# CALIFORNIA
# COOPERATIVE
# OCEANIC
# FISHERIES
# INVESTIGATIONS

## *Reports*

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## Part I

# REPORTS, REVIEW, AND PUBLICATIONS

## REPORT OF THE CALCOFI COMMITTEE

## NOAA HIGHLIGHTS

### CalCOFI Cruises

The CalCOFI program completed its fifty-seventh year with four successful quarterly cruises. All four cruises were manned by personnel from NOAA Fisheries Service Southwest Fisheries Science Center (SWFSC), Scripps Institution of Oceanography (SIO), and the California Department of Fish and Game (CDFG). The fall 2006 cruise was conducted on the Scripps vessel R/V *Roger Revelle* and covered the southern lines of the CalCOFI pattern. The winter 2006 cruise was conducted on the NOAA R/V *David Starr Jordan*. The *Jordan* covered line 93 to line 60 just north of San Francisco. The spring and summer 2006 cruises were on the Scripps vessel R/V *New Horizon*, and covered the standard CalCOFI pattern. The spring CalCOFI cruise was conducted in conjunction with the first coast-wide survey (see below). The R/V *David Starr Jordan* was used to perform the northern extension of the CalCOFI pattern, while the R/V *Oscar Dyson* surveyed from Vancouver, Canada, to San Francisco.

Standard CalCOFI protocols were followed during the four quarterly cruises. Over the year a total of 374 bongo tows, 298 manta tows, 316 pairovet tows, 424 CTD casts, and 40 trawls were conducted. In addition to the usual CTD casts and net tows, measurements were collected on a variety of other parameters including but not limited to primary productivity, salinity, dissolved oxygen, acoustics, and weather. Both seabird and marine mammal observers also collected data on each cruise.

### Coast-wide Sardine Survey

The first coast-wide survey of the California Current pelagic ecosystem was conducted from 1 April–8 May 2006, spanning from Baja California, Mexico, to British Columbia, Canada. The survey was carried out with three U.S. vessels. The R/V *David Starr Jordan* traveled from San Diego, California, north to San Francisco, California. The R/V *Oscar Dyson* departed Seattle, Washington, and surveyed from Vancouver Island, Canada, south to San Francisco, California. In addition, the SIO vessel R/V *New Horizon* conducted the regular spring CalCOFI survey concurrently.

Scientists aboard the R/V *David Starr Jordan* and the R/V *Oscar Dyson* conducted plankton net samples of eggs, larvae, and zooplankton, and vertical profiles of temperature, salinity, oxygen, and chlorophyll. Transect observations included continuous egg pump samples, continuous multi-frequency acoustic samples of adults and possibly juvenile fish, and continuous measurements of sea surface and meteorological conditions. Trained observers on both ships surveyed for marine mammals and sea birds during daylight hours.

The data collected on Pacific sardine (*Sardinops sagax*) were used to generate an estimate of the spawning stock biomass, which resulted in an updated stock assessment. The total DEPM-based spawning biomass during April–May 2006 was estimated to be 1,304,806 mt (CV = 0.47) within an 885,523 km$^2$ spawning area from San Diego to British Columbia. Sardine eggs and adults were not found north of Coos Bay, Oregon. The standard DEPM sampling region off California (San Diego to San Francisco) had a spawning area of 336,774 km$^2$ and a spawning biomass of 1,081,612 mt (CV = 0.47). Thus, the portion of spawning biomass from San Francisco to British Columbia was approximately 223,194 mt (Hill et al., 2006).

This survey is unique in that it is the first to provide a snapshot of the physical and biological environment of the California Current ecosystem spanning the bulk of its range. The next coast-wide survey is scheduled for April 2008 with the R/V *David Starr Jordan* and the R/V *Miller Freeman*.

### CalCOFI Ichthyoplankton Update

To make the CalCOFI ichthyoplankton data base more user-friendly, the Ichthyoplankton Ecology group at SWFSC has undertaken a project to update all larval fish identifications to current standards. The fish larvae have always been identified to the lowest taxon permitted by current knowledge. However, when taxonomic resolution has improved, it usually has not been possible to revisit and update earlier samples, with the result that many taxa must be aggregated back to genus, family, or ordinal level in order to perform analyses using the entire CalCOFI ichthyoplankton data set. This reidentification effort is a multi-year project that ultimately will provide taxonomic consistency throughout the CalCOFI ichthyoplankton time series. To date, all fish larvae from all CalCOFI samples collected between January 1972 (cruise 7201) and July 2007 (cruise 0707) have been identified to current standards. Larvae collected during the 1969 CalCOFI cruises are now being re-identified.

Larval fish overall were only about half as abundant during the 2006 CalCOFI survey as they had been in the 2005 survey. In 2005, the abundance of northern anchovy (*Engraulis mordax*) larvae increased substantially and it replaced Pacific sardine as the most abundant species collected. It was the most abundant species again in 2006, although less than one-quarter of its overall abundance in 2005. Larval Pacific sardine were about half as abundant in 2006 compared with 2005, but remained the second most abundant species collected. Ichthyoplankton data suggested the possibility that the region of peak Pacific sardine spawning began to shift southward from central California in 2005, and this was even more apparent in 2006. Preliminary results of the spring 2007 cruise suggest that again this year Pacific sardine spawning was highest off southern California.

### PaCOOS

The Pacific Coast Ocean Observing System Board of Governors continues to focus on the data management of NOAA West Coast biological and physical data as well as expanding to include euphausiid data collected by academics along the California coast. With funds from the NOAA IOOS Program, three websites have been created to house NOAA-generated data. The data are either available now or will soon be available in 2007. All will be accessible through the PaCOOS website (www.pacoos.org) as well as through the following home servers:

1. Habitat data: http://tomcat.coas.oregonstate.edu/
2. Pelagic data: http://oceanwatch.pfeg.noaa.gov/PaCOOS/
3. National Marine Sanctuary physical data: http://portal.ncddc.noaa.gov/wco/

More historical data will be added to these portals as they go through proper QA/QC and metadata procedures. The euphausiid data will be available at a later date through the Scripps Institution of Oceanography.

Ecological forecast development remains a top priority for PaCOOS and there were some new, modest developments in this area as well. The *Atlantis* and *Ecosim* models remain the primary focus for NOAA scientists to eventually augment existing fish and marine mammal stock assessments. Collaboration and partnerships between NOAA and academic scientists remains the primary means of developing the next generation of ecosystem forecasts with external funding.

The governance structure of PaCOOS continues to evolve. Representatives from Canada's Department of Fisheries and Oceans and from IMECOCAL, CalCOFI's sister survey program along Baja California, Mexico, were invited to join the Board of Governors. The addition of representatives from Canada and Mexico will round out representation along the entire California Current Large Marine Ecosystem.

## CDFG HIGHLIGHTS

The Marine Region of the California Department of Fish and Game (CDFG) in 2006 experienced increased funding primarily from the California legislature. These funds were used to hire 44 full time staff, increasing the staff of the Region by almost 25% and restoring the Region's operating budget. The major focus of these new positions is expanding the resource assessment capabilities of the CDFG. At the same time, the Region underwent a structural reorganization aligning it with the CDFG. The new structure is based on a resource assessment project which is responsible for the CalCOFI program.

The California Ocean Protection Council continues to partner with the Marine Region and others since its inception following the passage of the California Ocean Protection Act. The Council hosted the California and the World's Ocean Conference in Long Beach, California, in September 2006. In 2006 and early 2007, the Council adopted resolutions to fund research on cooling of power plants using seawater and its impact on the pelagic organisms contained in the water, as well as addressing marine debris such as lost fishing gear. The Council is partnering with the CDFG to jointly fund $10 million in resource assessment, data management, and program support. Along with these actions, in September 2006 the three West Coast governors signed an historic agreement on Ocean Health including the "expansion of ocean and coastal scientific information, research, and monitoring."

The Marine Region hosted the 2006 CalCOFI conference this year as it does every third year. The conference was held at Asilomar in Pacific Grove, California, in December 2006. The theme of the symposium of the conference was "Ecological Interactions Useful For Marine Ecosystem-Based Management: The Roles of Positive Species Interactions, Ecosystem Engineers and Species Diversity." In the symposium, themes such as biodiversity and the role of ecosystem engineers in structuring and providing goods and services within marine communities were explored as they relate to fisheries productivity.

### California State Legislature and White Sturgeon

In response to preliminary information suggesting a decline in the white sturgeon population in the San

Francisco Bay-Delta, the California Fish and Game Commission established several new sportfishing regulations for this species in 2006. In addition to fishing pressure, white sturgeon are known to be at risk from habitat loss and degradation, and are also subject to poaching and illegal commercialization. The allowable slot size was reduced from 46 to 72 inches to a smaller slot size of 46 to 66 inches, and an annual limit of three fish per angler per year was instituted. Additionally, a report card program was established which requires that every angler targeting or possessing white sturgeon record catch and other fishery information. In an effort to improve enforcement of the new annual bag limit, the report card comes affixed with three tags which are to be attached to any legally taken and retained white sturgeon.

### Marine Protected Areas

On 13 April 2007, in a landmark decision, the California Fish and Game Commission adopted regulations to create a new suite of marine protected areas (MPAs) designed for the Central Coast of California, the second region considered for the State. This move effectively launches the state's Marine Life Protection Act (MLPA) Program, which is designed to conserve marine resources for their long-term sustainability while enhancing outdoor recreation and ocean research opportunities along the coast.

The Fish and Game Commission voted unanimously in favor of its preferred alternative: 29 MPAs representing approximately 204 square miles (or approximately 18 percent) of state waters with 85 square miles designated as no-take state marine reserves along the Central Coast, which ranges from Pigeon Point in San Mateo County south to Point Conception in Santa Barbara County.

The newly established Central Coast MPAs represent the culmination of a two-year public process with nearly 60 public meetings held for stakeholders and scientists, as well as the oversight of the MLPA Blue Ribbon Task Force, convened by Secretary for Resources Mike Chrisman.

The California Department of Fish and Game, the lead agency charged with managing the state's marine resources, will be responsible for implementing the MLPA program, including all enforcement and research and monitoring activities. The Central Coast MPA regulations will go into effect this summer after the appropriate filings with the Office of Administrative Law and Secretary of State.

### Ocean Salmon Project

In 2006, the ocean salmon fisheries were severely constrained primarily by ocean abundance of Klamath River Fall Chinook salmon from Point Sur, California, to the California-Oregon border. The Salmon Fishery Management Plan requires that ocean fisheries be regulated to allow a minimum of 35,000 natural adult spawners to return to the Klamath Basin; however, even without any fisheries in 2006, the Klamath Ocean Harvest Model predicted that this goal couldn't be attained. As a result, NMFS took emergency action in March to allow ocean fishing and advised the Pacific Fisheries Management Council to regulate the commercial and recreational fisheries so that no less than 21,000 Klamath River Fall Chinook natural adults returned to spawn. Ocean landings were centered on the San Francisco port area (61% of all estimated landings). An estimated 158,300 Chinook were landed in all ocean fisheries during 2006.

### Fishery-Independent ROV Assessment Project

For the fourth consecutive year, the California Department of Fish and Game and the Marine Applied Research and Exploration (MARE) program, in partnership with the the Channel Islands National Marine Sanctuary, The Nature Conservancy, and Kingfisher Foundation, used a remotely operated vehicle (ROV) to survey fish populations in the Channel Islands National Marine Sanctuary. The objective of our ongoing research is to monitor changes in finfish density within areas of predominantly rocky habitat that are beyond the depth limit of scuba-based sampling. Our work will provide data for the evaluation of the Channel Islands Marine Protected Areas Monitoring Plan and will make available archival video for future research and monitoring.

During the 2006 survey, we measured substrate and finfish abundance within 10 priority sampling sites in the northern Channel Islands. Five of the sites are located within Marine Protected Areas (MPAs) near San Miguel, Santa Rosa, Santa Cruz, and the Anacapa Islands, and the other five reference sites are outside and adjacent to our MPA sites. In general, our permanent sampling sites are rectangles 500 meters wide spanning a depth range from 20 to 70 meters. Each year we plan to survey randomly selected 500 meter track lines to create finfish density transects over predominantly rocky habitat at each of the 10 sites.

In August and September of 2006 we worked aboard the CDFG's patrol vessel *Swordfish* to quantitatively sample seven sites, completing 65% of the total planned survey. In September and October of 2006, our work continued aboard the Sanctuary's R/V *Shearwater*, completing the season's remaining quantitative survey and two additional experiments aimed at developing a method for calculating habitat relief and sizing fish from video.

In addition, we continue to locate lost fishing gear that the CDFG, the Sanctuary, and marine debris removal groups have been working to remove. One such piece of gear located last year was a large 4,000 pound purse seine net which was later removed off the eastern end of Santa Rosa Island from a depth of 23 to 30 meters.

For more information on ROV sampling protocols and research cruises, see (www.dfg.ca.gov/mrd) and the MARE web site (www.maregroup.org).

### Kelp Surveys

During 2006 the CDFG completed the fifth annual coast-wide survey of California's kelp beds. The results of ongoing aerial assessments are available to GIS users on the Department's web at: http://ftp.dfg.ca.gov/Public/R7_MR/Natural_Resources/Kelp/

### 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. The development and implementation of CRFS has been a collaborative effort of the California Department of Fish and Game and the Pacific States Marine Fisheries Commission (PSMFC) with funding from state and federal sources.

The CRFS produced monthly estimates for 2006 and field samplers conducted more than 100,000 angler interviews and examined over 200,000 fish. The CRFS data were used to manage California's marine fisheries. Because catch and effort are reported by six geographical districts, managers were able to track catches in each district and to provide increased fishing opportunities in some areas while protecting overfished stocks.

In 2006, the CDFG began conducting studies to validate the catch and effort estimates and to verify the assumptions made in designing the sampling program. In addition, the CDFG began a review of the CRFS in 2006 to ensure that CRFS data and estimates address management needs and conform to the best available science. The review is examining each part of the CRFS program: sample design, survey methods, statistical methods, estimation procedures, computer programs, data and documentation needs, and outreach. For more information, go the CDFG's Marine Region website: http://www.dfg.ca.gov/mrd/crfs.html

### Aquaculture and Bay Management

The Aquaculture and Bay Management Project completed the California Pacific Herring Commercial Fishing Regulations Supplemental Environmental Document (SED) for the 2006–07 season. The SED included the herring spawning biomass estimates for San Francisco, Tomales, and Humboldt Bays for the 2005–06 season, spawning population and commercial catch assessment, and the results of sub-aquatic vegetation surveys in key herring spawning areas for Humboldt and San Francisco Bays. The spawning biomass estimate for San Francisco Bay of 145,054 tons (including catch) for the 2005–06 season is the largest recorded estimate in the history of the roe herring fishery.

### Invertebrate Fisheries

In 2006, the Marine Region reprioritized the invertebrate species groups within the Marine Life Management Act Master Plan. Spiny lobster (*Panuliris interruptus*), subtidal snails including *Kelletia* and *Megastrea*, and marine bivalves including gaper, pismo, and razor clams, were listed as top priorities for future research and assessment efforts. In conjunction with this, the Invertebrate Program has initiated the hiring of a plankton sorter to work within the CalCOFI program to sort for lobster larvae (phyllosoma and puerulus stages).

The Dungeness crab (*Cancer magister*) industry, with assistance from the Invertebrate Management Project, began exploring the possibility of a trap limit program, following the lead of Oregon and Washington. A number of meetings were held up and down the coast in an effort to create a series of alternative plans. However, northern and central California crabbers have competing interests with regard to a trap limit program and those differences have yet to be reconciled. Also, during 2006, legislation was passed and signed into law that extends the authority of a California Dungeness crab permit out to 200 miles (into the EEZ) off California.

### Abalone

In 2006, the implementation of the Abalone Recovery and Management Plan (ARMP) began after its adoption by the Fish and Game Commission in late 2005. The Commission adopted the ARMP, opting to select an alternative to begin development of a potential limited fishery for red abalone at San Miguel Island. The Department embarked on the limited fishery consideration process by collaborating with interested constituents. The collaborative process included a joint "Snap-shot Survey" of the red abalone resource at the island. A total of 187 survey stations with 371 transects were completed during the five-day cruise. In addition, an abalone advisory group (AAG) and a Technical Panel were formed. The AAG is a constituent representative body charged with providing recommendations to the Department and the Commission on the potential fishery.

## SIO HIGHLIGHTS

Dr. Tony Koslow joined the CalCOFI Committee this year, after taking up a position in January 2007 as Research Professor and Director of CalCOFI at SIO. Tony's links with CalCOFI and the California Current extend back to the late 1970s, when he was a graduate student at SIO, working on the feeding of northern anchovy schools and its influence on the zooplankton. His principal mentors were Mike Mullin, John Isaacs, Paul Smith, John Hunter, and Joe Reid. After graduating, Tony Koslow served as fishery oceanographer in the Oceanography Department at Dalhousie University in Halifax, where his research focused on large-scale climatic influences on recruitment to cod and haddock stocks in the northwest Atlantic. In 1989, Tony joined Australia's Commonwealth Scientific and Industrial Research Organization (CSIRO) Division of Marine and Atmospheric Research, where he led projects on deepwater fisheries, seamount ecology and conservation, and the biological oceanography off Western Australia.

Elizabeth Venrick stepped down from the CalCOFI Committee, after passing the baton to Tony Koslow. She has represented SIO on the Committee since 2001, when she stepped into the breach left by Mike Mullin's tragic and unforeseen death. She guided SIO's CalCOFI program through the exceptionally difficult period of California's budget crisis, when State support for CalCOFI was slashed. Remarkably, the program was maintained without loss of a single cruise.

### SCCOOS

Funding from the Southern California Coastal Observing System (SCCOOS) continued to fund work at nine nearshore stations that are occupied on CalCOFI cruises. The larval fish community at these stations, which are located along the 20 m isobath, is distinct from that observed at the standard coastal CalCOFI stations somewhat further offshore. In the future, samples at these stations may prove useful in providing baseline data on these communities prior to the establishment of nearshore marine protected areas (MPAs), as well as in monitoring their future impact.

For the first time in more than 25 years, spiny lobster phyllosoma will be routinely removed from CalCOFI samples, and historical CalCOFI samples will be sorted for them at selected stations. There are indications that spiny lobster recruitment to southern California fishing grounds is strongly influenced by ENSO, but this has never been documented. There are also no fishery-independent data on historical trends in the abundance of spiny lobster off California.

The spiny lobster population spawns from around Point Conception to southern Baja California from July through October. The phyllosoma larvae remain within the plankton for approximately eight months, the late stages being found primarily between April and June. The phyllosoma then metamorphose into the puerulus stage, which swims inshore, settles out of the plankton, and develops into a juvenile lobster. Our knowledge of the development and early life history of the spiny lobster is based largely on studies carried out by Martin Johnson, during the first seven years of the CalCOFI program (1949–55).

The abundance of early stage phyllosoma will be used to develop an index of the abundance of spiny lobster in their nearshore spawning habitat, and the abundance of late stage phyllosoma will be examined for their utility as an index of recruitment. These time series can be used to assess changes to the spiny lobster population off southern California since the early 1950s, as well as to examine the influence of climate variability and the fishery on recruitment. Collaboration with colleagues in Baja California is foreseen, in an effort to understand the dynamics of this species over the extent of its range. Progress on this project has been accelerated by the discovery in the Scripps Library Archives of unpublished phyllosoma data from Martin Johnson, based on CalCOFI cruises between 1974 and 1981.

### CCE-LTER Program

The California Current Ecosystem Long Term Ecological Research (CCE-LTER) program has augmented sampling on CalCOFI cruises since the fall of 2004. The objective of this work is to characterize in greater detail lower trophic level communities and processes, along with the dynamics of the carbon system. In the spring of 2007 the CCE-LTER program conducted its second process cruise off Point Conception, following the pattern of the previous year's cruise. It was initially hoped that the cruise would sample the California Current (CC) during an El Niño, but the weak equatorial El Niño did not materialize in the CC. However, the primary objective, to study processes in the CC, was met successfully.

All CalCOFI Atlases up to Atlas 35 (2002), except Atlas 33, are now available as pdf files that can be downloaded from the CalCOFI website. See: http://www.calcofi.org/newhome/publications/Atlases/atlases.htm

## REFERENCES

Hill, K. T., N. C. H. Lo, B. J. Macewicz, and R. Felix-Uraga. 2006. Assessment of the Pacific sardine (*Sardinops sagax caerulea*) population for U.S. management in 2007. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-396. 102 pp.

# REVIEW OF SOME CALIFORNIA FISHERIES FOR 2006: COASTAL PELAGIC FINFISH, MARKET SQUID, DUNGENESS CRAB, SPOT PRAWN, HIGHLY MIGRATORY SPECIES, OCEAN SALMON, CALIFORNIA HALIBUT, NEARSHORE LIVE-FISHES, CABEZON, SURFPERCHES, AND LEOPARD SHARK

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## SUMMARY

In 2006, commercial fisheries landed an estimated 152,088 metric tons (t) of fishes and invertebrates from California ocean waters (fig. 1). This represents an increase of nearly 15% from the 132,600 t landed in 2005, and a 40% decline from the peak landings of 252,568 t in 2000. The preliminary ex-vessel economic value of commercial landings in 2006 was nearly $130 million, an increase of 19% from the $109 million in 2005. This is mainly the result of a delay in the start of the 2005–06 Dungeness crab season until 2006.

Market squid was once again the largest fishery in the state by volume, at over 49,000 metric tons (t), and second in ex-vessel value at $26.9 million. The other top five were: Pacific sardine at nearly 46,600 t, northern anchovy at over 12,800 t, Dungeness crab at 11,900 t, and Pacific whiting at 5,400 t. Dungeness crab was the highest valued fishery in the state at $45 million. The ex-vessel value of market squid dropped to second in 2006 at $26.9 million, a decline of 14% from 2005. Other top five valued fisheries include California spiny lobster at over $8.1 million, Chinook salmon at nearly $5.2 million, and red sea urchin at $5.1 million.

The start of the 2005–06 Dungeness crab season was delayed by the California Department of Fish and Game (CDFG) until the last day of 2005 due to poor crab condition. This delay, however, did not result in decreased landings, as the season was the third largest since records began in 1915, and the largest in economic value.

In 2006, California salmon fisheries were nearly eliminated due to the low ocean abundance of the Klamath River Fall Chinook stock. The National Marine Fisheries Service (NMFS) took emergency action in March to allow ocean fishing and advised the Pacific Fisheries Management Council (PFMC) to regulate the commercial and recreational fisheries so that no less than 21,000 natural adults returned to spawn. Thus salmon fishing seasons in California were significantly constrained in 2006, resulting in an 80% reduction in commercial landings and a 70% reduction in recreational landings compared to 2005.

California's commercial groundfish harvest for 2006 was over 12,000 t, an 8% decrease from 2005 landings. The groundfish harvest consisted mainly of Pacific whiting, Dover sole, sablefish, and rockfishes. The ex-vessel value of groundfish landings for 2006 was $14.7 million, 6% higher than in 2005 ($13.8 million).

For highly migratory species, commercial and recreational landings of albacore decreased by 57% and 79%, respectively, from 2005. Landings of all other tuna species also declined. However, landings of swordfish increased 83% over 2005. In 2006, the PFMC adopted bag limits for both albacore (10, south of Point Conception; 25, north of Point Conception) and Pacific bluefin tuna (10).

In this review, an effort was made to highlight some of the lesser reported fisheries that have been the focus of recent conservation measures or management decisions. For California halibut, new regulations closed portions of the traditional halibut trawl grounds and implemented a restricted access program. Cabezon recently underwent a stock assessment which found that the southern stock was slightly above an overfished condition. In order to ensure that landings do not exceed the total allowable catch of 69.0 t, reductions in monthly allotments were imposed. For surfperches, better sampling, identification, and reporting methods have led to better insights into management of the major species in the surfperch family caught in California. And finally, for leopard sharks, a multi-agency investigation led to the curtailment of an illegal poaching ring that took over 50,000 leopard shark pups for the marine aquarium trade.

In 2006, the California Fish and Game Commission (Commission) undertook 12 rule-making actions that address marine and anadromous species. The Commission adopted changes to salmon, groundfish, sea urchin, lobster, herring, and rock crab regulations and added a non-transferable light boat permit to the market squid restricted access fishery. The Commission also received a large amount of public testimony on the creation of marine protected areas in central California, from Pigeon Point in San Mateo County south to Point Conception in Santa Barbara County, under the Marine Life Protection Act. In addition, the Commission instituted emergency regulations to protect green and white sturgeon.

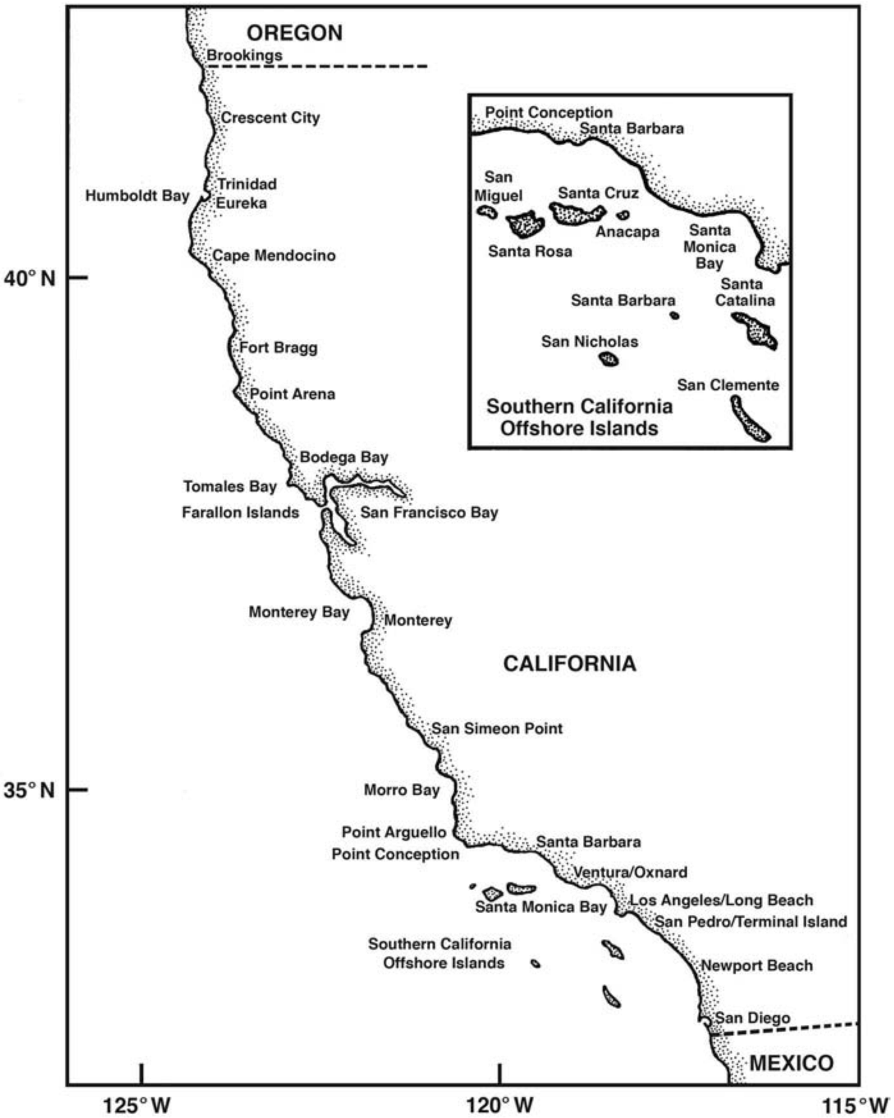

Figure 1. California ports and fishing areas.

## Coastal Pelagic Finfish

Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and northern anchovy (*Engraulis mordax*) form a finfish complex known as coastal pelagic species (CPS). These species are jointly managed by the PFMC and NMFS. In 2006, the combined commercial landings of CPS finfish totaled 66,560 t (tab. 1), and the ex-vessel value exceeded $7.4 million. The Pacific sardine fishery continues to be the most valuable fishery among these four species, contributing 70% of the total tonnage. For the four CPS finfish, Pacific sardine represented 68.8%, northern anchovy 17.5%, Pacific mackerel 11.1%, and jack mackerel 2.7% of the total ex-vessel revenues.

***Pacific Sardine.*** The Pacific sardine fishery extends from British Columbia, Canada, southward into Baja California, México (BCM). Although the bulk of the catch is landed in southern California and Ensenada, BCM, landings in the Pacific Northwest have been increasing. The Pacific sardine harvest guideline (HG) for each calendar year is determined from the previous year's stock biomass estimate (of ≥1-year-old fish on 1 July) in U.S. and Mexican waters. The 1 July 2006 stock biomass estimate for Pacific sardine was 1.1 million metric tons (t). The recommended U.S. HG for the 2006 season was 118,937 t. Given that there are inherent uncertainties in both the fishery and the Pacific sardine population that can affect long-term projections, a formal review of the new allocation structure will occur in 2008.

Following the new allocation scheme for the U.S. West Coast, decided by PFMC for the 2006–07 season, 35% (41,628 t) of the total U.S. HG was allocated coastwide

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

| Year | Pacific sardine | Northern anchovy | Pacific mackerel | Jack mackerel | Pacific herring | Market squid | Total |
|---|---|---|---|---|---|---|---|
| 1977 | 5 | 99,504 | 5,333 | 44,775 | 5,200 | 12,811 | 167,628 |
| 1978 | 4 | 11,253 | 11,193 | 30,755 | 4,401 | 17,145 | 74,751 |
| 1979 | 16 | 48,094 | 27,198 | 16,335 | 4,189 | 19,690 | 115,542 |
| 1980 | 34 | 42,255 | 29,139 | 20,019 | 7,932 | 15,385 | 114,764 |
| 1981 | 28 | 51,466 | 38,304 | 13,990 | 5,865 | 23,510 | 133,163 |
| 1982 | 129 | 41,385 | 27,916 | 25,984 | 10,106 | 16,308 | 121,828 |
| 1983 | 346 | 4,231 | 32,028 | 18,095 | 7,881 | 1,824 | 64,405 |
| 1984 | 231 | 2,908 | 41,534 | 10,504 | 3,786 | 564 | 59,527 |
| 1985 | 583 | 1,600 | 34,053 | 9,210 | 7,856 | 10,275 | 63,577 |
| 1986 | 1,145 | 1,879 | 40,616 | 10,898 | 7,502 | 21,278 | 83,318 |
| 1987 | 2,061 | 1,424 | 40,961 | 11,653 | 8,264 | 19,984 | 84,347 |
| 1988 | 3,724 | 1,444 | 42,200 | 10,157 | 8,677 | 36,641 | 102,843 |
| 1989 | 3,845 | 2,410 | 35,548 | 19,477 | 9,046 | 40,893 | 111,219 |
| 1990 | 2,770 | 3,156 | 36,716 | 4,874 | 7,978 | 28,447 | 83,941 |
| 1991 | 7,625 | 4,184 | 30,459 | 1,667 | 7,345 | 37,388 | 88,668 |
| 1992 | 17,946 | 1,124 | 18,570 | 5,878 | 6,318 | 13,110 | 62,946 |
| 1993 | 13,843 | 1,954 | 12,391 | 1,614 | 3,882 | 42,708 | 76,392 |
| 1994 | 13,420 | 3,680 | 10,040 | 2,153 | 2,668 | 55,395 | 85,929 |
| 1995 | 43,450 | 1,881 | 8,667 | 2,640 | 4,475 | 70,278 | 131,391 |
| 1996 | 32,553 | 4,419 | 10,286 | 1,985 | 5,518 | 80,360 | 135,121 |
| 1997 | 46,196 | 5,718 | 20,615 | 1,161 | 11,541 | 70,257 | 155,488 |
| 1998 | 41,056 | 1,457 | 20,073 | 970 | 2,432 | 2,895 | 68,646 |
| 1999 | 56,747 | 5,179 | 9,527 | 963 | 2,207 | 91,950 | 164,945 |
| 2000 | 53,586 | 11,504 | 21,222 | 1,135 | 3,736 | 118,827 | 209,144 |
| 2001 | 51,811 | 19,187 | 6,924 | 3,615 | 2,715 | 86,203 | 170,080 |
| 2002 | 58,353 | 4,643 | 3,367 | 1,006 | 3,339 | 72,878 | 143,586 |
| 2003 | 34,292 | 1,547 | 3,999 | 155 | 1,780 | 44,965 | 88,741 |
| 2004 | 44,293 | 6,793 | 3,569 | 1,027 | 1,596 | 40,324 | 99,606 |
| 2005 | 34,331 | 11,091 | 3,243 | 199 | 217 | 54,976 | 104,057 |
| 2006 | 46,672 | 12,815 | 5,904 | 1,169 | 732 | 49,248 | 115,845 |

on 1 January 2006. On 1 July, 40% (47,575 t) of the HG, plus the uncaught remainder of the previous allocation (20,207 t) was allocated coastwide. The remaining 25% (29,734 t) of the HG, plus the unharvested remainder of the previous allocations (50,828 t), was allocated coastwide on 15 September. By 31 December 2006, 69% (82,323 t) of the HG had been caught coastwide.

In 2006, 46,672 t of Pacific sardine, with an ex-vessel value of more than $5 million, was landed in California. This represents a 26.1% increase in commercial sardine landings over 2005 (34,479 t). In California, commercial sardine landings averaged 45,471 t over the ten-year period from 1996–2006 (fig. 2). Similar to previous years, the majority (95.5%) of California's 2006 catch was landed in Los Angeles (57.5%; 26,836.1 t) and Monterey (38.0%; 17,748.1 t) port areas (tab. 2).

California exported a total of 38,543 t of sardine product to 22 countries in 2006. Most of this product was exported to Australia (21,335 t), Japan (6,023 t), Croatia (3,213 t), and Thailand (2,331 t). These amounts represent over 81% of the total export value of over $21.6 million.

A total of 35,648 t of Pacific sardines, with an ex-vessel value exceeding $3.5 million, was landed in Oregon during 2006. Although Oregon's sardine landings have been increasing steadily over the past few years (fig. 3), the landings for 2006 were down 21.0% from 2005 (45,110 t). Washington landed 4,362 t in 2006 with an ex-vessel value of $437,424.

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

| | Pacific Sardine | | Pacific mackerel | |
|---|---|---|---|---|
| Area | Landings t | % Total t | Landings t | % Total t |
| Eureka | 0.0 | 0.0 | 0.0 | 0.00 |
| San Francisco | 131.0 | 0.3 | 0.4 | 0.01 |
| Monterey | 17,748.1 | 38.0 | 31.2 | 0.53 |
| Santa Barbara | 1,938.4 | 4.2 | 146.4 | 2.48 |
| Los Angeles | 26,836.1 | 57.5 | 5,724.8 | 96.98 |
| San Diego | 17.7 | 0.0 | 0.5 | 0.01 |
| Total | 46,671.3 | 100.0 | 5,903.3 | 100.00 |

***Pacific Mackerel.*** The U.S. fishing season for Pacific mackerel is from 1 July through 30 June of the following year. The majority of Pacific mackerel are landed in southern California and Ensenada, BCM, and occasionally in Oregon and Washington. At the beginning of the 2006–07 season (1 July 2006), the biomass estimate was 112,700 t and the HG was set at 19,845 t. Since Pacific mackerel are often landed incidentally to other CPS, the HG was divided into a directed fishery and an incidental fishery. The directed fishery was allo-

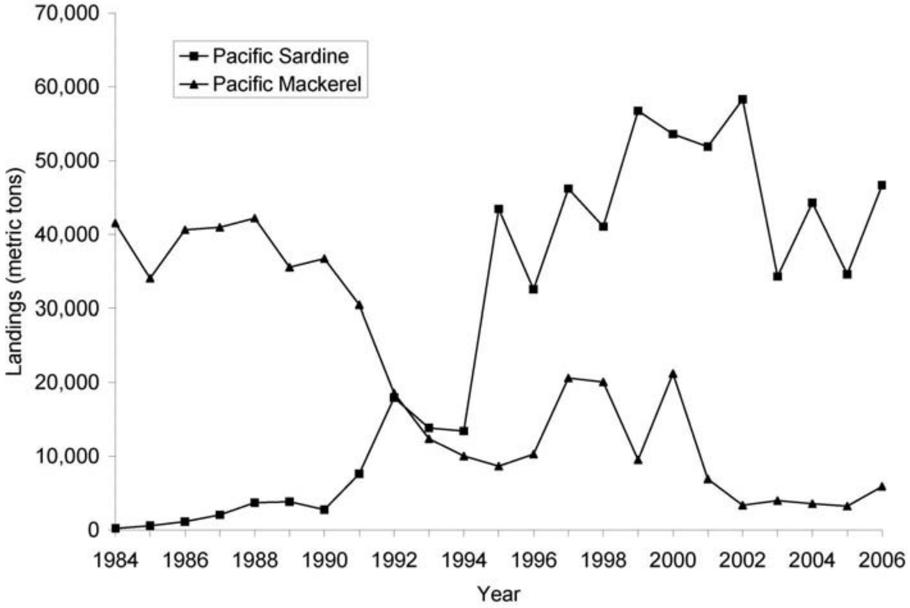

Figure 2. California commercial landings of Pacific sardine (*Sardinops sagax*) and Pacific mackerel (*Scomber japonicus*), 1984–2006.

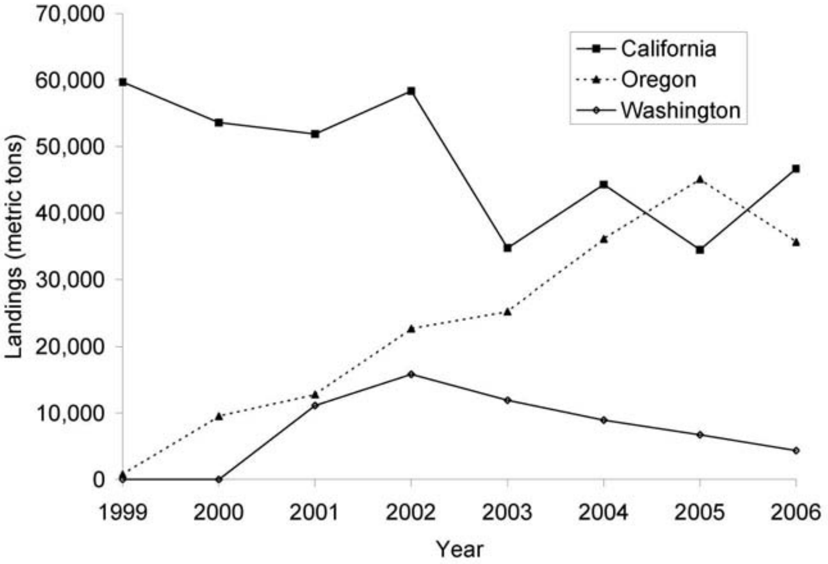

Figure 3. Commercial landings of Pacific sardine (*Sardinops sagax*) in California, Oregon, and Washington, 1999–2006.

cated 13,845 t and the remaining 6,000 t were set aside for an incidental catch rate of 40% when landed as a mixed load.

Although California landings of Pacific mackerel have been declining since the early 1990s (fig. 2), 5,904 t were landed during 2006 representing a 5-year high and a 45.1% increase over 2005 (3,243 t). The 2006 Pacific mackerel landings in California had an ex-vessel value of $819,594, with 97% (5,725 t) landed in the Los Angeles port area (tab. 2).

California exported 2,377 t of mackerel product to sixteen countries worldwide. The majority (67%) of this product was exported to Australia (834 t), Indonesia (386 t), and China (381 t). Mackerel exporters generated over $1.8 million in export revenue in 2006.

Since 1999, an average of 202 t of Pacific mackerel has been landed in Oregon, and 655 t were landed during 2006. In Washington, annual landings of unspecified mackerel averaged 144 t over the five-year period from 2001–2005; with no reported landings for 2006.

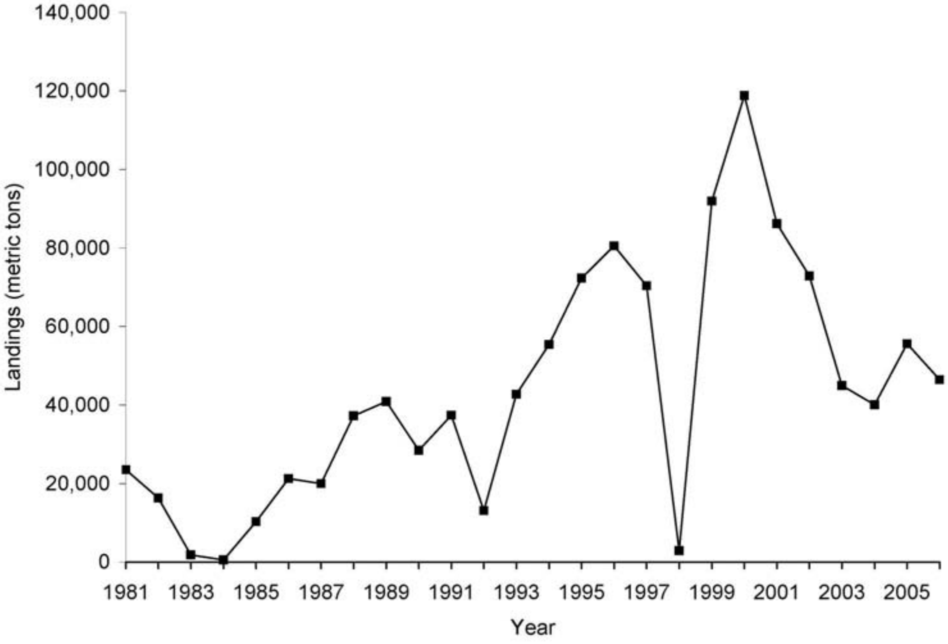

Figure 4. California commercial market squid (*Loligo opalescens*) landings, 1981–2006.

***Jack Mackerel.*** In 2006 jack mackerel landings in California were 1,169 t. This represents an 83.0% increase over 2005 (199 t). Ex-vessel revenues in 2006 totaled $196,361, a 25.9% increase over 2005 revenues. In Oregon, landings of jack mackerel totaled 5.3 t with an ex-vessel value of $2,598. This represents a 95.6% decrease in landings from 2005 and a 92.1% decrease from 2004. There were no reported landings of jack mackerel in Washington during 2006.

***Northern Anchovy.*** Over the past decade, landings of northern anchovy in California have varied widely. Anchovy landings in 2006 (12,815 t) increased 12.8% over the previous year (11,178 t). Ex-vessel revenues for northern anchovy totaled $1.3 million, making this species the second most valuable CPS finfish in 2006 after Pacific sardine. In 2006, there were no landings of northern anchovy in Washington. Oregon landed 8.6 t valued at $24.

California exported 1,083 t of anchovy product, valued at $792,120, to three countries in 2006. This was an increase in weight of 85.3% and almost one and a half times the export value of 2005. Ninety-one percent of California's anchovy export product was shipped to Australia (986.9 t; $597,182).

***Pacific Bonito.*** Landings of the Pacific bonito (*Sarda chiliensis lineolata*) in California waters have been minimal since the late 1980s. From the 1960s to the 1980s, bonito was a major component of the recreational fishery because it is easy to catch and is a strong fighter when hooked. In late 2005 and 2006, large schools of bonito were observed migrating northward from México into the Southern California Bight and were targeted by coastal pelagic fishermen. A total of 2,500 t were taken in 2006 with an ex-vessel value of $1.5 million. This is a sharp increase from the 10.4 t taken in 2005 (ex-vessel value $6,000) and represents the largest landings of bonito since 1990 (4,500 t). Recreational fishermen on Commercial Passenger Fishing Vessels (CPFVs) caught a total of 201,703 bonito in 2006, with 14% (27,259) of that total coming from trips in Mexican waters. This represents nearly 7% of all fishes caught on CPFVs in 2006. In contrast, a total of 75,353 were taken by CPFVs in 2005, representing only 2.8% of the total catch.

***Krill.*** Primarily euphausiids, krill are small shrimp-like crustaceans that serve as the basis of the food web for many commercially fished species, as well as marine mammals and birds. In 2005, the PFMC recommended that krill be managed under the Coastal Pelagic Species Fishery Management Plan (CPS FMP). In March 2006, the PFMC adopted a complete ban on commercial krill fishing and specified essential fish habitat for krill. The PFMC initiated the prohibition which took the form of Amendment 12 to the CPS FMP adding krill as a prohibited species. These actions followed a request from NOAA National Marine Sanctuaries to prohibit krill fishing in the exclusive economic zone (EEZ) around the three marine sanctuaries off central California. Washington, Oregon, and California had previously adopted state laws prohibiting fishing for krill in state waters and the landing of krill. However, commercial fishing of krill continues to exist in other parts of the world such as Antarctica, Japan, and off the west coast

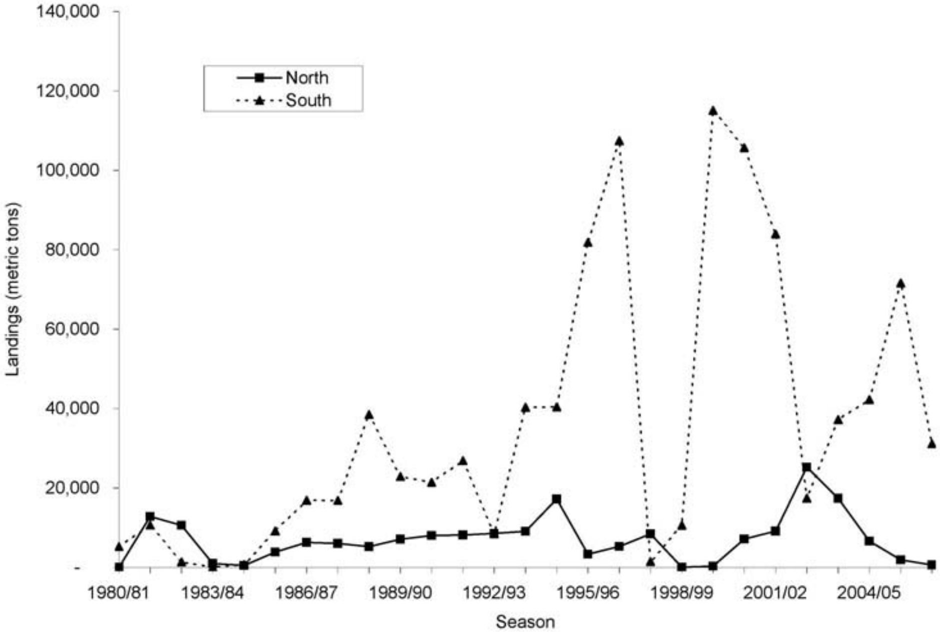

Figure 5. Comparison of market squid landings for northern and southern fisheries by fishing season (1 April–31 March), from 1980–81 to 2006–07 seasons.

of Canada, where it is primarily used for fish bait, pet food, cultured fish, and livestock.

## California Market Squid

In 2006, market squid (*Loligo opalescens*) was the state's largest fishery in terms of quantity but dropped to second in ex-vessel value. Total landings in the market squid fishery were 12% less than in 2005, decreasing from 55,606 t to 49,145 t (fig. 4). The ex-vessel price averaged $554/t (a decrease from the 2005 average of $569/t). The 2006 ex-vessel value was approximately $27.2 million, a 14% decrease from 2005 ($31.6 million). Market squid is used domestically for food and as bait by the recreational fishery, and remains an important international commodity. Approximately 22,562 t of market squid were exported for a value of $28.8 million in 2006. Asian countries were the main export market with about 49% of the trade going to China (8,894 t) and Japan (2,148 t). Switzerland was the second largest export market (4,200 t), accounting for 19% of the trade. This sharp decline in exports compared to 2005 (43,131 t of market squid exported at a value of $54.6 million) is probably due to the drop in international demand for California market squid since the resurgence of the Falkland Islands squid fishery.

The fishery uses either seine or brail gear that is usually combined with attracting lights to capture aggregations of adult squid spawning in shallow water in areas over sandy substrate. While most fishing effort occurs at night, spawning in some areas has been observed during the day. And, with advances in sonar technology, the fishery has been able to target market squid aggregations during daylight hours without using attraction lights. Spawning may occur year-round, however, the fishery is most active from April to September in central California and from October to March in southern California. This seasonal shift in location has produced two distinct northern and southern fisheries. The fishing permit season for market squid extends from 1 April through 31 March of the following year. During the 2006–07 season (as opposed to the 2006 calendar year), 31,786 t were landed, a 55% decrease from the 2005–06 season (70,972 t). There was a 70% decline in catch from the northern fishery near Monterey in the 2006–07 season with only 628 t landed (fig. 5). As in previous seasons, total catch was greater in southern California, with 31,158 t landed (98% of the catch) during the 2006–07 season (fig. 5). In 2006–07, market squid fishing was predominantly centered in areas around the northern Channel Islands near Santa Cruz and Santa Rosa Islands, and also along the coast of Los Angeles and Orange Counties. This varies from the 2005–06 season where market squid fishing took place primarily around Catalina Island.

Market squid are sensitive to changes in their environment, particularly to shifts to water that is warm and poor in nutrients. As a result, the fishery fluctuates with fishing patterns and landings reflecting the changing oceanic conditions and temperature variances. In 2006, a regional warm-water event similar to an El Niño, but without the characteristic equatorial warming, started in September and lasted until early 2007. A similar phenomenon occurred in 2005. In April 2006, when up-

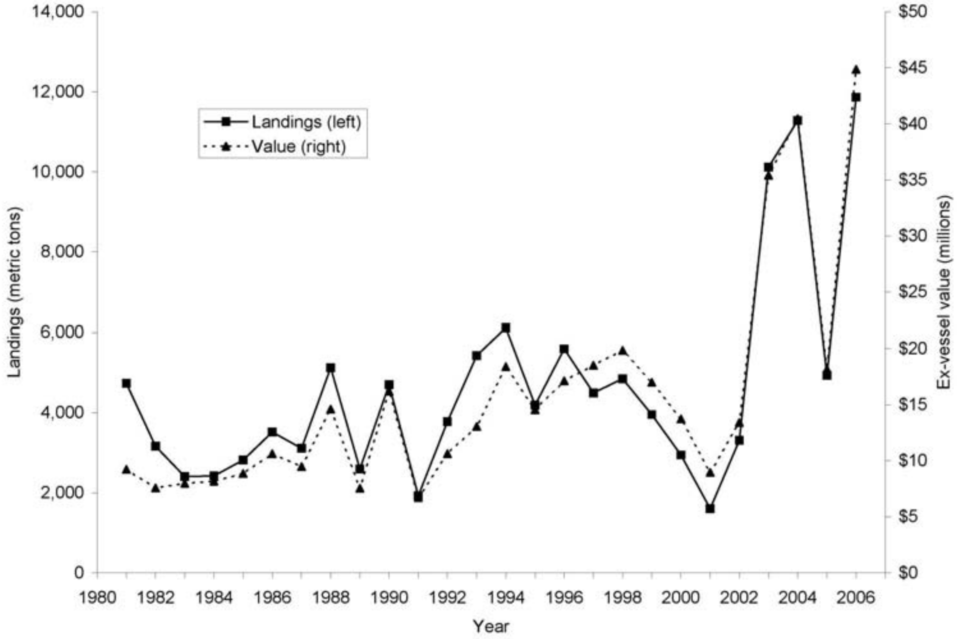

Figure 6. California commercial Dungeness crab (*Cancer magister*) landings, 1981–2006.

welling has usually started in central California, spawning market squid in Monterey were not found in great numbers and body size was small. By July, when upwelling had finally strengthened, a lack of market orders caused most market squid fishermen to shift their focus to sardine and salmon in Oregon and Alaska. The northern fishery in central California ended in August. In southern California, vessels began targeting market squid in June and July. Landings dropped off in August as market squid became less available and fishermen switched their fishing efforts to a local summer run of bonito. Landings decreased during September as the warm-water event developed with a rapid warming of the upper-ocean water. At the end of November, squid were found around the Channel Islands, but they were deep and hard to find. The regional warm-water event began to show signs of weakening in early 2007. In January and February, market squid were caught in abundance along the coast which attracted more permitted vessels from out of town, and increased the fishing pressure. Bad weather hampered fishing efforts for the rest of the season. By the end of March, market squid size and landings had decreased.

To protect and manage the squid resource, a market squid fishery management plan (MSFMP) was adopted by the Commission in 2004. The measures implemented in the MSFMP include: a seasonal catch limit of 107,047 t (118,000 short tons) to prevent the fishery from over-expanding; monitoring programs designed to evaluate the impact of the fishery on the resource; weekend closures that provide for periods of uninterrupted spawning; gear regulations regarding light shields and wattage used to attract squid; a restricted access program that includes provisions for initial entry into the fleet, permit types, permit fees, and permit transferability that produces a moderately productive and specialized fleet; and a seabird closure restricting the use of attracting lights for commercial purposes in any waters of the Gulf of the Farallones National Marine Sanctuary. In 2006, a total of 169 restricted access permits were issued: 76 transferable vessel permits, 12 non-transferable vessel permits, 14 transferable brail permits, 64 light boat permits, and 3 experimental non-transferable vessel permits.

## Dungeness Crab

Landings of Dungeness crab (*Cancer magister*) totaled 11,867 t in 2006, a 140% increase from the 4,933 t landed in 2005 (fig. 6). However, the 2005 catch total is misleading in that it is an artifact of the statutory postponement of the northern California 2005–06 season opening, due to poor crab condition. The 2005–06 northern California season opener was delayed by CDFG (for the first time since given that authority in 1995), until the last day of 2005 to allow ample time for crab condition to improve. The central California fishery opens in mid-November and is not subject to the statutory postponement provision. When examined on a seasonal basis, the 2005–06 crab season actually went on to become the third highest season since records began in 1915, with 10,784 t landed, mostly in 2006. Ex-vessel revenues for 2006 were $44.9 million, the highest on record. The average price per kilogram paid to fishermen increased to $3.78 ($1.71/lb), up 3% from $3.68 (1.66/lb) in 2005.

Mature male Dungeness crabs go through their annual molt in the summer and then begin putting on weight in their new shells. While the timing of this process can vary from year to year, the 1 December fishery opening on most of the West Coast usually results in adequately filled-out crabs reaching the markets. However, commencing with the 1995–96 season, the California legislature authorized industry-funded preseason crab condition testing to help ensure that crabs were ready for harvest by season's start. The states of Oregon, Washington, and California, the member states of the Pacific States Marine Fisheries Commission Tri-State Crab Committee, have agreed that the crab meat-to-whole crab drained weight recovery rate must be 25% by 1 December for the fishery to open on time. The assessment of crab condition is initiated each year around 1 November; if the crab meat recovery is less than 25%, another test is mandated. Approximately two weeks later the second test is conducted, and if the pick-out is still below 25%, the season opening is delayed 15 days. This procedure can continue until 1 January, when no more tests can be made and the season must be opened on 15 January in northern California (north of the Mendocino County southern border). In 2006, northern California crabbers asked CDFG to conduct the tests earlier than in previous years so that results would be available prior to the central California opening day in mid-November. A decision to delay the northern opening day would adversely affect northern crabbers who chose to fish the central California opener because of a penalty clause in the statutes. Tests were conducted on 26 October and 8 November, 2006, prior to the 2006–07 season. The second test yielded an average recovery of greater than 25%, leading to a consensus opinion by the Departments of the three states and the industry that the crab would be ready to harvest on 1 December.

The Dungeness crab fishery in California is managed using a combination of technical measures: a suite of size, sex, and season restrictions. Only male Dungeness crabs are harvested commercially, and the minimum commercial harvest size is 159 mm (6.25 in) carapace width. The minimum size limit is designed to protect sexually mature male crabs from harvest for several seasons, and the timing of the season is designed to provide some measure of protection to crabs when molting is most prevalent. The commercial season runs from 1 December to 15 July in northern California and from 15 November to 30 June in the remainder of the state (central area). In addition to these technical measures, fishery participation is managed by restricted access. While large fluctuations in catches occur on a cyclical basis, they are apparently due to stochastic factors independent of stock size. Studies have shown that despite the presumption that most males of legal size are taken each season, almost all of the sexually mature females are fertilized.

Landings in northern California in the 2005–06 season totaled 8,074 t or 75% of the statewide catch. A catch comparison between the 2005–06 season and the previous season shows only a 9 t difference despite the one month seasonal delay. About 77% of the near record northern California catch was taken in the first two months of the abbreviated season, an increasing trend and indication that there is an abundance of fishing power and gear available in this fishery. A total of 416 vessels made landings during the 2005–06 season, up from the 30-year low of 385 vessels in the 2001–02 season.

Limited entry for the Dungeness crab fishery was established by the California legislature in 1995, with most permits transferable. There were 537 resident permits and 85 non-resident permits as of 2006. Central California fishermen have in the past several years unsuccessfully tried to legislate a limit on the number of traps allowed in their area. Northern crabbers have generally been opposed to this measure, particularly those larger boats that fish central California during the 2 weeks prior to the northern opener. Industry leaders estimate that there were about 150,000 traps in the fishery in 2006. There is renewed interest state-wide to pursue some type of trap limit program, following on the recent programs adopted by Washington and Oregon.

A California law passed in 2006, effective 1 January 2007, requires all vessels commercially fishing Dungeness crab in the EEZ off California to possess a California Dungeness crab permit. The other two states in the Tri-State Committee enacted reciprocal regulations. These laws, known as LE200 (limited entry 200 miles), complement trap limit programs enacted by Oregon and Washington with the goal of eliminating un-permitted out-of-state vessels who would not be subject to their trap limits, from their respective EEZs.

### Spot Prawn

Preliminary 2006 spot prawn (*Pandalus platycerous*) landings were 148.9 t, a 47% increase from 2005 (101 t) (fig. 7). Until 2002, spot prawn were harvested by trawl and trap gear. In 2003, the use of trawl gear for the take of spot prawn was eliminated because of the bycatch of rockfish, particularly the overfished bocaccio (*Sebastes paucispinus*). Consequently, 2003 spot prawn landings were the lowest since 1987 when trapping was just getting underway in southern California. Current harvest levels are well below those of the mid- to late-1990s and appear to be sustainable.

Spot prawns are currently caught only with trap gear, although a small amount occurs as bycatch in the ridgeback (*Eusicyonia igentis*) trawl fishery (<0.5 t). Spot prawn

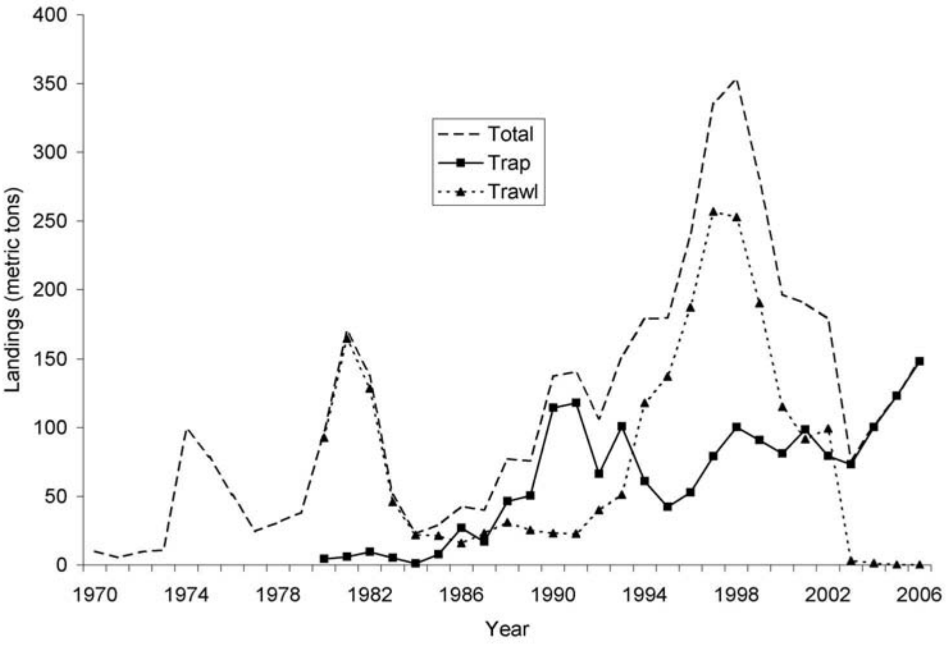

Figure 7. California landings of spot prawn (*Pandalus platycerous*) by gear type, 1970–2006.

traps were required to be made of plastic or wire mesh with an inside measurement of at least 2.22 × 2.22 cm (7/8 × 7/8 in.). The traps may not exceed 1.8 m in any dimension. In December 2005, the regulatory language requiring that prawn traps be made of plastic or wire webbing was amended so that other materials could be used as webbing. The baited traps are fished in strings at depths of 180–305 m (100–167 fathoms) along submarine canyons or shelf breaks. Each string consists of a groundline with anchors and a buoy at one or both ends, and 10 to 30 traps attached. No other species may be taken in a prawn trap, and all bycatch must be returned to the water immediately.

A two-tiered restricted access trap vessel permit program was initiated in 2002 based on participation in the fishery. Tier 1 permittees may use no more than 500 traps, unless fishing in state waters north of Point Arguello where they are only allowed the use of 300 traps. Eighteen trap vessel owners originally qualified and purchased these permits, and 17 remained when they became transferable on 1 April 2005. Two permits have been sold on the open market for approximately $200,000. The CDFG receives a transfer fee of $50.00 when a permit is sold.

Tier 2 vessel permittees are limited to an annual harvest quota of just over 2 t. Permittees may use no more than 150 traps and the permits are non-transferable. Initially there were six permittees, but only three Tier 2 permittees remain.

When the use of trawl gear for the take of spot prawn was prohibited, the Commission directed the CDFG to develop a conversion program for the trawl fleet. A conversion program went into effect in 2005, which allowed the owners of 11 former spot prawn trawl vessels to purchase Tier 3 spot prawn trap vessel permits in 2005. Tier 3 permittees may use no more than 500 traps, unless fishing in state waters north of Point Arguello where they are only allowed the use of 300 traps. Ten Tier 3 permittees remain. The fee for the Tier 3 permit was $1,066.25 in 2006, and the permits are non-transferable. Whereas, both Tier 1 and Tier 2 vessel permits were $266.50 in 2006.

In 2006, 22 trap permittees landed spot prawn. Fifteen of the 17 Tier 1 trappers landed 84% of the catch with each vessel landing an average of 8.3 t. All three Tier 2 fishermen fished, landing an average of 1.4 t. Only four of the Tier 3 permittees fished, landing almost 13% of the catch. Over half of the Tier 3 permittees have not had the financing necessary to purchase traps.

Almost all spot prawn harvested is sold live, with ex-vessel prices ranging from $2.22 to 30.00/kg ($10.00 to $13.50/lb). Fresh dead spot prawn generally sells for half the price of live. Most trap permittees have invested in live tanks and chillers on their vessels to keep the prawns in top condition for the live market.

The trap fishery in southern California (south of Point Arguello) is closed from 1 November to 31 January to provide protection for gravid females. North of Point Arguello, the spot prawn trap season is closed from 1 May to 31 July, an accommodation to prevent serious fishing gear conflicts in the Monterey Bay area. A 0.023 t allowance of spot prawn while trawling for ridgeback prawn is still legal, but spot prawn may not be landed as bycatch when trawling for pink shrimp (*Penaenus duorarum*).

## Highly Migratory Species

***Albacore.*** Albacore (*Thunnus alalunga*) is the most abundant tuna caught in both commercial and recreational fisheries in California. In 2006, 98% of the commercial caught albacore came from hook and line gear (jig/bait/troll). A total of 207 t were commercially landed in California ports in 2006, a decrease of over 200% compared to 483 t landed in 2005. This total is but a fraction of the North Pacific landings estimated at over 12,000 t for 2006. Ex-vessel value was $535,638 and price-per-kilogram remained constant at an average of $3.46/kg ($1.57/lb) in 2005 and 2006. Although some high-grade fresh caught albacore was sold for the restaurant trade, most of this catch was exported for processing and canning.

Historically, there have been no bag or size limits on sport-caught albacore in California. In late 2006, the PFMC adopted bag limit conservation measures for albacore (10 fish south of Point Conception, 25 fish north of Point Conception). These regulations, along with comparable state regulations, are currently being promulgated. Most of the recreational take of albacore comes from sportfishing in Mexican waters, which has a 5-fish daily bag limit. The 2006 sport fishing season started off early but the fish moved through and northward quickly. As a result, only 20,925 albacore were reported taken by California's CPFV fleet in 2006, one quarter of the 98,611 landed in 2005.

***Yellowfin Tuna.*** Commercial landings of yellowfin (*Thunnus albacares*) totaled 75 t in 2006, far less than the 286 t landed in 2005. Purse seine vessels caught 75% of the total yellowfin landed, while hook and line gear caught the remaining 25%. Ex-vessel value totaled $175,642 and price-per-kilogram was far better for the 2006 catch at an average $4.93/kg ($2.24/lb) compared to the $2.78/kg ($1.25/lb) paid in 2005. Some yellowfin is sold to the restaurant trade, however, most of the catch is processed into canned consumer product. Exports of fresh frozen yellowfin tuna from California went to México for processing. Currently there are no canneries operating in California. CPFV logbook data indicate recreational anglers landing 46,411 yellowfin, some 10,000 less than that reported in 2005.

***Skipjack Tuna.*** Commercial landings of skipjack (*Katsuwonus pelamis*) totaled 48 t in 2006, a dramatic decline from 533 t in 2005. The variable catch success is likely due to seasonal fluctuation in abundance of fish within range of southern California vessels. The total ex-vessel value increased to an average $1.22/kg ($0.55/lb) in 2006 from the $0.93/kg ($0.42/lb) average paid in 2005. Purse seine vessels catch almost all of the skipjack landed in California. Frozen skipjack are exported for processing into canned product. CPFV logbook data indicate that recreational anglers landed 4,541 fish in 2006, a decrease of 23% from 2005 (5,906 fish).

***Bluefin Tuna.*** Commercial landings of bluefin (*Thunnus thynnus*) totaled just 0.8 t in 2006, far less than the 207 t landed in 2005. Ex-vessel value was $3,790, and price-per-kilogram was greater in 2006 with an average $4.84/kg ($2.18/lb) paid for the few fish landed. In contrast, $3.33/kg ($1.51/lb) was the average paid for bluefin in 2005. Purse seine vessels caught 97% of the bluefin landed in 2005, while the drift gillnet fleet accounted for 65% of the 2006 landings.

CPFV logbook data indicate that recreational anglers landed 7,356 bluefin, up 28% from the 5,748 fish landed in 2005. Currently in California, there are no bag or size limits on sport-caught bluefin tuna. In late 2006, the PFMC adopted a 10-fish bag limit conservation measure for bluefin tuna. These regulations, along with comparable state regulations, are currently being promulgated.

***Swordfish.*** Swordfish (*Xiphias gladius*) is the most valuable fish taken in the California highly migratory species (HMS) fishery. In 2006, the commercial catch was valued at $2.7 million. In 2006, 82% of the commercial catch came from drift gill net gear; harpoon fishermen landed the remainder. In 2006, commercial landings totaled 371 t, up 83% from the 203 t landed in 2005. The price-per-kilogram decreased in 2006; an average of $8.93/kg ($4.02/lb) compared to $12.93/kg ($5.82/lb) in 2005. Swordfish caught by harpoon is considered more valuable than gill net caught fish. Ex-vessel price-per-kilogram can exceed $11.11/kg ($5.00/lb) for harpooned fish. The recreational catch of swordfish is unknown but is considered to be very few in number.

***Common Thresher Shark.*** Common thresher shark (*Alopias vulpinus*) is the most common and most valuable shark taken in the California HMS fishery. In 2006, 99% of the commercial catch of common thresher shark came from gill net vessels. Commercial landings decreased in 2006 to 93 t, compared to 105 t landed in 2005, an 11% decline. The ex-vessel value totaled $298,843, and price-per-kilogram increased from an average of $3.02/kg ($1.36/lb) in 2005 to $3.16/kg ($1.42/lb) in 2006. CPFV logbook data indicate that 27 fish were landed recreationally in 2006 and 23 reported for 2005, indicating that this mode of fishing is a minor component of the fishery.

***Shortfin Mako Shark.*** Shortfin mako shark (*Isurus oxyrinchus*) is the second most common shark landed in the California HMS fishery. In 2006, 67% of the commercial catch of mako shark came from drift gill net gear and 12% from set gill nets. Commercial landings increased in 2006 to 32 t, compared to 23 t in 2005, a

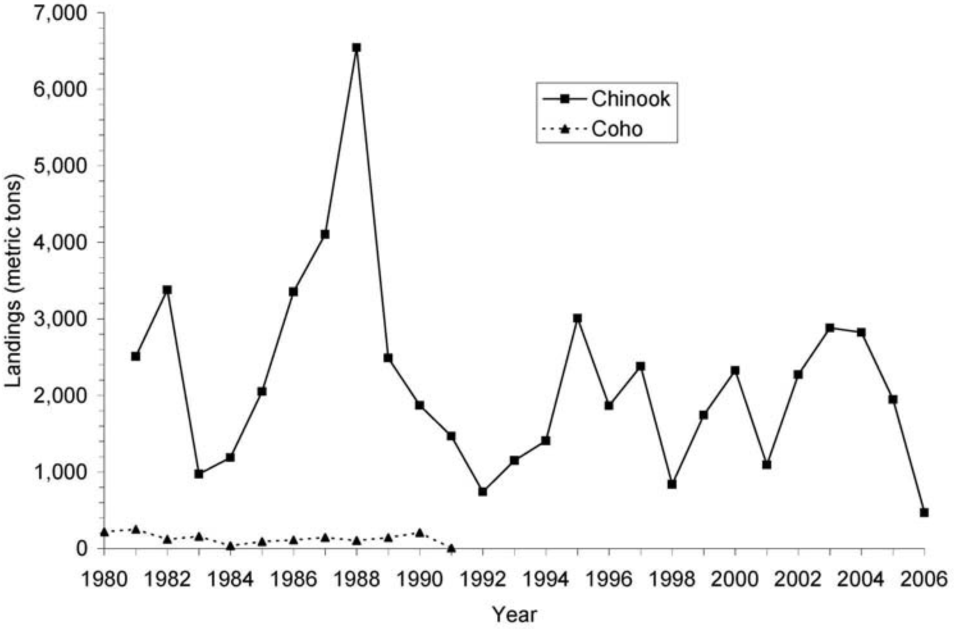

Figure 8. California commercial landings of ocean salmon, 1980–2006. Note: Commercial fishery landings of coho salmon were prohibited since 1992 to protect California coho salmon stocks.

39% increase. The ex-vessel value was $79,144, and price-per-kilogram remained constant at an average of $2.44/kg ($1.10/lb). According to CPFV logbook data, 238 mako sharks were taken in 2006, a 47% increase compared to 162 in 2005.

***Dorado (dolphinfish).*** Commercial landings of dorado (*Coryphaena hippurus*) totaled 2.8 t in 2006, an increase from the 0.2 t landed in 2005. The ex-vessel value was $17,945, and the price-per-kilogram remained constant at $6.98;kg ($3.10/lb). 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 waters. Local seafood restaurants purchase dorado when available. CPFV logbook data indicate that recreational anglers landed 45,569 dorado in 2006, a seven-fold increase from the 6,654 fish landed in 2005.

***2006 HMS Fishery Management Highlights.*** The PFMC's highly migratory species fishery management plan (HMS FMP) was approved by NMFS in March of 2004. Adoption of the HMS FMP provided for implementation of new management and conservation measures, consolidation of existing state and federal regulations, and international agreements for HMS. In 2006, PFMC activity was focused on implementing the HMS FMP.

The PFMC took action in response to NMFS declarations that bigeye (*Thunnus obesus*) and yellowfin tuna are being overfished in the Eastern Pacific Ocean. An HMS FMP amendment was adopted that calls for a Pacific-wide response to overfishing of bigeye tuna with emphasis on reductions to high seas longline and purse seine fisheries. In addition, the PFMC moved to amend the FMP to address Eastern Pacific Ocean overfishing of yellowfin tuna. The amendment process will be coordinated with activities of the Western Pacific Fishery Management Council and the Inter-American Tropical Tuna Commission. The PFMC also adopted bag limit conservation measures for the recreational harvest of albacore and bluefin tunas. These measures, which affect only California sport anglers, will be implemented in the 1 April 2007–31 March 2009 management cycle.

## Ocean Salmon

Ocean salmon fisheries in California primarily target Chinook salmon (*Oncorhynchus tshawytscha*). The retention of coho salmon (*O. kisutch*) has been prohibited in the commercial and recreational fisheries since 1993 and 1996, respectively. Pink salmon (*O. gorbuscha*) are taken occasionally in the fisheries, usually in odd years.

Each season, the PFMC and Commission regulate California ocean fisheries so that the conservation objectives of the Salmon Fishery Management Plan (Salmon FMP) are met for Klamath River fall Chinook (KRFC) and Sacramento fall Chinook stocks. In addition, the fisheries must meet the NMFS ESA consultation standards for listed stocks, including Sacramento winter Chinook (endangered), Central Valley spring Chinook (threatened), California coastal Chinook (threatened), and Central/Northern California coho stocks (threatened).

In 2006, California salmon fisheries were significantly constrained by low ocean abundance of KRFC. The Salmon FMP requires that ocean fisheries be regulated

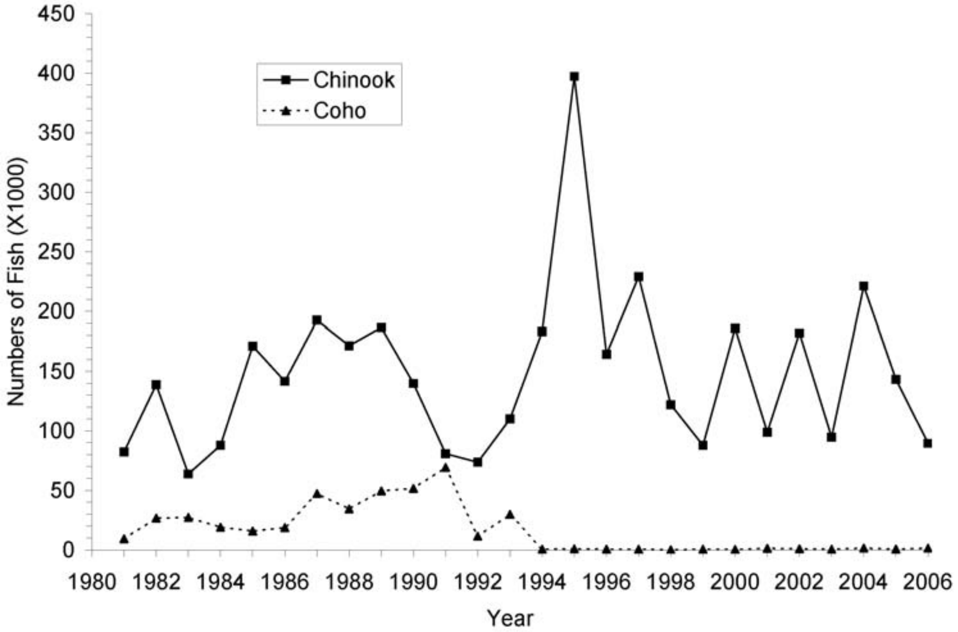

Figure 9. California recreational landings of ocean salmon, 1981–2006. Note: Landings of coho salmon were prohibited after 1996 to protect California coho salmon stocks. Numbers reported since 1996 are illegal harvest.

to allow a minimum of 35,000 natural adult spawners return to the Klamath Basin; however, even without any fisheries in 2006, the Klamath Ocean Harvest Model predicted that this goal couldn't be attained. As a result, NMFS took emergency action in March to allow ocean fishing and advised PFMC to regulate the commercial and recreational fisheries so that no less than 21,000 KRFC natural adults returned to spawn. Thus, commercial and recreational salmon fishing seasons in California were much shorter in 2006 than in 2005.

The commercial fishing season was reduced by 25 days in the Fort Bragg area (Horse Mountain to Point Arena), 20 days in the San Francisco area (Point Arena to Pigeon Point), 20 days in the Monterey area (Pigeon Point to Point Sur), and completely closed in the Klamath Management Zone (KMZ; Horse Mountain to the California-Oregon border). The season south of Point Sur remained the same because KRFC impacts are non-existent.

An estimated 68,800 Chinook salmon (467 t) were landed during the 2006 commercial season (fig. 8), which was approximately 20% of total commercial landings in 2005. The average weight per fish was 6.8 kg (15.0 lbs), the highest observed since the PFMC began reporting these data in 1976. Almost 70% of all salmon were landed in the San Francisco port area. Commercial effort was estimated to be almost 8,200 boat-days fished and the average price was $11.36/kg ($5.11/lb), a 72% increase over the $6.60/kg ($2.97/lb) paid in 2005. The total ex-vessel value of the fishery in 2006 was estimated to be $5.3 million, approximately 40% of the $12.9 million made by the salmon fleet in 2005.

The 2006 recreational fishing season was reduced by 17 days in the KMZ, 17 days in the Fort Bragg area, 4 days in the San Francisco area, and 9 days in the Monterey area compared to the 2005 season. Anglers were allowed two salmon per day of any species except coho. Single-point, single-shank barbless hooks were required north of Point Conception and anglers fishing with bait and by any means other than trolling were required to use circle hooks. The minimum size limit was 20 in. total length (TL), except in the KMZ where the minimum size limit was 24 in. TL.

An estimated 89,500 Chinook were caught by 120,400 sport anglers in 2006 (fig. 9). This represents a 38% decrease from total landings in 2005 while total effort also decreased to approximately 70% of 2005 levels. Sport anglers also reported contacting numerous coho salmon during the season, especially during June and July.

Approximately 1,400 coho were landed illegally during 2006, primarily by anglers who improperly identified their salmon as Chinook. This is twice the number of coho landed in 2005. It's assumed that the majority of these fish were part of the mass-marking production of coho currently occurring in Oregon and Washington; most were missing their adipose fin and many did not contain a coded-wire tag (only a small percentage of mass-marked coho contain coded-wire tags).

## California Halibut

California halibut (*Paralichthys californicus*) is an important flatfish species in both the commercial and recreational fisheries of central and southern California. It is

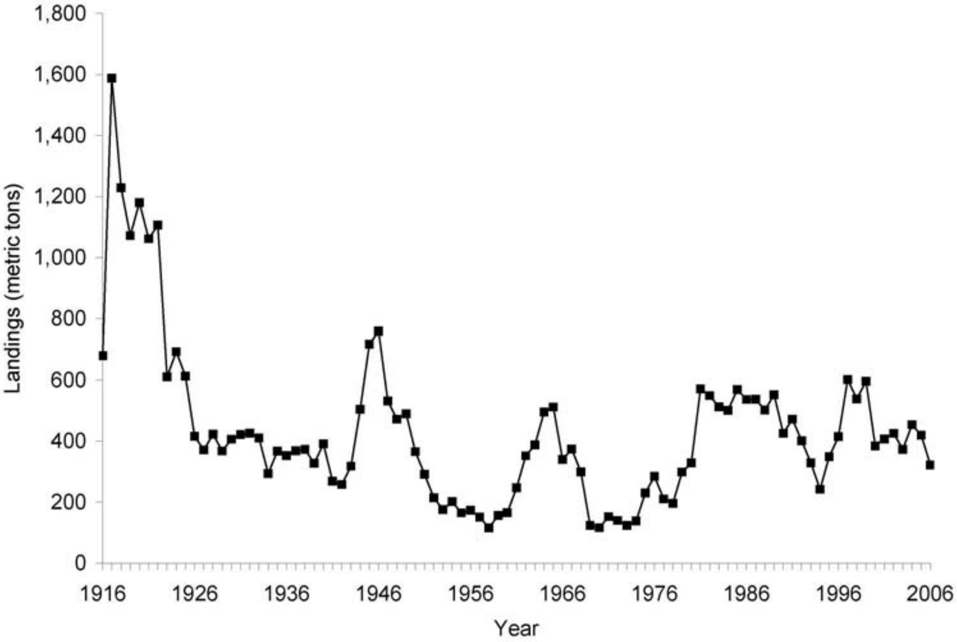

Figure 10. California commercial California halibut (*Paralichthys californicus*) landings, 1916–2006.

TABLE 3
**Annual commercial landings (metric tons) of California halibut (*Paralichthys californicus*) by major port complex for 2005 and 2006 and ten-year average (1997–2006).**

| | 2005 | | 2006 | | Ten-Year Average (1997–2006) | |
|---|---|---|---|---|---|---|
| Area | Landings (t) | Ex-vessel ($) | Landings (t) | Ex-vessel ($) | Landings (t) | Ex-vessel ($) |
| Eureka | 0.2 | $ 1,482 | 0 | $ 456 | 4 | $ 12,469 |
| Fort Bragg | 0 | $ 0 | 0 | $ 703 | 0 | $ 5,745 |
| Bodega Bay | 8 | $ 50,602 | 2 | $ 18,951 | 8 | $ 43,916 |
| San Francisco | 279 | $1,587,465 | 180 | $1,231,769 | 199 | $ 959,829 |
| Monterey | 31 | $ 221,253 | 31 | $ 222,136 | 46 | $ 318,435 |
| Morro Bay | 4 | $ 30,786 | 8 | $ 61,334 | 19 | $ 135,465 |
| Santa Barbara | 54 | $ 556,751 | 66 | $ 782,822 | 102 | $ 729,783 |
| Los Angeles | 30 | $ 314,318 | 27 | $ 286,351 | 58 | $ 483,134 |
| San Diego | 14 | $ 107,088 | 9 | $ 83,750 | 16 | $ 131,602 |
| Total Landings | 420 | $2,869,745 | 322 | $2,688,272 | 452 | $2,540,812 |

found in nearshore waters from Almejas Bay, Baja California Sur, to the Quillayute River, Washington. However, it is most common south of Bodega Bay, with distribution centered off northern Baja California. California halibut can grow to 1.5 m (5 ft) TL and weigh as much as 33 kg (72 lb).

California halibut is the target of three principle commercial fishing gears: trawl, gill net, and hook and line. While historical landings were estimated at nearly 1,600 t in 1917, recent landings have decreased from a peak of 602 t in 1997 to a low of 322 t in 2006 (fig. 10 and tab. 3). During this same period, the annual ex-vessel value averaged $2.5 million and totaled $2.7 million in 2006 (tab. 3). While landings decreased 23% in 2006 compared to 2005, the ex-vessel value decreased just 6%. This reflects the demand for halibut in 2006, which kept the price-per-kilogram at an average of $8.36/kg ($3.79/lb), compared to the $6.38/kg ($3.10/lb) in 2005. The live market fetched the highest average ex-vessel unit price of $13.29/kg ($6.03/lb). Trawl vessels operating out of ports in southern California supplied a majority (46%) of the live fish, followed by gill net (30%) and hook and line (23%) gears (fig. 11).

Since 1916, commercial landings follow a periodic shift between the central and southern California port complexes. Over the past decade, central California ports have received a majority of the landings, except for 2001 when landings were higher in southern California ports. In 2006, the San Francisco port complex received 56% of the total catch followed by the Santa Barbara (20%), the Monterey (10%), and the Los Angeles port complexes (8%) (tab. 3).

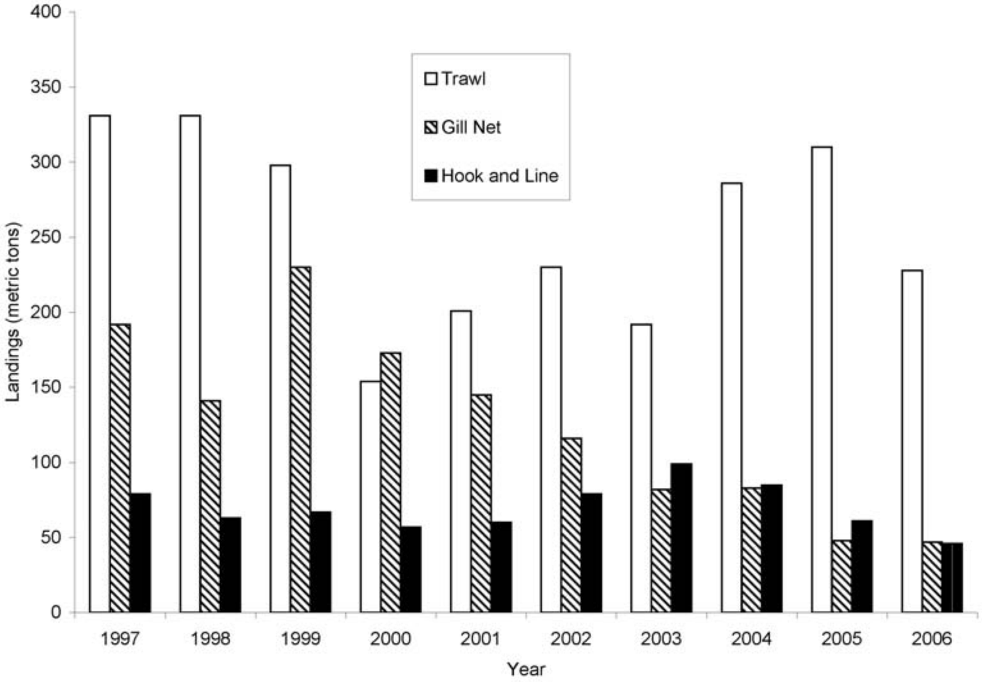

Figure 11. Commercial landings of California halibut, (*Paralichthys californicus*) by gear type, 1997–2006.

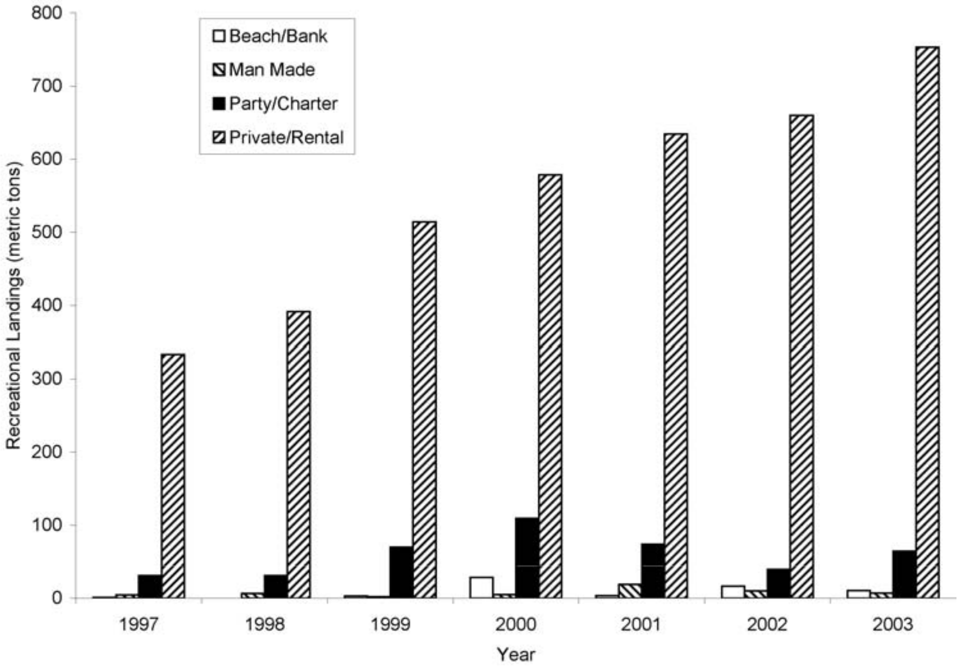

Figure 12. Recreational landings of California halibut, (*Paralichthys californicus*) as reported in the Marine Recreational Fisheries Statistical Survey (MRFSS), by four different fishing modes, 1997–2003.

The bottom trawl fleet has historically landed the majority of California halibut annually. Landings over the past decade have declined from 331 t in 1997 to a low of 154 t in 2000 (fig. 11). The volume and number of trawl landings varied throughout ports in California, however, the San Francisco port complex received a majority (70%) of the landings in 2006, followed by the Santa Barbara (14%) and the Monterey port complexes (11%).

Annual landings of gill net caught fish have also declined (fig. 11). The gill net portion of the total annual catch decreased from 31% in 1997 to 15% in 2006.

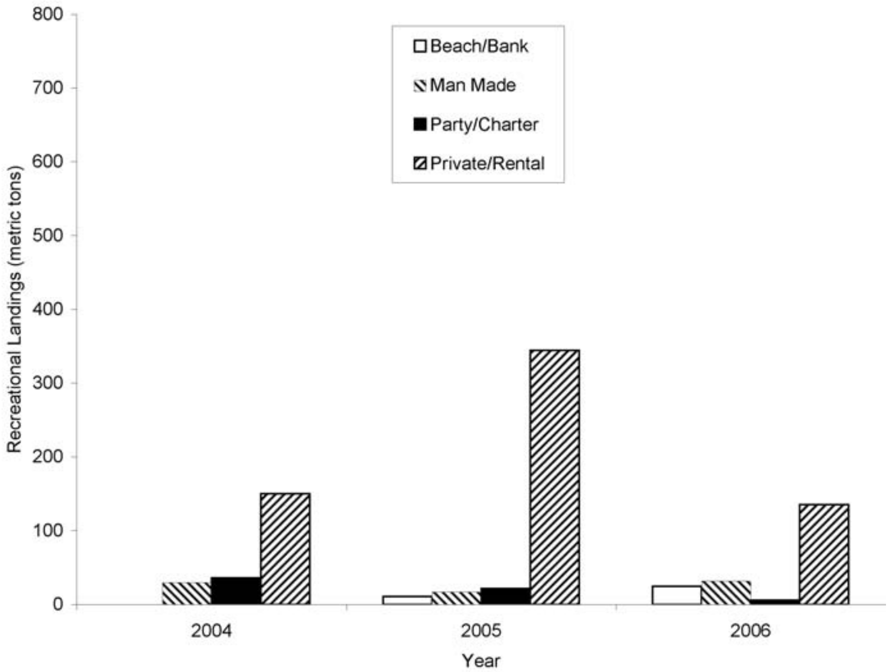

Figure 13. Recreational landings of California halibut (*Paralichthys californicus*) as reported in the California Recreational Fisheries Survey (CRFS), by four different fishing modes, 2004–06.

Southern California ports received almost 100% of the halibut caught in 2006. A series of depth restrictions in recent years along the central California coast has greatly affected the gill net fleet, which is evident by the lack of landings made north of Point Arguello since 2002.

Annual landings reported by the hook and line fleet have been relatively stable over the past decade (fig. 11). Hook and line landings by the top three port complexes were San Francisco (39%), Santa Barbara (27%), and Los Angeles (17%).

The recreational take of halibut, as reported in the Recreational Fisheries Information Network (RecFIN), from the Marine Recreational Fisheries Statistical Survey (MRFSS), showed a strong increase in fish landed from 1997 to 2003 (fig. 12). Anglers fishing from private and rental boats landed, on average, 84% of all the halibut during this time period. In 2004, the California Recreational Fisheries Survey (CRFS) replaced the MRFSS. Recreational catch estimates obtained from RecFIN show that anglers fishing from the shore modes, party/charter modes, and private/rental modes caught 197 t of halibut statewide in 2006, a 50% decrease from 2005 (fig. 13). CRFS data also show private/rental vessels catch the majority of the recreationally caught halibut.

Since the MRFSS and CRFS survey methods are not comparable, historical trends (spanning the last ten years) for the recreational catch of halibut can be determined by Commercial Passenger Fishing Vessel (CPFV) logbook data. CPFV logbook data provide a direct census of the recreational catch by anglers fishing from CPFVs (party/charter mode). Reported landings from 1997 to 2003 were fairly stable with a peak of 21,000 fish (83 t) in 2001. However, in 2004 a 62% decrease from the previous year occurred and the catch remained low throughout the next two years. Estimated weights, provided by RecFIN, were applied to the logbook landings (numbers of fish) to obtain metric tons.

***2006 Halibut Fishery Management Highlights.*** Beginning in 2000, a series of gill net depth restrictions were implemented in state waters less than 60 fathoms, from Point Reyes (Marin County) to Yankee Point (Monterey County) and from Point Sal (Santa Barbara County) to Point Arguello (Santa Barbara County). By 2002, the gaps between these areas were also closed and gill nets were not allowed in waters less than 60 fathoms between Point Reyes to Point Argeullo. These regulations were implemented to protect sea otters, common murres, and other marine life. These closures complement the 1994 southern California prohibition on gill net gear, within state waters, from Point Arguello to the U.S./Mexican border.

A new bottom trawl regulation implemented in 2005 closed small portions of the California halibut trawl grounds located between Point Arguello (Santa Barbara County) and Point Mugu (Ventura County) in state waters. A limited entry halibut trawl permit was implemented in 2006. The permit is required for bottom trawling within the designated halibut trawl grounds in state waters. Additionally, the permit is required for landings of halibut in excess of 331 kg (150 lb) that were

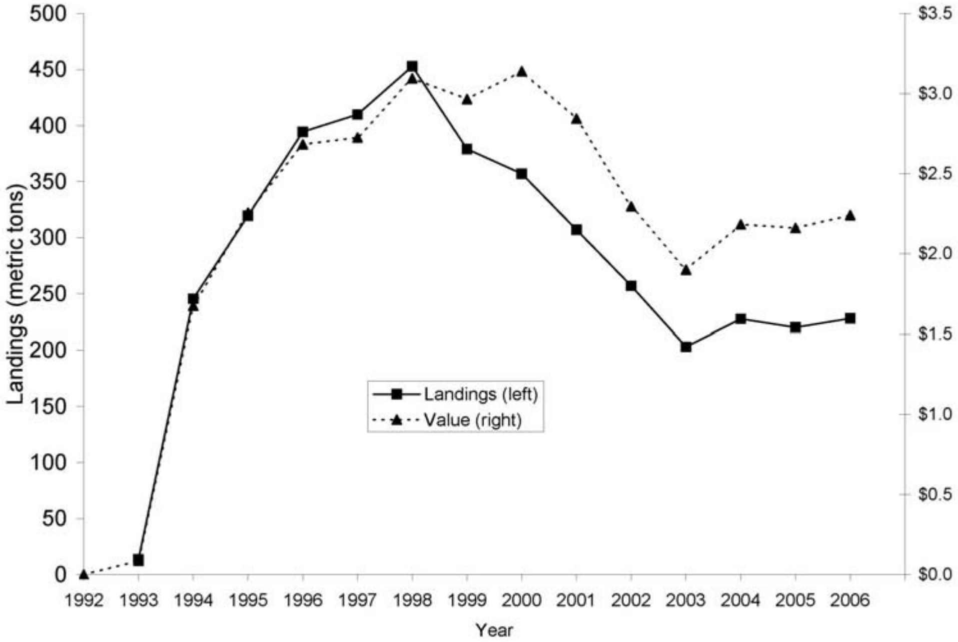

Figure 14. California nearshore live-fish landings in metric tons (left) and ex-vessel value (right), 1993–2006.

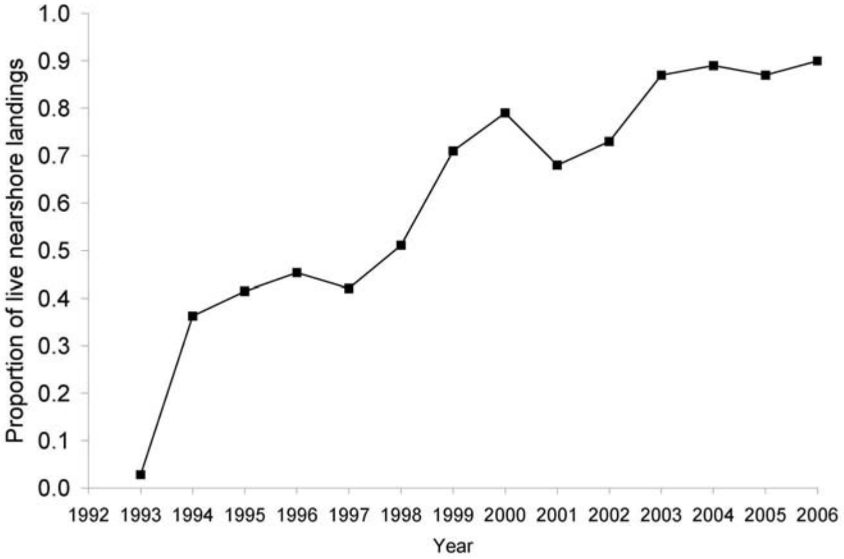

Figure 15. Proportion of fish landed live in the nearshore live fishery, 1993–2006.

caught in federal waters. A total of 60 permits were issued in 2006, and of these, 40 were active.

## Nearshore Live-Fishes

In 2006, statewide commercial landings of nearshore live finfish totaled approximately 228 t (fig. 14). Of that, a total of 206 t (90%) (fig. 15) were recorded as live landed fishes and 22 t or 10% were recorded as dead landed. The 2006 landings were 10% less than 2005 landings (254 t). The total ex-vessel value for the 2006 landings was $2.24 million, of which $2.18 million was paid for live fish (fig. 14). This represents a slight decrease in the total 2005 ex-vessel value of $2.26 million, but a slight increase in the amount paid for live fish ($2.16 million).

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 multimillion-dollar industry by the early 1990s, reaching its peak in 1998 (fig. 14). Part of the reason for this boom was the

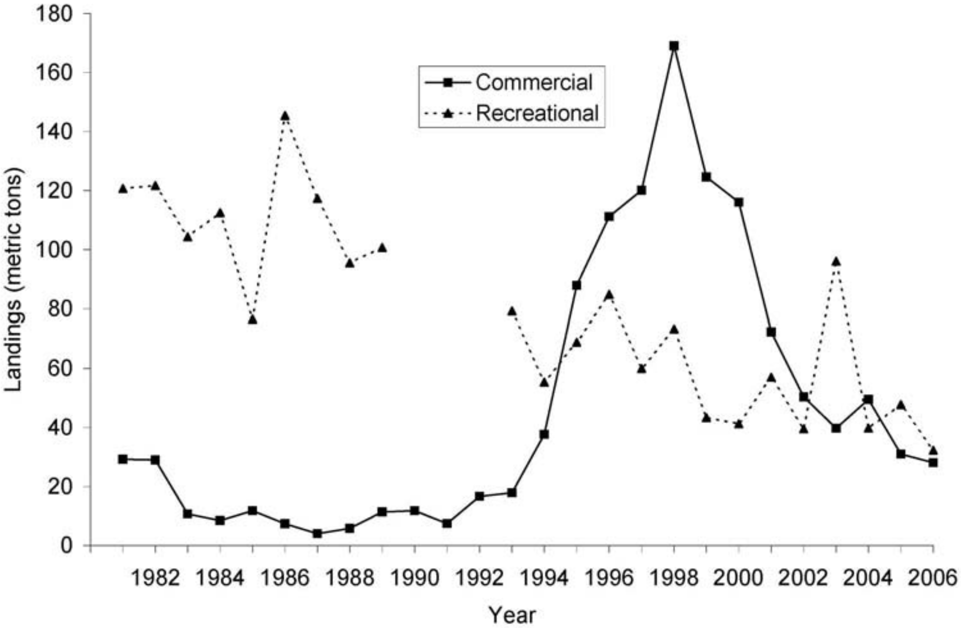

Figure 16. California commercial and recreational landings of cabezon (*Scorpaenichthys marmoratus*), 1981–2006. No recreational catch data are available for years 1990–92.

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 unit of weight paid to fishermen upon landing of catch) for live fish. In 2006, grass rockfish demanded the highest average price paid for a pound of live fish ($9.09 or $20.20/kg); whereas the highest average price paid for a pound of dead fish was $2.86 ($6.36/kg) (brown rockfish *Sebastes auriculatus*).

Black rockfish (*Sebastes melanops*) were landed in the greatest quantity (52 t), representing 25% of the total statewide nearshore live fish landings, the bulk of which were landed in the northern region of the state. In dollars, the top three species landed in the statewide live fishery for 2006 were grass rockfish ($0.38 million, 17.3%), California sheephead ($0.36 million, 16.6%), and cabezon ($0.34 million, 15.6%).

Hook and line and trap gear were the primary means to land nearshore fish species. Hook and line gear primarily consisted of rod and reel, vertical and horizontal longlines, and weighted stick gear. All hook and line gears combined landed 165 t of live nearshore fish. All trap gears combined landed 39 t of live nearshore fish. These two gear types accounted for 80% and 19% of the total nearshore live fish landed in 2006, respectively.

***2006 Nearshore Fishery Management Highlights.*** The nearshore fishery, as defined by California's Nearshore Fishery Management Plan (NFMP, adopted by the Commission in 2002), 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 eel (*Cebidichthys violaceus*), and the following rockfishes (*Sebastes* spp.): black (*S. melanops*), black-and-yellow (*S. chrysomelas*), blue (*S. mystinus*), brown (*S. auriculatus*), calico (*S. dallii*), China (*S. nebulosus*), copper (*S. caurinus*), gopher (*S. carnatus*), grass (*S. rastrelliger*), kelp (*S. atrovirens*), olive (*S. serranoides*), quillback (*S. maliger*), and treefish (*S. serriceps*). All except California sheephead, monkeyface prickleback, and rock greenling are designated as groundfish species under the PFMC's fishery management plan for Pacific coast groundfish.

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

In 2005, the first-ever gopher rockfish stock assessment was completed and the assessment results indicated the stock was healthy. Because of these findings, the harvest target was increased for the shallower, nearshore rockfish species south of Cape Mendocino (40°10'). This addition begins in 2007 and 2008 and does not affect data presented for 2006.

The first California scorpionfish stock assessment was completed in May 2005. The assessment indicated the stock was healthy. In addition, the stock assessment indicated that the recent removal rates were near to or

TABLE 4
**Annual commercial cabezon (*Scorpaenichthys marmoratus*) landings, ex-vessel value, and average unit price for years 1981–2006.**

| Average unit price for years 1981–2006 | Landings t | Ex-vessel value | Avg price/kg | Avg price/lb |
|---|---|---|---|---|
| 1981 | 29 | $ 10,551 | $ 0.34 | $0.16 |
| 1982 | 29 | $ 12,105 | $ 0.33 | $0.15 |
| 1983 | 11 | $ 5,060 | $ 0.33 | $0.15 |
| 1984 | 8 | $ 4,028 | $ 0.43 | $0.20 |
| 1985 | 12 | $ 6,473 | $ 0.46 | $0.21 |
| 1986 | 7 | $ 4,436 | $ 0.53 | $0.24 |
| 1987 | 4 | $ 2,777 | $ 0.72 | $0.33 |
| 1988 | 6 | $ 5,591 | $ 0.79 | $0.36 |
| 1989 | 11 | $ 9,910 | $ 0.84 | $0.38 |
| 1990 | 12 | $ 9,429 | $ 0.86 | $0.39 |
| 1991 | 7 | $ 13,602 | $ 1.23 | $0.56 |
| 1992 | 17 | $ 55,921 | $ 3.71 | $1.68 |
| 1993 | 18 | $ 123,860 | $ 6.40 | $2.90 |
| 1994 | 38 | $ 274,638 | $ 6.70 | $3.04 |
| 1995 | 88 | $ 665,879 | $ 6.75 | $3.06 |
| 1996 | 111 | $ 843,466 | $ 6.96 | $3.16 |
| 1997 | 120 | $ 860,486 | $ 6.48 | $2.94 |
| 1998 | 169 | $1,231,597 | $ 6.42 | $2.91 |
| 1999 | 125 | $1,014,731 | $ 7.40 | $3.35 |
| 2000 | 116 | $1,128,939 | $ 8.63 | $3.92 |
| 2001 | 72 | $ 718,146 | $ 8.97 | $4.07 |
| 2002 | 50 | $ 485,218 | $ 8.86 | $4.02 |
| 2003 | 40 | $ 416,652 | $ 9.13 | $4.14 |
| 2004 | 49 | $ 505,536 | $ 9.06 | $4.11 |
| 2005 | 31 | $ 343,124 | $10.04 | $4.55 |
| 2006 | 28 | $ 341,724 | $11.10 | $5.03 |
| Average | 46 | $ 349,765 | $ 4.75 | $2.15 |

below the fishing mortality rate for maximizing catch biomass. In 2006, the Pacific Fisheries Management Council set a separate optimum yield for the California scorpionfish based on the 2005 assessment results.

## Cabezon

Cabezon (*Scorpaenichthys marmoratus*) is one of the 19 species of nearshore finfish as defined by California's NFMP discussed in the nearshore live fishery section. Historically, the vast majority of cabezon caught in California have been by recreational fishers. Recently, however, commercial landings increased, and by 1995 commercially-landed cabezon (88 t) exceeded the statewide catch by sport anglers (69 t) for the first time (fig. 16). The commercial fishery peaked over the period 1995 through 2002, reaching a high of 169 t in 1998 with an overall average of 106 t for those years. This sharp increase in commercial landings can be attributed to the advent of the nearshore live fishery beginning in the mid 1980s.

Accordingly, average unit price per pound for cabezon has increased from $0.56 (1.24/kg) in 1991 to $5.03 (11.10/kg) in 2006 (tab. 4), and unit prices have been recorded as high as $10/lb ($22.02/kg) to $12/lb ($26.67/kg) most recently. Cabezon are one of the top four live-caught species groups in price per pound over the last five years, ranking only behind greenlings, rockfish, and flatfish.

Commercial cabezon catch has leveled off in the last few years, at least partially due to tighter regulations, but total catches have not dropped back to the lower catch amounts typical of the fishery prior to the emergence of the live fish market. However, commercial landings of cabezon have dropped below that of sport catch for the past three or four years. Preliminary 2006 commercial landings of cabezon totaled 28 t (ex-vessel value $341,724). Of the total commercial catch taken in 2006, 24 t (87%) were brought to market in a live condition. The primary gear types used to land cabezon are hook and line and trap. From 2001 through 2006, 172 t of cabezon were landed using hook and line gear and 97 t were landed using trap gear. For 2006, hook and line gear produced 23 t with trap gear generating 5 t. Although other gear types, such as trawl and miscellaneous net gear, were used to land cabezon over this period, their contribution to the overall catch was negligible.

Recreational landings data are available from 1980 to 2006 for CPFV and private boat anglers as well as from shore (beach/bank) and pier/jetty (man-made) anglers. Over this period, recreational total landings for cabezon peaked in 1986 but generally declined since then, with the exception of a smaller peak in 2003 (fig. 16). Statewide landings for 2006 amounted to 32 t for cabezon, a decrease of 33% from 2005 (48 t). For both 2005 and 2006, approximately 90% of sport-caught cabezon came from northern California (north of Point Conception).

Private boat fishermen continually take the majority of sport-caught cabezon in California. Over the 25-year period 1981–2006, the average annual catch for the private boat fishery was 34,279 fish, compared to 20,145 and 5,230 fish for beach/bank and man-made modes of fishing, respectively. The number of cabezon landed by private boaters peaked in 1984 at 55,445 fish and the lowest annual catch for this group was 9,841 fish landed in 2006.

Cabezon are prized by sport divers for their edibility, size, and ease of capture. Their significant numbers in shallow, inshore waters make them a popular target for free divers, in addition to those using scuba. Data collected at central California free diving spearfish competitions from 1958 through 2003 indicate that 2,988 cabezon were taken, ranking it the eighth most frequently captured species out of 52 species landed total. Locations of competitions ranged from San Luis Obispo County in central California to Mendocino County in northern California.

At present, CPFVs generally do not target cabezon and thus take a small amount of them compared to the total sport catch. Estimates from RecFIN data show that

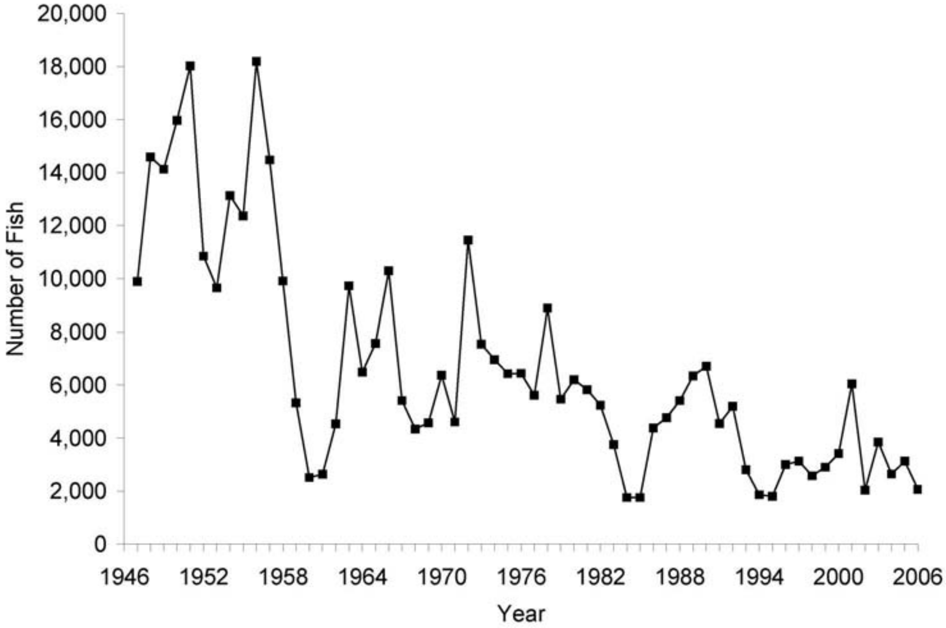

Figure 17. California commercial passenger fishing vessel (CPFV) cabezon (*Scorpaenichthys marmoratus*) catch (number of fish), 1947–2006.

in recent years the number of CPFV-landed cabezon have contributed less than 10% to the total annual sport catch for this species. With the exception of CPFVs, there is little statewide historical data for cabezon prior to 1980 available for other modes of fishing. Consistent CPFV data collected from logbooks are available starting from 1947 and show that landings of cabezon have, at times, been much more significant than they have been since the 1980s. Statewide CPFV landings of cabezon surpassed 10,000 annual fish eleven times prior to 1960, but only twice since then, and not once since 1972 (fig. 17). This trend, prior to significant sport take regulations enacted beginning in 1999, may reflect a fishery on the decline. A total of 2,069 cabezon were landed on CPFVs statewide in 2006, a 34% decrease from 2005.

***2006 Cabezon Fishery Management Highlights.*** The most recent California stock assessment on cabezon was completed in 2005. For this assessment cabezon were treated as different northern and southern California substocks based on differences in total removals, ecology, and current management needs. Point Conception was used as the delineation line between the two regions. Reproductive output of the cabezon resource off northern California was estimated to be about 40% of the unfished stock indicating a healthy fishery. Southern California's stock was estimated to be at about 28% of the unfished level, but due to greater uncertainty in the assessment for the southern population, no absolute conclusions could be drawn. Both estimates are above the estimated 25% unfished biomass level under which a fishery is defined as "overfished" by NMFS.

Under state management by the Commission, the cabezon is managed as a separate harvest group with specific regulations. The total allowable catch (TAC) for cabezon in 2006 was 69.0 t (152,100 lbs), of which the commercial fishery was allocated 26.9 t (59,300 lbs) and the recreational fishery was allocated 42.1 t (92,800 lbs). In past years the commercial cabezon fishery closed early due to projected catch exceeding the TAC. To avoid this, a mid-season reduction in trip limit amounts was adopted for September through October 2006. The change reduced the 2-month allotment from 408 to 90 kg (900 lbs to 200 lbs) total take per license holder. Accordingly, the commercial cabezon fishery was allowed to remain open through the end of the year. Recreational bottom-fishing seasons and/or depth restrictions were relaxed to some extent for all regions in California in 2006, allowing for increased fishing opportunity. There was no change in the 1-fish bag limit and 38.1 cm (15-in.) minimum size limit for cabezon for sport anglers.

### Surfperches

Historically, commercial landings of fish in the family Embiotocidae (surfperches) have been of minor importance compared to the recreational catch. In 2006, of the estimated 292 t of surfperch landed in California, 95% (276 t) was recreational and 5% (16 t) was commercial (fig. 18). Recreational landings are typically reported in numbers of fish and have been converted to weight (based on length-weight relationships and length-frequency distributions of sampled fish) for comparison.

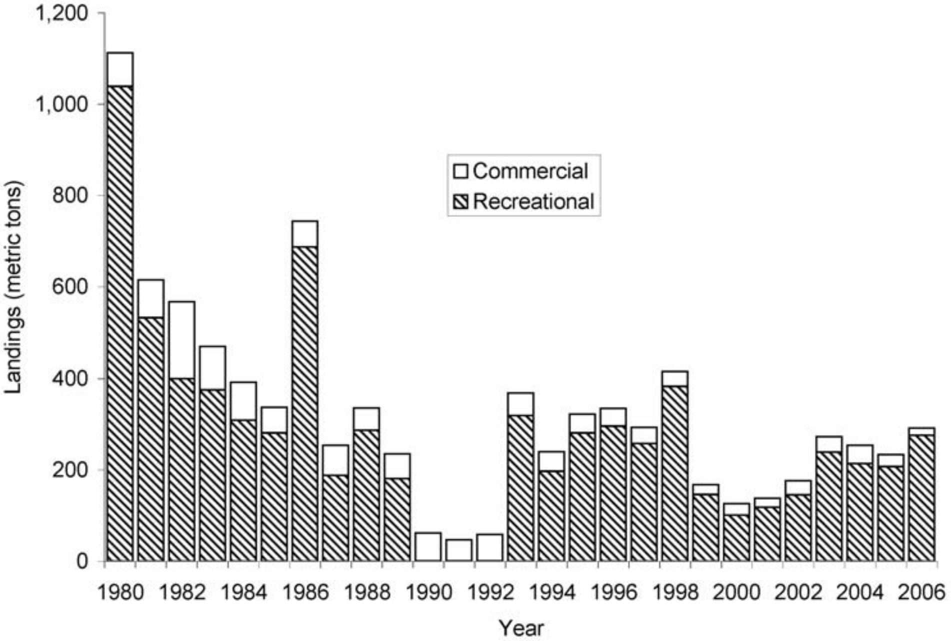

Figure 18. California commercial and recreational landings of surfperch in metric tons, 1980-2006. No recreational data were available for 1990–92.

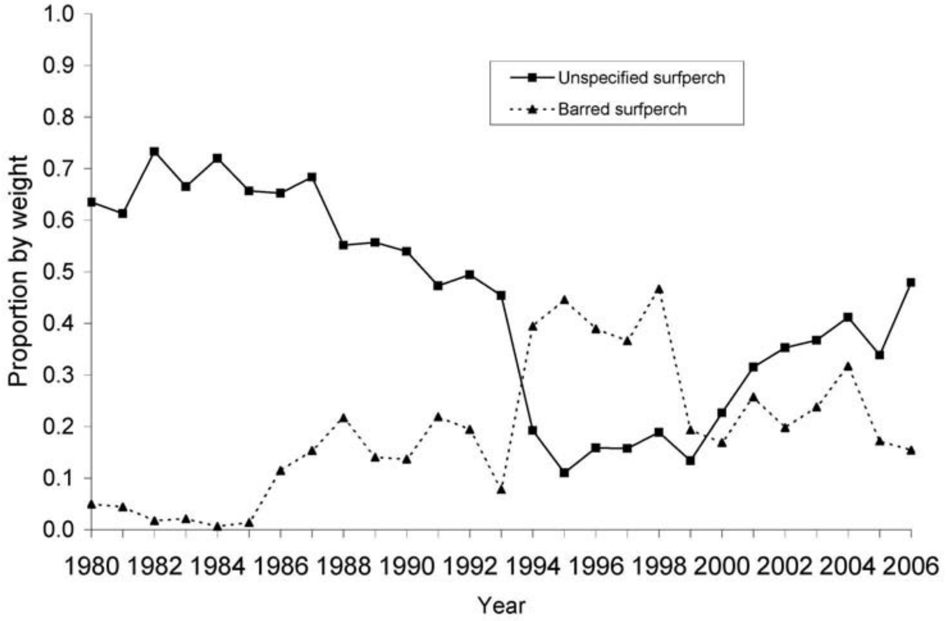

Figure 19. Historical commercial landings of unspecified surfperch compared to barred surfperch in California, 1980–2006.

In 2006, commercial surfperch fisheries accounted for only 0.01% of all commercial landings by weight. An estimated 16 t of surfperch were landed in 2006, a decrease of 38% from 2005. Barred surfperch and redtail surfperch accounted for nearly all the landings in which species were identified. An "unspecified surfperch" market category is used occasionally by dealers, and species composition is unknown. Over 99% of the 2.5 t of barred surfperch caught during 2006 in California were landed in the Santa Barbara and Morro Bay port areas. Barred surfperch landings statewide decreased by 50% from those in 2005. In 2006, 99% of the 6 t of redtail surfperch were landed in the Eureka port area. Historically, redtail surfperch landings have comprised more than 98% of all surfperch landings in Eureka. Landings of redtail surfperch decreased by 47% in this area compared with 2005.

Unspecified surfperch comprised 48% of the commercial landings by weight in 2006 and 34% in 2005.

TABLE 5
**Estimated number (in thousands) of surfperches caught in California marine recreational fisheries, 1996–2006.**

| | North of Point Conception | | South of Point Conception | |
|---|---|---|---|---|
| | No. | % | No. | % |
| Barred surfperch | 1,653 | 30 | 1,929 | 47 |
| Black perch | 273 | 5 | 586 | 14 |
| Calico surfperch | 109 | 2 | 20 | – |
| Pile perch | 107 | 2 | 51 | 1 |
| Rainbow seaperch | 86 | 2 | 7 | – |
| Redtail surfperch | 217 | 4 | 0 | – |
| Rubberlip seaperch | 132 | 2 | 61 | 1 |
| Shiner perch | 990 | 18 | 315 | 8 |
| Silver surfperch | 303 | 5 | 42 | 1 |
| Striped seaperch | 533 | 10 | 8 | – |
| Walleye surfperch | 626 | 11 | 773 | 19 |
| White seaperch | 123 | 2 | 123 | 3 |
| Other surfperches | 398 | 7 | 199 | 5 |
| All surfperches | 5,550 | 100 | 4,114 | 100 |

The majority of the unspecified surfperch was landed in San Francisco and Santa Barbara area ports. The past few decades have shown fluctuations in unspecified surfperch landings which appear to be inversely proportional to reported barred surfperch landings (fig 19); this may be indicative of the species composition of the unspecified market category, although landings were not sampled. In 1994, new landing receipts, with more specific market categories listed, were issued to buyers in an attempt to reduce the amount of landings reported as unspecified. This seemed to be effective at first, although recent landings are again being reported as unspecified. The average ex-vessel price for surfperch over the past 10 years has increased by 39% from $0.60/kg ($0.27/lb) in 1996 to $0.98/kg (0.44/lb) in 2006.

The primary gear used to catch surfperch is hook and line, which accounts for over 90% of the commercial landings. Much of the hook and line fishing occurs from shore. Other gears used include brail nets, fish traps, and longlines.

According to the 2006 commercial fishing statutes and regulations, the commercial surfperch fishery is closed from 1 May to 31 July, with the exception of the shiner perch fishery which is open year-round. It is illegal to take barred, redtail, and calico surfperches south of Point Arguello for commercial purposes.

Based on estimates from CRFS, nearly 10%, by number, of finfish caught statewide by recreational anglers in 2005 and 2006 were surfperch. The total surfperch harvest was approximately 1.1 million fish in 2005 and 1.3 million fish in 2006. By weight, in 2006 the total recreational catch of surfperch increased nearly 8% from that in 2005. Surfperch composed nearly 6% of the total recreational catch of finfish by weight for 2006 as compared to 5% in 2005.

The top surfperch species caught recreationally differed in central/northern California from that caught in southern California (Point Conception south to Mexican border) (tab. 5). Barred surfperch (*Amphistichus argenteus*) catch was substantial in both regions, but more so in southern California where it made up, on average, 47% of all surfperch from 1996 to 2006. Walleye surfperch (*Hyperprosopon argenteum*) and black perch (*Embiotoca jacksoni*) also contributed significantly to the catch in southern California, averaging 19% and 14%, respectively, of the total. There were more species taken in significant numbers (i.e., at least 5% of the catch) in central/northern California; in addition to barred surfperch (30%) and walleye surfperch (11%), the catch included 18% shiner perch (*Cymatogaster aggregata*) and 10% striped seaperch (*Embiotoca lateralis*) by number. A significant improvement in estimating recreationally-caught finfishes in California occurred in 2004 with the establishment of the CRFS program. While the actual catch estimates from MRFSS are not comparable to CRFS, the species composition data are reliable.

## Leopard Shark

The leopard shark (*Triakis semifasciata*) is a member of the Triakidae (houndshark) family, distinguished by its grey body covered in black saddlebars and spots. This species occurs from Oregon to Mazatlan, México, including the Gulf of California. It is common in nearshore waters, bays, and estuaries throughout California. Sexual maturity is reached at 7 to 15 years, and development is viviparous, with litters of 7 to 36 pups. Leopard sharks are targeted by small-scale commercial hook and line fisheries, recreational anglers, and marine aquaria collectors.

Leopard sharks are one of six elasmobranch species under the management authority of the PFMC Groundfish Fishery Management Plan (Groundfish FMP). Although this species is defined as a groundfish, harvest of leopard shark is not actively managed under the Groundfish FMP. However, the State of California has management measures in place, such as size and bag limits, to protect the leopard shark resource.

From 1991 to 2006, California commercial landings ranged from a high of 24 t in 1993 to a low of 6 t in 1996, averaging 12 t annually over the past 15 years. Reported landings totaled 9 t in 2006, compared to 11 t in 2005. However, the ex-vessel value increased from $1.74/kg ($0.78/lb) in 2005 to $2.27/kg ($1.02/lb) in 2006. Gill net gear contributed the majority of landed catch at 56% in 2006; hook and line gear contributed 33% of landings; while trawl gear contributed 11%. Most of the 2006 catch south of San Francisco was taken by gill net gear targeting halibut, while much of the catch from San Francisco north occurred in hook and line

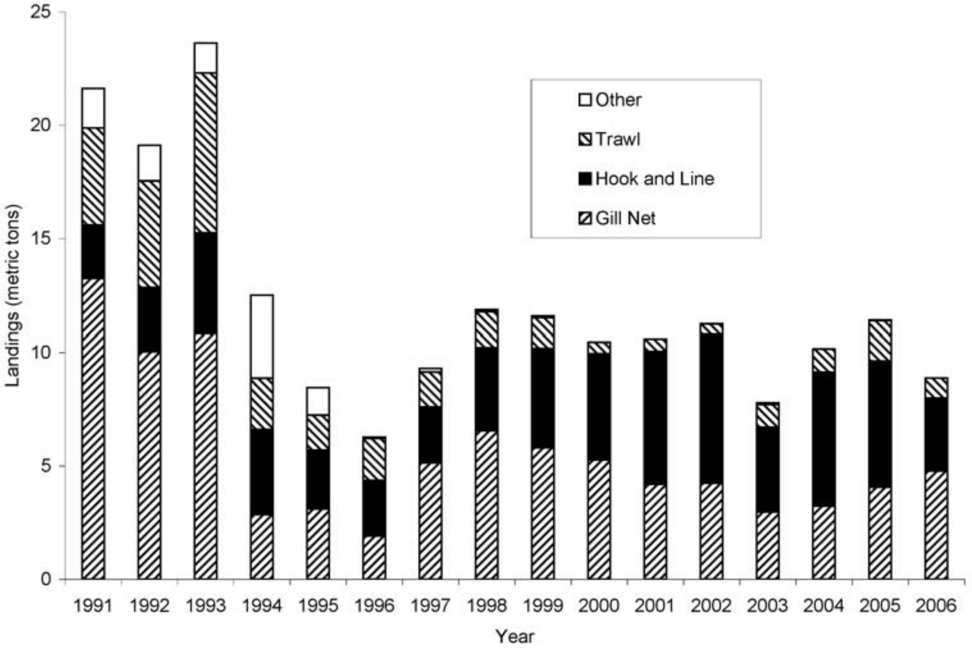

Figure 20. California commercial landings of leopard shark (*Triakis semifasciata*) by gear type, 1991–2006.

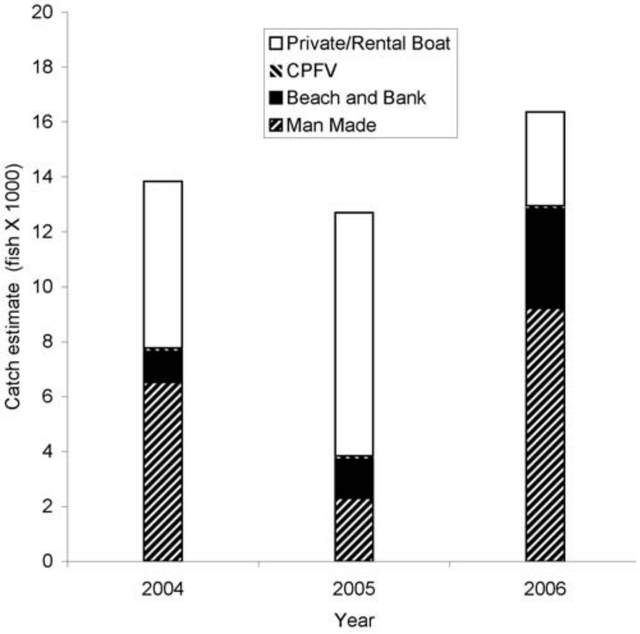

Figure 21. California recreational landings of leopard shark (*Triakis semifasciata*) as reported from CRFS, 2004–06.

fisheries targeting nearshore groundfish and flatfish trawl fisheries. It should be noted, however, that leopard shark landings are subject to reporting bias, since an unknown number are lumped with other shark species in the "shark, unspecified" market category on commercial landing receipts.

In 1994, the introduction of a minimum commercial size limit of 91 cm (36 in) TL and the exclusion of gill net gear in State waters south of Point Arguello resulted in a dramatic drop in commercial landings (fig. 20), but landings have remained relatively stable since 1994. In 2002, the use of gill net gear was also prohibited from Point Reyes to Point Arguello in 110 m (60 fathoms) of water or less, which appears to have further stabilized gill net landings.

Recreational catches for leopard shark are greater than commercial landings. Most sport-caught leopard sharks are taken using baited hooks, although some are also taken by divers using spears and by fishers using bow and arrow. A recreational size limit of 91 cm (36 in) TL and a three-fish daily bag limit have been in effect since 1992. Beginning in 2005, recreational groundfish closures and depth restrictions were applied to all federally managed groundfish to allow overfished stocks to rebuild. However, exceptions were incorporated into the regulations that allowed the take of leopard sharks during groundfish closures within specified enclosed bays.

Catch estimates (CRFS) indicate that from 2004 to 2006 (fig. 21), an average of 14,300 fish (65 t) were taken annually. In 2006, an estimated 16,400 fish were taken. This is 15% above the three-year average, and 25% above the 2005 catch, estimated at 12,700 fish. The CRFS data also indicate that private boaters land the majority (53%) of leopard sharks in the recreational fishery, followed by shore-based anglers (46%) and CPFVs (1%). Catch estimates (MRFSS) from 1993 through 2003 show a similar pattern (fig. 22). These surveys indicate anglers fishing from San Francisco to Eureka catch a majority of the leopard sharks in bays, while anglers fishing

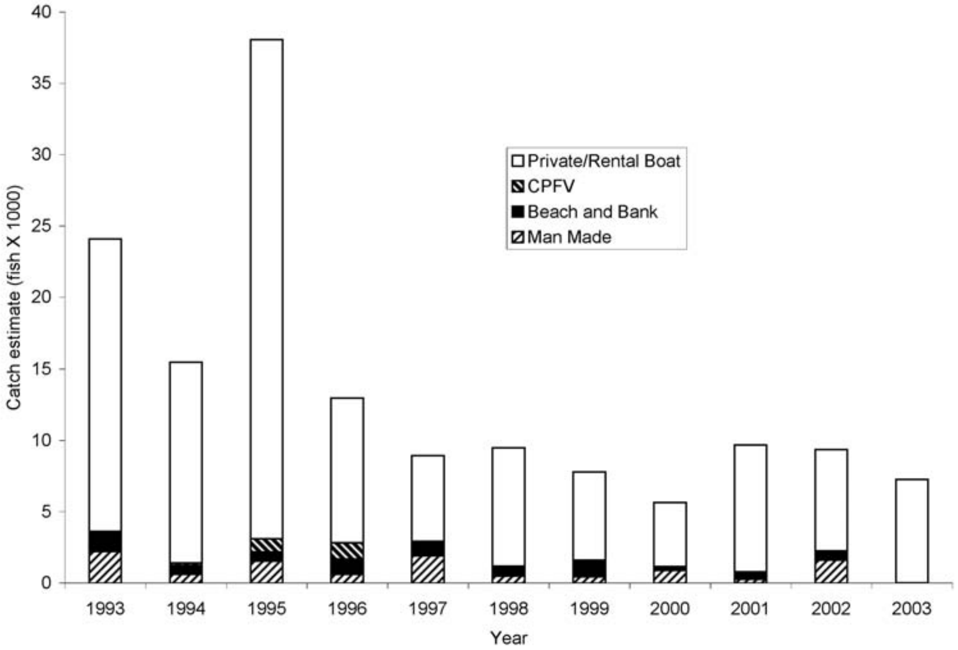

Figure 22. California recreational landings of leopard shark (*Triakis semifasciata*) as reported from MRFSS, 1993–2003.

south of San Francisco catch leopard sharks in nearshore coastal waters.

Marine aquaria collectors target leopard shark pups due to their desirability as aquarium fish. Collecting pups for marine aquaria display became illegal in 1994, when the size limit went into effect. However, a black market for pups continues today. In 2006, a three-year investigation involving the CDFG, NMFS, U.S. Fish and Wildlife Service, as well as investigators in the United Kingdom, Netherlands, and elsewhere resulted in the arrest and prosecution of six individuals charged with violating the Lacey Act. The Lacey Act is the Federal law that prohibits the possession, take, purchase, or sale of any wildlife taken in violation of any state or federal regulation. Investigators estimate that from 1992 to 2004, 20–25,000 leopard shark pups were poached from San Francisco Bay by the two groups investigated, and from 1992 to 2003, 30–33,000 pups were poached by various groups along the Los Angeles, Ventura, and Santa Barbara County coasts. These estimates are significant when compared to recreational and commercial leopard shark landings. However, the recent convictions appear to have resulted in curtailment of most of the large-scale illegal take of leopard shark pups.

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# THE STATE OF THE CALIFORNIA CURRENT, 2006–2007: REGIONAL AND LOCAL PROCESSES DOMINATE

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## ABSTRACT

The state of the California Current System (CCS) between Oregon and Baja California is summarized in this report, covering spring 2006 to spring 2007. Observations reported here are based on contributions from various ocean observing programs along the West Coast of North America. Basin-scale indicators were variable or neutral over the last year. This indeterminate forcing was reflected in conditions in the CCS where no coherent patterns emerged, i.e., no single "state" could be ascribed to the system. Rather, regional or local processes dominated observed patterns. Similar to last year, delayed upwelling off Oregon and central California dramatically affected higher trophic levels: euphausiid recruitment was delayed and as a likely consequence seabird productivity off Central California was extremely depressed. For example, Cassin's auklet had a complete reproductive failure, similar to 2006. Observations during the spring of 2007 demonstrate that these patterns were ephemeral since upwelling was normal and seabird productivity improved. Off southern and Baja California, upwelling-favorable winds were also weak or delayed during 2006, but biological consequences appear to have been relatively minor.

## INTRODUCTION

This report summarizes the climatology, oceanography, and biology of the California Current System (CCS) between the spring of 2006 and the summer of 2007. It is based on observations taken between Oregon and Baja California (fig. 1A). Participating programs or institutions include the Pacific Fisheries Environmental Laboratory (PFEL) providing basin- and coast-wide climatologies, the NOAA/Stock Assessment Improvement Program working off Oregon, the Point Reyes Bird Observatory (PRBO) studying seabirds off central and southern California, the CalCOFI program working off southern California, and the Investigaciones Mexicanas de la Corriente de California program (IMECOCAL) working off Baja California. The objective of this report is to describe the state of the CCS over the last year, to compare this to long-term conditions, and to relate changes of the state of the ecosystem to forcing by climate.

Over the last decade the CCS has experienced dramatic changes. The system entered a cool phase after the El Niño of 1997–98 (Hayward et al. 1999). This cool state was reflected by strong negative values of the Pacific Decadal Oscillation (PDO, fig. 2) and by negative sea surface temperature (SST) anomalies throughout the CCS. Off Oregon and southern California, the transition into a cold regime was accompanied by dramatic changes in zooplankton biomass and community structure (Brinton and Townsend 2003; Lavaniegos and Ohman 2003; Peterson and Schwing 2003). However, concentrations of chlorophyll *a* (Chl *a*), a proxy for phytoplankton biomass, did not respond significantly to this change from a warm to a cool phase.

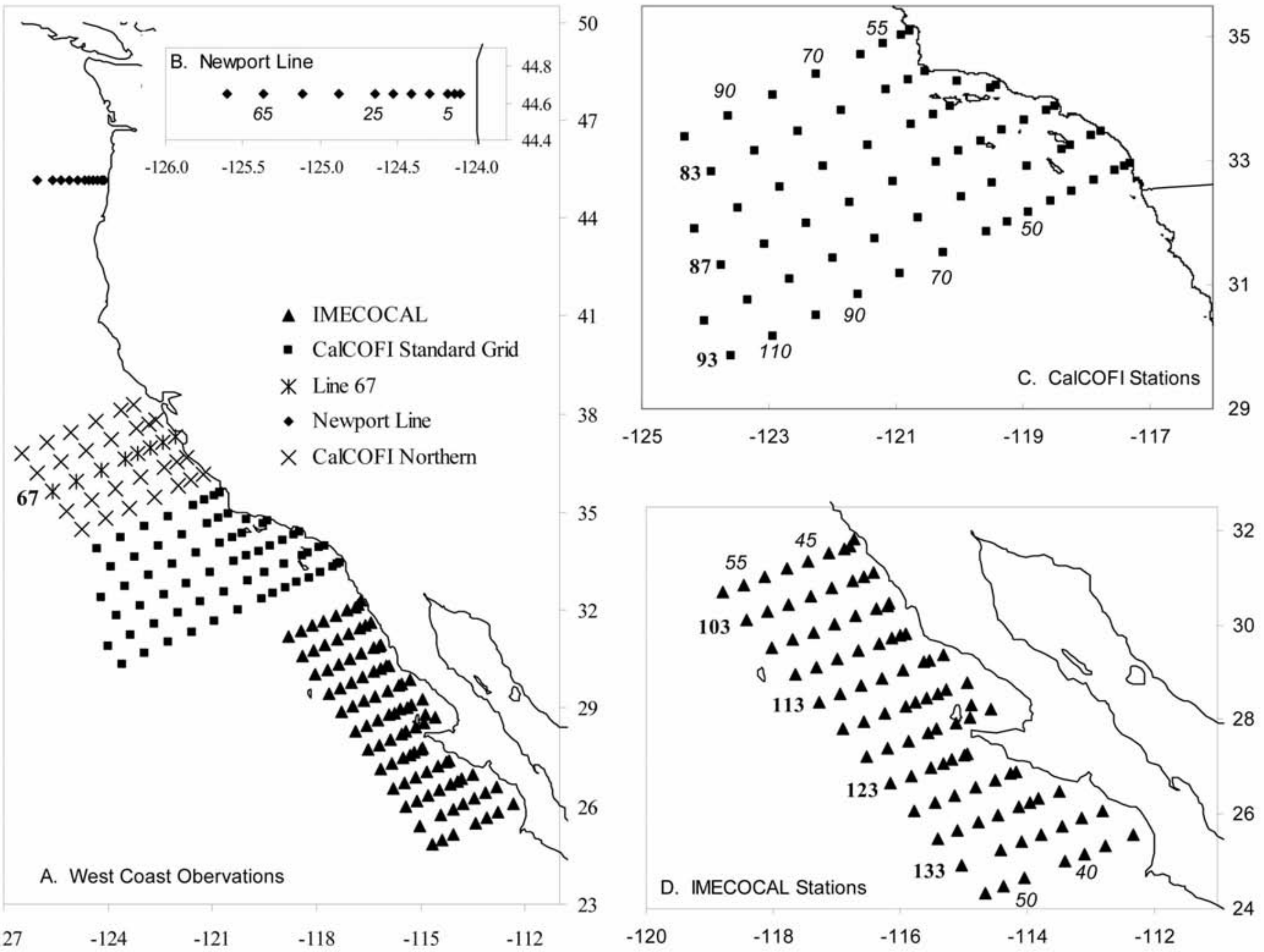

Figure 1. Location of stations where observations were made for this year's report. Observational lines are labeled using bold numbers positioned west of the line terminus; stations are labeled using numbers in italics immediately below or above the respective stations. Line and station numbers for the IMECOCAL and CalCOFI programs are following the CalCOFI line and station nomenclature. The IMECOCAL program covers all lines out to stations 60, i.e., the westernmost station on any IMECOCAL line is 60. The CalCOFI program covers lines 93 and 90 out to station 120, lines 87 and 83 to stations 110, and lines 80 and 77 to lines 100. 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 station 25 and occasionally further offshore.

This cool phase lasted for about three years (Goericke et al. 2004). In 2002–03 a weak El Niño developed in the equatorial Pacific and the PDO became positive. Off Oregon SST anomalies also became positive, and off southern California SSTs increased. This switch of the PDO was not accompanied by any dramatic changes of zooplankton biomass or indicators of zooplankton community structure. Seabird communities, however, showed a shift from temperate-cold species to subtropical species. Central California male sea lion activity patterns responded to the warmer water, concurrent with geographic shifts in prey distribution (Brodeur et al. 2006). Chlorophyll *a* off southern California was not affected by this change. Off Oregon, summertime chlorophyll *a* has been variable but has not changed systematically over the last decade. Thus, these time series showed no responses to the positive PDO in 2002.

Over the last four years, PDO signals have varied little (fig. 2). Significant events during the last four years were often driven by regional or local factors. The intrusion of subarctic surface waters into the CCS (Venrick et al. 2003) significantly affected concentrations of nutrients and chlorophyll *a* off Oregon. Off southern California the salinity anomalies were strong but confined only to the upper 200 m. These were accompanied by unusually low concentrations of silicic acid, which may have affected the growth of diatoms (Goericke et al. 2005). Off Baja California a pronounced negative salinity anomaly was observed but no other effects were

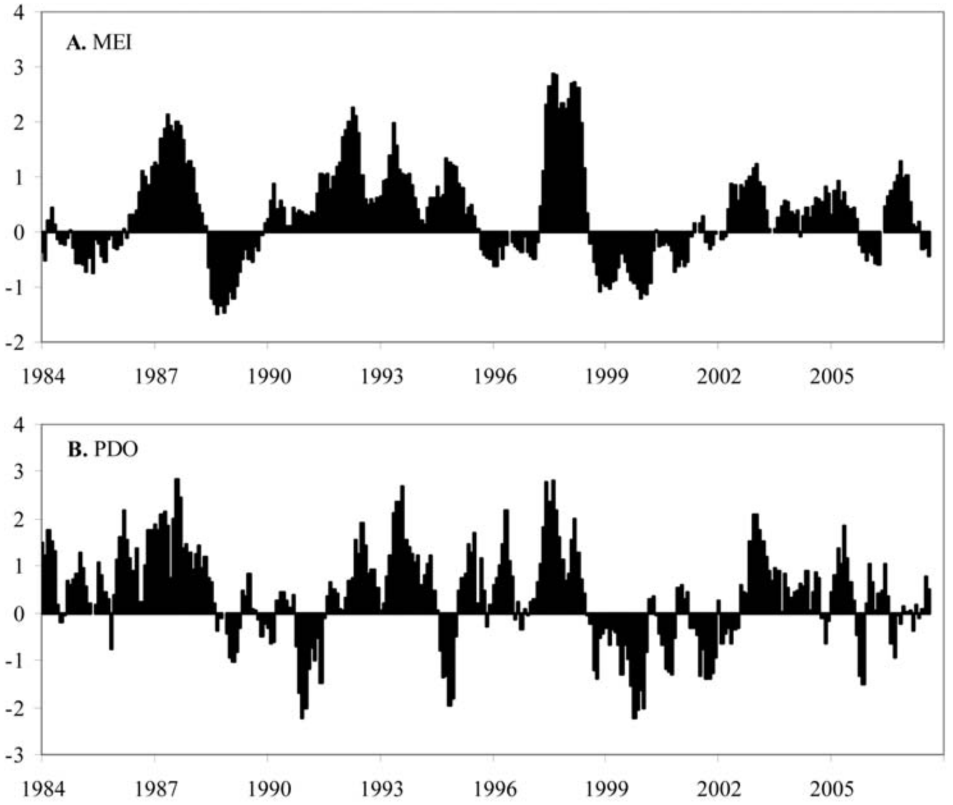

Figure 2. Time series of (A) the Multivariate ENSO Index (MEI, http://www.cdc.noaa.gov/people/klaus.wolter/MEI/) and (B) the Pacific Decadal Oscillation (PDO, http://jisao.washington.edu/pdo/PDO.latest) for the time period 1984 to August 2007.

reported. Upwelling off Oregon has been variable over the last four years, possibly affected by the position of the Jet Stream (Peterson et al. 2006). A delayed onset of upwelling in 2005 was accompanied by low abundances of euphausiids off Oregon and central California. The absence of these key prey species may have led to the unprecedented failure of Cassin's Auklet (*Ptychoramphus aleuticus*) recruitment at the Farallon Island colony in central California (Sydeman et al. 2006).

## DATA SETS AND METHODS

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 1968–96. Monthly upwelling indices and their anomalies for the North American West Coast (21°–52°N) are calculated relative to 1948–67. 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.

### Regional Analyses–Oregon

Regular sampling of the Newport Hydrographic (NH) line along 44.65°N (fig. 1A) continues on a biweekly basis along the inner portions of the line, at 7 stations, ranging from 1 to 25 nautical miles from shore. Methods and measurements are the same as listed in last year's report (Peterson et al. 2006).

Since 1998, pelagic forage and predatory fish have been sampled every ten nights from mid-April through mid-July. Four stations are occupied along each of two transects off the Columbia River and southern Washington. At each station, a 30 minute pelagic rope trawl is towed between the surface and 20 m. Additional details may be found in last year's report.

### Regional Analyses–Central California

CTD sections extending offshore off Monterey Bay to a distance of 315 km (CalCOFI Line 67, fig. 1B) have been carried out on a regular basis since 1997. CTD station spacing is 10 n. miles and the water column is sampled to a depth of 1000 m.

### Regional Analyses–CalCOFI

The CalCOFI program continues to occupy 66 standard stations (fig. 1C) on a quarterly basis. Results from

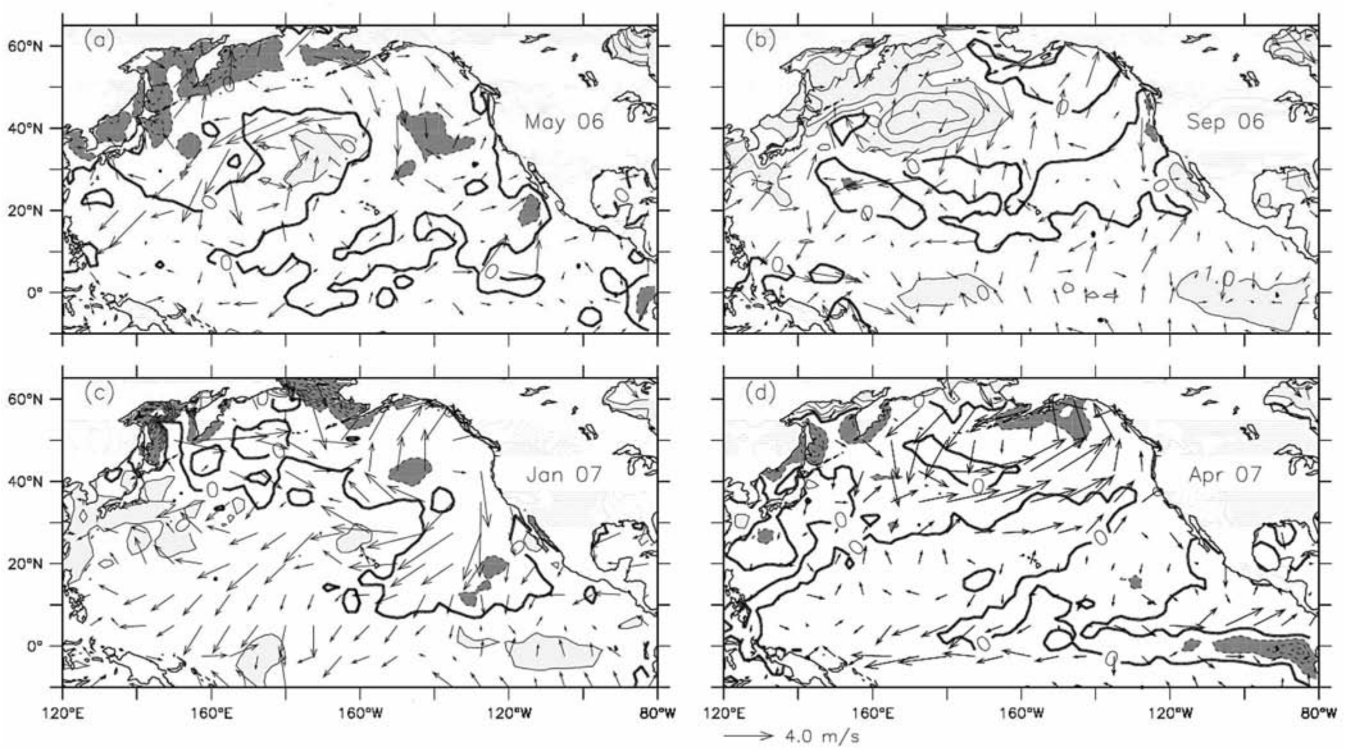

Figure 3. Anomalies of surface wind velocity and sea surface temperature (SST) in the north Pacific Ocean, for (A) May 2006, (B) September 2007, (C) January 2007, and (D) April 2007. Arrows denote magnitude and direction of wind anomaly. Contours denote SST anomaly. Contour interval is 1.0°C. Negative (cool) SST anomalies are shaded. Wind climatology period is 1968–96. SST climatology period is 1950–79.

cruises in April, July, and November of 2006 and January 2007 are presented here. At each station, bottom depth permitting, water column properties (conductivity, temperature, pressure, oxygen, fluorescence, and light transmission) are continuously measured to a depth of ~ 525 m; salinity, dissolved oxygen, and nutrients are determined throughout the water column from 20 water samples; chlorophyll is determined from the top 14 bottles; and standard (505 µm mesh) oblique bongo tows are conducted to 210 m depth. Detailed descriptions of sampling and analytical protocols and data reports from past cruises are archived on the CalCOFI website (http://www.calcofi.org).

Results are presented as contour maps of properties and as time series of cruise averages over all 66 stations, or as anomalies with respect to the 1984–2006 time series. The mixed-layer (ML) depth is calculated using a density criterion and set either to 12 m or to the halfway point between those 2 sampling depths where the sigma-theta gradient first reaches values larger than 0.002 per m, whichever is larger. The 12 m cutoff avoids including the diurnal thermocline in the analysis. This procedure will introduce a positive bias in calculating the ML depth, but, because the bias is consistent, it will not affect the interpretation of patterns. The nitracline depth is defined as the depth where concentrations of nitrate reach values of 1 µM, calculated from measurements at discrete depths using linear interpolation. Anomalies are based on the period 1984–present. Two hundred meter anomalies are based on data from all offshore stations (numbers 60 and higher). Mesozooplankton displacement volumes were reprocessed for this year's analysis. Previously, untransformed values were averaged and plotted, at times on a log scale. For this year's analysis, displacement volumes for individual stations were log-transformed and then averaged over all stations. Individual data points are different, but major seasonal and interannual features are unchanged.

## Regional Analyses–IMECOCAL

The IMECOCAL monitoring program began in autumn 1997, consisting of quarterly cruises surveying 93 stations off Baja California, México (fig. 1D). The core oceanographic data set collected at each station includes a conductivity-temperature-depth (CTD)/Rosette cast to 1000 m depth, with sensors for pressure, temperature, salinity, dissolved oxygen, and fluorescence. Water samples from the upper 200 m are collected with 5 liter Niskin bottles at 0, 10, 20, 50, 100, 150, and 200 m depths to determine dissolved oxygen, chlorophyll *a*, nutrients (NO3, NO2, PO4, SiO3), and primary production. IMECOCAL cruises schedules, data collection, methods, and analyses are fully described at http://imecocal.cicese.mx.

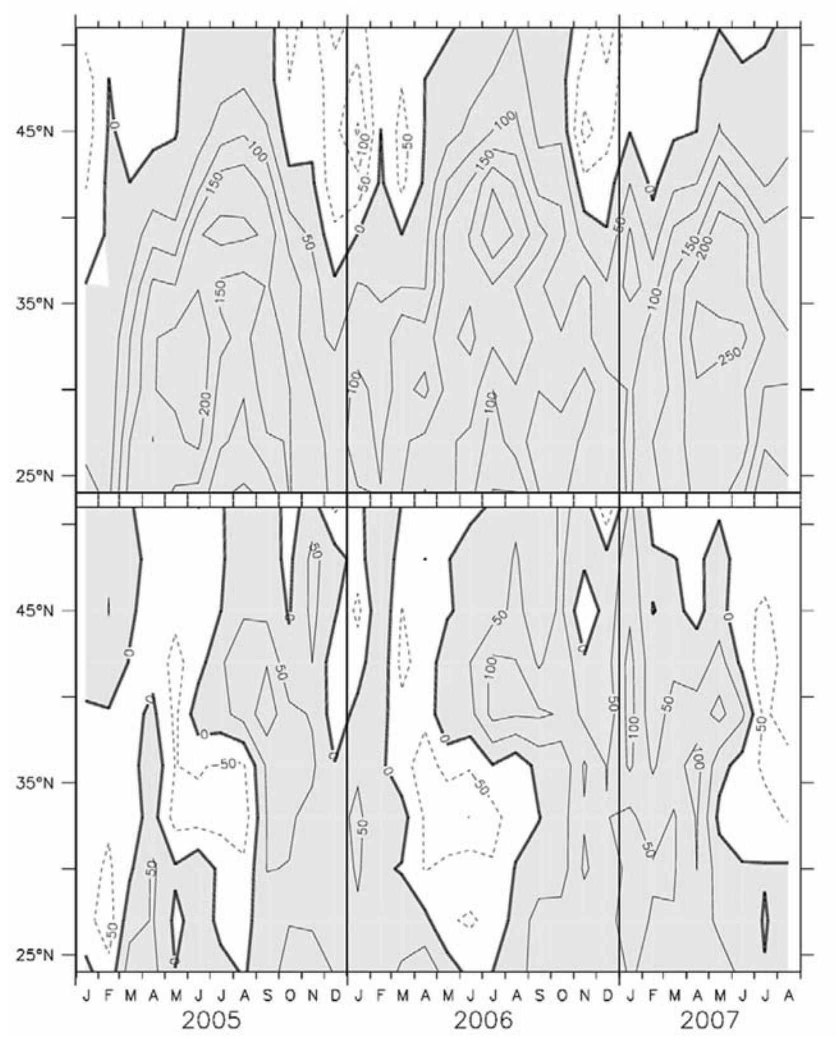

Figure 4. Monthly upwelling index and upwelling index anomaly for January 2005–August 2007. Shaded areas denote positive (upwelling-favorable) values in upper panel, and positive anomalies (generally greater than normal upwelling) in lower panel. Anomalies are relative to 1948–67 monthly means. Units are in m³/s per 100 km of coastline.

## Fish Egg Surveys off California

In 2006, a coast-wide survey for sardine was conducted in April–May to cover the area from San Diego, U.S., to British Columbia, Canada, with ichthyoplankton samples taken aboard the NOAA RV *Oscar Dyson* (11 April–8 May) and the NOAA RV *David Starr Jordan* (5–28 April), plus the routine CalCOFI cruise aboard SIO RV *New Horizon* (1–18 April). The *Dyson* occupied 17 transects from latitude 51°N to 30.7°N. The *Jordan* occupied 10 CalCOFI lines (95.0–51.7°N). CUFES samples were taken aboard the *Dyson* and *Jordan* but not on the *New Horizon*.

## California Sea Lion

Diet studies of California sea lion (*Zalophus californianus*) have been conducted in central California from 1997 to the present. Included are sites in Monterey Bay from 1997 to 1999 and Año Nuevo Island (37°6'N, 122°20'W) from 2001 to 2006, which is one of the largest haul-out sites for sea lions in central and northern California (Weise 2000; Lowry and Forney 2005). Annual variation in sea lion diet was determined by identifying fish otoliths and cephalopod beaks found in fecal samples collected at Año Nuevo Island. Prey hard parts were measured and species-specific correction factors were used to estimate standard length and mass of prey consumed (Orr and Harvey 2001). To detect changes in sea lion diet in relation to climatic forcing, each prey species in the diet for each year was expressed as an anomaly of the mean percentage of the total ingested mass (%M) of that prey species.

## Avifauna

Systematic surveys of the distribution and abundance of marine birds have been made on CalCOFI cruises since spring of 1987 (Hyrenbach and Veit 2003). Personnel from the Point Reyes Bird Observatory–Conservation Science (PRBO) conducted at-sea surveys during 2006. Additionally, PRBO has monitored the reproductive performance and diet of seabird populations breeding at the Farallon Islands (37°N, 123°W) since the early 1970s (Sydeman et al. 2001).

## LARGE-SCALE PATTERNS

The North Pacific was dominated in recent months by an unusually strong North Pacific high pressure system, which created anomalously strong clockwise winds over the northeast Pacific (fig. 3). This was particularly strong during the fall and winter of 2006–07. Associated with this wind pattern were unusually cool sea surface temperatures (SST) through much of the northeast Pacific (fig. 3).

The large-scale climate indices commonly used to assess the interannual state of the Pacific were generally unremarkable in 2006 and 2007. The Multivariate ENSO Index (MEI; fig. 2A; Wolter and Timlin 1998) indicated weak equatorial Pacific El Niño conditions through the end of 2006, and an ENSO-neutral state since. A positive Northern Oscillation Index (NOI), indicative of La Niña-like conditions and upwelling-favorable winds in the CCS, has been seen throughout 2006–07. Much of the tropics have been dominated by the 60–90 day signal of the Madden-Julian Oscillation (MJO), and Pacific SSTs have been described as "extremely volatile." The PDO signal (fig. 2B) remained positive (warm phase) for the first half of 2006, but switched signs briefly in July 2006 and has been neutral since the fall of 2006.

The regional expressions of this large-scale pattern are anomalously strong southward coastal winds and stronger than normal upwelling along the West Coast over the last year (fig. 4). After a period of anomalously weak upwelling in spring and early summer of 2006, particularly in the Southern California Bight, the CCS experienced stronger-than-normal upwelling in late summer and fall. Unlike 2005 and 2006, when the onset of seasonal upwelling in spring was up to two months later than usual (Schwing et al. 2006), the 2007 upwelling season began early, and upwelling remained unseasonably strong through May.

Conditions at coastal NDBC buoys have reflected these large-scale patterns. Buoy winds have been generally upwelling-favorable (southward), with a number of very strong upwelling episodes (fig. 5). 2007 has been unusual in its relative lack of relaxation events, which are periods of northward (downwelling) wind when onshore recruitment of pelagic larval stagescan occurs. Buoy SSTs have been anomalously cool during 2007 (fig. 6). Note especially the cool SSTs in May 2007 compared to those in May of the past two years.

***Projection:*** SST and other measures of the equatorial Pacific suggest developing La Niña conditions as of fall 2007 (NOAA CPC Climate Diagnostics Bulletin, http://www.cpc.ncep.noaa.gov). Most models project a weak La Niña pattern for the next several months. Although upwelling reduced substantially in June and July, the cumulative upwelling for the 2007 season was greater than normal. An important implication of this could be greater ecosystem productivity and reproductive success for many populations.

## REGIONAL STUDIES

### Oregon

From November 2002 through April 2006, SST anomalies off Oregon (fig. 6, NOAA buoy 46050 which is 22 miles off Newport in 140 m water depth) were 1° to 2°C above normal, at times exceeding those seen during the 1998 El Niño event. In 2006, coastal upwelling began in early May, somewhat earlier than usual, but after two weeks, atmospheric conditions changed and several strong southwesterly storm events moved up the coast, erasing any signature of upwelling. Sustained upwelling was not initiated until the end of May, and remained weak through late June. Winds were strong and persistent from July through September, favoring upwelling, albeit late. By July 2006, SST anomalies once again turned negative, and they remained either negative or neutral through May 2007, consistent with the pattern throughout the northeast Pacific (fig. 3).

A time series of temperature measured at a depth of 150 m at a shelf break station off Newport (NH 25; 300 m water depth) shows a strong seasonal cycle as well as interannual variations (fig. 7). Temperatures at 150 m depth were cool during summers of 1999–2002 (ranging from 7.39°C in 1999 to 7.24°C in 2002). Following this, the deep waters in summer warmed to 7.56°C (2003), 7.71°C (2004), 7.65°C (2005) and 7.69°C (2006). Cooler temperatures (7.3°C) have been seen through June 2007. Winter temperatures were cooler in 2005–06 and 2006–07 by 0.5°C. Salinity at 150 m at the same station showed the opposite pattern, with relatively high values during summers 1999–2002 (averages ranged from 33.92 to 33.96 psu), decreasing to 33.90 psu in 2003, and 33.89 psu in 2004. A slight increase was seen in 2005 (33.93 psu), 2006 (33.95 psu), and 2007 (33.95 psu through June). For the winter months, there was a trend towards increased salinity from 2003–04 until present. Thus, the trend seems to be towards colder and saltier water in 2006 and 2007, similar to that observed from 1999–2002. From this (albeit limited) data set, it appears that relatively warmer and fresher water occurs at depth during the positive phase of the PDO and colder and saltier water during the negative phase, supporting

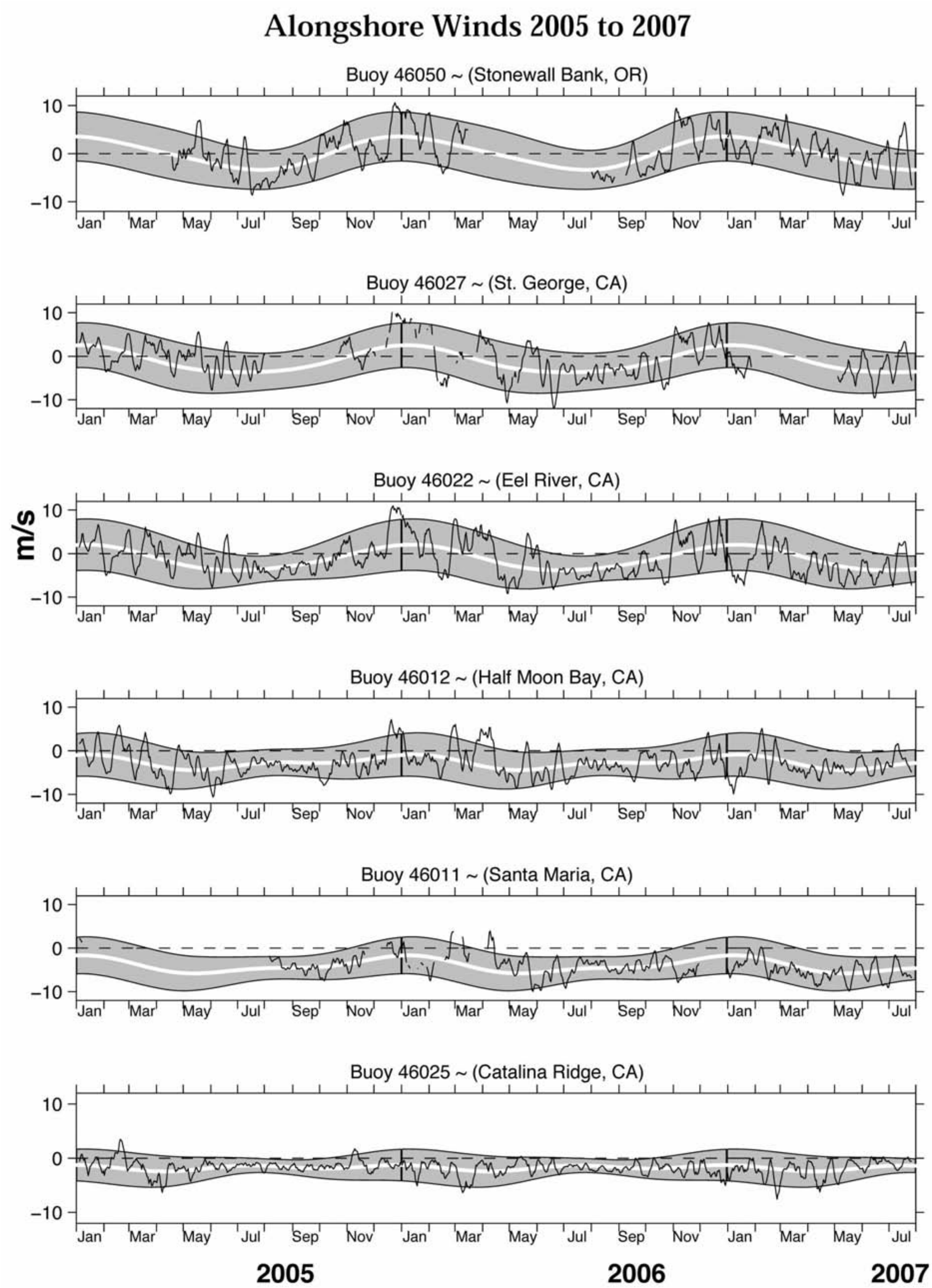

Figure 5. Time series of daily-averaged alongshore winds for January 2005–July 2007 at selected NOAA National Data Buoy Center (NDBC) coastal buoys. Bold lines are the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. Series have been smoothed with a seven-day running mean. Data provided by NOAA NDBC.

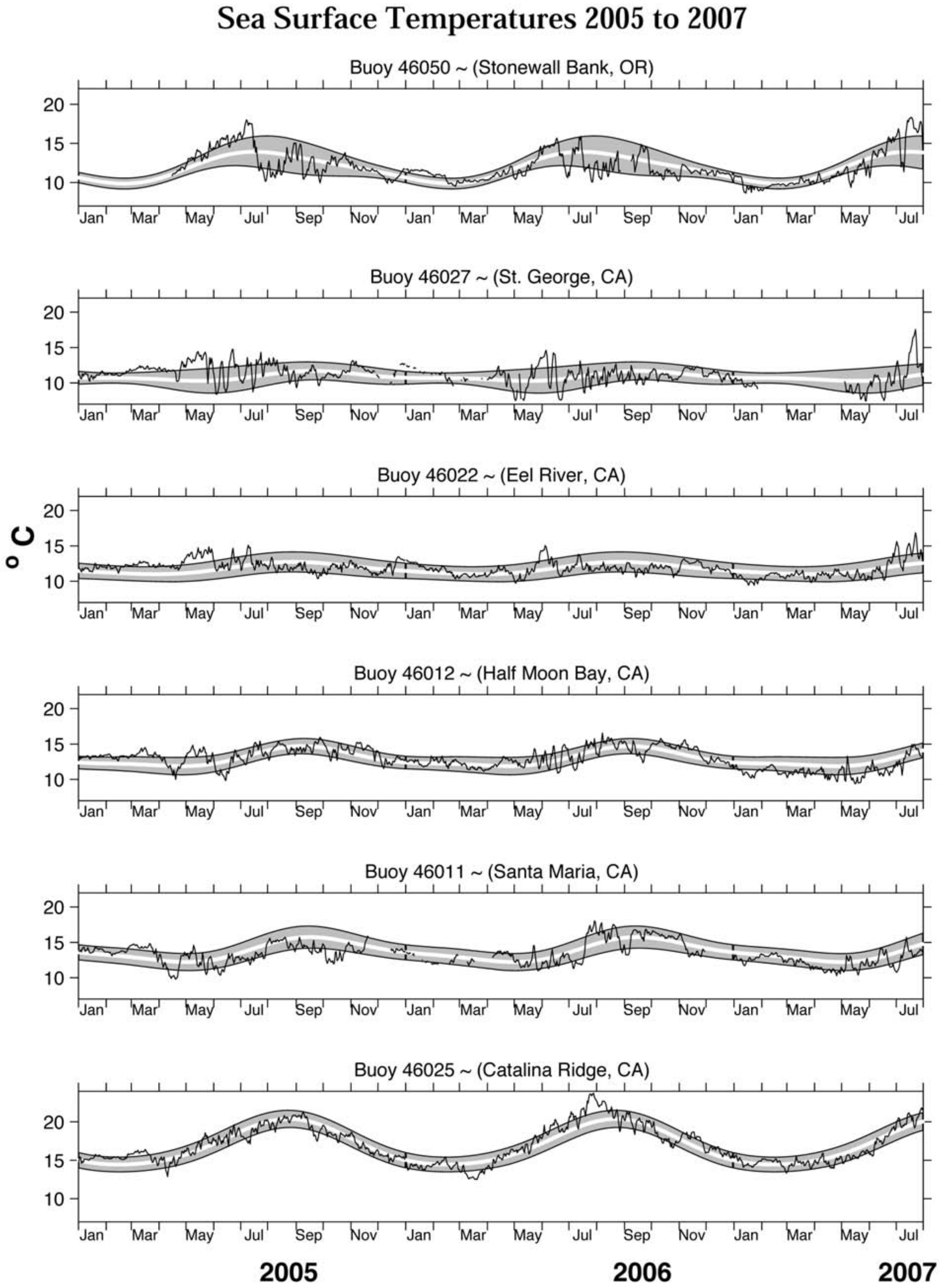

Figure 6. Time series of daily-averaged SST for January 2005–July 2007 at selected NDBC coastal buoys. Bold lines are the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. Data provided by NOAA NDBC.

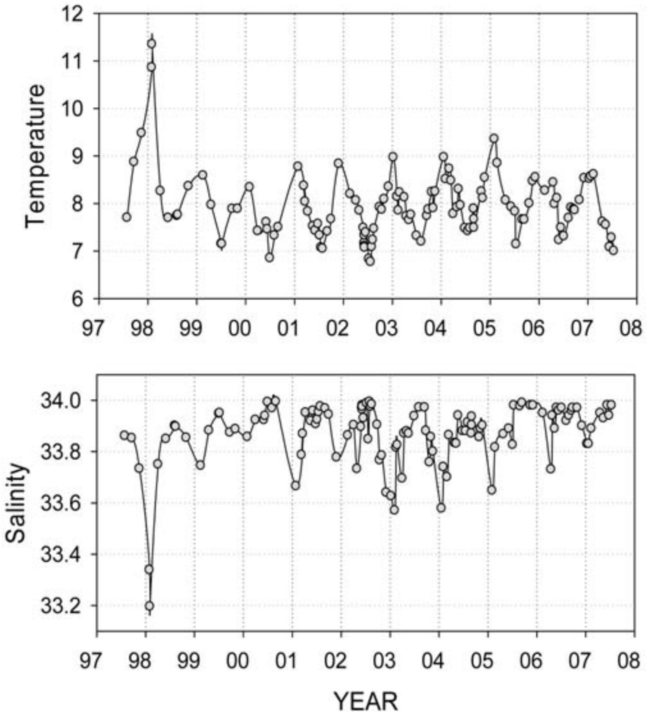

Figure 7. Time series of temperature (upper panel) and salinity (lower panel) measured at a depth of 150 m at station NH 25 (25 miles off Newport); station depth is 297 m.

a hypothesis that different water types occur off Oregon as a function of the phase of the PDO.

## Central California

CTD sections extending offshore of Monterey Bay have been carried out on a regular basis since 1997. Mean temperature-salinity curves for each cruise are shown in Figure 8A. The regular features of the temperature-salinity curves include: (1) an upper layer (T > 10°C) with strong seasonal and year to year variability, (2) a strong halocline between S = 33.6 to 33.4, (3) a region of rapid temperature change between 6°C to 8°C, and (4) a lower layer where T < 6°C. The temporal variabilities of the mean properties of these four layers are shown in Figure 8B-D. The salinity of the upper layer (fig. 8B) appears to have been near normal levels in 2006–07, ~33.3 psu, while the salinity of the thermocline and deeper layer (fig. 8D) appears to have leveled off after a decade of steadily increasing salinity. The mean temperature of the halocline (fig. 8C) was highly variable although the cruises in June and July 2007 indicated a temperature of 8.8°C, near the minimum observed. Based on these data, it appears that transport of equatorial intermediate waters into the region has leveled off while the upper waters remain near normal conditions.

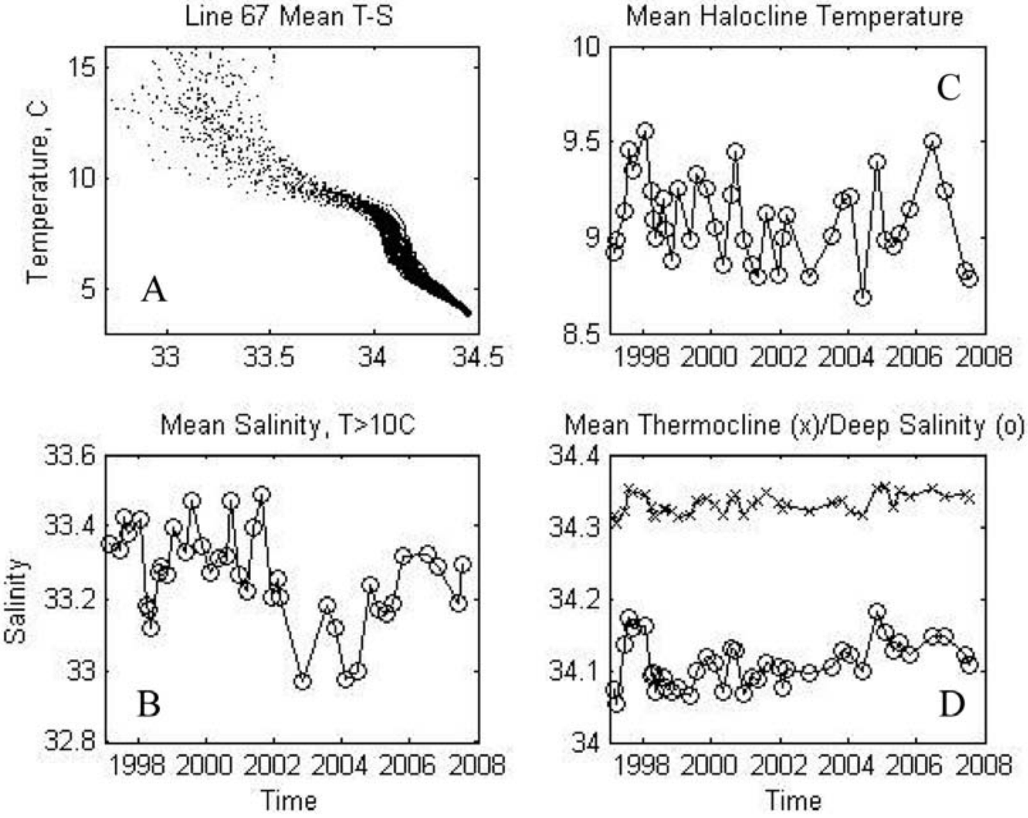

Figure 8. Conditions along Line 67 off Monterey Bay. (A) Mean temperature-salinity curves for all cruises since 1997. (B) Salinity of the upper layer (T > 10°C). (C) Mean halocline temperature. (D) Salinity of the thermocline region and the deeper layers.

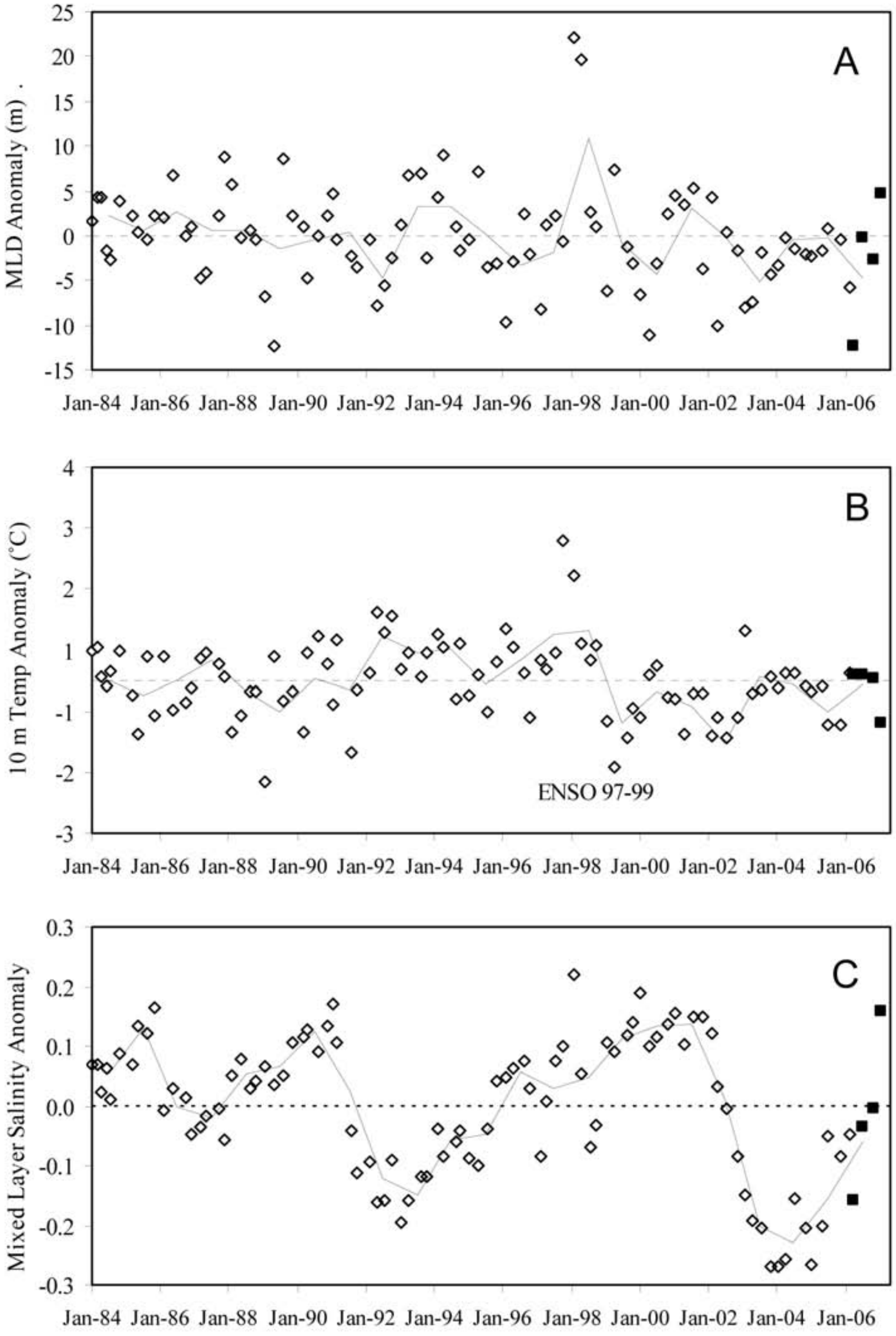

Figure 9. Anomalies of mixed-layer (ML) depth (A), 10 m temperature (B), and ML salinity (C). Data from the last four cruises are plotted as solid symbols, data from previous cruises are plotted as open diamonds. The solid lines represent the annual averages and the dotted lines the climatological mean which in the case of anomalies is zero.

## Southern California

***CalCOFI Overview:*** Anomalies of mixed-layer depth (MLD) over the last year were variable. After a low value in January, anomalies returned to near normal (fig. 9A). Temperature anomalies at a depth of 10 m (fig. 9B) were also close to zero. The trend of increasing temperatures is significant for the time period January 1984 to August 1998 ($p < 0.05$), continuing the trend since 1949, the beginning of CalCOFI data (Roemmich and Mc Gowan 1995). When the period of the strong 1998–99 ENSO event is excluded from the analysis, the trend is not (yet?) significant for the time period of August 1999 to the present. Temperature anomalies at a depth of 200 m were slightly but not sig-

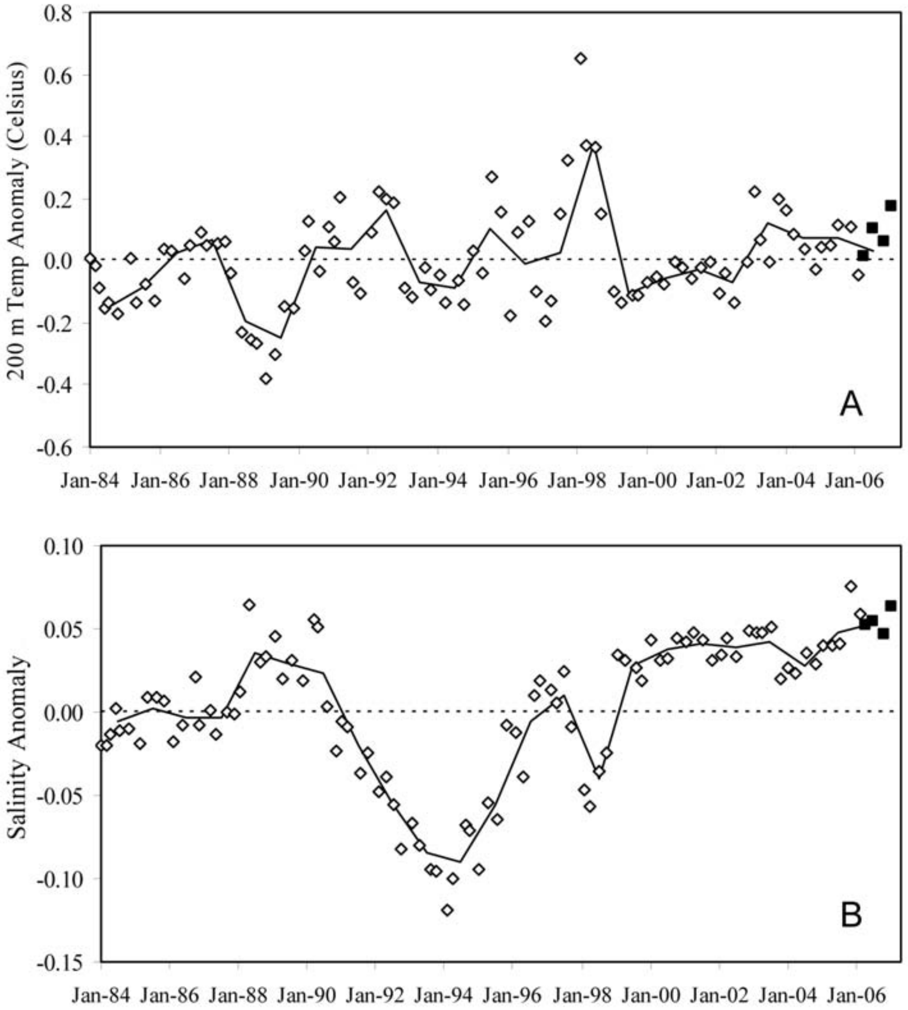

Figure 10. Anomalies of temperature (A) and salinity (B) at a depth of 200 m, calculated and presented as described above for Figure 9.

nificantly positive during the last year, with values similar to those observed since 2003 (fig. 10A). Anomalies of mixed-layer salinities had returned to zero (fig. 9C) after a period of strong negative values between 2003 and 2005. This return of salinities to values close to their long-term averages was seen throughout the CalCOFI region (fig. 11), with the exception of the edge of the Central Gyre of the North Pacific (fig. 11). Salinity anomalies at 200 m were slightly higher than those observed since 1999 (fig. 10B). Note that the 2003–06 negative sea surface salinity anomaly (fig. 9C) is virtually absent from salinities at 200 m (fig. 10B), illustrating the shallow nature of this anomaly.

***CalCOFI Cruise 0604 (1–18 April 2006; fig. 12).*** The California Current was strongly expressed throughout the study domain in April 2006. Across line 77 it was located close to the coast, making a large meander out to station 100 across line 87 and jetting further inshore, crossing line 93 in the vicinity of stations 70 to 90. Close to the coast the poleward countercurrent was present. In contrast with recent years, the relatively cool temperatures and elevated concentrations of nitrate that indicate upwelling were not evident at the inshore stations of lines 77 to 83. Only the inshore stations of lines 87 and 90 showed signs of recent upwelling (SST < 13°C, nitrate 5 to 8 μM). High concentrations of chlorophyll *a* were only observed in the vicinity of the Santa Barbara Basin and along the inshore sections of lines 83 to 90. The spatial restriction of elevated concentrations of chlorophyll *a* and rates of primary production were a likely consequence of the restricted upwelling.

***CalCOFI Cruise 0607 (7–25 July 2006; fig. 13).*** During the summer flow, patterns of the California Current were similar to those observed during the spring, with the exception of the large meander which was no longer observed. Poleward flow close to the coast was stronger than in the spring, similar to previous years. Spatial patterns and values of SST and chlorophyll *a* were

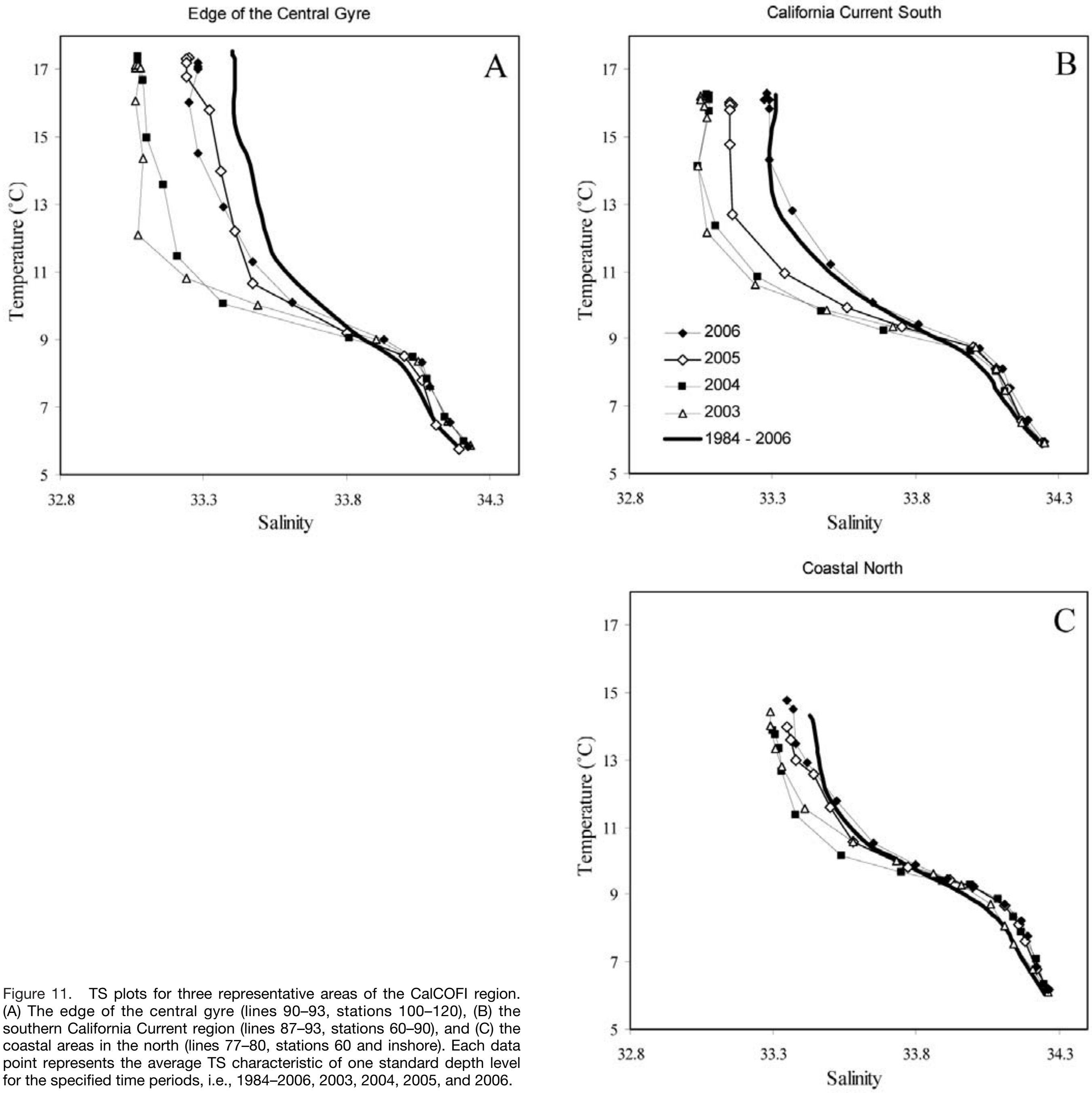

Figure 11. TS plots for three representative areas of the CalCOFI region. (A) The edge of the central gyre (lines 90–93, stations 100–120), (B) the southern California Current region (lines 87–93, stations 60–90), and (C) the coastal areas in the north (lines 77–80, stations 60 and inshore). Each data point represents the average TS characteristic of one standard depth level for the specified time periods, i.e., 1984–2006, 2003, 2004, 2005, and 2006.

typical for this season—with the exception of higher-than-normal SST along the inshore section of line 90.

***CalCOFI Cruise 0610 (21 October–6 November 2006; fig. 14).*** Data for this cruise are preliminary. By fall, the California Current had split with one weak branch entering the study domain along line 77 close to the coast and another entering at the northwest corner. The stronger offshore branch meandered in and out of the domain at its western edge, merging with the inshore branch along line 93. The Southern California Eddy was centered on stations 90.35 and 87.40. The coastal countercurrent was typical for this time of the year. Concentrations of chlorophyll *a* were low in the offshore areas; high values were only found close to the coast.

***CalCOFI Cruise 0701 (12 January–3 February 2007; fig. 15).*** Data for this cruise are preliminary. In January, the California Current was located in the offshore portion of the study domain, entering between stations 77.09 and 77.100 and exiting the domain through the

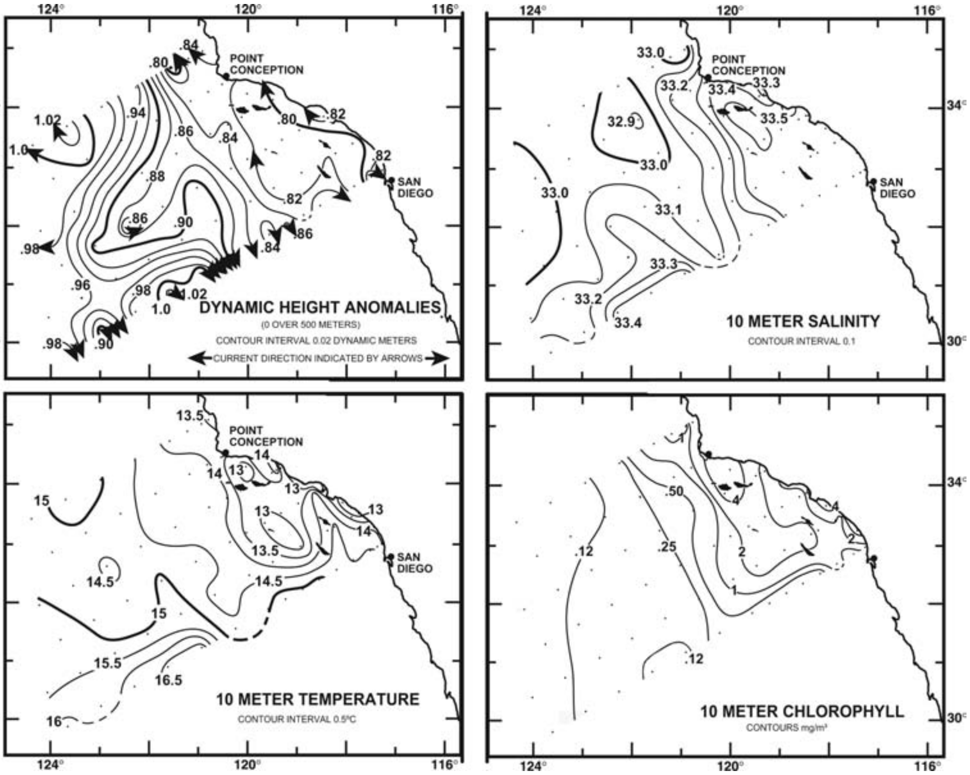

Figure 12. Spatial patterns for CalCOFI cruise 0604 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*.

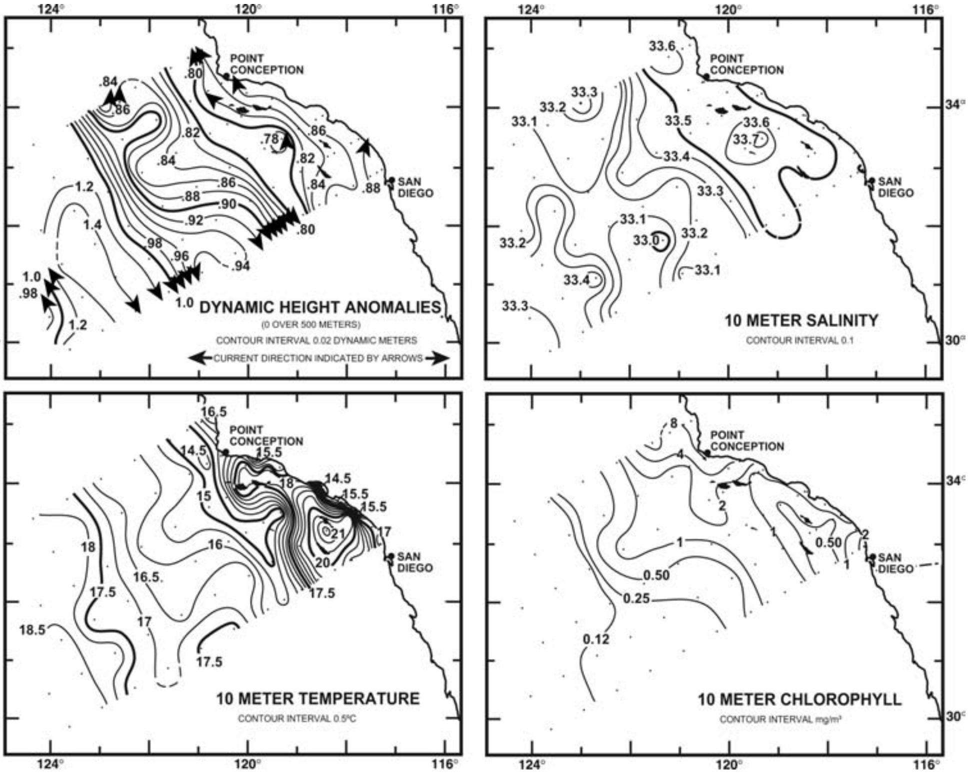

Figure 13. Spatial patterns for CalCOFI cruise 0607 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*.

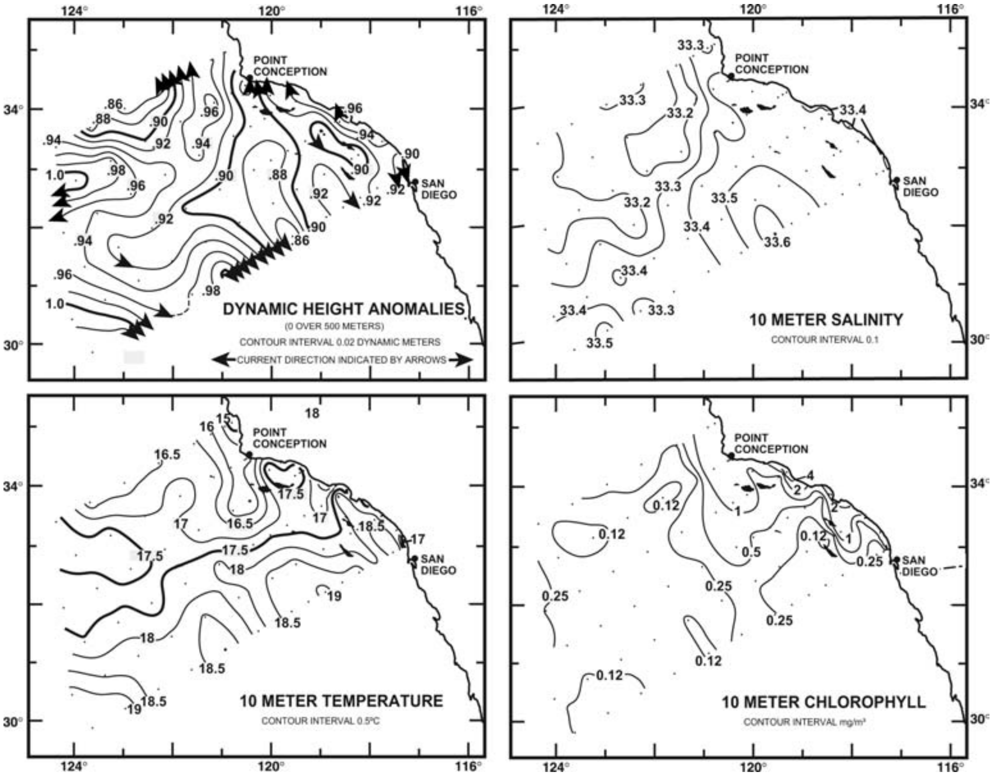

Figure 14. Spatial patterns for CalCOFI cruise 0610 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*. Data used for these plots are still preliminary.

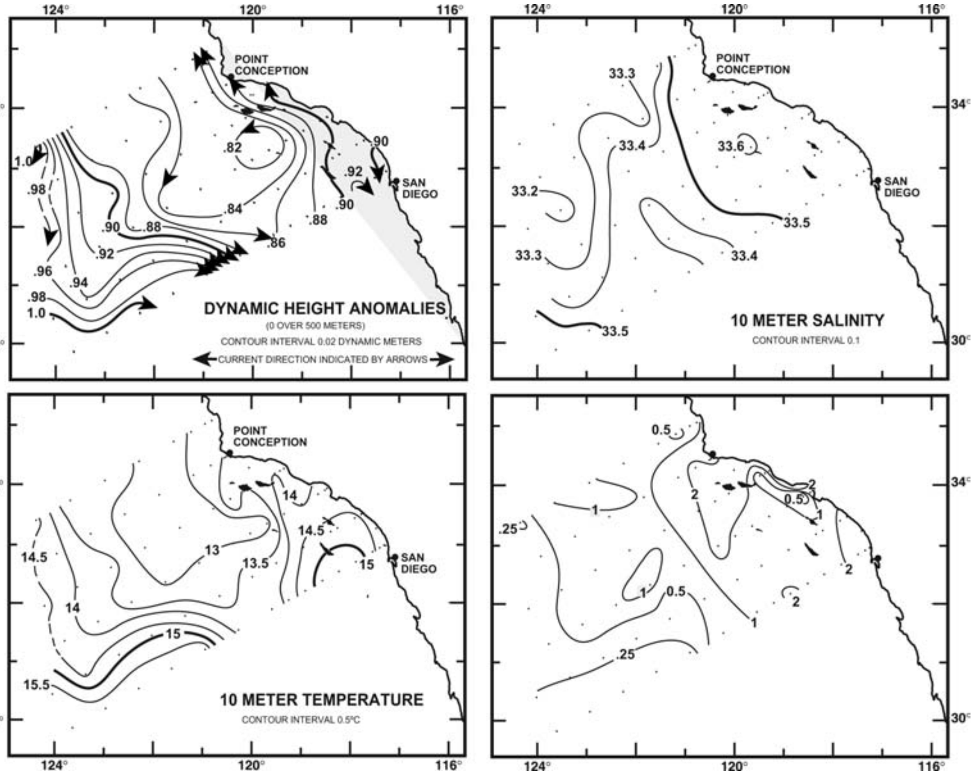

Figure 15. Spatial patterns for CalCOFI cruise 0701 including upper-ocean geostrophic flow estimated from the 0/500 dbar dynamic height field, 10 m salinity, 10 m temperature, and 10 m chlorophyll *a*. Data used for these plots are still preliminary.

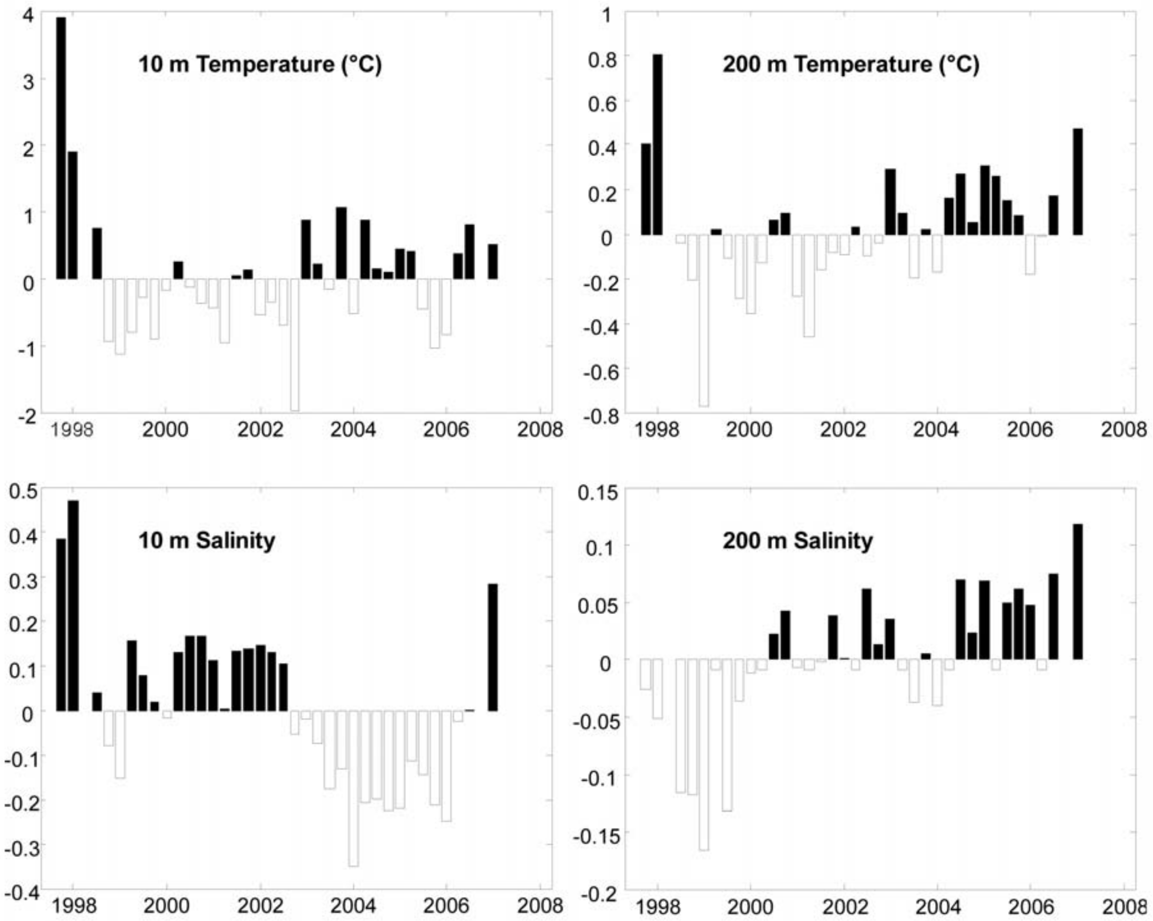

Figure 16. Temperature and salinity anomalies at 10 m and 200 m for the entire IMECOCAL survey area off Baja California. Anomalies are based on the time period 1997–2007.

center of line 93. Flows in the center of the domain were weak. The Southern California Eddy was centered on stations 87.50 to 55. A strong poleward current extended from the inshore section of line 87 to north of Point Conception. Temperatures at a depth of 10 m along the coast ranged from 13.0° to 14.5°C and concentrations of nitrate and chlorophyll *a* were low, suggesting that upwelling was insignificant.

### Baja California

***IMECOCAL Overview:*** IMECOCAL surveys were completed in April and July 2006 and January 2007 off Baja California (fig. 1D). Data shown here are relative to the climatology of 1997–2005. The most relevant feature during this period is a clear transition to warmer conditions as of April 2006, reflected in positive temperature anomalies at depths of 10 and 200 m (fig. 16). Salinity anomalies at 10 m were neutral for most of the year after a 4-year period of strong negative anomalies (fig. 16). There was a strong positive anomaly in January 2007. Temperature anomalies at continental shelf stations show tendencies similar to those observed in the offshore region (not shown). Also evident was the anomalous advection of warm and saltier water at depth from the south in January 2007 (fig. 16). As usual, April showed the highest chlorophyll *a* values due to upwelling, decreasing values in July, and minimum values in January 2007.

***IMECOCAL 0604 (19 April–3 May 2006; fig. 17).*** The circulation in April was dominated by the California Current, which was stronger offshore. The water mass associated with its core had low temperature (16.5ºC–17.0ºC) and low salinity (33.4 psu). Inshore 10 m water temperatures below 16ºC and salinities of 33.45 psu were probably related to upwelling in the northern region. Temperatures in the study domain at 10 m ranged from 16º to 17.5ºC; corresponding salinities ranged from 33.4 to 33.5 psu. High chlorophyll *a* concentrations (~2 mg $m^{-3}$) were associated with the coastal upwelling in the northern part off Ensenada, and in the central Peninsula inside Vizcaino Bay with values up to 6 mg $m^{-3}$. In the offshore areas chlorophyll *a* reached values as low as 0.12 mg $m^{-3}$.

***IMECOCAL 0607 (7–27 July 2006; fig. 18).*** A cyclonic eddy off Punta Eugenia perturbed the main south-

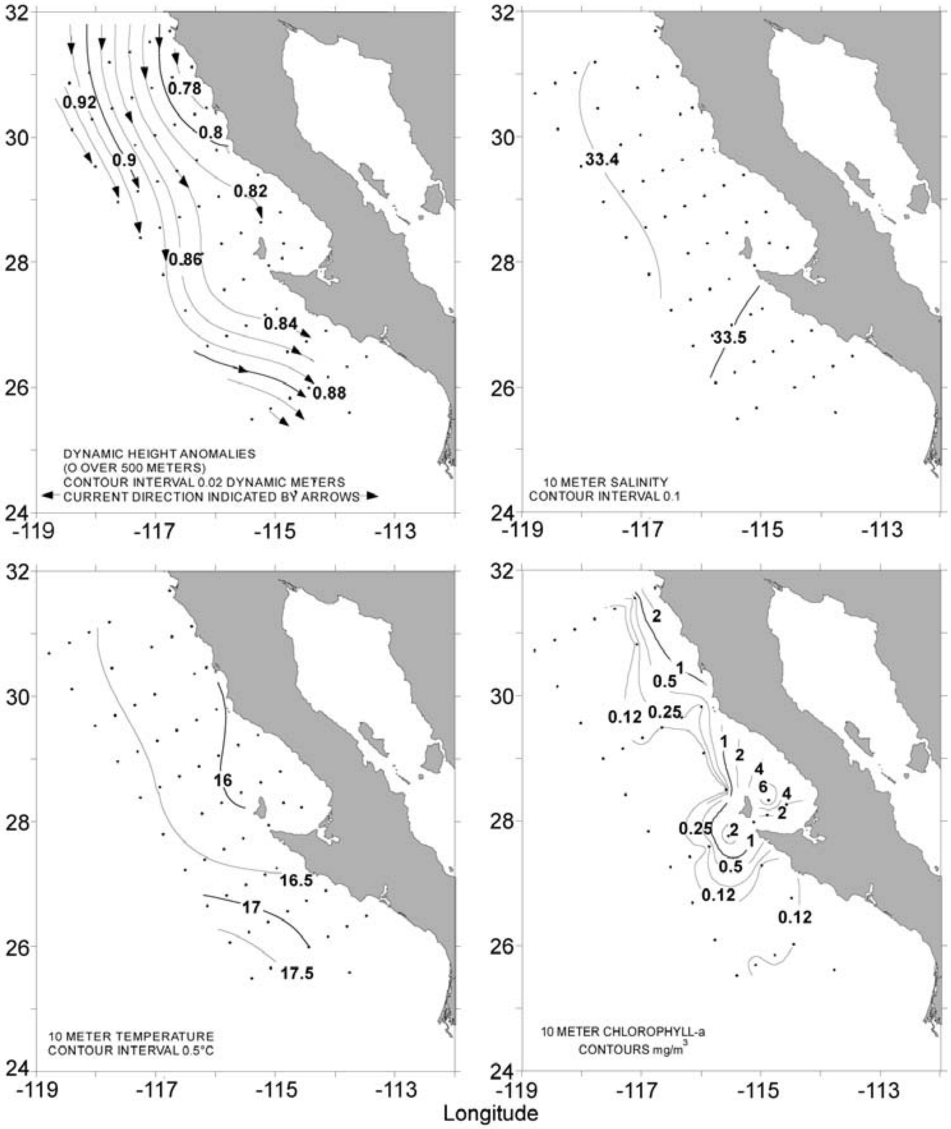

Figure 17. Spatial pattern for IMECOCAL cruise in spring 2005, showing upper ocean geostrophic flow estimated from the 0/500 dynamic height field, 10 m temperature, 10 m salinity, and 10 m chlorophyll *a*.

ward flow. The center of the eddy was characterized by high surface temperature (21°C) and low salinity (33.5 psu). North of the eddy, the core of the California Current was deflected shoreward at 29°N. South of the eddy, the California Current veered inshore at 26°N. Temperatures in the study domain ranged from 18° to 23°C, while salinities varied from 33.5 to 33.9 psu. High chlorophyll *a* concentrations (~2 mg $m^{-3}$) were observed along most of the coast, probably as a response of upwelling during this period. Chlorophyll *a* in the domain ranged from 0.12 to 4 mg $m^{-3}$.

***IMECOCAL 0701 (23 January–12 February 2007; fig. 19).*** The surface-circulation pattern showed a weak southward flow inshore. The 10 m salinity field shows strong gradients west and northwest of Punta Eugenia, suggesting that warm salty water had been advected into this region prior to the cruise. Temperatures ranged from 15° to 20.5°C, while salinities varied from 33.5 to 34.4 psu. Chlorophyll *a* concentrations, ranging from 0.25 to 2 mg $m^{-3}$, were low, typical of the winter, with highest values in the Vizcaino Bay region and south of Punta Eugenia.

## BIOLOGICAL PATTERNS AND PROCESSES

### Macronutrients, Chlorophyll *a* and Primary Production

***Oregon:*** Sea surface nitrate concentrations at station NH 05 in spring 2006 (April–June) were the highest measured during the spring, averaging 10.1 µM (tab. 1).

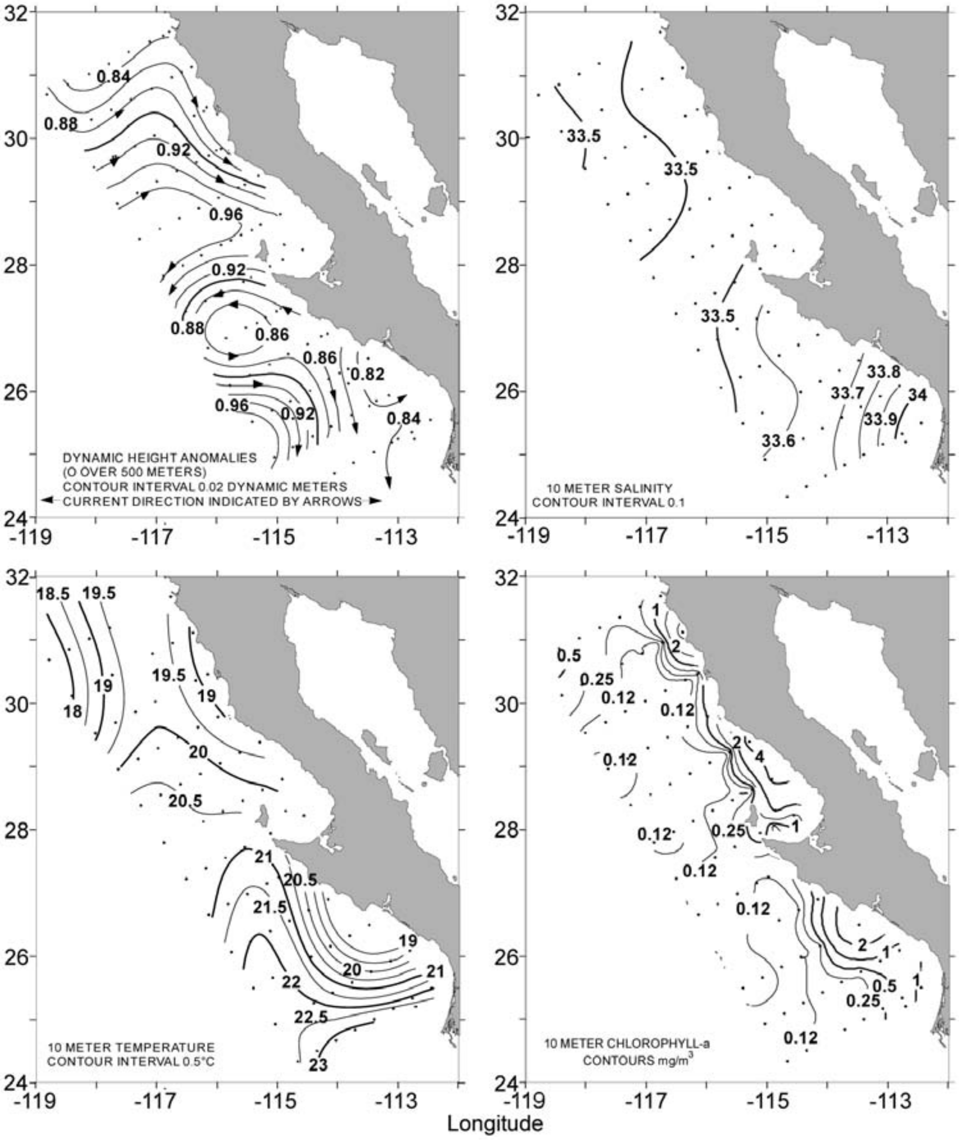

Figure 18. Spatial pattern for IMECOCAL cruise in summer 2006, showing upper ocean geostrophic flow estimated from the 0/500 dynamic height field, 10 m temperature, 10 m salinity, and 10 m chlorophyll *a*.

This is in strong contrast to spring 2005 when the lowest concentrations of our time series were found. During July–August, the two months when upwelling is usually the strongest, nitrate concentrations averaged 11.7 μM, one of the highest values observed in those months.

Average chlorophyll *a* values were 2.2 μg $L^{-1}$ during the spring (April–June) and 10.1 μg $L^{-1}$ during the summer (July–August) of 2006. These values are typical of most years (tab. 1). Nitrate and silicate concentration at 150 m at station NH 25 increased from the 1997–98 El Niño period until 2002 (fig. 20). These trends match those observed at 200 m both in the Monterey region and CalCOFI/Southern California Bight (see below and Peterson et al. 2006). Since late 2003, the concentra-

TABLE 1

**Average nitrate (μM) and chlorophyll (μg chl-a $L^{-1}$) concentrations measured at the sea surface at station NH 05, five miles off Newport, in spring (April–June) and summer (July–August) for the years 1997–2006.**

| | Nitrate (μM) | | Chlorophyll *a* (μg chl-*a* $L^{-1}$) | |
|---|---|---|---|---|
| YEAR | April–June | July–August | April–June | July–August |
| 1997 | 5.21 | 7.95 | 1.14 | 6.1 |
| 1998 | 1.91 | 2.25 | 2.23 | 10.5 |
| 1999 | 4.95 | 10.20 | 1.79 | 5.5 |
| 2000 | 8.65 | 12.00 | 1.93 | 8.4 |
| 2001 | 4.16 | 9.43 | 6.59 | 9.0 |
| 2002 | 4.28 | 11.49 | 6.09 | 10.9 |
| 2003 | 4.37 | 10.30 | 2.99 | 9.7 |
| 2004 | 3.62 | 8.41 | 4.92 | 8.1 |
| 2005 | 0.67 | 11.70 | 2.63 | 8.7 |
| 2006 | 10.10 | 11.74 | 2.22 | 10.1 |

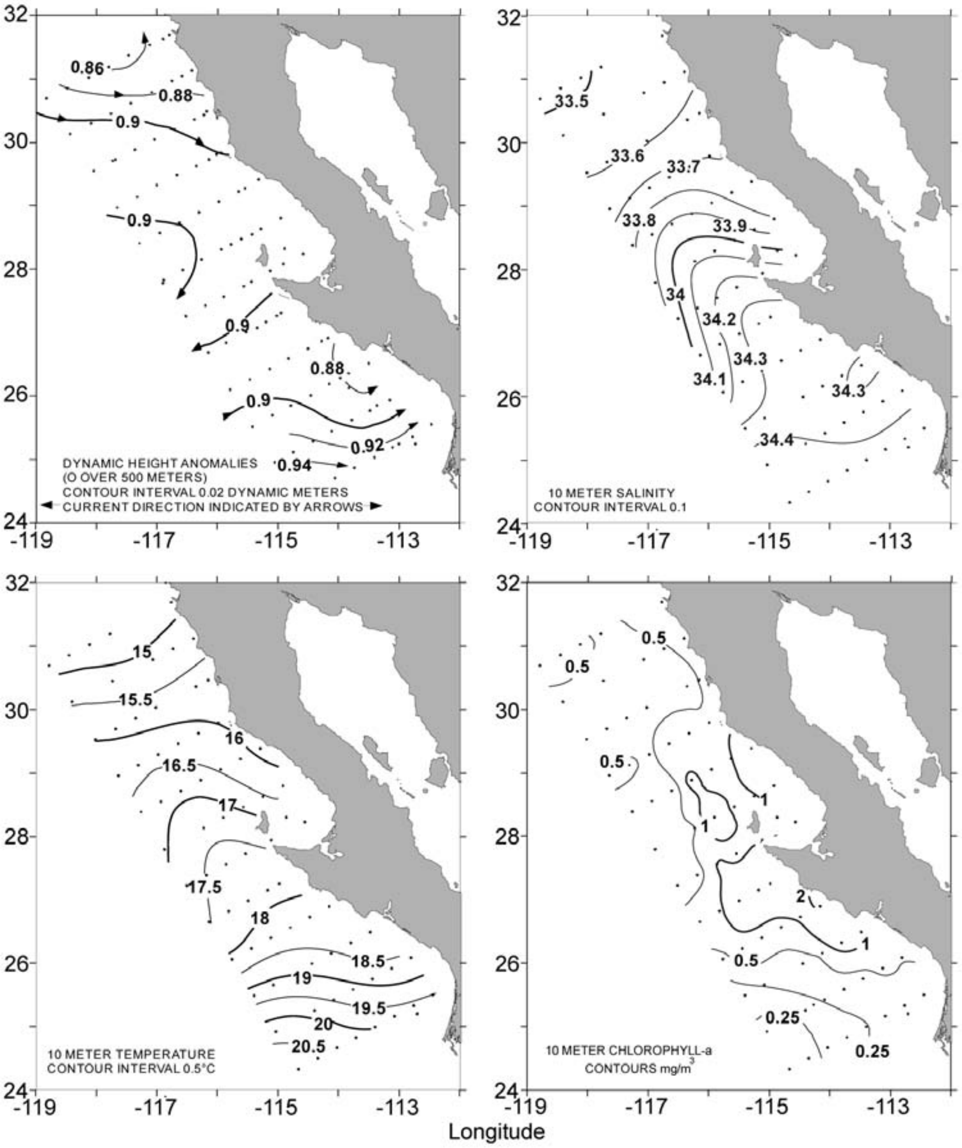

Figure 19. Spatial pattern for IMECOCAL cruise in winter 2007, showing upper ocean geostrophic flow estimated from 0/500 dynamic height field, 10 m temperature, 10 m salinity, and 10 m chlorophyll *a*.

tions have stabilized: recent values (including 2006) fall into the range of the long term average of 30–35 µM for nitrate and 40–50 µM for silicate.

***CalCOFI:*** Nitracline depth anomalies for the whole CalCOFI region were slightly negative over the last year (fig. 21) with values similar to those observed since 2000. Anomalies of nitrate in the mixed layer were close to zero (fig. 22A), and anomalies of phosphate were slightly negative (fig. 22B). The trend of decreasing phosphate since 2003 continued. Anomalies of silicic acid have increased to zero after unusually negative anomalies during 2003 to 2005 (fig. 22C). Recent trends in silicic acid concentrations mirror those observed for salinity.

Anomalies of chlorophyll *a* were variable, about zero during the past year (fig. 23A). Anomalies of depth-integrated rates of primary production were slightly negative (fig. 23B), similar to those observed over the last three years. The apparent decoupling between concentrations of chlorophyll *a* and rates of primary production is puzzling, suggesting either a change in insolation or a change in phytoplankton community structure over the last 20 years. The subsurface chlorophyll *a* maximum at the edge of the central gyre (fig. 24A) was 20 m above the long-term average, similar to 2003. In other areas (e.g., fig. 24B), concentrations were above long-term averages, consistent with the long-term trend in chlorophyll *a* standing stocks. Noteworthy are relatively low concentrations of chlorophyll *a* in the Northern Coastal region below the mixed layer (fig. 24C). It is possible that these low concentrations of chlorophyll *a* are related

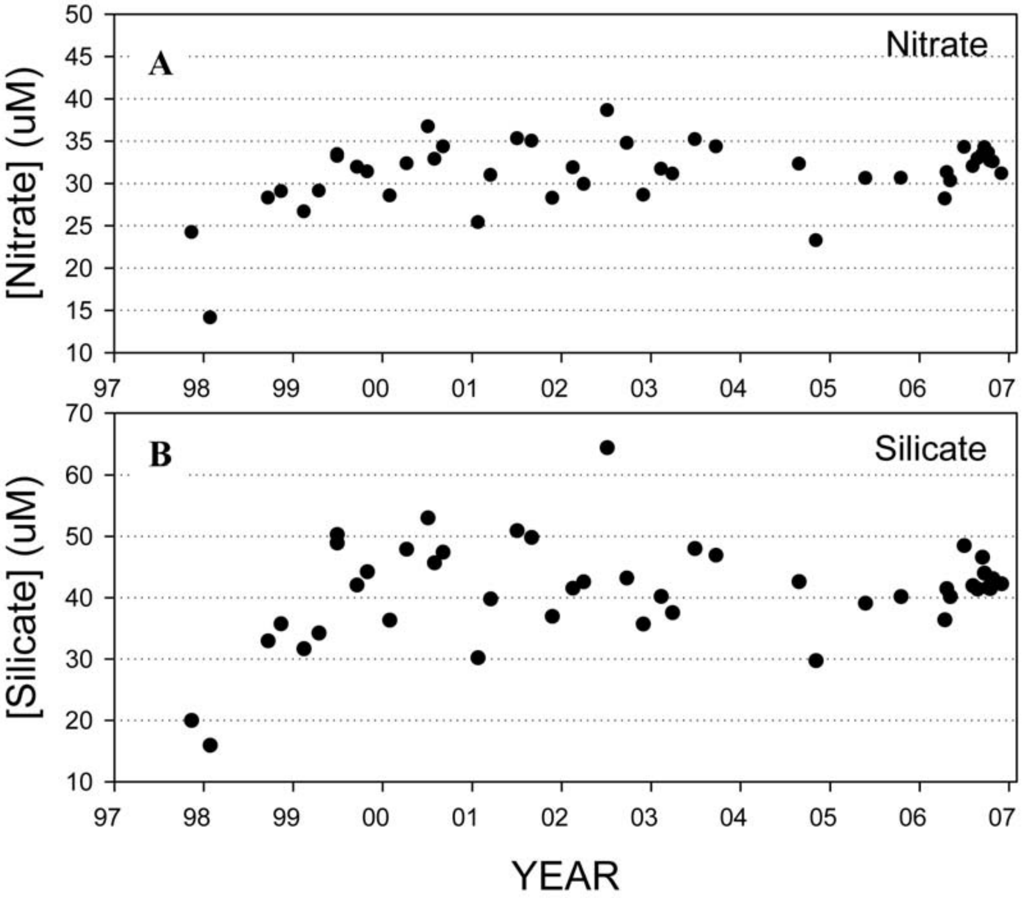

Figure 20. Time series of nitrate and silicate concentrations from station NH 25 (25 miles off Newport). Data from 1998–2003 are from P. Wheeler (Oregon State University, GLOBEC, LTOP Program, the years 1997–2003); the remainder are from the Newport Time Series.

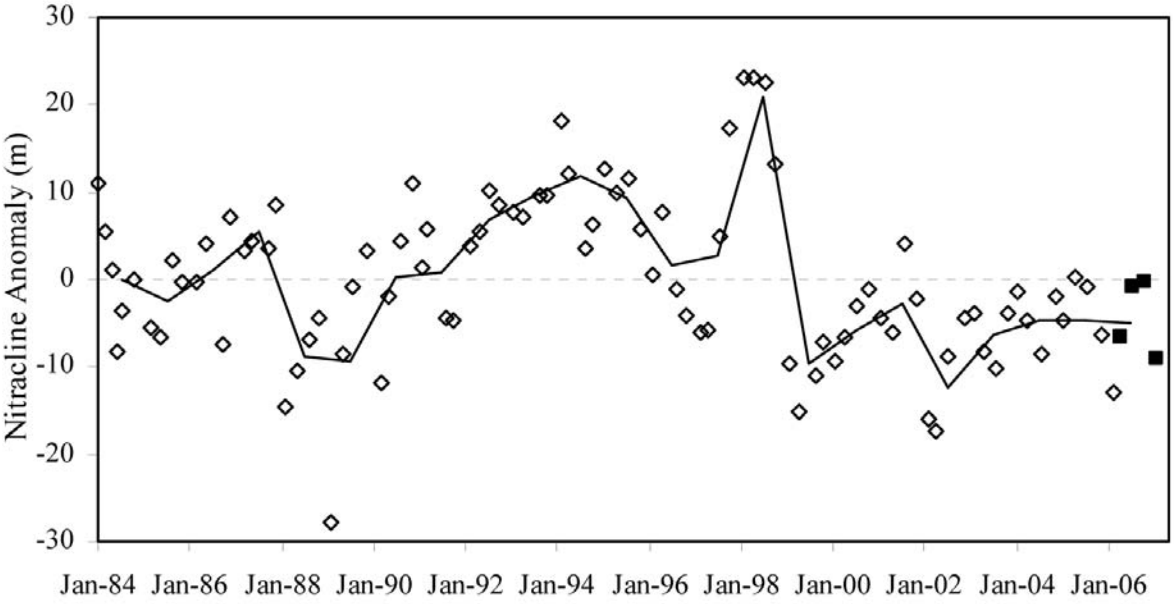

Figure 21. Cruise averages for nitracline depth anomaly. The nitracline depth was assumed to be the depth where nitrate reached values of 1 µM. Data are plotted as described in Figure 9.

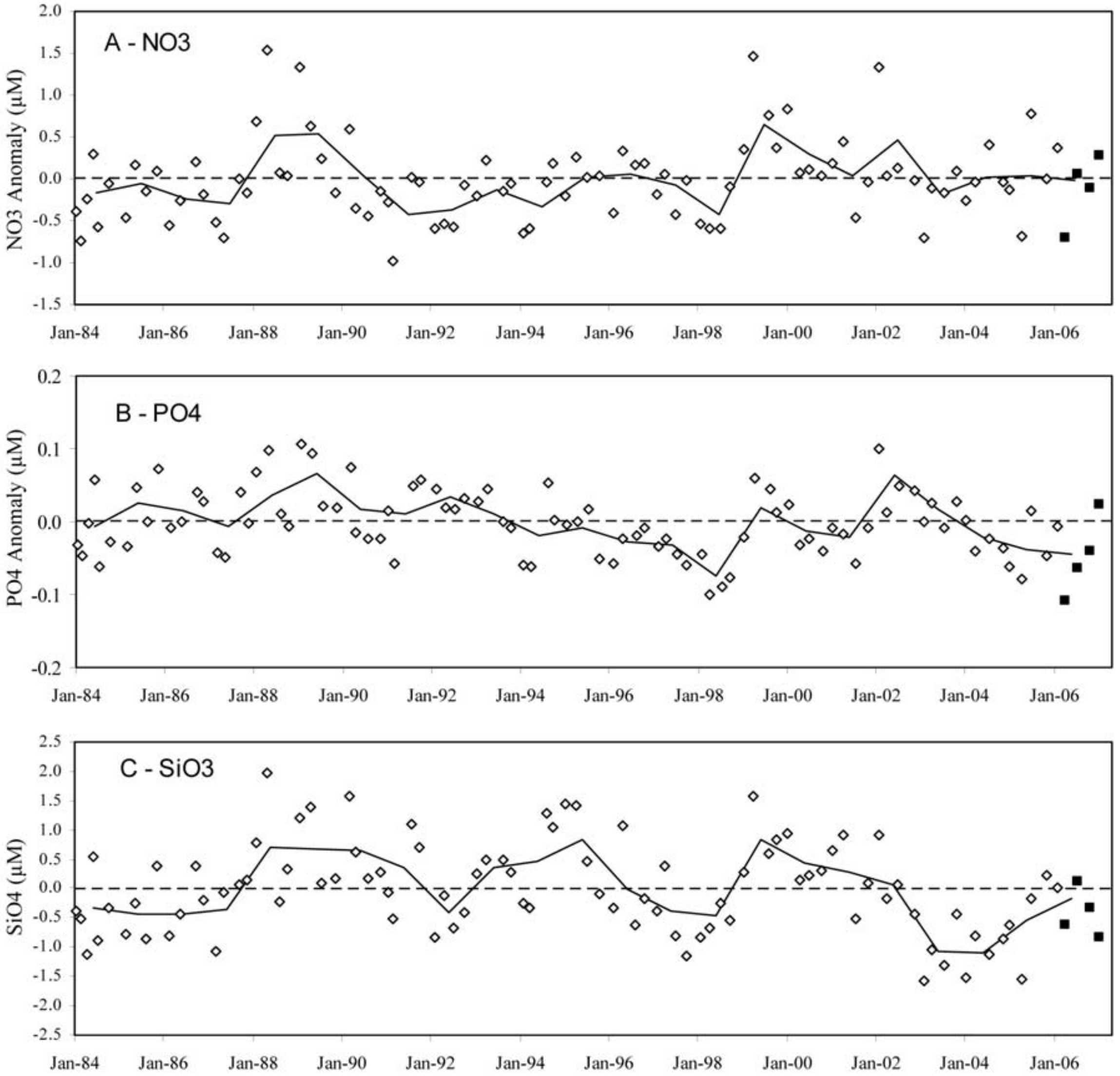

Figure 22. CalCOFI region anomalies for concentrations of (A) nitrate, (B) phosphate, and (C) silicate in the mixed layer. Data are plotted as described in Figure 9.

to weak and upwelling-unfavorable winds off southern California in 2006 (fig. 4).

### Macrozooplankton

***Oregon:*** Copepod biomass varied seasonally, with peaks in July–August, and interannually (fig. 25A). Lowest averages for summers (May–September) were seen from 1996–99, and were highest during the summers of 2000–04 (fig. 25B). The summer of 2005 had the lowest biomass of any summer on record due to the delayed upwelling. With stronger, albeit interrupted, upwelling in 2006, biomass rebounded to values twice those observed in 2005, and close to values observed from 2000–04 (fig. 25). Although copepod biomass was higher than average in 2006 (usually related to cool conditions with good reproduction), copepod biodiversity remained high (usually related to warm conditions, see fig. 26B). Thus, although the "physical spring transition," as measured by a drop in sea level, was somewhat early, the "biological" transition, as measured by changes in the species composition of the zooplankton, from a warm-water winter community to a cold-water summer community, was delayed.

Copepod species richness off Oregon covaries with the SST off Newport (Peterson 2006). Copepod species richness was low from 1999 until 2002, high from 2003 until the fall of 2006, turning negative in autumn 2006 and remaining negative (fig. 26B). These patterns may be related to transport processes in the northern California Current: anomalously low numbers of copepod species are associated with the transport of coastal subarctic water into the coastal waters of the northern California Current

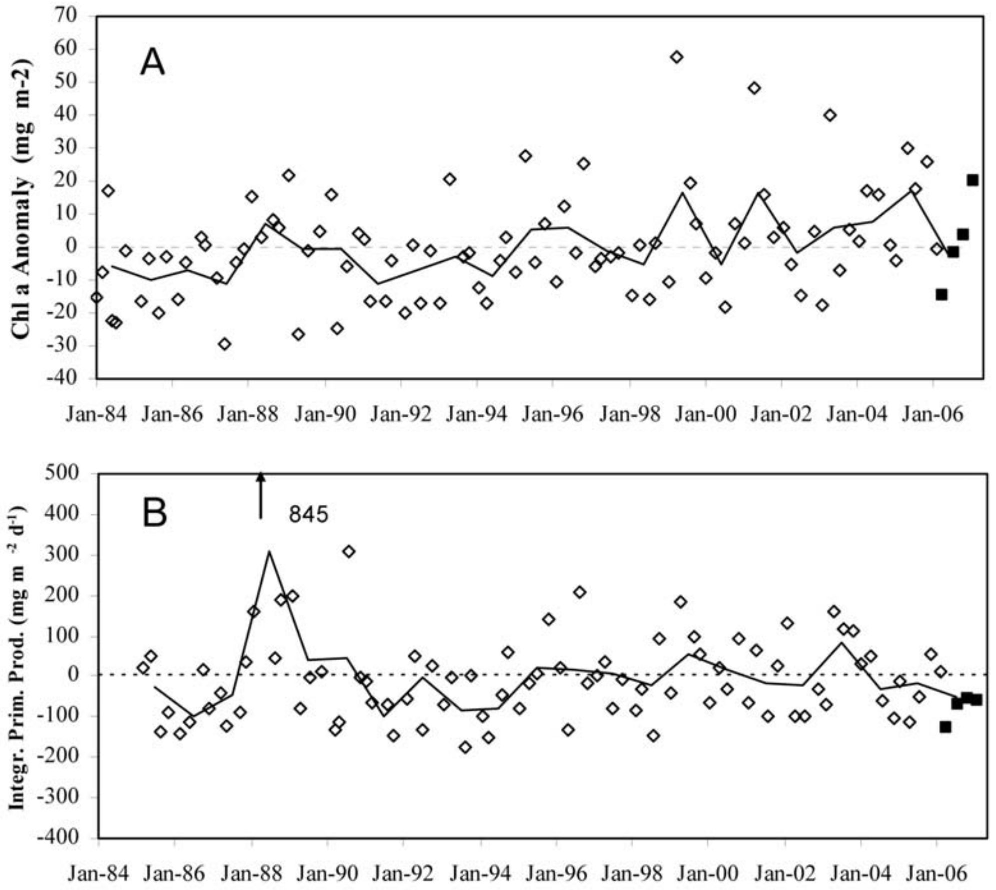

Figure 23. CalCOFI region averages for standing stocks of chlorophyll *a* (A) and rates of primary production integrated to the bottom of the euphotic zone (B) plotted against time. Data and symbol codes are the same as those in Figure 9.

(as in 1999–2002), whereas anomalously high numbers of species are associated with either a greater amount of onshore transport of warm, offshore, subtropical water, or northward transport of subtropical coastal neritic water along a coastal corridor (as happened in late 2002–early 2006). Copepod species richness may also be related to the PDO (fig. 26A), lagging that index by about six months.

Interannual variability of euphausiid egg abundances is very high off Oregon (station NH 05, fig. 27). Seasonal averages of egg abundances vary by orders of magnitude among years (tab. 2). The year 2005 was extraordinary in that large numbers of eggs were found early in the year (900 per cubic meter in February), but few eggs in March through June. Once upwelling was initiated (in mid-July) euphausiids began to spawn, and by September average egg abundances were among the highest of any summer. 2006 saw the continuation of a trend to very high concentrations of euphausiids at this inner-to-mid shelf station. We attribute the enhanced egg concentrations to higher numbers of adults in coastal waters during late summer 2005 and into the summer of 2006.

TABLE 2

**Abundance of euphausiid eggs (number $m^{-3}$) at station NH 05 on the Newport line, averaged for spring (March–June), summer (July–August), and for the May–September upwelling season.**

| Year | Mar–Jun | Jul–Aug | May–Sep |
|---|---|---|---|
| 1996 | 0.4 | 45.2 | 24.2 |
| 1997 | 0.6 | 50.0 | 30.6 |
| 1998 | 0.2 | 0.5 | 1.2 |
| 1999 | 99.3 | 27.3 | 23.8 |
| 2000 | 22.9 | 437.7 | 220.0 |
| 2001 | 11.4 | 52.1 | 24.5 |
| 2002 | 3.8 | 112.5 | 62.5 |
| 2003 | 0.2 | 18.2 | 8.4 |
| 2004 | 6.9 | 154.1 | 66.2 |
| 2005 | 0.2 | 38.8 | 302.4 |
| 2006 | 0.8 | 867.0 | 416.7 |

***CalCOFI:*** Macrozooplankton displacement volumes were reprocessed for this year's report as described in methods. Macrozooplankton displacement volumes were below expected values for the respective seasons in July 2006 and January 2007 and close to expected values for the summer and fall of 2006 (fig. 28A). Lower-than-expected values during the summer may have been due to upwelling-unfavorable conditions off southern

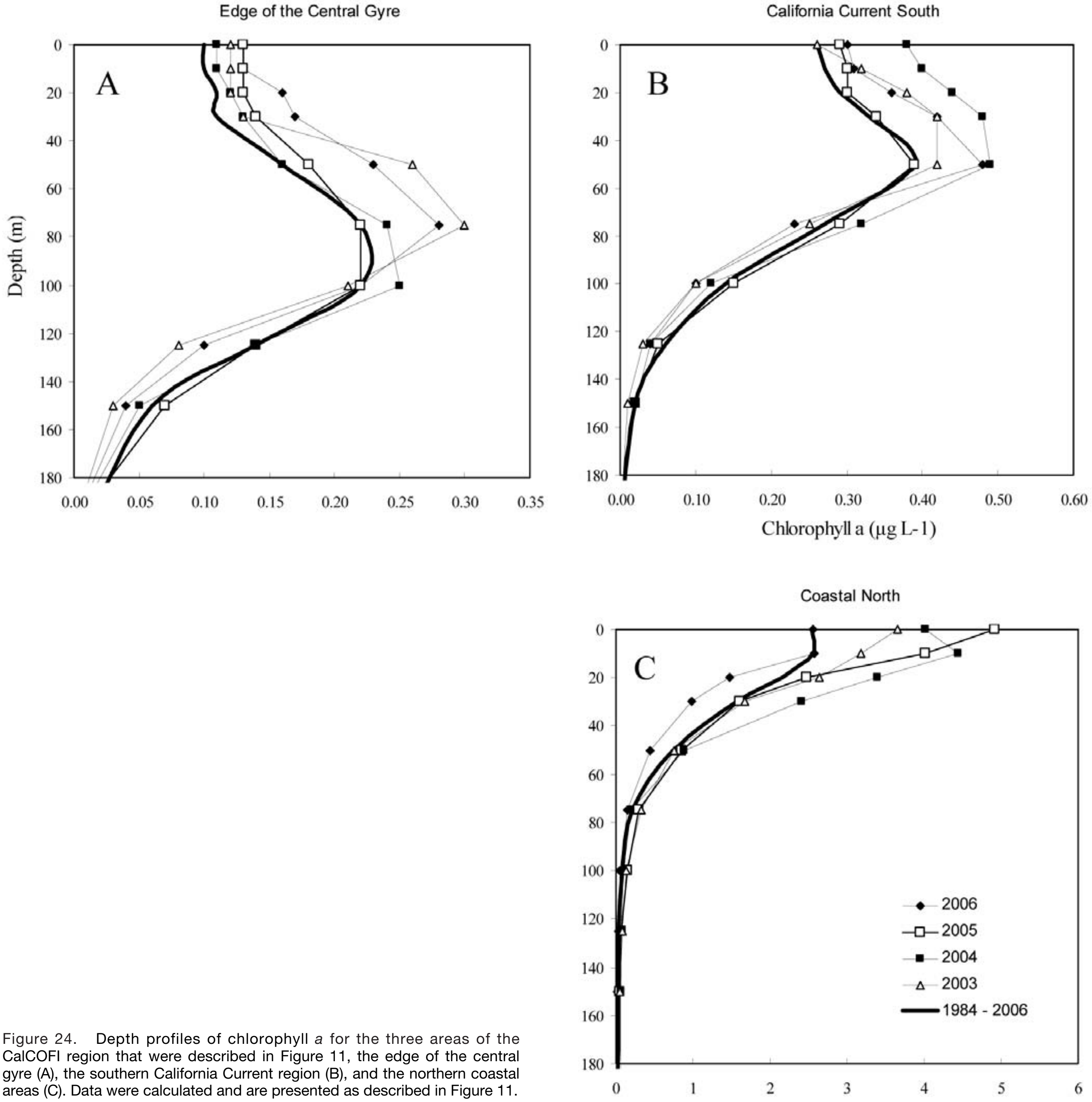

Figure 24. Depth profiles of chlorophyll *a* for the three areas of the CalCOFI region that were described in Figure 11, the edge of the central gyre (A), the southern California Current region (B), and the northern coastal areas (C). Data were calculated and are presented as described in Figure 11.

California during this time (fig. 4). Average macrozooplankton displacement volumes for 2006 continued the trend of declining zooplankton volumes observed since the beginning of 2000 (Peterson et al. 2006). Trends of declining zooplankton volume observed in the time periods (A) 1984 to 1998 and (B) 1999 to 2007 (fig. 28B) are clear ([A] $r^2 = 0.32$; [B] $r^2 = 0.33$). Excluding data corresponding to the 1997–98 El Niño does not change regressions (data not shown).

## Fish

***Washington-Oregon: Forage Fish species (whitebait smelt, herring, anchovies, sardines):*** Very low numbers of all species of small pelagic fishes were seen during the 1998 El Niño event and during 1999 (fig. 29A). As temperatures cooled, stocks increased by factors ranging from 5.6 (sardines) to 240 (whitebait smelt) in 2000, and they remained high through 2003. Following the change to warm ocean conditions in 2003, they declined

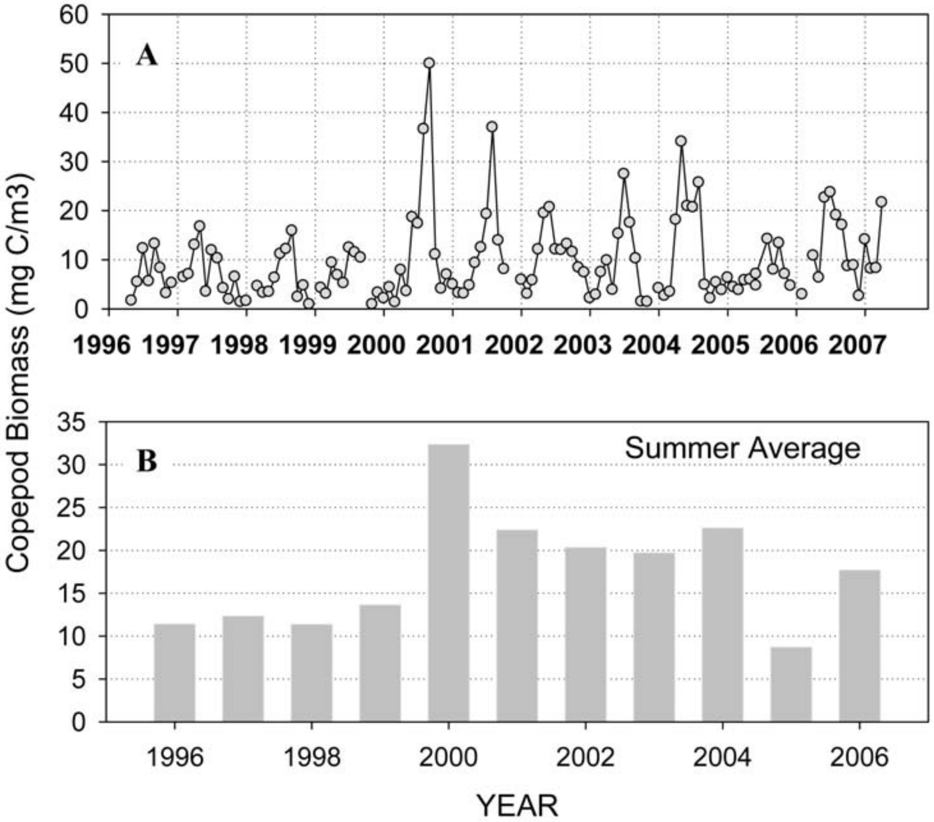

Figure 25. Newport Time series of monthly-averaged values of copepod biomass measured at a mid-shelf station, NH-05, from 1996–present, along with summer-averaged values of copepod biomass measured at NH-05.

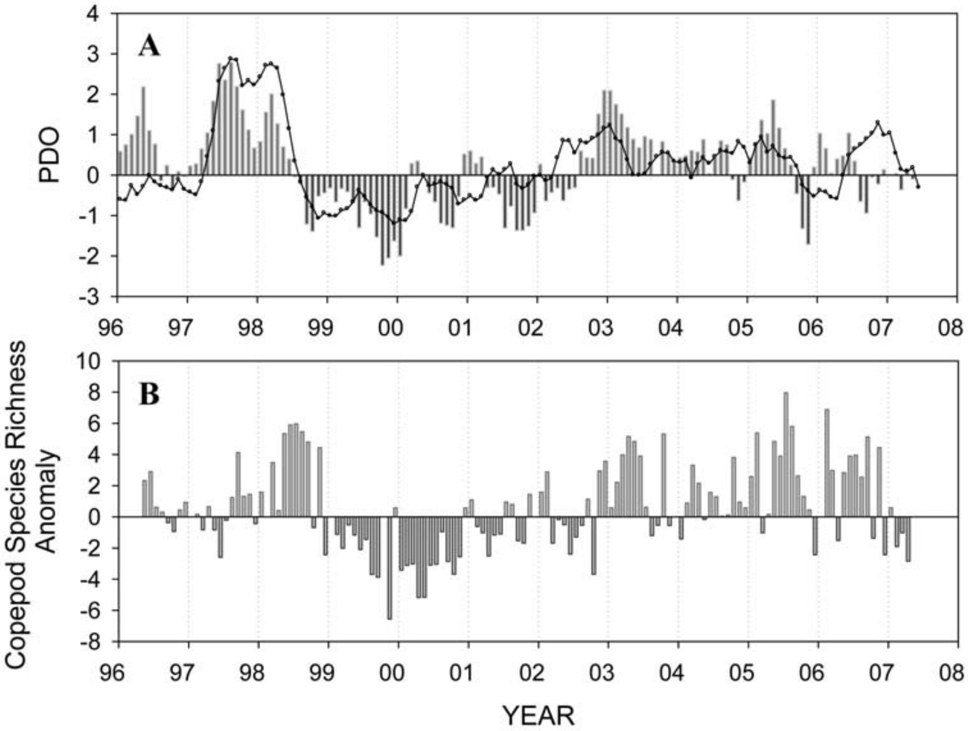

Figure 26. Newport. Time series of the Pacific Decadal Oscillation (upper panel, bars), Multivariate ENSO Index (upper panel, line), and monthly anomalies of copepod species richness at station NH-05, from May 1996 through March.

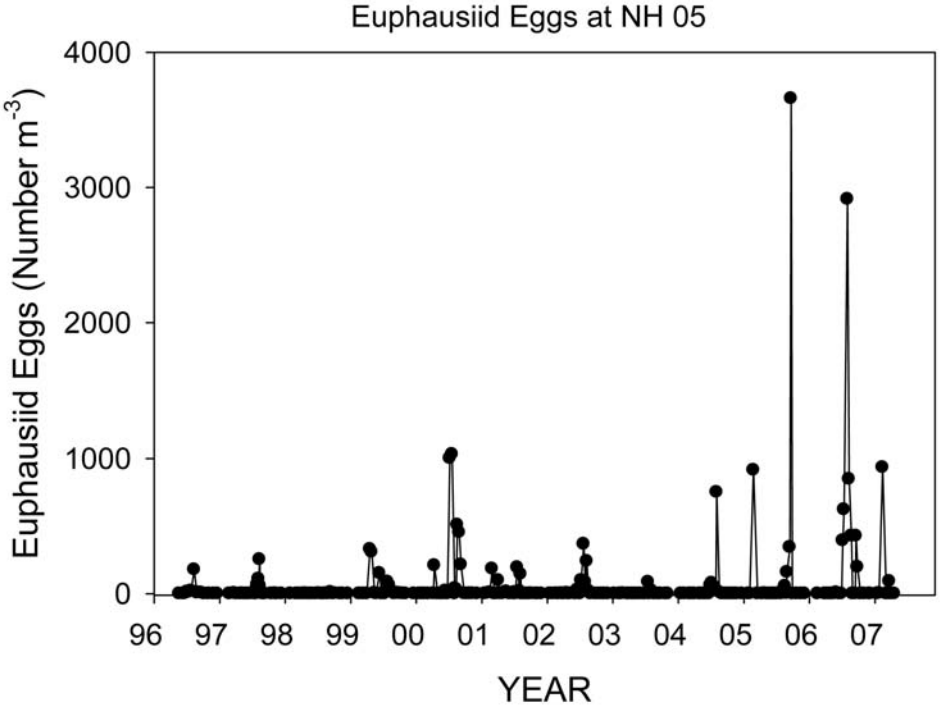

Figure 27. Time series of euphausiid eggs at station NH 05, from 1996 to spring 2007. Note the extraordinary peaks in summer 2005 and 2006.

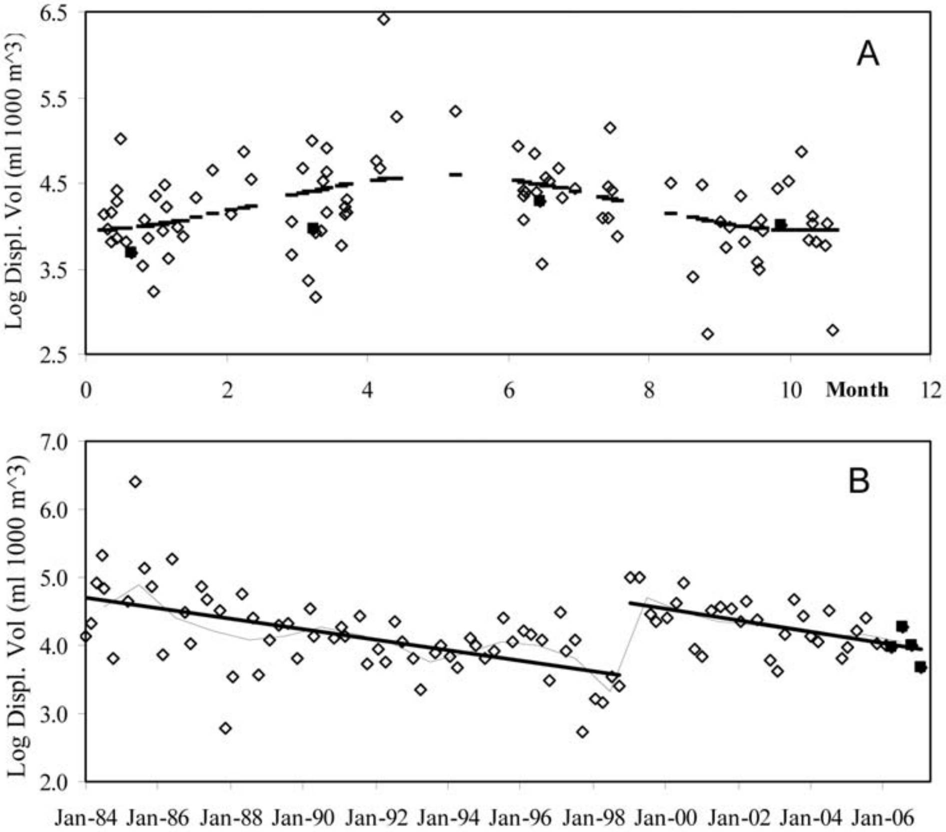

Figure 28. The Log of CalCOFI cruise mean macrozooplankton displacement volumes plotted against the time (A) and the month of the year (B). Annual averages are connected by solid lines; long term trends for the time periods 1984 to 1997 and 1998 to 2006 are indicated using the two straight lines.

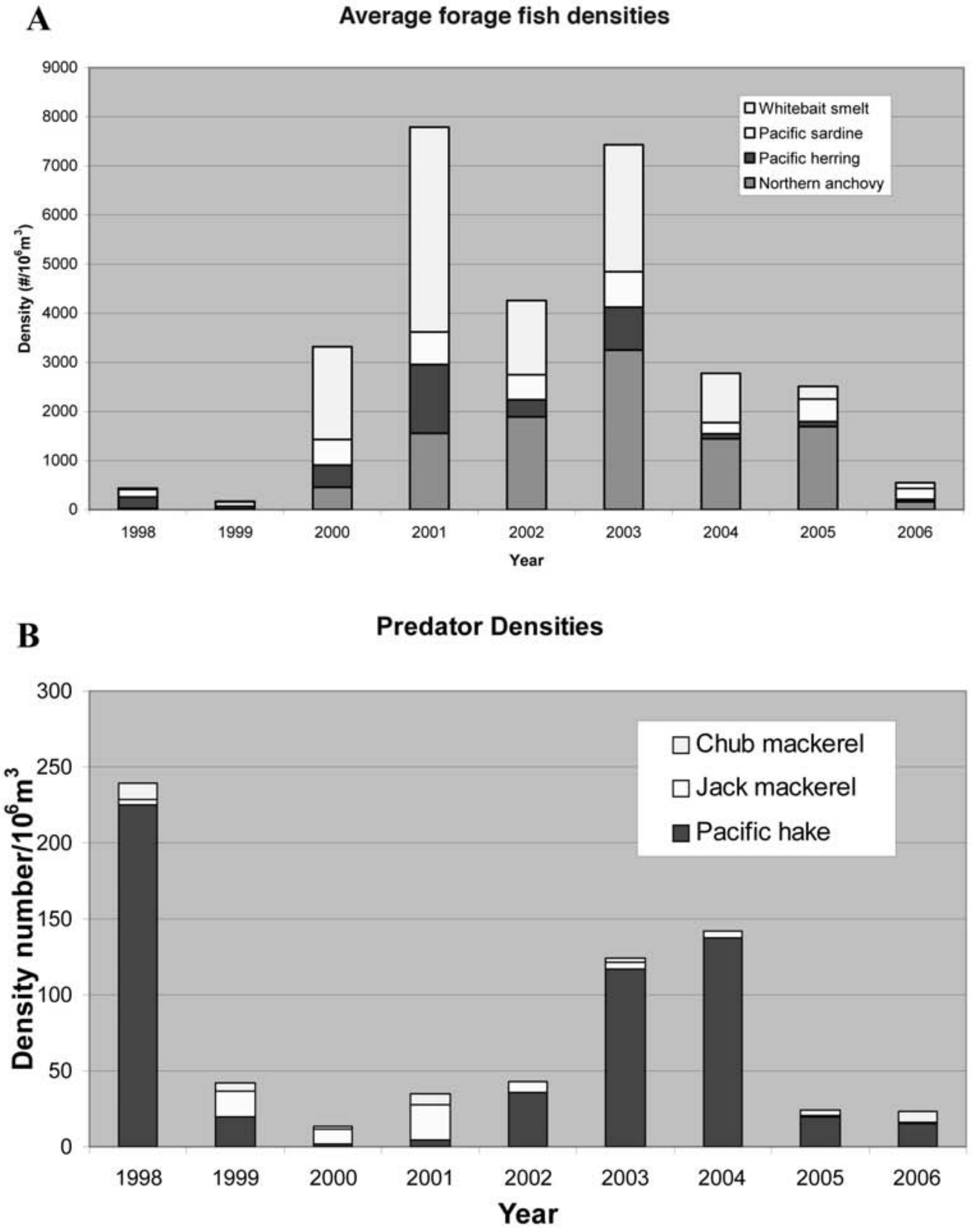

Figure 29. Densities of forage fish (A) and predatory fish (B) from rope trawl surveys conducted in coastal waters off southern Washington.

in 2004–05. Numbers of anchovies and sardines remained relatively high through 2005, whereas herring and whitebait smelt declined to 10% of the maximum numbers observed in 2001. Forage fish numbers in 2006 were among the lowest of the nine-year time series.

Because most forage fish recruitment (i.e., the larval-to-juvenile transformation in summer and fall) happens after our survey period (spring and summer), we do not catch most forage fishes in our trawls until they are at least one year old. Thus, forage fish densities appear to reflect oceanographic conditions from the previous year. Very low values observed in 2006 (fig. 29A) are almost certainly due to very poor forage fish recruitment from adults that spawned in 2005, due to the very warm and poor ocean conditions in spring and early summer of 2005.

***Washington-Oregon: Predatory Fish:*** The pelagic rope trawl also captures Pacific hake, jack and chub mackerel, and spiny dogfish. Catches of adult Pacific hake were somewhat related to ocean conditions. High catches occurred during the warm 1998 El Niño event, low catches during the subsequent cool years (1999–2002). Although increasing abundances were seen during the warm years of 2003–04 (fig. 29B), numbers were re-

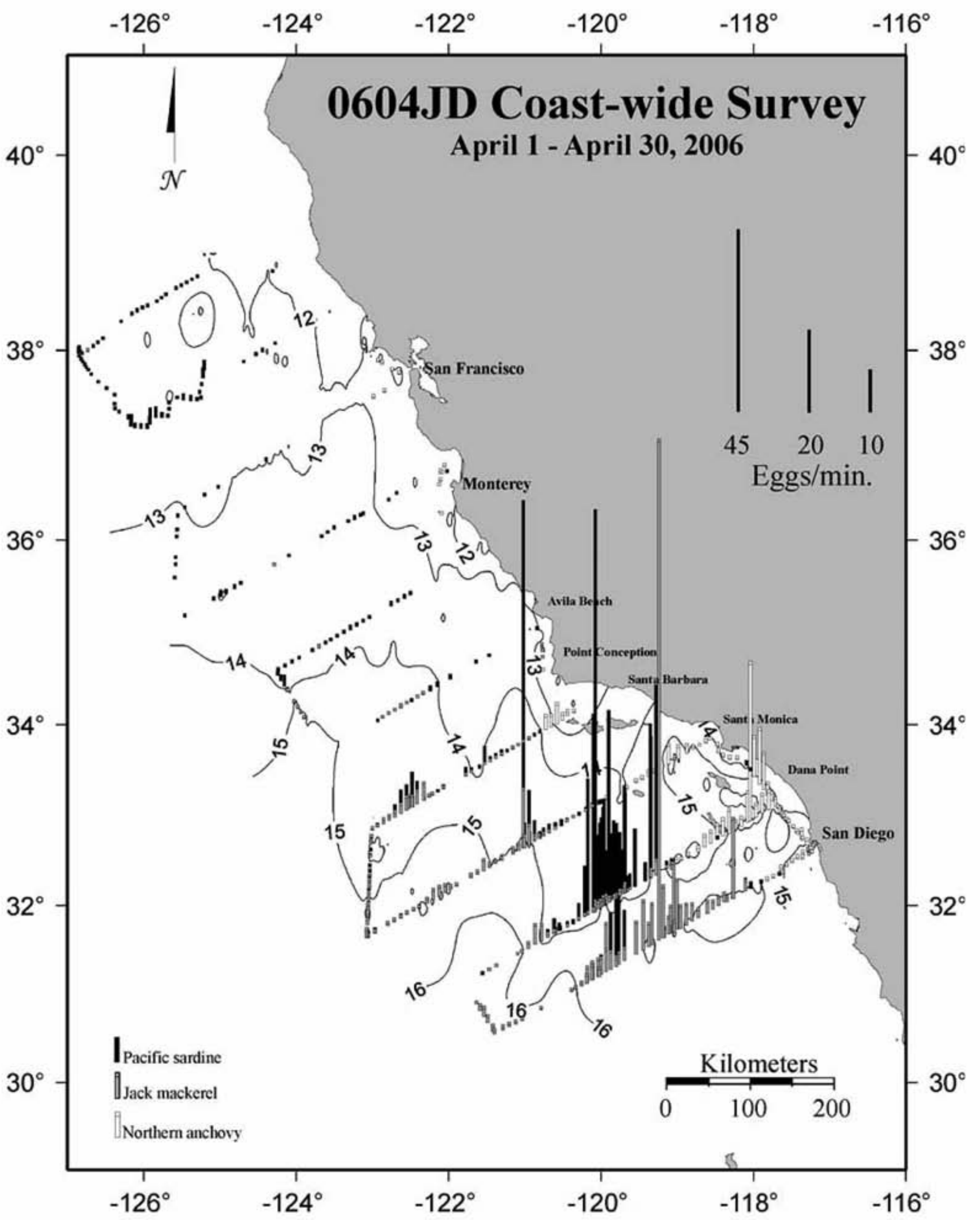

Figure 30. Rate of occurrence of eggs of Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), and jack mackerel (*Trachurus symmetricus*) sampled with the continuous underway fish egg sampler (CUFES) and sea surface temperatures in 1–30 April 2006. One egg per minute corresponds to approximately three eggs per cubic meter.

duced in both 2005 and 2006, also warm years. We had expected to see increased numbers of adult Pacific hake in 2005 and 2006, because hydrographic conditions and zooplankton species composition resembled the 1998 El Niño event. However, this expectation was not met and we do not have an explanation.

***California: Spawning of small pelagics:*** In the spring of 2006, eggs of sardine and jack mackerel were more abundant than anchovy during early April (fig. 30). In late April to early May few sardine eggs were observed south of Cape Mendocino, yet relatively abundant anchovy and jack mackerel were observed south of Point Conception, with anchovy near the shore in the California Bight and jack mackerel offshore (fig. 31). Sardine eggs were concentrated in two areas: between CalCOFI lines 95–86.7, and a narrow strip between 40°N and 42°N latitude (fig. 30 and 31). The area with low density of eggs north of CalCOFI line 86.7 had high egg density in 2005 (Lo and Macewicz 2006), and the distribution of sardine eggs in 2006 differed from

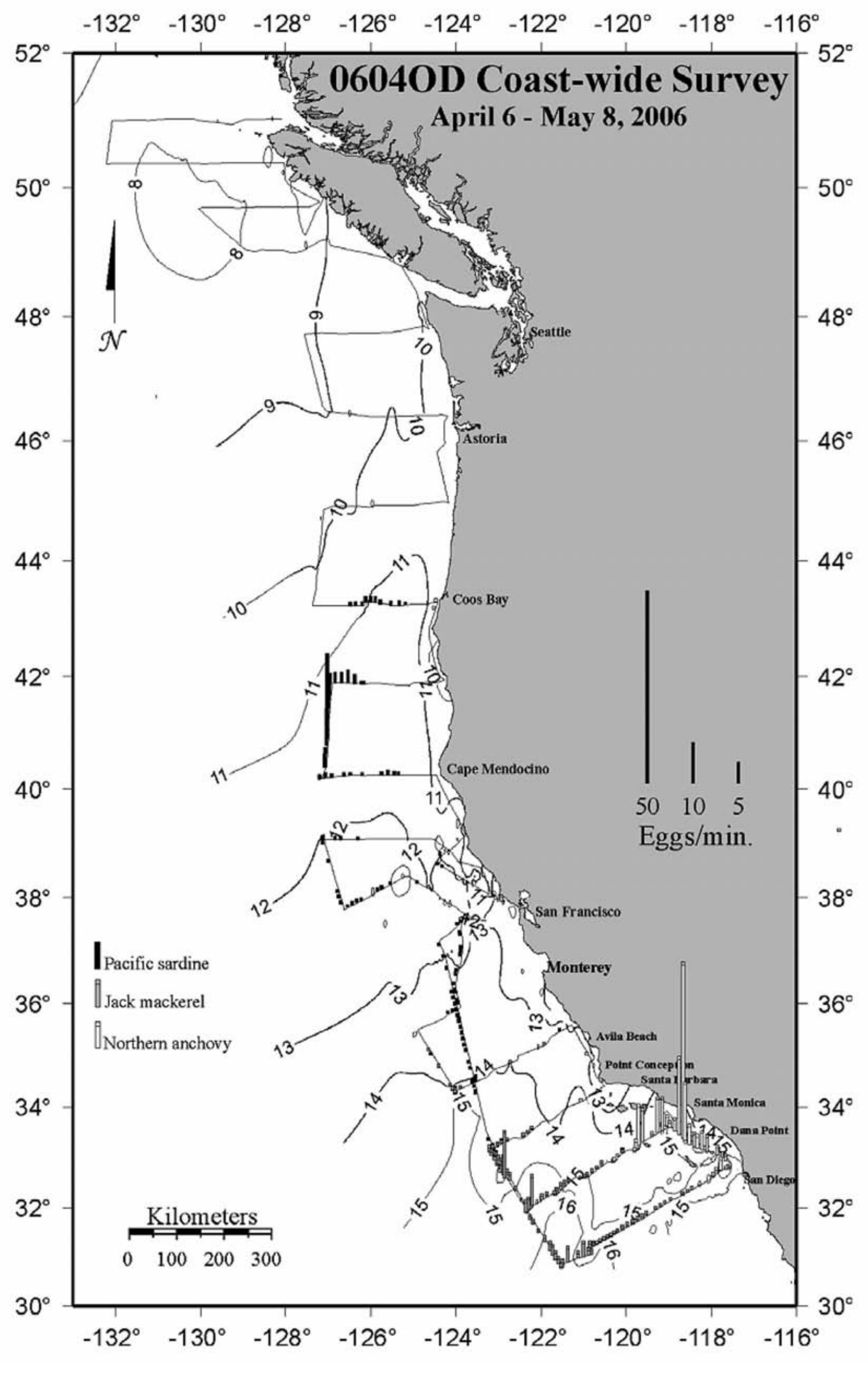

Figure 31. Rate of occurrence of eggs of Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), and jack mackerel (*Trachurus symmetricus*) sampled with the continuous underway fish egg sampler (CUFES) and sea surface temperatures in April 6–May 8, 2006.

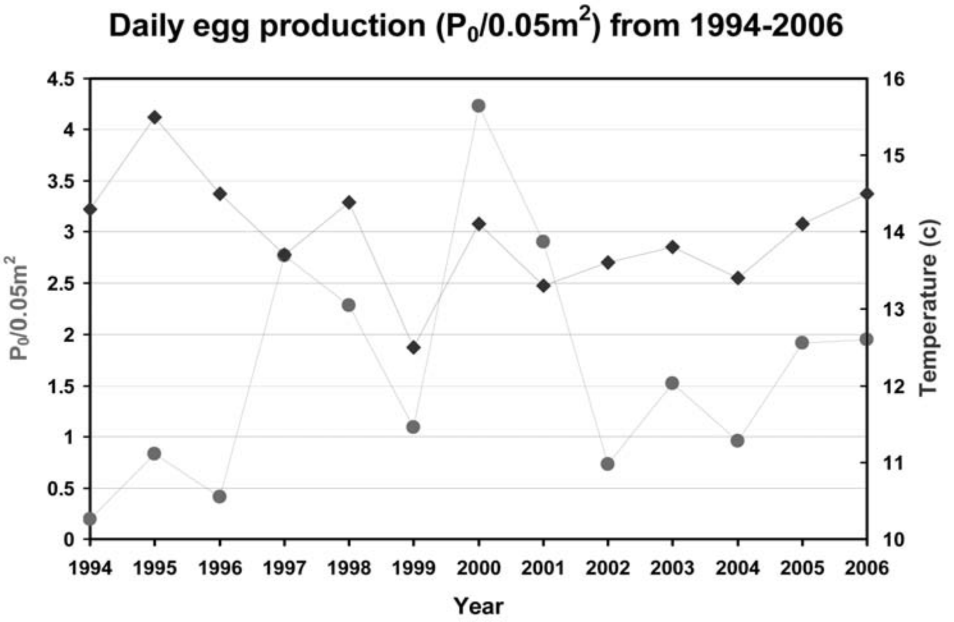

Figure 32. Daily egg production/0.05m$^2$ of Pacific sardine (*Sardinops sagax*) (circle) and average sea surface temperature (°C) (diamond) during March–May CalCOFI cruises and DEPM surveys from 1994–2006.

the past two years because very few were collected between CalCOFI lines 73.3 and 60 (fig. 30). This could be due to the shift of the spawning grounds, or to the delay of coverage of the central California area by the NOAA RV *David Starr Jordan*. The area north of 40°N latitude has been sampled relatively little using ichthyoplankton net tows. The high concentration of sardine eggs in this area was an indication of a spawning ground for sardine (fig. 2). In addition, unlike recent years, spawning activity in 2006 was strong in the southern part of the survey area off San Diego. The extent of spawning south of San Diego will not be known without information from Mexican surveys, i.e., IMECOCAL.

The spawning biomass of Pacific sardine, a fishery-independent population index, is positively related to the daily egg production, in particular if the number of oocytes per biomass weight remains constant (Lo et al. 2007). Daily egg production and the average SST during 1994–2006 are not directly related. However, in most years, except 1997 and 2002, year to year changes in daily egg production are inversely related to changes of sea surface temperature (fig. 32). This relationship is consistent with the assertion that high temperature is favorable for the Pacific sardine (Jacobs and MacCall 1995).

## California Sea Lions

California sea lions are one of the most abundant apex predators in the California Current System, with an estimated 237,000 to 244,000 sea lions in U.S. waters (Carretta et al. 2006). Sea lions respond to climatic forcing with changes in diet, movement, and foraging behavior, highlighting the utility of this predator as a sentinel

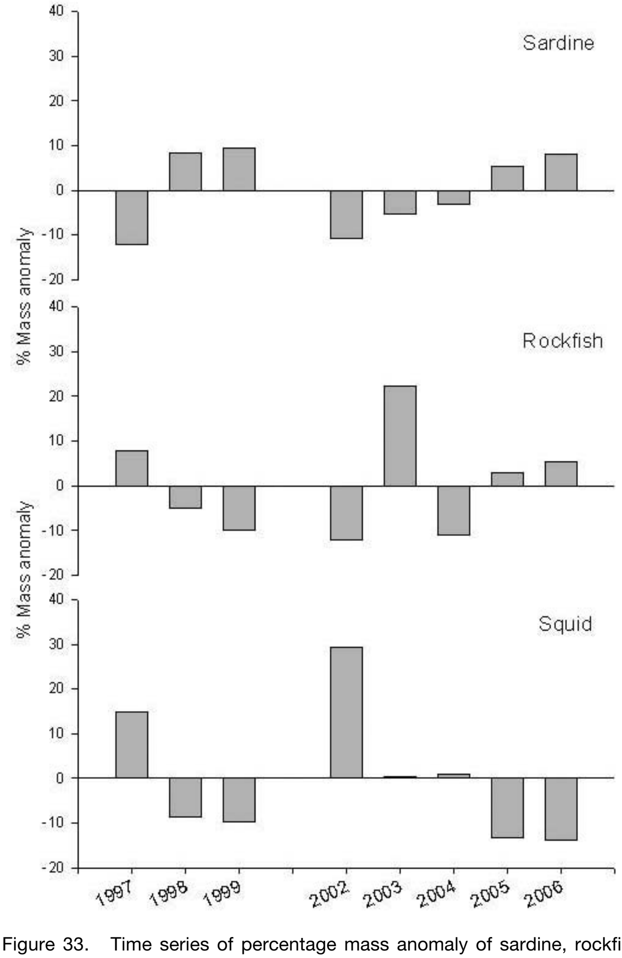

Figure 33. Time series of percentage mass anomaly of sardine, rockfish (*Sebastes* spp.), and market squid in the diet of California sea lions, Monterey Bay, 1997 to 1999 (Weise 2000; Weise and Harvey, In Review) and Año Nuevo Island 2002, to 2006 (Weise 2006; Weise and Harvey unpublished data).

TABLE 3
**Mean, standard deviation, and sample size of prey species identified in California sea lion (*Zalophus californianus*) fecal samples collected in Monterey Bay from 1997 to 1999 (Weise 2000; Weise and Harvey, In Review) and Año Nuevo Island from 2002 to 2006 (Weise 2006; Weise and Harvey unpublished data).**

| | Rockfish | | | Sardine | | | Squid | | | Anchovy | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean (cm) | SD (cm) | n | Mean (cm) | SD (cm) | n | Mean (mm) | SD (mm) | n | Mean (cm) | SD (cm) | n |
| 1997 | 29.2 | 9.9 | 79 | 22.8 | 3.8 | 99.0 | 117.2 | 11.4 | 623 | 10.8 | 2.4 | 107 |
| 1998 | 16.7 | 8.2 | 268 | 19.0 | 3.4 | 949.0 | 70.7 | 15.1 | 707 | 11.3 | 2.1 | 305 |
| 1999 | 22.2 | 9.3 | 35 | 18.5 | 2.2 | 394.0 | 100.8 | 19.8 | 55 | 11.9 | 2.0 | 221 |
| 2002 | 25.5 | 10.2 | 195 | 22.3 | 4.8 | 47.0 | 108.1 | 23.8 | 1422 | 12.8 | 1.7 | 72 |
| 2003 | 18.4 | 28.4 | 260 | 19.0 | 5.4 | 110.0 | 90.8 | 38.6 | 596 | 10.9 | 2.2 | 141 |
| 2004 | 14.2 | 4.3 | 6 | 23.9 | 5.4 | 8.0 | 108.6 | 15.9 | 174 | 10.2 | 1.7 | 122 |
| 2005 | 24.8 | 12.1 | 17 | 16.9 | 8.6 | 62.0 | 86.5 | 25.4 | 33 | 11.5 | 1.7 | 298 |
| 2006 | 25.8 | 4.4 | 36 | 18.3 | 4.0 | 185.0 | 82.2 | 15.8 | 22 | 11.2 | 2.1 | 642 |

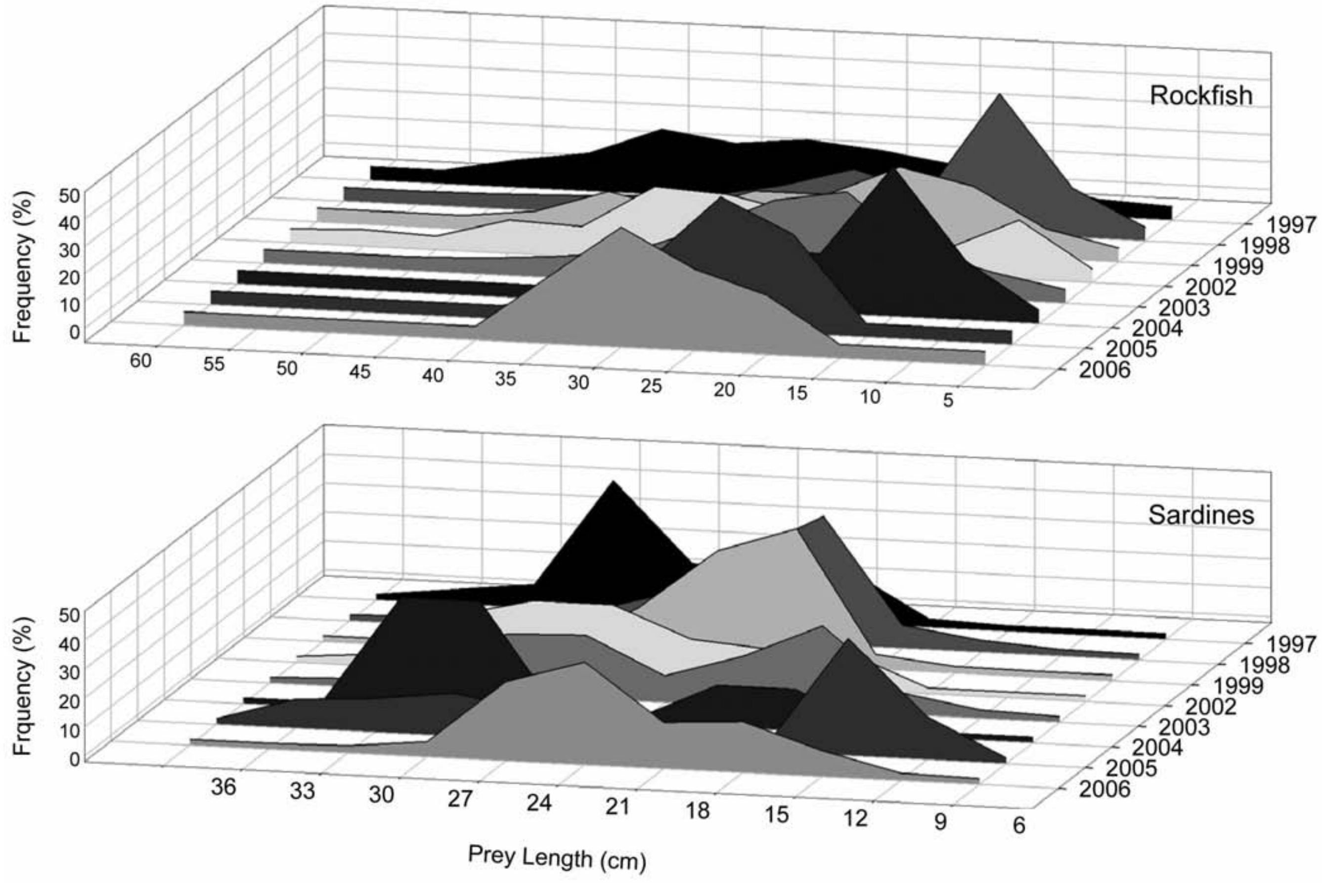

Figure 34. Time series of the size distribution of sardines and rockfishes (*Sebastes* spp.) utilized as prey by California sea lion reconstructed from sea lion fecal samples collected in Monterey Bay, 1997 to 1999 (Weise 2000; Weise and Harvey, In Review), and Año Nuevo Island, 2002 to 2005 (Weise 2006; Weise and Harvey unpublished data).

of climatic and biological variability and change (Weise et al. 2006).

The diet of California sea lions during 2006 off central California was similar to 2005. Anomalous oceanographic conditions early during the season resulted in positive anomalies in the consumption of rockfish (*Sebastes* spp.) and sardines (*Sardinops sagax*), and negative anomalies in market squid (*Loligo opalescens*; fig. 33). These species dominated the overall diet with rockfish constituting 27.5% of the total mass consumed and sardines 25.6%. Although northern anchovies (*Engraulis mordax*) were the most important prey item in 2005 (31.2%), in 2006 they had only a slightly positive percentage mass anomaly and they had decreased to the third most important prey species (20.6%); however, length of anchovy consumed remained unchanged between years (tab. 3).

Decreased anomaly of market squid and increased anomaly of sardine in the diet during 2005 and 2006 were similar to trends observed in sea lion diet during the 1997–98 El Niño (fig. 33). Size of sardine consumed in 2006 were adults (27–36 cm) and similar in size to those eaten during 1997–98 El Niño (ANOVA, Tukey MSD Multiple comparisons, $F = 25.83$, $p = 0.228$, $n = 1846$), but smaller than sardines consumed during 2005 ($p = 0.178$; tab. 3, fig. 34). Squid were comparatively smaller in size during 2005 and 2006 and were similar to sizes consumed during the 1997–98 El Niño (tab. 3). Sizes of rockfish consumed in 2006 were similar to those eaten during 2005 (ANOVA, Tukey MSD Multiple comparisons, $F = 31.83$, $p = 1.000$, $n = 1003$), but larger than rockfish consumed during the 1997–98 El Niño ($p < 0.001$). Similar diet anomalies during 2005 and 2006 in central California may reflect the late onset of upwelling during both years. This work highlights the plasticity of the sea lion diet, and how it varies with climatic and biological conditions.

## Avifauna

The 2005 breeding failure of planktivorous auklets on the Farallon Islands was unprecedented (Sydeman et al. 2006). To further explore the relationships between breeding and foraging, we focus on a comparison between reproductive success of seabirds on the Farallones and summer-time distribution and abundance of birds at sea in the CalCOFI region, using the data from 2006. To provide a longer-term perspective we also compare recent observations to reproductive and community dynamics in the cold-water period (August 1998–July 2002) and subsequent warm-water period (August 2002–September 2005).

***Farallon Island Seabird Productivity, 2006.*** The productivity of 6 species of seabirds at southeast Farallon Island has been monitored for the last 37 years by the PRBO. For comparative purposes we grouped species according to a basic life history pattern: those producing a single egg clutch, i.e., a conservative life history, such as Cassin's auklet (*Ptychoramphus aleuticus*), common murre (*Uria aalge*), and rhinoceros auklet (*Cerorhinca monocerata*); and those producing multiple-egg clutches, i.e., flexible life histories, such as Brandt's cormorant (*Phalacrocorax penicillatus*), pigeon guillemot (*Cepphus Columba*), and pelagic cormorant (*Phalacrocorax pelagicus*). Five of these six species experienced pervasive breeding failures or significant reductions in breeding success in 2006, with only the Brandt's cormorant performing at a level comparable to the previous eight years. Most notably, the Cassin's auklet experienced nearly complete breeding failure in 2006 for the second year in a row. Productivity for this species has increased slightly in 2007 (~0.3 chicks/pair; PRBO unpublished data), but is still well below the 36-year average of ~0.7 chicks per pair (Sydeman et al. 2001, 2006). The pelagic cormorant also essentially failed to reproduce (0.09 chicks/breeding pair), and common murre, pigeon guillemot, and rhinoceros auklet showed substantial negative productivity anomalies (fig. 35).

Clustering of seabird productivity data over the eight-year period revealed three distinct clusters. The last two years (2005 and 2006), characterized by pervasive reductions in productivity, clustered together (fig. 36) and contrasted sharply with the first two years (1999 and 2000) of high seabird productivity for all species. Three years of intermediate productivity (2001, 2002, and 2004) clustered together, despite some year-to-year fluctuations. The only year that stood alone was 2003, a warm-water year characterized by a decline in seabird productivity from the previous year (2002) for all the six seabird species monitored. The cluster analysis demonstrates the tremendous variability in seabird productivity observed over the past eight years, corresponding to a number of oceanographic and atmospheric anomalies.

***Pelagic Seabirds in the CalCOFI Region.*** To illustrate fluctuations in marine bird communities, we focus on four "indicator" species with different water mass and biogeographic affinities (fig. 37), as observed during the summer CalCOFI cruises. The subtropical pink-footed shearwater (*Puffinus creatopus*) occurs off southern California waters between spring and fall, and in the past has become more abundant three to six months before warm water arrives in the regions (Hyrenbach and Veit 2003). The Cook's petrel (*Pterodroma cookii*) also occurs off southern California during spring–fall and moves shoreward during periods of warm water (Hayward et al. 1999). We also consider two species that breed on the Farallones: the Cassin's auklet and the common murre (Sydeman et al. 2001). Off southern California these latter species are more abundant during cold-water periods (Hyrenbach and Veit 2003). To assess the responses of these species to oceanographic variation, we correlated their summertime densities with the mean 10 m water temperature along CalCOFI line 90 using Spearman rank correlations.

The summer densities of the two warm-water indicators (Cook's petrel and pink-footed shearwater) varied substantially from year to year (fig. 37). The petrel occurred at densities above average during 2002–2004, and was slightly below average in 2006. Conversely, this warm-water species occurred at very low densities (<0.1 bird km$^{-2}$) during the cold-water years of 1999–2001. Overall, Cook's petrel densities were significantly correlated with line 90 near surface temperatures for the period ($r_s = 0.65$, $n = 8$). The abundance of the pink-footed shearwater peaked in 2001 (>1 bird km$^{-2}$) with low densities (0.1–0.5 bird km$^{-2}$) during the rest of the

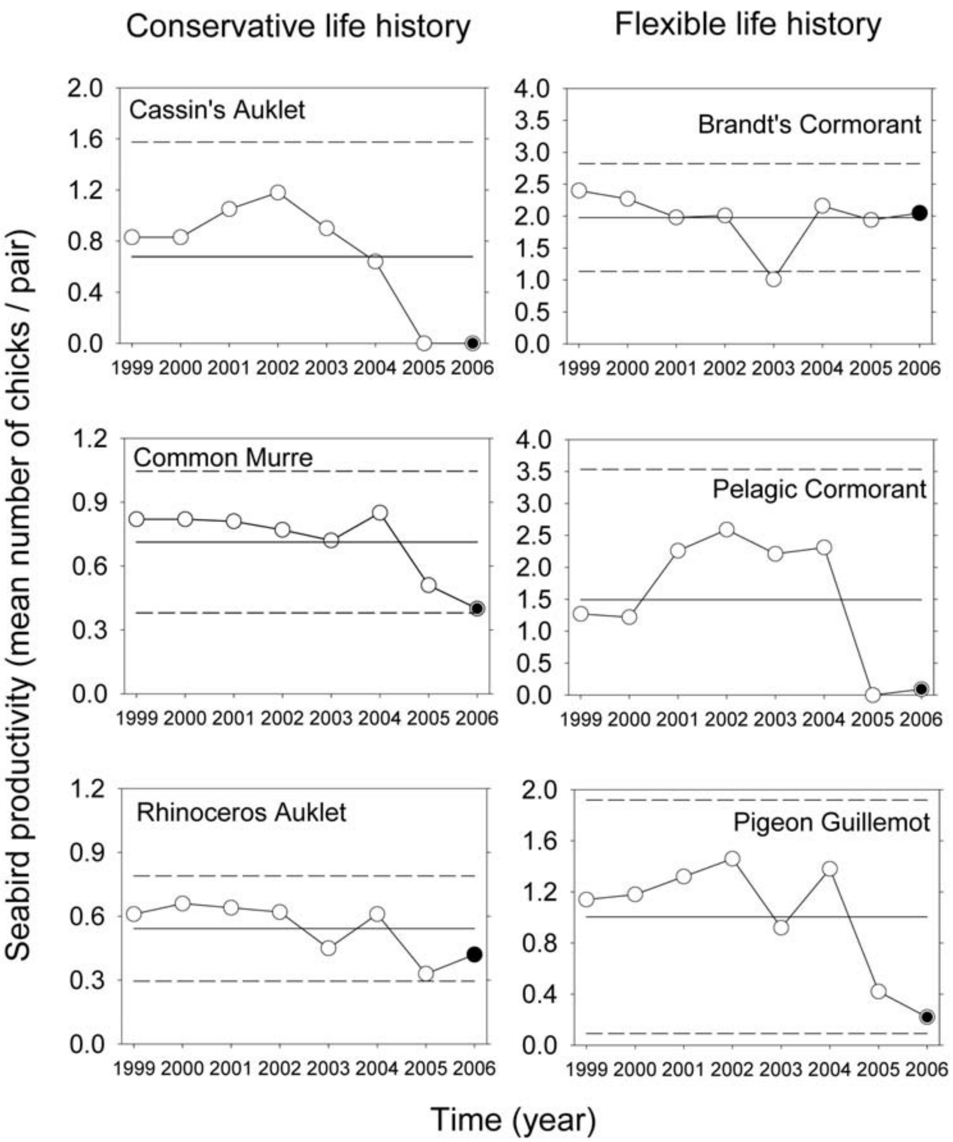

Figure 35. Productivity of six seabird species breeding at southeast Farallon Island (central California). The average (1999–2006) productivity is depicted by the solid horizontal lines and the hatched lines illustrate the year-to-year variability (mean ± 2 S.D.). Filled circles highlight productivities in 2006.

time series. Shearwater densities and concurrent water temperature were not significantly correlated ($r_s$ = + 0.02, $n$ = 8). The Cassin's auklet was anomalously abundant in 2005 and especially 2006, with densities well above the long-term mean. While the auklet abundance was not correlated with concurrent water temperature ($r_s$ = + 0.37, $n$ = 8), we found a significant negative correlation between auklet reproductive success at the Farallones and density at sea during summertime CalCOFI cruises ($r_s$ = –0.63, $n$ = 8). This result reinforces the idea put forth by Sydeman et al. (2006) that during the recent years (2005 and 2006) of catastrophic reproductive failure at the Farallones, auklets dispersed south and occurred in exceptionally high densities off southern California. Other auklet colonies breeding on

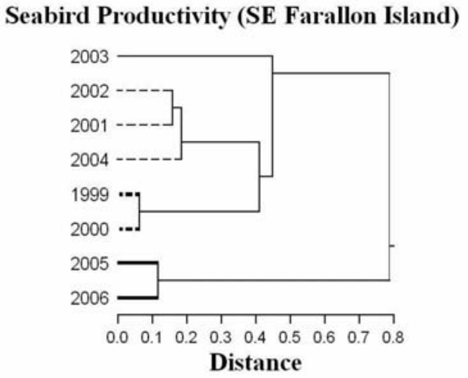

Figure 36. Cluster tree of marine bird productivity for the sea birds breeding in the Gulf of the Farallones. The Euclidean distances are based on the hierarchical clustering technique, with the median linkage algorithm. The thickness and hatching of the lines identify years that clustered together.

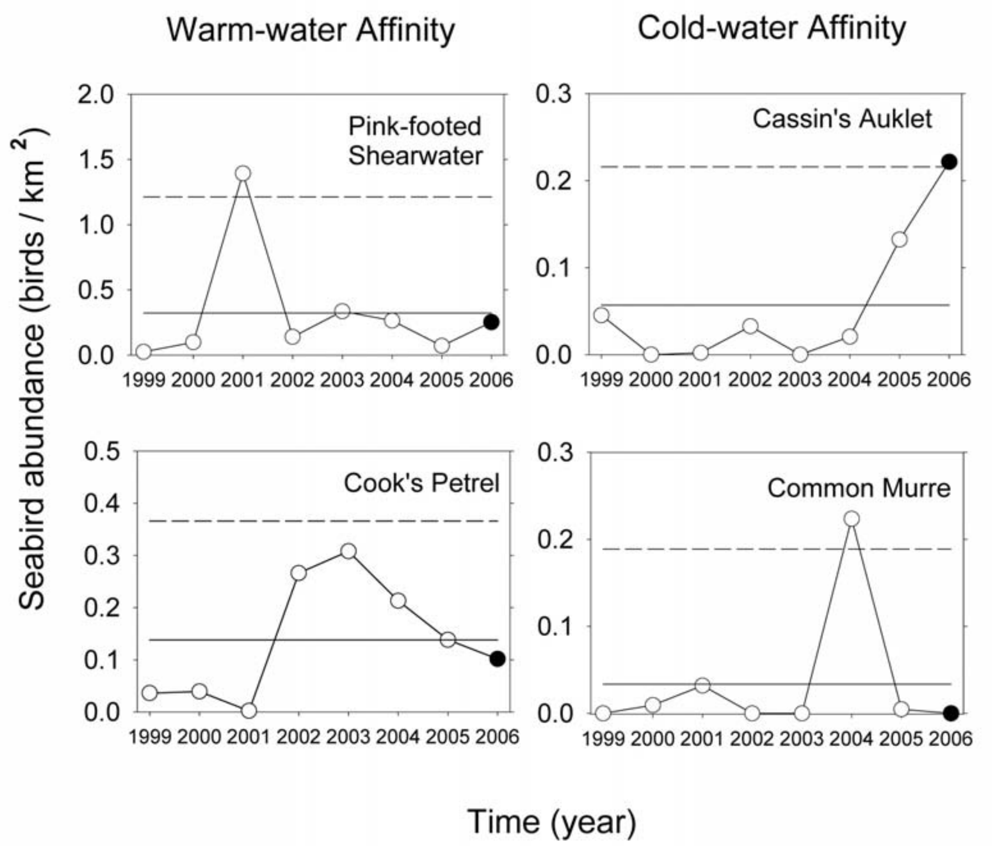

Figure 37. CalCOFI area at-sea abundance of four seabird species with different water temperature affinities during the summer. The average (1999–2006) densities are depicted by the solid horizontal lines and the hatched lines illustrate the year-to-year variability (mean ± 2 S.D.). Filled circles highlight abundances in 2006.

the Channel Islands and south of the Southern California Bight (San Benitos Islands, Mexico) also showed reproductive failures in 2006 (J. Adams and S. Wolf, pers. comm.). The Farallones population is the largest population, and is thus the most likely source of birds observed in the Southern California Bight, but some birds may have originated from the south. The common murre was anomalously abundant during the summer of 2004, but was essentially absent in other years, including 2005 and 2006. Murre abundance was weakly negatively correlated with concurrent water temperatures ($r_s$ = –0.46, *n* = 8).

## DISCUSSION

External forcing acting on the CCS includes local forcing with time scales on the order of months to years, forcing by ENSO events with time scales on the order of a year, and basin-scale changes on the order of years to decades, which may or may not be cyclical. In addition, global temperatures are increasing. The last years have been unusual in the California Current System. Basin scale climate indicators were neutral. Coherent patterns did not emerge for the whole CCS; no single "state" could be ascribed to the whole system. The last event that affected the CCS as a whole was the intrusion of fresh and cold water from the subarctic (Venrick et al. 2003). Corresponding salinity anomalies were evident in all time series collected along the coast from about 2002 until 2005 or 2006, depending on location. These salinity anomalies have returned to normal in all regions.

Observations over the last few years have shown that regional and local processes can dominate events in the different parts of the CCS, although biological interactions may spread local effects more broadly. For example, off Oregon and central California the dominant event over the last three years has been the onset of upwelling (Schwing et al. 2006; Peterson et al. 2006; this report). A late onset of upwelling in 2005 and 2006 caused delays or failures in the development of euphausiid populations. The absence of these prey items during time periods critical for breeding seabirds led to significant reductions and even total failures of seabird reproduction (Sydeman et al. 2006; this report). The productivity of Cassin's auklets and pelagic cormorants on the Farallon Islands was virtually zero during these two years. The significant increase of auklet populations off southern California during the summers of 2005 and 2006 suggests that populations based on the Farallon

Islands may have migrated south in search of feeding grounds (Sydeman et al. 2006; this report). The early and strong onset of upwelling off Oregon and central California in 2007 and the partial recovery of auklet productivity suggest that the 2005 and 2006 upwelling anomalies and their effects were ephemeral.

Upwelling-favorable winds were also weak or delayed off southern and Baja California during 2005 and 2006, but the biological consequences appear to have been relatively minor (this report).

In coming years, the dominant aspect of change in the CCS may be that which is driven by global climate change. As global temperatures have been increasing, so have local temperatures, at least in the areas of the CCS with sufficiently long temperature records (Roemmich and McGowan 1995; this report). It is likely, though difficult to prove, that these local changes are linked to global forcing. Other system properties are co-varying with these changing temperatures (e.g., nitracline depth, chlorophyll *a*, zooplankton displacement volume), suggesting that changing temperatures have significant impacts, directly or indirectly, on ecosystem structure. Currently our understanding of the linkages between temperature and ecosystem function are rudimentary, yet they are essential for accurate prediction of ecosystem response to global change. We conclude this annual report with a plea to all working in the CCS to search for relationships between changing temperatures and various indices of ecosystem function so that we may arrive at a deeper understanding of these when we synthesize these data for future reports.

## ACKNOWLEDGMENTS

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## Part II

# SYMPOSIUM OF THE CALCOFI CONFERENCE, 2006

### Asilomar Conference Grounds
### Pacific Grove, California
### 5 December 2006

## ECOLOGICAL INTERACTIONS USEFUL FOR MARINE ECOSYSTEM-BASED MANAGEMENT: THE ROLE OF POSITIVE SPECIES INTERACTIONS, ECOSYSTEM ENGINEERS, AND SPECIES DIVERSITY

Many fisheries in the United States and worldwide are in decline (Jackson et al. 2001; Rosenberg et al. 2006; Myers et al. 2007), spurring the U.S. Congress (Ecosystem Principles Advisory Council 1999), the Pew Oceans Commission (2003), and the U.S. Commission on Ocean Policy (2004) to recommend that ecosystem-based approaches be incorporated into fisheries management. In theory, these approaches will take into account interactions between target species, non-target species (including humans), and their environment. However, because they represent a fundamental shift away from the single-species management approaches that have traditionally been the mainstay of natural resource managers (Ricker 1954; Beverton and Holt 1957; Pella and Tomlinson 1969), are difficult to define (Larkin 1996), and will likely require additional data, these new ecosystem-based strategies have proven difficult to implement. Furthermore, changes in the physical environment are likely to have profound effects on species composition, interactions, productivity, and ecosystem processes (Hunter et al. 1988; Francis and Hare 1994), and these changes will need to be considered as managers formulate ecosystem-based approaches to fisheries management.

Recent advances in marine ecology and in modeling trophic interactions have led to new perspectives on marine community and ecosystem processes which can be incorporated into ecosystem-based management. For example, the presentations at CalCOFI's 2006 symposium highlighted aspects of marine systems, including species interactions, facilitation, and biodiversity, which have ramifications for ecosystem-based management. Two of the symposium presentations, Steven Palumbi's talk on "The ecosystem function of marine biodiversity," and Fiorenza Micheli's discussion of "Marine ecosystem-based management: theory and practice," were not submitted for publication, but we encourage readers to examine their related recent papers (e.g., Mumby et al. 2006; Worm et al. 2006).

Traditional approaches to fisheries management consider only species which are targeted for fishing and typically do not include interactions between target species and other organisms in the marine environment. In her contribution, Baskett (2007) examined both multispecies fisheries models and marine reserve models to examine the effects of incorporating species interactions on yields, fishing rates, and marine reserve size. She included a model which incorporated a positive interaction—the effect of red algae on spiny lobster recruitment—and examined the ways in which facilitation affects model outcomes.

Bracken et al. (2007) also considered the beneficial effects of habitat-forming species on fisheries stocks. Using data from groundfish test fisheries, they found that fish catches were higher where habitat-forming deep-water corals were present. Bracken et al. used the same dataset to evaluate the relationship between the diversity of fish caught and the abundance of both target (sablefish) and total fish caught. Based on these analyses, and a meta-analysis of the effects of foundation species in a variety of marine ecosystems, they propose ways in which species diversity and the presence of foundation species can be incorporated into fisheries management strategies.

Negative interactions between commercially harvested species also occur, and models that incorporate these interactions are usually consistent with lower yields of one or more species. For example, Emmett and Sampson (2007) used a trophic model to simulate interactions between Pacific hake, juvenile salmon, and forage fish. They found that multiple factors, including species interactions, river flows, and sea-surface temperatures, explained annual variation in marine survival of salmon. Their work highlights the necessity of incorporating both physical and biological variables into management strategies.

Finally, Ruzicka et al. (2007) examined trophic interactions in the Oregon upwelling system using trawl surveys and the Ecopath modeling framework. They found that large jellyfish are the major consumers of zooplankton during the late summer, diverting zooplankton production away from higher trophic levels. This research suggests that jellyfish and other non-target species can play dominant roles in mediating ecosystem functions and, ultimately, fisheries productivity.

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# SIMPLE FISHERIES AND MARINE RESERVE MODELS OF INTERACTING SPECIES: AN OVERVIEW AND EXAMPLE WITH RECRUITMENT FACILITATION

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## ABSTRACT

Accounting for species interactions is a key component of ecosystem-based management. Simple models of species interactions provide a framework for making qualitative comparisons and identifying critical dynamics. A review of multispecies-fisheries and marine-reserve models indicates that incorporating species interactions leads to decreased theoretical predictions for sustainable yield and harvest rates and to increased theoretical predictions for the reserve size necessary to protect populations; ontogenetic shifts in interactions also have a significant effect on multispecies model predictions. While previous models have explored negative species interactions (i.e., predation and competition), this paper presents an example marine reserve model with a positive interaction: a spiny lobster-sea urchin-red algae trophic chain where red algae facilitate lobster recruitment. Model results indicate that recruitment facilitation primarily affects the time scale of the species dynamics and the lobster spillover from reserves to harvested areas; the direction of these changes depends on the no-facilitation baseline. Overall, these models indicate the importance of incorporating species interactions into fisheries and reserve management decisions.

## INTRODUCTION

Global declines in harvested species have led to a call for a more holistic, ecosystem-based approach to fisheries management (Botsford et al. 1997; Pikitch et al. 2004). One of the central components of ecosystem-based management (EBM) is a multispecies approach (Larkin 1996; Pikitch et al. 2004; Marasco et al. 2005). In general, interspecific biodiversity is vital to marine ecosystem functional properties, such as productivity and stability (Worm et al. 2006). In addition, interactions between species may affect management metrics such as maximum sustainable yield (Hollowed et al. 2000) and, when overfishing occurs, could impede the recovery of depleted stocks (Walters and Kitchell 2001; Heino and Godø 2002; MacCall 2002).

Simple models provide insight into how species interactions may affect management decisions. For the purposes of this paper, simple models have few (two to four) species or aggregated groups of species (e.g., trophic guilds), follow deterministic dynamics on the level of populations (as opposed to individuals), and have a limited number of parameters (e.g., May et al. 1979), in contrast to large-scale simulations which have complex food web structure and/or variable climatic and oceanographic conditions (e.g., Field et al. 2006). While these approaches represent extremes on a continuum of possible model complexity, most models fall into one of these two categories.

Models, from simple community models to large-scale simulations, are always a simplified representation of the biological reality. While simple community models are less realistic, they can make important contributions to management decisions. For example, simple models can provide qualitative predictions, in some cases with the same degree of accuracy as more complicated simulations (Essington 2004; May 2004). This relative accuracy is possible because including the dynamics that have the greatest impact on model outcomes is more important to theoretical predictions than including a high level of biological detail in complicated simulations that neglect such key dynamics (for examples from disease management, see May 2004).

Furthermore, while the parameters in simple community models may be more abstract and therefore more difficult to measure (Whipple et al. 2000), the existence of fewer dynamics and parameters allows for more sensitivity analysis than possible in complicated simulations. In some cases, an analytic solution can be derived, which enables all potential outcomes to be determined. Overall, simple models provide greater insight into which dynamics and parameters have a large impact on model predictions. Therefore, such models help determine which processes may be necessary to incorporate into complicated simulations in order to ensure predictive power, and they help identify some key ecological processes or variables to estimate empirically (Whipple et al. 2000; Essington 2004).

The goal of this paper is to explore the effect of incorporating species interactions in simple models relevant to marine management. The incorporation of species interactions into traditional (non-spatial) fisheries management models has been reviewed by Bax (1998), Hollowed et al. (2000), Whipple et al. (2000), and Latour et al. (2003); the more recent development of incorporating species interactions into marine reserve models has been reviewed by Baskett et al. (2007). Because these approaches have previously been reviewed only separately, this paper provides a brief synopsis of the conclusions from these models and reviews and synthesizes the conclusions from both fisheries and marine reserve models. In addition, this paper presents a new example model.

As with theoretical ecology in general (Bruno et al. 2003), multispecies marine management models have focused on the negative interactions of predation and competition, while positive interactions are relatively under-explored despite their prevalence in marine ecosystems (with exceptions, e.g., see Thompson et al. 2006 for a mutualistic model relevant to marine populations, and see Rogers-Bennett and Pearse 2001 for an empirical study of the influence of facilitation on species responses to marine reserve establishment). Therefore, the example model I present incorporates recruitment facilitation into the dynamics of interacting species in marine reserves and harvested areas. Specifically, the model follows the trophic dynamics of spiny lobsters (*Panulirus interruptus*), sea urchins (*Strongylocentrotus* spp.), and red algae (*Gelidium* spp.), as well as the potential for spiny lobsters to preferentially recruit to red algae. Generalities arising from the overview and example model indicate how species interactions may affect marine management and help to identify topics for future research.

## Overview of existing models

### *Interacting species in fisheries models*

The interspecific dynamic most frequently incorporated into fisheries management models is predation (e.g., Larkin 1966; May et al. 1979; Brauer and Soudack 1981; Shirakihara and Tanaka 1981; Beddington and Cooke 1982; Yodzis 1994; Ströbele and Wacker 1995; Spencer and Collie 1996; Basson and Fogarty 1997; Dai and Tang 1998; Flaaten 1998; Essington 2004). In addition, some models account for competition directly (e.g., Larkin 1963; Shirakihara and Tanaka 1978; Kirkwood 1982; Ströbele and Wacker 1991; Semmler and Sieveking 1994) or indirectly in trophic models with multiple predators and/or prey (e.g., Collie and DeLong 1999), and a few models account for mutualism (e.g., Ströbele and Wacker 1991; Wacker 1999). Because of the additional predation mortality incorporated, the primary effect of including trophic interactions in the modeled species' demography is an increase in mortality rates; incorporating trophic interactions has little effect on the average recruitment of the modeled species (Hollowed et al. 2000). Incorporating species interactions such as predation can provide a mechanistic explanation for some of the variability in recruitment, mortality, age structure, and size structure (Hollowed et al. 2000).

The additional mortality factored in when incorporating predation into models causes decreases in the predicted yield per recruit and in spawner biomass per recruit and increases in the predicted recovery time compared to single species approaches (Hollowed et al. 2000). Furthermore, the total yield and maximum sustainable yield (MSY) in simple multispecies models with trophic and/or competitive interactions are less than the equivalent yield predictions from the analogous single-species models summed over all species (Pope 1975; May et al. 1979; Kirkwood 1982; Collie and DeLong 1999). How much predation affects yield predictions depends on the type of predation assumed (Yodzis 1994; Flaaten 1998). Landings and MSY predictions can also be lower than single-species predictions in more complicated community simulations such as Ecosim models, but the opposite trend is possible as well with the added food web complexity (Walters et al. 2005).

In addition, the harvest rates that maximize yield in single-species models are often unsustainable in the corresponding multispecies models that account for competitive and trophic interactions, both (1) because the single-species models overestimate sustainable harvest rates (May et al. 1979; Ströbele and Wacker 1991; Essington 2004) and (2) because the multispecies models have the capacity to have unstable equilibria, multiple stable states, and limit cycles when assuming strong and/or nonlinear species interactions (Shirakihara and Tanaka 1978; Brauer and Soudack 1981; Shirakihara and Tanaka 1981; Beddington and Cooke 1982; Kirkwood 1982; Semmler and Sieveking 1994; Spencer and Collie 1996; Basson and Fogarty 1997; Dai and Tang 1998). Overestimates of sustainable harvest rates generally result from species negatively affecting each others' productivities and, in trophic models, from the potential for harvest on a prey species to decrease the food availability and, therefore, productivity of a predator species; these dynamics are ignored in single-species models but accounted for in multispecies models (note that increased sustainable harvest rates can occur in mutualistic models due to the positive impact of the species on each others' productivities; Ströbele and Wacker 1991). Second, when unstable equilibria, multiple stable states, and limit cycles are possible, the dynamics of interacting species can create the potential for fishing to cause sudden shifts to an undesirable ecological state, such as a state with lower or collapsed populations of target species ("ecologically unsustainable yield" sensu Zabel et al. 2003). Similarly, Ecosim simulations indicate that fishing every species at its single-species MSY harvest rate would lead to a collapse in top predators in more complex food webs (Walters et al. 2005). Overall, species interactions can have a profound impact on the basic metrics of sustainable fisheries management.

### *Interacting species in marine reserve models*

Fisheries substantially alter the structure of marine ecosystems through direct take and indirect impacts that cascade through species interactions (Pauly et al. 1998; Jackson et al. 2001). One of the primary goals of no-take marine reserves is to protect biodiversity and ecosystem structure and function (Allison et al. 1998; Leslie 2005). Therefore, multispecies marine reserve models often address the question of how to design reserves to protect marine communities given the ecosystem impacts of fisheries outside reserves and before the reserves are established (the focus of the review by Baskett et al. 2007). This focus on conservation goals of reserves differs from single-species marine reserve models (reviewed by Guénette et al. 1998; Gerber et al. 2003), which primarily address the potential for reserves to reduce uncertainty in or enhance sustainable fisheries yield. While including the insights into designing reserves to achieve conservation goals from multispecies models, the overview below highlights model results that relate to sustainable fisheries management.

As in the fisheries models reviewed above, multispecies marine reserve models focus on negative species interactions (i.e., predation and competition) which reduce the modeled species' productivities. Because species are assumed to have negative effects on each other, incorporating species interactions increases the predicted reserve size necessary to protect self-sustaining populations, both in simple models (Baskett et al. 2006; 2007) as well as in more complex simulations such as Ecospace models (Walters 2000). Species interactions also alter reserve placement criteria. For example, incorporating predation on inshore juveniles for a species with an ontogenetic shift from inshore to offshore habitats changes the relative effectiveness of inshore and offshore reserves (Mangel and Levin 2005). In addition, a predator-prey model in which trophic level shifts with age indicates that reserve placement may need to be based on the current densities of the interacting species, including unfished prey species, to ensure the recovery of overfished predators (Baskett et al. 2006).

Along with reserve design, simple multispecies models provide insight into expectations after reserve establishment and, therefore, into appropriate goals for monitoring and determining reserve success. For example, two models predict the potential existence of alternative stable states, with or without a targeted species (Baskett et al. 2006; 2007). In this case, species interactions, such as competition, may impede the recovery of depleted species, depending on the species' densities at reserve establishment (Baskett et al. 2006; 2007). However, when that recovery does occur, reserves may promote resilience of the targeted species population to any overfishing in the harvested areas outside reserves (Baskett et al. 2006).

In another example, a simple trophic model demonstrates that spillover from reserves to harvested areas is more likely for top predators when assuming both a predator and its prey were fished before the reserve was established because, subsequently, the productivity of the predator population within the reserve benefits from both reduced mortality and increased prey availability (Baskett et al. 2007). Furthermore, while reserves are generally expected to reduce variation in catch (e.g., see single-species models by Sladek Nowlis and Roberts 1999; Mangel 2000), incorporating predation into a stochastic marine reserve predator-prey model may increase variation in dispersal and, therefore, spillover to harvested areas (Greenville and MacAulay 2006). Therefore, species interactions affect expectations for both the recovery of community structure within reserves and the potential for reserves to promote sustainable fisheries in harvested areas.

Finally, both simple trophic models and complicated ecosystem simulations predict that trophic cascades, and therefore declines of some species, are feasible after reserves are established (Walters 2000; Micheli et al. 2004; Baskett et al. 2007). This potential for cascades may be overestimated because simple trophic models often ignore additional biological dynamics that typically reduce the potential for cascades, such as omnivory and refugia from predation (Polis et al. 2000). For example, incorporating prey size refugia, or the potential for larger prey to escape predation, greatly decreases the theoretical likelihood of trophic cascades after reserve establishment (Baskett 2006). Because fewer prey are available to predators when incorporating prey size refugia, predators recover more slowly in reserves and, in the absence of reserves, the threshold harvest mortality for fishing predators to depletion is lower (Baskett 2006). In this model, as well as in the models by Mangel and Levin (2005) and Baskett et al. (2006), the size/age-dependency of the interaction is critical to predicting how species interactions affect both reserve design issues, such as monitoring, and fisheries management issues, such as sustainable harvest.

## Example model:
## Incorporating positive interactions

Multispecies fisheries and marine reserve models have focused on predation and competition, and positive interactions are under-explored. Unlike negative interactions, incorporating positive interactions into models can lead to increases in the interacting species' productivities. Therefore, it might be expected that incorporating positive interactions may have the opposite effect compared to negative interactions on management decisions, such as an increase in sustainable harvest rates (e.g., Ströbele and Wacker 1991) and/or a decrease in the reserve size necessary to protect populations. Metacommunity models of mutualism and habitat destruction confirm this expectation by showing that critical patch size, and therefore critical reserve size, decreases with increasing mutualism strength (e.g., Prakash and de Roos 2004). However, such metacommunity models assume that areas outside reserves are uninhabitable, which differs from marine systems with habitable, but harvested, regions outside reserves. Accounting for dynamics outside reserves is particularly important in the context of a multispecies approach in managing marine systems because of the potential for unharvested species to have non-reserve populations that, given movement such as larval dispersal, affect reserve populations of harvested species (Baskett et al. 2007).

One type of positive interaction common to marine systems is recruitment facilitation (Bruno and Bertness 2001). Specifically, dispersing larvae of a wide range of fish and invertebrates often preferentially recruit to the habitat formed by invertebrates and algae (Bruno and Bertness 2001; Carr and Syms 2006). In many temperate rocky subtidal systems, these positively interacting species are also components of trophic cascades, where herbivores graze algae and consumers prey on herbivores, and the reduction of consumer populations through fisheries often leads to herbivore increases and algal declines (Pinnegar et al. 2000). Given recruitment facilitation, declines in algae from fisheries-induced trophic cascades (plus the myriad of other direct anthropogenic impacts on algae such as habitat disturbance from fishing gear and sedimentation) can lead to reduced recruitment of targeted species (Planes et al. 2000). Therefore, protection of recruitment habitat in marine reserves can also help protect community structure and harvested species (Planes et al. 2000).

As an initial step toward exploring the potential effect of positive interactions on marine management decisions, this paper presents an example multispecies marine reserve model with and without facilitation. In particular, the model focuses on a trophic (producer-herbivore-consumer) chain where both the herbivore and consumer are harvested and the producer facilitates the recruitment of the consumer. The model parameters are based on a Northeast Pacific rocky subtidal system with two harvested invertebrates, spiny lobsters (*Panulirus interruptus*) and sea urchins (*Strongylocentrotus* spp.), and red algae (*Gelidium* spp.), where red algae facilitate spiny lobster recruitment (fig. 1A). Harvesting of urchin predators such as spiny lobsters can shift this ecosystem from diverse kelp forests (with high densities of many algae such as *Gelidium* spp.) to urchin-dominated barrens (with low densities of many algae); a goal of marine reserve networks is to protect the kelp forest community from such shifts (Behrens and Lafferty 2004a, b).

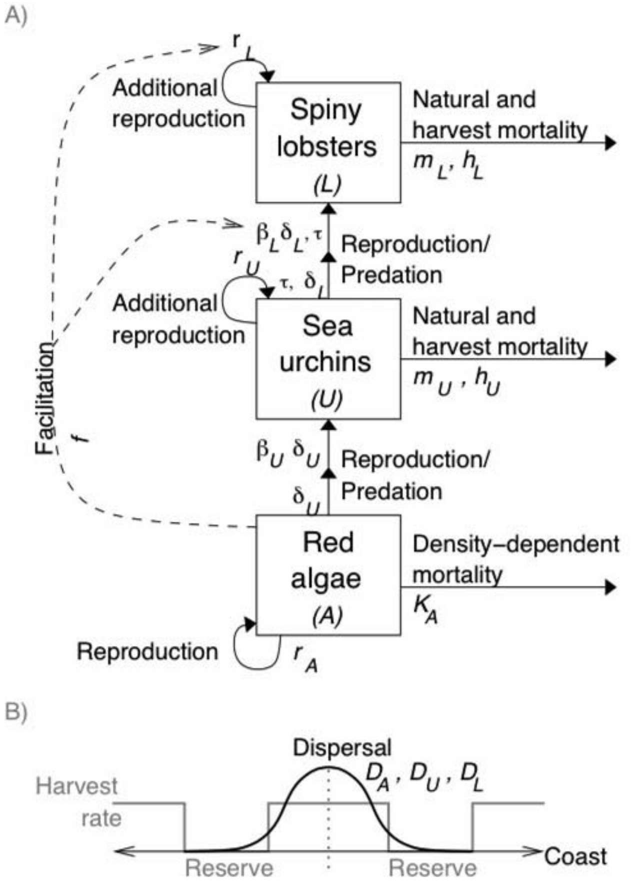

Figure 1. Outline of the spiny lobster–sea urchin–red algae facilitation model (equations 1–3). (A) ecological dynamics; (B) spatial dynamics.

In the model, sea urchins and spiny lobsters prey on red algae and sea urchins, respectively, and convert that predation into reproductive capacity which increases the rate of recruitment above a baseline amount (as predation on red algae and sea urchins are each one of many sources of urchin and lobster reproduction; Sousa et al. 1981, Tegner and Levin 1983). For the spiny lobster, this total recruitment (which is the predation-to-reproduction conversion plus the constant baseline) indicates the maximum possible recruitment. In the model with facilitation, how much of this recruitment occurs depends on the red algae population size. Specifically, given the preferential recruitment of *P. interruptus* to *Gelidium* spp. (Castañeda-Fernández de Lara et al. 2005), the facilitation model assumes that an increased density of red algae indicates increased algal cover, and therefore increases the rate at which lobster larvae encounter their preferred settlement habitat; thus, increasing the density of algae

TABLE 1
**Parameter values for the spiny lobster–sea urchin–red algae facilitation model (fig. 1; equations 1–3).**

| Description | Parameter | Value | Source* |
|---|---|---|---|
| Red algae recruitment | $r_A$ | 10/yr | |
| Urchin constant recruitment | $r_U$ | 0.4/yr | Pfister and Bradbury (1996) |
| Lobster constant recruitment | $r_L$ | 0.3/yr | Tegner and Levin (1983) |
| Lobster–red algae facilitation constant | $f$ | $0.05/A$ | Castañeda-Fernández de Lara et al. (2005) |
| Red algae carrying capacity | $K$ | $3\ A$ | Castañeda-Fernández de Lara et al. (2005) |
| Urchin natural mortality | $m_U$ | 0.5/yr | Kenner (1992) |
| Lobster natural mortality | $m_L$ | 0.35/yr | |
| Urchin harvest mortality | $H_U$ | 0.1/yr | Morgan et al. (2000) |
| Lobster harvest mortality | $H_L$ | 0.1/yr | |
| Urchin predation on red algae | $\delta_U$ | $0.2/U$/yr | Sousa et al. (1981) |
| Lobster predation on urchins | $\delta_L$ | $0.1/L$/yr | Tegner and Levin (1983) |
| Lobster predation handling time | $\tau$ | $10^{-8}$ yr | |
| Urchin predation-recruitment conversion | $\beta_U$ | $0.4\ U/A$ | Kenner (1992) |
| Lobster predation-recruitment conversion | $\beta_L$ | $0.1\ L/U$ | |
| Red algae average dispersal distance | $V_A$** | 1 km | Kinlan and Gaines (2003), Sosa et al. (1998) |
| Urchin average dispersal distance | $V_U$** | 10 km | Edmands et al. (1996) |
| Lobster average dispersal distance | $V_L$** | 10 km | |

*Parameter values are based on both the values reported in these sources and the values that produce biologically reasonable dynamics in the model.
**Diffusion constant for each species $D_X$ ($X = A$, $U$, or $L$ for algae, urchins, or lobsters) calculated from average dispersal distance $V_X$ by $D_X = (\pi/4)(V_X/Y)^2$ (Lockwood et al. 2002), where $Y = 1{,}000$ km is the length of the coastline.

increases the realized proportion of the potential spiny lobster recruitment beyond a baseline recruitment proportion. In addition, spiny lobsters and sea urchins experience natural and harvest mortality, and red algae experience density-dependent mortality. Finally, in the model, spiny lobster, sea urchin, and red algae movement occurs as diffusion along an idealized linear coastline to represent random (larval and adult) dispersal, and harvest varies in space in order to model harvested areas interspersed with no-take reserves (fig. 1B).

### *Model details*

Let $L$, $U$, and $A$ represent the spiny lobster, sea urchin, and red algal densities, respectively. In addition, let $\delta_U$ and $\delta_L$ be the urchin and lobster predation rates, respectively, on algae and urchins, with linear (type-I functional response) predation by urchins and lobster predation saturating with handling time $\tau$ (type-II functional response), as handling time is more likely to affect lobster consumption of urchins than urchin grazing of algae. Predation is converted into reproduction with efficiencies $\beta_U$ and $\beta_L$, while $r_U$ and $r_L$ are the constant recruitment rates for urchins and lobsters, respectively. The recruitment rate for the red algae is $r_A$, and its carrying capacity is $K$. $m_U$ and $m_L$ are the natural mortality rates for the urchins and lobsters, respectively; the urchin and lobster harvest mortalities, $h_U(x)$ and $h_L(x)$, vary with location $x$ such that they are equal to the constant-effort harvest rates, $H_U$ and $H_L$, for $x$ outside reserves and equal to zero for $x$ inside reserves. Algae, urchin, and lobster dispersal in space occurs according to diffusion constants $D_A$, $D_U$, and $D_L$ on a linear coastline. Note that these diffusion constants are independent of life-history stage and therefore represent both adult movement and larval dispersal. Finally, the proportion of the total possible lobster recruitment beyond a baseline amount increases linearly with algal density according to the constant $f$. Given the above definitions, the model dynamics are shown below (fig. 1). One mathematical constraint in the above model is that the baseline reproductive rates ($r_U$, $r_L$) must be less than the mortality rates ($m_U$, $m_L$) to avoid exponential growth in the sea urchins and spiny lobsters. Therefore, while red algae and sea urchins are not the only resources available for sea urchins and spiny lobsters, respectively, their presence is necessary for the predators' persistence.

$$\frac{\partial L}{\partial t} = D_L \frac{\partial^2 L}{\partial x^2} + \left(\left(\frac{1+fA}{1+fK}\right)\left(r_L + \frac{\beta_L \delta_L U}{\beta_L \delta_L U}\right) - (m_L + h_L(x))\right)L \qquad (1)$$

$$\frac{\partial U}{\partial t} = D_U \frac{\partial^2 U}{\partial x^2} + \left(r_U + \beta_U \delta_U A - \left(\frac{\delta_L U}{1+\tau\delta_L U} + (m_U + h_U(x))\right)\right)U \qquad (2)$$

$$\frac{\partial A}{\partial t} = D_A \frac{\partial^2 A}{\partial x^2} + \left(r_A\left(1 - \frac{A}{K}\right) - \delta_U U\right)A \qquad (3)$$

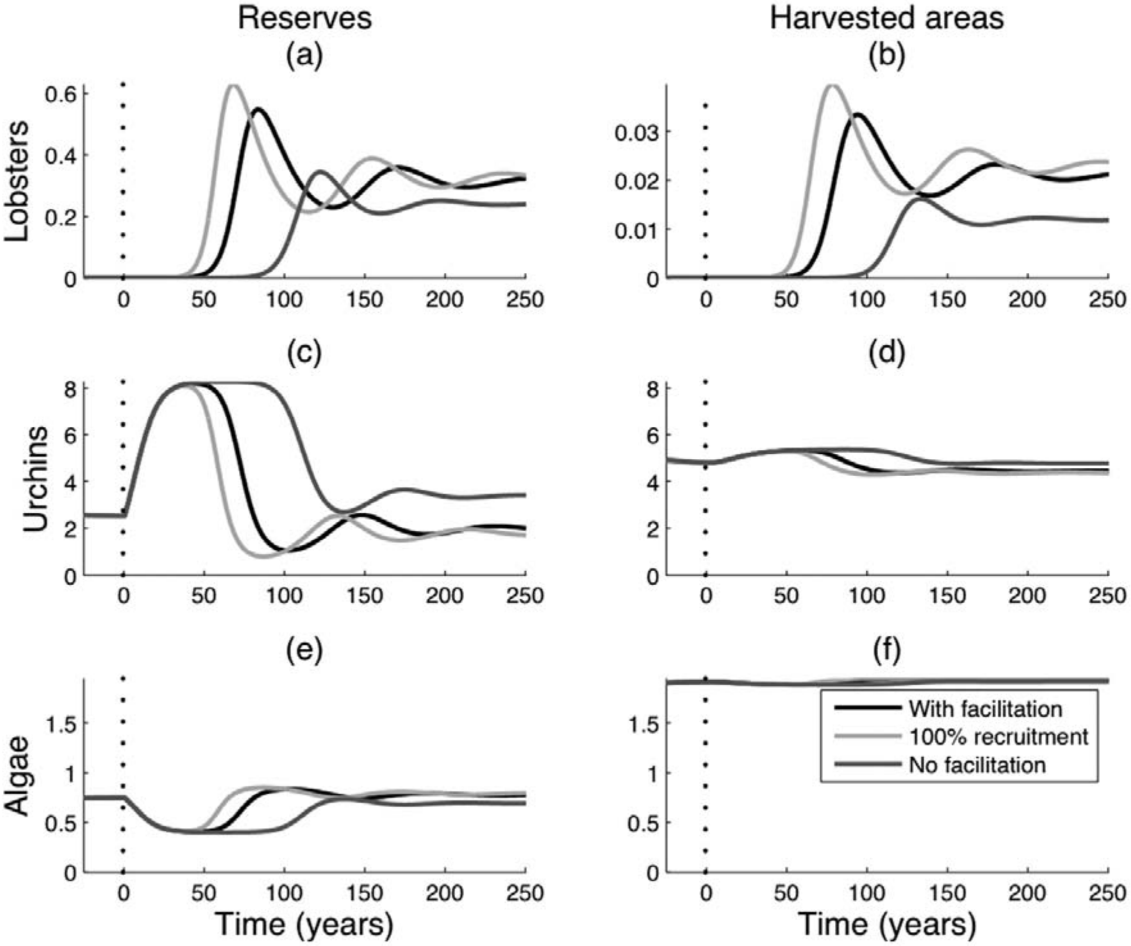

Figure 2. Sample time trajectories of the facilitation model (in black) and the two baseline simulations without facilitation: none of the otherwise red algae-facilitated recruitment happens (in dark grey) or all of the otherwise red algae-facilitated recruitment happens (in light grey). (A-B) spiny lobster densities (note different y-axes); (C-D) sea urchin densities; (E-F) red algae densities; (A, C, and E) densities within reserves; (B, D, and F) densities within harvested areas. Dotted lines indicate time of reserve implementation.

I numerically analyzed the lobster, urchin, and algal dynamics given parameter values within biologically feasible ranges for *P. interruptus*, *Strongylocentrotus* spp., and *Gelidium* spp., respectively (tab. 1; Sousa et al. 1981; Tegner and Levin 1983; Kenner 1992; Edmands et al. 1996; Pfister and Bradbury 1996; Sosa et al. 1998; Morgan et al. 2000; Kinlan and Gaines 2003; Castañeda-Fernández de Lara et al. 2005). I assumed absorbing boundary conditions (moving beyond the edge of the habitat is fatal) on the linear habitat (coastline). First, I initialized all population densities at the expected (locally stable) equilibrium densities with fishing in the spatially implicit version of the model (i.e., $D_A = D_U = D_L = 0$). Second, I numerically integrated the system with harvesting along the entire coastline beyond the time where the system reaches an equilibrium with spatial dynamics (100 years). Third, I implemented spatially variable harvest rates in order to model reserves and continue numerical integration beyond the time where the system has reached the new equilibrium (250 years). In addition to sample time trajectories, I present equilibrium results for varying reserve size and number of reserves in a reserve network.

*Model results*

In order to compare model results with facilitation to those without facilitation, I established two baseline models without facilitation, i.e., where spiny lobster recruitment is independent of red algae. In the first baseline, none of the additional recruitment that happens in the presence of red algae in the facilitation model occurred (i.e., $A = 0$ in equation 1; the "no-facilitation-recruitment" model). In the second baseline, spiny lobster recruitment always occurred at the maximum possible amount regardless of the red algae density (i.e., as if the red algae density were at its carrying capacity in the facilitation model, or $f = 0$ in equation 1; the "100% recruitment" model).

Given the parameter values used here, regardless of the inclusion of facilitation, the reserve populations fol-

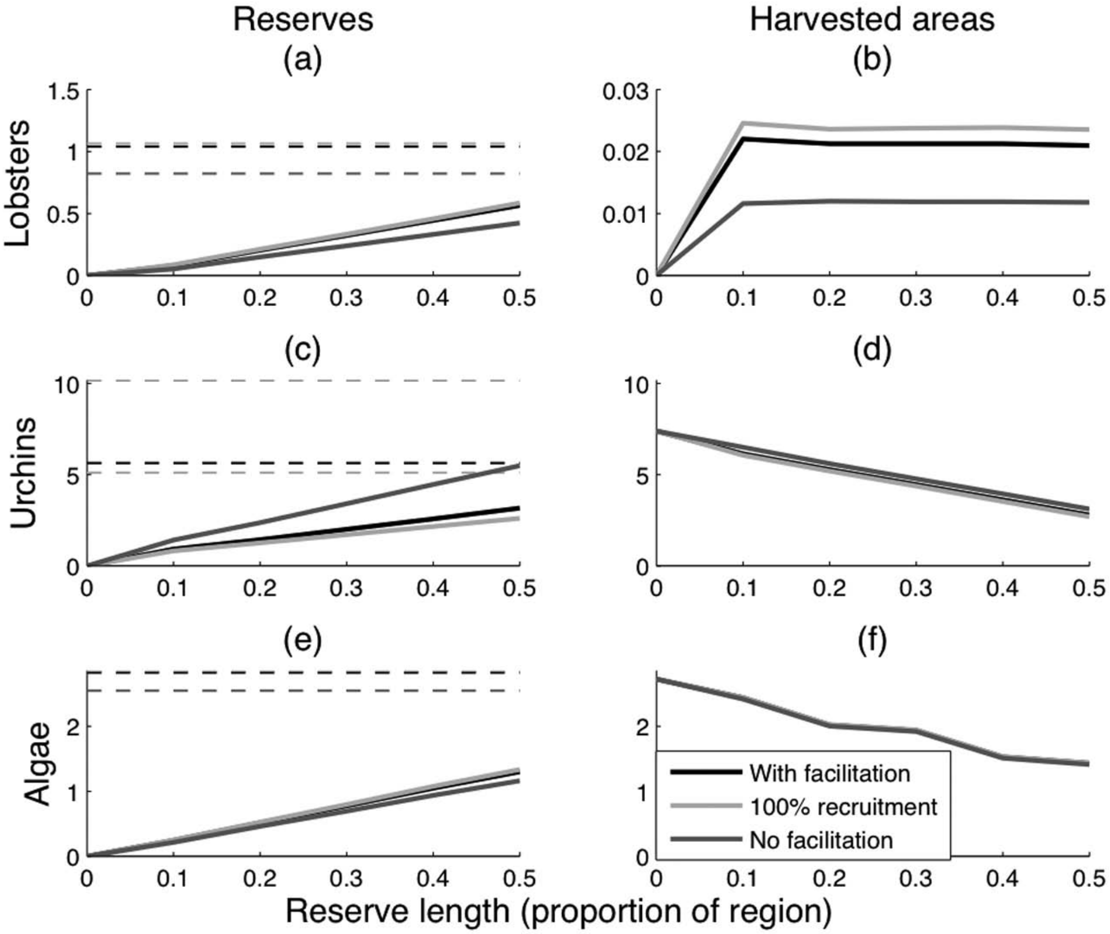

Figure 3. Equilibrium densities as a function of reserve size (proportion of the coastline protected in a single no-take reserve) for the facilitation model (in black) and the two baseline simulations without facilitation: none of the otherwise red algae-facilitated recruitment happens (in dark grey) or all of the otherwise red algae-facilitated recruitment happens (in light grey). (A-B) spiny lobster densities (note different y-axes); (C-D) sea urchin densities; (E-F) red algae densities; (A, C, and E) densities within reserves; (B, D, and F) densities within harvested areas. Broken lines indicate equilibrium density with no harvesting at any location (i.e., the expected natural state).

low time trajectories after reserve establishment where initially sea urchins increase and red algae decreases; then once the spiny lobsters start to increase, a cascade of decreasing sea urchins and increasing red algal occurs, with such oscillations eventually damping out to an equilibrium (fig. 2A, C, E). Harvested populations follow similar dynamics with lower magnitude oscillations (fig. 2B, D, F), probably due to the lower spiny lobster population sizes. While the inclusion of facilitation does not affect which populations increase or decrease, it does affect their time scale, with an intermediate response in the facilitation model; the fastest response was in the 100% recruitment model (where the lobsters have the greatest productivity), and the slowest response in the no-facilitation-recruitment model (where the lobsters have the lowest productivity).

In addition, facilitation has little effect on the reserve size necessary for the recovery of spiny lobsters and community structure (fig. 3A, C, E). However, facilitation does affect the predicted spiny lobster population densities in harvested areas, which are connected to the amount of larval and adult spillover from reserves; harvested-area spiny lobster density increases with potential lobster productivity (i.e., no-facilitation-recruitment less than facilitation less than 100% recruitment; fig. 3B). If the total area protected is constant and the reserve network is fragmented into smaller, more numerous reserves, lobster populations in the reserve decrease and harvested populations increase due to greater export from reserves to harvested populations and less self-replenishment within reserves (fig. 4A, B). Eventually reserves may become too fragmented to protect populations within reserves and therefore provide a source population for harvested areas; this potential loss of lobster reserve spillover is less likely in the simulations with facilitation or 100% recruitment than in the simulations with no-facilitation-recruitment (fig. 4B).

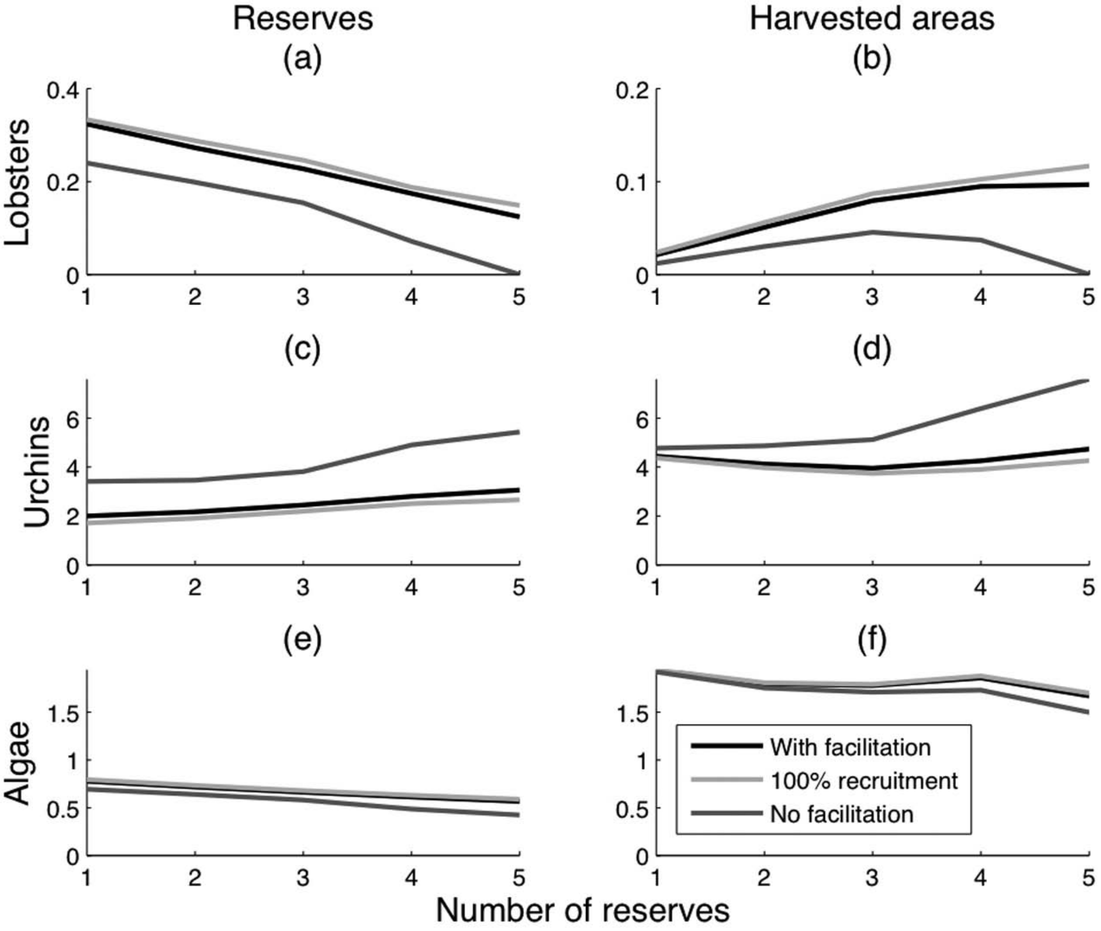

Figure 4. Equilibrium densities as a function of number of reserves in a reserve network with 30% of the coastline protected in total for the facilitation model (in black) and the two baseline simulations without facilitation: none of the otherwise red algae-facilitated recruitment happens (in dark grey) or all of the otherwise red algae-facilitated recruitment happens (in light grey). (A-B) spiny lobster densities (note different y-axes); (C-D) sea urchin densities; (E-F) red algae densities; (A, C, and E) densities within reserves; (B, D, and F) densities within harvested areas.

## DISCUSSION

### Conclusions from the facilitation model

In the example marine reserve multispecies model presented here, a spiny lobster–sea urchin–red algae trophic chain, recruitment facilitation of the spiny lobster to red algae primarily affects the time scale of the community recovery within reserves (fig. 2) and the potential for spiny lobster spillover (due to adult movement and larval dispersal) from reserves to harvested areas (fig. 3B). The potential for interspecific facilitation to affect the rate of recovery parallels both multispecies fisheries models (Hollowed et al. 2000) and multispecies marine reserve models (e.g., Baskett 2006), which indicates that negative species interactions may reduce the rate of species recoveries from intensive fishing. Furthermore, single-species marine reserve models predict similar results to those presented here where increasing network fragmentation into more, smaller reserves may initially increase spillover and reserve benefits to harvested populations (e.g., Hastings and Botsford 2003; Neubert 2003; Gaylord et al. 2005), while the concurrent reduced protection within reserves may eventually cause reduced spillover potential in highly fragmented reserve networks (e.g., DeMartini 1993). The results here indicate that such negative effects of fragmentation are less likely when the target species has a higher productivity, such as through recruitment-enhancing facilitation (fig. 4).

The direction of these changes when facilitation is included depends on the assumed baseline. Specifically, incorporating recruitment facilitation leads to a faster (fig. 2) and greater (fig. 3) response compared to ignoring all recruitment that may occur with facilitation, as one would expect for a positive interaction. The greater equilibrium density of spiny lobsters both outside and inside reserves associated with this greater response with facilitation indicates a potential for enhanced yield from lobsters in harvested areas and an enhanced ability for reserves to buffer against environmental variability, and therefore reduce uncertainty in fisheries yield, which is a potential benefit of reserves suggested by single-species models (e.g., Sladek Nowlis and Roberts 1999; Mangel 2000). However, incorporating recruitment facilitation leads to a slower (fig. 2) and slightly smaller (fig. 3) response compared to assuming that the maximum facilitation-associated recruitment always occurs. In either case, these effects on the time scale and the extent of response indicate that variation in the strength of facilitation and trophic interactions may partly explain variation in how species such as spiny lobsters respond to reserve establishment. Overall, empirical research on recruitment facilitation that explores the outcome without the attracting species as well as on the faciliatory interaction would help determine how facilitation may affect expectations for reserve establishment.

The simple model used here ignores many biological realities, from additional dynamic species in the system to variable oceanic conditions. In addition, our results only apply to the parameter values used in the numerical analysis. How the magnitude of harvest before reserve establishment and outside reserves varies with species can be particularly important to predicting the effect of reserve establishment in multispecies models (Baskett et al. 2007). If, for example, urchin harvest exceeds lobster harvest, establishing a reserve may lead to an increase in urchin populations and a decrease in red algae, which may negatively affect lobster recruitment in the facilitation model. Given the prevalence of facilitation in marine ecosystems both specific to recruitment dynamics and in general (Bruno and Bertness 2001; Carr and Syms 2006), the effect of facilitation on fisheries and marine reserve management decisions warrants future theoretical and empirical investigations. As highlighted above, the results presented here indicate that a careful consideration of the no-facilitation baseline is necessary to accurately predict the effect of facilitation on any future model predictions.

### Overall conclusions

Simple models can help identify key dynamics that have a substantial effect on theoretical predictions. The simple multispecies models discussed here indicate that species interactions are themselves such key dynamics: predation, competition, and facilitation have the potential to affect basic fisheries management decisions such as sustainable harvest rates (e.g., May et al. 1979), reserve design decisions such as size (e.g., Baskett et al. 2006), and interpretation of the response of species and communities to reserve establishment. Within reserve models, the exchange between protected and unprotected areas is critical to predicting both reserve benefits to harvested areas (as occurs with single-species models; e.g., Attwood and Bennett 1995; Gaylord et al. 2005) and the reserve design necessary to achieve conservation goals such as protecting community structure (Baskett et al. 2007).

Finally, ontogenetic shifts in habitat use (Mangel and Levin 2005), trophic level (Baskett et al. 2006), and predation susceptibility (Baskett 2006) are critical to effective reserve placement, size, and expectations after establishment. Similarly, ontogenetic shifts can be important to model predictions in single-species reserve models (e.g., St. Mary et al. 2000) and non-spatial multispecies fisheries models (Bax 1998). Therefore, such size/age-dependent dynamics may be particularly important to explore further with simple models, incorporate into more complicated multispecies simulations (e.g., Bax and Eliassen 1990; Christensen and Walters 2004; Pope et al. 2006), and investigate in empirical research (Field et al. 2006).

While quantitative predictions from multispecies models are rarely possible without in-depth empirical investigation of species interactions, qualitative trends across multiple models provide potential management recommendations. For example, in both fisheries and marine reserve models, negative species interactions tend to increase recovery time from any overfishing that may occur. Therefore, the species dynamic with the slowest time scale should determine the monitoring time scale (May et al. 1979), and empirical investigations of the time scale as well as the strength of species interactions would help inform multispecies management decisions.

In addition, incorporating negative species interactions decreases the maximum sustainable yield and sustainable harvest rates in fisheries models and increases the reserve size necessary to protect self-sustaining populations in marine reserve models. Positive species interactions may have the opposite effect, but the results from the recruitment facilitation example model suggest that the magnitude of this effect is uncertain and its direction depends on the baseline considered. Therefore, when data on key species interactions are not available, one management action may be to put a precautionary buffer into management decisions, such as harvest rate and reserve size, based on traditional single-species approaches (Baskett et al. 2007).

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# SPECIES DIVERSITY AND FOUNDATION SPECIES: POTENTIAL INDICATORS OF FISHERIES YIELDS AND MARINE ECOSYSTEM FUNCTIONING

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## ABSTRACT

Recent calls to incorporate ecosystem-based approaches, which consider multiple physical and biological aspects of a system instead of a single stock, into fisheries management have proven challenging to implement. Here, we suggest that managers can use the diversity of species in an area and the presence of foundation species as two indicators of marine ecosystem functioning. We used data from the 2006 sablefish (*Anoplopoma fimbria*) test fishery in the inside waters of southeastern Alaska to evaluate the relationship between the diversity of fish species present in an area and the abundance of both target and total fish caught. We found that areas where more fish species were present were characterized by higher catch levels of both sablefish and total fish, suggesting that diversity may be a reasonable indicator of fishery yields and productivity. Furthermore, because the incidence of deep-water coral was also logged in the surveys, we explored the relationship between coral, which provides habitat for groundfish, and catch levels. We found that abundances were highest where coral was present. Finally, we conducted meta-analyses of the importance of marine foundation species, such as corals, kelps, seagrasses, and oyster reefs, in promoting the diversity and abundance of associated taxa and found that diversity was 1.4-fold higher and abundances were 3.4-fold higher where these habitat-forming species were present. Together, these results suggest that biodiversity and the presence of foundation species can serve as useful indicators of a marine ecosystem's ability to provide the goods, services, and functions that we and other organisms rely on. We therefore suggest that these indicators be incorporated into fisheries management strategies.

## INTRODUCTION

Ecosystem-based management has been proposed as an improvement over traditional single-species approaches to resource management. Dramatic failures in single-species management, such as the collapse of the northwest Atlantic cod fishery (Walters and McGuire 1996; Myers et al. 1997), have highlighted the need for alternative approaches. The Sustainable Fisheries Act of 1996 calls for each of the major marine ecosystems in the United States to be managed using an ecosystem-based approach which considers the whole functioning system instead of individual fishery stocks (Ecosystem Principles Advisory Panel 1999). Furthermore, in response to demonstrated declines in fisheries stocks in the United States (Rosenberg et al. 2006), the Pew Oceans Commission (2003) and the U.S. Commission on Ocean Policy (2004) both indicated that ecosystem-based approaches are necessary to curb these declines. Despite this need, scientists and managers still grapple with what ecosystem-based management is and how it can be meaningfully applied.

The difficulties associated with defining and applying ecosystem-based management are compounded because the approaches contrast dramatically with traditional single-species fisheries management strategies (e.g., Ricker 1954; Beverton and Holt 1957; Pella and Tomlinson 1969). Even the more recent complex stochastic models, which use available data from fisheries catches and research surveys along with variability in year-class strength to determine the probability of future stock levels (e.g., Hilborn et al. 1994; Powers 2004), and the $F_{35}\%$ or $F_{40}\%$ harvest strategies commonly used over the last decade to manage fisheries (Clark 1991, 2002), predict only the future (fishable) abundance of single species or, at best, assemblages of closely associated species. They do not take into consideration the ecological integrity of the systems in which the fished species live (Larkin 1996).

Incorporating ecosystem principles into fisheries management therefore represents a substantial change in perspective and poses equally substantial challenges. Given these challenges, we suggest that the results of recent ecological research into the factors influencing ecosystem processes can provide some insights into indicators, such as biodiversity, of an ecosystem's ability to provide crucial goods, services, and functions. Motivated by global declines in biodiversity (Pimm et al. 1995; Vitousek et al. 1997), ecologists have been collecting an increasingly robust body of evidence regarding the ecosystem-level consequences of changing biodiversity (Loreau et al. 2001; Naeem 2002; Hooper et al. 2005). Because different organisms uniquely mediate biogeochemical processes (e.g., nutrient cycling, carbon fluxes), it has become clear that the diversity of organisms in an ecosystem has important ramifications for how that system functions (Kinzig et al. 2002).

Whereas most of the research on the relationships between diversity and ecosystem function has been conducted in terrestrial systems (Naeem and Wright 2003; Gessner et al. 2004), recent work indicates that similar relationships can be found in marine systems (Worm et al. 2006). For example, the number and identity of seaweed species in a marine community influence rates of nitrogen uptake and primary productivity (Bruno et al. 2005; Bracken and Stachowicz 2006); the diversity of native fouling organisms inhabiting a subtidal habitat mediates the ability of invasive organisms to successfully recruit (Stachowicz et al. 2002); and the number of predator species in a kelp-forest community influences the strength of trophic cascades (Byrnes et al. 2006). In fact, a recent synthesis of evidence from marine systems supports an overall positive effect of diversity on a variety of ecosystem functions and suggests that fishery yields and resilience are higher in more diverse ecosystems (Worm et al. 2006).

In benthic marine systems, the majority of habitat complexity is provided by foundation species (sensu Dayton 1972). These species, including coral reefs (Idjadi and Edmunds 2006), seagrass beds (Orth and Heck 1980; Reed and Hovel 2006), kelp forests (Carr 1989; Estes and Duggins 1995; Graham 2004), and oyster reefs (Lenihan and Peterson 1998; Grabowski et al. 2005; Kimbro and Grosholz 2006), provide biogenic structure, thereby facilitating the diversity and abundance of associated organisms. Foundation species are often threatened by anthropogenic stressors (e.g., coral bleaching, fishing, eutrophication), and their depletion can have cascading effects throughout an ecosystem. For example, because the physical structure of oyster reefs elevates oysters and associated organisms above the oxygen-depleted bottom layer of the water column, destructive fishing by oyster dredges exposes both oysters and associated fish and invertebrates to lethal hypoxic conditions (Lenihan and Peterson 1998). In benthic marine systems foundation species can therefore serve as indicators of an ecosystem's ability to provide the goods, services, and functions on which we and other organisms rely (Lubchenco et al. 1995; Coleman and Williams 2002).

In this study, we used fishery survey data and meta-analyses to evaluate the potential utility of these concepts—the relationship between biodiversity and ecosystem function and presence/absence of foundation species—in explaining the abundance and diversity of fish and other marine species, and in exploring their contribution to ecosystem-based management. Specifically, we evaluated the relationships between the diversity of groundfish species and the abundance of both target and total fish caught in longline surveys to evaluate whether regions with higher catch diversity were characterized by higher catch abundances. We also used the same data set, which included information on the presence of deep-water corals, to examine whether a foundation species facilitated the abundance of groundfish. Finally, we conducted meta-analyses to quantify the degree to which marine foundation species enhance the abundance and diversity of associated taxa.

## MATERIALS AND METHODS

### Fisheries benefits of diversity and foundation species

We examined the relationships between diversity, foundation species, and fishery catches using data from the 2006 sablefish (*Anoplopoma fimbria*, Pallas, 1814) test fisheries in the inside waters of southeastern Alaska (Holum, in press; O'Connell and Vaughn, in press). Sablefish is a high-value deep-water species, with adult fish most abundant at depths of between 600 and 800 m (Stocker and Saunders 1997). This species has been commercially harvested in southeastern Alaska since the early 1900s, and catch records indicate that the fishery was well-established by 1907 (Bracken 1983).

In 1988, the Alaska Department of Fish and Game began to conduct annual sablefish stock assessment surveys in two areas of southeastern Alaska's inside waters, Chatham Strait (also known as the Northern Southeast Inside [NSEI] Area) and Clarence Strait and Dixon Entrance (also known as the Southern Southeast Inside [SSEI] Area) (Bracken et al. 1997; fig. 1). Commercial longline gear has been used to survey these populations, and the gear has been standardized to the same specifications used by NOAA Fisheries to survey sablefish in the offshore waters of the Gulf of Alaska (C. Brylinsky, ADF&G, pers. comm.).

Each set of conventional benthic longline gear consisted of 25 skates of 45 #13/0 Mustad circle hooks. The vessel crew attached new hooks to all skates prior to each set as needed to replace missing hooks. The bait consisted of 100–200 g squid (Argentina *Illex* spp.). The head and tentacles were discarded, and the remainder was cut into 4–5 cm pieces and placed on the hooks at a rate of approximately 5.7 kg per 100 hooks. The gear was set on stations previously determined by random selection within the known habitat range of adult sablefish in the survey areas. The gear was deployed by commercial fishing vessels under contract to the Alaska Department of Fish and Game. Multiple vessels were contracted to ensure that all stations within an area could be fished within a seven-day period. Sets were made at 44 stations in the NSEI Area and 38 stations in the SSEI Area.

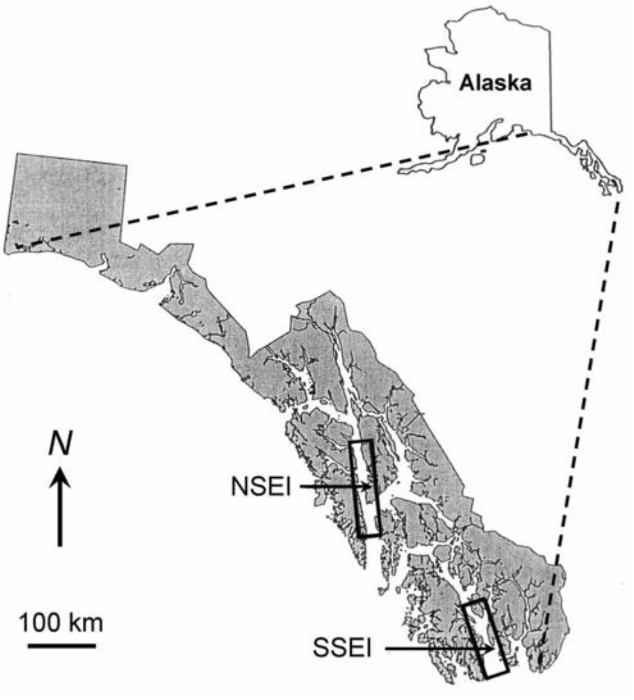

Figure 1. Sablefish (*Anoplopoma fimbria*) test fishery areas in southeastern Alaska. Data are from the 2006 surveys of 44 stations in the Northern Southeast Inside (NSEI) and 38 stations in the Southern Southeast Inside (SSEI) Areas.

For each set, the number of deployed hooks was recorded, and we used this number as a covariate in all analyses. As each set was brought onboard, the number of sablefish and a variety of other groundfish and by-catch species (including Pacific cod, dover sole, flounders, halibut, sharks, skates, and thornyhead rockfish) were recorded. Because these longlines run along the substratum, they occasionally snagged pieces of deep-water corals, which were subsequently brought onboard. In the SSEI survey, researchers logged the occurrence of corals in each set, and we used this as an indicator of biogenic habitat.

Based on these data, we used general linear models to examine the relationships between the number of fish species caught on a particular set and the abundance of both the target species (sablefish) and all fish species together, after accounting for the number of hooks deployed and regional differences (NSEI versus SSEI). We did not include an intercept in our models, because when species richness is zero, catch must, by definition, be zero. However, including the y-intercepts did not change the results, as the intercepts were indistinguishable from zero ($t < 0.13$, $P > 0.898$). Additionally, we compared abundances of both sablefish and total fish caught on sets where coral was present and absent to evaluate the potential role that deep-water corals play as foundation species that provide essential habitat for groundfish species.

In correlative studies like this one, it is difficult to determine whether diversity drives abundance or vice versa. For example, diversity could be positively related to abundance simply because higher catches are characterized by an increased probability of sampling rare species (Sanders 1968). Based on the observed diversity and abundance of species at each sampling station, we calculated diversity-abundance curves based on 1,000 iterations of a rarefaction algorithm (Gotelli and Entsminger 2001). We then used those curves to interpolate the diversity at each station to the minimum catch (15 individuals) recorded in any longline set.

### Effects of marine foundation species on diversity and abundance

While many independent studies have demonstrated important effects of individual foundation species on the diversity and abundance of associated taxa in various marine habitats, no studies to date have synthetically and quantitatively evaluated the effects of foundation species across all marine systems. We therefore used meta-analytical techniques to synthesize the existing evidence for foundation species' roles in enhancing the diversity and abundance of other marine organisms.

Studies for this analysis were selected by examining the abstracts of all papers returned from searches on ISI Web of Science and Aquatic Sciences and Fisheries Abstracts databases for terms such as "ecosystem engineer," "foundation species," and "biogenic habitat." We searched those papers and the literature cited therein for observational or experimental comparisons of either diversity or abundance of taxa where habitat-forming species were present (or at high abundances) or absent (or at low abundances). Based on these criteria, we identified 30 separate studies conducted in marine systems (there were often multiple studies within a given paper) which quantified the effect of foundation species on abundances and 41 separate studies which quantified effects on diversity (see Appendix A for a complete list of studies). Where possible, we used species richness as the metric of diversity. Where richness data were not available, we used the Shannon-Wiener diversity index. Our data set allowed us to quantify the collective effects of a variety of marine foundation species, including bivalves, corals, hydroids, kelps, seagrasses, seaweeds, snails, tubeworms, and tunicates.

We used the log response ratio as our effect-size metric. This metric is one of the most widely used effect metrics in ecological meta-analyses (Hedges et al. 1999; Shurin et al. 2002; Borer et al. 2006). Unlike Hedge's *d* (another commonly used metric), the log response ratio does not require a measure of sample variability, which was important because many studies did not report variances. Furthermore, the log ratio is easily interpretable (it represents the proportional change in the response variable), it shows the least bias of the meta-analysis metrics, and its sampling distribution is approximately normal (Hedges et al. 1999).

We calculated our effect sizes for abundance ($E_A$) and diversity ($E_D$) as follows:

$$E_A = \ln\left(\frac{A_1}{A_0}\right) \tag{1}$$

where $A_1$ was the abundance of organisms where the foundation species was present and $A_0$ was the abundance where it was absent, and

$$E_D = \ln\left(\frac{D_1}{D_0}\right) \tag{2}$$

where $D_1$ was the diversity of organisms where the foundation species was present and $D_0$ was the diversity where it was absent. Thus, effect-size metrics greater than zero indicate positive effects on abundance or diversity and metrics less than zero indicate negative effects. We averaged the effect sizes for each study to calculate the grand mean effects of foundation species (±95% confidence intervals) on abundance and diversity. We also separately analyzed the effects of producers and consumers as foundation species. Note that not all effects of ecosystem engineers are positive. Many habitat-forming species shade out or otherwise negatively affect other species (Bégin et al. 2004; Eriksson et al. 2006; Riesewitz et al. 2006), and our average effects take into consideration both positive and negative effects of foundation species.

## RESULTS

### Fisheries benefits of diversity and foundation species

When we used catch data from sablefish test fisheries to evaluate relationships between the number of fish species caught on a longline set and the abundances of both sablefish and total fish, and after accounting for regional differences and the number of hooks on a set, we found that the catch of both sablefish ($F_{1,78} = 3.9$, $P = 0.051$) and all species together ($F_{1,78} = 16.5$, $P < 0.001$) was higher in sets where more groundfish species were caught (fig. 2). Eliminating an obvious outlier, the set in the SSEI survey where only 15 individuals (all sablefish) were caught, did not affect this result. On average, each unit increase in groundfish species richness was associated with an additional 11.5 ± 5.8 (mean ± s.e.) sablefish and 29.5 ± 7.3 total fish caught.

When we used a rarefaction algorithm (Gotelli and Entsminger 2001) to interpolate the number of species caught in each set to the minimum number of individuals ($n = 15$) caught in any set and after adjusting for differences in catch levels at each location, we found a similar relationship between diversity and both total catch ($F_{1,81} = 314.0$, $P < 0.001$) and sablefish catch ($F_{1,81} = 204.1$, $P < 0.001$) to the one we describe above, but only when the diversity-catch function was forced through the origin. After including an intercept variable in the model and accounting for regional differences and the number of hooks on a set, there was no relationship between the number of fish species caught and the catch of either sablefish ($F_{1,78} = 3.0$, $P = 0.087$) or all species together ($F_{1,78} = 1.9$, $P = 0.169$). We were therefore unable to completely rule out the possibility that sites with higher catch rates are likely to have more species, simply due to the increased probability of sampling rare species.

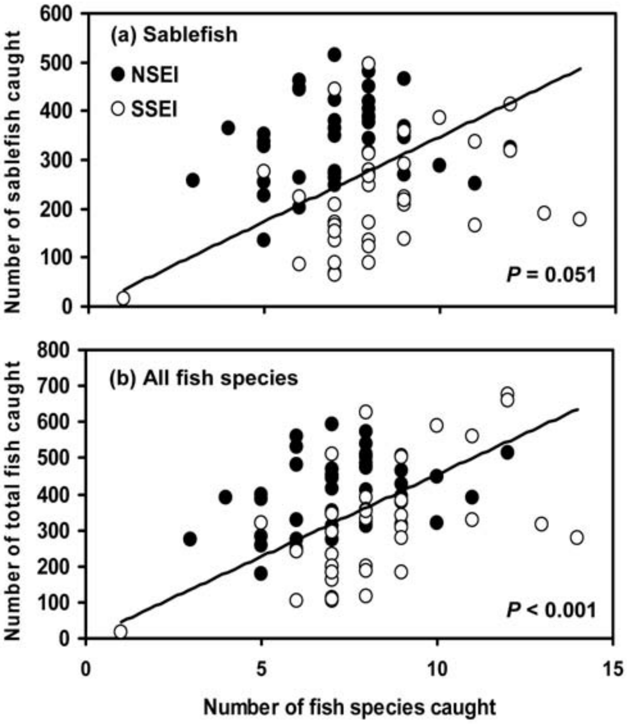

Figure 2. The number of both target and non-target fish caught in a longline set increased with the number of fish species caught. Data are from longline surveys conducted in 2006 in the Northern Southeast Inside (NSEI) and Southern Southeast Inside (SSEI) sablefish (*Anoplopoma fimbria*) test fisheries in Alaska. After accounting for regional differences and the number of hooks on each longline, catch of both (A) sablefish and (B) all species pooled was higher in sets where more fish species were caught ($F_{1,78} = 3.9$, $P = 0.051$ and $F_{1,78} = 16.5$, $P < 0.001$, respectively).

In the SSEI test fishery we used the record of coral pieces caught on the longline sets to assess the potential for deep-water corals to serve as foundation species, enhancing the catch of both sablefish and total fish because corals provide structural complexity on the seafloor. After accounting for the number of hooks, we found that sablefish ($F_{1,35} = 7.65$, $P = 0.009$) and total fish ($F_{1,35} = 5.77$, $P = 0.022$) catches were higher on sets where corals

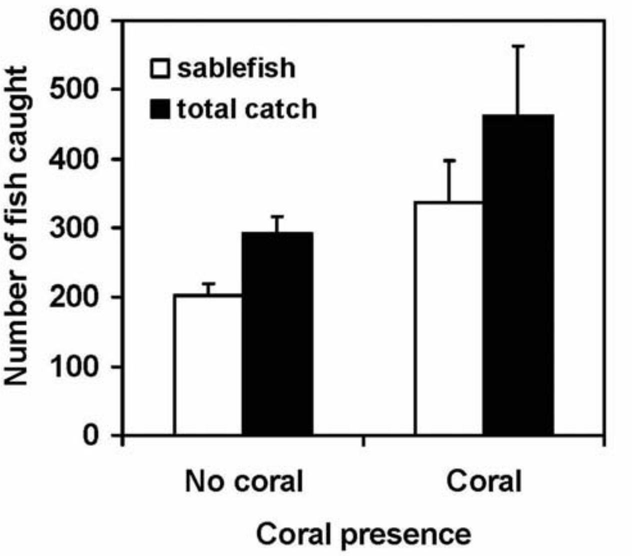

Figure 3. The number of both target and non-target fish caught in a longline set was higher where deep-water corals were present. Data are from longline surveys conducted in 2006 in the Southern Southeast Inside sablefish (*Anoplopoma fimbria*) test fishery in Alaska. Values are means ± standard errors. After accounting for the number of hooks on a given set, catches of both sablefish and total fish were higher ($F_{1,35}$ = 7.65; $P$ = 0.009 and $F_{1,35}$ = 5.77, $P$ = 0.022, respectively, after log-transformation) where coral was present.

were snagged and brought to the surface (fig. 3). The presence of corals was associated with a 67% higher catch of sablefish and a 58% higher total catch.

### Effects of marine foundation species on diversity and abundance

When we used meta-analyses to evaluate the effects of habitat-forming species, including corals, kelps, oysters, and seagrasses, we found that they enhanced both the abundance ($t$ = 4.33, $df$ = 29, $P$ < 0.001) and the diversity ($t$ = 2.59, $df$ = 40, $P$ = 0.013) of associated organisms, particularly invertebrates and fishes (fig. 4a). These analyses (i.e., after back-calculating from the log response ratios) indicated that species' abundances were 3.1-fold higher, and their diversity was 1.4-fold higher when foundation species were present compared to when they were not.

When the roles of consumers and producers as foundation species were analyzed separately, we found similar positive effects of consumers (e.g., bivalves, corals, and tubeworms) on the diversity ($t$ = 3.29, $df$ = 12, $P$ = 0.006) and abundance ($t$ = 5.257, $df$ = 16, $P$ < 0.001) of associated taxa. Species abundances were 2.6-fold higher, and diversity was 1.7-fold higher where heterotrophic foundation species were present (fig. 4b). Producers (e.g., seaweeds and seagrasses) were associated with a 3.7-fold increase in the abundance of associated taxa ($t$ = 2.789, $df$ = 12, P = 0.016) but had no consistent effect on diversity ($t$ = 1.308, $df$ = 27, $P$ = 0.202) (fig. 4b). Thus, whereas the effects of producers and consumers on associated taxa were fairly comparable for both abundance ($t$ = 0.749, $df$ = 28, $P$ = 0.460) and diversity ($t$ = 1.319, $df$ = 39, $P$ = 0.195), producers had a slightly greater positive effect on abundance, and consumers had a slightly greater (and statistically significant) effect on diversity.

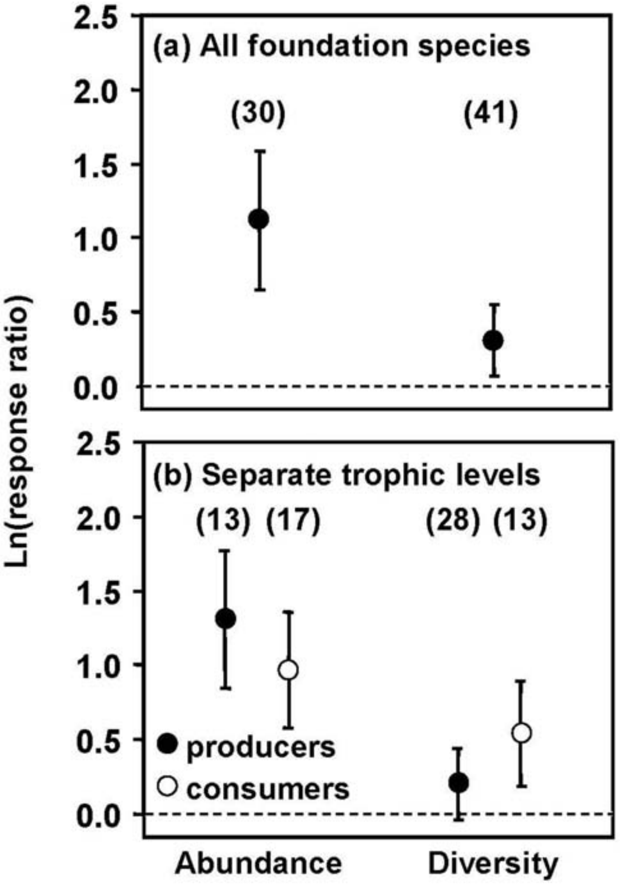

Figure 4. Abundance and diversity of marine organisms are higher in the presence of foundation species. Data are from meta-analyses of studies describing the enhanced abundance and diversity of organisms associated with foundation species. Mean log-response ratios (foundation species present versus absent) ± 95% confidence intervals are shown for (A) all foundation species together and (B) producers and consumers analyzed separately. Sample sizes for each log-response ratio are shown in parentheses. Overall, foundation species were associated with a 3.1-fold increase in species abundance ($t$ = 4.33, $df$ = 29, $P$ < 0.001) and a 1.4-fold increase in diversity ($t$ = 2.59, $df$ = 40, $P$ = 0.013).

## DISCUSSION

Based on fishery survey data from southeastern Alaska, we found that the abundances of both target and total fish caught at a site were higher at locations where more fish species were present (fig. 2) and where deep-water corals were snagged in the gear (fig. 3). These data suggest that the diversity of organisms in an ecosystem and the presence of foundation species can have important ramifications for the goods, services, and functions provided by that system. We therefore propose that marine biodiversity and presence of foundation species can serve as potential indicators of fisheries productivity and should be incorporated into fisheries management strategies. Below, we discuss the potential use of biodiversity and foundation species as indicators of marine ecosystem functioning and their consequent usefulness for ecosystem-based management.

### Fisheries benefits of marine biodiversity

Our work supports other recent findings on the importance of marine biodiversity to fisheries. Worm et al. (2006) examined fisheries catches at the scale of Large Marine Ecosystems and found that fisheries in species-rich systems (>500 species) collapse less rapidly than those in species-poor systems (<500 species). Furthermore, both catches and rates of recovery after collapse were higher for fisheries in more diverse Large Marine Ecosystems. Together with our data from the southeastern Alaska sablefish test fishery, these results suggest that the link between species diversity and fishery yields may be a general phenomenon.

Many studies have demonstrated mechanistic links between the diversity of organisms and the rates of ecosystem processes in a system (Loreau et al. 2001; Hooper et al. 2005), and it is tempting to suggest that similar mechanisms (e.g., partitioning of resources such as food or available habitat) may be operating here. However, the relationship between diversity and functioning is reciprocal; diversity both influences and is influenced by the rates of key biogeochemical processes (Naeem 2002). Especially given the correlative nature of our data and the fact that we were not able to definitively rule out the potential effect of abundance on diversity using rarefaction, we cannot demonstrate a causal effect of diversity on the number of fish caught, highlighting the need for experiments to evaluate the mechanisms underlying this relationship. Nevertheless, the fact that more fish were caught in areas where more fish species were present suggests that diversity can, at the very least, be used as an indicator of an area's potential for higher fisheries yields. Conversely, a decrease in diversity could be an indicator of ecosystem stress.

### Roles of foundation species in marine ecosystems

Both our analysis of the role that foundation species play in mediating the abundance and diversity of marine organisms (fig. 4) and the enhanced groundfish catches we observed in areas where deep-water corals were found suggest that more attention needs to be paid to the potential fisheries benefits of habitat-providing organisms and other positive species interactions in marine ecosystems (Bertness and Leonard 1997). Whereas our data relating sablefish and total catch to coral presence are correlative, they indicate that where corals were definitively present—we cannot know for sure that corals were absent at locations where they were not brought onboard—catches were higher, indicating that either the presence of corals or the habitat associated with them (i.e., corals only grow on rocky substrata) was more suitable for groundfish. Seagrass beds and kelp forests are known to be crucial nursery habitats for many commercially important species (Orth and Heck 1980; Carr 1989; Graham 2004), and both scientific (fig. 4) and anecdotal (see below) evidence suggests that both the diversity and abundance of fish is higher where foundation species are present.

When we considered the foundation-species effects of producers (e.g., seaweeds and seagrasses) and consumers (e.g., bivalves, tubeworms, and corals) separately, we found no differences in the effects of producers and consumers on either abundance or diversity (fig. 4b). However, producers did not have a consistent positive effect on the diversity of associated taxa, largely due to occasional negative effects of canopy-forming seaweeds on both understory algae and fish. This result highlights the fact that organisms can have both positive and negative effects on associated taxa. Furthermore, the relative importance of positive versus negative interactions is likely to vary with environmental and ecological context (e.g., Bertness et al. 1999).

Furthermore, fishing activities can have direct impacts on the abundances of foundation species. For example, the spine canopy of sea urchins provides physical structure for invertebrates, including juvenile abalone (Rogers-Bennett and Pearse 2001), and this biogenic habitat is lost when urchins are fished. Prior to the collapse of the Pacific Ocean perch (*Sebastes alutus*) stocks in the Gulf of Alaska, commercial fishermen knew that *S. alutus* were more abundant in areas where deep-water corals were present. However, it was difficult to trawl those areas because the gear became fouled on the corals. A heavy cable was therefore connected to two boats and dragged across the bottom, eliminating the corals before the area was trawled to capture the rockfish (anonymous fisherman, pers. comm.). The destruction of foundation species by fishing, especially trawling, has been likened to the clear-cutting of forests (Watling and Norse 1998). Clearly, the absence of foundation species has negative impacts on both marine biodiversity and fishery productivity, suggesting that the importance of foundation species and the essential fish habitat they provide should be incorporated into ecosystem-based management strategies (National Marine Fisheries Service 1997).

### Ecosystem-based management

While more work is necessary to evaluate the generality of our findings, we suggest that biodiversity and foundation species can be used as metrics of a system's productivity, functioning, and potential fisheries yields. One of the most difficult aspects of managing functioning ecosystems is the fact that conventional indicators of ecosystem change, such as production rates, cannot be used as indicators of a system's ability to provide goods, services, and functions, because once these processes are altered, the system has often been irreversibly changed (Schindler 1990). Instead, more sensitive indicators, such as species diversity and (especially in marine systems) the presence of foundation species, can serve as useful indicators of a system's functioning.

Diversity data, in particular, are easily obtainable from the test fishery and catch data that serve as the basis for many current marine fisheries management decisions (e.g., Holum, in press; O'Connell and Vaughn, in press). Given that diversity is a metric that can be quantified in space and time, biodiversity can then be managed for, giving fisheries managers and research biologists a tool for implementing ecosystem-based management plans. Fisheries biologists are also beginning to pay more attention to the habitat requirements of species (Mangel et al. 2006), though many of these efforts have focused on the physical structure provided by rocky reefs (e.g., Johnson 2006; Love et al. 2006; O'Connell et al. 2007). Because of the importance of foundation species in promoting the diversity and abundance of associated organisms (fig. 4), including many commercially targeted species (e.g., fig. 3), we suggest that surveys of both living and non-living habitat be used to predict the ability of a system to sustain abundant and diverse fish stocks.

We suggest that these sorts of indicators of ecosystem functioning, with clear ramifications for fisheries productivity, can play a major role in management strategies, such as fisheries ecosystem plans (Field et al. 2001), that consider entire ecosystems instead of separate stocks. Our work and the analysis of large marine ecosystem fisheries data by Worm et al. (2006) suggest that managers need to explicitly consider the diversity and abundance of both fished and unfished species. Furthermore, because foundation species provide essential habitat for fish, the habitat they provide needs to be considered in management plans, as mandated by the Sustainable Fisheries Act (National Marine Fisheries Service 1997).

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## APPENDIX A
### Studies Used in the Meta-Analyses

| Study | Foundation species | Common name | Response taxa | Response (A = abundance, D = diversity) | Citation |
|---|---|---|---|---|---|
| 1 | *Mytilus edulis* | mussel | invertebrates | A | 1 |
| 2-3 | *Lessonia trabeculata, Macrocystis integrifolia* | kelps | fishes | A, D | 2 |
| 4-7 | *Agarum cribrosum, Alaria escuelenta, Desmarestia viridis, Ptilota serrata* | kelps and other seaweeds | invertebrates | D | 3 |
| 8 | *Zostera marina* | seagrass | fishes | A | 4 |
| 9-10 | *Macrocystis pyrifera* | kelp | fishes | A, D | 5 |
| 11-12 | *Cladophora columbiana* | seaweed | invertebrates | A, D | 6 |
| 13-16 | *Halecium* spp., *Hydrallmania falcata, Nemertesia* spp., *Sertularella* spp., *Sertularia cupressina* | hydroids | invertebrates | A, D | 7 |
| 17-18 | *Macrocystis pyrifera* | kelp | fishes | A, D | 8 |
| 19 | *Pyura praeputialis* | tunicate | all taxa | D | 9 |
| 20-21 | *Carpophyllum flexuosum* | seaweed | fishes | A, D | 10 |
| 22-23 | *Musculista senhousia* | mussel | invertebrates | A, D | 11 |
| 24-28 | *Fucus vesiculosis* | seaweed | seaweeds | A, D | 12 |
| 29-30 | *Ecklonia radiata* | kelp | invertebrates | D | 13 |
| 31 | *Crassostrea virginica* | oyster | invertebrates | A | 14 |
| 32 | *Macrocystis pyrifera* | kelp | all taxa | D | 15 |
| 33 | *Centrostephanotus coronatus* | urchin | fish | A | 16 |
| 34-35 | *Laminaria hyperborea* | kelp | all taxa | A, D | 17 |
| 36-37 | *Agaricea agaricites, Montastraea annularis, Porites astreoides* | corals | invertebrates | A, D | 18 |
| 38 | *Ostreola conchaphila* | oyster | invertebrates | D | 19 |
| 39-40 | *Austrovenus stuchburyi* | cockle | invertebrates | A, D | 20 |
| 41-42 | *Zostera marina* | seagrass | fishes | A, D | 21 |
| 43-44 | *Zostera marina* | seagrass | invertebrates | A, D | 22 |
| 45-47 | *Agarum cribrosum, Laminaria* spp. | kelps | fish | D | 23 |
| 48-51 | *Chaetopterus variopedatus, Macreoclymene zonalis* | tubeworms | invertebrates | A, D | 24 |
| 52-55 | *Cystophora torulosa, Hormosira banksii* | seaweeds | all taxa | D | 25 |
| 56 | *Mytilus californianus* | mussel | all taxa | D | 26 |
| 57-58 | *Laminaria hyperborea* | kelp | invertebrates | A, D | 27 |
| 59-62 | *Ecklonia radiata* | kelp | fishes | A, D | 28 |
| 63-66 | *Modiolus modiolus* | mussel | infauna | A, D | 29 |
| 67-69 | *Batillaria attramentaria* | snail | various taxa | A | 30 |
| 70-71 | *Lanice conchilega* | tubeworm | invertebrates | A, D | 31 |

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# THE RELATIONSHIPS BETWEEN PREDATORY FISH, FORAGE FISHES, AND JUVENILE SALMONID MARINE SURVIVAL OFF THE COLUMBIA RIVER: A SIMPLE TROPHIC MODEL ANALYSIS

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## ABSTRACT

A trophic model that simulates interactions between a predatory fish (Pacific hake, *Merluccius productus*), forage fish, and juvenile salmon off the Columbia River was constructed to identify if trophic interactions could account for marine mortality of Columbia River juvenile salmon. The model estimates the number of juvenile salmon that are eaten annually by Pacific hake off the Columbia River for a given hake and forage fish population. Model results indicate that the presence of high numbers of Pacific hake could account for high mortality of some juvenile salmonid species/stocks leaving the Columbia River, and that this mortality would be much reduced when forage fish are abundant. Estimates of hake and forage fish abundance, based on field data collected from 1998–2005, were used in the model to derive annual estimates of the number of salmon possibly eaten by hake. A multiple regression analysis using the output from the trophic model and average May/June Columbia River flows accounted for much of the annual variation in Columbia River fall Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon marine survival ($p < 0.05$, $R^2 > 60\%$), but not spring or summer Chinook salmon. For these two stocks, average May/June sea-surface temperature was the best predictor of marine survival. Results support the hypothesis that for some Columbia River salmon species/stocks, marine survival is predation-driven and affected by the interaction between the abundance of Pacific hake, forage fish, Columbia River flows, and possibly ocean turbidity. Future modeling work should include predation estimates of other large fishes, marine mammals, and sea birds.

## INTRODUCTION

Pacific salmon run sizes are determined by mortality in fresh and marine waters, with both habitats being equally important (Bradford 1997; Lawson et al. 2004). While causes of juvenile salmon mortality in fresh water have been extensively studied, the causes of mortality in the marine environment remains one of the least resolved questions in Pacific salmon biology (Groot and Margolis 1991; Pearcy 1992; Beamish and Mahnken 2001; Logerwell et al. 2003; Beamish et al. 2004). To address this question, we initiated a pelagic fish ecosystem study off the Columbia River in 1998. The primary objective of this study was to identify the abundance and feeding habits of potential predators of juvenile salmonids (Emmett and Krutzikowsky, in press), and how fluctuations in physical and biological oceanographic conditions affected the distribution and abundance of predatory and forage fishes (Emmett et al. 2006).

We now have seven years of information on the physical oceanographic conditions, temporal distribution and abundance of fishes, and the feeding habits of predatory fishes offshore of the Columbia River. We have observed that Pacific hake (*Merluccius productus*), a limited salmonid predator (Emmett and Krutzikowsky, in press), is at times very abundant in this region, and hypothesize that it may be responsible for the death of many juvenile salmonids (Emmett et al. 2006). We also observed wide fluctuations in the abundance of forage fishes, which predators can consume as “alternative prey” instead of salmonids (Fisher and Pearcy 1988; Pearcy 1992; Svenning et al. 2005). The alternative-prey hypothesis proposes that when forage fishes are abundant, predators will eat forage fishes instead of salmonids because predators would rarely encounter juvenile salmonids relative to forage fishes. This appears to be particularly true for the California Current System, where forage fish are at least two orders of magnitude more abundant than juvenile salmon, versus the Alaska Coastal Current, which has relatively low forage fish abundance (Orsi et al. 2009).

Columbia River salmon runs showed large annual fluctuations from 1998–2005, which appeared to reflect changing ocean conditions (ocean temperatures, upwelling, primary production, fish production, etc.) (Williams et al. 2005). These observations suggest that marine survival of salmon off the Columbia River, and perhaps the Pacific Northwest, may be influenced by interactions between forage and predatory fish populations. As such, we hypothesize that marine survival of juvenile Columbia River salmon is largely controlled by marine predation, but when forage fish populations are high, large predatory fishes should consume primarily forage fishes instead of juvenile salmonids (fig. 1). The

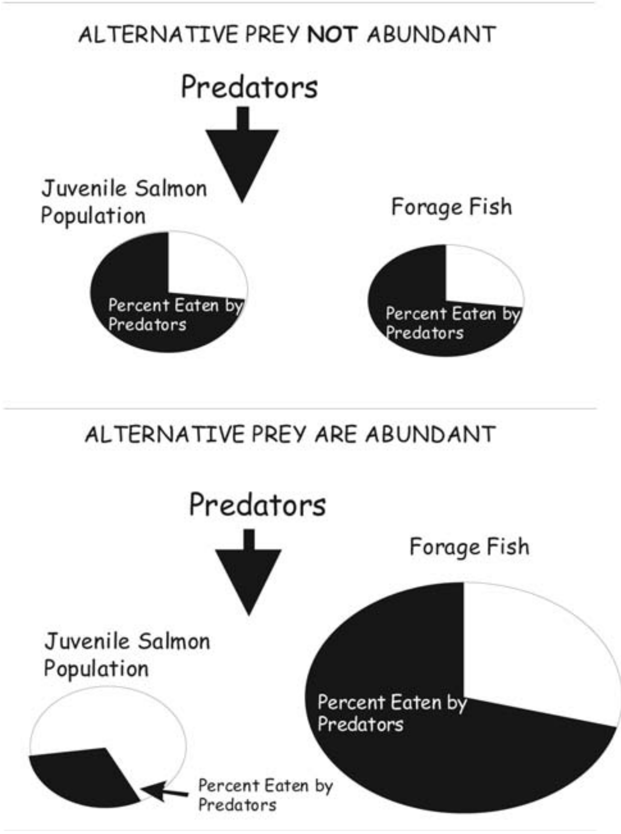

Figure 1. Diagram of the hypothesized role that alternative prey (forage fishes) play in reducing predation on juvenile salmonids in the marine environment.

purpose of our research was to explore this hypothesis by using a dynamic trophic model in conjunction with pelagic fish data collected off the Columbia River.

Predation can play an important role in structuring marine ecosystems (Estes and Palmisano 1974; Bogstad and Mehl 1997; Ware and McFarlane 1995; Bax 1998; Estes et al. 1998; Livingston and Jurado-Molina 2000). However, documenting predator effects (e.g., distinguishing relative importance of top-down processes versus bottom-up processes) in the marine environment has been difficult (Walters et al. 1978; Worm and Myers 2003). Studies of marine bird (Collis et al. 2002) and marine mammal (Riemer and Brown 1997) feeding in the Northwest indicate they can be important predators of juvenile salmonids at specific locations, but they do not appear to account for a significant proportion of the juvenile salmon marine mortality in the Pacific Northwest. There have been few actual observations of predation on juvenile salmon by large marine fishes in the Pacific Northwest (Brodeur et al. 1987; Beamish et al. 1992; Beamish and Neville 1995, 2001; Pearcy 1992; Emmett and Krutzikowsky, in press). For example, from 1998–2004 only seven juvenile salmonids were identified from 7,402 predator fish stomachs collected off the Columbia River (Emmett and Krutzkowsky, in press). Nevertheless, the negative correlation between marine predator fish abundance and salmon marine survival in the Pacific Northwest provides correlative evidence that fish predation may be important (Emmett and Brodeur 2000; Emmett et al. 2006).

Ecosystem and population models provide one method to investigate how environmental factors might control juvenile salmon marine survival. The juvenile salmon marine survival model of Gertseva et al.[1] found that salmon growth, migration, and mortality were important parameters affecting survival. They concluded that salmon marine survival was determined primarily by top-down mechanisms (predation). Field (2004) developed an ecosystem-based model of the northern California Current using a mass-balance modeling approach (Ecopath/Ecosim) (Christensen and Pauley 1992). Field et al. (2006) evaluated the effect of changing hake distributions and abundance on hake prey resources by running model simulations, and concluded that hake can affect the abundance of forage fish resources, especially if climate effects are included.

Our research considers three questions. First, can Pacific hake, the most abundant fish predator in the California Current ecosystem, be responsible for a large percentage of the marine mortality of Columbia River juvenile salmonids? Second, can the abundance of forage fish alter hake predation rates on juvenile salmonids? Finally, do Columbia River plume conditions affect these predation interactions? We explored these questions by building a dynamic trophic model containing interactions between Pacific hake, forage fish, and juvenile salmon. The model is limited to the area around the Columbia River (fig. 2) and the April–July 120-day period. During this initial ocean entry period, juvenile salmon are similar in size to forage fish and thought to be most vulnerable to predation (Pearcy 1992; Weitkamp 2004; Emmett and Krutzikowsky, in press). While the model provides a simplistic view of a complex ecosystem, it presents what are believed to be the major pathways and begins to identify general properties of the pelagic ecosystem off Oregon and Washington.

## METHODS

To develop a model of predator fish/prey fish interactions off the Columbia River, it was necessary to obtain fish abundance estimates and food habit information. Predator and forage fish population estimates were acquired by conducting regular night-time surface trawling and determining predator feeding habits by taking

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[1] Gertseva, V. V., T. C. Wainwright, and V. I. Gertsev. 2004. Juvenile salmon survival in the Northeast Pacific Ocean: top-down or bottom-up control? Unpublished manuscript. NOAA Fisheries, Newport, Oregon.

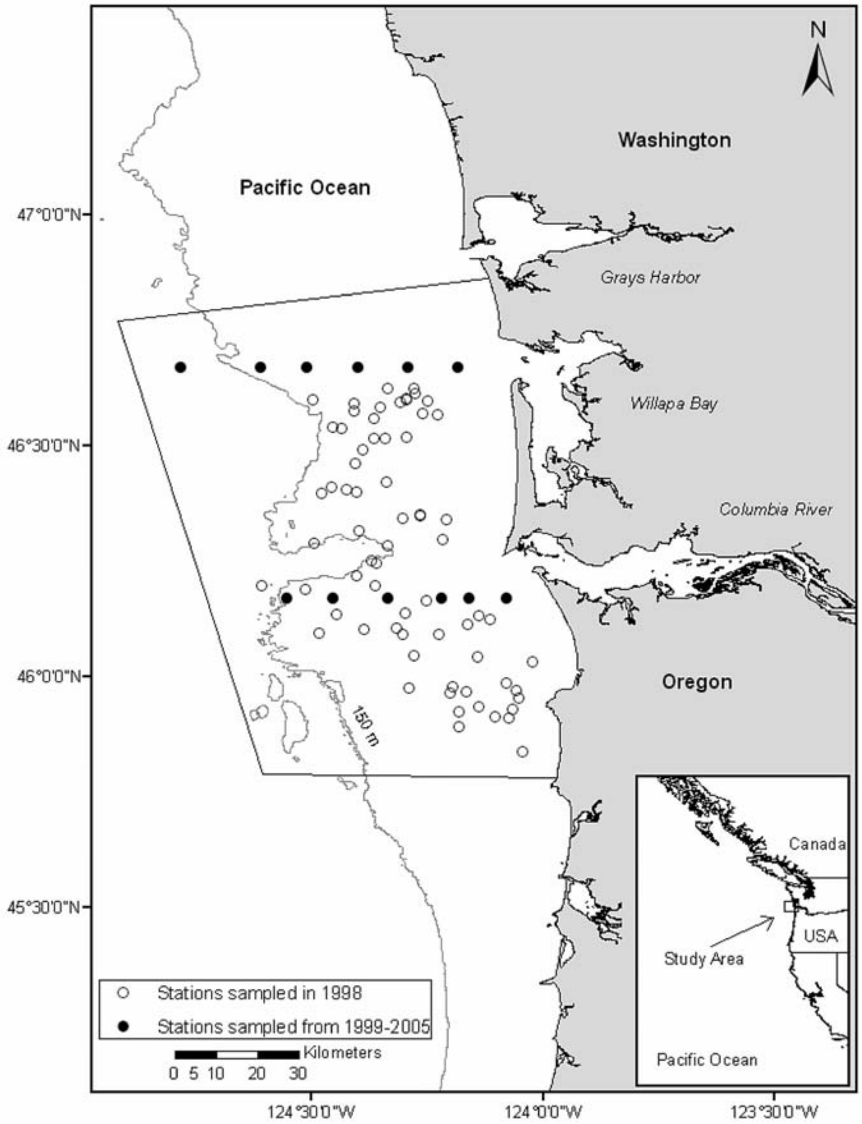

Figure 2. Location of stations off the Columbia River region sampled by surface trawl at night during spring/summer 1998–2005. Also shown is the estimated total coastal area represented by the trawl data and the 150 m depth contour.

fish stomachs from late April–July 1998–2005. These efforts provided seasonal density estimates for forage fishes, Pacific hake, and other predatory fishes. Juvenile salmon densities were not determined from fishing data, but extrapolated from estimates of Columbia River natural production, hatchery releases, migration timing, and freshwater survival.

### Study area

Much of the marine mortality of juvenile salmon is thought to occur during the first days or months that smolts enter the ocean (Pearcy 1992; Beamish and Mahnken 2001; Weitkamp 2004). Thus, we located our study site off the Columbia River (fig. 2), a river basin with relatively large salmon runs. We also conducted our field collections during spring/early summer, the time when most coho and Chinook salmon smolts emigrate from the Columbia River (Dawley et al. 1986). The study site is situated in the northern portion of the California Current ecosystem, and has seasonally variable winds and currents: in the summer, winds come from the northwest, currents move southerly, and upwelling occurs; in the winter, winds come from the south, currents move northerly, and downwelling occurs (Hickey 1989; Hickey and Banas 2003). The low-salinity Columbia River plume is a dominant feature of the study area, and is typically located on the continental shelf off Washington during winter and beyond the shelf off Oregon during summer (Hickey and Banas 2003). Columbia River flows are generally highest in

May/June and lowest in August/September. Flows are presently highly regulated (by dams) and high flows are now much lower than historical levels (Sherwood et al. 1990).

### Fish collections

During 1999–2005, we collected forage and predatory fishes at fixed stations along two transect lines, one just south of the Columbia River and the second approximately 80 km north (fig. 2). Six stations were sampled along each transect, with the first station as close to shore as possible (30 m deep), and the farthest station approximately 55.6 km from shore. In 1998, the first year of our study, we sampled at a variety of stations along a broad arc from Willapa Bay, Washington, to Tillamook Head, Oregon. During this year, part of our research was to identify the appropriate trawl equipment and station locations for collecting predator and forage fishes. We tried a variety of trawls before choosing a 264-rope trawl. Only data collected by rope trawl are reported. All sampling was conducted at night, dusk to dawn, approximately every 10 days from mid-April through July/early-August, for a total of 20 sampling days, for a maximum of 10 sampling cruises per year. Sampling was conducted at night because hake, clupeids, and other forage fishes make diel migrations from depth to surface waters (Blaxter and Holliday 1963; Averson and Larkins 1969).

All samples were collected by surface trawling with a chartered commercial trawler. The trawl equipment was a NET System 264-rope trawl with 3 m foam-filled Lite doors. This gear has also been used to capture juvenile salmonids and associated fishes off southeast Alaska (Murphy et al. 1999) and California (MacFarlane and Norton 2002). The trawl is 100 m long with a fishing mouth area 28 m wide and 12 m deep. The effective mouth area (336 $m^2$) was measured in earlier work using a backward-looking net sounder (Emmett et al. 2004). The net was fished close to the surface, but the head rope depth was usually 1–1.5 m deep (Krutzikowsky and Emmett 2005). Mesh size ranges from 126.2 cm in the throat of the net near the jib lines to 8.9 cm in the cod end. A 6.1 m long, 0.8 cm stretch knotless web liner was sewn into the cod end to capture small fishes and invertebrates. The 264-rope trawl was fished by towing it 137 m (75 fathoms) behind the vessel, which traveled at approximately 2.9 knots (1.5 m/s) for 30 minutes. However, starting in 2001, haul times were shortened to 15 minutes because longer tows resulted in very large catches of forage fishes. Large catches increased our fish processing time and reduced our ability to trawl at every sampling site before daylight.

From each haul, all fish species were identified and enumerated, and 30 random fish of each species were measured. However, when haul catches were large (~>200), a random sample of 30 individual fish from each species was measured, and a subsample of each species (approximately 5–30 kg, depending on fish size) was counted and weighed, and then the remaining fish of that species were weighed. The total numbers of each species captured for that haul were determined by adding the number counted to the estimated number that was weighed (i.e., mass weight divided by the average weight/individual).

### Fish abundance estimates

Fish densities for each haul were calculated by dividing the number of fish captured by the water volume of each haul. Volume of each haul was calculated by multiplying the distance fished by the effective mouth area. The distance each haul fished was identified by the geographic positioning system. We assumed a net efficiency of 1.0 (i.e., all fish at the mouth of the net were captured). Because the fish catch data were highly skewed, average monthly densities of forage and predator fishes were calculated using the delta-distribution method (Pennington 1996). This method uses a lognormal model to first calculate the mean and variance of the non-zero catch data (i.e. hauls where the fish catch was not zero) and then adjusts these values using the proportion of non-zero hauls. Because we sampled approximately every 10 days, monthly densities were calculated using data from two or three cruises (24 or 36 hauls). Estimates of total fish abundance in the study area were calculated by multiplying the average May/June densities by the total volume of the study area. Total water volume of the study area ($1.56 \times 10^{11}$ $m^3$) was calculated by multiplying the study area ($1.3 \times 10^{10}$ $m^2$) (fig. 2) by an assumed surface-trawl sampling depth of 12 m.

Forage fish migration into the study area begins in early May and peaks in late May (Emmett et al. 2006). The model incorporates these fluctuations by gradually increasing forage fish numbers until the end of May (fig. 3), after which forage fish immigration is discontinued. Recruitment, the addition of 0-age juveniles, to forage fish populations occurs in the fall after our study period (Emmett et al. 2005; Emmett, unpubl. data), so the model assumes no recruitment of forage fish during the model period.

### Juvenile salmonid abundance estimates

Surface trawling at night does not collect juvenile salmonids effectively (Krutzikowsky and Emmett 2005), so surface trawl catches of juvenile salmonids were not used to estimate their abundance. Total counts or estimates of juvenile salmonids, hatchery releases plus wild production, leaving the Columbia River are not available. However, in 2004 an estimated 157 million hatch-

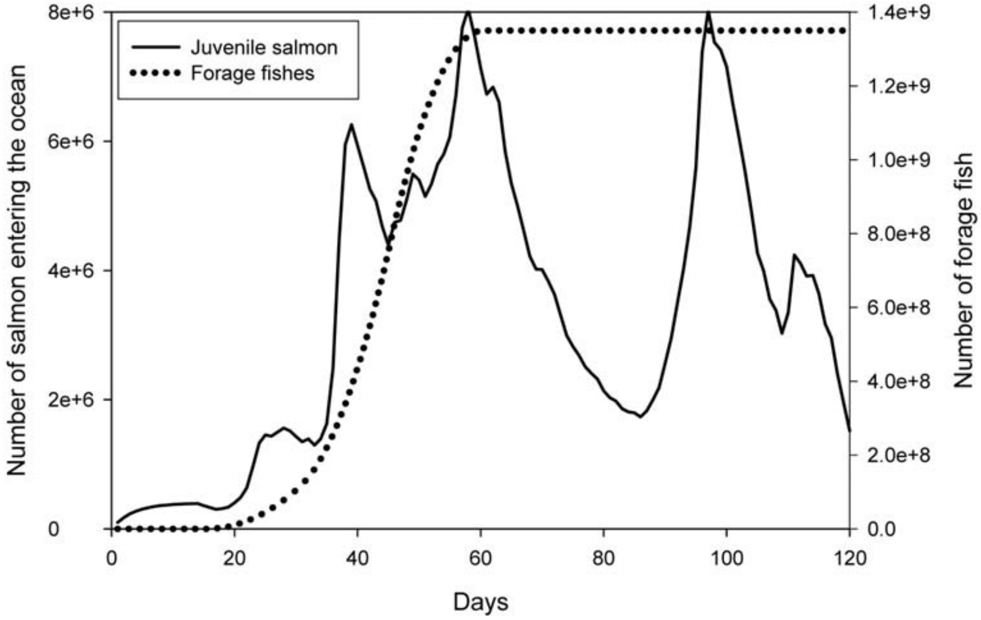

Figure 3. Graphic representation of how the trophic model populated the study area off the Columbia River with number of juvenile salmon entering per day and number of forage fish off the Columbia River. Zero on the *x* axis corresponds to 1 April.

ery salmon smolts were released in the Columbia River (NPCC 2004). Approximately 75% of juvenile salmonids in the Columbia River are of hatchery origin, thus ~50 million (25%) are wild smolts (Memo. from J. Ferguson, NOAA/NMFS, Seattle, Washington, to J. Lecky, NOAA/NMFS, Portland, Oregon, 25 August 2005). This provides a total estimate of 200 million smolts entering the Columbia River annually. However, approximately half of all smolts die before they reach the ocean (Douglas Marsh, NOAA/NMFS, Seattle, Washington, pers. comm.), so we estimated that about 100 million smolts entered the ocean from the Columbia River in 2004, and we assumed that smolt numbers were similar in other years. Columbia River hatchery and wild production, along with riverine survival of juvenile salmon, does vary annually, but specific estimates of the number of smolts entering the ocean each year are presently unavailable.

The annual smolt (juvenile salmon) migration through the Columbia River estuary is well documented. Yearling (coho and spring Chinook salmon) and older (steelhead, *O. mykiss*) smolts begin migrating in April, with peak migration in May, and decline through June (Dawley et al. 1986). Subyearling Chinook salmon smolts migrate primarily from June through September, with a peak in July (Dawley et al. 1986). The number of smolts that migrate into the ocean each day (fig. 3) was calculated by multiplying 100 million times the percent of Columbia River juvenile salmon that migrate each day. The percent of the juvenile salmon that migrate each day was modeled using the percent of the salmon-smolt run passing Bonneville Dam each day in 2002, and assumed to be similar each year. These data were obtained from the Fish Passage Center, Portland, OR (http://www.fpc.org/). It takes approximately three days for juvenile salmon to travel from Bonneville Dam to the ocean, so the ocean entry date was adjusted accordingly.

Juvenile salmon are known to migrate out of the study area and generally move directly offshore (steelhead), or move north (Pearcy and Fisher 1988; Fisher and Pearcy 1995) after spending time in the Columbia River plume, or move south for a short period. Unfortunately, no empirical data are available on the residence time of individual smolts in the study area. We assumed that 25% of the juvenile salmon leave the study area (fig. 2) per day, implying that only 13.3% of the juvenile salmon will be left in the study area after one week, assuming no predation. We believe this estimate of percent migration/day may be high. Decreasing the migration rate would increase predation rates on juvenile salmon in the study area. By using 25% we are making a conservative estimate of residence time.

### Large fish consumption rates

Pacific hake consumption rates were obtained from the literature (Francis 1983; Rexstad and Pikitch 1986), but modified by our own stomach analysis findings. For example, the literature indicated that Pacific hake consume ~1.0–2.5% of their body weight/day. For the average Pacific hake that we captured, which weighed ~500 g, this consumption rate implies that they ate only 5–10 g/day, but our stomach analysis showed that Pacific hake could consume a least 5.0% of their body weight

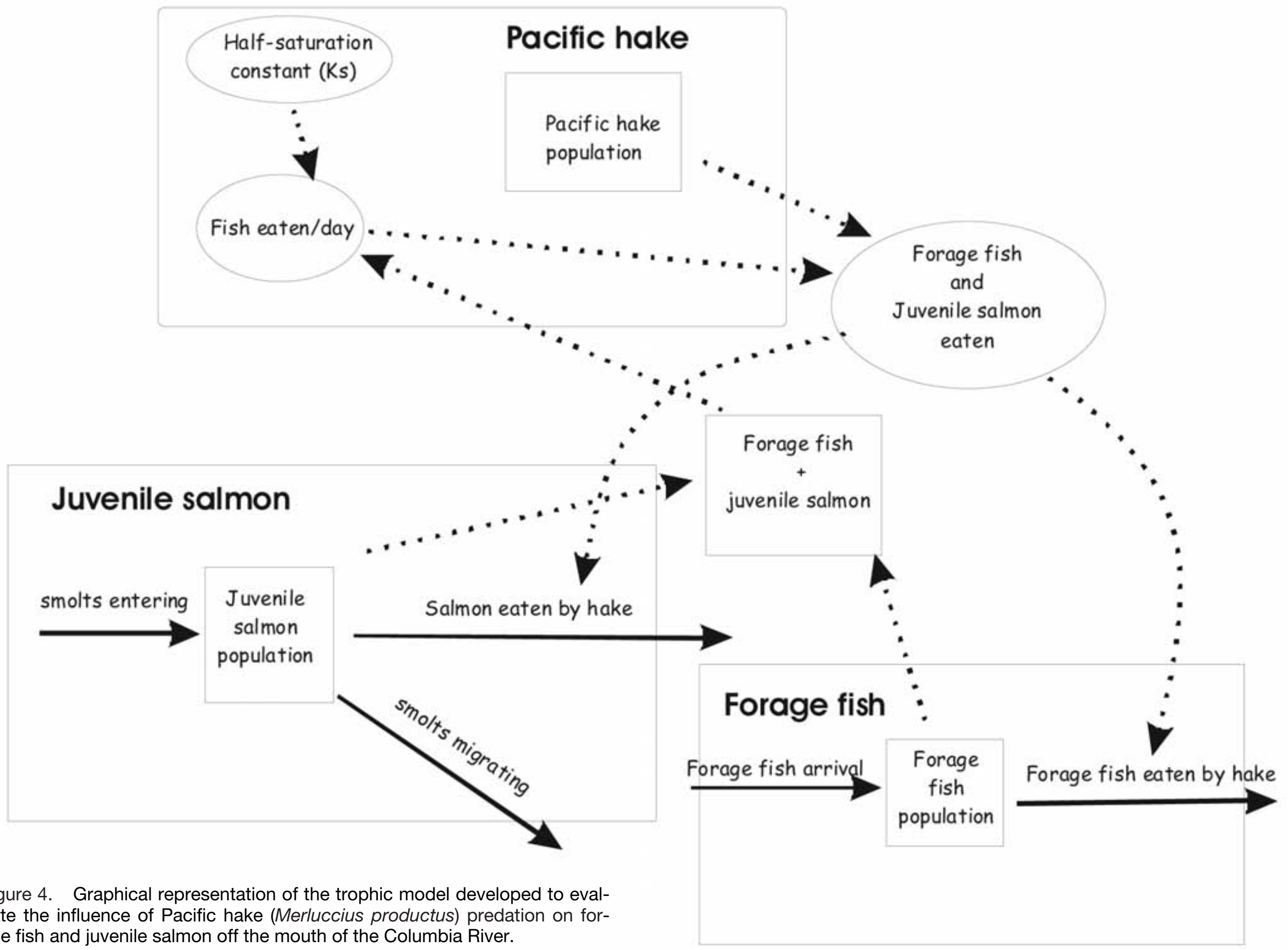

Figure 4. Graphical representation of the trophic model developed to evaluate the influence of Pacific hake (*Merluccius productus*) predation on forage fish and juvenile salmon off the mouth of the Columbia River.

during one meal. Cartes et al. (2004) reported that European hake (*Merluccius merluccius*) ate 1.01–5.51% of their body weight/day. As such, we estimated that our average Pacific hake had a maximum daily consumption rate of approximately 25 g/day, similar to the value in Field (2004). Since the average northern anchovy (*Engraulis mordax*), a primary prey of Pacific hake (Emmett and Krutzikowsky, in press), was approximately 25 g (our unpublished data), we estimated that Pacific hake had a maximum consumption rate of one forage fish per day.

### Model overview

All model development and mathematical calculations were conducted using the STELLA software package (High Performance Systems 1997). The model describes the pelagic food web off the mouth of the Columbia River for 120 days (April through July), the period when most Columbia River juvenile salmonids first enter the ocean (Dawley et al. 1986) and when mortality is thought to be high (Pearcy 1992). The model has one major predator (*Hake*) and two prey groups, *Salmon* and *Forage Fish* (*FF*) (fig. 4). Pseudo-code for the STELLA mathematical model is available by contacting the first author.

Predatory fishes have been shown to be primarily selective for prey size, not species (Ursin 1973; Sogard 1997), so juvenile salmon were considered a member of the forage fish, or prey, community. As such, we grouped forage fish (*FF*) and juvenile salmonid (*Salmon*) populations into one prey population variable (*FFSalmon*). Hake were allowed to prey on this mixed population, and the number of juvenile salmonids eaten by hake was derived by multiplying the number of fish eaten (*FFSalmon_Eaten*) by the proportion of *FFSalmon* composed of juvenile salmon:

$$Salmon\_Eaten = FFSalmon\_Eaten * (Salmon/FFsalmon) \quad (1)$$

The total number of forage fish and salmon eaten per day (*FFSalmon_Eaten*) can be calculated by multiplying the number of hake in the study area (*Hake*) by feeding rate (*FR*):

$$FFSalmon\_Eaten = Hake * FR \quad (2)$$

Feeding Rate (*FR*) changed as prey (*FFSalmon*) abundance changed. This was accounted for by using a (Michaelis-Menton) function:

$$FR = MaxFF \times FFSalmon/(Ks + FFSalmon) \quad (3)$$

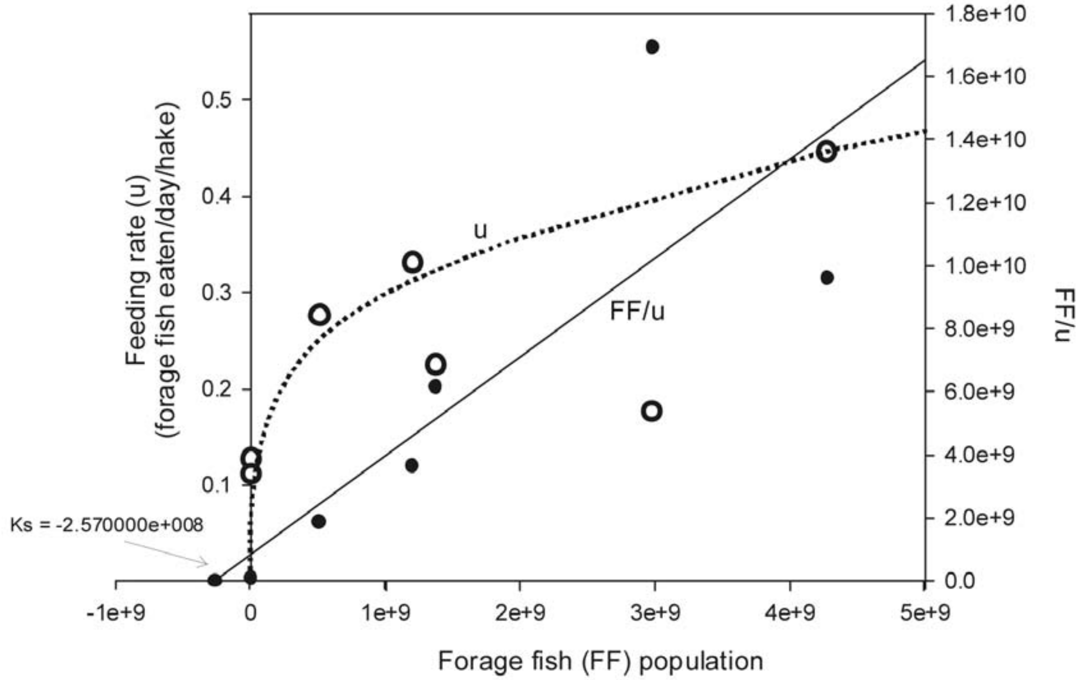

Figure 5. The relationship between the relative number of Pacific hake (*Merluccius productus*) feeding on fishes (○) (estimated hake fish feeding rate) at various forage fish population abundances. The straight line is the regression of the forage fish population/hake fish feeding rate ratio versus forage fish population abundance (●) from which the Michaelis-Menton *K*s (half-saturation feeding constant) was estimated.

Since the maximum feeding rate (*MaxFF*) was estimated to be equal to one forage fish/day, it can be ignored in the equation. The half-saturation feeding constant, *Ks*, was estimated by subtracting the intercept from a linear regression of the observed annual average percent of hake with fish in their stomachs (i.e., an estimate of hake fish-feeding rate) regressed against the observed ratios of the number of forage fish plus juvenile salmon (*FFsalmon*) over the hake fish-feeding rate (Eppley and Thomas 1969) (fig. 5). At very high forage fish and juvenile salmon densities, *FR* approaches 1. At low prey densities, *FR* approaches 0 and the number of forage fish and juvenile salmon consumed also approaches 0.

The total number of juvenile salmon (*Salmon*) in the study area on any day (*t*) was calculated as:

$$Salmon(t) = Salmon(t-1) + Salmon\text{n}\_Entering(t) - Salmon\_Eaten(t) - Salmon\_Migrating(t) \qquad (4)$$

for $t = 1$ to 120.

The total number of forage fish (*FF*) in the study area was calculated as:

$$FF(t) = FF(t-1) + Forage\_Fish\_arriving\ (t) - Forage\_Fish\_eaten(t) \qquad (5)$$

A list of parameter and constant values is provided in Table 1.

## Model evaluation

***Calibration/Confirmation.*** This model serves as an initial "framework" to evaluate if a dynamic trophic model, describing the relationships between hake and forage fish, could account for annual fluctuations in marine mortality of Columbia River juvenile salmon. The model predicts how many smolts would be eaten by hake under different levels of abundance for hake and forage fish populations. We used linear regression to compare the annual number of salmon eaten as predicted by the model, the independent variable, with four observed measures of salmon marine survival: the Oregon Production Index Area (OPI) of hatchery coho salmon (*Oncorhynchus kisutch*) marine survival (PFMC 2005), and spring, summer, and fall Chinook (*O. tshawytscha*) salmon jack counts at Bonneville Dam. Since annual production of smolts in the Columbia River is approximately constant (Douglas Marsh, NOAA/NMFS, Seattle, Washington, pers. comm.), jack counts, which

TABLE 1
**Constants and parameters for model simulations.**

| Parameter or constant | Description | Value |
|---|---|---|
| *Ks* | Half-saturation feeding constant | $2.3 \times 10^9$ |
| Percent Migration | Percent of smolts migrating from the study area per day | 25% |
| *Max FF*/day | Maximum number of forage fish eaten by the average hake per day | 1 |

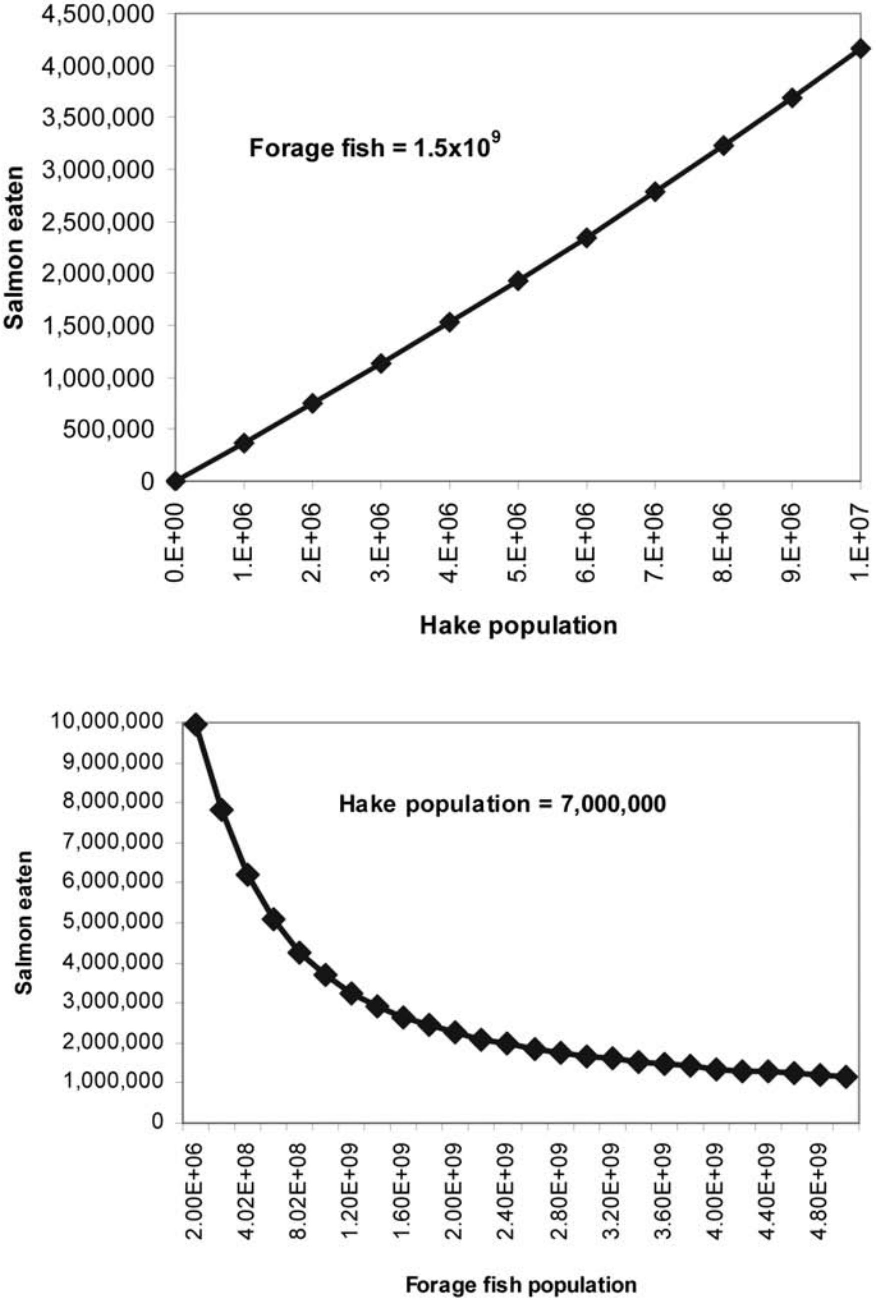

Figure 6. Model output showing the estimated number of salmon eaten at various Pacific hake (*Merluccius productus*) population sizes (top) and when the forage fish population is 1.5 x $10^9$, and at various forage fish population sizes (bottom) when Pacific hake are constant.

are the number of precocious males that have spent one summer at sea, are generally a good predictor of annual salmon marine survival for Chinook salmon. Annual Chinook salmon jack counts at Bonneville Dam were obtained from the Columbia River Data Access in Real Time (DART) homepage (http://www.cbr.washington.edu/dart/dart.html), maintained by the University of Washington. Before conducting the statistical analysis, the model-predicted number of salmon eaten by hake was log-transformed to normalize the data.

Using multiple regression models with Columbia River Chinook salmon jack returns or coho salmon marine survival as dependent variables, we also investigated if the annual numbers of salmon eaten, as predicted by the trophic model, with Columbia River flow (average May/June flows) or average May/June sea surface temperature (SST), could account for much of the observed variation in salmon marine survival

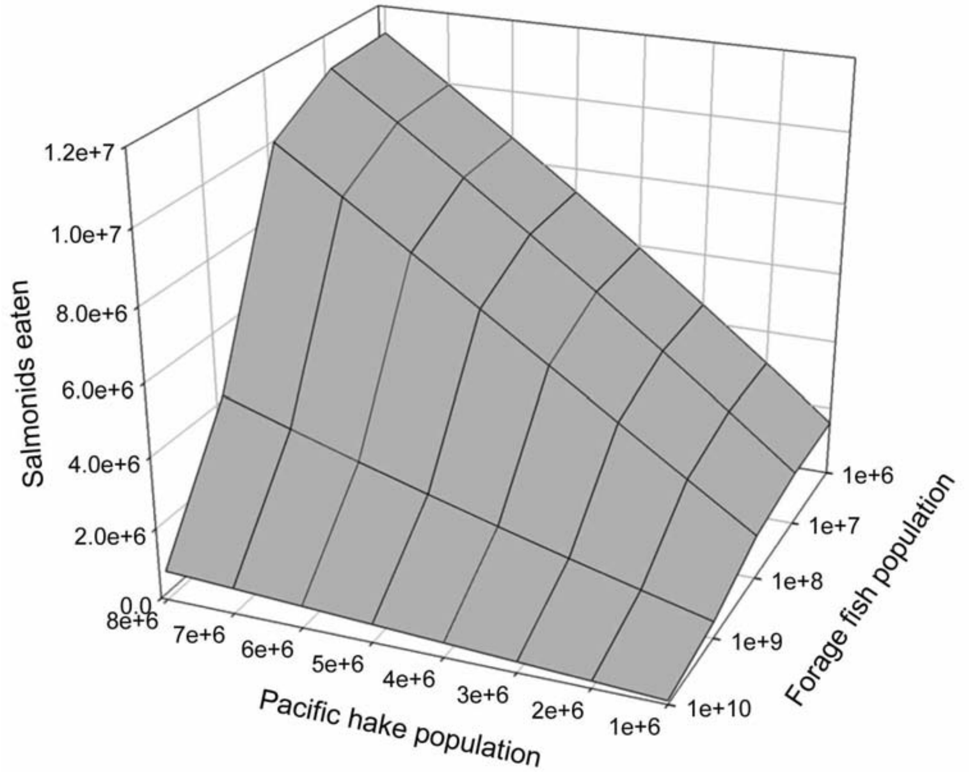

Figure 7. Output from the trophic model of Pacific hake, forage fish, and juvenile salmon interactions. Shown is the estimated number of salmon eaten under various population sizes of Pacific hake (*Merluccius productus*) and forage fishes.

## RESULTS

### Model simulations

We ran a variety of model scenarios to simulate how varying hake and forage fish abundances influence the number of juvenile salmon eaten. At a given level of forage fish abundance, the model predicts that the number of juvenile salmon eaten is directly related to hake population abundance (fig. 6, top panel). The model also predicts that juvenile salmon mortality is inversely related to forage fish abundance in a curvilinear fashion (fig. 6).

Under “good” ocean conditions—when hake numbers are less than $1.0 \times 10^6$ and forage fish are abundant—hake eat relatively few salmonids (fig. 7). However, when hake are abundant and forage fish are not, the number of salmon eaten by hake rises sharply (fig. 7). When forage fish are very abundant (greater than $1.0 \times 10^9$), they serve as strong alternative prey and, for a wide range of values for hake abundance, few salmonids are eaten (fig. 7).

### Model estimates of salmon mortality versus salmon marine survival indexes

Seven years of average annual May/June abundance estimates for hake and forage fish in the study area were used in the model to generate model predictions of the numbers of salmon eaten. These resulting model estimates of salmon mortality were then compared with four annual measures of salmon survival (tab. 2). The regression analysis found that Oregon OPI hatchery coho salmon marine survival was negatively correlated with the predicted number of salmon eaten (regression, $p = 0.05$, $R^2 = 0.42$). However, fall Chinook salmon jack counts at Bonneville Dam were only weakly related to the predicted numbers of salmon eaten ($p = 0.18$, $R^2 = 0.16$), and spring and summer Chinook salmon jack counts at Bonneville Dam were poorly related to the model predictions; $p = 0.91$, $R^2 = 0.0$ and $p = 0.28$, $R^2 = 0.05$, respectively.

The results of these simple regressions indicate that the simulation trophic model did not accurately mimic the observed variability in salmon marine survival. However, if average spring (May/June) Columbia River flows were included with the model-predicted numbers of salmon eaten in a multiple regression model, significant predictive relationships were obtained for OPI hatchery coho salmon smolt to adult returns ($p = 0.01$, $R^2 = 0.75$), and fall Chinook salmon jack counts ($p = 0.04$, $R^2 = 0.61$), but not spring and summer Chinook salmon jacks (fig. 8). In contrast, jack counts of Columbia River spring and summer Chinook salmon were strongly related only to May/June SST; $p = 0.002$, $R^2 = 0.79$ and $p = 0.01$, $R^2 = 0.61$, respectively (fig. 9).

TABLE 2

**Average spring (May/June) abundance estimates of Pacific hake (*Merluccius productus*) and forage fishes off the mouth of the Columbia River from surface trawls 1998–2005. Trophic model predictions are the annual number of salmon eaten from 1 April through 1 August, along with observed coho salmon (*Oncorhynchus kisutch*) hatchery Oregon Production Index (OPI) area percent smolt to adult returns (SAR), and Bonneville Dam spring, summer, and fall Chinook salmon (*O. tshawytscha*) jack counts (corrected for year of ocean entry).**

| Observed | | Model prediction | | Observed | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Year | Pacific hake | Forage fish | Salmon eaten | Coho salmon OPI % SAR | Spring Chinook salmon | Summer Chinook salmon | Fall Chinook salmon | Average Columbia River May/June flows ($m^3$/sec) | Average May/June SST anomaly |
| 1998 | 47,655,442 | 8,867,411 | 43,572,056 | 1.09 | 11,081 | 2905 | 23,582 | 10,082 | 0.28 |
| 1999 | 3,266,796 | 7,508,749 | 4,841,367 | 2.29 | 28,472 | 10450 | 55,538 | 10,497 | –0.94 |
| 2000 | 81,414 | 1,378,052,066 | 31,283 | 4.33 | 22,000 | 11840 | 74,496 | 7,695 | –0.26 |
| 2001 | 144,068 | 4,280,770,092 | 26,110 | 2.47 | 11,308 | 6141 | 40,215 | 4,621 | –0.49 |
| 2002 | 505,760 | 1,202,111,144 | 212,987 | 3.76 | 22,245 | 10058 | 47,722 | 8,913 | –0.42 |
| 2003 | 7,882,295 | 2,984,177,499 | 1,909,801 | 2.58 | 16,928 | 9501 | 38,557 | 7,991 | –0.26 |
| 2004 | 3,065,483 | 513,088,377 | 2,223,774 | 1.89 | 7,016 | 3439 | 21,214 | 7,293 | 1.00 |
| 2005 | 544,005 | 598,909,525 | 345,270 | 2.01 | 3,856 | 3,407 | 25,549 | 7,461 | 1.10 |

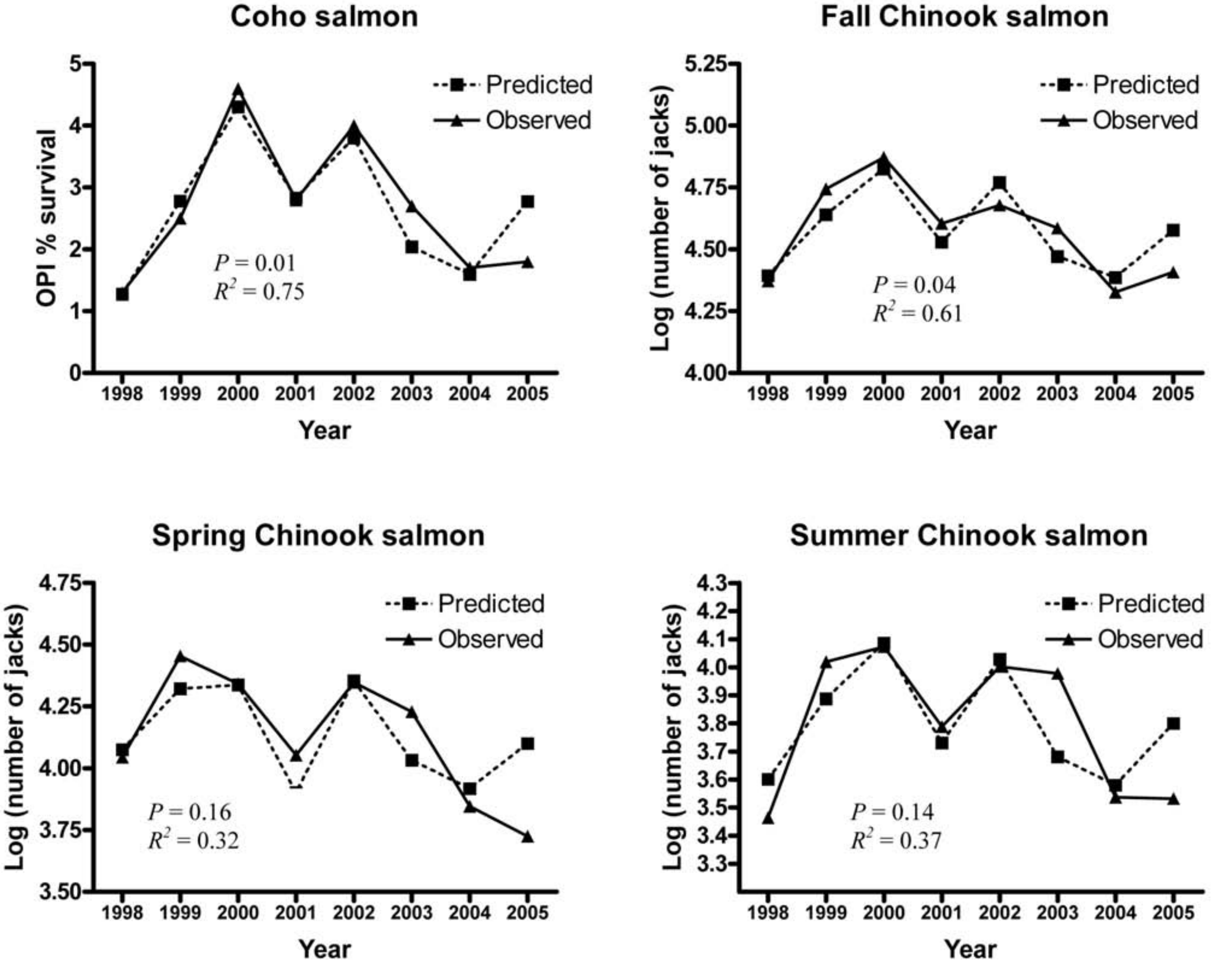

Figure 8. The relationship between observed marine survival of Oregon Production Index hatchery coho salmon (*Oncorhynchus kisutich*), and Columbia River fall, spring, and summer Chinook salmon (*O. tshawytscha*) jack counts versus values predicted from multiple regression using trophic model output and Columbia River flows.

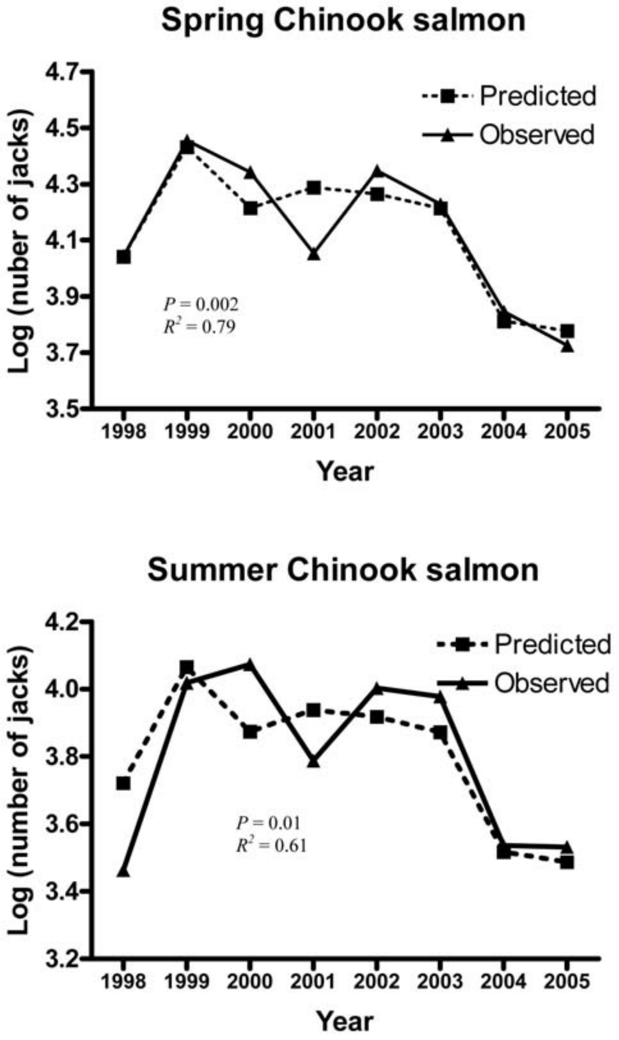

Figure 9. The relationship between observed jack counts of Columbia River spring and summer Chinook salmon (*Oncorhynchus tschawytscha*), and that predicted using average annual May/June sea surface temperatures collected off the Columbia River 1998–2005.

## DISCUSSION

The goal of this study was to evaluate if predation by Pacific hake could be responsible for a large portion of the marine mortality of Columbia River salmon smolts, and if forage fish populations play a role in this mortality. We also wanted to investigate if a simple trophic predation model could replicate observed annual salmon marine survival using the hake and forage fish population data collected off the Columbia River (Emmett et al. 2006).

The model predicted relatively poor salmon survival when hake populations were abundant and forage fish populations were low in the study area. The model also predicted relatively low salmon mortality when hake were abundant, provided that forage fish were very abundant (~100 times more abundant than hake). Overall, the model indicated that hake ate relatively few salmon smolts relative to the number migrating out of the Columbia River. However, our study area was relatively small compared to the coastal area that salmon smolts migrate through on their way north (Washington and British Columbia, Canada). If hake and forage fish densities in the coastal area are similar to those off the Columbia River, then total salmon mortalities directly related to hake predation would be proportionally higher than our estimates. Similar studies on the abundance of hake and forage fish in other locations would be of value.

A factor that strongly influences model results is the variable *Feeding Rate*, which alters the percentage of forage fish consumed by each hake as forage fish populations fluctuate. For example, when forage fish and salmon become less abundant, *Feeding Rate* declines and predators consume fewer forage fish and salmon. While stomach data indicate that the rate at which hake consume forage fish declines as forage fish become less abundant, we presently have only seven annual observations on how predator *Feeding Rate* actually changes with fluctuating predator/forage fish numbers. Laboratory studies of hake feeding at different prey concentrations would be helpful. Other estimated constants, such as residence time and number of smolts, when changed, produced smaller model responses. For example, a doubling of residence time doubled the number of salmon smolts eaten. However, holding forage fish densities constant but doubling the number of smolts did not double the number of smolts eaten, indicating that a possible "swamping" of predators can occur.

Feeding rates of large piscivorous predatory fishes are strongly affected by turbidity, while feeding rates of small fishes (juvenile salmon and forage fish) are not (De Robertis et al. 2003). In freshwater and estuarine habitats, juvenile salmon have been shown to be less vulnerable to predation at high turbidity levels (Gregory and Levings 1998). Coastal survey data indicate that juvenile salmon and forage fish are generally most abundant in nearshore turbid environments (Brodeur et al. 2004; Emmett et al. 2006), suggesting these fishes may use turbid marine waters to evade predators and for feeding. These nearshore areas also have higher zooplankton densities than offshore habitats (Lamb and Peterson 2005). We did not include turbidity in the simulation model, but doing so seems a sensible extension and it would be useful for future oceanographic surveys to measure turbidity. Laboratory experiments of predator/forage fish/juvenile salmon feeding interactions under various turbidity conditions in the Columbia River plume would also be valuable. We suspect that coastal turbidity levels are directly related to average May/June SSTs and upwelling, and to the high correlation between SSTs and spring and summer Chinook salmon jack counts.

The predictions from the simulation model correlated well with the marine survival of coho and fall Chinook salmon, but only after Columbia River flows were included in a multiple regression model. This suggests that Columbia River flows strongly influence predator/prey interactions in the Columbia River plume. Several mechanisms could be at work. Under high flow conditions juvenile salmonids would be carried quickly out of the study area and away from predators (see Pearcy 1992). Furthermore, the plume water is generally more turbid when flows are high, thus limiting Pacific hake and other predators' ability to see and capture near-surface prey (salmonids) (Gregory 1993; Gregory and Levings 1998; De Robertis et al. 2003).

In our model, we estimated that the total number of juvenile salmonids leaving the Columbia River was 100 million/year, with daily migration reflecting the numbers passing Bonneville Dam. While sufficient for this simple modeling effort, accurate estimates of the number of juvenile salmon migrating out of the Columbia River on a daily and annual basis would be extremely valuable for this model and Columbia River salmon management. Salmon runs in the Columbia River are dominated by hatchery production, so while adult salmon run sizes fluctuated widely during our study period, the actual number of juvenile salmonids migrating to sea probably did not fluctuate much. However, having the actual number of salmon smolts migrating to sea that were produced from large adult salmon returns would help parameterize our model.

The model was particularly poor at predicting salmon marine survival in 2005 (fig. 8). During that year, anomalous ocean conditions existed off the Pacific Northwest (Geophysical Research Letters special publication: http://www.agu.org/contents/sc/ViewCollection.do?collectionCode=CALIFCUR1&journalCode=GL). In particular, upwelling was delayed (Kosro et al. 2006; Schwing et al. 2006), zooplankton populations were low and contained few northern taxa (Mackas et al. 2006), and fish (Brodeur et al. 2006), marine birds (Sydeman et al. 2006), and marine mammals (Newell and Cowles 2006; Weise et al. 2006) were negatively affected. From these 2005 reports it was clear that the ecosystem off the Northwest was not operating "normally" but with conditions similar to an El Niño period, suggesting that during 2005 another biological mechanism, perhaps predation by Humboldt squid (*Dosidicus gigas*) or sharks (Brodeur et al. 2006), may have provided additional sources of salmon mortality.

The general trophic model we developed provides a good beginning framework to understand interactions between forage fish, predators, environmental conditions, and juvenile salmon off the Columbia River and the Pacific Northwest. As discussed above, many refinements need to be made to create a more "realistic" model. This includes additional information on fish encounter rates and feeding efficiencies, turbidity effects, Columbia River plume size and structure, large predator/prey patches, predator and forage fish population abundances, the actual number of juvenile salmons migrating to the ocean, and their migration rates. To make the model representative of the entire Pacific Northwest, we need additional information on Pacific hake, such as better information on feeding rate, population estimates on the shelf during spring and summer, feeding behavior, and forage fish abundance. We also need information on other large fish predators, predatory birds and mammals, and forage fishes for the entire Pacific Northwest, including British Columbia. Many predators, including hake and mackerel, also eat large numbers of euphausiids. Unfortunately, estimates of Northwest euphausiid populations are presently not available, but euphausiids are important in this ecosystem because they are a primary prey for hake (Tanasichuk 2002) and many other species, and may determine the spatial distribution and movements of hake (Benson et al. 2002; Swartzman and Hickey 2003) and other predators.

This simple ecosystem trophic model is a preliminary investigation into how the Pacific Northwest pelagic fish ecosystem functions. While the trophic model appears to successfully predict marine survival of two Columbia River species/stocks of salmon, it was not successful for two other stocks. This indicates that Columbia River salmon species/stocks probably do not behave similarly nor inhabit identical coastal marine habitats. Other ecosystem processes (e.g., feeding and growth) or other piscivorous predators (e.g., marine mammals or birds) are probably acting to limit marine survival for these salmon stocks. As fishery managers move to ecosystem-based fishery management, it will be essential to identify and quantify these processes. Relatively simple trophic models, similar to the one presented here, will be useful tools to clarify which ecosystem processes are important.

## CONCLUSIONS

Our trophic model indicates that predation by Pacific hake, interacting with forage fish and juvenile salmonids, and influenced by Columbia River May/June flows may help determine OPI coho salmon and Columbia River fall Chinook salmon marine survival. River flows and associated turbidity and other physical factors probably play an important role in these predator/prey interactions, and are influenced by Columbia River hydropower operations. Future ecosystem research should further quantify existing variables and explore whether adding other variables to this or other ecosystem models can produce more accurate predictions of salmon marine survival. Furthermore, this type of model would be a useful tool to evaluate how alternative Columbia River hydropower operations could affect predator/prey interactions in the estuary and plume, and thus, salmon marine survival.

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# SEASONAL FOOD WEB MODELS FOR THE OREGON INNER-SHELF ECOSYSTEM: INVESTIGATING THE ROLE OF LARGE JELLYFISH

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## ABSTRACT

We developed two seasonal food-web models, spring and summer, within the Ecopath framework for the Oregon upwelling ecosystem to investigate the role of large jellyfish as competitors for zooplankton prey. We used information about fish and jellyfish biomass, distribution, and diet derived from pelagic trawl survey data. Information about lower trophic-level production was acquired from zooplankton survey data. The models indicate that in spring, jellyfish are a modest consumer of zooplankton, and forage fishes dominate the system in terms of biomass and consumption. By late summer, jellyfish become the major zooplankton consumers, and they consume 17% of the summer zooplankton production while forage fish consume 9%. Jellyfish appear to divert zooplankton production away from upper trophic levels. Only 2% of the energy consumed by jellyfish is passed to higher trophic levels. However, the role of jellyfish as competitors may be moderate; a large proportion of zooplankton production (40%–44%) is not consumed but lost to detritus.

## INTRODUCTION

The northern California Current (NCC) off Oregon and Washington supports a seasonally productive and open ecosystem. Upwelling-favorable winds dominate along the Oregon and Washington coasts after the spring transition during March or April, and continue through October or November when downwelling conditions normally occur (Strub et al. 1987). During the upwelling season, the NCC is home to a diverse pelagic fish community, including the juveniles of important salmon stocks, resident species such as anchovies, smelts, and herring, and transient species migrating from the south such as sardines, hake, and mackerels (Brodeur et al. 2005). Ecosystem productivity and food-web structure vary on seasonal-to-decadal time scales due to the timing and strength of seasonal alongshore winds and forcing by basin-scale physical processes (e.g., El Niño, Pacific Decadal Oscillation) and longer-term climate trends (Batchelder et al. 2002). These variations affect the survival and productivity of all members of the pelagic community in the NCC.

Jellyfish biomass has increased dramatically in many ecosystems around the world in the past two decades (Mills 2001; Brodeur et al. 2002; Kawahara et al. 2006; Attrill et al. 2007). Jellyfish have several characteristics that place them in a unique and influential position within an ecosystem, which can have negative affects upon pelagic fish: high rates of reproduction and growth, generally broad diets that can overlap with planktivorous fish, and few predators. Increases in jellyfish biomass are generally accompanied by decreases in fish biomass (e.g., Lynam et al. 2006), which suggests substantial fish-jellyfish interactions that may affect fish growth, survival, and distribution. Thus, there is a recognized need to understand the role of jellyfish in pelagic ecosystems, the causes of jellyfish proliferation, and the potential consequences to ecosystem functioning and to fisheries when jellyfish biomass blooms. Jellyfish may have a negative impact upon pelagic fishes as both predators and competitors (Purcell and Arai 2001). Jellyfish, in particular, can obtain a high biomass and may become an important energy pathway diverting zooplankton production away from pelagic fishes (Mills 1995, 2001; Lynam et al. 2006).

Here, we examine the role of jellyfish in the NCC upwelling ecosystem off the Oregon coast. Jellyfish represent a major portion of the pelagic biomass in the NCC (Shenker 1984; Suchman and Brodeur 2005), although neither their long-term trends in biomass nor their trophic role in the ecosystem has been well studied. Suchman et al. (in press) examined the diet of several dominant jellyfish in this region and compared their consumption to available zooplankton. They found that these species can have a major impact on production of several zooplankton taxa. Brodeur et al.[1] compared the diets and distribution of these jellyfish to those of co-occurring pelagic fishes and found that the potential for competitive interactions can be substantial due to high dietary and spatial overlap.

The goals of this study are to: (1) develop two mass-

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[1] Brodeur, R. D., C. L. Suchman, D. C. Reese, T. W. Miller, and E. A. Daly. Submitted-a. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. Mar. Biol. NOAA/NMFS/NWFSC, Newport, Oregon.

balance food-web models of the northern California Current upwelling ecosystem with focus upon the pelagic sub-system using data from large-scale surveys for biomass, distribution, seasonal patterns of biomass change, and local and contemporary diet information, (2) investigate change in trophic structure during the early (spring) and late (summer) upwelling season, and (3) investigate the importance of large jellyfish within the northern California Current upwelling ecosystem, their impact on lower trophic levels, their importance as competitors with planktivorous fishes, and their impact upon higher trophic levels.

## MATERIALS AND METHODS

### Model Overview

Two seasonal-scale food-web models have been developed for the inner-shelf of the Oregon upwelling ecosystem within the Ecopath framework (Christensen and Walters 2004). The models represent the spring (April-June) and summer (July-September) periods for a composite of the years 2000 and 2002; these are the most recent years during which pelagic fish surveys were conducted over the full North-South extent of the Oregon shelf. The models' domain extends from 46°N to 41.8°N (southern Oregon border) and excludes the mouth of the Columbia River which has its own distinct and important physical and ecological characteristics (Hickey and Banas 2003). Offshore, the models extend to the 125 m isobath, encompassing an area of approximately 9,650 $km^2$.

Ecopath is a software package for synthesizing diet, production, and metabolic information into a mass-balanced system of interactions between all trophic groups that define an ecosystem (Christensen and Walters 2004). The Ecopath master equation allocates the productivity of each trophic group to fishery harvest, transfer to higher trophic level via predation, emigration out of the ecosystem, growth, and other mortality (e.g., senescence):

$$B_i \bullet (P/B)_i - \sum_{j=1}^{n} B_j \bullet (Q/B)_j \bullet DCji -$$

$$(P/B)_i \bullet B_i \bullet EE_i - Y_i - E_i - BA_i = 0 \qquad (1)$$

where, for each trophic group ($i$), $B$ is the biomass, $P/B$ is the mass-specific production rate, $Q/B$ is the mass-specific consumption rate, $DC_{ji}$ is the fraction of prey ($i$) in the diet of predator ($j$), $Y$ is the fishery harvest rate, $E$ is the emigration rate, $EE$ is the ecotrophic efficiency (the fraction of production consumed within the system), and $BA$ is the biomass accumulation rate. The term:

$$\sum_{j=1}^{n} B_j \bullet (Q/B)_j \bullet DCji$$

is the total predation mortality rate, and the term $(P/B)_i \bullet B_i \bullet EE_i$ is the non-predation mortality rate (Christensen and Walters 2004). As input parameters for each trophic group, Ecopath requires the weight-specific diet composition, the fishery harvest rate, and at least three of the following parameters: $B$, $P/B$, $Q/B$, or $EE$. As an assumption of steady-state community composition is not made in the seasonal models developed here, biomass change rate ($BA$) from endemic growth and mortality and emigration (or immigration) rates ($E$) are also required. Ecopath also accounts for the energy flow within individual trophic groups:

$$\text{consumption} = \text{production} + \text{respiration} + \text{egestion}, \qquad (2)$$

where egestion is assumed to be 20% for all groups in the present models.

The two seasonal models presented here each consist of one producer group, 48 consumer groups, two egg groups, and three detritus groups. They are based upon the annual-scale northern California Current models developed by Field and colleagues within the Ecopath framework (Field 2004; Field and Francis 2005; Field et al. 2006). The benthic food web (trophic groupings, diet, physiological rate parameters) is modified from the Field models as are the marine mammal and seabird groups. The information required to develop the pelagic food web was obtained from a variety of sources: recent pelagic fish and plankton survey studies off Oregon, local diet information, fishery records, the literature, and other northeast Pacific food-web models.

### Community Composition

***BPA and GLOBEC pelagic trawl surveys:*** The composition of the pelagic nekton and jellyfish community on the Oregon shelf in spring and summer (2000 and 2002) was estimated from the Bonneville Power Administration (BPA) ocean salmon survey program and the GLOBEC pelagic survey program. The BPA ocean salmon survey sampled three transect lines in May, June, and September from 45.7°N to 44.6°N and from the 30 m isobath onto the continental slope. The GLOBEC survey consisted of four cruises (June 2000 and 2002, September 2000 and 2002) from 44.4°N to 42°N from the 30 m isobath onto the continental slope. Both survey programs quantitatively sampled the upper 20 m of the water-column using an 18 × 30 m Nordic Rope trawl during daylight hours. Detailed trawl and sampling protocol information for both programs are provided by Emmett et al. (2005). The combined sampling area is shown in Figure 1.

Total wet weights of individual species in each trawl

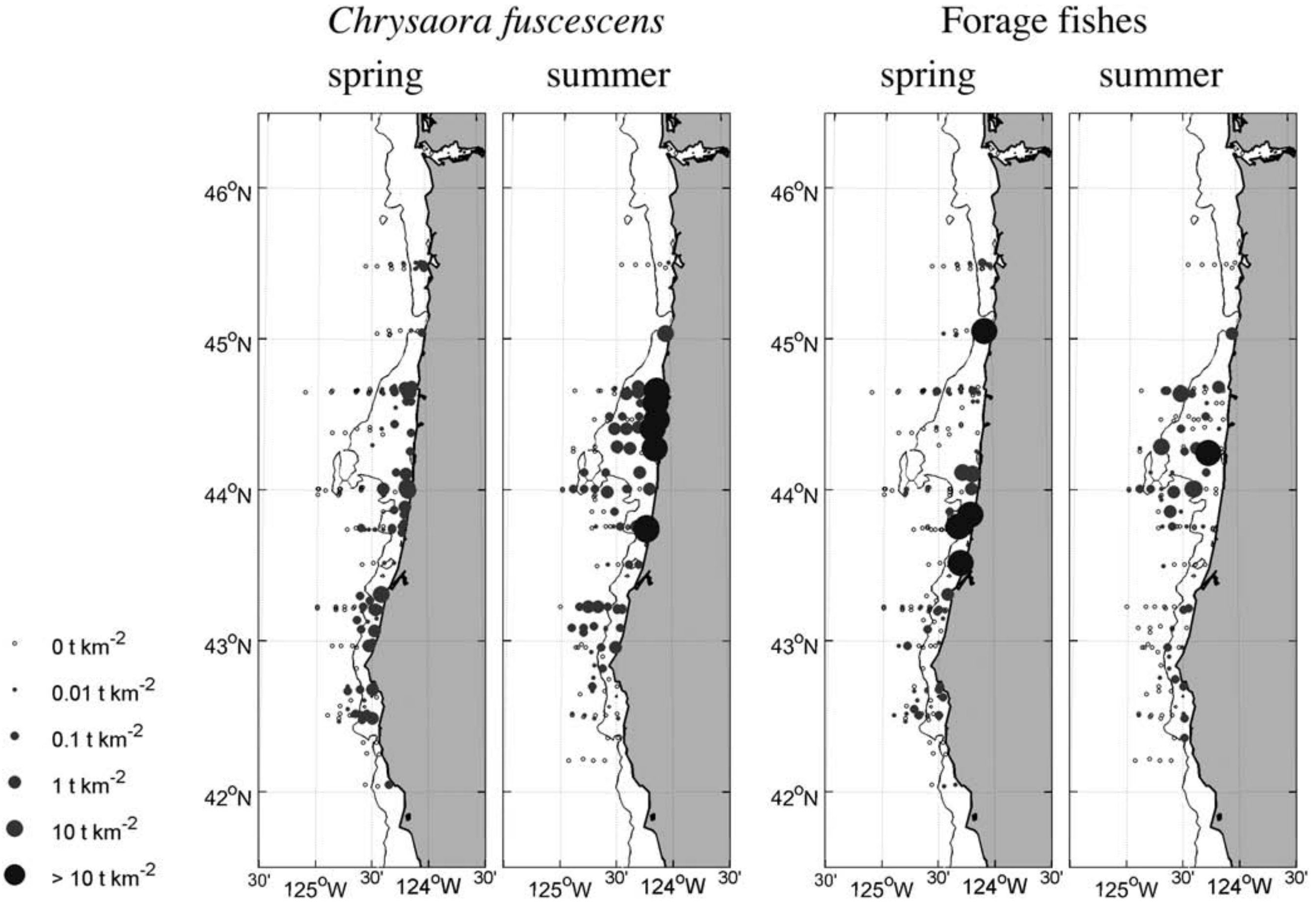

Figure 1. Spring and summer distribution of sea nettle jellyfish (*Chrysaora fuscescens*) and forage fishes (smelt, shad, sardine, herring, anchovy) off the Oregon coast sampled during the BPA and GLOBEC pelagic surveys in 2000 and 2002 (years pooled). Line indicates 125 m isobath.

were calculated from length-distribution data by applying species-specific empirical length-weight relations from the literature and FishBase (http://www.fishbase.org). Trawl data from years 2000 and 2002 were pooled to calculate the mean spring (141 trawls) and summer (103 trawls) areal density and biomass after the method of Pennington (1996) for survey data that include trawls with zero catch and non-zero trawls that are lognormally distributed. The areal biomass and density estimates for groups informed by the BPA and GLOBEC pelagic surveys and not adjusted for catchability are presented in Table 1 (see Appendix for details of pelagic fish biomass values used in models).

***Newport Hydrographic line (NH-line):*** The seasonal biomasses of phytoplankton, copepods, and euphausiids were estimated from time-series data collected along the Newport Hydrographic line (NH-line) across the central Oregon shelf (44.67°N). The phytoplankton and copepod biomass values used in the models are the spatial and seasonal mean values observed during bi-weekly surveys at stations NH-05 (60 m), NH-10 (80 m), and NH-15 (90 m) in the spring and summer seasons of 2000 through 2004 (W. T. Peterson et al., NOAA/NMFS, Newport, Oregon, unpub. data). See Appendix for details and Table 2.

***BPA zooplankton survey:*** Information about larval euphausiids, fish eggs, pelagic amphipods, and individual macro-zooplankton groups was provided by zooplankton surveys conducted as part of, and at the same stations as, the BPA ocean salmon survey in northern Oregon and Washington (C. Morgan, OSU, Newport, Oregon, unpub. data). Zooplankton were collected using a 1 m, 335 µm mesh ring-net towed obliquely from 20–30 m to the surface at 3.7 km/h. The detailed laboratory protocol is described by Schabetsberger et al. (2003). Total wet weights of individual species in each tow were calculated from length-distribution data by applying species-specific empirical length-weight or length-carbon relations (from the literature and W. T. Peterson et al., NOAA/NMFS, Newport, Oregon, unpub. data) and assuming dry:wet weight = 0.19 (Omori 1969). Areal biomass estimates for zooplankton groups measured during the BPA/GLOBEC zooplankton survey and not adjusted for biomass below the tow depth are

TABLE 1
**Areal density and biomass of pelagic fishes and jellyfish as estimated from GLOBEC and BPA pelagic trawl surveys over the Oregon inner-shelf during the spring and summers of 2000 and 2002. Estimates are derived from 141 spring trawls and 103 summer trawls. Both survey years are pooled. These estimates are unadjusted for catchability.**

| | SPRING | | SUMMER | |
|---|---|---|---|---|
| Group | biomass (t/km$^2$) | density (ind./km$^2$) | biomass (t/km$^2$) | density (ind./km$^2$) |
| Forage fishes | | | | |
| smelt | 0.0181 | 24,544 | 0.0086 | 8,569 |
| shad | <0.0001 | 44 | 0.0001 | 54 |
| sardine | 0.0421 | 7,990 | 0.2514 | 251,405 |
| herring | 0.4088 | 1,157,243 | 0.0635 | 39,763 |
| anchovy | 0.0001 | 85 | 0.0001 | 130 |
| saury | <0.0001 | 8 | 0.0007 | 742 |
| Jellyfish | | | | |
| sea nettle | 0.0646 | 690 | 1.5723 | 2,282,936 |
| moon jelly | 0.0791 | 800,732 | 0.5115 | 919,137 |
| egg-yolk jelly | 0.0041 | 15,110 | 0.0716 | 71,630 |
| water jelly | 0.0421 | 37,531 | 0.0241 | 33,509 |
| Salmon | | | | |
| coho | 0.0104 | 106,655 | 0.0214 | 21,427 |
| Chinook | 0.0587 | 445,669 | 0.0448 | 44,791 |
| other salmon | 0.0079 | 54,463 | 0.0001 | 97 |
| juvenile salmon | 0.0030 | 5,348 | 0.0089 | 24,910 |
| Piscivorous fishes | | | | |
| mackerels | 0.0093 | 5 | 0.0859 | 49 |
| sharks | 0.0234 | 23,447 | 0.0106 | 10,609 |

TABLE 2
**Areal density and biomass of zooplankton as estimated from NH-Line and BPA zooplankton surveys over the Oregon and Washington inner shelf during the spring and summers of 2000 and 2002. Values presented here are un-scaled to account for biomass beneath the tow depth. See Appendix for details on biomass estimations used in models.**

| | SPRING | | SUMMER | |
|---|---|---|---|---|
| Group | biomass (t/km$^2$) | density (ind./km$^2$) | biomass (t/km$^2$) | density (ind./km$^2$) |
| phytoplankton[a] | 26.9923 | — | 74.2414 | — |
| copepods[a] | 12.8749 | — | 17.6110 | — |
| *Euphausia pacifica* (adult)[b] | 0.7082 | $4.31 \cdot 10^{7}$ | 6.9833 | $2.67 \cdot 10^{8}$ |
| *Thysanoessa spinifera* (adult)[b] | 1.1739 | $7.70 \cdot 10^{6}$ | 6.4549 | $7.27 \cdot 10^{7}$ |
| euphausiid (larvae)[c] | 0.0554 | $4.51 \cdot 10^{8}$ | 0.1405 | $7.22 \cdot 10^{8}$ |
| euphausiid (eggs)[d] | 0.2223 | $4.05 \cdot 10^{9}$ | 0.0010 | $1.85 \cdot 10^{7}$ |
| pelagic amphipods[c] | 0.0096 | $4.45 \cdot 10^{6}$ | 0.0170 | $4.69 \cdot 10^{6}$ |
| meroplankton[c] | 0.1398 | $6.70 \cdot 10^{8}$ | 0.0479 | $1.60 \cdot 10^{9}$ |
| chaetognaths[c] | 0.0417 | $9.80 \cdot 10^{7}$ | 0.0691 | $1.44 \cdot 10^{8}$ |
| pteropods[c] | 0.0083 | $1.08 \cdot 10^{8}$ | 0.0076 | $1.15 \cdot 10^{8}$ |
| ichthyoplankton[c] | 0.0028 | $1.50 \cdot 10^{6}$ | 0.0005 | $1.42 \cdot 10^{6}$ |
| fish eggs[d] | 0.2032 | $1.39 \cdot 10^{8}$ | 0.0237 | $1.73 \cdot 10^{7}$ |

[a] NH-line (mean 2000-2004, NH-05, NH-10, NH-15) (W. T. Peterson, NOAA/NMFS, Newport, Oregon, unpub. data)
[b] NH-line (median 2001-2004, NH-20) (T. Shaw, OSU, Newport, Oregon, unpub. data)
[c] BPA (Oregon & Washington; 2000 & 2002 pooled; 43 spring tows, 36 summer tows) (C. Morgan, OSU, Newport, Oregon, unpub. data)
[d] BPA (Oregon; 2000 & 2002 pooled; 13 spring tows, 6 summer tows) (C. Morgan, OSU, Newport, Oregon, unpub. data)

presented in Table 2 (see Appendix for details of zooplankton biomass values used in models).

***NOAA West Coast bottom trawl survey:*** Information about the summer abundance of demersal fishes and hake was provided by the 2001 NOAA West Coast bottom trawl survey (Weinberg et al. 2002). The coast-wide survey was organized latitudinally into five statistical areas defined by the International North Pacific Fisheries Commission (INPFC) and cross-shelf into three depth strata. Survey biomass data is reapportioned into the Oregon inner-shelf model domain using a strategy in which the biomass of all INPFC areas and depth strata that overlap the model domain are scaled by the fractional area of overlap and summed. Bottom trawl surveys are limited in their ability to accurately survey semipelagic species (e.g., hake, some rockfish species) and do not sample inshore of the 55 m isobath. Our efforts to account for these limitations for individual trophic groups are detailed in the Appendix.

## Trophic Group Parameters

The definitions and the parameter details of individual trophic groups are provided in the Appendix. Physiological rate parameters, production ($P/B$), consumption ($Q/B$), and growth efficiency ($P/Q$), were obtained from the literature, other ecosystem models, or calculated from local and contemporary data. Production rate parameters ($P/B$) were calculated for juvenile salmon and carnivorous jellyfish based on data from the BPA and GLOBEC mesoscale surveys and local observations of jellyfish growth rates (Suchman and Brodeur 2005). Physiological parameters of zooplankton and pelagic fishes were obtained from the literature and other Northeast Pacific models (e.g., Pauly and Christensen 1996; Aydin et al. 2003; Preikshot 2005). Parameters for demersal fishes, seabirds, and mammals came from Field (2004).

Biomass accumulation rates ($BA$) were calculated as the change in the seasonal mean biomass from the spring to the summer. For most plankton groups, $BA$ was attributed to local net production (but see Appendix for euphusiids). For other groups, $BA$ was attributed partially to local net production and partially to migration. For forage fishes, 10% of the local production (calculated from $P/B$) contributes to $BA$. For salmon and sharks, $BA$ was attributed entirely to migration. For dogfish, mackerel, and hake, $BA$ was attributed entirely to migration in the spring and partially to net production in the summer. For juvenile salmon, $BA$ was attributed entirely to migration in the spring (smolts entering from rivers) and entirely to net local production in the summer.

The parameter set for the balanced spring and summer food-web models are presented in Table 3 and include parameters estimated by Ecopath: trophic level

TABLE 3

**Parameter-set for the balanced spring and summer food-web models for the Oregon inner-shelf ecosystem. Underlined values are estimated by the model. *P/B* = production rate, *Q/B* = consumption rate, *P/Q* = gross growth efficiency, *B* = biomass, *TL* = trophic level, *EE* = ecotrophic efficiency, *BA* = biomass accumulation rate, *EM* = spring emigration rate (summer emigration rate in parentheses if different).**

| | | | | SPRING MODEL | | | SUMMER MODEL | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *P/B* per yr | *Q/B* per yr | *P/Q* | *B* t/km$^2$ | *TL* | *EE* | *B* t/km$^2$ | *TL* | *EE* | *BA* t/km$^2$/yr | *EM* t km$^{-2}$yr$^{-1}$ |
| phytoplankton | 180 | — | — | 26.989 | 1.00 | 0.48 | 74.244 | 1.00 | 0.26 | 187.480 | 0.000 |
| copepods | 37 | 148 | 0.25 | 12.875 | 2.00 | 0.50 | 17.611 | 2.00 | 0.50 | 18.791 | 0.000 |
| *E. pacifica* (adult) | 5.8 | 23.2 | 0.25 | 0.709 | 2.08 | 0.78 | 6.984 | 2.08 | 0.85 | 24.895 | –24.895 |
| *T. spinifera* (adult) | 7 | 28 | 0.25 | 1.174 | 2.08 | 0.95 | 6.455 | 2.08 | 0.94 | 20.951 | –16.760 |
| euphausiid (larva) | 69.8 | 279.2 | 0.25 | 0.055 | 2.00 | 0.82 | 0.141 | 2.00 | 0.92 | 0.338 | 0.000 |
| pelagic amphipods | 7 | 28 | 0.25 | 1.965 | 2.05 | 0.90 | 1.426 | 2.05 | 0.90 | 0.000 | 0.000 |
| macro-zooplankton | 7 | 28 | 0.25 | 4.063 | 2.67 | 0.90 | 6.474 | 2.67 | 0.90 | 0.000 | 0.000 |
| small jellyfish | 9 | 30 | 0.3 | 3.078 | 2.00 | 0.90 | 8.945 | 2.00 | 0.90 | 0.000 | 0.000 |
| large jellyfish | 15 | 60 | 0.25 | 0.855 | 2.80 | 0.86 | 3.269 | 2.80 | 0.29 | 9.581 | 0.000 |
| pandalid shrimp | 3 | 12 | 0.25 | 1.052 | 2.69 | 0.90 | 4.062 | 2.70 | 0.90 | 0.000 | 0.000 |
| benthic shrimp | 3 | 12 | 0.25 | 2.019 | 3.06 | 0.90 | 4.405 | 3.06 | 0.90 | 0.000 | 0.000 |
| Dungeness crab | 1 | 4 | 0.25 | 2.649 | 3.27 | 0.21 | 2.649 | 3.24 | 0.20 | 0.000 | 0.000 |
| epifauna | 3 | 12 | 0.25 | 8.967 | 2.46 | 0.90 | 15.227 | 2.46 | 0.90 | 0.000 | 0.000 |
| infauna | 3 | 12 | 0.25 | 25.050 | 2.00 | 0.90 | 44.652 | 2.00 | 0.90 | 0.000 | 0.000 |
| cephalopod | 3 | 12 | 0.25 | 0.773 | 3.36 | 0.90 | 1.242 | 3.29 | 0.90 | 0.000 | 0.000 |
| smelt | 2 | 8 | 0.25 | 0.904 | 3.19 | 0.51 | 0.428 | 3.18 | 0.88 | –1.890 | 2.031 |
| shad | 2 | 8 | 0.25 | 0.002 | 3.02 | 0.66 | 0.003 | 3.04 | 0.88 | 0.002 | –0.002 |
| sardine | 2 | 8 | 0.25 | 2.107 | 2.69 | 0.69 | 12.570 | 2.70 | 0.77 | 41.509 | –40.338 |
| herring | 2.2 | 8.8 | 0.25 | 20.442 | 2.66 | 0.34 | 3.175 | 2.62 | 0.89 | –68.502 | 70.545 |
| anchovy | 2 | 8 | 0.25 | 0.005 | 2.64 | 0.75 | 0.005 | 2.64 | 0.94 | 0.000 | 0.001 |
| juvenile salmon | 6.5 | 30 | 0.217 | 0.018 | 3.75 | 0.49 | 0.053 | 3.69 | 0.92 | 0.139 | –0.139 (0.000) |
| juvenile rockfish | 2 | 8 | 0.25 | 0.699 | 3.18 | 0.90 | 2.255 | 3.18 | 0.90 | 0.000 | 0.000 |
| juvenile fish other | 2 | 8 | 0.25 | 2.994 | 2.98 | 0.90 | 5.523 | 2.91 | 0.90 | 0.000 | 0.000 |
| coho | 2.5 | 16.5 | 0.152 | 0.063 | 3.76 | 0.46 | 0.129 | 3.70 | 0.38 | 0.263 | –0.263 |
| Chinook | 0.75 | 5 | 0.15 | 0.352 | 3.70 | 0.48 | 0.269 | 3.67 | 0.68 | –0.331 | 0.331 |
| other salmon | 1.9 | 14.5 | 0.131 | 0.047 | 3.40 | 0.22 | 0.001 | 3.43 | 0.20 | –0.185 | 0.185 |
| shark | 0.2 | 5 | 0.04 | 0.023 | 4.24 | 0.01 | 0.011 | 4.33 | 0.79 | –0.051 | 0.051 |
| dogfish | 0.1 | 2.5 | 0.04 | 0.177 | 3.98 | 0.88 | 0.237 | 4.00 | 0.95 | 0.238 | –0.238 (–0.233) |
| mackerel | 0.5 | 7 | 0.071 | 0.093 | 3.33 | 0.80 | 0.859 | 3.32 | 0.23 | 3.041 | –3.041 (–3.012) |
| hake | 0.8 | 5 | 0.16 | 1.815 | 3.76 | 0.87 | 13.659 | 3.51 | 0.39 | 44.568 | –44.568 (–43.599) |
| mesopelagics | 0.6 | 3 | 0.2 | 1.938 | 3.08 | 0.90 | 2.349 | 3.13 | 0.90 | 0.000 | 0.000 |
| sablefish | 0.09 | 2.1 | 0.043 | 2.589 | 3.67 | 0.51 | 2.589 | 3.71 | 0.51 | 0.000 | 0.000 |
| lingcod | 0.3 | 2.4 | 0.125 | 0.107 | 4.23 | 0.89 | 0.107 | 4.21 | 0.81 | 0.000 | 0.000 |
| skates & rays | 0.2 | 2 | 0.1 | 0.155 | 3.97 | 0.93 | 0.155 | 3.95 | 0.71 | 0.000 | 0.000 |
| small benthic fishes | 0.5 | 2.5 | 0.2 | 2.539 | 3.35 | 0.90 | 3.469 | 3.35 | 0.90 | 0.000 | 0.000 |
| shelf piscivore rockfish | 0.13 | 2.2 | 0.059 | 2.404 | 3.77 | 0.90 | 2.404 | 3.61 | 0.87 | 0.000 | 0.000 |
| shelf planktivore rockfish | 0.13 | 2.2 | 0.059 | 0.837 | 3.20 | 0.83 | 0.837 | 3.21 | 0.90 | 0.000 | 0.000 |
| slope planktivore rockfish | 0.08 | 2.1 | 0.038 | 0.080 | 3.72 | 0.67 | 0.080 | 3.42 | 0.81 | 0.000 | 0.000 |
| flatfish (benthic feeder) | 0.301 | 1.669 | 0.181 | 2.393 | 3.18 | 0.84 | 2.393 | 3.18 | 0.88 | 0.000 | 0.000 |
| flatfish (water-column feeder) | 0.345 | 2.008 | 0.172 | 0.533 | 3.98 | 0.94 | 0.533 | 4.12 | 0.84 | 0.000 | 0.000 |
| flatfish (small) | 0.5 | 2.5 | 0.2 | 1.774 | 3.43 | 0.84 | 1.774 | 3.43 | 0.90 | 0.000 | 0.000 |
| alcids | 0.1 | 129 | 0.001 | 0.009 | 3.76 | 0.30 | 0.009 | 3.77 | 0.30 | 0.000 | 0.000 |
| gulls | 0.12 | 122 | 0.001 | 0.002 | 3.74 | 0.00 | 0.002 | 3.70 | 0.00 | 0.000 | 0.000 |
| shearwaters | 0.1 | 138 | 0.001 | 0.014 | 3.77 | 0.00 | 0.021 | 3.76 | 0.00 | 0.027 | –0.027 |
| harbor seals | 0.08 | 8.3 | 0.01 | 0.037 | 4.17 | 0.00 | 0.037 | 4.22 | 0.00 | 0.000 | 0.000 |
| sea lions | 0.07 | 17.4 | 0.004 | 0.032 | 4.30 | 0.00 | 0.032 | 4.32 | 0.00 | 0.000 | 0.000 |
| gray whales | 0.04 | 8.9 | 0.004 | 0.090 | 3.44 | 0.00 | 0.090 | 3.44 | 0.00 | 0.000 | 0.000 |
| baleen whales | 0.04 | 7.6 | 0.005 | 0.043 | 3.27 | 0.00 | 0.043 | 3.31 | 0.00 | 0.000 | 0.000 |
| toothed whales | 0.07 | 28.9 | 0.002 | 0.014 | 4.18 | 0.00 | 0.014 | 4.20 | 0.00 | 0.000 | 0.000 |
| euphausiid eggs | — | — | — | 0.077 | 1.00 | 0.93 | 0.468 | 1.00 | 0.90 | 0.000 | 0.000 |
| fish eggs | — | — | — | 0.203 | 1.00 | 0.93 | 0.024 | 1.00 | 0.76 | 0.000 | 0.000 |
| pelagic detritus | — | — | — | 9.072 | 1.00 | 0.02 | 9.072 | 1.00 | 0.01 | 0.000 | 0.000 |
| fishery offal | — | — | — | 9.072 | 1.00 | 0.02 | 9.072 | 1.00 | 0.03 | 0.000 | 0.000 |
| benthic detritus | — | — | — | 9.072 | 1.00 | 0.11 | 9.072 | 1.00 | 0.06 | 0.000 | 0.000 |

TABLE 4

**Diet matrices for the spring and summer models. Values are wet weight percent (rounded to nearest whole percent) of each prey group (left column) in the diet of each predator group (top row). First value given is for the spring model, second value given is for the summer model when different, T = trace (<0.5%). Prey not shown are gulls, shearwaters, and mammals (groups 43–49) which have no predators in the models.**

| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 phytoplankton | 100 | 90 | 90 | 100 | 15 | 33/34 | 75 | | | | | | | | | |
| 2 copepods | | 8 | 8 | | 5 | 55/46 | | 43 | 29/23 | | | | | 50/41 | 36/25 | 92/62 |
| 3 *E. pacifica* | | | | | | 1/4 | | | 1/3 | | | | | 2/13 | 2/1 | 3/19 |
| 4 *T. spinifera* | | | | | | 1/4 | | | 1/3 | | | | | 2/13 | 2/16 | 4/17 |
| 5 euphausiid-larvae | | | | | T | T | | 5/4 | T | | | | | T | T | |
| 6 pelagic amphipod | | | | | | 2 | | | 1 | | | | | 1 | 15 | 1 |
| 7 macro-zooplankton | | | | | | 1 | | 3 | 3 | | | | | 12/10 | 20 | T |
| 8 small jellyfish | | | | | | 5 | | 29 | | | | | | | 20 | |
| 9 large jellyfish | | | | | | 1/2 | | | | | | | | | | |
| 10 pandalid shrimp | | | | | | | | | | | | | | 4/3 | | |
| 11 benthic shrimp | | | | | | | | | | | 20 | 1 | | 3/2 | | |
| 12 Dungeness crab | | | | | | | | | | | 1 | | | | | |
| 13 epifauna | | | | | | | | | 6 | 44 | 23 | 1 | | 1 | T | |
| 14 infauna | | | | | | | | | 25 | 40 | 40 | 42 | | | | |
| 15 cephalopod | | | | | | | | | | | T | | | T | | 1 |
| 16 smelt | | | | | | | | | | | T | | | 2 | | |
| 17 shad | | | | | | | | | | | | | | | | |
| 18 sardine | | | | | | | | | | | | | | 1/2 | | |
| 19 herring | | | | | | | | | | | 2/1 | | | 13/3 | | |
| 20 anchovy | | | | | | | | | | | | | | | | |
| 21 juvenile salmon | | | | | | | | | | | | | | T | | |
| 22 juvenile rockfish | | | | | | | | | | | T | | | 2 | | |
| 23 juvenile fish | | | | | | | | | | 1 | 1 | | | 4 | 5/3 | |
| 24 coho | | | | | | | | | | | | | | | | |
| 25 chinook | | | | | | | | | | | | | | | | |
| 26 other salmon | | | | | | | | | | | | | | | | |
| 27 shark | | | | | | | | | | | | | | | | |
| 28 dogfish | | | | | | | | | | | | | | | | |
| 29 mackerel | | | | | | | | | | | | | | | | |
| 30 hake | | | | | | | | | | | | | | | | |
| 31 mesopelagics | | | | | | | | | | | | | | 5/4 | | |
| 32 sablefish | | | | | | | | | | | | | | | | |
| 33 lingcod | | | | | | | | | | | | | | | | |
| 34 skates & rays | | | | | | | | | | | | | | | | |
| 35 benthic fish-small | | | | | | | | | | | 1 | | | | | |
| 36 rockfish-piscivore | | | | | | | | | | | | | | | | |
| 37 rockfish-shelf plank. | | | | | | | | | | | | | | | | |
| 38 rockfish-slope plank. | | | | | | | | | | | | | | | | |
| 39 flatfish-benthic | | | | | | | | | | | T | | | | | |
| 40 flatfish-water-column | | | | | | | | | | | | | | | | |
| 41 flatfish-small | | | | | | | | | | | 1 | | | | | |
| 42 alcids | | | | | | | | | | | | | | | | |
| 50 euphausiid-eggs | | 2 | 2 | | | 1 | | 21/22 | 1 | | | | | | T | |
| 51 fish-eggs | | | | | | 1 | | T | | | | | | | | |
| 52 pelagic detritus | | | | | 80 | 1 | 25 | | | | | | | | | |
| 53 fishery offal | | | | | | | | | | | 2 | 1 | | | | |
| 54 benthic detritus | | | | | | | | | 35 | 15 | 9/11 | 55 | 100 | | | |

TABLE 4 (continued)

**Diet matrices for the spring and summer models. Values are wet weight percent (rounded to nearest whole percent) of each prey group (left column) in the diet of each predator group (top row). First value given is for the spring model, second value given is for the summer model when different, T = trace (<0.5%). Prey not shown are gulls, shearwaters, and mammals (groups 43–49) which have no predators in the models.**

| | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 phytoplankton | 38 | 38/44 | 38/40 | | | 11/18 | | | | | | | | | | |
| 2 copepods | 47/40 | 47/30 | 40/19 | 15/8 | 57/54 | 65/56 | | | 14/11 | | | 53/32 | | 78/55 | | |
| 3 *E. pacifica* | T/5 | 1/6 | T/5 | 1/8 | 1/2 | T/1 | 3/9 | 6/12 | T/3 | | 4/8 | 6/25 | 1/17 | 1/15 | 2/4 | |
| 4 *T. spinifera* | T/3 | 1/8 | T/15 | 1/8 | 1/2 | T/1 | 3/8 | 6/11 | T/3 | | 5/8 | 1/6 | 2/25 | T/8 | 3/5 | |
| 5 euphausiid-larvae | T | T | | T | T/1 | T | | | | | | | | T/1 | | |
| 6 pelagic amphipod | 1 | 4 | T | 2 | 8 | 2 | 1 | 1 | 16 | | T | 1 | | 5/3 | T | |
| 7 macro-zooplankton | 12 | 7/6 | 5 | 6/5 | 25 | 10 | 15 | 5 | 2 | | 3/0 | 10 | 8 | 5/6 | T | |
| 8 small jellyfish | 1 | | 15 | 2/1 | 6 | 4 | 1 | 1 | 25 | | | 1 | 2 | 7/6 | 5/4 | |
| 9 large jellyfish | | | | | | | | T | 1 | | 3/2 | | 0/1 | 1 | 2/4 | |
| 10 pandalid shrimp | | | | | | | | | | | 4/2 | | 11/13 | | 6 | 1/2 |
| 11 benthic shrimp | | | | | | 1 | | | | | 4/2 | T | 5/9 | | 4 | 2 |
| 12 Dungeness crab | | | | | | | | | | 1 | 4/3 | | | | 2/3 | 5/6 |
| 13 epifauna | | | | | | 2 | | | | | 16/11 | | | | 4 | 6 |
| 14 infauna | | | | | | 1 | | | | | | | | | 2 | |
| 15 cephalopod | | | T | T | | | 10 | 2/3 | 10/15 | 2 | 1 | 2 | 5/2 | 3/5 | 5 | 16/15 |
| 16 smelt | | | | 2/1 | | | 3/4 | 3 | 1 | 2/1 | 1/T | 1/T | 1/0 | | 2/t | 1 |
| 17 shad | | | | T | | | | T/0 | | | | | | | | |
| 18 sardine | | | | 1 | | | 5/20 | 6/25 | 2/10 | 4/15 | 2/8 | 2/7 | 4/11 | | 3/12 | 1/5 |
| 19 herring | | | | 4/2 | | | 47/12 | 53/12 | 21/5 | 34/8 | 15/3 | 10/2 | 49/2 | | 25/4 | 10/4 |
| 20 anchovy | | | | 1/T | | | 0/T | T | | | | | | | | |
| 21 juvenile salmon | | | | | | | | | | 1 | 1 | 1 | T | | T | |
| 22 juvenile rockfish | | | | 11 | | | 3/5 | 5 | 1/2 | T | 1 | 1/2 | 5/4 | | 1 | 3 |
| 23 juvenile fish | T | 1 | | 54/53 | 2 | 2 | 10/15 | 13/16 | 4/5 | 1 | 3 | 11 | 6 | | 2 | 3 |
| 24 coho | | | | | | | | | | 2/3 | | | | | | |
| 25 chinook | | | | | | | | | | 4 | | | | | | |
| 26 other salmon | | | | | | | | | | 1/0 | | | | | | |
| 27 shark | | | | | | | | | | | | | | | | |
| 28 dogfish | | | | | | | | | | 2 | | | | | | |
| 29 mackerel | | | | | | | | 0/2 | | 5/7 | | | | | | |
| 30 hake | | | | | | | | 1/4 | | 20/30 | 10/24 | | | | 3/13 | 8/10 |
| 31 mesopelagics | | | | | | | | | 2 | 3 | | | 1 | 1 | 2 | |
| 32 sablefish | | | | | | | | | | | | | | | | |
| 33 lingcod | | | | | | | | | | 2 | 2/1 | | | | T | |
| 34 skates & rays | | | | | | | | | | 1 | 1 | | | | | |
| 35 benthic fish-small | | | | | | | | 1 | | 3 | 7 | | 1 | | 8 | 25 |
| 36 rockfish-piscivore | | | | | | | | | | 2/1 | T | | | | 2/1 | 2/1 |
| 37 rockfish-shelf plank. | | | | | | | | | | 1/T | T | | | | T/0 | 1/T |
| 38 rockfish-slope plank. | | | | | | | | | | | | | | | T/0 | |
| 39 flatfish-benthic | | | | | | | | | | 5/7 | 6 | | | | 3/4 | 8 |
| 40 flatfish-water-column | | | | | | | | | | 4/6 | 3 | | | | 1/2 | 1 |
| 41 flatfish-small | | | | | | | | | | 4 | 6/4 | | T | | 2/1 | 10 |
| 42 alcids | | | | | | | | | | | | | | | | |
| 50 euphausiid-eggs | 1 | 1/T | 1 | | 1 | 1 | | | | | | T | | | | |
| 51 fish-eggs | | 1/T | 1 | T | | 1 | | | | | | T | | 1 | | |
| 52 pelagic detritus | | | | | | | | | | | | | | | | |
| 53 fishery offal | | | | | | | | | | | | | | | 10 | |
| 54 benthic detritus | | | | | | | | | | | | | | | 1 | |

TABLE 4 (continued)

**Diet matrices for the spring and summer models. Values are wet weight percent (rounded to nearest whole percent) of each prey group (left column) in the diet of each predator group (top row). First value given is for the spring model, second value given is for the summer model when different, T = trace (<0.5%). Prey not shown are gulls, shearwaters, and mammals (groups 43–49) which have no predators in the models.**

| | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 phytoplankton | | | | | | | | | | | | | | | | |
| 2 copepods | | | | 53/21 | | 1 | | 17/11 | 2/5 | | | | | | 56/27 | |
| 3 *E. pacifica* | | | 3/10 | 4/12 | 2/24 | | 1/2 | 1/3 | T | T/1 | 3/5 | | | | 2/18 | |
| 4 *T. spinifera* | | | 3/20 | 4/30 | 2/24 | | 1/2 | 1/3 | T | 1 | 3/5 | | | | 3/17 | |
| 5 euphausiid-larvae | | | | | | | | | | | | | | | T | |
| 6 pelagic amphipod | | | 2/1 | 2 | 4/2 | | T | 1 | | | | | | | 1/T | |
| 7 macro-zooplankton | | | 5/4 | 10 | 11/15 | | T | 1 | | 1 | 3/8 | | | | 3 | |
| 8 small jellyfish | | | 6 | 15 | 2 | T | | 1 | | | | | | | | |
| 9 large jellyfish | | | 1 | 2 | T | | | | | | 1 | | | | | |
| 10 pandalid shrimp | 6/7 | 1/2 | 7/5 | 4/2 | 18/7 | 1 | 11/9 | 1 | | | | | | | | |
| 11 benthic shrimp | 20 | 4/6 | 6/3 | | 15/5 | 2 | 10/9 | 6 | | | | | | | | |
| 12 Dungeness crab | 8 | 1 | 1 | | | T | 1 | 2 | | | | 5 | 1/2 | | | |
| 13 epifauna | 23 | 58/55 | 4/3 | | 15/10 | 34 | 5 | 49 | | 1 | | 2/4 | 1/2 | 98 | | |
| 14 infauna | 3 | 30 | | | | 63 | T | 12 | | | | | | 3 | | |
| 15 cephalopod | 1 | T | 6/3 | 3 | 5 | | 2/1 | 1 | 3/7 | 17/20 | 10/11 | 5 | 20/18 | | | 20/21 |
| 16 smelt | T | | 1 | T | 5/T | | 2/1 | T | 3/2 | 2/1 | 5/1 | 2/t | 2 | | 1 | 2/1 |
| 17 shad | | | | | 0/T | | | | | | | | | | | |
| 18 sardine | T/4 | | 3/12 | T/2 | 1 | | 5/10 | T/2 | 7/35 | 5/30 | 7/31 | 4/15 | 3/12 | | 3/22 | 3/20 |
| 19 herring | 4/1 | 1/0 | 27/7 | 2/T | 15/1 | | 25/4 | 3/1 | 71/30 | 49/20 | 58/20 | 29/6 | 23/4 | | 28/6 | 32/6 |
| 20 anchovy | | | | | | | | | | | | | | | | |
| 21 juvenile salmon | | | 0/T | | | | T | | 1 | T | 0/T | T | T | | | T |
| 22 juvenile rockfish | | T/1 | 3/3 | T | 1 | | 2 | T | 10 | 10 | 2/5 | 1/2 | 1/2 | | 1/2 | 1/3 |
| 23 juvenile fish | 6 | 2 | 5 | T | 1 | | 3 | T/1 | 1/7 | 3 | 5/10 | 2/5 | 2/4 | | 2/5 | 2/5 |
| 24 coho | | | | | | | | | | T | | 5/6 | 7/6 | | | 4 |
| 25 chinook | | | | | | | T | | | 1 | | 10/8 | 10/8 | | | 5/6 |
| 26 other salmon | | | | | | | | | | T/0 | | 1/0 | 2/0 | | | 1/0 |
| 27 shark | | | | | | | | | | | | | | | | |
| 28 dogfish | | | | | | | T | | | | | | 2/3 | | | T/1 |
| 29 mackerel | | | | | | | | | | | | | 2 | | | 5 |
| 30 hake | 4/5 | | 1/4 | 1 | | | 5/35 | | | | | 6/16 | 10/23 | | | 9/16 |
| 31 mesopelagics | | | 5/2 | 1 | 1 | | 1/T | | 1/2 | 2 | | | 2 | | | 5 |
| 32 sablefish | | | | | | | 6/T | | | | | | 1 | | | 3 |
| 33 lingcod | | | | | | | | | | | | | 1 | | | T |
| 34 skates & rays | | | | | | | 1/T | | | | | | 1/2 | | | T |
| 35 benthic fish-small | 5 | | 4 | | 2 | | 4 | 3 | T/1 | | | 5 | 2 | | | 2 |
| 36 rockfish-piscivore | | | T | | | | 1 | | | | 3 | 1 | 3 | | | 2 |
| 37 rockfish-shelf plank. | | | T | | | | 1/T | | | | T | 1/T | 1/T | | | T |
| 38 rockfish-slope plank. | | | | | | | | | | | | | | | | |
| 39 flatfish-benthic | 6 | | 3 | | | | 6 | T | | | | 10/11 | 3/2 | | | 2/1 |
| 40 flatfish-water-column | 1 | | | | | | 2/1 | | | | | 1 | 1 | | | 2/T |
| 41 flatfish-small | 12/10 | 1 | 3 | T | | T | 5 | 2 | | | | 10 | 1/2 | | | 1 |
| 42 alcids | | | | | | | | | | T | | | | | | |
| 50 euphausiid-eggs | | | | | | | | | | | | | | | | |
| 51 fish-eggs | | | 1 | | | | | | | | 1 | | | | | |
| 52 pelagic detritus | | | | | | | | | | | | | | | | |
| 53 fishery offal | | | | | | | | | | 8/10 | | | | | | |
| 54 benthic detritus | | 2/3 | | | | | 1 | | | | | | | | | |

(*TL*), ecotrophic efficiency (*EE*), and biomass for groups that could not be determined empirically. Model-estimated biomasses were calculated using assumed ecotrophic efficiencies. In these cases, biomass accumulation rates were held at zero even though the model-derived biomass may differ between the spring and summer models.

### Diet

Diet data for pelagic fishes (forage fish, salmon, sharks) came from observations made off the Oregon coast (Brodeur et al. 1987; Miller 2006). The diet data of the large jellyfish off the Oregon coast came from Suchman et al. (in press) and were converted from numerical fractions to weight fractions. The diets of demersal fishes, seabirds, and marine mammals came from the NCC food-web model of Field and Francis (2005). Diet matrices are presented in Table 4.

### Fisheries

Quarterly commercial fisheries data were provided by the Pacific Coast Fisheries Information Network (PacFIN; http://www.psmfc.org/pacfin/). PacFIN landings data are organized north to south into five INPFC statistical regions as well as two broadly defined areas, the Oregon coast region and coast-wide landings for which no specific area has been recorded. The fraction landed in Oregon was estimated using a fractional area-overlap strategy. For non-salmon landings from unknown areas, 10% was assumed landed in Oregon and Washington and 63% of that was assumed landed in Oregon (by fraction of area within the 1,280 m isobath). For salmon landed from unknown areas, 90% was assumed landed north of California and 20% of that from Oregon in accord with the proportion of coho landings between Oregon and Washington in 2000 and 2002 (PFMC 2006a). The fraction of commercial landings inshore of the 125 m isobath was assumed based upon general trends apparent from the BPA and GLOBEC pelagic surveys, triennial groundfish survey, or best logical assumption: 100% inshore for smelt, shad, Dungeness crab; 75% inshore for shelf planktivore and piscivore rockfish, sardine, pandalid shrimp, infauna, epifauna; 25% inshore for shark, sablefish, miscellaneous small benthic fishes, lingcod, herring, flatfishes, dogfish, salmon, benthic shrimp; 10% inshore for skates and rays, mackerel, hake, cephalopods, anchovy; and 5% inshore for slope planktivorous rockfish.

Bi-monthly Oregon marine recreational landings data were acquired from the Pacific States Marine Recreational Fisheries Information Network (RecFIN; http://www.psmfc.org/recfin/). The fraction of recreational landings inshore of the 125 m isobath was estimated in the same manner as commercial landings.

Harvest rates used in the spring and summer models were the mean of the 2000 and 2002 rates. Discards were assumed to be 10% of landings.

### Ecosystem Analysis

At the level of individual trophic groups, Ecopath calculates energy flow into and out of each group, accounting for all energy sources and destinations, and organizes this information as an energy consumption matrix. Ecopath also calculates ecotrophic efficiency (*EE*) or estimates the unknown biomass of a group as that required to support higher trophic levels given an assumed *EE*. Finally, each group's fractional Trophic Level (*TL*), or position in the food web relative to its distance from primary producers (or detritus), is calculated as 1 + (the weighted average of the trophic levels of all prey organisms). By definition, *TL* = 1 for primary producers and detritus groups.

Ecosystem structure and status were analyzed in terms of energy flow and fate metrics: ecosystem size in terms of energy flow, energy flow between major sub-systems and trophic groups, source of consumed energy (primary production, detritus), and fate of consumed energy. The defined sub-systems are the primary producers, detritus, the pelagic sub-system (zooplankton, jellyfish, pelagic fishes, cephalopods, mesopelagic fishes, seabirds, and mammals), and the benthic sub-system (epifauna, infauna, demersal fishes). Energy flow metrics were calculated from the consumption matrix generated by Ecopath. The primary metric of overall ecosystem size is the Total System Throughput (TST), the sum of all energy flows within the ecosystem (Ulanowicz 1986).

Mixed Trophic Impact (MTI) analysis quantifies the total strength of direct and indirect linkages between every component of the ecosystem (Ulanowicz and Puccia 1990). The MTI matrix provides an index of the relative positive or negative impact that a small, hypothetical increase in the biomass of one trophic group would have upon every other group and can be considered a class of sensitivity analysis.

## RESULTS

### Balanced Models

A simplified version of the summer trophic network is illustrated in Figure 2. The simplified model is formed by aggregating similar trophic groups for illustrative purposes; subsequent analyses and discussion refer to the full models. Trophic groups are arranged along the y-axis by trophic level, box height is proportional to biomass, and the connecting lines are proportional to the log-scaled energy flow rate.

While the pelagic sub-system is almost exclusively supported by phytoplankton, most energy supporting the benthic sub-system is detrital in origin. Within the

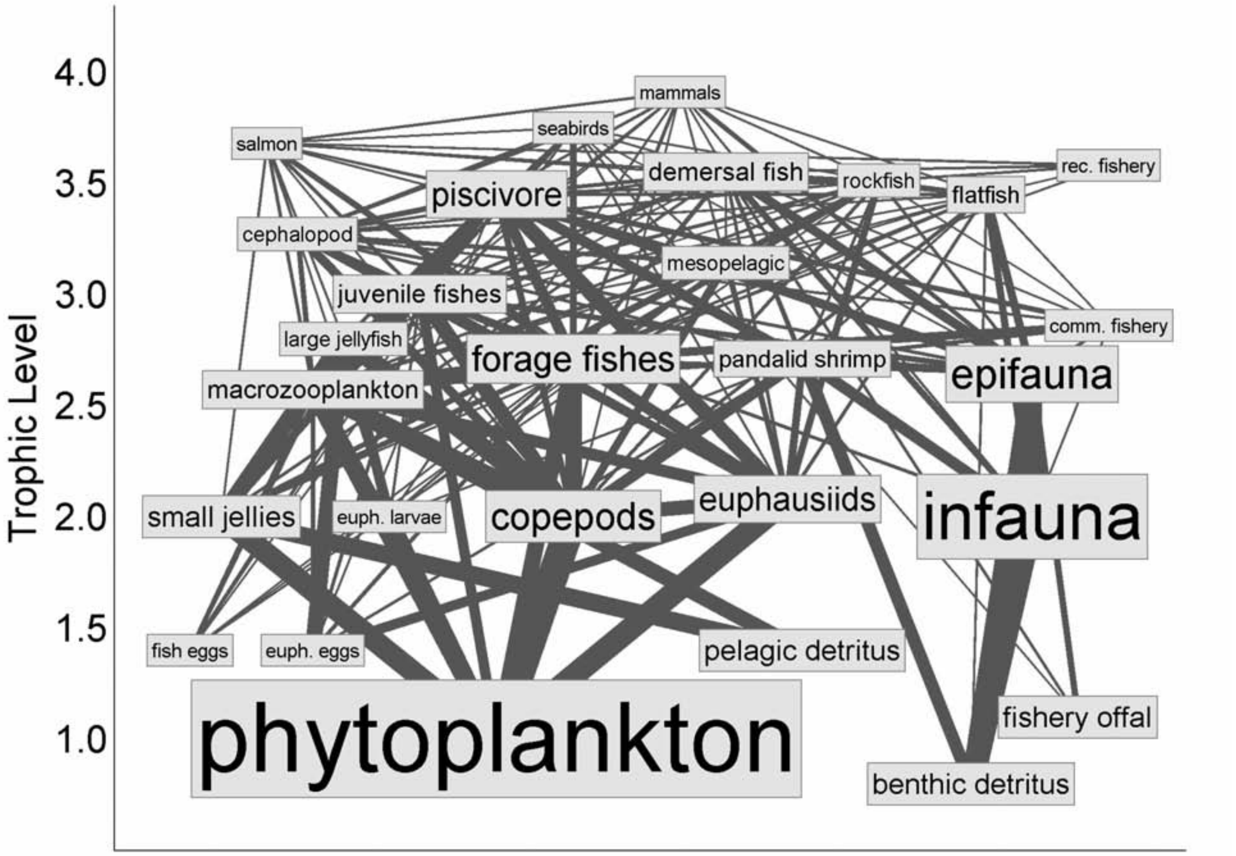

Figure 2. A simplified summer food-web model for the Oregon inner-shelf ecosystem. Box height is proportional to trophic group biomass, and box position along the y-axis marks the group's trophic level. Line width is proportional to the log of the energy flow rate. The pelagic system groups are to the left and are largely supported by phytoplankton production, the benthic system groups are to the right and are supported by detritus.

pelagic sub-system, jellyfish and forage fishes are at similar trophic levels (2.8–3.2). Seals, sea lions, and sharks occupy the highest trophic levels (>4.2) and have low *EE*s, indicating that little of the energy they consume is further used in the system. Within the benthic subsystem, lingcod and the water-column feeding flatfish (Pacific halibut, arrowtooth flounder, petrale sole) occupy high trophic levels (4.0–4.3) due to their fish-rich diet that includes piscivorous hake; however, unlike other high-*TL* groups, their high *EE*s show that much of their production is further used in the system.

### Ecosystem Size

System-level metrics and indices for the spring and summer models are provided in Table 5. From spring to summer, the ecosystem doubles in size in terms of biomass (from 138 to 254 t/km$^2$, respectively) and nearly triples in size in terms of total energy flow (total system throughput, TST; 14,304 to 40,333 t/km$^2$/yr) and in terms of total production (5,615 to 14,573 t/km$^2$/yr).

The size of the living heterotrophic ecosystem, excluding primary production, the flow of material to detritus, and fisheries extraction, may be defined as the

TABLE 5

**System-level metrics of the spring and summer food-web models for the Oregon inner-shelf ecosystem.**

| | SPRING | SUMMER | units |
|---|---|---|---|
| Total biomass (excluding detritus) | 137.60 | 253.90 | t/km$^2$ |
| ENERGY FLOW METRICS | | | |
| Total net primary production | 4857.97 | 13363.92 | t/km$^2$/yr |
| Sum of all production | 5615.47 | 14573.02 | t/km$^2$/yr |
| Total System Throughput (TST) | 14303.58 | 40332.53 | t/km$^2$/yr |
| Sum of all consumption | 3036.10 | 4838.78 | t/km$^2$/yr |
| total pelagic sub-system consumption | 2551.28 | 3976.56 | t/km$^2$/yr |
| total benthic sub-system consumption | 484.82 | 862.22 | t/km$^2$/yr |
| Sum of all exports | 2922.77 | 10483.31 | t/km$^2$/yr |
| Sum of all respiratory flows | 1671.87 | 2661.18 | t/km$^2$/yr |
| Sum of all flows into detritus | 6672.51 | 22348.91 | t/km$^2$/yr |
| Flow INTO detritus (excluding flow between detritus pools) | 3415.94 | 11295.35 | t/km$^2$/yr |
| Flow FROM detritus (excluding flow between detritus pools) | 438.46 | 765.24 | t/km$^2$/yr |
| FISHERY STATUS INDICES | | | |
| Total catches | 2.23 | 9.18 | t/km$^2$/yr |
| Mean trophic level of the catch | 3.19 | 2.88 | |
| Gross efficiency (catch/net primary production) | 0.000459 | 0.000687 | |

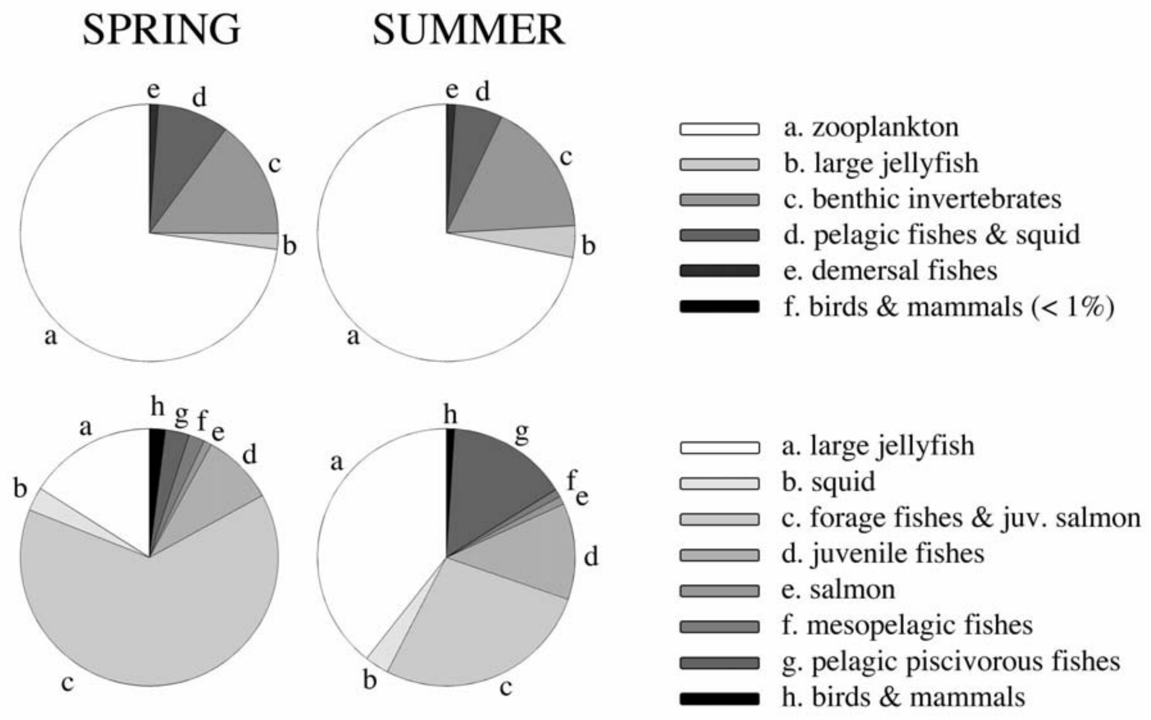

Figure 3. (Top) The relative sizes of the major trophic groups in terms of consumption rates within the spring and summer models: zooplankton (copepods, euphausiids, pelagic amphipods, macro-zooplankton, small jellies), pelagic fishes and squids (squid, forage fishes, juvenile fishes, salmon, piscivorous fishes, mesopelagic fishes), benthic invertebrates (pandalid shrimp, benthic shrimp, Dungeness crab, epifauna, infauna), benthic fishes (sablefish, lingcod, skates and rays, rockfishes, flatfishes). (Bottom) The relative sizes of groups within just the pelagic subsystem (excluding zooplankton) showing substantial changes from spring to summer in the relative sizes of the large jellyfish and forage fish groups.

total consumption by all trophic groups and grows by 60% from spring to summer (3,036 to 4,839 t/km$^2$/yr). The living ecosystem is dominated by the zooplankton (copepods, euphausiids, pelagic amphipods, macro-zooplankton, and small jellyfish) and benthic invertebrates (pandalid and benthic shrimp, Dungeness crab, epifauna, and infauna) which account for 88% of the energy flow through the ecosystem in both spring and summer. Pelagic fishes and squids (6–9%), jellyfish (2–4%), demersal fishes (1%), and seabirds and mammals (<1%) account for the balance of the energy flow (fig. 3, top). The pelagic sub-system (zooplankton, jellyfish, pelagic fish and squid, birds and mammals) is five times larger than the benthic sub-system (benthic invertebrates, demersal fishes) in both seasons, though there are substantial seasonal changes in the pelagic sub-system within the trophic levels above zooplankton. In the spring, the dominant consumers are the forage fishes (64%) and the jellyfish (16%). In the summer, jellyfish (39%) become the dominant consumers followed by forage fishes (27%), pelagic piscivores (15%), and juvenile fishes (12%) (fig. 3, bottom). The total consumption among the higher trophic level groups in the spring and summer models is illustrated in Figure 4. Readily apparent is the increasing importance of the large jellyfish as the dominant consumer as the upwelling season progresses.

### Predation upon Zooplankton

The relative importance of the different groups that prey upon the zooplankton community within the pelagic environment is presented in Figure 5. The importance of fish and jellyfish as predators upon different zooplankton groups appears to depend upon season as well as the size and swimming ability of the zooplankton prey. Jellyfish are the dominant consumers of euphausiid eggs and larvae and of small jellies in both seasonal models. Fishes remain the dominant consumers of adult euphausiids, macro-zooplankton, and pelagic amphipods in both seasons. As forage fishes become less abundant over the inner-shelf in the late summer, other pelagic fishes (e.g., juvenile fishes, hake, and mackerels) become the dominant consumer of these large-bodied zooplankton groups rather than the rapidly growing jellyfish population. For copepods and fish eggs, the relative importance of jellyfish as predators increases modestly as the overall abundance of the forage fishes declines.

### Energy Flow Through the Ecosystem

The fate of energy consumed by a trophic group or sub-system is one of the following: to be passed on to higher trophic levels via predation, passed on to detritus through egestion or non-predation mortality, used for metabolism, stored as accumulated biomass, or

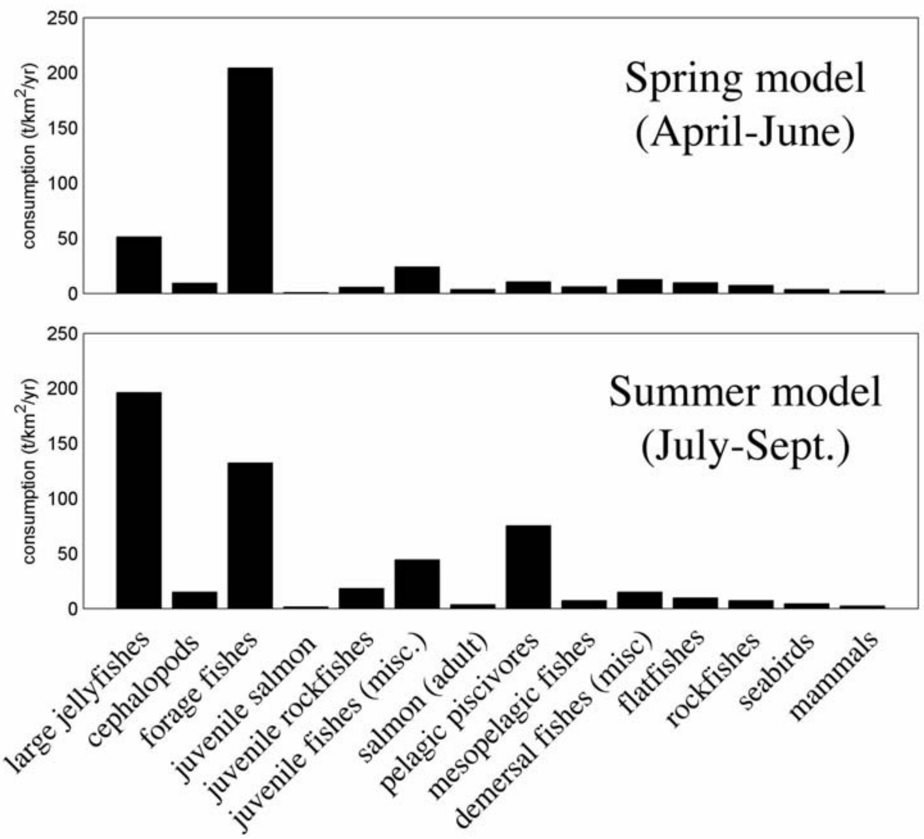

Figure 4. Consumption rates of upper trophic levels excluding plankton and benthic invertebrates (t/km²/yr). While the amount of energy flowing through the small pelagic forage fishes decreases from spring to summer, the amount flowing through the large jellyfish increases dramatically.

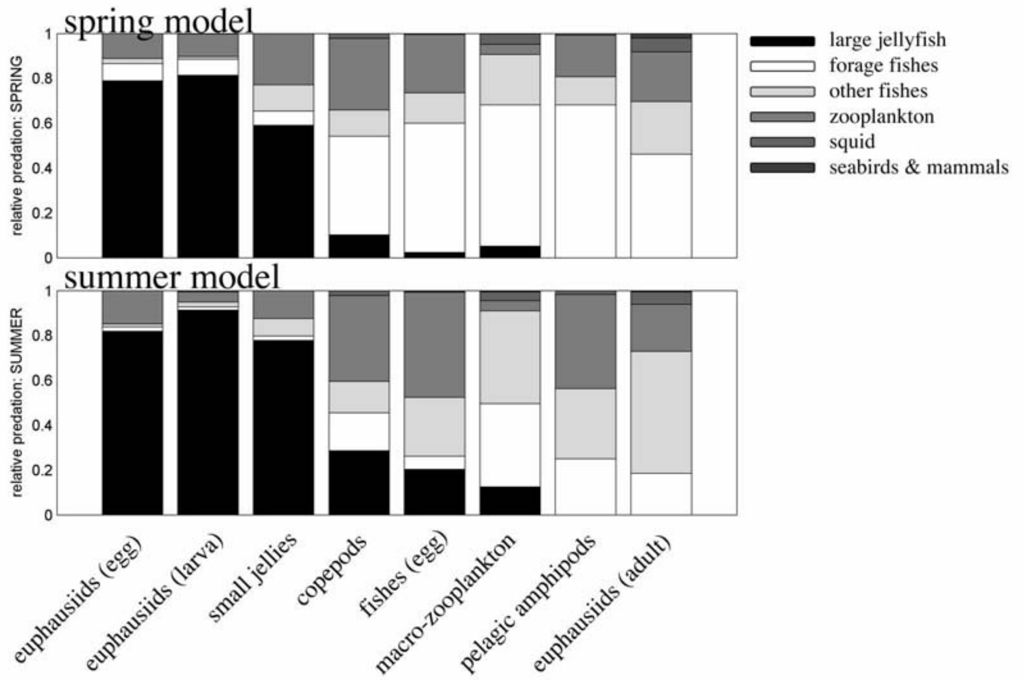

Figure 5. Relative predation upon zooplankton groups by upper trophic levels in the spring and summer food-web models. In the spring model, small pelagic forage fishes are an important consumer of lower trophic-level production; in the summer model, their importance is supplanted by large jellyfish and other pelagic fishes.

TABLE 6
**Flow and fate of gross energy consumption (input) to unassimilated egestion, respiration, detritus (non-predation mortality), somatic growth, benthic predation, pelagic predation, or fishery harvest organized by major trophic aggregation or sub-system (t/km$^2$/yr).**

| | input | output | | | | to upper trophic levels | | |
|---|---|---|---|---|---|---|---|---|
| | | egestion | respiration | detritus | growth | benthic | pelagic | fishery |
| SPRING | | | | | | | | |
| primary production | 4858.0 | | | 2512.0 | 187.5 | 0.0 | 2158.5 | 0.0 |
| pelagic environment (total) | 2551.3 | 510.3 | 1401.7 | 281.7 | 36.3 | 15.7 | 304.4 | 1.2 |
| zooplankton | 2231.4 | 446.3 | 1222.6 | 246.5 | 23.3 | 8.5 | 284.1 | 0.0 |
| large jellyfish | 51.3 | 10.3 | 28.2 | 1.8 | 9.6 | 0.2 | 1.2 | 0.0 |
| pelagic fish & squid (total) | 263.0 | 52.6 | 146.4 | 33.4 | 3.4 | 7.0 | 19.1 | 1.2 |
| squid | 9.3 | 1.9 | 5.1 | 0.2 | 0.0 | 0.8 | 1.3 | 0.0 |
| forage fish | 204.6 | 40.9 | 112.5 | 31.8 | 3.4 | 4.3 | 11.2 | 0.4 |
| juvenile fishes | 29.5 | 5.9 | 16.2 | 0.7 | 0.0 | 1.2 | 5.5 | 0.0 |
| salmon | 3.5 | 0.7 | 2.3 | 0.3 | 0.0 | 0.0 | 0.2 | 0.0 |
| pelagic piscivores | 10.3 | 2.1 | 6.7 | 0.2 | 0.0 | 0.4 | 0.2 | 0.7 |
| mesopelagic fishes | 5.8 | 1.2 | 3.5 | 0.1 | 0.0 | 0.4 | 0.6 | 0.0 |
| birds & mammals | 5.7 | 1.1 | 4.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| benthic environment (total) | 484.8 | 97.0 | 270.2 | 13.8 | 0.0 | 98.7 | 4.2 | 1.0 |
| benthic invertebrates | 455.7 | 91.1 | 250.6 | 13.2 | 0.0 | 96.1 | 3.8 | 0.7 |
| demersal fish (total) | 29.2 | 5.8 | 19.5 | 0.6 | 0.0 | 2.5 | 0.4 | 0.3 |
| misc. demersal fishes | 12.4 | 2.5 | 8.3 | 0.2 | 0.0 | 1.1 | 0.1 | 0.1 |
| flatfishes | 9.5 | 1.9 | 5.8 | 0.3 | 0.0 | 1.3 | 0.1 | 0.1 |
| rockfishes | 7.3 | 1.5 | 5.4 | 0.1 | 0.0 | 0.2 | 0.1 | 0.1 |
| SUMMER | | | | | | | | |
| primary production | 13363.9 | | | 9894.9 | 187.5 | 0.0 | 3281.5 | 0.0 |
| pelagic environment (total) | 3976.6 | 795.3 | 2183.3 | 402.2 | 37.4 | 28.8 | 521.6 | 7.9 |
| zooplankton | 3478.0 | 695.6 | 1899.5 | 351.0 | 23.3 | 22.1 | 486.4 | 0.0 |
| large jellyfish | 196.2 | 39.2 | 107.9 | 35.1 | 9.6 | 0.3 | 4.1 | 0.0 |
| pelagic fish & squid (total) | 295.8 | 59.2 | 170.7 | 16.1 | 4.5 | 6.3 | 31.1 | 7.9 |
| squid | 14.9 | 3.0 | 8.2 | 0.4 | 0.0 | 0.6 | 2.8 | 0.0 |
| forage fishes | 133.4 | 26.7 | 73.4 | 6.8 | 3.5 | 2.5 | 14.3 | 6.3 |
| juvenile fishes | 62.2 | 12.4 | 34.2 | 1.6 | 0.0 | 1.6 | 12.4 | 0.0 |
| salmon | 3.3 | 0.7 | 2.1 | 0.3 | 0.0 | 0.0 | 0.2 | 0.1 |
| pelagic piscivores | 74.9 | 15.0 | 48.6 | 7.0 | 1.0 | 1.5 | 0.4 | 1.5 |
| mesopelagic fishes | 7.0 | 1.4 | 4.2 | 0.1 | 0.0 | 0.2 | 1.0 | 0.0 |
| birds & mammals | 6.6 | 1.3 | 5.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| benthic environment (total) | 862.2 | 172.4 | 477.8 | 23.2 | 0.0 | 168.5 | 19.0 | 1.3 |
| benthic invertebrates | 830.8 | 166.2 | 456.9 | 22.6 | 0.0 | 166.1 | 18.0 | 0.9 |
| demersal fish (total) | 31.5 | 6.3 | 20.9 | 0.6 | 0.0 | 2.4 | 0.9 | 0.4 |
| misc. demersal fishes | 14.7 | 2.9 | 9.7 | 0.3 | 0.0 | 1.1 | 0.6 | 0.1 |
| flatfishes | 9.5 | 1.9 | 5.8 | 0.2 | 0.0 | 1.3 | 0.3 | 0.1 |
| rockfishes | 7.3 | 1.5 | 5.4 | 0.1 | 0.0 | 0.1 | 0.1 | 0.2 |

removed from the system via fishery extraction. The total flow and fate of the energy passing through the major ecosystem groups are summarized in Table 6 as a set of energy budgets. For every group, most consumed energy is used for respiration (55–80%), followed by the non-assimilated fraction (20%).

The relative fraction of energy lost to detritus or passed upwards to higher trophic levels varies from group to group. As top predators, seabirds and marine mammals are energetic dead-ends; less than 1% of the energy they consume is passed upwards. Jellyfish are also an energy-loss pathway even though they are not at a high trophic level (*TL* = 2.8); they are preyed upon by few other groups and only 2% of the energy consumed by jellyfish is passed on to higher trophic levels. In contrast, 10–15% of the energy consumed by pelagic fishes and cephalopods is transferred upwards. At the sub-system level, the benthic sub-system is more efficient than the pelagic sub-system, passing to higher trophic levels on average 21–22% of the energy consumed compared to 13–14% for the pelagic sub-system.

Seasonally, there is little change in the relative efficiency in which each group passes along consumed energy. The notable exception is the forage fishes. In the spring, only 8% of the energy consumed by forage fishes is transferred, whereas in the summer 17% is transferred. The low spring transfer efficiency may be attributed to export from the system via migration out of the model domain,

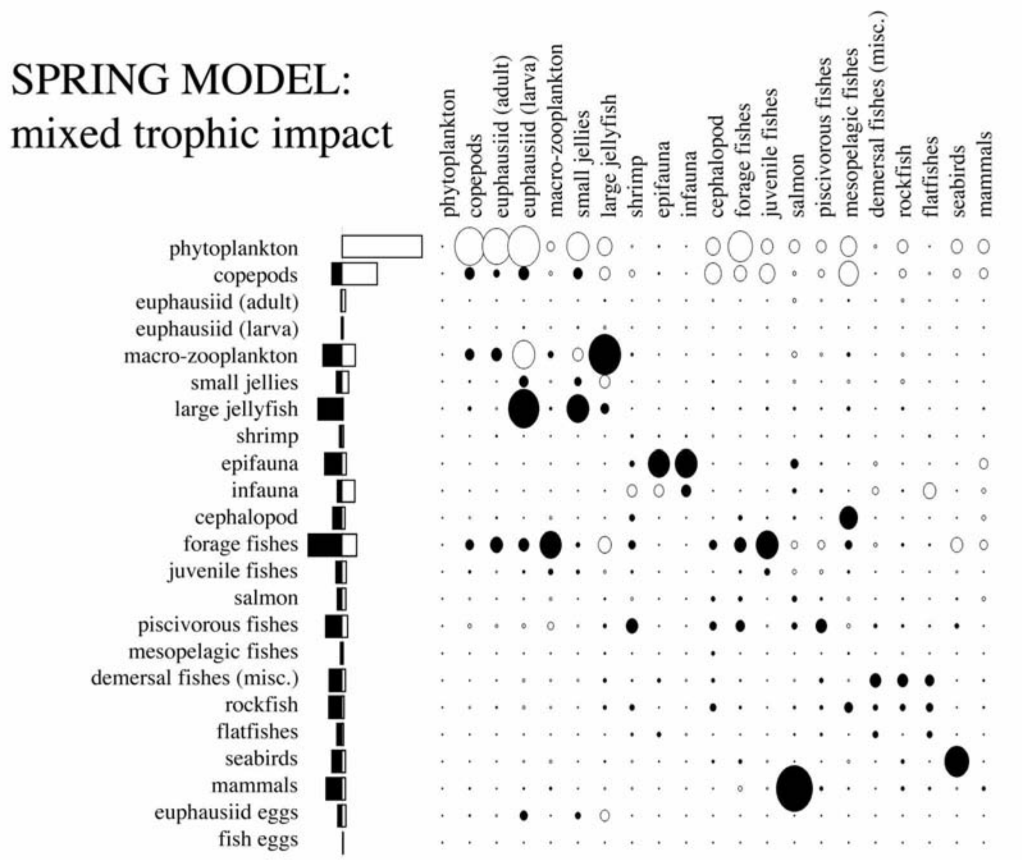

Figure 6. The Mixed Trophic Impact matrix (MTI) showing the relative impact, direct and indirect, that a small change in the biomass of a given trophic group will have throughout the spring food-web model. Rows down the side are the impacting groups and columns across the top are the impacted groups. White ovals represent positive impacts, black ovals represent negative impacts; oval size is proportional to impact strength. The bar chart represents the summed impact that each group has throughout the food web, positive or negative.

especially by herring. In the models developed here, the decline in forage fish biomass from spring to summer is assumed to be due to migration rather than predation.

## Mixed Trophic Impact (MTI)

The mixed trophic impact matrices generated from the simplified spring and summer models (see above) are presented in Figures 6 and 7, respectively. The MTI matrices show the combined direct and indirect impacts that a hypothetical small increase in the biomass of one group will have on the biomass of every other group in the ecosystem. The impact units are dimensionless but allow the relative scale of impact across all groups in the ecosystem to be compared directly. An increase in phytoplankton biomass has a positive impact throughout the food web. The diagonal running from upper left to lower right shows that all groups, except phytoplankton, have negative impacts upon themselves.

Jellyfish exerted top-down influence upon zooplankton, especially upon euphausiid larvae and the small jellyfish. However, they had relatively little bottom-up impact upon higher trophic levels nor strong negative impact upon forage fishes even in the summer months when jellyfish biomass (and potential competition for prey) was highest.

Forage fishes have a negative impact upon lower trophic levels, especially upon the macro-zooplankton. This top-down influence is greater in the summer. They have an indirect positive impact upon the large jellyfish that can be attributed to forage fish predation upon macro-zooplankton, which include species that consume jellyfish as a small part of their diet. Forage fishes have a positive, bottom-up impact upon salmon, seabirds, and mammals during the summer. Interestingly, the impact of forage fishes upon the piscivorous fishes changes from positive in the spring to weakly negative in the summer, perhaps because of the negative impact forage fish have upon euphausiids, which become a more important part of the piscivorous fish diet in the summer model.

The largest change in the ecosystem from spring to summer is related to the seasonal migration of pelagic piscivores (sharks, hake, mackerel) into the region. The negative impact that piscivorous fishes have upon squid, forage fish, salmon, and piscivorous fishes themselves increases from modest in the spring to strong in the sum-

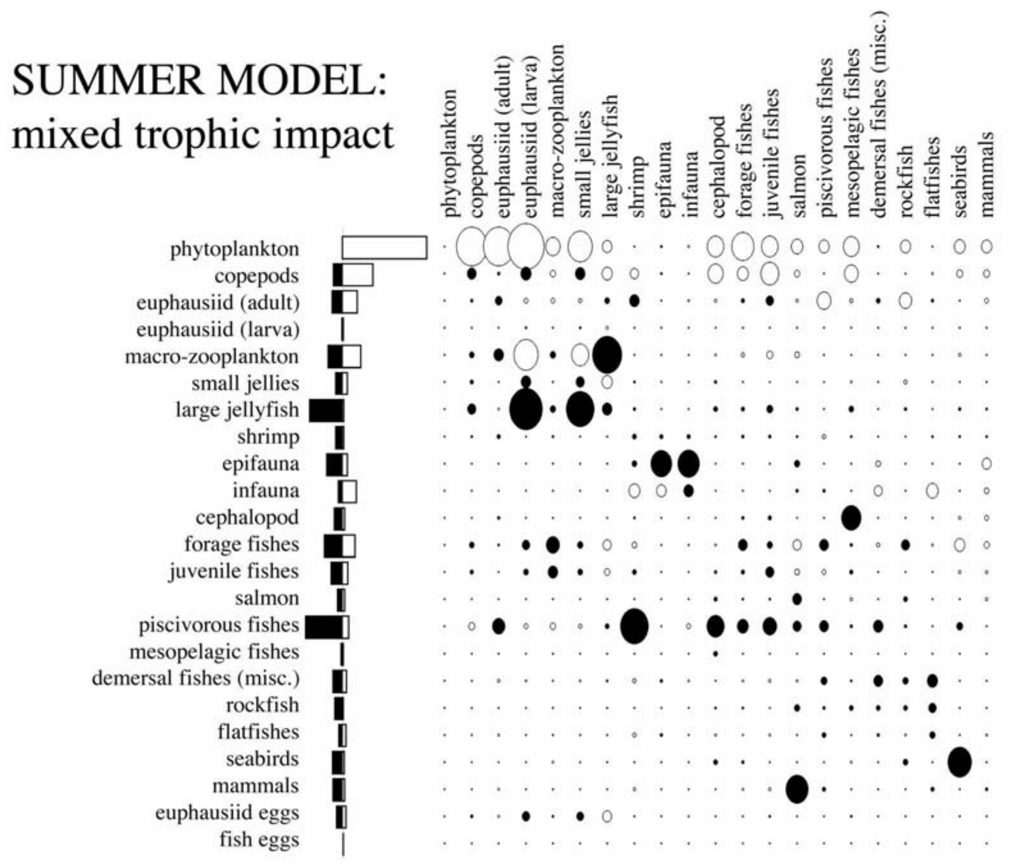

Figure 7. The Mixed Trophic Impact matrix (MTI) showing the relative impact, direct and indirect, that a small change in the biomass of a given trophic group will have throughout the spring food-web model. Rows down the side are the impacting groups and columns across the top are the impacted groups. White ovals represent positive impacts, black ovals represent negative impacts; oval size is proportional to impact strength. The bar chart represents the summed impact that each group has throughout the food web, positive or negative.

mer. Predation upon forage fish engenders an indirect positive impact by piscivorous fishes upon zooplankton in spring and summer. However, while piscivorous fishes have an indirect positive impact upon adult euphausiids in the spring, increased predation by piscivores upon adult euphausiids, particularly by hake, leads to a strong, direct negative impact in the summer model.

## DISCUSSION

### Importance of Jellyfish to the Ecosystem

Jellyfish are important predators in both high- and low-productivity ecosystems (Mills 1995). Most medusae are passive, generalist predators and show positive selection for fish eggs and larvae as these prey are relatively large (enhancing predator-prey encounter rates) and have little or no escape ability (Purcell and Arai 2001). Purcell and Grover (1990) have measured *Aequorea victoria* predation on larval herring within an embayment on Vancouver Island as over 50% of the standing stock per day. Off the Oregon coast, jellyfish predation impact upon fish recruitment has not been quantified, but observations off Oregon showed virtually no fish eggs nor larvae in jellyfish diets (Suchman et al. in press), likely because of the scarcity of these potential prey compared to zooplankton rather than selection against fish eggs and larvae (C. Suchman, Virginia Institute of Marine Science, Gloucester Point, Virginia, pers. comm.). Also, fish larvae in this region are most abundant in early spring (Brodeur et al.[2]) before jellyfish biomass reaches high levels. However, consumption of larvae by younger stages of jellyfish than those examined by Suchman et al. (in press) could be occurring during the spring.

Generally, the predation impact upon copepods by jellyfish is too low to cause populations to decline (Purcell and Arai 2001; Purcell 2003). Other zooplankton groups can be more vulnerable, lacking the refuge of small size or the escape behavior of copepods (Suchman and Sullivan 2000; Hansson et al. 2005; Suchman et al. in press). In Prince William Sound, Alaska, jellyfish have been observed to consume up to 7% of the larvacean standing

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[2] Brodeur, R. D., W. T. Peterson, T. D. Auth, H. L. Soulen, M. M. Parnel, and A. A. Emerson. Submitted-b. Abundance and diversity of ichthyoplankton as indicators of recent climate change in an upwelling area off Oregon. Mar. Ecol. Prog. Ser. NOAA/NMFS/NWFSC, Newport, Oregon.

stock per day but only 0.3% per day of the copepod standing stock (Purcell 2003). Off Oregon, Suchman et al. (in press) observed that mean predation on the copepod standing stock by *Chrysaora fuscescens* was less than 1% per day but predation upon small jellyfish and euphausiid larvae was 10–12% per day. Jellyfish showed positive selection for euphausiid eggs and a grazing rate upon egg standing stock as high as 32% per day, suggesting that jellyfish have the potential to deplete euphausiid eggs over the inner-shelf (Suchman et al. in press). Adult euphausiids comprise a major share of the diet of many pelagic species in this system (Brodeur and Pearcy 1992; Miller 2006; Miller and Brodeur, 2007) and substantial consumption of their eggs by jellyfish could translate into reduced availability of adult euphausiids to pelagic predators.

Jellyfish predation on zooplankton may have more of an impact on ecosystem structure and energy flow than does predation on fish eggs and larvae. For example, *Aurelia aurita* is a top predator in the western Baltic Sea and in years of high abundance can initiate a trophic cascade that alters both zooplankton composition and phytoplankton abundance (Schneider and Behrends 1998). As they are preyed upon by few species, jellyfish could be a trophic dead-end. For example, Coll et al. (2006) found that in the Adriatic Sea, jellyfish is the major consumer in the pelagic sub-system and is an important trophic pathway, diverting production to the detritus and reducing the ecosystem-level transfer efficiency of energy to upper trophic levels. In our Oregon summer food-web model, when jellyfish biomass is at its peak, only 2% of the energy consumed by jellyfish was passed to higher trophic levels compared to 17% for forage fishes, or in absolute terms, while jellyfish consume almost 150% as much energy as the forage fish, they passed only 17% as much (calculated from values in tab. 6). Jellyfish have the potential to divert energy from the living ecosystem, increase the level of competition, and possibly reshape the trophic interactions within higher trophic levels.

This comparison supposes that the food value of jellyfish is comparable to other trophic groups. However, while the carbon content of copepods is roughly 9% of the wet weight (given dry : wet weight = 0.19 (Omori 1969) and C : dry weight = 0.45 (Uye 1982)), the carbon content of the jellyfish *Chrysaora fuscescens* is only 0.28% of the wet weight (Shenker 1985). Further, arthropods have more than five times the caloric value of jellyfish (Arai et al. 2003). The consequence is that if biomass were to be expressed in carbon or calories, the present models may overestimate the small fraction of jellyfish production returning to the living food web.

Besides energy density, food value is also a function of ease of digestion. The digestion rate of jellies (ctenophores) by chum salmon is more than 20 times that of pandalid shrimp; ctenophores and larger jellyfish could be as important an energy source as other zooplankton despite their low energy content (Arai et al. 2003) if jellies were eaten at that much higher rate.

Could predation upon large jellyfish be higher than we estimate here? Gelatinous zooplankton are likely underrepresented in most diet studies due to their rapid digestion (Arai et al. 2003). However, almost all the studies to date that have shown that the fish that consume gelatinous zooplankton in any appreciable amount generally feed on smaller forms such as ctenophores, salps, and siphonophores, and few feed on the large medusae we consider here. A comprehensive study of the diets of 25 pelagic fish predators off the Oregon coast (Miller and Brodeur, 2007) found that gelatinous material never contributed more than 3% of the diet of any predator, and most of that contribution was from ctenophores. Dogfish may be important jellyfish predators (Arai 1988), but off the Oregon coast, gelatinous prey appear to make up less than 1% of their diet (Brodeur et al., in press). The majority of pelagic fish predators off the Oregon coast appear to be particulate feeders that consume whole prey (crustaceans, small fishes, small jellyfish). They lack the biting teeth to pull jellyfish apart. At the typical size of the sea nettle jellyfish (*Chrysaora fuscescens*) observed during surveys off the southern Oregon coast (>10 cm bell diameter, Suchman and Brodeur 2005), few of these are likely to be eaten whole by most fish or seabirds. Other species known to feed heavily upon large scyphozoa, ocean sunfish (Arai 1988), and sea turtles are present, but rare in Oregon waters. The carbon tied up in jellyfish, thus, is generally not available to the pelagic system, although it may provide a substantial nutrient input to the benthic food web when the medusae die and sink to the bottom of the ocean.

### Do Jellyfish Compete with Planktivorous Fishes for Zooplankton Resources?

One hypothesis for the increasing jellyfish biomass within ecosystems worldwide is that overfishing of planktivorous fishes has reduced competition for zooplankton and opened niche-space which, by virtue of their rapid growth potential, jellyfish have been able to rapidly colonize (Mills 2001; Purcell and Arai 2001). As one example, overfishing of sardines and anchovies in the northern Benguela Current upwelling ecosystem may have led to their permanent replacement by jellyfish which now exceed the fish stocks in biomass (Lynam et al. 2006). There are few direct comparisons of jellyfish and forage fish diets (Purcell and Arai 2001). For example, Purcell and Sturdevant (2001) have observed a high degree of diet overlap between jellyfish and forage fishes in Prince William Sound, Alaska. Off Oregon, stable isotope analyses show that jellyfish are at a similar trophic level as forage fishes, while a comparison of the stomach contents of jellyfish and many common forage fish shows a high similarity in their diets (Brodeur et al.[1]). The food-web models we have developed incorporate these Oregon diet data in addition to growth and consumption rate estimates and show the extent of the potential for competition between jellyfish and forage fish.

The food-web models suggest that during the summer, jellyfish are responsible for eating more of the zooplankton production than are the forage fishes; jellyfish consume 17% of the total zooplankton production (excluding euphausiid and fish eggs) and forage fishes consume 9%. While in the spring, jellyfish consume 7% and forage fishes consume 22% of the zooplankton production. In terms of copepods alone, jellyfish consume 1.3% of the standing stock of copepods per day which amounts to 13% of the summer copepod production. This level of predation pressure is somewhat higher than Suchman et al.'s (in press) estimate that, off Oregon, *C. fuscescens* graze less than 1% of the copepod standing stock per day. This difference may be partly attributed to the model's aggregation of the four large jellyfish species.

While the models suggest that more zooplankton production flows through jellyfish than forage fishes, they do not show that competition for zooplankton prey actually occurs to a large enough degree as to cause the decline of forage fish stocks. Competition requires that zooplankton prey are limited by predation (Purcell and Arai 2001), and the models suggest that this was not the case in the early 2000s. A large proportion of the potential prey resource is not used by the living ecosystem; 44% of zooplankton production is lost to the detritus in the spring model and 40% is lost in the summer model. The MTI analysis (figs. 6 and 7) illustrates the modest impact that jellyfish have upon upper trophic levels. While jellyfish have a very strong negative impact on most zooplankton groups, they have very little impact on the upper trophic levels including the forage fishes.

## Comparison to Other Upwelling Ecosystems

Trophic models have been developed for the four major eastern boundary upwelling ecosystems: the Benguela Current, the Humboldt Current, the California Current, and the Canary Current upwelling systems. From a set of inter-calibrated Ecopath models, the whole of the California Current system is shown to be the smallest of the four major upwelling ecosystems, an observation that may be partly attributed to the system's seasonality (Jarre-Teichmann et al. 1998). The seasonal models developed here for the northern California Current ecosystem off Oregon show that the total system throughput during the productive summer season is comparable to the annual mean size of the southern Benguela Current ecosystem and the Humboldt Current ecosystem off Peru, as estimated by Jarre-Teichmann et al. (1998).

Comparison of ecosystem structure among upwelling systems has revealed common traits: forage fishes dominate biomass and energy flow, there is generally low transfer efficiency of production to upper trophic levels, and upwelling systems are generally in a state of low maturity (Jarre-Teichmann et al. 1998). As in other upwelling systems, forage fishes are the major consumers in the spring model for the Oregon inner-shelf (fig. 4). However, by summer, jellyfish become the major consumer. A similar situation has occurred in the northern Benguela Current ecosystem in recent years where jellyfish consumption has become as great as that of the small planktivorous fishes (Moloney et al. 2005). One major difference between the northern California Current and the northern Benguela Current ecosystems, already stated, is the seasonality of the former. At present we can only speculate if this could moderate the impact that any future increase in jellyfish biomass could have off Oregon. Lynam et al. (2006) has hypothesized that the replacement of forage fishes by jellyfish in the northern Benguela ecosystem is irreversible due to the direct predation by jellyfish upon fish eggs and larvae, whereas the seasonal mismatch in jellyfish and ichthyoplankton abundance in the northern California Current ecosystem (Brodeur et al.[1]) may offer some immunity from jellyfish predation.

## Model Assumptions and Limitations

We have attempted to construct our seasonal models to incorporate the most complete and recent information available about the composition of the pelagic zooplankton and nekton community over the inner-shelf of Oregon based upon recent information from the BPA and GLOBEC pelagic surveys (Emmett et al. 2005) and the Newport Hydroline time-series data set (Keister and Peterson 2003). The efficiency of the rope-trawl used during the surveys is not known and catchability had to be assumed for each group. To the extent that independent estimates of biomass are available for the northern California Current (e.g., coast-wide stock assessment reports and acoustical surveys), they were used to inform our best guess of appropriate scaling factors to apply to catch-based biomass estimates. Attributing the change in community composition to local population growth (or mortality) or to migration was also a matter of making our best guess based upon what is known about the distribution and behavior of individual groups.

There are some particular processes and considerations that these models neglect and which could be incorporated in future model improvements. One of the most important of these processes is production export via Ekman transport during periods of strong upwelling. Surplus production that is lost to detritus in the current models may be more realistically assigned to export production. Zooplankton production rate estimates used in these models, or any similar mass-balance food-web model for an upwelling ecosystem, may need to be increased to allow biomass advected offshore to be replaced. With respect to the seasonal change in biomass of some groups observed during ocean surveys, we assume the relative importance of immigration versus local growth and mortality as the cause. Resolving this issue for the most mobile groups will ultimately require incorporating real observations of growth rates and migration patterns during the model coverage years. In the absence of detailed information, we must rely upon more general observations or informed hypotheses of migration behavior. For groups in which empirical biomass data were unavailable and biomass was estimated by the model, we chose not to incorporate the hypothetical biomass accumulation rate when spring and summer estimates differed and avoided compounding our assumed biomass with assumed growth, mortality, and migration rates.

## SUMMARY

The two seasonal food-web models developed here quantify direct and indirect trophic interactions with large jellyfish that are not amenable to direct observation. By summer, jellyfish become the major zooplankton consumer in the entire pelagic ecosystem, consuming nearly twice the zooplankton production as the pelagic forage fishes (anchovy, herring, sardine, smelt, and shad). In our model, jellyfish are an important pathway that diverts lower trophic level production away from upper trophic levels and reduces the efficiency of the entire ecosystem. Only 2% of the energy consumed by jellyfish is passed on to higher trophic levels while 10–15% of the energy consumed by forage fishes is transferred upwards. However, the impact of jellyfish upon the pelagic fish community as competitors may be moderate as more than a third of zooplankton production is not consumed at all but lost to the detritus. The strength of direct and indirect trophic linkages between large jellyfish and all other groups revealed by mixed-trophic impact analysis shows that jellyfish have a strong negative impact on most zooplankton but very little impact on upper trophic levels including forage fishes.

Food-web models provide a platform for testing the ramifications of our assumptions about physiological rates, diet, and migration, and for exploring ecosystem response to changes in any of these parameters, in community composition, or to other forcing phenomena. Future model development can and should address these questions: What if jellyfish, being easily digested and not easily quantified in diet studies, are consumed at a higher rate than supposed? At what level of jellyfish grazing does competition for zooplankton production limit the productivity and survival of small pelagic fish? Finally, data on long-term changes in jellyfish biomass are very sparse and do not provide evidence of dramatic increases in the biomass off Oregon in recent years (Shenker 1984; Suchman and Brodeur 2005). However, given that jellyfish biomass has increased dramatically in other ecosystems around the globe, including upwelling ecosystems, modeling efforts to investigate the consequences of future jellyfish outbreaks to fisheries and throughout the food web are valuable.

### Appendix: Data sources and parameters for trophic groups

The models developed here are based upon the northern California Current models developed by Field and colleagues (Field 2004; Field and Francis 2005; Field et al. 2006), but with expanded detail in the pelagic subsystem that incorporates recent pelagic survey data and is recast into a seasonal framework. Ecopath food-web models are typically developed to represent a full year, or several years. Physiological rate parameters are usually yearly averages. The models developed here are seasonal. They apply to the most productive half of the year, therefore production and consumption rate parameters are elevated above those used in other models. Seasonal models must also account for seasonal changes in biomass, expressed as biomass accumulation. Biomass accumulation, in turn, must be attributed to local production (or mortality), to immigration into the model domain (or emigration), or to a combination of both processes.

***Phytoplankton:*** The phytoplankton group aggregates all taxa. Phytoplankton biomass is estimated from surface chlorophyll samples collected by the NH-line study (Peterson et al. 2002) assuming Chl *a* : N = 2.19 (Dickson and Wheeler 1995), C : N = 7.3 (Geider and La Roche 2002), wet weight : C = 10 (after Dalsgaard and Pauly 1997), and mixed layer depth = 26 m. Biomass accumulation from spring to summer is assumed to be due entirely to local production. $P/B$ = 180/yr based upon a doubling time of two days during the upwelling season.

***Copepods:*** The copepod group is the aggregate of all copepod species present in the nearshore upwelling community and is dominated by boreal neritic species (*Pseudocalanus mimus*, *Calanus marshallae*, *Centropages abdominalis*, *Acartia longiremis*, *Acartia hudsonica*) (Peterson and Miller 1977; Keister and Peterson 2003; Morgan et al. 2003). Copepod biomass is estimated from the NH-line study; copepods were sampled with a 0.5 m ring-net towed vertically from near the sea floor (Peterson and Miller 1975; Keister and Peterson 2003; Peterson and Keister 2003). Copepod wet weight biomass is calculated from carbon biomass assuming C : dry weight = 0.45 and dry : wet weight = 0.19 (Omori 1969). Biomass accumulation from spring to summer is assumed to be due entirely to local production. $P/B$ = 37/yr is based upon a growth rate of 0.1/d at 10°C (Hirst and Bunker 2003). Gross growth efficiencies ($P/Q$) for zooplankton groups generally range between 0.1 and 0.4 (Parsons et al. 1984). Consumption rates ($Q/B$ = 148/yr) for copepods and other zooplankton groups were calculated assuming an intermediate growth efficiency, $P/Q = 0.25$.

***Euphausiid juveniles and adults:*** The dominant euphausiid species off Oregon are *Euphausia pacifica* and *Thysanoessa spinifera* (Peterson et al. 2000). Each species is modeled individually since *T. spinifera* is a coastal species, and *E. pacifica* is most abundant over the outer shelf and shelf-break. *T. spinifera* is the only euphausiid common within the 150 m isobath off southwestern Vancouver Island (Mackas 1992). Off central Oregon, *T. spinifera* is in greatest abundance over the inner-shelf, and *E. pacifica* is in greatest abundance near the shelf-break (Smiles and Pearcy 1971; Peterson and Miller 1976).

Adult and juvenile euphausiid biomass is estimated from median monthly time-series density data collected at station NH-20 (128 m) from 2001 through 2004 (T. Shaw, OSU, Newport, Oregon, unpub. data). Vertical bongo tows from 20 m were conducted at night as euphausiids undergo diel vertical migration (Alton and Blackburn 1972), and vertically integrated concentrations are calculated assuming they are concentrated within the upper 20 m at night (W. T. Peterson, NOAA/NMFS, Newport, Oregon, unpub. data). Wet weights of juvenile and adult *E. pacifica* (6.31 mg, 66.51 mg) and *T. spinifera* (12.38 mg, 166.98 mg) are calculated from average juvenile and adult body lengths (*E. pacifica*, 7 mm and 18 mm, *T. spinifera*, 8 mm and 20 mm; T. Shaw, OSU, Newport, Oregon, unpub. data), applying an empirical length-carbon relation (Ross 1982), and assuming C : dry weight = 0.45 and dry : wet weight = 0.19 (Omori 1969).

Seasonal biomass accumulation in the model of *E. pacifica* is assumed to be entirely due to immigration via transport within bottom waters onto the inner-shelf during periods of upwelling (see Feinberg and Peterson 2003). Given that *T. spinifera* is a more coastal species, *T. spinifera* biomass accumulation is attributed to 20% local production and 80% immigration. $P/B$ = 5.8/yr for *E. pacifica* adults (Tanasichuk 1998a), and $P/B$ = 7.0/yr for *T. spinifera* (Tanasichuk 1998b) (excluding molt production). $Q/B$ = 23.2/yr for *E. pacifica* and 28.0/yr for *T. spinifera* (assuming growth efficiency, $P/Q = 0.25$).

***Euphausiid larvae:*** Euphausiid larval biomass is estimated from the BPA zooplankton survey (see Methods), and seasonal biomass accumulation is assumed to be due entirely to local production. Areal biomass estimates assume larvae are concentrated within the sampled surface layer (30 m) (Lu et al. 2003; Lamb and Peterson 2005). $P/B$ = 69.8/yr is the mean of larval *E. pacifica* and *T. spinifera*, excluding molt production (Tanasichuk 1998a, b). $Q/B$ = 279.2/yr (assuming growth efficiency, $P/Q = 0.25$).

***Euphausiid eggs:*** Euphausiid eggs are found off the central Oregon coast throughout the year, but the major spawning event occurs in late summer and has increased in the spring season following the northern Pacific climate regime shift in 1999 (Feinberg and Peterson 2003). After spawning, eggs hatch within two days at temperatures typical for the Oregon coast upwelling ecosystem (Feinberg et al. 2006). Estimates from the BPA zooplankton survey off northern Oregon in 2000 and 2002 suggest euphausiid egg biomasses of 0.2223 t/km$^2$ and 0.0010 t/km$^2$ in the spring and summer, respectively (tab. 2; C. Morgan, OSU, Newport, Oregon, unpub. data), and higher densities to the north off Washington. In our Oregon shelf models, we use estimates from central Oregon coast observations. Feinberg and Peterson (2003) report the mean spring euphausiid egg densities at NH-line stations NH-5 and NH-15 from 1999–2001 as 51.3/m$^3$ and 11/m$^3$, respectively, and summer densities as 132.6/m$^3$ and 186/m$^3$. Assuming that the negatively buoyant eggs (Gomez-Gutierrez et al. 2005) are distributed throughout the water-column, these mean areal densities of $2*10^9$/km$^2$ in the spring and $1*10^{10}$/km$^2$ in the summer provide the biomass estimates used in the models: $B_{spring}$ = 0.077 t/km$^2$ and $B_{summer}$ = 0.468 t/km$^2$. The assumed mean euphausiid egg wet weight (0.039 mg) is based upon the median *E. pacifica* and *T. spinifera* egg diameter of 415 μm (Gomez-Gutierrez et al. 2005) and a density of 1.039 g/cm$^3$ is from *Thysanoessa raschii* (Marschall 1983).

Within Ecopath, euphausiid eggs are handled as a non-feeding group in the same manner as a detritus group, following the example of Okey and Pauly for herring eggs (1999). Egg production rates are set as a detritus input rate parameter during model balancing to offset predation under an assumed ecotrophic efficiency of ≈ 0.9.

***Pelagic amphipods, macro-zooplankton, and small jellies:*** Pelagic amphipods include both hyperiid and gammarid amphipods in the planktonic community. Species most encountered during the BPA survey are *Themisto pacifica* and *Hyperia medusarum*. The macro-zooplankton group is an aggregation of meroplankton (crab zoeae and megalopae, barnacle larvae, mysid shrimp larvae, and echinoderm larvae), chaetognaths (e.g., *Sagitta* spp.), pteropods (e.g., *Limacina* spp., *Carinaria* spp., *Corolla spectabilis*, *Clione* spp.), ichthyoplankton, and pelagic polychaetes. The small jellyfish group includes salps, larvaceans, and ctenophores and has not been well sampled off Oregon (encountered during the BPA survey are *Cyclosalpa bakeri*, *Salpa fusiformis*, *Thetys vagina*, *Oikopleura* spp., *Pleurobrachia* spp., *Beroe* spp.). Because of uncertain sampling efficiency and unknown biomass below the sampling depth of recent zooplankton surveys, seasonal biomass values of these groups are estimated by Ecopath under assumed ecotrophic efficiencies of 0.9. Model-derived biomass estimates (tab. 3) are substantially greater than estimates derived from the BPA zooplankton survey (tab. 2). For amphipods and macro-zooplankton, $P/B = 7/\text{yr}$ is from a British Columbia shelf model for carnivorous zooplankton (Preikshot 2005), and $Q/B = 28/\text{yr}$ is estimated under an assumed zooplankton growth efficiency ($P/Q = 0.25$). For the small jellyfish, $P/B = 9/\text{yr}$ and $Q/B = 30/\text{yr}$ is borrowed from the Fisheries Centre's (UBC, Vancouver, British Columbia) British Columbia shelf model for salps (Pauly and Christensen 1996).

***Fish eggs:*** Fish egg biomass is obtained from the BPA zooplankton survey off northern Oregon assuming C : dry weight = 0.45 and dry : wet weight = 0.073 (as found for cod eggs, Thorsen et al. 1996) and eggs are concentrated within the surface 30 m. Within Ecopath, fish eggs are handled as a non-feeding, detritus-like group. Egg production rates are set as a detritus input-rate parameter during model balancing to offset predation under an assumed ecotrophic efficiency of ≈ 0.9.

***Large jellyfish:*** The large jellyfish group is an aggregate made up of the scyphomedusae *Chrysaora fuscescens* (sea nettles), *Aurelia labiata* (moon jellyfish), and *Phacellophora camtschatica* (egg yolk jellyfish), and the hydromedusa *Aequorea* spp. (water jelly). Abundance and biomass data is provided by the BPA and GLOBEC pelagic trawl surveys. Individual jellyfish wet weight and growth from spring to summer is provided by Suchman and Brodeur (2005). These size data were collected during the same GLOBEC cruises off southern Oregon as used in the present food-web models. Remotely Operated Vehicle observations over the Oregon shelf show that *Chrysaora fuscescens* extend throughout the water-column with peak abundance at or just below the depth sampled by the pelagic trawl survey (C. Suchman, Virginia Institute of Marine Science, Gloucester Point, Virginia, pers. comm.). To account for jellyfish below the trawl depth, biomass is conservatively scaled upward by a factor of 1.5. Being smaller in spring, jellyfish are sampled with less efficiency by the rope-trawl in spring than in the summer (Brodeur, NOAA/NMFS, Newport, Oregon, pers. obs.). The spring jellyfish biomass is further scaled upward relative to the summer biomass; the appropriate scaling factor is unknown but a factor of 3 implies a conservative estimate of productivity. Jellyfish biomasses used in the models are: $B_{\text{spring}} = 0.855$ t*km$^2$, $B_{\text{summer}} = 3.269$ t*km$^2$.

The unscaled change in biomass observed during the BPA and GLOBEC pelagic surveys over 0.25 yr from spring to summer (tab. 1) implies a production rate of $P/B = 12.3/\text{yr}$, assuming biomass accumulation to be strictly endemic production and $B_{\text{mean}} = 0.643$ t*km$^2$. Larson (1986) found the spring net jelly production rate in Saanich Inlet, Vancouver Island, to be 15/yr to 36/yr (ctenophores, hydromedusae, siphonophores). The rescaled biomasses used in the present models imply lower productivity than measured by Larson or as calculated from the unscaled BPA and GLOBEC observations, but the latter are minimum productivity estimates that do not account for mortality and advection losses. Both the spring and summer models use $P/B = 15/\text{yr}$, which is at the low end of the range observed by Larson (1986). For our model, $Q/B = 60/\text{yr}$ (assuming growth efficiency, $P/Q = 0.25$).

***Benthic invertebrates (pandalid shrimp, benthic shrimp, epifauna, crabs, infauna):*** The biomasses of pandalid shrimp, benthic shrimp, epifauna and infauna are estimated by Ecopath based on assumed ecotrophic efficiencies of 0.9. For pandalid shrimp (primarily *Pandalus jordani*) and benthic shrimp, $P/B = 3/\text{yr}$ are from natural mortality estimates for pandalid shrimp in Oregon (1.0–2.5/yr, and increased assuming higher productivity in spring and summer) (Hannah 1995), and $Q/B = 12/\text{yr}$ (assuming growth efficiency, $P/Q = 0.25$). Dungeness crab biomass is re-estimated from Field (2004); $P/B = 1/\text{yr}$ is increased from Field (2004) assuming higher productivity in spring and summer, and $Q/B = 4/\text{yr}$ (assuming growth efficiency, $P/Q = 0.25$). For epifauna and infauna: $P/B = 3/\text{yr}$ and is increased from Field (2004) assuming higher productivity in spring and summer, and $Q/B = 12/\text{yr}$ (assuming growth efficiency, $P/Q = 0.25$).

***Forage fishes:*** The sampling efficiency of the trawl-system used in the BPA and GLOBEC pelagic surveys has not been tested for forage fishes (anchovy, smelt, herring, shad, sardines, and saury), and there are few independent estimates of forage fish biomass off Oregon against which to compare our biomass estimates. Nevertheless, these surveys remain unique in the NCC region for specifically targeting the pelagic fish community. During model balancing, we scale the total estimated forage fish biomass by a factor of 50, keeping the relative contribution of each forage fish group constant. Employing this scaling factor, the spring biomass in Oregon and Washington out to the 1,280 m isobath would be 382,000 t, or 7.5 t*km$^2$ (19.5 t*km$^2$ inshore, 1.2 t*km$^2$ offshore; BPA and GLOBEC survey data for offshore and Washington regions not shown). Preliminary estimates of the coastal pelagic species biomass as estimated from a coastwide acoustical survey in the spring of 2006 is approximately 2,000,000 t for the entire West Coast, most of which occurs south of Oregon (D. Demer, NOAA/NMFS, La Jolla, California, pers. comm.). Our forage fish biomass estimate would put 19% of the total West Coast biomass off Oregon and Washington. Similarly, we estimate that the summer sardine biomass off Oregon and Washington would be 158,000 t, or 15% of the entire 2000 and 2002 West Coast sardine biomass of 1,057,000 t, as reported in the most recent stock assessment (Hill et al. 2006). Saury are largely offshore species and were encountered inshore in greater-than-trace numbers only in summer 2002 off southern Oregon; they are excluded from the inner-shelf models.

$P/B$ ratios of 2/yr for smelt, shad, sardine, and anchovy are from the small pelagics group in the Fisheries Centre's (UBC, Vancouver, British Columbia) Strait of Georgia model (Pauly and Christensen 1996) and $P/B$ = 2.2/yr for herring is from their British Columbia shelf model. $Q/B$s are estimated under an assumed growth efficiency ($P/Q$ = 0.25).

***Salmon, adults and juveniles:*** For coho, Chinook, and "other" salmon (sockeye, chum, steelhead), a very crude estimate of the trawl-capture efficiency is calculated by comparing the summer coho biomass estimates from the pelagic surveys to the sum of the terminal run biomass (spawning returns plus freshwater landings) and ocean landings off Oregon and Washington (PFMC 2006b, 2007). These values (not shown) suggest a scaling factor of 3 to 6 between 2000 and 2002, and we use a scaling factor of 6. Juvenile salmon catchability is assumed to be the same as for adults and similarly scaled.

$P/B$ = 2.5/yr, $Q/B$ = 16.5/yr for coho and $P/B$ = 1.9/yr, $Q/B$ = 14.5/yr for other salmon (chum) are from Aydin et al. (2003). $P/B$ = 0.75/yr and $P/Q$ = 0.17 for Chinook are from Great Lakes studies (Rand and Stewart 1998).

***Mesopelagic fishes, squid, and non-salmonid juvenile fishes:*** Information about abundance and biomass of non-salmonid juvenile fishes (< 5cm), mesopelagic fishes, and squid from the BPA/GLOBEC pelagic surveys are considered non-quantitative due to capture efficiency limitations and net-avoidance. Biomasses are estimated by Ecopath under an assumed ecotrophic efficiency of 0.9.

$P/B$ = 3/yr for squid is borrowed from the Eastern Subarctic Pacific model of Aydin et al. (2003). $P/B$ = 2/yr for non-salmonid juvenile fishes is borrowed from the small pelagics group in the Strait of Georgia model (Pauly and Christensen 1996). Consumption rates for squid and juvenile fishes are calculated under assumed growth efficiencies ($P/Q$ = 0.25). $P/B$ = 0.6/yr and $Q/B$ = 3/yr for mesopelagic fishes are modified from Field (2004).

***Sharks:*** BPA and GLOBEC catch data are assumed to reflect regional biomass and are not adjusted for catchability. The species encountered during the pelagic surveys are the soupfin shark (*Galeorhinus galeus*), blue shark (*Prionace glauca*), common thresher shark (*Alopias vulpinus*), and salmon shark (*Lamna ditropis*). $P/B$ = 0.2/yr is from estimated natural mortality rates (PFMC 2003).

***Hake and mackerels:*** The mackerels, jack mackerel (*Trachurus symetricus*) and Pacific mackerel (*Scomber japonicus*), are aggregated into a single group as in Field's (2004) NCC model. Hake (*Merluccius productus*) and mackerel biomasses from the BPA and GLOBEC pelagic surveys are considered underrepresented due to capture efficiency limitations and net avoidance during daylight trawls. Summer hake biomass is from the 2001 NOAA triennial bottom trawl survey and scaled by a factor of 1.25 to conservatively account for the pelagic population not sampled in the bottom trawl. The spring hake biomass is back-calculated based upon the relative rate of change observed during the BPA and GLOBEC surveys. Mackerel biomass is estimated from the BPA and GLOBEC pelagic surveys and scaled by a factor of 10. Both the hake and mackerel biomass densities are lower than used in Field's 1990s model but reflect the decline in piscivorous fish abundance observed during NOAA groundfish surveys in the late 1990s and during night-time pelagic surveys off northern Oregon and southern Washington after 1998 (Field 2004; Emmett et al. 2006).

$P/B$ = 0.8/yr and $Q/B$ = 5/yr for hake are from the Fisheries Centre's (UBC, Vancouver, British Columbia) British Columbia shelf model (Pauly and Christensen 1996). $P/B$ = 0.5/yr for the mackerels is from estimates of Pacific mackerel natural mortality (Parrish and MacCall 1978), $Q/B$ = 7/yr is from Pauly and Christensen (1996).

***Rockfishes:*** Rockfish are aggregated into three groups based upon general cross-shelf distribution and diet: shelf planktivores (stripetail, redstripe, greenstriped, canary, shortbelly, widow), shelf piscivores (bocaccio, chilipepper, cabezon, black, blue, China, quillback, black-and-yellow, gopher), and slope planktivores (darkblotched, splitnose, yellowmouth, sharpchin, Pacific ocean perch, aurora, blackgill, shortraker, rougheye). Biomasses are estimated from the 2001 NOAA groundfish survey with a 2X catchability adjustment for shelf piscivore and slope planktivore rockfish and a 6X catchability adjustment for shelf planktivore rockfish (assuming a higher density inshore of the 55 m isobath survey limit). Physiological parameters are modified from Field (2004).

***Demersal fishes (dogfish, sablefish, lingcod, skates and rays, flatfishes, misc. small demersal fish):*** The defined demersal fish groups, their diets, and their physiological parameters are modified from Field (2004). The flatfishes are aggregated into three groups based upon diet: benthic feeders (English sole, Dover sole, rex sole), water-column feeders (Pacific halibut, arrowtooth flounder, petrale sole), and small flatfish (sanddabs, starry flounder, rock sole, slender sole, sand sole, butter sole). The miscellaneous small demersal fishes include sculpins, tomcod, eelpout, and snailfish, and their biomass is estimated by Ecopath based upon an assumed ecotrophic efficiency of 0.9. The biomass of all other demersal fish groups is estimated from the 2001 NOAA groundfish survey.

***Seabirds and marine mammals:*** The dominant seabirds (alcids, gulls, shearwaters) and marine mammals (harbor seals, sea lions, gray whales, baleen whales, toothed whales) parameters are modified slightly from Field (2004). Shearwaters are migratory and their relative spring and summer biomasses are adjusted to reflect this fact. The biomasses of other groups are adjusted to reflect the 125 m isobath offshore limits of the present models.

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## Part III

# SCIENTIFIC CONTRIBUTIONS

# RANGE EXPANSION AND TROPHIC INTERACTIONS OF THE JUMBO SQUID, *DOSIDICUS GIGAS*, IN THE CALIFORNIA CURRENT

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## ABSTRACT

Although jumbo squid (*Dosidicus gigas*) have been occasional visitors to the California Current over the last century, their abundance and distribution increased between 2002 and 2006. We report several time series of jumbo squid relative abundance from commercial and recreational fisheries as well as resource surveys and food habits studies. To evaluate the trophic relationships of jumbo squid, we report the results of 428 stomach samples collected between 2005 and 2006 at various locations and seasons along the U.S. West Coast. Prey were identified using hard parts, primarily squid beaks and otoliths, and prey sizes were estimated where possible. While jumbo squid forage primarily on small midwater and forage fishes, they also prey on adult groundfish such as Pacific hake (*Merluccius productus*), shortbelly rockfish (*Sebastes jordani*), and other species with semi-pelagic life histories. As their ability to prey on larger items suggests potential impacts on ecosystems, we also consider the role of jumbo squid in a food web model of the northern California Current.

## INTRODUCTION

The jumbo squid (*Dosidicus gigas*) is one of the largest and most abundant nektonic squid in the epipelagic zone throughout the Eastern Tropical Pacific (ETP). As such, jumbo squid are an important component of subtropical food webs, representing a conduit of energy transfer from the mesopelagic food web to higher trophic level tunas, billfish, sharks, and marine mammals (Nesis 1983; Nigmatullin et al. 2001; Olson and Watters 2003). Jumbo squid also support major fisheries in the Gulf of California, the ETP, and the coastal waters of Peru and Chile, although catches are highly variable in space and time. Like most cephalopods, jumbo squid are characterized by rapid growth and short life spans. In the Gulf of California, growth rates of 1 to 1.5 mm dorsal mantle length (DML) per day were estimated for squid in 50 to 70 cm size classes, consistent with lifespans of 1.5 to 2 years (Markaida et al. 2005). There is general consensus that females are more abundant and grow larger than males, with DMLs as large as 100 to 120 cm, corresponding to weights of 30 to 50 kg (Nigmatullin et al. 2001). Nigmatullin et al. (2001) described some apparent population structure of jumbo squid, with individuals growing to a smaller size and maturing earlier in the core of their range in the ETP, and growing (and maturing) larger at the poleward fringes of their range, consistent with the observation by O'dor (1992) that squid tend to grow larger and reproduce later in cooler waters.

Gilly et al. (2006) found that while squid spent most daylight hours at depths greater than 250 m and foraged in near-surface waters at night, they often made short-term vertical migrations from surface waters to depth throughout the night. Their results demonstrated a greater appreciation for the extent of diel movement and the tolerance of jumbo squid for a wide range of both temperature and oxygen levels over short time periods. Tagging results also demonstrate that jumbo squid are capable of migrating up to 30 miles a day for several days in a row (Markaida et al. 2005; Gilly et al. 2006). The usual range of jumbo squid extends from central Chile through the coastal and pelagic waters of the ETP, and into the Gulf of California. However, the distribution and density of jumbo squid throughout their range are characterized by irregular migratory incursions of large numbers of squid at the fringes of their habitat in both hemispheres (Nesis 1983; Ehrhardt 1991; Nigmatullin et al. 2001; Ibáñanez and Cubillos 2007).

Jumbo squid were described as "not uncommon" to the waters of southern and central California by Berry (1912) and Phillips (1933), and were particularly abundant for several years in the mid 1930s, when they were described as a nuisance to salmon, tuna, rockfish, and recreational charter boat fishermen (Clark and Phillips 1936; Croker 1937). There are few records of their presence in California waters between the late 1930s and 1950s (Phillips 1961), although episodic strandings and fisheries occurred sporadically throughout the 1960s and 1970s (Fitch 1974; Anderson 1978; Nesis 1983; Mearns 1988), and their presence in the Southern California

Bight was episodic throughout most of the 1980s and 1990s. During the 1997–98 El Niño event, jumbo squid were observed in substantial numbers off California, as well as in coastal waters off of Oregon and Washington states (Pearcy 2002). In situ video observations taken from remotely operated vehicle (ROV) surveys from the Monterey Bay region show that jumbo squid continue to be present and sporadically abundant since the 1997–98 El Niño, particularly between 2003 and 2006. Their presence in the surveys has been associated with declines in observations of Pacific hake (*Merluccius productus*) (Robison and Zeidberg[1]). Since 2003, jumbo squid have been frequently reported in beach strandings, commercial and recreational fisheries, and resource surveys along the West Coast and through southeast Alaska (Cosgrove 2005; Brodeur et al. 2006; Wing 2006).

In this study, we report several time series of jumbo squid relative abundance from commercial and recreational fisheries as well as resource surveys and food habits studies in order to evaluate the trophic relationships of jumbo squid along the U.S. West Coast.

## METHODS

To consider trends in jumbo squid abundance throughout the California Current, we evaluated several sources of landings and trend information for jumbo squid from commercial and recreational fisheries, resource surveys, and food habits studies. We evaluated catch records from Commercial Passenger Fishing Vessel (CPFV) records north and south of Point Conception from 1980 through 2006.[2] We also discussed the spatial and temporal distribution of squid with a large number of commercial and recreational fishermen. Jumbo squid have also been noted in food habits studies of predators in the California Current; Antonelis and Fiscus (1980) described them as common in the diets of northern fur seal (*Callorhinus ursinus*) off of California, and both Tricas (1979) and Harvey (1989) noted their presence (albeit rare) in the diets of blue sharks (*Prionace glauca*) collected off of the Channel Islands and Monterey Bay respectively in the mid 1970s. Consequently, we considered the frequency of occurrence of jumbo squid in the diets of California sea lions (*Zalophus californianus*) on San Clemente and San Nicolas Islands, based from quarterly monitoring from 1981 to the present (as described in Lowry and Carretta 1999), as well as in the food habits of shortfin mako shark (*Isurus oxyrinchus*) collected from gillnet fisheries off of southern California from 2002–05 (A. Preti, NOAA/NMFS/SWFSC, La Jolla, California, pers. comm.).

Fisheries resource surveys have provided both quantitative and qualitative estimates of abundance for many commercially and ecologically important species relevant to this study. We compiled data from pelagic midwater trawl surveys for juvenile groundfish conducted in May and June off of the central California coast by the NOAA Fisheries Southwest Fisheries Science Center (SWFSC) since 1983 (Sakuma et al. 2006), and a comparable midwater trawl survey conducted by the NOAA Fisheries Northwest Fisheries Science Center (NWFSC) off of Oregon and Southwest Washington between May and November from 2004–06 (Brodeur et al. 2006). Finally, bycatch monitoring data by fisheries observers on commercial at-sea catcher-processors targeting Pacific hake off of Oregon and Washington, including average weights per haul, are available from 1991 to the present, although jumbo squid were only routinely identified to species in 2006. In recent years, catches of squid have increased substantially, with hauls of 25 to 75 tons of squid not uncommon, and most large squid hauls were composed primarily of jumbo squid (V. Wespestad, At-Sea Processors Assn., pers. comm.). Consequently, we evaluated a range of factors including the relative catches of squid to hake, the frequency of occurrence of hauls with large volumes of squid, and the size composition of the squid catch during years for which no reliable taxonomic identity of squid bycatch are available (V. Tuttle, At-Sea Hake Observer Program NOAA/NMFS/NWFSC, pers. comm.).

To evaluate food habits, stomach samples were collected from jig-caught jumbo squid in CPFV and commercial fisheries off of southern and central California, as well as from jig, midwater, and bottom trawl gear aboard the resource surveys described above. The locations, dates, depths (including a range where appropriate), number of specimens collected, and size information for collected specimens are provided in Table 1 and Figure 1. Although size (DML, in cm) was recorded for all specimens, weight (kg) and sex were recorded only for a subset of specimens due to the opportunistic nature of most collections. Weights were estimated with the standard weight ($w$) to length ($l$) relationship based on 85 specimens ranging from 35 to 82 cm mantle length, where:

$$w = al^b \qquad (1)$$

Whole squid or stomachs alone were frozen at capture, although in many instances stomach removal was delayed by 1 to 2 hours. Upon thawing and weighing, stomach contents were washed through a 0.45 mm mesh sieve. Identification of prey items was made from otoliths, squid beaks, scales, bones, and other hard parts based on

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[1] Robison, B. H. and L. D. Zeidberg. 2006. Invasive range expansion by the jumbo squid, *Dosidicus gigas*, in the Eastern North Pacific: ecological impact in Monterey Bay. Eos Trans. AGU, 87(36) Ocean Sci. Meet. Suppl.

[2] California landings from CPFV electronic summary files extracted Jan. 2006 and updated May 2007 by W. Dunlap, California Department of Fish and Game, Marine Region.

TABLE 1
**Sampling locations, dates, collection gear, number of animals sampled, and average mantle length of animals for samples in which animals were collected. For gear type, jig represents sport or commercial line jigging, MT represents midwater (survey) trawls, BT represents bottom (survey) trawls.**

| | | | | | length | |
|---|---|---|---|---|---|---|
| Location | Month/year | Depth (m) | gear | number | mean | range |
| Nine mile bank | 2/2005 | 200 | jig | 27 | 60 | 50–69 |
| Carmel Canyon | 2/2006 | 250 | jig | 21 | 69 | 65–75 |
| Pioneer Canyon 1 | 1/2005 | 200–300 | jig | 46 | 65 | 56–75 |
| Pioneer Canyon 2 | 2/2005 | 200–300 | jig | 33 | 66 | 59–74 |
| Pioneer Canyon 3 | 6/2005 | 200 | MT | 20 | 54 | 46–63 |
| Pioneer Canyon 4 | 2/2006 | 200–300 | jig | 19 | 68 | 50–78 |
| Pioneer Canyon 5 | 3/2006 | 200–300 | jig | 12 | 63 | 57–70 |
| Pioneer Canyon 6 | 9/2006 | 200–300 | jig | 9 | 66 | 61–70 |
| Pioneer Canyon 7 | 12/2006 | 200–300 | jig | 11 | 72 | 66–76 |
| Cordell Bank 1 | 2/2005 | 200–300 | jig | 9 | 66 | 57–70 |
| Cordell Bank 2 | 1/2006 | 200–300 | jig | 16 | 71 | 63–81 |
| Cordell Bank 3 | 2/2006 | 200–300 | jig | 20 | 66 | 56–80 |
| Cordell Bank 4 | 3/2006 | 200–300 | jig | 34 | 66 | 57–79 |
| Cordell Bank 5 | 6/2006 | 1200 | MT, jig | 37 | 57 | 35–65 |
| Cordell Bank 6 | 11/2006 | 200–300 | jig | 21 | 70 | 62–82 |
| Arena Canyon, offshore | 5/2006 | 3000 | MT, jig | 18 | 51 | 46–59 |
| Arena Canyon, nearshore | 9/2006 | 400 | jig | 41 | 54 | 38–68 |
| Cape Mendocino | 6/2006 | 60 | MT, jig | 30 | 54 | 49–61 |
| Heceta Bank | 8–9/2006 | 950 | MT | 29 | 54 | 45–64 |
| Astoria Canyon | 8–9/2006 | 900 | MT | 21 | 58 | 51–68 |
| Coastwide | 6–10/2005–2006 | 100–600 | BT | 29 | 61 | 55–68 |

published guides to fish otoliths (Fitch 1964, 1969; Harvey et al. 2000), squid beaks (Pinkas et al. 1971; Wolff 1982; Clarke 1986), and other sources (McGowan 1968), as well as reference collections. The number of individuals consumed was reported based on the maximum number of upper or lower beaks for cephalopods, and the maximum number of left or right sagittal otoliths for fishes. Only the presence or absence was recorded for euphausiids or small unidentifiable crustaceans, as digestion typically made meaningful enumeration impossible. The frequency of occurrence and the number of prey items was enumerated for all other prey. We also report the percentage of stomach contents weight to the estimated predator size, where empty or trace contents were those with less than 0.001% of body weight, and very full stomachs were those in which stomach weight was greater than 1% of total body weight. Finally, we recorded qualitative estimates of prey digestion state for most samples, in which the degree of digestion was ranked from 1 for recently ingested prey to 5 for trace prey material.

As larger prey items are typically bitten into smaller pieces when consumed, and squid tend to have extremely rapid digestion rates, weighing of prey items is impractical, and was not attempted in this study. Consequently, commonly reported indices, such as the index of relative importance (Pinkas et al. 1971), are not available. However, an alternative index, the geometric index of importance (Assis 1996; Preti et al. 2004), was used, in which

$$GII_j = \frac{\left[\sum_{i=1}^{n} V_i\right]_j}{\sqrt{n}} \tag{2}$$

where $GII_j$ represents the geometric index of importance for the $j$th prey category, $V_i$ represents the vectors for the relative measures of prey quantity (here % frequency occurrence and % of total number), and $n$ is the number of relative measures of prey quantity used (in this case, 2). Additionally, standard lengths (for fishes), DML (for cephalopods), and prey weights were reconstructed based on fitted regressions against otolith lengths and beak rostral lengths where measurements could be taken (to the nearest 0.1 mm), and for which regression information was available (Wolff 1982; Wyllie-Echeverria 1987; Harvey et al. 2000; W. Walker unpubl. data; J. Field unpubl. data; M. Lowry, NOAA/NMFS/SWFSC, La Jolla, California, pers. comm.). Finally, the resulting information was integrated into an existing food web model of the shelf and slope ecosystem of the northern California Current (Field et al. 2006b), and trophic relationships were compared to those in a food web model of the ETP (Olson and Watters 2003).

## RESULTS

Trends in jumbo squid abundance include the number of jumbo squid landed by recreational fishers in CPFV fisheries north and south of Point Conception,

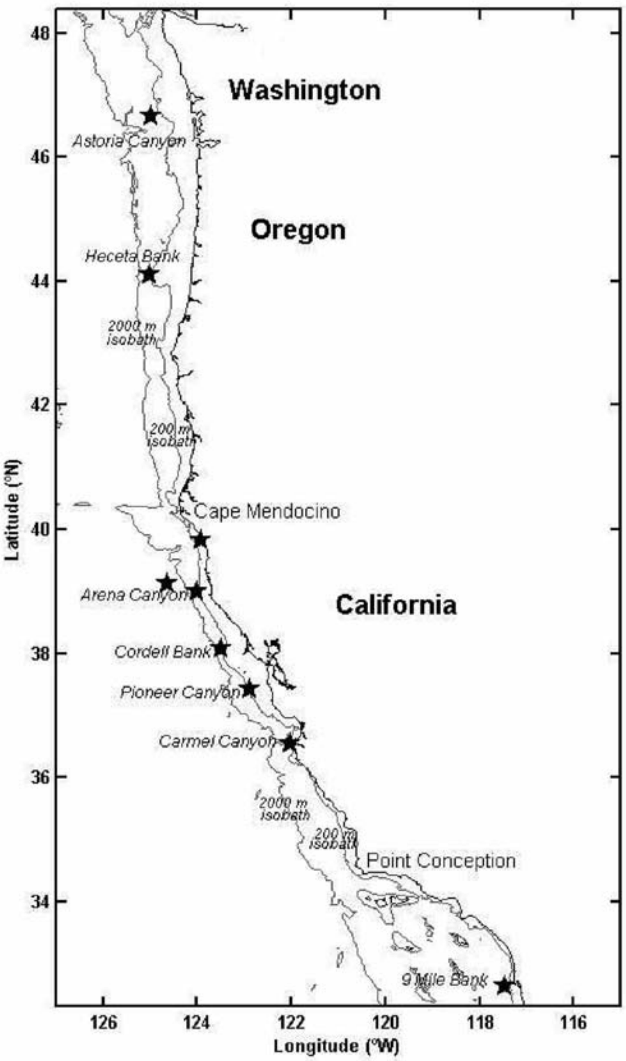

Figure 1. Collection locations of jumbo squid (*Dosidicus gigas*) for food habits studies in 2005 and 2006.

California (fig. 2A). Anecdotal information suggests that the high numbers of squid landed south of Point Conception in 2002 were smaller animals caught primarily in summer months, while catches from 2005–06 were caught almost exclusively in winter months and tended to be large (50–82 cm DML). Information from food habits studies off of southern California are consistent with these trends (fig. 2B), including data from California sea lion foods (1981–2003) and mako sharks (2002–05). Jumbo squid first appeared in the diets of California sea lions in 1995, increased in 1997–98, and increased again from 2002–03. Although the data for mako sharks extends only from 2002 through 2005, jumbo squid were among the most frequently encountered prey item for each of these years, indicating a sustained presence of squid in the offshore waters of southern California throughout this period.

Jumbo squid have also been increasingly encountered in resource surveys along the West Coast, and data from two pelagic midwater trawl surveys are shown (fig. 2C). In the SWFSC survey, jumbo squid were encountered for the first time in 2005, and frequently in 2006, while in the NWFSC midwater survey they were encountered frequently from 2004–06. Although the NWFSC survey shown here began in 2004, comparable midwater trawl surveys in this region prior to 2003 did not encounter jumbo squid (Brodeur et al. 2006). The discrepancy between the northern and southern surveys can be explained largely by their seasonality; although the SWFSC survey occurs in a continuous 45-day period during May and June (between San Diego and Cape Mendocino), the NWFSC survey occurs monthly from May through November (from central Oregon to southwest Washington). In the NWFSC survey, squid were encountered in only 2% of hauls made from May through August, but 14% of hauls made between September and November.

These trends in the seasonality of jumbo squid catches were consistent with those observed from monitoring data from the at-sea fishery for Pacific hake, in which catch rates of all squids in all years are an average of twenty times greater from September through November relative to April through August. Figure 2D shows the total catch of all squid as a percentage of the total catch of hake (to control for changes in year-to-year catches and monitoring coverage), as well as the frequency of occurrence of large catches of squid, defined as tows in which squid represented 10% or more of the total catch of hake by weight. Although jumbo squid were only identified to species in 2006, when they accounted for over 90% of all squid caught, the distribution of average sizes (collected in bycatch monitoring programs) of squid caught in the hake fishery between 2002–05 is much more consistent with the size of jumbo squid relative to the (larger) robust clubhook squid (*Moroteuthis robusta*) or the smaller species seen through most of the 1990s.

A total of 503 stomach samples were collected for food habits studies from 2005–06. From the 85 samples in which weight and length were recorded, the weight-length relationship was estimated ($a = 7.83 * 10^{-6}$, $b = 3.33$, $R^2 = 0.94$). Digestion state and stomach fullness relative to the inferred body weight of samples by gear type are shown in Figure 3. Although only a modest number of stomachs (29) were collected with bottom trawls, over 60% of these stomachs contained recently ingested prey (digestion state of 1), and another 16% had relatively recently ingested prey (digestion state of 2). Along with obvious incidents of cannibalism, this suggests that most prey items from samples collected in bottom trawls represented opportunistic net feeding. Net feeding was also inferred in many of the midwater trawl

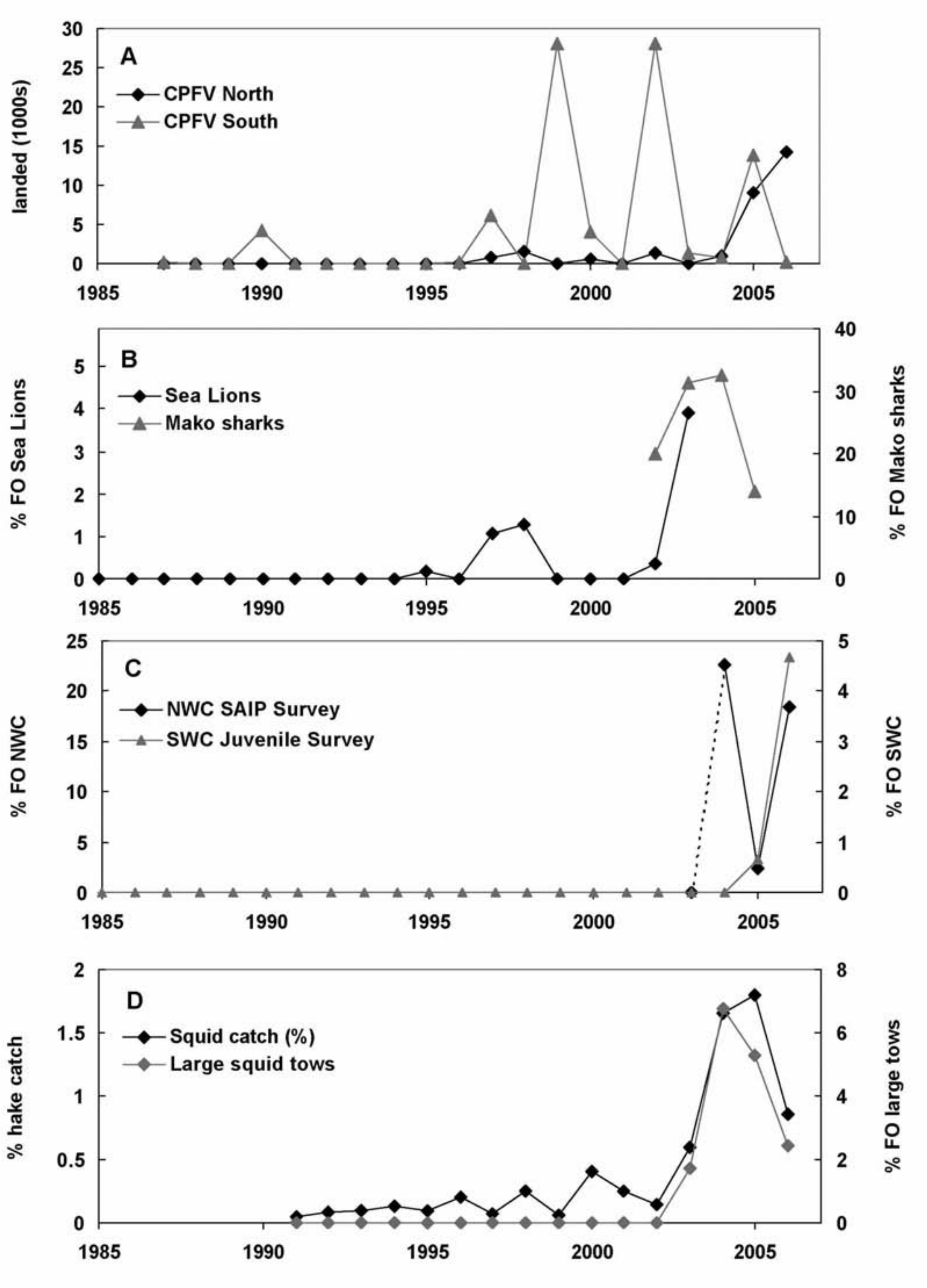

Figure 2. Indices of relative jumbo squid (*Dosidicus gigas*) abundance from (A) California commercial passenger fishing vessels (CPFV) north and south of Point Conception (note that 1999 and 2002 CPFV landings south of Conception were approximately 50,000 and 200,000 squid respectively), (B) frequency of occurrence of jumbo squid in sea lion (*Zalophus californianus*) and shortfin mako shark (*Isurus oxyrinchus*) food habits studies, (C) SWFSC and NWFSC pelagic midwater trawl surveys, and (D) catch statistics from the observer program for the at-sea processing sector of the Pacific hake (*Merluccius productus*) fishery.

collected species, with 28% of stomachs including very recently ingested prey, and 18% including relatively recently ingested prey. By contrast, recently ingested prey items were infrequent (5%) in jig-caught specimens, and in many cases represented cannibalism. Although factors such as seasonality, time of day, and behavior are also relevant, we excluded all samples collected with bottom trawl (*n* = 29) as well as samples collected with midwater trawl with digestion state codes of 1 or 2 (*n* = 46) from further analysis.

The resulting prey composition from 428 samples (375 jig-caught and 53 midwater trawl) are consistent

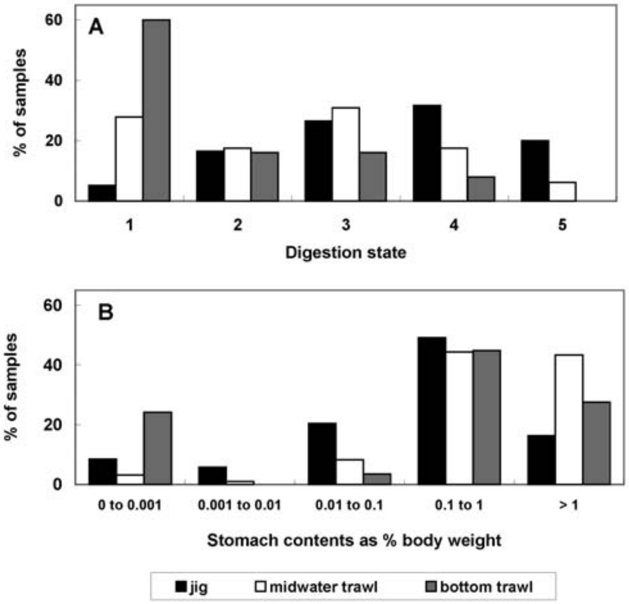

Figure 3. Qualitative estimate of digestion state for all three gear types used to collect jumbo squid (*Dosidicus gigas*), (A) where 1 represents recently ingested prey and 5 represents well digested or trace fragments of prey, and (B) stomach contents as a percentage of predator body weight.

with the expectation that jumbo squid are opportunistic predators, capable of feeding on a wide range of prey items throughout the waters of the California Current. The fifteen most frequently encountered prey items (excluding cannibalism) are presented as Table 2, and a complete taxonomic breakdown of over 60 prey items identified to the genus or species level, with corresponding general prey category groupings and size (length, weight) information is included as Appendix A. Pacific hake was the most numerically important prey item, followed by northern lampfish (*Stenobrachius leucopsarus*), northern anchovy (*Engraulis mordax*), blue lanternfish (*Tarletonbeania crenularis*), and Pacific sardine (*Sardinops sagax*). Although other jumbo squid were present in 11% of samples, cannibalism may be overestimated from many jig-caught cephalopods (Nesis 1983; Dawe et al. 1997; Markaida and Sosa-Nishizaki 2003), and all instances were of bite-size pieces of other large squid, rather than predation on smaller jumbo squid of the size ranges encountered for other cephalopods. Pteropods, euphausiids, and other unidentified crustaceans were all important prey items that could rarely be identified to species or accurately enumerated due to digestion. Additionally, many rockfish could not be identified to the species level, as otoliths of larger individuals were rarely recovered. Given the well armored nature of most rockfish heads, and the tendency of many cephalopods to discard the heads of larger prey items (Dawe et al. 1997), this result is not surprising. Finally, among the more unique remains were bird feathers, which were present in two samples. Observations from commercial fishermen confirm that jumbo squid will attack seabirds (F. Bertroni, F/V *Santina*, Fort Bragg, California, pers. comm.), although the observation of feathers alone in stomachs may suggest unsuccessful attempts.

Some insights with respect to the patchiness of food habits over space and time can be inferred from Table 3, which lists the frequency of occurrence for the eight most frequently encountered prey items, and aggregations of remaining prey items as delineated in Appendix A, for each of the major collection sites described in Table 1. These results show that Pacific hake tended to be important prey across all space and time, as only two location/time combinations did not include their presence. Mesopelagics tended to be ubiquitous, while northern anchovy tended to be more frequently encountered

TABLE 2

**The percent frequency of occurrence (FO) and total number (*N*) of the fifteen most important prey items of jumbo squid (*Dosidicus gigas*) based on a geometric index of importance. A complete taxonomic summary of all prey items, including length and weight information, is provided in Appendix A.**

| Species or taxonomic group | GII | %FO | %*N* | FO | *N* |
|---|---|---|---|---|---|
| Pacific hake (*Merluccius productus*) | 30.9 | 22.7 | 20.9 | 96 | 305 |
| Northern lampfish (*Stenobrachius leucopsarus*) | 21.5 | 20.1 | 10.3 | 85 | 150 |
| Northern anchovy (*Engraulis mordax*) | 19.9 | 16.3 | 11.9 | 69 | 173 |
| Blue lanternfish (*Tarletonbeania crenularis*) | 15.3 | 13.5 | 8.2 | 57 | 119 |
| Pacific sardine (*Sardinops sagax*) | 9.2 | 9.7 | 3.4 | 41 | 49 |
| Euphausiids (Euphausidae) | N/A | 9.0 | N/A | 38 | N/A |
| Shortbelly rockfish (*Sebastes jordani*) | 8.6 | 8.7 | 3.4 | 37 | 50 |
| California headlightfish (*Diaphus theta*) | 8.3 | 6.9 | 4.9 | 29 | 71 |
| Pteropods (*Clio* spp.) | 7.5 | 7.8 | 2.8 | 33 | 41 |
| Broadfin lampfish (*Nannobrachium ritteri*) | 6.3 | 5.7 | 3.3 | 24 | 48 |
| Rockfish spp. (*Sebastes* spp.) | 5.4 | 5.9 | 1.7 | 25 | 25 |
| Pelagic shrimp (Decapoda) | 4.4 | 4.5 | 1.8 | 19 | 26 |
| Clubhook squid (*Onychoteuthis borealijaponicus*) | 3.9 | 2.6 | 2.9 | 11 | 42 |
| California lanternfish (*Symbolophorus californiensis*) | 3.6 | 3.8 | 1.4 | 16 | 20 |
| California market squid (*Loligo opalescens*) | 3.2 | 3.1 | 1.5 | 13 | 22 |

TABLE 3

**Prey frequency of occurrence (%) by sampling site and number of samples. Differences between this table and Table 1 reflect exclusion of net feeding samples from midwater trawl collections. The top eight most frequently encountered prey from Table 2 are provided, with aggregated groups of remaining prey items.**

| | Nine Mile Bank | Carmel Canyon | Pioneer Canyon 1 | Pioneer Canyon 2 | Pioneer Canyon 3 | Pioneer Canyon 4 | Pioneer Canyon 5 | Pioneer Canyon 6 | Pioneer Canyon 7 | Cordell Bank 1 | Cordell Bank 2 | Cordell Bank 3 | Cordell Bank 4 | Cordell Bank 5 | Cordell Bank 6 | Arena Canyon offshore | Arena Canyon nearshore | Cape Mendocino | Heceta Bank | Astoria Canyon |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| # samp | 27 | 21 | 46 | 33 | 11 | 19 | 12 | 9 | 11 | 9 | 16 | 20 | 37 | 23 | 21 | 18 | 41 | 30 | 11 | 13 |
| gear | jig | jig | jig | jig | MT | jig | jig | jig | jig | jig | jig | jig | jig | MT | jig | MT | jig | jig | MT | MT |
| *Merluccius productus* | 8 | 10 | 17 | 16 | | 47 | 42 | 67 | 36 | 22 | 6 | 20 | 33 | 4 | 32 | | 5 | 47 | 45 | 62 |
| *Stenobrachius leucopsarus* | 8 | 10 | 26 | 38 | 27 | 6 | 33 | 11 | 55 | 11 | 6 | 20 | 11 | 22 | 32 | | 27 | 20 | 27 | 8 |
| *Engraulis mordax* | 36 | 38 | 26 | 25 | 73 | | 8 | 22 | 55 | | 6 | | | | 26 | | 20 | 3 | | |
| *Tarletonbeania crenularis* | | | 9 | 22 | 36 | 6 | | | 18 | 22 | 6 | | 8 | | 42 | 6 | 29 | 7 | 36 | 46 |
| *Sardinops sagax* | 4 | | | | | | | | 9 | | 6 | 45 | 50 | 26 | | 6 | | 7 | 9 | 8 |
| Euphausidae | | | 4 | 6 | | 6 | 17 | | | | | | | | 5 | 6 | 39 | 3 | 9 | 8 |
| *Sebastes jordani* | | 24 | 7 | 13 | | | 25 | 56 | 27 | | | 5 | | | | 6 | 17 | 7 | 9 | |
| *Diaphus theta* | 4 | | 28 | 28 | | 18 | 17 | | 36 | 11 | 6 | 5 | | | 11 | | | | | |
| other crustaceans | | | 7 | | | | | | 0 | | | | | 4 | 11 | | 2 | | 9 | 15 |
| pteropods | 12 | | | | | | | | 9 | | | 15 | 19 | | | 11 | 37 | | 9 | 38 |
| cephalopods | 16 | 62 | 28 | 28 | 73 | 12 | 33 | 22 | 36 | 22 | 25 | 20 | 22 | 30 | 42 | 17 | 44 | 13 | 27 | 46 |
| other coastal pelagics | 4 | | 2 | 3 | | 18 | | | 18 | | 6 | | | 4 | | | 5 | | 18 | |
| other mesopelagics | 12 | 14 | 4 | 16 | 18 | 53 | | 67 | 9 | | 6 | 30 | | 9 | 5 | 22 | 37 | 10 | 136 | 15 |
| other rockfish | | 5 | 13 | 19 | 9 | 6 | | 44 | 55 | | 19 | 10 | 6 | | 5 | 6 | | 3 | | |
| flatfish | | | 4 | 16 | | | | | 9 | | 6 | | 6 | | 5 | | | | | 8 |
| other or unidentified | 8 | 14 | 39 | 22 | 9 | 6 | 25 | 11 | 18 | 33 | 25 | 10 | 17 | 9 | 21 | 6 | 10 | 13 | 18 | 38 |

in nearshore and canyon areas (Carmel Canyon, Nine Mile Bank, and Pioneer Canyon) and Pacific sardine were more frequently encountered in offshore areas (particularly Cordell Bank). Shortbelly rockfish were most frequently encountered in Pioneer Canyon, long known to be a region of high abundance for that species (Chess et al. 1988), while other rockfish and small flatfish were most frequently seen at both Pioneer Canyon and Cordell Bank, generally in winter months.

Of the 1,293 fish and cephalopod prey items that could be identified to a species or genus level, 1,122 (87%) could be associated with length and weight information. The resulting length frequencies for several of the more frequently encountered species of commercial importance are shown in Figure 4. Most Pacific hake were less than 15 cm standard length, primarily young-of-year and age-1 fishes, although hake as large as 42 cm were observed. While most of the rockfish are shortbelly rockfish, an unfished species, other rockfish species were present, and many of the unidentified rockfish are unlikely to be shortbelly due to the large size inferred by vertebral remains. Pacific sardine were observed primarily in the 15 to 21 cm size classes, corresponding to age 1–3 sardines, which are age classes commonly targeted in commercial fisheries.

As Pacific hake and other groundfish for which lengths and weights could be reconstructed tended to be considerably larger than those for mesopelagic fishes, coastal pelagics, and cephalopods, a comparison of the relative importance of prey by weight is insightful. Figure 5 shows binned length classes of all prey items that could be associated with a length and weight by their general taxonomic groups described in Appendix A (where groundfish includes rockfish and flatfish). While small mesopelagics were numerically the most important prey item (accounting for 34% of all measured prey items), their estimated mass represented less than 5% of the mass of all measured prey. By contrast, groundfish other than Pacific hake represented only 9% by number, but 41% by mass. Similarly, smaller (0–20 cm) hake represented 22% of measured prey by number but only 9% by mass, while larger (>20 cm) hake represented only 4% by number but 21% by mass. Other cephalopods represented 13% of prey by number and 7% by mass, while coastal pelagics represented 20% by number and 17% by mass. Although clearance rates for larger prey items could be extended relative to smaller prey, these results indicate that larger prey items are likely to make a greater contribution to squid diets than might be expected by the frequency-of-occurrence information alone. The relationships between the mantle length of jumbo squid and standard length (for fish) or mantle length (for cephalopods) of prey are shown in Figure 6, along with smoothed 10th, 50th, and 90th percentiles of prey size by preda-

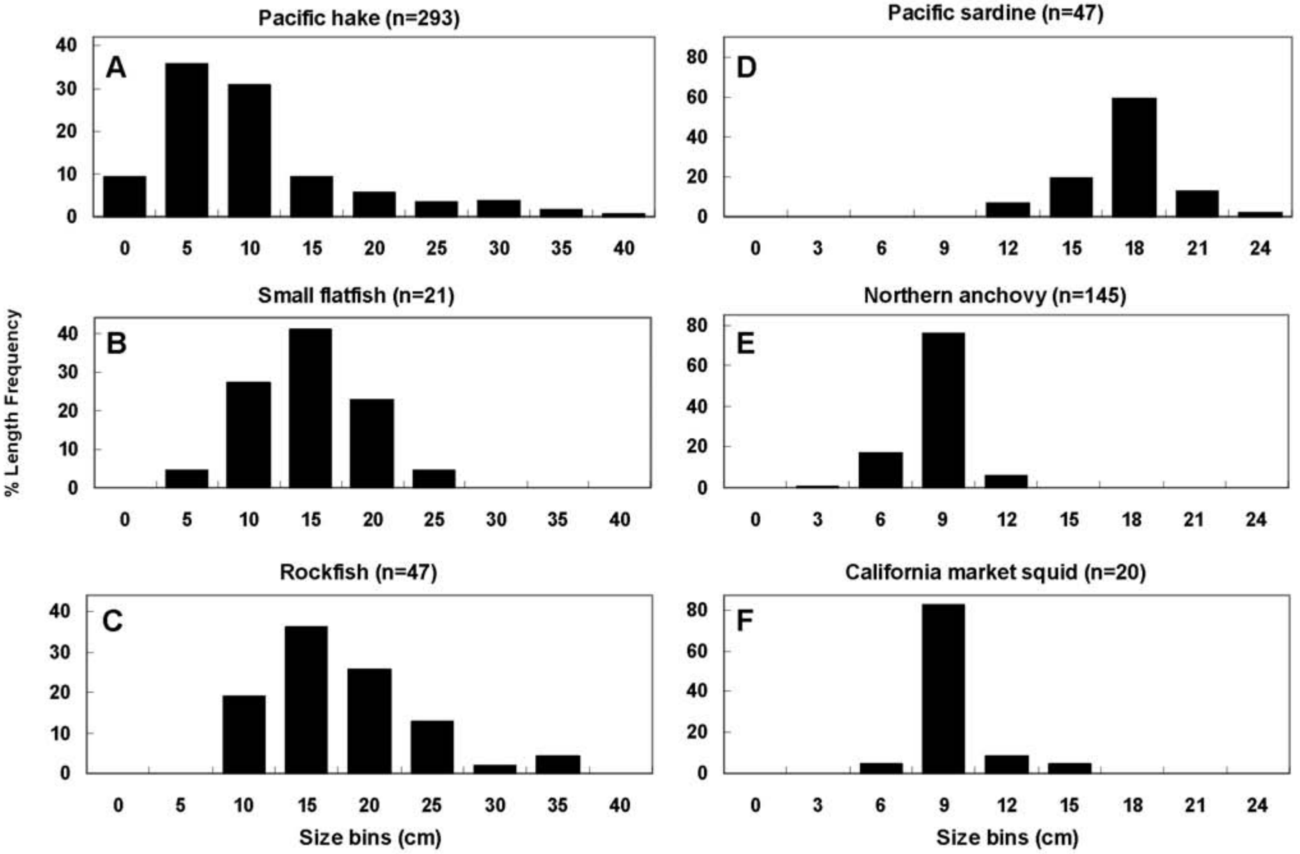

Figure 4. Size composition of most frequently consumed species of commercial interests, including, (A) Pacific hake (*Merluccius productus*), (B) small flatfish, (C) rockfish, (D) Pacific sardine (*Sardinops sagax*), (E) Northern anchovy (*Engraulis mordax*), and (F) California market squid (*Loligo opalescens*). Sizes are based on otolith length/standard length regressions for fishes, and rostrum length/mantle length regressions for market squid. Length bins are labeled by the lower end of the bin, such that 5 represents fish from 5 to 9.9 cm.

tor size (in 5 cm bins). The relationship suggests a log-normal distribution across the prey spectrum, such that the size classes of the vast majority of prey items changes little with size, while the distribution of the prey spectrum extends towards larger prey items with size.

The role of jumbo squid in the ecosystem, including an estimate of trophic level, was evaluated by adding jumbo squid to a food web model of the northern California Current (Field et al. 2006b). To arrive at an estimate of prey composition we made the following assumptions. First, as the rapid digestion rates of soft-bodied prey complicate enumeration or weighing of those prey items, we assumed that the frequency of occurrence represented a plausible composition for euphausiids (9%), macrozooplankton (5%), and gelatinous zooplankton (8%). For the remaining prey items, we scaled the product of the frequency of occurrence and the percentage of total number by the average weight of all prey items

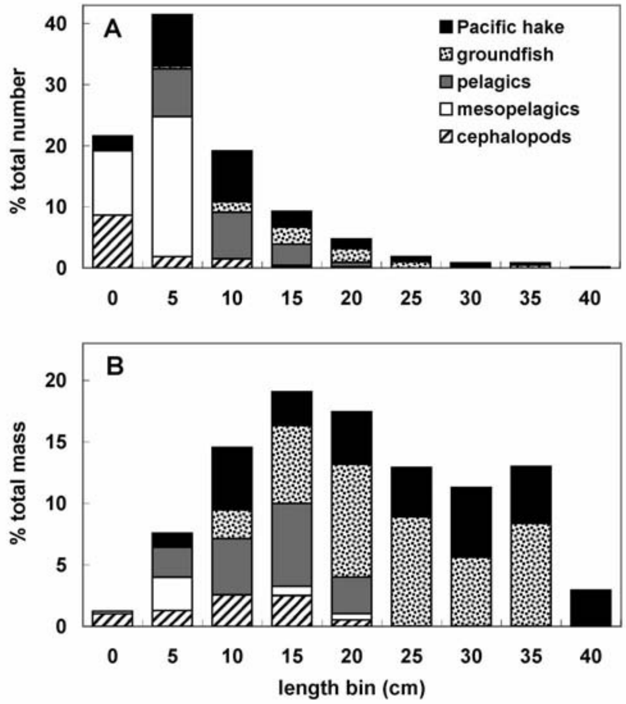

Figure 5. Size composition of all measured jumbo squid (*Dosidicus gigas*) prey items in aggregated groups, (A) by the percentage of the total number of measured prey, and (B) with respect to the reconstructed total mass of prey.

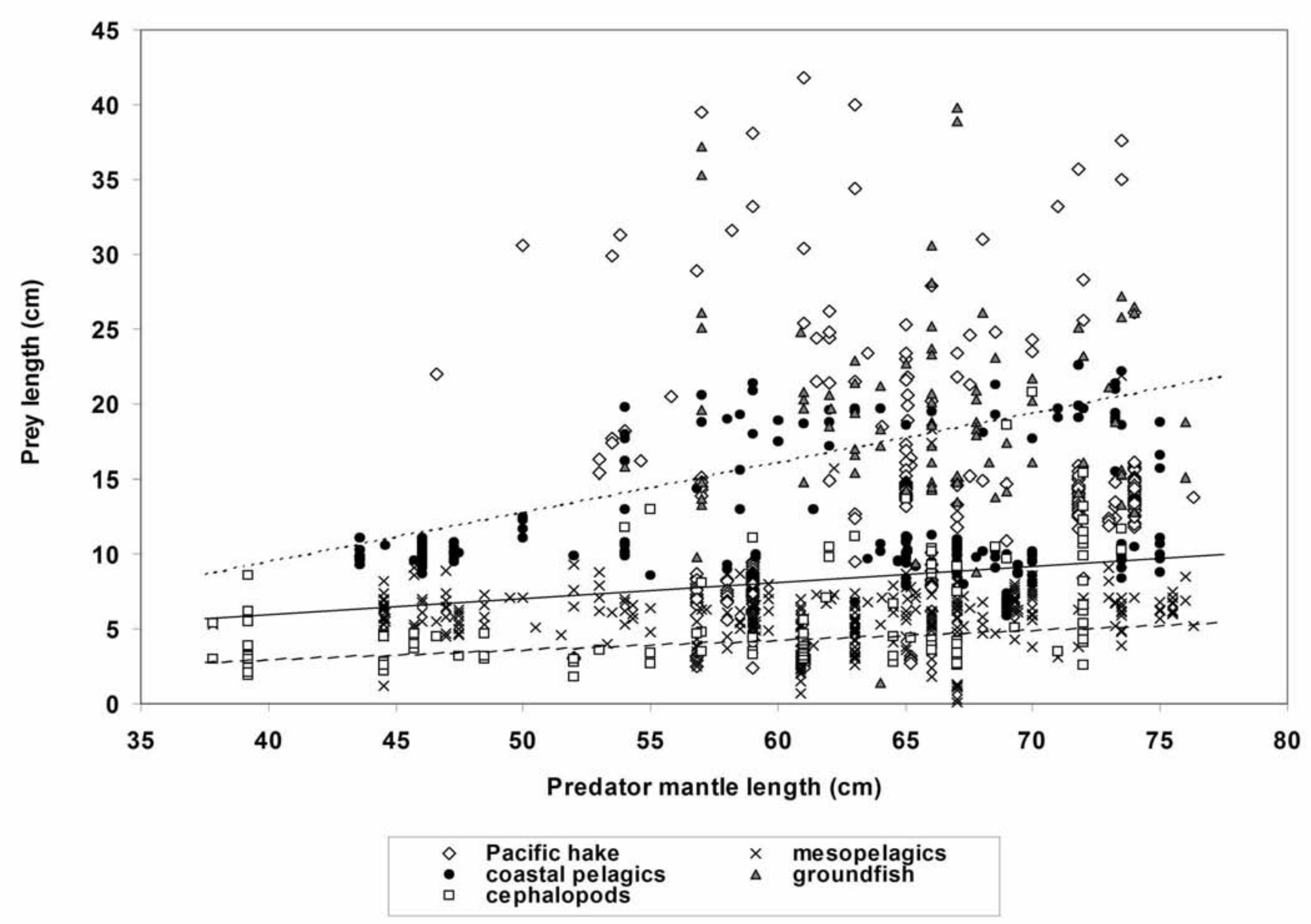

Figure 6. Jumbo squid (*Dosidicus gigas*) dorsal mantle length plotted against the standard length (for fish) and dorsal mantle length (for cephalopods) of 992 different prey items. Lines represent smoothed estimates of the 10th (dotted), 50th (solid line), and 90th (dashed) percentiles for predator length groups when dorsal mantle length was aggregated into 5 cm bins.

in that assemblage. This resulted in a diet composition (by mass) of 28% Pacific hake, 17% rockfish, 13% cephalopods, 7% mesopelagics, 6% anchovy and other forage fishes, 5% sardine, 1% mackerel, and 1% small flatfish (cannibalism was excluded from this model). Predators include the fisheries and pinnipeds discussed earlier, toothed whales[3], coastal sharks, and albacore (Pinkas et al. 1971). The abundance, consumption, and production parameters were based on Olson and Watters (2003), but do not affect the static model result.

The resulting food web model (fig. 7A) represents a plausible means of visualizing the role of adult jumbo squid in the California Current ecosystem. A comparable model of the ETP (Olson and Watters 2003), in which only predators with significant amounts of jumbo squid in their diets are highlighted, is also presented (fig. 7B). Although jumbo squid were not modeled independently of other cephalopods in the ETP, they do represent a major fraction of the cephalopod biomass in that ecosystem, and parameters for cephalopods in the ETP model were based on data for jumbo squid (Nesis 1983; Ehrhardt 1991). Finally, Figure 8 presents the resulting model estimates of trophic levels (excluding producers and lower trophic level consumers) increasing from left to right along the *x*-axis, with estimates of production to biomass (PB) ratios on the *y*-axis. To some extent, PB ratios integrate life history characteristics of growth and mortality, and it is rapidly apparent that the relative PB ratio of cephalopods in the ETP is within the distribution of PB values for many populations at comparable trophic levels, while in the California Current model the PB ratio of jumbo squid is considerably higher than populations at comparable trophic levels.

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[3] Sperm whales (*Physeter catodon*) are key predators of jumbo squid throughout their usual range (Ruiz-Cooley et al. 2006 and references therein). Rissos dolphin (*Grampus griseus*) were observed in high numbers along the central California coast in 2005, particularly by CPFV vessels targeting squid, and the stomachs of several stranded animals contained very high numbers of jumbo squid beaks (J. Harvey, Moss Landing Marine Laboratory, Moss Landing, California, pers. comm.)

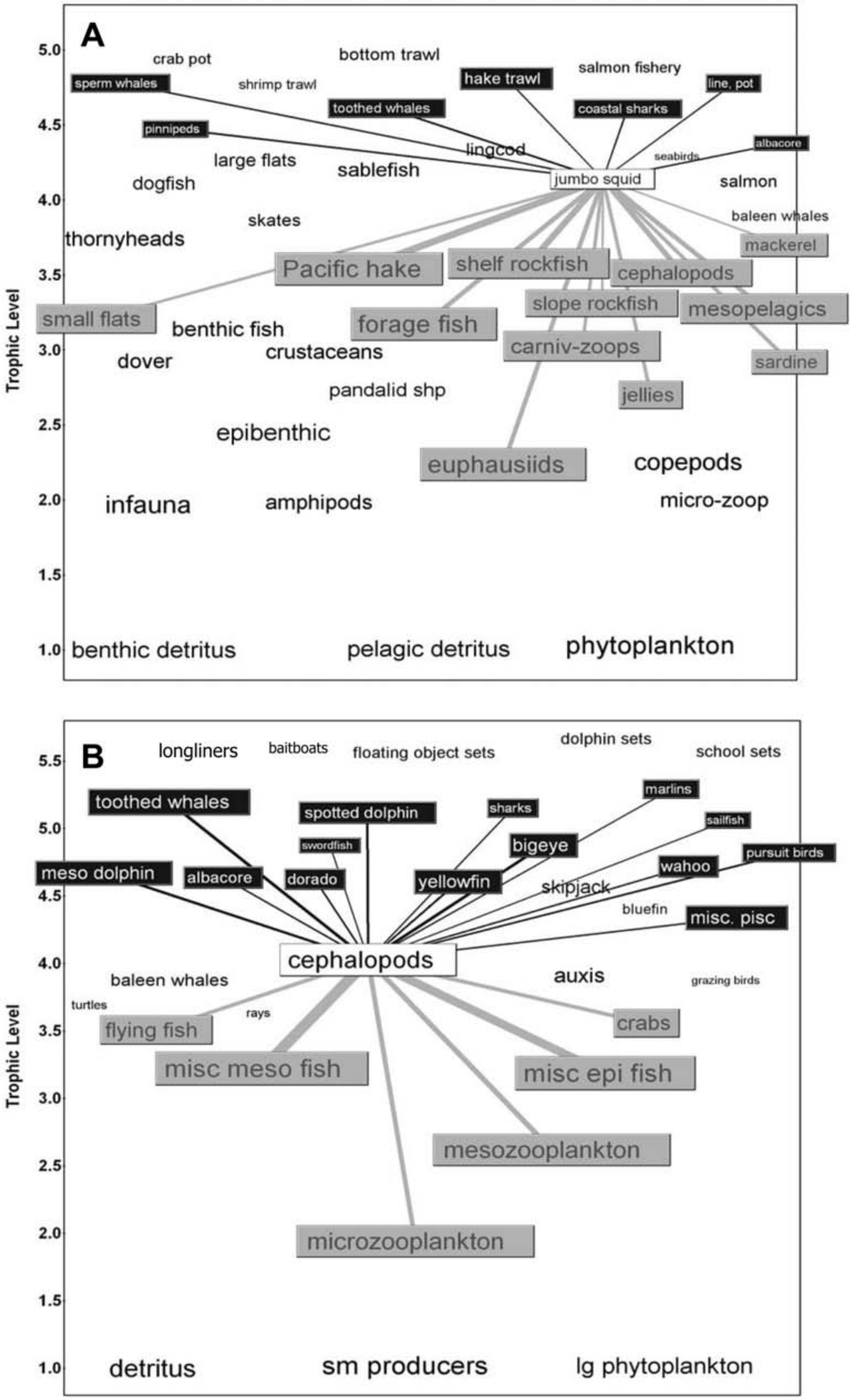

Figure 7. Food web models of the (A) Northern California Current and, (B) Eastern Tropical Pacific (ETP), with estimated trophic level along the y-axis. Jumbo squid (*Dosidicus gigas*) are in white and central (including other cephalopods in the ETP), known predators are in black, and prey items are in grey. The relative sizes of boxes are proportional to the log of their standing biomass, and the width of the lines represent relative energy flow, after Aydin et al. (2003).

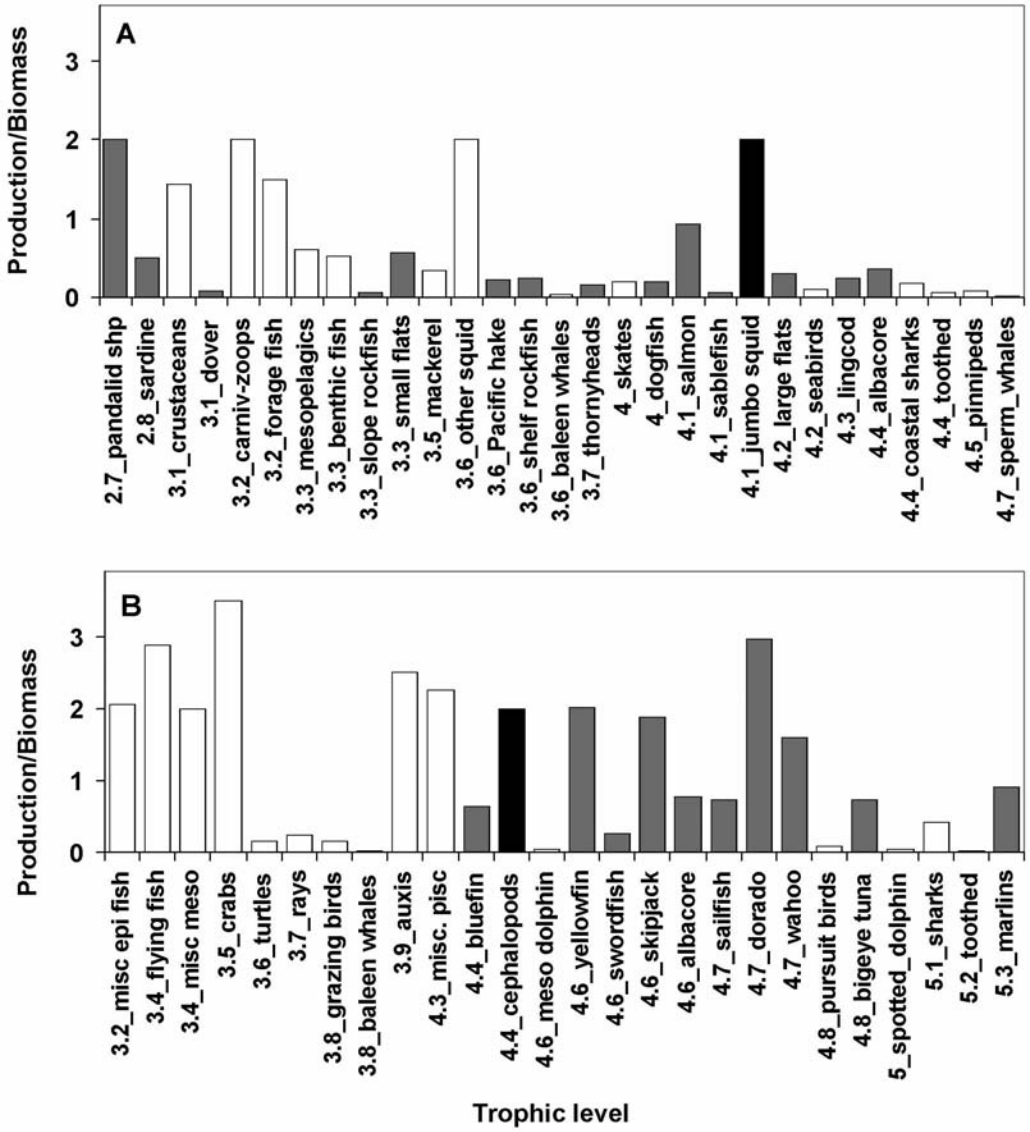

Figure 8. Production to Biomass (PB) ratio plotted against trophic level for two Pacific Ocean ecosystem models, (A) the Eastern Tropical Pacific (ETP), and (B) the Northern California Current (NCC). Jumbo squid (*Dosidicus gigas*) (modeled with other squids in the ETP, but as a single component in the NCC) are designated in black, and grey boxes symbolize ecosystem components with the significant commercial or recreational fisheries landings.

## DISCUSSION

Several studies have noted the rapid spread in the distribution and abundance of jumbo squid throughout the California Current over the past decade (Cosgrove 2005; Brodeur et al. 2006; Wing 2006), and the results shown here from recreational catches, food habits, resource surveys, and bycatch monitoring programs are highly consistent with these findings. Fishers targeting albacore (*Thunnus alalunga*) in offshore waters during late summer and fall have also reported that jumbo squid have been abundant in the tuna fishing grounds off of Washington and Oregon since at least the mid- to late-1990s. Off of central California there are similarities between the events in the mid 1930s and the 2002–06 period, with animals first showing up for several years in summer and fall months in the south, and later becoming more frequently encountered in fall and winter months over shelf break and slope habitats, particularly near canyons and offshore banks (Croker 1937). However, the extent of the northerly range expansion appears unprecedented, and raises questions about the abundance and distribution of this population in the future.

Food habits studies in general, and those for cephalopods in particular, suffer from a broad array of potential shortcomings and biases. The method of collection is clearly among these; for example, trawl gear is generally a poor method for collecting specimens, as larger squids in particular tend to attack and ingest potentially atypical prey items while trapped within the codend of the trawl (Breiby and Jobling 1985). Such behavior has also been observed in jumbo squid caught in purse seine fishing operations, with squid attacking small tunas not otherwise known to be squid prey (Olson et al. 2006). Other biases may include changes in stomach fullness associated with both the time of day and the gear used in capture, as digestion and elimination of food is rapid and hungry squid may be more likely to attack jigs than satiated animals (Markaida and Sosa-Nishizaki 2003), as well as a potential to overestimate cannibalism as described earlier. Bias may also result when heads are not consumed in larger prey, and the size and shape of otoliths may also lead to variable retention rates (Dawe et al. 1997). Perhaps more significantly, the likelihood of underestimating the importance of soft-bodied organisms relative to organisms that leave hard remains can be a major source of bias (Tanasichuk 1999; Arai et al. 2003). For example, the frequent presence of pteropod shells suggests that other gelatinous zooplankton could also be important prey items, as has been observed (albeit infrequently) for other cephalopods (Heeger et al. 1992). Despite such shortcomings, the results presented here are unique relative to food habits studies from most other areas of the range of this animal.

Previous studies have shown that while jumbo squid are opportunistic predators, the primary prey of adults are smaller pelagic and mesopelagic fishes, other cephalopods (including other jumbo squid), and pelagic crustaceans (Wormuth 1976; Nesis 1983; Ehrhardt 1991; Nigmatullin et al. 2001; Markaida and Sosa-Nishizaki 2003; Markaida 2006). Our results are limited to a relatively narrow spatial and temporal window, yet they demonstrate that jumbo squid also prey quite heavily on moderately-sized (15–45 cm) groundfish. Submersible observations of squid predation on adult Pacific hake and sablefish (*Anoplopoma fimbria*) in the waters off of Cordell Bank in September 2005 also confirm this (R. Starr, California Sea Grant, Moss Landing, California and D. Howard, Cordell Bank National Marine Sanctuary, Point Reyes, California, pers. comm.). Consequently, these results diverge from those observed throughout most of the range of this animal, where consumption of large fish is minimal, and reflect the widely held perception of jumbo squid being a highly flexible predator with the ability to rapidly adapt to new environmental conditions during range expansions (Nesis 1983; Ehrhardt 1991; Nigmatullin 2001).

Although technically considered groundfish; Pacific hake, shortbelly rockfish, Pacific sanddab (*Citharichthys sordidus*), and slender sole (*Lyopsetta exilis*) are well known to have semi-pelagic life histories (Pearcy and Hancock 1978; Bailey et al. 1982; Chess et al. 1988), indicating that even in mid-latitude coastal waters jumbo squid may retain a foraging strategy focused on pelagic prey. However, the presence of more benthic-oriented animals, such as English sole (*Parophrys vetulus*), eelpouts (*Zoarcidae* spp.), and spotted ratfish (*Hydrolagus colliei*) in squid diets does indicate some predation on bottom-oriented prey, as did the submersible observations described above. Results also suggest that larger hake and rockfish may be more frequently consumed during winter months off of central California, consistent with the migratory pattern of Pacific hake, the observation that squid caught in winter months tend to be larger, and the suggestion that larger squid have a greater tendency to feed at higher trophic levels (Ruiz-Cooley et al. 2006).

Wilhelm (1954) noted that during range expansions in the southern hemisphere in the early part of the 20th century, jumbo squid off of the central portion of the Chilean coast (a latitudinal range similar to that of California) fed on Chilean hake (*Merluccius gayi gayi*) and ling (*Genypterus* spp.), among other prey. More recently, jumbo squid have again been observed in large numbers off of the central portion of the Chilean coast, along a latitudinal range similar to that of California (Ibáñanez and Cubillos 2007). As a consequence, predation on Chilean hake by jumbo squid has been described as potentially contributing to a decline in the hake resource in that region.[4] Rodhouse and Nigmatullin (1996) suggest that cephalopod predation is an important variable affecting natural mortality and recruitment success of many fish stocks, particularly clupeids, scombrids, and gadoids in continental shelf ecosystems, and this may be particularly true where there is a strong mismatch between subtropical and temperate life history strategies (e.g., growth rate, metabolism, swimming speed). Such impacts are also subject to high interannual variation due to the short lifespans and widely variable cohort strength that characterize most large oceanic squid populations.

Although the reorganization of energy pathways in coastal ecosystems as a result of fishing has been postulated as leading to increases in high turnover of cephalopod populations (Caddy and Rodhouse 1998), the coincidence of poleward range expansions of jumbo squid in both hemispheres suggests a physically-induced forcing mechanism. Climate change has already been shown to force the range expansions of many marine species towards the poles, with animals with the greatest turnover rates showing the most rapid distributional responses to warming (Perry et al. 2005). Observed

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[4] Paya, I. Chilean Hake Stock Assessment. Institute for Fisheries Development (IFOP), 2005. Chile; H. Arancibia, Universidad de Concepción, Chile, pers. comm.

warming trends in the California Current (Mendelssohn et al. 2003; Field et al. 2006a), and the likelihood of continued warming in the future, may have facilitated the ongoing range expansion and could lead to the establishment of a permanent population or increased frequency of future incursions. However, the broad thermal tolerance of adult squid in the Gulf of California (Gilly et al. 2006) suggests that the mechanism responsible for the ongoing range expansion may not be as simplistic as changes in mean temperature alone.

Consideration of the role of jumbo squid in food web models suggests that while they tend to be predators of commercially important species in the California Current, they are principally prey to commercially important species in the ETP (figs. 7 and 8). Furthermore, the PB ratio of squid in the ETP is consistent with the distribution of PB values for many other model components in that subtropical ecosystem. By contrast, the PB ratio of jumbo squid in the California Current is anomalously high in an ecosystem that tends to be dominated by long-lived and slow-growing species at higher trophic levels. Currently there is insufficient information to estimate plausible or possible impacts on California Current food webs, due to a lack of abundance information and incomplete knowledge of how movement and food habits may differ across seasons and between inshore and offshore waters. However, that jumbo squid are opportunistic predators with high turnover rates and high consumption rates, and that among their important prey are several of the current (and historically) largest fisheries by volume along the U.S. West Coast, suggest that impacts are plausible. Such impacts could drive changes at both higher and lower trophic levels; for example Barlow and Forney (in press) show that the abundance of sperm whales (*Physeter macrocephalus*) in the California Current roughly doubled in 2001 and 2005 survey estimates, relative to those conducted in the 1990s. Future management approaches should recognize that fundamental changes in ecosystem structure and dynamics are likely to occur, particularly in the face of future global change. Quantifying trophic relationships represents an important contribution in understanding such interactions, and facilitating a rational response by managers and stakeholders.

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## APPENDIX A

**Taxonomic summary of prey, with the frequency of occurrence (FO), total number, and size (average length in cm, weight in gm, range of length and weight) where available. Broad groupings include mesopelagics (MS), coastal pelagics (CP), crustaceans (CR), rockfish (RK), pteropods (PT), cephalopods (CE), flatfish (FL), and other (OT).**

| Taxa | group | GII | %FO | %N | FO | N | length mean | range | weight mean | range |
|---|---|---|---|---|---|---|---|---|---|---|
| Arthropoda | | | | | | | | | | |
| Crustacea | | | | | | | | | | |
| Decapoda | CR | 4.4 | 4.5 | 1.8 | 19 | 26 | – | – | – | – |
| Euphausidae | CR | N/A | 9.0 | N/A | 38 | N/A | – | – | – | – |
| Mollusca | | | | | | | | | | |
| Pteropoda | | | | | | | | | | |
| *Clio* sp. cf *C. pyrimida* | PT | 7.5 | 7.8 | 2.8 | 33 | 41 | – | – | – | – |
| *Cresis* sp. | PT | 1.1 | 1.2 | 0.4 | 5 | 6 | – | – | – | – |
| *Limacina* sp. | PT | 0.4 | 0.5 | 0.1 | 2 | 2 | – | – | – | – |
| Cephalopoda | | | | | | | | | | |
| Enoploteuthidae | | | | | | | | | | |
| *Abraliopsis felis* | CE | 2.4 | 2.4 | 1.0 | 10 | 14 | 4 | 2–8 | 3 | <1–15 |
| Ommastrephidae | | | | | | | | | | |
| *Dosidicus gigas* | CE | N/A | 11.4 | N/A | 49 | N/A | – | – | – | – |
| Onchyoteuthidae | | | | | | | | | | |
| *Onychoteuthis borealijaponicus* | CE | 3.9 | 2.6 | 2.9 | 11 | 42 | 4 | 3–13 | 11 | 2–136 |
| Loliginidae | | | | | | | | | | |
| *Loligo opalescens* | CE | 3.2 | 3.1 | 1.5 | 13 | 22 | 11 | 9–15 | 23 | 14–42 |
| Gonatidae | | | | | | | | | | |
| *Gonatus onyx* | CE | 1.8 | 0.9 | 1.6 | 4 | 23 | 4 | 2–9 | 2 | <1–19 |
| *Gonatus berryi* | CE | 1.1 | 0.9 | 0.6 | 4 | 9 | 5 | 6 | 10 | 40 |
| *Gonatopsis borealis* | CE | 0.9 | 0.9 | 0.3 | 4 | 5 | – | – | – | – |
| *Gonatus* spp. | CE | 2.3 | 1.9 | 1.3 | 8 | 19 | – | – | – | – |
| Histioteuthidae | | | | | | | | | | |
| *Histioteuthis hoylei* | CE | 0.4 | 0.5 | 0.1 | 2 | 2 | 14 | 7–21 | 91 | 8–173 |
| Cranchidae | | | | | | | | | | |
| *Cranchia scabra* | CE | 0.3 | 0.2 | 0.1 | 1 | 2 | – | – | – | – |
| *Galiteuthis* sp. cf *G. phyllura* | CE | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| Chiroteuthidae | | | | | | | | | | |
| *Chiroteuthis calyx* | CE | 0.2 | 0.2 | 0.1 | 1 | 1 | 3 | – | 20 | – |
| Octopoteuthidae | | | | | | | | | | |
| *Octopoteuthis deletron* | CE | 2.4 | 2.6 | 0.8 | 11 | 11 | 10 | 4–19 | 269 | 24–792 |
| Argonautidae | | | | | | | | | | |
| *Argonauta* sp. | CE | 0.4 | 0.5 | 0.1 | 2 | 2 | – | – | – | – |
| Cephalopoda unidentified | CE | 5.9 | 6.4 | 2.0 | 27 | 29 | – | – | – | – |
| Chordata | | | | | | | | | | |
| Chondrichthyes | | | | | | | | | | |
| Chimaeridae | | | | | | | | | | |
| *Hydrolagus colliei* | OT | 0.2 | 0.2 | 0.1 | 1 | 1 | 31 | – | 1873 | – |
| Osteichthyes | | | | | | | | | | |
| Clupeidae | | | | | | | | | | |
| *Clupea pallasii* | CP | 1.3 | 1.4 | 0.4 | 6 | 6 | 18 | 16–19 | 84 | 51–106 |
| *Sardinops sagax* | CP | 9.2 | 9.7 | 3.4 | 41 | 49 | 19 | 13–23 | 54 | 16–97 |
| Engraulidae | | | | | | | | | | |
| *Engraulis mordax* | CP | 19.9 | 16.3 | 11.9 | 69 | 173 | 10 | 6–13 | 12 | 4–23 |
| Argentinidae | | | | | | | | | | |
| *Nansenia* sp. cf. *N. crassa* | MS | 0.3 | 0.2 | 0.1 | 1 | 2 | – | – | – | – |
| Bathylagidae | MS | 2.5 | 2.6 | 1.0 | 11 | 14 | – | – | – | – |
| *Bathylagus wesethi* | MS | 0.4 | 0.5 | 0.1 | 2 | 2 | – | – | – | – |
| *Bathylagus pacificus* | MS | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| *Leuroglossus stilbius* | MS | 0.6 | 0.7 | 0.2 | 3 | 3 | – | – | – | – |
| *Lipolagus ochotensis* | MS | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| Stomiidae | | | | | | | | | | |
| cf. *Tactostoma macropus* | MS | 1.0 | 0.9 | 0.4 | 4 | 6 | – | – | – | – |
| Scopelarchidae | | | | | | | | | | |
| *Benthalbella dentata* | MS | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| Paralepididae | MS | 1.9 | 2.1 | 0.6 | 9 | 9 | – | – | – | – |
| *Arctozenus risso* | MS | 1.5 | 1.2 | 0.9 | 5 | 13 | – | – | – | – |
| *Lestidiops ringens* | MS | 0.9 | 0.9 | 0.3 | 4 | 4 | – | – | – | – |
| *Magnisudis* sp. cf. *M. atlantica* | MS | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| Myctophidae | | | | | | | | | | |
| *Ceratoscopelus townsendi* | MS | 2.2 | 2.4 | 0.8 | 10 | 11 | 3 | 2–6 | 4 | <1–9 |
| *Diaphus theta* | MS | 8.3 | 6.9 | 4.9 | 29 | 71 | 4 | <1–9 | 2 | <1–11 |
| *Nannobrachium ritteri* | MS | 6.3 | 5.7 | 3.3 | 24 | 48 | 4 | 1–8 | 2 | <1–15 |

APPENDIX A (continued)
**Taxonomic summary of prey, with the frequency of occurrence (FO), total number, and size (average length in cm, weight in gm, range of length and weight) where available. Broad groupings include mesopelagics (MS), coastal pelagics (CP), crustaceans (CR), rockfish (RK), pteropods (PT), cephalopods (CE), flatfish (FL), and other (OT).**

| Taxa | group | GII | %FO | %N | FO | N | length mean | range | weight mean | range |
|---|---|---|---|---|---|---|---|---|---|---|
| *Protomyctophum crockeri* | MS | 1.0 | 0.9 | 0.4 | 4 | 6 | – | – | – | – |
| *Symbolophorus californiensis* | MS | 3.6 | 3.8 | 1.4 | 16 | 20 | 8 | 7–9 | 7 | 4–11 |
| *Stenobrachius leucopsarus* | MS | 21.5 | 20.1 | 10.3 | 85 | 150 | 6 | 2–9 | 2 | <1–5 |
| *Tarletonbeania crenularis* | MS | 15.3 | 13.5 | 8.2 | 57 | 119 | 6 | 2–8 | 4 | <1–9 |
| Merlucciidae | | | | | | | | | | |
| *Merluccius productus* | PH | 30.9 | 22.7 | 20.9 | 96 | 305 | 13 | 2–42 | 39 | <1–520 |
| Ophidiidae | | | | | | | | | | |
| *Chilara taylori* | OT | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| Zoarcidae | | | | | | | | | | |
| *Bothrocara brunneum* | OT | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| *Lycodes* sp. cf *L. pacificus* | OT | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| Batrachoididae | | | | | | | | | | |
| *Porichthys notatus* | MS | 1.0 | 0.9 | 0.4 | 4 | 6 | 15 | 9–22 | 74 | 14–168 |
| Scomberesocidae | | | | | | | | | | |
| *Cololabis saira* | CP | 0.7 | 0.7 | 0.3 | 3 | 5 | – | – | – | – |
| Melamphaidae | | | | | | | | | | |
| *Melamphaes lugubris* | MS | 0.2 | 0.2 | 0.1 | 1 | 1 | 9 | – | 3 | – |
| *Melamphaes* sp. cf. *M. lugubris* | MS | 0.6 | 0.7 | 0.2 | 3 | 3 | – | – | – | – |
| *Scopelogadus mizolepis bispinosus* | MS | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| Scorpaenidae | | | | | | | | | | |
| *Sebastes aurora* | RK | 0.9 | 0.9 | 0.3 | 4 | 4 | 21 | 13–27 | 285 | 69–471 |
| *S. jordani* | RK | 8.6 | 8.7 | 3.4 | 37 | 50 | 20 | 14–28 | 109 | 32–289 |
| *S. paucispinis* | RK | 0.2 | 0.2 | 0.1 | 1 | 1 | 13 | | 79 | |
| *S. rufus* | RK | 0.3 | 0.2 | 0.1 | 1 | 2 | 36 | 35–37 | 968 | 904–1032 |
| *S. zacentrus* | RK | 0.3 | 0.2 | 0.1 | 1 | 2 | – | – | – | – |
| *Sebastes* spp. | RK | 5.4 | 5.9 | 1.7 | 25 | 25 | – | – | – | – |
| Carangidae | | | | | | | | | | |
| *Trachurus symmetricus* | CP | 0.2 | 0.2 | 0.1 | 1 | 1 | 22 | – | 198 | – |
| Embiotocidae | | | | | | | | | | |
| *Zalembius rosaceus* | OT | 0.5 | 0.5 | 0.2 | 2 | 3 | 10 | 10–11 | 147 | 143–151 |
| Gempylidae | | | | | | | | | | |
| *Gempylus* sp. cf *G. serpens* | MS | 0.2 | 0.2 | 0.1 | 1 | 1 | – | – | – | – |
| Scombridae | | | | | | | | | | |
| *Scomber japonicus* | CP | 0.6 | 0.7 | 0.2 | 3 | 3 | 19 | | 223 | |
| Bothidae | | | | | | | | | | |
| *Citharichthys sordidus* | FL | 1.9 | 1.7 | 1.0 | 7 | 14 | 17 | 13–21 | 85 | 39–133 |
| Pleuronectidae | | | | | | | | | | |
| *Lyopsetta exilis* | FL | 1.3 | 1.4 | 0.5 | 6 | 7 | 15 | 18 | 45 | 77 |
| *Glyptocephalus zachirus* | FL | 0.2 | 0.2 | 0.1 | 1 | 1 | 25 | – | 139 | – |
| *Parophrys vetulus* | FL | 0.2 | 0.2 | 0.1 | 1 | 1 | 14 | – | 43 | – |
| Unidentified Osteichthyes | OT | 8.1 | 8.5 | 2.9 | 36 | 42 | – | – | – | – |
| Aves (bird feathers) | OT | 0.4 | 0.5 | 0.1 | 2 | 2 | – | – | – | – |

# DAILY LARVAL PRODUCTION OF PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) OFF CALIFORNIA IN 1951–2006

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## ABSTRACT

Pacific hake (*Merluccius productus*) daily larval production at hatching per 10 $m^2$ from 1951–2006 was estimated based on data collected from California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys off the California coast from San Diego to San Francisco in January–April, the peak spawning time. CalCOFI cruises covered this area prior to 1985, and have covered it during January surveys since 2003 and other non-CalCOFI surveys. For some years between 1980 and 2003, the CalCOFI survey area reached only to just north of Morro Bay. For those years, the larval production at hatching was estimated using a conversion factor to scale to the entire area. The density of daily Pacific hake larval production fluctuated with major peaks in 1986 and 1987. Minor peaks were in 1952, 1958, 1972, and 1979. The density of daily larval production has been decreasing since 1987 and was particularly low in 2003–06. The decrease of Pacific hake larval production coincided with the increase of sea temperature since the 1980s. This fishery-independent time series should benefit assessments and provide a better understanding of the dynamics of the Pacific hake population.

## INTRODUCTION

Pacific hake (*Merluccius productus*) is a migratory species occurring off the west coast of the North American continent, primarily from Baja California to British Columbia; its larvae live primarily below the mixed layer in colder water (Ahlstrom 1959). Adults migrate south off California and Baja California to spawn in the autumn and migrate north off Oregon and Washington to feed in the summer (Hollowed 1992) (fig. 1). Pacific hake larvae were observed in the first California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey in 1949, ranked first in abundance in 1951 before the northern anchovy population began to increase, and ranked second from 1955–84 before the CalCOFI survey area was reduced to the current southern California pattern from San Diego to Point Conception (Moser et al. 1993; fig. 2). Pacific hake larvae were typically collected at temperatures above 10.5°C in the upper 150 m of the water column and have been observed as far offshore as 200–250 miles (Ahlstrom 1959; 1968). It is believed that the spawning center moves north during warm years, and south in cool years between mid-Baja California and San Francisco (Ahlstrom 1968; Horn and Smith 1997).

The time series of Pacific hake larval abundance and distribution by month from 1951–84 were reported by Moser et al. (1993), and spatial and temporal distributions of larvae from 1961–86 were analyzed by Hollowed (1992). For most years from 1985 to 2002, the CalCOFI survey area has been reduced to cover the area in the Southern California Bight (CalCOFI line 93–line 77; figs. 3 and 4), called the southern area in this study. In 2002, the National Oceanic and Atmospheric Administration's (NOAA) Fishery and the Environment (FATE) research program recommended an expansion of the January survey to cover the distribution of hake larvae. Beginning in 2003, the January CalCOFI cruise was extended north to the vicinity of San Francisco (CalCOFI line 93–line 60; fig. 2). This extended area is defined as the larger area in this study and provides a link to the historical time series of Pacific hake larval abundance. Other surveys, like surveys for sardine during April, also cover the area from San Diego to San Francisco (Lo et al. 2005).

Ideally, methods such as the daily fecundity reduction (DFR) method for demersal fishes should be used to estimate spawning biomass of Pacific hake (Lo et al. 1993; Zeldis 1993; Moser et al. 1994). This method requires data on fish-egg stages, duration, and abundance, plus the reproductive output of adult fishes (MacGregor 1966; MacFarlane and Saunders 1997). Due to the high patchiness of Pacific hake eggs, the difficult identification of early stages of the eggs, and the fact that their eggs were consistently identified only in the last 10 years, it is not possible to carry out a DFR analysis over the whole 1951–2006 time period. Fortunately, Pacific hake larval data from CalCOFI surveys are readily available from 1951 and comprehensive correction algorithms can be applied to reduce the possible biases of measurement, such as extrusion through the net mesh, avoidance of the net, etc. It seems reasonable to consider the larval production of Pacific hake as a possible index of spawn-

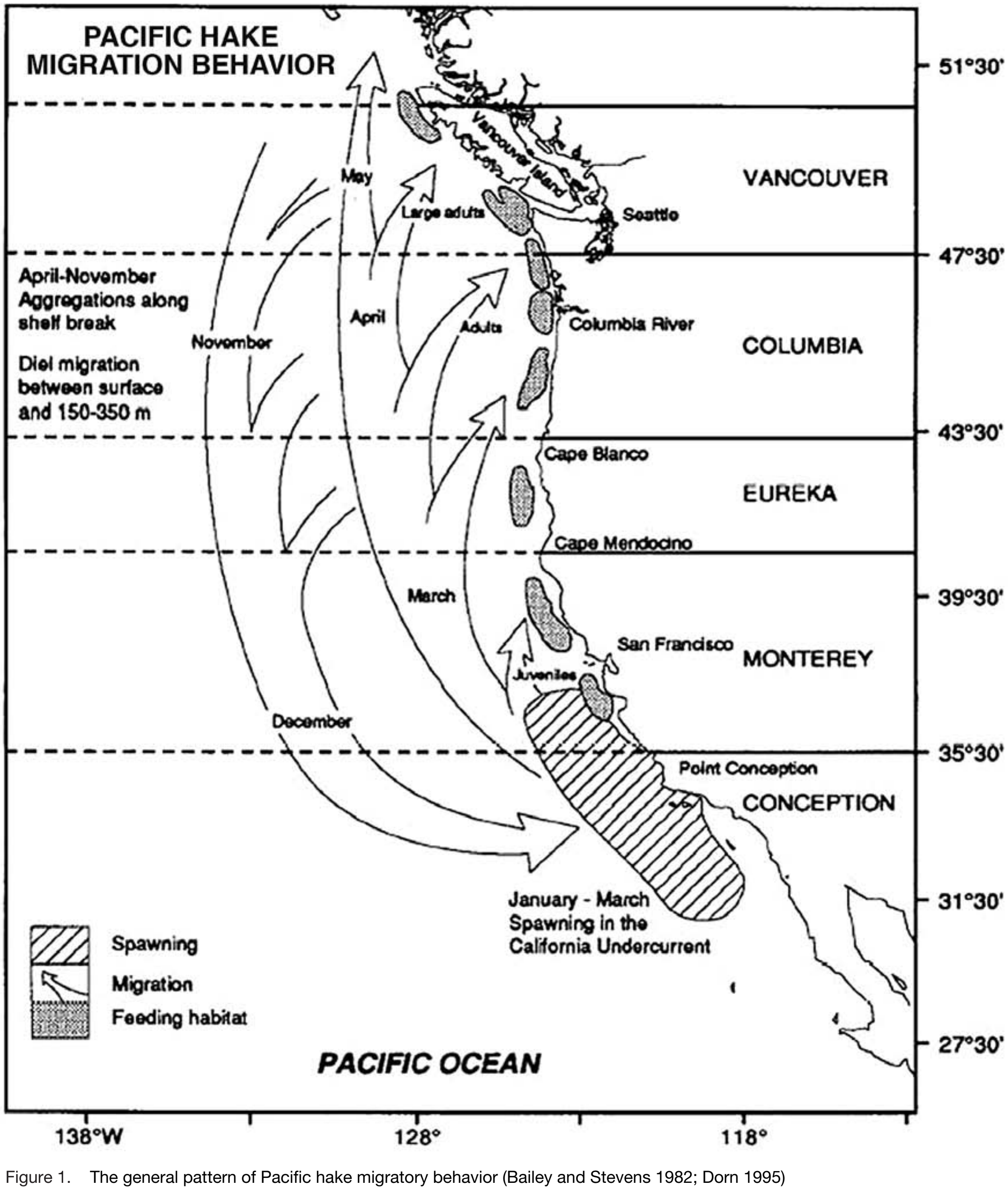

Figure 1. The general pattern of Pacific hake migratory behavior (Bailey and Stevens 1982; Dorn 1995)

ing biomass (Ahlstrom 1968) as has been done for many other fish populations (Smith 1972; Lo 1986; Lo et al. 1989). This time series can also be used to assess the role of environmental factors on the distribution and early survival rate of hake. In this paper, I analyze Pacific hake larval data from 1951–2006 for the larger area in January–April. Although this area is smaller than that of the historical CalCOFI survey (fig. 3), it encompasses the primary spawning area of Pacific hake (Moser et al. 1993) and should represent the whole Pacific hake population in most years.

## MATERIALS AND METHODS

The CalCOFI survey was conducted annually from 1949–66, after which it was conducted every three years through 1984, covering the area from Baja California to the north of San Francisco (fig. 3). Starting in 1985, the survey was conducted annually but covered only the southern area from San Diego to Avila Beach, north of Point Conception. Pacific hake is a migratory species, therefore, larval data from this southern area are not enough to assess its relative population abundance. However, in some years after 1984 various non-CalCOFI

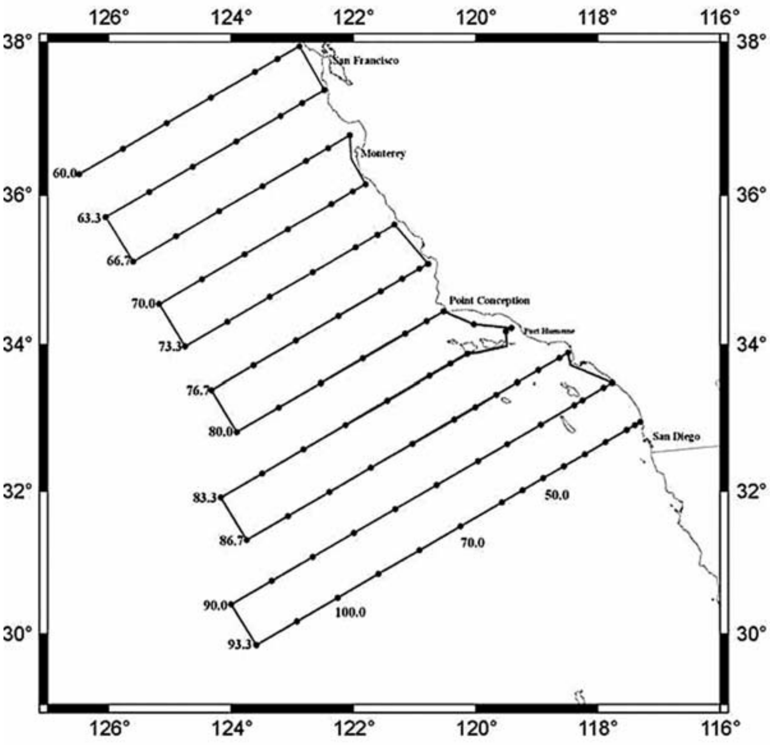

Figure 2. The larger area (CalCOFI lines 93.3–60.0) for January CalCOFI survey occupied since 2003. The southern area covers CalCOFI lines from 93.3–76.7, the regular CalCOFI Survey area since 1985. The northern area covers the path from Avila Beach to San Francisco.

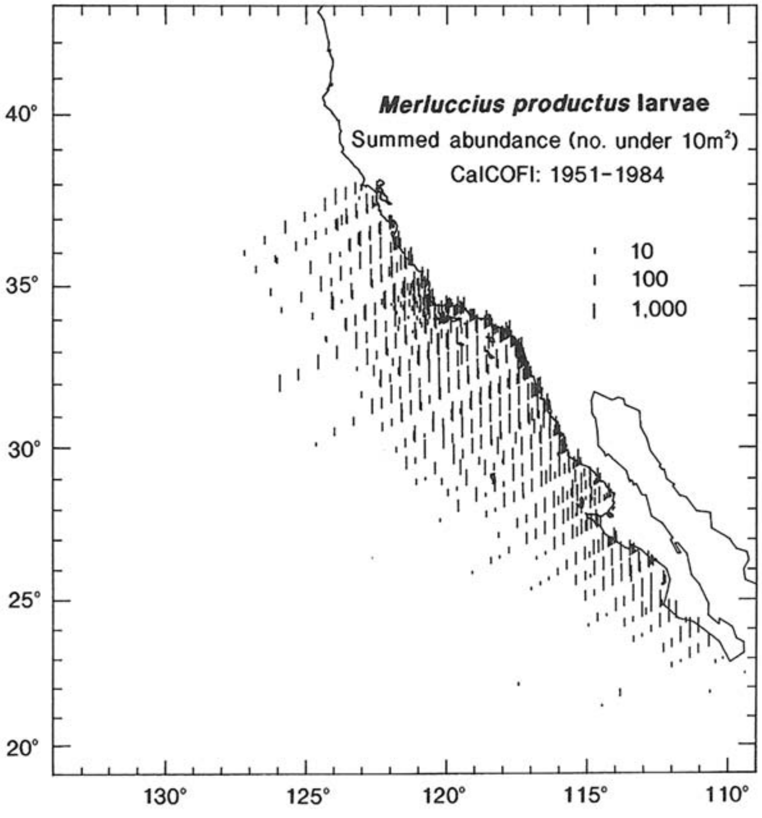

Figure 3. Pacific hake larval densities from CalCOFI surveys from 1951–84 (Moser et al. 1993).

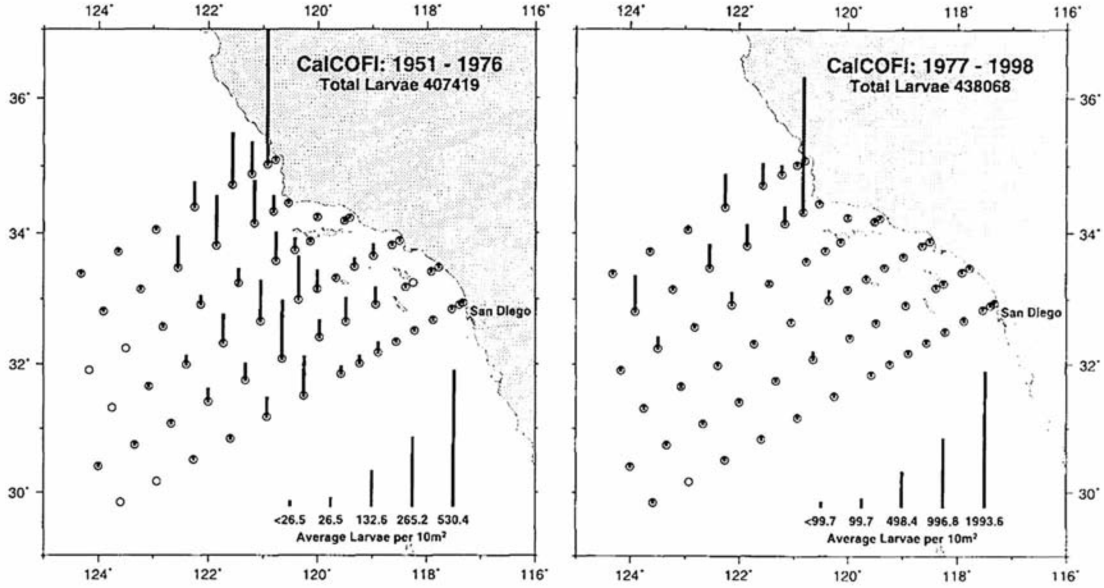

Figure 4. The mean Pacific hake larval densities in the current CalCOFI survey area from 1951–98 (Moser et al. 2001). Note the magnitudes of sticks in these two panels are different.

surveys were conducted in the area between Point Conception and San Francisco, e.g., cruises in 1987 and 1988 (Lo et al. 1993) and daily-egg-production-method anchovy or sardine surveys (Lo et al. 2005). Data from Bongo samples collected during those cruises were included in this analysis. Since 2003, the CalCOFI pattern has been expanded (figs. 2 and 5), and the survey area used in this study is this expanded area (from San Diego to San Francisco). It was reported that the spawning of Pacific hake in winter had been detected north of San Francisco between latitude 35°N–40°N in the early 1990s (Saunders and MacFarlane 1997). Therefore, the fluctuation of hake larval production in any particular area may be partially due to the expansion of the spawning area due to a regime shift, or just any recent anomalously warm temperatures.

For consistency, only January–April Pacific hake larval data from the CalCOFI database and other surveys in the same area were used in this study (Ahlstrom 1968; Moser et al. 2001). Larvae were collected by oblique tows with a 1 m ring net to 140 m from 1951–68; the depth was increased to 210 m in 1969. The 0.55 mm silk mesh net was replaced by a 0.505 mm nylon mesh net in 1969. The Bongo net replaced the 1 m ring net in 1978.

In the laboratory, samples were sorted for fish eggs and larvae. The fraction of the sample sorted depended on the amount of zooplankton: in general, if the displacement volume was less than 25 ml, the whole sample was processed. If the displacement volume was more than 25 ml, then the sample was split into 2 to 8 equal volumes for inshore stations (CalCOFI stations lower than 80) depending on the actual volume sizes. For offshore stations, the whole volume was examined regardless of zooplankton displacement volume. All fish eggs and larvae were sorted from the processed portion of each sample. For each collection, a maximum of 100 larvae of each targeted species (e.g., Pacific hake) were measured for length in 0.5 mm increments. If more than 100 larvae were sorted from the sample, the length distribution was prorated to the entire number sorted for that species.

A standard haul factor used to compute the number of larvae per 10 $m^2$ was intended to account for variability in the volume of water filtered per unit of depth (Ahlstrom 1948; Smith and Richardson 1975). Sampling biases caused by net selectivity for small larvae and gear avoidance for larger larvae were adjusted following the method of Lo (1985). Retention rates for extrusion can be expressed as functions of larval length and mesh size (Lenarz 1972; Zweifel and Smith 1981; Lo 1983), and those for avoidance can be expressed as functions of larval length and the diurnal time of capture (Hewitt and Methot 1982). All larval abundance data were adjusted to conform to the following standard condition: no extrusion, no day-night difference in avoidance, and a constant water volume filtered per unit depth. The data were then converted to daily production per 10 $m^2$ ($P_t$) by dividing the corrected total number of larvae in each length group by the duration (the number of days larvae remain within each length group). Each length category was converted to age after hatching based on growth curves reported by Bailey (1982) for young larvae and by Butler and Nishimoto (1995) for older larvae,

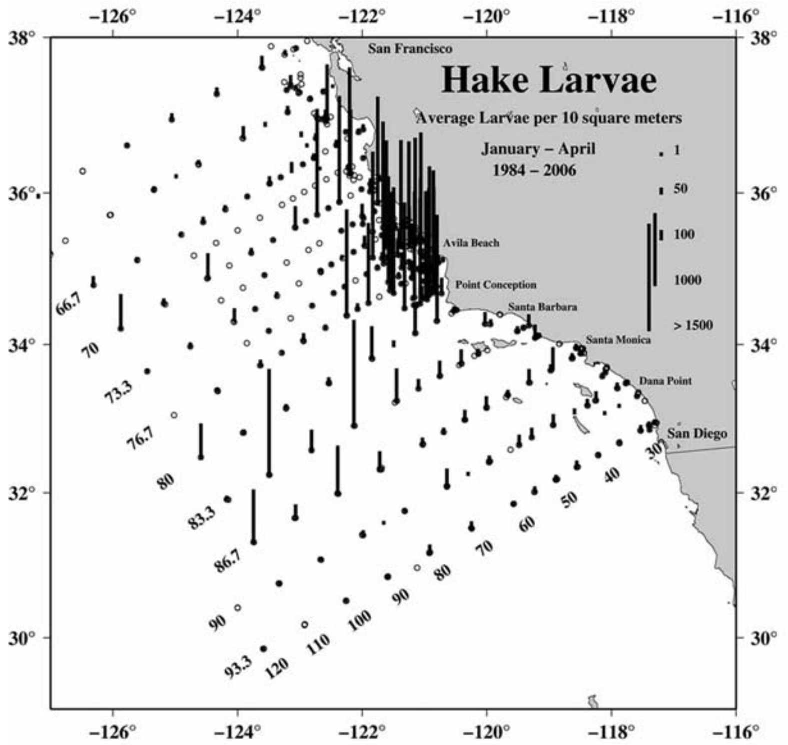

Figure 5. Pacific hake larval densities for the survey area from San Diego to San Francisco from Janurary–April, 1984, 1985, 1987, 1988, 1991, 1994, 2003–06 where the whole area was covered. For irregular stations, ata from northern area were from non-CalCOFI surveys.

after adjusting by temperature for the growth of yolk-sac larvae.

## Correction Factors

### *Extrusion*

There are no existing data on the length-specific extrusion rate for Pacific hake. Therefore, the retention coefficient of jack mackerel (*Trachurus symmetricus*) larvae due to extrusion was used as a proxy for Pacific hake. Jack mackerel larvae and Pacific hake larvae are approximately the same length at hatching and are superficially similar. Hewitt et al. (1985) reported that only the smallest size class of jack mackerel larvae (3.0 mm) was extruded to a significant degree through the 0.505 mm CalCOFI nets, with 28% of the catch in that size class retained in the net. The extrusion correction factor is equal to 1/0.28 or 3.571. The difference in extrusion of Pacific hake larvae between the 0.55 mm and 0.505 mm mesh nets is likely to be insignificant, as was the case for northern anchovy larvae (Lo 1983).

## Avoidance/Evasion

The correction factor for avoidance/evasion was estimated using the algorithm developed for northern anchovy (Lo et al. 1989). Because larvae are able to avoid or evade the net to the same degree under sufficient light to see, and larger larvae are better able to avoid the sampling gear, I used the Lo et al. (1989) model for the retention (or capture) coefficient of Pacific hake larvae for a specific larval length ($L$) and hour of the day ($h$): $R_{L,h}$:

$$R_{L,h} = \left(\frac{1+D_L}{2}\right) + \left(\frac{1-D_L}{2}\right) * \cos\left(\frac{2\pi * h}{24}\right), \qquad (1)$$

where $D_L$ is the noon/midnight catch ratio for length $L$. Data from positive tows from 1951 to 1984 in the larger area were used to model the catch ratio:

$$D_L = \frac{\bar{y}_{L,noon}}{\bar{y}_{L,night}} \qquad (2)$$

The numerator is the mean catch at noon (11:00 AM–1:00 PM) of larvae size $L$. The denominator is the mean catch in the night (9:00 PM–3:00 AM) of larval length $L$. I then used an exponential curve to model the relationship between $D_L$ and larval length, $L$.

## Shrinkage

Bailey (1982) reported on the percent shrinkage in the standard length of first-feeding larvae due to preservation and time of handling. Shrinkage was 8.9% for formalin-preserved larvae ($L$) and 3.6% for ethanol-preserved larvae ($L_e$). Because formalin is the standard

TABLE 1
**Summary of GAM for the relationship between temperature at depth and variables: line, station, month, depth and year.**

| Terms | Resid. Df | Resid..Dev | Test | Df | Deviance | F.Value | Pr.F. |
|---|---|---|---|---|---|---|---|
| s(line) + s(station) + s(year, df = 8) + s(month, df = 2) + s(depth) | 41880.99 | 5606423.59 | — | — | — | — | — |
| s(line) + s(station) + s(year, df = 8) + s(depth) | 41882.99 | 5782190.87 | -s(month, df = 2) | -1.9997 | -175767.27 | 656.62 | 0 |
| s(line) + s(station) + s(depth) | 41891.00 | 6536134.28 | -s(year, df = 8) | -8.0050 | -753943.42 | 703.57 | 0 |
| s(station) + s(depth) | 41895.00 | 8427943.31 | -s(line) | -4.0004 | -1891809.03 | 3532.68 | 0 |
| s(depth) | 41899.00 | 11384794.73 | -s(sta) | -4.0021 | -2956851.42 | 5519.17 | 0 |
| 1 | 41903 | 16652776.46 | — | -3.9988 | -5267981.73 | 9841.24 | 0 |

preservative used in regular CalCOFI surveys, a correction factor is needed to convert formalin-preserved length to ethanol-preserved length in order to apply the larval Pacific hake growth curves derived by Bailey (1982) and Butler and Nishimoto (1995). The multiplier applied to larvae from 2.5–11.5 mm from CalCOFI surveys is (1 – 0.036) / (1 – .089) = 1.058 to convert formalin-preserved length to ethanol-preserved length, i.e., $L_e = L * 1.058$ (see later section).

## Growth of Hake Larvae

*Growth curves*

In order to track the mortality curve of Pacific hake larvae, I first converted larval length to age, using the growth curve from Bailey (1982) for larvae < 3.16 mm (ethanol-preserved length):

$$L_e = 1.72 * \exp[3.15(1 - \exp(-0.02624t))], \qquad (3)$$

for $L_e < 3.16$ mm, where $t$ (days) is age from hatching and $L_e$ is the length (preserved in 80% ethanol). This equation was based on data collected in 1978–79 off the California coast (Bailey 1982).

For older larvae, I used the growth curve from Butler and Nishimoto (1995):

$$L_e = 3.16 * \exp[3.64(1 - \exp(-0.0101t))], \qquad (4)$$

for 3.16 mm < $L_e$ < 30 mm, where $t$ is age in days starting from length of 3.16 mm (preserved in 80% ethanol) or 3 mm (formalin–preserved length = 3.16 mm/1.058), near the size of yolk-sac absorption (Ahlstrom and Counts 1955). The age of a larva with length ($L_e$) = 3.16 mm would be 8.17 days after hatching, from the growth curve of Bailey (1982).

To convert length to age after hatching, I inverted the above two equations and obtained:

$$t_1 = -(1/0.02624)* \ln\{1-(1/3.15)*\ln(L*1.058/1.72)\}, \qquad (5)$$

for $L < 3$ mm and:

$$t_2 = -(1/0.0101)* \ln\{1-(1/3.64)*\ln(L*1.058/3.16)\} + t_{1|L=3}, \qquad (6)$$

for 3 mm ≤= $L$ < 28 mm, where $t$ is age after hatching and $L$ is formalin-preserved length.

### Depth Distribution of Yolk-sac Larvae and the Associated Sea Temperature

The growth of Pacific hake yolk-sac larvae ($L$ <= 3.25 mm) is temperature dependent (Bailey 1982; Zweifel and Lasker 1976). Pacific hake spawn at depths around 100 m (Ahlstrom and Counts 1955; Ahlstrom 1959; Bailey 1982; Moser et al. 1997). Estimated temperatures at the expected depth of capture in February were used in the model. Expected depth of capture was derived from a survey conducted during February 1996 in the Los Angeles Bight between 32°N–35°N and 118°W–121°W. Vertically stratified Multiple Opening/Closing Net and Environmental Sampling System (MOCNESS) samples were taken using 0.333 mm mesh nets. Based on 11 positive tows out of 25 tows, yolk-sac larvae were found between 25–100 m, with the modal depth at 50–75 m and the mean depth at 57.24 m (sd = 15 m) (Cass-Calay 2003; Cass-Calay pers. comm.). During regular CalCOFI cruises, the exact depths of yolk-sac larvae are unknown because all plankton tows are integrated tows. However, at each CalCOFI station, temperatures at depths of 20, 30, 40, 50, 75, and 100 m were recorded by hydrocast prior to 1985 and by CTD since then. I used a generalized additive model (GAM) to model the relationship of temperature and other variables: depth, CalCOFI line, station, month, and year. All factors are significant at the 5% level (tab. 1).

$$\begin{aligned} \text{Temperature} = {} & \text{s(line)} + \text{s(station)} \\ & + \text{s(depth)} + \text{s(Month, df = 2)} \\ & + \text{s(Year, df = 8)} \end{aligned} \qquad (7)$$

I estimated the depth of yolk-sac larvae collected at a station from a random number generated from a normal distribution with mean = 57.24 m and sd = 15 m. I then used the GAM to estimate the temperature that yolk-sac larvae experienced (equation 7) based on location of the tows, month (January–June), year (1951–2006), and estimated depth of yolk-sac larvae. Due to the randomly generated depths for yolk-sac larvae, the generated temperature experienced by yolk-sac larvae from each tow varies between analyses.

*Temperature-dependent growth of yolk-sac larval stage*

To account for the temperature-dependent growth of yolk-sac larvae (Lo 1983), I used the equation from Bailey (1982) for the relationship between the 50th percentile of time from fertilization to yolk-sac absorption ($H_{temp}$ in hours) and depth-dependent sea temperature experienced by yolk-sac larvae (*temp*; °C):

$$H_{temp} = 1269.52 * \exp\{-108.82 * [1 - \exp(-0.0016 * temp)]\} \quad (8)$$

Because the growth curve and age conversion from length (equation 3) were based on data collected in 1978–79 and the temperatures vary among years, I could not use equation 5 directly. Instead, I first computed the 50th percentile of time to yolk absorption for the temperature experienced by yolk-sac larvae at station $j$ (tow) for a given year $i$ ($H_{ij}$) (equation 8). I then estimated the age of yolk-sac larvae (2.5mm length group: 1.6−3.25 mm) ($t_{ij,1}$ or $t_{ij,2}$) as $t_1$ or $t_2$ (equation 5) multiplied by $H_{ij}/H_{1978-79}$, assuming that the ratio of age of yolk-sac larvae taken at any one station in any one year to that of 2.5 mm group from equation 5 ($t_{ij,1}/t_1$or $t_{ij,2}/t_2$) is equal to $H_{ij}/H_{1978-79}$ (Bailey, 1982). For yolk-sac larvae from $j$th tow in year $i$, the temperature-adjusted age will be:

$$t_{ij,1} = t_1 * (H_{ij} / H_{1978-79}), \quad (9)$$

for $L < 3$ mm and:

$$t_{ij,2} = t_2 * (H_{ij} / H_{1978-79}), \quad (10)$$

for 3 mm $<= L < 3.25$ mm, where $t_{ij,1}$ is the age of larvae before yolk-sac absorption and $t_{ij,2}$ is the age of larvae after yolk-sac absorption. Both $t_1$ and $t_2$ are ages computed from equation 5. $H_{ij}$ is the 50th percentile of age of larvae at the temperature for the $j$th tow in year $i$ (equation 8) and $H_{1978-79}$ was the 50th percentile at 12.55°C: the weighted temperature experienced by yolk-sac larvae (at mean depth of 57 m) with number of total larvae as the weight in January–April, 1978–79.

The larvae collected in each tow were grouped as 2.5 mm (up to 3.0 mm), 3.75 (3.5 and 4.0 mm), 4.75 (4.5 and 5.0 mm), etc. To obtain the final age of a larva, the actual length of a larva in each length group from each tow was generated by a random selection from a uniform distribution within each length category: for 2.5 mm, length was selected from 1.63–3.25 mm where 1.63 mm ($L$) was converted from 1.72 mm ($L_e$), the minimum length of larvae observed by Bailey (1982) (1.63 mm = 1.72 mm / 1.058). For 3.75 mm larvae, length was selected from 3.25–4.25 mm, etc.

*Size class duration and daily larval production*

The duration was estimated by the difference of the mid-ages where the mid-ages are the ages corresponding to the mid-lengths or the midpoint between two size groups. For example, the mid-length is 3.25 mm between 2.5 mm and 3.72 mm size groups. The daily larval production in each age group was the larval density in each age group divided by its duration, the time the larvae stayed in each size group.

## Daily Larval Production at Hake Hatching ($P_h$)

The daily larval production at hatching ($P_h$) was estimated for each year from a larval mortality curve, similar to that of northern anchovy (Lo 1985; 1986) from 1951–2006 when the survey encompassed the survey area from CalCOFI line 93.3–60.0 (fig. 2). Hollowed (1992) reported daily mortality rates for Pacific hake larvae of different stages and found that the Pacific hake larval mortality rate decreased with age as the larvae matured through the early (<4.25 mm), intermediate (4.25–11.25 mm), and late (11.25–15.5 mm) stages. Therefore, to construct a single mortality curve for Pacific hake larvae up to 11.75 mm, an age-dependent mortality rate, such as a Pareto function, would be more appropriate than an exponential function (Lo 1985; 1986). Larvae >11.75 mm in length were excluded because they constituted less than 5% of total larvae and their degree of evasion from the net is uncertain.

The Pareto function assumes that the instantaneous mortality rate at age $t$ from hatching ($Z_t$) is $\beta/t$. To account for the age zero of the youngest larvae, I chose the following form:

$$Z_t = \frac{\left(dP_t/dt\right)}{P_t} = \frac{\beta}{t+1} \quad (11)$$

and the mortality curve is:

$$P_t = P_h(t+1)^{-\beta}, \quad (12)$$

where $P_t$ is the daily Pacific hake larval production at $t$ days from hatching, and $\beta$ is the coefficient of instantaneous mortality rate, and is actually the instantaneous mortality rate at hatching ($Z_0$).

I fit the curve to all individual data points of $P_t$ and $t$ using a weighted nonlinear regression to estimate the $P_h$ and $\beta$ where the weight is 1/standard deviation for each 10-day interval for each age group: 0–10, 10–20. Since larvae 60 days or older typically occurred in less than 10% of the tows, the mortality curve was constructed based on larvae less than or equal to 60 days old, to avoid bias.

For other years when the CalCOFI survey covered only the southern area, the $P_h$ for the larger area was estimated from a conversion factor based on the relation-

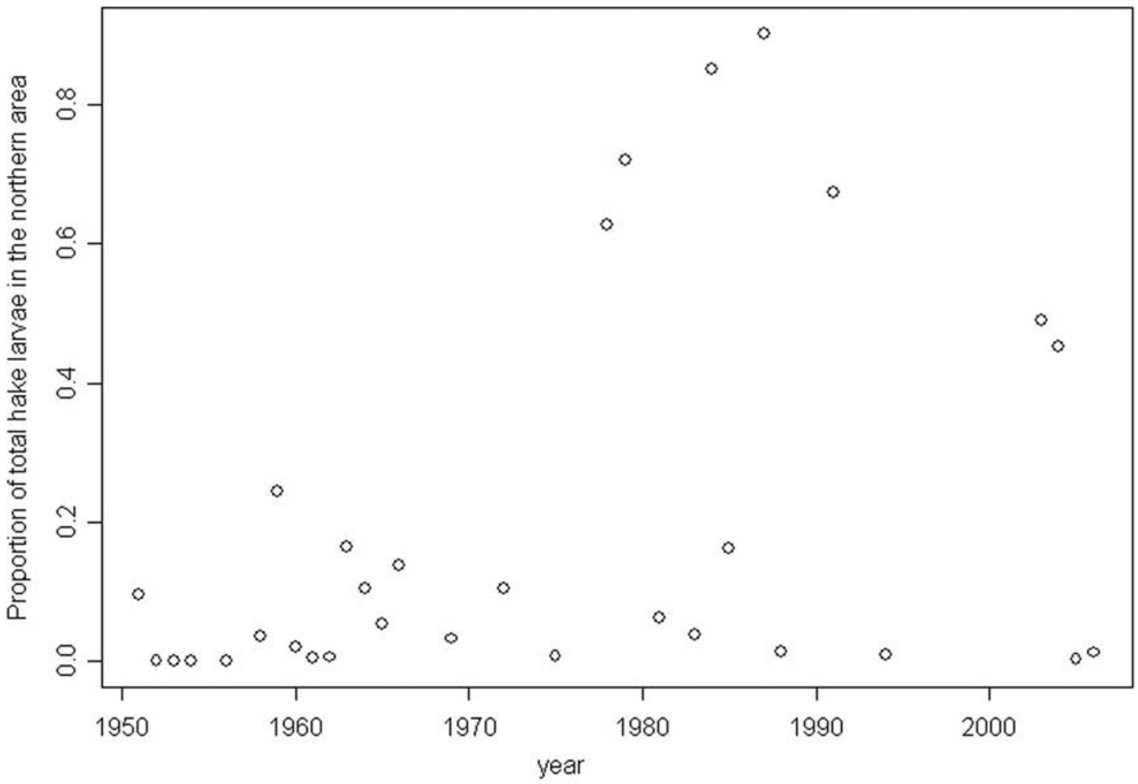

Figure 6. Percentage of Pacific hake larvae in the northern area (CalCOFI lines 76.7–60.0) from 1951–2006.

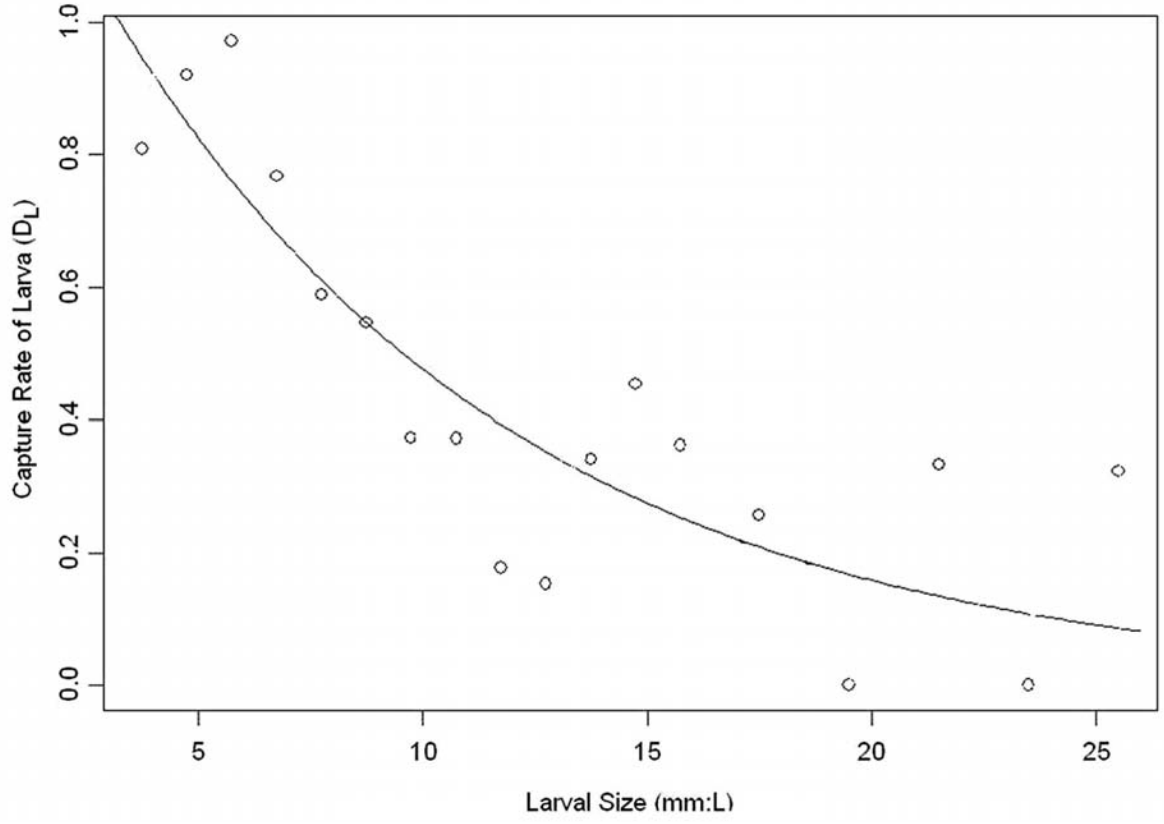

Figure 7. Capture rate of Pacific hake larvae ($D_L$) and larval length (mm), corrected for after avoidance.

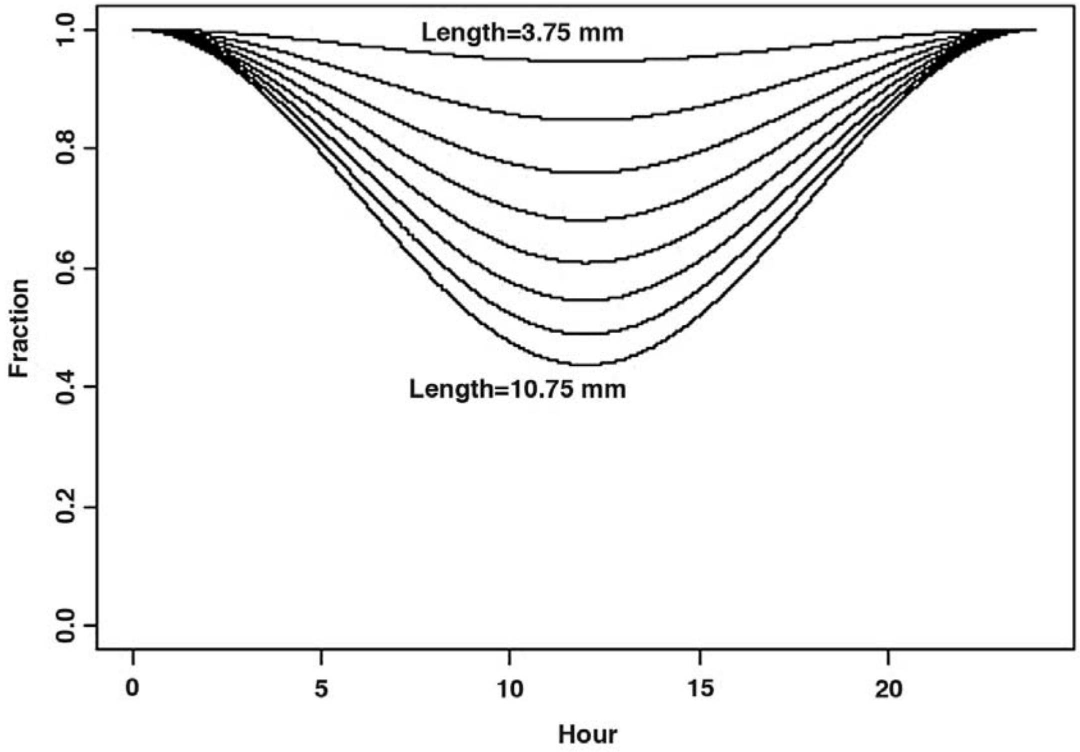

Figure 8. Fraction of Pacific hake larvae captured as a function of time of day.

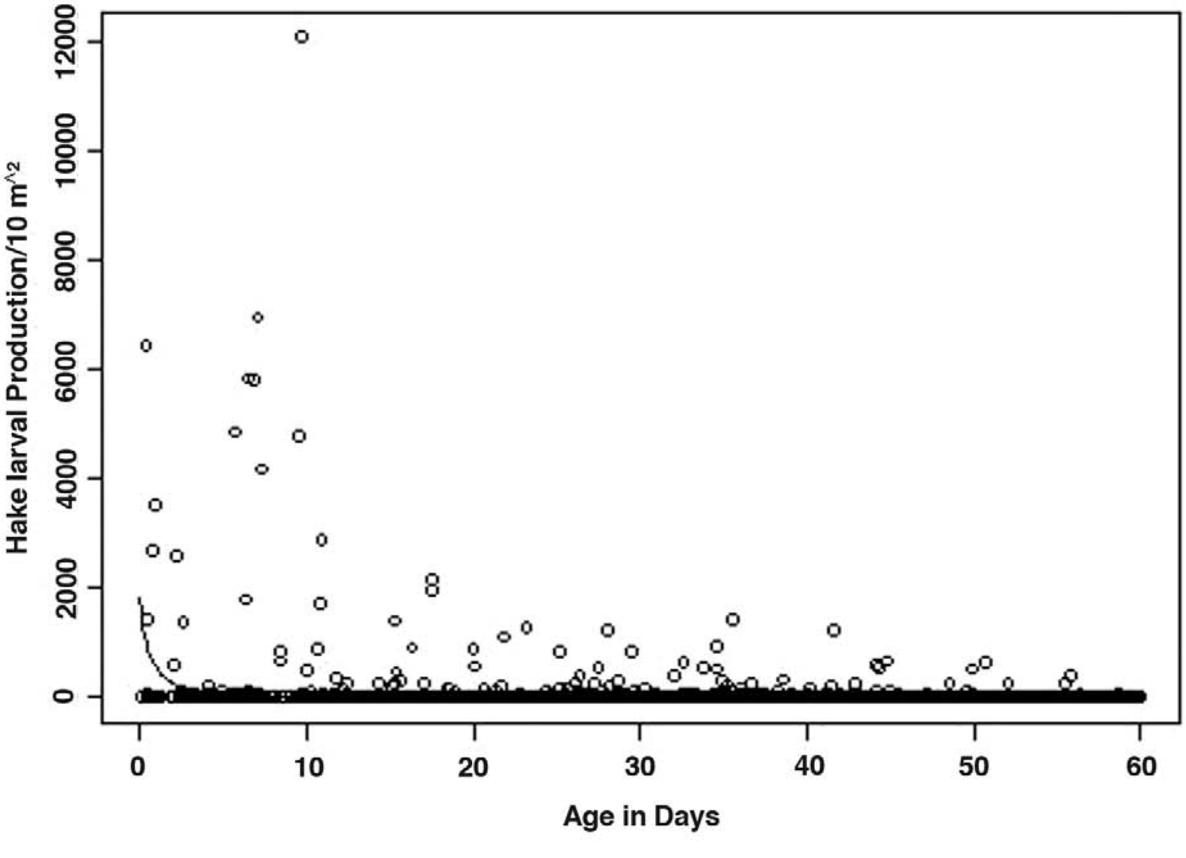

Figure 9. Daily larval production/10 m$^2$ and age with Mortality Curve ($pt = 1842\ (t+1)^{-1.17}$) in 1987.

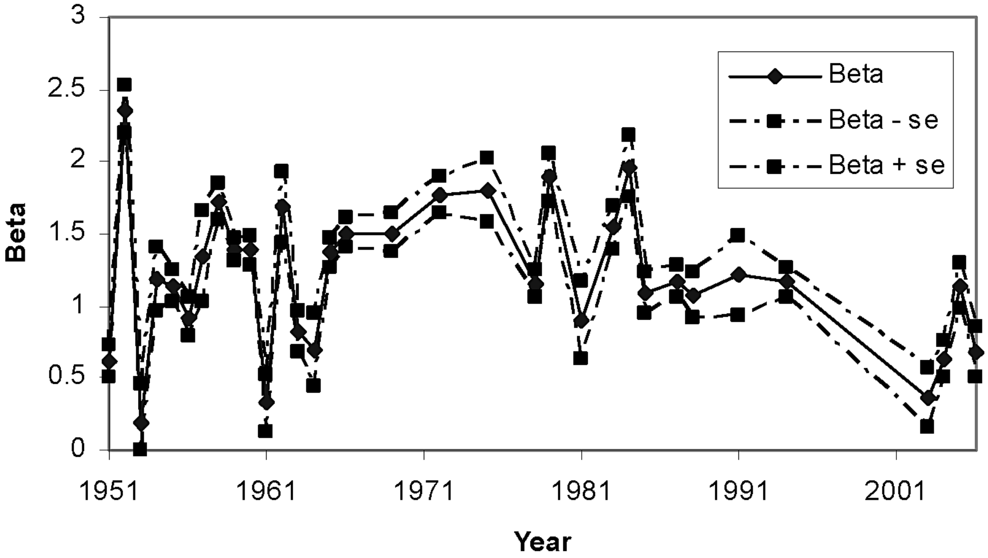

Figure 10. Time series of the estimated mortality coefficient ($\beta$ or Beta) +/– Standard error.

ship between $P_h$ of the larger area and the density of standing stock of Pacific hake larvae <11.75 mm in the southern area ($\bar{x}_s$), and the average temperature experienced by yolk-sac larvae (~57 m depth):

$$P_h = \alpha^* \bar{x}_s + \eta^* temp + \xi. \quad (13)$$

Although in some years more than 50% of Pacific hake larvae were found in the northern part of the study area, in most other years no more than 20% of larvae were found in the northern area (fig. 6). Moreover, the southern area is still the major spawning area (figs. 3 and 5).

## RESULTS

### Avoidance

The relationship between the mean noon/midnight catch ratio ($D_L$) and larval length ($L$) is:

$$D_L = 1.43\exp(-0.11L), \quad (14)$$

where the standard errors of two coefficients are 0.23 and 0.02. (fig. 7). The estimated capture rates of larvae by length and time of day (equation 1) are shown in Figure 8.

### *Mortality curves*

Mortality curves were constructed for each year the larger CalCOFI area was surveyed. The mortality curve and larval production with age for 1987 are provided in Figure 9. As mentioned earlier, the mortality of Pacific hake larvae is age dependent (equation 11) and the mortality coefficient, $\beta$, is also the daily instantaneous mortality rate of newly hatched larvae. The time series of $\beta$ fluctuated through the years with peaks in 1952, 1958, 1972, and 1979 (fig. 10, tab. 2). I also computed the mean instantaneous mortality rates for larvae <4.25 mm (Appendix) corresponding to the early larval category of Hollowed (1992). Mortality rates ranged from 0.03 in 1953 to 0.99 in 1984 (tab. 2).

### *Daily larval production*

For years when the CalCOFI surveys covered the larger area, the estimates of the daily larval production per 10 m$^2$ were the intercepts of the mortality curves (equation 12) (tab. 2). A comparison of the residual errors of the exponential and Pareto functions fit to observations shows that the Pareto function fit data better than the exponential function. For other years when the CalCOFI survey covered only the southern area from CalCOFI lines 76.7 through 93.3, the larval production of the larger area ($P_h$) was estimated from the mean number of larvae/10 m$^2$ in the southern area ($x$) in January–April (fig. 11), plus the error term ($\xi$). The temperature effect was insignificant and was excluded:

$$P_h = 0.3613^*\bar{x}_s+\xi, \quad (15)$$

where $P_h$ is the larval production at hatching in the larger area, and $x_s$ is the mean larvae/10 m$^2$ in the southern area for years when the survey covered the area from San Diego to San Francisco (tab. 2) with the coefficient 0.3613 (se = 0.0232). The variances of the residual ($\xi$) around the regression increase with the mean abundance of Pacific hake larvae. The standard deviations for the residuals in three intervals with two breakpoints of larval abundance in the southern area (50 and 600/10 m$^2$) were 2.99, 62.13, and 205.37 respectively. The error term was generated from the normal distribution, each

TABLE 2
**hake larval production at hatch ($P_h$), the mortality coefficient ($\beta$) and their standard errors (SE), total number of tows ($n$), positive tows ($n_p$), and mean temperatures experienced by yolk-sac larvae and sea surface. For years when only southern area was surveyed where $P_h$ was computed from equation 15 and no $\beta$ was estimated.**

| Year | $P_h$ | $\beta$ | Average Mortality for larvae <4.25 mm | SE($P_h$) | SE ($\beta$) | $n$ | $n_p$ | Mean Denisty (/10m²) for larvae of length <=11.75 mm | Mean Temp for ys larvae (˚C) | Wted. Temp for ys larvae (˚C) | Mean Sea surface Temp (˚c) | Mean Sea Surface Wted. Temp. (˚c) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1951 | 4.83 | 0.61 | 0.143 | 1.74 | 0.11 | 161 | 83 | 75.56 | 12.02 | 11.76 | 13.91 | 14.09 |
| 1952 | 450.36 | 2.36 | 1.334 | 271.11 | 0.17 | 134 | 72 | 625.04 | 11.91 | 12.3 | 13.41 | 13.97 |
| 1953 | 0.41 | 0.2 | 0.032 | 0.38 | 0.26 | 185 | 65 | s107.98 | 11.67 | 11.18 | 13.13 | 13.37 |
| 1954 | 5.34 | 1.18 | 0.401 | 3.78 | 0.22 | 189 | 89 | 41.3 | 11.72 | 12.87 | 13.80 | 14.37 |
| 1955 | 16.57 | 1.14 | 0.378 | 6.65 | 0.11 | 108 | 73 | 80.95 | 12 | 12.34 | 13.76 | 13.44 |
| 1956 | 1.67 | 0.92 | 0.263 | 0.76 | 0.13 | 157 | 56 | 18.82 | 11.94 | 13.17 | 12.72 | 13.49 |
| 1957 | 41.86 | 1.34 | 0.509 | 51.03 | 0.32 | 110 | 74 | 391.96 | 12.34 | 12.38 | 14.26 | 14.53 |
| 1958 | 201.34 | 1.73 | 0.79 | 95.81 | 0.13 | 219 | 171 | 448.33 | 12.19 | 12.12 | 14.68 | 14.51 |
| 1959 | 50.1 | 1.39 | 0.541 | 14.3 | 0.08 | 253 | 164 | 144.3 | 12.37 | 11.78 | 14.91 | 14.41 |
| 1960 | 25.89 | 1.39 | 0.539 | 9.64 | 0.1 | 301 | 176 | 88.46 | 12.4 | 12.73 | 13.88 | 14.17 |
| 1961 | 0.55 | 0.32 | 0.063 | 0.4 | 0.2 | 160 | 69 | 58.17 | 12.36 | 12.27 | 13.66 | 14.23 |
| 1962 | 66.9 | 1.68 | 0.759 | 56.92 | 0.25 | 150 | 90 | 229.06 | 12.43 | 12.3 | 13.14 | 13.70 |
| 1963 | 4.33 | 0.82 | 0.223 | 2.05 | 0.14 | 187 | 104 | 40.23 | 12.14 | 11.98 | 13.46 | 13.69 |
| 1964 | 1.83 | 0.69 | 0.168 | 1.67 | 0.26 | 283 | 174 | 63.26 | 11.8 | 12.91 | 14.22 | 14.85 |
| 1965 | 28.97 | 1.37 | 0.52 | 10.49 | 0.1 | 204 | 119 | 106.59 | 11.87 | 12.16 | 13.58 | 13.24 |
| 1966 | 214.57 | 1.51 | 0.616 | 79.06 | 0.1 | 215 | 166 | 752.39 | 11.89 | 12.08 | 13.60 | 13.33 |
| 1969 | 125.71 | 1.51 | 0.615 | 63.37 | 0.13 | 288 | 192 | 373.7 | 11.78 | 11.72 | 13.58 | 13.68 |
| 1972 | 250.5 | 1.77 | 0.817 | 116.85 | 0.13 | 323 | 179 | 625.03 | 11.52 | 11.38 | 12.64 | 12.97 |
| 1975 | 137.83 | 1.8 | 0.843 | 109.85 | 0.22 | 271 | 140 | 542.63 | 11.78 | 12.6 | 12.38 | 12.91 |
| 1978 | 36.24 | 1.15 | 0.394 | 12.35 | 0.1 | 288 | 153 | 190.58 | 12.38 | 12.1 | 14.85 | 14.34 |
| 1979 | 303.78 | 1.89 | 0.912 | 7.83 | 0.17 | 249 | 170 | 721.26 | 12.53 | 12.76 | 13.45 | 12.56 |
| 1980 | 130.815 | — | — | 95.89 | — | 116 | 80 | 96.72 | 12.92 | 12.44 | 14.54 | 14.57 |
| 1981 | 9.2 | 0.9 | 0.264 | 8.82 | 0.27 | 316 | 151 | 120.93 | 12.53 | 13.03 | 14.27 | 14.65 |
| 1982 | 1.45292 | — | — | 16.70 | — | 102 | 31 | 50.14 | 13.08 | 12.87 | 13.56 | 13.20 |
| 1983 | 11.1588 | 1.54 | 0.638 | 5.47 | 0.15 | 137 | 46 | 33.87 | 12.66 | 12.6 | 14.97 | 15.23 |
| 1984 | 138.45 | 1.96 | 0.989 | 111.61 | 0.22 | 280 | 85 | 282.17 | 12.66 | 12.21 | 14.36 | 13.69 |
| 1985 | 39.12 | 1.09 | 0.352 | 19.73 | 0.14 | 201 | 93 | 194.95 | 12.78 | 12.58 | 13.59 | 12.68 |
| 1986 | 1082.13 | — | — | 97.72 | — | 168 | 69 | 3173.01 | 12.83 | 11.57 | 14.92 | 13.97 |
| 1987 | 1842.39 | 1.17 | 0.4 | 690.03 | 0.11 | 126 | 90 | 16445.87 | 12.15 | 11.71 | 14.15 | 13.64 |
| 1988 | 131.14 | 1.07 | 0.349 | 77.50 | 0.16 | 136 | 92 | 644.72 | 12.35 | 12.72 | 13.53 | 12.92 |
| 1989 | 93.78 | — | — | 32.66 | — | 127 | 66 | 347.2 | 12.91 | 12.14 | 14.22 | 12.31 |
| 1990 | 64.01 | — | — | 38.59 | — | 107 | 56 | 70.44 | 12.7 | 12.24 | 14.45 | 13.35 |
| 1991 | 34.37 | 1.21 | 0.43 | 34.78 | 0.28 | 202 | 109 | 202 | 12.59 | 12.7 | 13.91 | 13.72 |
| 1993 | 154.47 | — | — | 132.53 | — | 132 | 47 | 60.76 | 13.31 | 12.62 | 15.23 | 14.41 |
| 1994 | 17.69 | 1.16 | 0.41 | 6.69 | 0.11 | 174 | 95 | 87.78 | 13.04 | 12.56 | 14.99 | 14.85 |
| 1995 | 62.25 | — | — | 16.54 | — | 119 | 49 | 215.97 | 13.43 | 13.59 | 15.01 | 15.20 |
| 1996 | 114.75 | — | — | 52.17 | — | 123 | 55 | 173.64 | 13.44 | 12.2 | 15.73 | 14.48 |
| 1997 | 74.64 | — | — | 6.55 | — | 129 | 63 | 218.15 | 13.42 | 12.22 | 15.04 | 13.56 |
| 1998 | 5.83 | — | — | 2.59 | — | 139 | 34 | 9.01 | 13.37 | 12.28 | 15.72 | 14.15 |
| 1999 | 6.98 | — | — | 0.61 | — | 126 | 48 | 18.11 | 13.11 | 13 | 13.57 | 13.02 |
| 2000 | 8.02 | — | — | 2.24 | — | 132 | 58 | 28.16 | 13.07 | 12.81 | 14.58 | 14.66 |
| 2001 | 9.11 | — | — | 1.99 | — | 128 | 54 | 19.84 | 13 | 12.08 | 14.12 | 13.34 |
| 2002 | 120.04 | — | — | 14.70 | — | 193 | 149 | 365.49 | 12.77 | 12.79 | 13.89 | 13.41 |
| 2003 | 0.21 | 0.37 | 0.074 | 0.15 | 0.21 | 256 | 61 | 4.82 | 12.45 | 12.23 | 14.62 | 14.62 |
| 2004 | 1.47 | 0.63 | 0.154 | 0.62 | 0.13 | 282 | 63 | 16.94 | 12.45 | 11.64 | 14.33 | 12.95 |
| 2005 | 1.97 | 1.13 | 0.379 | 1.09 | 0.16 | 338 | 54 | 18.52 | 12.25 | 11.93 | 14.60 | 14.65 |
| 2006 | 0.74 | 0.68 | 0.163 | 0.45 | 0.18 | 181 | 48 | 18.201 | 12.4 | 11.97 | 14.17 | 13.83 |

with mean zero and the associated variance: $N(0, 2.99^2)$, $N(0, 62.13^2)$, and $N(0, 205.37^2)$ respectively.

The time series of daily larval production ($P_h$/10 m²) from 1951–2006 off the California coast from San Diego to San Francisco fluctuated with the highest peak of 1842 larvae/day/10 m² in 1987 and minor peaks in 1952, 1958, 1966, 1972, and 1979 (tab. 2 and fig. 12). The larval production has been declining with moderate fluctuations since 1987 in this survey area. The mean water temperature experienced by yolk-sac larvae (~57 m depth) tended to increase from the mid-1970s to the mid-1990s and to decrease since the mid-1990's, while the sea surface temperature was more or less stable prior to 1980 and tended to increase through 2002. Both sets of temperatures have declined since 2003 (fig. 13). The larval production seems to be more related to the mean

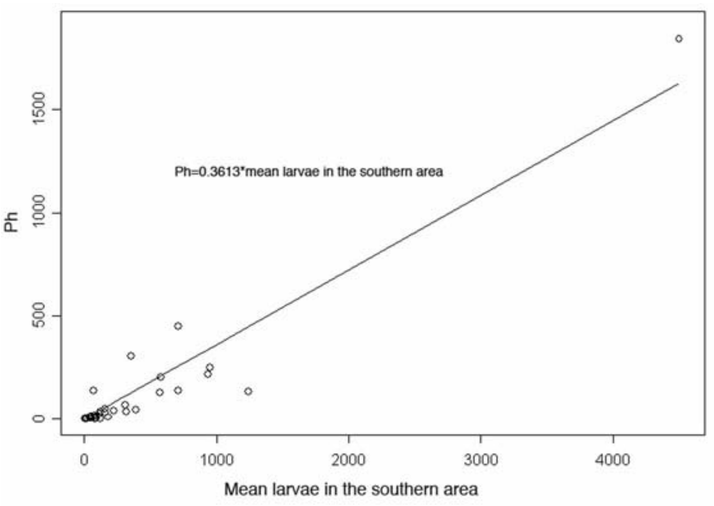

Figure 11. The relationship between $P_h$ and the mean larval abundance in the southern area for years when the larger area was covered.

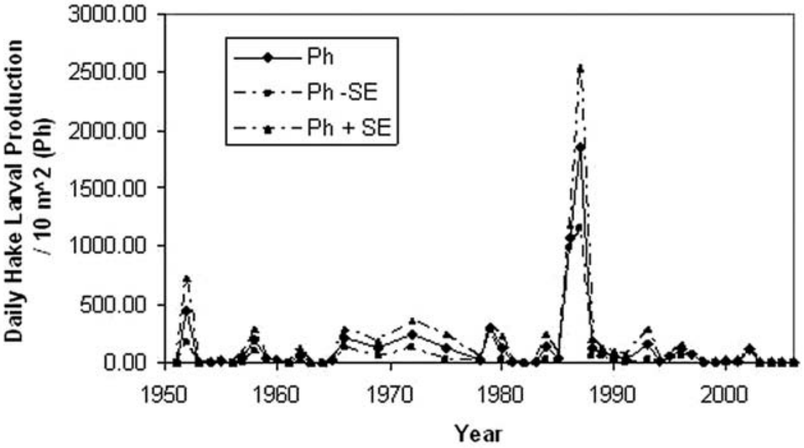

Figure 12. Pacific hake larval production/10 m² in the area from San Diego to San Francisco, in January–April from 1951–2006.

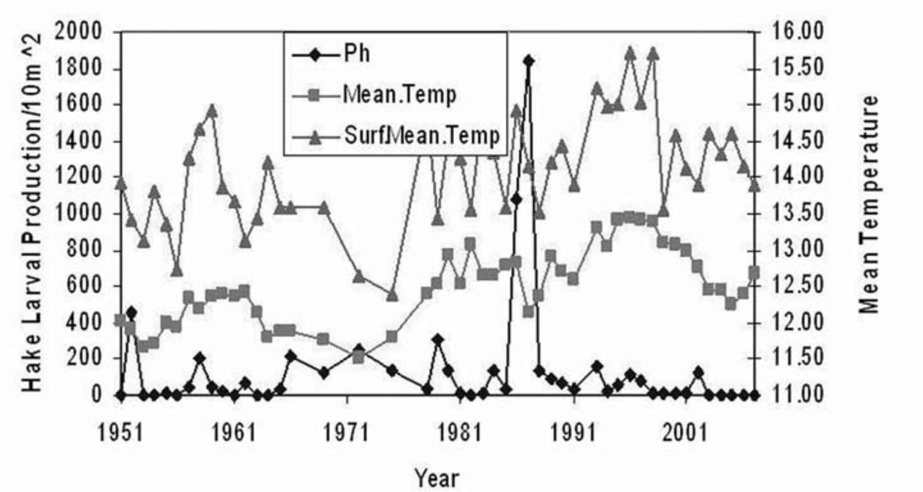

Figure 13. Pacific hake production/10 m² (diamond) and mean temperature experienced by yolk-sac larvae—57 m depth (square) and mean sea surface temperature (triangle) from 1951–2006.

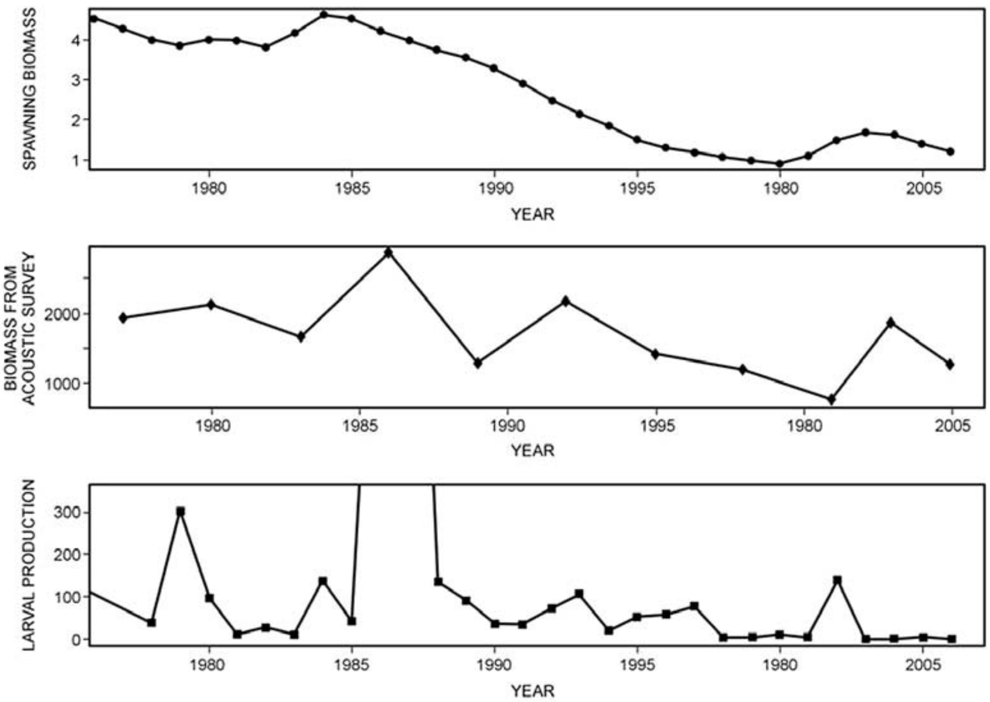

Figure 14. Time series of estimates of the spawning biomass (in million mt) from the stock assessment, biomass from the acoustic triennial survey (in thousand mt) and the larval production/10 m$^2$ for years from 1977–2006.

temperature experienced by yolk-sac larvae (~57 m depth temperature) than the sea surface temperature, with correlations of –0.26 and –0.17, respectively, although these correlations are not statistically significant. However, many of the peaks of larval production coincided with the low points of 57 m depth temperatures (tab. 2). The high larval production off central and southern California may be related to the migration of Pacific hake to California waters when the water temperature decreases (fig. 13).

## DISCUSSION

This analysis provides estimates of larval production of Pacific hake from 1951–2006 for the area covered by CalCOFI lines 93.3 through 60.0 (figs. 2 and 3), an area considered favorable to the survival of the larvae (Hollowed 1992) and which has been the major spawning ground. Pacific hake larval production should be updated each year and can be used to assess the Pacific hake population because: (1) samples were collected from a broader survey area than acoustic surveys covered (Helser[1]) as indicated by the observation of larvae offshore, although spawning is expected to be near-shore in most years; (2) this dataset requires nominal extra cost to process because data are readily available for every year compared to triennial data from the acoustic-trawl survey; and (3) the larval time series is consistent with the biomass estimates from the triennial acoustic-trawl survey with a simple correlation of 0.76, significant at the 5% level ($t = 3.17$; Zar 1984) and a Spearman correlation of 0.3 based on 9 years of data (Helser[1]) (fig. 14). The high peaks in 1986 for both time series indicate that Pacific hake in that year were productive. Yet, the triennial survey missed the high peak of larval production in 1987.

The estimates of $P_h$ for years when only the southern area was sampled (tab. 2) were computed from a simple linear regression: mean densities of Pacific hake larvae in the southern area plus the error term (equation 15). Estimates may be biased for years with extreme temperatures. The mean temperature experienced by yolk-sac larvae (at ~ 57 m depth) in the southern area was included in the original analysis. However, the temperature effect was not statistically significant and was therefore excluded in the final equation (equation 15). If the temperature coefficient had been kept in the equation, it would have a minus sign indicating an inverse relationship between $P_h$ in the survey area and temperature, a possible signor for the northern shift of the spawning center during warm years (fig. 6). More data are needed to verify the environmental effect on the migration of the Pacific hake population, and thus, the spatial distribution of its larvae.

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[1] Helser, T.E, I.J. Stewart, G. W. Fleischer, and S. Martell 2006. Stock Assessment of Pacific Hake (Whiting) in U.S. and Canadian Waters in 2006. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR 97201. http://www.pcouncil.org/groundfish/gfsafe0406/2006_hake_assessment_FINAL_ENTIRE.pdf

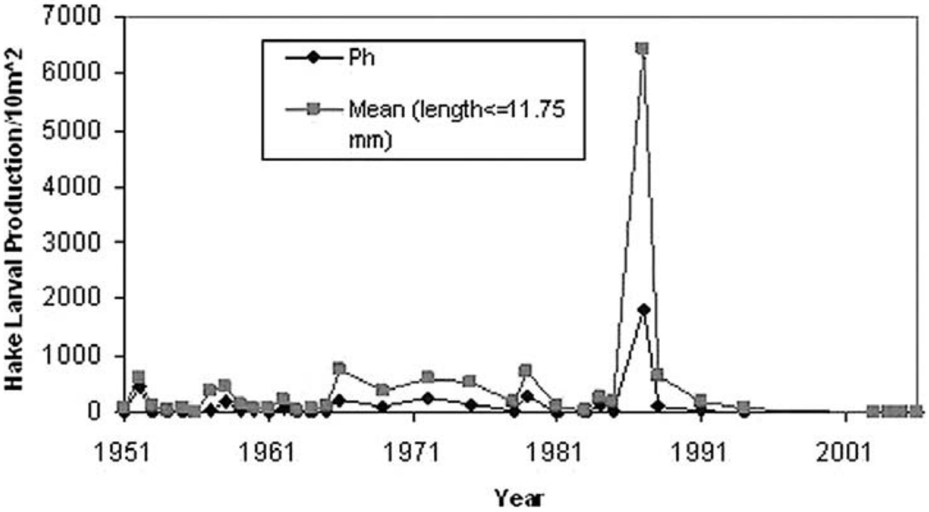

Figure 15. The time series of larval production at hatching ($P_h$) and the mean number of Pacific hake larvae/10 m$^2$ in the area from San Diego to San Francisco in 1951–2006. Gaps are years when only the southern area was surveyed.

For comparative purposes, I computed the mean counts of larvae <11.75 mm in length per 10 m$^2$ corrected for biases and the larval production ($P_h$). The time series of $P_h$ and mean counts of larvae for years when the survey covered the area from San Diego to San Francisco had similar trends but the time series of simple means was more variable than that of $P_h$ (fig. 15). Nevertheless, the fluctuations in the time series of Pacific hake larvae are partially due to Pacific hake being one of the most patchy pelagic species in the CalCOFI time series. The patches can be very large and dense (Horne and Smith 1997), persisting much longer in the depth range of highest larval abundance than in the mixed layer (Butler and Nishimoto 1997). On the other hand, the peaks in larval production tend to coincide with the biomass estimates from acoustic-trawl surveys (fig. 14).

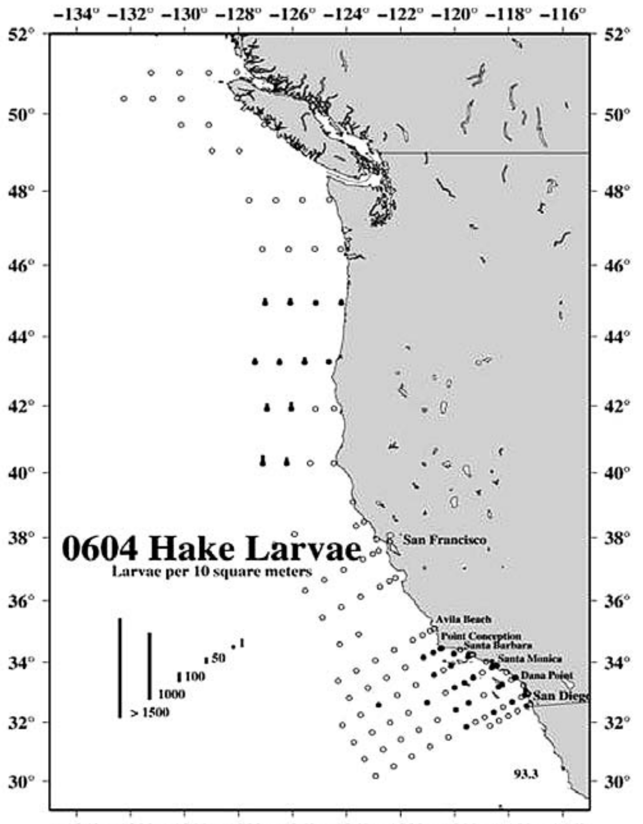

Figure 16. Pacific hake larvae density from the daily egg production method sardine coast wide survey in April–May, 2006

Analyses in this study were based on larval abundance corrected for all likely sources of bias. The extrusion factor was based on jack mackerel larval data, therefore I recommend obtaining direct measurements and verifying if the extrusion factor based on jack mackerel larvae is reasonable to use future surveys on Pacific hake larvae. The avoidance correction factor was based on 1951–1984 data, but I do not foresee a great difference if data from later years were to be included in the analysis. The cosine function was used to model the catchability by larval length. Methods like GAM can be considered in the future to model the length-related catchability, in particular to capture the catchability during the dawn and dusk periods (Watanabe and Lo 1989). Much of the effort was made on modeling the temperature-dependent growth of yolk-sac larvae because yolk-sac larvae are the stage closest to the newly hatched larvae. The effects of temperature on the yolk-sac larvae were modeled on the relationship between the 50th percentile for the time from fertilization to yolk-sac absorption and temperature (equations 8 and 9). Ideally, laboratory experiments on the growth of yolk-sac larvae at different temperatures should be conducted so that a temperature-dependent growth curve of yolk-sac larvae can be derived directly from laboratory experimental data, as was done for northern anchovy (Lo 1983).

As age was derived from growth curves reported in the literature (Bailey 1982; Butler and Nishimoto 1997), the errors associated with growth curves were not readily available and thus were not incorporated in the variance of the final estimates of $P_h$. As a result, the variances of the estimates of $P_h$ may be underestimated and the degree of this underestimation is unknown. It would be worthwhile to verify the applicability of any current data on the growth of Pacific hake larvae in early life stages to growth curves reported in the literature. The final estimates of larval production vary for each computation due to the randomly generated depth of yolk-sac larvae based on a mean depth of 57 m and a standard deviation of 15 m.

Hollowed (1992) computed the mortality rates for larvae that were less than 4.25 mm in length to be 0.23–0.41 for 1966–84. For comparison purposes, the mean instantaneous mortality rates for larvae less than 4.25 mm in length (Appendix) were computed (tab. 2). Estimates from this study ranged from 0.26–0.98 for 1966–84. The difference in the estimates of mortality rates between this study and that of Hollowed may be due to the theoretical mortality curves used; Hollowed (1992) used an exponential curve and I used a Pareto curve. Hollowed's estimates were based on 14°C whereas I used the temperatures found around 57 m depth, which were lower than 14°C (tab. 2).

The spawning center of Pacific hake is believed to move to the north during warm years and to the south during colder years in the area between CalCOFI lines 60.0 and 136.7 (roughly Point Reyes, California, to somewhat north of Cabo San Lazaro, Baja California Sur, Mexico) based on data of larval abundance and temperature at 100 m depth during 1951–84 (http://test.parsus.com/noaa/hake/SummaryData.aspx; P. Smith, pers. comm. fig. 3). In this study, most of data for the larger area came from surveys conducted in 1951–79 and direct estimates of $P_h$ were primarily made prior to 1980. Since 1980, spawning activities have been reported north of CalCOFI line 60.0: off Oregon and Washington during the springs of 1983–84 between 40°N–48°N (Hollowed 1992) during the El Niño period, and around Cape Mendocino at 35°N–40°N in February 1990 and 1991 (Saunders and MacFarlane 1997). Pacific hake were widely distributed from 36°N to 54°N in 1998 during the summer acoustic-trawl survey (Cooke et al. 2006), and Pacific hake larvae were observed between 40°N and 45°N during a coast-wide sardine survey in April to May 2006 (fig. 16; Lo et al. 2007). Thus, estimates of $P_h$ for the population from the current survey area may be biased downward during the few El Niño years after 1980, e.g. $P_h$ in 1983, 1998, and 1999 (tab. 2). For future surveys, the ichthyoplankton survey should be extended both to the north of San Francisco and to the south of San Diego during the winter-spring spawning season. This extended survey area will ensure the accuracy of the estimates of the larval production for the west coast of the North American continent and shed light on the effects of oceanographic conditions on the dynamics of Pacific hake spawning activities, and thus the spawning biomass.

A GAM was used to model the relationship between the larval production and three variables: spawning biomass from the 2006 stock assessment (Helser[1]), temperatures experienced by yolk-sac larvae close to 57 m depth, and "year". The year effect encompassed effects of factors other than the spawning biomass and temperature on the larval production, e.g. ocean conditions. The residual plots from the GAM are the relationship between larval production and a particular variable after the effects of other variables were removed. These residual plots, although not statistically significant and all nonlinear, suggested that the larval production in the survey area was inversely related to temperature (if the spawning biomass and year effects were held constant), and positively related to the spawning biomass (fig. 17A and B). If the spawning biomass and temperature were held constant, larval production in the survey area increased from the 1970s to a peak in the 1990s and decreased in recent years (fig. 17C). Therefore the decrease of larval production in the survey area during recent warm years may have resulted from the decrease of spawning biomass and/or movement of some spawning biomass to the north of this survey area (figs. 14, 17B and C).

Correlation coefficients between the $P_h$ and recruits estimated from the stock assessment were also examined with various time lags to determine whether the specific recruitment predicts the subsequent larval production: the $P_h$ time series. The highest correlation was for a time lag of seven years with a correlation of 0.68. The two high peaks of larval productions in 1986 and 1987 may have resulted from the high recruitment event in 1980 with an aid from 1984 (fig. 18). The correlation of 0.68 was driven primarily by the two high values of larval production and recruits and more such events are needed to ascertain the significant time lag between recruits and larval production. Overall, the high Pacific hake larval production in 1986–88 roughly corresponds to a high level of spawning biomass in 1984–86. This increase was most likely the result of two very strong year classes that occurred in 1980 and 1984, which allows for three to four years maturity, and would result in the peak in female spawning biomass (T. Helser, pers. comm.).

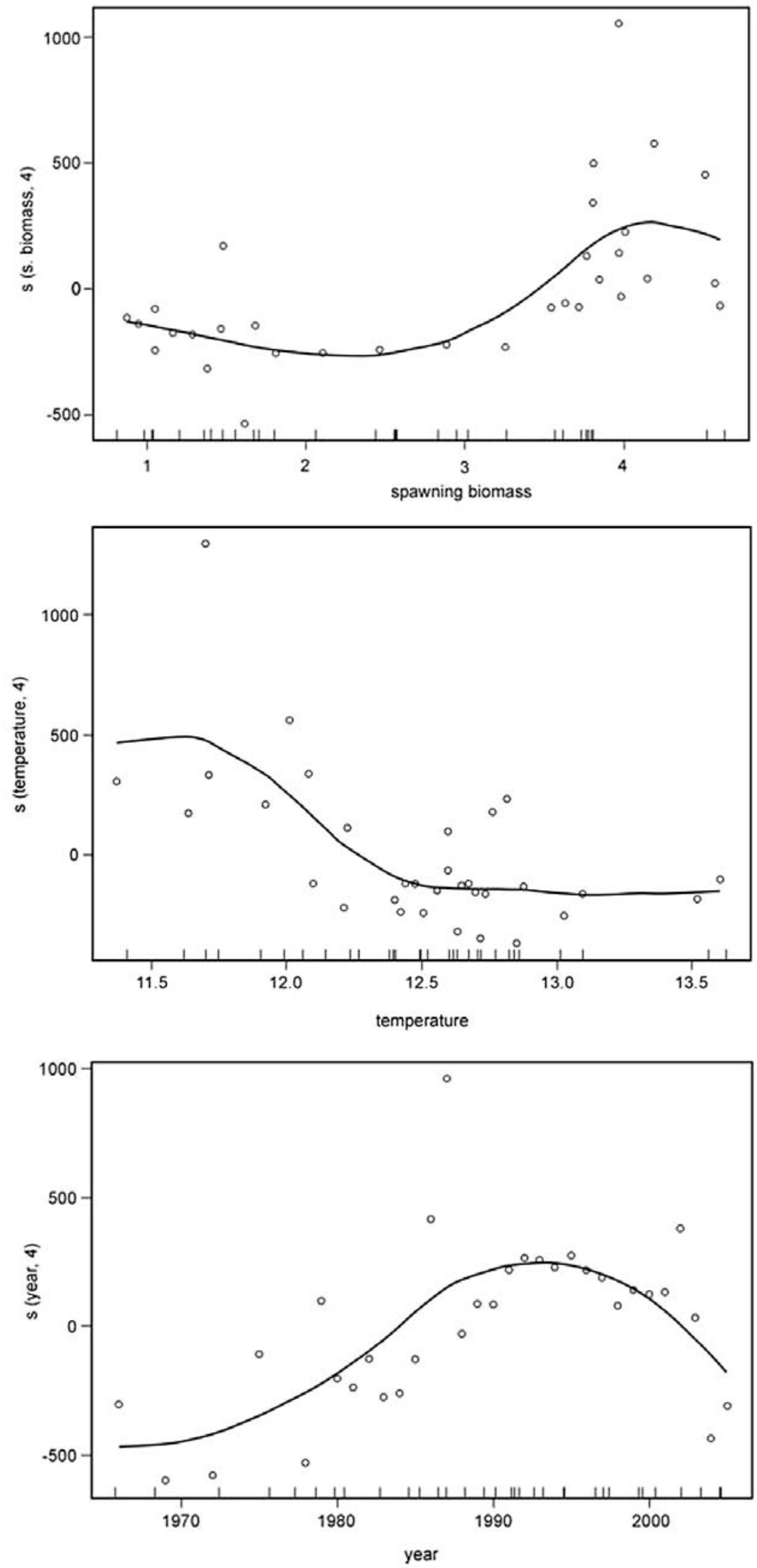

Figure 17. GAM residual of larval production as a smooth function of the spawning biomass (A) and the 57 m temperature (B) and a smooth function of year (C) for 1966–2006.

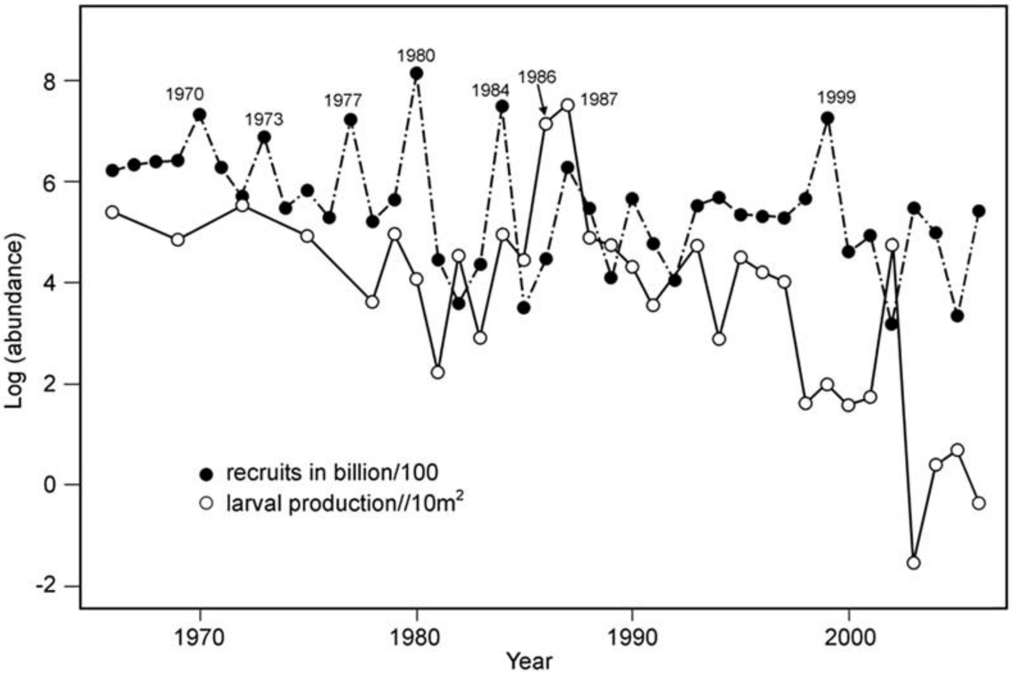

Figure 18. The time series of log (Pacific hake larval production/10 m$^2$) (solid line) and the log(abundance of 0 age recruits from 2006 stock assessment) (dash line) in 1966–2006

The larval indices and biomass estimates from acoustic-trawl surveys, two sets of direct observations, indicate that the Pacific hake population has been declining since the mid-1980s (figs. 13–15). The long time series of daily Pacific hake larval production, a fishery-independent population index obtained yearly, benefits the final estimate of the spawning biomass derived from the stock assessment of the Pacific hake population and improves our understanding of the dynamics of the Pacific hake population (Deriso and Quinn 1998).

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## APPENDIX

The average instantaneous mortality rate (equation 7) between age $t_1$ and $t_2$:

$$Z_t = \frac{\left(dP_t/dt\right)}{P_t} = \frac{\beta}{t+1}$$

$$EZ_t = \int_{t_1}^{t_2} Z_t \frac{P_1}{\int_{t_1}^{t_2} P_t dt} dt = \int_{t_1}^{t_2} Z_t \frac{Ph(t+1)^{-\beta}}{\int_{t_1}^{t_2} P_h(t+1)^{-\beta} dt} dt = \int_{t_1}^{t_2} \beta(t+1)^{-1} \frac{(1-\beta)(t+1)^{-\beta}}{(t_2+1)^{-\beta} - (t_1+1)^{-\beta}} dt$$

and

$$E(Z_t) = (\beta-1)\left[(t_2+1)^{-\beta} - (t_1+1)^{-\beta}\right] / \left[(t_2+1)^{1-\beta} - (t_1+1)^{1-\beta}\right] \qquad \text{(A1)}$$

Where $P_t = P_h(t+1)^{-\beta}$

# A CHARACTERIZATION OF THE FISH ASSEMBLAGE OF DEEP PHOTIC ZONE ROCK OUTCROPS IN THE ANACAPA PASSAGE, SOUTHERN CALIFORNIA, 1995 TO 2004, WITH EVIDENCE OF A REGIME SHIFT

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## ABSTRACT

During 1995, 1999, and 2001–04, using a manned research submersible, we surveyed the fish assemblage on rocky outcrops (situated at depths of 45–50 m) in the Anacapa Passage, southern California. We observed 40,132 fish and a minimum of 32 fish species. Rockfishes (*Sebastes* spp.) dominated the assemblage both in diversity and abundance. Squarespot rockfish (*Sebastes hopkinsi*), a schooling small-sized species, was the most abundant taxa, while blue rockfish (*S. mystinus*), blackeye goby (*Rhinogobiops nicholsii*), blacksmith (*Chromis punctipinnis*), halfbanded rockfish (*S. semicinctus*), vermilion rockfish (*S. miniatus*), rosy rockfish (*S. rosaceus*), senorita (*Oxyjulis californica*), lingcod (*Ophiodon elongatus*), and sharpnose/white seaperches (*Phanerodon atripes* and *P. furcatus*) were also characteristic species. The species assemblage on these outcrops represented a transition between that of the nearshore kelp beds and those more typical of deeper-water sites. The fish assemblage changed over time, due primarily to the addition of some species and increases in densities of many taxa. This occurred during a period where the oceanographic regime shifted from low productivity and warm water to high productivity and cool conditions.

## INTRODUCTION

The fish assemblages of several benthic marine habitats in southern California have been well described. Trawl surveys (e.g., Allen et al. 2002) have characterized soft sea floor assemblages and considerable attention has been given to the hard bottom fish assemblages in the shallow photic zone (30 m and less) (North and Hubbs 1968; Ebeling et al. 1980; Stephens et al. 1984). However, the fish assemblages of rocky outcrops below 30 m remain very poorly described. With the exception of a semi-quantitative survey of some rocky outcrop fishes on Tanner and Cortes banks (Lissner and Dorsey 1986), there have been no published accounts, based on underwater observations, of the fish communities that inhabit rocky outcrops in waters below about 30 m in the Southern California Bight.

Since 1995 we have conducted surveys of the fish assemblages of oil platforms and natural reefs in 30 to 360 m of water in southern California using a manned submersible. Usually, reefs were surveyed once or twice over this period. In contrast, a rocky area in the deep photic zone (45–50 m of water) in the Anacapa Passage (between Anacapa and Santa Cruz islands) was surveyed during six of the nine years. Our repeated visits to the

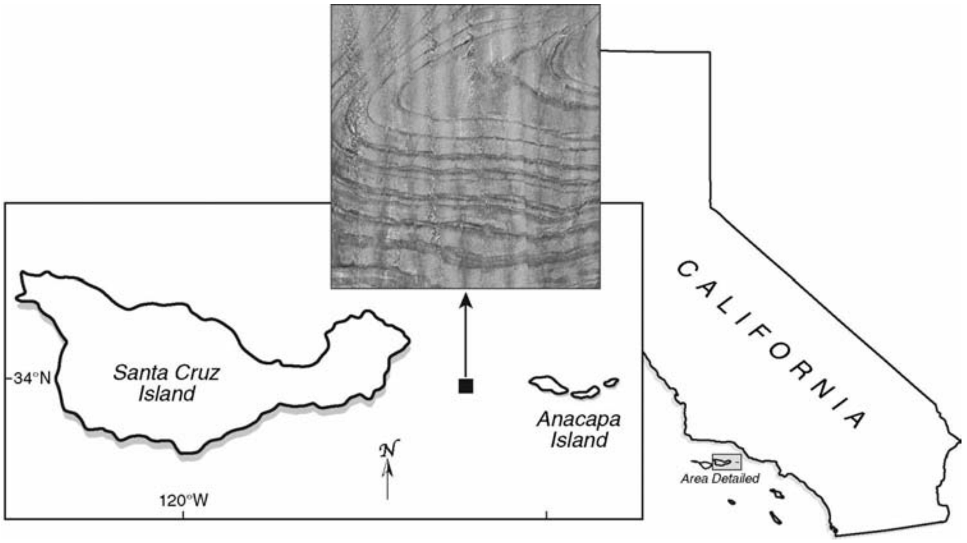

Figure 1. Location of survey site including sidescan sea floor image.

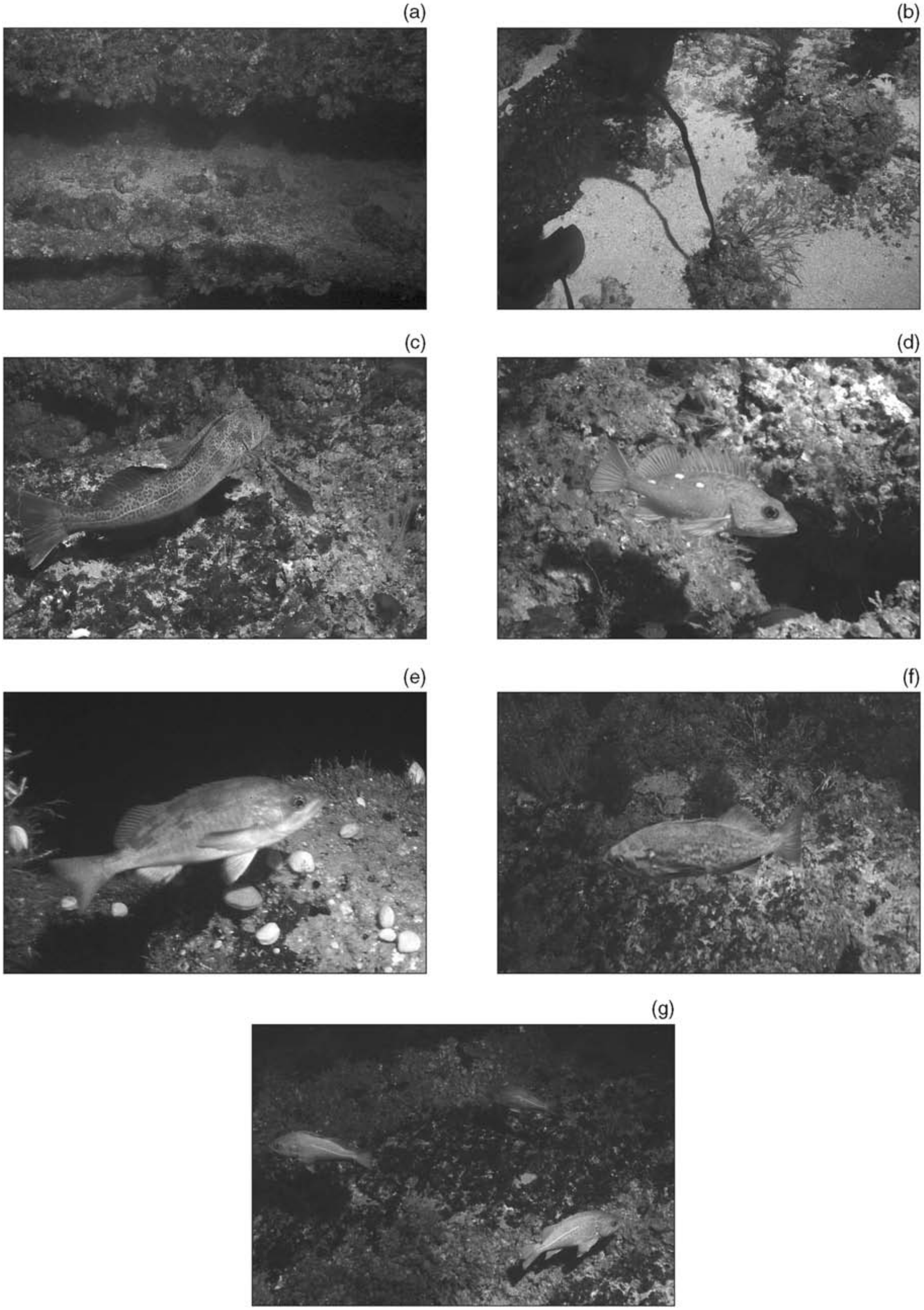

Figure 2. Typical habitat and fishes of the study site: (A) boulder and ledge habitat, (B) small boulders and sand with brown algae, (C) juvenile lingcod (*Ophiodon elongatus*), (D) rosy rockfish (*Sebastes rosaceus*), (E) squarespot rockfish (*S. hopkinsi*), (F) blue rockfish (*S. mystinus*), and (G) juvenile vermilion rockfish (*S. miniatus*).

Anacapa Passage site have provided us with an opportunity to both characterize this previously little-known fish community and to observe how that community changed over the study period; it is that which we explore in this study.

## METHODS

***Study area:*** The study area is located at approximately 33°59.9'N, 119°28.6'W (fig. 1). The outcrops lie at depths of 45–50 m and some extend more or less unbroken for at least 1,500 m. The features are sedimentary rock that extends 1–2 m above the sandy sea floor forming ledges with shelter holes and overhangs. The rock has been differentially eroded with some layers sticking up through thin sediment, forming long, linear ridges (fig. 1). The layers that are most easily eroded form low areas filled with coarse sediments (Cochrane et al. 2003). Some of the outermost sections of exposed strata have collapsed, adding boulders to the ledge habitat (fig. 2). Cobble surrounds some of these features. The outcrops support locally high densities of brown algae (including *Laminaria farlowii*), foliose red algae (*Plocamium cartilagineum*), articulate coralline algae (*Bossiella californica*), branching coralline algae (probably *Calliarthron tuberculosum*), and encrusting coralline algae. Sponges, red urchins, gorgonians, and bryozoans also dot the outcrops.

***Field sampling:*** We surveyed fish assemblages using the *Delta* research submersible, a 4.6 m, two-person vessel, operated by Delta Oceanographics of Oxnard, California. Aboard the *Delta*, we conducted 15-minute-long (10 minute 1995) belt transects about 2 m from the substrata, while the submarine maintained a speed of about 0.5 knots. We conducted surveys in 1995, 1999, and 2001–04. Four transects were conducted in every year except 1999 and 2001, when three transects were made. Within the study area, we selected ridges more or less randomly and transects were run parallel to these structures. In every year except 2002, surveys were conducted in October; in 2002 surveys occurred in November. Late fall is the optimal time to conduct surveys because of generally good weather and water clarity. In addition, many fish species have completed their seasonal juvenile recruitment by this time.

In each year, submersible surveys were conducted during daylight hours between 1400 and 1700. The same observer (D.S.) conducted all of the transects during all years. During each transect, the researcher made observations from a viewing port on the starboard side of the submersible. An externally mounted hi-8 mm video camera with associated lights filmed the same viewing fields as seen by the observer. The observer identified, counted, and estimated the lengths of all fishes and verbally recorded those data onto the video tape. All fishes in a volume 2 m from the seafloor upwards and from the submarine outwards were counted. Fish lengths were estimated using a pair of parallel lasers mounted on either side of the external video camera. The projected reference points were 20 cm apart and were visible to both the observer and the video camera. Transect lengths were computed by counting the number of 20 cm laser segments in 15 second subsamples (one per minute) throughout the transect, calculating speed based on those counts and averaging it over the whole transect, and multiplying that average speed by the transect duration.

An environmental monitoring system aboard the submarine continuously recorded date and time, depth, and altitude of the vessel above the sea floor. The environmental data was overlaid on the original videotape upon completion of each survey. Transect videos were reviewed aboard the research vessel or in the laboratory and observations transcribed into a database. For each fish, we recorded species and estimated its total length in 5 cm increments. All individuals were identified to species. The common and scientific names of all species observed are listed in Table 1.

***Statistical analyses:*** Interannual relationships in the Anacapa Passage fish assemblage were investigated using

TABLE 1
**Common and scientific names of species observed in this study.**

| Common Name | Scientific Name |
|---|---|
| Blackeye goby | *Rhinogobiops nicholsii* |
| Black perch | *Embiotoca jacksoni* |
| Blacksmith | *Chromis punctipinnis* |
| Blue rockfish | *Sebastes mystinus* |
| Bocaccio | *Sebastes paucispinis* |
| California scorpionfish | *Scorpaena guttata* |
| California sheephead | *Semicossyphus pulcher* |
| Copper rockfish | *Sebastes caurinus* |
| Deepwater blenny | *Cryptotrema corallinum* |
| Flag rockfish | *Sebastes rubrivinctus* |
| Gopher rockfish | *Sebastes carnatus* |
| Halfbanded rockfish | *Sebastes semicinctus* |
| Honeycomb rockfish | *Sebastes umbrosus* |
| Kelp rockfish | *Sebastes atrovirens* |
| Lingcod | *Ophiodon elongatus* |
| Olive rockfish | *Sebastes serranoides* |
| Painted greenling | *Oxylebius pictus* |
| Pile perch | *Rhachochilus vacca* |
| Pink seaperch | *Zalembius rosaceus* |
| Pygmy rockfish | *Sebastes wilsoni* |
| Rainbow seaperch | *Hypsurus caryi* |
| Rosy rockfish | *Sebastes rosaceus* |
| Rubberlip seaperch | *Rhachochilus toxotes* |
| Senorita | *Oxyjulis californica* |
| Sharpnose seaperch | *Phanerodon atripes* |
| Squarespot rockfish | *Sebastes hopkinsi* |
| Starry rockfish | *Sebastes constellatus* |
| Treefish | *Sebastes serriceps* |
| Unidentified ronquil | |
| Unidentified seaperches[1] | *Phanerodon* sp. |
| Vermilion rockfish | *Sebastes miniatus* |
| White seaperch | *Phanerodon furcatus* |
| Wolf-eel | *Anarrhichthys ocellatus* |

[1] Probably both sharpnose and white seaperches.

hierarchical cluster analysis and non-metric multidimensional scaling (MDS) plots. We fourth-root transformed fish densities (the full species set was used) to reduce the impact of extremely abundant species, and then constructed a triangular similarity matrix among year-pairs using the Bray-Curtis index (Bray and Curtis 1957). The Bray-Curtis index is useful in ecological analyses because joint absences of species between sample pairs are not used in similarity calculations (joint absences being difficult to interpret biologically). Of further benefit, the Bray-Curtis index is robust to non-linear species responses (Faith et al. 1987). Using this similarity matrix, we constructed a dendrogram of all transects using a hierarchical agglomerative procedure, with group-average linking (McCune and Grace 2002), to determine if transects grouped randomly or were nested within years. Next, we displayed similarities using MDS plots to illustrate relationships among all transects and among years (using the mean of either three or four transects surveyed during each year) in two dimensions. The usefulness of the two-dimensional display is represented by the stress statistic, where stress values <0.1 are reliable depictions of relationships, and stress values >0.2 are unreliable depictions of relationships (Clarke 1993). Both MDS plots show the minimum stress calculated from 1,000 random starts.

We tested the significance of among-year similarities in the structure of the Anacapa Passage fish assemblage by using a one-way analysis of similarity (ANOSIM; Clarke and Warwick 1994). We further investigated among-year differences in density and size structure of the most abundant fish species observed during the study. Density analyses used either a fixed-factor, one-way analysis of variance (ANOVA), or its nonparametric equivalent, the Kruskal-Wallis ANOVA, to test for significant differences in density among years. Density data were transformed when appropriate to meet ANOVA assumptions of normality and heterogeneity.

The PRIMER statistical package was used to calculate similarities, generate the dendrogram and MDS ordination plots, and to calculate ANOSIMs. The software program SPSS was used to conduct ANOVA and Kruskal-Wallis tests.

## RESULTS

Over the course of the study, we observed 40,132 fish representing a minimum of 32 fish species (tab. 2). Rockfishes, genus *Sebastes*, dominated the assemblage (fig. 2), comprising almost half (15 of 32) of all species observed. Rockfishes made up 91.2% of all fishes surveyed. Over all years, squarespot rockfish, a schooling dwarf species, was by far the most abundant; it comprised a minimum of 78.4% of all fishes seen. Even when squarespot rockfish were subtracted from the observations, rockfishes still comprised 59.4% of all fishes. Other particularly abundant species included blue rockfish, blackeye goby, blacksmith, and halfbanded rockfish. Vermilion and rosy rockfishes, senorita, lingcod, and sharpnose/white seaperches comprised the remaining top ten species or species complexes.

Many of the species we observed recruited as young-of-the-year (YOY) to the study reefs (we defined recruited fish as those less than 10 cm long, except for 5 cm for blackeye gobies). Of the most abundant fishes, species that at least occasionally recruited as YOYs included blue, halfbanded, rosy, and squarespot rockfishes, blackeye goby, blacksmith, and sharpnose/white seaperch (not figured) (fig. 3). Of the less abundant species, we also observed some recruitment of flag, pygmy, rosy, and starry rockfishes, treefish, pink seaperch, painted greenling, and deepwater blennies. Recruitment from the plankton was sporadic among years and some species, such as blacksmith, recruited in only one year. Among the more abundant species, we did not observe YOY recruitment of lingcod, vermilion rockfish, and senorita.

Assemblages of fishes on transects exhibited consistent temporal patterns as indicated in both cluster and MDS plots (figs. 4A, B). The ANOSIM showed that the Anacapa Passage fish assemblage changed significantly over the course of the study, though, not surprisingly, pairwise comparisons revealed that years close together in time were similar (tab. 3). Through 2004, the fish assemblage continued to diverge, becoming increasingly unlike that of the earlier years (fig. 4C). Many of the changes we observed were caused by an increase both in the overall number of species living on the reefs and in the density of many species (tab. 2). In particular, the densities of blue (*Sebastes mystinus*), halfbanded (*S. semicinctus*), rosy (*S. rosaceus*), squarespot (*S. hopkinsi*), starry (*S. constellatus*), and vermilion (*S. miniatus*) rockfishes, blackeye goby (*Rhinogobiops nicholsii*), blacksmith (*Chromis punctipinnis*), lingcod (*Ophiodon elongatus*), painted greenling (*Oxylebius pictus*), and treefish (*S. serriceps*) all increased over time.

Of the eleven species with the highest mean density over all years, eight species varied significantly through time (tab. 4), and this variability was generally on the order of one magnitude (tab. 2). For species that had significant changes, we used density information along with size distributions to infer potential sources of density variability.

For squarespot rockfish, the dominant species in the Anacapa Passage assemblage, inspection of size distributions showed that years with the highest densities (2001, 2003, 2004) were characterized by strong YOY classes (tab. 2, fig. 3A). Due to the diminutive maximum size of squarespots, size classes were too coarse to follow pulses of YOY recruitment through time. The year of

TABLE 2

**Numbers, densities, and mean total lengths (standard deviations in parentheses) of the species observed in the Anacapa Passage, 1995, 1999, 2001–04. Species ordered by overall abundances. Unidentified species are listed at the end of the table.**

| Common Name | | 1995 | 1999 | 2001 | 2002 | 2003 | 2004 |
|---|---|---|---|---|---|---|---|
| Squarespot rockfish | Total | 1313 | 3231 | 868 | 255 | 12,609 | 13,177 |
| | Density | 50.48 (64.4) | 121.90 (84.9) | 28.89 (33.8) | 13.22 (4.3) | 236.00 (204.3) | 351.99 (332.5) |
| | TL | 14.94 (3.3) | 10.45 (1.7) | 11.29 (4.5) | 13.25 (3.6) | 5.17 (1.2) | 12.41 (4.4) |
| Blue rockfish | | 75 | 218 | 182 | 444 | 1275 | 127 |
| | | 2.95 (2.1) | 8.45 (3.8) | 5.93 (4.2) | 23.30 (10.7) | 23.18 (17.3) | 3.29 (1.4) |
| | | 24.77 (4.3) | 17.80 (9.0) | 22.80 (4.4) | 23.20 (5.0) | 23.50 (3.0) | 22.26 (3.6) |
| Blackeye goby | | 8 | 64 | 73 | 273 | 95 | 692 |
| | | 0.33 (0.3) | 2.42 (1.2) | 2.37 (1.4) | 14.05 (10.9) | 1.60 (1.7) | 18.74 (9.3) |
| | | 12.13 (3.2) | 10.23 (1.1) | 11.30 (2.8) | 10.53 (2.6) | 11.32 (3.3) | 10.03 (1.4) |
| Halfbanded rockfish | | — | 5 | — | — | 810 | 266 |
| | | — | 0.19 (0.2) | — | — | 15.27 (16.1) | 6.86 (5.8) |
| | | — | 10.00 (0.0) | — | — | 5.00 (0.0) | 10.08 (1.1) |
| Blacksmith | | — | — | 294 | 213 | 554 | 41 |
| | | — | — | 9.40 (8.1) | 11.28 (12.6) | 8.63 (7.5) | 1.11 (0.8) |
| | | — | — | 18.18 (2.9) | 19.91 (2.1) | 17.05 (5.9) | 19.39 (2.3) |
| Senorita | | 202 | 13 | 23 | — | 27 | 2 |
| | | 7.98 (15.7) | 0.49 (0.7) | 0.65 (0.9) | — | 0.47 (0.7) | 0.05 (0.1) |
| | | 20.00 (0.0) | 10.77 (2.8) | 18.48 (3.2) | — | 20.00 (0.0) | 20.00 (0.0) |
| Sharpnose/White seaperch | | 21 | 38 | 98 | 3 | 4 | 76 |
| | | 0.94 (1.8) | 1.50 (2.1) | 2.64 (5.1) | 0.16 (0.1) | 0.07 (0.1) | 2.03 (2.2) |
| | | 10.00 (5.5) | 11.18 (5.8) | 5.10 (1.0) | 6.67 (1.7) | 10.00 (5.8) | 10.13 (4.8) |
| Rosy rockfish | | 6 | 44 | 42 | 66 | 65 | 111 |
| | | 0.25 (0.2) | 1.66 (1.4) | 1.36 (1.0) | 3.41 (1.6) | 1.11 (0.8) | 3.01 (1.5) |
| | | 19.17 (3.8) | 19.32 (4.0) | 18.81 (2.7) | 18.94 (2.7) | 18.98 (2.7) | 18.83 (2.8) |
| Vermilion rockfish | | 15 | 34 | 21 | 98 | 175 | 50 |
| | | 0.60 (0.2) | 1.30 (0.5) | 0.69 (0.7) | 5.09 (1.8) | 3.06 (1.1) | 1.35 (0.6) |
| | | 38.00 (5.6) | 34.26 (6.6) | 30.71 (5.1) | 26.73 (4.8) | 28.24 (6.1) | 28.90 (6.2) |
| Lingcod | | 18 | 8 | 49 | 64 | 78 | 50 |
| | | 0.73 (0.1) | 0.31 (0.1) | 1.58 (0.9) | 3.34 (0.2) | 1.40 (0.7) | 1.35 (0.4) |
| | | 52.50 (17.8) | 38.75 (9.5) | 38.85 (11.0) | 41.75 (9.0) | 44.49 (7.6) | 38.67 (11.9) |
| California sheephead | | 8 | 16 | 15 | 16 | 61 | 11 |
| | | 0.34 (0.2) | 0.62 (0.5) | 0.46 (0.2) | 0.83 (0.2) | 1.12 (0.8) | 0.29 (0.2) |
| | | 29.38 (10.2) | 24.69 (12.0) | 21.67 (5.6) | 28.75 (7.6) | 28.81 (8.4) | 22.27 (2.6) |
| Treefish | | — | — | 35 | 24 | 4 | 26 |
| | | — | — | 1.15 (0.9) | 1.26 (0.4) | 0.07 (0.1) | 0.71 (0.3) |
| | | — | — | 24.29 (3.2) | 22.92 (4.2) | 22.50 (5.0) | 22.12 (2.9) |
| Starry rockfish | | — | 2 | 10 | 14 | 5 | 50 |
| | | — | 0.08 (0.1) | 0.33 (0.3) | 0.73 (0.3) | 0.08 (0.1) | 1.36 (0.7) |
| | | — | 15.00 (7.1) | 25.00 (4.7) | 26.07 (6.6) | 22.00 (2.7) | 15.80 (9.0) |
| Painted greenling | | 1 | 8 | 10 | 9 | 21 | 22 |
| | | 0.04 (0.1) | 0.30 (0.2) | 0.31 (0.3) | 0.47 (0.3) | 0.37 (0.1) | 0.61 (0.4) |
| | | 15.00 (0.0) | 13.13 (3.7) | 16.00 (2.1) | 14.44 (1.7) | 14.52 (3.1) | 15.23 (3.3) |
| Copper rockfish | | 5 | 7 | 3 | 15 | 13 | 9 |
| | | 0.22 (0.3) | 0.27 (0.1) | 0.10 (0.1) | 0.78 (0.4) | 0.22 (0.1) | 0.23 (0.2) |
| | | 26.00 (8.9) | 28.57 (3.8) | 18.33 (2.9) | 23.33 (4.1) | 24.62 (3.2) | 20.00 (5.6) |
| Gopher rockfish | | 1 | 11 | 8 | 15 | 7 | 6 |
| | | 0.04 (0.8) | 0.41 (0.5) | 0.25 (0.2) | 0.78 (0.0) | 0.11 (0.1) | 0.17 (0.2) |
| | | — | 24.55 (5.7) | 19.38 (4.2) | 23.00 (2.5) | 22.86 (2.7) | 21.67 (2.6) |
| Rubberlip seaperch | | 1 | — | 3 | 14 | 26 | 4 |
| | | 0.04 (0.1) | — | 0.10 (0.1) | 0.74 (0.6) | 0.47 (0.7) | 0.11 (0.2) |
| | | 40.00 (0.0) | — | 31.67 (2.9) | 31.43 (3.1) | 26.15 (5.5) | 32.50 (2.9) |
| Olive rockfish | | 8 | 2 | 2 | 8 | 5 | 7 |
| | | 0.32 (0.2) | 0.08 (0.1) | 0.05 (0.1) | 0.41 (0.5) | 0.08 (0.1) | 0.19 (0.1) |
| | | 38.13 (7.0) | 40.00 (0.0) | 27.50 (3.5) | 27.5 (4.6) | 29.00 (8.2) | 27.86 (2.7) |
| Pile perch | | 12 | — | 1 | 4 | 2 | — |
| | | 0.47 (0.4) | — | 0.03 (0.1) | 0.21 (0.1) | 0.04 (0.0) | — |
| | | 25.50 (7.3) | — | 30.00 (0 .0) | 31.25 (7.5) | 27.50 (3.5) | — |
| Black perch | | 8 | — | — | — | — | — |
| | | 0.31 (0.2) | — | — | — | — | — |
| | | 23.75 (2.3) | — | — | — | — | — |
| Pygmy rockfish | | — | 12 | — | — | — | — |
| | | — | 0.45 (0.8) | — | — | — | — |
| | | — | 10.00 (0.0) | — | — | — | — |

TABLE 2 (continued)

**Numbers, densities, and mean total lengths (standard deviations in parentheses) of the species observed in the Anacapa Passage, 1995, 1999, 2001–04. Species ordered by overall abundances. Unidentified species are listed at the end of table.**

| Common Name | 1995 | 1999 | 2001 | 2002 | 2003 | 2004 |
|---|---|---|---|---|---|---|
| California scorpionfish | — | — | 1 | — | 5 | 7 |
| | — | — | 0.03 (0.1) | — | 0.08 (0.0) | 0.19 (0.1) |
| | — | — | 30.00 (0.0) | — | 27.00 (2.7) | 24.29 (1.9) |
| Flag rockfish | 1 | — | 2 | — | 6 | 1 |
| | 0.04 (0.1) | — | 0.06 (0.1) | — | 0.12 (0.2) | 0.03 (0.1) |
| | 10.00 (0.0) | — | 15.00 (0.0) | — | 21.00 (9.6) | 20.00 (0.0) |
| Deepwater blenny | — | — | 2 | — | 3 | 1 |
| | — | — | 0.06 (0.1) | — | 0.04 (0.1) | 0.03 (0.1) |
| | — | — | 15.00 (0.0) | — | 15.00 (0.0) | 10.00 (0.0) |
| Kelp rockfish | — | — | 1 | — | — | 1 |
| | — | — | 0.03 (0.1) | — | — | 0.03 (0.1) |
| | — | — | 25.00 (0.0) | — | — | 25.00 (0.0) |
| Honeycomb rockfish | 1 | — | 1 | — | — | 1 |
| | 0.04 (0.1) | — | 0.04 (0.1) | — | — | 0.03 (0.1) |
| | 20.00 (0.0) | — | 15.00 (0.0) | — | — | 20.00 (0.0) |
| Rainbow seaperch | — | — | — | — | — | — |
| | — | — | — | — | — | — |
| | — | — | — | — | — | — |
| Wolf-eel | — | — | — | — | — | — |
| | — | — | — | — | — | — |
| | — | — | — | — | — | — |
| Pink seaperch | 1 | — | 1 | — | — | — |
| | 0.04 (0.1) | — | 0.03 (0.1) | — | — | — |
| | 15.00 (0.0) | — | 5.00 (0.0) | — | — | — |
| Bocaccio | 1 | — | — | — | — | 1 |
| | 0.04 (0.1) | — | — | — | — | 0.02 (0.1) |
| | 100.00 (0.0) | — | — | — | — | 25.00 (0.0) |
| Unidentified young-of-year rockfishes | — | 11 | — | — | 386 | 162 |
| | — | 0.42 (0.3) | — | — | 6.95 (6.9) | 4.25 (4.9) |
| | — | 5.00 (0.0) | — | — | 5.00 (0.0) | 5.00 (0.0) |
| Unidentified rockfishes | — | 18 | 3 | 4 | 36 | 14 |
| | — | 0.68 (0.5) | 0.09 (0.1) | 0.21 (0.2) | 0.57 (0.4) | 0.38 (0.2) |
| | — | 10.00 (0.0) | 20.00 (10.0) | 15.00 (8.7) | 15.59 (5.0) | 16.15 (5.5) |
| Unidentified fishes | — | 6 | 1 | 1 | 28 | 10 |
| | — | 0.23 (0.2) | 0.04 (0.1) | 0.05 (0.1) | 0.47 (0.3) | 0.27 (0.3) |
| | — | 16.67 (19.2) | 15.00 (0.0) | — | 7.14 (5.0) | 6.00 (2.1) |
| Unidentified seaperches | 59 | 57 | 1 | 1 | 11 | 1 |
| | 2.37 (4.4) | 2.28(3.9) | 0.03 (0.1) | 0.05 (0.1) | 0.19 (0.1) | 0.03 (0.1) |
| | 5.42 (1.4) | 10.35 (2.7) | 5.00 (0.0) | 20.00 (0.0) | 10.91 (5.8) | 15.00 (0.0) |
| Unidentified ronquils | 1 | 1 | — | — | — | 5 |
| | 0.04 (0.1) | 0.04 (0.1) | — | — | — | 0.14 (0.1) |
| | 20.00 (0.0) | 25.00 (0.0) | — | — | — | 16.00 (5.5) |
| Unidentified sculpins | 24 | — | — | — | — | 3 |
| | 1.00 (1.6) | — | — | — | — | 0.08 (0.2) |
| | 5.83 (3.2) | — | — | — | — | 6.67 (2.9) |

lowest squarespot rockfish density (2002; tab. 2) coincided with the year of greatest density of piscivorous species (lingcod and various large rockfishes). However, it is not clear if this inverse relationship is due to a reduction of individuals through predation, behavioral shifts by squarespots to areas of lower predator density, or some other reason.

A suite of five species (blackeye goby, lingcod, and blue, rosy, and vermilion rockfishes) generally increased in density during the study, with 2002 the strongest year for all species. In particular, we can see effects of the 1999 oceanographic conditions, which have been noted as a good year for survival for lingcod and blue and vermilion rockfish juveniles in the Southern California Bight

TABLE 3

**Multivariate analysis of similarity (ANOSIM) to detect differences in fish assemblage structure among years. Bars beneath pairwise comparisons between years show levels of significance greater than $P = 0.05$.**

| Factor | Sample Statistic (Global *R*) | Number of Permutations[a] | | Significance Level (*P*) | |
|---|---|---|---|---|---|
| Year | 0.567 | 0/1000 | | 0.001 | |
| 1995 | 1999 | 2001 | 2002 | 2003 | 2004 |

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[a] The number of permuted statistics ≥ to the sample statistic out of a random sample from a large number of possible permutations.

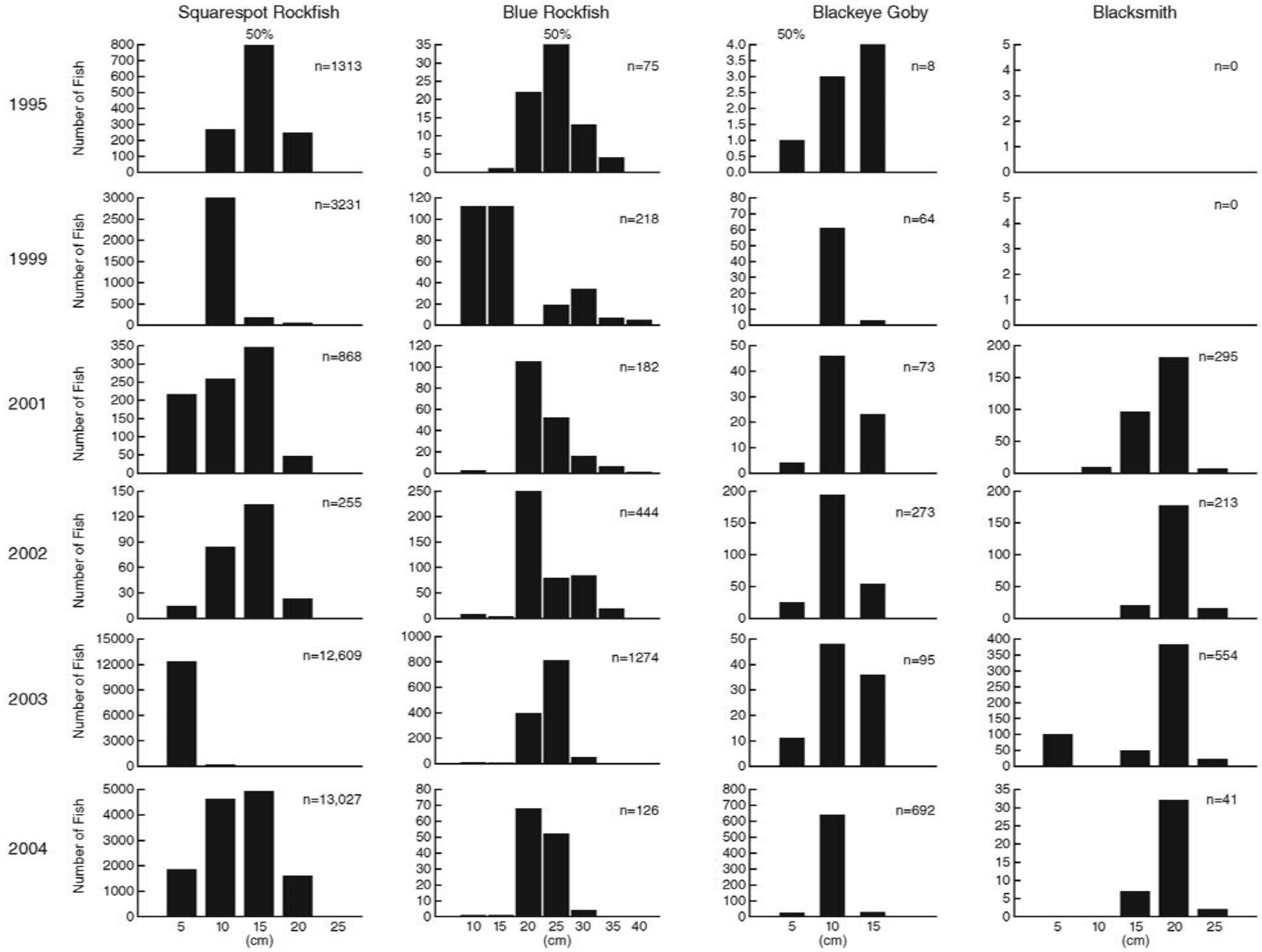

Figure 3. Size-frequency histograms of some major species observed in this study. Individuals 10 cm or less were assumed to be young-of-the-year for all species except blackeye goby (*Rhinogobiops nicholsii*) (young-of-the-year were 5 cm long). Also noted are the sizes at 50% maturity (data for halfbanded (*Sebastes semicinctus*), rosy (*S. rosaceus*), squarespot (*S. hopkinsi*), and vermilion (*S. miniatus*) rockfishes are from Love et al. (2002); blue rockfish (*S. mystinus*) from Miller and Geibel (1973); blackeye goby from Wiley (1970); lingcod (*Ophiodon elongatus*) from Silverberg et al. (2001); and blacksmith (*Chromis punctipinnis*) from Limbaugh (1955)).

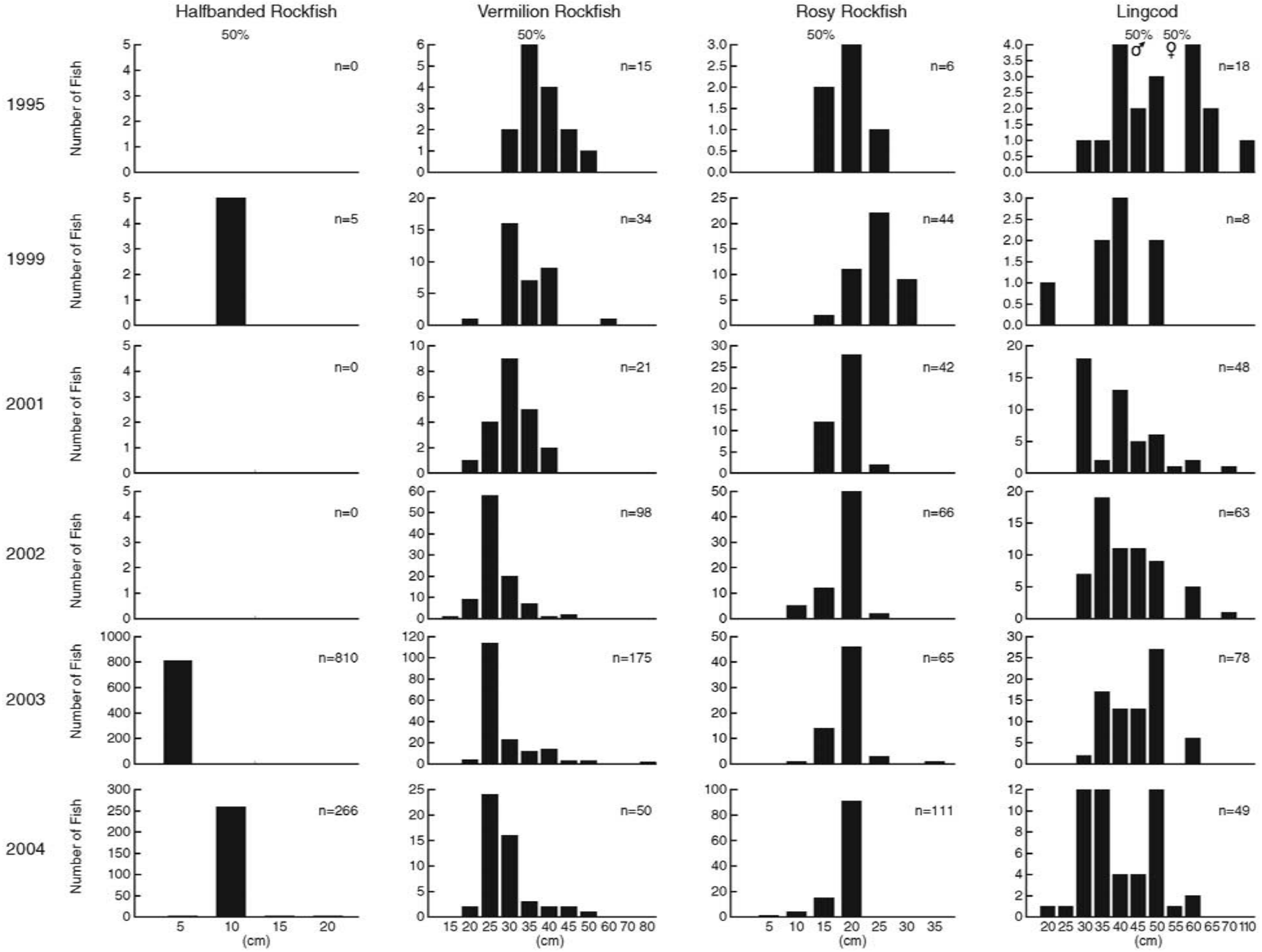

Figure 3. Size-frequency histograms of some major species observed in this study. Individuals 10 cm or less were assumed to be young-of-the-year for all species except blackeye goby (*Rhinogobiops nicholsii*) (young-of-the-year were 5 cm long). Also noted are the sizes at 50% maturity (data for halfbanded (*Sebastes semicinctus*), rosy (*S. rosaceus*), squarespot (*S. hopkinsi*), and vermilion (*S. miniatus*) rockfishes are from Love et al. (2002); blue rockfish (*S. mystinus*) from Miller and Geibel (1973); blackeye goby from Wiley (1970); lingcod (*Ophiodon elongatus*) from Silverberg et al. (2001); and blacksmith (*Chromis punctipinnis*) from Limbaugh (1955)).

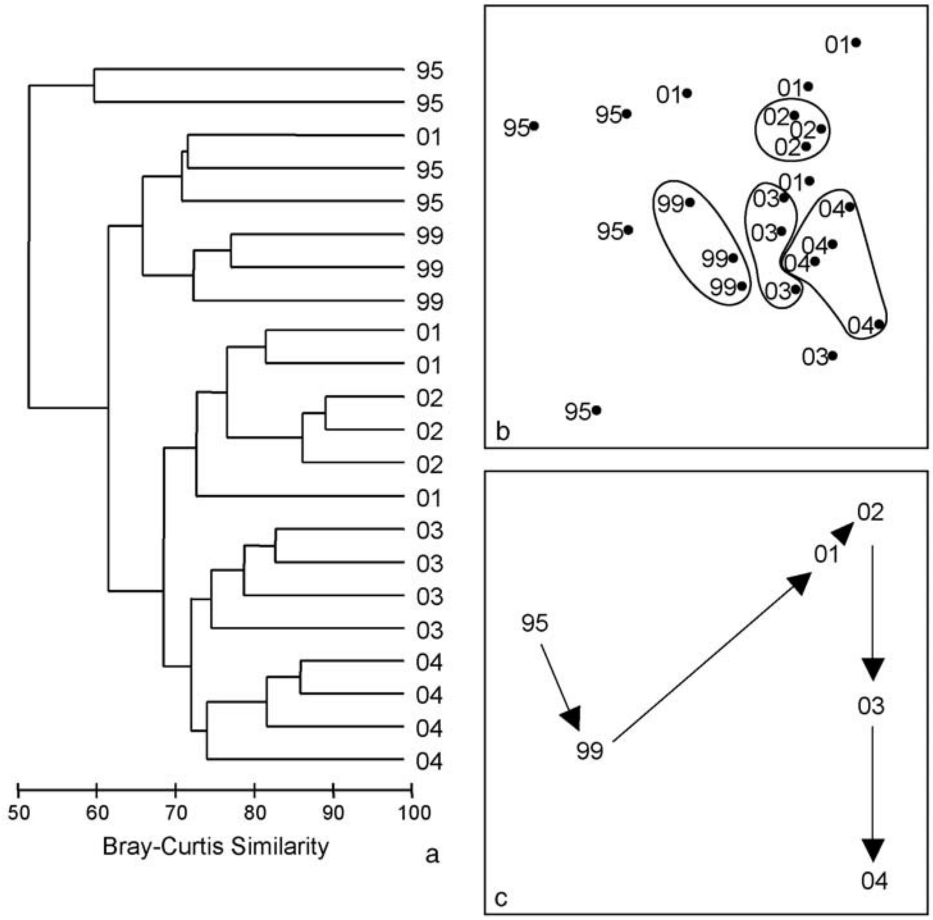

Figure 4A. Dendrogram from standard hierarchical cluster analysis using Bray-Curtis similarities on fourth-root transformed fish densities for all transects.
Figure 4B. MDS ordination of Bray-Curtis similarities showing fish assemblage relationships among all transects. Stress = 0.15.
Figure 4C. MDS ordination showing fish assemblage relationships among years. Arrows indicate shifts of assemblage in hyperspace through time. Stress = 0.0.

TABLE 4
**Summary of results from analyses of variance (ANOVA and Kruskal-Wallis ANOVA) testing interannual significance on density of selected species in the Anacapa Passage fish assemblage. P values in bold are significant at the <0.05 level.**

| Common Name | Mean no. fish/ $100m^2$ (all years) | Data transformation | Test | *F* or chi-square | *P* |
|---|---|---|---|---|---|
| Squarespot rockfish | 133.7 | log(*x*+1) | ANOVA | 3.765 | 0.019 |
| Blue rockfish | 11.2 | log(*x*+1) | ANOVA | 6.091 | 0.002 |
| Blackeye goby | 6.6 | log(*x*+1) | ANOVA | 14.832 | 0.000 |
| Halfbanded rockfish | 7.4 | | Kruskal-Wallis | 18.096 | 0.003 |
| Blacksmith | 7.6 | | Kruskal-Wallis | 14.935 | 0.011 |
| Senorita | 1.9 | | Kruskal-Wallis | 5.682 | 0.338 |
| Sharpnose/White seaperch | 1.2 | | Kruskal-Wallis | 2.702 | 0.764 |
| Rosy rockfish | 1.8 | none | ANOVA | 4.147 | 0.013 |
| Vermilion rockfish | 2.0 | | Kruskal-Wallis | 16.366 | 0.006 |
| Lingcod | 1.5 | | Kruskal-Wallis | 14.427 | 0.013 |
| California sheephead | 0.6 | none | ANOVA | 2.497 | 0.075 |
| Treefish | 0.8 | | Kruskal-Wallis | 17.326 | 0.004 |
| Starry rockfish | 0.5 | log(*x*+1) | ANOVA | 14.306 | 0.000 |
| Painted greenling | 0.4 | log(*x*+1) | ANOVA | 2.631 | 0.064 |
| Copper rockfish | 0.3 | log(*x*+1) | ANOVA | 3.274 | 0.032 |
| Gopher rockfish | 0.3 | | Kruskal-Wallis | 9.585 | 0.088 |
| Rubberlip seaperch | 0.3 | | Kruskal-Wallis | 5.995 | 0.307 |
| Pile perch | 0.2 | | Kruskal-Wallis | 17.539 | 0.004 |
| Black perch | 0.3 | | Kruskal-Wallis | 14.826 | 0.011 |
| California scorpionfish | 0.1 | | Kruskal-Wallis | 16.515 | 0.006 |

(Love et al. 2002, 2003; Jagielo and Wallace 2005; MacCall 2005). Blackeye goby and rosy rockfish did not show any pattern between density and size structure, perhaps because the size classes were too coarse to detect patterns.

Blue rockfish YOY recruited strongly to the Anacapa Passage in 1999. In 2001 and 2002, 20 cm fish dominated the size distribution, with 25 cm showing strongly in 2003. This pulse of blue rockfish sizes corresponds to sizes we might expect from fish recruiting in the 1999 year class. Densities of 20 cm and 25 cm fish are greater than the original density of YOY fish, suggesting that fish which recruited as juveniles to other habitats (perhaps nearby kelp beds) immigrated to deeper reefs as they matured. A few blue rockfish YOY were observed in 2001, 2003, and 2004.

For vermilion rockfish, high density years were dominated by 25 cm fish, which is in the size range that we would expect from fish recruiting in 1999. As we observed in blue rockfish, it appears that vermilion rockfish recruit as juveniles to other and shallower habitats, and immigrate to deeper reefs as they grow larger. There are low densities of adult vermilion rockfish, perhaps suggesting that the majority of larger fish seek out even deeper reefs.

Blacksmith were completely absent in 1995 and 1999, but then showed a spike in 2001. Densities of blacksmith then declined over the final years within the study. Halfbanded rockfish density varied sporadically across years, which may reflect the amount of sandy habitat in transects, and not reflect real population trends in time. The senorita and sharpnose/white seaperch complex showed no significance among years, probably due to its patchy spatial distribution. Finally, we note that sheephead did not show significant differences among years.

## DISCUSSION

The fish assemblage living on the Anacapa Passage reefs represents a transition between that found in southern California kelp beds and nearshore outcrops and that of deeper-water features. Of the relatively abundant species in our study, blackeye goby, blacksmith, blue and gopher rockfishes, senorita, California sheephead, painted greenling, and rubberlip seaperch are also abundant in shallower waters. On the other hand, rosy, squarespot, starry, and post-YOY vermilion rockfishes rarely inhabit shallower waters in southern California and all have ranges that extend much deeper than our survey sites. Two species, blacksmith and kelp rockfish, were near their maximum depth ranges on these outcrops and our observations of both rainbow seaperch and rubberlip seaperch comprised new maximum depth records (Love et al. 2005). A number of species that commonly occur on shallow hard features at Anacapa and Santa Cruz islands, such as black-and-yellow rockfish (*Sebastes chrysomelas*), garibaldi (*Hypsypops rubicunda*), kelp bass (*Paralabrax clathratus*), opaleye (*Girella nigricans*), and rock wrasse (*Halichoeres semicinctus*) (Ebeling et al. 1980; Kushner et al. 2001) were absent from these outcrops. Similarly, several species (i.e., greenspotted, *S. chlorostictus*, and swordspine, *S. ensifer*, rockfishes) typical of nearby outcrops in 80–100 m of water did not occur at our study site.

The Anacapa Passage assemblage was structured both by species that recruit as YOY to the study reefs and by somewhat older individuals that recruit elsewhere and immigrated to these reefs. Most or all of some species, such as halfbanded and squarespot rockfishes and blackeye goby, originated as YOY recruits to the study reefs. Pelagic juveniles of both halfbanded and squarespot rockfishes rarely settle in to shallower waters. On the other hand, some species (e.g., blacksmith and blue rockfish) rarely recruit into these relatively deep waters and the occurrence of very young fishes was relatively uncommon. All members of some species, such as vermilion rockfish (which are known to recruit to shallower waters, Love et al. 2002) and lingcod (which recruit to a wide range of depths but usually to low relief, Miller and Geibel 1973) settled elsewhere and immigrated to the reefs. We did not observe species that likely settled deeper and then swam into shallower waters. Thus, the species assemblage of our study site reflects recruitment success both on our study outcrops and at other, mostly shallower, sites. Clearly there is connectivity between the relatively deep reefs we studied and those that are shallower, as the densities of some species that live on the Anacapa Passage outcrops are dependent on more shallow-water productivity. On the other hand, it can be argued that the year-class success of some species that recruit to nearshore waters, such as vermilion rockfish, may be dependent on larvae from adults living on deeper reefs.

Most of the changes in the assemblage represented increasing densities of a number of species, probably reflecting increased productivity in nearshore waters, rather than a turnover in species composition. It is likely that at least some of the alteration in fish assemblages was linked to recent changes in oceanographic conditions that were conducive to increased larval survivorship. Bograd et al. (2000) noted that between 1997 and 1999 oceanographic conditions off southern California "shifted dramatically off southern California" from low productivity and warm water to high productivity and cool conditions. During 1999, we made extensive scuba and submersible fish assemblage surveys throughout the Santa Barbara Channel, northern Channel Islands, and off Points Conception and Arguello around both oil platforms and over natural outcrops. During these surveys we noted higher young-of-the-year densities of a number of species compared to what we had seen between 1995 and

1998 (Love et al. 2001; Schroeder 2001). Species that recruited more heavily in that year included blue, flag, halfbanded, olive, vermilion, and widow (*S. entomelas*) rockfishes, cowcod (*S. levis*), bocaccio (*S. paucispinis*), lingcod, and kelp greenling (*Hexagrammos decagrammus*). During that same year, relatively high recruitment of blue, olive, and vermilion rockfishes and treefish was also noted around some of the northern Channel Islands (Kushner et al. 2001).

The fate of the present fish assemblage, which reflects the highly productive and cooler waters that began in 1999, is unclear. Regarding much of the California Current, Peterson et al. (2006) stated that the "dramatic shift to cold ocean conditions that lasted for a period of four years (1999–2002)" was followed by a "more subtle but persistent return to warm ocean conditions initiated in October 2002." If these warm conditions, which led to reduced fish recruitment in many areas, persist, we might expect overall fish densities to decline and perhaps a return to the assemblages of earlier years.

Diminutive fishes dominated our study reefs. Dwarf species, such as squarespot and halfbanded rockfishes, or blackeye goby, were very abundant and comprised most of the assemblage. Among species that grow to substantial sizes, such as lingcod and vermilion rockfish, we observed relatively few large individuals. In southern California, larger vermilion rockfish and lingcod are only rarely found in nearshore waters. On our study reefs, it is likely that at least some of the larger adults of these species migrate into deeper waters. However, we believe that at least part of this phenomenon is due to substantial fishing pressure acting on local fish populations. The Anacapa Passage is located close to four mainland harbors and is usually protected from prevailing winds. For many decades these outcrops have been heavily fished by commercial passenger fishing vessels, private vessel recreational anglers, and, to a lesser extent, by commercial fishermen (Love et al. 1985; Schroeder and Love 2002). On our study reefs, fishing may not alter the species composition of the assemblage (i.e., removing the last member of a species). Rather it may crop and thus reduce the abundance of larger individuals and allow for increased densities of smaller fishes. However, this pattern is not limited to outcrops in the Anacapa Passage; many reefs off California are dominated by small fishes, reflecting intense fishing pressure (Yoklavich et al. 2000; Love and Yoklavich 2006).

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# ASPECTS OF THE LIFE HISTORY OF TREEFISH, *SEBASTES SERRICEPS* (SEBASTIDAE)

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## ABSTRACT

In this paper, we report the reproductive seasonality, maturity, length-age and length-weight relationships, and the parameters for converting between total and standard lengths for *Sebastes serriceps* from the Southern California Bight. Our data indicate that the von Bertalanffy age-length parameters are $L_\infty$ = 30.64 cm, $k$ = 0.233, and $t_0$ = –1.167. Females were reproductively active between at least February and May, and ovaries were found to contain eyed larvae in March. Males were reproductively active between October and at least December. The oldest fish we collected was 25 years of age; the age at 50% maturity was 4 years for females and 3 years for males; and the total length at 50% maturity was 19.0 to 19.9 cm for both sexes. We found no evidence of sexual dimorphism in mean length, growth, or the length-weight relationship. These findings are consistent with the life history traits of ecologically similar species of *Sebastes*.

## INTRODUCTION

More than 63 species of rockfish in the genus *Sebastes* (Sebastidae) inhabit the northeastern Pacific Ocean (Love et al. 1990). Members of this genus share characteristics such as viviparity, slow growth, and long life expectancy. Over fifty-five species of *Sebastes* have been reported within the Southern California Bight (Love et al. 1990), and the present study describes aspects of the life history of one species, the treefish (*Sebastes serriceps*).

Although the range of *Sebastes serriceps* extends from San Francisco, California, U.S.A., to Isla Cedros, Baja California, Mexico (Miller and Lea 1972), it is most common in the Southern California Bight (Jordan and Evermann 1898; Leet et al. 2001; Love et al. 2002) (fig. 1). *S. serriceps* is one of the larger benthic rockfishes, found inhabiting caves and crevices on rocky reefs usually shallower than 50 m (Miller and Lea 1972; Love et al. 2002), although it has been observed to 97 m on an oil platform (Love et al. 2000). The solitary adults are most likely territorial (Haaker 1978; Leet et al. 2001; Love et al. 2002), and are ambush predators that feed between dusk and dawn on benthic invertebrates and fishes (Hobson et al. 1981; Kosman et al. 2007).

Like other rockfish, *Sebastes serriceps* is viviparous. Females extrude preflexion, planktonic larvae, and pelagic juveniles may associate with drifting kelp mats (Hobday 2000; Love et al. 2002) before settling to adult habitat between June and August (Moser 1967; Boehlert 1977; Gunderson et al. 1980; Hobday 2000; Love et al. 2002). Prior to this study, information about the life history of *S. serriceps* was limited to observations of the maximum observed length (40.64 cm total length; Phillips 1957) and age (23 years; Love et al. 2002), and counts of ova in one individual (MacGregor 1970). MacGregor's study also provided minimal information about the seasonality of reproduction in *S. serriceps* given that the single gravid female was collected in March.

The goal of this study was to quantify aspects of the life history of *Sebastes serriceps*. Reproductive maturity and seasonality were investigated and length-age, length-weight and length-length relationships characterized. Because specimens were collected from several distinct regions within the Southern California Bight, the above relationships were compared between areas where possible. In addition, growth, longevity, and reproductive seasonality were compared between *S. serriceps* and ecologically and genetically similar species of rockfish.

## METHODS

Between 1978 and 2005, 365 *Sebastes serriceps* specimens were collected from as far south as Ensenada, Baja California, Mexico (lat. 31°51'N; long. 116°37'W), and as far north as San Gregorio, California, U.S.A. (lat. 37°33'N; long. 122°40'W) (fig. 1). The majority of the specimens were collected from the Southern California Bight by SCUBA divers using pole spears between March 2003 and March 2005 ($n$ = 321). Other specimens were collected by hook and line or gillnet. Specimens were put on ice immediately after capture, frozen within ten hours, and later thawed and processed. Sagittal otoliths were removed, cleaned, and stored dry. Whole specimens were weighed to 0.1 g, and their total and standard lengths measured to 1 mm. Gonads were removed and their weights recorded to 0.01 g, although for young fish this was not always possible. To maximize the accuracy of our length-weight, length-length, and length-

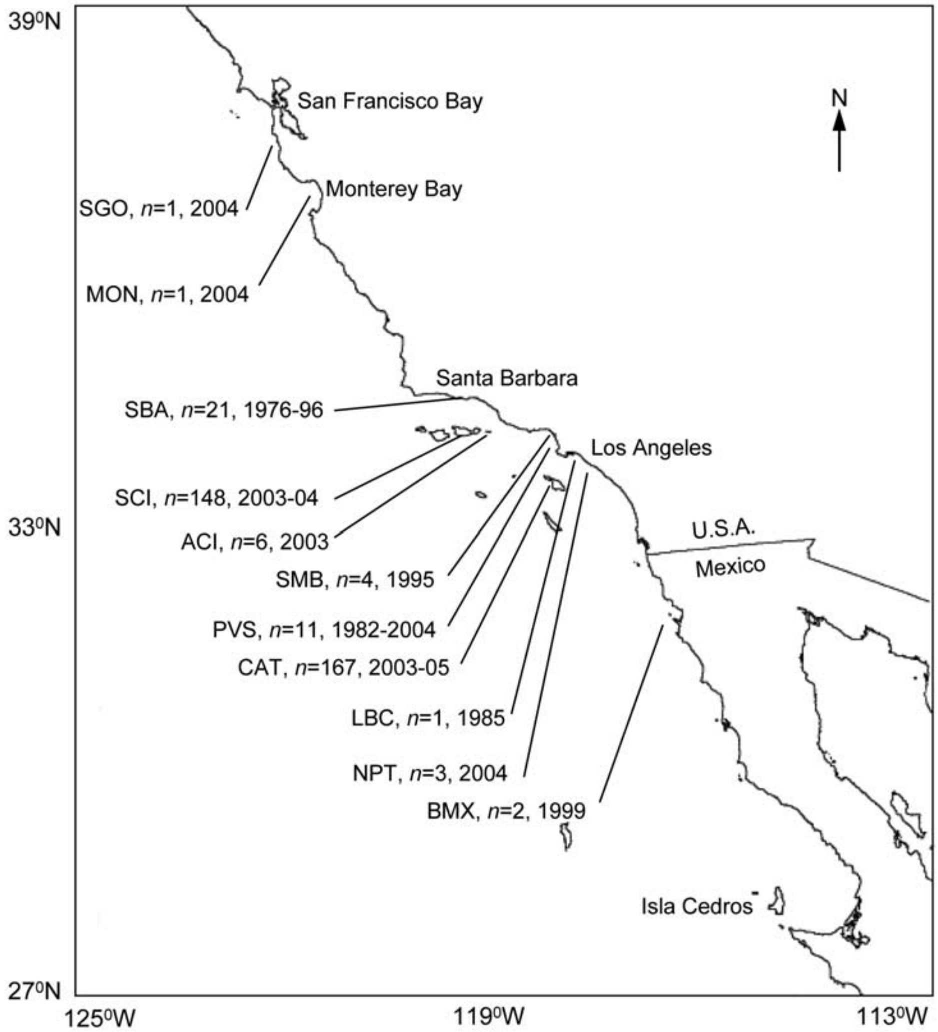

Figure 1. Collection sites with number of specimens and years in which collections were made. SGO = San Gregorio; MON = Monterey; SBA = Santa Barbara; SCI = Santa Cruz Island; ACI = Anacapa Island; SMB = Santa Monica Bay; PVS = Palos Verdes; CAT = Santa Catalina Island; LBC = Long Beach; NPT = Newport; and BMX = Ensenada, Baja California, Mexico.

age relationships, we included in our analyses 34 very young fish by recognizing that their total weight is approximately equal to their somatic weight; gonads of one-year-old specimens weighed at most 0.4% of their total weight. These specimens were assigned gender by grouping them based on month of capture, and randomly designating them male or female.

## Age

Sagittal otoliths have been found to give the most consistent ages for several species of rockfish (Six and Horton 1977) and it has become standard practice to use them to age fishes (Love et al. 2002). In this study, we estimated the ages of *Sebastes serriceps* by counting the annuli on sagittae. March 1st was chosen as the birth date of *S. serriceps* as this corresponds to the presence of eyed larvae in ovaries (this paper).

Treefish sagittae are difficult to analyze because they grow thick and strongly curved, and contain many "false checks" (Kimura et al. 1979). This is particularly true of older specimens. In order to obtain the most accurate estimate of specimens' ages, we employed several methods to read treefish otoliths. As has been found for other species (Six and Horton 1979; Boehlert and Yoklavich 1984; Wilson and Boehlert 1990; Laidig et al. 2003), surface readings were only accurate for younger fish, here defined as fish less than six years old. Sagittae from older specimens, here defined as fish of at least six years of age, were treated separately. Every otolith, irrespective of age, was read at least three times before an age was determined. Readings were separated by at least one week and up to six months to ensure that the reader did not remember the ages previously assigned to the specimens.

The otoliths of younger specimens were placed in a black-bottom watch glass, immersed in water and examined using direct light at magnifications of 120× to 500×. Otoliths were tilted in order to view annuli on the outermost edge (Boehlert and Yoklavich 1984). An opaque zone followed by a translucent (hyaline) zone was considered to represent one year in the life of the specimen (Six and Horton 1977). The surfaces of otoliths from all younger fish were examined at least three times, and specimens with different ages for the second and third readings were read again. Of the specimens that had been read four times, those that had no single age in the majority were read a fifth time. Specimens that remained inconsistent after five reads were not included in the analysis ($n = 2$).

Two techniques are commonly employed for analyzing otoliths from older specimens: break and burn (MacLellan 1997) and sectioning (e.g., Love and Johnson 1998). Sectioning is more precise, particularly when the otoliths are thick and strongly curved, and was therefore selected as the more appropriate method for this study. We took transverse sections of otoliths from older specimens and from a representative sample of younger fish ($n_{\text{total}} = 218$). The sectioned otoliths from younger samples of known age (i.e., specimens which had been read as the same age multiple times) were used to calibrate the sectioned otolith reading method. These specimens were examined by a reader who knew the age of the specimen and used this information to separate true annuli from "false checks" (Kimura et al. 1979). This ensured that the two methods were comparable.

Otolith sections were embedded in clear resin on a waxed paper tag and sliced using a Buehler Isomet low-speed saw. A dorso-ventral transverse section through the nucleus was cut from each otolith using two diamond-edge blades separated to 0.06 cm by plastic shims. Sections were affixed to slides using Cytoseal, ground, polished, brushed with mineral oil, and read twice using a compound microscope at 240× magnification. Digital photographs of otolith sections were taken using a Nikon Eclipse E600 microscope connected to a Spot RT Slider digital camera and imported using Spot Advanced (ver. 4.0.1). These photographs were imported into Microsoft PowerPoint (2003) and viewed beneath a grid that had been calibrated to 2.5 mm × 2.5 mm using a photograph of a stage micrometer taken with the same equipment. This allowed the reader to take measurements of the otolith and annuli. The total length of the transverse section, the length of the nucleus, and the total length across the nucleus from the inside curve of each hyaline ring were measured. From these data, frequency diagrams were constructed and means computed for measurements at each age. These measurements were used to aid the identification of annuli associated with early years (Boehlert and Yoklavich 1984). Identifying these early annuli improved the accuracy of the readings of sagittae from older specimens. The sagittae of younger specimens of known age were again used to validate that the sectioned otoliths were read in a method consistent with whole otoliths.

All sectioned otoliths from older fish were read at least once using the calibrated grid. Those specimens that had the same age estimate for the first three reads (twice using a compound microscope and once with the grid) were deemed that age. Those specimens for which the ages were inconsistent were read up to four times using the grid. Specimens that had four readings with a range of four were read a fifth time. Otoliths that remained inconsistent were not included in the analysis ($n = 6$).

Several researchers have validated the deposition of one hyaline band per year on an otolith by examining the edges of otoliths collected over the course of a year (e.g., Kimura et al. 1979; Pearson et al. 1991; Laidig et al. 2003). To validate that a single opaque band was deposited annually on treefish otoliths, the edges of whole otoliths from younger fish ($n = 189$) were examined at 240× magnification using a dissecting microscope. After examining the dorsal edge, the otolith was classified as either having a translucent or opaque outer band. If the edge was half opaque and half translucent, the ventral edge was also examined. Whenever possible, both otoliths were inspected. As a secondary validation, age-length frequencies were plotted for different locations and examined to see if clear age modes were apparent.

### Mortality

A nonlinear catch curve of abundance against age was constructed using FISHPARM (Prager et al. 1989). Mortality was estimated from the equation:

$$N_t = N_o(e^{-Zt}) \tag{1}$$

where $N_t$ = population size at age $t$ (years);
$N_o$ = the theoretical population size at age 0; and
$Z$ = instantaneous rate of mortality.

### Sexual Dimorphism

We examined the effect of gender on the length-weight, length-length, and length-age relationships. Details of these analyses can be found in their respective sections below. We also examined whether the mean total length of females ($n = 162$) was different from the mean total length of males ($n = 148$) using an independent samples t-test and data pooled from Santa Catalina, Santa Cruz, and Anacapa islands. It was easier to identify small female fish than small males because immature ovaries are easier to locate than testes. To account for this bias, small specimens were included and assigned genders according to the methods outlined above.

TABLE 1
**Independent Variables Used to Explore the Length-weight Relationship of *Sebastes serriceps*.**

| Independent Variable | Categories | *n* | Description |
|---|---|---|---|
| Location | CAT | 180 | Santa Catalina Island |
| | SBA | 17 | Santa Barbara |
| | SCB | 16 | Long Beach, Newport, Palos Verdes, Santa Monica Bay |
| | SCI | 160 | Santa Cruz Island and Anacapa Island |
| Time | FMA | 125 | February, March, April |
| | MJJ | 92 | May, June, July |
| | ASOND | 154 | August, September, October, November, December |
| Gender | M | 156 | Male |
| | F | 177 | Female |

### Length-weight Relationship

The relationship between length and somatic weight, calculated as total body weight less gonad weight, was fitted using the allometry equation in FISHPARM (Prager et al. 1989):

$$W = aL^b \tag{2}$$

where W = somatic weight (g);
$L$ = total length (cm); and
$a$ and $b$ = constants.

To examine whether gender, location, and time of year had an effect on the length-weight relationship, a multiple linear regression was performed (SPSS ver. 11.5) ($n$ = 333). The dependent variable was $\log_{10}$(somatic weight), and the independent variables were $\log_{10}$(total length), location, season, and gender (tab. 1). A scatterplot of standardized residuals indicated that the data were normally distributed and that there were two outlying data points. Mahalanobis distances (Pallant 2002) were used to determine that these data points should be kept in the analysis. Very young specimens were included as described above.

### Length-length Relationship

Studies on the life history of fishes vary in the methods used to measure length (e.g., Kimura et al. 1979; Pearson et al. 1991). To facilitate comparisons with other studies, the length-length conversion parameters for treefish were computed. The relationship between total length (cm) and standard length (cm) was found by fitting a linear regression for all fish from Santa Catalina, Santa Cruz, and Anacapa islands ($n$ = 310). Small fish were assigned a gender as outlined above. A two-way analysis of covariance (ANCOVA) was used to examine whether sex or location (Santa Cruz + Anacapa Island vs. Santa Catalina Island) affected the length-length relationship.

### Length-age Relationship

The relationship between length and age was estimated using the von Bertalanffy growth function (VBGF; Ricker 1975) fitted using FISHPARM (Prager et al. 1989):

$$L_t = L_\infty[1 - e^{-k(t - t_o)}] \tag{3}$$

where $L_t$ = length at age t (years);
$L_\infty$ = theoretical maximum length;
$k$ = rate of increase in length increments; and
$t_0$ = theoretical age at which $L_t$ = 0.

Small fish were included using the previously described methods. As sex and latitudinal variation have been shown to affect growth, the VBGF was fitted to nine combinations of data: (1) all specimens from southern California ($n$ = 311); (2) females from southern California ($n$ = 166); (3) males from southern California ($n$ = 145); (4) all samples from Santa Catalina Island ($n$ = 158); (5) all samples from Santa Cruz Island ($n$ = 146); (6) females from Santa Catalina Island ($n$ = 89); (7) males from Santa Catalina Island ($n$ = 60); (8) females from Santa Cruz Island ($n$ = 74); and (9) males from Santa Cruz Island ($n$ = 71).

An analysis of the residual sums of squares was used to compare VBGFs between sexes and locations (Chen et al. 1992). An F-statistic was computed as:

$$F = \frac{(RSS_p - RSS_s) \div (DF_p - DF_s)}{(RSS_s) \div (DF_s)} \tag{4}$$

where $RSS_p$ = RSS of VBGF fitted to pooled growth data;
$RSS_s$ = sum of RSS of each VBGF fitted to separate samples;
$DF_p$ = degrees of freedom for VBGF fitted to pooled growth data; and
$DF_s$ = sum of degrees of freedom of each VBGF fitted to sample data.

The degrees of freedom for the critical $F$-statistic were $3(K\text{-}1)$ and $N\text{-}3K$ for the numerator and denominator respectively, where $K$ is the number of samples being compared, and $N$ is the sample size used to obtain the pooled VBGF.

### Reproduction and Maturity

Gonads were staged while fresh using a dissecting microscope, stored in 90% ethanol, and reexamined between six and 18 months after the initial staging. The stage of gonad development was identified using categories from Wyllie Echeverria (1987). Males were classified as mature if their testes were staged as spermatogenic, spawning or recently spawned, or if their

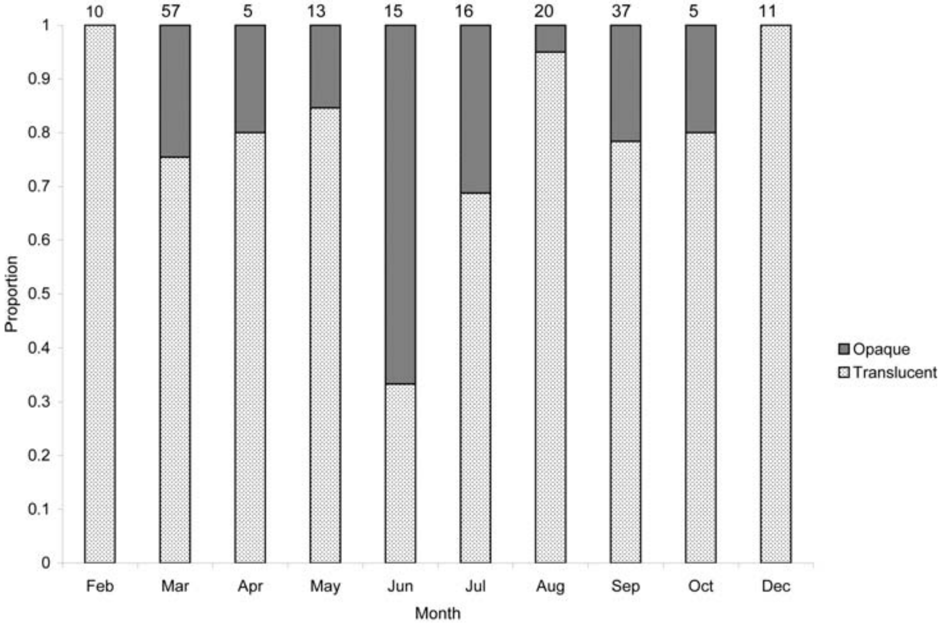

Figure 2. Frequency of edge state (opaque vs. translucent) for otoliths from *Sebastes serriceps* aged zero to five years, demonstrating the seasonal deposition of opaque band. Numbers above columns indicate sample sizes.

testes were relatively large and staged as resting. Females were classified as mature if the ovaries were staged as fertilized or in parturition. Ovaries staged as vitellogenic, spawned, or resting that contained evidence of residual eyed larvae or that had thick ovary walls were also considered mature. Some females appeared to have vitellogenic ovaries with no evidence of reproduction during the previous year, such as residual pigments or thick ovary walls. Following the recommendations of Bobko and Berkeley (2004), these fish were staged as first year/vitellogenesis, and classified as immature because it is impossible to predict whether they would reproduce during the year.

Differentiating between the immature and resting stages of rockfish gonads can be difficult (Love and Johnson 1998). In this study we followed the recommendations of Gunderson et al. (1980) and used only mature specimens to determine length and age at maturity: testes from mature fish collected between August and December ($n = 55$), and ovaries from mature specimens collected between February and May ($n = 68$).

A gonosomatic index (GSI) was calculated using the equation from Love et al. (1990):

$$\text{GSI} = 100[(W_g) \div (W_T)] \qquad (5)$$

where $W_g$ = gonad weight; and
$W_T$ = total body weight.

GSI values were calculated for all mature fish from southern California ($n = 213$) and changes in GSI by month were plotted for males ($n = 105$) and females ($n = 108$).

GSI values from mature females ($n = 30$) during months of peak reproductive output (February to May) were examined for trends. Because a $\log_{10}$-transformation of the GSI values only served to normalize three of the five stages (fertilization, parturition, and recently spawned; Kolmogorov-Smirnov $p = 0.137$, $p = 0.200$, and $p = 0.200$ respectively), a Kruskal-Wallis H test was used to examine the effect of each gonad stage upon GSI values.

## RESULTS

### Age

Like all other species of *Sebastes* studied thus far, *S. serriceps* deposits annual growth rings on its sagittae, allowing the sagittae to be used to measure its age. Edge analysis revealed that one opaque band was deposited annually during the summer months, usually in June (fig. 2). Length-age frequency plots revealed distinct size modes that, particularly for younger ages, consisted largely of one year class (fig. 3). Measurements taken from photographs of transverse sections of otoliths revealed a similar pattern relating otolith size to specimen age (fig. 4). Our aging methods thus validated, we identified the youngest individual in this study as less than 1 year old and the oldest as 25 years old. Previously, *S. serriceps* was posited to attain a maximum age of 23 years (Love et al. 2002).

### Mortality Rate

The instantaneous rate of mortality was estimated by fitting a nonlinear catch curve using FISHPARM (Prager

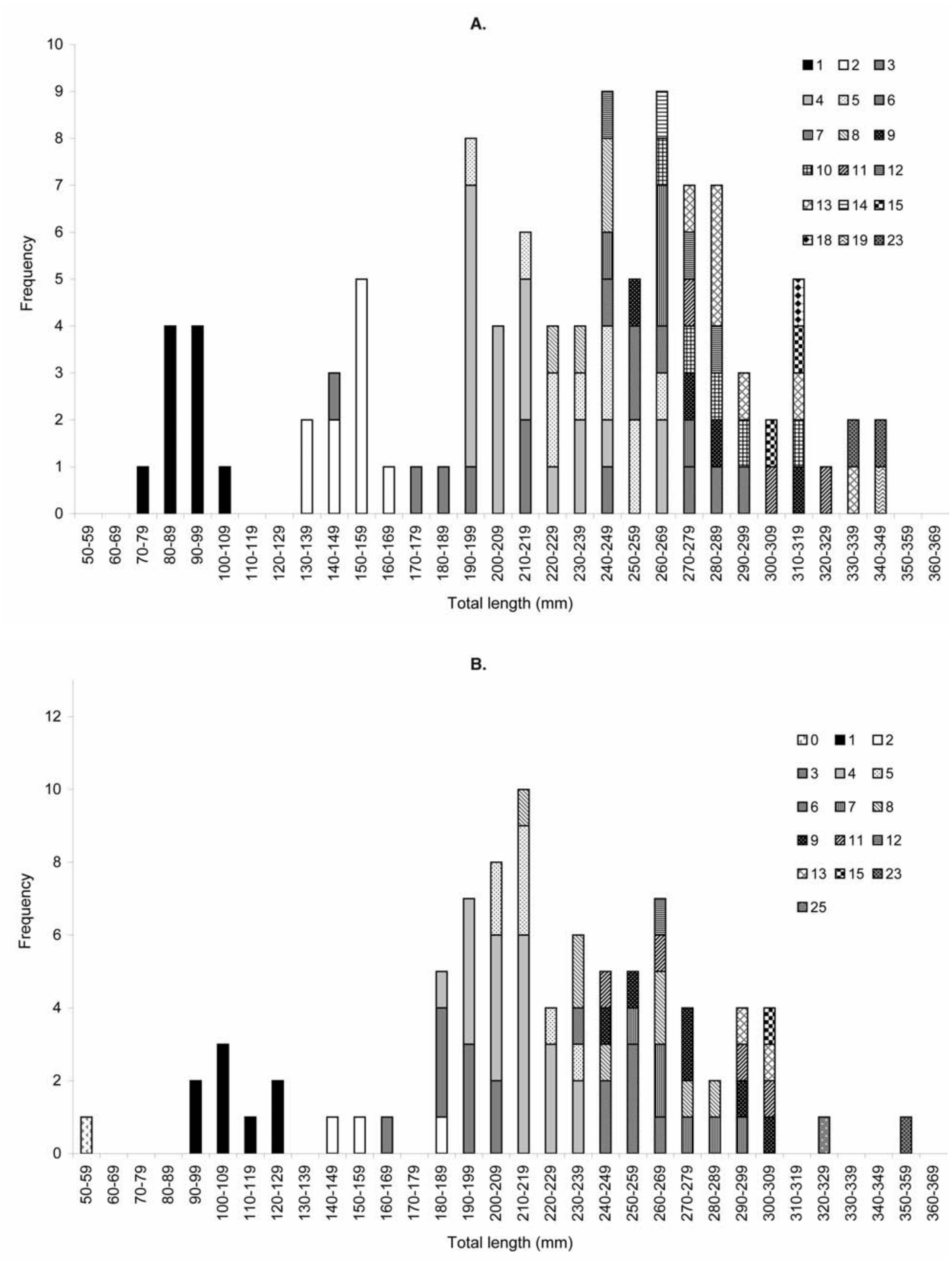

Figure 3. Length-frequency plots by age (years) for *Sebastes serriceps* from Santa Catalina, Santa Cruz, and Anacapa Islands for three seasons: A. February, March, and April; B. May, June, and July; and C. September, October, and December.

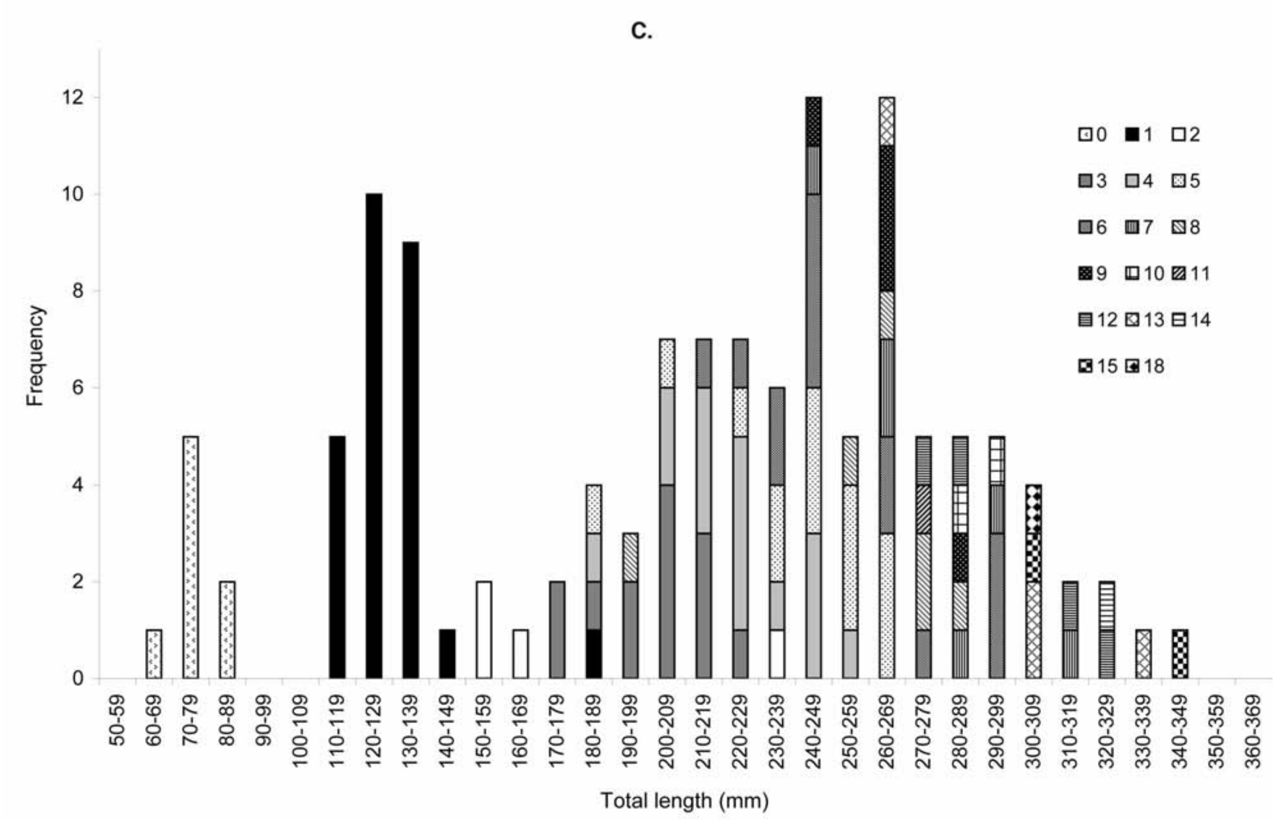

Figure 3 (continued). Length-frequency plots by age (years) for *Sebastes serriceps* from Santa Catalina, Santa Cruz, and Anacapa Islands for three seasons: A. February, March, and April; B. May, June, and July; and C. September, October, and December.

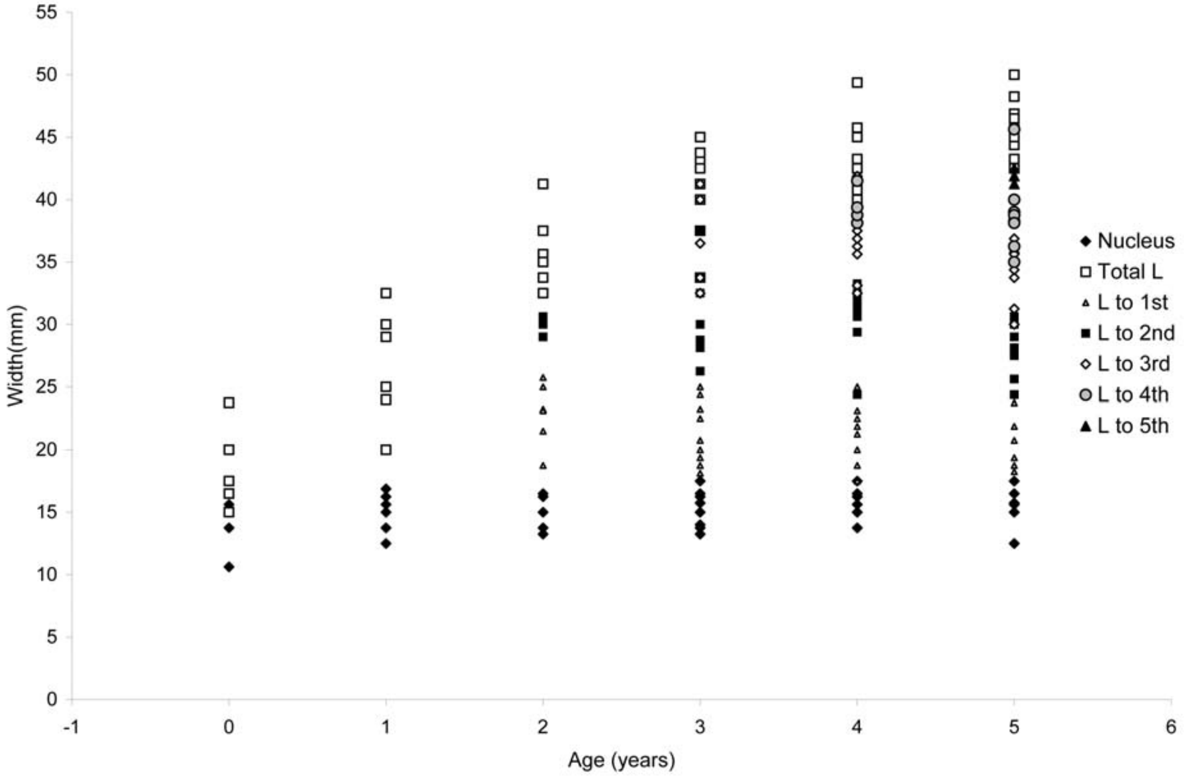

Figure 4. Measurements of total section width, and the distance across the nucleus and annuli for transverse otolith sections from *Sebastes serriceps*, based on photographic images measured by overlain grids using PowerPoint.

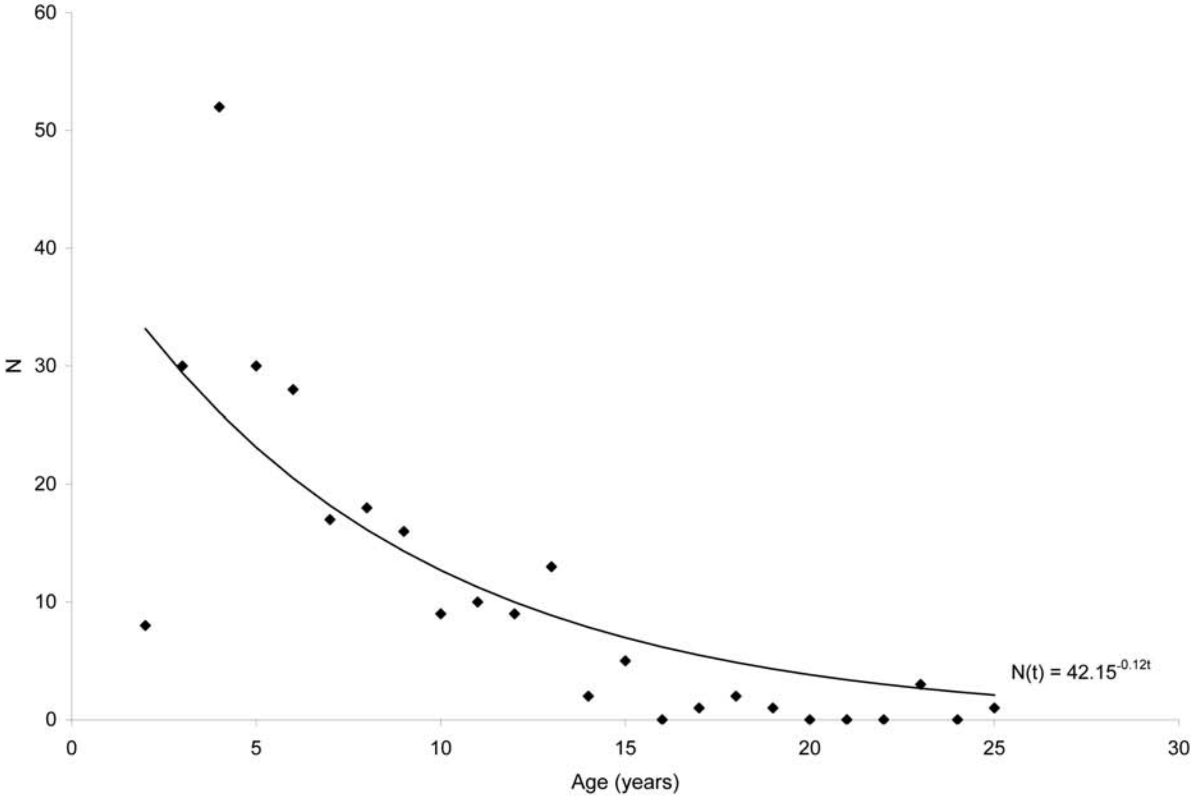

Figure 5. Catch curve for *Sebastes serriceps* in the Southern California Bight.

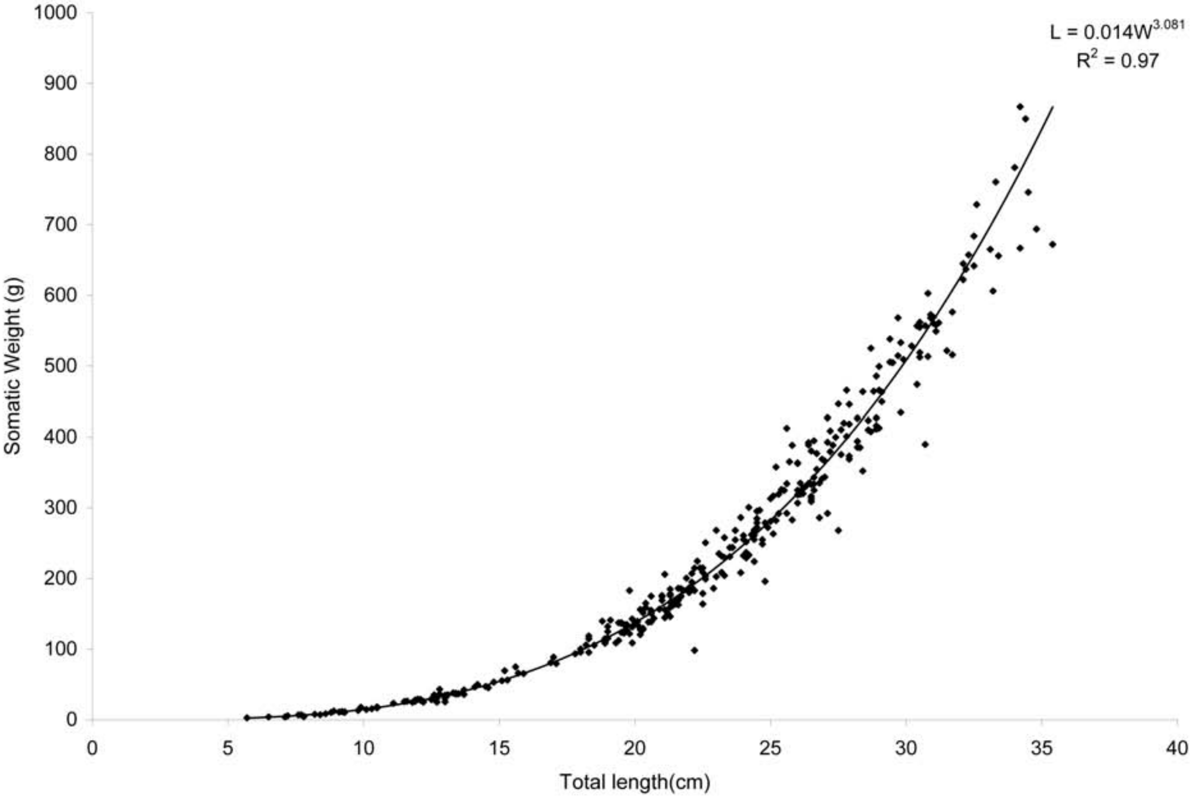

Figure 6. Length-weight relationship for *Sebastes serriceps* collected in southern California.

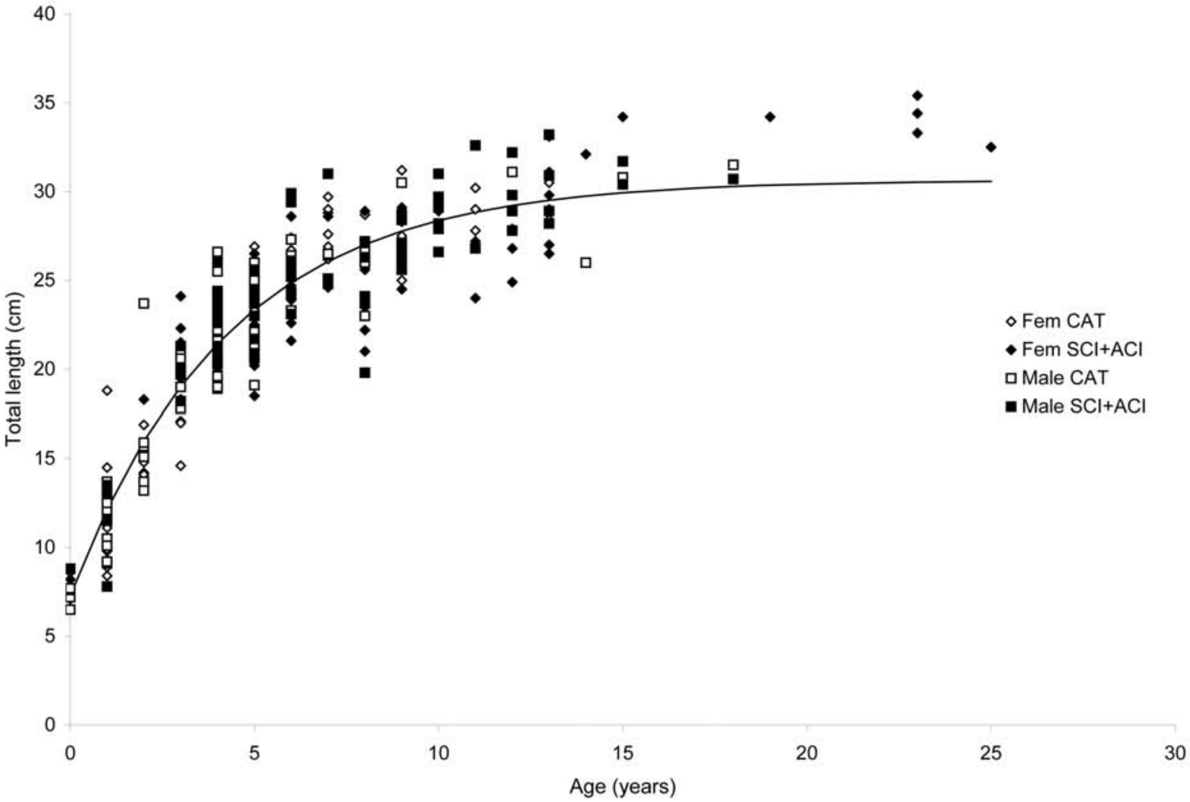

Figure 7. Von Bertalanffy growth curve for *Sebastes serriceps* from southern California.

et al. 1989). The data were described by equation 1, with the instantaneous rate of mortality $Z = 0.12$ and the constant $N_o = 42.15$ for *Sebastes serriceps* within the Southern California Bight (fig. 5).

## Length-weight Relationship

The weight and length data were fitted using equation 2. For *Sebastes serriceps*, $a = 0.014$ and $b = 3.081$ (fig. 6). A two-tailed Student's *t*-test did not quite reject the null hypothesis that $b = 3.0$ ($t = 0.0595$, $df = 335$), indicating that growth of *S. serriceps* cannot be distinguished from isometric growth. A stepwise, multiple linear regression was performed to ascertain whether gender, location, and/or season affected the length-weight relationship. Total length accounted for 99.7% of the variance in somatic weight ($\beta = 0.997$, $p < 0.0005$). None of the other variables had a significant effect on somatic weight (location: $\beta = -0.010$, $p = 0.109$; gender: $\beta = 0.001$, $p = 0.870$; season: $\beta = 0.001$, $p = 0.906$).

## Sexual Dimorphism

We found no difference between the mean length of female ($\overline{x} = 21.9$ cm TL; SD ± 6.5) and male ($\overline{x} = 22.2$ cm TL; SD ± 6.6) treefish using an independent samples *t*-test ($t = -0.42$, $p = 0.67$).

## Length-length Relationship

A two-way ANCOVA revealed that neither sex nor location significantly affected the relationship between standard and total lengths (sex: $F = 0.067$, $p = 0.796$; location: $F = 0.147$, $p = 0.702$). Therefore, parameters for length-length conversions are reported for all fish collected from the Southern California Bight ($n = 310$). The relationship between total length and standard length was described by the equation $y = ax + b$, where $y$ and $x$ are lengths, and $a$ and $b$ are conversion parameters. The equation to determine total length (TL) given standard length (SL) is: $\mathrm{TL} = 1.22(\mathrm{SL}) + 0.17$; and to compute standard length given total length is: $\mathrm{SL} = 0.82(\mathrm{TL}) - 0.07$. $R^2 = 1.00$ for both conversion relationships.

## Length-age Relationship

An analysis of residual sums of squares indicated that there was no statistically significant difference between the VBGFs of males and females ($F = 0.6529$, $\upsilon_1 = 3$, $\upsilon_2 = 305$). Similarly, no significant difference between the VBGFs of specimens from Santa Catalina Island and Santa Cruz Island was found ($F = 2.9070$, $\upsilon_1 = 3$, $\upsilon_2 = 298$), nor was a significant difference found between sexes at either location (Catalina: $F = 0.7846$, $\upsilon_1 = 3$, $\upsilon_2 = 152$; Santa Cruz Island: $F = 1.1458$, $\upsilon_1 = 3$, $\upsilon_2 = 140$). Given the lack of difference between

TABLE 2
**Weight-length Relationship Variables for Several *Sebastes* Species.**

| | Weight-length variables | | | von Bertalanffy growth function parameters | | | |
|---|---|---|---|---|---|---|---|
| Species | $a$ | $b$ | Max total length (cm) | Sex | $L_\infty$ | $k$ | $t_o$ |
| *Sebastes carnatus*[†] | 0.0186 | 2.957 | 42.5 | n/a | n/a | n/a | n/a |
| *S. caurinus*[†] | 0.0172 | 3.018 | 26.4 | Both | 50.00 | 0.120 | n/a |
| *S. chrysomelas*[†] | 0.0081 | 3.257 | 39.6 | F | 21.50 | 0.21 | –0.72 |
| | | | | M | 19.90 | 0.28 | –0.28 |
| *S. nigrocinctus*[†] | 0.0090 | 3.205 | 63.5 | n/a | n/a | n/a | n/a |
| *S. rastrelliger*[§] | 0.045 | 2.77 | 55.9 | Both | 51.3 | 0.11 | –2.41 |
| *S. rosenblatti*[¥] | 0.01103 | 3.10572 | 48.3 | F | 57.99 | 0.053 | –2.468 |
| | | | | M | 56.11 | 0.058 | –2.103 |
| *S. rubrivinctus* | 0.0146[★] | 3.000[★] | 44.0[†] | n/a | n/a | n/a | n/a |
| *S. serriceps*[‡] | 0.01404 | 3.081 | 40.6 | Both | 30.6 | 0.23 | –1.2 |

[¥]Love et al. 1990; [§]Love and Johnson 1998; [†]Love et al. 2002; [★]www.fishbase.org; [‡]This study.

these groupings, VBGF parameters are reported for *Sebastes serriceps* from the Southern California Bight (tab. 2). The von Bertalanffy growth parameters (standard errors) are $L_\infty$ = 30.64 cm TL (0.44), $k$ = 0.233 (0.01), and $t_o$ = –1.167 (0.01) (fig. 7). $L_{max}$ for the species is reported to be 41 cm TL (Miller and Lea 1972). The largest fish in this study was a 23-year-old female that measured 35.4 cm total length. The four oldest specimens (age 19 to 25 years) were all females; the oldest male was 18 years old.

## Reproduction and Maturity

The smallest mature female was 19.0 cm total length and 4 years old. The smallest mature male was 19.7 cm total length and 3 years old. The age at 50% maturity was 4 years for females and 3 years for males. The total length at 50% maturity was 19.0 to 20.9 cm for both males and females. All females were mature by 23 cm total length and 5 years old, and all males were mature by 25 cm total length and 7 years old.

Testes were found to be undergoing spermatogenesis from September to at least December, and more males spawned during December than any other month. One male was found to be spermatogenic in March and one in July; one male was found to be spawning in March and one in May. There is evidence that spawning occurred as early as October because recently spawned males were observed during this month. During June, July, and August, all testes were classified as either recently spawned or resting (fig. 8A).

Ovaries were observed to contain eyed larvae only during the month of March, although fertilized ovaries were observed from February to March, with peak occurrence in February. Females were found in vitellogenesis year-round, with the exception of April, during which all female fish were classified as resting (fig. 8B). Young-of-the-year *Sebastes serriceps* were observed at Santa Catalina Island as early as June (Jana Cobb, pers. comm.[1]), suggesting that larvae and juveniles spend at least three months in the plankton before recruiting to the benthos.

TABLE 3
**Results From a Kruskal-Wallis H Test Examining the Effect of Gonad Stage on the Gonosomatic Index for Mature Female *Sebastes serriceps*.**

| Gonad stage | $n$ | Mean rank |
|---|---|---|
| Vitellogenesis | 11 | 15.09 |
| Fertilization | 6 | 35.33 |
| Parturition | 7 | 38.43 |
| Spawned | 17 | 17.35 |
| Resting | 3 | 16.00 |

Gonosomatic indices varied with month (fig. 9). The peak GSI for females occurred in February and March, which corresponded to maximum fertilization and parturition (fig. 8B). The peak for males occurred in October and is most likely associated with spermatogenesis and the onset of copulation (fig. 8A). The maximum (13.39) and minimum (0.04) GSI for females were both higher than the maximum (9.61) and minimum (0.01) GSI for males. A Kruskal-Wallis test to ascertain the affect of gonad stage on GSI was significant at the Bonferonni-adjusted $\alpha = 0.017$ level (chi-square = 23.910, $df = 4$, $p < 0.0005$). Mean ranks indicated that females in parturition had the highest GSI values and females in vitellogenesis the lowest (tab. 3).

## DISCUSSION

Using edge analysis and length-frequency plots, the annual deposition of rings on the sagittae of *Sebastes serriceps* was validated for fish less than 6 years of age, suggesting that analyzing sagittal otoliths is an appropriate method for estimating the age of *S. serriceps*. Although there is some variation in opaque band deposition, it is similar to that observed for other rockfish

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[1] **Jana Cobb, Department of Biology, California State University, Northridge, CA**

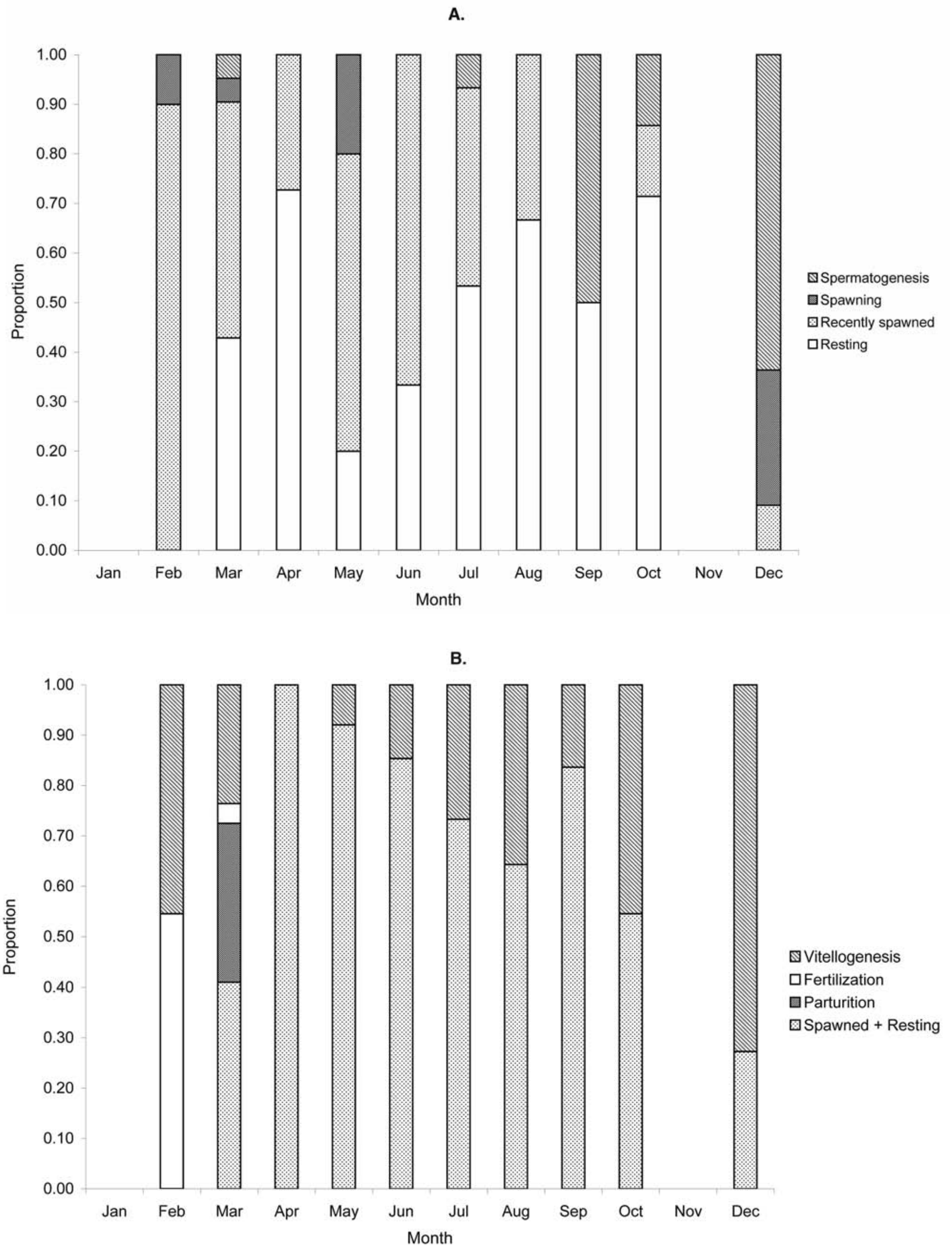

Figure 8. Seasonal variation in gonad stage of *Sebastes serriceps*: A. males; and B. females.

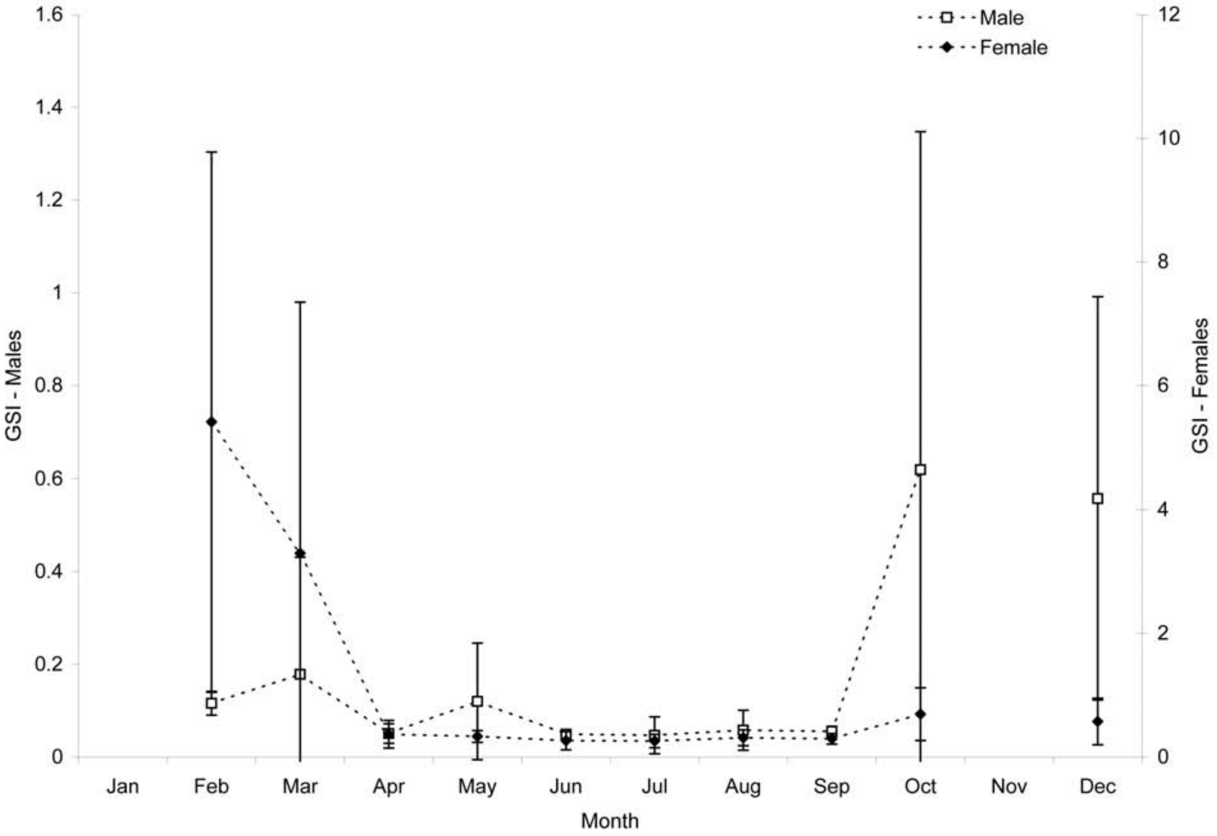

Figure 9. Changes in the average gonosomatic indices of male and female *Sebastes serriceps* from California. Error bars are ±1 standard deviation.

species (Kimura et al. 1979; Pearson et al. 1991; Laidig et al. 2003). Since *S. serriceps* appears to be residential, tagging studies could be used to further validate age determination for older fish.

Several trends in growth and life history have been reported for *Sebastes*. While most rockfish are slow-growing and have VBGF *k*-values between 0.1 and 0.3, Love et al. (1990) found variation in growth rates within the genus, reporting that smaller-bodied species grow more quickly than larger-bodied species. As a mid-sized rockfish, the treefish has a mid-range *k*-value of 0.23, which is similar to that of the ecologically similar *S. chrysomelas* (tab. 2). The length-weight relationship of *S. serriceps* is also similar to other species of solitary, benthic rockfishes as well as to two species closely related to treefish, *S. rubrivinctus* and *S. nigrocinctus* (R. Vetter, pers. comm.[2]) (tab. 2). Love et al. (2002) reported that longevity in rockfishes is positively correlated with body size, northern or cooler water, and deeper depth distribution. *S. serriceps* is a mid-sized rockfish that inhabits the warmer waters of southern California and has a relatively shallow depth distribution. Compared to *S. serriceps*, *S. nigrocinctus* has a more northerly distribution and *S. rubrivinctus* inhabits deeper waters (Love et al. 2002). *S. nigrocinctus* has been aged to 116 years and *S. rubrivinctus* to 38 years (Love et al. 2002). One of the smallest rockfish species, *S. emphaeus*, grows no larger than about 18 cm and lives up to 22 years; one of the largest species, *S. borealis*, reaches up to 120 cm in length and has been aged to 157 years (Love et al. 2002). The maximum reported size for *S. serriceps* is 41 cm and it has been aged to 25 years. When compared with congeners and assessed in light of the trends described above, the aspects of the life history of *S. serriceps* quantified in this study are as expected.

We found no evidence of sexual dimorphism in *Sebastes serriceps*. Males and females did not differ significantly in their mean total lengths. No difference between sexes was found in the length-weight relationship, which is not surprising considering that Love et al. (1990) found no sex-related difference in the length-weight relationship of 14 of the 19 species they examined. Comparison of von Bertalanffy growth functions (VBGF) also revealed no sexual dimorphism in the length-age relationship. This lack of sexual dimorphism in growth is unusual but not unheard of in the genus. Love et al. (2002) reported that six of the 39 species for which data were available showed no difference in length at age be-

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[2] Dr. Russell D. Vetter, NOAA, Southwest Fisheries Science Center, La Jolla, CA

tween males and females. In addition, Love and Johnson (1998) report no significant difference between the growth rates of male and female *S. auriculatus* and *S. rastrelliger*, although they did report that the oldest fish for both species were females. *S. serriceps* seems to be similar; the four oldest individuals collected were female, yet no difference was found between male and female growth rates (fig. 7). Sexual dimorphism may be related to some combination of fecundity and territoriality (Lenarz and Wyllie Echeverria 1991). *S. serriceps* is known to exhibit aggressive behavior (Haaker 1978; J. Hyde, pers. comm.[3]) and is likely to defend territories. All else being equal, if both sexes defend territories, it is expected that they would be of equal size, as observed in *S. chrysomelas* and *S. carnatus* (Larson 1980). However, there are species, such as *Hypsypops rubicundus*, that exhibit little sexual dimorphism although only one sex is territorial (Clarke 1971). Additional research is necessary to ascertain whether both treefish sexes defend territories.

Parturition in rockfish generally occurs in winter or spring (Moser 1967; Wyllie Echeverria 1987) and *Sebastes serriceps* appears to be no exception to this rule, with peak parturition observed in March, and the peak in female gonosomatic index (GSI) in February and March. The autumn peak of male GSI and observed spermatogenesis suggests that, as with other species of *Sebastes* (Moser 1967; Wyllie Echeverria 1987; Bobko and Berkeley 2004), *S. serriceps* is capable of sperm storage for at least three months (fig. 8). Although several congeners have been reported to produce multiple broods per year (Moser 1967; Love et al. 1990), there was no evidence that *S. serriceps* reproduces more than once per year: no eyed larvae were observed undergoing resorption in the presence of vitellogenic eggs (Wyllie Echeverria 1987). However, like *S. rastrelliger* and *S. auriculatus* (Love and Johnson 1998), *S. serriceps* exhibits vitellogenic ovaries throughout the year (fig. 8B). Treefish ovaries staged as vitellogenic between May and December most likely belong to females that did not reproduce during the year (Love and Johnson 1998). In many species of rockfish, males mature at a younger age than females (Wyllie Echeverria 1987; Love et al. 1990). Such a pattern of maturity was not readily apparent for *S. serriceps*: the total length range at 50% maturity was the same for both sexes.

In conclusion, the aspects of the life history of *Sebastes serriceps* examined in this study were similar to comparable species of *Sebastes*. As a shallow-water, medium-sized rockfish with a southerly distribution, it does not exhibit the extreme longevity found in deeper-water, larger, or more northerly distributed species. As with other territorial rockfish in which both sexes defend territories, it does not exhibit sexual dimorphism in its mean length, or weight-length and size-at-age relationships. Areas that warrant further investigation include patterns of geographic variation in life-history characteristics such as growth, mortality, and reproduction. Finally, while *S. serriceps* is part of the recreational and commercial fisheries of California, its fishery has not been formally assessed. With the life-history information now available, an initial assessment of the fishery status of *S. serriceps* is possible.

## ACKNOWLEDGEMENTS

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# CHARACTERIZING SPAWNING HABITATS OF JAPANESE SARDINE (*SARDINOPS MELANOSTICTUS*), JAPANESE ANCHOVY (*ENGRAULIS JAPONICUS*), AND PACIFIC ROUND HERRING (*ETRUMEUS TERES*) IN THE NORTHWESTERN PACIFIC

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## ABSTRACT

We analyzed sea surface temperature, salinity, and depth in the spawning grounds of three small pelagic fishes, Japanese sardine (*Sardinops melanostictus*), Japanese anchovy (*Engraulis japonicus*), and Pacific round herring (*Etrumeus teres*), to compare species-specific characteristics of spawning based on a long-term dataset of egg surveys off Japan from 1978 to 2004. A total of 133,294 samples were obtained by vertical tows of plankton nets. Temperature-salinity-depth plots of the spawning grounds of the three species indicated broad temperature and salinity ranges for anchovy, reflecting a wide distribution from coastal to offshore waters, compared to sardine. Spawning activities of round herring were observed in similar temperature but narrower salinity ranges compared to anchovy. These species-specific temperature/salinity characteristics reflect differences in the location and bottom depth distribution of their spawning grounds. Differential spawning strategies are also reflected in the species-specific relationships between spawning area and egg abundances.

## INTRODUCTION

Small pelagic fish are generally characterized by marked fluctuations in population size. Such cyclic patterns seem to reflect or be influenced by climate changes, as indicated by long-term landing histories (Lluch-Belda et al. 1989; Schwartzlose et al. 1999). In any given ecosystem, however, the timing of population fluctuations and their extent differ between co-existing species of small pelagic fish. A typical example is the alternating dominance of sardine and anchovy in various regions of the world (Kawasaki 1983). In the northwestern Pacific, Japanese sardine (*Sardinops melanostictus*) populations peaked in 1988 and then abruptly decreased to near collapse in recent years, while Japanese anchovy (*Engraulis japonicus*) populations increased during the sardine's collapsing phases (fig. 1; Anonymous 2005). Conversely, the Pacific round herring (*Etrumeus teres*) population has had a smaller but stable biomass during the same periods, although its spatial distribution from the larval to adult stage overlaps with the Japanese sardine and Japanese anchovy along the coastal area (Hanaoka 1972; Tanaka et al. 2006).

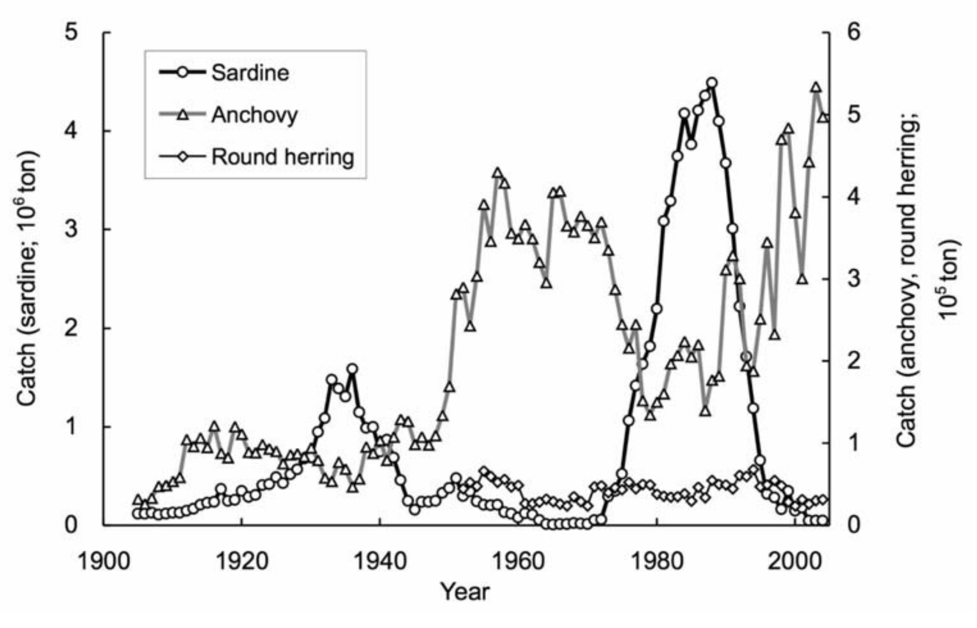

Fig. 1. Landing records of Japanese sardine (*Sardinops melanostictus*: circle), Japanese anchovy (*Engraulis japonicus*: triangle), and Pacific round herring (*Etrumeus teres*: diamond) off Japan from 1905 to 2004.

These patterns tend to be consistent with patterns in other ecosystems dominated by small pelagic fish and are attributed to differential responses to climate-related environmental changes. In this regard, characterizing spawning habitats of co-occurring small pelagic fish species appears critical to understanding these patterns, assuming that the physical conditions of the spawning habitats, crucial to their reproduction and subsequent survival of offspring, play a role in characterizing the spawning habitats.

The characteristics of the spawning grounds of pelagic fish have been described for temperature, salinity, bottom depth, and distance from coasts, and compared between different current systems (cf. van der Lingen et al. 2005). Temperature and salinity records are useful for detecting differences in the spawning habitats of small pelagic fishes with different population fluctuation patterns (Checkley et al. 2000). Sardine distributed in the northern Pacific might be a good example, as the characteristics of the spawning grounds in the northwestern Pacific are thought to be different from those in the northeastern Pacific, because these two populations increased simultaneously even though the temperature fluctuation patterns of the two areas have been quite different (Chavez et al. 2003). Sea surface temperature (SST) and salinity (SSS) in the spawning grounds of these fishes may provide information important to analyzing the synchrony of their population fluctuations.

The spatial overlap between the anchovy and sardine spawning grounds might be crucial from this point of view. However, the species-specific utilization of the spawning grounds should be analyzed before interpreting the consequences of the spatial overlap. There are two specific issues to be considered: the cross-shelf spatial preference and the area of the spawning ground. Spawning ground spatial preferences have been studied in several current systems (cf. van der Lingen et al. 2005), but no detailed analysis has been done in the northwestern Pacific. Relationships between spawning area (SA) and egg abundance (EA) have been analyzed for sardine and anchovy (Mangel and Smith 1990; Watanabe et al. 1996; Zenitani et al. 1998; Zenitani and Yamada 2000). Watanabe et al. (1996) reported a positive relationship between SA and EA for sardine; Zenitani and Kimura (1997) also reported a positive relationship between SA and EA for anchovy. However, the relationship between SA and EA among species has not yet been compared.

Long-term spawning data have been accumulated in various regions of the world to investigate spawning of small pelagic fish. The Japanese Fisheries Agency has conducted egg surveys of small pelagics since 1947, and small pelagic spawning habitats and egg production from 1978 to 1996 have been reported (Mori et al. 1988; Kikuchi and Konishi 1990; Ishida and Kikuchi 1992; Zenitani et al. 1995; Kubota et al. 1999). Recent information on the spawning habitats and egg productions off the Pacific coast of Japan has been reported in a series of Fisheries Research Agency annual reports (Anonymous 1997–2004). These reports suggested that the spawning area was affected by population size. However, the differences in the spawning habitat cannot be resolved by looking at the spawning ground distribution and estimates of egg production alone.

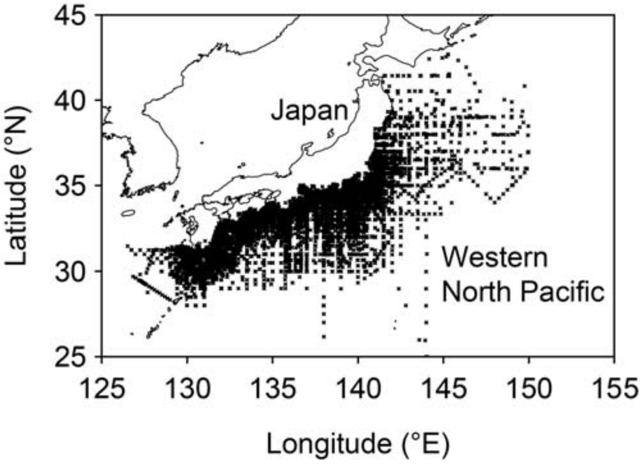

Fig. 2. Sampling stations of egg and larval surveys off the Pacific coast of Japan from 1978 to 2004. Both fixed and unfixed stations are shown together. Redrawn from Takasuka et al. (2007).

The present study characterizes the spawning habitats of three major small pelagic fishes (Japanese sardine, Japanese anchovy, and Pacific round herring), using Japanese Fisheries Research Agency datasets from 1978 to 2004. These long-term datasets, which covered the low and high population periods of both sardine and anchovy, were used to compare the species-specific environmental characteristics of the spawning grounds.

## MATERIALS AND METHODS

Egg and larval surveys along the Pacific coast of Japan have been historically conducted by 18 prefectural fisheries research laboratories and two national research institutes of the Fisheries Research Agency since 1947. We use data from these surveys. The survey areas covered the major spawning grounds of Japanese anchovy and sardine off the Pacific coast (fig. 2), and survey cruises were conducted monthly, with more intense sampling during early spring. Egg and larva samples were obtained using vertical tows of a net with 0.33 mm or 0.335 mm mesh size from 150 m depth (or just above the bottom) to the surface, equipped with a flowmeter to estimate the water volume filtered. Sampling nets varied throughout the time period: from 1947 through 1990, “Marutoku-B” net (45 cm mouth diameter, 80 cm-long conical net), “Marunaka” net (60 cm mouth diameter, 150 cm-long conical net), and NORPAC net (45 cm mouth diameter, 180 cm-long conical net) was used (Nakai 1962); since 1991, long NORPAC net (45 cm mouth diameter, 65 cm + 130 cm-long cylindrical-conical net) were used for all egg survey cruises. Despite the changes of sampling gears, sampling efficiency was not significantly different throughout the years (Matsuoka 1995a, b; Zenitani 1998). For all survey years, net samples were identified, sorted, and counted for eggs of small pelagics. Temperatures and salinities at several layers were measured by reversing thermometers or CTD.

Temperature-salinity-depth plots for eggs of the three species were described using all SST, SSS, and bottom-depth data at the sampling station along with egg density (individuals per m$^3$) from 1978 to 2004 off the Pacific coast of Japan (from 29°N 129°E to 42°N 145°E). Data from 1947 to 1977 were not used because the number of samples was limited (<800 stations per year) and because a portion of tows lacked flow-meter records. Egg densities (individuals per m$^3$) were estimated from flow-meter filtering rates, towing distance, and tilt angle of the wire. Depth data were obtained from the website of the Japan Oceanographic Data Center (http://www.jodc.go.jp/data_set/jodc/jegg_intro_j.html, accessed on 8 Nov. 2006) from which average depth for each 0.01-square degree was estimated. Due to the large number of small islands and the complex topography of the area, bottom depth was used as a proxy for the distance from the coast.

Quotient analyses of bottom depth class were plotted to compare differences in distance from shore of the spawning grounds of the three species. The frequency of positive egg samples for all sampling stations (% eggs $_D$) was divided by the frequency (%) of this depth class in all sampling stations (% sampling station $_D$). The quotient in each depth class ($Q_D$) was calculated as (Twatwa et al. 2005):

$$Q_D = \frac{\%\ eggs_D}{\%\ sampling\ station_D} \tag{1}$$

Monthly egg abundance was calculated for each 15' square. The resolution has been updated from the 30' latitude × 30' longitude squares that have previously been used in the annual reports of egg and larval surveys (e.g., Mori et al. 1988; Kubota et al. 1999). Our calculation procedures were similar to Mori et al.'s (1988) and Kubota et al.'s (1999) except for the spatial resolution. First, the number of eggs was standardized to densities per m$^2$ for each tow. Then, egg density per 1 m$^2$ was calculated for each 15' × 15' square by arithmetically averaging egg densities of all tows conducted in the square for each month. Egg abundance in the 15' × 15' square $i$ in month $j$ ($E_{ij}$) was calculated using the egg density (number per m$^2$) in the square in that month ($D_{ij}$), with egg incubation time and survival rate being considered (Nakai and Hattori 1962):

$$E_{ij} = \frac{1}{s} \bullet \frac{d_j}{d'_{ij}} \bullet A_i \bullet D_{ij} \tag{2}$$

where $s$ is the survival rate during egg stage (day$^{-1}$), which was 0.571 for sardine, 0.600 for anchovy and 0.571 for round herring (Watanabe 1983; Mori et al. 1988; Kubota et al. 1999; Watanabe T. unpubl. data), $d_j$ is the number of days in month $j$, $d'_{ij}$ is the egg incubation time in days in the square $i$ in month $j$, and $A_j$ is the area of the square $i$ (m$^2$). Mortality during egg stages was estimated from the long-term datasets providing egg stage. Estimated survival rates were used to compare relationships between egg abundance and spawning area between the three species. Area value of each square was estimated by the 20 m mesh GIS data (25000V; Hokkaido-chizu Co., Ltd.). Egg incubation time was estimated using a function of SST based on the Arrhenius' equation (Hattori 1983; Uehara and Mitani 2004; Watanabe T. 1983):

$$d_{ij} = \frac{1}{24} \bullet 10^{\left(\frac{a}{t_{ij}+273} - b\right)} \tag{3}$$

where $t_{ij}$ is the mean SST weighted by egg occurrence, $a$ and $b$ are constants ($a$ = 4760, $b$ = 14.6 for sardine, $a$ = 4060, $b$ = 12.2 for anchovy and $a$ = 3656, $b$ = 10.7 for round herring).

Annual relationships between spawning area and egg abundance were examined both for the total egg counts for each year and for the egg count during the peak spawning month of the three species. Total spawning area and egg abundance in a given year were calculated by simply summing up the monthly data from January to December for anchovy and from October of the previous year to September of the given year for sardine and round herring based on their specific spawning seasons (see Results). The relationships between total spawning area (during the whole spawning period) and annual spawning stock biomasses (SSB), estimated through virtual population analyses (Anonymous 2005), were also analyzed for sardine and anchovy. Relationships between spawning area, egg abundance, and SSB were also analyzed for the peak egg abundance month, which is February for sardine and June for anchovy.

## RESULTS

A total of 133,294 stations were covered by the survey and 126,080 net samples were available for the present analyses (fig. 2). Mean sampling area coverage (sum of areas of 15' latitude × 15' longitude squares in which

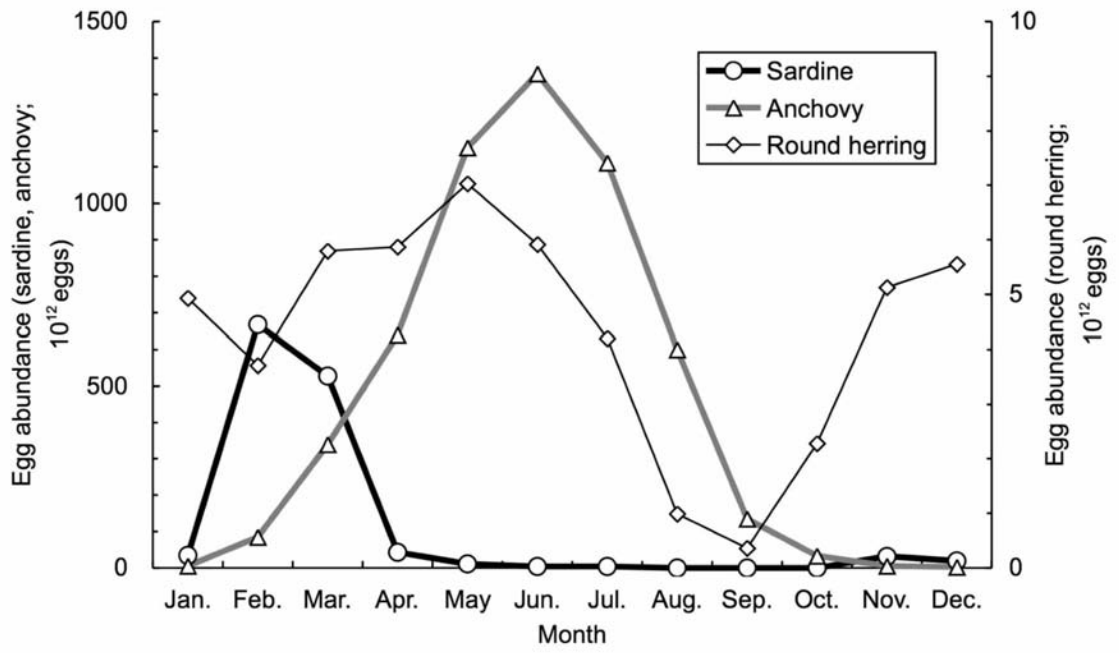

Fig. 3. Mean monthly egg abundance of Japanese sardine (*Sardinops melanostictus*: circle), Japanese anchovy (*Engraulis japonicus*: triangle), and Pacific round herring (*Etrumeus teres*: diamond) along the Pacific coast of Japan from 1978 to 2004.

sampling was conducted) ranged from 7.05 × $10^4$ $km^2$ (September) to 14.58 × $10^4$ $km^2$ (February). Number of samples (frequency of plankton net tows) per month during 1978 to 2004 ranged from 253 (September) to 456 (February). Annual total sampling area coverage and number of samples (summed for all months) have been almost constant since 1978, ranging from 92.50 × $10^4$ $km^2$ (1978) to 128.31 × $10^4$ $km^2$ (2004) and from 3,188 (1997) to 4,308 (1982), respectively.

A total of 10,890 positive samples were collected for spawning sardine, 24,718 for anchovy, and 10,420 for round herring from 1978 to 2004. Mean egg abundance per month indicated that the sardine spawning season, estimated as the period in which more than 95% of eggs were spawned, was from November to April, with peak spawning in February (fig. 3). The main spawning season of anchovy was from March to August with peak spawning in June. For round herring, the main spawning season was from October to July with a peak in May. While our recorded months of peak spawning for sardine and anchovy are slightly different from those in previous studies (Watanabe et al. 1996; Zenitani and Kimura 1997), the main spawning seasons are stable and thus the months of peak spawning calculated from the long-term data are appropriate for characterizing species-specific spawning behaviors.

Temperature-salinity-depth plots of the spawning grounds were described from the positive sampling data for the three species from 1978 to 2004 (figs. 4–6). Spawning activities of Japanese sardine were observed in the SST range of 10° to 25°C, and the abundant egg distributions were observed mainly at salinities of 33.5 to 35.5 psu (fig. 4). Abundant spawning activities were not only observed in the shallow coastal waters but also in the surface waters of offshore areas over bottom depths of up to 5000 m. The salinity of the spawning ground was not, however, lower than 31 psu. The SST range in the offshore areas (deeper than 1000 m depth), was between 15° to 21.5°C, but abundant spawning (>100 eggs per $m^3$) was only observed in SSTs of 18° to 21.5°C and in the high salinity waters.

The temperature-salinity-depth plots of the spawning grounds of Japanese anchovy indicated very wide temperature and salinity ranges, from 12° to over 30°C and mainly from 23 to 34.5 psu, respectively (fig. 5). Spawning activities of anchovy were observed both in shallow coastal areas and deep offshore areas (up to 5000 m bottom depth), and high egg abundances were not only observed in shallow, low salinity areas (less than 33 psu), but also in the high salinity offshore waters (up to 35.5 psu).

Temperature ranges of the round herring spawning grounds were from 10° to 30°C, which was similar to those of anchovy, although the eggs were concentrated only in a narrow SSS range of 30 to 35.5 psu (fig. 6). High densities of eggs were not observed in the surface waters of areas deeper than 3000 m, and spawning was not active in low salinity, coastal areas (<25 psu).

Results of the bottom depth quotient analyses of the spawning grounds indicated marked contrasts among the three species (fig. 7). The highest values of the anchovy depth quotient were found at the shallowest sampling

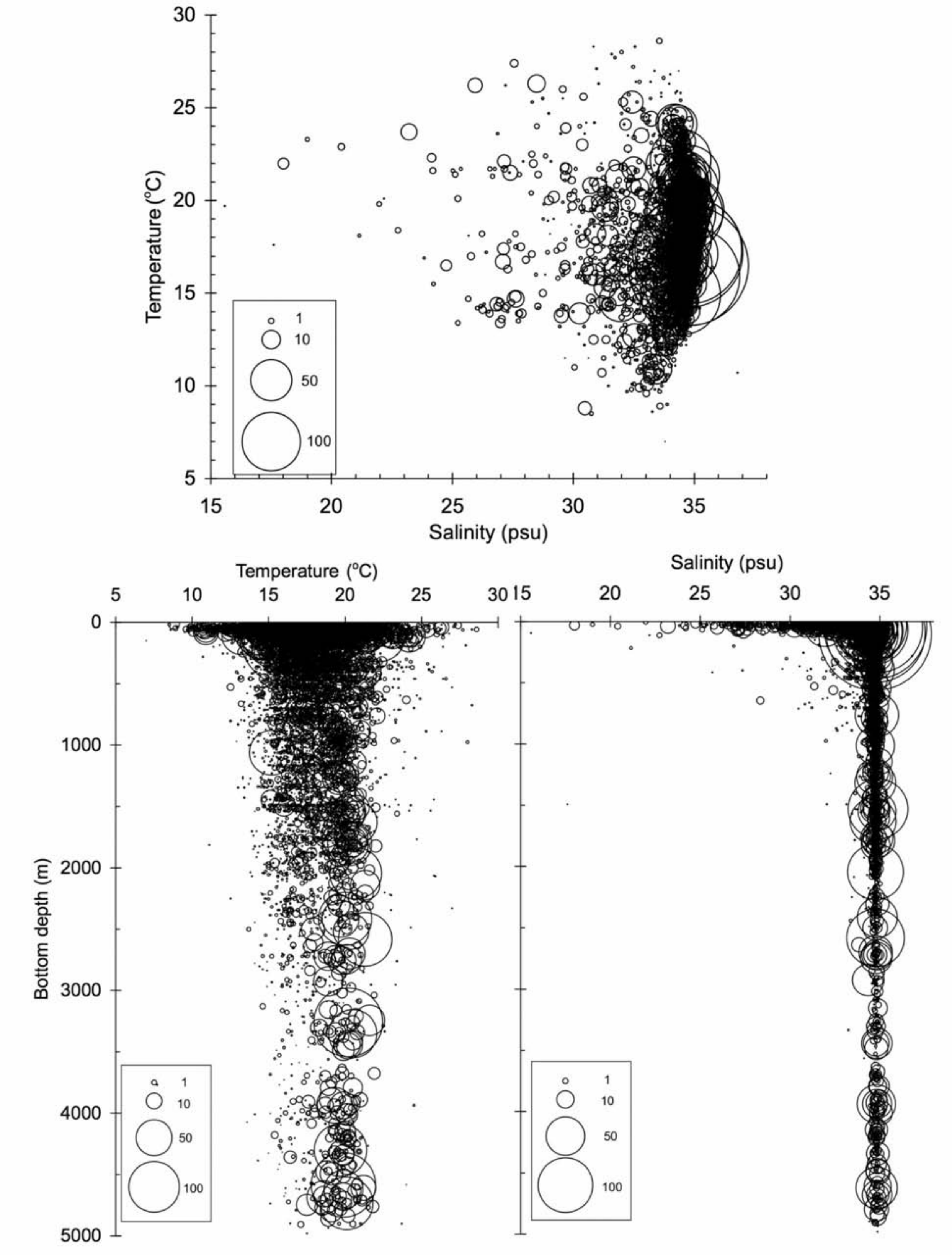

Fig. 4. Temperature-salinity-depth plots of the spawning grounds of Japanese sardine (*Sardinops melanostictus*) along the Pacific coast of Japan from 1978 to 2004. Circle size indicates egg density (individuals per $m^3$) calculated from each net sampling towed from 150 m depth (or just above the bottom) to the surface. Station depth (m) indicates the bottom depth of each station.

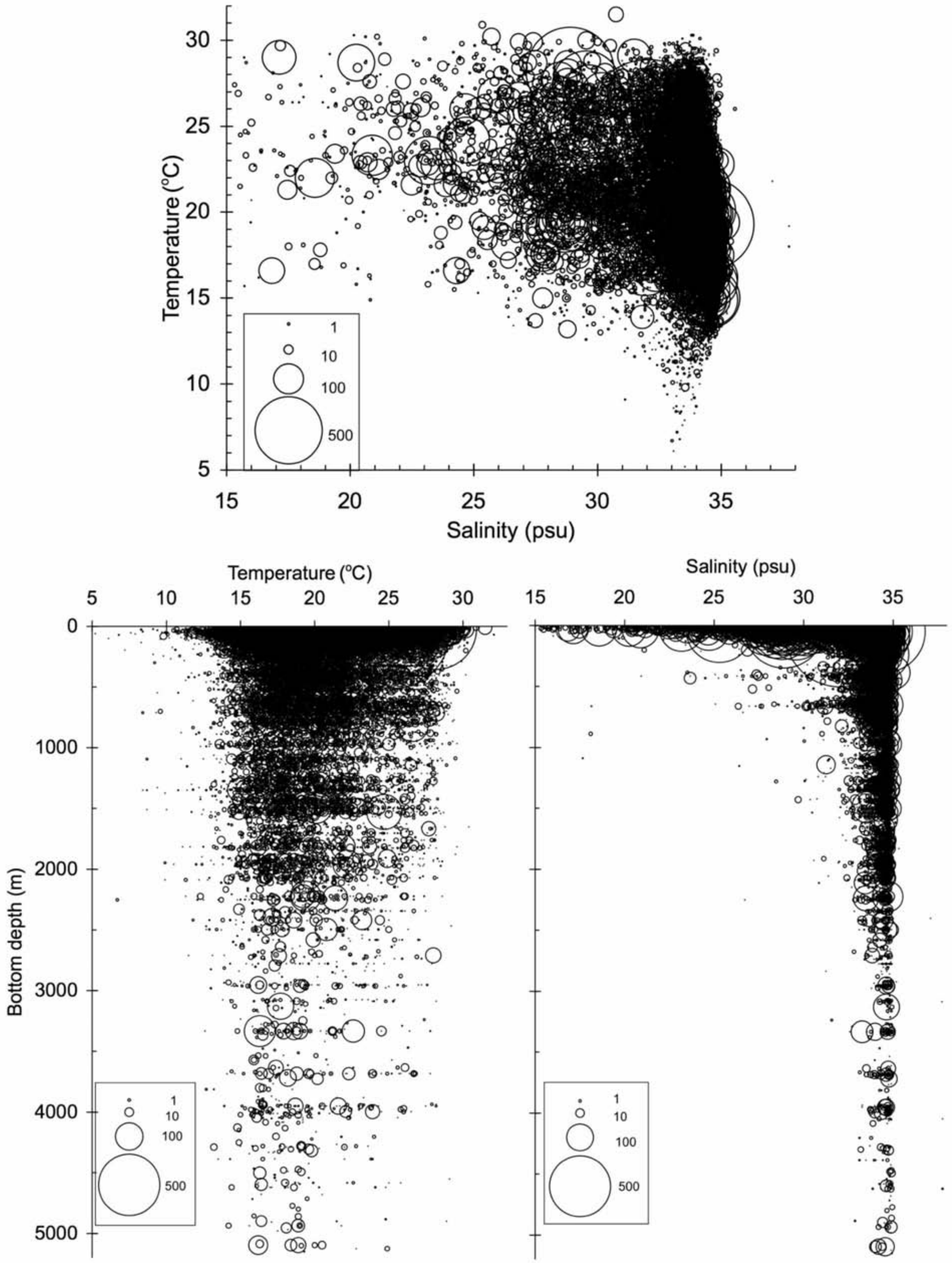

Fig. 5. Temperature-salinity-depth plots of the spawning grounds of Japanese anchovy (*Engraulis japonicus*) along the Pacific coast of Japan from 1978 to 2004. Circle size indicates egg density (individuals per m$^3$) calculated from each net sampling towed from 150 m depth (or just above the bottom) to the surface. Station depth (m) indicates the bottom depth of each station.

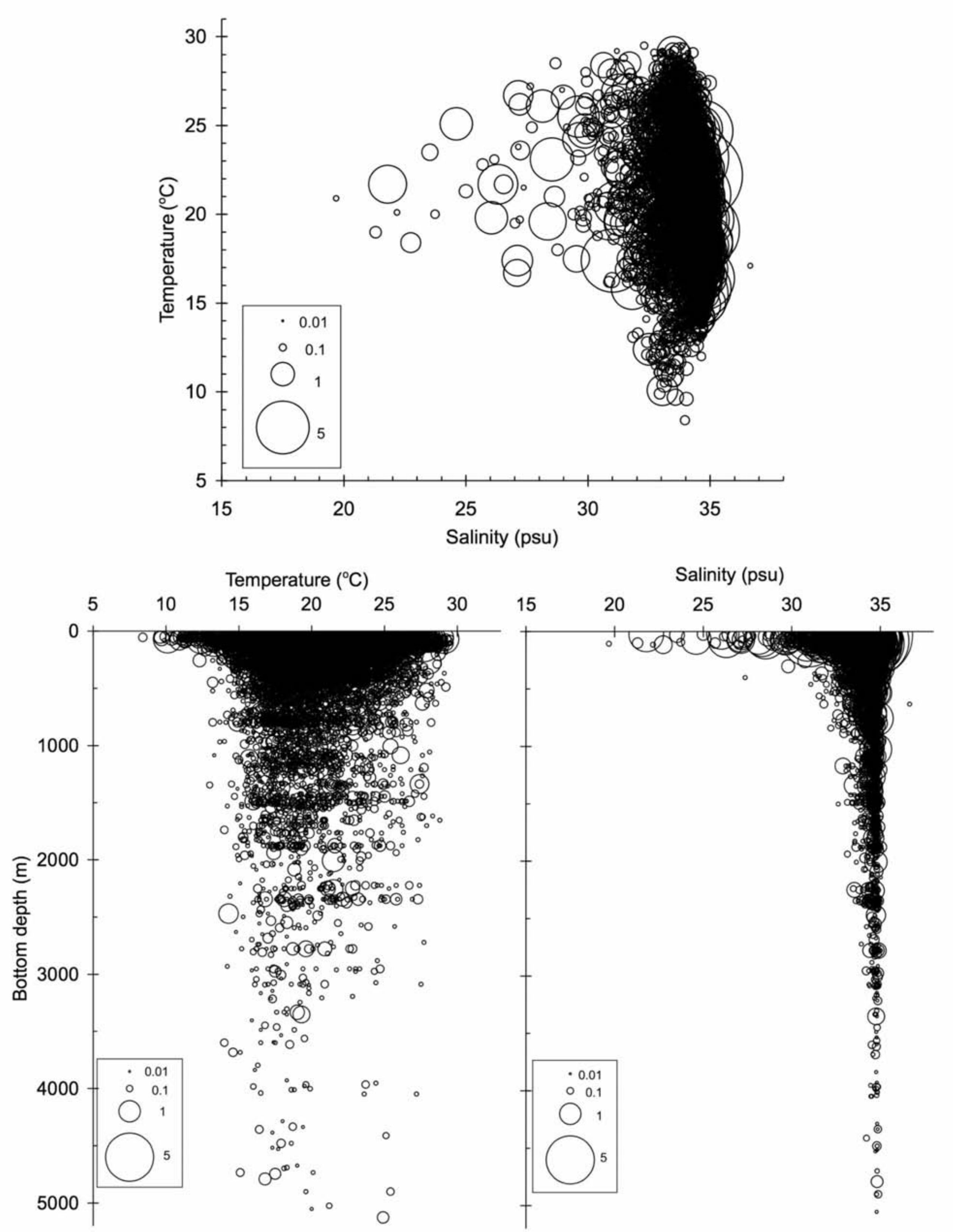

Fig. 6. Temperature-salinity-depth plots of the spawning grounds of Pacific round herring (*Etrumeus teres*) along the Pacific coast of Japan from 1978 to 2004. Circle size indicates egg density (individuals per m$^3$) calculated from each net sampling towed from 150 m depth (or just above the bottom) to the surface. Station depth (m) indicates the bottom depth of each station.

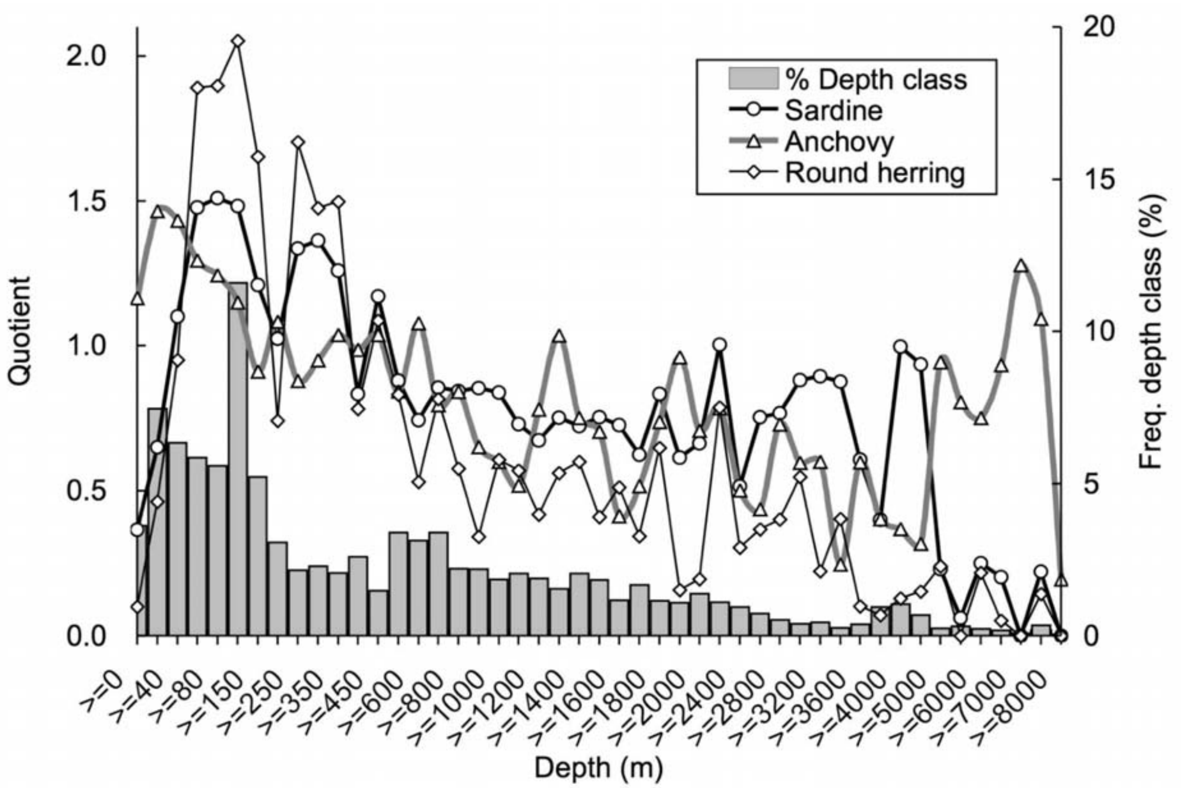

Fig. 7. Frequency distribution of depth class (histograms) and egg abundance/depth quotients (symbols and lines) for sardine (circle), anchovy (triangle), and round herring (diamond) along the Pacific coast of Japan from 1978 to 2004.

station (<60 m depth); for round herring they were at stations 80–400 m depth; and for anchovy they were around 1.0 at the same stations. Both sardine and anchovy had similar stable quotient values of less than 1.0 at stations 400 to 4000 m depth. The quotient for sardine decreased at stations deeper than 5500 m, although this was not the case for anchovy.

Significant species-specific log-linear relationships between egg abundance (EA) and the spawning area (SA) were observed for both sardine and anchovy, although no significant relationship between EA and SA was found for round herring because of its narrow egg abundance range in the time series (fig. 8). Relationships between EA and SA in the peak spawning period were not markedly different between sardine and anchovy. However, the total annual SA for anchovy was larger than that of the sardine because of its longer spawning season (fig. 8).

Significant species-specific relationships between SA and SSB both in the peak-spawning month and in the annual total were similar for sardine and anchovy (fig. 9). SA for anchovy was larger than that for sardine at the same SSB level, although the annual variance and the maximum value of SSB were much larger for sardine than for anchovy. Plots for round herring could not be computed due to uncertainties in stock estimation.

## DISCUSSION

Temperature-salinity (TS) plots of the spawning grounds indicated differential patterns among the three species. Sardine spawning was characterized by a stenohaline pattern in the higher salinity range associated with offshore waters, and by a eurythermal pattern in the relatively low temperature of 10° to 25°C. Nakai et al. (1955) analyzed three years of egg survey data from 1949 to 1951 and reported that SST for sardine spawning ranged from 11.1° to 19.1°C and SSS ranged from 33.06 to 35.04 psu, while spawning mainly occurred at temperatures of 13° to 16°C and salinities of 34.00 psu. Ito (1961) summarized data to show that the main spawning temperature varied depending on latitude: from 17°–19°C in the southern areas, and from 14°–17°C in the northern areas of the Pacific coast of Japan. Kuroda (1991) reported that the temperature range of sardine spawning grounds was from 11° to 21°C and that the main spawning temperatures from 15° to 19°C were along the Pacific coast of Japan. These previous findings agree well with the present results and the temperature and salinity ranges analyzed in this study. Overall, SSTs of 10° to 25°C and salinities of 33.5 to 35.5 psu are typical Japanese sardine spawning grounds. The main spawning temperature range indicated in this study, 15°–21.5°C, also coincides with laboratory studies. Zenitani (1995)

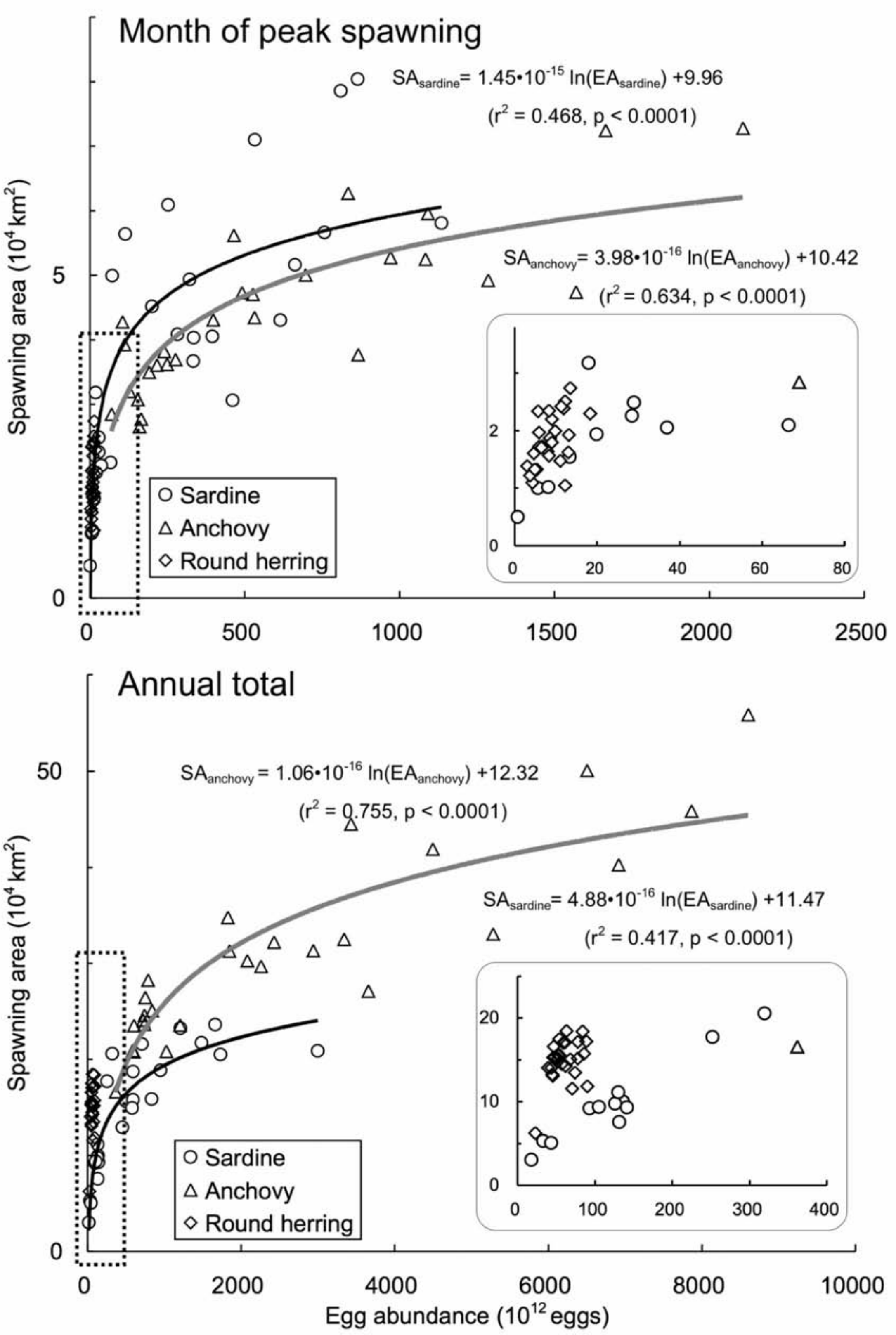

Fig. 8. Relationships of spawning area to egg abundance for Japanese sardine (*Sardinops melanostictus*: circle), Japanese anchovy (*Engraulis japonicus*: triangle), and Pacific round herring (*Etrumeus teres*: diamond) in the Northwestern Pacific from 1978 to 2004. Upper panel indicates the data in the month of egg abundance peak (February for sardine, June for anchovy, and May for round herring). Lower panel indicates data summed from October of the previous year to September for sardine and round herring and from January to December for anchovy. A close-up of the range enclosed by dotted line is shown in each panel.

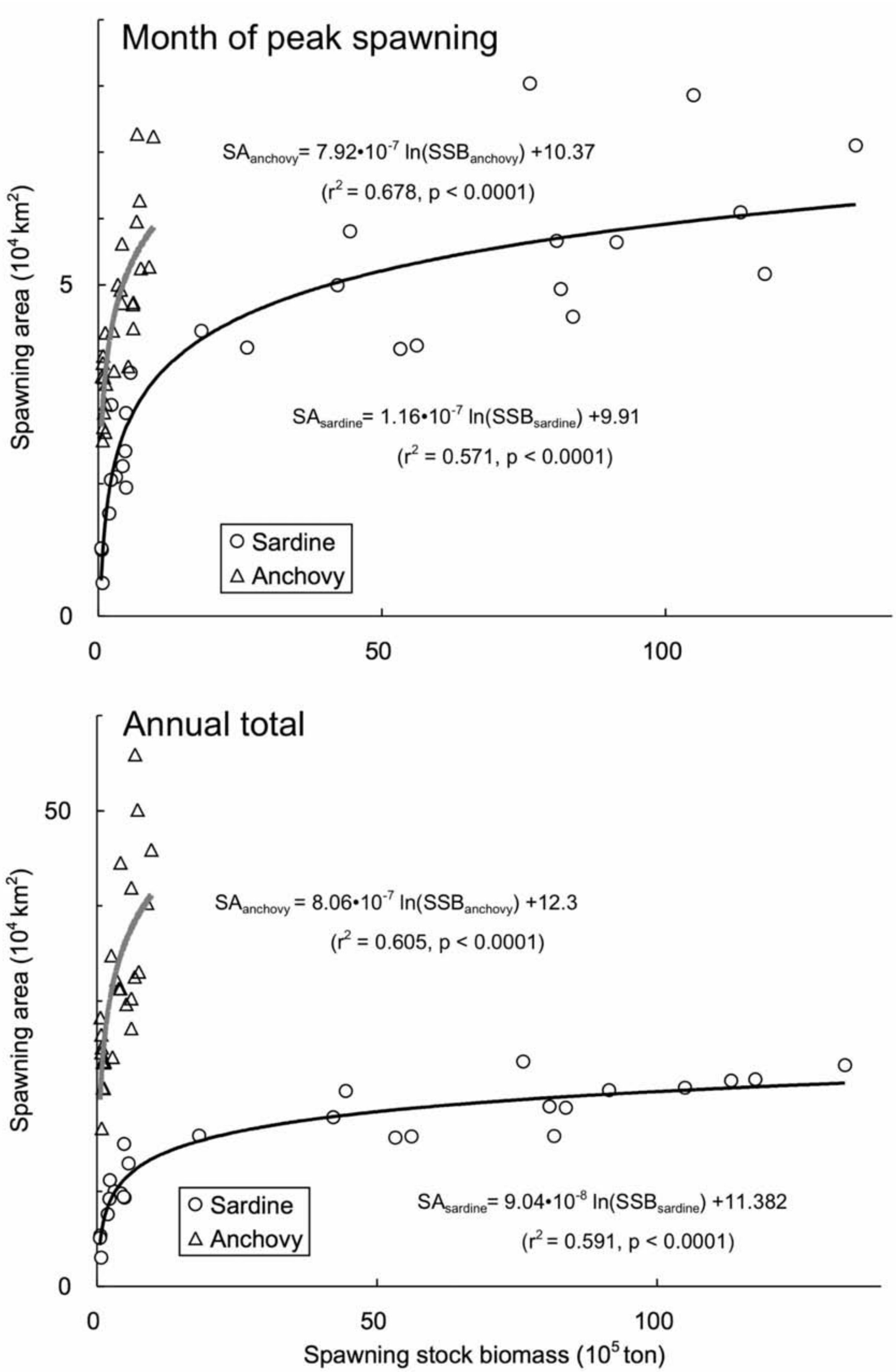

Fig. 9. Relationships of spawning area to spawning stock biomass for Japanese sardine (*Sardinops melanostictus*: circle), and Japanese anchovy (*Engraulis japonicus*: triangle) in the Northwestern Pacific from 1978 to 2004. Upper panel indicates the data in the month of egg abundance peak (February for sardine, and June for anchovy). Lower panel indicates the data summed from October of the previous year to September for sardine and round herring and from January to December for anchovy.

reported that embryo length and the yolk-sac volume of larvae hatched at 19°C was significantly larger than those that hatched at 15° and 23°C. Takasuka et al. (2007) pointed out that the optimum growth temperature was 16.2°C for Japanese sardine larvae. Therefore, the TS plot of the sardine spawning grounds reflects the physical environment preferable for larval growth.

Data from anchovy spawning grounds indicated a euryhaline pattern from estuarine (lower salinity) to offshore waters (higher salinity), and also a eurythermal pattern from 12° to over 30°C. Nakai et al. (1955) reported that the temperature and salinity in anchovy spawning areas was from 12.0° to 24.7°C (peak temperature: 17.7°C) and from 26.74 to 35.23 psu, respectively. Both temperature and salinity ranges were broader for anchovy than for sardine. Long-term data analyses in this study confirmed these results and indicated that the ranges of spawning temperature and salinity were broader than those reported in Nakai et al. (1955).

Spawning grounds of round herring were characterized by a eurythermal pattern from 10° to over 30°C, which is broader than the range previously reported in Nakai et al. (1955; 14° to 23°C). It was confirmed, however, that the salinity range of round herring spawning grounds was from 30.35 to 35.23 psu (Nakai et al. 1955), and that round herring are located in the high salinity stenohaline area between estuarine and offshore waters.

The different environmental characteristics of the spawning grounds of the three species could be associated with their specific spawning ground locations. This is particularly evident in the bottom depth of the spawning ground, used as a proxy for the distance from the coast. Both sardine and anchovy have the ability to expand their spawning grounds offshore, unlike round herring. Differences in TS where spawning activity occurred, however, reflect differences in the locations of sardine and anchovy spawning. TS plots of sardine spawning grounds, which indicated a stenohaline pattern in high salinity and a eurythermal pattern at relatively low temperatures, are consistent with a lack of spawning in the low-salinity and high-temperature coastal waters. The broader temperature adaptability of anchovy reflects active use of low-salinity coastal waters, along with offshore waters, for spawning. On the other hand, round herring can use neither near-coastal waters, because of its stenohaline spawning behavior, nor offshore waters.

The species-specific characteristics of the spawning grounds differ from other current systems, even when compared within the same genus. In upwelling-dominated systems, spawning grounds both for sardine and anchovy are characterized by relatively high salinity waters (>33 psu, van der Lingen et al. 2005). For example, off California, *Sardinops sagax* and *Engraulis mordax* spawned in a narrow salinity range from 32.5 to 33.5 psu, with sardine spawning in relatively lower-salinity offshore waters compared to anchovy (Checkley et al. 2000); and the main spawning temperature for anchovy was lower than that for sardine (Lluch-Belda et al. 1991). Similar spawning ground separation between *Sardinops sagax* and *Engraulis encrasicolus* was reported for the southern Benguela area, with sardine spawning located inshore and anchovy spawning offshore, although this pattern may not be consistent historically (Barange and Hampton 1997; Barange et al. 1999). These differences potentially are the result of adaptation to different current systems, i.e., western and eastern boundary currents, and may help explain the synchronicity in population fluctuations between areas related to fluctuating environmental characteristics. Further studies are needed to compare species-specific biological characteristics of small pelagics among different current systems.

Relationships between spawning area (SA), egg abundance (EA), and spawning stock biomass (SSB) also reflect the species-specific use of the spawning grounds. The present results indicated species-specific relationships between SA and EA, reflecting differential use of spawning grounds. Our results confirmed the positive relationship reported as $SA = 60.9\ EA^{0.181}$ for sardine (Watanabe et al. 1996). Anchovy utilize a larger spawning area than the sardine (per unit of egg abundance) for the whole spawning season, although in the peak spawning month no large differences were observed between sardine and anchovy. The difference thus may be explained by the duration of spawning seasons, which was two months for sardine and five months for anchovy. The difference in spawning season duration might be attributable to the wide ranges of temperature and salinity of anchovy sardine spawning. Barange et al. (2005), however, proposed that differences in the use of space between anchovy and sardine might be due to more complex factors, such as different school structures of *Sardinops sagax* and *Engraulis encrasicolus* in the southern Benguela. The relationship between SA and SSB presented in this study also suggests a similar phenomenon where anchovy utilized a larger spawning area than the sardine.

Our results indicate that the preferred environment for spawning was partially explained by species-specific inshore-offshore spawning patterns, but also reflected species-specific patterns of space use, in terms of spawning area per unit of biomass. Furthermore, there is a possibility that species-specific physiological preferences may determine when, where, and how long small pelagic fish spawn eggs. Concerning this issue, Bellier et al. (2007) analyzed historical shifts of spawning grounds of *Engraulis encrasicolus* and *Sardina pilchardus* and concluded that the shifts in spawning grounds reflected changes in population size and demography as well as environmental conditions. Watanabe et al. (1996) also reported the historical shifts of spawning grounds of Japanese sardine, showing that age structures of the spawners changed as population size fluctuated. The present study showed differences in spawning habitats among small pelagic fish in the Northwestern Pacific. Although spatial and temporal dynamics of spawning habitats needs further study, the species-specific patterns that are presented here are an essential step toward describing the spawning strategies of small pelagic fish in different ecosystems.

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# COMPARISON OF UPWELLING INDICES OFF BAJA CALIFORNIA DERIVED FROM THREE DIFFERENT WIND DATA SOURCES

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## ABSTRACT

We compared the NOAA Southwest Fisheries Science Center's Environmental Research Division (formerly Pacific Fisheries Environmental Laboratory: PFEL) coastal upwelling indices along the northern Baja California coast with those derived from winds measured by coastal meteorological stations and estimated by the QuikSCAT satellite. With the exception of the PFEL series at 33°N, the three data sets compare reasonably well, having similar typical year patterns, correlations >0.6, and significant coherences for periods three to five days or longer. By contrast, the seasonal variations, the timing and magnitude of maximum upwelling, and the variability of the PFEL indices at 33°N are significantly different compared to all the other time series, including QuikSCAT at that location. The performance of the QuikSCAT winds close to shore was evaluated using the coastal meteorological station data. Although large root-mean-square (RMS) errors in direction were found for the QuikSCAT winds, both datasets have properties similar to the variance ellipses, and show reasonable coherences for frequencies in the weather band and lower, particularly south of 33°N.

## INTRODUCTION

Winds near the Pacific Coast off Baja California blow predominantly from the north-northwest, causing an offshore Ekman transport that results in year-round upwelling of cold, relatively saline and nutrient-rich waters in the coastal region (Lynn 1967; Bakun and Nelson 1977; Huyer 1983; Schwing et al. 1996; Strub and James 2000). Coastal upwelling helps explain the large productivity along the North American coast and upwelling intensity has been linked with variability in fish stocks and other factors affecting coastal ecosystems (e.g., Reid et al. 1958; Ryther 1969; Longhurst 1998). Researchers have also used upwelling variability to explain zooplankton population spatial processes in coastal systems (Peterson et al. 1979), and more recently a link between latitudinal variability in coastal upwelling and intertidal larval supply, population dynamics, and community structure has been hypothesized (Roughgarden et al. 1988; Connolly et al. 2001).

Coastal Upwelling Indices (CUI) at 15 standard stations along the North American coast have been generated since 1945 by the NOAA Fisheries Southwest Fisheries Science Center's Environmental Research Division (formerly the Pacific Fisheries Environmental Laboratory: PFEL), and are publicly available at its website (http://www.pfel.noaa.gov/). The indices are estimates of the offshore Ekman transport obtained from geostrophic winds, which in turn are derived from the surface pressure fields of the operational atmospheric model provided by the U.S. Navy Fleet Numerical Meteorology and Oceanography Center (FNMOC), Monterey, California. For historic reasons, and to be consistent with previous references, we will refer to the Environmental Research Division coastal upwelling indices as the "PFEL indices."

The PFEL indices have been widely accepted, with more than 50 regular users each month, several dozens of additional requests for the data each year, and more than 400 scientific publications referencing them (Schwing et al. 1996). The studies cover topics ranging from descriptions of coastal circulation patterns, climate change, and linkages between environmental and biological variability. They have been particularly popular in linking physical forcing with marine population variability (e.g., Ainley et al. 1993; Parrish and Mallicoate 1995; Rau et al. 2001; Koslow et al. 2002; Ladah and Zertuche 2004).

The limitations of the PFEL indices have been discussed elsewhere (e.g., Schwing et al. 1996). The most important may be the fact that upwelling is the combined effect of two processes: the offshore Ekman transport due to the alongshore component of the winds (which is what the PFEL indices represent) and the Ekman pumping that results from the curl of the winds near the coast. The latter may be an equally or even more important contributor to surface Ekman divergence and upwelling, especially downstream of islands, capes, and other coastal promontories (Bakun and Nelson 1991; Enriquez and Friehe 1995; Schwing et al. 1996; Münchow 2000; Pickett and Paduan 2003; Koracin et al. 2004; Pickett and Schwing 2006).

PFEL indices off California have been compared with the offshore Ekman transport derived from satellite winds close to the PFEL indices grid points (Pickett and Schwing 2006), and the offshore Ekman transport and Ekman pumping close to shore using the 9 km resolution Coupled Ocean/Atmospheric Mesoscale Prediction System (COAMPS) model (Pickett and Paduan 2003; Pickett and Schwing 2006). Pickett and Schwing (2006) found reasonable agreement between weekly averages of the PFEL indices and the corresponding offshore Ekman transport derived from satellite winds on the PFEL grid, although a better comparison was found using the model winds (instead of the geostrophic winds used for the PFEL indices). On the other hand, the high resolution model showed narrow bands (about 20 km offshore by 50 km alongshore) of strong wind stress and wind stress curl adjacent to major coastal promontories, suggesting that Ekman pumping may be as large a contributor to upwelling as offshore Ekman transport. Nevertheless, Pickett and Paduan (2003) found a significant correlation, similar means, and seasonal variations between the PFEL indices and the net upwelling (offshore Ekman transport plus Ekman pumping), in spite of the fact that the PFEL indices do not include Ekman pumping. They attribute this similarity to an overestimation of the offshore Ekman transport by the PFEL indices, given that the winds generally increase with offshore distance, resulting in stronger winds at the PFEL grid than in the coastal zone.

These studies conclude that the PFEL indices are reasonable estimates of the regional upwelling off North America, but higher spatial resolution models are needed to accurately represent the magnitude and variability of local coastal upwelling.

Finally, intertidal ecologists have used PFEL indices to explain temporal and latitudinal variation in invertebrate recruitment. This usage is problematic because PFEL indices do not accurately represent nearshore hydrodynamics where invertebrate larvae are most likely to be found; PFEL indices are unlikely to capture the small-scale flows and the vertical variability that transport larvae and influence larval distribution. Moreover, the usage is also problematic because settled individuals suffer large mortalities which are time- and space-dependent, and these post-settlement mortalities are disregarded when linking PFEL indices with recruitment.

In this study we focus only on the offshore Ekman transport component of coastal upwelling, although the spatial variability of the winds and their effect on the offshore Ekman transport estimates will be discussed. We compare the daily PFEL indices with the average daily offshore Ekman transport from wind data measured both by coastal meteorological stations and satellites for the northern Baja California region. The objective is to evaluate the differences between the three different estimates, and discuss how representative they are of the coastal upwelling in the region between La Jolla, California, and Punta Eugenia, Baja California. In addition, the performance of satellite winds near the coast is evaluated using the coastal meteorological stations data.

## DATA AND METHODS

The Coastal Upwelling Index (CUI) has been defined as the cross-shore Ekman transport per 100 m coastline, positive for offshore transport, i.e., upwelling conditions. Its units are $m^3/s$ per 100 m coastline (Bakun 1975):

$$CUI = \frac{\tau}{\rho f} \times 100 \tag{1}$$

where $\rho = 1025\ kg/m^3$ is the mean density of the upper water layer, $f$- the Coriolis parameter, and $\tau$ is the alongshore wind stress (defined positive when directed towards the equator) estimated as in Bakun and Nelson (1977):

$$\tau = \rho_a C_d U_{10} \| U_{10} \| \tag{2}$$

here $\rho_a = 1.22\ kg/m^3$ is the density of air; $C_d$ is the drag coefficient, which for the PFEL historical 3° upwelling index has been used as a constant ($C_d = 0.0013$); and $U_{10}$ is the alongshore wind speed at 10 m (positive towards the equator).

Daily coastal upwelling indices were estimated from three different data sources: winds measured directly by coastal meteorological stations, winds estimated from scatterometer satellite data, and geostrophic winds calculated from an atmospheric operational model. The study period was from 30 August 2000 through 16 March 2004.

### Pacific Fisheries Environmental Laboratory indices

The daily Coastal Upwelling Indices provided by the NOAA Southwest Fisheries Science Center's Environmental Research Division (formerly the Pacific Fisheries Environmental Laboratory [PFEL]) were used for this study. The indices result from the geostrophic winds derived from six-hourly synoptic surface atmospheric pressure fields. The pressure fields were provided on a global spherical 1° mesh by the U.S. Navy Fleet Numerical

TABLE 1
**Meteorological stations information**

| Station name | Position of sensor (lat, lon, height) | Angle with coast (relative to east) | Angle of maximum variance (relative to east) |
|---|---|---|---|
| La Jolla | 32.9°N, 117.3°W 20m | −39° (−65°) | −62° |
| Punta Banda | 31.7°N, 116.7°W 20m | −60° | −69° |
| Punta Baja | 29.9°N, 115.8°W 19m | −65° (−51°) | −55° |
| Morro Santo Domingo | 28.2°N, 114.1°W 56m | −41° | −34° |

Location of the meteorological stations (latitude, longitude, and height above sea level). The angle with the coast is used to estimate alongshore wind stress. In La Jolla and Punta Baja, those angles are the ones used for the PFEL indices at those latitudes; the angles derived from a linear fit to the coastline 0.5° north and south of those stations are in parenthesis.

Meteorological and Oceanographic Center (FNMOC), Monterey, California. The historical daily indices were derived from a 3° mesh that was interpolated from the daily averages of the wind-driven cross-shore transports obtained from the six-hourly FNMOC 1° pressure fields (http://www.pfel.noaa.gov). We used the CUI values at 33°N, 119°W; 30°N, 119°W; and 27°N, 116°W (fig. 1). These locations are 110 km, 275 km, and 130 km from shore, respectively (Pickett and Schwing 2006). The angles (rel. to east) used to obtain the along-shore component of the wind were −39°, −65°, and −63°, respectively (Bakun 1975). We will refer to these time series as the PFEL indices.

## Meteorological stations

Winds were sampled at four coastal meteorological stations and averaged every hour (tab. 1, fig. 1). The meteorological stations were set in well-exposed locations, on top of lighthouses at capes and points along the coast. The La Jolla data came from the meteorological station located on the Scripps Oceanographic Institution pier. We obtained the alongshore component of the wind using the angles shown in Table 1. At Punta Banda, the angle was obtained by making a linear fit to the coastline 0.5° north and south of the station, while at Morro Santo Domingo the mean angle of the coastline between Punta Baja and the meteorological station in question was used. We used the same angles for La Jolla and Punta Baja as the corresponding angles used for the PFEL indices at those latitudes. A linear fit to the local coastline gives a different angle than the angles used by the Bakun indices, especially off La Jolla (tab. 1). This is the case given that the PFEL indices use the mean direction of the coastline within the 3° box containing the grid point, and the coastline north of San Diego has a strong change of direction towards the northwest north of 33°N, while it has more of a north-south orientation to the south. At the four stations, the axes of maximum variance of the winds were closely aligned with the direction of the coast, more so than with the angle used by PFEL.

The daily upwelling indices result from daily averages of the indices calculated from the hourly alongshore wind stress. In this report, the time series of upwelling indices derived from the meteorological station data is called MET. In addition, a time series of daily wind averages was produced to compare with the QuikSCAT satellite-derived winds.

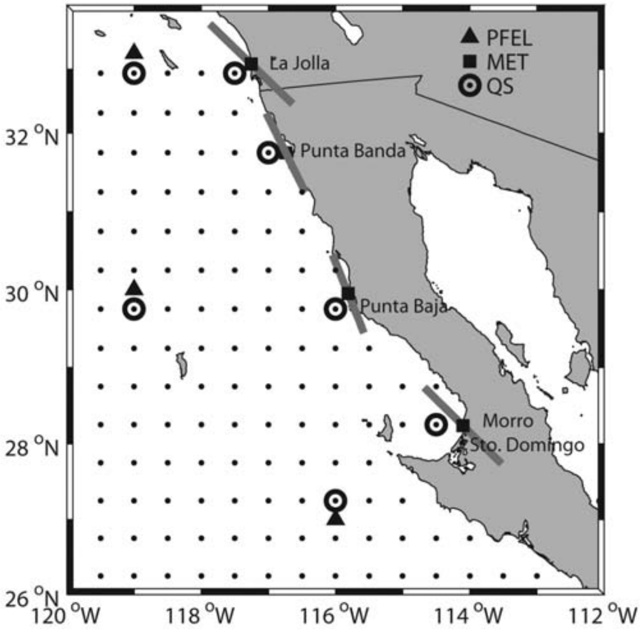

Figure 1. Position of the PFEL grid points (triangles), meteorological stations (squares), and QuikSCAT grid (dots). The open circles denote the QuikSCAT grid points closest to the PFEL and coastal meteorological stations. The dark gray lines at the coastal stations show the angle of the coastline used to obtain the alongshore component of the wind. At 33°N and 30°N, the angles are the ones used for the calculation of the PFEL indices.

## QuikSCAT winds

We use gridded and interpolated QuikSCAT Level 3 data (0.5° × 0.5° and 12 hour resolution) provided by the Jet Propulsion Laboratory Air-Sea Interaction & Climate Team (http://airsea.jpl.nasa.gov/DATA/QUIKSCAT/wind/). The accuracy of the measurement is 2 m/s in magnitude and 20° in direction for speeds larger than 3 m/s.

Near the coast, land contamination and other technical difficulties restrict scatterometer data to within a few tens of kilometers from land. Data analysis has shown that QuickSCAT vector wind measurements are accurate within approximately 25–30 kilometers of the coastline (Tang et al. 2004). Tang et al. (2004) argue that this increase in error near the coast is likely because the geophysical model function is inadequate and the removal scheme in addressing coastal conditions and light wind situations is ambiguous. In addition to the technical difficulties in determining winds near the coast, the increase in small-scale time and space variations associated with land (e.g., sea-land breezes, topographically induced variations) can be smoothed by the satellite space-averaging process and aliased by the twice-daily sampling that compounds the problem (e.g., Pickett et al. 2003). In fact, standard QuikSCAT products are the result of across-track sweeps averaged in 25 × 25 km wind vector cells, and the outputs are not used if any part of the fields of view is contaminated by land.

Time series of QuikSCAT winds were obtained for the grid points closest to the PFEL and MET locations (see fig. 1). Upwelling indices for the 12 hourly winds were derived with equation 1, using the angles for the alongshore component that correspond to the PFEL and MET series, and averaged to produce daily time series (which we refer to as QS). Daily means of each wind component were also produced, to compare with meteorological stations' winds. The PFEL stations are 150 to 280 km from the coast, while the MET stations are on the coast. We refer to the PFEL and corresponding QS points as the "offshore stations," while the MET and corresponding QS points will be called "coastal stations." Separation between the shore and QS coastal stations are: 26 km at San Diego, 25 km at Punta Banda, 29 km at Punta Baja, and 39 km at Morro Santo Domingo, all of these near to the accuracy limit of satellite winds close to land. Hence, we compared them with the corresponding meteorological station data to see how well they reproduce the coastal winds off Baja California.

Finally, we also derived upwelling indices for the entire QuikSCAT grid within the region of interest, using the angles shown in Figure 2, to obtain the alongshore component of the wind.

### Coherences

Coherences were estimated to compare the datasets on the frequency domain. The time series were divided into 20 segments, each smoothed with a Hanning window. The coherences were estimated for each window, using the periodogram method to calculate the corresponding spectral power densities. The final coherence is the ensemble average over all segments, with 20 equivalent degrees of freedom, and a frequency resolution of 0.015 cpd (Emery and Thomson 2001).

To make sure that the above coherences did not depend on the time period sampled, the series were divided in four segments of 323 days each, and the coherences for each segment were calculated with the method described above (20 equivalent degrees of freedom and a frequency resolution of 0.063 cpd). The mean of the coherences for the four segments represented the coherence for the entire time series in most cases. Both estimates are in the results for comparison. Please note that by "coherence" we mean the "squared coherence" or "coherence spectrum" (Julian 1975; Emery and Thomson 2001).

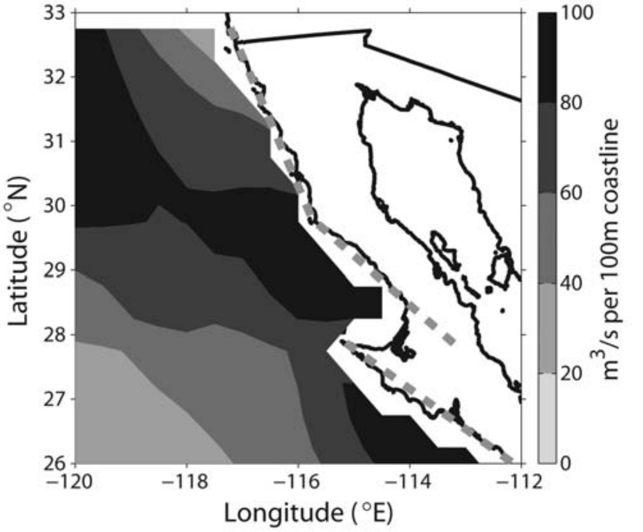

Figure 2. Mean offshore Ekman transport calculated from the QuikSCAT gridded field, using the dotted gray lines as the direction of the coastline.

We also calculated the clockwise and counterclockwise rotary spectral components for the QuikSCAT coastal and meteorological station winds. To determine how similar the circularly polarized rotary components of the two vector series were, the inner-coherence (between the co-rotating components) and outer-coherence (between the counter-rotating components) were obtained (Emery and Thomson 2001).

## RESULTS

### Coastal Upwelling Indices

***Spatial pattern from QuikSCAT*** The mean of the indices calculated with the QuikSCAT winds shows the spatial variations in the coastal upwelling estimates that result from the large-scale shear of the wind (fig. 2). Although the QuikSCAT grid may not resolve effects on the shear of the wind due to islands, headlands, capes, and friction with coastal topography, it is clear that the large-scale spatial pattern shows variations on the magnitude of the upwelling indices both along the coast and with distance from shore. Off La Jolla, the indices increase steadily away from the shore. The offshore maximum observed at that latitude is a consequence of the strong jet that separates from the coast at Point

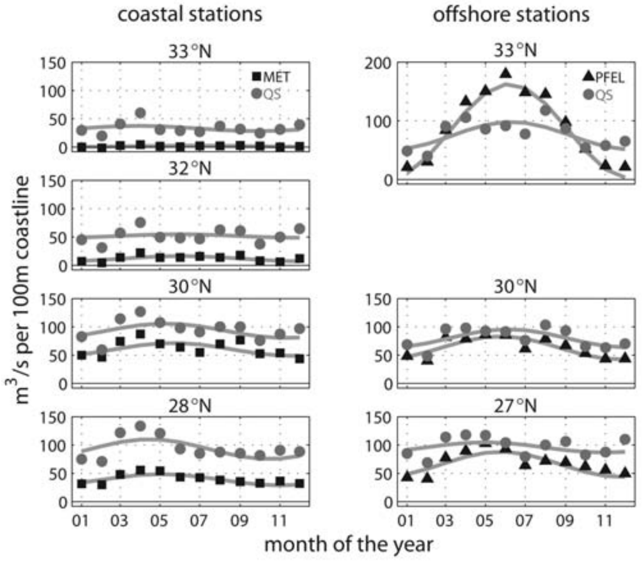

Figure 3. Typical year for the coastal upwelling indices. Each point represents the 3-year mean (2001–03) of the monthly averages. The light gray lines show the corresponding annual fit. Left panels: meteorological stations (squares) and coastal QuikSCAT stations (circles). Right panels: PFEL (triangles) and offshore QuikSCAT stations (circles).

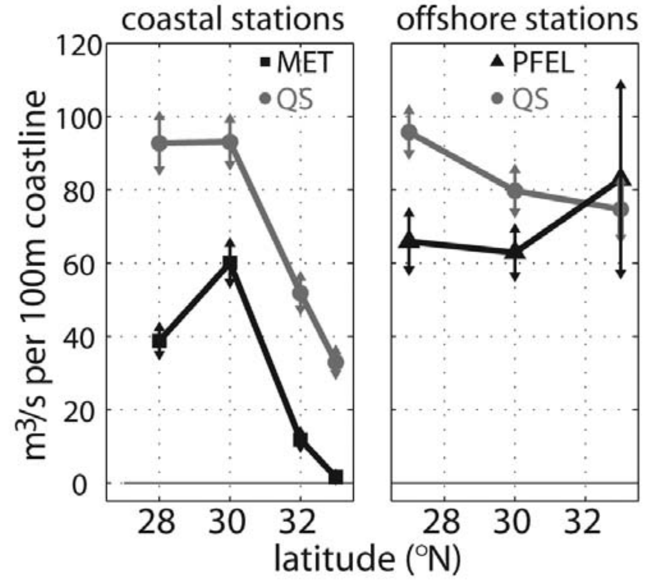

Figure 4. Mean upwelling indices with corresponding 95% interval for the coastal (left panel) and offshore stations (right panel). Meteorological stations (squares), PFEL (triangles), and QuikSCAT estimates (circles).

Conception (~34.5°N), caused by the 90° turn of the coastline (Winant and Dorman 1997; Münchow 2000). From Punta Baja southwards, the pattern reverses, with the largest indices found near the shore. This spatial pattern is maintained throughout the year, only varying in magnitude.

***Typical year and basic statistics*** Monthly means were obtained and averaged over the three complete years of the time series. Figure 3 shows the resulting typical year for the offshore and coastal stations, including the annual cycle fit obtained with harmonic analysis. The mean for the entire length of the time series with a 95% confidence interval is plotted in Figure 4. For the coastal stations, the typical year for the MET and QS series follow the same general pattern; maximum values in April, a secondary maximum in August-September (in most cases), and minimum values in February. A third maxima in December is usually found in the QuikSCAT series. The annual cycle fit explains less than 50% of the variance, except at the southernmost meteorological station, where the fit is better because the series has less of a bimodal character (the late summer maxima is small). Finally, the QS values are larger than the corresponding MET values by a near constant offset of 30–60 $m^3/s$ per 100 m coastline (fig. 4). Note that the indices tend to get smaller towards the north, with minimum values at 33°N (figs. 3 and 4). The highest values are observed at 30°N, although QS shows no major difference between Punta Baja (30°N) and Punta Eugenia (28°N).

For the offshore stations, QS also shows maximum values in April and August-September. The difference with the coastal stations is that both maxima have similar magnitudes. By contrast, the PFEL series show the first maxima later, especially off La Jolla (33°N) where the indices peak in June. That particular PFEL series stands out from the rest, with a strong annual cycle (explaining 98% of the variance), and the largest upwelling index values of all (larger than 150 $m^3/s$ per 100 m coastline in June). At this location, the monthly PFEL indices generally exceed the QS values, with a mean offset of 10 $m^3/s$. By contrast, the QS indices have slightly larger values than the corresponding PFEL values at the two southern stations (mean offset of 20–30 $m^3/s$ per 100 m coastline, figs. 3 and 4). While a decline towards the north is suggested by the MET series and by the QS indices both offshore and near the coast, the PFEL indices suggest that the strongest upwelling of the entire region occurs in the summer at 33°N. The large variability for PFEL at that station also stands out as anomalous compared to the results from the other stations and datasets.

***Correlations and coherences*** Figures 5 and 6 show the correlation and coherences for time series of offshore PFEL versus QS stations, and the coastal MET versus QS stations. The lowest correlations are found at 33°N (0.60 offshore, 0.45 coastal), and the highest at 30°N (around 0.70 both offshore and coastal). QuikSCAT shows better correlations offshore with the PFEL time series than with MET at the coastal stations.

The coherences (fig. 6) are generally significant for frequencies smaller than 0.2–0.3 cpd (periods larger than 3–5 days), and the series vary nearly in phase for those

TABLE 2
**Basic statistics for the daily upwelling indices**

| Station name | Database | Mean | Standard deviation | Variance explained by annual cycle |
|---|---|---|---|---|
| **Coastal Stations** | | | | |
| La Jolla (33°N) | MET | 2.0 ± 0.6 | 7.0 ± 0.4 | 20% |
| | QS | 33 ± 3 | 29 ± 2 | 11% |
| Punta Banda (32°N) | MET | 12 ± 2 | 20 ± 1 | 43% |
| | QS | 52 ± 4 | 38 ± 3 | 3% |
| Punta Baja (30°N) | MET | 60 ± 5 | 44 ± 4 | 37% |
| | QS | 93 ± 6 | 54 ± 5 | 28% |
| Morro Sto. Dom. (28°N) | MET | 39 ± 4 | 25 ± 3 | 67% |
| | QS | 93 ± 7 | 51 ± 5 | 43% |
| **Offshore Stations** | | | | |
| La Jolla (33°N) | PFEL | 83 ± 26 | 89 ± 21 | 98% |
| | QS | 75 ± 8 | 58 ± 6 | 53% |
| Punta Baja (30°N) | PFEL | 63 ± 6 | 53 ± 5 | 72% |
| | QS | 80 ± 6 | 52 ± 4 | 46% |
| Punta Eugenia (27°N) | PFEL | 66 ± 8 | 45 ± 6 | 67% |
| | QS | 96 ± 6 | 54 ± 4 | 17% |

The mean and standard deviations are shown with the 95% confidence interval. Units are in $m^3/s$ per 100 m coastline. The percentage of variance explained by the annual fit corresponds to the ratio of the variance of the typical year to the variance of the annual fit. PFEL–NOAA Southwest Fisheries Science Center's Environmental Research Division (formerly Pacific Fisheries Environmental Laboratory) coastal upwelling indices; MET–upwelling indices derived from the coastal meteorological stations' wind data; QS—upwelling indices derived from QuikSCAT winds close to the PFEL locations (offshore) and the meteorological stations (coastal).

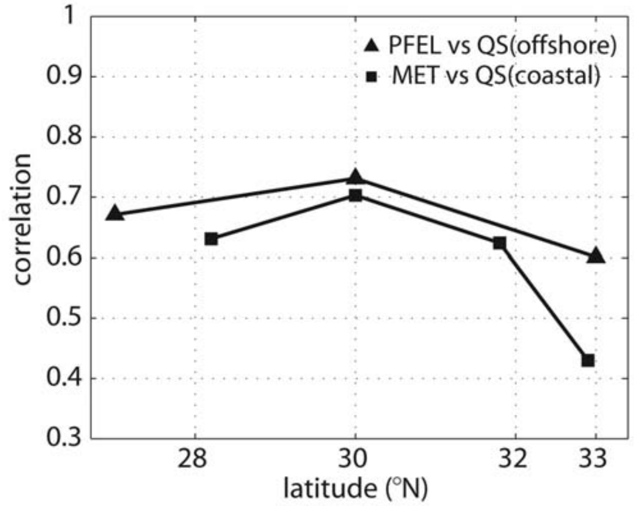

Figure 5. Correlations between PFEL and offshore QuikSCAT upwelling indices (triangles), and meteorological stations versus coastal QuikSCAT upwelling indices (squares).

frequencies, with lags mostly shorter than two days (phases <40°). The lowest coherences both offshore and at the coastal stations are found at 33°N (values less or equal to 0.6), while at the rest of the stations the values are generally larger than 0.5.

***Coastal versus offshore*** To compare the offshore versus the coastal estimates of the upwelling indices, we calculated the mean difference, correlations, and coherences between the PFEL and the corresponding MET time series, and between the offshore and coastal QS time series (figs. 7 and 8). The comparison between the QS series provides information about the differences in the estimates due to the large-scale shear of the winds (i.e.,

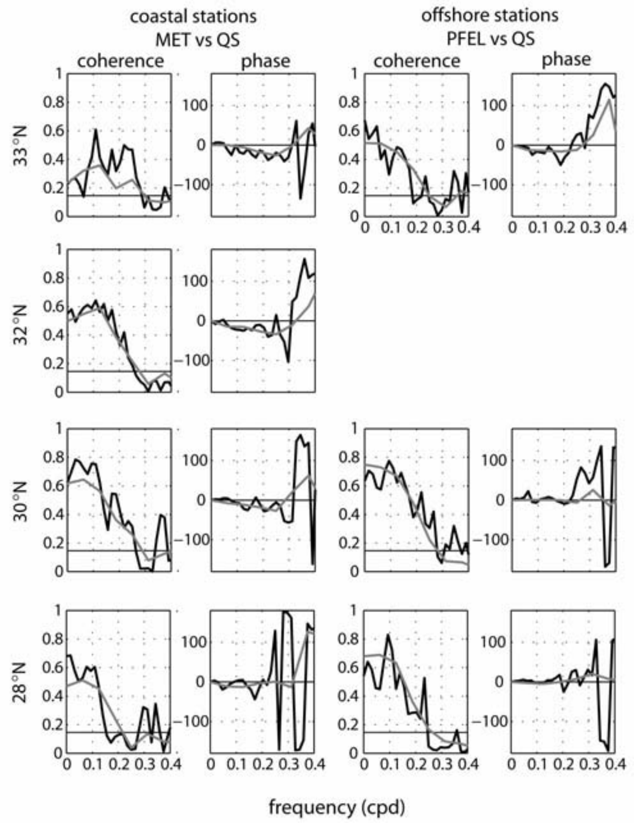

Figure 6. Point-by-point coherences and phases (in degrees) of the upwelling indices. The thick black lines show the calculation over the entire length of the time series, while the light gray lines show the average over the coherences and phases for each 323-day segment. The coherences were calculated using the averaged periodogram method with 20 degrees of freedom (see text for more details). Left panels: meteorological versus QuikSCAT coastal stations. Right panels: PFEL and QuikSCAT offshore stations. Positive phases indicate that the QuikSCAT series leads for both the left and right panels.

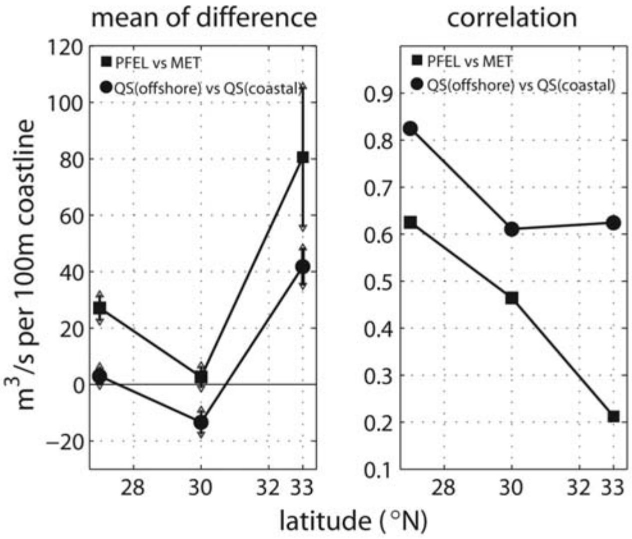

Figure 7. Comparisons between the offshore and coastal estimates of the upwelling indices. Left panel: mean of the difference between the PFEL and meteorological time series (squares, positive for PFEL > MET) and offshore minus coastal QuikSCAT series (circles), with corresponding 95% confidence interval. Right panel: correlations between the PFEL and meteorological time series (squares), and between the offshore and coastal QuikSCAT time series (squares).

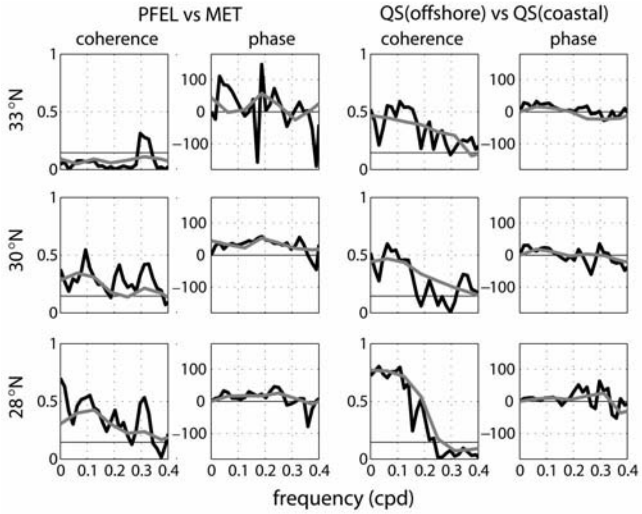

Figure 8. Coherences and phases between the offshore and coastal stations upwelling time series. The thick black lines show the calculation over the entire length of the time series, while the light gray lines show the average over the coherences and phases for each 323 day segment. The coherences were calculated using the averaged periodogram method with 20 degrees of freedom (see text for more details). Left panels: PFEL versus meteorological stations. Right panels: QuikSCAT offshore versus coastal stations. Positive phases indicate that the coastal stations lead the offshore stations.

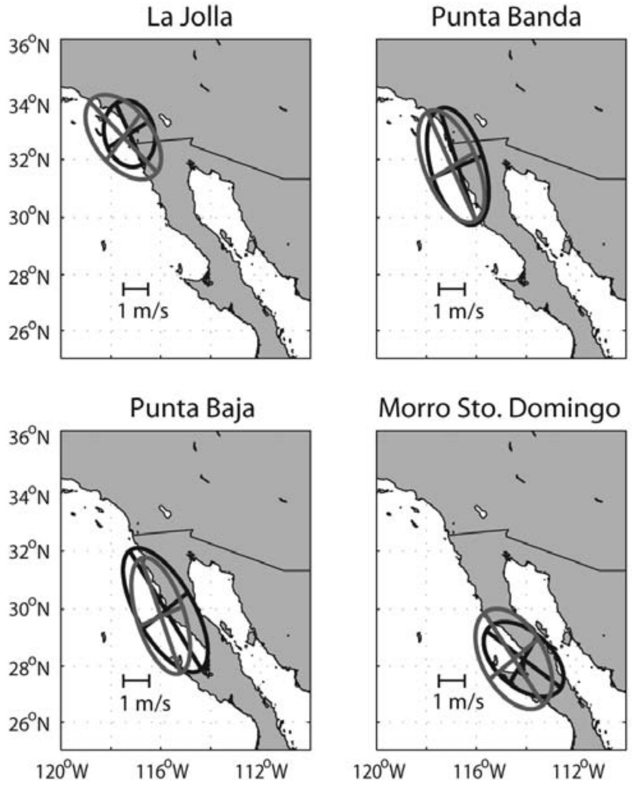

Figure 9. Ellipses showing the orientation of the principal axes and standard deviation along principal axes for the meteorological (black) and coastal QuikSCAT (gray) stations winds.

variations in the winds with distance from shore), while the comparison of the PFEL and MET indices provides information about the difference in estimates due to both the large-scale shear of the wind and differences between the two data sources.

At 33°N the indices calculated on the offshore station render a much larger value than the coastal station, the QS stations (40 unit bias), and the PFEL and MET stations (80 unit bias). For other latitudes, the differences are less than 30 m$^3$/s (per 100 m of coastline), in some cases not significantly different than zero (QS at 28°N), including a 15 m$^3$/s (per 100 m of coastline) larger mean value at the coast than offshore for QS at 30°N. Correlations are higher between the QS offshore and coastal stations (>0.6) than between the PFEL and MET stations (<= 0.6). The higher correlations for both comparisons are observed in the southernmost station (fig. 7).

Coherences between PFEL and MET at 30° and 28°N are generally significant for frequencies less than 0.3 cpd, while at 33°N they are nearly zero (fig. 8). QS shows significant coherences at the three latitudes, but mostly for frequencies less than 0.2 cpd. In both comparisons, higher coherences are found at the southernmost station (fig. 8). For the frequencies where the coherence is significant, the series vary more-or-less simultaneously (lags less than two days, which correspond to phases <40°).

## QuikSCAT versus meteorological station winds

To see how well the coastal QS winds represent those measured by the meteorological stations, the variance ellipses for both time series were calculated (fig. 9). Except for the northernmost station, the eccentricity

TABLE 3
**RMS errors for the QuikSCAT coastal stations**

| | La Jolla (33°N) | Punta Banda (32°N) | Punta Baja (30°N) | Morro Sto. Domingo (28°N) |
|---|---|---|---|---|
| Direction (degrees) | 109 | 91 | 34 | 36 |
| Magnitude (m/s) | 3.1 | 3.1 | 2.1 | 2.8 |

Root-mean-square differences between the QuikSCAT winds at the coastal stations and the winds measured by the coastal meteorological stations. Accuracy of QuikSCAT winds is 2m/s in magnitude and 20° in direction.

and magnitude of the ellipses' axes are similar, and correlations are larger than 0.6 for the winds along the major axis (figs. 9, 10A, E, and F). Off La Jolla (33°N), the variability along the major and minor axes is pretty much equal for the winds measured by the meteorological station, while the QS winds show larger variability in the alongshore direction. At this station, the correlation along the major axis drops below 0.4 (figs. 10A, C, E, and F).

The mean of the QS winds along the major axis of variance is 2–4 m/s larger than for the MET winds (fig. 10D). The angles of the major axis differ by 7° to 21° at all stations, with the MET winds generally more aligned with the local direction of the coastline (fig. 10B). Table 3 shows the root-mean-square (RMS) differences between the two datasets, where it is clear that the direction of the wind at the coast is badly represented by the QS dataset at 32°N and 33°N, mainly due to larger variability in direction for the MET winds.

The inner-coherences that result from the co-rotating components of the vector series are shown in Figure 11. They are significant for frequencies less than 0.2 cpd, with values larger than 0.5 south of Punta Banda (32°N), particularly for the clockwise components (negative phase). Phase lags are generally less than two days ($|\text{phase}| < 40°$). Figure 12 shows the outer-coherence (which measures the stability between the ellipse orientations of the two vector series for each frequency band: Gonella 1972; Mooers 1973), and the absolute mean difference in orientation of the ellipses. Significant outer-coherences are found for frequencies less than 0.2 cpd for all locations with the exception of 33°N, although the outer-coherence is barely significant for the southernmost station. The mean difference in orientation of the ellipses is generally less than 30°, with smaller and less variable differences at 28° and 32°N.

## DISCUSSION AND CONCLUSIONS

The satellite data show the position of maximum alongshore winds to be more than 100 km from the coast off La Jolla, getting progressively closer to shore towards the south, and resulting in maximum winds within 50 km from the coast south of Punta Baja (fig. 2). This pattern of strong northwesterly winds downstream of Point Conception (the point at which the northwesterly oriented central California coastline makes a sharp 90° turn to the east: ~34.5°N), and weak winds near the eastward coast of the Southern California Bight, has been observed in previous studies (e.g., Bakun and Nelson 1991; Winant and Dorman 1997; Münchow 2000; Pickett and Paduan 2003; Capet et al. 2004; Koracin et al. 2004; Pickett and Schwing 2006).

Midway down the Baja California peninsula, the wind profile seems closer to that observed off the Northern California coast by aircraft measurements (Beardsley et al. 1987; Enriquez and Friehe 1995) and high resolution atmospheric models (Koracin et al. 2004), where upwelling-favorable wind maxima were observed 20 km from shore. The northern California nearshore jet seems to be the consequence of a sharp narrowing towards the shore of a shallow marine boundary layer (Beardsley et al. 1987), and tends to behave as a supercritical channel flow. As a result, changes in direction of the coastline result in expansion fans with corresponding acceleration of the northerly winds downstream of Point Arena (Winant et al. 1988).

Winant et al. (1988) point out that the principal requirements for supercritical flow are (1) a shallow marine layer capped by a strong inversion, (2) coastal mountain ranges higher than the marine boundary layer, and (3) wind speeds close to the shallow-water wave speed. They also refer to some early studies that suggest the presence of a thin marine layer along the coastal region of Baja California. Although our data cannot verify this hypothesis, the presence in the spring and summer of a layer of dense fog, capped by a sharp boundary which separates it from the clear skies above, suggests a sharp-and-shallow temperature inversion, which can persist until late in the day. The fog is usually trapped by the coastal mountain ranges, which can reach heights over 600 m. In addition, the meteorological station at Punta Baja recorded mean wind speeds of 5 m/s, with most of the hourly winds falling in the 4–8 m/s window. These values correspond to the shallow wave speed for a layer 100–300 m thick, assuming a value of 0.3 $m/s^2$ for the reduced gravity as in Winant et al. (1988), so supercritical flow conditions seem likely. If this were the case, the supercritical conditions in combination with the change in the coastline direction may explain the nearshore wind stress maximum observed downstream of Punta Baja by satellite (figs. 2 and 3), coastal meteo-

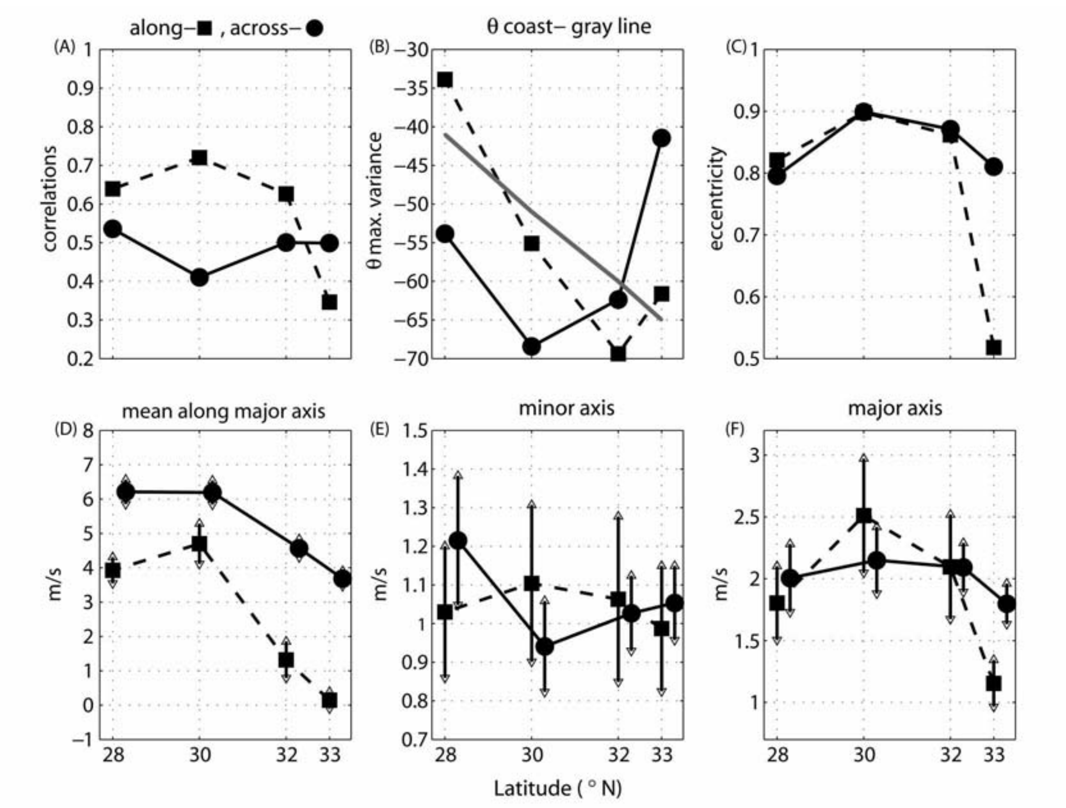

Figure 10. Comparisons between the meteorological and coastal QuikSCAT station winds. Except in (A), circles denote QuikSCAT winds while squares correspond to the meteorological stations winds. (A) correlations along the major (squares) and minor (circles) axis of the wind variance ellipses, (B) angle of maximum variance (relative to the east, the gray line shows the local direction of the coast), (C) eccentricity of the variance ellipses, (D) mean and 95% confidence interval along the direction of maximum variance, (E) and (F) magnitude and 95% confidence interval of the minor and major axis, respectively.

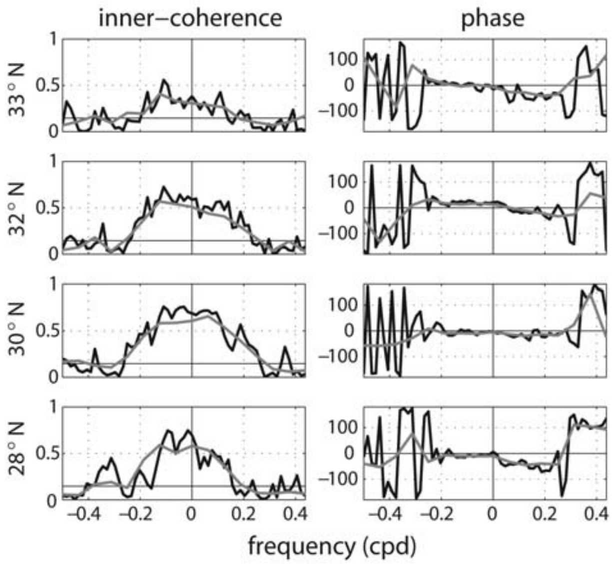

Figure 11. Inner-coherence and phase between the meteorological and QuikSCAT station winds. Negative (positive) frequencies correspond to the coherences of the counterclockwise (clockwise) rotary spectra. The 95% confidence limit is shown as a thin horizontal line. Positive phases mean the winds from the meteorological stations lead the QuikSCAT winds. The thick black lines show the calculation over the entire length of the time series, while the light gray lines show the average over the coherences and phases for each 323 day segment. The coherences were calculated using the averaged periodogram method with 20 degrees of freedom (see text for more details).

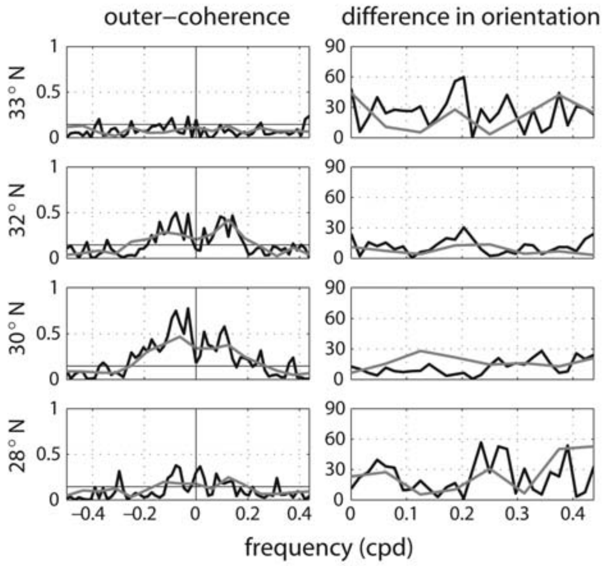

Figure 12. Left panels: outer-coherence between the meteorological and QuikSCAT station winds. Negative (positive) frequencies correspond to the coherences between the counterclockwise rotary spectra of the meteorological stations winds (QuikSCAT winds) and the clockwise rotary spectra of the QuikSCAT winds (meteorological stations data). The 95% confidence limit is shown as a thin horizontal line. Right panels: mean absolute difference in ellipse orientation (in degrees) between the meteorological and QuikSCAT stations winds. The thick black lines show the calculation over the entire length of the time series, while the light gray lines show the average over the calculations for each 323 day segment (see text for more details).

rological stations (figs. 3 and 4), historical ship reports (Nelson 1977; Bakun and Nelson 1977), and high resolution model winds (Koracin et al. 2004). This remains to be tested.

Similarly, the strong northwesterly winds downstream of Point Conception seem to result from separation of the supercritical flow due to the sharp change in the coastline orientation (Winant and Dorman 1997; Münchow 2000; Koracin et al. 2004).

The comparison of the offshore Ekman transports calculated from the coastal QuikSCAT stations and meteorological station winds is almost the same as the comparison between the PFEL and offshore QuikSCAT indices. This is a bit surprising, given that both the PFEL and QuikSCAT upwelling estimates are derived from smooth gridded fields, while the meteorological stations are point measurements. Also, land effects such as the sea breeze and small changes in local topography introduce additional variability to the local coastal winds not present a few kilometers offshore. Finally, satellite winds tend to have large errors near the land boundaries, especially in direction (Pickett et al. 2003). This is reflected in the large RMS errors found between the QuikSCAT and meteorological station winds, which for the northernmost stations were up to five times larger than the accuracy in wind direction of the satellite measurements (20°). Nevertheless, at the stations south of 33°N the variance ellipses have the same eccentricity, their orientation differing by at most 20°, the winds along the major axes correlate reasonably well (correlations >0.6) and, for periods larger than five days, the inner-coherences have values ≥0.5, the outer-coherences are generally significant, and the difference in orientation of the ellipses for each frequency band remained generally below 30°.

The three datasets tend to illustrate the same characteristics in a typical year: maximum upwelling in April and, with the exception of the southernmost coastal winds, a secondary maximum in August-September. The main differences are (1) that the PFEL indices peak later (May-June), (2) that the late summer-fall maxima is of similar (or even larger) magnitude than the spring maxima for the offshore QuikSCAT stations, and (3) that QuikSCAT shows a third maximum in December. The PFEL series at 33°N stands out from the rest, having the strongest annual cycle and the maximum values of upwelling of all. At this latitude, we find the lowest coherences and correlations between the PFEL series and meteorological and QuikSCAT time series.

The above results draw attention to the PFEL indices at 33°N. The spatial wind pattern suggests weak offshore Ekman transport near the shore of the U.S.-México border, increasing steadily towards Punta Baja in the Baja California Peninsula (fig. 2). Sea surface temperature satellite images support the idea of reduced upwelling on the southernmost California coastal region: the monthly composites for March-June (1999–2004) rarely show the presence of cold upwelled waters near the coast between Los Angeles and San Diego, while south of Ensenada (32°N) cold upwelled waters are always present (not shown, see http://coastwatch.pfel.noaa.gov/sst_comp_low.html). This pattern is also observed in the sea surface temperatures taken by the CalCOFI cruises, which in spring and summer show maximum temperatures along the coast in the southern part of the Southern California Bight (Winant and Dorman 1997). By contrast, the satellite images and the CalCOFI data generally show cold waters extending southeastwards of Point Conception, and along the northern coast of the Southern California Bight.

Contrary to this, a 50-year analysis of the PFEL indices along the North America West Coast (21°N–60°N) found the upwelling maximum at 33°N (Schwing et al. 1996). We think this discrepancy is partially due to the position of the PFEL grid point, which is closer to the offshore maximum downstream of Point Conception than it is to the eastern coastline, resulting in an overestimation of the coastal upwelling driven by offshore Ekman transport. But this does not explain why the seasonal variations, the timing and magnitude of maximum upwelling, and the variability of the PFEL indices at 33°N are significantly different compared to all the other time series, including QuikSCAT at that location.

Finally, we join others in cautioning biological oceanographers and marine ecologists on the use of PFEL indices. These indices vary at large spatial scales (>100 km), and they do not capture the small-scale patchiness that is pervasive in marine ecological systems or the high-frequency physical processes that are common in nearshore environments. Use of these indices as independent variables explaining ecological-system response poses problems, as the processes the indices try to capture, such as primary productivity and offshore larval drift, are complex, and often determined by unresolved biological and physical processes. For example, nearshore larvae may not drift offshore in response to suspected upwelling detected by PFEL indices because (1) the indices do not capture accurately the nearshore winds (e.g. this contribution for 33°N), (2) larvae may not be transported offshore by upwelling flows (i.e., they may be transported along-shore, not transported at all, or transported onshore, depending on larval vertical and cross-shore distribution), (3) flows by unaccounted small-scale transport processes dominate larval transport, or simply because (4) there are no larvae to be transported offshore. Hence, larval transport and dispersal of invertebrate and fish larvae are unlikely to be captured by PFEL indices or other large-scale descriptors such as satellite imagery. Before using PFEL indices and large scale descriptors as independent variables to explain processes such as primary production, fish biomass or intertidal community dynamics, researchers should resolve observationally the relevant biological and physical processes. Use of these indices without observational knowledge of the pelagic processes influencing the biological variables risks perpetuating unsupported hypotheses.

We conclude that the daily PFEL indices at 33°N do not seem representative of the offshore Ekman transport in the coastal region between Los Angeles and San Diego, and that caution should be taken when correlating them with events in the eastern Southern California Bight. On the other hand, the three databases compare reasonably well in Punta Banda and southwards. The QuikSCAT winds in the grid points closest to shore have large RMS errors in direction when compared to the meteorological wind data, but show similar properties of the variance ellipses and have reasonable coherences for frequencies in the weather band and lower, particularly south of 33°N.

## ACKNOWLEDGMENTS

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# RECENT PRE-RECRUIT PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) OCCURRENCES IN THE NORTHERN CALIFORNIA CURRENT SUGGEST A NORTHWARD EXPANSION OF THEIR SPAWNING AREA

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## ABSTRACT

Coastal Pacific hake (*Merluccius productus*) are known to spawn in the southern California Bight from January to March, migrate north during late spring and summer to feed off Oregon, Washington, and British Columbia, and then move back to southern California in the fall. Juvenile Pacific hake nursery areas have been found to occur along the coastal shelf and slope of California, and occasionally into southern Oregon during strong El Niño events. In this paper, we combine information from several studies that captured larval and high abundances of young-of-the-year (YOY) Pacific hake in the northern California Current from 2003–06. These preliminary results suggest that spawning and recruitment of Pacific hake have expanded northward and this will likely have major economic and ecological consequences in the northern California Current (NCC).

## INTRODUCTION

There are at least three distinct stocks of Pacific hake (*Merluccius productus*) in the eastern Pacific Ocean: (1) coastal, (2) Puget Sound, and (3) Strait of Georgia (Bailey et al. 1982). The coastal stock ranges from southern California to British Columbia and is the largest of the three stocks. Pacific hake (also known commercially as Pacific whiting) is an important species that supports a major fishery off the west coast of the United States and Canada. The 2005 biomass was estimated to range between 2.5 and 4.0 million metric tons (mt), and since 2000 the annual catch in the non-tribal Pacific hake fishery has averaged about 160,000 mt per year (Helser et al. 2006). Ecologically, Pacific hake represent the largest fish biomass in the northeastern Pacific Ocean (Agostini et al. 2006). It is generally accepted that Pacific hake spawn within the southern California Bight from January to March, migrate north to Oregon, Washington, and British Columbia during the summer to feed, and then move back to southern California in the fall (Bailey and Francis 1985; Ressler et al., in press).

Juvenile Pacific hake (i.e., >31 mm and sexually immature) nursery areas have been identified to be principally along the coastal shelf and slope of California (Bailey and Francis 1985). However, there have been occasional observations of eggs, larvae, and low abundances of YOY Pacific hake in the northern California Current (NCC) off Oregon and Washington prior to 2003. Typically the occurrence of larvae coincided with strong El Niños, such as the 1973, 1983–84, and 1998 events (Richardson et al. 1980; Pearcy and Schoener 1987; Doyle 1995; Dorn et al. 1999; Doyle et al. 2002). Although there have been occasional documented occurrences of YOY Pacific hake up to 40°N off northern California and off British Columbia (see Discussion), until recently there have not been significant occurrences of Pacific hake reported for Oregon and Washington waters despite intensive sampling of this region (e.g., Brodeur and Pearcy 1986; Brodeur et al. 2003; Ressler et al., in press).

The NCC is a highly dynamic system that exhibits extreme biological and environmental fluctuations on a variety of time scales (Brodeur et al. 2005). In this paper, we combine information from several studies that suggests that, in general, the distribution of YOY Pacific hake has expanded north in recent years in response to changing ocean conditions. Furthermore, the occurrence of larval and YOY Pacific hake in large numbers in the NCC implies that the Pacific hake spawning area may have expanded north. We also discuss the potential effects this northern geographic expansion may have on Pacific hake recruitment and other biological components of the NCC ecosystem.

## METHODS

### Larval Pacific hake collections

We used previously unpublished data on larval Pacific hake that were collected during three different research surveys in the NCC: (1) the NOAA Fisheries, Newport Hydrographic (NH) Line Biweekly Survey from 1996 to 2004, (2) the NOAA Fisheries, Northwest Fisheries Science Center (NWFSC) Stock Assessment Improvement Program (SAIP) Larval/Juvenile Survey from 2004 to 2006, and (3) the Pacific Coast Ocean Observing System (PaCOOS) Survey from 2004 to 2006.

#### *(1) NOAA Fisheries, NH Line Biweekly Survey*

NH Line Biweekly Survey samples were collected with a variety of standard ichthyoplankton equipment. Gear ranged in size from 1 m diameter ring to 20 cm diameter bongo nets with 0.200–0.333 mm mesh nets. Samples were taken with vertical and oblique tows from a single transect at 44.65°N from 9–18 km offshore (see Hooff and Peterson 2006 for detailed methods).

#### *(2) NOAA Fisheries, NWFSC SAIP Larval/Juvenile Survey*

SAIP Larval/Juvenile Survey samples were collected from spring to fall in 2004–06 at stations 5–85 km (typically 10–55 km) offshore ranging from 44.00° to 46.67°N (fig. 1). A 60 cm diameter bongo net with 0.332 mm mesh was fished obliquely from ~100 m depth to the surface (or within 5 m of the bottom at stations <100 m) primarily during the night.

#### *(3) PaCOOS Survey*

The PaCOOS Survey sampled the hydrographical and biological conditions of the central and northern California Current during May 2004, 2005, and 2006 at stations 3.5–121 km offshore ranging from approximately 39° to 47°N latitude (fig. 1). A 70 cm diameter bongo with 0.333 mm mesh and a 1 $m^2$ Tucker trawl with 0.335 mm mesh were fished obliquely from ~100 m depth to the surface (or within 5 m of the bottom at stations <100 m) during the day and night.

Ichthyoplankton samples collected during all surveys were preserved in a 10% buffered-formalin seawater solution at sea. Fish larvae were sorted under either a dissecting microscope or sorting tray in the lab, identified, enumerated, and measured to the nearest 0.1 mm notochord (NL) or standard (SL) length.

### YOY Pacific hake collections

YOY Pacific hake were collected during four different research surveys conducted from May to November over multiple years: (1) the NOAA Fisheries, Southwest Fisheries Science Center (SWFSC) Juvenile Rockfish Survey, (2) the NOAA Fisheries, NWFSC SAIP Larval/Juvenile Survey, (3) the NWFSC and the Pacific Whiting Conservation Cooperative (PWCC) Survey, and (4) the NOAA Fisheries, Predator Survey. Sampling stations ranged from 4–157 km offshore and 32.72°–48.00°N (fig. 1). Samples were collected by midwater (30–50 m depth stratum) or surface trawling at night with nets that had codend mesh liners from 3–10 mm. Tow durations were 15–30 min.

#### *(1) NOAA Fisheries, SWFSC Juvenile Rockfish Survey*

The NOAA Fisheries SWFSC has conducted a midwater trawl survey along the central California coast (36.50°–38.33°N) every year since 1983 (1986–2006 data presented). The survey was designed to measure the annual relative abundance of pelagic juvenile rockfishes (*Sebastes* spp.), but also captured YOY Pacific hake (Sakuma et al. 2006). Standardized 15 min midwater trawls with the headrope set at a depth of 30 m were conducted at a series of standard stations with a 9.5 mm mesh liner. The survey was expanded substantially in 2004 to cover a much larger spatial area (i.e., from San Diego to Point Delgada: 32.75°–40.00° N) (fig. 1). During each cruise, the catch was sorted at sea and YOY Pacific hake enumerated. Beginning in 1994, SL (mm) measurements were taken from a subsample of the Pacific hake catch (Sakuma et al. 2006).

A three-way analysis of variance (ANOVA) model (without interaction) was fitted to the SWFSC midwater trawl survey data to summarize the overall spatial and temporal variation in YOY Pacific hake catch rates. The advantage of fitting a simple model to the data, as opposed to calculating individual cell means, is that fewer parameters are estimated (i.e., the main effects only) and missing data are treated in a balanced fashion. Specifically, the fitted ANOVA model was:

$$log_e\,(N_{ijk\lambda} + 1) = Y_i + S_j + D_k + E_{ijk\lambda},$$

where $N_{ijk\lambda}$ is the number of YOY Pacific hake caught during a standard 15-minute haul (λ), $Y_i$ is a year effect, $S_j$ is a station effect, $D_k$ is a calendar date effect, and $E_{ijk\lambda}$ is a normal error term. Main effects from the model were summarized as marginal means (Searle et al. 1980) and back-transformed to the arithmetic scale with bias correction (Miller 1984).

The Pacific hake length data collected as part of the midwater trawl survey were summarized by: (1) calculating the proportion of fish in 1 mm SL size intervals

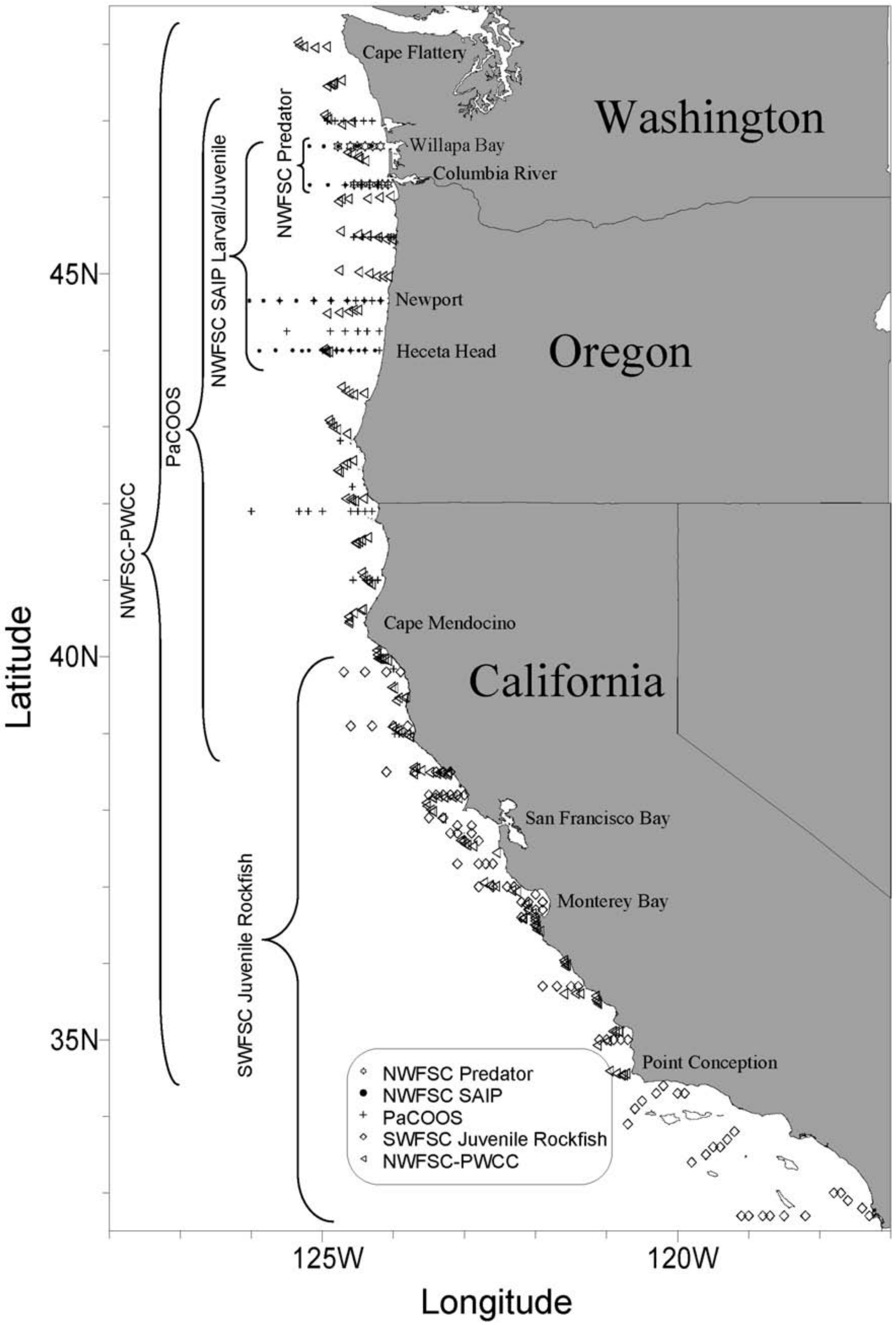

Figure 1. Location of the sampling efforts from the various fish studies along the west coast of the U.S. The NWFSC-PWCC Survey stations varied slightly from year to year. The stations presented are from 2006.

by year and haul, (2) multiplying the proportions by $N_{ijk\lambda}$, (3) summing over all hauls conducted in a year, and (4) expressing the results as annual relative length-frequency distributions.

To illustrate the interaction between year and sampling location on YOY Pacific hake catch rate (fish/trawl), the midwater trawl data were partitioned by year ($y$) and 1° latitudinal bins ($l$). The number of observations ($n$) in each partition was transformed (i.e., $log_e\ [N_{yln} + 1\ ]$) and the mean, standard deviation, and standard error calculated for each year-latitudinal combination. These values were then back-transformed with bias correction.

*(2) NOAA Fisheries, NWFSC SAIP Larval/Juvenile Survey*

In 2004, the NWFSC Fish Ecology Division initiated a study of the ecology of larvae and juvenile fish off central Oregon and Washington. Juvenile fishes were sampled with midwater trawls from summer to fall of 2004–06. Several stations were sampled along four transects off Heceta Head (44.00°N), Newport (44.65°N), the Columbia River (46.16°N), and Willapa Bay (46.67°N) (fig. 1). Stations started approximately 20 km offshore, extending out to about 100 km on each transect.

At each station, either a Nordic 264 rope trawl or a modified Cobb trawl was towed for 15–30 min with the headrope at a depth of 30 m. The Nordic 264 rope trawl had an effective fishing mouth of 12 m high and 28 m wide (336 $m^2$) using net mensuration equipment (Emmett et al. 2004; 2006), and a 6.1 m long, 3 mm mesh stretched knotless web liner sewn into the cod end. After removing all fish and invertebrates >10 cm in length, the catch was subsampled as follows: samples with a remaining volume of unsorted catch $\leq$0.25 $m^3$ were collected in their entirety, while samples with a remaining volume of unsorted catch >0.25 $m^3$ were subsampled in the amount of 0.25 $m^3$ or 20% of the entire sample (whichever was larger). The retained unsorted catches were frozen at sea, and later thawed and sorted in the lab. All YOY Pacific hake were identified, enumerated, and at least 30 randomly chosen individuals were measured to the nearest 1 mm SL.

Midwater trawl methods during the first year of the SAIP project differed slightly from 2005 and 2006. Trawl duration was 30 min for all tows in 2004. For June, August, and September cruises in 2004, only the NH and Heceta Head transects were sampled, and they extended from 8–160 km offshore. A modified Cobb trawl was used in the 2004 July and August cruises, and a Nordic 264 rope trawl was used for all other cruises. The Cobb trawl had an effective fishing mouth area of ~130 $m^2$, which was ~1/3 that of the Nordic trawl.

Pacific hake densities were determined by multiplying the distance of the tow (as determined by a flowmeter) by the mouth opening of the net, and converting that to number of Pacific hake $10^6/m^3$. During the first cruise of 2004 a flowmeter was unavailable, and length of the tow was determined from the vessel's global positioning system.

Pacific hake length-frequency histograms were created for each sampling period based on all individuals measured.

*(3) NWFSC-PWCC Survey*

The NWFSC-PWCC Survey started in 1999 as a cooperative study between (1) PWCC, (2) NOAA Fisheries, NWFSC Fishery Resource Analysis and Monitoring Division, and (3) NOAA Fisheries, SWFSC Juvenile Rockfish Survey. The NWFSC-PWCC Survey expanded the previously described SWFSC Juvenile Rockfish Survey to more outer shelf stations in order to target YOY Pacific hake. The NWFSC-PWCC Survey conducted in May–June covered an area from 34.50° to 44.50°N from 2001 to 2003, 34.50° to 46.50°N in 2004, and 34.50° to 48.00°N in 2005 and 2006 (fig. 1). A minimum of five stations were sampled across the continental shelf transects at 55.6 km (30 nm) intervals. Juvenile fishes were captured using a midwater trawl identical to that used in the SWFSC Juvenile Rockfish Survey, towed at a target headrope depth of 30 m for 15 min. Detailed methods are described in Sakuma et al. (2006).

To summarize catch distributions, YOY Pacific hake counts were binned into 1° latitude cells, standardized for each cell, and converted into a percentage to remove recruitment variability between years.

*(4) NOAA Fisheries, NWFSC Predator Survey*

This survey was conducted approximately every 10 days from mid-April through early-August 1998–2006. Twelve sampling stations were located 7–56 km offshore along two transect lines off Willapa Bay and just south of the Columbia River (fig. 1). From 1998 to 1999, surface trawls were 30 min in duration. However, starting in 2000, some hauls were shortened to 15 min because of very large catches of forage fish. A Nordic 264 rope trawl with an 8 mm mesh web liner was towed close to the surface to collect nekton samples. The volume of water fished was calculated as the distance the trawl traveled multiplied by the trawl area (336 $m^2$).

The first 30 Pacific hake of each class (YOY, subadult, and adult) captured in each haul were measured to SL or total length (TL) (mm). YOY Pacific hake that were measured in TL were converted to SL with the following equation generated from preserved samples:

$$SL = 1.0619 * \mathrm{TL} + 2.0747;\ \mathrm{R}^2 = 0.998.$$

To summarize length distributions, measured fish were binned into 10 mm groups. When variable size-classes

TABLE 1

**Abundances (number/10 m²), mean lengths (mm), and sampling station details where larval Pacific hake (*Merluccius productus*) were collected in the central and northern California Current from 1967–2006. Data are separated between years by solid lines. For gear type, BON 60 = 60-cm diameter bongo net, BON 70 = 70-cm diameter bongo net, 1-m = 1-m diameter ring net, and TT = 1-m² mouth-opening Tucker trawl. The Richardson et al. (1980) abundance data represents the mean for all stations sampled in April 1973.**

| Cruise/Source | Gear | Date | Station | Station depth (m) | Dist. from shore (km) | Latitude (°N) | Longitude (°W) | Number | Abundance (number/ 10 m²) | Mean length (mm) |
|---|---|---|---|---|---|---|---|---|---|---|
| Richardson et al. 1980 | BON 70 | Apr-73 | | | | | | 1 | 0.3 | |
| Doyle 1992 | BON 60 | 27-Apr-83 | G024A | 500 | 60 | 47.00 | 125.00 | 1 | 7.9 | 8.5 |
| Doyle 1992 | BON 60 | 4-Apr-84 | G118A | 3250 | 94 | 40.00 | 125.72 | 32 | 213.4 | 3.5 |
| Doyle 1992 | BON 60 | 2-Apr-84 | G104B | 1250 | 57 | 41.33 | 124.92 | 2 | 13.6 | 6.1 |
| Doyle 1992 | BON 60 | 2-Apr-84 | G105A | 2280 | 53 | 41.00 | 124.90 | 2 | 12.2 | 3.1 |
| NOAA NH line | 1-m | 21-Apr-98 | NH10 | 79 | 18 | 44.65 | 124.30 | 2 | 1.6 | 7.3 |
| NOAA NH line | 1-m | 12-May-98 | NH05 | 55 | 9 | 44.65 | 124.18 | 1 | 0.8 | 10.5 |
| PaCOOS | TT | 06-May-04 | PA02 | 100 | 14 | 39.00 | 123.83 | 5 | 13.6 | 3.9 |
| PaCOOS | TT | 06-May-04 | KP02 | 105 | 4 | 40.10 | 124.21 | 3 | 9.5 | 3.3 |
| PaCOOS | TT | 05-May-04 | FR02 | 95 | 7 | 38.48 | 123.35 | 3 | 8.7 | 19.9 |
| PaCOOS | TT | 06-May-04 | PA04 | 638 | 27 | 39.00 | 123.98 | 1 | 5.7 | 14.1 |
| PaCOOS | TT | 08-May-04 | CC04 | 481 | 33 | 41.90 | 124.60 | 1 | 2.1 | 30.0 |
| PaCOOS | TT | 08-May-04 | CC03 | 137 | 24 | 41.90 | 124.50 | 1 | 2.0 | 26.0 |
| PaCOOS | TT | 09-May-04 | NH65 | 2882 | 121 | 44.65 | 125.60 | 1 | 1.8 | 3.6 |
| PaCOOS | TT | 25-May-05 | EU02 | 91 | 19 | 41.00 | 124.30 | 1 | 0.7 | 5.9 |
| SAIP | BON 60 | 10-Jun-05 | NH55 | 2889 | 102 | 44.65 | 125.36 | 1 | 4.0 | 3.7 |
| PaCOOS | BON 70 | 09-May-06 | NH65 | 2882 | 121 | 44.65 | 125.60 | 20 | 53.0 | 15.4 |
| PaCOOS | TT | 13-May-06 | CC07 | 989 | 66 | 41.90 | 125.00 | 31 | 50.7 | 23.5 |
| PaCOOS | BON 70 | 09-May-06 | NH85 | 2904 | 157 | 44.65 | 126.05 | 7 | 20.5 | 12.7 |
| PaCOOS | BON 70 | 09-May-06 | CR40 | 854 | 75 | 46.16 | 124.92 | 5 | 16.6 | 25.8 |
| PaCOOS | BON 70 | 10-May-06 | NH25 | 300 | 47 | 44.65 | 124.65 | 3 | 8.1 | 22.7 |
| PaCOOS | BON 70 | 11-May-06 | HH04 | 112 | 53 | 44.00 | 124.80 | 1 | 3.5 | 15.3 |
| PaCOOS | BON 70 | 11-May-06 | HH05 | 920 | 69 | 44.00 | 125.00 | 1 | 3.3 | 21.0 |
| PaCOOS | TT | 10-May-06 | NH35 | 477 | 66 | 44.65 | 124.88 | 1 | 2.2 | 15.4 |
| PaCOOS | TT | 10-May-06 | NH25 | 300 | 47 | 44.65 | 124.65 | 1 | 2.2 | 19.8 |
| SAIP | BON 60 | 16-May-06 | WB40 | 910 | 71 | 46.67 | 124.98 | 1 | 2.1 | 12.4 |

of Pacific hake were captured, at least 30 of each size-class were measured.

## RESULTS

### Larval Pacific hake collections

A total of 91 Pacific hake larvae were collected in the three ichthyoplankton surveys conducted in the central and northern California Current region from 1996–2006: 1998 = 3, 2004 = 15, 2005 = 2, and 2006 = 71. Pacific hake larvae were only collected during spring (April–June). Larvae were collected between 39.00°N and 46.67°N. Larval abundances were generally higher offshore (>200 m depth) than nearshore (<200 m depth) (tab. 1), although too few larvae were collected to conduct statistical comparisons.

### YOY abundances and distributions

*(1) NOAA Fisheries, SWFSC Juvenile Rockfish Survey*

Catch rates of YOY Pacific hake observed in the core area of the SWFSC Juvenile Rockfish Survey were

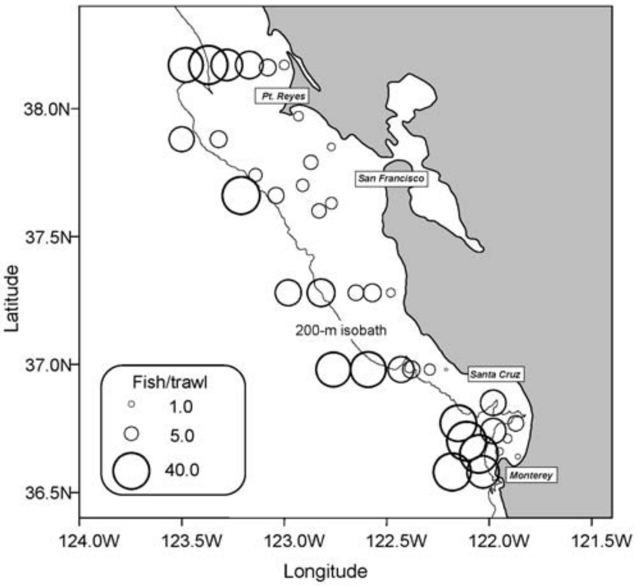

Figure 2. Average catch-per-unit-effort (CPUE; based on ANOVA) of YOY Pacific hake (*Merluccius productus*) by station of NOAA Fisheries, SWFSC Juvenile Rockfish Survey core (central California) stations, 1986–2006.

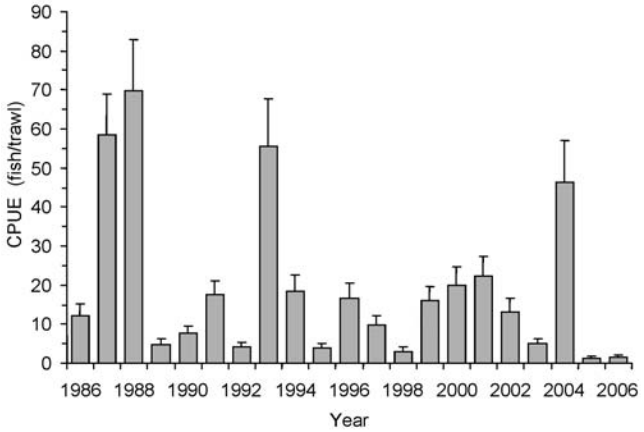

Figure 3. Average catch-per-unit-effort (CPUE; based on ANOVA) of YOY Pacific hake (*Merluccius productus*) by year of NOAA Fisheries, SWFSC Juvenile Rockfish Survey core (central California) stations, 1986–2006 (± 1 standard error).

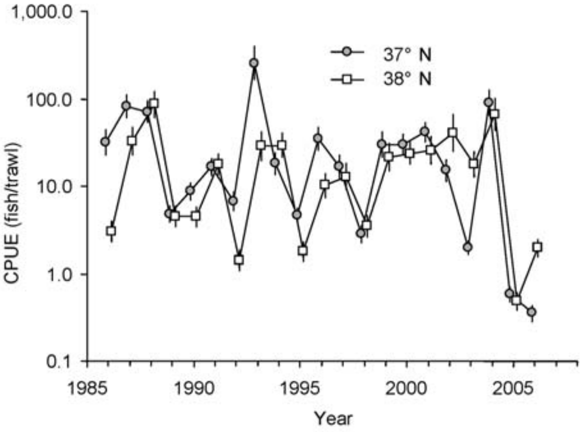

Figure 4. Average catch-per-unit-effort (CPUE; based on means of $log_e$ [$N$ + 1]) of YOY Pacific hake (*Merluccius productus*) by year in 1° latitude bins of NOAA Fisheries, SWFSC Juvenile Rockfish Survey core (central California) stations, 1986–2006 (± 1 standard error).

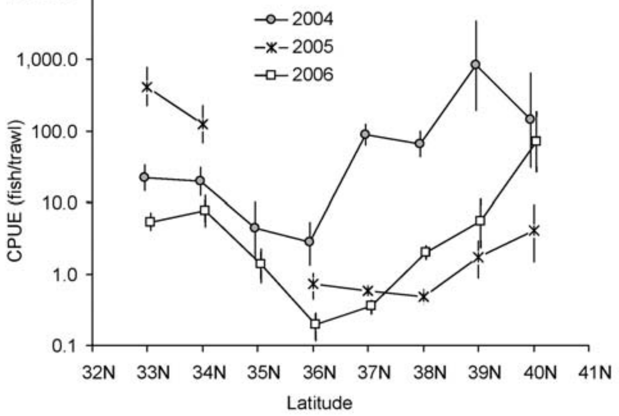

Figure 5. Average catch-per-unit-effort (CPUE; based on means of $log_e$ [$N$ + 1]) of YOY Pacific (*Merluccius productus*) hake by 1° latitude bins from the NOAA Fisheries, SWFSC Juvenile Rockfish Survey expanded coverage area, 2004–06.

strongly affected by bottom depth as shown in the back-transformed station effects from the fitted ANOVA model (fig. 2). Note that catches from stations located at, and seaward of, the continental shelf break (200 m isobath) have historically been much higher than those from stations located on the shelf proper. In addition, elevated catches of YOY Pacific hake were taken regularly in the offshore waters of Monterey Bay.

Interannual catch rates of YOY Pacific hake in the core area of the survey varied markedly (fig. 3). Catch rates in excess of 40 YOY Pacific hake/trawl were observed in 1987, 1988, 1993, and 2004. Conversely, very low catch rates were encountered in many years, including the 1992 and 1998 El Niños, and especially during the 2005 and 2006 surveys (1.2 and 1.4 fish/trawl, respectively). These two most recent surveys produced the lowest YOY Pacific hake catch rates in the entire 21-year time series.

The interaction between year and sample location (i.e., 1° latitudinal bins) within the traditional core area of the SWFSC midwater trawl survey is shown in Figure 4. The figure shows general agreement between the time series of catch rates of YOY Pacific hake observed at 37°N and 38°N, with the exception of 1992–93, when catch rates at 37°N were somewhat higher than at 38°N, and in 2003 and 2006, when the opposite pattern was observed.

Results of the expanded SWFSC Juvenile Rockfish Survey illustrate the geographic extent of YOY Pacific hake catches during the last three years (fig. 5), when survey sampling was conducted from 33° to 40°N. There was large interannual variability in the distribution and abundance of YOY Pacific hake. Catches in the northern portion of the survey area (37°–40°N) in 2004 were >65 fish/trawl and, conversely, were <22 fish/trawl in the southern area. In 2005 however, the opposite pattern was observed, with catches >120 fish/trawl taken south of Point Conception (33°–34°N) and catches <5 fish/trawl taken at all stations to the north. During 2006, catches in the traditional core area of the survey were lower than either to the north or the south.

In addition to fluctuations in catch rate, there was substantial interannual variability in the size composition of YOY Pacific hake (fig. 6). Some years (e.g., 1995, 1998, and 2006) were characterized by an abundance of small fish (20–30 mm), whereas in other years (e.g., 1997, 2002, and 2003) fish were much larger (30–50 mm). Likewise, in some years (e.g., 1994) there was a substantial range in the size of fish caught, whereas in other years (e.g., 2006) the fish were much more uniform in size.

### *(2) NOAA Fisheries, NWFSC SAIP Larval/Juvenile Survey*

The NWFSC SAIP Larval/Juvenile Survey captured a total of 14,429 YOY Pacific hake from 2004–06 from

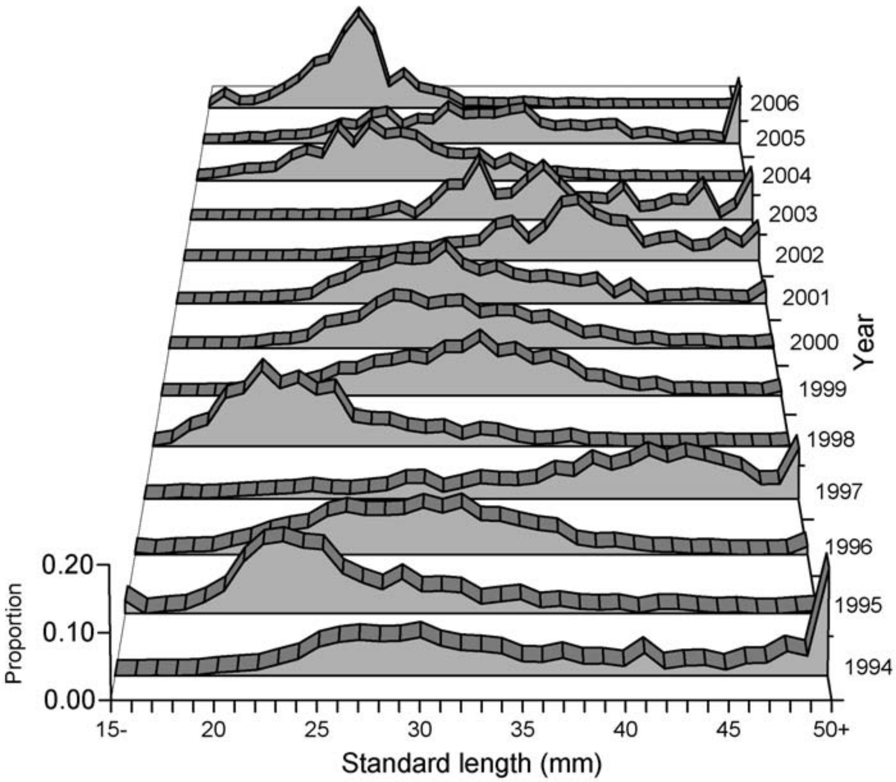

Figure 6. Annual length-frequency distributions of YOY Pacific hake (*Merluccius productus*) captured in the NOAA Fisheries, SWFSC Juvenile Rockfish Survey, 1994–2006.

TABLE 2
**Cruise summaries of NOAA Fisheries NWFSC, Stock Assesment Improvement Program (SAIP) YOY Pacific hake (*Merluccius productus*) captured off Oregon and Washington from 2004–2006. Data are separated between years by solid lines. n = number of tows, and n+ = number of tows that captured YOY hake. For gear types, MCT = modified Cobb Trawl, and NRT = Nordic 264 rope trawl.**

| Cruise | Trawl type | n | n+ | No. caught | Abundance (number/$10^6$ m$^3$) | No. measured | Mean SL (mm) | SL S.D. (mm) | ±95% C.I. (mm) |
|---|---|---|---|---|---|---|---|---|---|
| Jun–04 | MCT | 5 | 3 | 5262 | 514.4 | 90 | 44.0 | 5.2 | 1.1 |
| Aug–04 | MCT | 13 | 5 | 1912 | 110.9 | 103 | 54.7 | 8.3 | 1.6 |
| Sep–04 | NRT | 15 | 0 | 0 | – | – | – | – | – |
| Nov–04 | NRT | 20 | 0 | 0 | – | – | – | – | – |
| Jun–05 | NRT | 21 | 5 | 55 | 2.1 | 51 | 42.1 | 8.6 | 2.4 |
| Jul–05 | NRT | 15 | 4 | 183 | 16.6 | 36 | 63.2 | 10.7 | 3.6 |
| Aug–05 | NRT | 11 | 1 | 1 | 0.2 | 1 | 27.0 | – | – |
| Sep–05 | NRT | 20 | 1 | 2 | 0.4 | 2 | 76.5 | – | – |
| Oct–05 | NRT | 14 | 2 | 2 | 0.2 | 2 | 57.5 | – | – |
| May–06 | NRT | 4 | 3 | 40 | 3.0 | 38 | 24.4 | 2.3 | 0.7 |
| Jun–06 | NRT | 7 | 6 | 1079 | 49.3 | 147 | 36.1 | 5.2 | 0.8 |
| Aug–06 | NRT | 18 | 7 | 5720 | 207.7 | 143 | 61.4 | 8.0 | 1.3 |
| Sep–06 | NRT | 20 | 5 | 173 | 8.9 | 101 | 80.4 | 9.5 | 1.9 |
| All cruises | | 183 | 42 | 14429 | 94.7 | 714 | 52.4 | 17.5 | 1.3 |

central Oregon to southern Washington (tab. 2). YOY Pacific hake were captured in 42 of 183 tows with estimated density per tow ranging from 1091.0 fish $10^6$/m$^3$ June 2004 to 0.1 fish $10^6$/m$^3$ October 2005 (fig. 7). Density average per cruise ranged from 0.2 to 514.4 fish $10^6$/m$^3$, and the average density for all tows was 94.7 fish $10^6$/m$^3$ (tab. 2). For all years, Pacific hake catches were higher nearshore as the season progressed. In 2004, the highest YOY Pacific hake density observed was 65 nm offshore. Although the greatest sampling coverage was in 2005, this year had the lowest densities of YOY Pacific hake (fig. 7).

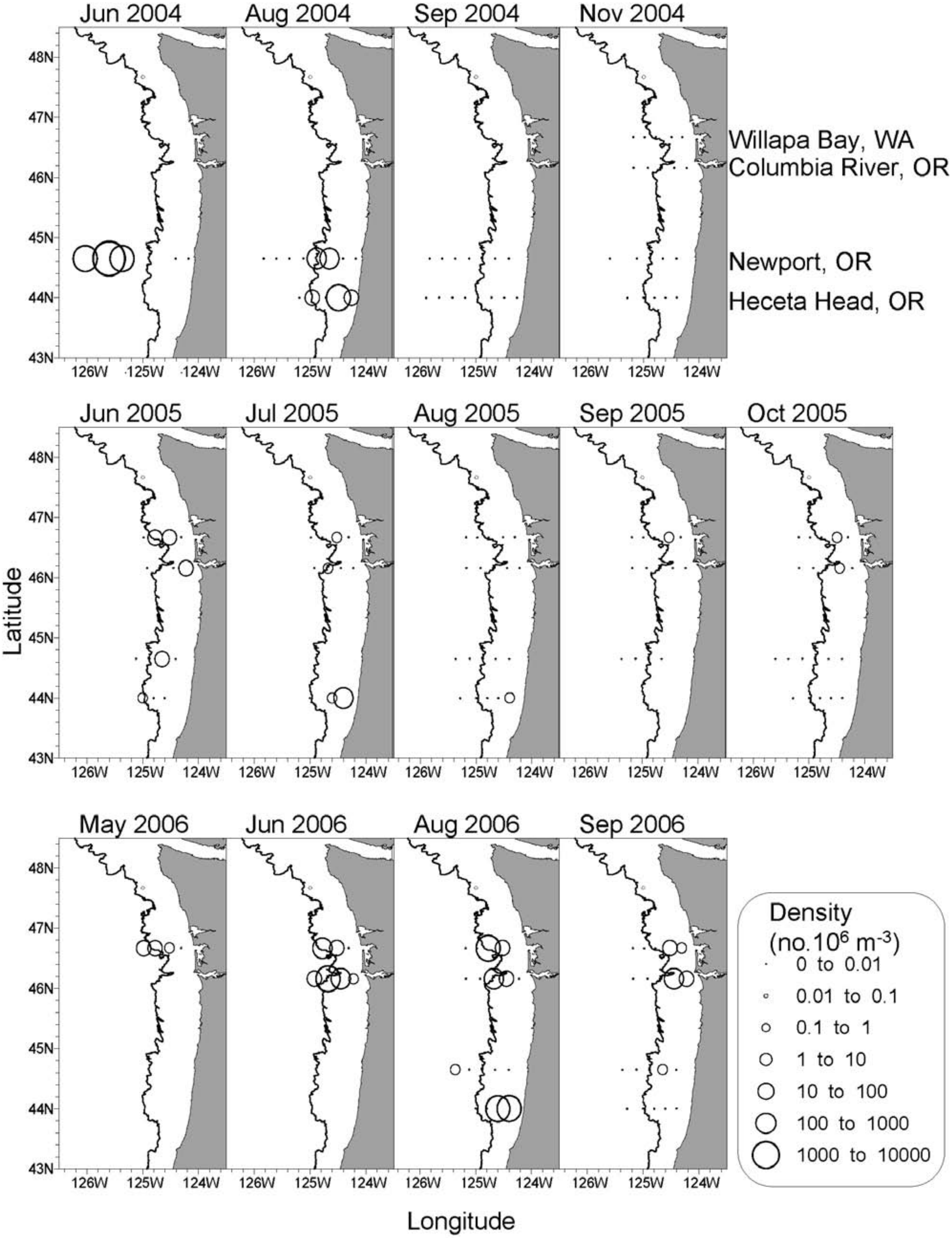

Figure 7. Densities (no. $10^6/m^3$) of YOY Pacific hake (*Merluccius productus*) observed during the NOAA Fisheries, NWFSC SAIP Larval/Juvenile Survey off Oregon and Washington by cruise. Solid dots indicate no catch and the size of the circles are proportional to the YOY Pacific hake densities, 2004–06.

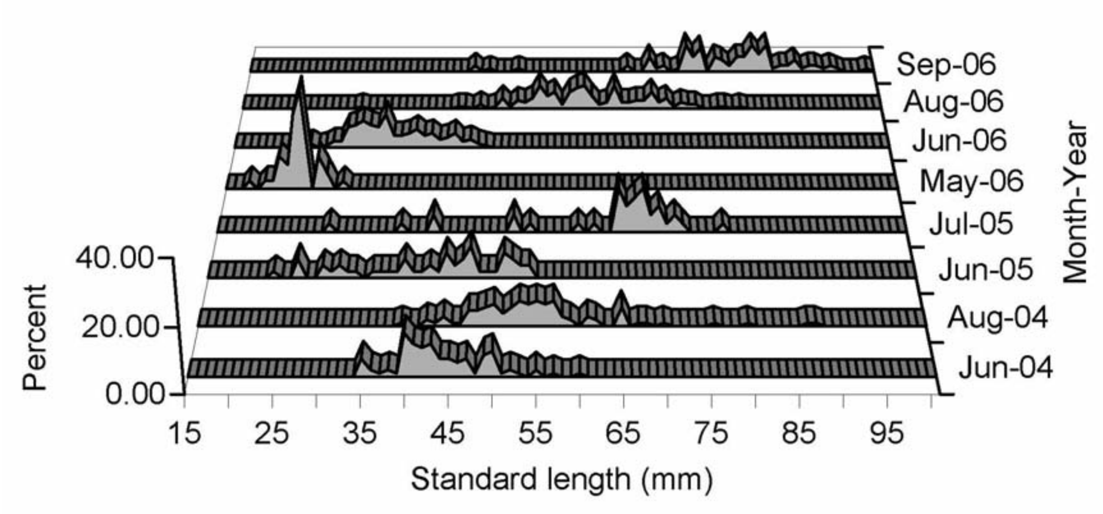

Figure 8. Monthly length-frequency distributions of YOY Pacific hake (*Merluccius productus*) captured in the NOAA Fisheries, NWFSC SAIP Larval/Juvenile Survey off Oregon and Washington, 2004–06.

The YOY Pacific hake captured during the NWFSC SAIP Larval/Juvenile Survey ranged in length from 18–100 mm with an average length of 52.4 mm (fig. 8 and tab. 2). All years showed cohorts of YOY Pacific hake growing throughout the season (fig. 8). In 2004, YOY Pacific hake were present, but sampling was limited to the southern two transects until November, and YOY Pacific hake were not encountered after August. In 2006, there was one dominant size mode and one smaller size mode. The dominant mode was encountered in all cruises, whereas the smaller size mode was represented by a single Pacific hake caught in August (102 km offshore) and four Pacific hake caught in September (46 km offshore) along the NH line, and these were likely spawned late in the season.

### (3) *NWFSC-PWCC Survey*

Catches of YOY Pacific hake by latitude indicated a northward distributional shift from 2001 to 2006 (fig. 9). YOY Pacific hake were caught as far north as 48°N in 2005 and 2006, but prior to 2005, few YOY Pacific hake were captured north of 42°N. In 2005, the largest concentrations of YOY Pacific hake occurred between 45°N and 39°N (i.e., approximately central Oregon to Cape Mendocino, California). The distribution of YOY Pacific hake was similar in 2006, but with more of the fish located in the northern portion of this range. South of Cape Mendocino, YOY Pacific hake were taken in only a few hauls and in low numbers in 2005 and 2006.

### (4) *NOAA Fisheries, NWFSC Predator Survey*

Length-frequency distributions from the NWFSC Predator Survey showed the presence of YOY Pacific hake off northern Oregon and southern Washington beginning in 2004 (fig. 10). A total of 12,039 YOY Pacific hake (30–113 mm SL) were collected between 2004 and 2006. Adult Pacific hake (generally >300 mm) were collected during all years, and during both 1998 and 1999 some age-1 Pacific hake (140–160 mm) were captured, probably reflecting recruitment during the 1997–98 El Niño event. Age-1 Pacific hake were observed in 2005, but were nearly absent in 2006, indicating that Pacific hake spawned in 2005 may not have successfully recruited that year off Oregon and Washington.

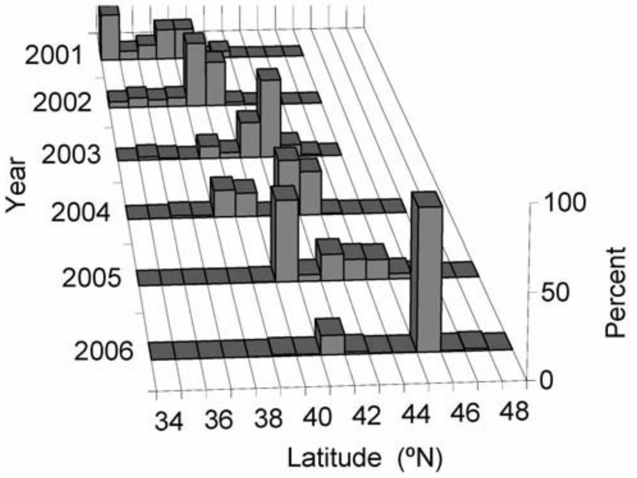

Figure 9. Distribution of YOY Pacific hake (*Merluccius productus*), represented as a percentage of annual catch by 1°-latitude bins, captured in the NWFSC-PWCC Survey, 2001–06. From 2001 to 2003 the survey covered an area from 34.50° to 44.50°N, in 2004 coverage was expanded to 46.50°N, and further expanded to 48.00°N in 2005.

## DISCUSSION

### Larval Pacific hake collections

Despite relatively intense sampling for fish larvae in the central and northern California Current from 1967

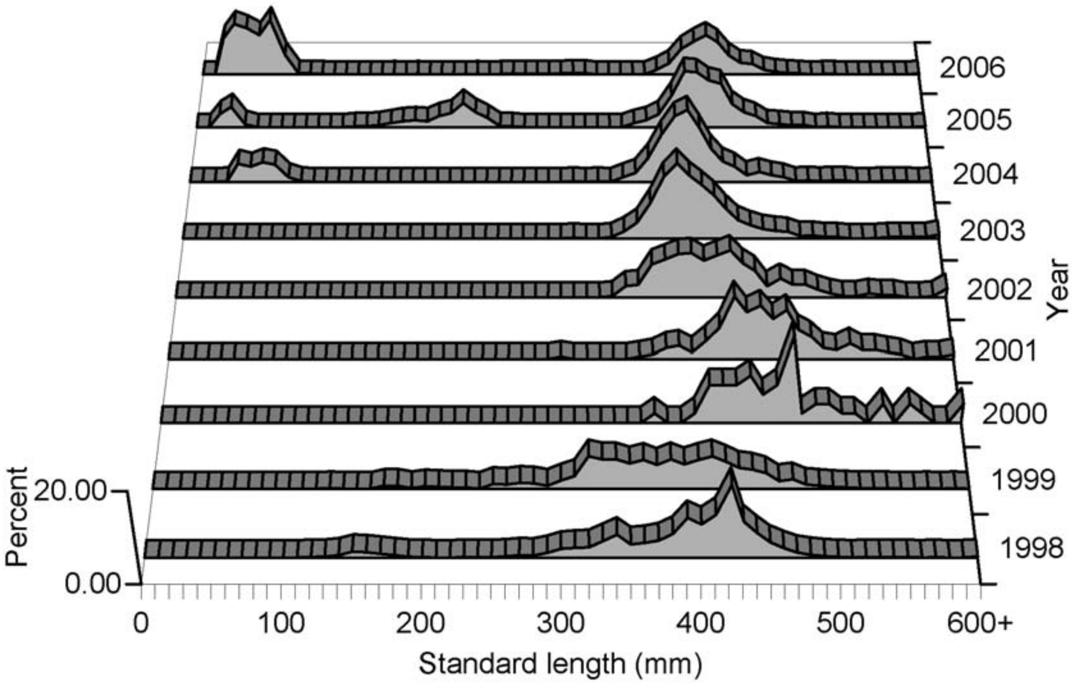

Figure 10. Annual length-frequency distributions of Pacific hake (*Merluccius productus*) captured in the NOAA Fisheries, NWFSC Predator Survey off Oregon and Washington, 1998–2006.

to 2006 (tab. 3; Auth and Brodeur 2006; Auth et al. 2007), Pacific hake larvae have only been collected during years having positive Multivariate El Niño Index (MEI) values (e.g., Doyle 1995). In the last four decades prior to 2004, only 38 larval hake were captured in over 2000 tows. Since 2004, larval Pacific hake were captured in 91 of approximately 300 tows off Oregon during weak El Niño periods, but when ocean conditions were anomalously warm (Peterson et al. 2006; Pierce et al. 2006). The biota was characterized by the presence of numerous southern or offshore fish and zooplankton species (Brodeur et al. 2006; Mackas et al. 2006). Despite not sampling in the correct place or at the appropriate time (deepwater, offshore, and in February and March), we have still captured more larvae since 2004 than had previously been encountered in the area. During 2004–06, larval Pacific hake were collected at increasingly northern locations, with the largest larval Pacific hake numbers (*n* = 71) recorded off the coast of Oregon in 2006. Larval Pacific hake were captured as far north as 45° N during the coast-wide sardine egg survey in 2006 (Lo 2007).

Pacific hake larvae of the size collected were not likely to have migrated from southern California spawning grounds, but likely spawned in northern waters. The mean lengths of larval hake captured during the PaCOOS and SAIP Larval/Juvenile Surveys in 2004–06 were 4.8 mm in 2004, 9.9 mm in 2005, and 20.92 mm in 2006. Using the growth curve from Butler and Nishimoto (1997), we determined that the average ages of the larvae collected off Oregon were 12 days in 2004, 37 days in 2005, and 72 days in 2006. Agostini et al. (2006) calculated most poleward flow in the California undercurrent waters occupied by Pacific hake to be 0.025–0.075 m/s and Pierce et al. (2000) calculated the overall mean poleward flow in the California undercurrent to be 0.10 m/s in July–August 1995. Larvae 72 days old would have to drift north at a rate of 0.15 m/s, or 13 km/d in a constant heading to travel the 1000 km from the California Bight to Oregon waters. So it is unlikely that drift alone would explain this northern shift in their distribution.

Although larval Pacific hake were collected as close as 4 km from shore, most were found in offshore waters. The mean length of larvae along the NH line during the May 2006 PaCOOS Survey decreased from 22.7 to 12.7 mm SL with increasing distance from shore (tab. 1). This suggests that larval Pacific hake spawned in offshore waters were either actively or passively transported into nearshore waters through ontogeny. Nearshore movement of larval Pacific hake in the north is consistent with oceanographic conditions and findings in the south (Bailey 1981; Grover et al. 2002), and further reduces the likelihood that large larval Pacific hake observed off of Oregon were transported from southern California.

## Juvenile Pacific hake collections

Few studies captured YOY Pacific hake north of 40°N in the NCC prior to 2003, and the surveys that did captured relatively few (tab. 3). The NOAA Fisheries, Alaska Fisheries Science Center (AFSC), Resource Assessment and Conservation Engineering (RACE) Division's triennial bottom trawl survey captured a total of 146 YOY Pacific hake (<100 mm) between 1977 and 2001 north of 40°N. In 2004, the triennial bottom trawl survey (conducted by the NWFSC Fishery Resource Analysis and Monitoring-[FRAM]-Division) captured 3,991 YOY Pacific hake (<100 mm) north of 40°N (M. Wilkins, NOAA Fisheries, AFSC, RACE Division 7600 Sand Point Way N.E. Seattle, Washington 98115 pers. comm., 2007). Between 1977–2001, the NOAA Fisheries, AFSC RACE Division West Coast acoustic survey captured a single YOY Pacific hake north of 40°N (M. Guttormsen, NOAA Fisheries, AFSC, RACE Division 7600 Sand Point Way N.E. Seattle, Washington 98115 pers. comm., 2007). Though not quantified, the Canadian Department of Fisheries and Oceans (DFO) Pacific hake survey from 1984–2006 captured YOY Pacific hake (<8 cm) in 1993, 1994, 1997, and 2006 off of Vancouver Island (G. A. McFarlane, Fisheries and Oceans, Canada, Pacific Biological Station, Nanaimo, BC, V9T 6N7 pers. comm., 2007). During the 1997–98 El Niño event, the NOAA Fisheries NWFSC Predator Survey captured a few age-1 hake but no YOY Pacific hake were caught in these surveys until 2004 (fig. 10).

Our data suggest that a northerly expansion in the spawning location of Pacific hake has occurred in the NCC, especially during 2003–06. Over the last decade, YOY Pacific hake distributions have expanded ~1000 km north. We conclude that it is unlikely this observed expansion was due to increased northerly current transport; this is supported by the findings of several fishery surveys: (1) the yearly occurrence and recruitment of YOY Pacific hake in the NCC captured in the NWFSC SAIP Larval/Juvenile Survey, the NWFSC-PWCC Survey, and the NWFSC Predator Survey starting in 2003; (2) the reduction in the abundance of larvae (≤11.75 mm) from 2003 to 2006 in the southern California spawning region (Peterson et al. 2006; Lo 2007); (3) the shoreward rather than northward transport of larvae (PaCOOS and NWFSC SAIP Larval/Juvenile Surveys); and (4) the low abundance of YOY Pacific hake in the NCC prior to 2004 in other surveys (see tab. 3).

The northerly shift of Pacific hake spawning and recruitment is likely related to increased winter/spring temperatures in the NCC. Hollowed (1992), Horne and Smith (1997), and Benson et al. (2002) hypothesized that Pacific hake shift their spawning location north during warm ocean years. Historically, warm years also tend to produce strong year classes, possibly due to relaxed upwelling or expansion of the spawning range (Methot and Dorn 1995; Ressler et al., in press).

YOY Pacific hake (7.5–8.0 mm mean length) were captured by a commercial fishing vessel as far north as Vancouver Island in 2005 (K. Cooke, Fisheries and Oceans, Canada, Pacific Biological Station, Nanaimo, BC, V9T 6N7, pers. comm., 2007). High densities of YOY Pacific hake were also found in the most southern regions of the SWFSC Juvenile Rockfish Survey in the same year (fig. 5), and low densities of YOY Pacific hake were encountered in the areas in between. In the 2006 coast-wide sardine survey, there appeared to be two distinct groups of larval Pacific hake (Lo 2007). The coastal stock may be splitting into two distinct spawning groups or possibly ocean-current patterns are causing a split in distribution. However, a longer time series is needed to confirm either hypothesis.

### NCC occurrences of age-1 Pacific hake in 2007

It appears that the 2006 year-class of Pacific hake is successfully recruiting in the NCC based upon recent widespread, high density occurrences not previously reported for this region. Age-1 Pacific hake have been collected from at least central California to Washington. The Predator Survey captured over 8,700 age-1 Pacific hake in a single midwater tow 24 km off of the Columbia River in May 2007. The 2007 NWFSC-PWCC Survey also caught large numbers of age-1 Pacific hake from Monterey Bay to Newport, and a 15-min test tow on light acoustic sign caught 225 kg of age-1 Pacific hake (Wespestad, pers. obs.). Commercial shrimp trawlers have been capturing large numbers of age-1 Pacific hake as bycatch in their trawls and it is negatively affecting the fishery; in some tows the majority of the catch has been age-1 Pacific hake, and the entire tows were discarded. The large catches of age-1 hake in the commercial shrimp fishery have occurred from south of Cape Blanco, Oregon to Destruction Island, Washington (Steve Jones, Oregon Department of Fish and Game, 2040 SE Marine Science Drive, Newport, Oregon 97365 pers. comm., 2007). Thus, the 2006 Pacific hake year class appears to be negatively affecting the commercial shrimp fishery, and will likely affect several other fisheries in the NCC in future years.

### Implications for the ecosystem and management

A northerly shift in the spawning and recruitment of Pacific hake will have major implications on the NCC ecosystem. Pacific hake larvae and juvenile survival may increase, and both adults and juveniles will not have to migrate as far to reach their traditional northern feeding grounds and will thus expend less energy migrating. Alternatively, Pacific hake year-class strength may be negatively affected due to: (1) cannibalism (Buckley and Livingston 1997), (2) predation, since YOY Pacific hake will encounter a new suite of predators not experienced off California, and (3) environmental conditions that

TABLE 3

**Surveys that captured or were capable of capturing early life-stages of Pacific hake (*Merluccius productus*) collected in the central and northern California Current from 1961–2006. TH = total number of hauls. n = number of larvae or YOY hake collected. For sampling gear, IKT = Isaacs-Kidd trawl, BON = bongo net, TT = Tucker trawl, PRT = Polish rope trawl, MAT = modified anchovy trawl, NRT = Nordic 264 rope trawl, S = surface trawl, MW = midwater trawl, and B = bottom trawl. N/A = data not avaliable.**

| Survey | Source | Sampling Gear, Mouth opening ($m^2$) | Mesh size (mm) |
|---|---|---|---|
| **Larval surveys** | | | |
| NOAA Fisheries, NWFSC | Waldron 1972 | 1-m ring net, 1.0 | 0.7 |
| School of Oceanography, OSU | Richardson 1973 | IKT (MW), 36 | 0.571 |
| School of Oceanography, OSU | Richardson 1973 | 0.7-m BON, 0.39 | 0.571 |
| School of Oceanography, OSU | Richardson 1973 | 1-m ring net, 0.79 | 0.571 |
| School of Oceanography, OSU | Mundy 1984 | 0.2 or 0.7-m BON, 0.03-0.39 | 0.233–0.571 |
| School of Oceanography, OSU | Richardson & Pearcy 1977 | 0.7-m BON, 0.39 | 0.571 |
| School of Oceanography, OSU | Richardson et al. 1980 | 0.7-m BON, 0.39 | 0.571 |
| School of Oceanography, OSU | Lyczkowski-Shultz unpublished[1] | 1-m square net, 1.0 | 0.240 |
| NOAA Fisheries, AFSC | Doyle 1992 | 0.61-m BON, 0.29 | 0.505 |
| School of Oceanography, OSU | Boehlert et al. 1985 | TT, 0.71 | 0.505 |
| School of Oceanography, OSU | Brodeur et al. 1985 | 0.7-m ring net, 0.39 | 0.333 |
| NOAA NH line | Brodeur et al. unpublished | 0.61-m ring or 0.7-m BON, 0.29-0.39 | 0.333 |
| NOAA Fisheries, NWFSC (BPA) | Brodeur et al. unpublished | 1-m ring net, 0.79 | 0.335 |
| NOAA Fisheries, NWFSC (SAIP) | Auth unpublished | 0.61-m BON, 0.29 | 0.333 |
| PaCOOS | Auth unpublished | TT, 1.0 | 0.335 |
| PaCOOS | Auth unpublished | 0.7-m BON, 0.39 | 0.571 |
| **Juvenile surveys** | | | |
| Micronekton Surveys, OSU | Brodeur et al. 2003 | IKT (MW), N/A | 5.0 |
| NOAA Fisheries, NWAFC, RACE Division | Guttormsen unpublished[2] | Cobb trawl (MW), 130 | 32.0 |
| NOAA Fisheries, NWAFC, RACE Division | Guttormsen unpublished[2] | Siedlecki bottom trawl, 90 | 32.0 |
| NOAA Fisheries, AFSC, RACE Division | Weinberg et al. 2002 | Poly Nor'Eastern trawl (B), 105 | 32 |
| NOAA Fisheries, NWAFC, RACE Division | Guttormsen unpublished[2] | Norse (MW), 800 | 46.0 |
| School of Oceanography, OSU | Brodeur & Pearcy 1986 | Purse seine, N/A | 32 |
| NOAA Fisheries, NWAFC, RACE Division | Guttormsen unpublished[2] | 3/4 Norse (MW), NA | 32.0 |
| DFO (Hake Surveys) | Saunders & McFarlane 1997: and unpublished. | PRT (MW), 120 | 9.5 |
| NOAA Fisheries, AFSC, RACE Division | Guttormsen unpublished[2] | Alaska diamond (MW), NA | 32.0 |
| NOAA Fisheries, SWFSC (Juvenile Rockfish) | Sakuma et al. 2006 | MAT (MW), 100 | 9.5 |
| NOAA Fisheries, AFSC, RACE Division | Guttormsen unpublished[2] | Northern gold (MW), NA | 32.0 |
| Columbia River Plume salmon survey | Brodeur et al. 2003 | NRT (S), 336 | 3.0 |
| NOAA Fisheries, NWFSC (Predator) | Emmett et al. 2006 | NRT (S), 336 | 3.0 |
| NOAA Fisheries, AFSC, RACE Division | Guttormsen unpublished[2] | Nylon Nor'eastern (Bot), 105 | 32.0 |
| NOAA Fisheries, AFSC, RACE Division | Guttormsen unpublished[2] | Marinovich (MW), 37 | 3.2 |
| NOAA Fisheries, AFSC, RACE Division | Guttormsen unpublished[2] | Aleutian wing trawl (MW), 850 | 4.8 |
| NOAA Fisheries, AFSC, RACE Division | Guttormsen unpublished[2] | Methot, 5.3 | 1.0 |
| NOAA Fisheries, AFSC, RACE Division | Guttormsen unpublished[2] | Aleutian wing trawl (MW), 850 | 32.0 |
| NOAA Fisheries, AFSC, RACE Division | Guttormsen unpublished[2] | Poly Nor'eastern (Bot), 130 | 32.0 |
| NOAA Fisheries, NWFSC (GLOBEC) | Reese & Brodeur 2006 | NRT (S), 336 | 3.0 |
| NWFSC-PWCC | Sakuma et al. 2006 | MAT (MW), 100 | 9.5 |
| NOAA Fisheries, NWFSC (SAIP) | Phillips unpublished | Cobb trawl (MW), 130 | 3.0 |
| NOAA Fisheries, NWFSC (SAIP) | Phillips unpublished | NRT (MW), 336 | 3.0 |

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may not favor larval or YOY Pacific hake survival in the highly advective NCC (Hickey and Banas 2003).

Potential impacts of increased numbers of juvenile Pacific hake in the NCC ecosystem will vary. Pacific hake juveniles may compete for prey with other commercially important species, such as juvenile salmon and rockfish. Adult Pacific hake become increasingly picivorous with age, and may prey upon juvenile salmon and forage fishes, thus reducing their abundances (Livingston 1983; Livingston and Bailey 1985; Emmett and Krutzikowsky, in press).

Ultimately, if the distance that Pacific hake migrate south to spawn is reduced, it is likely that a larger percentage of the coastal stock of the Pacific hake population will spend more time in Canadian waters. Presently, the American Pacific hake fishery is the largest single-species fishery off the west coast of the U.S., and the U.S. and Canada coordinate to define the annual total

TABLE 3 (continued)

**Surveys that captured or were capable of capturing early life-stages of Pacific hake (*Merluccius productus*) collected in the central and northern California Current from 1961–2006. TH = total number of hauls. n = number of larvae or YOY hake collected. For sampling gear, IKT = Isaacs-Kidd trawl, BON = bongo net, TT = Tucker trawl, PRT = Polish rope trawl, MAT = modified anchovy trawl, NRT = Nordic 264 rope trawl, S = surface trawl, MW = midwater trawl, and B = bottom trawl. N/A = data not avaliable.**

| Years of sampling | Season of sampling | Total cruises | Latitude range (°N) | Area or depth coverage offshore (km or m) | TH | n | Years of capture |
|---|---|---|---|---|---|---|---|
| Larval surveys | | | | | | | |
| 1967 | April to May | 2 | 42–51 | Nearshore–550 km | 88 | 0 | |
| 1969 | May to October | 6 | 42–46 | Nearshore–>100 km | 127 | 0 | |
| 1969 | May to October | 6 | 42–46 | Nearshore–>100 km | 62 | 0 | |
| 1969 | May to October | 6 | 42–46 | Nearshore–>100 km | 99 | 0 | |
| 1969–1972 | Biweekly | 74 | 44.67 | 2–18 km | 273 | 0 | |
| 1971–1972 | Monthly | 18 | 44.65 | 2–111 km | 287 | 0 | |
| 1972–1975 | March & April | 6 | 43–46 | 2–56 km | 306 | 1 | 1973 |
| 1977–1978 | November to June | 10 | 44.65 | 5–10 km | 25 | 0 | |
| 1980–1987 | Mostly Spring | 10 | 42–46 | 2–46 km | 1086 | 37 | 1983, 1984 |
| 1982 | April–July | 5 | 44.67 | 9–18 km | 6 | 0 | |
| 1983 | April to September | 11 | 44.67 | 6–18 km | 39 | 0 | |
| 1996–2006 | Biweekly | 159 | 44.67 | 9–18 km | 261 | 3 | 1998 |
| 1999–2004 | Biweekly (typically spring and summer) | 47 | 46.16 | 20–30 km | 85 | 0 | |
| 2004–2006 | Spring to Fall | 9 | 44–46.67 | 5–75 (typically 10–55) km | 138 | 1 | 2005 |
| 2004–2006 | May | 3 | 38.48–47 | 4–121 km | 106 | 49 | 2004–2006 |
| 2004–2006 | Spring to Fall | 5 | 44–46.67 | 5–85 (typically 10–55) km | 76 | 38 | 2006 |
| Juvenile surveys | | | | | | | |
| 1961–1969 | Monthly | 175 | 42.1–46.4 | 28–165 km | 623 | 0 | |
| 1977 | July to September | 1 | 34.10–49.75 | 75 m to > 1,500 m | 116 | 0 | |
| 1977 | August to September | 1 | 39.07–48.22 | 75 m to > 1,500 m | 65 | 0 | |
| 1977–2004 | Summer | 10 | 34.5–49.5 | 55–500 m | 5215 | 18645 | 1977–2004 |
| 1979–1980 | August to September | 2 | 37.22–49.32 | 75 m to > 1,500 m | 107 | 81 | 1980 |
| 1979–1984 | June to September | 15 | 43–48.33 | 6–56 km | 843 | 0 | |
| 1980–1986 | July | 3 | 36.98–48.99 | 75 m to > 1,500 m | 48 | 0 | |
| 1984–2006 | July & August | 35 | 48–50.5 | Nearshore–>100 km | N/A | N/A | 1993–94, 1997, 2004, 2006 |
| 1986–1989 | July | 2 | 37.00–49.13 | 75 m to > 1,500 m | 46 | 0 | |
| 1986–2006 | Spring | 24 | 32.75–45.0 | Nearshore–140 km | 2241 | 530513 | 1986–2006 |
| 1989–1992 | July to August | 2 | 34.83–51.49 | 75 m to > 1,500 m | 78 | 0 | |
| 1998–2006 | May to September | 26 | 44–47 | Across shelf | 1259 | 0 | |
| 1998–2006 | April to August | 85 | 46.16–46.67 | 7–56 km | 941 | 12039 | 2004–2006 |
| 1992–1995 | July to August | 2 | 35.78–51.06 | 75 m to > 1,500 m | 52 | 0 | |
| 1992–2001 | July to August | 3 | 42.30–54.82 | 75 m to > 1,500 m | 6 | 0 | |
| 1995 | July | 1 | 32.53–37.80 | 75 m to > 1,500 m | 17 | 318 | 1995 |
| 1995–2001 | July | 3 | 34.79–55.00 | 75 m to > 1,500 m | 103 | 0 | |
| 1995–2001 | June to September | 3 | 37.14–54.83 | 75 m to > 1,500 m | 237 | 0 | |
| 1995–2001 | June to September | 3 | 36.30–54.57 | 75 m to > 1,500 m | 38 | 5 | 1998 |
| 2000, 2002 | June & August | 4 | 42–22.67 | 2–70 km | 343 | 0 | |
| 2001–2006 | Spring | 6 | 34.5–48 | Across shelf | 782 | 237764 | 2001–2006 |
| 2004 | July to August | 2 | 44–44.67 | 5–85 km | 18 | 7174 | 2004–2006 |
| 2004–2006 | Spring to Fall | 11 | 44–46.67 | 5–85 (typically 10–55) km | 165 | 7255 | 2004–2006 |

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allowable catch (TAC). Under this agreement, 26.12% of the TAC is allocated to Canada (Helser et al. 2006). A more northerly spawning Pacific hake population may result in more Pacific hake in Canadian waters (Benson et al. 2002), thus affecting the proportion of the population available to the U.S.

It is too soon to ascertain whether this northward shift in the occurrence of larvae and YOY Pacific hake represents a permanent life-history feature in the California Current, or is a short-term response to warming ocean conditions. Similar northerly shifts in fish distributions have been observed in other systems such as the U.S. East Coast (Murawski 1993), the North Sea (Perry et al. 2005), and the Mediterranean Sea (Sabatés et al. 2006). Detailed studies of the effects of fish distributional shifts on other ecosystem components are clearly warranted in order to manage these systems properly.

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