of equatorial temperature at 100 m, Aug. 1996–Apr. 2002. Anomalies are shown for 5°N–5°S region along equator (120°E–75°W), based on the Global Temperature-Salinity Profile Program database, for a base period 1945–96. Contour interval is 2°C. Shading denotes negative anomalies.

Paita, Peru (5°S), jumped from 15°C to 21°C in March (F. Chavez, pers. comm., see <http://www.mbari.org/bog/Projects/Peru/peru02_03.htm>). This warming has reportedly affected Peruvian marine fisheries, where warm-water species have replaced the cold-water anchovy. However, South American SSTs and sea levels have returned to more normal values in April 2002 (F. Chavez, pers. comm.; D. Enfield, pers. comm.; see also <www.aoml/noaa.gov/phod/epac>), suggesting that these earlier warm temperatures may have been a short-lived event rather than the onset of a new El Niño.

The thermocline deepening and warming of upper ocean waters in the eastern equatorial Pacific in early 2002 was due to an oceanic Kelvin wave that propagated eastward from the central equatorial Pacific starting in mid-December (NCEP 2002). This Kelvin wave was triggered by a westerly wind burst associated with intraseasonal (30–60 day) variability known as the Madden-Julian Oscillation (MJO). Whereas MJO activity was evident globally throughout the tropics during winter 2001–2002, and more generally since late 1998, the MJO was not active during March 2002. However, late spring is a critical time, when MJO-related westerly wind bursts or other short-lived westerly wind activity can generate Kelvin waves, and ultimately initiate El Niño. If MJO activity increases, a more rapid evolution toward mature El Niño conditions might occur through the spring and summer of 2002. Without such activity, the prospects of El Niño are greatly diminished.

Several dynamical and statistical models indicate a gradual evolution toward weak or moderate El Niño conditions during the next several months, although some analyses indicate that conditions will remain near neutral or even return to a weak La Niña state for the remainder of 2002. One scenario is for further development toward a weak to moderate mature El Niño, continuing into early 2003. However, one-third of El Niño–like events die off within a few months (K. Wolter, pers. comm.). This possibility is enhanced by the fact that we are currently in the negative (cool CCS and northeast Pacific) phase of the PDO (Mantua et al. 1997), a pattern that is thought to reduce/enhance the formation of strong El Niño/La Niña events. The continuing development of El Niño can be monitored online at <http://www.cpc.noaa.gov/products/analysis_monitoring/enso_advisory/> or <http://www.pmel.noaa.gov/tao/jsdisplay>.

COASTAL CONDITIONS

Monthly coastal upwelling indexes (Bakun 1973; Schwing et al. 1996) have indicated generally stronger than normal upwelling in the CCS since the onset of La Niña in late 1998 (Hayward et al. 1999; Bograd et al. 2000; Durazo et al. 2001). Following record upwelling during 1999 (Schwing and Moore 2000; Schwing et al. 2000), upwelling was again extremely strong during the 2000 and 2001 upwelling seasons from about San Diego to the Columbia River, and off southern Baja California (fig. 6). The mean summer (May–Aug.) upwelling index at 36°N since 1999, for example, has been 275 $m^3/s/100$ m (33% above average), compared to 201 $m^3/s/100$ m for 1991–98. Other than the record 1999 upwelling, 2001 featured the highest mean summer upwelling index since 1981. The period following the 1997–98 El Niño has been the highest 4-year mean on record, extending back to 1946. Weaker than normal upwelling prevailed off northern Baja California in the 2001 upwelling season. April 2002 indexes indicate that the latest upwelling season is off to another strong start.

National Data Buoy Center (NDBC) coastal buoy winds in the CCS display the short-term variability associated with synoptic (1–2 week) atmospheric events, superimposed on the annual climatological cycle of strong southward winds in summer and northward or weak southward winds in winter. Wind vectors align strongly with the local coastline (tab. 1), so we show time series of the alongshore component of wind (fig. 7), the component directly linked with coastal upwelling. Coastal winds during 2001 displayed the typical pattern of stronger magnitudes and higher synoptic to annual variability off northern California, and weaker and less variable winds within the Southern California Bight. The general impression from these series is that the spring transition occurred in early March. Visually, alongshore wind events during 2001 appear to be biased toward stronger than normal upwelling. This is supported by the monthly upwelling index anomalies (fig. 6).

The multiyear trend of below-normal temperatures in the CCS since 1998, described in previous reports, has continued through 2001 (fig. 8). On a seasonal scale, coastal SSTs during 2001 were unusually cool, with extended periods of near- or above-normal values in May, July, and September. Coastal SSTs cool/warm on synoptic scales in response to local upwelling/downwelling winds (fig. 7). Winter SSTs in early and late 2001 remained very steady despite strongly fluctuating winds. Strong downwelling episodes occurred in February, November, and December 2001 over most of the CCS. However, these did not have an obvious effect on buoy SSTs (fig. 8). Synoptic variations in SST are more evident in the upwelling season. Extended wind relaxation events (periods of weak upwelling-favorable wind) in May, July, and September 2001 did produce warmer SSTs. These are particularly evident south of Monterey Bay.

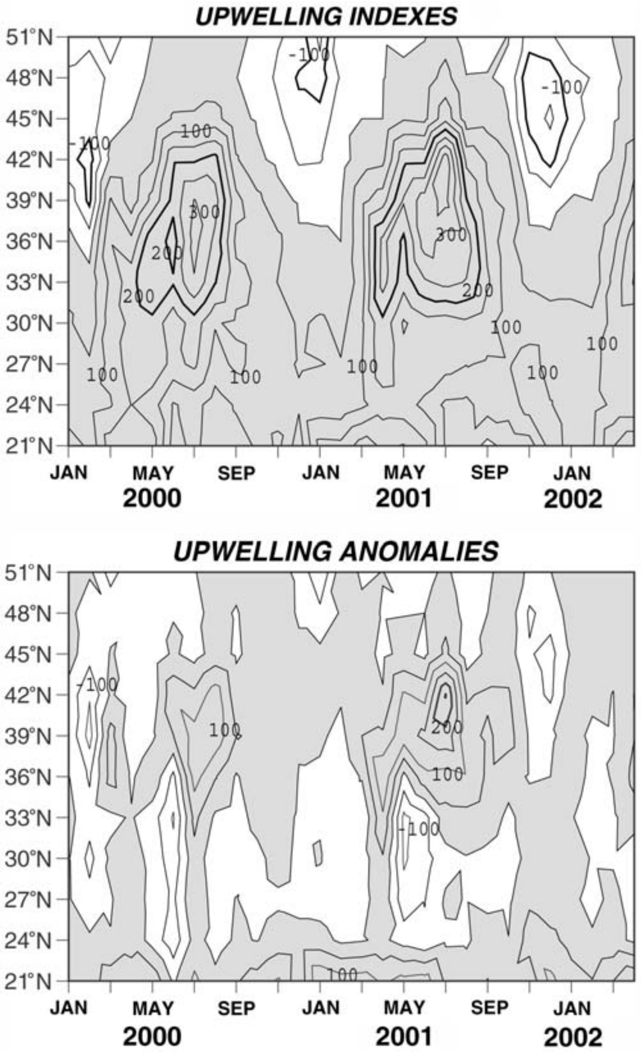

Figure 6. Monthly upwelling index and upwelling index anomaly for Jan. 2000–Apr. 2002. Shaded areas denote positive (upwelling-favorable) values in upper panel, and positive anomalies (generally greater than normal upwelling) in lower panel. Anomalies are relative to 1948–67 monthly means. Units are in m^3/s per 100 km of coastline.

CALCOFI SURVEY CRUISES

0101 (7–26 Jan. 2001)

Although this cruise was reviewed in last year's report (Durazo et al., 2001), it is included here to show the strong change in coastal circulation that took place between the winter and spring 2001 cruises. The position of the main California Current jet is revealed by the

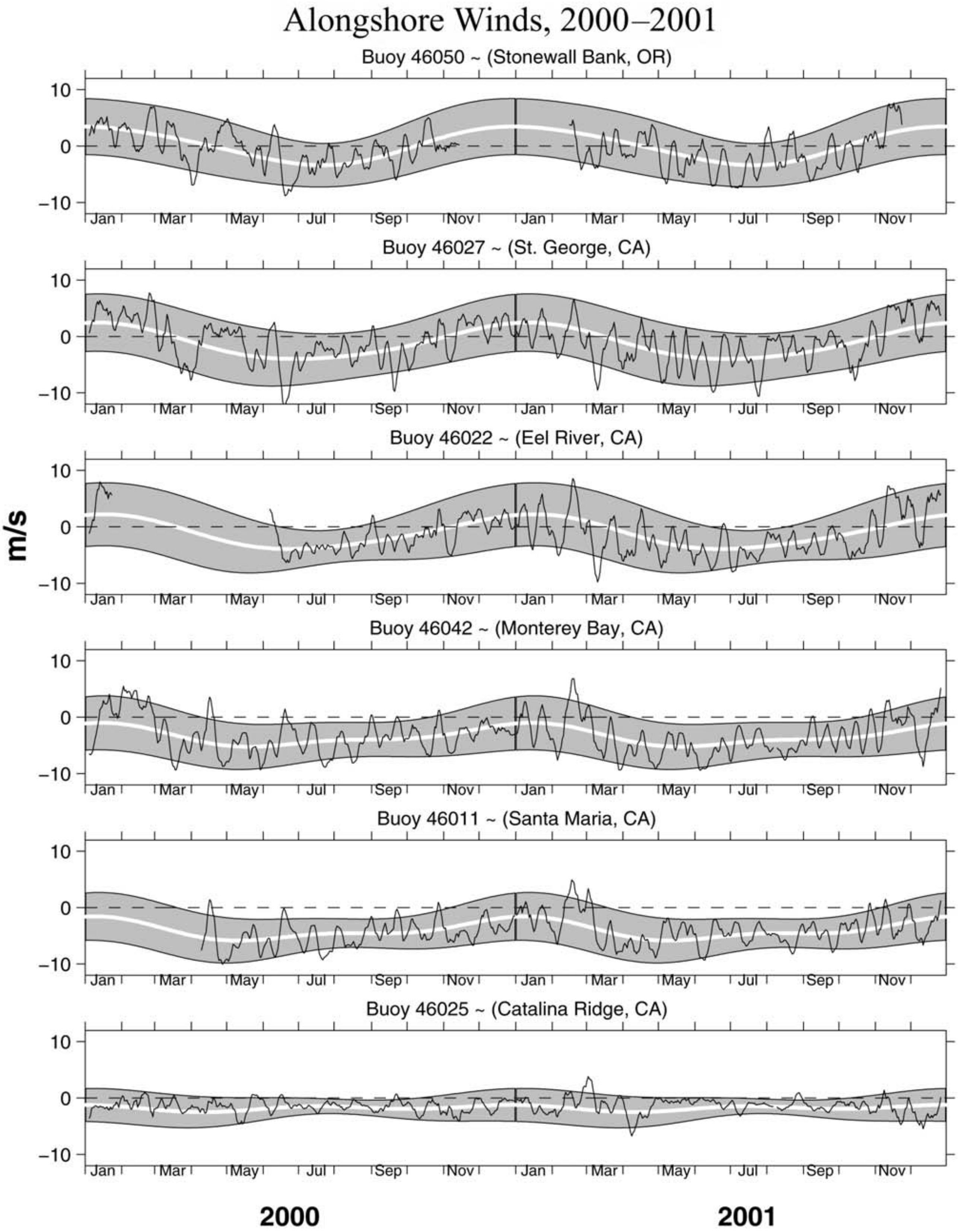

Figure 7. Time series of daily-averaged alongshore winds for Jan. 2000–Dec. 2001 at selected NOAA National Data Buoy Center (NDBC) coastal buoys. Bold white lines are the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. Series have been smoothed with a 7-day running mean. The periods used for calculating the climatology at each site and the alongshore angle are shown in table 1. Data provided by NDBC.

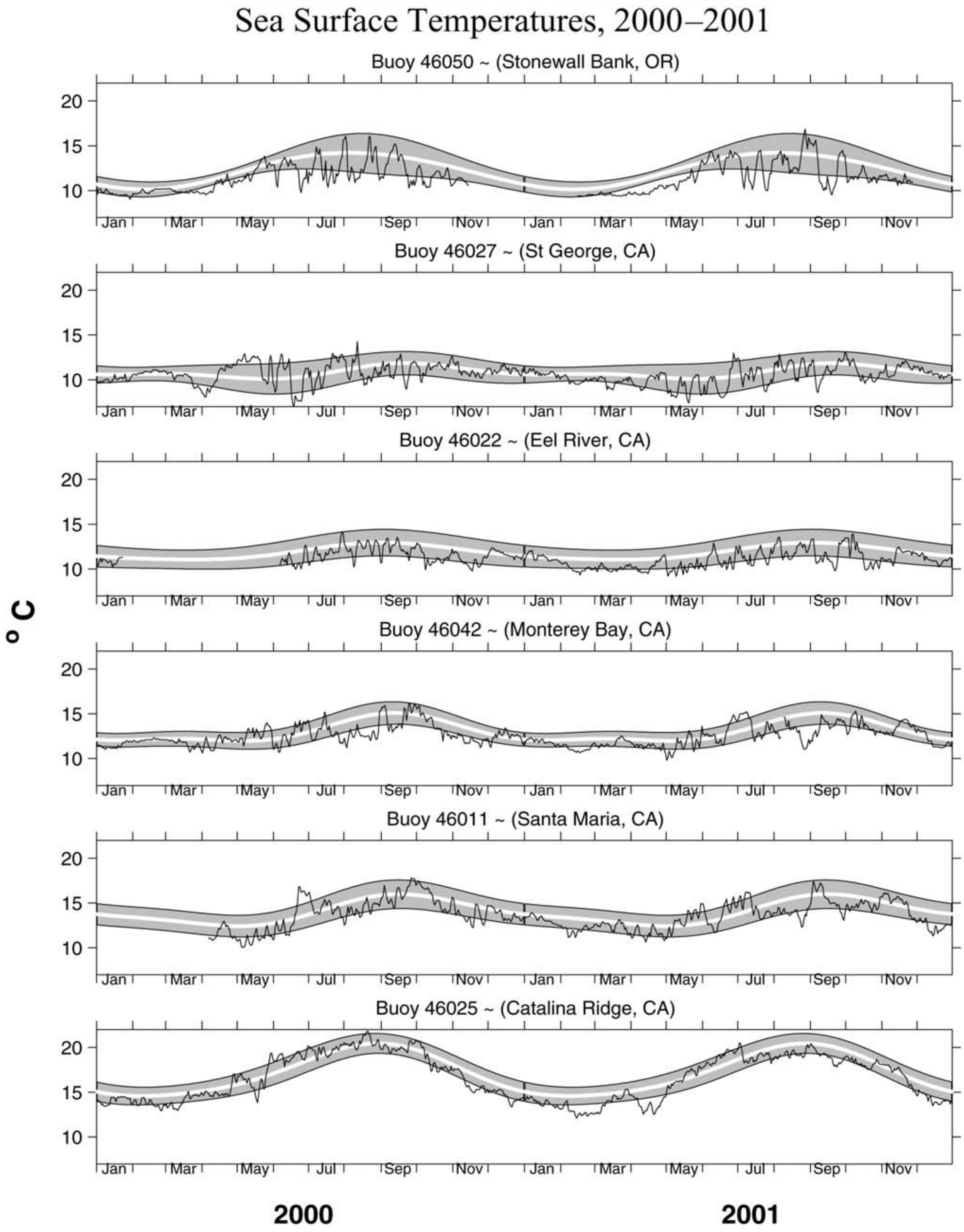

Figure 8. Time series of daily-averaged SST for Jan. 2000–Dec. 2001 at selected NDBC coastal buoys. Bold white lines are the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. The periods used for calculating the climatology at each site are shown in table 1. Data provided by NDBC.

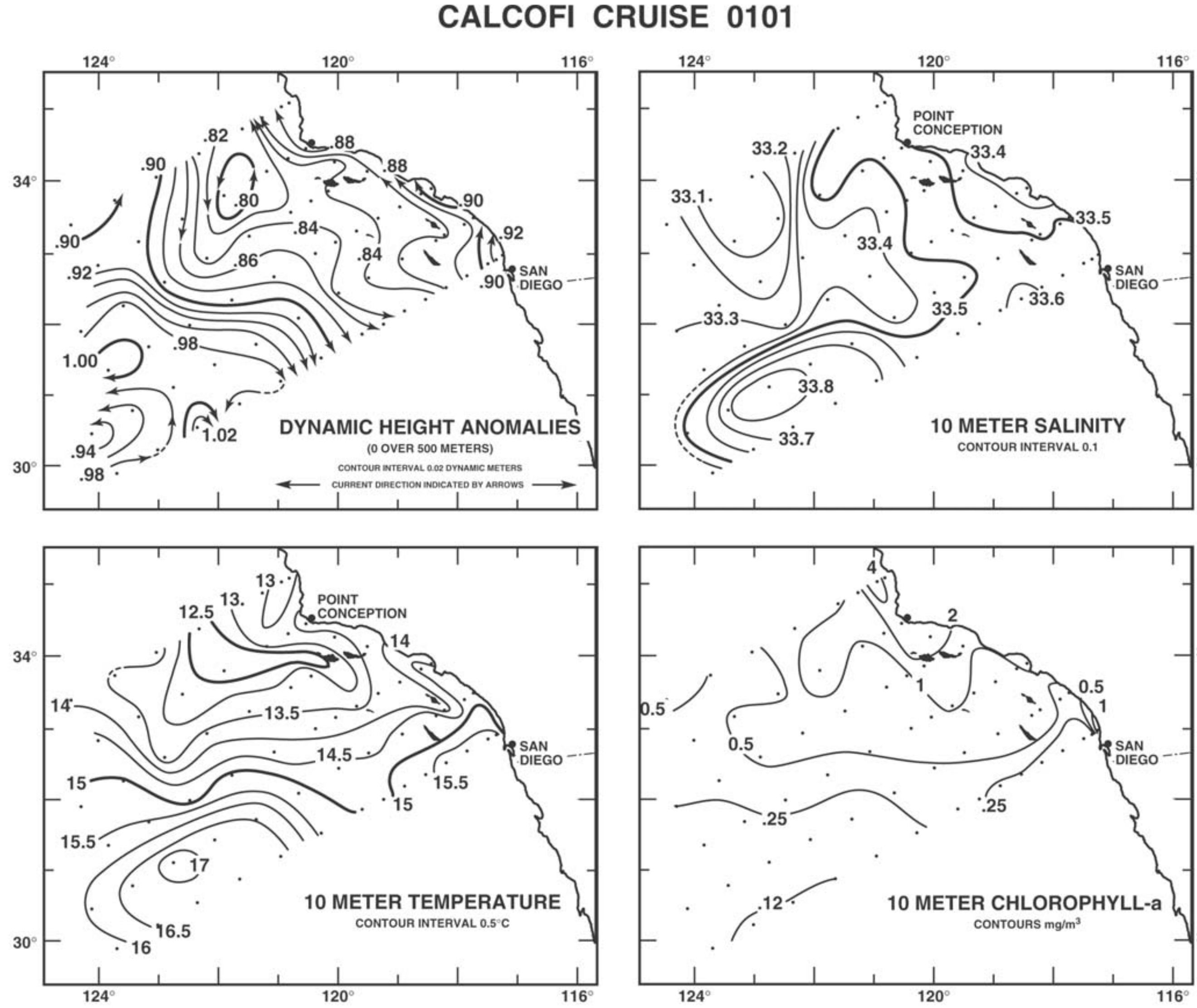

Figure 9. Spatial patterns for CalCOFI cruise 0101 (7–26 Jan. 2001), including upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height field, 10 m chlorophyll *a*, 10 m temperature, and 10 m salinity.

strong lateral gradient in the 0/500 dbar dynamic height contours through the middle of the cruise pattern, and by the location of the low-salinity water (<33.4) advected into the region from the north (fig. 9). A warm and saline eddy is seen in the southwest corner of the pattern, offshore of the main flow of the California Current. A broad northward coastal countercurrent was present between the coast and station 90.53. Near-coastal water between 100 and 300 m off San Diego was warmer and more saline than usual, an indication that the coastal undercurrent was also strong with an influx of water from the south. Surface chlorophyll was high off Point Conception and in the Santa Barbara Channel. Overall, the cruise-mean integrated chlorophyll and primary productivity were above normal (fig. 10a). SSTs were generally cooler than normal for the third consecutive winter.

0104 (6 Apr.–3 May 2001)

Although the April offshore circulation and salinity were similar to January, the coastal flow was southward (fig. 11). Associated with this strong flow was intense coastal upwelling, as shown by very cool coastal temperatures and high salinities (greater than 33.8 in the Santa Barbara Channel). The nearshore countercurrent that defines the Southern California Eddy was not evident; the dynamic height pattern shows only a slight suggestion of northward flow. An isolated cyclonic eddy was present, centered at station 80.90 (ca. 33°N 123°W). Surface chlorophyll was exceptionally high in April, especially at the shallow continental shelf stations. The cruise-mean integrated chlorophyll was exceeded only by the 1999 cruise mean (fig. 10a). SST anomalies were cooler than the long-term means throughout the region,

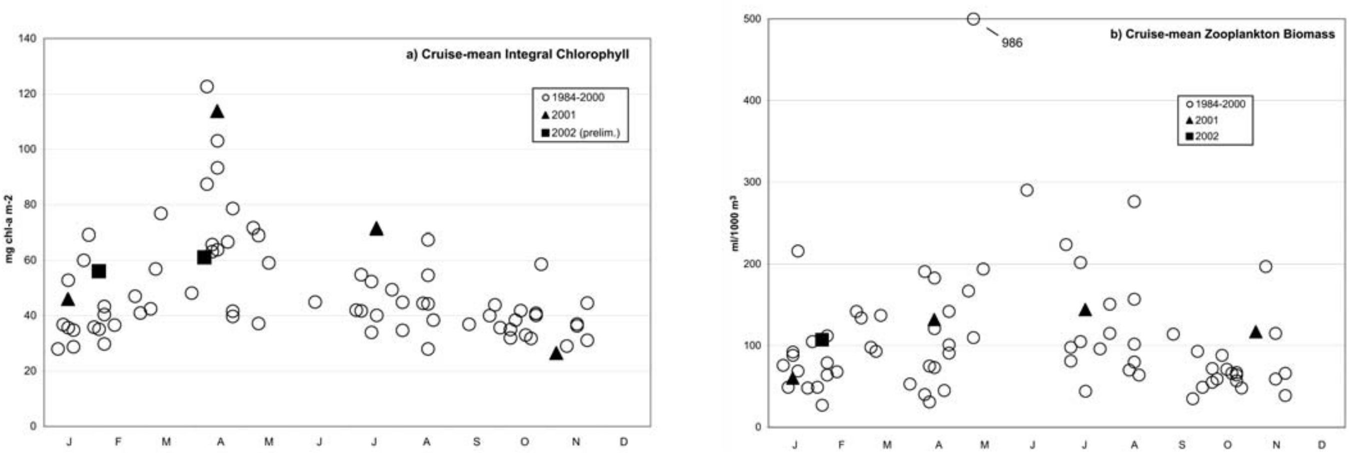

Figure 10. Cruise means of (*a*) vertically integrated chlorophyll and (*b*) macrozooplankton biomass plotted versus month for CalCOFI cruise from 1984 to Apr. 2001 for chlorophyll *a* and Jan. 2001 for zooplankton. Each point represents the mean of all measurements on a cruise (usually 66). Open circles indicate the 1984–2000 cruise values. Solid triangles and rectangles indicate values from 2001 and 2002, respectively.

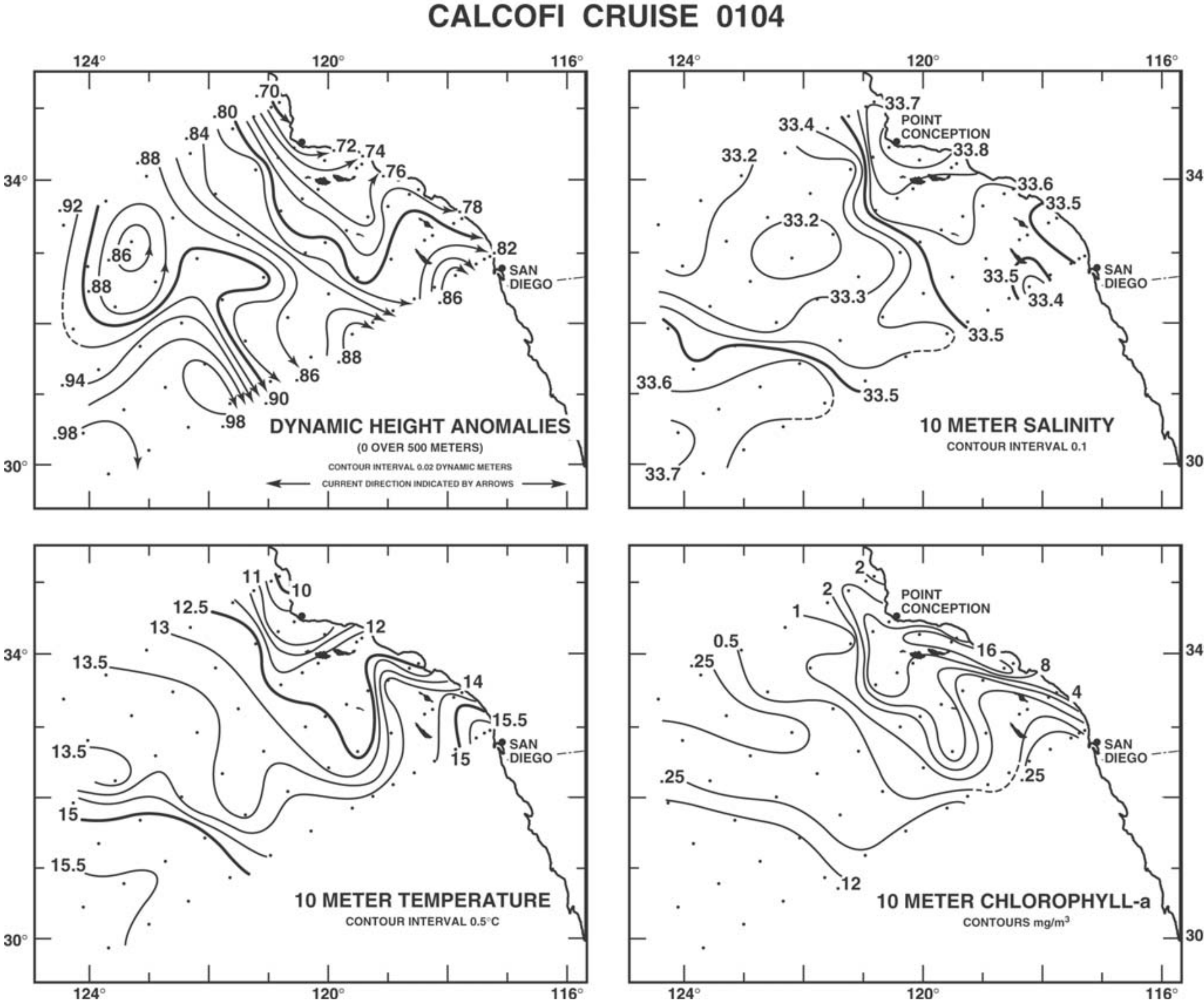

Figure 11. Spatial patterns for CalCOFI cruise 0104 (6 Apr.–3 May 2001), including upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height field, 10 m chlorophyll *a*, 10 m temperature, and 10 m salinity.

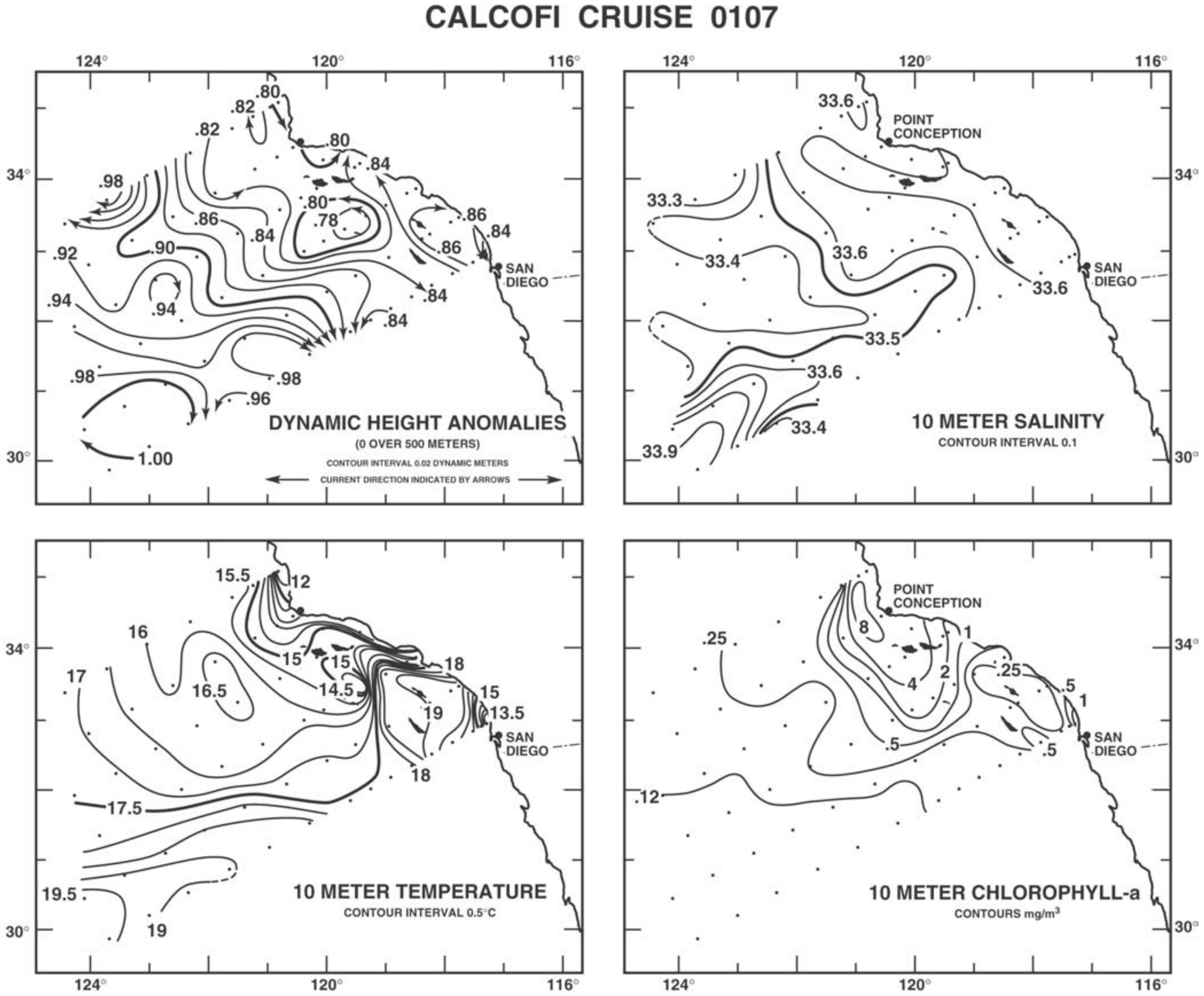

Figure 12. Spatial patterns for CalCOFI cruise 0107 (10–27 July 2001), including upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height field, 10 m chlorophyll *a*, 10 m temperature, and 10 m salinity.

exceeding 2°C below normal on the shelf stations of line 87.

0107 (10–27 July 2001)

The circulation in July reverted to a more normal state for the season, with a southern California cyclonic eddy present but with southward flow on the shelf north of Santa Barbara and off San Diego (fig. 12). Both of these shelf areas were unusually cool; a cold patch was also seen in the center of the cyclonic eddy, at stations 87.45 and 87.50 near San Nicolas Island. The flow from the offshore edge of the pattern was largely zonal, bringing in relatively low salinity (<33.4) water along the northwestern edge and warm high salinity (>33.7) water from the southwestern corner. Both signals were carried eastward well into the region. The shallow warm patch of water in the southeast part of the pattern is typical for summer. The temperature-salinity curve there is quite close to the long-term historical mean. Surface chlorophyll, cruise-mean integrated chlorophyll (fig. 10a), and primary productivity were very high for summer.

0110 (25 Oct.–9 Nov. 2001)

The California Current in October featured a wide meander, with offshore flow on the outer part of line 77 and an eastward flow between lines 80 and 83 that turns southward between stations 60 and 90 of line 83 (fig. 13). The Southern California Eddy, centered at station 87.45 on cruise 0107, had moved south and was centered on station 90.53. The northward coastal coun-

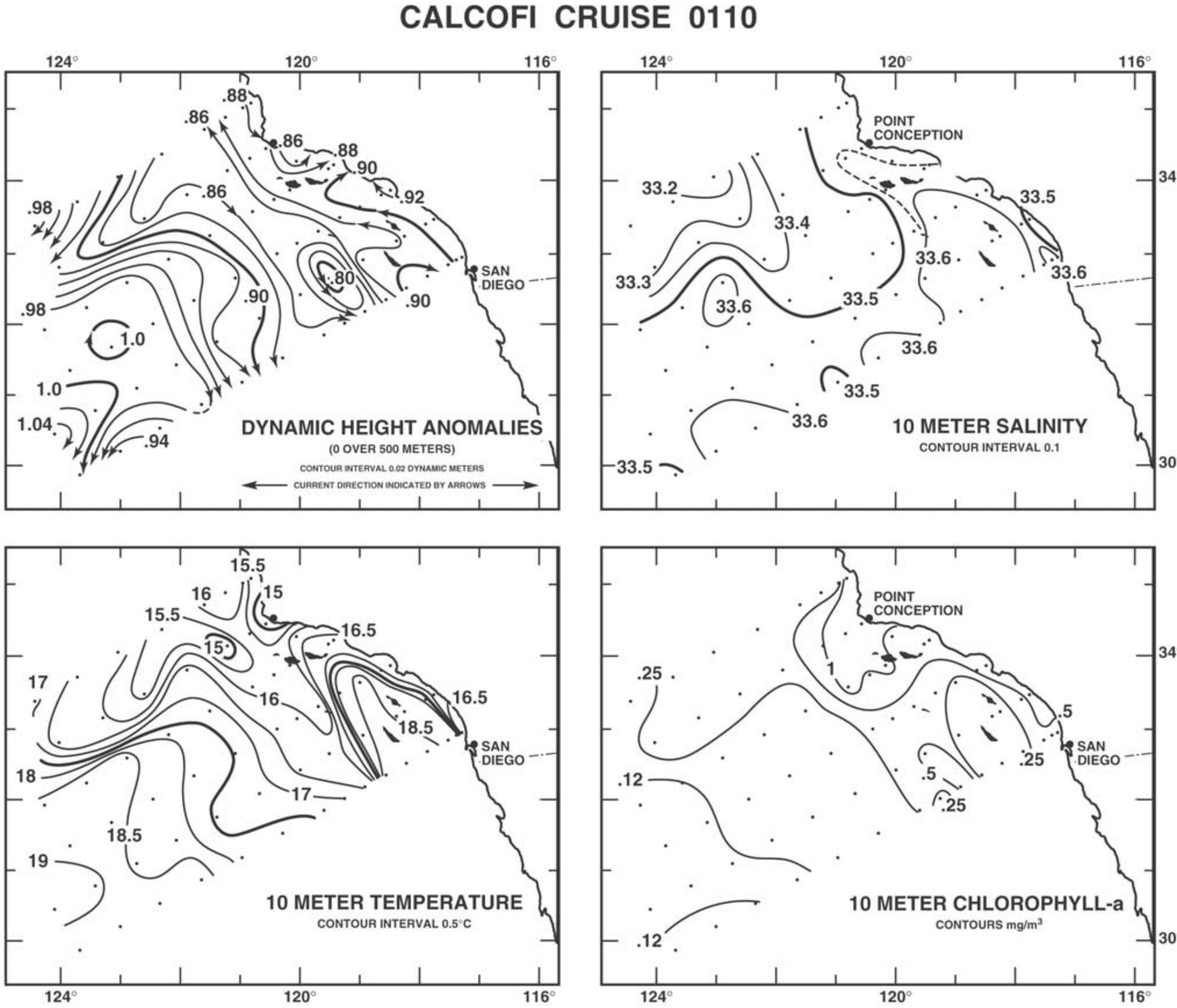

Figure 13. Spatial patterns for CalCOFI cruise 0110 (25 Oct.–9 Nov. 2001), including upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height field, 10 m chlorophyll *a*, 10 m temperature, and 10 m salinity.

tercurrent was wide and resumed the typical fall pattern. Surface chlorophyll also subsided to low values that are typical of fall.

0201 (24 Jan.–11 Feb. 2002)

The surface dynamic height field again shows a strong meander in the outer part of the pattern (fig. 14), but this was shifted compared to October. Whereas the flow was offshore on line 77 during the previous fall, it was now eastward, turning westward between lines 80 and 83. The northward nearshore countercurrent was present but somewhat further offshore than usual. A cyclonic/anticyclonic pair of eddies was seen in the southwest corner of the pattern. Along the coast, chlorophyll levels were again quite unseasonably high, especially near Point Conception. There was also a patch of elevated chlorophyll (greater than 0.5 μg/l) offshore in the region where surface chlorophyll is usually low. This was in the vicinity of the cyclonic current loop.

0204 (27 Mar.–12 Apr. 2002)

The offshore circulation map for April 2002 (fig. 15) shows the same zonal current loops that were present in January, perhaps shifted slightly southward. These cruise data are in the preliminary stages of being processed, so the 0/500 dbar dynamic heights were not available. The temperature at 100 m depth has been a useful proxy for the surface circulation in the past, especially in relation to the California Current jet. However, it is less successful in depicting the coastal countercurrent. Nonetheless, there was an apparent absence of any surface countercurrent and the Southern California eddy. These

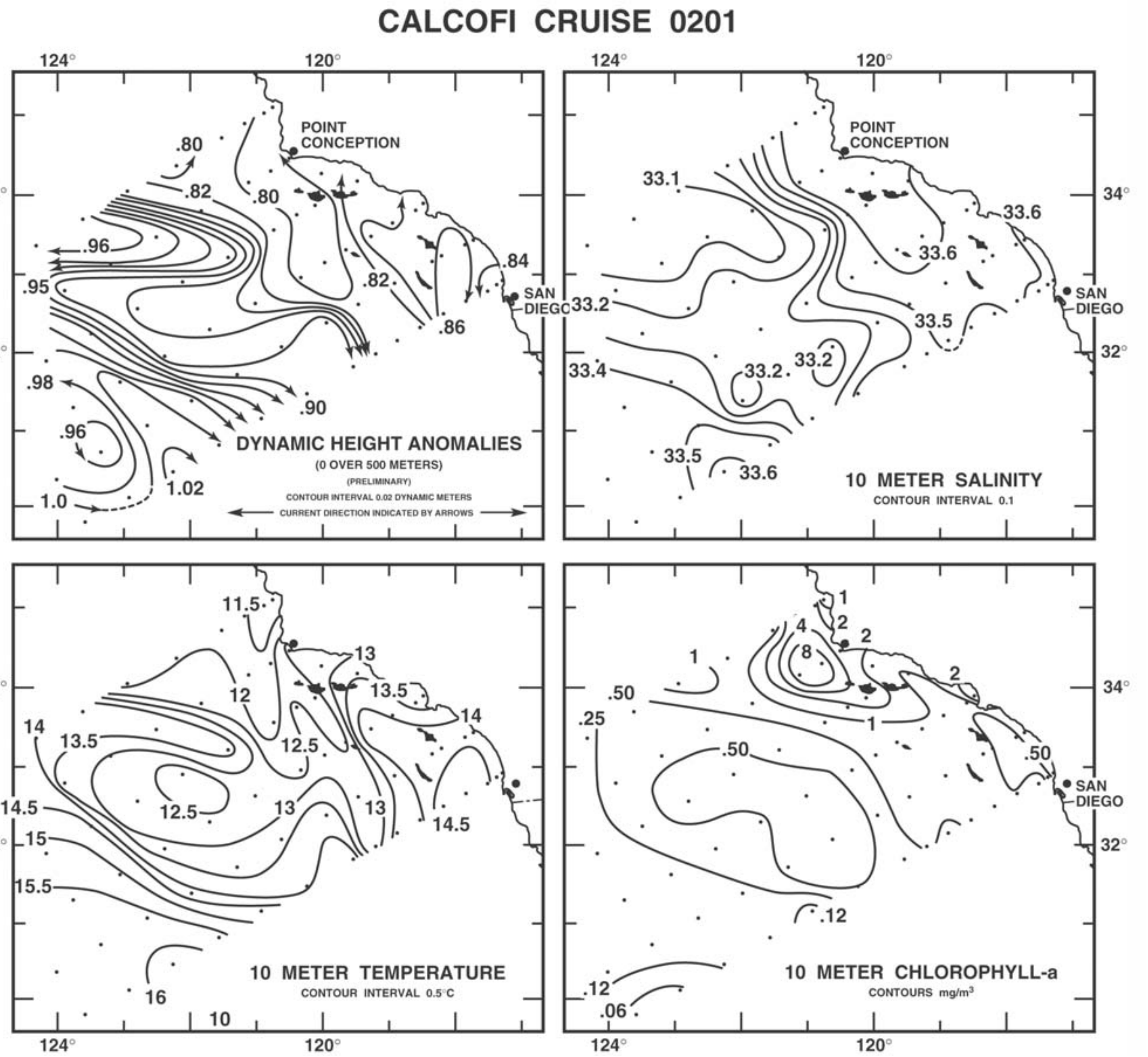

Figure 14. Spatial patterns for CalCOFI cruise 0201 (24 Jan.–11 Feb. 2002), including upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height field, 10 m chlorophyll *a*, 10 m temperature, and 10 m salinity.

near-surface patterns are somewhat unusual for spring, with the main core of the California Current apparently well offshore and little evidence of an equatorward upwelling jet. Upwelling was strong, with cooler than normal nearshore temperatures and high surface salinities. Chlorophyll levels were very high around the northern Channel Islands, where the phytoplankton was dominated by *Pseudonitzschia australis* instead of species in the genus *Chaetoceros* that are more usual in spring; *P. australis* exceeded 1,000 cells/ml at station 83.51, south of Santa Rosa Island. Another unusual biological observation was the high abundance of the chondrophore *Velella velella* over much of the survey region. The cruise track was extended another 40 nmi offshore on lines 77 and 80 to sample sardine egg concentrations. An unscheduled sample taken at 79.110 (not plotted) showed surprisingly high surface chlorophyll (0.45 µg/l) for a station so far offshore, whereas relatively low chlorophyll was present in the anticyclonic loop seen on the offshore ends of lines 80 and 83. That current loop is also the only part of the cruise that has positive 10 m temperature anomalies. The rest of the region remained cooler than normal, as it has been for the previous three springs.

TEMPERATURE AND SALINITY TIME SERIES 1995–2001: STATION 90.37

The temperature and salinity time series over the upper 500 m at station 90.37, which lies between San Clemente and Catalina Islands, represent events within the Southern California Bight. Water mass properties

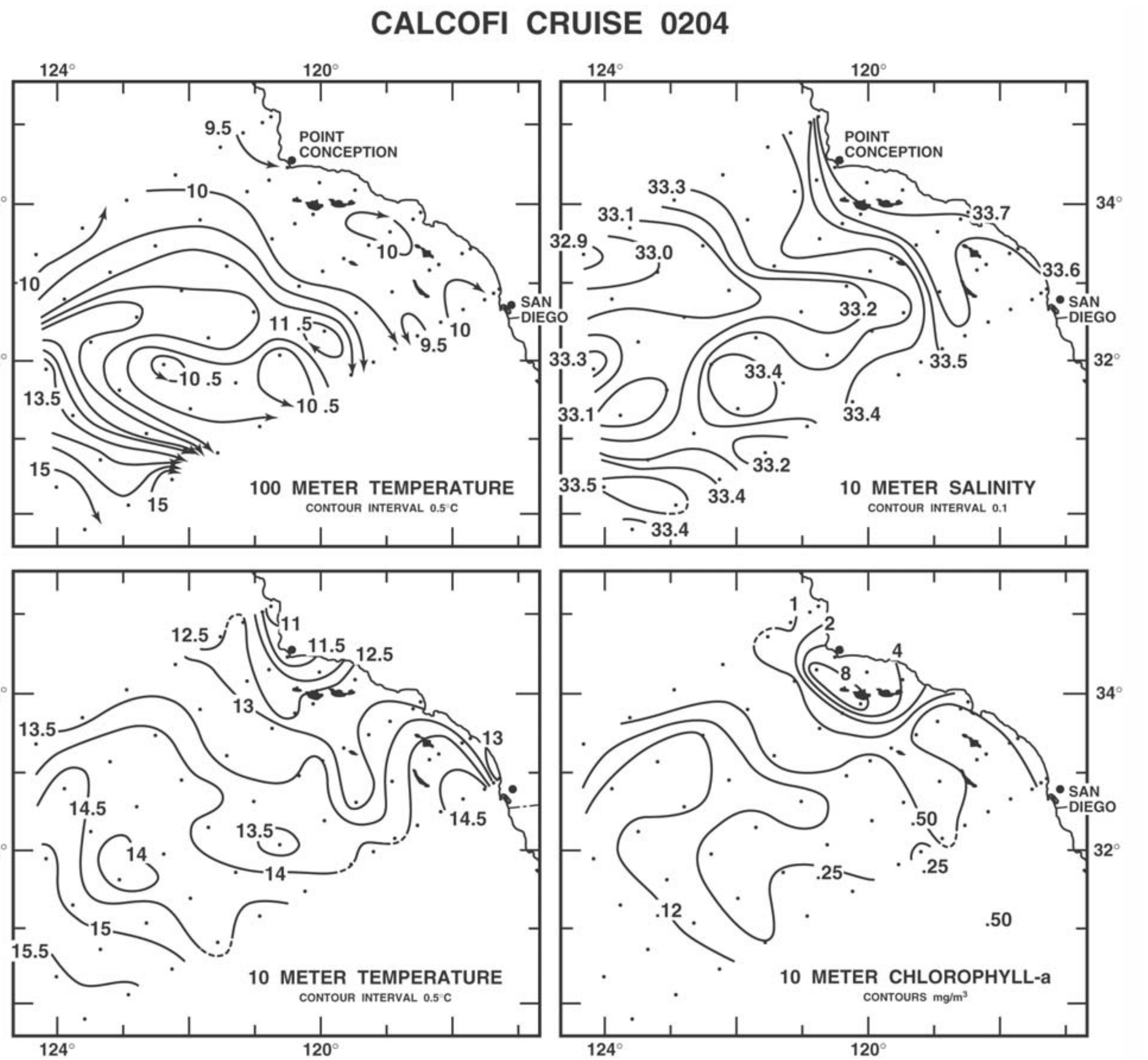

Figure 15. Spatial patterns for CalCOFI cruise 0204 (27 Mar.–12 Apr. 2002), including 100 m temperature (proxy for upper-ocean geostrophic flow), 10 m chlorophyll *a*, 10 m temperature, and 10 m salinity.

are influenced by seasonal, interannual, and episodic circulation events, all evident in Figure 16. Seasonal cooling/warming and an associated salinity decrease/increase are evident above 30 m, associated with stronger upwelling in spring and summer/weaker upwelling in fall and winter. The strong 1997–98 El Niño followed by a strong La Niña provide the strongest signals at mid-depths. Anomalously warm and saline waters initially appeared at depth (175–250 m) in July 1997. The surface manifestation of El Niño appeared during the fall and winter of 1997.

After mid-1998, La Niña produced a strong freshening and unseasonable cooling from the surface to 400 m. The seasonal cycle in temperature between 150 m and 400 m that existed prior to the 1997–98 El Niño does not appear afterward. The early period variation is likely related to seasonal variability in the geostrophic balance of the California Undercurrent. Since mid-1998, this portion of the water column has also been cool and fresh relative to the 1995–97 observations shown here. One explanation for this is a reduction in the transport of the Undercurrent beginning in 1998, resulting in more subarctic water in the Bight. An examination of these time series suggests that an expanded study using this methodology would be of some interest.

IMECOCAL SURVEY CRUISES

0104 (3–15 Apr. 2001)

Only a few stations were occupied during this survey because of unfavorable sea conditions and continuous ship problems. The core of the California Current was

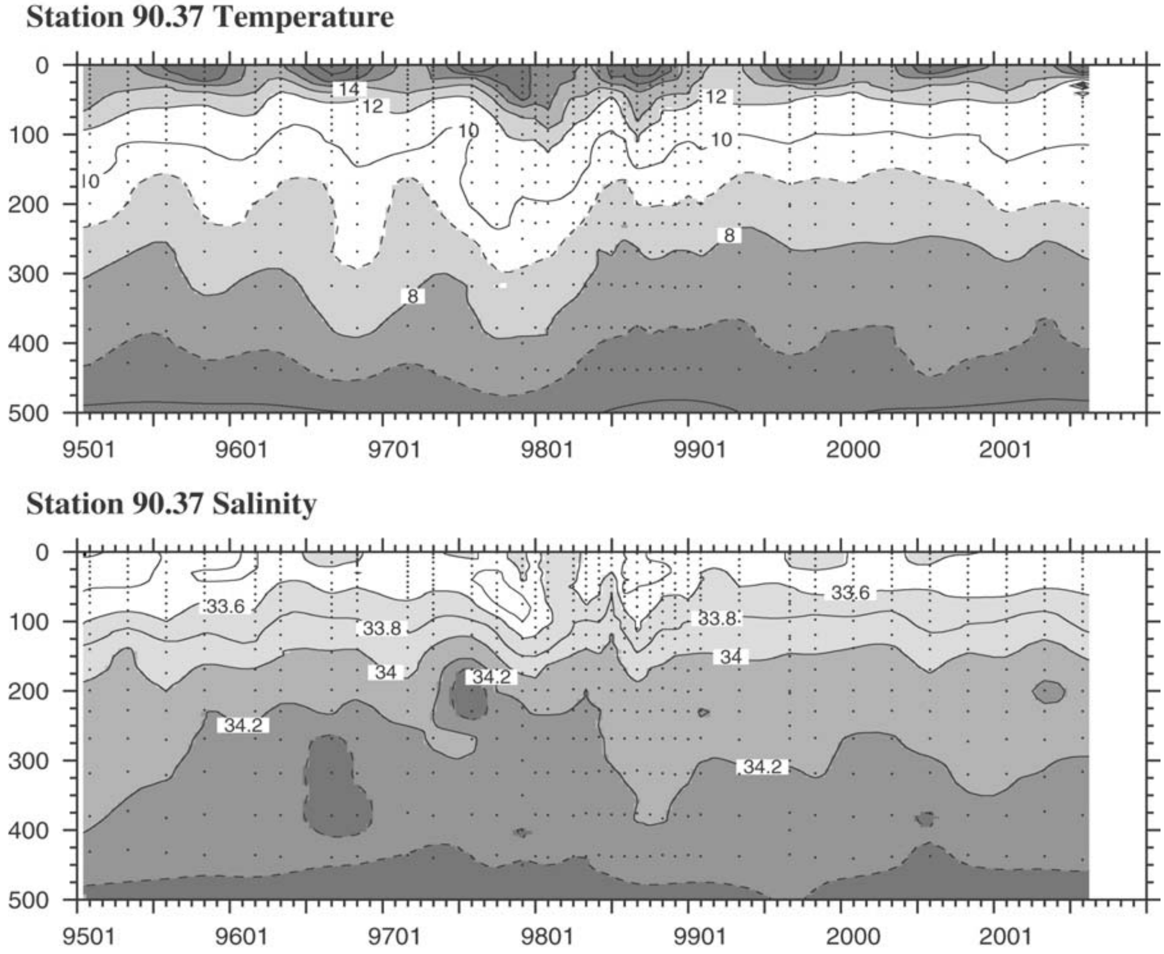

Figure 16. Time series of temperature and salinity over the upper 500 m at CalCOFI station 90.37 (between San Clemente and Catalina Islands), 1995–2001. Temperature contour interval is 2°C for T >10°C, 1°C for T < 10°C. Salinity contour interval is 0.2. Dots denote positions of samples.

located about 100 km off Punta Colonet (3°N) (fig. 17), in association with low SST (14.0–15.0°C) and salinity (33.50–33.60). Inshore 10 m water temperatures below 14.0°C and salinities up to 33.70 were related to upwelling in the northern region. Inshore waters had high dissolved oxygen (>6.0 ml l^{-1}) (fig. 17), and high phytoplankton biomass (10 m chlorophyll *a*) with concentrations above 8.0 mg m^{-3} (fig. 18). These values indicate high production off Baja California for spring 2001. During April, zooplankton biomass in northern Baja California was relatively low (<70 ml/1,000 m^3), with only a local patch of high biomass off Punta Colonet (fig. 19).

0106 (26 June–17 July 2001)

Inshore of the core of the California Current, which was still ~100 km off Punta Colonet, a cyclonic eddy had developed (fig. 20). This eddy had a lens of relatively high salinity (33.60) and high surface water temperature. Off Punta Eugenia, the core of the California Current was pushed offshore by a stronger cyclonic eddy. This eddy also had a warm (>20°C) saline lens. The temperature field shows an upwelling-type pattern over most of the IMECOCAL region. The warmest water (>20°C) occurred from Punta Eugenia to the south in the offshore region, associated with two high saline (34.0) cores. One was entering the region from the west and the other from the south. The 10 m dissolved oxygen distribution was homogeneous, with some high concentrations (>6.0 ml l^{-1}) near the coast. High (>8.0 mg m^{-3}) chlorophyll values were found in inshore waters off southern Baja California (fig. 18). In July, an increase of zooplankton biomass was observed in the entire sampled area, but was particularly high near the coast (fig. 19). Zooplankton biomass exceeded 1,000 ml/1,000 m^3 at some stations off southern Baja California. The main centers of high zooplankton biomass appear to be associated with high 10 m chlorophyll concentrations in coastal areas along the Baja California Peninsula.

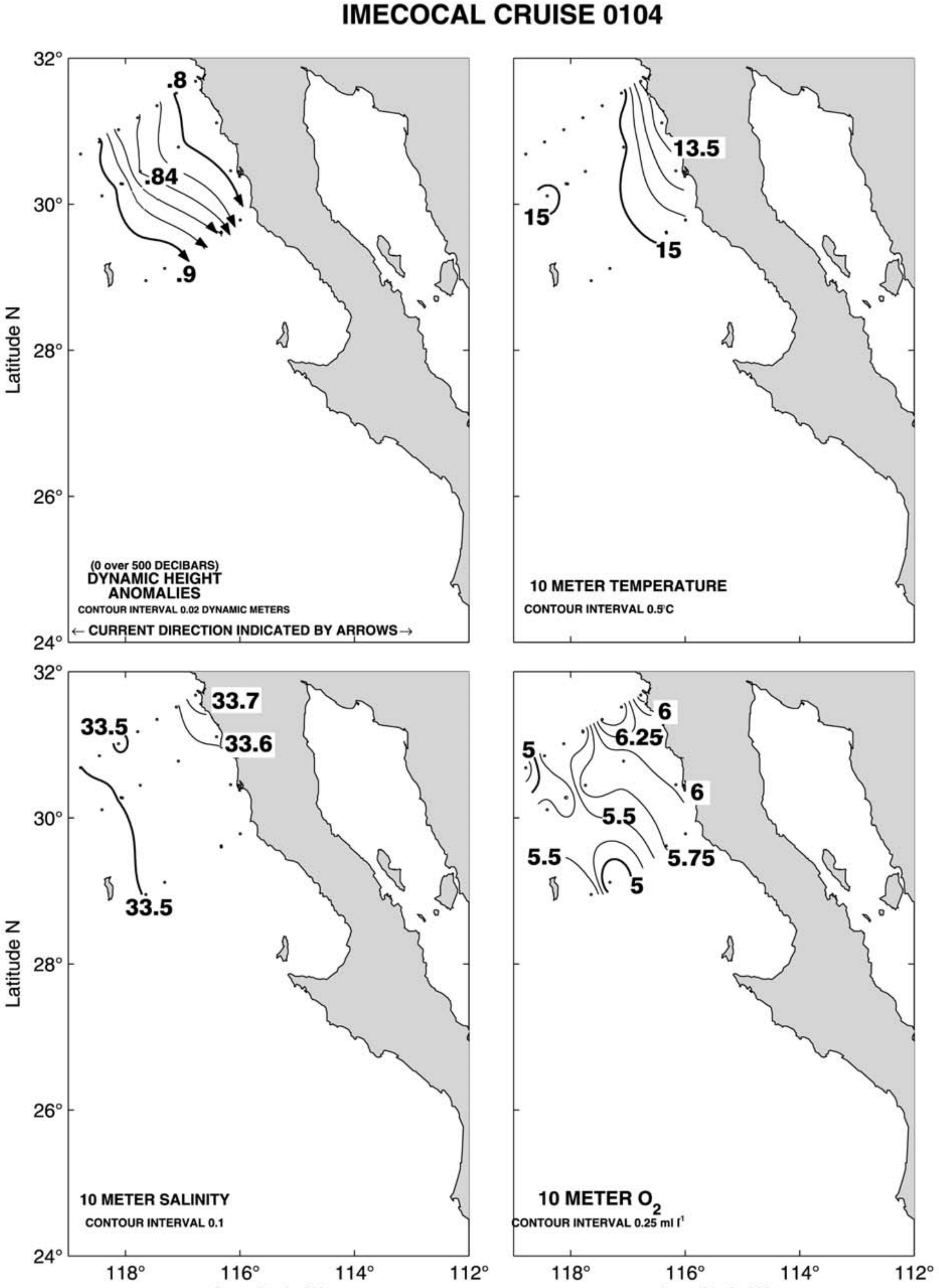

Figure 17. Spatial patterns for IMECOCAL cruise 0104 (3–15 Apr. 2001), including upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height anomalies, 10 m temperature, 10 m salinity, and 10 m oxygen.

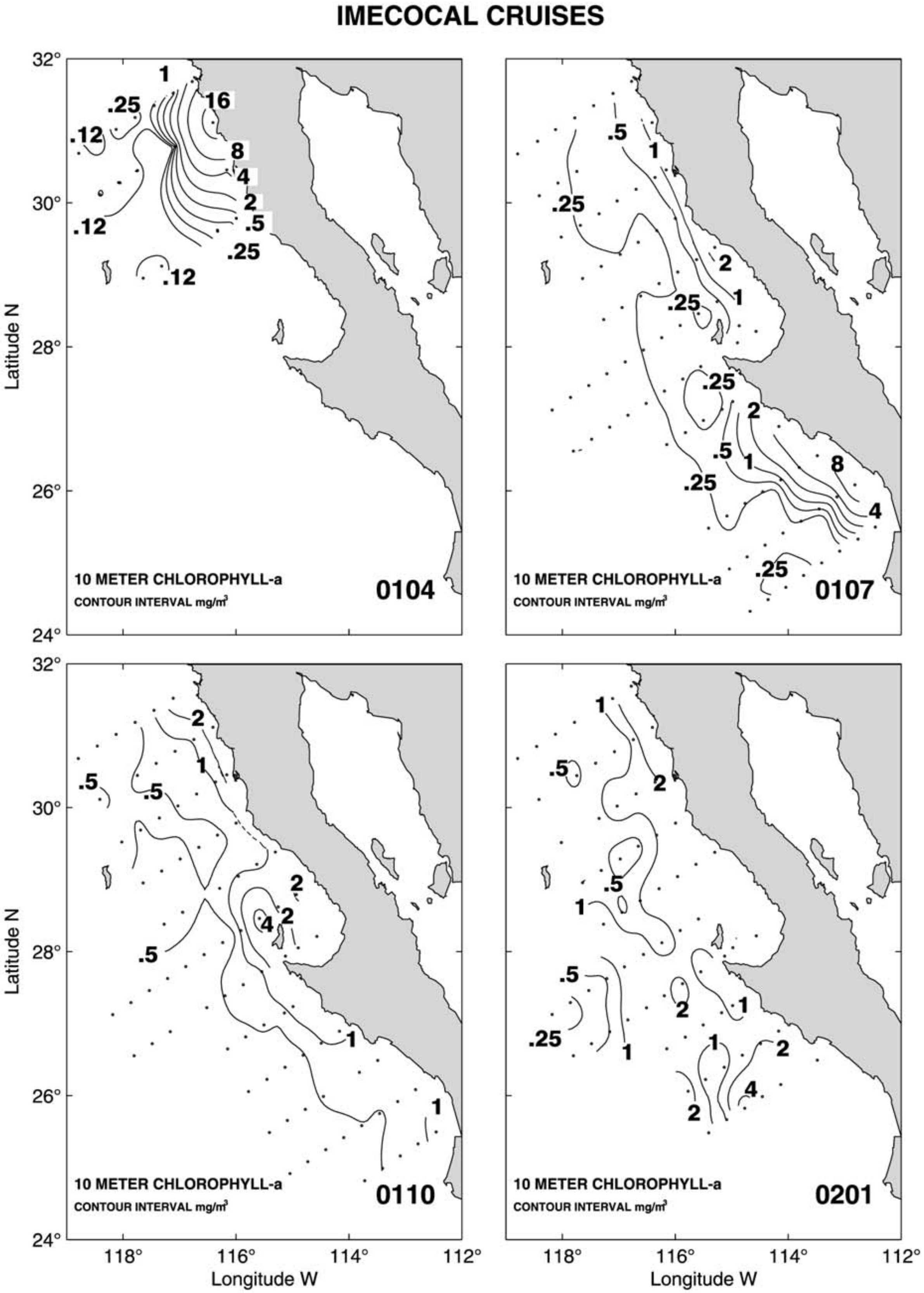

Figure 18. 10 m Chlorophyll *a* measured during the IMECOCAL surveys of Apr., July, and Oct. 2001, and Jan. 2002 in the southern region of the California Current.

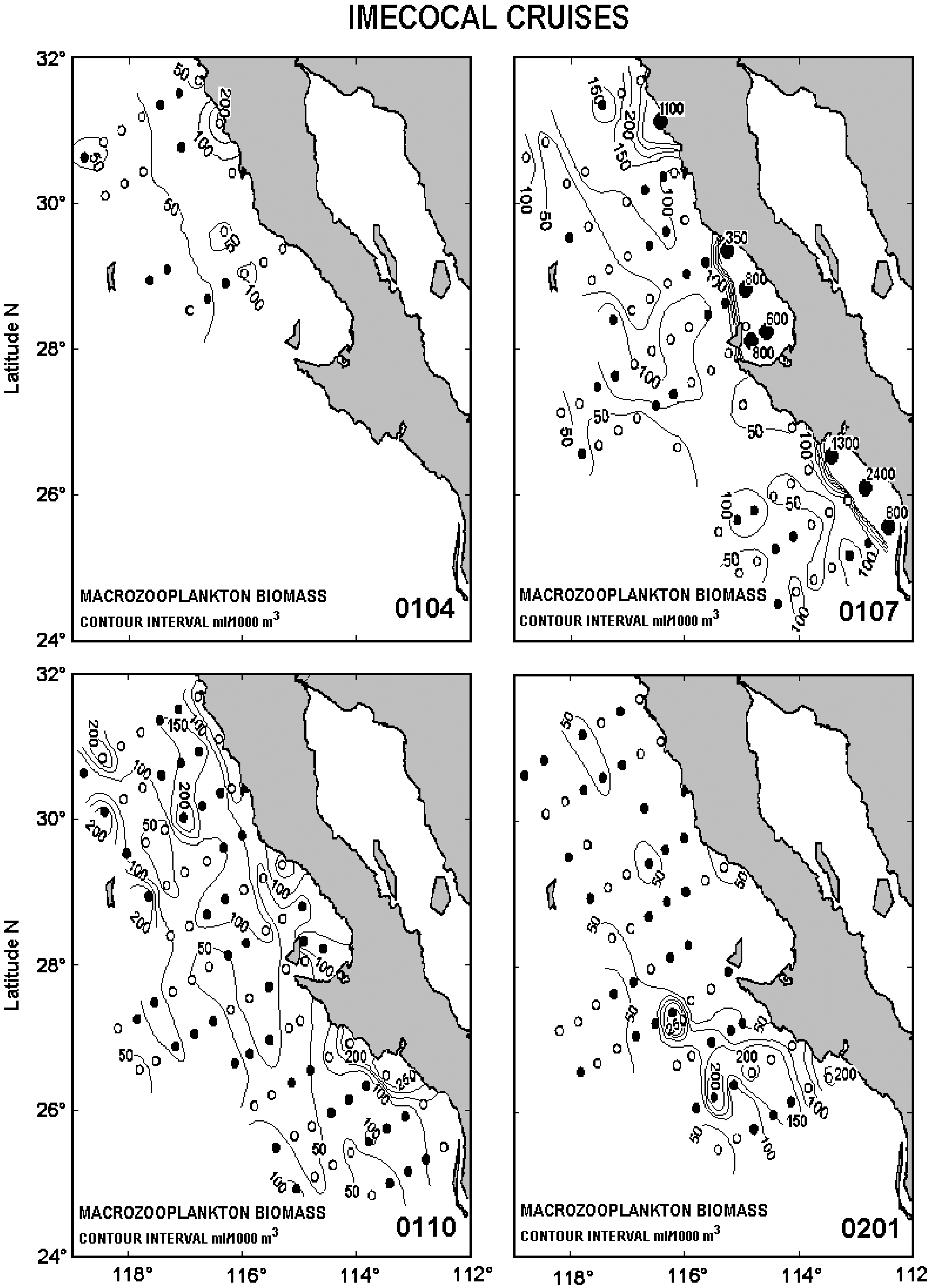

Figure 19. Macrozooplankton biomass distribution off Baja California during Apr., July, and Oct. 2001, and Jan. 2002. The open circles represent the stations visited during daylight hours, and the solid circles, nighttime. The large dots in the upper-right diagram represent very high biomass values.

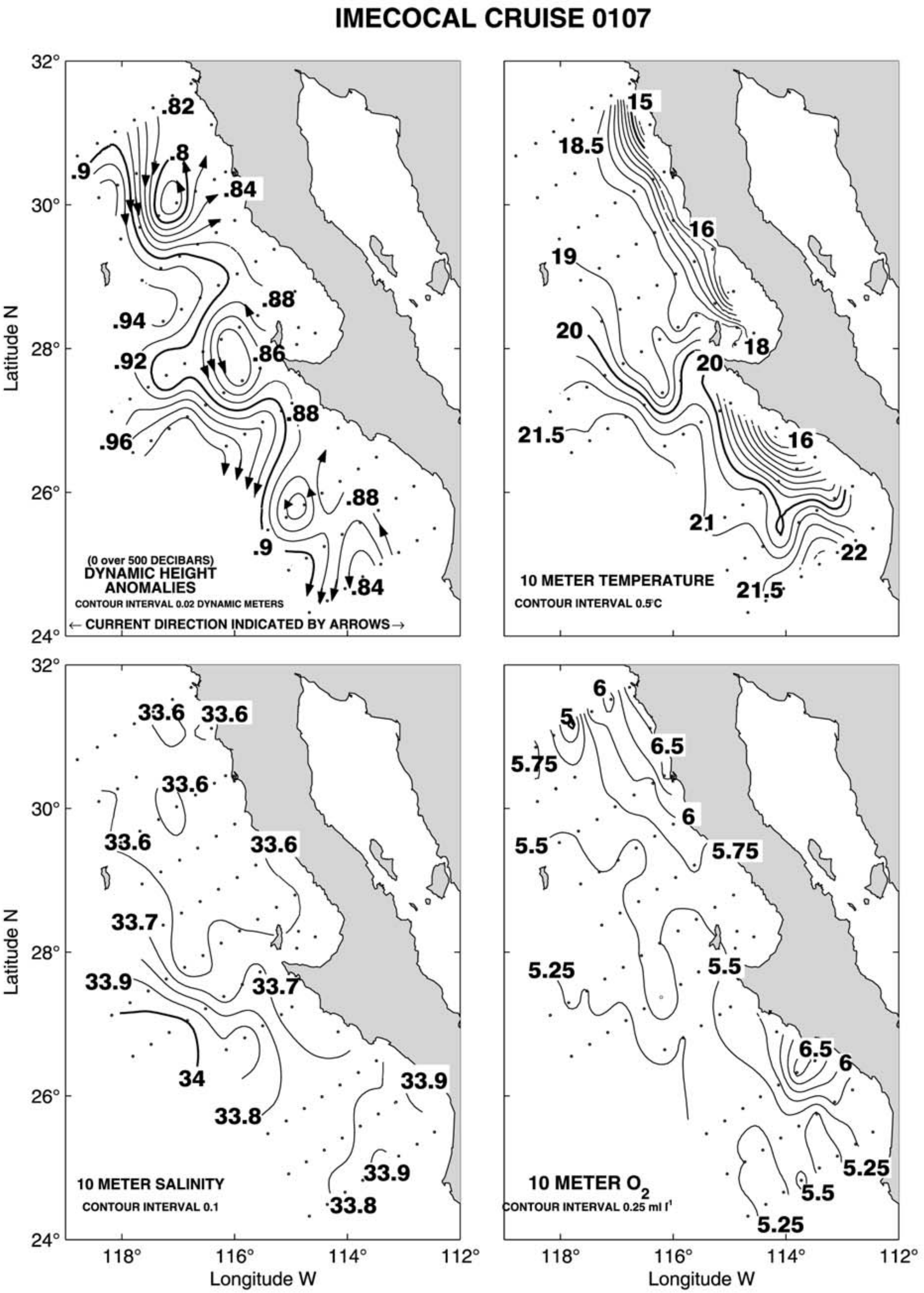

Figure 20. Spatial patterns for IMECOCAL cruise 0107 (26 June–17 July 2001), including upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height anomalies, 10 m temperature, 10 m salinity, and 10 m oxygen.

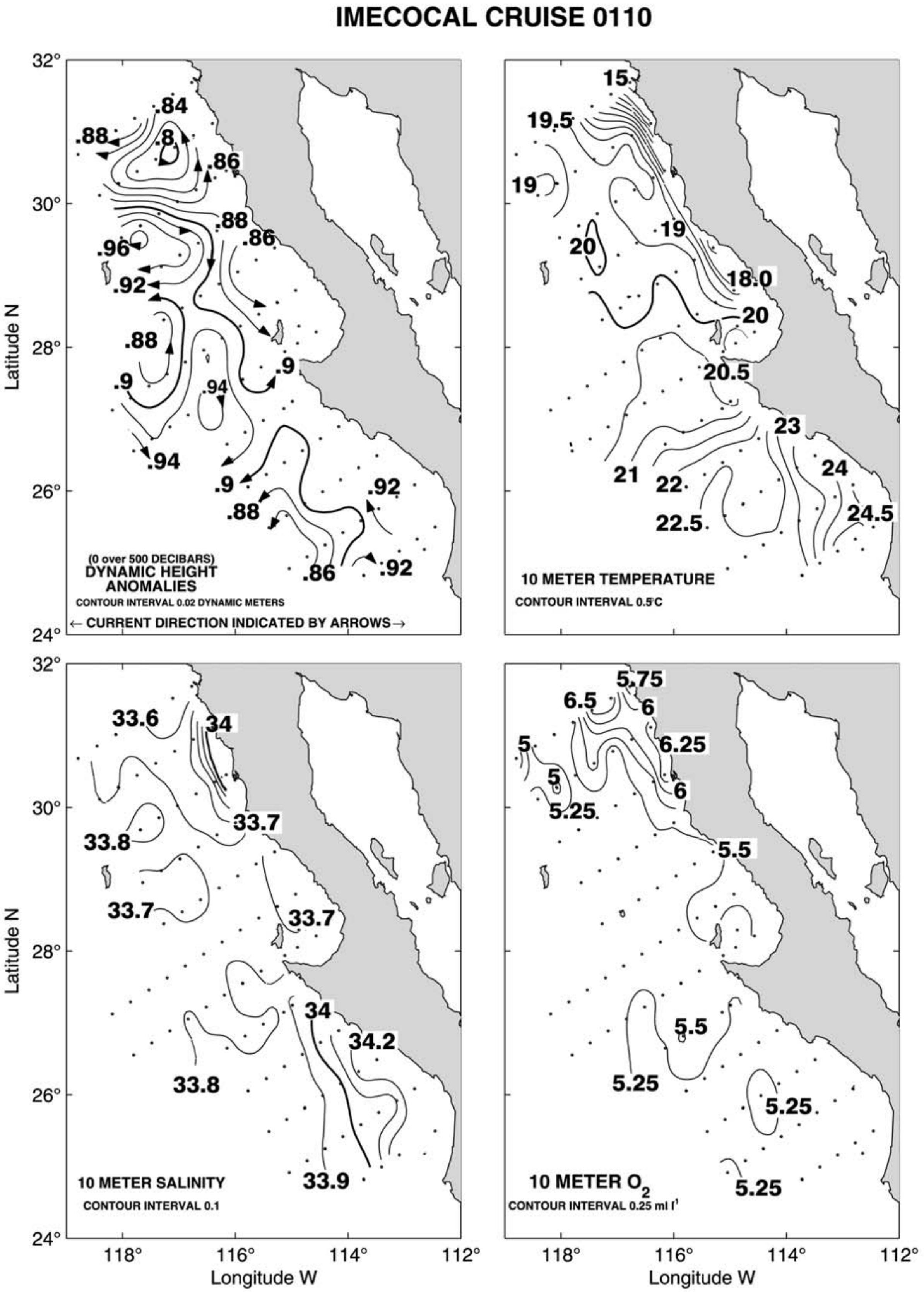

Figure 21. Spatial patterns for IMECOCAL cruise 0110 (3–24 Oct. 2001), including upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height anomalies, 10 m temperature, 10 m salinity, and 10 m oxygen.

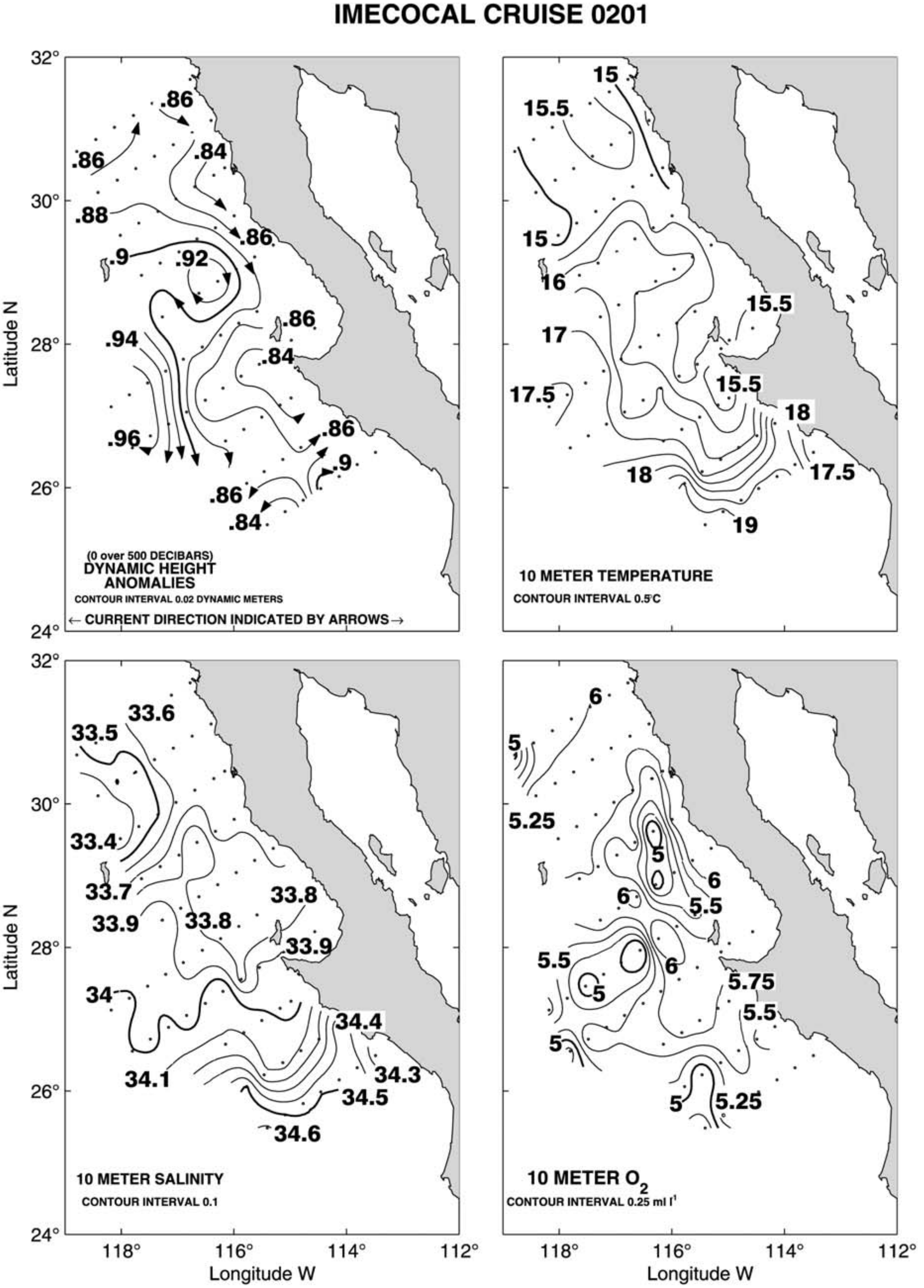

Figure 22. Spatial patterns for IMECOCAL cruise 0201 (19 Jan.–7 Feb. 2002), including upper-ocean geostrophic flow estimated from 0/500 dbar dynamic height anomalies, 10 m temperature, 10 m salinity, and 10 m oxygen.

0110 (3–24 Oct. 2001)

During fall, the core of the California Current, characterized by the 19.5°C isotherm and 33.7 isohaline, was located offshore of Punta Colonet (fig. 21). The eddy off Punta Colonet was now stronger than during summer. From Punta Baja to Ensenada, the high salinity (>34.0), low temperature (<14.5°C), high dissolved oxygen, and high chlorophyll (>2 mg m^{-3}; fig. 18) fields show the occurrence of coastal upwelling. An eddy off Punta Eugenia, characterized by low dissolved oxygen (<5 ml l^{-1}), was pushed offshore by an intrusion of the California Current (fig. 21). An inshore frontal zone was established south of Punta Eugenia, characterized by high salinity (34.3) and temperature (24.5°C). In this region, the main geostrophic flow was northward, turning to the west off Punta Eugenia. During October, zooplankton biomass near the coast continued to be uncharacteristically high (fig. 19), with patch concentrations up to 300 ml/1,000 m^3. Some patchy zooplankton distribution was noted from Guadalupe Island to the north.

0201 (19 Jan.–7 Feb. 2002)

During winter the core of the California Current was reestablished in the northern part of the IMECOCAL region. A clockwise eddy was established off Punta Baja (fig. 22), and the Punta Eugenia eddy had vanished. The frontal region south to Punta Eugenia was stronger during this period than it was in October and was associated with high temperature (>18.5°C) and salinity (>34.5), anomalous low dissolved oxygen (<5 ml l^{-1}) (fig. 22), and high 10 m chlorophyll (>4.0 mg m^{-3}; fig. 18). In January 2002, the tendencies in zooplankton biomass were strikingly different from north to south, with most values below 50 ml/1,000 m^3 north of Punta Eugenia (fig. 19). In the southern region, zooplankton biomass was up to 250 ml/1,000 m^3 in the frontal region described above. The usually rich zooplankton region of Bahia Vizcaino was not sampled in this survey.

The intensity of the California Current from April 2001 to January 2002 in the IMECOCAL surveys was very similar to the earlier period reported by Durazo et al. (2001). The main differences were in the southern region of Baja California, where a strong frontal zone developed during October 2001 and has remained at least until January 2002. In this frontal region a westward flow was evident during the last two reported seasons and was associated with high near-surface temperature and salinity. During the 2001–2002 surveys, 10 m dissolved oxygen varied between 5.2 ml l^{-1} and 6.2 ml l^{-1}; the higher values were seen at inshore stations during spring, summer, and fall. Only during winter (Jan.–Feb. 2002) were the values very similar over the whole area, with a wide zone of values higher than 6.0 ml l^{-1} extending offshore of the northern region. During January 2002, 10 m dissolved oxygen concentrations were about 0.6 ml l^{-1} higher than those reported by Hayward et al. (1999) during winter 1998–99. Dissolved oxygen in the IMECOCAL area increased during winter 1999 to 5.6–5.9 ml l^{-1} (Hayward et al. 1999), with a similar tendency in winter 2002. Chlorophyll values for spring 2001 were very similar to those reported during 2000 (Durazo et al. 2001), with higher concentrations for inshore waters (fig. 18). Moreover, chlorophyll values during summer 2000 in the chlorophyll maximum area in Bahia Vizcaino were 5- to 8-fold higher than for 2001 but only twice as large as 2001 south of Punta Eugenia (fig. 18). The high-chlorophyll frontal region located south of Punta Eugenia during January 2002 was absent during January 2001.

CENTRAL CALIFORNIA SURVEY CRUISES

Off Central California, data have been collected along CalCOFI Line 67 by the Naval Postgraduate School and the Monterey Bay Aquarium Research Institute from April 1988 to April 1991 and from January 1997 to January 2002. Temperature and salinity variations for these data are shown on the 2, 80, and 450 dbar surfaces in Figures 23 and 24, respectively. At 2 dbar, seasonal heating and cooling dominate temperature variability, and coastal upwelling increases the salinity of surface water during spring and summer at the coast as well as reducing its temperature. The most distinctive feature of the line 67 time series was the 1997–98 El Niño, which extended the seasonal warming at the surface through the fall of 1997 and early winter of 1998 and depressed the thermocline, resulting in warming at 80 and 450 dbar. The El Niño warming was accompanied by an increase in salinity. The warming ended abruptly in March 1998 when cooler, fresher water appeared along line 67. The upper ocean remained cooler in 1999, and the salinity increased.

Subsequently, conditions along Line 67 appear to be returning to those observed during the 1988–92 period. The 80 dbar surface is sensitive to the depth of the thermocline and halocline. Features observed at this surface during 1988–91 included warming (temperature >10°C) and freshening (salinity <33.4) to within 150 km from shore in fall as well as nearshore winter warming (T>10°C). The offshore features appeared in summer 2000 and late fall 2001, although the 80 dbar salinity remained higher than observed during 1988–91. In late 2001 the fresh (salinity <33) near-surface subarctic waters reappeared along the outer portion of line 67, and by late January 2002 these waters had penetrated to within about 150 km of shore. The salinity patterns observed at 2 and 80 dbar were similar.

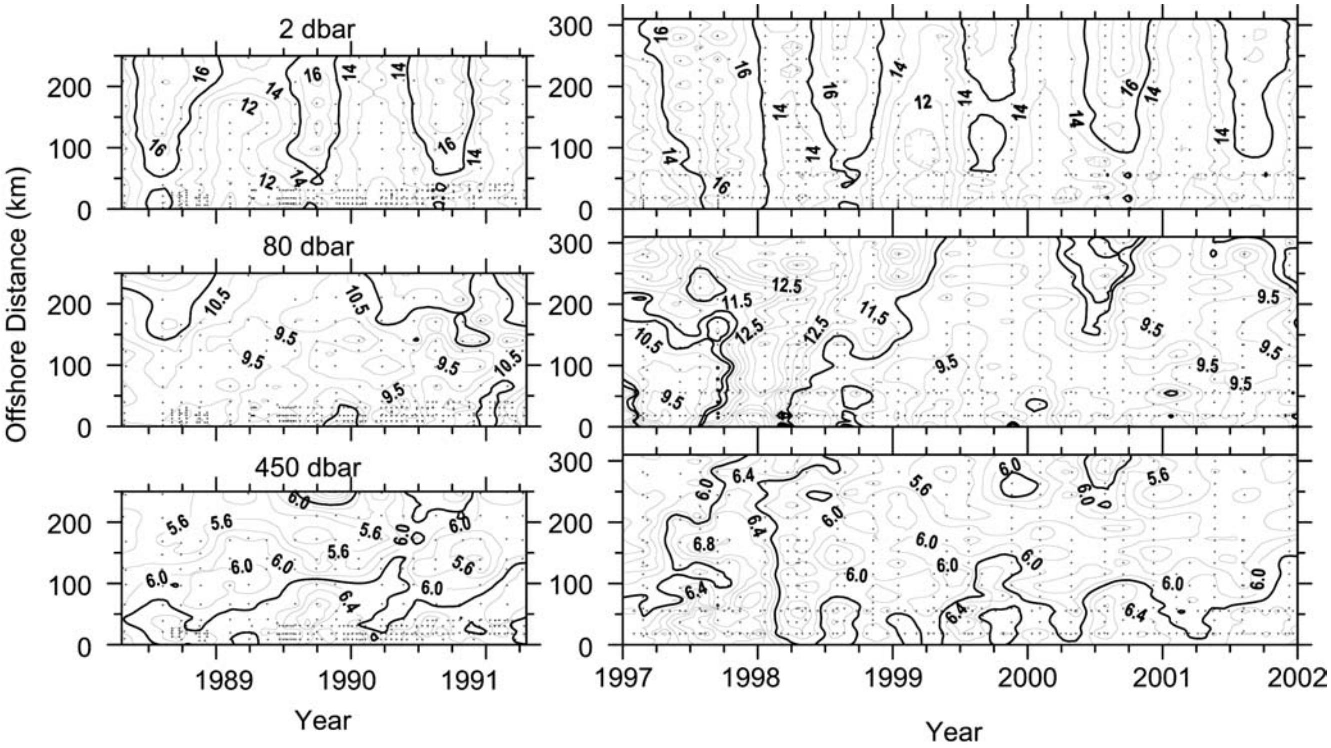

Figure 23. Time series of temperature at 2, 80, and 450 dbar surfaces along CalCOFI line 67 (off Monterey Bay), Apr. 1988–Apr. 1991 and Jan. 1997–Jan. 2002. Vertical axis is distance from coast. Contour interval is 1.0, 0.5, and 0.2°C at 2, 80, and 450 dbar, respectively. The 15, 11, and 6.2°C isotherms are highlighted at 2, 80, and 450 dbar, respectively. Dots denote sample positions.

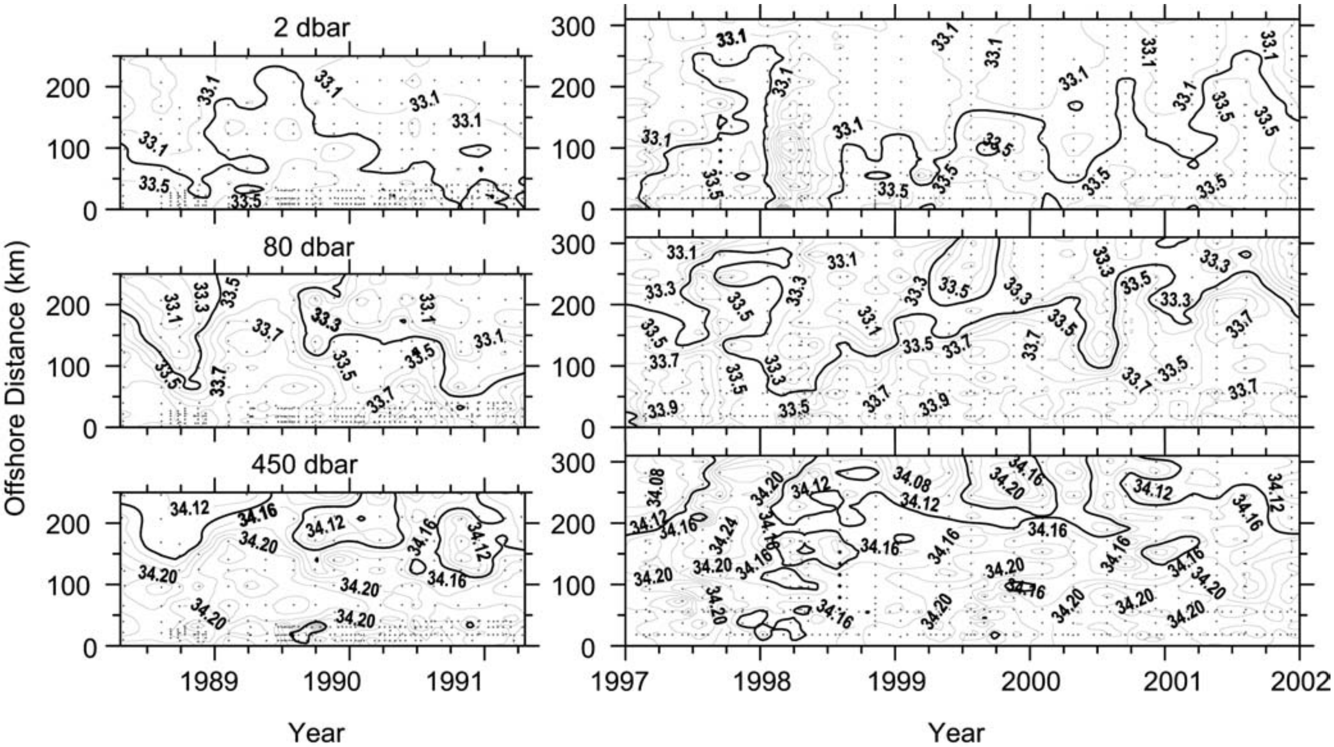

Figure 24. Time series of salinity at 2, 80, and 450 dbar surfaces along CalCOFI line 67 (off Monterey Bay), Apr. 1988–Apr. 1991 and Jan. 1997–Jan. 2002. Vertical axis is distance from coast. Contour interval is 0.2, 0.1, and 0.02 at 2, 80, and 450 dbar, respectively. The 33.3, 33.4, and 34.14 isohalines are highlighted at 2, 80, and 450 dbar, respectively. Dots denote sample positions.

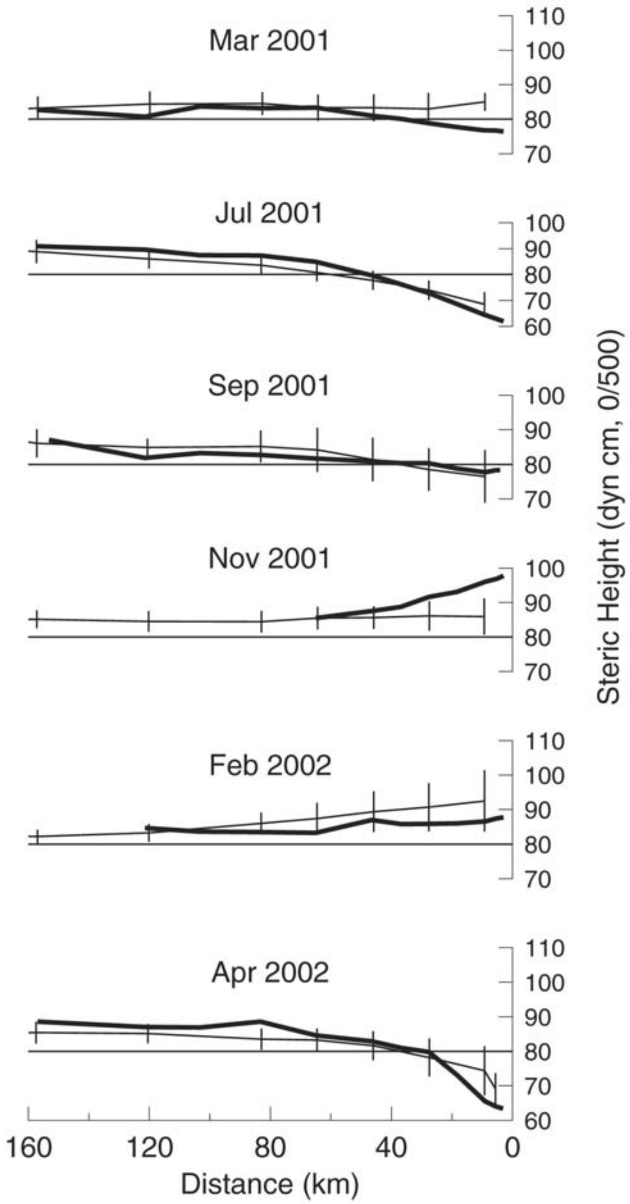

Figure 25. Steric height profiles of the sea surface relative to 500 dbar along the NH line at 44.65°N since Mar. 2001 (heavy line) shown with the long-term (1961–71) seasonal or monthly average provided by Smith et al. (2001). Vertical bars indicate one standard deviation above and below the average. Values over the shelf and upper slope were calculated by the method of Reid and Mantyla (1976). For the incomplete section of Feb. 2002, we estimated the profile by assuming that the surface steric height at the most offshore (65 km) station was the same as the 1961–71 average.

GLOBEC LTOP CRUISES

Previous observations on the NH line off Oregon (44.65°N) have shown the impact of the 1997–98 El Niño in this portion of the California Current, peaking in midwinter 1997–98 and receding by the following winter (Huyer et al. 2002). Between March and early April 2001, steric sea surface heights along the NH line were generally within one standard deviation of 1961–71 seasonal average values (fig. 25). Recall that the reference period for this line coincided with the negative phase of the PDO (Mantua et al. 1997), when the CCS is typically in a relatively cool state. There were three exceptions—March 2001, when the inshore steric height was lower than normal, presumably because seasonal upwelling had begun before the survey; November 2001, when inshore steric heights were high because of a series of winter storms; and April 2002, when offshore values were above normal, though very low inshore values reflect the onset of strong upwelling.

Temperature distributions along the NH line (fig. 26) show the typical seasonal cycle: deep mixed layers with weak horizontal gradients in winter and very strong stratification in the upper 50 m in summer with temperature decreasing shoreward over the shelf. The March 2001 section is typical for the end of winter; surface waters are uniformly cool, although isopycnals bend upward over the continental margin. The distribution of normalized temperature anomalies for 2001–2002 (calculated by subtracting the 1961–71 seasonal or monthly average and dividing this difference by the corresponding standard deviation) shows that temperatures at most depths and most stations were not significantly different from the 1961–71 epoch; values of >2 (corresponding to 95% significance) were observed in relatively small regions (fig. 27).

One exception was in midsummer at a depth of 100–200 m, seaward of the shelf break, where anomalously warm water suggested enhanced poleward advection by the California Undercurrent. A second major exception was a large pool of anomalously warm water at a depth of 400–500 m near the continental slope in April 2002. Note that the offshore end of the 5.5°C isotherm was 75–100 m deeper in April 2002 than in any other section since April 2000 (fig. 26; see also Durazo et al. 2001, fig. 22).

Regional surveys were made in March and September 2001; a survey planned for July was aborted because of ship propulsion failure. The early spring survey (fig. 28) took place very soon after the spring transition (cf. fig. 7). Near-surface temperatures were nearly uniform and about 1°C colder than in April 2000 (cf. Durazo et al. 2001, fig. 23). Values of geopotential anomaly decreased toward shore, particularly in the region south of Coos Bay, indicating that the coastal upwelling jet had already formed. The jet was not as wide, nor as far offshore, as in April 2000. Near-surface salinities were nearly uniform, with values of 32.5–33.0, typical of subarctic waters. A very weak salinity minimum extended southward along the coastal jet, that is, along the 7.8 or 8.0 contour of geopotential anomaly. The salinity minimum was much less pronounced than in April 2000. This is likely due to the 2000–2001 winter drought, which greatly

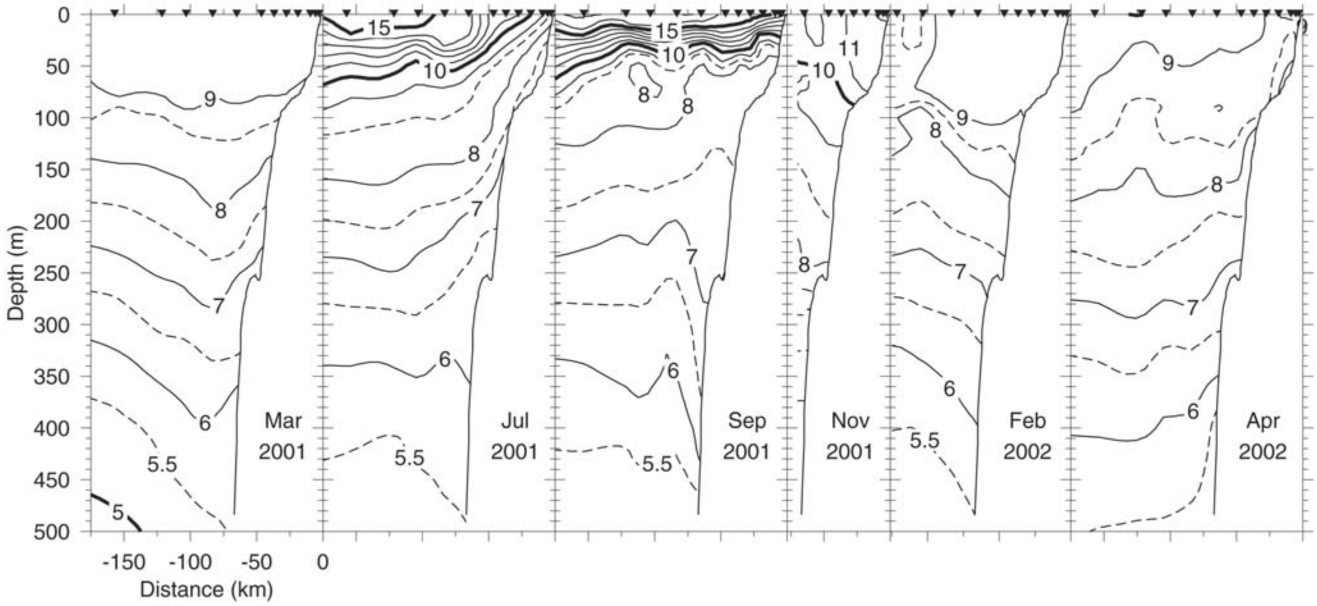

Figure 26. Temperature along the NH line at 44.65°N, for sections since Mar. 2001. Inverted triangles at top show the location of CTD stations.

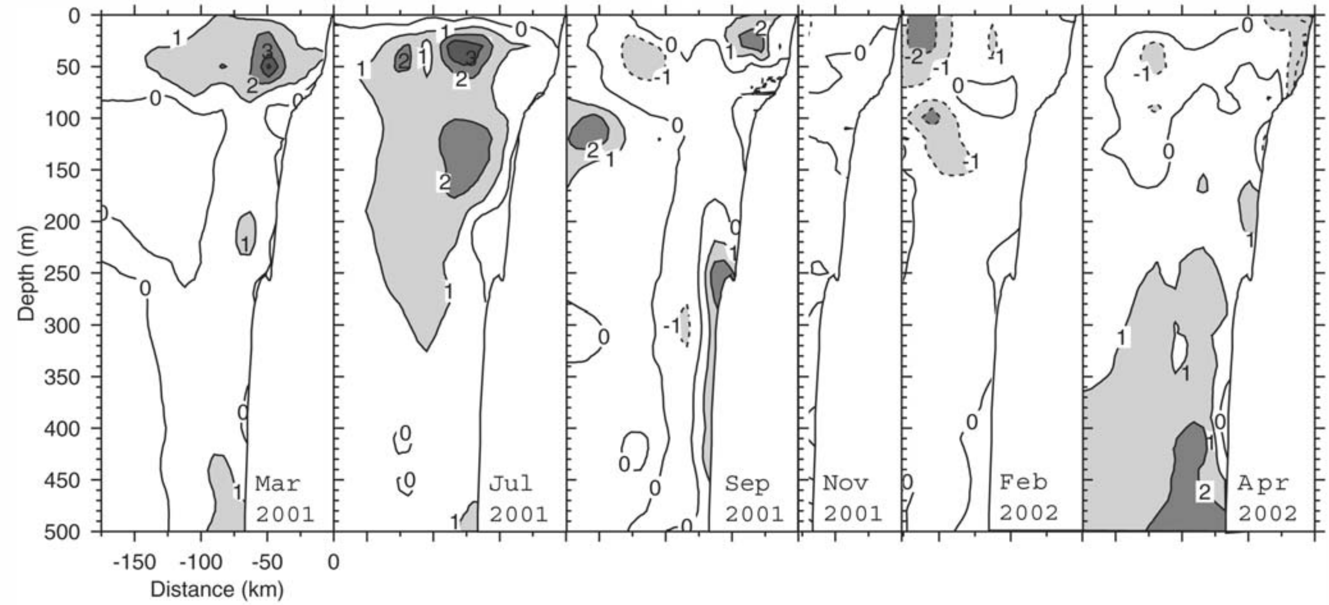

Figure 27. Normalized temperature anomalies for the NH line at 44.65°N. Positive (negative, dashed contours) anomalies indicate that present values are warmer (colder) than the historical (1961–71) seasonal or monthly averages. Values greater than 1 (2, 3) are significant at the 90% (95%, 99%) level, and shaded.

reduced Columbia River discharge in spring 2001. Chlorophyll values were substantially lower in March 2001 than in April 2000, perhaps reflecting the 2001 survey's occurring two weeks earlier in the season.

Surface waters in September 2001 (fig. 29) were generally cooler than in September 2000 (cf. Durazo et al. 2001, fig. 23). As in the previous year, the coastal jet was wider and lay farther from shore in September than in early spring. There were offshore anticyclonic eddies off Coos Bay and off Crescent City, and there was a weak cyclonic eddy offshore of Heceta Bank at 44°N. The thermal front lay far offshore at 42°N (Crescent City) and over the inner shelf at 44.65°N (off Newport), congruent with generally stronger upwelling favorable winds in the south. The 14°C and 15°C isotherms and the 31.5°C isohaline also lay far offshore at 44°N, over or beyond the shelf-break of Heceta Bank. Waters over Heceta Bank were relatively cool, salty, and enriched in

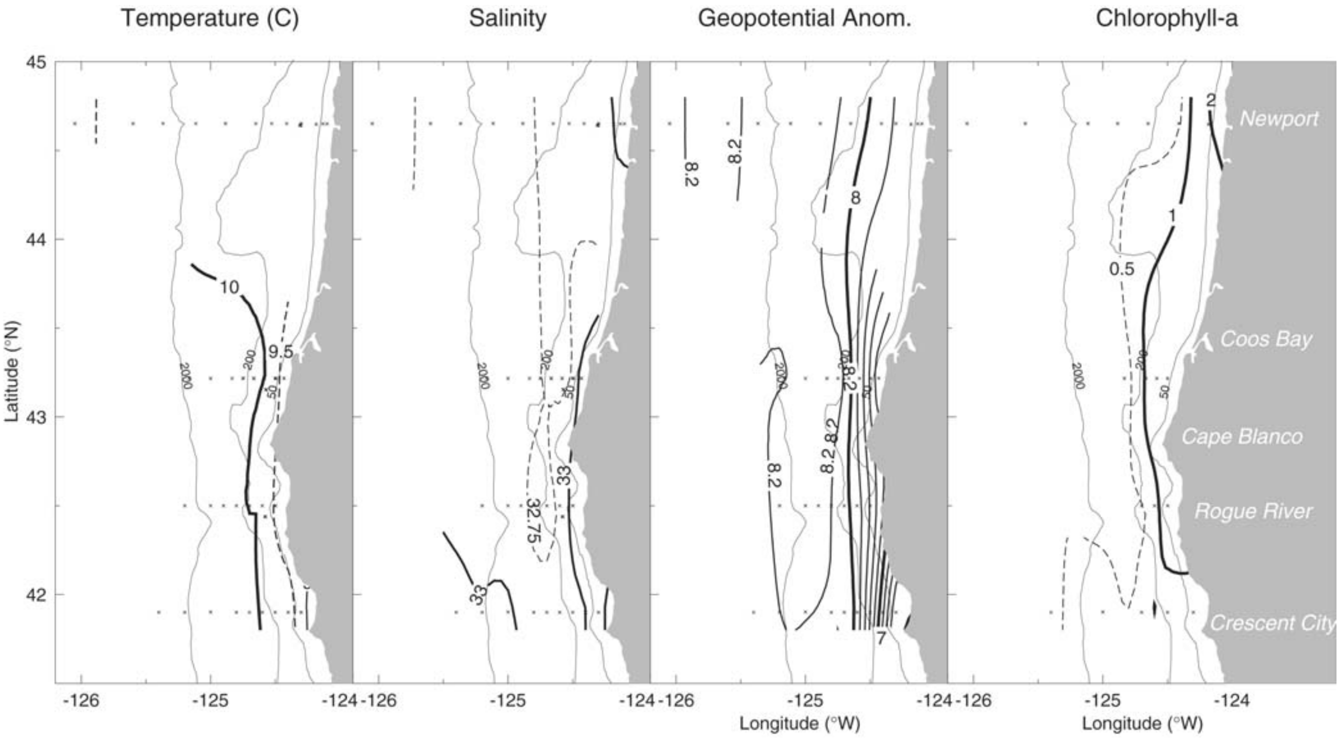

Figure 28. Temperature, salinity, and chlorophyll *a* at 10 m, and geopotential anomaly (J/kg) of the sea surface relative to 500 dbar, 15–24 Mar. 2001.

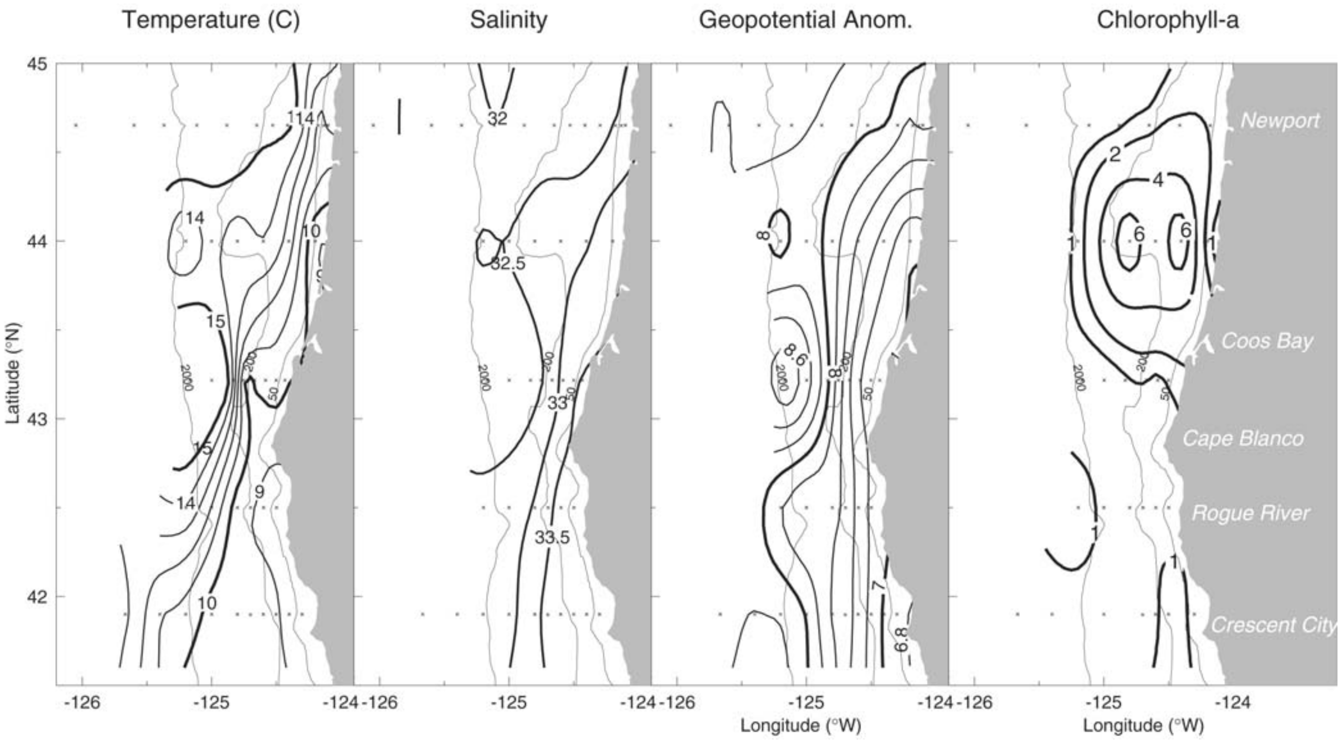

Figure 29. Temperature, salinity, and chlorophyll *a* at 10 m, and geopotential anomaly (J/kg) of the sea surface relative to 500 dbar, 4–10 Sept. 2001.

chlorophyll compared to adjacent waters. Chlorophyll concentrations over the Bank were much higher (>7 mg/l) in September 2001 than in September 2000.

As mentioned earlier, a deepening of the thermocline on the equatorial Pacific, suggestive of an ocean Kelvin wave, reached South America in March 2002. This may have propagated poleward along the North American west coast as a coastal Kelvin wave. The downward translation of isotherms and subsurface warming at a depth of 400–500 m (fig. 26) in April 2002 may represent the arrival of this remote signal. Otherwise, most of the northern CCS during 2001 and early 2002 was not significantly warmer or colder than it was during 1961–71.

BIOLOGICAL PATTERNS

Chlorophyll and Macrozooplankton

Surface maps from recent CalCOFI surveys indicate that chlorophyll *a* concentrations were elevated during 2001 and have been elevated in 2002. Area means of vertically integrated (0–200 m) chlorophyll *a* for each cruise support this conclusion, when compared to past cruise means since 1984 (fig. 10a). The summer and spring 2001 cruise means had the highest and second highest chlorophyll *a* values for their seasons, respectively. The preliminary estimate for spring 2002 is near the seasonal median for this period. Chlorophyll levels in early 2001 and 2002 were also unseasonably high.

These relatively high concentrations of chlorophyll may be part of a longer term tendency of higher production in the CCS. As a preliminary step toward assessing the possibility of a regime shift following the 1997–98 El Niño, we compare the average cruise-mean chlorophyll concentration by season (winter is Jan.–Mar., spring is Apr.–June, etc.) for the 1998–2001 period to the previous two 7-year periods (fig. 30). CalCOFI observations indicate that recent levels are substantially higher than historical values. The spring and summer means for the past 4 years represent a 14% increase from 1991 to 1997, and a roughly 40% enhancement over the period prior to 1991. For reference, summer coastal upwelling at 36°N during 1998–2001 was 27% stronger than during 1991–97.

Cruise mean macrozooplankton biomass has also rebounded in recent years (fig. 10b), especially when compared with the record low biomass during 1998 (Bograd et al. 2000; Durazo et al. 2001). Compared to zooplankton levels prior to 1991, recent biomass values remain relatively modest. However, biomass since 1998 is 20–30% higher than during 1991–97, depending on the season. There is considerable interannual variability within these longer periods. Nevertheless the recent increases in zooplankton biomass and, especially, primary production suggest that monitoring must be sustained to assess whether the postulated regime shift in 1998 continues and is reflected in the biological productivity of southern California.

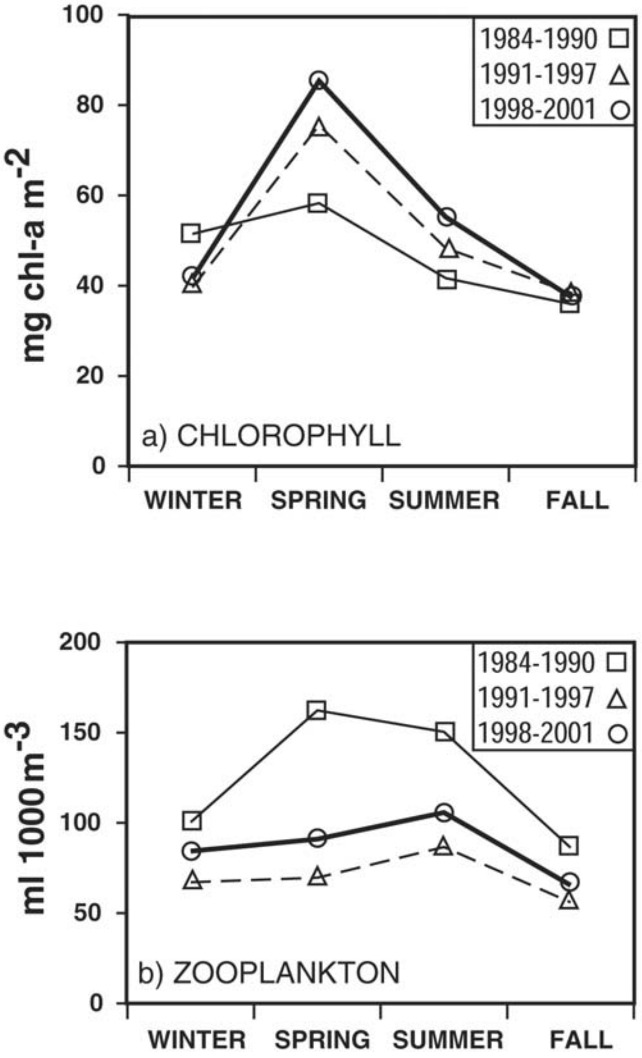

Figure 30. Seasonal averages of (*a*) chlorophyll *a* and (*b*) macrozooplankton biomass from the CalCOFI cruise means, comparing seasonal means for 1984–90 (*squares*), 1991–97 (*triangles*), and 1998–2001 (*circles*).

Analysis of individual salp species collected by CalCOFI nets in the southern portion of the CCS reveals remarkable long-term variations in abundance (fig. 31). The biomass values have been corrected for the 1.68-fold greater abundance of salps collected by the bongo net (post-1977) relative to the ring net (pre-1977; see Ohman and Lavaniegos, this volume). Salps tend to show highly aggregated distributions (Berner 1967; Andersen 1998), hence there is considerable uncertainty associated with biomass estimates. Moreover, the absence of individuals from a species in these springtime collections does not imply that they were not present in the CCS, but only that their abundance was below our detection threshold in this region.

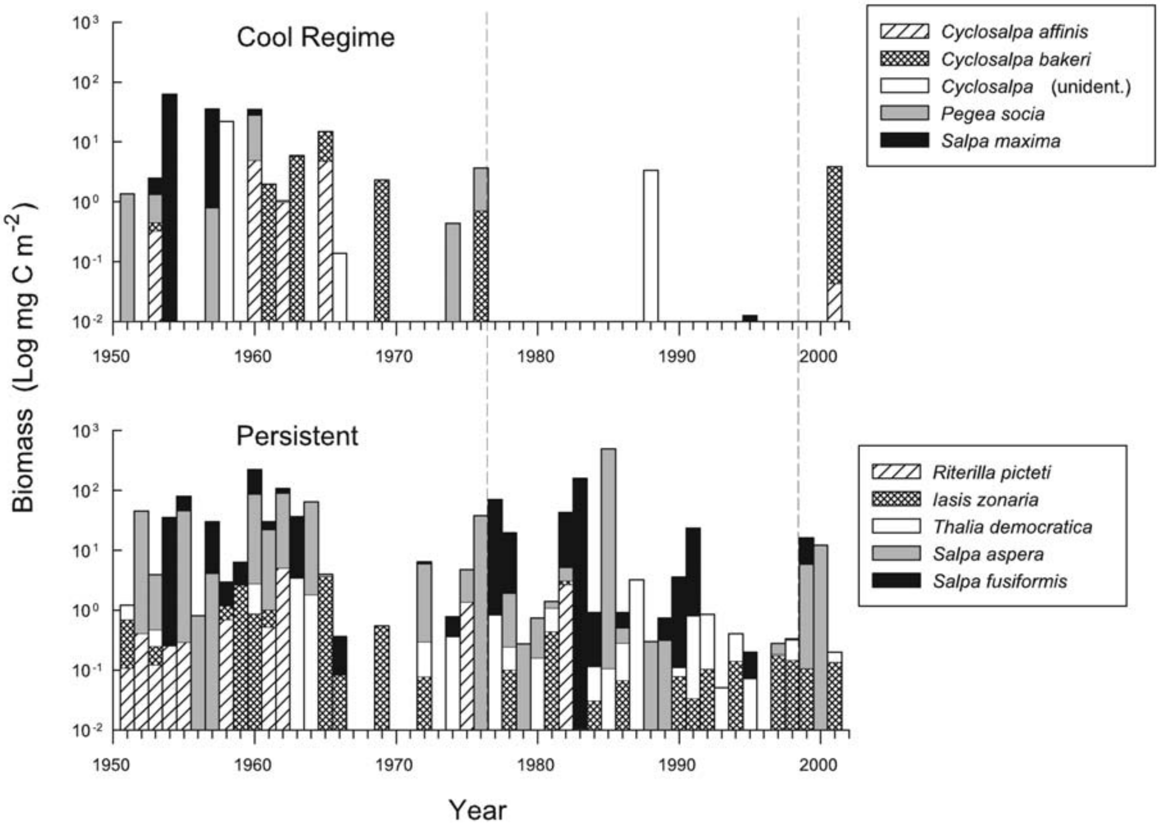

Figure 31. Interannual variation in springtime biomass of nine species of salps from CalCOFI samples in the southern sector of the California Current. The stations analyzed extended offshore to station 70, from lines 80 through 93, inclusive. Dashed lines indicate previously proposed transitions between ecosystem states in the northeast Pacific. Biomass was reconstructed from enumerations by species and size class, with application of length-carbon regressions from Madin and Deibel 1998 and references therein (see also Lavaniegos and Ohman, *Long term changes in pelagic tunicates of the California Current* [manuscript]).

The salps cluster into two species groups. The first group consists of five persistent species (*Ritteriella picteti*, *Iasis zonaria*, *Thalia democratica*, *Salpa aspera*, and *Salpa fusiformis*) that were found irregularly but recurred throughout the 50-year time period. The second group (*Cyclosalpa affinis*, *Cyclosalpa bakeri*, *Pegea socia*, *Salpa maxima*) was markedly abundant from 1951 to 1976, after which all four species became essentially undetectable for 24 years until *C. bakeri* and *C. affinis* were positively identified in spring 2001. An unidentifiable species of *Cyclosalpa* occurred in the spring 1988 samples, and a very small number of *S. maxima* were found in spring 1995. However, most species of this second group were below our detection limits for an extended period of time corresponding to the warm phase of the northeast Pacific associated with a positive PDO and negative NOI (fig. 4) and have begun to reappear in the more recent period since the cooling trend that began in late 1998. Although this analysis is restricted to salps, it suggests that components of the zooplankton assemblage may have changed over time, in addition to the fluctuations in overall biomass seen in the CalCOFI surveys.

In the context of the September 1997–January 2002 IMECOCAL cruises, macrozooplankton biomass values during April 2001 and January 2002 were the lowest in the record (fig. 32). The mean zooplankton biomass of January 2002 was markedly lower than the January 1998 mean, the highest in the IMECOCAL record (1997–2002). This is an atypical response of the Baja California region to El Niño conditions, perhaps due to the increase of subtropical zooplanktonic groups usually inhabiting the sampled area. Regarding the seasonal pattern, we have only information for spring 1999 and 2000, and April 2001 was sampled only in the most northern lines. The mean biomass during the 0104 and 0201 IMECOCAL cruises was lower than the 95% confidence limit of the long-term (1951–84) mean for the CalCOFI cruises. The lowest summer and fall values were obtained during La Niña in 1999, suggesting again the importance of the subtropical component in our study area. Baja California appears to have responded positively during the 1997–98 El Niño but negatively during the 1999–2000 La Niña. The low zooplankton biomass values during 0104 and 0201 are also unex-

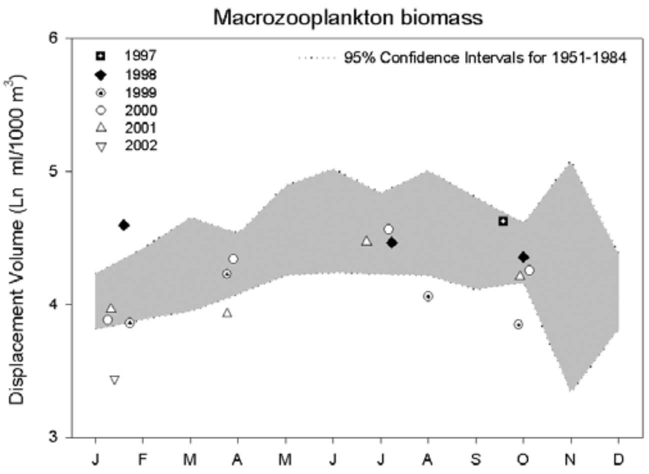

Figure 32. Mean zooplankton biomass of the seventeen IMECOCAL cruises performed from Sept. 1997 to Jan. 2002. The shaded area represents the 95% confidence interval for the historic mean (1951–84) of CalCOFI surveys realized in the area off Baja California. All data were transformed to logarithms.

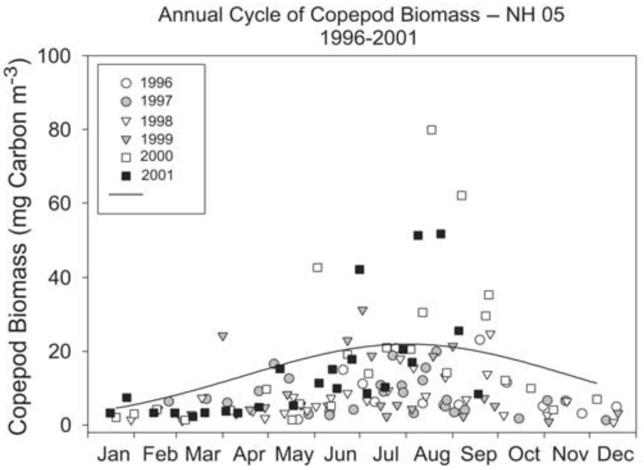

Figure 34. Annual cycle of copepod biomass at station NH 05 (60 m water depth) off Newport, Oregon, shown as a composite for 6 years of data.

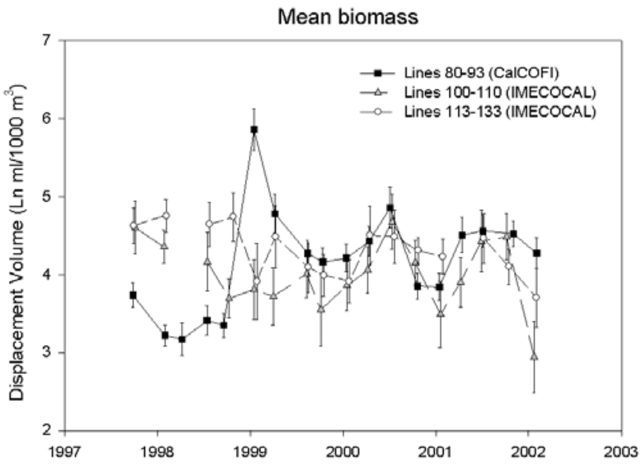

Figure 33. Mean zooplankton displacement volume in three regions of the California Current: CalCOFI surveys (lines 80–93), and IMECOCAL surveys (lines 100–110, and 113–133) performed from Sept. 1997 to Jan. 2002. The bars indicated the 95% confidence interval of the mean.

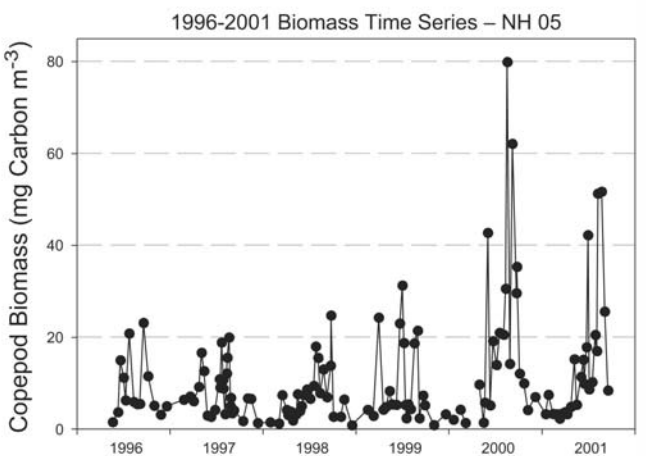

Figure 35. Time series of copepod biomass at station NH 05 (60 m water depth) off Newport, Oregon, 1996–2001.

pected, and further analysis of the taxa composition and biophysical interactions is required to understand these low values. The time tendencies were different between the southern California (Lines 80–93), northern Baja California (Lines 100–110), and central Baja California (Lines 113–133) regions during the 1997–98 El Niño event (fig. 33). In this particular event, southern California waters were poor in zooplankton biomass, but biomass was high in Baja California waters. In contrast, zooplankton biomass remained low in Baja California during the 1998–99 La Niña, while the southern California region experienced a strong rebound.

Oregon Copepod Biomass

The seasonal cycle of copepod biomass at Station 5 (water depth 60 m) on the NH line off Oregon is shown in Figure 34. 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 seen usually in August through October, near the end of the upwelling season. These observations suggest that there is considerable loss of biomass (and production) 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.

Over the period of our 6-year time series (fig. 35), copepod biomass was constant for the first 4 years but has increased by 200% during the past 2 years. Averaged over the period May through September, biomass for the first 4 years of our sampling was approximately 10 mg carbon per cubic meter (9.2 mg carbon per cubic meter in 1996, 9.7 in 1997, 10.1 in 1998, and 11.0 mg per cubic meter during the summer of 1999). Although dramatic changes in species composition did take place in 1999 (Peterson et al. 2002), it was not until summer 2000 that dramatic changes in biomass occurred. Copepod biomass averaged 25.5 mg carbon per cubic meter during that summer and remained high through 2001, averaging 21.5 mg per cubic meter.

What does this mean for the state of the California Current? During 1996 and 1997, and during the 1997–98 El Niño, copepod biomass was low and copepod species that are indicators of productive conditions (i.e., species with affinities for more northern waters) had negative abundance anomalies (Mackas et al. 2001; Peterson and Mackas 2001). The dominant members of this group include species that dominate the waters of the Bering Sea shelf, the coastal Gulf of Alaska, British Columbia coastal waters, and the Washington-Oregon coastal upwelling zone—*Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae*. Species with southern and offshore affinities were unusually abundant in coastal water from 1996 to 1998. This group includes *Mesocalanus tenuicornis*, *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus pergens*, *Clausocalanus arcuicornis*, and *Clausocalanus parapergens*. This suggests that at least during the 3-year period 1996–98 reduced coastal upwelling and low productivity characterized shelf waters of the northern California Current. However, since the onset of cool, La Niña–like conditions, copepod biomass has doubled, and positive anomalies in the abundance of northern copepod species are now the norm for shelf waters off Newport (and off Vancouver Island; Mackas et al. 2001), suggesting increased transport out of the coastal Gulf of Alaska and/or greater coastal upwelling.

Coincidently, 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.[2] Salmon stocks have also increased in abundance, as evidenced by greatly increased survival rates of coho salmon and near-record return rates of chinook salmon. Numbers seen during the past 2 years rival those not seen since the high productive years of the 1960s and 1970s.

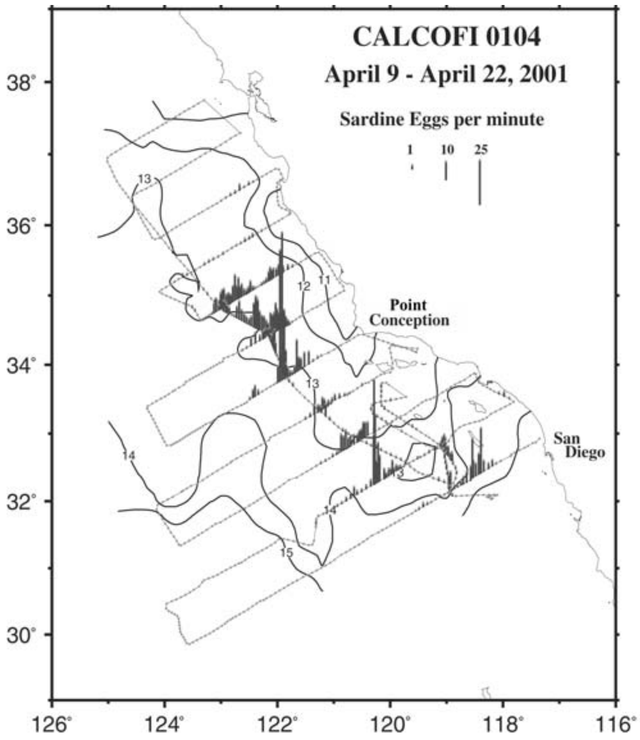

Figure 36. Distribution of sardine eggs as collected by the continuous underway fish egg sampler (CUFES) for CalCOFI survey 0104.

Sardine Spawning

The use of the continuous underway fish egg sampler (CUFES) on CalCOFI surveys, which began in 1996, has served to document the offshore expansion of sardine spawning north of Point Conception (Durazo et al. 2001). During the 1997–98 El Niño, sardine eggs were compressed toward the coast and shifted to the north, presumably in association with a general warming (Lynn et al. 1998). In contrast, eggs observed during the 1999 survey were spread very far offshore, probably in response to strong coastal upwelling, unusually cool waters, and the offshore displacement of the core of the California Current. SST in the entire CCS north of 32°N—the area where most of the eggs occur—was less than 12°C (Durazo et al. 2001). The distribution of eggs in spring 2000 was again relatively extensive along the core of the California Current, and generally farther offshore. However, the cross-shore distribution of high egg counts was not as broad as it was in 1999. SSTs in 2000 were 13–15°C in the spawning area off California.

The April 2001 survey revealed that sardine eggs were once again centered very far offshore (fig. 36), similar to the distribution in 1999. The entire spawning area was located in surface waters with temperatures greater than 12°C, and the peaks straddled the 13°C isotherm.

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[2] Feinberg, L., and W. Peterson. 2002. Year-to-year variations in abundances of euphausiid eggs from 1996 through 2001 in coastal waters off central Oregon. (manuscript)

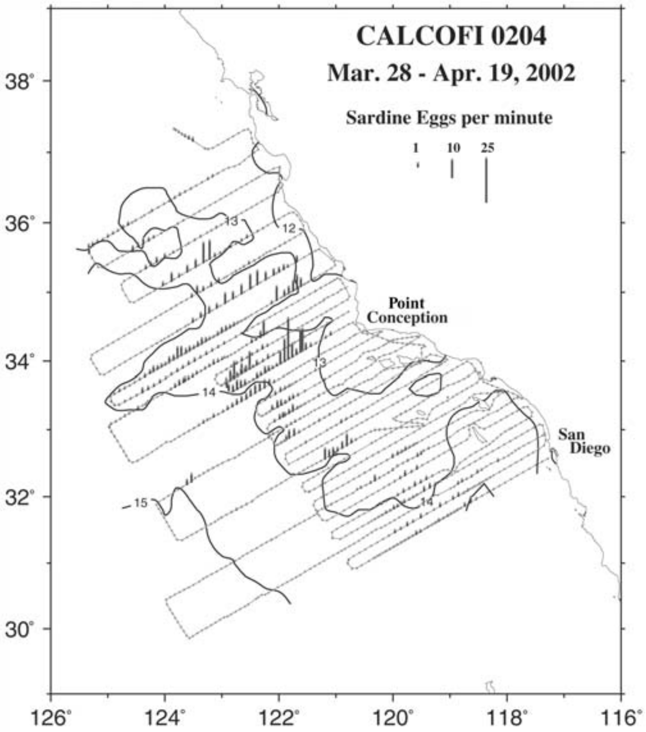

Figure 37. Distribution of sardine eggs as collected by the CUFES for CalCOFI survey 0204.

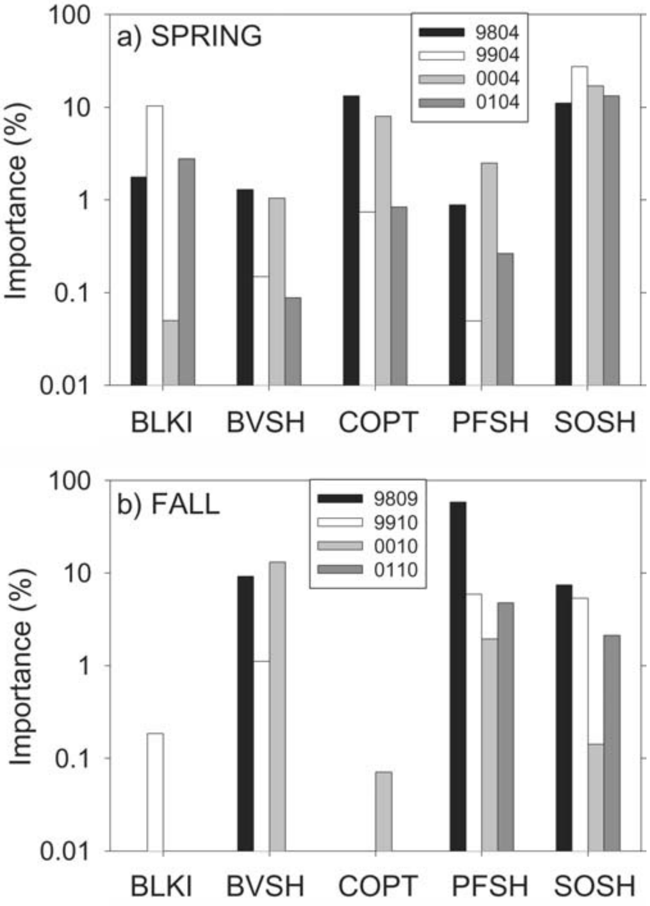

Figure 38. Relative abundance of five seabirds with an affinity for distinct temperature and biogeographic domains off southern California, for (*a*) spring and (*b*) fall surveys, 1998–2001. Importance was computed by dividing the number of individuals of a given species by the total number of seabirds sighted during each cruise. Subtropical/warm-water taxa: black-vented shearwater (BVSH), pink-footed shearwater (PFSH), Cook's petrel (COPT); subarctic/cold-water taxa: sooty shearwater (SOSH), black-legged kittiwake (BLKI).

The area was roughly in the main flow of the California Current and immediately offshore of the salinity front and high chlorophyll zone (fig. 11). In 2001, 13°C SSTs extended much farther offshore than in the previous spring (cf. Durazo et al. 2001). The survey indicated spawning had occurred at least as far south as the U.S.–Mexico border (fig. 36). However, very few eggs were found north of line 73.

As in 2001, the center of the sardine egg distribution in spring 2002 was about 100 km off Point Conception (fig. 37). However, there were several notable differences between the 2 years. Peak values in 2002 were much lower than in 2001, and the overall number of eggs in the survey region may have been reduced. The cross-shore extent over which eggs were found in 2002 was wider, roughly within the 13–14°C isotherms. Eggs were found unusually far offshore along line 77 in what was possibly an upwelling filament, based on its physical character and relatively high surface chlorophyll concentrations (fig. 15). Unlike 2001, when the core of the California Current southwest of the Southern California Bight displayed high counts (fig. 36), very few eggs were found in 2002 south of 33°N (fig. 37). An onshore intrusion of low salinity water was seen along lines 80 and 83 (fig. 15).

Avifauna

At-sea (CalCOFI) surveys of marine bird communities suggest that the changes in community structure observed during 1999 were transient fluctuations, apparently in response to enhanced upwelling and cool water conditions associated with La Niña. By spring 2000, however, the marine bird community reverted back to the preceding warm-water El Niño event (Bograd et al. 2000). This return to a more subtropical community was particularly evident during spring 2000, with a concurrent increase in the relative abundance of three southern species with an affinity for warm water—black-vented shearwater (*Puffinus opisthomelas*), Cook's petrel (*Pterodroma cooki*), and pink-footed shearwater (*Puffinus creatopus*)—and a decrease in the importance of two northern cold-water indicators—sooty shearwater (*Puffinus griseus*) and black-legged kittiwake (*Rissa tridactyla*) (fig. 38a). This

TABLE 3
Comparison of the Productivity of Six Seabird Species Breeding at the Farallon Islands, Central California, in Conjunction with the 1998 Regime Shift

Seabird species	Productivity (chicks fledged/pair) (mean ± SD) (1990–98)	(1999–2001)	Proportional change (%)[a]	Mann-Whitney U	*P* value
Brandt's cormorant	1.38 ±0.93	2.22 ±0.22	+60	4	0.079
Cassin's auklet	0.62 ±0.24	0.90 ±0.13	+45	2	0.033
Common murre	0.66 ±0.27	0.82 ±0.01	+24	10	0.509
Pelagic cormorant	0.54 ±0.64	1.58 ±0.59	+193	2	0.032
Pigeon guillemot	0.54 ±0.38	1.21 ±0.09	+123	2	0.033
Rhinoceros auklet	0.48 ±0.16	0.64 ±0.03	+31	3.5	0.064

[a] The proportional change in seabird productivity was quantified as PC = 100% * [(after) − (before) / (before)]. Positive PC values are indicative of increasing productivity.

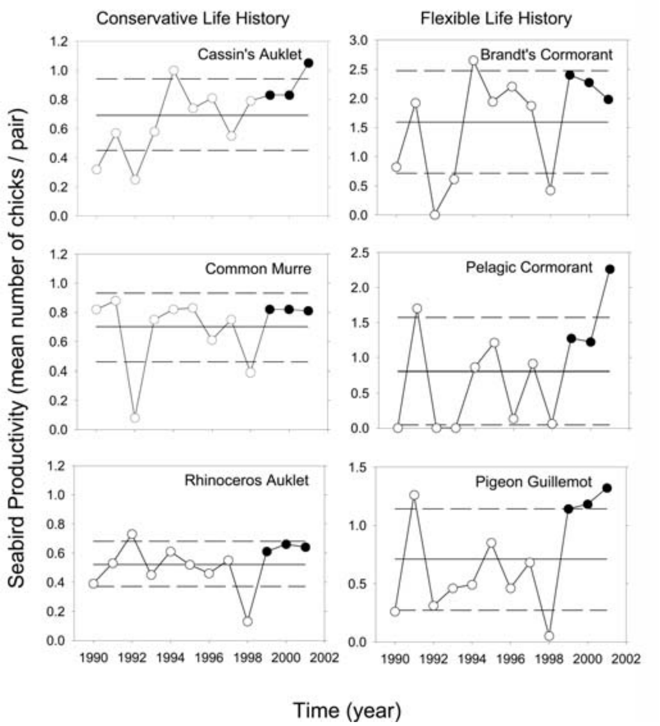

Figure 39. Anomalies of productivity for six seabird species breeding at the Farallon Islands (central California). The long-term averages (1990–2001) are depicted by the solid horizontal lines, and the variability (mean ± SD) by the dashed lines. Solid circles highlight productivity anomalies after 1998.

mixed avifauna, intermediate between the warm-water and cold-water communities observed during the preceding El Niño and La Niña events, respectively, was also evident during fall 2000. This period was characterized by positive (+2–3°C) temperature anomalies off southern California, resulting in the increased importance of subtropical species. Most notably, subtropical Cook's petrels were observed within the CalCOFI region, and the subtropical black-vented shearwater increased to account for over 10% of all birds censused (fig. 38b). Conversely, at-sea observations during spring 2001, when SSTs were near-normal, were suggestive of a subarctic avifauna, with concurrent increases/decreases in the proportional abundance of cold water/warm water (fig. 38).

Prey availability during egg-laying, incubation, and chick-rearing periods influences the reproductive performance of these species (Ainley et al. 1995; Sydeman et al. 2001). Marine bird productivity (mean number of offspring produced per breeding pair per year) provides an integrated measurement of reproductive performance and prey availability to seabirds throughout the breeding season (ca. Mar.–Sept.). Productivity during 2001 was high at the Farallon Islands, central California (fig. 39, tab. 3). In particular, annual mean productivity reached the highest value in the entire time series (1971–2001) for the Cassin's auklet (*Ptychoramphus aleuticus*), with an average of 1.05 chicks fledged per breeding pair. 2001 represents the third consecutive year of positive seabird productivity anomalies across the board.

Productivity data from 2001 continues to show enhanced seabird productivity after the 1998 regime shift (Durazo et al. 2001; PRBO unpublished data). The period 1999–2001 yielded significant increases in the productivity of three seabirds—Cassin's auklet, pelagic cormorant (*Phalacrocorax pelagicus*), and pigeon guillemot (*Cepphus columba*), and marginally significant ($0.10 < p < 0.05$) increases in the productivity of two additional species—Brandt's cormorant (*Phalacrocorax penicillatus*) and rhinoceros auklet (*Cerorhinca monocerata*). Only one species, the common murre (*Uria aalge*), did not display a significant increase in productivity after 1998 (tab. 3).

To assess whether marine bird populations have changed in conjunction with the hypothesized regime shift, we compared the normalized variances in productivity before and after the winter of 1999. Reproductive performance is less variable after 1998 for the six species considered in this analysis (tab. 4). Locally breeding seabird populations have experienced a sustained period of enhanced productivity since 1998 (tab. 3, fig. 39). This pattern contrasts sharply with the large interannual fluctuations and lower overall productivity evident during the preceding warm-water decade (tab. 4).

TABLE 4
Changes in the Dynamics of Six Seabird Species Breeding at the Farallon Islands, Central California, in Conjunction with the 1998 Regime Shift

	Variability of productivity (Coefficient of variation)	
Seabird species	(1990–98)	(1999–2001)
Brandt's cormorant	67.06	9.70
Cassin's auklet	38.45	14.06
Common murre	40.91	0.71
Pelagic cormorant	118.27	37.04
Pigeon guillemot	70.95	7.79
Rhinoceros auklet	33.33	3.950

Note: Variability in seabird productivity during the warm-water (1990–98) and the cold-water (1999-2001) periods was quantified using the coefficient of variation, C.V. = 100% * (SD/mean). A paired nonparametric Wilcoxon test revealed that seabird productivity, when all species were considered, was more variable during the warm-water decade than after 1998 ($Z = -2.201$, $df = 5$, $p = 0.028$).

Hierarchical clustering of the seabird productivity data for 1990–2001 provided more evidence of a shift in 1998 (fig. 40). The first cluster (1990, 1992, 1993, and 1998) is characterized by low overall bird productivity and warm-water conditions (Lynn et al. 1995, 1998; Hayward et al. 1999). Breeding failures were frequent in taxa with flexible life histories (i.e., larger clutches and broader diets), with zero reproductive success in 33% (4/12) of the instances and 67% of the productivity below one chick/pair. Species with conservative life histories (i.e., fewer eggs per clutch and narrower diets) were also impacted during these "bad" years. Overall, 58% of the productivity values for the common murre, the Cassin's auklet, and the rhinoceros auklet fell below 0.5 chicks per pair.

The second cluster included 1994 and 1996, 2 years of intermediate productivity. Two of the species with flexible life histories (pelagic cormorant and pigeon guillemot) had low reproductive success, below one chick per pair, in these years. Conversely, Brandt's cormorant had high productivity, well above two chicks per pair. This species appears to be somewhat buffered from the impact of low ocean productivity by its use of bays and estuaries within a larger foraging range (Ainley et al. 1995; Sydeman et al. 2001). Similarly, taxa with conservative life histories did well during 1994 and 1996, with 83% (5/6) above 0.5 chicks per pair.

The third cluster included all breeding seasons after 1998, as well as 1991, 1995, and 1997. Productivity for species with conservative life histories surpassed 0.5 chick per pair every year, whereas reproductive success of taxa with more conservative life histories exceeded one chick per pair on 83% (15/18) of the instances. These results suggest that breeding seabird populations have responded to the recent shift in conditions in 1998. However, it is not clear how the breeding seasons before and after the winter of 1999 compare. All the years in the second and third clusters were characterized by positive/negative values of the NOI/PDO (fig. 4), suggestive of large-scale cool conditions over the north Pacific.

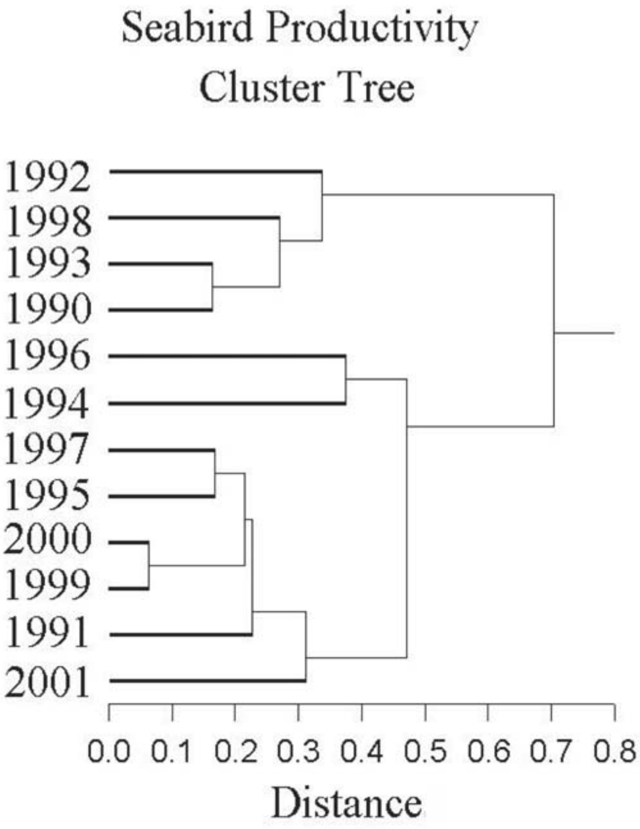

Figure 40. Cluster trees of seasonal marine bird productivity for six species breeding at the Farallon Islands (central California), between 1990 and 2001. The euclidean distances are based on a hierarchical clustering technique using the median linkage algorithm.

Recent colony-based and at-sea observations have provided additional evidence that seabird populations of the CCS responded to the 1998 regime shift. Conditions during 1999–2001 were characterized by episodic increases in the relative abundance of subarctic species at sea (fig. 38) and by enhanced seabird productivity at local colonies (fig. 39). The change in seabird productivity was particularly striking, suggesting that breeding populations have benefited from the prolonged period of enhanced upwelling and ocean productivity after the regime shift (tab. 3). Because seabird populations integrate the variability in ocean and prey conditions during the breeding season, annual mean productivity responds strongly to interannual changes in ocean productivity and prey availability (Ainley et al. 1995; Sydeman et al. 2001). The response of at-sea communities to the regime shift is more difficult to detect. Overall, the seabird community is in an intermediate state with episodic changes in ocean conditions favoring a cold-water community in 1999 and 2001 and a warm-water community in 2000.

DISCUSSION

Most of the physical data from the CCS, from Oregon to Baja California, indicate that 2001 and early 2002 have been uncharacteristically cool and featured stronger than normal coastal upwelling. These anomalous temperatures are part of a pattern that covers the entire Pacific and that is consistent with concurrent atmospheric anomalies. This pattern also represents a continuation of conditions that developed during the 1998–99 La Niña, and is very similar to patterns typically seen during La Niña events (Schwing et al. 2002b), as well as the decadal-scale SST anomaly pattern defined as the negative phase of the PDO (Mantua et al. 1997). Although some signs indicate a new El Niño developing in the equatorial Pacific, it is unlikely to impact the CCS during the productive upwelling season of 2002. Prospects for El Niño in the winter of 2002–2003 are less certain. However, if the climate has shifted to a cooler state in the northeast Pacific, as suggested initially by Schwing and Moore (2000), the coming winter may look much like the previous one.

There is some evidence of a higher level of biological productivity in much of the CCS, based on comparisons of recent chlorophyll concentrations and macrozooplankton biomass to values over the past 19 years. In particular, productivity during the past 4 years has been substantially higher than in the 1990s. Changes in copepod biomass, species composition, spawning, and salmon production point to a major shift in the carrying capacity of the northern CCS.[3] This is possibly aided by more favorable conditions for reproduction by subarctic zooplankton species. The striking change in seabird productivity in the CCS suggests that breeding populations have benefited from enhanced upwelling and ocean productivity after 1998. Marine bird communities respond to changes in ocean temperature within a few months (Veit et al. 1996; Hyrenbach and Veit, in press) because seabirds are highly mobile predators capable of adjusting their distributions in response to transient oceanographic conditions.

Paradoxically, zooplankton concentrations in the waters off Baja California were very low in 2001 and 2002, perhaps because the unusually cool conditions have depressed the numbers of subtropical fauna. During El Niño conditions, this relationship seems to reverse, with higher/lower zooplankton biomass off Baja California/Oregon and California. If subtropical species decline under cooler conditions, then the role of higher primary production in raising total zooplankton biomass (mainly through more subarctic animals) will be mitigated in the southern domain of the CCS. This may be responsible for less prey for sardines, hence a lack of spawning south of about 33°N. At the same time, cooler water could be reducing the spawning habitat from the north (i.e., off Monterey). If this pattern continues for many years—for example, as a "cool" PDO regime—it could lower the sardine population in a pattern reminiscent of the 1940s. Likewise, a cooler CCS is trophically more favorable for seabirds off central California than off southern California.

Although it may be too soon to declare that a regime shift has occurred, it is noteworthy that the present "extended" La Niña is now in its fourth year. Additional research is necessary, however, to determine the mechanisms linking large-scale physical forcing with changes in the availability of prey and the feeding success and reproductive energetics of marine populations.

We are still trying to understand and appreciate the fine distinctions between interannual and long-term climate variability. There is no argument that the CCS and greater Pacific have experienced a series of La Niña–like years since 1998 and these have apparently led to a lengthy period of cooler-than-normal conditions in the CCS and a notable swing in ecosystem structure. What is less certain over this short period (in the climate context) is whether we have witnessed a persistent shift in the state of the CCS or merely a series of weak La Niña and near-neutral years that were a respite from an El Niño–favorable climate state that culminated in the "El Niño of the century " in 1997–98. Change may be afoot once again, as signs of an El Niño appear on the horizon. If this does occur, it will be with a new background characterized by a negative PDO pattern. A natural experiment will take place in the coming months, as interannual and decadal climate processes battle it out for control of future conditions in the CCS.

The future of CalCOFI, and of multidisciplinary monitoring of the California Current in general, has been the subject of intense discussion over the past year. There are important societal rationales for continuing the CalCOFI survey program and even expanding it north toward its historical domain. This is an economically important region for commercial and recreational fishing, shipping, and recreation. Variations in marine conditions impact coastal erosion, water quality, and weather patterns. Intrinsically, the CCS is a vital marine ecosystem that is threatened by overfishing, oil spills and pollution, and harmful algal blooms. Of course, there is a basic scientific motivation for monitoring interannual and longer-term climate variability.

Two meetings have been held (Monterey, Jan. 2002, and Seattle, Mar. 2002) in an attempt to assess and fos-

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[3] Peterson and Schwing. (manuscript)

ter interest in a coordinated CCS monitoring system, resulting in the creation of the Alliance for California Current Ecosystem Observation (ACCEO, <http://swfsc.nmfs.noaa.gov/frd/acceo/acceo1.htm>). Participants at these meetings have agreed on the following mission statement for ACCEO:

> To facilitate and coordinate monitoring of the pelagic ecosystem of the entire California Current, to promote integration of California Current regional pelagic monitoring programs to the larger benefit of all, to understand the dynamics of the California Current and its populations, and to determine how the chemistry and biology of the California Current populations are affected by interdecadal to seasonal changes in physical forcing and water mass distributions.

Discussion also centered on the logistics of a synoptic, California Current–wide monitoring program, leading to the development of a preliminary plan anchored around CalCOFI and other ongoing regional programs (fig. 41). Although there is widespread recognition of the need for such a program, the funding and logistics required to see it materialize are not yet in place. ACCEO will proceed through the collective and coordinated effort of scientists involved in its component programs, as well as through proposals for external funding.

Thanks to some external support, the 2003 January CalCOFI survey will be extended north to San Francisco to cover the lines historically occupied by CalCOFI prior to 1985. This resumption of a major portion of the former January CalCOFI pattern will provide much better coverage of the spawning areas of hake and various groundfish species and will enlarge the survey area for evaluating the 1998 regime shift and monitoring future El Niño/La Niña events. Plans are also forming to conduct baseline plankton surveys of the Cowcod Conservation Area off southern California in February 2003.

There is a clear and urgent need for an integrated sampling program comprising the *entire* California Current System. Observations over the past two decades have shown that variability in the physical environment over a spectrum of time scales—from changes in the seasonal cycle, to El Niño/La Niña events, to regime shifts—leads to a pronounced but varying ecosystem response in different parts of the CCS. A holistic understanding of physical-biological coupling in the CCS requires a synoptic, California Current–wide sampling that the ACCEO plan would only minimally accomplish. A more comprehensive monitoring of the CCS, in real-time, will require the West Coast deployment of a large-scale, multiplatform, moored observation network similar in concept to the TOGA-TAO array in the equatorial Pacific.

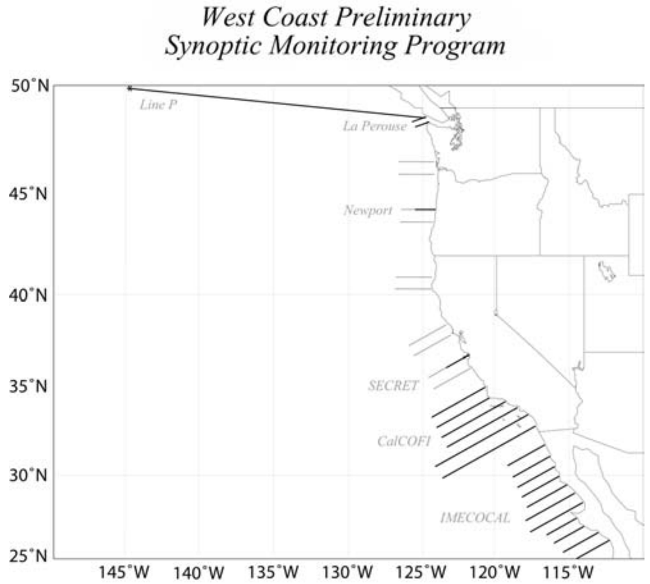

Figure 41. A preliminary monitoring plan for the California Current System, developed for ACCEO discussion in spring 2002. Programs with ongoing ship surveys on standard lines are shown in black. Ten additional lines (gray) have been proposed for U.S. waters (with Canadian participation anticipated), each located near existing marine laboratories to simplify logistics. Proposed lines extend approximately 300 km offshore (varying with latitude to assure sampling of the CCS) and consist of ten stations 30 km apart. Maximum benefit would be achieved with quarterly, synoptic occupations of all lines and sampling following standard CalCOFI protocol.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE, 2001

Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California
6 November 2001

REBUILDING CALIFORNIA'S ABALONE STOCKS

> The red abalone extend in such an abundant quantity along the coast . . . that it would be impossible to materially reduce their number, as they live in water beyond the depth to which a hunter can go; and their habits and methods of propagation are such that the spawn would immediately repopulate a district if it could be fished out, which, however, is impossible.
>
> —Dr. Harold Heath, Stanford University, 1925[1]

Abalone stocks in southern California have been severely depleted since the peak of the fishery in the 1960s and 1970s (Karpov et al. 2000), culminating in the closure of the recreational and commercial fisheries in southern California in 1997 (CDFG Code 5521). Since then, abalone populations have not recovered, indicating the need for a comprehensive restoration program. Population assessments have been hampered by a lack of both current and historic population surveys for fished species, including red abalone (*Haliotis rufescens*), pink abalone (*H. corrugata*), black abalone (*H. cracherodii*), and green abalone (*H. fulgens*), as well as three minor species in the abalone fishery complex. In 2000 a status review of the white abalone (*H. sorenseni*) (Hobday and Tegner 2000) resulted in the listing of this species as the first federally endangered marine invertebrate. The black abalone (*H. cracherodii*) has been proposed for listing, and the threaded abalone (a subspecies of the pinto abalone, *H. k. kamtschatkana*) may now be even more rare than the white abalone.

The reproductive potential of abalones was once thought to render them extinction proof (Heath 1925); however, we now have evidence that this is not the case for abalone (Campbell 2000; Shepherd et al. 2001) or for other marine organisms (Carlton et al. 1999; Roberts and Hawkins 1999). Reproductive failure may occur at any stage during the recruitment process, including fertilization (Babcock and Keesing 1999), larval development, settlement, and postsettlement. Measures of recruitment success suggest that abalones may go for years, sometimes decades, without a major recruitment event (Tegner et al. 1989). A comprehensive understanding of the factors affecting recruitment remains elusive, despite significant interest for nearly a century in the recruitment of marine organisms (Hjort 1914; Houde 1987). We know that survival of juvenile abalone is highly spatially variable, suggesting that site-specific conditions such as predators and food availability are important (Schiel 1993). Spatial patterns in abalone productivity have been quantified using fishery data in an effort to identify prime restoration sites in southern California (Rogers-Bennett et al. 2002). Nearshore sites, however, have been dramatically altered by anthropogenic impacts such as pollution and fishing operations, which may have both direct and indirect effects (Dayton et al. 1998). Indirect effects such as the removal of red sea urchins has been shown to reduce the survival of juvenile abalone (Rogers-Bennett and Pearse 2001; Day and Branch 2002).

In drafting a recovery plan for California's abalone stocks, choices will have to be made from among enhancement options that include aggregation of adults, captive rearing and seeding, and no human intervention. Key information gaps will need to be filled in order to implement an effective restoration program. The white abalone, for example, now exists on deep offshore reefs, but are these remnant populations reproducing successfully or should some of these individuals be collected for captive rearing, and are there enough individuals for aggregation? We have filled one gap through our extensive knowledge of spawning and rearing methods developed by the abalone aquaculture industry (Hahn 1989; McCormick et al. 1994; Leighton 2000). This

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[1] Heath 1925.

may make captive rearing a plausible option for most species of abalone in California (except perhaps black abalone). Yet, many challenges remain for broodstock aggregation and captive rearing, including protecting aggregations from illegal fishing and tracking reproduction (Henderson et al. 1988; Tegner 1992) and maximizing the survival of captive-reared abalone in the wild (Tegner and Butler 1989; Davis 1995; Rogers-Bennett and Pearse 1998; Tegner 2000). Restoration programs will need to address a suite of factors , such as (1) quantifying the success of enhancement programs, (2) investigating the genetic structure of wild and seeded populations, (3) restoring populations within the range of the lethal disease withering syndrome, (4) knowledge of range expansions of sea otter populations, (5) preventing the introduction of diseases and parasites into the wild (such as sabellid polychaetes), and (6) protecting wild and seeded abalone from illegal fishing. While these tasks will be challenging, some populations are at such drastically low levels that what we do or do not do now may dictate the success of our efforts to save California's abalone from extinction.

The articles in this section are based on presentations given at CalCOFI's 2001 symposium, "Rebuilding California's Abalone Stocks."[2] Laura Rogers-Bennett et al. estimate baseline abundances of abalone in the past to help set goals for restoration. Population surveys are rarely conducted prior to the start of a fishery, and perceptions of what baseline abundances were tend to shift downward over time (Pauly 1995; Dayton et al. 1998; Jackson et al. 2001). Abalones are particularly sensitive to ocean temperature and storm conditions, which impact growth, reproduction, and food availability. Alistair Hobday and Mia Tegner report on the results of an individual-based model exploring the effects of sea surface temperature, fishing pressure, and reserve size on two populations of red abalone in the northern Channel Islands. The two model populations decreased during the warm-water conditions of the last 20 years, and fishing intensified this decline. Fishery reserves and larval connectivity, however, ameliorated the decline. Warm-water conditions also enhanced the expression of the lethal disease withering syndrome, which has decimated black abalone populations in southern California. Moore et al. review the current state of knowledge regarding withering syndrome and the implications of this disease for abalone recovery programs. Plans for abalone restoration must take into account the susceptibility of abalone to this disease as well as the distribution of the causative agent (a prokaryote), which is now enzootic in the ocean south of San Francisco. Finally, the information from this symposium, sharing abalone restoration experiences from around the world, coupled with the continued cooperation among multiple agencies, universities, and foundations, will be critical to establishing a comprehensive abalone restoration strategy for California.

The articles presented here were refereed by at least two external reviewers and edited by Laura Rogers-Bennett, John Butler, and Joni Harlan. We wish to thank all the symposium participants for their contributions.

Laura Rogers-Bennett
John Butler

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THE WARM AND THE COLD: INFLUENCE OF TEMPERATURE AND FISHING ON LOCAL POPULATION DYNAMICS OF RED ABALONE

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ABSTRACT

We developed an individual-based, spatially explicit population-dynamics model to explore the effects of temperature, fishing pressure, and reserve size on red abalone (*Haliotis rufescens*) populations at two of the northern Channel Islands off the coast of California. The model locations represent the "warm" Santa Cruz Island, which has a fishing history of declining abalone stocks, and the "cold" San Miguel Island, which has a history of stable catches. We investigated the effects of three temperature scenarios for 100-year periods on the behavior of each population. In the first scenario we used the real temperature environment (sea surface temperature, SST) from the last 100 years; results showed a decline in both model populations over the last 20 years, with and without fishing. In the second scenario model runs using an SST time series generated from current conditions at the islands showed that in the absence of larval connectivity the warm population would go extinct within 75 years regardless of fishing level. The final SST scenario involved a range of constant, potential SSTs that could occur in the future; abalone populations persisted when the SST was between 11°C and 16°C.

The influence of temperature on the model populations and the latitudinal range of suitable SST suggest a northward migration of the real red abalone range as SST increases over the next 100 years. Efforts to rebuild or protect populations for the future should consider which West Coast regions would provide suitable red abalone habitat given rising ocean temperatures.

INTRODUCTION

Abalone are long-lived, broadcast-spawning coastal gastropods that live in relatively predictable and accessible locations (reviewed by Tegner 1989). They are a valuable fishery resource, yet overexploitation has been a problem in every producing country in the world (e.g., Breen 1986; Tegner 1989). California once supported fisheries for five species of abalones, but all commercial harvesting was halted in 1997 (Tegner 2000). One of these over-exploited species, white abalone (*Haliotis sorenseni*), recently became the first marine invertebrate in the United States to be listed as an endangered species under the federal Endangered Species Act (Hobday et al. 2001). Recovery efforts for this and other abalone species are underway in California.

Abalone fisheries have typically been managed by regulating a minimum size for capture, although quotas now exist in regions where harvesting continues (e.g., Tasmania, South Africa, New Zealand). The size-limit approach was intended to allow several years of reproduction before capture was possible. This approach may succeed if recruitment is frequent, but the combination of abalone life-history characters—specifically, long life span and broadcast spawning—indicate that high recruitment does not occur every year (Hobday et al. 2001). Successful reproduction in broadcast spawning invertebrates also depends on proximity between spawning individuals and their gametes (e.g., Pennington 1985; Babcock and Keesing 1998; Levitan 1998; Claereboudt 1999). Intense fishing can increase the distance between neighbors such that fertilization cannot occur, leading to recruitment failure (e.g., Shepherd and Brown 1993; Hughes and Tanner 1998). Recruitment failure over a period of time is likely to lead to dramatic population decline and loss of the fishery resource (Shepherd et al. 1998). Fishing has often borne the sole blame for stock collapse in many regions.

It is important to note that recruitment failure can occur in the absence of fishing, and some investigators suggest that variation in the environment may be a causative factor in irregular recruitment of abalone (e.g., Shepherd et al. 1998). Indeed, the life history characteristics that allow abalone to persist evolved well before human exploitation began, and so irregular recruitment may be a natural process, offset by long-lived adults. The role of the environment has not been clearly demonstrated in the population dynamics of these marine invertebrates, in part because manipulating and monitoring subtidal populations is difficult. Population models are one tool that may improve our understanding of these complex natural patterns (e.g., Claereboudt 1999).

Our goal in this study was to develop a model that incorporated abalone population dynamics, environmental variation, and level of fishing to explore production characteristics of abalone populations. The

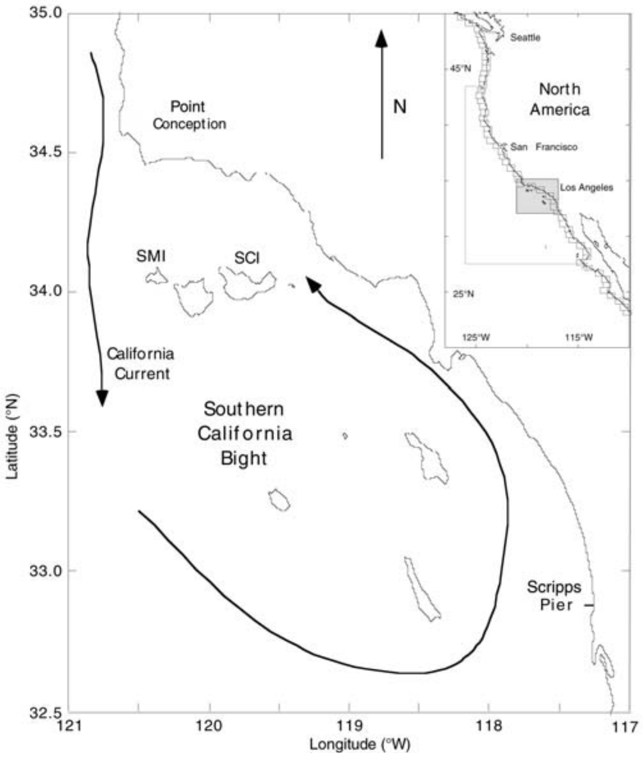

Figure 1. Model abalone populations were located at San Miguel Island (SMI) and Santa Cruz Island (SCI). Shown are the location of the Scripps Pier SST time series and two currents within the southern California Bight (California Current and Southern California Eddy). Inset map shows range of red abalone (*Haliotis rufescens*), from Sunset Bay, Oregon, in the north to Punta Banda, Mexico, in the south; shaded box is area expanded in main panel. Mean monthly SST was extracted from Pathfinder satellite images in each 0.5° latitude box along the West Coast.

model was intended to represent two populations of red abalone (*H. rufescens*)—one at San Miguel Island and the other at Santa Cruz Island, both off southern California (fig. 1). Red abalone have been exploited at these islands since at least 1950 (Karpov et al. 2000). Despite exposure to similar levels of fishing (Karpov et al. 2000), each location has a different catch history. By 1996, commercial catches of red abalone at Santa Cruz Island declined to less than 1% of the peak catch; at San Miguel Island catches were maintained at higher levels and were 23% of the peak catch when the fishery was closed in 1997 (Karpov et al. 2000). San Miguel Island is under the influence of the cold, southward flowing California Current, whereas Santa Cruz Island experiences the warmer waters circulating in the Southern California Bight (Haaker 1994; Harms and Winant 1998) (fig. 1). The difference in water temperature (approximately 1°C) has been suggested as a factor influencing the differences in abalone productivity and harvest sustainability at these two locations (Tegner et al. 1989). Abalone recovery and future management efforts will benefit from a more complete understanding of the influence of fishing and the environment on population dynamics.

MODEL FRAMEWORK AND GOALS

To create an individual-based, spatially explicit population-dynamics model we used MATLAB (from MathWorks). We took this approach because it was important to incorporate fertilization processes at the scale of the individual, and we needed to track the position and size of each individual while it persisted in the population. The model was designed to explore the following scenarios:

1. Given the sea surface temperature (SST) environment at the "warm" and "cold" islands over the last 100 years, what can be observed about red abalone population dynamics? What would have happened to these populations in the absence of fishing?
2. Given recent SST conditions at the islands, and assuming these conditions continue, what would happen to the abalone populations with and without fishing? What would be the effect of a marine reserve on these populations if fishing occurs?
3. If, as seems likely, SST continues to rise for the next 100 years, what is the potential fate of the "warm" and "cold" abalone populations with and without fishing? This scenario will allow "critical SST" to be identified; this has implications for management responses, such as setting SST trigger points for short-term closure if there is a fishery. Results from this scenario may provide guidance for selecting regions where red abalone restoration and reserve efforts should be concentrated, namely, where the SST environment is likely to remain suitable for red abalone into the future.

MODEL PARAMETERS AND ASSUMPTIONS

Model Area and Reserve Proportion

The model domain for each population was a continuous plane 100 m by 100 m (10,000 m^2 = 1 ha) (tab. 1) and was uniformly suitable for abalone. This area represents between 1% and 10% of the red abalone habitat at each island and is the size within which recruitment is driven by local abundance (Prince et al. 1987). The model was initiated by randomly allocating 1,000 abalone of random size and sex to each area. A portion of each area could be protected from fishing (tab. 1). Abalone larger than the legal harvest size could only be removed by fishing from the nonreserve portion.

Abalone Size

Settlement size of abalone was set at 1 mm (Shepherd and Daume 1986). First-year growth was not calculated; abalone were assumed to recruit throughout the year

TABLE 1
Parameters and Values Used in the Abalone Model

Parameter	Value	Reference
General		
Fishing mortality	Range: 0–70% per year	
Larval connectivity	0 or 5%	Tegner and Butler 1985; Hobday 2000
Reserve fraction	0 or 25%	
Habitat quality	Uniform	Tegner et al. 1989
Model area	10,000 m^2	
Maximum adult density	0.1 m^{-2}	Davis 1995; Guzman del Proo 1992; Tegner et al. 1989; Karpov et al. 1998; Karpov et al. 2001
Maximum adult population	Area x max. adult density	
Initial population size	1,000	
Size and growth		
Settlement size	1 mm	Shepherd and Daume 1996
Maximum first-year size	30 mm	Davis 1995; Tegner et al. 1989
Emergent size	80 mm	Tegner et al. 1989; Karpov et al. 1998
Adult size	90 mm	Owen et al. 1984
Harvest size (commercial)	197 mm	Haaker et al. 1998; Tegner et al. 1989.
Maximum size, $L\infty$	225 mm	Haaker et al. 1998; Tegner 1989
K (von Bertalanffy)	0.27	Tegner et al. 1989
± SE (in K)	0.03	Haaker et al. 1998
Fecundity	$F = aL^b$	
a	0.0004650	Tegner et al. 1989
b	4.518	Tegner et al. 1989
Fertilization		
Lowest rate	0	
Highest rate	90%	*Haliotis laevigata*; Shepherd and Partington 1995; Babcock and Keesing, 1999
Fertilization radius	4 m	*Haliotis laevigata*; Babcock and Keesing 1999
Survival		
Larval survival	0.0001	unknown
Juvenile survival	50%	Davis, 1995; Tegner and Butler 1985
Adult survival	85%	Tegner et al. 1989
Density-dependence settlement	0.5 max. adult density	unknown
Environmental effects		
Optimum adult SST for growth and survival	12°C	Haaker et al. 1998; Tegner et al. unpubl.
Optimum larval SST	15°C	Leighton 1974; Ebert and Hamilton 1983
Optimum fecundity SST	12°C	Owen et al. 1984
Larval period	Year-round	Boolootian et al. 1962; Davis 1995
Fecundity period	Year-round	Leighton 1974; Boolootian et al. 1962

Note: Values, discussed further in the text, are for red abalone, *Haliotis rufescens*, unless otherwise noted.

(Leighton 1974; Davis 1995), and initial size at the end of the year was a random size between settlement size and the maximum observed size after 1 year, 30 mm (Leighton 1972; Davis 1995) (tab. 1). Sex was randomly assigned to each settled abalone, mimicking a 1:1 sex ratio, as is the case for most large abalone populations (e.g., Tegner et al. 1989; Shepherd et al. 1995).

Abalones initially occupy cryptic habitats when they settle and later emerge to a more exposed position (Cox 1962). Red abalone become emergent at 70–80 mm (Tegner et al. 1989; Karpov et al. 1998); an emergent size of 80 mm was used here to represent the size when survival changed from the juvenile to the adult level (tab. 1).

Adult size, when sexual maturity occurs, is reached at approximately 60–90 mm for red abalone (Owen et al. 1984). A size of 90 mm was used in this model. In the 1980s and 1990s, when the California abalone fishery was still operating, commercial size for red abalone harvest was 197 mm (Haaker et al. 1998). The legal size for recreational harvest was smaller, but the catch by noncommercial fishers was minor (Karpov et al. 2000) and not considered in this model.

The maximum size of red abalone has been reported to be 300 mm (Cox 1962); however, growth models for red abalone in southern California typically report maximum size as about 200 mm (e.g., Tegner et al. 1989; Haaker et al. 1998). A maximum size of 225 mm was used in this model, as it allowed abalone to grow large enough for legal harvest.

Growth

The Von Bertalanffy growth equation is commonly used to describe abalone growth (e.g., Day and Fleming

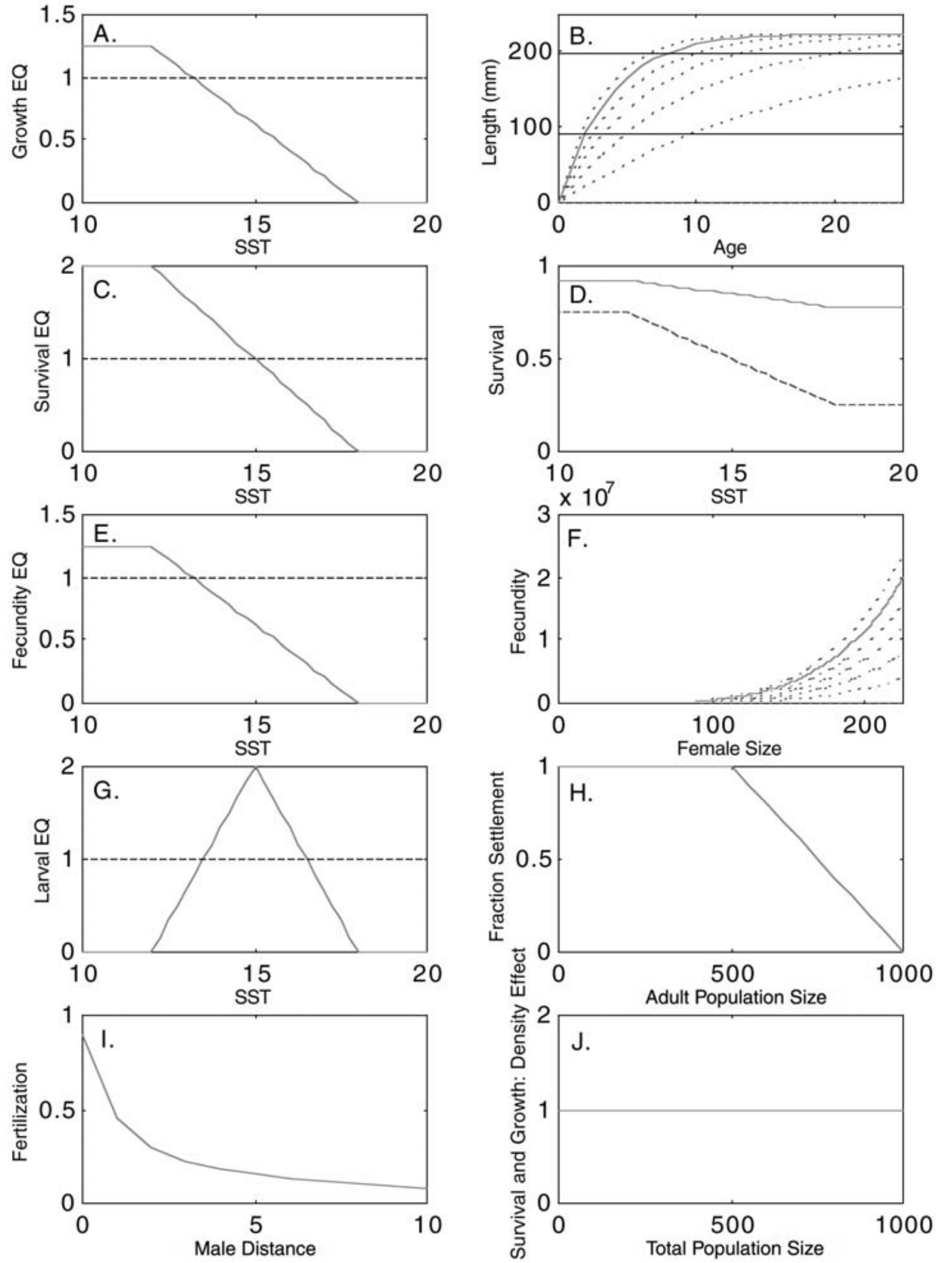

Figure 2. Influence of SST on model parameters: *A*, growth rate multiplier as a function of SST. *B*, growth relationships for a range of environmental qualities, with the lowest dashed line indicating lowest quality, and the solid line representing the base condition. *C*, survival multiplier as a function of SST. *D*, actual survival for juveniles (*solid line*) and adults (*dashed line*) as a function of SST. *E*, fecundity multiplier as a function of SST. *F*, size-fecundity relationships for a range of environmental qualities; dashed lines represent a range of environmental qualities, and the solid line represents the base condition. *G*, larval survival multiplier as a function of SST. *H*, proportion of recruit settlement as a function of adult density; the proportion of recruits that settle declines linearly from 1 to 0 between half and the maximum adult density. *I*, proportion of eggs fertilized by a single male as a function of distance from the female. *J*, juvenile and adult survival rates are independent of adult density.

1992) and was used in this model. Variation in the growth rate constant, K, was selected randomly for each individual each year from a normal distribution with mean of 0 and a maximum value of 0.06, after considering the range of values in Haaker et al. (1998).

The SST influenced *K*, increasing it in "good" years and decreasing it in "bad" years, according to a year-quality scaling factor ranging from 0 to 1.25 (fig. 2a). Thus, the minimum value for *K* was 0 at high SST, and the maximum value was 1.25 times the "normal *K*" at low SST (fig. 2b). Optimum growth for red abalone has been reported at high SST (15–18°C) (Leighton 1974), but a value of 12°C was used here based on recent work by Haaker et al. (1998) and Tegner et. al.[1]

Survival

Postsettlement juvenile and adult survival were set at an annual baseline value of 50% (Tegner and Butler 1985; Davis 1995) and 85% (Tegner et al. 1989), respectively (tab. 1). The SST environment influenced both survival values in the model, linearly increasing or decreasing baseline mortality (1-survival) by up to 50% for good and bad years, respectively (fig. 2c,d). Each year, each abalone was randomly allocated a survival probability from a uniform distribution (value 0–1). Individuals that had a survival probability greater than the mortality level were retained.

Fishing and Catch

We investigated a range of fishing levels (0–70% of all surviving legal abalone caught per year) and used the survival probabilities for each abalone to "catch" animals if fishing was included in the model. Abalone larger than legal harvest size (and not in the reserve portion, if it existed) were removed from the population if the individual survival value was less than the sum of the fishing level and the population survival value (i.e., fishing occurred after natural mortality). Exploitation was thus randomly distributed over the model area, which is reasonable given the scale of this model. Fishing began at year 50 in each model run to allow extinction to occur in the absence of exploitation. There was no poaching or mortality of undersized (sublegal) abalone due to fishing in the model, although the model could be adjusted to include this variation if such information existed.

Fecundity

Abalone fecundity is related to female size and in the model is described by the commonly used relationship

$$E = aL^b \tag{1}$$

where E is individual fecundity (number of eggs), L is female length, and a and b are constants fit to data (e.g., Shepherd et al. 1992). These constants were available for red abalone (tab. 1). Red abalone are fecund year-round off southern California (Boolootian et al. 1962; Leighton 1974) except in warm years (Cox 1962). Fecundity was influenced by SST in the model; individual female fecundity was multiplied by a scaling factor of 0–1.25, according to the fecundity year quality, Q_F (fig. 2e,f).

Fertilization Success

Fertilization success in broadcast spawning marine invertebrates is influenced by a number of factors, including the local density of each sex, water movement, degree of synchrony, and sperm and egg densities (e.g., Levitan and Sewell 1998; Levitan 1998; Claereboudt 1999). In population models, fertilization success has most often been calculated using the overall density of adults or the distribution of cluster sizes (e.g., Shepherd and Partington 1995). If a more biologically realistic local distribution is used, the number and distance of males surrounding each female is required, and this local distribution needs to be translated into a proportion of eggs fertilized during spawning. Most information exists for echinoderms (e.g., Pennington 1985; Levitan et al. 1992), but there are a few abalone studies (e.g., Levitan and Sewell 1998; Babcock and Keesing 1999) though none specific to red abalone. Declining fertilization success with increasing male-female separation has been generally observed. For example, fertilization success in *H. laevigata* dropped rapidly with increasing distance from the sperm source, from a high of 80–97% at 0 m to a low of 3% at 16 m (Babcock and Keesing 1999). The effect of increased male abundance (aggregation) close to the spawning female is less well understood. The closest male that spawns will likely have the highest fertilization rate, but males farther away may also contribute to fertilization of the remaining unfertilized eggs.

In this model we used the local abundance of male abalone to estimate female fertilization success. The fertilization relationship was based on a number of studies, though none specific to red abalone (Pennington 1985; Shepherd and Partington 1995; Babcock and Keesing 1999). The distance of all males within the fertilization radius of each female (tab. 1) was determined and these female-male distances ranked. The contribution of the closest male to fertilization of the eggs declined with distance according to the relationship

$$F = [1/(d_m + 1)] \cdot F_m \tag{2}$$

where F is the proportion of eggs fertilized, d_m is the distance to that male, and F_m is the maximum fertilization rate (fig. 2i). Subsequent males were evaluated individually by distance from the female, and the remaining portion of unfertilized eggs was fertilized according to equation 2. The total fertilization was obtained by summing the contribution of each male. The model assumed that each female spawned annually, and spawning synchrony between each female and the males within the fertilization distance was 100%.

Abalone aggregation may occur during the spawning season (e.g., *H. laevigata*; Shepherd 1986), although evidence is inconclusive for this behavior in red abalone.

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[1] M. Tegner., K. Riser, and L. Vilchis, unpubl. data.

In the model there was no movement or aggregation after abalone settlement.

Larval Survival, Duration, Connectivity, and Settlement

Larval survival is unknown, and values of 0.01–0.0001% were tested in this model to allow some population persistence in the absence of fishing before a single base value was selected (tab. 1). This base larval survival was influenced by the year quality (Q_L) in the model; it was highest at 15°C and declined linearly to zero at 15°C ± 3°C (fig. 2g). This is the SST range within which red abalone larvae survive (Leighton 1974).

Larval connectivity between the two islands is unknown. Studies by Tegner and Butler (1985) using drift cards, and Hobday (2000) using satellite-tracked drifters, indicate less than 5% of larvae at the surface would disperse between populations on San Miguel and Santa Cruz Islands within the larval duration. Larvae may be benthic, which would further restrict dispersal. There is evidence for local, but not delayed, settlement in abalone (Prince et al. 1987). The likely scale of dispersal is less than 100 m for larvae that are close to the bottom with a larval duration of 4–7 days (Prince et al. 1987; but see Shepherd et al. 1992), which is the lifetime for red abalone (Leighton 1974; Jaeckle and Mananhan 1989). In this study, connectivity (*C*) between populations was fixed in each run at either 0 or 5% (tab. 1).

Recruitment of red abalone has been reported as occurring throughout the year (Boolootian et al. 1962; Davis 1995). Settlement of red abalone at small scales does not seem to be influenced by the presence of adults, but given dispersal patterns it is likely to be from local sources. In this model, larvae settled at random locations in each model area, were randomly designated male or female, and were given a size between settlement size and maximum first-year size (tab. 1), which simulates continuous settlement. Overall, the number of recruits produced by each population was

$$R_{\text{local}} = \sum(E \cdot F) \cdot S_L \cdot Q_L \tag{3}$$

where *E* is the individual fecundity, *F* the fertilization success of individual females, S_L the larval survival, and Q_L the scaling factor for the larval environment quality. The total number of recruits to each population is the sum of the local recruits plus the proportion due to larval connectivity (*C*) between the populations:

$$R_{\text{total}} = R_{\text{local}} + C \cdot R_{\text{other}} \tag{4}$$

Maximum Density

The maximum density of red abalone under natural conditions is highly variable (e.g., Karpov et al. 2000) and is complicated by surveying problems, predators, fishing or poaching, and regional or local variation (e.g., Karpov et al. 1998). The overall density of abalone in the model was constrained at adult densities greater than 0.1 adults per square meter (Tegner et al. 1989; Guzman del Proo 1992; Davis 1995; Karpov et al. 1998), with settlement not allowed (tab. 1). Density dependence in settlement also occurred below this maximum adult density, with recruitment declining linearly from a factor of one at half the maximum adult density to zero at the maximum adult density (fig. 2h). Density did not influence growth or survival (fig. 2j). Biologically, this model condition represents lack of space and bulldozing by adults, either at settlement or when juvenile abalone become emergent.

Environmental Data

The current SST scenario data for the islands represented in the model was monthly SST from National Weather Service SST analyses between 1982 and 1999[2] averaged to create an annual time series. Because this SST dataset was only 18 years long, 8-year segments were randomly selected and appended to simulate 100-year time series. This preserved some of the structure of interannual variation in the SST signal. New SST time series were generated for each run of the model.

The longest historical SST time series available for southern California is from the Scripps Institution of Oceanography Pier (1920–98). We increased the length of this time series to 100 years by adding the first 22 years to the beginning of the time series. We then used this time series to simulate the last 100 years of SST conditions at the islands by adding the mean difference between each island and the Scripps Pier time series for the overlapping period (1982–98) to the whole Scripps Pier time series. Finally, future SST scenarios were evaluated using 100-year constant-value SST time series between 11°C and 18°C, in 0.5°C increments.

For each scenario we calculated the year quality factor for juvenile and adult growth and survival using the annual SST for each population. For fecundity and larval survival we used the mean SST value for the fecundity and spawning months (Jan.–Dec. for red abalone) to determine the year quality factor (tab. 1 and fig. 2). Year quality values greater or less than 1 adjusted the base parameter values explained earlier and represented "good" and "bad" conditions, respectively.

Using satellite SST data for the west coast of North America we explored the potential latitudinal ranges for red abalone under future SST conditions. The data were extracted from the NOAA Pathfinder monthly data set for the period 1987–99 (http://podaac.jpl.nasa.gov). The

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[2] J. Engle, unpubl. data.

median SST for 0.5° latitude boxes extending 0.5° offshore (fig. 1) was found each month and averaged to provide annual values by latitude.

Model Experiments and Runs

Each model run was for 100 years with the population characteristics updated each year. Ten replications of each run were undertaken for each set of parameter values. The parameter values we investigated in detail were fishing level, larval connectivity, and reserve size. Simulation experiments were chosen that would represent the range of choices that might be possible through management decisions, such as creating a reserve area, and to show the impact of fishing.

We conducted three experiments for the past 100 years and for current SST environment scenarios:

1. Range of fishing levels (0–70%), no larval connectivity, no reserve area
2. Range of fishing levels (0–70%), 5% larval connectivity, no reserve area
3. Range of fishing levels (0–70%), 5% larval connectivity, 25% reserve area

For future SST scenarios, we conducted four experiments:

1. No fishing, no larval connectivity, no reserve area
2. No fishing, 5% larval connectivity, no reserve area
3. 30% fishing level, 5% larval connectivity, no reserve area
4. 30% fishing level, 5% larval connectivity, 25% reserve area

Model Output

Output from the model simulations for each population included the mean and final total adult and legal abalone population sizes, proportion of recruits from the local population, mean year quality, frequency of and mean time to extinction, proportion of females with eggs fertilized, number of years with fertilization and recruitment, and total catch. Population sizes are reported as numbers of individuals; these can be converted to densities (individuals per square meter) by dividing by the model area (10,000 m^2).

RESULTS

Differences in the SST Environment

The mean annual SST using the in situ time series between 1982 and 1998 was 14.8°C at San Miguel Island and 15.8°C at Santa Cruz Island. During this period, the Scripps Pier SST was 2.04°C warmer than Santa Cruz Island (r = 0.72) and 3.02°C warmer then San Miguel Island (r = 0.71) (fig. 3). The difference for each island was subtracted from the Scripps Pier SST to create the past 100-year time series for each island population.

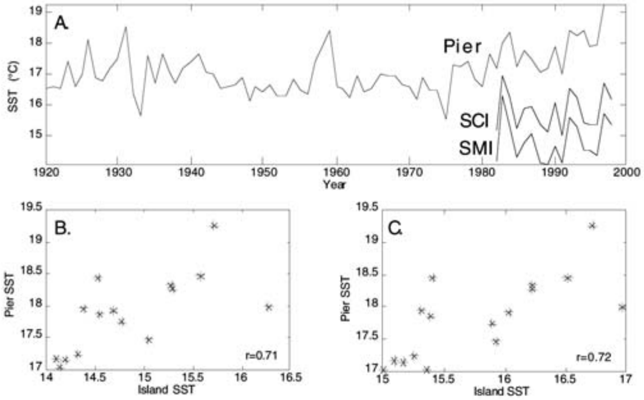

Figure 3. Real SST time series: *A*, annual Scripps Pier SST and island SST; *B*, relationship between San Miguel Island and Scripps Pier SST (1982–98); *C*, relationship between Santa Cruz Island and Scripps Pier SST (1982–98).

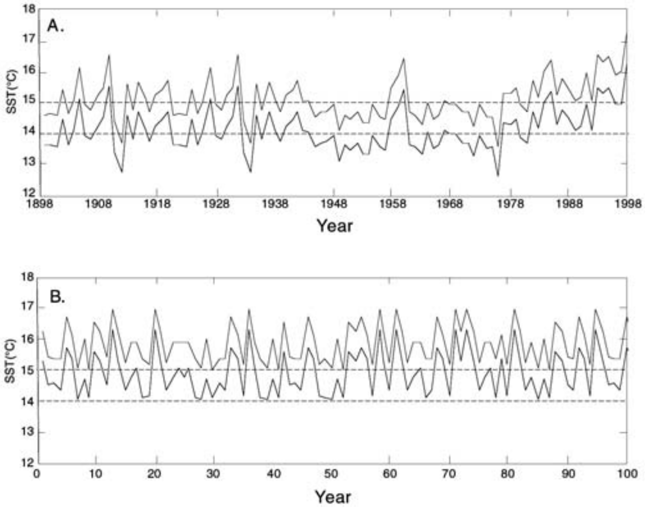

Figure 4. SST time series: *A*, scenario 1. *B*, scenario 2; the upper (lower) time series in each panel is SST at the warm (cold) location. The upper dashed line on each panel represents the SST optimal for larval survival; the lower dashed line represents the SST that divides good and bad conditions for postsettlement survival, growth, and fecundity.

Scenario 1: Last 100 Years

The SST time series for the last 100 years had warm and cold events but the temperature was reasonably stationary until about 1976, when it began to increase steadily (fig. 4a). The mean year quality during this period for the warm Santa Cruz Island was 1.15, and 1.47 for the cold San Miguel Island (fig. 5o). Appendix 1 shows a representative model run, with fishing removing 30% of the surviving legal animals each year and 5% larval connectivity. The decline in the size of the "warm" population occurred as the SST increased over the last 20 years and was also observed in the absence of fishing. ***Range of fishing levels, no larval connectivity, no reserve.*** The level of fishing exploitation ranged from 0 to 70% of surviving legal abalone removed each year. The cold population size was larger than the warm population at

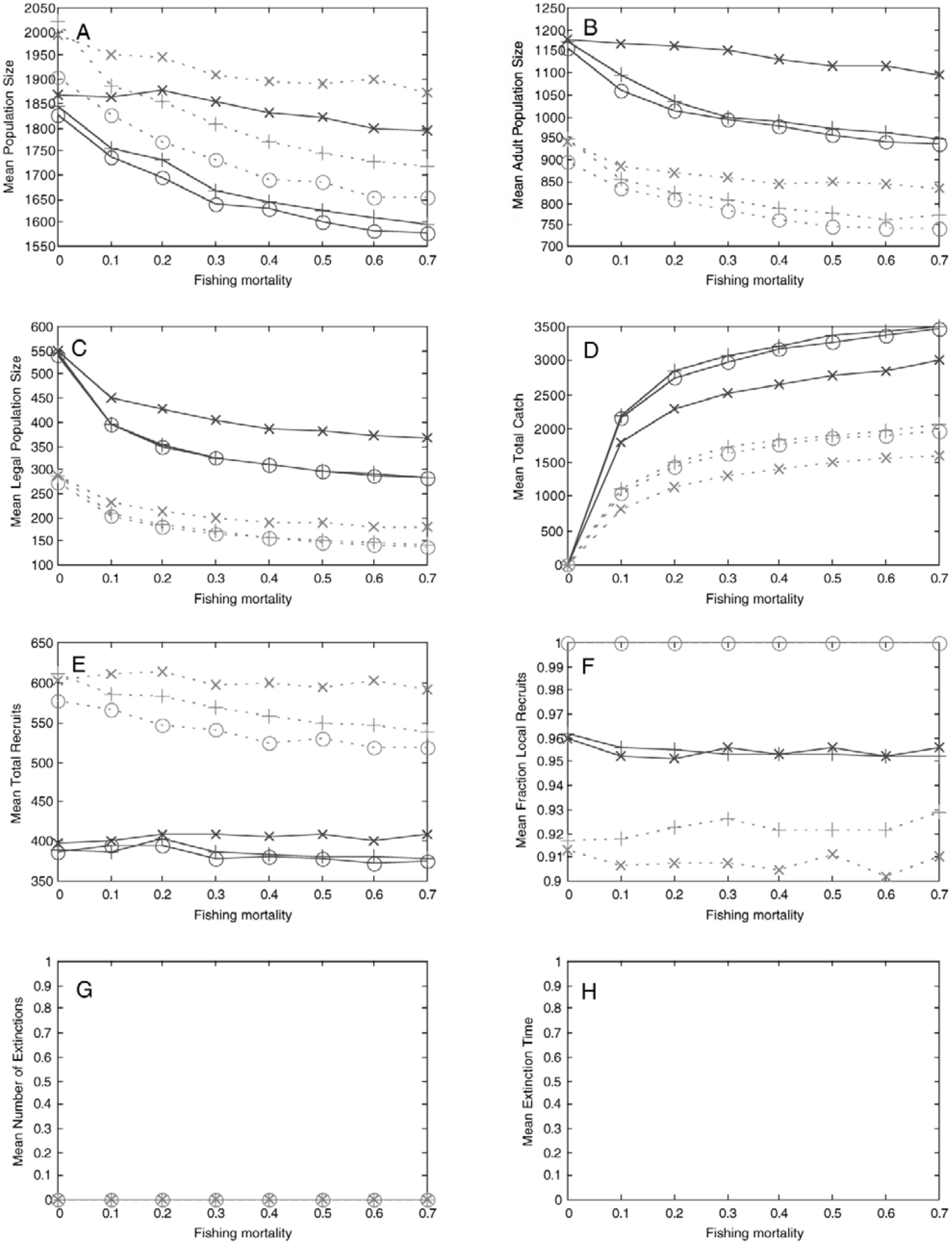

Figure 5. Scenario 1. Population dynamics based on the last 100 years of SST at the warm (*dotted*) and cold (*solid*) islands for a range of fishing levels. Symbols on each line refer to the version of the scenario. (o) no larval connectivity, (+) 5% larval connectivity, and (x) 5% larval connectivity and 25% reserve area.

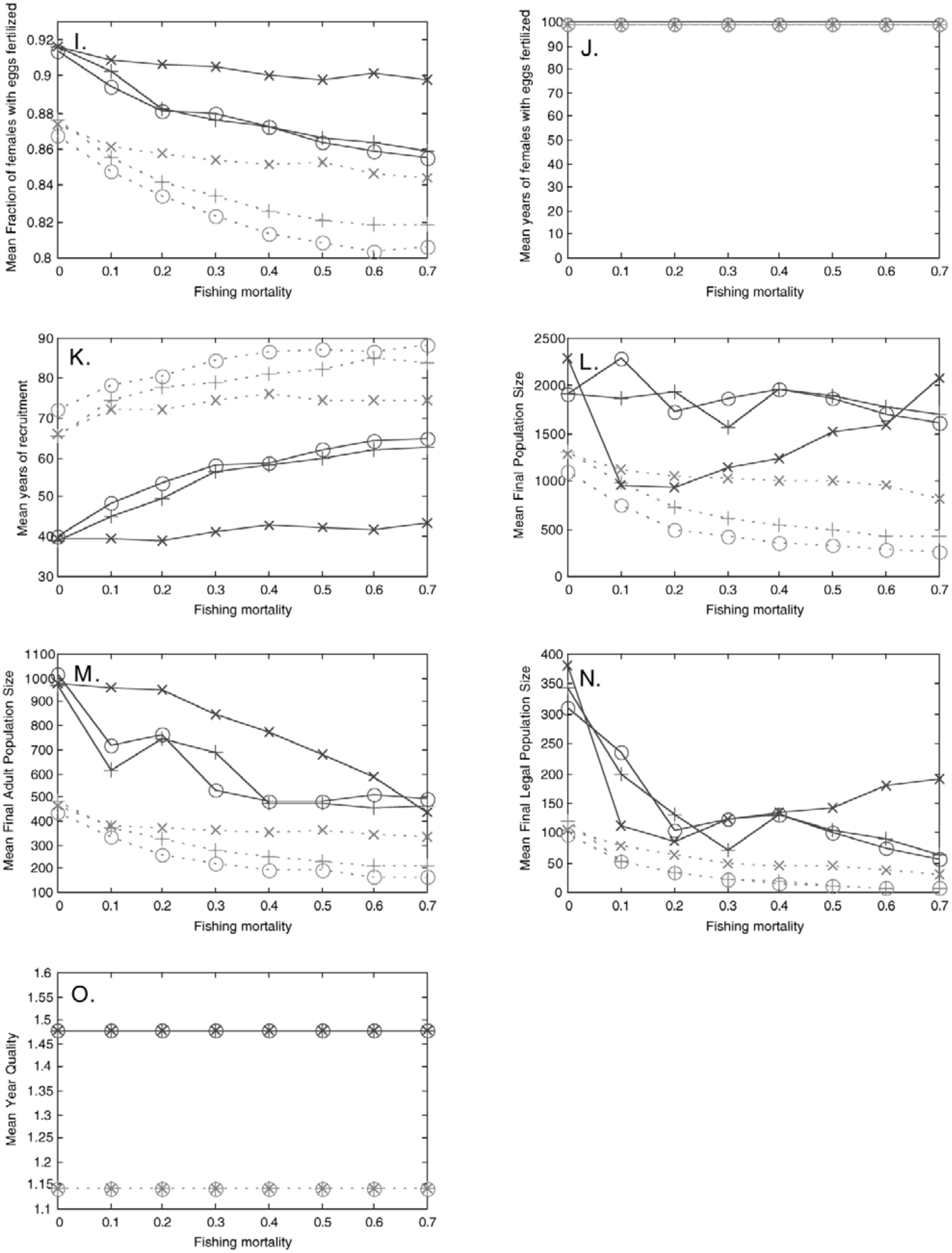

Figure 5. *Scenario 1, continued.*

all levels of fishing exploitation. Mean total, adult, and legal population sizes decreased with increasing fishing level, and the decline in adult and legal population size was lower at fishing levels above 30% removal (fig. 5a–c). Total catch increased with fishing level, although the increase was small above the 20% fishing level (fig. 5d). The warm population had a higher average number of recruits (fig. 5e), because the smaller size of the adult population allowed more density-dependent settlement. The average number of warm recruits declined with increasing fishing level but for the cold population remained similar at all fishing levels. All recruits were from the local population because there was no larval exchange in this experiment (fig. 5f) and there were no extinctions in either population (fig. 5g,h). The proportion of females with eggs fertilized was higher in the cold population (fig. 5i) with a larger adult population size, and this proportion decreased in both populations as fishing level increased. Eggs from at least some females were fertilized in all years (fig. 5j). The number of years in which recruitment occurred actually increased with increasing fishing pressure (fig. 5k) because the reduction in population size allowed settlement to occur more often. The final total, adult, and legal population sizes were higher for the cold population, and the size of both populations declined with fishing pressure (fig. 5l–n). Little further decline occurred at fishing levels above 30%. In the warm population, the final population size of legal animals was very low above this fishing level.

Range of fishing levels, 5% larval connectivity, no reserve. With the inclusion of larval exchange in the models using the last 100 years of SST data, there was a reduction in the decline of the warm population representing Santa Cruz Island. At all levels of fishing the size of the cold population was still larger than the size of the warm population; however, the population size patterns were very similar to those observed when there was no larval exchange (fig. 5a–e). With no fishing the cold and warm populations supplied about 96% and 92%, respectively, of their own recruits; this remained constant across the range of fishing levels (fig. 5f). There were no extinctions in either population (fig. 5g,h). The proportion of females with eggs fertilized was higher in the cold population, although the proportion decreased with increased fishing level as for the models without larval exchange (fig. 5i), and eggs from at least some females were fertilized in all years for both populations (fig. 5 j). The number of years in which recruitment occurred increased with increasing fishing pressure (fig. 5k). The final total, adult, and legal population sizes were larger in the cold population and declined in both populations when fishing level increased (fig. 5l–n). The final population sizes were slightly larger in this experiment than in the one without larval exchange.

Range of fishing levels, 5% larval connectivity, 25% reserve area. For both populations, including larval exchange and reserving part of the model area from fishing did not prevent declines in the mean total, adult, and final population sizes as fishing level increased. The adult and legal population sizes were still larger in the cold population than in the warm population at all levels of fishing; however, both populations were larger than when there was no reserve (fig. 5a–c). The total catch was less than it was in cases without a reserve across the range of fishing levels (fig. 5d). Patterns of total recruits and proportion of local recruits were similar to the preceding case, although the proportion of local recruitment was slightly lower at all fishing levels (fig. 5f), indicating that each population was less self-dependent. As for the two previous cases, extinction did not occur in either population (fig. 5g,h). The proportion of females with eggs fertilized was higher in the cold population than in the warm (fig. 5i); however, both populations had a higher proportion of females with eggs fertilized compared with the nonreserve cases. As before, eggs from at least some females were fertilized in all years for both populations (fig. 5j). The number of years in which recruitment occurred increased with increasing fishing pressure (fig. 5k) but was lower than the nonreserve cases because of the larger adult population and density-dependent settlement. The final total, adult, and legal population sizes were larger in the cold population, and the size of both populations declined with increasing fishing level (fig. 5l–n). These final population sizes were larger than observed in cases without a reserve.

Scenario 2: Current Conditions

The SST time series for the current island conditions was stationary because it was formed from appending random portions of the same 20-year time series (fig. 4b). The mean year quality differed slightly for each run because the exact composition of the SST time series changed; for all experimental combinations the warm Santa Cruz Island population was ≈ 0.9, whereas for the cold San Miguel Island population year quality was ≈ 1.22 (fig. 6o).

Range of fishing levels, no larval connectivity, no reserve. Using the current SST conditions, the cold population had larger mean total, adult, and legal population sizes than the warm population at all fishing levels (fig. 6a–c). Only the cold population declined with increasing fishing level; the size of the warm population was small at all levels. The total catch increased with increasing fishing level for the cold population, though the increase was small when the fishing level was above 30% (fig. 6d). The catch was low at all levels for the warm population. The average number of recruits was higher for the cold population than for the warm population, and in both

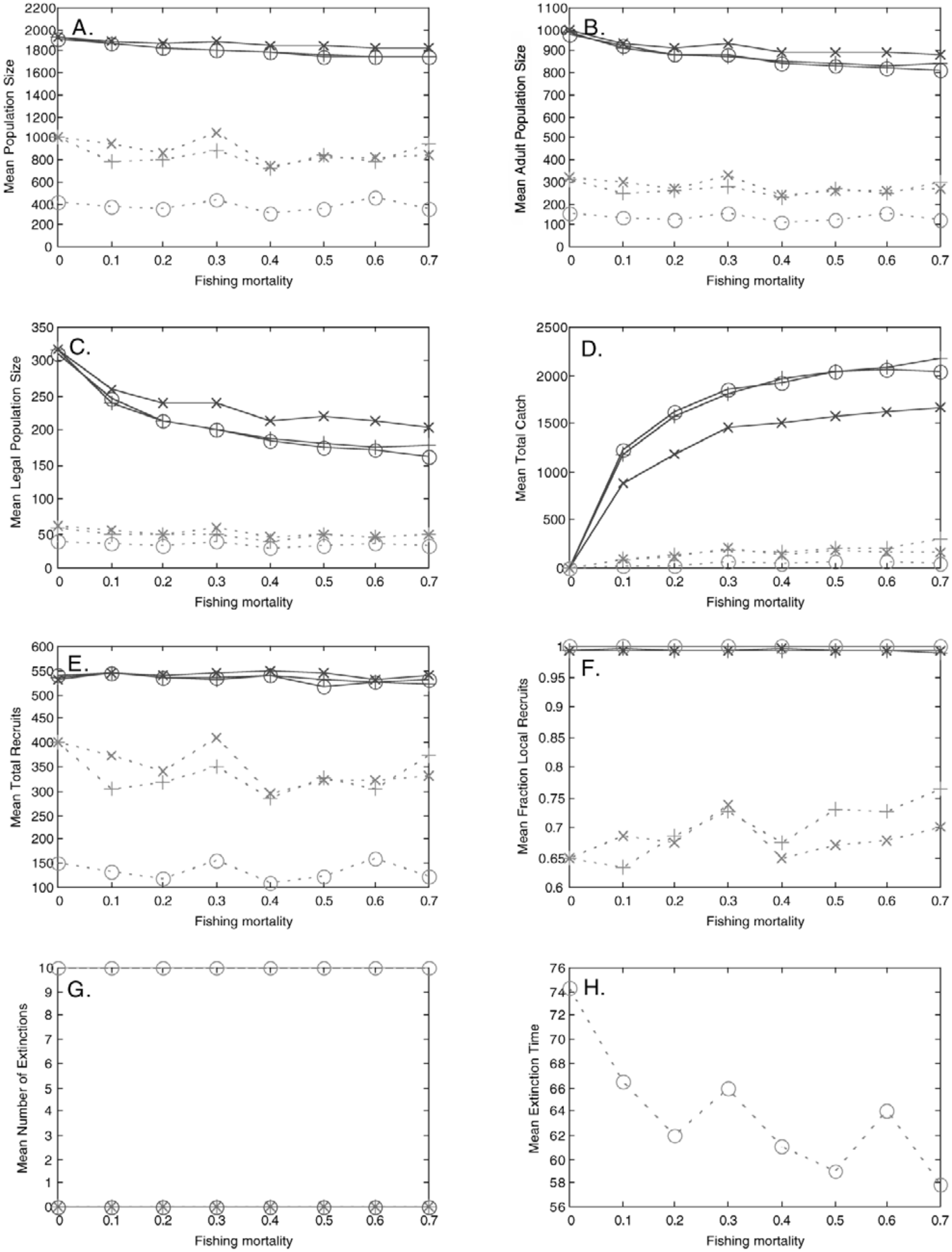

Figure 6. Scenario 2. Population dynamics based on 100 years of current SST conditions at the warm (*dotted*) and cold (*solid*) islands for a range of fishing levels. Symbols on each line refer to the version of the scenario. (o) no larval connectivity, (+) 5% larval connectivity, and (x) 5% larval connectivity and 25% reserve area.

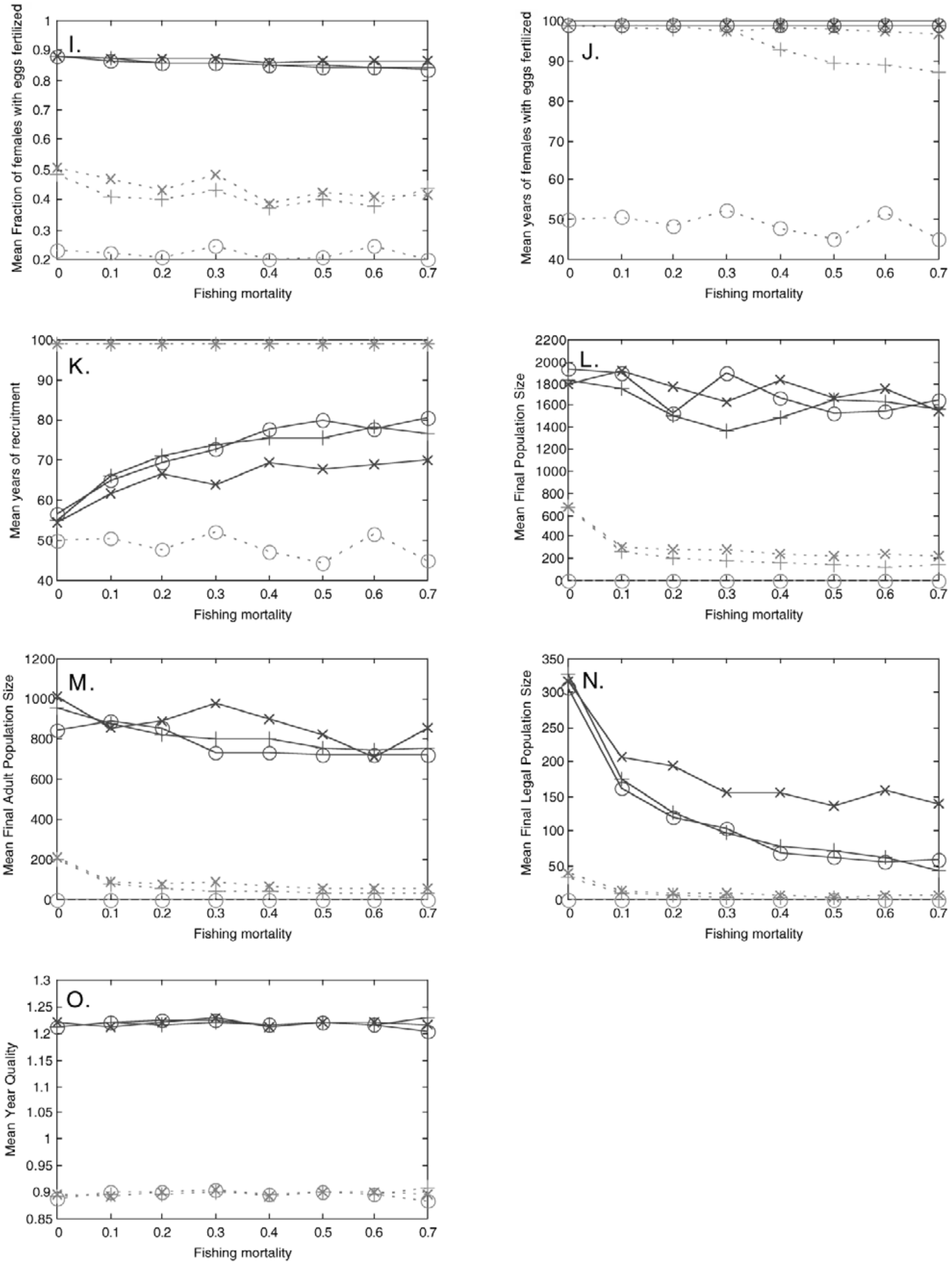

Figure 6. *Scenario 2, continued.*

populations the number was constant across the range of fishing levels (fig. 6e). All recruits were from the local population as there was no larval exchange in this simulation (fig. 6f). The cold population never went extinct, whereas the warm population became extinct in every run regardless of fishing pressure (fig. 6g), though the time to extinction decreased as fishing pressure increased (fig. 6h). At the highest level of fishing, the warm population was extinct within ten years of fishing activity. The proportion of females with eggs fertilized was higher in the cold population than in the warm, and in both populations the proportion changed little with changes in fishing level (fig. 6i). Eggs from at least some females were fertilized in all years for the cold population, whereas in the warm population the number of years in which eggs were fertilized was much lower (fig. 6j) due to the reduced persistence of this population. The number of years in which recruitment occurred increased with increasing fishing level for the cold population (fig. 6k) as a consequence of reduced population size, which allowed increased settlement; in the warm population it was again low and similar to the persistence time of the population. The final total, adult, and legal population sizes were zero for the warm population since it went extinct in all cases, whereas for the cold population the total and adult population sizes remained similar with increased fishing level (fig. 6l,m). As might be expected, the final legal population size declined as fishing level increased, with the minimum population size reached at a fishing level of about 40% (fig. 6 N).

Range of fishing levels, 5% larval connectivity, no reserve. Including larval connectivity in the model simulations did not change the outcome for the cold population for any of the variables considered because the warm population was unable to supply sufficient recruits to make an impact (fig. 6a–n). Larval connectivity did make a difference for the warm Santa Cruz Island population, increasing the mean total, adult, and legal population sizes threefold at all levels of fishing (fig. 6a–c). Even with larval connectivity, total catch was still low for the warm population (fig. 6d). The average number of recruits in the warm population increased to 80% of the cold population at low levels of fishing pressure, and declined to about 50% at high levels (fig. 6e). Over 99% of the recruits in the cold population were local compared with about 70% in the warm population (fig. 6f). Larval connectivity with the cold population prevented the warm population from extinction regardless of fishing level (fig. 6g). The proportion of females with eggs fertilized was higher in the cold population (90%) than in the warm one (about 50%), and both changed little with changes in the fishing level (fig. 6i). Eggs from at least some females were fertilized in all years for the cold population and in all years of the warm population at low fishing levels (fig. 6j). Recruitment to the warm population occurred in all years at all fishing levels (fig. 6k) because of the larval contribution from the cold population. The final total, adult, and legal warm population sizes were low compared with the cold population and were sharply reduced with any fishing (fig. 6l–n).

Range of fishing levels, 5% larval connectivity, 25% reserve area. Including both a reserve area and larval connectivity in the simulations did not change the outcome compared with including only larval connectivity for the cold San Miguel Island population for most of the variables considered (fig. 6a–n). The exceptions were a 25% decrease in the total catch (fig. 6d) and a greater than 50% increase in the final legal population size (fig. 6n) as fishing level increased. There was also little effect on the warm Santa Cruz Island population, apart from a slight increase in the final legal population size compared with the case without a reserve (fig. 6n).

Scenario 3: Future Conditions

The SST time series for the future scenario were constant for each set of ten runs and ranged from 11°C to 18°C in 0.5°C increments within each experiment, for a total of 150 runs per experiment. The two-population case can be understood by recalling the 1°C difference in SST between them; that is, when SST is 15°C at the cold population, it is 16°C at the warm population. At low SST the mean year quality was 2, whereas at the highest SST considered it was zero (fig. 7o).

No fishing, no larval connectivity, no reserve. In the absence of any fishing, larval connectivity, and reserve area the mean total population size was greatest at 15°C (fig. 7a), just below the temperature at which larval recruitment was greatest (15.5°C, fig. 7e). Adult population size was greatest at 14°C (fig. 7b), whereas the legal population size was greatest at 13°C (fig. 7c). Recruitment was constrained to be entirely local (fig. 7f). At temperatures below 12.5°C, approximately half the model's population runs ended in extinction (fig. 7g) in 80–90 years (fig. 7h). At SST above 15.5°C all the population runs ended in extinction, with the time to extinction decreasing with increasing SST. The populations all persisted when the SST was between these values. At the temperatures where the population persisted ≈ 90% of females had eggs fertilized (fig. 7i) in all years (fig. 7j). The number of years in which recruitment occurred was highest at the best SST for maximum recruitment (fig. 7k). The number of years of recruitment was actually reduced in the middle of the SST range due to the increase in population size, which reduced settlement. The final total, adult, and legal population sizes were largest at 14°C, 13.5°C, and 13°C, respectively (fig. 7l–n).

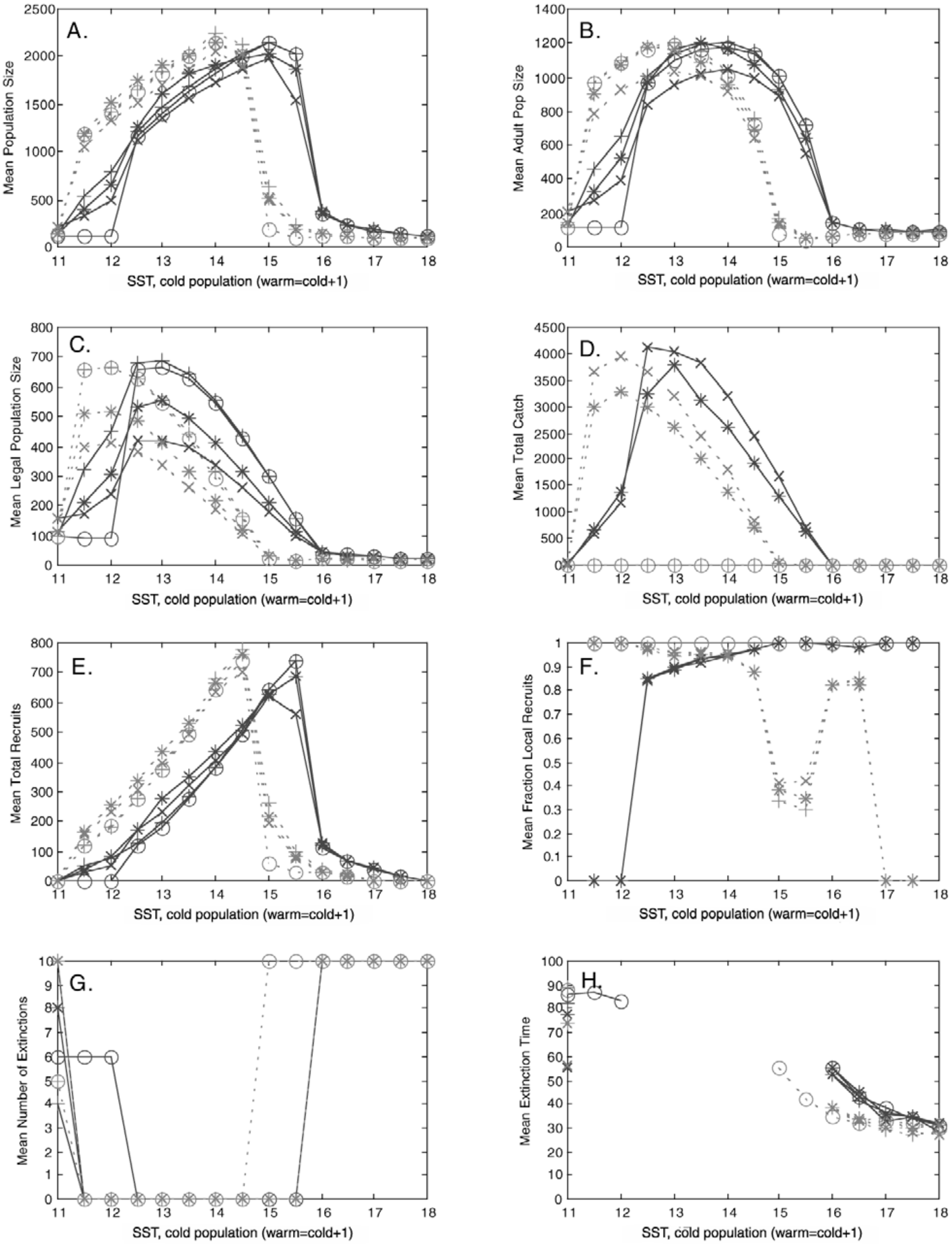

Figure 7. Scenario 3. Population dynamics based on 100 years of future SST conditions at the warm (*dotted*) and cold (*solid*) islands for a range of SST. Symbols on each line refer to the version of the scenario. (o) no fishing, no larval connectivity; (+) no fishing, 5% larval connectivity; (x) 30% fishing, 5% larval connectivity; and (*) 30% fishing, 5% larval connectivity, and 25% reserve area.

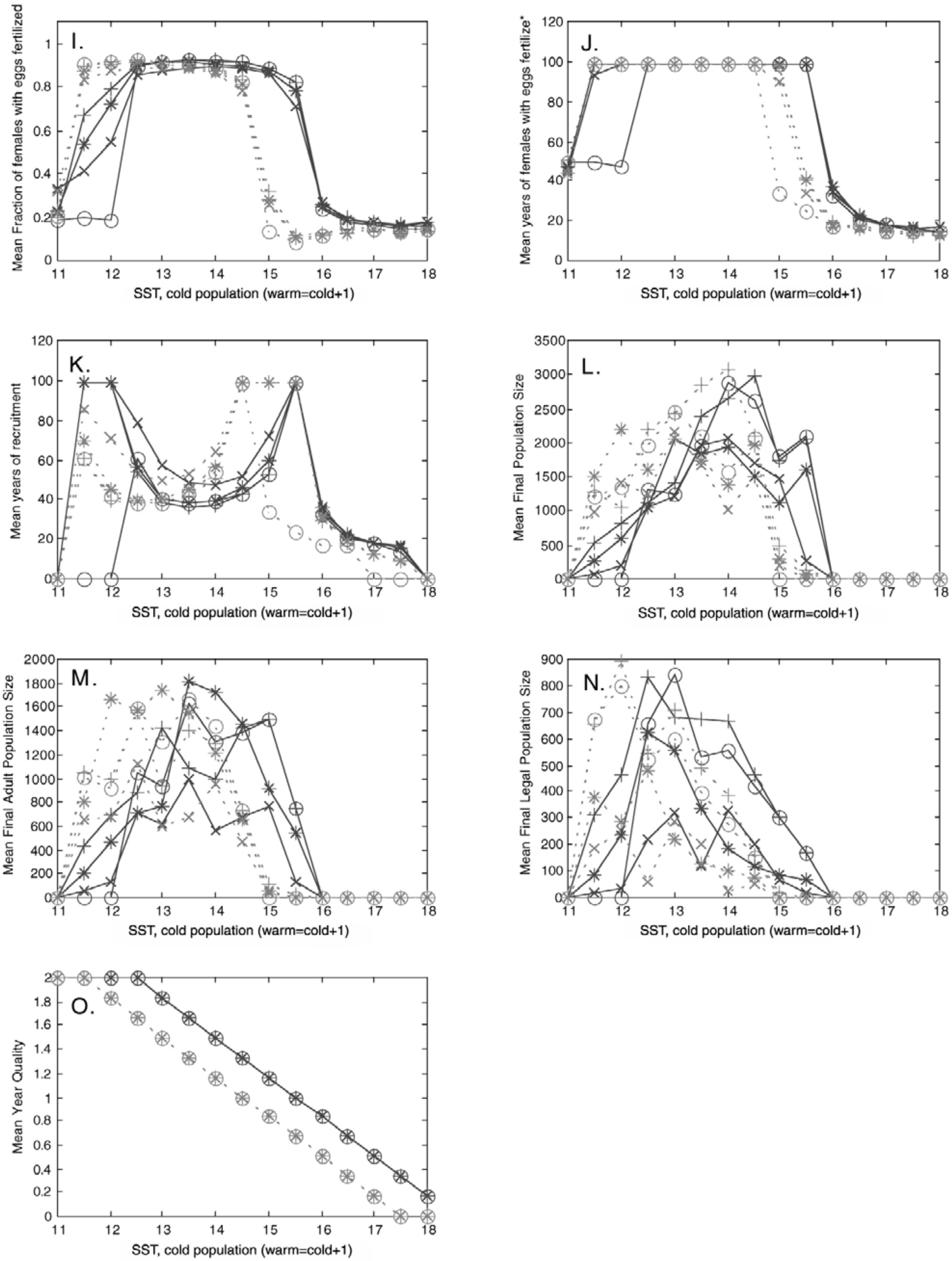

Figure 7. *Scenario 3, continued.*

No fishing, 5% larval connectivity, no reserve. Larval connectivity allowed both populations to persist at a greater range of SST. Mean total population size was largest at the same temperatures for the case with no larval connectivity (fig. 7a–c). The proportion of local recruitment was highest at the extreme SST values (while extant) because no larvae were produced by the other population (extinct), and lowest when one population was at unfavorable SST (fig. 7f). At temperatures lower than 11.5°C, approximately half of the populations went extinct (fig. 7g) after 90 years (fig. 7h). At SST at and above 16°C all the population runs ended in extinction, with the time to extinction decreasing with increasing SST. The populations all persisted between these SST values. For temperatures at which the population persisted, 90% of females had eggs fertilized (fig. 7i) in all years (fig. 7j). The number of years of recruitment was highest at the same SST for highest recruitment (fig. 7k). The number of years of recruitment was reduced in the middle of the SST range due to the increase in population size, which reduced density-dependent settlement. The final total, adult, and legal population sizes were largest at 14.5°C, 15°C, and 12.5°C respectively (fig. 7l–n).

30% fishing level, 5% larval connectivity, no reserve. With 30% of the surviving legal-sized abalone removed every year, and with larval connectivity between the populations, there was little difference in mean total population size compared with the previous two cases (fig. 7a). Mean adult and legal population sizes were largest at the same temperatures as before; however, the values were lower (fig. 7b,c). Total catch was greatest at 12.5°C for the cold and 13°C for the warm population (fig. 7d). Recruitment patterns were similar to the previous cases (fig. 7f). At temperatures lower than 11.5°C, both populations went extinct (fig. 7g) after about 50–60 years (fig. 7h). As before, at SST above 16°C all the population runs ended in extinction, with the time to extinction decreasing with increasing SST. The populations all persisted when the SST was between these values. Fertilization and recruitment patterns were similar to the previous cases (fig. 7i–k). The final total, adult, and legal population sizes were largest at 14°C, 13.5°C, and 13°C, respectively, and were reduced at all SSTs compared with the previous cases (fig. 7l–n).

30% fishing level, 5% larval connectivity, 25% reserve area. The final future SST scenario included 25% of the model area reserved from fishing, in addition to 30% of the legal-sized abalone removed every year and 5% connectivity between the population. This reserve portion somewhat compensated for the fishing, with mean total and adult population sizes the same as the first two cases, across the SST range (fig. 7a,b). The mean legal population size was now halfway between the fishing and no-fishing versions across the SST range (fig. 7c). Total catch was only slightly reduced compared to the previous version and was greatest at 13°C for both populations (fig. 7d). Recruitment patterns were similar to the previous cases (fig. 7f). At temperatures lower than 11.5°C, both populations went extinct (fig. 7g) but persisted longer than without a reserve, about 80 years (fig. 7h). As before, at or above 16°C all the model runs ended in population extinction, with the time to extinction decreasing with increasing SST and little difference in extinction time compared with the previous cases. Fertilization and recruitment patterns were again similar to the previous cases (fig. 7i–k). The final total, adult, and legal population sizes were greatest at 13.5°C, 13.5°C, and 13°C, respectively, and were either the same or higher than the nonfishing experiments across the SST range (fig. 7l–n).

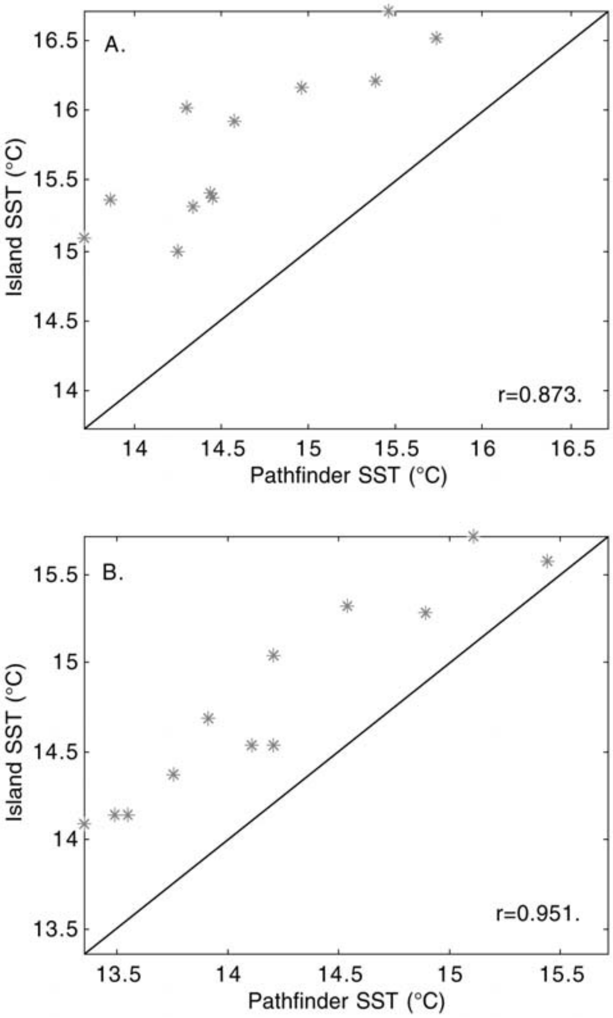

Figure 8. Correlation between the island SST and the Pathfinder SST extracted for the box closest to the island location (1987–98). *A*, Santa Cruz Island. *B*, San Miguel Island.

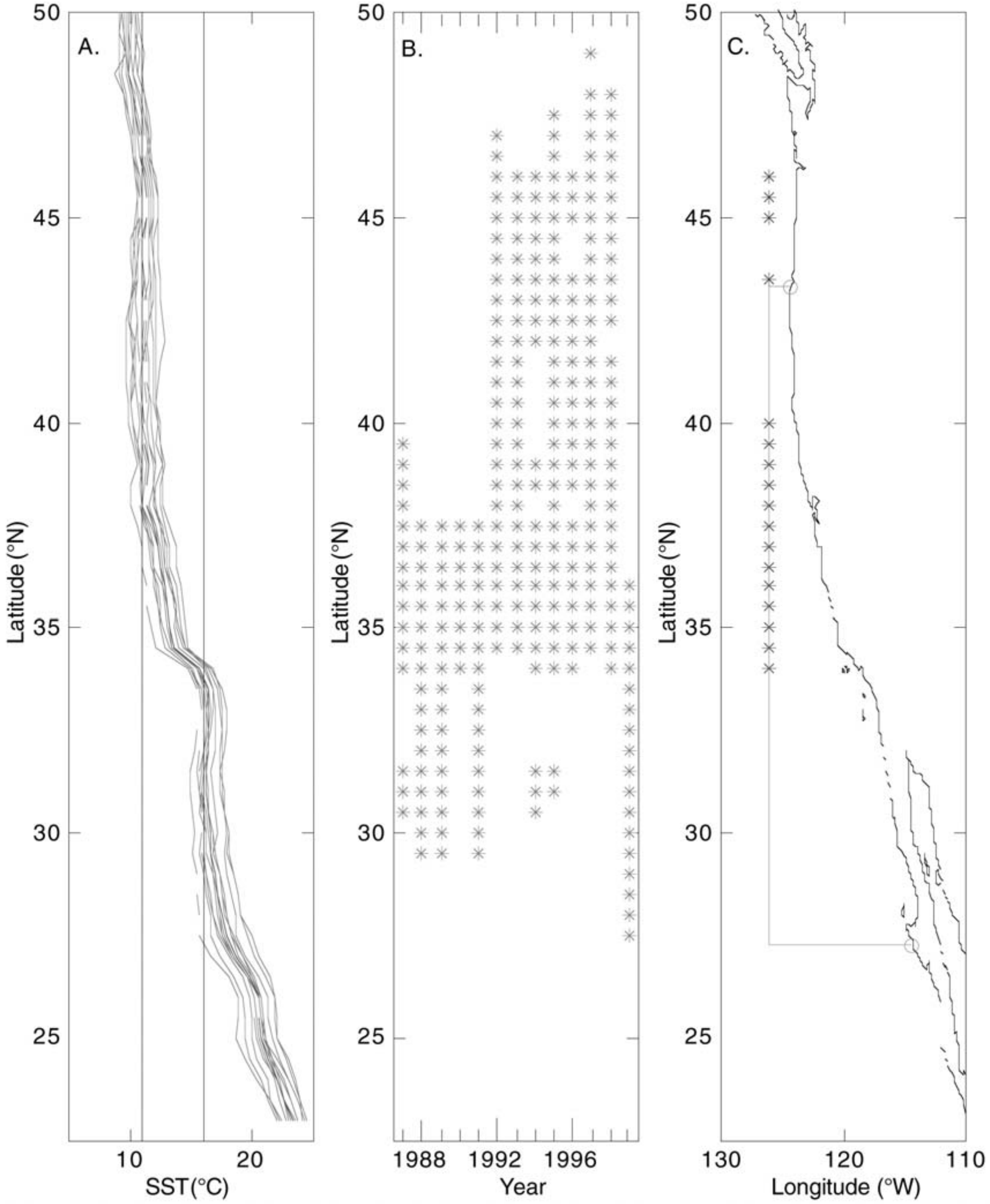

Figure 9. Corrected Pathfinder data extracted for 0.5° latitude bins along the west coast of North America (1987–99). *A*, SST by latitude for each year of data. The vertical lines indicate the suitable abalone SST range (11–16°C) estimated from Scenario 3 models. *B*, Latitudinal ranges for model red abalone within the suitable SST range. *C*, Suitable overall mean SST along the coast for model abalone (*stars*), together with the historical latitudinal range for red abalone (*H. rufescens*) (*line*).

Future SST and Range Changes

The correlation between the overlapping 12 years of island SST and Pathfinder SST for a similar latitude was high ($r = 0.873$ at Santa Cruz Island, $r = 0.951$ for San Miguel Island) (fig. 8). The Pathfinder data showed slightly cooler temperatures than the in situ data at these two locations (1.14°C and 0.57°C, respectively), perhaps because the Pathfinder data was averaged over a larger area and thus included regions where upwelling occurs. With a slight correction of the average difference over the latitudinal range considered (+ 1°C), the (corrected) Pathfinder SST data was suitable for extrapolating the abalone model findings based on the island data to the whole coast.

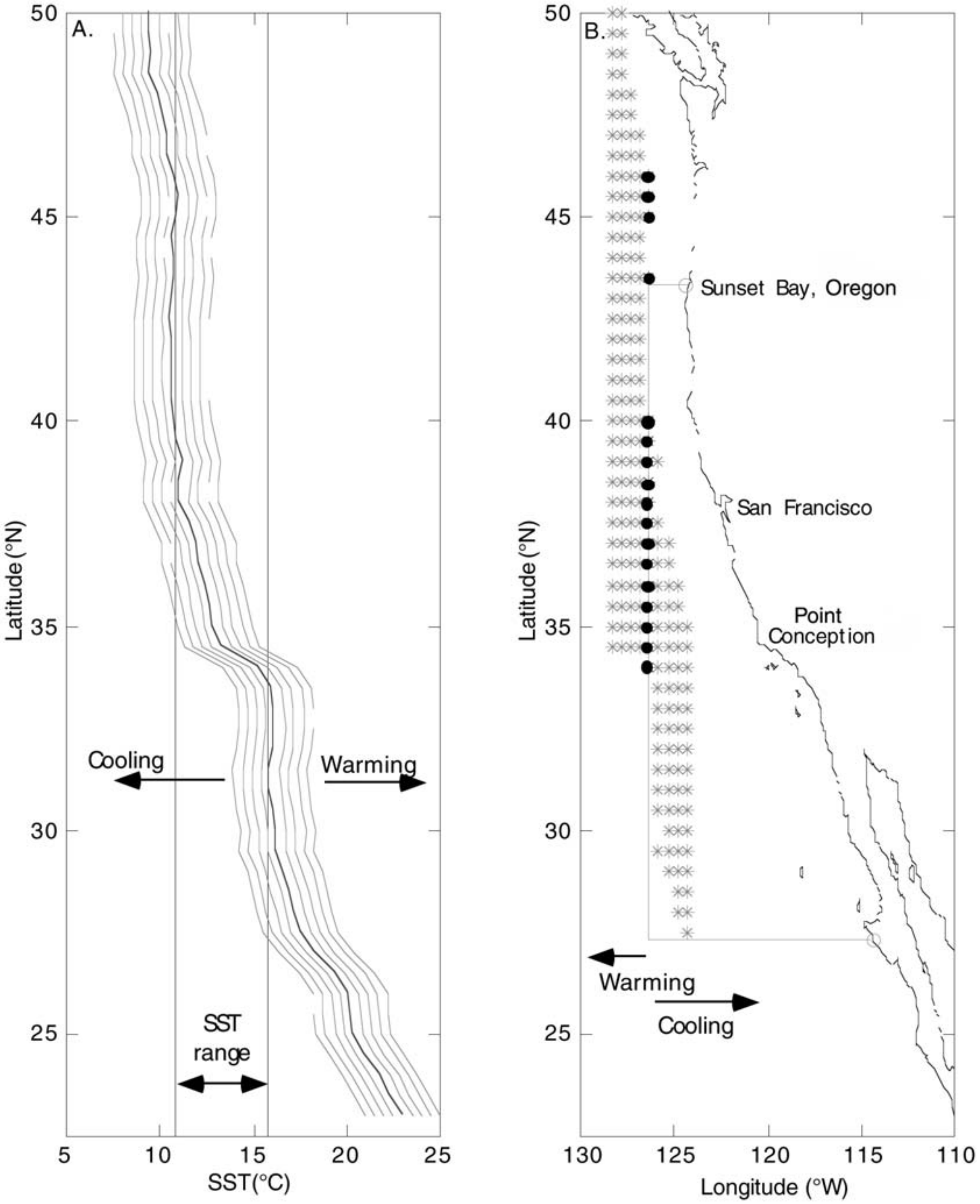

Figure 10. Potential future red abalone (*H. rufescens*) latitudinal ranges. *A*, Expected changes in SST with latitude for 0.5°C changes above and below current mean SST from corrected Pathfinder data (1987–99). Vertical lines indicate the suitable model abalone SST range (11–16°C). *B*, Expected changes in the latitudinal range of suitable red abalone habitat. The two open circles at the coast indicate the historical range, and filled circles indicate the current range of suitable SST; vertical columns of asterisks (*) to the left and right of the filled circles indicate the expected latitudinal range for increasing or decreasing SST respectively (± 2°C incremented by 0.5°C).

Analysis of mean annual SST by latitude (fig. 9a) showed that if red abalone populations can persist at temperatures between 11°C and 16°C (as indicated by the results of scenario 3), the suitable range along the U.S. west coast would be from 27.5°N to 49°N (fig. 9b), which is similar to the historical range. If the median of the annual range limits based on these temperature limits is used to define a latitudinal range for the model populations, then under current mean SST conditions the suitable range has moved north compared with the historical red abalone range (fig. 9c).

If climate change causes a general increase in SST, it will likely increase SST at each latitude. Increases in SST of 0.5°C and the subsequent northward migration of the southern limit of the range of red abalone indicate that southern portions of its range will soon be unsuitable (fig. 10a,b).

DISCUSSION

These model scenarios indicate patterns that might occur in real red abalone populations under similar circumstances. Although red abalones do not generally live at the surface, and so SST may not be a direct measure of this species' environment, they do live at depths where temperatures are similar to those observed at the surface. At worst these SST values are a correlated proxy for the actual conditions.

The results reported here were for a model area of 1 ha, which allowed experiments to be completed in a timely fashion (6 hours per experiment). The results were very similar to those obtained when the model was run for smaller areas, with the exception that extinction occurred slightly more frequently in smaller domains. Real populations of abalone exist at these smaller scales, as well as at larger ones. Model results for simulations with areas up to 10 ha were identical; however, the assumption of random settlement over these larger areas may not be valid and would need to be modified. Density dependence in settlement was required to constrain the model, and similar results were obtained when higher densities were allowed.

Summary, Scenario 1

All model runs based on the SST signal over the past 100 years showed a decline in population size with increasing fishing pressure, although the inclusion of a 25% reserve area reduced this decline. In both populations this reserve proportion led to a 15–20% decline in total catch across a range of fishing levels. The models with a reserve also showed an increase in the proportion of females with eggs fertilized as a result of higher densities within the reserve area. The inclusion of larval connectivity between the two populations did not markedly change the outcomes, suggesting that under this SST environment both populations are self-supporting. The final adult population size in the absence of fishing was close to the maximum allowed adult density for the cold San Miguel population, and about half the maximum allowed for the warm Santa Cruz population. In the absence of fishing, both populations persisted under this SST scenario. With the addition of fishing, the cold adult population was reduced to about half the maximum density, and the warm population was reduced to about 20% of maximum density.

Summary, Scenario 2

The model simulations based on the current island SST conditions showed large impacts on the warm population representing Santa Cruz Island. Without larval connectivity this population went extinct in all cases, and the process was accelerated if fishing was permitted. Allowing some larval connectivity increased the size of the warm population but did little for the cold population, which served only as a larval source for the warm population (hence a sink). Under these SST conditions, inclusion of a 25% reserve area also did little to increase the size of the warm population and changed little in the cold population.

In general, the size of the cold population was reduced to levels found for the warm population in the previous 100 years (scenario 1), and the size of the warm population was reduced to very low levels if there was any fishing exploitation. These results are similar to the real situation observed at these two islands (Karpov et al. 2000).

Summary, Scenario 3

The range of model versions using SST environments different from those currently found at the islands assume there is no evolution or adaptation to the changing conditions. If adaptation occurs, the results will be conservative. In general, all the models showed that the population at the cold location persisted, whereas at the warmer location an increase of only 1°C dramatically reduced the population. Larval connectivity slightly increased the range of temperatures at which the population could persist. At SST values higher than 16°C and lower than 11°C the populations did not persist. Fishing reduced the population sizes and decreased the time to extinction where it occurred. Adding a reserve component somewhat compensated for the effect of fishing, and only slightly reduced the total catch, by about 10–15% for a 25% reduction in fishing area. This indicates that within the range of suitable SST, a reserve would be an effective tool but outside that range it was obviously of no consequence.

Summary, All Scenarios

All scenarios showed that model populations of red abalone are sensitive to changes in SST. Declines of real exploited abalone stocks have also been linked to changes in SST (Shepherd et al. 1998; Tegner et al. 1989). Larval connectivity and fishing influenced the model outcomes, buffering or increasing the sensitivity of the populations to changes in the environment to varying degrees. The historical level of fishing is unknown in these real populations, so we used a range of possible values in this study. At even moderate fishing levels, however, the most dramatic changes had already occurred, suggesting the results are robust to uncertainty about the real level of fishing, which was certainly high (Karpov et al. 2001).

Although fertilization of eggs occurred often in the model runs, the frequency of recruitment was lower than fertilization. This was due to density-dependent settlement and environmental conditions unsuitable for larval survival. These two factors often compound to make stock-recruitment relationships of little value in real abalone population management (e.g., Shepherd 1990; but see Shepherd and Partington 1995). In real populations, irregular recruitment has been observed (Tegner et al. 1989; McShane 1992; Shepherd and Daume 1996) and is indicated by size-frequency distributions that are strongly skewed with an accumulation of old individuals; both were features of model runs in this study.

The proportion of recruitment that is local is an indicator of source/sink population status. Scenarios based on SST from the last 100 years and from the current period show that the warm population received more of its recruits from the cold population and can be considered a sink population. Protecting a sink population, perhaps through a marine reserve, at the expense of a source population is undesirable (Jennings 2001).

This abalone model incorporated local fertilization, and higher fertilization occurred when local adult density was high. Fishing reduces the density of adult abalone, and it has been suggested that fishers who target abalone aggregations can decrease reproductive success (Prince et al. 1987; Sluczanowski 1984; Shepherd 1986). Reserves are the best solution for the maintenance of natural aggregations for species like abalone where the ability to aggregate after settlement is low (e.g., Jennings 2001). This model could be further refined to explore the outcome under various reserve proportions.

The effects of abalone facilitators, competitors, and predators were ignored in this simulation study; however, the abundance of sea otters and urchins, for example, has fluctuated in the last century (e.g., Tegner and Dayton 2000) and this may also influence the population dynamics of red abalone (Rogers-Bennett and Pearse 2001). Alternative hypotheses for the decline of red abalone populations, such as that it is due to the fishing-related reduction in red urchins (*Strongylocentrotus franciscanus*) that provide spine canopy protection to juvenile abalone (Tegner and Dayton 1977, 2000; Rogers-Bennett and Pearse 2001) remain unexplored. More complex ecosystem models may provide insight on the effects of other species on abalone population dynamics.

Trigger Points for Management

These model simulations demonstrate the sensitivity of red abalone populations to the SST environment. When the environment is poor, extra pressure through fishing exploitation increased the magnitude of model abalone population declines. A management option might be to close an area to fishing when environmental conditions deteriorate (e.g., Shepherd et al. 1998). This would then protect the remaining animals at a time when recruitment, growth, and survival are in jeopardy. Management would need to be regional; since temperature varies regionally only some portions of the range would need to be closed to fishing at any one time.

With the future SST scenarios, trigger points for closure can be identified, such as temperatures at which the population would not persist if the conditions persisted. Under such criteria, trigger points for temporary fishery closure for these model populations would be 11°C > SST > 16°C. Alternative trigger criteria might include SST values that would lead to a 50% decline in population size at a certain fishing level or when recruitment fell to 50% of the maximum.

If a trigger point for closure for the year was 16°C, then based on the time series for the past 100 years (scenario 1) the cold population at San Miguel Island would have been closed to harvesting once and the warm Santa Cruz Island closed on ten occasions. Closures would have occurred in the El Niño years of 1958, 1983, and 1993, when observations indicated abalone growth and reproduction was reduced (Cox 1962; Haaker et al. 1998). There would have been no closures based on the lower trigger point of 11°C. Considering just the 18 years of in situ SST data at the islands, there would have been seven closures at Santa Cruz Island and one closure at San Miguel Island. Extrapolating to the 100-year periods used in scenario 2, closures would have occurred for 39% and 6% of years, respectively, at the warm and cold populations. As SST increases, so does the number of years of closure in the southern portion of the range. Model simulations could incorporate such management strategies to evaluate their effectiveness, comparing them to simulations with the same number of randomly selected closure years.[3] In an operational sense, a potential problem is that in situ SST data is only available after the fact; however, SST forecasts are now available and could be incorporated into management decision frameworks.[4]

Future SST and Range Changes

Increases in SST and the likely northward migration of the southern range limit for red abalone indicate that some portions of the historic range will soon be unsuitable, as they are for other marine species along the California coast (e.g., Barry et al. 1995; Veit et al. 1996; Oedekoven et al. 2001). The current mean SST for Santa Cruz Island (15.8°C) suggests that this abalone population is at the limit of suitable SST, with the caveat that real populations in California will be influenced by adap-

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[3] A. Hobday, unpubl. data.

[4] See, for example, Scripps Institution of Oceanography's Joint Environmental Data Analysis Center, <www.acw.ucsd.edu>.

tation as well as protected in refuges created as a result of submergence (moving to deeper, cooler waters) and localized upwelling.

Red abalone is only one of several species of abalone currently at risk in California. Commercial fishing is prohibited for all species, but if the environment is also contributing to population declines for the other species, then different management action must be taken. It is assumed, based on past observations (Roemmich and McGowan 1995; Levitus et al. 2000), that climate change will increase surface water temperatures more than temperatures at depth. Thus, the shallow-living abalone species, black (*H. cracherodii*) and green (*H. fulgens*), are more likely to be affected by temperature changes than those living deeper, pink (*H. corrugata*) and white (*H. sorenseni*) abalone. In fact, increased water temperature has already been shown to increase the susceptibility of green[5] and black abalone to disease (Alstatt et al. 1996; Friedman et al. 1997).

Management strategies that rely on restricting fishing or creating marine reserves may be unsuccessful in conserving abalone stocks if potential changes in the environment (such as SST) are not considered. Efforts to restore depleted red and other abalone populations should focus on locations where the environment is likely to be suitable over the long term. In the case of red abalone such locations are likely to be north of Point Conception (34.5°N) if SST increases by more than 1°C from current levels. An additional conservation problem for red abalone is that in several locations north of Point Conception, predation by sea otters is a significant additional source of abalone mortality (e.g., Wendell 1994).

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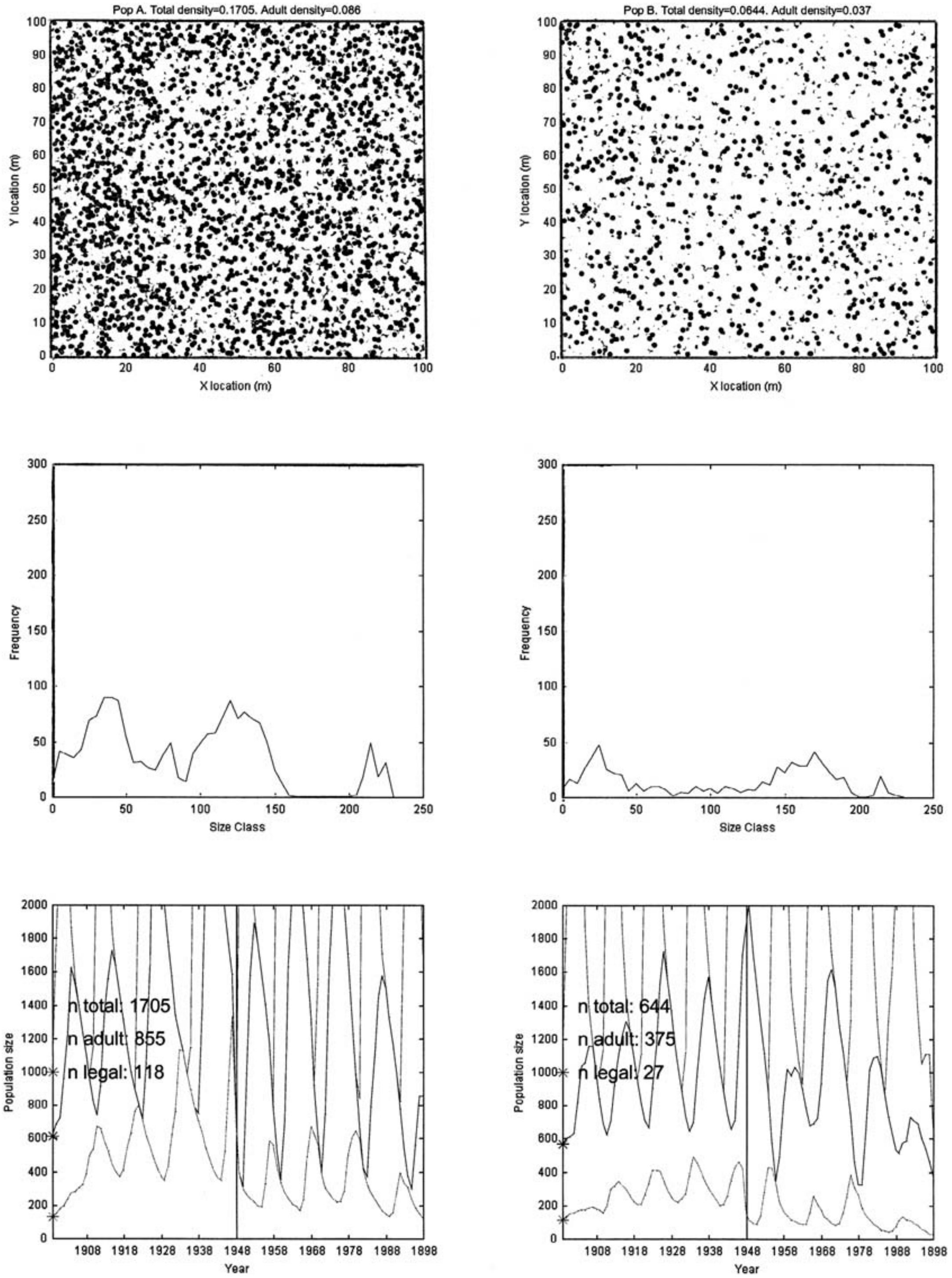
APPENDIX 1

Population dynamics model for red abalone. Example output from one model run of scenario 2 (100 years of current SST), where fishing level was 30% and larval connectivity was 5%. Panels on the right show the cold population, those on the left the warm population. The top two panels show the final distribution of abalone in each model area, the middle two the size distribution at the end of the run, and the bottom two the population trajectories. In the bottom panels, the upper line is the size of the total population, the middle the adult population, and the lower the legal population; the vertical line at year 50 indicates the start of fishing.



ESTIMATING BASELINE ABUNDANCES OF ABALONE IN CALIFORNIA FOR RESTORATION

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> Under our present laws the abalone is being exterminated.
>
> —Dr. Charles L. Edwards, University of Southern California, 1913

ABSTRACT

Abalone populations in California have declined dramatically; however, reliable estimates of baseline abundances are lacking. The lack of sufficient time scales seriously limits the value of most baselines. We use historical data to define baselines for abalone in California and to evaluate current abundances and suggest restoration targets. Using the fishery as a "sampling tool," we estimate that baseline abundances for pink abalone (*Haliotis corrugata*) were 9.3 million, black abalone were 3.5 million (*H. cracherodii*), green abalone (*H. fulgens*) were 1.5 million, white abalone (*H. sorenseni*) were 360,000, and threaded abalone (*H. kamtschatkana assimilis*) were

Pierce Brothers Abalone processing shop, ca. 1933. © Pat Hathaway, <http://caviews.com>. Used by permission.

21,000. All of these species now number less than 1% of their estimated baselines. For species poorly represented in the fishery, we use survey data to estimate that baseline abundances for pinto abalone (*H. k. kamtschatkana*) were 153,000, and for flat abalone (*H. walallensis*) were 71,000. Our modern surveys suggest that pinto abalone populations have undergone a ten-fold decline and that flat abalone populations remain similar to their baseline. These baselines underline the dramatic declines in abalone populations and thus define the magnitude of the challenges we face in restoring formerly abundant species. The identification of rare species brings into question the wisdom of fishing species in the absence of baseline information. This approach may serve to help set restoration targets for other depleted species for which we have limited data.

INTRODUCTION

Abalone populations in California once supported a major commercial fishery, with landings exceeding 2,000 metric tons (t) a year (Cox 1962; Karpov et al. 2000); however, population declines forced the closure of the recreational and commercial fishery in the south in 1996 (CDFG Code 5521). Estimates of baseline abundances (or natural benchmarks) are desperately needed to assess population declines and to establish restoration goals (Dayton et al. 1998); however, estimating abundances is difficult because times series are rare and there is little information available on historical abundances (Dayton et al. 1998; Jackson et al. 2001; Pitcher 2001). Furthermore, our perspective of baseline levels can be distorted by what Pauly (1995) terms "shifting baseline syndrome," that is, the undocumented decline of population abundances that have been vastly reduced from historic baseline abundances over time. As a result of this lack of historical data, restoration targets are frequently set based on temporally limited monitoring studies that rarely span a career.

Changes in baseline abundance resulting from overfishing can include severe population decline, local extirpation, and even global extinction (Carlton et al. 1999; Jackson et al. 2001). Stellar's sea cow (*Hydrodamalis gigas*), for example, once heavily fished, has been globally extinct since 1768 (Anderson 1995). Sea turtles were once so numerous that they impeded the progress of Columbus's ships in the late 1770s, whereas today many species are in danger of extirpation (Jackson 1997). The large barndoor skate (*Raja laevis*) is now close to extinction as a result of trawling in the northwest Atlantic (Casey and Myers 1998). The Chesapeake Bay oyster (*Crassostrea virginica*) has declined more than 50-fold as a consequence of intensive mechanical dredging of Chesapeake Bay that began in the 1870s, pre-dating such threats as poor water quality and oyster disease (Rothschild et al. 1994). Spiny lobsters have declined in southern California such that 260 traps in 1888 once yielded the same biomass as 19,000 traps yielded in 1975 (Dayton et al. 1998). Abalone processors after World War II imposed buying limits of 100 dozen a day per hard-hat diver, and novice divers fished 50 dozen a day: abundances unimaginable today.[1] From these anecdotes of high baseline abundances (Pauly 1995) we can see that some modern nearshore communities have become nearly devoid of many exploited species and now resemble "ghost communities" (Dayton et al. 1998; Tegner and Dayton 2000) much like portions of the Amazon, which as a result of overhunting of large mammals and birds has become an "empty forest" (Redford 1992).

The seas were once perceived as inexhaustible and the fecundity of marine organisms boundless (Roberts and Hawkins 1999), creating the false notion that marine organisms are resilient to population declines. Scientists once upheld this notion regarding abalone; Heath (1925), for example, stated that "the life of the abalone is dependent principally upon the amount of seaweed, and as this is practically inexhaustible, there is a very remote possibility indeed that the shell fish will ever become extinct." We now know that the white abalone (*Haliotis sorenseni*) was not inexhaustible despite its being a broadcast spawner and one of the most fecund of all the abalone species in California, with each female producing an estimated 3.7–6.5 million eggs a year (Tutschulte 1976; Hobday et al. 2001). From 1971 to 1976 overfishing appears to have reduced the population of white abalone below a self-sustaining level (Hobday et al. 2001), and in 2001 it became the first marine invertebrate to be placed on the federal endangered species list.[2]

Abalone appear to be particularly susceptible to overexploitation, and in many parts of the world abalone fisheries have collapsed (Campbell 2000; Karpov et al. 2000; Shepherd et al. 2001). In California serial depletion occurred within the abalone complex as declines in red abalone (*H. rufescens*) and later pink abalone (*H. corrugata*) landings were bolstered by increased landings of rarer species and in distant fishing grounds, masking the inevitable collapse of the species complex (Dugan and Davis 1993; Karpov et al. 2000). In Alaska, pinto abalone (northern abalone, *H. k. kamtschatkana*) landings were not sustainable, which resulted in repeated reductions in fishery limits (quotas) from the peak of 172 t in 1979 to just 7 t when the fishery was closed in 1995 (Woodby et al. 2000). Likewise, pinto abalone landings in British Columbia peaked at 481 t in 1977 and then declined dramatically to the 47 t quota set in 1985, prior

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[1] D. Parker, pers. comm.

[2] *Federal Register* 66 (103) 29046, 29 May 2001.

to the fishery's closure in 1990 (Campbell 2000). Recent surveys in British Columbia show that even after the closure of the fishery populations have continued to decline except in "reserve" areas (such as those adjacent to a heavily guarded prison, a de facto reserve). This finding suggests that poaching may be widespread (Wallace 1999). Nowhere is poaching more problematic than in South Africa, where political and ecological factors have converged to negatively impact abalone populations (Tarr 2000).

Commercial extinction, the cessation of fishing when it becomes unprofitable (Safina 1998), was once thought to ensure that fished species would never suffer global extinction. This was not the case with abalone in southern California where sea urchin divers held dual permits allowing them to search for abalone during sea urchin fishing operations, a practice that sustained catch per unit effort (Dugan and Davis 1993). Today, sea urchin landings have also declined dramatically (Kalvass and Hendrix 1997), and the dive fishery is pursuing other invertebrate species. Despite the emerging dive fishery for wavy turban snails (*Megastrea undosa*, formerly *Lithopoma*), little information exists about the baseline abundance of this species (Taniguchi and Rogers-Bennett 2001).

Our purpose in this study was to determine baseline abundances for abalone in California. We combined peak fishery landings over a ten-year period to estimate baseline abundances of white (*H. sorenseni*), pink (*H. corrugata*), black (*H. cracherodii*), green (*H. fulgens*), and threaded (*H. kamtschatkana assimilis*) abalone. We assumed that abalone populations were at least as large as the numbers taken in the commercial and recreational fishery. For species that were poorly represented in fishery-dependent data, such as flat abalone (*H. walallensis*) and pinto abalone (*H. kamtschatkana kamtschatkana*), we analyzed fishery-independent density data from the past to estimate historic baseline abundances. To assess modern densities of flat and pinto abalone we conducted dive surveys in northern California and compared our results with previous density estimates. We assessed the status of each abalone species by comparing baseline estimates of abundance from the past with present day (fishery-independent) estimates of abundance, where possible. Finally, we discuss how population abundances have changed over time for each of the six species (and one subspecies) in California and the prospects for restoring abundances to baseline levels.

ABALONE EXPLOITATION IN CALIFORNIA

Abalone have a long history of human exploitation within coastal Californian ecosystems. Radio-carbon dating of abalone shells provides archaeological evidence that humans were exploiting abalone in the late Pleistocene (ca. 10,500 years B.P.) in the Channel Islands (Erlandson et al. 1996), 5,000 years B.P. in central California, and 1,000–2,000 years B.P. in northern California.[3] Red abalone (*H. rufescens*) shells in middens from Santa Rosa Island date from 5,370–7,400 years B.P. (Orr 1960). This evidence indicates that human fishing may have affected local abalone populations and kelp forest communities in prehistoric time (Erlandson et al. 1996).

THE INTERTIDAL FISHERY

Early records set the start of the abalone fishery in the 1850s when Chinese immigrants began gathering red, black, and green abalone in the intertidal zone off central California. Abalone were dried and consumed locally or exported to China (Bonnot 1930). The first-recorded commercial abalone venture occurred in 1853, when, according to the *Daily Alta California*, 500–600 Chinese men were gathering abalone (Lundy 1997). Croker (1931) reported that Chinese fishers set out to "gather every available abalone on the coast of southern California." This fishery peaked in 1879 at 1,860 t (Cox 1962; Cincin-Sain et al. 1977). Chinese fishers also collected abalone in Baja California, Mexico, in the 1860s, using San Diego as a base (Lundy 1997). In the 1880s, however, in an effort to reduce fishing pressure on abalone, the Mexican government began assessing a $60 annual tax on U.S. fishing boats fishing in Mexican waters. And in 1888 the U.S. Congress passed the Scott Act, making it illegal for Chinese workers to enter or re-enter the United States (Lundy 1997). These actions led to the demise of the Chinese fishing industry, and by 1893 only one Chinese junk was still fishing in San Diego County (McEvoy 1977). In 1900 concern in California regarding overfishing lead to ordinances prohibiting abalone fishing in shallow waters; in 1913 the export of abalone was banned, and by 1915 abalone drying was forbidden, ending the Chinese intertidal fishery for abalone (Bonnot 1930).

THE DIVE FISHERY

Japanese immigrants began commercial abalone operations in California in 1898 and introduced diving to the industry (Croker 1931; Lundy 1997). Initially the Japanese divers tried traditional free-diving gear, including goggles and shirts, but the cold waters of California forced them to use hard-hat helmets and deep-sea dive suits (Lundy 1997). In 1898 the Point Lobos Canning Company was started by Mr. Kodani, a marine biologist from Japan, and Mr. Allen, who owned land at Whaler's Cove at Point Lobos south of Monterey (Lundy 1997). They used three Japanese hard-hat helmet divers to fish for red abalone (Lundy 1997).

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[3] M. Kennedy, pers. comm.

During the early years of the industry it was not uncommon for divers to fish 40–50 dozen abalone a day (Lundy 1997). One account tells of diver Duke Pierce's first dive experience, when he came up with 50 dozen abalone (Lundy 1997). Divers typically worked in shifts, with six to seven men topside and one diver below. The boats worked approximately 15 days a month for six to eight hours a day. In 1903 a group of Japanese divers moved to the Mendocino area (Dark Gulch) in northern California. One diver working six hours could collect an average of 2,300 red abalone a day (Lundy 1997). In 1913 Japanese divers began diving in Baja California, Mexico. One fisher described what these divers saw: "Abalone [were] found in abundance. It was common to find them in layers of twelve or thirteen. . . . At that time the divers used to catch five to six tons a day" (Estes 1977).

Abalone imported into California from Baja California, Mexico, increased from 1,724 t in 1923 to 3,357 t in 1929 (Bonnot 1930). In 1913, with red abalone stocks declining, Japanese divers began fishing for the smaller green and pink abalone. These abalone, according to Edwards (1913), were extremely abundant. One observer stated, "I have seen the diver send the net up, filled with about fifty green and corrugated (pink) abalones, every six or seven minutes. During his shift below the diver gathers from thirty to forty basketfuls, each containing one hundred pounds of meat and shell, or altogether one and one-half to two tons."

The first abalone cannery opened in 1915 in Cayucos, California, and two years later five canneries were operating, from Monterey to San Diego (Cox 1960, 1962). By 1928, however, the number of canneries was down to three, and in 1931 the only cannery still open—Point Lobos, at Monterey—was closed (Cox 1960, 1962). In 1907 the first abalone reserve was established in central California, the Monterey Bay Shellfish Refuge between Point Piños and Seaside, Monterey County; the take of all shellfish was prohibited within the reserve. There was also an abalone closure at Venice Beach, Los Angeles County, California (Edwards 1913). By 1930 several laws had been passed establishing restricted districts for abalone fishing, outlining fishing methods, imposing minimum size limits and maximum bag limits, and providing for a closed season (Croker 1931; Lundy 1997). According to Croker (1931), "the passage of these laws, which was a gradual evolution, came too late to preserve the abalones of southern California in numbers sufficient to support a commercial fishery, but there are enough left to provide shellfish for amateur fishermen."

THE RECREATIONAL FISHERY

Around 1915 recreational abalone fishing became increasingly popular in California. According to a California Department of Fish and Game (CDFG) report, "For every commercial diver, there are 1,000s of sportsmen. . . . Partial policing results in many arrests and confiscation of many 1,000s of undersized abalone. . . . It is not difficult to understand why the abalone has literally disappeared from the littoral zone." It was at this time that a daily catch limit was imposed on sport takers (Lundy 1997). By 1930 recreational abalone fishing was thriving. Croker (1931) reports that at every low tide during the open season "many hundreds of tourists and ranchers can be seen going over every accessible reef and ledge with a fine-toothed comb. State and county authorities are hard-pressed to enforce the laws on limits and minimum size which are so easily broken by thoughtless people."

The 1970s and 1980s brought a huge surge in the number of recreational scuba divers as gear became safer and easier to use and as training became more available. Between 1965 and 1985 the number of recreational scuba divers searching for abalone increased by 400%, and the catch increased by 250% (Coastal Ecology Group 1985). In northern California recreational divers and shorepickers took an annual average of 533,000 red abalone (906 t) from 1985 to 1989 (Tegner et al. 1992).

THE MODERN FISHERY

In 1928, 11 dive permits were issued in the Monterey area; by 1937 the number had risen to 27 and by 1954 to 294; in 1960, CDFG issued 505 commercial permits (Cox 1962). The number of permits issued peaked at 880 in 1966 and then declined to 119 prior to the closure of the fishery in the mid-1990s. Japanese-American divers dominated the California red abalone fishery until World War II when many were sent to internment camps (Cox 1962). During the war many areas previously closed to commercial abalone fishing were opened to meet the wartime demand for protein sources. In 1945 more than 77,465 red abalone (132 t) were landed in Sonoma and Mendocino Counties in northern California. Northern California towns such as Bodega Bay had a commercial fishery during the war[4] as did such southern California cities as Newport Beach, Avalon, and Santa Barbara (Lundy 1997). These newly opened areas in the south contained large numbers of pink, green, white, and black abalone rather than the red abalone that comprised most of the commercial catch from northern areas.

In 1893 the U.S. Commission of Fish and Fisheries reported commercial landings of abalone at 141 t (Lundy 1997). Landings gradually increased, and in 1916 CDFG reported that the commercial fishery landed just under 454 t. Prior to 1940 only red abalone were documented in records of commercial landings. Green, pink, white,

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[4] R. Mantua, pers. comm.

and black abalone first appear in records in 1940, 1944, 1959, and 1956, respectively. Little information is available for white abalone landings prior to 1959 because landing receipts did not contain a specific category for white abalone so this species may have been recorded as pink abalone.[5] Landings for pink abalone peaked in 1952 at 1,509 t; for green abalone, in 1971 at 511 t; for white abalone, in 1972 at 65 t; and for black abalone, in 1973 at 868 t. Green and white abalones continued to be fished even after their landings fell in 1985 to less than 12,000 and 300 animals, respectively. White abalone landings fell to such a low level that in 1978 mandatory reporting requirements for this species were dropped (Tegner 1989), further exacerbating problems documenting the decline of this species.

Fishery closures were not enacted in California until the mid 1990s despite severe declines in landings. The commercial and recreational fisheries for black abalone were closed in 1993 due to severe population declines caused by commercial fishing pressure and the devastating effects of the lethal abalone disease Withering Syndrome (Haaker et al. 1992). The commercial and recreational fishery for green, pink, and white abalone was closed in 1996 (effective in 1997) south of San Francisco (CDFG Code Sec. 5521). Today, an Abalone Restoration and Management Plan is being drafted in California (CDFG Code Sec. 5522), and a federal recovery plan is being drafted for white abalone (NOAA, NMFS).

METHODS FOR ESTIMATING BASELINE ABUNDANCES

We generated estimates of baseline abundances for abalone in California by combining landings from the commercial and recreational fisheries over a ten-year peak period (fig. 1, tab. 1). We assume that abalone populations were at least as large as the number taken in the fishery. There is information available for commercial landings of red, pink, green, black, white, and threaded abalone from 1950 to the close of the fishery, and for recreational landing from 1971 to the close of the fishery (except for 1984 and 1986). Prior to 1950 red abalone dominated the landings records. Landings were recorded in pounds, using conversions from numbers of abalone to pounds as follows: 45 lb represented a dozen animals for red abalone; 25 lbs, a dozen pink, green, and black abalone; 20 lb, a dozen white abalone; and 15 lb, a dozen threaded, pinto, and flat abalone (Pinkas 1974). Prior to 1959 the conversion factor was 35 lb per dozen for pink abalone and 50 lb per dozen for red abalone (Cox 1962).

We made two simplifying assumptions about abalone populations during the ten-year time period used to generate all the baseline estimates. First, we assumed that the fishery over a ten year period in effect "sampled" all size classes of the population. Even though the fishery was forced to take only large legal-size animals because of minimum legal sizes, the majority of juveniles and sublegal adults present in the first year of the time period grew to legal size and were subsequently taken in the fishery by the end of the ten-year time period.

TABLE 1
Commercial and Recreational Abalone Landings in California During the Peak Landings Decade

Species	Peak decade	Commercial landings	Peak decade	Recreational landings
Pink	1950–59	9,318,587	1950–59	—[a]
Green	1966–75	1,473,732	1971–75	30,947
Black	1972–81	3,537,126	1972–81	6,729
White	1969–78	354,973	1971–78	5,503
Threaded	1971–80	21,066	1971–80	—[a]

Note: Recreational landings are from commercial passenger dive vessels.
[a] No data available.

Second, we assumed that we were not sampling abalone that had been added to the population by reproduction during the ten-year time period because newly settled abalone typically take more than ten years to grow to the minimum legal size. Abalone grow slowly (Tutschulte 1976; Haaker et al. 1998), and estimates (using the von Bertalanffy growth model) of the age at which abalone reach commercial legal size range from 20 years for green abalone at 178 mm to 9 years for white abalone at 159 mm in length (Tutschulte 1976; Tutschulte and Connell 1988). The length of time may be even longer since the von Bertalanffy growth model overestimates juvenile growth (Yamaguchi 1975; Ebert 1999).

We were unable to construct baseline information for abalone that also occur in Mexico because we were unable to acquire complete commercial fishery records (but for white abalone, see Hobday et al. 2001). Flat and pinto abalone are not well represented in the commercial fishery data. For these species we used fishery-independent data to determine baseline estimates of abundance from 1971, the earliest subtidal surveys we are aware of in northern California.

WHITE ABALONE

A conservative estimate of baseline abundance of white abalone, using landings data during the peak of the fishery, 1969–78, is 360,476 animals; this includes the 5,503 abalone taken in the recreational fishery (tab. 1). We assumed that during the ten year period (1) the majority of the population was "sampled" by the fishery and (2) no new individuals were added to the population. This species is estimated to have a maximum life span of 35–40 years (Tutschulte 1976), and individuals are likely to attain older ages.

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[5] B. Owen, pers. comm.

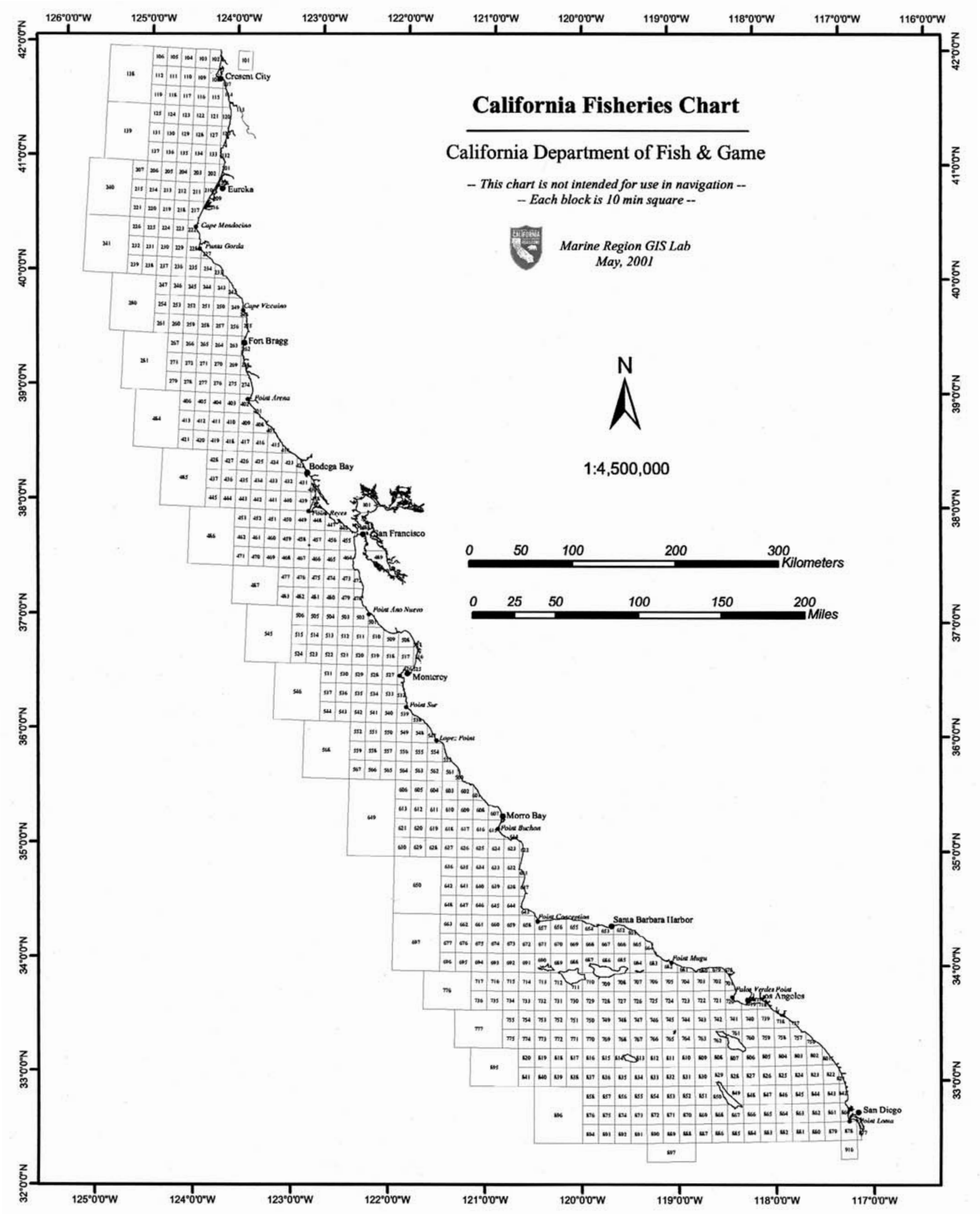

Figure 1. Map of California showing fishery landing blocks.

TABLE 2
Abundance and Density Estimates for White Abalone in California, 1970s to the Present

Study/year	Abundance estimate	Density[a] (abalone per ha)
Tutschulte, 1967	644,464[b]	857
Tutschulte, 1971-73	1,729,600[c]	2,300
Current study, 1969-78	360,476	479
Davis et al. 1980-81	15,792	21
Davis et al. 1992-93	1,256	1.67
Haaker 1996-97	880	1.17
Hobday et al. 2001	2,053	2.73

[a] Deep (25–65m) rocky reef habitat for white abalone in California is estimated at 752 ha (Davis et al. 1998); recent side-scan sonar estimates of deep habitat are six times as large (R. Kvitek, pers. comm.).
[b] Based on three white abalone within a 5 × 7 m quadrat.
[c] Based on seven white abalone within three $10\ m^2$ quadrats at Santa Catalina Island.

Combining this abundance estimate with previously published estimates of habitat area (752 ha) (Davis et al. 1998; Hobday et al. 2001) suggests that population density in California in 1969 was approximately 479 animals per hectare. Most white abalone (271,051 abalone) over the ten-year period (approximately 75%) were taken from San Clemente Island. This island has an estimated total shelf area of 5,557 ha[6] within the 25–65 m depth range (Rogers-Bennett et al. 2002). If we assume that 3% of this area is suitable rocky substrate (Davis et al. 1998), then white abalone habitat would comprise 167 ha (Rogers-Bennett et al. 2002), and the density of abalone at San Clemente Island in 1969 would have been 1,623 abalone per hectare. In contrast, if all of the habitat at this depth is suitable white abalone habitat (5,557 ha), then the density falls to 49 abalone per hectare in 1969.

For white abalone we are able to compare our baseline estimate (479 white abalone per hectare) with other estimates derived from published data. The earliest study during the 1970s (Tutschulte 1976) estimated abundance at 2,300 animals per hectare, almost five times greater than our estimate derived from fishery data (tab. 2). One possible explanation for the discrepancy is that Tutschulte's fishery-independent estimate was based on a limited sample of three quadrats ($10\ m^2$) at Santa Catalina Island in which seven white abalone were found (Tutschulte 1976; Hobday et al. 2001).

Modern Estimates

Modern estimates of white abalone abundance suggest that populations have declined dramatically since the 1960s. In the late 1990s, submersible surveys found 157 white abalone and estimate that there are now 21 white abalone per hectare (Davis et al. 1996, 1998). Fishery-independent population estimates have been made using small submarines in southern California (Davis et al. 1996; Davis et al. 1998; Haaker et al. 1998). These estimates suggest that less than 3,000 white abalone exist throughout their range in southern California and Mexico (Hobday et al. 2001). Despite our limited knowledge of modern abundances, today's estimates are less than 1% of our baseline estimate generated from fishery landings (1969–78) and less than 0.1 % of Tutschulte's (1976) estimate.

PINK ABALONE

An estimate of baseline pink abalone population abundance using landings data during the peak of the fishery, 1950–59, is 9.3 million animals (tab. 1). There are no records of recreational pink abalone fishing during this period. We assumed that during the ten year period (1) the majority of the population was "sampled" by the fishery and (2) no new individuals were added to the population. Pink abalone are estimated to reach the minimum legal size of 159 mm (6.25 in.) in 16 years (Tutschulte 1976; Tutschulte and Connell 1988).

There are currently no estimates of subtidal rocky habitat for pink abalone in southern California, but kelp canopy occurs primarily over rocky reefs of intermediate depth, suitable habitat for pink abalone; we therefore used kelp canopy area as a highly conservative proxy for pink abalone habitat. We examined aerial photographs of kelp surface canopy taken in the spring and summer of 1967 and found approximately 14,000 ha of kelp coverage in southern California from Point Arguello south to the Mexican border (8,500 ha) and at the offshore islands (5,500 ha) (kelp data provided by CDFG). Using this crude method of estimating habitat area, we estimated that pink abalone density in the 1950s would have been at most 664 animals per hectare. This estimate would be greatly reduced if pink abalone habitat estimates were revised upward. One additional caveat is that local densities may have been much higher, as earlier qualitative records suggest (see sections on early abalone exploitation).

Modern Estimates

To estimate current densities of pink abalone we used data from fishery-independent surveys conducted in 2001 by the Kelp Forest Monitoring Program. Divers found no pink abalone at 15 of the 16 sites surveyed at five northern Channel Islands (fig. 2). Pink abalone were found only at Landing Cove within the Anacapa Island Ecological Reserve, at a density of 42 animals per hectare. Using this density and averaging it with densities at two other locations at Anacapa Island, both of which lacked pink abalone, we calculated an average density for the entire island of 14 animals per hectare.

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[6] This is four times larger than previous estimates of white abalone habitat at San Clemente Island (40 ha) (Davis et al. 1998).

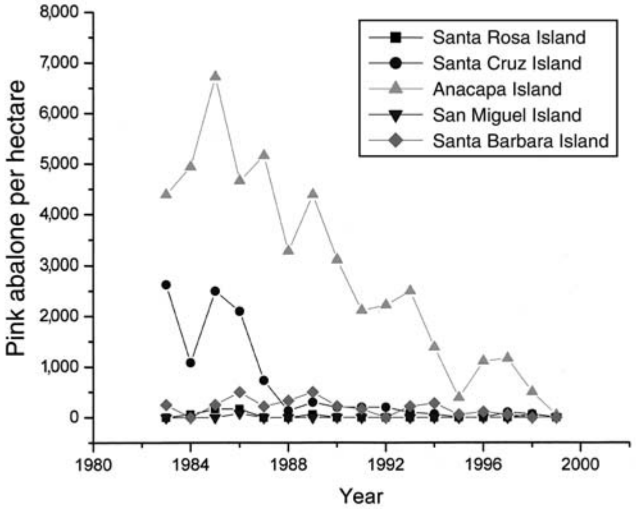

Figure 2. Density of pink abalone at subtidal Kelp Forest Monitoring Program survey sites at northern Channel Islands.

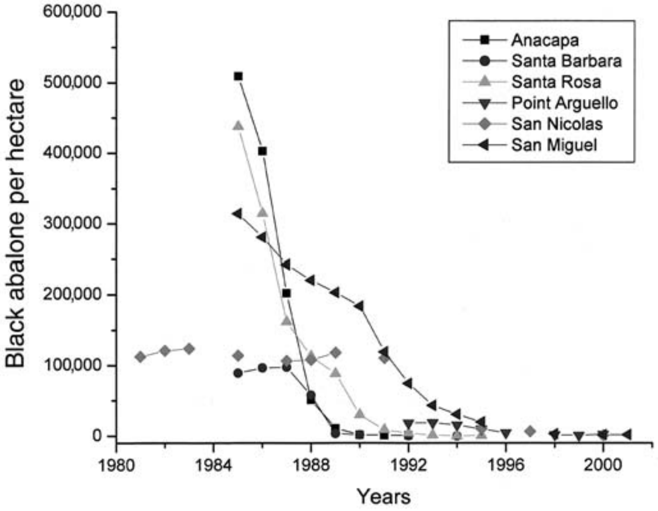

Figure 3. Density of black abalone at intertidal survey sites in southern California.

To estimate the size of potential habitat for pink abalone at Anacapa Island we used two different methods. First, we examined aerial photographs of kelp canopy coverage taken in October 1989 by ECO Scan.[7] These showed approximately 27 ha of kelp canopy around Anacapa Island. Using the abalone density data discussed above, we estimated a modern abundance of 378 pink abalone in the northern Channel Islands for 2001. No data were available for other islands or mainland locations.

The second method of estimating potential habitat at Anacapa Island was developed by the U.S. Geological Survey GIS program for southern California habitats. The subtidal rocky areas along the northern side of Anacapa island have been mapped, and it is estimated that 115 ha of subtidal rocky substrate occur at 10–50 m depth (Cochrane et al., in press); extrapolating from this, we estimate that 230 ha of suitable habitat occurs around the entire island. This area is ten times the habitat area we estimated based on kelp surface area (27 ha). It yields a modern abundance estimate of 3,220 pink abalone at the northern Channel Islands. Regardless of the method one chooses to estimate suitable pink abalone habitat area, however, modern estimates of abundance are less than 0.01% of the estimated 9.3 million pink abalone that occurred in the 1950s.

BLACK ABALONE

A conservative estimate of the baseline abundance of black abalone, using landings data from the peak of the fishery, 1972–81, is 3.54 million animals (tab. 1). Black abalone was the last species of abalone to be exploited; landings peaked in 1973. We assumed that no new individuals were added to the population during the ten-year peak of the fishery for this species. Black abalone are slow-growing animals, and mean asymptotic length (152 mm) appears to be smaller than minimum legal size for sites at San Miguel Island and Point Arguello in the late 1980s (Haaker et al. 1995).

Modern Estimates

Based on three data sets from population surveys in the intertidal zone at five islands and one mainland site, populations have severely declined since the late 1980s (fig. 3). Using fishery-independent surveys of black abalone abundance we find that three of the six areas now have no black abalone. In the three areas with black abalone surveyed in 2000, densities have dropped more than 99%, from hundreds of thousands per hectare prior to 1985 to 2,500 per hectare at Point Arguello, 1,706 per hectare at San Miguel Island,[8] and 953 per hectare at San Nicolas Island[9] (fig. 3).

GREEN ABALONE

A conservative estimate of baseline green abalone abundance, using landings data during the peak of the fishery, 1966–75, is 1.5 million animals (tab. 1). We assumed that during the ten-year period (1) the majority of the population was "sampled" by the fishery and (2) no new individuals were added to the population. Green abalone appear to be the slowest growing of the five commercially exploited southern abalone species and are estimated to reach the minimum legal size of 178 mm (7 in.) in 20 years (Tutschulte 1976; Tutschulte and Connell 1988; Shepherd et al. 1991).

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[7] ECO Scan Resources Data, Box 1046, Freedom, CA 95019, (831)728-3289.

[8] CDFG, unpubl. data.

[9] CDFG, unpubl. data; and G. VanBlaricom, unpubl. data.

Modern Estimates

There are few estimates of current green abalone abundance. In the early 1970s abundance estimates were made by divers conducting timed swims at Santa Catalina and San Clemente Islands; however, no density information was provided. Abundance at each of four sites at Santa Catalina Island in 1974 averaged 130 green abalone per hour; at San Clemente Island in 1973 abundance averaged 126 green abalone per hour.[10] In comparison, timed swims in 1995 at Santa Catalina Island at four sites yielded 26 green abalone during 1,172 min of search time (1.33 per hour), and in 1997 at San Clemente Island only 2 green abalone were found during 458 min of search time (0.26 per hour). Using these data we were unable to determine estimates of abundance for comparison with our estimated baseline abundance for this species, but clearly abundances have declined dramatically. Modern density surveys of green abalone are desperately needed.

THREADED ABALONE

A conservative estimate of baseline population abundance for threaded abalone, using landings data during the peak of the fishery, 1971–80, is 21,000 animals (tab. 1). Within this ten-year period 99.6% of all the threaded abalone taken by the fishery had been landed. After 1980 only 66 threaded abalone were landed We assume that during the ten year period (1) the majority of the population was "sampled" by the fishery and (2) no new individuals were added to the population. Threaded abalone landings were not recorded in the recreational landings database. Threaded abalone, like white abalone, is a deepwater species. The distribution of threaded abalone extends farther north than white abalone and not as far south (Geiger 1999), so habitat estimates generated for white abalone cannot be used for threaded abalone. At present, there are no reliable estimates of threaded abalone habitat that can be used to estimate population density.

Modern Estimates

Few fishery-independent estimates of threaded abalone exist. This species appears to have been rare even in the 1970s. A survey conducted in 1974 found that of 1,877 abalone quantified during more than nine hours of search time at Santa Catalina and San Nicolas Islands, only one was a threaded abalone (tab. 3).[11]

In 2001 the Kelp Forest Monitoring Program found five threaded abalone for the first time since their surveys began in 1972: four inside abalone-recruitment modules and one on rocky substrate.[12] Divers found another 11 threaded abalone at a site near Santa Barbara on the mainland. All ranged in size from 50 to 82 mm. We are not aware of any other fishery-independent data for this subspecies. The data suggest that this subspecies may now number in the hundreds and may be at least as rare as white abalone, if not more so.

TABLE 3
Abundance of Threaded Abalone from Fishery-independent Abalone Surveys in 1974 at Two Channel Islands in Southern California

	Abalone Species					
Survey site	Red	Pink	Green	Black	White	Threaded
San Nicolas Island[a]	760	214	0	0	5	1
Santa Catalina Island[b]	0	352	453	89	3	0

[a] Surveys at San Nicolas Island ranged in depth from 5 to 21 m during 6.6 hr of search time.
[b] Surveys at Santa Catalina Island ranged in depth from 2 to 14 m during 3.9 hr of search time.

FLAT AND PINTO ABALONE

Commercial data on flat and pinto abalone are limited and may not accurately reflect the take by the fishery. The total number of flat abalone reported in the commercial abalone landings database is 130 animals, all taken from 1973 to 1994. The bulk of this information is likely reporting error, since only 0.6% of the landings are reported from blocks north of Point Conception. Reports of pinto abalone in commercial landings also appear to be spurious since of the 549 abalone taken from 1973 to 1996 only 3% are reported from blocks north of Point Conception. Furthermore, there are some flat and pinto abalone landings reported from blocks far offshore at depths deeper than abalone exist. These species are not recorded in the southern recreational landings database. Flat and pinto abalone are small in size compared with red abalone and rarely reach 179 mm shell length. Flat abalone have always been considered rare (McMillen and Phillips 1974). For these reasons neither pinto nor flat abalone were targeted by the recreational fishery in northern California. Therefore, we do not use fishery-dependent landing information to determine historical baseline abundances for these species.

Northern California

We compiled fishery-independent information for flat and pinto abalone to estimate baseline abundances in northern California. Fishery-independent estimates of abalone density were made in 1971 and 1975 in northern California (tab. 4). Surveys in 1971 quantified abalone abundance along transects of known size, resulting in

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[10] CDFG, unpubl data.

[11] Burge, R. 1974. Abalone-lobster investigations. 74-KB-15 and 74-M-3. Unpublished cruise report, Calif. Dept. Fish Game, Long Beach, Calif., 6 p.

[12] D. Kushner, pers. comm.

estimates of density at three fished sites in northern California: Fort Ross State Park (FRSP) in Sonoma County and Point Arena (PA) and Van Damme State Park (VDSP) in Mendocino County. Abalone surveys in 1971 were conducted using differing protocols. The first survey examined abalone density within 38 subtidal transects (each 4 m × 30 m), covering an area of 4,560 m^2. The second survey examined abalone density using 2 m × 30 m transects and 30 m^2 arcs, covering an area of 2,070 m^2. The third survey in 1975 enumerated abalone abundances and species composition during timed swims (but did not report density) at seven areas in northern California that encompassed both fished (including FRSP and VDSP) and reserve sites.

No direct estimates of abalone habitat exist for northern California, although subtidal maps are currently being generated.[13] To arrive at a conservative estimate of abalone habitat area we used the abundance of kelp canopy as determined from aerial photographs taken flying over the land-sea interface in 1989. We estimated a minimum of 1,480 ha of rocky subtidal habitat along the north coast including Marin, Sonoma, Mendocino, and Humboldt Counties.

We used the 1971 estimate of flat and pinto abalone density in northern California to generate early estimates of population size (the 1975 surveys did not estimate density). Population size estimates were generated using Jolly-Seber methods; we input estimates of total habitat area, probability of type I error (alpha = 0.05), and sampling with replacement parameters into the empirical calculation.

Our baseline estimate of abundance for flat abalone in northern California (1,480 ha of habitat) in 1971 using Jolly-Seber estimates is 71,000 (upper 95% confidence interval: 133,000; lower 95% confidence interval: 10,000). Our baseline abundance estimate for pinto abalone in 1971 is 156,000 (upper 95% confidence interval: 341,000; lower 95% confidence interval: 29,000). The population estimates based on data from 1971 have extremely large confidence intervals. The patchy nature of the abundance data, with only a few patches occupied by flat and pinto abalone, along with the limited sampling in 1971, contributed to this wide confidence interval.

Modern Estimates

We compared these early surveys with our modern estimates (1999–2001) of abundance and density from five sites: Bodega Marine Life Refuge and Cabrillo Marine Reserve, Fort Ross State Park, Salt Point State Park in Sonoma County, and Van Damme State Park in Mendocino County. We used transects of two sizes: large emergent transects 2 m × 30 m (60 m^2) and small invasive transects 2 m × 5 m (10 m^2). A total of 163 large and 120 small transects were surveyed (roughly 32 and 24 per site, respectively). Surveyors searched smaller transects invasively, moving cobbles, rocks, and corallines and turning over red sea urchins (*Strongylocentrotus franciscanus*) to look for small abalone (tab. 4).

TABLE 4
Abundance of Flat, Pinto, and Red Abalone by Depth in Northern California

		Abundance (no. of animals)		
Survey year and type	Species	< 8.5 m depth (shallow)	> 8.5 m depth (deep)	Total (all depths)
1971[a]				
Emergent	Flat	17	5	22
	Pinto	7	41	48
	Red	701	32	733
1971-72[b]				
Emergent	Flat	5	16	21
	Pinto	11	56	67
	Red	327	85	412
1975[c]				
Timed swim	Flat		149	23
	Pinto	101	105	206
	Red	9,598	1,086	10,684
1999-2001[d]				
Emergent	Flat	9	2	11
	Pinto	1	8	9
	Red	3,849	1,241	5,090
Invasive	Flat	3	2	5
	Pinto	0	2	2
	Red	761	313	1,074

[a] Surveys covered an area of 4,560 m^2 along 38 transects (30 m × 4 m) at two sites (CDFG, unpubl. data).

[b] Surveys covered an area of 2,070 m^2 at one site, Point Arena, in northern California (Gotshall et al. 1974).

[c] Surveys during 33 timed swims covered an area of approximately 5,406 m^2 at seven study sites (Schultz and Burge, unpubl. data).

[d] Both large emergent transects (30 m × 2 m) and small invasive transects (5 m × 2 m) were surveyed. Investigators surveyed a total of 163 emergent and 120 invasive transects, examining 10,980 m^2 of area at the same five sites in northern California as were examined in 1975 and 1971 (Rogers-Bennett et al., current study).

Density estimates suggest that populations of flat abalone, which were not targeted by the fishery have remained consistent over time in northern California from the baseline estimate of 71,000 animals in 1971 to the present estimate of 83,845 animals (upper 95% confidence interval: 99,000; lower 95% confidence interval: 69,000). In contrast, pinto abalone populations appear to be declining in northern California, dropping nearly ten-fold from a baseline abundance of 156,000 in 1971 to 18,000 in 1999–2001 (upper 95% confidence interval: 22,000; lower 95% confidence interval: 13,000). Modern estimates have narrower confidence intervals because abalone were more evenly distributed and more transects were sampled.

DISCUSSION

Our estimates of baseline abundance for all species of abalone examined indicate that populations were larger

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[13] R. Kvitek, pers. comm.

in the past than they are today (tab. 1). In the case of white abalone, modern dive surveys estimate densities of 21 animals per hectare (Davis et al. 1996) and submersible surveys in 1996–97 and 1999 yield fewer than 3 animals per hectare (Haaker 1998); this is in marked contrast to our estimates of 479 animals per hectare in 1969. These findings suggest that white abalone now occur at less than 5% of their previous density (tab. 2). If we examine densities at San Clemente Island where 75% of the white abalone catch was taken, we find that densities have dropped from a high of 1,623 per hectare in 1969. Clearly at such low densities, Allee effects will be of concern for population recovery of this free-spawning invertebrate (Hobday and Tegner 2001).

The present distribution of white abalone at deep depths may be problematic for recovery. Remnant populations of adult white abalone remain only at the deepest portions (at depths > 33 m) of their former distribution, whereas divers report that they previously occurred at shallower depths.[14] Moreover, laboratory work indicates that larval development is arrested at temperatures below 12°C (Leighton 1972), which is common at depths (beyond 30 m) where adult broodstock have recently been collected.[15] In the laboratory, no larval settlement was observed at 10°C, whereas only 57–66% settled at 12°C after 15 days, and those larvae did not survive beyond day 30 (Leighton 1972). Furthermore, no signs of recruitment had been observed for two decades until 2000, when two juvenile white abalone were observed at Yellow Banks, Santa Cruz Island, at a depth of 10 m, and again in 2001, when one juvenile was observed at this location.[16] Although this is an indication that some recruitment is occurring at shallower depths, this is far less than the percentage of juveniles (15%) in samples ($N = 20$) collected in the early 1970s (Tutschulte 1976). Clearly, these few juveniles will not sustain the population. Today, a captive-rearing program is underway at the Channel Islands Marine Resources Institute with 8 wild adults and 18,000 hatchery-raised abalone. Withering syndrome reduced the number of hatchery-raised abalone from 100,000 to 18,000 in 2002.[17]

Pink abalone were once landed in quantities as large as 1.2 million per year during the peak of this fishery (1952) but are now absent from many survey areas in the northern Channel Islands. Fishery-independent declines of pink abalone preceded the fishery collapse (Davis et al. 1992) as did fluctuations in recruitment and recruitment failure (Davis 1995), suggesting that warning signs were present in the early 1990s. In 2000, diver surveys found pink abalone at only 1 site, inside the Anacapa Island Ecological Reserve (42 per hectare), of the 16 sites surveyed around five islands (fig. 2). This protected site, despite having fewer pink abalone than the nearby fished site when the fishery-independent surveys began in 1983, had significantly more abalone, of a greater mean size yielding higher estimates of egg production, than the nearby fished site by the end of the surveys (Rogers-Bennett et al. 2002). Abalone inside protected areas have been shown to have greater reproductive potential than those in fished areas (Wallace 1999; Rogers-Bennett et al. 2002), as has been observed with fin-fishes (Roberts and Polunin 1991; Paddack and Estes 2000). Once abalone abundances fall too low, however, populations may not recover, as was demonstrated by the failure of abalone restoration efforts using a fishery closure from the Palos Verdes Peninsula to Dana Point in southern California (Tegner 1993, 2000).

Restoration experiments aggregating 600 pink abalone broodstock were begun in 1995 in Channel Islands National Park. Preliminary results suggest that recruitment occurred in 1998 and that adult densities still exceed 2,000 animals per hectare; however, the population is declining at about 15% a year, presumably due to attrition through old age (Davis 2000). Time will tell the fate of this aggregation experiment.

Black abalone densities have been reduced by 99% (fig. 3) as a result of the combined impacts of fishing and Withering Syndrome (Haaker et al. 1992; Davis et al. 1992; Altstatt et al 1996; Moore et al. 2000). Mass mortalities associated with Withering Syndrome were first observed in 1986 at Anacapa Island; the disease spread north to central California (Steinbeck et al. 1992; Altstatt et al. 1996) and then to other offshore islands (VanBlaricom et al. 1993) and to other species. Increases in sea water temperature have been shown in the laboratory to exacerbate mortality from this disease (Friedman et al. 1997; also see Moore et al., this volume). At Anacapa, Santa Barbara, and Santa Rosa Islands, populations at intertidal sampling sites fell to zero in the mid-1990s, and at San Miguel Island, the coldest of the Channel Islands, densities at three sites average 0.18 animals per square meter in 2001.[18]

Today, survivors of the disease are at exceptionally low densities at sites that once supported 27–74 abalone per square meter (Richards and Davis 1993). It is unknown whether survivors are resistant to the disease, and if so whether this resistance can be passed on to produce disease-resistant progeny. Artificial spawning efforts with black abalone have been unsuccessful to date.[19] Repopulation without intervention seems unlikely since

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[14] B. Owen, pers. comm.

[15] L. Rogers-Bennett, pers. observ.

[16] D. Kushner, pers. comm.

[17] T. McCormick, pers. comm.

[18] Kelp Forest Monitoring Program data.

[19] C. Friedman, pers. comm.

TABLE 5
Abundance of Flat, Pinto, and Red Abalone Observed in Northern California

		Number of abalone			Percentage of total	
Survey period	Investigators	Flat	Pinto	Total[a]	Flat	Pinto
1971	CDFG et al.	22	48	803	3%	6%
1971–72	Gotshall et al.	21	67	500	4%	13%
1975	Schultz and Burge	172	206	10,963	2%	2%
1996–97	Rogers-Bennett and Pearse[b]	57	0	2,162	3%	0
1999–2001	Current study	16	11	6,191	< 1%	< 1%

[a] Flat, pinto, and red abalone combined.
[b] Study conducted at shallow depths more suitable for flat abalone than for pinto abalone.

dispersal distance appears to be short, as indicated by the genetic differentiation of neighboring populations of black abalone in central California (Hamm and Burton 2000). Aggregating resistant broodstock in the wild may facilitate spawning success, yet this could also facilitate the spread of the disease by increasing adult density. A status report on black abalone has recently been funded by the NMFS and will likely be completed in 2003.

Green abalone populations have been greatly reduced from a baseline estimate of 1.5 million; however, there are few current sources of data to compare with this baseline estimate. We know that early in the 1900s green abalone near Avalon on Catalina Island were stacked 4–5 deep in the intertidal zone but were absent just 13 years later (Edwards 1913). These observations along with current low densities and the species shallow-water distribution suggest that this species is particularly susceptible to overfishing. A captive-breeding program has begun for green abalone in southern California (Lapota et al. 2000).

Threaded abalone, which appear to have been even more rare than white abalone, were also occasionally landed in the fishery. The baseline abundance of this species is estimated to have been 21,000 animals in 1971. Had this been known prior to the 1970s, the species could have been excluded from the fishery. In fishery-independent surveys as early as 1974 only one threaded abalone was seen out of 1,876 abalone observed (tab. 3), indicating that this subspecies was rare even in the 1970s.[20] The fishery removed 21,000 threaded abalone from 1969 to 1995, apparently the bulk of the population in southern California. In 2002 only 16 threaded abalone were documented in California, all at depths greater than 20 m.[21] Captive breeding may be the only option for recovery of this subspecies since populations appear to be at such low numbers. Since invertebrate conservation is often species driven, the decisions by taxonomists to “lump or split “ (Murphy 1991) threaded abalone from pinto abalone will be relevant to the conservation status of threaded abalone.

In northern California, pinto and flat abalone both occur at low densities (< 50 per hectare), and recent surveys indicate that they comprise less than 1% of the total abalone population (tab. 5). Populations of flat abalone have remained low in northern California but do not appear to have declined from 1972 levels. In contrast, flat abalone populations in central California have fallen dramatically from 31% to 6% of the population in just 30 years, raising concerns about their persistence in this region.[22] Pinto abalone in northern California have fallen from 13% of the total abalone population in the early 1970s to less than 1% today (tab. 5). Population estimates in northern California suggest that densities of pinto abalone have fallen ten-fold in 30 years. Previous reports suggest that pinto abalone were also found in southern California in the northern Channel Islands, but they have not been observed there for the past two decades.[23] Similarly, pinto abalone have not been observed in central California for at least 30 years (tab. 5). Pinto abalone in northern California may have declined due to light fishing pressure. It was not until 1999 that pinto and flat abalone were effectively excluded from the recreational fishery in northern California as a result of an increase in the minimum legal size limit from 102 mm (4 in.) for flats and pintos to 178 mm (7 in.) for all species.

Pinto abalone, though rare in northern California, also occur in portions of Oregon, Washington, British Columbia, and Alaska. Surveys conducted in British Columbia in the late 1990s estimate densities ranging from 200 to 2,900 pinto abalone, with a mean density of close to 1,000 per hectare (Campbell 2000b; Lucas et al. 2000). The fishery in all these areas is now closed, and restoration programs including stocking have been proposed (Campbell 2000a),[24] an indication that declines in this species are widespread.

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[20] Burge, R. 1974. Abalone-lobster investigations. 74-KB-15 and 74-M-3. Unpublished cruise report, Calif. Dept. Fish Game, Long Beach, Calif., 6 p.

[21] D. Kushner, pers. comm.

[22] L. Rogers-Bennett, unpubl data.

[23] D. Parker, pers. comm.

[24] M. Banks, pers. comm.

IMPLICATIONS FOR RESTORATION OF ABALONE STOCKS

A network of marine reserves, or no-take areas, has been recommended for a number of fisheries to protect against their collapse and aid in restoration (Roberts and Polunin 1991; Rogers-Bennett et al. 1995; Roberts 1997; Lauck et al. 1998). Scientists advocated establishing a network of abalone reserves in California as early as 1913: "It would be very advantageous to establish a number of protected reservations, similar to those at Monterey Bay and at Venice, at regular intervals [a network] along the coast" (Edwards 1913). A network of reserves was never established. Today, the California Fish and Game Commission is considering establishing a network of no-take reserves along the California coast under the Marine Life Protection Act (AB 993). Already, the commission has approved reserves in the Channel Islands.

Positive multispecies interactions (Bertness and Leonard 1997) can be maintained inside marine reserves (Rogers-Bennett and Pearse 2001). Juvenile abalone, for example, have been observed in close association with the spine canopy of adult red sea urchins (Ebert 1968; Tegner and Dayton 1977). Established marine reserves in northern California with red sea urchins present had significantly more juvenile red abalone and rare flat abalone than fished sites (Rogers-Bennett and Pearse 2001). Sea urchins appear to be vital for the survival of small wild abalone in the 5–20 mm size class (Rogers-Bennett and Pearse 2001; Day and Branch 2002) and hatchery-reared abalone stocked in the ocean (Kojima 1981; Rogers-Bennett and Pearse 1998). This suggests that marine protected areas where red sea urchins are not fished may be essential habitat for abalone and could play a crucial role in restoration efforts. Furthermore, molluscs, such as abalone, may be a good indicator group when selecting marine reserves that could benefit multiple species (Gladstone 2002). Areas that at one time had high numbers of abalone may indicate productive subtidal sites that could be set aside as no-take reserves for multiple species (Rogers-Bennett et al. 2002).

Benthic invertebrates such as abalone, sea urchins, queen conch, and scallops must occur in dense patches to successfully reproduce, suggesting that Allee effects (or depensation) are important (Tegner et al. 1996; Hobday et al. 2001; Levitan et al. 1992; Stoner and Ray-Culp 2000; Stokesbury and Himmelman 1993). Aggregation size and distance between neighbors, in addition to abundance, play important roles in the population dynamics of abalone (Shepherd et al. 2001). Experiments have shown that fertilization may be limiting in populations of *H. laevigata* when distances separating spawning individuals are greater than 2 m (Babcock and Keesing 1999). Studies estimate that if 11% of the remaining white abalone are close enough to a conspecific for successful fertilization, then only 73 pairs of the remaining 3,000 animals have the potential to reproduce successfully (Hobday et al. 2001). Minimum viable population density for *H. laevigata* has been estimated at 2,000 animals per hectare, below which recruitment collapses (Shepard and Brown 1993). More work must be done to set appropriate density goals for abalone restoration in California since reliable estimates of habitat area are lacking in most subtidal areas.

Collapsed populations of abalone worldwide are in need of restoration. In California, restoring abalone (other than those species currently federally listed) will be guided by the state's Abalone Recovery and Management Plan (CDFG Code 5522), which is now under review (Dec. 2002). This study helps to define the challenges of restoring populations to 20% or 40% of baseline. Furthermore, restoration efforts will need to consider the potential impacts of climate change (Tegner et al. 2001), sea otter expansion (Wendell 1994), and illegal take. Restoration will need to be completed prior to the re-opening of abalone fisheries, but restoration to what level? In 1903 a Japanese hard-hat diver in the Mendocino area in northern California could collect an average of 2,300 red abalone in 6 hr (360 min) (Lundy 1997); almost 100 years later (in 2000) only 406 red abalone were found in the same area in 326 min.[25] In 1953 biologists concluded that "too few abalones" were found in northern California in comparison to central and southern California (Cox 1962). These examples reinforce the concern that our perception of abundance, so critical to restoration efforts in southern California and management in northern California, may have become the victim of shifting baselines. The challenge for managers in this and other fisheries will be to set restoration and management goals at baselines that do not rely solely on the limited perspective of modern data but instead take into account historical abundances. The reintroduction of long-lived and high-value species such as abalone in nearshore ecosystems along the northeastern Pacific may be required if they are to get "back to the future" (Pitcher 2001).

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[25] L. Rogers-Bennett, unpubl. data.

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WITHERING SYNDROME AND RESTORATION OF SOUTHERN CALIFORNIA ABALONE POPULATIONS

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ABSTRACT

Withering syndrome is a chronic wasting disease of California abalone (*Haliotis* spp.) first observed in the Channel Islands in the mid-1980s. This fatal disease played a significant role in the demise of southern California black abalone and may also be contributing to the lack of recovery of other species following their severe depletion by overfishing. The causative agent of withering syndrome is an intracellular Rickettsiales-like prokaryote that infects gastrointestinal epithelia. The entire southern California region is considered endemic for this pathogen, and therefore all abalone restoration plans for this area need to consider the implications of its presence. Here we review the current state of knowledge regarding withering syndrome and discuss its potential impact on species recovery programs.

INTRODUCTION

Before the arrival of Europeans, large abalone in southern California were preyed upon primarily by aboriginal peoples and sea otters. During the 1800s the aboriginal peoples were relocated from the Channel Islands and the sea otters were hunted to local extinction. This resulted in higher local population densities of black abalone (*Haliotis cracherodii*) and probably other species than previously experienced in recent history (Davis et al. 1992). Throughout the mid- to late-1900s various abalone species were serially depleted by commercial harvesting (Karpov et al. 2000). Withering syndrome first appeared in the mid-1980s at the Channel Islands in high-density populations of black abalone. Here we review the current state of knowledge regarding withering syndrome and the implications of this disease for abalone recovery programs.

WITHERING SYNDROME

In the mid-1980s large numbers of dying black abalone with severe pedal atrophy and the empty shells of recently deceased black abalone were observed in populations along the central Channel Islands. The term *withering syndrome* (WS) was coined to describe the phenomenon (Haaker et al. 1992). The disease spread throughout the Channel Islands (Lafferty and Kuris 1993; VanBlaricom et al. 1993) and to the mainland (Steinbeck et al. 1992; Alstatt et al. 1996) throughout the early 1990s. Although overfishing had already greatly reduced many black abalone populations in southern California, WS nearly eliminated the remaining populations throughout the Channel Islands and off central California (Haaker et al. 1992; Richards and Davis 1993; Alstatt et al. 1996). Overfishing was responsible for population declines of pink (*H. corrugata*), green (*H. fulgens*), and red abalone (*H. rufescens*) in southern California prior to the appearance of WS (Karpov et al. 2000). WS signs have been observed in all three species (Pete Haaker, pers. comm.), and the impact of WS on the natural recovery of their populations remains unclear. Overfishing had also depleted populations of white abalone (*H. sorenseni*) before the appearance of WS (Davis et al. 1998). In 2001 this species became the first marine invertebrate to be listed under the federal Endangered Species Act (Federal Register 66 (103), 29046-29055, 29 May 2001). Although two shrunken white abalone were collected from Santa Catalina Island in 1993 (cited in Hobday et al. 2001), and 20 freshly dead, undamaged shells were collected from Farnsworth Bank in 1990 (Tegner et al. 1996), shrunken animals can occur for reasons other than WS. Further studies are needed to determine the susceptibility of white abalone to WS. During the 1997–98 El Niño, red abalone farms from Mexico to central California experienced high mortality rates, and animals showed signs of WS (Moore et al. 2000).

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THE ETIOLOGIC AGENT OF WS

During the late 1980s to early 1990s three potential causes of WS were proposed: pollution, starvation (reduced drift algae supply in association with the severe 1982–83 El Niño), and an infectious agent (Davis 1993). Lafferty and Kuris (1993) integrated data sets on WS presence in black abalone, black abalone mortality rates, temperature, kelp abundance, urchin abundance, distance to ports, and current patterns. They concluded that an infectious agent must be responsible for the disease and that elevated temperature, though not a sole cause, resulted in accelerated mortality rates. A coccidian parasite of the kidney (Friedman et al. 1995) was examined as a potential cause but was found to be unassociated with signs of WS (Friedman et al. 1993). Gardner et al. (1995) reported that a Rickettsiales-like prokaryote (WS-RLP) infecting gastrointestinal tissue was present in black abalone from a WS-affected (Channel Islands) population and absent in black abalone from an unaffected population (Ano Nuevo Island, north of Santa Cruz), and that infection intensity was correlated with severity of disease signs. In studies with laboratory-held black abalone, Friedman et al. (1997) reported complex relationships between WS signs, WS-RLP intensity, temperature, and food supply, with some evidence for a role of WS-RLP. In a subsequent study, Friedman et al. (in press) verified that WS-RLP presence is required for WS expression in black abalone, suggesting its etiologic role in this species. Correlation between disease signs and WS-RLP intensity were observed in farmed red abalone during the 1997–98 El Niño (Moore et al. 2000). A series of studies directly implicating WS-RLP in red abalone with WS was reported by Moore et al. (2001). Clinical WS signs and WS-related mortality were seen only in animals with severe WS-RLP infections whereas WS-RLP-free animals remained healthy. Data and observations on pathogenesis, ultrastructure (Friedman et al. 2000), and DNA-based detection (Andree et al. 2000; Antonio et al. 2000) indicate that the bacterium infecting red and black abalone hosts is a single species. WS-RLP infections have been detected in pink and green abalone (CDFG, unpubl. observ.), whereas the susceptibility of white, flat, and pinto abalone remains unknown. The region from central California to northern Mexico can be considered endemic for WS-RLP. Therefore, any abalone restoration activities in southern California need to address the potential impact of this disease.

PHYLOGENY OF WS-RLP

Friedman et al. (2000) named WS-RLP "*Candidatus* Xenohaliotis californiensis" and described its phylogenetic placement within the order Rickettsiales based on morphological characteristics and the DNA sequence of its 16sRNA gene. The term "*Candidatus*" in the taxon indicates that the species was described largely on morphological and DNA sequence-based data and that the serological and biochemical analyses necessary for a complete description is lacking (Murray and Stackebrandt 1995). The order Rickettsiales comprises a large and diverse group of obligate intracellular, gram-negative bacteria, often pathogenic for one or more host species while exhibiting benign infections in closely related species. This group contains the agents of Rocky Mountain Spotted Fever, scrub typhus, Q fever, and typhus in humans, a wide variety of diseases in other mammals (Krieg and Holt 1984), piscirickettsiosis in salmon (Fryer and Lannan 1994), stained prawn disease (Bower et al. 1996), necrotizing hepatopancreatitis in shrimp (Brock et al. 1986), and a large number of poorly described pathogens in many aquatic animal taxa (Sparks 1985). Rickettsiales-like prokaryotes are common in branchial and digestive epithelia of marine molluscs where they often appear benign (Elston 1986; Fryer and Lannon 1994; Sparks 1985).

Nearly all Rickettsiales-like prokaryotes with terrestrial hosts require an arthropod vector (e.g., mosquitoes, fleas, lice, ticks) for spread between individuals. This characteristic is related to their intracellular location and to the inability of most to survive even transient desiccation. Our studies with WS-RLP in black and red abalone suggest that no arthropod vector is required—that is, direct transmission occurs between individuals (Moore et al. 2001; Friedman et al., in press). This finding is in agreement with findings on other marine Rickettsiales-like prokaryotes (e.g., *Piscirickettsia salmonis* of salmon [Cvitanich et al. 1991] and two that infect shrimp [Brock et al. 1986; Bower et al. 1996]). WS-RLP infects gastrointestinal epithelium. WS-RLP inclusions, each containing thousands of individual bacteria, are readily observed bursting into the lumen of the gastrointestinal tract. As with most gastrointestinal pathogens the spread of WS-RLP between individuals is likely fecal-oral.

ORIGIN AND POTENTIAL RESERVOIRS OF WS-RLP

The devastating impact of WS-RLP on black abalone populations suggests that it is a nonnative pathogen. Although we lack historical data to determine whether WS-RLP was present in Channel Island abalone populations before the arrival of WS, we have documented its sudden appearance off the central California coast. Until the mid-1990s, high population densities of black abalone at Vandenberg Air Force Base, resulting from restricted access and the absence of sea otters, were similar to population densities at the Channel Islands prior to the appearance of WS. WS-RLP was absent from this population until approximately 1994, when the first observations of WS were made (Friedman, unpubl. obs.; Alstatt et al. 1996). Abalone are taxonomically placed within the family Haliotidae, which is in the order Archeogastropoda of class Gastropoda, phylum Mollusca. Intracellular bacterial pathogens such as those in the order Rickettsiales do not have extremely broad host ranges, and the original host species of WS-RLP is likely another haliotid, archeogastropod, or gastropod mollusc. It is possible that nonhaliotid gastropods in southern California are susceptible to infection and could act as reservoirs for the pathogen even in the absence of abalone. This could have important implications for abalone species recovery programs. We have examined a limited number of limpets and other gastropods after cohabitation with infected abalone and have not detected WS-RLP, although further studies are needed to conclude a lack of susceptibility of nonhaliotid gastropods.

FACTORS AFFECTING DISEASE EXPRESSION

The key factors governing WS expression in abalone are (1) the presence of WS-RLP, (2) host species, and (3) temperature, clearly the most important environmental factor. Among local black abalone populations, animals with WS signs were seen exclusively within the heated seawater discharge plume of the Diablo Canyon Power Plant, where temperatures measured up to 11°C above ambient (Steinbeck et al. 1992). Mortality was positively correlated with temperature among Channel Islands black abalone populations experiencing WS (Lafferty and Kuris 1993). Elevated mortality and lower relative weights occurred during El Niño events in black abalone populations at Santa Cruz Island (Tissot 1995). Friedman et al. (1997) reported that elevated water temperature accelerated the mortality rate in laboratory-held black abalone, but animals in colder water also eventually succumbed. The red abalone culture industry has provided insight into the dynamics of WS in this species. Southern and central California red abalone farms typically experience some degree of WS in the summer or fall. Severity is associated with water temperature; the 1997–98 El Niño with temperatures above 23°C was particularly devastating. In a 220-day experiment, red abalone held at 18.5°C had higher mortality, more WS signs, and higher WS-RLP burdens than those held at 14.7°C (Moore et al. 2000). Although low temperature clearly provides a thermal refuge from the pathogenicity of WS-RLP infection in red abalone during the first several years of life, the effect of low-level, chronic infection over a multidecade potential life span remains undetermined. Temperature fluctuations due to seasonality, El Niño/La Niña events, and potential global warming make the long-term impact of WS in red abalone difficult to assess. Temperature likely plays a significant role in WS expression in pink and green abalone, though these species have yet to be studied. The true success of future southern California abalone restoration activities can only be gauged after populations have experienced the broad range of environmental temperatures that occur over multiyear or multidecade cycles. We have detected WS-RLP in experimentally exposed red abalone as small as 3 mm shell length (J. Moore and C. Finley, unpubl. obs.), but further research is needed to determine the life stages at which different species of abalone are susceptible to WS-RLP infection and clinical expression of WS.

POTENTIAL DEVELOPMENT OF RESISTANCE

Black abalone have nearly disappeared from southern California. Since WS-RLP is now endemic throughout southern California, restoration of black abalone (and probably other species) will depend upon natural or hatchery-assisted development of resistant stocks. When a severe selection pressure, such as epidemic disease, sweeps through a population, genetic diversity between individuals can result in survival of a proportion that are "resistant." This previously indistinguishable subset can become the founder population if sufficient numbers of survivors with sufficient genetic diversity remain. The resistance is typically graded rather than absolute—for example, some individuals may survive only slightly longer than average before succumbing to a disease, and others may be able to reproduce before doing so. The disease caused by *Bonamia ostreae*, a protozoan that parasitizes hemocytes in European oysters, *Ostrea edulis*, provides an example. The disease, bonamiasis, was first described in Brittany in 1979 (Comps et al. 1980), the pathogen apparently arriving via the introduction of infected oyster seed from California (Elston et al. 1987). Bonamiasis caused catastrophic declines in native oyster populations throughout most of Europe, reaching Ireland in the 1980s. Culloty et al. (2001) challenged two naive Irish oyster strains and one selectively bred from survivors that had been exposed to *B. ostreae* since the 1980s. In laboratory and field trials, the selected strain showed lower pathogen prevalence, infection intensity, and mortality compared to the naive strains. Similarly, some selective development of resistance to infectious agents of *Crassostrea virginica* has been detected (e.g., Ford 1988; Davis and Barber 1999). Bower et al. (1999) reported on laboratory and field trials investigating the virulence of the protozoan parasite *Perkinsus qugwadi* to nonnative Japanese scallops *Patinopecten yessoensis* that were either naive (with no history of exposure) or progeny of survivors of a *P. qugwadi* epidemic. The latter group of animals had a lower prevalence and lower intensities of infection after challenge by injection or following deployment in a *P. qugwadi* endemic region. The resistant strain tended to have more intense hemocyte responses to infection, suggesting that resistance was associated with immune system function.

It is important to note that nearly all work concerning development of disease resistance in molluscs has focused on bivalves and the enhancement of managed populations for aquaculture, not on restoring wild populations. In fact, despite the observations above, most experience with oyster disease paints a relatively grim picture with respect to recovery of natural populations via the development of resistance. Two protozoan parasites, *Haplosporidium nelsoni* and *Perkinsus marinus*, remain virulent pathogens severely impacting Atlantic *Crassostrea virginica* populations decades following initial mortality events, and no European populations of *Ostrea edulis* have recovered to levels approaching those before the introduction of bonamiasis, although other pathogens have also contributed. As a result of these experiences, the deployment of a naturally resistant nonnative oyster species is being considered to boost the Atlantic oyster culture industry (Calvo et al. 2000).

There is anecdotal evidence for potential WS-RLP resistance in black abalone. WS was first observed in the Vandenberg Air Force Base population in 1994 (Alstatt et al. 1996). During the 1997–98 El Niño, a large mortality event occurred with up to 80% of individuals exhibiting signs of WS (CDFG, unpubl. obs.). By 1999 densities were less than 1% of the pre-epidemic levels, but those that remained appeared healthy. Animal densities may be too low for this population to recover on its own, and hatchery-based production may be necessary to determine whether these abalone harbor genetically based resistance to WS-RLP. It is important to note that the heritability of this resistance should not be assumed; micro-geographic conditions, food availability, and any number of other nonheritable factors may contribute to realized disease resistance.

SPECIFIC RESTORATION APPROACHES IN SOUTHERN CALIFORNIA

Restoration activities being considered for the recovery of California abalone populations include (1) establishing (or continuing the existence of) protected areas where populations could recover on their own; (2) aggregation of animals to create densities necessary for successful fertilization; and (3) outplanting of hatchery-reared larvae, juveniles, or adults. For white abalone and southern California black abalone, passive methods alone are unlikely to achieve population recovery. Although aggregation increases the likelihood of WS-RLP transmission between individuals, this approach to restoration may be preferable to taking no action because current population densities of white abalone and southern California black abalone are too low to achieve successful fertilization. Outplanting activities for any species must consider the effect of WS on the outplanted animals, taking into account the inevitable occurrence of severe El Niño events. Outplanting of abalone into the WS-RLP-endemic region will be a viable option only if animals do not succumb to WS, which is dependent on thermal regime and species susceptibility. For black abalone, outplanting of animals of any age that are not resistant to WS-RLP may be futile. For red, pink, green, and white abalone, the ecology of WS in each species, particularly with respect to thermal modulation, needs to be determined and considered in the restoration planning process. The health status of any farm-reared abalone should be closely assessed before they are considered for restoration activities. Outplanting of WS-RLP-infected individuals of any species should be carefully considered even if the animals appear healthy. Fortunately, recently developed oral and injection treatments with oxytetracycline have been shown to be very effective against WS-RLP (Friedman et al. 2000) and could be used to eliminate the pathogen from broodstock. While outplanting efforts will always carry some degree of infectious disease risk, this can be minimized by applying knowledge gained about interactions between hosts and potential pathogens.

KEY RESEARCH NEEDS

White Abalone

White abalone is the first marine invertebrate to be listed as endangered under the federal Endangered Species Act. Studies are needed to determine the susceptibility of this species to WS-RLP infection and the role of temperature in WS progression. This information is essential for devising a rational recovery plan.

Pink and Green Abalone

As with white abalone, the relationship between temperature and WS progression in pink and green abalone needs to be determined in order to guide the design of recovery plans for these species.

Nonlethal Diagnostic Methods

To minimize further loss while monitoring natural populations, we need to develop nonlethal diagnostic methods for detecting WS-RLP. These would also be useful for monitoring the WS-RLP status of captive broodstock and their progeny in abalone culture facilities. A polymerase chain reaction-based detection assay (Andree et al. 2000) could provide a foundation for such methods.

Identification and Production of Resistant Stocks

For black abalone and perhaps other species, identification and production of WS-RLP-resistant stocks may offer the only hope for population recovery in southern California. Resistance should be investigated among survivors of WS epidemics.

Variation Among WS-RLP Isolates from Different Regions or Host Species

WS is currently being managed under the assumption that the pathogen is homogeneous throughout its range. This could be investigated through the development of a polymerase chain reaction-based method of detecting nucleic acid variation and periodic sampling within the endemic region.

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Part III

SCIENTIFIC CONTRIBUTIONS

DEEPWATER HABITAT AND FISH RESOURCES ASSOCIATED WITH THE BIG CREEK MARINE ECOLOGICAL RESERVE

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ABSTRACT

Big Creek Marine Ecological Reserve (BCER), located off the central California coast, has been closed to fishing since January 1994. We used side scan sonar and an occupied submersible to collect baseline information on species-habitat relationships, density, and species and size composition of fish inside and outside BCER. Forty-three dives were made in the fall of 1997 and 1998, at depths of 20–250 m. From 142 video transects, we identified over 70,000 fish from 82 taxa, including 36 species of rockfish. About 93% of the 25,159 fish inside BCER were rockfishes representing at least 20 species. Young-of-the-year rockfishes dominated rock outcrops in 20–90 m depth inside and outside BCER. Four distinct fish assemblages were associated with (1) fine, smooth sediment in deep water; (2) bedrock with uneven surface in deep water; (3) sand waves and shell hash in shallow water; and (4) boulders and organic habitats on rock in shallow water. There were no significant differences in fish density among locations (inside and outside BCER) and depths or between years. Density was significantly higher in high-relief rock habitat than in low-relief soft and mixed sediments, regardless of location. There were no consistent patterns of larger fish inside compared to outside the protected area. We recommend development of a monitoring program to continue these surveys after increased time of protection and with increased assessment effort in the appropriate habitats of economically valuable species. In addition, extending the boundaries of BCER seaward would protect habitats and fish in water depths greater than 100 m.

INTRODUCTION

Marine reserves (also known as no-take areas, marine protected areas [MPAs], and harvest refugia) are being considered as a supplement to traditional resource management practices on the West Coast, as well as throughout the world (Rowley 1994; Yoklavich 1998; Murray et al. 1999; Parrish et al. 2000). Reserves serve as undisturbed areas for research on natural populations and as fishery exclusion zones where fish have refuge from exploitation. Marine reserves have demonstrably enhanced fish populations within their borders by (1) increasing fish abundance, size, and reproductive output; (2) protecting critical spawning stocks and habitats; and (3) providing multispecies protection (Dugan and Davis 1993; Halpern in press; Murawski et al. 2000). In addition, fisheries have been identified as a critical threat to biodiversity (Boehlert 1996; Bohnsack and Ault 1996) and to the structure and function of coastal marine ecosystems (Jackson et al. 2001); marine reserves may help to conserve and restore these systems. Unharvested areas also could provide the means to separate the effects of fishing and other human activities on fish populations from the effects of natural changes in the environment. While not as well documented, it also has been suggested that reserves could serve as sources of replenishment to fisheries in unprotected areas.

The Big Creek Marine Ecological Reserve (BCER), located on the central California coast, has been closed to fishing since January 1994. This has afforded researchers the opportunity to collect baseline information on fish species composition, densities, and size, and to initiate an evaluation of potential benefits of BCER to its resources.

Many benthic fish species have affinities for specific seafloor substrata, the type and extent of which can help determine species distribution, abundance, and richness (Richards 1986; Pearcy et al. 1989; Stein et al. 1992; Yoklavich et al. 2000). Studies of marine fish assemblages and their habitats are limited by available technology. Most studies on fish-habitat specificity have been conducted using scuba in shallow (<30 m depth) subtidal environments (e.g., Larson 1980; Carr 1991); surveys in deep water have been logistically more difficult. In recent years a foundation for a systematic approach to characterizing marine habitats and fish assemblages has been developed in deep water using in situ submersible observations and remote geophysical mapping techniques (Yoklavich et al. 1997; Greene et al. 1999; Yoklavich et al. 2000).

Characterizing and quantifying elements of habitat, such as substratum type and water depth, and the association of fish assemblages with habitat are critical in evaluating the effectiveness of BCER in maintaining local fish resources. The overall goal of our research was to inventory and describe fishes and habitats in deep water (i.e., >20 m depth) of BCER. This baseline information will be useful when evaluating future changes to BCER populations of benthic fishes, and particularly to the assessment of nearshore species, as required by the California Department of Fish and Game's new nearshore management plan.

Our objectives during this study were (1) to verify and revise our interpretations of seafloor substrata made from side scan sonar images collected during a previous geophysical survey; (2) to estimate relative abundance and distribution of seafloor habitats; (3) to quantify fish density (number of fish per habitat-specific area), size structure, and species composition and diversity, relative to depth and substrata; (4) to compare these variables between 2 years of continued protection; (5) to test the null hypothesis that there is no difference in fish assemblages (numbers and sizes) between BCER and adjacent unprotected areas to the north and south of BCER.

METHODS

Study Site

BCER is about 8 km^2 in area, located within the Monterey Bay National Marine Sanctuary and about 90 km south of Monterey (fig. 1). It is contiguous with the University of California Landels-Hill Big Creek Reserve, which protects about 16 km^2 of coastal terrestrial habitats. The boundary of BCER extends for 4.5 km along the coast from 36°05.31'N and 121°37'W to 36°03.65'N and 121°35.6'W, and due west offshore to about 100 m water depth.

Our study site was situated on a relatively narrow part of the continental shelf, which leads into several steep submarine canyons along the continental slope. Surveys were conducted during 29 September–4 October 1997 and 20–25 September 1998 inside BCER at water depths of 20–100 m, as well as in areas adjacent to BCER at similar depths; these areas comprised 4.8 km^2 inside the reserve, 7.6 km^2 to the north, and 7.4 km^2 to the south. We also surveyed fishes and habitats in about 4.8 km^2 seaward of these three areas at water depths of 100–250 m.

Distribution and Abundance of Seafloor Substrata

A map of seafloor substratum types was produced from a side scan sonar survey conducted in our study site in June 1996 (Yoklavich et al. 1997). During our recent research we verified and revised our interpretations of this map by direct observations made from the *Delta* submersible. Submersible dive tracks were positioned precisely using acoustic track-point navigation and a differential global positioning system (dGPS). We used this map to quantify the amount of various types of substrata and to locate dive sites for fish and habitat surveys.

Fish and Habitat Surveys

Methodologies to assess benthic fishes and associated habitats in the BCER study site were similar to those used previously during surveys of deepwater fishes and habitats in submarine canyons (Yoklavich et al. 2000). Dives of 1–2 h duration were made in the *Delta* submersible during daylight to avoid bias due to diel activity patterns of some species. Dives were documented continuously with a high-8-mm video camera externally mounted on the starboard side of the submersible. We conducted 1–4 10-min strip transects during each dive, 1–2 m off the seafloor at 0.5–1.0 knots. Transects were verbally annotated by the scientific observer, who identified, counted, and estimated size of all fish within a 2-m strip of the viewing field.

Two parallel lasers were installed on either side of the video camera at 20 cm apart. The laser spots were projected onto the seafloor and were visible to the observer and on the videotape. We made measurements by comparing the size of a fish or habitat feature to the known spacing of the two bright laser spots when the object was perpendicular to the camera and lasers (Tusting and Davis 1993; Yoklavich et al. 2000). We estimated the length of each transect, independent of submersible speed and bottom currents, by counting the number of laser spot intervals as they moved along the seafloor in the video transect.

The type of substratum associated with each fish in the transect was characterized from the videotapes; these included boulder, rock outcrop, vertical rock pinnacle, cobble, sand, hash, organic (e.g., understory algae), and

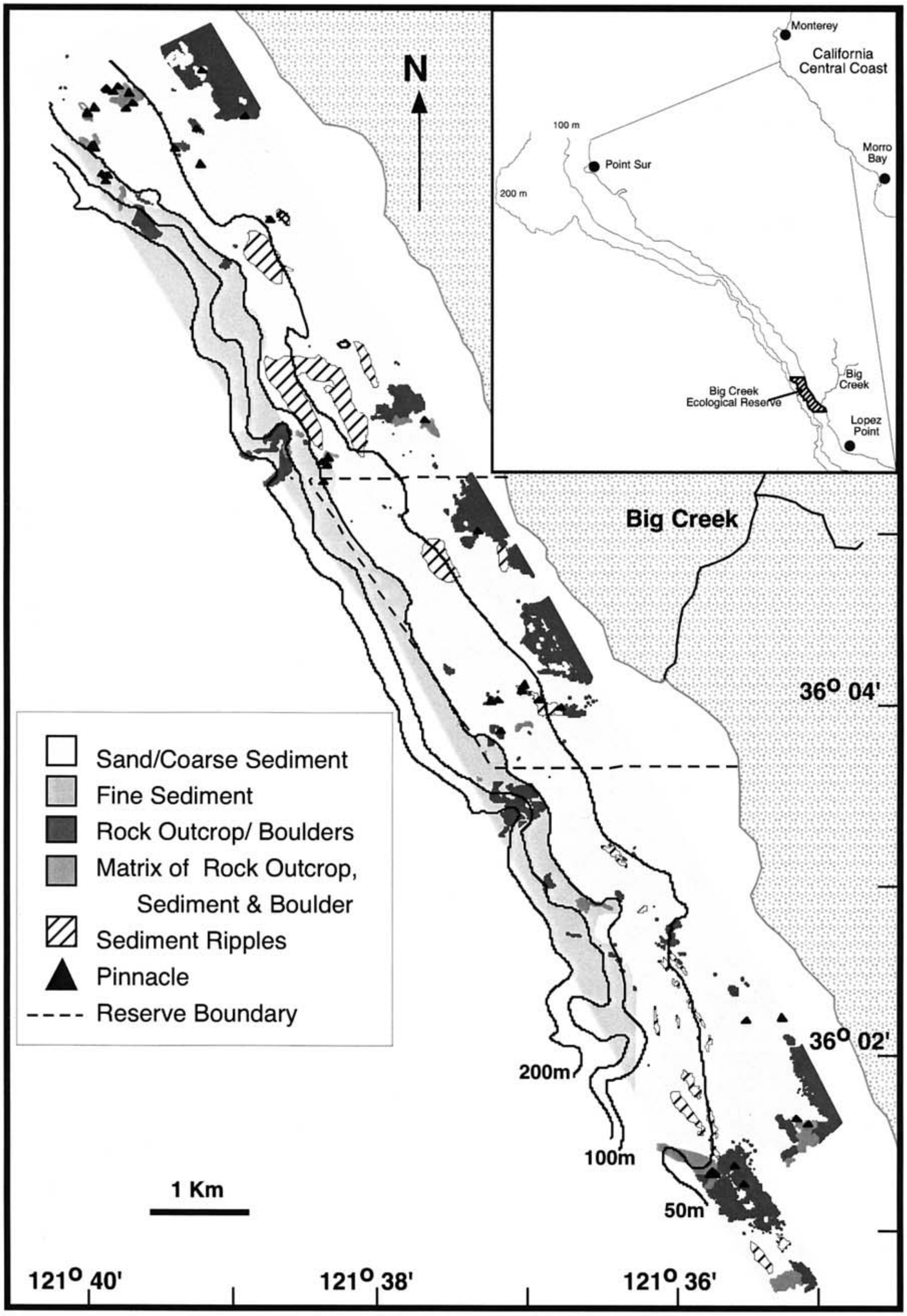

Figure 1. BCER study site off central California (inset modified from Pomeroy 1999). Seafloor substratum types identified from side scan sonar and observations from *Delta* submersible.

fine sediment, as described in Greene et al. (1999). Secondarily, surface morphology also was described as either smooth, uneven (i.e., sediment, rock, or organic substratum with holes, depressions, caves, crevices, ledges, and other rugosities), and sediment waves and ripples.

Various combinations of substrata were categorized according to primary (at least 50% of the area viewed) and secondary (>20% of the area viewed) microhabitat, following the protocol of Stein et al. (1992) and Yoklavich et al. (2000). Areas of uniform substratum composition were quantified along each transect and were used as the sample unit. Species-specific abundance was standardized per area of uniform substratum.

Data Analyses

Canonical correlation analysis (CCA) was used to identify patterns in associations among fishes and characteristics of their habitat. This analysis uses a matrix of species by habitat variables to describe assemblages of fishes. Species were included in analyses if they were nonschooling (i.e., nonpolarized aggregations or solitary individuals) benthic fishes that occurred in at least 5% of all possible habitat patches. Unidentified young-of-the-year rockfishes were not included in these analyses. "Year" (i.e., 1997 and 1998) was included as a covariate; its effect was removed by using a partial CCA to best describe the fish-habitat associations.

We used Analysis of Variance (ANOVA), with balanced design and log transformation of data where appropriate, to compare fish density among location (inside, north, and south of BCER), habitat type, water depth (<35 m, 35–100 m), and year (1997 and 1998). We did not include those species that were particularly mobile and difficult to accurately count (i.e., tubesnout, Pacific saury, Pacific hake, Pacific argentine, young-of-the-year rockfishes, and shortbelly rockfish). Based on the results of the CCA, we defined three groups of habitat types (1) low-relief soft sediments of primarily shell hash and sand; (2) low-relief mixed sediments of cobbles, organic understory, sand, shell hash, and flat rock; and (3) high-relief rock substratum primarily composed of boulders and rock outcrop. We used Tukey post-hoc multiple comparisons of cell means with Kramer's modification to identify specific locations, habitat types, depth, or year that contributed to significant factors in the models.

Overall richness (number of species), Shannon-Wiener diversity index, and evenness (Krebs 1999) were calculated for species assemblages at 15 discrete areas, as identified by depth and substrata on the habitat map.

We used a Kolmogorov-Smirnov goodness-of-fit test to compare size frequency distributions of economically valuable species that occurred at 20–100 m depths inside and outside BCER in each year. Because there was a statistical difference in the size of blue rockfish from <35 m and 35–100 m water depths, we analyzed size distributions from these two depth strata separately.

RESULTS

We completed 142 10-min video transect surveys of fishes and associated habitats during 43 dives (tab. 1). Thirty-nine transects were conducted inside BCER; the rest were located to the north (68 transects) and south (35 transects) of BCER.

Distribution and Abundance of Seafloor Substrata

From submersible observations, we verified our interpretation of 24.6 km^2 of seafloor and modified pre-existing maps to accurately reflect substratum types in 20–250 m water depth (fig. 1). Sand (grain size = 0.06–2 mm diameter) substratum of low relief was located almost entirely on the shelf in water depths <100 m; sand represented 64% of the seafloor types within the reserve (tab. 2). We could not distinguish fine and coarse sediments (grain size <0.06 mm) from the side scan sonar images; however, our observations from the submersible revealed that fine sediment typically occurred at water depths >100 m, and coarse sediments were found at depths <100 m. Sediment was distinct from sand substratum in both the side scan sonar and video images. Ninety percent of the seafloor in water depth > 100 m was identified as fine sediment (tab. 2).

TABLE 1
Distribution of Submersible Dives and Strip Transects Conducted Inside and Adjacent to BCER, 1997 and 1998

			Adjacent to BCER					
	Inside BCER		North		South		Total	
	1997	1998	1997	1998	1997	1998	1997	1998
No. of dives	5	5	8	13	7	5	20	23
No. of transects								
depth <35 m	6	5	4	7	2	0	12	12
depth 35–100 m	11	17	10	21	9	7	30	45
depth >100 m	0	0	12	14	10	7	22	21
Total	17	22	26	42	21	14	64	78

TABLE 2
Occurrence of Each Substratum Type as Determined by Surveys Using Side Scan Sonar and Observations from a Submersible

	Within BCER		Adjacent to BCER, depth >100 m		North of BCER, depth <100 m		South of BCER, depth <100 m	
Substratum type	**km²**	**%**	**km²**	**%**	**km²**	**%**	**km²**	**%**
Fine sediment	0.02	0.5	4.37	90.4	0.07	1.0	0.10	1.4
Sand	3.08	63.6	0.01	0.1	1.49	19.7	2.70	36.6
Coarse sediment	0.99	20.5	0.14	3.0	4.68	61.6	3.60	48.9
Boulders	0.01	0.2	0.00	0.1	0.03	0.3	0.08	1.1
Rock outcrop	0.55	11.5	0.29	5.9	0.56	7.3	0.49	6.7
Rock/sediment	0.05	1.1	0.02	0.4	0.10	1.3	0.18	2.5
Sediment ripples	0.13	2.7	—	—	0.67	8.8	0.21	2.8
Total area	4.84		4.83		7.60		7.37	

TABLE 3
Total Number (*n*), Relative Abundance (%), and Rank Abundance of Fish Taxa Observed from the *Delta* Submersible, Fall 1997 and 1998 (data ordered by total number from 1997)

a. Inside BCER

		1997			1998		
Scientific name	**Common name**	*n*	%	Rank	*n*	%	Rank
Sebastes spp. (YOY)[a]	unidentified rockfishes	8,235	64.6	**1**	2,044	16.5	**3**
Sebastes semicinctus (YOY)	halfbanded rockfish	2,236	17.5	**2**	667	5.4	**5**
Sebastes mystinus	blue rockfish	918	7.2	**3**	755	6.1	**4**
Citharichthys stigmaeus	speckled sanddab	359	2.8	**4**	65	0.5	12
Sebastes wilsoni	pygmy rockfish	200	1.6	**5**	118	1.0	**9**
Aulorhynchus flavidus	tubesnout	153	1.2	**6**	—		
Rhinogobiops nicholsii	blackeye goby	146	1.1	**7**	127	1.0	**8**
Oxylebius pictus	painted greenling	115	0.9	**8**	73	0.6	11
Citharichthys sordidus	Pacific sanddab	91	0.7	**9**	52	0.4	16
Sebastes serranoides	olive rockfish	73	0.6	**10**	89	0.7	**10**
Pleuronectiformes	unidentified flatfishes	37	0.3	11	21	0.2	20
Sebastes carnatus	gopher rockfish	23	0.2	12	33	0.3	18
Sebastes spp.	unidentified rockfishes	18	0.1	13	343	2.8	**6**
Pisces	unidentified fishes	18	0.1	13	248	2.0	**7**
Sebastomus spp.[b]	*Sebastomus* rockfishes	16	0.1	15	55	0.4	15
Embiotoca lateralis	striped surfperch	15	0.1	16	5	<0.1	32
Ophiodon elongatus	lingcod	13	0.1	17	25	0.2	19
Sebastes semicinctus	halfbanded rockfish	12	0.1	18	3,938	31.8	**1**
Damalichthys vacca	pile surfperch	9	0.1	19	4	<0.1	37
Embiotocidae	unidentified surfperches	9	0.1	19	3	<0.1	38
Cottidae	unidentified sculpins	9	0.1	19	—		
Hexagrammos decagrammus	kelp greenling	8	0.1	22	5	<0.1	32
Sebastes caurinus	copper rockfish	6	0.1	23	59	0.5	13
Sebastes atrovirens	kelp rockfish	6	0.1	23	6	0.1	31
Sebastes rosaceus	rosy rockfish	4	<0.1	25	58	0.5	14
Citharichthys spp.	unidentified sanddabs	4	<0.1	25	17	0.1	23
Semicossyphus pulcher	California sheephead	4	<0.1	25	7	0.1	27
Sebastes miniatus	vermilion rockfish	3	<0.1	28	13	0.1	24
Enophrys taurina	bull sculpin	2	<0.1	29	5	<0.1	32
Zalembius rosaceus	pink surfperch	2	<0.1	29	5	<0.1	32
Sebastes pinniger	canary rockfish	2	<0.1	29	1	<0.1	47
Lepidopsetta bilineata	rock sole	2	<0.1	29	—		
Oxyjulis californica	señorita	2	<0.1	29	—		
Phanerodon atripes	sharpnose surfperch	1	<0.1	34	7	0.1	27
Embiotoca jacksoni	black surfperch	1	<0.1	34	1	<0.1	47
Pleuronichthys spp.	turbots	1	<0.1	34	1	<0.1	47
Hypsopsetta guttulata	diamond turbot	1	<0.1	34	—		
Parophrys vetulus	English sole	1	<0.1	34	—		
Sebastes melanops	black rockfish	1	<0.1	34	—		
Sebastes jordani[c]	shortbelly rockfish	—			3,416	27.5	**2**

Note: Boldface indicates a ranking in the top ten.
[a] Young of the year.
[b] The seven species of rockfish within the *Sebastomus* complex that occur off central California are difficult to discern without close examination.
[c] Likely *S. jordani*, but some could be juvenile *S. goodei*.

TABLE 3 (*continued*)

a. Inside BCER

		1997			1998		
Scientific name	Common name	*n*	%	Rank	*n*	%	Rank
Sebastes paucispinis	bocaccio	—			38	0.3	17
Zaniolepis spp.	unidentified combfishes	—			20	0.2	21
Zaniolepis latipinnis	longspine combfish	—			18	0.2	22
Agonidae	unidentified poachers	—			8	0.1	25
Sebastes crameri (YOY)	darkblotched rockfish	—			8	0.1	25
Sebastes crameri	darkblotched rockfish	—			7	0.1	27
Sebastes hopkinsi	squarespot rockfish	—			7	0.1	27
Sebastes carnatus/caurinus[d]	gopher/copper complex	—			5	<0.1	32
Argentina sialis	Pacific argentine	—			3	<0.1	38
Lyopsetta exilis	slender sole	—			3	<0.1	38
Phanerodon furcatus	white surfperch	—			3	<0.1	38
Sebastes ruberrimus	yelloweye rockfish	—			3	<0.1	38
Hydrolagus colliei	spotted ratfish	—			2	<0.1	43
Sebastes flavidus	yellowtail rockfish	—			2	<0.1	43
Sebastes saxicola	stripetail rockfish	—			2	<0.1	43
Zaniolepis frenata	shortspine combfish	—			2	<0.1	43
Micrometrus minimus	dwarf surfperch	—			1	<0.1	47
Raja spp.	unidentifed skates	—			1	<0.1	47
Rathbunella alleni	stripefin ronquil	—			1	<0.1	47
Scorpaenichthys marmoratus	cabezon	—			1	<0.1	47
Sebastes chlorostictus	greenspotted rockfish	—			1	<0.1	47
Sebastes ensifer	swordspine rockfish	—			1	<0.1	47
Total no. of fish		12,756			12,403		
Total no. of rockfish		11,753	(92%)		11,669	(94%)	
Minimum no. of taxa		30			44		
Minimum no. of rockfish species		11			19		

[d] These two similar-looking species are sometimes difficult to discern under water.

Sediment waves and ripples, clearly identified in images from side scan sonar and video, represented 3% of the seafloor inside BCER.

Complex substratum types of relatively high-relief (e.g., boulders [>0.25 m diameter], pinnacles, rock outcrop, and a matrix of rock outcrop, boulder, cobble, and sediment) comprised about 12.8% of the 4.8 km^2 of seafloor that was surveyed inside BCER (tab. 2). Similar proportions of complex rock bottom types were represented in our study areas to the north (8.9%) and south (10.3%) of the reserve at the same water depth. Complex rock outcrop and boulders comprised about 6.4% of the seafloor in water depths >100 m and were found exclusively in the heads of submarine canyons outside BCER.

Fish and Habitat Associations

We identified 70,094 individual fish representing 82 taxa from all video transects (tab. 3). These included at least 36 species of rockfish (genus *Sebastes*). About 93% of the 25,159 fish (representing 49 taxa) counted inside BCER were rockfish comprising at least 20 species (tab. 3a). From those transects conducted at similar water depths (i.e., <100 m), in general there was a greater number of fish and rockfish species inside and to the north of BCER compared to the assemblage surveyed to the south of the reserve (tab. 3b). From 30% to 82% of the fish surveyed in water depths <100 m, both inside and outside BCER, were young-of-the-year rockfishes. We were unable to identify most of these young-of-the-year to species. Young-of-the-year rockfishes represented only 0.7–1.9% of the total number of fish counted in water depths >100 m (tab. 3c).

The most abundant rockfish species (>0.1% of total number of fish) inside BCER in both years included halfbanded, blue, pygmy, olive, and gopher rockfishes. Bocaccio and shortbelly, copper, and rosy rockfishes were relatively abundant (>0.1% of total number of fish) only in 1998. Relatively abundant non-rockfish species inside BCER included speckled and Pacific sanddabs, blackeye goby, and painted greenling. Similar species were relatively abundant outside the reserve to the north at depths <100 m (i.e., halfbanded, blue, pygmy, olive, gopher, copper, and rosy rockfishes), as well as widow, squarespot, and vermilion rockfishes. While far fewer fish and species were surveyed to the south of the reserve at similar depths, species composition was similar.

TABLE 3 (*continued*)

b. North and South of BCER, depth <100 m		North of BCER						South of BCER					
		1997			1998			1997			1998		
Scientific name	Common name	*n*	%	Rank	*n*	%	Rank	*n*	%	Rank	*n*	%	Rank
Sebastes spp. (YOY)[a]	unidentified rockfishes	7,223	64.4	**1**	11,846	74.9	**1**	8,001	80.9	**1**	551	45.8	**1**
Sebastes semicinctus (YOY)	halfbanded rockfish	1,052	9.4	**2**	154	1.0	**8**	20	0.2	11	11	0.9	14
Sebastes mystinus	blue rockfish	474	4.2	**3**	311	2.0	**5**	1,255	12.7	**2**	26	2.2	**8**
Sebastes hopkinsi	squarespot rockfish	459	4.1	**4**	383	2.4	**4**	—			12	1.0	11
Sebastes spp.	unidentified rockfishes	439	3.9	**5**	991	6.3	**2**	12	0.1	18	186	15.4	**2**
Citharichthys spp.	unidentified sanddabs	285	2.5	**6**	45	0.3	14	26	0.3	**9**	—		
Sebastes semicinctus	halfbanded rockfish	214	1.9	**7**	195	1.2	**7**	30	0.3	**8**	175	14.5	**3**
Cololabis saira	Pacific saury	200	1.8	**8**	—			—			—		
Sebastes wilsoni	pygmy rockfish	134	1.2	**9**	747	4.7	**3**						
Phanerodon atripes	sharpnose surfperch	100	0.9	**10**	—			32	0.3	**7**	—		
Sebastes entomelas	widow rockfish	81	0.7	11	298	1.9	**6**	2	<0.01	25	—		
Sebastes serranoides	olive rockfish	59	0.5	12	46	0.3	13	141	1.4	**3**	44	3.7	**5**
Citharichthys stigmaeus	speckled sanddab	58	0.5	13	137	0.9	**10**	23	0.2	**10**	1	0.1	19
Sebastes rosaceus	rosy rockfish	51	0.5	14	62	0.4	11	15	0.2	16	20	1.7	**9**
Zaniolepis spp.	unidentified combfishes	41	0.4	15	—			—			—		
Citharichthys sordidus	Pacific sanddab	40	0.4	16	57	0.4	12	—			—		
Zalembius rosaceus	pink surfperch	37	0.3	17	11	0.1	24	—			—		
Pleuronectiformes	unidentified flatfishes	36	0.3	18	40	0.3	15	6	0.1	19	1	0.1	19
Ophiodon elongatus	lingcod	34	0.3	19	35	0.2	19	20	0.2	11	5	0.4	15
Oxylebius pictus	painted greenling	21	0.2	20	39	0.2	16	108	1.1	**4**	29	2.4	**7**
Pisces	unidentified fishes	19	0.2	21	35	0.2	19	15	0.2	16	12	1.0	11
Sebastes jordani[b]	shortbelly rockfish	17	0.2	22	2	<0.01	39	—			—		
Damalichthys vacca	pile surfperch	16	0.1	23	3	<0.01	36	5	0.1	20	1	0.1	19
Sebastomus spp.[c]	*Sebastomus* rockfishes	15	0.1	24	38	0.2	17	16	0.2	14	4	0.3	16
Sebastes miniatus	vermilion rockfish	14	0.1	25	37	0.2	18	17	0.2	13	13	1.1	**10**
Sebastes caurinus	copper rockfish	14	0.1	25	35	0.2	19	5	0.1	20	4	0.3	16
Rhinogobiops nicholsii	blackeye goby	12	0.1	27	147	0.9	**9**	40	0.4	**6**	53	4.4	**4**
Cottidae	sculpins	9	0.1	28	3	<0.01	36	3	<0.01	24	1	0.1	19
Sebastes carnatus	gopher rockfish	8	0.1	29	23	0.2	22	16	0.2	14	12	1.0	11
Semicossyphus pulcher	California sheephead	6	0.1	30	—			5	0.1	20	—		
Sebastes saxicola	stripetail rockfish	6	0.1	30	—			—			—		
Embiotoca jacksoni	black surfperch	5	<0.01	32	1	<0.01	45	2	<0.01	25	—		
Enophrys taurina	bull sculpin	4	<0.01	33	11	0.1	24	—			—		
Sebastes paucispinis	bocaccio	4	<0.01	33	3	<0.01	36	—			—		
Sebastes pinniger	canary rockfish	3	<0.01	35	6	<0.01	28	1	<0.01	28	3	0.3	18

Note: Boldface indicates a ranking in the top ten.

[a] Young of the year.

[b] Likely *S. jordani*, but some 1998 could be juvenile *S. goodei*.

[c] The seven species of rockfish within the *Sebastomus* complex that occur off central California are difficult to discern without close examination.

TABLE 3 (*continued*)

b. North and South of BCER, depth <100 m		North of BCER						South of BCER					
		1997			1998			1997			1998		
Scientific name	Common name	*n*	%	Rank	*n*	%	Rank	*n*	%	Rank	*n*	%	Rank
Embiotocidae	surfperches	3	<0.01	35	1	<0.01	45	4	<0.01	23			
Oxyjulis californica	señorita	3	<0.01	35	—			64	0.7	5	36	3.0	6
Argentina sialis	Pacific argentine	2	<0.01	38	16	0.1	23	—			—		
Hexagrammos decagrammus	kelp greenling	2	<0.01	38	4	<0.01	32	2	<0.01	25	1	0.1	19
Icelinus filamentosus	threadfin sculpin	2	<0.01	38	1	<0.01	45	—			—		
Zaniolepis latipinnis	longspine combfish	1	<0.01	41	7	<0.01	27	—			—		
Agonidae	unidentified poachers	1	<0.01	41	6	<0.01	28	1	<0.01	28	—		
Pleuronichthys spp.	unidentified turbots	1	<0.01	41	5	<0.01	31	1	<0.01	28	—		
Sebastes ruberrimus	yelloweye rockfish	1	<0.01	41	4	<0.01	32	—			—		
Embiotoca lateralis	striped surfperch	1	<0.01	41	1	<0.01	45	1	<0.01	28	1	0.1	19
Rathbunella alleni	stripefin ronquil	1	<0.01	41	1	<0.01	45	—			—		
Parophrys vetulus	English sole	1	<0.01	41	—			—			—		
Sebastes elongatus	greenstriped rockfish	1	<0.01	41	—			—			—		
Psettichthys melanostictus	sand sole	—			9	0.1	26	—			—		
Sebastes flavidus	yellowtail rockfish	—			6	<0.01	28	—			—		
Lyopsetta exilis	slender sole	—			4	<0.01	32	—			—		
Synodus lucioceps	California lizardfish	—			4	<0.01	32	—			—		
Anarrichthys ocellatus	wolf-eel	—			2	<0.01	39	—			—		
Glyptocephalus zachirus	rex sole	—			2	<0.01	39	—			—		
Microstomus pacificus	Dover sole	—			2	<0.01	39	—			—		
Sebastes helvomaculatus	rosethorn rockfish	—			2	<0.01	39	—			—		
Sebastes rufus	bank rockfish	—			2	<0.01	39	—			—		
Icelinus tenuis	spotfin sculpin	—			1	<0.01	45	—			—		
Sebastes chlorostictus	greenspotted rockfish	—			1	<0.01	45	—			—		
Sebastes constellatus	starry rockfish	—			1	<0.01	45	—			—		
Sebastes serriceps	treefish	—			1	<0.01	45	—			—		
Symphurus atricaudia	California tonguefish	—			1	<0.01	45	—			—		
Torpedo californica	Pacific electric ray	—			1	<0.01	45	—			—		
Sebastes miniatus/pinniger[d]	vermilion/canary complex	—			—			1	<0.01	28	—		
Sebastes nebulosus	China rockfish	—			—			1	<0.01	28	—		
Hydrolagus colliei	spotted ratfish	—			—			—			1	0.1	19
Sebastes carnatus/caurinus[d]	gopher/copper complex	—			—			—			1	0.1	19
Total no. of fish			11,210			15,826			9,891			1,204	
Total no. of rockfish			10,269 (92%)			15,194 (96%)			9,533 (96%)			1,062 (98%)	
Total no. of taxa			38			46			24			19	
Minimum no. of rockfish species			16			20			10			9	

[d] These two similar-looking species are sometimes difficult to discern under water.

TABLE 3 (*continued*)

c. Outside BCER, depths >100 m

		1997			1998		
Scientific name	**Common name**	*n*	%	**Rank**	*n*	%	**Rank**
Merluccius productus	Pacific hake	1,098	23.8	**1**	6	0.3	34
Sebastes jordani[a]	shortbelly rockfish	1,007	21.8	**2**	201	9.2	**3**
Sebastes spp.	unidentified rockfishes	297	6.4	**3**	224	10.3	**2**
Sebastes semicinctus	halfbanded rockfish	232	5.0	**4**	114	5.2	**7**
Sebastes wilsoni	pygmy rockfish	207	4.5	**5**	356	16.3	**1**
Pleuronectiformes	unidentified flatfishes	206	4.5	**6**	141	6.5	**4**
Sebastomus spp.[b]	*Sebastomus* rockfishes	173	3.7	**7**	127	5.8	**5**
Sebastes miniatus/pinniger[c]	vermilion/canary complex	155	3.4	**8**	—		
Sebastes saxicola	stripetail rockfish	118	2.6	**9**	20	0.9	20
Agonidae	unidentified poachers	97	2.1	**10**	93	4.3	**8**
Sebastes crameri	darkblotched rockfish	92	2.0	11	28	1.3	17
Sebastes spp. (YOY)[d]	unidentified rockfishes	88	1.9	12	15	0.7	25
Argentina sialis	Pacific argentine	83	1.8	13	42	1.9	16
Sebastes helvomaculatus	rosethorn rockfish	77	1.7	14	68	3.1	**9**
Sebastes elongatus	greenstriped rockfish	71	1.5	15	47	2.2	15
Sebastes chlorostictus	greenspotted rockfish	67	1.5	16	67	3.1	11
Sebastes entomelas	widow rockfish	64	1.4	17	2	0.1	42
Microstomus pacificus	Dover sole	54	1.2	18	61	2.8	13
Zoarcidae	unidentified eelpouts	44	1.0	19	24	1.1	18
Citharichthys spp.	unidentified sanddabs	44	1.0	19	—		
Lyopsetta exilis	slender sole	38	0.8	21	15	0.7	25
Sebastes paucispinis	bocaccio	35	0.8	22	8	0.4	31
Pisces	unidentified fishes	34	0.7	23	125	5.7	**6**
Citharichthys sordidus	Pacific sanddab	31	0.7	24	5	0.2	36
Hydrolagus colliei	spotted ratfish	23	0.5	25	12	0.5	29
Sebastes hopkinsi	squarespot rockfish	22	0.5	26	24	1.1	18
Zalembius rosaceus	pink surfperch	20	0.4	27	18	0.8	21
Sebastes rufus	bank rockfish	18	0.4	28	58	2.7	14
Zaniolepis spp.	unidentified combfishes	17	0.4	29	14	0.6	27
Glyptocephalus zachirus	rex sole	16	0.3	30	65	3.0	12
Sebastolobus spp.	unidentified thornyheads	10	0.2	31	—		
Ophiodon elongatus	lingcod	9	0.2	32	14	0.6	27
Sebastes rosenblatti	greenblotched rockfish	9	0.2	32	8	0.4	31
Lycodes cortezianus	bigfin eelpout	9	0.2	32	7	0.3	33
Sebastes pinniger	canary rockfish	8	0.2	35	1	0.0	49
Sebastes ruberrimus	yelloweye rockfish	7	0.2	36	11	0.5	30
Zaniolepis latipinnis	longspine combfish	6	0.1	37	16	0.7	23
Sebastes zacentrus	sharpchin rockfish	5	0.1	38	68	3.1	**9**
Rajiformes-egg cases	skate egg cases	5	0.1	38	—		
Cottidae	unidentified sculpins	4	0.1	40	18	0.8	21
Eptatretus stoutii	Pacific hagfish	4	0.1	40	4	0.2	38
Chilara taylori	spotted cusk-eel	3	0.1	42	2	0.1	42
Sebastes ovalis	speckled rockfish	2	<0.1	43	1	0.1	49
Stichaeidae	unidentified pricklebacks	2	<0.1	43	1	0.1	49
Enophrys taurina	bull sculpin	1	<0.1	45	6	0.3	34
Sebastes constellatus	starry rockfish	1	<0.1	45	4	0.2	38
Sebastes levis	cowcod	1	<0.1	45	2	0.1	42
Sebastolobus alascanus	shortspine thornyhead	1	<0.1	45	2	0.1	42
Porichthys notatus	plainfin midshipman	1	<0.1	45	1	0.1	49
Raja spp.	unidentified skates	1	<0.1	45	1	0.1	49
Pleuronichthys spp.	unidentified turbots	1	<0.1	45	—		
Raja inornata	California skate	1	<0.1	45	—		
Sebastes ensifer	swordspine rockfish	—			16	0.7	23
Sebastes diploproa	splitnosed rockfish	—			5	0.2	36
Zaniolepis frenata	shortspine combfish	—			4	0.2	38
Sebastes miniatus	vermilion rockfish	—			3	0.1	41
Anoplopoma fimbria	sablefish	—			2	0.1	42
Sebastes nigrocinctus	tiger rockfish	—			2	0.1	42

Note: Boldface indicates a ranking in the top ten.

[a] Likely *S. jordani*, but some in 1998 could be juvenile *S. goodei*.

[b] The seven species of rockfish within the *Sebastomus* complex that occur off central California are difficult to discern without close examination.

[c] These two similar-looking species are sometimes difficult to discern under water.

[d] Young of the year.

TABLE 3 (*continued*)

c. Outside BCER, depths >100 m

		1997			1998		
Scientific name	Common name	*n*	%	Rank	*n*	%	Rank
Synodus lucioceps	California lizardfish	—			2	0.1	42
Icelinus filamentosus	threadfin sculpin	—			1	0.1	49
Parophrys vetulus	English sole	—			1	0.1	49
Sebastes babcocki	redbanded rockfish	—			1	0.1	49
Sebastes gilli	bronzespotted rockfish	—			1	0.1	49
Total no. of fishes			4,619			2,185	
Total no. of rockfishes			2,756 (60%)			1,482 (68%)	
Minimum no. of taxa			39			49	
Minimum no. of rockfish species			19			25	

The CCA of fish density constrained by habitat data revealed a primary separation of species by depth (fig. 2; axis 1 accounted for 62% of the total variance) and a secondary separation of species based on combinations of substrata, seafloor morphology, and degree of slope (axis 2 accounted for 16% of the variance). All species to the right of the vertical line (fig. 2a) occurred in relatively deep water; the depth gradient increased from the center point to the right in Figure 2b. There were two deepwater groups (the two quadrants on the ordination) within the deepwater assemblage: (1) Dover, rex, and slender soles, poachers, and Pacific hake were found on deep, smooth, fine sediment; unidentified flatfishes also were found on smooth, fine sediments of various depths; and (2) the rockfishes (rosethorn, greenspotted, bank, yelloweye, squarespot, and darkblotched) occurred in relatively deep, sloping habitats primarily comprising bedrock and some cobble with uneven surface morphology. In addition, pygmy rockfish stood out as an idiosyncratic species that also was related to deep rock habitats with uneven surfaces. Stripetail, sharpchin, and greenstriped rockfishes occurred in the deepwater assemblage but were not strictly associated with either rock or fine sediments.

Within the relatively shallow fauna, there also were two groups: (1) speckled and Pacific sanddabs and unidentified sculpins were found on sand waves and ripples and shell hash; and (2) the rockfishes (olive, blue, gopher, rosy, copper, vermilion, and halfbanded), painted greenling, blackeye goby, sharpnose surfperch, and señorita were associated with boulders and organic habitats (such as kelp and understory algae) that overlay rock outcrop.

From these primary (depth) and secondary (substratum type) habitat characteristics, the seafloor along each transect was categorized into three general types of habitats: high-relief rock; low-relief mixed sediments; and low-relief soft sediment. Relative percentage of each of these habitat types varied by depth and location (tab. 4).

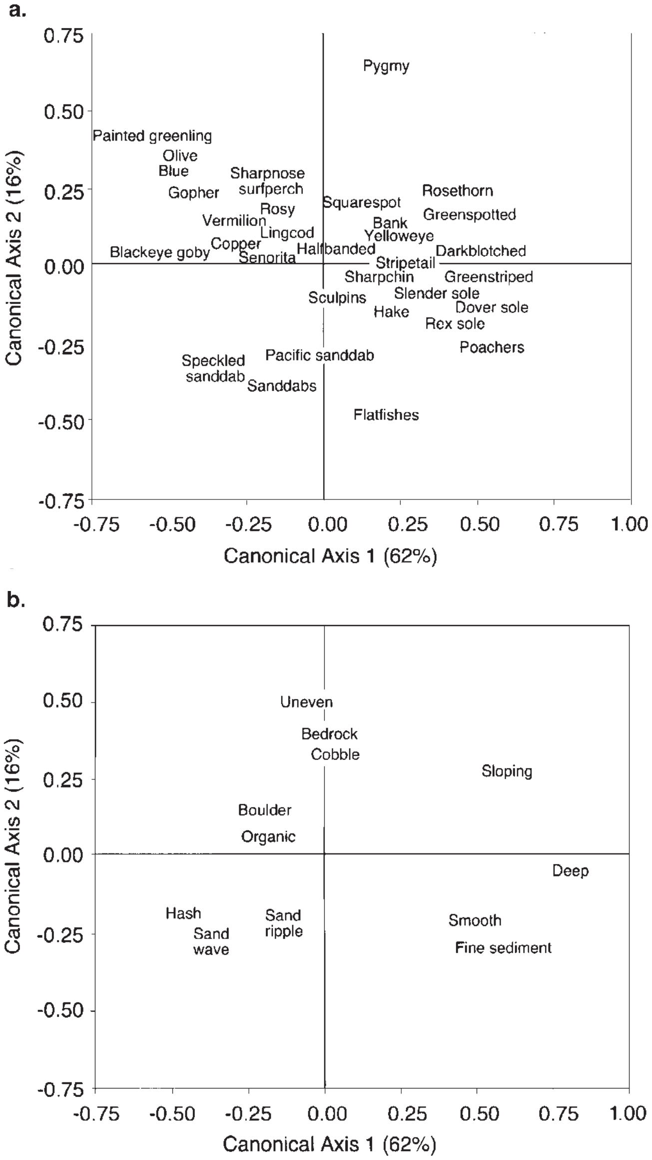

Figure 2. Results of canonical correlation analysis of fish-habitat data. (*a*) Coefficients (scores) for species; (*b*) coefficients for habitat variables.

TABLE 4

Total Area (m^2) Surveyed During Quantitative Transects Inside and Adjacent to BCER, by depth and habitat type

		Inside BCER			North of BCER			South of BCER			
Year	Depth (m)	Rock	Mixed	Soft	Rock	Mixed	Soft	Rock	Mixed	Soft	Total
1997	<35	1,287	52	693	618	283	748	183	68	599	4,529
	35–100	1,019	654	2,530	835	1,011	1,980	1,411	1,262	1,339	12,040
	>100	—	—	—	1,624	549	2,470	1,167	621	2,379	8,810
1998	<35	1,244	192	779	579	390	1,332	—	—	—	4,517
	35–100	1,488	377	3,587	1,313	128	6,156	973	625	959	15,606
	>100	—	—	—	2,188	182	3,710	562	148	1,890	8,680
Total		5,038	1,274	7,589	7,157	2,544	16,395	4,295	2,723	7,166	54,182

TABLE 5

Results of Analysis of Variance (ANOVA) and Tukey Post Hoc Multiple Comparison (with Kramer's Modification) of Fish Density (no. fish/m^2) in 1997

Location: North, inside, south of BCER
Substrata: High-relief rock, low-relief mixed rock, low-relief soft sediment
Depth: 1 = <35 m, 2 = 35–100 m

	ANOVA				
Source	Sum-of-squares	df	Mean-square	*F*-ratio	*p* value
Location	0.024	2	0.012	0.546	0.580
Substrata	0.553	2	0.276	12.825	**0.000**
Depth	0.011	1	0.011	0.516	0.474
Location*Substrata	0.041	4	0.010	0.474	0.755
Location*Depth	0.022	2	0.011	0.507	0.603
Substrata*Depth	0.008	2	0.004	0.187	0.829
Depth*Substrata*Location	0.001	4	0.000	0.017	0.999
Error	3.622	68	0.022		

Note: Boldfacing indicates statistical significance.

Tukey Post Hoc Multiple Comparison (with Kramer's Modification) to Test Fish Density Among Substrata Categories

	High-relief rock	Low-relief mixed rock	Low-relief soft sediment
Adj. least squares mean	0.205	0.084	0.042
SE	0.023	0.027	0.024
N	69	54	63

Overall we visually surveyed 13,901 m^2 of seafloor inside BCER during 1997 and 1998, and 15,373 and 7,410 m^2 to the north and south in similar water depths (20–100 m) as BCER, respectively. While the relative percent of low-relief soft sediment generally was high in these surveys, we focused effort in the complex habitats with high species density and diversity. Low-relief mixed sediment habitat occurred to a lesser amount in the study area and consequently was surveyed to a lesser extent than the other two categories. In deep water outside the reserve, we surveyed mostly high-relief rock habitat and low-relief soft sediment.

Fifteen discrete areas were identified by depth and various substratum types (rock outcrop, sand, pinnacle, etc.) on the habitat map of the entire study site (fig. 3). Overall fish density (excluding young-of-the-year rockfishes) was higher over rock substrata than over sand and fine sediment. The shallow-water assemblages in general were more diverse over rock outcrops than over sand. Some of the shallow-water assemblages were dominated by one or two species (e.g., blue rockfish on shallow pinnacles or outcrops and sanddabs over shallow sand areas), which resulted in low evenness indexes. In general, diversity was higher in deepwater assemblages than in shallow water.

Young-of-the-year rockfishes dominated the fish assemblages on rock outcrops and pinnacles at 20–90 m depth, especially at sites 1, 2, 9, 11, 12, and 15, both inside and outside BCER (fig. 4). Density of young-of-the-year at these sites ranged from 27 to 857 fish per 100 m^2 and represented 38–93% of all fish on the outcrops. Low-relief fields of coarse sand and sea pens in about 70 m of water (site 12) appeared to be a nursery ground for stripetail rockfish in particular (one of the few species of rockfish that was identified from young-of-the-year).

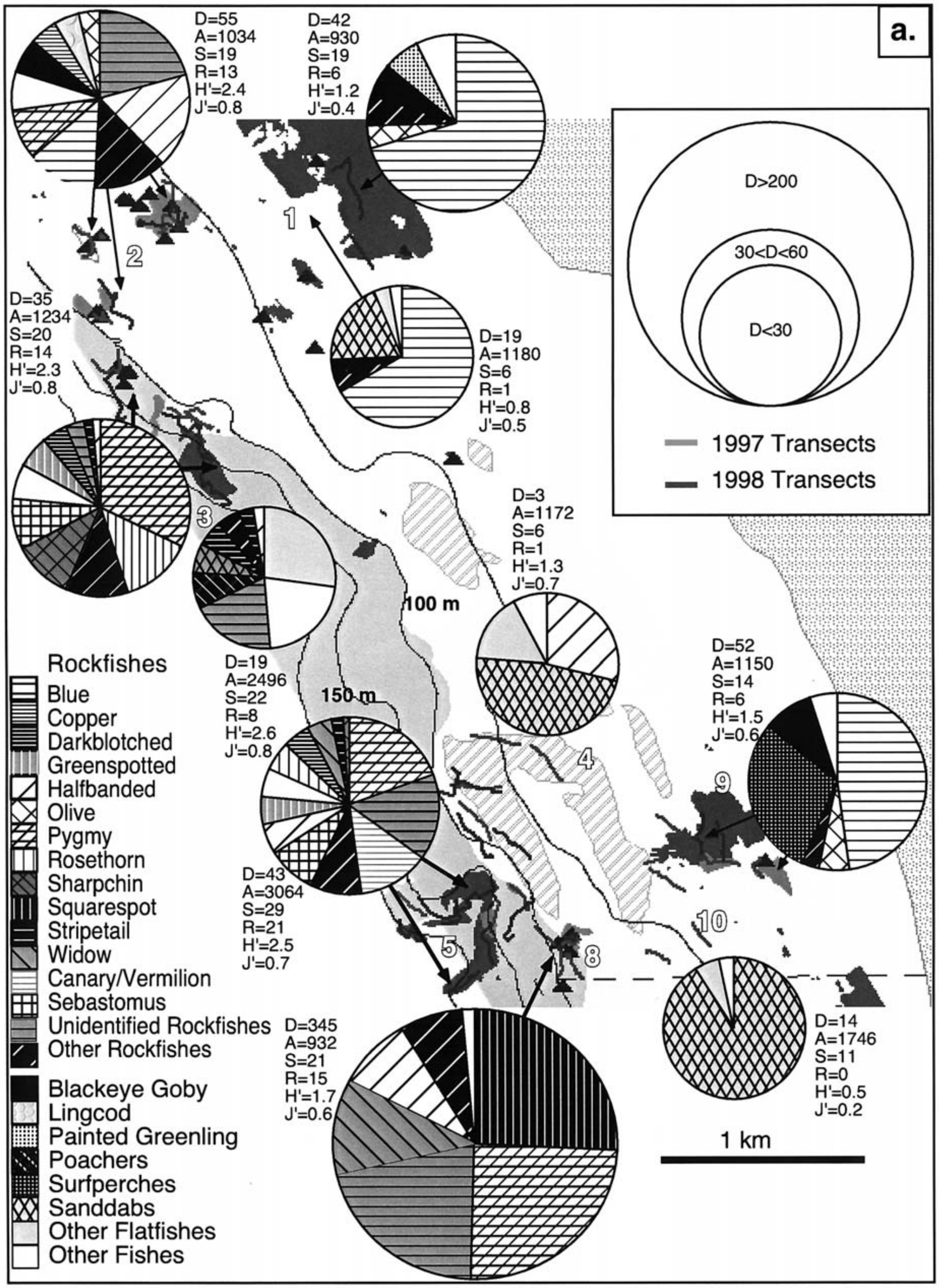

Figure 3. Average density and diversity of benthic fishes at 15 sites in BCER study area. Size of pie diagrams is scaled by density (D = number of fish/100 m^2); A = amount (m^2) of area surveyed; S = minimum number of fish species; R = minimum number of rockfish species; H' = species diversity index; and J' = species evenness index. (a) Sites north of BCER; (b) sites inside and seaward of BCER; and (c) sites south of BCER. (See fig. 1 for seafloor substratum types.)

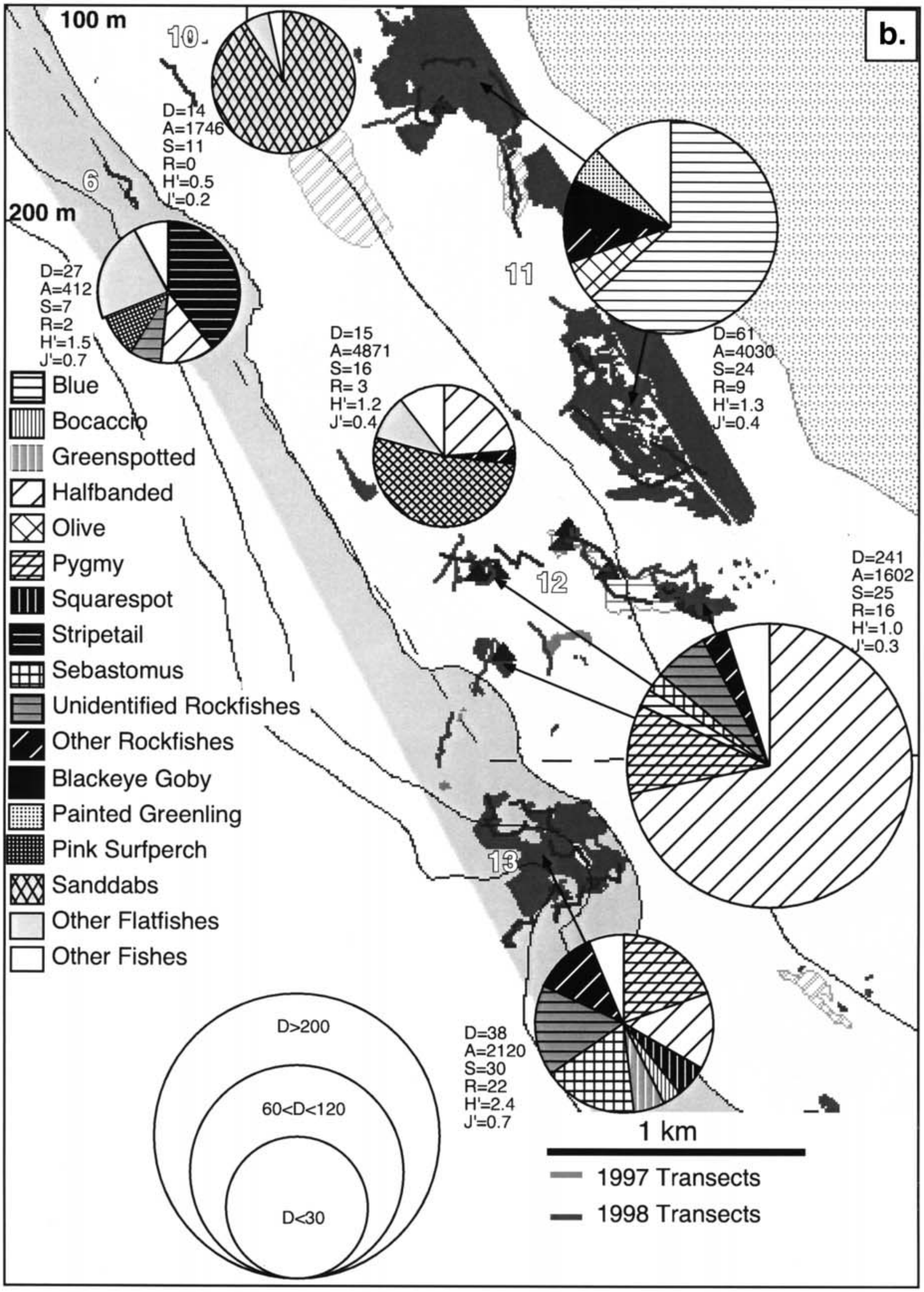

Figure 3. (*continued*)

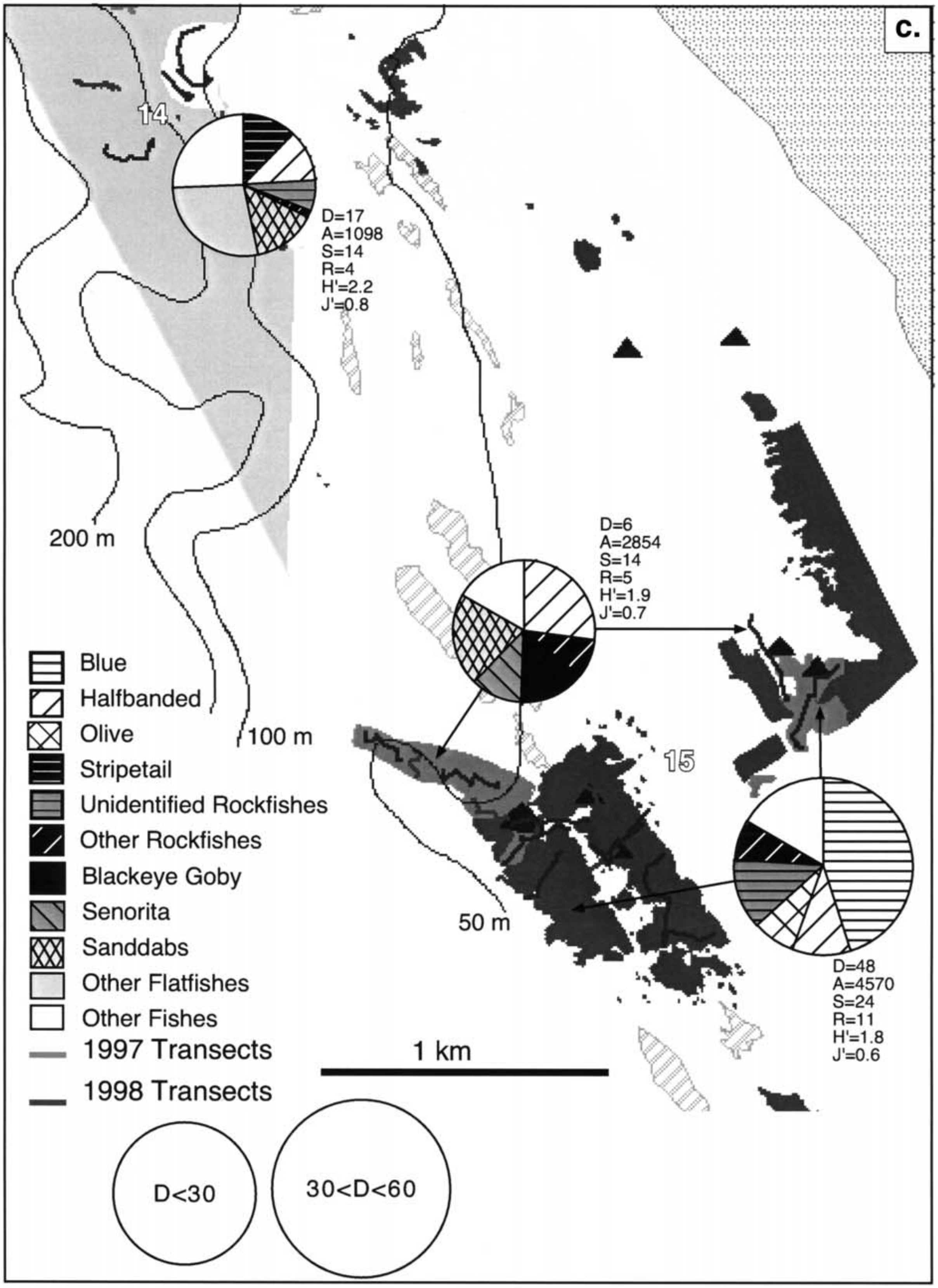

Figure 3. (*continued*)

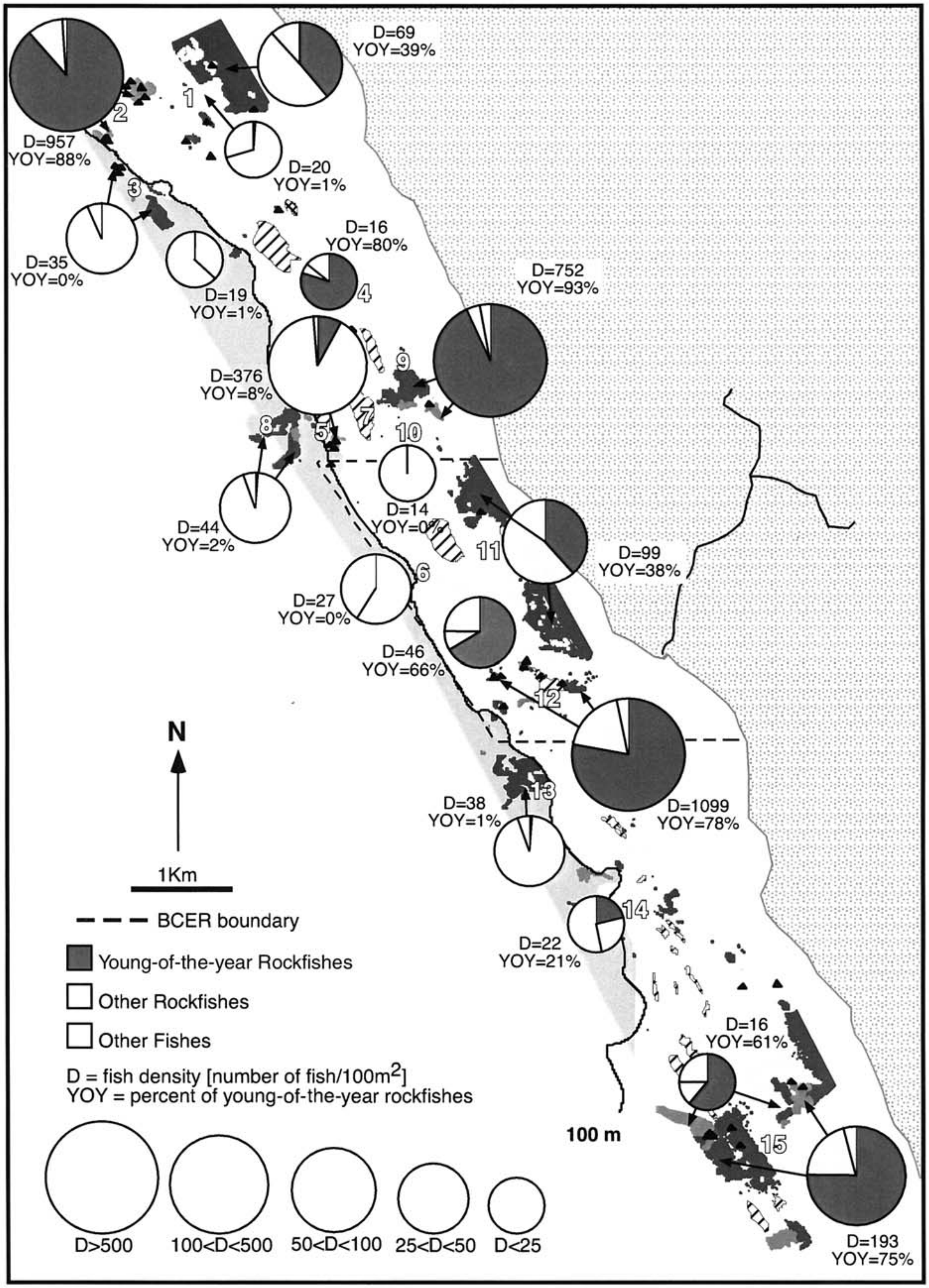

Figure 4. Distribution and average density of young-of-the-year rockfishes, all adult rockfishes, and all other adult fishes at 15 sites in the BCER study area. Pie diagrams are scaled by fish density (D).

TABLE 6
Results of ANOVA and Tukey Post Hoc Multiple Comparison (with Kramer's Modification) of Fish Density (no. fish/m^2) at Depths of 35–100 m

Location: North, inside, south of BCER
Substrata: High-relief rock, low-relief mixed rock, low-relief soft sediment
Year: 1997, 1998

	ANOVA				
Source	Sum-of-squares	df	Mean-square	*F*-ratio	*p* value
Location	0.089	2	0.044	1.587	0.207
Substrata	1.902	2	0.951	34.010	**0.000**
Year	0.080	1	0.080	2.848	0.093
Location*Substrata	0.415	4	0.104	3.707	**0.006**
Location*Year	0.048	2	0.024	0.851	0.428
Substrata*Year	0.177	2	0.088	3.156	**0.045**
Year*Substrata*Location	0.657	4	0.164	5.870	**0.000**
Error	6.040	216	0.028		

Note: Boldfacing indicates statistical significance.

Tukey Post Hoc Multiple Comparison (with Kramer's Modification) to Test Fish Density Among Substrata Categories

	High-relief rock	Low-relief mixed rock	Low-relief soft sediment
Adj. least squares mean	0.266	0.114	0.048
SE	0.020	0.028	0.018
N	85	52	97

Fish Densities in BCER and Unprotected Areas

In a first ANOVA, we compared total fish densities among locations, substratum types, and depths in 1997. Data from 1998 were not included because we did not have an orthogonal sample design; depth was not represented in all combinations of the other factors. There was a significant difference in densities among the three substratum types (tab. 5). Fish density was significantly higher in high-relief rock than in the low-relief soft sediments and mixed rock habitats; densities were not significantly different between the two low-relief habitats. These patterns applied to both depth categories and all three locations (fig. 5). Fish density was not significantly different among locations or between depths, and there were no significant interactions among the factors.

In a second ANOVA, we compared total fish densities at one depth range (35–100 m) between years and among substrata and locations. Both depth categories were not used in this comparison because the shallow depth category (<35 m) was not represented in all combinations of the other factors. Again, the only significant difference among main factors was that of substrata (tab. 6). High-relief rock harbored greater fish densities than low-relief mixed rock and soft sediments; density in low-relief mixed rock was greater than that in low-relief soft sediments (fig. 5). These differences in density with substratum varied with year and location (i.e., there was a significant interaction term in the ANOVA; tab. 6). This variation was due largely to the high densities of fish (notably halfbanded rockfish) in 1998 in high-relief rock inside and north of BCER. There were no significant differences in fish densities among locations and between years (tab. 6).

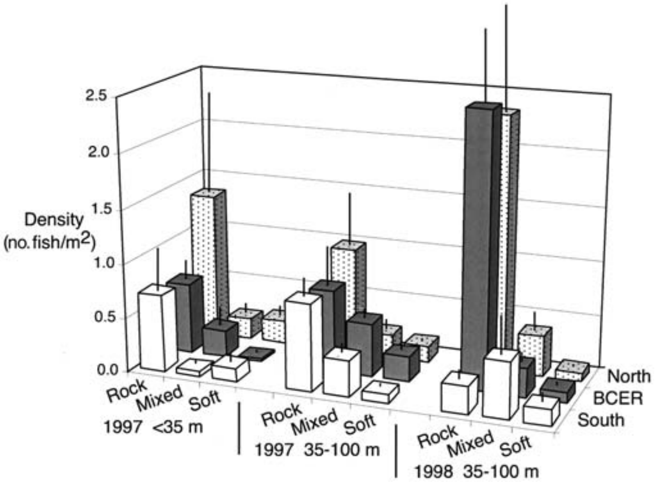

Figure 5. Mean density (no. fish/m^2) of fishes on three types of substratum (high-relief rock [Rock], low-relief mixed rock [Mixed], and low-relief soft sediment [Soft]), at three locations (north of, south of, and inside BCER) in 1997 (at water depths of <35 m and 35–100 m) and 1998 (at water depths of 35–100 m). Error bar is 1 SEM.

In a third ANOVA, we compared densities of eight species of commercial and recreational economic value, including rockfishes (blue, olive, vermilion, canary, gopher copper, and yellowtail), and lingcod, that occurred on high-relief rock substrata among locations and between years. There were significant differences in fish

TABLE 7
Two-factor ANOVA Comparing Fish Density (no. fish/m^2) of Economically Valuable Species (i.e., blue, olive, vermilion, canary, gopher, copper, and yellowtail rockfish and lingcod) on High-Relief Rock Substrata Among Three Locations (north, south, and inside BCER) and Over Two Years (1997 and 1998)

	ANOVA				
Source	Sum-of-squares	df	Mean-square	*F*-ratio	*p* value
Location	0.006	2	0.003	0.163	0.850
Year	0.288	1	0.288	14.720	**0.000**
Location*Year	0.016	2	0.008	0.398	0.673
Error	2.211	113	0.020		

Note: Boldfacing indicates statistical significance.

density between years; adjusted least square mean density was higher in 1997 than in 1998 (tab. 7). Interestingly, the declines in mean densities from 1997 to 1998 were greatest in both areas outside the reserve; mean density of economic species in 1998 was greater inside BCER than outside (fig. 6). No differences in density were found among locations, and there were no significant interaction terms.

Fish Size in BCER and Unprotected Areas

The size distributions of blue rockfish were significantly different inside and outside BCER, during both years and at both depth strata (fig. 7a,b). However, only in deep water in 1998 (fig. 7b) were sizes skewed toward larger fish inside BCER (in 1998, 50% of 134 blue rockfish were 30 cm total length inside BCER compared to no fish of that size outside the reserve).

Size distribution of olive rockfish also differed significantly inside and outside the reserve in both years (fig. 7c). In 1997, the distribution outside BCER was skewed toward larger size classes (>30 cm) compared to inside. However, this pattern was reversed in 1998, and the largest size classes (>35 cm) were truncated in the size distribution of olive rockfish outside the reserve. There was no significant difference in size structure of gopher rockfish in and out of BCER in either 1997 or 1998 (fig. 7d).

Comparisons of size distributions could not be made for copper, vermilion, and rosy rockfishes in 1997 because of low sample sizes of estimated lengths inside BCER. Distributions of rosy and vermilion rockfishes in 1998 were not significantly different in and out of the reserve, and the largest vermilion rockfish occurred in the surveys outside the reserve. Size distributions of lingcod, a more vagile species than many of the rockfishes, were statistically similar inside and outside the reserve in both years.

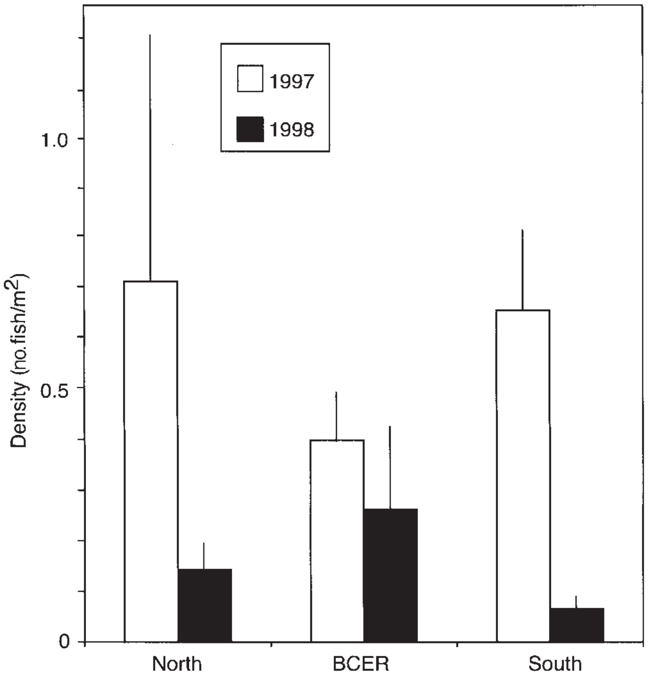

Figure 6. Mean density (no. fish/m^2) of economically valuable species (i.e., blue, olive, vermilion, canary, gopher, copper, and yellowtail rockfishes and lingcod) on high-relief rock substratum among three locations (north of, south of, and inside BCER) in 1997 and 1998. Standard error bar is included.

DISCUSSION

In situ video methods for surveying from an occupied submersible were effective in characterizing benthic habitats of BCER and adjacent areas on a spatial scale (microscale of <1 m to macroscale of 1–10 m) relevant to associated fish species. Seafloor substratum types were not distributed uniformly within the reserve, nor were they equal in relative abundance. The shallow high-relief rock habitat, although limited in distribution and abundance, supported a diverse and abundant fish fauna, including many species of economic value to nearshore fisheries. This shallow rock habitat also harbored high numbers of young-of-the-year rockfishes and may serve as a nursery for these newly settled fish. To increase protection of these nearshore species associated with limited amounts of rock habitat, the boundaries of BCER could be extended both north and south.

Substantial amounts of high-relief rock outcrop habitat also are located just outside BCER in deepwater heads of submarine canyons. The boundaries of BCER could

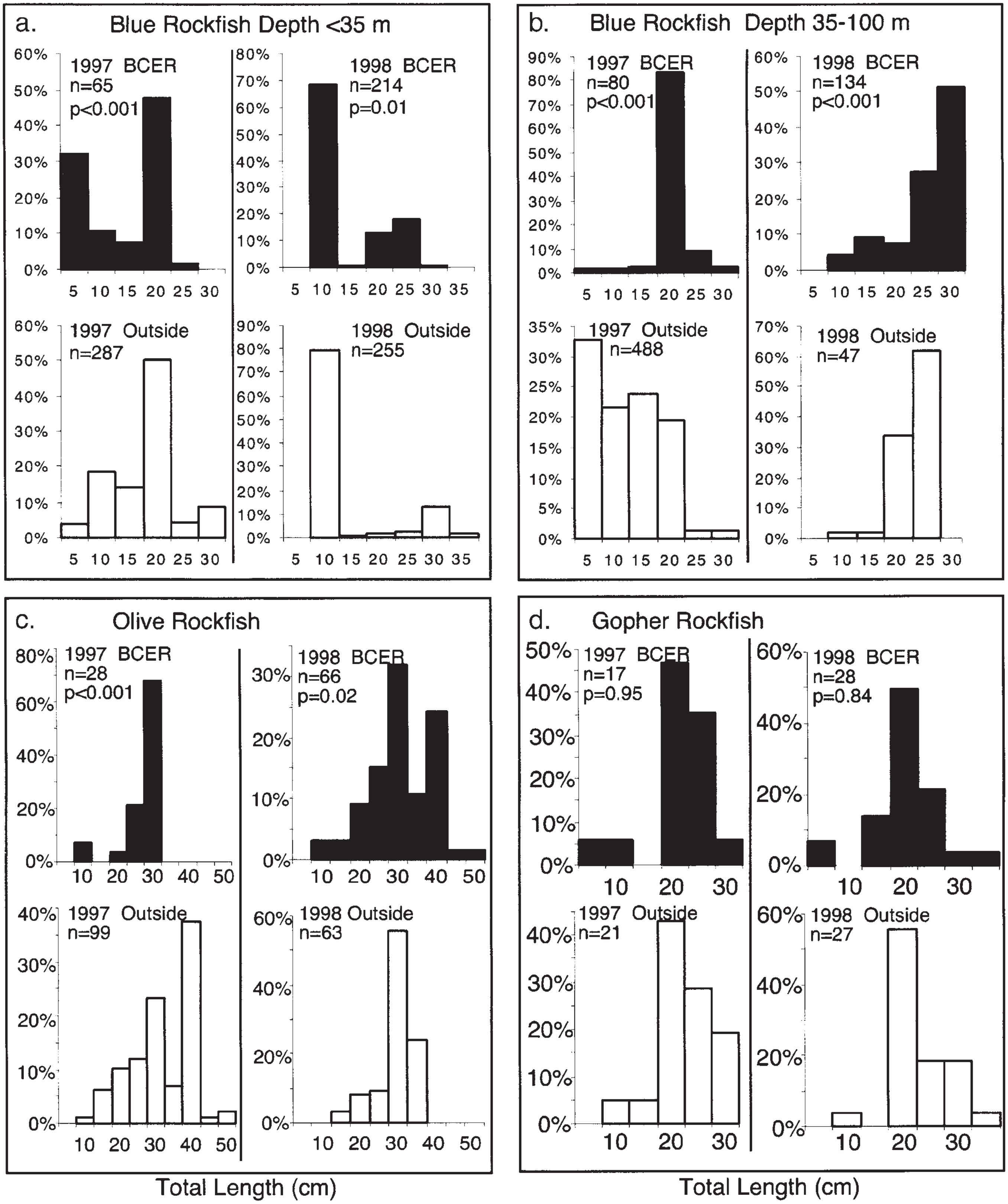

Figure 7. Frequency distributions (%) of total length of rockfishes inside (black) and outside (north and south; white) BCER in 1997 and 1998. (a) blue rockfish, <35 m water depth; (b) blue rockfish, 35–100 m water depth; (c) olive rockfish, 20–100 m water depth; and (d) gopher rockfish, 20–100 m water depth. *P* values are from Kolmogorov-Smirnov goodness-of-fit comparisons between sizes inside and outside the reserve. Sample size denoted as *n*.

be extended offshore to encompass the highly diverse deepwater canyon assemblages of fish associated with rock crevices and overhangs and those species most abundant over soft fine sediment on the canyon walls.

Presently there are no marine reserves that afford protection to those habitats and associated fauna at depths greater than 100 m off California (McArdle 1997; 1998) or off the entire West Coast. From results of our past research in Monterey Bay, rock outcrops on relatively steep canyon walls can offer natural refuge to some economically valuable species in deep water (Yoklavich et al. 2000). These deepwater assemblages include several species whose populations are in severe decline (i.e., bocaccio, cowcod, and canary and yelloweye rockfish; Ralston 1998; MacCall et al. 1999).

Fish densities and sizes were similar inside and outside BCER, and there are various explanations for this. First and most important, the recovery time (or time from the reserve's closure to fishing) could be inadequate to reflect significant effects. There is evidence elsewhere on the West Coast that some rockfish species and lingcod protected for much longer periods of time within a few existing no-take marine reserves have greater abundance or size, and consequently increased spawning biomass and reproductive potential, compared with those in adjacent fished areas.

For example, the reproductive potential of copper rockfish inside a 27-year-old marine reserve in shallow water in Puget Sound, Washington, was 55 times greater than that of copper rockfish subject to heavy fishing pressure outside the reserve (Palsson 1998). The enhanced reproductive potential resulted from greater densities and larger sizes of copper rockfish inside the reserve. Similarly, lingcod, especially large individuals, were more abundant inside a tiny 6-year-old no-take reserve in the San Juan Islands, Washington, compared to adjacent unprotected areas (Palsson and Pacunski 1995). Lingcod nests were denser inside the refuge than in the fished area. Copper rockfish were more abundant in the refuge than at the fished site, but large fish were no more common in any treatment. Positive benefits for lingcod also have been documented in small reserves off British Columbia (Martell et al. 2000).

Reproductive potential for black-and-yellow and kelp rockfishes was significantly greater inside both the Point Lobos State and Ecological Reserve (closed to fishing for more than 20 years prior to study) and Hopkins Marine Life Refuge (closed to fishing for 12 years prior to study) than in heavily fished areas immediately outside these reserves off central California (Paddack and Estes 2000). These researchers found no significant differences in the reproductive potential of these same species in shallow water (14 m) inside and outside BCER, which was closed to fishing for only 1–2 years prior to their surveys.

This suggests that the 3.5 years of protection prior to our surveys in deep water of BCER in 1997 and 1998 may not have been long enough to reflect differences in density, size, and subsequent reproductive potential. Length of time of protection is especially critical when evaluating effects of reserve protection on rockfish. Many rockfish species, particularly those in deep water, have maximum longevity of 50–205 years (Love et al. 2002). In general, rockfishes are slow growing, mature at older ages (6–12 years; Wyllie Echeverria 1987), and are relatively unproductive. The magnitude of recruitment of young rockfish varies greatly from year to year and is linked to environmental factors (Ralston and Howard 1995).

Because of these life history characteristics, the positive effects of areas protected from harvest could take years to accrue. For example, the expected median time to rebuild two of the most depleted populations of rockfishes to 40% of their original biomass in the absence of fishing is estimated to be 91 years for bocaccio[1] and 158 years for yelloweye rockfish.[2] Because BCER was closed to fishing for a relatively short period before we initiated our study, our inventory of habitats and associated fishes can be considered a valuable baseline from which to evaluate future changes to BCER populations of benthic fishes in deep water and the expectations of BCER to maintain species and habitat diversity.

Second, while we do not have estimates of fishing rates along the Big Sur coast, especially relative to BCER, this remote area with limited access likely receives relatively less fishing pressure than similar types of habitat closer to fishing ports. The expected positive effects of marine protected areas, such as increased abundance and sizes inside the protected area compared to adjacent unprotected areas, in large part depend on the contrast in fishing pressure between the two areas. This contrast might not have been great, particularly in deep water at the study site. It is especially important to continue to monitor this reserve and adjacent areas if fishing pressure is expected to increase along this coast.

Third, the size of BCER may not encompass the home range and movements of some benthic fish species and therefore may not adequately protect these fishes. We did not assess the movements of fishes within BCER, but many of the nearshore rockfish species are thought to be relatively sedentary (Stanley et al. 1994; Lea et al. 1999). Extent of movement depends on season for some species, temperature, food supplies, and developmental stage (young fish generally are more mobile than older

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[1] MacCall, A. D. 2002. Status of bocaccio off California in 2002. Unpublished report. National Marine Fisheries Service, 110 Shaffer Rd., Santa Cruz, Calif. 95060.

[2] Wallace, F. 2002. Rebuilding analysis for yelloweye rockfish. Unpublished report. Washington Department of Fish and Wildlife, 48 Devonshire Rd., Montesano, Wash. 98563.

stages). A recent tracking study of electronically tagged greenspotted rockfish and bocaccio in deep water of Monterey submarine canyon documented considerable short-term variation in movement (Starr et al. 2002). Even infrequent movements of fishes outside the boundaries of BCER could impede detection of reserve effect. Other small reserves did eventually demonstrate increased abundance and size of rockfishes (as noted above), but only after several years of protection. Increasing the size of BCER by extending the boundaries could reduce the percentage of time that fish move outside the boundaries and become vulnerable to fishing.

Finally, illegal fishing is known to occur within the boundaries of BCER (Paddack and Estes 2000; for a discussion on enforcement issues and marine reserves, see Proulx 1998). Although we have no good estimates of the extent of poaching in BCER, this activity could diminish fish densities and sizes inside the reserve and consequently conceal or negate any positive reserve effects. Conversely, the continued presence of an on-site reserve manager at BCER and the positive support of the local community likely serve to reduce the likelihood of poaching in this remote area. To further facilitate compliance with reserve regulations, the boundaries should be placed at more easily recognized points than is now the case. For example, the northern boundary could be made contiguous with the Landels-Hill Big Creek Reserve (a terrestrial protected area adjacent to BCER) and the southern boundary extended to Gamboa Point to make it clearly recognizable from sea.

The methodologies and results from this study will be valuable in the implementation of recent fishery management and marine reserve legislation in California (Marine Life Management Act and Marine Life Protection Act). Assessing habitat availability and species-specific habitat associations is paramount to locating marine reserves and evaluating their effectiveness. Results of our work can improve the effective design and monitoring of marine protected areas. For example, from our data we estimated that a minimum of 14 samples (independent estimates of abundance of the group of seven economically valuable species) from complex rock habitat in each of the three locations will be required to detect a two-fold (100%) difference in abundance inside and outside BCER; in contrast, to detect just a 50% change in abundance, 52 samples per location will be necessary. This information will be useful when developing monitoring plans for BCER and other similar reserves elsewhere off California.

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DISTRIBUTIONS OF PLANKTONIC FISH EGGS AND LARVAE OFF TWO STATE ECOLOGICAL RESERVES IN THE SANTA BARBARA CHANNEL VICINITY AND TWO NEARBY ISLANDS IN THE CHANNEL ISLANDS NATIONAL MARINE SANCTUARY, CALIFORNIA

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ABSTRACT

We conducted a study in 1998–99 to identify planktonic fish eggs and larvae, and to describe their temporal and spatial distributions, in the vicinities of Vandenberg and Big Sycamore Canyon Ecological Reserves and two nearby islands, Anacapa and San Miguel, in Channel Islands National Marine Sanctuary. We conducted surveys in late winter and early summer each year using an underway sampler and a bongo net towed vertically at fixed stations. A neuston sampler was added in 1999. We used bongo net data, thought to give the best estimates of ichthyoplankton abundance, as the primary data to identify distributions.

Cluster analyses showed that season was the major environmental signal in the ichthyoplankton data, with clear indications of the El Niño/Southern Oscillation events of 1998 and 1999, and more tenuous suggestions of adult habitat preferences and faunal affinities. Between- and within-site adult habitat preferences were apparent in analyses of individual taxa. Eggs and larvae of rocky-bottom and kelp forest taxa were most abundant at the islands where those habitats are available, and the eggs and larvae of soft-bottom taxa were more abundant at the Big Sycamore Canyon site, where that habitat predominates. It appears that no significant production of planktonic fish eggs and larvae occurred in the vicinity of Vandenberg Ecological Reserve. At the Big Sycamore Canyon site, eggs of a few taxa clearly are produced from the reserve but probably not in higher numbers than from adjacent nonreserve areas.

INTRODUCTION

The California Marine Resources Protection Act of 1990 required the establishment of marine reserves along the California coast. Two reserves created in 1994 are Vandenberg Ecological Reserve, centered on Point Arguello, and Big Sycamore Canyon Ecological Reserve, in the southeastern Santa Barbara Channel near Point Mugu. An argument often cited in favor of marine reserves is that they provide protected areas for adults of exploited species. Planktonic propagules of these species presumably disperse from the reserve to "reseed" adjacent fished areas outside the reserve, thereby helping to maintain or augment stocks of the exploited species outside the reserve (e.g., Agardy 1994; Sladek Nowlis and Yoklavich 1998, 32–40; Sladek Nowlis and Roberts 1999). Commonly, it is simply assumed that the reserves must function in this way; studies designed to quantify the abundances and distributions of planktonic propagules in the reserve vicinities rarely are undertaken. This study addresses the lack of information about ichthyoplankton in the immediate vicinities of Vandenberg and Big Sycamore Canyon Ecological Reserves by producing quantitative descriptions of the small-scale temporal and spatial distributions of planktonic fish eggs and larvae around the reserves. These data also provide a baseline against which any future ichthyoplankton studies in the area can be compared.

To accomplish the primary goal of our study we adapted sampling techniques commonly used for large-scale studies in deep coastal and offshore waters (e.g., Smith and Richardson 1977; Checkley et al. 1997) to a small-scale study in shallow inshore waters; we also developed criteria for identifying the planktonic shorefish eggs (Moser [1996] provided descriptions of the larvae of most of the taxa expected, as well as descriptions of some of the eggs). Watson et al. (1999) addressed these points, described temporal spawning patterns, and provided preliminary descriptions of spatial distributions of the eggs of several taxa using data from the first year of the study. Here, we focus on the distributional information obtainable from the ichthyoplankton assemblage and on the specific spatial distributions of some individual taxa selected for their fishery value and/or abundance. Coincidentally, the strong El Niño and La Niña events of 1998 and 1999 occurred during the study, and we note apparent affects of those events on the ichthyoplankton as well.

MATERIALS AND METHODS

We conducted four surveys aboard the NOAA research vessels *David Starr Jordan* (JD) and *McArthur* (M4) in 1998 and 1999, during late winter (9803JD, 19 Feb.–4 Mar. 1998; 9903M4, 25 Feb.–10 Mar. 1999) and early summer (9806JD, 12–24 June 1998; 9907JD, 28 June–11 July 1999). We sampled four sites: the vicinities of

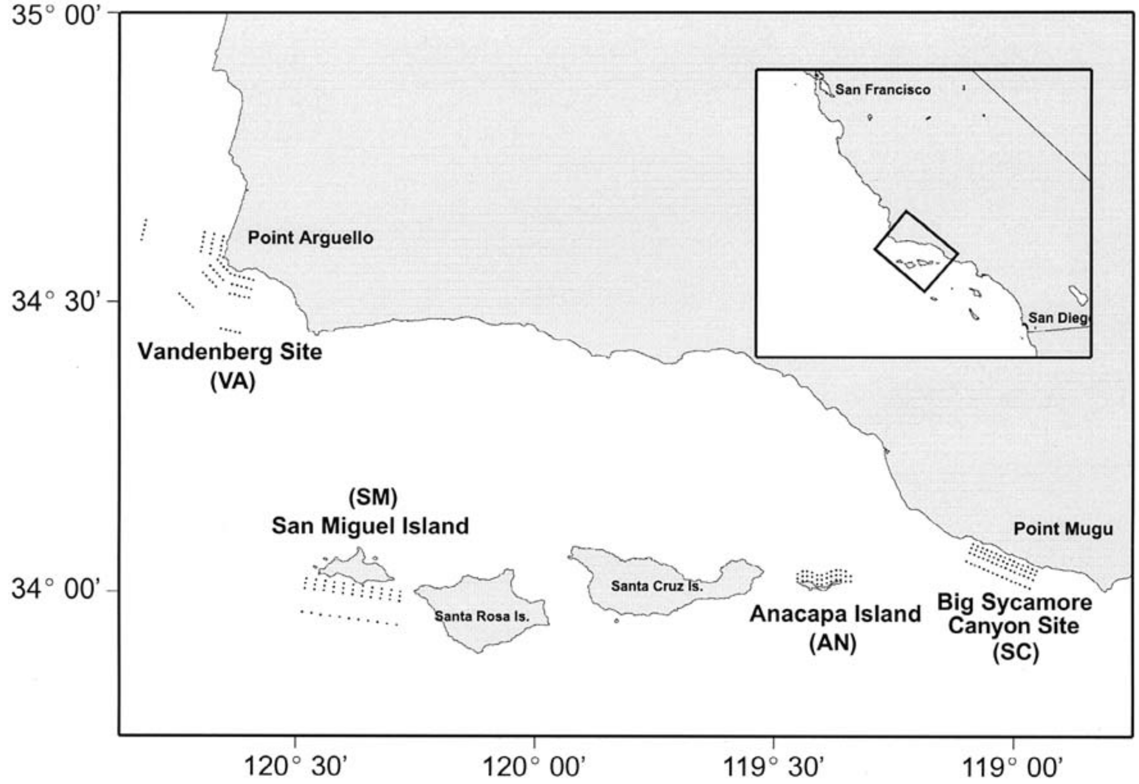

Figure 1. Study site showing station array at each site.

Big Sycamore Canyon and Vandenberg State Ecological Reserves, and Anacapa and San Miguel Islands in the Channel Islands National Marine Sanctuary (fig. 1). Big Sycamore Canyon is a low-relief site adjacent to a sandy beach, and it contains little hard-bottom or kelp habitat; the reserve itself is entirely a soft-bottom habitat. Vandenberg also contains little kelp but does have rocky headlands, somewhat more hard bottom than Big Sycamore Canyon, and some patchy surf grass. Coastal currents at both sites flow primarily alongshore, predominantly southerly in spring and summer and northerly in autumn and winter (Hendershott and Winant 1996). Both of the island sites have more hard-bottom habitat than the mainland sites (about 20% compared with < 5% shoreward of the 100 m isobath; Cochrane et al. 2002) and more extensive kelp coverage.

A station grid was established at each site (fig. 1). Station placement is described in Watson et al. (1999, 2002). Briefly, four lines of stations were placed approximately parallel to shore in the vicinities of the 20, 40, 60, and 200 m isobaths. There were three groups of five stations each corresponding to "downcoast," "reserve," and "upcoast" blocks along each line, for a total of 60 stations each at Big Sycamore Canyon and Vandenberg. There were 44 stations at San Miguel Island (11 per line), and 35 at Anacapa Island (12 each on the two shoreward lines, 11 on the next line; the most offshore line was not occupied). The reserve at Big Sycamore Canyon extends seaward to the 37 m (20 fm) isobath and the inshore line passes through the reserve. The reserve at Vandenberg extends offshore to approximately the 18 m (10 fm) isobath; concern for vessel safety precluded sampling within it.

Two samplers, an underway pump system (continuous underway fish egg sampler, CUFES; Checkley et al. 1997) and a bongo net, were used on all surveys. Watson et al. (1999, 2002) describe the use of both. Briefly, the CUFES drew water continuously from a depth of 3 m, and samples usually were collected at 10 min intervals as the vessel steamed along the station lines at about 2.5 m/s (5 kn). With few exceptions, a full CUFES pattern (all station lines) was sampled twice during the day and twice at night at each site (Watson et al. 2002). The 71 cm bongo net (McGowan and Brown 1966), equipped with 0.333 mm mesh nets and cod ends and a calibrated flowmeter, was used to make a vertical plankton tow at each station. Sampling was done without regard to day or night. Nearly all scheduled bongo samples were collected (Watson et al. 2002). A CUFES sample usually was collected with each bongo sample for calibration between the gear types.

A manta net (Brown and Cheng 1981) was added as a surface sampler in 1999 because the eggs of some taxa are strongly positively buoyant, and the larvae of some are neustonic (e.g., cabezon, *Scorpaenichthys marmoratus*; lingcod, *Ophiodon elongatus*) and may be poorly sampled by the vertically towed bongo net. The standard CalCOFI manta net used (see Moser et al. 2002) was equipped with a 0.333 mm mesh net and cod end and a calibrated flowmeter. There were 12 manta stations at each site: 3 per line at Big Sycamore Canyon, Vandenberg, and San Miguel Island, and 4 per line at Anacapa Island. Use of the manta net is described in Watson et al. (2002). All scheduled manta samples were collected.

Samples were preserved in 10% sodium borate-buffered seawater-formalin. In the laboratory, fish eggs and larvae were sorted from whole samples and stored in 2.5% sodium borate-buffered formalin. All fish eggs and larvae were identified to the lowest possible taxon and counted. Eggs were assigned to 11 developmental stages according to the criteria of Moser and Ahlstrom (1985), and larvae were assigned to yolk-sac, preflexion, flexion, or postflexion stages (Moser 1996). All fish eggs and larvae and all collection and count data are archived at the National Marine Fisheries Service Southwest Fisheries Science Center (SWFSC). These data ultimately will be made available through the SWFSC Fisheries Resources Division Web site.

Count data were converted to concentration (number per 1 m^3 or per 100 m^3 of water filtered) for the CUFES and manta samples, and to abundance (number under 10 m^2 of sea surface) for the bongo samples. For most analyses only "total eggs" and "total larvae" categories were used for each taxon; for some analyses egg stages were pooled into "early" (stages I–III), "middle" (stages IV–VII), and "late" (stages VIII–XI) categories. The standardized count data were transformed by log ([abundance or concentration] + 1) prior to statistical analyses (results evaluated at $\alpha = 0.05$) using ANOVA and the Bonferroni multiple comparisons procedure (Mathsoft, Inc. 2000) to examine between- and within-site distributions of selected taxa. Taxa were selected for analysis on the basis of their sport or commercial fishery value and/or abundance. Results for the eggs of six taxa and the larvae of two collected with the bongo net are presented here. Most of the fish eggs and larvae collected have little or no direct fishery value, or were relatively rare, or both. To explore alongshore abundance patterns, we grouped stations into the "downcoast," "reserve," and "upcoast" blocks at the reserve sites as described above, and into "east," "center," and "west" blocks at the islands (four stations per line in each block, except three in the "east" block on the offshore line at Anacapa Island; four per line in the "east" and "center" blocks, and three per line in the "west" block at San Miguel Island). CUFES data were used for supplemental descriptions of egg distributions but were not analyzed statistically.

Agglomerative hierarchical clustering of Euclidean distance values with complete (furthest-neighbor) linkage was performed on the bongo and manta net data to examine the organization of the egg and larval assemblages. Taxa used in the bongo cluster analyses were those that occurred on ≥ 2 cruises, at ≥ 10% of the stations at ≥ 1 site. Criteria for the manta data were the same except that occurrence on only one cruise was sufficient. This resulted in deletion of the rare taxa; the "unidentified" and "disintegrated" categories were deleted as well. Three egg categories, *Atractoscion nobilis*, *Sphyraena argentea*, and their indistinguishable early stages ("Perciformes"), were combined. This left 21 egg and 25 larval taxa for analysis in the bongo data set, and 26 egg and 19 larval taxa in the manta data set. The mean number of "total eggs" or "total larvae" of each taxon under 10 m^2 (bongo) and per 100 m^3 (manta) along each station line was calculated, and the means were log-transformed prior to analysis.

A secondary goal of the study was to assess the utility of the CUFES in generating descriptions of small-scale distributional patterns and in estimating abundances of nearshore planktonic fish eggs. This was done with linear regressions of CUFES catch data on bongo catch data. The rationale for using the bongo catch data as the independent variable was that the bongo sampled nearly the entire water column and thus was thought to provide the best estimate of egg abundance in the water column. We analyzed untransformed count data (number per minute for CUFES; number per 10 m^2 for bongo net) for four taxa regularly collected with both samplers. We included only stations with a positive collection for at least one of the samplers.

RESULTS

Ichthyoplankton Assemblage

In total, 236,596 fish eggs of at least 48 taxa, and 8,932 fish larvae of 109 taxa were collected with the three samplers during the four cruises (Watson et al. 2002). Overall, northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), white croaker (*Genyonemus lineatus*), speckled sanddab (*Citharichthys stigmaeus*), and California halibut (*Paralichthys californicus*) eggs occurred most frequently and were among the most abundant during the winter surveys. In summer, señorita (*Oxyjulis californica*), California sheephead (*Semicossyphus pulcher*), and white seabass (*Atractoscion nobilis*) plus California barracuda (*Sphyraena argentea*) eggs were among the most common, although during the cool summer of 1999 northern anchovy, speckled sanddab, and California halibut eggs remained common. Northern anchovy, California smoothtongue (*Leuroglossus stilbius*), northern lampfish (*Stenobrachius leucopsarus*), Pacific hake, and rockfishes (*Sebastes* spp.) were the most common fish larvae during both winter surveys; larval northern anchovy remained relatively common during summer (especially 1999), and rockfishes were common in summer 1999. The most common shorefish eggs at the mainland sites were white croaker, speckled sanddab, and California halibut during winter, with señorita replacing white croaker in summer. Common shorefish larvae at the mainland sites in winter included rockfishes, white croaker, and English sole (*Parophrys vetulus*); none was particularly common during summer. At the islands the most common shorefish eggs included speckled sanddab and California halibut in winter, and white seabass plus California barracuda (primarily at Anacapa), señorita, and California sheephead during summer, with speckled sanddab and California halibut remaining common in summer 1999. Common shorefish larvae at the islands during winter were rockfishes, white croaker (1999), and, at Anacapa Island, blackeye goby (*Coryphopterus nicholsii*); during summer larval blacksmith (*Chromis punctipinnis*) were common at Anacapa Island.

In the cluster analyses of bongo net egg data, when collections were classified according to the similarity of the egg catches within each collection, the primary separation was between winter and a group predominantly (94%) of summer collections (fig. 2). Within the summer collection group, a subgroup mostly (82%) of 1998 (El Niño) collections was distinguished from another of exclusively 1999 (La Niña) collections, probably reflecting mainly the higher abundances and frequencies of occurrence of the eggs of northern anchovy and several flatfish species (e.g., California halibut, speckled sanddab) in 1999. Within these subgroups smaller sets of exclusively island collections were distinguished from sets predominantly of mainland collections (91% in 1998, 80% in 1999). In the El Niño subgroup the island collections were characterized by more señorita and California sheephead eggs—both taxa require the hard-bottom/kelp habitats that are common at the islands but rare at the mainland sites. The mainland collections, especially those at Big Sycamore Canyon, had higher abundances of California halibut eggs—a soft-bottom species. In the La Niña subgroup the island collections were characterized by more labrid, white seabass, and California barracuda eggs, while the predominantly mainland subset contained somewhat more eggs of a few flatfish species.

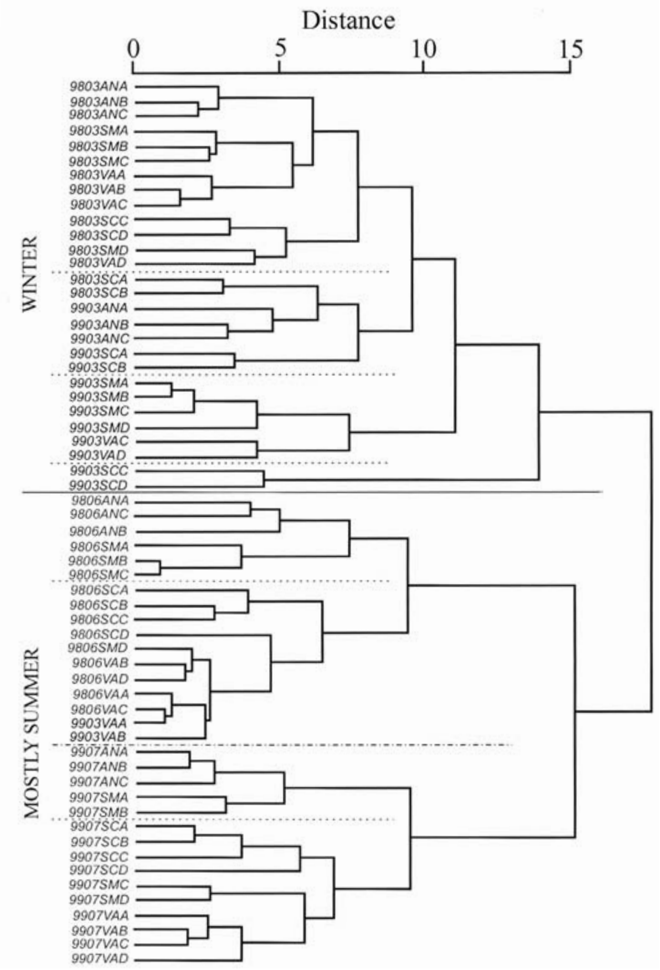

Figure 2. Dendrogram of bongo collections classified according to the similarity of fish egg catches within the collections. "Distance" refers to the Euclidean distance value and is a measure of dissimilarity. Collections are identified by numbers indicating the year and month of the cruise plus letters indicating sampling site (AN = Anacapa Island, SC = Big Sycamore Canyon, SM = San Miguel Island, VA = Vandenberg) and station line (A, nearest to shore, through D, farthest from shore).

Within the winter group collections tended to form chains, but four subgroups could be distinguished: (1) the two offshore station lines at Big Sycamore Canyon in 1999, perhaps reflecting an unusually high abundance of white croaker eggs; (2) San Miguel Island and the offshore two lines at Vandenberg in 1999, characterized primarily by a lack of northern anchovy eggs and very low abundances of white croaker eggs; (3) the inshore two lines at Big Sycamore Canyon plus all three lines at Anacapa Island in 1999, all with high abundances of California halibut eggs; and (4) a catch-all group containing the remaining 1998 collections. The reverse classification, of taxa by the collections in which they occurred, yielded little information apart from spawning season, with three or four groups: year-round spawners; species that spawn primarily in winter and spring; summer-autumn spawners; and a mixed group with peak spawning during some period from spring through autumn (Watson et al. 2002).

The primary separation in the classification of manta net egg collections was between summer collections and a group mostly (83%) of winter collections (fig. 3). The summer group contained a subgroup of mainland collections and one predominantly (71%) of island collec-

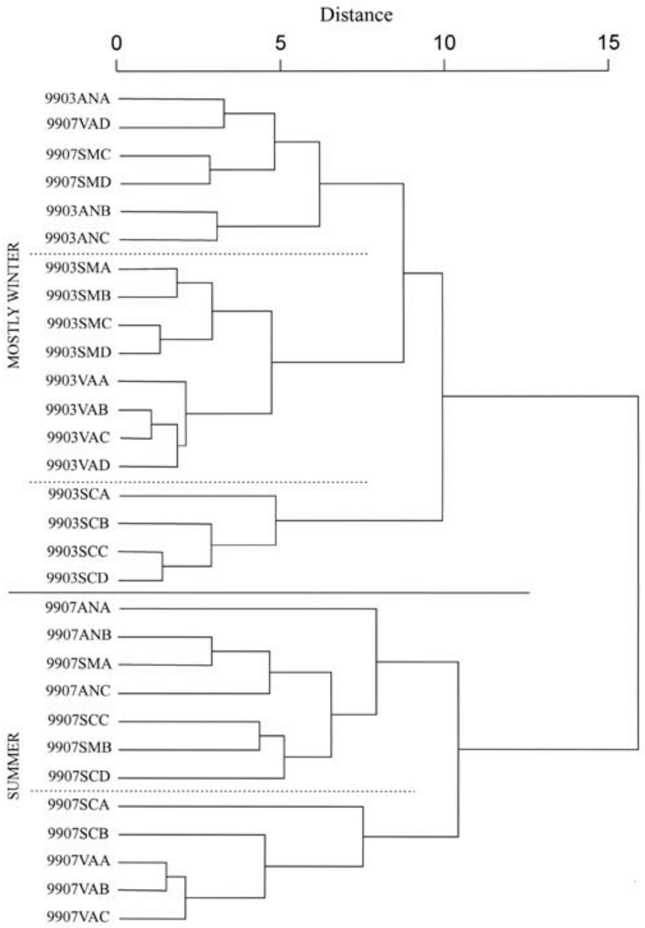

Figure 3. Dendrogram of manta collections classified according to the similarity of fish egg catches within the collections. “Distance” refers to Euclidean distance and is a measure of dissimilarity. For key to collection codes, see fig. 2.

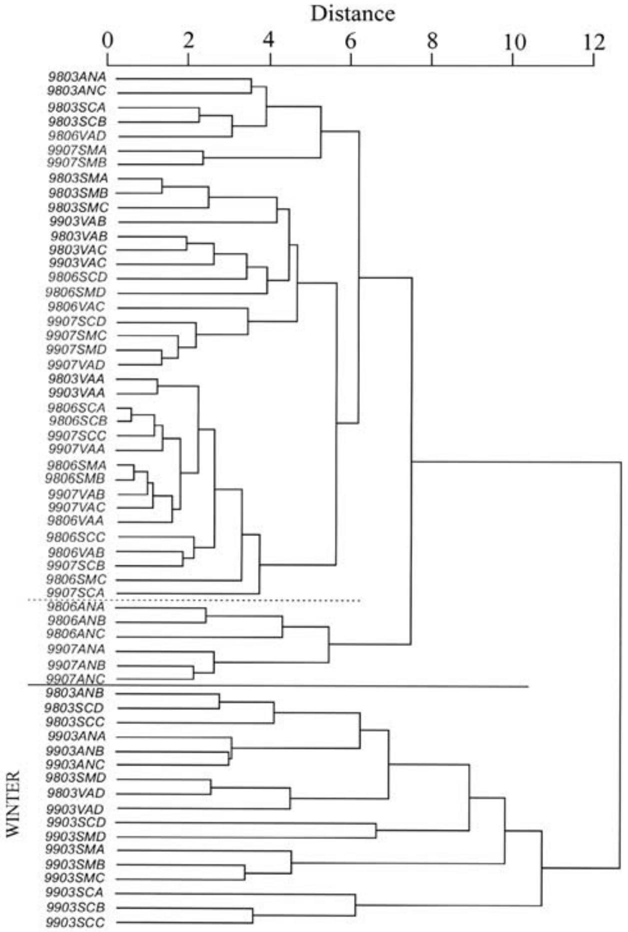

Figure 4. Dendrogram of bongo collections classified according to the similarity of larval fish catches within the collections. “Distance” refers to Euclidean distance value and is a measure of dissimilarity. For key to collection codes, see fig. 2.

tions. The mainland subgroup was characterized by higher abundances of some flatfish eggs, primarily hornyhead turbot (*Pleuronichthys verticalis*) and California tonguefish (*Symphurus atricaudus*). The island subgroup was characterized primarily by higher abundances of labrid and C-O sole eggs but also had somewhat higher abundance of northern anchovy and cusk-eel (Ophidiidae) eggs, which may account for inclusion of the two offshore Big Sycamore Canyon station lines in the island subset. Within the winter group the Big Sycamore Canyon collections formed a subgroup characterized by high abundances of soft-bottom species, including speckled sanddab, English sole, hornyhead turbot, and especially white croaker. Another subgroup contained the winter collections at San Miguel Island and Vandenberg, characterized by low abundances of the eggs of several taxa (e.g., speckled sanddab, California halibut, English sole), the near absence of white croaker eggs, and complete absence of northern anchovy eggs. A third subgroup included the remaining collections.

Thus, in the fish egg data seasonal spawning and El Niño/La Niña influences were apparent, with some suggestions of spawner habitat preferences and perhaps faunal affinity. Cluster analyses of the larval fish data yielded more ambiguous results. In the classification of bongo collections (fig. 4) the primary separation was between a winter group and a large, poorly defined group containing a mixture of seasons (67% summer) and sites (58% mainland). The winter group consisted primarily of 1999 collections (71%) at all sites, possibly reflecting higher abundances of larval California smoothtongue, northern lampfish, Pacific hake, white croaker, and rockfishes in winter 1999, except that Vandenberg was poorly represented (12%), possibly reflecting the very low abundance of larval white croaker at that site. Collections within the other group formed two subgroups: (1) Anacapa Island in summer, where all of the larval blacksmith collected during the study were taken; and (2) the remainder, with no readily interpretable pattern or subgroups.

In the reverse classification the primary separation was

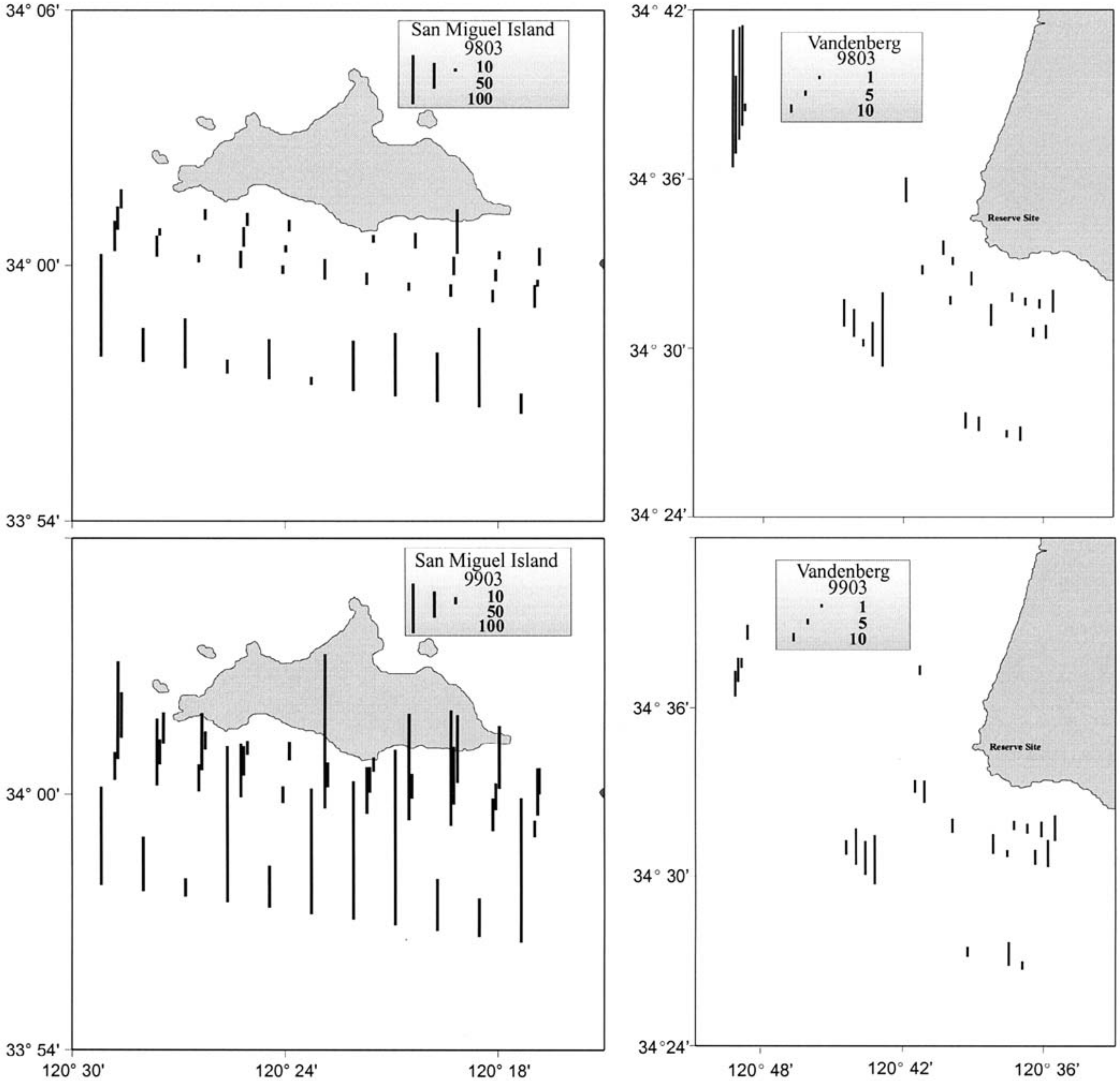

Figure 5. Abundance (number per 10 m^2) of larval rockfishes (*Sebastes* spp.) collected with a vertically towed bongo net at the Vandenberg and San Miguel Island study sites in February–March 1998 (*upper*) and 1999 (*lower*).

between: (1) six taxa that were most abundant and occurred most frequently in winter; and (2) all the others. The first group contained three subsets: the ubiquitous northern anchovy; three flatfish species, white croaker and Pacific argentine (*Argentina sialis*), all most abundant at Big Sycamore Canyon; and the remainder, most of which were more abundant at the islands (Watson et al. 2002). Owing to the numerous "zero" observations, no meaningful results were obtained in the analyses of manta larval fish data.

Individual Taxa

***Sebastes* spp.** Most *Sebastes* larvae cannot be identified to species, and the composite could include as many as 40–50 species in this data set. Abundances of rockfish larvae differed significantly among sites: there were more at the islands than at the mainland sites and more at Vandenberg than at Big Sycamore Canyon (tab. 1). No statistically significant spatial patterns were detected at Anacapa Island, and no significant alongshore patterns were detected at the other sites, but at all three abun-

TABLE 1
Summary of ANOVA and Multiple Comparisons Tests on Bongo Net Abundance Data

		ANOVA				Bonferroni			
						Abundance least <——> most			
Taxon	Site	df	rmse	*F*	*P*				
Sebastes spp.	All	3 site	107.64	42.43	< .01	SC	VA	AN	SM
		781 residual	2.54						
	SM	3 line	15.56	3.96	.01	A	B	C	D
		163 residual	3.93						
	VA	3 line	42.77	26.66	< .01	A	B	C	D
		219 residual	1.60						
	SC	3 line	20.00	20.01	< .01	A	B	C	D
		225 residual	1.00						
Genyonemus lineatus Eggs	All	3 site	383.15	190.67	< .01	SM	AN	VA	SC
		392 residual	2.01						
	SC	3 line	12.00	4.58	< .01	D	A	C	B
		105 residual	2.62						
	VA	2 position	15.22	6.33	< .01	R	U		Do
		108 residual	2.41						
G. lineatus Larvae	All	3 site	60.24	31.68	< .01	SM	VA	AN	SC
		392 residual	1.90						
	SC	3 line	12.89	2.99	.03	D	B	C	A
		105 residual	4.31						
Atractoscion nobilis + *Sphyraena argentea*	All	3 site	284.70	231.91	< .01	VA	SM	SC	AN
		385 residual	1.23						
	AN	2 position	13.81	6.70	< .01	E	W		Ce
		61 residual	2.06						
Oxyjulis californica	All	3 site	322.36	119.41	<< .01	SC	VA	SM	AN
		385 residual	2.70						
	SM	3 line	86.35	23.44	<< .01	D	C	B	A
		76 residual	3.68						
Semicossyphus pulcher	All	3 site	153.59	68.87	< .01	VA	SC	SM	AN
		385 residual	2.23						
	SM	3 line	33.53	12.23	< .01	D	C	B	A
		2 position	10.82	3.95	.02	E	Ce		W
		76 residual	2.74						
	SC	3 line	2.66	3.07	.03	D	C	A	B
		2 position	12.18	14.04	< .01	R	U		Do
		6 interaction	2.11	2.43	.03		no	test	
		108 residual	0.87						
"Early eggs"	SC	3 line	2.03	4.29	<< .01	D	C	B	A
		2 position	3.82	8.06	<< .01	U	R		Do
		6 interaction	2.03	4.29	<< .01		no	test	
		108 residual	0.47						
Citharichthys stigmaeus	All	3 site	129.41	24.50	<< .01	SM	VA	AN	SC
		781 residual	4.87						
	SM	3 line	15.08	4.46	< .01	D	C	B	A
		2 position	3.92	1.16	.32				
		165 residual	3.38						
Paralichthys californicus	All	3 site	298.94	69.54	< .01	VA	SM	AN	SC
		781 residual	4.30						
	SC	2 position	17.99	5.87	< .01	U	R		Do
		225 residual	3.06						
"Early" eggs	SC	3 line	20.26	6.35	<< .01	D	C	B	A
		2 position	29.89	9.37	<< .01	U	R		Do
		225 residual	3.19						
	SM	2 position	20.85	5.52	< .01	W	C		E
		163 residual	3.78						

Note: Only statistically significant ANOVA results are shown. Abundances at underlined locations in the multiple comparisons results do not differ significantly.
Site codes: AN = Anacapa Island, SC = Big Sycamore Canyon Ecological Reserve, SM = San Miguel Island, and VA = Vandenberg Ecological Reserve.
Station lines are sequential from A (nearest to shore) to D (farthest from shore).
Alongshore position codes: Ce = center, Do = downcoast, E = east, R = reserve, U = upcoast, and W = west.

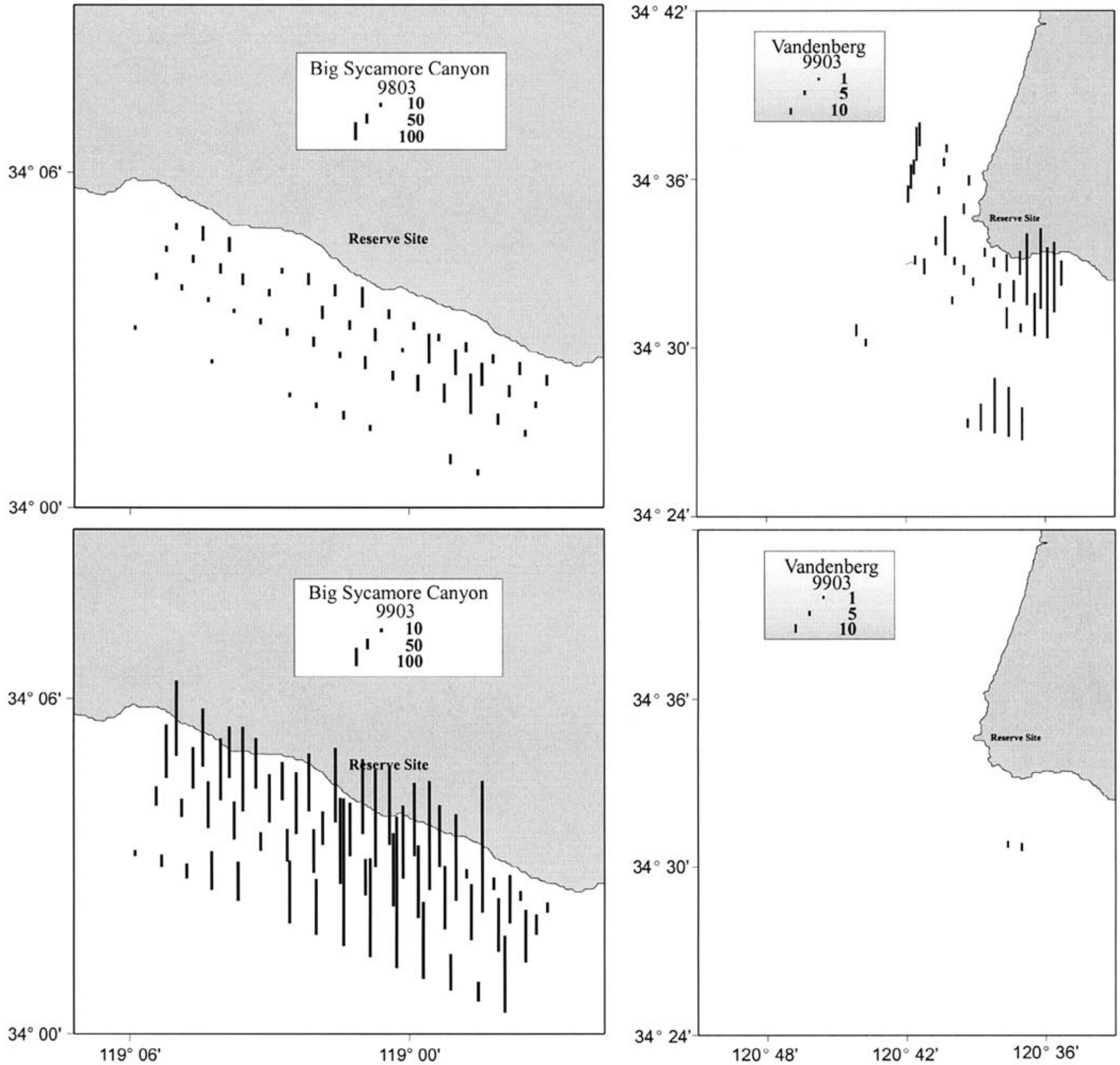

Figure 6. Abundance (number per 10 m^2) of white croaker (*Genyonemus lineatus*) eggs collected with a vertically towed bongo net at the Big Sycamore Canyon and Vandenberg study sites in February–March 1998 (*upper*) and 1999 (*lower*).

dance increased significantly in the seaward direction. At Vandenberg (fig. 5) and Big Sycamore Canyon abundance was higher along the most offshore station line than on the other three lines. At San Miguel Island (fig. 5) the change was more gradual, with abundance along the most offshore line significantly higher than along the most inshore line, but not significantly different from the other two station lines (tab. 1).

Genyonemus lineatus. White croaker eggs and larvae were much more abundant at Big Sycamore Canyon than elsewhere (tab. 1). Eggs were significantly rarer at San Miguel Island than at Anacapa Island and Vandenberg, but larval abundances were low at all three sites and did not differ significantly among them. At Big Sycamore Canyon statistically significant cross-shelf patterns were apparent for eggs and larvae, but no alongshore patterns were detected. Egg abundance was significantly lower along the most offshore line but did not differ significantly among the other three lines (tab. 1; fig. 6). Larvae were significantly more abundant along the most inshore line than along the most offshore line but did not differ significantly between other pairs of

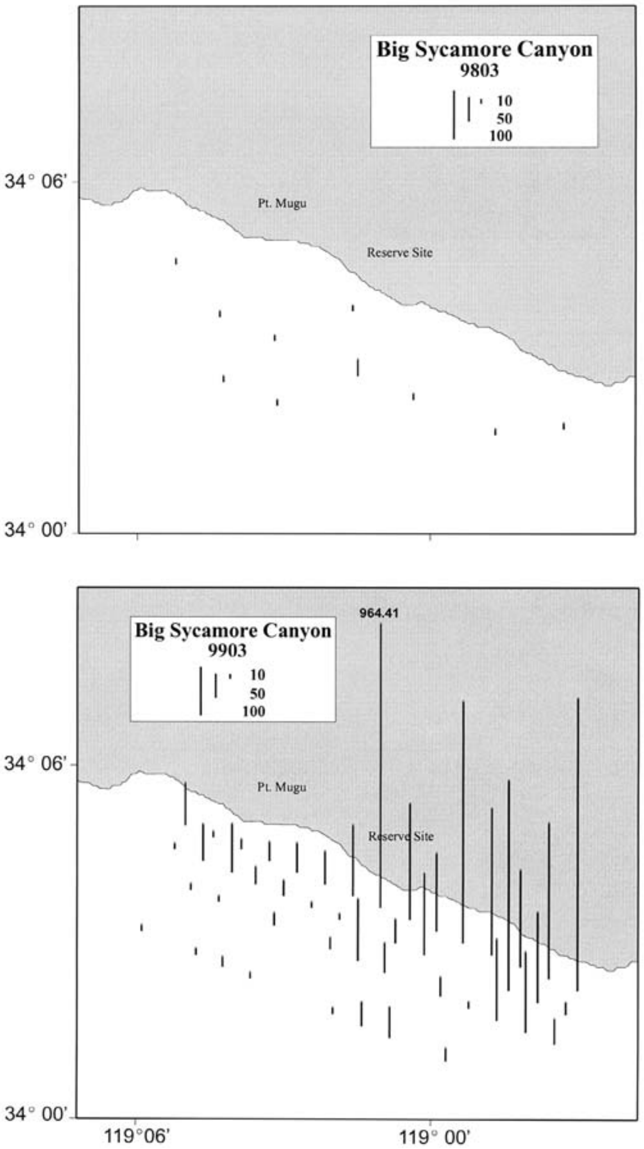

Figure 7. Abundance (number per 10 m²) of white croaker (*Genyonemus lineatus*) larvae collected with a vertically towed bongo net at the Big Sycamore Canyon site in February–March 1998 (*upper*) and 1999 (*lower*).

station lines (tab. 1; fig. 7). At Vandenberg, there were significantly more eggs at the "downcoast" stations in the western Santa Barbara Channel than in the other station blocks (tab. 1; fig. 6), but no significant cross-shelf pattern. No statistically significant patterns were detected for eggs at Anacapa Island, and low abundances of larvae at Anacapa Island and of both eggs and larvae at San Miguel Island precluded analyses of those data.

***Atractoscion nobilis* + *Sphyraena argentea*.** Eggs of these species often are indistinguishable in field collections until about midway through development (stage VII) when diagnostic embryonic pigmentation forms. Because the older, identifiable embryonic stages of both had similar distributions, the two were combined. Eggs of both were common in summer, but only one larval white seabass and no larval California barracuda were collected during the study. (No larvae of either species were collected at nearby stations during the 1998 and 1999 summer CalCOFI cruises, although larvae of both were collected south of our study area in 1998: Charter et al. 1999; Ambrose et al. 2001). Eggs were significantly more abundant at Anacapa Island than elsewhere, and significantly more abundant at Big Sycamore Canyon than at San Miguel Island and Vandenberg (tab. 1). There were no significant alongshore or cross-shelf patterns at Big Sycamore Canyon and San Miguel Island, and the Vandenberg data were not tested because too few eggs were collected at that site. There was no cross-shelf pattern at Anacapa Island, but abundance was significantly higher in the center of the pattern (tab. 1; Watson et al. 2002).

***Oxyjulis californica*.** Señorita eggs were most abundant at the islands, especially Anacapa Island, and least abundant at Big Sycamore Canyon (tab. 1). A statistically significant spatial pattern was detected only at San Miguel Island where abundance was highest inshore, decreasing in the seaward direction (tab. 1). Only a few larval señorita were collected, all at the islands during the 1999 summer survey.

***Semicossyphus pulcher*.** California sheephead eggs were common in summer, but only three larvae were collected (few were collected anywhere during the 1998 summer CalCOFI cruise, but they were more abundant in autumn; no larvae were collected in 1999; Charter et al. 1999; Ambrose et al. 2001). Eggs were more abundant at Anacapa Island than elsewhere, and more abundant at San Miguel Island than at the mainland sites, which differed insignificantly (tab. 1). There were no significant spatial patterns at Anacapa Island, and very low abundance at Vandenberg precluded analyses at that site. At San Miguel Island abundance was significantly higher on the inshore station line than on the offshore two lines, and higher along the next most inshore line than on the most offshore line (tab. 1; fig. 8). Abundance also was higher at the "west" stations than at the "east" stations; neither block differed significantly from the center (the same alongshore pattern was observed for señorita eggs but was not statistically significant: $p = 0.06$). At Big Sycamore Canyon almost all of the eggs taken with the bongo net were collected from the inshore three lines at the "downcoast" stations (fig. 9). They were significantly more abundant "downcoast" (tab. 1), but did not differ significantly in the cross-shelf direction. Abundance of "early" stage eggs was significantly highest on the most inshore line and in the "downcoast" block (tab. 1). CUFES data confirmed that eggs were more abundant toward shore and downcoast, but also suggested a broader distribution at Big Sycamore Canyon.

***Citharichthys stigmaeus*.** Speckled sanddab eggs were among the most abundant collected and larvae occurred

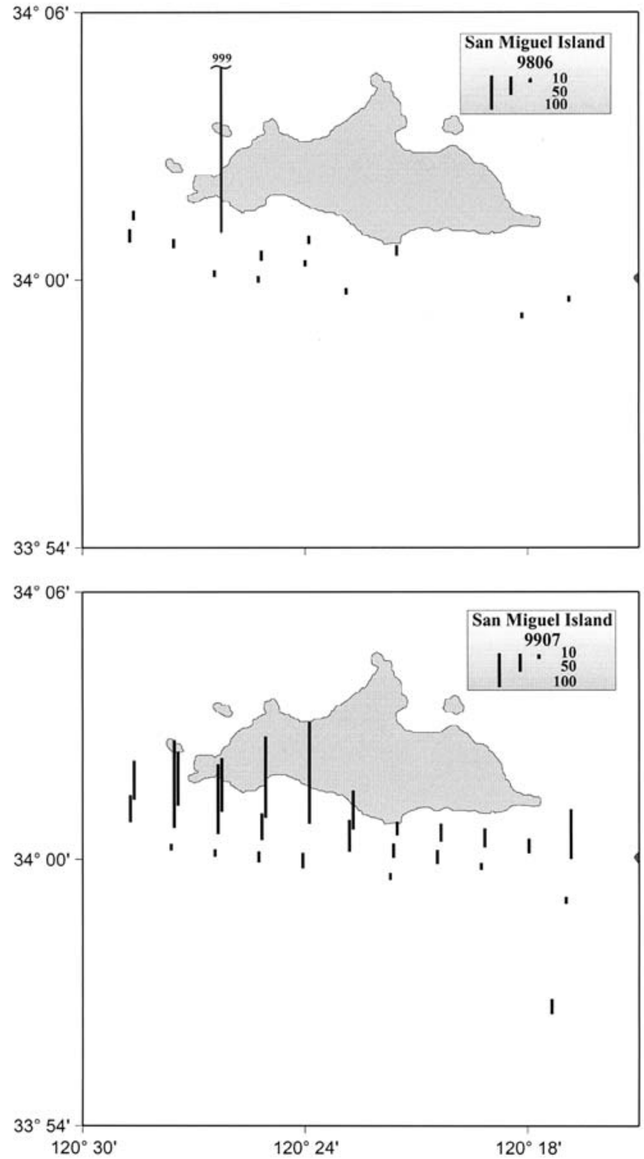

Figure 8. Abundance (number per 10 m^2) of California sheephead (*Semicossyphus pulcher*) eggs collected with a vertically towed bongo net at San Miguel Island in June 1998 (*upper*) and June–July 1999 (*lower*).

relatively commonly as well, but in small numbers. Eggs were more abundant at Big Sycamore Canyon than elsewhere (tab. 1); abundances differed insignificantly among the other sites. Statistically significant alongshore patterns were not detected at any site, and a significant cross-shelf difference was detected only at San Miguel Island, where abundance was higher along the two inshore lines than on the most seaward line (tab. 1).

Paralichthys californicus. California halibut eggs were common, but few larvae were collected (larvae were more common in CalCOFI collections in 1998, primarily north and south of our study area, but none was collected in 1999; Charter et al. 1999; Ambrose et al. 2001). Significantly more eggs were collected at Big Sycamore Canyon than elsewhere, and more at Anacapa Island than at San Miguel Island and Vandenberg, which did not differ significantly (tab. 1). No statistically significant spatial patterns were detected at Anacapa Island and Vandenberg, and no significant cross-shelf patterns were apparent at Big Sycamore Canyon and San Miguel Island, but significant alongshore differences were detected at both sites (tab. 1). At Big Sycamore Canyon abundance was higher at the "downcoast" stations than at the "upcoast" stations (fig. 10) but was not significantly different in either group from the "reserve" stations. After deletion of two offshore "downcoast" stations with extremely high abundances (fig. 10, lower left panel) the alongshore pattern remained, and a significant cross-shelf pattern, with higher abundance toward shore, resulted. CUFES data also showed higher abundance toward shore and downcoast (more apparent in 1998 than in 1999). Analyses of "early" stage eggs yielded essentially the same results (tab. 1). At San Miguel Island abundance was significantly higher at the eastern stations than in the other blocks (tab. 1), which differed insignificantly.

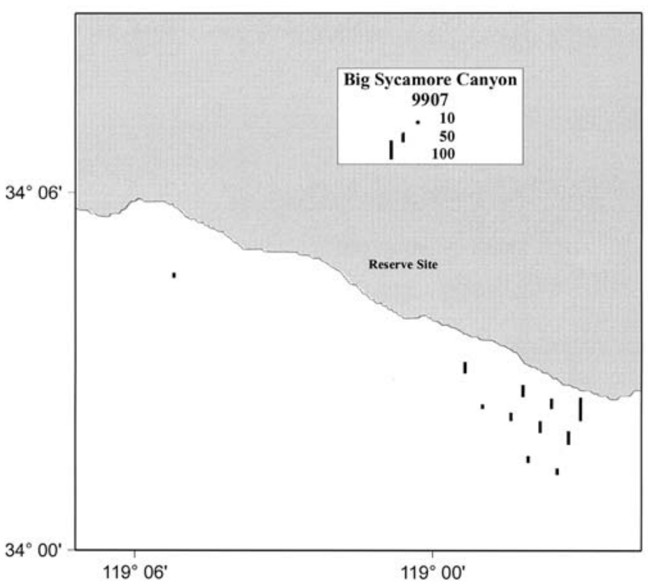

Figure 9. Abundance (number per 10 m^2) of California sheephead (*Semicossyphus pulcher*) eggs collected with a vertically towed bongo net at the Big Sycamore Canyon site in June–July 1999.

CUFES-Bongo Net Comparison

In the evaluation of CUFES catch data, the regressions of CUFES catches on bongo net catches (tab. 2) showed a strong relationship between the CUFES and bongo for northern anchovy, a moderate relationship for speckled sanddab, a weak relationship for California halibut, and no relationship for C-O sole. Thus the CUFES is a good sampler for the eggs of some taxa and a poor sampler for others; its utility must be assessed on a species-by-species basis.

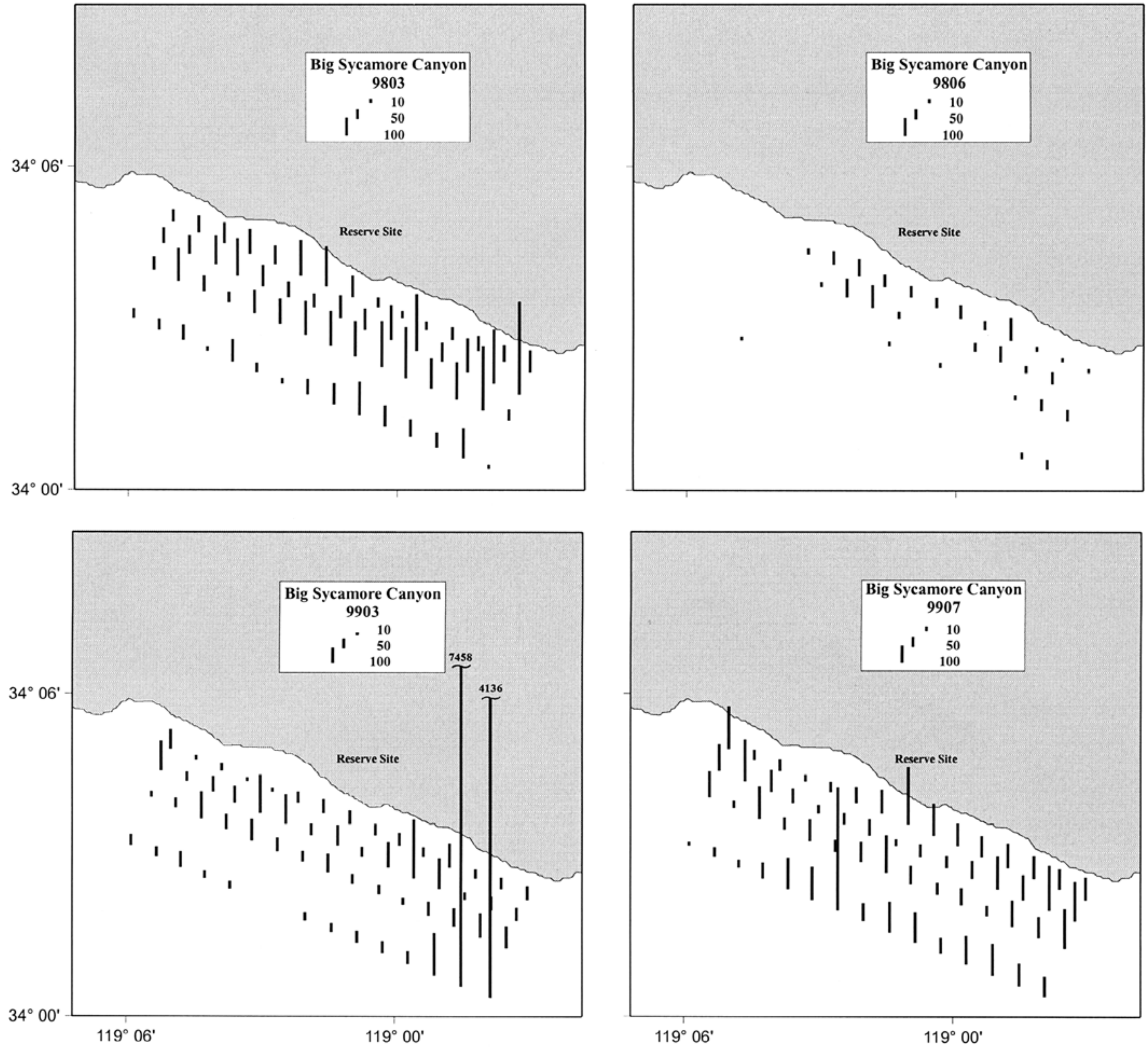

Figure 10. Abundance (number per 10 m^2) of California halibut (*Paralichthys californicus*) eggs collected with a vertically towed bongo net at the Big Sycamore Canyon site in February–March (*upper left*) and June (upper right) 1998, and February–March (lower left) and June–July (*lower right*) 1999.

DISCUSSION

At the level of the ichthyoplankton assemblage the dominant environmental signal was season: winter versus summer. Within summer the 1998–99 El Niño/ Southern Oscillation (ENSO) events were apparent in the bongo data. There were hints of adult habitat preference, most apparent in summer, when the rocky-bottom/kelp habitats at the islands tended to separate from the soft-bottom habitats at the mainland sites. Faunal affinity was apparent, more so in winter, with Anacapa Island and Big Sycamore Canyon in the San Diegan faunal province tending to group in the bongo data set, and San Miguel Island and Vandenberg at the southern limit of the Oregonian faunal province tending to group in the manta and bongo net data sets. All these patterns were apparent primarily based on the eggs, which are well sampled by both vertical bongo and manta net tows. The more ambiguous results for larvae may reflect, in part, the fact that vertical bongo net tows are not the most effective method for sampling fish larvae.

In addition to our study, only Lavenberg et al. (1987) and McGowen (1993) addressed the distributions of

TABLE 2
Results of Linear Regressions of CUFES Fish Egg Catches (number per minute) on Bongo Net Fish Egg Catches (number per 10 m²)

Taxon	R^2	df	F	P	Regression equation
Engraulis mordax	0.630	1,394	671.9	$<< 0.05$	CUFES = 0.005 (bongo) − 0.175
Citharichthys stigmaeus	0.408	1,378	260.4	$<< 0.05$	CUFES = 0.008 (bongo) + 0.303
Paralichthys californicus	0.027	1,442	12.2	$<< 0.05$	CUFES = 0.005 (bongo) + 0.610
Pleuronichthys coenosus	0.005	1,126	0.7	0.42	

planktonic fish eggs in coastal waters of the Southern California Bight (SCB). This small number of studies probably is largely attributable to the difficulty of identifying to species the eggs of the majority of planktonic spawners. Coastal fish larvae in the SCB have been studied more extensively (e.g., Gruber et al. 1982; Schlotterbeck and Connally 1982; Barnett et al. 1984; Lavenberg et al. 1986; Walker et al. 1987; McGowen 1993). Two studies in the nearshore zone (Walker et al. 1987; McGowen 1993) included analyses of the whole assemblage, and both identified season as a dominant environmental signal, as we did. McGowen (1993) demonstrated characteristic cross-shelf distributions for different groups but found little evidence for alongshore patterns within the SCB, and Gruber et al. (1982), whose study included stations near shore and seaward of the shelf, showed that on-offshore location is at least as important as season in determining larval fish assemblages. These results contrast somewhat with ours: we found little evidence for cross-shelf pattern at the assemblage level in that inshore and offshore collections did not form separate groups, although alongshore pattern was suggested in the tendency for winter collections at the northwestern sites (San Miguel Island and Vandenberg) to group separately from those at the southeastern sites (Anacapa Island and Big Sycamore Canyon). The difference between McGowen's (1993) study and ours with respect to alongshore pattern may reflect location in the SCB: the former was located entirely within the San Diegan faunal region, whereas ours included a transitional zone between the San Diegan and Oregonian faunal regions. There was an indication of cross-shelf location for two larval fish groups in our classification of taxa collected with the bongo net. The six primarily winter taxa (group 1) are broadly distributed across the shelf and tend to be more abundant over the outer shelf; this group is essentially the same as McGowen's (1993) STENOBRACHIUS assemblage, described as most abundant in winter and spring in the seaward half of his study area, and it includes all four Group 01 taxa of Gruber et al. (1982), described as an offshore/cosmopolite, winter to summer group. All but one (*A. sialis*) of the five taxa identified as a possible subset of larval group 2 in our analysis are most abundant over the inner shelf; among these only white croaker was included in McGowen's (1993) study, as part of an assemblage (GENYONEMUS) described as most abundant within the 15–36 m depth zone.

Cross-shelf and habitat-specific distributions were more apparent for individual taxa, both among and within sites. Señorita and California sheephead eggs were most abundant at the inshore stations at one or more sites, and broader distributions encompassing all three shoreward lines were apparent for white croaker eggs and larvae (highest egg abundance in the vicinity of the 40 m isobath and highest larval abundance in the vicinity of the 20 m isobath at Big Sycamore Canyon suggests that larvae concentrated shoreward of the principal spawning zone, as has been suggested elsewhere: e.g., Watson 1982; Barnett et al. 1984). Early stage California halibut eggs were significantly more abundant toward shore at Big Sycamore Canyon despite very large catches of stage I and II eggs offshore on the night of 26 February 1999, but total eggs were not significantly more abundant inshore, perhaps reflecting some dispersal after spawning. Rockfish larvae were more abundant offshore than inshore. These distributions generally are consistent with results of other studies of SCB coastal ichthyoplankton (e.g., Gruber et al. 1982; Barnett et al. 1984; McGowen 1993).

Habitat-specific distributions were apparent primarily for taxa with strong adult habitat affinity. Generally, eggs and larvae of soft-bottom taxa, such as white croaker and California halibut, were most abundant at the largely soft-bottom Big Sycamore Canyon site, while the eggs and larvae of taxa with strong rocky-bottom and kelp forest affinity, such as rockfishes and California sheephead, were most abundant at the islands where that habitat is located. Faunal affinity was apparent for some taxa. For example, California halibut, white seabass, and California barracuda have warm-water affinity, and their eggs were most abundant at the warmer, southeastern sites. California sheephead has warm-water affinity, and its eggs were more abundant at Anacapa Island than at San Miguel Island; rockfishes and lingcod have cool-water affinities, and their larvae were more abundant at San Miguel Island than at Anacapa Island. Within-site habitat specificity was apparent for California sheephead eggs at Big Sycamore Canyon, where the largest collections were at the eastern stations in the vicinity of the only suitable adult habitat. Señorita eggs, another rocky-bottom/kelp forest species, also tended to be more abundant at the eastern stations than elsewhere at Big Sycamore Canyon, but like California sheephead, they were relatively rare at that site compared with the islands.

Influences of the 1998–99 ENSO events on egg and larval abundances were most apparent for taxa with cool-water affinity, such as rockfishes and white croaker, which were most abundant in 1999 (La Niña). Interestingly, eggs of California sheephead and señorita were more abundant in 1999 as well, despite the warm-water affinity of those species, perhaps reflecting a greater influence of the increased plankton production (e.g., Bograd et al. 2000), expanding kelp coverage at the islands, and generally improved, albeit cooler, conditions in 1999.

A striking feature of the two state reserves is their relatively low productivity in eggs and larvae of most commercially and recreationally valuable shorefishes, which they were intended to protect. This especially was the case at Vandenberg, which seemingly provided poor habitat even for the soft-bottom species that might have been expected there. In contrast, production of eggs and larvae of many of the shorefishes of fishery value was high at the islands, especially at Anacapa Island. To provide some crude perspective on the mainland reserve-island contrast, we calculated the mean abundances of total eggs or larvae of a few species taken in the vertical bongo net tows within hypothetical reserves at the four sites. These hypothetical reserves were 3.7 km alongshore and extended offshore to the second station line (~ 40 m isobath)—similar to the actual Big Sycamore Canyon Ecological Reserve. Two were sited where the two existing state reserves are, one was at Anacapa Island on the northern side of East Anacapa, continuing along about the eastern third of Middle Anacapa, and one was centered along the southern side of San Miguel Island. Relative to the hypothetical Big Sycamore Canyon reserve, the hypothetical Vandenberg reserve was 85% as large, the hypothetical San Miguel Island reserve 55% as large, and the hypothetical Anacapa Island reserve 40% as large (the Anacapa "reserve" includes an actual no-take reserve at East Anacapa, in place since 1978, that constitutes about 10% of the area of the hypothetical reserve). Within these areas, the mean number of California sheephead eggs in summer was 71.6 million (130.2 eggs per 10 m^2) at Anacapa Island, 78.5 million (103.9 eggs per 10 m^2) at San Miguel Island, and none at Big Sycamore Canyon and Vandenberg. Respective values for white seabass plus California barracuda eggs were 216.5 million (393.7 eggs per 10 m^2) at Anacapa Island, 1.6 million (2.1 eggs per 10 m^2) at San Miguel Island, 32.2 million (23.5 eggs per 10 m^2) at Big Sycamore Canyon, and none at Vandenberg. There would have been 76.3 million rockfish larvae (138.8 larvae per 10 m2) on average during winter-spring in the hypothetical Anacapa Island reserve, 24.7 million (32.7 larvae per 10 m^2) at San Miguel Island, 1.5 million (1.1 larvae per 10 m^2) at Big Sycamore Canyon, and 5.7 million (4.9 larvae per 10 m^2) at Vandenberg. California halibut would have fared better at the mainland sites: 281.2 million eggs (205.3 eggs per 10 m^2) at Big Sycamore Canyon compared with 138.7 million (252.1 eggs per 10 m^2) at Anacapa Island (but recall that the hypothetical Anacapa Island reserve is less than half the size of the hypothetical Big Sycamore Canyon reserve), and 92.8 million (79.3 eggs per 10 m^2) at Vandenberg compared with 42.4 million (56.1 eggs per 10 m^2) at San Miguel Island.

The vicinity of Vandenberg Ecological Reserve, as noted, apparently is not a particularly productive area in planktonic fish eggs and larvae. Many taxa were least abundant, and only a few uncommon taxa were most abundant, at that site, for example, eggs of smalleye squaretail (*Tetragonurus cuvieri*), an epipelagic species, and larvae of pricklebreast poacher (*Stellerina xyosterna*), an inshore, soft-bottom benthic species, whose rare occurrence happened to be at Vandenberg. The Vandenberg site is a high-energy area with strong currents, strong sand transport, and relatively poor fish habitat. We found no evidence to suggest significant production of planktonic fish eggs or larvae from the vicinity of the Vandenberg Ecological Reserve.

The Big Sycamore Canyon Ecological Reserve vicinity is a more benign environment, and soft-bottom shorefish species of fishery value, such as California halibut (Moser and Watson 1990; Barsky 1990; Helvey and Witzig 1990), might, a priori, be expected to benefit from the exclusively inshore, soft-bottom reserve. California halibut and other soft-bottom species including white croaker, a species of modest, primarily sport fishery, value (Love et al. 1984; Aseltine-Neilson 2000, 23–24) clearly spawn in the reserve; however, egg abundance is higher outside the reserve, suggesting that more are produced outside the reserve than inside. Furthermore, the soft-bottom species are unlikely to have much site fidelity to a small reserve surrounded by extensive, similar habitat, and it seems unlikely that production of eggs or larvae of these species from the reserve will be significantly enhanced relative to adjacent areas in the future. As an exclusively soft-bottom, inshore site, Big Sycamore Canyon Ecological Reserve has little potential to function as a reserve for most nearshore species subject to fishery exploitation because most of them (e.g., nearshore rockfishes, cabezon, lingcod, California sheephead) have rocky-bottom habitat affinities. Placement of a large artificial reef in the reserve could dramatically alter its potential value for these species, especially if the reef were colonized by giant kelp, *Macrocystis*. If such a reef, with kelp, were present, high abundances of California sheephead eggs, probably similar to those at Anacapa Island, eventually might be expected. Alternatively, expansion of the reserve southeastward to include the rocky-bottom/kelp habitat downcoast from the present reserve may have a similar effect (Cochrane et al. 2002). Nearshore rockfishes, cabezon, white seabass, and California barracuda also might be expected to benefit from either method of including a reef within the reserve.

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THE COLOR SIGNATURE OF THE ENSENADA FRONT AND ITS SEASONAL AND INTERANNUAL VARIABILITY

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ABSTRACT

Using monthly composites of the ocean color sensor Coastal Zone Color Scanner, we generated time series of pigment concentrations for three transects and 22 locations off Baja California and the southern California coast in order to describe the signature of the Ensenada Front and its seasonal and interannual variability. We used averaging maps of pigment concentrations for non-El Niño and El Niño years to compare the differences between those periods. Our results show that the Ensenada Front signature has an M-shape and its spatial and seasonal displacement can be followed using the 0.25 and 0.5 mg m^{-3} chlorophyll-*a* concentration isolines. For El Niño years the M-shape is not very clear because of the strong penetration of Subtropical Pacific Waters along Baja California and the California coast, except during April, when upwelling is stronger. Such features were confirmed using SeaWiFS LAC images of chlorophyll-*a* concentration.

INTRODUCTION

Phytoplankton pigment concentration derived from satellites images can be used to describe surface oceanographic structures and their temporal and spatial variations (Traganza et al. 1980; Johannessen 1996; Luch-Cota et al. 1997; Müller-Karger and Fuentes-Yaco 2000). Peláez and McGowan (1986) first described one of the most spectacular examples of such structures in the California Current System (CCS), between Point Conception, California, and Punta Vizcaino, Baja California, México (fig. 1a). Pigment concentrations from July 1979 to April 1982, obtained from the sensor Coastal Zone Color Scanner (CZCS/NASA), were used to describe a frontal region separating oligotrophic (south)

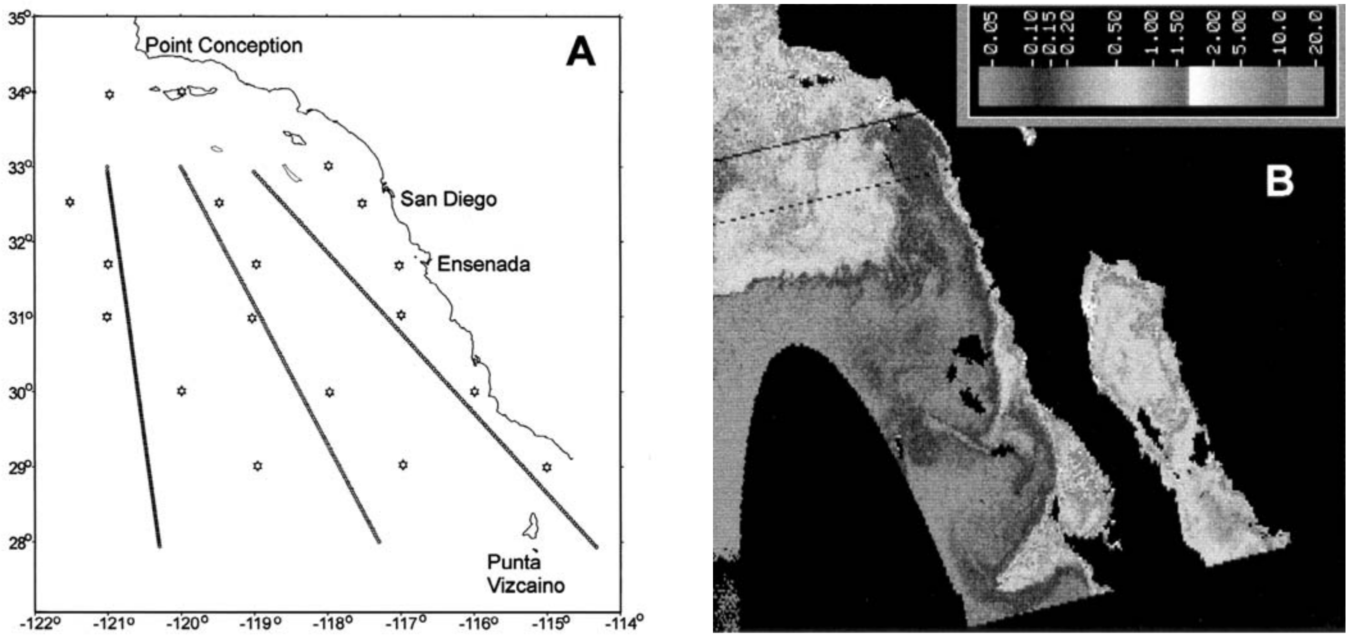

Figure 1. *A*, Study area showing the location of transects and points (*stars*) from which temporal series of pigment concentration were taken; and *B*, CZCS image with its corresponding color palette.

and eutrophic waters (north) (fig. 1b), which was considered a persistent structure throughout the year.

The northern and southern parts of this frontal zone were described later in more detail by Thomas and Strub (1990), who also used CZCS imagery from 1979 to 1983 and 1986. Their results showed stronger signals in the northern area of the frontal zone, where pigment concentrations are above 2.0 mg m^{-3} while in the southern area pigment concentrations are always below 1.0 mg m^{-3}. The front is detectable most of the year, but it is strongly developed from late March to early July and shows a latitudinal displacement of about 150 km throughout the year (Thomas and Strub 1990; Haury et al. 1993). However, there is an abrupt change that always comes north off the Baja California coast; it is referred to as the Ensenada Front (Haury et al. 1993).

Although several studies have been made in this zone (Pelaez and McGowan 1986; Thomas and Strub 1990; Gaxiola-Castro and Alvarez-Borrego 1991; Haury et al. 1993; Thomas et al. 1994; Kahru and Mitchell 2000; Kahru and Mitchell 2001), they do not describe the Ensenada Front signature in detail. Therefore, the goal of the present work is to evaluate the ocean color signature of the Ensenada Front and its seasonal and interannual variation, considering events like El Niño.

DATA AND METHODS

Monthly composites of pigment concentration from CZCS imagery, from November 1978 to June 1986, were used to generate time series for three transects (600 km) and 22 locations in the Ensenada Front area (fig. 1a). These locations and transects were chosen according to visual observation of CZCS images, like those shown in Figure 1b, and with the objective of avoiding artifices of false color palette. The spatial resolution of CZCS images was 4 km processed as explained in Santamaría-del-Angel et al. (1994).

Non-El Niño and El Niño periods were defined according to time series extracted from Sea Surface Temperature (SST) imagery. We extracted data for the transects described above (fig. 1a) from monthly composites with 18 km of spatial resolution obtained from the Advanced Very High Resolution Radiometer (AVHRR/NOAA), for the period from June 1982 to June 1986. We calculated SST anomalies following Santamaría-del-Angel et al. (1994) and used these to separate non-El Niño months from El Niño months. No AVHRR data were available from November 1978 to May 1982; we classified these months following Lenarz et al. (1995) indications.

We calculated an average picture for each period (non-El Niño and El Niño) using time series extracted from CZCS images for those locations indicated in Figure 1a. We did that using monthly average pigment concentration for each month corresponding to a non-El Niño and El Niño event.

Image composting over a long time period (e.g., a month) produces significant smearing and aliasing of fronts and may even create artificial fronts. We used LAC (Local Area Coverage) data from the ocean color sensor Sea-viewing Wide Field-of-view Sensor (SeaWiFS/NASA) to confirm the results obtained with CZCS monthly composites. We processed images from September 1997 to November 2001 that include the El Niño event of 1997–98. We processed chlorophyll maps at 1.1 km nadir resolution, using SeaDAS version 4.1 (released on 9 Nov. 2001).

RESULTS AND DISCUSSION

Considering SST anomalies, the period from July 1982 to December 1984 and from January to June 1986 were El Niño months. 1985 was considered a non-El Niño year. According to Lenarz et al. (1995), November 1978 to June 1982 were also non-El Niño months. Our calculations for typical average months for each period (non-El Niño and El Niño) were based on the time series taken from the transects and locations indicated above (fig. 1a). Figure 2 shows contour maps of these average pigment concentrations for April, August, and November, both for non-El Niño (fig. 2a) and El Niño (fig. 2b) periods. Such months were chosen to represent different hydrographic and climatic conditions. August was related to summertime, November to wintertime, and April is the month when upwelling events off Point Conception are strongest (Dugdale et al. 1997).

We used contour maps (fig. 2) to follow the latitudinal displacement of the frontal zone where the 0.25 mg m^{-3} isoline appears to delimit two areas. The southern area is characterized by low pigment concentrations and relatively homogeneous conditions, whereas the northern area is more structured and graded. This pattern has been previously noted not only with CZCS imagery (Pelaez and McGowan, 1986; Thomas and Strub 1990; Kahru and Mitchell 2000) but also by modern ocean color sensors like the Ocean Color and Temperature Sensor (OCTS) (Kahru and Mitchell 2000) and SeaWiFS (Kahru and Mitchell 2001). In situ data of chlorophyll-*a* concentration (Gaxiola-Castro and Alvarez-Borrego 1991; Haury et al. 1993; Kahru and Mitchell 2001), inorganic nutrients (Traganza et al. 1980; Haury et al. 1993), and temperature (Haury et al. 1993) have corroborated those satellite data.

An M-like shape characterizes the 0.25 mg m^{-3} isoline, mainly for non-El Niño periods (fig. 2a). The valley between the "M" oceanic and coastal peaks aforementioned can usually be observed between 119° and 121°W, which corresponds to the average longitude of Point Conception (see fig. 1). This region in the South-

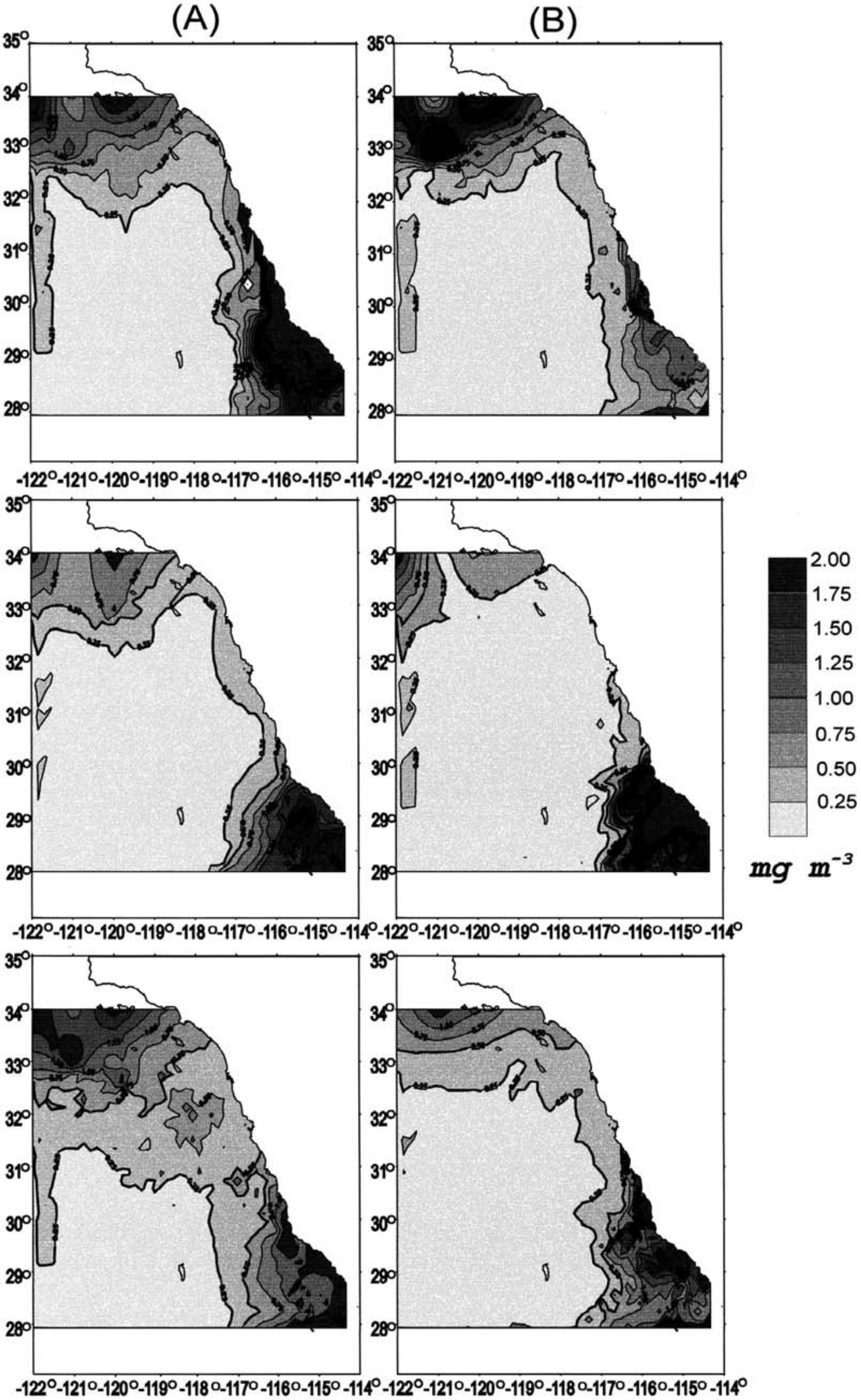

Figure 2. Contour plots of average pigment concentrations (mg m^{-3}) for April, August, and November during non-El Niño (*A*) and El Niño (*B*) periods.

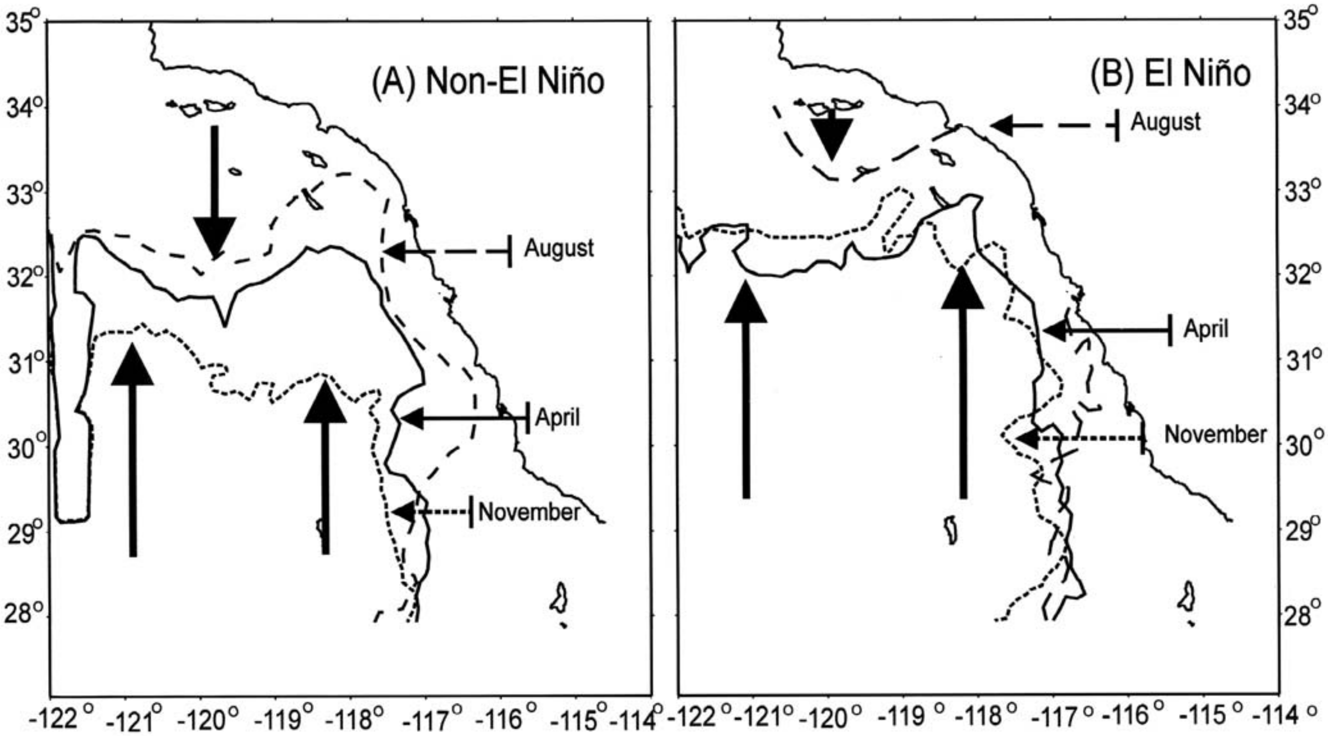

Figure 3. Schematic representation of 0.25 mg m^{-3} isoline seasonal migration during non-El Niño (*A*) and El Niño (*B*) years. Arrows indicate the direction of movement of water masses.

ern California Bight (SCB) corresponds to a break point in the coastal morphology, which promotes upwelling events (Dugdale et al. 1997). Cold, nutrient-rich, low-chlorophyll waters are upwelled close to the coast and moved offshore as a plume with increasing chlorophyll concentration (Dugdale et al. 1997).

This region is also associated with the Southern California Eddy (SCE) (Batteen 1997), a cyclonic gyre that promotes the flux of coastal waters to the south. The SCE originates through the interaction between the Coastal Counter Current (CCC), which flows from south to north, and the SCB coastal morphology off Point Conception. The main effect of this interaction is a change in the direction of the CCC, which makes a U-turn. The SCE effect helps to extend this upwelling plume southwards to promote the valley effect on the Ensenada Front M-shape, which is enclosed by the oligotrophic waters of the two external M-peaks.

Temporal variability of the 0.25 mg m^{-3} isoline is clearly visible in Figures 2 and 3. For non-El Niño months (fig. 3a) it can be seen that from winter (November) to summer (August) there is a northward migration of the frontal zone, which moves from 30–31°N to 32°30'N. However, the oceanic peak of the "M" is slowed down while the coastal one moves farther north, probably as a result of the effect of the SCE and the southwards flux of the upwelling plume on the shape of the frontal zone.

During El Niño months (fig. 3b) the M-shape is clearly visible in April, and the temporal variability of that boundary is slightly different. During August the low concentration zone (below 0.25 mg m^{-3} isoline) moves north (around 33°N) and closer to the coastline, whereas in November it is observed just below the latitude of 33°30'N and more to the north than during a non-El Niño November (fig. 3a). Comparing both periods, it is clear that in El Niño months the 0.25 mg m^{-3} isoline is moved farther north enclosing the eutrophic waters of the SCE to latitudes above 33°N. This can be associated with the intrusion of the oligotrophic Subtropical Pacific Water to northern California during El Niño periods, as previously reported by several researches (Emery and Hamilton 1985; Huyer and Smith 1985; Wyrtki 1985; Rienecker and Mooers 1986; Johnson and O'Brien 1990; Thomas and Strub 1990; Kahru and Mitchell 2000; Kahru and Mitchell 2001; Mitchell 2000).

Kahru and Mitchell (2000) summarized the effects of El Niño on the CCS. They observed the influence of two separate effects: (1) the reduction of the eutrophic areas throughout the region off Point Conception due to reduction in upwelling; (2) the increasing extent of an offshore bloom off Baja California. Their results are

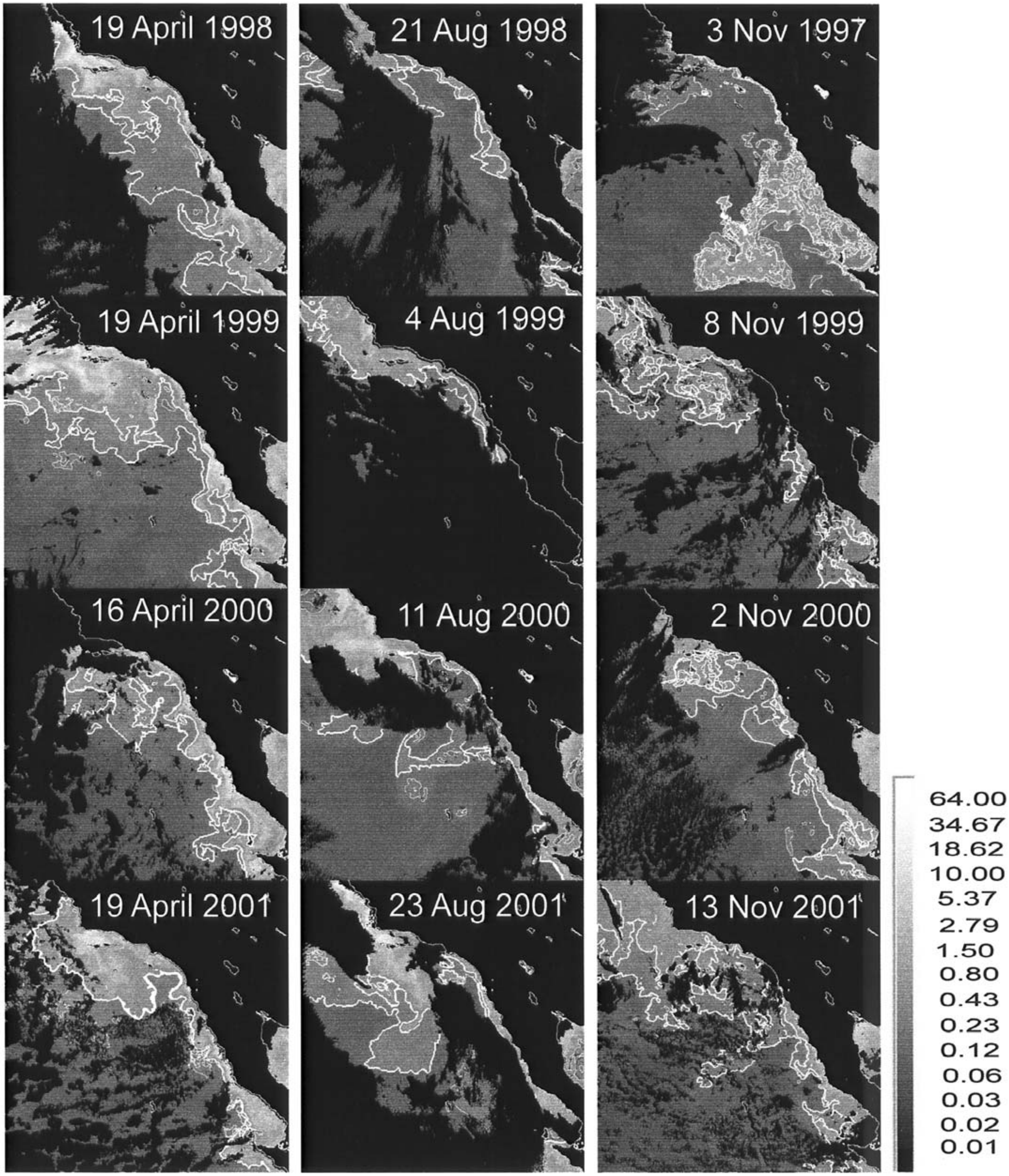

Figure 4. SeaWiFS LAC images of chlorophyll-*a* concentration (mg m^{-3}) from 1997 to 2001. Land and clouds were masked black.

also evident in our schematic representation shown in Figure 3b, which shows that pigment concentrations above 0.25 mg m^{-3} during summer are very close to Point Conception and that during April, when upwelling conditions are stronger, the M-shape of the 0.25 mg m^{-3} concentration is clearly visible. Besides, it is during November that the influence of the offshore bloom can be noted at approximately 30°N (November arrow in fig. 3b).

The ocean color sensor SeaWiFS, launched in September 1997, is part of a new generation of ocean color sensors that have a better radiometric resolution than CZCS. Besides, monthly composites of CZCS images could lead to significant smearing and aliasing of fronts or could even have created artificial fronts. To confirm those results obtained with CZCS, we processed SeaWiFS LAC images (1.1 km spatial resolution) from 1997 to 2001 (fig. 4) for the same months used for calculating average pigment concentration (fig. 2). We superposed 0.25 and 0.5 mg m^{-3} isolines over the images to enhance front migration and for comparison with Figures 2 and 3. Those images from 1997 and 1998 correspond to El Niño years, and it is possible to observe the same pattern discussed earlier, such as stronger upwelling in April off Point Conception and oligotrophic conditions off California and north of Baja California during winter and summer. The image of 3 November 1997 clearly shows the strong offshore bloom off Baja California, which has been previously associated with El Niño years by Kahru and Mitchell (2000). During this time the typical Ensenada Front is practically unrecognizable.

For non-El Niño months, the M-shape of the Ensenada Front is also clearly visible, following not only the 0.25 mg m^{-3} but also the 0.5 mg m^{-3} isoline. The stronger effect of the upwelling plume is observed in April, as noted previously, with exception for August 2001 when its intensity was comparable to that from April. This behavior confirms the strong interannual variability of the Ensenada Front in this zone.

The use of specific pigment (CZCS) or chlorophyll (SeaWiFS) concentration isolines to follow the displacement of the Ensenada Front is somewhat subjective considering the differences in algorithms for biomass retrieval between sensors, and for comparison with others in the future. For example, the parameter calculated for CZCS is “pigment” (chlorophyll-*a* + phaeopigments), whereas for SeaWiFS it is chlorophyll-a (Chl-*a*). In general, CZCS pigment underestimates the SeaWiFS chlorophyll-*a* at low Chl-*a* and overestimates at high Chl-*a* (Kahru and Mitchell 2000). Despite these constraints, it is possible to follow the position of the Ensenada Front using the 0.25 and 0.5 mg m^{-3} isolines and using both sensors because such Chl-*a* concentrations are in the middle of the range where CZCS and SeaWiFS seem to have the best agreement. However, a better representation of the position of the frontal zone could be obtained using an edge-detection method such as that described by Cayulla and Cornillon (1992), which was firstly applied for SeaWiFS images by Miller (2000). This subject has to be addressed by future investigations.

CONCLUDING REMARKS

This study showed the characteristic M-shape of the Ensenada Front, whose signature can be followed by observing the 0.25 and 0.5 mg m^{-3} isolines of chlorophyll-*a* concentration. Its latitudinal displacement was followed using CZCS imagery first, and later confirmed by SeaWiFS. In addition, it is important to consider that in El Niño years the front position (0.25 mg m^{-3} isoline) is located farther north than during non-El Niño years, mainly during November (winter) and April (upwelling). These results will be very useful for future cruise planning considering the strong seasonal and interannual variability of the front position. However, for a better representation of the frontal zone position, we suggest the use of an edge-detection method such as that described by Cayulla and Cornillon (1992) and Miller (2000).

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COMPARATIVE ZOOPLANKTON SAMPLING EFFICIENCY OF A RING NET AND BONGO NET WITH COMMENTS ON POOLING OF SUBSAMPLES

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ABSTRACT

We analyzed the comparative sampling efficiency of CalCOFI 1 m diameter ring nets and bongo nets in a series of paired comparisons from the California Current. Seventeen major taxa of holozooplankton were enumerated and species-specific analyses were carried out for hyperiid amphipods. The only consistent difference detected between these two nets was a significant increase in abundance of salps in the bongo net. In contrast with comparisons of abundance, the species diversity of hyperiid amphipods was higher when estimated from ring net than from bongo net collections, at higher numbers of individuals enumerated. Analysis of a sample pooling procedure revealed that the average abundance of the more numerous taxa was generally similar, whether determined by enumerating plankton samples individually or from a pooled sample comprising quantitative splits of individual samples. The average abundance of rare taxa was not well represented in the pooled sample. Sample pooling is particularly inappropriate for studies of pelagic species diversity.

INTRODUCTION

There is growing recognition that low-frequency perturbations in the ocean can have significant consequences for marine populations and ecosystems (e.g., Ebbesmeyer et al. 1991; Roemmich and McGowan 1995; Mantua et al. 1997; Planque and Taylor 1998; Lavaniegos and Ohman 1999; Hare and Mantua 2000; Rebstock 2001). Such studies depend upon measurement methods that document ocean properties in a consistent manner over many tens of years. Against this need for analytical consistency is the need for the development of new measurement methods that improve upon the accuracy, precision, or temporal/spatial resolution of traditional methodologies. As old methodologies give way to new, it becomes of particular importance to understand and intercalibrate measurements taken by different methods if a long temporal history is to be reconstructed.

Our interest in understanding decadal-scale variations in pelagic ecosystem structure in the California Current System has led us to examine the effects of changes in zooplankton sampling methods over the course of the CalCOFI time series. Historical variations in CalCOFI zooplankton sampling methods have been summarized (Ohman and Smith 1995). Here, we turn our attention to the possible influence of a change in net types on the measured abundances of different zooplankton taxa. In December 1977 the bridled 1-m diameter ring net used by CalCOFI since 1949 was replaced by a 0.71-m bridleless bongo net (McGowan and Brown 1966) for standard CalCOFI zooplankton collections. The two nets are illustrated in Brinton and Townsend (1981), who also explored the relative catchability of 12 species of euphausiids by the two nets. Hewitt (1980) compared the differential avoidance of the two nets by larval anchovy, Rebstock (2001) analyzed the capture efficiency of 28 species of calanoid copepods, and Ohman and Smith (1995) compared the relative efficiency of the two net designs for collection of total zooplankton biomass (measured as displacement volume). Here, our objective is to understand the catchability of all major holozooplankton taxa censused by the two nets, in order to improve our ability to detect long-term variability in pelagic ecosystem structure. In addition to our attention to major taxa, we analyzed hyperiid amphipods catches by the two nets because of our interest in reconstructing the temporal history of hyperiids and their gelatinous hosts in the water column (Lavaniegos and Ohman 1999).

Accurate taxonomic identification of zooplankton is a labor-intensive process and means to reduce the time spent in such identifications would be broadly welcomed. We sought to evaluate the feasibility of combining quantitative splits of a group of individual zooplankton samples into one pooled sample for enumeration, in order to reduce the amount of sample processing needed to obtain measures of mean abundance. Here, we present the results of our comparisons of pooled sample counts in relation to abundance estimates derived from the analysis of individual plankton samples.

METHODS

We based our analysis on samples collected by CalCOFI at selected stations in Alta California and Baja California waters. Paired, metered tows were carried out

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using a 1-m diameter ring net with a preceding bridle in comparison to a bridleless bongo net. The diameter of the bongo frame was 0.60 m in 1975 and 0.71 m in 1978. Both nets were of 0.505 mm Nitex mesh and were towed obliquely from the surface to 210 m and back to the surface, maintaining a wire angle close to 45°. The net catch was preserved in buffered formaldehyde and a total of 62 samples analyzed by microscope (tab. 1). Only nighttime samples were considered, to avoid issues of light-mediated net avoidance and differential vertical migration. Sample pairs were collected within 30–40 min of each other (for further sampling details see Brinton and Townsend 1981; and Ohman and Smith 1995).

Zooplankton groups were counted and measured from the complete sample when individual body size exceeded 25 mm in length. After removal of these large specimens, samples were split with a Folsom splitter and one-eighth, one-sixteenth, or one-thirty-second of the original sample enumerated. Specimens less than 25 mm in length were identified to taxon and recorded in intervals of length class (0.5 mm or 1.0 mm, depending on the taxon). In the case of hyperiid amphipods the complete sample was analyzed and all specimens identified to species following Brusca (1981) and Vinogradov et al. (1996).

Counts were standardized to individuals per square meter of sea surface. To estimate mean abundance and 95% confidence intervals, data were first Log (x+1) transformed. Diversity of hyperiid amphipods was estimated using modified rarefaction curves as proposed by Hurlbert (1971):

$$E(S_n) = \sum_{i=1}^{S} \left[1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right]$$

where $E(S_n)$ is the expected number of species in a sample of n individuals from a collection containing N individuals and S species, and N_i is the number of individuals of the ith species ($i = 1, 2,.,S$).

The effect of pooling samples from different stations compared to samples counted individually was analyzed using 13 spring nighttime samples from CalCOFI cruise 9804 (i.e., Apr. 1998). The pooled sample was constituted with 10.5–12.1% of each sample. The fraction removed from each corresponded to 50 m^3 of water filtered in the ocean (cf. Rebstock 2001). Zooplankton groups were counted and measured from complete individual samples when individual body size exceeded 25 mm in length. After removal of these large specimens, subsampling was done with a 5 ml Stempel pipette until one-eighth of the original sample had been enumerated. In the case of hyperiids, the complete sample was analyzed and all individuals identified to species. In the pooled sample, subsampling was done with a 5 ml Stempel pipette for small-sized individuals, but the complete sample was counted for large size categories and for hyperiid species.

TABLE 1
Zooplankton Samples Used in the Net Comparison Analysis and Portion of Each Sample Analyzed

Cruise	Stations	Number of paired tows	Portion analyzed 1 m ring net	Bongo net
7501	73.60	5	1/32	1/16
	103.60	5	1/16	1/16
7507	70.60[a]	4	1/32	1/16
	103.65	5	1/32	1/16
7804	83.60	1	1/8	1/8
	87.60	1	1/8	1/8
	90.30	1	1/8	1/8
	90.60	1	1/8	1/8
	103.30	1	1/8	1/8
	103.90	1	1/8	1/8
7805	73.60	1	1/8	1/8
	80.90	1	1/8	1/8
	83.60	1	1/8	1/8
	87.60	1	1/8	1/8
	90.30	1	1/8	1/8
	103.60	1	1/8	1/8

[a]Only copepods and amphipods were counted.

RESULTS

Bongo Versus Ring Net

Comparisons of the capture of 15 different major taxa of zooplankton by the bongo net and ring net in nighttime collections are illustrated in Figure 1, accompanied by a 1:1 line. Analysis of the catches of matched pairs of zooplankton samples by the Wilcoxon signed-rank test revealed no consistent bias in collection of any major taxon except salps ($p < 0.0001$, $N = 205$; see tab. 2) and pteropods (thecosomes plus gymnosomes, $p < 0.05$, $N = 154$). The alpha level has not been corrected for multiple testing. In both cases the bongo net collected more individuals than the ring net. For many taxa there was considerable scatter in the relationship between the two nets; this arises partly because of the finely subdivided length categories in which organisms were enumerated, leading to fewer individuals per category and a consequent greater susceptibility to subsampling error. In the case of the salps, where the variability was considerable, we combined all size classes from each net sample and again compared abundances (fig. 2). As with the results from individual size classes, combined abundances were significantly higher in the bongo net than in the ring net ($p < 0.02$, Wilcoxon signed-rank). In some comparisons for every taxon, specimens of a given length class were captured by one net but not by the other. A higher proportion of such instances generally occurred

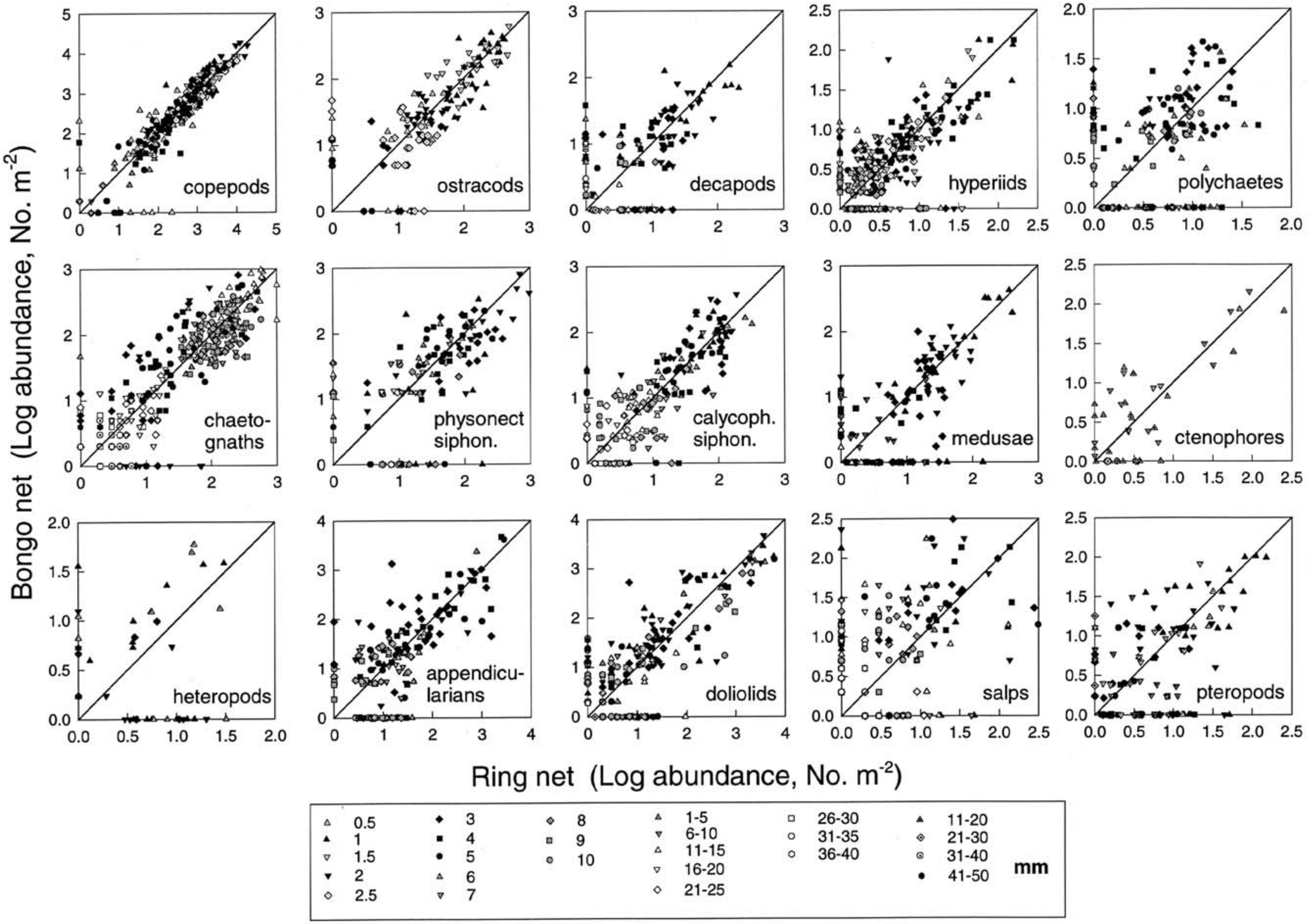

Figure 1. Comparative abundances of different zooplankton taxa captured by the bongo net and ring net. Comparisons are made by size classes of organisms, ranging from 0.5–1 mm to 41–50 mm. Diagonal is a 1:1 line. Note differences in scales among taxa.

TABLE 2
Comparison of Bongo and Ring Net Catches

	Wilcoxon matched-pairs signed-rank tests[a]		Ratio of bongo to ring net[b]		
Taxon	*N*[c]	*p* value	*N*[c]	Median	95% C.I.[d]
Copepoda	284	> 0.10	265	1.02	0.93–1.11
Ostracoda	154	> 0.10	124	0.97	0.84–1.16
Decapoda	180	> 0.10	78	1.39	0.93–1.68
Hyperiid Amphipoda	335	> 0.10	215	1.13	1.00–1.23
Polychaeta	214	> 0.10	108	1.23	0.98–1.47
Chaetognatha	462	> 0.10	390	0.99	0.89–1.11
Physonect Siphonophora	141	> 0.10	101	1.12	0.86–1.23
Calycophoran Siphonophora	198	> 0.10	159	1.06	0.86–1.15
Medusae	132	> 0.10	72	1.14	0.94–1.35
Ctenophora	49	> 0.10	25	1.29	0.75–1.65
Heteropoda	52	> 0.10	17	2.01	1.26–3.10
Appendicularia	173	> 0.10	122	1.07	0.87–1.47
Doliolida	234	> 0.10	140	1.30	0.97–1.54
Salpa	205	< 0.0001	91	2.68	1.66–3.38
Pteropoda (Gymnosomata + Thecosomata)	154	< 0.05	75	1.09	0.90–1.24
Radiolaria	92	> 0.10	72	1.07	0.83–1.40
Cladocera	33	> 0.10	22	0.95	0.44–1.67

[a] Excludes cases where a size class was missing from both net types.
[b] Excludes cases where a size class was missing from either net type.
[c] Number of paired comparisons including all available length classes within a taxon.
[d] Confidence intervals, based on the binomial distribution (Zar 1999).

with the rarer taxa (heteropods, gymnosomes and thecosomes, polychaetes, hydromedusae, decapods) and with taxa that were not necessarily rare but tend to have highly patchy distributions (salps, doliolids) or are associated with patchily distributed hosts (hyperiid amphipods). Such scatter did not occur in the copepods, which were generally abundant in all size classes.

The average ratio of bongo to ring net catch of each major taxon is also reported in Table 2. The median catch ratio did not differ significantly from 1.0 for any taxa except salps and heteropods. For calculations of the median catch ratio, cases where the catch of either net was zero had to be eliminated. This resulted in a different sample size from the comparisons with the Wilcoxon matched-pairs signed-rank test. After elimination of these cases, the average catch of pteropods was no longer different between nets. All heteropods in the 3 mm size class or below were members of the genus *Atlanta*, and all larger heteropods were carinariids and pterotracheids. Heteropods were generally too rare to make a conclusive assessment of catch ratios.

The shapes of the size frequency distributions of the major taxa enumerated did not differ appreciably between the two net types (fig. 3) for most taxa. However, in the case of salps the bongo net caught consistently higher numbers in all size classes but one, although not all such comparisons were significantly different (at $\alpha < 0.05$) in a Wilcoxon matched-pairs test. Significant differences at $\alpha < 0.05$ were detected for single length classes of ostracods, hyperiid amphipods, polychaetes, physonect siphonophores, and calycophoran siphonophores, and for two length classes of copepods and chaetognaths. Such differences in isolated length categories or in noncontiguous length classes, which are not upheld when corrected for multiple testing by the Bonferroni criterion, suggest that these results may be artifacts of large numbers of statistical tests. Note that the test results reported with asterisks in Figures 3 and

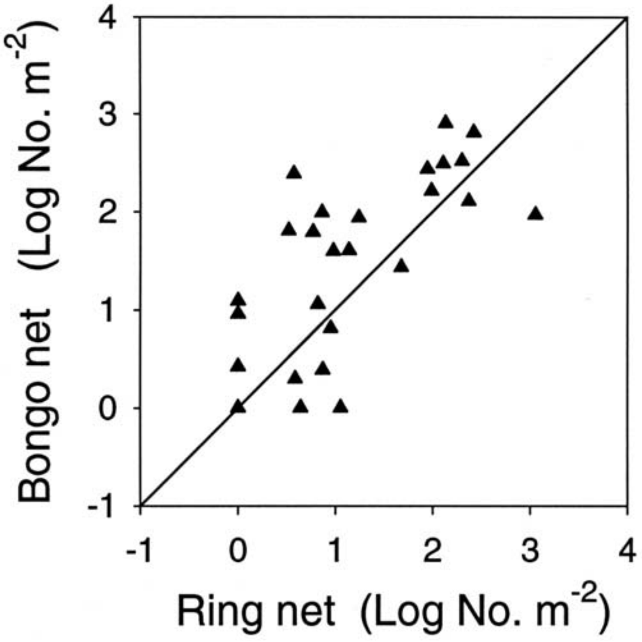

Figure 2. Comparative abundance of salps captured by the bongo net and ring net. All size classes from fig. 1 have been combined from each sample in the present plot. Diagonal is a 1:1 line.

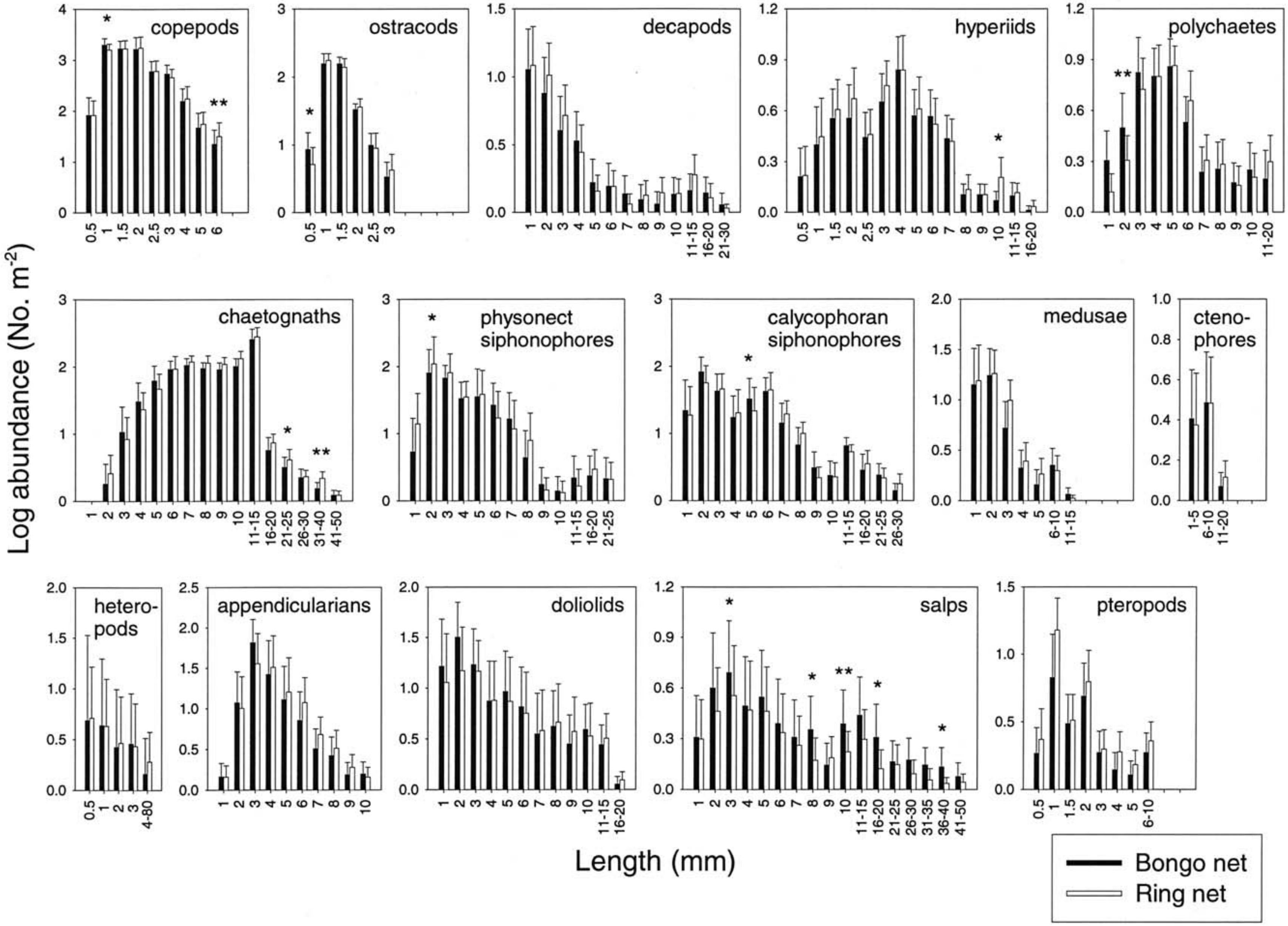

Figure 3. Comparative size-frequency distributions of different zooplankton taxa captured by the bongo net (filled bars) and ring net (open bars), ± 95% confidence intervals. Illustrated distributions are based on all samples combined without regard to specific pairing of bongo and ring net samples taken adjacent in time. Note the differences in scales among taxa. Asterisks indicate significant differences ($p < 0.05$ (*) or $p < 0.01$ (**)) from a separate paired-comparisons test (Wilcoxon matched pairs), which utilizes the specific pairing of individual bongo and ring net samples and is not based on the combined frequency distributions shown here.

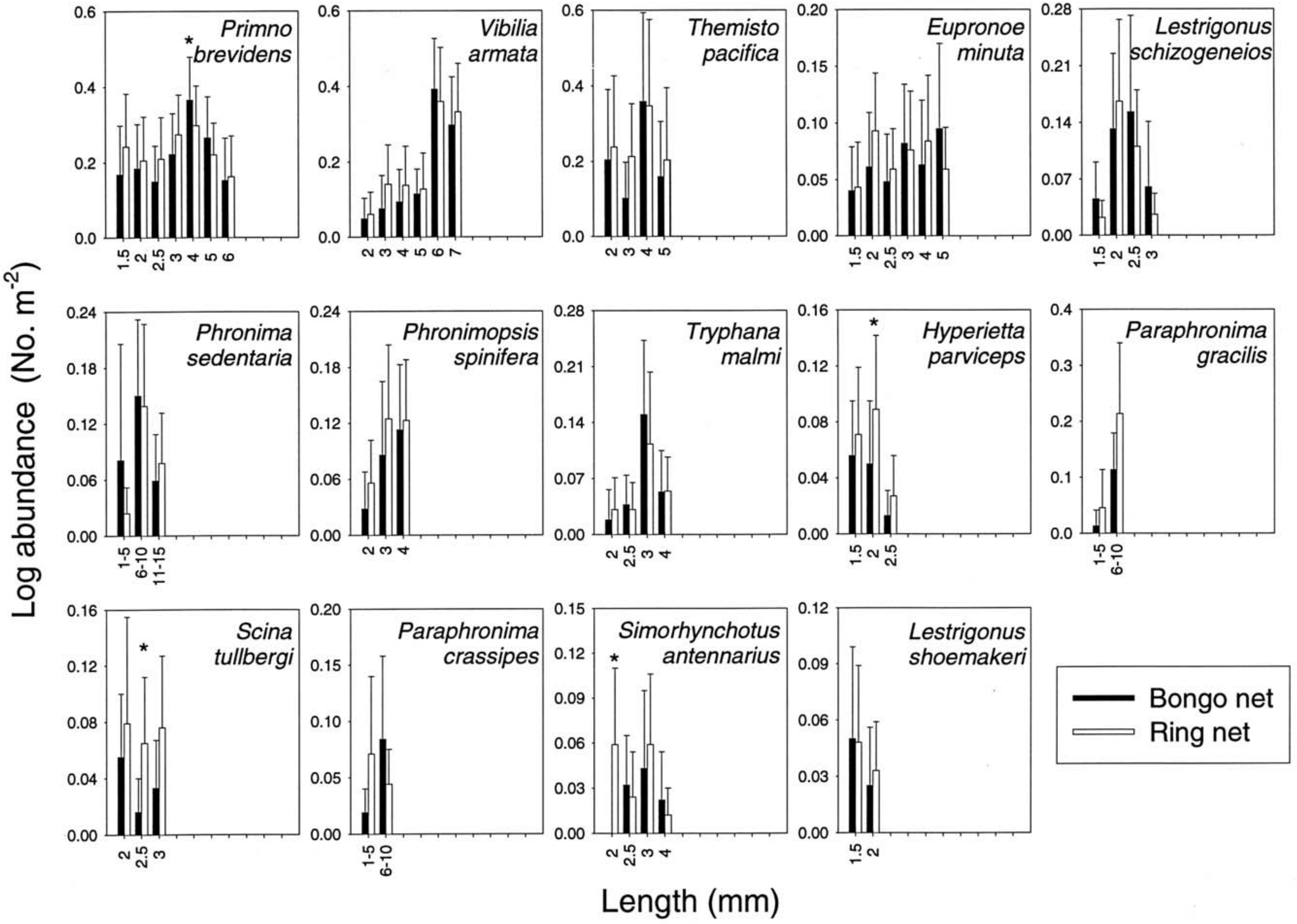

Figure 4. Comparative size-frequency distributions of different hyperiid amphipod species captured by the bongo net (filled bars) and ring net (open bars), ± 95% confidence intervals. Illustrated distributions are based on all samples combined without regard to specific pairing of bongo and ring net samples taken adjacent in time. Note the differences in scales among taxa. Asterisks indicate significant differences ($p < 0.05$ (*)) from a separate paired-comparisons test (Wilcoxon matched pairs), which utilizes the specific pairing of individual bongo and ring net samples and is not based on the combined frequency distributions shown here.

TABLE 3
Comparison of Bongo and Ring Net Catches of Hyperiid Amphipods

	Wilcoxon matched-pairs signed-rank tests[a]		Ratio of bongo to ring net[b]		
Taxon	*N*[c]	*p* value	*N*[c]	Median	95% C.I.[d]
Primno brevidens	141	> 0.10	66	1.27	1.13–1.66
Vibilia armata	90	> 0.10	48	1.35	1.00–1.71
Themisto pacifica	41	> 0.10	23	1.28	0.70–1.65
Eupronoe minuta	71	> 0.10	19	1.66	1.00–3.08
Lestrigonus schizogeneios	40	> 0.10	16	1.49	1.00–2.38
Phronima sedentaria	29	> 0.10	15	1.10	0.52–1.51
Phronimopsis spinifera	31	> 0.10	15	1.51	0.84–2.38
Tryphana malmi	35	> 0.10	10	1.22	0.50–2.05
Hyperietta parviceps	29	< 0.05	10	0.91	0.38–1.71
Paraphronima gracilis	25	> 0.10	7	1.69	0.75–3.31
Scina tullbergi	34	> 0.05	6	1.70	0.59–2.48
Paralycaea gracilis	8	> 0.10	4	1.30	—
Paraphronima crassipes	22	> 0.10	3	1.55	—
Scypholanceola aestiva	8	> 0.10	3	2.21	—
Vibilia propinqua	7	> 0.10	3	1.03	—
Phrosina semilunata	4	> 0.10	3	1.54	—
Vibilia chuni	6	> 0.10	3	3.42	—
Simorhynchotus antennarius	27	> 0.10	2	1.47	—
Lestrigonus shoemakeri	18	> 0.10	2	2.12	—
Hyperoche medusarum	10	> 0.05	2	0.96	—
Lycaeopsis themistoides	8	> 0.10	2	3.59	—
Vibilia australis	8	> 0.10	2	1.78	—
Phronima stebbingi	7	> 0.10	2	1.25	—
Euthamneus rostratus?	6	> 0.10	2	1.44	—
Vibilia stebbingi	5	> 0.10	2	1.63	—
Dairella californica	8	< 0.05	1	0.68	—
Streetsia challengeri	12	> 0.10	1	2.44	—
Hyperoche martinezi	9	> 0.05	1	1.51	—
Parascelus edwardsi	9	> 0.10	1	3.38	—
Hyperioides longipes	8	> 0.10	1	2.13	—
Hyperia medusarum	7	> 0.10	1	2.38	—
Phronima pacifica	7	> 0.10	1	0.44	—
Vibilia gibbosa	6	> 0.10	1	0.77	—
Parapronoe parva	5	> 0.10	1	2.05	—
Phronima atlantica?	5	> 0.10	1	0.55	—
Hyperoche mediterranea	4	> 0.05	1	1.19	—
Oxycephalus clausi	4	> 0.05	1	0.51	—
Primno latreillei	4	> 0.10	1	2.21	—
Lycaea pulex	8	> 0.10	0	—	—
Scina borealis	7	> 0.10	0	—	—
Phronima bucephala	6	> 0.10	0	—	—
Lycaea pachypoda	4	> 0.05	0	—	—

[a] Excludes cases where a size class was missing from both net types.

[b] Excludes cases where a size class was missing from either net type.

[c] Number of paired comparisons including all available length classes within a taxon.

[d] Confidence intervals, based on the binomial distribution; too few comparisons were available to estimate nonparametric confidence limits of the median for most species.

4 are from the Wilcoxon matched-pairs test of paired comparisons, whereas the overall length-frequency distributions in those figures are based on means and 95% confidence limits of combined abundances in each length class from all samples combined.

We considered 42 individual species of hyperiid amphipods. Many were too rare to obtain valid pairwise comparisons. The only species for which there were detectable overall differences in abundance between the two net types were *Hyperietta parviceps* (Wilcoxon matched pairs, $p = 0.019$, $N = 29$ pairs) and the much rarer *Dairella californica* ($p = 0.012$, $N = 8$ pairs). Neither of these comparisons would be considered statistically significant if corrected for multiple testing. Analysis of the bongo to ring net ratio showed that for only one species (*Primno brevidens*) was this ratio significantly greater than 1.0 (tab. 3), although the lower confidence limit for this ratio was exactly 1.00 for three other species. Notably, the results from the Wilcoxon test and the net ratios did not agree. The size frequency distributions of the 14 most abundant hyperiid species, for which sufficient counts were obtained to make size-based comparisons,

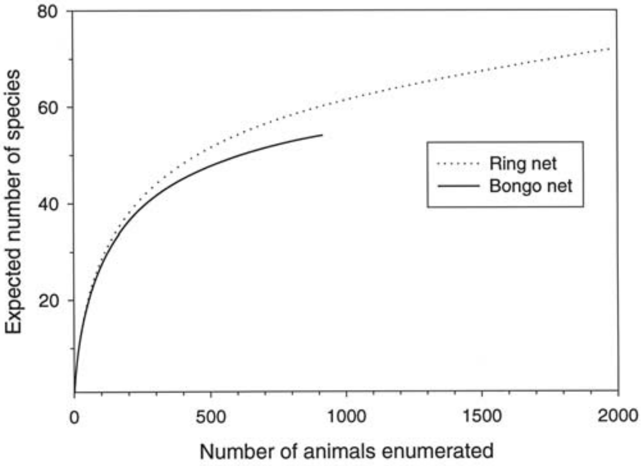

Figure 5. Rarefaction curves for hyperiid amphipods captured by the bongo net (*solid line*) and 1 m ring net (*dotted line*), for all net comparison samples combined.

showed similar distributions. When the matched ring–bongo net pairs were compared with a Wilcoxon test, we detected only isolated differences in size composition between the two net types (asterisks in fig. 4). In one case (*Simorhynchotus antennarius*) the smaller size class was not detected in the bongo net, probably due to the rarity of these individuals.

Comparison of the hyperiid amphipod species diversity as assessed by the two nets is shown in the rarefaction curves in Figure 5. At lower numbers of individuals counted (< 100 per sample) the two curves are virtually indistinguishable, but the increased species diversity as assessed by the ring net becomes clear at higher abundances (> 200–300 individuals counted). The total number of hyperiid individuals collected by the two nets differs because of the two-fold greater mouth area of the 1 m ring net than the 0.71 m bongo net, hence double the volume of water filtered for a tow of the same duration.

Sample Pooling

The mean abundance of all major taxa was determined on one cruise by two methods. One involved enumeration of each of the nighttime samples from the study region individually. The other involved subsampling a pooled sample containing a quantitative split of each of the preceding samples. For most (17 out of 21) taxa, the average abundance assessed from the pooled sample was within the 95% confidence limits of the mean of the samples analyzed individually (fig. 6). The exceptions were pteropods, radiolarians, appendicularians, and foraminifera. We attribute the differences in mean abundance of foraminifera and radiolaria to a tendency to adhere to other particulate matter and thus to clump, which makes completely randomized subsampling difficult. The differences found for pteropods (thecosomes and gymnosomes) and appendicularians appear to be a consequence of random processes in the subsampling procedure that led to the presence of slightly more individuals in some subsamples than in others.

Consideration of the effect of pooling on the estimated abundance of individual species of hyperiid amphipods yielded rather different results. Generally, the six most common species were reasonably represented by the abundance estimates from the pooled sample (fig. 7a). However, numerous rare species were found only in the individual samples and not detected at all in

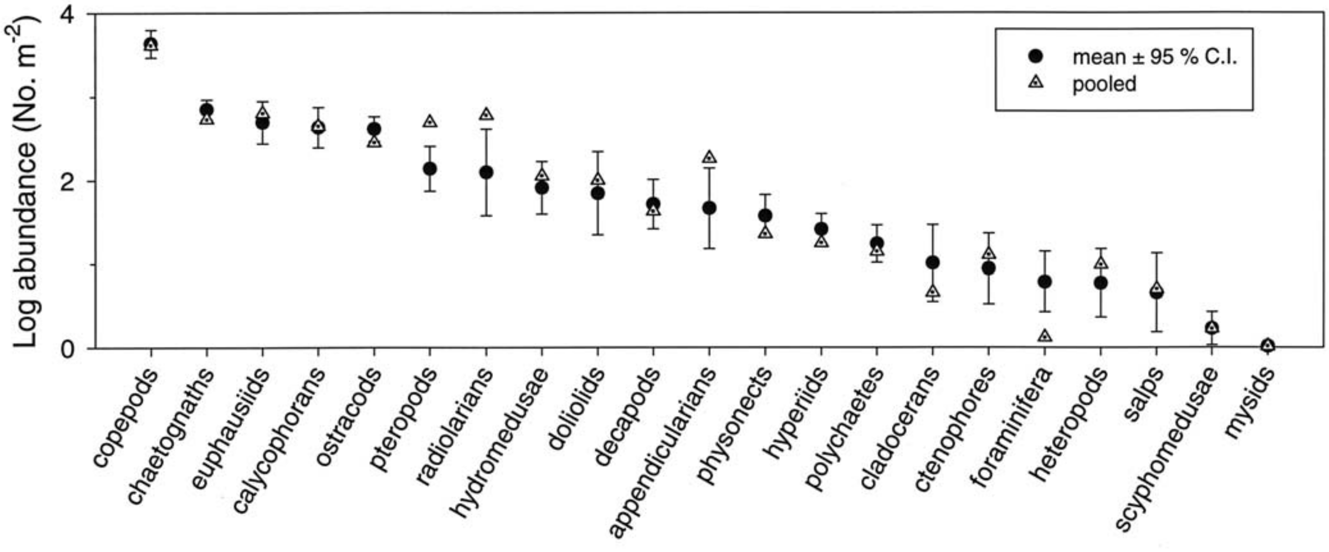

Figure 6. Pooling experiment from cruise 9804. Comparative abundances of different zooplankton taxa following enumeration of aliquots from all samples individually (*circles*, mean ± 95% confidence interval) and from a single pooled sample (*triangles*).

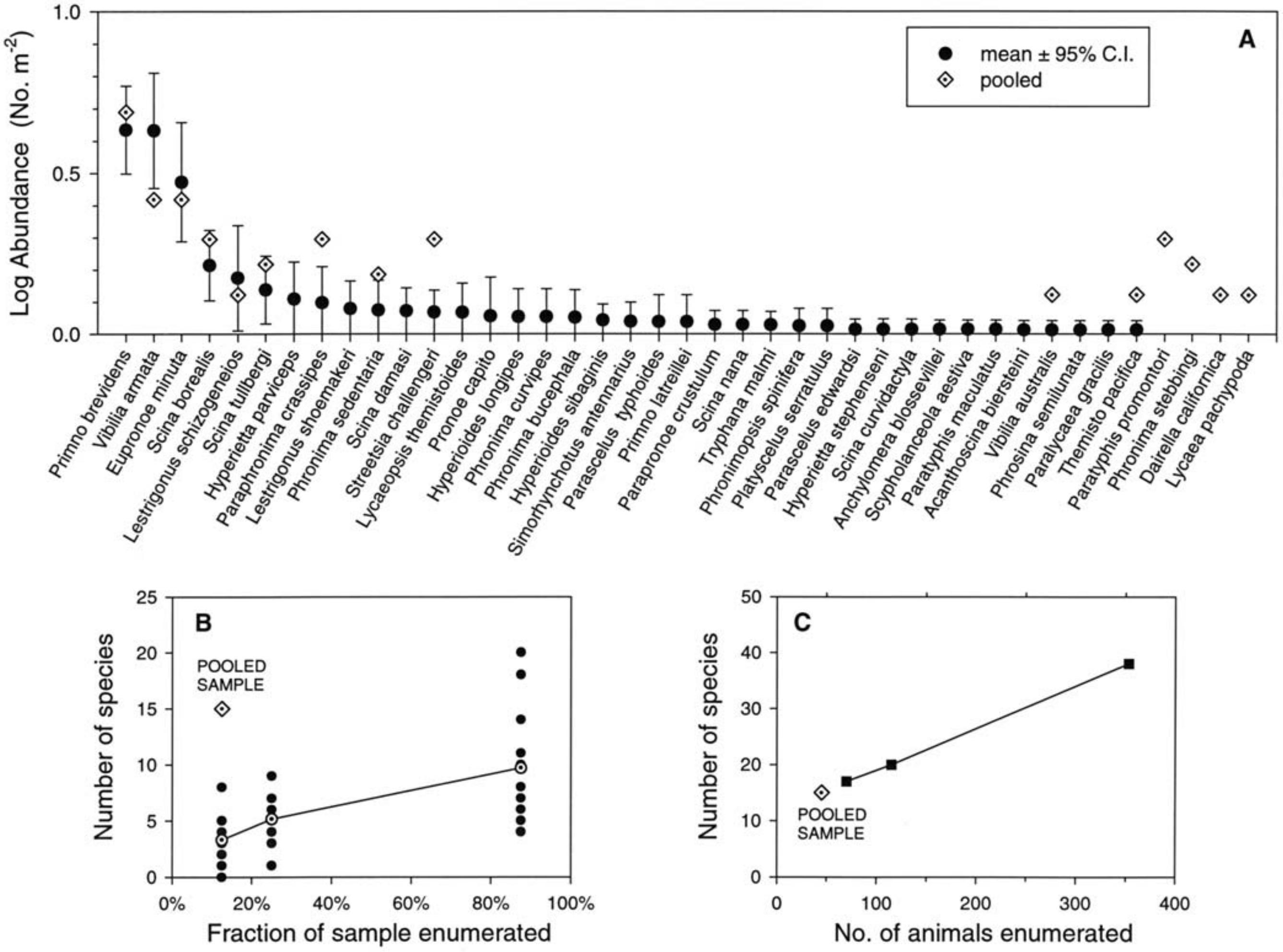

Figure 7. Pooling experiment from cruise 9804. *A*, comparative abundances of different species of hyperiid amphipods following enumeration of aliquots from all samples individually (*circles*; mean ± 95% confidence interval) and from a single pooled sample (*diamonds*). *B*, number of hyperiid amphipod species detected as successively larger fractions of individual plankton samples are enumerated (*filled circle*; *open circles* and *solid line* connect the mean of 13 samples); also indicated is number of species detected in the pooled sample. *C*, number of hyperiid amphipod species detected as a function of the number of individuals enumerated, for all samples in the pooling experiment combined; also indicated is number of species detected in the pooled sample.

the pooled sample. In addition, four species were found in the pooled sample that were not detected in any of the individual samples. The latter result reflects the fact that 10–12% of each sample was removed for pooling before enumerating each individual sample. Thus, by chance alone, rarer species could have been transferred into the pooled sample, leaving none in the 90% of the original sample that remained. Analysis of successively larger fractions of each sample, from 12.5% to 87.5%, resulted in an increase in the mean number of species detected (fig. 7b). The corresponding number of species detected in analysis of 12.5% of the pooled sample was appreciably higher than in the average of individual samples. The total number of species recognized was directly proportional to the number of individuals enumerated (Fig. 7c).

DISCUSSION

Comparison of the capture efficiency of different nets is complicated by the perennial difficulty in sampling precisely the same parcels of water and associated plankton patches. However, paired samples were usually taken within half an hour, which is as almost as closely spaced in time as was practicable with these nets. In instances where more abundant taxa are enumerated, such differences in time/space should have relatively little consequence, provided individuals do not have highly aggregated spatial distributions when abundant. For rarer taxa, or others with aggregated distributions, the consequence can easily be the absence of an individual in a net of one type and its presence in another. Such an effect was frequently seen with salps, doliolids, appendicularians, and pteropods. Overall, the primary consequence of slight temporal/spatial differences in waters sampled will be increased variability in the catch ratios of the two nets, but the median catch ratios should remain unbiased provided that a sufficient number of comparisons are made.

A statistical consequence of such variability in catch ratios is that the power of a test such as the Wilcoxon matched-pairs signed-rank test will be lessened. Rebstock (2001) analyzed the power efficiency of the Wilcoxon test for comparisons of calanoid copepods collected in these same samples. She found that the power of the test is relatively low, with power to detect differences between net types of a factor of 1.5 to vary between about 5% and 90%, depending on the species considered and its variability. This result suggests that caution be used before accepting the null hypothesis of no difference between nets. Our comparison of copepod collections in the two net types differs from that of Rebstock (2001), in that she counted primarily adult calanoids, whereas we counted and sized all copepods collected. This may account for the bongo to ring net ratio she observed (0.93), which was not significantly different from 1.0 (0.82–1.02 bootstrapped confidence intervals), whereas we observed a ratio of 1.02 (0.93–1.11, confidence interval based on the binomial distribution).

Another component of variability in such net comparisons is within-laboratory splitting and subsampling error. Our comparisons between pooled and separately enumerated samples is affected by this bias alone. For all of the abundant categories of higher taxa, and for the most abundant hyperiid species, the consequences of subsampling were relatively minor. We can conclude for the more abundant taxa that the mean abundance from the pooled sample generally approximates the mean abundances that would result from analysis of numerous replicate samples. However, for rare taxa, and most notably the rarer species of hyperiid amphipods, sample pooling is quite unsatisfactory. Sample pooling in the manner conducted here should not be carried out in studies of species diversity, in particular, where the presence or absence of rare taxa materially affects the outcome of the analysis.

We have not explored the possibility of differences in sampling efficiency by year, season, geographic area, or diameter of bongo net (0.60 m vs. 0.71 m). There were not sufficient paired comparison samples available to explore any of these factors in detail and we expect that such differences will be relatively minor. Concerning differences in the diameter of the bongo net, Ohman and Smith (1995) found no difference in the biomass ratio of 0.60 m diameter bongo net to 1 m ring net versus 0.71 m bongo to 1 m ring net.

The most consistent difference detected in the comparisons between net types was the improved collection of salps by the bongo net. The bongo net was a more efficient collector of many salp size classes. We infer that this difference is attributable to the lack of a three-point wire bridle and hydrowire immediately in front of the bongo net mouth, unlike the 1 m ring net. The hydrowire and bridle preceding the ring net would serve to break up and disperse salp chains and probably generate lower abundances inside the net itself. Hydrodynamic disturbances generated by the hydrowire could also lead to enhanced net avoidance, although it does not seem likely that the escape responses of salps are sufficiently rapid to permit avoidance (Wiebe et al. 1979). Salps were identified to species only on cruises 7501 and 7507. The dominant species present was *Thalia democratica*, and other species identifiable were *Salpa fusiformis*, *Iasis zonaria*, *Cyclosalpa bakeri*, *Salpa aspera*, and *Ritteriella picteti*. We note that net sampling is to be avoided altogether if the objective is to collect salp specimens in optimal condition for physiological and behavioral research (Madin and Kremer 1995), but this was not the purpose of the present study.

The extreme variability in the bivariate plot of salp abundances collected by the two nets illustrates, in part, the notoriously patchy distributions of these organisms (Andersen 1998). This complicates the assignment of an average catch ratio between the two nets that could be used to correct the ring net catches for equivalent bongo catches. However, assuming that the median value is an unbiased measure of central tendency, and that a comparable collection bias against salps collected by a ring net exists for other salp species, the average correction factor of 2.68 could be applied to ring net abundances to make them correspond approximately to bongo collections for time series studies.

The apparent difference in abundance of gymnosomatous and thecosomatous pteropods between bongo and ring nets is not robust to correction for multiple testing and was not sustained in the analysis of catch ratios, for which missing values from either net had to be excluded. Conversely, for heteropods, there were no significant between-net differences by the Wilcoxon test, in which only double zeroes were excluded, whereas the median catch ratios were significantly different from 1.0. However, since only 17 paired comparisons with positive heteropod abundance remained after elimination of cases of zero abundance for either net, the power of the test was low and this result must be considered inconclusive.

Of the hyperiid amphipod species that were sufficiently abundant to test for net differences, only *Hyperietta parviceps* suggested a significant change, but this comparison does not withstand correction for multiple testing. Most hyperiids utilize gelatinous zooplankton as hosts (Laval 1980; Harbison et al. 1977; Lavaniegos and Ohman 1999) or are associated with marine snow particles in the water column (Laval 1980). If hosts are (or are not) collected equally by both types of nets, one would expect the pattern of amphipod collections to follow. It is not clear whether *H. parviceps* has well-defined hosts, although members of the genus have been found to be associated with radiolarians (Laval 1980; Lavaniegos and Ohman 1999). We found no difference between net types in catches of radiolarians. In light of the lack of overall significant difference in collections of total hyperiids by the two net types, as well as the preponderance of individual species where no such bias was detectable, we conclude in general that there was little detectable effect of net changes on the collection of hyperiid amphipods.

The difference in species diversity, as estimated by rarefaction curves from all individuals collected by the two nets, is somewhat surprising. This difference is negligible at low total numbers of individuals compared. The time series analysis of hyperiid diversity by Lavaniegos and Ohman (1999) was based on the expected number of hyperiid species in a sample of 88 individuals (E_{88}), and the results above indicate that the difference between net types would have contributed a 3.9% bias in expected number of species at E_{88}. The long-term changes observed by Lavaniegos and Ohman were considerably larger than this, and thus their conclusions are not affected by the change in nets. However, at much larger numbers of individuals enumerated, an appreciably higher expected number of hyperiid species are found in the ring net samples. This may be related to either the bongo net's tendency to collect more salp specimens of all size classes or the weak (but nonsignificant) tendency of the bongo to catch more doliolids, and the importance of such gelatinous organisms as hosts for hyperiids. If a tendency existed for more individuals of a given host species to be collected in a bongo net tow, this could result in more individuals of the associated parasitoid species, and thus fewer species present for the same cumulative number of individuals counted.

The present results, together with the study of Brinton and Townsend (1981) help explain the findings of Ohman and Smith (1995) that the total zooplankton biomass collected by the bongo net was 1.366 times that collected by the ring net. Brinton and Townsend found that the bongo net generally caught more juvenile and adult euphausiids (due to diminished avoidance of the bongo), but the ring net usually caught more larval euphausiids. Considering 12 euphausiid species, and addressing biomass rather than abundance, the average difference was 1.6 times greater biomass collected by the bongo than the ring net (range 0.7–3.1, depending on the species). Here, the bongo net collected approximately 2.7 times greater abundance of salps but probably due to decreased disruption of colonies by the bongo net rather than to diminished avoidance of the bongo. Little difference in overall abundance or size classes of copepods (results above) or in individual copepod species (Rebstock 2001) has been found, or in other holozooplankton taxa. Hewitt (1980) found that the bongo net was a preferred collector for larger larvae of the northern anchovy, but larval fish were removed from the samples prior to our analyses, so they were not a contributor to the augmented biomass. Thus, the previously documented 36.6% increased biomass collected by the bongo net is principally attributable to its increased collection efficiency of salps and euphausiids.

The results of sample pooling suggest that the mean abundances of the more abundant taxa are generally relatively well approximated by enumerating the combined sample. The abundances of the rare taxa, however, and, in particular assessments of the diversity of rarer species, are not represented in a satisfactory manner in the pooled sample. The results from Rebstock's (2001) and Venrick's (2002) studies are consistent with this conclusion. Sample pooling is to be avoided where measures of species richness are required.

In summary, we have detected few consistent differences in collection efficiency of holozooplankton between CalCOFI collections by the 1 m diameter ring net and the bongo net. We must temper this conclusion with the recognition that the statistical power of such comparisons is limited. The bongo net is the preferred collector of adults and juveniles of most species of euphausiids (Brinton and Townsend 1981) and of salps. Appropriate correction factors can be found in Brinton and Townsend (1981), Ohman and Smith (1995), and in the present study.

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THE REPRODUCTIVE PATTERN OF BARRED SAND BASS (*PARALABRAX NEBULIFER*) FROM SOUTHERN CALIFORNIA

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ABSTRACT

Sea basses of the genus *Paralabrax* are either gonochores or protogynous hermaphrodites. This study sought to determine which, if either, reproductive strategy prevails in barred sand bass (*Paralabrax nebulifer*). A total of 436 specimens were collected from June 1996 through April 1997 from seven different locations along the southern California coast. Of these, only two (< 0.1%) transitional individuals were found. All males examined exhibited testes with a membrane-lined central cavity and a sperm sinus in the gonadal wall; our findings suggest that these individuals may have passed through a female-like juvenile stage prior to maturation. In addition, 52% of the males examined had atretic bodies. However, males and females were equally distributed throughout the age classes collected. Based on all evidence, we conclude that barred sand bass in southern California are functional gonochores that possess a latent, perhaps ancestral, ability to change sex.

INTRODUCTION

The barred sand bass (*Paralabrax nebulifer*) is a common species in the nearshore marine environment and an important part of the marine recreational fishery of southern California. It ranked second in the number of fish taken by sport-fishers in the state in 1989 and remains one of the most frequently caught species (Oliphant 1990). The barred sand bass together with the kelp bass (*Paralabrax clathratus*) comprised more than 90% of the general "rock bass" recreational catch in the first half of the twentieth century (Frey 1971). Barred sand bass range from Santa Cruz, California, south to Magdalena Bay, Baja California Sur, including Guadalupe Island (Miller and Lea 1972), and occupy a variety of different habitats, including kelp beds and sand flats on the open coast to inland harbors and bays. They are benthic, relatively sedentary fish and are rarely found more than 3 m above the substrate, closely associated with bottom structure and sand (Turner et al. 1969; Feder et al. 1974; Larson and DeMartini 1984). Barred sand bass are oviparous broadcast batch spawners that breed from April to August, with a peak in July (Love et al. 1996). They tend to form large breeding aggregations over soft bottom areas at depths of 15–30 m during their spawning season. Their eggs and larvae are pelagic, drifting in open water, and juveniles appear in shallow water from late summer to early winter (Love 1991). In this species, 50% of males matured at 219 mm, and 50% of females matured at 239 mm. Males mature between the ages of 2 and 4 years and females between the ages of 2 and 5 years (Love et al. 1996).

The barred sand bass is a warm temperate member of the family Serranidae (sea basses) and one of the three species of *Paralabrax* that occur along the southern California coast. Many species of the family Serranidae have specialized reproductive strategies. Some species are protogynous hermaphrodites and hence spend the early part of their lives as females and later change sex to conclude their lives as males. Oda et al. (1993) suggested that barred sand bass might be protogynous hermaphrodites based on a relatively small number of specimens ($N = 81$). They found six specimens that had gonads containing both ovarian and testicular tissue. Four of these were believed to be active males with primary oocytes in the testes. Proliferating testicular tissue was found in the remaining two specimens, one of which was an immature individual. This finding led Oda et al. (1993) to conclude that barred sand bass may be capable of both pre- and post-maturational sex change. However, based on the criteria for hermaphroditism established by Sadovy and Shapiro (1987), Oda et al. concluded that there was insufficient evidence to identify barred sand bass as a protogynous hermaphrodite. Their histological evidence was certainly suggestive of that conclusion. The major weakness of this study was born out of the relatively small sample size, which made it impossible to examine sex ratios over size classes and, particularly, age classes. We sought to address these shortcomings by using a much larger sample and determining the age of each specimen.

Studies on the other two temperate *Paralabrax* species have shown varying results (DeMartini 1987). Kelp bass (*P. clathratus*) are found in nearshore coastal waters usually associated with hard substrate and kelp. They have been termed "secondary gonochores," believed to have evolved from protogynous ancestors and do not change sex (Smith and Young 1966). Spotted sand bass (*P. mac-*

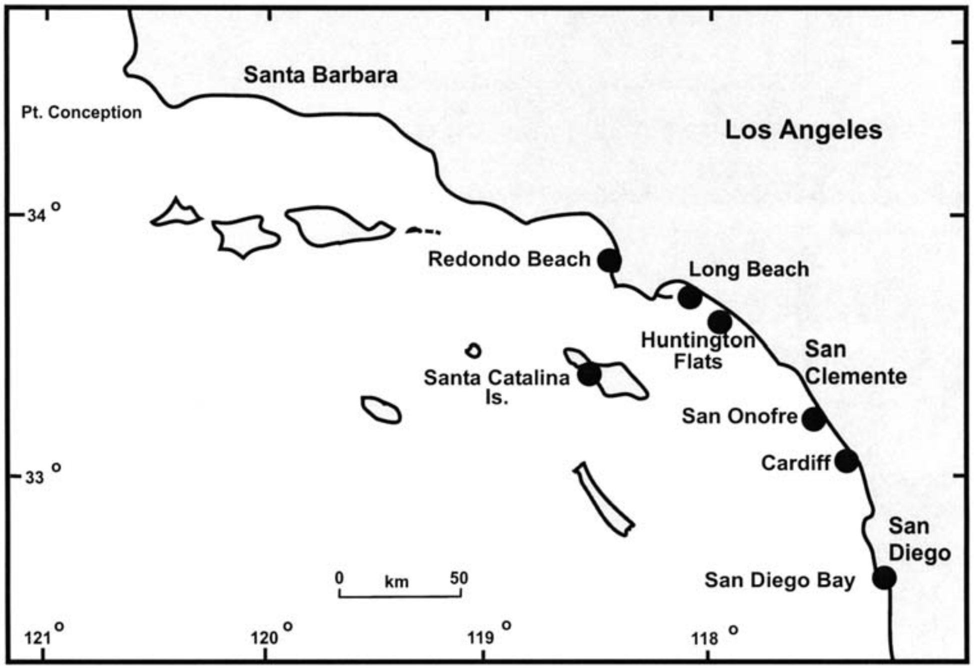

Figure 1. Sampling locations along the southern California coast for barred sand bass (*Paralabrax nebulifer*) reproductive study.

ulatofasciatus) found in harbors and bays (Allen et al. 1995) have specific populations that are protogynous hermaphrodites and others that appear to be gonochoric (Hastings 1989; Hovey and Allen 2000). The presence of protogynous hermaphrodites in *P. maculatofasciatus* was hypothesized to be related to population structure and mating system at various locations.

Our main objective in this study was to determine whether protogynous hermaphroditism occurs in barred sand bass and, if so, to what extent. To that end, we will present both histological evidence and age structure data from a large sample of barred sand bass collected primarily from breeding aggregations off the coast of southern California.

Knowledge of the reproductive strategy used by a species is important for proper management of the fishery. Fisheries are managed to protect the species and to provide sustainable yields. Management strategies assuming gonochorism may not be appropriate for fish populations with protogynous hermaphroditism. Species with the latter may have numerous small females and fewer larger males rather than equal ratios of males and females by length and age. Such species may require special protective measures to ensure sufficient numbers of both genders.

METHODS

A total of 436 specimens were collected by hook and line from June 1996 through April 1997 along the coast of southern California at Redondo Beach, Long Beach, Huntington Flats, Santa Catalina Island, San Onofre, Cardiff, and San Diego Bay (fig. 1). Each specimen was weighed to the nearest gram, measured to the nearest millimeter standard length, and preliminarily sexed. Gonads were removed, weighed, and preserved in 10% formalin for later histological examination.

Gonads were fixed by immersion in Davidson's solution (20% formaldehyde, 10% glycerin, 30% EtOH, 10% glacial acetic acid, and 30% deionized water) for two weeks then transferred to 70% ethyl alcohol. Cross-sectional tissue samples (4 mm thick) were removed from the mid area of each gonad and placed in Tissue Tek tissue cassettes. Using the Tissue Tek tissue-fixing unit, cassettes were emersed in a series of increasing concentrations (70%, 80%, 95%, and 100%) of ethyl alcohol with a final emmersion in xylene. The processed tissue was embedded with paraffin (at 56°C) and placed in a vacuum infiltrate for 1 h. The surface of the tissue block was then exposed and samples were soaked in a detergent bath for 10–14 days. Samples were sectioned at 6–12µm using an 820 Spencer microtome and mounted on slides. The slides were placed in an oven and allowed to dry for 7 days at 35°C. They were then stained using Mayer's alum hematoxylin and eosin, allowed to dry, and sealed with cytosol and a cover slip. Gonad morphology was examined using a compound microscope under 100–400× power. Initial sex determination was confirmed based on the finding of ovarian tissue (females), testicular tissue (males), and indeterminate tissue (immature individuals).

TABLE 1
Number, Size, and Sex of Barred Sand Bass (*Paralabrax nebulifer*) Collected in Reproductive Biology Study, June 1996–April 1997

Location	Total no. specimens	Size range (mm)	No. of males	Size range (mm)	No. of Females	Size range (mm)	No. of Immatures	Size range (mm)	No. of transitionals	Size range (mm)
Cardiff	80	170–310	46	200–290	33	170–310	1	183	0	
Catalina	18	158–395	11	158–395	6	171–300	1	178	0	
Huntington Flats	233	191–362	106	191–322	127	198–362	0		1	273
Long Beach	4	202–328	3	202–297	1	328	0		0	
Redondo	6	250–405	5	250–405	1	285	0		0	
San Diego	51	78–335	17	121–308	12	169–335	22	78–201	1	306
San Onofre	44	155–460	20	230–460	19	230–375	5	155–190	0	
Total	436	78–460	208	121–460	199	169–375	29	78–201	2	273–306

Potential hermaphroditism was diagnosed following the criteria outlined in Sadovy and Shapiro (1997). The following features were considered strongly indicative of protogynous hermaphroditism: (1) transitional individuals; (2) atretic bodies in stages 1, 2, or 3 of oocytic atresia within the testes; (3) a membrane line central cavity in the testes; and (4) sperm sinuses in the gonadal wall. A fifth feature, population structure, can also add support to a diagnosis of hermaphroditism, if indicated. We examined all samples to determine the presence of any of these features.

Sagittal otoliths were also removed from each specimen and mounted onto wood blocks using cyanoacrylate and sprayed with an accelerant for instant curing. Otoliths were then sectioned using a Buehler isomet low-speed saw. A dorso-ventral, 1.0 mm cross section was cut through the focus and perpendicular to the sulcus, using two diamond-edge blades separated by a stainless steel shim. Sections were polished with 3M lapping film and water. Sections were then placed in a black bottom, water-filled dish and read under a dissecting microscope at 50× magnification. Sections were aged by identifying the first translucent annulus and counting sequential growth zones from the center to the dorsal edge. Otoliths were then re-read by a second reader, with 85% agreement as outlined by Allen et al. (1995). These ages were then used to calculate sex ratios based on age class. Sex ratios were also calculated based on standard length. Sex ratios were examined for each individual location as well as for the population as a whole.

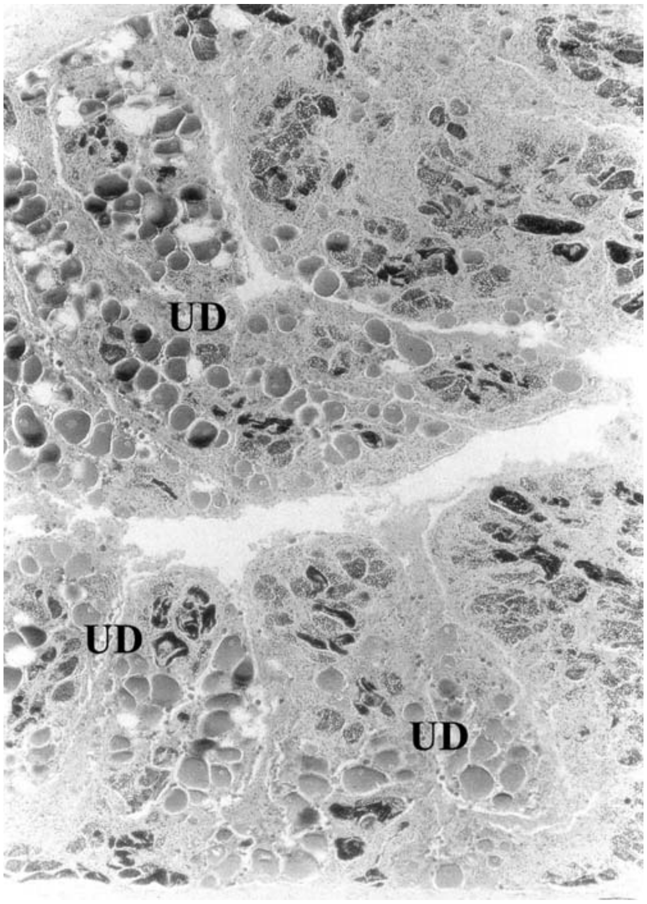

Figure 2. Immature gonad morphology in barred sand bass (*P. nebulifer*) showing undeveloped tissue (UD) resembling immature female features.

RESULTS

A total of 208 males, 199 females, 29 immatures, and 2 transitional individuals were examined (tab. 1). The majority of the fish (males and females) were collected from breeding aggregations at Huntington Flats, just southeast of Los Angeles–Long Beach Harbor. Immature individuals were only taken at Cardiff, Catalina, San Diego and San Onofre, with the majority being collected in San Diego. Overall, fish ranged in size from 78–460 mm SL. A 5-year-old, 273 mm SL transitional individual was taken from Huntington Flats and a 4-year-old, 250 mm SL transitional individual was taken from San Diego. Both transitional individuals were larger than the size at first maturity (Love et al. 1996).

Histological sections of ovaries in females showed typical primary, secondary, and vitellogenic oocytes. Testes of males exhibited typical spermatocytes, seminiferous

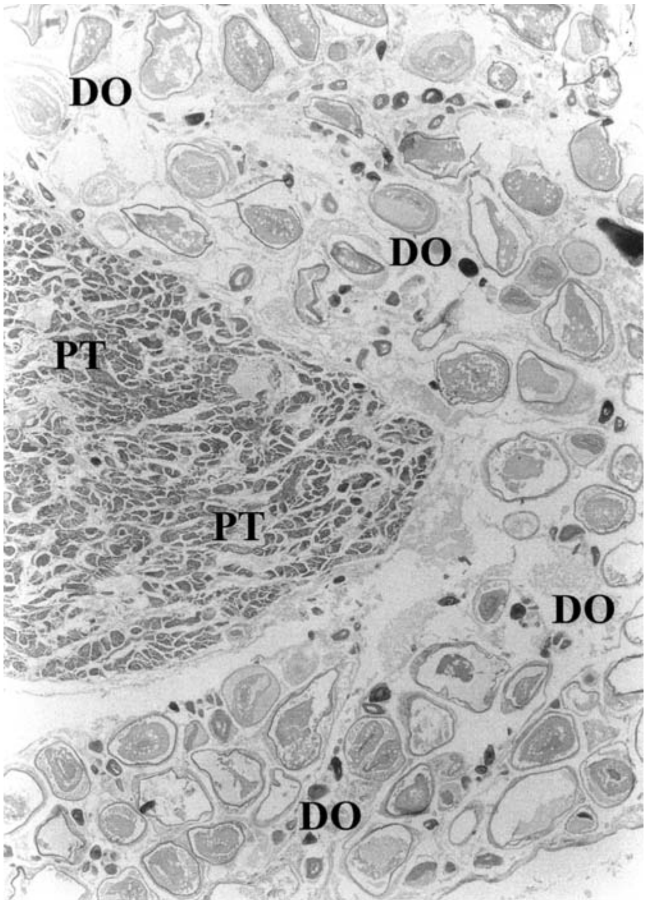

Figure 3. Transitional individual in barred sand bass (*P. nebulifer*) showing degenerating ovarian tissue (DO) surrounding proliferating testicular tissue (PT).

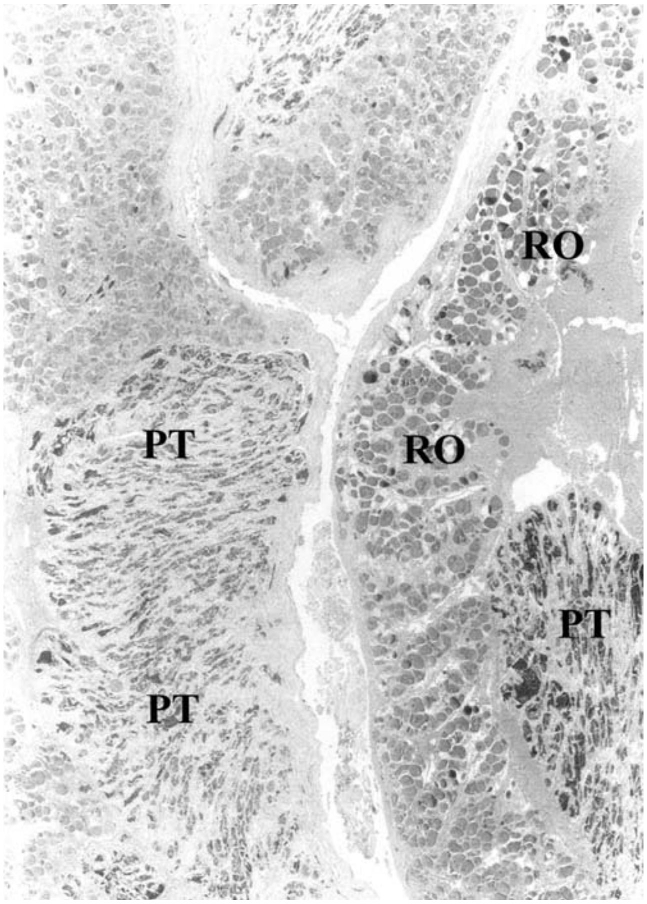

Figure 4. Transitional individual in barred sand bass (*P. nebulifer*) showing resting ovarian tissue (RO) and proliferating testicular tissue (PT).

tubules, sperm sinuses, and the crypts containing the developing sperm. All immature individuals were found to pass through a female-like stage of developing tissue with female features (fig. 2).

The gonad of the first transitional individual contained proliferating testicular tissue (developing sperm, sperm sinuses, and spermatocytes) and vitellogenic oocytes representing the degenerating ovarian tissue (fig. 3). This specimen was taken from Huntington Flats in August 1996 (during the later part of the breeding season). The second transitional individual exhibited resting ovarian tissue (rather than vitellogenic oocytes) and proliferating testicular tissue (fig. 4). This individual was taken off the coast of San Diego in April 1997 outside the breeding season.

A membrane-lined central cavity (gonadal lumen) with squamous epithelium cells was found in all males examined (fig. 5). The gonadal lumen was found to be used for the transportation of sperm in some of the males examined (fig. 6). The presence of a sperm sinus in the gonadal wall containing developing sperm surrounded by a muscle layer was also found in all males examined (fig. 7). Atretic bodies, found in 52% of all males examined, showed the characteristic yellow-brown pigment, granulose cells, and basophilic nuclei (fig. 8).

Sex ratios were examined based on standard length and age class (fig. 9). Individual locations showed comparable proportions of males and females throughout the size (ANCOVA, $F = 0.90$, $p = 0.35$) and age ($F = 0.88$, $p = 0.36$) classes allowing locations to be combined. In general, males and females were found to be distributed throughout the size and age classes for the entire sample (fig. 10). Most importantly, sex ratios did not differ significantly with age ($\chi^2 = 12.48$, df = 9, $p = 0.19$). Interestingly, females were actually better represented than males in the larger size classes ($\chi^2 = 25.59$, df = 8, $p < 0.001$). This distribution pattern is the opposite of what would be expected in a protogynous strategy. The presence of large females actually argues against protogyny and is likely due to sampling bias in this case. Samples were obtained primarily by hook and line in breeding aggregations where smaller, aggressive males tend to be captured at higher frequencies. Furthermore, these aggregations, once found, are targeted by commercial

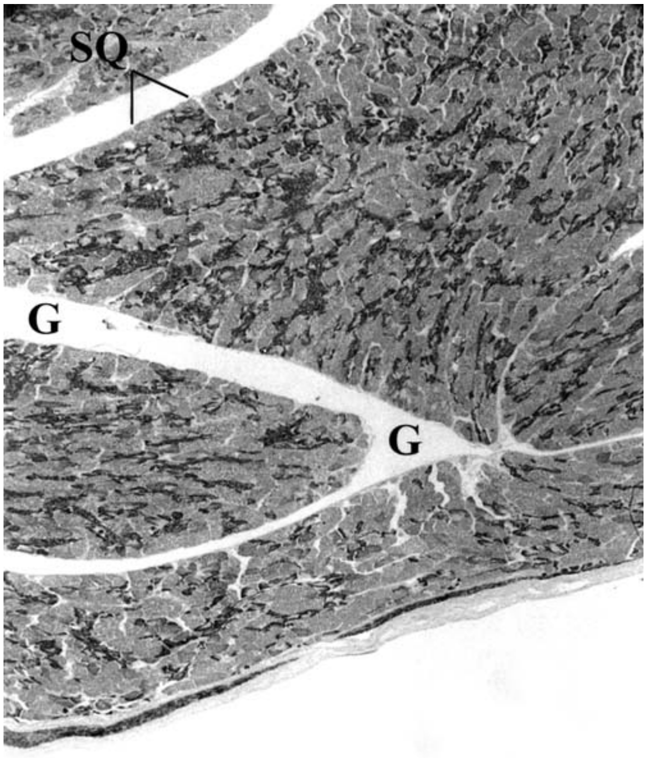

Figure 5. Gonadal lumen in male tissue of barred sand bass (*P. nebulifer*) showing gonadal lumen (G) and squamous epithelium cells (SQ).

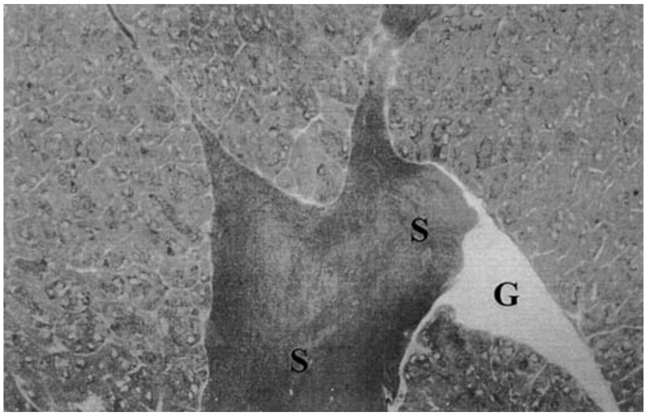

Figure 6. Gonadal lumen (G) functioning for the transport of sperm (S) in male tissue of barred sand bass (*P. nebulifer*).

passenger fishing vessels (CPFVs) over successive days, which probably removes males preferentially over time on the spawning grounds.

DISCUSSION

The first and strongest criterion used to indicate sex change is the presence of transitional individuals (i.e., individuals in the process of changing sex) (Sadovy and Shapiro 1987). The gonadal tissue of protogynous hermaphrodites will show a degeneration of the initial ovarian tissue and a proliferation of testicular tissue. Our finding two transitional individuals during this study was predictable because transitional individuals are relatively uncommon in field studies. They are more typically seen in laboratory studies where sex change is experimentally induced (Sadovy and Shapiro 1987). The fact that we found transitional individuals at all supports the hypothesis that at least a portion of the population of barred sand bass can change sex.

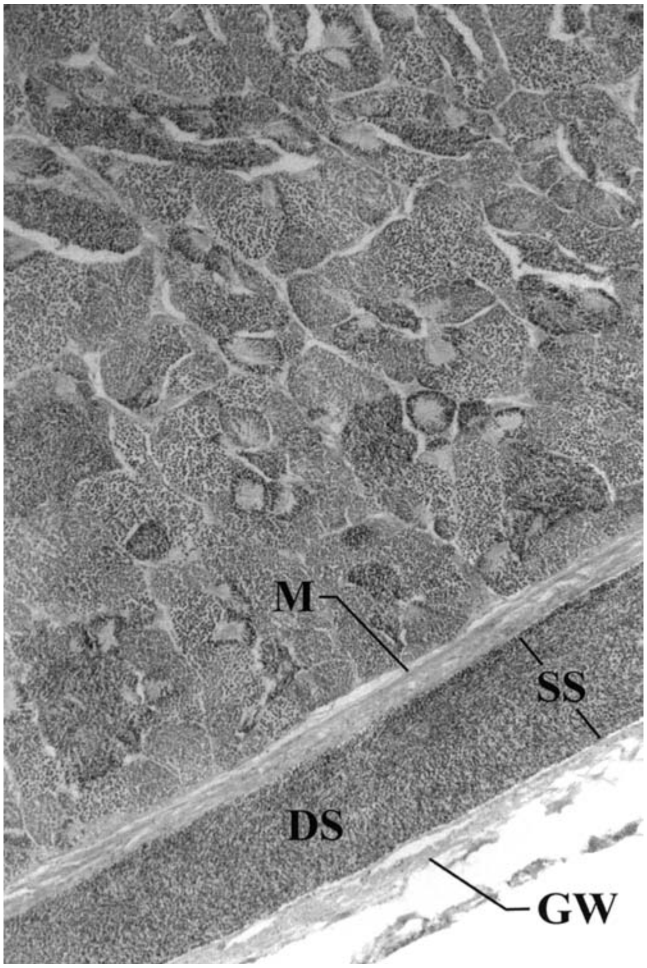

Figure 7. Sperm sinus (SS) in the gonadal wall of a male barred sand bass (*P. nebulifer*) containing developing sperm (DS) surrounded by the muscle layer (M) and gonadal wall (GW).

The second criterion examined was the presence of a membrane-lined central cavity (gonadal lumen) in the testes. The gonadal lumen is thought to be a remnant of the ovarian lumen, which is used for egg transportation in females. All males examined were found to have gonadal lumens. The presence of a gonadal lumen is only a valid criterion if it is nonfunctional in males. Sperm was found in this cavity in some of the males ex-

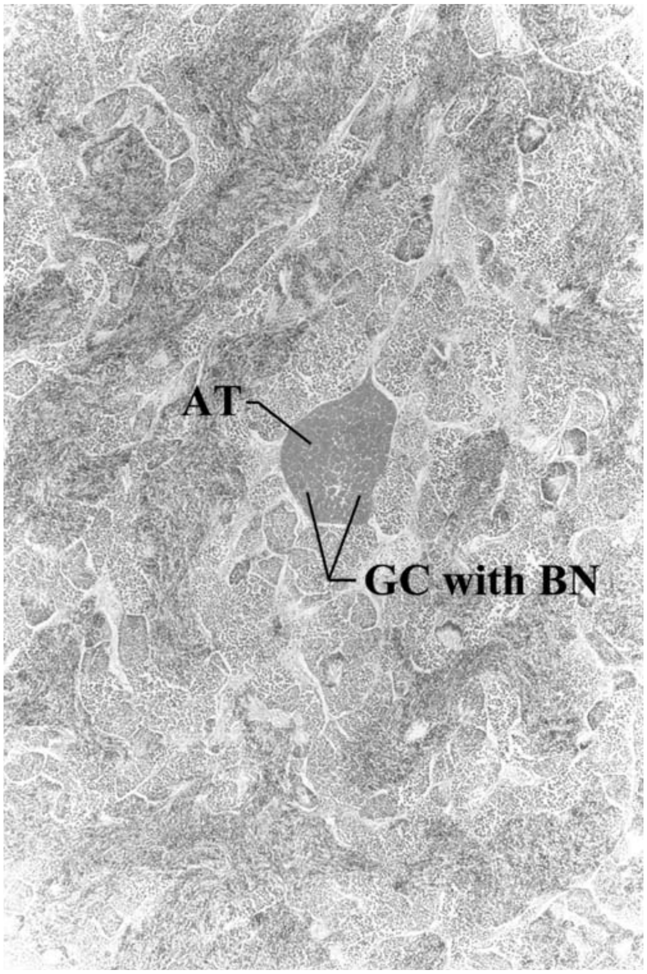

Figure 8. Atretic bodies (AT) in male barred sand bass (*P. nebulifer*) tissue showing the characteristic yellow-brown pigment, granulose cells (GC), and basophilic nuclei (BN) surrounded by advancing follicle degeneration.

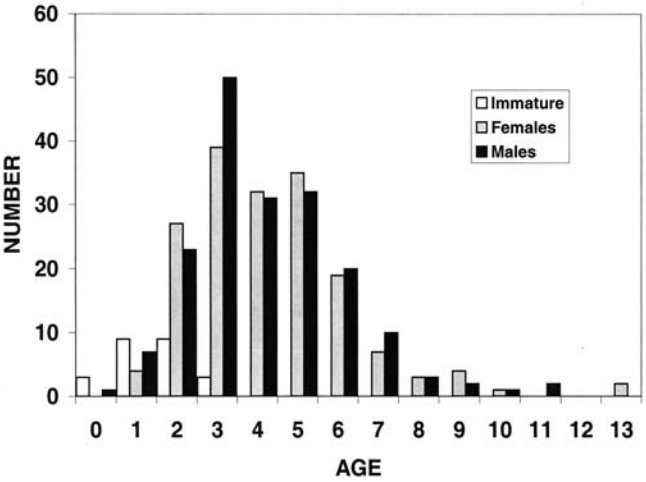

Figure 9. Number of immature, female, and male barred sand bass (*P. nebulifer*) specimens from southern California used in this study by age class ($N = 436$).

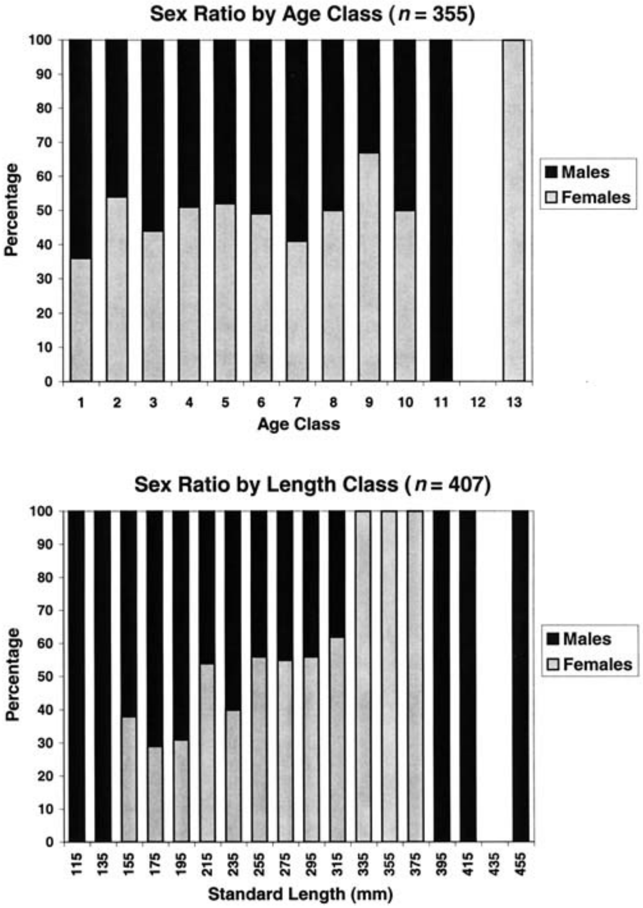

Figure 10. Sex ratios for the total sample of barred sand bass (*P. nebulifer*) showing the percentages of females and males by age class (*above*) and by length class (*below*).

amined, indicating that the cavity was used for the transportation of sperm in some individuals. Thus this criterion was not met.

The third criterion examined was the presence of the sperm sinus in the gonadal wall of the males. This sperm sinus is thought to develop from the splitting of the muscle layers of the ovarian capsule. All males examined were found to have a sperm sinus in the gonadal wall.

All males examined in this study contained gonadal lumens and sperm sinuses in the gonadal wall. There are two hypotheses other than hermaphroditism that can account for the presence of these two features in all males examined. First, these features may be evolutionary remnants from hermaphroditic ancestors. As mentioned earlier, species falling into this category have been termed "secondary gonochores" (Smith and Young 1966). Second, these features may result from all individuals passing through a female-like juvenile stage (Sadovy and Shapiro 1987). The gonads of all immature individuals examined in this study appeared to be passing through a female-like stage, supporting the second hypothesis.

The final criterion examined was the presence of atretic bodies. Atretic bodies were found in 52% of males examined. These structures are thought to be germ cell remnants of the initial sex that are retained after the sex change has occurred. Atretic bodies are not retained indefinitely, and as more time passes following change of sex, fewer germ cell remnants are present. These remnants can be caused by degenerating oocytes (going through atresia) but may also result from the degeneration of other types of cells (Smith and Young 1966). Alternative explanations for the presence of atretic bodies other than oocytic atresia include parasitic encystation (Atz 1964), sperm degeneration (Warner 1975b), and nonspecific tissue degeneration (Smith 1965).

Typical protogynous populations exhibit a bimodal distribution, with females making up a greater portion of the smaller, younger individuals and males making up a greater portion of the larger, older individuals (Sadovy and Shapiro 1987). We found an equal distribution of males and females throughout the age classes. While the sex distribution among length classes was significantly different, this is not the pattern of bimodality typically seen in protogynous populations. Factors that may obscure bimodality in protogynous populations are (1) lack of sexual dimorphism, (2) alternative pathways of male sexual development, (3) bisexual juveniles, (4) variation in size at sex change (Sadovy and Shapiro 1987), and (5) perhaps in this case, sampling bias. Thus, protogyny may not be completely ruled out on the basis of the sex-frequency distributions. However, the distributions found in this study favor a functionally gonochoric pattern of reproduction.

Typically in species that form breeding aggregations, individuals gather together during the breeding season in a central location to release their gametes. Protogyny is advantageous where larger males are able to dominate access to females (Warner 1975). In large breeding groups with an increased number of males present, it becomes difficult for larger males to monopolize access to females. Through mobbing and sneaking techniques, smaller males are able to gain access to females. All individuals may potentially release their gametes, and size does not appear to be an issue. Therefore, this arrangement tends to favor a gonochoric reproductive strategy. Kelp bass and barred sand bass are known to gather in large schools during spawning off California (Limbaugh 1955), and both species appear to be functionally gonochoric. Studies conducted on the spotted sand bass showed protogynous hermaphroditism to be most prevalent in large isolated populations where spawning may occur over large spatial and temporal scales (Hovey and Allen 2000).

In conclusion, the barred sand bass appears to possess many of the gonadal attributes of hermaphroditism, including the presence of transitional individuals and a large percentage of males possessing atretic bodies. However, transitional individuals are present very infrequently in their populations. Additionally, the presence of atretic bodies has been shown to be a weak indicator of sex change because atretic bodies may be formed by methods other than oocytic atresia, and a designation of a reproductive strategy cannot be determined using this characteristic alone. Barred sand bass were found to go through a female-like juvenile stage that may account for the presence of female tissue structures (gonadal lumen and sperm sinus) in all male individuals. The population-sex-by-age structure clearly follows a gonochoric pattern. Based on this population structure, the infrequent, hermaphroditic tissue conditions, and the data presented by Oda et al. (1993), we conclude that barred sand bass in southern California are functional gonochores that exhibit a latent ability to change sex.

The presence of hermaphroditic gonadal attributes, whether pre- or post-maturational, lends support to the "secondary gonochore" designation as proposed by Smith and Young (1966). However, additional information regarding the phylogeny of the genus *Paralabrax* is necessary before the validity of this term can be judged.

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RECREATIONAL FISHING AND MARINE FISH POPULATIONS IN CALIFORNIA

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ABSTRACT

We present and review information regarding recreational angling and exploited marine fish populations in California. A comparison of rockfish assemblages among three differently fished areas (one open to all fishing, another open only to recreational fishing, and a de facto marine protected area) revealed large differences in fish density, size structure, and species composition. The area open to all fishing harbored the highest density of rockfishes (7,212 fish/ha), although the size structure and species composition were dominated by small fishes. The area open only to recreational fishing had the lowest rockfish density (423 fish/ha) and a size structure also dominated by small fishes. The de facto protected area possessed high fish density (5,635 fish/ha), but here the size structure and species composition shifted toward larger fishes compared with the two fished areas. Two species federally listed as overfished, cowcod and bocaccio, had 32-fold and 408-fold higher densities, respectively, in the de facto reserve than observed inside the recreational fishing area, and 8-fold and 18-fold higher densities, respectively, than observed in the area open to all fishing. For 17 nearshore fish species, we compared landings by recreational anglers and commercial harvesters and found that, for 16 species, recreational angling was the primary source of fishing mortality. We illustrate the potential damaging effects of mortality associated with catch-and-release programs on long-lived fish populations. Based on this information, we recommend that legislators and natural resource managers reject the assumption that recreational fishing is a low or no impact activity until specific studies can demonstrate otherwise.

INTRODUCTION

The history of fisheries management on the West Coast of the United States records a steady allocation battle between recreational and commercial fishers (e.g., Clark and Croker 1933). This battle recently intensified with the formation of federal and state policies giving marine protected areas (MPAs) a leading role in managing and rebuilding fisheries. Since the extent of protection provided by MPAs varies greatly and often generates semantic confusion, we use the term MPA in this report to mean areas of "no take," that is, where all extraction activities are prohibited. One response to the increasing popularity of federal and state MPA policies is the proposed Freedom to Fish Act. This act would critically modify the Magnuson-Stevens Fishery Conservation and Management Act by allowing areas to be closed to recreational fishing only when there is clear demonstration that recreational anglers contribute to overfishing and all other management options, such as seasonal closures and bag and size limits, have been exhausted. Implicit in this type of legislation are the assumptions that overfishing is caused primarily by commercial harvesting and that recreational fishing does not interfere with other common goals of spatial closures, including (1) creating sustainable fisheries, (2) protecting essential fish habitat, (3) protecting marine ecosystem structure (biodiversity, trophic structure), (4) establishing scientific control areas necessary to distinguish between changes in marine populations caused by anthropogenic or natural sources, (5) creating marine wilderness areas, and (6) enhancing enjoyment of nonconsumptive activities, including educational activities. A null hypothesis of no impact to marine populations and habitats from recreational fishing places a logistical and legal hardship on resource managers and consequently must undergo careful examination before any agency endorsement.

The dynamics of fish populations and fisheries are complex, and predicting the dynamics of complex systems usually contains a measure of scientific uncertainty. Fisheries management decisions must therefore allocate risk, with allocations often reflecting various social values (Ludwig et al. 1993). By seeking to maximize fishery yields, traditional fisheries management places most of this risk burden onto fish populations (Dayton 1998). Such a tendency has been injudicious because (1) fisheries can be overexploited before managers and scientists have sufficient data to indisputably document declining population trends, and (2) overexploited fisheries rarely recover after collapse (Hutchings 2000). In contrast to the history of commercial fisheries, there is little information on the need for management or its effectiveness in recreational fisheries. Thus, it is unclear whether policy regarding recreational fishing and resource protection warrants a precautionary approach.

In this report, we examine data regarding fishing and marine resources in California to assess whether a default policy assumption that recreational anglers have little or no impact is justified. We also illustrate how small increases in mortality associated with catch-and-release programs can affect long-lived fish populations. Such scrutiny is timely given the passage of two acts by the state legislature that reorganize marine resource management in California. The first is the Marine Life Protection Act (MLPA), which requires the California Department of Fish and Game (CDFG) to simplify and expand the current network of marine spatial closures, and the second is the Marine Life Management Act (MLMA), which gives the California Fish and Game Commission new authority and direction to manage certain important fisheries, some of which are exploited by both recreational and commercial fishers.

THREE CASE STUDIES

Differences in Rockfish Population Structures Among Three Areas: An Area Open to All Fishing, an Area Open Only to Recreational Fishing, and a De Facto Marine Protected Area

Mosqueira et al. (2000) reviewed the effects of MPAs on marine populations and consistently found that mean density and size of exploited fishes within protected areas exceeded that of fished areas. These results manifested under extremely broad conditions and across many biogeographic regions. Therefore, if recreational angling has little impact on marine populations, we would expect an observable "reserve effect" of more and bigger fish in areas that restrict commercial harvest but permit recreational angling when compared to areas that permit all types of fishing. We tested for this reserve effect by comparing fish density, total length size structure, and species composition of rockfishes (*Sebastes* spp.) residing in three differently fished areas (open to all fishing, open only to recreational fishing, and de facto MPA) in the Southern California Bight. We then compared densities of two rockfish species federally listed as overfished, cowcod (*S. levis*) and bocaccio (*S. paucispinis*). Recreational and commercial fishers target many of the 70 species of rockfish that inhabit the northeastern Pacific. Most of these exploited rockfish species are long-lived and residential (Love et al. 2002). Thus, a comparison among differently fished areas provides a good test of recreational angling impacts because species such as rockfishes are sensitive to overfishing (Leaman 1991).

We extracted data from a six-year survey of fishes living on deep natural outcrops and around oil platforms within the Southern California Bight. To quantify fish abundance and associated habitat, we used the *Delta*, a two-person submersible, to perform belt transects of 15-min duration. Each transect was continuously documented with a hi-8 mm video camera and externally mounted lights. From the starboard viewing port, observers verbally annotated each videotape, identifying, counting, and estimating sizes of all fishes within 2 m of the submersible. Two paired lasers were mounted on either side of the external video camera at a fixed distance of 20 cm apart. Lasers projected visible spots onto the seafloor, and these were used to calibrate fish size during the surveys and to calculate transect length in post-dive analyses. Video tapes were used to quantify habitat type in post-dive analyses.

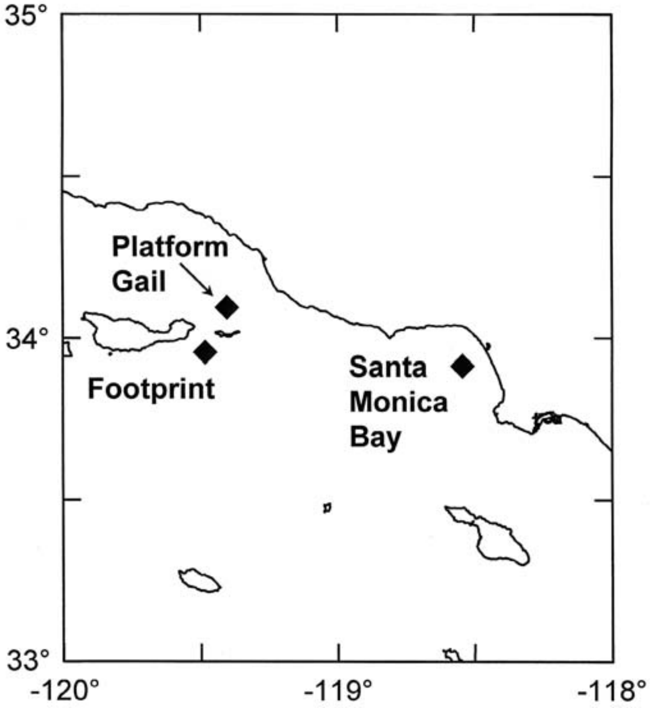

Figure 1. Location of areas where rockfish assemblages were surveyed using the *Delta* submersible. The Footprint is open to all fishing, Santa Monica Bay is open only to recreational fishing, and Platform Gail is a de facto marine protected area.

We compared differently fished areas positioned within similar depths and exposed to similar water masses (fig. 1). The Footprint, an offshore rocky ridge located in the southern Anacapa Passage, is open to all fishing activities and has historically produced large numbers of cowcod and bocaccio to both recreational and commercial fishers. Fish surveys at the Footprint were performed at depths of 100–300 m during 1995, 1998, 1999, and 2000. Since the 1950s, Santa Monica Bay has been closed to commercial fishing activities that use trawls, drag nets, gill nets, and traps, except for a small live-bait fishery that uses lampara nets. Handlines with more than two hooks have also been banned in this region. As our area

TABLE 1
Mean Number of Rockfish per Hectare (+1 SE) at Three Sites in the Southern California Bight

	Commercial and recreational fishing area	Recreational fishing only area	De facto marine protected area
All rockfishes	7,212 (1,300)	423 (69)	5,635 (1,908)
Cowcod	12 (3)	3 (7)	96 (43)
Bocaccio	70 (15)	3 (7)	1,225 (231)

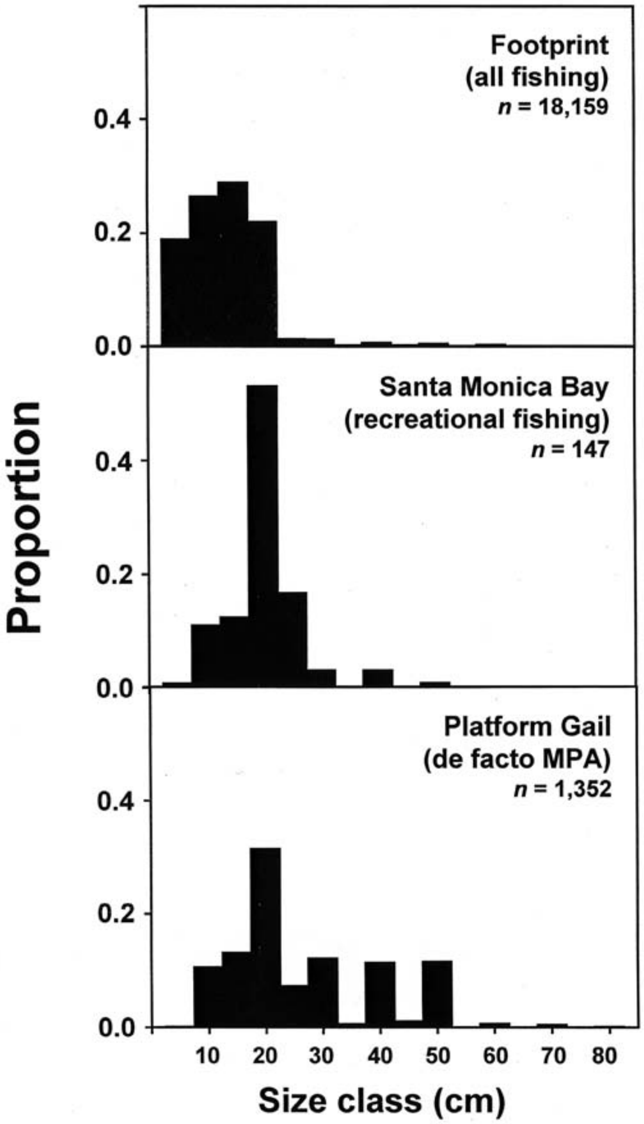

Figure 2. Size structure (total lengths) of all rockfishes observed among three differently fished areas.

open only to recreational fishing, we analyzed transects performed in Santa Monica Bay at depths of 100–300 m from fish surveys conducted in 1997 and 1998. Reef areas surveyed in Santa Monica Bay consisted of high rocky relief and are popular fishing spots with private boat owners and the commercial passenger fishing vessel (CPFV) fleet. At the time of our fish surveys, no deep reef habitat off California had been officially designated as an MPA. However, the offshore oil platforms in the Southern California Bight form de facto reserves. Benthic fishing effort near offshore platforms is very low because platform operators discourage marine vessels from entering a 150 m radius buffer zone around oil platforms. In addition, platform architecture and typically strong offshore currents hamper successful deployment and retrieval of fishing gear to the seafloor adjacent to the structure. As the de facto MPA, we quantified rockfish density only around the base of Platform Gail, which is situated in a depth of 230 m. Other offshore oil platforms in the eastern Santa Barbara Channel are not located at depths suitable for adult cowcod and bocaccio rockfishes. We conducted fish surveys around Platform Gail during 1995, 1996, 1997, 1999, and 2000. Mean rockfish densities from transects surveyed at each area were standardized to number of fish per hectare.

The density of all rockfish species combined was highest at the Footprint, which is open to all types of fishing (tab. 1). Species composition was dominated (67%) by dwarf varieties, such as squarespot (*S. hopkinsi*), swordspine (*S. ensifer*), and pygmy (*S. wilsoni*) rockfishes. The size structure of rockfish total lengths at the Footprint reflects this dominance of small species (fig. 2). In Santa Monica Bay, the density of all rockfish species was an order of magnitude less than rockfish density at the Footprint (tab. 1). Size structure was similar between the two fished areas in that the distribution is sharply truncated at sizes greater than 20 cm (fig. 2). Sixty-three percent of fish observed in Santa Monica Bay belonged to the subgenus *Sebastomus*. At Platform Gail, rockfish densities were also high (tab. 1), but the size structure here was skewed toward a greater proportion of large rockfish (fig. 2). The most commonly observed taxa at Platform Gail were the greenspotted/greenblotched species complex (*S. chlorostictus* and *S. rosenblatti*), which formed 41% of the assemblage.

Striking differences in density were found in cowcod and bocaccio densities among the three areas surveyed. Cowcod densities at Platform Gail, the de facto reserve, were 32 times greater than densities observed at Santa Monica Bay, the area open only to recreational fishing, and nearly 8 times greater than densities at the Footprint, the area open to all fishing (tab. 1). Bocaccio densities observed at Platform Gail were an extraordinary 408-fold greater than Santa Monica Bay estimates, and an 18-fold greater density than Footprint estimates (tab. 1). Composition was also quite different among the three areas: bocaccio constitute 22% of the total number of fish at Platform Gail, compared with 0.7% and 1% at Santa Monica Bay and the Footprint, respectively.

While performing fish surveys at the Footprint, we observed large amounts of gear debris (traps, longlines, trawl nets, and gill nets) from commercial fishing and many dislodged or damaged sponges. Evidence of recreational fishing activity (lead weights, artificial lures, monofilament line, and Budweiser beer cans) was also commonly encountered at the Footprint. In Santa Monica Bay surveys, we observed only recreational fishing debris. Sessile macroinvertebrate populations (sponges, branchiopods, gorgonians, etc.) within Santa Monica Bay appeared abundant and undamaged, perhaps due to the exclusion of trawling gear.

Using the same *Delta* submersible survey methods described earlier, Love (unpub. data) reports that the highest numbers of bocaccio and cowcod occurred on remote sites (near Point Arguello and distant offshore banks) where inclement weather prevents intense fishing effort. Conversely, large tracts of rocky reef in close proximity to harbors and ports contained no or very few large rockfishes. Off central California, Yoklavich et al. (2000) compared deepwater fish assemblages (mainly rockfishes) between a natural refuge and an offshore bank exploited by both recreational and commercial fishers and reported high densities of economically important fish only at the refuge.

Circumstantial evidence cannot demonstrate causation, so we now consider alternative hypotheses to fishing mortality in explaining observed differences in fish populations among surveyed areas. Two alternatives frequently suggested by stakeholders as the primary cause of declining rockfish populations are high pollution levels and changing oceanographic conditions. There is no scientific evidence that pollutants in the Southern California Bight appreciably affect population dynamics of rockfishes. Symptoms that indicate a contaminated environment (fin erosion, ulcers, and tumors) were not observed in any reef fish assemblage (our and others' personal observations). Furthermore, due to increasingly strict discharge regulations, offshore water quality in the Southern California Bight has been steadily improving over the last 20 years at the same time that many fished rockfish populations have been declining. Oceanographic processes that drive fish population dynamics, such as El Niño/Southern Oscillation (ENSO) events or the Pacific Decadal Oscillation, occur over large spatial scales (Cowen 1985; Hollowed et al. 2001). If changing oceanographic conditions were the only cause of observed rockfish decline, we would expect large-scale forcing across all areas and not the pattern where the highest densities and largest fish were found where lowest fishing effort occurs (oil platforms and remote natural reefs).

Could differences in habitat structure among surveyed areas be the primary cause in observed patterns of fish density? Habitat along transects conducted at the Footprint and Santa Monica Bay was characterized by rocky substrate and high density of crevices and shelter holes compared to the somewhat simpler habitat found at the base of Platform Gail. If habitat complexity alone were driving patterns of fish density, we might expect lower fish abundance at Platform Gail rather than the natural reef habitats. Indeed, a comparison of fish assemblages among the shallow portions of nine platforms and nine natural reefs in the Santa Barbara Channel region showed platforms to have on average 42% lower habitat value (as defined by the density, mean size, and persistence of fish species) and 24% lower species diversity than natural reefs (Schroeder et al. 2000).

Although our fish surveys were not originally designed to test for effects of recreational fishing, the existence of a spatial pattern in deepwater rockfish assemblages congruent with a spatial pattern in fishing pressure warrants further experimental investigation into the mechanisms generating such patterns, and this can only be done by establishing MPAs.

Relative Fishing Pressure Between Recreational Anglers and Commercial Harvesters in California's Nearshore Fishery

If recreational angling contributes little to overall fishing mortality, we would expect the relative catch of exploited species by recreational anglers to be much less than that of the commercial sector, especially in instances where stocks may be depleted. To test this hypothesis, we compared landings in California's nearshore fishery from 1980 to 2000 between these two groups using data compiled by CDFG for the Draft Nearshore Fishery Management Plan. The MLMA defines nearshore waters to be from the shoreline out to 20 fathoms (36 m). A suite of 19 species that inhabit these depths for at least part of their life cycle form the nearshore fishery (tab. 2). Due to declining aggregate catches and widespread anecdotal evidence of overexploitation, conflict and allocation battles frequently arise in this fishery among recreational anglers, commercial harvesters, and nonextractive users.

Recreational landing summaries in the nearshore fishery were based on data from the Recreational Fisheries Information Network (RecFIN), maintained by the Pacific States Fishery Management Council as part of the federal Marine Recreational Fisheries Statistics Program. The RecFIN database provides estimates by area and user group (CPFV, private/rental boat, beach, and man-made structures) of total effort (angler-days and angler-hours) and the total number of fish taken. These estimates are calculated using field and telephone interview surveys. Numbers of fish are converted into weights by multiplying catch by average weight. Commercial landing summaries in the nearshore finfish fishery were

TABLE 2
Fish Species in California's Nearshore Fishery

Common name	Scientific name
Monkeyface prickleback	*Cebidichthys violaceus*
Kelp greenling	*Hexagrammos decagrammus*
Rock greenling	*Hexagrammos lagocephalus*
California scorpionfish	*Scorpaena guttata*
Cabezon	*Scorpaenichthys marmoratus*
Kelp rockfish	*Sebastes atrovirens*
Brown rockfish	*Sebastes auriculatus*
Gopher rockfish	*Sebastes carnatus*
Copper rockfish	*Sebastes caurinus*
Black-and-yellow rockfish	*Sebastes chrysomelas*
Calico rockfish	*Sebastes dallii*
Quillback rockfish	*Sebastes maliger*
Black rockfish	*Sebastes melanops*
Blue rockfish	*Sebastes mystinus*
China rockfish	*Sebastes nebulosus*
Grass rockfish	*Sebastes rastrelliger*
Olive rockfish	*Sebastes serranoides*
Treefish	*Sebastes serriceps*
California sheephead	*Semicossyphus pulcher*

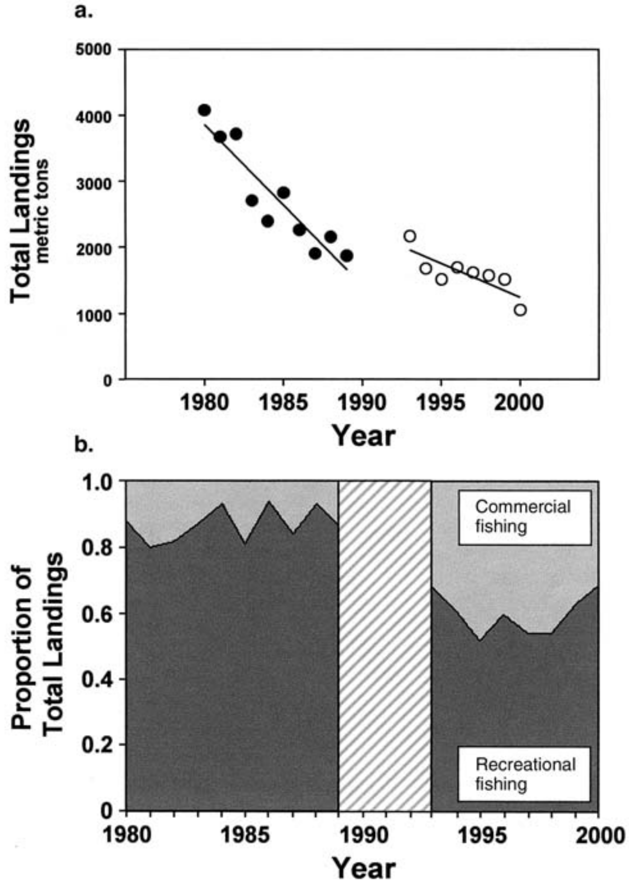

Figure 3. Annual landings in the nearshore fishery off California. No recreational data were collected in 1990–92. (*a*) Total landings, summing both recreational and commercial catches. Straight lines for each data set were calculated using the least squares method. (*b*) Proportion of total landings caught in each year by recreational or commercial fishers.

based on the Pacific Fisheries Information Network (PacFIN) database, also maintained by the Pacific States Fishery Management Council. This database collates information on commercial landing receipts, vessel registration, and permit information, and is supplemented by data sources that supply species composition and catch-by-area proportions developed from port sampling and trawl logbook data systems.

Suspension of the Marine Recreational Fisheries Statistics Program occurred during 1990 to 1992. This three-year data gap coincides with the development of the commercial live/premium finfish market, which began conspicuous participation in the nearshore fishery in the early 1990s. We summarize data within two time periods 1980–89 (hereafter "the 1980s"), and 1993 to 2000 (hereafter "the 1990s"), to reflect this development.

Total landings of 17 nearshore species decreased considerably over the time frame examined. Mean total landings during the 1990s were 42% less than mean total landings during the 1980s. The decline observed in the 1980s, before the establishment of a large live/premium finfish market, was much steeper than the decline observed in the 1990s (fig. 3a), although the 1990s decline may have been somewhat stemmed by stricter total-allowable-catch regulations in 1999. A change in the relative catch between recreational anglers and commercial harvesters occurred with the advent of the live/premium finfish market. During the 1980s, recreational anglers caught about 87% of the total landings, but this decreased to 60% of total landings in the 1990s. However, recreational catch still exceeded commercial catch in all years (fig. 3b).

Greater variability in patterns of exploitation among user groups emerged when species were examined separately. The 1990s recorded an increase in relative commercial landings in all species, with the largest shifts occurring in seven species: California sheephead, cabezon, and grass, quillback, black and yellow, china, and copper rockfishes (fig. 4). At the other end of the spectrum, recreational anglers landed 75% or more of the total catch in seven species: California scorpionfish, kelp greenling, treefish, and calico, blue, olive, and kelp rockfishes (fig. 4).

In light of these data trends, one can easily understand the alarm of recreational anglers about the nearshore environment. A steep decline in landings combined with an increasing proportion of the catch going toward commercial harvesters is such that in the 1990s, the average recreational angler in California caught 65% less in the nearshore than what he or she might have caught in the 1980s. Nevertheless, it remains clear that in the aggregate, recreational fishers impacted nearshore populations more than commercial harvesters.

Recreational anglers dominate other fisheries that show signs of depletion. Karpov et al. (1995) report that

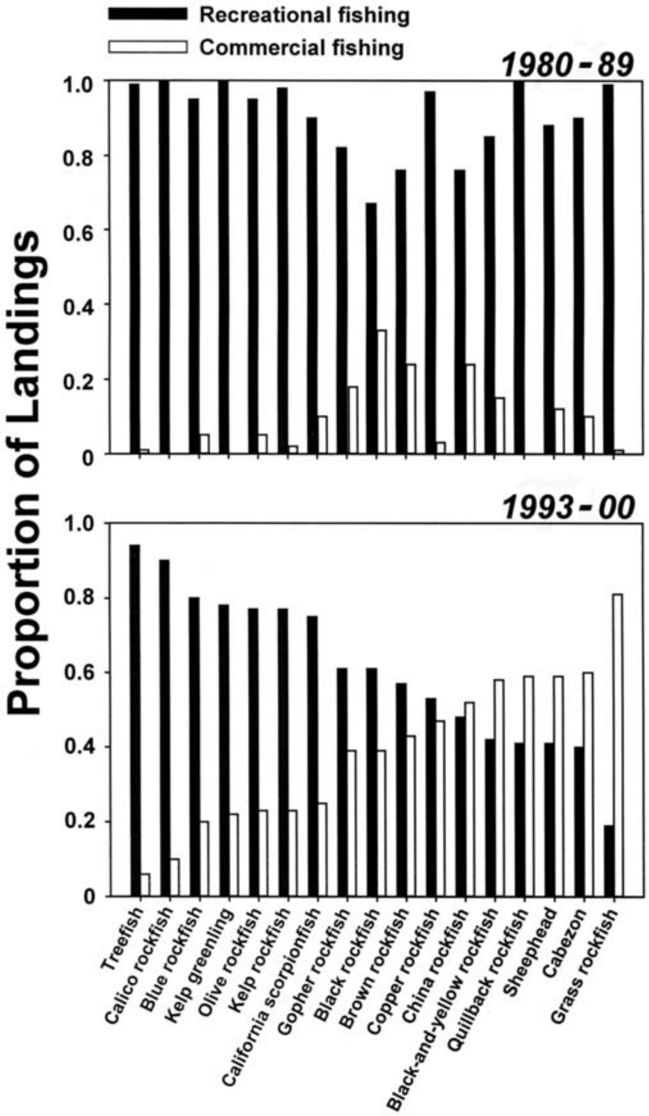

Figure 4. Proportion of fish landings for 17 nearshore species by either recreational or commercial fishers from landings summed during the time periods 1980–89 and 1993–2000. No data were available for monkeyface prickleback or rock greenling.

total surfperch landings from northern and central California during the period 1981–86 were 240 metric tons for recreational fishing and 56 metric tons for commercial harvesters.

Multiple causal factors may be contributing to landing declines in the nearshore fishery, including adverse oceanographic conditions, deteriorating coastal habitats, sustained high fishing mortality, and changing economic or social factors. Regrettably, there are few fishery-independent data that permit us to directly assess how trends in landings correlate with trends in stock abundance. Love et al. (1998a) reported a steep decline in impingement rates of some species of rockfishes at southern California electrical-generating stations in the 1980s and 1990s. This decline mirrored declines in CPFV landings in southern California (Love et al. 1998b). A few other information sources provide demographic clues to the existence of depleted nearshore stocks and implicate overfishing as contributing to this depleted state. The annual CalCOFI survey of early larval fishes has described a steady decline in abundance of some rockfish taxa over the last few decades, suggesting that spawner abundance has also declined (Moser et al. 2000). Abundance of pelagic juveniles for some nearshore rockfish species has also declined (Ralston and Howard 1995). On localized rocky outcrops, depletion in olive rockfish populations has been described by Love (1978), who found a complete lack of mature individuals in areas heavily fished by recreational anglers; lightly fished areas had many mature fish. Finally, Paddack and Estes (2000) compared fish populations inside and outside central California MPAs and suggested that fishing pressure significantly alters size structure and reproductive output of some nearshore fish stocks (*S. atrovirens* and *S. chrysomelas*).

Although the landing data reviewed above suffers from a number of technical uncertainties, we consider it to possess sufficient strength to persuade marine resource managers to consider the activities of recreational anglers nontrivial sources of fishing mortality.

Potential Impact of Catch-and-Release Programs

Catch-and-release (CR) is a popular management strategy in recreational fisheries. Public comment workshops during the MLPA process revealed a common stakeholder perception that catch-and-release fishing is not harmful to fish populations and should be allowed in MPAs. We address this supposition in this section.

Fish that have been hooked, landed, and released by anglers may still die from tissue trauma, bacterial infection, or increased vulnerability to predation resulting from a CR event (Muoneke and Childress 1994). Factors important in determining post-hooking mortality rate include position of hook location, bait type (natural or artificial), hook type (circle, "j," barbless, or treble), handling time, angler experience, water temperature, depth of capture, salinity, swim bladder deflation, and size, age, and species of fish (Gitchlag and Renaud 1994; Muoneke and Childress 1994; Render and Wilson 1994; Wilson and Burns 1996; Diggles and Ernst 1997). Published CR mortality rates range from zero to 100%, suggesting that managers should conduct a case-by-case evaluation of CR impacts for each fishery. If such a study is not available, managers have used a 20% mortality rate per CR event (e.g., Schirripa and Legault 1999), a factor that seems conservatively reasonable given that many published CR mortality rates in marine fishes are equivalent or greater than this value.

We now consider the effects CR mortality may have on protected fish populations by examining a case study of giant sea bass (*Stereolepis gigas*). An area along the north shore of Anacapa Island has recently been designated as a no-take MPA, in part due to numbers of giant sea bass frequently observed there. These fish attract recreational (nonspearfishing) scuba divers and play an increasingly important role in the education and outreach program at the Channel Islands National Marine Sanctuary (K. deWet-Oleson, pers. comm.). The take of giant sea bass has been prohibited in recreational and commercial fishing since 1981, after the species had already plummeted to catastrophically low levels (Crooke 1992). Giant sea bass live to at least 75 years and probably longer (Love 1996). They are the largest reef fish in California, and adults feed on a variety of fishes, decapod crustaceans, and cephalopods. Numerous videos taken by recreational divers suggest that most giant sea bass observed near Anacapa Island are from one successful year class that recruited during the 1983–84 ENSO event.

The effect of a small increase in mortality rate on population dynamics may be difficult to visualize because such rates are compounded through time, causing populations to decline in an exponential manner rather than in a linear one. This means that very small CR rates may have considerable impact on long-lived fish populations. Ironically, a fishing public that does not differentiate between a 6% and 7% annual mortality rate may immediately recognize the considerable difference between a 6% and a 7% annual interest rate on a 30-year mortgage, even though both examples compound rates through time. We therefore choose to use graphical methods to demonstrate the potential consequences of CR mortality to giant sea bass under five different demographic regimes: natural mortality only, and natural mortality plus one of four CR mortality rates (1%, 5%, 10%, or 20%). There are no estimates of natural mortality in giant sea bass, so we used Hoening's (1983) regression formula, which predicts annual mortality rate, m, on the basis of maximum age, $t_{\max}$, by the formula $\ln(m) = a + b \ln(t_{\max})$, where $a = 1.44$ and $b = -0.982$. A maximum age of 75 years translates into an annual mortality rate of 6%. We also lack information on CR mortality rates of this species, although a scientific tagging study on these fish around Anacapa Island recorded one fatality among six tagged individuals in 2000 (S. Fangman, pers. comm.). Given the low numbers of giant sea bass, their aggressive nature, the close proximity of Anacapa Island to several major harbors, and the large number of fishers present in the northern California Channel Islands, it is reasonable to assume that each giant sea bass at Anacapa Island is hooked once per year. This assumption allows the CR mortality rate and the natural mortality rate to be on the same temporal scale.

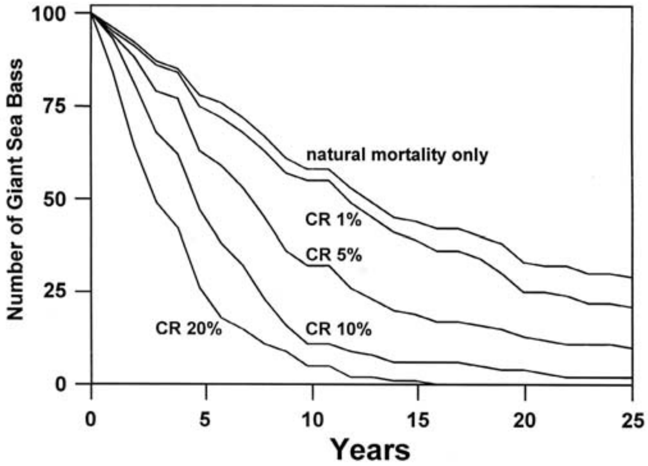

Figure 5. Population trajectories of giant sea bass (*Stereolepis gigas*) under five different mortality regimes: natural mortality only, and natural mortality plus one of four catch-and-release (CR) mortality rates.

We projected population abundance through time by exposing each giant sea bass in the model population to independent mortality risks at each yearly time step. The population projection lasted 25 years, during which time we assume no immigration of individuals (juvenile or adult) from other areas. The baseline population began with 100 fish that endured only the estimated natural mortality rate; that is, at each time step, each fish had a 6% chance of dying from natural causes. The baseline population trajectory was then exposed to varying rates of additional mortality (1–20%) to delineate changes in population dynamics that may be associated with a catch-and-release program for this species.

After 25 years, 29 giant sea bass remained alive in the baseline population; the addition of any CR mortality changes this number considerably (fig. 5). A 20% CR mortality rate causes extinction of the giant sea bass population after 16 years. A 10% CR mortality rate leaves two fish remaining at the end of the time period considered, and a 5% CR mortality rate leaves 10 fish. A CR rate of only 1% reduces the baseline population by 28%, down to 21 fish (fig. 5). It may be that in southern California, juvenile recruitment of giant sea bass is only significant during strong ENSO events. Consequently, without steady juvenile recruitment events, a small amount of CR mortality added to giant sea bass population dynamics may perilously delay population recovery or even cause local extinction.

The sea bass example presented here is one possible scenario; other fish species may tolerate a CR program quite successfully. Important variables likely to affect tolerance to a CR program include mean fish life span, degree of density dependence in demographic rates, and the rate at which individuals within a population experience a CR event.

CONCLUSION

In California waters, the view that recreational angling has no or little impact on marine populations is not supported by the best scientific information available. Our results agree with other reports that find recreational anglers capable of measurably impacting marine resources (Buxton and Clarke 1991; Bennett 1993; Sluka and Sullivan 1998; Young et al. 1999; Jouvenel and Pollard 2001). California has the third largest number of recreational anglers in the United States, with approximately 1.7 million anglers making nearly 6 million fishing trips during 2000 (MFRSS database). With such large numbers of fishers pursuing limited numbers of fish, the results we present here are not unexpected.

Our findings also suggest that recreational angling may be incompatible with some common goals of spatial closures, such as protecting marine ecosystem structure, and establishing scientific control and marine wilderness areas. Large predators may disappear when a reef is fished even lightly, and this in turn may alter ecosystem structure through top-down, trophic cascades (Dayton et al. 1995; Boehlert 1996; Pinnegar et al. 2000). Local depletion of California sheephead and subsequent changes in sea urchin and giant kelp dynamics may be an example of this phenomenon (Pinnegar et al. 2000). Places that permit substantial recreational angling cannot be considered marine wilderness areas, nor would these places provide suitable scientific controls to separate anthropogenic impacts from the natural variability of marine systems.

Many of California's exploited marine species possess life history traits (e.g., long life or irregular juvenile recruitment) that may inhibit timely population recovery once overfishing occurs. We thus conclude this report by strongly advising legislators and natural resource managers to adopt a precautionary approach in managing California's fisheries, where any source of fishing mortality, recreational or commercial, is assumed to be significant until specific studies demonstrate otherwise.

ACKNOWLEDGMENTS

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