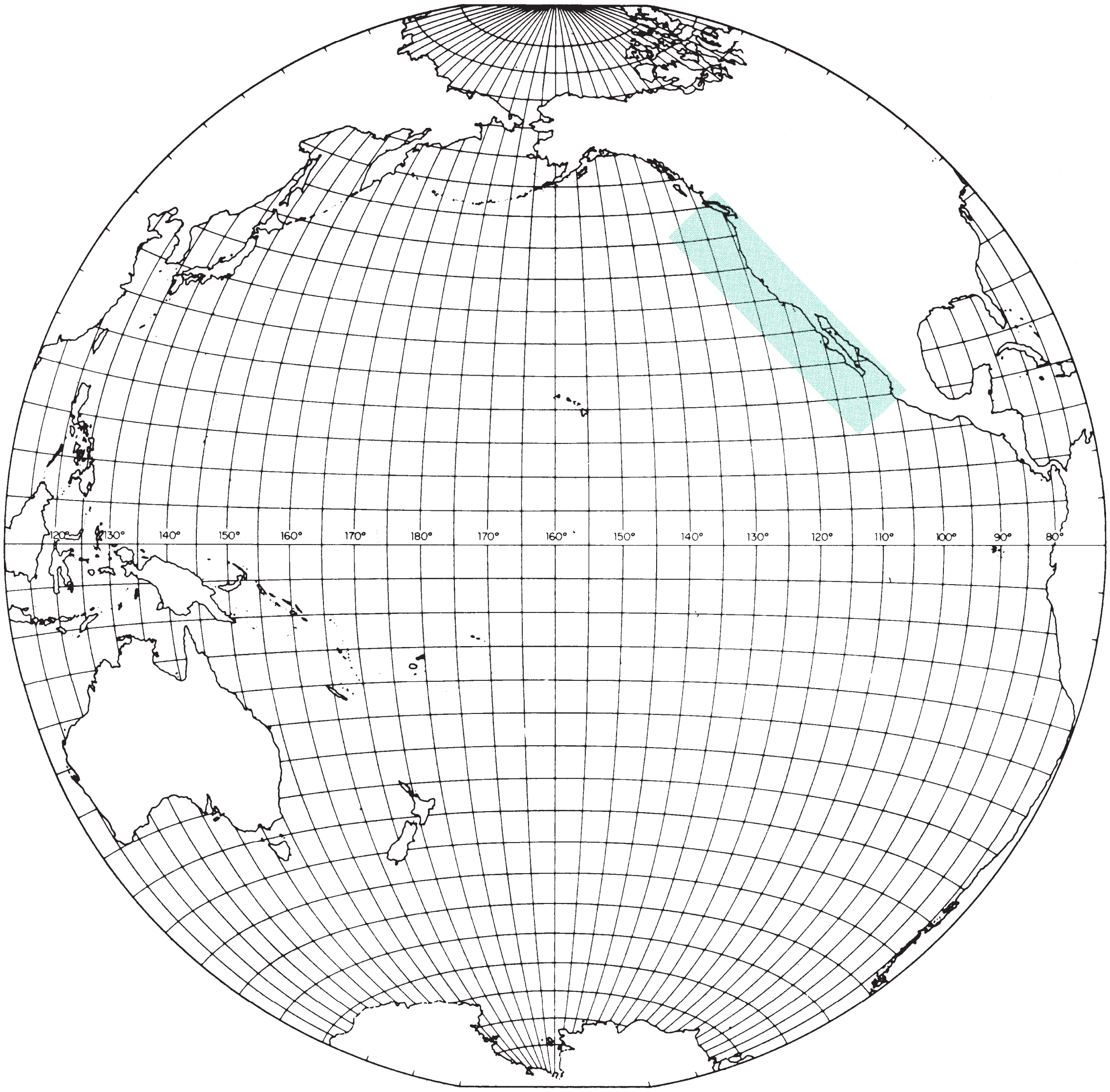

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Reports

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE 2009

NOAA HIGHLIGHTS

CalCOFI Cruises

The beginning of the field season for CalCOFI's 60th year saw the remnants of a weak La Niña condition which became ENSO-neutral by May of 2009. Neutral conditions were short lived as a weak El Niño system developed by July and persisted throughout the remainder of 2009. The 2009 field season saw the successful completion of the standard quarterly surveys and the Pacific sardine (*Sardinops sagax*) biomass survey using a total of four research vessels but also was noted for several milestones.

The field season of 2009 will be remembered for the final research cruise of the NOAA Ship *David Starr Jordan*. Due to budget constraints, the *Jordan* was placed on limited operational status during 2008 which kept her in San Diego but sitting idle at the Nimitz Marine Facility. By early 2009 it was decided that the ship would be moved up to Seattle, Washington, for storage until a decommissioning date was determined. The spring CalCOFI/sardine biomass survey was scheduled to go out on the NOAA ship *Miller Freeman* but due to major mechanical problems during the ship's dry dock period the *Freeman* was unable to fulfill its obligations. In order to complete a spring CalCOFI survey, the *Jordan* was reactivated one last time in March 2009 for her final cruise. The *David Starr Jordan* was built by the Christy Corporation in Sturgeon Bay, Wisconsin, and launched in 1964 for the U.S. Bureau of Commercial Fisheries which later became a part of NOAA as the National Marine Fisheries Service. Since her commissioning in 1966 in San Diego, the *Jordan* has covered over 1.5 million nautical miles. Many of those miles were earned during CalCOFI surveys so it seems fitting that the *Jordan* completed her long and successful life with one last CalCOFI survey. The *Jordan* now sits up in Lake Washington in Washington State, and is scheduled to be decommissioned in early August 2010.

Figure 1. NOAA Ship *David Starr Jordan*

The Ship Operations group at the Southwest Fisheries Science Center said goodbye to Ron Dotson as he headed off into retirement starting in 2010. Ron caps off an illustrious 39-year career with the Federal Government which began back in 1970 with the Bureau of Commercial Fisheries. Ron was hired on to the original albacore group by Ron Lynn while he was still a student at San Diego State University. Ron played a vital part in the early albacore studies as well as the development of the early aerial spotter surveys and has been a mainstay within the CalCOFI program. Prior to Ron's departure he was tasked with one last responsibility: to develop and implement a marine mammal excluder device to be installed in the Nordic 264 mid-water trawls used extensively by the Division for adult sardine assessments. With the help of many people within NMFS and the fishing industry, Ron was able to pull together a successful, working system that was used throughout the 2009 field season without incident (this process published in NOAA Tech. Memo. 455). Ron will surely be missed but we wish him only the best in his well earned retirement.

Over the course of the 2009 calendar year a total of five individual surveys (the four standard CalCOFI surveys and one Daily Egg Production Method survey) were completed using four different vessels: SIO's R/V *New Horizon*, the NOAA Ship *David Starr Jordan*, the NOAA Ship *McArthur II*, and the chartered fishing vessel F/V *Frosti*. Throughout these combined surveys a total of 656 Bongo samples, 318 Pairovet tows, 261 Manta tows, 404 CTD casts, and 1,127 CUFES samples were collected. In addition, 59 surface trawls were conducted netting approximately 377 kilograms of adult and juvenile Pacific sardine for the annual spawning biomass estimate.

CalCOFI Ichthyoplankton Update

The continuing SWFSC Ichthyoplankton Ecology group projects to update larval fish identifications to current standards from 1951 to the present, and to identify eggs of Pacific whiting (hake) and jack and Pacific mackerels collected in the CalCOFI bongo net samples are now complete from 1987 to the present for the eggs and 1967 to the present for the larvae.

Since 1997 we have identified market squid paralarvae in all CalCOFI samples (since 1981 for surface samples), and other cephalopod paralarvae from time to time in some samples. Beginning in 2008 we are now identifying all cephalopod paralarvae in all samples and including them in the ichthyoplankton database. The presence or absence of jumbo squid paralarvae has been of particular interest in recent years; ommastrephid paralarvae are rare in CalCOFI collections and although most are too small to identify below the level of family with any certainty, the few larger specimens appear to be *Ommastrephes* rather than *Dosidicus*.

We are working cooperatively with Ron Burton's group at SIO, who are developing a system for molecular identification of ichthyoplankton in the California Current Ecosystem with the ultimate aim of providing near real-time identifications of the 100 most common taxa. When developed, this method should be especially useful for fish eggs collected with the CUFES, particularly for taxa whose eggs are difficult to distinguish during early developmental stages, such as Pacific hake and Pacific mackerel, or white seabass and California barracuda.

PaCOOS—Pacific Coast Ocean Observing System

In 2009 the focus for PaCOOS was to continue to serve biological data via the internet as well as increase survey coverage in support of the California Current (CC) ecological observing system. Data access and data interoperability underlie ecological forecasts and integrated ecosystem assessments in the California Current. Collaboration and partnerships within NOAA and between NOAA and academic scientists remains the primary means of developing these forecasts and assessments.

Data management activities in 2009 centered on merging and access to the historical CalCOFI biological and physical data housed at the Southwest Fisheries Science Center and the Scripps Institution of Oceanography, respectively. In addition, PaCOOS hosted a zooplankton data management meeting of researchers and data managers along the California Current. A summary will be available on the PaCOOS website. The final activity to highlight is the quarterly reporting of climate and ecosystem science and management activities in the California Current that started as a pilot project in 2008. The quarterlies are now a regular feature of the program and can also be accessed on the PaCOOS website.

The 2010 plans for PaCOOS include continued coordination with the Regional Associations on joint proposal development with an emphasis on data management, ecological forecasting and assessment, and increasing ocean observing data when opportunities arise. Two assessments to highlight are: 1) the second annual ecosystem status report that was included in the Coastal Pelagic Stock Assessment and Fisheries Evaluation (SAFE) document for the Pacific Fisheries Management Council; and 2) a second module for the California Current Integrated Ecosystem Assessment developed by the Farallon Institute and funded by the NOAA IOOS Program.

Other Surveys Conducted in the California Current

Lines 60 and 67. MBARI, NPS, and UCSC scientists continue to occupy Line 67 off Monterey and Line 60 off San Francisco with NOAA and MBARI funding. A consistent suite of samples has now been collected quarterly along Line 67 since 1997, and nearshore since 1989. In recent years this shipboard work has been augmented by mooring, AUV, and glider programs. The focus has been on: 1) seasonal/interannual/decadal temporal variations; and 2) Monterey Bay/upwelling system/California Current spatial variations. The data document California Current and Upwelling System dynamics over several ENSO cycles as well as a decadal to multidecadal shift.

In 2009, the retirement of the NOAA Ship *David Starr Jordan* left the winter and spring occupations of Line 67 in peril. The winter occupation was salvaged by an occupation aboard the MBARI vessel *Western Flyer* (s109). MBARI and UCSC personnel collected nutrient, phytoplankton and zooplankton samples during summer cruise aboard the NOAA Ship *McArthur II* (0907-s209) as part of the annual coast-wide sardine survey. Finally a fall cruise out to 67–155 (500 km from shore) was made aboard the MBARI vessel *Western Flyer* (s309). Data from the three cruises have been processed and quality-controlled, and are available both in the MBARI Biological Oceanography database and online. 2009 was a near-normal year, although with a strong spring upwelling season, and the effects of the 2009–10 El Niño are not obvious (temperature, salt, chlorophyll, primary production). MBARI moorings seem to have detected the first arrival of El Niño as a thermocline anomaly in mid-October. As analysis and publication proceed, the 2009 work will enable data-based exploration of: 1) the 2009–

10 El Niño; 2) the putative decadal shift to cool conditions after 1998; and 3) secular climate change.

Trinidad Head Line. NOAA's National Marine Fisheries Service, Southwest Fisheries Science Center and Humboldt State University continue collaborative ocean observing efforts off northern California. Data are collected at roughly monthly intervals along the Trinidad Head line, which consists of six stations along a transect extending approximately 27 nm due west from Trinidad Head. Standard sampling protocols include CTD casts to a maximum depth of 150 m, collection of zooplankton samples by oblique bongo tows (505 um to formalin and 335 um mesh to EtOH) from a maximum depth of 100 m and vertical 0.5 m ring net tows from a maximum depth of 100 m (200 um mesh to formalin). These observations are being augmented by CTD data and ring net samples collected at the first five stations during research cruises lead by Dr. Jeff Abell (HSU, Oceanography) to quantify ocean acidity and other hydrographic and chemical parameters under a grant funded through the Ocean Protection Council. All cruises in 2009 and into 2010 were conducted aboard Humboldt State University's R/V *Coral Sea*. Sampling of offshore stations occurs after dark, but sampling over the shelf is conducted during daylight hours.

Here we report hydrographic and chemical data for Station TH02 (41°3.50'N, 124°16.00'W). Observations found warmer, fresher water along the coast during late 2009 and early 2010, consistent with the timing of El Niño effects in the California Current. This pattern is also apparent at other stations along the Trinidad Head Line and reflects substantial onshore transport associated with numerous strong storm systems. Warming in summer 2009 contrasted starkly with the cool conditions observed the previous year. Evidence of renewed upwelling is apparent moving into spring 2010, and cruises scheduled in June 2010 were prevented by severe northerly winds that presumably drove intense upwelling going into early summer 2010.

Shark Surveys. The SWFSC's shark research group is responsible for collecting data to support the management of blue (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and common thresher sharks (*Alopias vulpinus*), all of which are common in off the U.S. West Coast and taken in regional fisheries, primarily as juveniles. Common thresher and mako sharks have the greatest commercial value and are also targeted by sport fishers. Although the blue shark has little market importance in the United States, it is a leading bycatch species in a number of U.S. fisheries and is targeted in Mexico. One of the primary methods used by NOAA Fisheries to collect data on the three species is fisheries independent surveys. These surveys provide catch data that allow us to track trends in abundance. Use of fisheries data alone for estimating population status is complicated by changes in regulations, fishing methods, and areas over time. The surveys also provide the opportunity to deploy conventional and electronic tags, obtain biological samples, and conduct studies on age and growth.

In August 2009, the SWFSC conducted its sixteenth juvenile mako and blue shark survey since 1994. Working aboard F/V *Southern Horizon*, the team of scientists and volunteers fished a total of 5,575 hooks during 27 daytime sets inside seven focal areas within the Southern California Bight. Average water temperature during the 2009 survey was the second highest on record, although in only three other years were survey sets conducted during the month of August (1995, 1996, and 1997) when surface temperatures tend to be warmer. From the catch data, the index of relative abundance for juvenile sharks, defined as catch per 100 hook-hours, was calculated for the seven target survey areas. Survey catch totaled 100 shortfin makos, 67 blue sharks, 31 pelagic rays (*Pteroplatytrygon violacea*), and seven opah (*Lampris guttatus*). Nearly all of the sharks caught were injected with OTC for age and growth studies, tagged with conventional tags, and released. In addition, satellite tags were deployed on 14 mako sharks and 10 blue sharks. The nominal survey catch rate for makos was 0.453 per 100 hook-hours and for blue sharks was 0.314 per 100 hook-hours. The nominal CPUE for blue sharks dropped substantially from 2008 and was the second lowest in the survey's history. There is a declining trend in nominal CPUE for both species over the time series of the survey.

In September 2009, the SWFSC conducted its fifth thresher shark nursery area survey in the Southern California Bight. The team worked aboard the F/V *Outer Banks* and fished fifty longline sets in relatively shallow nearshore waters from Point Conception to the Mexico border. Over the 18-day cruise, shark catch included 216 common thresher, 11 soupfin (*Galeorhinus galeus*), seven shortfin mako, three spiny dogfish (*Squalus acanthias*), one leopard (*Triakis semifasciata*), and one Pacific angel (*Squatina californica*) shark. The average nominal catch rate by set was 2.13 per 100 hook-hours for common thresher sharks. This is down from 2008 when the catch rate was 3.32 per 100 hook-hours. The distribution of common threshers is very patchy and areas of high abundance are not consistent across years. In all years, a large percentage of the catch has been neonates, which were found in all areas surveyed. In addition to providing important information on abundance and distributions, the thresher shark pre-recruit survey enhances other ongoing research at the SWFSC, including age and growth, feeding, and habitat utilization studies. Two hundred and six sharks were tagged with conventional tags; 190 sharks were marked with OTC for age validation studies; 212

DNA samples were collected. In addition, colleagues from Scripps Institute of Oceanography tagged 17 neonate common thresher sharks with mini PSATs to study their movement patterns.

West Coast Midwater Trawl Survey. The twenty-eighth annual west coast midwater trawl survey was conducted during the peak of the upwelling season from May 1 through June 12, 2010. This coast-wide survey represents a major geographical expansion of the traditional SWFSC Fisheries Ecology Division's pelagic juvenile rockfish survey, which was conducted in the central California region between Carmel and Bodega Bay from 1983 through 2003. A total of 136 midwater trawls and 235 CTD casts, as well as zooplankton samples, seabird and mammal observations, and continuous underway data collections were conducted during this year's cruise. The survey targets pelagic juvenile rockfish for fisheries oceanography studies and for developing indices of year class strength for stock assessments, however the focus of the survey has expanded to an ecosystem survey focusing on the productivity of the forage assemblage in recent years.

The survey has in recent years spanned the entire U.S. west coast, by pooling effort between the SWFSC survey and a cooperative survey by the NWFSC and the Pacific Whiting Conservation Cooperative (PWCC). The expanded survey has been conducted using two vessels, usually the NOAA Ship *David Starr Jordan* (SWFSC) and the F/V *Excalibur* (NWFSC/PWCC). However, last year the SWFSC portion of the survey was conducted on the NOAA Ship *Miller Freeman*, and this year's survey was conducted on a chartered research vessel, the F/V *Frosti.* Moreover, the NWFSC/PWCC portion of the survey was not conducted in 2010, thus data for 2010 span only the region covered by the SWFSC survey, from San Diego, CA (lat. 32°42'N) to Delgada, CA (39°50'N). Future surveys are anticipated to take place on the new NOAA Ship *Bell M. Shimada*, and the use of this suite of new ships will necessitate future inter-vessel calibrations to maintain the integrity of the time series.

Sampling is focused on young-of-the-year (YOY) groundfish, particularly rockfishes (*Sebastes* spp.), Pacific whiting (*Merluccius productus*), lingcod (*Ophiodon elongatus*), rex sole (*Glyptocephalus zachirus*), and sanddabs (*Citharichthys* spp.). Data are used in stock assessments for several of these species. In addition, a wide variety of other epipelagic micronekton are captured and enumerated, including krill (*Euphausia pacifica* and *Thysanoessa spinifera*), market squid (*Loligo opalescens*), lanternfishes (*Diaphus theta*, *Tarletonbeania crenularis*, *Stenobrachius leucopsarus*, *Lampanyctus* spp.), northern anchovy (*Engraulis mordax*), and Pacific sardine (*Sardinops sagax*). The entire assemblage is analyzed to develop indicators of ecosystem state and productivity, which relates the productivity of higher trophic level species that forage on much or all of this assemblage. As with the 2009 data, results from this year continue to represent a return to cool, high productivity conditions similar to the 1999 to 2003 period for many groups, while others are at moderate levels that approximate long term mean conditions.

Ongoing efforts also include focused research on krill, which are being done in collaboration with the Farallon Institute for Advanced Ecosystem Research (FIAER). These efforts have focused on developing a geographic atlas of krill abundance and hotspots using both net and hydroacoustic data, and currently a decade of krill abundance data representing 28,000 nautical miles of transects have been processed. These data will be used to develop dynamic habitat models for higher trophic level predators in the California Current, including seabirds and salmon. Additional information on these data and efforts are reported in the State of the California Current report in this volume.

SIO HIGHLIGHTS

Four CalCOFI cruises went out over the last 12 months. The standard CalCOFI measurements were made on all 4 cruises; however, the number of depths sampled had to be reduced during the spring 2010 cruise since the ship, NOAA's *Miller Freeman*, could not handle the weight of the 24 bottle CalCOFI CTD rosette. Instead a 12-place rosette had to be used. The limited number of bunks on *Miller Freeman* forced us to leave the Marine Mammal group ashore during the spring 2010 cruise and curtail efforts of the California Current Ecosystem Long-Term Ecosystem Research (CCE-LTER) group as well. However, these two ancillary programs were able to carry out their work on the other three cruises, giving us estimates of the abundance of marine mammals in the region and a much more detailed look at the structure of the pelagic ecosystem. Along with measurements of total inorganic carbon, alkalinity and sea surface pCO2, measurements of sea surface pH were made for the first time on the fall 2009 cruise by Todd Martz. These measurements will be made on future cruises using funds provided by the CCE-LTER program. This spring the CCE-LTER program received very encouraging news from NSF that it is to be continued for the next 6 years. Over this time period measurements of the inorganic carbon system and fluorescence-based measurements of phytoplankton community structure and physiological status will be integrated into the CalCOFI program.

The most interesting oceanographic event during 2009–10 was the El Niño which was followed closely by NOAA and SIO scientists. Preliminary analyses of the CalCOFI data suggest that effects of the El Niño on the Southern California Bight were limited to changing stratification which did not have dramatic impacts on mixed layer hydrographic properties or phytoplankton or zooplankton biomass. Similar to previous years, the timing and strength of the upwelling off Pt. Conception was the most significant control on phytoplankton biomass. It appears that we will be heading for La Niña conditions. It will be interesting to compare the 2007–08 La Niña period, which was not preceded by strong El Niño conditions, with the upcoming conditions.

NOAA conducted a formal review of the CalCOFI program, March 2–4, 2010, led by Dr. Stephen Murawski. The external review committee was chaired by Dr. Anne Hollowed (NOAA, Alaska Fisheries Science Center, Seattle) and consisted of Drs. Enrique Curchitser (Rutgers University), Robert Cowen (Rosenstiel School of Marine and Atmospheric Science, Miami), Anthony Richardson (CSIRO and University of Queensland, Australia), and Michael Sinclair (Bedford Institute of Oceanography, Canada). The review was very positive about the program and its strong scientific legacy, stating that the CalCOFI program has been very responsive to the mission to provide a scientific understanding of human impacts and the influence of variability and climate change on the living marine resources of the California Current. Its overall recommendation was that the core CalCOFI Program should be continued for the foreseeable future. The review also made a number of specific recommendations:

- A review paper or book should be prepared to document the major scientific advances that stemmed from CalCOFI monitoring and research.
- A workshop should be convened to thoroughly assess the strengths and weaknesses of each of the three survey methods: aerial surveys, acoustic surveys and the DEPM. The Panel was skeptical that an acoustic survey could be conducted without trawl validation of targets. It therefore recommended that additional work should be conducted to confirm that cameras and 3-dimensional imaging provide accurate depictions of the length composition of the aggregation.
- If acoustics become part of the assessment tool box, then the assumption that target–strength to length relationships for Atlantic stocks are suitable for Pacific sardine and northern anchovy should be evaluated.
- The stock assessment authors should examine the relationship between sardine size at age and indices of prey availability, and the species composition of the diet relative to available prey.
- The historical data should be used to assess the most parsimonious sampling grid that would minimize ship time, while preserving the data needed to monitor climate impacts on the CCS.
- Some funds should be secured that could be devoted annually to high priority research projects. This could take the form of graduate student stipends, or research fellowships.
- To formally align the mission of CalCOFI with the shifting priorities of the three partner agencies, the Panel recommends that the Mission Statement for the CalCOFI program be modified.
- If the mission statement is broadened to encompass ecosystems, the title (not the acronym) should be revisited.
- A CalCOFI Scientific Steering Committee (SSC) should be formed to provide strategic direction to the program.
- The core CalCOFI surveys should be considered a part of the national backbone of oceanographic sampling.
- The new stock assessment expert/ecosystem modeling at SIO should play an important role in facilitating a link between resource managers the developing science of ecosystem assessment.
- When considering the plausible range of management alternatives for IEAs, CalCOFI scientists can inform analysts who are developing technical interaction models that track how the existing or planned management constraints would limit the range of management actions.
- Analysts responsible for gathering the information for the IEA should carefully consider the content and timeframes necessary for an adequate assessment.
- Dedicated funds should be identified to maintain and modernize the database.
- Dedicated funds should be identified to support research focused on applied science that would be useful in stock assessments or ecosystem assessments.
- Ancillary sampling programs should be encouraged because these programs provide added value to the CalCOFI surveys by addressing issues of spatial aggregation and seasonality.
- SIO should consider offering a course on ecosystem monitoring and assessment.
- Once a model is transitioned from research to use in routine operational activities, funding and staffing for this activity should be external from core CalCOFI program.

The CalCOFI Committee is reviewing the recommendations and considering how best to adopt them.

With funding from the California Conservancy Ocean Protection Council, several related projects are nearing completion. The Scripps and NOAA CalCOFI databases have been merged and are now available on the web. Phyllosoma of the California spiny lobster have been removed from the summer CalCOFI cruises, and the data will be used to develop a management plan for the fishery. Ichthyoplankton data for the coastal region have been combined from several sources, including

CalCOFI, NOAA, Los Angeles County Museum, and Tenera. Multivariate analyses were carried out to examine onshore-offshore and alongshore variability. Consistent with other studies, Pt. Conception was found to be a major biogeographic break point. A distinct nearshore assemblage was also found inshore of approximately 25 m depth. These results will be used in planning monitoring strategies for marine protected areas in the region.

CDFG HIGHLIGHTS

The California Department of Fish and Game's Marine Region was established in 1999. At that time two major pieces of legislation were passed by the Legislature that guide work within the region. The first is the Marine Life Management Act (MLMA), which mandates that fisheries management will focus on sustainability, taking an ecosystem perspective and be science-based. The second is the Marine Life Protection Act (MLPA) which directs the state to redesign its system of Marine Protected Areas (MPAs) to function as a network to protect marine life and habitats.

California's 2006 Budget Act appropriated $8 million to the California Ocean Protection Council (OPC) for the implementation of the MLMA and MLPA. An additional $2 million was appropriated to DFG to fulfill these same goals. The OPC-DFG Joint Work Plan was developed focusing on collecting, analyzing, and applying data essential to the implementation of the MLMA and the MLPA. Work plan projects focus on three activities and will end in 2010: 1) improving methods and collection of fishery-dependent and fishery-independent data; 2) monitoring to inform the management of MPAs; and 3) equipment improvements to ensure capacity to collect and manage data.

This funding helped to develop a joint research program to quantify the presence of larval spiny lobsters in CalCOFI samples. Lobster phyllosoma larvae were quantified from 1948 to the present. Dr. Martin Johnson began this work sorting lobster larvae in the samples for two decades. Drs. Koslow and Rogers-Bennett will work to: 1) identify patterns in larval abundance with oceanographic indexes; 2) identify trends relative to commercial catch of adult lobsters; and 3) work to incorporate these data into stock assessment modeling efforts in DFG.

Severe budget problems have impacted work within the Marine Region in 2009 requiring travel restrictions and limited hiring. Due to the state budget crisis Governor Schwarzeneggar froze state contracts temporarily and issued Executive Order S-13-09 which put DFG employees on unpaid furlough and closed offices statewide for the first, second, and third Friday of each month. Further reductions in salaries and other cuts are anticipated for 2010.

Marine Life Protection Act Project

As the lead agency in the state for the MLPA, the Department is responsible for Marine Protected Area planning, designing, and management. A Memorandum of Understanding established in 2004 created a unique public-private partnership among the following entities: the Department, the California Natural Resources Agency, and the Resources Legacy Fund Foundation. This partnership, known as the MLPA Initiative, continues to implement public policy through a series of regional planning processes. Each planning process includes input from a broad-based Regional Stakeholder Group, scientific advice from the Master Plan Science Advisory Team (SAT), and oversight and policy advice by a Blue Ribbon Task Force (BRTF). The final decision-making body for each planning process is the California Fish and Game Commission (Commission).

Two of five regional MLPA planning processes have been completed thus far. MPAs in the first planning region—the central coast study region spanning state waters from Point Conception (Santa Barbara County) to Pigeon Point (San Mateo County)—became effective in September 2007. MPAs in the second planning region, the north central coast study region (encompassing state waters from Pigeon Point [San Mateo County] to Alder Creek [Mendocino County]), were implemented in May 2010.

The south coast study region, which extends from Point Conception (Santa Barbara County) to the U.S./Mexico border, is the third region to undergo the planning process. Planning for this region commenced in June 2008 and the BRTF forwarded their integrated preferred alternative (IPA) as well as all South Coast Regional Stakeholder Group proposals to the Commission in December 2009. The Commission directed the Department to prepare the regulatory package including CEQA process using the IPA as their preferred alternative. Regulations are expected to be adopted in late 2010.

The fourth planning region, the north coast study region, which spans state waters from Alder Creek (Mendocino County) to the California/Oregon border, began in July 2009 with a series of informational public workshops. As was done in past study regions, the North Coast Regional Stakeholder Group will be developing alternative MPA proposals for the north coast study region. The SAT, Department, and California Department of Parks and Recreation (State Parks) will evaluate these proposals relative to how well they meet scientific guidelines developed by the SAT and follow Department and State Parks feasibility criteria, as well as the proposals' ability to meet the MLPA goals and objectives. An iterative MPA proposal process will continue through August 2010 that will be forwarded to the Commission at the end of 2010.

The San Francisco Bay study region is the last of the study regions to undergo the planning process and is set to commence in late 2010. See http://www.dfg.ca.gov/mlpa for more information.

Ocean Salmon

In April 2009, the Pacific Fishery Management Council (Council) and the California Fish and Game Commission (Commission) closed all commercial and severely limited recreational ocean salmon fishing, to protect Sacramento River Fall Chinook (SRFC). The 2009 10-day recreational fishery (August 29 through September 7, 2009) occurred in the coastal waters north of Horse Mountain to the California/Oregon border. The 10-day season was designed to target relatively abundant Klamath River fall Chinook, while minimizing impacts on recovering SRFC. The 2009 recreational ocean salmon fishery landed 672 Chinook salmon in 5,359 angler-days. In 2009, only 39,530 SRFC adults returned to spawn in the Central Valley, the lowest return on record. A total of 9,216 jacks (age-2 fish) returned. Based on these data the Council and the Commission will allow recreational and limited commercial fisheries in 2010. The fisheries result in a projected spawner escapement of 180,003 SRFC adults, which satisfies both the 2010 NMFS guidance and the Councils guidance to target 180,000 adult spawners.

Fishery-Independent and ROV Assessment Project

In 2009, Project staff, the Pacific States Marine Fisheries Commission (PSMFC), and partners continued Remotely Operated Vehicle (ROV) deep water quantitative surveys within and adjacent to the northern Channel Islands Marine Protected Areas. From 2005–2008, 7 of 11 finfishes that are targeted by fishermen had significantly higher densities in the reserves relative to outside fished areas. Project staff, PSMFC, and the National Park Service conducted the first year of exploratory ROV surveys in the North Central Coast Study Region at Tomales Point, Point Reyes Headlands, and Duxbury Reef. Project staff and PSMFC conducted the third year of ROV surveys in the Central Coast Study Region within and adjacent to MPAs from Monterey Bay to Point Buchon. For more information see http://www.dfg.ca.gov/marine/fir/dss.asp.

Project staff developed regression equations to evaluate vertical parameters as predictors of fish length. Due to a fish's continuous lateral flexion while swimming and angle to the viewer, its length is often difficult to estimate from videos. In many cases, vertical morphometric parameters such as depth at mid-orbit and depth at anal fin origin may be measured more accurately than horizontal parameters. Relationships between each vertical parameter and fork length were strongly correlated ($r > 0.973$) for kelp greenling (*Hexagrammos decagrammus*), lingcod (*Ophiodon elongatus*), blue rockfish (*S. mystinus*), black rockfish (*S. melanops*), and combined rockfish species ($r > 0.947$).

Kelp canopy aerial survey data were collected along the north coast from Pigeon Pt. to Alder Creek near Pt. Arena in the fall of 2009. In this region the surface area of both Nereocystis and Macrocystis kelp canopy was high at 7.7 km^2 with 2009 being the third highest in the eight-year record compared with the low in 2005 of 2.3 km^2, and an average of 5.3 km^2. Data are available on the DFG web site, http://www.dfg.ca.gov/marine/gis/naturalresource.asp, including metadata that describes methods and areas surveyed by year.

Invertebrate Fisheries Management Project

Invertebrate Project biologists completed a number of significant projects and reports in 2009, and continued progress on numerous ongoing activities. Lobster study biologists began catch and effort based modeling in 2009, initiated at a December 2009 spiny lobster stock assessment workshop at UCSB. First season (2008–09) lobster recreational fishery report card results have been processed and will be integrated into the stock assessment along with 2009–10 catch and effort estimates as they become available. Lobsters use eelgrass and rocky habitat in San Diego Bay, where commercial fishing is prohibited, making the bay a potential *de facto* reserve that may buffer San Diego's lobster population from declines. Project staff continued a joint study with San Diego State on lobster movement patterns within San Diego Bay in 2009. The size of the lobster population in the bay, and movement rates of lobsters between bay and coastal habitats are two goals of this research. In addition, a collaborative program using commercial lobster fishermen to collect biological and CPUE data from their catches was initiated.

The abalone project, divided into northern and southern California components, continued stock assessment work in both regions. Southern California staff continued the San Miguel Island Red Abalone Cooperative Tagging Study with quarterly monitoring beginning January 2009: onsite monitoring is conducted over a period of 1–2 days of diving using the R/V *Garibaldi* or R/V *Irish Lord*, in cooperation with California Abalone Association boats. The Pink/Green Abalone Translocation/Aggregation Study begun in 2008 includes monitoring of study sites for one year. Study sites for green abalone are at Catalina Island and pink abalone sites are at San Clemente Island. This study is funded in part by NOAA. The northern California abalone staff biologists completed revisions to the draft northern California abalone triennial status of the fishery report to the Fish and Game Commission. Ongoing field work consisted of assessing three index stations and the abalone recruitment modules.

Project staff participated in the Dungeness Crab Task Force, a committee formed to discuss commercial crab management and make recommendations to the state by January 2010. Dungeness crab megalopae trapping continued in Humboldt Bay in an effort to establish a predictive population abundance index, complementing similar research in Bodega Bay begun in 2007, and coastal Oregon. Gaper clam and razor clam fisheries in Humboldt County were assessed by both creel census and transect surveys using methods developed earlier by Department biologists and researchers from Humboldt State.

California Recreational Fisheries Survey

The California Recreational Fisheries Survey (CRFS) began in January 2004 to provide catch and effort estimates for marine recreational finfish fisheries. This is the updated version of the marine recreational finfish fisheries statistical survey (MRFSS), which started in 1980. The CRFS uses field and telephone sampling to generate monthly estimates of total recreational finfish catch for four modes of fishing (private and rental boats, beaches and banks, man-made structures such as piers, and commercial passenger fishing vessels) for six geographic districts along California's 1,000 plus miles of coast. In 2009, approximately 40 samplers worked statewide to gather the field data. The CRFS samplers interviewed more than 66,000 anglers at more than 400 sites, and examined almost 207,000 fish. The licensed angler telephone survey completed almost 26,000 interviews.

In 2009, CRFS completed two pilot studies to improve the current methods of determining catch and effort for anglers who depart from marinas, mooring, and docks that CRFS field samplers cannot access (i.e., private-access). A Marina Study used field-based counts of the number of returning recreational fishing boats at seven southern California marinas to generate monthly estimates of private-access fishing effort. Those estimates were compared to estimates currently generated from the licensed angler telephone survey and a report has been drafted. In general the Marina Study verified the relative accuracy of the telephone survey's estimates of angler effort, however, the Marina Study's estimates tended to be more precise in months of low fishing effort. A Saltwater Angler Logbook Study used more than 1,000 volunteers representing publicly accessible boat sites and private-access sites to compare catch and discard rates by species between the two populations. The data analysis and report writing are in progress. The comparisons will provide a better understanding of the similarities and differences and can be used to refine the current methods. For more information: http://www.dfg.ca.gov/marine/crfs.asp.

Aquaculture and Bay Management

The Aquaculture and Bay Management Project (ABMP) completed the California Pacific Herring Commercial Fishing Regulations Supplemental Environmental Document (SED) for the 2009–10 season. The SED included the herring spawning biomass estimates, spawning population, and commercial catch assessment. In addition, the SED included the results of sub-aquatic vegetation surveys in key herring spawning areas for San Francisco Bay for the 2008–09 season. Despite improved oceanic conditions reported for 2008, the spawning population exhibited further decline to a new historic low. The spawning biomass estimate for the 2008–09 season is 4,844 tons, less than ten percent of the historic average (1978–79 season to present) of 49,428 tons. The estimate is a 57 percent decrease from the previous season's estimate of 11,183 tons.

Coastal Pelagics: Sardine and Squid

The Pacific sardine, *Sardinops sagax*, fishery existed from the early 1900s, crashed in the 1940s, and saw resurgence in the late 1980s. In 2009, sardine was California's second largest fishery by volume and sixth in ex-vessel value. Statewide landings in 2009 were 82.8 million pounds (37,543 metric tons) with an ex-vessel value of approximately $5.6 million. This was a 35 percent decrease in volume from 2008, in which landings were estimated at 127.4 million pounds (57,803 metric tons) with an ex-vessel value of approximately $7.6 million.

In 2009, the coastwide harvest guideline (HG), as adopted by the Pacific Fishery Management Council (PFMC), was completely taken. This is the second time since its resurgence that the sardine HG had been achieved. In November 2008, the Council adopted a total HG of 66,932 metric tons for the 2009 Pacific sardine fishery, which extends from California to Washington. The behavior of the fishery in 2009 was characteristic of a "derby" style fishery, leading to a temporally shortened directed fishery. The directed Pacific sardine fishery was officially closed by NOAA Fisheries on September 23, 2008.

In November 2009, the Council adopted a HG of 72,039 metric tons for the 2010 Pacific sardine fishery based on a biomass estimate of 702,024 metric tons and the harvest control rule in the Coastal Pelagic Species Fishery Management Plan. This HG also incorporates a set-aside allocated for dedicated Pacific sardine research consisting of a coast-wide aerial survey with accompanying point sets during closed periods.

The California commercial market squid fishery in 2009 was the largest volume fishery and most valuable fishery in the state. Statewide, over 200 million pounds (93,371 metric tons) of market squid were landed in 2009 with an ex-vessel value of $56.4 million. In 2008, the fishery landed 84 million pounds (38,100 metric tons) and was worth $26.4 million. From 1999 to 2008, the market squid fishery averaged $20.7 million in value and 142.7 million pounds (64,730 metric tons) in landings. The average price per pound decreased from $0.31 in 2008 to $0.28 in 2009.

The presence of market squid is strongly correlated with environmental factors, such as water temperature and nutrient availability. Although the majority of landings usually occur in southern California, landings in Monterey have been considerably lower since 2005. The decline in squid landings have been attributed to the cyclical nature of the market squid population and changes in environmental conditions.

Market squid is a federally monitored species and a state managed fishery. In 2005, the California Fish and Game Commission adopted the Market Squid Fishery Management Plan (MSFMP), which implemented a series of fishery control rules. A harvest guideline of 236 million pounds (107,048 metric tons) for each fishing season (April 1 through March 31 of the following year) was enacted along with weekend closures, gear closure areas to protect squid spawning a light boat wattage restriction, and shielding requirements as well as a limited entry program.

The CalCOFI Committee:
Russ Vetter, NMFS
Tony Koslow, SIO
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REVIEW OF SELECTED CALIFORNIA FISHERIES FOR 2009: COASTAL PELAGIC FINFISH, MARKET SQUID, RED ABALONE, DUNGENESS CRAB, PACIFIC HERRING, GROUNDFISH/NEARSHORE LIVE-FISH, HIGHLY MIGRATORY SPECIES, KELP, CALIFORNIA HALIBUT, AND SANDBASSES

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SUMMARY

In 2009, commercial fisheries landed an estimated 160,615 metric tons (t) of fish and invertebrates from California ocean waters (fig. 1). This represents an increase of nearly 14% from the 141,377 t landed in 2008, and a 39% decline from the peak landings of 252,568 t observed in 2000. The preliminary ex-vessel economic value of commercial landings in 2009 was nearly $144 million, an increase of 29% from the $112 million in 2008.

Pacific sardine landings experienced a 35% decrease in volume during 2009. This was largely due to a more restrictive harvest guideline (HG) based on declining stock abundance. Similar to 2008, the fishery exhibited the characteristics of a "derby." Other coastal pelagic finfish that also experienced a drop in landings were Jack mackerel and Northern anchovy. Pacific mackerel and Pacific bonito, on the other hand, registered increases in landing totals.

California market squid emerged as the largest volume and highest value fishery in the state with over 92,000 t landed and an ex-vessel value of approximately $56.5 million, a two-fold increase from the $26.5 million of 2008. Such increases can be attributed to favorable environmental conditions.

California's recreational red abalone fishery, while tightly managed, remains the only abalone fishery still open. Critical data are collected from fishery independent dive surveys, fishery dependent creel surveys, and a report card system. Additional regulations in 2008 mandated tagging of retained abalone as well as a report card for all fishery participants.

Dungeness crab landings decreased 26% in 2009 compared to 2008, but still remained one of the more valuable state fisheries with an ex-vessel value of $14.7 million. Concerns regarding increased effort in the fishery have prompted strong support for a statewide, tiered trap limit program. Currently, discussions among constituents are ongoing. Preliminary data suggest an upturn occurring within the fishery.

In 2009, Pacific herring fisheries experienced one of the lowest landings in the history of the 35 year old fishery. California Department of Fish and Game (Department) surveys in the San Francisco Bay indicated drastic (57%) declines in the spawning biomass. This was the lowest ever estimate for the fishery. Following these alarming declines, the fishery was closed by the California Fish and Game Commission (Commission) for the first time ever.

Commercial nearshore live-finfish landings, consisting of 19 species, totaled 242 t in 2009, a 19% decrease from 2008. A large percentage of the nearshore finfish are sold live at premium prices resulting in a fishery valued at $2.25 million.

Albacore was the most abundant tuna caught in California waters, as well as along the west coast. Commercial landings totaled 12,262 t with an ex-vessel value $0.9 million. Recreational albacore landings in California from Commercial Passenger Fishing Vessels (CPFV) totaled 33,679 fish.

The commercial kelp harvest totaled 4,200 t in 2009, a steep decrease from the high of 38,000 t in 2000. Fewer commercial kelp harvesters rather than unfavorable oceanographic conditions are responsible for this decline. Commercial landings of California halibut in 2009 totaled 278 t with an ex-vessel value of $2.6 million, while recreational landings were 211 t (58,000 fish). In 2009, the Department began compiling data to support the first statewide stock assessment of California halibut.

Sandbasses have not supported a commercial fishery since the 1950s due to steep declines in landings. However, barred sand bass have ranked among the top recreational species caught by southern California CPFV anglers for the past two decades. They also ranked first in terms of number of fish kept. Spotted sand bass, in contrast, rank high among the species not kept with 94% released. Recreational fishing pressure on these species continues to increase over the last two decades.

In 2009, the Commission undertook ten rule-making actions that addressed marine and anadromous species. The Commission adopted changes to salmon, halibut, lobster, herring, white seabass, and sport fishing regulations. For two anadromous species, delta smelt status was upgraded from threatened to endangered under the California Endangered Species Act, and longfin smelt was

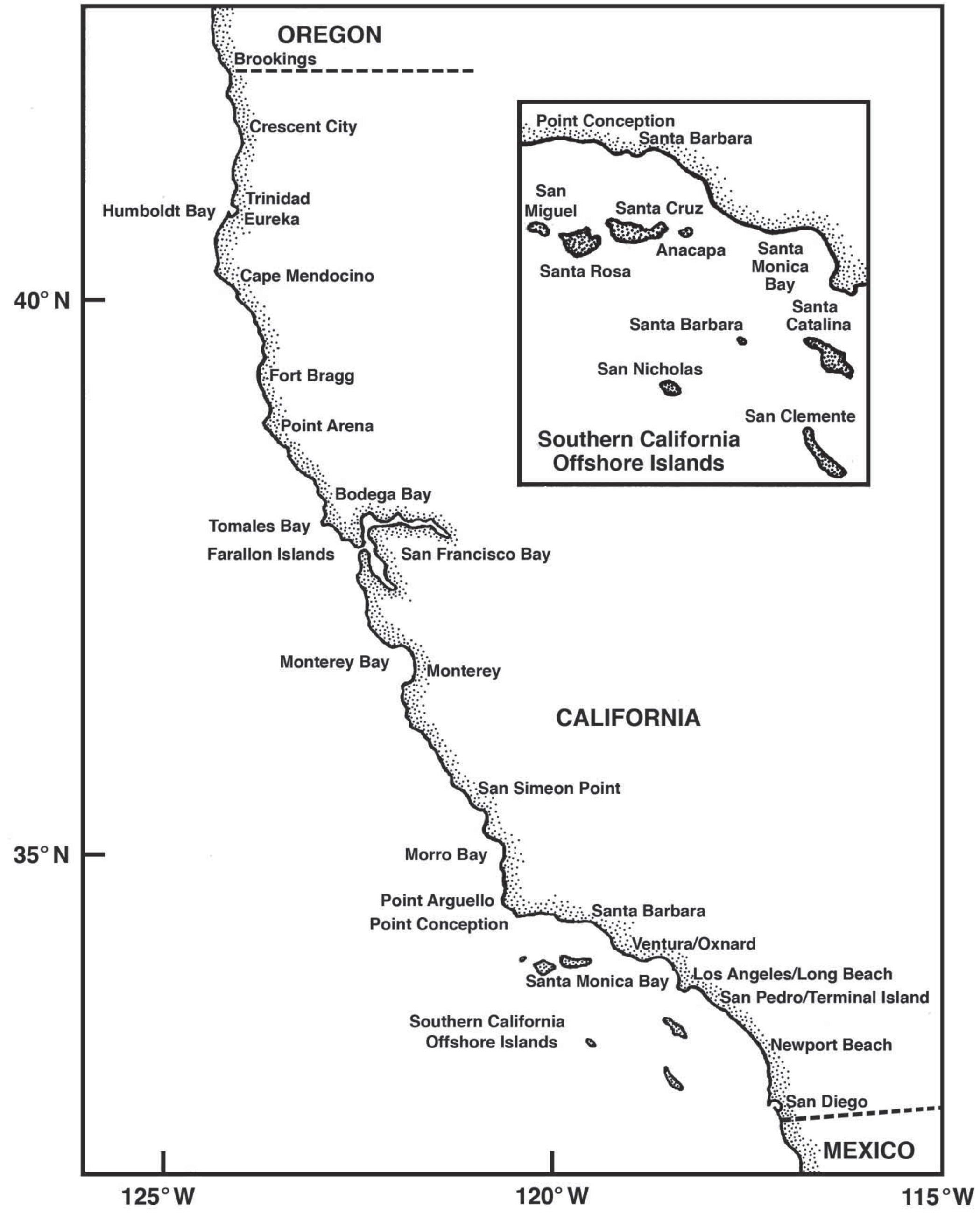

Figure 1. California ports and fishing areas.

listed as threatened. Emergency regulatory action was taken to close the open ocean herring fishery to protect the San Francisco Bay herring stock due to the dramatic decline in biomass. The Commission also implemented a series of 24 marine protected areas (153 square miles) in the north central coast region, defined as state waters between Point Arena (Mendocino County) and Pigeon Point (San Mateo County) under the Marine Life Protection Act (MLPA). The MLPA is a process to consolidate and establish marine protected areas in California state waters.

Coastal Pelagic Finfish

Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), northern anchovy (*Engraulis mordax*), and Pacific herring (*Clupea pallasi*) form a finfish complex known as coastal pelagic species (CPS). These species, with the exception of Pacific herring, are jointly managed by the Pacific Fishery Management Council (Council) and the National Marine Fisheries Service (NMFS). In 2009, total commercial landings for these four CPS equaled 45,444 t (tab. 1), and was worth $6.9 million in ex-vessel

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

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Unspecified mackerel	Pacific herring	Herring roe	Market squid	Total
1977	2	101,132	3,316	47,615		5,286		12,811	170,163
1978	1	11,439	8,241	34,349	48	4,473		17,145	75,696
1979	51	48,880	22,404	21,548	301	4,257		19,982	117,424
1980	21	42,946	25,739	24,181	56	8,061		15,385	116,389
1981	34	52,308	35,257	17,778	132	5,961		23,510	134,980
1982	2	42,150	17,667	19,618	18,398	10,604		16,308	124,747
1983	1	4,427	17,812	9,829	23,659	8,024		1,824	65,576
1984	1	2,889	26,043	9,149	18,038	3,847		564	60,532
1985	6	1,626	18,149	6,876	19,624	7,984		10,275	64,540
1986	388	1,535	22,095	4,777	25,995	7,658		21,278	83,727
1987	439	1,390	26,941	8,020	19,783	8,420		19,984	84,978
1988	1,188	1,478	30,127	5,068	20,736	8,641		37,233	104,471
1989	837	2,449	21,067	10,746	26,661	9,296		40,893	111,950
1990	1,664	3,208	31,077	3,223	9,039	7,436		28,447	84,094
1991	7,587	4,014	31,680	1,693	339	7,347		37,389	90,048
1992	17,950	1,124	18,574	1,209	3	6,319		13,110	58,289
1993	15,346	1,958	11,798	1,673		3,846	0	42,722	77,345
1994	11,644	1,789	10,008	2,704	0	77	2,874	55,508	84,603
1995	40,328	1,886	8,625	1,728		3	4,664	72,433	129,667
1996	32,559	4,421	9,597	2,178	4	249	5,162	80,784	134,954
1997	43,246	5,718	18,398	1,160	1	0	9,147	70,387	148,057
1998	42,956	1,457	20,515	824		0	2,009	2,895	70,656
1999	59,493	5,179	8,688	953	0		2,279	91,950	168,542
2000	53,612	11,754	21,916	1,269	0	26	3,450	118,816	210,843
2001	51,894	19,277	6,925	3,624	1	0	2,768	86,385	170,873
2002	58,354	4,643	3,367	1,006	2	0	3,324	72,920	143,615
2003	34,732	1,676	3,999	156	0	34	1,808	45,061	87,467
2004	44,305	6,793	3,570	1,027	0	60	1,581	41,026	98,362
2005	34,633	11,182	3,244	199		219	136	58,391	108,005
2006	46,577	12,791	5,891	1,167	0	37	694	49,159	116,316
2007	80,981	10,390	5,018	630	1	336	261	49,474	147,091
2008	57,806	14,285	3,530	274	0	131	626	38,101	114,754
2009	37,578	2,668	5,079	119	1	74	460	92,338	138,317

Data Source: Commercial Fisheries Information System (CFIS)

value. Compared to 2008 landings, this represents a 40% and 30% decrease in quantity and ex-vessel value, respectively. Once again Pacific sardine ranked as the largest fishery among these four species, contributing 83% of the combined quantity and 79% of the combined ex-vessel value.

Pacific Sardine. In 2009, the total tonnage of Pacific sardine landed (37,578 t) was 35% lower than in 2008 (57,803 t) due in large part to an HG that was 25% lower than in 2008. California landings of Pacific sardine generated an ex-vessel value of approximately $5.6 million. From 2000–2009, commercial landings of sardine averaged 49,994 t (fig. 2). Nearly all (97%) of California's 2009 sardine catch was landed in Los Angeles (33%, 12,418 t) and Monterey (64%, 24,151 t) port areas (tab. 2). California exports of sardine product in 2009 decreased by 34% over 2008 exports (51,844 t). A total of 33,909 t of sardine product was delivered to 35 countries. Nearly 80% of this product was exported to Thailand (13,923 t), Australia (6,582 t) and Japan (6,417 t). These three countries represent 75% of the total export value of $19 million.

The Pacific sardine fishery ranges from British Columbia, Canada, southward to Baja California, Mexico (BCM). Since the 1970s, the majority of landings have occurred in southern California and northern Baja California. In 1999, fishing pressure and landings increased in the Pacific Northwest. The 2009 combined landings of Pacific sardine for California, Oregon, and Washington totaled 67,050 t, which is a 23% decrease from 2008 (87,189 t). The Pacific sardine HG for each calendar year is determined from the previous year's stock biomass estimate (of ≥1-year-old fish on 1 July). The HG for the 2009 season was 66,932 t based on a biomass estimate of 662,886 t. The Pacific sardine HG was apportioned coast-wide through the year with 35% allocated from 1 January through 30 June, 40% plus any portion not harvested allocated from 1 July through 14 September, and the last 25%, plus any portion not harvested from the first two allocations, released on 15 September.

In 2009, the U.S. west coast fishery harvested all of the HG. The 1st allocation (Jan 1–June 30) lasted 51 days, and the 2nd (July 1–Sept 14) and 3rd (Sept 15–Dec 31) allocations spanned 17 and 9 days, respectively. Increased fishing efforts, such as vessels making multiple landings per day, were observed during all allocation periods. During the 2nd and 3rd allocation periods, fishing

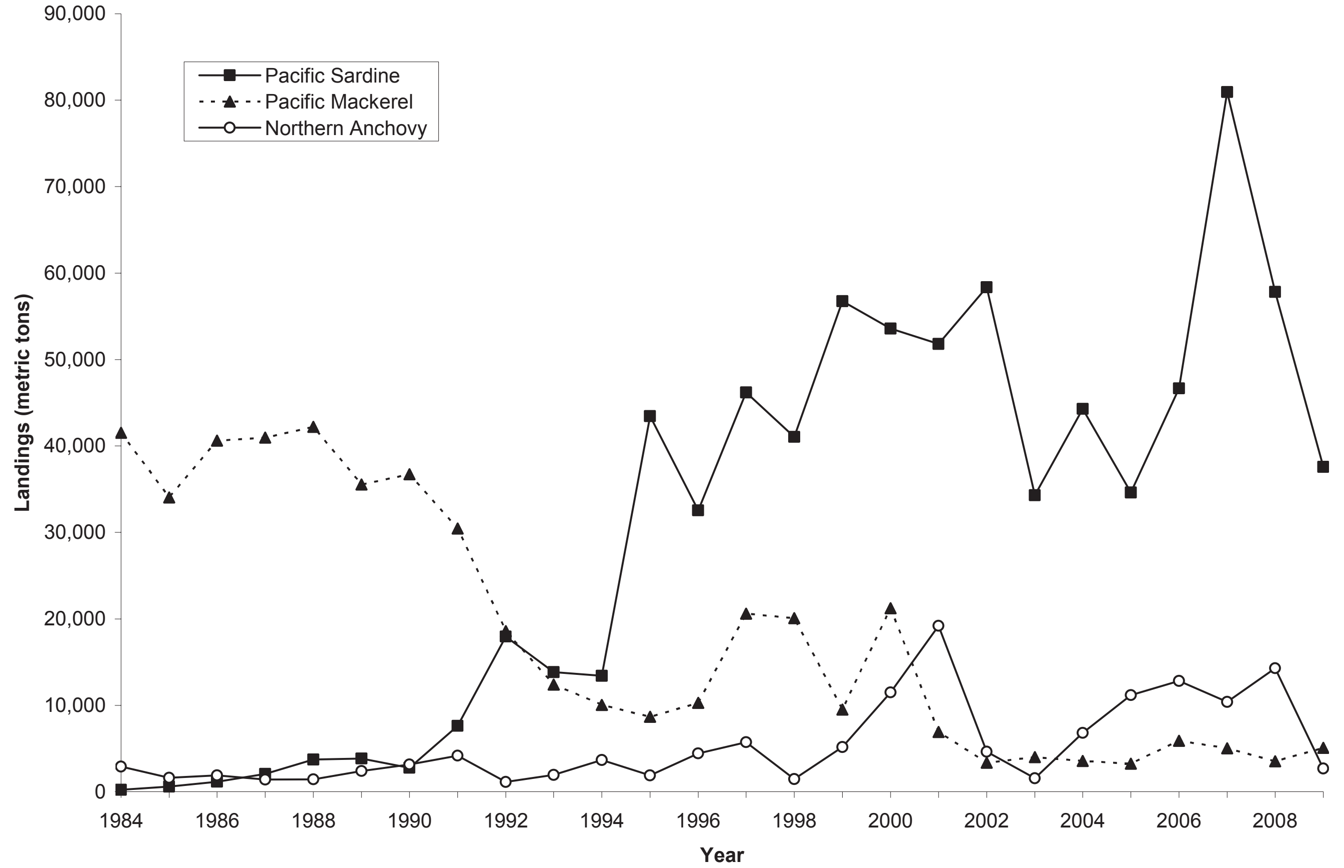

Figure 2. California commercial landings of Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), and northern anchovy (*Engralis mordax*), 1984–2009.

TABLE 2
Landings (metric tons) of Pacific sardine (*Sardinops sagax*) and Pacific mackerel (*Scomber japonicus*) at California port areas in 2009.

	Pacific sardine		Pacific mackerel	
Area	Landings	% Total	Landings	% Total
San Francisco	861	2		0
Monterey	24,151	64	14	0
Santa Barbara	147	0	53	1
Los Angeles	12,418	33	5,012	99
Total	37,577	100	5,079	100

Data Source: CFIS

effort continued during weekends, a period normally not fished by the CPS California fleet. Since the 2008 reduction in the HG, the fishery has become a "derby," resulting in early closures of the directed fishery within each allocation period. The directed Pacific sardine fishery during the 2009 third allocation was officially closed by the NMFS on September 23, 2009; however, incidental take of sardine (up to 20% by weight) was allowed until December 23, 2009.

The steady increase of sardines landed in Oregon since 1999 has slowed in the last three years (fig. 3). Sardine catch in Oregon totaled 21,481 t in 2009, which is slightly less than 2008 (22,949 t). In 2009, Oregon exported 1,901 t of sardine product worth a little over $1.7 million.

Washington landings of Pacific sardine decreased to 8,026 t in 2009 since a peak in 2002 (15,832 t, fig. 3). This is an increase from 2008 (6,435 t). Washington exported more sardine (25,146 t) than was landed; the product was most likely sardine landed in Oregon or the previous year.

In November 2009, the Council adopted an HG of 72,039 t for the 2010 Pacific sardine fishery. The HG was based on a biomass estimate of 702,024 t and was calculated from the harvest control rule in the CPS. This HG is a 7% increase from the 2009 HG. The HG also includes a 5,000 t set-aside allocated for an industry sponsored aerial research project. Data from the 2009 aerial survey were included in the 2009 sardine stock assessment.

The 2009 recreational Pacific sardine catch as sampled from the California Recreational Fisheries Survey (CRFS) was 50 t (739,000 fish), a 72% (24%, by number of fish) increase from 2008. The majority of the fish landed were from man-made structures, such as piers.

Pacific Mackerel. In 2009, 5,079 t of Pacific mackerel were landed in California (tab. 1, fig. 2). The major-

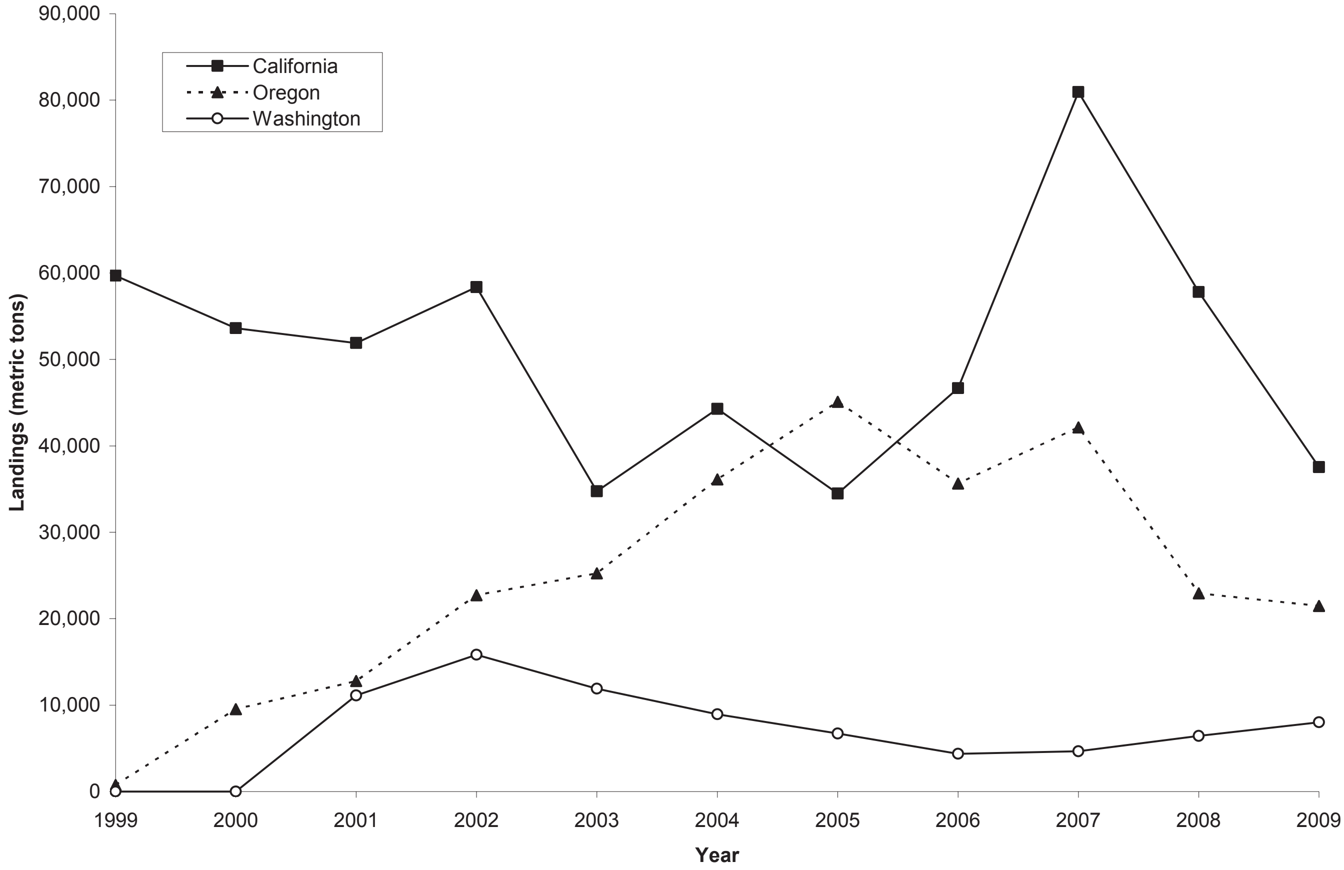

Figure 3. Commercial landings of Pacific sardine (*Sardinops sagax*) in California, Oregon, and Washington, 1999–2009.

ity of landings were made in Southern California port areas (tab. 2). The ex-vessel value in 2009 was $1.1 million. Industry exported 1,093 t of mackerel product, valued at $1 million, to 29 countries. Egypt (432 t), Jamaica (143 t), and Mexico (76 t) received 60% of this product.

Oregon reported 53 t of Pacific mackerel landed in 2009 for a total ex-vessel value of $4,766. This is similar to catch in 2008 (58 t). No landings of mackerel have been reported in Washington since 2005 (unspecified mackerel). Washington landings of Pacific mackerel are typically low, with the greatest landings occurring in 2001 (371 t).

Similar to sardines, the majority of Pacific mackerel landings occur in southern California and Ensenada, BCM. In the U.S., the fishing season for Pacific mackerel is 1 July to 30 June the following year. At the start of the 2009–2010 season, NMFS estimated the biomass at 282,049 t and the Council set the HG at 8,000 t, with a 2,000 t set-aside for incidental landings in other fisheries, much lower than the prior season's HG of 40,000 t. Landings above the HG would be constrained by an incidental catch rate of 45% by weight when landed with other CPS.

The 2009 recreational Pacific mackerel catch as sampled from CRFS was 118 t (659,000 fish), a 59% (65%, by number of fish) decrease from 2008. A total of 43,000 fish were reported landed on CPFVs.

Jack Mackerel. In 2009, jack mackerel landings represented less than 1% of the total catch of federally managed CPS finfish in California with 119 t landed. The ex-vessel revenue for jack mackerel was $17,962 for California. Landings in Oregon continue to be low with 3 t landed in 2009 (no ex-vessel value). Washington reported no landings of jack mackerel during 2009.

The 2009 recreational jack mackerel catch as sampled from CRFS was 4 t (46,000 fish), a 20% (47%, by number of fish) decrease from 2008. A total of 3,000 fish were landed on CPFVs.

Northern Anchovy. Historically, anchovy was primarily reduced to oil or fish meal. When sardine landings have been low in the past, anchovy landings have increased. In the early 1970s, annual harvest exceeded 100,000 t during some years. Presently, landings of northern anchovy are relatively low, averaging about 9,500 t per year over the last 10 years (fig. 2). The majority of landings occur in California on the central sub-population. Landings in Oregon and Washington on the north-

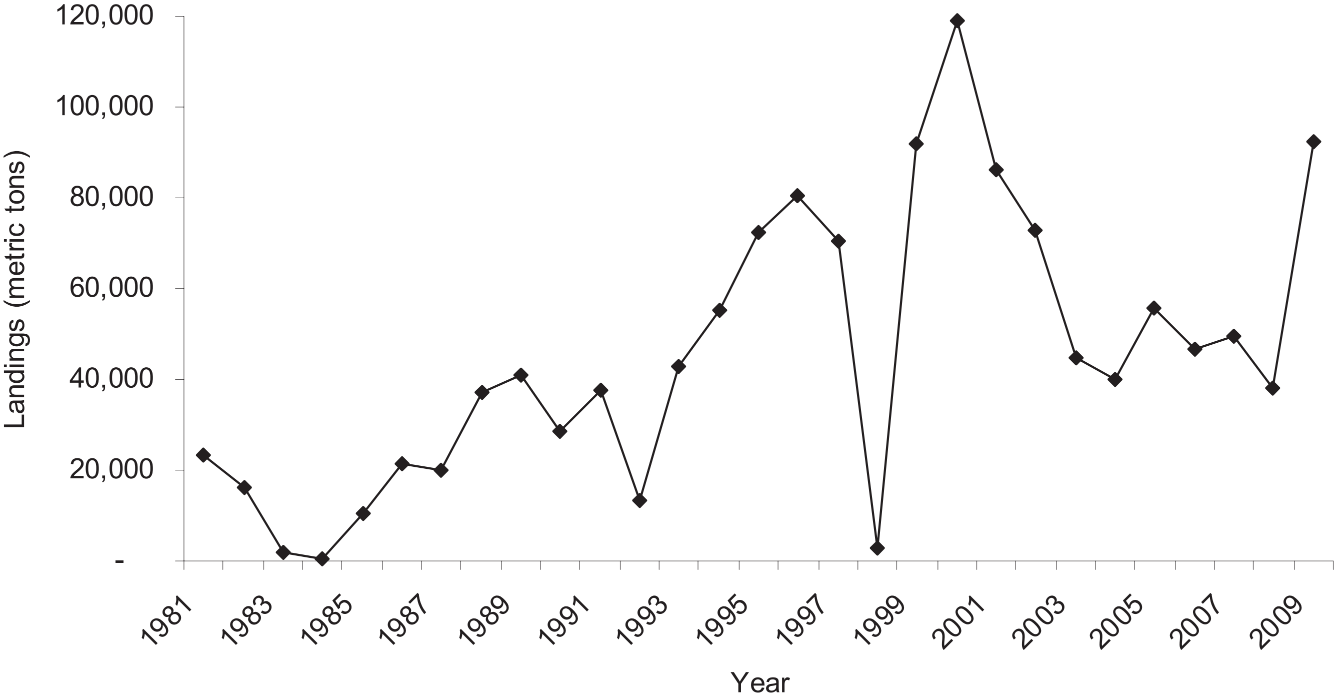

Figure 4. California commercial market squid (*Loligo opalescens*) landings, 1981–2009.

ern sub-population have been increasing in recent years. Anchovy are currently used for human consumption, animal food, and bait. A high-end product of anchovies, marinated in a traditional Spanish style, called "boquerones" has recently been introduced in Oregon and Washington markets.

California landings of northern anchovy in 2009 totaled 2,668 t (tab. 1) with an ex-vessel value of nearly $369,725. This is an 81% decrease from 2008 landings (14,285 t). Exports of northern anchovy product from California totaled 474 t for an export value of $283,346. Three countries received anchovy product from California; Australia received the majority at 77%.

For 2009, Oregon landed 39 t ($8,678 ex-vessel value). Oregon exported 23 t to China with a value of $80,505. Washington reported 810 t valued at $133,400 ex-vessel value for 2009. Approximately 121 t was exported to China, Malaysia, Australia, Canada, and Thailand with a value of $127,007.

Pacific Bonito. Annual Pacific bonito (*Sarda chiliensis lineolata*) landings has averaged 609 t from 2000 to 2009. In 2009, landings totaled 2,132 t, an increase of 165% from 2008. The landings generated an ex-vessel value of $1.7 million. No landings of Pacific bonito were reported from Oregon or Washington in 2009. The California recreational catch for Pacific bonito in 2009 was 146 t (42,000 fish), a 67% (44%, by number of fish) decrease from 2008. A total of 15,000 fish were landed on CPFVs.

California Market Squid

In 2009, California market squid, *Loligo (Doryteuthis) opalescens*, was the state's largest fishery in terms of volume landed and ex-vessel value. Total landings increased 42% from 2008, increasing from 38,100 t to 92,338 t (fig. 4). The 2009 ex-vessel value was approximately $56.5 million, a 113% increase from $26.5 million in 2008. The average ex-vessel value was $640/t, a slight increase from $639/t in 2008. Market squid is used domestically for food and as bait in the recreational fishery, and remains an important international commodity. California fish businesses exported 40,630 t of market squid to 36 countries in 2009 for a value of just over $52 million. This increased from 2008 in which 25,371 t were exported for a value of $35.8 million. China was again the leading importer accounting for 72% (29.13 t) of the trade. Vietnam, Greece, Spain, and the United Kingdom were the only other countries importing more than 1.26 t each.

The market squid fishery is naturally divided into northern and southern regions, which coincide with the optimal environmental conditions for squid spawning. The northern region (north of Point Conception) is centered in and around Monterey Bay during spring and summer months, while the southern region (south of Point Conception) is centered in the Southern California Bight during fall and winter months. Although the fishery has its historical origins in Monterey Bay, it has been dominated by the southern region in recent years (fig. 5).

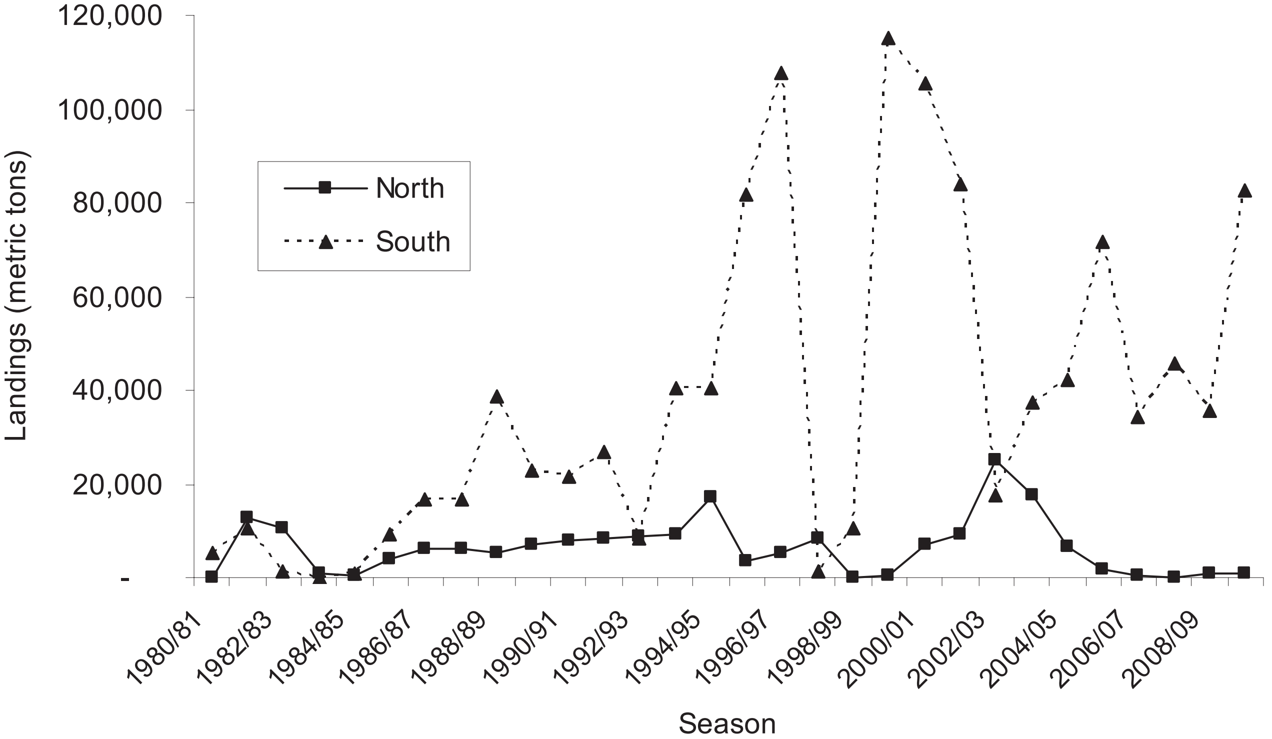

Figure 5. Comparison of market squid landings for northern and southern fisheries by fishing season (1 April–31 March), from 1980–81 to 2009–10 seasons.

The fishery targets adult market squid during spawning events usually in shallow water over sandy substrate. The fishery primarily uses purse and drum seine vessels with attracting lights to catch market squid. These vessels often work with smaller light boats, which use bright lights to aggregate squid near the surface. Depending on weather conditions and regulations, seine vessels and some light boats also brail the squid using dip nets to scoop the squid from the surface. This technique also supports an existing commercial live bait fishery for market squid. Although, the amount of squid harvested and the value of the fishery is largely unknown, the live bait fishery is likely a low-volume, high-value endeavor, as recreational anglers are willing to pay up to $85 for a "scoop" of live squid.

To protect and sustain the resource and fishery, market squid have been managed by the state of California under the Market Squid Fishery Management Plan (MSFMP) since 2005. The MSFMP instituted fishery control rules including an annual catch limit of 107,048 t, monitoring programs designed to evaluate the impact of the fishery on the resource, weekend closures, light restriction and area closures for seabirds, and a restricted access permit program, with transferable and non-transferable permits based on participation in the fishery. Vessels are required to have a permit to possess or land over 1.8 t of squid. In 2009 a total of 167 restricted access permits were issued including 83 vessels, 63 light boat, and 21 brail permits. Of the 83 vessel permits issued, 70 vessels made commercial landings, with 50 vessels making approximately ninety percent of the landings.

Red Abalone

The northern California recreational red abalone (*Haliotis rufescens*) fishery is the only abalone fishery currently open in California. The moratorium placed on commercial and recreational take of all abalone south of San Francisco in 1997 remains in effect. Management of the recreational fishery and recovery of southern abalone stocks are administered under the Abalone Recovery and Management Plan (ARMP), which was adopted by the Commission in 2005. This plan sets management guidelines and triggers for Total Allowable Catch (TAC) adjustments based on 3 criteria: density, recruitment, and catch per unit effort (CPUE). Data for these criteria come from fishery independent dive surveys, fisherman report cards combined with a systematic telephone survey, and fishery dependent creel surveys.

Dive surveys are conducted at eight index sites, with all sites visited on a rotating triennial basis. These surveys are the primary method for providing density and recruitment data for population abundance estimates. The completion of the 2008 and 2009 surveys revealed declines in the abalone abundance index to 0.53 abalone/m^2 (5,300 abalone/hectare) in contrast to densities of 0.68 abalone/m^2 (6,800 abalone/hectare) from sur-

TABLE 3
Northern California abalone population survey densities (abalone/m²) compared to abalone Recovery and Management Plan critical density values of Total Allowable Catch (TAC).

	Deep Transects (>8.4m)		All Depths		Recruitment Density
Site/Year	Number of Transects	Density (abalone/m²)	Number of Transects	Density (abalone/m²)	0–177 mm (abalone/m²)
Todds Point 2006	18	0.16	34	0.43	0.12
Caspar Cove 2008	24	0.19	50	0.43	0.11
Van Damme 2007	14	0.16	28	0.69	0.30
Arena Cove 2007	19	0.45	36	0.64	0.23
Salt Point 2008	21	0.15	41	0.39	0.15
Ocean Cove 2007	19	0.42	36	0.86	0.39
Timber Cove 2009	20	0.27	35	0.43	0.09
Fort Ross 2009	22	0.17	43	0.33	0.10
Average		0.25		0.53	0.19
Critical Values for TAC decrease		**0.25**		**0.50**	

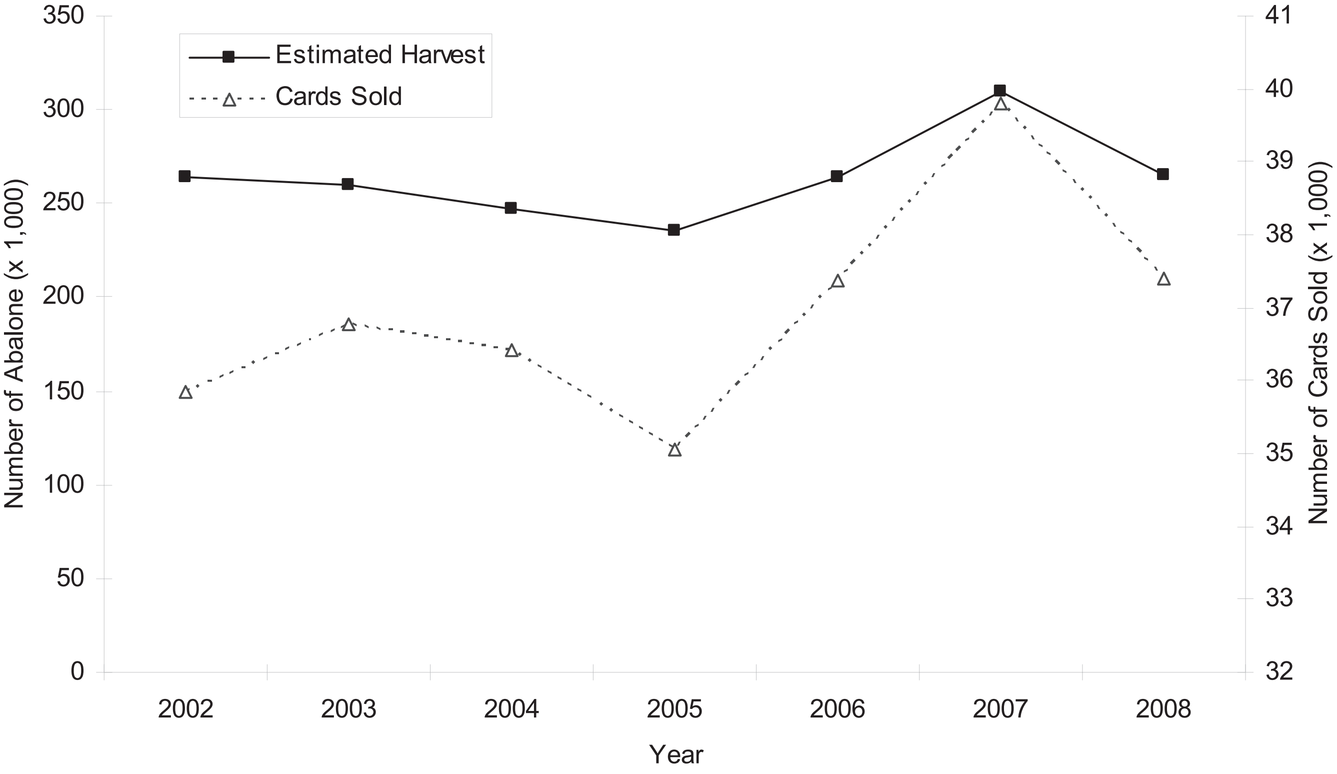

Figure 6. Annual harvest of red abalone (*Haliotis rufescens*) as estimated from combined report card and telephone survey results and number of report cards sold annually.

veys completed between 2005 and 2007 (tab. 3). Using the most recent surveys of all eight index sites, overall densities show declines in abalone at the refuge depth (>8.4 m) and at all depths surveyed, to levels close to the ARMP trigger to reduce the TAC (0.25 and 0.50 abalone/m², respectively) (tab. 3). The 2010 dive surveys will complete a second triennial index site rotation and will provide crucial data to direct management actions regarding the future TAC.

Report card data combined with a systematic telephone survey of report card purchasers provide an estimate of the total harvest per year since 2002 (fig. 6). The telephone survey provides data on report card purchasers who fail to turn their cards in at the end of the season. The most recent catch data available are from the 2008 season in which an estimated 265,066 abalone were harvested, a 14.3% decrease from the 2007 estimated harvest of 309,449 abalone. The number of abalone harvested per picker per year decreased by 7.8% from 8.9 to 8.2 abalone from 2007 to 2008. The number of cards sold in 2008 decreased by 6% from 39,789 sold in 2007, the highest annual sale of cards since 2002, to 37,408 cards

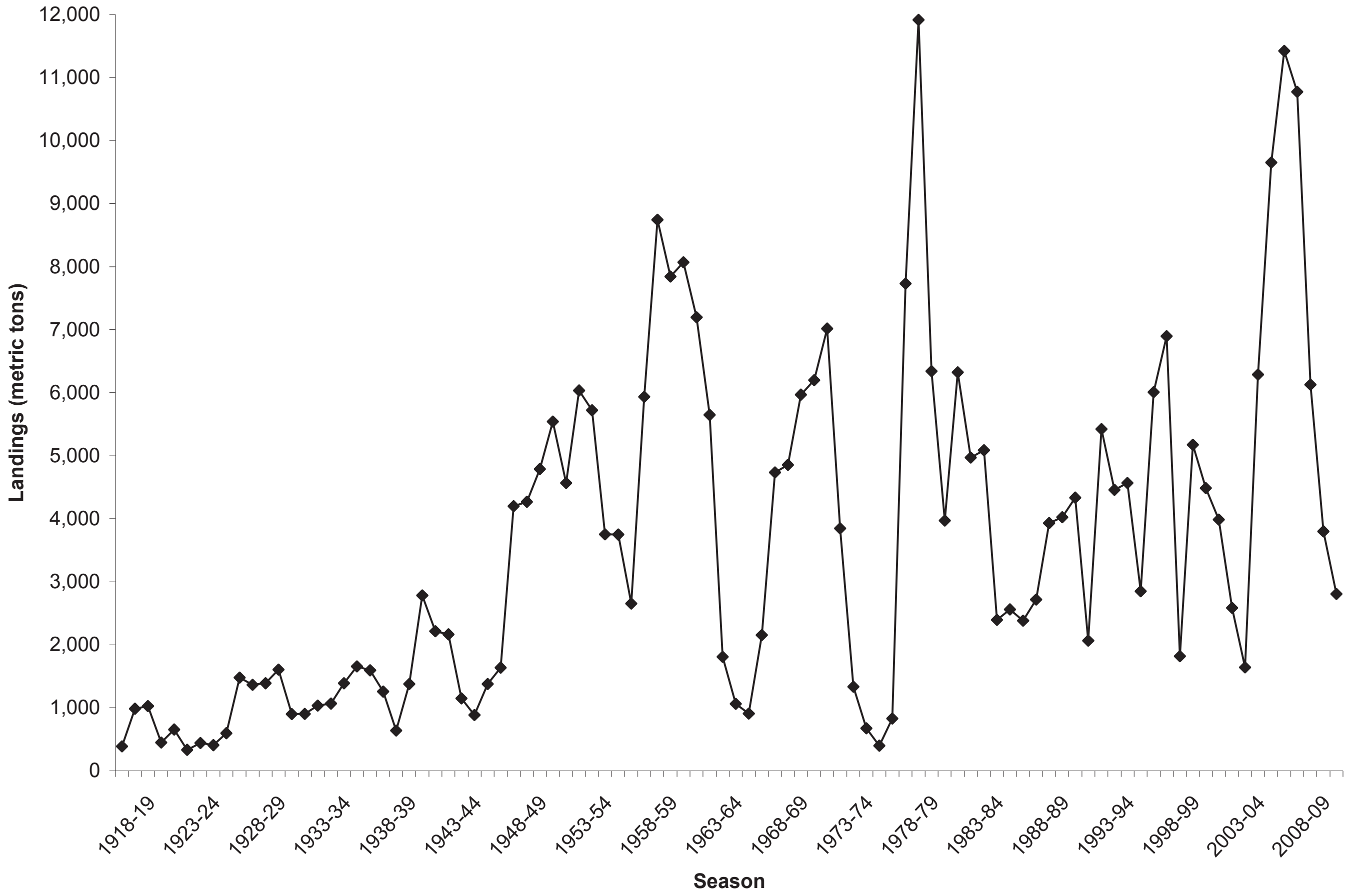

Figure 7. California commercial Dungeness crab (*Cancer magister*) landings, 1915–16 to 2008–09.

sold in 2008. This decrease accounts for only a portion of the harvest decline between those two years.

Creel surveys are completed in alternate years and are used to collect CPUE data in the form of take per picker day or take per picker hour by fishing mode, as well as detailed catch location information and catch size frequencies. The 2009 diver take per day declined by 11% from 2007 while the shore picker take per day decreased by 18%. CPUE in take per hour also decreased between 2007 and 2009. Overall take per hour declined by 24%, with a 16% and 32% drop by divers and shore pickers, respectively. Variations in year to year CPUE can be influenced by ocean conditions during the survey periods. For management decisions, CPUE is compared statistically using blocks of several years and in conjunction with CPUE from the report cards.

New regulations requiring the tagging of each abalone retained were implemented in 2008 to help reduce illegal take and ensure compliance with the daily bag and annual limits of 3 and 24 abalone, respectively. Also new as of 2008, cards are required for everyone taking abalone, regardless of age, in order to provide more accurate take estimates.

Dungeness Crab

The Dungeness crab (*Cancer magister*) fishery is highly cyclical and ranges from Alaska to Monterey, California. California commercial landings of Dungeness crab for the 2008–09 season totaled 2,807 t (fig. 7), well below both the 10-season and 50-season moving averages of 5,908 t and 4,523 t, respectively. This was the fourth consecutive season in decline, a 26% decrease from the 2007–08 catch. The average price paid to fishermen was $5.24/kg ($2.38/lb) resulting in a total ex-vessel value of $14.7 million, a 36% decrease from the previous season. The decline in landings and value can be attributed to a disproportionate drop in central California's catch from 1,622 t caught in the 2007–08 season to 498 t in 2008–09. Typically, the central California catch is lower in volume than in northern California, but the statewide fishery value can be disproportionately affected by varying geographical ex-vessel prices. Initial data from the 2009–10 season indicates an upturn in the fishery. Preliminary numbers show the season in progress has already surpassed the 10-season average by at least 2,500 t.

The commercial Dungeness crab fishery is managed through the state legislature and is California's largest commercial crab fishery. The commercial fishery regulations are comprised of size, sex, and seasonal restrictions, along with restricted access to the fishery. Only male crabs larger than 159 mm (6.25 in) carapace width can be harvested commercially. The minimum size limit is designed to protect sexually mature male crabs from harvest for at least one season. Studies have shown that, despite the presumption that nearly all legal sized male crabs are harvested each season, most sexually mature female crabs are fertilized each year. The timing of the central (south of the Mendocino/Sonoma County line) and northern (north of the Mendocino/Sonoma County line) California seasons protects the portion of the lifecycle when most crabs are molting or soft-shelled, and thus vulnerable to predation and handling mortality.

Of the 585 vessels with a 2010 commercial Dungeness Crab Vessel Permit, 395 boats made at least one landing in the 2008–09 season. The Dungeness crab fishery has evolved into a derby fishery where much of the total catch is caught in a relatively short period of time at the beginning of the season. For example, in the 2006–07 season, 79% of the total catch was landed within two months of the northern season opener. There is no limit to the number of traps a vessel may fish or the frequency with which they are fished, and no reliable estimates of either effort level. As the groundfish industry has declined, larger multi-purpose vessels have devoted more effort to Dungeness crab. According to a 2003 CalCOFI report based on a fisherman survey, there were at least 172,000 traps being fished in California during the 2001–2002 season. In Oregon's comparable Dungeness crab fishery, the estimated number of traps soared from 150,000 in 2002 to 200,000 in 2005 before implementation of a trap limit. Reports of overcrowded fishing grounds, in central California in particular, have increased in recent years

Concerns over of the number of crab traps deployed in both central and northern California has led to management recommendations from fishery constituents. Recommendations included support for controlling total allowable commercial effort, defining latent permits, putting special restrictions on latent permits, defining vessel size expansion, preventing permit transfers to fish processors, continuing current management schemes (size, sex, season), and, most notably, a strong recommendation for an industry funded, statewide, tiered trap limit program.

The recreational Dungeness crab fishery is managed through size, season, and bag limit regulations by the Commission. The minimum size for sport fishing is 146 mm (5.75 in) and, unlike the commercial fishery, the take is not legally limited to male crabs. California is the only state on the west coast to allow sport take of female crabs. The daily bag limit and possession limit is ten crabs. Sport fishers on CPFVs, whose activities in catching crab have increased in the last decade, are generally subject to the same regulations, except that when fishing from Sonoma County south, the bag limit is reduced to six. In November 2009, CRFS began sampling Dungeness crab sport fishing from shore and private, rental and CPFV vessels. Expanding sampling to include Dungeness crab as part of the regular CRFS program was motivated by a November 2008 regulation change that opened the sport fishery statewide on the first Saturday of November. Previously, counties north of Sonoma County opened on the fourth Saturday of November, which provided little opportunity for sport fishermen to set their traps before commercial gear dominated the crab grounds.

Pacific Herring

California's Pacific herring (*Clupea pallasi*) fisheries in 2009 had the second lowest landings in the 35 year history of the modern fishery. During the 2008–09 sac roe season (December 2008 through March 2009) the San Francisco Bay fleet landed 459.9 t, 74% of their 2007–08 landings (623.2 t) (fig. 8), and only 49.8% of the 924.4 t quota. There was no fishing effort in Tomales Bay, Humboldt Bay, or Crescent City Harbor during the 2008–09 season.

The forecast base price for roe herring is a good indicator of the economic status of the fishery, and a factor in whether fishermen will participate in the fishery. Ex-vessel prices for roe herring are set using a base price with an additional roe percentage point bonus. The base price is set per short ton of roe herring with a minimum roe percentage of 10%. Roe herring that are landed, which exceed the minimum roe recovery level, are given a bonus for each percentage point exceeding 10%. Ex-vessel prices in the herring sac roe fishery can vary greatly based on roe recovery rates. The 2008–09 base price for roe herring with 10% or greater roe recovery was $771/t ($700/short ton) landed, with an additional $70 paid for each percentage point above the 10% baseline. The average roe count for the 2008–09 season was 13.5% resulting in an ex-vessel value of $1,043/t ($946/short ton). Due to a decrease in landings, the statewide ex-vessel value of the herring sac roe fishery fell from $587,852 in 2008 to $479,446 in 2009.

The San Francisco Bay herring eggs-on-kelp fishery landed 3.0 t which was only 19% of their 16.0 t quota; whereas, in the previous season 13.7 t of the 15.4 t quota was landed. Price paid for eggs-on-kelp ranges from $13.23–39.68/kg ($6–18/lb) depending on the quality of the product. The total estimated value of the 2008–09 eggs-on-kelp harvest was approximately $41,588 based on an average ex-vessel price of $13.78/kg ($6.25/lb).

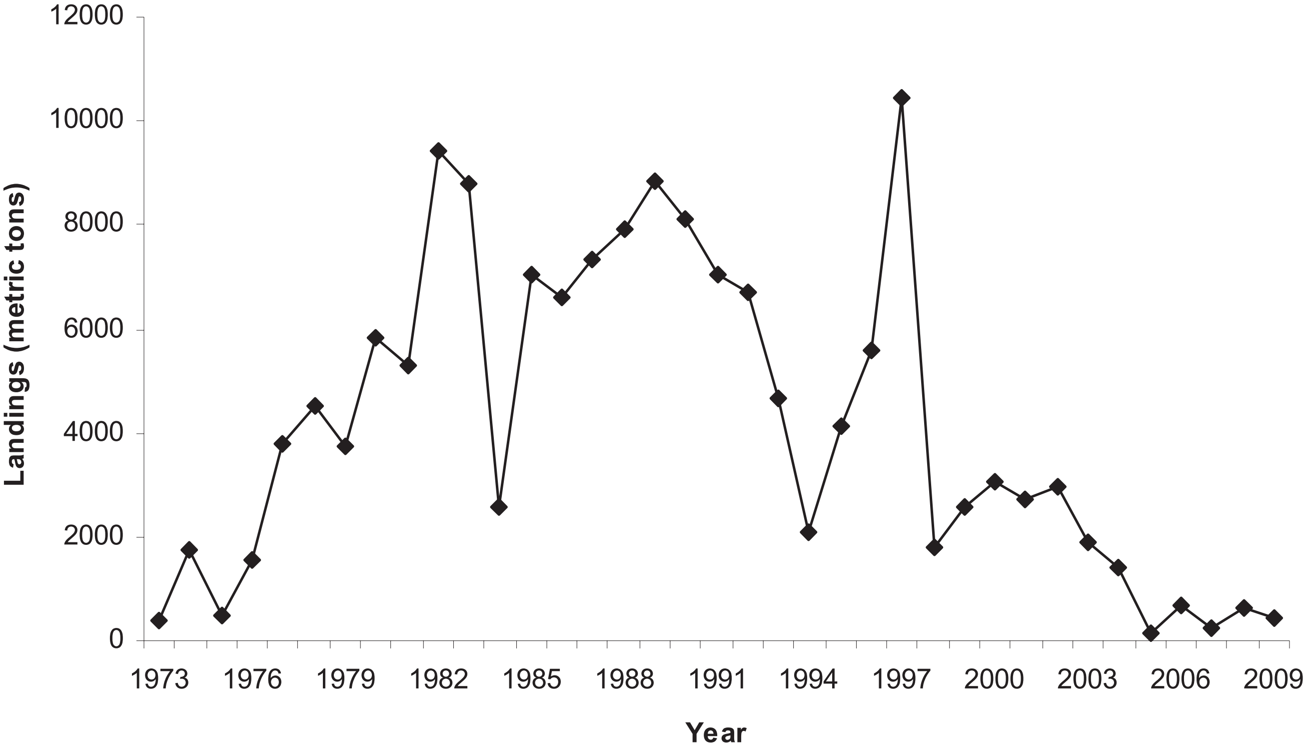

Figure 8. San Francisco Bay commercial Pacific herring (*Clupea pallasi*) sac roe, 1972–2009.

During the 2008–09 season the Department conducted spawn deposition surveys in San Francisco Bay to estimate the spawning biomass of the herring stock. The spawning biomass estimate for San Francisco Bay is 4,394 t, a 57% decrease from last season's estimate of 10,145 t. This estimate is the lowest recorded estimate in the history of the roe herring fishery (1973–74 season to present). No spawning biomass estimates were made for Tomales Bay, Humboldt Bay, or Crescent City in 2008–09.

The Department and the Director's Herring Advisory Committee (composed of fishing industry representatives) recommended a zero harvest or no fishery option for the 2009–10 season, due primarily to concerns over the low biomass estimate. The Commission adopted this recommendation and closed the San Francisco Bay herring sac-roe and herring-eggs-on-kelp fisheries for the 2009–10 season and the ocean waters fishery for 2010 and beyond. This was the first time a herring roe fishery closure was approved by the Commission since the fishery began in 1972–73. This precaution was enacted so that the San Francisco stock can be rebuilt to a level that provides long term sustainability of the fishery. In addition, potential impacts from the Cosco Busan oil spill remain unresolved, as the results from the Natural Resources Damage Assessment study on oil impacts to herring resources have yet to be released.

Prior to closing the San Francisco Bay herring roe fishery, the Commission took emergency regulatory action to close the remainder of the 2009 ocean waters fishery beginning in July. This herring fishery occurs during the non-spawning season primarily in the waters of Monterey Bay and was the only herring fishery with no quota limit. From 1998 to 2002, intermittent herring landings have been made from ocean waters, accounting for approximately 0.2 percent of California's overall herring catch. However, between 2005 and 2008, approximately 35 percent of the overall California commercial herring catch was landed by this fishery. Due to the increase in overall California catch by the ocean waters fishery, the emergency action was sought by the Department to protect the remaining herring stock.

Groundfish/Nearshore Live-fish

The nearshore fishery, as defined by California's Nearshore Fishery Management Plan, includes a select group of finfish: cabezon (*Scorpaenichthys marmoratus*), California scorpionfish (*Scorpaena guttata*), California sheephead (*Semicossyphus pulcher*), kelp greenling (*Hexagrammos decagrammus*), rock greenling (*Hexagrammos lagocephalus*), monkeyface prickleback (*Cebidichthys violaceus*), and the following rockfishes (*Sebastes* spp.): black (*S. melanops*), black-and-yellow (*S. chrysomelas*), blue (*S. mystinus*), brown (*S. auriculatus*), calico (*S. dalli*), China (*S. nebulosus*), copper (*S. caurinus*), gopher (*S. carnatus*), grass (*S. rastrelliger*), kelp (*S. atrovirens*), olive (*S. serranoides*), quillback (*S. maliger*), and treefish (*S. serriceps*). All except California

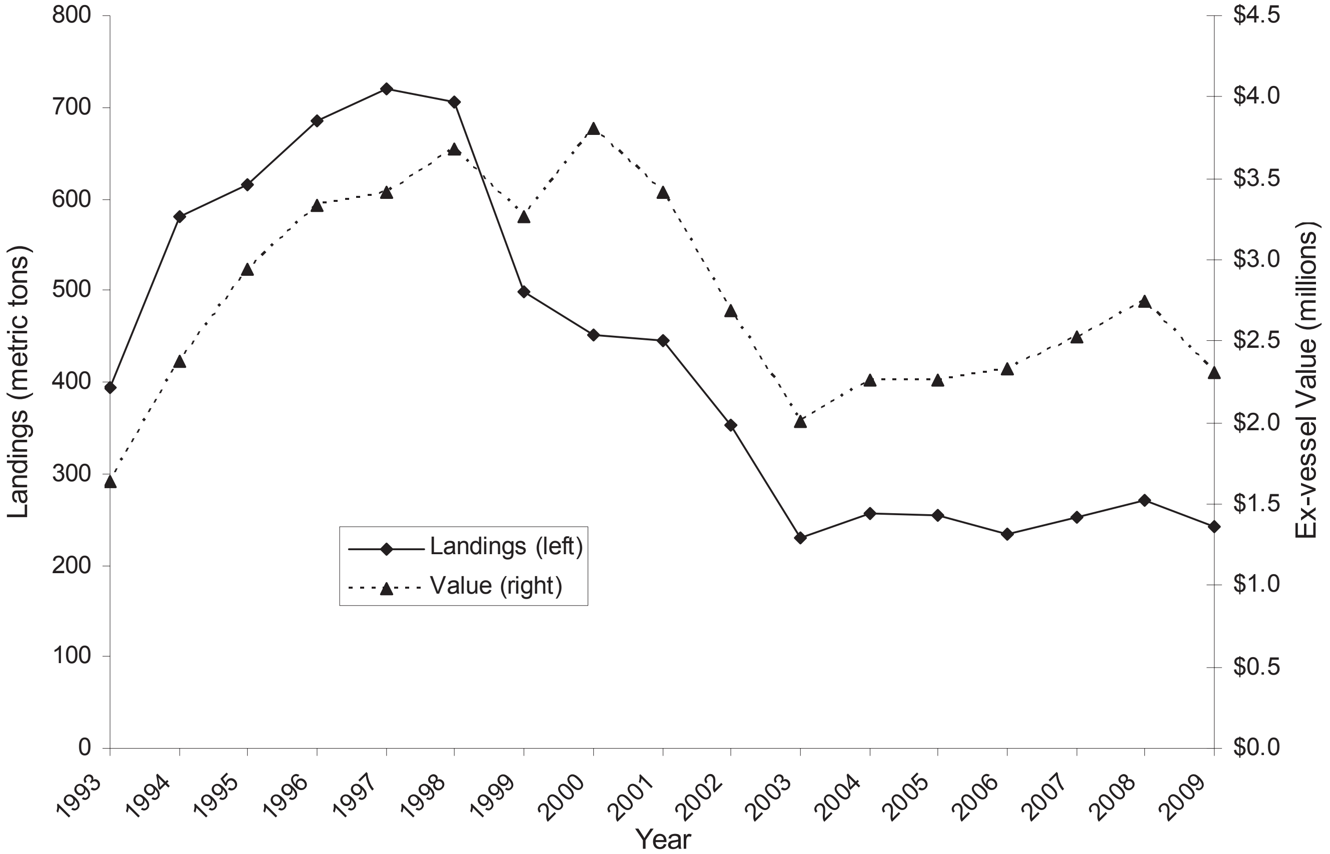

Figure 9. California commercial landings and ex-vessel value of nearshore live finfish, 1993–2009.

sheephead, monkeyface prickleback, and rock greenling are also federally designated as groundfish species under the Council's fishery management plan for Pacific coast groundfish.

These 19 species represent the most commonly landed fish in the nearshore live-fishery. Many are primarily found in shallow waters less than 20 fathoms and are associated with structures such as kelp beds or rocky reefs. Many are slow-growing, long-lived, and territorial, making them potentially vulnerable to overfishing even at low exploitation rates.

In 2009, statewide commercial landings of nearshore live-finfish totaled approximately 242 t (fig. 9). Of that, a total of 219 t or 90% (fig. 10) was recorded as live-landed fishes and 23 t or 10% were recorded as dead-landed. The 2009 landings were 10% less than the 2008 landings (270 t). The total ex-vessel value for the 2009 landings was $2.32 million, of which $2.25 million was paid for live fish (fig. 9). This represents a decrease from the 2008 total ex-vessel value of $2.75 million, where $2.64 million was paid for live fish. Proportionally, in 2009, 97% of the ex-vessel value can be attributed to live landings; a slight increase from 2008 when 96% of ex-vessel value was attributed to live landings.

The nearshore live-fish fishery evolved from the demand for specialty foods in Asian restaurants and markets in southern California. What started out as an alternative fishery quickly expanded into a multi-million dollar industry by the early 1990s, reaching its peak in the late 1990s (fig. 9). Part of the reason for this boom was the willingness of consumers to pay a much higher price for live fish than dead fish of certain species, particularly plate-sized fish. That premium was passed on to fishermen in the form of higher ex-vessel prices (price per pound paid to fishermen upon landing of catch) for live fish. In 2009, live grass rockfish commanded the highest average price per kilogram of live fish ($19.16/kg or $8.69/lb); whereas the highest average price paid for a kilogram of dead fish was $5.34 ($2.42/lb) (quillback rockfish).

Black rockfish were landed in the greatest quantity (94.3 t), representing 39% of the total statewide nearshore live fish landings, the bulk of which was landed in the northern region of the state. In dollars, the top three species landed in the statewide live fishery for 2009 were black rockfish ($0.40 million, 17.4% of total revenue), gopher rockfish ($0.37 million, 16.1% of total revenue) and California sheephead ($0.33 million, 14.3% of total revenue).

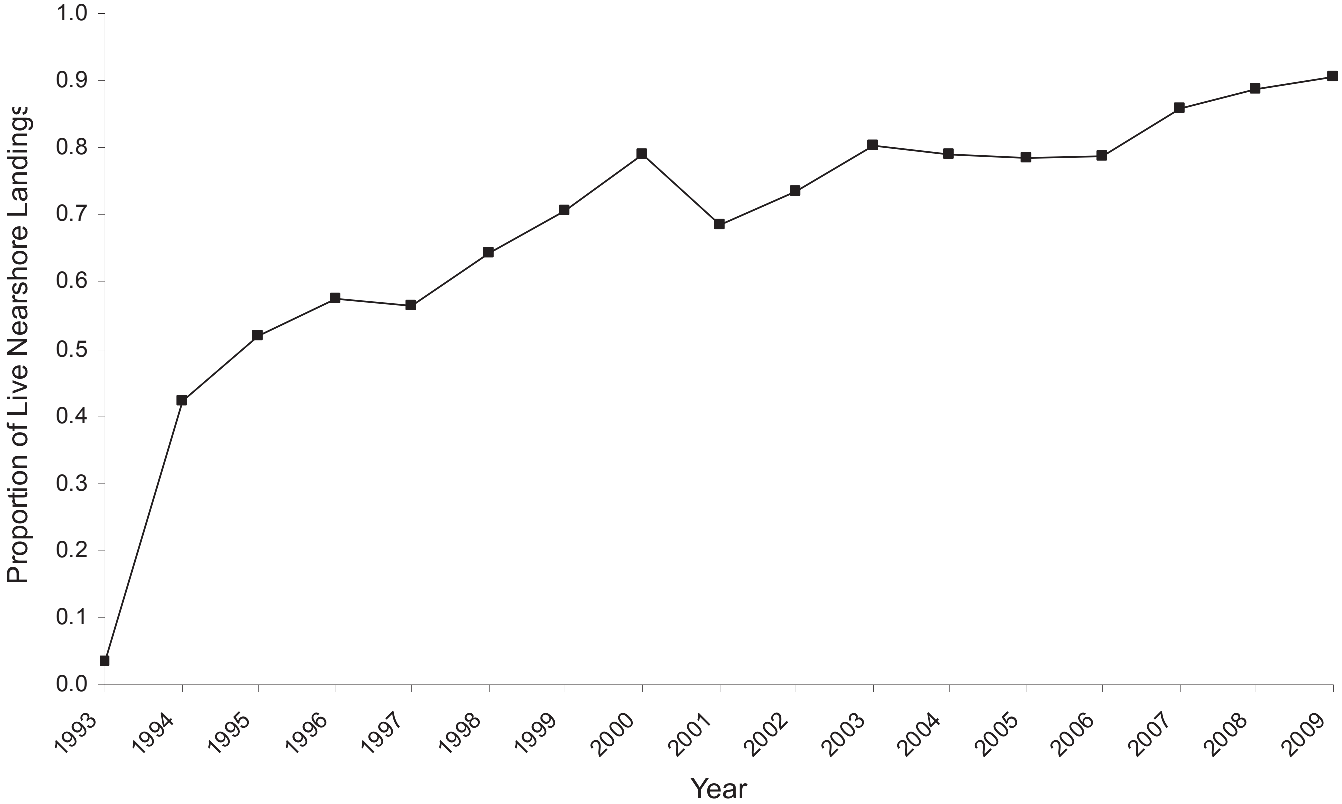

Figure 10. Proportion of commercially landed finfish recorded as live, 1993–2009.

Hook-and-line and trap gear were the primary means used to catch and land nearshore fish species. Hook-and-line gear primarily consisted of rod and reel, vertical and horizontal longlines, and weighted stick gear (although stick gear is commonly used in the nearshore fishery it does not have a designated gear code in the commercial landings database, and is recorded as "hook-and-line gear"). All hook-and-line gears combined were used to land 204 t of live nearshore fish. All trap gears combined resulted in 36.5 t of live nearshore fish. These two gear types accounted for 84% and 15% of the total nearshore live fish landed in 2009, respectively.

2009 Nearshore Fishery Management Highlights. Staying within optimum yields (OY) and total allowable catch (TAC) allocations while avoiding impacts to overfished species are the driving forces behind management of the nearshore fishery at both the state and federal levels. One tool to stay within TAC allocations is to close a fishery if landings are projected to exceed the allotted amount; in 2009, the commercial fishery for kelp and rock greenling was closed on 1 September to stay within its annual statewide TAC allocation. Conversely, if a fishery is not expected to attain its OY or TAC allocation, trip limits or other management measures may be changed to increase access to the fishery. In 2009, depth restrictions for the nearshore fishery north of 40°10'N. lat. required participants to stay in waters shallower than 20 fathoms to minimize impacts to yelloweye rockfish (*S. ruberrimus*) (an overfished species). The black and minor nearshore rockfish trip limit north of 40°10'N. lat. was restructured to allow greater access to the healthy black rockfish stock while minimizing take of other minor nearshore rockfish species. This increase in opportunity required close monitoring to ensure the fishery stayed within the statewide harvest guideline for blue rockfish, which is commonly caught in conjunction with black rockfish.

In 2009, a full cabezon stock assessment off the coast of California was conducted. Results of this new stock assessment will be used to determine the management measures (trip limit and season structure) for use in the 2011–2012 management cycle.

Highly Migratory Species

Albacore. Albacore (*Thunnus alalunga*) is the most abundant tuna caught in both commercial and recreational fisheries in California and along the west coast. In the commercial fishery albacore are caught primarily using hook and line gear (jig/bait/troll), but they can also be caught using drift gill net or a purse seine. Along the entire west coast 12,262 t were commercially landed in 2009 (fig. 11). This is an increase of almost

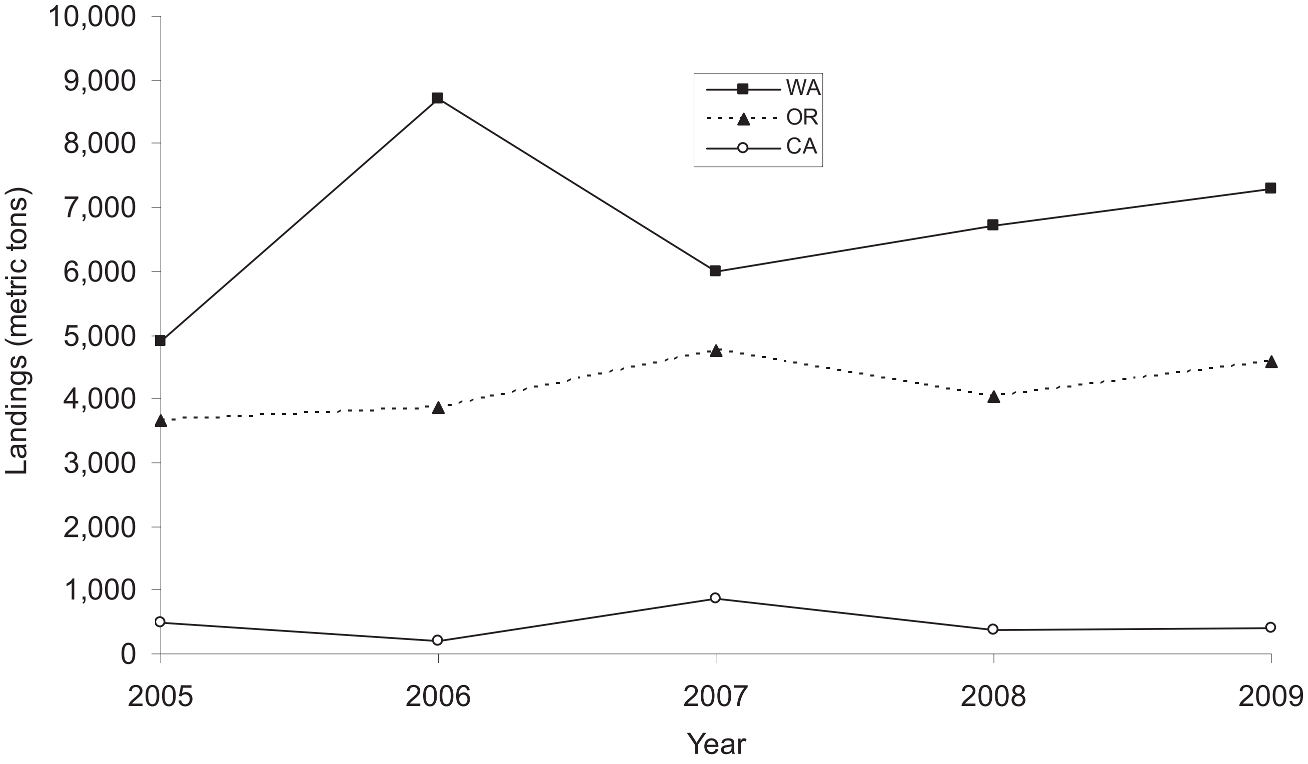

Figure 11. West coast commercial landings of Albacore (*Thunnus alalunga*), 2005-2009.

10% coastwide. California landings held steady from last year, but are still about 50% of the 5 year high of 856 t in 2007. In 2009 the ex-vessel value in California was $0.9 million and price-per-kilogram decreased slightly to $2.41/kg ($1.09/lb), just slightly higher than the coastwide average. Most of this catch was exported for processing and canning, but a small percentage was sold for the restaurant trade.

The Council and the state of California have adopted bag limit conservation measures for albacore (10 fish south of Point Conception, 25 fish north of Point Conception). Most of the recreational take of albacore comes from sportfishing in Mexican waters, which has a 5-fish daily bag limit. In 2009, 33,679 albacore were reported taken by California's CPFVs, which is only a slight decrease from 35,873 fish taken in 2008 (fig. 12). While the California CPFV fishery saw a slight decrease in albacore landings in 2009, all other areas of the recreational fishery in Oregon and California saw increased landings of approximately 25%. RecFIN estimates 9,000 fish were caught in CA, which is primarily from fishing modes other than CPFVs since trips longer than a day are underrepresented in the estimates. A total of 42,000 fish were caught in Oregon and no fish were caught in Washington in 2009.

Yellowfin Tuna. Coastwide commercial landings of yellowfin (*Thunnus albacares*) decreased again in 2009 to 45 t, the lowest commercial landings in 5 years. Over 96% of the landings were in California, by hook and line (64%), purse seine (34%), and drift gill net (<1%). Ex-vessel value totaled $166,281 and price-per-kilogram increased to an average $3.81/kg ($1.73/lb) compared to $1.92/kg ($0.87/lb) in 2008. Most of the catch was processed into canned consumer product, with some sold to the restaurant trade. Exports of fresh frozen yellowfin tuna from California went to México for processing as there are currently no canneries operating in California. CPFV logbook data indicate recreational anglers landed 77,286 yellowfin, a 48% increase from 2008 and a 5 year high. Recreational landings of yellowfin tuna were on a decline for many years hitting a low of 20,124 in 2007, but have seen significant increases in 2008 and 2009.

Skipjack Tuna. West coast commercial landings of skipjack (*Katsuwonus pelamis*) in 2009 all occurred in California (primarily southern) and increased slightly to 5 t from 3 t in 2008, but this is still significantly lower than the 5 year high of 523 t in 2005. The variable catch success is likely due to seasonal fluctuation in abundance of fish within range of southern California vessels. The ex-vessel value decreased to an average of $1.03/kg ($0.39/lb) from $1.24/kg ($0.56/lb) average paid in 2008. Skipjack is primarily landed in California by purse seine vessels. Frozen skipjack are exported for processing into canned product. CPFV logbook data indicate

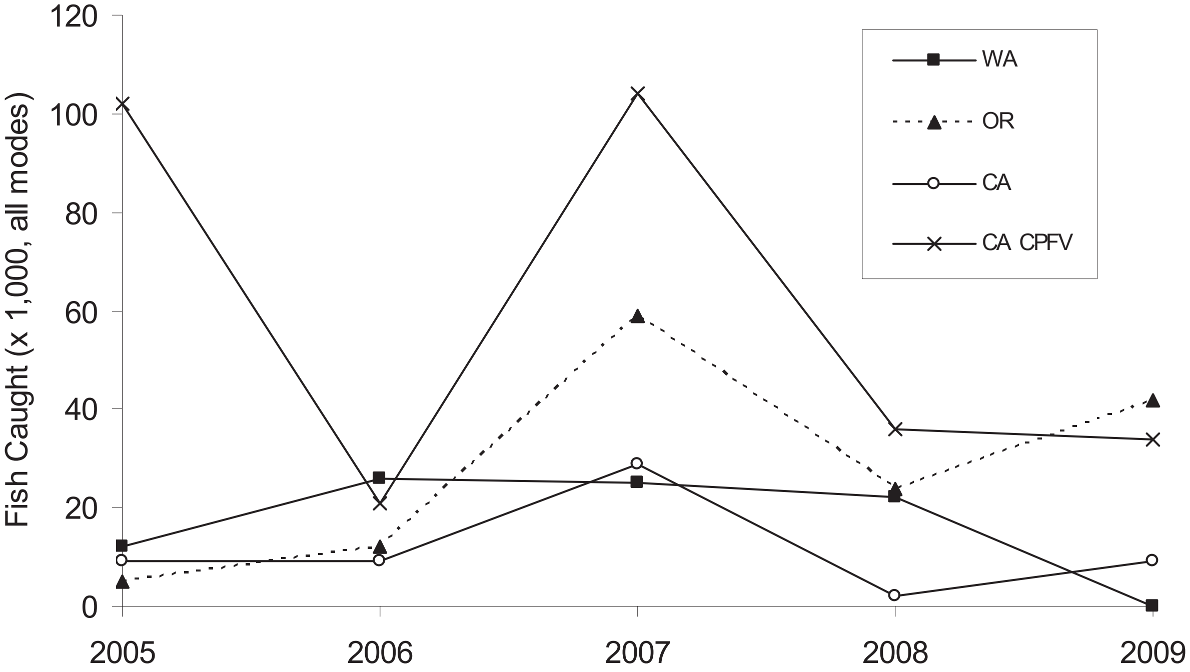

Figure 12. West coast recreational landings of Albacore (*Thunnus alalunga*), 2005–2009. State totals are from RecFIN, all fishing modes. CA CPFV values are from CPFV logbooks and include albacore caught in Mexico.

that recreational anglers landed 9,751 fish in 2009 a 67% increase from 2008 (5,845 fish).

Bluefin Tuna. Commercial landings of bluefin (*Thunnus thynnus*) increased to 414.7 t in 2009 (from 0.8 t in 2008), the greatest annual landings in the past 5 years (99% of this was caught in California). Ex-vessel value was $441,383, and price-per-kilogram decreased to $1.06/kg ($0.48/lb) from an average $4.07/kg ($1.85/lb) in 2008. Purse seine vessels caught 99% of the bluefin landed in 2009. This is commonly seen in years where the fish are plentiful enough to target, in less abundant years bluefin are only caught incidentally to other fisheries on hook-and-line and drift gillnet. California recreational anglers landed 10,739 bluefin in 2009, up from 10,268 fish landed in 2008.

Swordfish. Swordfish (*Xiphias gladius*) is the most valuable fish taken in the California highly migratory species (HMS) fishery. In 2009, commercial landings totaled 404 t, 282 t in California. This was a 23% decrease both coastwide and in California from 2008 (531 t and 366 t respectively). In 2009, the California commercial catch was valued at $1.9 million and was taken using drift gill net gear (62%), hook-and-line gear types (26%) and by harpoon (12 %). The price-per-kilogram increased in 2009 to an average of $6.83/kg ($3.10/lb) compared to $6.44/kg ($2.93/lb) in 2008. Swordfish caught by harpoon is considered more valuable than gill net caught fish. Ex-vessel price-per-kilogram exceeded $13.50/kg ($6.10/lb) for harpooned fish. The recreational catch of swordfish is very low along the entire west coast for the past 5 years. There have only been recreational landings in California and none recorded in 2009. In April, the Council took final action not to authorize a shallow-set longline fishery seaward of the West Coast Exclusive Economic Zone in the Pacific Ocean.

Common Thresher Shark. Common thresher shark (*Alopias vulpinus*) is the most common and most valuable shark taken in the California HMS fishery. In 2009, 90% of the commercial catch of common thresher shark came from gill net vessels. Commercial landings decreased to 62 t in 2009 from 86 t in 2008. The ex-vessel value totaled $194,788, and price-per-kilogram dropped from an average of $3.23/kg ($1.47/lb) in 2006 to $3.14/kg ($1.42/lb). CPFV logbook data indicate that 58 fish were landed recreationally in 2009, down from 81 in 2008 and about the same as 2007 (54). Significantly higher landings are seen in RecFIN landings, which are primarily fishing modes other than CPFV. In 2009 an estimated 4,000 thresher sharks were caught in southern California, twice what was caught in 2008. Over the last five years we have seen a steady increase in the recreational fishery with the likely potential for future growth.

Shortfin Mako Shark. Shortfin mako shark (*Isurus oxyrinchus*) is the second most common shark landed in the California HMS fishery. In 2009, commercial landings decreased 17% along the entire west coast and in California from 35 t in 2008 to 29 t in 2009. In California 75% of the 20 t commercial catch of mako shark

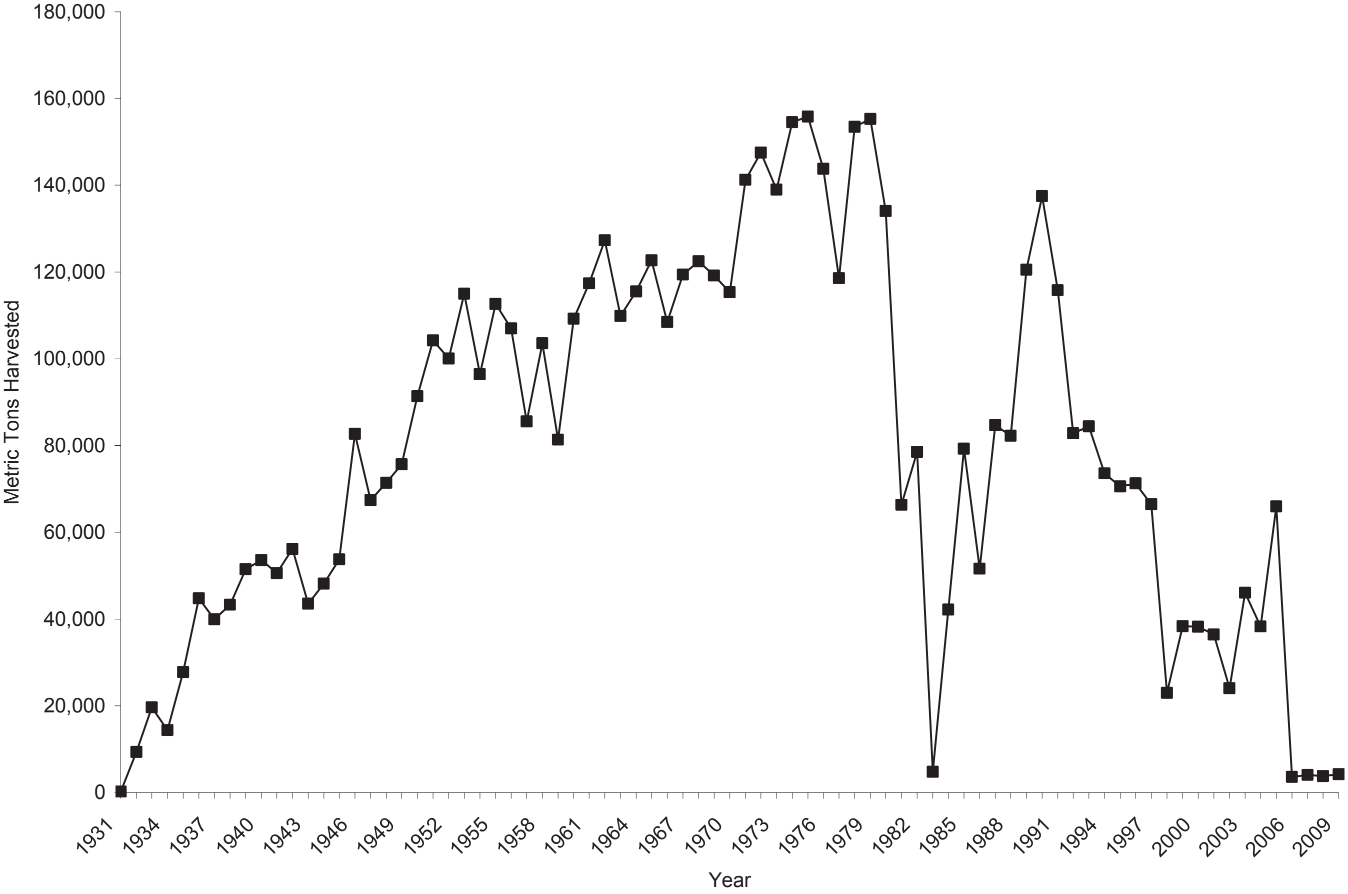

Figure 13. Total California commercial kelp harvest, 1931–2009.

came from drift gill net gear, 12% from set gill nets, 10% from hook-and-line gear types and 3% from harpoon. The ex-vessel value also decreased to $51,352, with a small drop in the price-per-kilogram from an average of $2.69/kg ($1.22/lb) in 2008 to $2.54/kg ($1.16/lb) in 2009. According to CPFV logbook data, 292 mako sharks were taken in 2009, a 17% decrease compared to 351 in 2008.

***Dorado* (dolphinfish).** Commercial landings of dorado (*Coryphaena hippurus*) totaled 0.6 t in 2009, a 66.6% decrease from the 1.8 t landed in 2006. All of these landings occurred in California. The ex-vessel value was $3,769, and the price-per-kilogram increased to $6.14/kg ($2.79/lb) from $5.11/kg ($2.32/lb) in 2008. Historically, dorado landings have been a relatively small component of the HMS fishery and vary from year to year, primarily depending on cyclic intrusions of warm water into the southern California region. Local seafood restaurants purchase dorado when available. CPFV logbook data indicate that recreational anglers landed 7,217 dorado in 2009. This shows how drastically the catch can vary from year to year (31,678 fish landed in 2008 and 7,217 in 2007).

Kelp

The commercial harvest of giant kelp (*Macrocystis pyrifera*) has shown a sharp decline over the past decade from approximately 38,000 t in 2000 to approximately 4,200 t in 2009 (fig. 13). The sharpest decline occurred in 2005 when one company, ISP Alginates (aka Kelco), moved out of California for economic reasons. Kelp harvesting for algin products was the major purpose for kelp harvesting prior to 2005. ISP Alginates harvested the majority of the kelp for use in its production of alginates. Since 2005, the majority of kelp harvesting has been for the purpose of providing food for abalone aquaculture. Most of this kelp is now harvested from leased beds in central California using small mechanized harvesters. One harvester based in northern California uses a skiff to harvest bull kelp (*Nereocystis luetkeana*). The remaining 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 has increased statewide from approximately 5.5 t in 2001 to 23 t in 2009. Kelp is also harvested for recreational use. However, with a cur-

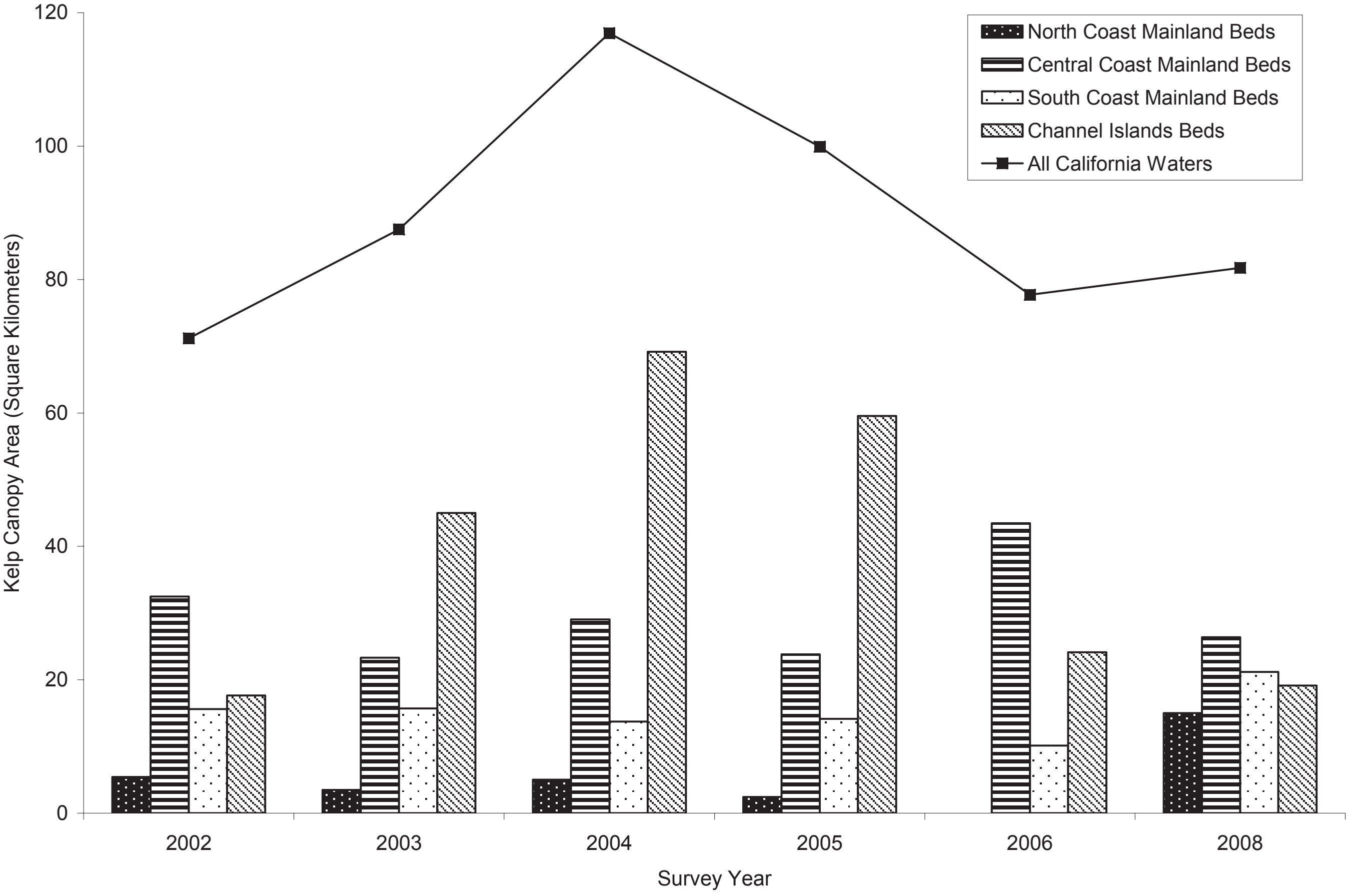

Figure 14. California surveyed kelp canopy area, 2002–2008.

rent 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 kelp fishery. Recreational harvesters generally collect drift kelp that has been cast ashore.

From 2002 to 2009, generally favorable oceanographic conditions (relatively cool conditions in the mixed layer and a shallow nitracline) should have resulted in productive kelp beds, especially those in the southern California Bight (SCB). However, the total amount of area occupied by kelp canopy in this region is still far below levels documented in the twentieth century. In 1967, 1989, and 1999 Department statewide kelp canopy surveys indicated kelp coverage at 181 km^2, 105.4 km^2 and 46 km^2 respectively. This long-term decline can be attributed both to natural disturbances, such as warm-water stress and intense storms associated with one El Niño Southern Oscillation (ENSO) event in the 80s and two ENSO events in the 90s. Declines in kelp bed area can also be attributed to human-induced disturbances, such as dredging/sand disposal onto beaches, increased ocean turbidity and siltation in some urban areas, coastal developments, pollution, and commercial/recreational fishing activities. Some fishing activities remove animals, such as California sheephead and California spiny lobster, which help sustain kelp forests through trophic ecosystem interactions.

The Department began annual kelp aerial surveys statewide in 2002 using multi-spectral imagery to document the abundance and distribution of kelp during the late summer when most beds have reached their maximum canopy potential. Survey images were georeferenced, and used to map and monitor the health of this economically and ecologically important resource. The survey methods have changed over the years in order to provide better data accuracy. The Department has conducted one statewide kelp survey annually from 2002 to 2008, although 2007 data has not been published yet, and no survey was conducted in 2009. Regardless, preliminary results suggest that south coast mainland beds have not increased (recovered) in the same manner that the Channel Island beds have since the last ENSO event in 1997–98 (fig. 14). The kelp beds of the mainland south coast and Channel Island areas are thought to both be subject to the same relative oceanographic conditions and any changes between the two areas might

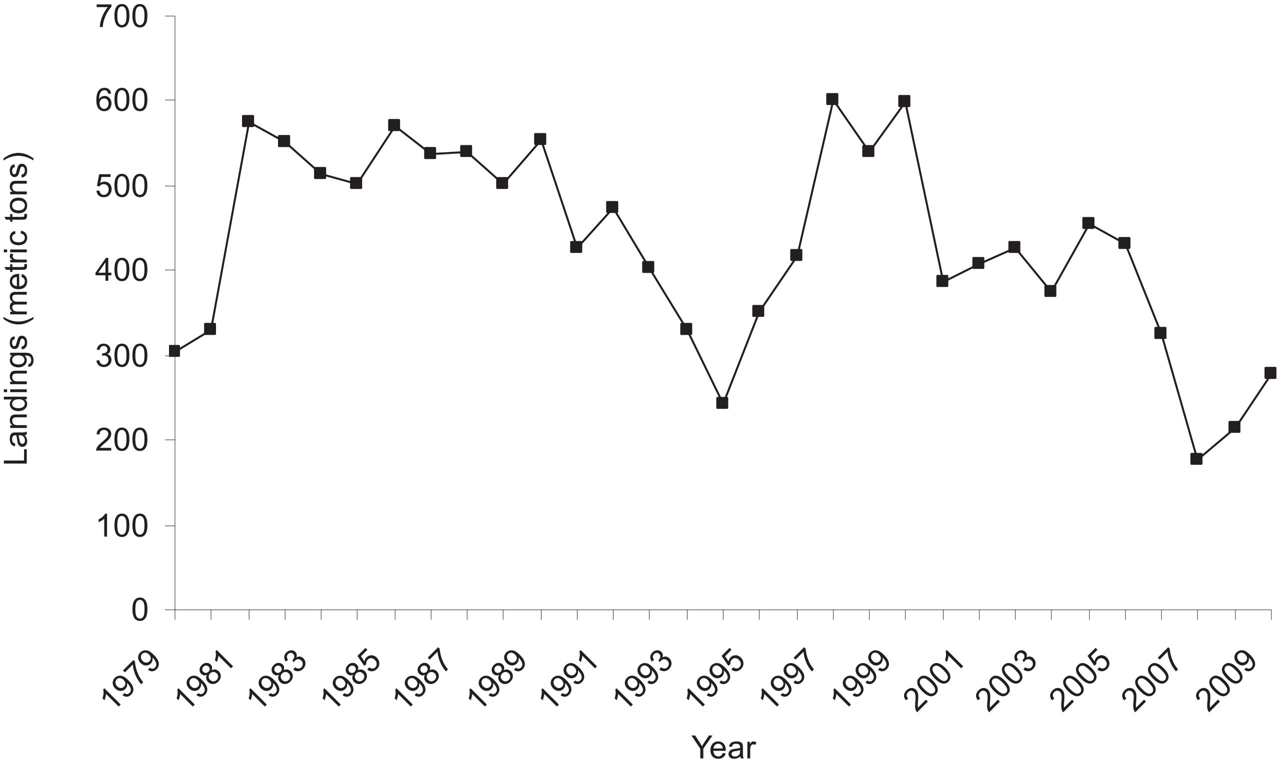

Figure 15. California commercial landings of California halibut (*Paralichthys californicus*), 1979–2009.

suggest other causes, such as differential warming within the SCB or coastal anthropogenic effects. The Department intends to continue annual monitoring of kelp beds statewide in 2010.

California Halibut

The California halibut (*Paralichthys californicus*) is an important and relatively shallow flatfish species to commercial and recreational fisheries in central and southern California. They are found in nearshore waters from Almejas Bay, BCM to the Quillayute River, Washington, but are most common south of Bodega Bay, California. Individual fish can grow up to 1,524 mm (5 ft) in total length (TL) and weigh as much as 32.7 kg (72 lb).

In the commercial fishery, California halibut are harvested using three primary gears: trawl, hook-and-line, and set gill net. Over the past 30 years, total annual landings of California halibut peaked at 602.4 t with a value of $3.26 million in 1997, with a low of 176.3 t valued at $1.84 million in 2007 (fig. 15). Total landings for 2009 were 279.7 t with an ex-vessel value of $2.57 million. In 2009, the three principle gears comprised 99% of halibut landings. Trawl was the dominant gear used to harvest halibut in 2009, accounting for 52% of the total catch. Hook-and-line and set gill net accounted for 28% and 19%, respectively.

Over the past 30 years, bottom trawls have produced more California halibut landings than any other gear type; landings have fluctuated from a high of 331.3 t in 1997 to a low of 63.4 t in 1979 (fig. 16). At the peak of the halibut trawl fishery (1997), 112 vessels made at least one halibut landing. In the year of lowest trawl landings (1979), 58 vessels made at least one halibut landing. In 2009, a total of 37 trawl vessels landed 145.8 t of halibut compared to 40 trawl vessels that landed 93.1 t in 2008. The San Francisco port complex received a majority (58%) of the landings in 2009, followed by the Santa Barbara (32%) port complex, with Morro Bay accounting for 8% of the trawl catch. Directed trawling for halibut is by Department-issued permit only. Currently there are 48 permitted vessels, but not all actively fish. Vessels with a federal groundfish permit may take up to 150 lb of halibut incidentally while fishing for groundfish.

Gill net landings generally have declined in the past 30 years, from a high of 421.7 t in 1985 to a low of 44.1 t in 2007. A series of depth restrictions, enacted to protect sea bird and sea otter populations along the central California coast and prohibiting set net gear in 60 fm or less, greatly impacted the gill net fleet. This is evident by the lack of landings made north of Point Arguello since 2002. Statewide gill net landings increased slightly in 2009 with 40 gill net vessels landing 54.0 t in 2009

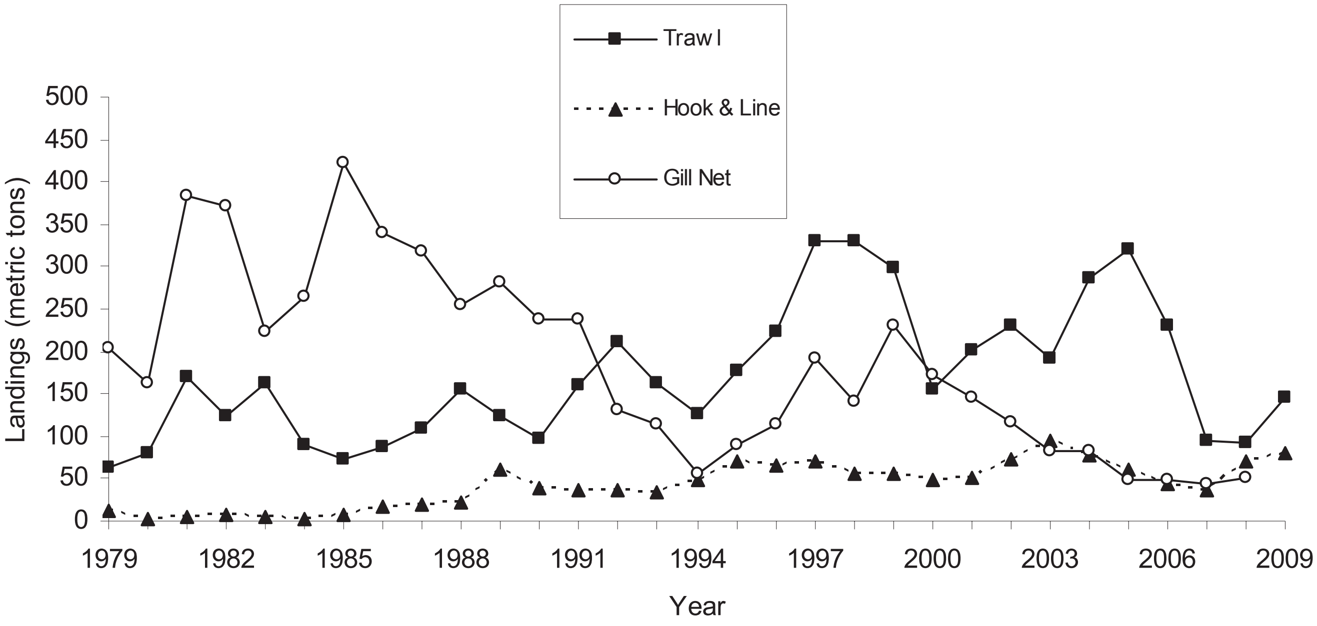

Figure 16. California commercial landings of California halibut (*Paralichthys californicus*) by gear type, 1979–2009.

compared to 42 gill net vessels landing 50.7 t in 2008. The gill net fishery now operates only in southern California, with the Santa Barbara port complex receiving 73% of 2009 landings, followed by the San Diego (14%) and Los Angeles (13%) port complexes.

Annual landings reported by the hook-and-line fleet have fluctuated over the past three decades, ranging from a high of 94.4 t in 2003 to a low of 3.3 t in 1984. From the high of 2003, landings dropped to 37.1 t in 2007, but increased to 71.0 t in 2008 and 78.8 t in 2009. This recent increase in landings can be largely attributed to an increase in effort in the San Francisco Bay fishery, possibly due to displaced salmon fishermen looking for alternate sources of income during the salmon fishery closure of 2008 and 2009. In 2009, 249 hook-and-line vessels landed 78.8 t statewide. The top two port complexes for hook-and-line landings were San Francisco (52%) and Santa Barbara (15%). The hook-and-line fishery is open access; no special permit other than a commercial fishing license is required.

Recreational anglers target California halibut from shore, private and rental skiffs, and CPFVs using hook-and-line gear. Some catch also occurs from scuba divers and free divers using spear guns or pole spears. From 1980 to 2004, the method for estimating recreational catch was the Marine Recreational Fisheries Statistical Survey (MRFSS). During this period, the highest estimated annual recreational catch was 1,062 t (337,000 fish) in 1995 and the lowest estimated annual catch was 122 t (40,000 fish) in 1984 (fig. 17). There are no MRFSS data available for 1990 through 1992. The predominant fishing mode for 1980 through 2004 was private/rental skiff, followed by CPFV. In 2004, the CRFS replaced the MRFSS. CRFS and MRFSS data and estimates are not comparable.

Preliminary data for the 2009 recreational fishery indicate that an estimated 211 t (58,000 fish) of California halibut was landed for all fishing modes statewide (fig. 18). CRFS data indicate that private and rental boats continued to be the primary mode within the recreational halibut fishery.

For both the commercial and recreational fisheries, a minimum size limit of 559 mm (22 inches) total length is required for retention. Recreational anglers are limited to five California halibut per day south of Point Sur (Monterey County) and three California halibut per day north of Point Sur.

In 2008, the Commission, at the request and with the assistance of industry, adopted regulations which defined the parameters of legal trawl gear ("light touch") for the California Halibut Trawl Grounds (CHTG) in southern California. The CHTG is the only area within state waters in which bottom trawling is allowed; all other bottom trawling occurs in federal waters. The "light touch" trawl gear allowed within the CHTG must have a minimum cod-end mesh of 190.5 mm (7.5 inches), a headrope less than 27.4 m (90 ft) in length, webbing on any portion of the trawl less than 7 mm (0.28 in.) in diamter, any chain attached to the footrope not exceeding in diamter of the link material, trawl doors not exceeding 226 kg (500 lbs.) in weight, and no rollers or bobbins

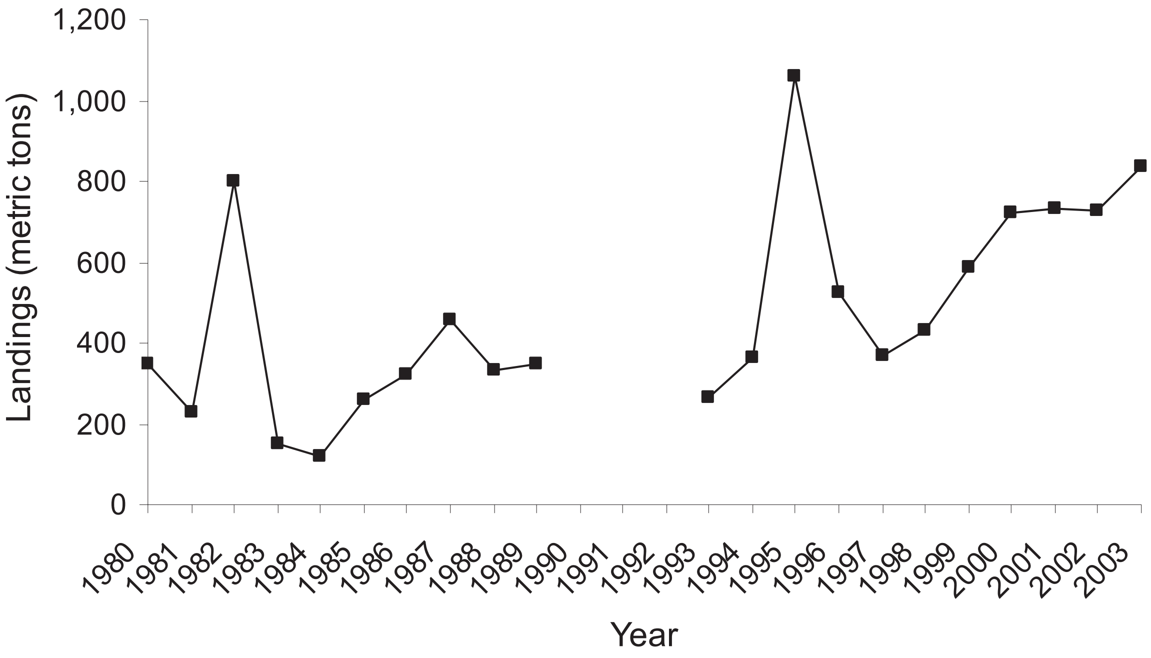

Figure 17. California recreational landing estimates of California halibut (*Paralichthys californicus*), from 1980–2003 as reported by MRFSS. No recreational data from MRFSS were available from 1990–1992.

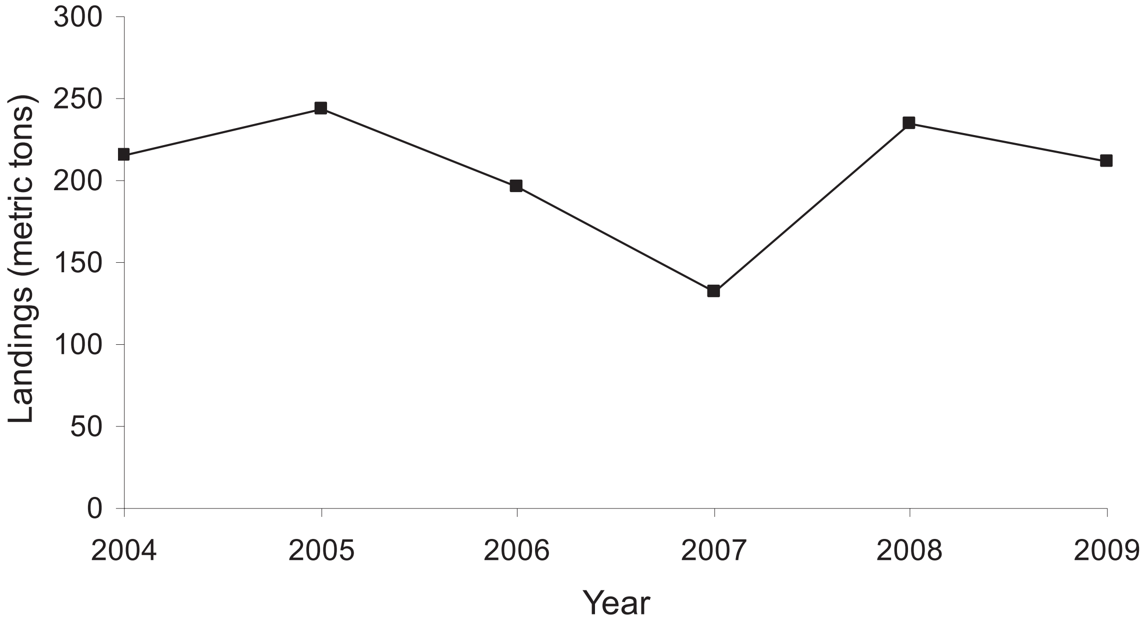

Figure 18. California recreational landing estimates of California halibut (*Paralichthys californicus*), from 2004–2009 as reported by CRFS.

In 2007, the Department began to sample the commercial fishery in central California for the first time for length, weight, age, and sex composition. The Department also resumed ongoing, but discontinuous, sampling of the southern California commercial fishery. Further more, in late 2009, the Department began an aging study for California halibut from central and southern California using cross-sectioned otoliths. The Department is compiling this essential fish information for a statewide stock assessment of California halibut which is expected to be completed in late 2010.

Sandbasses

Barred Sand Bass. Barred sand bass (*Paralabrax nebulifer*) is a common species in the nearshore marine environment and an important part of the recreational fishery

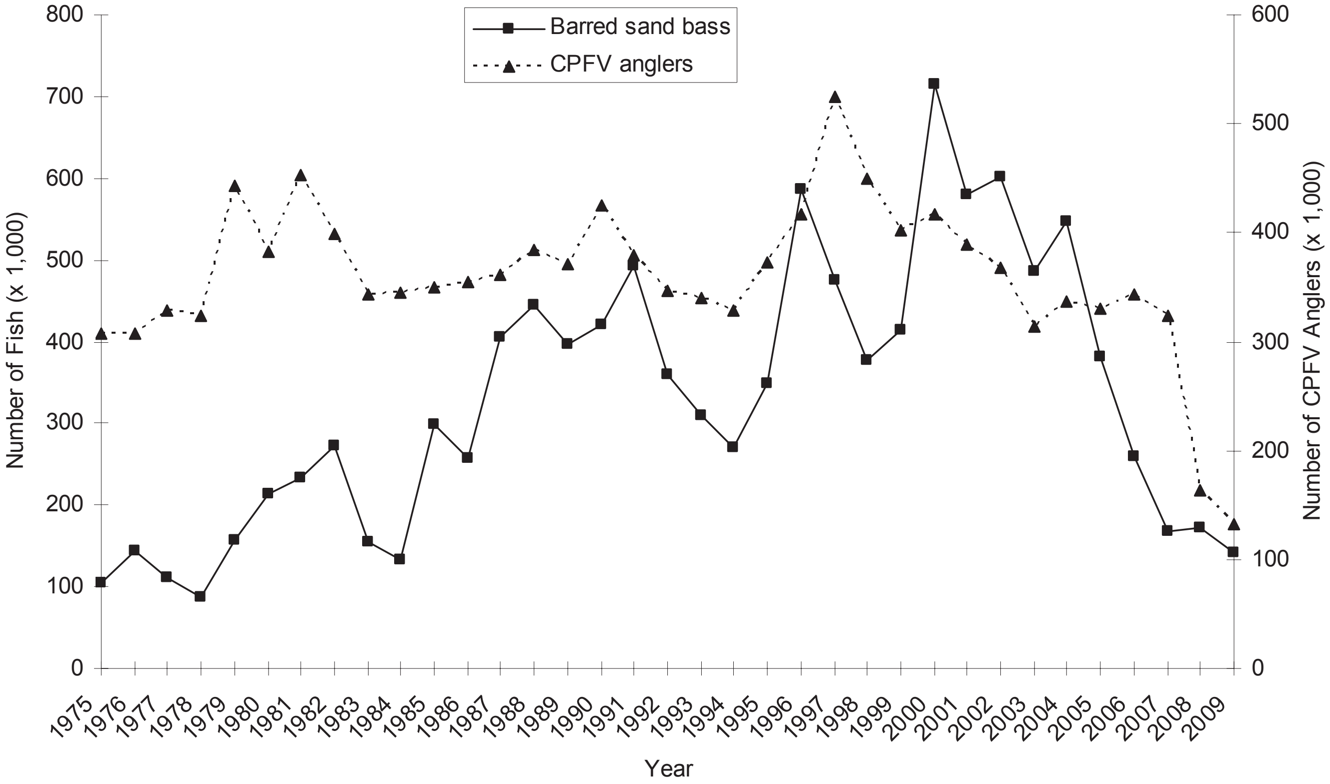

Figure 19. Number of barred sand bass (*Paralabrax nebulifer*) kept by CPFVs in thousands of fish and effort (in thousands of CPFV anglers) in southern California for trips in which barred sand bass were caught. Data are based on CPFV logbooks (1975–2009) for fish caught in U.S. waters. 2009 data are preliminary.

of southern California. Barred sand bass is a warm temperate member of the family Serranidae (sea basses) and one of three species of *Paralabrax* that occurs in southern California. Barred sand bass range from Santa Cruz, California south to Bahia Magdalena, BCM; however, their occurrence is rare north of Pt. Conception. They inhabit waters from the shallow subtidal to about 183 m (600 ft), but are most common less than 30 m (100 ft) and tend to be closely associated with sand/rock interfaces of deep reefs and artificial structures. In the summer months, barred sand bass form large breeding aggregations over specific, sandy bottom sites in depths of 15 to 30 m (~50–100 ft). Barred sand bass are oviparous batch spawners that breed from April through November, with a peak usually in July. They can grow up to 647.7 mm (25.5 in) and weigh up to 6 kg (13.2 lb).

Barred sand bass were fished commercially and recreationally until 1953 when it became illegal to commercially fish for barred sand bass, spotted sand bass (*Paralabrax maculatofasciatus*), and kelp bass (*Paralabrax clathratus*) in California due to a sharp decline in landings of these species. By the mid-1950s the recreational barred sand bass fishery gained popularity and in 1959 a 10-fish bag limit and a 30.5 cm (12 in.) TL minimum size limit were imposed on all bass species to offset declining numbers and a shrinking size composition. The CPFV fishery responded positively to this management approach, and the landings of legal-sized kelp bass and barred sand bass began to increase substantially in the 1960s and 1970s. The minimum size limit is still in effect today, as well as the bag limit which allows a maximum of 10 barred sand bass, spotted sand bass, and/or kelp bass in combination per day for each angler.

Catch estimates for barred sand bass are available through CPFV logbooks from 1935 to the present, but barred sand bass were not differentiated from the other bass until 1975. Prior to 1975, barred sand bass were recorded in a general "rock bass" category which included kelp bass and spotted sand bass. CPFV logbook data indicate annual barred sand bass catch from 1975 to the present has fluctuated showing a steady increase starting in the mid-1980s and expanding more than five fold and peaking in 2000 with 735,690 fish kept (fig. 19). After 2000 a substantial decline in CPFV barred sand bass catch occurred with numbers going below 200,000 fish per year from 2007–2009, the lowest annual catch since 1984. A corresponding decline in number of anglers occurred in 2008–09.

In addition to CPFVs, barred sand bass are also caught from other sport fishing modes including shore (piers, jetties, and beach/bank), and private/rental boats. From 1980 to 2003, MRFSS data indicate that CPFVs com-

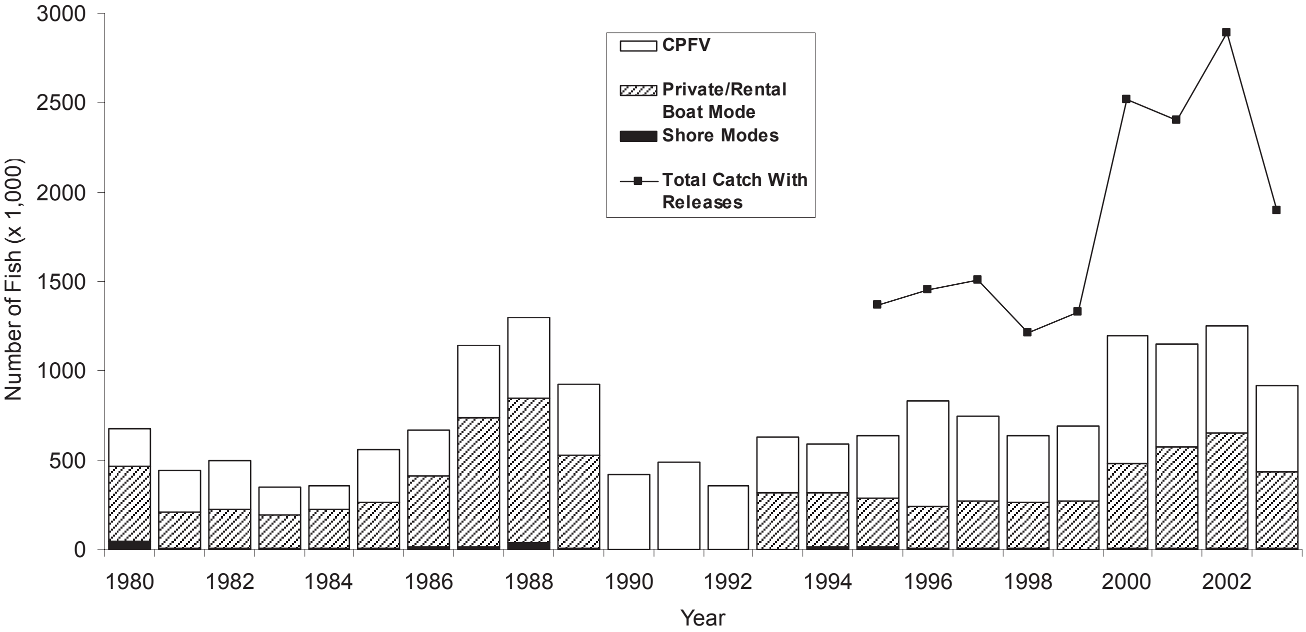

Figure 20. Recreational catch estimates of barred sand bass (*Paralabrax nebulifer*) in southern California in thousands of fish as reported by MRFSS for private/rental boats and shore modes, and by CPFV logbooks, 1980–2003. No recreational data from MRFSS were available from 1990–1992 and for January–February 1995. Data for total combined catch with fish released alive were only available from 1995–2003.

prise the majority (55%) of the catch, with private/rental boats comprising 44% and shore modes comprising 1%. More recent CRFS data indicate a similar pattern with shore based modes comprising less than 10% of the total kept barred sand bass catch annually from 2004–2009, and CPFVs comprising 62% of the annual average catch. MRFSS and CPFV logbook data in aggregate representing all fishing modes from 1980 to 2003 indicate a fluctuating trend with peak catches for kept fish in 1988 and 2002, with 1,295,022 and 1,253,900 fish, respectively (fig. 20). From 1995 to 2003 a substantial number of landed fish were released, resulting in a combined peak total of kept and released fish of 2,893,400 in 2002; CPFV logbook data does not include releases prior to 1995. The mean proportion of released fish differed by fishing mode with 88% for shore based fishing, 68% for private/rental boats, and 12% for CPFVs. Catch estimates (CRFS) and CPFV logbook data in aggregate from 2004 to 2009 show a substantial decline in the number of kept fish for all fishing modes (fig. 21). During this time period the number of fish kept showed a 72% decrease from 694,900 in 2004 to 191,800 in 2009. The mean proportion of released fish by fishing mode from 2004–2009 was similar to 1980–2003 with shore based fishing releasing 86%, private/rental boats releasing 72% and CPFVs releasing 13% of fish annually.

Barred sand bass have consistently ranked among the top species caught by southern California CPFV anglers during the past 20 years. Despite the relatively low catch numbers in the last years, barred sand bass ranked first in terms of number of fish kept. Over the past years, the port of Long Beach had the highest number of barred sand bass caught by CPFVs comprising approximately 21% of the total state catch (tab. 4). The ports of Newport/Balboa and San Pedro ranked 2nd and 3rd in average catch with 18% and 13% of the total catch, respectively. A large number of barred sand bass are landed in these ports from Mexican waters. From 2000–2009 17% of kept fish on CPFVs for all southern California ports and almost 40% from San Diego ports were taken in Mexican waters, primarily off northern Baja California.

Spotted Sand Bass. Spotted sand bass (*Paralabrax maculatofasciatus*) is an important sportfish for nearshore anglers in southern California. Spotted sand bass range from Monterey, California to Mazatlan, Mexico including the Gulf of California; however, this species is rarely found north of Santa Monica Bay. Southern California populations are typically restricted to sandy or mud bottom habitat within shallow bays, harbors, lagoons, and quiet sections of open coast where there is extensive cover such as eelgrass, surfgrass, and rock relief.

Adults usually inhabit waters from 0.6 m–9.1 m (2–30 ft); however, specimens have been taken from waters as deep as 70 m (200 ft) in the Gulf of California. Primary spotted sand bass fishing sites in southern California include Mission and San Diego bays (San Diego County) and Newport and Anaheim Bays (Orange County). These sheltered areas act as warm-water refuges for this generally sub-tropical species.

TABLE 4
Number of barred sand bass (*Paralabrax nebulifer*) kept by California commercial passenger fishing vessels (CPFVs) in southern California by port for 2008 and 2009 and the 10-year average (2000–2009). Data were taken from CPFV logbooks for fish caught in U.S. waters.

	2008		2009*		10-Year Average (2000–2009)	
Port Name	No. Fish Caught	% Total	No. Fish Caught	% Total	No. Fish Caught	% Total
Santa Barbara/Ventura	2,366	1%	927	1%	25,006	6%
Marina Del Ray	8,502	5%	10,502	7%	26,606	7%
Redondo Beach	13,536	8%	7,667	5%	25,019	6%
San Pedro	15,484	9%	16,723	12%	51,759	13%
Long Beach	40,438	24%	39,447	28%	85,016	21%
Newport/Balboa	38,359	22%	24,670	17%	73,270	18%
Dana Point	17,388	10%	15,497	11%	49,081	12%
Oceanside	5,938	3%	6,511	5%	22,029	5%
San Diego	29,760	17%	19,757	14%	42,352	10%
Other	180	0%	181	0%	5,100	1%
Total CPFV Catch	171,951	100%	141,882	100%	405,239	100%

Data Source: CFIS
*2009 data are preliminary.

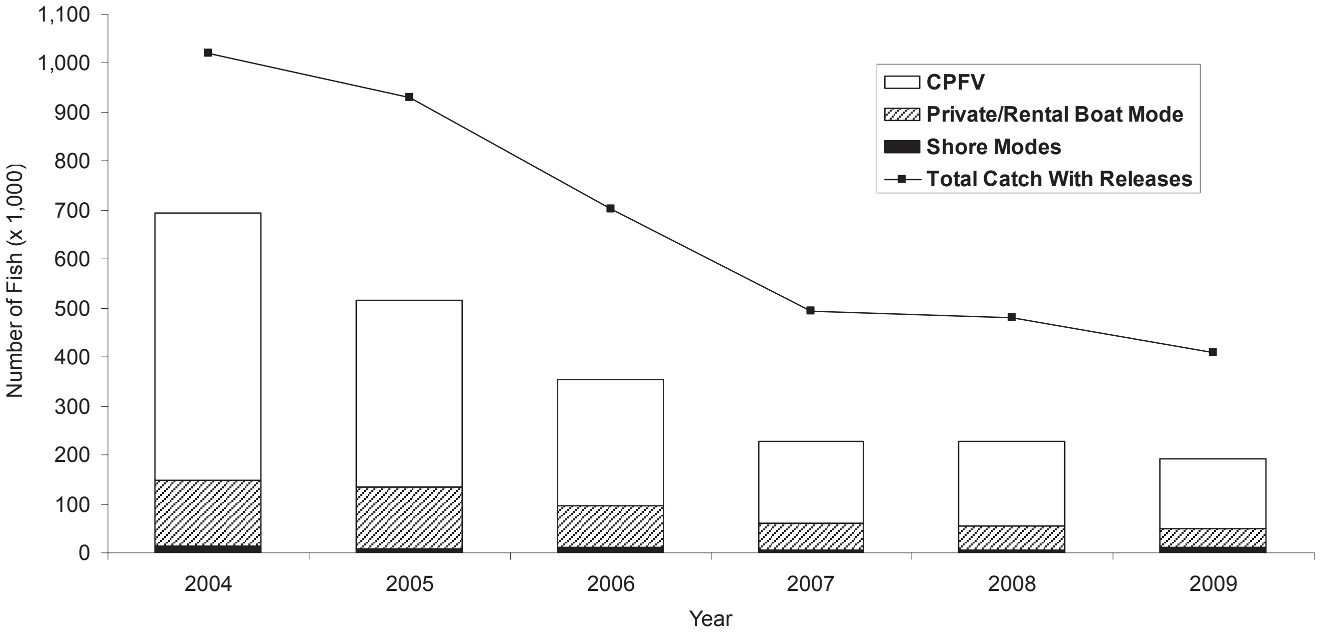

Figure 21. Recreational catch estimates of barred sand bass (*Paralabrax nebulifer*) in southern California in thousands of fish as reported by CRFS for private/rental boats and shore modes, and by CPFV logbooks for party/charter boats, 2004–2009. 2009 data are preliminary.

The spawning season for spotted sand bass occurs in the warm summer months from late May to early September in southern California when spotted sand bass gather to breed at or near entrances of bays and lagoons. The reproductive strategy for spotted sand bass is complex with individual populations in southern California displaying varied patterns. In San Diego Bay spotted sand bass utilize protogynous hermaphrodism, where individual fish start their lives as females and after a period of time change into males. In Anaheim and Newport Bays, spotted sand bass do not exhibit this reproductive strategy resulting in an equal distribution of males and females throughout the age and size classes in the population. Spotted sand bass can grow up to 560 mm (22 in) and up to 3.1 kg (6.8 lb). Significant morphological and genetic differentiation has occurred among spotted sand bass populations throughout their geographic range; populations in the Gulf of California appear to be distinct from those on the Pacific coast and in southern California. This sub-population structure suggests that spotted sand bass exhibit limited dispersal from their restricted habitats.

The spotted sand bass fishery began to gain popularity in the mid-1950s in southern California for shore and small skiff anglers due to the species' aggressive behavior and fighting ability. Adequate landing data for

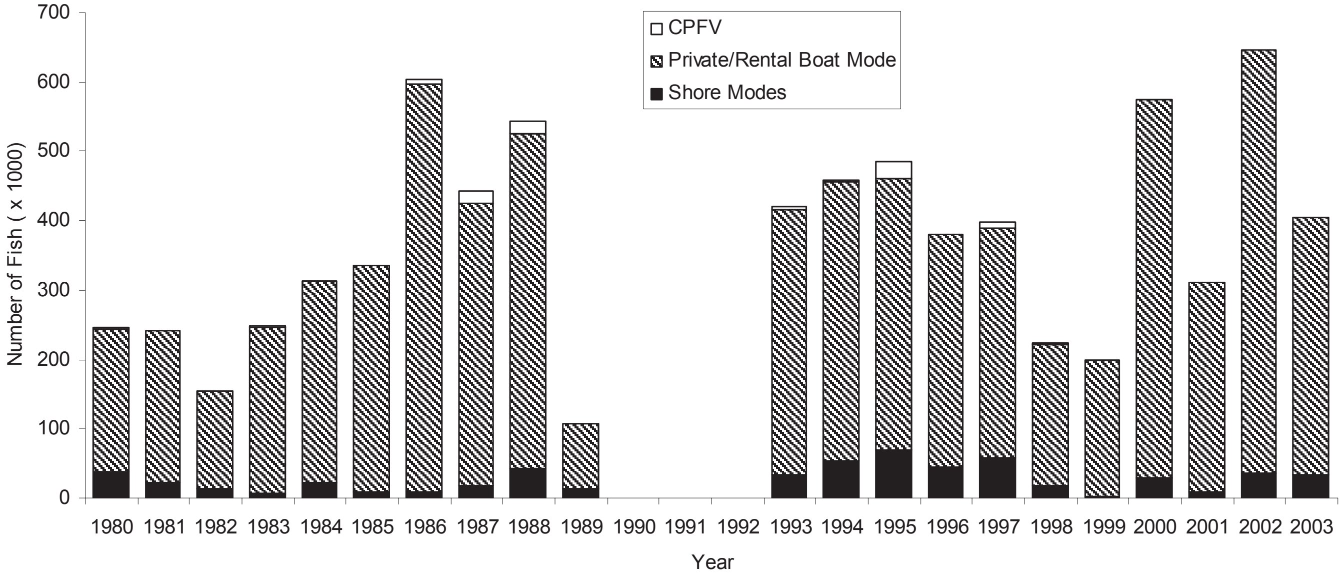

Figure 22. Recreational catch estimates (including kept and released fish) of spotted sand bass (*Paralabrax maculatofasciatus*) in southern California in thousands of fish as reported by MRFSS for private/rental boats and shore modes, and by CPFV logbooks for party/charter boats, 1980–2003. No recreational data from MRFSS were available from 1990–1992 and for January–February 1995.

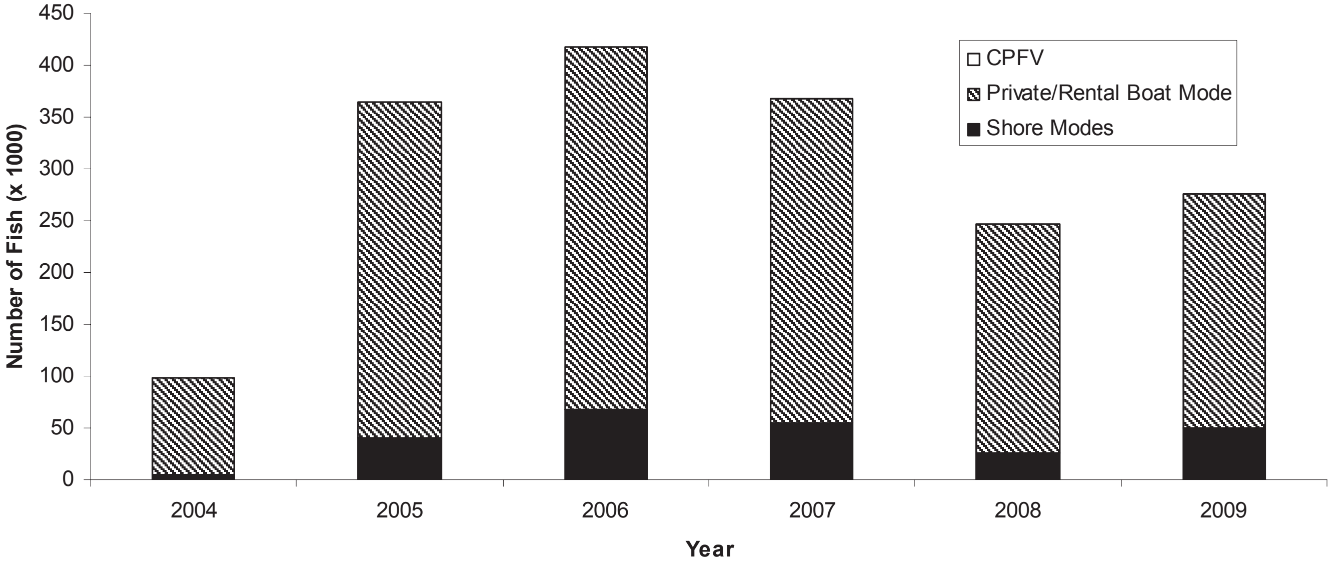

Figure 23. Recreational catch estimates (including kept and released fish) of spotted sand bass (*Paralabrax maculatofasciatus*) in southern California in thousands of fish as reported by CRFS for private/rental boats and shore modes, and by CPFV logbooks for party/charter boats, 2004–2009. CPFV catch is not apparent due to the small contribution to total catch (1%). 2009 data are preliminary.

this species are not available prior to the mid-1970s because early landing data were lumped with the other two *Paralabrax* species or not consistently reported. Surveys conducted by the Department on skiff fishing estimated that annual catch of spotted sand bass in southern California ranged from 12,790 to 23,933 fish between 1976 and 1981. After this time recreational angling for the spotted sand bass has seen a dramatic increase, resulting in angling tournaments that target spotted sand bass exclusively.

MRFSS catch estimates from 1980 to 2003 show that an average of 368,500 spotted sand bass were caught annually. During this time period peak catch occurred in 1986 with 603,800 fish caught (kept and released) and in 2002 with 646,400 fish (fig. 22). The majority of fish (91%) were caught by private/rental boat anglers, with shore based anglers catching 8% and CPFVs catching 1% of the total catch. CRFS data from 2004 to 2009 (fig. 23) show a similar pattern with private/rental boats comprising 86% of spotted sand bass catch and with shore based anglers and CPFVs comprising 14% and less than 1%, respectively. Catch estimates from this time period show a peak catch in 2006 with 417,700 fish and an annual average catch of 295,200 fish.

Although recreational fishing pressure for spotted sand bass has dramatically increased in the last two decades, CRFS data from 2004–2009 indicate that most of these fish are released (94%). This release rate is dramatically higher than reported for kelp bass (71%) and barred sand bass (55%) during this time period. When comparing CRFS catch estimates (kept and released) for all fishing modes in southern California for the three *Paralabrax* species the last five years, spotted sand bass comprises the smallest proportion of the total estimated sea bass catch with 17%. Barred sand bass and kelp bass comprised 38% and 45%, respectively.

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STATE OF THE CALIFORNIA CURRENT 2009–2010: REGIONAL VARIATION PERSISTS THROUGH TRANSITION FROM LA NIÑA TO EL NIÑO (AND BACK?)

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ABSTRACT

This report summarizes observations of the California Current System (CCS) from Baja California, Mexico to Oregon for the period from spring 2009 through spring 2010. During this period, changes in the state of the CCS reflected a transition from cool La Niña conditions into and through a short-lived, relatively weak El Niño event. Weaker than normal upwelling and several extended relaxation events contributed to warming over much of the CCS during summer 2009, especially in the north. Moderation of La Niña conditions in the CCS coincided with the development of El Niño conditions in the equatorial Pacific, yet manifested well in advance of any evidence for direct effects of El Niño on the CCS. Responses to El Niño in fall 2009 and winter 2009–2010 appear to have varied substantially with latitude: conditions off southern California returned to near climatological values with the decline of La Niña, and did not indicate any subsequent response to El Niño, yet the northern CCS warmed subtantially following the decline of La Niña and was strongly affected by intense downwelling during winter 2009–2010. The 2009–2010 El Niño diminished rapidly in early 2010, and upwelling off central and southern California resumed unusually early and strongly for a spring following an El Niño, but recovery from El Niño in early 2010 appears to be less robust in the northern CCS. Thus, despite dynamic changes in the overall state of the California Current, 2009–2010 continued the recent pattern of strong regional variability across the CCS.

INTRODUCTION

This report reviews oceanographic conditions and ecosystem responses in the California Current System (CCS) from spring 2009 through spring 2010 based on observations collected and analyzed by a diverse range

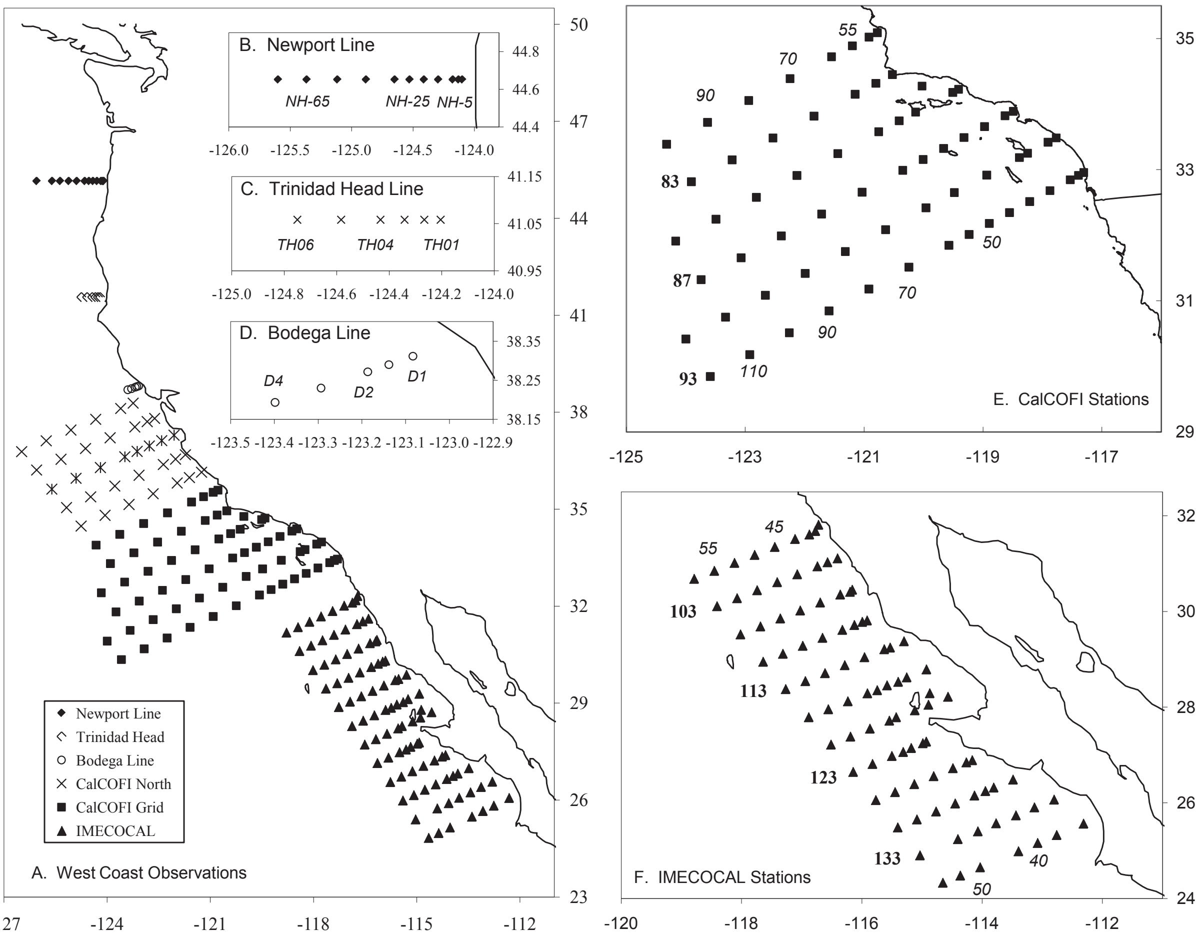

Figure 1. Location of stations for ship-based observing programs that contributed data to this year's report. Observational lines are labeled using bold numbers positioned west of the line terminus; stations are labeled using numbers in italics immediately below or above the respective stations. Line and station numbers for the IMECOCAL and CalCOFI programs are following the CalCOFI line and station nomenclature. The Newport Line station names designate distance (nm) from shore. The 66 standard CalCOFI stations (black squares in A) are occupied on all cruises, weather permitting. During the winter and spring cruises the pattern is extended north for observations of hydrographic properties and distributions of fish eggs and larvae (crosses). The Monterey Bay Aquarium Research Institute monitors conditions along line 67 off Monterey Bay. The Newport Line is covered biweekly out to St 25 and occasionally further offshore. The Trinidad Head Line is occupied at monthly or shorter intervals. The Bodega Line is occupied at quarterly or shorter intervals.

of government, academic, and private research programs. Programs or institutions that have contributed data and analysis to this and previous reports in this series include the Environmental Research Division, Fisheries Resources Division and Fisheries Ecology Division of the Southwest Fisheries Science Center (SWFSC) of NOAA's National Marine Fisheries Service (NMFS), Humboldt State University, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program off southern California, the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) program off Baja California, the Monterey Bay Aquarium Research Institute (MBARI) off central California, the NMFS Northwest Fisheries Science Center (NWFSC), and the Farallon Institute for Advanced Ecosystem Research. In keeping with the tradition of extending the scope of information brought to bear in evaluating the state of the CCS, this year's report includes for the first time observations of surface currents derived from a network of HF radar systems along the Oregon and California coasts, and data collected along the recently established Bodega Line by researchers at the University of California, Davis Bodega Marine Laboratory.

As in previous reports in this series, the focus here is on reviewing recent observations in the context of historical observations as a means of identifying changes in the state of the CCS ostensibly related to recent climatic conditions. This review emphasizes evaluation of augmented or new time series of observations. Where necessary for additional context, insights from spatial patterns are described in general terms in the text; supporting maps and other "snapshots" of the CCS, including more detailed information on specific cruises, are available online at observing programs' websites (indicated in footnotes). The data sets reviewed herein are the subject of ongoing research to understand links between climate and ecosystem processes, work that is well beyond the scope of the present paper. This review, therefore focuses on description and preliminary synthesis of available observations, and therefore offers only sparse information on methods related to data collection (primarily in footnotes). For many ongoing observing programs, more detailed descriptions of methods are available in previous State of the California Current reports or online.

The report is organized as follows. First, we review recent historical conditions and long-term indices of large-scale climate modes (e.g., the Pacific Decadal Oscillation or PDO), followed by more detailed, recent basin-scale information from the tropical and northern Pacific Ocean. This review provides a broad temporal and spatial context for observations that focus more specifically on patterns and structure in physical forcing and responses at scales that span the entire CCS. Second, proceeding from south to north, we summarize the state of the CCS based on physical, chemical and biological observations collected in the course of repeated ship-based surveys that occupy designated stations on a more or less regular schedule (fig. 1). Third, we summarize information on the status of higher trophic levels whether derived from data collected on one (or rarely two) targeted large scale surveys, in conjunction with ongoing large-scale surveys of the CCS, or aggregated from a suite of survey-based, fishery-based, and other sources. Finally, in the Discussion, we summarize the evolution of the state of the CCS through the last year, including the oceanographic and ecological consequences of the 2009–2010 El Niño, and peer briefly into the future.

Recent Evolution of the State of the California Current

A shift to cool conditions following the 1997–1998 El Niño (Bograd et al. 2000; Peterson and Schwing 2003) drove ecosystem responses consistent with those expected for such a transition, e.g., increased zooplankton production, as well as occasional shifts in zooplankton community structure (Brinton and Townsend 2003; Lavaniegos and Ohman 2003). Two events impinged on the CCS in 2002–2003: an intrusion of subarctic waters (the signature of which was detectable in parts of the CCS into 2007) and a mild tropical El Niño (Venrick et al. 2003). Strong ecosystem responses to the intrusion of anomalously cool, fresh, and nutrient-rich waters (e.g., enhanced productivity) were observed only in the northern CCS (e.g., off Oregon); it is thought that the effects of El Niño were likely to have countered any similar responses off southern California and Baja California (Venrick et al. 2003; Wheeler et al. 2003; Bograd and Lynn 2003; Goericke et al. 2004). Since 2004, regional variability has dominated over coherent CCS-wide patterns (Goericke et al. 2005, Peterson et al. 2006; Goericke et al. 2007; McClatchie et al. 2008; 2009). The late onset of upwelling in 2005 and 2006 led to delayed spin-up of productivity in coastal waters, with strongly negative consequences for higher trophic levels in the northern CCS (Peterson et al. 2006; Sydeman et al. 2006; Goericke et al. 2007; Lindley et al. 2009). Cool conditions associated with La Niña prevailed from mid-2007 through 2008 into early 2009, but regional variability was again dominant: increases in productivity in the northern CCS were not matched by similar responses off southern California and Baja California despite evidence of hydrographic effects of La Niña (McClatchie et al. 2008, 2009).

In contrast to the consistently warm conditions that dominated the CCS prior to the strong 1997–1998 El Niño, the Pacific Decadal Oscillation (PDO; Mantua et al. 1997) index suggests that the North Pacific has since been in a generally cooler state. However, the PDO has been for the past decade fluctuating at intervals of approximately two to four years between cool states marked by negative values of the PDO index and associated negative anomalies in sea surface temperature throughout the CCS (e.g., 1998–2001, 2008–2009) and warmer states of positive PDO and positive SST anomalies (e.g., 2003–2006) (fig. 2, and see next page). Over this period, variability in PDO exhibits a high degree of coherence with the Multivariate El Niño Southern Oscillation Index (MEI) (fig. 2). Whether a sustained "cool regime" has been in place for the CCS remains an open question. The North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008) index declined in late 2008 and fell to values near zero for much of spring and summer 2009 before slowly increasing into early 2010 to levels comparable to those observed through much of 2008 (fig. 2).

BASIN-WIDE CONDITIONS

Equatorial Pacific

The 2009–2010 El Niño was preceded by weak La Niña conditions during the winter 2008–2009. The tropical Pacific returned to near-normal conditions during boreal spring 2009, but then transitioned into weak El Niño conditions (NINO3.4 > 0.5°C)[1] during boreal summer 2009. The evolutions of the equatorial sea surface temperature (SST), zonal wind stress, and heat content (upper 300 m temperature average) anomalies from spring 2009 to spring 2010 are shown in Figure 3. The June–July–August seasonal mean SST anomaly (SSTa) was about +1.2°C in the far eastern equatorial Pacific. The positive SSTa in the central-eastern equatorial Pacific strengthened rapidly in October–November

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[1] The NINO3.4 index is the average sea surface temperature anomaly over a region of the equatorial Pacific bounded by 5°N–5°S latitude and 120°W–170°W longitude.

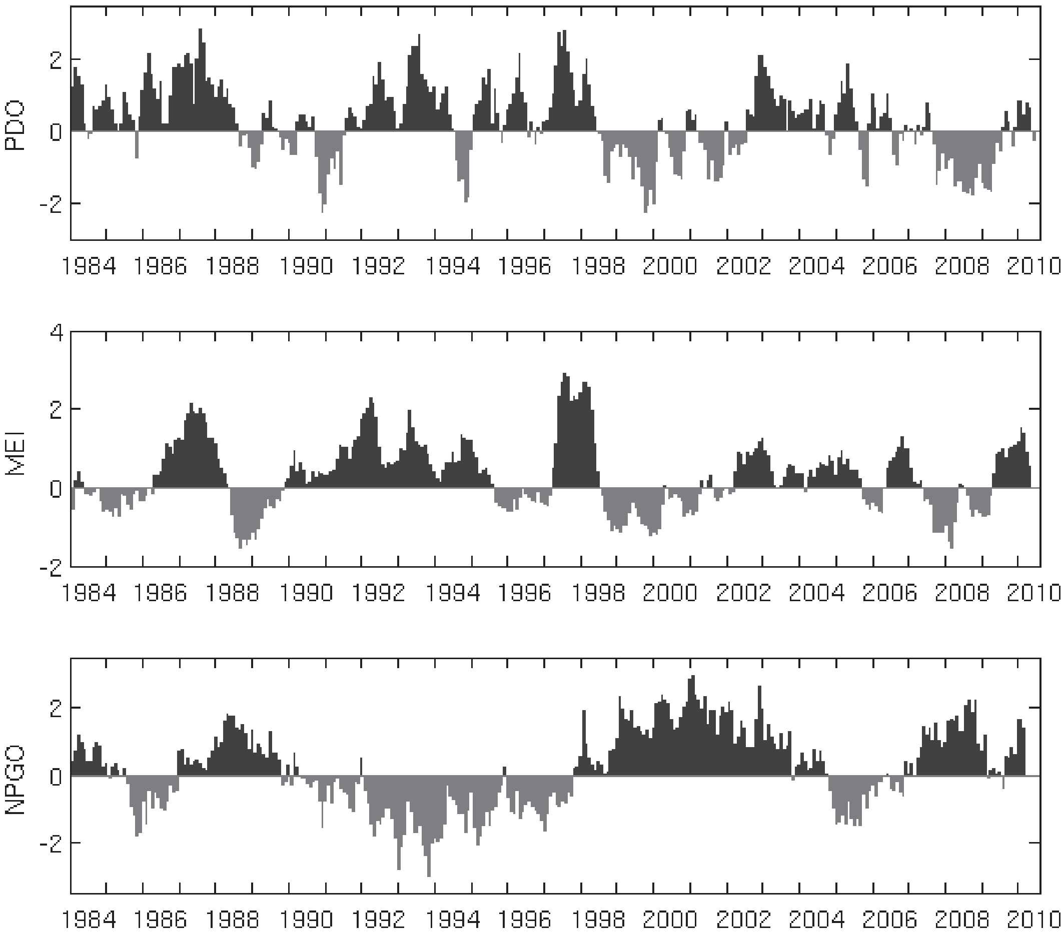

Figure 2. Time series of the Pacific Decadal Oscillation (PDO; top panel; data retrieved from http://jisao.washington.edu/pdo/PDO.latest), the Multivariate ENSO Index (MEI; middle panel; data downloaded from http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/table.html), and the North Pacific Gyre Oscillation (NPGO; bottom panel; downloaded from http://www.o3d.org/npgo/data/NPGO.txt) for January 1984–May 2010 (March 2010 for the NPGO).

2009, and the 3-month-running mean NINO3.4 SST was about 1˚C above-normal in September–November 2009, indicating a moderate strength of El Niño. Coincident with the positive SSTa, the positive zonal wind stress anomalies persisted in the western Pacific and positive heat content anomalies persisted across the equatorial Pacific (fig. 3).

Since June 2009 there have been five episodes of downwelling oceanic Kelvin waves associated with westerly wind burst events that are believed to have contributed to the maintenance and strengthening of the 2009–2010 El Niño (fig. 3)[2]. The El Niño reached a peak phase during December 2009, and the SSTa pattern since January 2010 falls into the category of the central-Pacific event or Modoki event (Ashok et al. 2007) in which the largest warming is centered near the Dateline. Niño indices continued to decline through winter and spring of 2010 and approached zero in May 2010.

North Pacific Climate Patterns[3]

In the extratropical North Pacific, SST anomalies[4] in summer 2009 were generally cool (–0.5 to –1.0˚C) along the North American coast and warm (>+1˚C) in the central northeast Pacific (fig.4a), a pattern that had persisted through 2008 and into the first half of 2009. This pattern also reflects the negative phase of the Pacific Decadal Oscillation (PDO) in place during this period. Concomitant with the development of the tropical El Niño in summer 2009, the negative-PDO pattern broke down in the northeast Pacific. Typical of El Niño periods, the Aleutian Low deepened in autumn 2009, leading to anomalously strong cyclonic winds in the northeast Pacific (fig.4b). Cool SSTs remained in the

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[2] See also "Monthly Ocean Briefing" PPT by Climate Prediction Center (CPC), NCEP, at http://www.cpc.ncep.noaa.gov/products/GODAS.

[3] Further details on month-to-month and interannual global ocean climate variability can be found at CPC's "Monthly Ocean Briefing" archive (http://www.cpc.ncep.noaa.gov/products/GODAS).

[4] Large-scale patterns are summarized from the National Center for Environmental Prediction reanalysis fields (Kistler et al. 2001) and from the NOAA-CIRES climate Diagnostics Center (http://www.cdc.noaa.gov/). The reanalysis fields are monthly-gridded (approximately 2˚ × 2˚) anomalies of sea surface temperature (SST) and surface winds. The base period is 1968–1996.

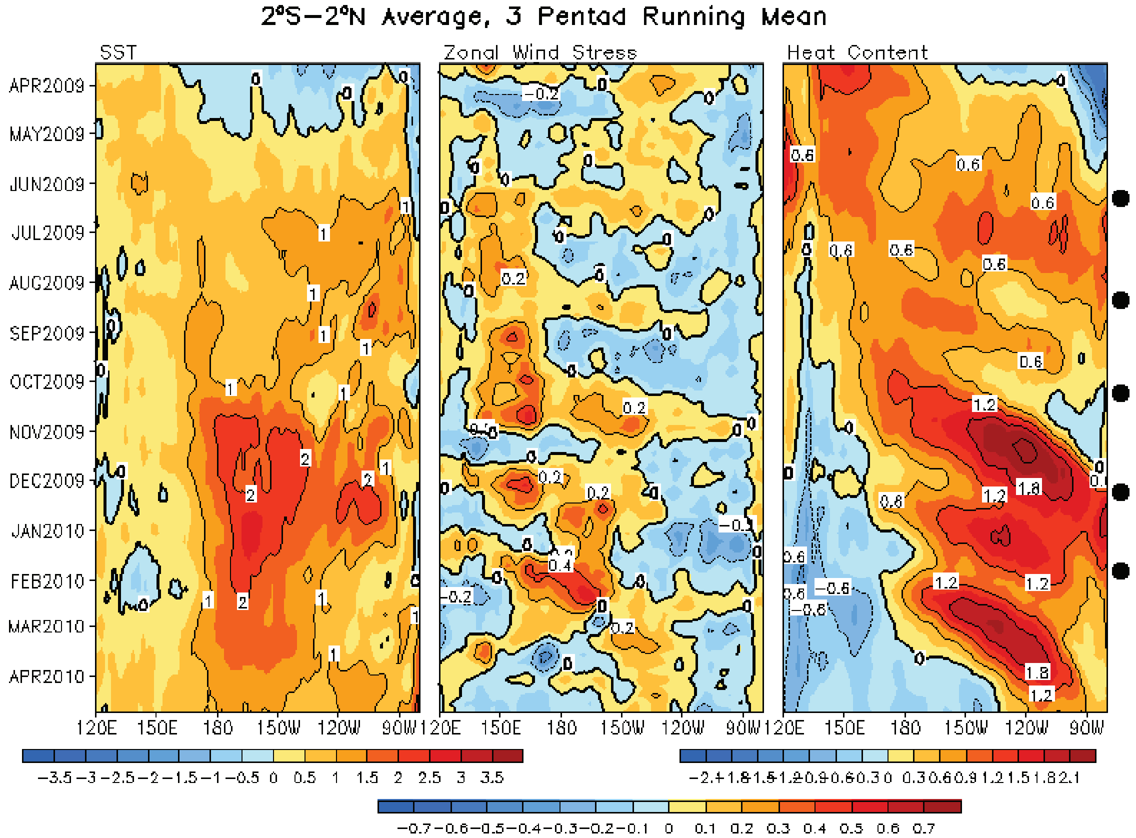

Figure 3. Time-longitude plots of 3-pentad-running mean of SST (left), zonal wind stress (middle) and heat content (upper 300 m temperature average, right) anomalies averaged in 2˚S–2˚N. SSTs are from the weekly 1˚ Optimum Interpolation (OI) analyses of (Reynolds et al. 2002), heat contents from the NCEP GODAS (Behringer and Xue 2004), and zonal wind stresses from the NCEP Reanalysis 2 (Kanamitsu et al. 2002). Anomalies for SST, zonal wind stress and heat content were calculated for the base periods of 1971–2000, 1982–2004, and 1982–2004 respectively. Black dots to right of plot indicate approximate timing of wind bursts and subsequent onset of downwelling Kelvin waves.

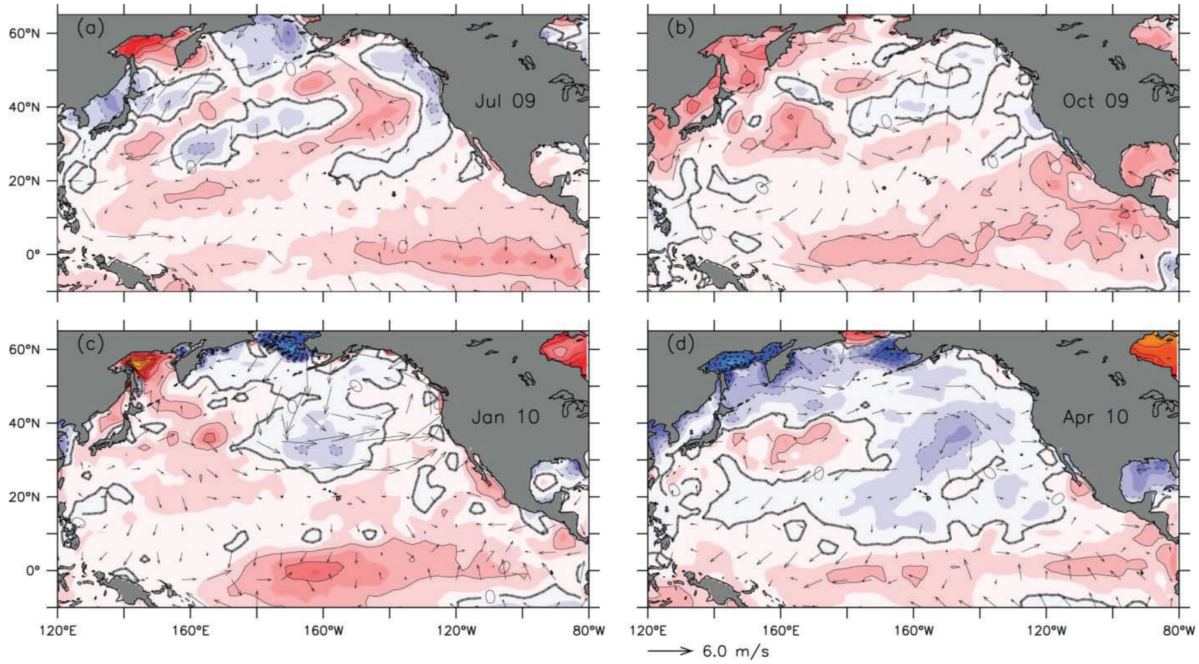

Figure 4. Anomalies of surface wind velocity and sea surface temperature (SST) in the north Pacific Ocean, for (a) July 2009, (b) October 2009, (c) January 2010, and (d) April 2010. Arrows denote magnitude and direction of wind anomaly. Contours denote SST anomaly. Contour interval is 1.0˚C. Negative (cool) SST anomalies are shaded blue; positive (warm) SST anomalies are shaded red. Wind climatology period is 1968–1996. SST climatology period is 1950–1979. Monthly data obtained from the NOAA-CIRES Climate Diagnostics Center.

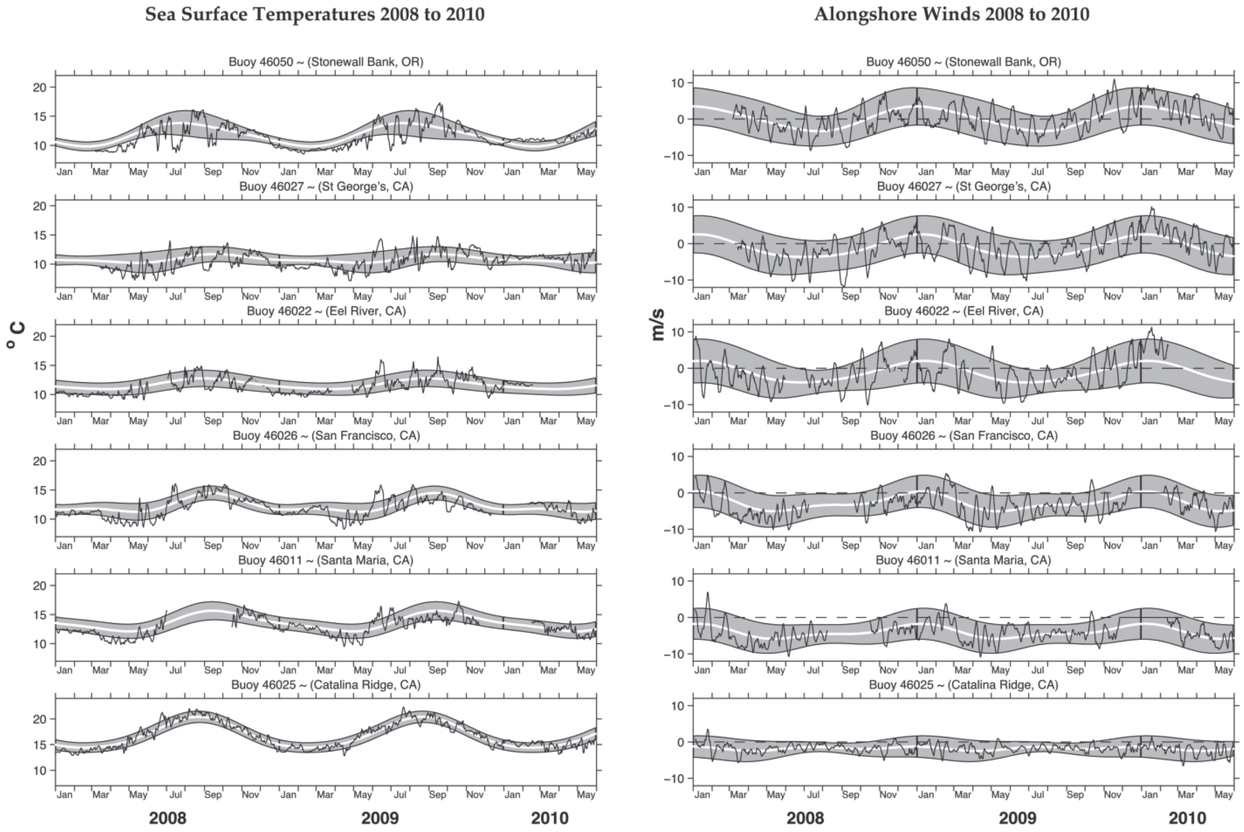

Figure 5. Time series of daily-averaged SST (left) and alongshore winds (right) for January 2008–April 2010 at selected NOAA National Data Buoy Center (NDBC) coastal buoys. Bold lines are the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. Series have been smoothed with a 7-day running mean. Data provided by NOAA NDBC. Coordinates for buoy locations are at http://www.ndbc.noaa.gov/to_station.shtml.

California Current, but anomalies were weaker than in the summer. At the time of peak tropical El Niño conditions (December 2009–January 2010), strong cyclonic wind anomalies dominated the northeast Pacific, resulting in warm SST anomalies (~0.5˚C) in the California Current and eastern Gulf of Alaska, and cool SSTs near the dateline (fig. 4c). This pattern changed rapidly in late winter and early spring 2010, as the North Pacific High developed unseasonably early and strong anticyclonic (upwelling-favorable) wind anomalies prevailed by March–April 2010, leading to a return to slightly cooler than normal SSTs in the California Current (fig. 4d).

CALIFORNIA CURRENT

Atmospheric Forcing, Upwelling, and Sea Surface Temperature Responses

In 2009, the spring transition to upwelling conditions, estimated from trends in cumulative upwelling indices and changes in sea level[5], occurred during the second half of March. Strong event-scale variability prevailed in summer 2009, as it had in 2008, with numerous upwelling and relaxation events and corresponding variations in SST. This strong cycle of upwelling/downwelling events has been evident since 2007, and might be linked to an active period of the intraseasonal Madden-Julian Oscillation[6], which is characterized by 30–60 day variability in the tropics. Conditions at coastal NDBC buoys[7] have reflected these large-scale patterns, with high volatility in both surface winds and SST (fig. 5).

The numerous extended relaxation events resulted in anomalous warming of nearshore waters (cf. SST at NDBC Buoy 46050 off Oregon, fig. 5), effects of which are apparent in the warm SST anomalies observed near the coast in the northern CCS (north of Point Arena) in summer 2009 (fig. 4a). An unusually late upwelling event in late September and early October generated the cool anomalies observed in fall 2009 (fig. 4b). Off central California, anomalously cool conditions prevailed in April and May, and transitioned to anomalously warm, fresh waters in June and July before conditions settled

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[5] See http://www.cbr.washington.edu/data/trans.html for methods of estimating spring transition.

[6] http://www.cpc.noaa.gov/products/precip/CWlink/MJO/mjo.shtml.

[7] The daily alongshore wind component and SST are from the NOAA National Data Buoy Center (NDBC). Values from six representative buoys from the CCS are plotted against the harmonic mean of each buoy.

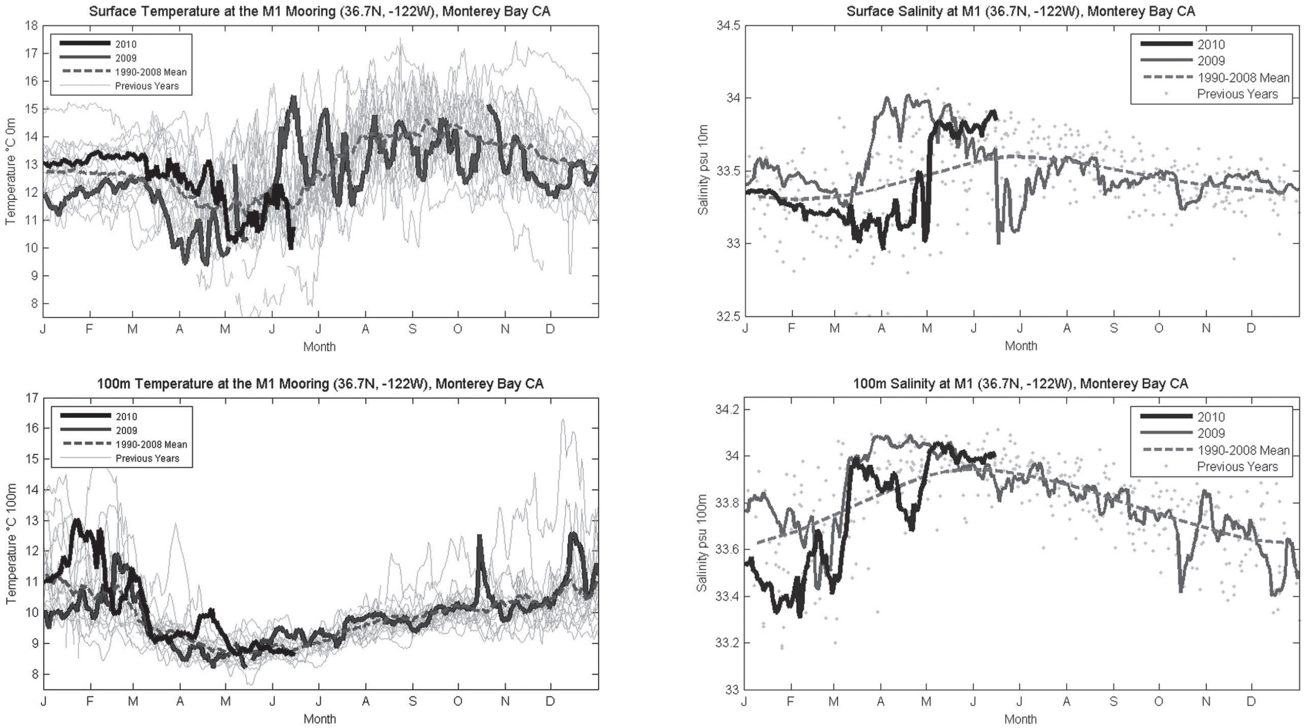

Figure 6. Daily 2009 (thick grey line) and 2010 (thick blue) temperatures (left hand panels) and salinities (right hand panels) at the surface (top panels) and at 100 m (bottom panels) measured by the M1 mooring in Monterey Bay compared to climatological values (grey) from shipboard measurements.

towards climatology in late summer (fig. 6; see also SST at NDBC Buoy 46026 off San Francisco, fig. 5). Overall, the highly variable upwelling and extended relaxation events yielded anomalously weak upwelling during the summer of 2009, particularly in the northern CCS. Coastal SSTs in the southern CCS were above normal (fig. 4a).

The rapidly changing atmospheric forcing in the northeast Pacific through winter 2009–2010 is reflected in California Current upwelling[8]. The strong Aleutian Low in winter 2009–2010 resulted in anomalously strong downwelling in the northern California Current, especially north of Point Arena (~39°N) where a series of intense winter storms contributed to downwelling comparable in magnitude to that observed during winters of 1997–1998 and 1998–1999 (fig. 7). SSTs in winter 2010 were anomalously warm, reflecting the strengthened Aleutian Low and strong downwelling. The generally weaker upwelling (and strong downwelling in the northern California Current) observed in 2009 is typical of an El Niño year.

Rapid development of a strong North Pacific High drove resumption of upwelling earlier and more strongly than is usual following an El Niño event, especially in the central California Current (fig. 7) and likely reflects the rapid decay of the tropical El Niño. Observations along the coast show that the water column remained anomalously warm and fresh at the surface from winter 2009–2010 until the spring transition to upwelling in late April/early May 2010 (approximately a month later than in 2009). Anomalously strong southward wind stress, associated with a well-developed North Pacific High, produced negative SST anomalies throughout most of the CCS. Observations off central California indicate that recovery from El Niño conditions may have begun earlier at depth: anomalies >2°C at 100 m in Monterey Bay (M1 mooring) had returned to normal by early March 2010 (fig. 6). Observations elsewhere in the northern CCS corroborate this pattern (e.g. Trinidad Head Line; data not shown). Moreover, observations in the northern CCS also also suggest that upwelling was weak and intermittent following the 2010 spring transition; upwelling has generally been weaker than normal through the spring of 2010 over much of the CCS (fig. 7).

HF Radar Surface Current Observations[9]

In spring 2009, enhancement of upwelling jets south of major capes was observed as regions of strong mean

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[8] Monthly upwelling indices for the North American West Coast (21°–52°N) and methods for their calculation are available at http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html. Anomalies are calculated relative to 1948–1967.

[9] HF Radar currents presented herein are calculated hourly at 6 km resolution using optimal interpolation (Kim et al. 2008; Terrill et al. 2006) and further averaged to 20 kilometer resolution prior to display. Real-time displays of HF-Radar surface currents can be viewed at the regional association websites: http://www.sccoos.org/data/hfrnet/ and http://www.cencoos.org/sections/conditions/Google_currents/ and at websites maintained by the institutions that contributed data reported here (listed in Acknowledgments).

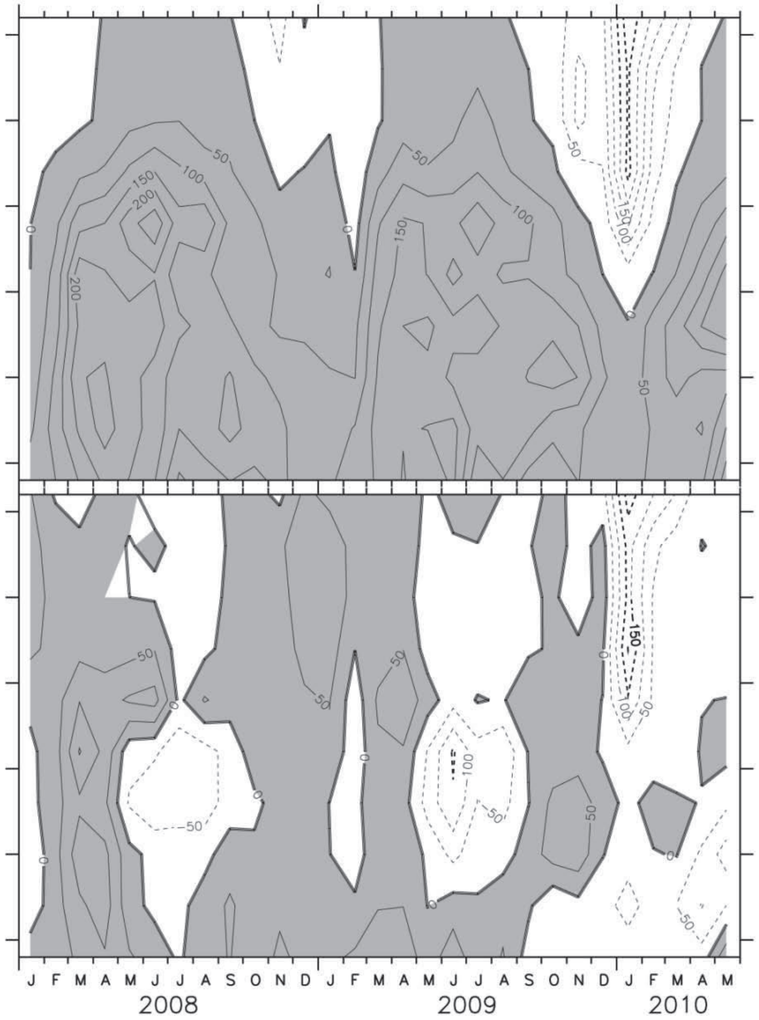

Figure 7. Monthly upwelling index (top) and upwelling index anomaly (bottom) for January 2008–April 2010. Shaded areas denote positive (upwelling-favorable) values in upper panel, and positive anomalies (generally greater than normal upwelling) in lower panel. Anomalies are relative to 1948–1967 monthly means. Units are in m^3/s per 100 km of coastline.

flow extending south from Cape Blanco, Cape Mendocino, Point Arena, Point Reyes and Point Sur (fig. 8). During summer 2009, the spatial extent of strong mean flow increased somewhat north of Cape Mendocino, but mean flows (and locally enhanced upwelling jets) generally weakened into summer and fall. Only the mesoscale feature south of Cape Mendocino persisted robustly through summer and into the fall, associated with the persistence of a clockwise mesoscale eddy (Halle et al. 2010). In the winter (December to February), northward mean flow was evident throughout the California Current region. Spatial variability in the magnitude of poleward surface currents corroborates the difference in intensity of downwelling between the northern and southern portions of the CCS (fig. 7; fig. 8).

Southward flow over the outer shelf off Point Reyes was strong in the summer of 2009 (comparable or greater in magnitude to that observed during the preceding two years, and clearly stronger than in 2005 and 2006), but anomalously strong in April 2009 with a monthly average of 0.7m/s (fig. 9). These flows reflect interactions between the California Current and wind-forced flow over the continental shelf in this region, and therefore provide an index of periods when the California Current has a more or less energetic influence on coastal waters (Largier et al. 1993; Kaplan et al. 2009; Halle and Largier 2010). Strong equatorward flows over the outer shelf were consistent with the strongly positive NPGO and negative PDO during winter 2008–2009 and associated large-scale circulation patterns. Strong poleward flow over the outer shelf in early 2010 coincided with downwelling in the northern CCS (fig. 9). In contrast, alongshore flow over the inner shelf, which generally repsonds more strongly to local wind forcing and includes poleward "relaxation" flows, diminished rapidly from spring 2009 and was weaker in summer

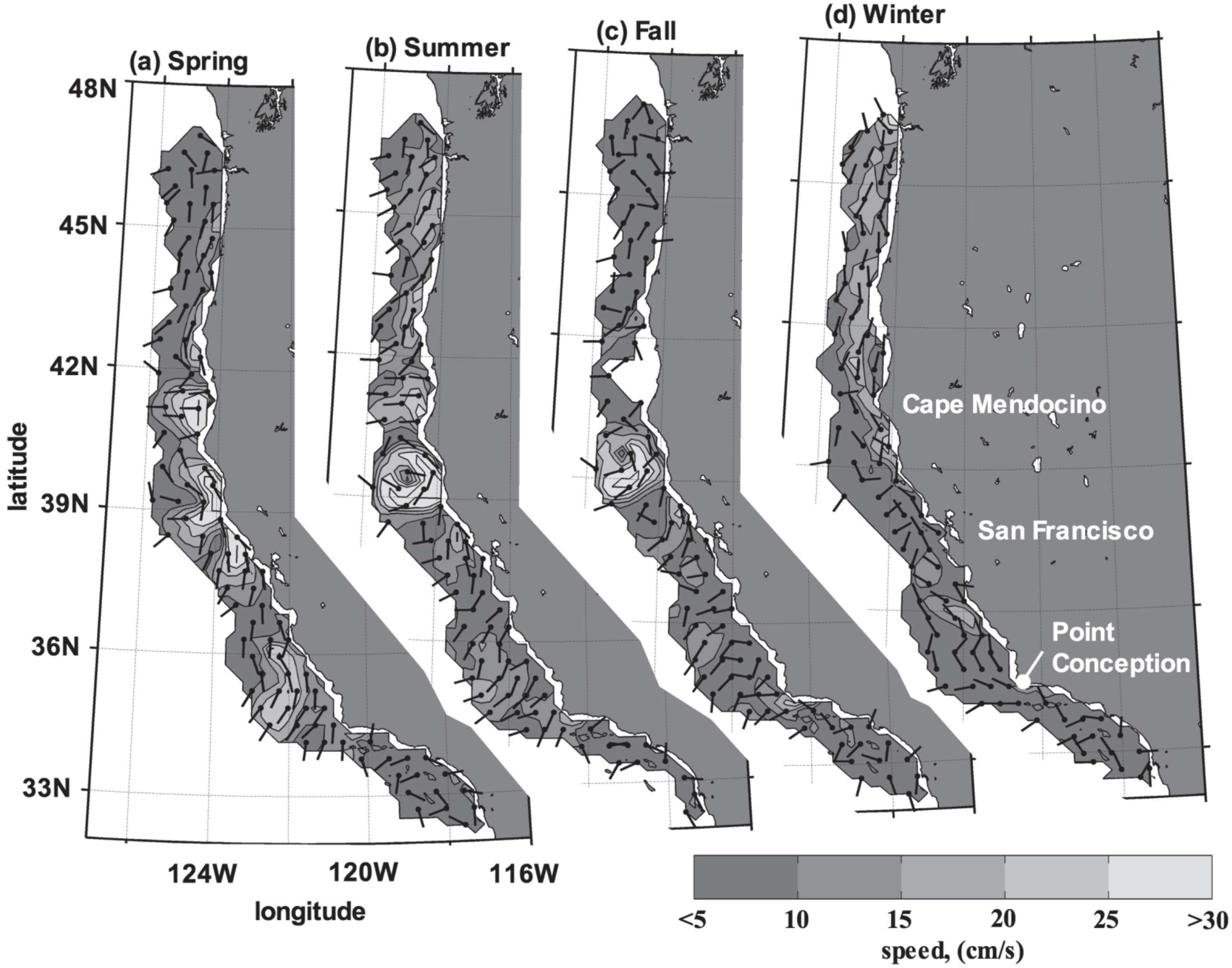

Figure 8. Mean seasonal maps of surface currents observed throughout the CCS with coastal HF radar for March 2009 through February 2010. The seasons are spring (March–May), summer (June–August), fall (September–November), and winter (December–February). Mean surface currents are calculated at 20 km resolution using hourly HF radar observations. Current speeds are indicated by shading. Current direction is given by direction of lines extending from black dots that indicate the location of the measured currents. For clarity, roughly one-sixth of the directions associated with the gridded 20 km currents are shown.

2009 than in the preceding two years (fig. 9). By 2010, strong southward flow had returned to the inner shelf, reflecting the resumption of upwelling winds along the north-central California coast (fig. 9).

El Niño Impacts in the California Current

Although the El Niño of 2009–2010 appears to have been relatively weak and short-lived, evidence of direct, physical effects was observed in the California Current. Time series of coastal sea level from Panama (Balboa) to Washington (Neah Bay) include a number of high sea level events (e.g., mid-October, late January) that plausibly indicate the propagation of coastally-trapped waves triggered by downwelling equatorial Kelvin waves (fig. 10). These events are corroborated by coincident pulses of anomalously warm, fresh water in the upper 100 m of the water column in Monterey Bay (fig. 7). The timing of these events is more or less consistent with the expected arrival of equatorial downwelling Kelvin waves on the coast of South America (cf. fig. 3) and subsequent poleward propagation of resulting coastally trapped Kelvin waves. However, coastal sea levels also vary in response to local wind forcing (e.g., storm passage) and additional work is needed to evaluate whether and to what degree the observed high sea level events did in fact mark the passage of coastally-trapped Kelvin waves. If these events are shown by subsequent analysis to represent the effects of Kelvin waves, they represent the in-water arrival of El Niño at various points along the west coast of North America.

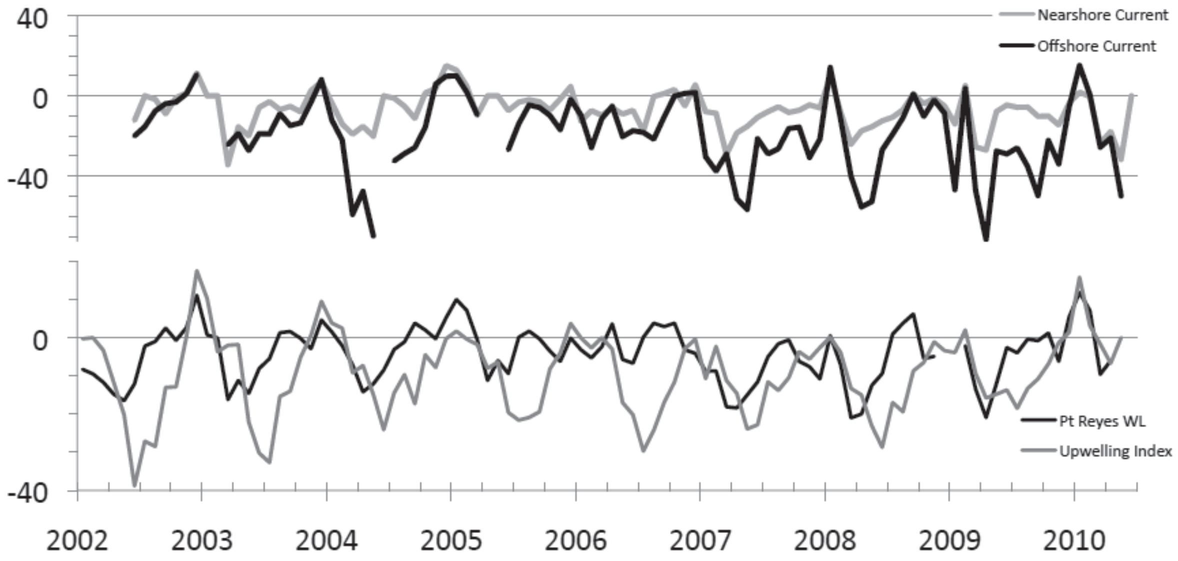

Figure 9. Upper panel: Monthly average surface flow past Point Reyes, CA (positive indicates northward flow, cm/s) between 0 to 15 km offshore (38˚00’ to 38˚00’N and 123˚00’ to 123˚10’W; grey line) and between 30 and 60 km offshore (38˚00’ to 38˚00’N and 123˚20’ to 123˚40’W; black line). Lower panel: Sea level at Point Reyes relative to 1 m above MLLW (units cm; black line) and negative upwelling index for 39˚N, i.e., positive values indicate onshore Ekman transport (units m^3/s per 10 m of coastline; grey line).

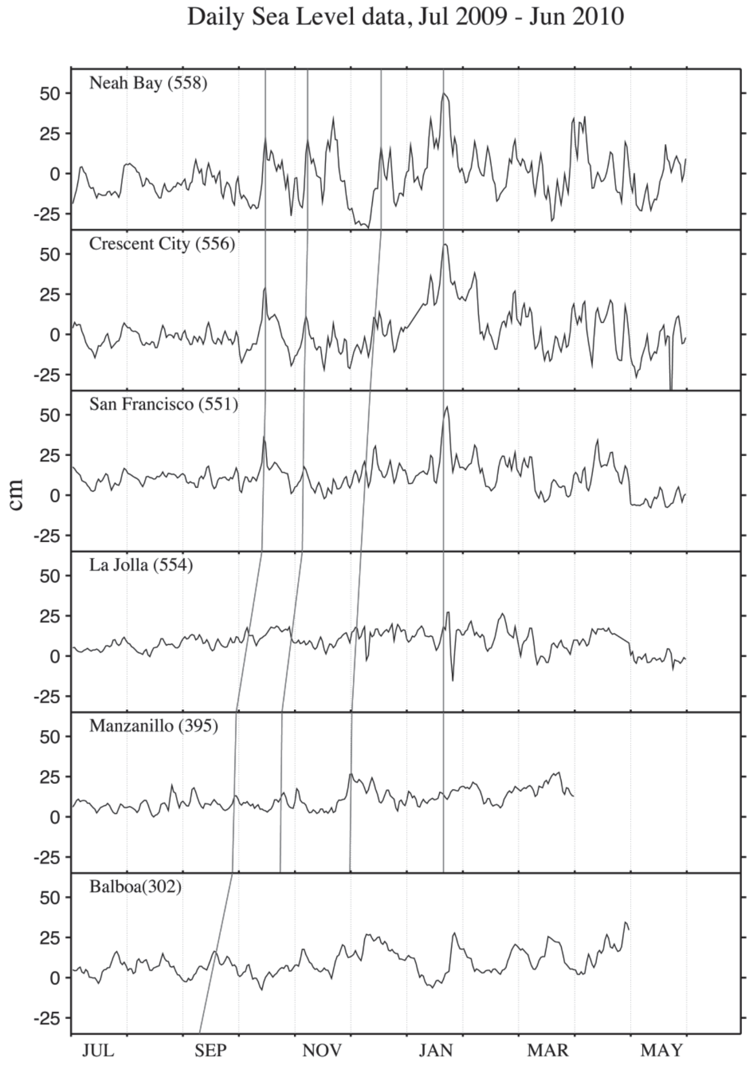

Figure 10. Daily adjusted sea levels (cm) at six locations along the North American continent. High sea level events that might correspond to passage of coastally-trapped Kelvin waves are indicated by lines connecting peaks across time series.

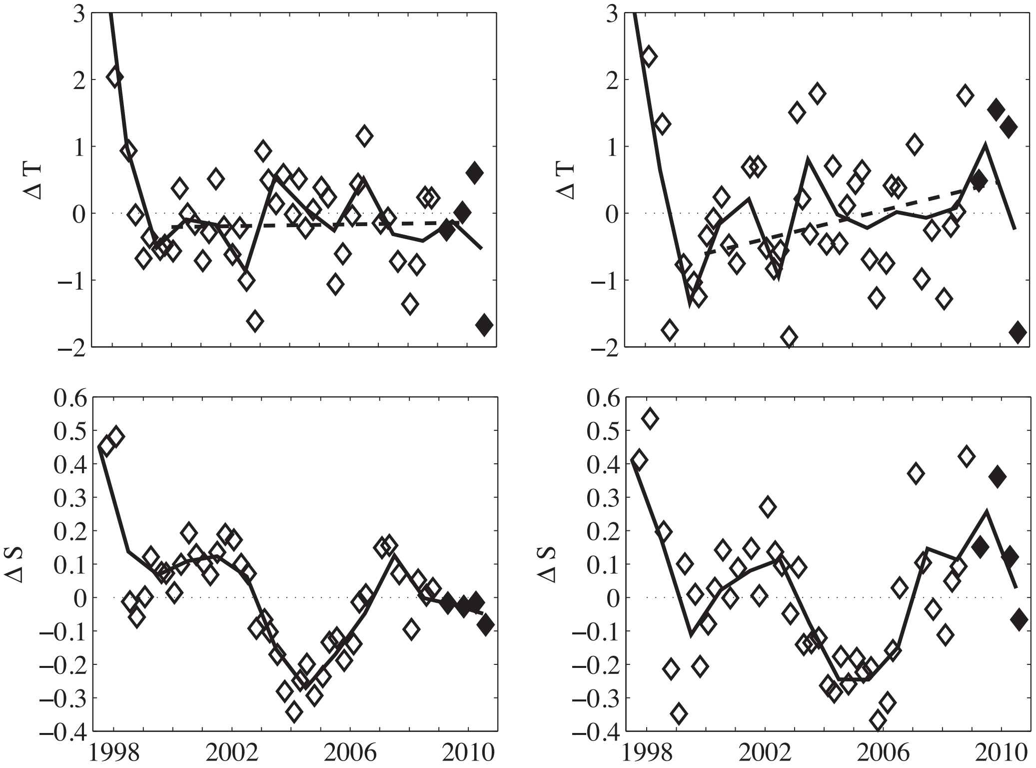

Figure 11. Time evolution of regional 10-m temperature (˚C), salinity, and phytoplankton chl-a anomalies (mg m^{-3}). Northern region values were obtained by averaging anomalies from lines 103, 107, 110 and 113. Southern region values were obtained from observations along sections 123, 127, 130 and 133. Anomalies were computed by contrasting measured values at each depth/location to climatological means obtained from all available data (44 cruises) in the period 1998–2010.

REGIONAL SURVEY OBSERVATIONS

Baja California – IMECOCAL Surveys[10]

Time series of mixed layer temperature and salinity anomalies[11] illustrate the effects of El Niño in 1997–1998, La Niña 1999–2002, freshening of the upper layer in 2002–2006, and the short-termed La Niña event in late 2007–early 2008 throughout the IMECOCAL study region, and contrasting responses in the temperate and subtropical subregions north and south of 28°N, respectively (Durazo 2009) (fig. 11). Starting in late 2008, data in the northern region show slightly positive temperature anomalies and near normal salinities. For the southern region, the effects of El Niño are indicated by the larger positive anomalies ($\Delta T \sim 1$–2°C, $\Delta S \sim 0.4$), with peak values in October 2009.

A dissimilar pattern was apparent in anomalies for chl a at 10-m (data not shown). In the northern region, chl a concentrations shifted from anomalously large values in spring 2009, through values very near the long term mean in autumn 2009, to large negative anomalies (~1.0 mg m^{-3}) in spring 2010. In the southern region, chl a values were near long term means throughout 2009, with slightly negative anomalies in spring 2010. The trend in chl a anomalies during 2002–2006 is related to patterns described by Gaxiola-Castro et al. (2008).

Analysis of cross-shelf sections (data not shown) shows that large positive salinity anomalies were most apparent near the coast in the southern region. These anomalies increased in strength between April 2009 to October 2009 (maximum anomalies $\Delta S \sim 0.5$ occured at southern nearshore stations in October 2009), but were replaced by negative anomalies ($\Delta S \sim -0.1$ to -0.5) near the coast by April 2010. Complex eddy structure was observed throughout the region during October 2009, and included features that are likely to have contributed to the strong nearshore salinity anomalies through entrainment of more saline water from south of the IMECOCAL region. These flows differ from circulation patterns observed during the 1997–1998 El Niño, during which waters of tropical and subtropical charac-

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[10] The IMECOCAL study region spans 93 stations off Baja California, México (fig. 1). IMECOCAL cruise schedules, data collection protocols, analysis methods, and additional substantiating data are fully described at http://imecocal.cicese.mx. Zooplankton data were not available at the time of writing, and will be presented elsewhere.

[11] Mixed layer temperature and salinity anomalies were calculated for regions north and south of 28°N using a method similar to that employed by CalCOFI (described below). Results for the southern region include some variability associated with inter-annual differences in station occupancy. Climatological means are computed from hydrographic data gathered by the IMECOCAL program in the period 1998–2010.

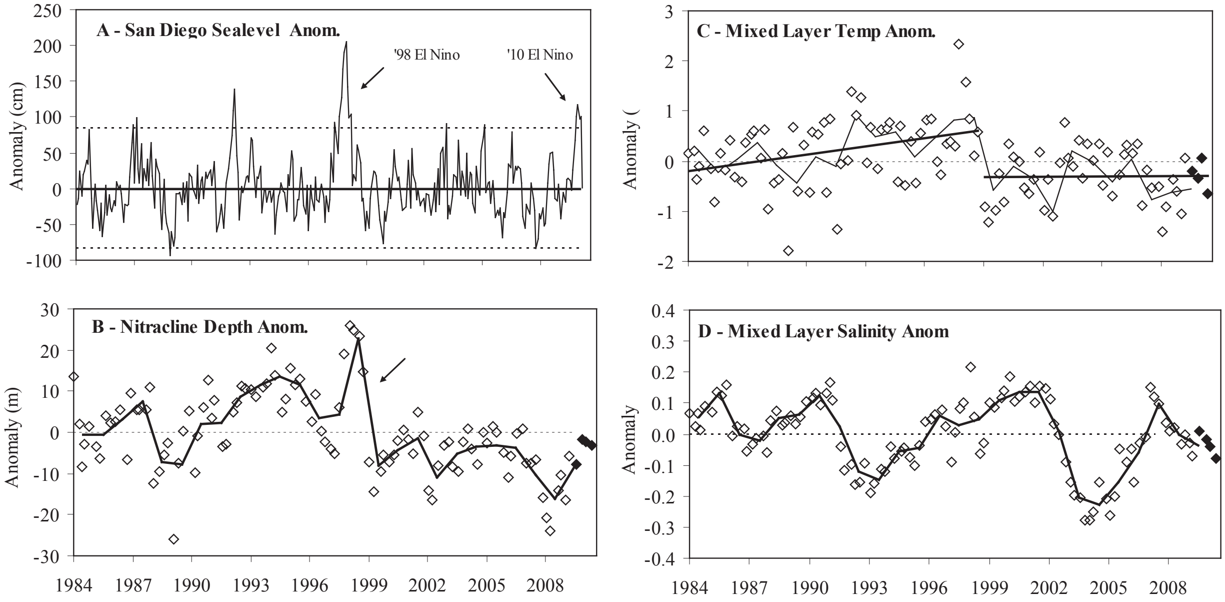

Figure 12. Anomalies of detrended San Diego sea level (A), nitracline depth (B), mixed layer (ML) temperature (C), and ML salinity (D) off Southern California (CalCOFI standard grid; fig. 10). Data from the last four CalCOFI cruises are plotted as solid symbols, data from previous cruises are plotted as open diamonds. The thin solid lines represent the annual averages, the dotted lines the climatological mean, which in the case of anomalies is zero and the straight solid lines long-term trends.

teristics coalesced into a coastal, poleward current north of Punta Eugenia (Durazo and Baumgartner 2002). In contrast, geostrophic circulation patterns in April 2009 and April 2010 were dominated by meandering equatorward flows.

Southern California – CalCOFI Surveys[12]

Sea level anomalies serve as useful indicators of local El Niño effects off southern California. The 2009–2010 El Niño started having an effect on local sea levels in the fall of 2009, reached its peak in late 2009 and by the spring of 2010 sea levels had receded to normal values (fig. 12a). Despite this clear signal of the El Niño event, no noticeable effects on mixed layer temperature or nitracline depth were observed (fig. 12b,c); values of both properties were close to their long-term means. Mixed layer salinity, which is not expected to be affected by ENSO, also was similar to long-term averages (fig. 12d).

Over the last year, temperatures and salinities at 200 m were slightly higher and lower, respectively, than long-term averages, similar to patterns observed during the 1997–1998 El Niño (fig. 13). However, these signals were driven by changing isopycnal depths (fig. 14) rather than changing properties on any isopycnal. Rather, in contrast to observations during the 1997–1998 El Niño, hydrographic and chemical properties did not change significantly at representative isopycnals during the 2009–2010 El Niño. Spatial patterns of isopycnal depth anomalies during the 2009–2010 El Niño were similar to those observed during 1997–1998, i.e. during the winter, deeper than normal isopycnal depths (positive anomalies), were observed primarily in the Southern California Bight (data not shown). In the spring, positive anomalies were primarily found in the offshore regions of the study area (data not shown). Averaged over the CalCOFI area, these spatial patterns contributed to the persistence of overall positive anomalies in isopycnal depth after the dissipation of El Niño conditions (fig. 14).

Temperature-salinity (TS) diagrams for different regions within the CalCOFI study area reflect these processes. During 2009, temperature and salinity differed from long-term averages only at intermediate depths. These patterns were consistent across all different regions of the study area (shown in Figure 15 for the edge of the central gyre, the southern California Current and the northern coastal region). The freshening of the thermocline at the edge of the Gyre, however, can not be attributed solely to the El Niño since a similar stratification was observed during 2008. This likely reflects the influence of the California Current which extended further offshore than usual (cf. McClatchie et al. 2009).

Nitracline depths in the CalCOFI area were similar to mean values observed since 1999. Thus, nitracline depth responded significantly to the La Niña conditions of 2007–2008 but not to the El Niño conditions of 2009–2010 (fig. 12b). Concentrations of nutrients in the mixed layer were likewise similar to long-term averages

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[12] Results are presented here as cruise averages over all 66 stations (fig. 1C) or as anomalies with respect to the 1984–2008 time series to augment ongoing time series of observations. Detailed descriptions of the cruises and methods used to collect data and analyze samples are given in previous reports and are available at http://www.calcofi.org.

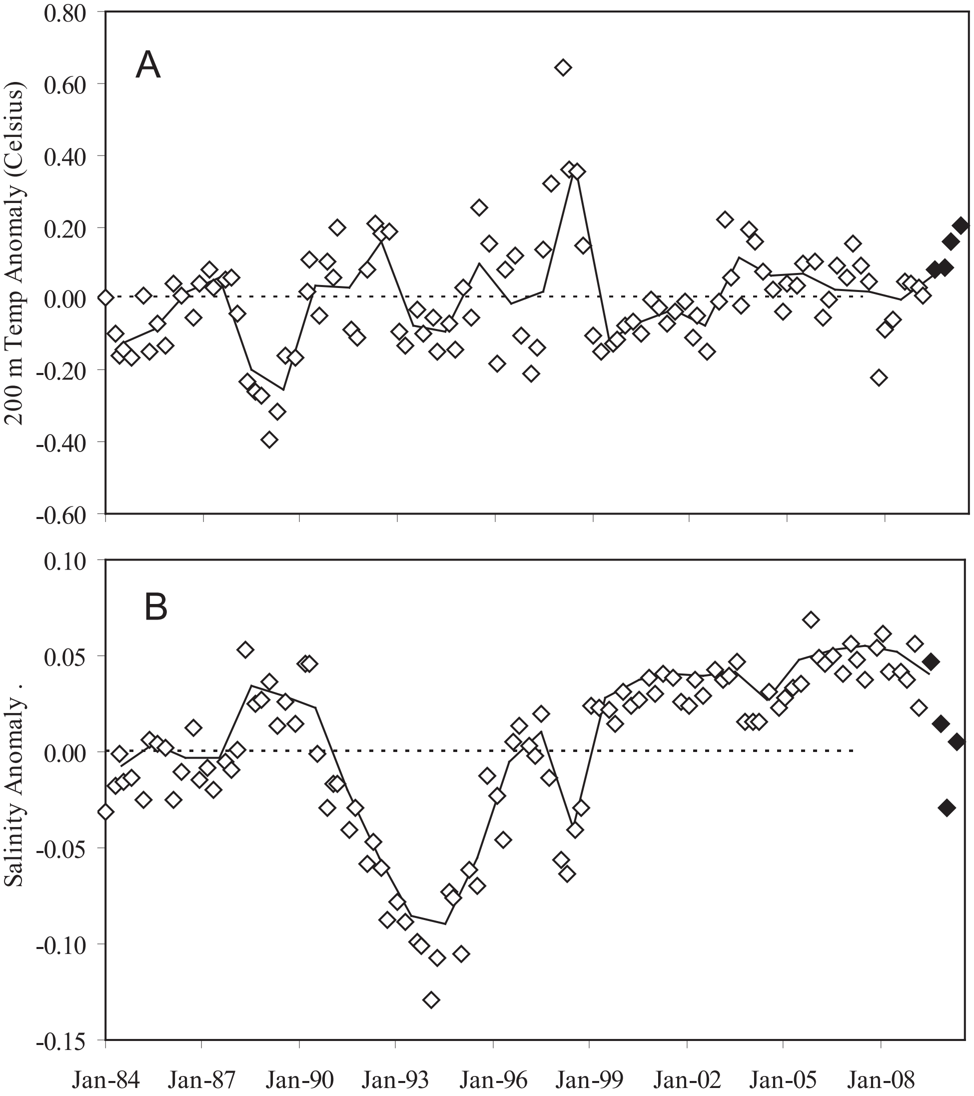

Figure 13. Anomalies of temperature (A) and salinity (B) at a depth of 200 m, calculated and presented as described at left for Figure 12.

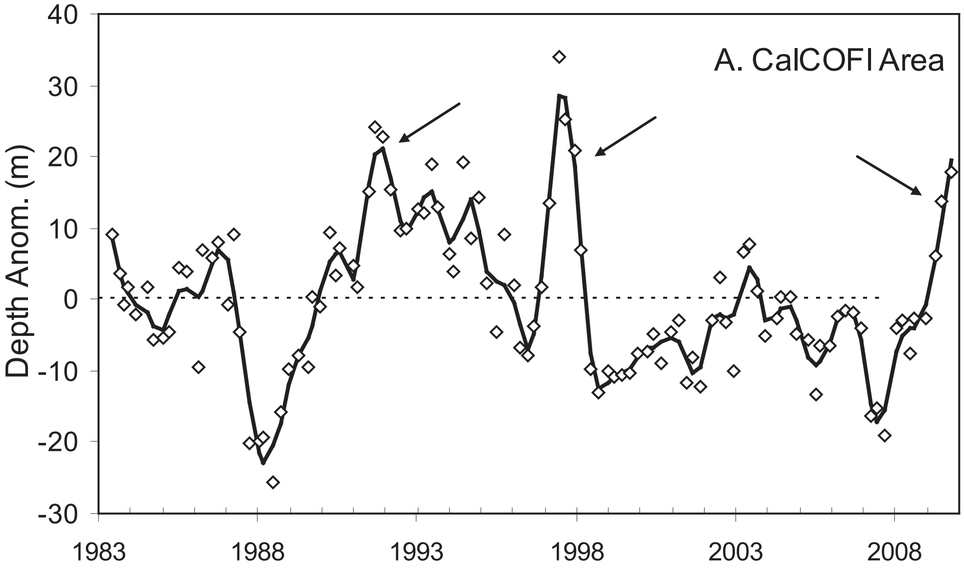

Figure 14. Depth anomalies of the σ_t 26.4 isopycnal calculated and presented as described at left for Figure 12. Arrows indicate the last three strong El Niños.

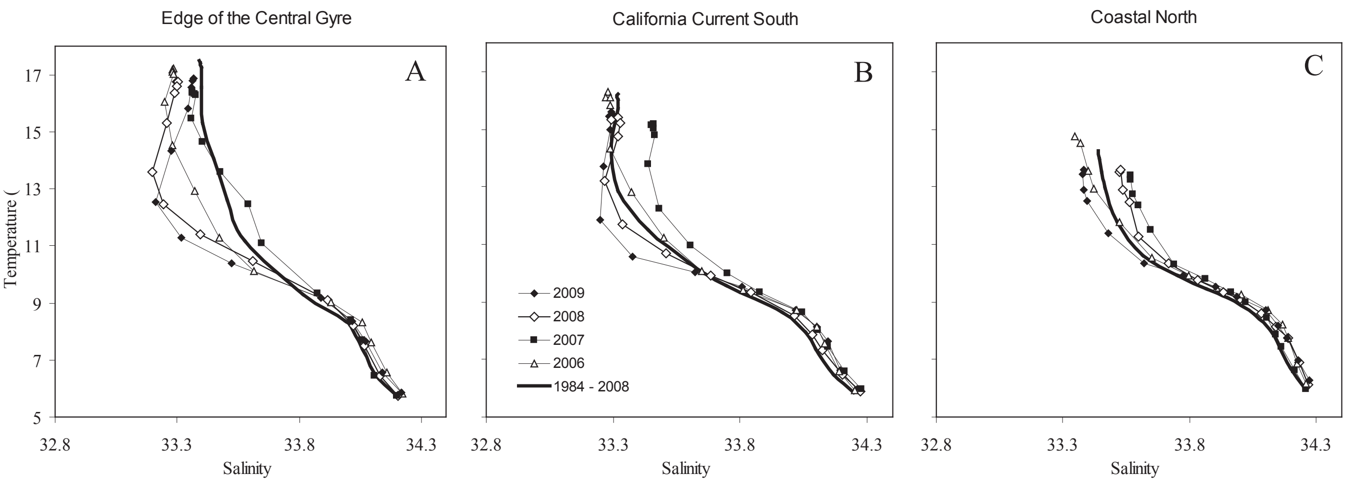

Figure 15. TS plots for three representative areas of the CalCOFI region. A. The edge of the central gyre (Lines 90–93, Stations 100–120), B. the southern California Current region (Lines 87–93, Stations 60–90) and C. the coastal areas in the north (Lines 77–80, Stations 60 and inshore). Each data point represents the average TS characteristic of one standard depth level for the specified time periods, i.e., 1984–2008, 2006, 2007, 2008 and 2009.

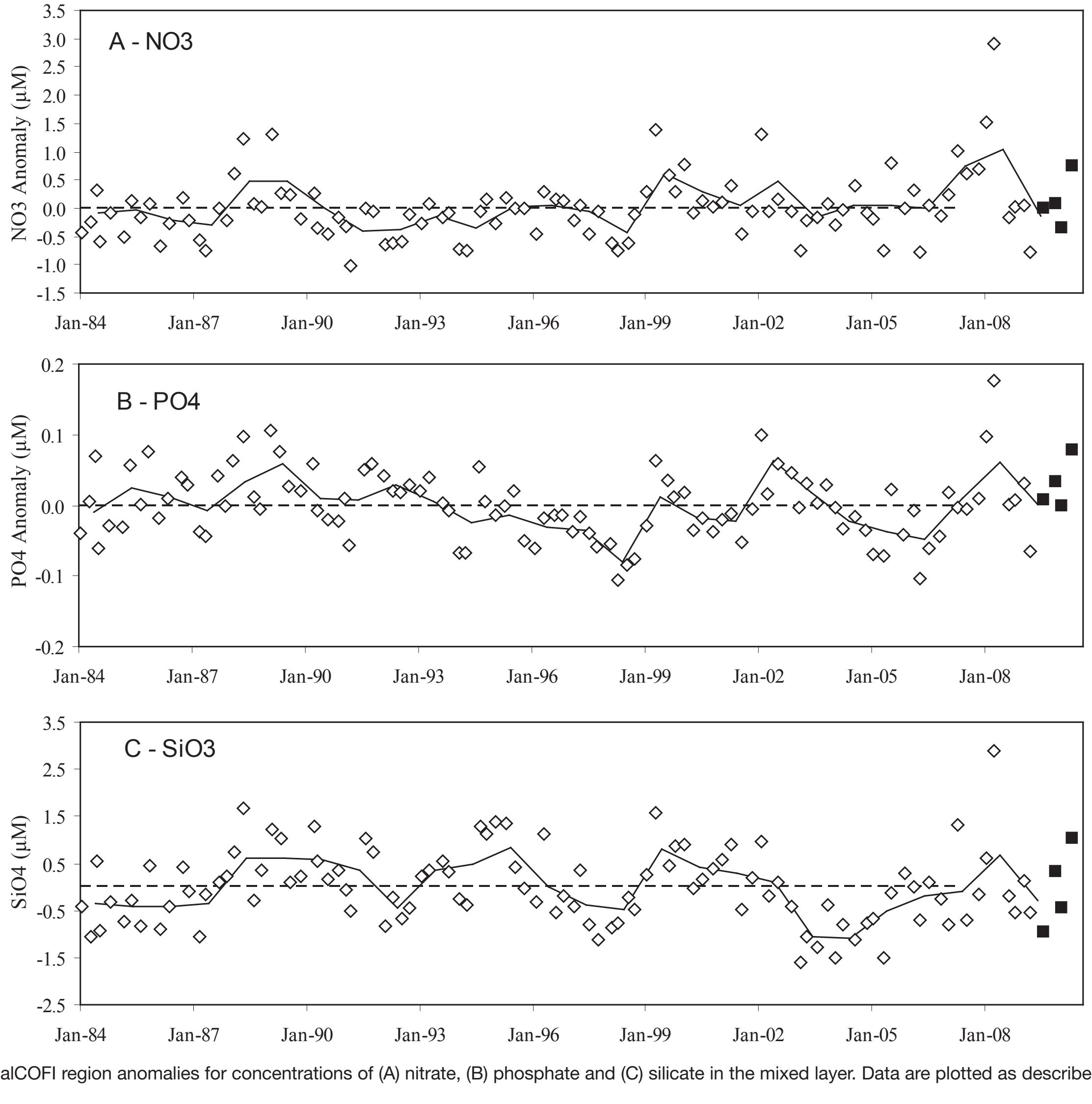

Figure 16. CalCOFI region anomalies for concentrations of (A) nitrate, (B) phosphate and (C) silicate in the mixed layer. Data are plotted as described in Figure 12.

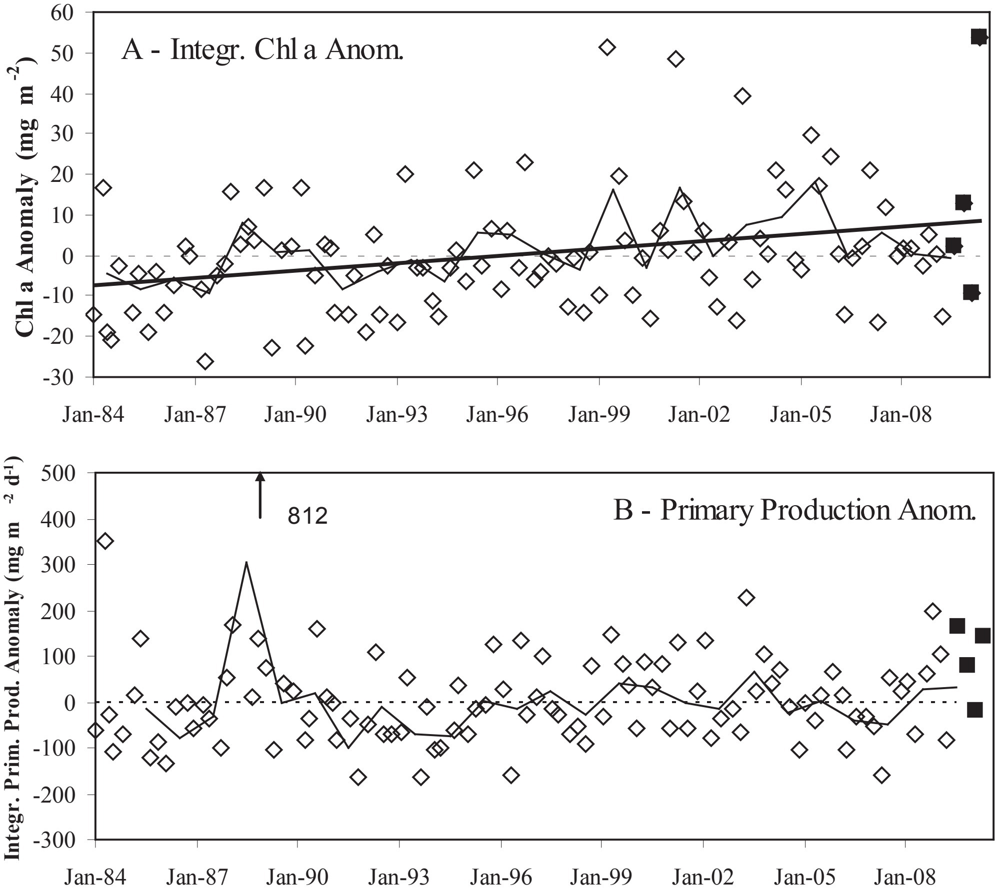

Figure 17. CalCOFI region averages for standing stocks of Chl *a* (A) and rates of primary production (B) both integrated to the bottom of the euphotic zone, plotted against time. Data and symbol codes are the same as those in Figure 13.

(fig. 16). The slightly elevated concentrations observed during the April/May 2010 cruise were due to strong upwelling observed west and southwest of Point Conception during the cruise. Strong upwelling also contributed to the very high chl a concentrations observed during the April/May 2010 cruise (fig. 17a), a signal primarily driven by enhanced phytoplankton growth in the coastal areas. Coincident observations of extremely low zooplankton displacement volumes southwest of Pt Conception on the April/May 2010 cruise are also likely to reflect the effects of transport associated with this upwelling event (data not shown). With the exception of those observed during the winter of 2009–2010, rates of primary production were slightly above long-term averages (fig. 17b).

Zooplankton displacement volumes over the past 12 months have been similar to long-term averages for the respective months (fig. 18a). Anomalies of zooplankton displacement volumes are consistent with the long-term trend of declining values observed since 1999 (fig. 18b). Spatial patterns in zooplankton displacement volume anomalies[13] suggest that recent trends of declining zooplankton displacement in the CalCOFI study area are due to trends of increasing zooplankton biomass in the offshore areas, declining biomass in the California Current regions and stable biomass in the Southern California Bight; this pattern continues to hold, with smaller average anomalies, in data from the past 12 months. What factors control zooplankton biomass in these different areas are currently not known.

Central California: Monterey Bay and Line 67[14]

The 2009 spring transition to upwelling conditions occurred in the later half of March at the surface in both temperature and salinity and seems to have been anticipated at 100 m. Anomalously cool, salty conditions in April and inconsistently May 2009 were somewhat cooler and saltier than normal, whereas summer

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[13] Anomalies of zooplankton displacement volumes are calculated relative to the base period 1984 to 2008.

[14] Data on temperature and salinity at the surface and 100 m for Monterey Bay are based on MBARI monthly cruises and mooring data. CalCOFI Line 67 was occupied three times in 2009 and twice so far in 2010; three of these occupations were regular CalCOFI cruises and the data have not been included here.

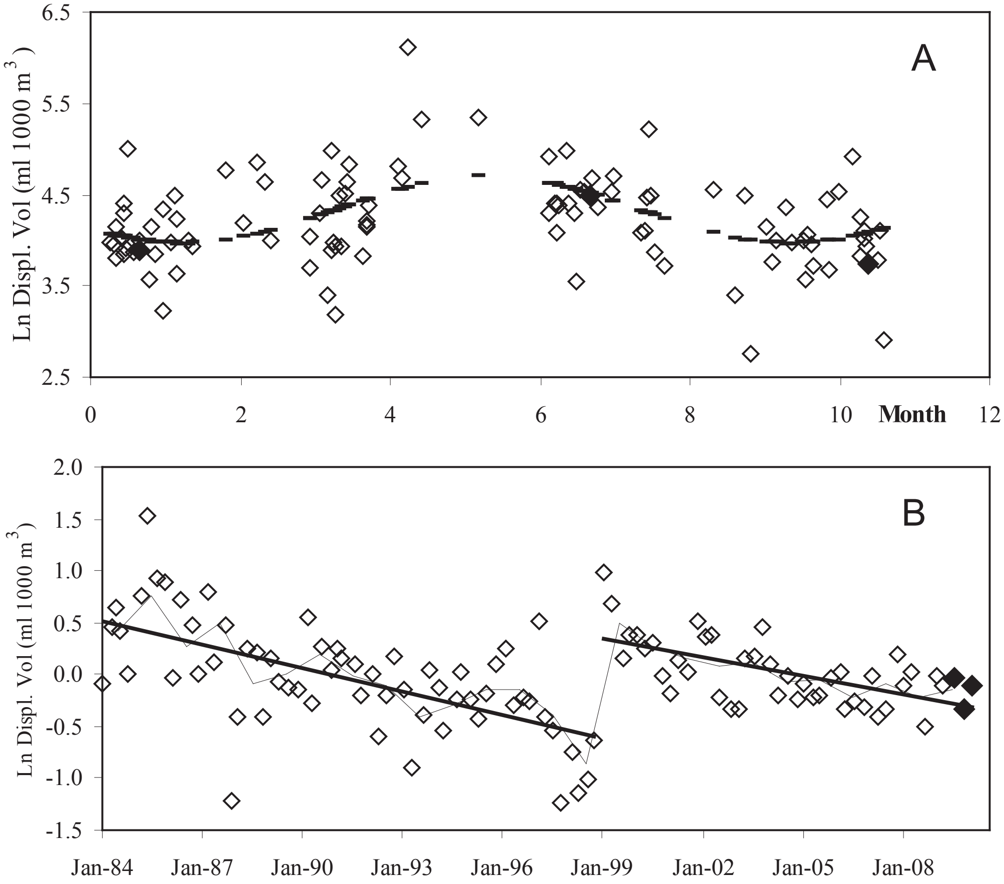

Figure 18. CalCOFI log cruise-mean macrozooplankton displacement volumes plotted against the month of the year (A) and time (B). Symbols are as described for Figure 12, except that data for cruise 2010-04 are not yet available. The dashed line in A is the harmonic fit to the data. Straight lines in B represent long term trends for the periods 1984 to 1998 and 1999 to 2009.

was close to climatology (fig. 6). In both 2009 and 2010, spring chl a[15] concentrations were lower than average, but 2009 summer chl a concentrations were close to climatology, although still lower than during the most recent 4–5 years (fig. 21). Five warm, fresh pulses were observed in the upper 100 m of the water column in winter 2009–2010, and the water column remained anomalously warm and fresh at the surface until the spring transition occurred in late April/early May (fig. 6). It appears, however, that the conditions began to return to normal earlier at depth: anomalies >2°C at 100 m had disappeared by early March 2010.

NORTHERN CALIFORNIA CURRENT

Newport Hydrographic Line

Observations along the Newport Hydrographic Line[16] reveal that bottom waters over the inner- to mid-shelf were on average warmer and fresher during summer 2009 than in the previous two summers (data averaged over May to September; fig. 19) and relatively fresh in fall 2009 (October to December; fig. 20) compared to recent fall conditions. Further offshore, mid-water salinity anomalies do not indicate any influx of subtropical water related to the El Niño event (fig. 22). Except for observations on two separate cruises (6 March 2009 and 19 March 2010), salinity anomalies were small during 2009 and early 2010, in contrast to the strong, sustained freshening observed during the 1997–1998 El Niño.

Monthly averaged values of copepod species richness off Oregon[17] continue to track the PDO and SST quite closely, with cold conditions dominated by a few sub-

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[15] Chlorophyll concentrations reported here are based on measurements at major stations (C1, H3, M1, 67–50, M2, 67–55) occupied at approximately 3 week intevals. The data have been averaged by day, gridded to 14 days, and smoothed with a 9-point moving average. Climatology is based on observations from 1990–2008.

[16] Regular sampling of the Newport Hydrographic (NH) line along 44.65°N continued on a biweekly basis along the inner portions of the line, at seven stations ranging from 1 to 25 nautical miles from shore. Details on sampling protcols are available in previous reports and at http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/ka-hydrography-zoo-ichthyoplankton.cfm. Temperature anomalies along the Newport line are based on the Smith et al. (2001) climatology.

[17] Samples were collected with a 0.5 m diameter ring net of 202 µm mesh, hauled from near the bottom to the sea surface. A TSK flowmeter was used to estimate distance towed.

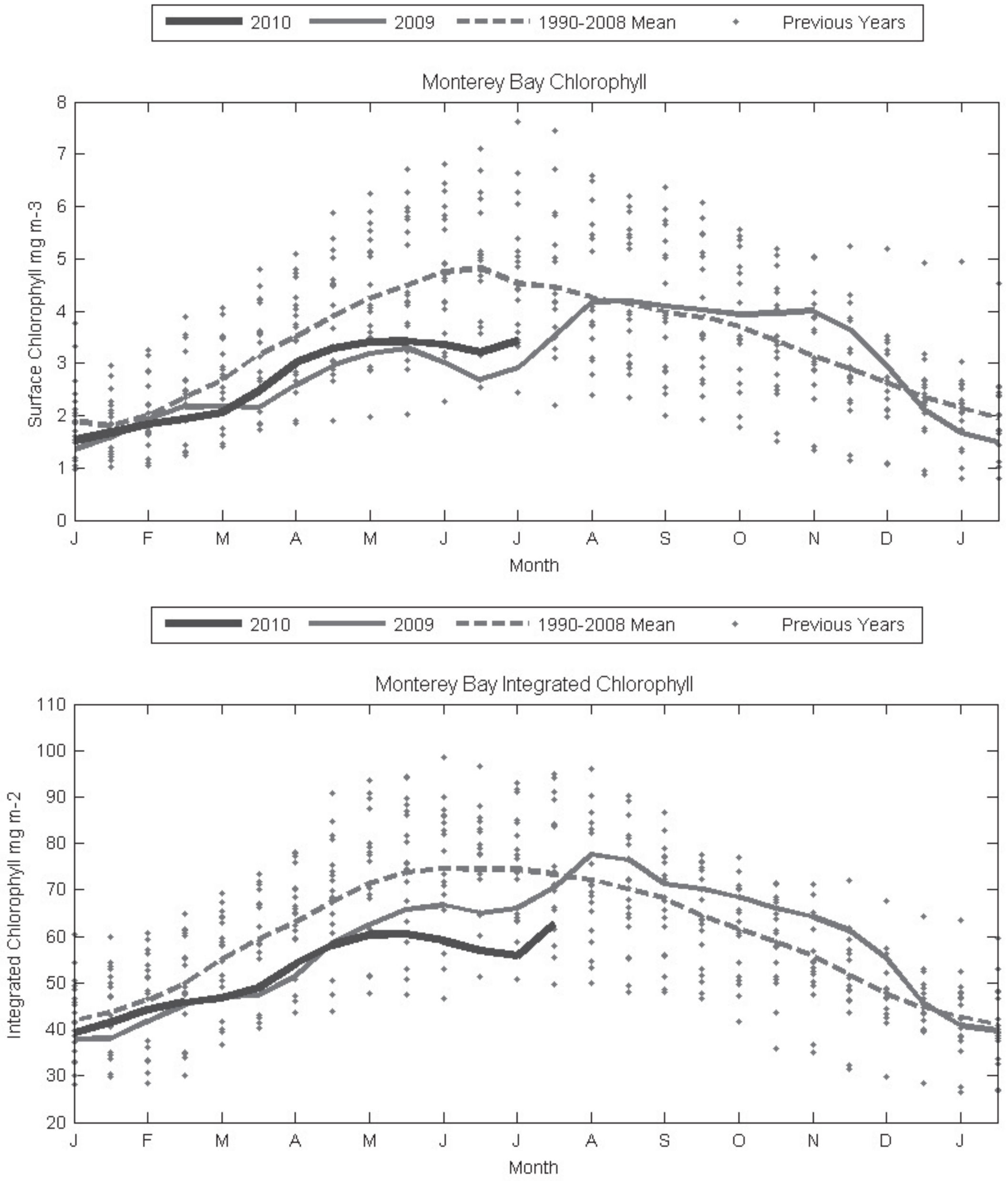

Figure 19. Surface (upper panel) and water column (lower panel) chlorophyll concentrations from Monterey Bay, California for 2009 and 2010 compared to the 1990–2008 seasonal mean.

arctic taxa and warmer conditions dominated by a more speciose subtropical assemblage (fig. 23). Moderately low species–richness values were observed during 2009 but not as low as during 2008. The winter and early spring of 2010 show anomalously high values of species richness, comparable to values observed during 1997–1998 El Niño and most of 2003 through 2006.

Trinidad Head Line[18]

Observations along the Trinidad Head Line indicate similar patterns to those reported above for the Newport Hydrographic Line. Specifically, available data show a greater degree of warming and freshening over the mid-shelf during winter in 2009–2010 than had been observed in the previous three winters, and indicate that warming of coastal waters began to develop in the late summer and early fall of 2009 and persisted until the transition to upwelling observed in April 2010. Salinity measurements at depths of 120–150 m at station TH04 (410 m depth) corroborate patterns in salinity observed over the slope off Oregon (data not shown).

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[18] Details on sampling protocols for the Trinidad Head Line are available in previous reports and at http://swfsc.noaa.gov/HSU-FisheriesOceanography.

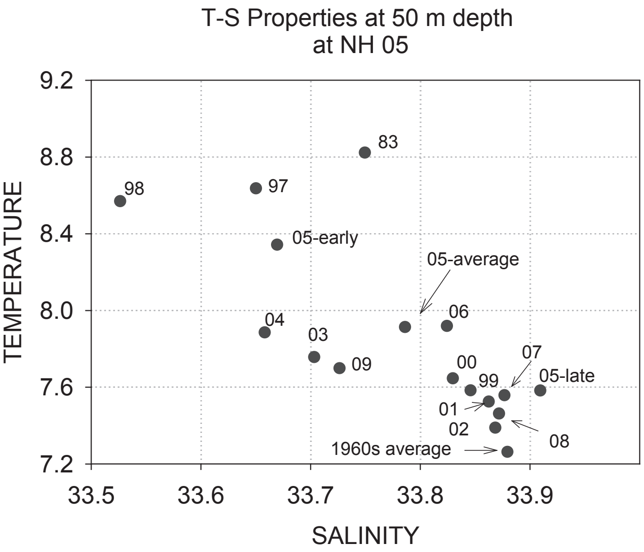

Figure 20. T-S characteristics at a depth of 50 m at a mid-shelf station (NH-05) off Newport OR, averaged over cruises in May through September.

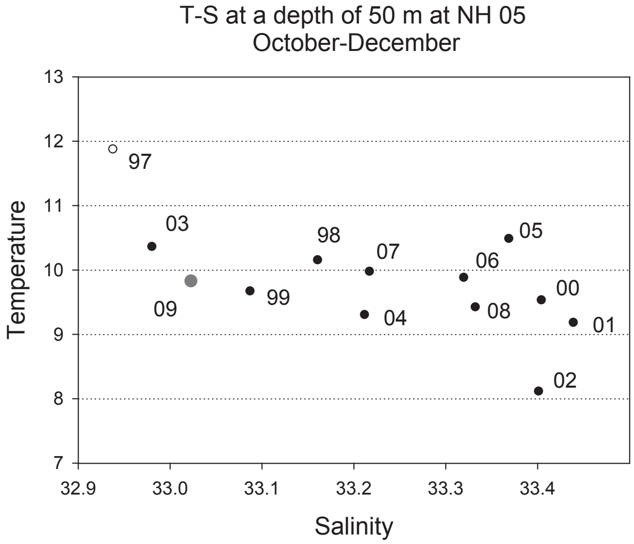

Figure 21. T-S characteristics at a depth of 50 m at a mid-shelf station (NH-05) off Newport OR, averaged over cruises in October through December of the year indicated. Autumn 2009 was characterized by the presence of relatively cool but fresh water, although temperature was similar to that observed in most other years.

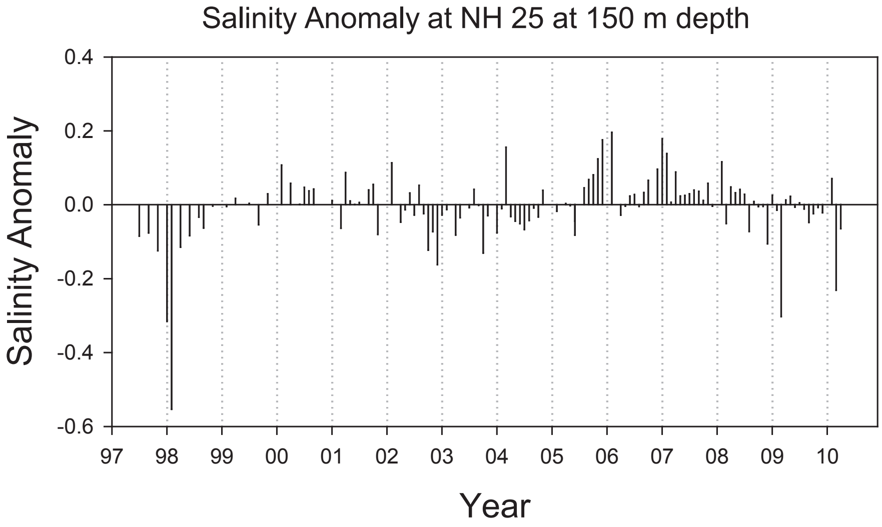

Figure 22. Time series of salinity anomalies at a depth of 150 m at a slope station, NH 25, 25 miles from shore in 300 m of water.

Comparison of copepod assemblages off northern California and Oregon. Copepod assemblages observed at mid-shelf stations off northern California[19] and Oregon continued to show marked seasonal variation, with high abundances developing over the summer and into the fall and subsequently declining over the winter (fig. 24). Total abundance of copepods over the shelf appears to have been lower or later in developing in summer 2009 than in 2008 in sampled areas of the northern CCS.

Patterns in assemblage structure, as indicated by the abundance of species particular biogeographic affinities (e.g., southern (warm) v. northern (cold), neritic v. oceanic; Hooff and Peterson 2006), show a substantial degree of coherence since 2008, particularly at stations north of Cape Mendocino. Compared to winter 2009, the composition of copepod assemblages off Oregon and northern California shifted strongly towards being dominated by southern and oceanic species by winter 2010 (fig. 23). Southern taxa were abundant off Bodega in late 2008, coincident with warm temperatures, but largely disappeared from mid-shelf waters in early 2009, possibly as a consequence of intense transport

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[19] Zooplankton samples were collected along the Trinidad Head Line and Bodega Line following protocols as implemented on the Newport line. Prior to October 2008, samples off Trinidad Head were collected using a 0.25 m PairoVET net fitted with 202 µm mesh and a General Oceanics flowmeter.

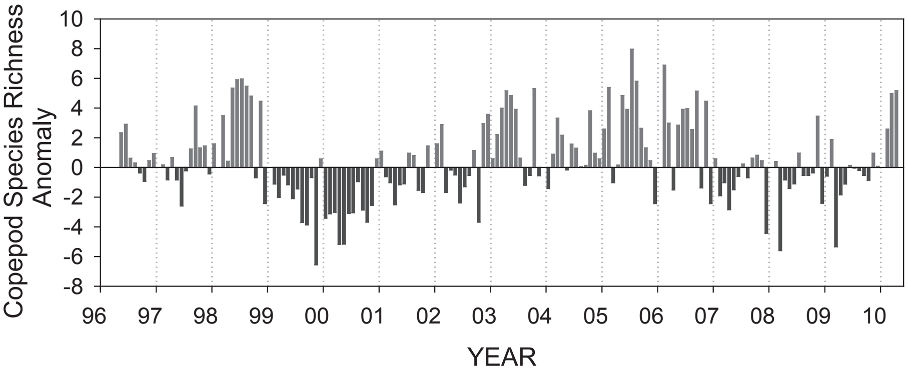

Figure 23. Monthly averaged copepod species richness anomalies at Station NH-5 off Newport, OR.

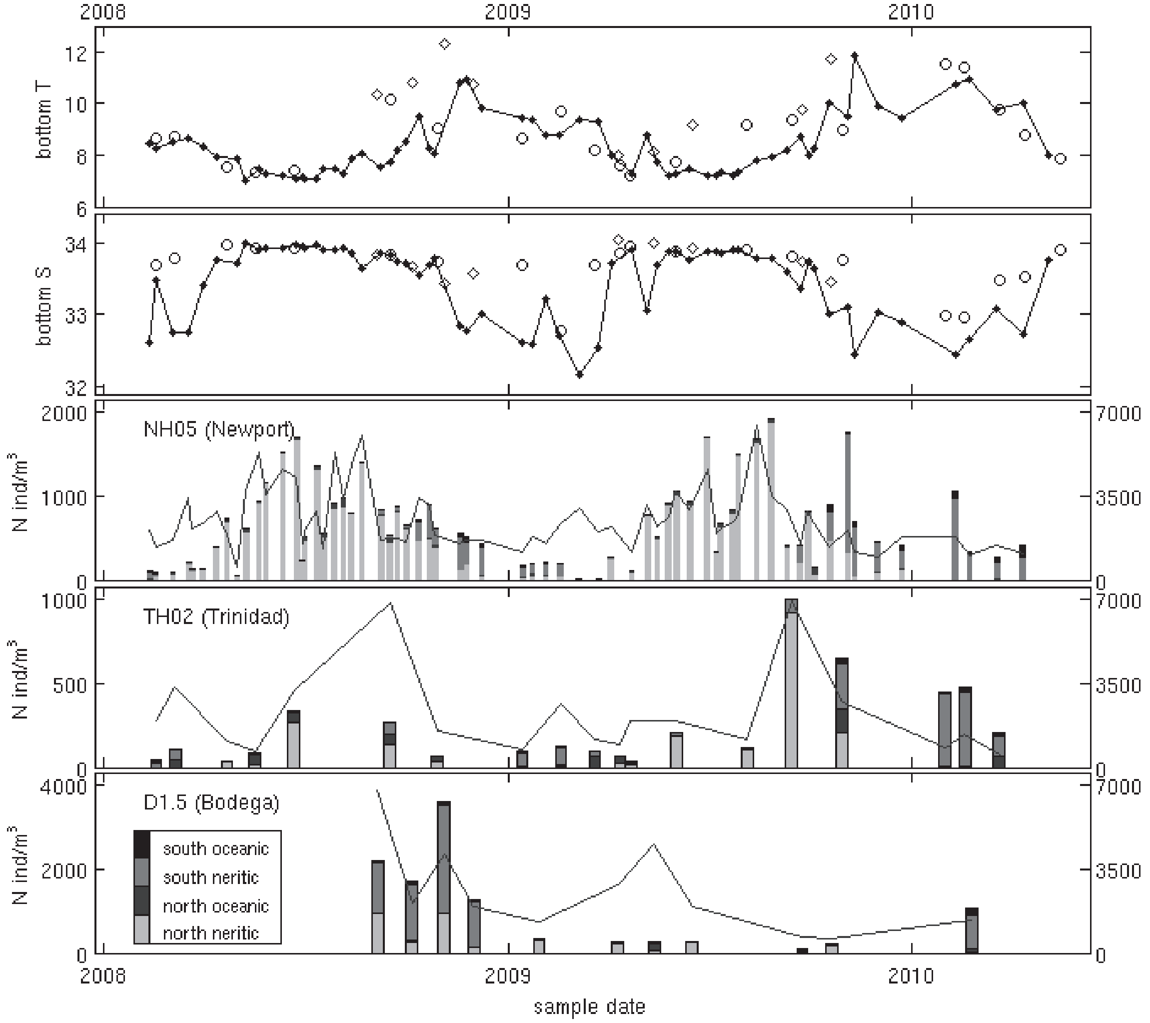

Figure 24. Top two panels: near-bottom temperature and salinity for stations NH05 (solid line with dots), TH02 (open circles), and D1.5 (open diamonds). Bottom three panels: copepod density in vertical ring-net samples collected at stations NH05 (Newport Line, 44.65°N, 124.18°W, 77 m), TH02 (Trinidad Head Line, 41.06°N, 124.27°W, 77 m) and D1.5 (Bodega Line, 38.29°N, 123.20°N, 83 m), respectively. Shaded bars (left hand y-axis) indicate density of selected species indiciative of assemblages identified in Hooff and Peterson (2006): northern neritic (*Calanus marshallae, Acartia longiremis, Acartia hudsonica, Centropages abdominalis*), northern oceanic (*Metridia pacifica, Microcalanus pusillus*), southern neritic (*Acartia tonsa, Ctenocalanus vanus, Paracalanus parvus, Corycaeus anglicus*), southern oceanic (*Acartia danae, Calanus pacificus, Clausocalanus spp, Eucalanus californicus*). Lines (right hand y-axis) indicate total copepod density.

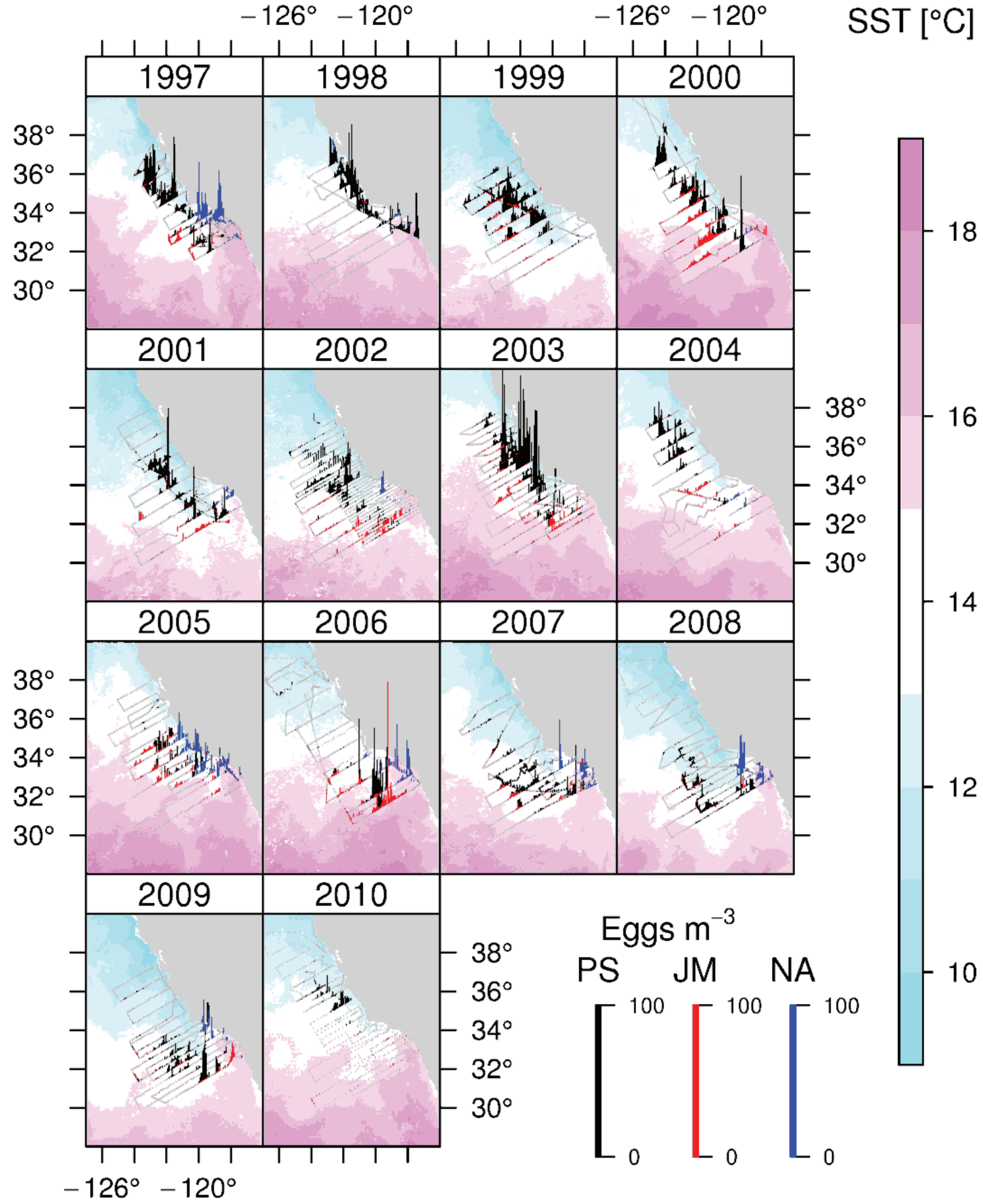

Figure 25. Density of eggs from Pacific sardine, northern anchovy and jack mackerel collected with CUFES (all on the same scale) overlaid on satellite SST derived from a monthly composite of April AVHRR Pathfinder imagery (1997–2008) and a blended SST product (2009–2010). PS = Pacific sardine (*Sardinops sagax*), JM = jack mackerel (*Trachurus symmetricus*), and NA = northern anchovy (*Engraulis mordax*).

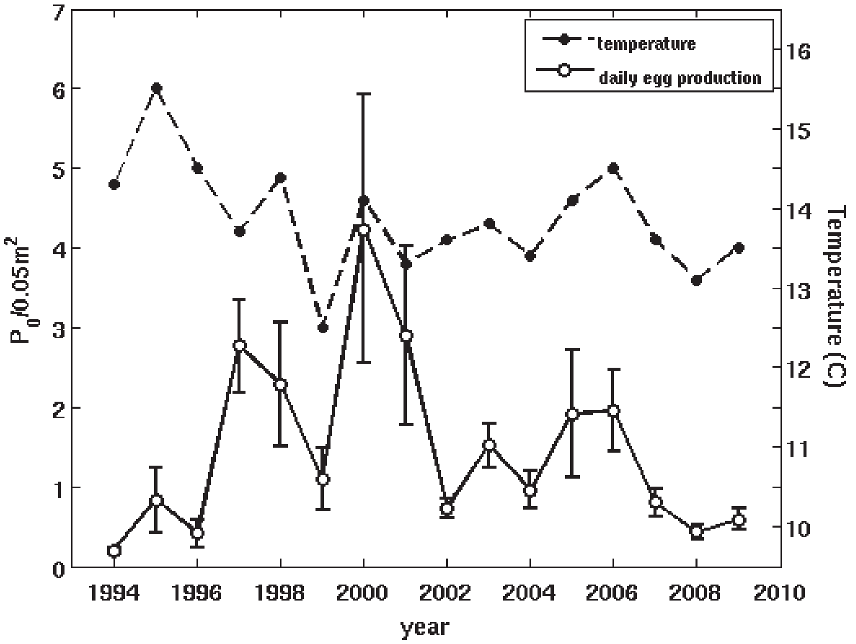

Figure 26. Daily egg production/0.05m^2 of Pacific sardine (open circles, solid line; error bars indicate +– 1 SE) and average SST (°C) (closed circles, dashed line) during March–April DEPM-CalCOFI cruises from 1994–2009.

(fig. 9). Although warm water and reduced flows were observed in summer 2009 off Bodega, total copepod abundance did not reach high abundances and southern taxa did not assume a dominant place in the assemblage until winter 2010.

ECOSYSTEM SURVEYS & HIGHER TROPHIC LEVELS

Small Pelagic Fish Spawning

The spatial distribution of sardine (*Sardinops sagax*) eggs with respect to sea surface temperature varies substantially from year to year in the CCS (fig. 25)[20]. In 2009, the concentration of sardine eggs off southern California indicated that the spawning ground was similar to 2006–2008 when the distribution of sardine spawning was almost entirely restricted to latitudes south of Point Conception (Lo et al. 2007a, 2007b, 2008; McClatchie et al. 2009). By contrast, in 2010 the distribution of sardine spawning was similar to 2004, being well north of Point Conception. The early part of the time series shows sardine spawning at latitudes from San Diego to San Francisco. Northerly extension of sardine spawning out of the Southern California Bight to along the central California coast does not appear to be consistently related to variation in temperature. Qualitative examination of sardine egg distributions suggests that 5 of 8 anomalously warm years (1998, 2000, 2003, 2004 and 2010) showed northern extension of sardine spawning; the remaining 3 years (1997, 2005, 2006) were ambiguous or contradicted the expected pattern (fig. 25).

Spawning grounds of northern anchovy (*Engraulis mordax*) and jack mackerel (*Trachurus symmetricus*) also exhibit substantial variation over time as indicated by the spatial distribution of their eggs (fig. 25). In spring 2009, anchovy eggs appeared to be concentrated in the Southern California Bight, and in spring 2010, anchovy eggs were nearly absent from the study region (fig. 25). These patterns contrast sharply with the broader extent of anchovy spawning grounds observed in 2005–2008 (fig. 25). In spring 2009, jack mackerel eggs were broadly distributed throughout the southwestern area of the survey at low densities, showed an unusual degree of overlap with the distribution of sardine eggs, and occurred in high densities inshore of the sardine spawning grounds in the southern portion of the survey region (fig. 25). The latter pattern was also observed in 2000, and substantial overlap between sardine and jack mackerel spawning also occurred in 2005,

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[20] During spring cruises from 1997–2010 fish eggs were collected from 3 m depth with the Continuous Underway Fish Egg Sampler (CUFES), manually identified and counted, and converted to densities (eggs m^{-3}). Temperature anomalies were calculated from monthly composites of April SST for each year using AVHRR Pathfinder v5 (4.4km resolution) for the years 1997–2008, and a blended SST product (0.1° resolution) for 2009 and 2010. The imagery were gridded to the same resolution (Weber and McClatchie 2009), and an SST anomaly at each pixel location was calculated by subtracting the monthly mean of all years at each location from the monthly mean for each year at that location. We overlaid densities of sardine, anchovy and jack mackerel eggs on both the SST and the SST anomalies.

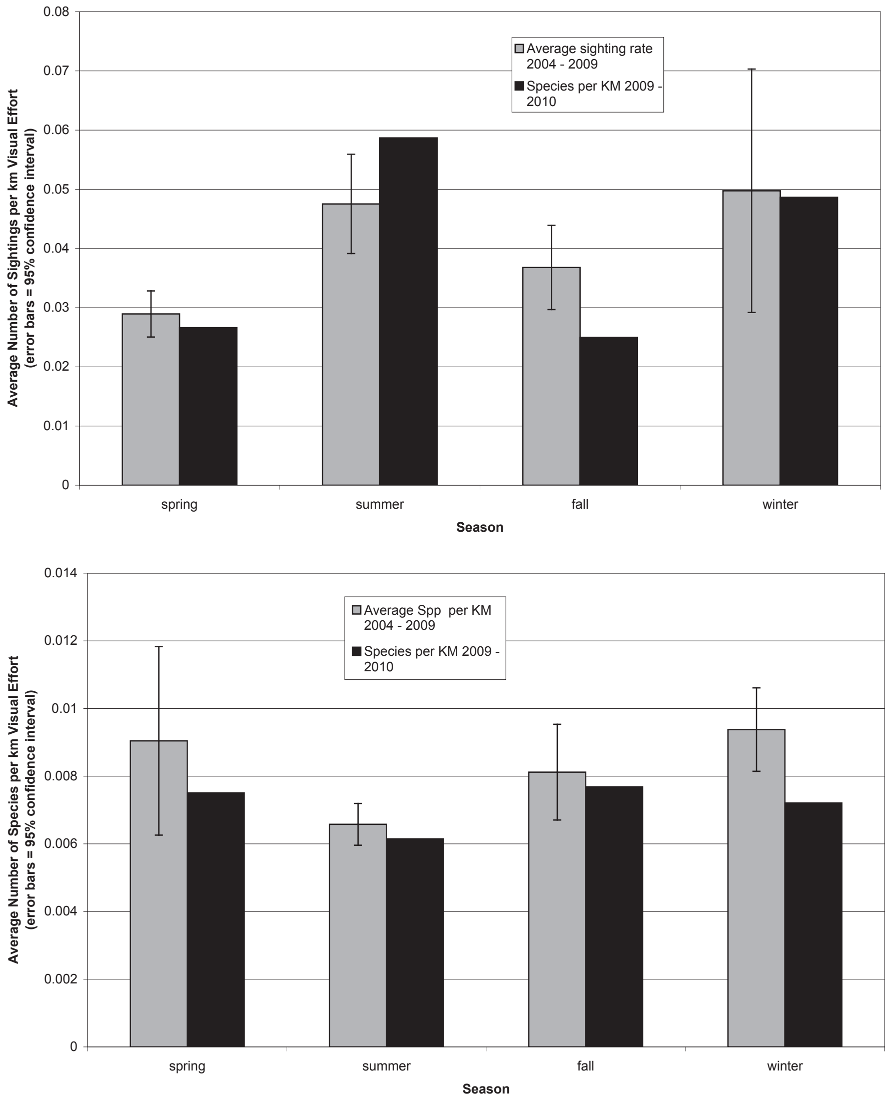

Figure 27. Comparison of the average sighting rates (top panel) and average species richness (bottom panel) for July 2004–January 2009 (grey) and for Spring 2009–Winter 2010 (black). Error bars indicate 95% confidence interval.

2007, and 2008. Jack mackerel eggs occurred only south of Point Conception in 2010.

These patterns need to be quantified for all three species, but pose possible challenges to three commonly held views. Specifically, these data suggest that sardine spawning does not necessarily shift northwards in warmer years, that anchovy spawning is not always associated with coastal upwelling areas, and that jack mackerel do not always spawn further offshore than sardine.

Based on analysis of data and samples from the 2009 survey, estimated daily egg production rates suggest a slight increase in 2009[21], coincident with overall warmer temperatures than the preceding year (fig. 26). The relationship between sea surface temperature and changes in estimated daily egg production rates remained consistent over the period 1994 to 2009, with the exception of 1997 and 2002. Given that the spawning biomass of Pacific sardine is positively related to the daily egg production, in particular if the number of oocytes per biomass weight remains constant (Lo et al. 2009), estimated daily egg production rates suggest that spawning biomass of Pacific sardines is presently at relative low levels compared to recent historical estimates (fig. 26). The extent of spawning south of San Diego depends on the local environmental conditions (Baumgartner et al. 2008) and will not be known until

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[21] In 2009, the spring CalCOFI cruise was conducted from March 7–22, 2009, and so estimates of daily egg production of Pacific sardines were estimated using only data from the April 15–May 9 2009 sardine biomass survey. Sardine eggs were collected aboard the chartered fishing vessel F/V *Frosti* using CalVET, CUFES, and Bongo nets during the April 15–May 9 2009 sardine biomass survey. The survey was conducted south of San Francisco down to San Diego (CalCOFI lines 63.3 to 95.0) and extended offshore to CalCOFI station 90 and 100 in the areas north and south of Point Conception, respectively (fig. 1).

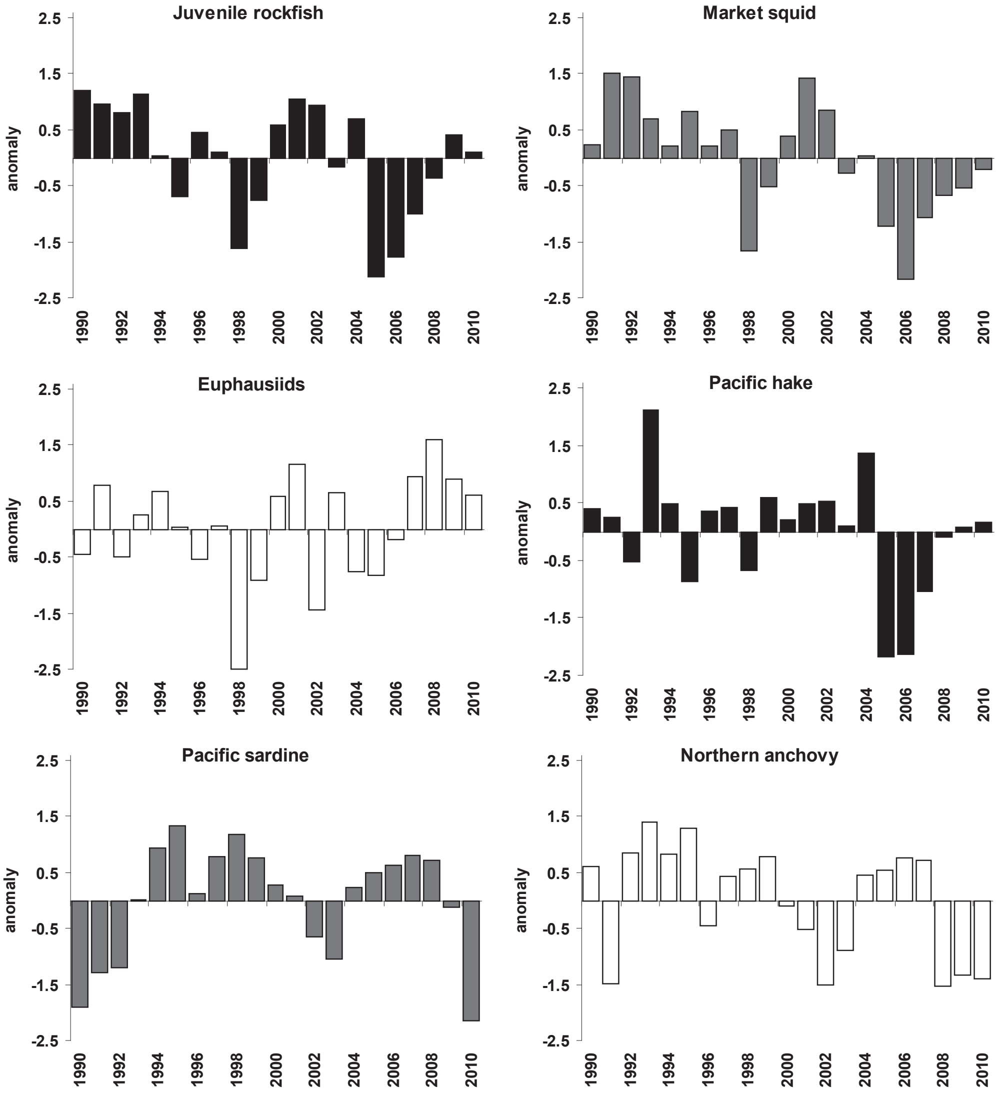

Figure 28. Long-term standardized anomalies of several of the most frequently encountered pelagic forage species from the central California rockfish recruitment survey in the core region (1990–2010 period only).

information from Mexican surveys, i.e. IMECOCAL becomes available for recent years. To update previous reports, we note that analysis of CUFES samples collected during IMECOCAL survey 0804 suggests that little sardine spawning occurred in the IMECOCAL area in April 2008.

Southern California Cetaceans

Visual surveys[22] for cetaceans on quarterly CalCOFI cruises did not detect changes in the cetacean assemblage off southern California. Species richness (average number of species per km of effort) of cetaceans observed on all four cruises for 2009–2010 was similar to richness in all previous years (not shown); however, species richness observed during the winter 2010 cruise was lower than in previous winters despite a relatively high sighting rate (fig. 27). For most species, 2009–2010 was not unusual. Relative to other cetaceans, Dall's porpoise (*Phocoenoides dalli*), which is generally restricted to cold/temperate waters, were abundant in the spring 2009 and winter 2010 cruises. During the summer cruise we observed remarkably high numbers of blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales, and common (*Delphinus* spp.), striped (*Stenella coeruleoalba*) and bottlenose (*Tursiops truncatus*) dolphins. Northern right whale dolphins (*Lissodelphis borealis*), gray whales (*Eschrichtius robustus*) and sperm

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[22] Marine mammal surveys have been carried out as part of quarterly Southern California CalCOFI cruises since 2004. Methods are standard across years: two trained marine mammal observers use binoculars (7X and 18–25X) and the naked eye to scan the area forward of the ship's beam for marine mammals during daylight hours while the ship is underway (~10 km). Opportunistic sighting data are also recorded.

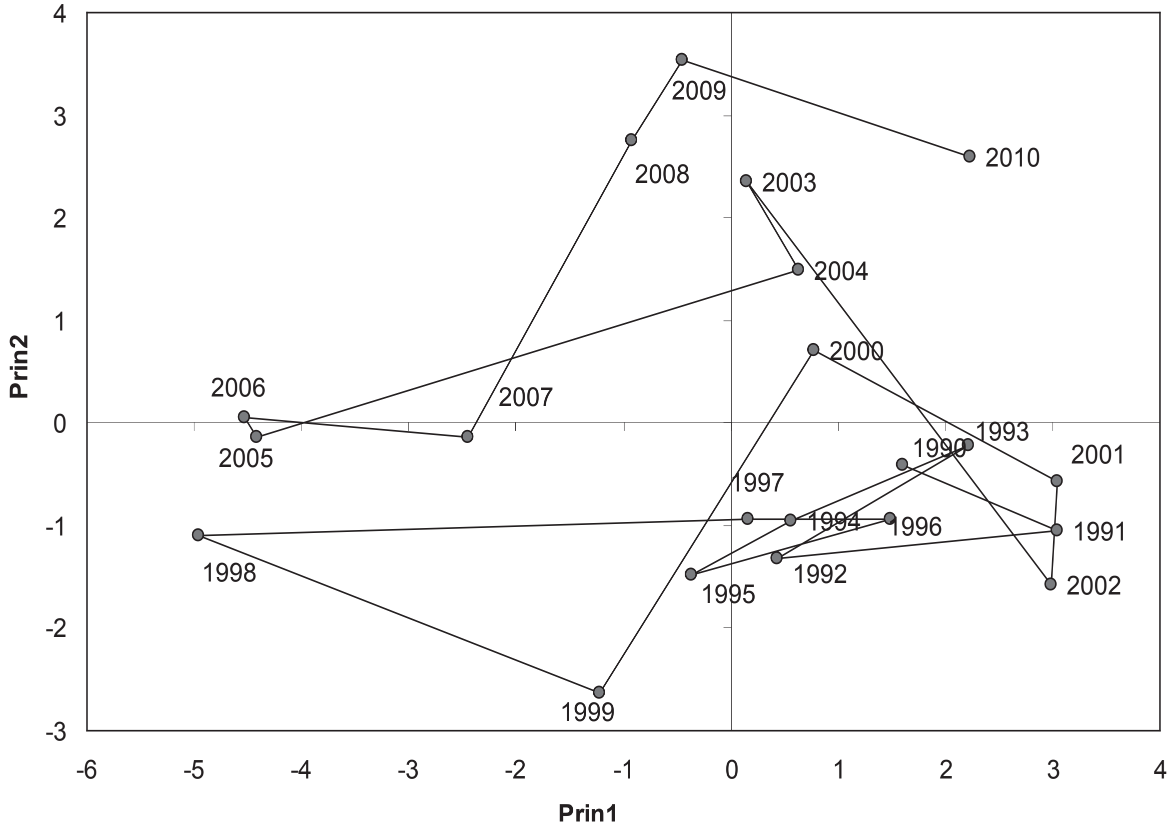

Figure 29. Phase plot of first two principal component scores for the fifteen most frequently encountered species groups captured between 1990 and 2010 in the core area of the Fisheries Ecology Division Midwater Trawl Survey off central California.

whales (*Physeter macrocephalus*) were unusually abundant during the winter 2010 cruise.

Central California Pelagic Ecosystem

Analysis of catch composition and abundance of key taxa from annual mid-water trawl surveys off central California[23] indicated that trends in 2009 and 2010 were of increasing abundance for the species and assemblages that tend to do better with cool, productive conditions, including juvenile rockfish, juvenile Pacific hake, market squid and krill (fig. 28). However, while the trend in relative abundance for rockfish and squid has been increasing since record low values in the 2005–2006 period, this increase has been only to levels close to the long term mean, and has not continued into 2010 for all taxa (fig. 28). Of the taxa favored by cool conditions, only krill appear to have recovered strongly, with very high catches in recent years. By contrast, the coastal pelagic forage species (adult life history stages of northern anchovy and Pacific sardine) typically observed in greater numbers during warmer, less productive periods were at low levels in 2009 and 2010, either as a result of lower abundance, a more offshore or southerly distribution, or both (fig. 28).

Trends observed in these six indicators are consistent with trends across a number of other taxa within this region. Results from a Principal Components Analysis of annual catch data[24] highlight changes in the midwater assemblage over time: the clupeoid-mesopelagic group was prominent during the 1998 El Niño and during the anomalously warm years 2005–2007, while the groundfish group prospered during the early 1990s, the cool-phase between 1999 and 2003, and most recently from 2009 through 2010 (fig. 29). As with the 2009 data, results from 2010 continue to represent a return towards

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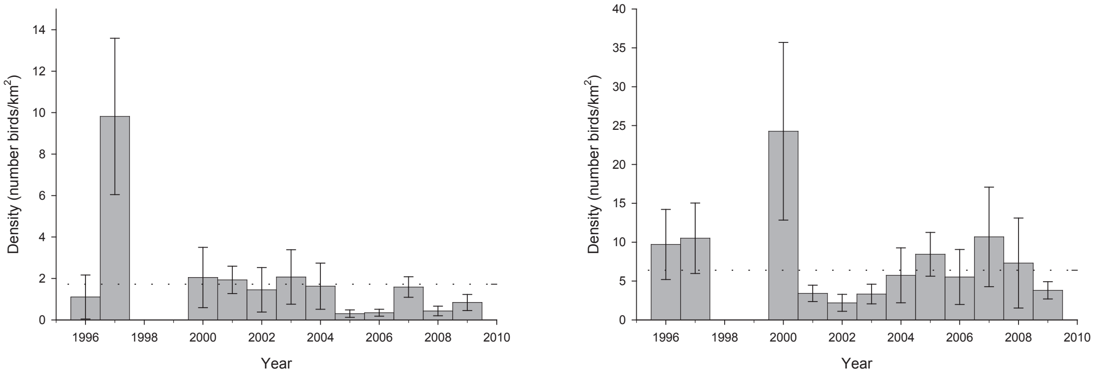
[23] Observations reported here are based on midwater trawl surveys conducted off central California (a region running from just south of Monterey Bay to just north of Point Reyes, CA, and about 60 km offshore) since 1990 (see Sakuma et al. 2006 for methods and details on spatial extent of survey). Most cruises have been conducted on the NOAA ship *David Starr Jordan* (1990–2008), the NOAA Ship *Miller Freeman* (2009) and the 2010 cruise took place on the F/V *Frosti* (2010). Data for the 2010 survey presented here are preliminary, and neither 2009 nor 2010 data account for potential vessel-related differences in catchability. Data are reported as standardized anomalies from the log of mean catch rates. Most taxa reported are considered to be well sampled, but the survey was not designed to accurately sample krill.

[24] Principal Components Analysis (PCA) was applied to the covariance among fifteen of the most frequently encountered species and species groups, yielding strong loadings for various young-of-the-year groundfish taxa (rockfish, Pacific hake, rex sole and sanddabs), cephalopods, and euphausiids, with slightly weaker (and inverse) loadings for Pacific sardine, northern anchovy, and several species of mesopelagic fishes. The first and second components explain 39% and 14% of the variance in the data respectively.

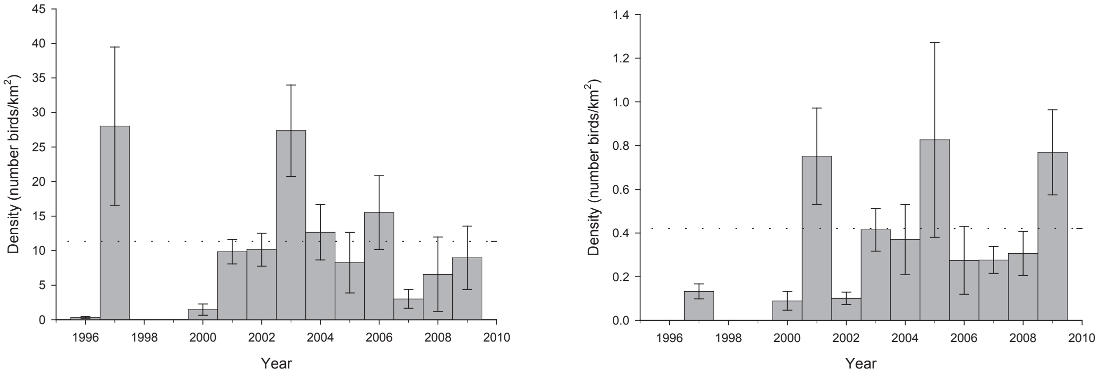
a) Cassin's Auklet density

b) Common Murre density



c) Sooty Shearwater density

d) Pink-footed Shearwater density



e) Density, all species

f) Density anomaly, all species

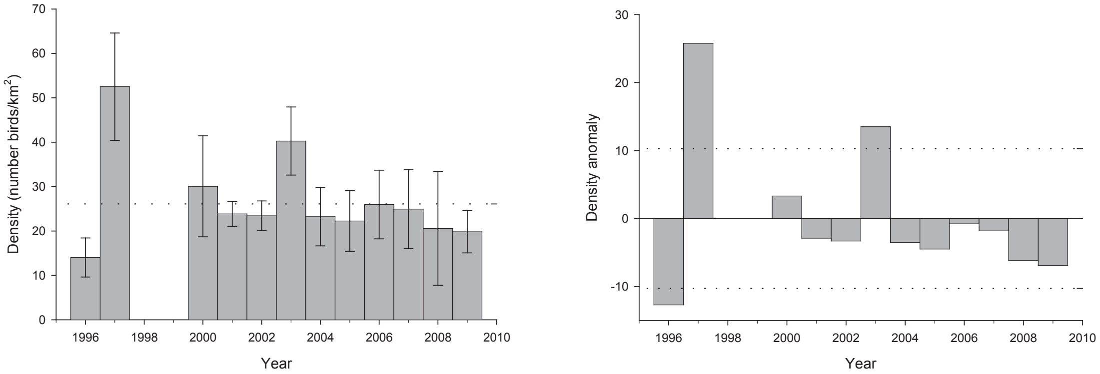


Figure 30. Variation in density of seabirds in the greater Gulf of the Farallones region (Pt. Sur to Pt. Arena), May–June, 1996–2009. Annual mean at-sea density (birds km^{-2} day^{-1}) of (a) Cassin's auklet, (bb) common murre, (c) sooty shearwater, (d) pink-footed shearwater and (e) combined avifauna, and (f) anomaly for combined avifauna of 'all species' (a), and anomaly in annual mean at-sea density (birds m^{-2} day^{-1}) of all species (b), CAAU (c), COMU (d), SOSH (e), and PFSH (f) are illustrated. Dashed lines in (a–f) show the long-term average density for each species and the overall seabird community.

conditions similar to the 1999 to 2003 period for many groups, while others are at moderate levels that approximate long term mean conditions.

Seabirds Off North-Central California

Analysis of at-sea counts of seabirds off central California[25] indicated significantly greater densities of pink-footed shearwater (*Puffinus creatopus*) in 2009 than in the previous three years (fig. 30). Pink-footed shearwater tend to be associated with warmer water, which suggests that this increase may be associated with warming of surface waters observed in summer 2009. Trends in at-sea counts of other seabirds (fig. 30) corroborate observations made at breeding colonies on the Farallon

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[25] In conjunction the NOAA NMFS mid-water trawl survey, seabirds are are identified and enumerated as they enter a 300-m arc from the bow to 90° amidships while the vessel is underway at speeds >5 k per standard techniques (Tasker et al. 1984). Here, we report on seabird counts made in May and June of 1996–1997 and 2000–2009 for a "core" area between Point Sur (36° 18'N, 121° 53'W) and Point Arena (38° 57'N, 123° 44'W). Seabird counts are expressed as a density function per day (birds km^{-2} day^{-1}) and each day is considered the sampling unit.

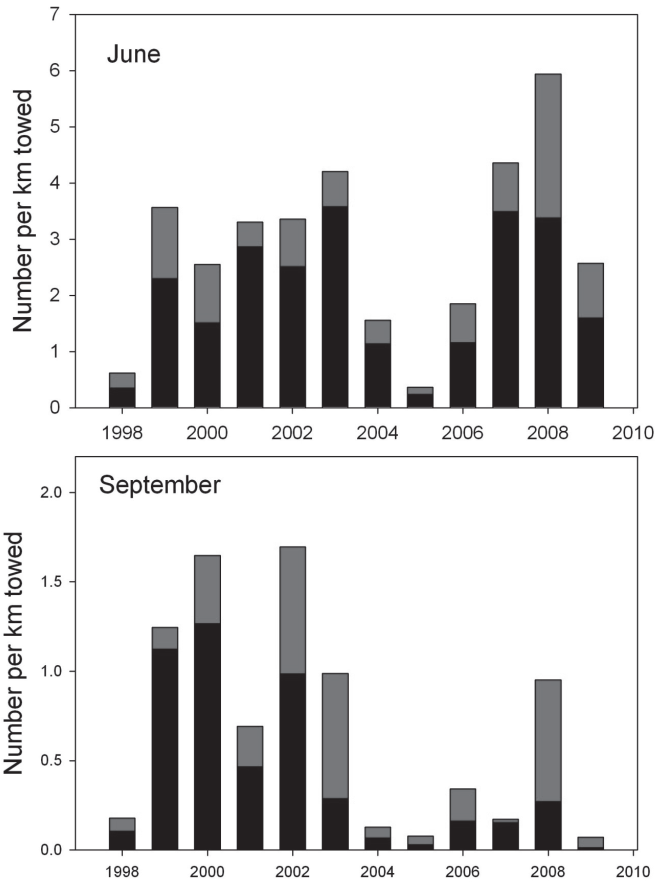

Figure 31. Average catches per unit effort of juvenile salmon partitioned among coho salmon (*Oncorhynchus kisutch* in black) and Chinook (*O. tshawytscha* in red) during June (upper panel) and September (lower panel) trawl surveys off the coast of Washington and Oregon from 1998 to 2009.

Islands (e.g., for murres and auklets; Warzybok and Bradley 2009), and support conclusions that abundance of sooty shearwaters has declined as has been observed for many years off southern California (Hyrenbach and Veit 2003; Sydeman et al. 2009) and more recently in central-northern California (Ainley and Hyrenbach 2010).

Breeding success of seabirds roosting on the Farallon Islands was mixed across species, with some species showing average to above average productivity while others showing diminished productivity and even complete failure in breeding (Warzybok and Bradley 2009). The breeding success of common murre (*Uria aalgae*) and Brandt's cormorant (*Phalacrocorax pennicillatus*) was essentially zero for 2009 (Warzybok and Bradley 2009). Interestingly, Brandt's cormorant breeding success was also near zero in 2008, a year of strong upwelling and cold SST (Warzybok and Bradley 2009). In both of these years, the abundance of northern anchovy (*Engraulis mordax*) was greatly reduced (fig. 28), which may have contributed to the cormorants' poor productivity. Thus, the decline in breeding success of Brandt's cormorant in 2009 may not have been related to the impending ENSO event, but rather factors that began to impact the birds in a previous year or during a time of the year well before any manifestation of El Niño was apparent off central California. In contrast, breeding success of Cassin's auklets (*Ptychoramphus aleuticus*) in 2009 was well above average (Warzybok and Bradley 2009). Hydroacoustic surveys in the greater Gulf of the Farallones indicated relatively high abundances of krill in the region (data not shown, but see fig. 28), which may have contributed to auklet breeding success.

Juvenile Salmon and Other Pelagic Fishes Off Oregon and Washington

Catches of juvenile salmonids in pelagic surface trawl surveys[26] were unusually low during September 2009. The fewest juvenile coho salmon (*Oncorhynchus kisutch*; 2 compared to maximum catch of 158 in 1999) and subyearling Chinook salmon (*O. tschawytschwa*; 2 versus 465 in 2001) were caught since the beginning of the time series in 1998 (fig. 31). Overall spring 2009 appeared to be relatively good for salmon marine survival but oceanographic conditions appear to have deteriorated for salmon by late summer 2009.

In 2009, annual average forage fish densities[27] off the Columbia River and Willapa Bay were the highest since 2005 (fig. 32). Northern anchovy (*Engraulis mordax*) and whitebait smelt (*Allosmerus elongates*) densities were the highest since 2004 which indicates successful recruitment in 2008. Pacific sardine (*Sardinops sagax*) and Pacific herring (*Clupea pallasi*) also made up a substantial portion of the catch. Overall forage fish densities were higher in 2009 than observed in 1998, 1999, 2006, 2007, and 2008 but still much lower from their very high abundance years 2000–2005.

In contrast, annual average predatory fish densities in 2009 were the lowest observed during the 12 year study period, in part because the abundant juvenile (yearling) Pacific hake (*Merluccius productus*) were too young to be counted as piscivores (fig. 32). Adult Pacific hake and jack mackerel (*Trachurus symmetricus*) were the two most abundant predatory fish taxa captured and were most abundant in July and August, respectively. Humboldt squid (*Dosidicus gigas*) were also present in appreciable numbers off northern Oregon/southern Washington during summer 2009 (see next page).

Humboldt Squid

Prior to the 1997–1998 El Niño, Humboldt squid was an infrequent visitor to the U.S. waters of the Cali-

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[26] For information on methods and sampling locations see http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/a-ecinhome.cfm.

[27] These results are based on ongoing bi-monthly surface trawls conducted from May to August off the Columbia River and Willapa Bay. As part of a broader sampling program, nektonic fishes are sampled using a Nordic 264 rope trawl (Net Systems, Bainbridge Island, WA) fished at the surface directly astern.

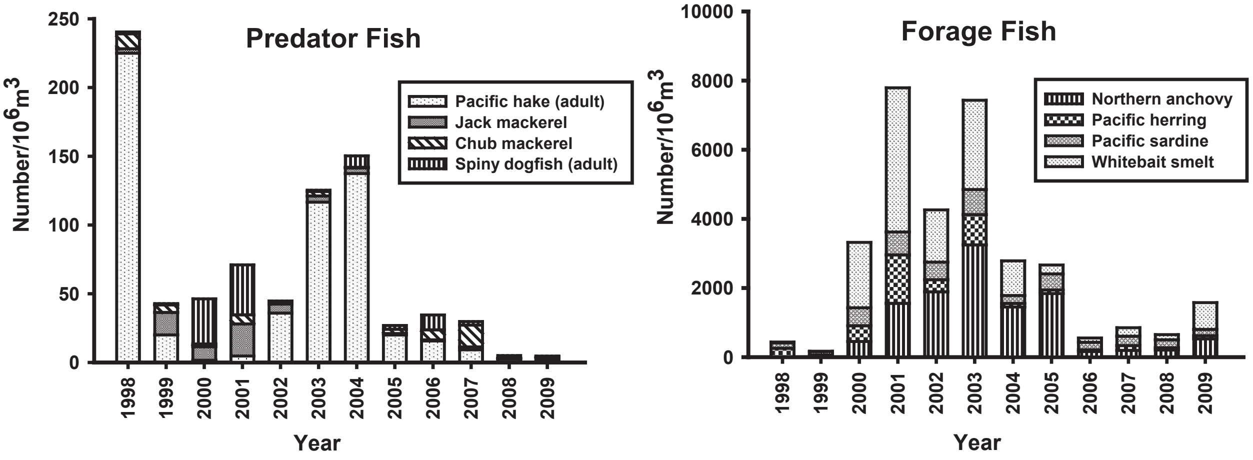

Figure 32. Annual average densities of predatory fishes (left panel) and forage fishes (right panel) captured off the Columbia River/Willapa Bay by bi-monthly surface trawling between May and September.

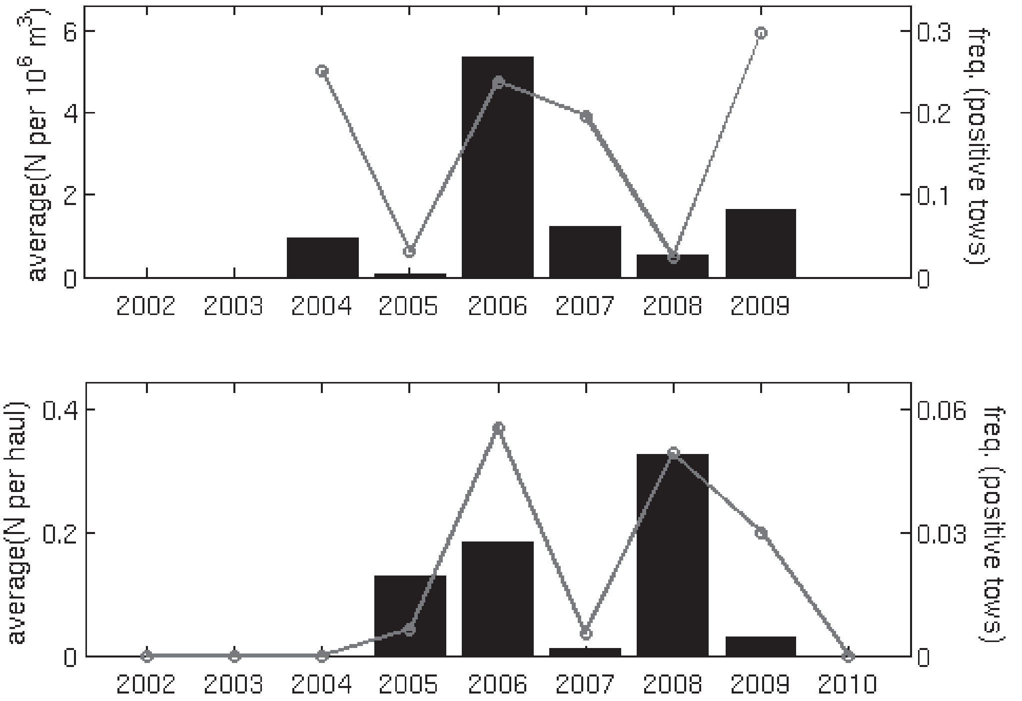

Figure 33. Indices of abundance for Humboldt squid (*Dosidicus gigas*) captured during surface trawl surveys in summer-fall surveys off Oregon and Washington (upper panel) and in mid-water trawl surveys during late spring-early summer off central California (lower panel). Bars indicate average density of squid. Lines indicate percent tows that captured at least one squid.

fornia Current System (CCS), yet since 2003 these animals have been regularly encountered in large numbers throughout the CCS in both the U.S. and Canada, and as far north as Southeast Alaska (Wing 2006; Zeidberg and Robison 2007; Field et al. 2007; fig. 33). The spatial and temporal extent of the present range of Humboldt squid is unprecedented in the historical record and may be related to an apparent expansion of the oxygen minimum zone (OMZ) throughout the CCS and elsewhere in the Northeast Pacific (Bograd et al. 2008).

Available data suggest that the movements and distribution of Humboldt squid in 2009 were consistent with general trends observed since 2003. Squid were encountered in both trawl and ROV surveys off of central California in modest numbers in spring and early summer 2009. Few squid were observed in the Pacific Northwest through the summer, however unusually large numbers of squid were observed in this region beginning in August 2009 in both commercial and recreational fisheries, various resource surveys and beach strandings. Strandings continued through the fall and winter of 2009. From November through December of 2009, squid were again abundant off of northern and central California, and in late December 2009 squid were again present off of San Diego (southern California), consistent with the proposed general southward migration during winter. By contrast, from spring through early summer (July) of 2010, Humboldt squid have been virtually absent from surveys and fisheries throughout the California Current, suggesting that cool conditions may be having an effect on squid abundance or distribution.

DISCUSSION

Changes in the state of the California Current System (CCS) since spring 2009 reflected a transition from cool La Niña conditions into and through a short-lived El Niño event. Responses to this climate sequence exhibited some consistent patterns across the CCS, but regional differences noted in recent State of the California Current reports appear to have persisted along the west coast of North America (cf. Goericke et al. 2007; McClatchie et al. 2009).

The transition from La Niña conditions appears to have unfolded well in advance of the arrival of direct effects of El Niño in the CCS in late 2009. Cool conditions related to the 2007–2008 La Niña abated in summer 2009, and, in general terms, hydrographic and ecological conditions from southern California north approached climatological values during summer 2009. Warmer than usual conditions had already developed off Baja California in 2008 and persisted into the current year, but showed similar directional responses to climate variability as did regions to the north. Overall, changes in the state of the CCS during 2009 coincide with the decay of La Niña conditions in the tropical Pacific.

In the context of the general pattern of transition from La Niña to El Niño, differences between the northern and southern regions of the CCS are readily apparent. Off southern California, the general trend was for mean hydrographic, chemical, and biological properties of the system to return to long-term average conditions during summer 2009. In contrast, the northern CCS, especially the region north of Point Arena, experienced anomalous warming of coastal waters and associated ecosystem responses, presumably as a consequence of anomalously weak and intermittent upwelling during 2009.

Likewise, regional differences and similarities are apparent from late fall 2009 through spring 2010, the period during which El Niño conditions propagated into the CCS and subsequently diminished. Off southern California, the arrival of El Niño was clearly indicated by anomalously high sea level, but responses to El Niño were limited to changes in isopyncnal depth—presumably related to the passage of poleward-propagating Kelvin waves and their lingering consequences. Coastal waters off Oregon and northern California were affected by unusually strong downwelling during winter 2009–2010. In neither case, however, was there any evidence for intrusion of unusual water masses such as had been observed during the strong 1997–1998 El Niño. Relatively strong positive anomalies in temperature and salinity off southern Baja California suggest that the 2009–2010 El Niño influenced the southern extent of the CCS, but these changes appear to have been a consequence of local circulation patterns rather than anomalous poleward flows.

Ecosystem observations offer further suggestion of regional variation in responses to El Niño, but it must be noted that such comparisons are limited by disparity in available data sets. Off southern California, estimates of nutrient concentrations, chl a standing stock, primary productivity, and zooplankton displacement volumes returned to "normal" levels, and did not show evidence for any decline associated with El Niño. In contrast, anomalies in chl a concentration shifted from positive to negative off Baja California, especially north of Point Eugenia, despite the lack of concomitantly strong changes in hydrographic conditions.

Responses at higher trophic levels are much more difficult to connect to simple indices of climate variability, but provide insight to the potential magnitude of ecosystem responses to conditions leading into spring 2009 and the consequences of the 2009–2010 El Niño relative to previous El Niños. Positive shifts in indices of abundance for the juvenile groundfish assemblage off central California and breeding success of Cassin's Auklet in 2009 are consistent with the persistence of cool conditions into spring 2009. Interestingly, the pelagic juvenile groundfish assemblage did not appear to collapse in 2010, suggesting that El Niño conditions did not substantially diminish productivity available to these taxa during critical life history stages during winter and early spring. In contrast, juvenile salmonids at sea in the northern region of the CCS appear to have fared poorly during the warmer than usual conditions of summer and fall 2009. Changes in the copepod assemblage off Oregon were consistent with warmer conditions that do not favor salmon production (Peterson and Schwing 2003; Peterson et al. 2010). Warmer conditions were also reflected in shifts in the marine avifauna off central California (i.e., elevated abundances of Pink-Footed Shearwaters, a species with warm-water affinities) and a northerly distribution of sardine spawning, although the latter observation may not represent a consistent response to temperature variability in the CCS. Humboldt squid (*Docidicus gigas*) continue to be seasonally common throughout the CCS, although it is not clear whether this pattern will persist into 2010.

In summary, the significant changes in the state of the CCS during 2009 and early 2010 appear to have been more closely associated with diminishment of La Niña conditions than direct effects of El Niño. The signature of the 2009–2010 El Niño throughout much of the CCS was substantially weaker than that of the strong 1997–1998 El Niño when influxes of more tropical waters were observed throughout the CCS. While the 2009–2010 El Niño is perhaps most comparable to the mild 2002–2003 El Niño, direct comparisons between the two events are confounded by the interaction of the 2002–2003 El Niño with a coincident intrusion of subarctic water that affected much of the CCS (Venrick et al. 2003). Indeed, the more dramatic changes observed during 2009–2010 in the northern CCS might reflect responses to atmospheric forcing favoring coastal warming absent countervailing subarctic influences. At the time of writing, a transition to moderate La Niña conditions is forecast for summer 2010.[28] It therefore appears that the past year might represent a temporary interruption of an otherwise cool period in the California Current.

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LITERATURE CITED

Ainley, D. G., and K. D. Hyrenbach. 2010. Top-down and bottom-up factors affecting seabird population trends in the California Current system (1985–2006). Prog. Ocean. 84:242–254.

Alarcón-Muñoz, R., L. Cubillos, and C. Gatica. 2008. Jumbo squid (*Dosidicus gigas*) biomass off central Chile: Effects on Chilean hake (*Merluccius gayi*). Calif. Coop. Oceanic Fish. Invest. Rep. 49: 157–166.

Ashok, K., S. K. Behera, S. A. Rao, H. Weng, & T. Yamagata, El Niño Modoki and its possible teleconnection. J. Geophys. Res. 112, C11007, doi:10.1029/2006JC003798 (2007).

Baumgartner, T., R. Durazo, B. Lavaniegos, G. Gaxiola, J. Gomez, and J. Garcia. 2008. Ten years of change from IMECOCAL observations in the southern region of the California Current Ecosystem. Globec International Newsletter. Vo. 14. no. 2. Global Ocean Ecosystem Dynamics. The scientific committee for oceanic research (SCOR) and the intergovernmental oceanographic commission of UNESCO (IOC) 64 p.

Behringer, D.W., and Y. Xue, 2004: Evaluation of the global ocean data assimilation system at NCEP: The Pacific Ocean. Eighth Symposium on Integrated Observing and Assimilation Systems for Atmosphere, Oceans, and Land Surface, AMS 84th Annual Meeting, Washington State Convention and Trade Center, Seattle, Washington, 11–15.

Bograd, S. J., P. M. DiGiacomo, R. Durazo, T. L. Hayward, K. D. Hyrenbach, R. J. Lynn, A. W. Mantyla, F. B. Schwing, W. J. Sydeman, T. Baumgartner, B. Lavaniegos, and C. S. Moore. 2000. The State of the California Current, 1999–2000: Forward to a new regime? Calif. Coop. Oceanic Fish. Invest. Rep. 41:26–52.

Bograd, S. J., and R. J. Lynn. 2003. Anomalous subarctic influence in the southern California Current during 2002. Geophysical Research Letters 30:8020.

Bograd, S.J., C.G. Castro, E. Di Lorenzo, D.M. Palacios, H. Bailey, W. Gilly, and F.P. Chavez. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophys. Res. Let. 35: L12607.

Brinton, E., and A. Townsend. 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. Deep-Sea Res. II. 50:2449–2472.

Di Lorenzo, E., N. Schneider, K. M. Cobb, K. Chhak, P. J. S. Franks, A. J. Miller, J. C McWilliams, S. J. Bograd, H. Arango, E. Curchister, T. M. Powell, and P. Rivere. 2008: North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophys. Res. Lett., 35, L08607, doi:10.1029/2007GL032838.

Durazo, R., and T. Baumgartner. 2002. Evolution of oceanographic conditions off Baja California: 1997–1999. Progress in Oceanography, 54, 7–31.

Durazo, R. 2009. Climate and upper ocean variability off Baja California, Mexico: 1997–2008. Progress in Oceanography, 83, 361–368, doi: 10.1016/j.pocean.2009.07.043.

Field, J. C., K. Baltz, A. J. Phillips, and W. A. Walker. 2007. Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 48: 131–146.

Gaxiola-Castro, G., R. Durazo, B. Lavaniegos, M. E. De-la-Cruz-Orozco, E. Millán-Nuñez, L. Soto-Mardones, J. Cepeda-Morales. 2008. Pelagic ecosystem response to interannual variability off Baja California. Cienc. Mar., 263–270.

Goericke, R., E. Venrick, A. Mantyla, S. J. Bograd, F. B. Schwing, A. Huyer, R. L. Smith, P. A. Wheeler, R. Hooff, W. T. Peterson, F. Chavez, C. Collins, B. Marinovic, N. Lo, G. Gaxiola-Castro, R. Durazo, K. D. Hyrenbach, and W. J. Sydeman, 2005. The state of the California current, 2004–2005: still cool? CalCOFI Reports, 46: 32–71.

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[28] http://www.cpc.noaa.gov/products/analysis_monitoring/enso_advisory.

Goericke, R., E.Venrick, T. Koslow, W. J. Sydeman, F. B. Schwing, S. J. Bograd, W. T. Peterson, R. Emmett, J. R. Lara Lara, G. Gaxiola Castro, J. Gómez Valdez, K. D. Hyrenbach, R.W. Bradley, M. J. Weise, J.T. Harvey, C. Collins, and N. C. H. Lo. 2007. The State of the California Current, 2006–2007: Regional and Local Processes Dominate, Calif. Coop. Oceanic Fish. Invest. Rep. 48:33–66.

Halle, C.M., and J. Largier. 2010. Large-scale surface circulation downstream of the Point Arena upwelling center, *submitted to J. Geophys. Res.*

Halle, C. M., J. L. Largier, and G. Crawford. 2010. A seasonal coastal/oceanic eddy near Cape Mendocino, California. (to be submitted to Geophs Res Letters).

Holmes, J., K. Cooke, and G. Cronkite. 2007. Interactions between jumbo squid (*Dosidicus gigas*) and Pacific hake (*Merluccius productus*) in the northern California Current in 2007. Calif. Coop. Oceanic Fish. Invest. Rep. 49: 129–141.

Hooff, R. C., and W. T. Peterson. 2006. Recent increases in copepod biodiversity as an indicator of changes in ocean and climate conditions in the northern California current ecosystem. Limnol. Oceanogr. 51:2042–2051.

Hyrenbach, K. D., and R. R.Veit. 2003. Ocean warming and seabird assemblages of the California Current System (1987–1998): response at multiple temporal scales. Deep-Sea Res. II. 50:2537–2565.

Kanamitsu M., W. Ebisuzaki, J. Woollen, S.-K. Yang, J. J. Hnilo, M. Fiorino, and G. L. Potter, 2002a: NCEP–DOE AMIP-II Reanalysis (R-2). Bull. Amer. Meteor. Soc., 83, 1631–1643. Xue, Y., T. M. Smith, and R. W. Reynolds, 2003: Interdecadal changes of 30-yr SST normals during 1871–2000. J. Climate, 16, 1601–1612.

Kaplan, D. M., C. Halle, J. Paduan, and J. L. Largier, 2009. Surface currents during anomalous upwelling seasons off central California. Journal of Geophysical Research, 114, doi:10.1029/2009JC005382.

Kim, S. Y., E. J. Terrill, and B. D. Cornuelle, 2008, Mapping surface currents from HF radar radial velocity measurements using optimal interpolation, J. Geophys. Res. 113, C10023, doi:10.1029/2007JC004244.

Kister, R., and co-authors. 2001. The NCEP-NCAR 50-year reanalysis: Monthly means CD-ROM and documentation, Bull. Am. Meteorol. Soc. 82: 247–268.

Largier, J. L., B. A. Magnell, and C. D. Winant, 1993. Subtidal circulation over the northern California shelf. Journal of Geophysical Research, 98(C10), 18147–18179.

Lavaniegos, B. E., and M. D. Ohman. 2003. Long term changes in pelagic tunicates of the California Current. Deep-Sea Res. II. 50:2493–2518.

Lee, D. E., N. Nur, and W. J. Sydeman. 2007. Climate and demography of the planktivorous Cassin's auklet *Ptychoramphus aleuticus* off northern California: implications for population change. J. Anim. Ecol. 76:337–347.

Lindley, S. T., C. B. Grimes, M.S. Mohr, W. Peterson, J. Stein, J.T. Anderson, L.W. Botsford, D. L. Bottom, C. A. Busack, T. K. Collier, J. Ferguson, J. C. Garza, A. M. Grover, D. G. Hankin, R. G. Kope, P. W. Lawson, A. Low, R. B. MacFarlane, K. Moore, M. Palmer-Zwahlen, F. B. Schwing, J. Smith, C. Tracy, R. Webb, B. K. Wells, and T. H. Williams. 2009. What caused the Sacramento River fall Chinook stock collapse? U. S. Department of Commerce, NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFSC-447, 121 pp.

Lo, N. C. H., B. Macewicz, and R. Charter. 2007a. Spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2006. Nat. Oceanic Atmos. Admin., U. S. Dep. Commer. Tech. Memo. NOAA-TM-NMFS-SWFSC-401. 32 pp.

Lo, N. C. H., B. Macewicz, and R. Charter. 2007b. Spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2007. Nat. Oceanic Atmos. Admin., U. S. Dep. Commer. Tech. Memo. NOAA-TM-NMFS-SWFSC-411. 31 pp.

Lo, N. C. H., B. Macewicz, and R. L. Charter. 2007. Spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2007. NOAA Tech. Memo. NOAA-TM-NMFX-SWFSC-411. 31 pp. http://swfsc.noaa.gov/publications/TM/SWFSC/NOAA-TM-NMFS-SWFSC-411.PDF.

Lo, N. C. H., B. Macewicz, D. Griffith, and R. Charter. 2008. Spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2008. Nat. Oceanic Atmos.Admin., U. S. Dep. Commer., Tech. Memo. NOAA-TM-NMFS-SWFSC-430. 33 pp.

Lo, N. C. H., B. Macewicz, and D. Griffith. 2009. Spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2008. Nat. Oceanic Atmos. Admin., U. S. Dep. Commer., Tech. Memo. NOAA-TM-NMFS-SWFSC-449. 31 pp.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteorological Soc. 78: 1069–1079.

McClatchie, S., R. Goericke, J. A. Koslow, F. B. Schwing, S. J. Bograd, R. Charter, W. Watson, N. Lo, K. Hill, J. Gottschalk, M. L'Heureux, Y. Xue, W. T. Peterson, R. Emmett, C. Collins, G. Gaxiola-Castro, R. Durazo, M. Kahru, B. G. Mitchell, K.D. Hyrenbach, W. J. Sydeman, R.W. Bradley, P. Warzybok, E. Bjorkstedt. 2008. The State of the California Current, 2007–2008: La Niña conditions and their effects on the ecosystem. CalCOFI Reports, 49: 39–76.

McClatchie, S., R. Goericke, F. B. Schwing, S. J. Bograd, W. T. Peterson, R. Emmett, R. Charter, W. Watson, N. Lo, K. Hill, C. Collins, M. Kahru, B. G. Mitchell, J. A. Koslow, J. Gomez-Valdes, B. E. Lavaniegos, G. Gaxiola-Castro, J. Gottschalk, M. L'Heureux, Y. Xue, M. Manzano-Sarabia, E. Bjorkstedt, S. Ralston, J. Field, L. Rogers-Bennett, L. Munger, G. Campbell, K. Merkens, D. Camacho, A. Havron, A. Douglas, and J. Hildebrand. 2009. The state of the California Current, 2008–2009: Cold conditions drive regional difference. CalCOFI Rep. 50: 43–68

Peterson, W. T., and F. B. Schwing. 2003. A new climate regime in Northeast Pacific ecosystems. Geophysical Research Letters. 30(17), 1896. doi:10.1029/2003GL017528.

Peterson, W.T., R. Emmett, R. Goericke, E.Venrick, A. Mantayla, S. J. Bograd, F. B. Schwing, R. Hewitt, N. Lo., W. Watson, J. Barlow, M. Lowry, S. Ralston, K. A. Forney, B. E. Lavaniegos, W. J. Sydeman, D. Hyrenbach, R. W. Bradley, P. Warzybok, F. Chavez, K. Hunter, S. Benson, M. Weise, J. Harvey, G. Gaxicola-Castro, R. Durazo. 2006. The State of the California Current, 2005–2006: warm in the north, cool in the south. Calif. Coop. Oceanic Fish. Invest. Rep. 47:30–74.

Peterson, W.T., C. A. Morgan, E. Casillas, J. L. Fisher, and J.W. Ferguson. 2010. Ocean Ecosystem Indicators of Salmon Marine Survival in the Northern California Current. http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/documents/peterson_etal_2010.pdf.

Reynolds, R. W., N. A. Rayner, T. M. Smith, D. C. Stokes, and W. Wang, 2002: An improved in situ and satellite SST analysis for climate. J. Climate, 15, 1609–1625.

Sakuma, K. M., S. Ralston, and V. G. Wespestad. 2006. Interannual and spatial variation in the distribution of young-of-the-year rockfish (*Sebastes* spp.): expanding and coordinating a survey sampling frame. California Cooperative Oceanic Fisheries Investigations (CalCOFI) Reports 47:127–139.

Santora, J. A., S. Ralston, and W. J. Sydeman. Interannual indices of central California Current krill spatial organization: an integrated approach. Submitted to ICES J. Mar. Sci.

Schwing, F. B., N. A. Bond, S. J. Bograd, T. Mitchell, M. A. Alexander, and N. Mantua. 2006. Delayed coastal upwelling along the U.S. west coast in 2005: a historical perspective. Geophys. Res. Lett. 33: L22S01, doi:10.1029/2006GL026911.

Smith, R.L, A. Huyer, J. Fleischbein. 2001. The coastal ocean off Oregon from 1961 to 2000: is there evidence of climate change or only of Los Niños? Prog. Oceanogr., Volume 49: 63–93.

Sydeman, W. J., M. M. Hester, J. A. Thayer, F. Gress, P. Martin, and J. Buffa. 2001. Climate change, reproductive performance, and diet composition of marine birds in the southern California Current system, 1969–1997. Prog. Oceanogr. 49:309–329.

Sydeman, W. J., R. W. Bradley, P. Warzybok, J. Jahncke, K. D. Hyrenbach, V. Kousky, M. A. Hipfner, and M. D. Ohman. 2006. Krill and Krill Predators: Responses of Planktivorous Auklets Ptychoramphus aleuticus to the Anomaly of 2005. J. Geophys. Res. 33, L22S09.

Sydeman, W. J., K. L. Mills, J. A. Santora, S. A. Thompson, D. F. Bertram, K. H. Morgan, B. K. Wells, J. M. Hipfner, and S. G. Wolf. 2009. Seabirds and climate in the California Current—A synthesis of change. CalCOFI Rep. 50:82–104.

Tasker, M. L., P. H. Jones, T. Dixon, and B. Blake. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. Auk. 101:567–577.

Terrill, E. J., M. Otero, L. Hazard, D. Conlee, J. Harlan, J. Kohut, P. Reuter, T. Cook, T. Harris, K. Lindquist, Data Management and Real-time Distribution in the HF-Radar National Network, OCEANS 2006, 2006, IEEE, 10.1109/OCEANS.2006.306883.

Venrick, E., S. J. Bograd, D. Checkley, R. Durazo, G. Gaxiola-Castro, J. Hunter, A. Huyer, K. D. Hyrenbach, B. E. Lavaniegos, A. Mantyla, F. B. Schwing, R. L. Smith, W. J. Sydeman, and P. A. Wheeler. 2003. The state of the California Current, 2002–2003: Tropical and Subarctic influences vie for dominance. Calif. Coop. Oceanic Fish. Invest. Rep. 44:28–60.

Warzybok, P. M., and R. W. Bradley. 2009. Status of seabirds on Southeast Farallon Island during the 2009 breeding season. PRBO Conservation Science, Petaluma, California. (available at http://www.prbo.org/cms/docs/marine/2009FarallonSeabirdReport.pdf).

Wheeler, P. A., A. Huyer, and J. Fleischbein. 2003. Cold halocline, increased nutrients and higher productivity off Oregon in 2002. Geophys. Res. Lett. 30:8021.

Wing, B.L. 2006. Unusual invertebrates and fish observed in the Gulf of Alaska, 2004–2005. PICES Press 14:2:26–28.

Wolter, K., and M. S. Timlin, 1998: Measuring the strength of ENSO events—how does 1997/98 rank? Weather. 53:315–324.

Xue, Y., T. M. Smith, and R. W. Reynolds, 2003: Interdecadal changes of 30-yr SST normals during 1871–2000. J. Climate, 16, 1601–1612.

Zeidberg, L.D., and B.H. Robison. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. Proc. Natl. Acad. Sci. USA 104: 12948–12950.

PUBLICATIONS
1 January–31 December 2009

Aksnes, D. L., and M. D. Ohman. 2009. Multi-decadal shoaling of the euphotic zone in the southern sector of the California Current System. Amer. Soc. of Limnol. and Oceanogr. 54(4):1272–1281.

Auth, T. D. 2009. Importance of far-offshore sampling in evaluating the ichthyoplankton community in the Northern California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 50:107–117.

Baker, K. S., and L. Yarmey. 2009. Data stewardship: Environmental data curation and a web-of-repositories. International Journal of Digital Curation. 4(2):12–27.

Barange, M., M. Bernal, M. C. Cercole, L. A. Cubillos, G. M. Daskalov, C. L. de Moor, J. A. A. De Oliveira, M. Dickey-Collas, D. J. Gaughan, K. Hill, et al. 2009. Current trends in the assessment and management of stocks. *In* Climate Change and Small Pelagic Fish, Chapter 9, pp 191–255. D. Checkley, J. Alheit, Y. Oozeki and C. Roy (Eds). Cambridge University Press. xii+ 372 pp.

Barange, M., J. Coetzee, A. Takasuka, K. Hill, M. Gutierrez, Y. Oozeki, C. van der Lingen, and V. Agostini. 2009. Habitat expansion and contraction in anchovy and sardine populations. Prog. Oceanogr. 83:251–260.

Barsky, K., D. Haas, M. Heisdorf, K. Hubbard, L. Laughlin, A. Louie, M. Michie, D. Neilsen, W. Miller, D. Ono, K. Penttila, V. Taylor, P. Ton. 2009. Review of selected California fisheries for 2008: Coastal pelagic finfish, market squid, ocean salmon, groundfish, California spiny lobster, spot prawn, white bass, kelp bass, thresher shark, skates and rays, Kellet's whelk, and sea cucumber. Calif. Coop. Oceanic Fish. Invest. Rep. 50:5–13.

Bowlin, N. M., W. Watson, R. L. Charter, and S. M. Manion. 2009. Ichthyoplankton and station data for surface (manta) and oblique (bongo) plankton tows for California Cooperative Oceanic fisheries Investigations survey cruises and California Current Ecosystem survey in 2006. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-442. 152 pp.

Broquet, G., C. A. Edwards, A. M. Moore, B. S. Powell, M. Veneziani, and J. D. Doyle. 2009. Application of 4D-variational data assimilation to the California Current System. Dyn. Atmos. Oceans. 48:69–92.

Checkley, D. M., Jr., J. Alheit, Y. Oozeki, and C. Roy. 2009. Climate Change and Small Pelagic Fish. Cambridge University Press. 372 pp.

Churnside, J. H., D. Griffith, D. A. Demer, R. L. Emmett, and R. D. Brodeur. 2009. Comparisons of Lidar, acoustic and trawl data on two scales in the Northeast Pacific Ocean. Calif. Coop. Oceanic Fish. Invest. Rep. 50:118–122.

Crone, P. R., K. T. Hill, J. D. McDaniel, and N. C. H. Lo. 2009. Pacific mackerel (*Scomber japonicus*) stock assessment for USA management in the 2009–10 fishing year. Pacific Fishery Management Council, Portland, Oregon, USA. 197 pp.

Di Lorenzo, E., J. Fiechter, N. Schneider, A. Bracco, A. J. Miller, P. J. S. Franks, S. J. Bograd, A. M. Moore, A. C. Thomas, W. Crawford, A. Pena, and A. J. Hermann. 2009. Nutrient and salinity decadal variations in the Central and Eastern North Pacific. Geophys. Res. Lett. 36: L14601, doi:10.1029/2009GL038261.

Dottori, M. C., and J. Allan. 2009. Rossby Waves and the interannual and interdecadal variability of semperature and salinity off California. J. Phys. Ocean. 39:2543–2561.

Emmett, R., and N. C. H. Lo. 2009. Proceedings of the 2008 Trinational sardine forum. NWFSC Adm. Rep. 89 pp.

Gay, P. S., and T. K. Chereskin. 2009. Mean structure and seasonal variability of the poleward undercurrent off Southern California. J. Geophys. Res. 114: C02007, 10.1029/2008JC004886.

Gilfillan, L.R., M. D. Ohman, M. L. Doyle, and W. Watson. 2009. Occurrence of plastic micro-debris in the Southern California Current System. Calif. Coop. Oceanic Fish. Invest. Rep. 50:123–133.

Glaser, S. M. 2009. Foraging ecology of North Pacific albacore in the California Current System. PhD Thesis. Biological oceanography. University of California San Diego. 231 pp.

Hill, K. T., N. C. H. Lo, P. R. Crone, B. J. Macewicz, and R. Felix-Uraga. 2009. Assessment of the Pacific sardine resource in 2009 for USA management in 2010. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-452. 221 pp.

Hsieh, C. H., H. J. Kim, W. Watson, E. Di Lorenzo, and G. Sugihara. 2009. Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the Southern California region. Global Change Biol. 15:2137–2152.

Jarvis, E. T., H. L. Gliniak, O. Horning, and C. Linardich. 2009. Occurrence of juvenile Mexican Lookdown, *Selene brevoortii* (Gill, 1863), in Seal Beach, California. California Fish and Game 95:188–192.

Johnston, T. M. S., O. M. Cheriton, J. T. Pennington, F. P. Chavez. 2009. Thin phytoplankton layer formation at eddies, filaments, and fronts in a coastal upwelling zone. Deep Sea Res. (II Top. Stud. Oceanogr.). 56:246–259.

Kahru, M., R. Kudela, M. Manzano-Sarabia, and B. G. Mitchell. 2009. Trends in primary production in the California Current detected with satellite data. J. Geophys. Res. 114: C02004, doi: 10.1029/2008JC004979.

Karpov, K. A., N. J. Kogut, and J. J. Geibel. 2009. Estimating fish length with vertical morphometric parameters. California Fish and Game, 95:161–174.

Kim, H. J., A. J. Miller, J. McGowan, and M. Carter. 2009. Coastal phytoplankton blooms in the Southern California Bight. Prog. Oceanogr. 82:137–147.

Koslow, J. A. 2009. The role of acoustics in ecosystem-based fishery management ICES. Journal of Mar. Sci. 66:966–973.

Koslow, J. A., R. Goericke, S. McClatchie, R. Vetter, and L. Rogers-Bennett. 2009. The California Cooperative Oceanic Fisheries Investigations (CalCOFI): the continuing evolution and contributions of a 60-year ocean observation program. OceanObs'09. ESA, Venice, Italy.

Koslow, J. A. 2009. Deepwater corals and the other CO2 problem. *In* Herr, D., G. R. Galland (Eds.), The Ocean and Climate Change: Tools and Guidelines for Action. IUCN, Gland, Switzerland, p. 19.

Lanz, E., M. Nevárez-Martínez, J. López-Martínez, and J. A. Dworak. 2009. Small pelagic fish catches in the Gulf of California associated with sea surface temperature and chlorophyll. Calif. Coop. Oceanic Fish. Invest. Rep. 50:134–146.

Lluch-Belda, D., P. del Monte Luna, and S. E. Lluch-Cota. 2009. 20th century variability in Gulf of California SST. Calif. Coop. Oceanic Fish. Invest. Rep. 50:147–154.

Lo, N. C. H., B. J. Macewicz, and D. A. Griffith. 2009. Spawning biomass of Pacific sardine (*Sardinop sagax*) off California in 2009. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-449, 31 pp.

Lo, N. C. H., B. J. Macewicz, and D. A. Griffith. 2010. Biomass and reproduction of Pacific sardine off northwest U.S. in 2003–2005. U.S. Fish. Bull 108(2):174–192.

Lo, N.C.H., P. E. Smith, and M. Takahashi. 2009. Chapter 6. Egg, larval and juveniles surveys in Fish Reproductive Biology. Implications for Assessment & Management edited by T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness. Wiley-Blackwell.

Mason, J.W., G. J. McChesney, W. R. Mclver, H. R. Carter, J. Y. Takekawa, R. T. Golightly, J. T. Ackerman, D. L. Orthmeyer, W. M. Perry, J. L. Yee, M. O. Pierson, and M. D. McCrary. 2009. At-sea distribution and abundance of seabirds off Southern California: A 20-year comparison. The Auk. 126(4):937–939.

McClatchie, S., R. Goericke, F. B. Schwing, S. J. Bograd, W. T. Peterson, R. Emmett, R. Charter, W. Watson, N. Lo, K. Hill, C. Collins, M. Kahru, B. G. Mitchell, J. A. Koslow, J. Gomez-Valdes, B. E. Lavaniegos, G. Gaxiola-Castro, J. Gottschalk, M. L'Heureux, Y. Xue, M. Manzano-Sarabia, E. Bjorkstedt, S. Ralston, J. Field, L. Rogers-Bennett, L. Munger, G. Campbell, K. Merkens, D. Camacho, A. Havron, A. Douglas, and J. Hildebrand. 2009. The state of the California Current, Spring 2008–2009: Cold conditions drive regional differences. Calif. Coop. Oceanic Fish. Invest. Rep. 50:43–68.

Mitchell, B. G., and M. Kahru. 2009. Bio-optical algorithms for ADEOS-2 GLI. Journal of the Remote Sensing Society of Japan, 29(1): 80–85.

Moore, A. M., H. G. Arango, E. Di Lorenzo, A. J. Miller, and B. D. Cornuelle. 2009. An adjoint sensitivity analysis of the Southern California Current circulation and ecosystem. J. Phys. Ocean. 39:702–720.

Munger, L. M., D. Camacho, A. Havron, G. Campbell, J. Calambokidis, A. Douglas and J. Hildebrand. 2009. Baleen whale distribution relative to surface temperature and zooplankton abundance off Southern California, 2004–2008. Calif. Coop. Oceanic Fish. Invest. Rep. 50:155–168.

Ohman, M. D., B. E. Lavaniegos, and A.W. Townsend. 2009. Multi-decadal variations in calcareous holozooplankton in the California Current System: Thecosome pteropods, heteropods, and foraminifera. Geophys. Res. Let. 36: L18608, doi:10.1029/2009GL039901.

Peterson, W. T. 2009. Copepod species richness as an indicator of long-term changes in the coastal ecosystem of the Northern California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 50:73–81.

Rago, T.A., R. Michisaki, B. Marinovic, M. Blum, and K. Whitaker. 2009. Physical, nutrient, and biological measurements of coastal waters off Central California in January 2009. Report of the Naval Postgraduate School. 46 pp.

Ralston, S., and B. R. MacFarlane. 2010. Population estimation of bocaccio (*Sebases paucispinis*) based on larval production. Can. J. Fish. Aquat. Sci. 67: 1005–1020.

Rosales-Casián, J.A., and C. Almeda-Jáuregui. 2009. Unusual occurrence of a green sturgeon, *Acipenser medirotris*, at El Socorro, Baja California, México. Calif. Coop. Oceanic Fish. Invest. Rep. 50:169–171.

Rykaczewski, R. 2009. Influence of oceanographic variability on the planktonic prey and growth of sardine and anchovy in the California Current Ecosystem. PhD Thesis. Biological Oceanography. University of California San Diego. 137 pp.

Suk, S. H., S. E. Smith, and D. A. Ramon. 2009. Bioaccumulation of mercury in pelagic sharks from the Northeast Pacific Ocean. Calif. Coop. Oceanic Fish. Invest. Rep. 50:172–177.

Sydeman, W. J., K. L. Mills, J. A. Santora, S. A. Thompson, D. F. Bertram, K. H. Morgan, J. M. Hipfner, B. K. Wells, and S. G. Wolf. 2009. Seabirds and climate in the California Current—a synthesis of change. Calif. Coop. Oceanic Fish. Invest. Rep. 50:82–106.

Weber, E., and S. McClatchie. 2009. rcalcofi: Analysis and visualization of CalCOFI data in R. Calif. Coop. Oceanic Fish. Invest. Rep. 50:178–185.

Williamson, M., and J. A. McGowan. 2009–2010. The copepod communities of the North and South Pacific central gyres and the form of species-abundance distributions J. of Plankton Res. 32:273–283.

Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE, 2009

FORECASTING FISHERY PRODUCTIVITY IN THE CALIFORNIA CURRENT

Asilomar Conference Grounds
Pacific Grove, California
8 December 2009

The ability to forecast the productivity of fisheries has been a goal of fisheries managers for 100 years (Hjort 1914). Fisheries are challenging to predict for many reasons, including wide fluctuations in recruitment success between year classes, poorly known stock-recruit relationships and dramatic differences in ocean conditions between years (Cushing 1982, Fogarty et al. 1991, Mullin 1994). For many commercially important species, recruitment is irregular and strong year classes often sustain the fishery between recruitment droughts that may last a decade or more. Researchers are starting to find relationships between recruitment and physical oceanographic parameters as our understanding of the role of physical forcing on marine populations expands. In some cases, specific mechanisms linked to physical oceanographic conditions (forcing) appear to drive recruitment success (e.g., Gaines and Bertness 1993, Botsford et al. 1994, Peterson and Schwing 2003). This important first step, describing relationships between recruitment and ocean conditions, is in and of itself useful in forecasting fishery productivity. We know for example, that years with warm ocean temperatures are "good" for sardines and this can information has been incorporated into fishery harvest control rules (Conser et al. 2001). The 55-year CalCOFI time series encompasses a wide range of ocean conditions and is uniquely suited to examine relationships between larval abundances and ocean condition. The papers presented in this symposium explore a wide array of approaches examining the potential for and utility of forecasting productivity of various species of commercially important stocks.

Field et al. explore the use of four sources of data of juvenile bocaccio (*Sebastes paucispinus*) abundance to see if their inclusion improves stock assessment results. The current stock assessment model uses the age-structured Stock Assess III model which incorporates fishery-dependent and -independent data such as larval data (CalCOFI), trawl surveys and juvenile abundance data. Here they evaluate the performance of the 4 additional recruitment indices by re-running the model with and without the juvenile indices. Field et al. find that the re-run model results for biomass trends and recruitment estimates are nearly identical to those from the original stock assessment model. They also find that recruitment indices can overestimate recruitment before the year class shows up in the fishery-dependent size-frequency data. Bocaccio populations appear to be dominated by highly variable recruitment events which significantly impacts rebuilding targets.

Caselle et al. describe the development of an index of rockfish (*Sebastes* spp.) recruitment in southern and central California and relate this to indices of ocean condition. They focus on two groups of nearshore rockfishes recruiting to artificial collectors at 5 sites starting in 2000. They find that south of Point Conception annual recruitment of the two groups occurs together and is strongly correlated with upwelling in the summer months. In central California, annual recruitment in the two rockfish groups are not concordant, with one group correlating well to upwelling in the summer months while the other group had highly variable recruitment uncorrelated with physical oceanographic indices.

Hannah shows how a pre-recruitment index was used to improve forecasts of productivity in the Oregon ocean shrimp (*Pandalus jordani*) fishery. An index of pre-recruits (age-0) was developed in northern and southern Oregon from 1980 to the present. For northern Oregon, incorporation of the pre-recruit index into the best environmental model improved the model fit, while fit was not improved for the southern Oregon fishery model. The southern Oregon model while unable to predict recruitment failures during the 1983 and 1998 ENSO events was able to predict the strong year class in 2009.

Shanks et al. developed an index of Dungeness crab (*Cancer magister*) megalopae abundance in spring in southern Oregon. They examined the use of this index as a predictor of the strength of the commercial fishery four years later when the cohort recruited to the fishery. During the first 6 years there was a strong correlation between the larval index and the commercial catch four years later; strong commercial catches were associated with early onset of the spring transition and upwelling.

However, this correlation broke down in the last three years when annual larval numbers in the traps jumped from 1,000–80,000 (1997–2001) to 1.2–2.4 million (2007–2009). There was a strong negative correlation with day of the spring transition and megalopae index in 1997–2001 but this relationship also breaks down during the high catches in 2007–2009. These new megalopae catches equate to a commercial catch greater than 10 times the record catch, however density-dependent mortality of juvenile crabs may affect recruitment more strongly during large recruitment years.

Lastly, White and Rogers-Bennett explore the use of physical oceanographic variables as proxies for recruitment success in both traditional and spatially explicit models of fishery productivity. Using Caselle et al.'s results for kelp rockfish as an example, they find that when the proxy is a good predictor ($r > 0.8$) of actual larval survival there was a strong correlation between the proxy and recruitment especially when recruitment was variable. In the spatially explicit model, the same held true for incorporating the proxy into the model and larval dispersal distances did not influence the utility of the proxy. The use of the proxy improved the model predictions over years in which there was recruitment information but was less effective beyond the time to grow into the fishery. This paper provides an example of how oceanographic indices reflecting ocean condition can be incorporated into fishery models.

The papers in this symposium are examples of advances being made in our understanding of how fisheries productivity and major recruitment events are influenced or driven by ocean conditions. These papers also illustrate some of the challenges that remain, primarily understanding the scale over which productivity indices operate. It is also clear that strongly predictive indices may break down in the face of long-term oceanographic regime changes, and/or may not extend to oceanographically distinct regions. Working with these caveats will be crucial to moving forward in our understanding of the links between oceanographic conditions and fisheries. We encourage future research to build on the work presented here to develop indices as predictive tools for improving fisheries ecology and management.

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LITERATURE CITED

Botsford, L. W., C. L. Moloney, A. Hastings, J. L. Largier, T. M. Powell, K. Higgins, and J. F. Quinn. 1994. The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. Deep-Sea Res. II 41: 107–145.

Conser, R. J., Hill, K. T., Crone, P. R., and Bergen, D., 2001. Stock Assessment of Pacific Sardine with Management Recommendations for 2002: Executive Summary. Pacific States Fishery Management Council, Portland, OR. 97201.

Cushing, D. H. 1982. Climate and Fisheries. Academic Press, London.

Fogarty, M. J., M. P. Sissenwine, and E. B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends Ecol. Evol. 6: 241–246.

Gaines, S. G., and M. Bertness. 1993. The dynamics of juvenile dispersal: why field ecologists must integrate. Ecology 74: 2430–2435.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapp. P.-V. Reun. Cons. Inst. Explor. Mer. 20: 1–13.

Mullin, M. M. 1994. Webs and scales: Physical and ecological processes in marine fish recruitment. Washington Sea Grant Program/University of Washington Press, Seattle and London.

Peterson, W. T. and F. B. Schwing. 2003. A new climate regime in northeast Pacific ecosystems. Geophys. Res. Lett. 30:1896.

BOCACCIONOMICS: THE EFFECTIVENESS OF PRE-RECRUIT INDICES FOR ASSESSMENT AND MANAGEMENT OF BOCACCIO

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ABSTRACT

Bocaccio (*Sebastes paucispinis*) has been one of the most important species of rockfish to both commercial and recreational fisheries in California Current waters over the last century. Actions taken to rebuild the stock of bocaccio residing off of California have been responsible for dramatic changes on both commercial and recreational groundfish management and total allowable yields of most groundfish species in California waters over the last decade, including a virtual cessation of commercial and recreational fishing in 2003. In retrospect, it was determined that a strong 1999 year class was moving through the fishery at that time, resulting in high catch rates during a period in which management sought to drastically reduce catch. This results in a paradox, in which rebuilding requires strong year classes, which requires further constraints on fishing during periods in which the condition of the stock seems to be improving. Although this paradox exists for all stocks undergoing rebuilding, it is particularly pronounced for bocaccio as they have among the greatest variability in recruitment observed in any species of West Coast rockfish, as well as very rapid growth and very young age at recruitment to the recreational fishery. Consequently, accurate indices of the strength of incoming year classes both improve stock assessment estimates of future (near term) abundance trends, as well as aid regulators in making management decisions during those infrequent periods of high abundance of young fish. We discuss several indices of recruitment strength based on data on young bocaccio, evaluate their relative performance in the early detection of strong year classes, and consider both the oceanographic factors that may drive recruitment variability, as well as the spatial patterns of recruitment events which may aid in interpreting these indices.

INTRODUCTION

Bocaccio (*Sebastes paucispinis*) have long been one of the most important targets of both commercial and recreational fisheries in California waters, accounting for between 25 and 30% of the commercial and recreational rockfish (*Sebastes* spp.) catch over the past century. However, this percentage has declined in recent years as a result of stock declines, restrictive management actions and the development of alternative fisheries. Catches and abundance began to fall during the 1980s and declined rapidly in the 1990s, due to a combination of high harvest rates and poor ocean conditions (MacCall 2003; Field et al. 2009). More recently, since the southern sub-stock of bocaccio (currently representing the population of bocaccio south of Cape Blanco, OR)[1] was declared overfished by the Pacific Fishery Management Council (PFMC) in 1999,[2] management measures have been responsible for even more significant reductions of both commercial and recreational catches. Management measures included a virtual cessation of most commercial and recreational fishing in 2003, following a very pessimistic assessment of stock status in 2002 (MacCall et al. 2002).

The landings limitations and area closures that followed the 2002 assessment led to considerable economic hardships during a period in which many fishermen complained bitterly that bocaccio were "more abundant than ever before." Management constraints implemented to rebuild bocaccio, as well as six other species of rockfishes that were declared overfished, have substantially reduced rockfish landings coastwide since then (Berkeley et al. 2004, Punt and Ralston 2007). Although the stock is still estimated to have been in an overfished condition throughout the 1990s, the most recent assessment indicates that the population was not as depleted as estimated in the 2002 assessment (MacCall 2003, Field et al. 2009). Additionally, it is now clear that a relatively strong (relative to parental biomass) 1999 year class had indeed been moving through the fishery at that time, following a decade of record-low recruitment

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[1] This paper investigates the recruitment and abundance trends of the southern sub-stock of bocaccio only, currently defined as waters south of Cape Blanco, Oregon to the U.S./Mexico border (Field et al. 2009). Bocaccio in U.S. waters north of Cape Blanco are likely to be more connected from a population perspective to bocaccio off of British Columbia, Canada, for which abundance has also been estimated to be at very low levels (Stanley et al. 2009).

[2] The PFMC is the management body charged with implementing the requirements of federal law for west coast groundfish fisheries, and defines a stock or population as being "overfished" if the stock is at or below the minimum stock size threshold (MSST). The MSST for West Coast rockfish is currently defined as 25% of the estimated spawning biomass or spawning potential that would occur in an unfished condition.

levels that began in 1990. Thus, the fishermen's complaints had validity, in that the bocaccio population was undergoing a significant increase in abundance during a period in which management sought to drastically reduce catch.

Consequently, management of bocaccio in recent years has been complicated by both changes in management regimes and objectives, and variable population trajectories driven (to a large extent) by highly variable recruitment. Despite the significant socio-economic hardships, management actions have been effective at reducing mortality. This combined with several recent strong year classes (1999, 2003, 2005), have resulted in an increase in abundance and spawning output over the past decade. Although the current estimate of abundance is substantially higher than those of the 1990s, the population will remain in "rebuilding" status until it has recovered to the target level of abundance, currently set to 40% of the unfished abundance for West Coast groundfish (Punt and Ralston 2007; Field and He 2009). In an analysis of the likely time to rebuild to this target level, recruitment variability remains among the most significant factors contributing to rebuilding success or failure by the currently adopted management target of 2026 (Field and He 2009). Rebuilding plans and targets are developed by simulating forward projections of the population under a variety of harvest rates to determine the probability of recovering to target abundance levels (40% of the unfished spawning potential) by target years that are defined by law (Punt 2003; Punt and Ralston 2007). For bocaccio, the current target is the year 2026, and while the most recent assessment projects that this rebuilding target has a greater than 75% probability of being met (at current harvest rates), this leaves an approximately 25% probability of not achieving this target. Most of the uncertainty regarding the probability of rebuilding is a consequence of recruitment stochasticity and the inability to accurately forecast future recruitment events.

Information regarding the magnitude and the determinants of impending year class strength can be of utility for tactical management actions, such as short-term catch projections and consideration of seasonal and area closures, particularly with respect to avoiding the mismatch between stock trends and management actions that took place following the 1999 year class and the overfishing declaration. In this manuscript, we will first briefly describe the early life history of bocaccio and introduce four fishery-independent sources of information regarding recruitment success as indexed by the abundance of young-of-the-year (YOY) bocaccio, and describe the methods typically used to develop recruitment indices from these data. Next we will provide a short overview of the structure and results of the most recent bocaccio assessment, including biomass trends and exploitation rates, but with a focus on the estimation of recruitment in either the most recent or in past stock assessments. Then we will evaluate the relative performance of the recruitment indices in predicting impending strong year classes (assuming that the stock assessment estimates of recruitment based on length composition data represent "true" recruitment). Finally, we will consider the performance of recruitment indices, including the spatial patterns of recruitment events and how these indices may relate to climate variables, and discuss how these indices could or should be used in future assessments and management.

DATA AND METHODS

Life history

Like all rockfish, bocaccio are primitively viviparous and bear live young at parturition. Copulation typically takes place during September–October, although fertilization is often delayed, and parturition occurs during the winter months (Moser 1967; Wyllie Echeverria, 1987). Figure 1 provides a conceptual overview of early life history stages of bocaccio following parturition. Early stage larvae (pre-flexion, approximately 0 to 20 days) are weak swimmers, however post-flexion late-stage larvae do have some swimming capabilities. Bocaccio are one of a very few number of *Sebastes* species for which data on larval abundance and distribution are available from 1951 to the present from California Cooperative Oceanic Fisheries Investigation research collections, as the larvae of most *Sebastes* species cannot be distinguished using morphological characteristics (Moser et al. 1977). These data have long been used as an indicator of population abundance in stock assessments (MacCall 2003; Field et al. 2009), under the assumption that larval abundance is a reflection of the female reproductive effort and thus spawning biomass. More recently, Ralston and MacFarlane 2010 have used these data to estimate total (rather than relative) spawning biomass. However, as year class strength for most California Current fish populations is thought to be set following parturition (Lasker 1977, Hollowed 1992), larval abundance data are not considered a reliable indicator of recruitment.

Both larval and juvenile stages are typically found in the mixed layer from 10 to 100 meters depth, (Ahlstrom 1959; Ross and Larson 2003). Pelagic juveniles are capable swimmers, and there is some evidence that both larval and juvenile stages of bocaccio tend to occur in the shallower sections of the water column (Ross and Larson 2003), which would imply greater dispersal relative to more deeply oriented larval and juvenile rockfish based on the propagule dispersal models

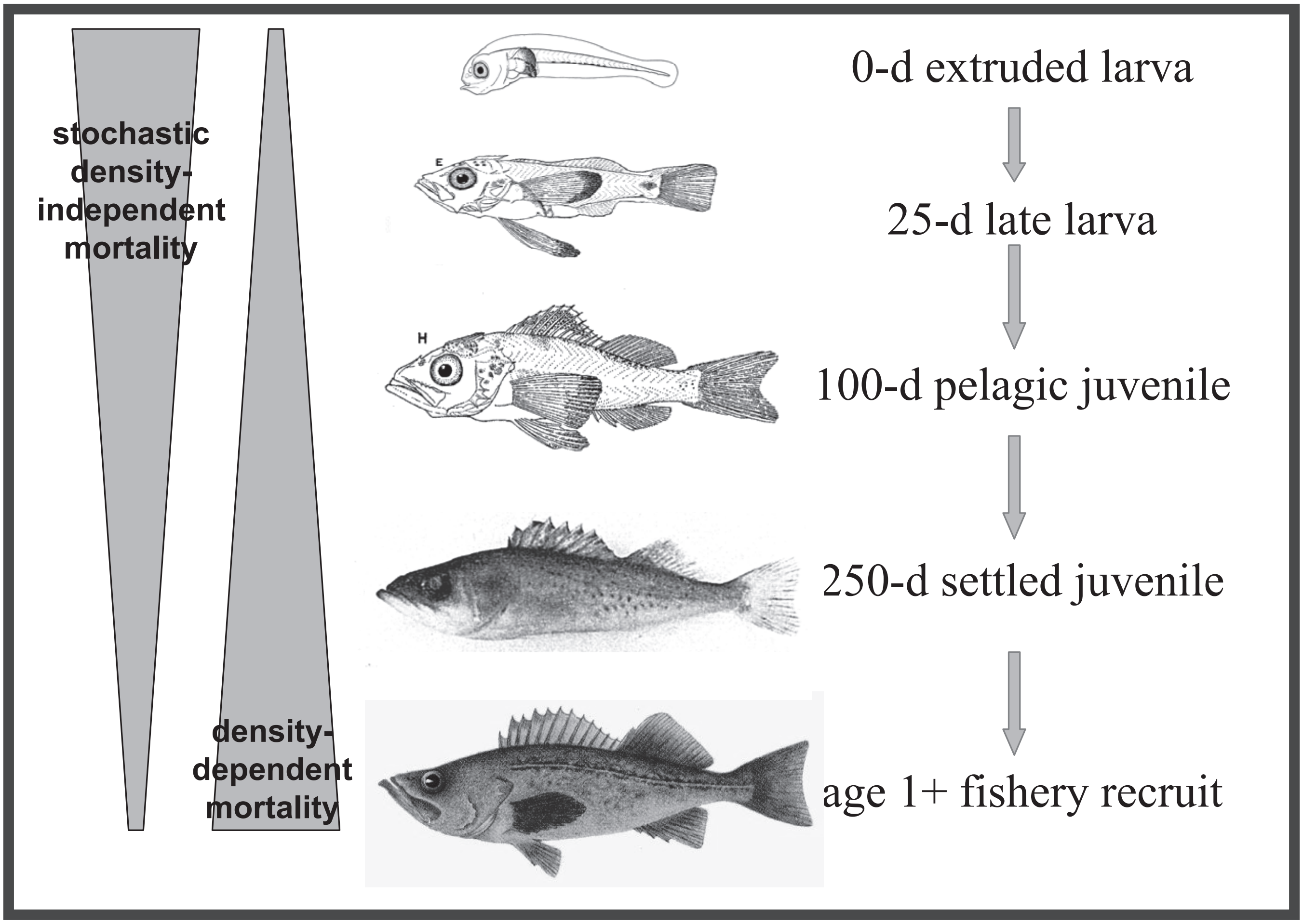

Figure 1. Ontogenetic sequence of bocaccio life history stages, as related to a conceptual model of the nature of density dependent and density independent mortality sources for each stage.

of Peterson et al. (2010). This may also lead to relatively greater dispersal to nearshore habitats immediately prior to settlement to benthic habitats, as bocaccio are entrained in surface waters that are pushed closer to the coastline than waters at depth. Settlement to nearshore and demersal habitats begins in late spring and extends throughout the summer months. Pelagic YOY typically recruit to shallow habitats, and subadult bocaccio are more common in shallower water than adults, with an apparent ontogenetic movement of adults to deeper water with size and/or age. Adult bocaccio occur in a broad range of habitats and depths, including midwater, although high densities tend to be more associated with more complex (e.g., rocky, high relief) substrates.

The rapid growth of bocaccio is also initiated at the juvenile stage; Woodbury and Ralston (1991) describe linear species-specific growth rates (and interannual variability in the same) for juvenile rockfish in approximately the first 50 to 150 days of life. Bocaccio growth rates ranged from 0.56 to 0.97 mm/day, the highest rate amongst the *Sebastes* species. This rapid growth continues into the settled juvenile and young adult stages, with fish growing to a mean size of 27 and 36 cm (fork length) by ages 1.5 and 2.5 respectively, the most rapid growth of any West Coast *Sebastes*. As bocaccio have been proven to be very difficult to age (Andrews et al. 2005; Piner et al. 2006), and age data are consequently not routinely developed or used in assessments, this rapid growth provides the primary means of estimating recruitment variability and year-class (cohort) strength from length frequency data (Ralston and Ianelli 1998). Such rapid growth is fueled by almost exclusive piscivory; Phillips (1964) reported that recently settled YOY typically preyed on other YOY rockfishes, surfperches (Embiotocidae), jack mackerel (*Trachurus symetricus*) and other small inshore species, and that such patterns of piscivory are retained throughout their life.[3]

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[3] Juvenile rockfish appear to dominate the prey spectrum of juvenile bocaccio, as the original food habits notes of Phillips report that *Sebastes jordani, S. goodei, S. mystinus* and other species represented more than 60% of all prey, while the *Sebastes* genus, primarily *S. jordani*, represented 40% of the prey of adult *S. paucispinis*. Access to Phillip's original notes was graciously provided by Tim Thomas of the Monterey Maritime Museum.

Stock assessment results

The most recent bocaccio assessment was adopted as the scientific basis for management actions by the PFMC in September 2009 (Field et al. 2009). The resulting abundance trends and recruitment estimates were highly consistent with previous assessments (MacCall 2003; MacCall 2007), although changes in the estimated catch history resulted in a generally more optimistic perception of the stock status and productivity. The modeling framework used in this assessment (and most other West Coast groundfish assessments) is the age structured model Stock Synthesis III (Methot 2009a, 2009b). The model treats a cohort, or year class, as a collection of fish whose size-at-age is characterized by a mean and a variance, such that the numbers at age are distributed across defined length bins. Several sources of both fishery-dependent (catch per unit effort data) and fishery independent (surveys of larval abundance, trawl surveys, and juvenile abundance indices) information are available for this species, and there are hundreds of thousands of length observations across various fisheries and surveys which inform population structure and estimates of recruitment. In order to evaluate the performance of the recruitment indices independently from their effect in the assessment model, the adopted stock assessment model was re-run with the recruitment indices removed. This is done to avoid contaminating the estimated "true" recruitment time series,[4] based exclusively on fishery and survey abundance and length frequency data, to recruitment indices derived solely from the suite of juvenile (age-0) abundance data explored in this manuscript.

Juvenile abundance data

We evaluate four sources of juvenile abundance data for consideration as indices of impending recruitment for bocaccio assessment and management. The first is an index of pelagic juvenile abundance based on data from a standardized midwater trawl survey specifically designed to estimate the abundance of pelagic juvenile rockfishes, and to develop indices of year-class strength for use in groundfish stock assessments (Ralston and Howard 1995). The remaining three indices reflect a slightly later life history stage for YOY rockfish, as settling or recently settled juveniles from power plant impingement studies, recreational pier fisheries, and submersible (*in situ*) surveys of fish abundance at both oil platforms and natural reef habitats in the Southern California Bight. We develop these data sources into relative recruitment indices, and subsequently contrast them with the recruitment estimates from the statistical catch-at-age model in order evaluate their performance in early detection of recruitment events. Each of these four datasets represents a different region of the range of the population of bocaccio subpopulation (fig. 2), although most of the data overlap spatially. Although the southern subpopulation is currently considered to range from the U.S./Mexico border to Cape Blanco, Oregon, recruitment of YOY bocaccio is rarely observed north of 38°N, the approximate northern boundary of the midwater trawl survey. Recruits are rarely observed between this region and the apparent center of the northern subpopulation off of Vancouver Island, Canada.

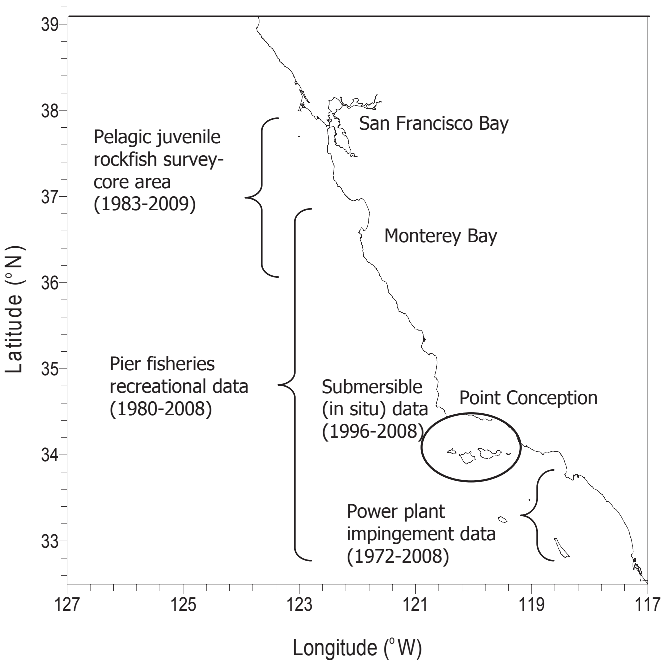

Figure 2. Spatial distribution of the four sources of data on juvenile abundance used to develop recruitment indices.

The midwater trawl survey samples YOY rockfish when they are ~100 days old, an ontogenetic stage that occurs after year-class strength is established from the larval stage, but well before cohorts recruit to commercial and recreational fisheries. This survey has encountered strong interannual variability in the abundance of the rockfishes that are routinely indexed, as well as high apparent synchrony in abundance among the ten most frequently encountered species. This synchronicity appears to be related to physical climate indicators (S. Ralston and J. Field, unpublished data). Several past assessments have used this survey as an index of year-class strength, including assessments for widow rockfish (*Sebastes entomelas*, He et al. 2005), Pacific hake (*Mer-*

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[4] In most age structured stock assessment models, annual recruitment estimates are estimated with parameters that represent lognormally distributed deviations around the "expected" recruitment based on the spawner recruit relationship (Maunder and Deriso 2003, Methot 2009). The standard deviation of these parameters, σ_R, defines the magnitude of recruitment variability. For bocaccio this value is fixed at 1 and estimated to be (effectively) slightly greater (1.1).

luccius productus, Helser et al. 2006[5]), shortbelly rockfish (*S. jordani*, Field et al. 2007) and chilipepper rockfish (*S. goodei*, Field 2008). The midwater trawl survey has taken place during May–June every year since 1983, with a historical range (1983–2003) between 36°30' to 38°20' N latitude (approximately Carmel to just north of Point Reyes, CA). Beginning in 2004, the spatial coverage expanded to effectively cover a broader range of the California Current, from Cape Mendocino in the north to the U.S./Mexico border in the south (Sakuma et al. 2006). Although the expanded survey frame is considered to be a more appropriate index for use in stock assessments[6], the time series of the expanded survey is thus far insufficient to accurately assess performance relative to the time series from the core area. Consequently, we focus on the long-term data for this evaluation, in order to address the long-term performance of the index. The survey index is calculated after the raw catch data are adjusted to a common age of 100 days to account for interannual differences in age structure (Ralston and Howard 1995).

The power plant impingement index represents data collected from coastal cooling water intakes at five Southern California electrical generating stations from 1972 to 2008 (and ongoing). These data have been previously described and published by Love et al. (1998) and Miller et al. (2009) with respect to trends in abundance of *Sebastes* species and queenfish (*Seriphus politus*), respectively (See either of these manuscripts for additional information, and the precise location of the facilities). The dataset includes observations on over 13 million fish encountered in three basic types of power plant impingement surveys (E. Miller unpublished data). The three principle "types" of survey data include fish sampled off of intake screens during normal operations (typically over a 24 hour period, however we aggregated normal operations data by month for any given plant), fish abundances estimated during heat treatments (a periodic event in which a given volume of water is treated at high temperatures to kill off biofouling organisms [mussels, barnacles, etc.; Graham et al. 1977], and all fishes are subsequently enumerated), and a third set of impingement survey data that are unique to the San Onofre power plant but were not used in this analysis due to the low frequency of occurrence of bocaccio in those data (Miller et al. 2009). Fish are identified to the lowest possible taxon, and standardized length measurements are obtained for all species. The frequency of all of these sampling methods is irregular, as a result of changes in operating schedules, regulatory requirements and changes in ownership over time, however the time series is uninterrupted at the annual scale from 1972–2008.

Recreational fisheries catch, and often target, bocaccio of all sizes throughout their range, including high catches of YOY bocaccio in pier fisheries in central and southern California during good recruitment years. Since 1980 (but excluding 1990–1992), these pier fisheries have been sampled, first by the Marine Recreational Fisheries Statistics Survey (MRFSS) and then by the California Recreational Fisheries Survey (CRFS), with data analyzed and made available on the RecFIN internet site. The stock assessment also incorporated data from studies in the 1950s and 1960s that were insightful with respect to several large historical recruitment events.[7] Catches of bocaccio typically take place during infrequent strong recruitment years from San Mateo county (south of the entrance to San Francisco Bay) through Ventura county (somewhat north of Palos Verdes peninsula in the Southern California Bight), with the highest catch rates being observed in San Luis Obispo county. Juveniles were rarely observed at piers south of Los Angeles County, and in analyzing spatial patterns of recruitment, MacCall (2003) concluded that there was no evidence of separate recruitment events north and south of Point Conception in these data. For this analysis, RecFIN records of bocaccio catch per angler hour were summarized by years, 2-month sampling periods ("waves," using only waves 3, 4 and 5, corresponding to data from May through October, as bocaccio catches in other waves were very infrequent), and counties, such that each combination constitutes a single record.

In southern California, settling juvenile bocaccio recruit to a variety of habitats, including both natural reefs and oil platforms, often in large numbers during strong recruitment years. Observational data collected from submersible (*in situ*) surveys have been used to assess the abundance of rockfish and other species on both natural reefs and oil platforms to develop absolute abundance indices for other species of rockfishes (e.g., Love et al. 2005; Yoklavich et al. 2007) and to characterize assemblages of rockfish communities (Love et al. 2009); details of the survey methods and results can be found in those publications. Over the course of these

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[5] The index evolved to a coastwide index following the 2006 assessment, but has not been used on the most recent assessment (Hamel and Stewart 2009), although it continues to be reported in the assessment documentation.

[6] See discussion in J. Hastie and S. Ralston, 2006, "Summary Report of Pre-Recruit Survey Workshop, September 13-15, 2006, Southwest Fisheries Science Center Santa Cruz, California," prepared for the PFMC (reported in April 2007 in the NWFSC Supplemental Science Report, Agenda Item E.1.b) and available online at http://www.pcouncil.org/bb/2007/0407/E1b_NWFSC3_sup.pdf.

[7] URL for recfin: http://www.recfin.org/data.htm. Historical data are from Miller and Gotschall (1965), who reported large numbers of YOY bocaccio in piers throughout central California in 1956 and 1957; an event also observed by one of the coauthors (M. Love). Large numbers of bocaccio were also observed in pier fisheries in the Central California region during the fall of 1966, for which bocaccio accounted for 26% of the 1.3 million fish estimated to have been caught in pier fisheries in that year (Miller and Odemar 1968).

surveys, bocaccio catches have been shown to be very patchily distributed, with the highest catch (observation) rates at oil platforms relative to natural reef habitats (Love et al. 2006). For all of the submersible data, we obtained dive-specific "catch" (observation) rates, which were standardized to reflect observations per 100 square meters. Only bocaccio smaller than 30 cm were included in developing the catch rate index.

All of the recruitment indices were developed using a Delta-GLM (generalized linear model) approach, consistent with the approach used in past assessments (MacCall 2003; Field et al. 2009). The Delta-GLM approach combines a binomial model for presence/absence information with a model of catch per unit effort for positive observations (Stefansson 1996, Maunder and Punt 2004). Akaike's Information Criterion (AIC) was used to determine the appropriate error distributions and to assess the most parsimonious model with respect to the number of covariates (Dick 2004). Year effects are independently estimated covariates which reflect a relative index of abundance for each year, error estimates for these parameters are developed with a jackknife routine. Seasonal (or temporal) effects are estimated using month, two-month periods, or season as covariates depending upon the resolution of the original data. For the midwater trawl survey, which takes place over an approximate 50 day period in May and June, bins of 10 Julian day periods are used, while two month periods ("waves") were used for the recreational pier fisheries data, one month periods were used for the impingement data, and no temporal effects were used for the submersible data (which only takes place during weather windows in late fall). Similarly, spatial effects are described by spatial covariates, represented by individual trawl stations for the midwater trawl survey data, counties for the recreational pier fishery data, individual power plants for the impingement data, and habitat types (oil rig base, oil rig midwater, and natural reef) as well as depth for the submersible data. For the impingement data, "survey type" was also included as a factor, with only two types estimated, these being the "normal operations" and "heat treatment" types described previously.

The resulting recruitment indices were compared to the estimated recruitments from the stock assessment. The natural logarithm of both the predictor (indices) and response (assessment recruits) values were used for the regression, to best mimic the behavior of stock assessment models which perform maximum likelihood parameter estimations (Maunder and Punt 2004, Methot 2009). In addition to comparing the results of the recruitment indices to the results of the assessment, we evaluate the extent to which the recruitment indices improve the predictive ability of the stock assessment model. This is done by retrospectively estimating the magnitude and confidence in estimates of one of the strongest recruitment events in recent years, the 1999 year class, when data are sequentially removed from the model going backwards in time. By sequentially removing entire years of data for two models with and without the recruitment indices we can compare both the absolute recruitment estimates and the confidence in those estimates. The estimated precision of the absolute values of annual recruitment are provided by the asymptotic approximation used in the stock synthesis model (Methot 2009a, b). This allows us to better evaluate how well the recruitment indices may, or may not, perform with respect to predicting strong incoming year classes of bocaccio.

RESULTS

The bocaccio stock assessment model that was re-run without the recruitment indices suggested a biomass trend and recruitment estimates nearly identical to those from the adopted assessment model (fig. 3). As with bocaccio assessments done over the past 10 years, the results indicate that the spawning output (a reflection of the spawning biomass, accounting for the greater fecundity of larger fish) fluctuated significantly through the 1960s and 1970s, peaking near 1970 and declined rapidly through the rest of the 1980s and 1990s. These declines were primarily a result of high exploitation rates, although a period of anomalously poor recruitment appears to have taken place throughout most of the 1990s. The estimated recruitment time series illustrates that recruitment has a high degree of interannual variability, but that the relative size of the strong recruitment events have declined in concert with the decline of spawning output through the year 2000. Since that time, fishing mortality has declined markedly due to severe management restrictions, and the stock has been increasing at a fairly rapid rate coincident with a series of several relatively strong year classes (1999, 2003, 2005). Note that the differences in the magnitude of recruitment events in the late 1950s and early 1960s, shown in Figure 3, results from exclusion of the recreational pier fishery time series in the model used for evaluating the performance of recruitment indices, as there were a mix of qualitative and quantitative data used in the full assessment.

For all of the models, several alternative model structures were explored and evaluated using AIC, and the most parsimonious model (explaining the greatest amount of relative variance with the lowest number of parameters) was used. Similarly, for each of the recruitment data sources, the year effects from the delta-GLM models led to an improvement in the AIC, indicating that the year effects provided information potentially usable as a recruitment index. We provide a summary

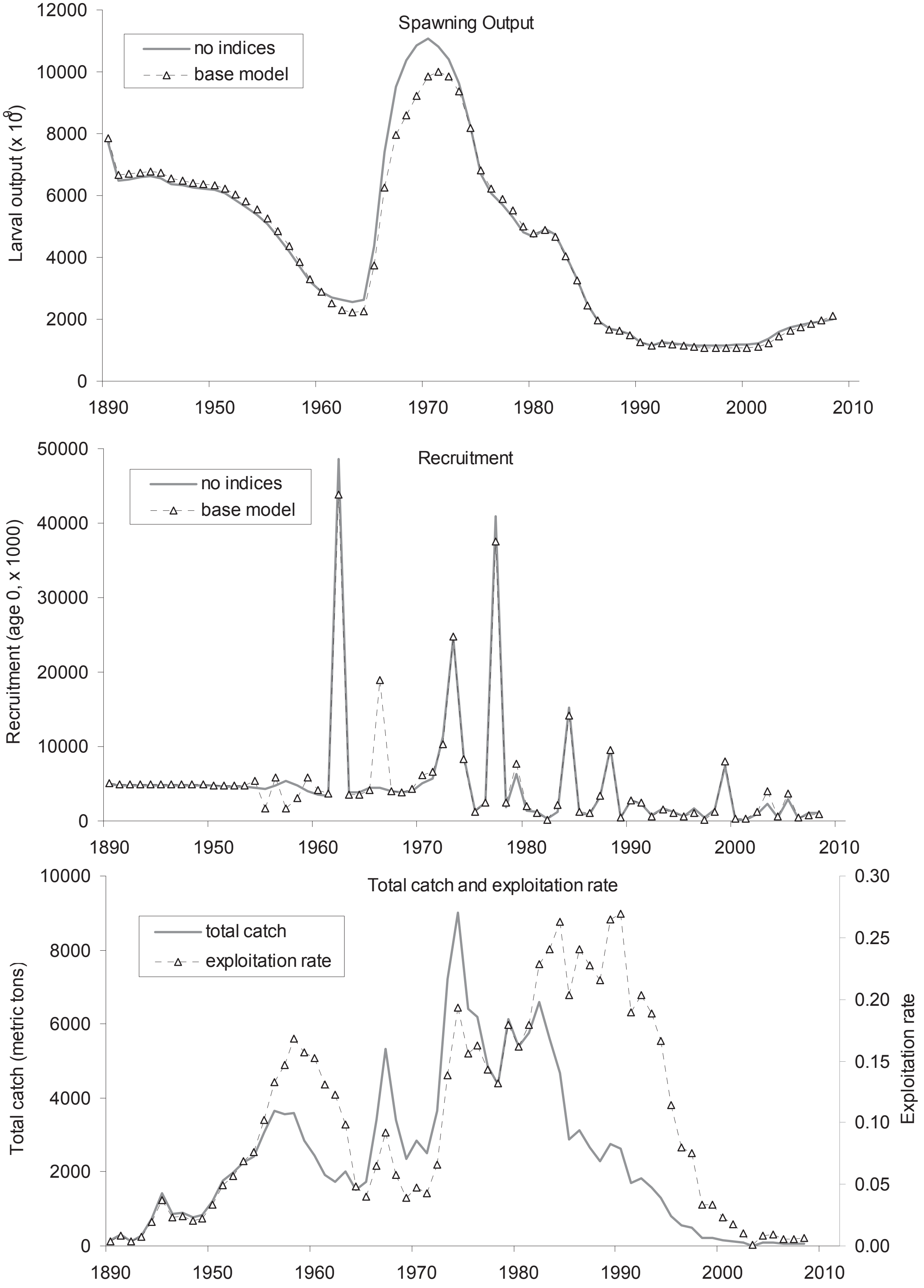

Figure 3. Estimated reproductive potential (spawning output) and recruitment of bocaccio from the base 2009 model (dashed lines) relative to the same model in which all juvenile indices are removed (solid lines), to avoid confounding the performance of the various indices.

TABLE 1
Summary of data availability, the number of parameter estimated, and GLM model performance for the four recruitment indices.

	Pelagic trawl	Recreational Pier	Power Plant Impingement	Delta Submersible
Time period	1983–2008	1980–2008	1972–2008	1995–2008
Number of years*	17	19	31	13
Temporal parameters	6	0	12	0
Spatial parameters	34	6	6	7
Data points	2225	312	2628	914
Coefficients of variation				
average	0.56	0.73	0.60	0.41
maximum	0.87	1.11	0.83	0.63
minimum	0.34	0.40	0.37	0.30
Change to AIC				
Remove year				
binomial	123.3	0.2	36.7	6.4
positive	75.4	3.9	78.2	5.0
Remove spatial				
binomial	18.9	45.6	25.5	41.3
positive	–9.0	66.2	–5.7	87.6
Remove temporal				
binomial	0.5	n/a	5.8	n/a
positive	7.6	n/a	14.3	n/a
Null model				
binomial	142.7	66.2	71.6	51.3
positive	93.1	49.6	167.4	92.8

of available data for each index, listing the time period for which data are available, the number of observations, the number of covariates used in the GLM, and both the null and final model AIC (tab. 1). The mean, and range, of the estimated coefficients of variation that result from the jackknife routine are also reported in this table. We focus subsequent discussion on the year effects (covariates) for each model, although the intra-annual (seasonal) and spatial covariates are also relevant.

All four of the resulting indices tracked most of the strong recruitment events estimated from the assessment model (fig. 4a-d). All of the indices were significantly correlated to the assessment estimates of recruitment (at the $p<0.05$ level), with coefficients of determination (R^2) values ranging from 0.28 for the pier fishery index to 0.58 for the power plant impingement data, with the juvenile trawl survey and submersible survey having coefficients of 0.35 and 0.41 respectively. One particular challenge with this type of model is how to deal with missing data. Many indices have years with insufficient numbers of positive observations to estimate a year effect (generally speaking, two positive observations in a given year are necessary), despite having fairly comprehensive sampling coverage (and data) overall. For the correlations shown here, those years have been dropped, although one approach to including that information is to use some fraction of the minimum estimated value for years with insufficient numbers of positive observations (for example, half). This is consistent with the practice frequently used in stock assessments. Although admittedly ad-hoc, this approach recognizes that there is information in the data regarding the relative strength of a given year class when data are collected and no juveniles are observed (the year class is presumably weak in such circumstances, although differences in sampling intensity are also relevant). The juvenile trawl survey index, the pier fishery index and the impingement survey index have eight, ten, and five years that meet this criteria respectively (there are no years of submersible data with this problem); if half of the minimum estimated values are used for these years and added to the regressions, the resulting R^2 values are 0.21, 0.45 and 0.46 respectively. Thus, the information content of the juvenile survey and the impingement survey are slightly degraded, that of the pier fishery is slightly improved, if this approach is adopted.

Another challenge is how to address the problem of errors in variables (EIV). In ordinary regression models, the independent variables are assumed to be measured without error, such that all error is a function of the dependent variable. This issue has a deep history in fisheries science and in the fisheries literature (Ricker 1975, Hilborn and Walters 1992), a comprehensive review of which is beyond the scope of this manuscript, but it is worth noting that the issue remains generally unresolved (Kimura 2000). We explored several approaches to addressing the issue, ultimately settling upon reporting both the "standard" linear regression relationship and the geometric mean estimate of the functional regression (GM regression; Ricker 1975), both of which are presented in Figure 4. Note that the coefficients of variation are unchanged among the two models, it is

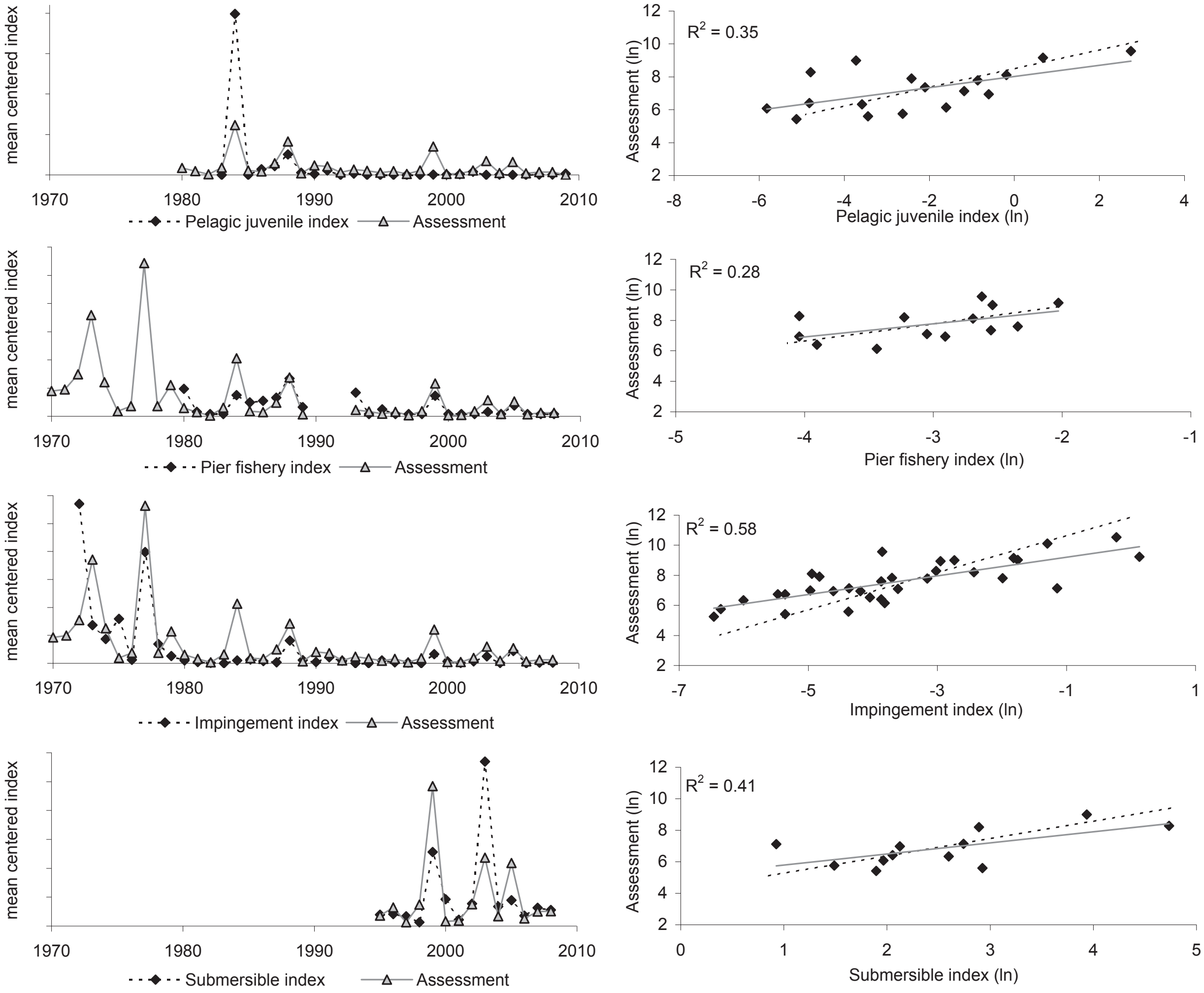

Figure 4. Mean-centered estimates of recruitment from the base stock assessment model (absent recruitment index data) relative to mean-centered indices of juvenile abundance from the data sources reported here (left panels). Corresponding regression results for each index (right panels), with both ordinary least squares regression (solid grey line) and geometric mean regression (dotted black line).

only the slope and intercept parameters that differ, and neither of these parameters are utilized further for the purposes of this manuscript.

While the recreational pier fishery index has a relatively modest correlation to assessment estimates of recruitment, this index does capture the magnitude of the 1984, 1988 and importantly the 1999 year class. The midwater trawl survey was among the noisier of indices (R^2 = 0.35), although this index captured the magnitude of the 1984 and (perhaps to a lesser extent) the 1988 year classes, there have been very few bocaccio juveniles observed in the catches since that time. Consequently, this index did not detect the strong year classes observed in 1999, 2003 and 2005, which may be an artifact of changes in the relative distribution of spawning biomass (and subsequent recruitment) over recent years. In fact, the failure of the juvenile survey to capture the magnitude of the 1999 year class for bocaccio or any other species contributed to the decision to expand the geographic range of the juvenile rockfish survey, under the assumption that expanding the survey accross space would lead to more effective predictions of coastwide recruitment events (Sakuma et al. 2006). The power plant impingement index also compares favorably with the stock assessment estimates of recruitment (R^2 = 0.58), and as the only index that precedes the 1980s it is reassuring to observe that the index does particularly well with respect to capturing the magnitude of the 1973, 1977 and 1988 year classes. This index also captures apparently strong recruitment in 2005 and 2007, which are now showing up in fishery data. Interestingly, this index appears to miss the magnitude of the 1984 and 1999 year classes, although it does recognize some recruitment in both of those years. Finally, although it is the shortest of the time series evaluated here, the submersible index also performs fairly

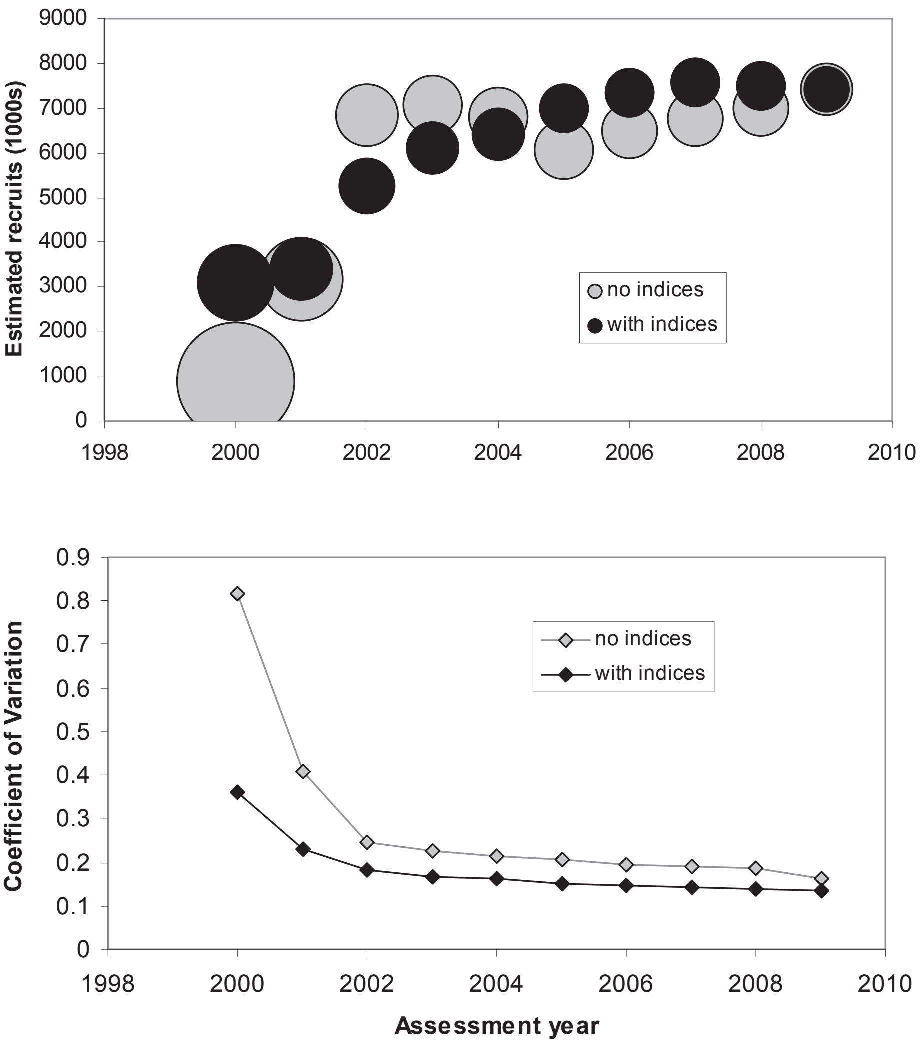

Figure 5a (top). Relative information content of the 1999 recruitment from retrospective bocaccio assessment models with (black) and without (grey) the juvenile indices developed in this manuscruipt. Size of bubbles corresponds to the CV of the estimates, which are also shown in Figure 5b (bottom).

well in capturing the magnitude of large year classes (R^2 = 0.41), although it overestimates the 2003 and underestimates the 1999 year class.

The comparison of estimates of the magnitude of the 1999 year class with retrospective model runs with and without all of the recruitment indices is shown (fig. 5a), along with the estimates of the CV of that recruitment point estimate in subsequent years. Here, we can see that the information content of informative indices is limited to the first 1–2 years before fish show up in fishery and survey data. For example, an assessment done in 2000 using data through 1999 would predict considerably greater recruitment with the recruitment indices than without them, due to the limited information available on that cohort available in length frequency data and the statistical "penalties" imposed on data with low information content in the model (thus the first two years represent primarily a recruitment estimation drawn from the spawner recruit curve), with considerably greater confidence (CV of 0.38 versus 0.85). However, by 2001 fishery-based length frequency data for bocaccio have already demonstrated the presence of the 1999 year class, and although the recruitment indices lead to a smaller variance estimate of that year class strength, the magnitude is generally well established based on simply the recreational fishery length composition data alone. As this example includes all of the recruitment indices in the model simultaneously, which would not necessarily be an optimal approach in a typical assessment, the difference among the estimated recruitments after the second year is negligible. That these recruitment events appear so strongly defined so early in the fishery reflects the unique life history of bocaccio, which grow very rapidly and are encountered by sport fisheries in particular at very young ages, whereas other *Sebastes* species are typically not vulner-

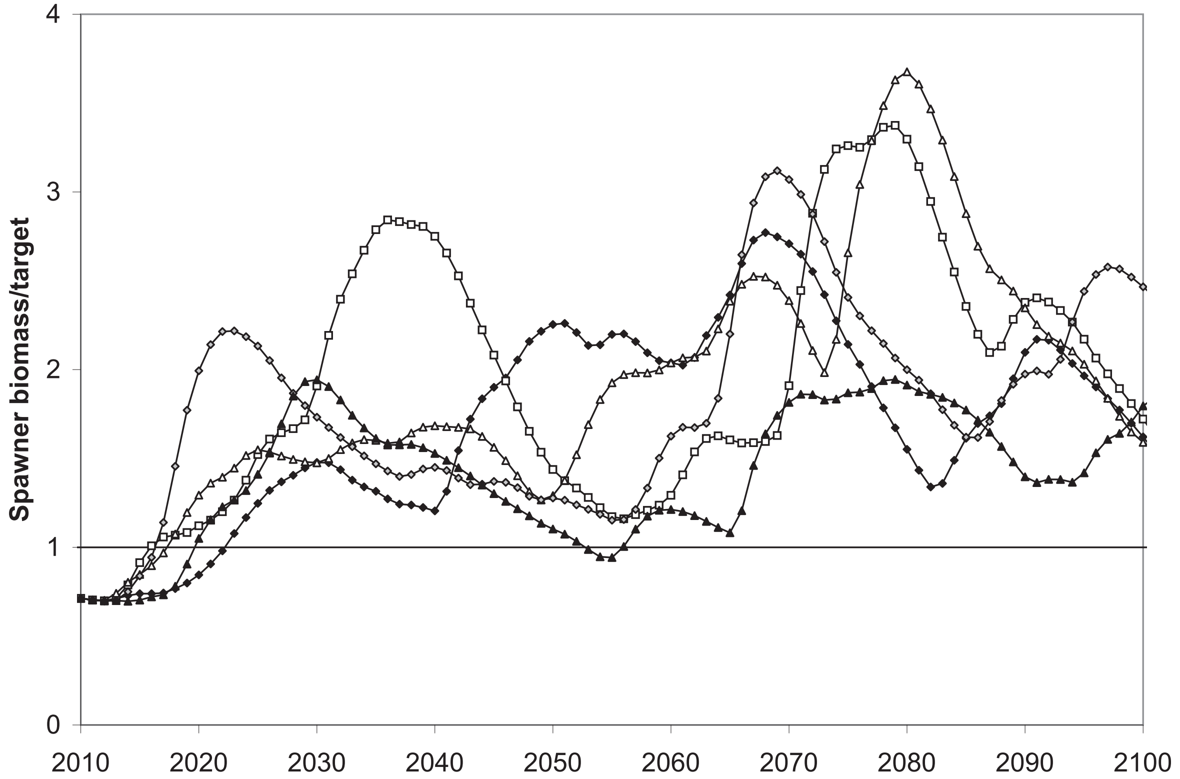

Figure 6. Five example trajectories, of the thousands simulated in the rebuilding analysis for bocaccio rockfish, illustrating the significance of highly variable recruitment events on population trends (harvest rates are constant set to current level in all scenarios). These individual trajectories are used to assess the probability of rebuilding by management targets.

able to fisheries until individuals reach ages of 3–10 years. For such slower-growing species, recruitment indices would be more useful in assessing abundance and productivity in the long term. For bocaccio, the period in which recruitment indices are useful in forecasting productivity is relatively brief (one to two years), although given the significance of changing bocaccio bycatch rates on other fisheries, improved forecasting of such recruitment events is still of great importance to resource management activities.

DISCUSSION

The southern bocaccio population is fortunate to have multiple sources of informative data that can provide estimates of the magnitude of recruitment events. As such, bocaccio are a good case study for evaluating the effectiveness of pre-recruit indices for West Coast groundfish, particularly as the correlation coefficients from this evaluation are comparable to or considerably greater than the correlations between the spawner recruit curve and subsequent recruitments. Currently, only two of these indices (the midwater trawl survey, albeit an index based on greater spatial resolution and shorter duration, and the recreational pier fishery index) are used are used in the stock assessment. Both of the other indices described here hold considerable potential for future assessments, and should be evaluated accordingly in the future. Moreover, the performance of most these indices is consistent with what DeOliveira and Butterworth (2005) describe as a reasonable threshold for the application of indicators (albeit, environmental indicators in their case) for improving stock assessment models, for which indicators should be able to explain approximately 50% or more of the total variation in recruitment.

Moreover, the data from these recruitment indices could provide insights into the physical and biological conditions that either enable or repress strong recruitment events. The high recruitment variability exhibited by this species leads to considerable uncertainty with respect to the estimated time to rebuild to target levels for this stock, as illustrated by five equally plausible trajectories of stock biomass developed as a part of a comprehensive rebuilding analysis (fig. 6, from Field and He 2009). Essentially, thousands of these individual trajectories are used to assess the probability of rebuilding by management targets, using the methods developed in Punt (2003). The rebuilding analysis also indicates that upon rebuilding to target biomass levels, the chance of returning to an overfished condition in the future remains significant if the default harvest policies are followed, simply due to the highly variable nature of recruitment for this stock. Comparable results have been described for Pacific hake (*Merluccius productus*), another species with highly variable recruitment and population trajectories (Haltuch et al. 2008). Consequently, for stocks with such high variability in recruitment, such that harvest policies based on constant harvest rates may not be optimal for either ecological or socio-economic stability.

The potential for bocaccio recruitment indices to provide insights beyond just the bocaccio stock should also be explored. Several other commercially and ecologically important species have recruitment trends that covary with bocaccio rockfish, including chilipepper and Pacific hake. There is also some synchrony in recruitment variability of other species, for example nearly all of the assessed groundfish stocks on the U.S. west coast experienced good to excellent recruitment in 1999, and most also experienced strong recruitment in 1980 and 1984. Similarly, there tends to be poor recruitment during strong El Niño events, such as those 1982–83, 1986–87 and 1997–98 El Niño events (it is noteworthy to consider that many of the strongest recruitment events for West Coast groundfish have taken place in years that immediately followed these El Niño events). However, thus far the degree of synchrony in groundfish recruitment has been relatively modest; the leading principal components explain 25–45% of the variance for groundfish recruitment deviations for well-informed stocks (range reflects the subset of stocks evaluated), which is comparable to results for other regions (Mueter et al. 2007). While suggestive of some generalized response to ocean conditions, this fraction of the total variance is relatively modest in comparison to the high amount of synchrony observed in juvenile rockfish abundance in the pelagic stage, where the leading principle component explains 85% of the variance for the ten most abundant rockfish species (J. Field and S. Ralston, unpublished data). The spatial component of recruitment for shelf rockfish has also been shown to be strongly coherent over broad spatial scales (Field and Ralston 2005), although this reflects post-settlement and recruitment based primarily on fishery data and may not reflect the patchy nature of recruitment prior to dispersal. All of these observations suggest that many of the processes contributing to variable year class strength for rockfish, and perhaps other groundfish, occur at the post settlement stage, and vary considerably among species, again consistent with expectations for most marine species more generally (Ralston and Howard 1995, Houde 2008). For bocaccio, a closer evaluation of both the synchrony and the spatial structure of strong recruitment events using the different indices could lead to insights regarding the nature of the physical and biological ocean conditions that lead to strong year classes.

The geographic frame of the various indices also appears to be informative with respect to stock structure trends. The data used in the most recent assessment suggest that the stock biomass south of Point Conception appears to be rebuilding at a more rapid rate than to the north, based on the relative influence of data from these respective regions. The patterns observed in the recruitment index time series are consistent with this, in that the strong recruitment in 1984 seemed to be a "northern" recruitment event. This recruitment event was strongest in the central California data, including both the midwater trawl survey and the recreational pier fishery index (particularly Santa Cruz and San Luis Obispo counties). Since the 1990s however, the signal from the pier survey index has been dominated by San Luis Obispo and Santa Barbara Counties, and both the impingement index and the visual survey index suggest that recruitment south of Point Conception is strongly correlated with the model estimates of recruitment for the entire stock. This too is consistent with the abundance indices that suggest greater population increases in the southern part of the stock range relative to the central portion (Field et al. 2009), indicating that both recruitment and rebuilding may have a regional component.

With respect to further utility of these recruitment indicators, it may be that they are also useful for managers contemplating the duration of fishing seasons and seasonal depth restrictions. As one of several rebuilding species of rockfish on the West Coast, bocaccio is a constraining species for fisheries on healthy populations, and regulations focus on minimizing the catch of bocaccio while allowing opportunities to exploit more productive stocks. Thus, effective forecasting catches of this constraining species is key for maintaining fishing opportunities, while avoiding the chance of exceeding the allowable catch of bocaccio. Given the dramatic spikes in both catch rates and the percentage of the total southern California rockfish catch that is bocaccio following strong recruitment events (fig. 7)[8], improved predictions of future catch rates of constraining species could be of considerable value not only in assessments that include future year projections, but in year-to-year management activities as well. The latter point may be particularly true in a management regime in which the bocaccio stock assessment is performed every two years at most, and with a greater lag between the data and the time period in which the results are applied to management, making "fine tuning" of management measures

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[8] There are statistically significant relationships among these variables, the R^2 between the assessment recruitment and a one-year lagged change in the percentage of all southern California rockfish (with an arcsine transform to account for proportionality) is 0.34, while the R^2 between recruits and one year lagged catch per angler hour is 0.35. However, a linear regression may be too simplistic, as both relationships show signs of non-linearity.

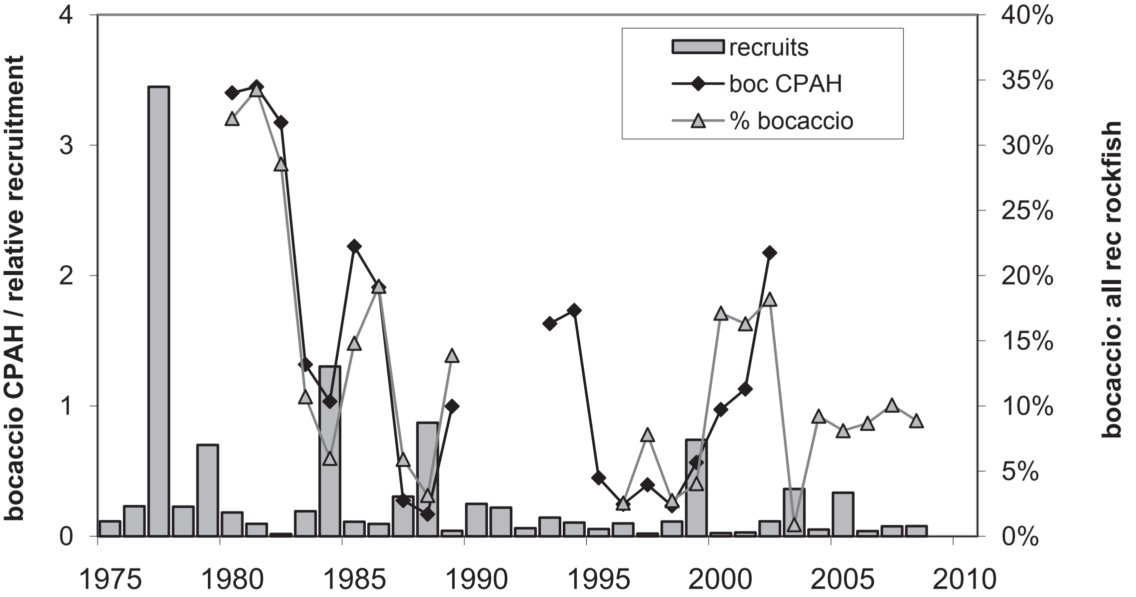

Figure 7. Estimated annual recruitment (grey bars) relative to Southern California recreational fishery catch rates (catch per angler hour, black line) and to the percentage of the total recreational catch represented by bocaccio (grey line).

in response to changing conditions even more important. In such a scenario, integrating all of the indices into a single indicator of impending recruitment, using principle components analysis or comparable means, might be more useful for management with respect to predicting spikes in bocaccio catches in recreational fisheries.

We have shown that there are several sources of information that could improve the prediction of strong year classes in stock assessment of bocaccio. Such information is useful to assessing stock status and productivity, to tracking rebuilding success, and likely to improving real time management of commercial and recreational fisheries that routinely encounter large numbers of young bocaccio during strong recruitment events. Additionally, these data could be informative with respect to recruitment trends for species of groundfish that tend to covary with bocaccio, and could ultimately lead to an improved understanding of the oceanographic processes that drive variable recruitment. In the long term, such information should aid both scientists and managers, by improving the ability to monitor and respond to the variable abundance and catch rates of bocaccio, as well as by leading to a greater appreciation for the connectivity between environmental changes in coastal ecosystems and fisheries productivity.

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LITERATURE CITED

Ahlstrom, H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv. Fish. Bull. No. 161, 60:107–146.

Berkeley, S. A., M. A. Hixon, R. J. Larson and M. S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29:23–32.

DeOliveira, J. A. A. and D. S. Butterworth. 2005. Limits to the use of environmental indices to reduce risk and (or) increase yield in the South African anchovy fishery. Afr. J. Mar. Sci. 27:191–203.

Dick, E. J. 2004. Beyond 'lognormal versus gamma': discrimination among error distributions for generalized linear models. Fish. Res. 70:351–366.

Dorn, M. W. 2002. Advice on West Coast rockfish harvest rates from Bayesian meta-analysis of stock-recruit relationships. N. Amer. J. Fish. Man. 22:280–300.

Field, J. C. 2008. Status of the Chilipepper rockfish, *Sebastes goodei*, in 2007. *In* Status of the Pacific Coast Groundfish Fishery Through 2007, Stock Assessment and Fishery Evaluation: Stock Assessments and Rebuilding Analyses Portland, OR: Pacific Fishery Management Council.

Field, J. C. and S. Ralston. 2005. Spatial variability in California Current rockfish recruitment events. Can. J. Fish. Aq. Sci. 62:2199–2210.

Field, J. C. and X. He. 2009. Bocaccio Rebuilding Analysis for 2009. Pacific Fishery Management Council Stock Assessment and Fishery Evaluation. Portland, OR.

Field, J. C., E. J. Dick, M. Key, M. Lowry, Y. Lucero, A. MacCall, D. Pearson, S. Ralston, W. Sydeman and J. Thayer. 2007. Population dynamics of an unexploited rockfish, *Sebastes jordani*, in the California Current. pp 451–472 in J. Heifetz, J. Dicosimo, A.J. Gharrett, M.S. Love, V. M. O'connell and R.D. Stanley (editors) Proceedings of the Lowell-Wakefield Symposium on the Biology, Assessment and Management of North Pacific Rockfish. University of Alaska Sea Grant: Anchorage, Alaska.

Field, J. C., E. J. Dick, D. Pearson and A. D. MacCall. 2009. Status of bocaccio, *Sebastes paucispinis*, in the Conception, Monterey and Eureka INPFC areas for 2009. Pacific Fishery Management Council Stock Assessment and Fishery Evaluation. Portland, OR.

Graham, J. W., J. N. Stock, and P. H. Benson. 1977. Further studies on the use of heat treatment to control biofouling in seawater cooling systems. Oceans '77 23A:1–6.

Haltuch, M. A., A. E. Punt and M. W. Dorn. 2008. Evaluating alternative estimators of fishery management reference points. Fish. Res. 94:290–303.

Hamel, O. S. and I. J. Stewart. 2009. Stock Assessment of Pacific Hake, *Merluccius productus*, (a.k.a. Whiting) in U.S. and Canadian Waters in 2009. *In* Status of the Pacific Coast Groundfish Fishery Through 2007, Stock Assessment and Fishery Evaluation: Stock Assessments and Rebuilding Analyses Portland, OR: Pacific Fishery Management Council.

He, X., D. Pearson, E. J. Dick, J. Field, S. Ralston and A. D. MacCall. 2006. Status of the Widow Rockfish Resource in 2005. *In* Volume 3: Status of the Pacific Coast Groundfish Fishery Through 2005, Stock Assessment and Fishery Evaluation: Stock Assessments and Rebuilding Analyses Portland, OR: Pacific Fishery Management Council.

Helser, T., I. J. Stewart, G. Fleischer and S Martell. 2006. Stock Assessment of Pacific Hake (Whiting) in U.S. and Canadian Waters in 2006. *In* Volume 7: Status of the Pacific Coast Groundfish Fishery Through 2005, Stock Assessment and Fishery Evaluation Portland, OR: Pacific Fishery Management Council.

Hilborn, R. and C. J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall: New York.

Hollowed, A. B. 1992. Spatial and temporal distributions of Pacific hake, *Merluccius productus*, larvae and estimates of survival during early life stages. Calif. Coop. Oceanic Fish. Invest. Rep. 33: 100–123.

Houde, E. D. 2008. Emerging from Hjort's Shadow. J. Nw. Atl. Fish. Sci. 41:53–70.

Kimura, D. K. 2000. Using nonlinear functional relastionship regression to fit fisheries models. Can. J. Fish. Aquat. Sci. 47: 160–170.

Lasker, R. 1987. Use of fish eggs and larvae in probing some major problems in fisheries and aquaculture. Pages 1–16 in R. D. Hoyt, editor. 10th Annual Larval Fish Conference, American Fisheries Society Symposium 2, Bethesda, Maryland.

Love, M. S., J. E. Caselle and K. Herbinson. 1998. Declines in nearshore rockfish recruitment and populations in the southern California Bight as measured by impingement rates in coastal electrical power generating stations. Fish. Bull. 96:492–501.

Love, M. S., M. Yoklavich, and L. K. Thorsteinson. 2002. The rockfishes of the northeast Pacific. University of California Press, Berkeley.

Love, M. S., D. M. Schroeder and W.H. Lenarz. 2005. Distribution of bocaccio (*Sebastes paucispinis*) and cowcod (*Sebastes levis*) around oil platforms and natural outcrops off California with implications for larval production. Bull. Mar. Sci. 77:397–408.

Love, M. S., D. M. Schroeder, W. Lenarz, A. MacCall, A. S. Bull and L. Thorsteinson. 2006. Potential use of offshore marine structures in rebuilding an overfished rockfish species, bocaccio (*Sebastes paucispinis*). Fish. Bull. 104:383–390.

Love, M. S., M. Yoklavich and D. M. Schroeder. 2009. Demersal fish assemblages in the Southern California bight based on visual surveys in deep water. Env. Bio. Fish. 84:55–68.

MacCall, A. D. 2002. Status of bocaccio off California in 2002. *In* Status of the Pacific Coast Groundfish Fishery Through 2002 Stock Assessment and Fishery Evaluation Vol 1. Pacific Fishery Management Council.

MacCall, A. D. 2003a. Status of bocaccio off California in 2003. *In* Status of the Pacific Coast Groundfish Fishery Through 2003, Stock Assessment and Fishery Evaluation: Stock Assessments and Rebuilding Analyses Portland, OR: Pacific Fishery Management Council.

Maunder, M. N. and R. B. Deriso. 2003. Estimation of recruitment in catch-at-age models. Can. J. Fish. Aq. Sci. 60:1204–1216.

Maunder, M. N. and A. E. Punt. 2004. Standardizing catch and effort data: a review of recent approaches. Fish. Res. 70:141–159.

Methot, R. D. 2009a. Stock assessment: operational models in support of fisheries management. *In* R.J. Beamish and B.J. Rothschild (editors) The Future of Fisheries Science in North America, 137 Fish & Fisheries Series. Springer Science and Business Media.

Methot, R. D. 2009b. User manual for Stock Synthesis Model Version 3.03a. May 11, 2009.

Miller, D. J. and D. Gotshall. 1965. Ocean sportfish catch and effort from Oregon to Point Arguello, California. California Department of Fish and Game Fish Bulletin 130: 135 pp.

Miller, D. J. and M. W. Odemar. 1968. Ocean sportfish catch and effort from the Golden Gate to Yankee Point, Monterey County, California for the year 1966. California Department of Fish and Game Marine Resources Operations Reference No. 68–15.

Miller, E. F., J. P. Williams, D. J. Pondella and K. T. Herbinson. 2009. Life History, Ecology, and Long-term Demographics of Queenfish. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 1:187–199.

Moser, H. G. 1967. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773–797.

Mueter, F. J., J. L. Boldt, B. A. Megrey and R. M. Peterman. 2007. Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation and regime shifts. Can. J. Fish. Aq. Sci. 64:911–927.

Peterson, C. H., P. T. Drake, C. A. Edwards and S. Ralston. 2010. A numerical study of inferred rockfish larval dispersal along the central California coast. Fish. Oceanogr. 19:21-41.

Phillips, J. B. 1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Cal. Dep. Fish Game Bull. 126:1–70.

Punt, A. E. 2003. Evaluating the efficacy of managing West Coast groundfish resources through simulations. Fish. Bull. 101:860–873.

Punt, A. E. and S. Ralston. 2007. A management strategy evaluation of rebuilding revision rules for overfished rockfish stocks. Pp. 329–353 *In* J. Heifetz, J. Dicosimo, A. J. Gharrett, M. S. Love, V. M. O'Connell and R. D. Stanley (editors) Proceedings of the Lowell-Wakefield Symposium on the Biology, Assessment and Management of North Pacific Rockfish. University of Alaska Sea Grant: Anchorage, Alaska.

Ralston, S. and D. F. Howard. 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. Fish Bull. 93:710–720.

Ralston, S. and J. N. Ianelli. 1998. When lengths are better than ages: The complex case of bocaccio. Pp. 451–468 *In* F. Funk, T. J. Quinn II, J. Heifetz, J. N. Ianelli, J. E. Powers, J. F. Schweigert, P. J. Sullivan, and C.-I. Zhang (eds.), Fishery Stock Assessment Models. Alaska Sea Grant College Program report No. AK-SG-98-01. Univ. of Alaska, Fairbanks. 1037 pp.

Ralston, S. and B. R. MacFarlane. 2010. Population estimation of bocaccio (*Sebastes paucispinis*) based on larval production. Can. J. Fish. Aquat. Sci. 67: 1005–1020.

Ricker, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409–434.

Ross, J. R. M. and R. J. Larson. 2003. Influence of water column stratification on the depth distributions of pelagic juvenile rockfishes off central California. Calif. Coop. Oceanic Fish. Invest. Rep. 44:65–75.

Sakuma, K. M., S. Ralston, and V. G. Wespestad. 2006. Interannual and spatial variation in young-of-the-year rockfish, *Sebastes* spp.: expanding and coordinating the sampling frame. Calif. Coop. Oceanic Fish. Invest. Rep. 47:127–139.

Stanley, R. D., M. McAllister, P. Starr and N. Olsen. 2009. Stock assessment for bocaccio (*Sebastes paucispinis*) in British Columbia waters. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/055. http://www.dfo-mpo.gc.ca/csas.

Stefansson, G. 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. ICES J. Mar. Sci. 53:577–588.

Woodbury, D. P., and S. Ralston. 1991. Interannual variation in growth rates and back-calculated birthdate distributions of pelagic juvenile rockfish (*Sebastes* spp.) off the central California coast. Fish. Bull. 89:523–533.

Wyllie Echeverria, T. 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. Fish. Bull. 85:229–250.

Yoklavich, M., M. Love, and K. Forney. 2007. A fishery-independent assessment of an overfished rockfish stock, cowcod (*Sebastes levis*), using direct observations from an occupied submersible. Can. J. Fish. Aq. Sci. 64:1795–1804.

CAN WE PREDICT INTERANNUAL AND REGIONAL VARIATION IN DELIVERY OF PELAGIC JUVENILES TO NEARSHORE POPULATIONS OF ROCKFISHES (GENUS *SEBASTES*) USING SIMPLE PROXIES OF OCEAN CONDITIONS?

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ABSTRACT

Rates of larval delivery and population replenishment of many marine species, including nearshore temperate reef fishes are notoriously variable between years and across geographic ranges. The inability to explain and predict this variation hampers our understanding and forecasting of population dynamics and our attempts to manage fisheries proactively. Environmental proxies of interannual and regional variation in rates of population replenishment may provide scientists and managers with tools to forecast regional stock dynamics and adjust rates of fishing mortality to maintain sustainable fisheries. Rockfish (genus *Sebastes*) constitute important fisheries throughout the California Current large marine ecosystem. Since 2000, we monitored rates of onshore delivery of pelagic juveniles (defined here as settlement) of two groups of nearshore rockfishes (kelp, gopher, black and yellow and copper [KGBC] and olive, yellowtail, and black [OYTB]) using artificial collectors placed just offshore of rocky reefs at five locations ranging from Southern California to Northern Monterey Bay. These species complexes are based on similarities in their life history and larval attributes. We attempt to relate interannual patterns of settlement to easily accessible, regional indices of ocean conditions including upwelling, alongshore transport, sea surface temperature (SST) and Chlorophyll-a (Chl-a). In the Santa Barbara channel locations (south of Pt. Conception), interannual variation in settlement of the two species groups is concordant and settlement is strongly and positively correlated to regional upwelling in summer months. North of Pt. Conception, timing of settlement of the two species groups is less concordant. In that region, settlement of KGBC was also positively correlated with summer upwelling, while that of the OYTB group was highly variable and poorly related to any ocean indices. In general, upwelling and alongshore transport were better predictors of delivery than SST or Chl-a. Our results indicate that (1) readily available oceanographic metrics like upwelling indices can be used as reasonable proxies for explaining and forecasting actual rates of replenishment (i.e. delivery of pelagic juveniles to nearshore adult populations) and (2) recognition of the regional variation in these relationships will better inform efforts to more accurately forecast stock dynamics, especially at regional spatial scales.

Keywords: Larval delivery, Settlement, Rockfish, *Sebastes*, Upwelling, Alongshore transport, Chl-a, Temperature, Ocean indices, Proxies

INTRODUCTION

The rate at which young are delivered to and replenish populations is highly variable in time and space and is a critically important determinant of population size and dynamics for many marine organisms (Doherty and Williams 1988; Roughgarden et al. 1988; Caley et al. 1996; Doherty 2002; Osenberg et al. 2002). However, understanding the dynamics of marine populations is often difficult, when input of new individuals is fluctuating in seemingly unpredictable ways. Physical and biological processes affecting growth, survival, and transport of pelagic stages have been shown to affect recruitment and hence, population sizes, for coral reef and temperate fishes (Doherty and Fowler 1994; Chambers 1997; Carr and Syms 2006) as well as marine invertebrates (Connell 1985; Ebert and Russell 1988).

For fisheries species, the inability to accurately predict or forecast the strength of recruitment to a fishery has hampered management efforts. It is clear for most nearshore, demersal fisheries, that reliance on stock-recruitment relationships is inadequate to forecast year class strength (Frank and Leggett 1994). This is due, in part, to the spatially heterogeneous and 'open' nature of these stocks and their associated fisheries. In addition, stock recruitment relationships are confounded by environmental factors affecting survival of pelagic larvae and delivery to settlement habitats.

Given declines in many nearshore fisheries, including rockfishes on the west coast of North America (Love et al. 1998; Mason 1998; Berkeley et al. 2004), improved knowledge of larval recruitment may allow more proactive management measures. The ability to predict patterns of intra- and interannual variation in delivery of larvae or pelagic young to adult populations offers the potential to dramatically improve fisheries management by allowing for better predictions of year class strength and future stock biomass. For example, Shanks and Roegner (2007) and Shanks et al. (this volume) correctly predicted catch rates of *Cancer magister* based on measurements of settlement and timing of the onset of spring upwelling four years prior. Similar lagged correlations between larval or juvenile abundance and commercial harvest have been made for western rock lobster in Australia (Morgan et al. 1982) and for a number of temperate fish species (Mearns et al. 1980; Parrish et al. 1981; Hollowed et al. 1987; Ralston and Ianelli 1998; Jenkins 2005; Laidig et al. 2007; Hare and Able 2007). Moreover, population dynamics of exploited species can be more sensitive to recruitment dynamics because of their typically truncated size distribution (Hsieh et al. 2006).

While recent increases in ocean observing networks are providing accessible environmental data at unprecedented spatial and temporal scales, monitoring interannual and geographic patterns of larval and/or pelagic juvenile replenishment for nearshore marine species at scales relevant to management, remains a challenging and potentially costly endeavor. Thus, understanding the strength and form of linkages between environmental variability and delivery of young may allow the use of 'proxies' for rates of population replenishment that are both easier and cheaper to measure. The utility of simple proxies will increase if the spatial scale and geographic areas for which they apply are identified.

In this study, we test the ability of simple oceanographic proxies to predict rates of delivery of pelagic juveniles of two groups of nearshore rockfishes (genus *Sebastes*) by investigating correlations between delivery to onshore adult populations and four, readily available, regional indices of ocean conditions that have previously been shown to influence delivery of young rockfish to reefs (Laidig et al. 2007; Caselle et al. 2010) on the West Coast of North America: upwelling, alongshore transport, sea surface temperature (SST) and Chl-a. Specifically, we document annual and geographic variability in rates of delivery of pelagic juvenile rockfish across roughly 400 km from central California to southern California, relate interannual patterns to readily available, regional indices of ocean conditions, and discuss the predictive ability of these indices among species and locations. This is the first study to explore potential relationships between oceanographic drivers and actual rates of larval delivery to populations of rockfishes on shallow rocky reefs at such large regional geographic scales.

METHODS

Pelagic juvenile rockfish species complexes

Rockfishes (genus *Sebastes*) are a speciose group of cold temperate fishes, most common in the Northeast Pacific (Love et al. 2002). Rockfishes undergo internal fertilization, bear live, feeding larvae, and have a gestation period that likely depends on water temperature (Sogard et al. 2008). Females of the rockfish species in this study are thought to release larvae once per season (Larson 1992; Gilbert et al. 2006). Two groupings of nearshore rockfishes are common settlers to rocky reefs in the study region, each with a distinct set of shared morphological and early life-history characteristics.

The OYTB group consists of three species, olive, yellowtail, and black rockfishes (*Sebastes serranoides*, *S. flavidus* and *S. melanops*, respectively). All share similar larval characteristics including larval release during the winter, pelagic duration ranging from 3.5–4 months and large size at settlement (2.8–5cm TL). This group settles from early to late spring in central California (Anderson 1983; Carr 1991; Ammann 2004) and from spring through the summer, with most settlement occurring in the late spring, in the Channel Islands (Love et al. 2002; Caselle et al. 2010).

The KGBC group includes kelp, gopher, black-and-yellow and copper rockfishes (*Sebastes atrovirens*, *S. carnatus*, *S. chrysomelas*, and *S. caurinus*). These species range from Alaska (*S. caurinus*) or northern California (the other three species) in the north to central Baja California in the south. KGBC rockfish release larvae from late winter through spring and following larval durations of approximately 1–3 months (Moser 1996; Gilbert 2000), fish settle to kelp canopy and rocky reef habitat at lengths of less than 2cm total length (TL). Settlement of these species occurs from late spring through late summer (Anderson 1983; Carr 1991; Love et al. 2002; Ammann 2004; Caselle et al. 2010) with the majority of settlement occurring in June through August (Ammann 2001; Caselle et al. 2010; Carr and Caselle, unpublished data). Although there is evidence that timing of delivery of *S. caurinus* may be as similar to that of the OYTB complex as it is to the other members of the KGBC complex in central CA (Anderson 1983; Carr 1991), previous work (Ammann 2004) suggests that this species responds to oceanographic drivers more similarly with the KGB group than with the OYTB, perhaps reflecting more similar life history attributes and larval processes. For this reason, and because their timing of settlement overlaps substantially with *S. carnatus* and *S. chrysomelas* in central California, and overlaps completely with members of this complex in the Channel Islands, we included them in the "KGBC" group for analyses.

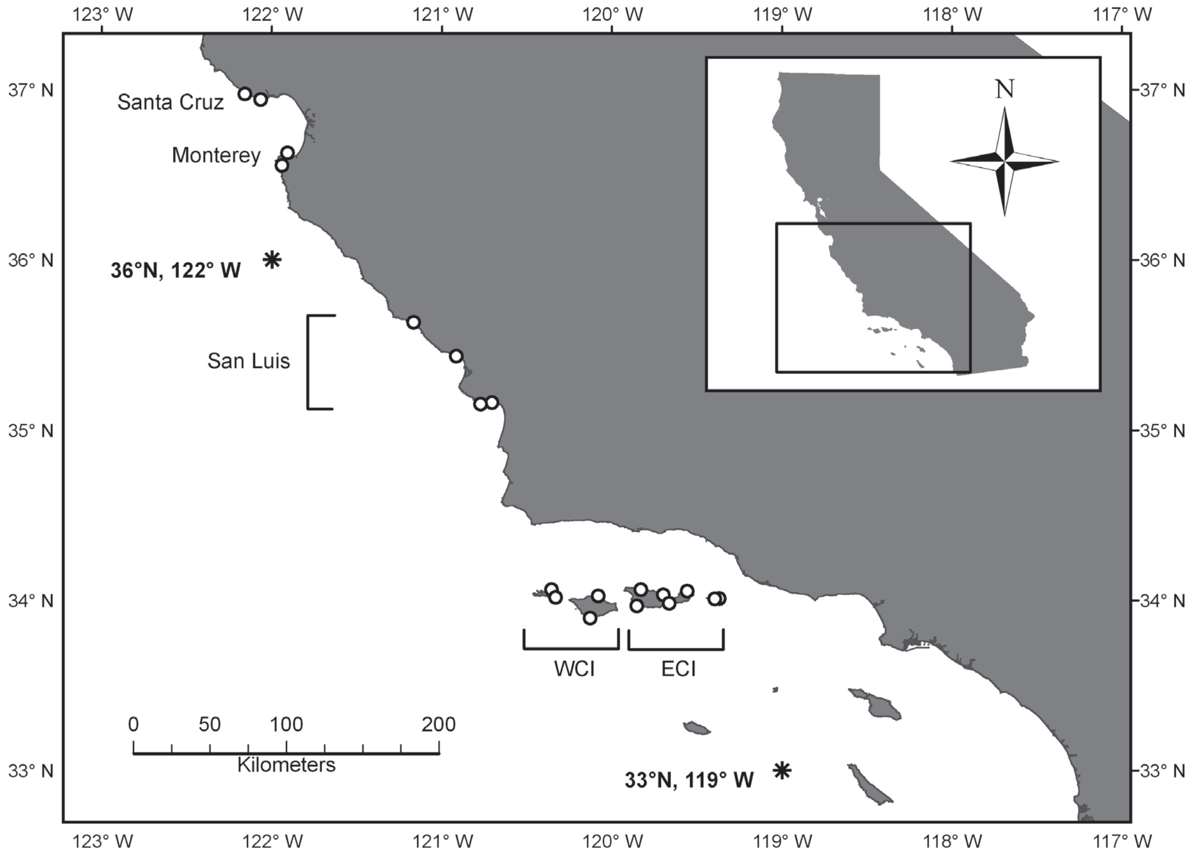

Figure 1. Map of study area. Gray circles show locations of settlement collection sites within each location. West Channel Islands (WCI) sites are on San Miguel and Santa Rosa and East Channel Islands (ECI) sites are on Santa Cruz and Anacapa. Stars mark the locations for the ocean indices: Southern California (So Cal:119W 33N) and Central California (Cen Cal: 122W 36N).

We present settlement data from these taxonomic groupings because (1) their combined abundances provide stronger statistical power to detect temporal and geographical patterns, (2) it is not possible to visually distinguish between all species within each group (e.g., gopher, [*Sebastes carnatus*], and black and yellow, [*Sebastes chrysomelas*], rockfish) and genetic analyses have not been completed for all samples, and (3) the species are treated as complexes in some fisheries (e.g., California recreational nearshore fishery).

Settlement to SMURFs

We monitored arrival of newly settled rockfishes on artificial collectors known as SMURFs (Standard Monitoring Units for Recruitment of Fishes; Steele et al. 2002; Ammann 2004) at 5 locations in California (fig. 1). Rates of settlement to SMURFs provide measures of delivery of competent larvae or pelagic juveniles in close proximity to adult populations, but independent of, and not confounded by, the availability and quality of nearby settlement habitat (Steele et al. 2002; Ammann 2004). Nonetheless, settlement to SMURFs can also correlate with recruitment to reefs as measured by visual surveys (Ammann 2001). Throughout this paper, we use the term 'settlement' to SMURFs to mean the rate at which young fish appear on the SMURFs and we interpret these measures as rates of onshore delivery of pelagic juveniles to the site where SMURFs are located.

All SMURFs were placed on individual mooring lines approximately 100–500 m from one another and 50–200 m offshore of kelp beds at sites where kelp was present, or 200–500 m from shore at sites where no kelp was present. Moorings were located in approximately 15 m of water depth and SMURFs were placed 3 m below the surface buoy. We sampled several sites within each location, ranging from 2 in Monterey and Santa Cruz to 7 in the East Channel Islands (fig. 1). Within each site, from three to eight replicate SMURFS were sampled. The sampling interval, the seasonal timing of collections, and the number of years sampled also varied slightly between locations. In the East Channel Islands (ECI), West Channel Islands (WCI) and San Luis locations, we removed fish settlers from each SMURF biweekly, while in Monterey and Santa Cruz sampling was approximately weekly. Earlier studies with daily sampling regimes indicated that biweekly sampling is suffi-

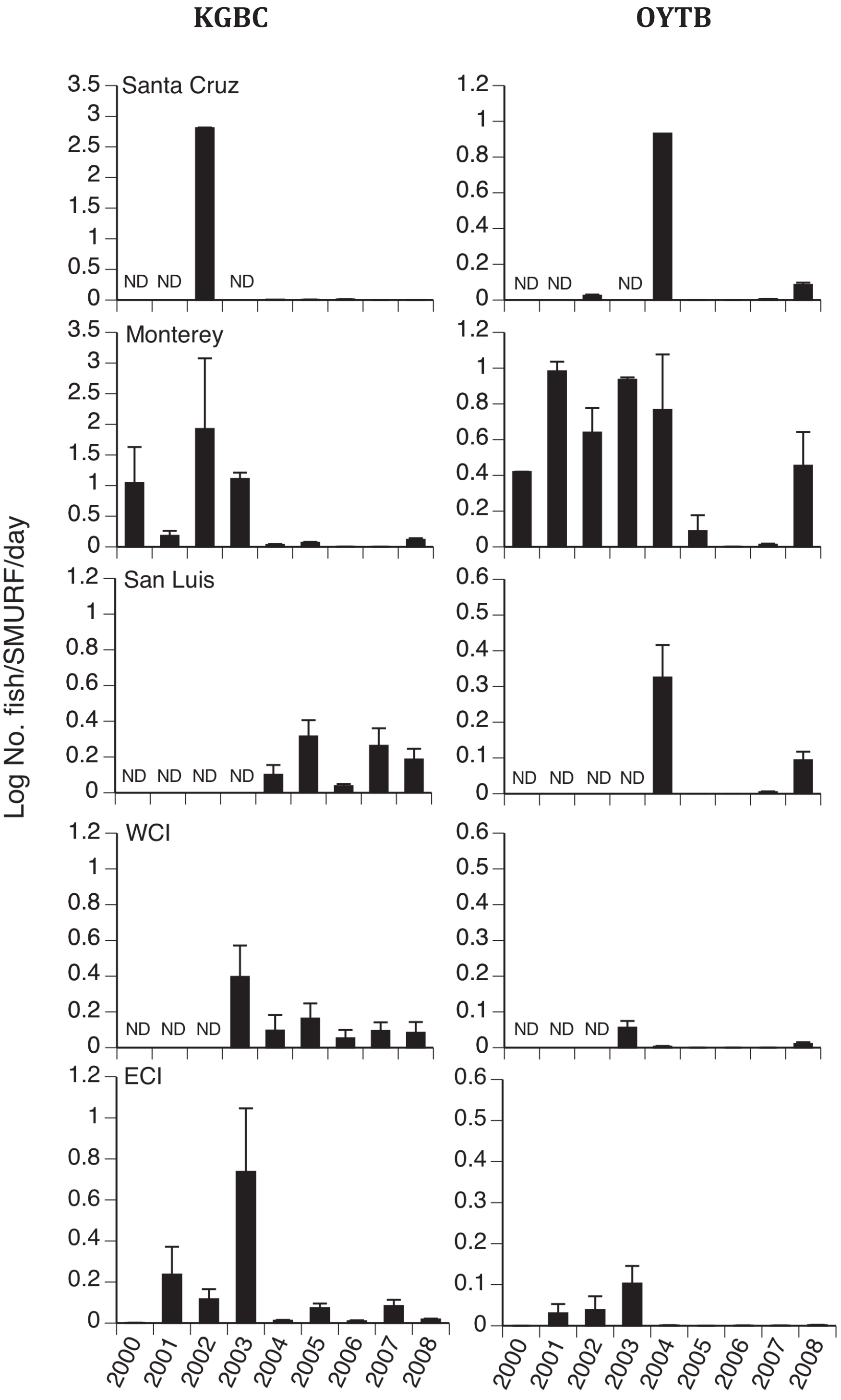

Figure 2. Mean number of settlers per SMURF per day + 1 SE (untransformed data) for KGBC (left panels) and OYTB (right panels). ND indicated = No data. Note different scales for y-axes.

ciently frequent to minimize post-settlement mortality on a SMURF (Steele et al. 2002; Ammann 2004). While variation in the sampling interval is unlikely to influence the relative abundance and interannual patterns of settlement, it may influence the number of fish settling and caution is suggested in comparing the absolute magnitude of settlement (i.e., rates of delivery) among sites. Sampling at all locations commenced in early- to mid-April and concluded in mid- to late-October. Sampling began in 2000 in Monterey and ECI followed by Santa Cruz in 2002, WCI in 2003 and San Luis in 2004. Years with missing data are noted on Figure 2.

Time series of oceanographic variables

We generated monthly means of four coastal oceanographic variables (hereafter referred to as "ocean indices") to test for relationships with regional interannual variation in settlement. These were offshore and alongshore components of upwelling, sea surface temperature (SST) and satellite derived estimates of Chlorophyll-a (Chl-a) concentration at the sea surface. Chl-a concentration was used as a near-term (monthly) proxy of productivity as it relates to availability of prey (i.e., zooplankton abundance). Upwelling indices were obtained from NOAA Fisheries Southwest Fisheries Science Center's Environmental Research Division (formerly the Pacific Fisheries Environmental Laboratory, publically available at http://www.pfel.noaa.gov/, Schwing et al. 1996) at 2 locations chosen to represent regional-scale variation around the settlement locations (fig. 1, southern California ('So Cal'): 119W 33N and central California ('Cen Cal'): 122W 36N). Chl-a and SST indices were calculated for the same locations (details below). These locations are 2 of 15 'historical' locations where ocean indices are routinely calculated and made accessible online (Perez-Brunius et al. 2007).

We used time series of both the offshore and alongshore components of upwelling. The magnitude of the offshore component of upwelling is considered to be an index of the amount of water upwelled from the base of the Ekman layer. Positive values are, in general, the result of equatorward wind stress. Negative values imply downwelling, the onshore advection of surface waters accompanied by a downward displacement of water. We refer to this index as the 'Bakun Index' throughout. We also used values for the alongshore component of upwelling with positive values indicating equatorward transport and negative values indicating poleward transport.

We used satellite-based measurements of SST and Chl-a concentration to develop indices of the thermal environment and phytoplankton abundance from the same two locations. To create the SST time series, we used weekly composite of daytime SST from NOAA Advanced Very-High-Resolution Radiometer (AVHRR) 18-km gridded satellite images (available at http://poet.jpl.nasa.gov/). We then calculated the mean monthly SST in a 1×1 degree box centered on each of the locations for direct comparison with the upwelling indices.

We described pelagic primary productivity in the 2 regions of interest using surface chlorophyll a (Chl-a) concentration from SeaWiFS (sea-viewing Wide Field-of-View Sensor, GeoEye, Dulles, Virginia, USA). We used the 8d, 4km standard mapped images available for research use (http://oceancolor.gsfc.nasa.gov/SeaWiFS/). Values of the Chl-a concentration derived parameter were again averaged over a 1×1 degree box centered on each the two locations and interpolated to a daily time interval. From that time series we calculated monthly averages.

Tests of relationships between oceanographic variables and settlement

Annual settlement density is expressed as the mean number of fish/SMURF/day to account for the differences among locations in sample interval and/or replication. In order to better visualize and test for coherence among locations and species groups over time, we standardized settlement density for each location as follows:

$$\text{Log (Annual Mean)} - \text{Log (Grand Mean)} / \text{Log (Standard Deviation of Grand Mean)}.$$

We used this standardized index of settlement in pairwise correlations among locations for each species group.

To investigate regional variation in interannual relationships between settlement and ocean indices, we first calculated pairwise Pearson correlation coefficients between mean annual settlement (log10 + 1 transformed, not standardized) for each species group at each location and the monthly averages of the four ocean indices. The log transform improved normality and reduced heterogeneity in variance. We used monthly averages for January through August, corresponding to times ranging from egg production through the period when the majority of settlement to SMURFs occurs for these species. Although SMURF sampling continued through October, very little settlement occurred after August in any year at any location (this study and see Ammann 2004; Wilson et al. 2008; Caselle et al. 2010). Here we present only the results of correlations between settlement to SMURFs at the three northern locations (i.e., San Luis, Monterey and Santa Cruz) with central California indices (Cen Cal: 122W 36N) and the two Southern locations (i.e., WCI and ECI) with southern California indices (So Cal: 119W 33N). We did not statistically correct for multiple comparisons (e.g., Bonferroni type corrections) because we are simply interested in the relative strength of the correlations and not statistical significance, *per se*. A number of monthly ocean indices were significantly correlated with settlement and we next used these significant variables in stepwise multiple regression models to assess the relative importance of particular indices across regions to assess their relative applicability to predicting interannual variation. Finally, we asked whether a composite of those ocean indices is a better predictor of settlement than any single, highly correlated variable. Using only data from the two locations with the longest time series,

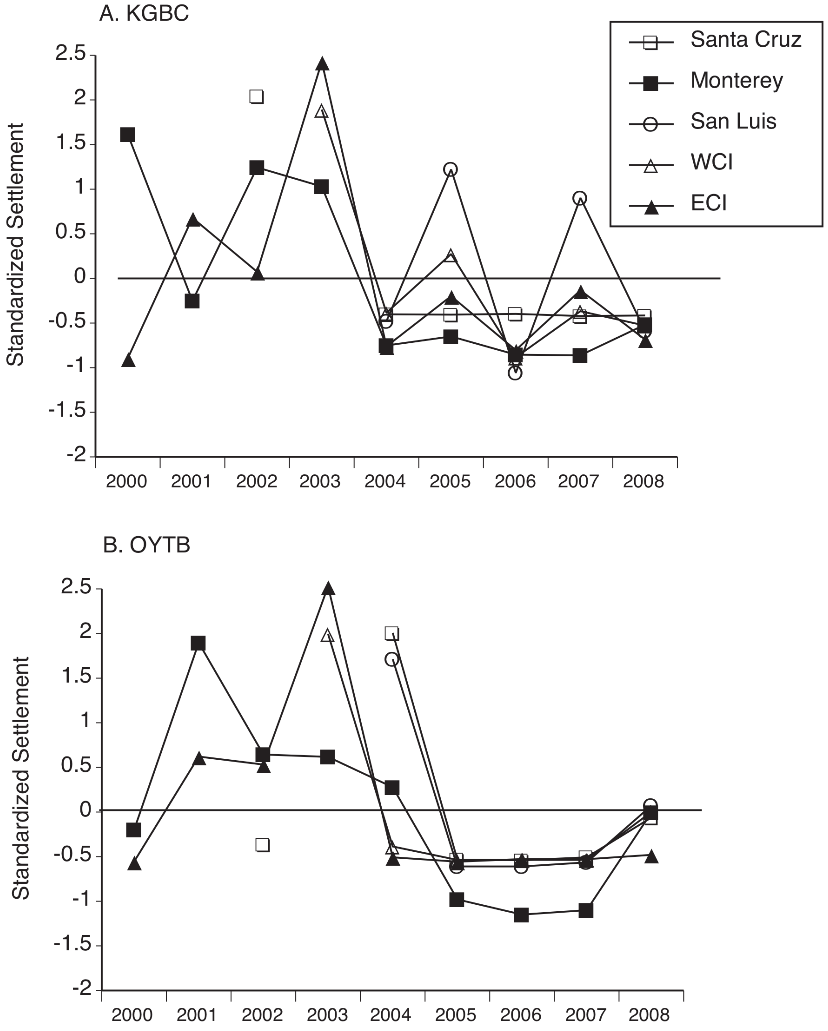

Figure 3. Standardized number of fish per SMURF per day for A. KGBC and B. OYTB. Standardization is described in the methods. Site legend is the same for both panels.

ECI and Monterey, we combined all individual variables that were significant in pairwise correlations into a single index using principal component analysis. The first principal component and the best single predictor (that with the highest correlation in the pairwise tests) were regressed against settlement and we compared the R^2 of the two relationships.

RESULTS

Spatial and temporal variation

Settlement of both groups of nearshore rockfishes was characterized by large interannual fluctuations (fig. 2). Most locations had one or a few strong years and little to no settlement in other years. The year of peak settlement differed among locations and species groups. Focusing on the two sites with a complete time series (Monterey and ECI sampled from 2000–2008) indicates that on average, settlement was higher prior to 2003, declining to low levels in 2004 (OYTB at ECI and KGBC at both locations) or 2005 (OYTB in Monterey) and remaining low. Although absolute abundance of settlers should be interpreted with some caution due to slight sampling differences, both species groups settle in greater numbers to the two northernmost locations (Monterey and Santa Cruz) compared with San Luis, ECI and WCI (fig. 2). OYTB rockfish, in particular settle in very low numbers in the two Channel Islands locations.

Standardized settlement densities allow easier visualization of temporal trends among locations (fig. 3). Again, most locations showed very low settlement of both species groups during the second half of the time series relative to the first part of the study. During the first half of the study, the peak years of settlement differed

TABLE 1
Pairwise Pearson correlation coefficients of standardized annual rockfish settlement among locations for A) KGBC and B) OYTB.

A. KGBC	Santa Cruz	Monterey	San Luis	WCI
Monterey	0.97**	.	.	.
San Luis	–0.49	0.02	.	.
WCI	–0.19	0.91*	0.84	.
ECI	0.62	0.41	0.96**	0.94**

B. OYTB	Santa Cruz	Monterey	San Luis	WCI
Monterey	0.68	.	.	.
San Luis	0.99***	0.90*	.	.
WCI	0.30	0.67	0.40	.
ECI	–0.15	0.58	0.55	0.98***

* $p<0.05$, ** $p<0.01$, *** $p<0.001$

between locations and species groups (fig. 3). Settlement of the KGBC group in Monterey was highest in 2000 and 2002 while in the ECI, settlement of this group was high in 2001, peaked in 2003 and was low in 2000 and 2002 (fig. 3A). For the OYTB group, settlement was more similar between the Monterey and ECI locations with high settlement density from 2000 through 2003 (for ECI) or 2004 (Monterey) and low to no settlement following those years (fig. 3B).

Settlement was significantly correlated between the two southern locations, WCI and ECI for both taxonomic groups (tab. 1A, B). Settlement to the two northernmost locations, Monterey and Santa Cruz, was significantly correlated for the KGBC group (tab. 1A) but not for the OYTB group (tab. 1B). The lack of a correlation for the OYTB group was driven by very low settlement in Santa Cruz in 2002. Sampling at Santa Cruz that year commenced relatively late in the summer, potentially resulting in an underestimate of OYTB settlement, which tends to occur in late spring/early summer. Settlement to the central location, San Luis, was more strongly correlated to the two southern locations for KGBC and to the northern locations for the OYTB group (tab. 1A, B). It must be noted the time series at San Luis was the shortest in the study (5 years) and occurred only during a period of apparently low settlement of both rockfish groups throughout the study region. In addition to spatial coherence between the WCI and the ECI for a given species complex, the two complexes settle contemporaneously at these locations but show more complex patterns and less coherent patterns at the three other locations (fig. 3).

Oceanographic proxies for settlement

Upwelling was greater, on average, from 2000 to 2003 and declined in both regions beginning in 2004 (fig. 4A, Mean Bakun index both regions: 2000–2003 = 138, 2004–2008 = 116). From 2000–2002, peak upwelling was greatest in the Cen Cal region (usually in June and July) while in subsequent years peak upwelling was equal or greater in the So Cal region (usually in April, May or June). Alongshore transport tended to be positive (equatorward) in the Cen Cal region and negative (poleward) in the So Cal region throughout the study period (fig. 4B). Chl-a concentration was greater on average as well as more variable in the Cen Cal region relative to So Cal but showed no obvious temporal trends over the study period (fig. 4C). SST was consistently lower in Cen Cal than in So Cal and increased slightly after 2002 in both regions (fig. 4D, Mean SST Cen Cal: 2000–2002 = 16°C, 2003–2008 = 16.5°C, So Cal: 2000–2002 = 13.3°C, 2003–2008 = 14.0°C).

Upwelling and alongshore transport were more strongly correlated with annual settlement of both taxonomic groups than SST or Chl-a (tab. 2, tab. 3). In addition, these indices for the summer months tended to correlate with settlement more strongly than either winter or spring months. Finally, we found stronger correlations between ocean indices and settlement for the KGBC group than for the OYTB group. The exception was at the two Channel Islands locations where settlement of both species groups was highly correlated and similarly related to the upwelling.

In the southern locations (ECI and WCI), the Bakun index in the summer months of June, July and August was strongly and positively related to settlement of both KGBC and OYTB groups (tab. 2, 3) respectively. In the ECI, KGBC settlement was also correlated with Chl-a in August, while OYTB settlement was significantly correlated with alongshore transport in May and June and Chl-a in August. In the WCI, KGBC settlement was positively correlated with alongshore transport in June and Chl-a in May, while OYTB settlement did not relate to any other indices beyond the Bakun index.

At the San Luis location, KGBC settlement was negatively related to Chl-a levels in July and August; no other indices were correlated (tab. 2). Interestingly, OYTB settlement at this location showed no significant correlations with any index (tab. 3).

Settlement of KGBC at Monterey and Santa Cruz was strongly and positively correlated with the Bakun

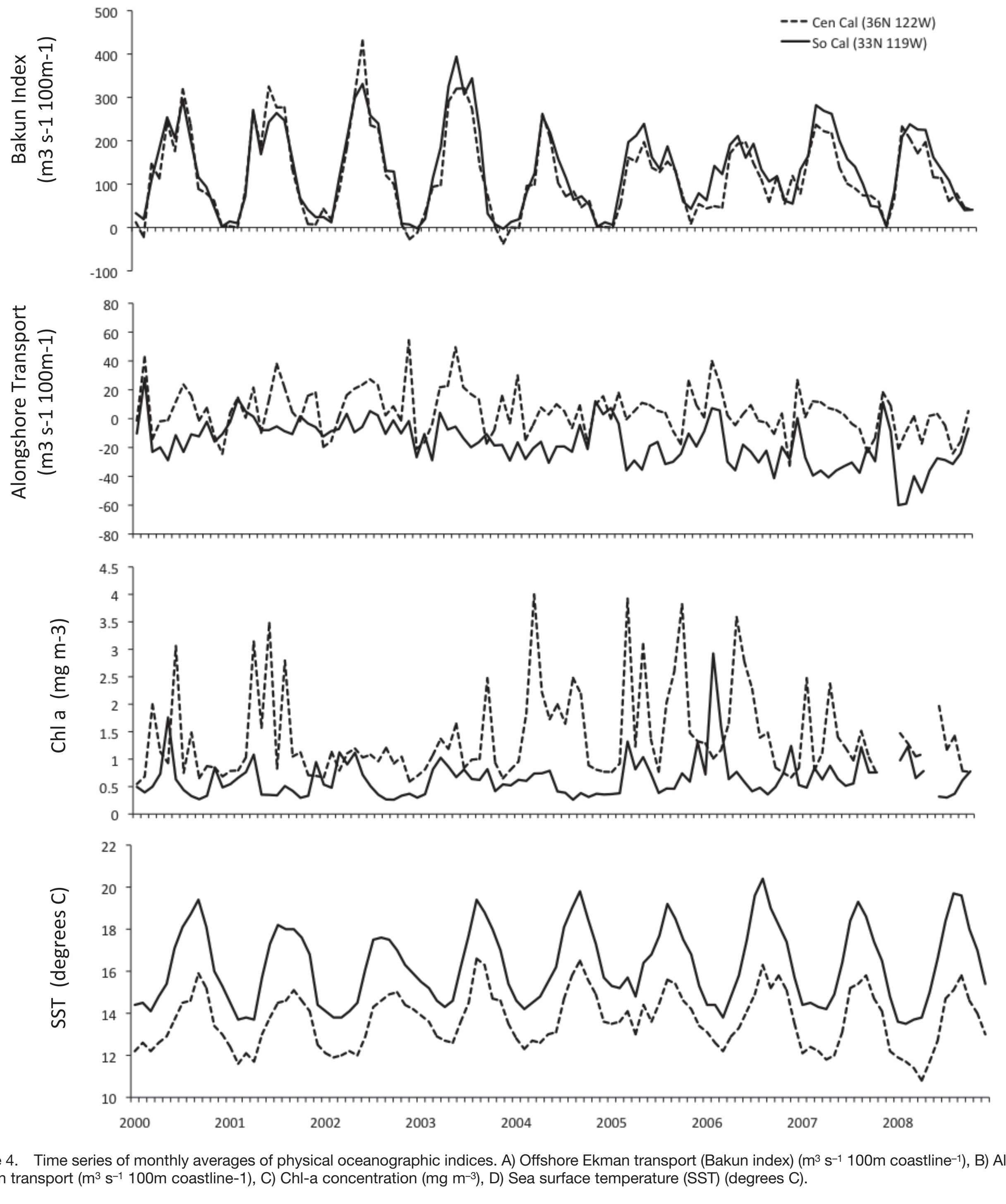

Figure 4. Time series of monthly averages of physical oceanographic indices. A) Offshore Ekman transport (Bakun index) (m^3 s^{-1} 100m $coastline^{-1}$), B) Alongshore Ekman transport (m^3 s^{-1} 100m coastline-1), C) Chl-a concentration (mg m^{-3}), D) Sea surface temperature (SST) (degrees C).

index in summer months, the same pattern found in the Channel Islands locations (tab. 2). This was not the case for the OYTB group (tab. 3). In marked contrast to the strong positive correlation of OYTB settlement with upwelling in the Channel Islands, OYTB settlement was not significantly correlated with the Bakun index at either Monterey or Santa Cruz. OYTB settlement did correlate with alongshore transport in July and August at Monterey. With the exception of the KGBC group in the Monterey, SST was not a good predictor of settlement for either group in any location.

Multiple regression allowed us to assess the relative importance of particular indices identified in the correlation analysis (tab. 4). For both species groups and most locations, upwelling during summer months explained the majority of variance in settlement, with partial R^2

TABLE 2
Pearson correlation coefficients of annual rockfish settlement (log10 + 1 transformed) and mean monthly oceanographic indices from January through August for KGBC at five locations. ECI and WCI locations show correlations with So Cal indices while San Luis, Monterey and Santa Cruz show correlations with Cen Cal indices.

Month	J	F	M	A	M	J	J	A
Bakun Index								
Santa Cruz	0.067	–0.239	–0.208	0.195	0.749	0.995	0.784	0.882
Monterey	–0.269	–0.426	0.011	–0.141	0.681	0.475	0.802	0.745
San Luis	0.245	–0.095	–0.062	0.625	–0.114	0.466	–0.223	–0.092
WCI	–0.601	–0.475	–0.357	0.056	0.780	0.943	0.897	0.812
ECI	–0.459	–0.242	–0.239	0.234	0.447	0.873	0.618	0.841
Alongshore transport								
Santa Cruz	–0.416	–0.683	–0.058	0.365	0.862	0.692	0.937	0.955
Monterey	–0.329	–0.136	–0.337	0.105	0.342	0.624	0.626	0.736
San Luis	–0.357	0.060	–0.003	–0.157	0.588	0.749	0.528	–0.489
WCI	–0.194	0.010	–0.081	0.362	0.726	0.856	0.511	0.401
ECI	–0.236	–0.153	0.051	0.444	0.646	0.568	0.375	0.115
Chl-a concentration								
Santa Cruz	–0.361	0.360	–0.478	–0.305	–0.230	–0.518	–0.526	–0.419
Monterey	–0.576	–0.242	–0.145	–0.391	–0.490	–0.244	–0.677	–0.339
San Luis	–0.802	–0.917	0.216	0.253	–0.474	0.164	–0.957	–0.969
WCI	–0.729	–0.820	–0.393	–0.220	0.865	–0.264	0.741	0.764
ECI	–0.420	–0.360	–0.184	–0.047	–0.201	–0.317	0.489	0.853
SST								
Santa Cruz	–0.360	–0.376	–0.228	–0.003	–0.343	–0.329	–0.656	–0.720
Monterey	–0.044	0.107	–0.115	0.165	–0.220	0.023	–0.671	–0.317
San Luis	0.161	0.620	0.639	0.137	0.290	–0.099	–0.005	–0.402
WCI	0.776	0.697	0.453	–0.094	–0.372	–0.517	–0.701	–0.364
ECI	0.613	0.372	0.168	–0.362	–0.401	–0.318	–0.440	–0.170

P<0.05 P<0.001

values as high as 0.99 (tab. 4). This result was particularly strong for the KGBC group compared to the OYTB group, in particular for the Channel Islands locations relative to the other more northern sites.

For the two sites with complete time series (ECI and Monterey), we asked whether a composite of multiple monthly indices was a better 'proxy' for settlement than any single monthly variable. To do this, we created an index using principal components analysis on all significant single monthly correlates (from tabs. 2 and 3) and compared that with the best single predictor by comparing R^2 values from regressions (figs. 5 and 6). Since the monthly ocean indices tend to correlate with one another, PC1 loadings were quite high (60%–90%). In the ECI, we compared the strength of the relationships between settlement vs. PC1 and settlement vs. June upwelling for the KGBC complex (fig. 5A–B) and settlement vs. PC1 and settlement vs. August upwelling for the OYTB complex (fig. 5C–D). Although all fits were good, settlement was more strongly related to the composite variable (PC1) than the single best predictor variable in all cases. This was particularly true for KGBC (fig. 5A–B: $R^2 = 0.92$ for PC1 vs. 0.76 for June Bakun Index). For Monterey, we contrasted PC1 vs. July Bakun Index for KGBC settlement (fig. 6A–B) and PC1 vs. July alongshore for OYTB settlement (fig. 6C–D). For the KGBC group both relationships were strong and significant and the difference between the R^2 values was negligible (fig. 6A–B: $R^2 = 0.77$ for PC1 vs. 0.74 for July Bakun Index). For OYTB in Monterey, both relationships were poor and R^2 values were equal (fig. 6C–D $R^2 = 0.36$ for both).

DISCUSSION

Spatial and temporal variation

Similar to previous studies (reviewed in Carr and Syms 2006), we found that settlement of two nearshore rockfish groups was highly variable among years. Yet notably, the 9 years of this study did not encompass any large climatic events such as ENSO (El Niño Southern Oscillation), which have previously been linked to extreme fluctuations in rockfish settlement and recruitment (Norton 1987; Lenarz et al. 1995; Ralston and Howard 1995; Carr and Syms 2006). We also documented good spatial coherence in interannual patterns of settlement for both species groups among the closely located study locations such as ECI–WCI and Monterey–Santa Cruz.

TABLE 3

Correlation coefficients of annual rockfish settlement (log10 + 1 transformed) and mean monthly oceanographic indices from January through August for OYTB at five locations. ECI and WCI locations show correlations with So Cal indices while San Luis, Monterey and Santa Cruz show correlations with Cen Cal indices.

Month	J	F	M	A	M	J	J	A
Bakun Index								
Santa Cruz	–0.449	–0.453	0.024	–0.317	0.382	–0.160	–0.532	–0.539
Monterey	–0.512	–0.370	–0.046	0.369	0.372	0.659	0.472	0.646
San Luis	–0.479	–0.465	0.080	–0.244	0.765	0.170	–0.680	–0.820
WCI	–0.538	–0.313	–0.083	–0.007	0.790	0.929	0.925	0.902
ECI	–0.465	–0.344	–0.248	0.079	0.517	0.893	0.693	0.912
Alongshore transport								
Santa Cruz	0.027	0.590	–0.543	–0.508	–0.055	–0.126	0.006	–0.197
Monterey	–0.063	–0.142	–0.443	0.222	–0.110	0.372	0.818	0.708
San Luis	–0.012	0.639	–0.631	–0.542	0.146	–0.096	0.429	–0.141
WCI	–0.208	–0.335	–0.293	0.417	0.683	0.797	0.404	0.211
ECI	–0.252	–0.215	0.024	0.565	0.734	0.674	0.491	0.253
Chl-a concentration								
Santa Cruz	–0.110	–0.088	0.309	0.592	0.817	–0.337	0.191	0.194
Monterey	–0.316	–0.192	–0.336	0.224	0.179	–0.204	–0.552	0.366
San Luis	–0.200	–0.024	0.260	0.534	0.760	–0.593	0.107	0.174
WCI	–0.531	–0.540	–0.135	–0.158	0.643	–0.648	0.602	0.729
ECI	–0.461	–0.312	–0.067	–0.082	–0.072	–0.425	0.370	0.743
SST								
Santa Cruz	0.040	–0.217	0.025	0.070	0.008	–0.277	–0.070	0.178
Monterey	–0.118	–0.438	–0.264	–0.307	–0.224	–0.067	–0.604	–0.376
San Luis	–0.104	–0.389	–0.090	–0.028	–0.131	–0.437	–0.266	–0.004
WCI	0.475	0.370	0.011	–0.323	–0.637	–0.459	–0.441	–0.089
ECI	0.500	0.253	–0.002	–0.345	–0.511	–0.336	–0.424	–0.218

P<0.05 P<0.001

TABLE 4

Results of multiple stepwise regressions of significant variables from pairwise correlations (Table 2 for KGBC, Table 3 for OYTB) on annual rockfish settlement of A. KGBC and B. OYTB.

A. KGBC

Site	Variable	Model Step	Sign	Partial R-Square	Model R-Square	F Value	Pr>F
Santa Cruz	Upwelling June	1	(+)	0.9904	0.9904	414.26	<.0001
	Alongshore transport May	2	(-)	0.0079	0.9983	13.97	0.0334
Monterey	Upwelling July	1	(+)	0.6428	0.6428	12.6	0.0094
San Luis	Chl-a conc. August	1	(-)	0.9333	0.9333	27.99	0.0339
WCI	Upwelling June	1	(+)	0.8893	0.8893	32.13	0.0048
	Chl-a conc. May	2	(+)	0.1067	0.996	79.6	0.003
	Alongshore transport June	3	(-)	0.0037	0.9997	23.84	0.0395
ECI	Upwelling June	1	(+)	0.7624	0.7624	22.46	0.0021
	Chl-a conc. August	2	(+)	0.1494	0.9119	10.17	0.0189

B. OYTB

Site	Variable	Model Step	Sign	Partial R-Square	Model R-Square	F Value	Pr>F
Santa Cruz	Chl-a conc. May	1	(+)	0.6681	0.6681	8.05	0.047
Monterey	Alongshore transport July	1	(-)	0.6699	0.6699	14.21	0.007
San Luis	N/A						
WCI	Upwelling June	1	(+)	0.863	0.863	25.21	0.0074
ECI	Upwelling August	1	(+)	0.8326	0.8326	34.81	0.0006
	Upwelling June	2	(+)	0.0837	0.9162	5.99	0.0499

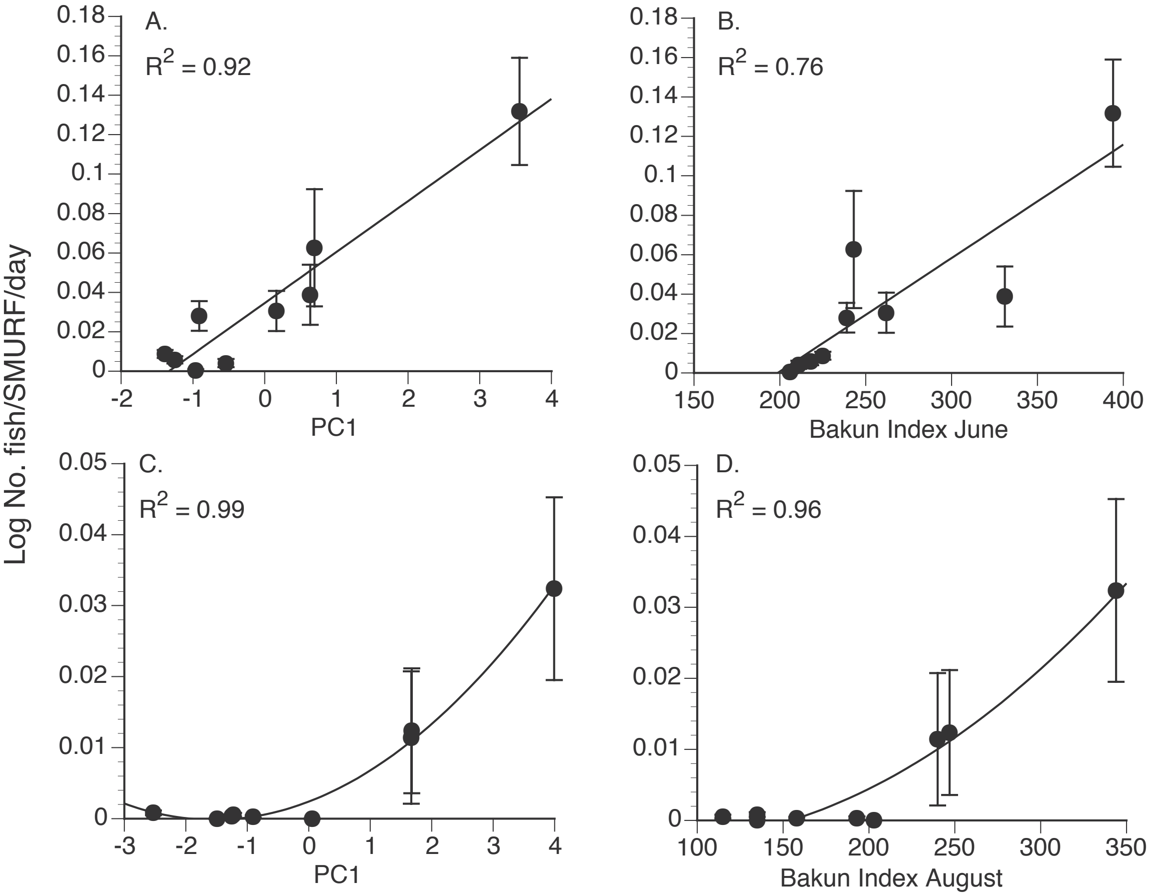

Figure 5. Comparisons of the performance of PC1 versus individual predictors for the East Channel Islands location (ECI). A) Settlement (log No. fish/ SMURF/ day) of KGBC vs. principal component 1 (PC1 of significant individual correlates for a given species group and location-see methods), B) Settlement of KGBC vs. Bakun index June, C) Settlement of OYTB vs. PC1, D) Settlement of OYTB vs. Bakun index August. R^2 values are shown.

Correspondence in the interannual patterns among larger regions (e.g. sites south of Pt. Conception versus sites north of Pt. Conception), which span a distance of approximately 400 km, were generally weaker. While we know of no other studies that compare settlement patterns of fishes in both Central and Southern California, the regional differences we see here corroborate regional differences in temporal patterns of recruitment among intertidal invertebrates recorded across the same geographic range (Broitman et al. 2008).

Although correlations between distant locations were weaker than closely spaced locations, the interannual patterns of settlement to SMURFs were broadly synchronous over time across the entire study region in that both species groups exhibited very little or no settlement in the later years of the study. The two locations with the longest times series (ECI and Monterey) show a precipitous decline in settlement beginning in 2004 or 2005. This was notable for the OYTB group in which settlement failed between 2004–2008 in the southern locations and between 2005–2007 in the northern locations. The lack of continuous SMURF settlement data from the other locations (WCI, San Luis and Santa Cruz) prior to 2003–2004 makes it difficult to assess the degree to which settlement may have declined at those locations relative to earlier years. However, interannual patterns of recruitment to kelp forests measured by SCUBA surveys (beginning in 2000 and corresponding to sites in Santa Cruz, Monterey and San Luis in this study) were similar to those observed from SMURFS and reflected the overall decline in the later years of this study even at sites with no SMURF sampling (Carr and Caselle, unpublished data, available at www.piscoweb.org). This is the first study to document coherent failures in rockfish settlement to nearshore areas at such large spatial scales.

The spatially extensive nature of the settlement failure likely indicates decline or failure in production and/or larval survival rather than changes in processes affecting larval transport or delivery, which are more likely to act at smaller spatial scales. Several studies have documented anomalous oceanographic conditions in the Northeast Pacific ocean in 2005 including delayed spring upwelling, increased water temperatures, low Chlorophyll-a, anomalous zooplankton concentrations and distributions as well as declines in recruitment of invertebrates and pelagic nekton (Brodeur et al. 2006; Schwing et al.

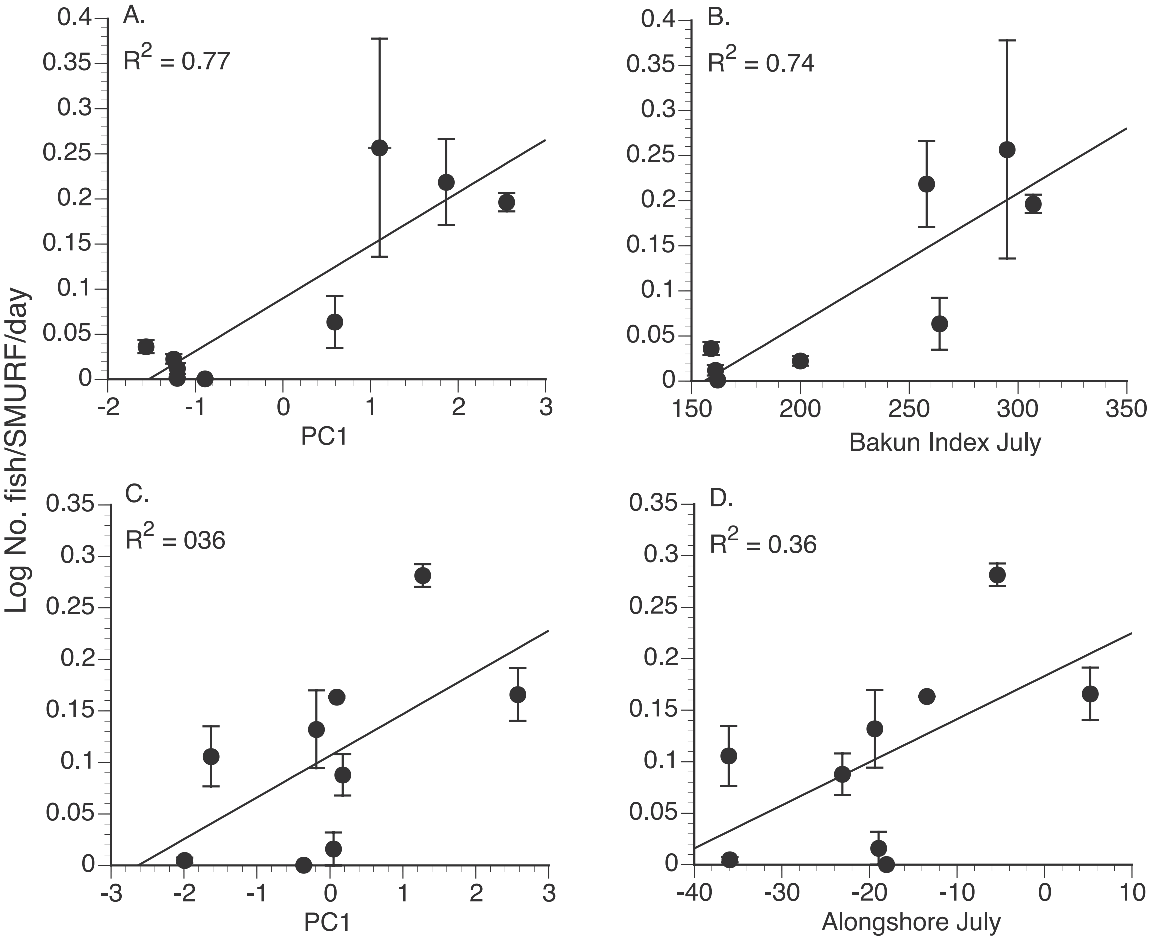

Figure 6. Comparisons of the performance of PC1 versus individual predictors for Monterey. A) Settlement (log No. fish/ SMURF/day) of KGBC vs. principal component 1 (PC1 of significant individual correlates for a given species group and location—see methods), B) Settlement of KGBC vs. Bakun index July, C) Settlement of OYTB vs. PC1, D) Settlement of OYTB vs. Alongshore transport July. R^2 values are shown.

2006; Barth et al. 2007). It appears from this study, that these anomalous conditions, especially those relating to late upwelling, also influenced survival and settlement of nearshore rockfishes. Further, our results indicate that the effects of conditions so well documented in 2005, continued in central and southern California at least until 2008, when settlement of the OYTB group recovered in the locations North of Pt. Conception.

Field and Ralston (2005) investigated the general assumption that, for populations with similar life histories and exposure to environmental variability, there is spatial synchrony in year class strength. They found broad spatial coherence in year class strength of winter spawning rockfishes (including yellowtail rockfish studied here) over scales of 500–1000 km. That study, which back-calculated year class strength from fishery landings data, and others (Hannah 1995; Hollowed and Wooster 1995; Botsford and Lawrence 2002) have suggested that large scale physical forcing mechanisms acting on scales of 1000s of kms are more important than regional or meso-scale processes in influencing recruitment to a fishery. However, the regional comparisons made by those studies are all to the north of Point Conception within an upwelling dominated section of the California Current. In contrast, the stronger regional differences in spatial synchrony of recruitment and oceanographic drivers that we observed in this and previous studies (Caselle et al. 2010), likely reflect our comparisons between regions to the north and south of Pt. Conception and the greater differences in conditions of the California Current, including upwelling dynamics.

While settlement failures were broadly coherent across all regions, during times of settlement, locations within regions tended to be more highly correlated to one another than across regions (e.g. WCI and ECI). While inferences from these comparisons are limited due to short time series at three of five locations, the strongest correlations within a region were between the two Channel Islands locations (i.e., south of Pt. Conception) for both species groups. Previous studies have documented a strong east-west gradient of environmental conditions over short geographic distances across the northern Channel Islands (Hickey et al. 2003; Broitman et al. 2005) resulting in differences in community structure (Blanchette et al. 2006; Blanchette et al. 2009; Hamilton et al. 2010) and recruitment (White and Caselle, 2008; Broitman et al. 2005) of both subtidal and intertidal organisms. Consequently, the eastern and western islands have a tendency to be treated as separate units when considering spatial management such as marine protected areas (Airamé et al. 2003). Despite differences in SST, productivity and exposure to storms between the eastern and western islands, we found very strong coherence in annual settlement in time and between species groups. This result has important implications for interpretation of changes to both populations and communities in a recently placed network of marine protected areas located in these islands (Hamilton et al. 2010).

Relationship to ocean environment

While a wide range of environmental parameters have been related to settlement of marine organisms, upwelling and downwelling circulation are among the more intensively studied processes for fishes and invertebrates in temperate coastal habitats (Norton, 1987; Ainley et al. 1993; Ralston and Howard 1995; Bjorkstedt et al. 2002; Mace and Morgan 2006). Previous work has also shown that year class strength for many rockfishes in the California Current system is likely set at some point during the larval phase (Ralston and Howard 1995; Yoklavich et al. 1996), prompting a number of studies focused on identifying environmental variables that may be related to the dispersal and survival of larvae, planktonic juveniles and settlers (Lenarz et al. 1995; Sakuma and Ralston 1995; Nishimoto and Washburn 2002; Laidig et al. 2007). For rockfishes, both the timing and the strength of coastal upwelling can influence successful recruitment and the relationships are complex (Yoklavich et al. 1996; Bjorkstedt et al. 2002). We found that a simple index of regional upwelling during summer months strongly correlated with rockfish settlement at locations both north and south of Pt. Conception, explaining more variance in combined models than indices of alongshore transport, SST or Chl-a. This study builds on earlier work that attempted to identify the spatial and temporal scales of influence of several oceanographic parameters on biweekly recruitment of nearshore rockfishes (similar to groups studied here) to the Santa Barbara Channel (Caselle et al. 2010). In that study, a number of wind-driven processes (e.g., Ekman upwelling and transport, Ekman pumping, and wind stress) were significantly related to settlement but with lags that varied between species groups (very short and very long for the KGB group, intermediate for the OYT group). In the simpler analyses done here, the Bakun index predicted settlement (more strongly for the KGBC group) but at relatively short lags for both groups. Unlike results of Laidig et al. (2007) in a study of rockfish recruitment to reefs in Northern California, we found that no ocean indices from winter or spring months (Jan through April) were correlated with settlement to any location. The strong positive relationship with the Bakun index occurring in the months directly preceding or even during settlement suggest that either the effects of upwelling on larval dispersal, delivery, or survival later in the pelagic stage are more important than effects on early larval phases and/or that the Bakun upwelling index, measured at regional scales is not a true measure of upwelling, *per se*, but describes or covaries with a number of processes that eventually determine larval settlement.

The coast of California is part of an Eastern boundary system characterized by persistent upwelling, especially from the Oregon border to Pt. Conception (Parrish et al. 1981). Coastal upwelling is typically described by low SST, high productivity and high offshore flow and can affect settlement of nearshore organisms negatively, by increasing offshore transport, or positively through increased availability of food resources. Whereas regions north of Pt. Conception are better characterized, fewer studies have documented oceanographic-recruitment correlations south of Pt. Conception (but see Stephens et al. 1984; Mearns et al. 1980; Broitman et al. 2005). South of Pt. Conception, the coastline runs in an east-west orientation, and although upwelling remains an important process, the typical pattern of upwelling-relaxation dynamics observed on the central and northern part of California (Davis 1985) is less prominent. Instead, wind-driven and other circulation processes interact with the unique geomorphology of the region to generate a variety of circulation patterns (Harms and Winant 1998). Thus, while the Bakun index measured at the central California location ("Cen Cal" in this study) may accurately reflect coastal upwelling (Bograd et al. 2009), the southern California index ("So Cal" in this study) may not represent upwelling per se (Perez-Brunius et al. 2007) but instead be a proxy for other processes that clearly relate to survival and/or transport of rockfish larvae in the region. The end result is that the Bakun upwelling index provides a very good proxy for settlement of these nearshore rockfish complexes in both the Monterey and the Channel Islands regions, although the actual mechanisms are likely to differ in the two regions.

In conclusion, our results suggest that simple oceanographic proxies can provide useful predictors of year-to-year variation in settlement of at least some nearshore rockfish species. However, the best oceanographic proxies for settlement varied both regionally and between species groups, indicating that a single metric applied across the entire range of a stock or for multiple species that differed markedly in key life history traits (e.g., larval duration, spawning season) would likely prove a poor predictor for regional patterns of settlement and recruitment of particular species. Nonetheless, our results suggest that such relationships, in contrast to the poor predictability of spawner-recruit relationships, could prove useful tools for forecasting year-class strength and population dynamics. The next step for these nearshore rockfish groups will be to determine the relationship between settlement variation and recruitment to the fishery. The growing time series used here and geographic extent of settlement monitoring will allow these relationships to be determined in the future. In conjunction with the increasing accessibility of ocean indices to fisheries ecologists and managers, their use for forecasting settlement, recruitment and year-class strength can greatly enhance our ability to adjust catch proactively to better correspond with stock dynamics. While we are not arguing here against pursuing a detailed mechanistic understanding of the causes of variation in larval delivery, settlement and recruitment, in the face of declining fisheries and ecosystems worldwide, the utility of simple, cheap and readily accessible proxies for these complex processes should not be ignored.

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LITERATURE CITED

Ainley, D. G., W. J. Sydeman, R. H. Parrish, and W. H. Lenarz. 1993. Oceanic factors influencing distribution of young rockfish (*Sebastes* spp.) in central California: a predator's perspective. Calif. Coop. Oceanic Fish. Invest. Rep. 34:133–139.

Airamé, S., J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. Mcardle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. Ecol. Appl. 13:S170–S184.

Ammann, A. J. 2001. Evaluation of a standard monitoring unit for the recruitment of fish in Central California. M.A. Thesis. University of California, Santa Cruz.

Ammann, A. J. 2004. SMURFs: standard monitoring units for the recruitment of temperate reef fishes. J. Exp. Mar. Biol. Ecol. 299:135–154.

Anderson, T. W. 1983. Identification and development of nearshore juvenile rockfishes (genus *Sebastes*) in kelp forests off central California. M.A. Thesis. California State University.

Barth, J. A., B. A. Menge, J. Lubchenco, F. Chan, J. M. Bane, A. R. Kirincich, M. A. McManus, K. J. Nielsen, S. D. Pierce, and L. Washburn. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proc. Natl. Acad. Sci. USA 104:3719–3724.

Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29:23–32.

Bjorkstedt, E. P., L. K. Rosenfeld, B. A. Grantham, Y. Shkedy, and J. Roughgarden. 2002. Distributions of larval rockfishes (*Sebastes* spp.) across nearshore fronts in a coastal upwelling region. Mar. Ecol. Prog. Ser. 242:215–228.

Blanchette, C. A., B. R. Broitman, and S. D. Gaines. 2006. Intertidal community structure and oceanographic patterns around Santa Cruz Island, CA, USA. Mar. Biol. 149:689–701.

Blanchette, C. A., P. T. Raimondi, and B. R. Broitman. 2009. Spatial patterns of intertidal community structure across the California Channel Islands and links to ocean temperature. *In* Proceedings of the 7th California Islands Symposium, C. C. Damiani and D. K. Garcelon, eds. Institute for Wildlife Studies, Arcata, CA. pp. 161–173.

Bograd, S. J., I. Schroeder, N. Sarkar, X. Qiu, W. J. Sydeman, and F.B. Schwing. 2009. Phenology of coastal upwelling in the California Current. Geophys. Res. Lett. 36:L01602.

Botsford, L.W., and C. A. Lawrence. 2002. Patterns of covariability among California Current chinook salmon, coho salmon, Dungeness crab, and physical oceanographic conditions. Prog. Oceanogr. 53:283–305.

Brodeur, R. D., S. Ralston, R. L. Emmett, M. Trudel, T. D. Auth, and A. J. Phillips. 2006. Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. Geophys. Res. Lett. 33:L22S08.

Broitman, B. R., C. A. Blanchette, and S. D. Gaines. 2005. Recruitment of Intertidal Invertebrates and Oceanographic Variability at Santa Cruz Island, California. Limnol. Oceangr. 50:1473–1479.

Broitman, B. R., C. A. Blanchette, B. A. Menge, J. Lubchenco, C. Krenz, M. Foley, P. T. Raimondi, D. Lohse, and S. D. Gaines. 2008. Spatial and temporal patterns of invertebrate recruitment along the west coast of the United States. Ecol. Monogr. 78:403–421.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the population dynamics of open marine populations. Annu. Rev. Ecol. Syst. 27:477–500.

Carr, M. H., 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. J. Exp. Mar. Biol. Ecol. 146:113–137.

Carr, M. H., and C. Syms. 2006. Recruitment. *In* The Ecology of Marine Fishes California and Adjacent Waters, L. G. Allen, D. J. Pondella II, and M. H. Horn, eds. U.C. Press. pp. 411–427.

Caselle, J. E., B. P. Kinlan, and R. R. Warner. 2010. Temporal and spatial scales of influence on nearshore fish settlement in the southern California Bight. Bull. Mar. Sci. 86:355–385.

Chambers, R.C. 1997. Environmental influences on egg and propagule sizes in marine fishes. *In* Early Life History and Recruitment in Fish Populations. R. C. Chambers and E. A. Trippel, eds. Chapman and Hall, New York. pp. 63–102.

Connell, J. H. 1985. The consequences of variation in initial settlement versus post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 93:11–45.

Davis, R. E. 1985. Drifter observations of coastal surface currents during CODE. J. Geophys. Res. 90:4741–4772.

Doherty, P. J., and D. McB. Williams. 1988. The replenishment of coral reef fish populations. Ocean. Mar. Biol. Ann. Rev. 26:487–551.

Doherty, P., and T. Fowler. 1994. An empirical test of recruitment limitation in a coral reef fish. Science 263:935–939.

Doherty, P. J. 2002. Variable replenishment and the dynamics of reef fish populations. *In* Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. P. F. Sale, Ed., Academic Press, San Diego, CA, pp. 327–355.

Ebert, T. A., and M. P. Russell. 1988. Latitudinal variation in size structure of the West Coast purple sea urchin: A correlation with headlands. Limnol. Oceanogr. 33:286–294.

Field, J. C., and S. Ralston. 2005. Spatial variability in rockfish (*Sebastes* spp.) recruitment events in the California Current System. Can. J. Fish. Aq. Sci. 62:2199–2210.

Frank, K. T., and W. C. Leggett. 1994. Fisheries ecology in the context of ecological and evolutionary theory. Ann. Rev. Ecol. Syst. 25:401–422.

Gilbert, E. A. 2000. Molecular genetic analysis of temporal recruitment pulses in juvenile kelp rockfish. M.A. Thesis, San Francisco State University, San Francisco, CA.

Gilbert, E. A., R. J. Larson, and J. C. Garza. 2006. Temporal recruitment patterns and gene flow in kelp rockfish (*Sebastes atrovirens*). Molec. Ecol. 15:3801–3815.

Hamilton, S. L., J. E. Caselle, D. P. Malone, and M. H. Carr. 2010. Incorporating biogeography into evaluations of the Channel Islands marine reserve network. Proc. Natl. Acad. Sci. USA. [doi/10.1073/pnas.0908091107].

Hannah, R. W. 1995. Variation in geographic stock area, catchability, and natural mortality of ocean shrimp (*Pandalus jordani*)—some new evidence for a trophic interaction with pacific hake (*Merluccius productus*). Can. J. Fish. Aq. Sci. 52:1018–1029.

Hare, J. A., and K. W. Able. 2007. Mechanistic links between climate and fisheries along the east coast of the United States: explaining population outbursts of Atlantic croaker (*Micropogonias undulatus*). Fish. Oceanogr. 16:31–45.

Harms, S., and C. D. Winant. 1998. Characteristic patterns of the circulation in the Santa Barbara Channel. J. Geophys. Res. 103:3041–3065.

Hickey, B., E. L. Dobbins, and S. E. Allen. 2003. Local and remote forcing of currents and temperature in the central Southern California Bight. J. Geophys. Res.: Oceans 108:[doi:10.1029/1200JC000313].

Hollowed, A. B., K. M. Bailey, and W. S. Wooster. 1987. Patterns in recruitment of marine fishes in the northeast Pacific Ocean. Biol. Oceanogr. 5:99–131.

Hollowed, A. B., and W. S. Wooster. 1995. Decadal-scale variations in the eastern subarctic Pacific: II. Response of northeast Pacific fish stocks. Can. Spec. Publ. Fish. Aquat. Sci. No. 121, pp. 373–385.

Hsieh, C-h., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006. Fishing elevates variability in the abundance of exploited species. Nature: 443:859–862.

Jenkins, G. P. 2005. Influence of climate on the fishery recruitment of a temperate, seagrass-associated fish, the King George whiting *Sillaginodes punctata*. Mar. Ecol. Prog. Ser. 288:263–271.

Laidig, T. E., J. R. Chess, and D. F. Howard. 2007. Relationship between abundance of juvenile rockfishes (*Sebastes* spp.) and environmental variables documented off northern California and potential mechanisms for the covariation. Fish. Bull. 105:39–48.

Larson, R. J. 1992. Other nearshore rockfish. *In* California's living marine resources and their utilization, W. S. Leet, C. M. Dewees, and C. W. Haugen, eds. California Sea Grant Extension Publication UCSGEP-92-12. pp. 130–131.

Lenarz, W. H., D. A. VenTresca, W. M. Graham, F. B. Schwing, and F. Chavez. 1995. Explorations of El Niño events and associated biological population dynamics off central Calif. Calif. Coop. Oceanic Fish. Invest. Rep. 36:106–119.

Love, M. S., J. E. Caselle, and W. Van Buskirk. 1998. A severe decline in the commercial passenger fishing vessel rockfish (*Sebastes* spp.) catch in the Southern California Bight, 1980–1996. Calif. Coop. Oceanic Fish. Invest. Rep. 39:180–195.

Love, M. S., M. Yoklavich, and L. Thorsteinson. 2002. The rockfishes of the northeast Pacific. Univ. California Press, Berkeley and Los Angeles. 404 pp.

Mace, A. J. and S. G. Morgan. 2006. Biological and physical coupling in the lee of a small headland: contrasting transport mechanisms for crab larvae in an upwelling region. Mar. Ecol. Prog. Ser. 324:185–196.

Mason, J. E. 1998. Declining rockfish lengths in the Monterey Bay, California, recreational fishery 1959–94. Mar. Fish. Rev. 60:15–28.

Mearns, A. J., M. J. Allen, M. D. Moore, and M. J. Sherwood. 1980. Distribution, abundance, and recruitment of soft bottom rockfishes (Scorpaenidae: *Sebastes*) on the southern California mainland shelf. Calif. Coop. Oceanic Fish. Invest. Rep. 21: 180–190.

Morgan, G. R., B. F. Phillips, and L. M. Joll. 1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of western Australia. Fish. Bull. 80:475–486.

Moser, H. G. 1996. Scorpaenidae: scorpionfishes and rockfishes. Pages 733–795 *In* H. G. Moser, ed. The early stages of fishes in the California Current region. CalCOFI Atlas No. 33. Allen Press, Lawrence, Kansas.

Nishimoto, M. M. and L. Washburn. 2002. Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA. Mar. Ecol. Prog. Ser. 241:183–199.

Norton, J. 1987. Ocean climate influences on groundfish recruitment in the California Current, Proceedings of the International Rockfish Symposium, Anchorage, Alaska (AK Sea Grant Rep 87–2), University of Alaska, Anchorage. pp. 73–99.

Osenberg, C. W., C. M. St. Mary, R. J. Schmitt, S. J. Holbrook, P. Chesson, and B. Byrne. 2002. Rethinking ecological inference: density dependence in reef fishes. Ecol. Lett. 5:715–721.

Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1:175–203.

Perez-Brunius, P., M. López, A. Parés-Sierra, and J. Pineda. 2007. Comparison of upwelling indices off Baja California derived from three different wind data sources. Calif. Coop. Oceanic Fish. Invest. Rep. 48: 204–214.

Ralston, S., and D. F. Howard. 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. Fish. Bull. U.S. 93:710–720.

Ralston, S., and J. N. Ianelli. 1998. When lengths are better than ages: the complex case of bocaccio. *In* Fishery stock assessment models. Alaska Sea Grant College Program, AK-SG-98-01, pp. 451–468.

Roughgarden, J., S. D. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. Science 241:1460–1466.

Sakuma, K. M. and S. Ralston. 1995. Distributional patterns of late larval groundfish off central California in relation to hydrographic features during 1992–1993. Calif. Coop. Oceanic Fish. Invest. Rep. 36:179–192.

Schwing, F. B., M. O'Farrell, J. Steger, and K. Baltz. 1996. Coastal Upwelling Indices, West Coast of North America 1946–1995, U.S. Dep. Comer., NOAA Tech. Memo., NOAA-TM NMFS-SWFSC-231, 207 pp.

Schwing, F. B., N. A. Bond, S. J. Bograd, T. Mitchell, M. A. Alexander, and N. Mantua. 2006. Delayed coastal upwelling along the US West Coast in 2005: a historical perspective. Geophys. Res. Lett. 33:1–5.

Shanks, A. L., and G. C. Roegner. 2007. Recruitment limitation in dungeness crab populations is driven by variation in atmospheric forcing. Ecology. 88:1726–1737.

Shanks, A. L., G. C. Roegner, and J. Miller. In press. Predicting the future commercial catch of dungeness crabs. Calif. Coop. Oceanic Fish. Invest. Rep.

Sogard, S. M., E. Gilbert-Horvath, E. C. Anderson, R. Fisher, S. A. Berkeley, and J. C. Garza. 2008. Multiple paternity in viviparous kelp rockfish, *Sebastes atrovirens.* Environ. Biol. Fish. 81:7–13.

Steele, M. A., J. C. Malone, A. M. Findlay, M. H. Carr, and G. E. Forrester. 2002. A simple method for estimating larval supply in reef fishes and a preliminary test of limitation of population size by larval supply in the kelp bass, *Paralabrax clathratus.* Mar. Ecol. Prog. Ser. 235:195–203.

Stephens, J. S. Jr., P. A. Morris, K. Zerba, and M. Love. 1984. Factors affecting fish diversity on a temperate reef: the fish assemblage of Palos Verde Point, 1974–1981. Environ. Biol. Fish. 11:259–275.

White, J. W., and J. E. Caselle. 2008. Scale-dependent changes in the importance of larval supply and habitat to abundance of a reef fish. Ecology 89:1323–1333.

Wilson, J. R., B. R. Broitman, J. E. Caselle, and D. E. Wendt. 2008. Recruitment of coastal fishes and oceanographic variability in central California. Est. Coast. Shelf Sci. 79:483–490.

Yoklavich, M. M., V. J. Loeb, M. M. Nishimoto, and B. Daly. 1996. Nearshore assemblages of larval rockfishes and their physical environment off central California during an extended El Niño event 1991–1993. Fish. Bull. 94:766–782.

USING MEGALOPAE ABUNDANCE TO PREDICT FUTURE COMMERCIAL CATCHES OF DUNGENESS CRABS (*CANCER MAGISTER*) IN OREGON

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ABSTRACT

We explore the possibility of predicting the commercial catch of Dungeness crabs (*Cancer magister*) from the abundance of returning megalopae. In the first six years of a nine-year time series (1997–2001, 2006–2009), there is a strong relationship between megalopal abundance and Oregon commercial catch, and early spring transitions led to higher numbers of returning megalopae. During this period, we could make reasonable predictions of commercial catch. In the last three years (2007–2009), megalopal abundance ranged from 1.2 to 2.4 million animals. The previous relationship between megalopal abundance and commercial catch is unlikely to hold given these huge abundances; density-dependent factors should lead to an asymptotic relationship between the number of returning megalopae and commercial catch and, if this holds, commercial catch should be predictable. The high abundances of megalopae do not appear to be due to improved larval growth conditions, but significant correlations between megalopal abundances and hydrographic and climatic indices suggest that reduced northward and enhanced southward transport during the pelagic phase may have contributed to the huge returns.

INTRODUCTION

This research explores the possibility of predicting the commercial catch of Dungeness crabs (*Cancer magister*) from a measure of the number of megalopae returning to shore. The data presented were collected during two periods. Data in the first year (1997) was part of a Masters thesis (Johnson and Shanks 2002) and during the next four years (1998–2001) were collected as part of the Pacific Northwest Coastal Ecosystem Regional Study (PNCERS) (Roegner et al. 2007). There was a hiatus of four years due to a lack of funding and then, with support from the Oregon Dungeness Crab Commission, the time series was restarted in 2006 and has continued to the present.

Methods, data and the initial model relating the numbers of settlers to the commercial catch were presented in a previous paper (Shanks and Roegner 2007). Following a description of the Dungeness crab life history and fishery in the California Current, which is based upon the review by Wild and Tasto (1983), the results and conclusions from the Shanks and Roegner study will be presented. In this present paper, the last four years of data will be combined with this initial time series and reanalyzed.

The following presentation of Dungeness crab life history relates to the the California Current portion of the species range; the species range extends up into coastal Alaska and here the life history characteristics are different (Swiney and Shirley 2001). In the California Current system mating occurs in spring during a female's molt. Males can mate with multiple females. Females store sperm until egg extrusion in the fall. Egg development takes three to four months with hatching occurring sometime in winter (Strathmann 1987). There are five zoeae stages and a megalopal stage. The larval period is from three to four months (Strathmann 1987). Larvae hatch close to shore and, as they develop, they move further offshore. By the late zoeae stages, many if not most larvae are present in waters beyond the continental shelf (Wild and Tasto 1983). In Oregon, megalopae begin returning to shore in spring and returning megalopae are usually present until October or November (Roegner et al. 2007). The daily abundance of megalopae at the shore (as measured with light traps, see Methods) is highly pulsed; pulses are one to several orders of magnitude larger than abundances between pulses. Pulses tend to occur between spring and neap tides suggesting that shoreward transport of megalopae is due to the internal tides (Roegner et al. 2007). In Oregon waters, crabs reach sexual maturity in about 1.5 years and male crabs enter the fishery at about four years of age (Wild and Tasto 1983).

The following description of the history of the Dungeness crab fishery is taken from the review by Wild and Tasto (1983). The commercial fishery for Dungeness crab began in San Francisco Bay in 1848. Initially, the fishery was entirely within the Bay, but within several decades this fishing ground was over-fished and the fishery moved to waters between the Golden Gate and the Farallon Islands. There was a steady increase in landings through the 1880s at which time landings began to drop and crabs became scarce. To protect the fishery, the California State Board of Fish Commissioners lim-

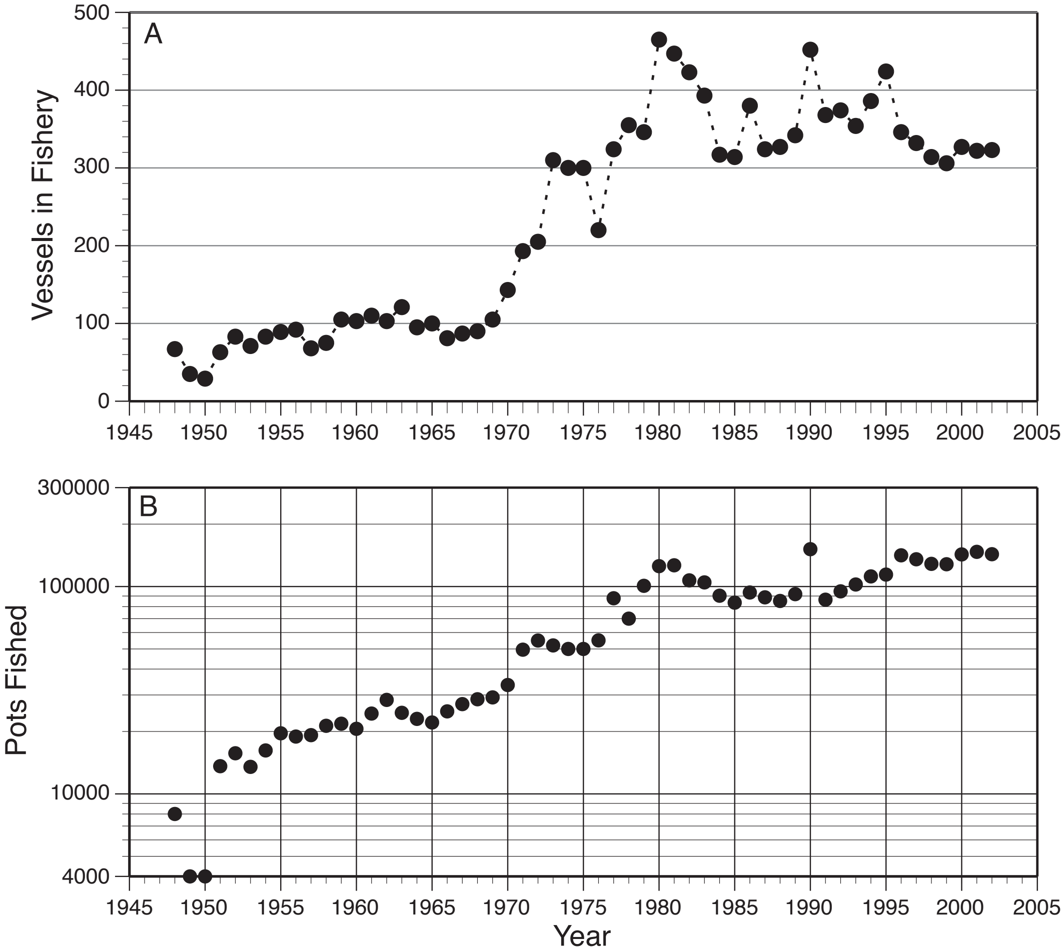

Figure 1. (A) Number of vessels participating in Oregon Dungeness crab fishery from 1947–2004 and (B) the number of crab pots fished over the same period (data are from the Oregon Department of Fish and Wildlife).

ited the catch to male crabs in 1897. The intense fishing pressure, however, continued to cause a decline in the population and additional restrictions were placed on the fishery. In 1903 the fishery was closed during September and October to prevent fishing when males are molting. In 1905 a size limit was placed on male crabs and in 1907 the size limit was increased to limit the take of female crabs (male crabs are significantly larger than female crabs). In addition, the larger size limit allows male crabs several opportunities to mate before they enter the fishery. These basic regulations, with minor changes, have been utilized in Dungeness crab fisheries throughout the California Current system. Starting in 1915, fish dealers were required to keep records of their transactions (landings). As the fishery expanded north into Oregon and Washington, similar record keeping was instigated in these states. These records provide an excellent time series of the commercial catch of Dungeness crabs in the California Current.

During the first half of the 20th century, the fishery expanded northward and the number of boats fishing crab increased. During the 1970s, following the initiation of the 200-mile economic exclusion zone, there was a rapid increase in the crab fishing fleet. For example, in Oregon (data from Oregon Dept. of Fish and Wildlife), the fishing fleet fluctuated around 100 boats during the 1960s. Between 1970 and 1975, the fleet increased to 300 boats and has remained between 300 and >400 boats since (fig. 1). During the 1960s, the fleet fished around 30 thousand crab pots, but > 100,000 pots have been fished since the growth of the fleet (fig. 1). Fishing pressure on Dungeness crabs is intense and has been since at least the 1970s. By the close of the fishing season, > 90% of the legal-sized crabs (four-year olds) have been caught and, as a consequence, annual catch is a good measure of the abundance of the four-year old cohort (Hackett et al. 2003). Despite the intense fishing pressure there is no indication that the crab population is suffering from overfishing. That is, while the size of the commercial catch has fluctuated over the years, there is no apparent downward trend in the size of the commercial catch (pers. obs.); the fishery appears to be

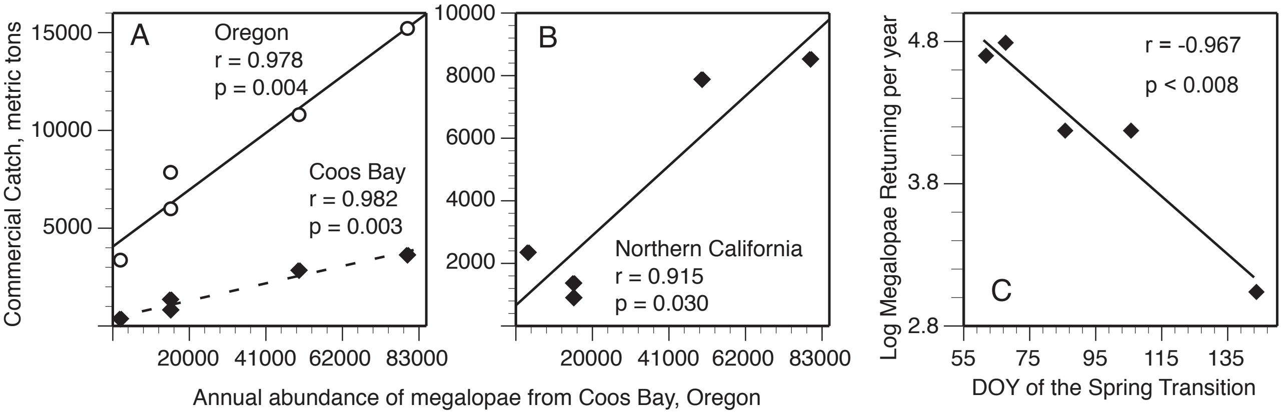

Figure 2. (A and B) The annual abundance of megalopae returning to Coos Bay, Oregon as measured as the sum of the daily catch of megalopae to a light trap plotted against the commercial catch landed in Coos Bay, all Oregon, and Northern California lagged four years to account for the growth of the megalopae to a legal-sized crab. (C) The day of the year of the spring transition plotted against the annual abundance of megalopae returning to Coos Bay, Oregon. Data are replotted from Shanks and Roegner (2007).

sustainable. A likely explanation for this is that the regulations limit the impact of the fishery on the reproductive output of the population.

Between 1997 and 2001, the annual return of megalopae to the shore as measured by the number of megalopae caught in light traps in Coos Bay, Oregon varied from 1000 in 1997 to nearly 80,000 in 2001. The number of returning megalopae was significantly, positively, and linearly correlated with the commercial crab landings in Coos Bay four years later (fig. 2), and was significantly correlated to landings in all Oregon and Northern California, and was nearly significantly correlated to landings in central California (Shanks and Roegner 2007). These correlations suggested three conclusions: (1) The size of the commercial catch (four-year old year cohort) was set by the relative success of the larvae as measured by the abundance of returning megalopae, (2) Over this range of returning megalopae, there were no obvious density-dependent effects; the relationship was linear, and (3) Whatever was driving the annual success of larvae was a process or processes consistent over a large portion of the West coast.

Off Oregon, larvae hatch in winter and move offshore during development such that by the megalopal stage most larvae are off the continental shelf. The timing of the pulsed return of megalopae to the shore suggests that shoreward transport is due to the internal tides, a hydrographic phenomena characteristic of the shelf (Roegner et al. 2009). Hence, the first step in the shoreward migration of megalopae appears to be transport from waters off the shelf back onto the shelf at which point internal tides could cause shoreward transport. We hypothesized that the spring transition might transport megalopae back onto the continental shelf. The spring transition occurs when winter winds from the south (downwelling favorable) are replaced by spring/summer upwelling favorable winds from the north. During this transition, the Davidson Current, which is present on the shelf during winter is replaced by the California Current moving back onto the shelf and the north winds begin the seasonal cycle of upwelling. These dramatic seasonal changes in the current regime might transport megalopae from waters seaward of the shelf onto the shelf. The spring transition varies from as early as March to as late as July. We hypothesized that if the transition was early (March), Dungeness crab larvae would spend a minimum time in the plankton and the return would be large. In contrast, if the transition was late (June or July) then larvae would spend additional months in the plankton during which a variety of mechanisms might cause increased mortality and the return of megalopae should be smaller. The day of the year of the spring transition was significantly correlated with the number of returning megalopae; when the transition was early, the return was large and, when it was late, the return was smaller (fig. 2). Interestingly, the return of the larvae of several taxa of nearshore or intertidal decapods (Shanks and Roegner 2007) and fishes (Shanks and Pfister 2009), species with larvae that remain close to shore during their development, had an opposite relationship with the date of the spring transition; in these taxa, when the transition was early, the return was low and when it was late, it was higher.

METHODS

A detailed description of the sampling methods used from 1997 to 2001 can be found in Shanks and Roegner (2007). Very similar sampling methods have been used since the time series was restarted in 2006. Using a light trap (fig. 3) placed in the Charleston small boat harbor in Coos Bay, Oregon crab megalopae were captured daily from roughly the beginning of April through September

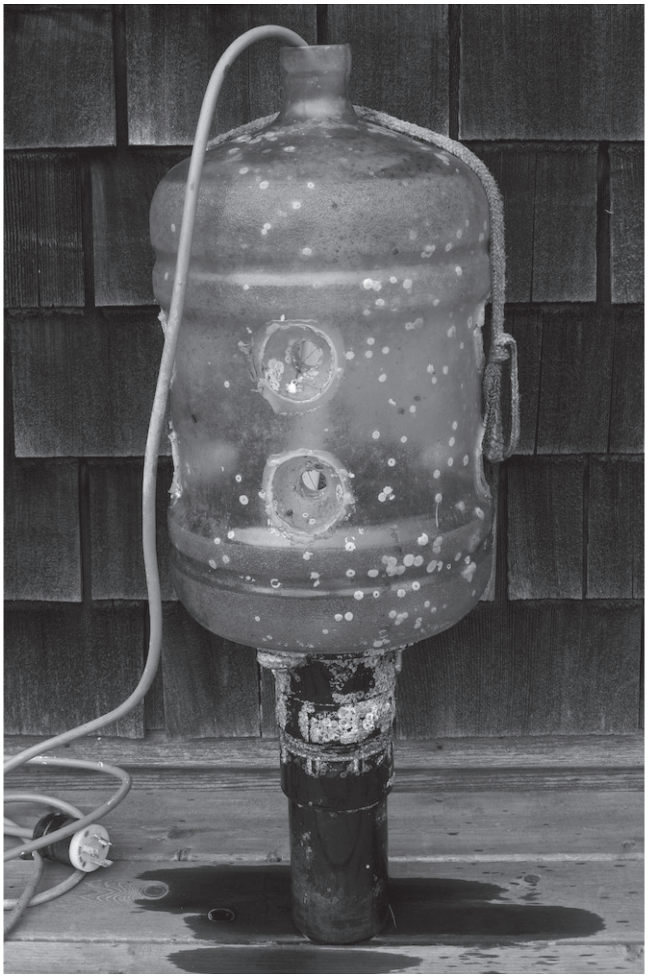

Figure 3. Light trap used to sample megalopae in Coos Bay, Oregon. The trap consists of a clear plastic water bottle into which are placed a number of funnels. The light source is a fluorescent lamp powered by an outlet on the dock. This trap had been deployed for about one month.

or October (Shanks and Roegner 2007). At the beginning of this study we sampled three replicate traps per day, but we found that the daily catch in these replicates was quite similar and that the greatly increased work required to process three replicates each day was unwarranted (Roegner et al. 2007; Shanks and Roegner 2007). The total number of megalopae captured in each settlement season was used as an index of the abundance of megalopae returning to the coast.

When a daily sample was < 2000 either the entire sample was counted or it was split using standard methods and then counted. Starting in 2007, the daily and annual abundance of megalopae increased dramatically with daily catches during pulses in the range of 10s of thousands of megalopae (5 to 10 liters of megalopae). We could not efficiently count these huge samples. To estimate the number of megalopae, we carefully drained off the water, weighted the entire sample, and then divided by the weight of 100 megalopae.

To test the hypothesis that population size is limited by the number of returning megalopae, we correlated the index of settling megalopae to the size of the Oregon commercial catch landed four years later. The Oregon Department of Fish and Wildlife provided commercial catch data.

We compared the index of settling megalopae with a variety of climate indices and oceanographic parameters. We correlated the index of settling megalopae to the date of the spring transition. The spring transition is apparent as an abrupt drop from high winter coastal sea levels following a period of steady winds from the north (Strub et al. 1987). As the date of the spring transition, we used the date on which sea level dropped 100 mm below the annual average and stayed there for at least seven days (Strub et al. 1987). We used sea level data for Crescent City, California obtained from the University of Hawaii Sea Level Center (http:/ilikai.soest.hawaii.edu). The strength of winter upwelling was estimated from summed monthly averages of the upwelling index for 42°N (http://www.pfeg.noaa.gov/pr). We correlated the index of settling megalopae with the Pacific Decadal Oscillation (PDO, http://jisao.washington.edu/pdo/PDO.latest), the North Pacific Gyre Oscillation (NPGO, http://eros.eas.gatech.edu/npgo/data/NPGO.txt), the Northern Oscillation Index (NOI, http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix_download.html?indx=NOI&time=1948+to+present&Submit=Show+List+%28entire+series%29), the East Pacific North Pacific index (EP/NP, http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.CPC/.Indices/.NHTI/) and the North Pacific index (NP, http://www.cgd.ucar.edu/cas/jhurrell/npindex.html). With the NP index we used the sum of the values from December through February, months when this index shows high inter-annual variability (Trendberth and Hurrell 1994). For all other indices we used the sum of the index from January through July, the entire pelagic larval period for Oregon crabs.

Starting in 2007, the return of megalopae increased dramatically. One possible cause of the large jump in annual return might be that the at-sea larval growth conditions were better in 2007–2009. If this were the case, we hypothesized that the returning megalopae may be larger in these years than in previous years. To test this hypothesis, we measured the length of megalopae caught on a number of days (about 20) during each recruitment season. Early in the recruitment season, when megalopae were abundant, we measured at least 100 haphazardly-selected animals (i.e., the first 100 animals removed from a sample), but late in the season, when returns were much lower, fewer individuals were available to be measured. In the data from the first six years of sampling, about a quarter of the dates had <100 animals, but in

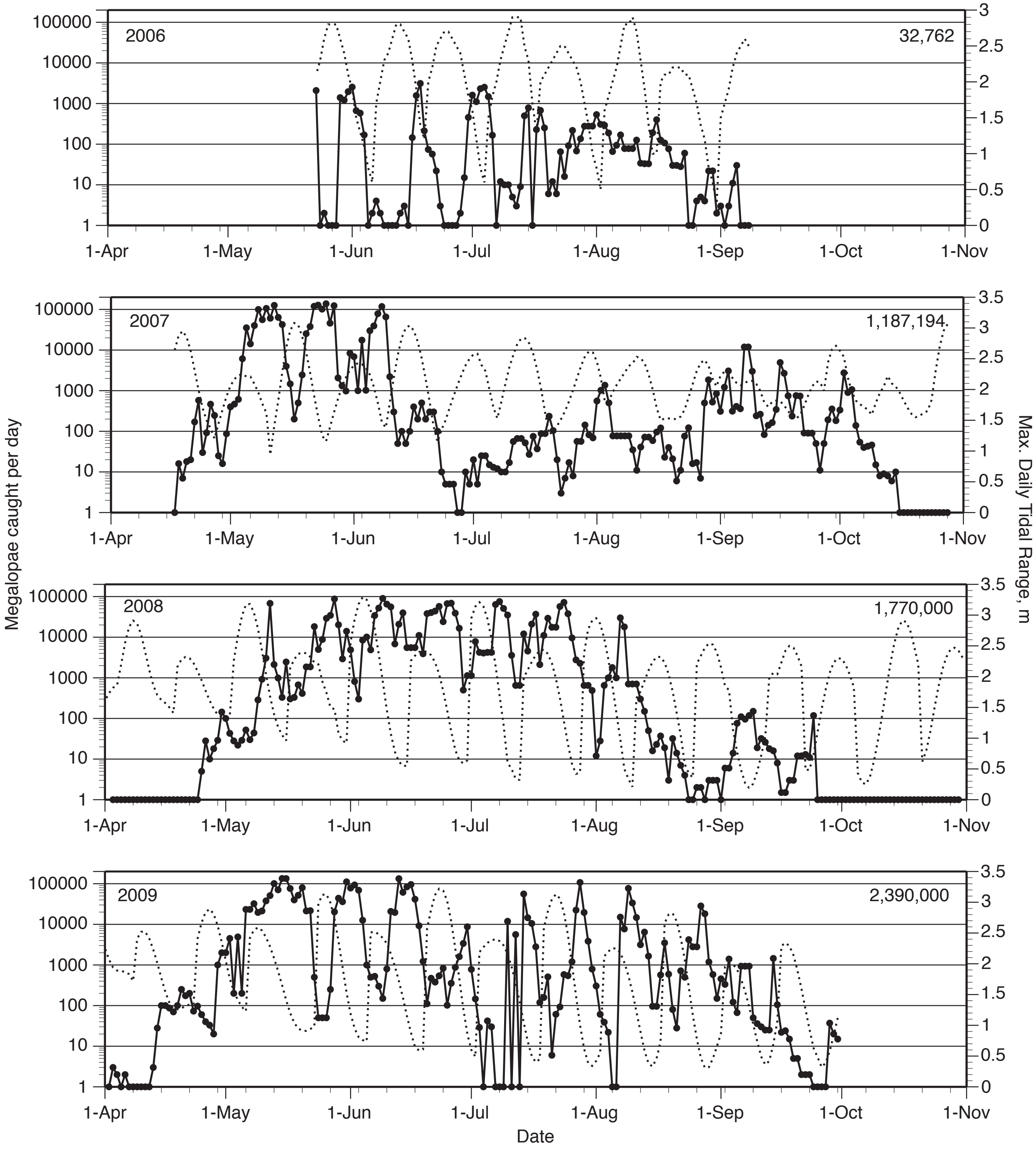

Figure 4. The daily catch of megalopae (solid line and circles) to a light trap in Coos Bay, Oregon during the 2006, 2007, 2008, and 2009 recruitment seasons plotted with the maximum daily tidal range (dotted line). Number in the upper right hand corner of each graph is the total number of megalopae caught each year.

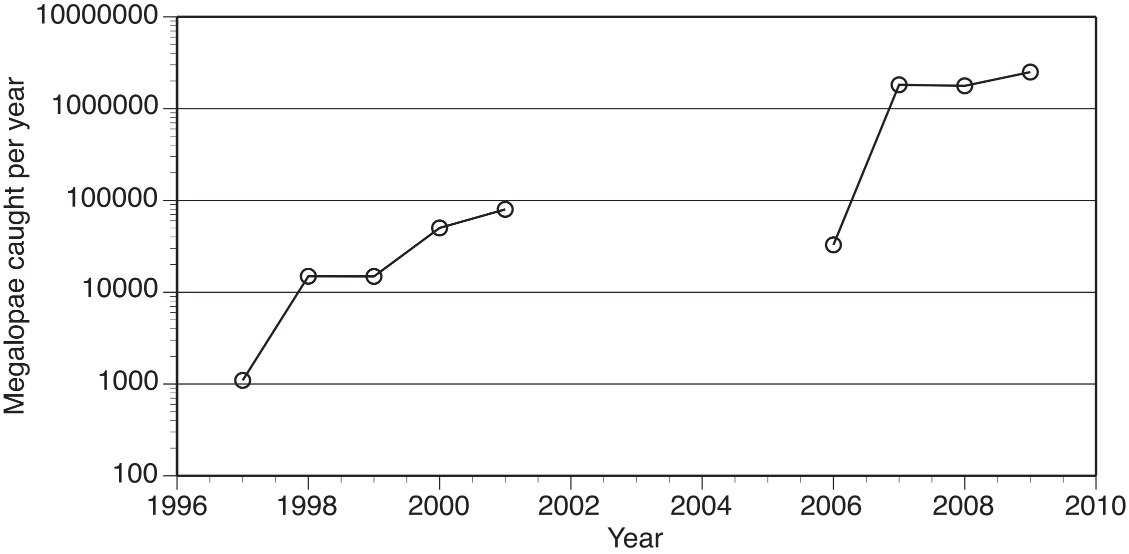

Figure 5. The annual catch of megalopae plotted by year. Prior to 2007, the annual catch ranged from 1000 to 80,000, but from 2007 onward, catch jumped to 1.2 to 2.4 million megalopae.

the last three years few dates had <100 animals. During the late season, we either used dates when we could measure at least 10 animals or combined adjacent dates to get at least 10 animals to measure. Length (tip of rostral spine to back of the carapace; DeBrosse et al. 1990) was measured using an ocular micrometer in a dissecting microscope.

One possible consequence of the very high settlement rates of 2007–2009 is that growth rates of juvenile crabs may have been slowed due to intense competition. To investigate this possibility, we measured the sizes (carapace width) of juvenile crabs photographed by an Oregon Department of Fish and Wildlife (ODFW) ROV deployed off Cape Perpetua, Oregon in August of 2007. The average size of these crabs was compared to historical size data for similar aged crabs.

RESULTS

The daily abundance of returning megalopae was highly pulsed (fig. 4). Significant negative cross correlations between the maximum daily tidal range and daily catch, with lags around –1 to –4 days, suggest that peak catches tended to occur between the neap and the spring tides as had been seen previously (Roegner et al. 2007).

In 2006, on the first day of trap deployment, over 2,000 megalopae were caught suggesting that the trap was deployed after the start of the recruitment season. Total catch in the light trap during the first three completely sampled pulses in 2006 averaged around 7,000 individuals suggesting that the first pulse may have been under sampled by about 5,000 animals. In 2007–2009, initial daily catches were between 0 and 10 individuals for at least several days before the first large pulse suggesting that the trap was deployed prior to the beginning of the recruitment season.

The total catch of megalopae in 2006 was similar to catches from previous years, 32,762 megalopae (figs. 4 and 5): given that the start of the season was missed, the annual return of megalopae was probably around 37,000. After 2006, the total annual catch was far larger than in any previous year; total catches in 2007, 2008, and 2009 were 1.2, 1.7, and 2.4 million megalopae, respectively (figs. 4 and 5). During the fortnightly pulses, daily catches ranged from 10s of thousands to > 100,000 individuals. These annual catches were >10X larger than the previous largest annual catch of around 80,000 megalopae (2001). Over nine years of sampling, the total annual return of megalopae varied by a factor of > 1,000 (fig. 5).

Of the last four years of sampling, we have both the annual catch of megalopae and an estimate of the year class strength from the fishery only for 2006 year of megalopae return. Given the past relationship between returning megalopae and commercial catch, the predicted commercial catch generated by the 2006 return of megalopae was 21,000,000 lbs (tab. 1), and the observed commercial catch as of the submission of this paper (1 June 2010) was 22,937,111 lbs. Historically, by this date ≈95% of the annual commercial catch has been landed, suggesting that the total catch for the 2009/2010 fishing season will ultimately be ≈24,100,000 lbs; similar to the catch predicted from the number of returning megalopae. We now have six years in which we have both the total return of megalopae and commercial catch (fig. 6) and the relationship between these two variables remains remarkably strong ($R^2 = 0.932$, n=6, $p< 0.01$).

TABLE 1

Predicted and observed Oregon commercial catch of Dungeness crab. Predictions were based on the models in Shanks and Roegner (2007) that utilized the date of the spring transition or the total number of megalopae caught in Coos Bay, Oregon during the annual recruitment season (roughly April through September).

Crab fishing year	Date of the spring transition 4 yrs earlier	Oregon predicted catch (lbs) using spring transition date	Oregon predicted catch (lbs) using catch of megalopae	Oregon observed catch (lbs)	Deviation from predicted catch (lbs) (% off)
2005–2006	14 March 2002	27,000,000		27,600,000	–600,000 (2%)
2006–2007	8 May 2003	12,000,000		15,400,000	–3,400,000 (28%)
2007–2008	4 March 2004	28,000,000		12,300,000	–15,700,000 (212%)
2008–2009	13 July 2005	5,500,000		12,500,000	+7,000,000 (127%)
2009–2010	22 April 2006	16,000,000	21,000,000	24,100,000	+8,000,000 or +3,000,000 (33 or 12%)
2010–2011	11 March 2007	26,000,000	>500,000,000		
2011–2012	29 March 2008	18,000,000	>500,000,000		
2012–2013	29 March 2008	18,000,000	>500,000,000		

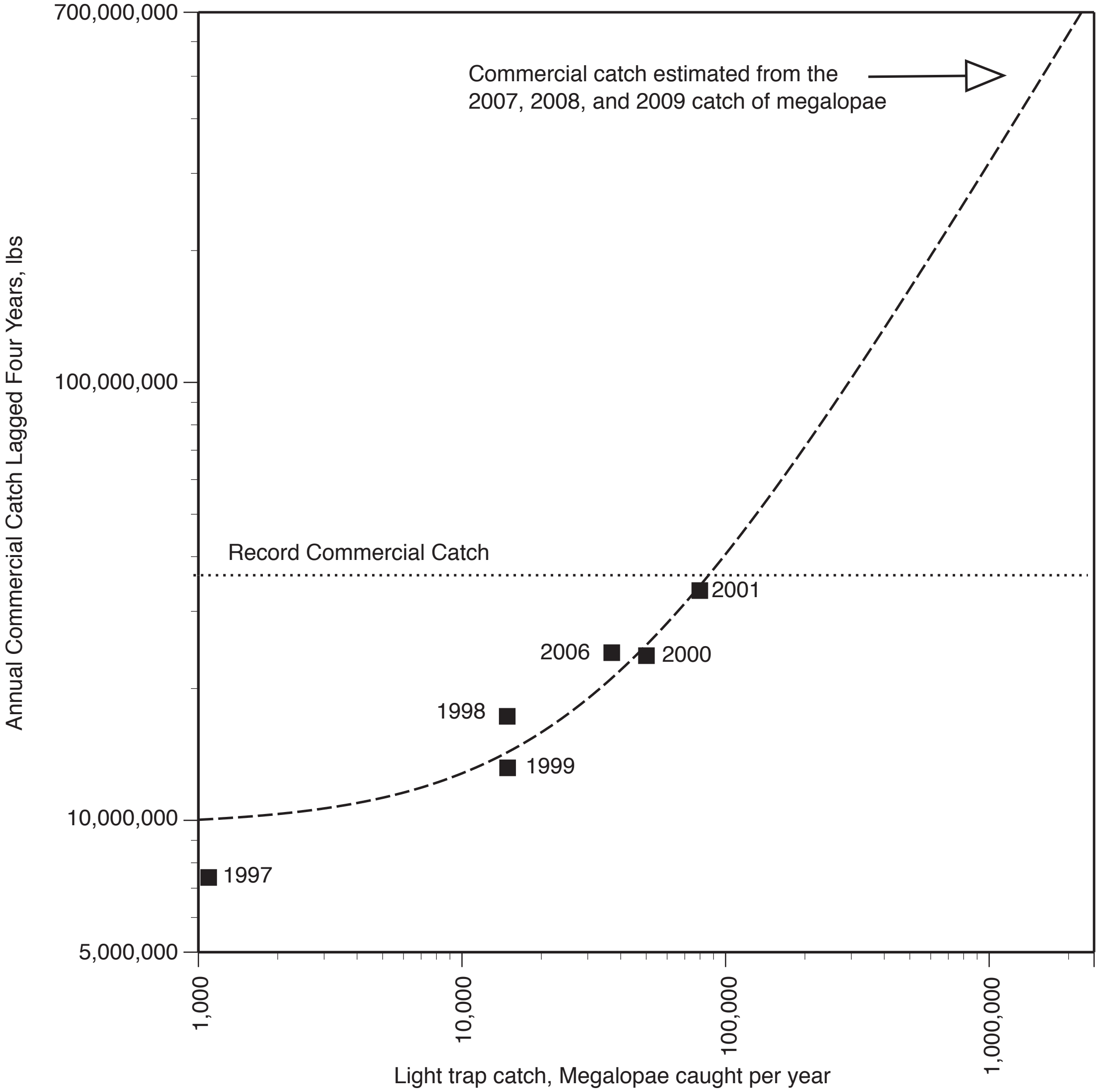

Figure 6. The annual light trap catch of megalopae plotted against the annual commercial catch of Dungeness crabs landed in Oregon lagged four years. From 2007 to 2009, the annual catch of megalopae ranged from 1.2 to 2.4 million individuals. Megalopae that settled during these years have yet to enter the fishery. The arrow indicates the approximate size of the commercial catch if the significant relationship ($R^2 = 0.943$, n=6, $p < 0.01$) for the years 1997 to 2001 and 2006 between the number of returning megalopae and commercial catch were applied. The commercial catch would be > 10 times larger than the current record commercial catch (indicated by the dashed line).

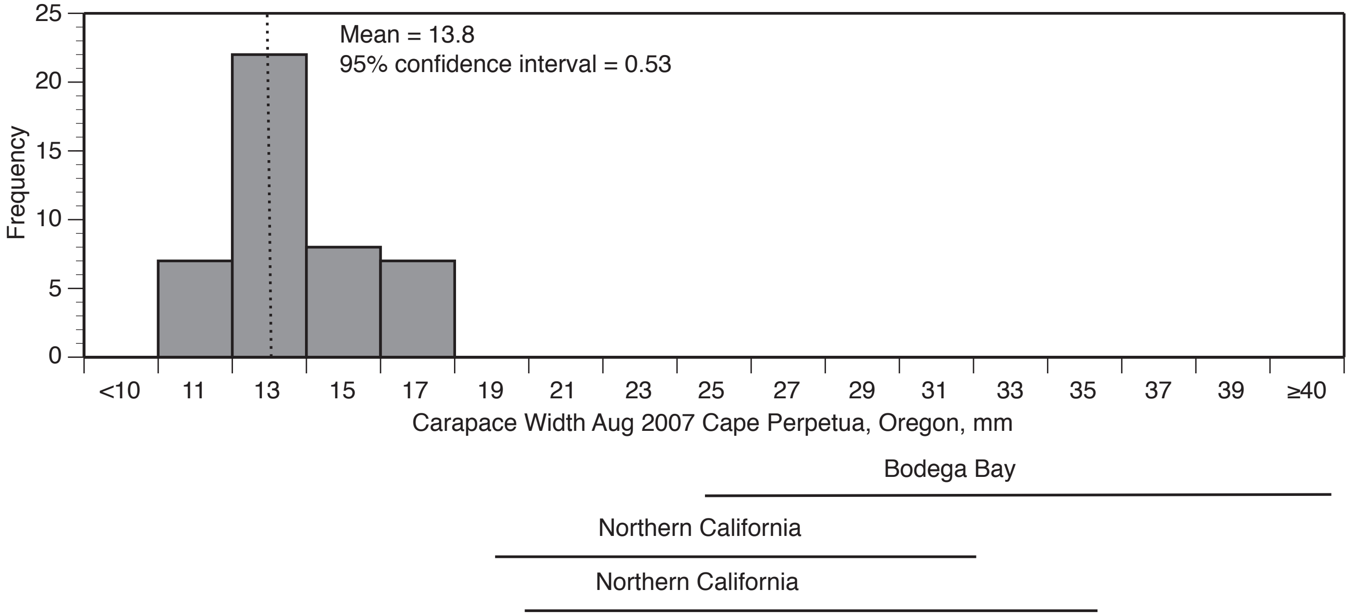

Figure 7. Size frequency distribution of juvenile crabs in August off Cape Perpetua, Oregon. Data are from an ROV video collected by the Oregon Dept. of Fish and Wildlife. The lines below this graph are size ranges for similarly aged juveniles reported in other studies in the California Current (Wainwright and Armstrong 1993).

At least within the range of 1,000 to 100,000 returning megalopae, the number of returning megalopae appears to be an excellent predictor of the commercial catch four years later, but will this relationship hold in the future given the recent huge returns of megalopae?

Using the present relationship between returning megalopae and commercial catch, we estimate that the future commercial catches generated by these huge returns of megalopae would be on the order of 500,000,000 lbs (fig. 6). Given that historically the largest commercial catch was 33,000,000 lbs, it is highly unlikely that such large commercial catches will occur; density-dependent effects, mortality due to predation and starvation and reduced growth rates, will likely modify the relationship between returning megalopae and commercial catch. Without systematic sampling of new-recruits as they grow into fishable-sized crabs, we have little evidence that can be used to investigate density dependence.

The 2007 ROV video from ODF&W provides one set of data. The video was shot in August off Cape Perpetua, Oregon. The average density of juveniles was 174 m^{-2} (n= 24, SE = 25, range 25 to 405 m^{-2}). These very high densities could lead to intense competition for food and reduced growth rate of juveniles. Using close-up images from the video, we generated a size frequency distribution of carapace widths (fig. 7). In August, the average juvenile was 13.8 mm wide (95% confidence interval = 0.5 mm), significantly smaller (10 to 20 mm smaller) than the reported sizes of similarly aged new-recruits within the California Current (Wainright and Armstrong 1993). The small size of the 2007 recruits is consistent with the hypothesis that competition for food was retarding their growth. It may take longer than four years for these recruits to enter the fishery.

What might have caused the huge return of megalopae in the last three years? There are at least three possibilities; mortality of larvae due to predation was much lower, growing conditions were much better than in previous years, and ocean currents were highly favorable and returned more larvae to the coast. There is not enough information on the predators of zoeae and megalopae of Dungeness crabs to address the first possibility, but we have some data with which we can investigate the other two potential causes.

If growth conditions during larval development were better during the last three years, then returning megalopae in these years may be significantly larger than in the years with smaller returns. We measured the sizes of megalopae over the recruitment season in 1998, 1999, 2001, and 2006 through 2009 (1997 and 2000 samples were unavailable). In each year, the largest megalopae were caught at the beginning of the season and returning megalopae decreased in size over the summer (fig. 8). If improved pelagic growth conditions translate into larger returning megalopae, then we would expect to see the size curves from the last three years (closed symbols, fig. 8) located above curves from years with smaller catches (open symbols, fig. 8). The size curve for megalopae from 2007, the first year of huge returns, is co-located with curves for years of lower catch. The curve for 2008 is mostly above curves for the lower catch years, and at the very beginning and toward the end of 2009, megalopae

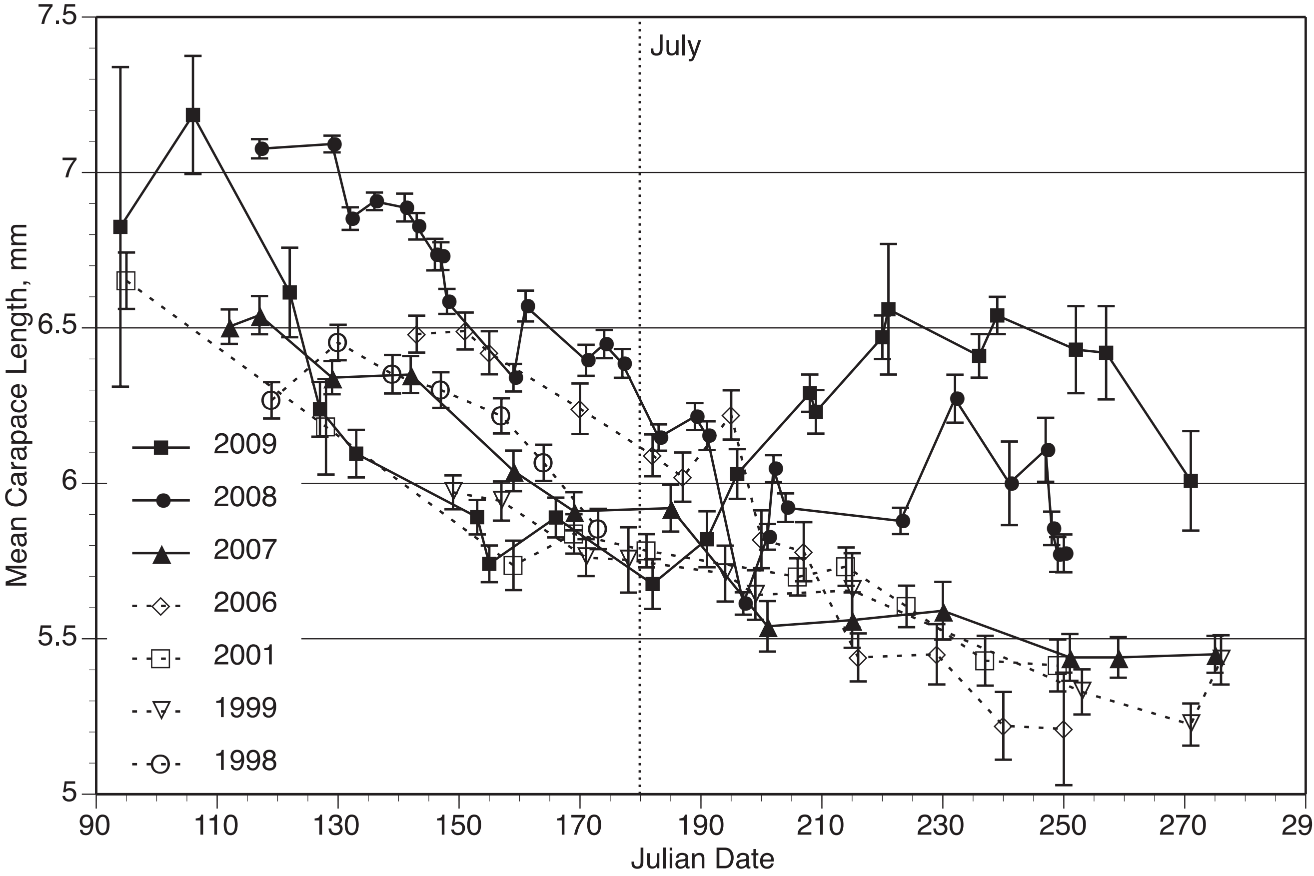

Figure 8. Mean carapace lengths (± 95% confidence interval) of megalopae caught in light traps placed in Coos Bay, Oregon plotted by Julian date. Closed symbols indicate years with very large (> 1 million) annual returns of megalopae and open symbols are years with < 100,000 megalopae returning.

were larger than those from years with lower catches, however, in the middle of the 2009 season, megalopae size was similar to that seen in the years with lower catches. While there are interesting patterns in these data, the results do not clearly support the hypothesis that returning megalopae were significantly larger in years with very high returns than in those with lower returns. If size of returning megalopae is a reflection of pelagic growth conditions then the data do not support the hypothesis that recent huge returns of megalopae were due to improved larval growth conditions.

We investigated a variety of hydrographic and climatic indices that might relate to the ocean transport of Dungeness crab larvae. Shanks and Roegner (2007) found a clear negative relationship between the day of the year of the spring transition and the number of returning megalopae. This relationship held through 2006 ($R^2=0.943$, n=6, $P<0.01$), but data points from the last three years of very large catches sit far above this relationship (fig. 9A). The East Pacific/North Pacific (EP/NP) index was negatively related to the number of returning megalopae, the relationship was significant through 2006 ($R^2=0.734$, n=6, $P<0.05$), and data points from the last three years sit well above this significant relationship (fig. 9B). Using all the data, the Pacific Decadal Oscillation (PDO) was significantly negatively related to the number of returning megalopae ($R^2=0.532$, n=9, $P<0.05$) with the PDO explaining about 50% of the variation in the catch of megalopae (fig. 9C). Using all the data, the summed monthly winter upwelling index was not significantly related to the number of returning megalopae (fig. 9D), with the one outlier point (1997) removed, however, the relationship is highly significant ($R^2=0.782$, n=8, $P<0.01$). The remaining indices were positively related to the number of returning megalopae. Neither the North Pacific Gyre Oscillation (NPGO) index nor the North Pacific index were significantly related to the number of returning megalopae (figs. 9E and G), but the relationship between the Northern Oscillation Index (NOI) and the number of returning megalopae was significant at the 0.10 level, but not at 0.05 ($R^2=0.417$, n=9, $P=0.060$).

DISCUSSION

In years when the number of returning megalopae was less than about 100,000, the index of returning meg-

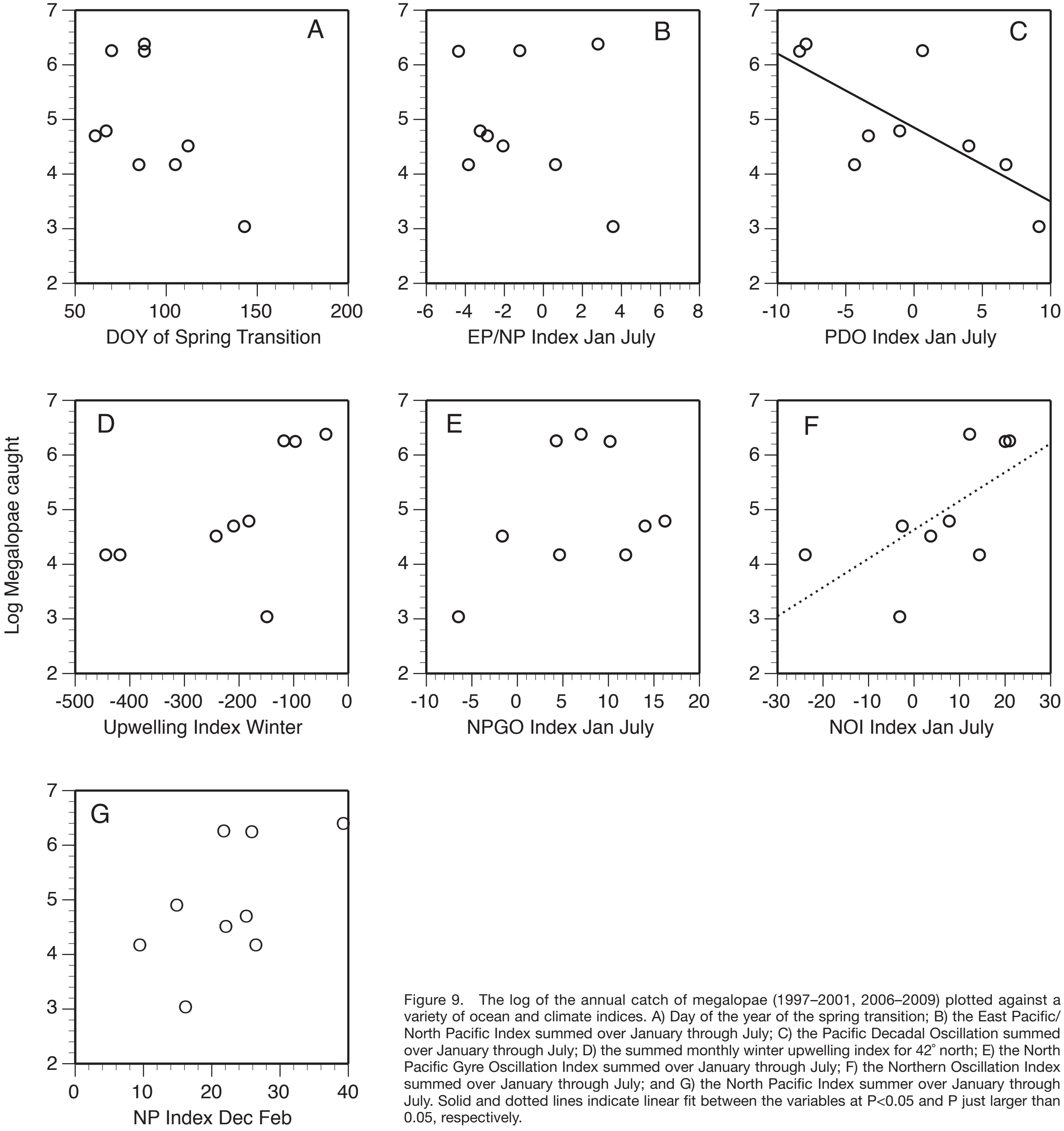

Figure 9. The log of the annual catch of megalopae (1997–2001, 2006–2009) plotted against a variety of ocean and climate indices. A) Day of the year of the spring transition; B) the East Pacific/North Pacific Index summed over January through July; C) the Pacific Decadal Oscillation summed over January through July; D) the summed monthly winter upwelling index for 42° north; E) the North Pacific Gyre Oscillation Index summed over January through July; F) the Northern Oscillation Index summed over January through July; and G) the North Pacific Index summer over January through July. Solid and dotted lines indicate linear fit between the variables at P<0.05 and P just larger than 0.05, respectively.

alopae has been a good predictor of commercial catch four years in the future. The technique for monitoring returning megalopae, a light trap in Charleston marina, is simple and cost effective. In addition, the time series has revealed fascinating and previously unobserved huge variations in annual larval success.

During the last three years, we have measured annual returns of megalopae in the millions; > ten times more megalopae returned in each of these years than in any previous year and, in fact, during settlement pulses, a day's catch was often larger than the entire annual catch in previous years. How these huge catches relate to the future commercial catch will not be clear until these recruits begin entering the fishery in fishing year

2010/2011, but the size of the commercial catch during the last two fishing seasons (2007/2008 and 2008/2009) offers some indication of what may occur.

We currently have two means of predicting the future commercial catch of Dungeness crabs. We can predict the commercial catch from the number of returning megalopae, but, given the strong relationship between returning megalopae and the day of the year of the spring transition, we can also predict commercial catch from the spring transition date. During the period when we did not have support to maintain sampling, this relationship was used to predict the commercial catch for the 2007/2008 and 2008/2009 fishing seasons (tab. 1). Given the early spring transition in 2004, the 2007/2008 season should have produced a large commercial catch, but the catch was only average. In contrast, the very late spring transition in 2005 (tab. 1) should have produced a very small commercial catch in the 2008/2009 season, but the catch in this year was much larger than predicted.

While we did not have light traps deployed in 2004, we did subjectively monitor recruitment. During this summer, there were vast numbers of megalopae around the docks in Coos Bay and, on sand flats near the docks, there were swarms of juvenile crabs. On a rising tide, at the water's edge, there was a continuous band of juvenile crabs 10 or more cm wide migrating into the intertidal zone to feed. The abundance of megalopae and juveniles suggests that the number of returning megalopae in 2004 was likely comparable to that in the last three years; we strongly suspect that the larval return in 2004 was in the millions. The observed juvenile densities were very high and likely led to stiff competition for food. The juveniles in the Cape Perpetua video were significantly smaller than the size of similarly aged juveniles reported in the literature (Wainright and Armstrong 1993). Off Oregon it typically takes four years for crabs to grow from larvae to commercial sized crabs, but, if densities on the bottom are high, competition may slow growth enough that some recruits may take five years to enter the fishery. The lower than predicted commercial catch in the 2007/2008 fishing season could be due to crabs taking five rather than four years to enter the fishery and the higher than predicted catch in the 2008/2009 fishing season might be due to an influx of five year old crabs that settled in 2004 subsidizing the commercial catch. The current model relationship between the number of returning megalopae and the commercial catch is based upon a four year lag between new settlers and commercial catch; obviously, if it takes four or five years for settlers to enter the fishery this model relationship breaks down and a new model will have to be developed.

The argument presented in the previous paragraph is, obviously, speculative; we will have to wait for the crabs that settled in the last three years to grow and enter the fishery before we can begin to develop an understanding of the relationship between huge settlement events and the size of the commercial catch. In addition, insights from the 2004 settlement event may not be applicable. In 2004, we had one apparently very high settlement year followed probably by a very poor settlement year (2005), but in the current situation we have three very high settlement years (2007, 2008, and 2009) in a row; repeated very strong settlement years would likely exacerbate density-dependent effects.

The most likely relationship between the number of megalopae and the commercial catch is that above some number of returning megalopae the relationship will be asymptotic (Caley et al. 1996). The earlier significant relationship between the number of returning megalopae and the future commercial catch would be the portion of the graph leading to the asymptote and would describe conditions under which the adult population is set by the relative success of the larvae. The current relationship between the huge returns of megalopae and the commercial catch will likely delineate an asymptote and would describe conditions under which settlement is so high that adult population size is not set by the relative success of the larvae, but by the relative success of the recruits; when the returns of megalopae are very high, density dependent effects will likely strongly influence the adult population size. This type of relationship between the annual return of larvae and the eventual size of the commercial catch is exactly what has been seen in the fishery for the Western Australian rock lobster (*Panulirus cygnus*) (Phillips 1986; Caputi et al. 1995). We will not know if this is true until we see how many adults are caught in the future; the first commercial catch from the recent large returns occurs in the 2010/2011 fishing year and will continue for several more years. If the relationship between the number of megalopae returning and the commercial catch is asymptotic then we should be able to predict the commercial catch with this more complete model relationship between number of returning megalopae and the size of the commercial catch.

Density dependent effects can take several forms, e.g., competition for food, increased predation, and the spread of diseases or parasites. The very high densities of recruits seen in the 2007 ROV video off Cape Perpetua, Oregon and their small size suggests that competition for food was reducing their growth rate. Competition for food may eventually lead to starvation or slower growth may lead to a longer period of vulnerability to predators on small crabs. Settling megalopae are preyed upon by young of the year Dungeness crabs (Fernandez et al. 1993; Fernandez 1999) as well as by predators of small crustaceans such as crabs and fish (Armstrong et al. 1995; Visser et al. 2004). Predation on Dungeness crab recruits has received some attention in estuarine habitats (Armstrong et al. 1995; Visser et al. 2004), but studies do not appear have taken place in coastal subtidal habitats. High densities of new-recruits could lead to predators, which do not normally prey on Dungeness crab recruits to target the bounty. This has not been investigated. Very high densities of recruits might also lead to the rapid spread of diseases or parasites, but this has also not been investigated.

What might have caused the amazingly large larval returns of the last three years? Ocean conditions were clearly far more favorable either to the survival of Dungeness crab larvae during their pelagic development or their return to the coast. As pointed out earlier, we know too little about predation on crab larvae to speculate on the contribution of decreased predation as a cause for the large returns of megalopae. We tested the hypothesis that the growing conditions may have been better during the past three years by assuming the sizes of returning megalopae were an indication of growing conditions; larger megalopae would indicate better growing conditions. Megalopae from the last three years were not consistently larger than megalopae from years with lower returns suggesting that, if our assumed relationship between megalopae sizes and growing conditions is correct, then growth conditions during the pelagic phase were not markedly better during the years of huge returns than those with lower returns.

While the size data do not indicate that growth conditions likely varied between years with higher and lower larval returns, the size data are curious. In all years, megalopae were largest at the start of the settlement season and, generally, decreased in size over the course of the spring and summer (fig. 8). It is not clear what might be causing this seasonal size decrease. Off Oregon, larval release is in winter and the larval period is about three months. If larval returns in Oregon are due to larval production from Oregon, then larval returns should end by July, but megalopae continue to settle into October and even November (fig. 4). By July, coastal flow is from the north suggesting that the source of these late summer settlers is to the north. Populations north of Oregon spawn later in the year (Strathmann 1987) and a limited set of measurements suggests that megalopae to the north (Washington and Puget Sound) are smaller than those caught off Oregon (DeBrosse et al. 1990). The very small megalopae caught at the end of the 2006 settlement season were similar in size to those from Puget Sound. The variation in size of megalopae over the settlement season may be due, at least in part, to different larval sources, but why source might affect megalopae size is unknown.

Larval transport may also affect the number of megalopae returning to the Oregon coast. From 1997 through 2006, the timing of the spring transition was clearly related to the number of settlers, suggesting that shoreward transport generated by the spring transition played a substantial role in determining larval success. In the last three years, however, this relationship is no longer true. We investigated the relationship between the number of settlers and a number of ocean and climate indices. Several of these correlations were either significant (summed PDO Jan. – July) or nearly so (summed winter upwelling index, and summed NOI Jan. – July) (fig. 9), and each of these climate or hydrographic variables can be interpreted as indicators of the amount of southward flow along the West coast. The PDO correlates with the amount of water from the North Pacific Drift that enters either the Gulf of Alaska (positive PDO) or the California Current (negative PDO) (Minobe and Mantua 1999); in years when more water is deflected to the California Current the return of megalopae was higher. The summed winter upwelling index indicates both the amount of water forced off- or onshore by the winds, but also the amount of wind-driven north- or southward flow over the shelf; during the winter months, when Dungeness crab larval are pelagic, weaker downwelling-favorable winds (less offshore and northward flow) led to higher numbers of returning megalopae. Positive (negative) values of the NOI tend to be associated with La Niña (El Niño) events, stronger (weaker) upwelling favorable winds along the West coast, and cooler (warmer) sea surface temperatures in the California Current (Schwing et al. 2002); higher returns of megalopae tended to occur when the NOI was more positive indicating more flow from the north. Tentatively—the time series of returning megalopae is short—these correlations suggest that when northward flow during the winter is weak or southward flow during the Dungeness crab larval development period is stronger, more megalopae return to the Oregon coast.

How might north/south flow during the pelagic larval phase affect the number of returning megalopae? Along the Oregon coast, larvae hatch during winter probably within several miles of shore (Wild and Tasto 1983). As development progresses, larvae are found progressively further from shore such that by late zoeae stages they are found seaward of the continental shelf (Wild and Tasto 1983). Early larval stages are, thus, in shelf waters in winter and will be transported northward by the Davidson Current. Northward transport will continue until larvae migrate off the shelf and into the southward flowing California Current present beyond the shelf. The amount of northward vs. southward transport the larvae will experience will be dependent on the amount of time spent in the Davidson Current vs. California Current and current speeds. Given the speed at which drifters are carried northward by the Davidson Current (Austin and Barth 2002), larvae released off Oregon may be transported to Vancouver Island before they migrate seaward of the continental shelf. If larvae experience enough northward transport, they may actually be carried north of the California Current in which case these larvae would settle well to the north of their release site, supplementing the Dungeness crab population along the coast of Vancouver Island. In addition, the amount of southward transport they may experience within the California Current may not compensate for the Davidson Current northward transport, which would again lead to larvae settling to the north of their release point. Whether larvae released in Oregon waters settle to the north or south or settle in Oregon waters may be dependent on the relative transport by the Davidson and California Currents.

The characteristics of the larval stage in Dungeness crabs (e.g., winter spawning, long larval duration, larvae present in the waters over the shelf and beyond, and recruitment to the benthos in spring and summer) are not unique to this species, but are characteristics shared by most shelf/slope species of fish and benthic crustaceans (Shanks and Eckert 2005). Hence, the relative amounts of northward and southward transport as well as processing affecting cross-shelf transport experienced by larvae of these species during their pelagic development may be amongst the critical factors determining the annual larval return at a site.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Armstrong, J. L., D. A. Armstrong, and S. B. Mathew. 1995. Food habits of esuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab, *Cancer magister.* Fish. Bull. 93:456–470.

Austin, J. A., and J. A. Barth. 2002. Drifter behavior on the Oregon-Washington shelf during downwelling-favorable winds. J. Phys. Oceanogr. 32:3132–3144.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. (1996) Recruitment and the local dynamics of open marine populations. Annual Review of Ecology and Systematics 27:477–500.

Caputi, H., R.S. Brown, and B.F. Phillips. (1995). Predicting catches of the western rock lobster (*Panulirus cygnus*) based on indices of puerulus and juvenile abundance. Shellfish Life History and Shellfishery Models. ICES Marine Science Symposia, New Brunswick, Canada. P. 287–293.

DeBrosse, G. A., A. J. Baldinger, and P. A. McLaughlin. 1990. A comparative study of the megalopal stages of *Cancer oregonensis* Dana and *C. productus* Randall (Decapoda: Brachyura: Cancridae) from the Northeastern Pacific. Fish. Bull. 88:39–49.

Fernandez, M. 1999. Cannibalism in Dungeness crab *Cancer magister*: effects of predatory-prey size ratio, density and habitat type. Mar. Ecol. Progr. Ser. 182:221–230.

Fernandez, M., D. Armstrong, and O. Iribarne. 1993. First cohort of young-of-the-year Dungeness crab, *Cancer magister,* reduces abundance of subsequent cohorts in intertidal shell habitat. Can. J. Fish. Aquat. Sci. 50:2100–2105.

Hackett, S., M. Krachey, C. Dewees, D. Hankin, and K. Sortais. 2003. An economic overview of Dungeness crab (*Cancer magister*) processing in California. Calif. Coop. Oceanic Fish. Invest. Rep. 44:86–93.

Johnson, J., and A. L. Shanks. 2002. Time series of the abundance of the post-larvae of the crabs *Cancer magister* and *Cancer* spp. on the southern Oregon coast and their cross-shelf transport. Estuaries 25:1138–1142.

Minobe, S., and N. Mantua. 1999. Interdecadal modulation of interannual atmospheric and oceanic variability over the North Pacific. Prog. in Oceanogr. 2:163–192.

Phillips, B.F. (1986) Prediction of commercial catches of the western rock lobster *Panulirus cygnus*. Canadian J. Fish. Aquat. Sci. 43:2126–2130.

Roegner, G. C., D. A. Armstrong, and A. L. Shanks. 2007. Wind and tidal influences on larval crab recruitment to an Oregon estuary. Mar. Ecol. Prog. Ser. 351:177–188.

Schwing, F. B., T. Murphree, and P. M. Green. 2002. The Northern Oscillation Index (NOI): A new climate index for the northeast Pacific. Prog. Oceanogr. 53:115–139.

Shanks, A. L., and G. Eckert. 2005. Life-History Traits and Population Persistence of California Current Fishes and Benthic Crustaceans; Solution of A Marine Drift Paradox. Ecol. Monogr. 75:505–524.

Shanks, A. L., and C. A. Pfister. 2009. Annual recruitment of three species of tidepool fishes is driven by variation in springtime coastal hydrodynamics. Limnol. Oceanogr. 54:1481–1487.

Shanks, A. L., and G. C. Roegner. 2007. Recruitment limitation in dungeness crab populations is driven by variation in atmospheric forcing. Ecology 88:1726–1737.

Strathmann, M. F. 1987. *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast*. U. of Washington, Seattle.

Strub, P., J. Allen, A. Huyer, and R. Smith. 1987. Large-scale structure of the spring transition in the coastal ocean off western North America. J. of Geophys. Res. 92:1527–1544.

Swiney, K. M., and T. C. Shirley. 2001. Gonad development of southeastern Alaskan Dungeness crab, *Cancer magister*, under laboratory conditions. J. Crust. Biol. 21:897–904.

Trendberth, K. E., and J. W. Hurrell. 1994. Decadal atmosperr-ocean variations in the Pacific. Climate Dynamics 9:303–319.

Visser, E. P., P. S. McDonald, and D. A. Armstrong. 2004. The impact of Yellow Shore crabs, *Hemigrapsus oregonensis*, on early benthic phase Dungeness crabs, *Cancer magister*, in intertidal oyster shell mitigation habitat. Estuaries 27:699–715.

Wainright, T. C., and D. A. Armstrong. 1993. Growth patterns in the Dungeness crab (*Cancer magister* Dana): Synthesis of data and comparison of models. J. Crust. Biol. 13:36–50.

Wild, P. W., and R. N. Tasto. 1983. Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with empahsis on the central California fishery resource. Calif. Dept. Fish and Game, Fish Bull. 172:1–352.

USE OF A PRE-RECRUIT ABUNDANCE INDEX TO IMPROVE FORECASTS OF OCEAN SHRIMP (*PANDALUS JORDANI*) RECRUITMENT FROM ENVIRONMENTAL MODELS

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ABSTRACT

I investigated the potential to improve forecasts of annual $\log_e$ recruitment to the ocean shrimp (*Pandalus jordani*) fishery using a pre-recruit index based on the percentage of age-zero shrimp from fishery samples in the year prior to recruitment. The index was incorporated into existing models in which $\log_e$ age-1 recruitment is forced by environmental variables related to the spring transition in coastal currents (negative correlation with April sea level height at Crescent City, California, $ASLH_{t-1}$) and the strength of April–July upwelling winds at 42°N. latitude (negative correlation, AJU_{t-1}) during the pelagic larval phase. For northern Oregon, the pre-recruit index improved model fit, increasing the coefficient of determination from 0.40 for a model based only on $ASLH_{t-1}$ to 0.62 for the combined model. For southern Oregon, the index did not improve the fit of a model based on $ASLH_{t-1}$ and AJU_{t-1}. However, the pre-recruit index alone had a higher correlation with age-1 recruits than the best environmental model (r^2 of 0.43 versus 0.27). Although precision of the final models was low, both correctly predicted a stronger than average 2009 recruitment.

INTRODUCTION

The trawl fishery for ocean shrimp (*Pandalus jordani*) is the second most valuable crustacean fishery operating in California Current waters, following only Dungeness crab (*Cancer magister*) in the average annual value of landings (The Research Group 2006). The ocean shrimp fishery is considered a "recruit fishery," in that annual catches are strongly influenced by the strength of the year class entering the fishery that year (Hannah and Jones 1991). Ocean shrimp are very short-lived, recruit to the fishery at age one and contribute to fishery landings for just 3 years (Dahlstrom 1973; Hannah and Jones 1991). Recruitment of ocean shrimp off Oregon has been linked to environmental variation in the California Current ecosystem, specifically to the timing of the spring transition in coastal currents (Huyer et al. 1979) that, on average, takes place shortly after ocean shrimp release their pelagic larvae (Dahlstrom 1973; Hannah 1993). The transition from predominantly northward to southward surface currents is forced by a similar shift in the predominant coastal winds in early spring, and is reflected in a sharp drop in coastal sea level height (Huyer et al. 1979). An early transition (generally in March or early April), results in a lower mean April sea level height (fig. 1, Crescent City, California, $ASLH_{t-1}$), which has been associated with strong age-1 recruitment of ocean shrimp in Oregon waters the following year (Hannah 1993). The mechanisms underlying this association are not well understood. However, an early spring transition, with associated coastal upwelling, can establish near-surface ocean conditions that are favorable to larval survival, including reduced sea surface temperatures (Rothlisberg and Miller 1983). A very late spring transition can result in continued northward transport of surface waters, possibly transporting larvae to areas where subsequent transport is unlikely to bring them back to areas off Oregon (Austin and Barth 2002).

Recently, recruitment success of ocean shrimp has also been shown to be negatively influenced by anomolously strong coastal upwelling during the pelagic larval phase (Hannah in press). Specifically, recruitment off southern Oregon was shown to be reduced in the years following the very high April–July upwelling values observed at 42°N. latitude in 1999 and in 2001–2003 (fig. 1). The mechanism underlying this relationship is also unknown, however, the excessive offshore transport of larvae is a reasonable hypothesis that has been proposed (Parrish et al. 1981; Hannah in press). This mechanism is also supported by data showing that large concentrations of ocean shrimp are typically found north of the zone of maximum upwelling, which is centered off California (fig. 2). In 1999 and in 2001–2003 the upwelling index at 42°N. latitude reached levels higher than had been observed previously in the complete available time series, starting in 1946. It's possible that these recent years with very strong spring upwelling represent normal extremes in local climate variability, however these observations are also consistent with a hypothesis that the zone of maximum upwelling may have shifted or simply expanded northwards, which in turn is consistent with predictions of many climate

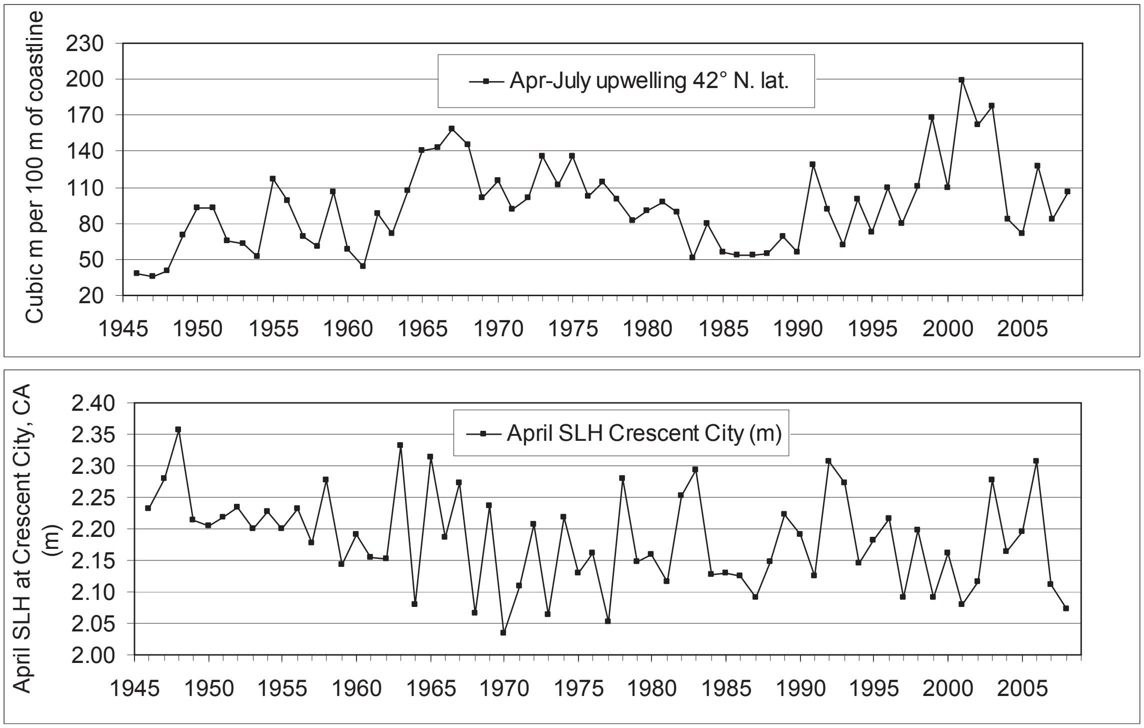

Figure 1. Time series of selected environmental variables, 1946–2008.

models under conditions of global warming (Yin 2005; Seidel et al. 2008; Hannah in press). Several researchers have suggested that global warming may have begun to intensify coastal upwelling off the U.S. west coast (Bakun 1990; Schwing and Mendelssohn 1997) and to alter its seasonal pattern (Snyder et al. 2003), with large potential effects on the California Current ecosystem (Barth et al. 2007).

The pelagic larval phase for ocean shrimp lasts from larval release in March and April through about August. Early stage shrimp larvae are found in near-surface waters (<150 m, Rothlisberg 1975) and occupy progressively deeper portions of the water column as they develop, however juveniles also migrate up into near-surface waters at night (Dahlstrom 1973; Rothlisberg 1975). By September and October, small age-0 ocean shrimp begin showing up in small numbers in commercial trawl catches. The fishery is closed each year from November through March to protect gravid females, so additional fishery-dependent information on the relative abundance of the incoming year class is unavailable until the fishery opens again in April. No fishery-independent surveys are conducted for ocean shrimp. The relative abundance of age-0 ocean shrimp in fall fishery samples has long been considered a questionable index of age-1 recruitment the following year (although see comments in Geibel and Heimann 1976). These young shrimp have not fully recruited to the near-bottom waters fished by trawls and have been considered too small to be completely retained by the mesh sizes typically used in ocean shrimp trawls (Rothlisberg 1975; Lo 1978; Jones et al. 1996). However, no research to try and relate the relative abundance of age-0 ocean shrimp in fall fishery samples to age-1 recruitment the following year has been conducted since the development of the recruit-environment models discussed above. The objective of this study was to develop a simple index of age-0 shrimp abundance from fall fishery samples and determine if it could be used to improve the forecasting ability of existing recruit-environment models for age-1 ocean shrimp.

It should be noted that the best fitting recruit-environment models for ocean shrimp have relatively low predictive power. This is not unexpected, as most recruit-environment relationships have been shown to break down over time (Myers 1998). The limitations of recruit-environment models are not surprising because the establishment of year class success is certainly a very complex process. It is unlikely to be fully captured in simple linear or non-linear recruit-environment models. For marine species with pelagic larvae, recruitment processes involve complex interactions between factors modulating larval mortality and transport in the open ocean, including interactions between life history, predation and larval behavior as well as variation in environmental conditions. The most recent research on recruit-environment relationships with ocean shrimp is a good example of this complexity. Prior to 1999,

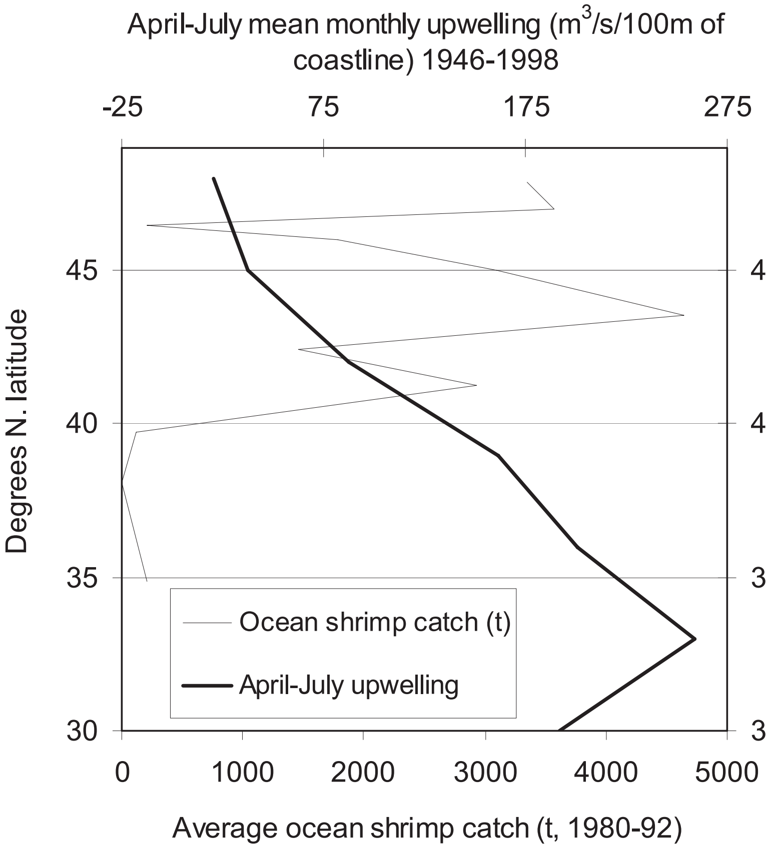

Figure 2. Comparison of latitudinal distribution of ocean shrimp catches (1980–92 average, t) and April–July upwelling (1946–98 average) for Oregon and California waters.

$ASLH_{t-1}$ predicted age-1 recruitment of ocean shrimp in Oregon waters fairly well. When spring upwelling increased to truly record levels in 1999 and 2001-2003 off southern Oregon, this simple relationship broke down for southern Oregon waters, probably because a different process was limiting local recruitment success in those years. A primary advantage of using pre-recruit indices to predict recruitment is that they may be able to indicate the final result of all of these complex processes that influence year class success.

METHODS

An index of the relative abundance of age-0 ocean shrimp was calculated as a simple average of the proportion of age-0 shrimp found in fishery samples for waters off northern and southern Oregon. First, the proportion of age-0 shrimp in September and October samples was averaged for each statistical area (fig. 3). Then these values were averaged for the three statistical areas off northern Oregon and the four statistical areas off southern Oregon, to provide a single index for each of the two larger areas each year. No adjustment was made for missing samples in some areas and years. The age-0 ocean shrimp index was highly skewed and was transformed using a Box-Cox transformation with an offset of 0.001 and 0.0005 for northern and southern Oregon waters, respectively. The Box-Cox transformation employs a log-likelihood function to find a power transformation that best normalizes the data (Sokal and Rolf 1981).

Age-1 recruitment of ocean shrimp was indexed using a simple virtual population estimate (VPE, a sum of catch-at-age, also called "utilized stock," Ricker, 1975) calculated from fishery-dependent data, after Hannah (in press). The index did not include catches of age-0 shrimp in fall samples so as to maintain statistical independence from the pre-recruit index detailed above. The age-1 recruitment index was calculated separately for northern and southern Oregon waters, which are separated by the large rocky reef system, Heceta Bank, where shrimping does not occur (fig. 3). Separate indices for northern and southern Oregon were used because recently, different environmental variables were linked to recruitment in the two areas (Hannah, in press). The successful use of fishery-dependent data to index recruitment of ocean shrimp has been demonstrated in several studies (Hannah 1993; Hannah 1999; Hannah in press) and is possible because of some rather unique characteristics of the stock and the fishery that targets it. The short life span of ocean shrimp and the

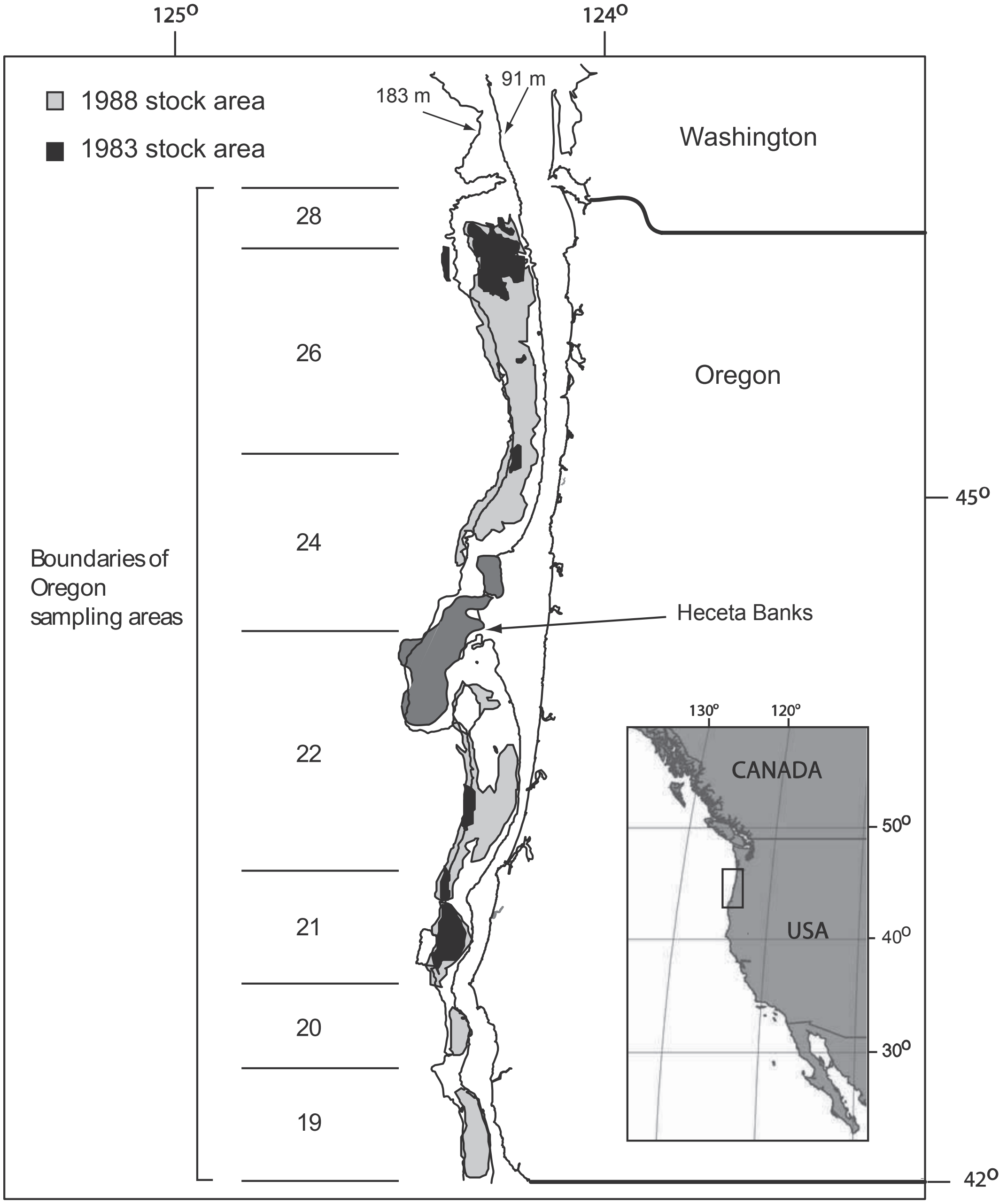

Figure 3. Map of the Oregon commercial fishing grounds for ocean shrimp at high (1988 recruitment, light grey) and low stock abundance (1983 recruitment, dark). Heceta Bank marks the division between northern and southern grounds.

strong dependence of trawl fishery catches on age-1 recruitment, creating a strong recruitment "signal" in the fishery, have already been mentioned. An active and ongoing fishery monitoring program in Oregon also provides high quality data including trawl logbook information that can be used, along with biological samples of the landed catch, to estimate catch-at-age by area (fig. 3). The ocean shrimp trawl fleet is also very mobile and searches widely for concentrations of shrimp (Hannah 1995). Major movements of ocean shrimp after settlement have not been shown and thus the distribution of age-1 shrimp captured in the fishery has been interpreted as roughly describing the distribution of newly-settled recruits (Hannah 1995). Limitations of the logbook data collected by the states of Washington and California after 1992 preclude the development of similar indices for waters off those states (Hannah 1999). Accordingly, this study was limited to the component of the stock found off of Oregon.

The utility of the pre-recruit index for improving forecasts of age-1 recruitment of ocean shrimp was evaluated in a straightforward manner. The coefficient of

TABLE 1

Ocean shrimp recruitment index (millions of age 1 recruits, VPE-based) and the mean proportion of age zero shrimp in fishery samples in September–October of the prior calendar year, for northern and southern Oregon waters (Figure 1), 1980–2006 (year of age-1 recruitment).

Year of age 1 recruitment	Northern Oregon recruit index (millions)	Mean proportion of age zero shrimp north (Sept.–Oct., t-1)	Southern Oregon recruit index (millions)	Mean proportion of age zero shrimp south (Sept.–Oct., t-1)
1980	728.6	0.0018	2,018.5	0.0276
1981	405.9	0.0000	1,158.9	0.0016
1982	360.4	0.0000	1,397.1	0.0133
1983	86.0	0.0000	91.3	0.0000
1984	422.4	0.0000	411.4	—
1985	1,207.0	0.0010	544.3	0.0078
1986	1,209.2	0.0200	1,162.6	0.0210
1987	3,459.2	0.0000	1,342.3	0.1102
1988	2,963.2	0.0045	2,563.2	0.0888
1989	1,997.4	0.0012	2,973.2	0.0438
1990	322.3	0.0000	262.2	0.0039
1991	815.0	0.0010	1,449.7	0.0801
1992	1,103.5	0.0010	4,072.7	0.0801
1993	123.1	0.0000	402.2	0.0033
1994	438.1	0.0000	1,106.7	0.0701
1995	296.6	0.0000	197.1	0.0016
1996	485.4	0.0010	1,106.7	0.0068
1997	376.5	0.0005	1,468.2	0.0275
1998	294.3	0.0000	197.1	0.0048
1999	2,005.9	0.0137	1,115.8	0.0158
2000	2,410.8	0.0057	644.1	0.0000
2001	1,502.3	0.0022	672.4	0.0000
2002	4,053.9	0.0027	488.7	0.0150
2003	2,529.0	0.0217	98.4	0.0185
2004	399.1	0.0038	79.1	0.0000
2005	2,249.1	0.0482	701.5	0.1308
2006	196.0	0.0015	209.9	0.0000
2007	—	0.0265	—	0.0255
2008	—	0.0000	—	0.0327
2009	—	0.0003	—	0.0603
1980–2006 average	1,201.5	0.0053	1,045.4	0.0297

determination was compared between the best-fitting recruit-environment models developed by Hannah (in press) for northern and southern Oregon waters with corresponding multiple regression models that incorporated the transformed pre-recruit index. As in Hannah (in press), the age-1 recruitment index was log-transformed prior to regression. The upwelling index was obtained from the Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/products-/PFEL/modeled/indices/upwelling). April SLH data were obtained from the National Oceanic and Atmospheric Administration (http://tidesandcurrents.noaa.gov). No recruitment index is yet available for the 2009 year class of ocean shrimp, however, catch rates and reports of very widespread and dense concentrations of ocean shrimp suggest a very strong year class in Oregon waters, especially off southern Oregon. Although further testing of the "best" models developed here will have to await more years of data, the prediction from each model for the 2009 year class was evaluated against a hypothesis of a strong recruitment event.

RESULTS

The mean proportion of age-0 shrimp in fishery samples was highly variable interannually and ranged from 0–0.0482 and from 0–0.1308 in samples collected from northern and southern Oregon, respectively, between 1980 and 2006 (year of age-1 recruitment unless noted, tab. 1). The generally higher proportions of age-0 shrimp off southern Oregon are consistent with faster growth at more southerly latitudes, resulting in more consistent retention in shrimp trawl gear (Hannah and Jones 1991). For northern Oregon, some samples were collected in every year, however, lack of fishing effort in all southern Oregon statistical areas in September and October of 1984 resulted in no samples being collected (tab. 1). Estimates of the mean proportion of age-0 shrimp were based on samples from multiple statistical areas in most years for both northern and southern Oregon. The age-0 index for southern Oregon was successfully normalized by transformation, however the index for northern Oregon was not. The age-1 recruitment index showed wide variation

TABLE 2

Regression models relating ocean shrimp recruitment indices to selected environmental variables (Hannah in press) and alternative models incorporating an index of pre-recruit abundance from September–October fishery samples in the year prior to recruitment (age zero index), by area, 1980–2006 (year of age 1 recruitment). April SLH_{t-1} and AJ $upwell_{t-1}$ are mean sea level height at Crescent City, California and mean April–July upwelling index at 42°N. latitude, respectively, for the year prior to recruitment.

Dependent variable	Parameters/variables	Coefficients	Standard error	R^2	P>F
Northern Oregon					
Log_e age-1 recruit index	Intercept	42.594	5.401		0.0001
	April SLH_{t-1}	-0.1021	0.025		0.0004
	Full model (1)			0.40	0.0004
Log_e age-1 recruit index	Intercept	37.806	4.610		0.0001
	April SLH_{t-1}	-0.075	0.022		0.0020
	Age zero index[1]	207.847	56.897		0.0013
	Full model (2)			0.62	0.0001
Southern Oregon					
Log_e age-1 recruit index	Intercept	35.091	6.366		0.0001
	April SLH_{t-1}	-0.063	0.029		0.0385
	AJ $upwell_{t-1}$	-0.011	0.005		0.0231
	Full model (3)			0.27	0.0228
Log_e age-1 recruit index	Intercept	30.774	5.963		0.0001
	April SLH_{t-1}	-0.035	0.028		0.2217
	AJ $upwell_{t-1}$	-0.006	0.005		0.1938
	Age zero index[2]	32.646	10.486		0.0051
	Full model (4)			0.49	0.0017
Log_e age-1 recruit index	Intercept	23.143	0.683		0.0001
	Age zero index[2]	40.303	9.526		0.0003
	Full model (5)			0.43	0.0003

[1] Fitted index = $((\text{proportion age zero}+0.001)^{-0.6}-1)/-7962.285941$

[2] Fitted index = $((\text{proportion age zero}+0.0005)^{0.2}-1)/8.343416$

in recruitment between years, as has been reported in previous studies (Hannah 1993; Hannah 1999; Hannah in press).

For ocean shrimp recruits off northern Oregon, incorporating the pre-recruit index into the best environmental model, which was based on just $ASLH_{t-1}$, increased the coefficient of determination from 0.40 to 0.62, a clear improvement (model 1 vs. model 2 in tab. 2). The sign of the coefficient for the pre-recruit index was positive, as expected. A plot of the residuals from the regression of loge recruits on $ASLH_{t-1}$ showed that the pre-recruit index, although correlated with subsequent age-1 recruitment, was very low in some years (untransformed proportion equal to 0), even when subsequent recruitment was above average (fig. 4A). Predictions from the model incorporating both independent variables (model 2 in tab. 2) matched the time series of the transformed recruitment index fairly well and correctly indicated an above-average recruitment event in 2009 (fig. 5A).

For southern Oregon waters, adding the pre-recruit index to the best environmental model did not result in an improved model (compare model 3 to model 4 in tab. 2), as neither environmental term contributed significantly to the combined model. The best fitting model for all combinations of these three independent variables was a simple regression of loge recruits on the transformed pre-recruit index (model 5 in tab. 2). This model was an improvement over the best environmental model statistically, raising the coefficient of determination from 0.27 to 0.43, while reducing the number of independent variables by one (tab. 2 and fig. 4B). However, this model does not fit the data well, in that predictions do not match the wide range observed in recruitment (fig. 5B). Particularly notable is the failure of the model to accurately predict major southern Oregon year class failures in 1983 and 1998, years of strong extra-tropical ENSO events, and also in 2003–2004 (fig. 5B). The model did, however, correctly indicate an above-average age-1 recruitment for 2009.

DISCUSSION

The brief analysis presented here suggests that a pre-recruit abundance index derived from fishery samples may have some utility in forecasting age-1 recruitment of ocean shrimp. Although improved coefficients of determination were achieved utilizing the pre-recruit index for both northern and southern Oregon waters, neither of the "best" models (models 2 and 5 in tab. 2) showed an excellent fit to the transformed recruitment index, suggesting a continued low ability to predict age-1 recruitment with accuracy. A reasonable expectation for the best-fitting models for both northern and southern Oregon is that they may be useful for indicating whether an incoming year class is likely to be above- or below-average, although additional years of

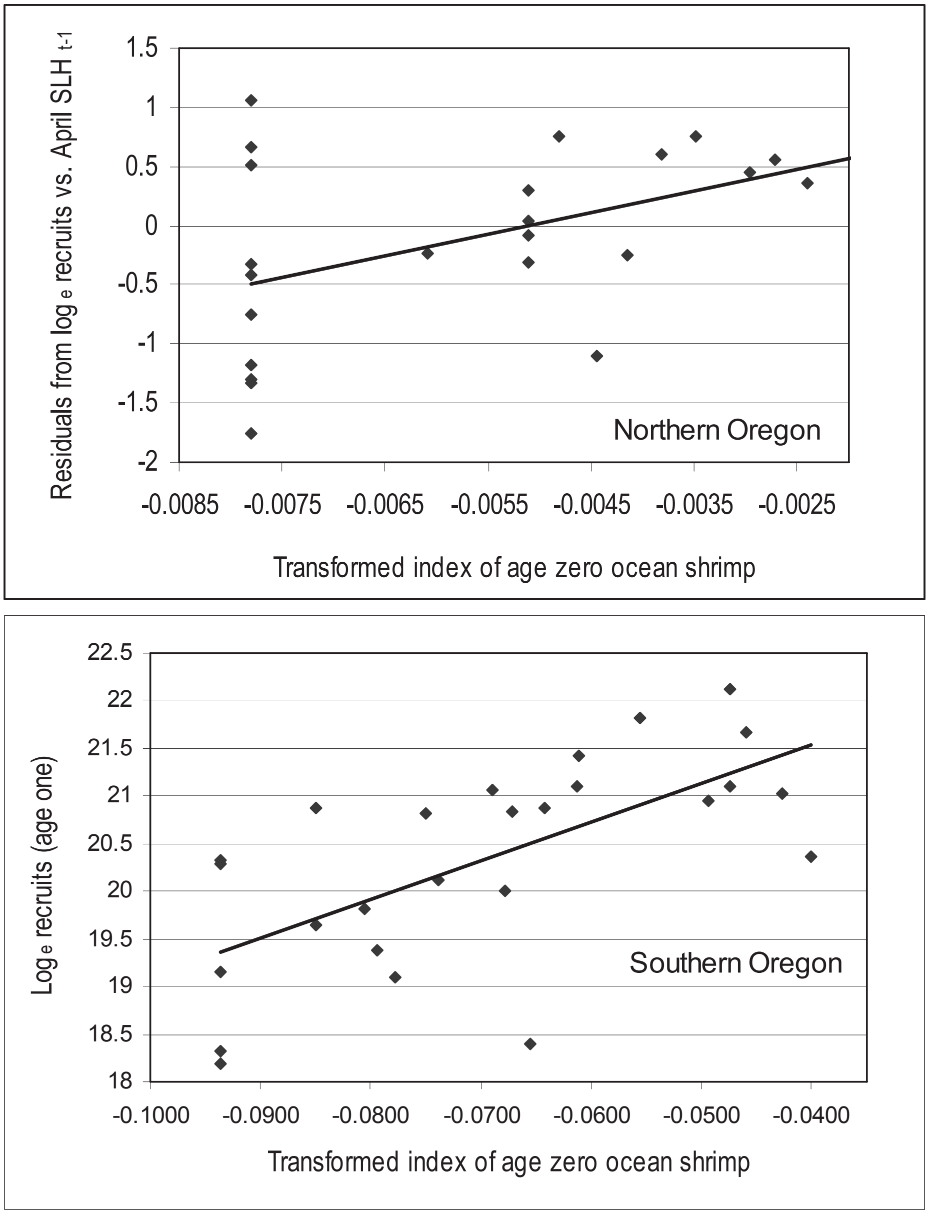

Figure 4. Linear regression of residuals from a regression of log$_e$ age-1 ocean shrimp recruits (northern Oregon) on April SLH$_{t-1}$ and log$_e$ ocean shrimp recruits (southern Oregon) on the ocean shrimp pre-recruit index.

data will be needed even to validate this modest predictive ability.

The modest success reported here for forecasting ocean shrimp recruitment based on the relative abundance of pre-recruits in fishery samples suggests that better forecasts could be developed with more extensive sampling for pre-recruits. Sampling levels of fishery landings could be increased to obtain somewhat better spatial coverage from September and October samples. However, shrimp trawling is usually directed at areas producing the best catches of age-1 shrimp, which may not correspond with areas in which age-0 shrimp are abundant. In some years, a wide geographic coverage simply cannot be obtained from fishery samples. However, fishery-independent sampling could be conducted to provide a more representative index of pre-recruits. To date, the economic value of accurate forecasts of ocean shrimp recruitment has not been considered sufficient to warrant spatially extensive fishery-independent sampling for pre-recruits.

Even though highly accurate forecasting of recruitment of ocean shrimp has not been achieved, the models presented here, both environmental models and those based on pre-recruits, do have some scientific utility. In this study, the statistical significance of the pre-recruit index provides additional support for the hypothesis that

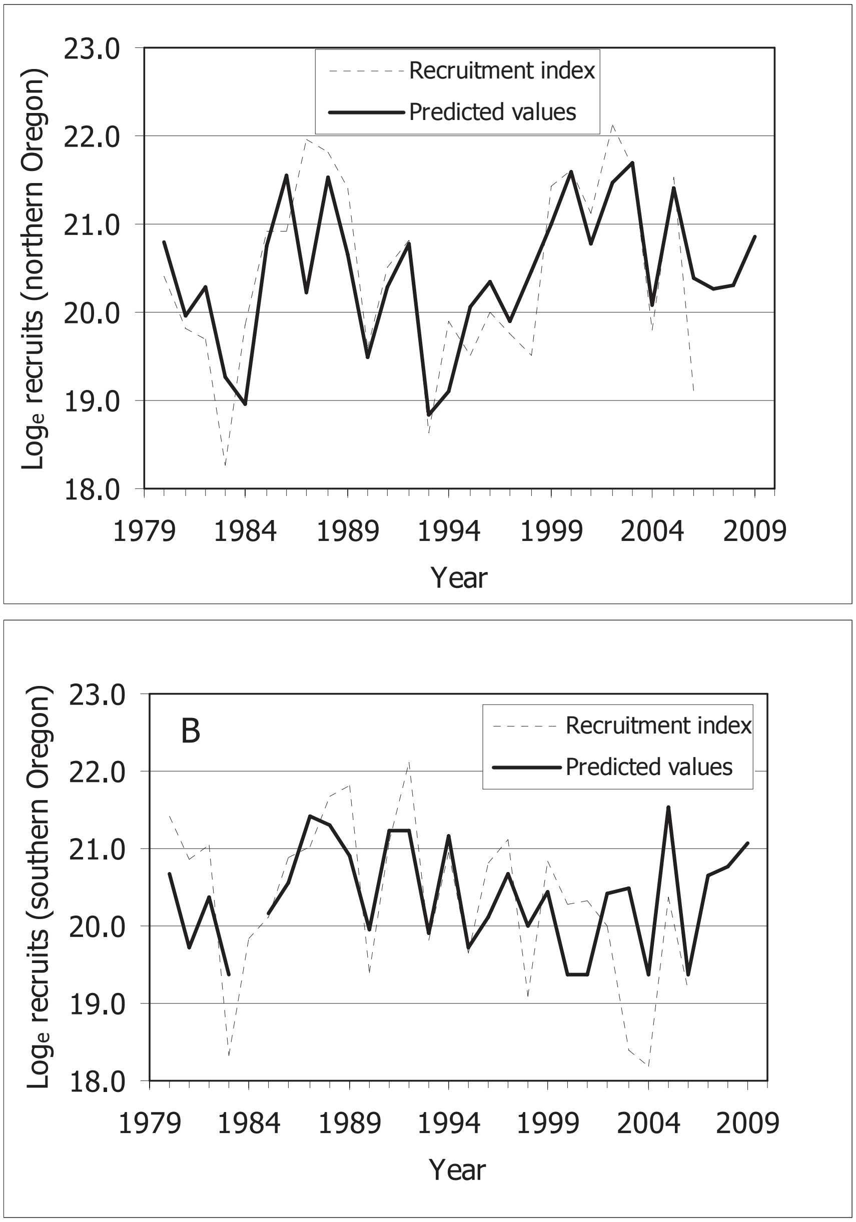

Figure 5. Comparison of the age-1 recruitment index for ocean shrimp with predicted values from the best models incorporating the pre-recruit index (models 2 and 5 in Table 2).

recruitment success of ocean shrimp is determined during the pelagic larval phase, as has been demonstrated for Dungeness crab (*Cancer magister*), another commercially important crustacean species found in California Current waters. It should be noted however, that the failure of the pre-recruit index to accurately predict major year class failures associated with strong extra-tropical ENSO events in 1983 and 1998 may indicate that under extreme environmental conditions, year class strength or geographical distribution of recruits may continue to be modified after settlement. The environmental models that formed the basis for this analysis show the dependence of successful recruitment of ocean shrimp on a timely spring transition in coastal currents and therefore on large-scale atmospheric forcing, another commonality with Dungeness crab (Hannah 1993; Shanks and Roegner 2007).

The primary benefit from exploring predictive recruitment models is the potential to identify, and perhaps eventually verify, hypotheses about how the ocean environment, species life history and anthropogenic effects like fishing interact to determine regional and local recruitment success. For example, the ocean shrimp recruit-environment models that have been developed suggest a link between southern Oregon recruitment failures and excessive offshore transport of larvae under extreme spring upwelling conditions (Hannah in press). If spring upwelling intensity off southern Oregon returns to record high levels in future years and is again associated with recruitment failure it will support this hypothesis, especially if ocean shrimp recruitment is not suppressed broadly by a weak or late spring transition. Similarly, in this study, the comparison of ocean shrimp pre-recruit indices with subsequent recruitment to the fishery showed that although pre-recruit indices have predictive value, they perform poorly at predicting severe year class failures associated with strong ENSO events, especially off southern Oregon (fig. 5). A possible explanation is that northward transport of ocean shrimp takes place during ENSO-influenced winters as a result of anomolously strong northward-flowing bottom currents. There is some evidence that this may have been the case in the extremely strong ENSO event of 1982/83 (Huyer and Smith 1985, Hannah 1993).

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LITERATURE CITED

Austin, J. A. and J. A. Barth. 2002. Drifter behavior on the Oregon-Washington shelf during downwelling-favorable winds. J. Phys. Oceanogr. 32:3132–3144.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. Science 247:198–201.

Barth, J. A., B. A. Menge, J. Lubchenco, F. Chan, F., J. M.Bane, A. R. Kirincich, M. A. McManus, K. J. Nielsen, S. D. Pierce and L. Washburn. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proc. Nat. Acad. Sci. 104(10):3719–3724.

Dahlstrom, W. A. 1973. Status of the California ocean shrimp resource and its management. Mar. Fish. Rev. 35:55–59.

Geibel, J. J. and R. F. G. Heimann. 1976. Assessment of ocean shrimp management in California resulting from widely fluctuating recruitment. Calif. Fish and Game. 62(4):255–273.

Hannah, R. W. 1993. The influence of environmental variation and spawning stock levels on recruitment of ocean shrimp (*Pandalus jordani*). Can. J. Fish. Aquat. Sci. 50(3):612–622.

Hannah, R. W. 1995. Variation in geographic stock area, catchability and natural mortality of ocean shrimp (*Pandalus jordani*): some new evidence for a trophic interaction with Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 52:1018–1029.

Hannah, R. W. 1999. A new method for indexing spawning stock and recruitment in ocean shrimp, *Pandalus jordani*, and preliminary evidence for a stock-recruitment relationship. Fish. Bull. 97:482–494.

Hannah, R. W. (in press). Variation in the distribution of ocean shrimp (*Pandalus jordani*) recruits: links with coastal upwelling and climate change. Fish. Ocean.

Hannah, R. W. and S. A. Jones. 1991. Fishery induced changes in the population structure of pink shrimp (*Pandalus jordani*). Fish. Bull. U.S. 89:41–51.

Huyer, A., J. C. Sobey and R. L. Smith. 1979. The spring transition in currents over the Oregon continental shelf. J. Geophys. Res. 84, No. C11. 6995–7011.

Huyer, A. and R. L. Smith. 1985. The signature of El Niño off Oregon, 1982–83. J. Geophys. Res. 90(C4): 7133–7142.

Jones, S. A., R. W. Hannah and J. T. Golden. 1996. A survey of trawl gear employed in the fishery for ocean shrimp *Pandalus jordani*. Oregon Dept. Fish Wildl., Information Rept. Ser., Fish. No. 96-6. 23 p.

Lo, N. C. H. 1978. California ocean shrimp mesh experiment. Calif. Fish Game 64:280–301.

Myers, R. A. 1998. When do environment-recruitment correlations work? Rev. Fish Biol. Fish. 8:285–305.

Parrish, R. H., C. S. Nelson and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1(2):175–203.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. No. 191. 382 p.

Rothlisberg, P. C. 1975. Larval ecology of *Pandalus jordani* Rathbun. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon. 117 p.

Rothlisberg, P. C. and C. B. Miller. 1983. Factors affecting the distribution, abundance, and survival of *Pandalus jordani* (Decapoda, Pandalidae) larvae off the Oregon coast. Fish. Bull. 81(3):455–472.

Schwing, F. B. and R. Mendelssohn. 1997. Increased coastal upwelling in the California Current System. J. Geophys. Res. 102(C2):3421–3438.

Seidel, D. J., Q. Fu, W. J. Randel and T. J. Reichler. 2008. Widening of the tropical belt in a changing climate. Nature Geosci. 1:21–24.

Shanks, A. L. and G. C. Roegner. 2007. Recruitment limitation in Dungeness crab populations is driven by variation in atmospheric forcing. Ecology 88:1726–1737.

Snyder, M. A., L. C. Sloan, N. S. Diffenbaugh and J. L. Bell. 2003. Future climate change and upwelling in the California current. Geophys. Res. Lett. 30, 15,1823, doi:10.1029/2003GL017647.

Sokal, R. R. and F. J. Rolf. 1981. Biometry. Freeman, New York.

The Research Group. 2006. Review of the west coast commercial fishing industry in 2004. Prepared for Pacific States Marine Fisheries Commission. September 2006.

Yin, J. F. 2005. A consistent poleward shift of the storm tracks in simulations of 21st century climate. Geophys. Res. Lett. 32,L18701, doi:10.1029/2005GL023684.

INCORPORATING PHYSICAL OCEANOGRAPHIC PROXIES OF RECRUITMENT INTO POPULATION MODELS TO IMPROVE FISHERY AND MARINE PROTECTED AREA MANAGEMENT

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ABSTRACT

Variability in larval supply introduces uncertainty into the management of marine fisheries. This variability can confound short-term population projections of both traditional and spatially explicit models of fishery productivity. A potential remedy is the use of physical oceanographic variables, such as an upwelling index or the Pacific Decadal Oscillation, as proxies for recruitment year class strength. We describe a method for incorporating proxy information into population models for fishery management. Our model of a conventional fishery (using kelp rockfish as an example) suggested that proxies were effective in predicting actual larval survival if there was a strong correlation between the proxy and larval survival ($r > 0.8$), when recruitment was highly variable. Model outputs were most useful when used to hindcast rather than forecast the population trajectory. A spatial extension of the model for marine protected areas (MPAs) confirmed those results and revealed that 1) larval dispersal distances did not affect the utility of the proxy, and 2) adult home range size influenced whether before:after or inside:outside biomass ratios provided a more effective metric of MPA success. We found that proxies greatly improved model projections over short time scales, but that projections beyond the time needed for recruits to enter the fishery were less effective. This work provides an example of how information about environmental variability affecting recruitment can be incorporated into fishery models to improve management.

INTRODUCTION

A major difficulty encountered in the management of marine fisheries is the uncertainty introduced by variability in recruitment. It has been suspected for more than 100 years that physical factors affecting larval survival and transport drive much of this variability (Cushing 1982; Mullin 1994; Fogarty et al. 1991) and there have been attempts to find environmental variables which can predict recruitment success (Cushing 1982). Strong year classes (recruitment pulses or booms) can propagate through a fishery for multiple years and may sustain the fishery (Hjort 1914; Shepherd and Cushing 1990). The precise mechanism by which physical factors affect recruitment success is not always known and tends to be species-specific, but investigators have determined the nature of the link in a few cases (e.g., Gaines and Bertness 1993; Botsford et al. 1994; Peterson and Schwing 2003). More often, investigators report a relationship between recruit year-class strength and a physical proxy variable. Examples of such relationships have been reported for several fished species on the Pacific coast of North America. These include a correlation between recruitment of Dungeness crab (*Cancer magister*) and the Bakun upwelling index (Botsford and Wickham 1974), the timing of the spring transition (Shanks and Roegner 2007), and the Pacific Decadal Oscillation (Shanks et al. 2010). Likewise, settlement of kelp bass (*Paralabrax clathratus*) and nearshore rockfishes (*Sebastes* spp.) in southern California is related to a suite of oceanographic predictors over a range of spatial and temporal scales, including sea surface temperature, Ekman transport, and offshore wind stress (Caselle et al. 2010a). Total annual settlement of those nearshore rockfish species is strongly correlated with both the offshore and alongshore components of upwelling-associated transport (Caselle et al. 2010b). The information contained in these physical proxies may be useful in understanding recruitment variability and improving fisheries management.

Conceptually, a close relationship between a physical proxy and recruitment could be used to predict the short-term trajectory of recruitment, biomass, and yield when forecasting the possible consequences of different management options in a decision analysis context (Peterman and Anderson 1999; Harwood and Stokes 2003; Drechsler and Burgman 2004). Furthermore, a past record of year-class size could be used to distinguish signal (due to management) from noise (due to recruitment variability) in hindcasting models used to evaluate management actions in an adaptive management (sensu

Walters 1997) context. To our knowledge, no physical proxy has yet been incorporated into a population model used for adaptive management. Physical proxies however, are starting to be used as indicators of overall fisheries productivity. For example, an environmental parameter based on sea surface temperature is used to determine the harvest guideline for Pacific sardine, *Sardinops sagax* (Hill et al. 2007; but see McClatchie et al. 2010).

Management strategy evaluations, which simulate both population dynamics and management responses (Sainsbury et al. 2000), reveal the consequences of variable recruitment for stock assessment and the adaptive management of fishery stocks. The management problem is that realistic levels of process error (sensu Hilborn and Mangel 1997) in annual recruitment can cause projected biomass to vary over several orders of magnitude among simulations with the same deterministic dynamics. Examples of this problem have been shown for the adaptive management of many species, including rockfishes (*Sebastes* spp.) from the U.S. Pacific coast (Punt and Ralston 2007), Gulf of Alaska walleye pollock (*Theragra chalcogramma*; A'mar et al. 2008) and several key fishery species in southeast Australia (Punt et al. 2000). Although the minimum value of spawning potential ratio (SPR) (expected lifetime egg production) needed for population persistence is uncertain and depends on larval processes, the SPR itself is not sensitive to interannual variations in recruitment (Hilborn et al. 2002). However, the management status of a stock is typically estimated in terms of biomass or catch (e.g., Ralston 2002; Rose and Cowan 2003; Punt and Ralston 2007), which are highly sensitive to physically-forced variability. Additional uncertainty is introduced when there is a time lag between spawning and recruitment. This introduces a lag between the implementation of a new management action and its effects on the fishery, and can lead to management that tracks noise rather than the deterministic signal (Punt and Ralston 2007).

The problems of recruitment variability are compounded in the management of marine protected areas (MPAs), which adds the spatial dimension. Management of MPAs ideally involves monitoring populations inside MPAs using a Before-After Control-Impact (BACI) design so that the deterministic effects of MPAs on fished populations can be distinguished from large-scale, environmental forcing across areas (Underwood 1994; Fraschetti et al. 2002; Grafton and Kompas 2005; Russ et al. 2008). However, monitoring may not start at the time of implementation (Fraschetti et al. 2002) and as a consequence it is common to measure trajectories of a response variable (e.g., biomass) inside and outside MPAs to quantify differences between fished regions and MPAs (e.g., Hamilton et al. 2010). However, the effectiveness of this approach is likely to be sensitive to 1) movement of adults and larvae between fished and unfished regions, 2) the intensity of fishing outside MPA boundaries, 3) the lag time between MPA implementation and recruitment, and 4) the strength of the signal:noise ratio introduced by recruitment variability. The first two factors make it difficult to measure the effects of MPAs over both long and short time scales (Botsford et al. 2001; Moffitt et al. 2009; White et al. 2010b); while factors 3 and 4 hold for both nonspatial and spatial management over the short term only. Here we focus primarily on the problems introduced by lag times and signal:noise ratios related to recruitment variability as the first two topics have been considered in detail elsewhere (Moffitt 2009; Moffitt et al. 2009; White et al. 2010b).

Here we develop a method for incorporating physical proxies of larval production into population models used for fishery management and assessment. We first develop a model of a conventionally managed fishery, then extend the model to include spatial management. In both cases we first illustrate the use of prospective modeling (forecasting), for decision analysis at the time of an initial management action. We then consider the use of retrospective modeling (hindcasting), in which we simulate the trajectory between an initial decision and a later observation. In this modeling work we use kelp rockfish, *Sebastes atrovirens,* as an example of a typical nearshore fished species for which physical proxies for recruit year-class strength exist (Caselle et al. 2010b). The goal of this modeling work is to determine if the addition of the physical proxy aids in distinguishing deterministic changes in recruitment from stochastic variability in order to evaluate its potential for guiding management decisions and implementing adaptive management.

METHODS

We implemented a discrete time, spatially explicit, age-structured, single-species model of a typical rocky reef species. We incorporated von Bertalanffy growth, a nonlinear length-weight relationship, and fecundity proportional to biomass. Adults spawn pelagic larvae during an annual reproductive period, larvae disperse according to a dispersal matrix, and settling larvae experience density-dependent survival following a Beverton-Holt survivorship function. The model follows the basic structure used by White et al. 2010b and can be summarized by the following equations, taking $\mathbf{N}_j(t)$ to be the vector of abundances of each of A age classes in spatial cell j (out of n total cells) at time t (Table 1 summarizes symbols used in this paper; boldface symbols indicate vectors and matrices). The number of larval settlers arriving at cell i, S_i, is

$$S_i(t) = \sum_{i=1}^{n} D_{ij} f(\mathbf{N}_j(t)) \frac{1}{1+e^{-\theta(t)}} \qquad (1)$$

TABLE 1
Symbols used in the paper

Symbol	Sub-element	Definition
State variables		
$\mathbf{N}(t)$	$\mathbf{N}_i(t)$	Abundance of each age classes in each cell at time t ($A \times n$ matrix)
$\mathbf{N}_i(t)$	$N_{i,a}(t)$	Abundance of each age class in cell i at time t ($A \times 1$ vector)
$S_i(t)$		Number of settlers in cell i at time t
$\mathbf{SSB}(t)$	$SSB_i(t)$	Spawning stock biomass in cell i at time t ($n \times 1$ vector)
Parameters		
α		Density-independent Beverton-Holt settler survival
a_0		Age at size 0
a_c		Age at recruitment into fishery
a_m		Mean age at maturity
β		Asymptotic Beverton-Holt maximum recruit density
b		Fecundity per unit biomass
γ		Length-biomass exponent
$\mathbf{D}$	D_{ij}	Probability of larval disperal from cell j to cell i
$F_i(a)$		Fishing mortality rate for age a individuals in cell i
$\widehat{F_i}(a)$		Effective fishing rate experienced due to home range movement
F_{MSY}		Value of F that produces maximum sustainable yield
h		Radius of adult homerange
k		von Bertalanffy growth rate
L_∞		von Bertalanffy Asymptotic maximum length
M		Natural mortality rate
q		Length-biomass coefficient
ρ		Correlation between $\boldsymbol{\theta}$ and $\boldsymbol{\phi}$
Other		
A		Number of age classes
$B(a)$		Biomass at age a
CRT		Critical replacement threshold
cv_θ		Coefficient of variation of $\theta(t)$
$f(\mathbf{N}_i(t))$		Fecundity at cell
$\lambda_{\mathbf{D}}$		Leading eigenvalue of $\mathbf{D}$
$L(a)$		Length at age a
LEP		Lifetime egg production
LEP_{pre}		Fraction of lifetime egg production (relative to unfished maximum) at $t \leq 0$
LEP_{post}		Fraction of lifetime egg production at $t > 0$
n		Number of spatial cells
$\boldsymbol{\phi}$	$\phi(t)$	Physical factor affecting larval survival
$p(a)$		Probability of maturity at age a
s_θ		standard deviation of $\theta(t)$
s_ϕ		standard deviation of $\phi(t)$
SPR		spawning potential ratio
$\boldsymbol{\theta}$	$\theta(t)$	Larval survival parameter
$\widehat{\boldsymbol{\theta}}$		Values of $\boldsymbol{\theta}$ predicted from a particular $\boldsymbol{\phi}$ without accounting for ρ
X'		Simulated value of variable X, incorporating process variability
X*		Actual value of variable X corresponding to simulated value X'

where D_{ij} is the i,j^{th} element of the dispersal matrix $\mathbf{D}$ and gives the probability of larvae dispersing from j to i. The term including $e^{-\theta(t)}$ represents larval survival and is explained below. The scalar $f(\mathbf{N}_j)$ is the total fecundity of the population at j:

$$f\big(\mathbf{N}_j(t)\big) = SSB_j(t)b \tag{2a}$$

$$SSB_j(t) = [p(1)B(1), p(2)B(2), \ldots p(3)B(A)] \times \mathbf{N}_j(t) \tag{2b}$$

where × represents vector multiplication, $SSB_j(t)$ is spawning stock biomass, b is fecundity per unit biomass, $p(a)$ is the probability of being reproductively mature at age a (assumed to be 0 for $a < a_m$ and 1 for $a \geq a_m$), and $B(a)$ is mean biomass at age a. Biomass is a function of length, $B(a) = qL(a)^r$, where q and r are constants. Length at age is given by a von Bertalanffy function with growth rate k, age at length zero a_0, and asymptotic maximum length L_∞:

$$L(a) = L_\infty \left[1 - e^{-k(a - a_0)}\right] \tag{3}$$

Note that for simplicity we assume there is no variability in length or biomass at age.

The updating step for the population is given by Equation 4 (see Equation 4, next page).

Note that the initial age class in $\mathbf{N}_j(t+1)$ is comprised of settlers $S_j(t)$ that survive Beverton-Holt density-dependent mortality (with density-independent survivorship α and asymptotic maximum settler density β). Post-settlement individuals have density-independent mortality rate M and experience fishing rate $F(a)$, which is a function of age such that $F(a) = 0$ for all $a < a_c$, the age at which individuals recruit to the fishery; $F(a)$ is constant for all $a \geq a_c$ and was varied to create different fishing scenarios (fishery mortality typically depends on length not age; because our model has deterministic growth, length and age are directly related by Equation 3, so age a_c corresponds to a particular length). Demographic parameter values were taken from literature estimates for kelp rockfish, *Sebastes atrovirens* (tab. 2). In all cases we assume data are fisheries-dependent, so direct observation of age classes younger than a_c is impossible.

The major difference in model structure from typical models of this type (e.g, White et al. 2010b) is that we explicitly modeled larval survival. Following the convention used in statistical survival analysis, we assumed that larval survival was a logit function of parameter $\theta(t)$, so that larval survivorship is equal to $\text{logit}^{-1}(\theta(t)) = 1/(1+\exp(-\theta(t)))$. This relationship allows $\theta(t)$ to vary widely but constrains survival to fall between 0 and 1; alternative functional forms could be substituted as appropriate for a specific study system. We assumed that $\theta(t)$ is a function of some physical oceanographic factor, and is correlated, with correlation coefficient ρ, to

$$\mathbf{N}_j(t+1) = \begin{bmatrix} 0 & & & & \\ e^{-(M+F(1))} & & & & \\ & e^{-(M+F(2))} & & & \\ & & \ddots & & \\ & & & e^{-(M+F(A-1))} & 0 \end{bmatrix} \times \mathbf{N}_j(t) + \begin{bmatrix} \dfrac{\alpha S_j(t)}{1+\dfrac{\alpha}{\beta}S_j(t)} \\ 0 \\ \vdots \\ 0 \end{bmatrix} \qquad (4)$$

TABLE 2
Life history parameters for kelp rockfish, *Sebastes atrovirens*, used in the model

Parameter	Estimate	Notes
Beverton-Holt settler survival		
$R = \alpha S/(1+(\alpha/\beta)S)$		
α	4.86	a
β	1	b
Length-at-age (cm)		
$L(a) = L_\infty\left(1 - \exp(-k(a-a_0))\right)$		
L_∞	37.8 cm	c
k	0.23 y^{-1}	
a_0	–0.7 y	
Weight-at-length (kg)		
$W = pL^q$		c
p	9.37×10^{-6} kg cm^{-q}	
q	3.172	
A	25 y	d
a_m	4 y	d
M	0.2 y^{-1}	e
a_c	4 y (29 cm)	f
$\bar{\theta}$	0.5	g

Notes:
a. Fitted to produce CRT = 0.25, given other demographic parameters
b. Arbitrary; this parameter defines spatial scale at which density is calculated but does not affect model results
c. Source: Lea et al. (1999)
d. Source: Love et al. (2002)
e. Not well known; value based on lifespan given in Love et al. (2002)
f. Based on California Department of Fish and Game regulations
g. Arbitrary; because *a* is scaled to produce a given CRT, model results are not sensitive to this value

some observable quantity $\phi(t)$, e.g., sea surface temperature, an upwelling index, the timing of a seasonal current shift, Pacific Decadal Oscillation, etc. For example, in kelp rockfish, Caselle et al. (this issue) have documented correlations between larval settlement (a function of larval survival) and the strength of the offshore component of upwelling transport with values of r as high as 0.99. For the purposes of the model, we assume that $\phi(t)$ is some generic quantity that is recorded annually. Thus, given past observations of $\phi(t)$, it is possible to re-create the pattern of $\theta(t)$ (with precision determined by ρ) and thus approximate the pattern of larval survival, even when observations of the resulting age classes are not yet available.

The persistence of an age-structured population with density-dependent recruitment requires that at low population densities, each individual produces on average at least one successful offspring within its lifetime (Hastings and Botsford 2006). Assuming that population density is low enough to ignore density-dependent factors, White (2010) showed that this requirement can be expressed as

$$\alpha\lambda_{\mathbf{D}}\,\mathrm{logit}^{-1}(\theta)\,LEP \geq 1 \qquad (5)$$

where $\lambda_{\mathbf{D}}$ is the leading eigenvalue of the dispersal matrix $\mathbf{D}$ and *LEP* is lifetime egg production, calculated as the sum of the product of survival to age *a* and fecundity at age *a* over all ages *A*.

The basic effect of fishing is to reduce *LEP*. For convenience we express both *LEP* and *SSB* as values relative to the maximum unfished value. The units of all other variables, such as α, are also scaled accordingly. Therefore the persistence threshold in Equation 5 can be expressed as

$$LEP \geq 1/\alpha\lambda_{\mathbf{D}}\,\mathrm{logit}^{-1}(\theta) \qquad (6)$$

The quantity $1/\alpha\lambda_{\mathbf{D}}\,\mathrm{logit}^{-1}(\theta)$ is referred to as the Critical Replacement Threshold (CRT). The CRT is mathematically related to the Goodyear compensation ratio and the steepness parameter, both of which are often used in fisheries models (White 2010); the CRT is interpreted as the minimum *LEP* required for population persistence. In order to keep our analysis general—rather than specific to kelp rockfish—we express fishing effort in terms of the *LEP* it produces, and parameterize α so that CRT = 0.25 in all model runs (cf. White et al. 2010b; note that White et al. referred to the scaled value of *LEP* as *FLEP*, the fraction of unfished lifetime egg production). In this way, the level of fishing is expressed relative to the persistence threshold, and results would be similar across species for the same value of *LEP* relative to CRT.

Simulated observations of stochastic larval survival

In all simulations described here, we assume that past observations of $S(t)$ and $\phi(t)$ had been made over some period with relatively constant larval production, so that estimating $\theta(t)$ over that period was possible. Therefore we now possess an estimate of the means, $\bar{\theta}$ and $\bar{\phi}$, and standard deviations, s_θ and s_ϕ, of $\theta(t)$ and $\phi(t)$ as well as an estimate of the linear relationship (including an estimate of the correlation coefficient ρ) between $\theta(t)$ and $\phi(t)$. We further assume that interannual variation in $\phi(t)$ and $\theta(t)$ is such that autocorrelation in those time series is negligible. If larval production varied greatly in the past, estimates of the parameters of $\theta(t)$ and $\phi(t)$ would be biased because variation in $S(t)$ due to production will be incorporated into estimates of s_θ, inflating it. As such, one should be cautious when estimating $\theta(t)$ and $\phi(t)$, and detrending or other processing of $S(t)$ may be necessary.

For clarity it will become important to distinguish between observed values of $\theta(t)$, $\phi(t)$, and $\mathbf{N}(t)$, and values that are simulated from other sources, which we denote with the 'prime' symbol. For example, given an observed vector of physical proxy values $\boldsymbol{\phi}$, we can simulate a corresponding time series $\boldsymbol{\theta}'$ such that $\boldsymbol{\phi}$ and $\boldsymbol{\theta}'$ have correlation ρ. Predicted population densities simulated using $\boldsymbol{\theta}'$ are denoted $\mathbf{N}'$ and predicted spawning stock biomass is $\mathbf{SSB}'$.

A goal of this analysis was to represent the uncertainty in $\theta'(t)$, introduced by the imperfect match between $\theta(t)$ and the proxy $\phi(t)$. We did this by simulating multiple time series $\boldsymbol{\theta}'$ for a given set of observations $\boldsymbol{\phi}$; each simulated $\boldsymbol{\theta}'$ represented one possible set of values with correlation ρ to $\boldsymbol{\phi}$, and by simulating population dynamics for each $\boldsymbol{\theta}'$ we obtained a distribution of possible outcomes $\mathbf{N}'(t)$. To simulate vector $\boldsymbol{\theta}'$ with correlation ρ to vector $\boldsymbol{\phi}$, we first assumed that the linear relationship between $\theta(t)$ and $\phi(t)$ is used to produce $\widehat{\boldsymbol{\theta}}$, an estimate of $\boldsymbol{\theta}$ that does not account for the correlation ρ between the two variables (for simplicity we let $\widehat{\boldsymbol{\theta}} = \boldsymbol{\phi}$, but this does not affect the results). We then used the following procedure to obtain simulated vectors $\boldsymbol{\theta}'$:

$$\boldsymbol{\theta}'' = \left[\widehat{\boldsymbol{\theta}} - \overline{\widehat{\boldsymbol{\theta}}}\right] \rho + R(0,s_\theta)[1-\rho^2]^{0.5}$$

$$\boldsymbol{\theta}' = \boldsymbol{\theta}'' - \overline{\boldsymbol{\theta}}'' + \overline{\widehat{\boldsymbol{\theta}}}\, \rho + \bar{\theta}\,(1-\rho) \qquad (7)$$

where $R(0,s_\theta)$ is a vector of the same length as $\boldsymbol{\phi}$ containing values drawn from a normal distribution with mean 0 and standard deviation s_θ. The first step produces a set of values with the correct standard deviation and correlation coefficient; the second step ensures that the mean of $\boldsymbol{\theta}'$ approaches the mean of $\widehat{\boldsymbol{\theta}}$ as ρ increases. The result of this is that if ρ is near 1, $\boldsymbol{\theta}'$ converges on $\widehat{\boldsymbol{\theta}}$. When ρ is near 0, $\boldsymbol{\theta}'$ is simply a random normal distribution with mean $\bar{\theta}$ and standard deviation s_θ, the best available prior estimates for those quantities. Note that in this effort we are accounting only for process error in $\boldsymbol{\phi}$ and error introduced by the strength of correlation ρ (represented by the distribution of $\boldsymbol{\theta}'$); we do not directly consider the effects of observation error in any of these processes or in the measurement of $\mathbf{N}(t)$.

In all cases where $\mathbf{N}'(t)$ is simulated, we also simulated an 'actual' value, which we denoted $\mathbf{N}^\star(t)$, so the accuracy and precision of the distribution of $\mathbf{N}'(t)$ could be estimated by comparison to $\mathbf{N}^\star(t)$. $\mathbf{N}^\star(t)$ was simulated by initializing the model in year $t = -50$ at the deterministic equilibrium (using $\theta(t) = \bar{\theta}$), then running forward in time with a time series $\boldsymbol{\theta}$ generated from random draws from a normal distribution with parameters $\bar{\theta}$ and s_θ. In the simulations presented here, $\bar{\theta}$ was held at a constant value of 0.5. The correction applied in Equation 6 ensures that the results are insensitive to the level of larval survival, because collapse depends only the relative values of *LEP* and CRT. For the sake of generality we describe variation in θ using the coefficient of variation, cv_θ, which is equal to $s_\theta / \bar{\theta}$. We considered values of cv_θ ranging from 0.1 (nearly deterministic) to 10, a range that brackets the observed level of interannual variability in recruitment reported by Caselle et al. (this issue) and Shanks et al. (this issue). Both studies reported levels of variability in recruitment with a coefficient of variability greater than 1; this is not directly comparable to cv_θ as we have defined it, but we know of no studies that have directly reported estimates of temporal variability in larval survival.

Nonspatial model

We first consider the case of a fished population managed in a conventional manner, i.e., assuming that the entire population in a geographical region is a well-mixed unit. As such, there is only a single subpopulation in the models in Equations 1–4 ($n = 1$), and the dispersal matrix $\mathbf{D}$ is a scalar with value 1.

The management scenario is thus: we presume that we are in year $t = 0$. The population has been fished for 30 years at level LEP_{pre}. In year $t = 0$, managers decide to adjust management in order to change *LEP* to one of several possible new values, LEP_{post}. We assume LEP_{pre} can be calculated empirically (e.g., O'Farrell and Botsford 2005), but it is difficult to manage fishing mortality, *F*, such that a precise value of LEP_{post} will be obtained (note that *LEP* as we have defined it here is equivalent to Spawning Potential Ratio, SPR, as used in the fisheries literature).

In practice, groundfish fisheries on the Pacific coast typically utilize control rules based on spawning biomass rather than *LEP* (or SPR) directly. The overall management target is a value of *F* that approximates maximum sustainable yield, F_{MSY}. For a particular value of CRT, F_{MSY} is obtained at a particular SPR; in turn, a target value of *SSB* (relative to unfished) is used as a proxy for SPR_{MSY}. For many Pacific groundfish, the target is SPR = 50% of unfished, and the spawning biomass target is 40% of unfished (Ralston 2002; Punt and Ralston 2007). Stocks which decline more than this spawning biomass

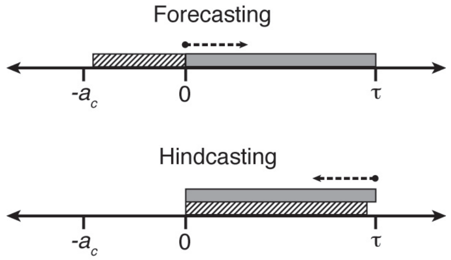

Figure 1. Diagram illustrating difference between forecasting and hindcasting predictions. In the forecasting approach, an observer in year 0 uses information on ϕ from years $t < 0$ (hatched region) to predict population dynamics in the years $0 > t \geq \tau$ (gray region). In the hindcasting approach, an observer in year τ uses information on ϕ from years $t \geq 0$ to predict population dynamics in the years $0 > t \geq \tau$.

target are said to be overfished and the fishery may be curtailed during a stock rebuilding phase. Henceforth we will express spawning biomass as a proportion of the unfished maximum (this is often referred to as 'spawning depletion'). With CRT = 0.25, MSY will actually occur at approximately $LEP = 0.27$ and $SSB = 0.35$. With those equivalencies in mind, we report *SSB* as the response variable in model analyses in order to approximate the type of data that would be used in actual management scenarios.

Forecasting model. In the forecasting scenario, we simulated a decision analysis process at year $t = 0$ and project the outcome (in spawning depletion) of different LEP_{post} targets at years $t = 1, 2, ...10$. These estimates would provide decision makers with estimates (and prediction intervals) of which values of LEP_{post} would produce the desired change in spawning depletion within certain time windows. This type of analysis would typically make forecasts over time periods greater than 10 years, but the shorter window is suitable for our purposes.

The first difficulty encountered in making this type of short-term projection is that the starting conditions, i.e., the full vector $\mathbf{N}(0)$, must be specified, even though the age classes younger than a_c are unobserved. Those pre-recruit age classes depend on the values of $\theta(t)$ at times $(-a_c) \leq t < 0$. To obtain the best estimate of $\mathbf{N}(0)$, we first used the values of M and F_{pre} to back-calculate $\mathbf{N}'(-a_c - 1)$ (i.e., $a_c + 1$ years in the past) from age classes $a > a_c$ in $\mathbf{N}^\star(0)$ (as mentioned earlier, an 'actual' time series of $\mathbf{N}^\star(t)$ was simulated first). This method leaves the age classes $A - a_c$ to A in $\mathbf{N}'(-a_c - 1)$ empty. We then obtain $\theta'(t)$ from $\phi(t)$ for the period $-(a_c + 1) \leq t < 0$, and use those values of $\theta'(t)$ and the starting conditions $\mathbf{N}'(-a_c - 1)$ to simulate dynamics forward for a_c years to obtain a full estimate of all age classes in $\mathbf{N}'(0)$ (fig. 1). Values for $a \geq a_c$ in $\mathbf{N}'(0)$ are then replaced with the actual values observed in $\mathbf{N}^\star(0)$.

To forecast forward in time from $\mathbf{N}'(0)$, we simulated 100 different time series $\boldsymbol{\phi}^\star$ for $t = 0, 1, ... 9$ using random draws from a normal distribution with mean $\overline{\phi}$ and standard deviation s_θ. For each time series $\boldsymbol{\phi}^\star$ we simulated 100 different predicted time series $\boldsymbol{\theta}'$, given a particular value of ρ. We also simulated an additional time series $\boldsymbol{\theta}^\star$ that was designated the 'actual' time series. This produced a distribution of 100 possible values of $\mathbf{N}'(t)$ for years $t = 1$ to 10 for comparison to a single 'actual' $\mathbf{N}^\star(t)$, repeated for 100 different realizations of the $\boldsymbol{\phi}^\star$ and $\mathbf{N}^\star(t)$ time series. This procedure was executed for a range of values of LEP_{pre} and cv_θ in order to represent the effects of prior management and environmental variation. For each combination of LEP_{pre} and cv_θ, we also modeled a range of values of LEP_{post} to simulate a decision analysis process wherein managers are presented with the range of possible outcomes for each management alternative.

Hindcasting model. We suppose that in year $t = \tau$ in the future there is a desire to manage adaptively by determining whether the management action taken at $t = 0$ met expected goals (i.e., whether the chosen target value of LEP_{post} produced the desired change in spawning biomass). In this case the difficulty is distinguishing the effects of stochastic variability in recruitment from changes in spawning biomass due to management. Therefore we simulate a "hindcasting" procedure, in which an observer at year τ models dynamics between years zero and τ to obtain a projection of the expected *SSB* at τ, accounting for recruitment variability in the intervening years (fig. 1). Note that we refer to this as hindcasting, but the hindcasting occurs from year τ ("future") back towards year 0 ("present") rather than from year 0 back towards years $t < 0$ ("past").

The population density $\mathbf{N}(\tau)$ is now observable (at least for ages $a \geq a_c$), but $\boldsymbol{\theta}$ for years $0 - \tau$ is unknown. We estimated the distribution of $\mathbf{N}'(\tau)$ using a procedure similar to that in the forecasting model. Starting with the same estimate of density at $\mathbf{N}'(0)$ used in the forecasting model, the observed values $\boldsymbol{\phi}$ for years 0 to $(\tau - 1)$ were used to simulate 100 different possible time series $\boldsymbol{\theta}'$, which were used in turn to obtain a distribution of values for $\mathbf{N}'(\tau)$. As before, the values of $\mathbf{N}'(\tau)$ for ages $\geq a_c$ were constrained to be equal to the observed values in $\mathbf{N}^\star(t)$, and the entire procedure was performed for 100 different time series of $\mathbf{N}^\star(t)$.

Together these forecasting and hindcasting analyses are similar to a management strategy evaluation, in that we consider the ability of managers to make correct inferences about fishery stock status in the face of environmental process error. However, unlike typical management strategy evaluations analyses, we only consider the consequences of a single change in management strategy (at time $t = 0$) and examine both the success of decision analysis at that time and managers' ability to detect the consequences of that action at an arbitrary point in the future.

Spatial model

We then considered the case of spatial management, including the use of no-take marine protected areas (MPAs). This introduces several changes into the model: $\mathbf{D}$ is now an $n \times n$ matrix of dispersal probabilities. We assumed that demographic parameters were constant across all n populations, and that the fishing rate, F, was also constant across space (except that $F = 0$ inside any MPA). Adult fish can move inside home ranges, so fish that settle inside MPAs can move across MPA boundaries and experience fishing pressure. We assumed that home range movement follows a Gaussian distribution with mean 0 and standard deviation $h/2$, so that fish spend 95% of their time within a radius h of their settlement location (cf. Moffitt et al. 2009; Freiwald 2009). Then the fishing pressure of a fish with home range centered at spatial cell i is given by

$$\widehat{F}_i = \frac{1}{h\sqrt{\pi/2}} \int_{-\infty}^{\infty} c_x F_x \exp\left[-\frac{4(x-x_0)^2}{h^2}\right] dx \qquad (7)$$

where $\widehat{F}_i$ is the effective fishing rate experienced by an individual with a home range centered at spatial cell i, F_x is the fishing rate at location x, $c_x = 0$ for reserves and 1 for fished areas, and x_0 is the center of cell i, and the integration is made over one-dimensional space x. The effective fishing rate $\widehat{F}_i$ was then used to calculate LEP_i and the expected fishery yield of recruits settling at each cell i. This is similar to the approach taken by Moffitt et al. (2009), but with a Gaussian rather than uniform distribution of home range movement.

We assumed a spatial domain consisting of a linear coastline with homogenous habitat. The coastline was simulated as a repeating unit of 40 spatial cells representing 40 km of coastline; dispersing larvae and adult home ranges wrapped around the edge of the domain, eliminating edge artifacts and making the coastline effectively infinite (very similar results would be obtained on a very long non-infinite coastline, but our approach is computationally much simpler). In principle, model results should be sensitive to this assumption; if the domain had absorbing boundaries then a species with long larval dispersal distances should lose many larvae off of the edge of the domain. This would results in lower overall larval replenishment and make it less likely that the species would persist. However, as described above, the model is parameterized such that the persistence threshold is precisely given by Equation 6, regardless of losses due to larval survival or transport processes. Therefore, we have avoided any sensitivity to assumptions about domain boundaries.

While MPA size and spacing have been examined for protected populations (e.g., White et al. 2010b), we were concerned with the effects of recruitment variability, so we considered only two different MPA configurations. The primary set of results were generated for MPAs that conformed to size and spacing guidelines from the California Marine Life Protection Act initiative (CDFG 2008): MPAs were 10 km wide and separated by 30 km of fished area. This produced MPAs that covered 25% of the coastline. For comparison with a smaller MPA scenario, we also simulated a coastline with 3 km wide MPAs, covering 7.5% of the 40 km coastline.

Larval dispersal was assumed to be purely diffusive and described by a Gaussian dispersal kernel with zero mean displacement a standard deviation d. Hereafter, d is referred to as "dispersal distance." For this type of model, the nature of deterministic population persistence depends on the spatial scale of movement relative to MPA size: if the scale of larval dispersal is much smaller than the scale of MPA width, then populations tend to exhibit self-persistence and MPAs are self-sustaining units. If the spatial scales of larval dispersal and/or adult home range movement are much larger than MPAs, then persistence depends on connectivity over space across multiple generations, termed a network effect, and is more sensitive to the fraction of the coastline in MPAs than to MPA size (Hastings and Botsford 2006; Moffitt et al. 2009; White et al. 2010). To capture this range of model behavior, we modeled four different life history scenarios, including each combination of long and short adult and larval dispersal distances ($d = 5$ km or $d = 40$ km and $h = 0.1$ km or $h = 10$ km).

In addition to the case of a simple homogenous coastline, the dynamics of which are well understood in deterministic models (e.g., Botsford et al. 2001; White et al. 2010b), we also considered a case in which the coastline has a recruitment 'hotspot' or retention zone. It is generally recommended that MPAs be placed in locations with high recruitment (e.g., Halpern and Warner 2003; Roberts et al. 2003) and there is some evidence from models that this strategy may be successful (White et al. 2010a), but such hotspots could amplify the effects of variable recruitment. We modeled the recruitment hotspot scenario by creating an oceanographic retention zone following the procedure for scenario "B" in White et al. (2010a): inside the retention zone—which was assumed to be contiguous with the MPA—the standard deviation of the Gaussian dispersal kernel was $d/2$ instead of d. This produces a higher degree of larval retention (and less spillover) in that area. We did not consider the case of spatial variation in recruitment, since recruitment patterns of nearshore California fishes are often coherent over large spatial scales within a year, even if the overall magnitude varies (Caselle et al., this issue).

We considered two types of output in the spatial model, both of which approximate commonly used measures of MPA effectiveness (Lester et al. 2009). The first

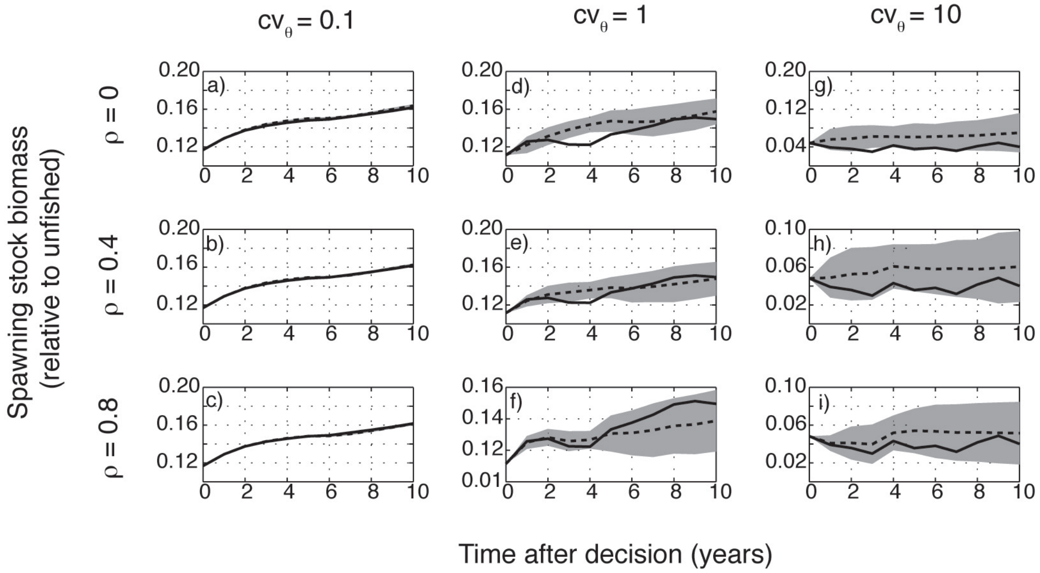

Figure 2. Time series from the nonspatial forecasting model. Panels depict the time series of actual spawning stock biomass (*SSB**; solid line) as well as the mean (dashed line) and 95% prediction interval (gray area) of model projections (*SSB*') for a particular combination of variability in larval survival (cv_θ) and the correlation (ρ) between actual larval survival and a physical proxy. Model projections are based on an initial observation of the fished population at time $t = 0$; for larger values of ρ, the model projections incorporate increasingly better proxy-derived estimates of the initial density of unfished age classes. The population was being overfished prior to $t = 0$ ($LEP_{pre} = 0.2$) and is then switched to sustainable fishing ($LEP_{post} = 0.35$).

is the log of the ratio of *SSB* after:before MPA implementation for a location inside the MPA. This measure captures the trajectory of increase (or decrease) in biomass inside the MPA relative to the baseline situation in $t = 0$. We report the log after:before *SSB* ratio for location $x = 5$, in the center of the MPA. The second metric is the log of the ratio of SSB at a location inside the MPA to *SSB* at a location outside the MPA. This metric is an attempt to account for large-scale environmental variability (such as variability in $\theta(t)$) that might dampen the effects of the MPA over short time scales (as measured by the after:before comparison), under the assumption that a well-performing MPA will still contain higher biomass than a fished location. In the 10 km MPA scenario we report this log inside:outside ratio for locations $x = 5$ (inside) and $x = 25$ (outside); for the 3 km MPA scenario we used locations $x = 2$ (inside) and $x = 17$ (outside).

The management scenario for the spatial model is similar to that in the nonspatial model: we assume that a population has been fished for 30 years at the level $LEP_{pre} = 0.2$ (i.e., overfished). In year $t = 0$ (the present day), managers choose to implement an MPA network along the coastline. At the same time, they also choose a new target value of LEP_{post} for the remaining fished areas of the coast. The level of fishing outside the MPA can greatly affect MPA performance, especially for species with large scales of larval or adult movement (White et al. 2010b). Thus projections of MPA performance must specify the expected level of LEP_{post}, and adaptive management of MPAs must account for the observed increase in SSB relative to that projection. Therefore, the spatial model was run for 3 values of LEP_{post} (0.2, 0.35, 0.5 ranging from overfished to sustainably fished), just as in the nonspatial model. Model performance was evaluated in terms of its ability to predict the correct log *SSB* ratio and distinguish among alternative log *SSB* ratios.

RESULTS

Nonspatial model

An example of the population dynamics forecasting model is provided in Figure 2, with lifetime egg production prior to $t = 0$, LEP_{pre}, equal to 0.2, and then $LEP_{post} = 0.35$ after $t = 0$, for a range of values with the correlation strength of the proxy, ρ, and variability in larval survival, cv_θ. In each panel, the range of projected outcomes for $t = 1$–10 years in the future is shown relative to the actual trend in spawning stock biomass, $SSB^\star(t)$, for a typical realization of actual larval survival values $\boldsymbol{\theta}$. When cv_θ was very low, dynamics were nearly deterministic, so incorporating information from the physical proxy did not improve model forecasting substantially (fig. 2a–c). Projections of $SSB'(t)$ had narrow prediction intervals that usually contained the actual value $SSB^\star(t)$, even when $\rho = 0$ (fig. 2a). As cv_θ increased, the proxy afforded a larger improvement in predictive skill (fig. 2d–i). For $cv_\theta = 1$, the predicted range of $SSB'(t)$ deviated from the actual value of $SSB^\star(t)$ in the absence of a proxy ($\rho = 0$); that is, the model incorrectly forecasted dynamics just 3–4 years into the future (e.g., fig. 2d). However, the range of model projections followed $SSB^\star(t)$ much

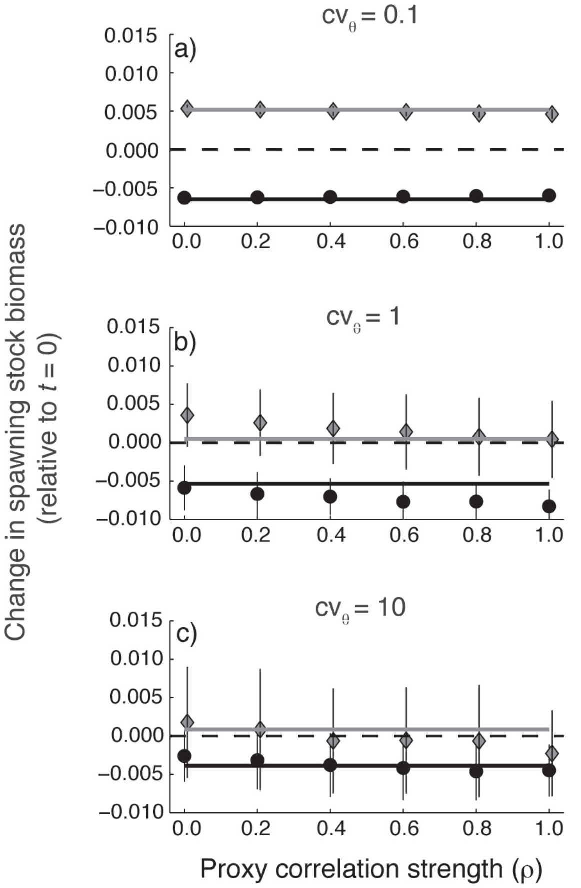

Figure 3. Results from the nonspatial forecasting model showing the deviation of model projections from actual values. Points depict the projected spawning stock biomass (SSB') at t = 10 years after fishery management switched from LEP_{pre} = 0.2 (overfishing) to an alternative level of fishing (LEP_{post}): 0.5 (light gray diamonds) or 0.2 (black circles). Projections are shown for a range of values of the correlation ρ between actual larval survival and a physical proxy. Error bars indicate 95% prediction interval for model projections. Solid lines indicate actual SSB^* values for the corresponding value of LEP_{post}. The level of variability in natural survival, cv_θ, differs among panels as indicated. SSB values are presented as deviations from SSB at time t = 0; no deviation indicated by dashed horizontal line. For decision analysis at t = 0, the quantity of interest is the degree of overlap in the range of projected outcomes for different levels of LEP_{post}. For adaptive management at t > 0, the quantity of interest is whether the range of projected outcomes for a particular LEP_{post} contain the actual value.

more closely with higher values of ρ. Similar patterns held for a much higher level of variability in survival, cv_θ = 10, but the range of projected model outcomes was much higher overall in this case, so projections were less precise but the range of values usually contained $SSB^\star(t)$ (fig. 2g–i). Regardless of the value of cv_θ and ρ, the improvement in predictive skill afforded by the proxy fell off after approximately 5 years, as indicated by a widening of the prediction interval around the model projection. This corresponds to the age at recruitment to the fishery, a_c. After a_c years, all of the pre-recruit cohorts present at t = 0 and estimated from observations of the physical proxy ϕ prior to t = 0 had entered the fishery. After this point ($t > a_c$), the proxy cannot provide any additional information on pre-recruit cohorts, because they were all spawned after t = 0. Consequently, the range of model outcomes became wider. Note also that simulations with low noise ($cv_\theta \leq 1$) exhibited an overall increase in SSB, consistent with a decrease in fishing switching from LEP_{pre} = 0.2 to LEP_{post} = 0.35, whereas in the higher-noise scenario (cv_θ = 10) this switch did not produce an obvious increase in SSB.

The predictive skill of model projections has two important components. First, projections must be sufficiently precise (i.e., narrow prediction intervals) so that the outcomes of alternative management scenarios (LEP_{post}) can be distinguished within a decision analysis setting at time t = 0. Otherwise, model uncertainty overwhelms the scope of potential management outcomes. Second, projections must be sufficiently accurate that the prediction intervals of projections for a particular management scenario (LEP_{post}) encompass the actual value for that management outcome, and not the value for other management outcomes. If not, the model might indicate that the observed spawning stock biomass corresponded to an incorrect level of LEP_{post}. That is, the model would be unable to account for process error in the dynamics, and would make an incorrect prediction.

To illustrate these two components of model skill, Figure 3 shows the mean and 95% prediction interval for forecast model projections for a range of values of LEP_{post}, correlation strength ρ and variability in larval survival cv_θ at 10 years post-decision, again using a single model realization for illustration (LEP_{pre} = 0.2). When variability in survival was low and dynamics were nearly deterministic (fig. 3a), model projections for each value of LEP_{post} did not overlap and closely matched the actual value at all time steps, regardless of the correlation strength of the proxy. These results also illustrate the general deterministic trend that $LEP_{\text{post}} < 0.35$ led to additional declines in SSB while $LEP_{\text{post}} \geq 0.35$ produced an increase in SSB. This result may be relevant not only for the rockfish model depicted in this case but may be more generally applicable.

For an intermediate level of variability (cv_θ = 1; fig. 3b), the prediction intervals of model projections for different values of LEP_{post} rarely overlapped, even for low correlation strength ρ. However, higher values of ρ produced a closer match between the model projection spawning stock biomass SSB' and the actual value $SSB^\star$.

When there was much greater natural variability in larval survival (cv_θ = 10; fig. 3c), the 95% prediction intervals for $SSB'(t)$ under different values of LEP_{post} overlapped considerably for low values of the correlation strength ρ, so that a decision analysis effort at t = 0 would predict that it is impossible to distinguish the effects of very different fishing rates on SSB over this time scale. Similarly, the prediction interval for a given

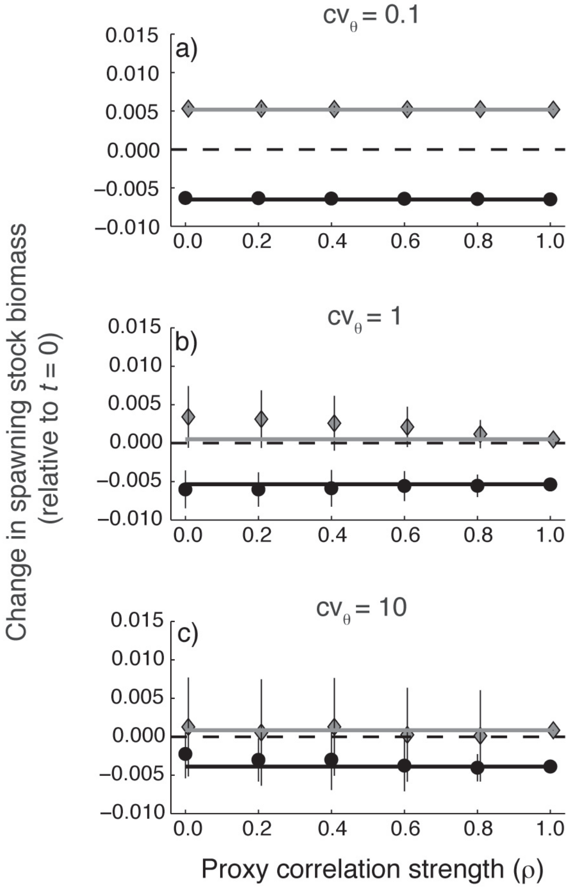

Figure 4. Results from the nonspatial hindcasting model showing the deviation of model projections from actual values. Each series of points depicts the projected spawning stock biomass (*SSB'*) at t = 10 years after fishery management switched from LEP_{pre} = 0.2 (overfishing) to an alternative level of fishing (LEP_{post}): 0.5 (light gray diamonds) or 0.2 (black circles). Projections are shown for a range of values of the correlation ρ between actual larval survival and a physical proxy. Error bars indicate 95% prediction interval for model projections. Solid lines indicate actual *SSB** values for the corresponding value of LEP_{post}. The level of variability in natural survival, cv_θ, differs among panels as indicated. *SSB* values are presented as deviations from *SSB* at time t = 0; no deviation indicated by dashed horizontal line. For decision analysis at t = 0, the quantity of interest is the degree of overlap in the range of projected outcomes for different levels of LEP_{post}. For adaptive management at t > 0, the quantity of interest is whether the range of projected outcomes for a particular LEP_{post} contain the actual value.

projection overlapped multiple values of $SSB^{\star}(t)$. Thus it would be impossible to determine from examining *SSB* at year 10 whether the desired value of LEP_{post} was being achieved, because uncertainty about the variability in recruitment would be too large. However, the prediction intervals on model projections diminished with increasing ρ, and both the accuracy and precision of model projections were much greater for $\rho > 0.8$.

Interestingly, over longer time scales (e.g., t = 10), it was possible for a strong correlation between the proxy and larval survival to actually introduce error into the model projection and produce a greater deviation from the actual value. This appears to occur because the relatively narrow prediction intervals on SSB' during the period t = 0 to $t = a_c$ constrain the model trajectory in later years, and slight errors during that early period can propogate through time, producing larger errors later (compare fig. 2e to 2f).

Results similar to those shown in Figure 3 for the forecasting model are also obtained in the hindcasting model (fig. 4), in which values of the physical variable $\phi(t)$ from years t = 1–10 are used as a proxy for $\theta(t)$ in those years. The notable differences are that prediction intervals around model projections are generally smaller, and projections always converge towards $SSB^{\star}$ as ρ approaches 1.

The general patterns illustrated in Figures 2–3 are summarized for 100 different realizations of the actual larval survival time series $\boldsymbol{\theta}^{\star}$ in Figure 5. In order to summarize the distribution of model projections for each model realization (i.e., each set of actual values $\boldsymbol{\theta}^{\star}$), the mean and standard deviation of predicted SSB' were compared to the actual value $SSB^{\star}$ using a standard normal deviate: $z = (\overline{SSB'} - SSB^{\star})/s_{SSB'}$. We then calculated the average z-statistic across all model realizations for a particular combination of LEP_{pre}, LEP_{post}, variability in larval survival cv_θ, correlation strength ρ, and time t. The p-value corresponding to this z-statistic indicates the probability that the actual value of $SSB^{\star}$ falls within the distribution of projected SSB' values; that is, the accuracy of the projections. Examination of these p-values (fig. 5a–e) indicates that model accuracy is maximal for $\rho > 0.6$ (note that the contour lines grow closer just above $\rho > 0.6$) and $t \leq 4$ (recall that the age at recruitment to the fishery, a_c, is 4). The p-values fall off sharply below the value of $\rho > 0.6$ over short time scales. Over longer time scales ($t > 4$), model accuracy is relatively constant across all values of ρ, but decreases somewhat for higher values of ρ after t = 8. This general pattern holds across all levels of variability cv_θ, and correspond to the patterns noted in Figure 3 for a single model realization.

We also employed the same z-statistic procedure to compare SSB' for LEP_{post} = 0.35 to the actual value of $SSB^{\star}$ for LEP_{post} = 0.2. In this case, the p-value measures the probability that an incorrect value of $SSB^{\star}$ would fall within the distribution of SSB' values, that is, the precision of the model projections. In this case, the p-values were uniformly low across all values of correlation strength ρ for low levels of natural variability (fig. 5f–h). For higher levels of variability ($cv_\theta \geq 5$), the pattern of this metric of model skill roughly matched that for the comparison of SSB' to the correct $SSB^{\star}$: p-values were high for low values of ρ early in simulations (indicating high overlap with the incorrect value) and moderate ($p \sim 0.15$) for most values of ρ in later years (fig. 5i–j). The major difference from the comparison shown in Figure 4a–e is that model skill remained high for high values of ρ ($\rho \geq 0.8$) across all time-steps.

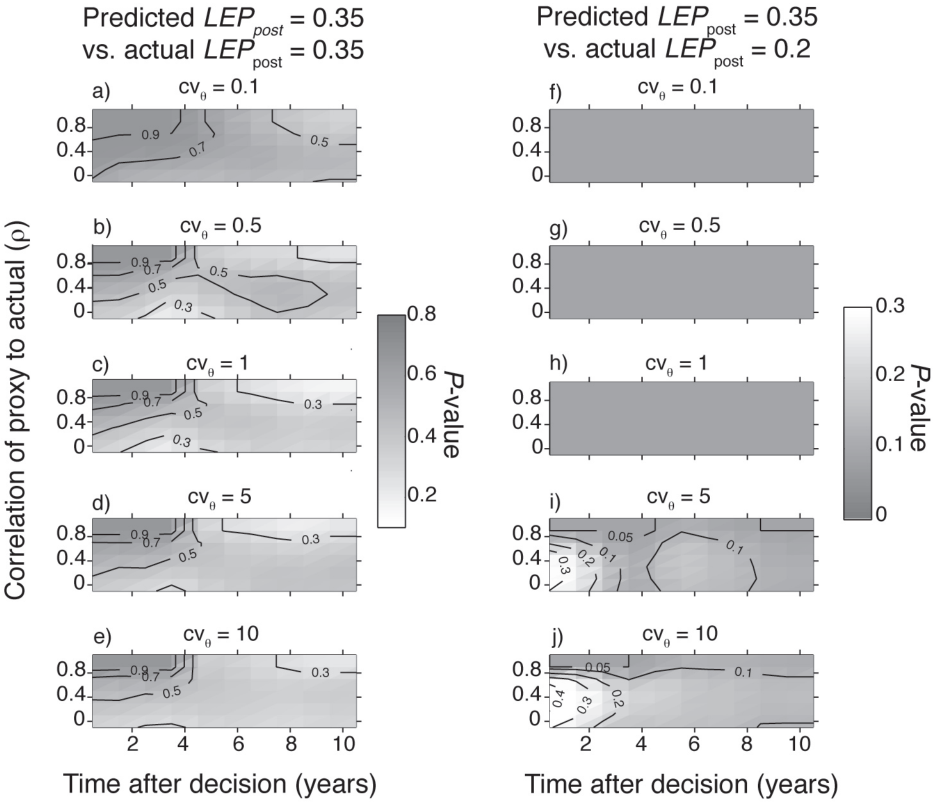

Figure 5. Results from multiple realizations of the nonspatial forecasting model showing the predictive skill of model projections. Model results were summarized as the standard normal deviate (*z*-statistic) for the deviation of the mean model projection from the correct actual value (a–e) or the actual value for an alternative level of *LEP*$_{post}$ (f–j). Each *z*-value was then translated into a *p*-value, representing the probability that the range of model projections contains the correct value (a–e) or an incorrect alternative value (f–j). Each panel shows the range of outcomes over time after *t* = 0 for increasing values of the correlation of actual larval survival rates to a physical proxy (*ρ*) and a given level of natural variability in larval survival (cv_θ). Note that shading in panels (a–e) is opposite that in (f–j); in both cases darker values indicate better model performance.

As in the example shown above (fig. 4), the overall behavior of the hindcasting model was similar to that depicted for the forecasting model in Figure 4, but with smaller prediction intervals and thus improved model performance (fig. 6). Additionally, high values of **ρ** were uniformly advantageous across all time-steps, and did not lead to a decrease in model performance at *t* = 10 (compare upper left corners of Figure 5a–e and Figure 6a–e).

Here we have presented results only for the case of LEP_{pre} = 0.2, in which the pre-decision population was undergoing overfishing. Model results for LEP_{pre} = 0.4 (sustainable fishing) exhibit nearly identical patterns of model accuracy with respect to **ρ**, cv_θ, and *t*, and for brevity we simply state this result without a figure.

Spatial model

An example of the behavior of the spatial model with diffusive dispersal and a 10 km wide MPA is shown in Figure 7. Overall, adult movement (defined by adult home range radius *h*) had a much greater effect on the spatial pattern of *SSB* than did variation in larval disperal distance (defined by dispersal distance *d*). Indeed, *SSB* was 3× greater for the model runs with small home range size compared with large (fig. 7a, b), but differed little between the two larval dispersal distances. The apparent lack of an effect of dispersal distance *d* is because the MPA in these model runs was large enough to be self-persistent for small *d* and covered enough area to be network persistent for large *d* (when home range size was small), so the population inside the MPA was persistent in either scenario. However, LEP_{post} did affect overall *SSB*, even inside the MPA, for all movement scenarios. The effects of LEP_{post}, and the tendency for recruitment variability to obscure those effects, were amplified with greater adult movement. Notice that for LEP_{post} = 0.2, the large-home-range case was not persistent despite the MPA (i.e., biomass continues to decline after MPA implementation), but with a moderate amount of recruitment variability (cv_θ = 1 in this example) the decline was not immediately evident in all simulations (fig. 7c, d).

The general patterns observed in the diffusive dispersal case were similar to those in the retention zone scenario (fig. 8), although densities within the MPA were slightly elevated by the shorter home ranges and shorter

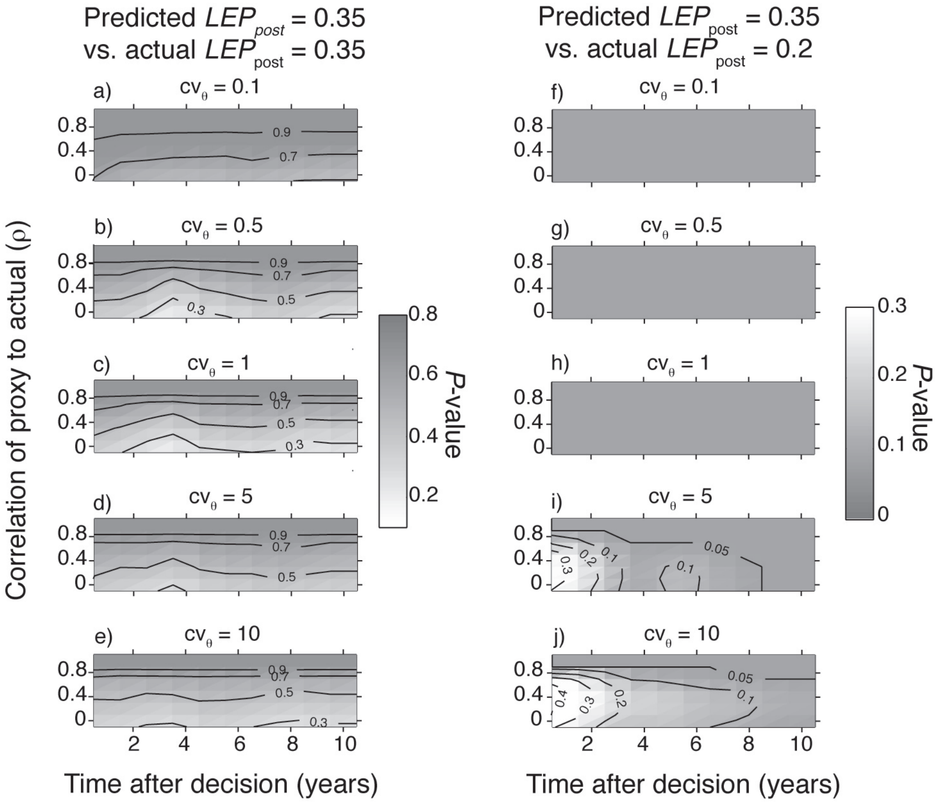

Figure 6. Results from multiple realizations of the nonspatial hindcasting model showing the predictive skill of model projections. Model results were summarized as the standard normal deviate (*z*-statistic) for the deviation of the mean model projection from the correct actual value (a–e) or the actual value for an alternative level of LEP_{post} (f–j). Each z-value was then translated into a *p*-value, representing the probability that the range of model projections contains the correct value (a–e) or an incorrect alternative value (f–j). Each panel shows the range of outcomes over time after $t = 0$ for increasing values of the correlation of actual larval survival rates to a physical proxy (ρ) and a given level of natural variability in larval survival (cv_θ). Note that shading in panels (a–e) is opposite that in (f–j); in both cases darker values indicate better model performance.

larval dispersal distances. Populations with large home ranges were persistent in the $LEP_{post} = 0.2$ case when larval dispersal was short (note the slightly increasing *SSB* in Figure 8c) but not long (fig. 8d); in the former case the additional recruitment afforded by the retention zone inside the MPA was sufficient to offset the fishing of individuals moving outside the MPA boundaries.

Evaluations of MPA performance typically take either or both of two forms: an after:before comparison of biomass within an MPA and an inside:outside comparison of biomass in the MPA relative to that in a fished control. The after:before comparison seeks to determine whether biomass is recovering inside the MPA, but that signal can be obscured by recruitment variability. The inside:outside comparison is intended to control for large-scale variability in recruitment and other processes, but assumes that there is a substantial difference in fishing pressure inside vs. outside. We simulated both of these types of comparisons. An example is given in Figure 9, showing the log ratio of *SSB*' after:before for a location inside the MPA (fig. 9a–c) and log ratio of *SSB*' inside:outside measured at a location in the center of the MPA and the center of the fished area (fig. 9d–f). The general patterns of accuracy and precision of the model projections were similar to those observed in the nonspatial model: the signal of deterministic change in *SSB*' due to LEP_{post} increased over time, that signal was more difficult to detect as recruitment variability (cv_θ) increased, and higher values of ρ increased the precision of model projections. As in the nonspatial model, the increase in precision afforded by the forecast estimate of $\theta(t)$ declined after $t = 5$ *y* ($t = t_c$). The major new pattern evident in the spatial model was that the value of LEP_{post} had a strong effect on the inside:outside ratio (fig. 9d–f) but only a minimal effect on the after:before ratio (fig. 9a–c; there was a slightly greater effect of LEP_{post} in the large home range scenario). There was also a strong effect of adult home range movement on the two response ratios, as summarized below.

As in the nonspatial model, we summarized the accuracy and precision of the spatial model results using *z* statistics to quantify whether A) model projections bracketed the actual value, and B) projections bracketed incorrect values associated with other values of

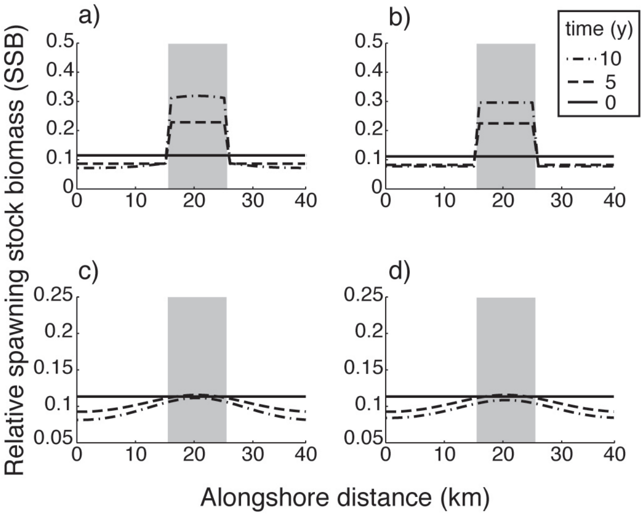

Figure 7. Results from spatial forecasting model with spatially homogenous larval dispersal and a moderate level of variability in larval survival ($cv_\theta = 1$). The mean value (across all simulations) of the actual value of SSB^* (relative to the unfished maximum) at each time is shown for $LEP_{pre} = 0.2$ and $LEP_{post} = 0.2$, at $t = 0$ (solid lines), 5 (dashed lines), and 10 (dot-dash lines) years after MPA implementation. Each panel shows results for a model species with a different combination of larval dispersal distance (*d*) and home range diameter (*h*): a) short d, short *h* ($d = 5$ km, $h = 0.1$ km); b) long *d*, short *h* ($d = 40$ km, $h = 0.1$ km); c) short *d*, long *h* ($d = 5$ km, $h = 10$ km); d) long *d*, long *h* ($d = 40$ km, $h = 10$ km). Gray shading indicates location of MPA within the 40 km repeating unit of infinite coastline.

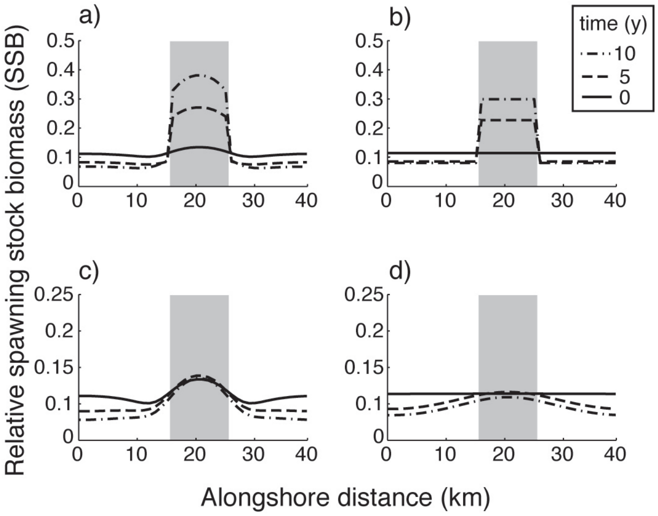

Figure 8. Results from spatial forecasting model with a larval retention zone and a moderate level of variability in larval survival ($cv_\theta = 1$). The mean value (across all simulations) of the actual value of SSB^* (relative to the unfished maximum) at each time is shown for $LEP_{pre} = 0.2$ and $LEP_{post} = 0.2$, at $t = 0$ (solid lines), 5 (dashed lines), and 10 (dot-dash lines) years after MPA implementation. Each panel shows results for a model species with a different combination of larval dispersal distance (*d*) and home range diameter (*h*): a) short *d*, short *h* ($d = 5$ km, $h = 0.1$ km); b) long *d*, short *h* ($d = 40$ km, $h = 0.1$ km); c) short *d*, long *h* ($d = 5$ km, $h = 10$ km); d) long *d*, long *h* ($d = 40$ km, $h = 10$ km). Gray shading indicates location of MPA within the 40 km repeating unit of infinite coastline. The MPA contains the larval retention zone, inside which larval dispersal distance *d* is reduced by 50%.

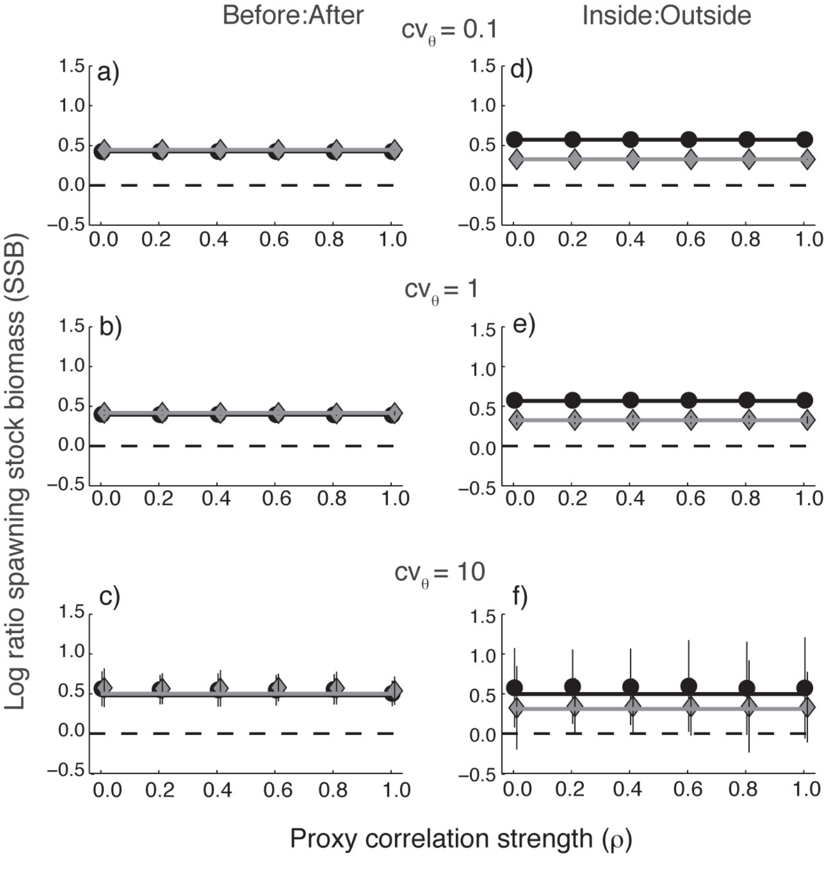

Figure 9. Results from the spatial forecasting model with spatially homogenous dispersal showing the deviation of model projections from actual values. Each series of points depicts the projected spawning stock biomass (SSB') at $t = 10$ years after MPAs were implemented and fishery management switched from $LEP_{pre} = 0.2$ (overfishing) to an alternative level of fishing (LEP_{post}): 0.5 (light gray diamonds) or 0.2 (black circles). Projections are shown for a range of values of the correlation ρ between actual larval survival and a physical proxy. Error bars indicate 95% prediction interval for model projections. *SSB* is expressed as (a–c) the log ratio of SSB before:after MPA implementation for a location inside the MPA (*t* vs $t = 0$), or (d–f) the log ratio of *SSB* inside:outside the MPA at the same time. Solid lines indicate actual values for the corresponding value of LEP_{post}. The level of variability in natural survival, cv_θ, differs among panels as indicated. These results were obtained using the forecasting model for a species with long larval dispersal distance ($d = 40$ km) and short adult home range ($h = 0.1$ km); the MPA was 10 km wide.

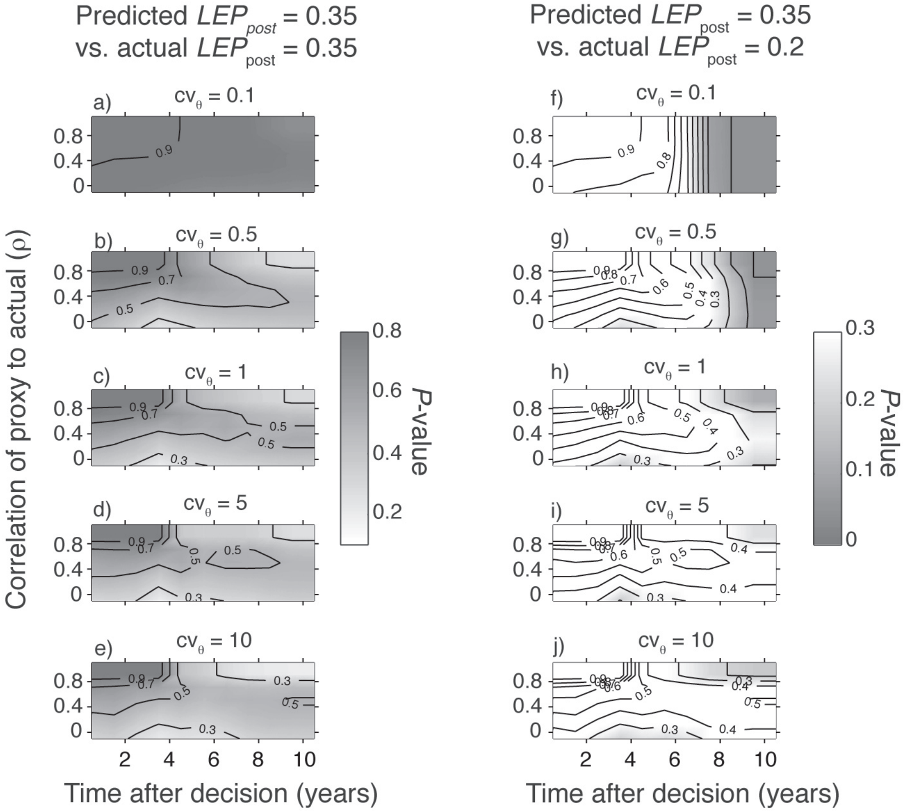

Figure 10. Results from multiple realizations of the spatial model with spatially homogenous dispersal showing the predictive skill of model projections for the ratio of *SSB* after:before MPA implementation. These results were obtained using the forecasting model for a species with long larval dispersal distance (d = 40 km) and short adult home range (h = 0.1 km); the MPA was 10 km wide. Model results were summarized as the standard normal deviate (z-statistic) for the deviation of the mean model projection of the *SSB* ratio for LEP_{post} = 0.35 from (a–e) the correct actual value for that level of LEP_{post}, or (f–j) the actual value for an alternative management scenario with LEP_{post} = 0.2. Each z-value was translated into a p-value, representing the probability that the range of model projections contains the correct value (a–e) or an incorrect alternative value (f–j). Each panel shows the range of outcomes over time after t = 0 for increasing values of the correlation of actual larval survival rates to a physical proxy (ρ) and a given level of natural variability in larval survival (cv_θ). Note that grayscale in panels (a–e) is opposite that in (f–j); in both cases darker values indicate better model performance.

LEP_{post}. Even though the MPAs modeled in these scenarios were big enough to support a persistent population in most cases (regardless of LEP_{post}), the value of LEP_{post} affects the *SSB* inside MPAs (cf. figs. 7–9). An adaptive management evaluation of MPA performance will require a model projection of how much *SSB* should have increased inside (or outside) the MPA. We first examine the results obtained from the diffusive dispersal scenario. There was essentially no effect of larval dispersal distance on the z statistics (data not shown), so we focus on the results for the two home range sizes and long larval dispersal distances (d = 40). For the short home range case (h = 0.1; fig. 10), forecast projections of the after:before *SSB*' ratio always had considerable overlap with the ratio associated with the correct LEP_{post} (fig. 10a–e), although the accuracy was somewhat better for correlation strength $\rho > 0.8$ over short timescales ($t < 5$ y). The distribution of after:before *SSB*' ratios also had considerable overlap with ratios associated with alternative values of LEP_{post} in early years ($t < 6$ y) for all values of correlation strength ρ and survival variability cv_θ (fig. 10f–j). This lack of precision is a consequence of the minimal deterministic effect of different LEP_{post} values on the after:before ratio in that initial time period. However, in high-noise ($cv_\theta \geq 1$) scenarios, an informative proxy ($\rho > 0.8$) did improve the precision of model projections after $t = 8$ y (fig. 10h–j). That is, the value of LEP_{post} had a long-term effect on MPA performance, but the trajectories of the after:before ratio associated with different values of LEP_{post} were only distinguishable within a reasonable time scale ($t < 10$ y) when an effective proxy for $\theta(t)$ was used.

The overall model skill in the short home range case was higher when *SSB*' was measured as the inside:outside ratio (fig. 11). Using that metric, forecast projections always had a high degree of overlap with the value associated with the correct LEP_{post} (fig. 11a–e) and very little overlap with ratios associated with alternative values of LEP_{post} (fig. 11f–j), except for very high values of cv_θ (fig. 11i–j). This result suggests that the inside:outside ratio does appear to control for environmental stochasticity when testing for the effects of an MPA. None-

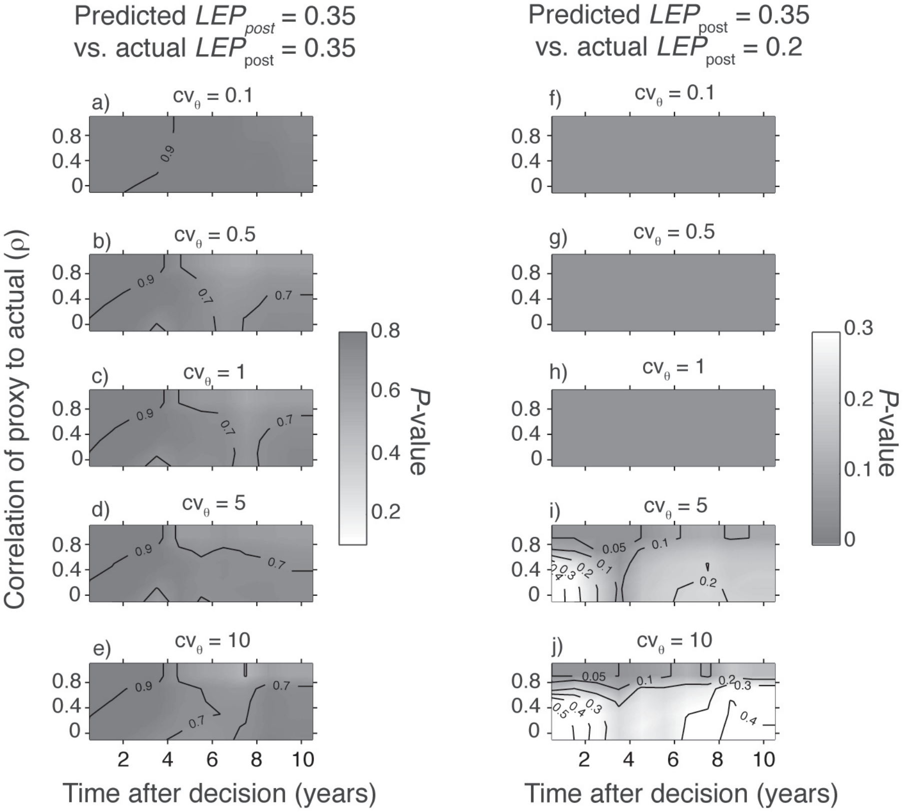

Figure 11. Results from multiple realizations of the spatial model with spatially homogenous dispersal showing the predictive skill of model projections for the ratio of *SSB* inside:outside the MPA. These results were obtained using the forecasting model for a species with long larval dispersal distance (d = 40 km) and short adult home range (h = 0.1 km); the MPA was 10 km wide. Other figure details as in Figure 10.

theless, the forecasts had greater precision in high noise situations ($cv_\theta > 1$) when an effective proxy was used ($\rho > 0.8$; fig. 11i–j).

The accuracy and precision of forecast projections were strikingly different for a species with a large home range (h = 10 km). This is because home range movement dilutes the protection of an MPA, so that the change in biomass inside the MPA is more sensitive to the level of fishing outside (Moffitt et al. 2009), producing a larger, more rapid divergence in *SSB*' among alternative values of LEP_{post}. When forecasting the after:before *SSB*' ratio, projections had far less overlap with the value associated with the actual LEP_{post} (fig. 12a–e) than in the small home range scenario, and use of a proxy with $\rho > 0.8$ yielded considerable improvement in accuracy over timescales shorter than t_c (i.e., $t \leq 4$ years). By contrast, the forecast after:before ratio had much less overlap with values associated with alternative LEP_{post}, and the proxy only improved precision over short time scales ($t < 4$ y) in high-variability scenarios ($cv_\theta > 1$; fig. 12f–j).

When the response variable was the inside:outside *SSB*' ratio, results were more similar to those for the small home range case: there was high accuracy for all values of survival variability cv_θ and proxy correlation strength ρ (fig. 13a–e), and high precision for low values of cv_θ (fig. 13f–g). However, when recruitment was more variable ($cv_\theta \geq 1$) precision was very low except when an effective proxy ($\rho \geq 0.8$) was used, although this only improved precision over short time scales (fig. 13h–j). This result is a consequence of home range movement tending to equalize biomass inside and outside of the MPA (e.g., fig. 7c–d). As a consequence, it would be difficult to distinguish successful from unsuccessful MPAs over short time scales using the inside:outside ratio unless an effective proxy were employed.

It is important to note that the use of the inside:outside ratio depends on the choice of sample locations. Comparing a location in the center of the MPA to a location far outside of the MPA boundary—as we have done here—will produce the highest contrast. The inside:outside ratio will be closer to zero (i.e., less informative) if either inside or outside observations were made closer to the MPA edge, especially for species with larger home ranges. This effect can be seen in Figure 6, which shows how a large home range produces a larger zone over which high "inside" values transition to low "outside" values; making observations inside this transi-

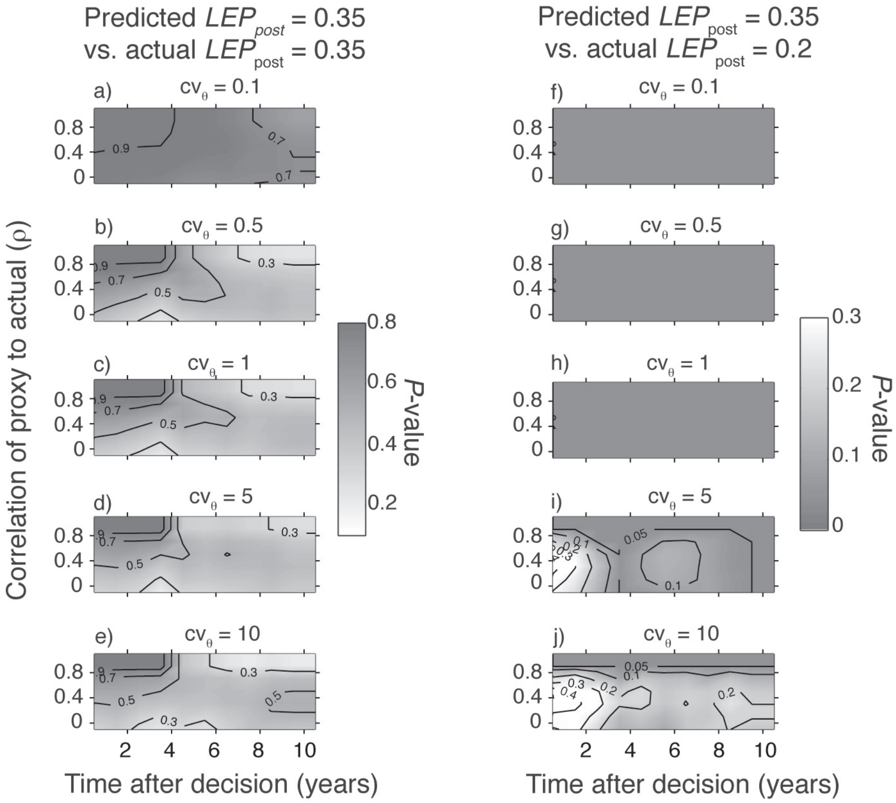

Figure 12. Results from multiple realizations of the spatial model with spatially homogenous dispersal showing the predictive skill of model projections for the ratio of *SSB* after:before MPA implementation. These results were obtained using the forecasting model for a species with long larval dispersal distance (d = 40 km) and large adult home range (h = 10 km); the MPA was 10 km wide. Other figure details as in Figure 10.

tion zone will produce a lower inside:outside ratio. This issue is addressed more formally by Moffitt (2009).

As in the nonspatial case, running the model in hindcast mode improved the accuracy and precision of the model projections, and projections made with a high-ρ proxy were accurate over the entire 10-year period rather than just the initial 4–5 years after the change in fishing pressure (i.e., $t \le t_c$). For example, in the large-home range (h = 10 km), long larval dispersal (d = 40 km) case, the after:before comparison had greater precision and accuracy, and the latter did not drop off after t = 4 y (this result is not portrayed in the figures). Similarly, the model skill for the inside:outside comparison was high for high values of ρ and cv_θ over the entire 10-year period rather than the first 4 years only.

In these simulations, there was very little effect of the larval retention zone on the efficacy of using the physical proxy, and results were generally similar to those with spatially homogenous dispersal. For comparison, the forecast after:before and inside:outside ratios for the short- and long-home range cases are shown in Figures 14–15. Larval retention can have a striking effect on population persistence within MPAs (White et al. 2010a), and the large home range/short larval dispersal case (h = 10 km, d = 40 km) was persistent with LEP_{post} = 0.2 in the retention zone scenario but not in the homogenous dispersal scenario. Despite the effects on population persistence, the degree of retention that we modeled was not sufficient to substantially alter SSB' for the other life history combinations or values of LEP_{post} we considered.

To explore the importance of persistence on the usefulness of the proxy, we also simulated dynamics for a coastline with a much smaller, 3 km wide MPA. This MPA was too small to be self-persistent for any of the larval dispersal distances we considered, although larval production in the fished region was sufficient (under all values of LEP_{post} we considered) for the population to be persistent in all cases except for the long larval dispersal distance and large home range case (d = 40 km, h = 10 km). Despite the lack of self-persistence, results for the small MPA were nearly identical to those for the larger, 10 km MPA. The only noticeable difference was for the inside:outside comparison in the high d, high h scenario, in which the population continued to decline after MPA implementation for all values of LEP_{post}. As a consequence, it was difficult to distinguish alternative LEP_{post} scenarios unless there was very little variability in survival or the proxy correlation strength ρ was very

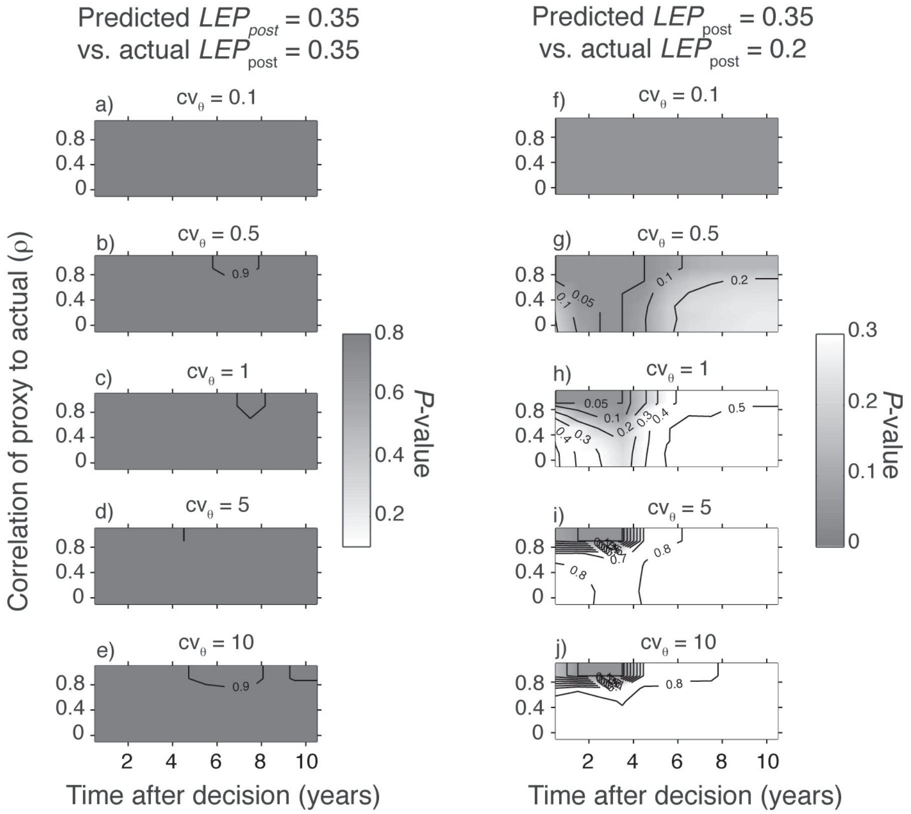

Figure 13. Results from multiple realizations of the spatial model with spatially homogenous dispersal showing the predictive skill of model projections for the ratio of *SSB* inside:outside the MPA. These results were obtained using the forecasting model for a species with long larval dispersal distance (*d* = 40 km) and large adult home range (*h* = 10 km); the MPA was 10 km wide. Other figure details as in Figure 10.

high; even with high ρ, the model skill was improved only during years 3–5 following implementation (these results are not portrayed in a figure).

DISCUSSION

Here we have outlined a general framework for incorporating physical proxy information into forecasts of recruitment year-class strength for fishery management. Our modeling results illustrated how variability in larval survival can make it difficult to distinguish the effects of different fishing rates on spawning stock biomass (*SSB*) and population persistence. Our proxy-based method may be useful because it accounts for some of this variability in order to obtain better projections of the response of a fished population to management decisions. These results support the development of good proxies of recruitment strength for fishery management. We anticipate that the application and effectiveness of this modeling approach in a real management scenario will depend on species- and location-specific particulars and as we have shown here will depend on how well the proxy describes recruitment.

Here we have found two consistent outcomes regarding the use of a physical recruitment proxy in forecast models. First, incorporating information from the proxy was most useful when the correlation, ρ, between the proxy and larval survival was high; ≥ 0.8. Correlations this high or higher have been reported for real datasets (e.g., Caselle, this issue; Shanks, this issue), so this approach is promising for implementation. Second, when forecasting for fishery management, the proxy only improves model accuracy out to approximately a_c years, the time to recruitment into the fishery (a time period of 4–5 years in this model). After this point there is a sharp decline in accuracy, because the pre-recruit age classes predicted by the proxy at time $t = 0$ have entered the fished population, and there is no proxy information on later age classes (i.e. those that were spawned after $t = 0$). Accuracy falls sharply because the model simulations were no longer tracking the actual population trajectories, despite the well behaved narrow prediction intervals.

Beyond this time ($t > a_c$), the model prediction interval expands, reflecting greater uncertainty about recruitment year class strength, and because the interval is so large it once again tends to encompass the actual value. This anomaly is a feature of the forecast model, but not the hindcast model, for which information on larval survival is available after $t = a_c$ and model accuracy is more

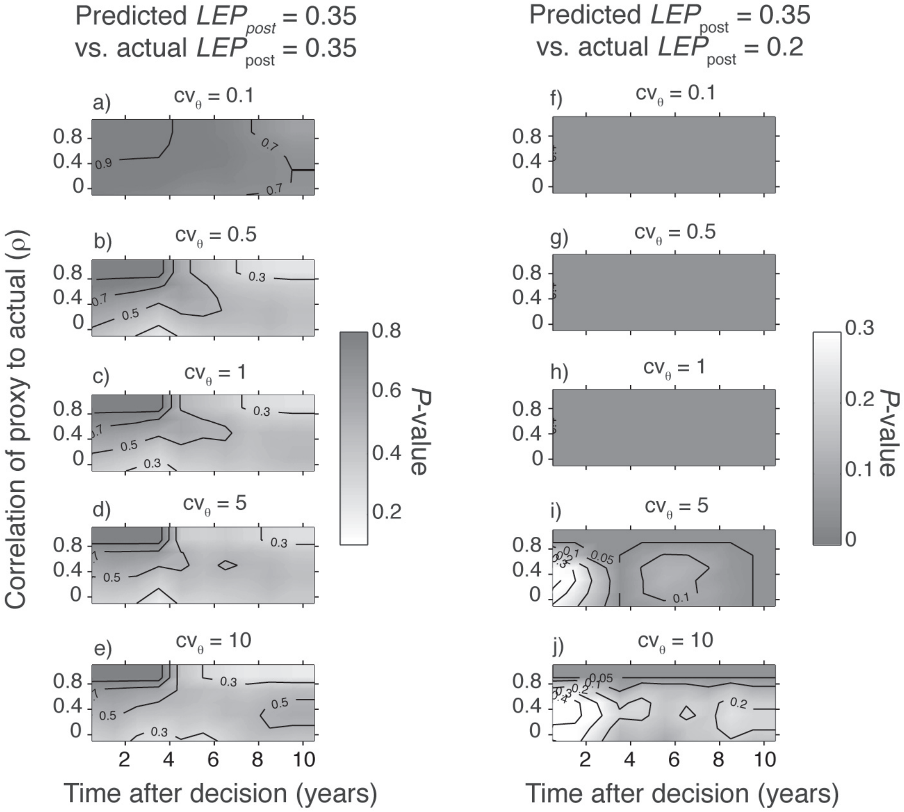

Figure 14. Results from multiple realizations of the spatial model with a larval retention zone showing the predictive skill of model projections for the ratio of SSB after:before MPA implementation. These results were obtained using the forecasting model for a species with long larval dispersal distance (*d* = 40 km) and large adult home range (*h* = 10 km); the MPA was 10 km wide. The MPA contains the larval retention zone, inside which larval dispersal distance *d* is reduced by 50%. Other figure details as in Figure 10.

consistent across time. Thus the use of the proxy is even more advantageous in hindcasting situations over longer periods of time. The time lag in recruitment to the fishery and the width of the prediction interval will be specific to the species examined and the time to enter the fishery. In the example modeled here, kelp rockfish enter the fishery after 4 years, making forecasts beyond this time less reliable. By contrast, a species such as red abalone (*Haliotis rufescens*) enters the fishery in 11 years (Rogers-Bennett et al. 2007), potentially making proxy-derived forecasts reliable over a longer time period.

It is important to note that our models did not account for observation error in the measurement of either physical variables, year class strength, or biomass. It is possible that actual proxies would require a correlation strength considerably better than 0.8 in order to overcome errors introduced by observation and possibly other processes not included in our model.

The use of a recruitment proxy could be especially valuable for short-term decision making with regard to MPAs. There is often little baseline observation data available prior to MPA implementation, especially data that are spatially explicit and collected both inside and outside of MPA sites (e.g., Hamilton et al. 2010). Furthermore, MPAs are politically contentious so there is often a short window for re-evaluation (e.g., 5 yr in California; CDFG 2008) within which recruitment variability could easily overwhelm any signal of an actual deterministic fishing effect within an MPA.

Several authors have recently advocated using inside:outside ratios to avoid the problem of minimal pre-monitoring (E. A. Babcock and A. D. MacCall, unpublished manuscript). Indeed, the inside:outside ratio can be predicted by models relatively well, even without a larval survival proxy, especially in low-variability cases (figs. 11 and 13). However, the use of the inside:outside ratio as a decision rule is predicated on the assumption that biomass inside the MPA is close to the unfished value or differs dramatically with the biomass inside the MPA at the final census period (e.g., 5 years). This will be true only over longer time scales and may not be true for all species (e.g., species with large home ranges; fig. 7c; White et al. 2010b). Additionally, the inside:outside ratios are sensitive to other factors which we did not address in this study, including the distribution of suitable habitat, the spatial distribution of fishing effort, and even the locations at which observations are made. Over short time scales following implementation, or in the case of

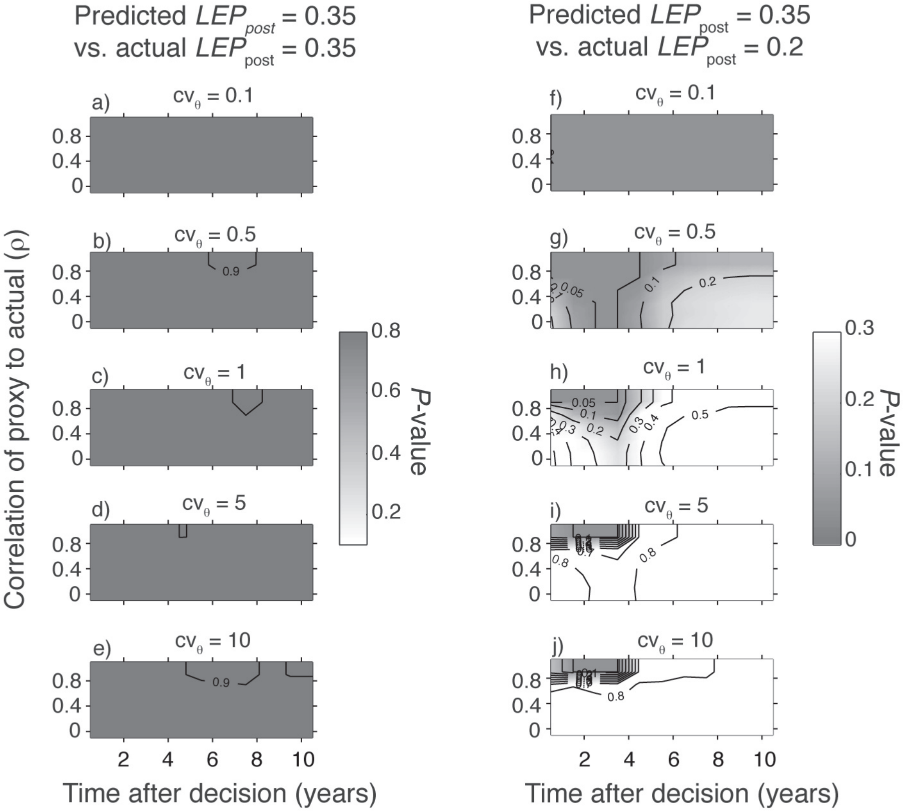

Figure 15. Results from multiple realizations of the spatial model with a larval retention zone showing the predictive skill of model projections for the ratio of SSB inside:outside the MPA. These results were obtained using the forecasting model for a species with long larval dispersal distance (d = 40 km) and large adult home range (h = 10 km); the MPA was 10 km wide. The MPA contains the larval retention zone, inside which larval dispersal distance d is reduced by 50%. Other figure details as in Figure 10.

ineffective MPAs, management strategy evaluations suggest that such ratio-based decision rules may produce unusual and incorrect results (E. A. Babcock and A. D. MacCall, unpublished manuscript). Consequently, we suggest there is value in using our proxy-based method to project results over the short time scales that are most relevant to adaptive management decisions. Ratios obtained from monitoring data could then be evaluated in the context of the expected trajectory of biomass inside and outside the MPAs, reducing the chance that managers draw incorrect inferences from the raw ratios in the absence of proxy information.

Prior modeling efforts have clearly demonstrated that the level of fishing outside MPA boundaries can have an effect on population persistence and biomass inside the MPA (Holland and Brazee 1996; Mangel 1998, 2000; Botsford et al. 2001; White et al. 2010b), just as we found in our spatial model. This result is generally borne out by empirical findings that species targeted by fisheries have a greater response to protection in MPAs (Micheli et al. 2004; Lester et al. 2009; Pelc et al. 2009; Hamilton et al. 2010). As a consequence, the adaptive management of MPAs must utilize model predictions that account for fishing rates outside MPAs. However, while the long-term deterministic trends in biomass associated with different fishing rates tend to be quite distinct (White et al. 2010b), our results show that stochastic variability in larval supply can make it difficult to discern those long-term trends from variability due to recruitment fluctuations over short time scales (e.g., fig. 7d; also see Moffitt 2009). Consequently, the predictions of deterministic models without proxy information should be used with caution in an adaptive management setting.

The Before-After Control-Impact (BACI) approach for detecting management effects is intended to control for the type of stochastic variation modeled here (Underwood 1994). However, our results suggest that the effectiveness of BACI depends on the life history of the species in question. For fishes with small home ranges, the before: after ratio had limited resolution. The prediction intervals of model forecasts for different levels of fishing (LEP_{post}) had considerable overlap, so it would be impossible to distinguish alternative outcomes (e.g., SSB might not differ significantly under different management scenarios) in an adaptive management setting. This is an important point for the implementation of this modeling approach. However, an inside:outside comparison was much more accurate and precise in the model forecasts. The opposite was true for species with larger home ranges: there was greater overall effect of LEP_{post} on biomass across the entire coast, so it was easier to resolve different model trajectories using the after:before ratio than using the inside:outside comparison. In general, increasing variability in larval survival impaired the model's prediction of either of these metrics, but substantially improved the model's predictions with the use of an accurate proxy ($\rho > 0.8$). Therefore, we advocate the use of larval survival information in fishery models particularly in cases where research has determined that larval survival is tightly linked to a physical proxy such as an index of upwelling.

A variety of recent spatially explicit modeling efforts have documented the effects of different larval dispersal patterns on MPA performance (McGilliard and Hilborn 2009; Costello et al. 2010; White et al. 2010a), yet we found relatively little effect of larval dispersal distance or larval retention on the accuracy and precision of different effectiveness metrics. In contrast, we did find a large impact of adult home range size on model outcomes, highlighting the importance of basic research describing home ranges of marine organisms. While we did not explore a full suite of larval dispersal distances, we did consider scenarios in which MPAs were large enough relative to the larval dispersal distance to support a self-persistent population as well as scenarios in which this condition was not me. Thus our results do illustrate an insensitivity to larval dispersal over a range of possible population outcomes. A wider range of combinations of MPA size and spacing could be simulated to further investigate this question, but given the potentially large number of parameter combinations involved, we advocate examining real-world scenarios of interest. While little is known about larval dispersal distances, many species with potentially long-distance dispersal (long larval stages) may be retained locally with few individuals dispersing long distances (Strathmann et al. 2002; Marko et al. 2007; Rogers-Bennett and Rogers 2008), so self persistence at the spatial scale of MPAs may be relatively common. In any case, our results suggest that there is not likely to be a strong effect of larval dispersal distance on the effectiveness of management efforts, but there may be an effect adult home ranges sizes.

In summary, our simulations suggested that a physical proxy with a correlation coefficient of greater than 0.8 does function to increase the short-term predictive skill of forecasting and hindcasting models in both the nonspatial and spatial model. In the spatially explicit model (with MPAs) the inclusion of a good physical proxy information improved model precision especially in cases of adults with short home-ranges. Our approach could be applied to adaptive management efforts over short time scales. Numerous authors have documented correlations between physical factors and recruitment year class strength that exceed this level of correlation. Several promising examples emerged from this CalCOFI Symposium, including correlations of up to $r = 0.99$ between annual settlement of KGBC rockfish (primarily kelp rockfish, *Sebastes atrovirens*) and a monthly upwelling index (Caselle et al., this issue), and correlations between Dungeness crab (*Cancer magister*) recruitment and the timing of the spring transition ($r = 0.97$, excluding three recent outlier years) and the Pacific Decadal Oscillation ($r = 0.73$; Shanks et al., this issue). Indices related to upwelling and the Pacific Decadal Oscillation are likely to be informative for many nearshore fisheries on the U.S. Pacific coast, but any number of other environmental indices may be useful for fisheries in other locations (e.g., Vance et al. 1985; Caputi et al. 2001; but see Myers 1998). Short-term predictive powers of these models may improve management performance more for extremely productive populations as opposed to less productive stocks (Walters 1989) and be more beneficial for populations with wide rather than narrow population fluctuations between years. It is precisely these types of fisheries that are challenging to manage. It seems obvious that ocean conditions have a large impact on recruitment and yet traditional fishery management does not incorporate this information into management. In the United States, federal managers have called for the incorporation of physical parameters into models for adaptive management (e.g., the Fisheries And The Environment [FATE] program; http://fate.nmfs.noaa.gov/) and the framework provided here helps to address this goal. This work provides a first step towards incorporating proxies of productivity driven by environmental forcing into modeling to improve fishery management.

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LITERATURE CITED

A'mar, Z. T., A. E. Punt, and M. W. Dorn. 2008. The management strategy evaluation approach and the fishery for walleye pollock in the Gulf of Alaska. Alaska Sea Grant College Program AK-SG-08-01: 317–346.

Botsford, L. W., and D. E. Wickham. 1974. Correlation of upwelling index and Dungeness crab catch. Fish. Bull. 73: 901–907.

Botsford, L. W., C. L. Moloney, A. Hastings, J. L. Largier, T. M. Powell, K. Higgins, and J. F. Quinn. 1994. The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. Deep-Sea Res. II 41: 107–145.

Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol. Lett. 4: 144–150.

California Department of Fish and Game (CDFG). 2008. California Marine Life Protection Act master plan for marine protected areas. http://www.dfg.ca.gov/mlpa/masterplan.asp. Accessed 4/4/2008.

Caputi, N., C.F. Chubb, and A. Pearce. 2001. Environmental effects on recruitment of the western rock lobster, *Panulirus cygnus*. Mar. Freshw. Res. 52: 1167–1175.

Caselle, J. E., B. P. Kinlan, and R. R. Warner. 2010. Temporal and spatial scales of influence on near-shore fish settlement in the Southern California Bight. Bull. Mar. Sci. 86: 355–385.

Caselle, J. E., B. P. Kinlan, R. R. Warner, D. Malone, and M. H. Carr. In press. Predictability of settlement of nearshore rockfishes (genus *Sebastes*) using simple indices of ocean conditions. Calif. Coop. Oceanic Fish. Invest. Rep.

Costello, C., A. Rassweiler, D. Siegel, G. De Leo, F. Micheli, and A. Rosenberg. 2010. The value of spatial information in MPA network design. Proc. Natl. Acad. Sci. USA. DOI: 10.1073/pnas.0908057107.

Cushing, D. H. 1982. Climate and fisheries. Academic Press, London.

Drechsler, M., and M. A. Burgman. 2004. Combining population viability analysis with decision analysis. Biodiv. Cons. 13: 115–139.

Fogarty, M. J., M. P. Sissenwine, and E. B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends Ecol. Evol. 6: 241–246.

Fraschetti, S., A. Terlizzi, F. Micheli, L. Benedetti-Cecchi, and F. Boero. 2002. Marine protected areas in the Mediterranean Sea: objectives, effectiveness and monitoring. Mar. Ecol. 23 (s1): 190–200.

Freiwald, J. 2009. Causes and consequences of the movement of temperate reef fishes. Ph.D. dissertation. University of California, Santa Cruz, CA, USA.

Gaines, S. G., and M. Bertness. 1993. The dynamics of juvenile dispersal: why field ecologists must integrate. Ecology 74: 2430–2435.

Grafton, R. Q., and T. Kompas. 2005. Uncertainty and the active adaptive management of marine reserves. Mar. Pol. 29: 471–479.

Halpern, B. S., and R. R. Warner. 2003. Matching marine reserve design to reserve objectives. Proc. R. Soc. Lond. B 270: 1871–1878.

Hamilton, S. L., J. E. Caselle, D. P. Malone, and M. H. Carr. 2010. Incorporating biogeography into evaluations of the Channel Islands marine reserve network. Proc. Natl. Acad. Sci. USA. DOI: 10.1073/pnas.0908091107.

Harwood, J., and K. Stokes. 2003. Coping with uncertainty in ecological advice: lessons from fisheries. Trends Ecol. Evol. 18: 617–622.

Hastings, A., and L. W. Botsford. 2006. Persistence of spatial populations depends on returning home. Proc. Natl. Acad. Sci. USA 103: 6067–6072.

Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, NJ.

Hilborn, R., A. Parma, and M. Maunder. 2002. Exploitation rate reference points for west coast rockfish: are they robust and are there better alternatives? N. Amer. J. Fish. Manag. 22: 365–375.

Hill, K. T., E. Dorval, N. C. H. Lo, B. J. Macewicz, C. Show, R. Felix-Uraga. 2007. Assessment of the Pacific sardine resources in 2007 for U. S. management in 2008. NOAA Technical Memorandum NMFS-SWFSC-413.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapp. P.-V. Reun. Cons. Inst. Explor. Mer. 20: 1–13.

Holland, D. S., and R. J. Brazee. 1996. Marine reserves for fisheries management. Marine Resource Economics 11: 157–171.

Lea, R. N., R. D. McAllister, and D. A. VenTresca. 1999. Biological aspects of nearshore rockfishes of the genus *Sebastes* from Central California with notes on ecologically related sport fishes. California Dept. Fish and Game Fish Bull. 177.

Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines, S. Airamé, and R. R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Mar. Ecol. Prog. Ser. 384: 33–46.

Love M. S., M. M. Yoklavich, and L. Thorsteinson. 2002. The rockfishes of the northeast Pacific. Berkeley, California: University of California Press. 404 pp.

Mangel, M. 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves Ecol. Lett. 1: 87–90.

Marko, P. B., L. Rogers-Bennett, and A. B. Dennis. 2007. MtDNA population structure and gene flow in lingcod (*Ophiodon elongatus*): limited connectivity despite long-lived pelagic larvae. Mar. Biol. 150: 1301-1311.

McClatchie, S., R. Goericke, G. Auad, and K. Hill. 2010. Re-assessing the temperature index for Pacific sardine (*Sardinops sagax*) stock assessment. Can. J. Fish. Aquat. Sci.

McGilliard, C. R., and R. Hilborn. 2009. Modeling no-take marine reserves in regulated fisheries: assessing the role of larval dispersal. Can. J. Fish. Aquat. Sci. 65: 2509–2523.

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004. Trajectories and correlates of community change in no-take marine reserves. Ecol. Appl.14: 1709–1723.

Moffitt, E. A. 2009. The design and implications of marine protected areas for mobile species: a theoretical approach. Ph.D. dissertation, University of California, Davis, CA, USA.

Moffitt, E. A., L. W. Botsford, D. M. Kaplan, and M. R. O'Farrell. 2009. Marine reserve networks for species that move within a home range. Ecol. Appl. 19: 1835–1847.

Mullin, M. M. 1994. Webs and scales: Physical and ecological processes in marine fish recruitment. Washington Sea Grant Program/University of Washington Press, Seattle and London.

Myers, R. A. 1998. When do environment-recruitment correlations work? Rev. Fish. Biol. Fish. 8: 285–305.

O'Farrell, M. R., and L. W. Botsford. 2005. Estimation of change in lifetime egg production from length frequency data. Can. J. Fish. Aquat. Sci. 62: 1626–1639.

Pelc, R. A., M. L. Baskett, T. Tanci, S. D. Gaines, and R. R. Warner. 2009. Quantifying larval export from South African marine reserves. Mar. Ecol. Prog. Ser. 394: 65–78.

Peterman, R. M., and J. R. Anderson. 1999. Decision analysis: a method for taking uncertainties into account in risk-based decision making. Hum. Ecol. Risk. Assess. Int. J. 5: 231–244.

Peterson, W. T., and F. B. Schwing. 2003. A new climate regime in northeast Pacific ecosystems. Geophys. Res. Lett. 30: 1896.

Punt, A., and S. Ralston. 2007. A management strategy evaluation of rebuilding revision rules for overfished rockfish stocks. Alaska Sea Grant College Program AK-SG-07-01: 329–351.

Punt, A. E., A. D. M. Smith, and G. Cui. 2002. Evalution of management tools for Australia's South East Fishery 1. modelling the South East Fishery taking account of technical interactions. Mar. Freshw. Res. 53: 615–629.

Ralston, S. 2002. West coast groundfish harvest policy. N. Amer. J. Fish. Manag. 22: 249-250.

Roberts, C. M., S. Andelman, G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, H. P. Possingham, M. Ruckelshaus, and R. R. Warner. 2003. Ecological criteria for evaluating candidate sites for marine reserves. Ecol. Appl. 13: S199–S214.

Rogers-Bennett, L., D. W. Rogers, and S. Schultz. 2007. Modeling growth and mortality of red abalone (*Haliotis rufescens*) in northern California. J. Shellfish Res. 26: 719–727.

Rogers-Bennett, L., and D.W. Rogers 2008. Modeling dispersal of cloning echinoderm larvae with a Gaussian distribution: Forever young? CalCOFI Reports 49: 232–240.

Rose, K. A., and J. H. Cowan, Jr. 2003. Data, models, and decisions in U.S. marine fisheries management: lessons for ecologists. Ann. Rev. Ecol. Syst. 34: 127–151.

Russ, G. R., A. J. Cheal, A. M. Dolman, M. J. Emslie, R. D. Evans, I. Miller, H. Sweatman, and D. H. Williamson. 2008. Rapid increase in fish numbers follows creation of world's largest marine reserve network. Curr. Biol. 18: R514–R515.

Shanks, A., G. C. Roegner, and J. Miller. In press. Predicting the future commercial catch of Dungeness crabs. Calif. Coop. Oceanic Fish. Invest. Rep.

Shepherd, J. G., and D. H. Cushing. 1990. Regulation in fish populations: myth or mirage? Phil. Trans. R. Soc. Lond. B. 330: 151–164.

Strathmann, R. R., T. P. Hughes, A. M. Kuris, K. C. Lindeman, S. G. Morgan, J. M. Pandolfi, and R. R. Warner. 2002. Evolution of local recruitment and its consequences for marine populations. Bull. Mar. Sci. 70 (Suppl): 377–396.

Underwood, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecol. Appl. 4: 3–15.

Vance, D. J., D. J. Staples, and J. D. Kerr, 1985. Factors affecting year-to-year variation in the catch of banana prawns *Penaeus merguiensis* in the Gulf of Carpentaria, Australia. J. Cons. Int. Explor. Mer 42: 83–97.

Walters, C. J. 1989. Value of short-term forecasts of recruitment variation for harvest management. Can. J. Fish. Aquat. Sci. 46: 1969–1976.

Walters, C. J. 1997. Challenges in adaptive management of riparian and coastal ecosystems. Cons. Ecol. 1: 1.

White, J. W. 2010. Adapting the steepness parameter from stock-recruit curves for use in spatially explicit models. Fish. Res. 102: 330–334.

White, J. W., L. W. Botsford, A. Hastings, and J.L. Largier. 2010a. Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal. Mar. Ecol. Prog. Ser. 398: 49-67.

White, J. W., L. W. Botsford, E. A. Moffitt, and D. T. Fischer. 2010b. Decision analysis for designing marine protected areas for multiple species with uncertain fishery status. Ecological Applications 20: 1523–1541.

Part III

SCIENTIFIC CONTRIBUTIONS

BIOECONOMIC ASSESSMENT OF THE RED SPINY LOBSTER FISHERY OF BAJA CALIFORNIA, MEXICO

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ABSTRACT

The red spiny lobster (*Panulirus interruptus*) is the most important fishery of northwestern Mexico, accounting for up to 2,000 t. The trap-based fishery occurs along most of the western coast of the Baja California peninsula. Fishing mortality results indicate that the stock has been overexploited for the last eight years, but is still a profitable activity. A bioeconomic assessment and simulation was made to provide the basis for a sustainable exploitation of the stock. The age structure was reconstructed by linking the biological, economic, and social variables. The maximum stock biomass of >1,600 t was recorded in 1999, followed by declining catch particularly after 2003. Therefore advice is required to ensure a sustainable fishery. Specific recommendations for a gradual decrease in fishing mortality and an increase in the minimum size are given. Their use would result in significant improvement in the volume of the catch and in profits.

INTRODUCTION

The red spiny lobster (*Panulirus interruptus*, Randall 1840) is distributed in waters off California and the western Baja California peninsula. Off the Baja California peninsula there is a well-developed fishery that yields > 80% of the catch of the Mexican Pacific spiny lobster, approaching up to 2,000 t in 2003, with a value > $26 million USD and providing jobs to about 1,160 fishers (fig. 1). The fishery is exploited along the coast of the Baja California peninsula, north of Bahía Magdalena. There are three other species of the spiny lobster off the west coast of Mexico south of Bahía Magdalena: the blue lobster (*P. inflatus*, Bouvier 1895), the green lobster (*P. gracilis*, Streets 1871), and the island spiny lobster (*P. penicillatus*, Olivier 1791). These are found in tropical waters of this coastline, and the catch volume is not significant as compared to that of the red spiny lobster. The fishery data in this paper is for *P. interruptus* only. Up to the present, the scientific research evaluating these stocks and identifying reference points for their sustainable exploitation has not been satisfactory.

Most spiny lobster harvested by the Baja California fishery are imported by Asian countries, mostly as live lobsters. Only about 5% is sold cooked and frozen to the USA and the European countries, with only a small portion sold raw and frozen to the Mexican market.

The increasing demand of new fishermen recruited to this activity and a growing demand by consumers has led to increased fishing intensity. For this reason, the red spiny lobster fishery off Baja California was evaluated. Earlier assessments of this resource have been based on local and sporadic attempts (Ayala et al. 1973; De la Rosa-Pacheco and Ramírez-Rodríguez 1996; Gluyas-Millán 1996; Vega et al. 1996; Vega et al. 2000; Arteaga-Rios et al. 2007), therefore an updated and more comprehensive evaluation was made by us. We identified the most useful bioeconomic-reference points for optimizing the fishery. The goals of the study were to evaluate the status of the red spiny lobster stock in Mexican waters, to evaluate the stock's potential production, to provide advice for a sustainable exploitation of the fishery, and to evaluate the fishing intensity that will maximize yields and profits over the long term.

METHODS

The assessment of the stock was made using catch data for the last fifteen years. The population parameter values were taken from published sources. Changes in abundance over time were determined using the catch data.

The red spiny lobster fishery along the Baja California peninsula is trap-based and is the only authorized means to exploit it. This may allow assessment of the stocks more accurately than for other fisheries where a variety of catch methods are in use. We found that the mean catch per fisher during a fishing season was 1,130 kg and they sell their landed whole lobster for $27.00 USD per kilo.

Trends in the fishing mortality (F) over time and the estimates of the total stock biomass were examined. The criteria for evaluation of fishing scenarios were based on the F and the age of first catch (tc) at the maximum-sustainable-yield level (F_{MSY}), an extreme reference point.

The population parameters plus the catch data were analyzed with the aid of a simulation model, imple-

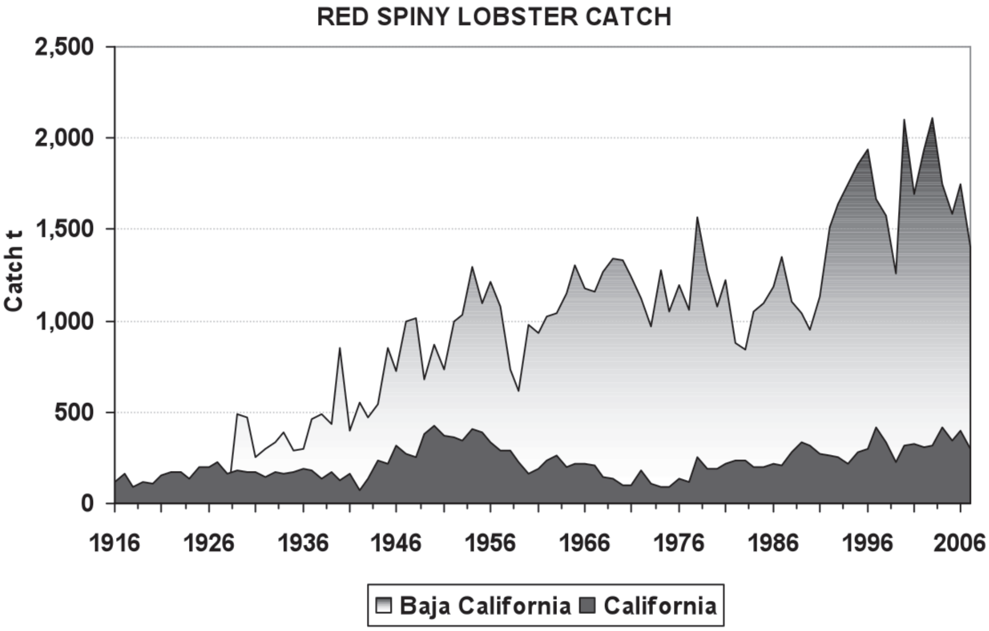

Figure 1. Red spiny lobster catch off California (1916 to 2007) and the Baja California peninsula (1929 to 2007), t.

mented in the semiautomated, age-structured simulation model FISMO (Chávez 2005). The age of first capture was 5 years and was maintained constant in the analysis of the catch records, though this value changes as required in the optimizing process and for designing exploitation policies. The age of first maturity has been estimated to be at about 65-mm carapace length.

Once the catch data and growth rate were known, estimates of the age composition of the catch were made. With these partial results the total mortality (Z_t) could be determined with the exponential decay model as

$$N_{a+1} = N_a \cdot e^{(-Z_t)} \qquad (1)$$

where N_{a+1} is the number of spiny lobsters of age a+1 and N_a is the number of spiny lobsters of age a in reconstructed age-groups. With the numbers per age known, the use of the von Bertalanffy growth equation allowed the determination of their corresponding lengths. These lengths were transformed into their respective weights by using the equation

$$W = 0.0404.L^3$$

where W = Total weight (g) and L = Total length (cm).

The time units are years. The age structures for each year were estimated assuming a constant, natural mortality. For setting the variables of the initial state, the abundance per age-class ($N_{a,y}$) was set using the age-specific abundance $N_a/\Sigma N_a$ obtained from equation (1). In subsequent years, the age structure was defined after the estimation of the number of one-year-old recruits. These values were used to calculate catch-at-age as proposed by Sparre and Venema (1992) and were integrated into the FISMO simulation model (Chávez 2005) as

$$Y_{a,y} = N_{a,y} \bullet W_{a,y} \; \frac{F_t}{(F_t + M)} \; (1 - e^{(-F_t - M)}) \qquad (2)$$

where $Y_{a,y}$ is the catch-at-age a of each year y, $N_{a,y}$ is the number of spiny lobsters at age a in year y, $W_{a,y}$ is the lobster weight equivalent to $N_{a,y}$, F_t is described, and M is the natural mortality. Given the established initial conditions, the values of $Y_{a,y}$ were adjusted by varying the initial number of recruits and linked to the equations described above until the condition of the following equation was fulfilled

$$\sum_{a}^{\lambda} Y_{a,y} = Y_{y(REC)}$$

where $Y_{y(REC)}$ is the yield recorded during the year y, a = 5 years, and $t_\lambda = 3/K$ or longevity, where K is the growth constant of the von Bertalanffy growth equation and $t_\lambda = 25$ years, which is found by assuming that a reasonable life expectancy (L_{max}) is when 95% of the population reaches 95% of $L\infty$, the asymptotic length. Thus by making $L_{max} = 0.95L\infty$ in the von Bertalanffy growth equation and finding the respective value of t the longevity was found. Use of the catch equation was made for each year in the time-series analyzed. For the estimation of the natural mortality (M), the criterion proposed by Jensen (1996, 1997) was adopted, where M = 1.5K = 0.1793 K is further described below. Estimations of the stock biomass and the exploitation rate

TABLE 1

Population parameter values used for the evaluation of the red spiny lobster fishery. To transform carapace length (CL) into total length (Lt), the equation Lt = (CL/0.0275) + 3.2 was used, giving $L\infty$ = 56 cm (Lt), which was the value used as an input in the model. The resulting W_∞ was obtained by using the length - weight equation, $W = 0.0404\ L^3$. To feed the model, five years was arbitrarily chosen as tc, the age of first catch*.

Parameter	Value	Units-Model	Source
K	0.1195	Bertalanffy	Vega et al. (2000)
$L\infty$ (mm, CL)	153	mm, tails-Bertalanffy	Vega et al. (2000)
$W\infty$ (g)	7,135	live weight-Bertalanffy	This paper
to	–0.210	Years-Bertalanffy	Vega et al. (2000)
a	0.0404	Length - weight	This paper
b	3.0	Length - weight	This paper
tc*	7 & 4	♀ and ♂ respectively	Years, Vega (2003)
Maturity age	5	Years	This paper
Longevity	25	Years	As 3/K, this paper
a'	0.25	Beverton & Holt	Estimated after age structure
b'	0.6	Beverton & Holt	Estimated after age structure
M	0.1793	Instantaneous rate	Jensen (1996, 1997)
Max. E (E_{max})	0.4556	$F_{MSY}/(M+F_{MSY})$	Exploitation rate at MSY, this paper
Phi'	2.6	Log K + 2Log L	Growth performance, this paper

E = [F/(M+F)] were made for each age-class in every fishing year analyzed by the model. These values were compared to the E value at the F_{MSY} level. A special case is when E is at the F_{MSY} level corresponding to the maximum exploitation rate that a fishery should attain before the stock is overexploited. A diagnosis of which years of the series the stock was under- or overexploited was then made, providing an easy way to recommend either a further increase or decrease of F of the fishery.

The annual cohort abundance ($N_{a,y}$) coming from ages older than age-at-maturity (tm = 5 years) were used to estimate the annual abundance of adults (S_y) over the years, whereas the abundance of the one-year-old group was used as the number of recruits (R_y). The stock-recruitment relationship was evaluated by using a slightly modified version of the Beverton and Holt (1957) model in the form

$$R_{y+1} = \frac{a'S_oS_y}{S_y + b'S_o} \qquad (3)$$

where R_{y+1} is the number of one-year-old recruits in year y+1, S_y is the number of adults in year y, S_o is the maximum number of adults in the population, and a' and b' are parameters modified from the original model where a' is the maximum number of recruits and b' is the initial slope of the recruitment line, which was constant through the simulation. The values of the parameters used as input are shown in Table 1.

The simulation was used to describe the main ecological processes underlying the stock dynamics. It allowed simulating exploitation scenarios under different combinations of fishing intensities and the age-at-first catch to maximize the biomass, the profits, and the social benefits. For this purpose, analytical procedures adopting the concepts and views of Chávez (1996, 2005) and Grafton et al. (2007) were used. The catch was displayed by the model, where the stock biomass and the fishing mortality for each year of the series were estimated.

The approach to the socioeconomics of the fishery was made through the explicit consideration of the costs of fishing per boat per fishing day, the number of boats, the number of traps, the number of fishermen per boat, and the number of fishing days during the fishing season. All of these variables impose the costs of the activity. The value is the price at the dock of the spiny lobster landed; the difference between the costs and the value is profit and the value (the benefit) divided by the cost is the B/C ratio. In the simulation, the costs of fishing and catch value were assumed constant over time.

The information from the 2008 fishing season allowed us to reconstruct the economic trend of this fishery for the last fifteen years with the aid of the simulation model, using the estimates of fishing mortality over time as a reference and its correspondence to the economic variables.

The changes in the population abundance using the number of survivors in each cohort were estimated. The initial condition is set by assignment of a seed value for F. The graphic display of the potential yield allowed us to find that for the current conditions of this fishery it was $F_{MSY} = 0.15$, allowing an estimation of an initial recruitment number and then estimations of abundance for each cohort for each year.

To evaluate the maximum number of traps, the Schaefer model (Sparre and Venema 1992), also known as the surplus-yield model, was used on this data series. The high variability of the data is characterized by two peaks of the catch over time, as shown in Figure 1, so we used the data series of 1940 to 2008 for this part of

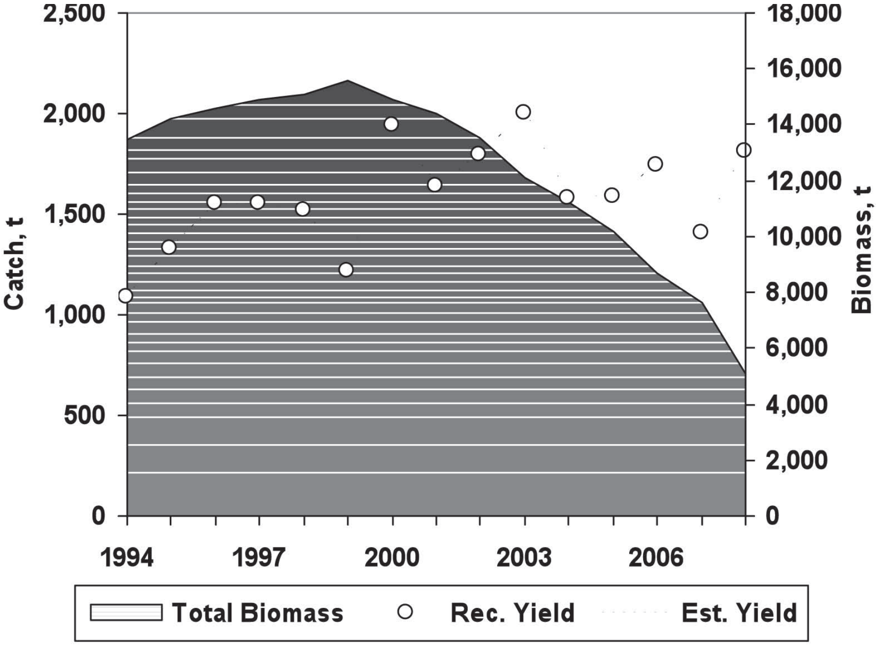

Figure 2. Stock biomass (right) and catch (left) in t by the red spiny lobster fishery off the Baja California peninsula.

the analysis. This model is based on the principle that the population-growth rate is described by a sigmoid curve, whose rate of change can be described by a quadratic equation ($Y = af + bf^2$) where the number of traps is used here as the independent variable and the catch is the dependent variable. The level where the rate of change is zero corresponds to the point where the fishery attains its maximum, equivalent to the MSY. The influence of climate seems to be great and makes the data appear noisy, but the analysis of this effect would be beyond the purpose of this paper.

Model Validation

The model was developed with 15 years of catch data. In the validation process, the 15th year was left out of the direct evaluation and its value was simulated as if it were unknown. Then the model was fitted to the whole series of 15 years. The difference between the recorded and simulated values on this 15th year provided a way to evaluate the uncertainty in the assessment made for 2008, the last year of the catch records analyzed.

Management Options

For comparison of some of the output variables, the condition for the 2008 fishing season was used as the reference. The management options were assessed for the year t + 1, (= 2009), which was used as the target of the fishery. The other three management options are that F_{MSY} is the combination of F and tc producing the highest catch, F_{MEY} is the combination of F and tc producing the highest profits, and F_{Traps} is the condition of the fishery if the number of traps in use were the number suggested by the use of the surplus-yield model.

RESULTS

Some Ecological Processes

We needed to define a parent-recruit relationship to link cohorts over time in the reconstruction of the age structure during the historical catch records and in the simulation process of the fishery. The number of recruits per adult over the fifteen years of data analyzed is 0.48. We saw an interesting variation of this ratio, because up to the year 2000 when the stock biomass was the highest, the value was 0.38, and after 2000, when the biomass was declining, this ratio increased to 0.61. These values could be interpreted as a density-dependence response of the stock biomass with an increase of the recruitment rate when the number of adults was low, and vice versa, but the data-series is not long enough to confirm this as a real pattern.

Condition of the Fishery

Stock biomass. The results show that the stock biomass had an increasing trend until 1999, then a declining trend after 2003. We believe the increasing trend is an artifact of the use of the catch equation, rather than a real one. We interpret the decline as caused by the high exploitation intensity, for if the stock were much larger, the fishing mortality would be negligible. The maximum

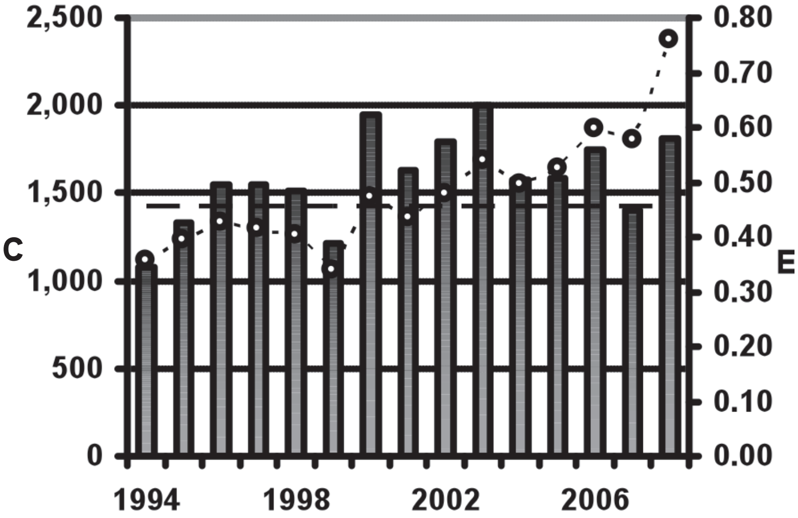

Figure 3. The exploitation rate (E) of the red lobster stock, with the E at the MSY level (0.46, horizontal line). For comparison, the catch (C) is also indicated with bars.

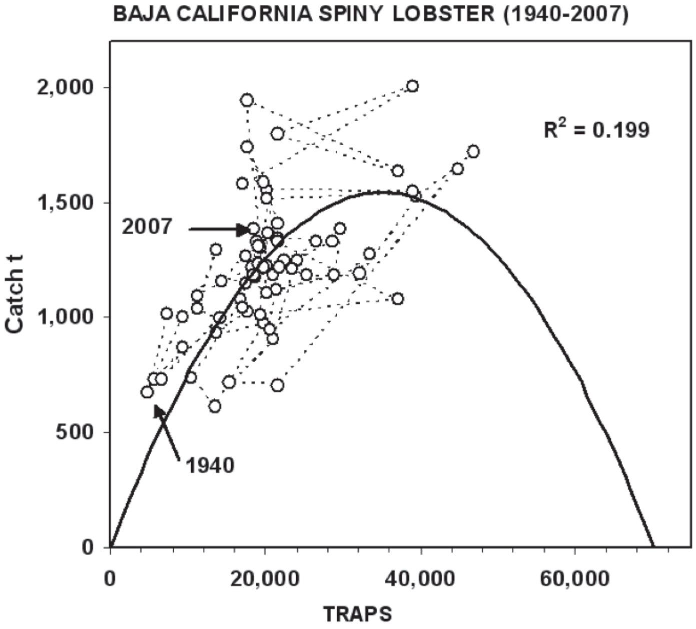

Figure 4. Catch as a function of the number of traps for 1940 to 2007. The parabola fitted to data describes the trend. The upper-catch value of the trend line indicates the maximum catch (1,540 t). According to this, the maximum number of traps/season (35,100, equivalent to 572 fishing boats carrying 38 traps for 85 days per season) is the maximum effort that should be used to avoid overexploiting the stock.

stock biomass of 16,800 t was measured in 1999 (fig. 2). As a consequence, the catch had two maximum values of about 2,000 t, one in 2000 and the other in 2003, declining after that until the last three years when the mean catch was 1,800 t. The difference between direct estimations of catch and those obtained by simulation was between –11% and +22%, with a mean value or mean error of 5%.

The intensity of exploitation indicates that the fishery has been overexploited consistently since 1999 and in particular since 2002, when the values of F increased, about which we need to be concerned. In consequence, the exploitation rate E lay between 0.36 in 1994 and 0.76 in 2008, with E = 0.46 at the MSY level, allowing us to conclude that the stock has been overexploited for the last seven years (fig. 3). A drastic reduction of fishing effort is suggested to keep the fishery healthy.

Further evidence of the overexploitation was examined using the increasing number of traps. The number of traps has increased from 6,000 in 1940 to 21,600 in

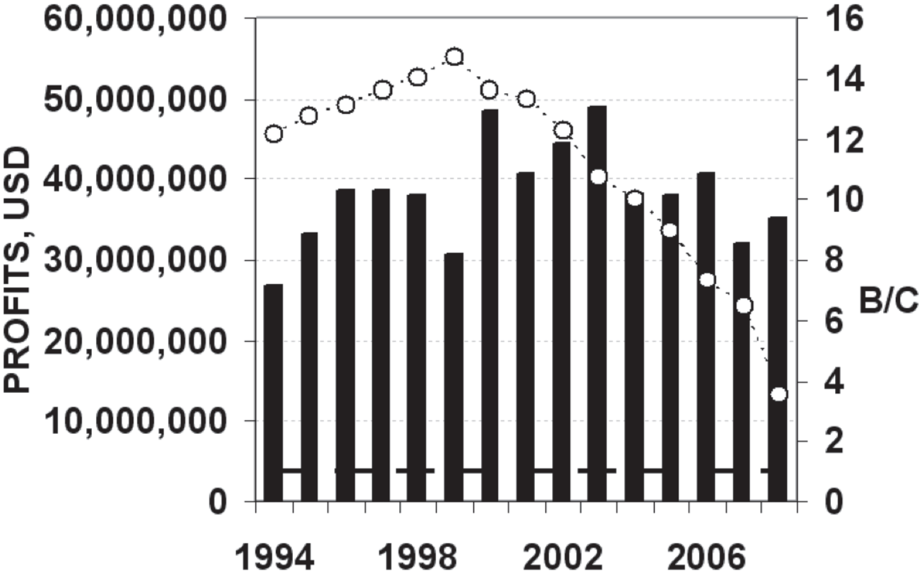

Figure 5. Reconstruction of total profits (bars and left scale) and the benefit/cost ratio over the last fifteen years of the spiny lobster fishery off the Baja California peninsula (dots, right scale), both in Y axis. The horizontal broken line is the B/C at the economic-equilibrium level, when B = C, as a reference to diagnose the economic condition of the fishery.

2007 with peaks of 37,000 and 39,000 in 1994 and 1997. Over 20,000 traps have been in frequent use since 1954 and in particular after 1963.

To determine the maximum number of traps to be used, the parabola was fitted to data as shown in Figure 4. As a result of this, we found that the trends are not as clear as expected. The data do not indicate overexploitation, as the age structure does, which is explained below, though the data of the last group of years suggests the need to enforce a limit for the maximum number of traps.

From the parabola fitted to the data, the quadratic equation ($Y = af + bf^2$) indicates that the maximum number of traps ($fmax = (-0.5 \star a/b)$) is 35,100, producing a maximum yield ($MSY = (-.25 \star (a^2/b))$) of 1,540 t. The trend of the last group of years of the series is interpreted as evidence of overfishing (see Sparre and Venema 1992 for further explanation). From this, the reduction of the fishing effort to maintain the condition of relative stability of the fishery is advised. The use of this evaluation of the maximum effort evidently is not suitable, because this underestimates the real effort and overestimates the exploitable biomass. The relative constancy in the number of traps and the lack of a decline in the catch per unit of effort over time also is evidence of excess fishing capacity, explaining why the use of the Schaefer model does not provide the expected results.

Bioeconomic analysis. In 2008, the fishery provided direct employment to 1,164 fishers on 572 boats, each boat working 85 days per fishing season. By examining raw data, we found that the cost of each fishing-day per boat is $112 USD and in 2008 total fishing effort was 122,572 days. The catch obtained was 1,810 t with a value of $48,951,000, producing profits of $35,226,168 with a benefit/cost ratio of 3.6, which is more than three times the cost of fishing operations. The cost of fishing is a variable depending on the stock size and fishing effort. This way, estimates of total profits and the benefit/cost (B/C) ratio were obtained as shown in Figure 5.

The trend shows that the highest profits obtained in 2000 and 2003 were about $50 million USD, but these years are only a short period of maximum profits, declining afterwards to $35.2 million in 2008. The B/C ratio shows a trend similar to the economic efficiency, with a maximum value of B/C = 14.7, recorded in 2000, and evenly declining afterwards, approaching the equilibrium level and a pending socioeconomic crisis, with a B/C = 3.57 in 2008, which is still very profitable. By projecting this trend on Figure 5 it is evident that it will attain the limit in only three or four more years.

To examine the stock response and its socioeconomic condition as a function of the fishing intensity (F), the simulation describes a series of 5 curves; the yield, the profits or economic benefit, the number of boats, the number of fishermen and the B/C ratio (fig. 6). In four of them (yield, profits, boats, and fishermen) the maximum value of F at the MSY is F = 0.15. The B/C ratio then attains its maximum value at the lowest F.

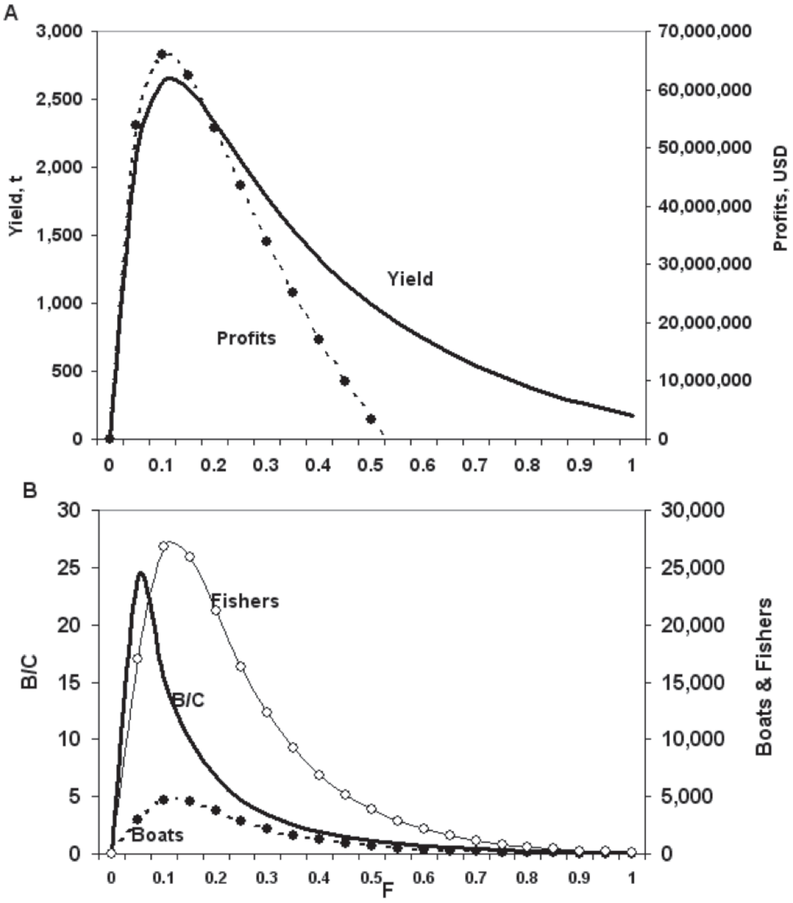

Figure 6. Stock response of the spiny lobster fishery off the Baja California peninsula, showing the trend of the potential yield and potential profits (A) and the number of fishermen, boats, and the B/C ratio (B) as a result of the intensity of fishing mortality. Maximum profits are attained at a lower level of F than the one required for the maximum yield. The number of fishermen and boats reach their maximum at the same value of F as the yield. The maximum B/C ratio is found at the lowest value of F and declines monotonically with a higher fishing intensity.

DISCUSSION

Many papers have documented overexploitation, overcapitalization, and threats to food security (Beddington and Kirkwood 2005). The dynamics of the spiny lobster stocks are strongly influenced by the overexploitation and overfishing as a rather general problem in the fisheries world-wide and though the solution seems straightforward and the benefits are clear, action is often taken after the stock had been driven to low levels (Rosenberg 2003). Unfortunately, most stock assessments use no quantitative information derived from previous experience on other fish stocks (Hilborn and Liermann 1998).

The intensity of recruitment depends to a great extent on the stock size, as part of an ecological mechanism related to density dependence and carrying capacity. By comparing these trends with the historical values of F, we found that the fishery has been overexploited since 2003, with the worst year 2008 when there was a fishing effort nearly two times greater than the one required for the MSY, dramatically leading the fishery to an economic crisis within a few more years. A well-known cause of overexploitation is the fishermen's opposition to a lower catch caused by stock rebuilding, requiring the finding of appropriate incentives to provide security and benefits to them during that process (Grafton et al. 2007).

Assessment

The model was fitted to data from the last fifteen years, from 1994 to 2008, allowing a direct estimation of F for each year. To evaluate the magnitude of uncertainty, the model was fitted again, but this time from data for 1994 until 2007. An estimation of the catch for 2008 was made by simulation and using the same value of F obtained with the previous fit. From this a new estimate of the catch was obtained. Coincidently with this approach, Beddington and Kirkwood (2010) stated that the simple relationships that can be used to estimate potential yield and the maximum sustainable fishing-mortality rate give information about the growth curve and the size at which fishing starts. Current fishery management is working well to achieve the legislated objec-

TABLE 2

Management scenarios for the red spiny lobster fishery off Baja California. The condition for the 2008 fishing season is used as reference. The management options are F_{MSY} = F at the MSY level at a tc = 11 years; F_{MEY} = F at the MEY level at a tc = 11 years; F_{Traps} = the condition of the fishery if the number of traps is 35,100 as suggested in Fig. 4, equivalent to F = 0.48. The days/boat/year are 85 in all cases. Costs and value are in USD.

Indicators	Current 2008	F_{MSY}	F_{MEY}	F_{Traps}
F (/y)	0.283	0.23	0.18	0.476
Age of 1st catch (tc)	5	11	11	5
Yield, t	1,813	3,638	3,562	1,066
Fishing days /y	122,572	3,638	75,300	199,005
Boats	572	449	351	109
Direct jobs	1,164	918	723	929
Catch Value	48,951,000	98,228,900	96,169,000	28,776,300
Costs	13,724,800	10,773,800	8,431,600	22,283,300
B/C	3.6	9.1	11.4	1.9
Profits	35,226,168	87,455,083	87,737,341	6,493,073
Profits/boat	61,580	194,770	249,680	6,990
Traps	21,620	16,970	13,280	35,100

tive of the MSY in some countries but is failing in others (Hilborn 2007).

The exploitation rate E was used as a criterion for the diagnosis of each fishery, where F_{MSY} is the F at the level producing the maximum yield at the apex of the production curve, or the maximum sustainable yield, as it is currently known. This is a useful extreme reference point for the diagnosis of a fishery, because it allows a quick and easy interpretation of the condition of any fishery. It varies under different ages at first catch, as we explained above. The maximum or limit value of E found was $E_{max} = 0.46$ and it was used as a reference for the diagnosis of the fishery. This criterion was used for the fifteen years of data.

Uncertainty of Assessment

Many fisheries at present are often characterized by an excessive investment in the fishing infrastructure, the profits are close to the economic-equilibrium limit, and new fishermen still have strong expectations of taking part in this activity. Our results show there is an excess number of boats and traps. The catch per unit of effort is not a good indicator of stock density and the large variance in the catch suggests that recruitment is variable, increasing the uncertainty of the estimates. The results of the use of the Schaefer model are evidence of this statement.

Some of the model outputs should be taken as trends rather than hard results. However, the analysis provides a consistent criterion, showing that without any doubt, the fishery is coming to a socioeconomic crisis if the access is not controlled.

Sustainability of the Fishery

Fisheries have rarely been 'sustainable' (Pauly et al. 2002). Ecological extinction caused by overfishing precedes all the other pervasive human disturbances to the coastal ecosystems, but the literature also demonstrates achievable goals for restoration and management (Jackson et al. 2001). There are substantial probabilities of the wrong identification of the condition of the stock being exploited (Punt 2000). Unsuccessful systems have generally involved open access, attempts at top-down control with a poor ability to monitor and implement regulations, or reliance on consensus (Hilborn et al. 2005a). New definitions of sustainability will attempt to incorporate the economic and social aspects of the fisheries (Quinn and Collie 2005), and our work is an example of such an approach. In this fishery, the F_{MSY} has been used as a reference point to evaluate the biological, economic, and social consequences of using the current fishing effort or other possible options, as shown in Table 2, where three different scenarios are compared to the current condition. The driving variables are F and tc and in each case successive changes in tc are tested until either the catch or the profits are chosen as the target to maximize, and reaches its maximum value. The values of all the other variables depend on F and tc so they should be considered as the consequence of any strategy chosen. The maximum social benefit is derived from the number of boats fishing, so their maximum number is multiplied by the number of fishermen per boat. The economic-equilibrium level indicates the value of F is at the limit of fishing intensity beyond which it becomes unprofitable. This is one of the reasons why it is unlikely to force a population to extinction as a sole consequence of the strong fishing pressure. Rights-based management is probably not appropriate for all fisheries (Hilborn et al. 2005b). With recent data on the catch and effort we were able to obtain the corresponding information on costs and profits of the fishing activity such that it allowed us to link this information to the simulation model and to evaluate the optimum bioeconomic-harvesting options.

Here, the so-called stock effect is a nonlinear function of yield and is difficult to estimate with a high level of precision (Hannesson 2007).

The maximum economic yield (MEY) was found by following the costs and benefits of the fishing activity and by depending on the stock biomass and the fishing effort. It usually is where $F_{MEY} \leq F_{MSY}$. In a well-managed fishery it is more convenient to adopt this as the target rather than the F_{MSY} because it implies a lower risk of overexploitation. The tc value producing MSY and MEY may look unreal in this fishery, because the model indicates that tc should be 11 years. Whatever may be the reason for this, it is impractical to wait until the spiny lobster reaches its 11th year to start exploiting this species. The maximum yield obtained currently with tc = 5 years is 3,640 t with a profit of $87 million USD. The use of this fishing strategy implies a significant decrease of 19% in the fishing effort compared to the current situation (tab. 2). Additionally, appropriate control regulations are required to control exploitation to maintain the lobster fishery as sustainable over time and space. In contrast, the option of using the MEY seems to be quite appealing because it provides a profitable economic activity ensuring the sustainability of the exploitation. It has the relative inconvenience that can be attained only with a tc = 11 years, which makes its use impractical. The conversion of scientific advice into policy, through a participatory and transparent process, is at the core of achieving fishery sustainability (Mora et al. 2009) and it is hoped that the results presented here can be used for a sustainable exploitation of the spiny lobster fishery off the Baja California peninsula.

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LITERATURE CITED

Arteaga-Ríos, L. D., J. Carrillo-Laguna, J. Belmar-Pérez, and S. A. Guzmán Del Próo. 2007. Post-larval settlement of California spiny lobster *Panulirus interruptus* in Bahía Tortugas, Baja California and its relationship to the commercial catch. Fisheries Research, 88: 51–55.

Ayala, M., J., B. Pineda, and S. A. Guzmán Del Próo. 1973. Explotación de la langosta roja en el estado de Baja California durante la temporada 1971–1972. Análisis de la composición por tallas de la captura comercial. Serie Informativa INP/SI.

Beddington, J., and G. Kirkwood. 2005. Introduction: fisheries, past, present and future. Phil. Trans. R. Soc. B 360: 3–4.

Beddington, J. R., and G. P. Kirkwood. 2010. The estimation of potential yield and stock status using life history parameters. Phil. Trans. R. Soc. B 2005(360): 163–170.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Investigations, London, Series 2, 19, 533 p.

Chávez, E. A. 1996. Simulating fisheries for the assessment of optimum harvesting strategies. Naga, International Center for Living Aquatic Resource Management 2:33–35.

Chávez, E. A. 2005. FISMO: A generalized fisheries simulation model. pp: 659–681. *In* G. H. Kruse, V. F. Gallucci, D. E. Hay, R. I. Perry, R. M. Peterman, T. C. Shirley, P. D. Spencer, B. Wilson, and D. Woodby (eds.), Fisheries assessment and management in data-limited situations. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Chávez, E. A. 2008. Socio-economic assessment for the management of the Caribbean spiny lobster. Proc. 60th Gulf and Caribbean Fisheries Institute: 193–196.

Chávez, E. A. 2009. Potential production of the Caribbean spiny lobster (Decapoda, Palinura) fisheries. Crustaceana 82(11):1393–1412.

De La Rosa-Pacheco, R., and M. Ramírez-Rodríguez. 1996. Ventanas de escape en trampas para la captura de la langosta roja, *Panulirus interruptus*, en Baja California Sur, México. Ciencias Marinas, 22(2):235–243.

Gluyas-Millán, M. G. 1996. Temporada 1989–1990 de pesca de langosta en la costa occidental de Baja California Sur, México. Ciencia pesquera, 12:1–4.

Grafton, R. Q., T. Kompas, and R. W. Hilborn. 2007. Economics of overexploitation revisited. Science, 317(5856):1601.

Hannesson, R. 2007. A Note on the "stock effect." Marine Resource Economics, 22: 69–75.

Hilborn, R. 2007. Reinterpreting the state of fisheries and their management. Ecosystems 10:1362–1369.

Hilborn, R., and M. Liermann. 1998. Standing on the shoulders of giants: learning from experience in fisheries. Reviews in Fish Biology and Fisheries 8:273–283.

Hilborn, R., J. M. Orensanz, and A. M. Parma. 2005a. Institutions, incentives and the future of fisheries. Phil. Trans. R. Soc. B 360:47–57.

Hilborn, R., J. K. Parrish, and K. Litle. 2005b. Fishing rights or fishing wrongs? Reviews in Fish Biology and Fisheries 15:191–199.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–638.

Jensen, A. L. 1996. Beverton and Holt life history invariants result from optimal trade off of reproduction and survival. Canadian Journal Fisheries and Aquatic Science, 53:820–822.

Jensen, A. L. 1997. Origin of the relation between K and Linf and synthesis of relations among life history parameters. Canadian Journal of Fisheries and Aquatic Sciences, 54:987–989.

Mora, C., R. A. Myers, M. Coll, S. Libralato, T. J. Pitcher, R. U. Sumaila, D. Zeller, R. Watson, K.J. Gaston, and B. Worm. 2009. Management effectiveness of the world's marine fisheries. PLoS Biol 7(6): e1000131.

Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. Nature (418):689–695.

Punt, A. 2000. Extinction of marine renewable resources: a demographic analysis. Population Ecology 42:19–27.

Quinn, T. J. Ii, and J. S. Collie. 2005. Sustainability in single-species population models. Phil. Trans. R. Soc. B 360:147–162.

Rosenberg, A. 2003. Managing to the margins: the overexploitation of fisheries. Front. Ecol. Environ. 1(2):102–106.

Sparre, P., and S. C. Venema. 1992. Introduction to tropical fish stock assessment. Part 1 Manual FAO Fisheries Technical paper, 306 (1), 376 p.

Vega, V. A. 2003. Reproductive strategies of the spiny lobster *Panulirus interruptus* related to the marine environmental variability off central Baja California, Mexico: management implications. *In* O. Tully, J. Freire, and J. Addison (eds.), Life Histories, Assessment and Management of Crustacean Fisheries Fisheries Research, 65: 123–135.

Vega, V. A., C. G. Espinoza, and R. C. Gomez-Rojo. 1996. Pesquería de la langosta (Panulirus spp.). *In* M. Casas Valdés and G. Ponce Díaz (eds.), Estudio del Potencial Pesquero y Acuícola de Baja California Sur, México. FAO/SEMARNAP/Gobierno de Baja California Sur Instituto Nacional de la Pesca, UABCS, CIBNOR, CICIMAR, CETMAR. 1: 227–262.

Vega, V. A., C. G. Espinoza, C. Gómez-Rojo, and P. Sierra-Rodríguez. 2000. Pesquería de langosta de Baja California. *In* P. Fuentes, and A. Díaz de León (eds.), "Sustentabilidad y Pesca Responsable en México: Evaluación y manejo 1997–1998" Instituto Nacional de la Pesca. SEMARNAP. México. 265–329.

PRELIMINARY STUDY ON THE USE OF POLISHED OTOLITHS IN THE AGE DETERMINATION OF PACIFIC SARDINE (*SARDINOPS SAGAX*) IN BRITISH COLUMBIA WATERS

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ABSTRACT

Accurate age estimates are fundamental to understanding stock dynamics of fish. This study compares two methods for estimating the age of Pacific sardine (*Sardinops sagax*) using the otolith surface and polished otolith methods. In addition, first and second annuli could be better identified using mean annulus measurements. Estimated ages ranged from 2 to 9 years using the otolith surface method and from 2 to 10 years using the polished otolith method. Individual fish ages estimated using the polished otolith method were generally 1 to 3 years older than corresponding otolith surface ages. Average percent error was lower (3.3) for the polished otolith method than for the otolith surface method (5.3). Accurate ages are essential for determining growth trajectories, age compositions and maturation schedules. Polishing the otolith surface enhanced the first two annuli, and greatly enhanced annuli near the edge in fish 5 years and older.

INTRODUCTION

The Pacific sardine (*Sardinops sagax*) supported the largest fishery in British Columbia from the 1920s to the mid-1940s. Catches during this period averaged 40,000t annually, then collapsed in 1947 as sardines disappeared from the British Columbia coast. The collapse of sardines off the west coast of North America was historically cited as an example of overfishing (Hilborn and Walters 1992) rather than a result of distributional change, and sardines were not expected to return to Canadian waters (Murphy 1966; MacCall 1979). Sardines first reappeared in British Columbia waters in 1992 in commercial and research catches of Pacific hake (*Merluccius productus*) (Hargreaves et al. 1994), and an experimental scientific fishery was opened in 1995. Research surveys targeting sardines were first conducted in 1997, capturing the fish in large numbers in surface waters. The abundance of sardines in British Columbia has continued to increase and has averaged 244kt since 2006 (Schweigert et al. 2010). This recent reappearance of sardines off British Columbia has been linked to changes in climate/ocean conditions (McFarlane et al. 2000; McFarlane and Beamish 2001).

Accurate age information is fundamental to stock assessment and management. Historically, the methods of estimating the age of Pacific sardine have changed from length-frequency analysis to annuli counts from either scales or otoliths (Butler et al. 1996). There is some evidence for the annual periodicity of otolith age increments for sardine captured in California waters. Otoliths were used to validate daily growth in juvenile sardines (Butler 1987), and Barnes and Foreman (1994) documented the periodicity of annuli in sardines up to age 3 using otolith surface readings. Yaremko (1996) postulated that because sardines are a relatively short-lived species, examination of the external surface of the otolith is a satisfactory technique for determining annual growth increments. However, she went on to point out that as the fish ages and otoliths grow, some deposition occurs across the entire otolith surface, and otolith thickness increases.

Additionally, grooves and spiny protuberances on the ventral interior surface of the otolith become more pronounced. This can lead to difficulty in identifying annuli (particularly in older fish). Without using additional characteristics to help identify annuli, Butler et al. (1996) proposed two potential sources of aging error: 1) variable periodicity for major growth increments, and 2) indistinct or ambiguous appearance of major growth increments. Butler et al. (1996) suggested these difficulties in interpreting otolith appearance were the greater source of error.

Larger (and presumably older) sardines migrate north into British Columbia waters during the summer feeding season (Beamish et al. 1999; McFarlane and Beamish 2001). No studies have examined the reliability of the otolith surface method for these larger fish in northern waters. Difficulties with identifying annuli in older fish have been a reoccurring problem in our studies. Given the importance of accurate ages for determining growth trajectories, age compositions and maturation schedules, we initiated a study to examine the reliability of the otolith surface method of age determination for sardines captured in British Columbia waters. This paper presents preliminary results of this study.

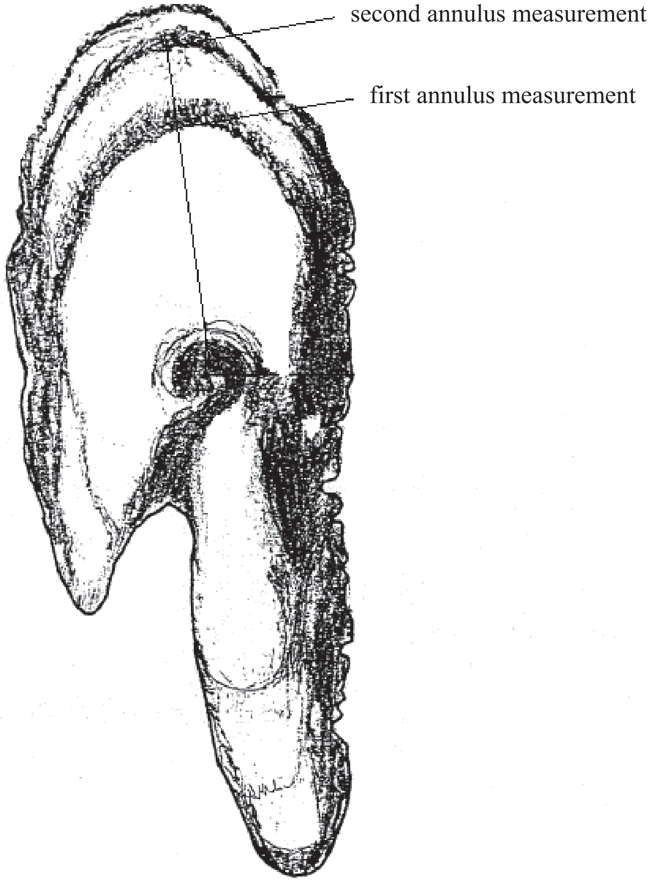

Figure 1. Schematic representation of the otolith surface for measurements of first and second annuli. Measurements are made from the centre of the focus to the interface between the translucent and opaque zone. (Figure modified from Yaremko, 1996).

METHODS

Sample Collection

Surface-trawl surveys have been conducted annually (with the exception of 2007) off the west coast of Vancouver Island, Canada, to determine the abundance, distribution and biology of sardines. In all surveys a model 250/350 14 mid-water rope trawl (Cantrawl Pacific Ltd, Richmond, British Columbia) was used. Fork length (mm) and sex were recorded for all fish sampled. Sardine otoliths were collected from randomly selected samples of 50–75 fish from randomly selected sets during each survey. Samples were collected throughout the entire range of the survey. For this study otoliths were selected from fish from 7 sets. These otoliths were collected from fish which covered a range in size. In addition, samples of small fish were selected for 1st and 2nd annuli measurements from sets conducted from 1999 to 2005.

Otolith Processing and Annulus Counts

Otoliths were extracted from sardines during onboard sampling, or were extracted in the laboratory from sardines that were frozen at sea, and processed at the Pacific Biological Station, Nanaimo, British Columbia. After otoliths were extracted, they were rinsed in water to remove tissue and stored dry for subsequent aging.

For surface aging, otoliths were placed under a film of water in a shallow container and observed under a dissecting microscope on 25X and 50X power with a 10X eye piece, using reflected light. Against a dark background, opaque zones appeared light, translucent zones appeared dark. Annuli were defined as the area consisting of one opaque zone (summer growth) and one translucent zone (winter growth).

For polishing, each otolith was mounted sulcus side down on a microscope slide using a thermal setting resin (Crystalbond™). Using fine sandpaper (ranging from 600 to 8000 grit), the otoliths were wet sanded to remove surface overburden and enhance underlying annuli (presumably on the outer edge). Polished otoliths were then aged as described above.

In larger (and presumably older) fish, it was sometimes difficult to identify the annuli (from checks) that would correspond to the first year or two of life. In these instances, the mean distance from the center of the focus to the interface between the translucent and opaque zone for the 1st and 2nd annuli measurement from young sardines in which these rings were clear were used to help identify the annuli.

Criteria for Annulus Determination

1. An annulus is defined as the interface between an inner translucent growth increment and a distal opaque growth increment (Collins and Spratt, 1969).
2. The translucent ring must be continuous along the entire structure. If the translucent ring merges with another or fails to go around the entire otolith, it is considered a false annulus, also called a check (Collins and Spratt 1969).
3. A surface-relief view of the otolith reveals a ridge for opaque depositions.
4. The outermost translucent ring is not counted as an annulus unless an opaque zone can be seen distally from it (Yaremko 1996).
5. Some parts of the otolith may have stronger formations than other areas. Age interpretations were based upon the examination of all parts of the otolith. Often the best ridging was observed on the antirostrum part of the otolith.
6. A January 1st birth date was used to avoid straddling the summer growth season.

Data Analysis

Cailliet and Goldman (2004) suggested that precision within a given study should be evaluated using an average percent error index. Both readings conducted

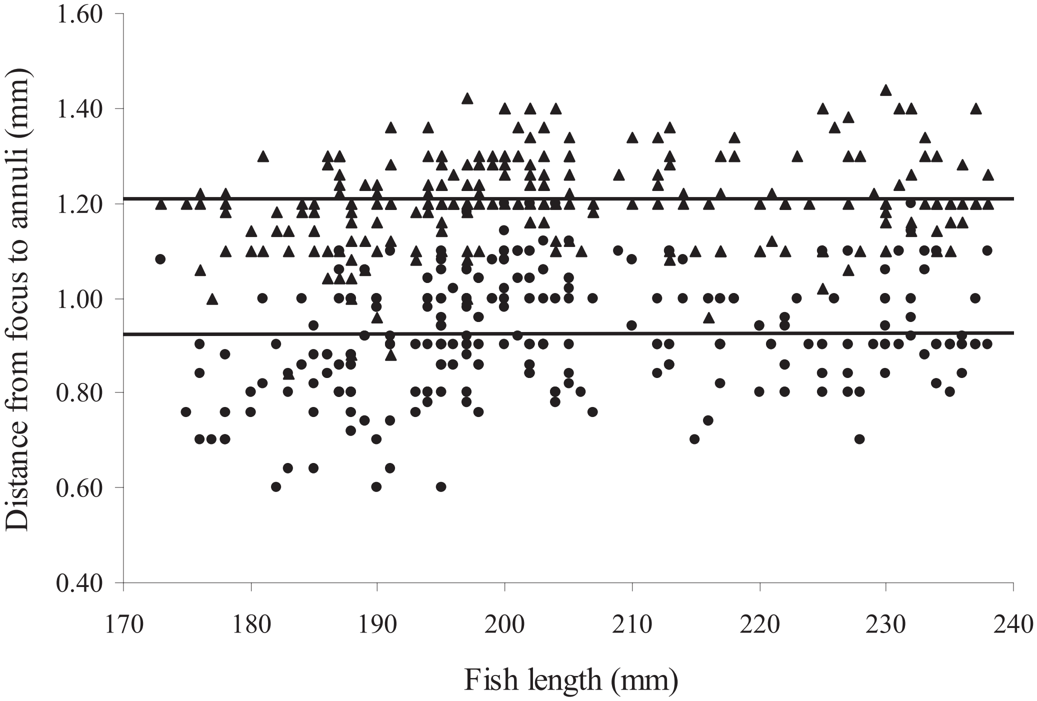

Figure 2. Scatterplot of distances (mm) from the focus to the first annulus (circles) and second annulus (triangles) for Pacific sardine.

in this study were done by a single reader so the precision between readings was evaluated using the average percent error index of Beamish and Fournier (1981). A student's t-test was used to evaluate the differences in the frequency of assigned ages between the otolith surface and polished otolith surface methods.

RESULTS

In this study, otoliths from 173 Pacific sardines were examined to compare the otolith surface and polished otolith methods for age determination. These fish were collected from research survey sets off the south west coast of Vancouver Island in 2003 (91 fish) and 2008 (82 fish), and ranged in length from 173 mm to 286 mm. In addition 252 small fish were sampled and the position of the 1st and 2nd annuli measured.

An annulus was defined as the interface between an inner translucent growth increment and the successive outer growth increment (Fitch 1951; Yarmenko 1996). Although numerous checks were present, using the criteria presented above, the first and second annuli were usually easily identified in smaller, younger fish. In older fish, as deposition occurs across the entire otolith surface, and otolith thickness increases, identification of annuli near the focus became increasingly problematic as it may be more difficult to distinguish checks. In addition, annuli near the edge of otoliths from older fish are close together, and may be faint due to increased deposition on the exterior surface of the entire otolith, as well as increased deposition on the ventral interior surface near the edges. Polishing the exterior surface of the otolith removed the surface deposition over the entire otolith surface and annuli (particularly near the edge) became clearer and easier to identify.

As it was sometimes difficult to identify the 1st and 2nd annuli we used the measurement criterion of Chilton and Beamish (1982) to locate the annuli (fig. 1). The mean first annulus diameter was 0.92 mm +/- 0.12 mm and the mean second annulus diameter was 1.21 mm +/- 0.10 (fig. 2). There was little overlap between the measured diameter and the two measures were significantly different (t-test; $p<0.05$).

For example, a 226 mm male sardine (fig. 3) was aged 4+ using the otolith surface method, and 6+ using the polished otolith method. In this case, the 1st annulus was not identified correctly, as it did not meet all the criteria used by the reader. In addition, the 4th annulus was missed and initially called a check. Once the otolith was polished the two annuli could be identified and the 1st annulus confirmed using annulus measurements.

A 242 mm, male sardine aged 5+ using the otolith surface method was aged 6+ using the polished otolith method (fig. 4). In this case, the 5th annulus near the edge was not detected until the otolith was polished; however the 1st and 2nd annuli were easily identified in both the otolith surface and polished otolith.

The most extreme example of undetected annuli in our study was a 265 mm male sardine (fig. 5) which

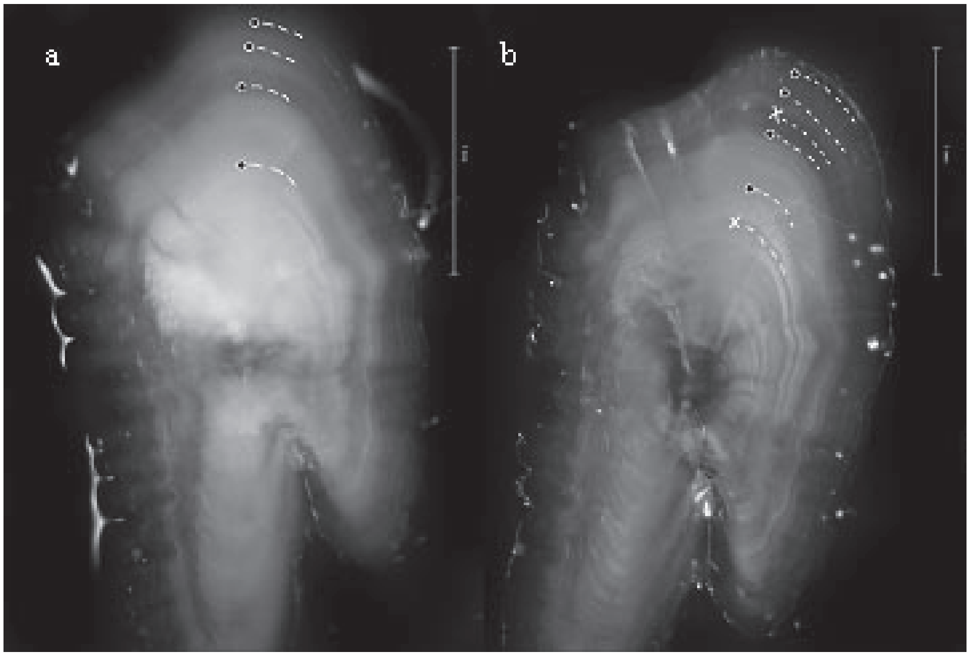

Figure 3. Otolith age estimates for a 226 mm male Pacific sardine showing (a) four distinct annuli using the otolith surface method to age the fish (b) six annuli using the polished otolith surface. X denotes the position of annuli which could not be identified using the surface method. Note: the first annulus was easily identified and confirmed on the polished surface using the annular measurement. (Scale bar=1 mm)

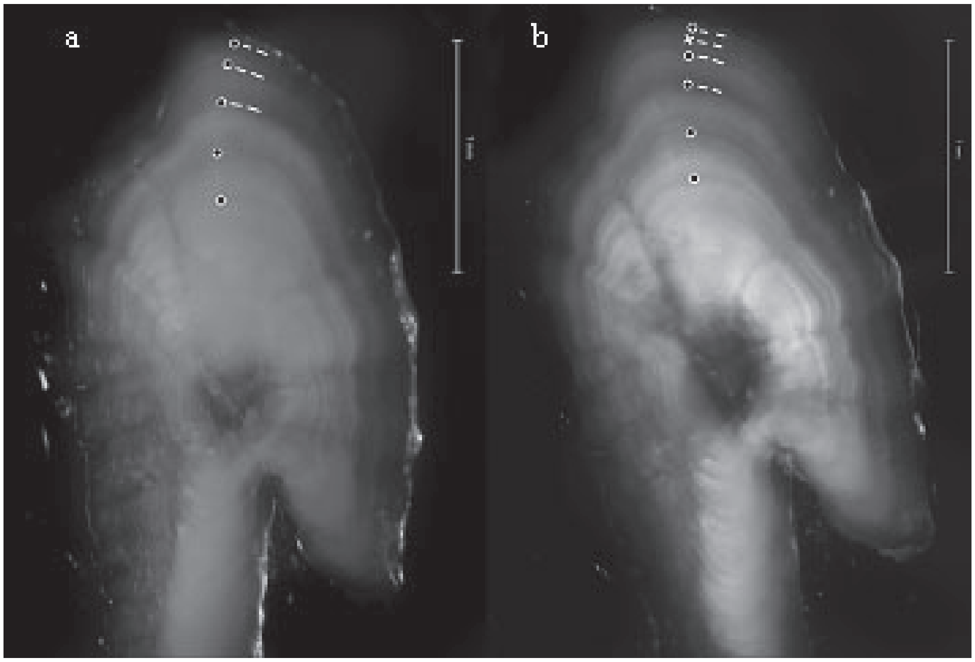

Figure 4. Otolith age estimates for a 242 mm male Pacific sardine showing (a) five distinct annuli using the otolith surface method to age the fish (b) six annuli using the polished otolith surface. X denotes the position of annuli which could not be identified using the surface method. (Scale bar=1 mm)

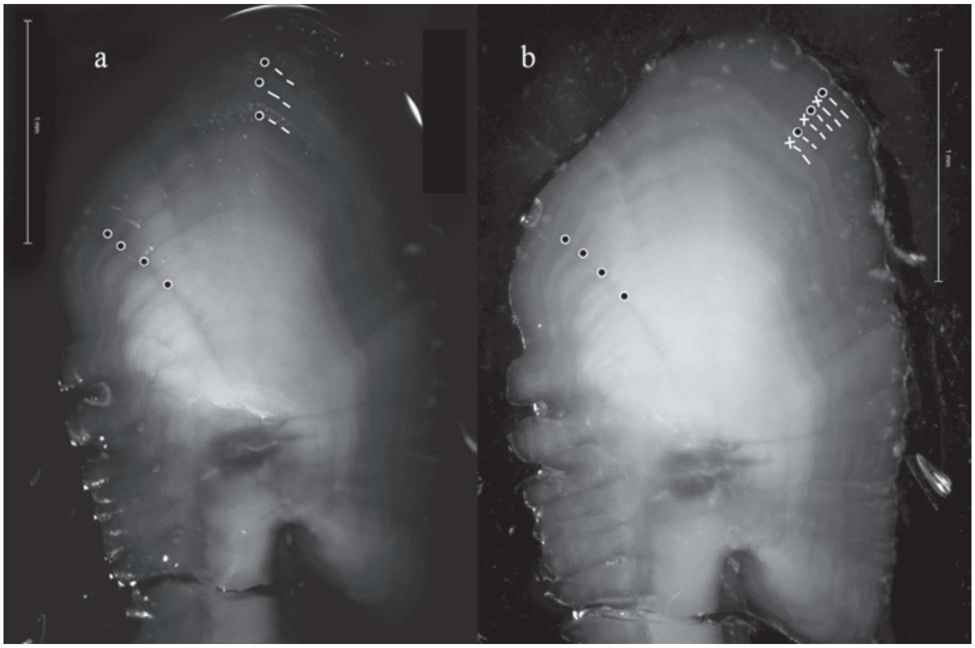

Figure 5. Otolith age estimates for a 265 mm male Pacific sardine showing (a) seven distinct annuli using the otolith surface method to age the fish (b) ten annuli using the polished otolith surface. X denotes the position of annuli which could not be identified using the surface method. (Scale bar=1 mm)

TABLE 1
Percent agreement and average percent error (APE) for reader 1 and reader 2 using surface otolith readings and polished otolith surface readings.

Method	Precision between reader 1 and reader 2	Number of fish	Percent Agreement	APE
Surface age	No difference	90	52%	
	+/-1	69	92%	5.3
	+/-2	14	100%	
Polished surface	No difference	158	81%	
	+/-1	14	98%	3.3
	+/-2	1	100%	

was aged 7+ using the otolith surface technique and 10+ using the polished otolith technique. All 3 undetected annuli were near the edge and were not visible on the otolith surface. Only after the edge was polished to reveal the otolith growth on the ventral interior portion of the edge were these annuli detected.

Reader Agreement

Reader agreement between first and second readings of the otolith surface was less precise than for the polished otolith surface method (tab. 1). Total agreement for the surface otolith method was 52% and agreement within +/- 1 year was 92%, similar to that presented by Butler et al. (1996). However, most fish aged by Butler et al. (1996) were less than 5 yrs. The index of average percent error (APE) (Beamish and Fournier 1981; Chang 1982) was 5.3 identifying an acceptable level of precision. Total agreement for the polished otolith surface method was 81% and agreement within +/- 1 year was 98%. The index of average percent error was 3.3, indicating a high level of precision.

Ages determined by using the annulus measurements in conjunction with the polished otolith surface were generally 1 to 3 years older, even in fish as young as 3 or 4 years (fig. 6). The age composition for ages determined using the polished otolith surface has a mode of 6 years a maximum age of 10 whereas the age composition for ages determined using the otolith surface had a mode of 5 yrs and a maximum age of 9 years (fig. 7). Older fish (>5+) comprised 57% of the polished otolith sample vs. 42% using the otolith surface. There was a significant difference between the ages estimated using the otolith surface and polished otolith surface methods (t-test; $p<0.05$).

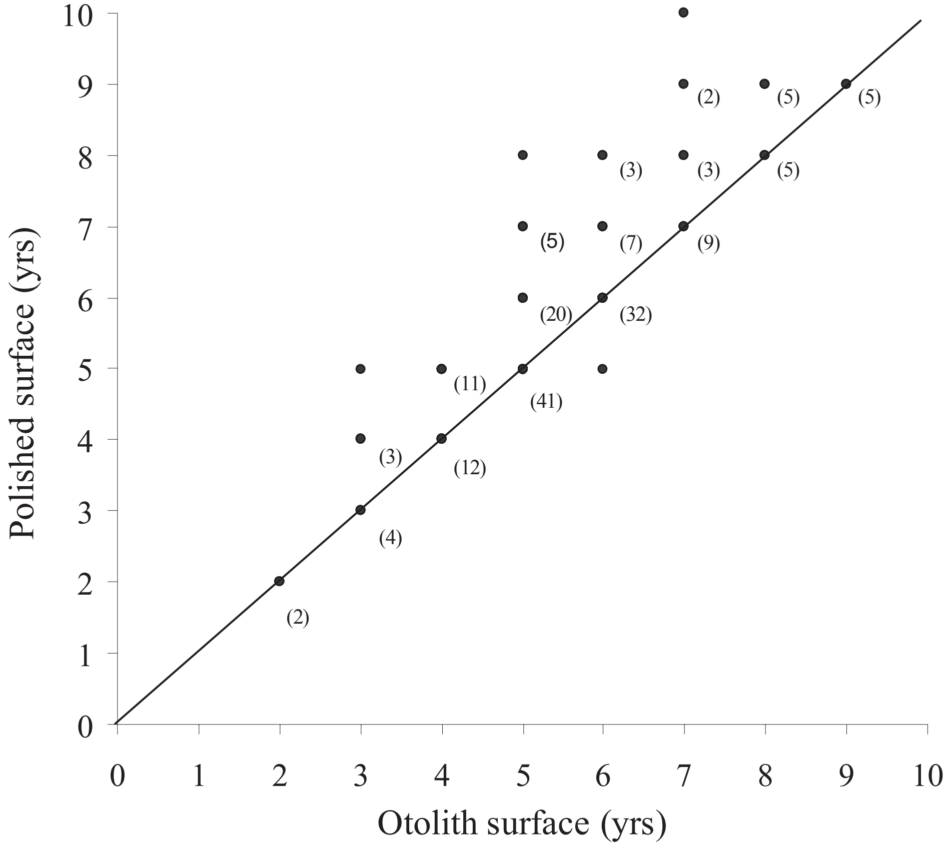

Figure 6. The relationship between age estimates using otolith surface method and polished otolith method for Pacific sardine. The number in brackets indicates number of fish at that point.

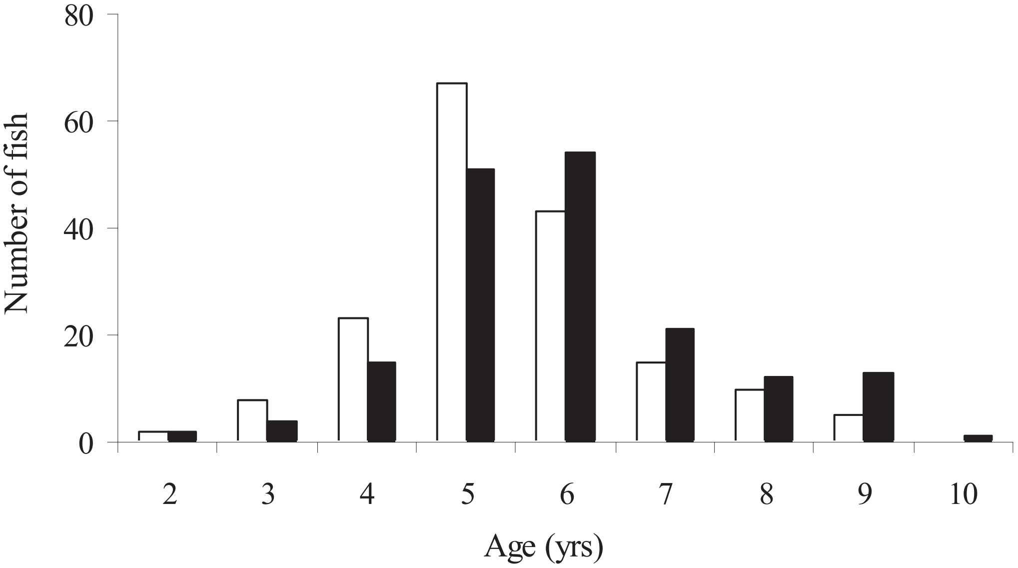

Figure 7. Age composition for 173 Pacific sardine using the otolith surface method (open bars) and the polished otolith surface (solid bars).

DISCUSSION

This study used standard age determination methodologies using otolith surface readings and polished otolith readings to estimate the ages of Pacific sardines. In general, the otolith surface readings produced ages 1 year younger than polished otolith readings, however some fish were aged 2 and 3 years younger. Although aging inaccuracies of one year might not be critical in long-lived species, they have serious stock assessment implications for shorter-lived species such as sardine (Tyler et al. 1989). This is likely true because shorter-lived species typically have only 3 to 5 year classes which dominate the fishery.

Butler et al. (1996) validated only growth rings in juvenile sardine and Barnes and Foreman (1994) validated annuli up to age 3. However, Butler et al. (1996) and Yaremko (1996) pointed out that difficulties associated with otolith growth made annuli identification in older fish difficult. In particular, we found that ring (annuli) clarity near the focus (first and second annuli) was sometimes compromised and that rings (annuli) close to the edge were close together, faint and difficult to identify. This was due to deposition (in older fish) along the entire surface of the otolith and increased thickness of the otolith on the ventral interior surface near the edge in older fish. Identification of the first and second annuli was improved by using mean annulus measurements to estimate the location of those annuli, and polishing the otolith surface enhanced those annuli, and greatly enhanced annuli near the edge in fish 5 years and older.

Despite the polished otolith method being slightly more time consuming than the otolith surface method, especially when doing production aging, we suggest that using these techniques when aging Pacific sardine will improve the accuracy of the age estimates. Future studies will include a re-evaluation of the cross sectioning of sardine otoliths using the break and burn method.

Although a systematic under-aging of sardine of 1 year and a small percentage of under-aging by 2 and 3 years does not appear, at first glance to be problematic—we believe that it could have serious consequences for understanding sardine dynamics and for stock assessment. For example, underestimates of age would overestimate mortality rates. If managers used a F=M strategy to estimate fishing yields, then overfishing would result (Tyler et al. 1989). If recruitment was estimated from catch-at-age analysis, erroneous age composition and overestimates of mortality would lead to overestimates of recruitment (Tyler et al. 1989). The use of annulus measurements and polished otoliths will also help us to assess the relative migration of older fish found in this stock.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Barnes, J. T., and T. J. Foreman. 1994. Recent evidence for the formation of annual growth increments in the otoliths of young Pacific sardines (*Sardinops sagax*). Calif. Fish and Game 80: 29–35.

Beamish, R. J., and D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Canadian Journal of Fisheries and Aquatic Sciences. 3: 982–983.

Beamish, R. J., G. A. McFarlane, and J. R. King. 1999. Fisheries Climatology. Understanding the Interannual and Decadal scale process that regulate British Columbia fish populations naturally. *In* Parsons, J. and P. Harrison [eds.]. Fisheries Oceanography. A Science for the New Millennium. Blackwell Scientific. 347 pp.

Butler, J. L. 1987. Comparison of the early life history parameters of Pacific sardine and northern anchovy with implications of species interactions. PhD Thesis, University of California, San Diego, 242 pp.

Butler, J. L., M. L. Granados-G., J. T. Barnes, M. Yaremko, and B. J. Macewicz. 1996. Age composition, growth and maturation of the Pacific Sardine, *Sardinops sagax*, during 1994. Calif. Coop. Oceanic Fish. Invest. Rep. 37:152–159.

Cailliet, G. M., and K. J. Goldman. 2004. Age determination and validation in Chondrichthyan fishes. *In* Carrier J., J. A. Musick, and M. R. Heithaus (eds). Biology of sharks and their relatives. CRC Press, Boca Raton. pp. 399–447.

Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences. 39: 1208–1210.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Science 60: 102 pp.

Collins, R. A., and J. D. Spratt.1969. Age determination of northern anchovies, *Engraulis mordax*, from otoliths. Pages 39–55 *In* J. D. Messersmith, ed. The northern anchovy (*Engraulis Mordax*) and its fishery, 1965–1968. Calif. Dept. Fish Game, Fish Bull. 147.

Fitch, J. E. 1951. Age composition of the southern California catch of Pacific mackerel 1939–40 through 1950–51. Calif. Dept. Fish Game, Fish Bull. 83: l–73.

Hargreaves, N. B., D. M. Ware, and G. A. McFarlane.1994. Return of the Pacific sardine (*Sardinops sagax*) to the British Columbia coast in 1992. Canadian Journal of Fisheries and Aquatic Sciences. 51: 460–463.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment. Chapman and Hall, New York, New York, USA.

MacCall, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. California Committee on the Fishing Industry Report 20: 72–82.

McFarlane, G. A., and R. J. Beamish. 2001. The reoccurrence of sardines off British Columbia characterize the dynamic nature of regimes. Progr. Oceanogr. 49: 151–165.

McFarlane, G. A., J. R. King, and R. J. Beamish. 2000. Have there been recent changes in climate? Ask the fish. Progr. in Oceanography. 47(2–4): 147–169.

Murphy, G. I. 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proceedings of the California Academy of Science Fourth series 34: 1–84.

Schweigert, J., G. McFarlane, and V. Hodes. 2010. Pacific sardine (*Sardinops sagax*) biomass and migration rates in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/088. iii, 14 p.

Tyler, A. V., R. J. Beamish, and G. A. McFarlane. 1989. Implications of age determination errors to yield estimates. *In* Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, R. J. Beamish, and G. A. McFarlane, eds. Can. Spec. Publ. Fish. Aquat. Sci.108: 27–35.

Yaremko, M. L. 1996. Age determination in Pacific sardine, *Sardinops sagax*. NOAA Technical Memorandum NMFS 223, 22 p.

DIET ANALYSIS OF PACIFIC SARDINE (*SARDINOPS SAGAX*) OFF THE WEST COAST OF VANCOUVER ISLAND, BRITISH COLUMBIA FROM 1997 TO 2008

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ABSTRACT

Trawl surveys for Pacific sardine were conducted off the west coast of Vancouver Island (northern terminus of the California Current System) from 1997 to 2008. Stomachs of 1670 sardines were collected and analysed using standardized laboratory procedures. Sardines are opportunistic feeders with dominant groups in the diet reflecting abundance and availability of prey. Major prey groups included euphausiid (and eggs), copepods and diatoms; however a total of 11 other functional prey groups were identified. Dominant prey groups varied seasonally and interannually. Sardines fed throughout the day and night, with a peak feeding event after dusk.

INTRODUCTION

Pacific sardine (*Sardinops sagax*) off the west coast of North America have fluctuated in abundance for at least the last 1600 years (Baumgartner et al. 1992; McFarlane et al. 2002). Over the last century, sardines were a dominant species from Baja California to British Columbia during the 1930s, 1940s and 1950s, and again from the early 1990s to the present (Hill et al. 2008). Their fluctuations in abundance have been related to climate/ocean conditions (Kawasaki 1983; McFarlane et al. 2002; Chavez et al. 2003), however, the underlying mechanism is poorly understood. A number of authors have argued that physical factors are the main causal mechanisms (see Rykaczewski and Checkley 2008, McFarlane et al. 2002, and Barange et al. 2009 for a review of the studies). Alternatively, a number of authors have proposed links to larval and juvenile diet (Lasker 1975, 1981; Watanabe and Saito 1998; McFarlane and Beamish 2001; Logerwell and Smith 2001). Clearly both physical and biological factors play a role in regulating sardine abundance (McFarlane et al. 2002).

It is equally clear that sardines play an important role in the California Current System (CCS). They are omnivores, feeding on both phytoplankton and zooplankton (Lasker 1970; McFarlane et al. 2005; Emmett et al. 2005), and can consume vast amounts of both primary and secondary production (Lasker 1970). To better understand the role of sardines in the CCS and the dynamics of the stock itself, requires information on the diet of sardines along their entire range (McFarlane and Beamish 2001; Emmett et al. 2005).

In this paper we provide diet data for sardines captured off the west coast of Vancouver Island (the northern terminus of the CCS) from 1997 to 2008. We believe this information will be useful in understanding the role sardines play in the system.

METHODS

Sardine diet information was collected from randomly selected samples of approximately 50 fish during trawl surveys conducted off the west coast of Vancouver Island (WCVI) during June, July or August from 1997–2008 (with the exception of 2000 and 2007) aboard the R/V *W.E. Ricker* or F/V *Frosti* (2005). In addition, during 1998, 1999 and 2001 samples were collected before and after the summer period (June–August) to examine seasonal differences. In August 2005, samples were collected every 2 or 3 hours in 2 areas over 3 days to examine day/night differences in feeding. Samples (150 fish) were also collected in August 2005 from 2 commercial fishing trips in inlets off the WCVI aboard the seiners F/V *Kynoc* and F/V *Ocean Horizon*.

Preservation and Laboratory Methods

All stomachs collected from each set were pooled by set. Stomachs were excised and preserved in 3.7% buffered formalin. In the laboratory, contents of the cardiac stomach region were extracted with curved end forceps onto a petri dish. A total volume of stomach contents was visually estimated in cubic centimetres (cc) using a syringe marked at every 0.1 cc. An estimate indicating a proportion of a full stomach was expressed as a percentage; where 0% denoted an empty stomach, and 100% signified a completely full stomach. Degree of stomach contents digestion was also expressed as a percentage, where 0% denoted fresh contents and 100% indicated completely digested contents.

Under a dissecting microscope, probe and forceps were used to pull apart the stomach mass and identify individual food items. Items were identified to the lowest taxonomic group possible, then collated to a major prey group (e.g. euphausiid, diatom, copepod, etc.), and the contribution of each major group was expressed as a percent of the total stomach volume. Similarly, unidentifiable contents (categorized as digested matter) were expressed as a percent of the total stomach volume.

In 1997 and 1998, sardine scales were included as a prey item, and were considered a component of the overall stomach contents volume. Since 1999, the volume of sardine scales present in the stomach has been recorded separately from the stomach contents volume. In order to standardize all years, the total stomach volume from 1997 and 1998 samples was recalculated to exclude sardine scales.

Data Standardization

We have omitted stomachs analyzed using methodology inconsistent with the described laboratory methods, along with stomachs collected in spring or fall, empty stomachs, and stomachs containing 100% scales or 100% digested material.

Prey items which were present in trace amounts were converted to represent 1% of the total stomach content volume. To accommodate this change, the proportion of digested matter was adjusted accordingly. In rare cases where digested matter was not present, the reduction was applied to the most abundant prey item in that stomach.

Minor prey items were combined into a category named "Other." Prey items included in the "Other" prey item category had to respect two conditions: (1) the prey item was present in less than 5% of the stomachs in each year, and (2) the prey item was present in no more than two of all survey years. Summer months (June, July and August) exclusively, were used for the inter-annual comparisons.

Diet Analysis

The relative importance of each prey group was determined using the King and Beamish (2000) modification of the Index of Relative Importance (IRI) (Pinkas et al. 1971). Similar to the IRI, the modified index of relative importance (RI) describes the quantity of a particular prey item in each individual fish, how many fish eat that prey item, and how much that prey item contributes to the total volume of food consumed by all the fish. The equation for RI is as follows: RI = %FOx (%C+%V) where; %FO = percent frequency of occurrence, or percentage of stomachs containing at least one of the prey items, %C = percentage of contents importance, or the average percentage volume per stomach made up by the prey item, %V = total volume importance, or the percentage ratio of the total volume of the prey item consumed by all fish to the total volume of all prey consumed by all fish (excludes digested matter volume). The %RI ranges from 0, where a prey item is not consumed at all, to 20 000 where a prey item is exclusively consumed. The equation for %RI is as follows: %RI = RI/20 000 x 100.

In this report, the RI values are expressed as a percentage of the maximum attainable value of 20 000 (%RI), to allow for a simpler comparison between values. It is important to note that the %RI values are not cumulative for prey groups within a year, and that the %RI values for all prey items within a year may add up to be greater than 100.

Sardine diet overlap was estimated among all years, using the Morisita-Horn index of overlap (Horn 1966; in King and Beamish 2000) to compare among years:

$$O = 2\Sigma^{n}_{i}\ p_{ij}\ p_{ik}\ /\ \Sigma^{n}_{i}\ p^{2}_{ij} + \Sigma^{n}_{i}\ p^{2}_{ik}$$

Where O = Morisita-Horn index of overlap between year j and year k, n = total number of prey item groups. p_{ij} = proportion of prey item i consumed by sardines in year j. p_{ik} = proportion of prey item i consumed by sardines in year k.

The Morisita-Horn index of overlap was calculated separately based on total volume importance (%V: reflects an overall contribution) and index of relative importance (%RI: provides integrated expression of diet) as the measurements of proportion of prey items. The overlap index ranges from 0 (absolutely no overlap) to 1.0 (complete overlap) (Landingham et al. 1998; King and Beamish 2000). For the purposes of this study values greater than 0.6 were considered to reflect significant overlap.

We used %V since it reflects an overall contribution and is not influenced by small prey items unless they are consumed often and in large quantities. We used the %RI since it is a composite measurement that provides an integrated expression of diet.

RESULTS

A total of 2169 stomachs were examined from research cruises off the WCVI from 1997 to 2008 (tab. 1). Of these, 1670 were examined using standardized laboratory procedures of which, 1405 stomachs were examined using standardized laboratory procedures and contained identifiable prey items. All fish were adults measuring from 173mm to 290mm fork length (FL) and a modal size of 240mm (FL) for male and female groups.

Interannual Comparison

A total of 1849 stomachs were examined from sardines collected during summer months (June to August)

TABLE 1
Summary of stomach analysis for Pacific sardines (*Sardinops sagax*) captured off WCVI, 1997–2008.

Year/ Month	# of stomachs	# of stomachs analyzed by standard lab method	# of empty stomachs	# of stomachs with 100% digested matter or 100% scales	# of stomachs summarized for report	Total volume (cc)	Volume of digested matter (cc)	Volume of identifiable prey items (cc)	Average volume per stomach including digested matter (cc)	Average volume of identifiable prey items per stomach (cc)
1997										
June	549	67	0	52	15	40.02	38.26	1.76	0.60	0.03
July	22	5	0	5	0	4.26	4.26	0.00	0.85	0.00
August	53	53	0	38	15	40.19	35.54	4.65	0.76	0.09
October	15	15	0	14	0	6.90	6.82	0.08	0.46	0.01
1997 Total	**639**	**140**	**0**	**109**	**30**	**91.37**	**84.88**	**6.49**		
1998										
May	14	14	3	3	8	6.90	0.50	6.40	0.49	0.46
June	57	57	0	3	54	25.20	5.26	19.94	0.44	0.35
August	14	14	1	0	13	11.40	0.05	11.35	0.81	0.81
September	95	95	13	2	80	2.33	1.36	0.97	0.02	0.01
October	20	20	1	10	9	4.90	3.66	1.24	0.25	0.06
1998 Total	**200**	**200**	**18**	**18**	**164**	**50.73**	**10.83**	**39.90**		
1999										
March	30	30	0	0	30	13.50	8.89	4.61	0.45	0.15
July	80	80	0	0	80	16.51	4.69	11.82	0.21	0.15
August	45	45	0	0	45	5.80	3.61	2.19	0.13	0.05
1999 Total	**155**	**155**	**0**	**0**	**155**	**35.81**	**17.19**	**18.62**		
2000										
September	74	74	0	0	0	9.50	8.97	0.53	0.13	0.01
2000 Total	**74**	**74**	**0**	**0**	**0**	**9.50**	**8.97**	**0.53**		
2001										
July	38	38	0	0	38	4.80	4.45	0.35	0.13	0.01
August	22	22	0	0	22	3.70	3.45	0.25	0.17	0.01
October	50	50	0	2	48	5.70	5.00	0.70	0.12	0.01
2001 Total	**110**	**110**	**0**	**2**	**108**	**14.20**	**12.90**	**1.30**		
2002										
August	80	80	0	0	80	136.10	45.75	90.35	1.70	1.13
September	22	22	0	0	0	21.20	15.18	6.02	0.96	0.69
2002 Total	**102**	**102**	**0**	**0**	**80**	**157.30**	**60.93**	**96.37**		
2003										
August	20	20	0	0	20	4.00	1.38	2.62	0.20	0.13
2003 Total	**20**	**20**	**0**	**0**	**20**	**4.00**	**1.38**	**2.62**		
2004										
July	20	20	0	1	19	12.20	7.40	4.80	0.61	0.37
2004 Total	**20**	**20**	**0**	**1**	**19**	**12.20**	**7.40**	**4.80**		
2005										
August (coastal)	179	179	0	0	179	224.00	70.78	153.22	1.25	0.86
August (inlet)	150	150	0	0	150	199.83	86.81	113.02	1.33	0.75
2005 Total	**329**	**329**	**0**	**0**	**329**	**423.83**	**157.59**	**266.24**		
2006										
July	20	20	0	0	20	35.40	8.35	27.05	1.77	1.35
August	260	260	0	20	240	373.80	63.71	310.09	1.56	1.29
2006 Total	**280**	**280**	**0**	**20**	**260**	**409.20**	**72.06**	**337.14**		
2008										
August	240	240	0	0	240	451.60	85.97	365.64	1.88	1.52
2008 Total	**240**	**240**	**0**	**0**	**240**	**451.60**	**85.97**	**365.64**		
Overall total	**2169**	**1670**	**18**	**150**	**1405**	**1659.74**	**520.10**	**1139.65**		
Summer total	**1849**	**1350**	**1**	**119**	**1230**	**1588.81**	**469.72**	**1119.11**		

(tab. 1). Of these, 1350 were examined using standardized laboratory procedures and contained identifiable items. Average volume per stomach ranged from 0.13cc (Aug 1999, July 2001) to 1.88cc (Aug 2008). The average volume of identifiable prey items ranged from 0.01 cc (2001) to 1.52 cc (2008). A total of 14 functional groups of prey items were identified during summer months. In general, the majority of identifiable stomach contents consisted of euphausiids, copepods and diatoms (tab. 2, fig. 1). However, the relative contribution of prey items varied considerably (fig. 1) between years. For example, euphausiids were important in the diet of sardine in 1997, 2006 and 2008 (%RI of 21.63, 23.57 and 40.71 respectively), with importance influ-

TABLE 2
Pacific sardine (*Sardinops sagax*) diet composition by year 1997–2008. Data from summer months (June–August) only.

	Euphausiid	Copepod	Diatoms	Euphausiid eggs	Oikopleura	Eggs	Crab zoea	Cladoceran	Barnacle nauplii	Barnacle cyprids	Fish eggs	Cyclopoid	Amphipod	Other*
1997: 30 stomachs														
%FO	56.67	6.67	0.00	0.00	0.00	20.00	26.67	0.00	0.00	0.00	0.00	0.00	3.33	40.00
%V	55.30	1.55	0.00	0.00	0.00	16.25	5.80	0.00	0.00	0.00	0.00	0.00	0.22	20.87
%C	21.05	0.50	0.00	0.00	0.00	5.33	3.67	0.00	0.00	0.00	0.00	0.00	0.33	9.93
RI	4326.78	13.67	0.00	0.00	0.00	431.67	252.52	0.00	0.00	0.00	0.00	0.00	1.85	1232.11
%RI	21.63	0.07	0.00	0.00	0.00	2.16	1.26	0.00	0.00	0.00	0.00	0.00	0.01	6.16
1998: 67 stomachs														
%FO	23.88	17.91	74.63	74.63	0.00	0.00	0.00	0.00	7.46	1.49	1.49	1.49	11.94	19.40
%V	35.25	3.12	33.18	19.88	0.00	0.00	0.00	0.00	0.32	0.03	0.02	0.08	1.68	6.44
%C	18.21	1.06	36.41	21.02	0.00	0.00	0.00	0.00	0.32	0.03	0.01	0.08	1.04	4.19
RI	1276.55	74.83	5193.82	3052.76	0.00	0.00	0.00	0.00	4.74	0.09	0.05	0.24	32.57	206.30
%RI	6.38	0.37	25.97	15.26	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.16	1.03
1999: 125 stomachs														
%FO	1.61	96.77	46.77	66.13	37.90	8.06	10.48	3.23	10.48	0.81	8.06	10.48	3.23	3.23
%V	0.36	31.08	5.52	20.25	36.36	2.12	1.17	0.25	0.22	0.07	1.64	0.23	0.50	0.23
%C	0.09	17.37	2.41	13.45	16.77	0.94	0.35	0.18	0.14	0.04	0.52	0.18	0.22	0.14
RI	0.73	4688.98	371.13	2228.33	2013.80	24.65	15.87	1.38	3.75	0.09	17.40	4.25	2.31	1.20
%RI	0.00	23.44	1.86	11.14	10.07	0.12	0.08	0.01	0.02	0.00	0.09	0.02	0.01	0.01
2001: 60 stomachs														
%FO	8.33	95.00	71.67	16.67	8.33	1.67	3.33	10.00	6.67	0.00	0.00	10.00	6.67	1.67
%V	8.70	35.45	32.44	2.84	1.84	2.51	8.53	1.51	1.17	0.00	0.00	2.01	2.68	0.33
%C	0.52	2.23	2.02	0.17	0.15	0.08	0.85	0.10	0.07	0.00	0.00	0.17	0.13	0.02
RI	76.77	3580.06	2469.50	50.16	16.58	4.32	31.26	16.05	8.25	0.00	0.00	21.73	18.73	0.59
%RI	0.38	17.90	12.35	0.25	0.08	0.02	0.16	0.08	0.04	0.00	0.00	0.11	0.09	0.00
2002: 80 stomachs														
%FO	81.25	98.75	100.00	37.50	72.50	0.00	8.75	58.75	67.50	23.75	3.75	7.50	0.00	5.00
%V	15.24	23.38	45.32	2.35	7.51	0.00	0.17	2.31	1.50	0.43	1.57	0.13	0.00	0.08
%C	9.63	19.58	25.19	1.11	5.21	0.00	0.14	2.01	1.13	0.28	0.28	0.08	0.00	0.16
RI	2020.27	4241.88	7051.02	129.83	922.13	0.00	2.73	253.67	177.92	16.63	6.92	1.56	0.00	1.21
%RI	10.10	21.21	35.26	0.65	4.61	0.00	0.01	1.27	0.89	0.08	0.03	0.01	0.00	0.01
2003: 20 stomachs														
%FO	15.00	100.00	100.00	90.00	90.00	0.00	80.00	95.00	70.00	5.00	0.00	15.00	0.00	30.00
%V	0.36	28.99	26.70	2.04	17.35	0.00	15.06	6.90	1.11	0.08	0.00	0.27	0.00	1.30
%C	0.24	20.75	15.50	1.39	11.00	0.00	12.38	4.35	0.70	0.05	0.00	0.35	0.00	1.30
RI	9.00	4973.55	4219.72	308.51	2551.78	0.00	2195.19	1069.05	126.42	0.63	0.00	9.25	0.00	77.90
%RI	0.04	24.87	21.10	1.54	12.76	0.00	10.98	5.35	0.63	0.00	0.00	0.05	0.00	0.39
2004: 19 stomachs														
%FO	31.58	94.74	78.95	0.00	10.53	0.00	31.58	0.00	0.00	5.26	0.00	0.00	10.53	78.95
%V	6.31	22.07	5.29	0.00	0.31	0.00	12.08	0.00	0.00	0.21	0.00	0.00	0.42	53.52
%C	1.89	10.32	2.21	0.00	0.11	0.00	4.00	0.00	0.00	0.05	0.00	0.00	0.11	17.12
RI	259.09	3068.52	592.10	0.00	4.40	0.00	507.74	0.00	0.00	1.37	0.00	0.00	5.49	5576.46
%RI	1.30	15.34	2.96	0.00	0.02	0.00	2.54	0.00	0.00	0.01	0.00	0.00	0.03	27.88
2005 (Coastal): 179 stomachs														
%FO	26.26	100.00	98.88	26.26	0.00	0.00	2.23	19.55	6.70	6.15	0.00	1.12	2.23	7.26
%V	59.97	18.26	16.61	2.78	0.00	0.00	0.06	0.27	0.06	0.06	0.00	0.01	0.34	1.58
%C	16.10	16.49	16.04	3.24	0.00	0.00	0.09	0.57	0.07	0.06	0.00	0.01	0.07	0.46
RI	1997.53	3475.36	3228.46	157.94	0.00	0.00	0.34	16.36	0.86	0.73	0.00	0.02	0.90	14.86
%RI	9.99	17.38	16.14	0.79	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.07
2005 (Inlets): 150 stomachs														
%FO	6.00	98.67	83.33	54.67	4.00	0.00	0.67	30.67	48.00	30.00	0.00	20.00	4.00	18.00
%V	0.94	18.51	62.22	11.55	0.23	0.00	0.01	0.88	2.22	1.37	0.00	0.87	0.39	0.81
%C	0.15	14.93	17.57	6.86	0.06	0.00	0.01	0.47	0.82	0.38	0.00	0.31	0.38	0.42
RI	6.54	3299.73	6649.41	1006.78	1.14	0.00	0.01	41.42	145.97	52.32	0.00	23.77	3.07	22.19
%RI	0.03	16.50	33.25	5.03	0.01	0.00	0.00	0.21	0.73	0.26	0.00	0.12	0.02	0.11
2006: 260 stomachs														
%FO	72.31	98.85	95.77	51.92	21.54	0.00	3.08	43.85	21.92	2.69	4.62	54.62	3.85	16.15
%V	43.52	19.47	29.29	3.70	0.22	0.00	0.09	1.68	0.47	0.04	0.11	0.97	0.05	0.38
%C	21.66	17.18	22.62	1.95	0.34	0.00	0.03	1.32	0.29	0.03	0.05	0.79	0.04	0.38
RI	4713.48	3622.95	4972.06	293.25	11.91	0.00	0.38	131.80	16.67	0.19	0.71	96.47	0.35	12.17
%RI	23.57	18.11	24.86	1.47	0.06	0.00	0.00	0.66	0.08	0.00	0.00	0.48	0.00	0.06
2008: 240 stomachs														
%FO	87.08	99.17	66.25	22.50	25.83	0.00	2.92	11.67	2.50	0.83	2.08	10.00	3.75	25.83
%V	57.62	22.27	17.12	1.23	0.26	0.00	0.07	0.13	0.03	0.00	0.02	0.08	0.05	1.14
%C	35.87	13.24	17.74	1.27	0.51	0.00	0.07	0.17	0.04	0.01	0.02	0.13	0.11	0.79
RI	8141.03	3521.00	2309.43	56.29	19.82	0.00	0.39	3.46	0.16	0.01	0.08	2.02	0.58	50.05
%RI	40.71	17.60	11.55	0.28	0.10	0.00	0.00	0.02	0.00	0.00	0.00	0.01	0.00	0.25

*Other prey items include: 1997 (crab megalops, pteropod, juvenile shrimp, larval shrimp, juvenile octopus, juvenile crab) 1998 (fish larvae, crab megalops, gastropod, algae filaments) 1999 (shrimp zoea, ostracod, algae filaments) 2001 (chaetognath) 2002 (chaetognath, shrimp zoea) 2003 (shrimp remains, shrimp larvae, juvenile octopus) 2004 (crab megalops, pteropod, shrimp remains, shrimp larvae, juvenile octopus) 2005 (crab megalops, pteropod, shrimp remains, shrimp larvae, juvenile octopus, peleypoda, ectoprocta, mysid) 2006 (rotifers, cumacea, larval shrimp, ectoprocta, chaetognath, gastropod, fish larvae) 2008 (chaetognath, shrimp remains, pteropod, crab megalops, pelecypoda, larval polychete, ectoprocta).

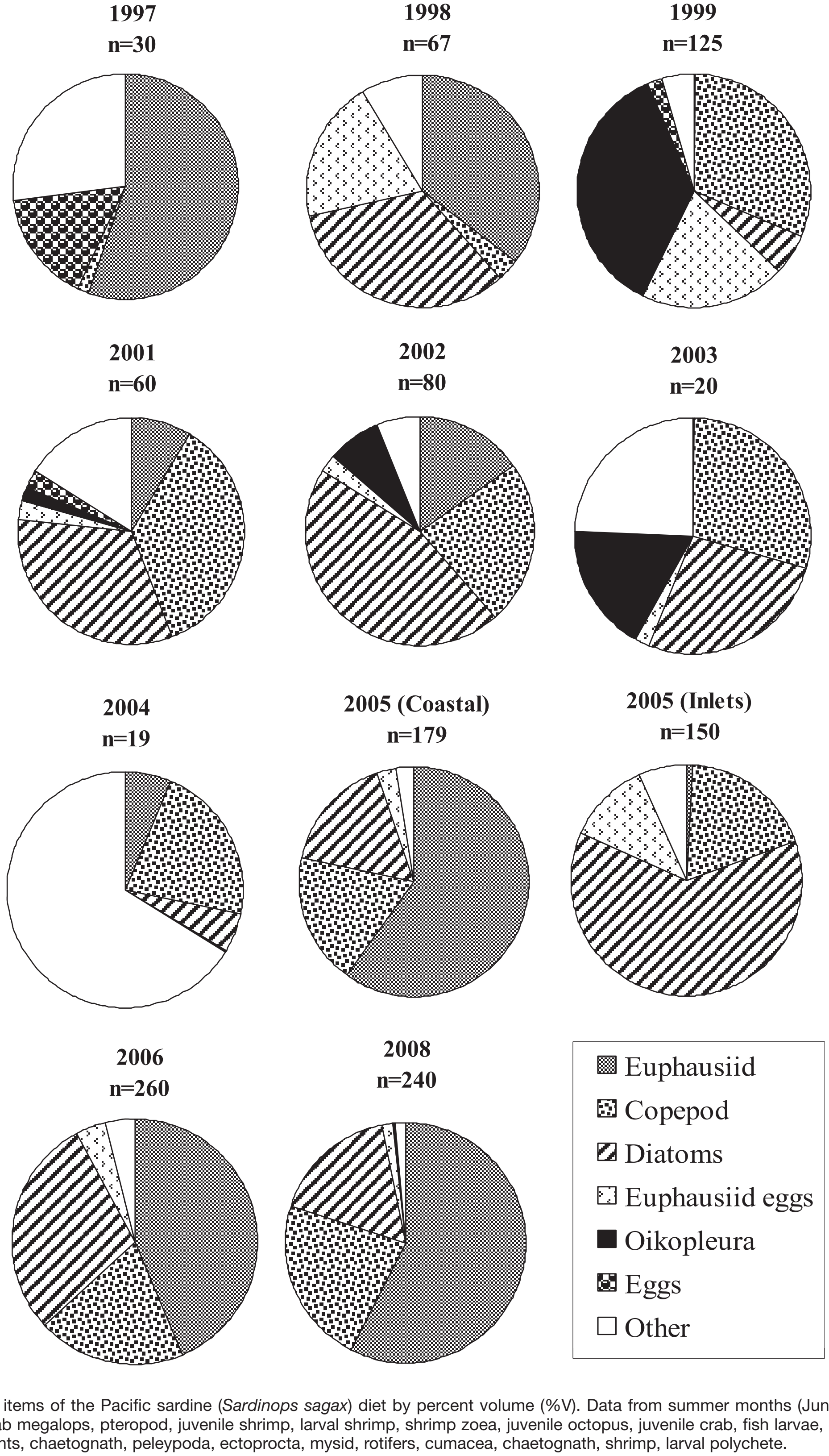


Figure 1. Major prey items of the Pacific sardine (*Sardinops sagax*) diet by percent volume (%V). Data from summer months (June–August) only. Other prey items may include: crab megalops, pteropod, juvenile shrimp, larval shrimp, shrimp zoea, juvenile octopus, juvenile crab, fish larvae, gastropod, algae filaments, ostracod, algae filaments, chaetognath, peleypoda, ectoprocta, mysid, rotifers, cumacea, chaetognath, shrimp, larval polychete.

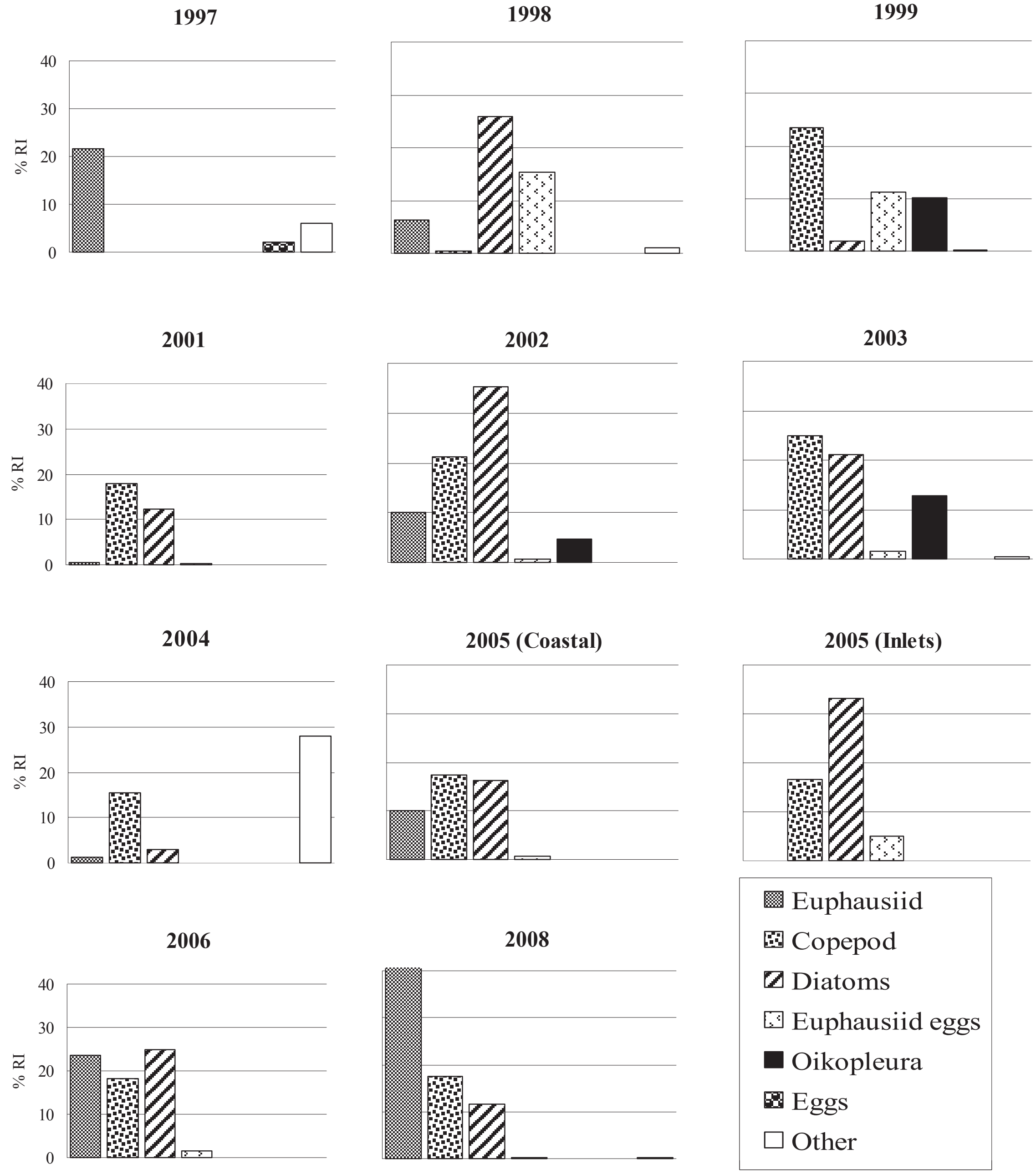


Figure 2. Major prey items of the Pacific sardine (*Sardinops sagax*) diet by total relative importance (%RI). Data from summer months (June–August) only. Other prey items may include: crab megalops, pteropod, juvenile shrimp, larval shrimp, shrimp zoea, juvenile octopus, juvenile crab, fish larvae, gastropod, algae filaments, ostracod, algae filaments, chaetognath, peleypoda, ectoprocta, mysid, rotifers, cumacea, chaetognath, shrimp, larval polychete.

enced mainly by %FO and %V (tab. 2, fig. 1), however it should be noted that night-time samples were included in the 2006 and 2008 data. Copepods were important components of diet in all years from 1999–2008 (but virtually absent in 1997 and 1998), with %RI ranging from 0.07 to 24.87 (tab. 2, fig. 2) again influenced mainly by %FO and %V. Diatoms were dominant in the diet in 1998, 2002, and 2006 (%RI of 25.97, 35.26, and 24.86 respectively), but were also important in 2001, 2003, 2005, and 2008 influenced by all measures (%FO, %V, %) (tab. 2, fig. 2). Interestingly, in 1999 and 2003, oikopleurids (larvaceans) were important components of the diet (%RI of 10.07 and 12.76, respectively) influenced by %V in 1999 and %FO in 2003. In the 2004 sample, the "Other" category dominated diet samples (%RI of 27.88), and was composed of 39.47% shrimp by volume.

Where identification to species within a prey cat-

TABLE 3
Taxonomic summary of prey items in the Pacific sardine (*Sardinops sagax*) by percent frequency of occurrence (%FO). Data from summer months (June–August) only.

Year	Group	Taxa	%FO
1998	Diatoms	*Coscinodiscus* sp.	45
	Copepods	*Calanus* sp.	4
		Pseudocalanus sp.	3
		Metridia sp.	1
		Epilabidocera longipedata	1
		Paracalanus parvus	1
	Euphausiids	*Euphausia pacifica*	22
		Thysanoessa spinifera	9
	Amphipods	*Parathemisto* sp.	12
1999	Diatoms	*Coscinodiscus* sp.	48
		Thalassiothrix sp.	3
		Rizosolenia sp.	2
		Dinoflagellates	1
	Copepods	*Acartia longiremis*	81
		Paracalanus parvus	31
		Pseudocalanus sp.	6
		Centropages abdominalis	6
		Metridia sp.	1
	Amphipods	*Parathemisto* sp.	2
		Calliopius sp.	1
	Cyclopoids	*Oithona* sp.	25
2001	Diatoms	*Coscinodiscus* sp.	72
	Copepods	*Acartia longiremis*	67
		Pseudocalanus sp.	17
		Centropages abdominalis	12
		Eucalanus bungii	8
		Paracalanus parvus	3
	Amphipods	*Parathemisto* sp.	7
	Cyclopoids	*Oithona* sp.	13
2002	Diatoms	*Thalassiosira* sp.	95
		Coscinodiscus sp.	75
		Skeletonema sp.	69
		Chaetocerus sp.	50
		Dinoflagellates	41
		Ditylum sp.	31
		Pseudo-nitzschia sp.	15
		Biddulphia sp.	5
		Thalassiothrix sp.	4
	Copepods	*Acartia longiremis*	84
		Paracalanus parvus	48
		Centropages abdominalis	28
		Pseudocalanus sp.	23
		Eucalanus bungii	3
		Metridia sp.	1
	Euphausiids	*Thysanoessa spinifera*	16
		Euphausia pacifica	3
	Cyclopoids	*Corycaeus anglicus*	9
		Oithona sp.	6
2003	Diatoms	*Dinoflagellates*	100
		Chaetocerus sp.	65
		Coscinodiscus sp.	55
		Thalassiosira sp.	45
		Skeletonema sp.	15
		Ditylum sp.	15
		Biddulphia sp.	5
	Copepods	*Paracalanus parvus*	60
		Pseudocalanus sp.	60
		Centropages abdominalis	40
		Acartia longiremis	35
	Cyclopoids	*Corycaeus anglicus*	5
	Crab zoea	*Porcellanidae*	80
		Brachyura	10
		Anomura	5
2004	Diatoms	*Dinoflagellates*	63
		Thalassiosira sp.	26
		Coscinodiscus sp.	21
		Skeletonema sp.	11
		Pseudo-nitzschia sp.	5
	Copepods	*Acartia longiremis*	74
		Centropages abdominalis	37
		Calanus sp.	21
		Eucalanus bungii	5
		Metridia sp.	5
	Amphipods	*Hyperiid*	5
		Themisto sp.	5
	Gastropods	*Limacina* sp.	5
	Crab zoea	*Anomura*	26
		Brachyura	11
		Cancridae	5
2005 (Coastal)	Diatoms	*Skeletonema* sp.	79
		Thalassiosira sp.	77
		Ditylum sp.	65
		Dinoflagellates	61
		Pleurosigma sp.	53
		Coscinodiscus sp.	25
		Chaetocerus sp.	11
		Pseudo-nitzschia sp.	7
		Thalassiothrix sp.	7
		Biddulphia sp.	1
	Copepods	*Acartia longiremis*	80
		Centropages abdominalis	39
		Paracalanus parvus	37
		Calanus sp.	21
		Metridia sp.	3
		Eucalanus bungii	2
		Pseudocalanus sp.	1
		Neocalanus cristatus	1
		Tortanus discaudatus	1
	Euphausiids	*Euphausia pacifica*	22
		Thysanoessa spinifera	21
	Amphipods	*Themisto* sp.	2
		Vibilia armata	2
	Cyclopoids	*Corycaeus anglicus*	1
	Gastropods	*Limacina* sp.	3
	Crab zoea	*Porcellanidae*	1
		Brachyura	1
		Cancridae	1
		Anomura	1
2005 (Inlets)	Diatoms	*Thalassiosira* sp.	74
		Skeletonema sp.	53
		Ditylum sp.	51
		Coscinodiscus sp.	41
		Pseudo-nitzschia sp.	33
		Thalassiothrix sp.	30
		Dinoflagellates	20
		Biddulphia sp.	17
	Copepods	*Acartia longiremis*	77
		Centropages abdominalis	22
		Pseudocalanus sp.	19
		Paracalanus parvus	10
		Calanus sp.	2
		Metridia sp.	1
		Eucalanus bungii	1
		Epilabidocera longipedata	1
	Amphipods	*Grammarid*	3
	Cyclopoids	*Corycaeus anglicus*	13
		Oithona sp.	5
	Crab zoea	*Brachyura*	1
2006	Diatoms	*Ditylum* sp.	94
		Thalassiosira sp.	90
		Skeletonema sp.	80
		Coscinodiscus sp.	68
		Thalassiothrix sp.	50
		Pseudo-nitzschia sp.	44

TABLE 3 (Continued)
Taxonomic summary of prey items in the Pacific sardine (*Sardinops sagax*) by percent frequency of occurrence (%FO). Data from summer months (June–August) only.

Year	Group	Taxa	%FO
		Dinoflagellates	43
		Chaetocerus sp.	27
		Pleurosigma sp.	17
		Biddulphia sp.	4
	Copepods	*Acartia longiremis*	89
		Paracalanus parvus	73
		Centropages abdominalis	47
		Calanus sp.	38
		Pseudocalanus sp.	37
		Metridia sp.	4
		Eucalanus bungii	3
		Tortanus discaudatus	2
	Euphausiids	*Thysanoessa spinifera*	28
		Euphausia pacifica	23
	Amphipods	*Hyperiid*	3
	Cyclopoids	*Oithona* sp.	50
		Corycaeus anglicus	4
		Oncaea borealis	1
2008	Diatoms	*Coscinodiscus* sp.	65
		Thalassiosira sp.	64
		Thalassiothrix sp.	50
		Chaetocerus sp.	46
		Dinoflagellates	48
		Skeletonema sp.	35
		Pseudo-nitzschia sp.	23
		Biddulphia sp.	6
		Ditylum sp.	2
	Copepods	*Calanus* sp.	54
		Acartia longiremis	50
		Pseudocalanus sp.	46
		Centropages abdominalis	18
		Paracalanus parvus	15
		Metridia sp.	13
		Eucalanus bungii	3
		Epilabidocera longipedata	2
		Neocalanus cristatus	1
	Euphausiids	*Euphausia pacifica*	37
		Thysanoessa spinifera	28
	Amphipods	*Hyperiid*	3
	Cyclopoids	*Oithona* sp.	8
		Corycaeus anglicus	1
	Gastropods	*Limacina helicina*	22

TABLE 4A
Morisita-Horn overlap indices using %RI of prey items of the Pacific sardine (*Sardinops sagax*) diet by year. Data from summer months (June–August) only. Values greater than 0.6 (bold) were considered to reflect significant overlap.

	1997	1998	1999	2001	2002	2003	2004	2005	2006
1998	0.20								
1999	0.00	0.26							
2001	0.02	0.47	**0.71**						
2002	0.19	**0.72**	0.47	**0.72**					
2003	0.02	0.50	**0.71**	**0.77**	**0.84**				
2004	0.26	0.12	0.4	0.42	0.31	0.4			
2005	0.37	**0.62**	**0.62**	**0.91**	**0.84**	**0.76**	0.39		
2006	0.51	**0.67**	0.43	**0.65**	**0.90**	**0.68**	0.30	**0.88**	
2008	**0.68**	0.37	0.30	0.37	**0.61**	0.39	0.23	**0.65**	**0.87**

TABLE 4B
Morisita-Horn overlap indices using %V of prey items of the Pacific sardine (*Sardinops sagax*) diet by year. Data from summer months (June–August) only. Values greater than 0.6 (bold) were considered to reflect significant overlap.

	1997	1998	1999	2001	2002	2003	2004	2005	2006
1998	**0.63**								
1999	0.04	0.25							
2001	0.20	0.59	0.55						
2002	0.26	**0.76**	0.46	**0.91**					
2003	0.06	0.42	**0.71**	**0.90**	**0.81**				
2004	0.43	0.26	0.24	0.37	0.26	0.36			
2005	**0.84**	**0.80**	0.21	0.51	0.59	0.32	0.25		
2006	**0.70**	**0.89**	0.29	**0.72**	**0.81**	0.53	0.26	**0.94**	
2008	**0.82**	**0.78**	0.25	0.56	**0.62**	0.36	0.26	**1.00**	**0.95**

egory was possible, euphausiids were composed of *Euphausia pacifica* and *Thysanoessa spinifera*; copepods were dominated by *Acartia longeremis*, *Centropages abdominalis*, *Paracalanus parvus, Calanus* sp. and *Pseudocalanus* sp. (tab. 3) and phytoplankton (ie. diatoms and dinoflagellates) were dominated by *Coscinodiscus* sp., *Thalassiosira* sp., *Chaetocerus* sp., *Ditylum* sp., *Skeletonema* sp., and dinoflagellates (tab. 3).

The amount of diet overlap based on %RI and %V, between years was substantial for most years examined (tab. 4a and 4b), with the exception of 1997 and 2004 when using %RI. Both these years were dominated by only one prey item (1997 euphausiids; 2004 "Other"). Based on a %V 1997 overlapped to a very high degree with 2005 to 2008, but showed less overlap with other years (ie. 1999, 2001, and 2003).

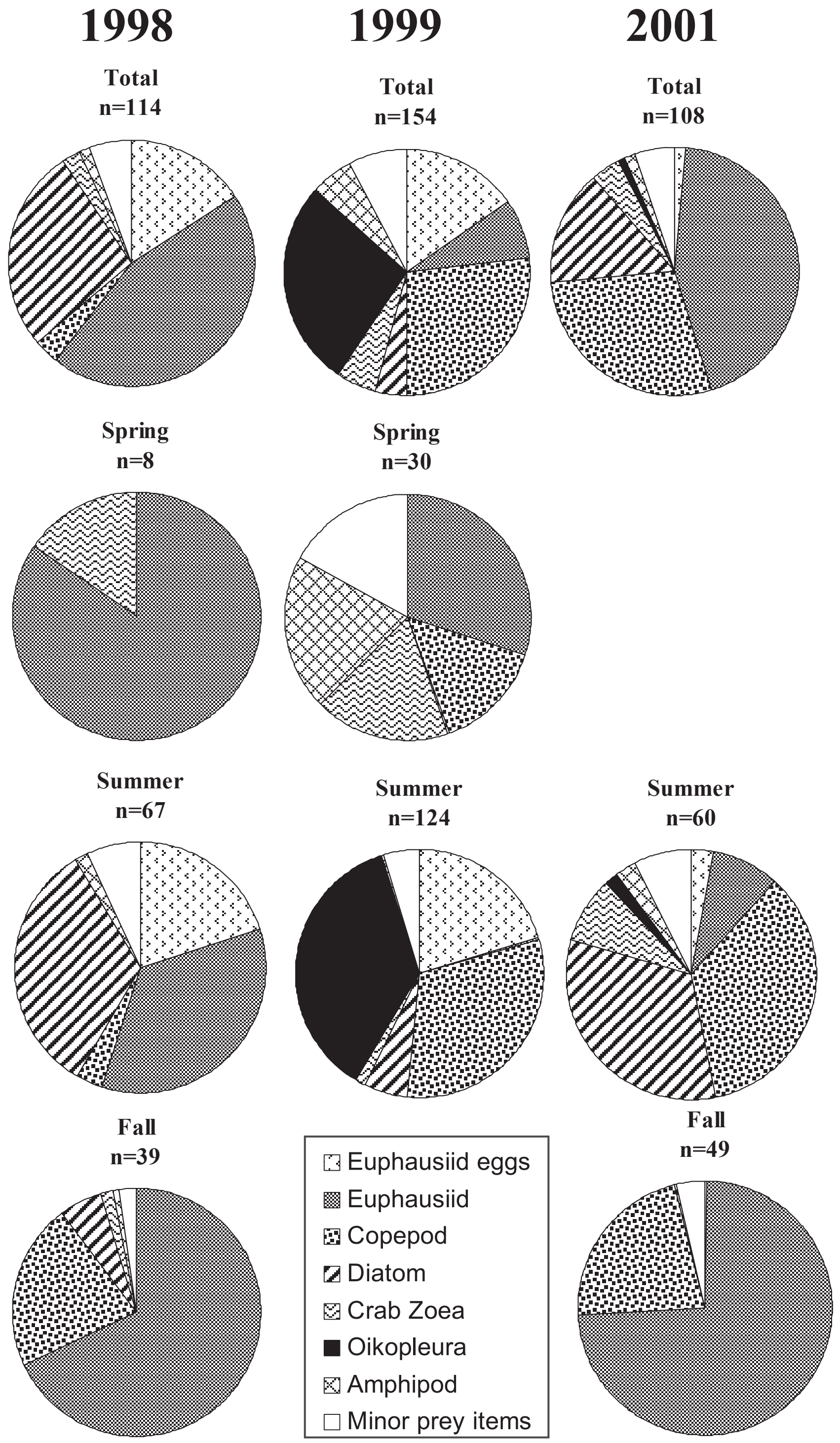
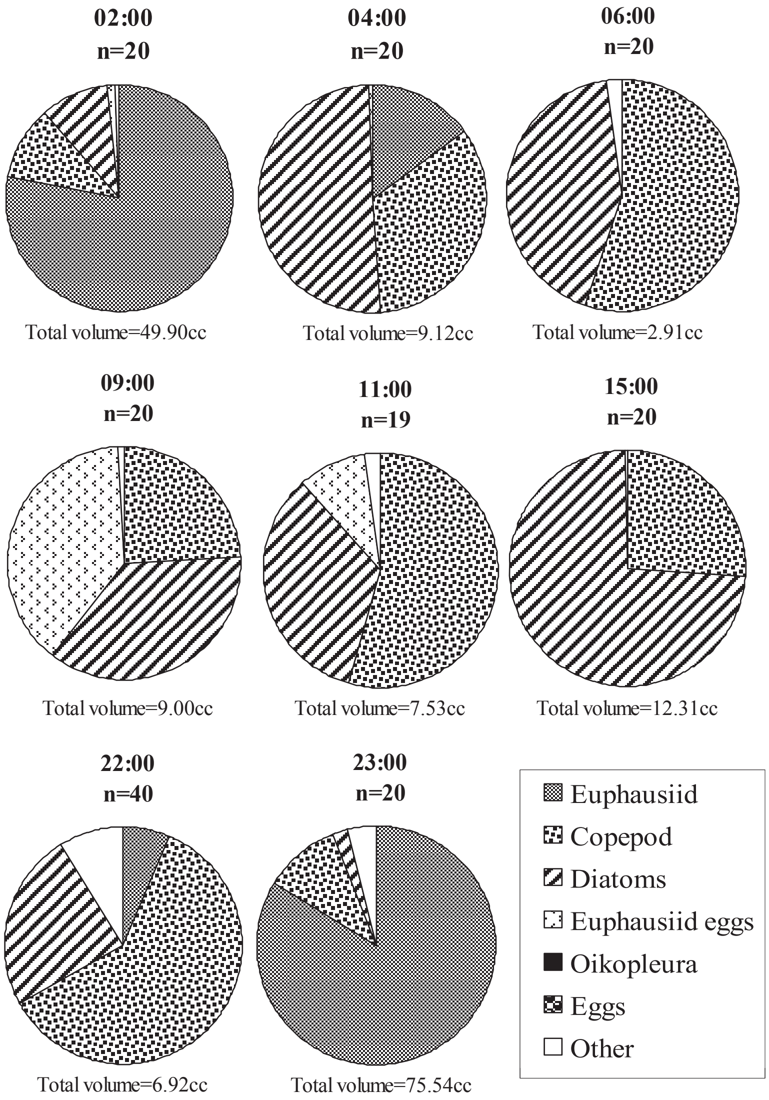


Figure 3. Seasonal summary of major prey items of the Pacific sardine (*Sardinops sagax*) diet by %V. Minor prey items include: cyclopoid, algae filaments, gastropods, barnacle cyprids and nauplii, fish eggs, crab megalops, shrimp zoea, unknown eggs, chaetognath, ostracod, cladoceran.

Seasonal Comparison

In 1998, samples were collected throughout the spring (May), summer (June, August) and fall (September, October). Euphausiids and crab zoea dominated (%V) in the spring, euphausiids, euphausiid eggs, and diatoms in the summer, and euphausiids and copepods in the fall (fig. 3).

For the three years (1998, 1999 and 2001), for which some seasonal diet information was available, prey items varied considerably between seasons and



02:00 n=20

04:00 n=20

06:00 n=20

09:00 n=20

11:00 n=19

15:00 n=20

22:00 n=40

23:00 n=20

Figure 4. Hourly summary of major prey items of the Pacific sardine (*Sardinops sagax*) diet by %V during one period in 2005. Other prey items may include: crab megalops, pteropod, shrimp remains, shrimp larvae, juvenile octopus, peleypoda, ectoprocta, mysid. Average total volume (cc) of food eaten is shown in parenthesis. Average sunrise and sunset times during this period were 06:05 PDT and 20:51 PDT respectively.

years (fig. 3). In 1998, euphausiids (44.63%) were dominant in sardine diets in all seasons. As well, crab zoea (15.63%) were important in the spring; and diatoms (33.18%) and euphausiid eggs (19.88%) in summer. Copepods (21.54%) were present in late fall (fig. 3). Similarly, in 2001, euphausiids were an important prey item in summer (8.70%) and fall (73.97%), with diatoms again being important contributing 32.44% in summer. However, copepods also accounted for (35.45%) of the summer diet. During 1999, euphausiids (29.99%), crab zoea (17.68%), copepods (14.53%) and also amphipods were important in spring. Of note, however, oikopleurids (larvaceans) were a major food item in summer contributing 36.36%, followed by copepods (31.08%) and euphausiid eggs (20.25%) (fig. 3).

Day/Night Comparison

During August 2005, 179 stomachs were collected over two 24 hour periods conducted over three days. As contents were similar from sets at similar times the data was combined (fig. 4). Diatoms and copepods dominated (%V) in samples collected from just prior to sunrise (0400 hrs) until just after sunset (2200 hrs). Samples taken from 2200 hrs to 0400 hrs were dominated by euphausiids. Average volume of prey items (stomach fullness) ranged from 0.5 cc to 1.0 cc from 0400 hrs to 2200 hrs but increased dramatically to 2.9 cc to 4.3 cc from 2200 hrs to 0400 hrs (fig. 5).

Inlet/Coastal Comparison

Sardines collected in 2005 aboard commercial vessels in WCVI inlets fed primarily (%V) on diatoms (62.22%)

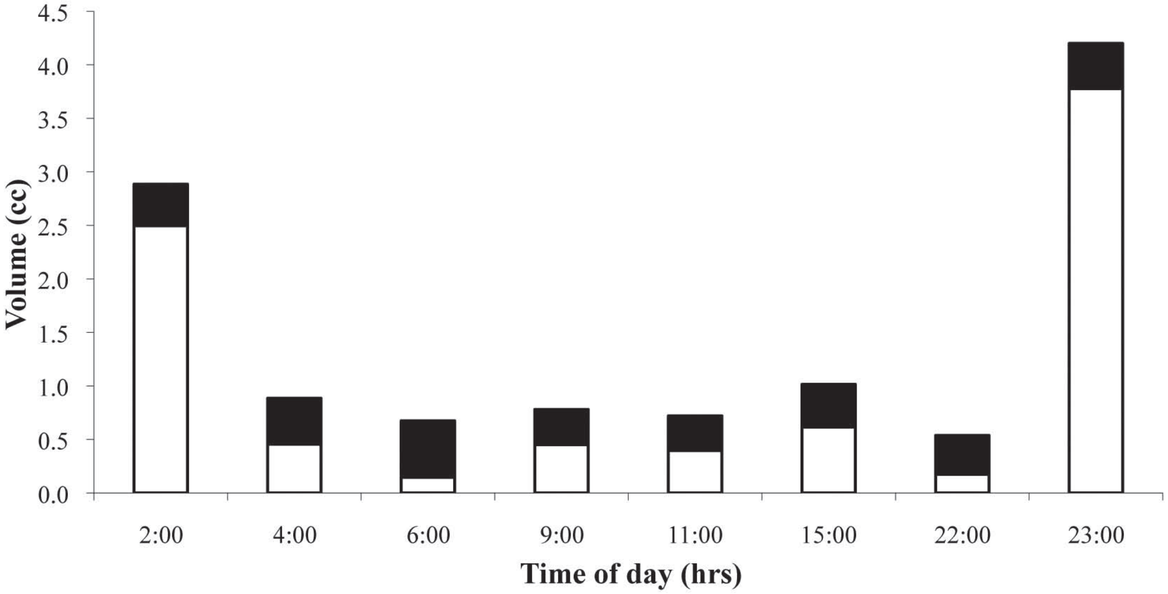


Figure 5. Hourly summary of average total stomach volume (open bar) and average volume of digested matter (dark bar) of the Pacific sardine (*Sardinops sagax*). Sample size of 20 stomachs for all hours with the exception of 11:00 and 22:00 where the sample sizes are 19 and 40 respectively. Average sunrise and sunset times during this period were 06:05 PDT and 20:51 PDT respectively.

composed mainly of *Thalassiosira* sp., *Skeletonema* sp. and *Ditylum* sp.; copepods (18.51%), mainly *A. longiremis* and *C. abdominalis*; and euphausiid eggs (11.55%). Sardines collected from coastal research sets at the same time fed mainly on euphausiids (59.97%), both *E. pacifica* and *T. spinifera*, and diatoms (16.61%) mainly *Skeletonema* sp., *Thalassiosira* sp., *Ditylum* sp., dinoflagellates, and *Pleurosigma* sp.; and copepods (18.26%) mainly *A. longiremis* (fig. 1). Although euphausiids dominated the diet of coastal samples by volume (fig. 1), %RI values show that they were slightly less important than copepods and diatoms (tab. 2, fig. 2).

DISCUSSION

In general, our study of sardine diets indicates sardines prey primarily on phytoplankton (diatoms), copepods and euphausiids (including euphausiid eggs), accounting for > 80% (by volume) of diet in most years. This confirms earlier preliminary work in this area (Hart and Wailes 1931; McFarlane et al. 2005), and is similar to previous studies in other areas of the northeast Pacific (Emmett et al. 2005) and Alaska (Wing et al. 2000). The relative contribution of primary prey items varied considerably seasonally and annually. For example, euphausiid were the most important prey item in 1997, 2005, 2006 and 2008 but were virtually absent in 1999, 2001, 2003 and 2004. In contrast, phytoplankton (mainly diatoms) were virtually absent in 1997, 1999 and 2004 but were the dominant prey item in 1998 and 2002 and important in sardine diet in all other years. Copepods were important in all years after 1999 but were rarely consumed in 1997 and 1998. Similarly, seasonal diet composition reflects the same changes in the relative contribution of dominant prey items. These seasonal and annual variations most likely reflect changes in availability and/or abundance of major prey groups illustrating the opportunistic feeding behaviour of sardines. Changes in the distribution and abundance of prey items have been linked to changes in ocean conditions (Peterson and Schwing 2003; King 2005; Mackas et al. 2009) indicating that sardine may be a key species for monitoring ocean productivity changes on annual and decadal scales.

Dominant prey groups found in sardine diet each year match groups identified by Mackas and Tsuda (1999) as major contributors to the zooplankton biomass throughout the oceanic subarctic Pacific, both locally and at a basin scale. Mackas et al. (2009) found most zooplankton taxa underwent large year–to-year variations in abundance during the study period off the WCVI. For example, the euphausiids *E. pacifica* and *T. spinifera* were low in abundance before 1987, increased in abundance in the late 1980s through the early 1990s, then levelled off or declined by the late 1990s (Mackas et al. 2009). In particular, *E. pacifica* was high in abundance in 1997 and 1998 and well below average or average from 1999 to 2003, followed by above average to average since. Our diet data indicate that *E. pacifica* and *T. spinifera* were important prey items in 1998 but declined in importance thereafter until 2004 when they dominated sardine diets once again.

Species assemblage shifts of copepods observed during our study period (Mackas et al. 2009) was only loosely correlated with prominent species present in sardine diets. This could be a reflection of the dominance of *A. longiremis*, *C. abdominalis* and *Pseudocalanus* sp. in the diet in all years since 1999, or a function of sample timing (seasonally and temporally).

We found no major shifts in the dominant phytoplankton species present in sardine diets over the study period with *Coscinodiscus* sp., *Thalassiosira* sp., *Skeletonema* sp. and *Ditylum* sp. dominating in all years. The lack of species identified in 1998 and 1999 is a refection of identification standards in the early years of our study and not an absence of phytoplankton in the diet.

We believe the overall seasonal and annual variation in major prey groups (but not major shifts in prey species within groups), coupled with the number of other prey groups which include unusual major contribution to sardine diet in some years (Oikopleurids in 1999 and 2003; shrimps in 2004) confirm the opportunistic feeding behaviour of sardines off Vancouver Island.

Given their opportunistic plankton feeding, it is not surprising that the diet comparison between years showed high or very high overlap for many years and low overlap for others. This is a reflection of the opportunistic nature of sardine predation and the variability in abundance (availability) of the major prey groups annually.

Analysis of stomach contents and fullness over two 24 hour periods in 2005 indicated sardines feed throughout the 24 hour period but had a peak in feeding activity after dusk (2200–0400 hrs). During this time, they preyed primarily on euphausiids. At all other times, they fed primarily on copepods and diatoms. This probably reflects movement of euphausiids upwards in the water column after dusk into the feeding regions of sardine.

Our study also indicated sardines showed inshore (inlets)/offshore differences in feeding, with phytoplankton (diatoms) and copepods dominating the inshore samples and offshore (coastal) sardines feeding more heavily on euphausiids, similar to feeding behavior reported by Emmett et al. (2005). This is a reflection of the abundance (availability) of these prey species in these areas, again indicating the opportunistic feeding behaviour of sardines.

The return or increase of large numbers of Pacific sardine (*Sardinops sagax*) to waters off California, Oregon, Washington and British Columbia, after an absence of almost 60 years, stimulated great interest in understanding the factors which influence both the numeric and geographic elements of sardine populations. Recent studies have shown that large-scale climate changes (regime shifts) can be associated with fluctuations in sardine abundance and distribution (McFarlane et al. 2002). Decadal scale changes in abundance and distribution of sardine populations in the North Pacific may be responding to these ecosystem changes in a fundamental, but as yet little understood, way. It is beyond the scope of this paper to specifically examine linkages between changes in ocean conditions and sardine dynamics. However, considering and answering the questions of natural variability in sardine stocks is key to understanding the underlying mechanisms of ecosystem change in the North Pacific.

One approach to examining the role of sardines in the CCS is to examine the feeding behaviour of sardine and their predators over the entire CCS and develop ecotrophic models which will allow us to test hypotheses regarding the expansion and contraction of this population. As mentioned, changes in distribution and abundance of plankton species have been linked to changes in oceanographic conditions (King 2005). Monitoring sardine diet may provide immediate feedback on changing ocean conditions, since sardines opportunistically prey on organisms directly impacted by these changes. We believe current studies along the west coast of North America from Canada to Mexico should be expanded to include detailed annual diet analysis with the goal of developing improved ecosystem assessments and management strategies.

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LITERATURE CITED

Barange, M., J. Coetzee, A. Takasuka, K. Hill, M. Gutierrez, Y. Oozeki, C. van der Lingen, and V. Agostini. 2009. Habitat expansion and contraction in anchovy and sardine populations. Prog. in Oceanogr. 83: 251–260.

Baumgartner, T. R., A. Soutar, and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. Calif. Coop. Fish. Invest. Rep. 33: 24–40.

Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and C. M. Niquen. 2003. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. Science 229: 217–221.

Checkley, D. M., Jr., J. Alheit, Y. Oozeki, and C. Roy (eds.) 2009. Climate Change and Small Pelagic Fish, Cambridge University Press. 372 pp.

Emmett, R. L., R.D. Brodeur, T. W. Miller, S.S. Pool, G.K. Krutzikowsky, P. J. Bentley, J. McCrae. 2005. Pacific Sardine Northwest Ecology Calif. Coop. Fish. Invest. Rep. 46: 122–143.

Hart, J. L., and G. H. Wailes. 1931. The food of the pilchard, *Sardinops caerulea* (Girard), off the coast of British Columbia. Contrib. Can. Biol.Fish. 7:245–254.

Hill, K.T., E. Dorval, N. C. H. Lo, B. J. Macewicz, C. Show, and R. Felix-Uraga. 2008. Assessment of the Pacific sardine resource in 2008 for U.S. management in 2009. Pacific Fishery Management Council, November 2008 Briefing Book, Agenda Item G.2.b. Supplemental Attachment 1. 147 pp.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Amer. Nat. 100: 419–424.

Kawasaki, T. 1983. Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuation from the viewpoint of evolutionary ecology. FAO Fisheries Report 291: 1065–1080.

King, J. (Ed.). 2005. Report of the Study Group on Fisheries and Ecosystem Responses to Recent Regime Shifts. PICES Sci. Rep. 28: 162 p.

King, J. R., and R. J. Beamish. 2000. Diet composition indicate a competitive interaction between Ocean Age – 0 chum and coho salmon. N. Pac. Anadr. Fish. Comm. Bull. No. 2: 65–74.

Landingham, J. H., M.V. Sturdevant, and R. D. Brodeur. 1998. Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia. Fish. Bull. 96: 285–302.

Lasker, R. 1970. Utilization of zooplankton energy by a Pacific sardine population in the California Current. *In* Marine Food Chains. J. H. Steele, Ed. Edinburgh: Oliver and Boyd, Ltd., pp. 265–284.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. 73: 453–462.

Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: Contrasting years 1975 through 1978. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 375–388.

Logerwell, E. A., and P. E. Smith. 2001. Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. Fish. Oceanogr. 10: 13–25.

McFarlane, G. A., and R. J. Beamish. 2001. The re-occurrence of sardines off British Columbia characterises the dynamic nature of regimes. Prog. Oceanogr. 49: 151–165.

McFarlane, G. A., L. Macdougall, J. Schweigert, C. Hrabok. 2005. Distribution and biology of the Pacific sardine (*Sardinops sagax*) off British Columbia, Canada. CalCOFI Rep., Vol. 46: 144–160.

McFarlane, G. A., P. E. Smith, T. R. Baumgartner, and J. R. Hunter. 2002. Climate variability and Pacific sardine populations and fisheries. Am. Fish. Soc. Symp. 32: 195–214.

Mackas, D. L., and A. Tsuda. 1999. Mesozooplankton in the eastern and western subarctic Pacific: community structure, seasonal life histories, and interannual variability. Prog. Oceanogr. 43: 335–363.

Mackas, D. L., M. Galbraith, and D. Faust. 2009. Zooplankton community returns to "cool-ocean" pattern off Vancouver Island. *In* W. R. Crawford and J. R. Irvine, State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems. CSAS Res.Doc. 2009/022: 129 pp.

Peterson, W. T., and F. B. Schwing. 2003. A new climate regime in northeast Pacific ecosystems. Geophys. Res. Letters Vol. 30 (17): 1896.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Fish. Bull. 152: 1–105.

Rykaczewski, R. R., and D. M. Checkley, Jr. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proc. Nat. Acad. Sci. 105: 1965–1970.

Watanabe, Y., and H. Saito. 1998. Feeding and growth of early juvenile Japanese sardines in the Pacific waters off central Japan. J. Fish. Biol. 52: 519–530.

Wing, B. L., J. M. Murphy, and T. Rutecki. 2000. Occurrence of Pacific sardine, *Sardinops sagax*, in southeastern Alaska. U.S.Fish. Bull., 98: 881–883.

UNPRECEDENTED MORTALITY OF CALIFORNIA SEA LION PUPS ASSOCIATED WITH ANOMALOUS OCEANOGRAPHIC CONDITIONS ALONG THE CENTRAL CALIFORNIA COAST IN 2009

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ABSTRACT

Between May and August 2009, an anomalous oceanographic event occurred along the central California coast. The event was characterized by the strongest negative upwelling observed in 40 years and uncharacteristically warm sea surface temperatures. The timing of the event coincided with the weaning and reproduction of California sea lions in the California Current System. We documented the effects of the event on sea lion pup production, pup mortality, female attendance, and diet at San Miguel Island, California. Simultaneous with the oceanographic event, we also documented a record number of strandings along the California coast of emaciated weaned pups born in 2008. We conclude that the response of California sea lions to the anomalous oceanographic conditions in 2009 was mediated through warmer SSTs that likely reduced availability of their usual summer prey and resulted in the high mortality of the 2008 and 2009 cohorts due to starvation.

INTRODUCTION

The California sea lion (*Zalophus californianus*) population has been growing steadily since its protection under the Marine Mammal Protection Act of 1972 (Caretta et al. 2007). During its period of rapid growth in the 1970s and 1980s, the population experienced significant declines in production during 1982–1983, 1992–1993 and 1998 that were associated with El Niño (EN) events (DeLong et al. 1991; DeLong and Melin 2000; Caretta et al. 2007). The response of California sea lions to EN conditions is presumably mediated through a change in the availability of fish and cephalopods, the primary prey of California sea lions (DeLong et al. 1991; DeLong and Melin 2000). In the California Current System (CCS), EN conditions are characterized by a change in sea level pressure that leads to increased coastal sea level height (Norton et al. 1985), delayed onset of the upwelling season (Bograd et al. 2009), a decrease in the upwelling strength, increased sea surface temperature (SST), and suppression of the thermocline (Norton et al. 1985). These changes result in lower productivity at lower trophic levels which results in reduced availability of fish and cephalopods at upper trophic levels (Barber and Chavez 1983; Chavez et al. 2002). However, anomalous oceanographic conditions also occur outside EN and can have similar effects on the marine community structure at local or regional scales (Schwing et al. 2006). In 2005, a delayed onset of the seasonal upwelling in the northern CCS resulted from a regional shift in oceanographic dynamics (Schwing et al. 2006) and declines in productivity at various trophic levels were reported (Brodeur et al. 2006; Mackas et al. 2006; Sydeman et al. 2006; Thomas and Brickley 2006).

In 2009, and EN in the tropics was confirmed in July (http://www.noaanews.noaa.gov/stories2009/20090709_elnino.html). But, a regional anomalous oceanographic event began two months earlier in the south and central CCS. After a normal start to the upwelling season with strong positive upwelling conditions from February through April in the CCS, a shift to negative upwelling occurred in May (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html). The negative upwelling intensified in June and became the strongest negative upwelling event in the past 40 years. SSTs along the central coast were uncharacteristically warm as a result of the reduced upwelling. By September, positive upwelling conditions and cooler SSTs had returned to the CCS. The timing of the event was simultaneous with the weaning and reproductive seasons for California sea lions breeding in the southern CCS. Here, we document the unprecedented mortality of pups born at San Miguel Island, California, and a record number of strandings of emaciated, weaned pups from the 2008 cohort along the central California coast that occurred during the event.

California Sea Lion Life History

California sea lions are permanent residents of the CCS, ranging from northern Mexico to southern Canada. In the United States, the primary breeding colonies are the California Channel Islands. Weaning

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and reproduction occur during late spring and summer, during the peak upwelling period in the CCS (Bograd et al. 2009). During the reproductive season, adult females give birth to a single pup during a 6-week period from late May to the end of June (Peterson and Bartholomew 1967). Lactation lasts up to 11 months or longer. During this time, lactating females travel to sea for 2–5 days to feed and return to the colony for 2 days to nurse their pup (Antonelis et al. 1990; Melin et al. 2000). The pup is solely dependent on its mother until about 6 months old and maintains a fasting cycle while the mother is on foraging trips. The weaning process is gradual and the timing of weaning is poorly known but it begins as early as 8 months old. Peak weaning occurs in April or May when pups are between 10 and 11 months old (Melin et al. 2000).

Adult females and pups from San Miguel Island generally remain south of Monterey Bay, California year-round and feed in coastal waters in the summer and move offshore in the winter (Melin and DeLong 2000; Melin et al. 2008). California sea lions in the Channel Islands feed on more than 30 fish and cephalopod species (Antonelis et al. 1984; Lowry et al. 1990; Antonelis et al. 1990; Lowry 1991) and generally feed within 75 m of the surface but have been reported to dive deeper than 480 m (Feldkamp et al. 1989; Melin et al. 2008).

Oceanographic Indices

The most dominant feature of the CCS is the seasonal upwelling that occurs between January and November each year (Lynn and Simpson 1987; Bograd et al. 2009). Off the central California coast (Point Conception to Cape Mendocino), peak upwelling and productivity usually occurs between April and July when California sea lion pups born the previous year are weaned and a new cohort is born.

During periods of strong negative upwelling in the CCS, such as during ENSO events, regional productivity declines and lactating female California sea lions travel farther from the colony, move farther offshore and dive deeper presumably in response to movement of their prey deeper in the water column or to more productive areas (Melin et al. 2008). Because lactating females are restricted in the distance they can travel and the time they are away from the colony by the fasting capabilities of their pups, movement of their prey outside their normal foraging range (spatially or temporally) results in longer foraging trips (Melin et al. 2000; Melin et al. 2008). This can have negative consequences for a dependent pup. If the duration of the foraging trip exceeds the fasting capability of the pup, the pup may die from starvation and if the female is unable to obtain enough prey or energy for self-maintenance and lactation, she may not be able to support her pup. For newly weaned pups, the movement of prey out of their foraging range or to deeper depths may result in starvation (Fowler et al. 2007). Thus, indices of upwelling strength and SST may provide proxies for prey availability and explain events like the unusually high pup mortality at San Miguel Island and high incidence of stranded yearlings observed along the central California coast in 2009. Here, we use oceanographic indices to explain annual patterns in pup production and mortality indices of the California sea lion population at San Miguel Island, California, and strandings of weaned pups along the central California coast between 1997 and 2009.

METHODS

California Sea Lion Population Indices

Study Sites We measured several population indices for the California sea lion population at San Miguel Island, California (34.03°N, 120.4°W). San Miguel Island represents the northern extent of the breeding range and is one of the largest colonies in the Channel Islands representing about 45% of the U. S. breeding population. As such, it is a useful colony to measure trends and population responses to changes in the marine environment. Because of the large size of the colony, we used index sites for measuring the population parameters. The East Adams Cove Study Area (EACS) is a long-term index site for measuring the timing of reproductive events of a small group of animals (~800 females). West Shelf Rock (WSR) is a small rocky cove where individually marked animals are easily observed and was used as the site for monitoring attendance cycles of females in 2009. The Point Bennett Study Area (PBSA) is used as a long-term index site for monitoring pup production and mortality. About 50% of the pup production that occurs at San Miguel Island takes place in this area, so it provides an index of trends for the entire colony.

Median Birthing Date Between 15 May and 20 July each year between 1997 and 2009, the total numbers of live and dead sea lion pups in the EACS were counted daily to obtain a cumulative count of pups born over the reproductive season. The median birth date was calculated as the date by which 50% of the pups were born. The temporal trend in births was described from the weekly maximum number of pups counted in the EACS. The long-term means for median birth date and maximum number of pups were calculated for 1997–2008, excluding 1998. We excluded 1998 from the long-term dataset because it was an ENSO year and the temporal pattern of births and median birth date were abnormal.

Female Attendance Cycle We conducted 12-hour daily observations of seven branded females at WSR between 19 June and 21 July 2009. Once a female gave birth, we monitored her attendance. If a female was observed at any time during the observation period, she was considered present for the full day. The small size of the cove and the intensive observation time each day made it unlikely that a female that was present would not be observed. The first foraging trip (post-natal trip) was shorter than subsequent trips for all females (Student's paired T-test, $p = 0.03$), so we calculated a mean for the first trip and a mean for all subsequent trips. A nested analysis of variance (ANOVA) with foraging trips nested within individual females was used to calculate the overall mean for the foraging trips that occurred after the post-natal trips. We compared the attendance pattern in 2009 with previous studies at San Miguel Island in the 1980s (Feldkamp et al. 1989; Antonelis et al. 1990).

Pup Mortality Pup mortality surveys were conducted every 2 weeks from 25 June to early August between 1997 and 2009 in the PBSA as an index of pup mortality for the population. A final survey was conducted the last week of September. Dead pups were removed from the breeding areas as they were counted so they would not be recounted on subsequent surveys. The total number of observed dead pups for each survey described the temporal trend in pup mortality and was an estimate of the cumulative mortality of pups at 5 weeks and 3.5 months of age.

Pup Production Live pups were counted in the PBSA after all pups were born (between 20–30 July) each year between 1997 and 2009. Observers walked through the PBSA, moved adults away from pups, and then counted individual pups. A mean number of live pups for the PBSA was calculated from the total number of live pups counted by each observer. Total production was the sum of the mean number of live pups and the cumulative number of dead pups counted up to the time of the live pup survey. Cumulative pup mortality at 5 weeks of age was calculated as the proportion of dead pups of those counted during the live pup survey. This mortality rate was used to model pup mortality trends over time.

Strandings of California Sea Lion Pups We compiled stranding data for animals that live stranded from San Luis Obispo to Mendocino counties in central California and that were transported to The Marine Mammal Center (TMMC) in Sausalito, California, for rehabilitation to describe trends in strandings of weaned pups between 1997 and 2009. We restricted the stranding dataset to those recovered by TMMC because they are responsible for strandings that occur over the largest area of the central coast and have had consistent recovery effort from 1997 to 2009. The stranding data represent the minimum number of animals that stranded in any year because strandings that occurred in remote areas are not reported and animals that died prior to collection were not included. We excluded dead animals because the cause of death could not be determined. We restricted the dataset to pups of the year that were evaluated by veterinarians at the TMMC to have stranded due to starvation. Pups were classified as animals that were between 0- and 1-year-old with a birth date of 15 June.

Diet Composition and Prey Identification We collected fecal samples from adult female California sea lion haul out areas at San Miguel Island in July or early August in the early 2000s (2000, 2001, 2002, 2004, 2005) and 2009 to examine the diet. Individual samples were placed in bags and frozen until they were processed for prey identification. Fecal samples contained in nylon paint strainer bags were washed in a washing machine to remove fecal matter and the remaining contents were washed through nested sieves to recover fish bones, fish otoliths and cephalopod hard parts that were then identified to family, genus or species (Orr et al. 2003). The similarity of key otolith structures and the degradation from digestion of *Sebastes* spp. otoliths made species identification difficult and we used the genus rather than risk misidentification of the species. Using all identifiable structures, the frequency of occurrence (FO) of each fish taxon was calculated as the number of samples containing the taxon of the total samples with identifiable prey remains. We used FO as a conservative relative measure of prey importance because of the biases associated with extrapolating from fecal contents to biomass or percent mass of prey consumed by pinnipeds (Laake et al. 2002; Joy et al. 2006). The primary fish taxons were defined as those that had FO greater than 10% in any year.

We calculated the diet composition as the percentage of samples that contained fish only, mixed fish and cephalopod, or cephalopod remains only. For each diet component and each fish taxon, a general linear model was constructed to test differences between 2009 and the other years.

Oceanographic Indices

Upwelling Index Anomaly We used a monthly coastal upwelling index (UWI) anomaly between 1997 and 2009 as an index of monthly productivity and prey availability (Schwing et al. 2006). The upwelling index anomaly dataset was obtained from NOAA's Pacific Fisheries Environmental Laboratory (http://pfel.noaa.gov). We used the 33°N 119°W and 36°N 122°W indices because they encompassed the foraging range of juvenile and lactating female California sea lions (fig. 1). The baseline index was calculated from monthly means of upwelling between 1946 and 1986. The

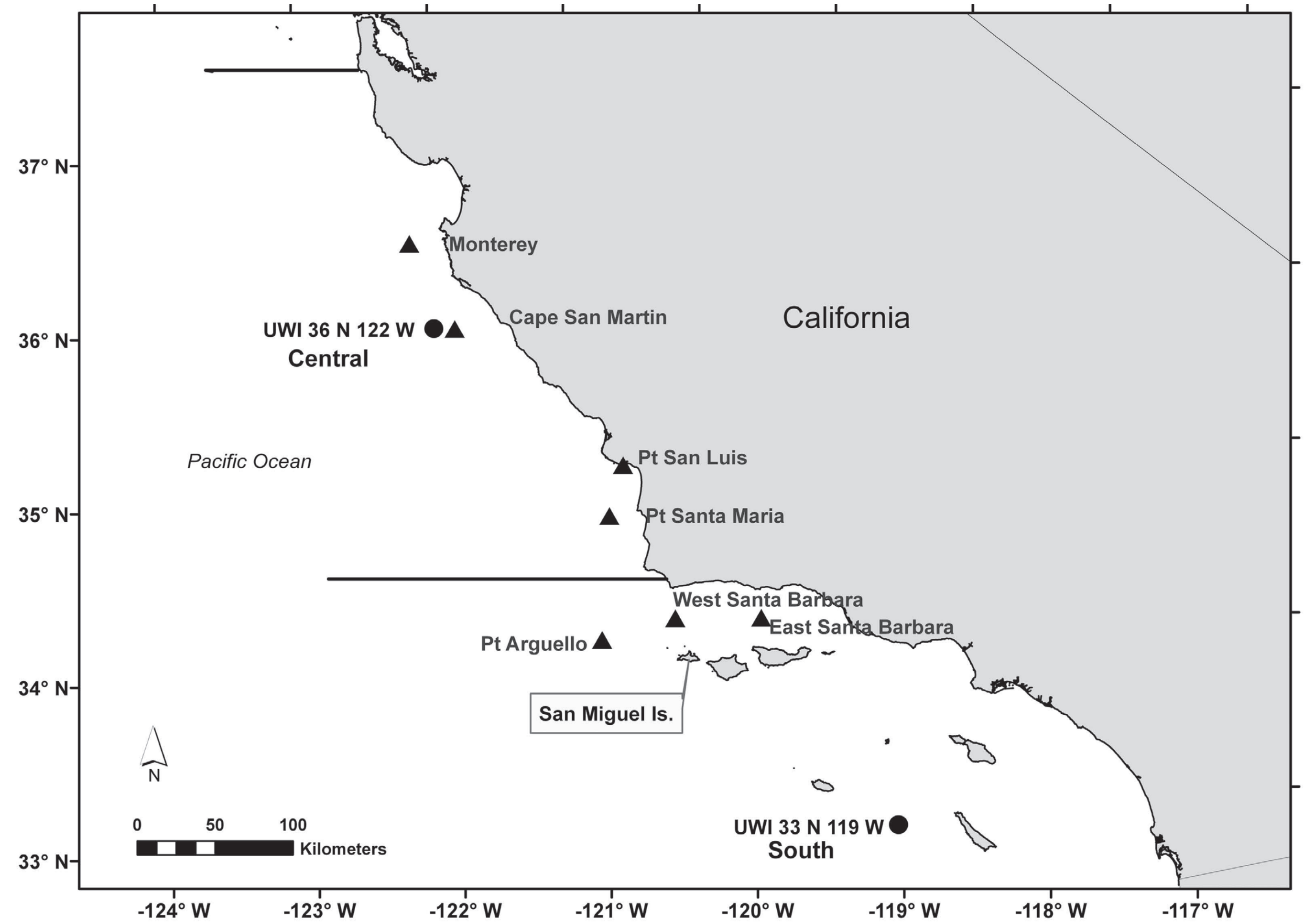

Figure 1. Positions of buoys used to calculate the monthly sea surface temperature index (SSTI) anomaly (▲) and center positions of the monthly upwelling index (UWI) anomaly (●) based on 3° grids. South and central regions for the UWI are defined by horizontal lines.

monthly upwelling anomalies within each year are the difference between the baseline mean and the annual monthly mean.

Sea Surface Temperature Anomaly We used SST anomalies as an indicator of prey availability. We calculated a daily mean SST from seven buoys along the central California coast (fig. 1). The buoy data were obtained from the NOAA National Data Buoy Center (http://www.ndbc.noaa.gov/rmd.shtml). We used the mean daily SST to calculate a mean monthly SST for each buoy and then created a monthly baseline SST for each buoy for the periods 1994 to 1996 and 1998 to 2008. Data for 1997 were not available for many of the months at several buoys, so it was excluded from the baseline calculation. For each buoy, the baseline monthly SST was subtracted from the mean SST value for each month in each year from 1997 to 2009 to construct a time series of anomalies. The anomalies were averaged across the buoys for each month to create a sea surface temperature anomaly index (SSTI).

Model of Early Pup Mortality and Oceanographic Indices

We used R (R Core Development Team 2009) to develop linear models that included year, SSTI and UWI indices to explain the variability in pup mortality at 5 weeks of age between 1997 and 2009. We created four temporal variables for SSTI and UWI to reflect lags in the response of sea lions to oceanographic changes. The variables were as follows: April to July, May to July, May to June, and June to July. We also created a June only and July only variable to account for an immediate impact of oceanographic changes on pup mortality. For the UWI, we created separate variables for 33°N 119°W and 36°N 122°W for each temporal variable. We used the Akaike Information Criterion

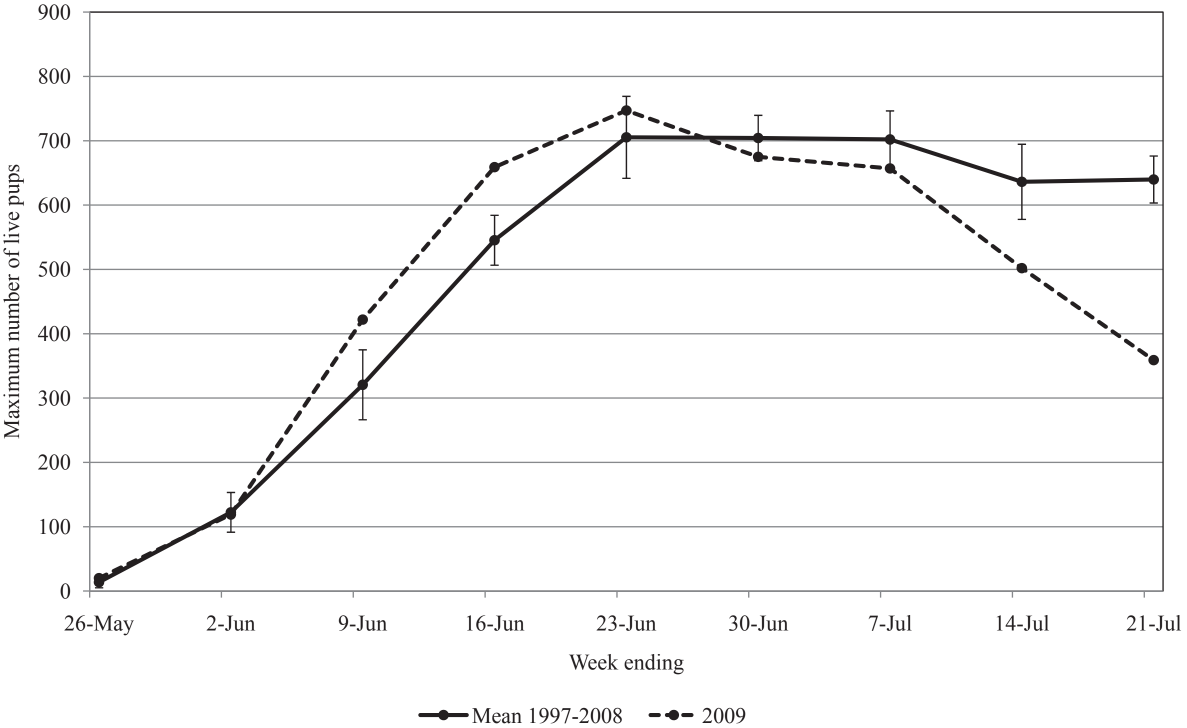

Figure 2. The weekly mean of the maximum number of live California sea lion pups counted in the East Adams Cove Study Area (EACS) at San Miguel Island, California, for 1997 to 2008 and the weekly maximum number of live pups counted in 2009. Error bars represent one standard error about the mean.

adjusted for small sample sizes (AICc) to select the best model (Burnham and Anderson 2002).

RESULTS

California Sea Lion Population Indices

Median Birthing Date Births in the EACS in 2009 followed the long-term pattern with females giving birth beginning in late May, a median birth date of 9 June (1997–2008: mean = 10 June, SE = 0.982 days), the maximum number of live pups occurring by 23 June, and birthing completed by 30 June (fig. 2). The decline in the number of live pups after 7 July in 2009 reflects the high early pup mortality that occurred in late June and early July.

Female Attendance Cycle Seven lactating females made between two and six foraging trips between 19 June and 21 July 2009. The mean post-natal foraging trip duration was 4.3 days (SE = 0.57 days). The mean of all subsequent trips was 7 days (SE = 1.89 days). The mean duration of the visits ashore was not different between the first visit after the post-natal foraging trip and subsequent visits (Student's paired T-test, $p = 0.57$) so the data were pooled. The mean visit ashore for the seven females was 1.9 days (SE = 0.82 days). Previous studies reported mean foraging trip durations of 3.1 days ($n = 25$ females, SE = 0.17 days; Antonelis et al. 1990) and 2.5 days ($n = 8$ females, SE = 0.49 days; Feldkamp et al. 1989) and visits ashore of 2.1 days (SE = 0.16 days; Antonelis et al. 1990).

Pup Production and Mortality The estimated 2009 pup production for the PBSA was 14651 pups. This was similar to the long-term mean between 1997 and 2008 of 14521 (SE = 695 pups) (fig. 3). But early pup mortality during the first 5 weeks of life was 74% in 2009, almost four times greater than the long-term average of 18.7% (SE = 1.6%) (fig. 3).

Pup mortality to 3.5 months of age in 2009 had a dramatically different temporal pattern and magnitude from the long-term average (fig. 4). Pup mortality normally declines slowly from birth, reaching 15% by 1 month of age (fig. 4). The mortality accelerates between 2 and 3 months of age, culminating in a pup mortality rate of about 33% at 3.5 months of age. In 2009, most of the pup mortality occurred early in the season with 65% of the mortality occurring by 1 month of age (fig. 4). By 3.5 months of age, 80% of the pups born in 2009 had died.

Strandings of California sea lion pups Strandings of emaciated pups from the 2008 cohort occurred in record numbers between San Luis Obispo and Mendocino counties in central California in 2009. The long-term mean from the 1997–2008 cohorts was 70 pups per year (SE = 24.0) but in 2009, 640 pups were recovered (fig. 5). Most of the strandings in 2009 occurred between May and August (92%) (fig. 6). Within this

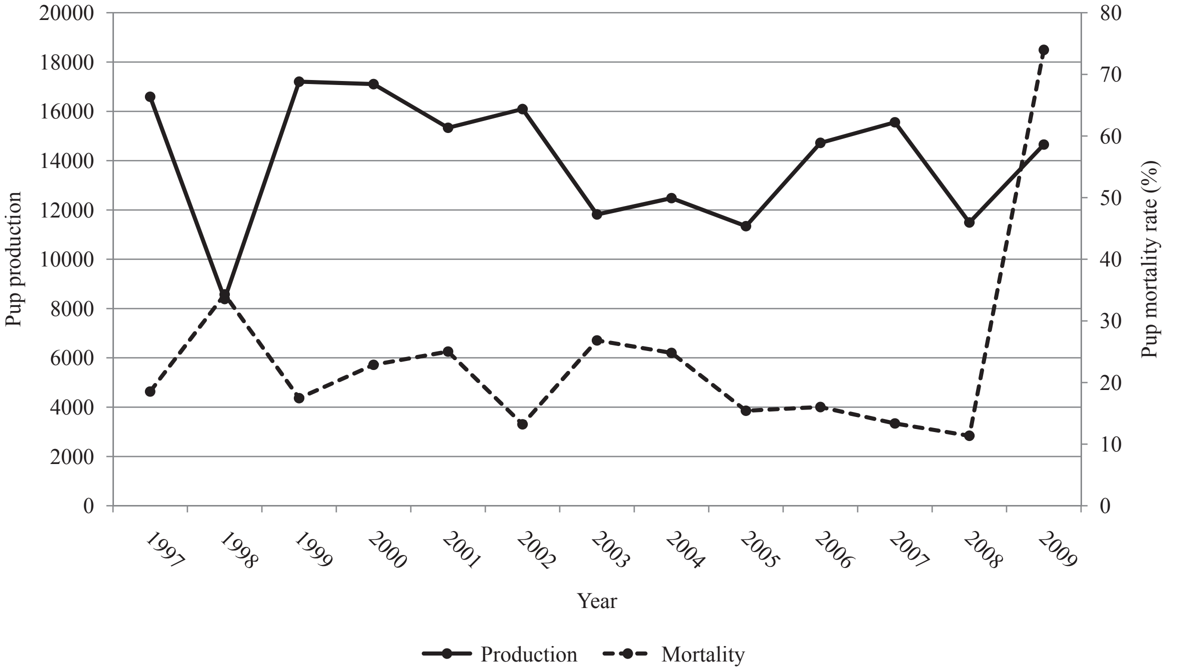

Figure 3. The pup mortality rate at 5 weeks of age and the annual pup production of California sea lions in the Point Bennett Study Area (PBSA) on San Miguel Island, California, between 1997 and 2009.

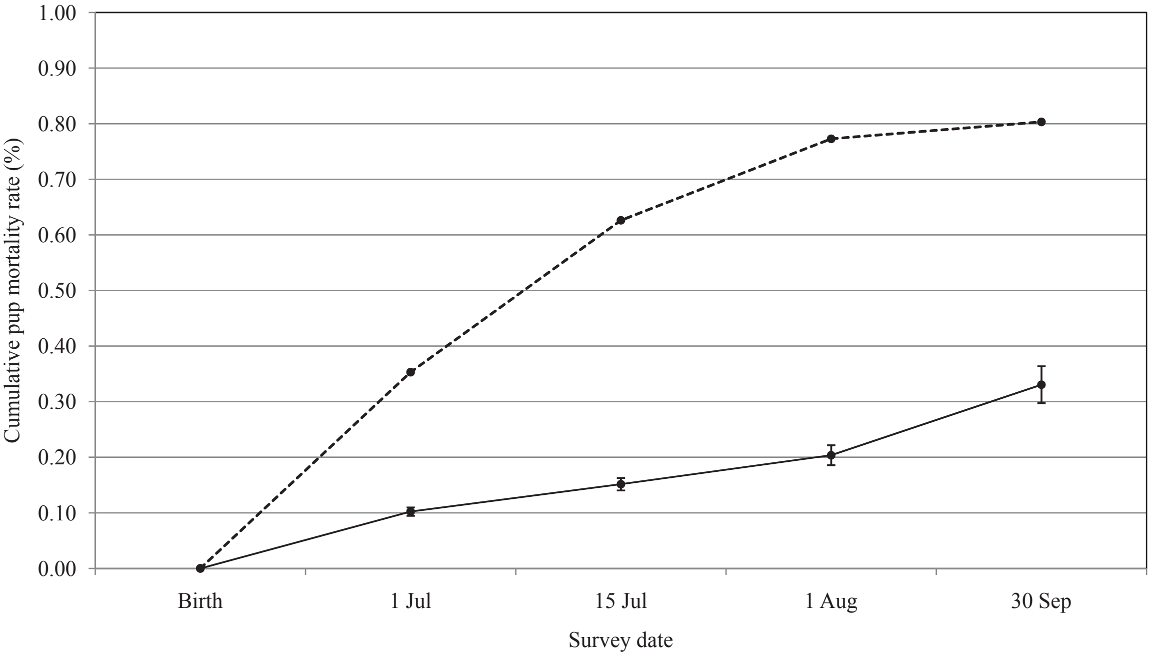

Figure 4. The mean cumulative pup mortality rate for California sea lion pups in the Point Bennett Study Area (PBSA) on San Miguel Island, California, between 1997 and 2008 and for 2009 from birth to 3.5 months of age. Error bars represent one standard error about the mean.

period, most of the strandings occurred in June corresponding to the period of the warmest SSTI and most negative UWI anomalies (figs. 7 and 8).

Diet Composition and Prey Identification We identified 36 fish taxons consumed by California sea lions including two new species not previously reported in the diet (tab. 1). Pacific hake, northern anchovy, Pacific sardine, rockfish, Pacific saury and jack mackerel comprised the primary fish prey. In the early 2000s, hake, anchovy and sardine dominated the fish diet, but in 2009 rockfish was the most frequent fish prey.

Fish and cephalopods comprised the diet of California sea lions during the summer and the frequency of the different components and primary fish prey varied

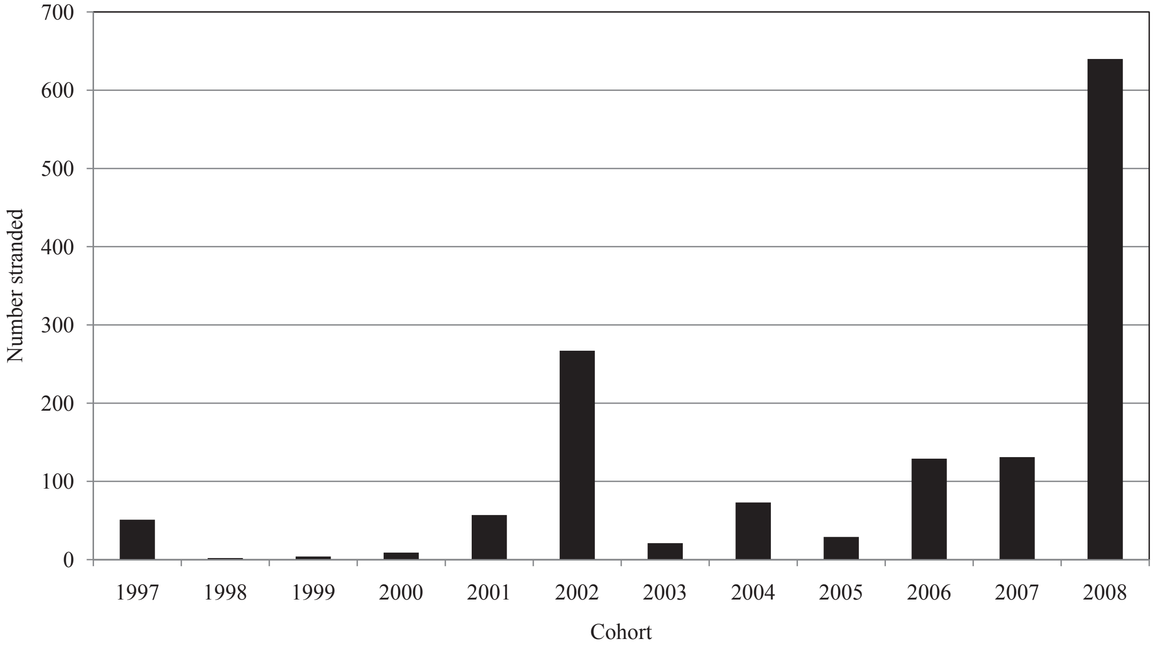

Figure 5. The annual number of weaned California sea lion pups by cohort that stranded due to emaciation between San Luis Obispo and Mendocino counties along the central California coast and that were evaluated by The Marine Mammal Center in Sausalito, California, between 1997 and 2009.

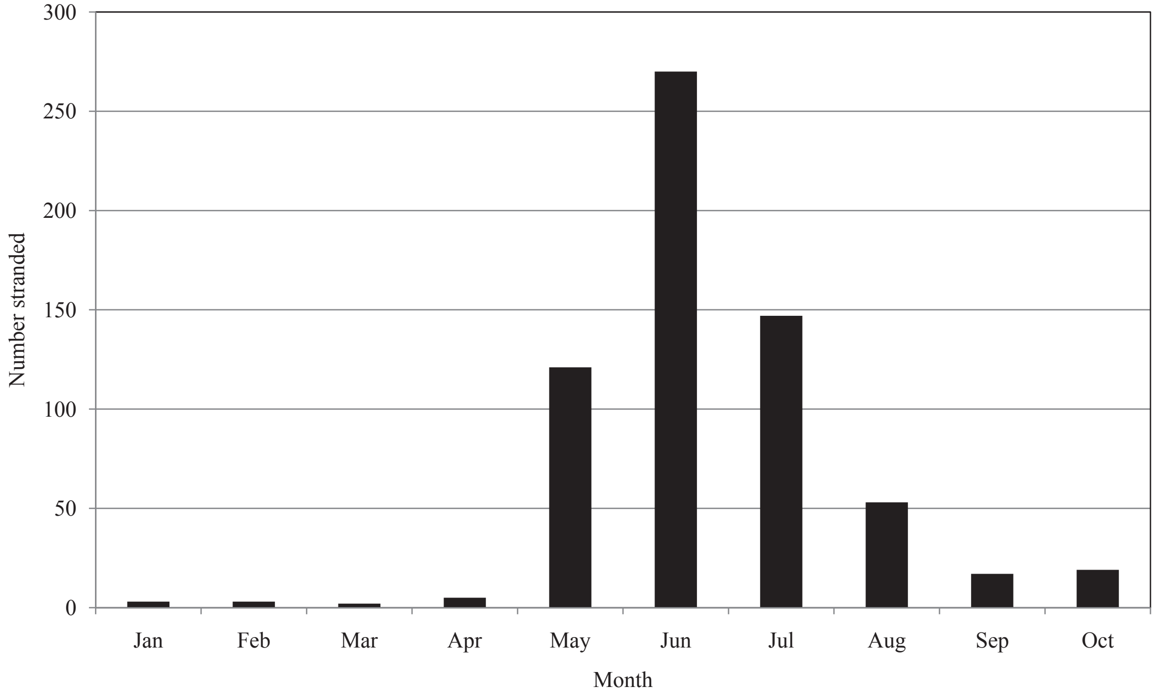

Figure 6. The monthly distribution of weaned California sea lion pups from the 2008 cohort that stranded due to emaciation between San Luis Obispo and Mendocino counties along the central California coast and that were evaluated by The Marine Mammal Center in Sausalito, California, in 2009.

significantly from 2009 for many of the years (tab. 2). In 2009, the diet was comprised of 30.7% fish, 30.8% cephalopod and 38.5% mixed fish and cephalopods (tab. 3). The percentage of cephalopod only in the diet was significantly higher in 2009 (ANOVA, p = 0.034). Rockfish was the only primary prey that was significantly different in 2009, occurring more frequently than in the early 2000s (ANOVA, p = 0.028) (tab. 3). The FO of northern anchovy, Pacific sardine, Pacific hake and Pacific saury were lower in 2009 than in the early 2000s but were not different for the two periods due to substantial annual variability in the frequencies of occurrence among the years (tab. 3).

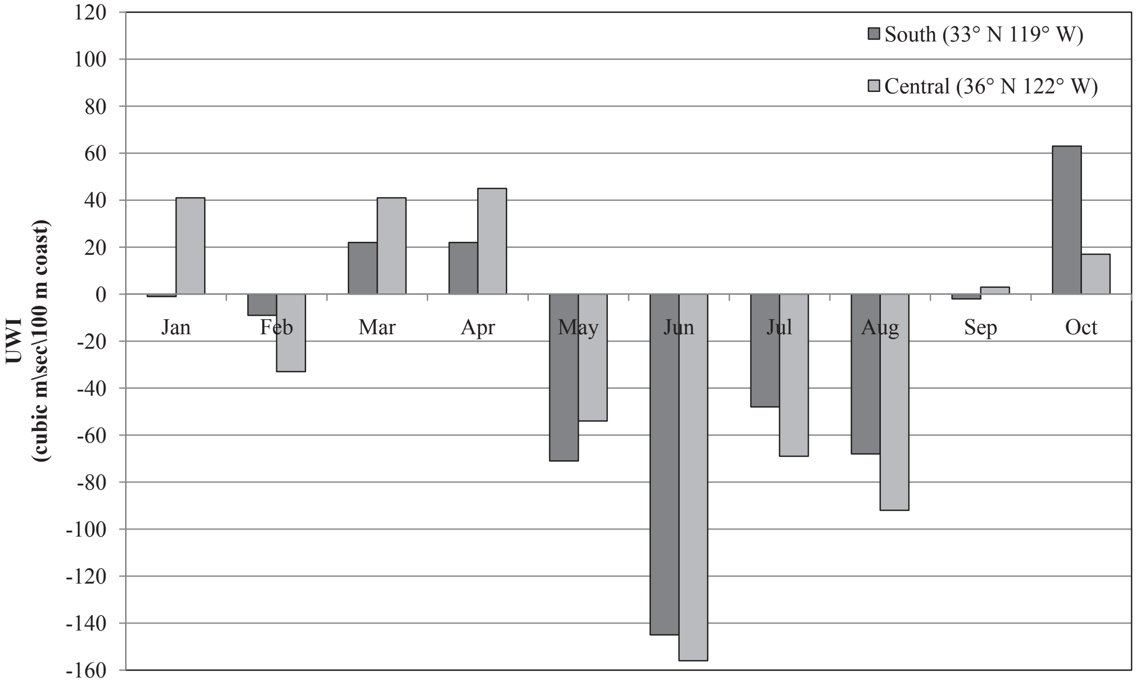

Figure 7. The monthly upwelling index (UWI) anomaly for the central and southern California coast in 2009. The baseline UWI anomaly was calculated for the years 1946 to 1986.

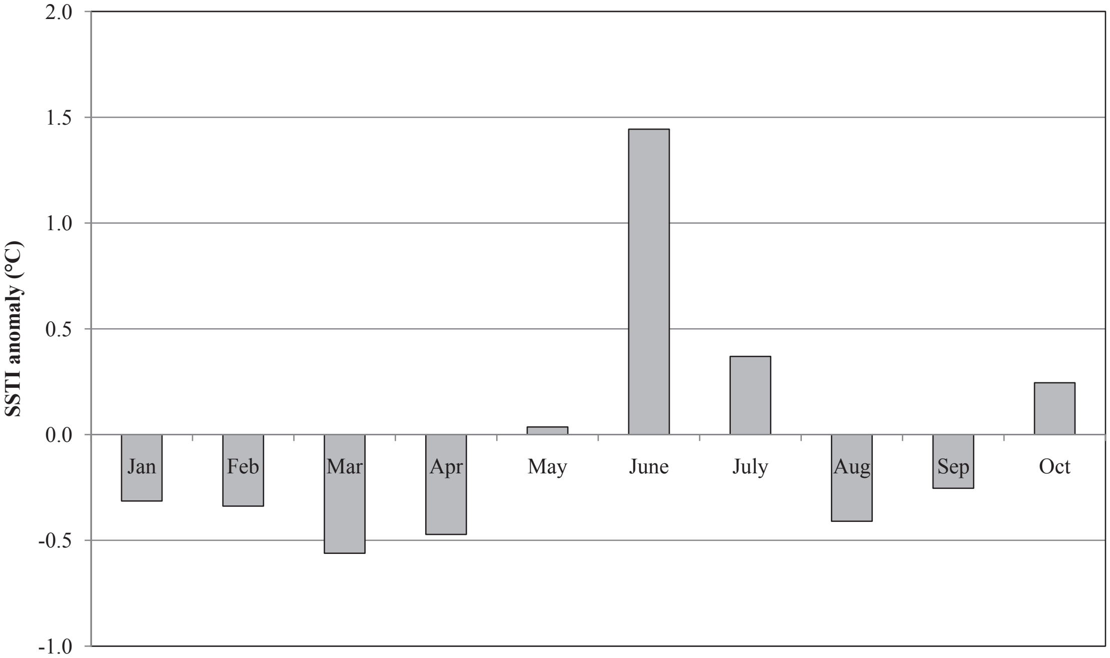

Figure 8. The monthly sea surface temperature index (SSTI) anomaly for seven buoys along the central California coast in 2009. The baseline SSTI anomaly is based on monthly means summarized for 1994–1996 and 1998–2008.

Oceanographic Indices

In 2009, the CCS experienced strong positive upwelling between January and April indicated by positive UWI anomalies (fig. 7). This is the normal pattern in the spring for the CCS. In May the central (36°N 122°W) and south (33°N 119°W) regions transitioned to a negative upwelling pattern indicated by negative UWI anomalies. The most negative UWI anomaly occurred in June. Upwelling anomalies remained negative through August, shifting to a positive upwelling pattern in September and October. SSTI anomalies were mostly negative during the strong positive upwell-

TABLE 1
Prey fish taxa consumed by California sea lions at San Miguel Island, California in July and early August in 2000, 2001, 2002, 2004, 2005 (Early 2000s) and 2009. Prey taxa were identified from hard parts recovered from fecal samples. '*n*' is number of fecal samples. '%FO' is percent Frequency of Occurrence. Primary prey indicated in bold. Shaded taxons are new species identified in the diet of California sea lions in the Channel Islands.

	% FO					
	Early 2000s					
Prey taxon	2000 (*n*=63)	2001 (*n*=61)	2002 (*n*=86)	2004 (*n*=91)	2005 (*n*=86)	2009 (*n*=44)
Rockfish, *Sebastes* spp.	**7.9**	**13.1**	**15.1**	**6.6**	**27.9**	**45.5**
Northern anchovy, *Engraulis mordax*	**68.3**	**23.0**	**10.5**	**67.0**	**39.5**	**25.0**
Pacific sardine, *Sardinops sagax*	**14.3**	**1.6**	**36.0**	**76.9**	**46.5**	**15.9**
Pacific hake, *Merluccius productus*	**55.6**	**80.3**	**40.7**	**28.6**	**55.8**	**13.6**
Pacific saury, *Cololabis saira*	**15.9**	**6.6**	**14.0**	**9.9**	**22.1**	**9.1**
Jack mackerel, *Trachurus symmetricus*	**1.6**	**9.8**	**0.0**	**2.2**	**10.5**	**6.8**
Northern lampfish, *Stenobrachius leucopsarus*	0.0	0.0	0.0	6.6	1.2	9.1
Pacific sanddab, *Citharichthys sordidus*	0.0	0.0	1.2	2.2	0.0	6.8
Spotted cuskeel, *Chilara taylori*	0.0	0.0	2.3	0.0	1.2	4.5
Sculpin, Cottidae	0.0	0.0	0.0	0.0	0.0	4.5
Slender barricudina, *Lestidiops ringens*	0.0	0.0	0.0	0.0	0.0	4.5
Blackbelly eelpout, *Lycodopis pacifica*	0.0	0.0	0.0	0.0	0.0	4.5
Dover sole, *Microstomus pacificus*	0.0	0.0	0.0	1.1	1.2	4.5
California laternfish, *Symbolophorus californiensis*	0.0	3.3	1.2	2.2	2.3	4.5
Blue lanternfish, *Tarletonbeania crenularis*	0.0	3.3	1.2	2.2	0.0	4.5
Sablefish, *Anoplopoma fimbria*	0.0	0.0	0.0	0.0	0.0	2.3
Surf perch, Embiotocidae	0.0	0.0	0.0	0.0	0.0	2.3
Rex sole, *Glyptocephalus zachirus*	0.0	0.0	0.0	0.0	0.0	2.3
Goby, Gobidae	0.0	0.0	0.0	1.1	0.0	2.3
English sole, *Parophrys vetalus*	0.0	0.0	0.0	0.0	0.0	2.3
Pacific blacksmelt, *Bathylagus pacificus*	0.0	0.0	0.0	0.0	1.2	0.0
Herring, Clupeidae	0.0	1.6	0.0	0.0	1.2	0.0
Pacific hagfish, *Eptatretus stoutii*	0.0	1.6	0.0	0.0	0.0	0.0
Greenling, Hexagrammidae	0.0	1.6	0.0	0.0	0.0	0.0
California smoothtongue, *Leuroglossus stilbius*	6.3	0.0	2.3	3.3	2.3	0.0
Duckbill barracudina, *Magnisudis atlantica*	1.6	0.0	0.0	0.0	0.0	0.0
Laternfish, Myctophidae	0.0	1.6	0.0	0.0	0.0	0.0
Smelt, Osmeridae	0.0	1.6	0.0	0.0	0.0	0.0
Pacific pompano, *Peprilus simillimus*	0.0	1.6	0.0	0.0	1.2	0.0
Righteye flounder, Pleuronectidae	0.0	0.0	0.0	0.0	1.2	0.0
Plainfin midshipmen, *Porichthys notatus*	0.0	0.0	1.2	0.0	0.0	0.0
Sand sole, *Psettichthys melanostictus*	0.0	1.6	0.0	0.0	0.0	0.0
Pacific mackerel, *Scomber japonicus*	1.6	6.6	0.0	0.0	0.0	0.0
Queenfish, *Seriphus politus*	0.0	1.6	1.2	0.0	0.0	0.0
Spiny dogfish, *Squalus acanthias*	3.2	0.0	0.0	0.0	0.0	0.0
Prickleback, Stichaeidae	0.0	1.6	0.0	0.0	0.0	0.0

TABLE 2
General linear model results comparing FO in 2009 for each diet component and primary fish taxon from California sea lion fecal samples against each year from the Early 2000s samples. Model for each diet component or fish taxon was y = 1+ year where 2009 was the intercept. Results are significant at α =< 0.05 and '–' is less than 2009, '+' is greater than 2009, or '0' is no difference from 2009.

	Early 2000s				
	2000	2001	2002	2004	2005
Diet Composition					
Mixed fish and cephalopod	0	+	0	–	0
Fish only	–	–	0	+	0
Cephalopod only	–	–	–	–	–
Primary Fish Taxa					
Rockfish (*Sebastes* spp.)	–	–	–	–	–
Northern anchovy (*Engraulis mordax*)	+	0	–	+	0
Pacific sardine (*Sardinops sagax*)	0	–	+	+	+
Pacific hake (*Merluccius productus*)	+	+	+	0	+
Pacific saury (*Cololabis saira*)	0	0	0	0	0
Jack mackerel (*Trachurus symmetricus*)	0	0	0	0	0

TABLE 3
Diet composition and primary fish taxa consumed by California sea lions at San Miguel Island, California in July and early August in 2000, 2001, 2002, 2004, 2005 (Early 2000s) and 2009. Prey taxa were identified from hard parts recovered from fecal samples. '%FO' is percent Frequency of Occurrence. Statistics are from Analysis of Variance (ANOVA) tests and compare 2009 to Early 2000s samples.

	% FO				
		Early 2000s			
	2009	Mean	S. E.	*P*	$F_{0.05,5}$
Diet Composition					
Mixed fish and cephalopod	38.5	50.5	8.8	0.606	0.313
Fish only	30.7	40.9	10.3	0.707	0.163
Cephalopod only	30.8	8.6	2.9	0.034	10.112
Fish Taxons					
Rockfish (*Sebastes* spp.)	45.5	14.1	3.8	0.028	11.405
Northern anchovy (*Engraulis mordax*)	25.0	41.6	11.6	0.589	0.345
Pacific sardine (*Sardinops sagax*)	15.9	35.1	13.1	0.582	0.357
Pacific hake (*Merluccius productus*)	13.6	52.2	8.7	0.144	3.290
Pacific saury (*Cololabis saira*)	9.1	13.7	2.7	0.520	0.497
Jack mackerel (*Trachurus symmetricus*)	6.8	4.8	1.7	0.733	0.134

TABLE 4
Top linear models predicting the annual mortality rate of 5-week old California sea lion pups at San Miguel Island, California, with explanatory variables of year, monthly sea surface temperature index (SSTI) anomaly, and monthly upwelling index anomaly at 36°N 122°W (UWI36N) and 33°N 119°W (UWI33N).

Model	Parameters	*F*-statistic	df	*P*	Adjusted R^2	AICc
obsmr ~Year+SSTI.Jun	3	9.197	10	0.005	0.577	-14.971
obsmr ~SSTI.Jun+UWI36N.Jun	3	7.484	10	0.010	0.519	-13.299
obsmr ~SSTI.Jun	2	8.629	11	0.014	0.389	-12.400
obsmr ~Year+SSTI.Jun+UWI36N.Jun	4	6.013	9	0.016	0.556	-11.371
obsmr~Year+SSTI.JunJul	3	5.590	10	0.024	0.433	-11.160
obsmr ~Year+SSTI.Jun+UWI33N.Jun	4	5.564	9	0.020	0.533	-10.707
obsmr ~SSTI.Jun+UWI33N.Jun	3	5.027	10	0.031	0.402	-10.450
obsmr ~Year+SSTI.MayJun	3	3.407	10	0.074	0.286	-8.1599
obsmr ~Year+SSTI.MayJul	3	3.330	10	0.078	0.280	-8.0390

ing between January and April. The negative upwelling between May and July resulted in warmer than average SSTI in June and July, with the greatest positive SSTI anomaly occurring in June. Negative SSTI anomalies returned in August and September as upwelling increased along the coast and SSTs cooled (fig. 8).

Model of Early Pup Mortality and Oceanographic Indices

The model that best explained the annual variability in pup mortality rates at 5 weeks of age between 1997 and 2009 included year and June SSTI as explanatory variables (tab. 4). The 10 best models included June SSTI. Pup mortality increased with increasing positive June SSTI anomalies (fig. 9). The highest positive June SSTI anomalies (> 1.4°C) in the ENSO year of 1998 and the unusually warm year of 2009 were associated with the highest mortality rates (fig. 9). Other suitable models included June SSTI only and June UWI at 36°N 122°W and June SSTI as explanatory variables for annual pup mortality.

DISCUSSION

The unprecedented mortality of California sea lion pups born at San Miguel Island, California and the record number of emaciated weaned pups that stranded along the central California coast in 2009 were associated with anomalous oceanographic conditions along the central California coast between May and August 2009. The conditions only persisted for 4 months but the timing and magnitude of the event relative to weaning and birthing of California sea lion pups resulted in 80% mortality of the 2009 cohort by 3.5 months of age at San Miguel Island. Although strandings of weaned pups occur regularly along the California coast during the spring and summer, in 2009, strandings were high throughout California. Along southern California coasts, more than 400 strandings occurred (J. Cordaro, NOAA, NMFS, personal communication) and we documented 640 strandings for central and northern California, almost 11 times the average between 1997 and 2008.

The positive upwelling and cooler SSTs along the central coast between January and April 2009 were

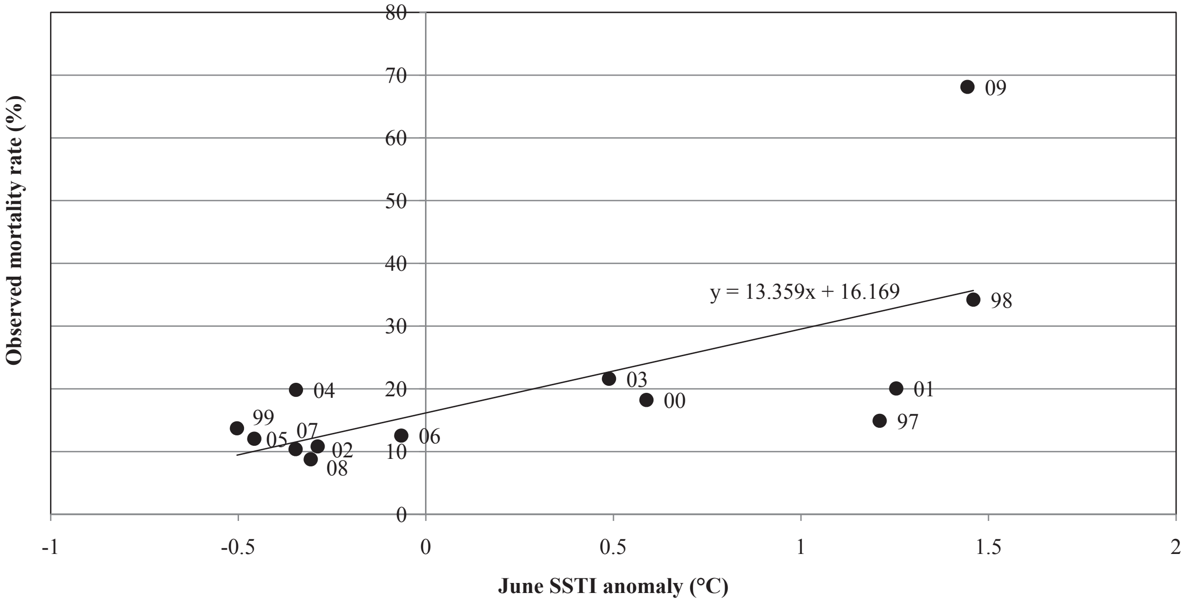

Figure 9. The relationship between observed California sea lion pup mortality at 5 weeks of age at San Miguel Island, California, and the June SSTI anomaly for the central and southern California Current System (CCS) between 1997 and 2009.

within the normal pattern for the CCS (Bograd et al. 2009). This likely lead to adequate prey availability for pregnant California sea lion females and resulted in normal patterns in the timing of births and pup production. We would have expected a later median birth date, a protracted birthing season, and lower pup production in addition to pup mortality if pregnant females had had difficulty finding enough food to support gestation and late lactation. When the oceanographic conditions transitioned to negative upwelling patterns and warmer SSTs in the summer, mothers responded with long foraging trips averaging 7 days, up to 4 days longer than trips in the 1980s (Feldkamp et al. 1989; Antonelis et al. 1990), that approached the maximum duration for which pups survive without nursing (9 days, Heath 1989). Although the methods of measuring trip duration were different among the studies (telemetry in the earlier studies vs. visual observation in this study), the magnitude of the difference was too great to be attributed to sampling method alone. Behavioral observations have been shown to underestimate trip duration by up to 7% in Antarctic fur seals (*Arctocephalus gazella*) (Boyd et al. 1991) and overestimate duration by 3.4% in Australian sea lions (*Neophoca cinerea*) (Higgins and Cass 1993) relative to telemetry derived durations. Biases of these magnitudes would not result in trip durations significantly different from those we observed. The longer foraging trips indicate that lactating females had difficulty finding sufficient prey or prey of adequate energetic value within their normal foraging range to energetically maintain themselves and sustain lactation. Because pups fast while their mother is away on foraging trips, repeated foraging trips lasting up to 7 days likely resulted in a nutritional deficit for the pups such that they succumbed to starvation within the first months of life. The duration of visits ashore was not different from other studies at San Miguel Island (Antonelis et al. 1990). Thus, longer absences by females were not compensated by longer periods ashore for nursing.

The primary prey of California sea lion females in the summers of our study were similar to previous studies with fish and cephalopods comprising the diet and Pacific sardine, northern anchovy, Pacific hake and rockfish representing the primary fish taxons (Antonelis et al. 1984, Lowry et al. 1990, Lowry 1991, Melin et al. 2008). The increased FO of cephalopods in the diet in 2009 (30.8%) compared to the early 2000s (8.6%) indicates that cephalopods were more available to California sea lions than usual during the summer of 2009. The FO of the fish taxons in the diet also changed in 2009. Most notably, rockfish became the dominant fish taxon and the importance of Pacific hake, Pacific sardine and northern anchovy was considerably less than in the early 2000s. The increase in rockfish in 2009 could be due to increased abundance of rockfish due to strong year classes of rockfish in 2003 and 2006 (Field et al. 2007), or it could reflect reduced availability of sardine, anchovy and hake due to the anomalous ocean conditions in the summer. The preferred summer diet with high FO of sardine, anchovy and hake likely provides an energy rich diet that allows females to support lactation. The high pup mortality in 2009 suggests that the combination of longer foraging trips and a diet principally of rockfish and cephalopods did not provide adequate energy for lactating females to support their pups.

The results of our model of pup mortality in which the SSTI in June predicted higher pup mortality, suggest that the response of prey to SST changes and the response of sea lions to a change in prey availability, are relatively immediate. For California sea lions, reduced prey availability or a diet of energetically inferior prey in June is likely to have a significant impact on pup survival because it may result in longer foraging trips for their mothers and possibly less energy transfer between mothers and pups at a time when the pups are solely dependent on their mothers for nutrition and have limited fasting capabilities.

The record number of emaciated weaned pups from the 2008 cohort that stranded along the central California coast in 2009 indicates that weaned pups had difficulty finding food in the summer shortly after they achieved independence from their mothers. Although weaning is a gradual process in California sea lions, dependent pups do not accompany their mothers to foraging areas (Melin et al. 2000). When pups are weaned, they are naïve to the location of foraging areas away from the colony and must learn to find them and to capture prey on their own. Weaned pups have limited physiological capabilities for diving and traveling (Fowler et al. 2006; Richmond et al. 2006) and thus, if they encounter poor foraging conditions before becoming proficient hunters, they may die from starvation.

Coastal upwelling processes are important determinants of local and regional SSTs which in turn affects the distribution and reproduction of marine species by influencing the distribution of their prey (Ainley et al. 1995; Ainley et al. 2005; Lluch-Belda et al. 2005; Wells et al. 2008). In 2009, the decreased upwelling along the central California coast produced warm, low nutrient water along the coast between May and August but the highest number of starving weaned pups and the highest pup mortality occurred during the period of the warmest SSTI and the most negative UWI anomalies in June 2009. This suggests that the response of California sea lions to the anomalous oceanographic conditions in 2009 was mediated through warmer SSTs that likely resulted in reduced availability of their prey. The association of changes in SSTs with prey availability and production or survival of predators has been documented for seabirds (Abraham and Sydeman 2004; Ainley et al. 2005; Sydeman et al. 2006; Mills et al. 2007; Wells et al. 2008) and marine mammals (Melin 2002; Beauplet et al. 2005; Weise et al. 2006). Though we did not conduct prey distribution studies in 2009, we observed that northern fur seals (*Callorhinus ursinus*) that breed at San Miguel Island at the same time as California sea lions and feed on similar prey (Antonelis et al. 1990) did not experience massive mortality of their pups in 2009. Northern fur seals feed offshore in the pelagic zone during the summer (Antonelis et al. 1990) unlike California sea lions that feed in coastal waters (Antonelis et al. 1990; Melin and DeLong 2000). This observation leads us to hypothesize that the primary prey moved offshore or northward in 2009 and was less available to lactating sea lion females due to the anomalous oceanographic patterns between May and August 2009. Future analyses will combine fishery landings data and fish larvae abundance surveys from the CalCOFI cruises in July 2009 within the foraging range of California sea lions to test this hypothesis.

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LITERATURE CITED

Abraham, C. L., and W. J. Sydeman. 2004. Ocean climate, euphausiids and auklet nesting: Interannual trends and variation in phenology, diet and growth of a planktivorous seabird, *Ptychorampus aleuticus.* Mar. Ecol. Prog. Ser. 274:235–250.

Ainley, D. G., R. L. Veit, S. G. Allen, L. B. Spear, and P. Pyle. 1995. Variations in marine bird communities of the California Current, 1986–1994. Calif. Coop. Oceanic. Fish. Invest. Rep. 36:72–77.

Ainley, D. G., L. B. Spear, C. T. Tynan, J. A. Barth, S. D. Pierce, R. G. Ford, and T. J. Cowles. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. Deep-Sea Res. Part II Top. Stud. Oceanogr. 52:123–143.

Antonelis, G. A., C. H. Fiscus, and R. L. DeLong. 1984. Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978–79. Fish. Bull. (Seattle) 82:67–76.

Antonelis, G. A., B. S. Stewart, and W. F. Perryman. 1990. Foraging characteristics of female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*). Can. J. Zool. 68:150–158.

Barber, R. T., and F. P. Chavez. 1983. Biological consequences of El Niño. Science 222:1203–1210.

Beauplet, G., C. Barbraud, M. Chambellant, and C. Guinet. 2005. Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate, and oceanographic conditions. J. Anim. Ecol. 74:1160–1172.

Bograd, S. J., I. Schroeder, N. Sarkar, X. Qui, W. J. Sydeman, and F. B. Schwing. 2009. Phenology of coastal upwelling in the California Current. Geophys. Res. Lett. 36:2008GL035933.

Boyd, I. L., N. J. Lunn, and T. Barton. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. J. Anim. Ecol. 60:577–592.

Brodeur, R. D., S. Ralston, R. L. Emmett, M. Trudel, T. D. Auth, and A. J. Phillips. 2006. Anomalous pelagic nekton abundance, distribution and apparent recruitment in the northern California Current in 2004 and 2005. Geophys. Res. Lett. 33: 2006GL026614.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. New York: Springer. 488 pp.

Caretta, J.V., K. A. Forney, M. S. Lowry, J. Barlow, J. Baker, B. Hanson, and M. M. Muto. 2007. California sea lion (*Zalophus californianus*): U.S. Stock. U.S. Pacific Marine Mammal Stock Assessments: 2007. U. S. Dept. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-414. 321 pp.

Chavez, F. P., J. T. Pennington, C. G. Castro, J. P. Ryan, R. P. Michisaki, B. Schlining, P. Walz, K. R. Buck, A. McFadyen, and C. A. Collins. 2002. Biological and chemical consequences of the 1997–1998 El Niño in central California waters. Prog. Oceanogr. 54:205–232.

DeLong, R. L., and S. R. Melin. 2000. Thirty years of pinniped research. Proceedings of the Fifth Channel Islands Symposium. Santa Barbara: Santa Barbara Museum of Natural History, pp. 401–406.

DeLong, R. L., G. A. Antonelis, C. W. Oliver, B. S. Stewart, M. S. Lowry, and P. K. Yochem. 1991. Effects of the 1982–83 El Niño on several population parameters and diet of California sea lions on the California Channel Islands. *In* Pinnipeds and El Niño: Reponses to environmental stress, F. Trillmich and K.A. Ono, ed., Berlin: Springer-Verlag, pp. 166–172.

Feldkamp, S. D., R. L. DeLong, and G. A. Antonelis. 1989. Diving patterns of California sea lions, *Zalophus californianus*. Can. J. Zool. 67:872–883.

Field, J. C., E. J. Dick, and A. D. MacCall. 2007. Stock assessment model for the shortbelly rockfish, *Sebastes jordani*, in the California Current. U. S. Dept. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-405, 108 pp.

Fowler, S. L., D. P. Costa, J. P. Y. Arnould, N. J. Gales, and C. E. Kuhn. 2006. Ontogeny of diving behavior in the Australian sea lion: trails of adolescence in a late bloomer. J. Anim. Ecol. 75:358–367.

Fowler, S. L., D. P. Costa, and J. P. Y. Arnould. 2007. Ontogeny of movements and foraging ranges in the Australian sea lion. Mar. Mamm. Sci. 23:598–614.

Heath, C. B. 1989. The behavioral ecology of the California sea lion, *Zalophus californianus*. PhD Dissertation, Santa Cruz: University of California, Santa Cruz, 255 pp.

Higgins, L.V., and L. Cass. 1993. Birth to weaning: parturition, duration of lactation, and attendance cycles of Australian sea lions (*Neophoca cinerea*). Can. J. Zool. 71:2047–2055.

Joy, R., D. J. Tollit, J. L. Laake, and A. W. Trites. 2006. Using simulations to evaluate reconstructions of sea lion diet from scat. *In* Sea lions of the world, A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea, and K. M. Wynne, eds., Fairbanks: Alaska Sea Grant College Program, pp. 205–221.

Laake, J. L., P. Browne, R. L. DeLong, and H. R. Huber. 2002. Pinniped diet composition: a comparison of estimation models. Fish. Bull. (Seattle) 100:434–447.

Lluch-Belda, D., D. B. Lluch-Cota, and S. E. Lluch-Cota. 2005. Changes in marine faunal distributions and ENSO events in the California Current. Fish. Oceanogr. 14:458–467.

Lowry, M. S., C. W. Oliver, C. Macky, and J. B. Wexler. 1990. Food habits of California sea lions *Zalophus californianus* at San Clemente Island, California, 1981–1986. Fish. Bull. (Seattle) 88:509–521.

Lowry, M. S. 1991. Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981–86. Fish. Bull. (Seattle) 89:339–346.

Lynn, R. J., and J. J. Simpson. 1987. The California Current System: The seasonal variability of its physical characteristics. J. Geophys. Res. 92:12947–12966.

Mackas, D. L., W. T. Peterson, B. M. Hickey, R. K. Sherman, and S. D. Price. 2006. Zooplankton anomalies in the California Current before and during the warm conditions of 2005. Geophys. Res. Lett. 33:2006GL027930.

Melin, S. R., R. L. DeLong, J. R. Thomason, and G. R. VanBlaricom. 2000. Attendance patterns of California sea lion (*Zalophus californianus*) females and pups during the non-breeding season at San Miguel Island. Mar. Mamm. Sci. 16:169–185.

Melin, S. R., and R. L. DeLong. 2000. At-sea distribution and diving behavior of California sea lion females from San Miguel Island, California. Proceedings of the Fifth California Islands Symposium. Santa Barbara: Santa Barbara Museum of Natural History, pp. 407–412.

Melin, S. R. 2002. The foraging ecology and reproduction of the California sea lion (*Zalophus californianus*). PhD Dissertation. St. Paul: University of Minnesota, 150 pp.

Melin, S. R., R. L. DeLong, and D. B. Siniff. 2008. The effects of El Niño on the foraging behavior of lactating California sea lions (*Zalophus californianus*) during the nonbreeding season. Can. J. Zool. 86:192–206.

Mills, K. L., T. Laidig, S. Ralston, and W. J. Sydeman. 2007. Diets of top predators indicate pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current System. Fish. Oceanogr. 16:273–283.

Norton, J., D. McLain, R. Brainard, and D. Husby. 1985. The 1982–83 El Niño event off Baja and Alta California and its ocean climate context. *In* El Niño North: Niño effects in the Eastern Subarctic and Pacific Ocean, W. S. Wooster and D. L. Fluharty, eds., Seattle: Washington Sea Grant. pp. 44–72.

Orr, A. J., J. L. Laake, M. I. Dhruv, A. S. Banks, R. L. DeLong, and H. R. Huber. 2003. Comparison of processing pinniped scat samples using a washing machine and nested sieves. Wildl. Soc. Bull. 31:253–257.

Peterson, R. S., and G. A. Bartholomew. 1967. The natural history and behavior of the California sea lion. Spec. Publ. No. 1 Am. Soc. Mammal. 79 pp.

R Core Development Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Richmond, J. P., J. M. Burns, and L. D. Rea. 2006. Ontogeny of total body oxygen stores and aerobic dive potential in Steller sea lions (*Eumetopias jubatus*). J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 176:535–545.

Schwing, F. B., N. A. Bond, S. J. Bograd, T. Mitchell, M. A. Alexander, and N. Mantua. 2006. Delayed coastal upwelling along the U.S. West Coast in 2005: A historical perspective. Geophys. Res. Lett. 33:2006GL026911.

Sydeman, W. J., R. W. Bradely, P. Warzybok, C. L. Abraham, J. Jahncke, K. D. Hyrenbach, V. Kousky, J. M. Hipfner, and M. D. Ohman. 2006. Planktivorous auklet (*Ptychoramphus aleuticus*) responses to the anomaly of 2005 in the California Current. Geophys. Res. Lett. 33:2006GL026736.

Thomas, A. C., and P. Brickley. 2006. Satellite measurements of chlorophyll distribution during spring 2005 in the California Current. Geophys. Res. Lett. 33:2006GL026588.

Weise, M. J., D. P. Costa, and R. M. Kudela. 2006. Movement and diving behavior of male California sea lions (*Zalophus californianus*) during anomalous oceanographic conditions of 2005 compared to those of 2004. Geophys. Res. Lett. 33:2006GL027113.

Wells, B. K., J. C. Field, J. A. Thayer, C. B. Grimes, S. J. Bograd, W. J. Sydeman, F. B. Schwing, and R. Hewitt. 2008. Untangling the relationships among climate, prey and top predators in an ocean ecosystem. Mar. Ecol. Prog. Ser. 364:15–29.

CHECKLIST AND BIOGEOGRAPHY OF FISHES FROM GUADALUPE ISLAND, WESTERN MEXICO

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ABSTRACT

Guadalupe Island, off Baja California, México, is an important fishing area which also harbors high marine biodiversity. Based on field data, literature reviews, and scientific collection records, we present a comprehensive checklist of the local fish fauna, which is comprised of 328 species from 219 genera, 105 families, 30 orders, and 3 classes. Of these, 156 species represent new records. Almost half of the species (154) are from tropical waters and the remainders are typical of warm and cold temperate regions. The island is the type locality of 18 fishes, represents the range limit of 48 taxa, and has 8 endemics. A biogeographic analysis comparing Guadalupe and the Baja California Peninsula indicates that the composition of reef fishes of the island is very similar to that found at 28°N, and suggests that Cedros, San Benito islands, and Punta Eugenia, might be the key sources of tropical immigrants to Guadalupe.

INTRODUCTION

Guadalupe Island, located off the western coast of the Baja California Peninsula, has a long tradition as a fishing ground (Aguirre-Muñoz et al. 2005; Salgado-Rogel et al. 2009), and sustains many high-value fisheries, such as abalone *Haliotis* spp., lobster *Panulirus interruptus* (Randall 1840), and sea cucumber *Parastichopus parvimensis* (Clark 1913). In addition, Gallo-Reynoso et al. (2005a, b) demonstrated that the island has a key conservation significance as a breeding habitat for marine mammals, such as the Guadalupe fur seal *Arctocephalus townsendi* (Merriam 1897) and the elephant seal *Mirounga angustirostris* (Gill 1866). More recently, this location has become an important tourist attraction (Domeier and Nasby-Lucas 2007) because of the presence of white sharks, *Carcharodon carcharias* (Linnaeus 1758). For all these reasons, in 2005, the Méxican federal government recognized the biological and ecological significance of Guadalupe Island, and declared it a Biosphere Reserve (SEMARNAT 2005).

Guadalupe Island is isolated, far away from the mainland and has limited logistic facilities to conduct scientific studies. In consequence (and despite its biological importance) there is still a very limited number of papers about the ecology and composition of its marine communities. A good example of this situation is the lack of a formal checklist for many invertebrate taxa, and of the bony and cartilaginous fish fauna of this insular region. In relation to the ichthyofauna, most published listings contain only partial information from occasional visits or literature reviews (Hubbs 1960; Miller and Lea 1972; Love et al. 2005), and the few studies that have specifically targeted Guadalupe Island, are focused on particular families (Hubbs and Rechnitzer 1958; Briggs 1965; Pietsch 1969; León-Castro et al. 1993). The lack of more complete information hinders the efforts of the Biosphere Reserve managers, who require comprehensive data to set adequate baselines for monitoring possible temporal changes in community composition, caused either by anthropogenic or natural forces. Furthermore, without a detailed inventory of fish species, any biogeographic analysis of the island is limited in scope. A comparison of the fish assemblages of Guadalupe Island and the mainland has never been adequately conducted, but might elucidate population linkages between Guadalupe Island and the mainland. Such studies would be an important contribution to the "Baja to Bering" initiative, devoted to create a multinational network of marine reserves in Canada, the United States, and México (Vásárhelyi and Thomas 2008). For the reasons specified above, the objective of this paper is to present an updated systematic list of the fish fauna of Guadalupe Island, based on field data, literature reviews, and scientific collection records.

STUDY AREA

Guadalupe Island is located in the Pacific Ocean, about 260 km west of the Baja California Peninsula, México (fig. 1). It is of volcanic origin, approximately 37 x 8 km in size (total area about 254 km^2), and oriented in a north-south direction with a mountainous topography and altitudes up to 1,300 m above sea level (fig. 1). The geology, vegetation, and terrestrial fauna of Guadalupe Island are well-studied and described elsewhere (Santos-del Prado and Peters 2005). There is no significant coastal shelf, except on the south end where a shallow platform connects the island to a series of small islets, such as El Toro and El Zapato (Castro et al. 2005). Offshore, the depth increases with an average slope of 70° to the ocean floor down to 3,600 m (Gallo-Reynoso et al. 2005a). The rugged subtidal environment consists of boulders and gray-black sandy bottoms intermixed with blocks, basaltic dikes, pavements, and walls with numerous caves and hollows that provide shelter to many species, including commercially important invertebrates.

Guadalupe Island is home to a great variety of fauna and flora, including many endemic species both in land and in the sea, and for that reason it was declared as a Biosphere Reserve by the Méxican government (Garth 1958; Ferreira 1978; Santos-del Prado and Peters 2005; Espinosa-Pérez and Hendrickx 2006). The weather and oceanic conditions at Guadalupe are influenced by the California Current system, which carries water from high latitudes to the south (Castro et al. 2005). Monthly average sea surface temperature range from 14°C to 22°C (yearly average 18.7°C); the warmest months are August, September, and October when temperatures are usually > 20°C, and the coldest months are January, February, and March when temperature is typically < 17°C (Hernández-de la Torre et al. 2005). It is interesting to note that positive local temperature anomalies > 5°C have been documented in El Niño Southern Oscillation years (Durazo and Baumgartner 2002; Durazo et al. 2005), and that the southern part of the island is almost half a degree warmer than the north, evidence of the cooling effect from the California Current (CONANP 2009). The water surrounding Guadalupe Island has chlorophyll concentrations from 0.25 to 0.50 mg/m^3, with the highest production in December and January and the lowest in August and September (Venrick et al. 2003). Total primary productivity is remarkably affected in El Niño years, decreasing to very low values (Hernández-de la Torre et al. 2005).

METHODS

The process followed to construct the fish checklist of Guadalupe Island encompassed three steps. First, we conducted a field survey on the island in 2008 and 2009. Second, we gathered information from electronic and in-house scientific collections from institutions in México and the United States, encompassing records from the 1950s to 2004. Third, we conducted an extensive literature review on the fish fauna of the location of interest.

For our field survey, we visited 16 sites during a six-day visit to the island in September 2008 (fig. 1). In each location, we performed four underwater visual censuses with hookah diving equipment: two "shallow" (0–10 m) and two "deep" (10–20 m); all were conducted inside belt transects of 25 x 4 m, and the total surveyed area was 6,400 m^2. In addition, during a second two-week visit to Guadalupe in April 2009, we surveyed tide pools at the southern tip and on the west coast. All fishes observed in the field were identified on the basis of illustrations in Miller and Lea (1972), Eschmeyer et al. (1983), Gotshall (2001) and Humann (2005).

In the case of museum data, we reviewed records from eleven collections, either electronically or by direct visits to the following institutions: Universidad Autónoma de Baja California (Ensenada); Scripps Institution of Oceanography (San Diego); Los Angeles County Natural History Museum (Los Angeles); California Academy of Sciences (San Francisco); National Museum of Natural History, Smithsonian Institution (Washington, DC); American Museum of Natural History (New York); Santa Barbara Museum of Natural History (Santa Barbara); Academy of Natural Sciences of Philadelphia (Philadelphia); Museum of Comparative Zoology (Cambridge); University of Kansas Natural History Museum (Kansas City); and Tulane University (New Orleans). We only used the information from those specimens caught within 50 km of the island, independent of the fishing method, depth or year; this choice was done to have a better list of possible species, because of the steep topography of the island, it is common to observe pelagic species near the coastline (Gallo-Reynoso et al. 2005b).

Finally, to complete the checklist we made a literature review of refereed journals and technical books from libraries at Universidad Autónoma de Baja California Sur (La Paz), Centro Interdisciplinario de Ciencias Marinas (La Paz), Centro de Investigaciones Biológicas del Noroeste (La Paz), Universidad Autónoma de Baja California (Ensenada), Centro de Investigación Científica y de Educación Superior de Ensenada (Ensenada), and Scripps Institution of Oceanography (San Diego). We only took into consideration species that were reported in papers explicitly referenced to Guadalupe Island, or specifically seen or collected in the island or its surroundings (50 km away). To eliminate synonyms and generate a systematic list consisting only of valid names, we checked each taxonomic name in

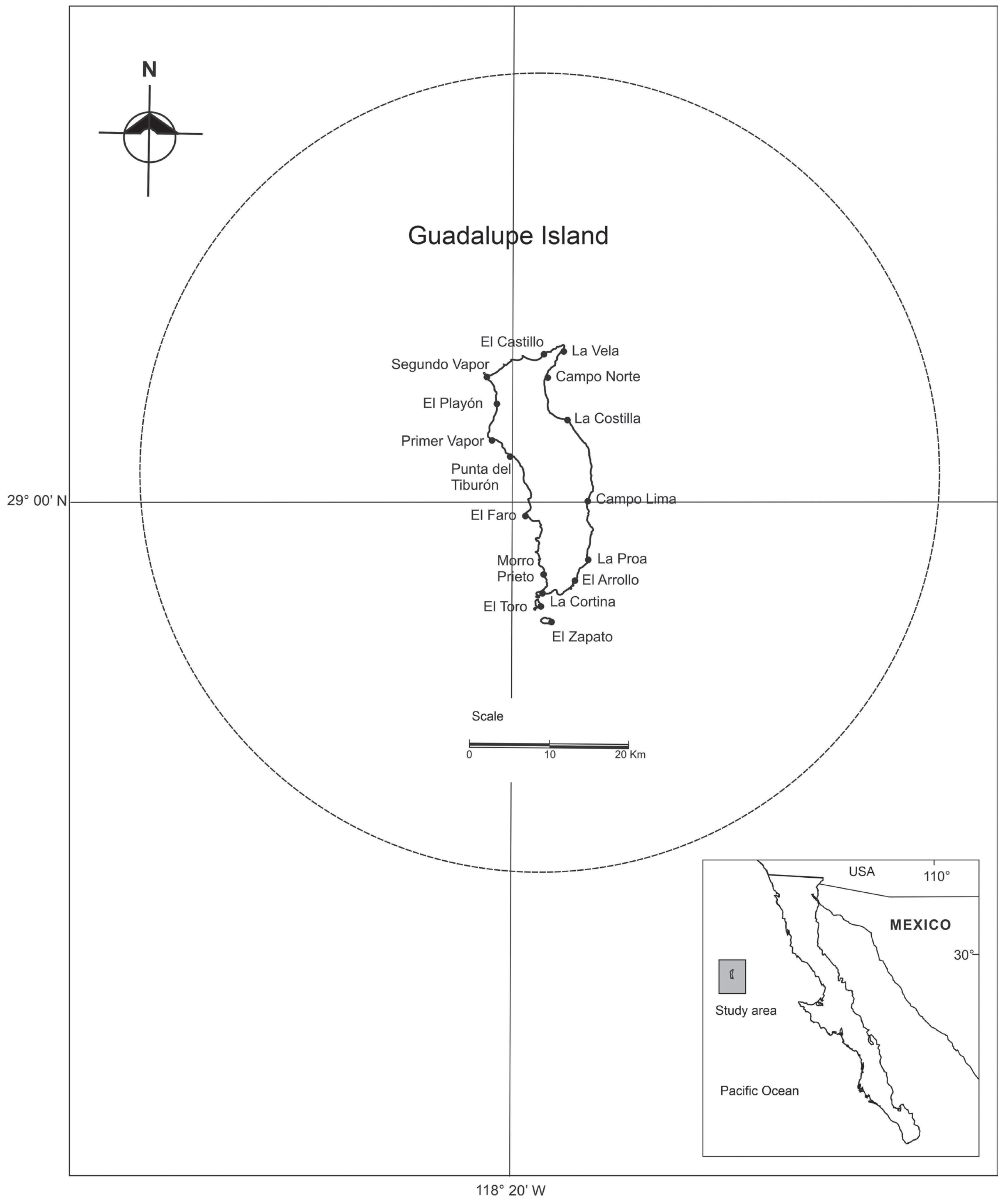

Figure 1. Locations of study area and sampling points at Guadalupe Island, Mexico. The circle indicates a 50 km radius around the island.

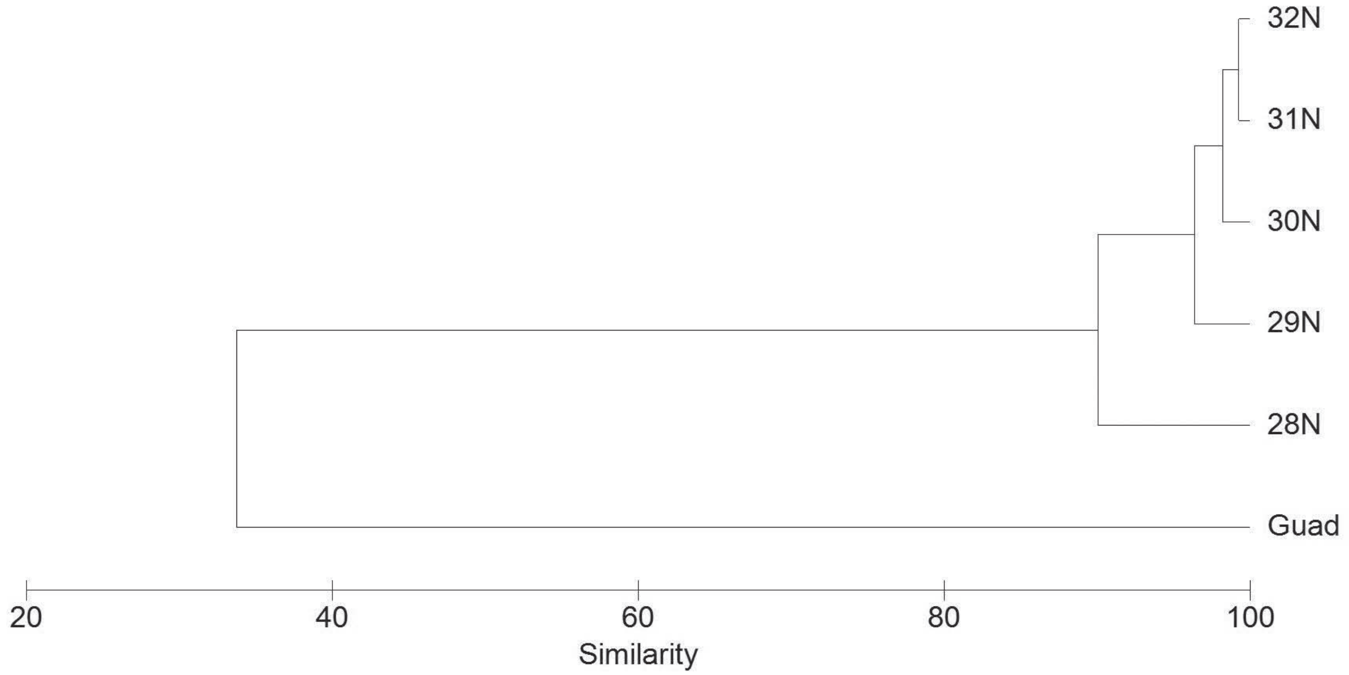

Figure 2. Dendrogram of similarity (Bray-Curtis) comparing the shallow and reef fish species of Guadalupe Island with the recorded in 1° grids of latitude of 28°N to 32°N. Specific richness per site: Isla Guadalupe: 141 species; 28°N: 327 species; 29°N: 294 species; 30°N: 280 species; 31°N: 278 species; 32°N: 280 species.

FishBase (Froese and Pauly 2009; www.fishbase.org) and the Catalog of Fishes of the California Academy of Sciences (Eschmeyer and Fricke 2009; http://research.calacademy.org/research/ichthyology/Catalog/fishcatmain.asp).

The biogeographical analysis of the data consisted of a numerical comparison of the composition of the shallow water (< 30 m depth) fish fauna among Guadalupe Island and six regions of the western Baja California peninsula. Based on published distribution data (Love et al. 2005; Allen et al. 2006; Horn et al. 2006; Robertson and Allen 2008), we constructed a matrix of the 360 species present at each latitude degree from 28°N to 32°N and on the island, and from these data we constructed a dendrogram of similitude using the Bray-Curtis coefficient and the UPGMA algorithm (Clarke and Gorley 2006). The selection of this particular group of species was born of necessity, as the most detailed occurrence records for fishes in the west coast of Baja California pertain to those distributed in rocky reefs and at depths safe for divers (Pondella et al. 2005; Robertson and Allen 2008).

RESULTS

Based on our field surveys, museum records, and literature review, we identified 328 species of marine fishes off Guadalupe Island from 219 genera, 105 families, 30 orders, and 3 classes (tab. 1). The island is the type locality for 18 species (5.5% of the fauna) and it also marks the northern or southern distributional limit for 23 and 25 species, respectively. Of the 328 documented species, 154 (46.9%) have tropical affinity and the remainder (174) are representative of temperate and cold waters. From a bathymetric perspective, 184 species (56.1%) are typically from deep (> 30 m) or pelagic waters while the remaining 144 (43.9%) are reef or shallow water fishes. Finally, Guadalupe Island has 8 endemic fishes (2.4% of the total, but 5.5% if the number refers only to rocky reef taxa): *Eptatretus fritzi* (Wisner and McMillan 1990), *Rimicola sila* (Briggs 1955), *Syngnathus insulae* (Fiitzsce 1980), *Psednos anoderkes* (Chernova and Stein 2002), *Psednos griseus* (Chernova and Stein 2002), *Psednos mexicanus* (Chernova and Stein 2002), *Psednos pallidus (*Chernova and Stein 2002) and *Brachyistius aletes* (Tarp 1952).

The literature review yielded 173 species reported for the island, while we observed 38 species in the field, and 269 records came from museums. Considering only unpublished information (data from collections and field work), Table 1 includes a total of 155 new records of fish species for Guadalupe Island, from 117 genera, 62 families, 24 orders, and 2 classes. Among the newly registered species are typical tropical reef or shallow water species, such as the leopard grouper *Mycteroperca rosacea* (Streets 1877), the large banded blenny *Ophioblennius steindachneri* (Jordan and Evermann 1898), the bullseye pufferfish *Sphoeroides annulatus* (Jenyns 1842), and the redtail triggerfish *Xanthichthys*

TABLE 1
Systematic list of the cartilaginous and bony fishes of Guadalupe Island, Baja California, Mexico. Classification according to Eschmeyer and Fricke (2009).

	Field observation (2008)	Museum data	References	Distribution area and bathymetric range	Notes
Phylum CHORDATA					
Clase MYXINI					
Order MIXINIFORMES					
Family Myxinidae					
Eptatretus deani (Evermann and Goldsborough, 1907)			13, 14	C, D	Southern limit
Eptatretus fritzi Wisner and McMillan, 1990		SIO	14, 18	E, D	Type location
Eptatretus stoutii (Lockington, 1878)		SIO		C, D	
Clase ELASMOBRANCHII					
Order HETERODONTIFORMES					
Family Heterodontidae					
Heterodontus francisci (Girard, 1855)	+	SIO, LACM	13, 28	C, S	
Order LAMNIFORMES					
Family Lamnidae					
Carcharodon carcharias (Linneus, 1758)	+		4, 28	C, S	
Isurus oxyrhynchus Rafesinque, 1810			28	T, S	
Lamna ditropis Hubbs and Follett, 1947			28	C, S	
Order CARCHARHINIFORMES					
Family Scyliorhinidae					
Cephaloscyllium ventriosum (Garman, 1880)		SIO, LACM	13, 28	T, S	
Family Triakidae					
Mustelus californicus Gill, 1864			28	C, S	
Triakis semifasciata Girard, 1855			28	C, S	
Family Carcharhinidae					
Carcharhinus leucas Muller and Henle, 1839			28	T, S	
Carcharhinus longimanus (Poey, 1861)			28	T, S	
Carcharhinus obscurus (Lesueur, 1818)			28	T, S	
Galeocerdo cuvier (Peron and Lesueur, 1822)			28	T, S	
Prionace glauca (Linneus, 1758)			28	C, S	
Family Sphyrnidae					
Sphyrna sp.			28	T, S	
Order SQUALIFORMES					
Family Dalatiidae					
Isistius brasiliensis (Quoy and Gaimard, 1824)			14, 18, 28	T, S	Northern limit
Somniosus pacificus Bigelow and Schroeder, 1944			28	C, S	
Family Squalidae					
Squalus acanthias Linneus, 1758			28	C, S	
Family Echinorhinidae					
Echinorhinus cookei Pietschmann, 1928			28	T, S	
Order TORPEDINIFORMES					
Family Torpedinidae					
Torpedo californica Ayres, 1855	+	SIO		C, S	*
Order RAJIFORMES					
Family Arhynchobatidae					
Bathyraja trachura (Gilbert, 1832)		USNM, AMNH	10, 13, 14	C, D	Southern limit
Family Myliobatidae					
Manta birostris (Walbaum, 1792)			13, 15	T, S	
Mobula japanica (Müler and Henle, 1841)		SIO	3	T, S	
Mobula thurstoni (Lloyd, 1908)			13, 15	T, S	
Myliobatis californica Gill, 1865	+	SIO		T, S	*
Clase ACTINOPTERYGII					
Order ANGUILLIFORMES					
Family Chlopsidae					
Thalassenchelys coheni Castle and Raju, 1975		LACM	14	C, D	Southern limit
Family Muraenidae					
Gymnothorax mordax (Ayres, 1859)	+	SIO	13, 14	C, S	
Gymnothorax panamensis (Steindachner, 1876)		SIO	14	T, S	Northern limit
Family Ophichthidae					
Scytalichthys miurus (Jordan and Gilbert, 1882)			14	T, S	Northern limit
Family Congridae					
Ariosoma gilberti (Ogilby, 1898)		SIO		T, D	*
Gnathophis cinctus (Garman, 1899)		SIO, LACM	13, 15	T, S	
Family Derichthyidae					
Derichthys serpentinus Gill, 1884		LACM		T, D	
Family Nemichthyidae					

Avocettina bowersi Garman, 1899		SIO		T, D	★
Avocettina infans (Günther, 1878)		SIO, LACM		C, D	★
Nemichthys larseni Nielsen and Smith, 1978		SIO		C, D	★
Nemichthys scolopaceus Richardson, 1848		SIO, LACM		T, D	★
Family Serrivomeridae					
Serrivomer sector Garman, 1899		SIO, LACM		T, D	★
Family Nettastomatidae					
Facciolella gilbertii (Garman, 1899)		LACM		T, D	★
ORDER SACCOPHARYNGIFORMES					
Family Cyematidae					
Cyema atrum Günther, 1878		SIO, LACM	17	T, D	★
Family Eurypharyngidae					
Eurypharynx pelecanoides Vaillant,1882		SIO, LACM		T, D	★
Family Saccopharyngidae					
Saccopharynx lavenbergi Nielsen and Bertelsen, 1985		SIO		T, D	★
Order CLUPEIFORMES					
Family Clupeidae					
Sardinops sagax (Jenyns, 1842)	+	SIO	13, 28	C, S	
Family Engraulidae					
Engraulis mordax Girard, 1854		SIO	19	C, S	
Pseudobathylagus milleri (Jordan and Gilbert, 1898)		SIO, LACM		C, D	★, Southern limit
Order OSMERIFORMES					
Family Microstomatidae					
Nansenia crassa Lavenberg, 1965		LACM		T, S	★
Family Opisthoproctidae					
Bathylychnops exilis Cohen, 1958			14	C, D	Southern limit
Macropinna microstoma Chapman, 1939		SIO		C, D	
Dolichopteryx longipes (Vaillant, 1888)		LACM		C, D	Southern limit
Family Bathylagidae					
Bathylagoides nigrigenys (Parr, 1931)		SIO		T, D	★
Bathylagus wesethi Bolin, 1938		SIO, LACM	22	C, D	
Bathylagus stilbius (Gilbert, 1890)		SIO, LACM		C, D	★
Lipolagus ochotensis (Schmidt, 1938)		SIO, LACM		C, D	★
Family Alepocephalidae					
Alepocephalus tenebrosus Gilbert, 1892		LACM	14	C, D	Southern limit
Bajacalifornia burragei Townsend and Nichols, 1925		LACM		T, D	★
Bathylaco nigricans Goode and Bean, 1896		LACM		C, D	★
Mirorictus taaningi Parr, 1947		SIO		T, D	★
Narcetes stomias (Gilbert, 1890)		LACM		T, D	★
Talismania bifurcata (Parr, 1951)		SIO, LACM		C, D	★
Family Platytroctidae					
Holtbyrnia latifrons Sazonov, 1976		SIO		T, D	★
Holtbyrnia macrops Maul, 1957		LACM		T, D	★
Holtbyrnia melanocephala (Vaillant, 1888)		LACM		C, D	★, New record eastern Pacific
Maulisia mauli Parr, 1960		LACM		T, D	★, New record eastern Pacific
Mentodus facilis (Parr, 1951)		LACM		T, D	★
Mirorictus taningi Parr, 1951		LACM		T, D	★
Sagamichthys abei Parr, 1953		SIO, LACM		T, D	★
Order STOMIIFORMES					
Family Gonostomatidae					
Cyclothone acclinidens Garman, 1899		SIO, LACM		T, D	★
Cyclothone atraria Gilbert, 1905		SIO, LACM		C, D	★
Cyclothone braueri Jespersen and Tåning, 1926		LACM		T, D	★
Cyclothone microdon (Günther, 1878)		SIO		T, D	
Cyclothone pallida Brauer, 1902		SIO, LACM		T, D	★
Cyclothone pseudopallida Mukhacheva, 1964		SIO, LACM		C, D	★
Cyclothone signata Garman, 1899		SIO, LACM		C, D	★
Gonostoma atlanticum Norman, 1930		LACM		T, D	★
Family Sternoptychidae					
Argyropelecus affinis Garman, 1899		SIO, LACM	17	T, D	
Argyropelecus hemigymnus Cocco, 1829		SIO, LACM		T, D	★
Argyropelecus intermedius Clarke, 1878		LACM		T, D	★
Argyropelecus lychnus Garman, 1899		SIO, LACM		T, D	★
Argyropelecus sladeni Regan, 1908		LACM		C, D	★
Danaphos oculatus (Garman, 1899)		SIO, LACM		T, D	★
Sternoptyx diaphana Hermann, 1781		SIO, UKNHM, LACM		C, D	★
Sternoptyx obscura Garman, 1899		SIO, LACM	17	T, D	★
Sternoptyx pseudobscura Baird, 1971		LACM		C, D	★
Valenciennellus tripunctulatus (Esmark, 1871)		SIO		T, D	★
Family Phosichthyidae					

Ichthyococcus irregularis Rechnitzer and Böhlke 1958	SIO, SBMNH, LACM		C, D	*
Vinciguerria lucetia (Garman, 1899)	SIO, UKNHM, LACM		T, D	*
Vinciguerria nimbaria (Jordan and Williams, 1895)	SIO, CAS		T, D	*
Vinciguerria poweriae (Cocco, 1838)	SIO		T, D	*
Woodsia nonsuchae (Beebe, 1932)	SIO, LACM		T, D	*
Family Stomiidae				
Aristostomias scintillans (Gilbert, 1915)	SIO, LACM		C, D	*
Bathophilus flemingi Aron and McCrery, 1958	LACM		C, D	*
Borostomias panamensis Regan and Trewavas, 1929	SIO, LACM		T, D	*
Chauliodus macouni Bean, 1890	SIO, LACM		C, D	*
Chauliodus sloani Bloch and Schneider, 1801	SIO		T, D	*
Idiacanthus antrostomus Gilbert, 1890	SIO, LACM		T, S	*
Photonectes margarita (Goode and Bean, 1896)	LACM		T, D	*
Stomias atriventer Garman, 1899	SIO, LACM	17	T, D	
Order AULOPIFORMES				
Family Scopelarchidae				
Benthalbella dentata (Chapman, 1939)	LACM	14	C, D	Southern limit
Rosenblattichthys volucris (Roffen, 1966)	SIO, LACM		C, D	*
Scopelarchus guentheri Alcock, 1896	LACM		C, D	*
Family Notosudidae				
Scopelosaurus adleri (Fedorov, 1967)	LACM		C, D	*
Scopelosaurus harryi (Mead, 1953)	LACM		C, D	*
Family Synodontidae				
Synodus lucioceps (Ayres, 1855)	SIO		C, D	*
Synodus scituliceps Jordan and Gilbert, 1882		14	C, S	Northern limit
Family Bathysauridae				
Bathysaurus mollis Günther, 1878		14	C, D	Southern limit
Family Paralepididae				
Lestidiops ringens (Jordan and Gilbert, 1880)	SIO, LACM		C, D	*
Family Anotopteridae				
Anotopterus pharao Zugmayer, 1911	LACM		T, D	*
Family Evermannellidae				
Evermannella ahlstromi Johnson and Glodek, 1975	LACM		T, D	*
Order MYCTOPHIFORMES				
Family Neoscopelidae				
Scopelengys tristis Alcock, 1890	SIO, LACM		C, D	*
Family Myctophidae				
Bolinichthys longipes (Brauer, 1906)	SIO, LACM		T, D	*
Bolinichthys pyrsobolus (Alcock, 1890)	LACM		T, D	*, New record eastern Pacific
Ceratoscopelus townsendi (Eigenmann and Eigenmann, 1889)	SIO, LACM		T, D	*
Diaphus theta Eigenmann and Eigenmann, 1890	SIO, LACM		C, D	*
Diogenichthys atlanticus (Taning, 1928)	SIO, LACM		T, D	*
Diogenichthys laternatus (Garman, 1899)	SIO, LACM		T, D	*
Gonichthys tenuiculus (Garman, 1899)	SIO, LACM		T, D	*
Hygophum atratum (Garman, 1899)	SIO, LACM		T, D	
Hygophum hanseni (Tåning, 1932)	LACM		T, D	*
Hygophum reinhardtii (Lütken, 1892)	SIO, LACM		T, D	
Lampadena urophaos (Paxton, 1963)	SIO, LACM		T, D	*
Lampanyctus festivus Tåning, 1928	SIO		T, D	*
Lampanyctus steinbecki Bolin, 1939	SIO		T, D	*
Lampanyctus tenuiformis (Brauer, 1906)	SIO		T, D	*
Loweina rara (Lütken, 1892)	SIO, CAS, LACM		T, D	*
Myctophum nitidulum Garman, 1899	SIO, LACM		C, D	*
Nannobrachium bristori Zahuranec, 2000	SIO		T, D	*
Nannobrachium hawaiiensis Zahuranec, 2000	SIO		C, D	*
Nannobrachium idostigma (Parr, 1931)	SIO, LACM		T, D	*
Nannobrachium regale (Gilbert, 1892)	SIO, LACM		C, D	*
Nannobrachium ritteri Gilbert, 1915	SIO, LACM		C, D	*
Notolychnus valdiviae (Brauer, 1904)	SIO, LACM		T, D	*
Notoscopelus resplendens (Richardson, 1845)	LACM		T, D	*
Parvilux ingens Hubbs and Wisner, 1964	SIO, LACM	14	C, D	Southern limit; type location
Protomyctophum crockeri (Bolin, 1939)	SIO, LACM		C, D	*
Stenobrachius leucopsarus (Eigenmann and Eigenmann, 1890)	LACM		C, D	*
Stenobrachius nannochir (Gilbert, 1890)	LACM		C, D	*
Simbolphorus californiensis Eigenmann and Eigenmann, 1889	SIO, LACM		C, D	*
Taaningichthys paurolychnus Davy, 1972	SIO, LACM		T, D	*
Tarletonbeania crenularis (Jordan and Gilbert, 1880)	LACM		C, D	*
Triphoturus mexicanus (Gilbert, 1890)	SIO, LACM	17	C, D	
Order LAMPRIFORMES				
Family Trachipteridae				

Desmodema lorum Rosenblatt and Butler, 1977	LACM		C, S	★
Order GADIFORMES				
Family Macrouridae				
Albatrossia pectoralis (Gilbert, 1892)	SIO		C, D	★
Coryphaenoides acrolepis (Bean, 1884)		13, 14, 15	C, D	Southern limit
Coryphaenoides armatus (Hector, 1875)	SIO		T, D	★
Coryphaenoides yaquinae Iwamoto and Stein, 1974	SIO		C, D	★
Mesobius berryi Hubbs and Iwamoto, 1977	LACM		T, D	★
Family Moridae				
Antimora microlepis Bean, 1890	SIO		C, D	★
Antimora rostrata (Günther, 1878)		2	T, D	
Family Melanonidae				
Melanonus zugmayeri Norman, 1930	LACM		C, D	★
Order OPHIDIIFORMES				
Family Ophidiidae				
Chilara taylori (Girard, 1858)	SIO		T, D	★
Lamprogrammus niger Alcock, 1891	LACM		T, D	★
Family Bythitidae				
Cataetyx rubrirostris Gilbert, 1890	LACM		C, D	
Grammonus diagrammus (Heller and Snodgrass, 1903)	SIO	13, 15	T, S	
Order BATRACHOIDIFORMES				
Family Batrachoidiidae				
Porichthys sp.		28		
Order LOPHIIFORMES				
Family Caulophrynidae				
Caulophryne pelagica (Brauer, 1902)		14	T, D	Northern limit
Family Oneirodidae				
Bertella idiomorpha Pietsch, 1973	CAS	21	C, D	Type location
Chaenophryne melanorhabdus Regan and Trewavas, 1932	LACM		T, D	★
Oneirodes acanthias (Gilbert, 1915)	SIO, LACM		C, D	★
Oneirodes basili Pietsch, 1974		14	C, D	Southern limit; type location
Phyllorhinichthys micractis Pietsch, 1969	LACM	14, 16, 20	C, D	Northern limit; type location
Family Gigantactinidae				
Gigantactis savagei Bertelsen, Pietsch, and Lavenberg, 1981	LACM		C, D	★
Order GOBIESOCIFORMES				
Family Gobiesocidae				
Gobiesox eugrammus Briggs, 1955	SIO, CAS	10, 13, 14, 15, 28	C, S	Type location
Gobiesox maeandricus (Girard, 1858)		13, 14, 15	C, S	Southern limit
Gobiesox rhessodon Smith, 1881	SIO	13, 15, 26	C, S	
Rimicola eigenmanni (Gilbert, 1890)	SIO		C, S	★
Rimicola sila Briggs, 1955		10, 14, 18	E, S	Type location
Order ATHERINIFORMES				
Family Atherinopsidae				
Atherinops affinis (Ayres, 1860)	CI-UABC, SIO, AMNH	8, 10, 13	C, S	
Atherinopsis californiensis Girard, 1854	SIO, LACM		C, S	★
Order BELONIFORMES				
Family Scomberesocidae				
Cololabis saira (Brevoort, 1856)	SIO, LACM		C, S	★
Family Exocoetidae				
Cheilopogon pinnatibarbatus (Bennett, 1831)	SIO	28	C, S	
Order BERYCIFORMES				
Family Anoplogastridae				
Anoplogaster cornuta (Valenciennes, 1833)	LACM		T, D	★
Order STEPHANOBERYCIFORMES				
Family Melamphidae				
Melamphaes acanthomus Ebeling, 1962	SIO, LACM		T, D	★
Melamphaes indicus Ebeling, 1962	LACM		T, D	★
Melamphaes janae Ebeling, 1962	SIO		T, D	★
Melamphaes longivelis Parr, 1933	SIO		T, D	★
Melamphaes lugubris Gilbert, 1891	SIO, LACM		C, D	★
Melamphaes parvus Ebeling, 1962	SIO, CAS, LACM	25	C, D	Type location
Poromitra crassiceps (Günther, 1878)	SIO, LACM		T, D	★
Scopeloberyx microlepis (Norman, 1937)	SIO		T, D	★
Scopeloberyx opisthopterus (Parr, 1933)	SIO		T, D	★
Scopeloberyx robustus (Günther, 1887)	SIO, LACM		T, D	★
Scopelogadus mizolepis (Günther, 1878)	SIO, LACM		T, D	★
Order CETOMIMIFORMES				
Family Barbourisiidae				
Barbourisia rufa Parr, 1945	SBMNH		C, D	★
Family Cetomimidae				

Ditropichthys storeri (Goode and Bean, 1895)		LACM		T, D	★
Gyrinomimus myersi Parr, 1934		SIO		T, D	★
Order SYNGNATHIFORMES					
Family Centriscidae					
Macrorhamphosus gracilis (Lowe, 1839)		SIO		T, S	★
Family Syngnathidae					
Syngnathus exilis (Osburn and Nichols, 1916)		SIO		C, D	★
Syngnathus insulae Fiitzsce, 1980		SIO	14, 18	E, S	Type location
Syngnathus leptorhynchus Girard, 1854		LACM		C, S	★
Order SCORPAENIFORMES					
Family Sebastidae					
Sebastolobus altivelis Gilbert, 1896		SIO, LACM		C, D	
Family Scorpaenidae					
Scorpaena guttata Girard, 1854	+	SIO, TUMNH, LACM	10, 13, 15	T, S	
Scorpaena histrio Jenyns, 1840		SIO	14	T, S	Northern limit
Scorpaena mystes Jordan and Starks, 1895	+			T, S	
Sebastes chlorostictus (Jordan and Gilbert, 1880)		CI-UABC, SIO	11, 13	C, D	
Sebastes constellatus (Jordan and Gilbert, 1880)		CI-UABC, SIO	11, 13	C, S	
Sebastes elongatus Ayres, 1859		CI-UABC, SIO	13	C, S	
Sebastes ensifer Chen, 1971		CI-UABC, SIO	11, 13	C, D	
Sebastes eos (Eigenmann and Eigenmann, 1890)		CI-UABC, SIO	13, 14	C, D	
Sebastes helvomaculatus Ayres, 1859			8	C, D	
Sebastes hopkinsi (Cramer, 1895)		SIO	6, 13, 14, 15	C, S	Southern limit
Sebastes lentiginosus Chen, 1971		SIO	14	C, S	Southern limit
Sebastes levis (Eigenmann and Eigenmann, 1889)	+	CI-UABC	13, 14, 15	C, D	
Sebastes macdonaldi (Eigenmann and Beeson, 1893)		CI-UABC, SIO	13	C, D	
Sebastes melanostomus (Eigenmann and Eigenmann, 1890)		CI-UABC, SIO	13	C, D	
Sebastes miniatus (Jordan and Gilbert, 1890)		CI-UABC, SIO	13	C, S	
Sebastes notius Chen, 1971		CI-UABC, SIO	11, 13, 14	T, D	Northern limit; type location
Sebastes ovalis (Ayres, 1862)		CI-UABC, SIO	13	C, D	Southern limit
Sebastes paucispinis Ayres, 1854		SIO	13, 14	C, S	
Sebastes rosaceus Girard, 1854		CI-UABC	11, 13	C, S	
Sebastes rosenblatti Chen, 1971		CI-UABC, SIO	11, 13	C, D	
Sebastes rufus (Eigenmann and Eigenmann, 1890)		SIO	13, 14, 15	C, D	
Sebastes simulator Chen, 1971		CI-UABC, SIO	11, 13, 14, 15,	C, D	
Sebastes umbrosus (Jordan and Gilbert, 1882)		CI-UABC, SIO	11, 13	C, S	
Scoepaenodes xyris (Jordan and Gilbert, 1882)	+	SIO	13, 14, 15	T, S	
Family Cottidae					
Chitonotus pugetensis (Steindachner, 1876)		SIO	15	C, S	
Clinocottus analis (Girard, 1858)	+	SIO, CAS	15	C, S	
Icelinus cavifrons Gilbert, 1890		SIO	7, 13, 15	C, S	
Ruscarius creaseri (Hubbs, 1926)		SIO	13, 15	C, S	
Family Liparidae					
Paraliparis rosaceus Gilbert, 1890		SIO	14	T, D	
Paraliparis ulochir Gilbert, 1896		SIO		C, D	★
Psednos anoderkes Chernova and Stein, 2002		SIO	14	E, D	Type location
Psednos griseus Chernova and Stein, 2002			14	E, D	Type location
Psednos mexicanus Chernova and Stein, 2002		LACM	14	E, D	Type location
Psednos pallidus Chernova and Stein, 2002		SIO	14	E, D	Type location
Order PERCIFORMES					
Family Howellidae					
Howella brodiei Ogilby, 1899		LACM		T, D	★
Family Polyprionidae					
Stereolepis gigas Ayres, 1859			15	T, S	
Family Serranidae					
Epinephelus labriformis (Jenyns, 1840)	+			T, S	★, Northern limit
Mycteroperca rosacea (Streets, 1877)	+	LACM		T, S	★, Northern limit
Mycteroperca xenarcha Jordan, 1888		SIO	15	T, S	
Paralabrax auroguttatus Walford, 1936		SIO		C, D	★
Paralabrax clathratus (Girard, 1854)	+	CI-UABC, SIO, AMNH	13, 23, 28	C, S	
Paralabrax nebulifer (Girard, 1854)			13, 15	C, S	
Pronotogrammus multifasciatus Gill, 1863		SIO		T, D	★
Family Priacanthidae					
Heteropriacanthus cruentatus (Lacepe`de, 1801)		SIO	14, 15	T, S	Northern limit
Priacanthus alalaua Jordan and Evermann, 1903			24, 28	T, S	Northern limit
Family Apogonidae					
Apogon atricaudus Jordan and McGregor, 1898		SIO	14	T, S	
Apogon guadalupensis (Osburn and Nichols, 1916)	+	SIO, AMNH	10, 13, 14, 15, 28	C, S	Type location
Family Malacanthidae					
Caulolatilus affinis Gill, 1865		SIO	14, 28	T, S	
Caulolatilus princeps (Jenyns, 1840)	+	SIO, AMNH, LACM	12	T, S	

Family Carangidae					
Decapterus muroadsi (Temminck and Schlegel, 1843)		SIO	13, 15, 26	C, S	
Elagatis bipinnulata (Quoy and Gaimard, 1825)			6	T, S	
Seriola lalandi Valenciennes, 1833	+	SIO	25, 28	T, S	
Trachurus symmetricus (Ayres, 1855)		SIO, AMNH, LACM	28	C, S	
Family Bramidae					
Brama japonica Hilgendorf, 1878			8	C, S	
Family Sparidae					
Calamus brachysomus Lockington, 1880		SIO		T, S	*
Family Sciaenidae					
Cynoscion sp.			28		
Genyonemus lineatus (Ayres, 1855)			28	C, S	
Pareques sp. (Gilbert, 1898)		SIO		T, S	*, Northern limit
Umbrina roncador Jordan and Gilbert, 1882			28	C, S	
Family Kyphosidae					
Girella nigricans (Ayres, 1860)	+	CI-UABC, SIO, CAS, AMNH, LACM	23, 28	C, S	
Kyphosus analogus (Gill, 1862)	+		18	T, S	*
Medialuna californiensis (Steindachner, 1876)	+	SIO, LACM	13, 15, 23	C, S	
Family Chaetodontidae					
Prognathodes falcifer (Hubbs and Rechnitzer, 1958)	+	SIO	11, 15, 28	T, S	Type location
Family Pomacantidae					
Holacanthus clarionensis Gilbert, 1891		SIO	6, 14	T, S	Northern limit
Holacanthus passer Valenciennes, 1846		SIO	14	T, S	Northern limit
Family Embiotocidae					
Brachyistius aletes (Tarp, 1952)		SIO, CAS, MCZ	10	E, S	Type location
Brachyistius frenatus Gill, 1862	+	SIO, USNM, AMNH	13, 14, 15, 23	C, S	
Embiotoca jacksoni Agassiz, 1853	+	SIO, CAS	13, 14, 15, 23, 24	C, S	
Embiotoca lateralis Agassiz, 1854	+	CAS		C, S	*, Southern limit
Hyperprosopon argenteum Gibbons, 1854		SIO	13, 14, 15	C, S	Southern limit
Rhacochilus toxotes Agassiz, 1854	+	SIO	14, 15	C, S	
Rhacochilus vacca (Girard, 1855)	+	SIO	7, 13, 14, 15	C, S	Southern limit
Zalembius rosaceus (Jordan and Gilbert, 1880)			13, 15	C, S	
Family Pomacentridae					
Azurina hirundo Jordan and McGregor, 1898	+	SIO	6, 10, 14, 24	C, S	
Chromis alta Greenfield and Woods, 1980			6	T, S	
Chromis atrilobata Gill, 1862			14	T, S	Northern limit
Chromis punctipinnis (Cooper, 1863)	+	SIO, AMNH	23, 28	C, S	
Hypsypops rubicundus (Girard, 1854)	+	CI-UABC, SIO, CAS, AMNH, TUMNH	13, 15, 23, 28	C, D	
Stegastes leucorus (Gilbert, 1892)	+	SIO	6, 14, 24	T, S	
Family Labridae					
Bodianus diplotaenia (Gill, 1862)		SIO	6, 14	T, S	Northern limit
Halichoeres insularis Allen and Robertson, 1992			28	T, S	Northern limit
Halichoeres nicholsi (Jordan and Gilbert, 1882)	+		6	T, S	Northern limit
Halichoeres semicinctus (Ayres, 1859)	+	CI-UABC, SIO, ANSP, TUMNH, LACM	13, 14, 15	C, S	
Oxyjulis californica (Günther, 1861)	+	SIO	23, 25	C, S	
Semicossyphus pulcher (Ayres, 1854)	+	CI-UABC, SIO, USNM, LACM	14, 15, 23, 24, 28	C, S	
Family Zoarcidae					
Melanostigma pammelas Gilbert, 1896		SIO		C, D	*
Pachycara bulbiceps (Garman, 1899)		SIO		C, D	*
Pachycara gymninium Anderson and Peden, 1988			14	C, D	Southern limit
Pachycara lepinium Anderson and Peden, 1988			14	C, D	Southern limit
Taranetzella lyoderma Andriashev, 1952			14	C, D	Southern limit
Family Pholidae					
Apodichthys anctaerosae (Gilbert and Starks, 1897)		SIO, CAS, AMNH	13, 14, 15, 18	C, S	Southern limit
Family Anarhichadidae					
Anarrhichthys ocellatus Ayres, 1855			28	C, S	Southern limit
Family Chiasmodontidae					
Kali indica Lloyd, 1909		SIO		C, D	*
Kali normani (Parra, 1931)		SIO	5	T, D	
Chiasmodon niger Johnson, 1864		SIO		T, D	*
Chiasmodon subniger Garman, 1899		SIO, LACM		T, D	*
Pseudoscopelus lavenbergi Melo, Walker, and Klepadlo, 2007		SIO		T, D	*
Family Tripterygiidae					
Enneanectes reticulatus Allen and Robertson, 1991		SIO	14	T, S	Northern limit
Enneanectes sp.			14		
Family Labrisomidae					
Alloclinus holderi (Lauderbach, 1907)	+	SIO	9, 15	C, S	
Malacoctenus ebisui Springer, 1959		SIO	14	T, S	Northern limit

Malacoctenus gigas Springer, 1959		SIO		T, S	⋆
Malacoctenus zacae Springer, 1959		SIO		T, S	⋆
Paraclinus integripinnis (Smith, 1880)		SIO, CAS	27	T, S	
Starksia guadalupae Rosenblatt and Taylor, 1971		SIO	14, 18	C, S	Northern limit; type location
Family Clinidae					
Gibbonsia elegans (Cooper, 1864)		SIO, USNM AMNH	10, 13, 14, 15, 30	C, S	
Gibbonsia montereyensis Hubbs, 1927		SIO, CAS, TUMNH	14, 30	C, S	Southern limit
Gibbonsia norae Hubbs, 1952			29	C, S	
Heterostichus rostratus Girard, 1854	+	CI-UABC, SIO, CAS	10, 13, 14, 15	C, S	
Family Chaenopsidae					
Chaenopsis alepidota (Gilbert, 1890)		SIO		C, S	⋆
Family Dactyloscopidae					
Gillellus semicinctus Gilbert, 1890		SIO	14	T, S	Northern limit
Family Blenniidae					
Hypsoblennius jenkinsi (Jordan and Evermann, 1896)		SIO		C, S	⋆
Ophioblennius steindachneri Jordan and Evermann, 1898		SIO	6	T, S	
Family Gobiidae					
Lythrypnus dalli (Gilbert, 1890)	+	SIO	13, 15	T, S	
Lythrypnus zebra (Gilbert, 1890)	+	SIO, TUMNH	13, 15	C, S	
Rhinogobiops nicholsii (Bean, 1882)			14	C, S	
Family Gempylidae					
Ruvettus pretiosus Cocco, 1833		SIO		C, S	⋆
Family Scombridae					
Acanthocybium solandri (Cuvier, 1832)			28	C, S	
Auxis thazard (Lacepède, 1800)			28	T, S	
Katsuwonus pelamis (Linnaeus, 1758)			28	T, S	
Scomber japonicus Houttuyn, 1782		SIO	28	C, S	
Thunnus alalunga (Bonnaterre, 1788)		SIO	13, 15	C, S	
Thunnus albacares (Bonnaterre, 1788)		SIO	13, 15, 28	T, S	
Thunnus obesus (Lowe, 1839)			1, 5	T, S	
Thunnus orientalis (Temminck and Schlegel, 1844)		SIO	7, 8, 13, 14, 15, 24, 28	T, S	
Thunnus thynnus (Linnaeus, 1758)			7,13, 15	T, S	
Family Istiophoriade					
Tetrapturus angustirostris Tanaka, 1915		SIO		T, D	⋆
Family Centrolophidae					
Icichthys lockingtoni Jordan and Gilbert, 1880		LACM		C, S	⋆
Order PLEURONECTIFORMES					
Family Paralichthyidae					
Citharichthys sordidus (Girard, 1854)		SIO, LACM		C, S	⋆
Citharichthys stigmaeus Jordan and Gilbert, 1882		SIO, LACM		C, S	⋆
Hippoglossina stomata Eigenmann and Eigenmann, 1890			13, 14, 15	C, S	
Paralichthys californicus (Ayres, 1859)		SIO		C, S	⋆
Family Pleuronectidae					
Microstomus pacificus (Lockington, 1879)		LACM	25	C, D	
Pleuronichthys coenosus Girard, 1854		SIO		C, D	⋆
Family Cynoglossidae					
Symphurus atricaudus (Jordan and Gilbert, 1880)		LACM		C, D	⋆
Order TETRAODONTIFORMES					
Family Balistidae					
Xanthichthys lineopunctatus (Hollard, 1854)				T, D	
Xanthichthys mento (Jordan and Gilbert, 1882)	+	SIO		T, S	⋆
Family Tetraodontidae					
Sphoeroides annulatus (Jenyns, 1842)		SIO		T, S	⋆
Family Molidae					
Mola mola (Linnaeus, 1758)		SIO		T, S	⋆

References: 1) Berdegué, 1956; 2) Briggs, 1965; 3) Castro-Aguirre and Espinosa-Pérez, 1996; 4) Domeier and Nasby-Lucas, 2007; 5) Godsil and Byers, 1944; 6) Gotshall, 1998; 7) Gotshall, 2001; 8) Hart, 1973, 9) Hubbs, 1954; 10) Hubbs, 1960; 11) Hubbs and Rechnitzer, 1958; 12) Johnson, 1969; 13) León Castro *et al.*, 1993; 14) Love *et al.*, 2005; 15) Miller and Lea, 1972; 16) Moser *et al.*, 1986; 17) Munz, 1958; 18) Nelson *et al.*, 2004; 19) Patton and Thomas, 1977; 20) Pietsch, 1969; 21) Pietsch, 1973; 22) Pietsch, 2004; 23) Quast, 1960; 24) Robertson and Allen, 2008; 25) Roedel, 1953; 26) Roedel and Fitch, 1952; 27) Rosenblatt and Parr, 1969; 28) Santos del Prado and Peters, 2005; 29) Stepien and Rosenblatt, 1991; 30) Stepien *et al.*, 1991.

Key to distribution range: T: Species of tropical affinity (midpoint of its distribution south of 24°N); C: Species of Cold-temperate affinity (midpoint of its distribution north of 24°N); E: Species endemic of Isla Guadalupe. Geographic ranges from Love *et al.*, (2005), Robertson and Allen (2008) and Fishbase (2009).

Key to bathymetric range: S: Shallow water species (resident from surface to 20 m deep); D: Deep water species (bathymetric limit higher than -20 m, or deeper). Data from Love *et al.*, (2005), Robertson and Allen (2008) and Fishbase (2009).

Key to museums: CI-UABC) Colección Ictiológica Universidad Autónoma de Baja California, Ensenada; SIO) Scripps Institution of Oceanography, San Diego; CAS) California Academy of Sciences, San Francisco; USNM) National Museum of Natural History, Smithsonian Institution, Washington; AMNH) The American Museum of Natural History; SBMNH) Santa Barbara Museum of Natural History, Santa Barbara; ANSP) The Academy of Natural Science of Philadelphia; MCZ) Museum of Comparative Zoology, Cambridge, Massachusetts; UKNHM) The University of Kansas Natural History Museum; TUMNH) Tulane University Museum of Natural History, Louisiana; LACM) Los Angeles Natural History Museum, Los Angeles.

Notes: Refers to records which Guadalupe Island marks the northern or southern limit of the distribution of the species, if the study area represents the type locality, or if this is a new record for the locality (⋆)

mento (Jordan and Gilbert 1882). Additionally, some new findings were from temperate environments, such as the California batray *Myliobatis californica* (Gill 1865), the California flounder *Paralichthys californicus* (Ayres 1859), and the striped seaperch *Embiotoca lateralis* (Agassiz 1854). There is even a new record from the circumglobal *Mola mola* (Linnaeus 1758). Many of the species that were newly identified on Guadalupe Island have known populations in similar or higher latitudes on the coasts of Mexico and the United States. It is also noteworthy that in this review we found out that *Xanthichthys lineopunctatus* (Hollard 1854) considered exclusive resident of the western Pacific, was collected on Guadalupe Island in the 1950s (SIO 53–173, SIO 54–219A). This record might be considered as doubtful until a more detailed review of the material is done.

The data base of the 360 shallow water fishes from the island and the peninsula demonstrated that Guadalupe has a markedly lower richness (144 species) than the continent (between 278 and 327, with higher numbers in lower latitudes). The Bray-Curtis coefficient and the dendrogram (fig. 2) showed that the Guadalupe Island ichthyofauna is most qualitatively similar to the one at the peninsular segment of 28°N, and that the likeness dropped gradually and reached its lowest value at the México-United States border (fig. 2). When we separated the fish fauna by class (elasmobranchs and bony fishes) the arrangement of the dendrograms from each one was consistent with that of Figure 2 (data not shown), and thus it was manifest that the biogeographical arrangement is followed by all kinds of fishes.

DISCUSSION

The comprehensive fish list of Guadalupe Island presented here (328 species) more than doubled the number reported in previous inventories (124, according to a poll of Gallo-Reynoso et al. 2005b; and Love et al. 2005 listings). One reason for the increase in nominal species richness is the inclusion of pelagic and deep water taxa in our review (tab. 1), as they inhabit areas that were not considered in previous studies of the island, which mostly focused on coastal rocky reefs (Hubbs and Rechnitzer 1958; Briggs 1965; Pietsch 1969; León-Castro et al.1993).

Nevertheless, the 144 shallow water reef fishes reported here still represent a small improvement to previous appraisals (124 species in total, from Gallo-Reynoso et al. 2005b; Love et al. 2005). In the group of 20 new records there are 12 tropical species and only 8 temperate ones. It is still early to affirm that this difference is an indication of asymmetrical incidence of colonization from tropical faunas or effects of global change, but the possibility opens new research avenues for the future.

The 144 species of shallow reef fishes reported here for Guadalupe (tab. 1) indicates that the island might be richer in such fishes than coastal lagoons on the Baja California Peninsula. According to the literature (Danemann and de la Cruz-Aguero 1993; Arellano et al. 1996; Rosales-Casián 1996; Galván-Magaña et al. 2000), San Ignacio has 81 species (26°N), Ojo de Liebre 58 species (28°N), and San Quintín has 90 (30°N). We suggest that the rocky substrate in the coastal waters of Guadalupe Island increases habitat heterogeneity and favors the occurrence of a higher number of fish species in relation to the cited lagoons, where large areas of soft bottom exists.

In contrast, Guadalupe reefs have less fish species than the coastal zone of southern California (34°N, 242 species, Horn et al. 2006), Magdalena Bay (24°N, on the Baja California Peninsula: 292 species, Galván-Magaña et al. 2000), and all one latitude degree bins of the peninsula from 28° to 32°N (238 to 327 species; fig. 2). The low species richness is also evident when comparing specific taxonomic groups resident in the island and the peninsula, like rays (6 on the island and 20 or more at each latitude degree on the peninsula), perchs and snappers (Lutjanidae; 1 on the island and 10 on the peninsula), and puffers (Tetraodontiformes; 3 on the island and 14 on the peninsula). The explanation for these differences is probably due to a series of factors. Isolation is one of the most feasible causes, since larval transportation and movement of adults must be more efficient in mainland reefs than to an island over 200 km away. However, there may be other reasons involved; for example, the lower latitude and larger relative size of Magdalena Bay and of the coastal sections of north Baja California might also contribute to its higher species richness compared to Guadalupe (Whittaker and Fernández Palacios 2007). Another reason for the discrepancies in fish diversity may be the disparity in habitat heterogeneity among areas. Along the peninsula it is possible to find mangrove forests, sea grasses, kelp forests, mollusk beds, and other biological features (Graham et al. 2007; Bizzarro 2008) all with relatively distinct faunas and in consequence, possibly working as enrichment factors (sources) for the reefs. In clear contrast, Guadalupe lacks kelps, extensive sea grasses beds or mangroves, and has a very narrow shelf where reefs can develop (Santos-del Prado and Peters 2005). The likeness in the bottom features might be the instrumental agent that brings about differences in fish species richness of the island and Baja California.

Shifting the perspective, it can be said that Guadalupe Island has low richness for an oceanic island in the eastern Pacific. This notion is exemplified by a comparison of fish diversity in shallow waters of Guadalupe Island (144 species) with that found in the rest of the region's oceanic islands (Galápagos, Ecuador; Cocos, Costa Rica; Malpelo, Colombia; and Revillagigedos, México), from where Robertson and Cramer (2009) reported a range of 203 to 363 species. The one exception to this trend is Clipperton Island with only 104 species present (Robertson and Allen 2008). Guadalupe is much larger than Malpelo and most of the Revillagigedo islands (Santos-del Prado and Peters 2005), and is nearer to the coast than Galápagos or Clipperton (Robertson and Cramer 2009); from these facts we discard the idea that the smaller diversity is due to an island size effect (Whittaker and Fernández Palacios 2007), or to mere isolation. It is more possible that the dominant pattern of currents and the difference in temperatures between the islands and the nearest mainland can explain the situation. All cited tropical islands can carry colonizers from the mainland and from about the same latitude, using branches of the California and Costa Rica currents (Kessler 2006). However, Guadalupe is surrounded by colder waters than the peninsula (a condition that may form a temporal barrier for dispersal), and in addition, the movement of the California Current is southwards, also making arrival more difficult.

In Guadalupe Island only 8 endemic fish species have been documented (tab. 1); this adds to 2.4% of the total although the figure rises to 5.5% when considering only reef taxa. Relating these data to those of coastal waters of the tropical eastern Pacific coast (Robertson and Cramer 2009), endemism in Guadalupe is quite low as most areas have over 10 endemics, and the oceanic islands usually exceed 25. However, the situation changes when the number is transformed to percentage of the total fauna; in this case Guadalupe contains a relatively high proportion of endemics, only surpassed by some reefs in Panamá and the oceanic islands Clipperton, Cocos, Galápagos, Malpelo and Revillagigedos (13% endemics or more in all cases). It can be hypothesized that Guadalupe Island is relatively isolated from the mainland and that has favored the presence of some unique species; notwithstanding, the somewhat low endemism may indicate that segregation is not permanent or not as efficient, especially during El Niño years, when the presence of tropical taxa (both as larvae and adults) has been reported (Hernández-de la Torre et al. 2005).

Regarding the biogeographic aspects of the fauna, a recent paper (Pondella et al. 2005) investigated reef fish species abundance and composition in a group of eight islands off the coast of California (USA) and Baja California (México), with data obtained from a census of conspicuous fishes conducted at each site. They report a total of 84 species, remark the existence of a clear faunistic division of tropical and temperate faunas between Coronado and San Martín islands in México (approximate latitude 31°N), and point out that San Benito Island might be the northernmost limit of tropical species that are much more common at lower latitudes in the peninsula. The referred study did not include Guadalupe Island, and thus we decided to perform a similar analysis of the fish structure, but this time using absence/presence data from one degree latitude bins, from which information is more readily available (Love et al. 2005). The resulting dendrogram (based on a data set of 360 species of the island and the peninsula from 28°N to 32°N; fig. 2) shows that the qualitative differences in fish composition along the peninsula are gradual and do not seem to evidence the break mentioned by Pondella et al. (2005), probably because of the difference in data sources, or as an artifact of the tree that joined the northernmost point in the north (32°N) to the next most similar one (31°N). In addition, Guadalupe Island was more related to the 28°N bin than to northern latitudes. This finding suggests that the most probable source of faunal exchange with the peninsula might be the area around Cedros Island, San Benito Island, and Punta Eugenia (all at 28°N). This hypothesis is supported by the range extensions of over 20 tropical species for which their nearest area of occurrence was that latitude (including the flag cabrilla *Epinephelus labriformis* and the leopard grouper *Mycteroperca rosacea*; Pondella et al. 2005; Robertson and Allen 2008; tab. 1). Further phylogeographic studies between Guadalupe Island and the Baja California coast have to be conducted in order to confirm this connection.

In conclusion, Guadalupe Island has a total of 328 documented fish species (144 of them residents of reefs or shallow water), a much higher figure than previously reported. The site has a low number of reported endemics (only 8), a fact that indicates low local speciation rates, probably as a consequence of gene flow from the mainland. Notwithstanding, it has one of the highest percentages of endemism in the tropical and warm temperate eastern Pacific (5.5% of the species). Finally, the qualitative similarity between the fish fauna at Guadalupe and that present at 28°N on the Baja California Peninsula, points toward the latter as the main source for potential immigrants from tropical regions.

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LITERATURE CITED

Aguirre-Muñoz, A., E. Ezcurra, E. E. Höflich, J. Soberón-Mainero, L. M. Salas-Flores, K. Santos-del Prado, E. Peters, L. Luna-Mendoza, B. Tershy, B. Keitt, C. García-Gutiérrez, and L. Aguirre-Bielschowsky. 2005. La construcción social de la conservación y el desarrollo sustentable de Isla Guadalupe. *In* La Isla Guadalupe. Restauración y conservación, K. Santos-del Prado and E. Peters, compilators. México, D.F.: SEMARNAT/INE/CICESE/GECI/SEMAR, pp. 239–253.

Allen, L. G., D. J. Pondella, and M. H. Horn. 2006. The ecology of marine fishes. California and adjacent waters. Berkeley: University of California Press. 660 pp.

Arellano-Martínez, M., J. de la Cruz-Agüero, and V. M. Cota-Gómez. 1996. Lista sistemática de los peces marinos de las lagunas Ojo de Liebre y Guerrero Negro, B.C.S. y B.C., México. Cienc. Mar. 22: 111–128.

Berdegué, A. J. 1956. Peces de importancia comercial en la costa nor-Occidental de México. México, D.F.: Comisión para el Fomento de la Piscicultura Rural, Secretaría de Marina. 345 pp.

Bizzarro, J. J. 2008. A review of the physical and biological characteristics of the Bahía Magdalena Lagoon complex (Baja California Sur, Mexico). Bull. So. Calif. Acad. Sci. 107: 1–24.

Briggs, J. C. 1965. The Clingfishes (Gobiesocidae) of Guadalupe Island, Mexico. Calif. Fish Game 51: 123–124.

Castro, R., A. Mascarenhas, A. Sánchez-Barba, R. Durazo, and E. Gil-Silva. 2005. Condiciones meteorológicas en el sur de Isla Guadalupe. *In* La Isla Guadalupe. Restauración y conservación, K. Santos-del Prado and E. Peters, compilators. México, D.F.: SEMARNAT/INE/CICESE/GECI/SEMAR, pp. 27–38.

Castro-Aguirre, J. L., and H. Espinosa-Pérez. 1996. Catálogo sistemático de las rayas y especies afines de México: Chondrichthyes: Elasmobranchii: Rajiformes: Batoideiomorpha. Listados Faunísticos de México 7: 1–75.

Clarke, K. R., and R. N. Gorley. 2006. Primer v6. User manual/tutorial. Primer-E Ltd. Plymouth. 190 pp.

CONANP. 2009. Programa de Manejo. Reserva de la Biosfera Isla Guadalupe. http://www.conanp.gob.mx/anp/consulta/Borrador%20PM%20RBIG%20agosto%2009.pdf.

Danemann, G. D., and J. de la Cruz-Agüero. 1993. Ictiofauna de la Laguna de San Ignacio, B.C.S., México. Cienc. Mar. 19: 333–341.

Domeier, L. M. and N. Nasby-Lucas. 2007. Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico), Mar. Biol. 150: 977–984.

Durazo, R., and T. R. Baumgartner. 2002. Evolution of oceanographic conditions off Baja California: 1997–1999. Prog. Oceanogr. 54: 7–31.

Durazo, R., G. Gaxiola-Castro, B. Lavaniegos, R. Castro Valdés, J. Gómez-Valdés, and A. da Silva-Mascarenhas. 2005. Oceanographic conditions west of the Baja California coast, 2002–2003: a weak El Niño and subarctic water enhancement. Cienc. Mar. 31: 537–552.

Eschmeyer, W. N., E. S. Herald, and H. E. Hammann. 1983. A field guide to Pacific coast fishes: a Peterson field guide. New York: Houghton Mifflin Harcourt. 352 pp.

Eschmeyer, W. N., and R. Fricke. eds. 2009. Catalog of Fishes electronic version (9 September 2009). http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp.

Espinosa-Pérez, M. C., and M. E. Hendrickx. 2006. A comparative analysis of biodiversity and distribution of shallow-water marine isopods (Crustacea: Isopoda) from polar and temperate waters in the East Pacific. Belg. J. Zool. 136: 219–247.

Ferreira, A J. 1978. The genus *Lepidozona* in the temperate eastern Pacific, Baja California to Alaska, with the description of a new species. Veliger 21:19–44.

Froese, R., and D. Pauly. eds. 2009. FishBase. World Wide Web electronic publication (14 September 2009). http://www.fishbase.org.

Gallo-Reynoso, J. P., B. J. LeBoeuf, A. L. Figueroa-Carranza, and M.O. Maravilla-Chávez. 2005a. Los pinnipedos de Isla Guadalupe. *In* La Isla Guadalupe. Restauración y conservación, K. Santos-del Prado and E. Peters, compilators. México, D.F.: SEMARNAT/INE/CICESE/GECI/SEMAR, pp. 171–202.

Gallo-Reynoso, J. P., A. L. Figueroa-Carranza, and M.P. Blanco-Parra. 2005b. Los tiburones de Isla Guadalupe. *In* La Isla Guadalupe. Restauración y conservación, K. Santos-del Prado and E. Peters, compilators. México, D.F.: SEMARNAT/INE/CICESE/GECI/SEMAR, pp. 143–169.

Galván-Magaña, F., F. Gutiérrez-Sánchez, L. A. Abitia-Cárdenas, and J. Rodríguez-Romero. 2000. The distribution and affinities of the shore fishes of the Baja California Sur lagoons. *In* Aquatic ecosystems of Mexico: status and scope, M. Munawar, S. G. Lawrence, I. F. Munawar and D. F. Malley, eds. Leiden: Backhuys, pp 383–398.

Garth, J. S. 1958. Brachyura of the Pacific coast of America. Oxyrhyncha. Allan Hancock Pac. Exped. 21: 1–673.

Godsil, H. C., and R. D. Byers. 1944. A systematic study of the pacific tunas. Calif. Div. Fish Game, Fish Bull. 60: 131 pp.

Gotshall, D. W. 1998. Marine animals of Baja California. A guide to the common fishes and invertebrates. Monterey: Sea Challengers. 113 pp.

Gotshall, D. W. 2001. Pacific coast inshore fishes. Monterey: Sea Challengers. 96 pp.

Graham, M. H., J. A. Vásquez, and A. H. Buschmann. 2007. Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. Ocean. Mar Biol. Ann. Rev. 45: 39–88.

Hart, J. L. 1973. Pacific fishes of Canada. Fish. Res. Board Canada Bull 180: 1–740.

Hernández-de la Torre, B., G. Gaxiola-Castro, R. Aguirre-Gómez, S. Álvarez-Borrego, J. R. Lara-Lara, and S. Nájera Martínez. 2005. Serie de tiempo de productividad (1970–2003) en el ecosistema marino de Isla Guadalupe. *In* La Isla Guadalupe. Restauración y conservación, K. Santos-del Prado and E. Peters, compilators. México, D.F.: SEMARNAT/INE/CICESE/GECI/SEMAR, pp. 135–142.

Horn, M. H., L. G. Allen, and R. N. Lea. 2006. Biogeography. *In* The ecology of marine fishes. California and adjacent waters, L. G. Allen, D. J. Pondella and M. H. Horn, eds. Berkeley: University of California Press. pp. 3–25.

Hubbs, C. L. 1954. Additional records of clinid fishes, with the description of a new species of *Cryptotrema* from the Gulf of California. Copeia 1: 17–19.

Hubbs, C. L. 1960. The marine vertebrates of the outer coast. Syst. Zool. 9: 134–147.

Hubbs, C. L., and A. B. Rechnitzer. 1958. A new fish, *Chaetodon falcifer,* from Guadalupe Island, Baja California, with notes on related species. Proc. Calif. Acad. Sci. 29:273–313.

Humann, P. 2005. Coastal fish identification. California to Alaska. Jacksonville: New World Publications. 208 pp.

Johnson, R. K. 1969. A review of the fish genus *Kali* (Perciformes: Chiasmodontidae) Copeia 2: 386–400.

Kessler, W. S. 2006. The circulation of the eastern tropical Pacific: a review. Prog. Oceanogr. 69: 181–217.

León-Castro H., G. Ruiz-Campos, J. Alanis-García, and O. A. Pedrin-Osuna. 1993. Escorpénidos (Pisces, Scorpaenidae) de Isla Guadalupe, Baja California. *In* Biodiversidad Marina y Costera de México, S. I. Salazar-Vallejo and N. E. González, eds. Chetumal: CONABIO/CIQRO, pp. 319–327.

Love, M. S., C. W. Mecklenburg, T. A. Mecklenburg, and L. K. Thorsteinson. 2005. Resource inventory of marine and estuarine fishes of the west coast and Alaska: A checklist on north Pacific and Arctic Ocean species from Baja California to the Alaska-Yukon border. Seattle: United States Geological Survey. 276 pp.

Miller, J. D., and N. R. Lea. 1972. Guide to the coastal marine fishes of California. Fish. Bull. 157: 1–249.

Moser, H. G., B. Y. Sumida, D. A. Ambrose, E. M. Sandknop, and E. G. Stevens. 1986. Development and distribution of larvae and pelagic juveniles of ocean whitefish, *Caulolatilus princeps*, in the CalCOFI survey region. CalCOFI Rep. 27: 162–169.

Munz, F. W. 1958. Photosensitive pigments from the retinae of certain deep-sea fishes. J. Physiol. 140:220–235.

Nelson, J. S., E. J. Crossman, H. Espinoza-Pérez, L. T. Findley, C. R. Gilbert, R. N. Lea, and J. D. Williams. 2004. Common and scientific names of fishes from the United States, Canada, and Mexico. 6th ed. Bethesda: American Fisheries Society, Special Publication 29. 386 pp.

Patton, S., and A. J. Thomas. 1977. Composition of lipid foams from swim bladders of two deep ocean fish species. J. Lipid. Res. 12:331–335.

Pietsch T. W. 1969. A remarkable new genus and species of deep-sea anglerfish (Family Oneirodidae) from off Guadalupe Island, Mexico. Copeia, 2: 365–369.

Pietsch, T. W. 1972. A review of the monotypic deep sea anglerfish family Centrophyrnidae: taxonomy, distribution and osteology. Copeia 1972: 17–47.

Pietsch, T. W. 2004. Revision of the deep-sea anglerfish Genus *Phyllorhinichthys* Pietsch (Lophiiformes: Ceratioidei: Oneirodidae), with the description of a new species from the Atlantic Ocean. Copeia 4: 797–803.

Pondella D. J., B. E. Gintert, J. R. Cobb, and L. G. Allen. 2005. Biogeography of the nearshore rocky-reef fishes at the southern and Baja California islands. J. Biog. 32: 187–201.

Quast, Jay C. 1960. The fishes of the family Hexagrammidae: their classification variation and osteology. PhD thesis, Univ. Calif. Los Angeles, 380 pp.

Robertson, D. R., and G. R. Allen. 2008. Shorefishes of the tropical eastern Pacific. http://www.stri.org/sftep.

Robertson, D. R., and K. L. Cramer. 2009. Shore fishes and biogeographic subdivisions of the Tropical Eastern Pacific. Mar. Ecol. Progr. Ser. 380: 1–17.

Roedel, P. M. 1953. Common ocean fishes of the California Coast. Fish. Bull. 91: 1–184.

Roedel, P. M., and J. E. Fitch. 1952. The status of the carangid fishes *Trachurus* and *Decapterus* on the Pacific Coast of Canada and the United States Copeia 1: 4–6.

Rosales-Casián, J. 1996. Ictiofauna de la Bahía de San Quintín, Baja California, México, y su costa adyacente. Cienc. Mar. 22: 443–458.

Rosenblatt, R. H., and T. D. Parr. 1969. The Pacific species of the clinid fish genus *Paraclinus* Copeia 1: 1–20.

Salgado-Rogel, M. L., J. S. Palleiro-Nayar, J. L. Rivera-Ulloa, D. Aguilar-Montero, E. Vázquez-Solórzano, and M. C. Jiménez-Quiroz. 2009. La pesquería y propuestas de manejo del pepino de mar *Parastichopus parvimensis* en Baja California, México. Cienc. Pesq. 17: 17–26.

Sánchez-Montante, O., O. Zaitsev, and M. Saldívar-Reyes. 2007. Condiciones hidrofísicas en el sistema lagunar Bahía Magdalena-Almejas. pp. 1–28, *In* R. Funes-Rodríguez, J. Gómez-Gutiérrez, and R. Palomares-García (eds.). Estudios ecológicos en Bahía Magdalena. CICIMAR/CIBNOR, México, D.F.

Santos-del Prado, K., and E. Peters (compilators). 2005. La Isla Guadalupe. Restauración y conservación. México, D.F.: SEMARNAT/INE/CICESE/GECI/SEMAR. 324 pp.

SEMARNAT. 2005. Decreto de Creación de la Reserva de la Biosfera Isla Guadalupe. http://www.semarnat.gob.mx/leyesynormas/La%20SEMARNAT%20en%20el%20Diario%20Oficial%20de%20la%20Federacin/250405.

Stepien, C. A., and R. H. Rosenblatt. 1991. Patterns of gene flow and genetic divergence in the northeastern pacific clinidae (Teleostei: Blennioidei), based on allozyme and morphological data. Copeia 4: 873–896.

Stepien, C. A., H. Phillips, J. A. Adler, and P. J. Mangold. 1991. Biogeographic relationships of rocky intertidal fishes in an area of cold water upwelling off Baja California, Mexico. Pac, Sci. 45: 63–71.

Vásárhelyi, C., and V. G. Thomas. 2008. Reflecting ecological criteria in laws supporting the Baja to Bering Sea marine protected areas network case study. Environ. Sci. Policy 11: 394–407.

Venrick, E.L., S. J. Bograd, D. A. Checkley, S. Cummings, R. Durazo, G. Gaxiola-Castro, J. Hunter, A. Huyer, K. D. Hyrenbach, B. E. Lavaniegos, A. Mantyla, F. B. Schwing, R. L. Smith, W. J. Sydeman, and P. A. Wheeler. 2003. The state of the California Current, 2002–2003: Tropical and subarctic influences vie for dominance, CalCOFI Rep. 44:28–60.

Whittaker, R. J. and J. M. Fernández Palacios. 2007. Island biogeography. Oxford: Oxford University Press. 416 pp.

COMPOSITION, DENSITY AND BIOGEOGRAPHIC AFFINITIES OF THE ROCKY INTERTIDAL FISHES ON THE WESTERN COAST OF THE BAJA CALIFORNIA PENINSULA, MEXICO

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ABSTRACT

The composition, density and biogeographic affinities of the rocky intertidal fishes of the western coast of the Baja California peninsula, Mexico, were studied from June 2006 to January 2009. A total of 5,489 specimens belonging to 48 species, 39 genera and 20 families were registered. *Clinocottus analis* was the dominant species on the northern and central coast (north to Punta Abreojos), and *Entomacrodus chiostictus* was dominant farther south. Based on distribution and density of permanent species, the area between Punta San Juanico and Bahia Magdalena represents the distributional boundary for northern (warm-temperate) and tropical fish elements. Most of species (85%) showed zoogeographical affinities with the San Diegan province, followed by species related to the Mexican (58%) and Cortez (56%) provinces. The known northernmost geographical ranges are extended for *Sargocentron suborbitalis*, *Labrisomus multiporosus* and *Bathygobius ramosus*; while the southernmost ranges extended for *Clinocottus analis*, *Oligocottus rubellio* and *Amphistichus koelzi*.

INTRODUCTION

The rocky intertidal zone is one of the most studied marine biotopes worldwide due to its easy access and the special adaptations of its biota to the dynamic environmental conditions (Gibson 1969, 1982; Stephenson and Stephenson 1972; Horn et al. 1999; Horn and Martin 2006). The fish fauna of these biotopes is characterized by having special physiological and morphological adaptations to inhabit the pools and crevices through the intertidal zone (Gibson 1969; Horn et al. 1999; Horn and Martin 2006).

The taxonomic and ecological studies of the rocky intertidal fish fauna in the Northeastern Pacific are well documented for the United States of America and Canada (cf. Chotkowski et al. 1999; Prochazka et al. 1999; Horn et al. 2006; Horn and Martin 2006; Blanchette et al. 2008) but insufficiently represented for the western rocky coast of Mexico. Recent studies on rocky tide pool fishes in northwestern region of the Baja California Peninsula (BCP) have been focused on taxonomical and ecological issues. Ruiz-Campos (1986) and Ruiz-Campos and Hammann (2002) analyzed the dynamics, composition and feeding relationships of the rocky intertidal fish community in Granada Cove (Punta Morro) at Bahia Todos Santos. For this same bay, Ruiz-Campos and Hammann (1987) reported 13 species, with the woolly sculpin *Clinocottus analis*, the most abundant fish. On the other hand, Stepien et al. (1991) found 19 species in a cold, upwelling area off Punta Clara (55 km SW of Ensenada) and remarked on the importance of this site in the Californian-Oregonian coastal marine zoogeographic transition. Recently, Ruiz-Campos et al. (2010) provided weight-length and length-length relationships for nine common rocky intertidal fish species of the western coast of the BCP. Except for the localities cited above, a long portion of the rocky shores of the BCP has not been quantitatively assessed for tide pool fishes. Briggs (1960) and Horn et al. (2006) identified Bahia Magdalena as a geographical distributional limit for boreal and tropical species; however this statement has not been properly documented for rocky tide pool fishes, with strong fidelity and connection to these biotopes (Pfister 1999). Pondella et al. (2005) analyzed the biogeography of the nearshore rocky-reef fishes at southern California and Baja California islands, and found that Punta Eugenia (Baja California Sur) showed a greater faunal break than Point Conception (California), as well as the presence of a clinal transition pattern in species composition from north to south throughout the San Diegan Province. Hastings (2000) established a significant correspondence between the ranges of chaenopsid fishes and the tropical eastern Pacific marine prov-

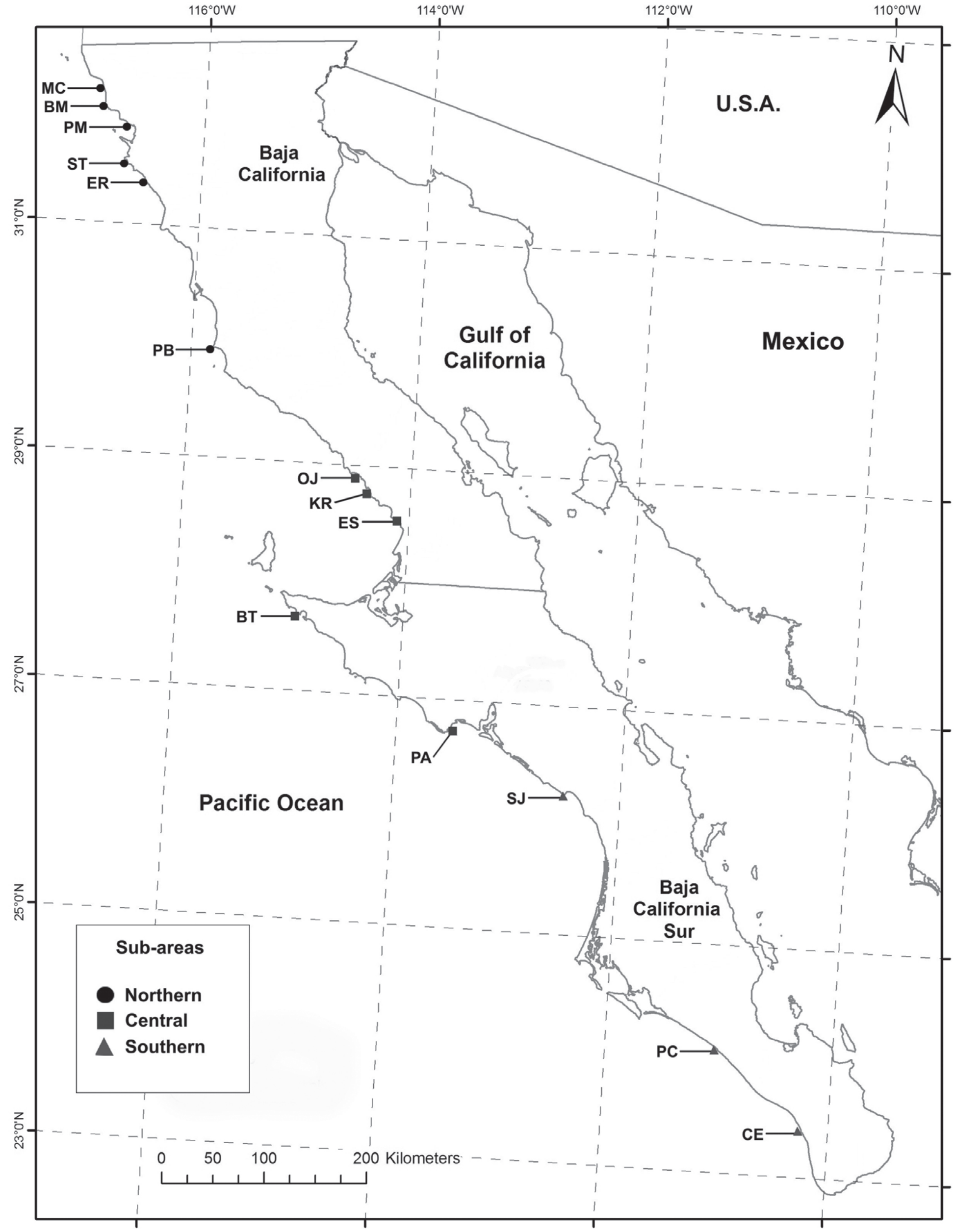

Figure 1. Sampling sites for rocky intertidal fishes in the western coast of the Baja California Peninsula, during June 2006 to January 2009. MC= Medio Camino, BM= Bajamar, PM= Punta Morro, ST= Santo Tomas, ER= Erendira, PB= Punta Baja, OJ= Los Ojitos, KR= Krutsio, ES= La Esmeralda, BT= Bahia Tortugas, PA= Punta Abreojos, SJ= San Juanico, PC= Punta [Playa] El Conejo, and CE= Los Cerritos.

inces, including the southern part of the BCP from Bahia Magdalena into the Cortez province.

We analyze here the taxonomic composition, density, zonation and zoogeographic relationships of the rocky intertidal fish communities through a latitudinal interval of nine degrees in the western coast of the BCP, in order to determine species' abundances and distribution patterns.

METHODS

Fish sampling was carried out in 14 rocky intertidal sites of the Baja California Peninsula (fig. 1) during low tide conditions from June 2006 to January 2009. The northernmost site was Medio Camino, Baja California (32°10'N) and the southernmost, Los Cerritos, Baja California Sur (23°20'N). The study area was divided into three sub-areas following Allen and Pondella (2006): northern (NS: Medio Camino to Punta Baja), central (CS: Los Ojitos to Punta Abreojos) and southern (SS: San Juanico to Los Cerritos). Fishes were sampled across mesolittoral zones (high, middle and low intertidal) established for this area by Ruiz-Campos (1986) and Ramírez-Valdéz (2009). In order to compare the species composition and abundances among sites, the length and width of each tide pool were measured. Fish were sampled using manual aspersion pumps, one containing a solution of 20% quinaldine (Gibson 1999) and the other 10% clove oil (Munday and Wilson 1997; Griffiths 2000). After 10 minutes of the application, narcotized fishes were removed from each tide pool using dip nets. The number of fishes collected in each pool was counted and expressed as average density (number of individuals captured per square meter of sampled pool) in each sub-area.

Specimens were fixed in 10%-formalin or 96%-ethanol, identified and deposited in the Fish Collection of the Universidad Autónoma de Baja California (UABC). Species identifications were based on Jordan and Evermann (1896), Bolin (1944), Hubbs (1952), Briggs (1955), Springer (1962), Miller and Lea (1972), Fischer et al. (1995), Allen and Robertson (1998), Thomson et al. (2000), and Robertson and Allen (2002). The taxonomic arrangement and nomenclature follows Nelson et al. (2004).

The species composition similarity among sites of the study area was calculated using the square root transformed average abundances of the permanent species, by means of the Bray–Curtis coefficient (Brower et al. 1997) and the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) clustering method. The determination of permanent species for the study sub-areas was based on Ramírez-Valdéz (2009).

RESULTS AND DISCUSSION

Species Accounts

A total of 5,489 fish belonging to 48 species, 39 genera and 20 families were collected throughout the study area. For each fish species, we present the following: *Distribution,* the known distribution range for the species as described by Love et al. (2005); *Records*, include the collection records for each species during the study period (June 2006 to January 2009), indicating for each locality the catalog record (UABC Fish Collection) with the highest number of specimens, denoted by square brackets; *Density*, average density of individuals/m² of sampled pool in the study sub-areas; *Zonation*, the distribution of the species crossing the intertidal zones described by Stephenson and Stephenson (1972): high intertidal (HI), middle intertidal (MI) and low intertidal (LI); *Affinity*, the zoogeographic region(s) and province(s) where the taxon is known to occur, following the marine coastal regionalization of Briggs (1974): California Region (CR) and its San Diegan (SDP) and Cortez (CP) provinces; Tropical Eastern Pacific Region (TEPR) and its Mexican (MP), Panamic (PP) and Galapagos Islands (IGP) provinces; Eastern Pacific Boreal Region (EPBR) and its Oregonian (OP) and Aleutian (AP) provinces; and Amphiamerican (AA).

Family Muraenidae

Gymnothorax mordax (Ayres, 1859). California moray
Distribution: Point Conception, California to Bahia Magdalena, Baja California. *Records*: Bahia Tortugas (1982 [1]). *Density*: 0.1 ind/m² [CS]. *Zonation*: LI. *Affinity*: CR (SDP).

Muraena lentiginosa (Jenyns, 1842). Jewel moray
Distribution: Bahia Magdalena, Baja California to Islas Lobos de Afuera, Peru, including Gulf of California, and Islas Galapagos. *Records*: Los Cerritos (2159 [1]). *Density*: 0.2 ind/m² (SS). *Zonation*: LI. *Affinity*: CR (SDP and CP) and TEPR (MP, PP and IGP).

Family Mugilidae

Chaenomugil proboscideus (Günther, 1861). Snouted mullet
Distribution: Bahia Magdalena, Baja California Sur to Panama, including the Gulf of California. *Records*: Los Cerritos (0814 [6]). *Density*: 0.1 ind/m² (SS). *Zonation*: HI. *Affinity*: CR (CP) and TEPR (MP and PP).

Mugil curema (Valenciennes, 1836). White mullet
Distribution: Atlantic and Pacific oceans; Newport Bay, southern California to Chile, including the Gulf of California and Islas Galapagos. *Records*: Los Cerritos (2001 [1]). *Density*: 0.2 ind/m² (SS). *Zonation*: HI. *Affinity*: AA.

Family Atherinopsidae

Atherinops affinis (Ayres, 1860). Topsmelt
Distribution: Near Sooke Harbour, Vancouver Island, British Columbia to Cabo San Lucas, Baja California Sur, with an isolated population in upper Gulf of California. *Records*: Punta Morro (1951 [19]) and Bahia Tortugas (2000 [17]). *Density*: 0.2 ind/m² (NS) and 0.4 ind./m²(CS). *Zonation*: HI. *Affinity*: EPBR (OP) and CR (SDP and CP).

Leuresthes tenuis (Ayres, 1860). California grunion
Distribution: San Francisco, northern California to Bahia Magdalena, Baja California Sur. *Records*: Punta Morro (1953 [17]), La Esmeralda (1954 [1]) and Bahia Tortugas (1762 [6]). *Density*: 0.1 ind/m² (NS) and 0.9 ind/m² (CS). *Zonation*: HI. *Affinity*: CR (SDP and OP).

Family Holocentridae

Sargocentron suborbitalis (Gill, 1863). Tinsel squirrelfish
Distribution: Gulf of California to Ecuador, including the southern end of the BCP and Islas Galapagos. *Records*: Los Cerritos (1833 [8]) and San Juanico (2148 [1]). *Density*: 0.4 ind/m² (SS). *Zonation*: HI and MI. *Affinity*: CR (CP) and TEPR (MP, PP and IGP).

Family Scorpaenidae

Scorpaena guttata (Girard, 1854). California scorpionfish
Distribution: Santa Cruz, central California to Gulf of

California. *Records*: San Juanico (2153 [1]). *Density*: 0.3 ind/m^2 (SS). *Zonation*: LI. *Affinity*: EPBR (OP) and CR (SDP and CP).

Familiy Cottidae

Clinocottus analis (Girard, 1858). Woolly sculpin
Distribution: Cape Mendocino, California to Punta Asuncion, Baja California Sur, including Isla Cedros and Isla Guadalupe (UABC-0398). *Records*: Bajamar (1734 [67]), Punta Morro (1862 [108]), Punta Santo Tomas (1828 [52]), Punta Baja (1693 [43]), Krutsio (1749 [64]), Los Ojitos (1815 [156]), La Esmeralda (1904 [68]), Bahia Tortugas (1984 [53]), and Punta Abreojos (1931 [25]). *Density*: 4.6 ind/m^2 (NS) and 4.7 ind/m^2 (CS). *Zonation*: HI, MI and LI. *Affinity*: EPBR (OP) and CR (SDP).

Clinocottus recalvus (Greeley, 1899). Bald sculpin
Distribution: Mill Beach near Brookings, southern Oregon to Punta Rompiente, Baja California. *Records*: Bajamar (1735 [11]), Punta Santo Tomas (1829 [4]) and Punta Baja (1694 [18]). *Density*: 1.0 ind/m^2 (NS). *Zonation*: HI, MI and LI. *Affinity*: EPBR (OP) and CR (SDP).

Oligocottus rubellio (Greeley, 1899). Rosy sculpin
Distribution: Fort Bragg, northern California to Isla San Martin, Baja California. *Records*: Punta Baja (1696 [1]). *Density*: 0.1 ind/m^2 (NS). *Zonation*: MI. *Affinity*: EPBR (OP) and CR (SDP).

Oligocottus snyderi (Greeley, 1898). Fluffy sculpin
Distribution: Chernabura Island, western Gulf of Alaska; Samsing Cove near Sitka, southeastern Alaska to Punta Cono, Baja California. *Records*: Punta Santo Tomas (1830 [9]), and Punta Baja (1805 [38]). *Density*: 0.3 ind/m^2 (NS). *Zonation*: MI and LI. *Affinity*: EPBR (AP and OP) and CR (SDP).

Family Serranidae

Epinephelus labriformis (Jenyns, 1840). Flag cabrilla
Distribution: San Diego and upper Gulf of California to Paita, Peru, including Islas Galapagos. *Records*: San Juanico (2154 [1]). Density: 0.3 ind/m^2 (SS). *Zonation*: LI. *Affinity*: CR (SDP and CP) and TEPR (MP, PP and IGP).

Family Pomacanthidae

Pomacanthus zonipectus (Gill, 1862). Cortez angelfish
Distribution: Redondo Beach, southern California and upper Gulf of California to Mancora, Peru and Islas Galapagos. *Records*: San Juanico (2152 [1]). *Density*: 0.3 ind/m^2 (SS). *Zonation*: MI. *Affinity*: CR (SDP and CP) and TEPR (MP, PP and IGP).

Family Kyphosidae

Girella nigricans (Ayres, 1860). Opaleye
Distribution: Otter Rock, Oregon to Cabo San Lucas, Baja California Sur, with an isolated population in the Gulf of California. *Records*: Punta Morro (1863 [85]), Punta Santo Tomas (1832 [6]), Punta Baja (1692 [85]), Krutsio (1842 [34]), Los Ojitos (1846 [37]), La Esmeralda (1633 [37]), Bahia Tortugas (1763 [33], Punta Abreojos (1898 [14]) and Punta Conejo (1949 [8]). *Density*: 2.1 ind/m^2 (NS), 1.2 ind/m^2 (CS) and 2.3 ind/m^2 (SS). *Zonation*: HI, MI and LI (juveniles and sub-adults). *Affinity*: CR (SDP and CP) and TEPR (MP).

Hermosilla azurea (Jenkins and Evermann, 1889). Zebraperch
Distribution: Klamath River estuary, California to Gulf of California. *Records*: Punta Morro (1707 [8]), Punta Baja (1691 [9]), La Esmeralda (1994 [19]), Los Ojitos (1745 [40]), Bahia Tortugas (2193 [7]), and Punta Abreojos (1899 [42]). *Density*: 0.6 ind/m^2 (NS and CS). *Zonation*: MI and LI (juveniles and subadults). *Affinity*: EPBR (OP), CR (SDP and CP) and TEPR (MP).

Family Cirrhitidae

Cirrhitus rivulatus (Valenciennes, 1855). Giant hawkfish
Distribution: Bahia Magdalena, Baja California Sur to Ecuador, including Gulf of California and Islas Galapagos. *Records*: Los Cerritos (1836 [4]). *Density*: 0.2 ind/m^2 (SS). *Zonation*: MI and LI. *Affinity*: CR (SDP and CP) and TEPR (MP, PP and IGP).

Family Embiotocidae

Amphistichus koelzi (Hubbs, 1933). Calico surfperch
Distribution: Cape Flattery, Washington to Arroyo San Isidro, Baja California. *Records*: Punta Morro (1928 [1]) and Los Ojitos (1927 [1]). *Density*: 0.1 ind/m^2 (NS and CS). *Zonation*: MI (juveniles). *Affinity*: EPBR (OP) and CR (SDP).

Hyperprosopon anale (Agassiz, 1861). Spotfin surfperch
Distribution: Seal Rock, Oregon to Bahia Blanca, Baja California. *Records*: Punta Baja (1924 [8]) and Los Ojitos (1926 [2]). *Density*: 0.1 ind/m^2 (NS and CS). *Zonation*: MI (juveniles). *Affinity*: EPBR (OP) and CR (SDP).

Hyperprosopon argenteum (Gibbons, 1854). Walleye surfperch
Distribution: Vancouver Island, British Columbia to Punta San Rosarito, Baja California, including Isla Guadalupe. *Records*: Punta Morro (1955 [1, juvenile]). *Density*: 0.6 ind/m^2 (NS). *Zonation*: MI. *Affinity*: EPBR (OP) and CR (SDP).

Micrometrus aurora (Jordan and Gilbert, 1880). Reef perch
Distribution: Tomales Bay, northern California to Isla Cedros, Baja California. *Records:* Punta Baja (1810 [13]). *Density*: 0.1 ind/m^2 (NS). *Zonation*: MI. *Affinity*: EPBR (OP) and CR (SDP).

Family Pomacentridae

Abudefduf declivifrons (Gill, 1862). Mexican night sergeant

Distribution: Bahia Magdalena, Baja California Sur and Gulf of California to Costa Rica. *Records*: Los Cerritos (1795 [173]). *Density*: 4.6 ind/m^2 (SS). *Zonation*: MI and LI (juveniles and adults). *Affinity*: CR (SDP and CP) and TEPR (MP and PP).

Abudefduf troschelii (Gill, 1862). Panamic sergeant major

Distribution: King Harbor, Redondo Beach, southern California to Pucusana, Peru, including Gulf of California and Islas Galapagos. *Records*: Punta Conejo (1825 [1], juvenile). *Density*: 0.3 ind/m^2 (SS). *Zonation*: MI. *Affinity*: CR (SDP and CP) and TEPR (MP, PP and IGP).

Hypsypops rubicundus (Girard, 1854). Garibaldi

Distribution: Monterey Bay, California to southwest corner of Gulf of California, Baja California Sur. *Records*: Punta Baja (2113 [1]). *Density*: 0.1 ind/m^2 (NS). *Zonation*: MI (juveniles). *Affinity*: EPBR (OP), CR (SDP) and TEPR (MP).

Microspathodon bairdii (Gill, 1862). Bumphead damselfish

Distribution: Gulf of California, including the southern tip of the BCP to Ecuador and Islas Galapagos. *Records*: Los Cerritos (1771 [1]). *Density*: 0.2 ind/m^2 (SS). *Zonation*: MI (juveniles). *Affinity*: CR (CP) and TEPR (MP, PP and IGP).

Stegastes flavilatus (Gill, 1862). Beaubrummel

Distribution: Isla Cedros and Rocas Chester, Baja California to Pucusana, Peru, including Gulf of California and Islas Galapagos. *Records*: Los Cerritos (2168 [3]) and San Juanico (2155 [1]). *Density*: 0.3 ind/m^2 (SS). *Zonation*: MI (juveniles). *Affinity*: CR (SDP and CP) and TEPR (MP, PP and IGP).

Family Labridae

Halichoeres notospilus (Günther, 1864). Banded wrasse

Distribution: Bahia San Juanico, Baja California Sur and Gulf of California to Islas Lobos de Afuera, Peru and Islas Galapagos. *Records*: San Juanico (2149 [1]). Density: 0.3 ind/m^2 (SS). *Zonation*: MI. *Affinity*: CR (CP) and TEPR (MP, PP and IGP).

Oxyjulis californica (Günther, 1861). Señorita

Distribution: Salt Point, California to Bahia Magdalena, Baja California Sur. *Records*: La Esmeralda (1998 [1]). *Density*: 0.1 ind/m^2 (CS). *Zonation*: LI. *Affinity*: EPBR (OP) and CR (SDP).

Thalassoma lucasanum (Gill, 1862). Cortez rainbow wrasse

Distribution: Islas San Benito and Isla Cedros, and Rocas Chester (27°53'N, 115°04'W), Baja California Sur to Ecuador, including Gulf of California and Islas Galapagos. *Records*: Los Cerritos (1968 [1]). *Density*: 0.2 ind/m^2 (SS). *Zonation*: LI. *Affinity*: CR (SDP and CP) and TEPR (MP, PP and IGP).

Family Pholidae

Apodichthys fucorum (Jordan and Gilbert, 1880). Rockweed gunnel

Distribution: Banks Island, British Columbia to Punta Escarpada, Baja California. *Records*: Punta Santo Tomas (1831 [1]) and Punta Baja (2146 [1]). *Density*: 0.2 ind/m^2 (NS). *Zonation*: MI. *Affinity*: EPBR (AP and OP) and CR (SDP).

Family Labrisomidae

Labrisomus multiporosus (Hubbs, 1953). Porehead blenny

Distribution: Laguna Guerrero Negro, Baja California Sur and Gulf of California to Islas Chincha, Peru, including Islas Galapagos. *Records*: Punta Morro (1868 [8]), Los Ojitos (1850 [3]), La Esmeralda (1690 [14]), Bahia Tortugas (2191 [8]), Punta Abreojos (1942 [14]), San Juanico (2156 [39]), and Los Cerritos (2161 [3]). *Density*: 0.2 ind/m^2 (NS), 1.0 ind/m^2 (CS) and 3.4 ind/m2 (SS). *Zonation*: MI and LI. *Affinity*: CR (SDP and CP) and TEPR (MP, PP and IGP).

Malacoctenus hubbsi (Springer, 1959). Redside blenny

Distribution: Bahia Sebastian Vizcaino, Baja California and upper Gulf of California to Acapulco, Mexico. *Records*: Los Cerritos (1958 [16]). *Density*: 0.5 ind/m^2 (SS). *Zonation*: MI and LI. *Affinity*: CR (SDP and CP) and TEPR (MP).

Paraclinus integripinnis (Smith, 1880). Reef finspot

Distribution: Santa Cruz Island and Naples (Santa Barbara County), southern California to Bahia Almejas, Baja California Sur. *Records*: Punta Morro (1858 [45]) and Punta Abreojos (1941 [6]). *Density*: 1.1 ind/m^2 (NS) and 0.6 ind/m^2 (CS). *Zonation*: MI and LI. *Affinity*: CR (SDP).

Family Clinidae

Gibbonsia elegans (Cooper, 1864). Spotted kelpfish

Distribution: Piedras Blancas Point, California to Bahia Magdalena, Baja California Sur, including Isla Guadalupe. *Records*: Punta Morro (1865 [13]), Punta Santo Tomas (1827 [18]), Punta Baja (1811 [6]), Krutsio (1752 [2]), Los Ojitos (1910 [4]), La Esmeralda (1997 [7]) and Bahia Tortugas (1980 [4]). *Density*: 0.5 ind/m^2 (NS) and 0.1 ind/m^2 (CS). *Zonation*: MI and LI. *Affinity*: EPBR (OP) and CR (SDP).

Gibbonsia montereyensis (Hubbs, 1927). Crevice kelpfish

Distribution: Vancouver Island, British Columbia to Punta Rompiente, Baja California Sur, including Isla Guadalupe. *Records*: Punta Morro (1916 [1]) and Los Ojitos (1912 [1]). *Density*: 0.5 ind/m^2 (NS) and 0.2 ind/m^2 (CS). *Zonation*: MI and LI. *Affinity*: EPBR (OP) and CR (SDP).

Heterostichus rostratus (Girard, 1854). Giant kelpfish

Distribution: British Columbia to Cabo San Lucas, Baja California Sur, including Isla Guadalupe. *Records*: Punta Morro (2176 [1]) and Bahia Tortugas (1981 [3]). *Density*: 0.3ind/m^2 (NS) and 0.1 ind/m^2 (CS). *Zonation*: MI and II. *Affinity*: EPBR (OP), CR (SDP) and TEPR (MP).

Family Chaenopsidae

Coralliozetus micropes (Beebe and Tee-Van, 1938). Zebraface blenny
Distribution: Bahia Magdalena, Baja California Sur and upper Gulf of California. *Records*: Los Cerritos (1959 [1]). *Density*: 0.2 ind/m^2 (SS). *Zonation*: MI. *Affinity*: CR (SDP and CP).

Family Blenniidae

Entomacrodus chiostictus (Jordan and Gilbert, 1882). Notchfin blenny
Distribution: Bahia San Ignacio, Baja California Sur and Gulf of California to Colombia, including the offshore islands, except Islas Galapagos. *Records*: Los Cerritos (1961 [69]). Density: 4.7 ind/m^2 (SS). *Zonation*: MI and LI. *Affinity*: CR (CP) and TEPR (MP, PP and IGP).

Hypsoblennius gentilis (Girard, 1854). Bay blenny
Distribution: Monterey Bay, California to Gulf of California. *Records*: Los Ojitos (1635 [1]). *Density*: 0.1 ind/m^2 (CS). *Zonation*: MI. *Affinity*: CR (SDP and TPER (MP).

Hypsoblennius gilberti (Jordan, 1882). Rockpool blenny
Distribution: Morro Bay, California to Bahia Magdalena, Baja California Sur. *Records*: Punta Morro (1871 [22]), Punta Baja (1976 [1]), Los Ojitos (1683 [10]), Krutsio (1843 [3]), La Esmeralda (1630 [5]), Bahia Tortugas (1765 [2]) and San Juanico (2192 [9]). *Density*: 0.9 ind/m^2 (NS), 0.2 ind/m^2 (CS) and 2.0 ind/m^2 (SS). *Zonation*: MI and LI. *Affinity*: EPBR (OP), CR (SDP) and TEPR (MP).

Hypsoblennius jenkinsi (Jordan and Evermann, 1896). Mussel blenny
Distribution: Morro Bay, California to Puerto Marques, Mexico, including Gulf of California. *Records*: Punta Morro (1741 [1]), La Esmeralda (1800 [5]), Punta Abreojos (1939 [7]), and Bahia Tortugas (1936 [2]). *Density*: 0.6 ind/m^2 (NS and CS). *Zonation*: MI. *Affinity*: EPBR (OP), CR (SDP and CP) and TEPR (MP).

Ophioblennius steindachneri (Jordan and Evermann, 1898). Panamic fanged blenny
Distribution: Isla Guadalupe [Reyes-Bonilla et al. 2010] and Arrecife Sacramento in Baja California, and upper Gulf of California to Islas Lobos de Afuera, Peru, including Islas Galapagos. *Records*: Punta Abreojos (1940 [1]), San Juanico (2151 [1]) and Los Cerritos (1837 [28]). *Density*: 0.1 ind/m^2 (CS) and 0.9 ind/m^2 (SS). *Zonation*: MI and LI. *Affinity*: CR (SDP and CP) and TEPR (MP, PP and IGP).

Family Gobiesocidae

Gobiesox papillifer (Gilbert, 1890). Bearded clingfish
Distribution: San Pedro, southern California to Bahia de Panama, including Gulf of California. *Records*: Punta Conejo (1824 [2]). *Density*: 2 ind/m^2 (SS). *Zonation*: MI. *Affinity*: EPBR (OP), CR (SDP and CP) and TEPR (MP and PP).

Gobiesox rhessodon (Smith, 1881). California clingfish
Distribution: Pismo Beach, California to Bahia Magdalena, Baja California Sur. *Records*: Punta Morro (11867 [31]). *Density*: 1.1 ind/m^2 (NS). *Zonation*: MI. *Affinity*: EPBR (OP) and CR (SDP).

Rimicola eigenmanni (Gilbert, 1890). Slender clingfish
Distribution: Palos Verdes, southern California to Bahia San Juanico, Baja California Sur. *Records*: Punta Morro (1908 [1]). *Density*: 0.8 ind/m^2 (NS). *Zonation*: MI. *Affinity*: EPBR (OP) and CR (SDP).

*Tomicodon boehlkei (*Briggs, 1955). Cortez clingfish
Distribution: Cabo San Lucas, Baja California Sur to upper Gulf of California. *Records*: Los Cerritos (1978 [37]). *Density*: 2.1 ind/m^2 (SS). *Zonation*: MI. *Affinity*: CR (CP) and TEPR (MP).

Tomicodon zebra (Jordan and Gilbert, 1882). Zebra clingfish
Distribution: Bahia Magdalena, Baja California Sur to Oaxaca, Mexico, including Gulf of California. *Records*: Los Cerritos (1969 [28]). *Density*: 0.8 ind/m^2 (SS). *Zonation*: MI. *Affinity*: CR (SDP and CP) and TEPR (MP).

Family Gobiidae

Bathygobius ramosus (Ginsburg, 1947). Panamic frillfin
Distribution: Bahia Magdalena, Baja California Sur and upper Gulf of California to Paita, Peru. *Records*: San Juanico (2150 [10]), Punta Conejo (1758 [18]) and Los Cerritos (1768 [32]). *Density*: 1.7 ind/m^2 (SS). *Zonation*: MI and LI. *Affinity*: CR (SDP and CP) and TERP (MP and PP).

Richness, Density and Similarity of Species

Of the 48 fish species registered in the study, the largest numbers were captured at Punta Morro (Baja California) and Los Cerritos (Baja California Sur) with 16 and 17 species, respectively. The lowest number of species (3) occurred at Bajamar (open coast). At the subarea level (combined sites), the number of species was 23 in the north, 17 in the center, and 25 in the south (tab. 1). The most speciose families were Blenniidae (5), Pomacentridae (5), Gobiesocidae (5), Cottidae (4) and Embiotocidae (4). These families have also been reported as the most dominant both in species rich-

TABLE 1

Fish density (individuals/m^2 of sampled tidepool) in rocky intertidal sites of the western coast of the Baja California peninsula, Mexico. M = mean, SD = standard deviation. Abbreviations of sites as in figure 1.

Sub-area			**NS**						**CS**				**SS**	
Sites	**MC**	**BM**	**PM**	**ST**	**ER**	**PB**	**OJ**	**KR**	**ES**	**BT**	**PA**	**SJ**	**PC**	**CE**
Number of sampling events	**1**	**4**	**14**	**2**	**3**	**4**	**5**	**2**	**6**	**2**	**2**	**1**	**1**	**3**
Taxa	M	M±SD	M±SD	M	M±SD	M±SD	M±SD	M	M±SD	M	M	M	M	M±SD
G. mordax										0.1				
M. lentiginosa														0.2 ±0.5
C. proboscideus														0.1 ±0.2
M. curema														0.2 ±0.4
A. affinis			0.2±0.5							0.4				
L. tenuis			0.1±0.5						0.1 ±0.3	1				
S. suborbitalis												0.3		0.4 ±0.2
S. guttata												0.3		
C. analis	17.9	4.8±3.2	5.5±2.5	11	1.4 ±1.3	1.9 ±0.5	5.1 ±2.6	5.7	2.2 ±1.8	14.6	0.1			
C. recalvus		0.7±0.6		0.3		0.2 ±0.4								
O. rubellio						0.1 ±0.2								
O. snyderi	4.1			0.7	0.1 ±0.1	0.8 ±0.1								
E. labriformis												0.3		
P. zonipectus												0.3		
G. nigricans	12.3		2.3±2.2	0.4	0.1 ±0.2	2.3 ±2.1	0.9 ±0.6	1.5	1.4 ±1.2	0.8	0.9		2.3	
H. azurea			0.2±0.3			0.1 ±0.2	0.5 ±0.6		0.3 ±0.5	0.6	0.8			
C. rivulatus														0.2 ±0.1
A. koelzi			0.6±0.2				0.1 ±0.2							
H. anale						0.1 ±0.1	0.1 ±0.4							
H. argenteum			0.6±0.2											
M. aurora						0.1±2.5								
A. declivifrons														4.6 ±7.3
A. troschelii												0.3	1.0	
H. rubicundus						0.1								
M. bairdii														0.2 ±0.4
S. flavilatus												0.3		0.5 ±0.4
H. notospilus												0.3		
O. californica									0.1					
T. lucasanum														0.2 ±0.4
A. fucorum				0.3		0.1								
L. multiporosus			0.8±0.2				0.3 ±0.5		0.5 ±0.5	2.9	0.2	13.2		0.1 ±0.1
M. hubbsi														0.5 ±0.6
P. integripinnis			1.1±1.2								0.6			
G. elegans			0.4±0.4	1.3		1.0-6.0	0.8 ±0.7	0.8	0.2 ±0.4	2.0				
G. montereyensis			0.5±0.2				0.2 ±0.2							
H. rostratus			0.3							0.1				
C. micropes														0.2 ±0.4
E. chiostictus														4.7 ±3.2
H. gilberti	12.3	0.3±0.6	1.2±0.6		0.8 ±0.7	0.8 ±0.1	0.1 ±0.1	0.1	0.2 ±0.1	2		2.4		
H. gentilis							0.1 ±0.2							
H. jenkinsi			0.6±0.2						0.1 ±0.2	0.8	0.7			
O. steindachneri											0.1	0.3		1.9 ±0.8
G. papillifer													2.0	
G. rhessodon			1.1±1.1											
R. eigenmanni			0.8±0.3											
T. boehlkei														2.1 ±1.1
T. zebra														0.8 ±1.1
B. ramosus												3.4	4.0	1.3 ±0.7

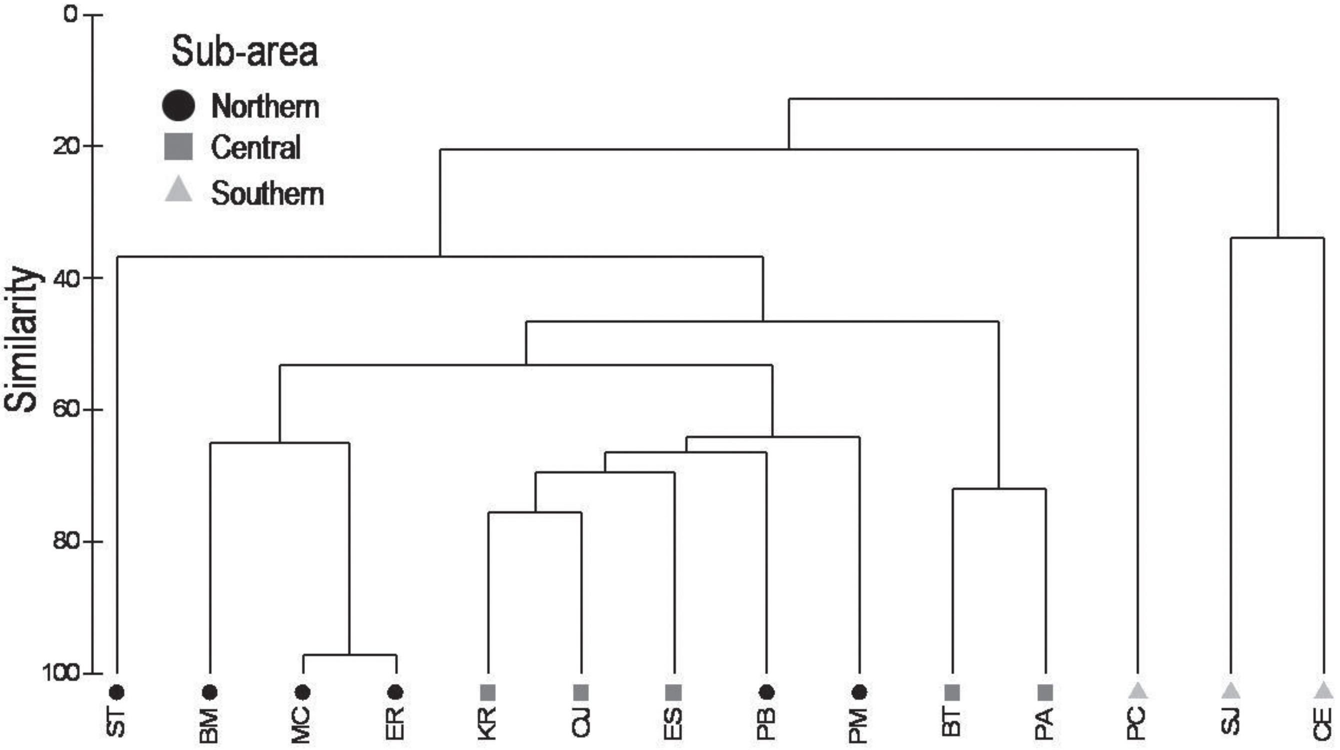

Figure 2. Cluster analysis of 14 rocky intertidal sites of the western coast of the Baja California peninsula, based on the composition of permanent fish species using Bray-Curtis index. Abbreviations of sites as in figure 1.

ness and abundance in tide pools from the northeastern Pacific (Yoshiyama 1981; Grossman 1986; Matson et al. 1986; Yoshiyama et al. 1986; Stepien et al. 1991; Polivka and Chotkoswski 1998; Chotkoswski et al. 1999; Allen and Pondella 2006).

Species with the highest densities in the northern sub-area (combined sites; tab. 1) were *Clinocottus analis*, *Girella nigricans*, *Paraclinus integripinnis* and *Gobiesox rhessodon*. In the central sub-area, *C. analis* and *G. nigricans* were again the most abundant species, followed by *Labrisomus multiporosus* and juveniles of *Leuresthes tenuis*. Finally, in the southern sub-area, *Entomacrodus chiostictus, Abudefduf declivifor*ns and *L. multiporosus* dominated in abundance. Two species exhibited a peculiar distribution pattern within the study area, where the boreal species *Clinocottus analis* was the most abundant fish for the northern and central sub-areas, while the tropical species *Labrisomus multiporosus*, was one of the three most abundant species for the southern sub-area. Both species coexist in tide pools in the central part of the study area (Punta Abreojos to Los Ojitos), where they possibly inhabit different microhabitats. The dominance of *Clinocottus analis* and *Girella nigricans* was also reported by Ruiz-Campos (1986) for intertidal sites in the northern sub-area (Bahia Todos Santos).

The cluster analysis of sampling sites (fig. 2) showed two major groups, the first formed by the two southern sites (Los Cerritos and San Juanico) and the second subdivided into five subgroups at a level of similarity >50%: (1) Santo Tomas, (2) Bajamar-Medio Camino-Erendira, (3) Krutsio-Los Ojitos-Esmeralda-Punta Baja-Punta Morro, (4) Bahia Tortugas-Punta Abreojos, and (5) Punta Conejo. The highest similarity values were registered among sites exposed to open coast (tab. 2): Medio Camino and Eréndira (100%), Punta Abreojos and Bahia Tortugas (80%), Krutsio and Medio Camino (75%), and Krutsio and Erendira (75%). Punta Conejo had low species similarities with other southern sites (San Juanico and Los Cerritos), which might be explained by differences in habitats; the intertidal at Punta Conejo is characterized by the formation of large shallow pools with cobble-pebble bottom and low exposure to sea swell, as well as containing a low number of species (4).

Zoogeographic Relationships and Considerations

Based on the zoogeographic regionalization scheme of Briggs (1974), we determined that the intertidal fish fauna of the western rocky coast of the Baja California Peninsula possesses a higher affinity to the San Diegan province (85%), followed by the Mexican (58%) and Cortez (56%) provinces. Likewise, 46% of the recorded species exhibited an affinity with the Oregonian province. Stepien et al. (1991) remarked on the importance of

TABLE 2
Percent of similarity (Bray-Curtis' index) for rocky intertidal fish species (permanent) among collecting sites in the western coast of the Baja California peninsula, Mexico. Values in bold indicate significant similarity (≥60%).

Collecting sites	MC	BM	PM	ST	ER	PB	OJ	KR	ES	BT	PA	SJ	PC
BM	57.1												
PM	31.6	22.2											
ST	40.0	50.0	12.5										
ER	**100.0**	57.1	31.6	40.0									
PB	**66.7**	54.5	34.8	22.2	**66.7**								
OJ	42.9	30.8	**64.0**	18.2	42.9	55.6							
KR	**75.0**	57.1	42.1	40.0	**75.0**	50.0	57.1						
ES	50.0	36.4	**69.6**	22.2	50.0	50.0	**66.7**	**66.7**					
BT	50.0	28.6	42.1	40.0	50.0	33.3	42.9	50.0	**66.7**				
PA	40.0	22.2	47.6	28.6	40.0	28.6	37.5	40.0	57.1	**80.0**			
SJ	13.3	14.3	15.4	0.0	13.3	10.5	19.0	13.3	21.1	13.3	23.5		
PC	25.0	0.0	10.5	0.0	25.0	16.7	14.3	25.0	16.7	25.0	20.0	26.7	
CE	0.0	0.0	6.3	0.0	0.0	0.0	7.4	0.0	8.0	9.5	17.4	35.7	9.5

Abbreviations: (MC) Medio Camino, (BM) Bajamar, (PM) Punta Morro, (ST) Santo Tomas, (ER) Erendira, (PB) Punta Baja, (OJ) Los Ojitos, (KR) Krutsio, (ES) La Esmeralda, (BT) Bahia Tortugas [El Playon], (PA) Punta Abreojos, (SJ) San Juanico, (PC) Punta Conejo, and (CE) Los Cerritos.

Punta Clara, an area of cold water upwelling ca. 55 km SW of Ensenada, in the Oregonian-Californian coastal marine zoogeographic transition; however this transition should be extended southward to Punta Baja (30°N), where upwelling also frequently occurs.

The zoogeographical affinities of the rocky intertidal fish fauna in the region were predominantly boreal both in the northern (87%) and central (71%) sub-areas, while in the southern sub-area affinities were predominantly tropical and subtropical (92%). Furthermore, it is notable that a high percentage (54%) of species occurs in both coasts of the BCP (amphipeninsular distribution; cf. Castro-Aguirre et al. 2005). These distributions reflect the ample zoogeographic transition zone that exists along the western coast of the BCP (Hubbs 1960; Briggs 1974; Brusca and Wallerstein 1979; Hastings 2000; Pondella et al. 2005; Castro-Aguirre and Espinosa Pérez 2006), with a remarkable change in the intertidal fish composition between Bahia San Juanico (Scorpion Bay) and Bahia Magdalena, where a number of species of northern (warm-temperate) and tropical affinities reach their respective distributional limits.

In relation to species' affinities based on their distribution ranges, a high percentage of the species are endemic to the Tropical Eastern Pacific Region (98%). Of particular interest is the fact that the austral distribution ranges of the following species with boreal affinity do not extend beyond Bahia San Juanico: *Clinocottus analis*, *C. recalvus*, *Oligocottus snyderi, O. rubellio*, *Amphisticus koelzi*, *Micrometrus aurora*, *Hyperprosopon anale*, *H. argenteum*, *Gibbonsia montereyensis*, *Apodichthys fucorum* and *Rimicola eigenmanni*. Also, the northern ranges of the following eleven species of sub-tropical or tropical affinity do not extend beyond Punta San Juanico: *Muraena lentiginosa*, *Chaenomugil proboscideus*, *Sargocentron suborbitalis*, *Cirrhitus rivulatus*, *Abudefduf declivifrons*, *Microspathodon bairdii*, *Halichoeres notospilus*, *Coralliozetus micropes*, *Tomicodon boehlkei*, *T. zebra* and *Bathygobius ramosus*.

The distribution ranges of six species recorded in this study are extended as follows: toward the north for *Labrisomus multiporosus* (500 km, until Bahia Todos Santos, 31°51'N), *Sargocentron suborbitalis* and *Bathygobius ramosus* (450 km and 420 km, respectively, until Punta San Juanico, 26°14'N); and toward the south for *Clinocottus analis* (85 km, until Punta Abreojos, 26°42'N), *Oligocottus rubellio* (65 km, until Punta Baja, 29° 57' N), and *Amphistichus koelzi* (370 km, until Los Ojitos, 28°52'N). The range extensions documented here could represent recent dispersals promoted by El Niño or La Niña oceanographic events (McClatchie et al. 2008; Durazo 2009) or simply reflect the limited sampling on the Pacific coast of the peninsula prior to this study (cf. Chotkowski et al. 1999). Our present records and observations based on voucher specimens might support future taxonomic, ecologic and biogeographic studies in this peninsular coastal region as well as for establishing the significance of the climatic changes on fish distributions.

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LITERATURE CITED

Allen, G. R. and D. R. Robertson. 1998. Peces del Pacífico Oriental Tropical. CONABIO-Agrupación Sierra Madre. México.

Blanchette, C. A., C. M. Miner, P. T. Raimondi, D. Lohse, K. E. K. Heady, and B.R. Broitman. 2008. Biogeographic patterns of rocky intertidal communities along the Pacific coast of North America. J. Biogeog. 35:1593–1607.

Bolin, R. L. 1944. A review of the marine cottid fishes of California. Stanford Ichthyol. Bull. 3: 1–135.

Briggs, J. C. 1955. A monograph of the clingfishes (Order Xenopterygii). Stanford Ichthyol. Bull. 6: 1–224.

Briggs, J. C. 1960. Fishes of worldwide (circumtropical) distribution. Copeia 1960: 171–180.

Briggs, J. C. 1974. Marine Zoogeography. New York: McGraw-Hill. 475 pp.

Brower, J. E., J. H. Zar, and C. N. von Ende. 1997. Field and laboratory methods for general ecology. 4th ed. Boston: WCB McGraw-Hill. 273 pp.

Brusca, R. C., and B. R. Wallerstein. 1979. Zoogeographic patterns of idoteid isopods in the northeast Pacific, with a review of shallow–water zoogeography for the region. Bull. Biol. Soc. Wash. 3:67–105.

Castro-Aguirre, J. L., and H. Espinosa Pérez. 2006. Los peces de la familia Atherinopsidae (Teleostei: Atheriniformes) de las lagunas neutras e hipersalinas de México. Hidrobiológica 16: 89–101.

Castro-Aguirre, J. L., A. F. González-Acosta, and J. De La Cruz-Agüero. 2005. Lista anotada de las especies ícticas anfipacíficas, de afinidad boreal, endémicas y anfipeninsulares del Golfo de California, México. Universidad y Ciencia 21: 85–106.

Chotkowski, M. A., D. G. Buth, and K. Prochazka. 1999. Systematics of intertidal fishes. *In* Intertidal fishes: life in two worlds, M. H. Horn, K. L. M. Marti, and M. A. Chotkowski, eds. San Diego: Academic Press, pp. 297–331.

Durazo, R. 2009. Climate and upper ocean variability off Baja California, Mexico: 1997–2008. Prog. in Oceanogr. 83: 361–368.

Fischer, W., F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem (eds.) 1995. Guía FAO para la identificación de especies para los fines de la pesca, Pacifico Centro-Oriental. 1st ed. Roma: Depto. de Pesca de la FAO, Vol. II, III.

Gibson, R. N. 1969. The biology and behaviour of littoral fish. Oceanogr. Mar. Biol. Ann. Rev. 1969: 367–410.

Gibson, R. N. 1982. Recent studies on the biology of intertidal fishes. Oceanogr. Mar. Biol. Annual Rev. 20: 363–414.

Gibson, R. N. 1999. Methods for studying intertidal fishes. *In* Intertidal fishes: life in two worlds, M. H. Horn, K. L. M. Marti, and M. A. Chotkowski, eds. San Diego: Academic Press, pp. 7–25.

Griffiths, S. P. 2000. The use of clove oil as an anesthetic and method for sampling intertidal rockpool fishes. J. Fish Biol. 57:1453–1464.

Grossman G. D. 1986. Food resource partitioning in a rocky intertidal fish assemblage. J. Zool. Lond. (B) 1:317–355.

Hastings, P. A. 2000. Biogeography of the tropical eastern Pacific: distribution and phylogeny of chaenopsid fishes. Zool. J. Linnean Soc. 128: 319–335.

Horn, M. H., and K. L. M. Martin. 2006. Rocky intertidal zone (Chapter 8). *In* The ecology of marine fishes: California and adjacent waters, L. G. Allen, D. J. Pondella II, and M. H. Horn, eds. Berkeley: University of California Press, pp. 205–226.

Horn, M. H., K. L. M. Martin, and M. A. Chotkowski. 1999. Intertidal fishes: life in two worlds. San Diego: Academic Press. 399 pp.

Horn, M. H., L. G. Allen, and R. N. Lea. 2006. Biogeography (Chapter 1). *In* The ecology of marine fishes: California and adjacent waters, L. G. Allen, D. J. Pondella II, and M. H. Horn, eds. Berkeley: University of California Press, pp. 3–25.

Hubbs, C. L. 1952. A contribution to the classification of the blennioid fishes of the family Clinidae, with a partial of the eastern Pacific forms. Stanford Ichthyol. Bull. 4: 41–165.

Hubbs, C. L. 1960. The marine vertebrates of the outer coast. Symposium: The biogeography of Baja California and adjacent seas. Syst. Zool. 9: 134–147.

Jordan, D. S., and B.W. Evermann. 1896. The Fishes of North and Middle America: A descriptive catalogue of the species of fish-like vertebrates in the waters of North America, north of the Isthmus of Panamá. Smithsonian Institution, Bull. U.S. Nat. Mus. Reprinted 1963, for the Smithsonian Institution by T.F.H. Publications, 47(I–IV): 1–3313.

Love, M. S., C. W. Mecklenburg, T. A. Mecklenburg, and L. K. Thorsteinson. 2005. Resource inventory of marine and estuarine fishes of the West coast and Alaska: A checklist of North Pacific and Arctic ocean species from Baja California to the Alaska–Yukon border. U. S. Department of the Interior, U. S. Geological Survey, Biological Resources Division, Seattle, Washington, 98104, OCS Study MMS 2005-030 and USGS/NBII 2005-001.

McClatchie, S., R. Goericke, J. A. Koslow, F. B. Schwing, S. J. Bograd, R. Charter, W. Watson, N. Lo, K. Hill, J. Gottschalck, M. L'heureux, Y. Xue, W. T. Petterson, R. Emmett, C. Collins, G. Gaxiola-Castro, R. Durazo, M. Kahru, B. G. Mitchell, K. D. Hyrenbach, W. J. Sydeman, R. W. Bradley, P. Warzybok, and E. Bjorkstedt. 2008. The State of the California Current, 2007–2008: La Niña conditions and their effects on the ecosystem. Calif. Coop. Oceanic Fish. Invest. Rep. 49:3 9–76.

Matson, R. H., C. B. Crabtree, and T. R. Haglund. 1986. Ichthyofaunal composition and recolonization in a central California tidepool. Calif. Fish Game 72: 227–231.

Miller, D. J., and R. N. Lea. 1972. Guide to the Coastal Marine Fishes of California., Calif. Fish Bull. 157.

Munday, P. L., and S. K. Wilson. 1997. Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis,* a coral reef fish. J. Fish Biology 51: 931–938.

Nelson, J. S., E. J. Crossman, H. Espinosa-Pérez, L. T. Findley, C.R. Gilbert, R.N. Lea, and J. D. Williams. 2004. Common and scientific names of fishes from the United States, Canada, and Mexico. 6th ed., Bethesda: American Fisheries Society, Special Publication 29. 386 pp.

Pfister, C. A. 1999. Recruitment of intertidal fishes. *In* Intertidal fishes: life in two worlds, M. H. Horn, K. L. M. Marti, and M.A. Chotkowski, eds. San Diego: Academic Press, pp 181–196.

Polivka, K. M., and M. A. Chotkowski. 1998. The effects of repeated tidepool defaunation on recolonization by Northeast Pacific intertidal fishes. Copeia 1998: 456–462.

Pondella, D. J. II, B. E. Gintert, J. R. Cobb, and L. A. Allen. 2005. Biogeography of the nearshore rocky-reef fishes at the southern and Baja California islands. J. Biogeogr. 32: 187–201.

Prochazka, K., M. A. Chotkowski, and D.G. Buth. 1999. Biogeography of rocky intertidal fishes. *In* Intertidal fishes: life in two worlds, M. H. Horn, K.L.M. Marti, and M.A. Chotkowski, eds. San Diego: Academic Press, pp. 332–355.

Ramírez-Valdéz, J. A. 2009. Ecología y biogeografía de las comunidades de peces del intermareal rocoso en la costa occidental de la Península de Baja California, México. Master of Sciences thesis, Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Ensenada, B.C., México. 203 pp.

Reyes-Bonilla, H., Y. R. Bedolla-Guzmán, L.E. Calderón-Aguilera, A. Ayala-Bocos, A. Ramírez-Valdéz, S. González-Romero, N. C. Olivares-Bañuelos, I. Sánchez-Alcántara, and M. Walther-Mendoza. 2010. Checklist and biogeography of fishes from Guadalupe island, western Mexico. Calif. Coop. Oceanic Fish. Invest. Rep. (in press).

Robertson, D. R., and G. R. Allen. 2002. Shorefishes of the tropical eastern Pacific: an information system. CDROM. Balboa, Panama: Smithsonian Tropical Research Institute.

Ruiz-Campos, G. 1986. Estructura, composición y dinámica de la comunidad íctica de las pozas de marea durante otoño-invierno en la playa rocosa de Granada Cove, Bahía Todos Santos, B.C., México. Master of Sciences thesis, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, B.C., Mexico. 112 pp.

Ruiz-Campos, G., and M. G. Hammann. 1987. Lista sistemática de los peces del intermareal rocoso de la Bahía de Todos Santos, Baja California, México. Cienc. Mar. 13: 61–69.

Ruiz-Campos, G., and M. G. Hammann. 2002. Hábitos y relaciones tróficas de un elenco íctico en el intermareal rocoso de la Bahía de Todos Santos, Baja California, México: otoño-invierno. *In* libro jubilar en honor al Dr. Salvador Contreras Balderas, M. L. Lozano-Vilano, ed. Monterrey, México: Universidad Autónoma de Nuevo León, pp. 87–101.

Ruiz-Campos, G., J. A. Ramírez-Valdéz, S. González-Guzmán, A. F. González-Acosta, and D. Acosta-Zamorano. 2010. Length–weight and length–length relationships for nine rocky tidal pool fishes along the Pacific coast of the Baja California Peninsula, Mexico. J. Appl. Ichthyol. 26:118–119.

Springer, V. G. 1962. A review of the blenniid fishes of the genus *Ophioblennius* Gill. Copeia 1962: 426–433.

Stephenson, T. A, and A. Stephenson. 1972. Life between tide marks on rocky shores. 1st ed. San Francisco: W.H. Freeman and Co. 425 pp.

Stepien, C. A., H. Phillips, J. A. Adler, and P. J. Mangold. 1991. Biogeographic relationships of rocky intertidal fish assemblage in an area of cold water upwelling off Baja California, Mexico. Pacific Sci. 45: 63–71.

Thomson, D. A., L. T. Findley, and A. N. Kerstitch. 2000. Reef fishes of the Sea of Cortez, the rocky-shore fishes of the Gulf of California. Austin: The University of Texas Press. 353 pp.

Yoshiyama, R. M. 1981. Distribution and abundance patterns of rocky intertidal fishes in Central California. Environ. Biol. Fish. 6: 315–332.

Yoshiyama, R. M., C. Sassaman, and R. N. Lea. 1986. Rocky intertidal fish communities of California: temporal and spatial variation. Environ. Biol. Fish. 17: 23–40.

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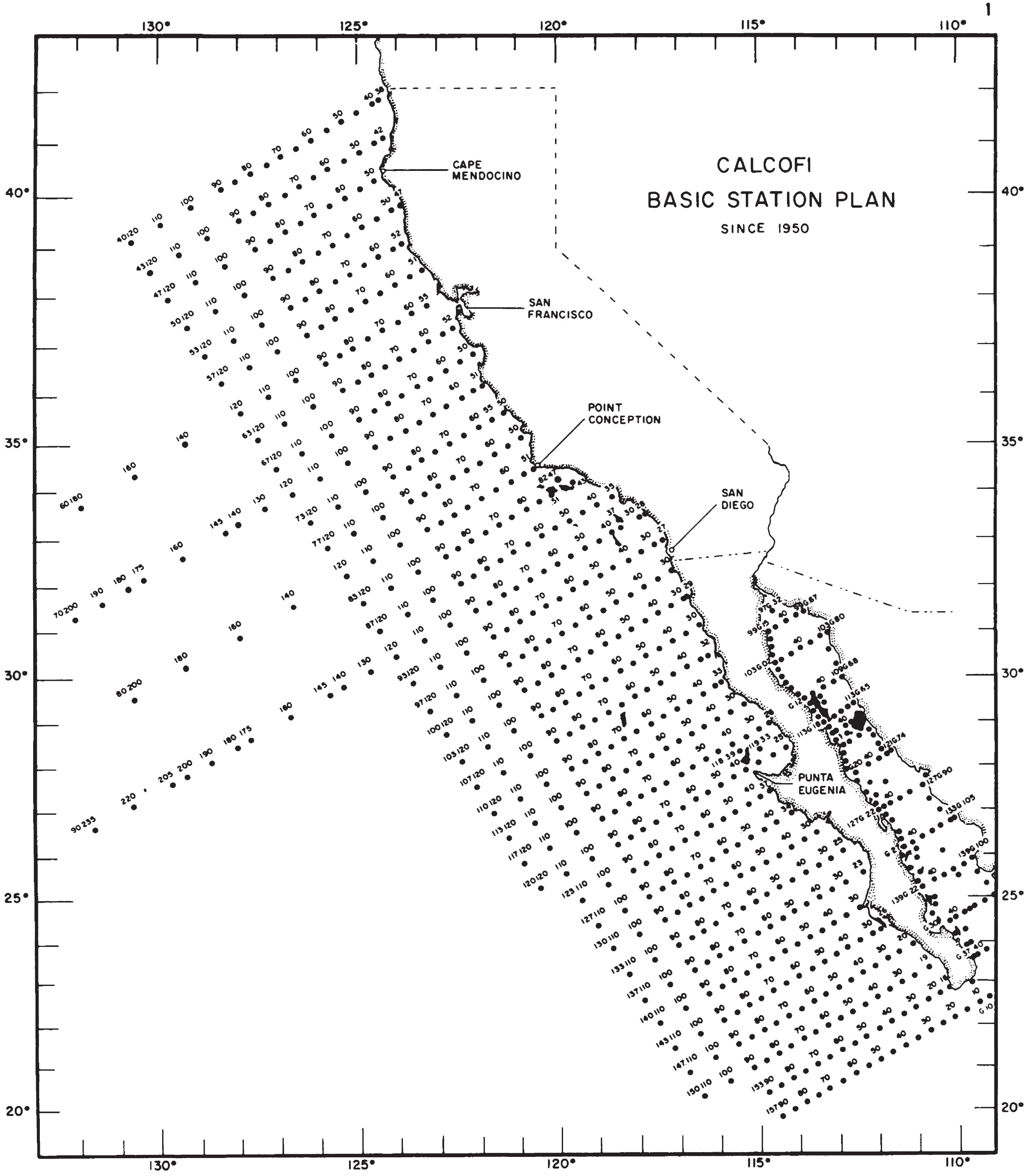

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