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REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

In April 1997 CalCOFI celebrated its three hundredth cruise in the California Current. This number includes neither the countless other cruises and expeditions inspired by the CalCOFI program nor the annual fisheries cruises to sample eggs and fish larvae along the coast of the Californias. Researchers on the April 1997 cruise sampled a portion of the sampling grid first established in 1949. That first sampling program has been modified over time to incorporate new technologies and to answer questions that have arisen since the program began. Owing to reductions in funding and modified priorities, the locations sampled today are a subset of those sampled at the outset. But the underlying scientific question that drives the program has remained constant: "What are the causes of changes in populations, over time, of commercially important fishes in California's coastal waters?" The constancy of the program has produced perhaps the largest, most robust multivariate marine fisheries database in the world. Scientists and policymakers all over the world refer to these data: during 18 months of operation, the CalCOFI Web pages have received over 25,000 hits from private industries, private scientific research laboratories, U.S. government agencies, state agencies, and universities around the world. Many of these organizations manifest a pattern that suggests serious data use.

Over the years, CalCOFI's researchers have demonstrated that episodic atmospheric and oceanic events significantly affect the biology of the California Current. The paper by Schwing et al. discusses the events and trends of the last year in the California Current from a perspective that is both interdisciplinary and global. Baduini discusses how such episodes affect the food chain in Monterey Bay.

Disciplines not normally associated with fishery oceanography in the strictest sense are often brought to bear in the open intellectual climate of CalCOFI. An example in this volume is the work by Lange et al., which, together with other studies of local anaerobic basins, helps us to understand how annual layers of sediment are deposited, and to expand our scope of inquiry backward in time through several centuries.

The commercially important species of fishes in the California Current must be managed by agencies of both the United States and Mexico. Thus a community of interest, speaking a common scientific language, has developed through several decades of transborder cooperation and education through the efforts of the CalCOFI member agencies and Mexican fisheries agencies (cf. Cotero-Altamirano and Green-Ruiz). The management of coastal lagoons and estuaries as nurseries for fishes is an important matter to both nations, and requires a common understanding of methods of measurement and analysis. Rosales-Casián collaborated with CalCOFI agencies in his research on two estuaries in Baja California.

Selected papers from last year's CalCOFI symposium on the biology of the Pacific hake (*Merluccius productus*) and related species worldwide constitute a valuable collection of contributions to our understanding of these commercially important species.

During the past year, scientists of the National Marine Fisheries Service (NMFS), the California Department of Fish and Game (CDFG), and the Scripps Institution of Oceanography have collaborated in several cruises. In autumn of 1996, the new research vessel *Roger Revelle* was inaugurated into the service of the University of California with a CalCOFI cruise. Instruments designed for use on the NOAA ship *David Starr Jordan* and the UC vessel *New Horizon* were successfully adapted for use on the *Revelle*. The ship's extra capacity resulted in increased participation from ancillary, extramurally funded programs whose researchers have become regular participants on CalCOFI cruises.

CalCOFI scientists are constantly seeking new methods of collecting data to optimize information gathering. A fish egg-pumping device has been incorporated into the routine underway operations of the cruises. Preliminary studies have shown exciting mesoscale relations between physical properties and fish eggs. The system has been tested on several NOAA cruises, and a similar system has been sent to South Africa for studies in the Benguela Current. In addition, NMFS and CDFG, together with NOAA's Office of Oceanic and Atmospheric Research, have tested airborne lidar (laser imaging) for detecting pelagic fish schools. A CDFG aircraft collected lidar data while an NMFS vessel collected acoustic data and high-speed trawl specimens for ship-

board identification. Shipboard acoustic data and lidar data were found to be comparable. Airborne lidar may prove to be an economical way to assess biomass.

Also in order to improve stock assessments, the CDFG has reached an informal agreement with the Mexican government's Instituto Nacional de la Pesca to include Port of Ensenada fisheries statistics and biological data in CDFG analyses. Additional cross-border cooperation included a summer 1996 larval mackerel survey in Baja California waters to determine the extent and intensity of chub mackerel spawning. Survey data were compared to data collected from 1951 to 1966. All historic larval data were entered into a common database, to hindcast abundances through that earlier sixteen-year period. This analysis vastly improved the accuracy of the model used for current-year estimates of abundance. On the basis of this new model, the estimate of mackerel abundance used for 1997 is nearly double, and the coefficient of variation was significantly reduced.

In addition, CDFG's fishery sampling was extended northward in response to increased sardine abundance and decreased chub mackerel abundance. In order to obtain additional biological information and size-at-age data, CDFG began sampling the Monterey fishery. Additional sardine and chub mackerel fishery data may be available from a new study of whiting bycatch, funded by the Pacific States Marine Fisheries Commission, and from experimental sardine fishery data collected by the Canadian Department of Fisheries in 1996.

This year, the Southwest Fisheries Science Center (SWFSC) began a new initiative to monitor egg and larval fish production in marine reserves near Ventura and Point Conception. These studies are designed to develop methods for testing the effectiveness of marine reserves as sources of adult spawning biomass that may reseed heavily exploited areas outside the reserves. The field research is designed to monitor spatial and temporal variation in egg production and the patterns of egg and larval dispersal from the reserves. These studies, supported by funds administered by California Sea Grant, draw upon methods that include the egg pump, satellite-tracked current drifters, and vertically hauled bongo nets.

The U.S. GLOBEC (Global Ocean Ecosystem Dynamics) program of the National Science Foundation and NOAA has long invoked concepts and methods similar to those of CalCOFI, but its field work has been limited to Georges Bank off Massachusetts. Plans for a new study off the U.S. west coast have stimulated CalCOFI investigators to consider how their expertise and experience may contribute to the GLOBEC study. The biogeographic center of the study is an area of historic CalCOFI interest and research, but is located north of the present CalCOFI study area, where a less complicated coastal structure simplifies the field studies and where salmon is a politically potent subject of investigation.

In July of 1996 the Ichthyoplankton Group at SWFSC, together with the CalCOFI Committee and the Allen Press, published the 1,517-page *CalCOFI Atlas 33*, titled *The Early Stages of Fishes of the California Current Region*. This tome, edited by Geoff Moser, treats the life history of 586 species in 158 families and 25 orders. The book includes 2,500 illustrations of eggs, yolk-sac larvae, preflexion larvae, flexion larvae, and post-flexion larvae. Parts of the book were over 40 years in development.

With new funding provided through the Saltonstall-Kennedy program of NMFS, the Ichthyoplankton Group is reexamining the preserved ichthyoplankton collection in order to update the time-series data for rockfish (*Sebastes*) larvae. New alcohol-preserved samples, taken simultaneously with formalin-preserved samples, will be used for studies of molecular genetic markers that may help identify fish eggs and larvae when visual methods are ineffective.

The committee thanks the officers and crews of the NOAA ship *David Starr Jordan*, the State of California research vessel *Mako*, and the University of California research vessels *New Horizon* and *Roger Revelle* for their excellent support of the CalCOFI field sampling program. Appreciation is also extended for the collaborative efforts of the hydrographic department of the Mexican navy and the Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California for their contribution to the article on the California Current (Schwing et al.). The committee and coordinator also thank the following people for their invaluable contribution of time and expertise in reviewing the manuscripts that are published in this volume: Shannon Cass-Calay, Loren Haury, George Hemingway, Roger Hewitt, Sharon Kramer, Uta Passow, Susan Picquelle, Drew Talley. And finally we thank the editor, Julie Olfe.

Portions of the *CalCOFI Reports*, as well as extensive data archives, calendars of operations, maps of cruises, animations, links to cooperating agencies, and general information about CalCOFI, are available online at *http://www-mlrg.ucsd.edu/calcofi.html*.

The CalCOFI Committee:
    Doyle Hanan, CDFG
    Michael Mullin, SIO-UCSD
    Michael Tillman, SWFSC-NMFS
    George Hemingway, Coordinator

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1996

CALIFORNIA DEPARTMENT OF FISH AND GAME
Marine Resources Division
8604 La Jolla Shores Drive
La Jolla, California 92037-1508

Total 1996 annual landings of fishes, crustaceans, echinoderms, and mollusks in California increased by 8% from 1995, to 208,440 metric tons (t). Ex-vessel economic value of California commercial landings rose 16% from the prior year's level, to $183.7 million.

Pelagic wetfish landings increased 3% from 1995. The largest share of this increase was attributed to a record level of market squid landings (78,825 t). Increases were also registered for northern anchovy, Pacific mackerel, and Pacific herring.

Groundfish fisheries declined slightly in 1996, and ex-vessel revenues remained stable at $34 million. Statewide, Dungeness crab landings changed little from the year before, remaining 40% above the ten-year mean of 4,348 t. Sea urchin landings continued an eight-year decline, falling an additional 11% in northern and southern California to 9,105 t. The spot and ridgeback prawn fishery registered a dramatic 39% increase in annual catch, to 511 t, as did the sea cucumber fishery, which rose to a 19-year record since the fishery's inception. Commercial landings of red abalone declined by an additional 33% in 1996, to just 75 t. Commercial and recreational fisheries for pink, green, and white abalones were closed by the California Fish and Game Commission as of March 1, 1996. The black abalone fishery had closed previously because of the population effects of withering syndrome disease.

Swordfish and mako shark landings registered small decreases, but thresher shark landings rose slightly in 1996, ending a decade-long decline. Drift gill nets accounted for an increasing proportion (70%) of these landings, at the expense of longline and harpoon gears.

California's live-fish fishery continued its expansive growth in 1996 with respect to total landings (+25%), number of target species (66 species, as compared to 54 species in 1995), fishing methods, and markets. Statewide landings of live fish were estimated at 562 t, with an estimated ex-vessel value of over $3.6 million.

PACIFIC SARDINE

Rebuilding of the sardine fishery continued in 1996, with the year's total landings of 34,128 t ranking as the second largest since the late 1950s (table 1). In southern California the sardine quota of 23,511 t was reached on November 5, and the fishery closed the same day. When the southern California directed fishery closed, only incidentally caught sardines (35% or less by weight) were authorized. In northern California the directed quota was set at 11,353 t. Only 78% of the quota was landed, thus the directed fishery remained open until year's end.

In 1996, sardines were used for frozen whole bait (54%), fresh fish for human consumption (31%), live

TABLE 1
Landings of Pelagic Wetfishes 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*	34,128	4,424	10,300	1,485	6,602	78,825	135,764

*Preliminary
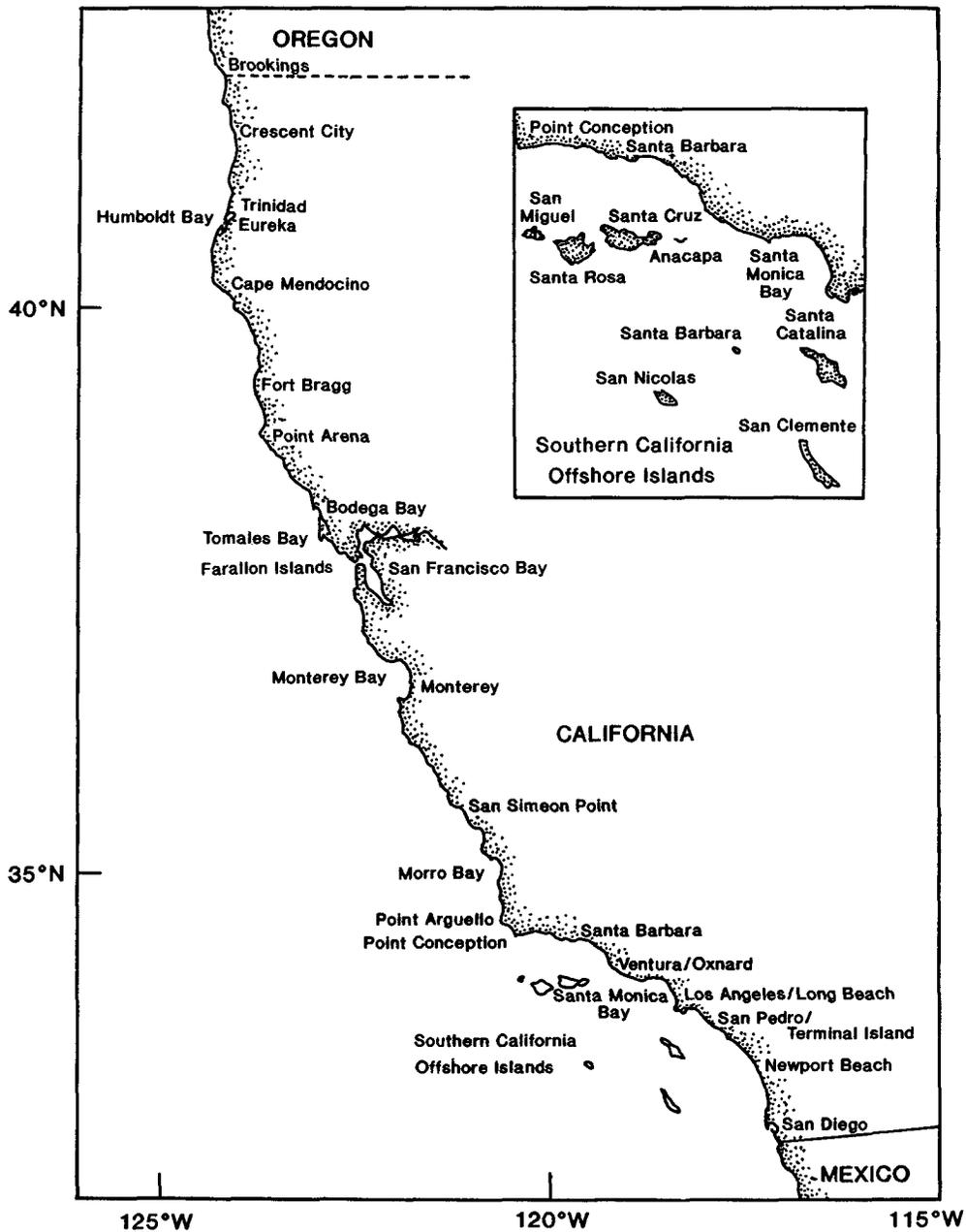
Figure 1.   California ports and fishing areas.

bait (10%), and canned pet food (5%). Only 6% of the total sardines landed were canned for human consumption. No California landings were used for the production of fish meal.

Fish and Game Code (Section 8150.8) states that annual sardine quotas shall be allocated two-thirds to southern California (south of San Simeon Point, San Luis Obispo County) and one-third to northern California (north of San Simeon Point; figure 1). During 1996, the formula generated an initial southern fishery quota of 21,212 t and a northern quota of 10,606 t. At midyear, the sardine stock assessment was updated and, as a result,

the 1996 quota was increased by 3,045 t. In October, the California Department of Fish and Game (CDFG) reallocated uncaught quota portions equally between north and south (table 2).

Sardine total biomass as of July 1, 1995, was estimated at 320,909 t on the basis of output from CANSAR (Catch-at-age ANalysis of SARdines model). CANSAR, a forward-casting stock assessment model, produces biomass estimates by incorporating both fishery-dependent and fishery-independent data, including catch and weight-at-age information, landings data, egg and larval abundance, and spotter pilot observations.

TABLE 2
Pacific Sardine Quota Allocations (Metric Tons)
in California, 1996

	Initial quota	Reallocated quota	Landings
North	10,606	11,353	8,904
South	21,212	23,511	25,224
Total	31,818	34,864	34,128

Current regulations give considerable latitude to CDFG in setting annual sardine quotas. When biomass is estimated to be over 20,000 t, Fish and Game Code requires that allowable catch must be consistent with resource rehabilitation. The 1996 quota was established from a formula of 20% of total estimated biomass.

Price paid to fishermen (ex-vessel price) for sardines remained low from 1995 to 1996, at approximately $70 per t at fresh fish markets and $77 per t at canneries. Other important target species for the southern California wetfish fleet include Pacific mackerel (*Scomber japonicus*) and market squid (*Loligo opalescens*) in the winter, and tunas during the summer. In northern California, Pacific herring (*Clupea pallasi*) is also an important target species from January to March. Species such as squid and tuna command significantly higher ex-vessel prices than sardines: $154–$330 per t for market squid and a minimum of $882 per t for tuna. During 1996 landings varied monthly due to availability, demand, and fleet participation in other fisheries.

In addition to the wetfish fishery for sardine, there is a small bait fishery that is not subject to a quota and usually takes less than 5,000 t annually. Live bait ex-vessel prices (about $680 per t) were approximately ten times greater than those for the directed fishery. In 1996, the ex-vessel value of the bait fishery exceeded the value of the directed fishery by approximately one million dollars.

In May 1996, nine months after closing because of bankruptcy, the only remaining southern California cannery capable of packing fish for human consumption reopened under new management. The cannery began processing sardines in October.

While some fish markets plan to expand production facilities to fill increasing sardine orders, others state that they cannot rely on a U.S. quota that could fluctuate widely from year to year due to unregulated Mexican fisheries. Recent sardine landings from Mexico have equaled or exceeded California's (except in 1995) and could ultimately affect allowable catch in state waters.

Industry representatives indicate that international interest in Pacific sardine is increasing. In 1996, 12,347 t of sardines were exported, slightly less than the 1995 export total of 12,563 t and a ninefold increase from the 1990–1994 average. The top three importers of frozen blocks of Pacific sardines are Australia, the Philippines, and Japan. Australia imports sardines to use as fish food in aquaculture facilities; the Philippines import sardines for human consumption; and Japan supplements its catch to meet consumer demand following the recent decline and near collapse of its sardine resource.

During 1996, the Pacific sardine sampling program expanded considerably. In California, sampling was extended to Monterey. Also, California scientists began a data exchange with Oregon and Washington scientists and informally with British Columbia, Canada. The Canadians tested a 200-t sardine fishery in 1996. The informal exchange of data with Ensenada, Mexico, scientists continues.

PACIFIC MACKEREL

Pacific mackerel (*Scomber japonicus*) is a transboundary stock supporting commercial fisheries in the United States and Mexico, and both have declined since the 1980s. Concurrently, the stock has more fully used the northernmost portions of its range in response to a warm regime in the northeast Pacific Ocean, and mackerel have been found as far north as British Columbia, Canada.

California landings during 1996 totaled 10,300 t, only slightly higher than the 19-year low of 8,667 t landed in 1995 (table 1). Over 90% of the statewide landings during 1996 were made by approximately 17 purse seine vessels based in the Los Angeles area, commonly known as the wetfish fleet. Twelve additional wetfish vessels based in Monterey accounted for most of the mackerel landings in northern California. Average ex-vessel price during 1996 was $147 per t, but large, high-quality fish such as those landed in July received better prices of $220 per t. Ex-vessel value of the 1996 California fishery was $1.51 million.

During the last few years, the principal causes of reduced catches have been low biomass and poor availability on the traditional fishing grounds in southern California waters. Cannery closures since 1993 may have diminished demand. In 1996, the wetfish fleet participated in lucrative winter squid and summer tuna fisheries, thus decreasing effort for mackerel during those months.

The mackerel fishing season is defined in the California Fish and Game Code as the 12-month period from July 1 through June 30 of the following calendar year. The harvest formula for mackerel specifies that when biomass is between 18,144 and 136,080 t, the season's quota shall be 30% of the total biomass in excess of 18,144 t. If total biomass is less than 18,144 t, no directed landings are allowed, and if total biomass is greater than 136,080 t, no limitation on total catch is imposed. Under the prescribed formula and the CDFG biomass projection for July 1, 1996, a commercial fishery quota of 8,700 t was established for the 1996–97 California fishing season.

When the 1996–97 season opened, abundant large mackerel off San Clemente Island and Santa Catalina Island increased landings compared to preceding months. July 1996 landings were 2,984 t—the highest monthly total since July of 1993. On March 12, 1997, the season quota was reached, and the Pacific mackerel directed fishery was closed for the first time since 1985, although regulations allowed incidental landings of mackerel mixed with landings of other wetfish species. Following the closure, the bycatch tolerance of 35% mackerel by weight limited incidental mackerel landings to about 600 t between the closure date and the end of April 1997. Incidental landings were allowed to continue at a 35% tolerance through the close of the 1996–97 season on June 30, 1997.

Examination of several information sources on the status of the mackerel stock suggests a decline in biomass compared to the late 1970s and 1980s. Landing statistics for both the U.S. and Mexican fisheries show reduced catches in recent years. Catch rates for the southern California commercial passenger fishing vessel (CPFV) fleet have also shown declining trends since the 1970s. Other fishery-independent data from aerial observations (spotter pilots) and plankton surveys (CalCOFI mackerel larvae samples) indicate lower abundance compared to the early 1980s.

A tuned virtual population analysis (VPA) model called ADEPT was used to estimate mackerel biomass and to determine the California quota for the 1997–98 fishing season. The model performs the best statistical fit between fishery-based, age-structured biomass estimates and the fishery-independent data listed above. On the basis of the estimated number of fish in each year class during the last quarter of 1996 (including the 1996 year class), and using certain assumptions for fishing mortality during the first half of 1997, mackerel biomass was projected to be 91,600 t at the beginning of the 1997–98 fishing season. Consequently, the CDFG set the 1997–98 quota at 22,000 t. There is a large degree of uncertainty in the 1997 biomass estimate because the youngest year classes made up much of the biomass.

In response to the northward range extension of recent years, in 1996 CDFG, the Oregon Department of Fish and Wildlife, and the Washington Department of Fish and Wildlife began a pilot study to examine geographic variation in growth and age composition. These studies are based on samples taken from the California directed mackerel fishery, mackerel bycatch in the Oregon and Washington whiting fishery, and mackerel caught by hook and line from Washington. Although mackerel catches in the Pacific Northwest have remained small (less than 500 t) compared to the directed fishery in California, bycatch in the whiting fishery has been notable in recent years. This higher bycatch rate lends support to the hypothesis that increased numbers of mackerel may be emigrating northward from the traditional southern California fishing grounds. Preliminary results from the pilot program suggest that mackerel in these northern waters are significantly older than those that dominate the southern California fishery.

In August 1996, CDFG conducted an icthyoplankton survey to determine the extent and intensity of mackerel spawning in waters off northern and central Baja California. The surveyed area was chosen to encompass the primary spawning grounds for the stock that also inhabits California waters and is vulnerable to the California commercial fishery. Preliminary findings—low densities of larvae—are in agreement with other information on the status of the stock.

PACIFIC HERRING

Annual statewide landings for Pacific herring (*Clupea pallasi*) were 6,602 t, an increase of 41.5% from the previous year (table 1). Statewide landings for the roe fisheries during the 1995–96 fishing season (December to March) totaled 6,003 t (table 1). Three gill net platoons (376 permittees) in San Francisco Bay's fishery landed 4,463 t, which was 14.8% over their 3,888-t quota. Twenty-six round haul (purse seine and lampara) permittees fishing in San Francisco Bay landed 7 tons more than their 1,123-t quota. The quota for Tomales Bay was 318 t, and the 39 Tomales Bay permittees landed 322 t. The four Humboldt Bay permittees landed 46 t, 14.8% less than their 54-t quota. Three Crescent City permittees landed 42 t, 53.6% more than their quota of 27 t.

Ex-vessel prices for herring with 10% roe recovery ranged from $2,000 to $2,300 per short ton during the 1995–96 fishing season; an additional $200 to $230 per short ton was paid for each percentage point over 10%. Total ex-vessel value of roe fisheries was $19.8 million, more than double the average value of approximately $9 million for the previous ten seasons.

Ten permittees participated in the San Francisco Bay herring eggs-on-kelp fishery and harvested their full quota of 97 t. Total estimated ex-vessel value of the eggs-on-kelp fishery was $2.2 million, with prices ranging from $10 to $20 per pound.

CDFG biologists used hydroacoustic and spawn-deposition surveys to estimate the spawning biomass of herring in San Francisco Bay and Tomales Bay. No surveys were conducted in Humboldt Bay or Crescent City Harbor.

The 1995–96 herring spawning biomass estimate for San Francisco Bay was 89,812 t, more than twice last season's estimate and one of the two highest estimates ever made. The increase in biomass was attributed to very large numbers of two-, three-, and four-year-old fish from the 1994, 1993, and 1992 year classes. These

three year classes constituted approximately 80% of the spawning population. The 1994 and 1993 year classes are the strongest ever observed in the population, an encouraging sign for the future.

Spawning biomass estimates have fluctuated widely in Tomales Bay since the reopening of the fishery in the 1992–93 season. The 1995–96 spawning biomass estimate for Tomales Bay (1,892 t) continued that tendency by decreasing 48% from last season's estimate of 3,610 t. The spawning biomass estimate was well below the 23-season average for the fishery of 4,103 t. The 1992 and 1993 year classes were relatively strong, but this was offset by a weak 1991 year class.

A dead bait and animal food fishery for Pacific herring is conducted during the summer months in Monterey Bay. Participants in this fishery landed 248 t in 1996, nearly equal to the peak landings of 250 t in 1982 and well over the 20-year average of 82 t. The estimated ex-vessel value of the 1996 landings was $295,000.

MARKET SQUID

In 1996, market squid (*Loligo opalescens*) surpassed red sea urchin (*Strongylocentrotus franciscanus*) as the state's most valuable fishery resource, with ex-vessel revenues of approximately $29.5 million. Landings were 78,825 metric tons, an increase of 12.2% over the 1995 previous record high of 70,278 t (table 1).

Squid are currently harvested by about 150 purse seine vessels, usually with a hold capacity of 35–70 t and a median length of about 15–20 meters. Fishing is done at night on spawning grounds when the squid aggregate to spawn. Squid typically spawn in semiprotected nearshore areas over sandy bottoms with rocky outcroppings. Fishing operations often involve two vessels: a light vessel with high-intensity lights to attract and hold the spawning schools near the surface, and a purse seiner to capture them.

Two distinct fisheries exist for market squid in California, separated geographically and seasonally. The southern California fishery, primarily a fall and winter fishery, historically dominates overall squid landings, accounting for 93.3% of the 1996 statewide total. The fishing grounds are nearshore areas from San Pedro to Point Conception, and around the Channel Islands. Port Hueneme was the most important southern California fishing port for market squid during 1996; San Pedro and Ventura accounted for most of the remainder. In contrast, the smaller northern and central California fishery takes place from spring through fall. Nearly all market squid in the northern fishery are landed in Monterey or Moss Landing.

Historically, market squid catches have fluctuated greatly and have been difficult to predict. Such extreme fluctuations are characteristic of a fishery that is dependent on each year's recruitment of short-lived, highly fecund animals. The market squid fishery in California has traditionally been open-access and is largely unregulated by the CDFG, except for weekend closures in the Monterey area. Consequently, purse seine vessels from Alaska, Washington, and Oregon that may have been displaced from salmon fisheries have moved into the expanding southern California squid fishery in recent years, prompting some resident squid fishermen to press for limited-entry regulations. In 1996 several bills were introduced in the state legislature to establish market squid management and provisions for limited entry. But no major management changes were enacted by year's end.

Price paid to fishermen remained steady during the first half of 1996, averaging between $240 and $280 per t. Price per t increased later in the year to $306 in August and $356 in November. In December, mean ex-vessel price rose to $602. Monthly landings in December reached a high for 1996 of 21,900 t, generating nearly $12 million in ex-vessel revenue. As in previous years, most squid was exported either in frozen blocks or in canned form for human consumption. Developing markets for squid continued to increase demand, particularly in China, Europe, and Japan.

SEA URCHIN

The 1996 statewide red sea urchin (*Strongylocentrotus franciscanus*) catch was 9,105 metric tons, with an ex-vessel value of $18.8 million. Catch was down 11%, and value was down 15% from the previous year. The number of dive permits renewed in 1996 declined by 9%, to 502. The other commercially fished sea urchin in California, the purple sea urchin (*Strongylocentrotus purpuratus*), accounted for 25 t in 1996, compared to 37 t in 1995.

Red sea urchin landings in southern California, south of the sea otter's range, fell by 8.3% from 1995, to 7,368 t, the lowest level since the El Niño–influenced year of 1984. Underlying this continuing decline was a steep drop in landings from the northern Channel Islands. In 1991, these islands produced about 7,000 t, representing over 60% of the southern California catch. By 1995, they produced only 25% of the 8,035-t catch. A shift in effort to the other Channel Islands, notably San Clemente Island, contributed to this decline. The distribution of landings among the mainland ports through time also reflects this shift. Preliminary 1996 landings data showed a decline of almost 500 t at the more northerly ports in the Oxnard-Ventura area. However, unlike 1995, landings at more southerly ports in the Los Angeles and San Diego areas did not increase.

The situation in northern California is equally bleak, as landings fell by 21% from 1995's catch to 1,737 t—the lowest level since the fishery began there in 1985. Modeling results suggest that most of the northern California sea urchin fishery areas are overfished. A sluggish

Japanese economy and competition from foreign sea urchin fisheries have combined to keep ex-vessel prices flat or depressed, particularly in northern California. The 1996 average ex-vessel price in northern California was $0.77 per pound, compared to $0.96 per pound in 1994. Catch-per-receipt and catch-per-diver-hour indices have remained stable in northern California since dropping by almost 50% between 1992 and 1993. In 1996, catch per diver-hour was 121 kg/hr. Despite this recent stability, the number of urchin permittees who devote their entire fishing time to northern California waters has declined from 85 in 1994 to just 69 in 1995 (statewide, there were 551 permittees in 1995).

GROUNDFISH

The California commercial groundfish harvest for 1996 was 27,820 metric tons, with an ex-vessel value of approximately $34 million. Total landings decreased by 4%, or 1,139 t, from 1995. Dover sole (*Microstomus pacificus*), thornyheads (*Sebastolobus* spp.), sablefish (*Anoplopoma fimbria*), rockfish (*Sebastes* spp.), and Pacific whiting (*Merluccius productus*) were the principal species harvested. Landings remained relatively steady in spite of restrictive Washington-Oregon-California (WOC) area landing regulations. Increased landings in some categories such as grenadier, other rockfish, English sole, and petrale sole were offset by decreases in bocaccio rockfish, widow rockfish, and Pacific whiting (table 3).

Most of the groundfish landed in California (83%) were taken with bottom trawl and midwater trawl gear. This is a slight decrease from the proportion landed by this gear in 1995 (85%). Line gear was used for 15% of the landings. This proportion is higher than in 1995 (11%), but below the highest proportion to date (18% in the 1992 season). Groundfish landings from gill and

TABLE 3
California 1996 Groundfish Landings (Metric Tons)

Species	1995	1996	Percent change
Dover sole	6,043	6,379	6
English sole	499	585	17
Petrale sole	593	817	38
Rex sole	691	502	−27
Other flatfish	1,253	995	−21
Widow rockfish	1,712	1,060	−38
Bocaccio	785	478	−39
Other rockfish	5,902	5,922	7
Thornyhead	3,609	3,270	−9
Lingcod	538	477	−11
Sablefish	2,716	3,172	17
Pacific whiting	4,091	2,901	−29
Grenadier*		1,133	
Other groundfish	527	129	−76
Total	28,959	27,820	−4

*Grenadier landings were reported previously in the "other groundfish" category.

trammel net gear (1%) have declined continuously since 1993 (5%), while the proportion of landings taken by trap gear has remained steady at just over 1%.

The license limitation program that the Pacific Fishery Management Council (PFMC) implemented in 1994 continued in 1996. Annual harvest guidelines were again allocated between a permitted limited-entry (LE) fleet and nonpermitted open-access (OA) fleet, and separate trip limits were established for each geographical area. The PFMC harvest guidelines affected the California fishery for Dover sole, shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*Sebastolobus altivelis*), sablefish, the *Sebastes* complex, widow rockfish (*Sebastes entomelas*), bocaccio rockfish (*S. paucispinis*), yellowtail rockfish (*S. flavidus*), canary rockfish (*S. pinniger*), lingcod (*Ophiodon elongatus*), and Pacific whiting. The PFMC continued to use cumulative landing limits and trip limits to provide a year-round groundfish fishery while staying within the annual harvest guideline. Two-month cumulative landing limits were established for most of the limited-entry fishery.

This was the final year of a three-year Pacific whiting allocation plan that reserves 40% of the annual harvest guideline for shore-based processing after the first 60% has been taken in open competition between at-sea and shore-based components. At-sea processing of whiting was again restricted to waters north of California. The 1996 WOC-area harvest of 197,456 t was near the 212,000-t harvest guideline. California's shoreside whiting fishery landed and processed 2,901 t, a 29% decline from 1995 landings. Five midwater trawl vessels, fishing off Eureka and Crescent City, landed over 99% of California's catch.

A whiting observation program, established in 1993 to monitor the bycatch of salmon and other species in the shoreside landings, documented 0.008 salmon per metric ton of Pacific whiting. This represented a sharp decrease from the bycatch observed last year (0.017 salmon per t). All salmon observed were chinook (*Oncorhynchus tshawytscha*). The non-salmon bycatch rate in observed landings declined to 5.2 lb/t from 28.8 lb/t during 1995.

Dover sole, longspine thornyhead, shortspine thornyhead, and trawl-caught sablefish (the DTS complex) management was similar to that carried out in 1995. The PFMC also imposed two-month cumulative limits of 70,000 pounds for the DTS complex in the area north of Cape Mendocino, and 100,000 pounds in the area south of Cape Mendocino. Thornyhead landings were further restricted to 20,000 pounds within the overall DTS two-month limits, of which no more than 4,000 pounds could be shortspine thornyhead. Trawl-caught sablefish was limited to 12,000 pounds per period. These limits remained in effect throughout 1996. To reduce Dover sole landings in the Columbia area, the PFMC

established a 38,000-pound, two-month limit for the area north of Cape Mendocino effective July 1.

The coastwide catch of Dover sole was 12,129 t, an increase of 1,585 t from 1995 landings and higher than the 1996 11,050-t harvest guideline. California's 1996 landings (6,379 t) represented a 6% increase over last year's total and were 53% of total WOC Dover sole landings, compared with last year's 57% share.

The longspine harvest guideline for 1996 remained at 6,000 t, and the shortspine thornyhead harvest guideline at 1,500 t. Total WOC-area landings of longspine thornyhead were 4,813 t; shortspine landings were 1,705 t. Shortspine landings exceeded the harvest guideline by 12%. California fishermen landed 3,270 t, or 50% of the total WOC thornyhead catch.

The total nontribal, WOC-area catch of sablefish (LE trawl, LE nontrawl, and OA) in 1996 was 8,226 t, 426 t over the combined LE/OA 7,800-t harvest guidelines. California fishermen accounted for 3,172 t, or 38% of the total WOC-area nontribal catch. The LE trawl sablefish allocation (3,803 t) was unchanged from 1995. WOC-area trawl sablefish landings were 4,126 t, about 8% over the harvest guideline. California trawl vessels landed 1,445 t, or about 35% of the WOC-area trawl landings.

The nontrawl LE sablefish fishery, except for the derby and mop-up fisheries, was again managed under a daily limit of 300 pounds north of 36°N latitude and 350 pounds south of 36°N. The LE derby opening date was moved from early August to September 1. The fishery, open for only five days, captured 2,381 t, or about 87% of the LE 2,754-t nontrawl allocation. The remainder of the allocation was used by the daily-trip-limit fishery and a cumulative-vessel-limit mop-up fishery following the derby. Total WOC area LE fixed-gear landings of 3,432 t were about 25% higher than the LE nontrawl allocation. California fishermen landed 1,231 t, or 36%, of the WOC, LE nontrawl sablefish harvest.

The OA sablefish fishery, under a daily trip limit of 300 pounds north of 36°N and 350 pounds south of 36°N, landed approximately 668 t, exceeding the 463-t open-access harvest guideline by 44%. California fishermen landed 496 t of the total WOC harvest.

On January 1, LE two-month cumulative limits were set at 200,000 pounds south of Cape Mendocino and 100,000 pounds north to Cape Lookout, Oregon, for the Sebastes complex (including yellowtail, canary, and bocaccio rockfishes, and excluding widow rockfish and shortbelly rockfish). Within the 200,000-pound limit, no more than 60,000 pounds could be bocaccio rockfish and no more than 18,000 pounds could be canary rockfish. Within the 100,000-pound limit, no more than 70,000 pounds could be yellowtail rockfish and no more than 18,000 pounds could be canary rockfish.

The OA cumulative limit was set at 40,000 pounds per month, and no more than 10,000 pounds per trip were authorized for line and pot gear. Bocaccio, yellowtail, and canary rockfish monthly limits were 50% of the two-month LE limits. California's Sebastes complex landings dropped from 8,863 t in 1992 to 6,293 t in 1994. In 1995, total landings increased to 6,687 t, but dropped again in 1996 to 6,400 t. The 1996 Sebastes complex harvest included 478 t of bocaccio, a 39% drop from 1995 landings (785 t).

The widow rockfish harvest guideline (6,500 t) remained unchanged from 1995, with a two-month cumulative limit set at 70,000 pounds. This continued in effect until September 1, when the limit was reduced to 50,000 pounds. The total 1996 catch in the WOC area (5,571 t) was 929 t below the harvest guideline. California landings of 1,060 t constituted 19% of the WOC total.

The lingcod WOC-area harvest guideline remained unchanged, at 2,400 t. The PFMC allotted 900 t within this guideline for recreational fisheries. The 22-inch size limit remained in effect for 1996, but trawlers were given a 100-pound allowance for fish under 22 inches. A two-month cumulative limit of 40,000 pounds for all commercial gear was in effect through 1996. Total WOC-area commercial lingcod landings (1,556 t) were slightly over the 1,500-t commercial allocation. California commercial fishermen landed 477 t, or 31%, of the WOC-area commercial allotment.

In 1997, the PFMC will consider (1) a capacity-reduction program for the groundfish industry, (2) the appropriateness of using $F_{35\%}$ as the proxy for maximum sustainable yield, and (3) amendments to provisions required by the Magnuson-Stevens Fishery Conservation and Management Act. The PFMC will also reassess widow rockfish, chilipepper rockfish, lingcod, Pacific whiting, and all four components of the DTS complex as a preliminary step in reevaluating harvest guidelines for 1998.

SWORDFISH AND SHARKS

Swordfish (Xiphias gladius) landings were 714 metric tons in 1996, 10% less than in 1995 (table 4). During the past decade the drift gill net fishery accounted for most of the catch. This year, 70% of the catch was taken with drift gill nets, up from last year's 65%. Longline landings constituted 22% of the catch. Fourteen vessels used longline gear outside the U.S. Exclusive Economic Zone (EEZ) and landed swordfish in southern California ports in 1996, but only three were based in California. As usual, harpoon landings constituted 8% of the catch. Fifty-seven percent of the swordfish catch was landed in southern California ports.

Gear type affected swordfish ex-vessel prices; typically, fishermen landing drift gill net–caught swordfish

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

	Swordfish	Common thresher shark	Shortfin mako shark
1986	1,749	276	215
1987	1,246	239	274
1988	1,129	250	222
1989	1,296	295	177
1990	851	210	262
1991	711	344	151
1992	1,068	179	97
1993	1,218	162	84
1994	1,165	194	88
1995	796	155	66
1996*	714	179	64

*Preliminary

received $3.00 to $5.50 per pound, whereas longline-caught fish commanded only $2.00 to $4.00 per pound. Fishermen landing harpoon-caught swordfish received the highest prices: $4.00 to $6.50 per pound.

Landings of common thresher shark (*Alopias vulpinus*) increased by 15%, ending a decade-long trend of decline. Thresher shark (*Alopias* spp.) are taken primarily with drift gill nets (73%), followed by set gill nets (17%), and assorted other gears (10%). Most landings (87%) continued to be made in southern California. Typically, ex-vessel price varied from $1.00 to $2.00 per pound, with an average of $1.50.

Shortfin mako shark (*Isurus oxyrinchus*) landings in 1996 were 64 t (table 4), a decrease of 2%. Most of the catch (83%) was landed in southern California ports, at ex-vessel prices between $0.50 and $1.75 per pound, with an average of $1.25. Mako sharks are caught primarily by the drift gill net fishery (85%). The remainder of the catch was landed with set gill nets (5%), hook and line gear (4%), longline vessels operating outside the EEZ (4%), and as incidental catch with other gears (2%).

LIVE-FISH FISHERY

The 1996 statewide landings for live fish were estimated at 562 metric tons, 25% more than in 1995 (table 5).

TABLE 5
Preliminary 1996 Landings of Live Fish (Metric Tons)

	Southern California	Northern California
Rockfish	132	65
Cabezon	92	13
California sheephead	89	<1
California halibut	65	<1
Lingcod	20	16
Thornyhead	27	<1
All others	35	6
Total	460	102

Sixty-six fish species were landed in live form and had an ex-vessel value of over $3.6 million. Field observations indicate that the documented landings underestimate the activity of this fishery. In addition, there is a new market for premium quality fresh fish (dead), which allows fishermen to sell their dead catch along with their live counterparts for virtually the same price. Future reviews will report on all premium quality landings in an attempt to more accurately describe the current demand for nearshore finfish species.

Ex-vessel prices averaged between $2.00 and $9.00 per pound. Larger fish previously sold at considerably reduced prices but are now gaining popularity as "large party" specialties at local restaurants. Prices fluctuated with market demand, fish size, fish condition, and weather conditions. Hook and line gear was used to capture 63% of the live fish landed statewide; trap gear landed 22%. These values are consistent with those from 1995.

Live-fish landings in southern California (Morro Bay southward) totaled 460 t, 22% more than in 1994. Target species for all gear types included California sheephead (*Semicossyphus pulcher*), California halibut (*Paralichthys californicus*), cabezon (*Scorpaenichthys marmoratus*), California scorpionfish (*Scorpaena guttata*), rockfishes (*Sebastes* spp.) and thornyheads (*Sebastolobus* spp.). Most of the 1996 catch was taken with hook and line (56%) and trap (26%) gears. Trapping accounted for 81% of all live California sheephead taken. Catches of these fish increased dramatically again this year: 323% for sablefish, 172% for thornyheads, 95% for cabezon, 50% for gopher rockfish (11% for the entire rockfish group), and 44% for lingcod. Grass rockfish was the only species with decreased landings (16%), and the California sheephead catch was virtually the same as last year. Live California halibut were caught with trawl and net gear and kept alive to ensure optimum freshness, then bled, iced, and quickly shipped overseas. Eighty percent of all live landings were delivered to Morro Bay and Santa Barbara/Ventura.

Live-fish landings in northern California (north of Morro Bay) totaled 102 t, 42% more than in 1994. Most landings (98%) were made by hook and line vessels employing vertical, horizontal, and troll longlines to harvest primarily rockfish along nearshore rocky reefs and offshore banks. Fishing pressure for these nearshore rockfish species continued to be intense, with landings increasing by 28% from the previous year. Principal species caught were gopher (*Sebastes carnatus*), China (*S. nebulosus*), and brown (*S. auriculatus*) rockfishes. Another notable landing increase from 1995 was cabezon (33%).

A total of 277 finfish trapping permits were sold in 1996 through the limited-entry program effective south of Point Arguello, Santa Barbara County.

ABALONE

Commercial landings for the red abalone were estimated at 75 metric tons during 1996, down from 1995 landings of 111 t. Four species (pink, green, white, and black abalone) are now prohibited from harvest throughout California. At the end of 1996, recreational fishery groups proposed a closure of recreational and commercial red abalone fisheries in waters south of San Francisco. This proposal will be considered by the Fish and Game Commission in 1997.

Abalone resources have declined to record lows since the present fishery was established in the early 1900s. The black abalone fishery was closed in 1993 because withering syndrome (WS) was causing mass mortalities throughout the black abalone range in California and Mexico. The closure was initiated to allow the potential development of natural resistance to WS, an unknown pathogen at that time. This strategy appears to have worked: researchers are finding continued black abalone recruitment and a few old, large individuals in some areas where WS was virulent. Future studies are planned to document persistence, and, it is hoped, the recovery process of some black abalone populations. Withering syndrome itself came under considerable study in 1996, and researchers are confident that the pathogen has been identified. Pathological studies of this rickettsial-like procaryote (RLP) are continuing.

Green abalone populations are also low in many parts of southern California. Green abalone have also been found to have symptoms of WS. This species' habitat overlaps that of black abalone. Researchers have observed large numbers of shells from abalone that appeared to have died in place. (Normally, shells are not left by human harvesters, so excessive numbers can indicate unusual natural mortality.)

Pink abalone inhabit subtidal areas to over 30-m depth. Withering syndrome is also known to occur in this species, but it appears not to have been as virulent as in other species. The broad depth distribution and low density of pink abalone may have reduced the spread of WS. This species' broad bathymetric and geographic distribution, as well as some areas of limited of abundance at several Channel Islands locations may increase the probability that pink abalone may be the best candidate for natural recovery of the species now prohibited from harvest.

The white abalone population is at an exceedingly low level. Diving surveys covering about three hectares of habitat over a several-year period found only five individuals, a density far below that necessary to assure successful reproduction. Surveys from the research submersible *Delta* at Anacapa and Santa Cruz Islands, also covering about three hectares, found only five white abalone in depths deeper than 50 m. More surveys are planned in other areas during 1997. This species may be a candidate for listing under the federal or California Endangered Species Acts.

Red abalone populations and the fishery have been spatially compressed in southern California. The red abalone is adapted to cooler water, maintaining its populations in locations where there is frequent upwelling or in areas influenced by cool, southerly-flowing currents. Populations in former locations such as the San Diego–La Jolla kelp beds and the Palos Verdes Peninsula have been adversely affected by ENSO conditions, reduced kelp availability, competition, and intensive harvest. These conditions also affect the remaining areas of red abalone harvest (e.g., around Point Conception and San Miguel Island). Concentrated fishery effort in these few remaining "productive" areas has raised concern for further protecting these stocks as a source of recruitment to other formerly productive areas.

SEA CUCUMBER

Statewide, sea cucumber landings were 376 metric tons in 1996, an increase of 108 t over 1995 landings (figure 2). This was the largest harvest of sea cucumbers in California since landings were first recorded in 1978. Much of the increase was due to a substantial increase in the numbers taken by divers. Commercial trawlers in southern California primarily harvested the giant red sea cucumber (*Parastichopus californicus*); divers harvested warty sea cucumbers (*P. parvimensis*) almost exclusively. The catch comprised 176 t of diver-harvested sea cucumber and 200 t taken by trawl vessel.

Most of the sea cucumbers were landed in the ports of Terminal Island, Ventura Harbor, and Santa Barbara Harbor. The main fishing grounds for the giant red sea cucumber were the Santa Barbara Channel and the Santa Catalina Channel at depths of 30 to 90 fm. The warty sea cucumber was harvested as far south as San Diego, but most of the harvest came from waters off the four northern Channel Islands at depths of 6 to 20 fm.
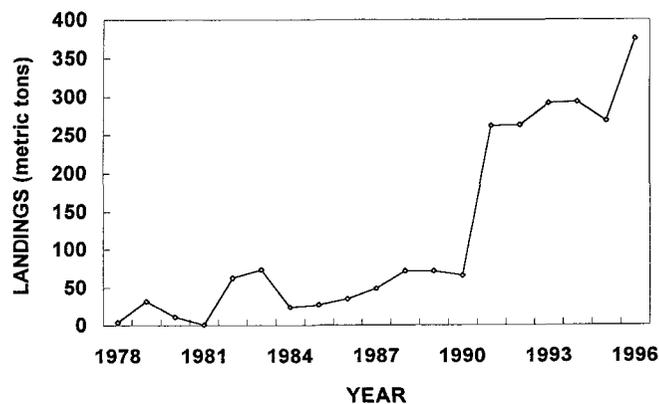

Figure 2. Commercial landings of sea cucumbers in California, 1978–96.

The average price for both warty and giant red sea cucumbers was $0.70 per pound and ranged from $0.40 to $1.20 per pound. Most of the sea cucumbers were dried and exported to Korea, Hong Kong, Taiwan, and mainland China. The end product, called *trepang*, can sell for $20 or more per pound. A small portion of the landings was distributed and sold within the United States.

The sea cucumber fishery began in California near Los Angeles around 1978, and averaged under 15 t annually until 1982, when a trawl fishery developed near Santa Barbara. During the next ten years, annual landings increased gradually. In 1991, an influx of trawlers, predominately out of the Los Angeles port area, greatly expanded the fishing effort and catch. From 1991 through 1996, landings exceeded 260 t. Since the 1992–93 season, the sea cucumber fishery has been a limited-entry fishery based on a previous minimum landing of 50 pounds. There were 129 sea cucumber permittees in 1996. Landing receipt data indicate that 84 permittees on 23 trawlers and 43 dive boats participated in the fishery during 1996.

Warty sea cucumbers inhabit the ocean bottom from the intertidal zone to 27 meters, and range from Monterey Bay to Baja California. The species is uncommon north of Point Conception. Giant red sea cucumbers inhabit the subtidal zone out to 90 meters, and range from the eastern Gulf of Alaska to Baja California. Both species feed on surface organic nutrients from mud, sand, and detritus. Warty sea cucumbers migrate annually between their shallow- and deep-water depth limits. Fishermen claim that giant red sea cucumbers make similar, large-scale movements over varying depth ranges, but this has not been verified by research.

Sea cucumbers have a short life span, low age of maturity, sporadic recruitment, and high natural mortality. Species with these characteristics can be vulnerable to overfishing, but it is expected that the southern California populations of warty and giant red sea cucumber can sustain current harvest levels, thanks to the effort-limiting permit restrictions placed upon the fishery.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1995–96 season totaled 6,861 metric tons, an increase of 930 t over the previous season, well above the ten-year average of 4,348 t.

In northern California, the crab season opened on December 1, and fishing commenced on December 5 after a price settlement of $1.25 per pound. Initial catches were very good; however, dealers terminated market orders on December 8 because of soft market conditions. On January 1, crab fishermen settled for a renegotiated price of $1.15 per pound. A fleet of 509 vessels landed approximately 5,935 t at Crescent City, Trinidad,

Eureka, and Fort Bragg. Crescent City accounted for 3,673 t, followed by Eureka (1,520 t), Trinidad (588 t), and Fort Bragg (154 t).

San Francisco-area Dungeness crab fishing opened on November 15, with fishermen agreeing to a price of $1.50 per pound. Total landings decreased by 445 t from the previous season, to 859 t. Crab fishermen landed 318 t at Bodega Bay and 541 t at ports in San Francisco Bay. Monterey and Morro Bay contributed 67 t to the statewide landings.

The Sustainable Fisheries Act, an amended version of the Magnuson Act authorized in October 1996, gave the states of Washington, Oregon, and California regulatory authority over their crab fisheries out to 200 miles, excluding any crab fishery limited-entry restrictions. The act also encouraged the development of a federal fishery management plan (FMP) for Dungeness crab to be completed by 1999. Not later than December 1, 1997, the Pacific Fisheries Management Council shall provide a report to the Committee on Commerce, Science, and Transportation of the Senate, and to the Committee on Resources of the House of Representatives describing progress in developing the FMP.

CALIFORNIA SPINY LOBSTER

The fishery for California spiny lobster (*Panulirus interruptus*) is one of California's oldest; catch records date from the late 1800s. Total landings for the 1995–96 season (first Wednesday in October through the first Wednesday after March 15) were 265 metric tons. This total is 13% greater than the 1994–95 season total of 238 t. Landings have generally increased since 1974–75, reaching a peak of 332 t in 1989–90. The average for the past ten seasons is 259 t.

Landings typically are highest early in the season. In the 1995–96 season 67% of the landings were made during the first two months, 12% in December, and the remaining 20% from January through March. Ports in San Diego County received 40% of the total landings; the remainder was equally divided between Los Angeles–Orange and Santa Barbara–Ventura counties. The coastal waters off Orange and San Diego counties are the most heavily fished and produced the highest capture-per-trap ratios.

There was a moratorium on new (additional) lobster operator permits for the season. The Fish and Game Commission has directed the CDFG to meet with the California Lobster and Trapfishermen's Association to develop proposals for a formal limited-entry lobster fishery. For the 1995–96 season only 366 lobster operator permits were issued by the CDFG, 97 fewer than for the previous season.

Ex-vessel price ranged from $6.50 to $10.00 per pound, and averaged $7.50 per pound. The season's catch

was worth approximately $4.4 million to the fishermen. A robust export market to Asian destinations has created increased demand and higher prices for California spiny lobsters. Consequently, high retail prices have nearly curtailed local consumption. A plentiful market exists for lower-priced Mexican product and East Coast American lobster.

SPOT AND RIDGEBACK PRAWN

The 1996 prawn fishery landings totaled 511 metric tons, a 39% increase from the 368 t landed in 1995. Approximately 419 t were landed in southern California ports, and 92 t in central/northern California ports. The statewide total is a combination of landings for two commercially important species of prawn: ridgeback prawn (*Sicyonia ingentis*) and spot prawn (*Pandalus platyceros*). Ridgeback prawn landings accounted for 54% (275.5 t) of the statewide total, and spot prawn landings accounted for 46% (235.5 t). Landings for both species increased in 1996: ridgeback prawn by 46% and spot prawn by 32%. All but 0.5 t of the ridgeback prawn landings were made in southern California ports. The spot prawn fishery was more widespread, with 144 t landed in southern California ports and 91.5 t in central/northern California.

Sixty-one vessels (48 trawl and 13 trap) landed most (84%) of the southern California combined-species catch at Santa Barbara area ports. Los Angeles area ports accounted for 12%, captured by 14 trawl and 19 trap vessels. Nineteen San Diego area vessels (2 trawl and 17 trap) landed the remaining 4% of the southern California total. Twelve San Francisco Bay area vessels (6 trawl and 6 trap) landed 60% of the central/northern California catch. Monterey Bay area vessels (12 trawl and 5 trap) landed 34%, with Eureka/Fort Bragg area vessels (2 trawl and 1 trap) landing 6% of the central/northern California total.

Spot prawn landings commanded the higher ex-vessel prices, averaging $6.77 per pound ($8.45 per pound for live and $5.58 per pound for dead prawns). Average ex-vessel prices increased by $0.52 per pound over the 1995 value of $6.25 per pound. The average ex-vessel price for ridgeback prawn landings was $1.33 per pound ($1.73 per pound for live and $1.20 per pound for dead prawns), a $0.17 rise from the 1995 price.

The San Francisco Bay area spot prawn fishery grew phenomenally in 1996 to an annual catch of 55.5 t, compared with a ten-year (1986–95) mean annual harvest of only 0.2 t. A major reason for the increased landings was an influx of trawl vessels to participate in the lucrative live-prawn fishery. Several of these shrimp vessels came from the Santa Barbara area and at least two from out of state. During August alone, two of these shrimp trawlers landed approximately 5.5 t—more than the catch for the previous ten years. Market receipt data revealed

that approximately 70% of the San Francisco Bay area spot prawns were landed live.

Regulation changes implemented in 1995 continued for the 1996 period. The Fish and Game Commission continued to allow the use of Fathom Plus traps. Additionally, Fish and Game Code Section 8842, which expired on April 1, 1997, was extended until April 1, 1999. This statute regulates the use of trawl nets for taking shrimp or prawns.

OCEAN SALMON

In 1996, the Pacific Fishery Management Council (PFMC) again enacted restrictive commercial and recreational ocean salmon regulations in California to (1) protect endangered chinook (*Oncorhynchus tshawytscha*) stocks—Sacramento River winter chinook and Snake River fall chinook, (2) ensure fall chinook spawner escapement goals for Klamath, Sacramento, and Oregon coastal rivers, and (3) protect depressed coho (*Oncorhynchus kisutch*) stocks coastwide. The regulations included increased minimum size limits, reduced seasons, and specific gear restrictions for the area between Horse Mountain and Point Conception. Under authority of the Endangered Species Act, NMFS required the PFMC to take specific action to reduce harvest impacts on the endangered Sacramento River winter chinook to increase the stock's spawning escapement by 35%.

In 1996, commercial fishing for ocean salmon in California was allowed everywhere except between Humboldt South Jetty and Horse Mountain, with various time and area closures (May 1–September 30). The minimum size limit was 26 inches through June 30, and 27 inches thereafter. Approximately 1,773 metric tons (365,300 fish) of dressed chinook were landed by commercial trollers, who fished approximately 19,900 days during 1996. Ex-vessel prices for dressed salmon averaged $1.44 per pound, and total ex-vessel value exceeded $5.6 million. Commercial fishing for coho salmon was not allowed in 1996.

Recreational fishing regulations in California were more restrictive than in 1995, with various time and area closures enacted (February 17–November 17). The fishing season south of Point San Pedro was shortened by more than two months (March 2–August 25) compared to 1995. Sport anglers could not retain coho salmon at any time during 1996. In the Klamath Management Zone (KMZ: Horse Mountain, California, to Humbug Mountain, Oregon) season management, rather than quotas, was enacted for the first time since 1991 because of improved chinook abundance in the fall. Statewide, recreational landings were less than half those of the previous year, but still totaled 164,200 chinook during 225,400 angler trips (CPUE: 0.73 fish/angler). Most salmon were caught south of the KMZ, where sport

anglers landed 153,300 chinook during 200,000 trips on CPFVs and private skiffs. Anglers were limited to two salmon per day, with a minimum size limit of 24 inches (total length) through July 1 and 26 inches thereafter, except in state waters (0–3 miles), where the 26-inch limit was not enacted until July 15.

In the KMZ, two separate seasons were provided: May 12–July 7 and August 18–September 21. The bag limit was one salmon per day and no more than four fish in seven consecutive days; a 20-inch size limit was in effect north of Horse Mountain. In the California portion of KMZ, anglers landed 10,800 chinook during 25,500 trips made primarily on private skiffs.

WHITE SEABASS

White seabass (*Atractoscion nobilis*) has been an important commercial and recreational species for more than a century. In 1959, more than 1,556 metric tons were landed commercially. Since then landings have decreased substantially (figure 3). Prior to 1982, Mexican waters often supplied much of the catch. Since 1982, U.S. fishermen have been unable to obtain fishing permits for Mexican waters, and less than 1% of the total catch per year since then has been reported from Mexico. Commercial landings of white seabass since 1987 have averaged 50 t. White seabass landings in 1996 were 43 t, a 30% increase over 1995.

Nearshore gill nets have taken the bulk of the commercial catch since purse seine nets became uneconomical in the 1920s. Set and drift gill nets are generally deployed in shallow waters along the mainland coast and around offshore islands. The Marine Resources Protection Act of 1990 restricted the use of gill nets inside three miles along the mainland coast south of Point Arguello and around the Channel Islands. After January 1, 1994, gill nets were prohibited inside those areas. In 1996, 19 commercial vessels expended 258 days of gill net effort to

take white seabass. That compares to 912 days fished in 1992, 700 in 1993, 326 in 1994, and 261 days in 1995. The primary gear was 6.5-inch multifilament drift gill net. In 1996, drift gill nets accounted for 65% of the total pounds landed; set gill nets and hook and line gear each captured 16%. The average ex-vessel value for white seabass in 1996 was $2.00 per pound.

Commercial landings in June and July accounted for 71% of the year's catch. Gill net log information indicates that most of the nets were fished offshore of San Diego County and around the Channel Islands. Although small populations of white seabass are known to occur around Santa Cruz and Morro Bay, less than 2% of the catch in 1996 was reported to be landed north of Point Conception.

Recreational catches reported from fishing logs for commercial passenger fishing vessels (CPFVs) have also decreased over time (figure 4). An average of 1,970 white seabass has been taken per year since 1987 by recreational anglers on CPFVs. In 1996, 1,605 fish were reported.

In 1983, the Ocean Resources Enhancement and Hatchery Program was created by the California legislature to promote basic and applied research into the artificial propagation of adversely affected marine fish species important to commercial and recreational fishing in southern California. In 1995, the California Marine Hatchery Institute in Carlsbad began producing young white seabass for eventual release into the ocean. Fish are raised to approximately three inches at the hatchery, then transferred to grow-out pens in marinas and harbors from San Diego to Santa Barbara. When the fish reach nine inches, 10% are tagged with external tags and released. All fish are injected with coded-wire tags before leaving the hatchery. Tag returns will provide information for assessing whether the hatchery is successful in significantly augmenting white seabass stocks in California waters.
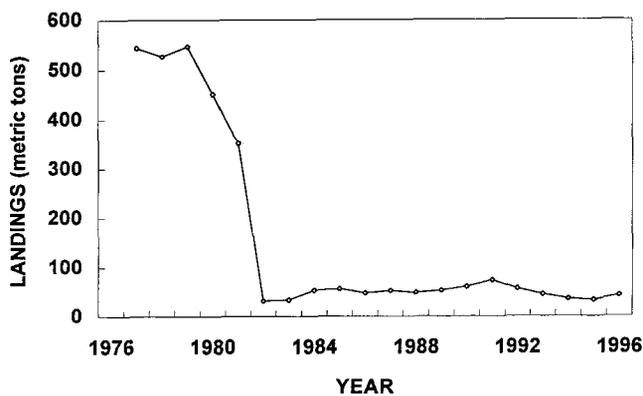

Figure 3. Commercial landings of white seabass in California (California and Mexican waters catch combined), 1977–96.
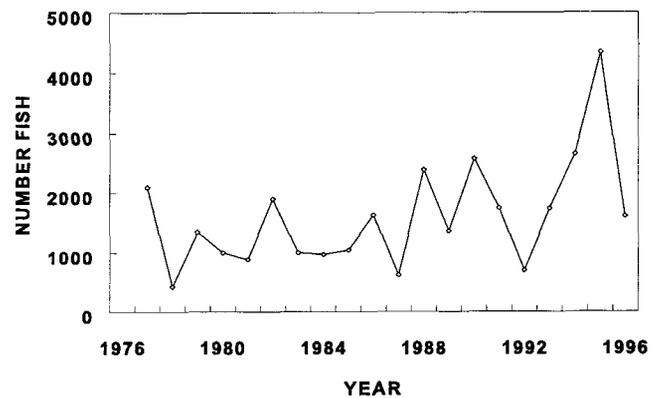

Figure 4. Numbers of white seabass reported caught by California commercial passenger fishing vessels, 1977–96 (California and Mexican waters).

RECREATIONAL FISHERY

Southern California

Southern California's large marine recreational fishery includes private recreational boat, beach-and-bank, pier, and CPFV modes. Approximately 40% of California's marine recreational landings come from CPFVs. In southern California and Baja California, traditional CPFV target species include California barracuda (*Sphyraena argentea*), barred sand bass (*Paralabrax nebulifer*), bluefin tuna (*Thunnus thynnus*), Pacific bonito (*Sarda chiliensis*), halfmoon (*Medialuna californiensis*), California halibut (*Paralichthys californicus*), kelp bass (*Paralabrax clathratus*), Pacific mackerel (*Scomber japonicus*), rockfishes (*Sebastes* spp.), spotted scorpionfish (*Scorpaena guttata*), California sheephead (*Semicossyphus pulcher*), skipjack tuna (*Euthynnus pelamis*), wahoo (*Acanthocybium solanderi*), ocean whitefish (*Caulolatilus princeps*), white seabass (*Atractoscion nobilis*), yellowfin tuna (*Thunnus alalunga*), and yellowtail (*Seriola lalandi*).

In 1996, 2,556,372 fish were landed south of Point Conception by CPFV anglers (table 6). Southern California CPFV catch represented 77% of the 3,294,935 fish landed statewide. Reported CPFV landings increased

17% in southern California, while increasing 5% statewide. Angler participation on CPFVs increased both statewide (1%) and in southern California (8%) in 1996. Approximately 494,091 CPFV anglers fished off southern California, representing 78% of statewide participation (632,236) for 1996.

The top ten ranking species comprised 93% of total landings by CPFV anglers in southern California (table 6). Barred sand bass dominated the landings in southern California, with reported catch increasing 72% from 1995. Approximately half of all barred sand bass were caught in the Huntington Flats area adjacent to Huntington Beach and Newport Beach. Rockfish landings increased 12% in 1996, but rockfishes dropped in relative importance from first to second rank for the first time in many years. Pacific mackerel reversed a recent downward trend, increasing 23%. Kelp bass returned to fourth rank in 1996. California barracuda dropped from third to fifth rank in relative importance. Spotted scorpionfish landings increased 27%. Ocean whitefish, primarily targeted on rockfish trips, dropped in importance to rank seven. Pacific bonito landings increased 82%, moving this species from rank eleven to eight. Yellowfin tuna landings were down. Yellowtail landings increased

TABLE 6
Southern California CPFV Landings (Number of Fish) in 1996 and 1995

| Species/species group | 1996 landings | | 1995 landings | | Percent change |
	Number	Rank	Number	Rank	
Barred sand bass	604,132	1	350,539	2	+72
Rockfishes, unspecified	455,040	2	407,678	1	+12
Pacific mackerel	329,146	3	267,731	4	+23
Kelp bass	282,673	4	231,687	5	+22
California barracuda	271,856	5	326,792	3	−17
Spotted scorpionfish	119,492	6	94,398	7	+27
Ocean whitefish	108,282	7	133,655	6	−19
Pacific bonito	72,664	8	39,995	11	+82
Yellowfin tuna	72,449	9	87,347	8	−17
Yellowtail	66,763	10	29,445	12	+127
Halfmoon	43,555	11	54,656	9	−20
White croaker	25,654	12	16,916	14	+52
California sheephead	23,450	13	23,735	13	−1
Dolphinfish	21,939	14	5,022	20	+337
Flatfishes, unspecified	11,052	15	4,664	22	+137
Lingcod	6,970	16	4,823	21	+45
Skipjack tuna	6,356	17	43,043	10	−85
California halibut	5,829	18	5,681	18	+3
Jack mackerel	5,403	19	5,330	19	+1
Blacksmith	4,926	20	3,150	24	+56
Wahoo	3,680	21	5,733	17	−36
Bluefin tuna	2,477	22	14,646	15	−83
Cabezon	1,501	23	769	26	+95
White seabass	1,448	24	4,264	23	−66
All others	9,635	—	26,064	—	—
Total number of fishes	2,556,372		2,187,763		+17
Number of anglers	494,091		455,545		+8
Reporting CPFVs	208		205		+1

TABLE 7
Central and Northern California CPFV Landings (Number of Fish) in 1996 and 1995

Species/species group	1996 landings		1995 landings		Percent change
	Number	Rank	Number	Rank	
Rockfishes, unspecified	621,070	1	767,313	1	−19
King salmon (chinook)	60,650	2	124,489	2	−51
Lingcod	22,764	3	25,719	3	−11
California halibut	13,263	4	13,664	4	−3
Striped bass	6,096	5	3,102	6	+49
Pacific mackerel	6,094	6	3,419	5	+44
Flatfishes, unspecified	2,285	7	3,099	7	−26
Cabezon	1,502	8	1,041	8	+44
Albacore	1,337	9	135	14	+890
Jack mackerel	1,226	10	765	9	+60
White croaker	669	11	168	13	+298
Shark, unspecified	363	12	613	10	−41
Sturgeon, unspecified	308	13	281	12	+10
Leopard shark	179	14	468	11	−62
All others	757	—	484	—	—
Total number of fishes	738,563		944,760		−22
Number of anglers	138,145		173,093		−20
Reporting CPFVs	121		121		0

127% in 1996, making this the tenth most frequently landed species. Yellowtail had a strong spring season (10,817 fish in May), with catch peaking again in August at 22,996 fish. Dolphinfish landings increased 337% in 1996, moving this favored species from rank 20 to 14.

Northern California

Northern and central California anglers fished aboard CPFVs, targeting chinook (king) salmon (*Oncorhynchus tshawytscha*), rockfishes (*Sebastes* spp.), lingcod (*Ophiodon elongatus*), striped bass (*Morone saxatilis*), California halibut (*Paralichthys californicus*), albacore (*Thunnus alalunga*), or white sturgeon (*Acipenser transmontanus*). Salmon, rockfish, lingcod, cabezon (*Scorpaenichthys marmoratus*), and other nearshore species were caught from coastal waters. Striped bass, leopard shark (*Triakis semifasciata*), and white sturgeon live mainly in estuarine waters and were caught almost exclusively in San Francisco Bay. Most California halibut were caught by CPFV anglers in San Francisco Bay, although some were caught along the coast. In previous years salmon catches included coho (silver) salmon (*Oncorhynchus kisutch*), but in 1996 coho salmon were prohibited. Albacore were caught primarily during summer in waters offshore (>20 nmi) of the Morro Bay and Monterey areas, where ocean temperatures are warmer than in nearshore areas.

The rockfish species group continued to dominate catches by northern and central California CPFV anglers, constituting 84% of the total number caught (table 7). Approximately 50% of the total rockfish catch was landed in the Monterey and Morro Bay areas. Order of rank abundance has changed slightly within the top eight species or species groups, which have remained consistent since 1994. The top four represented 95% of total reported landings. Albacore constituted 2% of the catch, increased 890% over the previous year, and increased in rank abundance to ninth from fourteenth.

Total catch in absolute numbers, as reported in logbooks, decreased by 22% over the previous year, primarily because of decreased landings of the top three species or species groups. The CDFG requires that CPFV captains report their catches in CDFG-provided logbooks and submit completed logbooks. Although compliance is less than 100%, the overall rate has not varied much among years, so it is likely that this apparent decrease in total catch represents a real decline. It is not clear if decreasing rockfish landings since 1992 reflect decreased abundance, because there has been a coincident increase in salmon landings, a preferred species. Total number of anglers decreased by 20% from 1995, and there was no change in the number of CPFVs reporting catches.

The high catch of California halibut in 1996 was 97% of the 1995 reported value and accounted for 2% of the total CPFV catch in 1996. These two years represented an average sixfold increase in landings over the average catch from 1980 to 1994. Recent warm-water years (related to an El Niño event) along the central and northern coast, high abundance of juvenile halibut in 1993, and the elimination in 1993 of alternative gear permits for commercial halibut fishing have probably contributed to this increase. Increases were also observed in catches of other important species or species groups, including striped bass, Pacific mackerel, cabezon, jack mackerel, white croaker (*Genyonemus lineatus*), and sturgeon. Catches of leopard sharks decreased by 62% from 1995 reported values.

Editors:

F. Henry and D. Hanan

Contributors:

T. Barnes, Pacific mackerel

K. Barsky, swordfish/shark

D. Ono, sea cucumber

S. Owen, white seabass

R. Dixon, salmon

P. Haaker, abalone

K. Hill, S. Calif. recreational

P. Kalvass, sea urchin

R. Leos, prawns

K. McKee-Lewis, live fish

C. Ryan, Pacific herring

D. Thomas, groundfish

R. Warner, Dungeness crab

D. Wilson-Vandenberg,
    N. Calif. recreational

M. Yaremko, market squid

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THE STATE OF THE CALIFORNIA CURRENT, 1996–1997: MIXED SIGNALS FROM THE TROPICS

FRANKLIN B. SCHWING
Pacific Fisheries Environmental Laboratory
National Marine Fisheries Service, NOAA
1352 Lighthouse Avenue
Pacific Grove, California 93950-2097

THOMAS L. HAYWARD
Marine Life Research Group
Scripps Institution of Oceanography, UCSD
9500 Gilman Drive
La Jolla, California 92093-0227

KEITH M. SAKUMA
Tiburon Laboratory
National Marine Fisheries Service, NOAA
3150 Paradise Drive
Tiburon, California 94920

TOM MURPHREE
Department of Meteorology
Naval Postgraduate School
254 Root Hall
589 Dyer Road
Monterey, California 93943-5114

AFFONSO S. MASCARENAS JR.
Instituto de Investigaciones Oceanológicas
Universidad Autónoma de Baja California
Apartado Postal 453
Ensenada, Baja California 22830
México

SERGIO I. LARIOS CASTILLO
Instituto de Investigaciones Oceanológicas
Universidad Autónoma de Baja California
Apartado Postal 453
Ensenada, Baja California 22830
México

ARNOLD W. MANTYLA
Marine Life Research Group
Scripps Institution of Oceanography, UCSD
9500 Gilman Drive
La Jolla, California 92093-0227

SHERRY L. CUMMINGS
Marine Life Research Group
Scripps Institution of Oceanography, UCSD
9500 Gilman Drive
La Jolla, California 92093-0227

FRANCISCO P. CHAVEZ
Monterey Bay Aquarium Research Institute
P.O. Box 628
7700 Sandholdt Road
Moss Landing, California 95039

KENNETH BALTZ
Pacific Fisheries Environmental Laboratory
National Marine Fisheries Service, NOAA
1352 Lighthouse Avenue
Pacific Grove, California 93950-2097

DAVID G. AINLEY
H. T. Harvey and Associates
906 Elizabeth Street
Alviso, California 95002

ABSTRACT

A large number of data sets from within the California Current region, and the large-scale fields that affect this region, are available for timely assessment of recent environmental conditions in this system. In addition to the long-running quarterly CalCOFI cruises, which featured the initial research cruise of RV *Roger Revelle*, several surveys off Baja California and central California have provided information on coastal areas adjacent to the present CalCOFI coverage. Conditions throughout the north Pacific and in the California Current are summarized and interpreted for the 1996–97 period.

Moderate to weak La Niña conditions have affected the north Pacific since late 1995. But this particular La Niña event displayed an unusual pattern of atmospheric heating in the tropical Pacific, compared to other La Niña events. This may have helped produce a different response over the north Pacific that was, in several important respects, different from a typical La Niña. The most notable differences were in the wind anomalies, which may have contributed to relatively high sea level and warm SSTs offshore of California and Mexico throughout this period. El Niño conditions began to develop in the tropics in early 1997. If this event continues to develop, significant effects on the California Current region can be expected.

Variability in coastal conditions is complex, and seems due to the combined effect of local processes and anomalies in large-scale atmospheric and ocean forcing. Coastal indices and time series show no dominant pattern of variability, and the anomalies from their long-term seasonal means were generally not remarkable. Upwelling indices and buoy time series suggest generally high upwelling in the spring and summer of 1996, and unusually high rates in early 1997. In May 1997, upwelling was dramatically reduced along the entire coast. At SIO Pier, SSTs were anomalously warm during the first half of 1996, but closer to the norm in late 1996 and early 1997. In spring 1997, SST and coastal sea-level anomalies began increasing, but it is premature to say this was related to El Niño forcing. What is certain is that warm, El Niño–like conditions have been observed in the region long before the initial development of this latest apparent El Niño. Winter sea-level heights were relatively high due to onshore winds and high freshwater discharge, and were connected with positive height anomalies extending across the entire north Pacific, a consequence of La Niña.

Oceanic circulation patterns observed in 1996–97 were similar to the long-term mean, and have featured relatively high mesoscale activity since early 1996. Salinities in the core of the California Current were noticeably lower than historical climatologies indicate. A strong coastal countercurrent was noted off southern California in August and October 1996 and April 1997, and along the Big Sur coast in June 1996. Warm, saline water that was low in chlorophyll was associated with this flow.

Despite reasonably high primary production based on chlorophyll concentrations, macrozooplankton biomass remains very low compared to historical levels in the

California Current. In recent years, there have also been reduced abundances of juvenile rockfish and seabird populations. High primary production is not clearly related to coastal time series or circulation patterns, and does not appear to be a good predictor of production at higher trophic levels in the California Current.

1. INTRODUCTION

Providing a timely summary and interpretation of basic environmental data sets that are applicable to ecological research is a high priority, particularly for the California Current system, where a number of interdisciplinary problems are being investigated. This report continues a series of annual papers in *CalCOFI Reports* (cf. Hayward et al. 1994, 1995, 1996) that describe and interpret recent atmospheric and oceanographic conditions in the California Current. Our objective is to provide an up-to-date assessment of environmental patterns and conditions. The primary period covered by this report is from April 1996 to April 1997, although some earlier data are included to compare recent structure to previous patterns and trends.

The fundamental emphasis is on results from the quarterly cruises that are part of the data-rich CalCOFI time series. Additional information obtained off central and Baja California during this period substantiates many of the features and patterns noted in the present CalCOFI sampling region, and gives a contemporary context to the historical CalCOFI data set that once extended from the Gulf of California and the southern tip of Baja California to the Oregon border and north. We also examine the large-scale atmospheric and oceanic conditions that force much of the variability in the California Current. Physical and biological patterns are related as well. We consider how these patterns differ from long-term means, and how biological structure may be linked to atmospheric forcing and ocean circulation.

Local patterns were affected by a weak La Niña in the tropics, which featured an unusual distribution of anomalies compared to typical La Niña events. Unlike conditions during the 1992–94 El Niño, no single dominant pattern was expressed throughout the California Current during the previous year.

2. DATA SETS AND METHODS

Coastal data include temperature and salinity at shore stations (Walker et al. 1994). La Jolla (SIO Pier) and Pacific Grove daily temperatures and their anomalies from the long-term harmonic mean (1916–93 for La Jolla and 1919–93 for Pacific Grove) are shown as time series. Coastal sea-level data from San Diego and San Francisco are shown as monthly anomalies from the 1975–95 mean, corrected for atmospheric pressure (data courtesy Patrick Caldwell, U. Hawaii Sea Level Center).

TABLE 1
Locations of SST and Alongshore Wind Time Series

Buoy	Position	Base period[a]	Alongshore angle (°N)[b]
46050 (Stonewall Bank, OR)	44.6°N, 124.5°W	(1991–96)	0
46027 (St. George, CA)	41.8°N, 124.4°W	(1983–96)	341
46013 (Bodega, CA)	38.2°N, 123.3°W	(1981–96)	312
46042 (Monterey Bay, CA)	36.7°N, 122.4°W	(1987–96)	328
46011 (Santa Maria, CA)	34.9°N, 120.9°W	(1980–96)	326
46025 (Catalina Ridge, CA)	33.7°N, 119.1°W	(1982–96)	294

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

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

Data from quarterly CalCOFI surveys in 1996 and 1997 are described. The CalCOFI monitoring program started in 1949; a brief history of the program is given in Hewitt 1988. The present program consists of quarterly (normally January, April, July, October) cruises that occupy a grid of 66 stations off southern California. The core time series data set now collected at each station includes a CTD/rosette cast with sensors for pressure, temperature, salinity, dissolved oxygen, photosynthetically active radiation, fluorescence, and transmissivity. Water samples are collected at 20-24 depths in the upper 500 m to determine salinity, dissolved oxygen, nutrients (NO_3, NO_2, PO_4, SiO_3), phytoplankton pigments (chlorophyll a and phaeophytin), and primary production (^{14}C uptake at one station per day). Oblique and surface (neuston) net tows (0.505-mm mesh) are taken at each station. Continuous near-surface measurements of temperature, salinity, and chlorophyll fluorescence are made from water pumped through the ship. Acoustic Doppler current profiler (ADCP) data are also recorded continuously, providing a measure of upper ocean currents as well as an estimate of zooplankton biomass based upon acoustic backscatter. The most recent data presented here are preliminary, and some changes may be made after the final processing and quality control checks. More details on the methods, information about recent activities, and CalCOFI hydrographic data can be accessed via the World Wide Web (*http://www-mlrg.ucsd.edu/calcofi.html*).

3. DYNAMICAL RESULTS

A. Large-Scale Oceanic and Atmospheric Climate Patterns

1995–97 La Niña. Large-scale surface anomalies are summarized from monthly fields, assembled from a variety of sources by the NOAA Climate Prediction Center

(NCEP 1997a, b). Monthly anomalies (figures 1, 2) are departures from the 1979–95 base period. Much of the physical variability—wind, sea-surface temperature (SST)—of the California Current region during 1996–97 appears to have been related to climate anomalies in the tropical Pacific. La Niña conditions appeared in the tropical Pacific about September 1995 and continued
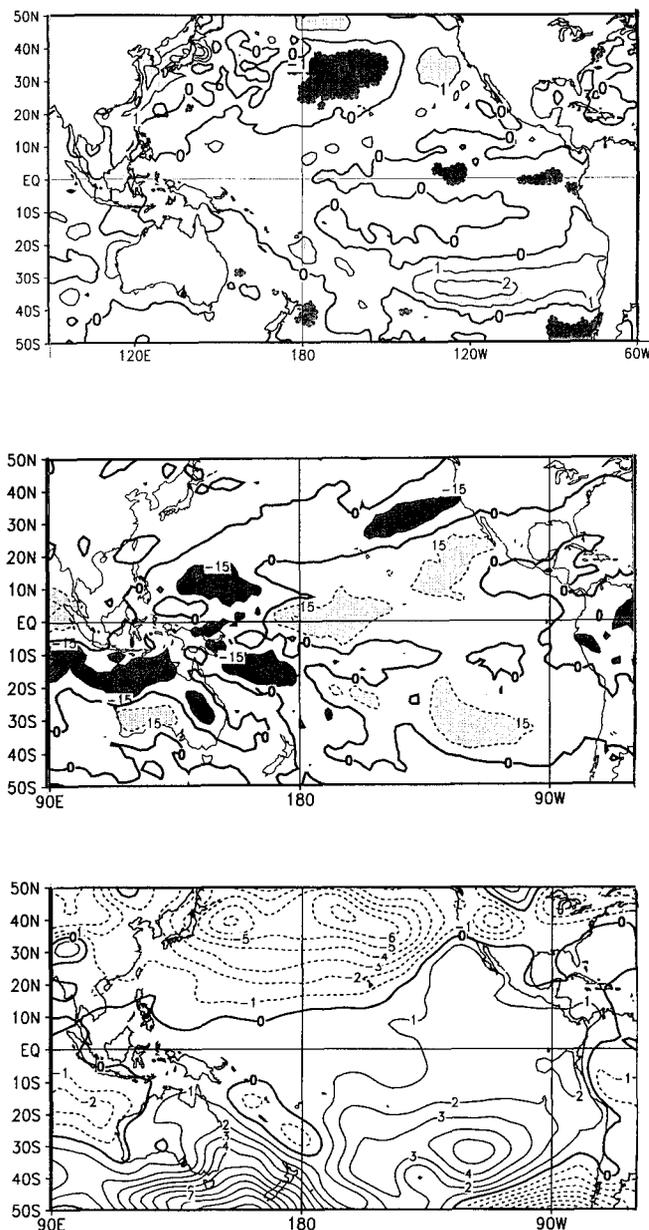
Figure 1. January 1997 Pacific Ocean anomalies of sea-surface temperature (SSTA; *top*), outgoing longwave radiation (OLRA; *center*), and sea-level pressure (SLPA; *bottom*). Anomalies are departures of monthly-averaged fields from the 1979–95 base period. Positive anomalies denote warmer than normal SST, lower than normal atmospheric heating, and higher than normal atmospheric pressure. Anomalous surface winds are approximately parallel with SLPA contours, and cyclonic (counterclockwise in Northern Hemisphere) around negative anomalies. Closer-spaced SLPA contours indicate faster anomalous winds. Adapted from NOAA National Centers for Environmental Prediction (NCEP 1997a).
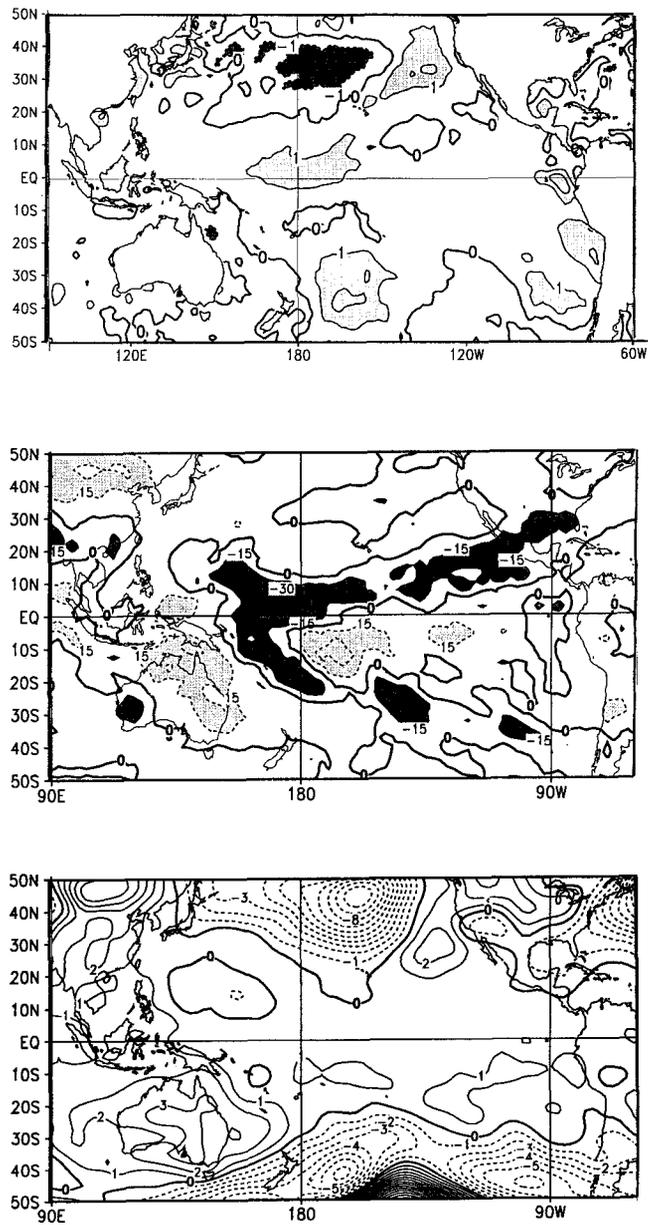
Figure 2. April 1997 Pacific Ocean anomalies of sea-surface temperature (SSTA; *top*), outgoing longwave radiation (OLRA; *center*), and sea-level pressure (SLPA; *bottom*). Anomalies are departures of monthly-averaged fields from the 1979–95 base period. Positive anomalies denote warmer than normal SST, lower than normal atmospheric heating, and higher than normal atmospheric pressure. Anomalous surface winds are approximately parallel with SLPA contours, and cyclonic (counterclockwise in Northern Hemisphere) around negative anomalies. Closer-spaced SLPA contours indicate faster anomalous winds. Adapted from NOAA National Centers for Environmental Prediction (NCEP 1997b).

through January 1997. La Niña conditions were moderate to weak until June 1996 and weak during the last eight months of this period. In February 1997, several tropical Pacific Ocean and atmospheric anomalies appeared that indicated a shift toward El Niño conditions. Throughout this period SSTs in and offshore of the California Current region were unusually warm, possibly because of La Niña conditions in the tropics that differed from those in a typical La Niña.

These tropical developments were indicated by the sea-surface temperature anomaly (SSTA) and the corresponding outgoing longwave radiation anomaly (OLRA) patterns in the tropical Pacific. Negative OLRAs indicate anomalously high tropical storm activity and high latent heating of the troposphere, or lower atmosphere (Murphree and Reynolds 1995), in essence greater than usual atmospheric heating. Anomalous atmospheric heating or cooling in the tropics may trigger a sequence of events that leads to significant disturbances of the extratropical ocean and atmosphere. In particular, OLRAs associated with El Niño and La Niña events may alter the atmospheric forcing and circulation of the mid-latitude north Pacific, including the California Current region (Murphree and Reynolds 1995). La Niña conditions, illustrated by the January 1997 fields, are indicated by positive SSTAs and negative OLRAs in the tropical western Pacific, along with negative SSTAs and positive OLRAs in the tropical central and eastern Pacific (figure 1). The transition toward El Niño conditions in early 1997 (e.g., April) is suggested by the development of positive SSTAs in the tropical central and eastern Pacific, positive OLRAs in the western Pacific, and negative OLRAs near the dateline (figure 2).

During most of the September 1995–January 1997 period, compared to other La Niña events, OLRAs were moderate to strong (more than normal atmospheric heating for La Niña) in the western region, but weak to moderate (less than normal heating for La Niña) in the central and eastern Pacific (figure 1). The uneven development of atmospheric heating anomalies over the tropical Pacific during 1995–97 may have helped produce a response over the north Pacific that was, in several important respects, different from that typically observed during La Niña.

The typical north Pacific winter response to a La Niña event includes a negative sea-level atmospheric pressure anomaly (SLPA) near Hawaii and a positive SLPA over the northeast Pacific, corresponding to a weaker Aleutian Low (Murphree and Reynolds 1995). But for most of the November 1995–January 1997 period, a negative SLPA occurred over much of the northeast Pacific. This negative anomaly frequently extended northeastward from the central north Pacific toward North America. Surface wind anomalies associated with the SLPAs

were cyclonic (counterclockwise), with generally northeastward and northward anomalies over much of the California Current region and the northeast Pacific (NCEP 1997a). Such anomalies should lead to reduced coastal upwelling and higher coastal sea level along the U.S. west coast. North Pacific sea-level height anomalies tended to be anomalously low on the north side of this region of anomalous wind, but high south of it (U. Hawaii, Sea Level Center, unpubl. data). Incidentally, the northeastward wind anomalies were also responsible for bringing warm, humid, subtropical air to much of the west coast during the 1995–96 and 1996–97 winters and the 1997 spring.

The extratropical north Pacific SSTA pattern from February 1995 to June 1997 was dominated by a negative SSTA in the central north Pacific, and a positive SSTA that extended northeastward from the tropical western Pacific across the northeast Pacific. These features were supplemented at times by monthly or seasonal SSTAs along western north America produced by upwelling episodes (e.g., in October 1996). The area of positive SSTA was roughly coincident with the region of anomalously high sea level.

During April–May 1997, the northeast Pacific warmed substantially in a roughly triangular region extending between Vancouver Island, Hawaii, and Cabo San Lucas (figure 2). By early June 1997, SSTAs in this region ranged from +0.5° to more than +4.0°C. Normally during spring, the North Pacific High migrates to the northwest from its winter position west of northern Baja California, while also expanding to the west. But during spring 1997, this migration and expansion was reduced, leading to northeastward winds and wind anomalies over much of the northeast Pacific and parts of the west coast (NCEP 1997b). This situation was especially pronounced in May 1997. This wind field is associated with more open-ocean downwelling, which may have contributed to these warm ocean anomalies as well as higher than typical sea level, identical to patterns seen in the previous La Niña.

The atypical response of the extratropical north Pacific to the 1995–97 La Niña may have been dominated by the effects of unusually well-developed positive tropospheric heating anomalies in the tropical western Pacific, and by the absence of well-developed cooling anomalies in the tropical central and eastern Pacific (Murphree and Gelaro, unpubl. model results). These extratropical responses include the negative SLPA in the northeast Pacific and its associated low-level wind, sea-level anomalies, and SST anomalies.

The extratropical North Pacific anomaly patterns observed during this La Niña period suggest that sea-level anomalies were controlled by Ekman pumping (divergence in the surface Ekman transport) produced by the

unusual winds. Increased open-ocean upwelling in much of the central north Pacific, but open-ocean downwelling and warmer surface waters offshore of California and Mexico are implied. While the interactions between these processes are complex, the ocean provides feedback to the atmosphere which may have helped sustain the La Niña pattern for over two years.

El Niño outlook. In late 1996 and early 1997 (November–May), eastward surface wind anomalies in the tropical western Pacific helped initiate a transition toward El Niño conditions. The early stages of an El Niño event were clearly indicated by positive SSTAs in the eastern and central equatorial Pacific in February–June 1997 (figure 2). By April, anomalies in surface pressure, wind, atmospheric heating, and ocean temperatures across much of the tropical Pacific were consistent with a shift toward El Niño conditions. Over a large area near Ecuador and Peru, SSTAs exceeded +2°C by late May, an increase in the anomaly of more than 3°C since the beginning of the year.

During early 1997, temperature anomalies at and near the thermocline propagated eastward through the equatorial Pacific (figure 3). These were associated with two equatorial Kelvin waves, whose downwelling phase is indicated by an anomalously deep mixed layer, each apparently forced by a relaxation in westward wind stress in the western equatorial Pacific (NCEP 1997b). The downwelling phase of the first wave reached South America in March 1997; the second arrived in April–May 1997. These waves would be expected to propagate poleward along the Americas as coastal Kelvin waves, with the first reaching southern California in mid-to-late April 1997 (the time of a CalCOFI cruise), and the second arriving in early June. The expected direct effects of these waves would include increased coastal sea level and northward flow, along with warmer and less saline water (Simpson 1992; Lynn et al. 1995). We stress, however, that SSTs were elevated throughout the most recent La Niña, and that the June 1997 warm anomalies off California have not been introduced by El Niño.

If El Niño conditions persist or strengthen during 1997–98, significant effects in the California Current region would be expected via atmospheric and/or oceanic teleconnection processes (Murphree and Reynolds 1995; Lau 1997). Several El Niño/Southern Oscillation forecast models run in early spring 1997 are predicting El Niño conditions for the second half of 1997 and early 1998, although other models have predicted cool to normal conditions for this period (Barnston 1997).

B. Coastal Conditions

Coastal upwelling indices. The monthly upwelling indices (Bakun 1973; Schwing et al. 1996) along the North American west coast since 1995 display the annual cycle
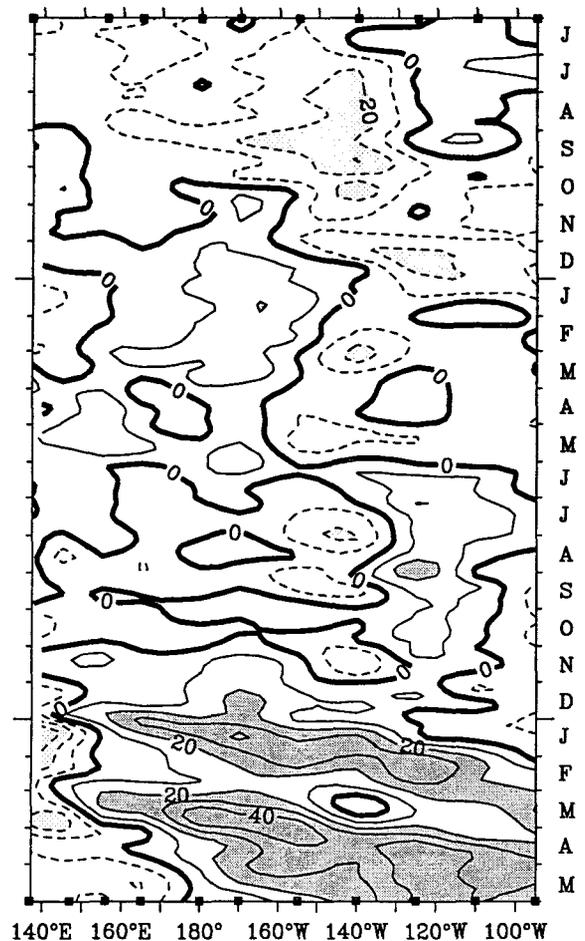
20°C Isotherm Depth Anomalies (m)

Figure 3. Depth of the 20°C isotherm between 2°N and 2°S for June 1995–May 1997. Analysis based on the five-day averages of moored time series data from the TAO (Tropical Atmosphere Ocean) array. *Shading* denotes isotherm depths more than 20 m deeper than the monthly climatology. Deeper than normal isotherms indicate the eastward propagation of the downwelling phases of two Kelvin waves across the equatorial Pacific in early 1997. Adapted from NCEP (1997b).

of increased upwelling during spring and summer, with generally higher values in 1996 than in 1995 (figure 4). Anomalies were generally positive (greater than normal upwelling) for the latter half of 1995, but reversed to slightly negative (weaker than normal upwelling) along the U.S. coast in early 1996. In May 1996, values became anomalously high at 36°N and north, but remained negative at 33°N. Weaker than normal upwelling off Baja California was suggested during the summer of 1996. Upwelling remained high along most of California during the biologically productive months of 1996. After negative anomalies in December 1996, the indices were unusually high in early 1997 south of Cape Mendocino (40°N). Winds were relatively calm in May 1997, leading to much weaker than normal upwelling along the entire west coast. The indices have been near zero off Oregon for the first six months of 1997.
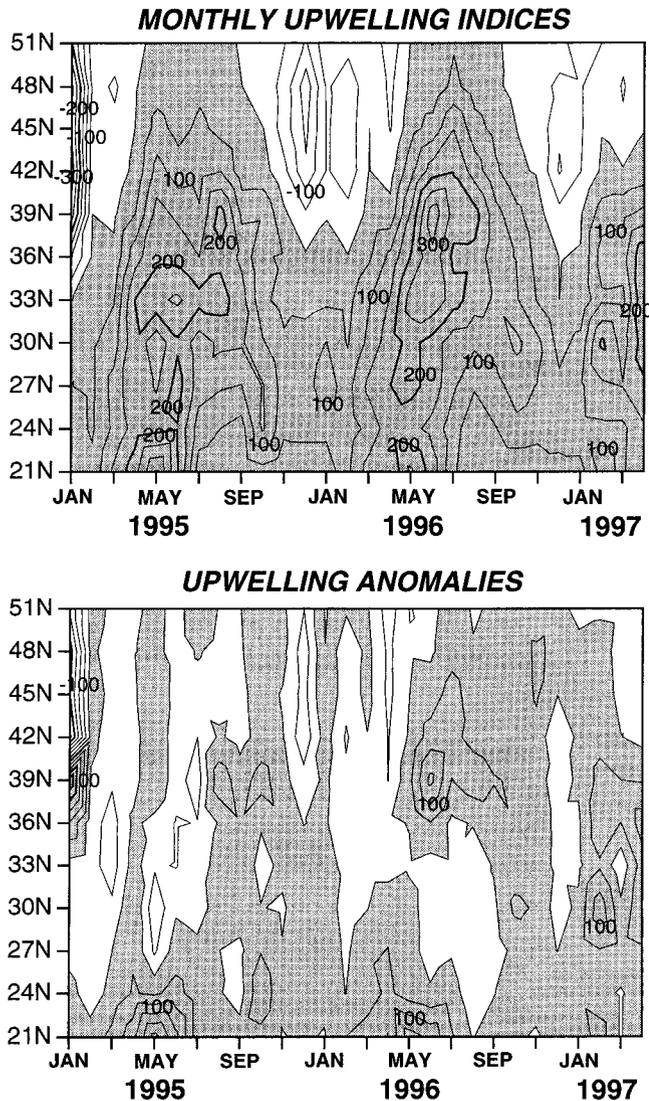
MONTHLY UPWELLING INDICES

UPWELLING ANOMALIES

Figure 4. Monthly upwelling index and upwelling index anomaly during 1995–97. Positive values imply coastal upwelling. *Shaded areas* denote positive (upwelling-favorable) values in *upper panel*, and positive anomalies (generally greater than normal upwelling) in *lower panel*. Units are in m³ sec⁻¹ per 100 km of coastline.

Coastal upwelling indices during this period do not correlate with the large-scale atmospheric anomalies described in section 3A. Thus at times coastal conditions (e.g., SST) may show a different pattern from that in the greater north Pacific. For example, strong coastal upwelling in early 1997 appears to have mitigated the warming effects of wind-forced Ekman downwelling in the northeast Pacific (figure 1).

Coastal buoy time series. Winds measured at NDBC buoys (table 1) along the U.S. west coast (figure 5) reflect the interannual differences, as well as the annual cycle, noted in the upwelling indices. Seasonal patterns observed in 1995 and 1996 correspond well to the long-term climatology of west coast buoys (Dorman and Winant

1995). Wind vectors align strongly with the local coastline, particularly off central and southern California. Winds within the Southern California Bight are weak and variable throughout the year, particularly in summer, relative to those north of Point Conception. Winter winds in 1995 and 1996 were highly variable over short time scales, a consequence of a series of strong winter storms that crossed the coast. On average, the winter winds were poleward and stronger than normal, particularly in early 1995. Summer winds were predominantly equatorward, or upwelling favorable, with occasional wind relaxation events or reversals to poleward flow. Coastwide reversals in April and May 1996 produced poleward winds for a brief period. Overall, the winds during 1996 were more upwelling favorable than during 1995, and featured stronger than usual velocities.

At the coastal buoys SSTs reflect both the large-scale anomaly patterns seen throughout the north Pacific, and changes in local wind forcing over time (figure 6). Maximum SSTs occur in late summer along the entire coast. But the minima are delayed off much of California, due to the cooling effect of coastal upwelling. The spring transition for 1995 arrived in mid-April; in 1996 it arrived in mid-March. During 1995 and 1996, as well as in the long-term climatology, SST variance was greater in summer than winter. This is probably due to the combined effect of upwelling/downwelling events that periodically advect the strong seasonal alongshore SST front separating upwelled and offshore water past the buoys, along with interannual variability associated with El Niño, La Niña, and other large-scale climate events. Generally, SSTs were warmer than normal in early 1995, but cooler than usual off southern California from spring through fall 1995. In early 1996, SSTs were unusually warm, particularly in the northern half of the California Current. Unusually cool SSTs, related to strong upwelling-favorable wind conditions (figures 4, 5), predominated for most of the summer of 1996; SSTs gradually returned to their long-term mean in December.

Shore time series. Unlike SSTs at the nearby coastal buoy (Catalina Ridge, figure 6), which featured cooling tendencies in early spring 1996, surface temperatures measured at the SIO Pier remained anomalously warm through the first half of 1996 (figure 7). This pattern was a continuation of the warm SSTs that commenced in fall 1995, and of the warm conditions noted over a large area of the north Pacific (figure 1). Exceptions to these warm anomalies in 1996 were a sharp decline in SST in May from strong positive to near-normal anomalies, and brief periods of very cool SST in July and August. Events like these are not unusual in the historical record. Variations in SST at SIO corresponded closely to anomalies at the Catalina Ridge buoy. Shore temperatures at Pacific Grove fluctuated about the seasonal norm during
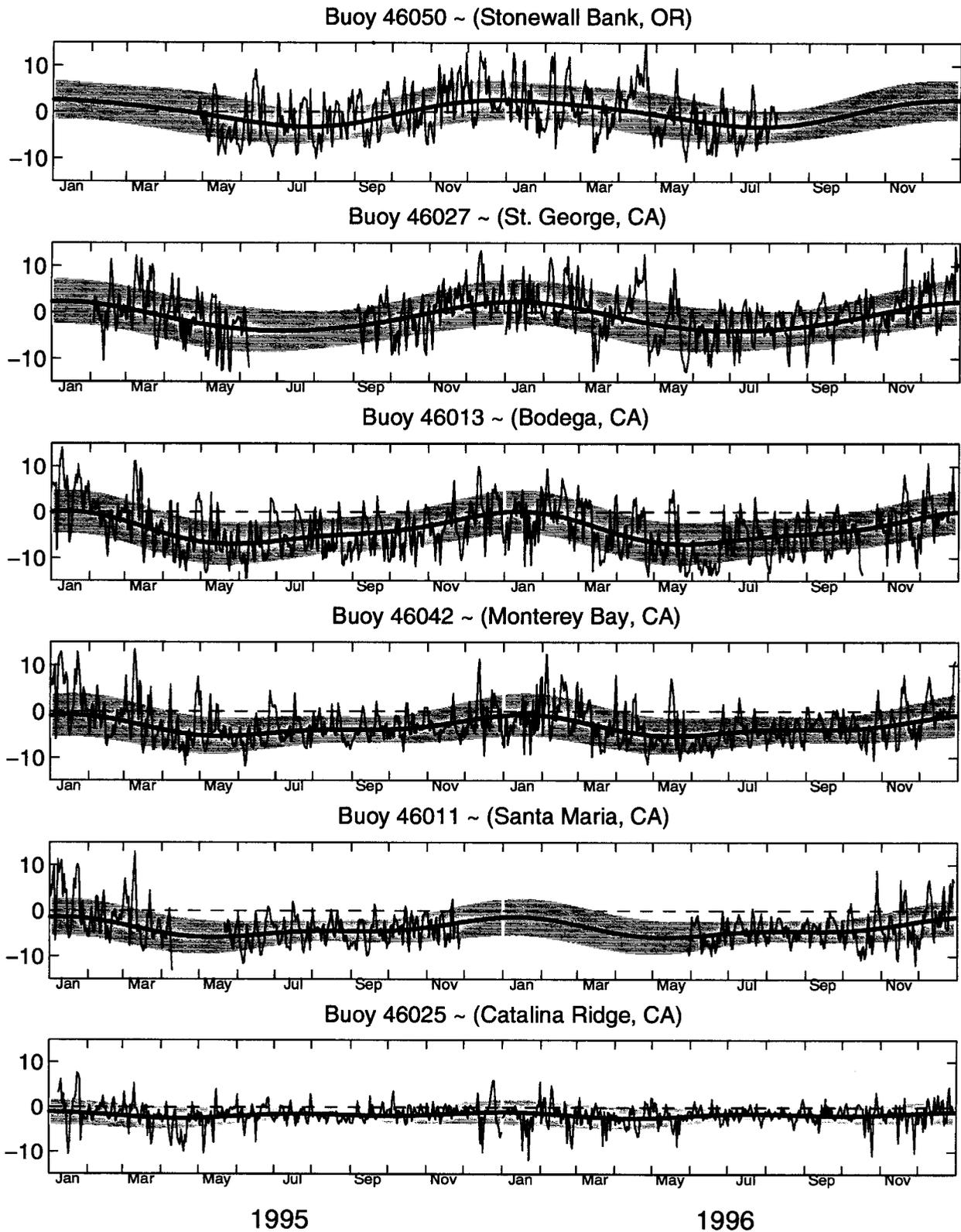
Alongshore Winds 1995 and 1996

Figure 5. Time series of daily-averaged alongshore winds for 1995–96 at selected NDBC buoys. *Bold lines* indicate the harmonic mean annual cycle for each buoy. *Shaded areas* are the standard error for each Julian day. The period used for calculating the mean at each site and the alongshore angle are shown in table 1.
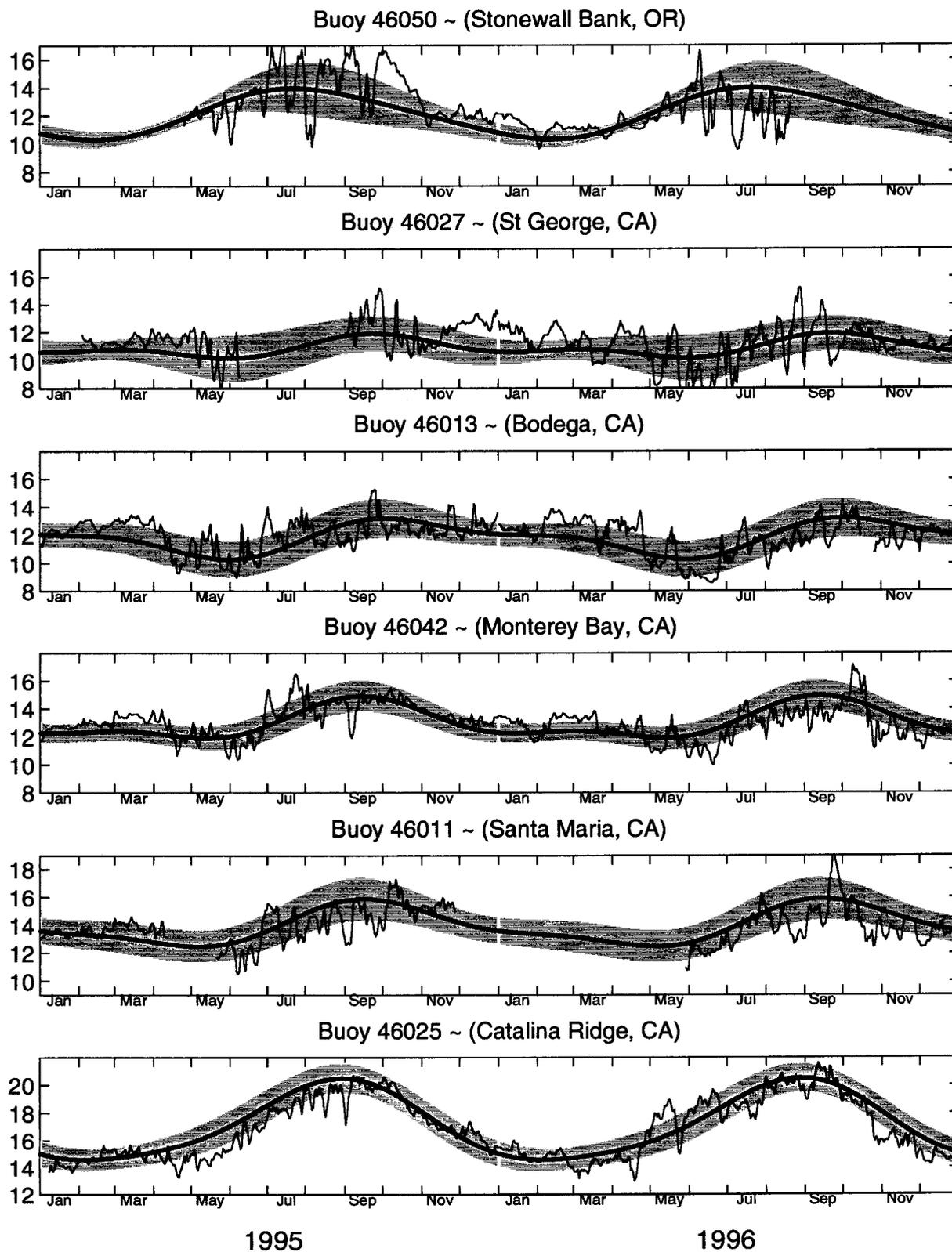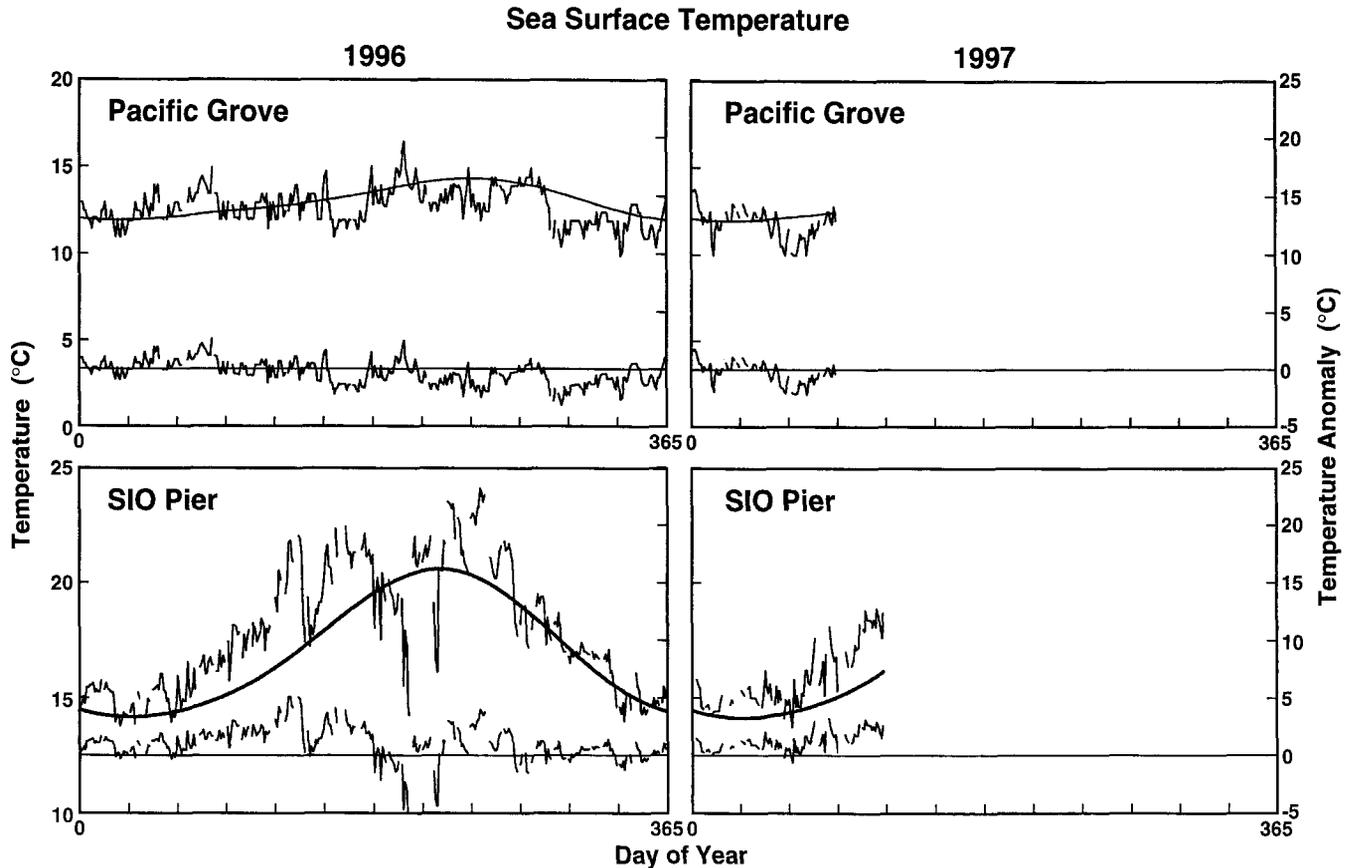
Sea Surface Temperatures 1995 and 1996

Buoy 46050 ~ (Stonewall Bank, OR)

Buoy 46027 ~ (St George, CA)

Buoy 46013 ~ (Bodega, CA)

Buoy 46042 ~ (Monterey Bay, CA)

Buoy 46011 ~ (Santa Maria, CA)

Buoy 46025 ~ (Catalina Ridge, CA)

1995   1996

Figure 6.   Time series of daily-averaged SST for 1995–96 at selected NDBC buoys. *Bold lines* indicate the harmonic mean annual cycle for each buoy. *Shaded areas* are the standard error for each Julian day. The period used for calculating the mean at each site is shown in table 1.

Sea Surface Temperature

Figure 7. Sea-surface temperature at Pacific Grove and La Jolla (SIO Pier) for 1996 and 1997. Daily temperatures and anomalies from the long-term harmonic mean (1919–93 for Pacific Grove and 1916–93 for La Jolla). The *heavy line* shows the harmonic mean annual cycle in SST.

the first half of 1996, and were slightly cooler than average during the latter half, presumably in response to the stronger than normal upwelling-favorable winds (figures 4, 5), and show a marked agreement with nearby buoy SSTs (figure 6). Seasonal anomalies for the buoy and shore series are not directly comparable because they are based on very different periods.

More recent coastal SSTs are available at a few locations. At Granite Canyon, an open site on the Big Sur coast that reflects upwelling events, SST jumped from 9.5° to 13.5°C over the course of several days in early May 1997 (Jerry Norton, pers. comm.). The 1971–94 mean for May at this site is 10.36° (David Newton, SIO, pers. comm.). The relatively cool SSTs in April and early May were associated with higher than normal upwelling indices, and the sudden increase was possibly due to the initiation of weak upwelling (figure 4).

Coastal sea levels at San Diego and San Francisco (figure 8) were near or slightly below average throughout most of 1996, and consistently lower than 1995 values at San Francisco. Note that the annual climatologies have been revised recently, so the anomalies do not correspond with those described in Hayward et al. 1996. San Francisco sea level was near normal from April through

October 1996. As in 1995, sea level at San Francisco was anomalously high in late winter 1996 and January 1997, presumably because of winter storm winds that favored onshore Ekman transport (figures 4, 5), along with high freshwater discharge through the Golden Gate in association with heavy rains and widespread flooding throughout northern California. San Diego sea level anomalies were slightly lower than normal in spring and relatively higher in winter during the past two years. High coastal sea levels in winter 1996–97 are consistent with a large area of positive height anomalies extending southwestward across the entire north Pacific (U. Hawaii Sea Level Center, unpubl. data) discussed in section 3A.

C. Conditions during the CalCOFI Surveys

In contrast to the relatively well-defined large-scale anomalies in the north Pacific associated with the 1992–94 La Niña, but perhaps in agreement with fairly typical seasonal values in the coastal time series discussed in section 3B, the quarterly CalCOFI surveys displayed no strong pattern. The circulation of the California Current appeared to feature relatively high mesoscale activity since early 1996. Over this same period, salinities in the core of the current were clearly lower than
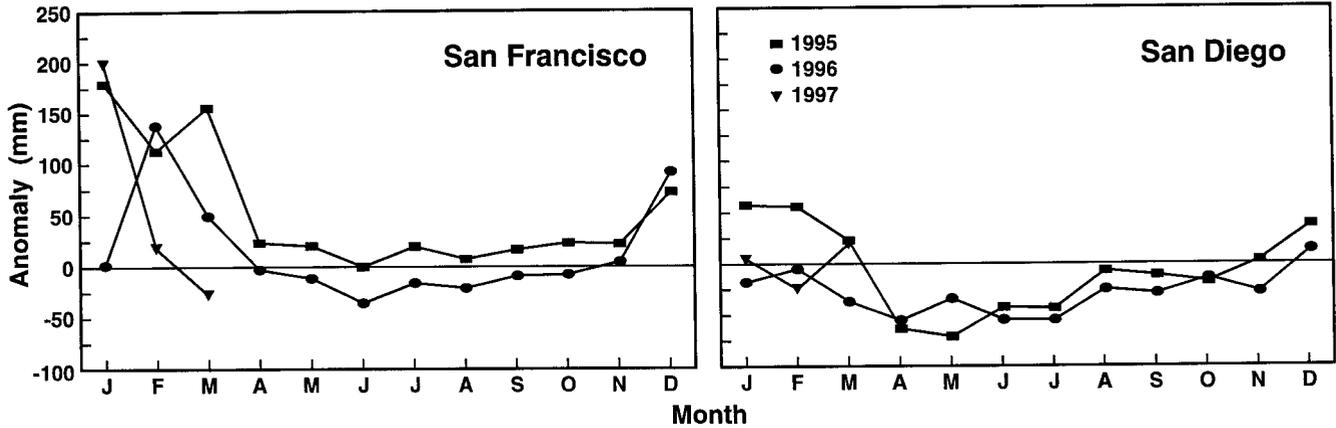
Monthly Sea Level Anomalies

Figure 8.   Monthly sea-level anomalies at San Francisco and San Diego for 1995, 1996, and 1997. The monthly anomalies are deviations from the period 1975–95, corrected for atmospheric pressure.
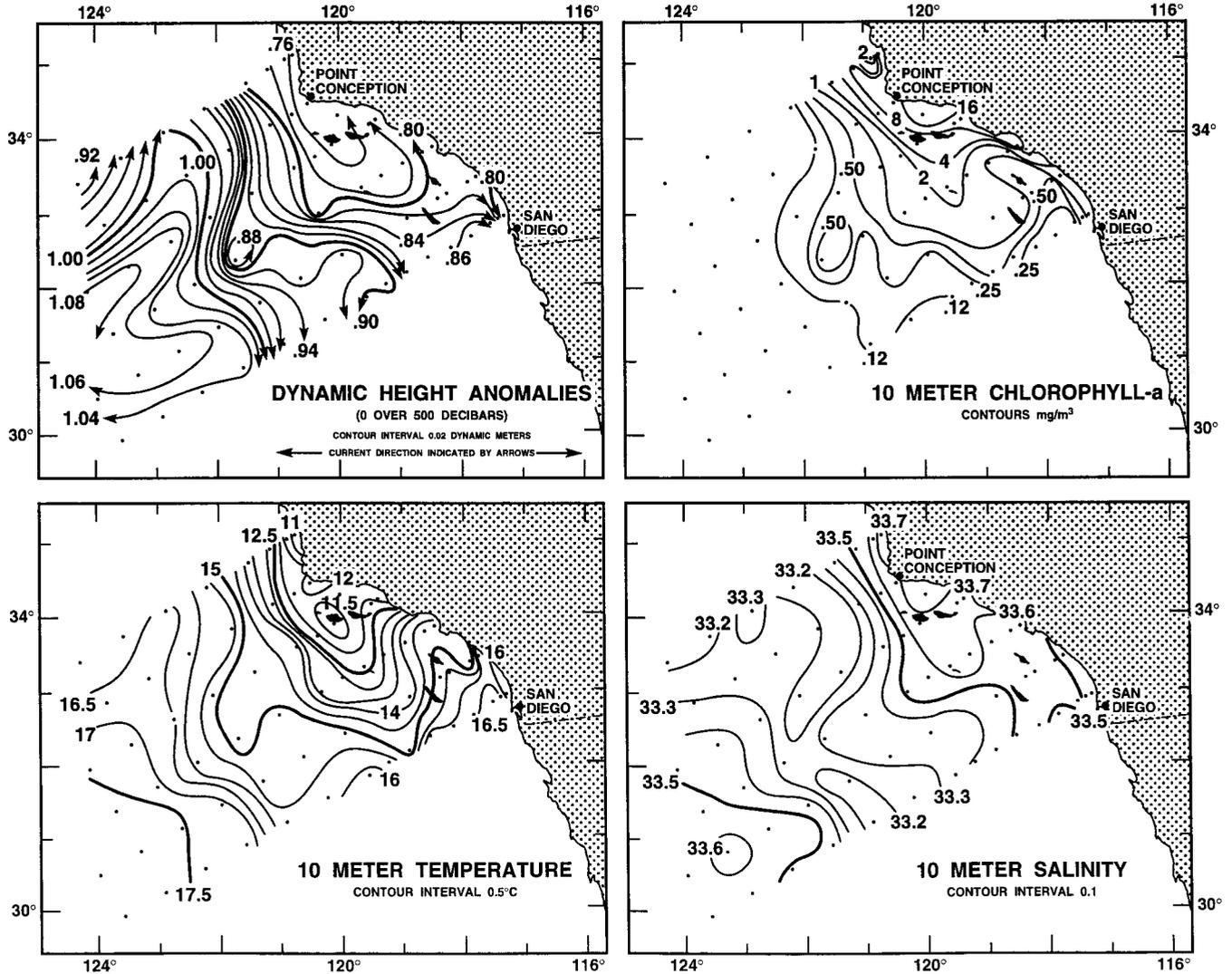
CALCOFI CRUISE 9604

Figure 9.   Spatial patterns for CalCOFI cruise 9604 (15 April–3 May 1996), including upper-ocean geostrophic flow estimated from 0 over 500-db dynamic height anomalies, 10-m chlorophyll, 10-m temperature, and 10-m salinity.
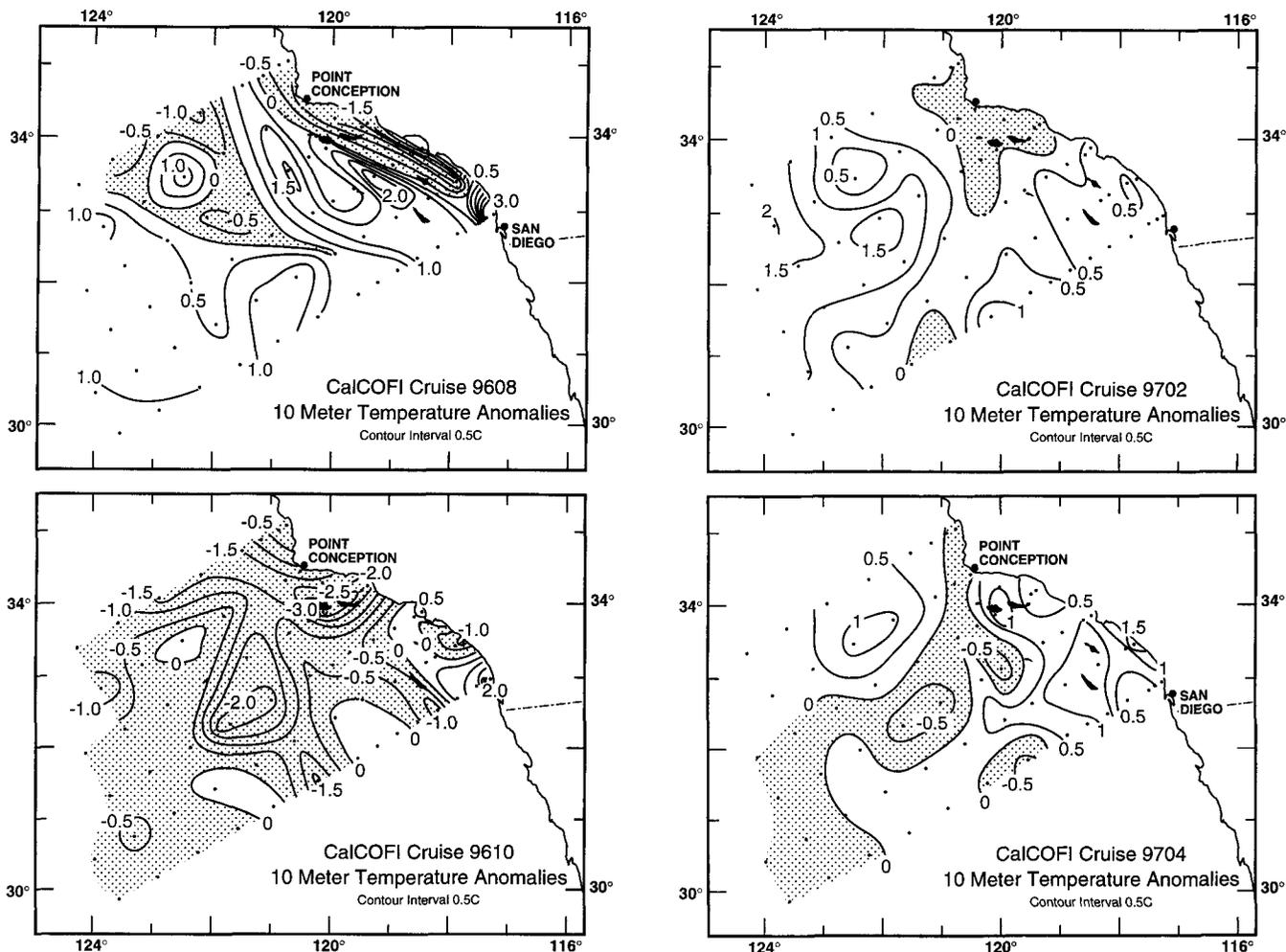
Figure 10.   Anomalies in SST (°C) for CalCOFI cruises 9608, 9610, 9702, and 9704.

normal, but temperature anomalies in the region varied with each cruise. Episodes of strong coastal countercurrent coincided with warm and saline water, and low chlorophyll near the coast.

Conditions prior to April 1996.   The CalCOFI cruises of 1995 and early 1996 were described in Hayward et al. 1996. The region's circulation during 1995 was fairly typical of the long-term mean. But by February 1996 the pattern shifted so that strong mesoscale eddy activity complicated the typical southward flow of the California Current and the northward coastal countercurrent. The region featured generally warm SST anomalies during this period. Chlorophyll concentrations were high, particularly in coastal waters, but macrozooplankton continued a decade-long trend of low biomass (Roemmich and McGowan 1995).

9604 (15 April–3 May 1996).   Preliminary data from this cruise were also included in last year's report (Hayward et al. 1996). Dynamic height anomalies (figure 9) support the conclusion that the core of the California Current, as defined by the southward velocity maximum and cor-

responding salinity minimum, was anomalously far offshore, and that the region had developed a strong mesoscale eddy field around the meandering southward jet. The core of the current in this area was unusually warm and fresh (cf. Lynn et al. 1982), a pattern seen in subsequent cruises as well (figure 10). Chlorophyll levels were high, especially in the coastal area north of the Channel Islands, where relatively cool, saline surface conditions suggested recent strong upwelling.

9608 (7–24 August 1996).   The California Current continued to be farther offshore than normal in the southern part of this survey (figure 11). The flow field featured strong meanders and weaker than normal southward flow off the Southern California Bight. Dynamic heights in the bight were higher than typical, and there appeared to be a stronger than usual coastal countercurrent. Most of the region was anomalously warm, but the spatial pattern included cool anomalies near the coast and near the core of the current. Salinities were higher than normal throughout the region, compared to the summer climatology of Lynn et al. (1982). Chlorophyll concen-
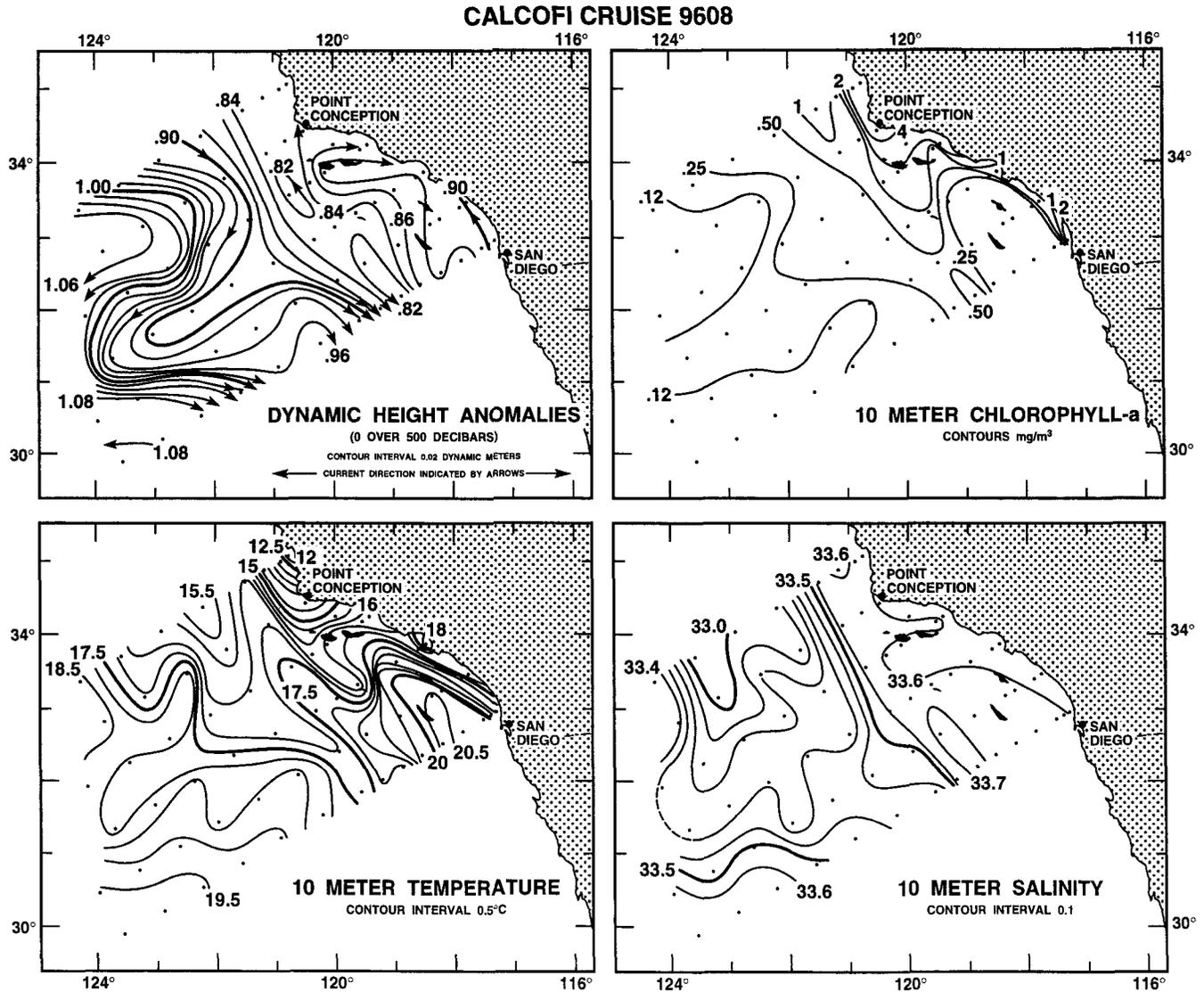
CALCOFI CRUISE 9608

Figure 11. Spatial patterns for CalCOFI cruise 9608 (7–24 August 1996), including upper-ocean geostrophic flow estimated from 0 over 500-db dynamic height anomalies, 10-m chlorophyll, 10-m temperature, and 10-m salinity.

trations were low in the bight, where surface water was warm and saline, but elevated in the cool, saline coastal waters near Point Conception and the Channel Islands. Concentrations were similar to those during the 9408 cruise and a little lower than during the 9507 cruise.

9610 (10 October–2 November 1996). This CalCOFI survey marked the inaugural research cruise of the new SIO research vessel *Roger Revelle*, and included an expanded sampling program with much more effort by cooperative programs. The circulation pattern was fairly typical of fall, but again featured a strong mesoscale eddy field (figure 12). A strong cross-shelf temperature front located off Los Angeles coincided with a very sharp inshore meander of the California Current, which fed into a strong coastal countercurrent. The result was an intense cyclonic circulation around the Channel Islands.

As in the previous survey, very warm (>2°C, figure 10) and saline anomalies were noted near San Diego. Most of the region, however, featured relatively large negative SST anomalies and lower than normal salinities. Near the Channel Islands, SSTs up to 3°C below normal were observed, and a large portion of the area had anomalies cooler than −1°C. Figure 13 presents NOAA polar orbiter images of gray-scaled radiometric SST (channel 4) for the 9610 cruise. The California Current jet and the offshore eddies found in the survey are clearly evident in the satellite image.

In terms of chlorophyll, this was one of the most anomalous cruises in the past decade. Fall is normally a time of low chlorophyll, but concentrations were quite high throughout this cruise. The pattern was much more similar to that in April 1996 and 1997, the seasonal peak
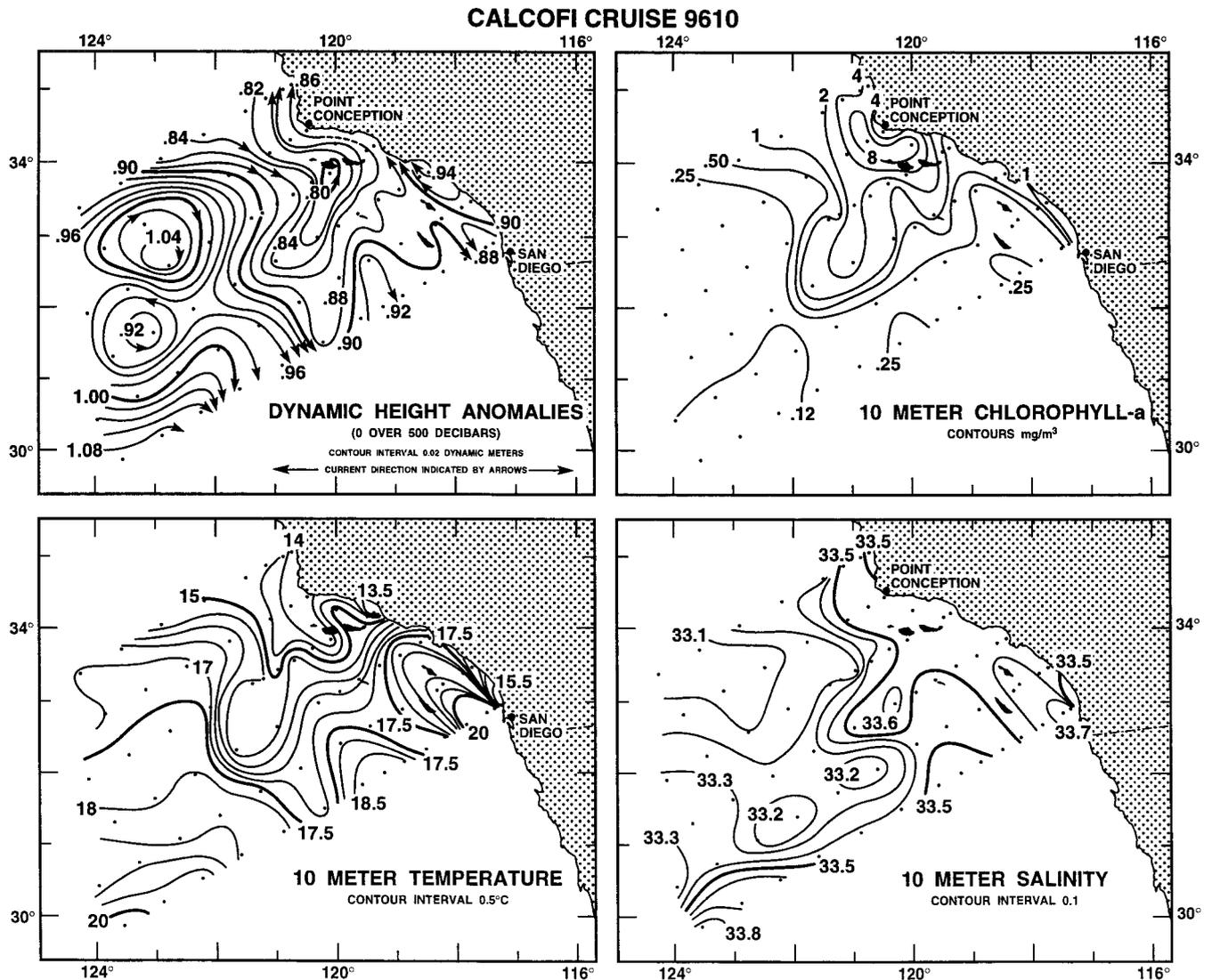
33

CALCOFI CRUISE 9610

Figure 12.   Spatial patterns for CalCOFI cruise 9610 (10 October–2 November 1996), including upper-ocean geostrophic flow estimated from 0 over 500-db dynamic height anomalies, 10-m chlorophyll, 10-m temperature, and 10-m salinity.

in chlorophyll. Chlorophyll values were particularly high in the coastal region near Point Conception. Compared to the previous year's cruise (9510), when 10-m values did not exceed 4 mg m^{-3}, during this cruise there was a large area of chlorophyll concentrations greater than 4 mg m^{-3}, with the highest concentrations being more than 12 mg m^{-3}. Buoy records were highly variable in time and space during October (figures 5, 6), further complicating the interpretation of this pattern.

9702 (29 January–15 February 1997).   Although dynamic height anomalies are not yet available for the 1997 cruises, the circulation patterns can be inferred from temperatures at 100 m. Strong mesoscale structure characterized this winter survey (figure 14), a continuation of the pattern seen in 1996. The normally strong seasonal coastal countercurrent was weak to nonexistent, especially in

the Southern California Bight. Chlorophyll was relatively low, as is typical of winter, with higher values in the coastal region in the northern part of the grid. The high chlorophyll concentrations of October 1996 had generally declined. However, the area where 10-m chlorophyll was greater than 2 mg m^{-3} was greater than at this time in 1995 and 1996. Throughout the area, SSTs were anomalously warm (+0.5° to 1.5°) except for the coastal region near the Channel Islands and Point Conception, which was slightly cooler than the norm (figure 10). A strong alongshore salinity front transected the survey. Seaward of this feature, the core of the California Current was 0.2–0.4 ppt fresher than historical means (Lynn et al. 1982). Although near-surface salinity was high north of Point Conception, nearshore waters were unusually fresh from Point
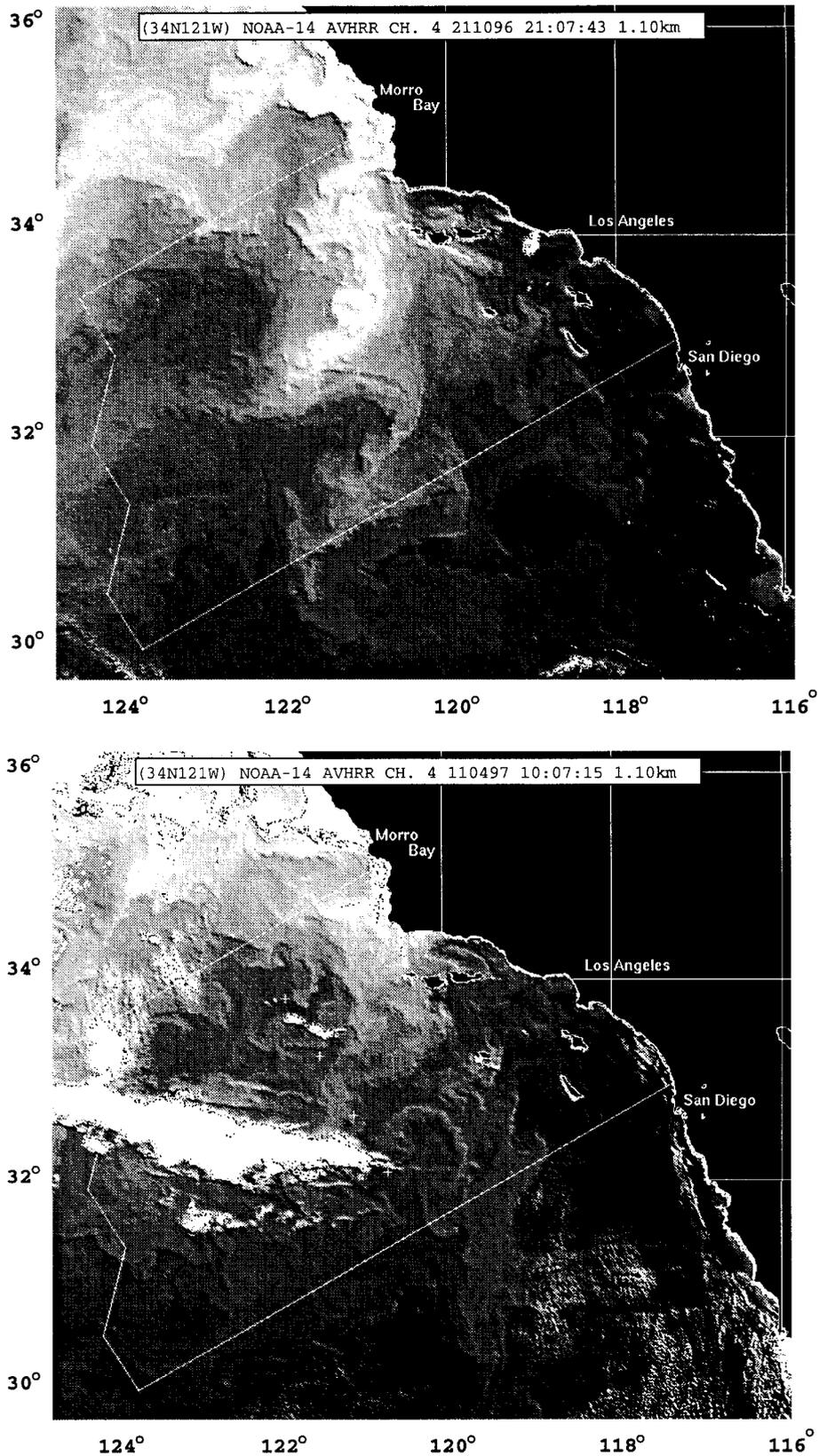
Figure 13. AVHRR channel 4 radiometric temperature from NOAA-14 polar orbiter satellite for 2107 UTC 21 October 1996 (*top*) and 1007 UTC 11 April 1997 (*bottom*). *Dashed lines* show extent of CalCOFI survey. *Grey levels* represent relative temperature differences (lighter shades denote cooler SST) and are not quantitative. Data provided by CoastWatch West Coast Node.
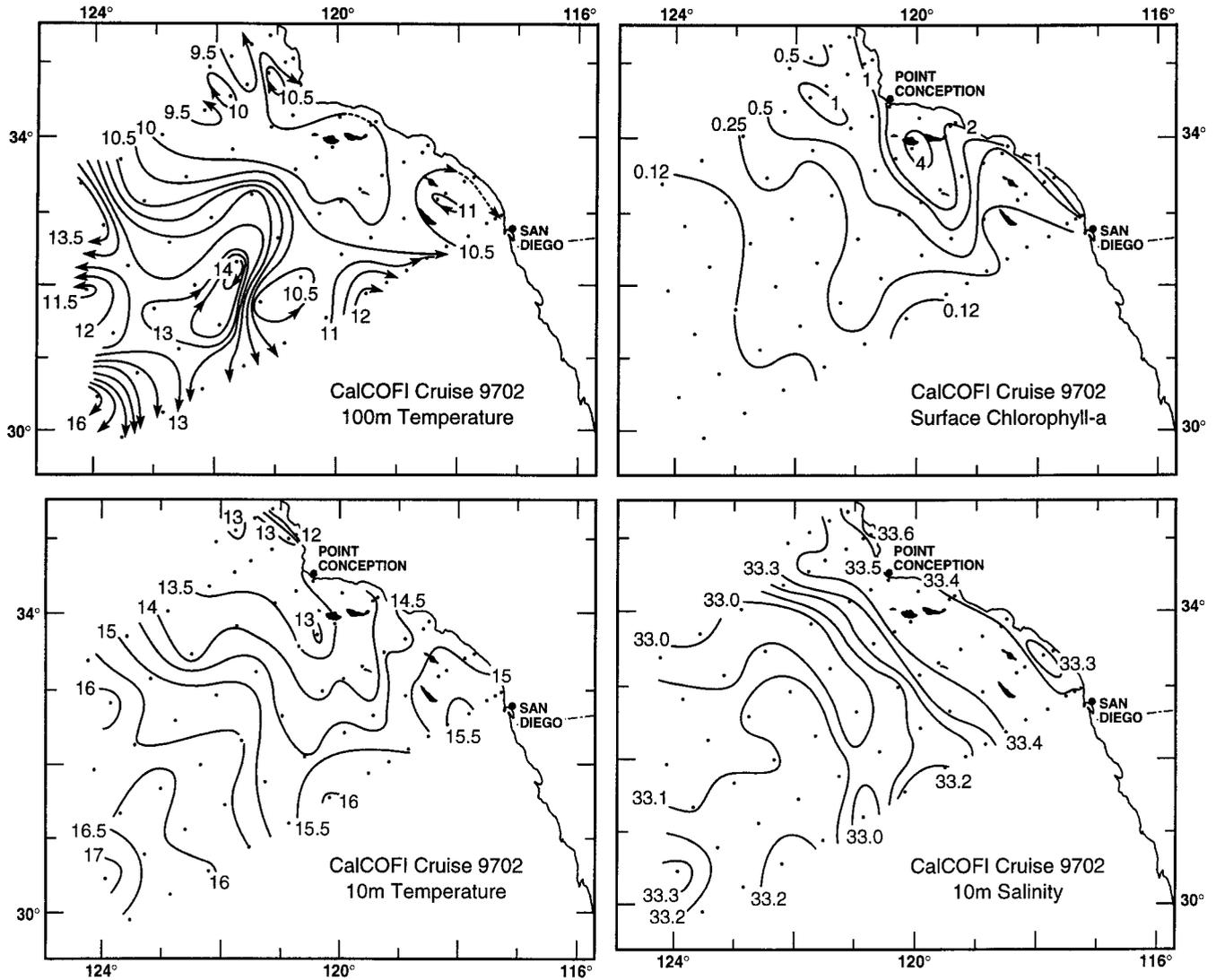
Figure 14. Spatial patterns for CalCOFI cruise 9702 (29 January–15 February 1997), including upper-ocean geostrophic flow estimated from the 100-m temperature, 10-m chlorophyll, 10-m temperature, and 10-m salinity.

Conception to San Diego, consistent with the reduced countercurrent.

9704 (2–20 April 1997). The data shown here are preliminary. The circulation pattern in April, inferred from the 100-m temperatures (figure 15), was anomalous in several respects. Poleward flow in the Southern California Bight was confirmed by ADCP data, which showed a northward coastal flow that appeared to be continuous around Point Conception (T. Chereskin, SIO, pers. comm.). The main flow of the California Current was strongly perturbed by mesoscale eddies and by a very sharp and unusual meander that brought the relatively warm (figure 10), low-salinity core of the current close to Point Conception. On the other hand, the main flow of the California Current was unusually far offshore in the southern part of the sample grid. Anomalously warm and saline water was seen in the Southern California

Bight region. This is consistent with the anomalously strong coastal countercurrent bringing in warmer and more saline water from the south, a relationship inferred in August and October 1996 as well. Unlike the October cruise, the circulation and thermal gradients observed during this cruise correspond less well to a midcruise AVHRR image (figure 13). The chlorophyll distribution during 9704 continued to be strongly influenced by the circulation pattern. Chlorophyll levels were again highest in the coastal region near the Channel Islands and Point Conception. The enriched area near Point Conception was compressed near the coast due to the inshore sweep of the California Current, but extended farther offshore and south of the Channel Islands because of the offshore meander of the current in that region. The 9704 pattern in the southern California region is not markedly different from the 9604 pattern.
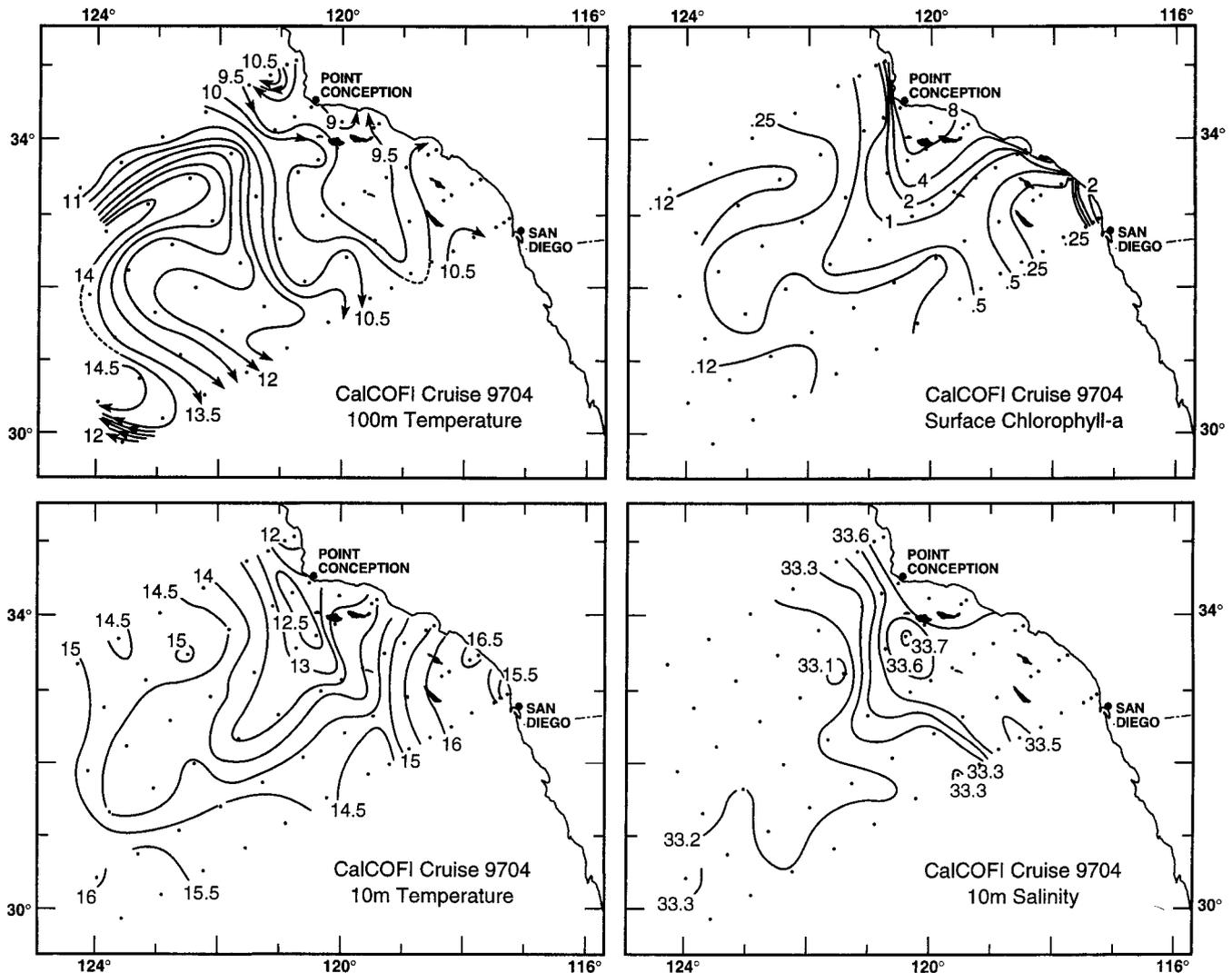
Figure 15.   Spatial patterns for CalCOFI cruise 9704 (2–20 April 1997), including upper-ocean flow field estimated from the 100-m temperature, 10-m chlorophyll, 10-m temperature, and 10-m salinity.

In addition to the quarterly CalCOFI cruises, several other notable oceanographic surveys were made in coastal waters south and north of the present CalCOFI region. Although these surveys were generally smaller in scale and confined closer to the coast, they do provide information about the spatial variability of patterns in the California Current.

D. Baja California Coastal Conditions

As part of a cooperative program to study the circulation variability on the Baja California continental shelf/ slope between Tijuana and San Quintín, the Estación de Investigación Oceanográfica de Ensenada of the Mexican navy (EIOE/SM) and the Instituto de Investigaciones Oceanológicas of the Universidad Autónoma de Baja California (IIO/UABC) initiated a series of oceanographic cruises in 1995. To date, three cruises

have been made; preliminary results from the October 1995 and June 1996 cruises are presented here. The coastal surveys off Baja California indicate that the circulation pattern was similar to the long-term mean.

Cruise 1095 (23 October–2 November 1995).   The lowest 0/500-db dynamic height anomalies during cruise 1095 (94 dyn. cm) are found near the coast (figure 16). The horizontal pattern of this field suggests an anticyclonic gyre off Punta Colnett and Cabo San Quintín (ca. 30.5°N) associated with a density anomaly of 23.75 kg/m^3 and a salinity of 33.35 ppt. There is a tendency for weak disorganized flow toward the south. According to Lynn and Simpson (1987), the strongest equatorward surface flow off Baja California typically appears in spring and summer, whereas the poleward surface coastal countercurrent and undercurrent both peak in fall and winter. The 200/500-db picture for October 1995 indeed
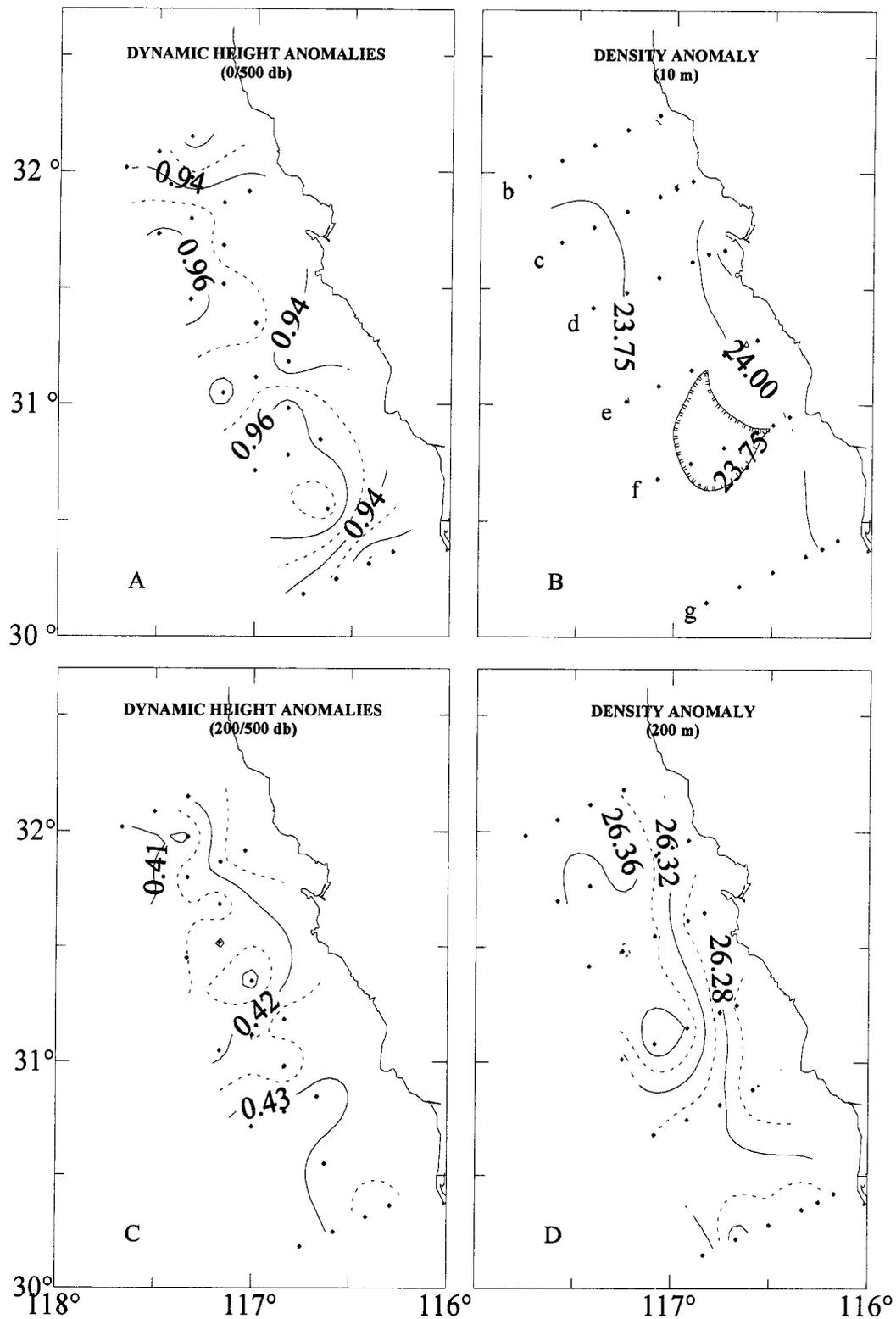
CRUISE 1095

Figure 16.   Spatial patterns for cruise 1095 (23 October–2 November 1995) off Baja California, including (A) upper-ocean geostrophic flow estimated from 0 over 500-db dynamic height anomalies, (B) 10-m density anomaly, (C) ocean geostrophic flow estimated from 200 over 500-db dynamic height anomalies, and (D) 200-m density anomaly.
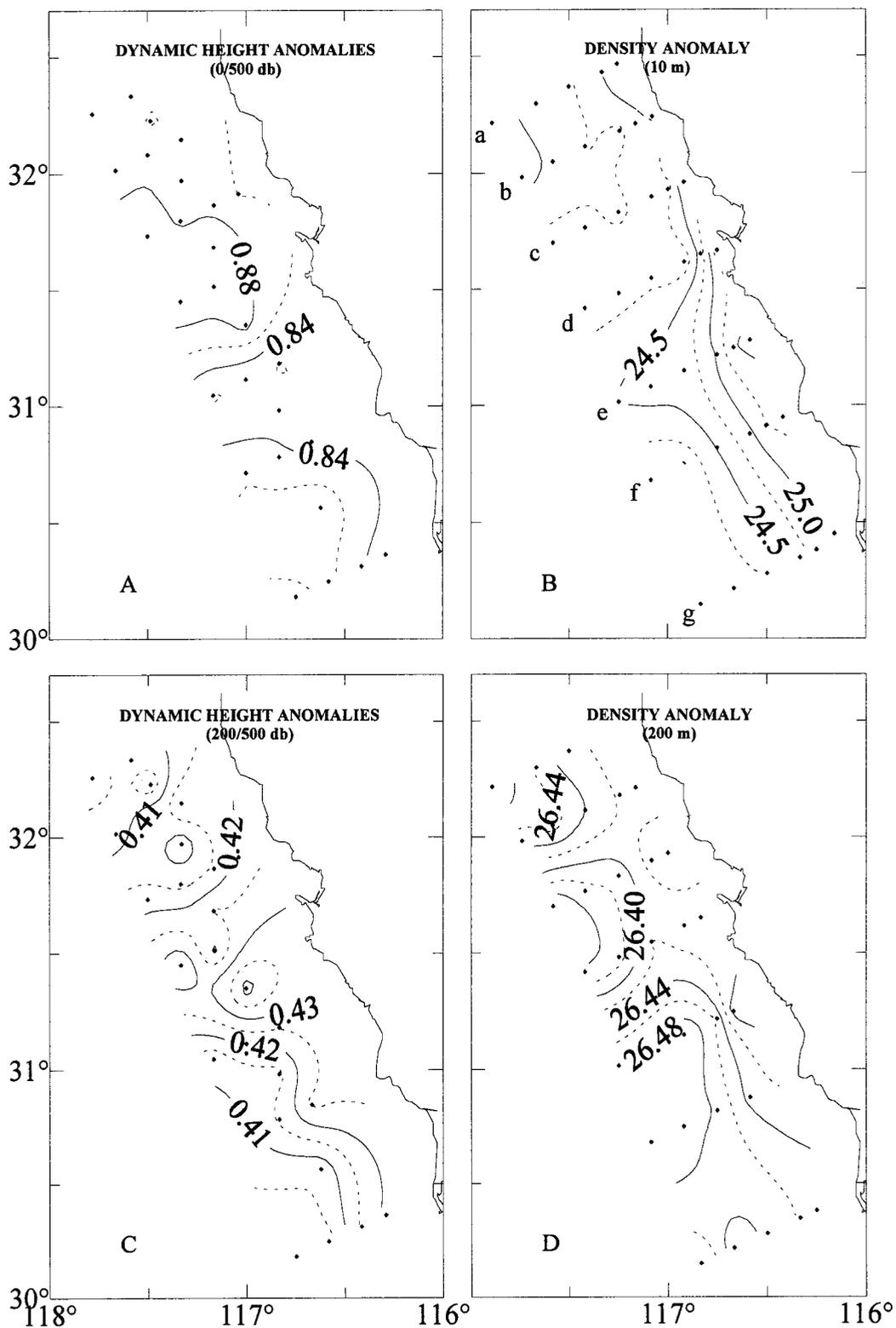
CRUISE 0696

Figure 17.   Spatial patterns for cruise 0696 (11–22 June 1996) off Baja California, including (A) upper-ocean geostrophic flow estimated from 0 over 500-db dynamic height anomalies, (B) 10-m density anomaly, (C) ocean geostrophic flow estimated from 200 over 500-db dynamic height anomalies, and (D) 200-m density anomaly.

shows a more organized pattern than the surface field, in spite of the weaker subsurface velocities. Dynamic heights are similar to those during CalCOFI Cruise 9510 (Hayward et al. 1996), and are comparable to the long-term mean pattern, with the same anticyclonic gyre and meandering trend. Vertical sections of geostrophic velocity show cores of northward velocity in the upper layer, particularly in the northern portion of the survey where the maximum value was about 10 cm sec^{-1}. Southward currents of 20 cm sec^{-1} were observed along line E (off Punta Cabras, ca. 31.2°N). The undercurrent could be observed in all lines, with geostrophic velocities reaching 10 cm sec^{-1}.

Cruise 0696 (11–22 June 1996). A southward flow was observed during cruise 0696 (figure 17), still disorganized but less so than during the 1095 cruise. The cross-shelf gradient was also larger (4 dyn. cm), indicating a stronger flow than in October. The apparent anticyclonic gyre during the 1095 cruise was not resolved with the June survey. The uplifting of isotherms and isohalines toward the coast in the upper 100 m was seen more clearly on the lines south of Ensenada (31.8°N). This area of upwelling can be contrasted with conditions in the northern portion of the survey in the 10-m isopycnal field. The 200/500-db dynamic height anomalies for this cruise show a pattern similar to those during the 1095 cruise. The range of values is the same, but the June field is a little more organized. Differences in the two cruises are better seen in the density fields, particularly north of 31°N. Differences in stratification are the result of higher salinities; temperatures did not change much. Vertical sections of geostrophic velocity show a better-developed undercurrent in the southern lines, reaching 10 cm sec^{-1} over the slope. A nearshore southward flow in the upper layer, with a maximum of 25 cm sec^{-1} in lines B and C, decreased to 10 cm sec^{-1} in the southern lines. While a salinity minimum indicative of the core of the California Current was not observed in the June cruise, a subsurface salinity maximum of 34.4 ppt was noted in lines E–G, the result of the better-organized countercurrent flow. This was not seen in October.

E. Central California Conditions

March–April 1996. An ADCP and CTD survey of the coastal current regime from San Diego to Point Sur was made by RV *David Starr Jordan* from 19 October to 7 November 1995 and repeated from 22 March to 7 April 1996 (data courtesy Ron Lynn, NOAA NMFS, La Jolla, and Terri Chereskin, SIO). The survey was designed to cross the basins and channels of the Southern California Bight and examine a series of better-resolved lines along the central California coast than is provided by the CalCOFI station grid. The area of coverage and the
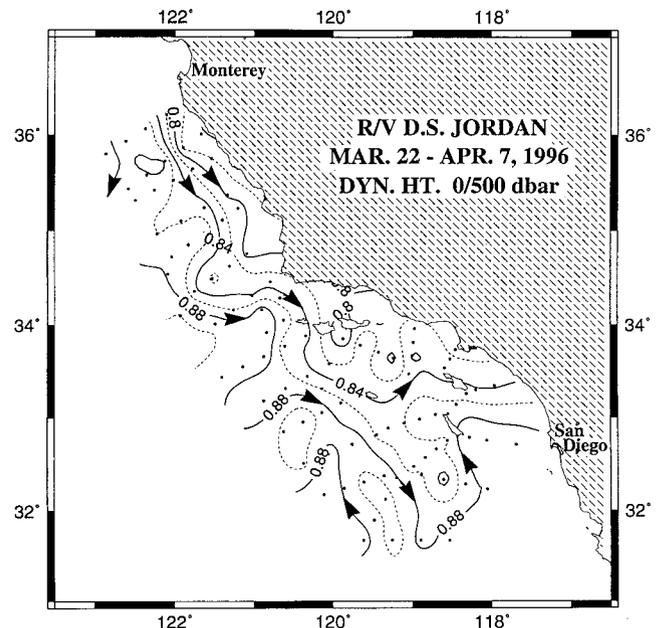

Figure 18. Upper-ocean geostrophic flow off southern and central California estimated from 0 over 500-db dynamic height anomalies for 22 March–7 April 1996.

geostrophic flow pattern for March–April are shown in figure 18. The field shows a flow meandering southward through a region of high mesoscale activity, similar in pattern and magnitude to the April–May 1996 CalCOFI cruise and the long-term mean (Lynn et al. 1982). One temporal difference was the stronger coastal counter-current noted near the Channel Islands during 9604, which was absent when this survey occupied the same area earlier.

May–June 1996. The region between Monterey Bay and Bodega Bay was surveyed three times from 18 May to 19 June 1996, as part of the SWFSC Tiburon Laboratory's annual surveys of pelagic young-of-the-year rockfish on RV *David Starr Jordan*, begun in 1983 (data courtesy Stephen Ralston, Tiburon Groundfish Analysis Task). Researchers conducted midwater trawls, CTD casts, and ADCP profiling during the survey. The May–June survey was repeated in 1997. The Tiburon Laboratory also surveyed in the Gulf of the Farallones in June and September 1996, as part of a program to monitor how dredge spoil disposal affects marine organisms.

Conditions off central California during May–June 1996 were cooler and more saline than average (Lynn et al. 1982), and suggest the greatest coastal upwelling rates since 1991. Upper-layer temperatures were 9°–10°C, 2°–4° cooler than during the same period in 1992. Near-surface salinities exceeded 34.0 ppt in upwelling centers. Wind and CTD observations indicate that upwelling also increased over the course of the survey's three sweeps. As in May–June 1995 and March–April 1996, high levels of winter precipitation led to considerable freshwater
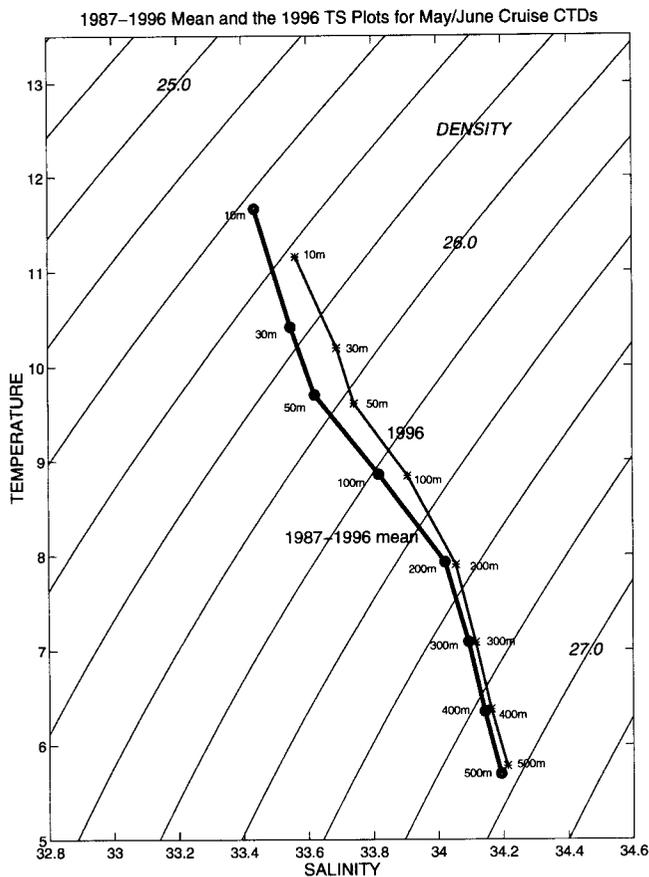
1987-1996 Mean and the 1996 TS Plots for May/June Cruise CTDs

Figure 19. Relationship of mean CTD temperature and salinity from May–June 1996 survey off central California. *Asterisks* connected by *thin line* are 1996 mean values at 10, 30, 50, 100, 200, 300, 400, and 500 m. *Solid dots* connected by *bold line* are mean of all CTD casts from 1987–96 cruises. Position of 1996 values to the right of long-term means shows that water in 1996 was relatively warm and saline on density surfaces.

input from the San Francisco Bay system; salinities of 32.5–33.0 ppt were found confined to the upper 10 m seaward of the Golden Gate. Water below the mixed layer was warmer and more saline in 1996 than in the past several years (figure 19), which suggests that the region contained a lower percentage of subarctic water. Midlevel water during the 1992–94 El Niño was cooler and fresher than average, which is attributed to an on-shore displacement of the core of the California Current during the event.

No unusual circulation features were evident off central California; geostrophic currents were very similar to those in previous years. The strongest feature in the geostrophic flow was an upwelling jet off Point Reyes that meandered generally southward during all three sweeps, although the magnitude of the current was much weaker than in 1995. A second relatively strong flow was an anticyclonic circulation associated with a recurring warm surface feature west of Monterey Bay (Rosenfeld et al. 1994). The 0/500-db dynamic heights continued to be depressed by 10 dyn. cm and more relative to those

during the recent El Niño and were typically 2–5 dyn. cm lower than in 1995. Although the 200/500-db heights were very similar to those in the previous year, the dynamic signature of the undercurrent off Monterey Bay in 1996 was noticeably stronger.

Farther south, off Big Sur, ocean conditions have been less well studied. This region was surveyed during 3–6 June 1996 as part of a multidisciplinary effort to describe the benthic fish habitat and ocean circulation near the Big Creek Ecological Reserve (Rago et al. 1997; Yoklavich et al. 1997; data courtesy Mary Yoklavich, NOAA NMFS PFEL). In a response to upwelling-favorable winds (figure 5), strong offshore jets with maximum speeds of nearly 40 cm sec^{-1}, extending to 100 m and greater, were observed in association with Point Sur and Lopez Point. Water on the southern side of these jets featured the lowest temperatures and highest salinities in the survey. Unlike the traditional view of a southward flowing California Current during this time of year, a coherent 10-to-20-km-wide poleward coastal current (10–15 cm sec^{-1}) was noted along the entire Big Sur coast from the surface to 200 m. This coastal flow coincided with a region of warm, saline water in the upper 50 m, implying a more southerly source. In the seaward portion of the survey, cool and less saline water consistent with the character of California Current water flowed south. These water types were separated by northward-moving water that appeared to have been recently upwelled. A similar region of coherent poleward coastal flow was noted in the summers of 1981 and 1984 (Chelton et al. 1988) and in October 1995 (Rago and Collins 1995). The results from this survey suggest an intriguing conceptual model of circulation, with a persistent poleward coastal flow and a series of recirculating cyclonic cells that move water and material offshore and return to the coast. Future surveys of this area will, we hope, test this model.

January 1997. During the late fall and early winter of 1996–97, an unusually large number of strong storms passed over the northeast Pacific. These storms produced strong poleward (downwelling-favorable) surface winds, along with heavy rain and snowfall that caused flooding from Washington south to central California. In California, the heaviest flooding occurred in December and January. A cruise was conducted by the Naval Postgraduate School during 22–29 January 1997 to assess the effects of flood waters leaving San Francisco Bay (data courtesy Curt Collins, Naval Postgraduate School, Monterey, CA). Observations showed a distinct cold, fresh plume extending from the Golden Gate and flowing into the northern portion of the Gulf of the Farallones. ADCP measurements indicated that the plume, which was confined to the upper 10 m of the water column, was advected northward along the coast at about 25 cm sec^{-1}. The minimum surface salinity
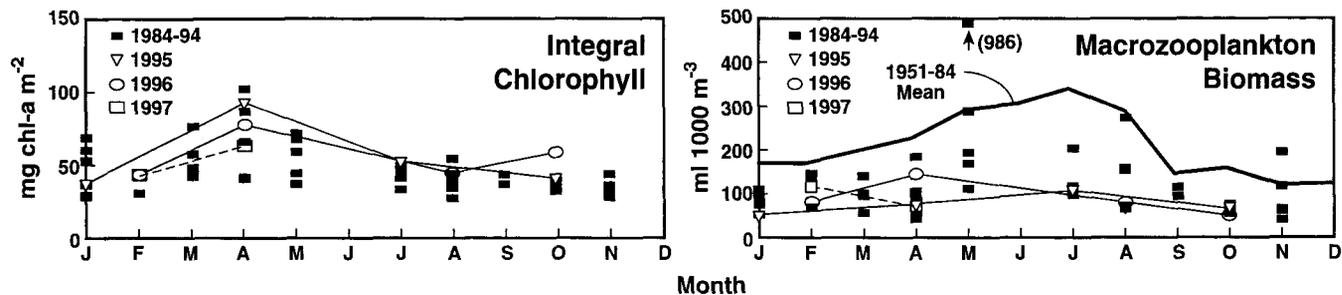
CalCOFI Cruise Means (1984-1997)

Figure 20. Cruise means of vertically integrated chlorophyll and macrozooplankton biomass plotted versus the month of CalCOFI cruises from 1984 to 1997. Each point represents the mean of all measurements on a cruise (normally 66). The *solid squares* show the cruises that took place from 1984 to 1994. The *open symbols* are cruises from 1995 to 1997; cruises from individual years are connected with lines. The *bold line* in macrozooplankton biomass indicates the monthly means for 1951–84.

observed at Point Reyes was 29 ppt. Anomalously high sea levels, reflected in San Francisco sea level (figure 8), characterized the region during this time (U. Hawaii Sea Level Center, unpubl. data).

4. BIOLOGICAL RESULTS

A. Biological Structure of the CalCOFI Region

The integral chlorophyll cruise means show that 9610 was anomalously high for fall (figure 20). This was probably the main surprise of the cruises. The first two cruises of 1997 continue the trend since 1995 of being within the range of, if not high relative to, integrated measurements made since 1984. Macrozooplankton biomass cruise means through 9704 continued the recent trend of being low both in the context of values prior to the mid-1970s (Roemmich and McGowan 1995) and relative to the past decade. This decline is continuing despite the fact that chlorophyll, and implicitly primary production (Mantyla et al. 1995), has been relatively high in the past few years compared to levels of the past decade.

Extensive red tide events were observed from San Diego to Monterey in early 1995 (Hayward et al. 1995) and from La Jolla south to Todos Santos Bay in April 1996 (G. Hemingway, pers. comm.). A dense red tide of *Lingulodinium polyedrum* (=*Gonyaulax polyedra*) was visible in the nearshore waters of the Southern California Bight from mid-March to mid-April 1997. This bloom began in December 1996, when elevated concentrations of this and other dinoflagellate species were observed near the coast. The densest cell concentrations were slow in developing, and did not appear to be correlated with rain or freshwater runoff. Indeed, the relatively strong winds that occurred during its development (figure 4) made this red tide all the more surprising, since red tide dinoflagellates are known to be sensitive to turbulence (Thomas and Gibson 1990). It is possible that dinoflagellates were exploiting recently upwelled nutrients,

although diatoms tend to dominate in upwelling assemblages. The bloom eventually dissipated in late April, although recurrences of red water were seen until late May. The cause of the bloom's decline is not known, although it did not appear to be related to meteorological forcing or grazing by other protists (e.g., *Noctiluca scintillans*). The bloom was quite patchy along the coast, and was recorded from the Mexican border to north of Los Angeles. The bioluminescence was spectacular, and chlorophyll concentrations reached nearly 100 mg m^{-3} in the dense red water.

B. Biological Conditions off Central California

Primary production. The annual pattern of primary production in Monterey Bay has been measured as part of the Monterey Bay Aquarium Research Institute's monitoring program. Time series of integrated chlorophyll and primary production for 1994–96, measured by ^{14}C uptake with methods described in Chavez et al. 1990, show a strong seasonality (figure 21).

The seasonal cycle in Monterey Bay during 1996 was similar in amplitude and phase to previous years. The 1994–96 period was relatively normal with respect to coastal upwelling and primary production. Anomalously high chlorophyll levels were observed in winter 1995–96. Primary production during this time was also higher compared to seasonal means but, because of lower seasonal light levels, was not as evident as the chlorophyll signal. Maximum values occurred in spring and summer 1996 following the initial spring bloom, although levels dropped off during the time of maximum upwelling (figure 4). Chlorophyll concentrations and primary production fell to their winter minima in late 1996 (figure 21).

Early measurements in 1997 suggest that this year should also be highly productive. A March 1997 cruise found levels of nutrients and phytoplankton in the Monterey Bay area elevated as far as 250 km from shore. By June 1997, conditions had changed significantly, with
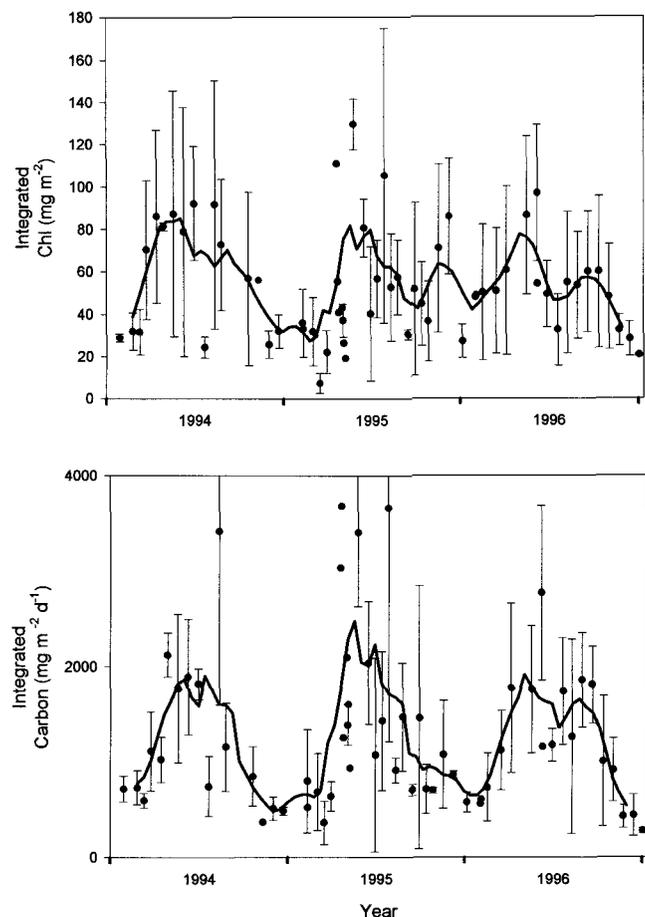
Figure 21. Integrated chlorophyll (top) and primary production (bottom) in Monterey Bay from 1994 to 1996 measured by ^{14}C uptake. Means and standard errors of two to five daily measurements are shown by *filled circles* and *error bars*. The *heavy line* represents a five-point running mean of the data interpolated to biweekly intervals.

the area of enhanced production having retreated to within 50 km of the coast. These differences can most likely be attributed to dramatically reduced coastal upwelling, which brought very warm water closer to the coast, possibly combined with the initial signature of the 1997 El Niño off central California.

Juvenile rockfish. Annual abundance indices of pelagic young-of-the-year rockfish (*Sebastes* spp.) off central California were estimated from trawls collected during the Tiburon Laboratory surveys described in section 3E (see Adams 1995 for methods). Indices were very low in 1996, continuing a trend of declining catch rates since 1994 (figure 22). The catch rate of *S. jordani* (the most common species collected) was slightly higher in 1996 than in 1995, but abundances of many rockfish species were the lowest observed in the 11 years of the surveys. In the past, poor recruitment (e.g., 1986 and 1992) has been associated with El Niño conditions. Such conditions occurred in the region in 1994 in association with the continuing El Niño, and the area experienced

El Niño–like conditions in 1995 and 1996 (figure 1), despite the presence of La Niña in the tropics. While northerly distributed species (e.g., *S. entomelas*, *S. flavidus*, and *S. pinniger*, figure 22, dotted lines), were quite abundant in 1991 (a year with colder than average temperatures and strong southerly transport via the California Current; Sakuma et al. 1995), their numbers have been substantially reduced since the 1992 El Niño. In contrast, relatively high abundances of southerly distributed species (e.g., *S. goodei*, *S. jordani*, and *S. saxicola*; figure 22, solid lines) were observed in the relatively warm 1993. Even so, catches of these southerly species have been substantially lower since 1994. The numbers of invertebrates and other fish species in the 1996 trawls were also relatively low.

Seabirds. Since 1994, several avifauna species have been observed off California that have not previously been reported here, even though search effort by ornithologists has remained largely constant for the past 10–15 years (see Ainley 1976 and Briggs et al. 1987).

The dark-rumped petrel (*Pterodroma phaeopygia*) breeds in the Galápagos Islands and is common and widespread at sea in the eastern tropical Pacific (ETP; Spear et al. 1995), rarely moving as far north as the subtropical waters west of the California Current (Pyle et al. 1993). Yet at least one dark-rumped petrel has been seen annually since 1994 in the pelagic waters just off the shelf break of central and southern California. During 1996, when five individuals were observed in the California Current, two other species also found normally in the ETP—the Parkinson's petrel (*Procellaria parkinsoni*) and the swallow-tailed gull (*Larus furcatus*), another Galápagos breeder—were sighted off central California. The only previous (unconfirmed) sighting of swallow-tailed gull was made in Monterey Bay 20 years ago (S. Terrill, H. T. Harvey & Assoc., Alviso CA, pers. comm.).

Seabirds in the ETP move their locations at sea in concert with shifts in the boundaries of current systems and water types, especially as forced by El Niño or La Niña (Ribic et al. 1992). Movements within the California Current in response to shifts in oceanographic climate are also well known (Ainley 1976). The warm temperatures of the California Current and temperate eastern Pacific during the past several months (figure 1) may be partly responsible for these changes in avifauna.

5. DISCUSSION

Many factors operating on a variety of time and space scales affect the California Current system. A wide range of atmospheric forces appears to produce a complex set of physical responses and even more complicated biological responses. Thus it is difficult to develop a single model that can describe the system's dynamics under all conditions. It can also be difficult to clearly identify
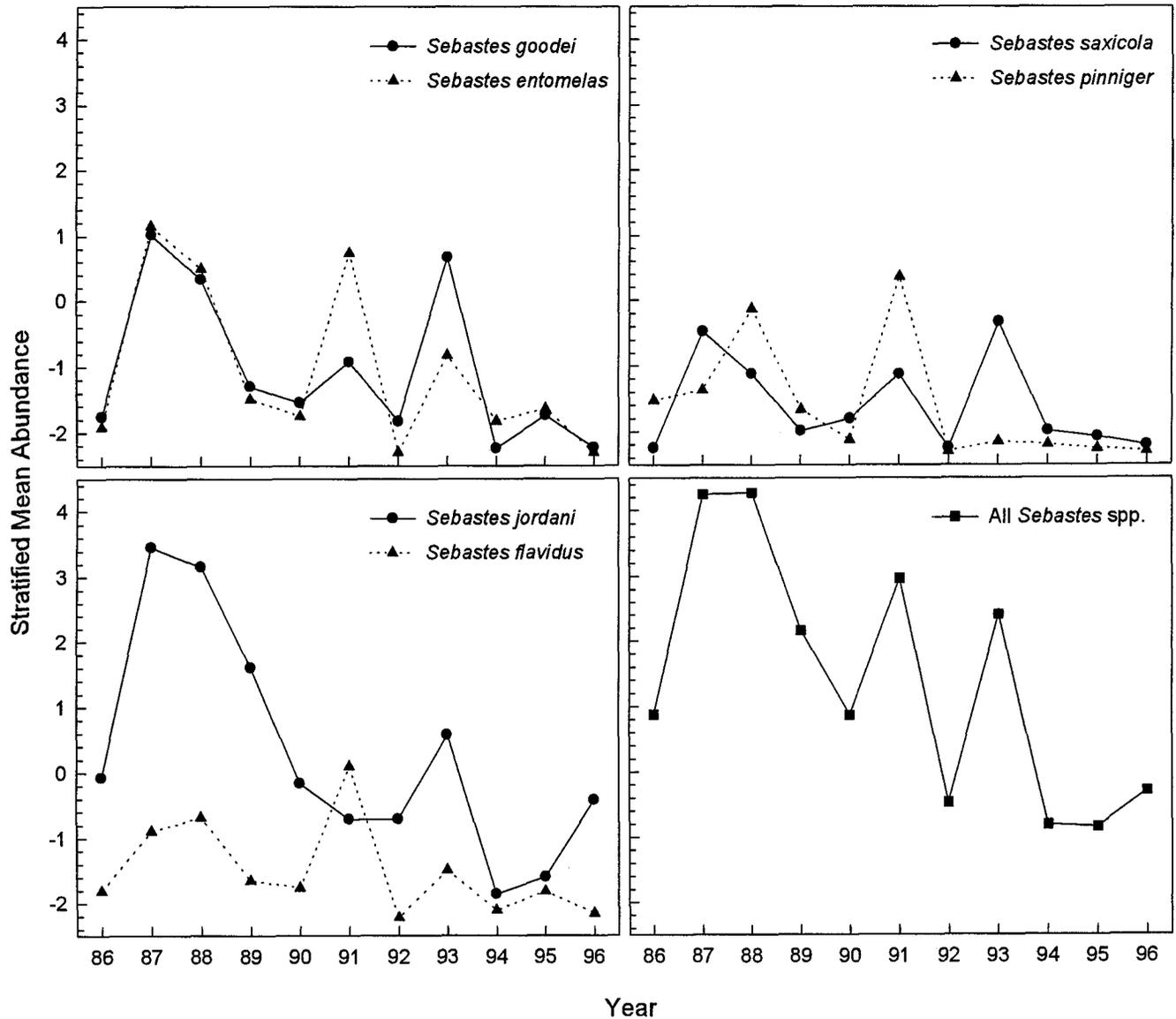
Figure 22. Annual abundance estimates of pelagic young-of-the-year rockfish, *Sebastes* spp., off central California for 1986–96, including individual estimates for three southerly distributed species (*solid lines with circles*) and three northerly distributed species (*dotted lines with triangles*). Abundances were adjusted according to Adams (1995) to account for interannual differences in size structure, and log-transformed by $\log_e (x + 0.1)$, where x is the length-adjusted catch.

the major signals within the system. This is partly due to a relative scarcity of data. Despite the large number of surveys in the CalCOFI time series, the number of observations is still quite small, given the complexity of the system being sampled. This makes it difficult, in a system with strong spatial and temporal variability, to calculate meaningful averages. This difficulty, in turn, makes it hard to identify anomalous conditions, since their calculation is based on the averages. These problems are increased when researchers use different data sets, since each set tends to have its own reference periods and sampling methods. Despite these difficulties, we have

taken the liberty of speculating on some of the more intriguing results presented here, in part to stimulate the reader to develop better ways of defining environmental variability and its relation to ecosystem elements.

Many variations in coastal parameters may be well explained by fluctuations in local atmospheric and oceanic conditions. But local factors clearly do not tell the whole story. Both large-scale and local dynamical processes contribute to variations in SST, sea level, currents, and other fields in the California Current region. For example, coastal upwelling, geostrophic adjustments in the coastal countercurrent and California Current, changes in wind

forcing over the central north Pacific, and equatorial El Niño and La Niña processes can all force large changes in coastal sea level and currents. However, since these processes operate at different space and time scales, it can be difficult to disentangle their coastal effects.

La Niña conditions in the tropical Pacific from late 1995 through early 1997 seem to have significantly affected the extratropical north Pacific (figure 1). Several tropical features of this La Niña event differed from those of a typical La Niña. These differences appear to have contributed to the formation of extratropical anomalies that were uncharacteristic for La Niña, most notably a large area of unusually warm SST that extended across much of the northeast Pacific. Again we emphasize that the warm SSTs off our coast at this time (June 1997) continue a pattern established and maintained by this unusual La Niña, and do not yet reflect an extratropical signal of the developing El Niño. The anomalous extratropical atmospheric processes helped produce unusually warm waters in the California Current region, although this coastal effect has been reduced somewhat since mid-1996 by higher than normal coastal upwelling along much of California.

Many of the observations in the California Current region during late 1996 and early 1997 were fairly close to the seasonal norms. This may have been partly because La Niña conditions in the tropical Pacific were weak or absent during this period. But significant anomalies may be expected in the region during 1997 and 1998, if the emerging El Niño event is maintained or strengthened. Since late 1996, two Kelvin waves have developed and propagated eastward across the equatorial Pacific, in association with the emergence of El Niño (figure 3). The downwelling phase of the first wave reached the west coast of South America in March 1997, and may have continued traveling poleward along the west coast of the Americas, arriving off southern California sometime in April. This may have contributed to the increase in sea-level anomalies at San Diego in March and the strong coastal countercurrent observed in the bight during April 1997. However, coastal Kelvin waves can be created by more local processes (e.g., extratropical coastal storms), so a careful analysis of the source of such anomalies is needed.

The circulation of the California Current appeared to switch in early 1996 to a pattern of relatively high mesoscale activity that has continued through the most recent cruises. Mesoscale features in the current were not geographically fixed during the 1996–97 cruises, although a strong onshore meander toward Point Conception was noted in three surveys (9608, 9610, 9704). But it is difficult to compare this mesoscale activity to the region's long-term circulation, and to know if this activity represents a shift to a new state. Over this same period, salin-

ities in the core of the current were clearly lower than in the climatologies for the region. There were also periods (August, October 1996, April 1997) in which a strong coastal countercurrent was associated with warm, saline water near the coast that was also low in chlorophyll. The countercurrent appears to have been an important mechanism for bringing more subtropical water into the Southern California Bight.

The high chlorophyll levels in the bight during October 1996 were not clearly related to the shore station data or to the general pattern of circulation. Coastal sea level and temperature were near seasonal norms at that time. Buoy winds in the bight showed no strong wind events, although the conditions at the Santa Maria buoy suggested a period of elevated upwelling north of Point Conception in October (figures 5, 6), in agreement with the upwelling index (figure 4). The circulation pattern was typical of the long-term mean, with a strong superimposed mesoscale eddy field. The mesoscale field has often been this strong before, but without elevated levels of chlorophyll. The spatial pattern of chlorophyll was strongly related to the circulation pattern and presumably the nutrient distribution, with the nutricline probably shallower than normal in the northern part of the grid. Much of the area of high chlorophyll is often found well offshore of the wind-driven coastal upwelling region, and in association with isopycnal shoaling along the inner edge of the California Current as it meanders into the CalCOFI region.

Although chlorophyll estimates are good indicators of primary production (Mantyla et al. 1995), chlorophyll is not a good predictor of higher trophic production in the California Current ecosystem. Despite the relatively high levels of phytoplankton production on some cruises, particularly during October 1996, the biomass at higher trophic levels appears to have been low compared to historical observations. Macrozooplankton biomass remains depressed in comparison to recent historical levels. The abundance of juvenile rockfish off central California has been at a low for the past decade. It also appears that decreases in plankton-feeding seabird species reported recently by Ainley et al. (1995) and Veit et al. (1997) continued during 1995–97 (Spear and Ainley, unpubl. data). Decreases are consistent with the decline in zooplankton reported by Roemmich and McGowan (1995) and with the aforementioned decreases in juvenile rockfish. The issue of why zooplankton, fish, and bird populations have been reduced for the past several years remains a pressing question in this system.

As part of the California Department of Fish and Game's Central California Marine Sport Fish Project-Refugia Study, scientists have been monitoring rockfish populations to determine the feasibility of marine reserves as a management tool (data courtesy David

VenTresca, CDFG, Monterey, CA). A statistically sig-
nificant relationship exists between the monthly up-
welling index at 36°N and the subsequent recruitment
of young-of-the-year blue rockfish (*Sebastes mystinus*)
in the Monterey Bay area (D. VenTresca, CDFG,
Monterey, CA, pers. comm.). Recruitment in Monterey
Bay was below normal in 1995, and very poor in 1996.
The March 1997 upwelling index (figure 4) indicates
that the 1997 recruitment of young-of-the-year blue
rockfish will be the highest since the exceptionally strong
1988 year class. In addition, recruitment of this fish in
1997 has been unusually early, possibly in conjunction
with the rather early transition to strong upwelling-
favorable conditions. Whether this early recruitment is
eventually reflected in other higher trophic level com-
ponents, or ultimately leads to a strong year class for
rockfish in general remains to be seen.

An encouraging note from the 1996–97 period was
the large number of projects that examined the oceanog-
raphy of various regions of the California Current. It is
critical that projects such as those off Baja California and
central California (described in previous sections) be
linked with the CalCOFI program to produce a result
that is greater than the sum of its parts. Independent
ocean data sets from different areas of the California
Current allow a better assessment of individual envi-
ronmental features and the processes that produce them.

The growing number of observations of the California
Current include a wide variety of data types and sources.
Researchers need to develop innovative ways to ana-
lyze and interpret the historical environmental data from
CalCOFI and the greater north Pacific region. One tech-
nological advance that has helped and will continue
to help is the increasing use of telecommunications and
the World Wide Web to make data more readily and
widely available. As mentioned in section 2, the CalCOFI
data are accessible on the Web, as are a growing num-
ber of other databases and products relevant to the
California Current.

We suggest a few ideas to encourage closer links be-
tween the area's numerous field research programs. First,
efforts should be made to standardize sampling methods
for basic physical and biological measurements, and to
attempt to include sampling of these basic variables on
all cruises. This may require the help of experts from
new disciplines on existing field research teams. If pos-
sible, cruise plans should include opportunities for adding
outside researchers to take samples that are part of the
standard set of critical measurements (e.g., chlorophyll
on fisheries surveys). Second, the Internet should be used
as an electronic bulletin board to post detailed cruise
plans so that independent but concurrent cruises can
be coordinated. Third, the California Current is highly
variable, and the most important results are often un-

expected. Chief scientists should communicate with sci-
entists of recently completed surveys regarding any un-
usual or anomalous findings, and cruise plans should
consider "adaptive sampling" strategies to further inves-
tigate these features. Finally, we encourage someone to
step forward to attempt a more complete assessment and
"model" of the California Current that incorporates var-
ious data sets such as those described here. This will re-
quire not only keen scientific insight but also the ability
to bring together a diverse group of researchers from a
wide variety of academic, government, and private in-
stitutions.

It is important for physical and biological oceanog-
raphers to continue working together; to join with sci-
entists in other disciplines to better understand long-term
(i.e., interannual to decadal) variability in the environ-
mental and biological components of the California
Current region; and to better describe how climate shifts
may affect the region and its living resources.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

Asilomar, California
October 30–31, 1996

THE 1996 HAKE SYMPOSIUM

Hake is one of the principal groundfishes of the world because of the large catch (the global take approaches 2 million tons annually); the high quality of the flesh, which is prized by the food-processing industry; and an apparent resistance to overfishing (Alheit and Pitcher 1995). Because of this global importance, our announcement of a CalCOFI symposium on hake drew a remarkable response. Participants came from Spain, Namibia, Norway, New Zealand, Mexico, and Canada, as well as from the east and west coasts of the United States. The symposium consisted of 6 poster presentations and 21 oral presentations, 11 of which appear as papers in this issue of *CalCOFI Reports*.

The idea of holding a CalCOFI symposium on the biology, ecology, and population dynamics of hake grew out of a plan we developed for a coastwide research program on Pacific hake, *Merluccius productus*. Our plan involved academic and fishery institutions extending from the Pacific Biological Station (Nanaimo, Canada) in the north to CICIMAR (La Paz, Mexico) in the south. The symposium documented the current involvement of many institutions in hake research, and indicated a great opportunity for integrating separate research areas into a comprehensive, basin-scale program on ocean forcing, productivity, and migration. Pacific hake are the largest (2–3 million tons) and most valuable fish population on the west coast of the conterminous United States.

The symposium clearly indicated that an integrated research program focusing on Pacific hake could yield practical methods for forecasting hake recruitment and migration and also would help clarify allocation issues between the United States and Canada. Areas likely to break new ground are studies of subsurface (50–100 m) zooplankton production systems (critical for larval hake); development of new biophysical models dealing with all life stages and changes in habitat boundaries; improved understanding of the euphausiid production systems along the West Coast (necessary for hake as well as many other species of fish and mammals); and a coor-

dinated coastwide (population-scale) approach to recruitment dynamics.

Our evening discussion session crystallized several research avenues. Long-term shifts in Pacific hake biomass could be manifested in two ways: (1) the frequency of strong year classes could be increased; or (2) strong year classes could continue at the same frequency, but the magnitude of the year class could be higher. Evidence suggests that both mechanisms may be influencing Pacific hake recruitment. The fact that strong year classes never occur during cool ocean conditions may limit the frequency of strong year classes during cool ocean regimes. The strongest year classes on record (1980 and 1984) occurred during the recent period of warm ocean conditions.

Distribution studies of Pacific hake revealed that larvae are distributed between 75 and 150 m below the surface, an environment where food is limited. The infrequent nature of strong year classes may be associated with occasional years of above average production in subsurface waters. Although Pacific hake spawn over a broad area, survivors may be concentrated in patches along the shelf break and slope. Thus the hake may have adopted a strategy of broadcast spawning to increase the probability that larvae will encounter a patch of suitable prey. Slow-growing larvae have lower rates of survival, and larval growth rates indicate marked interannual differences, which may be associated with the availability of prey patches. Strong year classes tend to be associated with accelerated growth rates. Recent analysis of hake juvenile and adult diets supports the hypothesis that cannibalism is an important element in the recruitment process. Migration studies presented during the symposium helped modify the existing conceptualization of Pacific hake migration and ontogeny. In recent years, one-year-olds have been captured off the coasts of Washington and Oregon. Studies of the spawning distribution suggest a stratification of fish by size-at-age. Research also showed that the center of spawning

concentration is influenced by subsurface temperature; the fish spawn farther south in cool years.

We thank the participants for their oral and written contributions. We thank George Hemingway, Diane Foster, and Mary Olivarria for help in coordinating the symposium; the many anonymous manuscript reviewers; and CalCOFI managing editor, Julie Olfe, for producing the symposium volume.

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John R. Hunter
Anne B. Hollowed

GEOGRAPHIC VARIATION IN THE DIET OF PACIFIC HAKE, WITH A NOTE ON CANNIBALISM

TROY W. BUCKLEY
University of Washington
School of Fisheries
Box 357980
Seattle, Washington 98195

PATRICIA A. LIVINGSTON
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way N.E., F\AKC2
Seattle, Washington 98115

ABSTRACT

We examined the stomach contents of Pacific hake collected from the Southern California Bight to Vancouver Island. Samples were taken during bottom trawl surveys in 1989, 1991, and 1992 and during a midwater trawl survey in 1995. We found increasing piscivory with size, and gross variation in the diet with latitude and season. Cannibalism by adults on juvenile (age 1 and young-of-the-year) Pacific hake was found in autumn 1992 south of Cape Mendocino. In summer 1995, we found adult cannibalism on juveniles (especially age 1) along the entire coast and cannibalism by age-1 on young-of-the-year Pacific hake between 33° and 36°N latitude. We discuss some of the implications of cannibalism by adjacent cohorts.

INTRODUCTION

Pacific hake (*Merluccius productus*), also known as Pacific whiting, is the largest single groundfish resource found off the U.S. Pacific coast (Dark and Wilkins 1994). Ecologically, Pacific hake is one of the most important fish species in the California Current ecosystem (Francis 1983; Livingston and Bailey 1985). Because of its large biomass, Pacific hake's predatory impact on some commercially important species can be extensive (Gotshall 1969; Francis 1983; Livingston and Bailey 1985; Rexstad and Pikitch 1986). Pacific hake preys on euphausiids, swimming crabs, pandalid shrimp, squid, schooling baitfish, and juvenile fishes, and is itself an important prey of birds, tunas, sharks, groundfish, and marine mammals (Best 1963; Livingston and Bailey 1985; Rexstad and Pikitch 1986).

Feeding habits of Pacific hake have been investigated because of their potential importance to other stocks (Livingston and Bailey 1985; Rexstad and Pikitch 1986). Quantitative assessments of the Pacific hake diet have been conducted off Vancouver Island, British Columbia (Outram and Haegele 1972; Livingston 1983; Tanasichuk et al. 1991); Washington and Oregon (Alton and Nelson 1970; Livingston 1983; Rexstad and Pikitch 1986; Brodeur et al. 1987); northern California (Gotshall 1969; Livingston 1983); and, for larvae only, southern California (Sumida and Moser 1980). The food habits of juvenile and adult Pacific hake off central and southern California have not been the object of any intensive study. However,

Best (1963) gives a list of common prey from observations in California waters, and Mearns et al. (1981) present the percent of total indices of relative importance (% IRI) for prey found in Pacific hake from the Southern California Bight.

Cannibalism by Pacific hake was noted only in the studies conducted in California waters (Best 1963; Mearns et al. 1981; 7.2% IRI). On the basis of migration patterns, overlapping distributions of large and small fish (a requisite for cannibalism) would be most likely off central and southern California, in late autumn, winter, and early spring (Francis 1983).

Our objectives were to (1) quantify the diet of Pacific hake, including samples from central and southern California, (2) examine variability in the diet by latitude, predator size, and season, and (3) describe the incidence of cannibalism in our samples and discuss some of its implications for determining year-class strength.

METHODS

Study Area

This study primarily encompasses the continental shelf and upper continental slope from Point Conception, California, to British Columbia. This broad latitudinal range extends over several statistical reporting areas of the International North Pacific Fisheries Commission (INPFC). These areas—Conception (U.S.–Mexico International Boundary to 36°00'N); Monterey (36°00' to 40°30'N); Eureka (40°30' to 43°00'N); Columbia (43°00' to 47°30'N); Vancouver (47°30' to 50°30'N); and Charlotte (50°30' to 54°30'N)—will frequently be referred to by name in this paper (figure 1).

Stomachs from Pacific hake were collected in these areas during three National Marine Fisheries Service bottom trawl surveys (figure 1). In 1989, the fifth triennial groundfish survey was conducted on the continental shelf (55–366 m, or 30–200 fm deep) from Point Conception, California, to central Vancouver Island, British Columbia (34°30' to 49°35'N) between July 7 and September 29 (Weinberg et al. 1994). From October 21 to November 18, 1991, a groundfish survey was conducted on the upper continental slope (550–732 m, or 300–400 fm deep) in the Columbia and Eureka statistical areas and on the shelf and slope (183–1,280 m, or
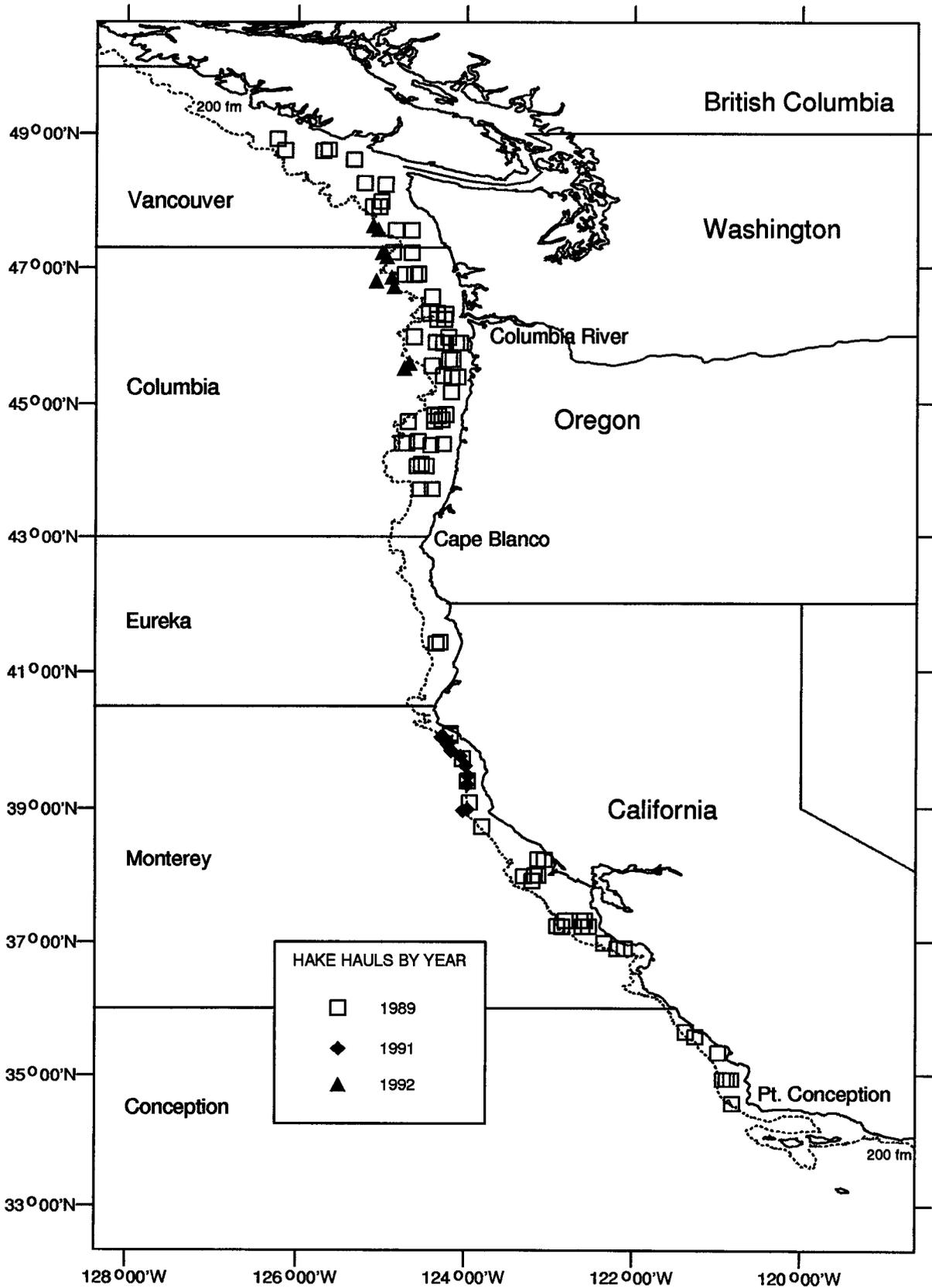
Figure 1.   Haul locations of the 1989, 1991, and 1992 bottom trawl surveys where Pacific hake stomachs were collected. The 200-fm isobath is shown with a *dotted line*.

100–700 fm) in the Monterey statistical area. From October 16 to November 13, 1992, a groundfish survey was conducted on the continental shelf and slope (183–1,280 m, or 100–700 fm) in parts of the Vancouver and Columbia statistical areas.

Samples were also collected during the 1995 echo-integration trawl survey. Midwater and bottom trawls were made from July 1 to September 1, extending along the Pacific coast from the Southern California Bight to Dixon Entrance, Alaska (32°30' to 54°30'N; Wilson and Guttormsen 1997). Although these samples were collected as part of a forthcoming detailed study of euphausiid predation by Pacific hake relative to euphausiid abundance, the cannibalism observed in these samples warranted inclusion in this study.

Sample Collection

The buccal cavities of individual fish were examined for signs of regurgitation or net-feeding before the stomachs were removed. Fish with everted stomachs or partially digested prey in the mouth or gills were discarded. Fish with completely undigested prey in the mouth or protruding from the esophagus were discarded. After opening the body cavity, we discarded fish if the stomach appeared partially everted or flaccid (evidence of recent regurgitation). If a sample was discarded because of evidence of regurgitation or net-feeding, we replaced it with an acceptable sample that contained food.

Stomachs that met these collection criteria, including empty or near-empty stomachs, were placed in a cloth bag with a specimen tag indicating the species, sex, and fork length (FL) of the fish, and also the vessel, survey, haul, and specimen numbers. A maximum of 15 stomachs, from fish representative of the size composition caught, were collected per haul in 1989, 1991, and 1992. In 1995, a maximum of 15 stomachs were collected per 10-cm size-interval per haul. Stomach samples were preserved in 10% formalin. In the laboratory, samples were rinsed in water for 24 hours, then stored in 70% ethanol.

Stomach Content Analysis

In the laboratory, stomach samples were rinsed with water, and the contents were removed, blotted, and weighed to the nearest one-hundredth of a gram (one-tenth of a gram for the 1989 samples). Prey were identified to the lowest practical taxon. Two procedures were used to determine the prey composition of the stomach contents. For the samples collected in 1991, 1992, and 1995, the weight and number of prey in every taxon were recorded. For the samples collected in 1989, only the fish and crab prey were counted and weighed, and the contribution of the remaining taxa to the stomach contents was estimated as a percentage of the total vol-

ume of the contents. Whenever possible, the standard length (SL) of fish prey was measured and recorded to the nearest millimeter. Some of the stomach contents were identified as offal (discarded parts from commercial fish-processing operations); these were treated as a single prey type.

Data Analysis

To examine the diet variation by latitude and survey, we calculated the diet composition, by weight, for broad prey categories in each INPFC area covered during the 1989, 1991, and 1992 surveys. To examine the diet variation by predator size, we combined the data from the Vancouver and Columbia areas (North of Cape Blanco) and the Eureka, Monterey, and Conception areas (South of Cape Blanco). We chose to combine the areas in this fashion because of the diet similarities between the Vancouver and Columbia areas, and because of the regional physical and biological processes (U.S. GLOBEC 1994). The diet data were aggregated into broad prey categories for each 10-cm predator-length group, and the diet composition was presented by weight. The percent frequency of occurrence of cannibalism was calculated for each sampled haul in the 1995 survey.

RESULTS

A total of 1,334 Pacific hake stomachs were examined from the bottom trawl surveys (table 1). Of the 1,096 stomachs collected in the summer of 1989, 100 (9%) were empty. Seven (5%) of the 138 stomachs collected in the autumn of 1991 were empty, and 26 (26%) of the 100 stomachs collected farther north in the autumn of 1992 were empty.

The diet, by weight, of the Pacific hake sampled in the summer of 1989 was generally dominated by fishes, but euphausiids, mostly *Euphausia pacifica* and *Thysanoessa*

TABLE 1
Size Ranges of Pacific Hake and Number of Stomachs Sampled from Bottom Trawls by Year, Season, and Location

| Year	Season	INPFC area	Size range (cm)	No. examined Non-empty	No. examined Empty
1989	Summer	Vancouver	25–70	155	19
		Columbia	34–75	539	32
		Eureka	42–51	23	7
		Monterey	23–70	203	36
		Conception	10–58	76	6
1991	Autumn	Monterey	18–60	131	7
1992	Autumn	Vancouver	42–51	26	4
		Columbia	35–59	48	22
1995	Summer	Charlotte	44–56	75	8
		Vancouver	18–73	422	72
		Columbia	21–76	532	36
		Eureka	20–65	122	29
		Monterey	23–73	162	52
		Conception	3–56	108	12
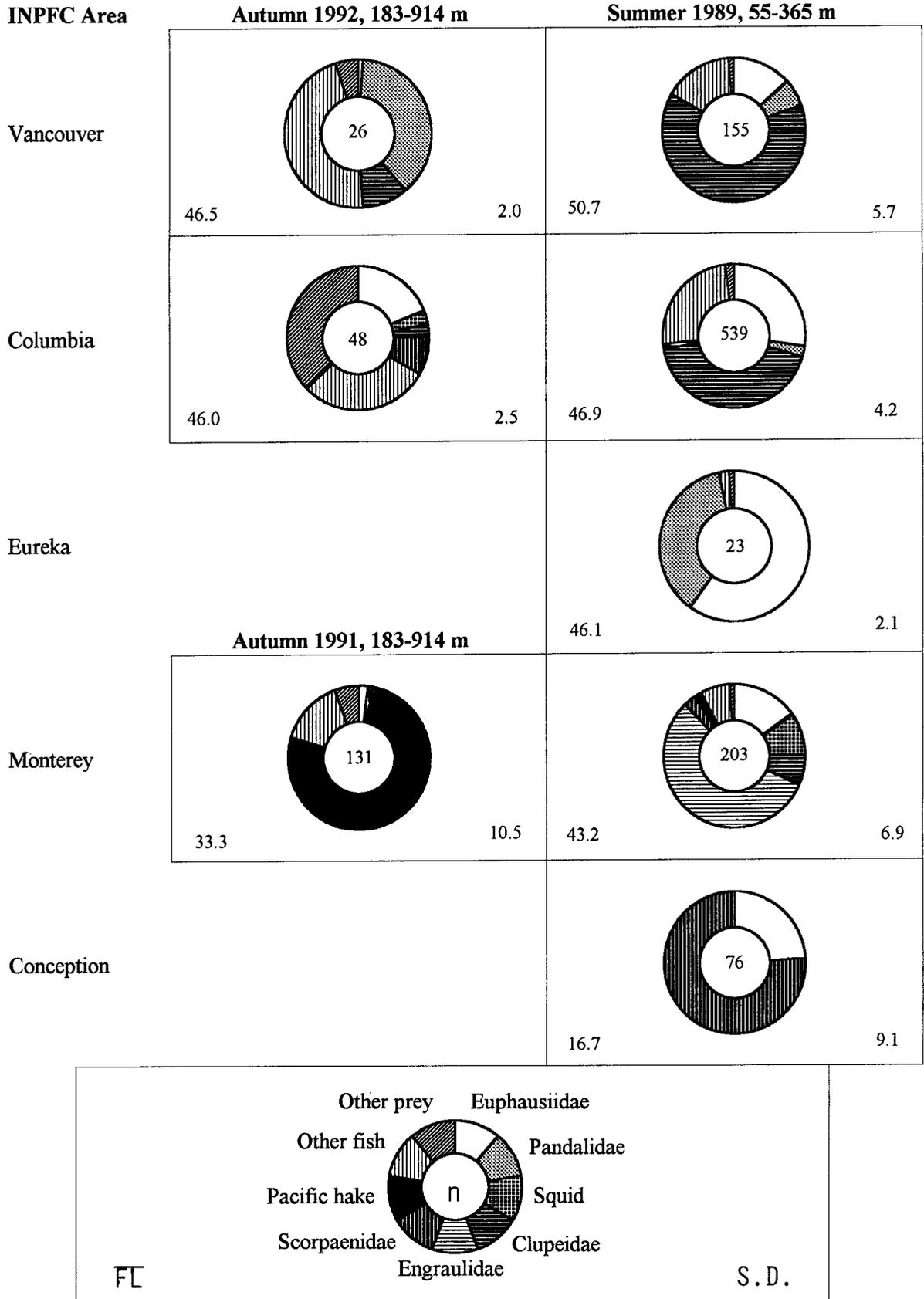
Figure 2.   Diet composition (by weight) of Pacific hake by survey and INPFC area. The number of non-empty stomachs is shown in the center of each ring. Mean of the fork lengths is shown on the lower left of each box, standard deviation on the lower right.

spinifera, consistently contributed to the diet in all areas (figure 2). In the Conception INPFC area, shortbelly (*Sebastes jordani*) and stripetail (*S. saxicola*) rockfishes (Scorpaenidae) were important prey. Shortbelly and stripe-tail rockfishes were also eaten in the Monterey INPFC area, but northern anchovy (*Engraulis mordax*; Engraulidae) dominated the diet. In the Eureka INPFC area, euphausiids and pink shrimp (*Pandalus jordani*; Pandalidae) constituted nearly the entire diet. Pacific herring (*Clupea pallasi*, Clupeidae) was the most important diet component by weight in the Columbia and Vancouver INPFC areas. The "Other fish" category comprised mostly smelts (Osmeridae), including eulachon (*Thaleichthys pacificus*) and whitebait smelt (*Allosmerus elongatus*), contributing 21% of the Pacific hake diet in the Columbia INPFC area and 10% in the Vancouver area.

A broad size range of Pacific hake co-occurred in the Monterey INPFC area in autumn 1991, and a high level of cannibalism was found (figure 2). Although two incidents of cannibalism were found in that area in summer 1989, the diet of Pacific hake in autumn 1991 differed considerably from the diet in summer 1989. We found the same pattern of diet differences when restricting the analysis to comparable bottom depths (183–365 m) in each survey.

The diet of Pacific hake in autumn 1992 appeared different from that in summer 1989 in the Columbia and Vancouver INPFC areas (figure 2). In the Columbia area, sergestid shrimp made up most of the "Other prey" category, contributing 32% to the diet by weight; and the bathypelagic lightfishes (Gonostomatidae) and lantern-fishes (Myctophidae) accounted for almost all of the "Other fish" by weight. Pacific saury (*Cololabis saira*), which are included in the "Other fish" category, and pink shrimp were very important in the Vancouver area.

Diet Variation with Predator Size

In the summer of 1989, euphausiids decreased in importance with increasing length of Pacific hake both north and south of Cape Blanco, and fishes increased (figure 3). As noted earlier, the fishes, by weight, were primarily Pacific herring north of Cape Blanco, and were mostly northern anchovy south of Cape Blanco. A similar pattern of increasing fish and decreasing euphausiid biomass in the diet was observed south of Cape Blanco in the Monterey area in autumn 1991. Cannibalism by larger Pacific hake was a main contributor to this pattern. The length frequency of the Pacific hake sampled north of Cape Blanco in autumn 1992 was too narrow to examine diet variability across a broad predator size range.

Cannibalism

In autumn 1991 a broad size range of Pacific hake co-occurred south of Cape Blanco in the Monterey INPFC

TABLE 2
Percent Frequency of Occurrence (% FO) and Percent Weight (% W) in the Diet of Cannibalized Pacific Hake for Two Predator Size Groups in Surveys Where Cannibalism Was Found

Year	Season	Latitudinal range (N)	Predator size (cm FL)	Cannibalism % FO	Cannibalism % W
1989	Summer	34°30'–49°35'	>40	<1	<1
			≤40	0	0
1991	Autumn	36°00'–40°30'	>40	39	84
			≤40	0	0
1995	Summer	32°30'–54°30'	>40	5	30
			≤40	4	3

area, and a high level of cannibalism was found (figure 2). Only larger Pacific hake (FL >40 cm) were cannibalistic (figure 3), and the frequency of occurrence of cannibalism was 39% for these larger fish (table 2). Many of the Pacific hake caught in the trawls were small juveniles, with modes at 18–19 and 23–29 cm FL, similar in length to the Pacific hake that were cannibalized. On the basis of growth rates of juvenile Pacific hake (Best 1963; Woodbury et al. 1995) the cannibalized hake are young-of-the-year (YOY) and small age-1 individuals. We found only two occurrences of cannibalism by large Pacific hake in the Monterey INPFC area during the summer of 1989.

Cannibalism was found in many locations during the summer 1995 echo-integration trawl survey (figure 4), and two types of interaction were typical (figure 5). The first common interaction was cannibalism by adult Pacific hake on fish with lengths typical of age-1 individuals. There was also a single occurrence of an adult cannibalizing three YOY Pacific hake (figure 4; 44°00'N latitude). Cannibalism by large Pacific hake (FL >40 cm) was found over a wide latitudinal range (figure 4); contributed 30% to the diet by weight; and occurred with a frequency of 5%. Although rates of cannibalism by smaller Pacific hake (FL ≤40 cm) were lower (table 2; 3% W and 4% FO) than those of larger individuals, the most common interaction among these smaller fish was between juvenile Pacific hake (23–32 cm FL; mostly age-1) and YOY individuals (30–70 mm SL; figure 5). In the Conception INPFC area, cannibalism by age-1 Pacific hake on YOY hake accounted for 14% of the diet by weight and occurred with a frequency of 18%. Cannibalism by age-1 Pacific hake was not found north of the Conception area. The number of YOY in the stomachs of age-1 Pacific hake ranged from one to five.

DISCUSSION

Although there is a considerable literature describing the food habits of Pacific hake, comparisons among the studies are difficult because of the many variables involved (year, season, area, and fish size; table 3). In our
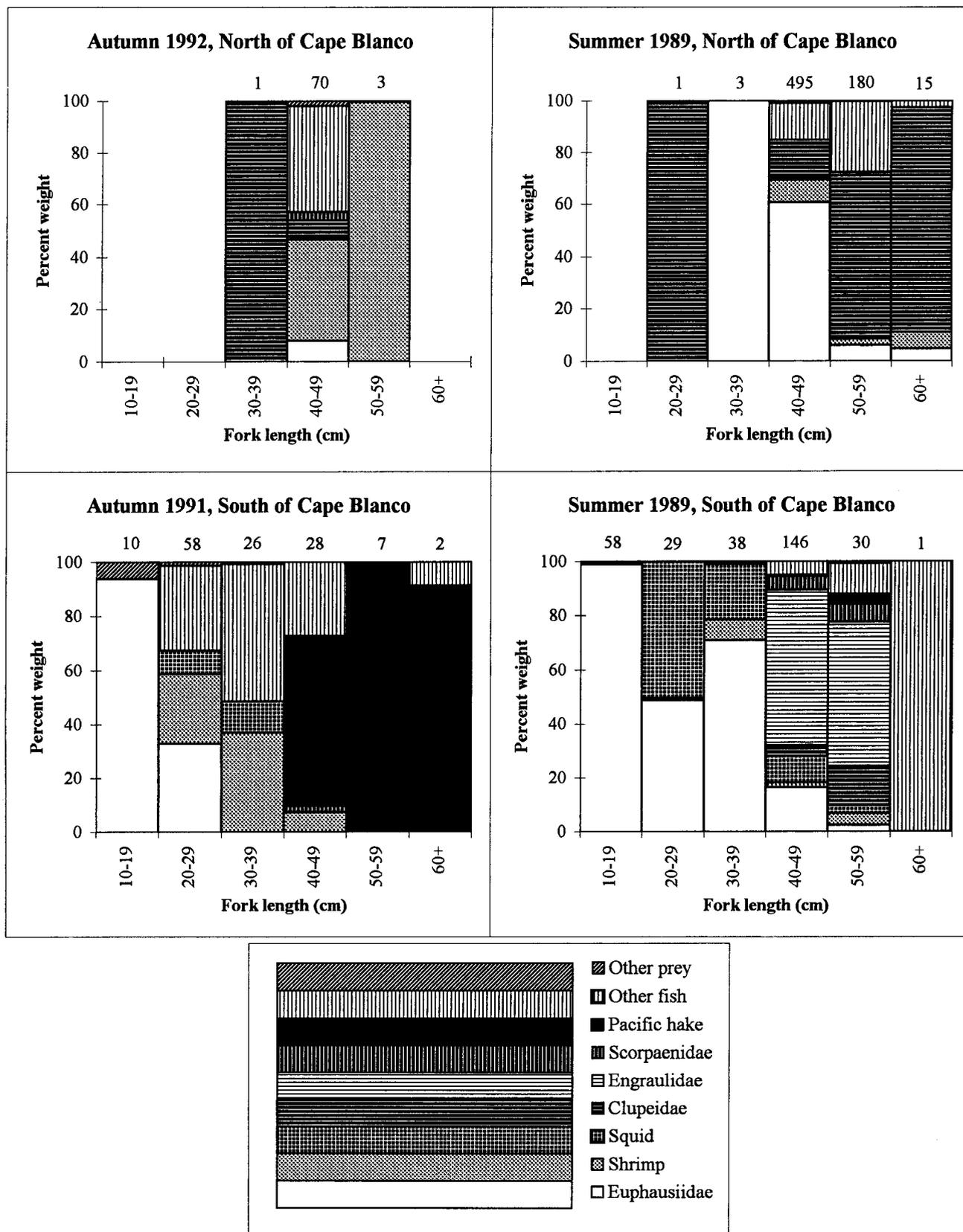
Figure 3. Diet composition (by weight) of Pacific hake length-groups from north of Cape Blanco (Vancouver and Columbia INPFC areas) in 1992 and 1989, and south of Cape Blanco in 1991 (Monterey INPFC area) and 1989 (Eureka, Monterey, and Conception INPFC areas).
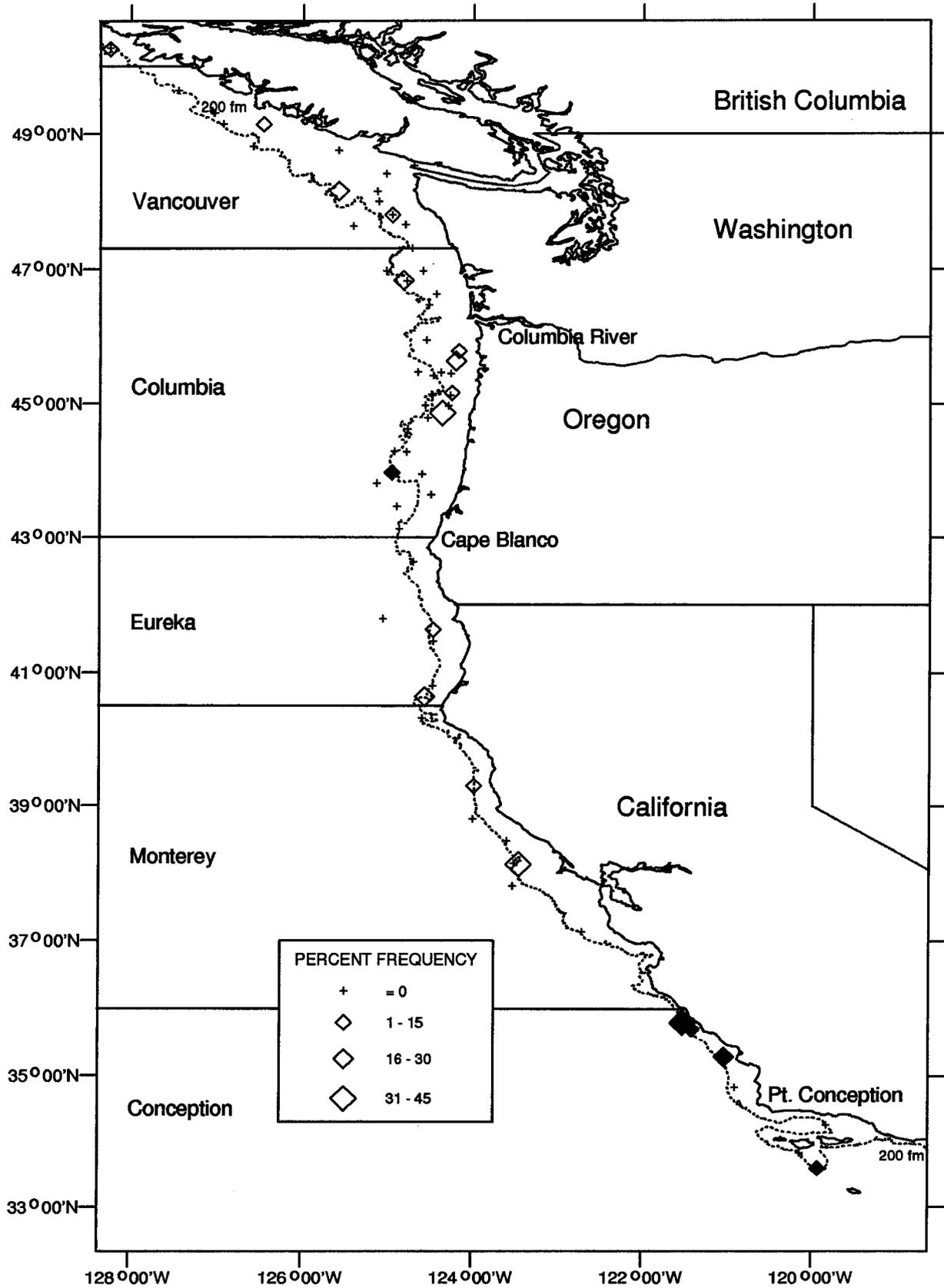
Figure 4.   The percent frequency of occurrence of cannibalism by Pacific hake at each haul location where Pacific hake stomachs were collected in 1995. The *black diamonds* indicate cannibalism of YOY Pacific hake. The 200-fm isobath is shown with a *dotted line.*
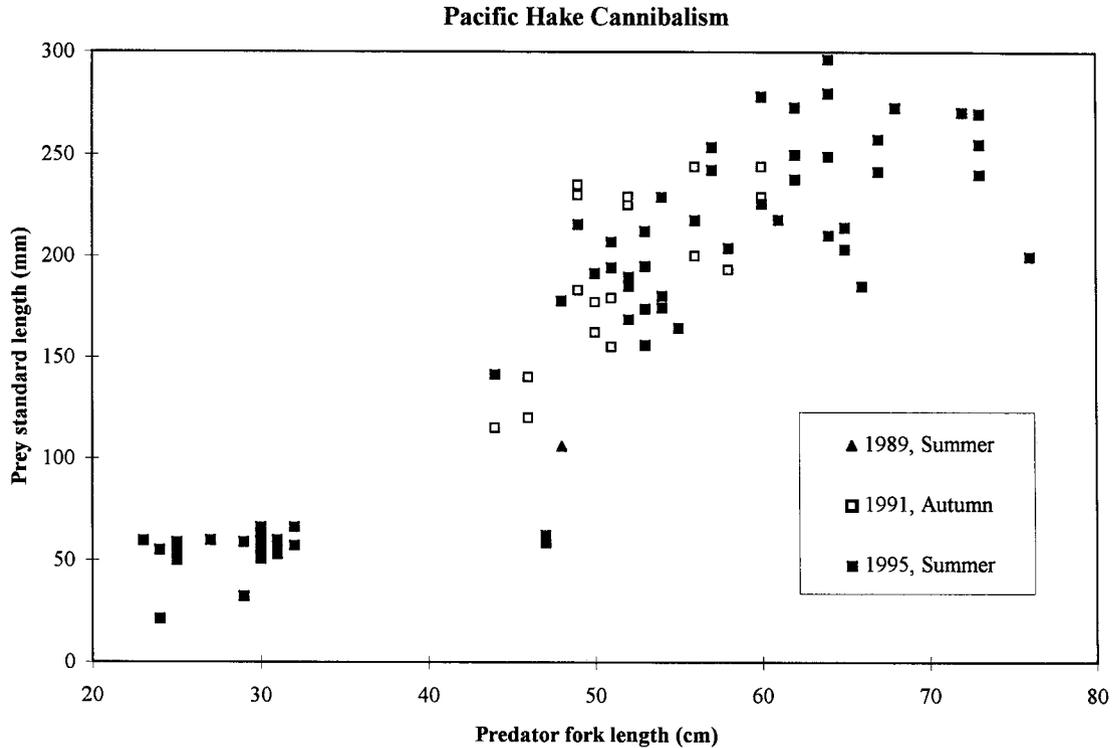
Figure 5. Scatterplot of prey size versus predator size in Pacific hake cannibalism from 1989, 1991, and 1995.

study, inferences about diet changes were limited because, in most cases, our samples were unique with respect to two or more of the following: year, season, area, depth, and fish size. Although we were able to cover a wide range of latitudes, water depths, and fish sizes in this study, stomach samples were not collected from Pacific hake feeding in water shallower than 55 m. In several years, adult hake have been seen gorging themselves on fishes schooling against the shoreline (De Witt 1952; Hobson and Howard 1989). This potentially important component in the feeding habits of Pacific hake remains poorly documented.

Pacific hake's reliance on euphausiids as a major food source in spring and summer is well known (Alton and Nelson 1970; Outram and Haegele 1972; Livingston 1983; Brodeur et al. 1987; Tanasichuk et al. 1991), as is their increasing piscivory with size (Livingston 1983; Livingston and Bailey 1985; Rexstad and Pikitch 1986; Tanasichuk et al. 1991). However, tremendous differences in diet composition can be found among these studies even when they cover the same geographic area. Although low sample sizes and differences in gear (purse seine, bottom trawl, or midwater trawl), sampling depth, and fish size may contribute to these differences, interannual variability may be the strongest influence. Interannual variability in the species composition of euphausiids in the diet can be dramatic, especially in strong

El Niño years (Brodeur et al. 1987). The volumetric and gravimetric proportion of fish in the diet of Pacific hake can vary widely among years (Brodeur et al. 1987; Tanasichuk et al. 1991), and fish species that dominate the sampled diet in some years can be absent in other years (Livingston 1983; Brodeur et al. 1987).

Apparent latitudinal differences in the diet may be confounded by the size of the Pacific hake sampled (Livingston 1983; Livingston and Bailey 1985; Rexstad and Pikitch 1986). The average size of Pacific hake generally increases with latitude (figure 2) because of seasonal and size-dependent migrations (Francis 1983). However, latitudinal differences in diet composition were apparent for predator-length categories that occurred both north and south of Cape Blanco (figure 3; 40–49 cm FL and 50–59 cm FL). Pacific herring constituted a large proportion of the diet, by weight or volume, north of Cape Blanco in several other studies (Livingston 1983; Rexstad and Pikitch 1986; Tanasichuk et al. 1991), and sometimes occurs in the Pacific hake diet south of Cape Blanco (Gotshall 1969). Northern anchovy occurs in the diet of Pacific hake off California (Best 1963; Gotshall 1969) and dominated the weight of the diet south of Cape Blanco in this study. Although northern anchovy contributed little to the diet north of Cape Blanco in this study, it can be very important in some years (Livingston 1983; Brodeur et al. 1987).

TABLE 3
Summary of Literature on the Diet of Pacific Hake by Location

Study	Months[a]	Year	Gear type[b]	Size-range in cm[a]	Sample size
SW Vancouver Island					
Outram and Haegle 1972	Aug.	1970	MW&B	42–71	1,196
Tanasichuk et al. 1991[c]	Aug.–Sept.	1983	MW&B	(40–65+)	1,362
	Aug.	1985	MW&B		801
	Aug.	1986	MW&B		2,244
	Aug.	1987	MW&B		1,698
	Aug.	1988	MW&B		3,629
	Aug.	1989	MW&B		2,696
	July–Nov.	1987	MW		15,551
	June–Oct.	1988	MW		20,153
SW Vancouver Island and Washington					
Livingston 1983	Aug.–Sept.	1980	MW&B	45–65	111
Washington					
Alton and Nelson 1970	May, Aug.	1965	MW&B	(46–66)	119
	June–Sept.	1966	MW&B		245
Livingston 1983	May–July	1967	MW	49–50	1,228
Washington and Oregon					
Rexstad and Pikitch 1986	Aug.–Sept.	1983	B	30–55+	347
Brodeur et al. 1987	(May–Sept.)	1981	PS	(31–63)	28
		1982	PS		58
		1983	PS		10
		1984	PS		60
Oregon					
Livingston 1983	Apr.–July	1967	MW	49–50	202
	Apr.–May	1980	B	35–65	53
Northern California					
Gotshall 1969	July, Oct.–Dec.	1964	MW&B	10–82	212
	Mar.–Sept.	1965	MW&B	40–76	238
Livingston 1983	Oct.	1980	B	10–20	40
Southern California					
Best 1963	Unk	Unk	Unk	Juv–adult	100's
Sumida and Moser 1980	Mar.	1975	MW	0.3–1.1	208
Mearns et al. 1981	Unk	Unk	Unk	Unk	14

[a]Information in parentheses is for all samples combined.
[b]MW = midwater trawl; B = bottom trawl; PS = purse seine.
[c]Includes all Pacific hake examined (empty and non-empty) except those with everted stomachs.

The latitudinal pattern for pandalid shrimp, as a proportion of diet, by weight, in the summer of 1989 (figure 2), is similar to that found in other studies. Gotshall (1969) found that pandalid shrimp made up 44% of diet volume of Pacific hake in the Eureka INPFC area, whereas studies in the Columbia and Vancouver INPFC areas found pandalid shrimp to constitute 0–8% of the diet by weight (Alton and Nelson 1970; Livingston 1983; Rexstad and Pikitch 1986; Brodeur et al. 1987).

Because most surveys are conducted in summer, detailed seasonal changes in the diet of Pacific hake are not well documented. Brodeur et al. (1987) found that euphausiids were almost absent from the diet in May, but were the dominant prey, by weight, from June through September off the coasts of Oregon and Washington. The proportion of euphausiids, by volume, in the diet in the Vancouver INPFC area decreased from summer highs (June through August or September) to lower values in October and November (Tanasichuk et al. 1991). Our findings follow a similar pattern: in the summer (of 1989)

euphausiids make up a higher percentage of the diet, by weight, than in the autumn (of 1991 and 1992; figure 2). This pattern remains when discrete size categories of Pacific hake are compared north and south of Cape Blanco (figure 3). However, the diet of juvenile Pacific hake (<20 cm FL) remained almost exclusively euphausiids in autumn 1991, similar to the diet observed by Livingston (1983) in October off California. Fishes are generally most important in the diet, by weight, in autumn (Gotshall 1969; Tanasichuk et al. 1991), winter (Gotshall 1969), and early spring (Gotshall 1969; Brodeur et al. 1987). Some observed seasonal changes in diet may be confounded by seasonal changes in size composition of the Pacific hake resulting from their seasonal migrations (Livingston 1983).

Cannibalism seems more common in the life history of Pacific hake than has been previously shown, and it may follow a seasonal pattern. We found a considerable degree of cannibalism south of Cape Blanco in the Monterey INPFC area in autumn 1991, but much less in summer 1989, even though a wide range of sizes were

in the area. Although little can be inferred directly from this seasonal comparison from two different years, it is consistent with patterns in the importance of fishes in the diet and the degree of spatial overlap of adult and juvenile Pacific hake. Intracohort cannibalism by larvae (Sumida and Moser 1980) and larger YOY (9–12 cm TL predator; unpubl. data) occurs, but not frequently.

Interannual changes in the abundance of age-1 Pacific hake available to adults could also explain the differing amounts of cannibalism observed in 1989, 1991, and 1995. The relative abundance of age-1 Pacific hake in those years can be judged from estimates of year-class size in the Pacific hake stock assessment (Dorn 1996), which show that the 1988 year class was weak and the 1990 year class was moderately strong. The 1994 year class is just now being assessed, and indications are that it is the strongest year class of Pacific hake since 1984 (M. Dorn, pers. comm., Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115). Cannibalism rates of age-1 fish observed in our study reflect the same trends. Determining the effect of cannibalism on the population dynamics of Pacific hake will require more sampling to better quantify seasonal and interannual differences in cannibalism rates.

Smith (1995) suggested that the negative interannual autocorrelation, lagged 1 year, in Pacific hake recruitment may be evidence for adjacent-cohort cannibalism or another control (competition for food) on recruitment rate. The cannibalism on YOY Pacific hake by the preceding cohort documented in this study supports, but does not confirm, this hypothesized mechanism. Competition for food may also weaken a cohort that follows a successful one. The diet of very small (33–60 mm TL) YOY indicates an early reliance on euphausiids (55%–79% by weight; unpubl. data) as a food source, and euphausiids constitute the main diet of larger juvenile Pacific hake (Livingston 1983; figure 3 of this study). Although predatory and competitive interactions affecting juveniles may be of secondary importance in determining year-class strength (Bailey and Francis 1985), this study indicates that both processes may be occurring between age-1 and YOY Pacific hake within the critical three to five months after spawning. Quantifying the importance of these interactions between age-1 and YOY Pacific hake will require field sampling to determine the degree of their spatial overlap, analysis of their growth and bioenergetics, and a better understanding of the production and availability of their common prey.

ACKNOWLEDGMENTS

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GROWTH AND COHORT DYNAMICS OF LARVAL PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*)

JOHN L. BUTLER AND ROBERT N. NISHIMOTO
National Marine Fisheries Service
Southwest Fisheries Science Center
P. O. Box 271
La Jolla, California 92038

ABSTRACT

Size-specific mortality rates and stage-based models predict that fast-growing fish larvae experience lower mortality than slow-growing larvae. We provide empirical evidence that supports this hypothesis, by comparing otolith size-at-age of young larval Pacific hake (*Merluccius productus*) with back-calculated otolith size-at-age from older larvae collected about 45 days later. The mean back-calculated size-at-age of the larvae surviving beyond 45 days was greater than the average population growth rate of younger larvae sampled earlier. Thus hake larvae with slow growth rates appear to have suffered higher mortality than larvae with faster growth rates.

INTRODUCTION

Size-selective mortality is a common topic in fishery biology, but most investigations focus on the effects of fishing (Parma and Deriso 1990; Rijnsdorp and Jaworski 1990; Buijse and Houthuijzen 1992; Hanson and Chouinard 1992). Correlations of body size and mortality indicate that larger organisms have lower mortality rates (Peterson and Wroblewski 1984). Individual-based models (Lomnicki 1978; DeAngelis et al. 1993; Cowan et al. 1996) and stochastic stage-based models (Lo et al. 1995) also predict that faster-growing individuals have higher survival rates.

Although size-selective mortality is believed to be a major factor in larval fishes (McGurk 1986; Houde 1987; Anderson 1988; Miller et al. 1988; Pepin 1988, 1989, 1991; Bailey and Houde 1989; Beyer 1989; Cowan et al. 1996), few field data exist to support this hypothesis. Both starvation and predation are size dependent (Rosenburg and Haugen 1982; Margulies 1993). Smaller larvae are more vulnerable to starvation because they have smaller energy reserves to withstand food deprivation (Beyer and Laurence 1980; Rosenburg and Haugen 1982; Margulies 1993). Smaller larvae are more vulnerable to predation (Shepard and Cushing 1980; Bailey and Batty 1983; Bailey 1984; Purcell 1986). Size-selective vulnerability to predation in hake larvae has been demonstrated in the laboratory (Bailey 1984). However, Brown and Bailey (1992) were unable to demonstrate size-selective mortality in walleye pollack larvae in the field.

Some evidence for size-selective mortality has been reported for juvenile fishes. Post and Prankevicius (1987) found evidence for size-selective mortality in one of two populations of yellow perch (*Perca flavescens*) on the basis of otolith growth history. West and Larkin (1987) reported evidence for size-selective mortality in juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. Their results were criticized by Mosegaard (1990) because the correlation between fish length and otolith length was too low for indirect selection on fish length to shift otolith sizes as much as was observed. Between-drainage differences in otolith size–fish size may explain West and Larkin's result (Mosegaard 1990). Fitzhugh and Rice (1995) could not reject the null hypothesis of no size-selective mortality when back-calculation variability was incorporated into simulations of juvenile southern flounder (*Paralichthys lethostigma*) growth. Size-selective mortality has been demonstrated for gulf menhaden (*Brevoortia patronus*) and king mackerel (*Scomberomorus cavalla*; Grimes and Isely 1996). Meekan and Fortier (1996) found selection for fast growth in larval Atlantic cod (*Gadus morhua*), and Campana (1996) found that year-class strength was correlated with faster growth of larval and juvenile Atlantic cod. Thus, although size-selective mortality is often incorporated in models, empirical evidence for this phenomenon in larval fish has only recently been reported.

Population dynamics of Pacific hake are characterized by large year classes separated by two to three years of poor recruitment (Dorn 1995). While the exact cause of this variability is unknown, the strength of an incoming year class is detectable in the first 1–3 months after spawning (Hollowed and Bailey 1989). Thus, growth rates may be critical to larval survival as well as in the dynamics of recruitment in the coastal stock of Pacific hake (Woodbury et al. 1995).

As part of an investigation on the recruitment of Pacific hake, we studied the growth of larvae during a 4-month period. To investigate whether hake larvae experience size-selective mortality, we compared the otolith size-at-age of young larval hake with repeated measures of otolith size-at-age of older larvae with the same back-calculated hatch dates collected in the same area approximately 45 days later.

METHODS

Larval hake were sampled on three cruises. During January 4–23, 1995, larvae were captured with a standard CalCOFI 1-m bongo net hauled obliquely between
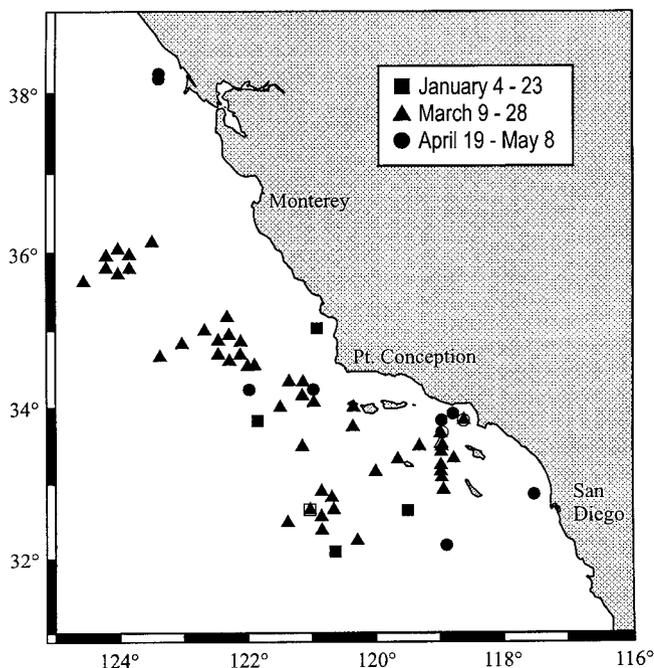
Figure 1. Locations of positive samples for Pacific hake (*Merluccius productus*) larvae during 1995 cruises: January (*squares*); March (*triangles*); and April–May (*circles*).

210 m and the surface. During March 9–28, 1995, larvae were collected with a standard CalCOFI 1-m bongo net and with a 1-m² multiple opening/closing net and environmental sensing system (MOCNESS) hauled obliquely between 300 m and the surface. During April 19–May 8, 1995, larger larvae were collected with a 10-m² MOCNESS hauled obliquely between 300 m and the surface. Samples were collected in the California Current between 32°5.1'N and 38°13.5'N and between 117°31.8'W and 124°33.1'W (figure 1).

Plankton samples from the bongo nets in January and March were preserved in 80% ethanol buffered with 20 millimolar tris(hydroxymethyl)aminoethane. Hake larvae were removed from the plankton at the shore laboratory and stored in 70% ethanol. Larvae collected with the 10-m² MOCNESS and bongo net in April–May were sorted at sea and preserved in buffered 80% ethanol.

To compare catch rates of hake larvae in the 505-micron-mesh, 70-cm bongo net and catch rates in the 3-mm-mesh, 10-m² MOCNESS, we compared the log of percent frequency of all hake larvae ($N = 124,064$) caught in the bongo during March and April from 1978 to 1986 to the log of percent frequency of hake larvae ($N = 1,435$) caught in March 1992 with the 10-m² MOCNESS. Catch rates were compared on the log scale to highlight any differences in the larger sizes.

Before removing the otoliths, we measured the standard length or length to the tip of the notochord of each larva to the nearest 0.1 mm with an ocular micrometer.

Otoliths were extracted with microprobes while the larva lay on a glass slide. After drying, the otoliths were fixed to the slide with the histological compound EUKITT.

Otolith increments were counted and measured with the technique of Methot and Kramer (1979). A high-resolution television camera mounted on a compound microscope projected the image of the otolith onto a monitor of a closed-circuit television system. Distance along a standardized path and the number of increments observed were recorded on a microcomputer interfaced to a video coordinate digitizer and television system. Data on average increment width were recorded and analyzed with a program that "counts" increments by evaluating the distance along the radius from the center to the outer edge of the otolith divided by average width at each radius (Methot 1981).

We counted increments on both sagittae whenever possible by placing nondrying immersion oil on the histological compound and using oil-immersion lenses of 40× and 63×. The sagittae had been mounted or remounted distal side up, and the increments were counted in a straight path from the focus to the tip of the rostrum on otoliths where the rostrum and postrostrum could be differentiated. For small larvae, where two of the three pairs of otoliths are nearly equal in size, and round, we selected two otoliths with the most visible increments, and counted in a straight line from focus to the edge of the otolith. When increments were difficult to see, we polished the otoliths with either 12- or 30-micron imperial lapping paper until the increments became visible. Widths were measured for two increments at a time along two transects for each otolith. One transect began at the focus and proceeded toward the outer edge, the other began at the margin and overlapped the first transect.

Since both otoliths may not have been recovered from each larva, results from left and right sagitta were tested to determine any bias. The percent agreement within ±1 day was 78.9, and the agreement within ±2 days was 93.8. Since the index of precision (Chang 1982) was 0.0142, results were average from both otoliths. If both otoliths were not recovered, we used the count for the single otolith.

The daily formation of otolith microincrements was validated by Bailey (1982). Hake larvae form the first increment 2–3 days after hatching (Bailey 1982). For the age in days, we used two more than the number of increments.

A Gompertz growth equation (Zweifel and Lasker 1976) was fitted to size-at-age data from the March and April–May cruises by means of nonlinear regression (figure 2). Because the variance was heteroscedastic, we used the reciprocal of the variance for each 10-increment segment to weight the regression.
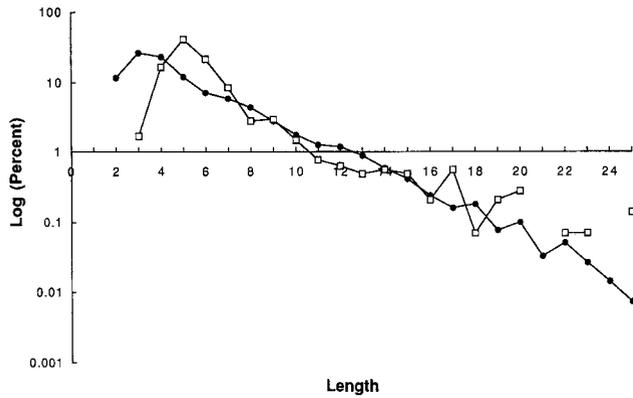
Figure 2. Percentage of Pacific hake (*Merluccius productus*) larvae in 1-mm size categories collected by 70-cm bongo nets (*filled circles; N* = 124,064) and 10-m² MOCNESS (*open squares; N* = 1,435).
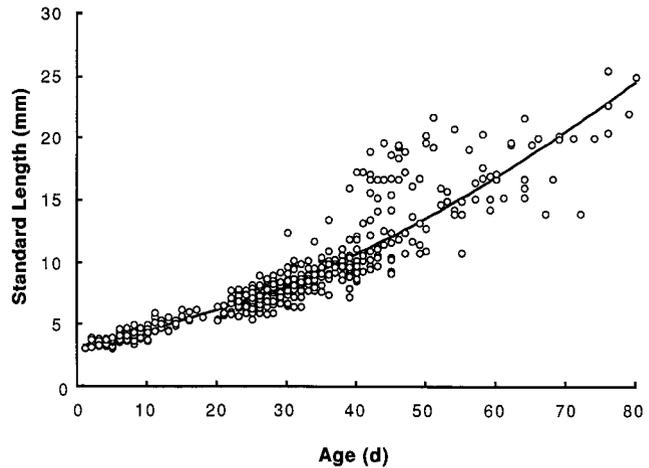

Figure 3. Size-at-age of Pacific hake (*Merluccius productus*) larvae. The Gompertz growth curve was fitted to all data. See text for details of fitted line.
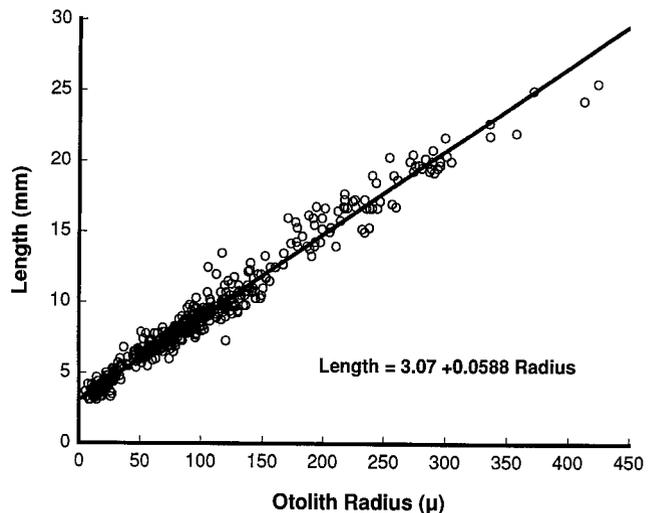

Figure 4. Allometric relation of body length and otolith radius of Pacific hake (*Merluccius productus*) larvae. Fitted line is geometric regression.

Hatch dates were back-calculated from the age and the date of capture. We compared the hatch date distributions from the March and April–May cruises to confirm that back-calculated growth rates were compared to size-at-age of larvae hatched during the same part of the spawning season (within-season cohort).

Otolith size was measured from the focus to the maximum radius of the otolith (rostrum). An allometric relation was fitted with geometric regression (Ricker 1973).

To test whether surviving larvae were larger at size than the population, we compared otolith size-at-age from larvae collected during the March cruise to otolith size-at-age from the April–May cruise by using repeated measure analysis of covariance (Chambers and Miller 1995). Body-length-at-age trajectories of surviving larvae were back-calculated from size at hatching to size at capture and plotted with size-at-age from the March larvae for illustrative purposes. Since few late larvae were collected north of Point Conception during the April–May cruise (figure 1), only larvae collected south of Point Conception from both the March and April–May cruises were included in the comparison. Large larvae, whose otoliths had begun to form secondary primordium, were also excluded.

RESULTS

The catch rates of the 70-cm bongo net and 10-m² MOCNESS differ greatly for the smallest larvae (figure 2). The bongo net catches many more 2- and 3-mm larvae than the MOCNESS because the smaller larvae are extruded through the 3-mm mesh of the MOCNESS. Larvae of 8 to 16 mm are represented equally in the catch of the two nets. In the size classes larger than 16 mm, the numbers of larvae are few, and the differences may represent sampling error.

The size-at-age of early larvae ($\leq$20 d) is not significantly different for the January and March cruises

(ANCOVA, $P >$ .05). Therefore, we pooled all specimens from both cruises. The growth rate is described by the linear equation

$$L = 3.02 + 0.156^{*}t$$

where L is body length in mm and t is time in days ($N =$ 187, $R^2 =$ .74, $p =$ .001).

The growth rate of hake larvae up to 89 days is best described by the Gompertz equation:

$$L = L_0 e^{(a(1 - e^{(-gt)}))}$$

where L is standard length, t is age in days, and L_0 is length at hatching (figure 3). For hake larvae from March and April–May 1995, $L_0 =$ 3.16, $a =$ 3.64, $g =$ 0.0101. The residual mean square of this regression is 1.00 ($r^2 \cong$ 0.76).

Fish size is linearly related to maximum otolith radius (figure 4). Residuals from this regression show no trend
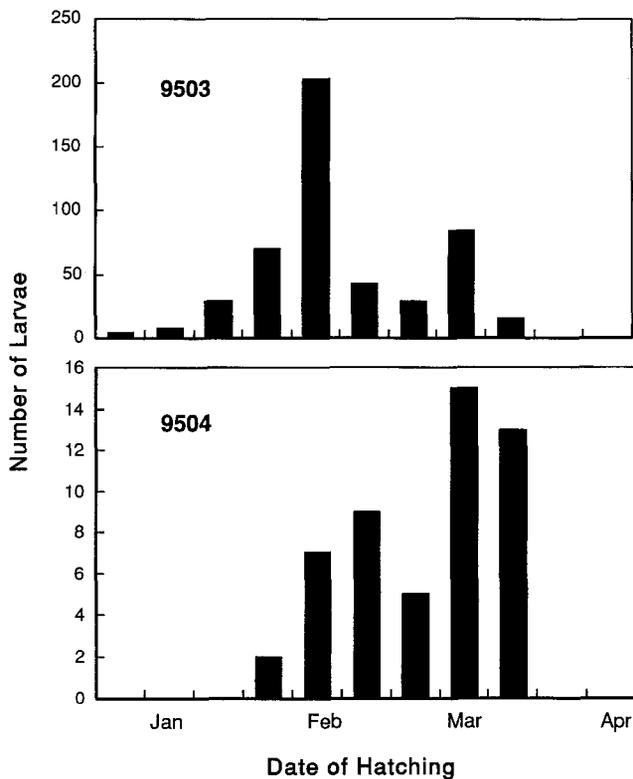
Figure 5. Hatch date distributions of Pacific hake (*Merluccius productus*) larvae for cruises 9503 and 9504. Histogram is based on ten-day intervals beginning January 1, 1995.

with otolith size (figure 5). A step-wise linear regression indicates that otolith size explained 96% of the variance of fish size (table 1). Variance in age accounts for only 3% of the variance in fish size (table 1). The geometric mean regression of length (*L*) on otolith radius (*R*) is:

$$L = 3.07 + 0.0588 \times R$$

The distributions of hatch dates are similar for the March and April cruises (figure 6). Both distributions are bimodal, with a peak in mid-February and a second peak in mid-March. The relative decrease in the first peak from the first cruise to the second cruise may be due to the greater total mortality of these older larvae. An alternative interpretation would be that the age of the older larvae has been underestimated. This would both shift the hatch date peak and overestimate the growth

TABLE 1
Step-Wise Linear Regression of Fish Length
on Otolith Radius and Age

Variable	Coefficient	Standard error	Standard coefficient	P(2-tail)
Constant	3.007	0.058	0.000	0.000
Radius	0.057	0.001	0.956	0.000
Age	0.009	0.004	0.034	0.047

rates of the survivors. The clarity of daily increments in larval hake otoliths makes that interpretation unlikely.

Mean otolith size-at-age from larvae caught in April–May is significantly different from otolith size-at-age from larvae collected in March (RM-ANCOVA *P* < 0.000). Back-calculated size-at-age trajectories of the April–May surviving larvae are plotted with size-at-age of March larvae in figure 6 to illustrate the difference. These differences in size-at-age indicate that slow-growing larvae survive less well than fast-growing larvae.

DISCUSSION

In order to demonstrate that survivors have higher growth rates than larvae sampled earlier, it is necessary to show that neither net selected for faster- or slower-growing larvae. The greatest difference in the catch curves of hake larvae in the two nets is in the smallest larvae (figure 2). Although there is significant extrusion of 3- and 4-mm hake larvae in the 10-m^2 MOCNESS, from 5 to 16 mm the catch rates of the two nets are virtually the same. Comparing the catch rate of larvae larger than 16 mm is difficult because of the few larvae represented in the 10-m^2 MOCNESS samples. To date, only 1,435 hake larvae have been collected with the MOCNESS; thus one larvae represents .07 percent. Because 124,064 larvae have been collected in the bongo net during the months of March and April since 1978, the bongo catch curve is accurate for larvae up to 25 mm. Since the 10-m^2 MOCNESS adequately samples larvae as small as 5 mm (figure 2), it is unlikely that the MOCNESS undersampled slower-growing individuals.

Size-at-age and growth rates of young hake larvae (≤20 d) did not differ in January and March and were almost identical to those reported by Bailey (1982). Thus the early growth of hake larvae may vary little from season to season. Size-at-age of field-collected larvae up to 80 days are also similar to those reported by Bailey (1982). However, Woodbury et al. (1995) have found significant interannual variation in growth rates of larvae older than about 80 days.

Size-selective mortality in larval fish has been an accepted fact since Houde (1987) speculated on its role in recruitment variability. Many models have incorporated size-selective mortality (Lo et al. 1995; Cowan et al. 1996), but direct empirical evidence for this phenomenon remains elusive. Many investigators have been unable to detect this phenomenon in the field, perhaps because of problems with back-calculation (Brown and Bailey 1992; Fitzhugh and Rice 1995). In this study, however, we used otolith size-at-age rather than back-calculated growth to detect size selection.

Back-calculated growth rates from larvae that have survived for at least a month are, however, significantly faster than those of the cohort. This is strong evidence
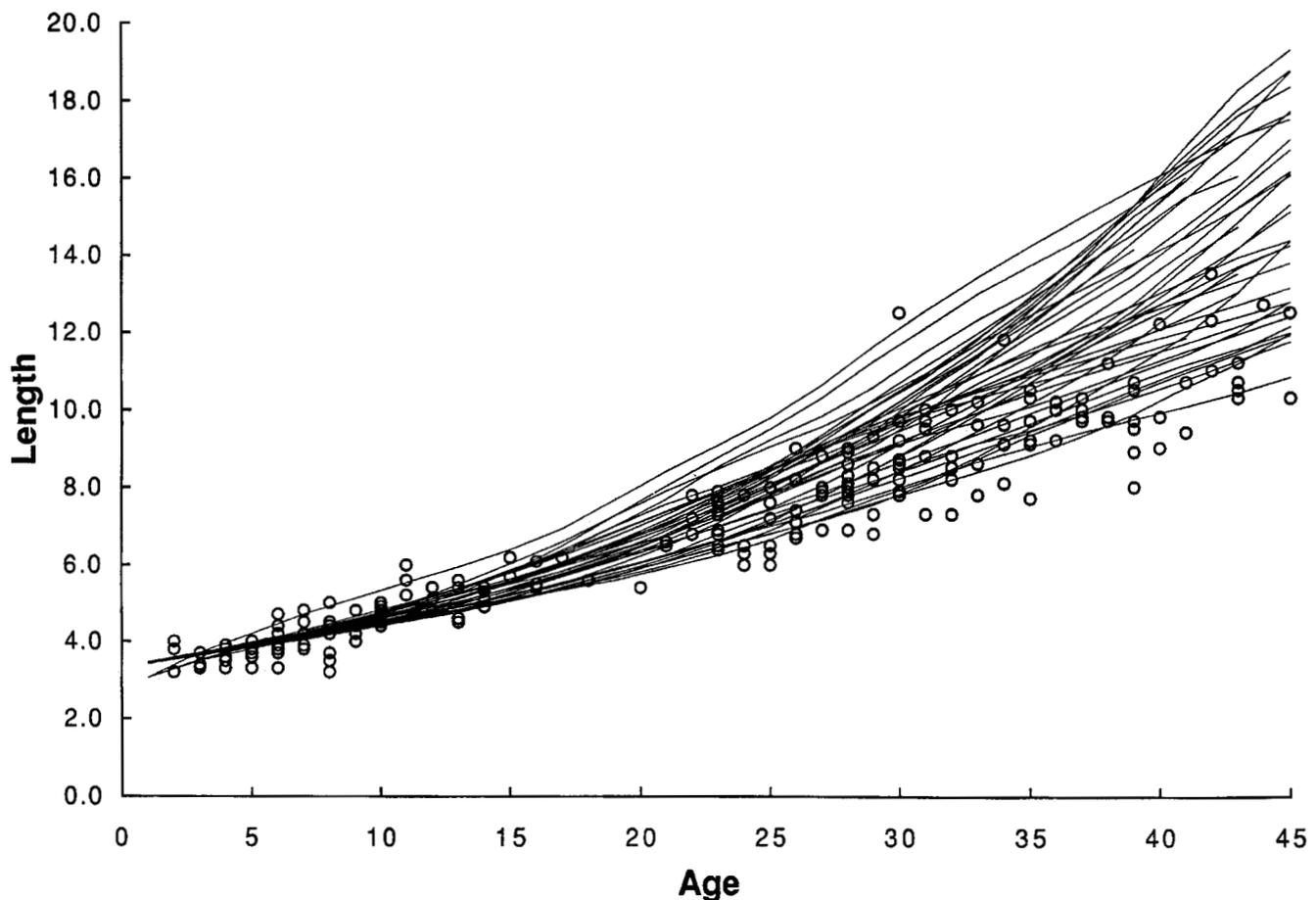
Figure 6. Size-at-age (*circles*) of 207 Pacific hake larvae collected south of Point Conception, and growth trajectories (*lines*) of larvae collected about 45 days later in the same area.

for size-selective mortality. The larvae with the fastest growth rates are the ones that survive. These data support conclusions of stochastic stage-based models (Lo et al. 1995) and individual-based models (Cowan et al. 1996).

Size-selective mortality in the early life history of fishes has also been demonstrated for fish eggs (Rijnsdorp and Jaworski 1990). In the case of fish eggs, mortality (predation) can be either neutral or positive for smaller eggs. In the case of fish larvae, mortality (predation and starvation) can be positive for smaller, slower-growing individuals. It is also conceivable that predation can be positive for larger, faster-growing, and more active individuals. This is certainly true for juveniles entering a fishery (Parma and Deriso 1990; Rijnsdorp and Jaworski 1990; Buijse and Houthuijzen 1992; Hanson and Chouinard 1992). Faster-growing, more active larvae may also be vulnerable to higher predation, if predators detect prey by their movements. In the case of Pacific hake larvae, the evidence from otolith size-at-age indicates that slower-growing larvae suffer higher mortality.

ACKNOWLEDGMENTS

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RELATION OF MEAN GROWTH RATE TO CONCENTRATION OF PREY-SIZED PARTICLES FOR LARVAE OF PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*)

SHANNON L. CASS-CALAY
Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive
La Jolla, California 92093-0208

ABSTRACT

During February 1996, a combined OPC/MOCNESS was used to sample Pacific hake larvae (*Merluccius productus*) at twelve stations within or just offshore of the Southern California Bight. The OPC/MOCNESS simultaneously measured the horizontal and vertical distribution of hake larvae, the fine-scale distribution of prey-sized particles, and the temperature and salinity of the water column. In order to examine the relation between growth and particle concentration, I measured the size-at-age for 60 larvae from 6 stratified samples collected at five different stations. Within the strata examined, the average particle concentrations ranged from 6.36 to 1.44 prey-sized particles L^{-1}, and the average temperatures ranged from 10.5°C to 12.4°C. Estimates of the average growth rate of larval hake contained within these samples ranged from 0.135 to 0.279 mm d^{-1}. Within the range of temperatures examined, the average growth rate of larval hake collected in a sample was not related to the average temperature of that sample ($r^2 = 2e^{-6}$, $p = 0.998$). In contrast, there was a significant, positive relation between the average growth rate of larval hake within a stratum and the average concentration of prey-sized particles in that stratum ($r^2 = 0.795$, $p < 0.02$).

INTRODUCTION

For many decades, scientists have examined the stock-recruitment dynamics of fish populations. In particular, they have searched for the underlying cause of the recruitment variability that often occurs independent of fluctuations in adult biomass. The Pacific hake (*Merluccius productus*) is one species in which such variability occurs. While the per capita recruitment rate of Pacific hake may vary 100-fold interannually (Methot and Dorn 1995; Smith 1995), these fluctuations are not obviously related to the spawning biomass, or to the number of eggs present in the sampling region (Hollowed and Bailey 1989; Hollowed 1992; Methot and Dorn 1995). Recruitment of Pacific hake is determined at a relatively young age. Bailey et al. (1986) report that the abundance of age-0 hake collected in southern California midwater trawl surveys is strongly related to the magnitude of the year class at recruitment. Furthermore, Hollowed and Bailey (1989) demonstrated that measuring the abundance of

hake larvae 11.50 to 15.75 mm long made it possible to predict the relative strength of the year class at age three. Thus processes that influence the survival of Pacific hake larvae determine, in part, the relative magnitude of recruitment to the adult population.

Many factors influence the survival of fish larvae, including genetic defect, disease (Sindermann 1970; Sissenwine 1984); predation (Hunter 1981; Houde 1987; Bailey and Houde 1989); adverse transport (Hjort 1914; Parrish et al. 1981); growth rate (Ware 1975; Shepherd and Cushing 1980); and starvation (Hjort 1914; Cushing 1975; Lasker 1975, 1978, 1981). Thus it is often difficult to determine the magnitude of any one source of mortality. Pacific hake larvae, however, possess a unique suite of characteristics that may modify their likely sources of mortality.

Hake larvae are generally distributed from 50 to 100 meters, well below the turbulent wind-mixed layer, and they are occasionally found as deep as 200 meters (Ahlstrom 1959). This subsurface habitat may protect them from Ekman drift and wind-driven transport (Smith 1995), factors that can increase mortality if larvae are advected from areas where temperature and prey concentrations are favorable for growth (Bailey 1981; Parrish et al. 1981). However, this subsurface habitat is also below the zooplankton biomass maxima located within the euphotic zone.

The diet of larval hake consists primarily of copepod nauplii, copepodites, and adult copepods (Sumida and Moser 1980). It has been estimated that first-feeding Pacific hake larvae must ingest 0.13 calories per day to balance the cost of metabolism and growth (Bailey 1982). Bailey predicts that this ration could be obtained by consuming 25 copepod nauplii, 15 small copepodites (or small adult copepods), or 1 large adult *Calanus* each day. Considering the limited mobility, small daily ambit, and poor ability of first-feeding larvae to capture prey, it is evident that the growth and survival of first-feeding hake larvae may be limited by the low prey concentrations often found at depth in the California Current region.

The objective of this study was to determine whether prey concentration limits the abundance and growth rate of Pacific hake larvae. Two questions were examined. (1) Was the concentration of larval hake within a stratum related to the average concentration of prey-sized
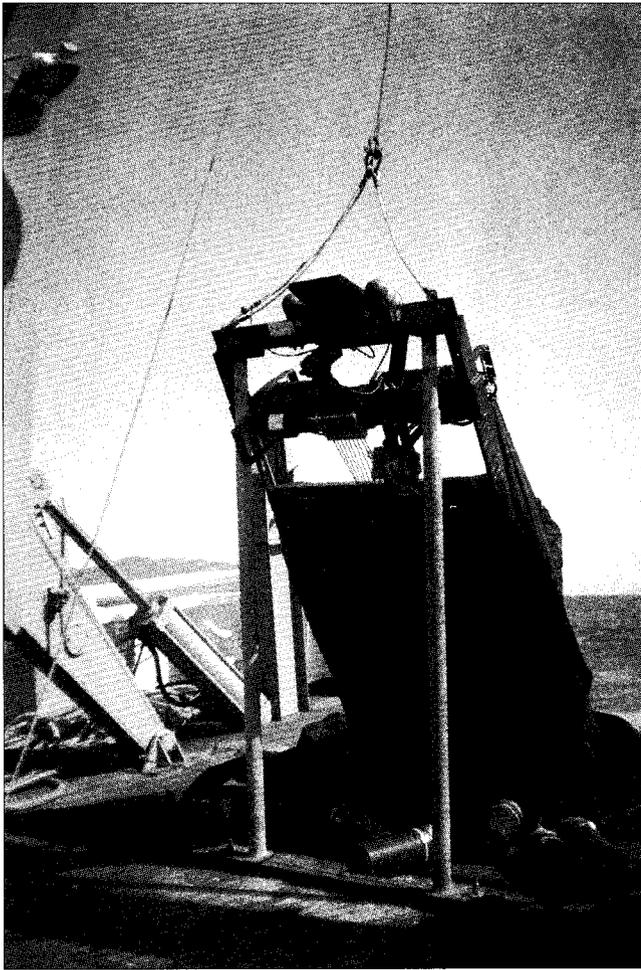
Figure 1. The OPC/MOCNESS. The optical particle counter can be seen atop the MOCNESS frame.

particles in that stratum? (2) Did hake larvae have higher average growth rates where the ambient concentration of prey-sized particles was elevated? Although the objective of this study is not novel, the approach is unique. The OPC/MOCNESS enables simultaneous measurements of both predator and prey. These data provide unique insight into the relation between prey concentration and the abundance and growth rate of Pacific hake larvae.

METHODS

Sampling with the OPC/MOCNESS

The horizontal and vertical distribution of Pacific hake larvae and the fine-scale distribution of particles were measured simultaneously with a combined opening/closing net and environmental sensing system (MOCNESS; Wiebe et al. 1976) and optical plankton counter (OPC; Herman 1988, 1992; figure 1). Pacific hake larvae were collected with a 1-m² MOCNESS with ten 333-μm-

mesh nets. The MOCNESS was deployed to a depth of 225 m, and sampled nine 25-m strata from 225 m to the surface. In addition, one net was open throughout the downcast. This net provided an integrated sample that was not examined.

Particles were counted with a Focal Technologies OPC attached directly to the MOCNESS frame. The OPC uses an array of light-emitting diodes to count particles. The light travels through a cylindrical lens and is focused into a parallel beam extending across the sampling tunnel, at the end of which it passes through a second lens and is refocused onto a photodiode receiver. The amount of light reaching the photodiode receiver is converted to a corresponding voltage. As a particle passes through the sampling tunnel, it attenuates the light beam by an amount proportional to the cross-sectional area of the particle and its transparency. In turn, the amount of light that reaches the photodiode receiver is reduced, as is the corresponding voltage. Each time the voltage is reduced, a particle is counted. The analog decrease in voltage is converted to a digital size for the particle (Herman 1988, 1992). By means of a standard calculation that assumes that all particles are spherical, the digital size can then be converted to an equivalent spherical diameter (ESD).

The OPC can be used to identify and estimate the abundance of specific taxa (Herman et al. 1993; Osgood and Checkley, in press). However, this is practical only when the species composition is limited to a few members with distinct optical attributes, or when most of the biomass is accounted for by a single species. Such was not the case during this study, so it was necessary to estimate the size range of particles that could be prey for larval hake.

Sumida and Moser (1980) state that adult copepods 110 to 600 μm in maximal width make up 73.8% of the gut volume of Pacific hake larvae 3 to 11 mm long. If one assumes that the volume of an adult copepod can be estimated by a cylinder with a height equal to three times its diameter (Mullin and Cass-Calay 1997), a copepod 600 μm wide would have an ESD equal to 1,000 μm. The smallest particle that can be routinely detected by the OPC has an ESD of 250 μm. This value corresponds to a copepod roughly 152 μm in diameter. Therefore I assumed that all particles with an equivalent spherical diameter ranging from 250 to 1,000 μm are "prey-sized particles." In addition, several other assumptions were necessary: (1) that hake larvae and particles are distributed randomly within a stratum; (2) that the amount of food available to the hake larvae within a stratum can be estimated by the average concentration of prey-sized particles within that stratum; and (3) that the distributions of hake larvae and prey persist over a period of days to weeks.

Calculating the Concentration of Prey-Sized Particles

By merging the OPC and MOCNESS data I was able to calculate the concentration of prey-sized particles in each stratum with the equation

$$\frac{N}{l} = \frac{N}{t} \cdot \frac{t}{v \cdot t \cdot A} \cdot 10^{-3}$$

where N is the number of prey-sized particles; l is the volume sampled (l); t is duration of the sampling interval (s); v is the net speed (m/s); and A is the area of the OPC aperture (m^2). The OPC/MOCNESS measurements provided one estimate of particle concentration every 3.6 seconds. Since each MOCNESS net was open for approximately 3 minutes, about 50 concentration estimates were made in each 25-m stratum. The average particle concentration within a stratum is simply the arithmetic mean of these estimates.

Preserving the Samples

In order to allow examination of both the gut content and growth rate of larval hake, it was necessary to split each MOCNESS sample into two equal portions. So the entire MOCNESS sample was rinsed out of the cod end into a 32-ounce jar. The sample was then poured into a containment reservoir. Before the sample settled, a stopcock was opened to shunt the sample into two 32-ounce collecting jars. All plankton was then carefully rinsed out of the splitter and into the two collecting jars. One portion was preserved in a solution of seawater containing 5%–10% formalin saturated with sodium borate. The second portion was strained, then preserved in 80% ethanol. The ethanol was replaced after 24 hours. To prevent dissolution of the calcium carbonate otoliths, the ethanol was buffered with a saturated solution of Sigma 7–9 tris buffer in deionized water. Eight milliliters of the saturated tris solution were added to every liter of 80% ethanol.

Measuring Size-at-Age

Because the hake larvae had been preserved in ethanol for several months, before microscopic examination they were soaked in deionized water for several minutes to restore the tissues to osmotic balance and to minimize shrinkage. I used a dissecting microscope with ocular micrometer to measure standard length. I used a dissecting microscope at 250× magnification, fitted with two polarizing filters, to remove the sagittal otoliths. The otoliths were then mounted on a glass slide, dried, and covered with a drop of liquid coverslip.

I used a digital analysis system at the NMFS/Southwest Fisheries Science Center to count growth increments. The digital analysis system included a compound microscope, a high-performance CCD camera, a high-resolution monitor, a video coordinate digitizer, and a computer to log data. To estimate the age of a larva, I examined several transects at 400× and 630× magnification across the widest part of both sagittal otoliths. The center and the edge of the otolith were digitized during each transect. Additional transects were made until every increment and the focus of the otolith were well resolved. I then used a software package designed to estimate the age and growth rate of larval fish to average the data.

Laboratory experiments have demonstrated that Pacific hake larvae form one growth increment each day (Bailey 1982). The first increment appears a few days after hatching, perhaps as feeding commences (Bailey 1982). Because otolith analysis can be somewhat subjective, otoliths were mounted on slides labeled with a random number. No depth, temperature, prey concentration, or size information was recorded on the slide. In addition, slides were analyzed in random order. Both sagittal otoliths were analyzed to minimize the variability in the age estimate. A single reader made all the measurements.

Estimating the Mean Growth Rate

The mean growth rate of the larvae within a given stratum was estimated as follows. A representative subsample was chosen haphazardly, so that a variety of sizes were examined. The size and age were determined for each fish, and a linear equation was fitted to the data. The slope of the fitted line was assumed to be equal to the mean growth rate. It should be noted that a Gompertz curve is generally fitted to size-at-age data in order to estimate growth rates. But I chose a linear equation to facilitate statistical analysis, and because the growth of Pacific hake larvae is described more accurately by a linear equation during the first 20 days after hatching (Bailey 1982).

RESULTS

Horizontal and Vertical Distribution of Hake Larvae

Samples were taken at twelve stations during February 3–14, 1996, in the region from 32° to 34°N and 118° to 121°W (figure 2). Station locations and times of occupation are summarized in table 1. The average volume of water filtered by the MOCNESS in each stratum was 154.1 ± 4.2 m^3 (mean ±SE). Although Pacific hake larvae were found at all stations, their abundance at a given station varied from 4 to more than 1,100 larvae per collection (table 1). The larvae were most common from a depth of 25 to 100 meters, and the center of the vertical distribution was approximately 50 meters (figure 3).

Temperature profiles were measured with a CTD attached to the MOCNESS frame. These data were used to estimate the depth of the mixed layer. At eleven of
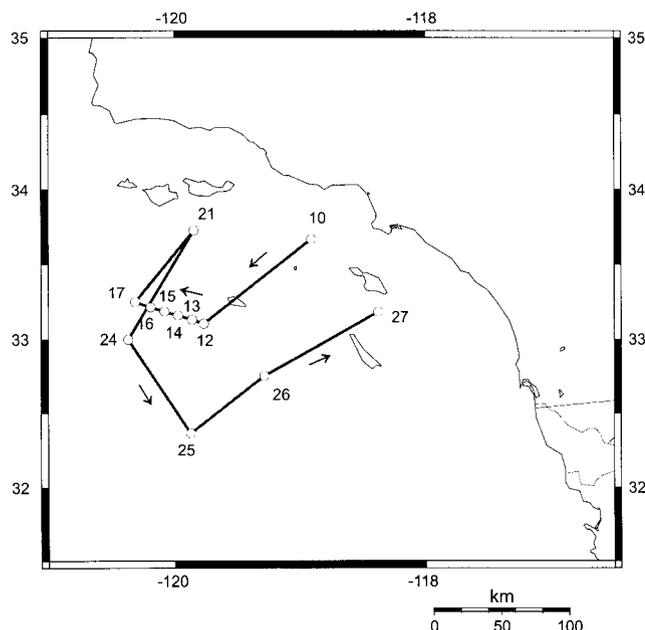
Figure 2. The OPC/MOCNESS cast locations. Twelve stations were occupied (station numbers 10–27) from February 3 to 14, 1996.
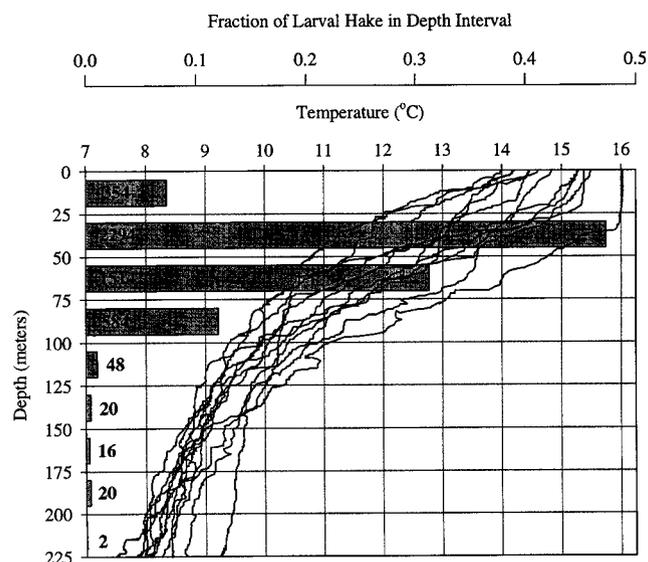

Figure 3. Vertical distribution of all Pacific hake larvae collected during this investigation. The boldface number is the total number of hake larvae found in a given depth interval. Superimposed is the temperature profile at each of the twelve stations.

twelve stations the mixed layer was less than 25 meters deep. At station 24 it was approximately 33 meters deep. Hake larvae were rare in the mixed layer, accounting for less than 7.3% of the larvae collected. More than 90.5% of the hake larvae collected were found in the stratified waters of the thermocline (figure 3).

Larval Abundance as a Function of Particle Concentration

For the following analyses, I examined 97 of the 106 strata sampled. Because the MOCNESS was accidentally reset during deployment, the software for merging the OPC/MOCNESS data malfunctioned. Thus it was impossible to calculate the concentration of particles at station 26. Therefore the nine strata sampled at that station could not be included.

TABLE 1
OPC/MOCNESS Station Locations, Dates, Times of Casts, and Total Numbers of Hake Larvae Collected in the Nine Stratified MOCNESS Nets

Station	Latitude	Longitude	Date	Time (PST)	Hake
10	33°40'.4N	118°59'.5W	2-8-96	2056	78
12	33°06'.2N	119°46'.0W	2-9-96	1045	394
13	33°07'.8N	119°51'.6W	2-9-96	1544	392
14	33°09'.6N	119°58'.3W	2-9-96	1807	566
15	33°11'.1N	120°04'.8W	2-9-96	2037	862
16	33°12'.9N	120°11'.4W	2-9-96	2310	1,108
17	33°15'.0N	120°18'.7W	2-10-96	0158	524
21	33°43'.9N	119°50'.7W	2-11-96	0054	180
24	32°59'.9N	120°22'.0W	2-12-96	0406	4
25	32°21'.9N	119°52'.3W	2-12-96	1257	72
26	32°45'.1N	119°17'.2W	2-12-96	2012	196
27	33°10'.9N	118°22'.7W	2-13-96	0852	476

To investigate the relation between prey availability and the abundance of feeding-stage hake larvae, I compared the average concentration of prey-sized particles in a sample to the concentration of feeding-stage hake larvae in that sample. To minimize the effect of strata sampled outside the spawning area (which would include no larvae regardless of prey concentration) I excluded all samples that contained zero hake larvae from the statistical analysis. In addition, since none of the 212 hake larvae larger than 3.9 mm SL examined by Sumida and Moser (1980) retained yolk-sac resources, I assumed that all hake larvae larger than 4 mm SL were capable of feeding.

An analysis of variance indicated that there was a significant, positive relation between the concentration of hake larvae larger than 4.0 mm SL in a given sample and the average concentration of prey-sized particles in that sample ($n = 47$, $r^2 = 0.158$, $p = 0.006$; figure 4). Thus, feeding-stage larvae became more abundant as the particle concentration increased.

I used the same procedure to examine the relation between prey concentration and the abundance of larvae smaller than 4.0 mm SL. Unfortunately, small hake larvae are very fragile, and they were not well preserved. Often the mouth and the gut, which may have contained a yolk sac, had been destroyed during collection, leaving only the more sturdy head and notochord. Therefore, one cannot assume that the fish included in this investigation were all yolk-sac-stage larvae. An analysis of variance indicated that the concentration of hake larvae smaller than 4.0 mm SL contained within a sample was
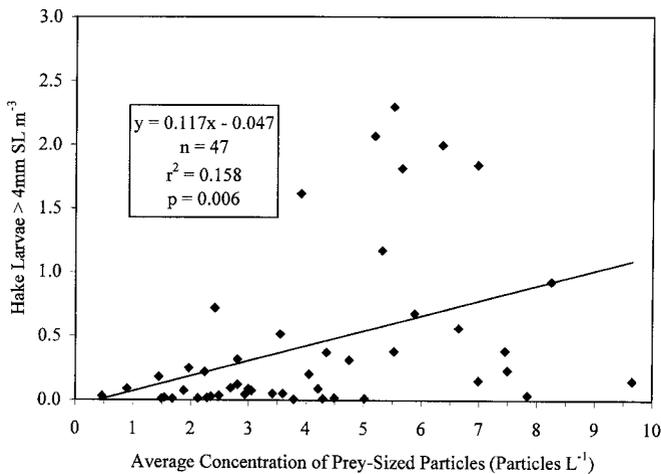
Figure 4. The abundance of larval hake larger than 4.0 mm SL as related to prey concentration. The data are the concentration of Pacific hake larvae larger than 4 mm SL found in a given stratum and the average concentration of prey-sized particles in that stratum. The *solid line* is the linear equation fitted to the data.
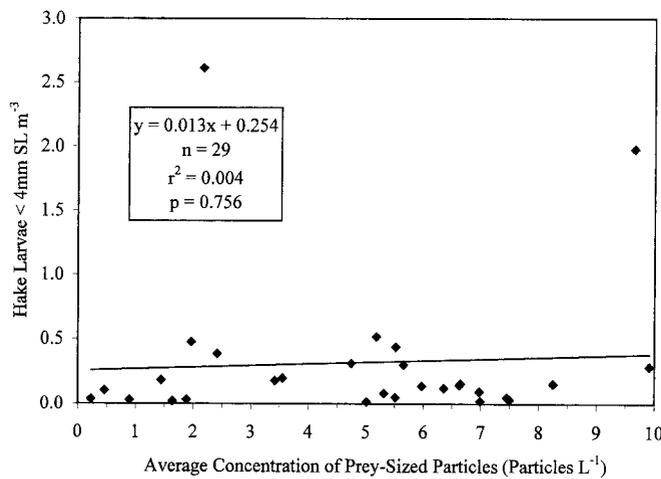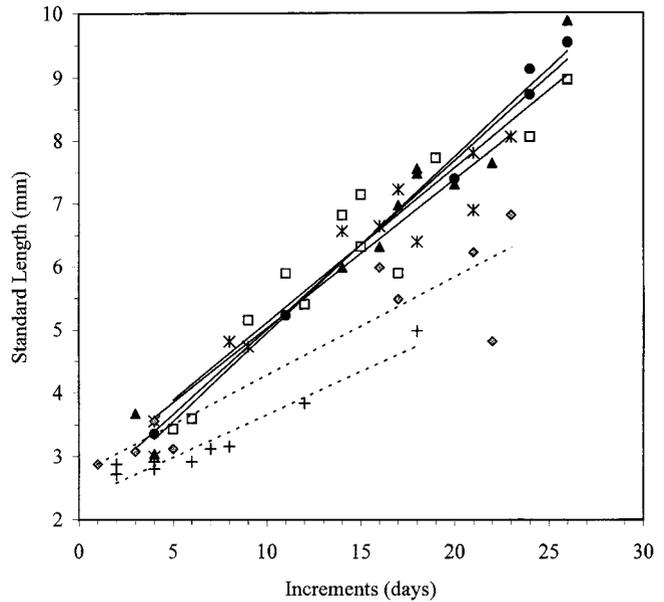

Figure 5. The abundance of larval hake smaller than 4.0 mm SL as related to prey concentration. The data are the concentration of Pacific hake larvae smaller than 4 mm SL found in a given stratum and the average concentration of prey-sized particles in that stratum. The *solid line* is the linear equation fitted to the data.

Figure 6. Size-at-age data for all fish analyzed. The various strata sampled are identified with symbols. The average particle concentration and temperature of the strata are given in the key. A linear equation was fitted to the data from each stratum. *Solid regression lines* indicate strata where the average prey concentration exceeded 2.40 prey-sized particles L^{-1}. *Dotted regression lines* indicate strata where the average prey concentration was less than 2.40 prey-sized particles L^{-1}.

not related to the average concentration of prey-sized particles in that sample ($n = 29$, $r^2 = 0.004$, $p = 0.756$; figure 5).

Growth as a Function of Temperature and Prey Concentration

Six stratified samples collected at five different stations were chosen for this analysis. The samples were not randomly selected. Instead, they were chosen to maximize the variation in the average temperature and particle concentration of the samples analyzed. Within the six strata sampled, the average temperature varied from 10.5°C to 12.4°C, and the average particle concentration ranged from 1.44 to 6.36 prey-sized particles L^{-1}.

The temperature range contained 70.8% of the hake larvae collected; the range of particle concentrations included 81.2% of the hake larvae.

The slope of a linear equation fitted to size-at-age data was used to estimate the average growth rate of the hake larvae within a sample. Although hake larvae do not grow in a strictly linear fashion, in every case the coefficient of determination, r^2, exceeded 0.845. It seems likely, therefore, that the size-at-age of hake larvae smaller than 11.0 mm SL can be adequately approximated by a monotonically increasing linear function, and that the average growth rate can be estimated with the slope of that function.

The average growth rates of hake larvae in the various strata ranged from 0.135 to 0.279 mm d^{-1}. Larvae grew at a rate of 0.235 to 0.279 mm d^{-1} in strata where the average particle concentration was ≥2.40 prey-sized particles L^{-1} (figure 6), but in strata with lesser concentrations the larvae grew more slowly. Below 2.40 prey-sized particles L^{-1}, average growth rates of 0.135 mm d^{-1} and 0.155 mm d^{-1} were measured (figure 6).
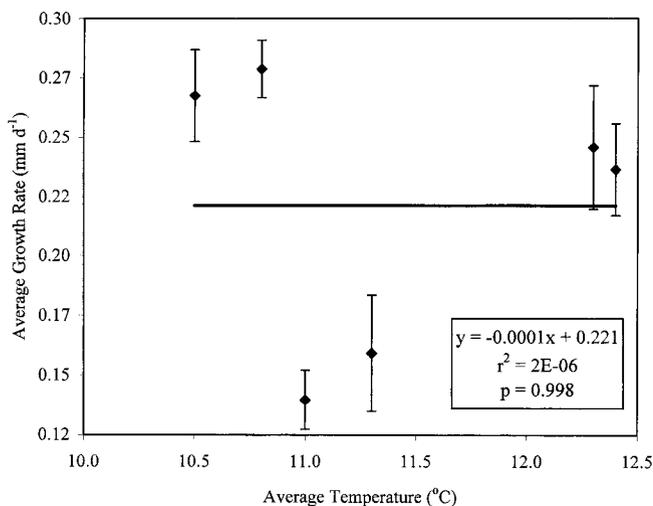
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Figure 7. The growth rate of hake larvae as related to temperature. Each data point shows the average growth rate of the larvae within a stratum and the average temperature of that stratum. The standard errors of the growth-rate estimates are shown. The *solid line* is the linear equation fitted to the data.
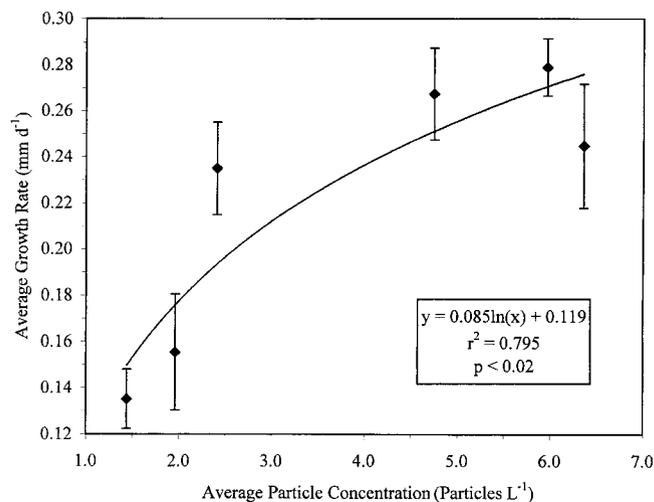

Figure 8. The growth rate of hake larvae as related to prey concentration. Each data point shows the average growth rate of the larvae within a stratum and the average particle concentration of that stratum. The standard errors of the growth-rate estimates are shown. The *solid line* is the logarithmic equation fitted to the data.

To examine the effect of temperature on the growth rate, I compared the average growth rate within each stratum to the average temperature of that stratum. I fitted a linear equation to the data, and tested the significance of the regression with an analysis of variance. The results of this analysis indicated that within the range of temperatures examined, the growth rate of hake larvae was not related to temperature (r^2 = 2E-6, p = 0.998; figure 7).

I used a similar analysis to examine the effect of particle concentration on the larval growth rate. I compared the average growth rate within a stratum to the average particle concentration of that stratum. These data indicated that hake larvae grew faster at elevated particle concentrations, but the relation was not linear. Instead, the results suggested a particle concentration above which the average growth rate did not increase. A logarithmic regression fitted to the data explained a large amount of the variance in the growth rate (r^2 = 0.795; figure 8). To test the significance of the logarithmic regression, I log-transformed the data and fitted a linear regression to the transformed data. An analysis of variance indicated a significant, positive relation between the average growth rate of hake larvae in a stratum and the average prey concentration of that stratum (r^2 = 0.786, p < 0.02). Therefore, it appears that particle concentration has a substantial influence on the growth rate of Pacific hake larvae.

DISCUSSION

The purpose of this study was to evaluate how prey concentration influences the abundance and growth rate

of Pacific hake larvae. This type of study has been attempted in the past for first-feeding clupeoid fishes that consume much smaller particles including diatoms and dinoflagellates (Lasker 1975, 1978, 1981), and for other gadoid fishes that, like the Pacific hake, consume copepod nauplii and larger zooplankton at first feeding (Buckley and Lough 1987; Canino et al. 1991). Unfortunately, previous attempts to understand the importance of starvation in natural fish populations have been confounded by the inability to simultaneously measure the small-scale distribution of both predator and prey. It has therefore been quite difficult to show that reduced availability of food inhibits the growth of fish larvae in the field. This study demonstrates that the OPC/MOCNESS makes it feasible to simultaneously collect Pacific hake larvae and make in vivo measurements of the abundance and fine-scale distribution of their prey.

This study indicated that Pacific hake larvae became increasingly abundant as the concentration of prey-sized particles increased. This relation could have been caused by several mechanisms. First, hake larvae may emigrate from areas where prey concentration is low, or move into regions where it is high. This mechanism seems unlikely because of the poor mobility of early-stage fish larvae and the large horizontal spatial scales of variability in prey concentration. But vertically, prey concentration varies over much smaller spatial scales (e.g., meters). Therefore this mechanism is feasible if hake larvae migrate vertically. Ahlstrom (1959) and Roberts and Ralston (unpublished data) indicate that there is no significant diel variation in the abundance of Pacific hake larvae captured in net collections. These results suggest that

hake larvae do not undergo diel vertical migration, but they may migrate on longer time scales.

Second, adults may choose to spawn in regions with high prey concentration. This also appears improbable, since the fish spawn at depths of 130 to 500 m (Bailey 1982), whereas larvae are abundant at 50 to 100 m (Ahlstrom 1959). In addition, because spawners do not appear to migrate vertically (Bailey 1982), they are unable to assess the adequacy of the nursery environment. Physical forcing could also cause aggregations of predator and prey. Unfortunately, this issue cannot be addressed with the data presented, but it remains a fascinating topic for future investigation.

This study suggests that elevated mortality caused the reduced abundance of feeding-stage larvae at low particle concentrations. Hake larvae larger than 4.0 mm SL have depleted their yolk-sac resources. Therefore, inadequate prey concentration can increase their mortality directly by increasing the starvation rate, and indirectly by lengthening the stages most vulnerable to predation, as well as by inhibiting the escape response (Ware 1975; Shepherd and Cushing 1980; Folkvord and Hunter 1986). This conclusion is further supported by the fact that there was no relation between the abundance of larvae smaller than 4.0 mm SL and prey concentration. A large portion of these small larvae were in the yolk-sac stage. Since larvae do not require exogenous food until yolk-sac resources are exhausted, there is no obvious mechanism to increase the mortality of yolk-sac larvae found at low prey concentrations.

It is difficult to relate larval growth rates to temperature and prey concentration. Changes in growth rates occur on time scales of days to weeks, whereas the average temperature and prey concentration of a stratum can change much more quickly (hours to days). My results indicate that in strata with high particle concentrations, larvae older than one week were larger than larvae of the same age collected from strata with lower particle concentrations. This trend persisted throughout the first month of life. There are two explanations for this finding: either it occurred by chance, or the ambient conditions where hake larvae are found persist over extended time scales (days to weeks). Since hake larvae are found in the stratified waters of the thermocline where wind-driven mixing is minimal, the latter explanation is reasonable.

This investigation demonstrates that there is a significant, positive relation between the growth rate of Pacific hake larvae and prey concentration. Where prey concentration exceeded 2.40 prey-sized particles L^{-1}, mean growth rates ranged from 0.235 to 0.279 mm d^{-1}. Below this concentration, growth was reduced by as much as 50%, to 0.135 to 0.155 mm d^{-1}. The lower values are consistent with a published average growth rate of 0.160

mm d^{-1} for hake larvae collected off southern California during 1977, 1978, and 1979 (Bailey 1982).

Recruitment of Pacific hake is positively related to a number of processes, including weak offshore transport in early winter (Bailey 1980, 1981; Bailey and Francis 1985; Hollowed and Bailey 1989); warm January sea-surface temperature (Bailey and Francis 1985; Hollowed and Bailey 1989); and increased upwelling in March (Hollowed and Bailey 1989). Bailey and Francis (1985) suggest that strong year classes often develop when water temperatures are warm; when spawning occurs at the northern extent of the potential spawning region, near Point Conception; and when larvae are abundant in the inshore regions. Arthur (1977) examined the distribution of microzooplankton in the California Current system and found that the abundance of microcopepods was 4 to 5 times higher in the inshore regions. In addition, Chelton (1981) reports that zooplankton biomass is generally higher in the northernmost region occupied by Pacific hake larvae and that zooplankton biomass decreases as one moves offshore, or to the south. Therefore, it is reasonable to conclude that the abundance of prey available to early-stage larvae determines, in part, the growth, survival, and eventual recruitment rates of Pacific hake.

ACKNOWLEDGMENTS

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MESOSCALE FISHING PATTERNS OF FACTORY TRAWLERS IN THE PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) FISHERY

MARTIN W. DORN
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, BIN C15700
Seattle, Washington 98115-0070

ABSTRACT

During 1991–95, up to 60% of the annual catch of Pacific hake (*Merluccius productus*) in the U.S. management zone was harvested by a U.S.–based fleet of factory trawlers. Optimal foraging theory was used to motivate a statistical analysis of movement patterns of these vessels. This study focused on the mesoscale characteristics of the environment (5–50 km), and vessel movement at these spatial scales. Geostatistical analyses of hake densities derived from the 1992 and 1995 National Marine Fisheries Service assessment surveys with quantitative echo-sounding techniques showed that strong spatial correlations of hake density do not extend beyond ~25–35 km. The range of Pacific hake spatial correlation suggests an association with mesoscale oceanographic features whose characteristic scale in the California Current system is determined by the Rossby radius of deformation (~25 km in mid-latitudes off the West Coast). The foraging patterns of factory trawlers can be described as a series of moves between trawling locations. The distance between successive hauls depends on whether the vessel continues fishing within a local area of high fish density, or moves to a different area. Generalized additive models (GAM) were used to examine influence of the catch rates of prior hauls on the distance between successive hauls. The GAM models suggested that deviations from the expected catch rate influence the decision to move from a local foraging area, as expected from optimization models of animal foraging. These decisions appeared to be based on relatively short time frames, such that information from only the most recent one or two hauls in the area is used. In addition, results indicated that the presence of other fishing vessels operating nearby reduces the probability that a vessel will leave an area.

INTRODUCTION

Factory trawlers—fishing vessels that both catch and process fish—are important in many fisheries worldwide (Garcia and Newton 1995). The advanced technology of these vessels (including hydraulic winches to set and retrieve extremely large nets, automated filleting machines, flash freezers, freezer holds, fish meal plants, electronic echo sounders, and GPS navigation and plotting equipment) enables them to efficiently catch and process

large quantities of fish (up to 500 metric tons per day). The ability of these vessels to operate independently of port services for extended periods is a significant advantage in harvesting migratory species like Pacific hake (*Merluccius productus*), whose spatial distribution can vary greatly from one year to the next. Since fish can be processed immediately after they are caught, these vessels produce a high-quality product from fish species whose flesh undergoes rapid proteolysis when held at ambient temperatures.

In this paper, I discuss the fishing patterns of factory trawlers as an example of the foraging behavior of animal predators. Although a factory trawler is, of course, a complex machine operated by a crew, from the perspective of its role in the ecosystem, it is reasonable to view it as a single agent—a midwater filter feeder that detects prey by using echolocation. A similar approach was used by Gillis et al. (1995a, b) to study discarding behavior in a trawl fishery subject to trip limits.

The foraging choices available to these vessels depend on the spatial and temporal scale of their assessment of the environment (Holling 1992). This paper focuses on the mesoscale characteristics of the environment (5–50 km) and vessel movement at these spatial scales. Since factory trawlers do not return to port regularly to deliver fish to a processing plant, their movement patterns at this scale are assumed to be a pure foraging process. Foraging behavior at this scale can be described as a series of movements between successive trawling locations. The focus of this paper is to develop statistical models for investigating the factors that influence these movements, particularly the movements which indicate that the vessel has left the area where it had been fishing previously.

The analyses of vessel movement presented in this paper are motivated by Arditi and Dacorogna's (1985, 1988) contribution to optimal patch foraging theory. Their work generalizes the marginal value theorem (Charnov 1976) to habitats with arbitrary prey distributions. Although they limit their consideration to one-dimensional habitats, this is not as restrictive an assumption as it seems. Many fisheries occur within relatively narrow depth limits parallel to the shelf break or the coastline. Arditi and Dacorogna (1988) show that when presented with an arbitrary prey distribution in a habitat, the optimal
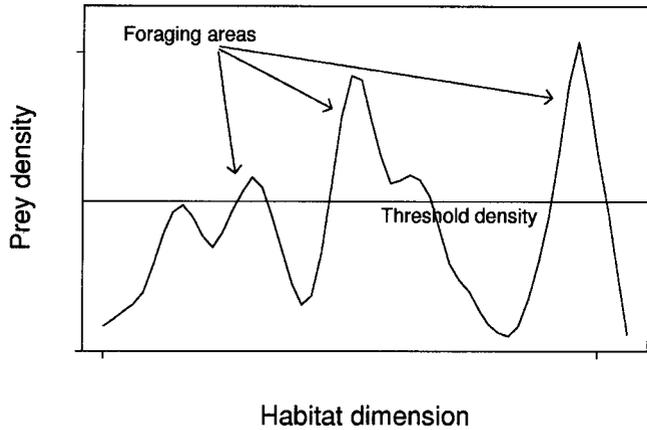
Figure 1.   Schematic of the Arditi and Dacorogna (1988) optimal foraging model. The threshold density partitions the habitat into areas of two types: those in which it is optimal to forage, and those where the optimal strategy is to transit as quickly as possible.

forager should partition the habitat into contiguous areas of two types: areas in which it is optimal to forage, and areas in which the optimal strategy is to traverse as quickly as possible without foraging.

In the areas where it is optimal to forage, the forager should move on when the density of prey declines below the critical density that partitioned the habitat into foraging and nonforaging regions (figure 1). The critical density is determined by the mean density of prey in the habitat as a whole (similar to the marginal value theorem) and by the forager's functional response curve. For a factory trawler, the functional response is the relation between fish density and surimi production, and is a nonlinear function of the capture efficiency of the net, the time required to set and retrieve the net, and the production capacity of the factory (Dorn, in press).

The Arditi and Dacorogna foraging model implies that the forager perceives its habitat as a "behavioral landscape" in which different activities are performed in different regions. This emphasis on the forager's perception is different from the marginal value theorem, where the pattern of the environment is assumed. The model suggests that the "patches" of classic optimal foraging theory may not be intrinsic to the environment, but a result of the forager's imposing a particular cognitive structure on the environment.

The critical threshold transforms an undifferentiated environment into a mosaic of two types of regions—foraging and nonforaging. The characteristic dimensions of those regions will depend on the spatial continuity of the prey population. A prey population with short-range spatial continuity would present the forager with many small patches to exploit. If the spatial correlation of the population extends to wider scales, the patches will be larger and fewer. Since the forager alternates between two patterns of movement (small-scale movements within

a foraging area, and larger-scale movements of transit between foraging areas) the spatial continuity of the prey population has important implications for how the forager moves.

The transition from the theoretical models of Arditi and Dacorogna (1988) to a statistical analysis of how catch rates affect vessel movement must confront the real complexity of the environment—that is, those important environmental characteristics not included in the theoretical model. Although the model allows the catch rate to decline in a foraging area only because of fishing activity, in fact, local changes in prey abundance may result from a variety of factors, many of them unrelated to fishing activity. Moreover, although the model assumes perfect knowledge of the environment, fishing vessels typically will not know in advance where prey density is high.

Catch rates for Pacific hake also follow a diel pattern, with the daytime rates about twice as high as nighttime rates when hake are dispersed through the water column. Catch rates vary between vessels because of differences in the nets used, horsepower, and other technological characteristics of the vessel. To standardize the catch rates by accounting for the diel trend and for differences in fishing power, a preliminary model was fit to the haul-by-haul catch rate data, with vessel and time of day as predictor variables. The residuals from this model were used in the analysis of vessel movement patterns. This approach follows Vignaux (1996a, b), who used a similar strategy to assess the spatial structure of fish distribution and to analyze fishing behavior in a trawl fishery off New Zealand.

The statistical analyses presented in this paper examine how catch rates and other information affect the decision to leave an area where a vessel is fishing. One might expect the catch rate of the target species to be the major factor in this decision, but other factors, such as the presence of other vessels nearby, may also be important. The first objective of the statistical analysis will be to evaluate how the catch rate of the most recent haul affects the decision to leave. Next, the effect of prior catch rates will be evaluated. Previous catches differ from the most recent catch by being farther away in space and time from the most recent catch. Since areas of higher than usual hake density are transient, fishermen may use a weighting function that assigns more emphasis to recent catches. An exponential weighting model has been used in theoretical work on other foraging situations (McNamara and Houston 1985) and will be evaluated here. In addition, how the presence of other vessels fishing nearby affects the decision to move will be evaluated. The presence of other vessels could induce the vessel to remain in the area longer than it would if the decision were based strictly on its own catch rate.

The subsequent sections of the paper are organized as follows. After a brief presentation of background information on the factory trawlers participating in Pacific hake fishery, results are presented from a geostatistical analysis of acoustic survey data to assess the spatial continuity of Pacific hake distribution. These results are used to select the appropriate spatial scale at which to assess vessel movement patterns. Then, from fishery data collected by at-sea observers, models are fit to the haul-by-haul catch rates of the factory trawler fleet during 1991–95, with time of day and a categorical term for individual vessels as predictor variables. The residuals from this model are then used in a generalized additive model (GAM) to predict the probability of movement from a foraging area. Other variables are also assessed in the model. Finally, the results are compared with those from other studies of spatial correlation and fishing behavior, and recommendations are offered about further research into fishing behavior.

FACTORY TRAWLERS AND PACIFIC HAKE

During 1991–95, an average of 14 factory trawlers and 5 mother ships participated in the Pacific hake at-sea fishery each year, with an average aggregate catch of 150,000 metric tons (t) per year. The factory trawlers in the Pacific hake fishery are large vessels (275–375 ft long), carry a crew of 70–100, and can remain at sea for several months. Between 50% and 70% of the crew is engaged in surimi production. Several work shifts operate the processing factory 24 h per day. Midwater trawls (mean trawl opening 90 × 55 m) are used exclusively for Pacific hake. The at-sea fishery operates as a "derby" fishery in which all vessels compete for the fleetwide quota. With the entry of U.S. factory trawlers and mother ships in 1991, the character of the at-sea fishery changed dramatically. Before 1991, the fishery had lasted for as long as 6 months; now it closes 3–4 weeks after the annual opening date of April 15.

As is usual with targeted midwater trawling, catches in the hake fishery are extremely pure, with bycatch typically amounting to less than 3% of the total catch by weight. The most common bycatch species are pelagic rockfishes and mackerels: yellowtail rockfish (*Sebastes flavidus*), widow rockfish (*Sebastes entomelas*), Pacific ocean perch (*Sebastes alutus*), jack mackerel (*Trachurus symmetricus*), and Pacific mackerel (*Scomber japonicus*). The bycatch is either discarded at sea or diverted to the fish meal plant. Although the bycatch of chinook salmon (*Oncorhynchus tshawytscha*) is low (4,000–6,000 fish per year), it is an important concern because of the extremely low abundance of many West Coast chinook salmon populations. Several West Coast chinook salmon runs are listed as endangered under terms of the U.S. Endangered Species Act (Waples et al. 1991; Fisher 1994).

METHODS

Analysis of Pacific Hake Spatial Pattern

Geostatistical techniques were used to assess the spatial continuity of Pacific hake by means of data from acoustic resource assessment surveys conducted by the NOAA research vessel *Miller Freeman* during July–September of 1992 and 1995 (Dorn et al. 1994; Wilson and Guttormsen 1997). Acoustic data were collected with a Simrad EK500 scientific echo-sounding system (Bodholt et al. 1989) that used a 38-kHz transducer mounted on the vessel's centerboard 9 m below the waterline. Acoustic data were processed on a SUN workstation with Simrad BI500 echo-integration and analysis software (Foote et al. 1991) to exclude non-hake sound-scatterers from the echo integration.

The survey design consisted of equally spaced east-west transects extending from 30 m to approximately 1,500 m bottom depth. Transects were spaced 10 nautical miles (nmi) apart for most of the survey, with higher-density spacing (5 nmi) in the Juan de Fuca Canyon–La Perouse region (48°–49°N lat.). Survey transects were run only during daylight hours because hake disperse at night. The acoustic backscatter attributed to Pacific hake by 0.5-nmi transect section was converted to fish density by means of a length-target strength relationship of $TS = 20 \log(length) - 68$ (Traynor 1996). Since 40–60 days are required to conduct a coastwide acoustic survey of Pacific hake, some redistribution of fish would be expected during the survey operations. But adjacent transects were almost always surveyed within one day, and usually within several hours, so the effect of fish redistribution should be relatively minor at scales less than the transect spacing. To analyze spatial correlation with acoustic survey data, it is necessary to assume that the data provide an instantaneous "snapshot" of Pacific hake distribution patterns.

Directional correlograms (Rossi et al. 1992) were estimated for mean hake density by 0.5-nmi transect section, $z(x_i)$, where x_i is location of the transect section. Separate correlograms were estimated for E-W (east-west) and (N-S) north-south directions, with a directional tolerance of $\pm 45°$. In the E-W direction, binning intervals of 2.5 km were used to a maximum distance of 50 km; in the N-S direction, binning intervals of 10 km were used to a maximum distance of 80 km. Different binning intervals were used because the survey design of parallel E-W transects yields fine-scale information on spatial correlation along the transect in the E-W direction, but relatively coarser information in the N-S direction (Pelletier and Parma 1994). Since the orientation of the shelf break is north-south in the area where the fishery operates, the N-S correlogram measures along-shelf spatial correlation, while the E-W correlogram measures the cross-shelf correlation.

In addition, I estimated an omnidirectional correlogram, using the same binning strategy as for the E-W correlogram. The estimation was restricted to acoustic data collected north of 41° and east of 127°W, an area roughly corresponding to the area where the fishery operates. The correlogram is a plot of the lag correlation, $\hat{\rho}(h)$, such that

$$\hat{\rho}(h) = \frac{\frac{1}{N(h)} \sum_{i=1}^{N(h)} [z(x_i) - m_{-h}][z(x_i + h) - m_{+h}]}{s_{-h}\, s_{+h}},$$

where $z(x_i)$ and $z(x_i + h)$ are pairs of hake densities separated by vector distance h; m_{-h} and m_{+h} are the means of the initial and terminal points of the vectors used to estimate the lag correlation; and s_{-h} and s_{+h} are the standard deviations of the initial and terminal points. Rossi et al. (1992) call this the non-ergodic correlogram to distinguish it from the more usual spatial correlogram where the global mean is subtracted out, and the global variance is used to scale the covariance. Rossi et al. (1992) recommend this form of the correlogram for ecological applications where nonstationarity in local means and variances is frequently encountered.

To demonstrate how the spatial structure in hake distribution might be perceived by fishing vessels, I used hake density by 0.5-nmi transect section to estimate structure functions. The structure function describes the spatial pattern of resources from the perspective of the forager (Mangel and Adler 1994). I applied an indicator transform to hake densities of the form

$$i(x;z) = \begin{cases} 1 & \text{if } z(x) \geq k \\ 0 & \text{if } z(x) < k \end{cases},$$

where the threshold density ($k = 635\ kg\ ha^{-1}$) is the value of hake density such that the median of all acoustic densities greater than the threshold is equal to the median density implied by the catch rates for factory trawlers during the fishery.

To obtain an expected density from the fishery catch rates, I determined the area swept by the net from the haul duration, towing speed, and the horizontal opening of the net (= 90 m, the mean net width recorded by several observers). Daylight hauls (between 0600 and 2000 Pacific Standard Time) made by factory trawlers during the 1991–95 seasons were used. Since a strong avoidance response has been reported for Pacific hake when encountering midwater trawl nets (Nunnallee 1991), the assumption of 100% capture efficiency is unjustifiable. To estimate the threshold density, I assumed that a commercial midwater trawl would capture 50% of the fish in the water column, and evaluated the sensitivity of the results to this assumption. It should be emphasized that the purpose here was to obtain a rough

approximation of the spatial pattern and geographic extent of the regions where fishing would be successful.

The structure function is defined as

$p(i(x + h) = 1 \,|\, i(x) = 1)) = $ Prop {resource at vector distance h away, given that there is resource at the current point}

$p(i(x + h) = 1 \,|\, i(x) = 0)) = $ Prop {resource at vector distance h away, given that there is no resource at the current point}.

In this definition, the structure function has been generalized from Mangel and Adler (1994) to allow the structure function to vary depending on the direction away from the current point. This broader definition of the structure function makes it possible to consider directional structure functions similar to directional correlograms. To estimate the structure function, I followed the algorithm of Mangel and Adler (1994):

$$\hat{\rho}(i(x + h) = 1 \,|\, (i(x) = 1)) = \frac{\sum_{k=1}^{N(h)} i(x_k + h)\, i(x_k)}{\sum_{k=1}^{N(h)} i(x_k)}.$$

In estimating the structure function, I used the same binning strategies that were used to estimate the directional correlograms.

Catch Rate Model

NMFS-certified observers are placed on all factory trawlers and mother ships in the at-sea fishery. While on board, observers maintain a complete record of the catch weight, duration, set and retrieval times, and retrieval location for each haul made by the vessel. Set location, however, is not recorded, which limits the spatial resolution of estimated distances between trawling locations. A tow that retraces the path of the previous tow in reverse direction could have a retrieval location farther than 10 km away. Alternatively, two tows that end at the same location could have trawled toward that location from opposite directions. Since all vessels carry observers, there is a complete record of all hauls during the fishery. This record is kept in the NORPAC database, an ORACLE relational database maintained by the North Pacific Observer Program at the Alaska Fisheries Science Center (7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070). The number of hauls in each fishing season by factory trawlers ranged between about 1,000 and 2,000 (table 1).

A generalized additive model (GAM) with Poisson error (Hastie and Tibshirani 1990) was used to standardize the catch rates. This form of GAM has been used in marine ecology applications to analyze trawl survey

TABLE 1
Number of Factory Trawlers and Mean Catch Rates in the 1991–95 Pacific Hake Fishery

Year	Number of factory trawlers	Number of hauls	Average catch rate (t/hr)
1991	9	1,940	41.8
1992	14	1,743	43.4
1993	13	1,227	44.2
1994	7	1,192	60.5
1995	9	954	39.6

data (Smith 1990; Swartzman et al. 1992). Poisson regression is a pragmatic choice for "count-like" data where the variance is proportional to the mean (McCullagh and Nelder 1983),

$$E[cr_i] = \mu(x_i)$$

$$\text{Var}[cr_i] = \phi \, \mu(x_i),$$

where cr_i is the catch rate in t hr^{-1} for the ith haul; $\mu(x_i)$ is the expected catch rate of the ith haul as a function of a vector of covariates x_i; and ϕ is an overdispersion parameter that models the additional variability in the data relative to the Poisson distribution, where the variance is equal to the mean (Lawless 1987).

The structural part of the model consisted of two additive terms: a categorical term for vessel, and a "smooth" function of time of day (average of set and retrieval times) estimated with the *loess* scatterplot smoother (Chambers and Hastie 1992). Because of the short duration of the at-sea hake fishery (3–4 wk), a seasonal effect was not considered necessary in the model. The additive part of this model is log-linear; that is, $\mu(x_i) = \exp[\eta]$, where η is the additive predictor. Separate models were fit for the 1991–95 seasons. A span width (fraction of the data used by *loess* to estimate local linear regressions) was fixed at 0.3 on the basis of a series of trial models in which the span width was varied systematically. A span width of 0.3 provided enough flexibility to capture the diel trend while at the same time excluding higher-frequency variation from the smooth term.

Statistical Models of Vessel Movement

Although the focus of this analysis is to determine the factors leading to a decision to leave a mesoscale aggregation of fish, without an extensive acoustic survey conducted at the same time as the fishery, it is difficult to know with certainty when this decision is made. Consequently, it was necessary to use some easily measurable proxy for this decision. If a critical distance between successive trawling locations is chosen appropriately, it should be possible to partition the intertrawl movements into those within an area and those representing a transit between areas.

For this research, a distance of greater than 30 km between haul retrieval locations was selected as the criterion for moving to a new area. This criterion was based on the examination of Pacific hake spatial patterns during the 1992 and 1995 acoustic surveys reported in the results, which suggests that strong spatial correlations do not extend beyond ~25–35 km. Consequently, the dependent variable in the statistical model is the geometric distance between successive haul retrieval locations recoded as 0-1 variable, where 0 denotes a distance of less than 30 km, and 1 denotes movement of greater than 30 km. Mean trawling distance, assuming the vessel travels in a straight line for the duration of the haul, was 16.2 km during 1991–95, which is roughly one-half the range of spatial correlation of 30 km.

Logistic regression is the primary statistical model for analyzing binary response data. Logistic regression predicts the probability of an event (movement greater than 30 km) based on a set of covariates. Since the Arditi and Dacorogna (1988) model suggests that a threshold catch rate triggers the decision to move, a flexible regression technique (the GAM described above) was used for the statistical analyses. The expectation and variance for logistic regression are

$$E[y_i] = \pi(x_i)$$

$$\text{Var}[y_i] = \pi(x_i)[1 - \pi(x_i)]$$

where y_i is the 0-1 response variable, and $\pi(x_i)$ is the probability of moving to a new area following the ith haul as a function of a vector of covariates x_i. In a GAM, the linear predictor of logistic regression is replaced by an additive predictor with the general form $\eta = f_1(x_1) + f_2(x_2) + \ldots + f_p(x_p)$, where $f_j(x_j)$ is a smooth function of x_j. As with the Poisson model, this "smooth" function is estimated with local linear regressions. The probability of the event is linked to the additive predictor by the logistic function $\pi(x_i) = \exp(\eta)/[1 + [\exp(\eta)]$. Potential covariates examined with this modeling framework were the catch rate residual for the ith haul, an exponentially weighted average of the catch residuals for previous hauls within 30 km, and the number of other vessels fishing nearby, where *nearby* is defined as the number of vessels within 15 km over the previous 6 hrs. Separate models were fit for the 1991–95 seasons. This model and the Poisson regression model for catch rates were fit by means of the statistical modeling language S-Plus (StatSci 1993).

RESULTS

Spatial Analysis

In 1992 and 1995 NMFS acoustic surveys, areas of high Pacific hake density were found mostly in a narrow
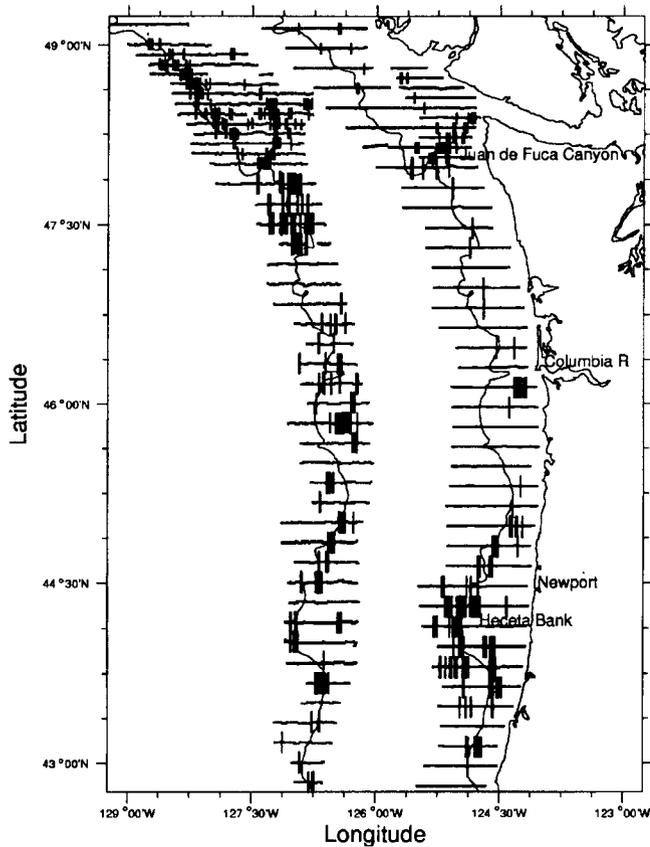
Figure 2. Pacific hake density in 0.5-nmi transect segments for the 1992 and 1995 NMFS acoustic surveys. To show both surveys, data for the 1992 survey is offset to the west by 2° longitude. Transect segments in which the Pacific hake density was greater than 635 kg ha^{-1} (the nominal density required to support fishing activity) are marked with *vertical bars*. The 300-m isobath and survey transects are also shown.

Figure 3. Directional correlograms for the 1992 and 1995 NMFS acoustic surveys of Pacific hake.

N-S band close to the continental shelf break (figure 2). Consequently, the E-W dimensions of the area where the fishery can operate are much narrower than its N-S dimensions. Interspersed regions of high and low density extend along the entire coast. Certain features along the shelf break tend to support higher densities of Pacific hake (e.g., Heceta Bank off central Oregon and Juan de Fuca Canyon off Cape Flattery), but high densities are not confined to these areas.

In 1992, densities in excess of 635 kg ha^{-1} represented 8.9% of the surveyed area north of 41°N and east of 127°W, but 18.2% of the area within the 150–600-m bottom-depth range, where most fishing occurs. In 1995, the percentages were 4.8% for the surveyed area and 11.4% for the area within the 150–600-m bottom-depth range. The decrease in the area of high fish density from 1992 to 1995 may be due to an estimated 23% decline in the total biomass within these depth and geographic boundaries. A relation between overall abundance and the proportion of potential habitat that is occupied has been observed for many fish populations (MacCall 1990).

The spatial correlograms support the depiction of hake spatial pattern in figure 2. The E-W directional correlogram for the 1992 survey declines from 0.56 at a distance of 0–2.5 km to near zero at ~25 km (figure 3). The N-S directional correlogram is similar to the E-W correlogram at larger distances (>8 km) where comparison is possible. Despite differences in overall abundance and the location of the higher-density areas in the 1995 survey, the directional correlograms for the 1995 survey show a similar pattern to the 1992 correlograms (figure 3). As with the 1992 correlograms, the E-W and N-S directional correlograms for the 1995 acoustic survey are similar at lag distances where comparison is possible. There is a slight positive correlation (~0.025) extending from 30 to 60 km in the 1995 survey that does not appear in the 1992 correlograms, but this correlation is only about 5% the correlation at a range of 0–2.5 km.

The data used to estimate the N-S correlation for the smallest lag distance (0–10 km) were collected along transects in the Juan de Fuca Canyon–La Perouse region, the only area where the transect spacing was 5 nmi in both the 1992 and 1995 surveys. Since this a bathymetrically complex region—with a narrow, steep-walled canyon and a large offshore bank—the correlation structure in this region may differ from other locations along the West Coast where the bathymetry is less complex. Additional acoustic data collected along transects oriented at angles to the usual survey grid are needed to adequately assess anisotropy. Although figure 2 suggests the presence of larger-scale N-S structure (that is, higher densities in the Heceta Bank and Juan de Fuca canyon area and lower densities elsewhere) the spatial statistics interpret these patterns as N-S trends rather than as a spatial correlation (Swartzman et al. 1992). From the perspective of the fishing vessel, the key spatial characteristics of the hake population would appear to be (1) a narrow, elongated region of potential occurrence, and (2) transient fishable aggregations of 20–30 km in size that can be fished on multiple times.
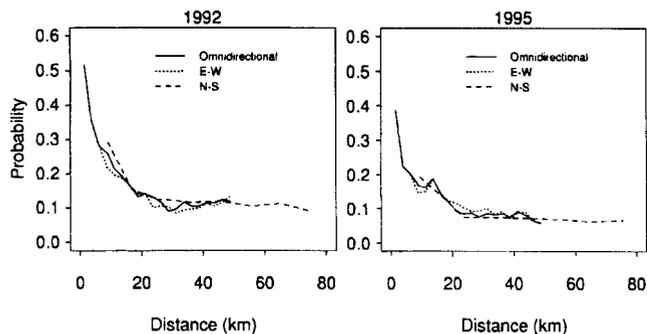
Figure 4. Directional structure functions for the 1992 and 1995 NMFS acoustic surveys of Pacific hake. Only the first part of the structure function is shown; that is, the conditional probability of finding hake densities higher than the threshold density at vector distance *h* away, given that the density is higher than the threshold at the current location.
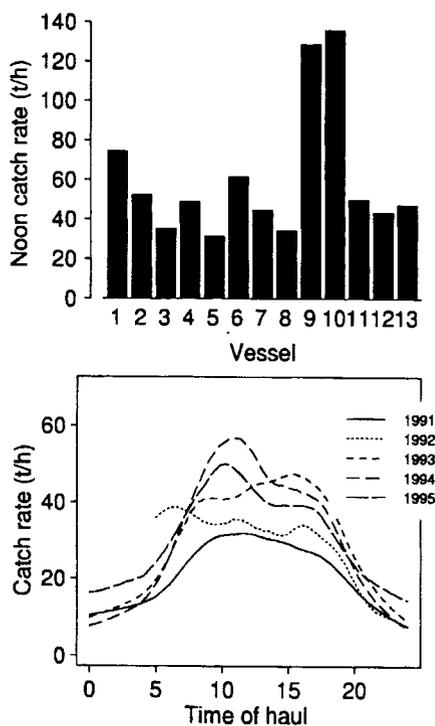

Figure 5. Poisson catch rate regression predictions for noon catch rate by vessel in 1993 and by time of haul for 1991–95 for a single vessel that fished in all years.

The directional structure functions for the 1992 and 1995 NMFS acoustic surveys are shown in figure 4. The E-W and N-S structure functions are similar for both surveys. The structure functions for 1992 and 1995 show similar patterns, with a conditional probability of 0.5–0.4 of finding high fish densities at short distances (<2.5 km) and a rapid decline to baseline levels at 25–35 km. This decline is slightly steeper than the decline in the correlograms. As distance increases, the conditional probability for finding high fish density approaches the unconditional probability (~0.10 in 1992 and ~0.05 in 1995).

The estimated structure functions are fairly robust to the choice of a threshold density in the range of plus or

minus 25% of 635 kg ha^{-1}. At higher threshold densities, there is a tendency for the conditional probability of high fish density to decline more rapidly than at lower thresholds, so that baseline levels are reached at ~20 km rather than 30 km. Consequently, inaccuracies of this magnitude in the length-TS relationship for hake or in the assumed 50% capture efficiency of midwater trawls would not cause a severe bias. These results suggest that if a vessel moves more than ~30 km away from its current fishing location, its probability of encountering high densities of hake is similar to the probability at a location chosen at random within potential hake habitat. Consequently, these results provide the rationale for the statistical analysis of vessel movement, where a movement of greater than 30 km between trawling locations is assumed to represent a decision by the fishing vessel to leave a local area of high density.

Catch Rate Model

Since the objective of fitting the Poisson regression model to the catch rates was to obtain a set of catch rate residuals for additional analysis, I present only general features of the model. For each year 1991–95, both terms in the model, vessel and time of day, are highly significant ($p < 0.001$). The high significance level indicates that vessel and time of day are important influences on the catch rate, but this result is at least partly due to the large amount of observational data available for fitting the model (table 1). The GAM analogue to the coefficient of determination—1.0 minus the ratio of the model deviance to the deviance for a null (mean) model (Swartzman et al. 1992)—ranged from 25.5% in 1991 to 43.9% in 1993. The relatively low r^2 values suggest that there is considerable variation in catch rates not explained by the model.

Model results are best interpreted by looking at model predictions rather than by directly examining the model coefficients. Most vessels tended to have similar predicted noon catch rates, although in each year, several vessels had predicted catch rates that were more than twice those of the rest of the fleet (figure 5). Figure 5 shows the predicted catch rates only for 1993, but the pattern for the other years was similar. In particular, vessels with higher catch rates in 1993 consistently experienced higher catch rates than the rest of the fleet throughout 1991–95. These variations may be explained by differences in vessel or net characteristics, variation in fishing skill, or differences in fishing strategy. For example, some vessels may spend more time searching, but target only the highest densities they encounter while searching.

The GAM smooth term for time of day (mean of set and retrieval times) generally shows an increase in catch rate at ~0600, and a decline at ~1800 (all times are Pacific Daylight Time, UTC+7; figure 5). Sunrise and
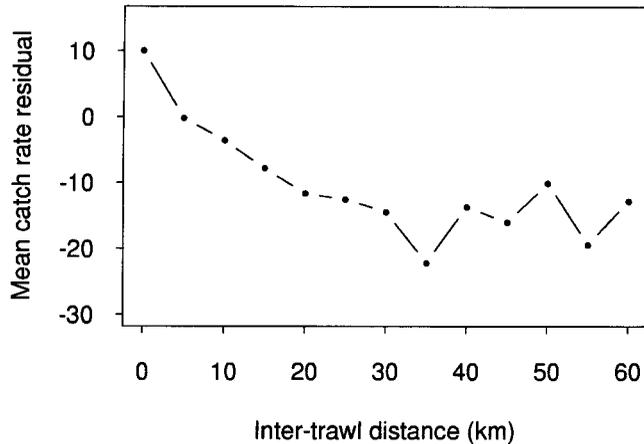
Figure 6. Mean catch rate residual versus intertrawl distance (distance between successive haul retrieval locations) for factory trawlers during 1991–95.

sunset on 1 May at 45°N, 125°W (the approximate location of Heceta Bank off central Oregon) occur at 0611 and 2024, suggesting that the diel variation in catch rates is closely coupled to ambient light levels. In 1992, fishing was prohibited during nighttime (from midnight to one hour after official sunrise) to reduce the bycatch of chinook salmon. In contrast to other years, the GAM smooth term for 1992 does not show an increase in the predicted catch rate at sunrise. In 1991, 1992, 1994, and 1995, catch rates peaked in midmorning (~1000), but in 1993, for reasons that are unclear, they peaked in the afternoon instead. Figure 5 shows the predicted diel pattern in catch rate for only a representative vessel in all years. Since the additive predictor for Poisson regression is log-linear, the pattern for other vessels would simply be scaled upwards or downwards by a multiplicative factor. The mean catch rates for the entire factory trawler fleet were similar in 1991–93 and 1995, whereas in 1994 the catch rate was 43% higher than the average for the other years (table 1).

The catch rate residuals $(cr_i - \hat{cr}_i)$ have a nearly symmetric distribution, with a mean of zero (as expected) and a median of -7.16 t hr^{-1}. There are a few extremely large positive residuals (maximum 1,628.0 t hr^{-1}), suggesting that some skewness is present. However, only 1% of the residuals are larger than 218.5 t hr^{-1}. A plot of the mean catch rate residual versus intertrawl distance provides additional support for the use of a 30-km intertrawl distance to indicate the decision to move to a new area (figure 6). For intertrawl distances less than ~30 km, the mean catch rate residual decreases with increased intertrawl distance, whereas at distances greater than ~30 km, the mean catch rate residuals are strongly negative, and show no consistent relationship with intertrawl distance. This suggests that the pattern of spatial correlation detected in the acoustic survey data is perceived in a similar way by fishing vessels.

GAM Models of Vessel Movement

The sequence of terms assessed in the models consisted of (1) the catch rate residual for the most recent haul; (2) a weighted average of previous hauls within 30 km, including an assessment of the appropriate exponential weighting coefficient to use; and (3) the number of other vessels operating nearby. This order was established so that the most recent information on the target species would be assessed first, while information that is less recent, or less sure (in the case of information on the activity of other vessels) would be addressed subsequently. Trial models with a term for the number of vessels added first showed smaller declines in deviance
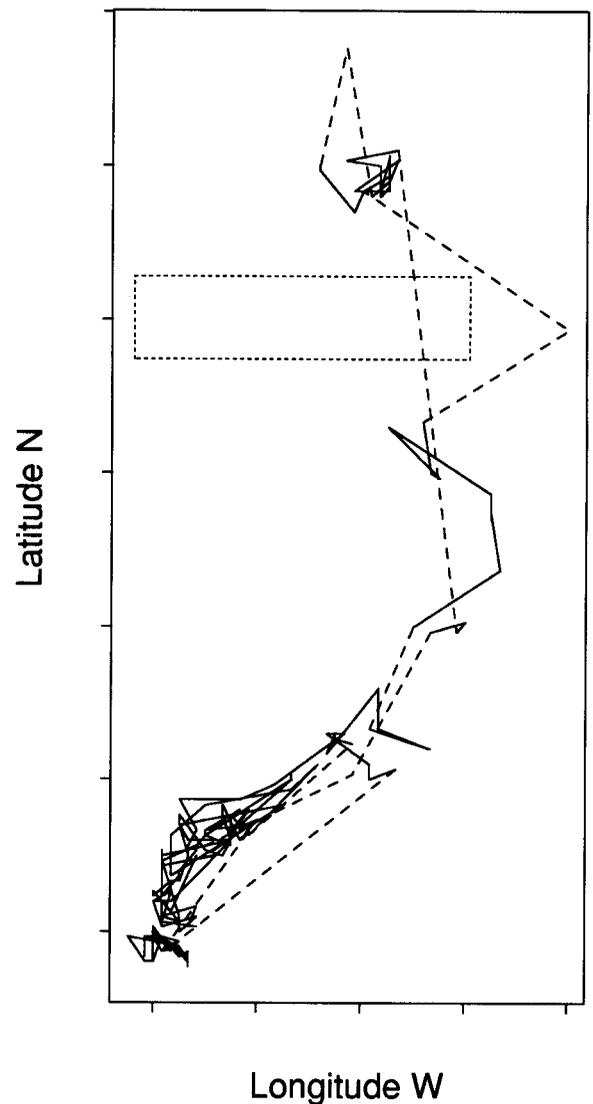

Longitude W

Figure 7. Path of a single factory trawler during a 28-day opening in 1994, constructed by connecting the haul retrieval positions with straight lines. Solid lines connect consecutive haul retrieval locations less than 30 km apart; dashed lines connect those farther than 30 km apart. The E-W scale on this figure has been expanded to better depict the fine-scale structure of the path. The box is 30 km square.

than models with a term for the catch rate residuals added first. This suggests that the order in which terms were evaluated was a reasonable approach.

Before fitting models, I conducted several exploratory data analyses. Figure 7 shows the path of a single vessel during a 28-day opening in 1994, constructed by connecting the haul retrieval positions with straight lines. Searching behavior between hauls would, of course, not appear on this figure. The distribution of between-trawl move distances during 1991–95 has a mean of 14.2 km, a median of 8.0 km, and is skewed significantly to the right (figure 8). Out of a total of 6,914 valid observations for 1991–95, 530 (7.7%) consisted of move distances greater than 30 km, the criterion assumed to indicate a decision to move to a new area.

A comparison of models with linear and smooth terms for the catch rate residual of the immediately preceding haul evaluated whether there was significant nonlinearity between the catch rate residual and the probability of movement. I selected a span width of 0.5 for the smooth term by fitting a series of trial models with varying span widths for the 1994 data, and choosing a width that provided enough flexibility to capture the nonlinearity in the data, but did not result in an excessive amount
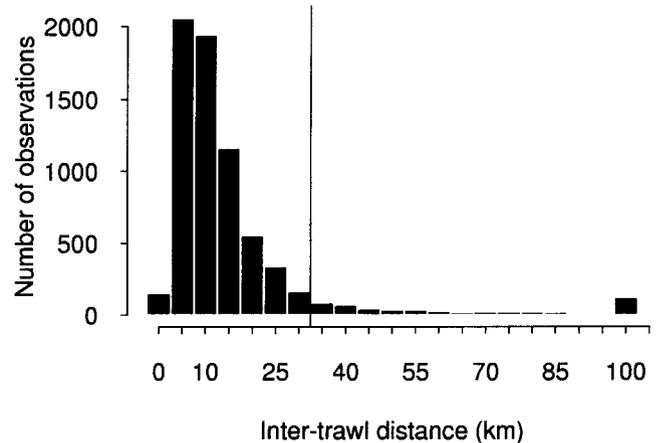
Figure 8. Frequency distribution of the distances between successive haul retrieval positions for factory trawlers in the Pacific hake fishery, 1991–95. The final bar of the histogram includes all distances greater than 100 km.

of roughness in the smooth term. The addition of a smooth term for the catch rate residual for the immediately preceding haul was significant at $\alpha = 0.05$ in the GAM models for four out of the five years (table 2). P-values based on likelihood ratio tests (Hastie and Tibshirani 1990) for adding the nonlinear smooth term ranged from <0.001 in 1991 to 0.128 in 1993.

TABLE 2
Analysis of Deviance for Logistic Regression GAMs for the Probability of Vessel Movement in 1991–95

Year	Model[a]	Residual df	Residual dev.	Δ df[b]	Δ dev.	P-value[c]
1991	Null	1908.0	1046.1	—	—	—
	+ linear CR	1907.0	1013.3	1.0	32.8	0.000
	± smooth CR	1902.2	991.1	4.8	22.2	0.000
	± AVGCR	1902.3	983.9	−0.2	7.2	No test
	± NVESS	1898.1	933.8	4.2	50.1	0.000
1992	Null	1680.0	1052.4	—	—	—
	+ linear CR	1679.0	1037.9	1.0	14.4	0.000
	± smooth CR	1673.6	1025.6	5.4	12.3	0.039
	± AVGCR	1673.7	1012.5	−0.1	13.2	No test
	+ NVESS	1670.4	970.7	3.3	41.8	0.000
1993	Null	1201.0	533.9	—	—	—
	+ linear CR	1200.0	527.8	1.0	6.1	0.014
	± smooth CR	1194.9	519.1	5.1	8.7	0.128
	± AVGCR	1195.0	516.1	−0.1	3.1	No test
	+ NVESS	1191.3	497.7	3.7	18.4	0.001
1994	Null	1176.0	468.2	—	—	—
	+ linear CR	1175.0	464.8	1.0	3.4	0.065
	± smooth CR	1170.0	446.1	5.0	18.7	0.002
	± AVGCR	1170.2	442.0	−0.2	4.1	No test
	+ NVESS	1166.8	435.2	3.4	6.7	0.107
1995	Null	943.0	603.1	—	—	—
	+ linear CR	942.0	582.1	1.0	21.1	0.000
	± smooth CR	937.5	570.5	4.5	11.6	0.030
	± AVGCR	937.4	556.1	0.1	14.4	No test
	+ NVESS	932.9	537.6	4.5	18.5	0.002

[a]Terms in additive predictor: null—intercept term only; linear CR—linear term for catch rate residual of the most recent haul; smooth CR—smooth term for catch rate residual; AVGCR—smooth term for the weighted average of catch rate residuals within 30 km using an exponential coefficient of 3.5; NVESS—smooth term for the number of vessels operating within 15 km over the previous 6 h. Terms were added to the models in the order they occur in the table. The "+" symbol indicates that the term has been added to the model; the "±" symbol indicates that the term replaces the previous term.
[b]The degrees of freedom for smooth terms quantify the degree of "smoothness" of the term (Hastie and Tibshirani 1990).
[c]P-values (from a $\chi^2_{\Delta df}$ distribution) are for a likelihood ratio test of the change in deviance between models.
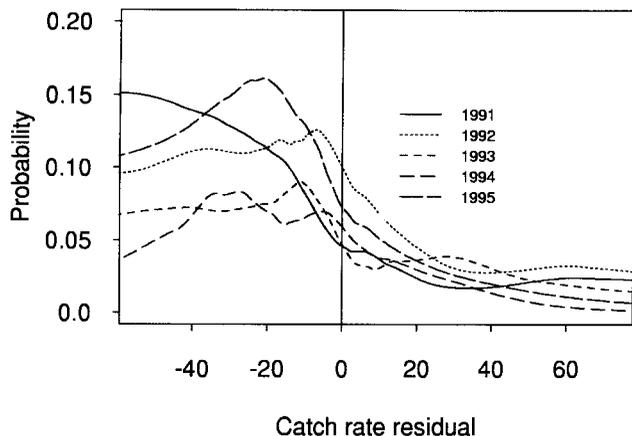
Figure 9. Generalized additive model (GAM) predictions of the probability of movement as a function of the catch rate residual for the most recent haul. The upper and lower limits of the x-axis are the 0.05 and 0.95 quantiles of the catch rate residual.
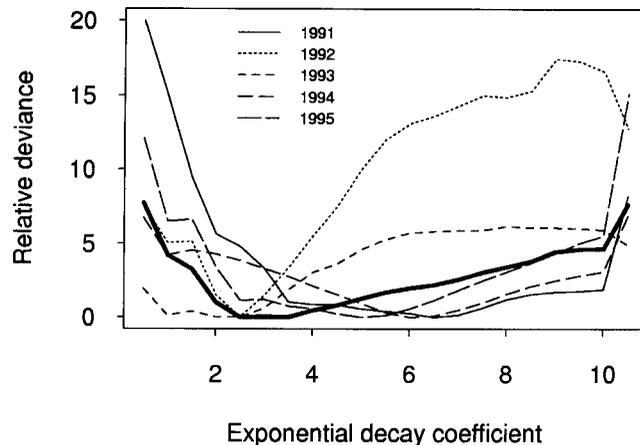

Figure 10. Deviance profiles for 1991–95 of the exponential coefficient (r) in the exponential average summarizing previous fishing experience. The farthest right point of the profile is the deviance for a model with only the most recent haul. The *bold line* is the mean for all years.

The smooth term for the catch rate residual for each year consistently shows an increased probability of movement with declining catch rates (figure 9). Although there are some differences between years, in general the predicted probability of movement is low when the catch rate residual is positive, increases relatively rapidly when the catch rate residual becomes negative, then remains stable at higher levels with further decreases in the catch rate residual. To address whether these results were being driven by the behavior of only a few vessels, models with individual terms for vessel were fit for 1993 and 1994 by means of regular logistic regression. Patterns of increasing probability of movement with declining catch rates were consistent for all vessels, although there was considerable variation in the slope and the inflection point of the logistic curves.

To model the role of earlier information in the decision to leave an area, it was necessary to consider which hauls would be used and how much influence they should have. Certainly, recent nearby hauls should receive the most weight, but during the course of a fishing season a vessel moves several times, and often returns to a location that was fished earlier in the season. The particular summary of previous experience used for this analysis was an exponentially weighted average, m_j, of previous hauls, such that the catch rate residual for the most recent haul received a weight of 1.0, and previous hauls within 30 km of that haul received progressively less weight the further back in time that they occurred:

$$m_j = \frac{\sum_{k=1}^{j} (cr_k - \hat{cr}_k)\, i_j(k)\, e^{-rt_j(k)}}{\sum_{k=1}^{j} i_j(k)\, e^{-rt_j(k)}} .$$

where $i_j(k)$ is an indicator function that takes the value 1.0 if the kth haul is within 30 km of the jth haul and zero otherwise; $t_j(k)$ is the time in days from the kth haul to the jth haul; and r is an exponential coefficient that governs the rate that the catch rate residuals from earlier hauls are down-weighted relative to the most recent haul. This summary of previous fishing experience was calculated on a vessel-by-vessel basis, not for the fleet as a whole.

The key parameter in this approach to modeling past information is the exponential coefficient, r. To gain some insight into the appropriate choice for r, I obtained deviance profiles across r for each year by varying r incrementally from 0.5 to 10 in steps of 0.5. Although the shape of the r profile differed between years, in each year there was a value of r that resulted in a lower deviance than the model which used only the most recent catch rate residual (figure 10). The minimum deviance r values were generally in the range of 2.0–6.5 (which imply half weights of 2.5–8 hrs). The value of r with minimum deviance for all years was 3.5, which results in a half weight of 4.8 hrs; that is, a haul retrieved 4.8 hrs before the current haul receives half the weight in the weighted average. The average time between haul retrievals on a factory trawler is usually about 5 hrs (mean haul duration 2.5 hrs, mean time between hauls 2.5 hrs). This suggests that the decision to leave an area is based on information from only the most recent 1–2 hauls. The change in deviance for $r = 3.5$ ranged between 3.1 in 1993 and 14.1 in 1995 (table 2), but no attempt was made to associate p-values with these changes in deviance. Determining the appropriate degrees of freedom for the likelihood ratio test is difficult because of correlation in the catch rates of successive hauls, and the choice of the exponential coefficient r used in the weighted average.
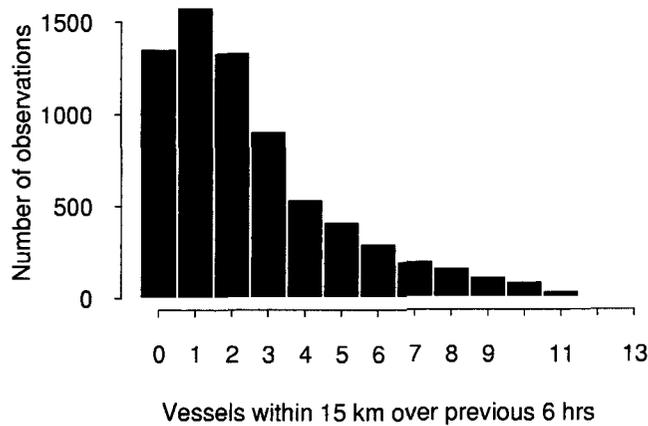
Figure 11. Frequency distribution of local fishing activity during 1991–95 (the number of vessels fishing within 15 km over the previous 6 hrs).
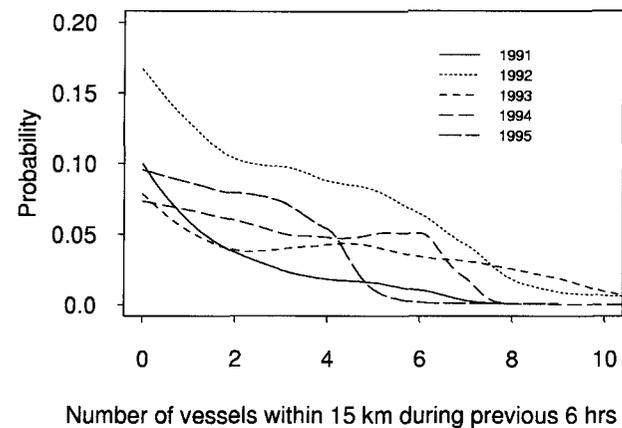

Figure 12. Generalized additive model (GAM) predictions of the probability of movement as a function of local fishing activity for 1991–95. Predictions are for a model with two terms: an exponential average of the catch rate residuals for previous hauls, and local fishing activity. The catch rate residual term was fixed at zero to produce the model predictions.

The influence of local fishing activity on the decision to leave an area was examined next. Similar issues about the choice of an appropriate spatial and temporal frame to summarize information on local fishing activity must be addressed. The summary of local fishing activity used for this analysis was a simple count of the number of unique vessels (both catcher processors and catcher boats delivering to mother ships) within 15 km that had conducted trawling operations within the previous 6 hrs. Fifteen kilometers is an approximation of the range of sight from a vessel at sea. This summary of local fishing activity ranged from 0 to 12 vessels, with a mean of 2.6 vessels (figure 11). Nineteen percent of the time there were no other vessels within 15 km. The GAM smooth terms for local fishing activity show a decrease in the probability of movement with increasing local fishing activity (figure 12). The smooth terms are fairly linear throughout their range. The smooth terms are significant at $\alpha = 0.05$ in all years except 1994 (table 2).

DISCUSSION AND CONCLUSIONS

The analysis of acoustic survey data indicated that the spatial correlation extended to 25–35 km. These results are generally comparable with other research on similar species. Sullivan (1991) found that spatial correlations of spawning pollock in Shelikof Strait, Alaska, extended to about 30 km. Other analyses of survey or fishery data have reported spatial-correlation ranges. For haddock on Georges Bank the range is 9 nmi (Polacheck and Vølstad 1993); for hoki off New Zealand, the range is 11 nmi (Vignaux 1996a).

The factors that produce spatial correlation in fish populations are poorly understood. Ultimately, the physical oceanography of the summer feeding habitat of Pacific hake probably determines its correlation structure. Instability in the California Current mean flow produces mesoscale meanders and eddies that are sites of enhanced primary production (Abbott and Zion 1987) and that create fronts which concentrate zooplankton, including euphausiids, the primary food of Pacific hake (Rexstad and Pikitch 1986; Mackas et al. 1991). The spatial scale of these mesoscale oceanographic features is determined by the baroclinic Rossby radius of deformation, which is ~25 km in midlatitudes off the West Coast (Thomson et al. 1992). If Pacific hake concentrate in areas of high zooplankton density, aggregations may occur in association with these mesoscale oceanographic features. However, this is an area of active research, and additional work is needed to elucidate the biophysical linkages between the physical environment and regions of high fish abundance.

The geostatistical analyses of Pacific hake spatial structure demonstrate the importance of considering the spatial characteristics of fish populations when interpreting vessel movement patterns. Other research on fishing behavior has usually imposed ad hoc models of decision making by looking at movement between arbitrary geographic blocks or statistical reporting areas, which may be unrelated to how fishermen perceive their environment (Hilborn and Ledbetter 1979; Gillis et al. 1993; Vignaux 1996b). Eales and Wilen (1986), however, examined fishing location choice in a shrimp fishery where the potential fishing area was divided into smaller regions based on fishing patterns. The structure function illustrates how the foraging landscape would be perceived by a fishing vessel that requires a threshold fish density in order to operate profitably. To estimate the structure function, however, it was necessary to link fishery catch rates with acoustically measured fish densities by making some fairly crude assumptions about the capture efficiency of commercial fishing gear. Independent information is needed about the level of fish density that can support fishing activity, such as might be obtained by placing a calibrated echo sounder on a commercial fishing vessel.

The results of the GAM models of vessel movement showed that there is a low probability that a vessel will leave a foraging area when its catch rate is higher than its expected catch rate. The probability of moving increases sharply when catch rate residuals become negative. This result generally agrees with the Arditi and Dacorogna (1988) prediction of a threshold prey density that triggers movement by the forager. But the results also suggest that there may be additional factors involved in the decision to move. Although the probability of moving is clearly a nonlinear function of the catch rate residual on a logistic scale, there is no evidence of a discontinuity. This may in part be due to the GAM approach to modeling, which estimates smooth terms in an additive predictor. Also, the probability of movement for negative catch rate residuals is between 0.05 and 0.15, which indicates that fishing vessels still have a fairly low probability of leaving an area when their catch rates are below average. Since factory trawlers usually target their midwater nets on acoustically detected aggregations of fish, the ability to locate a suitably dense aggregation may play an important role in the decision to move.

The GAM models of vessel movement showed that an exponentially weighted average of previous hauls with a half-weight of approximately 4.8 hours was more successful at predicting movement than only the catch rate residual of the most recent haul. This result suggests that vessels base their decisions on relatively short time frames. Evaluating different frame lengths is a new approach to interpreting fishing behavior, but similar approaches have been used with bumblebees in artificial foraging environments (Real 1991). Previous research on fishing behavior has assumed an arbitrary time window over which experience is averaged, typically one day (Eales and Wilen 1986; Vignaux 1996b) or one week (Hilborn and Ledbetter 1979; Gillis et al. 1993). The time frame that the vessels use to evaluate fishing success may be related to the temporal persistence of hake aggregations and also to the inherent stochastic variation in the catch rates. If hake aggregations are extremely transient, earlier information would rapidly become useless as a predictor of current conditions. A fishing vessel that used an inappropriate weighting scheme would remain too long in an area where the fishing is no longer good or, conversely, would leave too soon and spend an excessive amount of time in transit between areas.

The tendency for vessels to be less likely to leave an area if there are other vessels nearby is an advantageous strategy from two perspectives. First, the presence of other vessels in an area suggests high fish densities. Information on the local density of fishing vessels can be collected easily and quickly in comparison to surveying an area acoustically or by test fishing. Second,

each vessel fishing in the same area can be certain that no other vessel has a higher average catch rate than it does. This is particularly important in a fishery that is managed with a fleetwide quota. If only a few days remain to the close of season, a risk-averse strategy such as fishing near other vessels will guarantee that the remaining quota will be shared equally among vessels. Searching for a new area with higher catch rates runs the risk that the season will close before higher catch rates can compensate for the time spent searching or in transit. Since the north-south variance in trawling locations in the at-sea fishery typically decreases toward the close of the season, there is some evidence that the spatial distribution of fishing activity is affected by these considerations.

Vignaux (1996b) conducted a similar analysis of fishing behavior in a trawl fishery for hoki off New Zealand. Instead of using a GAM model to predict vessel movement as a function of catch rates, Vignaux (1996b) tested for differences in the probability of movement when the catch rates were below and above average. Vignaux's results regarding the effect of low catch rates were similar to those in this paper, suggesting that this may be a common characteristic of fishing behavior.

The GAM models for vessel movement developed in this paper offer advantages over the more ad hoc approaches that have been used up to now to study fishing behavior. The GAM models allow a more detailed examination of vessel response. For example, my evaluation of nonlinearity in the response to declines in catch rates would have been difficult with conventional approaches. Also, GAM models provide a unified framework for evaluating different sources of information and other attributes of the catch in addition to the catch rate.

One of the initial objectives of this research was to investigate vessel responses to salmon and rockfish bycatch. In addition to the catch rate of the target species, decision making may depend on the amount of bycatch and other attributes of the catch, such as the mean size or sex ratio of the target species. But it became evident that observer sampling procedures and record keeping do not provide enough information for such analysis. Since bycatch estimates are often derived from a small sample of the catch, sampling variability may occasionally result in unrealistic bycatch estimates for individual hauls. This sampling variability is not a problem when the objective is to estimate the bycatch for the entire fleet, but it does present difficulties for the statistical models developed in this paper, where accurate information is needed for each haul. In addition, observers sample only a subset of hauls for species composition, ranging from 35% to 70%. Consequently, it is difficult to assess decision making based on more than one haul. The cumulative bycatch over a number of hauls may be a

more important predictor of vessel response than by-catch from a single haul.

The spatial structure of salmon and rockfish distribution is also likely to differ in scale from that of Pacific hake. An analysis of the spatial correlation of bycatch species is a prerequisite for developing models of vessel response to bycatch. Methods developed by Vignaux (1996a) using fishery data to analyze spatial structure in the distribution of the target species may also be applicable to bycatch species. Since observers record only the retrieval locations of hauls, the spatial resolution of the observer database is not adequate to examine spatial correlation and vessel movement at smaller scales than those examined in this paper. Once the spatial scale of the bycatch species has been identified, vessel responses at this scale could be explored with the techniques developed in this paper. Since bycatch is an important concern in managing the Pacific hake fishery, expanded data collection procedures in the fishery should be considered.

ACKNOWLEDGMENTS

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SPACE AND TIME SCALES IN PACIFIC HAKE RECRUITMENT PROCESSES: LATITUDINAL VARIATION OVER ANNUAL CYCLES

JOHN K. HORNE
Great Lakes Center
SUNY at Buffalo State College
1300 Elmwood Avenue
Buffalo, New York 14222-1095

PAUL E. SMITH
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038-0271

ABSTRACT

Habitat of North Pacific hake (*Merluccius productus*) can be partitioned into three life-history zones: an adult feeding area along the coastal shelf and slope from California to British Columbia, a spawning area off central California south to Baja California, and a brood area extending along the coastal shelf and slopes of California and, at times, into Oregon. Recruitment is potentially influenced by a complex mixture of physical and biological processes that operate over a wide range of spatial and temporal scales. We quantify the relative importance of demographic (natality, mortality), growth (physical influences, food supply), and kinematic (passive motion with flow structures, active locomotion) processes that can influence recruitment of Pacific hake in scale diagrams of dimensionless ratios. We found that changes in larval hake biomass are dominated by mortality and drift with prevailing currents. Location of adult spawning is therefore important to survival. Changes in juvenile biomass are influenced more by changes caused by somatic growth and active locomotion. Annual survey data show multiyear trends in the latitudinal placement of spawn toward the equator (1951–55, 1959–64, 1980–83) or toward the pole (1955–59, 1964–69), but strong recruitment only in single years (1961, 1970, 1977, 1980, 1984, 1987, 1990, 1993). We surmise that sharp adjacent year changes in recruitment may not be induced by slow trends in spawning location. The center of adult spawning shifts toward the pole during warm years (>10°C at 100-m depth off Point Conception) and toward the equator during cold years. There has been an overall shift in the mid-spawning location of 444 km toward the pole during the 34-year period from 1951 to 1984. On average, three times as many recruits survive from warm years than from cold years. Unfortunately, a warm-water year does not guarantee higher than usual recruitment.

INTRODUCTION

As the most abundant fish species along the west coast of North America, North Pacific hake (*Merluccius productus*; referred to hereafter as hake) is commercially valuable and important to the biological oceanography of the region. Interest in hake as an exploitable resource began during the 1800s in localized fisheries and continues to the present day. Even though the commercial hake fishery represents a multimillion-dollar enterprise, efforts to quantify and explain recruitment to the adult stock have resulted from fortuitous sampling during other research programs. For example, the range of the hake stock was not understood until spawning grounds were delineated during California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises in 1951 (Ahlstrom and Counts 1955). Total spawning biomass was later estimated from ichthyoplankton samples as 2–3.5 million metric tons (Ahlstrom 1968).

Before the commercial hake fishery was fully established, Alverson and Larkins (1969) estimated that annual catch rates of 136,000–245,000 metric tons (t) would ensure a sustainable resource. These estimates have proven robust. Mean annual estimates of hake biomass have remained at approximately 2 million t for the past two decades, and the mean annual fishery yield over the past three decades has been 192,000 t (Dorn 1996). Despite extensive efforts to sample population abundance and to model population dynamics, processes influencing the success of hake recruitment are not fully understood.

Empirical evidence suggests that successful recruitment of a hake cohort depends on the interaction of biological and physical processes. Using Marsden square 120-2 January-to-March mean water temperatures, Bailey and Francis (1985) found that in eleven of the warmer than average years (>14.8°C at surface) recruitment was higher than average. In contrast, none of the seven colder than average years (<14.8° at surface) resulted in above average recruitment. Early data (Smith 1975; Bailey 1980) showed that colder water temperatures coincided with southern and offshore shifts in adult hake spawning, but it is uncertain whether the absence of large cohorts born during "cold years" is a direct or an indirect result of water temperature (cf. deYoung and Rose 1993).

Another mechanism influencing recruitment is demographic population structure. Shifts in population structure due to fishing mortality reduce the proportion of older and larger adults. A potential consequence of changing population structure is a shift in the location and extent of adult hake spawning (cf. McCall 1990; Hutchings and Myers 1994). Bailey and Francis (1985) recognized the importance of physical-biological coupling

to hake recruitment and recommended an examination of "temporal and spatial variability in [hake] spawning related to environmental conditions." Quantifying variability in hake recruitment success may improve precision of population abundance estimates.

Precision of population estimates depends on spatial and temporal scales of measurement. Scale-dependence in the variability of biological quantities such as population density is best summarized in a plot of variance as a function of spatial and temporal scale (e.g., Haury et al. 1978). This approach explicitly diagrams variability in a quantity of interest across a range of scales rather than concentrating on time and space scales of anthropocentric convenience (Smith 1978). The relative importance of biological and physical processes influencing the magnitude of biological variance can then be plotted as a set of dimensionless ratios over the same range of scales by means of a Lagrangian (Horne and Schneider 1994) or Eularian frame of reference. This technique diagrammatically summarizes ranges of scales over which concomitant processes dominate. This approach has not been used to examine processes influencing the recruitment of a commercially important fish species.

We use this technique to quantify the relative importance of biological and physical processes that potentially influence the survival of hake as a function of spatial and temporal scale. Results of this analysis prompted further examination of CalCOFI data to determine latitudinal variation in adult spawning activity. Pacific hake was chosen as an illustrative example because recruitment rates can vary over two orders of magnitude in adjacent years (Hollowed 1992; Dorn et al. 1993); it has the largest biomass of any fish species in its latitudinal range (25° to 55° north); it has a 37-year series of recruitment rates; and it has been monitored at spawning time since 1951.

METHODS

Analyses in this study can be divided in two parts. First, we qualitatively summarize the influence of physical and biological processes on changes in larval and juvenile hake biomass as a function of spatial and temporal scale. Values of dimensionless ratios are plotted and contoured in rate diagrams. A second set of analyses uses CalCOFI hake data from 1951 through 1984 to estimate the median position of larval hake distribution from cumulative abundance data as an index of adult mid-spawning latitude. Bootstrap techniques are then used to examine the utility of these estimates under variable sampling effort. Larval surveys were not conducted in 1967–68, 1970–71, 1973–74, 1976–77, 1979–80, and 1982–83. Quarterly larval surveys did not cover the usual latitudinal extent in 1985–94.

Rate Diagrams

Quantities of interest in this study are concentrations of larval B_l and juvenile B_j hake biomass in the eastern Pacific. We use a Eularian perspective and fix the frame of reference to encompass the total spawning and nursery area of hake in the eastern Pacific. Following the notation of Schneider et al. (1997), biomass concentration B is defined as the number N of organisms times the average mass of an individual M per unit volume V. Local change in biomass concentration is defined as

$$\frac{\partial B}{\partial t} = \frac{\partial M \cdot N}{\partial t} \tag{1}$$

Applying the conservation equation to an infinitesimally small water volume results in a local rate of change in the concentration of biomass defined by convergent or divergent movement of biomass, the density of the net reproductive rate R, and somatic growth rate M_0:

$$\frac{\partial B}{\partial t} = -\nabla \cdot (\mathbf{u}B) + M \cdot R + M_0 \cdot N \tag{2}$$

where $\mathbf{u}B$ is the flux of biomass through a volume per unit time, expressed as the product of biomass concentration B and a velocity vector $\mathbf{u}$ with components u,v,w in two horizontal (x,y) and one vertical (z) direction. If mass flux differs between two locations, a gradient is formed and biomass will converge or diverge between points. The term ∇ is a gradient operator (see Dutton 1975; ch. 5) with components $\frac{\partial}{\partial x}$, $\frac{\partial}{\partial y}$, and $\frac{\partial}{\partial z}$ in the x, y, and z directions. When combined, the term $\nabla \cdot (\mathbf{u}B)$ is the mass flux gradient that describes the accumulation or loss of biomass due to organism movement. Changes in the concentration of biomass are also due to changes in the net reproductive mass rate $M \cdot R$ and somatic growth rate $M_0 \cdot N$, where M_0 is change in mass per unit time and N is the population abundance.

Since organisms are discrete entities, calculations are simplified by partitioning the volume into small parcels and averaging variables within the volume. Integrating over volume V:

$$\int_V \frac{\partial B}{\partial t} dV = -\int_V \nabla \cdot (\mathbf{u}B) + \int_V M \cdot R dV + \int_V M_0 \cdot N dV \tag{3}$$

or

$$\frac{\partial B}{\partial t} = -B_s \frac{\partial V}{\partial t} + \oint \mathbf{n}(\mathbf{u}B) dA + M \cdot R + M_0 \cdot N \tag{4}$$

Equation 4 states that the local change in biomass within the volume is equal to the expansion or contraction of the volume occupied, the flux of organisms through boundaries of the volume, the net reproductive rate, and the somatic growth rate. In equation 4, B_s is biomass at

the surface of the volume; $\oint$ represents the surface integral; $\mathbf{n}$ is a unit vector perpendicular to the surface; $\mathbf{u}B$ is the biomass density flux across the surface; and dA is the area of the flux.

When the equation is divided by B, the local change in biomass concentration is described by the expansion or contraction of the occupied volume, immigration or emigration across the outer boundary, somatic growth, and demographics.

$$\frac{1}{B}\frac{\partial B}{\partial t} = -\frac{B_s}{B}\frac{\partial V}{\partial t} + \frac{1}{B}\oint(\mathbf{u}B)\,dA$$
$$+ \frac{1}{B}M\cdot R + \frac{1}{B}M_0\cdot N \qquad (5)$$

Since $B = M\cdot N$ then

$$\frac{1}{B}\frac{\partial B}{\partial t} = -\frac{B_s}{B}\frac{\partial V}{\partial t} + \frac{1}{B}\oint(\mathbf{u}B)\,dA$$
$$+ \frac{R}{N} + \frac{M_0}{M} \qquad (6)$$

where $\frac{R}{N}$ and $\frac{M_0}{M}$ are the per capita reproductive and growth rates. To simplify, each term is represented by a single symbol:

$$\underset{\substack{\text{biomass}\\\text{distribution}}}{\dot{B}_0} = \underset{\substack{\text{volume}\\\text{occupied}}}{-\dot{V}} + \underset{\text{flux}}{F} + \underset{\text{demographics}}{r} + \underset{\text{growth}}{m} \qquad (7)$$

Some of the terms in this equation can be further partitioned. Changes in biomass concentration in the two kinematic terms, $\dot{V}$ and F, can be categorized by changes due to passive drift with the surrounding fluid and by changes due to organism locomotion.

$$-\dot{V} + F = -\dot{V}_{fl} - \dot{V}_{loc} + F_{fl} + F_{loc} \qquad (8)$$

The demographic term r can be categorized into the per capita birth rate r_b and the per capita death rate r_d. If data exist, the per capita death rate can be further partitioned into natural r_n, predatory r_p, and harvesting r_h mortality.

$$r = r_b - r_n - r_p - r_h \qquad (9)$$

To determine the relative importance of these biological and physical sources of variation, dimensionless ratios (cf. Taylor 1974; Langhaar 1980) were formed with terms in equations 7 through 9. If all terms have the same units, ratios can be formed in any combination relative to a process of interest (e.g., Schneider 1992), in functional groups (Fischer et al. 1979), or through biological reasoning.

The first ratio of interest is the comparison of somatic growth to changes in population dynamics. In this study the range of observation is set to encompass total spawning and brood areas used by hake in the eastern Pacific

over the last three decades, and does not change. This eliminates any change in biomass concentration due to changes in total volume occupied V, and the term goes to zero. The resulting population dynamics term is a combination of recruitment and flux of individuals in or out of the population.

$$\frac{m}{r - F} \qquad (10)$$

The second ratio evaluates the relative importance of population dynamic processes by comparing demographic r to kinematic F terms.

$$\frac{r}{F} \qquad (11)$$

A demographic ratio compares changes in biomass due to recruitment with those due to mortality.

$$\frac{r_b}{r_d} \qquad (12)$$

Sources of mortality will not be partitioned in this study. The fourth ratio examines the relative importance of kinematic terms. Flux in biomass due to organism locomotion F_{loc} is compared to that due to passive drift with the fluid F_{fl}.

$$\frac{F_{loc}}{F_{fl}} \qquad (13)$$

Where possible, values for each ratio were calculated at discrete spatiotemporal scales for larval and juvenile hake from available hake data and published velocities of the California Current system. Additional values of dimensionless ratios were estimated from physiological limits. Order of magnitude calculations showed whether the absolute value of any dimensionless ratio was less than, equal to, or greater than 1 at a specified spatiotemporal scale. Nominal values (<1, $=1$, >1) for each ratio were plotted in rate diagrams as a function of spatial and temporal scale for larval and juvenile hake. Ratio values <1 indicate the predominance of processes in the denominator; values $=1$ indicate a potential interaction between processes in the numerator and denominator; and values >1 indicate that processes in the numerator prevail over those in the denominator. Contour lines drawn on rate diagrams indicate spatial and temporal scales where dimensionless ratios change value. Dotted lines extend contours across the range of scales lacking data to mark boundaries where ratios are believed to change value. The construction of a rate diagram is an iterative process. Ratio values and contour locations should be adjusted as additional data become available.

Hake Movement and Spawning

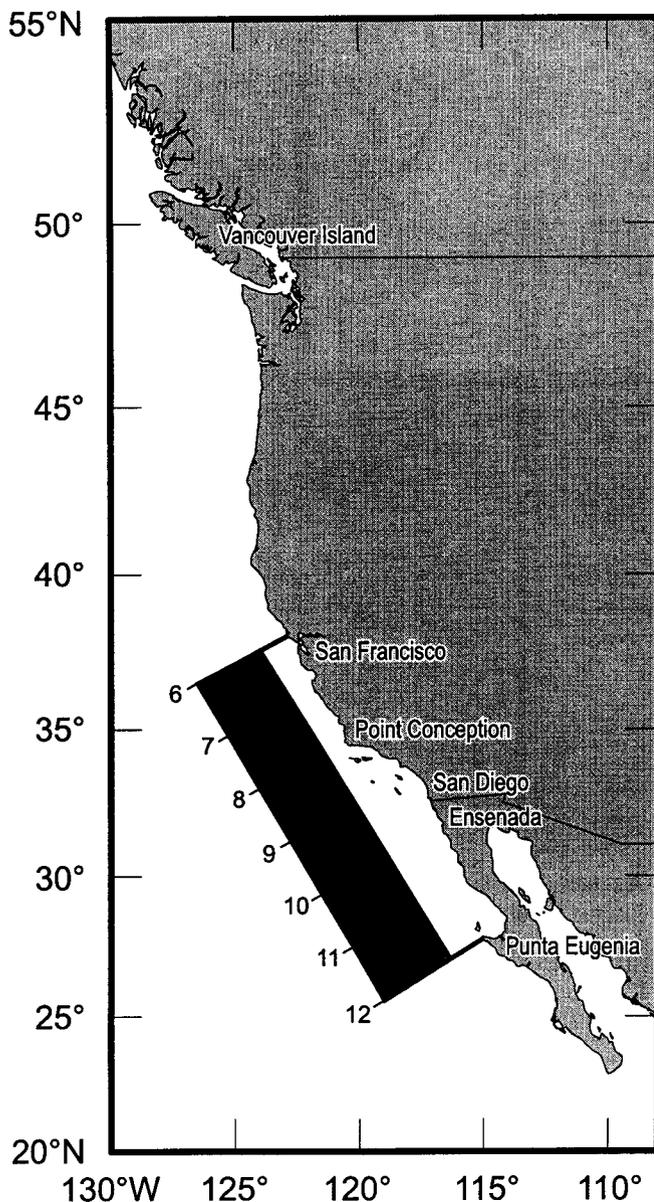In this study we arbitrarily define the spawning and brood boxes as the area encompassed by a southern

Figure 1. Pacific hake larval and juvenile habitat within the CalCOFI basic station plan. The arbitrary spawning area is shaded and extends from San Francisco (line 60) in the north to Punta Eugenia (line 120) in the south. The seaward boundary is set at station 120. The clear zone represents the brood area of older larvae and juveniles at the time of recruiting to the coastal slope and shelf habitat. The brood area boundary is set at station 60. The numbers at the left margin of the shaded habitat represent the latitudinal zones into which larval abundance is assembled for illustrating interannual changes in cumulative abundance from north to south.

boundary set at Punta Eugenia (line 120), a northern boundary at San Francisco (line 60), a seaward boundary at station 120, and the larval-juvenile boundary at station 60 (figure 1). We summarize the annual adult migration as 50% (183 days) in the feeding area, 39% (142 days) in transit and resident in the spawning area, and 11% (40 days) in transit to the adult feeding area. All spawning is assumed to occur within zones 6 to 12

(figure 1). We also assume that spawning rates per adult female and survival rates of eggs and larvae are constant. Larvae are defined as fish smaller than 20 mm (Smith 1995; Ambrose 1996).

We have further assumed that active swimming by adults and passive transport of eggs and larvae with water currents are uniform. Although not all swimming by adults results in progress toward the spawning area, we estimate that the distance traveled is 1,100 km and the rate of progress is 20 cm per second, or nominally 0.4 body lengths (bl) per second. Neither the stimuli to which the hake respond while migrating nor the stimuli that cause them to stop and spawn are known. What is known is that commercial fishing stops in mid-October and doesn't resume until mid-April (Dorn 1996). Larvae begin to appear in mid-December, and smaller larvae are not readily found after the first week of March (Smith 1995). Northerly movement by adults continues through the feeding season (Dorn 1996).

Owing to the extreme patchiness of hake larvae, we used two nonparametric methods to index adult mid-spawning locations: the median larva position, and bootstrap estimates of mean and variation of estimated annual larval distribution. The median larval index of adult spawning is defined as the 0.5 position of the cumulative proportion of hake larvae in each of six bands between line 60 off San Francisco and line 120 at Bahía Sebastián Vizcaíno. This covers a distance of 1,333 km (720 nautical miles) in a plane parallel to the North American west coast. The midpoint of larval distribution was determined with a precision of 222 km from this cumulative curve and was used as an index of adult mid-spawning location.

To classify annual surveys as warm- or cold-water years, we linearly regressed the annual mid-spawning location against the 100-m water temperature off Point Conception, California. Pacific hake live at depth during spawning. There is a tendency for cold anomalies from the California Current to flow at the surface, and for warmer countercurrent to flow at depth. Given the potential indirect relation between water temperature and hake spawning, we fit a linear function to the data from 19 survey years as an indicative rather than an analytical solution:

$$y = 4111 + 375x \qquad (14)$$

where y is the distance (km) of mid-hake spawning from Point Conception, and x is the water temperature (°C) at 100-m depth off Point Conception. Data from 19 years were used in the regression. The r^2 value of 0.64 has little value given the violated assumption of independent adjacent points and the comparison of values with measurement error in both horizontal and vertical sampling planes. Water temperature as an index of spawn-

ing location was used only to discriminate warm from cold years in figure 4.

Bootstrap estimates of mean spawning location are based on 12,535 stations regularly sampled during January–April from 1951 to 1984 in an area bounded by lines 60 off San Francisco and 116.7 in Bahía Sebastián Vizcaíno off central Baja California, and stations 24.8 and 130. The area extends from the coast to 780 km (421 nautical miles) offshore. Thirty bootstrap sets of 10,000 stations were chosen with replacement. Means and standard errors of spawning location were calculated in the usual way. One advantage of interannual bootstrap estimates of mean spawning location is that the standard error of the estimate is calculable when sampling effort differs among years. Intraseasonal variation in spawning location has been ignored.

Recruitment estimates do not exist for the highest-quality spawning data between 1951 and 1960. Conversely, high-quality data on spawning position have not been collected during the period of the greatest contrasting recruitment rates in the 1980s. For example, spawning data were insufficient to determine mid-spawning location in 1980, when recruitment was highest. Only the second highest recruitment of hake (1984) coincided with a larval survey that permitted calculation of spawning locations. Beginning in 1985, the CalCOFI survey design was changed from one that monitors abundance to one that monitors habitat. Off southern California, this represents approximately one-third of potential hake spawning habitat in an average year.

Estimates of the mid-hake spawning location were compared to subsequent recruitment of age-2 hake from 1958 to 1994, and to the number of recruits per ton of female spawning biomass from 1960 to 1994. Because the temporal and spatial sampling scales of the biological and environmental series differ, it is not appropriate to correlate recruitment with mid-spawning location or a water-temperature index.

RESULTS

Rate Diagrams

The rate diagram of the growth-to-population dynamics ratio (figure 2a) for hake indicates that changes in larval biomass concentration due to somatic growth exceed those due to demographic and flux processes at the scale of a spawning season. From the time that eggs are first laid until larvae are transported out of the spawning area, individual fish biomass increases from approximately 5×10^{-7} kg to 7×10^{-5} kg, or 140% of the birthweight (Smith 1995). Annual recruitment is 100% of the cohort, and virtually all of the biomass fluxes out of the spawning area. The resulting value of the ratio is much greater than one. At daily scales, changes in bio

mass due to somatic growth are less than those due to demographics and the flux of larvae out of the spawning area. The resulting ratio is less than one.

Changes in larval hake biomass due to demographics at temporal scales larger than an annual cycle are balanced by those due to kinematics in the spawning area (figure 2b). Over an annual cycle, changes in biomass due to active and passive flux ($\simeq 100\%$) greatly exceed those due to net recruitment ($\simeq 2.21\%$, see below). On a daily basis during an average spawning season of 76 days, the ratio of recruitment to kinematics is approximately equal. The spawning rate of hake averages 1.3% of eggs per day, and larval mortality averages 13% per day (Smith 1995), resulting in a net recruitment rate of 1.13% per day. Passive flux of larvae from the midline to the eastern boundary of the spawning box (222 km), based on a net eastern transport by the coastal jet (1 cm s^{-1} south) and the California Current (4 cm s^{-1} southeast), is 1.48% per day. If all surviving larvae leave the spawning area, total flux out of the spawning area is 2.21% per day averaged over the spawning season. At the scale of a spawning event, biomass changes due to egg deposition exceed those due to flux of eggs with water currents.

Persistence of a population requires that biomass changes due to somatic growth must equal or exceed those due to mortality at the largest temporal and spatial scales. Since there is a net flux out of the spawning area, the demographic ratio will exceed unity (figure 2c). At the scale of a spawning season (76 days) natality does not exceed 14% week^{-1}, and larval mortality is estimated at 13% day^{-1} (Smith 1995). The resulting value of the demographic ratio is less than one. During a spawning event by an aggregation ($\simeq 10^6$ m^2 over a 24-hour cycle) or a spawning pair ($\simeq 10^{-1}$ m^2, minutes), natality exceeds mortality, and the value of the ratio exceeds one. Ratio values are less than one at spatiotemporal scales of an individual organism's dying (seconds, mm^2).

The rate diagram of the kinematics ratio (figure 2d) indicates the dominance of passive flux over active locomotion across most spatiotemporal scales. Fluxes of larvae due to drift with tides, currents, and upwellings exceed fluxes due to active locomotion except over very short time scales. If eggs are released at the midpoint in the northern half of the spawning area, the net drift is 3.8 cm s^{-1} eastward. A total of 67.6 days would elapse for these larvae to drift 222 km to the boundary of the juvenile brood area. Residence time in the spawning area is 102 days (Smith 1995), so an additional 34.4 days can be attributed to active locomotion. There is a net 1% per day movement from the midline of the spawning area to the boundary of the juvenile brood area. The kinematic ratio will exceed unity only at the scale of a larval swimming burst.
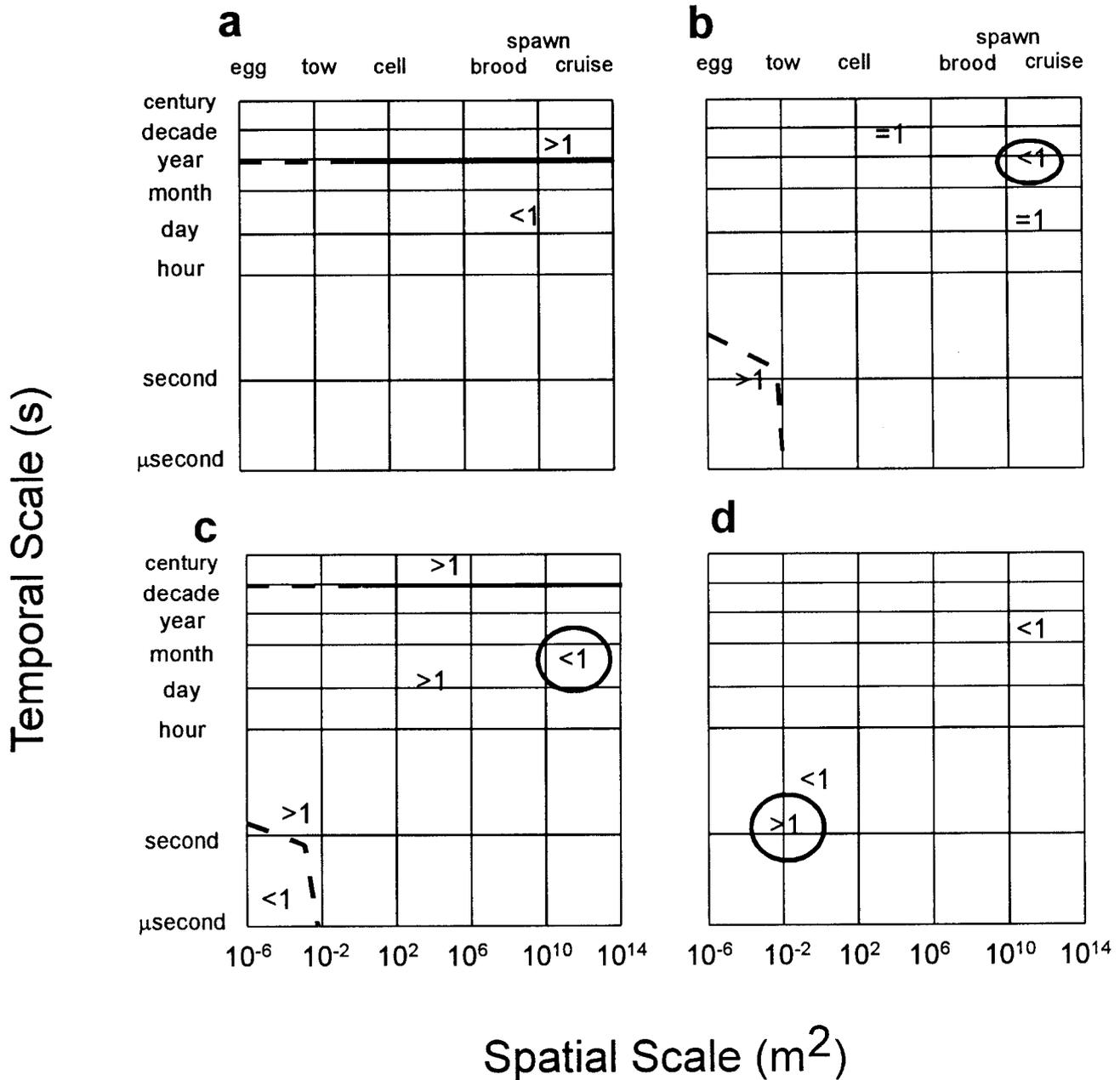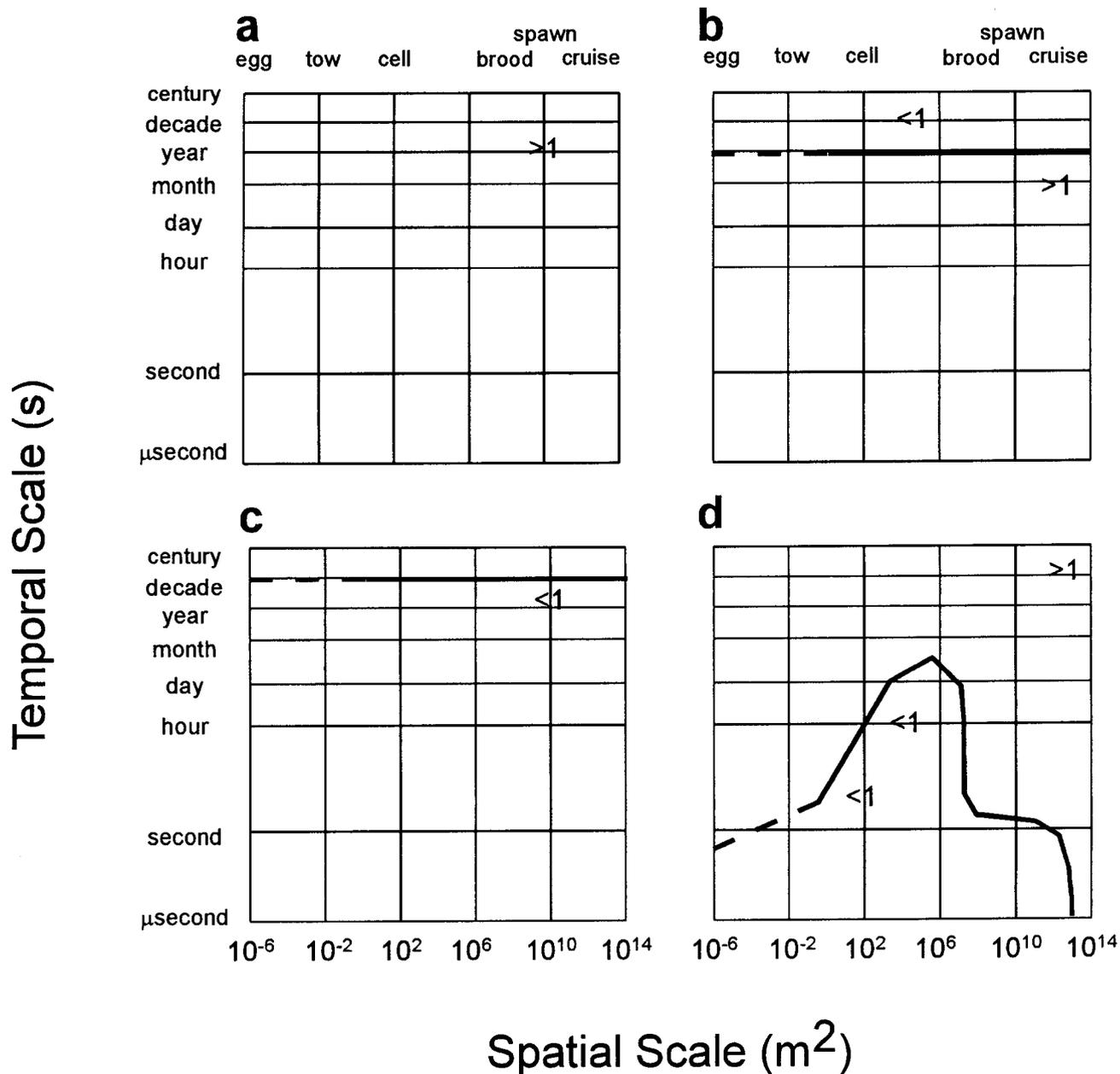
Figure 2.   Contoured rate diagrams of dimensionless ratio values for larval Pacific hake (*Merluccius productus*) biomass distribution in the eastern Pacific. Ratio values are contoured less than 1 (<1), equal to 1 (=1), and greater than 1 (>1). *Broken lines* extend contours across scales where data are lacking. Ratio of (*a*) somatic growth to population dynamics (demographics − kinematic fluxes), $m/r − F$; (*b*) demographic (natality, mortality) to kinematic fluxes (passive drift, active locomotion), r/F; (*c*) demographics, r_b/r_a; and (*d*) kinematic fluxes, F_{loc}/F_{fl}.

In the juvenile hake rate diagrams, the growth-to-population-dynamics ratio (figure 3a) is greater than one at the scale of the brood area. Changes in biomass due to somatic growth rate (500% over a two-year residence period; Smith 1995) exceed those due to changes in recruitment (58% mortality) and changes due to active flux (100%) of two-year-old fish to the adult population.

At spatiotemporal scales greater than a brood cycle, the rate diagram of the recruitment-to-flux ratio (figure 3b) indicates that changes in biomass due to the flux of juveniles into and out of the brood area (100% in two years) exceed those due to recruitment (58% mortality by age two; Smith 1995). Even if the flux of larvae into the brood area is considered juvenile "natality," changes in biomass due to natility and mortality do not exceed the net flux of biomass out of the brood area. A newly recruited juvenile hake weighs 7×10^{-5} kg when leaving the spawning area and 0.155 kg at the end of the second year of life (Smith 1995). At temporal scales less than a year, biomass changes due to mortality (41% year 1, 30%

Figure 3. Contoured rate diagrams of dimensionless ratio values for juvenile Pacific hake (*Merluccius productus*) biomass distribution in the eastern Pacific. Ratio values are contoured less than 1 (<1), equal to 1 (=1), and greater than 1 (>1). *Broken lines* extend contours across scales where data are lacking. Ratio of (*a*) somatic growth to population dynamics (demographics − kinematic fluxes), $m/r - F$; (*b*) demographic (natality, mortality) to kinematic fluxes (passive drift, active locomotion), r/F; (*c*) demographics, r_b/r_d; and (*d*) kinematic fluxes, F_{loc}/F_{fl}.

year 2) exceed those due to active or passive flux out of the brood box. The value of the ratio is greater than one.

The demographics rate diagram (figure 3c) depicts a ratio less than one at the scale of a brood cycle. Changes in biomass due to mortality over a biannual residence period will exceed those due to "natality" of juveniles from the spawning area.

The continuous presence of juvenile hake in the brood area over large temporal scales implies that absolute changes in biomass due to active flux exceed those due

to drift out of the area with the California Current (figure 3d). Episodic events (e.g., upwellings) and large-scale water movements (e.g., currents) will change the value of the ratio to less than one over shorter temporal scales throughout the brood area.

In summary, processes that influence changes in hake biomass switch between the spawning and brood areas at the scale of a spawning season. Changes in larval hake biomass are dominated by mortality and drift with prevailing currents. Location of adult spawning is therefore
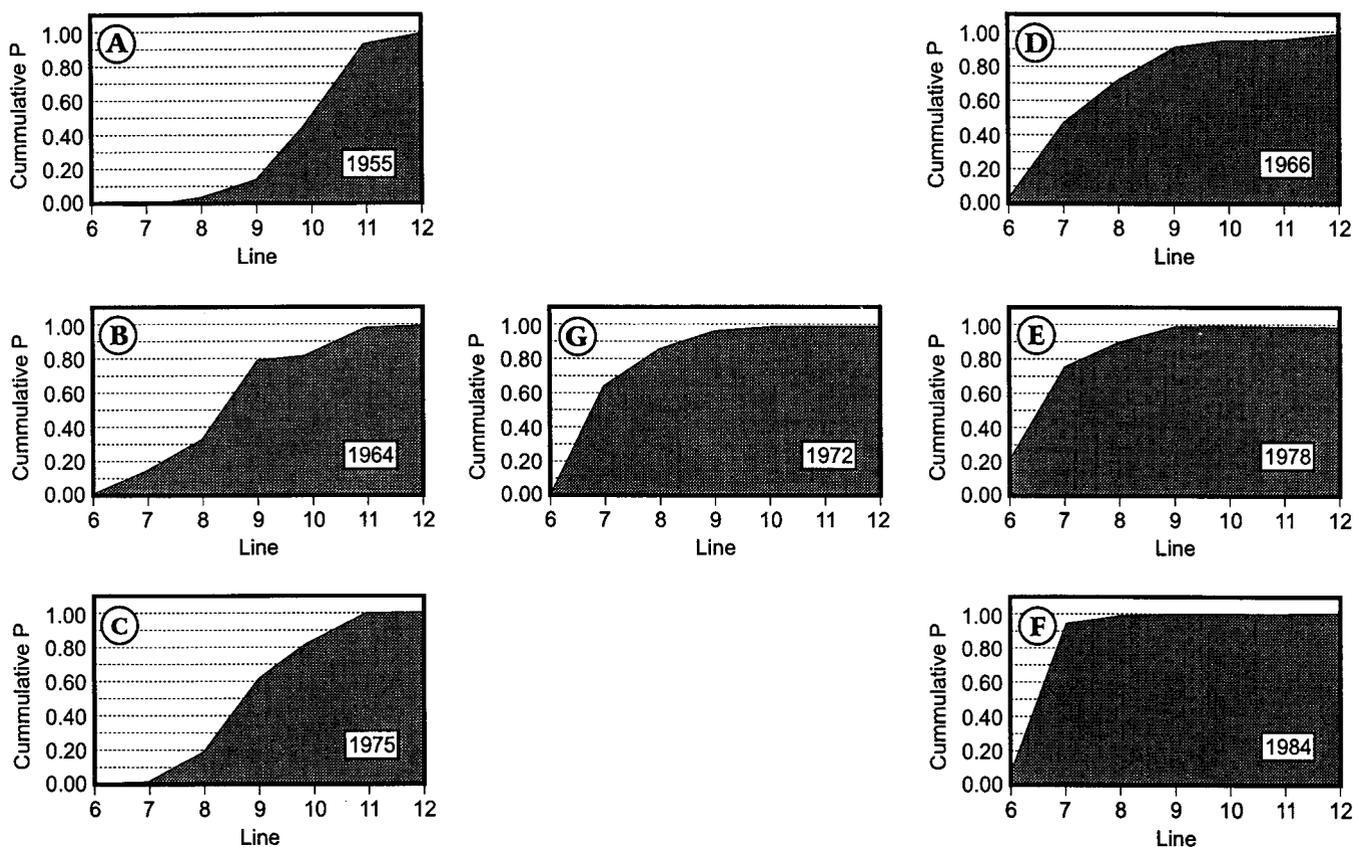
Figure 4.   Cumulative frequency distributions of hake spawning location as a function of latitudinal zone. Colder than average (<10°C) water temperatures at 100-m depth at Point Conception occurred during 1955 (A), 1964 (B), and 1975 (C). Warmer than average temperatures occurred during 1966 (D), 1978 (E), and 1984 (F). In 1984, hake spawning was reported north of the CalCOFI sampling grid off the coast of Oregon (Hollowed 1992). Fisheries analysis indicates that the largest year class on record recruited from 1984. The cumulative diagram from 1972 (G) shows an exceptional year in which hake spawning appeared to show a Southern Hemisphere El Niño response even though the surface temperature in the Northern Hemisphere eastern boundary did not (see text).

important to survival of individual hake. Changes in juvenile biomass are influenced more by changes due to somatic growth and to active locomotion.

Latitudinal Spawning Variation

The latitudinal distribution of hake larvae exhibits readily observable interannual changes (figure 4). Logistic constraints on survey frequency and latitudinal coverage probably underestimate the extent but not the nature of the variance in larval hake distribution and, by inference, adult spawning position. For example, in 1955, 1964, and 1975 (figure 4A–C) appreciable spawning activity occurred between lines 11 and 12. This suggests that there could have been considerable spawning south of the fully sampled area. By the same reasoning, in 1966, 1978, and 1984 (figure 4D–F) there is an indication that spawning occurred poleward of the CalCOFI survey. Spawning poleward of the survey area may have increased since 1984, but there are too few samples north of line 8 to quantify the trend.

The bootstrap time series of the midpoint of hake spawning is shown in figure 5. The best sampled seg-

ments of the time series (1951–61) show appreciable interannual continuity in changes of the center of spawning toward the equator (1952–55) and toward the pole (1955–59). Other latitudinal trends toward the pole occurred during 1964–69 and toward the equator during 1980–83. It is particularly notable that adjacent years are relatively similar and that no extreme northern spawning years are followed by extreme southern spawning years. Extreme changes in position of spawning never occurred in less than a three-year period. The overall trend of the time series is a poleward movement of approximately 444 km (240 nautical miles) over 34 years (1951–84). Standard errors of bootstrap estimates increase over time because of reduced sampling effort in both time and space.

Neither the time series of absolute recruitment of age-two hake (figure 6) nor the time series of hake recruitment per unit of female spawning biomass (figure 7) parallels trends observed in the hake latitudinal spawning position time series (figure 5). Single year spikes, defined as a doubling of recruitment in preceding and succeeding years, occurred in 1961, 1970, 1977, 1980,
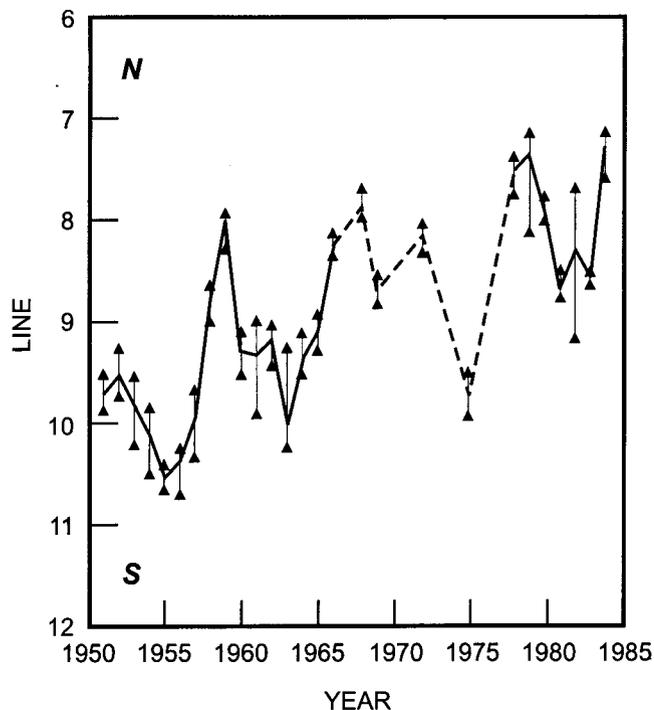
Figure 5. Bootstrap time series of hake larvae position (mean ± 2 SE). The numbers on the ordinate refer to positions along the coast (figure 1), with lower line numbers at the northern end (N) and higher numbers at the southern end (S). The broken line from 1965 to 1978 indicates years when annual surveys were not conducted. Surveys of larval hake were conducted two to four times during the spawning season in 1951–60, and triennially from 1966 to 1984. Larval surveys were not conducted in 1967, 1970–71, 1973–74, or 1976–77. Single surveys covering most of the latitudinal extent shown in figure 1 were conducted in 1968, 1979–80, and 1982–83. Quarterly larval surveys since 1985 have covered only the southern one-third of section 7, all of section 8, and the northern two-thirds of section 9, and therefore are not comparable.

Figure 6. Estimates of absolute age-2 recruitment (billions) of hake, based on appendix table 9 in Dorn 1996.
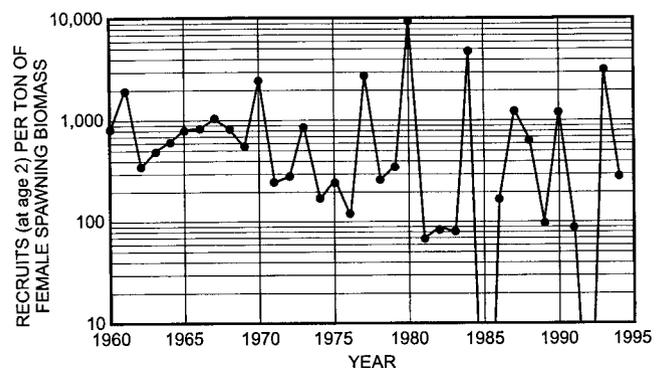

Figure 7. Recruitment rate of hake as recruits per ton of female spawning biomass, based on appendix table 9 in Dorn 1996. Hake recruits from the cohorts of 1985 and 1992 were virtually undetectable.

1984, 1987, 1990, and 1993. It appears that two to three years of poor recruitment follow each year of highly successful recruitment.

DISCUSSION

Identifying sources of variability in the recruitment of commercially important aquatic resources continues as a dominant theme in fisheries research. Variability in the survival of pre-recruit animals is accepted as a major influence on the size of adult population. Recruitment variability studies have examined biological (e.g., Ricker 1954; Beverton and Holt 1957), physical (e.g., Cushing 1980; Smith and Eppley 1982; Koslow 1984), or a combination of biological and physical (e.g., Lasker 1975; Sissenwine 1984; Rothschild 1986) processes that influence mortality and survival of larval and juvenile life stages.

Inferring causality from correlations between single environmental variables and biological responses deserves the bad reputation that Gulland (1953) gave it in the early days of fisheries hydrography. This problem has been accentuated by the massive availability of environmental data, personal computers, and exploratory sta-

tistical programs. It may become routine to explore many data series where at least one would contain a "significant" relationship at the 95% level. To illustrate using an example of hake and water temperature, the 1972 surface temperature in the Southern California Bight was the lowest since 1951. But surface temperature was not indicative of hake spawning activity, because the 100-m temperature at Point Conception was among the warmest recorded and coincided with the most northerly spawning of the Pacific hake (figure 4G).

An alternative to simple correlative analyses is to propose models of suitable complexity that reflect variability observed in biological quantities. To continue the hake and temperature example, the secular rise in California Current surface temperature could be characterized by sea level (Roemmich 1992), West Wind Drift (Chelton and Davis 1982), or coastally trapped waves (Enfield and Allen 1980; Pares-Sierra and O'Brien 1989; White 1994). If the usual range of the hake annual migration is 1,100 km and a linear regression model predicts a 375-km shift in the center of spawning distribution for each degree of change in water tempera-

ture at 100-m depth off Point Conception, then one could examine how variability in the California Current and the accompanying changes in water temperature affect hake spawning activity. One could also evaluate the consequences of variable coastal water flow during the southward and northward adult migrations. The adults could be swimming (1) against the current both ways, (2) with the current both ways, (3) with the current on the way to the spawning grounds and against it to the feeding grounds, or (4) against the current on the way to the spawning grounds and with it to the feeding grounds.

For this study we use rate diagrams to identify processes that influence the production, survival, and growth of hake larvae into juveniles from November through March when adults are in the spawning area. The relative importance of biological and physical processes to the survival and growth of adult hake is not evaluated. We surmise that the adaptive value of spawning at the southern limit of "hake habitat" is fast growth of embryos and larvae, and that the adaptive value of the northern end of the habitat is faster adult growth in the productive waters of the subarctic. Northward migration by adults after spawning is an attempt to seek larger and richer feeding grounds than those found off central California and Baja California. We infer support for this strategy from Robinson et al. (1993), who found that 90% of the productivity in British Columbian waters occurs during the upwelling months of April through October.

The use of rate diagrams avoids assumptions that single biological or physical processes are linked to observed patterns at any scale of interest and that biological and physical processes are coupled at characteristic spatial and temporal scales. Rate diagrams contain nominal values of dimensionless ratios that indicate the relative importance of two or more processes based on published knowledge, available data, and biological reasoning. Rate diagrams can be used to summarize current knowledge of spatial and temporal dynamics, to identify cogent space and time scales for any life-history stage in process-oriented research, and to identify processes that may influence distribution patterns over the range of scales where they dominate (Hatcher et al. 1987; Horne and Schneider 1994).

The application of rate diagrams to research design is best illustrated by example. It is relevant to ask, "Is drift important to the recruitment of hake, and if so, over what scales should drift be examined?" From hake life history we know that the adult spawning season lasts approximately 76 days each year and occurs offshore from the San Francisco area in the north to Baja California in the south. The northern and southern limits of spawning shift among years, but suitable spawning habitat is assumed along the length of the coast. If we assume that all initial larval movement inshore is net drift with currents, then potential larval transport is 3.87 cm s^{-1}, or 3.34 km day^{-1}. The spawning box covers an area of approximately 600,000 km^2. At the spatiotemporal scale of a spawning season, the rate diagram of larval growth to population dynamics ratio (figure 2a) indicates that demographic and kinematic processes are more important than growth processes. The ratio of demographic to kinematic rates (figure 2b) is less than one, although at smaller temporal scales demographic and kinematic processes may be important to the recruitment of hake. Further comparison shows that kinematic processes are dominated by flux out of the spawning area (figure 2d) and that mortality exceeds changes in biomass due to natality (figure 2c). When the focus is shifted to juvenile hake, changes in biomass due to somatic growth exceed those due to drift with currents (figure 3a). Over the course of a spawning season, research effort should focus on larval movement and mortality at scales of one day and more than one kilometer.

It is also important to realize what rate diagrams do not provide. Examining relative rates of biological and physical processes as a function of spatial and temporal scale results in dimensionless ratio values that are independent of geographic location and clock time. Dimensionless ratio values are not predictors of organism distribution patterns resulting from physical or biological processes. Rate diagrams have yet to be incorporated into models for predicting abundance or recruitment but can be used to identify important terms for inclusion across any range of scales.

Rate diagrams can be constructed from a Eularian (fixed) or Lagrangian (moving) perspective. The choice of perspective will influence terms that are included in the equation and terms used to form dimensionless ratios. Schneider (1991, 1993) and Horne and Schneider (1994) used a Lagrangian perspective to examine rates of change in aerial or volumetric distributions of marine bird, fish, and zooplankton biomass as a function of temporal and spatial scale. The difference in the Lagrangian formulation is that kinematic terms in the equation describing all potential variance-generating processes do not include fluxes of organisms or biomass. A moving perspective does not incorporate the crossing of outer boundaries by organisms within the volume of interest. Outer boundaries expand and contract to contain all organisms. The Eularian perspective used in this study allows us to quantify the flux of hake out of the spawning grounds, and the northern flux of juveniles into the feeding grounds. We arbitrarily set the outer limits of the spawning and brood areas to encompass all latitudinal variation in adult spawning due to variability in water temperature.

Water temperature is used as an index of important changes in absolute recruitment (figure 6) and recruitment rates per unit of spawning hake female (figure 7). Of the 61 billion recruits spawned during the 37 years from 1958 to 1994, 29 billion came from the three most successful years (1980, 1984, 1993) and less than 0.2 billion from the three least successful years (1981, 1985, 1992). Recruitment during the 16 years that were considered cold-water years averaged 0.8 billion recruits per year. An average 2.5 billion hake per year recruited during the 20 years considered warm-water years. Fishery yield models that use Los Angeles Bight surface temperatures have demonstrated that yields of 150,000 tons can be increased to 200,000 tons during higher-temperature years (Francis et al. 1982). Higher-temperature years were defined as those with annual average sea-surface temperature in the Southern California Bight between 15.67° and 16.81°C in the years 1931–79. The year 1970 was labeled warm at 15.46° because of the recruitment of a large hake year class from a small spawning biomass compared to small hake year classes at temperatures ranging from 13.5° to 15.59° (Francis et al. 1982). Unfortunately, predictions of hake recruitment based on water temperatures do not follow the same trend. Warm-water years tend to persist, but no large hake recruitment has consecutively followed a large hake recruitment (Smith 1995, appendix table 9; Dorn 1996). These order-of-magnitude changes in cohort success have been independent of the adult population size (Bailey 1981).

Present estimates of allowable Pacific hake catch are influenced by the success of hake recruitment since 1980. Extraordinary recruitment of the 1980, 1984, and 1993 cohorts coincides with the fundamental oceanic change in the Pacific (Venrick et al. 1987; Beamish 1995; Polovina et al. 1995). Before the 1975 transition, hake catches were more variable and ranged from 103,000 to 234,000 metric tons. Since 1975, catches have ranged from 90,000 to 359,000 metric tons (Wooster and Hollowed 1995; Dorn 1996).

It is uncertain what the effects of a return to the cold climate of 1950–56 would be in the presence of a fishery. The sustained harvest rates may have to be reduced if adult spawning shifted hundreds of kilometers to the south in response to colder waters or faster California Current flow along the coast. Catches above 10% of the adult spawning stock have only occurred since 1994. A longer migration path implied by cold water temperature may influence natural mortality rates of both adult and juvenile hake. Similarly, reductions in older age classes potentially reduce the occupancy of traditional spawning areas and may reduce the stabilizing factors that sustain the population in larger ocean areas.

Observations of successive recruitment of a large cohort followed by a small cohort suggests that Pacific hake abundance may be regulated by both bottom-up and top-down mechanisms of population control. Since adult abundance, mortality, or growth do not influence cohort variability, massive success of a first cohort is probably due to egg production or high survival of early life stages. Survival of embryonic, larval, or early juvenile hake may depend on temperature and movement of ambient water. Spawning in southerly latitudes has been associated with cold (<10°C) water temperatures at a depth of 100 m off central California. Northward shifts in spawning have been attributed to warming water and the reduction of older hake cohorts (Smith 1972, 1975; Bailey 1980). Since zooplankton crops are higher in cold years relative to those in warm years (figure 23 in Reid et al. 1958), latitudinal shifts in spawning imply that success of a cohort depends on the matching of spawning activity and subsequent larval transport with high plankton production. The absence of suitable food, or expatriation from suitable food may lead to the recruitment of a "typical" rather than a large hake cohort. The failure to produce a large cohort under similar conditions in a subsequent year may be due to increased abundance of predators, including cannibalistic juveniles from previous cohorts. Although there has been insufficient study of intercohort cannibalism, stomach contents of 1+ and 2+ Pacific hake show that when cohorts co-occur, cannibalism is common (Bailey et al. 1982; Buckley and Livingston, 1997).

Cannibalism among successive cohorts may affect hake population dynamics in two opposing ways. The ultimate success of a cohort may depend on the arrival of the subsequent cohort to serve as a food source at the brood area. The ensuing biomass depletion of the younger cohort may be insignificant relative to the biomass of the entire stock, but numeric losses from the younger cohort may have a significant demographic effect on the cohort and, at a larger temporal scale, on the population. Density-dependent population regulation appears to cycle on a bi- or triennial scale. If juvenile hake limit recruitment of succeeding cohorts, it may be advantageous to institute an occasional fishery on juvenile hake. Juvenile fishing mortality on one cohort may increase recruitment of a subsequent cohort through a reduction in density-dependent cannibalism. This might also benefit the rest of the ecosystem by reducing the consumption of euphausiid shrimp and larval or juvenile fishes of other species.

Hake research efforts are often designed to quantify abundances and identify habitat preferences of egg through adult stages. To estimate abundance it is crucial to choose a sampling resolution that will ensure maximum independence of adjacent samples as dictated by the central-limit theorem. Surveys should be designed to improve the discriminating power (precision) by in-

creasing the effective number of samples. If the sampling resolution is less than the autocorrelation lag distance, then adjacent samples are not independent; the standard error of the response variable should be decremented as a function of the autocorrelation; and sampling effort has been wasted. Sampling resolution may change among life-history stages but should not change with location unless distribution patterns differ regionally.

Given the opportunistic history of hake research, it is advantageous to examine how rate diagrams can help design surveys sampling geographic areas or multispecies communities. A simple extension of single-species rate diagrams overlays sets of rate diagrams for all species of interest to determine appropriate sample range and resolution. In an examination of energy flux from prey to seabird predators, Schneider (1995) identified processes that were important at critical time and space scales for marine birds. For sampling cruises in the CalCOFI program, rate diagrams of anchovy (*Engraulis mordax*), sardine (*Sardinops sagax*), and hake could be compared to ensure that samples will detect change in critical processes and extend over the range of a critical process such as the temporal and geographic boundaries of hake spawning activity. The use of rate diagrams during cruise planning should make the allocation of sampling effort less contentious by explicitly defining sampling requirements and highlighting sampling constraints.

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USING A RESTRICTED ADAPTIVE CLUSTER SAMPLING TO ESTIMATE PACIFIC HAKE LARVAL ABUNDANCE

NANCY C. H. LO, DAVID GRIFFITH, AND JOHN R. HUNTER
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

In adaptive sampling the procedure for selecting sample sites and allocating effort depends on data collected during the survey. From March 9 to 27, 1995, stratified adaptive sampling was used to survey Pacific hake larvae because the spatial distribution of the larvae is highly patchy and because adaptive sampling is an efficient means of surveying such a population.

The survey, conducted between Los Angeles and San Francisco and covering an area of 202,115 km² (59,540 n mi²), was designed to test the feasibility of adaptive sampling. Because of limited survey time, we used a restricted design imposing a maximum number of stations in each stratum. A stratified, two-stage cluster Horvitz-Thompson (HT) estimator and a simple stratified (SS) sample mean were used to determine mean catch per tow. The variance of the HT estimate included the variance resulting from subsampling within a cluster and was high. The mean density from SS sampling was biased downward, but its variance was a 2-fold reduction over what it would have been if the same number of samples had been allocated proportional to the area size within strata. Nonetheless, our adaptive sampling was relatively easy to implement, and it provided biological information within patches.

INTRODUCTION

The more patchy egg and larval distribution becomes, the larger a sample size is needed to maintain the same level of precision. Thus large sample sizes are needed to precisely estimate the abundance of eggs or larvae with a highly patchy distribution (Smith 1981). Of the fishes that have been studied in the California Current, the Pacific hake (*Merluccius productus*) has by far the most patchy egg and larval distribution. The standard deviation for hake larvae counts/10 m² is about 10 times the mean value (Smith 1995); i.e., the coefficient of variation (CV) = 10, whereas the standard deviation of anchovy and sardine larval counts is only 3 times the mean value. Owing to their highly contagious distribution, it may be impractical to achieve a reasonable level of precision (CV = 20%) for an estimate of hake larval abundance with conventional simple random sampling (SRS), because too many samples would be required (Stauffer 1985).

When a population has a patchy spatial distribution, the precision of abundance estimates may be improved by using adaptive sampling rather than SRS (Seber 1986). In an adaptive sampling design, the selection of sample sites and the allocation of sampling effort depends upon data collected during the survey. Adaptive sampling designs have been used for trawl surveys (Francis 1984; Thompson and Seber 1996) and forest surveys (Roesch 1993), and have been evaluated for waterfowl (Smith et al. 1995) and plant surveys (Brown 1996a, b), but they have not been evaluated for ichthyoplankton surveys.

The purpose of this paper is to examine the feasibility of using adaptive sampling to estimate abundance of the highly aggregated larval Pacific hake (Smith 1995). We empirically compare the relative efficiency of estimates based on adaptive sampling to estimates based on simple random sampling and conventional stratified sampling schemes. Because patch size may be estimated from clustered samples, we also provide an estimate of the size of patches of larval hake. The size of larval patch not only serves as a guide for future adaptive sampling strategies, but is also a useful early life-history parameter (Hewitt 1981).

THEORY OF ADAPTIVE CLUSTER SAMPLING

The conceptual basis of adaptive sampling was developed in the late 1960s (Basu 1969), and the theory has been improved considerably in recent years (Thompson 1992; Brown 1994, 1996a, b; Thompson and Seber 1996). Adaptive cluster sampling starts with a random sample of n units (net-tow stations in our application). If any of the initial observations exceeds or is equal to a predetermined critical value (number of larvae), sampling units in the neighborhood of that observation are also sampled.

The *neighborhood* can be any arbitrary pattern. The neighborhood relationship is symmetric; e.g., if unit a is in the neighborhood of unit b, then unit b is in the neighborhood of unit a. However, the units in the neighborhood could be noncontiguous (Thompson 1992; Thompson and Seber 1996). If any one of the additional observations meets the condition, then observations in its neighborhood are taken. This procedure continues until no observations meet the condition.

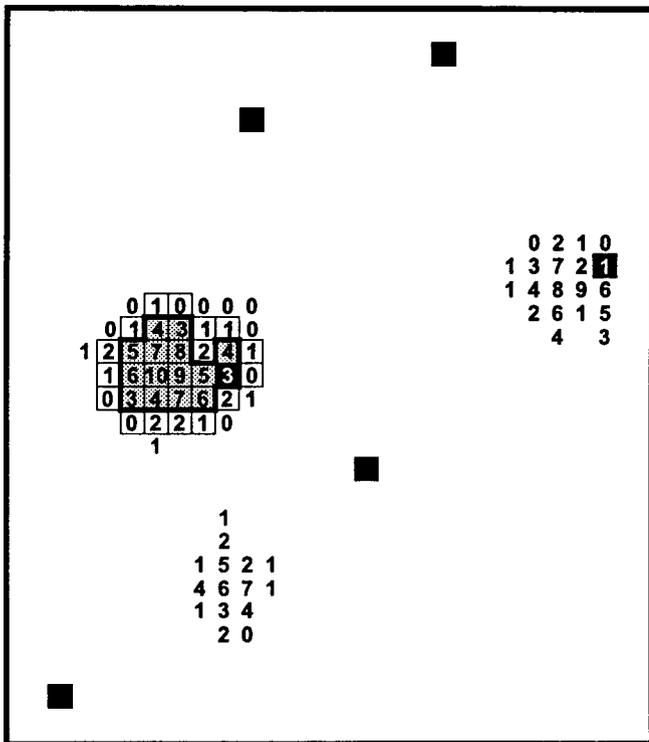All contiguous observations that meet the condition constitute a *network*, and observations that do not meet

Figure 1. An example of adaptive sampling with a complete enumeration of network encountered: dark squares are the initial random sample size of 6. There are three patches. Numbers in each square indicate the number of larvae. The critical value is 3. The neighborhood of a unit is four units each in the north-south and east-west directions. Two observations in the initial sample intersect with two patches. One observation was 3. The resulting network was outlined in bold. The edge units are units with fewer than 3 larvae, indicated by open squares. Notice that in this patch 3 larvae were not sampled. Another initial observation was 1, therefore no further observations were taken in its neighborhood.

the condition are called *edge units*. A network plus edge units makes up a *cluster*. A *patch*, in this paper, is a group of fish larvae. Therefore a network or a cluster can be a patch of different scale and a cluster may be a subset of a large patch. Edge units are not used in the computation unless they are part of the initial sample. A sampling unit that does not meet the condition but was included in the initial sample is considered as a network of size 1 (figure 1).

The estimators we used for larval density were a stratified, adaptive two-stage cluster Horvitz-Thompson (HT) estimator modified from the adaptive single-stage cluster estimator (Thompson 1990, 1991), even though our adaptive sampling design is a restricted one, and a simple stratified (SS) mean. The adaptive cluster sampling procedures proposed by Thompson (1992) require continuous sampling in the neighborhood until observations no longer meet the criteria. This approach will not be practical for population-scale studies of hake larvae in the open ocean if the neighborhood consists of adjacent sampling units, because ship time is limited and the potential spawning habitat is vast.

In this study, we did not use a single definition of *neighborhood*, and the neighborhood was not symmetric, as shown in figure 1. We considered that the sampling units which met the criteria were a random sample from a network, and we therefore used them to estimate the mean density per tow in the network. We then estimated the area covered by a network by measuring the area surrounding a group of stations where the catch was at least as great as a critical value.

TABLE 1

Mean, Standard Deviation (SD), and Number of Stations (*n*) from Initial Stations, Stratum Area, Stations Allocated (*n*) for Optimal Stratified (OSS), Proportional Stratified (PSS), and Unbiased Adaptive Stratified (UASS) Sampling; Mean and Standard Error (SE) for Horvitz-Thompson (HT) and Simple Stratified (SS) Sampling, March 9–15, 1995

Stratum	Initial A-stations Mean	Initial A-stations SD	*n*	Area (km²)	Number of stations (*n*) OSS	Number of stations (*n*) PSS*	Number of stations (*n*) UASS	Number of stations (*n*) HT or SS	HT Mean	HT SE	SS Mean	SS SE
1	2	2.65	3	15,635	3	4	3	3	2	1.53	2	1.53
2	4	5.29	3	13,764	5	3	2	3	4	3.05	4	3.06
3	9	12.73	2	10,952	9	3	5	2	9	8.98	9	9.00
4	4.5	2.12	2	10,952	2	2	5	2	4.5	1.50	4.5	1.50
5	0	0.00	2	10,952	0	3	2	2	0	0.00	0	0.00
6	0	0.00	2	10,952	0	3	2	2	0	0.00	0	0.00
7	0	0.00	2	10,952	0	2	2	2	0	0.00	0	0.00
8	1	1.41	2	10,952	1	3	2	2	1	1.00	1	1.00
9	16.5	23.30	2	13,764	17	3	2	8	19.19	19.75	10.75	6.05
11	0.33	0.58	3	13,764	1	3	5	3	0.33	0.33	0.33	0.33
12	4.5	6.36	2	10,952	5	3	2	2	4.5	4.50	4.5	4.50
13	0.5	0.71	2	10,952	1	2	2	2	0.5	0.50	0.5	0.5
14	0	0.00	2	10,952	0	3	2	2	0	0.00	0	0.00
15	2	1.41	2	10,952	1	3	2	2	2	1.00	2	1.00
16	12.5	0.71	2	10,952	1	2	2	6	6.43	6.11	6.5	2.20
17	5.5	0.71	2	10,952	1	3	5	2	5.5	0.50	5.5	0.50
18	0.67	1.15	3	13,764	1	3	3	3	0.66	0.66	0.66	0.38
Total or mean			38	202,115	48	48	48	48	3.61	1.51	3.04	0.73

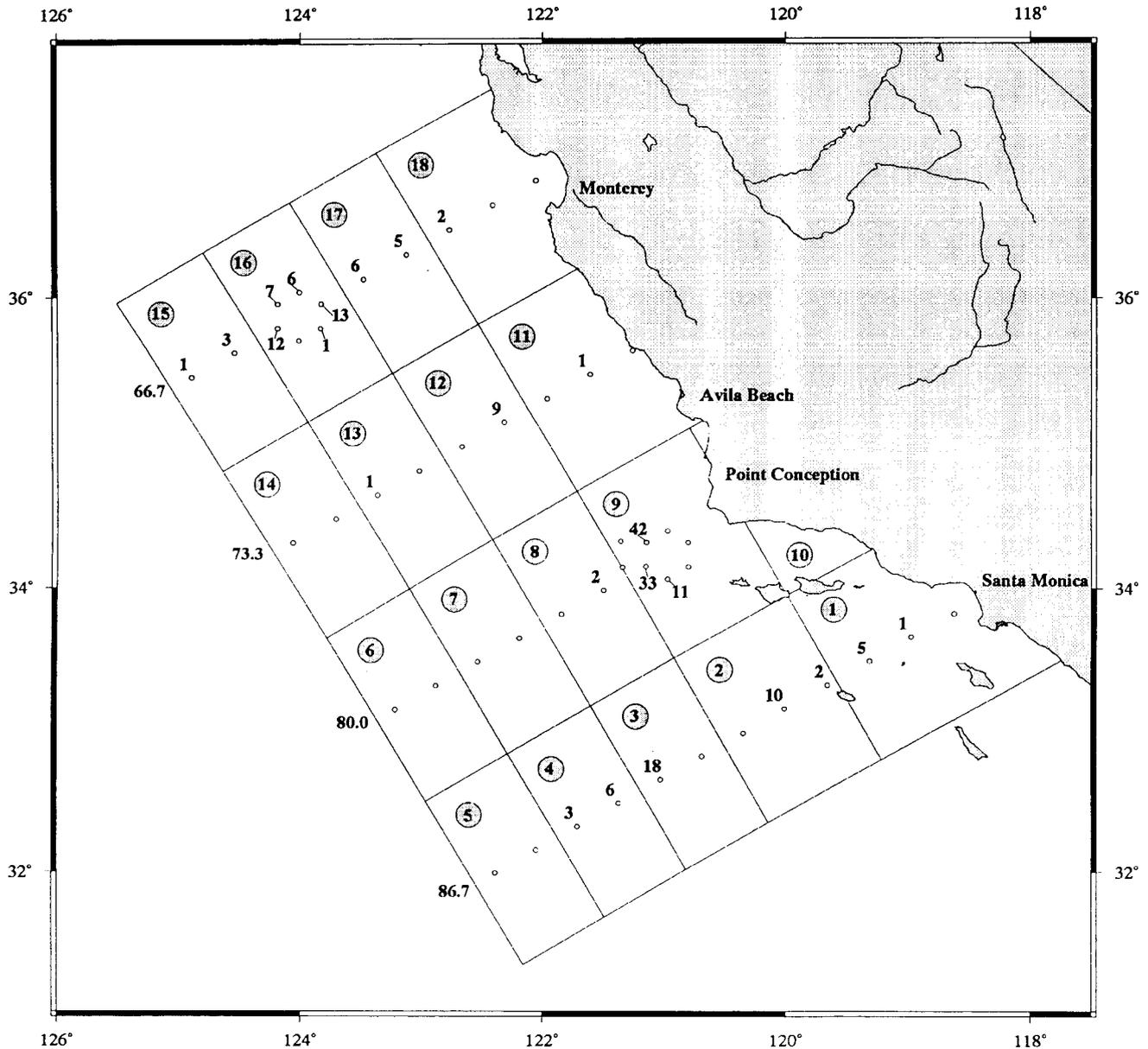*Number of stations was reduced from 3 to 2 for four strata, so that the total number of stations = 48.

Figure 2. Stations occupied within each of 18 strata in the survey for Pacific hake larvae, March 9–15, 1995. Small numerals indicate the number of larvae caught at each station. Circled numbers identify strata. Decimal numbers identify CalCOFI lines.

MATERIALS AND METHODS

Survey Design

In order to test the adaptive sampling technique, a survey was conducted during March 9–27, 1995, covering an area of 202,115 km^2 (59,540 n mi^2), from California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey line 66.7 south to line 86.7. Each line extended to 200 n mi offshore (table 1 and figure 2). The survey area was divided into 18 rectangular strata with two initial stations in each stratum except for strata 1, 2, 11, and 18, which had three initial stations each

(stratum 10 was excluded from analyses because only one station was occupied). The initial stations were on CalCOFI lines 86.7, 80.0, 73.3, and 66.7. Each stratum was approximately 10,952 km^2 (3,200 n mi^2). The initial stations (points A in figure 3) were 37 km (20 n mi) apart. Ichthyoplankton samples were taken at the initial stations in each stratum with bongo nets (71-cm-dia. opening with 505-μm-mesh nets) towed to a nominal depth of 212 meters (depth permitting) and retrieved obliquely (Smith and Richardson 1977). The Pacific hake larvae in each tow were identified and counted before the ship departed from the sampling station.
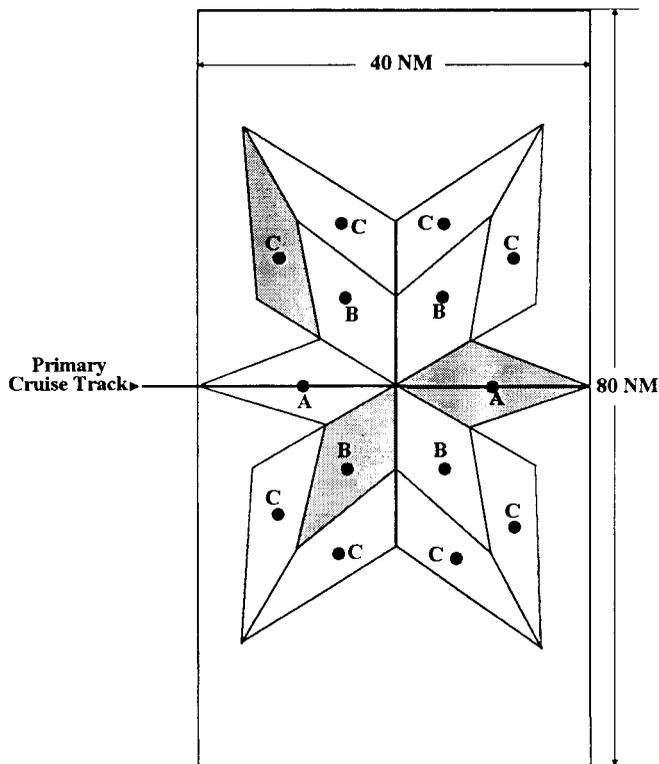
Figure 3. Diagram of survey pattern under adaptive sampling for Pacific hake larvae within a stratum. A-stations are the initial stations. B- and C-stations are added when catch in the previous station exceeds a critical value. Distance is 37 km (20 n mi) from A to A and is 18.5 km (10 n mi) from A to B, B to C, B to B, and C to C. *Shading* indicates the area represented by each station. Area for A and B is 312.47 km² (91.3 n mi²); area for C is 388.45 km² (113.5 n mi²).

If any of the samples from the initial stations (A-samples) contained a number of larvae more than or equal to a critical value, two additional B-stations (B-samples) were added to the north and south from each A-station (figure 3) to form a polygon. If any of the four B-stations contained more than or equal to the critical value, then two C-stations (C-samples) were added to the nearby area of a B-station (figure 3) so that the distance between adjacent stations was 18.5 km (10 n mi), except that the distance between two A-stations was 37 km (20 n mi). The distance between additional stations (18.5 km; 10 n mi) was our best guess of the maximum diameter of spawning hake schools from data provided by Stauffer (1985) and Mark Saunders (pers. comm.).

Adaptive cluster sampling (Thompson 1992) requires this procedure to continue until catches no longer meet the criterion, but in this study sampling stopped at C-stations. Such a stopping rule limits the number of un-scheduled samples, thereby limiting the ship time required to complete the survey. This restricted sampling design (Brown and Manly, in press) may bias the estimates of density (the extent of this bias could be estimated by simulation).

Selecting a Critical Value

Selecting a critical value (number of larvae needed for adding extra stations) required a consideration not only of the expected densities of hake larvae, but also of the time that could be devoted to taking extra samples while still completing all scheduled samples. We decided that we might not be able to complete the survey in the scheduled two weeks if more than four strata with extra stations were allowed. To estimate the critical value that would fill this requirement, we first divided the survey area of 1993 and 1994 CalCOFI surveys into strata. Each stratum had 2 to 4 stations, similar to the 1995 survey (figure 2).

Mean and standard deviation of larval hake catch for each stratum were obtained from data collected during the two CalCOFI surveys. We then followed the adaptive sampling procedures of increasing the number of samples by four each time the maximum larvae within a stratum exceeded or equaled a predetermined critical value. Applying critical values from 2 to 20, we obtained the total number of strata with maximum catch greater than or equal to a given critical value and the variance of the grand mean.

The final critical values were determined so that a maximum of five strata could include extra stations. Since the mean larval densities were different between 1993 (1.081/tow) and 1994 (6.61/tow), the final critical values differed. A critical value of 6 resulted in five strata with extra stations when 1993 data were used, while a critical value of 20 resulted in three strata with extra stations when 1994 data were used. For 1994 data, if the critical value was reduced from 20 to 15, the variance of the grand mean decreased only slightly. Assuming that the larval density in 1995 was close to the level of 1994, we decided to use a critical value of 20.

Actual results required us to change the critical value midway in the survey. After occupying half of the survey pattern (CalCOFI lines 86.7 and 80.0) we had taken only one set of additional samples (figure 2). Consequently, we lowered the critical value from 20 to 10. With the lower value, one additional set of samples was taken in stratum 16; the total number of samples used in our analyses was 48, taken from March 9 to 15.

Estimating Hake Larval Density

We estimated larval density with the two-stage cluster Horvitz-Thompson estimator (HT) and a simple stratified (SS) sample mean from the resulting stations within each stratum, recognizing that both are biased for the restricted adaptive sampling. We chose HT because it was designed to reduce the bias resulting from non-random sampling. The HT estimates were computed only for strata in which the number of larvae caught in at least one of the initial stations exceeded or was equal to

the critical value. For other strata, we used simple sample means. For comparison purposes, we also computed an unstratified SRS mean density from all initial stations.

Horvitz-Thompson (HT) estimator. The adaptive sampling procedure allocates larger sample sizes to strata where a large catch is observed at one of the initial stations. Therefore the probability that a station will be occupied depends on the catch at stations nearby; the probability is a function of the patch size and larval density. Each station does not have equal probability of being selected. This sampling procedure constitutes a probability sampling design (Overton and Stehman 1995). An unbiased estimator was first introduced by Horvitz-Thompson (1952; see also Cochran 1977). The original HT estimator for the population total, T, is

$$\hat{T}_y = \sum_{i \in s} \frac{y_i}{p_i}$$

where p_i is the inclusion probability for each observation y_i (e.g., the larval count from each station, or the total larvae from a network), and the summation is over the sample observed. The HT estimator downweights observations that are more likely to be observed than others. Since the observations are overrepresented in the sample, they are divided by their inclusion probability to reduce overrepresentation.

For adaptive sampling, Thompson (1992) modified the HT estimator to make use of observations that are less than the critical value only when they are included in the initial sample. In Thompson's procedure, the network in which one initial station is located is enumerated completely, so there is no sampling error in the total count of the network; this is a single-stage cluster sampling design.

In the case of hake larval sampling, without a single definition of neighborhood, when the number of larvae was equal to or greater than a predetermined value, two stations 10 n mi away from each initial station were sampled. Therefore the sampling scheme is an adaptive two-stage cluster sampling. A-stations are used to locate patches (stage 1), and B-stations and C-stations are used to subsample the patches (stage 2; figures 1, 3).

Any station where the larval count was equal to or greater than the critical value is denoted as a "G-station." The area surrounding adjacent G-stations was used to estimate the area of a network (network size). G-stations can be considered as a random sample from a network[1], and the average of number of larvae from G-stations is used to estimate the mean larvae per tow for that network. The probability that any of the initial

stations intersect a network is called the intersection probability (α; equation A2, appendix) rather than the inclusion probability, because stations that do not meet the condition will be included in the computation only if they are initial stations (Thompson 1992). The mean density of larvae per tow, $\hat{y}_i$, in the ith stratum is computed from equation A3 (appendix) as

$$\hat{y}_i = \frac{1}{A_i} \sum_{j=1}^{K} \frac{\overline{y}_j a_j z_j}{\alpha_j}$$

$$= \frac{1}{A_i} \sum_{j=1}^{k} \frac{\overline{y}_j a_j}{\alpha_j} \tag{1}$$

where K is the number of total patches in the ith stratum, which may never be known, and k is the total patches sampled. In the jth patch observed,

$$\overline{y}_j = \sum_{u=1}^{m_j} \frac{y_{ju}}{m_j}$$

is the sample mean per tow from m_j tows, and m_j is the number of G-stations sampled in the network, including the jth A-station. On the population level, z_j is equal to 1 if the jth network was sampled, and zero otherwise. Therefore $\alpha_j = p(z_j = 1)$ is the intersection probability for the jth network (equation A2 in appendix); A_i is the area for ith stratum; and a_j is the network size (km²), estimated by the total area represented by adjacent G-stations including the jth A-station.

The area size represented by A- and B-stations was determined so that A- and B-stations would represent equal areas, as indicated by the inner star in figure 3. We then defined the area for C-stations in a symmetric fashion. The area for one C-station, 388.45 km² (113.5 n mi²), was slightly larger than that for each A- and B-station, 312.47 km² (91.3 n mi²; figure 3).

The variance of $\hat{y}_j$ (equation 1) did not include the variance of estimated network size (equation A5), therefore the variance of $\hat{y}_j$ would be underestimated. For detailed derivation and the variance, see appendix.

We used the general formula for stratified sample mean to compute the overall mean density for the survey area. The stratified sample mean is

$$\overline{y} = \sum_{i=1}^{I} \overline{y}_i \frac{N_i}{\sum_{i=1}^{I} N_i}$$

$$= \sum_{i=1}^{I} \overline{y}_i \frac{A_i}{\sum_{i=1}^{I} A_i} \tag{2}$$

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[1]*Network* in this paper refers to a patch of units with larval counts greater than or equal to the critical value.

where in the ith stratum, $\bar{y}_i$ is the estimate of mean density per tow; e.g., $\bar{y}_i = \Sigma_j y_{ij}/n_i$ is the sample mean under simple random sample (SRS). N_i is the total possible sample size. A_i is the area of the ith stratum. The standard error (SE) of stratified sample mean for a sample size $n = \Sigma n_i$ is

$$SE = \sqrt{\sum_{i=1}^{I} se^2_i [\frac{A_i}{\frac{I}{\sum_{i=1}^{I} A_i}}]^2} \qquad (3)$$

$$= \sqrt{\sum_{i=1}^{I} \frac{\sigma^2_i}{n_i} [\frac{A_i}{\frac{I}{\sum_{i=1}^{I} A_i}}]^2} \quad \text{if } \bar{y}_i \text{ is simple sample mean}$$

where σ_i is the standard deviation in the ith stratum, and can be estimated by the sample standard deviation s_i from the initial stations.

Simple stratified (SS) sample mean. For simple stratified sampling, the sample mean $(\bar{y}_i)$ and standard deviation (s_i) were computed from all stations occupied in the ith stratum from the adaptive procedure. This estimate is biased for any adaptive sampling (Francis 1984; Thompson 1992) because sampling is not random and because extra samples are taken from areas of high abundance. Nevertheless, the simple stratified sample mean can be used as a relative index of mean density, and its variance can be compared with the variance of other stratified sample means (table 2).

Comparison of Adaptive Sampling with Standard Conventional Sampling

The standard approach to survey design requires the allocation of sample size to individual strata according to the area (A_i), the standard deviation (σ_i), and the cost of sampling within strata. Such statistical design, termed optimal stratified sampling (Cochran 1977), is seldom used in pelagic surveys because one rarely can anticipate what the variance may be in a given stratum. Nevertheless, we compared the results of adaptive sampling with those of optimal stratified sampling (OSS), proportional stratified sampling (PSS), and simple random sampling (SRS). We also included an unbiased adaptive stratified sampling (UASS) proposed by Thompson et al. (1992; table 2) in the relative efficiency comparison (see below).

Because the cost of sampling is the same among strata, the sample allocation for optimal stratified sampling is $n_i \sim \sigma_i A_i$, and for proportional stratified sampling it is $n_i \sim A_i$. For standard deviation within strata, we used sample standard deviation, s_i, computed from A-samples.

The UASS is a variation of a stratified adaptive sampling procedure for animal populations in which sample size in a given stratum depends on the observations obtained in the previous stratum. The conventional stratified sample mean is unbiased under such a sampling scheme (table 2). Under UASS, if in the previous stratum one of the A-samples exceeded or was equal to the critical value, we would add three extra stations randomly in space (table 1). The variance of the estimate was computed according to equation 3, where standard deviation was computed from A-stations. Therefore, except for HT, SS, and SRS, the difference in variances among sampling schemes was primarily due to the different sample size allocated to each stratum.

To compare the relative efficiency of any two estimates, say X_1 to X_2, we computed the ratio of the variance of X_2 to variance of X_1:

$$RE(X_1 \text{ TO } X_2) = var(X_2)/var(X_1) = (SE(x_2)/SE(x_1))^2 \qquad (4)$$

TABLE 2
Estimates of Hake Larval Density and Their Standard Errors (SE) from Horvitz-Thompson (HT), Simple Stratified (SS), and Unbiased Adaptive Stratified Sampling (UASS) under Adaptive Sampling, and Proportional Stratified Sampling (PSS), Optimal Stratified Sampling (OSS), and Simple Random Sampling (SRS)

Sampling design	Criteria of sample allocation	Density estimate (number/tow)	SE	Relative efficiency (SE(PPS)/SE)^2	n
Adaptive					
HT	Catch within stratum	3.61	1.51	0.48	48(39[a])
SS	Sample size from HT	3.04	0.732	2.06	48
UASS	Catch in previous stratum	—[b]	1.226	0.73	48
Conventional					
PSS	Area	—	1.051	1.00	48
OSS	Area and standard deviation	—	0.693	2.30	48
SRS		3.50	1.066	0.97	38
			0.948	1.23	48

Except HT and SS, the variances of estimates were computed from the within-stratum variance based on data collected at initial A-stations and allocated sample size in each stratum.
[a]Number of stations used in calculation.
[b]No actual survey took place. Only standard error was computed (see text).

For example, the relative efficiency of the HT estimate to a proportional stratified sampling estimate is Var(PSS)/Var(HT). Except for HT and SS, a total resulting sample size of 48 was allocated to each stratum according to each sampling scheme, and we then computed the variances of the stratified sample mean for each sampling scheme (equation 3).

RESULTS

Hake Larval Mean Density per Tow

The mean and standard deviation for the number of hake larvae per tow, computed from initial stations (A-samples) in each stratum (columns 2 and 3 of table 1), indicated that strata 9 and 16 had a high abundance of larvae. The HT adaptive sampling procedures were followed in strata 9 and 16, although a single high catch of 18 larvae occurred in stratum 3.

In stratum 9, the critical value was 20. At the first A-station, 33 larvae were caught, so a total of four B-stations were occupied (figure 2). The four B-samples each had catches of 42, 0, 0, and 11. Therefore two C-samples were taken 10 n mi away from one B-station with catch = 42. Two C-stations had zero catch. The other three B-stations were edge units, because catches were less than the critical value of 20.

We assumed that two stations with catches of 33 and 42 were from a single patch, and we computed the network size, a_1, as the total area represented by these two stations: 91.3 n mi^2 × 2 × (1.85 km/n mi)^2 = 624.94 km^2 (figures 2 and 3). The mean density of larvae in the first network, $\bar{y}_{9,1}$, is (33+42)/2 = 37.5. The catch of the second A-sample, $\bar{y}_{9,2}$, is zero ($\bar{y}_{9,2}$ = 0). Therefore, we sampled one patch from the first A-station in stratum 9.

For the HT estimate, the intersection probability for the one network was $\alpha_1 = 1 - (1 - 624.94/13764)^2 = 0.0887$ (equation A2). The HT mean density for the stratum, $\hat{y}_9$, is (37.5 × 624.94/0.0887/13764) + 0 = 19.19 (equation 1 and table 1). The sample variance of mean density was reduced to one term since there was only one nonzero network (equation A5): $SE(\hat{y}_9) = 19.75$.

In stratum 16, the critical value was set at 10. Two A-samples contained 12 and 13 larvae, respectively, which exceeded the critical value, so four B-samples were taken, resulting in catches of 7, 6, 1, and 0 (figures 2, 3). Since the number of larvae in B-samples was less than 10, these samples were treated as edge units, and no C-samples were taken. In this stratum, we assumed that the two A-samples came from one patch, therefore the area of the network is the area represented by two A-stations: $a_1 = 624.94$ km^2. The intersection probability, α_1, was 0.1108 (equation A2). The modified HT mean density, $\hat{y}_{16}$, for

the stratum is 12.5 × 624.94/0.1108/10952 = 6.43 (equation A3) with $SE(\hat{y}_{16})$ = 6.11 (equation A5).

The modified two-staged HT estimate of larval mean density for the entire survey area was 3.61 (SE = 1.51; equation 2 and table 1) calculated from 39 stations. The other two estimates of mean density were 3.04 (SE = 0.732) for simple stratified (SS) sampling, where within-stratum variance was computed from resulting stations by means of the restricted adaptive sampling design (columns 12 and 13 of table 1), and 3.50 (SE = $s/\sqrt{48}$ = 6.57/$\sqrt{48}$ = 0.948) for unstratified SRS where the standard deviation (s = 6.57) was computed from 38 A-samples (table 2 and figure 2).

Relative Efficiency

An estimated relative efficiency (equation 4) with respect to proportional stratified sampling (PSS) was computed for unstratified simple random sampling (SRS; n = 48), optimal stratified sampling (OSS), Horvitz-Thompson (HT), simple stratified (SS), and unbiased adaptive stratified sampling (UASS) designs (table 2). The standard error for OSS, PSS, and UASS was computed on the basis of sample standard deviation from initial A-stations and the sample size allocated to each stratum (tables 1, 2). The standard error was 1.051^2 for PSS, and 1.226 for UASS (table 2). The SE for the OSS estimate was 0.693, the lowest of all estimates. Standard errors for SRS with n = 38, HT and UASS were higher than proportional stratified sampling. The relative efficiency (HT to PSS) was 0.48. This means that HT was less efficient than proportional stratified sampling. The relative efficiency (SS to PSS) was 2.06, and the sample size for PSS had to be two times the sample size for SS to achieve the same precision.

If the UASS (Thompson et al. 1992) had been used, it would have produced unbiased estimates. The variance of UASS was high in this example because allocated sample size was small in strata 9 and 16, where the variance was high; and the allocated sample size was large in strata 11 and 17, where variance was low (table 1). If we had used a lower critical value, then additional stations would have been allocated to strata 9 and 16, and the variance of the estimate would be lower.

DISCUSSION

An important application of this restricted adaptive ichthyoplankton sampling would be to improve the precision of estimates of adult spawning biomass from daily or annual egg production methods, or from larval production methods (Hunter and Lo 1993) and to obtain biological information within patches. Improving the

[2]Sqrt((2.65^2/4 × 15635^2 + 5.29^2/3 × 13764^2 + ... + 1.15^2/3 × 13764^2)/20211^2) (columns 3, 5, and 7 of table 1)

precision of a larval or egg production estimate of biomass with adaptive sampling requires (1) that eggs or larvae of the target species can be identified rapidly on shipboard; (2) that the distributions of the egg or larval stages are sufficiently patchy to be worth the extra effort of adaptive sampling; (3) the computation of a suitable critical value; (4) minimization of the bias of sample mean estimates; (5) selection of an appropriate survey design; and (6) an estimate of the optimal distance between adaptive samples. The first two conditions require no elaboration, but the latter four warrant further discussion.

Critical Value

If we had set our critical value at 10 instead of 20 before starting our survey, we would have been able to include four instead of two patches in the survey. We expect this would have reduced the variance of the estimate both by increasing sample size and by sampling two more clusters. Fearing that we would use up all the available ship time without completing the pattern, we used our estimate from the 1994 survey (20 larvae) rather than the mean of the two critical values from the 1994 and 1993 surveys ($13 = \{20+6\}/2$).

Although we set our critical value too high, our mid-survey revision of the critical value did not affect the accuracy of the estimate of larval density because we used a stratified design. Thus critical value selection is important but not an irrevocable choice as long as a stratified design is used. Brown (1996a, b) suggested that a large critical value would increase the precision of an estimate, but only (we would add) as long as the value is not so high that it substantially reduces the chance of sampling patches.

An alternative to selecting a critical value prior to the survey is to use an order statistic from the initial random sample (Thompson and Seber 1996). The adaptive sampling will be performed in the neighborhood of initial sites whose observations have values greater than or equal to, say, the 90th percentile of the initial observations. This order statistic method was used for a terrestrial pollution survey (Thompson and Seber 1996) and may not be practical for marine surveys.

Bias

Although restricted adaptive sampling produces a biased estimate, in our example the mean densities from HT and SRS ($n = 38$) were very close: 3.61/tow and 3.5/tow. If, in stratum 16, two A-samples were assumed to belong to two separate patches, the mean density from HT would have been 3.91. Thus HT appears to reduce the bias under the restricted adaptive sampling. The simple stratified (SS) mean under the adaptive sampling was 3.04, lower than both the HT and SRS estimates (an apparent underestimate of the mean density). How-

ever, the SE of the SS mean was lower than that of the HT estimate (table 2). The results of the study demonstrated that the variance of HT under restricted sampling was higher than for other conventional sampling designs. Simulations are being done to verify our conclusions and to estimate the biases for HT and SS, and their variances.

Since the variance of the HT estimate includes the variance due to subsampling but not the variance for estimating network size, the variance of HT is underestimated and the magnitude of underestimation is unknown. Although 48 stations were occupied in leg 1 of the survey, for the HT estimate, only initial stations and one station that had met the conditions were included in the computation. As a result, the total number of stations used in HT was 39.

Survey Design

The retrospective comparison of relative efficiency indicated that SS was more efficient than most sampling designs, even though SS was biased downward. This still speaks well for adaptive sampling of ichthyoplankton, since the optimal sampling design (stratified sampling weighted by the mean and variance in each stratum) is unrealistic for pelagic species. The bias of SS can be estimated by simulation.

Our adaptive sampling plan was easy to implement because the location of each station was predetermined. We assumed that larval patches are randomly distributed in the ocean and that their locations are unknown prior to the survey. Fish larvae move much more slowly than the research vessel (Smith and Hewitt 1985); therefore a larval patch can be considered as stationary when it is sampled.

In our survey, B-stations were located between two A-stations to save survey time. Alternatively, B-stations can be centered around a single A-station with a catch equal to or greater than the critical value, which was the original intention of the adaptive sampling.

The restricted sampling plan is more practical to implement than one-stage cluster sampling when the neighborhood consists of adjacent sampling units (Thompson and Seber 1996), since the time required to completely enumerate each patch encountered may prevent sampling of more than one or two strata. But subsampling patches increases the variance of the HT estimate. In our example, the relative efficiency of the estimates from the restricted two-stage sampling is lower than for other stratified sampling. If an unrestricted adaptive cluster sampling procedure is to be used, the neighborhood should consist of stations with an optimal distance from stations where the catch is greater than or equal to the critical value, so that patches can be adequately sampled and the survey can be completed within a fixed time frame.

The unbiased adaptive stratified sampling (UASS; Thompson et al. 1992) might be a practical alternative to our sampling plan, because within a stratum, simple random sampling of a fixed number of stations should ensure that the survey is finished within a fixed time, and that means and variances are unbiased. This method requires taking additional samples in a stratum when the catches in the previous stratum meet or exceed the critical value. It is important to recognize that for UASS to be effective the stratum size must be smaller than the patch size, because high catch in the previous stratum must be linked to a high catch in the adjacent stratum. The critical value should be lower than in our restricted adaptive sampling, to ensure that additional stations are allocated to the strata with high abundance.

Patch Size

An important benefit of sampling adaptively is that one may use the data to estimate patch size. The sizes of egg and larval patches are an interesting biological characteristic of a species (Smith 1973, 1981; Hewitt 1981), as well as a property of their distributions that one needs to know in order to sample adaptively.

The distance between adjacent stations with catches greater than or equal to 10 larvae provides an estimate of the patch size of larval hake averaging 7.5 mm long (Cass-Calay, pers. comm.) and about 40 days old (Butler 1997). In stratum 9, one A-station and two B-stations had larval counts greater than 10. The distance between A- and B-stations was 10 n mi, and the distance between two B-stations was 15 n mi, so the diameter of the patch could be, say, 20 n mi. In stratum 16, we assumed that two A-stations were from one patch 20 n mi apart, each with larval counts greater than 10, so the diameter of the patch could be, say, 30 n mi. Thus the diameters of the patches of 40-day-old hake larvae were 37–55 km (20–30 n mi; figure 2). It seems remarkable that such distinct hake larval patches persist for 40 days in the open sea.

Patch diameter also dictates the optimal spatial interval between stations in an adaptive sampling design. The preferred distance is less than half of the diameter of patches. Too short a distance between stations may result in excessive time spent in one patch. If the distance is greater than half of the patch diameter, patches will not be adequately sampled. We selected 10 n mi as our interval; it seems to be a good guess, but there is room for improvement. If the survey were carried out on a regular basis we could greatly improve our estimates of patch size, and thereby improve the efficiency of subsequent adaptive sampling surveys.

CONCLUSIONS

Although it is an information-rich approach, requiring prior knowledge of density and patch size to be ef-

fective (Brown 1994, 1996a, b), adaptive cluster sampling is a way to improve the precision of pelagic egg and larval surveys while holding the maximum sample size constant. In our survey, adaptive cluster sampling of two patches of hake larvae resulted in a 2-fold reduction in the variance over the proportional stratified sampling. Adaptive ichthyoplankton sampling has several biological benefits in addition to the issue of precision. Increasing sampling effort in the area where catch was high not only provided an estimate of the dimension of the patch, but also yielded more specimens for biological studies (Moser et al. 1997; Cass-Calay 1997; Mullin 1997) than would have been obtained from other designs.

ACKNOWLEDGMENTS

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APPENDIX

Two-Stage Cluster Horvitz-Thompson Estimator and Its Variance

Following Thompson (1990), the unbiased estimator for total larvae summed over networks observed in a stratum is:

$$\hat{T} = \sum_{j=1}^{K} \frac{y^{\star}_j z_j}{\alpha_j}$$

$$= \sum_{j=1}^{K} \frac{\frac{\overline{y}_j}{0.4} a_j z_j}{\alpha_j}$$

$$= \sum_{j=1}^{k} \frac{\frac{\overline{y}_j}{0.4} a_j}{\alpha_j} \tag{A1}$$

where K is total number of patches, which was not observed in a stratum, and k is number of patches sampled in a stratum. z_j is 1 if the jth patch is sampled, and zero otherwise.

$$\overline{y}_j = \sum_{u=1}^{m_j} \frac{\overline{y}_{ju}}{m_j}$$

is the sample mean per tow from m_j tows; m_j is the number of G-stations sampled in the network, including the jth A-station. $Ez_j = \alpha_j(1-\alpha_j)$. 0.4 m^2 is the surface area covered by a bongo tow with 71-cm diameter. a_j is

the area of the jth network. The estimator of network total, $y^{\star}$, is computed from catch at G-stations:

$$y^{\star}_j = \frac{\overline{y}_j}{0.4} a_j \text{ and}$$

$$\alpha_j = 1 - C_q^{N-x_j}/C_q^N = 1 - \frac{(N-x_j)!}{(N-x_j-q)!q!} \frac{(N-q)q!}{N!} \tag{A2}$$

where q is the number of the initial stations and A is the total area for a given stratum. $N = A/0.4$ is the total number of tows in the stratum; $x_j = a_j/0.4$ is the total number of tows in the jth network. If q/N is small (p. 274 in Thompson 1992), then $\alpha_j \sim 1-(1-a_j/A)^q$. For example, for $q = 2$, we have

$$\alpha_j = 1 - C_q^{N-x_j}/C_q^N = 1 - \frac{(N-x_j)(N-x_j-1)}{N(N-1)}$$

$$\doteq 1 - \left(1 - \frac{x_j}{N}\right)^2 = 1 - \left(1 - \frac{a_j}{A}\right)^2$$

The estimated mean number of larvae per tow from (equation A1) is

$$\hat{y} = \frac{\hat{T}}{A/0.4} = \frac{1}{A/0.4} \sum_{j=1}^{K} \frac{\frac{\overline{y}_j}{0.4} a_j z_j}{\alpha_j}$$

$$= \frac{1}{A} \sum_{j=1}^{K} \frac{\overline{y}_j a_j z_j}{\alpha_j} \tag{A3}$$

The variance of $\hat{y}$ ($\text{var}(\hat{y})$) is

$$\text{var}(\hat{y}) = \frac{1}{A^2} \, \text{var}\left(\sum_{j=1}^{K} \frac{a_j}{\alpha_j} \overline{y}_j z_j \right) \qquad (A4)$$

$$\text{var}(\hat{y}) = \frac{1}{A^2} \left(\sum_{j=1}^{K} \frac{a_j^2}{\alpha_j^2} \text{var}[\overline{y}_j z_j] + \right.$$

$$\left. \sum_{i<j} 2 \frac{a_i a_j}{\alpha_i \alpha_j} \text{cov}[\overline{y}_i z_i, \overline{y}_j z_j] \right)$$

The unbiased estimate of $\text{var}(\hat{y})$ is (Thompson 1992)

$$\hat{\text{var}}(\hat{y}) = \frac{1}{A^2} \left[\sum_{j=1}^{K} \frac{a_j^2}{\alpha_j^2} \frac{z_j}{\alpha_j} \hat{\text{var}}(\overline{y}_j z_j) + \right.$$

$$\left. \sum_{i<j} 2 \frac{a_i a_j}{\alpha_i \alpha_j} \frac{z_i z_j}{\alpha_{ij}} \hat{\text{cov}}(\overline{y}_i z_i, \overline{y}_j z_j) \right] \qquad (A5)$$

where

$$\hat{\text{var}}(\overline{y}_i z_i) = \overline{y}_i^2 \text{var}(z_i) + z_i^2 \hat{\text{var}}(\overline{y}_i) - \hat{\text{var}}(\overline{y}_i)\text{var}(z_i)$$

(Goodman 1960).

$$\text{var}(z_i) = E z_i^2 - [E z_i]^2 = \alpha_i(1 - \alpha_i)$$

and

$$\hat{\text{var}}(\overline{y}_i) = \frac{s_i^2}{m_i} .$$

Assuming $\text{cov}(\overline{y}_i, z_j) = 0$ for $I \neq j$, we have

$$\text{cov}(\overline{y}_i z_i, \overline{y}_j z_j) = E\overline{y}_i E\overline{y}_j \text{cov}(z_i, z_j) +$$

$$E z_i E z_j \text{cov}(\overline{y}_i, \overline{y}_j) + \text{cov}(\overline{y}_i, \overline{y}_j)\text{cov}(z_i, z_j)$$

$$\hat{\text{cov}}(\overline{y}_i z_i, \overline{y}_j z_j) = \overline{y}_i \overline{y}_j (\alpha_{ij} - \alpha_i \alpha_j) \quad \text{if } \text{cov}(\overline{y}_i \overline{y}_j) = 0$$

where

$$\text{cov}(z_i, z_j) = (\alpha_{ij} - \alpha_i \alpha_j)$$

and

$$\alpha_{ij} = E(z_i z_j) = 1 - \left[\left(1 - \frac{a_i}{A}\right)^q + \left(1 - \frac{a_j}{A}\right)^q - \left(1 - \frac{a_i + a_j}{A}\right)^q \right]$$

(p. 274 in Thompson 1992).

FECUNDITY OF PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*)
FOR THREE STOCKS OFF THE WEST COAST OF NORTH AMERICA

GORDON A. MCFARLANE AND MARK W. SAUNDERS
Pacific Biological Station
Hammond Bay Road
Nanaimo, British Columbia
Canada V9R 5K6

ABSTRACT

We compare fecundity for the three major stocks of Pacific hake off the west coast of North America: the large, migratory offshore stock that ranges from California to British Columbia, and smaller, discrete stocks in Puget Sound and the Strait of Georgia. Estimates of total fecundity for these stocks are similar, but estimates of "effective" fecundity (number of yolked oocytes that are released to be fertilized) differ between stocks. All three stocks resorbed a proportion of their yolked oocytes, ranging from 10%–12% for the offshore stock to 38%–58% for the Strait of Georgia stock. Investigators using fecundity for stock assessment or other purposes must consider the effect that resorption of a large proportion of viable eggs will have on their studies.

INTRODUCTION

Foucher and Beamish (1980) examined oocyte development of Pacific hake (*Merluccius productus*) from the Strait of Georgia and reported that "relatively large numbers of large and small yolked oocytes remained in some ovaries after spawning and were completely resorbed so that a second spawning did not occur." Foucher and Beamish suggested that this could be related to the general condition of the stock (stock dynamics) and to environmental conditions such as temperature, and that this phenomenon should be considered in fecundity estimates for this and other stocks. Mason (1986) also reported resorbing oocytes in the same stock but considered it of minimal importance.

Fecundity relationships are often used in stock assessment to estimate stock abundance (Mason 1986), to estimate potential recruitment to the stock (Hunter and Macewicz 1985), and as an indicator of change in the dynamics of a stock (McFarlane and Franzin 1978; Leaman 1991).

The production of yolked oocytes destined to resorb indicates that the assumption used in fecundity estimates for Strait of Georgia hake and perhaps other stocks and species must be clearly defined. We therefore define fecundity as the number of yolked oocytes that are actually released to be fertilized, i.e., "effective" fecundity.

As part of our studies on Pacific hake in Canadian waters, we wanted to determine if the oocyte resorption reported by Foucher and Beamish (1980) could be

quantified for use in stock assessment, and if other stocks of Pacific hake showed the same phenomenon. In this paper we compare fecundity between three major stocks of Pacific hake off the west coast of North America and present estimates of "effective" fecundity for these stocks. The total potential fecundity of hake reported in this paper (all yolked oocytes) is considered to be the maximum number of oocytes that could be spawned in a season. We assume that during the spawning season no additional oocytes are recruited into the stock of eggs we have counted.

MATERIAL AND METHODS

Study Area

Three major stocks of Pacific hake were examined during 1983–85: Strait of Georgia (British Columbia), Puget Sound (Washington), and offshore (California to west coast of Vancouver Island). These stocks are considered discrete on the basis of growth; otolith morphology and the pattern of annuli formation; stock dynamics (year-class strength and spawning biology; McFarlane and Beamish 1985); size and age at maturity (Goni 1988); and the presence (or absence) of the myxosporean parasite *Kudoa paniformis* (Kabata and Whitaker 1981; Nelson 1985).

Fish Sampling

Pacific hake were collected with midwater trawls during February, March, and April 1983 and April 1985 in the Strait of Georgia; March 1983 and March, April 1985 in Puget Sound; and March 1983 and January, February 1984 off California (offshore stock).

Peak spawning in the Strait of Georgia and Puget Sound occurs in late March–early April (McFarlane and Beamish 1985; Goni 1988), and off California in late January–February (Woodbury et al. 1995). Therefore, ovaries were collected from ripe fish just prior to or during peak spawning, and from spent fish 2 to 3 weeks after peak spawning in all areas. All fish were sampled for length, sex, maturity, and paired otoliths for age estimation.

Ovaries were selected from ripe and spent fish according to the description of Foucher and Beamish (1977). Only fish that met the criteria for ripe or spent

TABLE 1
Macroscopic Characteristics of Different Stages in the Development of the Ovaries of the Pacific Hake (*Merluccius productus*)

Stage	Macroscopic characteristics
Immature 1 (I1)	Virgin; ovary small, light pink, and semi-transparent; no oocytes
Immature 2 (I2)	Same as above, but some yolkless oocytes visible
Ripening 1 (R1)	Ovary starting to enlarge up to 1/4 of volume of body cavity and light yellow; oocytes with yolk and opaque; blood vessels on ovary pronounced
Ripening 2 (R2)	Ovary filling more than 1/3 of body cavity and yellow; oocytes with yolk and opaque; blood vessels pronounced
Ripe (R)	Ovary fills 1/2 to 1/3 body cavity; yellow
1 Ripe (1R)	Ovary fills 1/2 to 1/3 body cavity; translucent yellow; less than half of the oocytes are translucent
2 Ripe (2R)	Ovary fills 2/3 body cavity, translucent yellow; more than half of the oocytes are translucent
Running ripe (RR)	Translucent oocytes flow from vent with slight pressure; ovaries almost fill body cavity; oocytes loose in translucent ovary
Spent (S)	Ovary bloodshot, purple, and flaccid; fills about 1/3 body cavity; some translucent oocytes may remain
Resorbing (Resb)	Fish has not spawned; ovaries large, about 1/2 of body cavity, soft and flaccid; oocytes large and watery
Recovering (Rec)	Ovaries not flaccid or bloodshot, moderately firm, filling less than 1/2 body cavity and returning to preripening size; oocytes small
Resting (Rest)	Ovaries less than 1/4 body cavity, moderately firm with white sheen on surface, not bloodshot

TABLE 2
Date and Maturity State of Samples Collected during 1983–85

Area	Year	Month	No. ripe	No. spent
Strait of Georgia	1983	Feb/Mar	23	—
	1983	Apr	—	22
	1985	Apr	—	16
Puget Sound	1983	Mar	12	—
	1985	Mar/Apr	13	30
Offshore	1983	Mar	4	43
	1984	Jan/Feb	15	—

as outlined in table 1 were selected. Ovaries were preserved in 10% formaldehyde solution and transferred to the laboratory. In the laboratory, the ovaries were transferred to modified Gilson's solution (Simpson 1951) for several months to allow breakdown of connective tissue.

We made the assumption that no fish categorized as ripe had spawned previously during the season, and that the estimates of total fecundity are unbiased. Although it is possible that some fish could have released eggs prior to sampling, we believe the timing of the collections and our adherence to the criteria (table 1) for selecting ripe fish would ensure that any bias would be small.

Ovary Processing and Fecundity Estimates

Ovaries were washed thoroughly in cold water over an 850-µm stainless steel screen onto a 40-µm nylon fabric screen. When necessary, eggs were gently separated by hand from ovarian tissue.

Eggs from each ovary pair were transferred to a preweighed shallow cup, vacuum dried for 4 minutes, and weighed to obtain total egg weight per fish. Five random subsamples (.05 or .1 gm) were removed. One subsample (.05 gm) was sized and counted in 50-µm

intervals of oocyte diameter. Four subsamples (.01 gm) were counted.

The total number of eggs in the ovary was calculated as the product of the mean subsample count per unit weight and the total egg weight per fish. The number of eggs in various size categories was obtained by applying the appropriate proportional value to the estimated total eggs in the ovary.

RESULTS

A total of 250 fish were collected during 1983 and 1985 in the Strait of Georgia; 225 fish during 1983 and 1985 in Puget Sound; and 95 fish during 1983 and 1984 offshore of California (offshore stock). Of these, 319 were female. Under the criteria of Foucher and Beamish (1977; table 1), 23 ripe and 38 spent ovaries were preserved from the Strait of Georgia, 25 ripe and 30 spent ovaries from Puget Sound, and 19 ripe and 43 spent ovaries from the offshore stock. In order to examine as representative a range of size and age as possible for each stock, we selected fish by size and pooled them for each stock by year and maturity for the analysis (table 2). The age composition of the female Pacific hake examined (figure 1) is representative of fish captured during commercial fishing in these areas (Francis and Hollowed 1985; McFarlane and Beamish 1985; Pedersen 1985).

Frequency Distribution of Oocyte Diameter

Ovaries of prespawning (ripe) fish from all three areas contained a bimodal distribution of oocyte diameters with peaks at about 100 µm and between 500 and 700 µm, similar to that described by MacGregor (1966), Foucher and Beamish (1980), and Mason (1986). Oocytes smaller than 150 µm contained no yolk and may constitute a reserve fund for future years (Foucher and Beamish 1980). All analyses were conducted on yolked oocytes only. In all three areas yolked oocytes were present in all size classes of oocytes from 150 to 840 µm, in approximately the same proportions between areas (figure 2).

Post-spawning (spent) fish from the three areas exhibited very different distributions of oocyte diameters
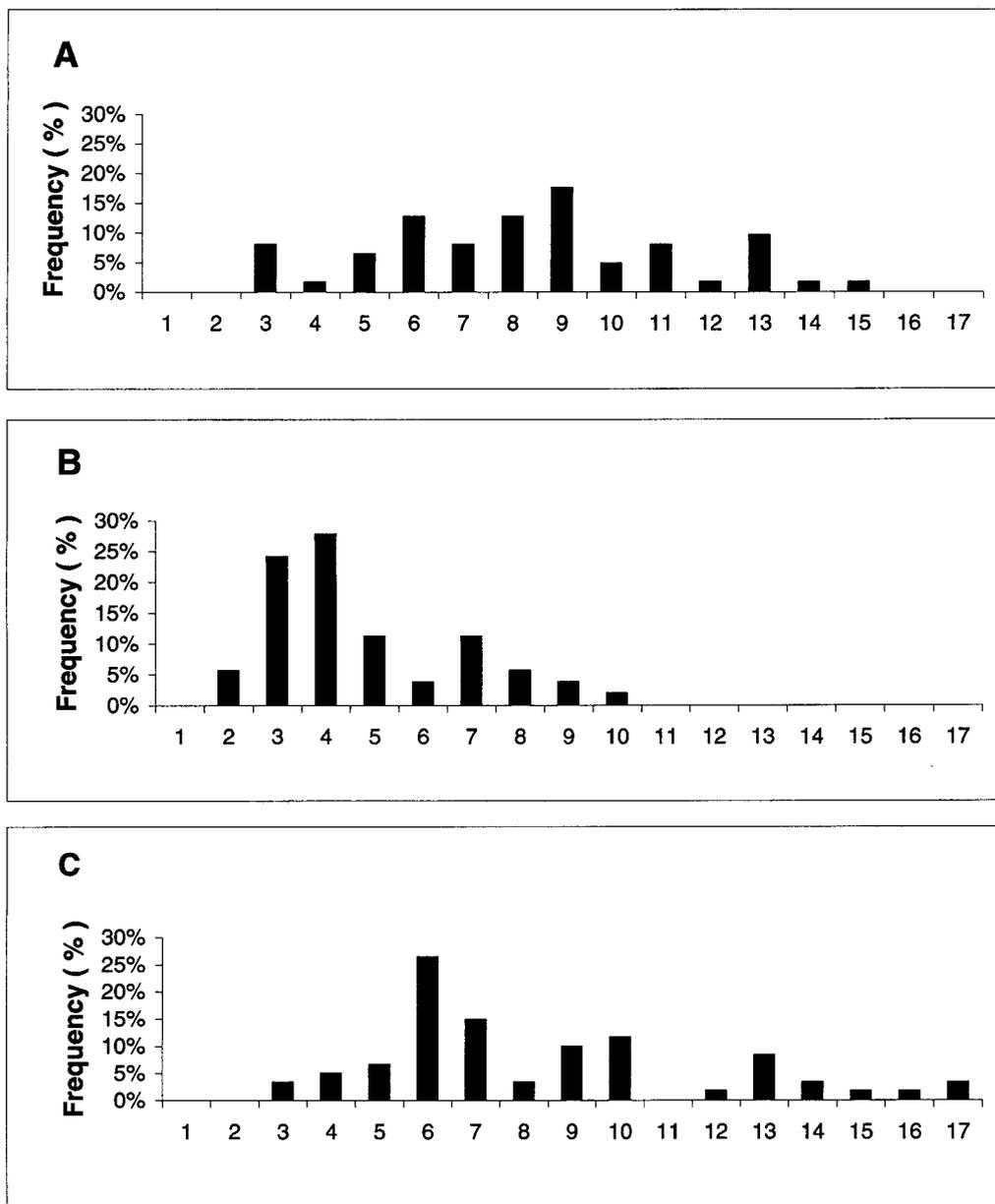
Figure 1.   Age composition of fish collected from A, Strait of Georgia (1983, 1985); B, Puget Sound (1983, 1985); and C, offshore (California; 1983, 1984).

(figure 2). Of the oocytes remaining in the ovaries of spent offshore fish, approximately 70% were in the smallest size class of yolked oocytes (150–280 μm). Few oocytes larger than 360 μm were present. Puget Sound fish exhibited a similar trend: 40% of resorbing eggs in the smallest size class remained, but higher percentages in the larger size classes remained. Strait of Georgia fish exhibited a more even distribution of resorbing eggs across all size categories, with a peak at the smallest size (30%) at 150–280 μm and a smaller, secondary peak at 520–680 μm.

Size-Specific Resorption

Spent ovaries examined for all three stocks contained yolked oocytes (figure 2). In the offshore stock the percentage of retained oocytes was constant across the size range of fish examined: approximately 10%–12% of ripe ovaries. But ovaries examined from both the Strait of Georgia and the Puget Sound stocks showed an increasing percentage of eggs retained with decreasing fish length (figure 3). For Puget Sound, fish between 32 and 36 cm long retained from 44% to 32% of their eggs. But fish approaching the size of mature offshore

RIPE

SPENT
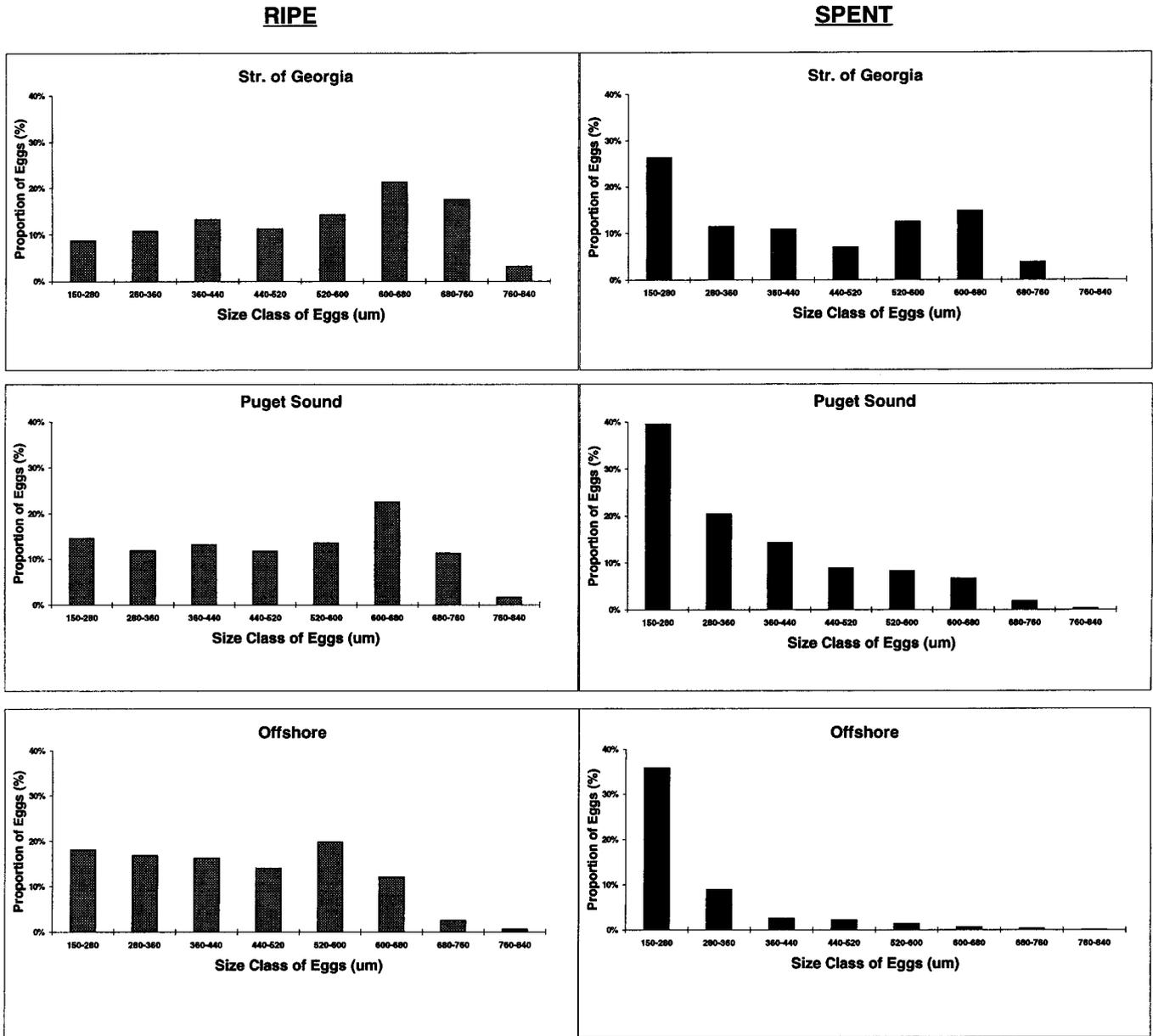
Figure 2. Representative frequency distribution of oocyte diameter from ovaries of Pacific hake collected in the Strait of Georgia, Puget Sound, and offshore (California).

fish retained a percentage of eggs similar to that of off-shore fish (figure 3). The Strait of Georgia stock retained a percentage of eggs considerably higher at all fish lengths than either the Puget Sound or the offshore stocks, averaging between 38% (largest fish) and 58% (smallest fish).

Estimates of Total and Effective Fecundity

The relation of total fecundity to fish size was similar for all three areas (figure 4). Total fecundity (all yolked oocytes >150 μm) increased with length as follows: Strait of Georgia ($y = 0.0001x^{3.9576}$); Puget Sound ($y =$

$0.0003x^{3.6233}$); offshore (California; $y = 0.047x^{2.4311}$), where $y =$ fork length in centimeters (figure 5).

The number of yolked oocytes (>150 μm) remaining in the ovaries of spent fish varied between areas (figure 5) and had the following relationships: Strait of Georgia ($y = 0.0013x^{3.1055}$); Puget Sound ($y = 3.6878x^{0.7117}$); offshore (California; $y = 4E-07x^{4.7875}$).

Our definition of effective fecundity—the number of yolked oocytes that are actually released for fertilization—suggests that the real, or effective, fecundity will be lower for all three stocks than previous estimates of fecundity or the estimates presented here as total fe-

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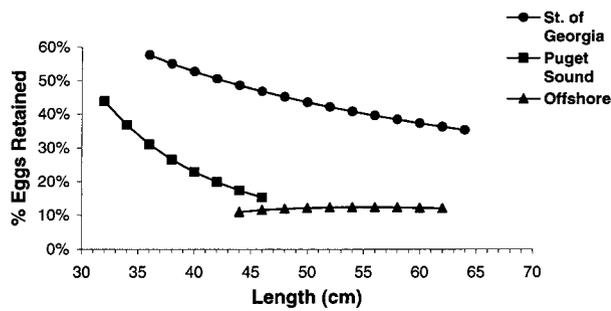
Figure 3. Percentage of oocytes retained in the ovaries of Pacific hake from the Strait of Georgia, Puget Sound, and offshore (California).
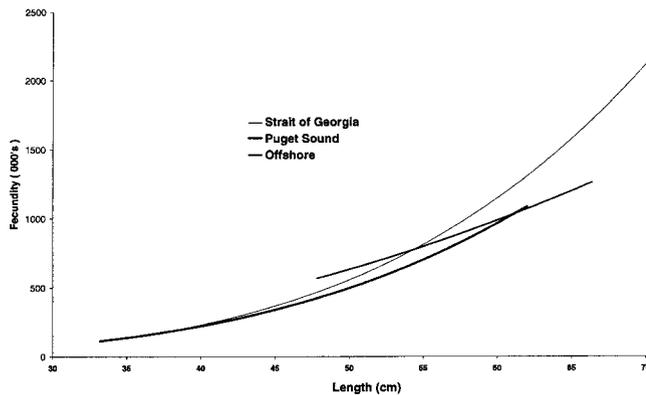
Figure 4. Estimates of number of yolked oocytes (>150 µm) in hake ovaries from the Strait of Georgia, Puget Sound, and offshore (California) plotted against fork length of female hake.

Figure 5. Estimates of number of yolked oocytes (>150 µm) in ripe and spent ovaries from A, Strait of Georgia; B, Puget Sound; and C, offshore (California) plotted against fork length of female hake.

cundity (figure 6). Effective fecundity increased with length as follows: Strait of Georgia ($y = 0.0035x^{4.6746}$); Puget Sound ($y = 0.0021x^{4.9268}$); offshore (California; $y = 46.713x^{2.4004}$).

We also examined the relation of only the larger size classes of yolked eggs to length, as other authors have suggested might be appropriate (MacGregor 1966; Mason 1986). We chose eggs larger than 360 µm because our observations indicated that most fish in two of the stocks (Puget Sound and offshore) retained only a small percentage of eggs larger than 360 µm in the ovary after spawning. The relation of eggs larger than 360 µm to length is: Strait of Georgia ($y = 0.0099x^{4.4254}$); Puget Sound ($y = 0.067x^{3.9623}$); offshore (California; $y = 133.8x^{2.0894}$).

DISCUSSION

Our estimates of total fecundity (all yolked oocytes >150 µm) are similar among stocks and comparable to the estimates presented by MacGregor (1966). For the Strait of Georgia our estimates of total fecundity are substantially higher (~30%) than those presented by Mason (1986), but the methods Mason used to estimate fecundity have been shown to consistently underestimate fecundity in other species (Leaman 1988).

Our study indicates that all three stocks of Pacific hake resorb a proportion of their yolked oocytes after spawning; the proportion ranges from 10%–12% for the offshore stock to 38%–58% for the Strait of Georgia stock.

The size-specific trend in resorption (retained eggs) in the Puget Sound and Strait of Georgia stocks may indicate a physiological response to maturation at a smaller size. The mechanisms for this are unknown; however, we do note that for the small fish in which this is most pronounced (Puget Sound: 32–35 cm) the impact on total or effective fecundity for the range of mature fish is small.

For some stocks of fish the effective fecundity, or number of viable eggs released to be fertilized, may be substantially less than the number of yolked oocytes produced in the ovary. It is important that investigators using fecundity to monitor the health of a stock, or to estimate abundance or potential recruitment for stock assessment be aware of how the resorption of a large percentage of seemingly viable eggs will affect their studies.
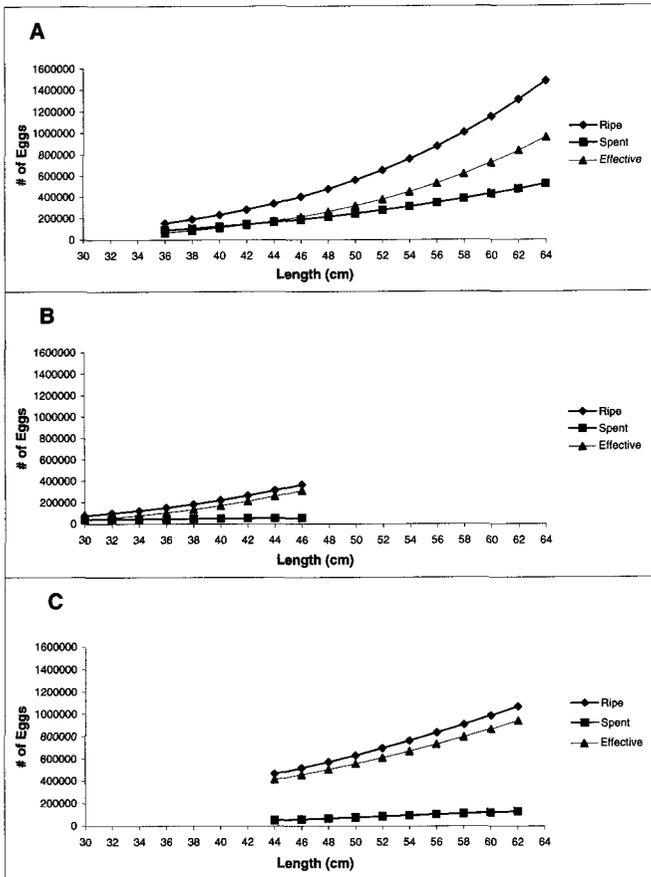
Figure 6. Relationship between total fecundity (ripe) and effective fecundity (ripe–spent) for Pacific hake in A, Strait of Georgia; B, Puget Sound; and C, offshore (California).

Other researchers have reported on this phenomenon for Pacific hake (Foucher and Beamish 1980; Mason 1986), other forms of *Merluccius* (Hickling 1930; Christiansen 1971), and other species (Hoar 1955). This study, to the best of our knowledge, is the first to attempt to quantify this resorption.

ACKNOWLEDGMENTS

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VERTICAL DISTRIBUTION OF PACIFIC HAKE EGGS IN RELATION TO
STAGE OF DEVELOPMENT AND TEMPERATURE

H. GEOFFREY MOSER, NANCY C. H. LO, AND PAUL E. SMITH
National Marine Fisheries Service
Southwest Fisheries Science Center
P. O. Box 271
La Jolla, California 92038

ABSTRACT

The vertical distribution of eggs of Pacific hake (*Merluccius productus*) was determined from 27 MOCNESS samples taken on cruises off southern and central California in March 1995 and February 1996. In 1995, nine depth strata (0–25, 25–50, 50–75, 75–100, 100–125, 125–150, 150–200, 200–250, and 250–300 m) were sampled. In 1996, nine 25-m depth strata were sampled down to 225 m. In 1995 Pacific hake eggs were taken in all strata down to 250–300 m; most of the eggs were found between 50 and 150 m, with the highest densities in the 50–75- and 75–100-m strata. Average temperatures for developing Pacific hake eggs were estimated to be 10.2°–11.3°C. Early-stage eggs were generally deeper in the water column than later-stage eggs. Most early-stage eggs were found between 75 and 150 m, with highest densities in the 125–150-m stratum. In contrast, mid- and late-stage eggs were most dense in the 50–75- and 75–100-m strata. Early-stage eggs were taken primarily in tows between 2200 and 0600 hrs, suggesting diel periodicity in spawning. On the 1996 cruise hake eggs had a slightly shallower distribution compared with 1995, and there was more overlap in vertical distribution between stages. Methods are given for separating Pacific hake eggs from similar eggs of other species, and criteria are described for staging Pacific hake eggs.

INTRODUCTION

The daily egg production method (DEPM) is an effective fishery-independent means of estimating the biomass of commercially important fish stocks (Hunter and Lo 1993). It has been applied principally to coastal pelagic fishes; however, a modification of this method, the daily fecundity reduction method (DFRM), has been used for demersal fishes such as Dover sole (Lo et al. 1993), orange roughy (Zeldis 1993), and sablefish (Moser et al. 1994). Application of the DFRM to Pacific hake may be confounded by the difficulty of sampling egg patches produced by the reputed large spawning aggregations about 100–400 m deep off central and southern California (observations of M. V. Stepanenko reported by Stauffer 1985).

During March 9–27, 1995, the Coastal Fisheries Resources Division, Southwest Fisheries Science Center, conducted Cruise 9503-JD (figure 1), partly to determine the vertical distribution of Pacific hake eggs in
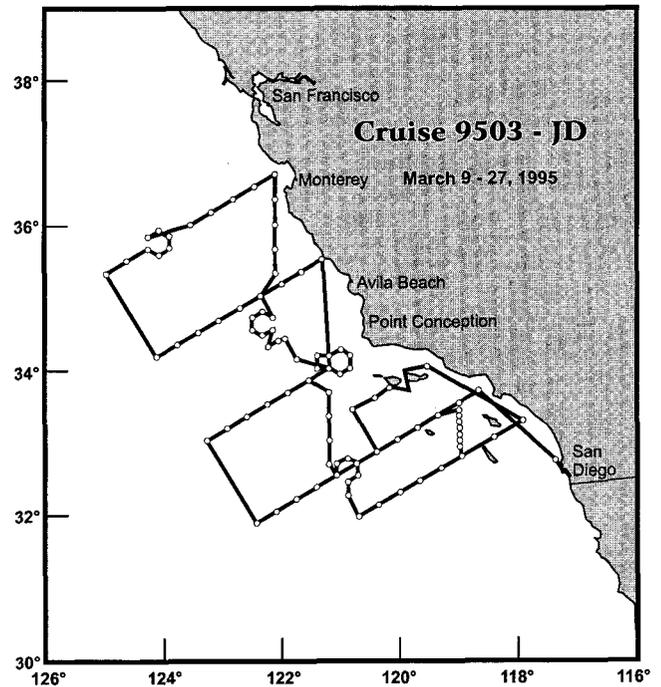
Figure 1. Sampling pattern for Cruise 9503-JD. Pacific hake eggs from MOCNESS stations indicated by the three hexagonal sampling areas extending northwest from Point Conception were used in this analysis.

relation to stage of development, age, and temperature; this information is needed to construct the mortality curves required for DFRM biomass estimation. Additional vertically stratified samples of Pacific hake eggs were obtained from a cruise (9602-RGS) conducted by Shannon Cass-Calay during February 8–13, 1996, in the Southern California Bight (Cass-Calay 1997).

In this paper we describe the methods of identifying Pacific hake eggs, the criteria for assigning developmental stages to them, and their vertical distribution on Cruises 9503-JD and 9602-RGS. The age of the eggs will be determined when a stage-to-age key becomes available.

METHODS AND MATERIALS

In 1995 a total of 102 oblique bongo net tows (505-µ mesh) was made on five onshore-offshore transects from Dana Point to Monterey, California. When live-sorting of these catches revealed high concentrations of Pacific hake larvae, a close-interval hexagonal set of six vertically stratified plankton tows was taken, sampling

nine depth strata (0–25, 25–50, 50–75, 75–100, 100–125, 125–150, 150–200, 200–250, and 250–300 m). Pacific hake eggs were identified and staged from these samples; eggs from the three sets taken off central California were used in this analysis. One of the 18 tows (station 19) produced >27,000 Pacific hake eggs; this tow was not included in our analyses of frequency distribution, because the extremely high number of eggs overshadowed the egg frequencies of the other tows.

Another source of material was a series of 10 vertically stratified tows (25-m strata to 225-m depth) taken in the Southern California Bight by Shannon Cass-Calay in 1996 (Cass-Calay 1997). Pacific hake eggs from these tows were identified and staged, and provided additional data for this study.

The sampler employed on both cruises was a MOCNESS-1 (Wiebe et al. 1976) with a 1-m^2 mouth opening and 505-μ mesh.

Identification of Pacific Hake Eggs

Pacific hake eggs were identified with criteria of Ahlstrom and Counts (1955), Matarese et al. (1989), Ambrose (1996), and several other criteria established in this study. Preserved eggs have a smooth shell (1.04–1.20-mm diameter); a relatively large oil globule (0.27–0.34-mm diameter) that is deep yellow to slightly orange; a deep yellow, homogeneous yolk; and a narrow perivitelline space.

Eggs of a bathylagid (*Leuroglossus stilbius*) commonly co-occur with Pacific hake eggs and overlap with them in size, but have a pale, segmented yolk and multiple oil globules that migrate and coalesce during development. In preserved early-stage eggs of both species, the yolk membrane is often broken, and in *L. stilbius* the membranes of the yolk segments may be broken, so that the yolk appears homogeneous. When no remnants of yolk segmentation are present the eggs of the two species may be difficult to separate. The oil globule is usually intact in Pacific hake eggs, whereas in *L. stilbius* it is fragmented and paler in color than in Pacific hake. In *L. stilbius* eggs the inner surface of the chorion is faintly ornamented with minute pustules (see Moser and Ahlstrom 1996), which are lacking in Pacific hake. Usually this ornamentation is visible in preserved eggs and can aid in separating eggs of the two species.

Early-stage eggs of Pacific mackerel (*Scomber japonicus*) are similar to those of Pacific hake and are difficult to distinguish from them. The oil globule is paler in Pacific mackerel than in Pacific hake. When pigment develops in mid-stage eggs, the two species are easily distinguished. In Pacific hake, melanophores are present on the yolk anterior to the head; head pigment extends forward to the snout; and pigment is absent on the tip of the tail. Pacific mackerel eggs lack yolk pigment for-

ward of the head and on the snout; melanophores on the head and body are larger and less dense than in Pacific hake; and pigment extends farther posteriad on the tail. In late-stage eggs, the pigment pattern is distinctive for these species.

Staging of Pacific Hake Eggs

Each egg was assigned to one of 11 developmental stages. Stage criteria were similar to those used for pelagic eggs of other species (Moser and Ahlstrom 1985; Lo et al. 1992; Lo et al. 1996), but some modification was required. In a large proportion of early stage 2 eggs the yolk membrane was broken and the blastodisc was disassociated, with the blastomeres scattered throughout the yolk and often partially or totally disintegrated. Because eggs in this condition could not be distinguished from stage 1 eggs, for practical purposes the two stages were combined as stage 2.

Stage 1: Begins with extrusion and fertilization and ends with the beginning of cell division. In the few intact stage 1 eggs in our samples, the cytoplasm is paler than the yolk and may contain minute granules that are easily distinguishable from the minute cells (blastomeres) that form the blastodisc of late stage 3 eggs.

Stage 2 (figure 2a): Begins with the initial division of the cytoplasm into two cells; ends when the individual blastomeres have undergone numerous divisions and the blastodisc has the appearance of tissue when viewed at 12 power with the dissecting microscope.

Stage 3: Begins when cell division has progressed to the point where the individual blastomeres are no longer apparent (viewed at 12 power); ends when the embryonic shield covers half of the blastodisc. The embryonic shield is a bell-shaped mass of cells that proliferates inward from the margin of the blastodisc, eventually forming the axis of the embryo.

Stage 4: The yolk mass begins to be covered by cell proliferation and movement of the blastoderm around the yolk (epiboly). Stage 4 begins when the germ ring (thickened margin of blastodisc) has progressed one-third of the way around the yolk mass. The embryonic shield becomes denser and begins to form the axis of the embryo.

Stage 5 (figure 2b): Begins when the germ ring has progressed two-thirds of the way around the yolk mass, and the embryonic axis extends to the edge of the germ ring. At the end of stage 5 the brain, optic vesicles, and trunk somites of the embryo are becoming apparent. Late in stage 5, melanophores form on the embryo and on the yolk anterior to the head (not shown in figure 2b).
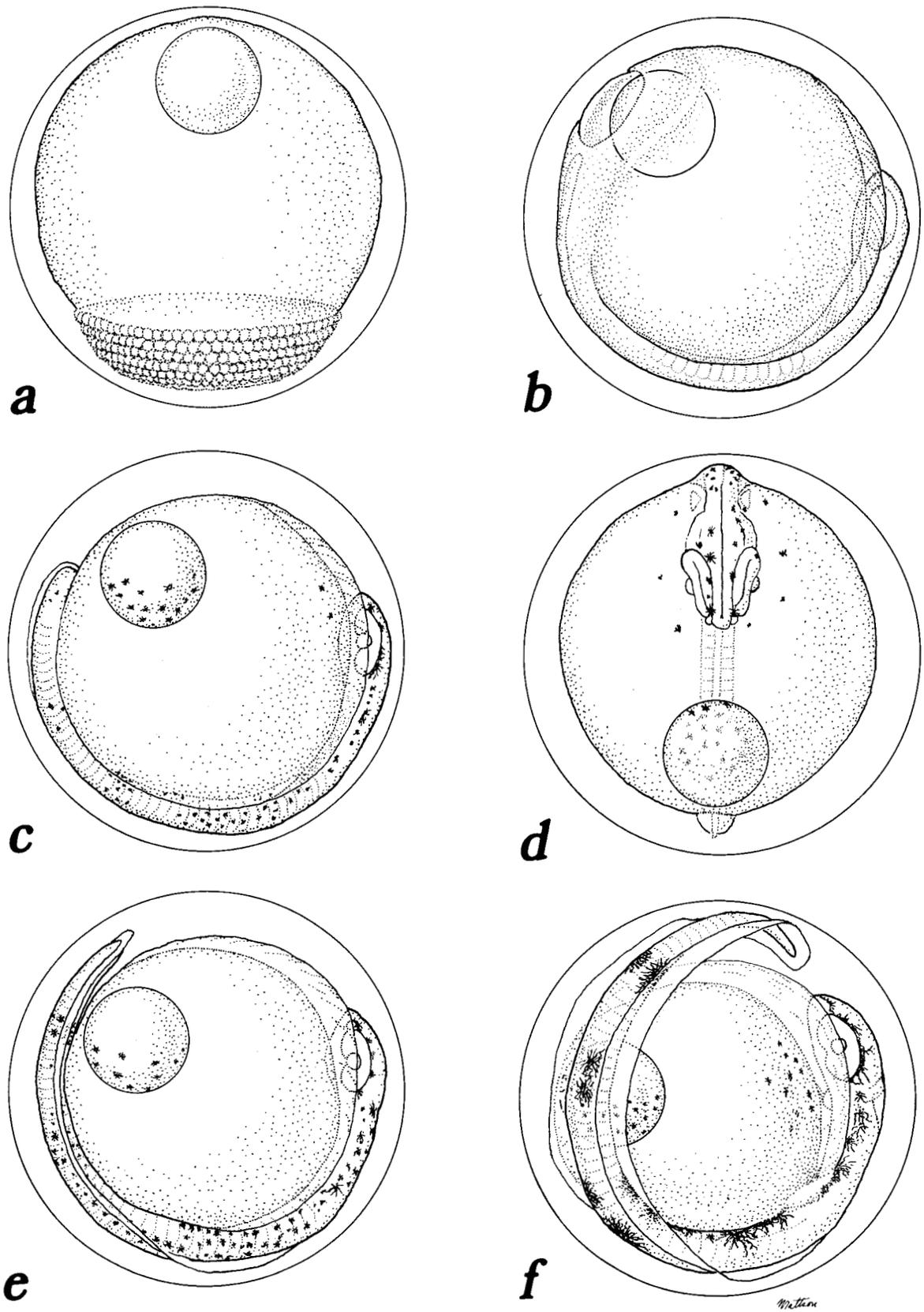
Figure 2. Examples of developmental stages of Pacific hake eggs: a, stage 2: b, late stage 5; c and d, lateral and front view of early stage 7; e, stage 9; f, stage 11. Illustrations from Ahlstrom and Counts (1955).

Stage 6: Begins with closure of the "blastopore" at the posterior tip of the embryonic axis. By the end of stage 6, the somites are present along most of the embryo; the brain has begun to differentiate; the lens primordia are forming in the eyes; and the tip of the tail has thickened slightly.

Stage 7 (figure 2c and d): Begins when the tip of the tail has become rounded and has begun to separate from the yolk mass. The tail becomes pointed as it lengthens.

Stage 8: Begins when the length of the free section of the tail (the portion that has separated from the yolk mass) is half the length of the head (head length defined for this purpose as the distance from the tip of the snout to the back of the midbrain).

Stage 9 (figure 2e): Begins when tail length is ≥head length.

Stage 10: Begins when the tail has reached halfway around the yolk mass. Pigment is becoming organized into a characteristic pattern.

Stage 11 (figure 2f): Begins when the tail has reached three-quarters of the way around the yolk mass. Pectoral fin primordia are obvious. The posterior pigment bar on the tail is distinct. Stage 11 ends at hatching.

RESULTS

On Cruise 9503-JD, Pacific hake eggs were taken in all strata down to 250–300 m. Most came from strata between 50 and 150 m, with the 50–75- and 75–100-m strata showing the highest densities (figures 3, 4). This is generally consistent with results of previous studies of the vertical distribution of Pacific hake eggs (Ahlstrom 1959; Bailey 1982). Early-stage eggs were generally deeper in the water column than later-stage eggs (figure 5). Most stage 2–3 eggs were found between 75 and 150 m, with highest densities in the 125–150-m stratum. In contrast, highest densities of mid- and late-stage eggs were found in the 50–75- and 75–100-m strata.

The Weibull distribution function (shown below) was used to model the distribution of eggs of four groups of stages (2–3, 4–6, 7–9, and 10–11) from Cruise 9503-JD in relation to depth and temperature (table 1).

$$y = 1 - \exp[-(x/p1)^{p2}]$$

Stages were grouped because data were sparse for some stages. In our model, y ($0 < y < 1$) is the cumulative proportion of eggs down to depth (m) or up to temperature (°C) where depth or temperature are denoted by x. The parameter $p1$ is the scale parameter, and $p2$ is the shape parameter. When $p2 = 1$, the Weibull distribution is reduced to an exponential distribution. The scale parameter $p1$ is the average of x for either $p2 = 1$ or for
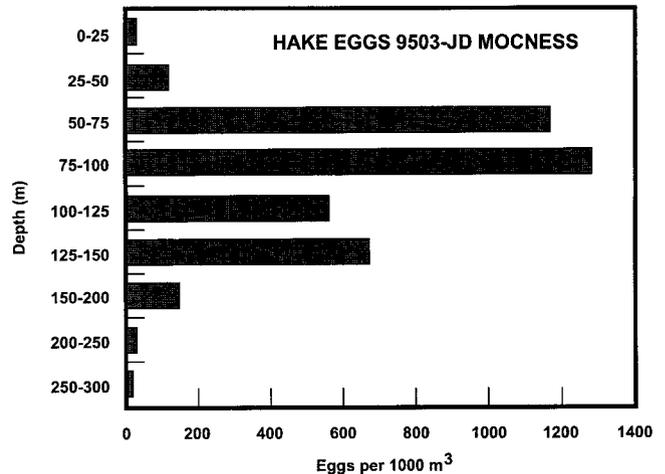
Figure 3. Vertical distribution of Pacific hake eggs based on 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995; values are average densities (eggs/1,000 m³) for each of 9 depth strata.
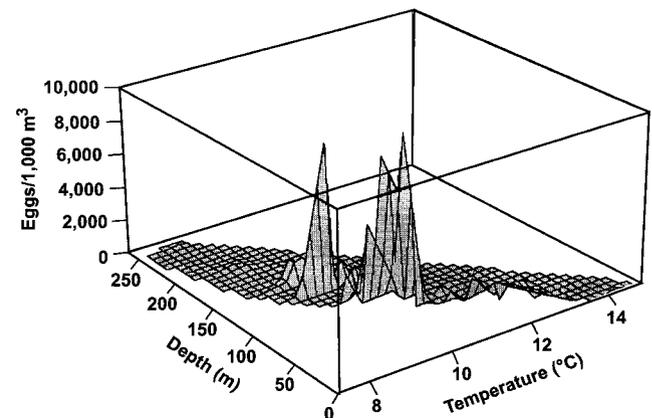
Figure 4. Relation of hake egg density to depth (m) and temperature (°C) based on hake eggs collected in 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995.
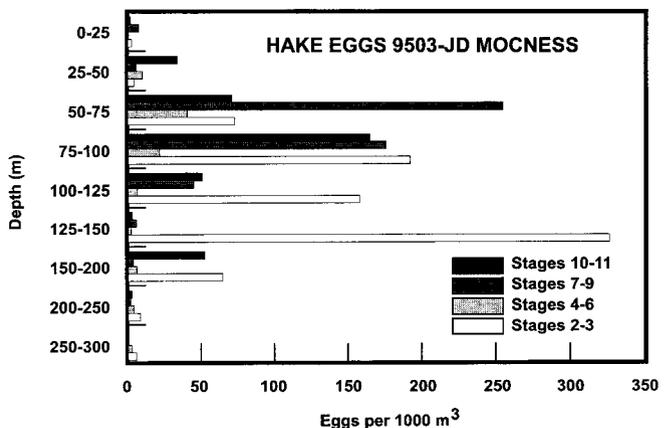
Figure 5. Vertical distribution of four stage-groups of Pacific hake eggs, based on 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995; values are average densities (eggs/1,000 m³) for each of 9 depth strata.

TABLE 1
**Parameter Estimates for Weibull Distribution Function[a]
Used to Calculate Cumulative Proportions of
Depth and Temperature for Eggs of Pacific Hake
Collected on Cruise 9503-JD**

Depth (m)

		$p1$			$p2$		
Stage	Estimate	Std. error	t value	Estimate	Std. error	t value	Mean
2–3	134.17	1.08	124.22	4.08	0.18	23.35	125.21 m
4–6	109.17	1.44	75.85	4.47	0.35	12.86	103.14 m
7–9	83.80	0.50	167.30	6.58	0.39	16.86	81.73 m
10–11	82.08	0.55	149.96	5.76	0.30	19.45	79.41 m
All	106.97	0.83	129.70	3.46	0.13	27.65	96.91 m

Temperature (°C)

2–3	10.29	0.03	408.06	19.38	0.96	20.25	10.23°C
4–6[b]	11.03	—	—	14.93	—	—	11.02°C
7–9	11.77	0.05	255.65	10.49	0.04	23.61	11.29°C
10–11	11.17	0.06	198.69	11.44	0.67	17.22	11.02°C
All	10.88	0.04	249.92	13.43	0.75	17.94	10.96°C

[a]See text for description of Weibull distribution function.
[b]The estimates of parameters were interpolated from values of stage-groups 2–3 and 7–9, because the estimates of parameters did not converge.

large values. In either case, $p1$ is similar to the average depth or temperature for Pacific hake eggs in each of the four stage-groups. The fitted curves for the depth distributions (figure 6) indicated that the shape parameters were greater than 1 (ca. 4), which means that the vertical distribution of each of the four groups was not exponential, and that $p1$'s were close to the mean depth. Based on $p1$ values, early-stage eggs were deeper in the water column than later stages, ascending from a mean depth of about 125 m to about 80 m (table 1).

Estimates of Weibull parameters for the temperatures associated with each stage-group were also obtained, and the estimates of the shape parameters, $p2$, were even greater than those of the depth distribution (figure 7). Therefore, $p1$ was close to its mean temperature. Younger stages encountered slightly colder temperatures (ca. 10.3°C) than older stages (ca. 11.0°–11.3°C; table 1). Slopes of the curves in figures 6 and 7 indicate that early-stage eggs were rather broadly distributed below the thermocline (figure 6), where they encountered a narrow range of temperatures (figure 7), but older eggs ascended and became mostly concentrated in a narrower depth zone in the lower part of the thermocline (figure 6), which had a broader range of temperatures (figure 7).

Pacific hake eggs from Cruise 9602-RGS had a slightly shallower distribution than those from Cruise 9503-JD (figures 3, 8). Eggs were taken in all strata down to 200–225 m, most from strata between 25 and 125 m. The 50–75- and 75–100-m strata showed the highest densities. Early-stage eggs were generally deeper in the water column than later-stage eggs, but there was more overlap in vertical distribution between stages than in Cruise 9503-JD (figure 9).
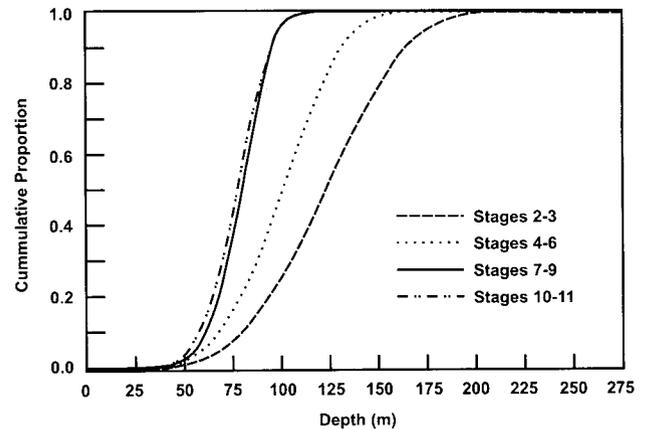
Figure 6. Cumulative proportion of Pacific hake egg density versus depth of collection for four stage-groups, based on 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995. Values are derived from Weibull distribution function (table 1).
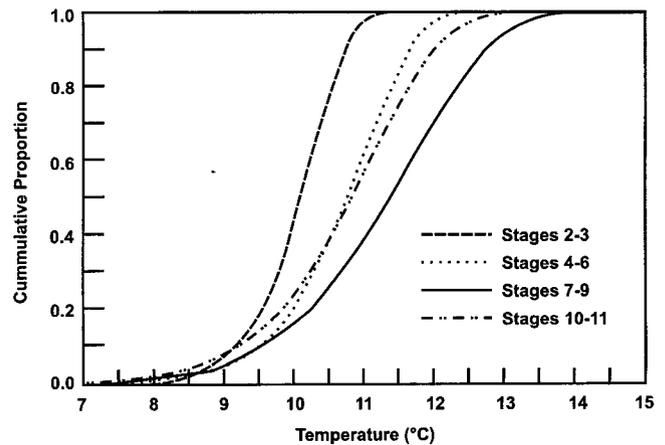

Figure 7. Cumulative proportion of Pacific hake egg density versus habitat temperature for four stage-groups, based on 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995. Values are derived from Weibull distribution function (table 1).
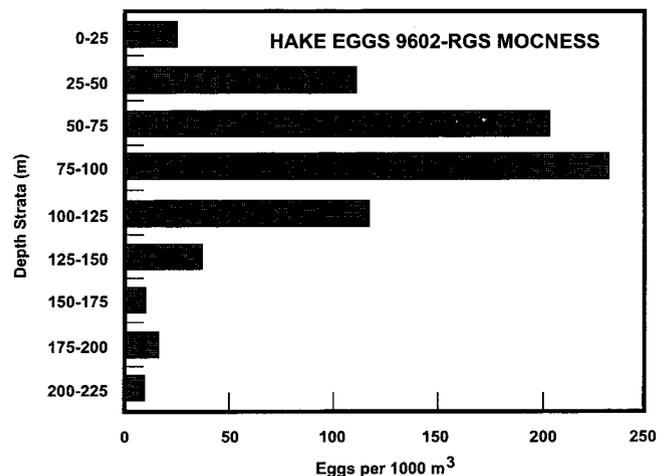

Figure 8. Vertical distribution of Pacific hake eggs based on 10 MOCNESS tows taken during Cruise 9602-RGS off southern California, February 8–13, 1996. Values are average densities (eggs/1,000 m³) for each of 9 depth strata.
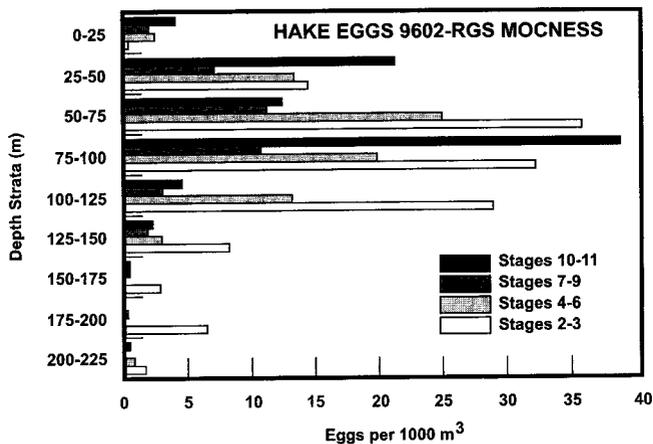
Figure 9. Vertical distribution of four stage-groups of Pacific hake eggs, based on 10 MOCNESS tows taken during Cruise 9602-RGS off southern California, February 8–13, 1996. Values are average densities (eggs/1,000 m³) for each of 9 depth strata.

DISCUSSION

March 1995 MOCNESS tows from central California show that Pacific hake eggs range from the surface to as deep as 250–300 m. Relatively few, however, occur below 200 m, the maximum depth of the standard CalCOFI oblique plankton tow. The eggs are most abundant between 50 and 100 m (lower limit of the mixed layer and thermocline). These findings correspond to those of Ahlstrom (1959), who found the highest abundance of Pacific hake eggs at about 75 m in two series of vertically stratified tows in the Southern California Bight. Eggs of the reproductively isolated Puget Sound population of *M. productus* occur at approximately the same depth as those off California, but in the bottom 25 m of the water column at a bottom depth of about 110 m (Bailey 1982). Coombs and Mitchell (1982) found the eggs of *M. merluccius* at about 50 and 150 m off the west coast of the British Isles.

Vertically stratified tows in 1995 showed highest densities for stage 2–3 eggs at 75–150 m, with some as deep as 250–300 m; in 1996 the highest densities for these stages were at 50–125 m. This suggests that newly spawned eggs may ascend from aggregations spawning in the 100–400-m depth range, as reported in Stauffer (1985). Thus, tows made for egg production biomass assessment should be taken to at least 300 m to assure that the vertical distribution is encompassed. Another consideration in developing sampling procedures in DEPM surveys is time of spawning. On Cruise 9503-JD, stage 2 eggs occurred primarily in tows taken between 2200 and 0600 hrs, suggesting diel periodicity, but more information is needed to determine the time of spawning.

Average temperatures encountered by developing Pacific hake eggs were estimated to be 10.2°–11.3°C. The incubation period for Pacific hake eggs developing

at this temperature is 4–5 days (Zweifel and Lasker 1976; Bailey 1982). Estimating the age of Pacific hake eggs with morphological criteria will require experimentally rearing eggs to allow development of a temperature-specific stage-to-age key.

Pacific hake eggs can be separated from eggs of other fishes present off California during the compressed spawning season in January–March, but early-stage eggs of Pacific mackerel may be indistinguishable from those of Pacific hake. This is most problematic when sampling is done after February off southern and central California. Although Pacific mackerel generally spawn later in the year than Pacific hake, we encountered late-stage eggs of both species in the same tows during March 1995 in the Southern California Bight; consequently, we did not use eggs from the MOCNESS tows in the Southern California Bight in our analysis. Other methods of species identification, such as genetic markers, would be required to separate eggs of these species where their eggs may co-occur.

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VERTICAL DISTRIBUTIONS OF ZOOPLANKTON AND LARVAE OF THE PACIFIC HAKE (WHITING), *MERLUCCIUS PRODUCTUS*, IN THE CALIFORNIA CURRENT SYSTEM

MICHAEL M. MULLIN AND SHANNON L. CASS-CALAY

Marine Life Research Group
Scripps Institution of Oceanography
9500 Gilman Drive
La Jolla, California 92093-0218

ABSTRACT

As part of an investigation of the vertical distributions of larval hake and potential food in March 1995, we used a pump to sample microzooplankton larger than 73 µm and an optical plankton counter (OPC) for zooplankton 250 µm or larger, at depths to 250 or 300 m at eight stations where larvae were found, and one other station. We also intercalibrated the two techniques for sampling potential food. Copepod nauplii and copepodids dominated the microzooplanktonic biomass. The greatest fraction of larval hake was found in the 50–75-m layer, together with the greatest fraction of the potential food (by either mensural technique) deeper than 50 m. The depth distributions of larvae and OPC-estimated zooplankton were positively correlated from 50 to 300 m, but this relation was not significant between the larvae and potential microzooplanktonic food caught by pumping. Because of a great abundance and relatively shallow distribution of larvae at one particularly rich station, however, there was an overall correlation between the abundance of larvae in a particular sample and the biomass of their food.

INTRODUCTION

The small-scale distribution of larval fish relative to their food supply has frequently been examined in attempts to determine whether availability of food during early life affects the success of eventual recruitment to the adult population. Larval Pacific hake (whiting), *Merluccius productus*, are particularly interesting in this regard, since they occur deeper in the water column than the larvae of most other commercially important species (Ahlstrom 1969), and therefore presumably experience quantitatively different environmental factors, including significantly lower concentrations of food, than do larvae living nearer the surface at the same locations.

Microzooplankton (heterotrophs a few tens to a few hundreds of µm in size, including proto- and metazoans) is awkward to sample—often too rare to enumerate precisely when sampled with water bottles, and too small to be retained in towed nets of commonly used mesh sizes. Yet one of the components (copepod nauplii) is perhaps the most important type of food for larval fish. One of the few investigations of the vertical distribution

of microzooplankton in the California Current system off southern California was conducted by Beers and Stewart (1969), who obtained samples of total seston, total chlorophyll, and organisms passing through a 202-µm mesh from six depth intervals between the surface and 200 m at three offshore stations. Most relevant for comparison to the present work are data concerning microzooplankton retained on a 103-µm mesh. Copepod nauplii and copepodites dominated this size category, and were more abundant above 50 m than below this depth. Radiolarians also contributed significantly to the total abundance of microzooplankton below 50 m, which was $\leq 5 \cdot L^{-1}$. We used similar methods and addressed many of the same questions, but did not attempt as complete an assessment of taxa or of trophic or size categories.

We also used an optical plankton counter (OPC) to categorize by size and to assess the vertical distributions of somewhat larger zooplankton, on which the larvae increasingly depend as they grow. Because the OPC was attached directly to the opening/closing net used to determine the vertical distribution of larval hake, it provided a direct measure of the concentration of various food-sized particles in the depth strata where larvae were (or were not) caught, together with estimates of variability at smaller scales within strata.

METHODS

Sampling the Larval Hake

Our study was conducted during a March 1995 research cruise organized by the Coastal Fisheries Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, on the RV *David Starr Jordan* (Lo 1997). We sampled a subset of the stations at which vertical distributions of larval hake were determined; this subset represented a variety of distributions and abundances (table 1).

The larval hake (along with other macrozooplankton) were sampled by a multiple opening/closing net and environmental sensing system (MOCNESS; Wiebe et al. 1976). This system was routinely deployed to 300 m, and nine depth strata were sampled between that depth and the surface—nominally strata 50 m thick below 150 m, and 25 m thick above that depth.

TABLE 1
Locations, Dates, Local Times of Samples, and Abundance of Larval Hake

Station	Lat., long.	Date (March 1995)	Time MOCNESS and OPC started	Time pump started	Larval hake/m²	Median depth stratum (m)*
80.0, 85.0	33°18.9'N 122°52.9'W	12	1017	1230	0	x
80.0, 60.0	34°09.0'N 121°09.0'W	13	0608	0800	17.5	50–75
80.7, 58.8	34°03.8'N 120°58.6'W	13	1346	1530	10.5	75–100
79.3, 58.7	34°19.0'N 121°08.8'W	14	0511	0700	18.2	50–75
66.7, 80.0	35°47.2'N 124°11.7'W	17	1212	1400	7.1	125–150
67.4, 78.8	35°42.2'N 124°01.2'W	17	1833	2030	4.1	100–125
66.0, 78.7	35°57.2'N 124°11.7'W	18	1119	1230	2.4	75–100
74.3, 68.8	34°50.9'N 122°27.4'W	20	0736	0930	43.7	50–75
75.7, 66.3	34°40.9'N 122°06.5'W	20–21	2204	0030	9.8	50–100

*Stratum fished by the MOCNESS where 50% of the larval hake occurred in that stratum or shallower, and 50% in that stratum or deeper.

Sampling by Pump

Samples for microzooplankton were taken by lowering the intake of a 3.8-cm-diameter hose attached to a weighted hydrographic wire to 240 m and then pumping water from each successively shallower depth through an on-deck centrifugal pump into a collecting tub (after allowing the hose to flush with water from each new depth). From the tub, the water passed through a flowmeter and into a 73-μm-mesh net (figure 1 in Star and Mullin 1981; Miller and Judkins 1981). Each net-concentrated sample was preserved in 5% formalin-seawater. A subsample of the flow from the tub was diverted into a bucket in which temperature was measured. Depths were generally chosen to correspond to depths fished by the MOCNESS, with some finer detail near the surface, but we took no samples of micro-zooplankton in the 250–300-m or 100–125-m strata sampled by the MOCNESS.

Some caution is necessary in interpreting the results. The issues are actual depth of sampling, sampling efficiency, and synchronism. The temperature of the deepest samples was usually higher than the temperature measured at comparable depths by the MOCNESS, even when the hose was vertical. Although this probably resulted from heating as the samples passed through warmer surface waters, plus perhaps some frictional heating in the hose, it is possible that some water leaked into the hose from shallower depths.

We did not assess avoidance by zooplankters, nor rig-

orously compare the catches to those of some other, more conventional device such as a net, though a comparison with samples collected by water bottle satisfied us that nauplii and small copepodites were not destroyed by the pump. But because the hose was shortened to 100 m when that depth was reached, the flow rate increased significantly, and thus it is possible that avoidance was less important above 100 m than in the deeper samples. We tested this possibility by comparing six catches taken from 100 m with 240 m of hose (flow rate 49 L·min⁻¹) with five preceding and five following catches from the same depth but with only 100 m of hose (flow rate 79 L·min⁻¹).

For each enumerated category, there was no significant difference between median abundance in samples taken at the slower flow rate (longer hose) or the faster flow rate ($p > 0.10$ of no difference by rank sum test in all cases). Hence, efficiency of capture, though unknown, did not change significantly when the hose was shortened. Horizontal patchiness of all enumerated categories of organisms is shown by the coefficients of dispersion (variance/mean), which ranged from 9 for the least abundant category to about 60 for the most abundant.

It is also worth noting that the vertical profiles obtained by pump followed the MOCNESS tow (table 1), and took up to three hours to complete. The ship's motion caused some vertical and horizontal integration during sampling. In spite of time lag and drift, we assume that each depth sampled by pump was assignable to the

stratum sampled by the MOCNESS which included that depth (i.e., an assumption that horizontal layering was the dominant form of variability on this scale).

Microzooplankters in each sample were enumerated and measured under a dissecting microscope by one of two people; the counters were unaware of the sample's identity, and counted the samples in haphazard order. They assigned organisms to one of the following categories of maximum width: eggs; protozoans (mainly dinoflagellates and radiolarians); copepod nauplii <160 μm and ≥160 μm; copepodites <160 μm, 160–400 μm, and >400 μm; and other metazoans <160 μm, 160–400 μm, and >400 μm. The categorization was based on width of the mouth and maximum width of food items found in the guts of larval hake of various lengths (Sumida and Moser 1980). The mouth of a 33-mm larva is approximately 400 μm wide, although prey that large were actually found only in guts of larvae >40 mm long, and probably do not become a frequent part of the diet until a larva reaches 100 mm. Of larvae shorter than 40 mm with prey in their guts, approximately half contained prey at least 160 μm wide (but smaller than 400 μm).

To calculate the biomass of particular kinds of food as sampled by the pump, or the sum of all kinds, we assumed (1) that the eggs and protozoans were 100-μm spheres; (2) that the nauplii were cylinders with height equal to twice the diameter, small nauplii were 120 μm in diameter, and large nauplii were 253 μm in diameter; and (3) that copepodids and "other" metazoans were cylinders with heights equal to thrice the diameters, and the respective diameters of small, medium, and large animals were 120, 253, and 450 μm.

Sampling by Optical Plankton Counter

Because the MOCNESS required a conducting cable for towing, we were able to record data from an optical plankton counter (OPC) mounted directly on the top of the MOCNESS frame while the MOCNESS was being fished. This also allowed us to use the rate of travel of the MOCNESS through the water, monitored by an electronic flowmeter, to estimate the volumetric rate of sampling of the OPC, and to monitor the depth of sampling.

The OPC provided data categorized only by size of particle (indeed, there is no proof that all the particles counted were individual, living zooplankters), but with much greater vertical resolution than did the pump, and with no horizontal offset from the samples of larval hake. In fact, the vertical resolution of OPC data within the stratum sampled by each MOCNESS net was of little use except to indicate the range of concentrations of potential prey for the larvae caught in that stratum.

The OPC is described by Herman (1988), and has been used fairly often on towed or lowered devices to count zooplankton in situ at sea (e.g., Herman et al. 1991;

Osgood and Checkley, in press). The size of particles detected by the OPC is expressed as equivalent spherical diameter (ESD), based on the calibration with spheres. Particles with ESDs 250 to 1,000 μm were counted in our application. The lower size limit is approximately equal, in terms of volume, to the separation between "small" and "large" nauplii and "small" and "medium" copepodites in the pump samples, described above. The upper size limit of the OPC is equivalent to a copepodid of 600-μm maximal width. Thus the particles detected by the OPC and the organisms counted microscopically from pumped samples overlap in size range.

We merged data from the OPC and MOCNESS sensors into 7.2-sec. time intervals, producing many estimates of the particle concentration experienced by the larval hake collected in a single sample, since a single MOCNESS net fished in a depth stratum considerably longer than this. We sorted the OPC data on sizes of particles into eight categories of ESD, in μm: 250–305, 305–398, 398–497, 497–602, 602–700, 700–803, 803–903, and 903–1,000. From the number of particles (n_i) detected in each size category (*i*), the mean ESD of that category (ESD_i), and the volume of water (v_t, m³) sampled by the OPC during each time interval, we estimated the total biomass of particles (mm³·m⁻³) as:

$$\text{Biomass} = \Sigma \; 1.33 \cdot \pi \cdot (0.5 \cdot ESD_i)^3 \cdot 10^{-9} \cdot n_i \cdot v_t^{-1}$$

We thus assume that the particles are spherical, and that all particles are suitable as food for some size of larval hake. These estimates of biomass were then averaged for all periods within one stratum sampled by one MOCNESS net.

We compared the biomass of optically counted microzooplankton in the 160–400-μm-diameter categories (large nauplii and medium copepodids and other metazoans) with mean biomass in the smallest two size categories (250–398-μm ESD) estimated by the OPC for the same depth stratum (figure 1). Differences in the size categories, or in the calculations of biomass from size, could account for a constant, linear offset from a 1-to-1 relation between the two methods, but the relation is curvilinear. The problem is not due solely to the calculations of biomass from abundances using different geometric approximations, since a plot of abundances of particles counted by the OPC versus abundances of zooplankters caught by the pump was similarly offset from 1-to-1 and curvilinear, and less variance was explained. A reasonable explanation is coincidence in OPC counting at high concentrations of particles: if two or more particles pass through the OPC's sensing zone within the instrument's response time, they will be counted as one larger particle. The curvilinearity, however, is due to a few data points at high concentrations, and other explanations for curvilinearity are plausible.
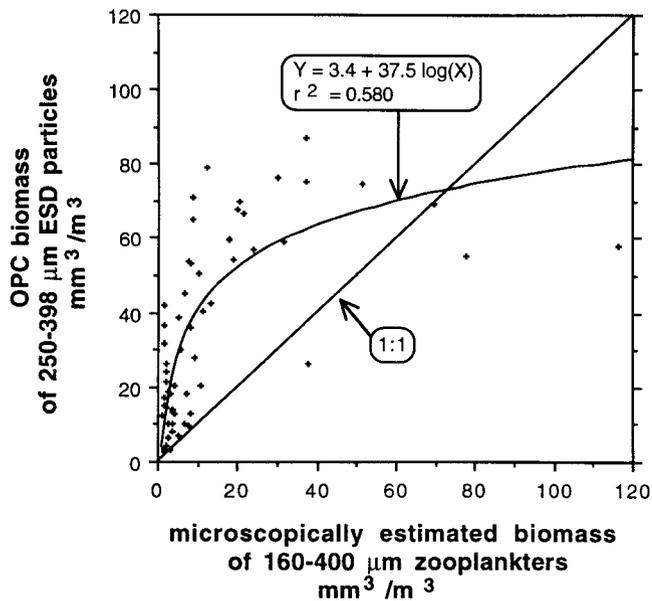
Figure 1. Biomasses of microzooplankton estimated by optical measurements and OPC. For optical measurements, the biomass represents the sum of biomasses of nauplii ≥160 μm, and copepodites and other metazoans 160–400 μm (see Methods). For OPC measurements, the biomasses are for particles 250–398-μm ESD (see Methods).

RESULTS

Pump Samples

As examples for detailed presentation, we selected three stations (table 1): one where larval hake were most abundant and relatively shallow (station 74.3, 68.8; 44 larvae·m^{-2}, median depth 50–75 m, some larvae in the upper 25 m); one where larvae were moderately abundant and relatively deep (station 66.7, 80.0; 7 larvae·m^{-2}, median depth 125–150 m, no larvae above 50 m); and one where the larvae were present but rare, and at an intermediate depth (station 66.0, 78.7; 2 larvae·m^{-2}, median depth 75–100 m). The histograms in figures 2–4 indicate the actual data (abundances of the enumerated categories, per unit volume of seawater at specific depths from which samples were pumped); the connecting lines are linear interpolations. Results are plotted to emphasize the vertical distribution of each individual category. Thus the axes for abundance differ between panels within each figure; analogous panels in different figures may have different axis values; and even within a panel there are usually differences in the volume of water to which the counts of different categories are referenced (except for "other" metazoans, all sizes of which were rare).

Many categories of food were more abundant at station 74.3, 68.8 than at the other two stations (see also figure 5), but there are few other differences clearly related to the occurrences of larval hake (see figure 5 for larval distributions). In particular, the vertical distribution of food at station 66.7, 80.0, where larvae were relatively deep, is not very different from that at station 74.3, 68.8, where the larvae were relatively near the surface, some even in the upper 25 m.

Figure 5 is a composite of data from all stations, showing vertical distributions of total prey biomass, calculated from abundances and geometric approximations of individual volumes, as described in Methods. The biomass of microzooplankton was least at the one station we sampled where no larvae were found (80.0, 85.0), but other differences are not obvious by inspection. Because this is a single station, and farther offshore than most of the
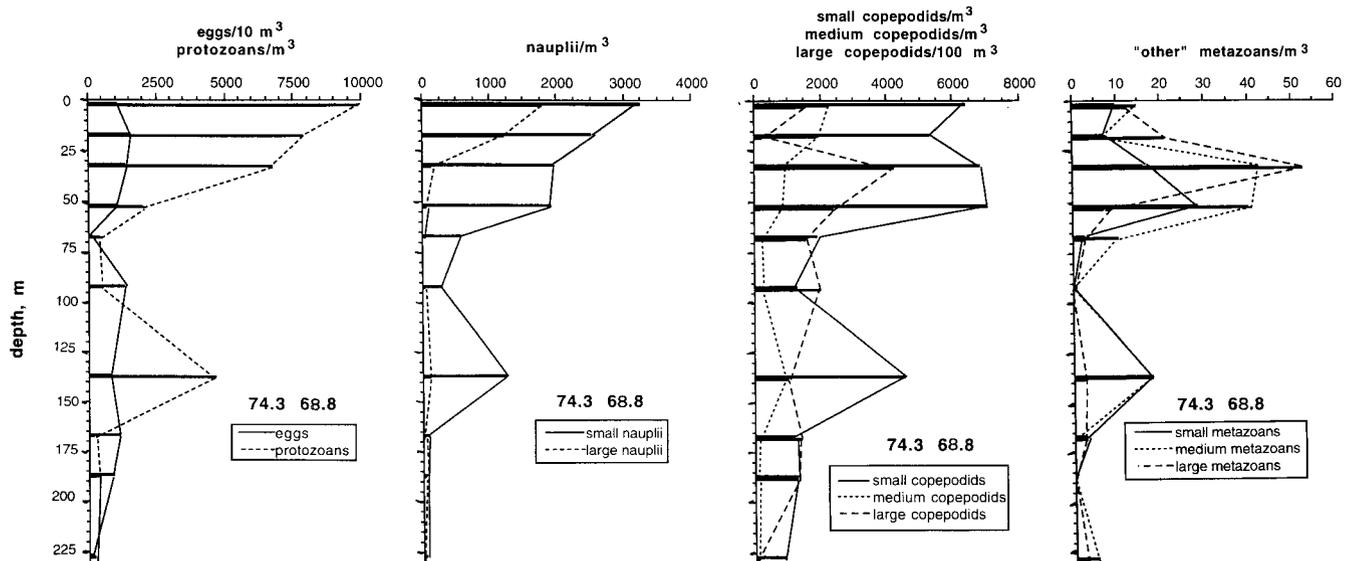

Figure 2. Vertical distributions of categories of microzooplanktonic food at station 74.3, 68.8 (see table 1 for location), where larval hake were abundant and relatively shallow (median depth 50–75 m). Note that volume basis for abundance differs between categories.
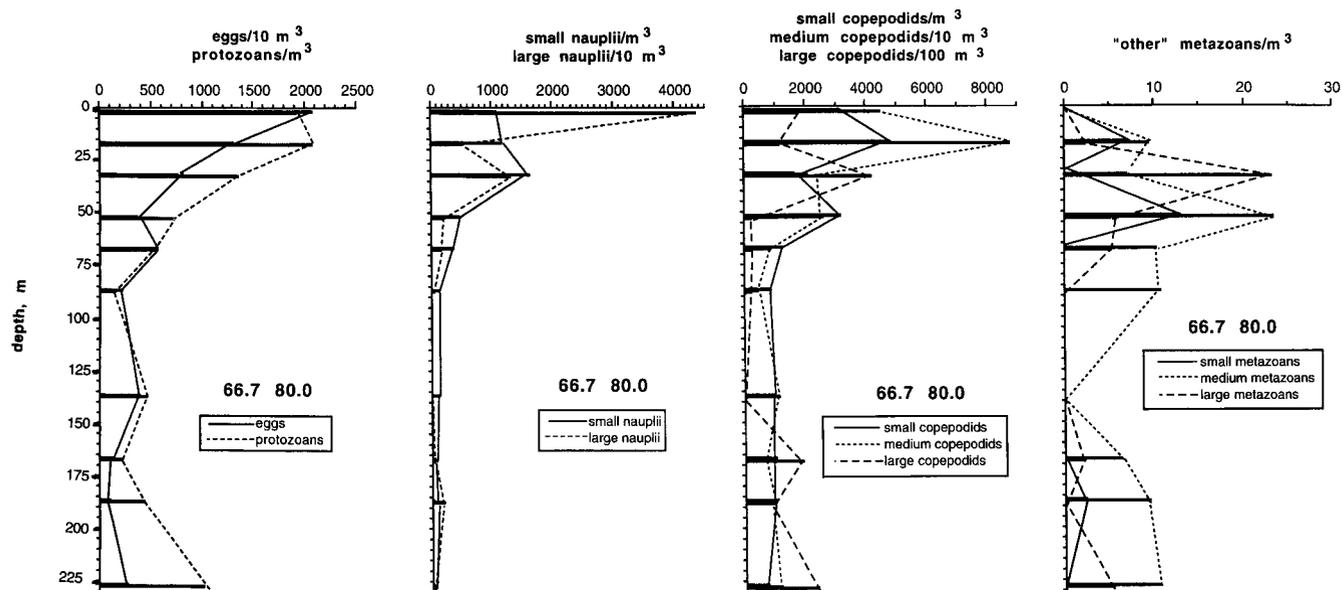
Figure 3. Vertical distributions of categories of microzooplanktonic food at station 66.7, 80.0 (see table 1), where larval hake were moderately abundant and deep (median depth 125–150 m).
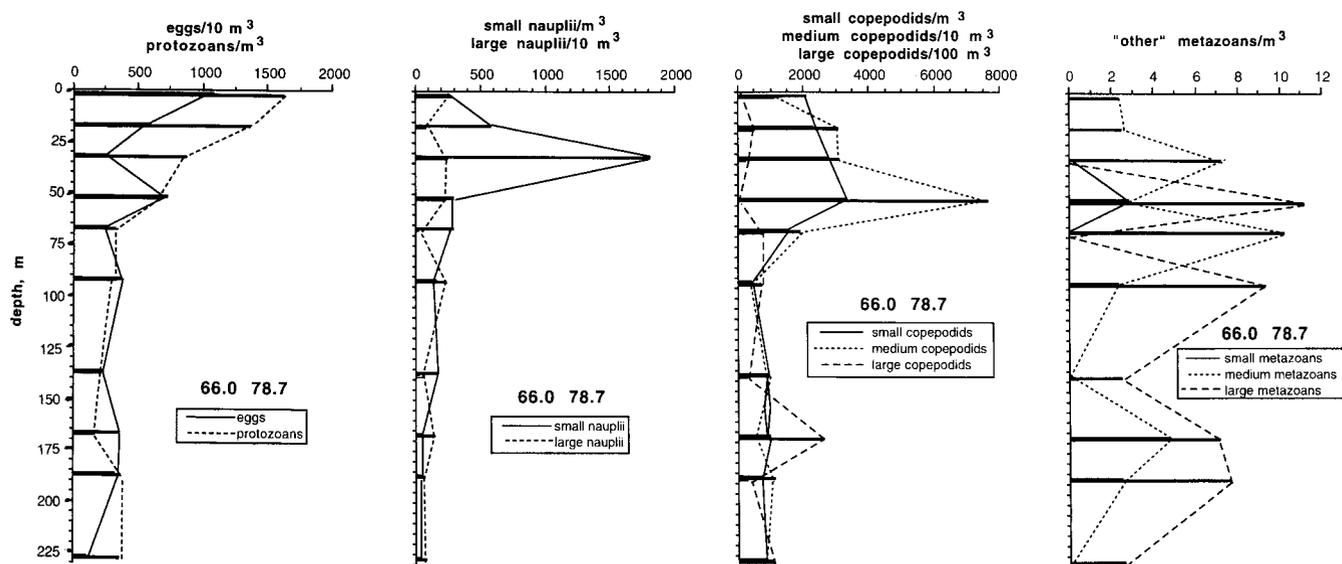

Figure 4. Vertical distributions of categories of microzooplanktonic food at station 66.0, 78.7 (see table 1), where larval hake were present, but rare and centered at an intermediate depth (75–100 m).

stations where larval hake were encountered, it is unrealistic to generalize from it to "hake-less" stations.

Larval hake were found from the 0–25-m stratum to the deepest stratum sampled (250–300 m) at some location within the subset of stations we sampled for microzooplankton (figure 5). Considering only the stations where larval hake were found, there was a significant, positive relation between their abundance and microzooplanktonic biomass (figure 6, left; 7 depths sampled at each of 8 stations). This relation combines the effects of the overall richness of a station, in terms of microzooplankton and larval hake, and the intensity and de-

gree of coincidence of layering of microzooplankton and larvae within stations. We recalculated this relation using only abundances of nauplii and small and medium copepodids as the estimate of available food, but less variance was explained.

There was also a positive relation (figure 6, center) between the integrated abundance of larvae at a station (0–300 m) and the integrated abundance of microzooplankton (0–250 m), as suggested by the comparison (summarized above) of three specific stations. But when we calculated so as to give each station equal weight in the outcome, there was no relation between the fraction
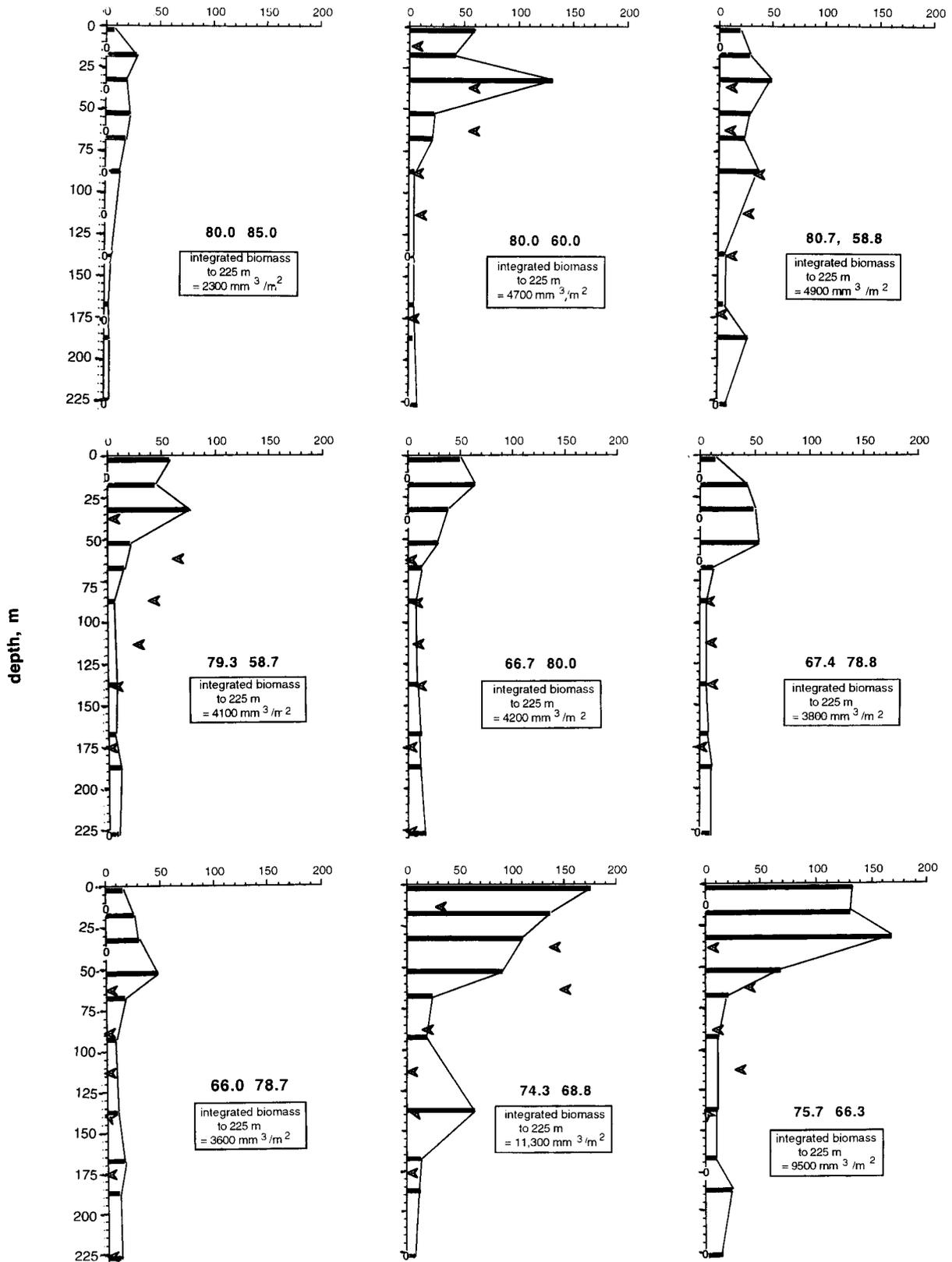
Figure 5.   Vertical distributions (at all stations) of total prey biomass sampled by pump ($mm^3 \cdot m^{-3}$, calculated from abundances and geometric approximations of individual volumes, as described in Methods) and of larval hake. *Arrowhead* = larvae present, *0* = larvae absent, larvae$\cdot(200$ m$)^{-3}$. The placement of the arrowhead indicates the midpoint of each OPC-sampled stratum.
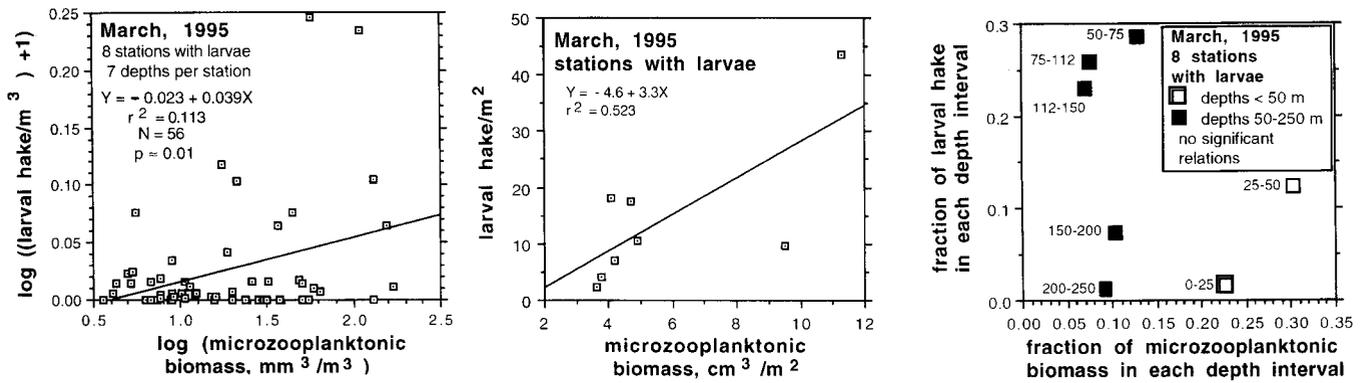
Figure 6. Correlations with pump-sampled microzooplanktonic biomass for stations where larvae were found. *Left*, Log-log correlation of larval hake abundances in specific strata at all stations vs. biomass of microzooplankton in those strata. The regression is significant. *Center*, Abundance of larval hake, integrated 0–300 m, vs. biomass of microzooplankton, integrated 0–250 m. The regression is significant ($p < 0.05$, 2-tailed). *Right*, Fraction of larval hake in each stratum vs. fraction of microzooplanktonic biomass in that stratum. Strata are indicated by numbers adjacent to points, and upper two strata are shown as open squares. The 100–125-m stratum, where larvae were sampled but not microzooplankton, is split between the adjacent strata.

of larvae in a particular stratum and the fraction of the available food that was there (figure 6, right). This was also true when the strata shallower than 50 m (open symbols in figure 6, right) were excluded, even though the 50–75-m stratum contained the greatest fraction of larvae and was richer in potential food than deeper strata.

On conceptual grounds, one would expect larvae to be particularly concentrated in the stratum with the greatest supply of food at those stations where food was scarce overall, and perhaps more broadly distributed where food was plentiful. This concept is not supported by the data. In fact, there is a *positive* correlation (though barely significant) between food available in the water column and the fraction of the column's total larvae that occurred in a single stratum.

OPC Samples

The relations between the vertical and areal distributions of larval hake relative to potential food, estimated as total biomass sensed by the OPC (figure 7) were very

similar to those where pump-sampled microzooplankton was taken as the measure of potential food (figure 6). Considering all depths sampled at stations where larvae were found, there was an overall correlation between the abundance of larvae and the zooplanktonic biomass estimated by the OPC (figure 7, left), and a tendency (though a nonsignificant one) for the abundance of larvae in the whole water column to be greater where depth-integrated biomass was greater (figure 7, center). At depths greater than 50 m, the fraction of larvae in a particular stratum was positively correlated with the fraction of biomass found there (figure 7, right). The analogous relation was not significant with respect to pump-sampled microzooplankton (figure 6, right), perhaps because the deepest stratum sampled by the OPC and the MOCNESS (250–300 m) contained the lowest fraction of larval hake and of biomass (figure 7, right), but was not sampled by pump.

The OPC also provides a dimension not attained by pump sampling in this study (except the assessment of
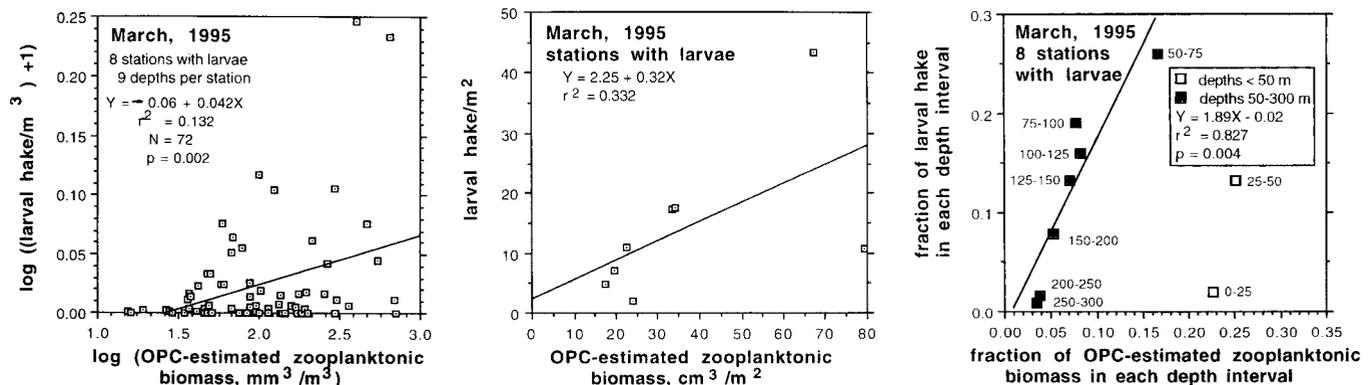

Figure 7. Correlations with zooplanktonic biomass (250–1,000-μm ESD) as estimated by OPC for stations where larvae were found (cf. figure 5). *Left*, Log-log correlation of larval hake abundances in specific strata at all stations vs. biomass of zooplankton in those strata. The regression is significant. *Center*, Abundance of larval hake vs. biomass of zooplankton, both integrated 0–300 m. The regression is not significant. *Right*, Fraction of larval hake in each stratum vs. fraction of zooplanktonic biomass in that stratum. Strata are indicated by numbers adjacent to points, and upper two strata are shown as open squares. When all strata were considered, the relation was not significant, but a significant regression (shown by the diagonal line and equation) was obtained for strata deeper than 50 m.
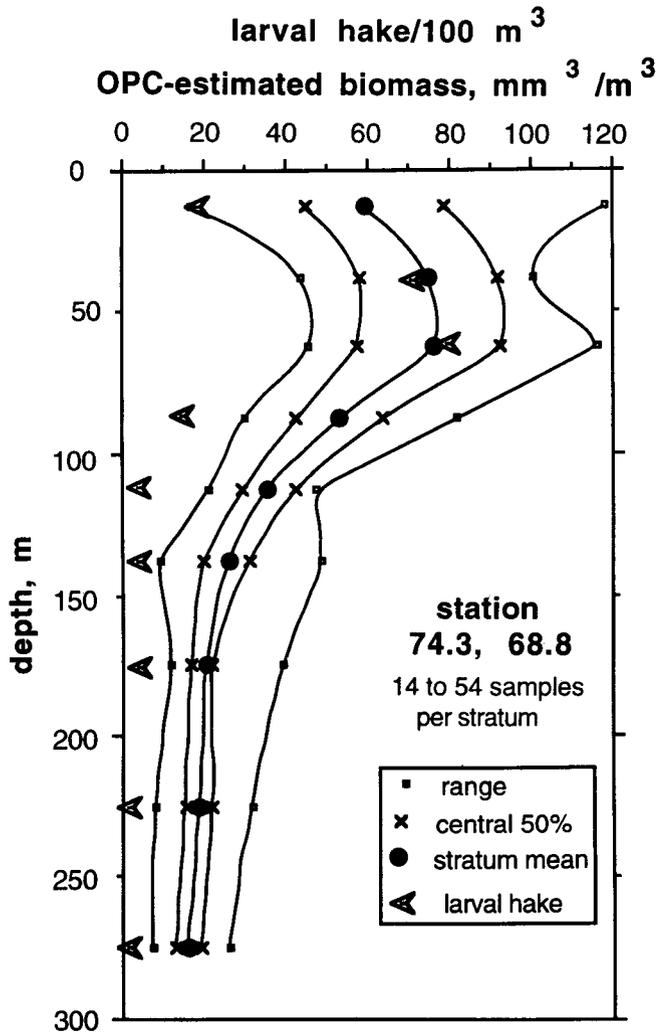
Figure 8. Variability in zooplanktonic food for larval hake at station 74.3, 68.8, based on 14–54 estimates of OPC biomass of particles 250–398-µm ESD per depth stratum sampled for larval hake. Shown for the midpoint depth of each stratum are the mean biomass (*large dot*), the envelope of the central 50% of all estimates (*x's*), the range of biomasses (*small squares*), and the abundance of larval hake (*arrowhead*).

avoidance as a function of length of hose, reported in Methods): a measure of variation due to patchiness or layering on scales smaller than the depth strata integrated in sampling the larvae, but still potentially relevant to the question of how or where larvae obtain sufficient food to survive. Figure 8 shows an example for station 74.3, 68.8, the richest station with respect to both microzooplankton and larval hake, and where the latter were concentrated in relatively shallow strata. The biomass of zooplankters 250–398 µm in ESD, integrated to 250 m, was 10,500 $mm^3 \cdot m^{-2}$, which can be compared to a biomass of 11,300 $mm^3 \cdot m^{-2}$ of pump-sampled microzooplankton at this station (figure 5). The range of biomasses within any stratum was approximately proportional to the mean biomass there; in fact, the range·(mean)$^{-1}$ ratio varied from 0.75 to 1.5, and had no trend with depth.

DISCUSSION

The purpose of this study was to evaluate the availability of food for larval hake, which are unusual in their deep distribution. In many regions, gadoid larvae use copepod nauplii as their earliest food, and indeed the growth and/or recruitment of larvae is sometimes correlated with the availability of nauplii, on a mesoscale (Buckley and Lough 1987; Canino et al. 1991), seasonally (Haldorson et al. 1989), or interannually (Ellertsen et al. 1990). In most cases, the larvae feed in the uppermost few tens of meters, and the concentrations of nauplii in which they feed can be quite high (e.g., for walleye pollock, up to $144 \cdot L^{-1}$ in Shelikof Strait, Alaska, Incze and Ainaire 1994; $60 \cdot L^{-1}$ in Auke Bay, Alaska, Paul et al. 1991; and 10–$20 \cdot L^{-1}$ in the Bering Sea, Dagg et al. 1984). Napp et al. (1996) report 20 $nauplii \cdot L^{-1}$ as minimally necessary for larval pollock, and Ellertsen et al. (1990) suggest a range from 10 to 50 $nauplii \cdot L^{-1}$ for Arcto-Scandian cod.

On the spatial scales of our study (tens of m vertically, tens of km horizontally), prey is much less concentrated in the environment where larval hake must find their first meals. The study of vertical distribution of microzooplankton by Beers and Stewart (1969), summarized above, indicated that prey for larval hake might be considerably less abundant than that for cod or pollock, and the present investigation confirms this. Even if the entire microzooplanktonic biomass below 50 m (≤ 100 $mm^3 \cdot m^{-3}$; figure 5) were made up of 253-µm-diameter nauplii, the greatest concentration below 50 m was equivalent to <3 $nauplii \cdot L^{-1}$, and typical concentrations were of the order $1 \cdot L^{-1}$. The greatest biomass of 250–398-µm ESD particles was 76 $mm^3 \cdot m^{-3}$ (figure 8), which is equivalent to only 4.3 $particles \cdot L^{-1}$ of 325-µm ESD.

The study by Beers and Stewart (1969) was conducted in the correct season (Feb.–Mar.) for comparison with present results, but their stations were either inshore or south of ours. They found concentrations of naupliar and postnaupliar copepods to be 1–$5 \cdot L^{-1}$ in samples from >50-m depth caught on 103-µm mesh netting, while the size fraction passing through 103-µm but retained on 35-µm mesh contained up to $30 \cdot L^{-1}$. For comparison, the abundance of these categories at 55 m at station 74.3, 68.8 (figure 2) was approximately $10 \cdot L^{-1}$ in our 73-µm-mesh samples, and less at greater depths or other stations (e.g., figures 3 and 4). Considering the differences in sampling between the two studies, this is reasonable agreement.

The data from the optical plankton counter are more difficult to compare with published studies because although a great range of sizes was included, the taxonomic composition is unknown. Within the size categories most readily compared, the relation between OPC-sensed particles and optically counted microzooplankton was not

good (figure 1). However, the relations between the larvae and their potential food were similar whether microzooplanktonic biomass or OPC-assessed total zooplanktonic biomass was considered as potential food. This similarity lends some confidence to the conclusions derived from sampling by pump, which was not truly coincident with sampling the larvae and was potentially more sensitive to within-stratum patchiness than was the sampling by OPC.

In addition to the paucity of food for larval hake (relative to other gadoid larvae), there are related trophic implications stemming from their depth. Though the water of the offshore California Current is usually more transparent than the more turbid, near-surface waters inhabited by other gadoid larvae, larval life below 50 m in late winter—early spring means that visual feeding must be possible at rather low intensities of light.

Further, a mechanism that has been invoked to explain high rates of feeding—turbulence-enhanced encounter between a larva and prey (Rothschild and Osborn 1988; Sundby and Fossum 1990; Sundby et al. 1994)— is also likely to be less important for larval hake than for near-surface species because of the decrease in turbulence with depth. Although the volume of water integrated in one of our samples is not unreasonable for the volume searched daily by a large hake larva, copepod nauplii and other prey are known to be patchy on still smaller scales (e.g., Owen 1989). It is therefore possible, at least in principle, that larval hake detect and feed on aggregations of prey on smaller scales than we sampled. Lack of turbulence would encourage the maintenance of such small-scale aggregations (e.g., Davis et al. 1991).

The OPC can sample these small-scale aggregations, though in the example shown in figure 8 there was no indication that patchiness was unusually pronounced (relative to the mean for the stratum) in the strata where larvae were concentrated. To determine the trophic significance of small-scale aggregations, it would be necessary to sample the larval hake, and to determine their feeding, on the various spatial scales of patchiness of food. This would permit tests for positive correlations on a substratum scale. Significant correlations would mean that the mean biomass of potential food in a stratum would underestimate the biomass most relevant to the feeding larvae. Going beyond correlations, one would also have to show that larvae do indeed detect and feed within small-scale aggregations frequently enough to permit observed growth rates.

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VERTICAL AND HORIZONTAL DISTRIBUTION OF JUVENILE PACIFIC WHITING (*MERLUCCIUS PRODUCTUS*) IN RELATION TO HYDROGRAPHY OFF CALIFORNIA

KEITH M. SAKUMA AND STEPHEN RALSTON
National Marine Fisheries Service
Southwest Fisheries Science Center
Tiburon Laboratory
3150 Paradise Drive
Tiburon, California 94920

ABSTRACT

The vertical and horizontal distributional patterns of young-of-the-year juvenile Pacific whiting, *Merluccius productus*, collected during midwater trawl surveys off California from mid-May through mid-June 1986–95 were examined. Comparison of 1992 MOCNESS tows and depth-stratified midwater trawls indicated that although larvae were most abundant below the mixed layer, juveniles were most abundant in the upper mixed layer. Abundance estimates from the midwater trawl surveys varied from year to year. Large numbers were consistently observed in the Monterey Bay area. The least-squared mean catch per year from a sampling stratum offshore of Monterey Bay was significantly correlated with recruitment to the commercial fishery two years later, suggesting that midwater trawl surveys could provide useful fishery-independent forecasts of year-class strength. Information collected with CTD recorders in 1987–95 indicated that juveniles were significantly less abundant in upwelled water than in non-upwelled water. This could be attributed to advection away from upwelling fronts, a behavioral response to avoid upwelled water, or a general offshore distributional pattern, irrespective of upwelling events. Plots of juvenile abundances and density (σ_t) contours showed substantial catches nearshore during periods of upwelling relaxation, whereas nearshore abundances were greatly reduced during strong upwelling events.

INTRODUCTION

The Pacific whiting[1], *Merluccius productus*, is an abundant, semipelagic species comprising four distinct stocks: Strait of Georgia, Puget Sound, southern Baja California, and coastal (Utter and Hodgins 1971; Vrooman and Paloma 1977; Stauffer 1985; Dorn 1996). The coastal stock is by far the most abundant and most important commercially within the California Current system, with an annual average of 191,925 tons landed off the west coast of the United States and Canada from 1966 through 1995 (Dorn 1996).

Adults migrate south from their summer feeding grounds off the Pacific Northwest to spawn off the coast of California and northern Baja California beginning in autumn (Bailey et al. 1982; Stauffer 1985). The northern and southern boundary of the spawning grounds can shift, depending on prevailing hydrographic conditions. In warmer years (often associated with El Niño events) the distribution shifts towards the north; in colder years it shifts south (Bailey et al. 1982; Dorn 1995). Most spawning occurs between January and March at depths of 130–500 m over the continental slope (Bailey et al. 1982).

Larvae hatch at a size of 2.4 mm notochord length (NL), and transform to the juvenile stage at approximately 30 mm standard length (SL; Matarese et al. 1989). Larval Pacific whiting (less than 30 mm SL) usually remain below the thermocline at depths of 60 m or greater (Ahlstrom 1959; Bailey 1982). However, larger larvae (longer than 12 mm SL) can be found near the surface (Bailey 1982), and early-stage juveniles (longer than 30 mm SL) are quite abundant in the surface layer at night (Lenarz et al. 1991).

Larval survival of Pacific whiting has been shown to be strongly correlated with recruitment success (Bailey and Francis 1985; Hollowed 1992). Bailey et al. (1986) indicated that young-of-the-year juvenile abundance estimated from midwater trawl surveys (Mais 1974) could also be useful in forecasting relative year-class success. Studies have shown that strong recruitment years are infrequent and that these strong year classes dominate the adult population for five to seven years (Bailey and Francis 1985; Francis and Hollowed 1985).

The prevailing hydrographic conditions during the first year of life have been shown to contribute to recruitment success (Bailey 1981; Bailey and Francis 1985; Hollowed 1992). Bailey and Francis (1985) observed that from 1960 to 1977, cold years with strong upwelling always led to poor recruitment of Pacific whiting, and that strong recruitment resulted only from spawning in warmer than average years (although not all warm years led to strong recruitment). Upwelling intensity has been shown to be a factor in the recruitment of other species, such as rockfishes (*Sebastes* spp.) and sanddabs (*Citharichthys* spp.; Ainley et al. 1993; Larson et al. 1994; Sakuma and Larson 1995).

Upwelling off the west coast of the United States is driven by northwesterly winds, which cause the offshore displacement of nearshore coastal waters of the upper

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[1] [Editors' note: The accepted common name for this species is now Pacific hake, but the name Pacific whiting is still widely used on the West Coast.]

mixed layer (generally 10–50 m, depending on location and time of year; Parrish et al. 1981; Husby and Nelson 1982). This displacement brings cold, nutrient-rich subsurface waters into the upper water column (Simpson 1987). Parrish et al. (1981) designated the region from Cape Blanco, Oregon, to Point Conception, California, as the region of maximal upwelling. This geographic region encompasses a large portion of the northern range occupied by young-of-the-year Pacific whiting (Dark et al. 1980; Bailey et al. 1982; Stauffer 1985).

The incidental collection of young-of-the-year juvenile Pacific whiting in midwater trawl surveys conducted during the upwelling season off central California by the National Marine Fisheries Service (NMFS), Tiburon Laboratory, (Wyllie Echeverria et al. 1990) provided an opportunity to examine spatial distributional patterns and their relation to prevailing hydrographic features such as upwelling fronts. It should be noted that the midwater trawl surveys were initially designed to sample juvenile rockfish, which have a more localized recruitment pattern than Pacific whiting. Therefore, only a small portion of the habitat occupied by the juvenile Pacific whiting population was sampled by these surveys. In this study we examined (1) the spatial and temporal abundance of juvenile Pacific whiting, (2) the vertical distribution of larvae and juveniles, (3) the effect of upwelling on juvenile abundance, and (4) horizontal distributional patterns in relation to specific hydrographic features.

METHODS

Data Collection

Juvenile Pacific whiting (longer than 30 mm SL) were collected aboard the National Oceanic and Atmospheric Administration (NOAA) research vessel *David Starr Jordan*, as part of the NMFS Tiburon Laboratory's annual midwater trawl surveys. A series of standard stations extending from Bodega Bay (38°20'N) to Cypress Point (36°35'N) were sampled at night with a 14 × 14-m modified Cobb trawl with a 12.7-mm stretched mesh codend liner (Wyllie Echeverria et al. 1990). These standard stations were grouped into seven distinct strata: Monterey outside (MO), Monterey inside (MI), shallow south (SS), deep south (DS), Gulf of the Farallones (GF), shallow north (SN), and deep north (DN; figure 1). Stratum designations were based on geographic location and bottom depth; each stratum contained at least five trawl stations.

Standard trawling depth was 30 m, except at nearshore shallow-water stations (bottom depths less than 60 m), where the standard trawling depth was 10 m. At four standard offshore sites (off Cypress Point, Davenport, Pescadero, and Point Reyes), a series of three depth-stratified trawls (depths = 10 m, 30 m, and 100 m) were conducted to examine vertical distributional patterns.
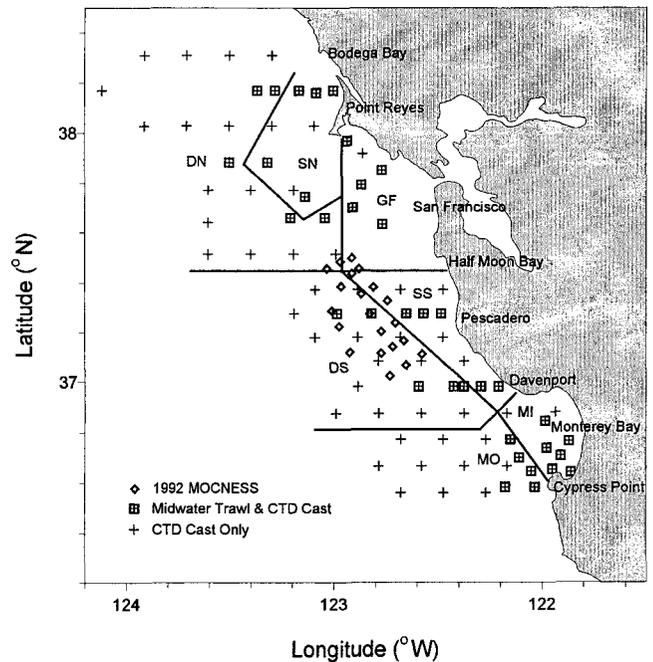

Figure 1. Map of the study area, showing locations of midwater trawl, MOCNESS, and CTD stations, and the strata boundaries (MO = Monterey outside, MI = Monterey inside, SS = shallow south, DS = deep south, GF = Gulf of the Farallones, SN = shallow north, and DN = deep north).

As time permitted, additional depth-stratified trawls were conducted at nonstandard stations. Trawling lasted 15 minutes at depth, and all trawls were completed between the hours of 2100 and 0600.

Stations were sampled from south to north during a 10-day sweep of the survey area. Three replicate sweeps were completed from mid-May through mid-June, 1986–95. Juvenile Pacific whiting were sorted and enumerated at sea.

Beginning in 1987, a conductivity, temperature, and depth (CTD) cast was made at each trawl station during each sweep to obtain temperature, salinity, and seawater density at depth. Additional CTD stations, interspersed between the trawl stations, were sampled during the day and repeated for each sweep. Beginning in 1991, the grid of daytime CTD stations was standardized and extended offshore (figure 1). Specifics of CTD deployment and data processing can be found in Sakuma et al. 1996.

To compare the vertical distribution of juvenile Pacific whiting from the depth-stratified trawls with that of early larvae (smaller than 12 mm SL), a 1.0-m² multiple opening/closing net and environmental sensing system (MOCNESS) with 0.505-mm mesh was deployed from the NOAA research vessel *David Starr Jordan* in 1992. Oblique tows were conducted around the clock at 21 stations bordering either side of the continental shelf break (approximately 200 m) between Half Moon Bay (37°30'N) and Davenport (37°00'N) from February 21 to 23. As dictated by bottom depth, up to seven nets

were used to sample the following depth bins: 400–300 m, 300–200 m, 200–160 m, 160–120 m, 120–80 m, 80–40 m, and 40–0 m. Samples were preserved in 95% EtOH, and larval Pacific whiting were sorted and enumerated at the NMFS Tiburon Laboratory.

Data Analysis

Catches of juvenile Pacific whiting from the midwater trawl surveys were transformed by $\log_e$(number/trawl+1). Due to changes in the width of the net opening with depth fished, the catches from the depth-stratified trawls were first adjusted as described by Lenarz et al. (1991) and then $\log_e$-transformed. Catches of larval Pacific whiting from the MOCNESS were adjusted to the number/1,000 m^3 water filtered and were then transformed by $\log_e$(number/1,000 m^3 + 1) for comparison with the $\log_e$-transformed catches of juveniles from the midwater trawls. We analyzed only midwater trawl stations at which all three depths had been successfully sampled, and MOCNESS stations where oblique tows were conducted through all seven depth bins. In addition, because the midwater trawls were conducted at night, we analyzed only the nighttime MOCNESS tows for comparison. We applied a two-way ANOVA to both sets of data, using depth and location of each collection as class variables. Tukey's studentized range tests were performed to identify significant differences in the mean catches among the different depths sampled.

In order to examine interannual and geographic variability in the catch of juvenile Pacific whiting, we analyzed only data collected at standard stations. An ANOVA with year and stratum as class variables and a year-stratum interaction was then performed. To evaluate the potential of using midwater trawl abundance data in forecasting year-class strength, we subset the data to include only the stratum (or strata) yielding the largest catches of juvenile Pacific whiting. An ANOVA, with year and sweep as class variables and a year-sweep interaction term, was then performed. The least-squared means (Searle et al. 1980) from these analyses were compared against the recruitment of two-year-old fish, as presented in the most recent Pacific whiting stock assessment (Dorn 1996).

We used CTD data to identify midwater trawls conducted in areas of recent upwelling. Schwing et al. (1991) defined recently upwelled water off central California as having surface temperatures less than 10.5°C and surface salinities greater than 33.6 psu. The combination of low temperature and high salinity in upwelled water leads to high density (σ_t) values. Because the salinity data recorded by the CTD were sometimes erratic at the surface (Sakuma et al. 1996), temperature and salinity values at 30 m were used for this analysis. This also allowed for a more direct comparison of the CTD data with the catches of juvenile Pacific whiting collected at the standard trawl depth of 30 m.

Because of the increased depth of the hydrographic comparison, we defined upwelled water as less than or equal to 10.0°C in temperature and greater than 33.7 psu in salinity. A t-test was performed on $\log_e$-transformed abundances in upwelled and non-upwelled water from each individual year and from all years combined (1987–95) to determine if there was a relation between upwelling and juvenile Pacific whiting abundance.

In order to get a general view of the abundance patterns of juvenile Pacific whiting and their relation to hydrographic features, we overlaid catches of juveniles onto contours of seawater density (σ_t) at 30 m for each sweep of each survey year. Density contours were generated from CTD data, postprocessed through Surfer for Windows (1995) with Kriging as the interpolation algorithm. A more complete description of contouring is presented in Sakuma et al. 1996. For the sake of brevity, we will not present an in-depth analysis of each sweep of each year. However, representative plots from the two best recruitment years and one of the worst recruitment years were compared and contrasted.

RESULTS

The ANOVA results from the MOCNESS indicated a significant effect of net depth on larval abundance ($P = 0.0001$, $r^2 = 0.82$). Tukey's studentized range test indicated that larval Pacific whiting were significantly more abundant between 40–160 m than at the shallowest depth (40–0 m) and at the deeper depths (greater than 160 m; $\alpha = 0.05$, df = 24; figure 2).

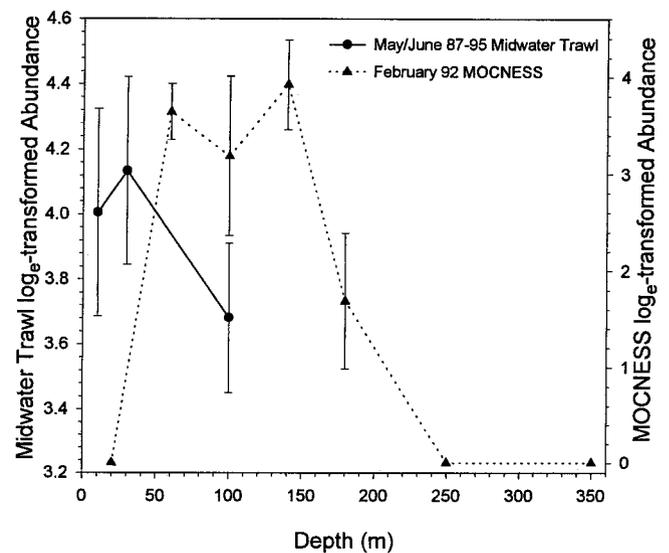There was also a significant depth effect on catch rate

Figure 2. Vertical distribution of Pacific whiting, *Merluccius productus*, larvae (collected by MOCNESS in February 1992) and juveniles (collected by midwater trawl in May/June, 1987–95). Mean abundance at depth and the standard error of the mean are shown.
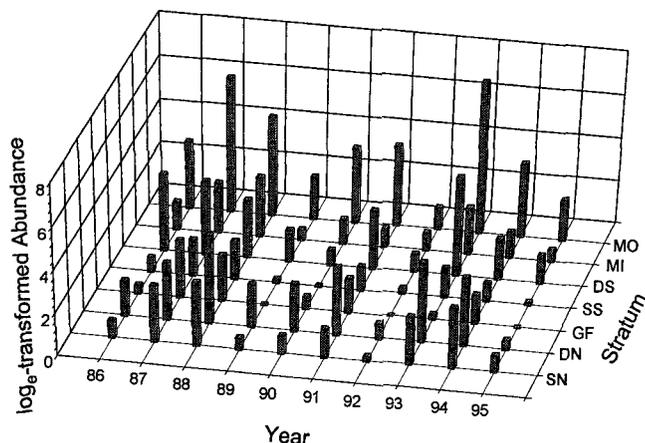
Figure 3. Annual least-squared mean abundance of juvenile Pacific whiting, *Merluccius productus*, collected in midwater trawls at various strata (MO = Monterey outside, MI = Monterey inside, DS = deep south, SS = shallow south, GF = Gulf of the Farallones, DN = deep north, and SN = shallow north), 1986–95.

of juvenile Pacific whiting in the depth-stratified mid-water trawls ($P = 0.0427$, $r^2 = 0.86$). Tukey's studentized range test showed that mean catches of juveniles at 100 m were significantly lower than those at 30 m ($\alpha = 0.05$, df = 138; figure 2). These results suggested an ontogenetic vertical shift in distribution, with larvae mostly below the upper mixed layer (the 40–0-m MOCNESS depth bin), and juveniles mostly within the upper water column (figure 2).

Results from the ANOVA used to examine the interannual and geographic variability of juvenile Pacific
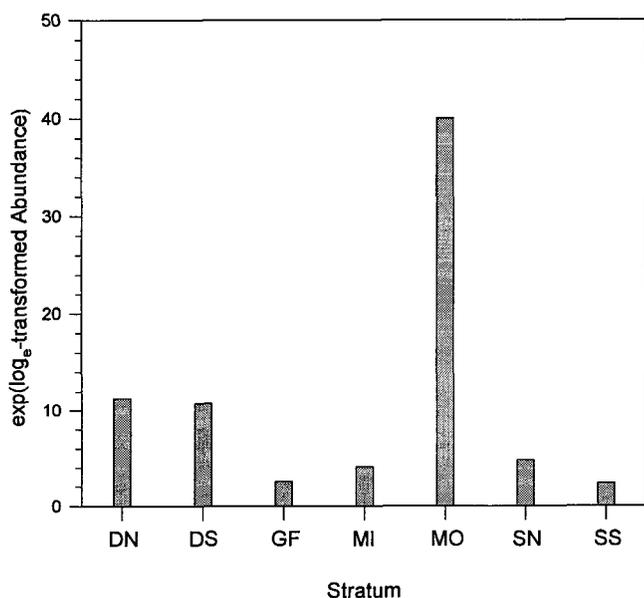
whiting had an r^2 of 0.40 and showed significant year ($P = 0.0001$) and stratum ($P = 0.0001$) effects, as well as a significant year-stratum interaction ($P = 0.0001$). The least-squared means for year and stratum indicated that abundances were greatest in 1987, 1988, and 1993 and lowest in 1989, 1992, and 1995; the largest catches consistently came from the MO stratum (figure 3). Back-transformation of the least-squared means, with bias correction (Miller 1984), showed that catches within the MO stratum were nearly four times greater than in the stratum with the next highest abundance (figure 4).

Because the largest catches consistently came from the MO stratum (figure 4), an ANOVA using only catches within this stratum was subsequently done; it yielded an r^2 of 0.62 with a significant year effect ($P = 0.0001$) and year-sweep interaction ($P = 0.0003$). Although a comparison of the recruitment index of two-year-old fish presented by Dorn (1996) with the least-square means from the ANOVA using all strata resulted in a non-significant ($P = 0.0632$) correlation of 0.68 (figure 5), a comparison with results from the ANOVA using only the MO stratum yielded a significant ($P = 0.012$) correlation of 0.82 (figure 6).

A comparison of Pacific whiting abundance from samples taken in upwelling and non-upwelling areas indicated that juveniles were significantly less abundant in upwelling areas over all years (table 1). Analysis of individual years showed significantly reduced abundance in upwelling areas versus non-upwelling areas in 1988, 1989, and 1990, but no significant differences in abundance in

Figure 4. Back-transformed stratum least-squared mean abundance of juvenile Pacific whiting, *Merluccius productus*, over all years combined, 1986–95. Strata designations are: DN = deep north, DS = deep south, GF = Gulf of the Farallones, MI = Monterey inside, MO = Monterey outside, SN = shallow north, and SS = shallow south.

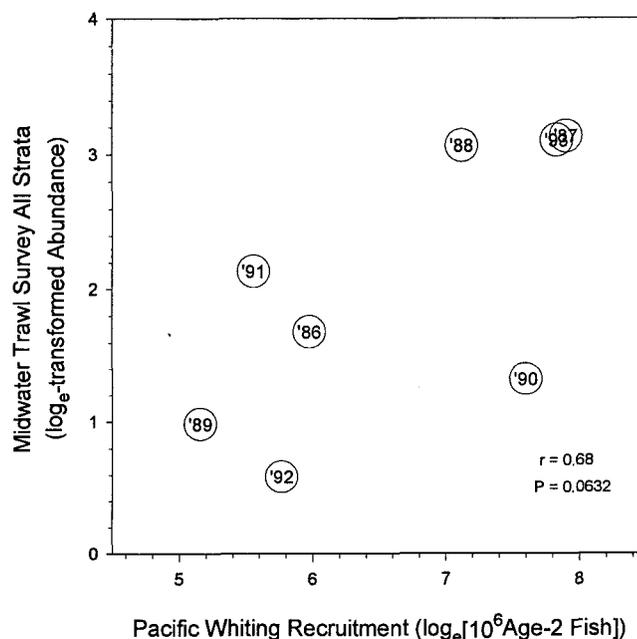Pacific Whiting Recruitment ($\log_e[10^6\text{Age-2 Fish}]$)

Figure 5. Comparison of the least-square mean abundance of juvenile Pacific whiting, *Merluccius productus*, collected from all strata, with the recruitment index of two-year-old fish presented by Dorn (1996).
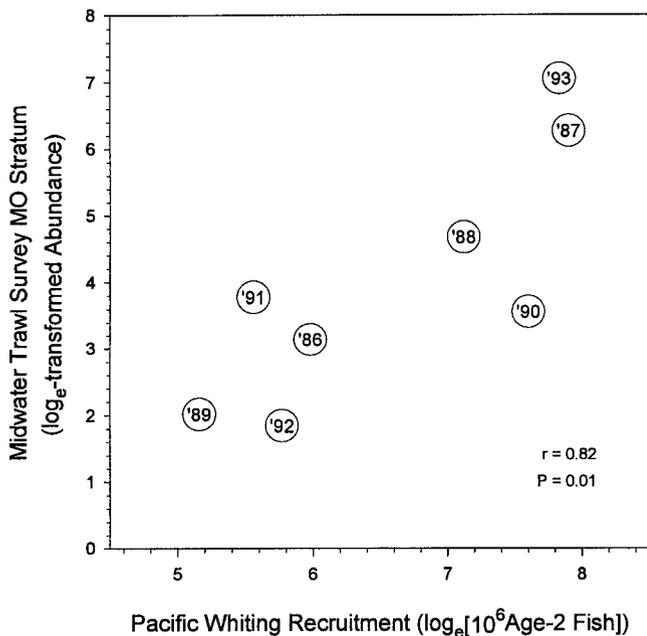
Figure 6. Comparison of the least-square mean abundance of juvenile Pacific whiting, *Merluccius productus*, collected from the Monterey outside (MO) stratum with the recruitment index of two-year-old fish presented by Dorn (1996).
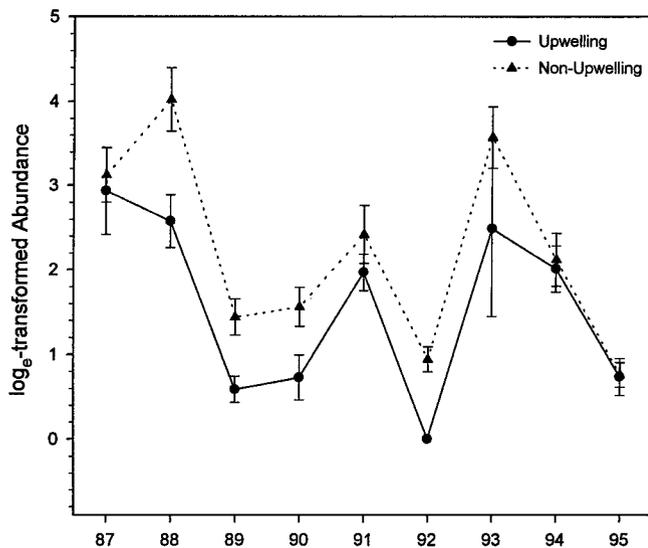

Figure 7. Comparison of juvenile Pacific whiting, *Merluccius productus*, abundance in upwelling areas versus non-upwelling areas. Upwelled water was defined as less than or equal to 10.0°C in temperature and greater than 33.7 psu in salinity at 30-m depth. The mean abundance and the standard error of the mean are shown.

TABLE 1
Results of t-tests on Pacific Whiting (*Merluccius productus*) Log_e-transformed Abundances in Upwelled and Non-upwelled Water, 1987–95

Year	N1	N2	t	df	P
1987	26	71	−0.2921	95.0	0.7709
1988	71	40	−2.8507	109.0	0.0052
1989	56	47	−3.2284	101.0	0.0017
1990	23	78	−2.3423	58.1	0.0226
1991	73	31	−1.1029	102.0	0.2726
1992	1	93	−0.6643	92.0	0.5082
1993	10	74	−1.0105	82.0	0.3152
1994	57	31	−0.2272	86.0	0.8208
1995	37	55	−0.0656	90.0	0.9479
1987–95	354	520	−2.3770	803.9	0.0177

N1 = the number of samples collected in upwelled water; N2 = the number of samples collected in non-upwelled water. Upwelled water was defined as less than or equal to 10.0°C in temperature and greater than 33.7 psu in salinity at 30-m depth.

years and were, moreover, difficult to characterize. In general, juveniles tended to be distributed in the offshore sections of the sampling area. However, in the Monterey Bay area moderate to large numbers of Pacific whiting were consistently observed both nearshore and offshore. A more in-depth analysis was done on the plots of juvenile abundance and density from the two best recruitment years (1987 and 1993) and one of the worst recruitment years (1989).

During sweep 1 of 1987, following the general pattern observed in all other years, juvenile Pacific whiting were distributed offshore, except for the Monterey Bay area (figure 8). In the Monterey Bay area, where the highest catches occurred, juveniles were numerous both nearshore and offshore. Juveniles were not observed within the upwelling plume off Point Reyes in the northern portion of the sampling area. In sweep 2 of 1987, upwelling intensity off Point Reyes had decreased and juveniles were observed in increased numbers in the northern trawl stations (figure 8). In addition, there appeared to be an onshore encroachment of the frontal zone between offshore California Current water and nearshore coastal water, with large numbers of juvenile Pacific whiting near shore. Furthermore, the highest catches, which came from the Monterey Bay area in sweep 1, were made in the central region of the survey area in sweep 2, indicating a possible northward shift in distribution. In sweep 3 of 1987, conditions off Point Reyes remained relatively the same as in sweep 2, and juvenile abundance apparently continued to shift northward, with the largest catches in the northern trawl stations (figure 8). Although the center of abundance appeared to shift northward during sweeps 2 and 3, moderate numbers of juvenile Pacific whiting were still evident in the Monterey Bay area.

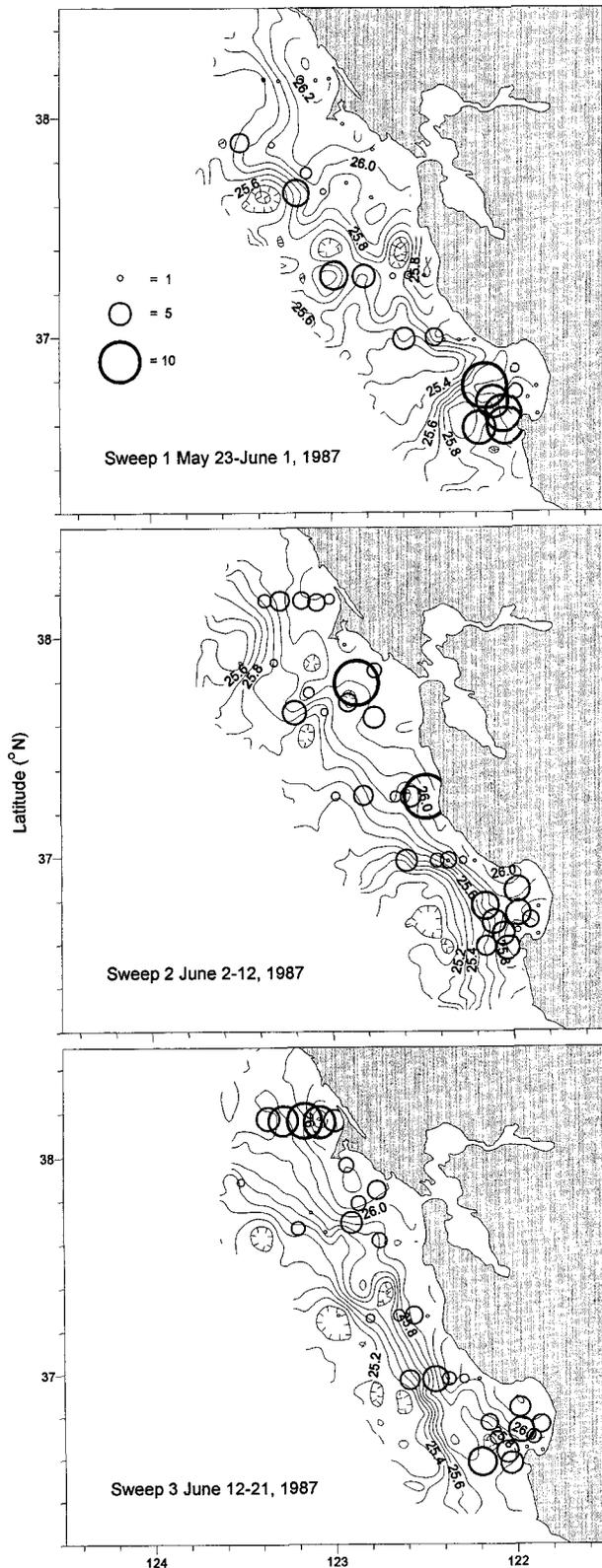The distributional pattern of Pacific whiting juveniles

1987, 1991, 1993, 1994, and 1995 (table 1 and figure 7). Because only one sample was taken in upwelled water in 1992, an accurate comparison of juvenile abundance in upwelling versus non-upwelling areas was not possible.

Horizontal spatial patterns of juvenile Pacific whiting abundance varied considerably among years and within

Figure 8. Juvenile Pacific whiting, *Merluccius productus*, abundance overlaid on contours of seawater density (σ_t) at 30 m from the 1987 midwater trawl survey. The size of the circle is proportional to the $\log_e$-transformed abundance. Hachured contour lines represent areas of lower-density water. Contour values greater than 26.0 kg/m³ indicate upwelling.

in sweep 1 of 1989 appeared similar to that of sweep 1 of 1987, except that catches were much reduced (figure 9). A strong upwelling plume was evident off Point Reyes, and juveniles were distributed offshore. The highest catches came from the Monterey Bay area and off Point Reyes. The moderate numbers of Pacific whiting juveniles in the northern trawl stations were found on the offshore side of the Point Reyes upwelling plume. Upwelling conditions persisted through sweep 2, and juveniles were again distributed offshore, with the largest catches made in the Monterey Bay area (figure 9). During sweep 3 of 1989, upwelling was still evident off Point Reyes, but appeared to have weakened in intensity (figure 9). Juvenile Pacific whiting remained predominately offshore and were still most evident in the Monterey Bay area and off Point Reyes. Latitudinal changes in abundance patterns could not be resolved in 1989 because of the much reduced catch rates.

During sweep 1 of 1993, upwelling was not evident off Point Reyes, but a strong frontal density gradient was apparent (figure 10). While the largest catches of Pacific whiting juveniles were made in the Monterey Bay area, moderate numbers were also caught in the northern trawl stations within the frontal region and throughout the central region. Although there was no evidence of recent upwelling, juveniles still showed a more offshore distribution. Upwelling was again absent in sweep 2 of 1993, and a strong frontal gradient was again evident off Point Reyes, with moderate numbers of juveniles in the northern trawl stations (figure 10). An additional front was observed offshore of San Francisco, south to Davenport, and an onshore distribution of juveniles in the Pescadero region seems to have been associated with this feature. Once again, the greatest abundances occurred in the Monterey Bay area.

During sweep 3 of 1993, strong upwelling-favorable winds at the end of the sweep reduced sampling effort in the northern portion of the survey area, particularly off Point Reyes. Because of high winds, only three of the five trawl stations were sampled, and many of the CTD stations were canceled. Therefore, contours of seawater density in the area off Point Reyes for sweep 3 are incomplete (figure 10). In the three trawl stations off Point Reyes that we were able to sample, catches of juveniles were small relative to catches in this region during the first two sweeps (figure 10). Prior to the last two days, wind conditions during sweep 3 had been similar to those observed in sweep 2. Elevated catches in sweep 3 appeared to be associated with two frontal gradients, one off San Francisco and the other off Pescadero and Monterey Bay. The large catch of Pacific whiting juveniles offshore of Davenport was associated with an eddylike feature evident within the frontal gradient (figure 10).
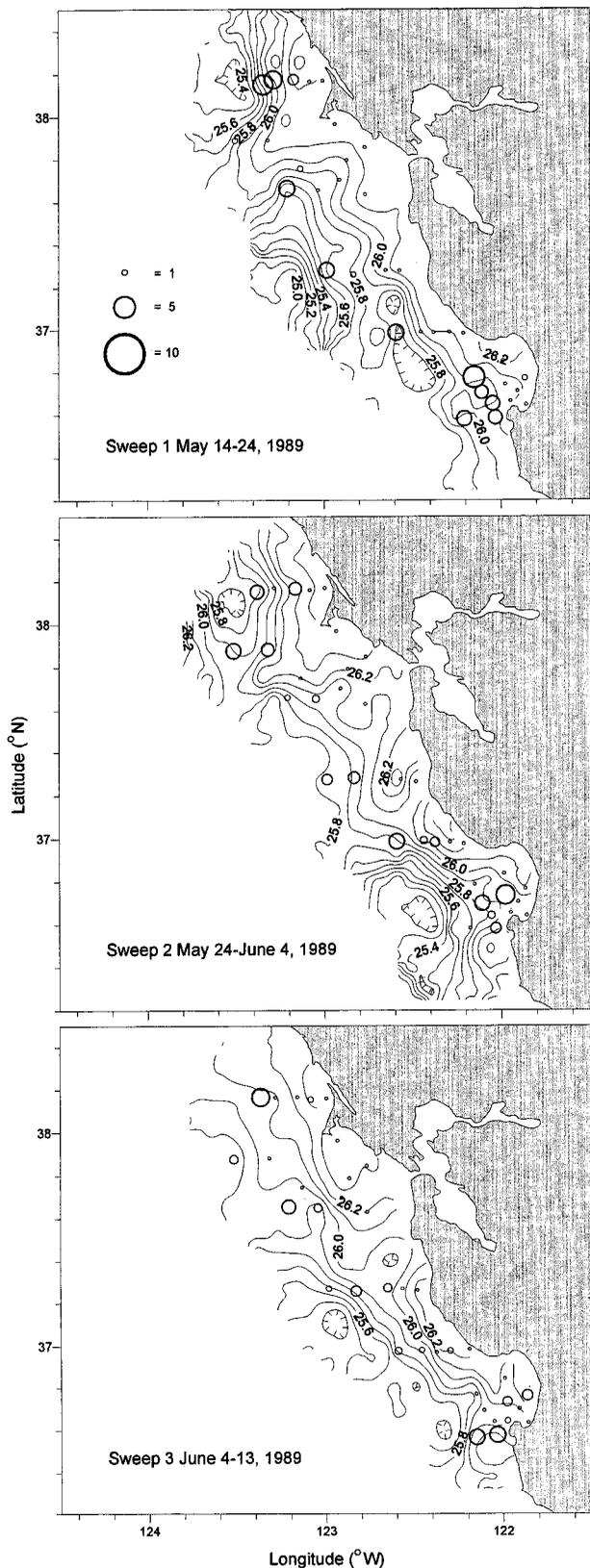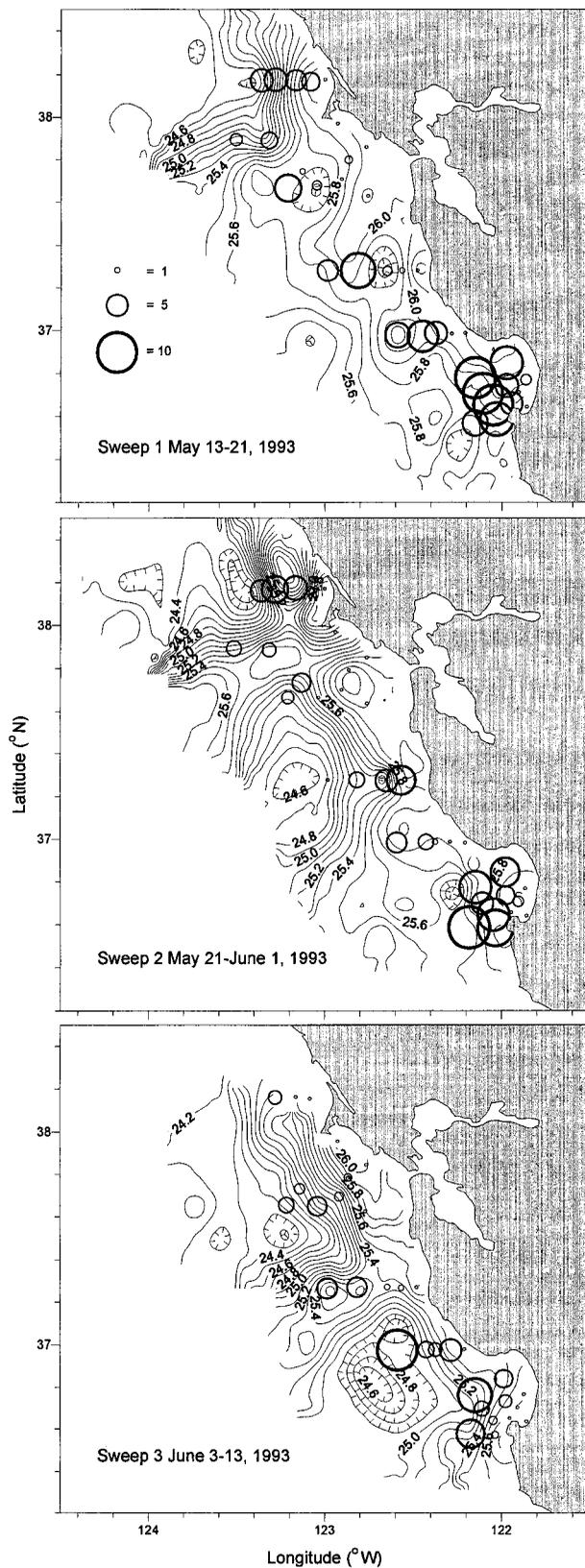
Figure 9.   Juvenile Pacific whiting, *Merluccius productus*, abundance overlaid on contours of seawater density (σ_t) at 30 m from the 1989 midwater trawl survey. The size of the circle is proportional to the $\log_e$-transformed abundance. Hachured contour lines represent areas of lower-density water. Contour values greater than 26.0 kg/m^3 indicate upwelling.

Figure 10.   Juvenile Pacific whiting, *Merluccius productus*, abundance overlaid on contours of seawater density (σ_t) at 30 m from the 1993 midwater trawl survey. The size of the circle is proportional to the $\log_e$-transformed abundance. Hachured contour lines represent areas of lower-density water. Contour values greater than 26.0 kg/m^3 indicate upwelling.

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DISCUSSION

Juvenile Pacific whiting were most abundant within the upper mixed layer; larvae were more abundant at depths presumably well below the mixed layer (figure 2). These results were consistent with the vertical distribution of larvae and juveniles reported by Ahlstrom (1959), Bailey (1982), and Lenarz et al. (1991). Such ontogenetic shifts in distribution are not uncommon and have been observed in other species, including shortbelly rockfish (*Sebastes jordani*; Lenarz et al. 1991), walleye pollock (*Theragra chalcogramma*; Sogard and Olla 1993), and Pacific and speckled sanddabs (*Citharichthys sordidus* and *C. stigmaeus*; Sakuma and Larson 1995). Although the relatively deep distribution of Pacific whiting larvae reduces the likelihood of offshore advection by upwelling (Smith 1995), the occurrence of juveniles within the upper water column would seem to leave them quite susceptible to such movements.

It should be noted that the vertical distribution of young-of-the-year juvenile Pacific whiting reported in this study resulted from collections made at night; daytime distributions could be quite different. Daytime midwater trawls conducted by the NMFS Tiburon Laboratory in May–June of 1988 at the same locations as the standard nighttime trawls yielded significantly lower catches of juvenile Pacific whiting (NMFS Tiburon Laboratory, unpublished data). Low catches during the day could have resulted from juveniles' ability to avoid the net, a more dispersed distribution, a deeper distribution than the standard trawl depth of 30 m, or a combination of these factors. Sogard and Olla (1996) observed that juvenile walleye pollock were more active and widely dispersed throughout the water column during the day, whereas at night they moved into the upper water column and became less active. Koeller et al. (1986) reported that young-of-the-year silver hake (*Merluccius bilinearis*) 20–30 mm long were distributed on the bottom during the day and migrated up into the water column at night.

Catch rates of juvenile Pacific whiting in the midwater trawl survey varied considerably among years, as well as between specific geographic regions (figure 3). The lack of a significant correlation between the year-effect from the ANOVA that incorporated all strata and the recruitment of two-year-old fish to the commercial fishery (Dorn 1996) was primarily due to the lack of correlation of the years 1988 and 1990 (figure 5). Dorn (1996) indicated that 1990 was a moderate year class, slightly better than that of 1988. In contrast, the midwater trawl surveys indicated that 1988 was one of the better years, whereas 1990 was relatively poor (figures 3 and 5). However, the midwater trawl survey data indicate that 1988 was a good year only because juvenile Pacific whiting were caught in moderate numbers in all strata (figure 3).
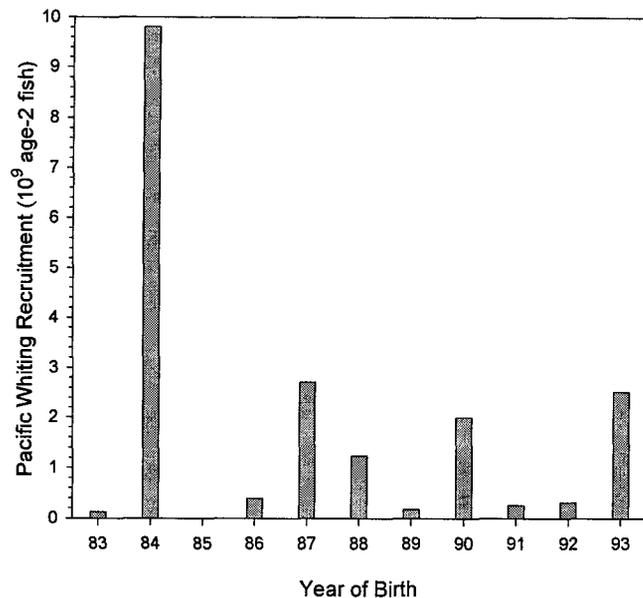

Figure 11. Recruitment index of two-year-old Pacific whiting, *Merluccius productus*, from 1983 through 1993, presented by Dorn (1996).

It could be argued that successful recruitment might depend on the survival of large localized aggregations of juveniles, rather than on the widespread occurrence of moderate-sized schools. A much better correlation with Dorn's (1996) results was produced by focusing on the MO stratum, where juvenile Pacific whiting persistently occurred (figure 6). This result, and the fact that strong recruitment years dominate the adult population for several years (Bailey and Francis 1985; Francis and Hollowed 1985), would seem to imply that the persistence of large schools of juveniles, as observed in the MO stratum, is important to year-class success.

It should be noted, however, that even the best year classes observed in this study do not compare on as great a scale as the dominant year class observed in 1984 (Dorn 1996; figure 11). Although the NMFS Tiburon Laboratory's midwater trawl surveys began in 1983, the current standardized set of stations was not incorporated until 1986 (Wyllie Echeverria 1990), and young-of-the-year juveniles were not routinely differentiated from adults until 1985. Therefore, a comparison of the 1984 midwater trawl data with Dorn's (1996) results is not possible. In addition, the midwater trawl survey focused on only a small portion of the juvenile Pacific whiting habitat. Latitudinal shifts in the spawning distribution, as reported by Bailey et al. (1982) and Dorn (1995), could greatly confound the estimation of year-class success in a study with limited geographic coverage.

Each year the largest catches of Pacific whiting juveniles came from the MO stratum (figure 3). This persistence could be caused by convergence due to localized hydrographic features (e.g., a mesoscale eddy);

a behavioral response to the abundance of predators or prey; or a combination of both factors.

Acoustic Doppler current profiler (ADCP) data showed evidence of an eddylike circulation pattern off Monterey Bay at 15–63 m during sweep 3 of 1994, at 95–111 m during sweep 2 of 1995, and at 15–63 m during sweep 3 of 1995 (Sakuma et al. 1995, 1996). Unfortunately, ADCP data prior to 1994 are unavailable, so an eddylike feature off Monterey Bay in other years cannot be verified. But the occurrence of a mesoscale eddy off Monterey Bay in both 1994 and 1995 (Sakuma et al. 1995, 1996) would seem to indicate that this might be a recurrent, predictable feature.

Mesoscale eddies might not necessarily entrain juvenile Pacific whiting, but may concentrate less mobile zooplankton and other food items within the Monterey Bay area. Huntley et al. (1995) observed enhanced zooplankton abundance associated with a mesoscale eddy located 185 km offshore of Monterey Bay in June 1993. Hayward and Mantyla (1990) observed increased primary production and phytoplankton biomass as a result of the combined effects of a coastal upwelling jet and a mesoscale eddy off Cape Mendocino in May 1987. The large numbers of juvenile Pacific whiting in the Monterey Bay area could result from an active response to increased prey availability, rather than from passive transport driven by hydrography. But passive transport due to prevailing currents probably has some effect on the distribution of juveniles, particularly smaller individuals, whose swimming abilities are less well developed.

Averaged over the years 1987–95, juvenile Pacific whiting were significantly less abundant in upwelled water than in non-upwelled water, although within any particular year, differences were not always evident (e.g., 1987, 1994, and 1995; table 1 and figure 7). Decreased abundance in upwelled water could result from the advection of juveniles away from upwelling fronts, a behavioral response to avoid upwelled water, or a general offshore distributional pattern that is independent of coastal upwelling events.

Juvenile Pacific whiting could migrate deeper into the water column and therefore appear to be absent in areas of recent upwelling. Changes in the vertical migration patterns of some species of larval and juvenile fish have been reported coincident with changes in the vertical thermal structure (Neilson and Perry 1990). But thermal stratification weakens during upwelling and would be more likely to cause juveniles to migrate into the upper water column rather than to constrain them to deeper depths.

The occurrence of moderate to large numbers of juveniles near the coast of Point Reyes during upwelling relaxation, and the absence of juveniles in this same region during periods of strong upwelling, as observed in 1987 and 1993, would suggest that these juveniles were subject to advection (figures 8, 10). Similarly, the offshore distribution of juvenile Pacific whiting in 1989 could have been due to advection as a result of the strong upwelling during that year (figure 9). Bailey et al. (1982) reported that the distance of Pacific whiting larvae offshore was positively correlated with upwelling indices. Offshore transport due to upwelling has been observed in small pelagic juvenile rockfish and in early pelagic metamorphic stages of sanddabs, although the same patterns were not evident in large pelagic juvenile rockfish and late pelagic metamorphic-stage sanddabs (Larson et al. 1994; Sakuma and Larson 1995). It is likely that Pacific whiting's susceptibility to offshore advection due to upwelling also depends on size or developmental stage.

In summary, we have shown that Pacific whiting appear to undergo a shift in vertical distribution, as evidenced by the absence of larvae in the upper mixed layer and the presence of large numbers of juveniles in this region (figure 2). These juveniles' presence in the upper water column may make them susceptible to advection by upwelling, as evidenced by their distribution offshore during upwelling episodes and nearshore during upwelling relaxation (figures 8–10). In the area off Monterey Bay juveniles are consistently observed in substantial numbers (figures 3, 8–10). This may be attributed to the episodic occurrence of a mesoscale eddy in this region, which might entrain juveniles or aggregate prey.

From this study, we conclude that data about juvenile abundance gathered from midwater trawl surveys could be a useful source of fishery-independent information for forecasting year-class strength.

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OBSERVATIONS ON THE SPAWNING DISTRIBUTION AND BIOLOGY OF OFFSHORE PACIFIC HAKE (MERLUCCIUS PRODUCTUS)

MARK W. SAUNDERS AND GORDON A. MCFARLANE
Pacific Biological Station
Hammond Bay Road
Nanaimo, British Columbia
Canada V9R 5K6

ABSTRACT

Two cruises were conducted in February 1990 and 1991 to examine the distribution and biology of spawning offshore Pacific hake. The fish spawned during winter, in the southern portion of their range, i.e., south of Cape Mendocino, and offshore of the shelf break over bottom depths exceeding 1,000 m. In 1990, the schools were 110–167 km (60–90 nmi) offshore in midwater depths ranging from 140 to 240 m, over bottom depths of 3,600 and 4,200 m. In 1991 there were six schools containing spawning hake from 35° to 40.5°N, spanning 720 km (390 nmi). There were more males than females in the spawning schools. In 1991 some schools of predominantly post-spawners were encountered; they tended to be inshore of the spawners and were mainly female. The most surprising of the results was the presence of a north-south cline in biological parameters during spawning similar to the one occurring in summer. We discuss the implications of our results for the present migration hypothesis.

INTRODUCTION

The offshore Pacific hake stock ranges from Baja California to southeastern Alaska. It is the most abundant of three stocks of Merluccius productus in the northeastern Pacific Ocean that support international, joint-venture, and domestic fisheries in Canadian and U.S. waters. In total, these fisheries have averaged 190,000 metric tons (t) annually, from 1966 to 1995.

The basic life history was first described by Alverson and Larkins (1969) from year-round observations of Russian and U.S. scientists participating in and assessing the international fishery during the 1960s. They reported that hake migrate annually between spawning grounds (located from central California to Baja California) and summer feeding grounds (located from central Oregon to northern Vancouver Island). During the summer feeding period adult hake are concentrated in large midwater feeding aggregations, centered on the shelf break from central Oregon to northern Vancouver Island (figure 1). There is a latitudinal cline in average age, mean size, and sex ratio; older, larger, and predominantly female fish are found farther north. Spawning, between January and March, centers on the California Bight, seaward of the shelf break as far offshore as 925 km (500
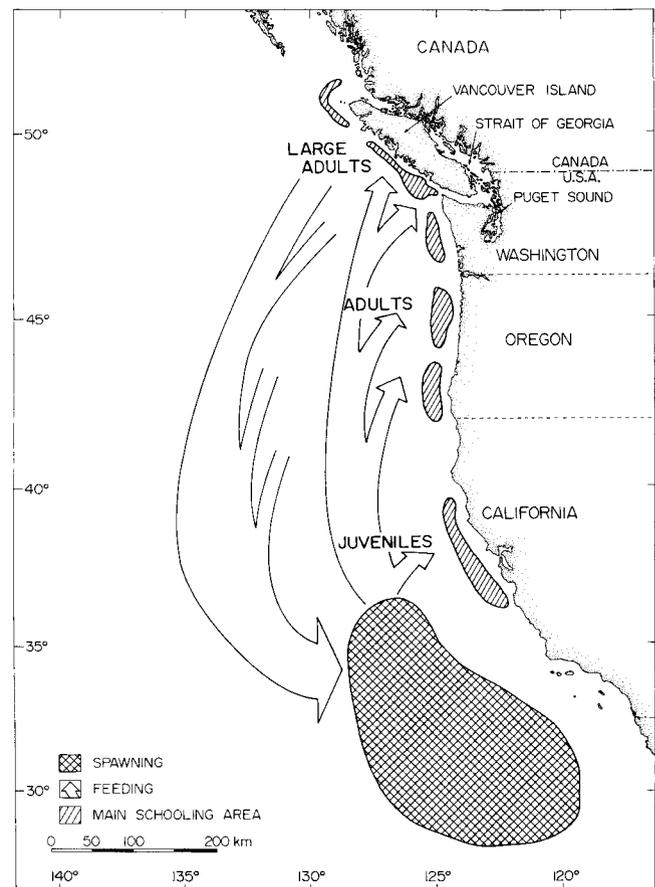

Figure 1. Migration pattern of Pacific hake (modified from Bailey et al. 1982).

nmi; figure 1). Juveniles (<3 years) frequent shelf locations in southern and central California and gradually migrate north and recruit to the main stock.

Alverson and Larkins (1969) synthesized these observations into a migration hypothesis:

1. The adult segment of the population exhibits a large-scale north-south movement: north during spring and summer, and south during late fall and winter.
2. Northward migration of adults is accompanied by movement towards shore and into shallower water.
3. The southward migration is accompanied by movement into deeper water and seaward.

4. Spawning occurs during the winter when hake occupy the southern portion of their geographic range.

The hypothesis was subsequently modified by Francis (1983), who introduced a swimming-speed argument, modified from Ware (1978), to explain the latitudinal cline in age- and size-related parameters. Since then the research has focused on the fishery, and related assessment surveys have been conducted during the summer. In particular, the National Marine Fisheries Service (NMFS) has conducted hydroacoustic surveys triennially since 1977 (Dark et al. 1980; Nelson and Dark 1985; Dark and Wilkins 1994), and the Department of Fisheries and Oceans (DFO) has conducted annual surveys of the Canadian zone since 1990 (e.g., Saunders et al. 1992). Spawning distributions have been inferred from CalCOFI surveys of egg and larval distributions (Bailey 1980, 1981a, 1982; Bailey et al. 1982; Hollowed 1992), and there have been no further direct observations of winter spawning distribution and biology.

Direct observations are desirable for testing the migration hypothesis. Consistent with the hypothesis, the current assessment model assumes that all the hake assessed during the summer return to southern California and contribute equally to spawning success. Harvest strategies have been developed on the basis of maintaining a specific spawner biomass. If the hypothesis is not correct then the basis for conserving the stock may be flawed.

To begin collecting data to test the hypothesis, two cruises were conducted in February 1990 and 1991 to examine the distribution and biology of spawning offshore hake. In this paper we present the results of the cruises, and discuss their implications to the current migration hypothesis.

METHODS

During both surveys a zigzag search pattern was used to locate hake schools in the area bounded on the north by 48°N, on the south by the U.S.–Mexico boundary (approximately 31°N), on the east by the 200-m isobath, and on the west by 130°W. The seaward boundary extended beyond any previous catch of spawning hake. Hull-mounted 38- and 50-kHz Simrad sounders were monitored continuously for midwater echosign. The survey was conducted 24 hours per day, since hake schools exhibit minimal diel behavior during spawning (McFarlane and Beamish 1985). The survey was conducted from the CSS *W. E. Ricker*, a 58-m, 2,500-hp research stern trawler.

When schools were located they were sampled with midwater trawl gear. In 1990, the trawl gear consisted of a Canadian Diamond 5 midwater mesh trawl with a 10-m vertical opening and 3.8-cm cod-end mesh, a pair of 4-m Superkrub midwater trawl doors, and 55-m sweep

wires with 167-kg chain weights. In 1991 we used a Canadian Diamond 7 midwater mesh trawl with 13.5-m vertical opening, 3.8-cm cod-end mesh, a pair of 5-m Superkrub midwater trawl doors, and 80-m sweeps with 300-kg chain weights.

Total catches were separated by species and weighed to the nearest kilogram. Random samples of hake fork length (cm), sex, maturity, and otoliths (for subsequent ageing) were collected. Otoliths were stored in a 50/50 glycerine/freshwater solution with thymol. Maturity states were visually assessed according to the criteria outlined in Weir et al. 1978. Stomach contents were identified to the lowest possible taxon, and the volume of each item was visually estimated to the nearest 0.5 cc. Hake otolith cross sections were aged with the break and burn method (Chilton and Beamish 1982).

We used the methods outlined in Kabata and Whitaker (1981, 1986) to assess the prevalence of infection with *Kudoa paniformes* and *Kudoa thrysites*.
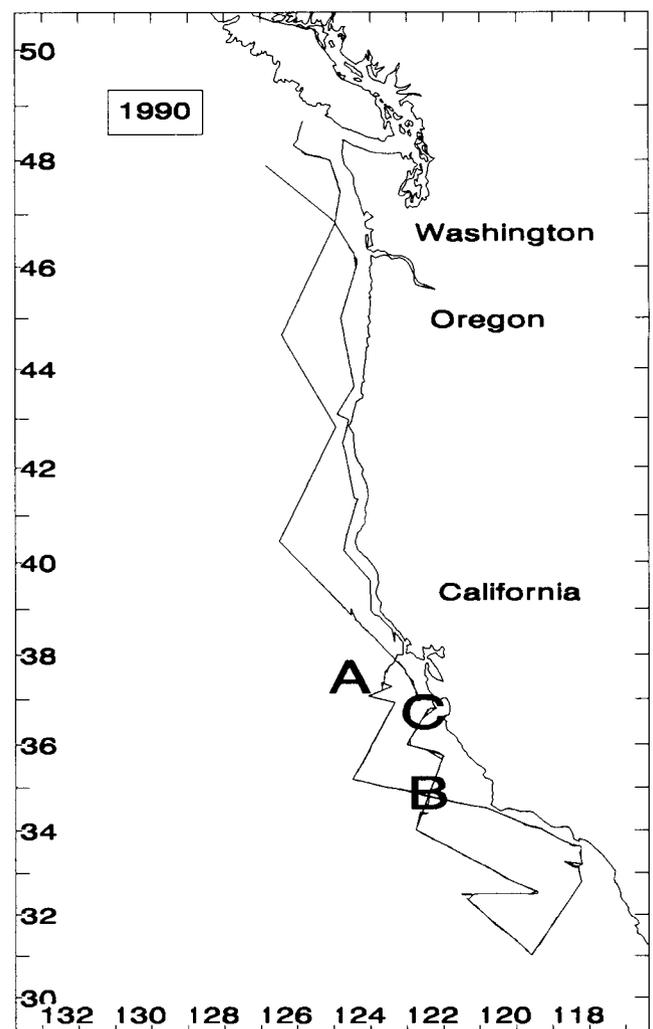

Figure 2. Tracklines sounded and Pacific hake schools (*letters*) encountered during the February 13–March 4, 1990, survey.

TABLE 1
Pacific Hake School Descriptions, by Year

School	Location	School dimensions (km)	Date fished	Fishing set	School depth (m)	Capture depth (m) of headrope
1990						
A	93 km SW of Pt. Reyes 37.3°N, 123.7°W Bottom depth ~3,600 m	6 × 9 = 54 km²	2/17	1	140–180	160
				2	140–180	165
B	200 km W of Pt. Conception 34.9°N, 122.9°W Bottom depth ~4,200 m	11 × 17 = 187 km²	2/19	6	220–240	220–232
				7	200–230	200–230
				8	190–205	200–220
1991						
A	100 km W of Cape Mendocino 40.8°N, 125.7°W Bottom depth ~2,962 m	4.1 × 4.1 = 16.8 km²	2/25	12	120–180	190–200
B	165 km W of Pt. Reyes 37.8°N, 124.9°W Bottom depth ~2,225 m	9.1 × 2.2 = 20.0 km²	2/24	11	180–200	200
C	NW Monterey Bay 37.0°N, 122.6°W Bottom depth 460 m	N/A	2/12	2 & 3	120–140	140–150
D	130 km W of Monterey 36.5°N, 123.5°W Bottom depth ~3,570 m	5.5 × 6.1 = 33.6 km²	2/21	10	280–300	350–380
E	130 km NW of Pt. Conception 34.9°N, 122.5°W Bottom depth ~4,500 m	2.4 × 9.8 = 23.5 km²	2/13	4	220–300	240–300
				5	200–280	250–280
F	60 km W of Cape San Martin (NW of Pt. Conception) 35.5°N, 122.0°W Bottom depth ~1,090 m	7.6 × 9.8 = 74.5 km²	2/20	8	280–350	350
				9	180–310	350
G	150 km SW of Pt. Conception 33.2°N, 121.4°W Bottom depth ~3,800 m	31.6 × 14.8 = 467.7 km²	2/15	6	380–400	380–450

RESULTS

Cruises were conducted from February 13 to March 4, 1990, and from February 7 to 28, 1991. In 1990, two large schools were encountered 280 km (150 nmi) apart, one at 37°N (school A) and another at 35°N (school B; figure 2). School C contained some spawners but primarily juveniles. The schools were 110–170 km (60–90 nmi) offshore in midwater depths ranging from 140 to 240 m, over bottom depths of 3,600 and 4,200 m (table 1). The thickness of the schools ranged from 10 to 50 m (figure 3).

In 1991 there were six schools containing spawning hake (schools A, B, D, E, F, and G in table 1 and figure 4) from 35° to 40.5°N, spanning 720 km (390 nmi). School C contained only juvenile fish. The depth of the spawners ranged from 120 to 300 m, and the schools were thinner (10–20 m) and less dense than in 1990 (table 1 and figure 5).

Maturity

In both years, the maturity condition of males was predominantly ripe-and-running and spent. The high-
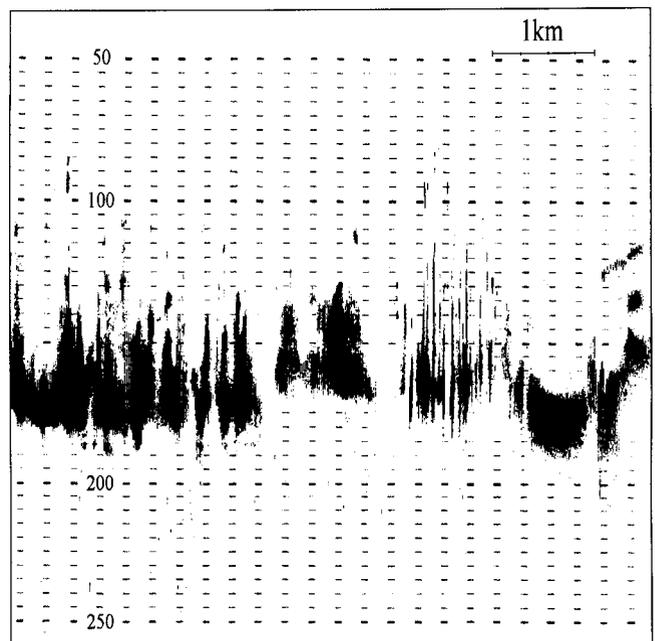

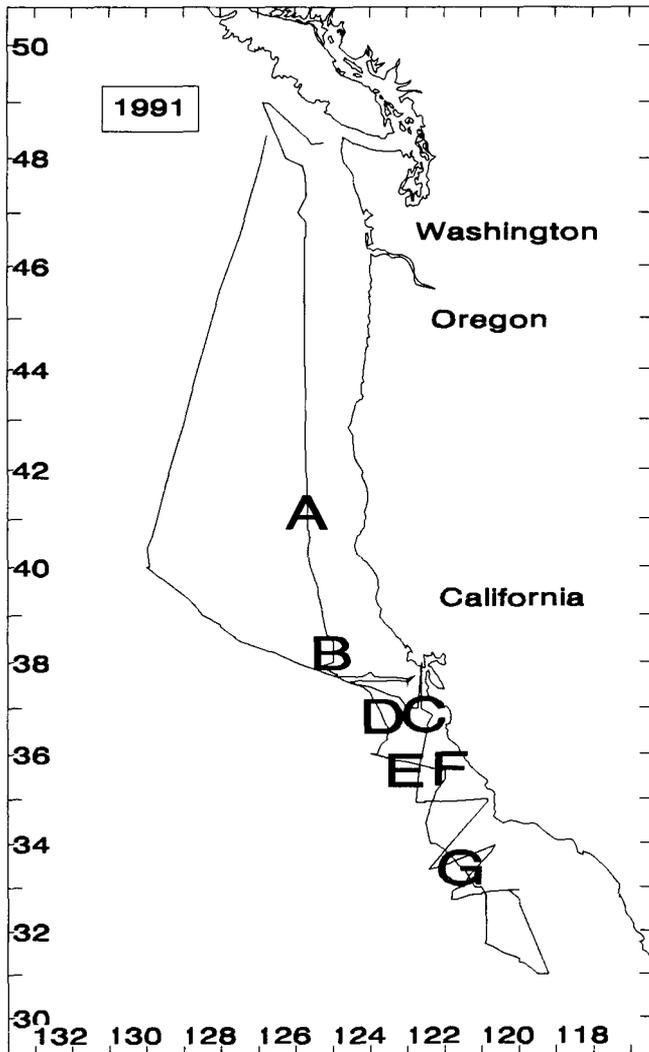Figure 3. Echogram of spawning Pacific hake, school A, February 17, 1990. Depth in meters.

Figure 4. Tracklines sounded and Pacific hake schools (*letters*) encountered during the February 7–28, 1991, survey.
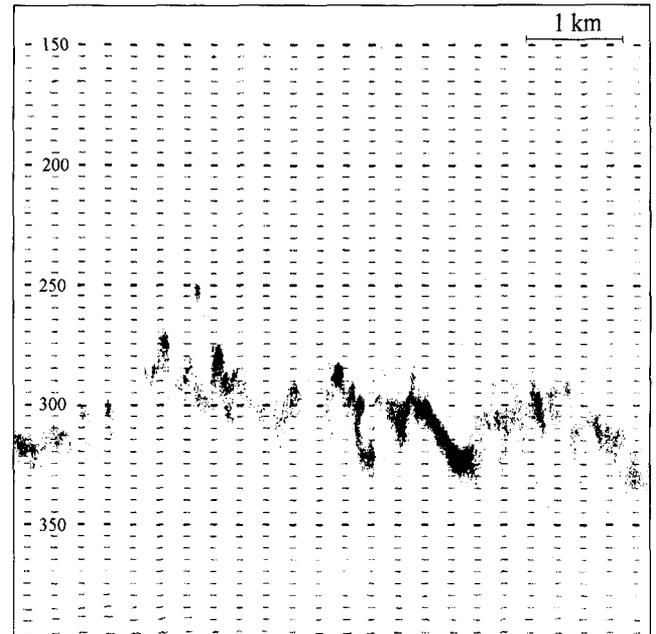

Figure 5. Echogram of spawning Pacific hake, school C, February 12, 1991. Depth in meters.

ing response to the vessel and trawl. This response made discrete depth sampling of the schools difficult.

Nevertheless, there was a clear difference between surveys. In 1990, the sex ratio of the spawning schools ranged from 10% to 28% females; in 1991, the range was much higher: 32%–55%. There is an indication that the proportion of females increases with latitude. At similar latitudes the inshore post-spawning school (F) had a much higher proportion of females than the offshore spawning school (E; table 2).

Age and Growth

The age compositions in both years were dominated by the strong 1980 and 1984 year classes (figure 8). In 1991, the percentage contribution of the older, 1981 year class as age 11's increased with latitude while the percentage of age 4's decreased with latitude.

The mean size of both males and females increased with latitude in 1991 (figure 9). Females increased from 45.4 cm at the southernmost point (school G) to 46.3 cm at the northernmost point (school A). Similarly, males increased from 44.0 cm to 45.5 cm. An ANOVA test of mean length by set found these differences to be significant ($P > .0001$) for both sexes.

Parasite Prevalence

The prevalence of infection with the two species of Kudoan parasites was examined from 50 fish samples collected from schools G, F, D, and A in 1991 (table 3). The proportion infected with *K. paniformes* decreased from south to north. The proportion infected with *K. thrysites*

est proportion of females were either ripe or spent; fewer than 10 percent were actively spawning (ripe-and-running; figures 6, 7).

In 1990, the more northerly school contained a larger proportion of males and females in pre-spawning condition (figure 6), a trend that was less obvious in 1991 (figure 7). In 1991 some schools of predominantly post-spawners were encountered; they tended to be inshore of the spawners except for school G, the southernmost school (figure 7).

Sex Ratio

The sex ratio varied considerably among sets (table 2). Pacific hake from the Strait of Georgia are known to stratify by sex within spawning schools (McFarlane and Beamish 1985), and it is possible that this is a contributing factor. We were, however, unable to demonstrate this for the offshore hake because of their very strong div-
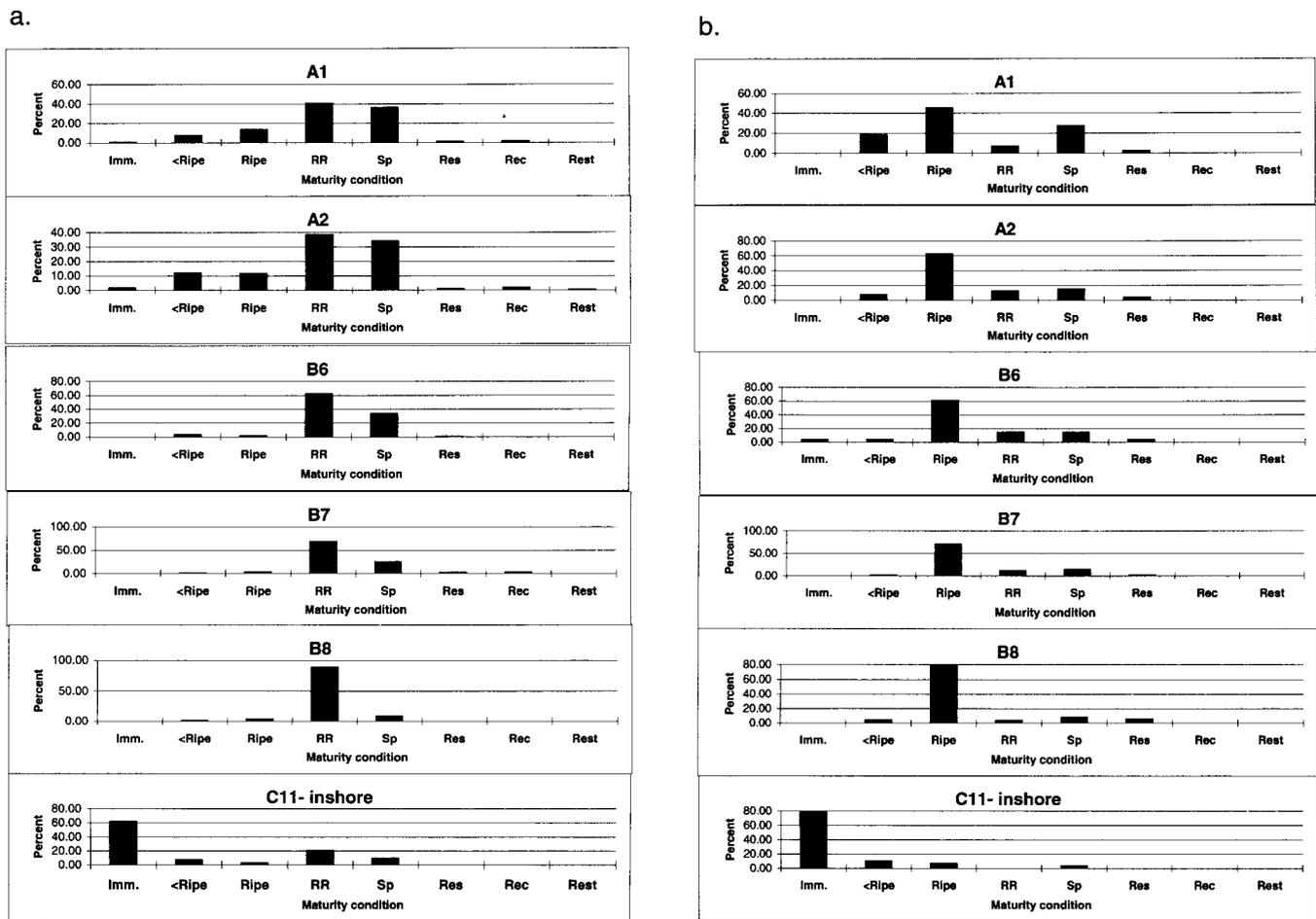
a.

b.

Figure 6.   Percent frequency of maturity condition by fishing set, February 1990, for (a) males and (b) females. Maturity conditions as defined by Weir et al. (1978): Imm = immature, RR = ripe and running, Sp = spent, Res = resorbing, Rec = recovering, Rest = resting. Sets are listed by school (letters) and set (numbers).

increased over the three northerly sets but was elevated for the southernmost school.

Feeding

In general, the stomachs of hake captured from the spawning aggregations were empty or everted. In 1990, such stomachs constituted 97%–99% of those sampled. The few food items present consisted of euphasiids, squid, and a sipunculid. In 1991, the percentage of empty and everted stomachs decreased and the diet was more varied (table 4). The change is associated with the samples dominated by post-spawners, suggesting that they had resumed feeding (school G; table 4).

DISCUSSION

Spawning Distribution

These surveys represent the first capture of spawning offshore Pacific hake reported since 1982 (Stepanenko

and Zinovyeva 1982). Our results support the original hypotheses of Alverson and Larkins (1969). Spawning occurred during the winter, in the southern portion of the range, i.e., south of Cape Mendocino, and offshore of the shelf break over bottom depths exceeding 1,000 m (table 1). The offshore locations (60–165 km), depth of the schools (120–400 m), and timing of spawning (February; table 1) were similar to the few direct observations of offshore spawning hake summarized by Bailey et al. (1982).

The presence of fish in spawning condition off Cape Mendocino (40.5°N) extends the northern spawning boundary from that of previous studies which found spawners as far north as 38°N (Anonymous 1969; Ehrich et al. 1980; Stepanenko 1981). This observation is consistent with larval distributions summarized by Bailey et al. (1982), who inferred that Cape Mendocino was the northern limit of spawning, and by Bailey (1980), who observed that Pacific hake spawning has moved farther
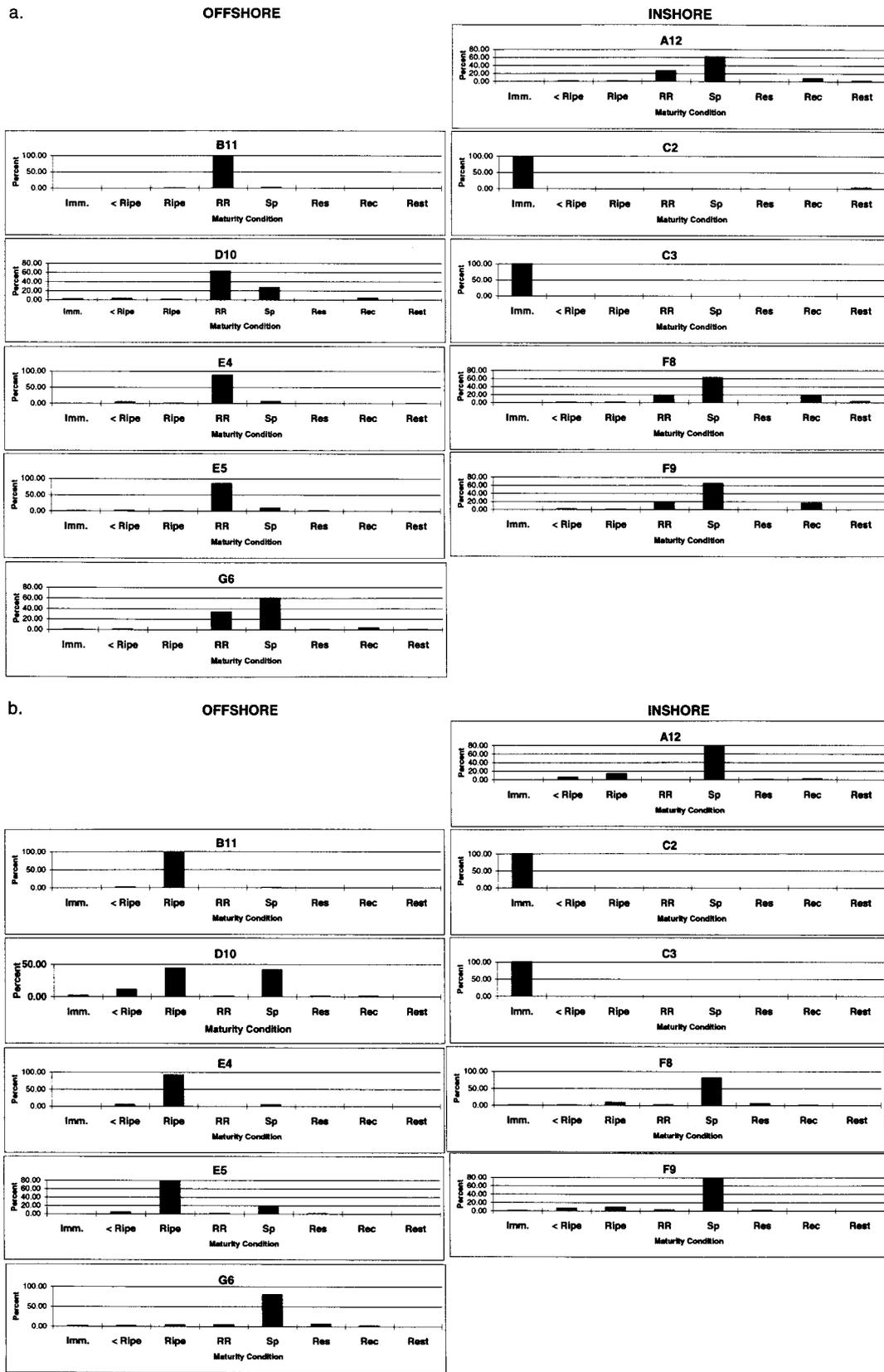
Figure 7.   Percent frequency of maturity condition by fishing set, February 1991, for (a) males and (b) females. Maturity conditions as defined by Weir et al. (1978): Imm = immature, RR = ripe and running, Sp = spent, Res = resorbing, Rec = recovering, Rest = resting. Sets are listed by school (letters) and set (numbers) and are presented in latitudinal sequence from north (top) to south (bottom).

TABLE 2
Percentage of Female Hake by Survey Year,
Position Offshore, School, and Fishing Set

Offshore				Inshore			
School	Status	Set	Percentage	School	Status	Set	Percentage
1990							
A	Spawning	1	10%	C	Juveniles	9	40%
		2	28%				
B	Spawning	6	17%				
		7	14%				
		8	23%				
1991							
B	Spawning	11	55%	A	Post-spawning	12	57%
D	Spawning & Post-spawning	10	53%				
E	Spawning	4	32%	F	Post-spawning	8	57%
		5	36%			9	54%
G	Post-spawning	6	39%				
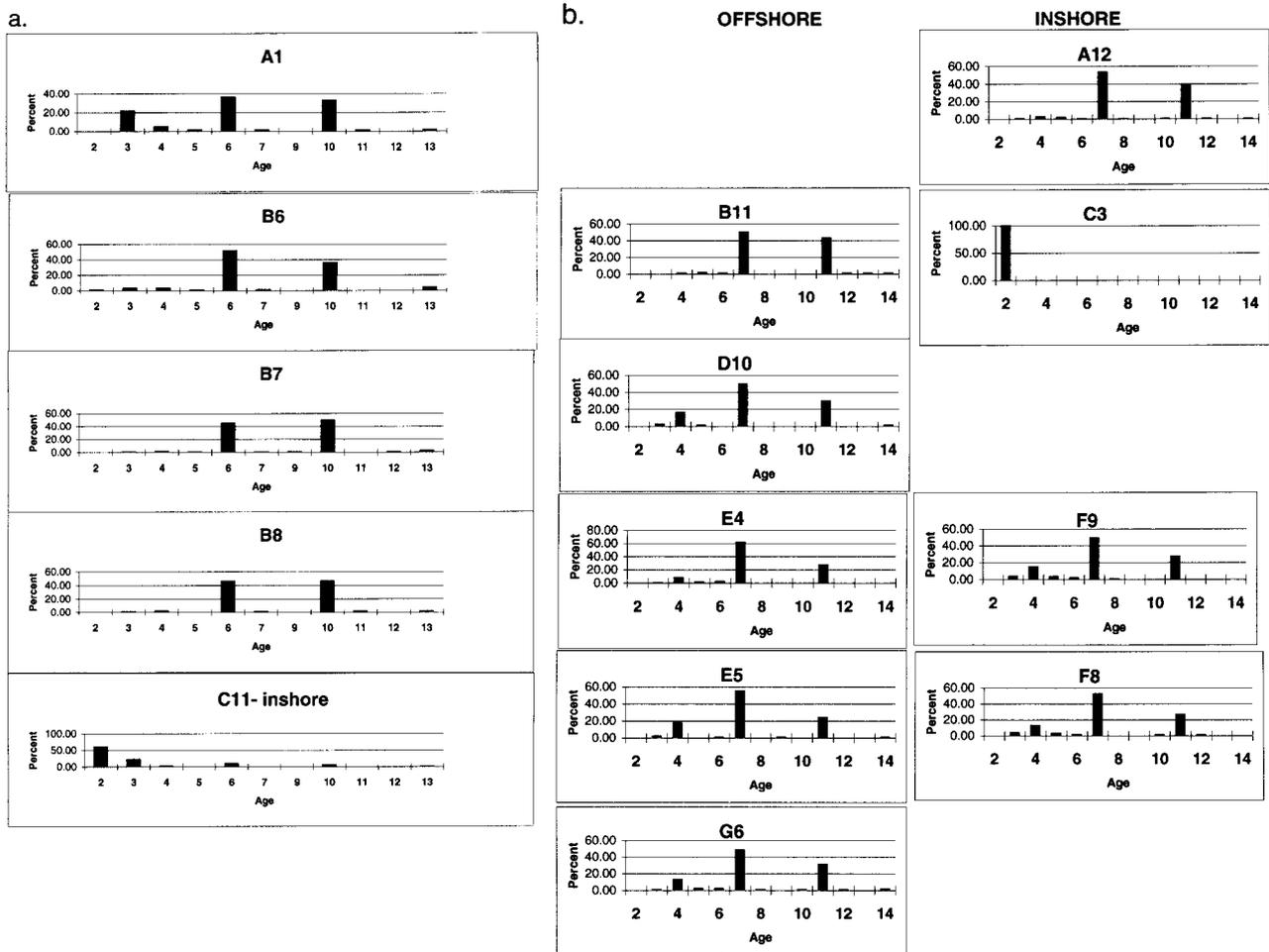
Figure 8.   Percent age-frequency compositions of Pacific hake, by set, during February 1990 (a) and 1991 (b). Sets are listed by school (letters) and set (numbers) and are presented in latitudinal sequence from north (top) to south (bottom).

north since the 1950s, when the fish spawned only between Point Conception and southern Baja California.

Although we were unsuccessful in finding hake above Cape Mendocino and below Point Conception, there are several indications that we did not sample the entire spawning population. CalCOFI surveys conducted during January, February, and April of both 1990 and 1991 found hake larvae throughout the California Bight (Paul Smith, pers. comm.), indicating unsampled spawners south of Point Conception.
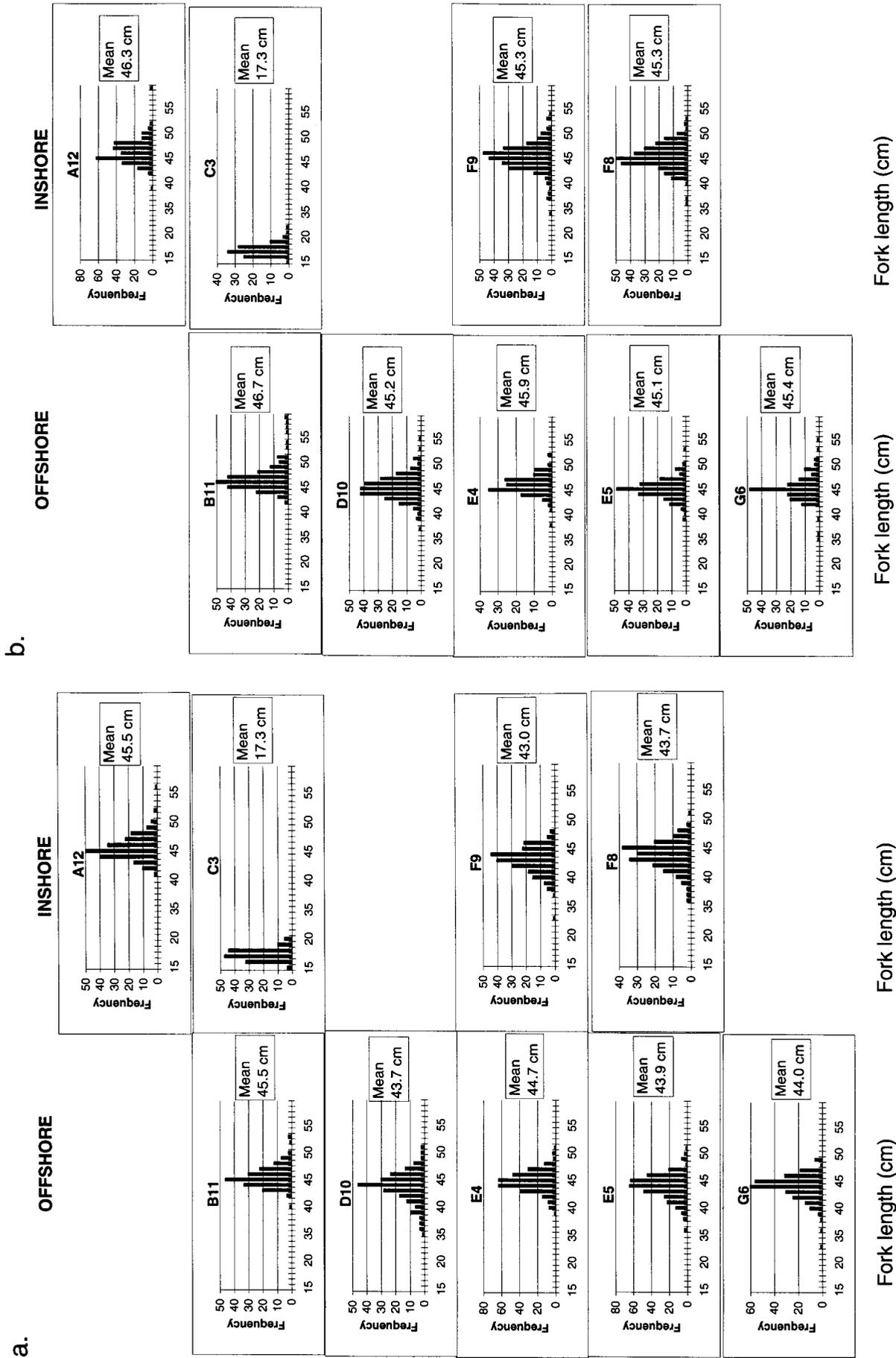
Figure 9. Percent length-frequency compositions of Pacific hake by set, February 1991, for (a) males and (b) females. Sets are listed by school (letters) and set (numbers) and are presented in latitudinal sequence from north (top) to south (bottom).

TABLE 3
Percentage of *Kudoa* Infection in Hake, by Set, 1991

Infection type	Set[a]			
	G6	F8	D10	A12
K. paniformes	44.9	34.0	38.0	25.0
K. thrysites	22.7	10.0	20.0	17.3
Mixed	14.3	28.0	28.0	28.8
Negative	30.6	28.0	14.0	28.8

[a]Set refers to school (letter) and fishing set (number).

In addition, there are aspects of the biological data that indicate we did not survey the older, larger segment of the population that is found in Canadian waters during summer. In the 1991 spawn survey, the mean length of females ranged from 45.4 to 46.3 cm in our sets (figure 9). These fish were comparable in mean size (45.7–46.5 cm) to the females sampled from the South Columbia to Vancouver INPFC areas (M. Dorn, NMFS, unpubl. data; figure 10), during the U.S. 1991 spring fishery. Hake sampled in the 1991 Canadian summer fishery were larger, averaging 48.7 cm (M. Saunders, unpubl. data). Similarly, the prevalence of Kudoan infection during our 1991 survey (table 3) was comparable to prevalence reported by Kabata and Whitaker (1986) for hake found during the summer from Cape Mendocino to northern Oregon. Whether the larger hake were north or south of our sampled distribution is unknown, but the presence of a cline in age- and size-related parameters that is similar in direction to the summer distribution discussed below provides some insight.

Latitudinal Trend in Biological Characteristics

A latitudinal trend in biological characteristics during the summer has been documented in detail (Dark 1975; Francis 1983; Dorn 1995) and explained with an optimal-swimming-speed argument developed by Ware (1978) and adapted for hake by Francis (1983). Briefly, larger fish have higher optimal rates of migration, therefore larger fish reach higher latitudes in summer (Smith 1975; Bailey 1980; Francis 1983; Dorn 1991, 1995).
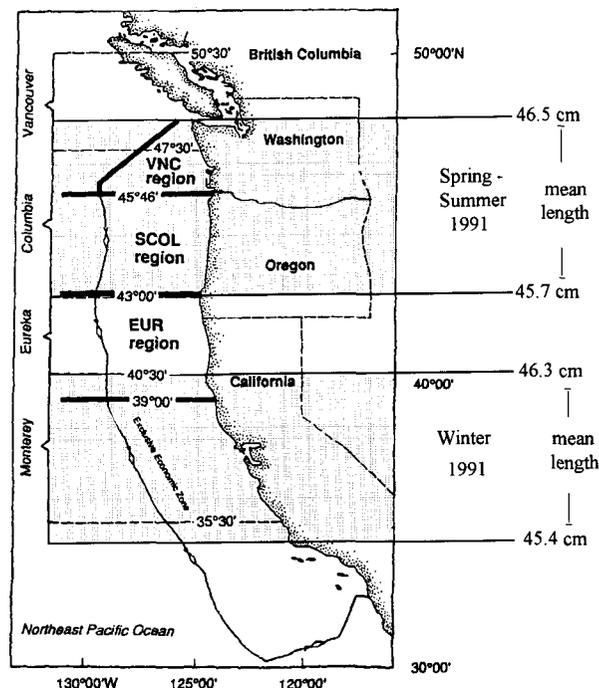

Figure 10. Comparison of the latitudinal range in mean length of spawning females during February 1991 and females of comparable size in the U.S. 1991 fishery. Base map of INPFC regions from Dorn (1991).

In the absence of winter observations, the expected winter latitudinal trends are drawn from conjecture. The current assessments (Saunders and McFarlane, in press; Dorn, in press) and research by Dorn (1995) have assumed that the optimal-swimming-speed argument applies to the southern migration, and that all of the hake return to the point of origin as a mixed stock (Dorn 1995). Smith (1975) hypothesized that the largest fish would migrate from the northern extreme of the feeding migration to the southern extreme of the spawner migration. He and Bailey (1980) suggested that the decline in larvae off Baja California was a result of the developing fishery in the Pacific Northwest, which selectively removed the older fish that would have spawned in the Baja California area.

TABLE 4
Percentage of Prey Occurrence during 1991 Survey

Prey	Set[a]							
	E4	E5	G6	F8	F9	D10	B11	A12
(Empty stomach)	20.0	70.0	50.7	77.5	52.5	40.0	45.0	67.5
(Everted stomach)	77.5	20.0	38.0	20.0	40.0	37.5	52.5	30.0
Euph.	2.5	7.5	0.0	0.0	5.0	10.0	0.0	2.5
Squid	0.0	0.0	0.0	0.0	0.0	10.0	0.0	0.0
Myctophid	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0
Fish Rem.	0.0	0.0	0.7	0.0	0.0	2.5	0.0	0.0
Unid.	0.0	2.5	2.1	0.0	2.5	0.0	0.0	0.0
Hatchet fish	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0
Unid. crust.	0.0	0.0	1.4	2.5	0.0	0.0	2.5	0.0
Totals	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

[a]Set refers to school (letter) and fishing set (number).

On this basis, biological characteristics of winter spawning schools were expected to either vary without latitudinal trend, or exhibit trends that were the inverse of the summer distribution. In 1990, we observed only two schools, 280 km (150 nmi) apart, and their biological characteristics were similar. This was not the case during the 1991 survey, when spawning aggregations observed over 720 km (390 nmi), were found to exhibit north-south clines in age composition, sex ratio, mean size, and parasite prevalence that were similar in direction to those during summer. Although based on only one year, our observations do not support the hypothesis that a swimming-speed mechanism alone causes complete mixing or a latitudinal trend in reverse of the summer direction.

We propose that the clines in population biological characteristics are the cumulative effect of four processes affecting individual fish:

One. Adult hake (3+) migrate onshore and northward to summer feeding grounds and offshore and southward to winter spawning grounds (Alverson and Larkins 1969).
Two. Annual displacement of an individual is dependent on body size and the speed of the alongshore components of the prevailing currents.

Given the considerable evidence that the extent of northern migration in summer is related to the strength of poleward-flowing currents (Smith et al. 1990; Dorn 1995), it seems reasonable that there are analogous mechanisms affecting the return migration. There is some support for a relation between oceanographic conditions and spawning distribution. Hollowed (1992) examined larval data and found that although Cape Mendocino appears to be the limit in most years, the boundary may shift north during anomalously warm years.

Specifically, Hollowed (1992) reported that NMFS ichthyoplankton surveys conducted off the coast of Oregon and Washington during the springs of 1980–84, between 40° and 48°N, found hake eggs in 1983 and 1984. Hollowed suggests that this northward shift may have been due to a shift in spawner distribution resulting from the 1982–93 El Niño. Similarly, the presence of young-of-the year during July 1994, from central Oregon to southern Vancouver Island (M. Saunders, unpubl. data), suggests a northward shift in spawning distribution associated with the warm 1992–93 period. This is consistent with 1992 and 1993 summer observations indicating a northern shift of the stock. In 1992 the triennial acoustic survey found approximately one million t in the Canadian zone—the highest proportion of biomass found there since the inception of the survey in 1977. During 1993, hake were pushed even farther north; there were commercial aggregations in the northern Canadian zone and southeast Alaska (Saunders and McFarlane 1995).

Three. The growth rate of an individual increases with latitude, because of decreased parasite load and/or increased primary and secondary production associated with more northerly waters.

Ware (1992) reports an increasing cline in primary production from southern to northern California which could translate into larger mean size-at-age, assuming that food supply is limiting. MacLellan and Saunders (1995) found that the mean size of the 1980 year class of offshore Pacific hake as age 3's increased with latitude, and hypothesized that the cline resulted from decreasing influence of the 1983 El Niño on productivity with increasing latitude, as reported by Pearcy and Schoener (1987).

Regarding parasite load, Kabata and Whitaker (1986) developed two competing hypotheses to explain the opposed clines in prevalence and intensity of infection of *K. thyrsites* and *K. paniformes*. One hypothesis assumes that California is the site of infection of *K. paniformes* and that a fish is not continuously infected over its life. They postulated that the more heavily infected fish might forgo their migration and cluster near the southern end of their range, as the result of parasite-induced debility.

The alternative hypothesis, based on the assumption that the more prevalent and intensive infection of hake occurs in the southern part of its range, is that part of the hake population fails to migrate. Remaining behind, at, or near the focus of infection, they continue to be exposed to the parasite and thus become more heavily infected. This latter hypothesis is consistent with a persistent north-south cline, with the southern fish remaining in the south and—more important—the largest fish not returning to southern California in most years.

Four. The annual northern displacement of females for a particular cohort is greater than the displacement of males due to sex-specific timing of the post-spawning migration.

If males remain with spawning aggregations longer than females—a behavior noted by McFarlane et al. (1983) for this species in the Strait of Georgia, and for other hake species by Martos and Peralta (1995) and Espino et al. (1995)—then females will have a longer period of northward migration and one which starts earlier. The sex ratios of hake encountered during these surveys provide some support, since spawning aggregations favored males and post-spawning schools favored females. Interestingly, the aggregations of post-spawners tended to be located inshore and were dominated by females. Since the speed of the California Undercurrent intensifies closer to shore, and is strongest during the spawning period (Lynn and Simpson 1987), females could be advected north in larger numbers than males. Bailey (1981b) postulated that hake spawn in the California Undercurrent, noting that bathymetric migrations reported by Ermakov (1974) and Alton (1972) are similar to the dynamics of the California Undercurrent.

Some fundamental aspects of offshore Pacific hake biology remain unresolved; they include the factors, both internal and external, that determine spawning distribution and cause the latitudinal stratification of biological characteristics. Until these aspects of the life history are more fully understood, we must be cautious in applying stock-assessment models which rely on assumptions about the migration that may be incorrect.

ACKNOWLEDGMENTS

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Part III

SCIENTIFIC CONTRIBUTIONS

SEDIMENTATION PATTERNS OF DIATOMS, RADIOLARIANS, AND SILICOFLAGELLATES IN SANTA BARBARA BASIN, CALIFORNIA

CARINA B. LANGE, AMY L. WEINHEIMER, FREDA M. H. REID

Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive
La Jolla, California 92093-0215

ROBERT C. THUNELL

University of South Carolina
Department of Geological Sciences
Columbia, South Carolina 29208

ABSTRACT

We report on fluxes of siliceous microorganisms (diatoms, radiolarians, and silicoflagellates), organic carbon, calcium carbonate, biogenic silica, and lithogenic particles in the Santa Barbara Basin (34°14'N, 120°02'W), offshore of California, in a sediment trap set 540 m deep, from August 1993 to November 1994. Although total mass flux was dominated by lithogenic components throughout the sampling period, we believe that overall flux variations at 540 m were closely coupled with oceanographic conditions at the surface. Organic carbon and biogenic silica fluxes show distinct variations, with maxima during the upwelling period, from May to July 1994, and low fluxes from September to March. Diatoms were the main contributor to the biogenic opal fraction (mean daily flux = 3.98×10^5 valves m^{-2} d^{-1}), followed by radiolarians (mean = 7.05×10^3 tests m^{-2} d^{-1}) and silicoflagellates (mean = 1.48×10^3 skeletons m^{-2} d^{-1}). Each group showed a distinct pattern, with marked production maxima at different times of the year: radiolarians in late summer and fall, silicoflagellates in winter, and diatoms in spring. In total, 150 diatom and 165 radiolarian taxa were identified. Species composition associated with flux peaks differed, reflecting seasonal changes in circulation patterns and the source of water masses in the basin. Spring upwelling is reflected by the co-occurrence of deep-living intermediate radiolarian fauna (mainly *Lithomelissa setosa*) and diatom resting spores (mainly *Chaetoceros radicans*). Non-upwelling conditions, summer through winter, with water entering the basin from the west or the east, are represented by a warm-water, surface-dwelling radiolarian fauna and diatoms that are typically found in temperate and temperate-warm offshore waters. The intra-annual sequence of events, each characterized by a distinct diatom assemblage, can be identified in the laminated sediments of the Santa Barbara Basin. *Chaetoceros* resting spores dominate fluxes in spring, the most productive season, in both the trap and sedimentary records. Thus the effect of preservation in the sedimentary record does not seem to remove information from the most productive season, as is the case in most other areas of the world. Since species in the plankton and in the trap occur simultaneously and are observed within the surface sediment layer in pristine conditions, we assume that dissolution is minimized by rapid descent through the water column. Dissolution seems to take place immediately below the sediment/water interface, and weakly silicified species are removed from the sedimentary record.

INTRODUCTION

In order to use the fossil record to interpret past climatic conditions it is necessary to understand the nature of seasonal representation in the sediments (see review of Anderson 1996). With the increasing interest in high-resolution paleoceanographic studies and the closer linkage to climate modeling, it is crucial to assess the quality and accuracy of the information preserved in the sedimentary record (Sancetta 1992). Transformations associated with the settling of biogenic material from the uppermost layers of the ocean to the seafloor provide clues for understanding mechanisms involved in the formation of sediments, the supply of food to the deep-sea benthos, and the formation and fate of new and recycled organic matter (Berger et al. 1989).

Work conducted by several investigators in different areas of the World Ocean indicates that in terms of abundance and diversity, the diatom assemblage reaching the ocean floor is not only impoverished with respect to the surface community, but also affected by dissolution at the sediment/water interface (e.g., Reimers et al. 1990; Sancetta 1992, 1995; Lange et al. 1994; Treppke et al. 1996). To resolve the questions of seasonal variability recorded in the sediments, it is necessary to examine the sequence from production in the upper water column, through vertical settling, to final burial in the sediment, at time scales of days to months. This is now possible with the use of moored sediment traps (see review in Lange and Boltovskoy 1995).

We report on fluxes of diatoms, radiolarians, and silicoflagellates in the Santa Barbara Basin (SBB), offshore of California, in a sediment trap set at about 500 m deep, from August 1993 to November 1994. Although several studies have used sediment traps to measure fluxes for short periods of time in the SBB (Soutar et al. 1977; Dunbar and Berger 1981; Dymond et al. 1981) our study represents the first attempt to monitor biweekly changes in the flux of siliceous microorganisms in this basin over
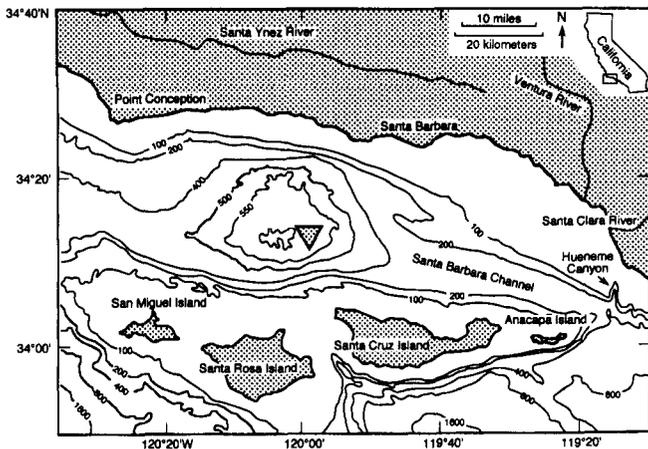
Figure 1. Bathymetry (in meters) of Santa Barbara Basin and location of sediment trap mooring (*triangle*).

Figure 2. Upper ocean temperature at sediment trap location, derived from biweekly conductivity-temperature-density casts from July 1993 to May 1995. Isotherms are in degrees centigrade.

a 15-month cycle. This work is part of an ongoing trapping program being carried out by the University of South Carolina (Thunell et al. 1995) with the goal of monitoring seasonal changes in sediment fluxes in the SBB and evaluating varve formation. We demonstrate that flux patterns of the siliceous components of the plankton are a response to changes in upper-ocean conditions in the SBB, and that the shifts in species composition reflect the complicated hydrography of the area. Our results should aid micropaleontologists in interpreting the climatic signal contained in the laminated sediments of the SBB.

STUDY AREA

The Santa Barbara Channel (SBC) is an elongated basin lying between the California coast and the Channel Islands. An approximately 500-m-deep basin occupies the western part of the central channel (Santa Barbara Basin; figure 1). The SBC is separated from the Southern California Bight to the east by a sill about 200 m deep between Anacapa Island and Port Hueneme. A sill about 400 m deep between Point Conception and San Miguel Island separates the SBC from the open ocean to the west. Below this deeper sill depth, the modern SBB contains oxygen-depleted waters which derive from the Pacific Intermediate Water mass and the Oxygen Minimum Zone off central California. Once within the basin, this low-oxygen (0.1 to 0.3 mL/L; Sholkovitz and Gieskes 1971) water mass is further depleted of oxygen by degradation of organic matter from the highly productive surface waters, rendering the seafloor inhospitable to benthic fauna and preventing bioturbation (Emery and Hülsemann 1962), thus allowing the seasonal sedimentation patterns to be preserved as annually laminated (varved) sequences.

The SBB underlies the highly productive waters of the California Current system, the strength of which
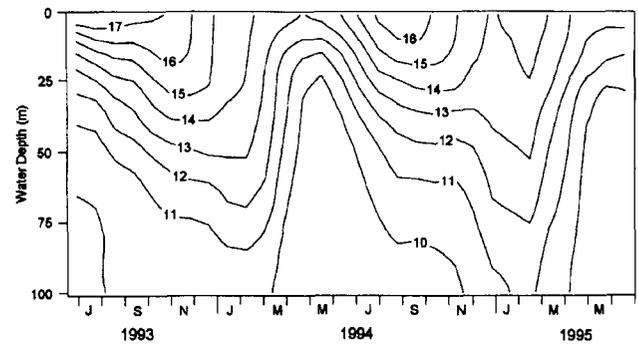
changes in response to seasonal variations in the winds (Huyer 1983). Prevailing winds around Point Arguello–Point Conception are equatorward, and almost always upwelling-favorable. They are strong and steady during spring and early summer, weaker and far more variable in winter (Hendershott and Winant 1996).

The surface waters of the SBC are primarily mixtures of warm and saline waters from the Southern California Bight, with colder and fresher waters upwelled near Point Conception and Point Arguello (Hendershott and Winant 1996). The California Current flows equatorward past the western mouth of the SBC.

The salient features of the surface circulation are summarized in Hendershott and Winant 1996. In general, surface flow at the eastern mouth of the SBC is poleward except in winter. At the western mouth, surface flow is poleward along the north shore of the channel, and equatorward along the north shore of the Channel Islands. Counterclockwise recirculation occurs here; it is strongest during spring through autumn. Episodes of vigorous eddy motion are frequent in the western half of the channel, especially in spring and summer. Upwelled waters near Points Arguello and Conception enter the SBC eastward along the Channel Islands as part of the recirculation.

During our study period (Aug. 1993–Nov. 1994) the upwelling interval was identified by the shoaling of isotherms (figure 2) and high chlorophyll a concentrations in surface waters (Hayward et al. 1994).

MATERIALS AND METHODS

Sediment trap samples were recovered from the center of the SBB (34°14'N, 120°02'W; figure 1) between 12 Aug. 1993 and 1 Nov. 1994, with a small gap of 12 days between 11 and 23 Aug. 1994. Samples were obtained with a cone-shaped trap with 13 cups and a collection area of 0.5 m²; they were poisoned with $HgCl_2$. Each trap sample represents a two-week period, and samples were collected continuously. The mooring was

deployed in 590-m-deep water, the trap positioned about 50 m off the bottom.

Siliceous microplankton analyses were carried out on 1/64 splits of total material in the original sample. The entire split was first washed with distilled water to remove salt and preservatives, and then acid-cleaned and prepared according to the method of Wigley (1984); permanent slides were mounted with Naphrax (for diatoms and silicoflagellates; refractive index 1.74) and Canada balsam (for radiolarians; refractive index 1.54). Quantitative analysis of the diatoms and silicoflagellates was performed with a Zeiss standard microscope with phase contrast illumination, at 250× magnification. *Chaetoceros* resting spores and occasional very numerous or extremely small diatom valves were counted at 650× magnification. Quantification and identification of radiolarians was done with a Zeiss Photomicroscope I, at 100× magnification. All counts refer to the ≥45-μm fraction. For each of the above taxonomic groups, several traverses across the microslide were examined, depending on abundance, and each organism was identified to the lowest taxonomic level possible. Two microslides per sample were scanned in this fashion.

Fluxes in each sample were determined for the three taxonomic groups surveyed, as well as for individual species; they were standardized to daily rates and are expressed in numbers m^{-2} d^{-1} (Sancetta and Calvert 1988). Relative abundances of individual taxa are given as percentages of the total diatom and radiolarian assemblages.

Specific diversity was computed for diatoms and radiolarians only, using Margalef's (1958) formula S_i-1/ln N_i, where S_i is the number of taxa in sample i and N is the total number of individuals in sample i. Diversity was not calculated for silicoflagellates, since only three species were present (*Dictyocha fibula*, *D. speculum*, and *Octactis octonaria* var. *pulchra*).

Radiolarian species were grouped into warm-water, transition, and intermediate environmental groups, according to their biogeographic distribution, as documented by Weinheimer (1994), following the oceanic provinces of McGowan (1974). Warm-water fauna includes species found in warm, high-salinity surface waters entering the California Current system from the west (gyre) or south (tropical waters). Transition fauna is found in cool, low-salinity waters transported southward within the California Current; it includes species from the Subarctic and Transition provinces, as defined by McGowan (1974). Intermediate fauna lives below the thermocline, in cold, high-salinity intermediate waters; along the California coast, it is vertically advected to shallower depths with the shoaling of the thermocline. Ecological affinities and biogeographic distribution of diatoms are well known and have been published elsewhere (e.g., Smayda 1958; Hasle 1976; Semina 1979);

we followed Cupp (1943), Round et al. (1990), and Hasle and Syvertsen (1996). Throughout this text, the term *neritic* refers to those diatoms mainly confined to inshore waters; *oceanic* refers to those typically found in the offshore, open-ocean realm. Each of them, neritic and oceanic, have representatives in cold, temperate, and/ or warm waters.

RESULTS

Particle Fluxes

Bulk-sediment flux data at the SBB mooring are summarized in figure 3, and include daily fluxes of organic carbon, calcium carbonate, biogenic silica, and lithogenic particles, as determined by Thunell et al. (1995). Total mass flux was dominated by lithogenic components (58%–80% range) throughout the sampling period. We contend, however, that overall flux variations at 540 m were closely coupled with oceanographic conditions at the surface. In particular, organic carbon and biogenic silica fluxes show distinct variations, with maxima from May to July (0.08–0.18 g m^{-2} d^{-1} and 0.3–0.9 g m^{-2}
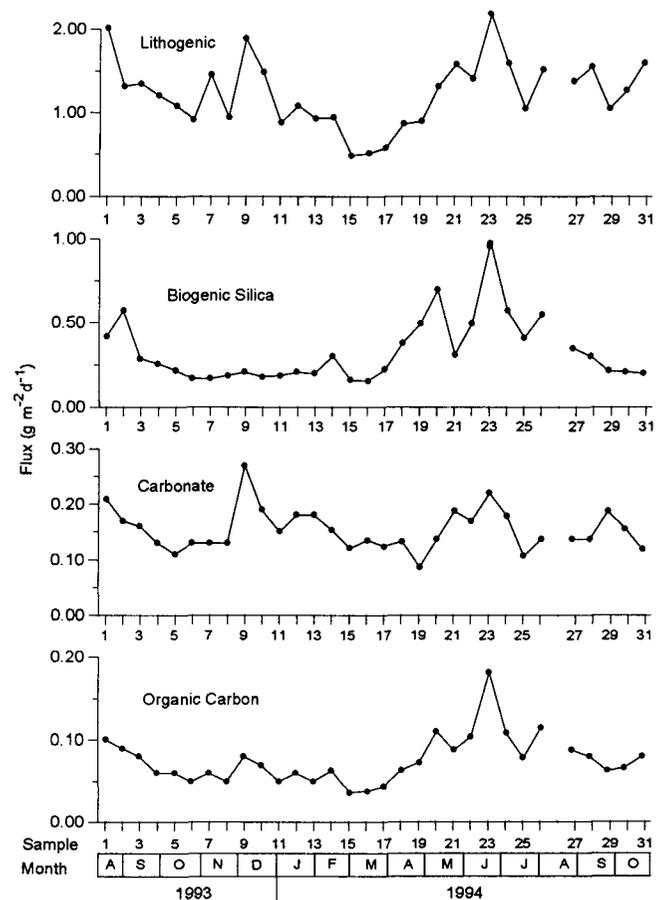

Figure 3. Organic carbon, carbonate, biogenic opal, and lithogenic fluxes (in g m^{-2} d^{-1}) measured in two-week-long samples at SBB sediment trap location (~540-m water depth), from August 1993 to November 1994.

d^{-1}, respectively) and low fluxes from September to March (Corg = 0.04–0.08 g m^{-2} d^{-1}; silica = 0.2–0.5 g m^{-2} d^{-1}). This variability reflects intra-annual changes in upper ocean conditions, with the highest fluxes occurring during the upwelling period (see Study Area). Silica fluxes were typically five times higher than organic carbon fluxes. In contrast, carbonate flux (primarily composed of foraminifers and coccolithophorids) did not vary significantly during the sampling period; the range of values is small (0.1–0.3 g m^{-2} d^{-1}), and the value peaked in winter.

Of relevance for the terrigenous input to our sampling site are the precipitation and runoff patterns into SBB. They are typically greatest during late fall and winter (Soutar and Crill 1977), and this was observed during our study (Thunell et al. 1995); high lithogenic fluxes occurred in October 1994 and November–December 1993 (figure 3). However, lithogenic flux showed a peculiar distribution pattern. In addition to the expected fall–winter peak mentioned above, high lithogenic fluxes were also measured in August 1993 and in spring–early summer 1994. Thunell et al. (1995) attributed this to both the incorporation of terrigenous material into fecal pellets and the scavenging of fine detrital particles from the water column by organic-rich aggregates. We found a good correlation (correlation coefficient r = 0.8) between the organic carbon and the lithogenic fluxes, indicating that sedimentation of terrigenous components may be linked to biological processes (Deuser et al. 1983; Wefer and Fischer 1993). Although fecal pellets and aggregates were not quantified, a casual inspection of the trap samples revealed that they are much more common in the April–June samples.

Fluxes of Siliceous Microorganisms

Diatoms were the main contributor to the biogenic opal fraction (mean daily flux = 3.98 × 10^5 valves m^{-2} d^{-1}), followed by radiolarians (mean = 7.05 × 10^3 tests m^{-2} d^{-1}) and silicoflagellates (mean = 1.48 × 10^3 skeletons m^{-2} d^{-1}). Each group showed a distinct pattern, with the timing of peak fluxes reflecting a clear succession of these microplankton groups (figure 4).

Flux maxima for radiolarians were observed in fall 1993, February 1994, and again in early fall 1994. Silicoflagellates peaked in winter 1993–94 and in early fall 1994 (together with radiolarians). Diatoms yielded four flux maxima—in February, two peaks during spring, and in autumn 1994. The highest value of 6.81 × 10^6 valves m^{-2} d^{-1} was measured in April (sample 19, out of scale in figure 4), in coincidence with the spring upwelling period (figure 2) and its associated high chlorophyll a concentrations at the surface (Hayward et al. 1994).

The specific diversity of diatoms and radiolarians was related to their flux (figure 5); positive correlation for
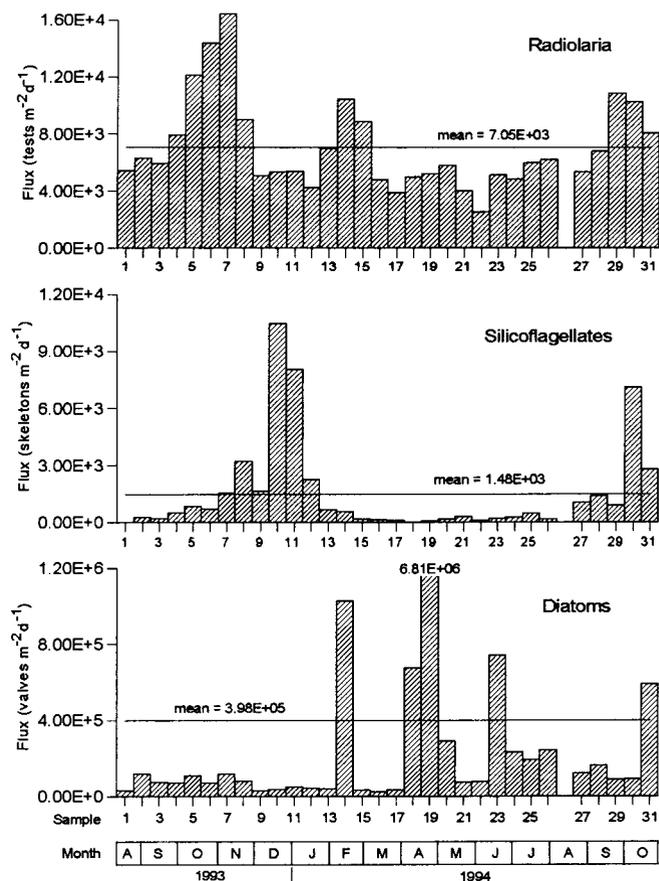

Figure 4. Time-series fluxes of radiolarians, silicoflagellates, and diatoms at SBB sediment trap location (~540-m water depth), from August 1993 to November 1994.
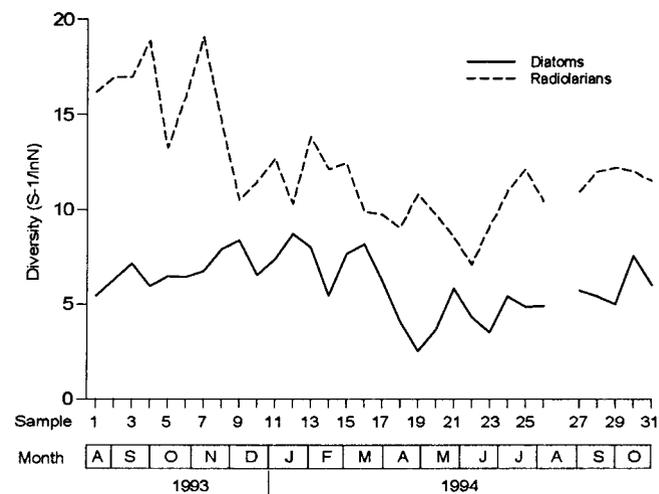

Figure 5. Radiolarian and diatom specific diversity, as measured by the Margalef (1958) index, at SBB sediment trap location (~540-m water depth), from August 1993 to November 1994.

radiolarians (r = 0.5) and negative correlation for diatoms (r = −0.5). In general, highest diatom fluxes yielded lowest diversities; this is especially noticeable in spring (diversity index <4; figure 5). In contrast, radiolarian

TABLE 1
Selected Diatom and Radiolarian Species
(Species or Species Groups with ≥5% in at Least
One Sample) Used in Cluster Analysis

Diatoms
Bacteriastrum elongatum
B. furcatum/delicatulum
Chaetoceros spp. resting spores: *C. affinis, C. compressus, C. debilis,*
C. diadema, C. lorenzianus, C. sp. cf.
C. lorenzianus, C. radicans, C. seiracanthus,
C. vanheurckii
Chaetoceros spp. vegetative cells: *C. concavicornis, C. radicans*
Coscinodiscus spp.: *C. centralis, C. perforatus, C. radiatus*
Rhizosolenia robusta
Thalassionema frauenfeldii
Non-planktonic diatoms: *Arachnoidiscus ehrenbergii, Aulacodiscus kittonii,*
Campylodiscus clypeus, Cerataulus turgidus,
Cocconeis scutellum, Navicula praetexta,
Pleurosira laevis, Rhabdonema adriaticum,
Stictodiscus californicus, Trigonium formosum
f. quadrangularis

Radiolarians
Arachnocorallium calvata group★
Botryostrobus aquilonarus
B. auritus/australis
Dictyophimus gracilipes
Larcopyle butschlii
Lithomelissa setosa
Pterocorys minythorax
Spongodiscid sp.
Spongopyle osculosa
Spongurus sp. cf. *S. elliptica*

★*A. calvata* group includes skeletons with a wide range of morphological vari-
ability, and probably combines closely related taxa (Boltovskoy and Riedel 1987).

diversity was higher overall (index range 7–19 vs. 2–9
for diatoms), and peaks in diversity were generally as-
sociated with flux maxima (except in late summer 1993).

In total, 150 diatom and 165 radiolarian taxa were
identified. These numbers may underestimate the actual
number of species present in the area, because they also
include instances where organisms were identified to
genus only (e.g., diatoms: *Navicula* spp., *Pleurosigma* spp.;
radiolarians: *Porodiscus* spp., *Lophophaena* spp.).

Annual Cycle of Species Assemblages

During the 15-month study (Aug. 1993–Nov. 1994)
diatom and radiolarian species showed clear changes in
their relative and absolute abundances. In order to de-
fine a monthly pattern, we performed a cluster analysis
of samples, based on the relative abundances of species
or species groups (e.g., *Arachnocorallium calvata* group,
nonplanktonic diatoms) present in the ≥45-μm fraction
with ≥5% in at least one sample (table 1), and the log-
transformed total fluxes of diatoms, radiolarians, and sil-
icoflagellates. Clusters were based on the correlation matrix
(distance metric is 1-Pearson correlation coefficient),
using average-linkage clustering (SYSTAT, Inc.). Five
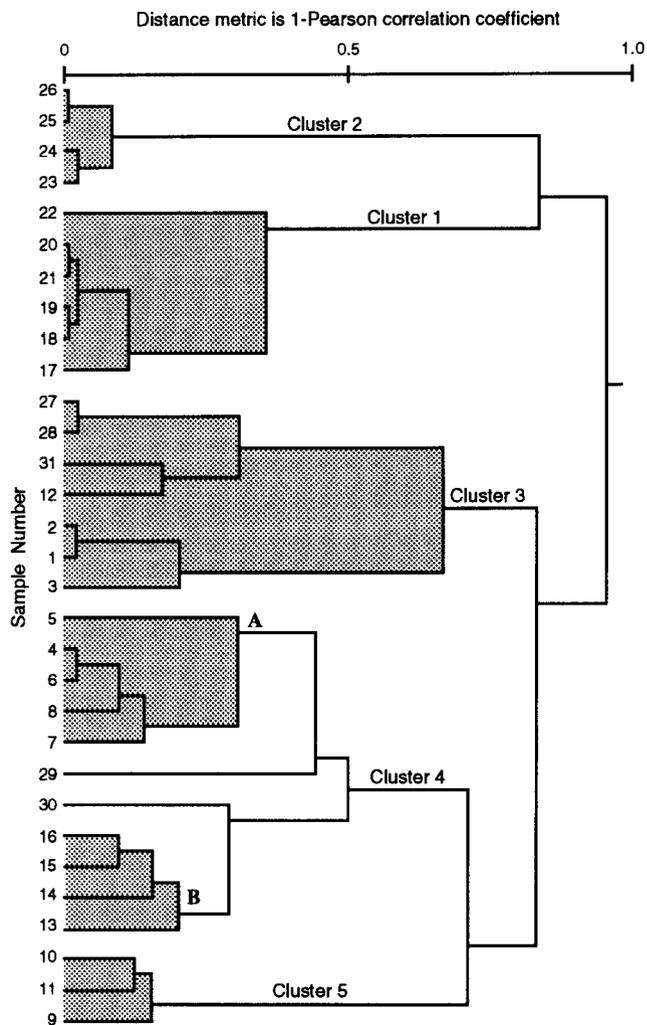distinct clusters can be defined (figure 6).

Figure 6. Cluster analysis (average-linkage clustering) of SBB sediment
trap samples based on the relative abundances of diatom and radiolarian
species or species groups with ≥5% in at least one sample (table 1), and the
log-transformed fluxes of total diatoms, radiolarians, and silicoflagellates (clus-
tering of samples as function of taxon assemblage and total microorganism
flux values).

The clustering of samples reflects the changes in hy-
drography and associated surface production, and species
makeup (figures 6, 7), as follows:

Cluster 1 (late March to mid-June; samples 17–22)
characterizes the spring upwelling period defined by a
shoaling of the thermocline (figure 2), high surface
chlorophyll *a* concentration (Hayward et al. 1994), high-
est diatom and low radiolarian fluxes (figure 4). High
relative abundances of *Chaetoceros radicans* resting spores
(>60%; figure 7A) and *Lithomelissa setosa* (~14%; figure
7B) dominate the diatom and radiolarian assemblages.
Chaetoceros radicans is a common member of the spring
diatom plankton in the southern California area (Cupp
1943), a typically coastal taxon indicative of newly
upwelled waters (Pitcher 1990). *Lithomelissa setosa* is a
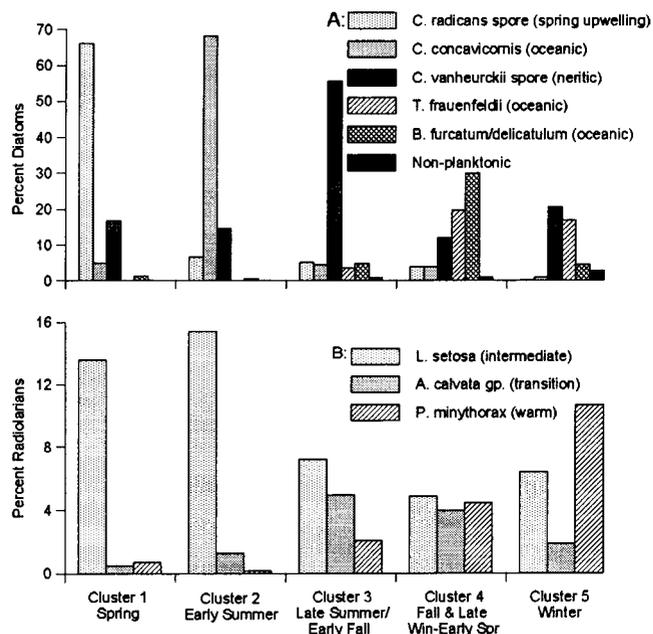deep-living radiolarian (intermediate fauna) brought to

Figure 7. Seasonal succession of selected diatom (A) and radiolarian (B) species and species groups based on the clustering of samples as a function of taxa content. For diatoms, resting spores of *Chaetoceros radicans* indicate the upwelling period; *Chaetoceros concavicornis* and *Bacteriastrum furcatum/delicatulum* are representatives of temperate waters, and *Thalassionema frauenfeldii* is representative of temperate-warm offshore waters. Spores of *Chaetoceros vanheurckii* represent coastal conditions after the spring bloom, mainly summer–fall. The category of non-planktonic diatoms encompasses all marine, epiphytic, epipsammic, benthic, and freshwater taxa (table 1). Selected radiolarian taxa—*Lithomelissa setosa*, *Arachnocorallium calvata* group, and *Pterocorys minythorax*—are indicators of upwelling, California Current waters, and warm waters, respectively.

shallower depths by upwelling. In the region of the California Current system, it lives below the salinity minimum, in cold, high-salinity waters that are upwelled along the California coast (Boltovskoy and Riedel 1980; Kling and Boltovskoy 1995). We believe that the co-occurrence of these two species represents a coastal upwelling-controlled assemblage characteristic of spring.

Cluster 2 (mid-June to August; samples 23–26) represents the early summer, a time when upwelling conditions fade, thermal stratification of the upper waters begins (figure 2), and pigment concentrations start to decline after the spring bloom (Thunell et al. 1995). Moderate radiolarian fluxes and high-moderate diatom fluxes are observed at this time (figure 4). The temporal coverage of this cluster includes the termination of the upwelling period given by a last spike of *L. setosa*, and the transition into summer conditions indicated by increased representation of *Arachnocorallium calvata*, a transition-group radiolarian (figure 7B). Large *Chaetoceros* cells (vegetative cells of *C. concavicornis*), representative of offshore waters (Cupp 1943), become important (relative abundances of ~70%; figure 7A).

Cluster 3 (mid-August to October; samples 1–3, 27, 28, 31) defines the midsummer through early fall pe-

riod, when surface waters in the SBB are warm (>16°C) and there is a strong stratification of the upper ocean (figure 2). Ten-meter chlorophyll a is moderately low (Hayward et al. 1994, 1995), and diatom fluxes are low (figure 4). At this time, the neritic diatom *Chaetoceros vanheurckii* reaches highest relative abundances (spores >50%), and small numbers of warm-water oceanic diatoms occur (figure 7A). A rather mixed radiolarian fauna is present; *L. setosa* abundances decline; and the shallow-dwelling species *A. calvata* and *Pterocorys minythorax* enter the basin (figure 7B).

Cluster 4 includes two groups of samples representative of fall (*cluster 4A*, late September to early December, samples 4–8) and late winter–early spring conditions (*cluster 4B*, February to mid-March, samples 13–16), before the onset of the upwelling period. In the fall, thermal stratification of the upper ocean is still strong, and water temperatures are still high (figure 2). Total radiolarians and warm-water radiolarians show highest fluxes and proportions (figures 4, 7B). The contribution of oceanic diatoms of temperate-warm origins, such as *Thalassionema frauenfeldii* (up to 58%), is greatest at this time (figure 7A). The late winter–early spring is a transitional period between true winter conditions (low temperatures and a deep thermocline), and true upwelling conditions (low temperatures and a shallow thermocline). A diverse flora and fauna is present (figure 5) and is represented by taxa of different ecological affinities (figure 7B). During both of these hydrographic regimes, surface chlorophyll concentrations are generally low (Hayward et al. 1994, 1995), and diatom fluxes are minimal (with the exception of sample 14; see below).

An unexpected diatom flux peak was observed in February 1994 (sample 14; figure 4); it was dominated by long chains of *Bacteriastrum furcatum/delicatulum*, an oceanic species of temperate origin (Cupp 1943), and the radiolarians *A. calvata* group and *L. setosa*. We speculate that this peak is related to a "flood east" circulation pattern described by Hendershott and Winant (1996), and that California Current water with its associated flora and fauna moved into the SBB for a short time (Winant, pers. comm.).

Cluster 5 (December to January; samples 9–11) is characteristic of the winter period, when surface waters in SBB cool and the upper 60–80 m of the water column become nearly isothermal (figure 2); chlorophyll concentrations are low (Hayward et al. 1994). Silicoflagellates peak at this time (figure 4); *Dictyocha fibula* dominates the assemblage. A mixed diatom assemblage composed of temperate-warm oceanic (*Thalassionema frauenfeldii*) and typically coastal taxa (spores of *C. vanheurckii*) is observed (figure 7A). Warm-water radiolaria, as represented by *P. minythorax*, reach highest relative abundances (>10%). Most probably, both warm-water flora and fauna were

brought into the SBB from the Southern California Bight through the eastern mouth of the channel (Hendershott and Winant 1996).

The contribution of non-planktonic diatoms is highest in December (reaching 6% of the entire diatom assemblage). We assume that their presence in the central SBB is associated with high precipitation and runoff into the basin characteristic of the winter rainy season (Soutar and Crill 1977). Of course, resuspension, downslope transport, and redeposition cannot be ruled out (Sancetta 1992), and may explain the moderately high (~20%) contribution of *C. vanheurckii* resting spores.

DISCUSSION

Santa Barbara Basin flux patterns described from the sediment trap data may reflect seasonal changes in upper ocean conditions. In particular, organic carbon and biogenic silica flux records showed distinct fluctuations, with low fluxes in the fall–winter period and high values in spring (upwelling period) that last into the summer. Diatoms dominated the biogenic silica fraction by at least an order of magnitude; they were followed by radiolarians and then silicoflagellates. Fluxes of the three groups showed a clear monthly sequence, with distinct production maxima at different times of the year: radiolarians in late summer and fall, silicoflagellates in winter, and diatoms in spring (figure 4).

Species composition associated with flux peaks differed, reflecting seasonal changes in circulation patterns and the source of water masses in the basin (figure 8). Following Hendershott and Winant's (1996) scheme of synoptic circulation patterns in the SBB, spring upwelling with strong eastward flow is reflected by the high fluxes of deep-living intermediate radiolarian fauna and *Chaetoceros* resting spores (mainly *C. radicans*; Cluster 1), and a shoaling of the thermocline (figure 8). Non-upwelling conditions (i.e., flood east/flood west, and cyclonic flow), summer through winter, with water entering the basin from the west or the east, are represented by a warm, surface-dwelling radiolarian fauna and oceanic diatoms (clusters 2–5); warm surface waters and a deep thermocline are characteristic of this period (figure 8). As an indication of the tight coupling between circulation and microorganism fluxes, a flood east event with California Current waters entering the basin took place in the winter of 1994 (Winant, pers. comm.) and was represented by anomalously high fluxes of temperate oceanic flora and intermediate fauna during an otherwise warm, low-productivity period.

Because the flux records presented here represent only 15 months of data collection, continued monitoring is being carried out to establish whether a seasonal pattern of fluxes and species assemblages does exist in the SBB, and to assess interannual variability in flux patterns.

Preliminary results for 1995–96 point to a repetition of the patterns described above, with high fluxes for the spring–summer period (Thunell, pers. obs.) and *Chaetoceros* species dominating the spring plankton assemblage (Venrick, pers. comm.).

Relevance of Trap Data to the Sediments

Sediment trap and biological oceanographic studies reveal that particle flux from the surface ocean to the deep sea is highly episodic (e.g., Berger and Wefer 1992; Berger et al. 1989), yet in most marine depositional environments, the combination of low sediment-accumulation rates and vigorous benthic mixing does not allow preservation of these short-term events, and makes most deep-sea sediments suitable only for studying millennial-scale climate change. High-resolution studies, with annual-to-century-scale resolution, are best achieved in marginal basins where discrete annual laminations (varves) of accumulating sediment are preserved in an oxygen-depleted depositional environment (see review in Kemp 1996).

According to Sancetta and Calvert (1988), the environment chosen for such a study should be one of high productivity and of marked seasonal variation, where organisms that produce preservable hard parts are a significant component of the plankton and are known to occur in local sediments. Moreover, sedimentation rates should be high so that a year of trap material can be compared directly with the equivalent accumulation in the surface sediments. The SBB represents an ideal setting for such a study. It is part of the CalCOFI time-series grid, and a well-known site for work on physical oceanography (e.g., Hendershott and Winant 1996); surface-water pigment concentration and primary productivity; zooplankton biomass; fish population dynamics (e.g., Hayward et al. 1996; McGowan et al. 1996; California Department of Fish and Game 1996); and the varved sedimentary record (Baumgartner et al. 1992; see review in Lange et al. 1996 and articles in Kennett et al. 1995).

Our results from a 15-month sediment trap study confirm earlier hypotheses that there is a significant intra-annual variability in both the quantity and composition of sedimentary particles delivered to the seafloor in the SBB (e.g., Hülsemann and Emery 1961; Soutar and Crill 1977). This variability plays an important role in the accumulation of sediment laminae. Laminated sediments in the SBB are characterized by intimate juxtaposition of light-colored (light olive to olive) biosiliceous layers and darker-colored (dark olive) layers enriched with terrigenous detritus, reflecting spring–summer and late fall–winter deposition, respectively (Hülsemann and Emery 1961; Emery and Hülsemann 1962; Soutar and Crill 1977; Reimers et al. 1990; Lange et al. 1996).
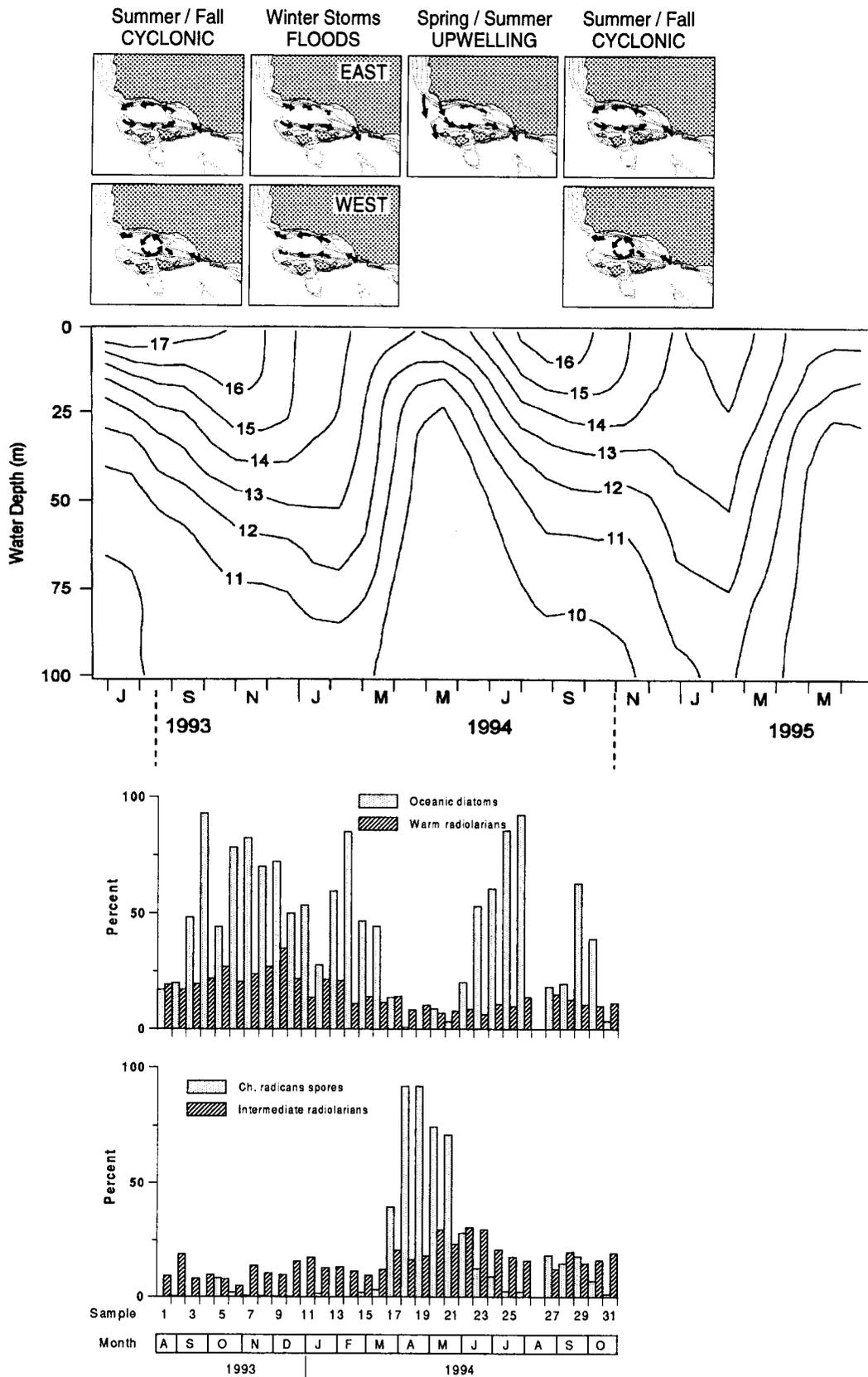
Figure 8. Summary of seasonal synoptic circulation patterns in the SBB (from Hendershott and Winant 1996), temperature profile, and associated diatom and radiolarian species groups representative of upwelling (intermediate radiolarians and Chaetoceros radicans) and non-upwelling (warm radiolarians and oceanic diatoms) conditions.

In the trap, we observed that during late fall and winter more than 80% of the total sediment flux is lithogenic material, while biogenic fluxes are low. This combination results in the deposition of dark laminae. In contrast, biogenic fluxes (organic carbon and silica) are highest and least diluted by detrital material during spring–summer, and we suggest that light laminae are formed at that time. Preliminary results of the 1995–96 trap monitoring program show a similar depositional pattern (Thunell, pers. comm.). Flux maxima of organic carbon and biogenic silica were measured in spring 1995 and 1996, and summer 1995. Lithogenic contribution ranged between 64% and 72% during spring–summer; it reached 86% of the total mass flux in winter 1995–96.

As for the biogenic assemblages contained in the varved sediments of the SBB, we need to know what processes resulted in the creation of any assemblage, and how accurately the fossil assemblage reflects the original living assemblages, before any paleoceanographic interpretation can be attempted.

Diatoms in the trap occur as short chains (e.g., *Pseudonitzschia*, *Chaetoceros*); as aggregates (mainly of *Chaetoceros* resting spores); as complete individual cells (with or without plastids); or as intact valves, or fragments (mainly *Thalassiothrix* and broken setae of *Chaetoceros* and *Bacteriastrum*). The occurrence at our 540-m-deep site of intact delicate radiolarian species (*Cladococcus* spp. and *Sethophormis* spp.), and of weakly silicified diatom species such as *Haslea* sp., *Leptocylindrus danicus*, *Nitzschia bicapitata*, as well as complete cells with chloroplasts argues against any significant dissolution and may reflect fast settling through the water column. Moreover, the fact that these species occur within the topmost surface sediment layer of the SBB in pristine conditions (Lange, pers. obs.) may indicate that dissolution is minimized by rapid descent from surface waters to the subjacent seafloor (sinking velocities > 100 m d^{-1}, Alldredge and Gotschalk 1989; see reviews in Bull and Kemp 1996; and Grimm et al. 1996).

Dissolution of the diatom assemblage does occur immediately below the sediment/water interface (Reimers et al. 1990), and weakly silicified species and the vegetative cells of *Chaetoceros* are rarely preserved in the sedimentary record. In addition, large taxa like the rhizosolenids are usually fragmented. However, and in contrast to other areas (e.g., offshore Oregon: Sancetta 1992; eastern equatorial Atlantic: Lange et al. 1994), the seasonal sequence of events, each characterized by distinctive diatom taxa (figure 7), can be identified in the sediment laminae of the SBB (e.g., Bull and Kemp 1996), as is also the case in Saanich Inlet and the Gulf of California (see review in Sancetta 1996). Commonly observed species in the varves belong to the Thalassiosiraceae and Coscinodiscaceae groups. However, the

Chaetoceros resting-stage assemblage is invariably the one that dominates the sedimentary imprint (Reimers et al. 1990; Bull and Kemp 1996; Grimm et al. 1996; Lange et al. 1996).

Chaetoceros resting spore ooze laminae, including setae-rich sublamina, are prominent in SBB sediment samples. Excellent preservation of fine ornamental structures indicates that they were deposited without being grazed (i.e., fecal pelleting is not the major mechanism of deposition) or affected by significant dissolution (Bull and Kemp 1996; Grimm et al. 1996). Each spore lamina is believed to represent a phytoplankton population that was sedimented by rapidly sinking flocs at the end of a discrete bloom event (Alldredge et al. 1995). The most common species identified in modern flocs (Alldredge and Gotschalk 1989), *Chaetoceros radicans*, is also the commonest species identified in the Pleistocene and Holocene diatom ooze laminae. It was the most abundant diatom taxon in the April plankton of CalCOFI station 82.47, reaching concentrations of 400,000 vegetative cells l^{-1} and about 29,000 resting spores l^{-1} (Venrick, pers. comm.). In the trap, this taxon accounts for 92% of the diatom assemblage from 8 April to 5 May 1994 (samples 18 and 19) and represents the most productive spring season (figures 3, 4, 7, 8). Thus, in the SBB the effect of preservation in the sediment record does not seem to remove information from the most productive season.

ACKNOWLEDGMENTS

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SPAWNING BIOMASS OF THE NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) IN THE GULF OF CALIFORNIA DURING 1991

CELIA EVA COTERO-ALTAMIRANO
Instituto Nacional de la Pesca, CRIP Ensenada
Apartado Postal 1306
Ensenada, Baja California
México

YANIRA GREEN-RUIZ
Instituto Nacional de la Pesca, CRIP Mazatlán
Apartado Postal 1177
Mazatlán, Sinaloa
México

ABSTRACT

The spawning biomass of northern anchovy (*Engraulis mordax*) in the Gulf of California during 1991 was estimated to be 105,079 metric tons (CV = 0.44), as determined by the daily egg production method.

The principal spawning regions were around the large islands in the north and in two smaller regions close to Guaymas in the south.

INTRODUCTION

The populations of small pelagic fishes are characterized by biomass fluctuations (Murphy 1966; Blaxter and Hunter 1982; Pedrín-Osuna et al. 1992). This variability has been attributed both to climatic change and to fishing pressure (Lasker 1981).

Northern anchovy were first detected in the Gulf of California during 1985 by Green-Ruiz and Aguirre-Medina (1989). The discovery of anchovy in the gulf coincided with declines in the availability of sardine and the decline of the sardine fishery in the Gulf of California (Cisneros-Mata et al. 1991; Nevárez-Martínez et al. 1993).

The identification of anchovy larvae in ichthyoplankton samples and the presence of adults in the fishery catches extended the known geographical range of the anchovy to the Gulf of California (Hammann and Cisneros 1989). Since then, approximately 40,000 metric tons of anchovy have been incidentally taken in the sardine commercial fishery (Cisneros-Mata et al. 1991; Nevárez-Martínez et al. 1993). Later paleoecologic studies by Holmgren-Urba and Baumgartner (1993) demonstrated the presence of the anchovy over 250 years, during alternating periods of high anchovy abundance and high sardine abundance in the Gulf of California.

The increased abundance of *Engraulis mordax* made the stock an alternative resource for the fishing industry and a matter of scientific concern in the Gulf of California. Mexican authorities and scientists decided to estimate its spawning biomass in the Gulf of California. This work was undertaken by the Small Pelagic National Research Program of the National Fishery Institute of Mexico.

Spawning biomass of northern anchovy in the gulf was first estimated with the larval census method (LCM) by Green-Ruiz and Aguirre-Medina (1990). Larval census has been the traditional method for estimating spawn-

ing biomass of small pelagic fish (Smith and Richardson 1977) on both the west coast of Baja California (Escudero-Diaz 1976; Olvera-Limas et al. 1983) and in the Gulf of California (Green-Ruiz and Aguirre-Medina 1990). In addition, hydroacoustic estimates of anchovy abundance have been made (Melcer et al. 1976). Data have been collected from fishery catches since the beginning of the incidental fishery (Cisneros-Mata et al. 1991; Nevárez-Martínez et al. 1993).

The daily egg production method (DEPM) for estimating spawning biomass of pelagic fish was developed in 1980 (Parker 1980; Stauffer and Picquelle 1980; Lasker 1985). The DEPM has been used to estimate the size of clupeoid populations in California (Picquelle and Hewitt 1983, 1984; Hewitt 1985a; Bindman 1986; Scannell et al. 1996; Lo et al. 1996); in Peru (Alheit et al. 1984; Santander et al. 1984); in Portugal (Cunha et al. 1992); in Spain (Uriarte and Motos 1991; Garcia et al. 1992; Santiago and Sanz 1992); in Africa (Armstrong et al. 1988); and in Mexico (Torres 1986).

The National Fishery Institute of Mexico decided to use the DEPM for anchovy in the gulf because the method is relatively precise and because of technical difficulties in converting hydroacoustic data to estimates of anchovy biomass. The DEPM was preferred over the larval census approach because it accommodates variability in the reproductive output of adults.

The DEPM offers additional advantages: (1) Ship time and the associated costs of ichthyoplankton samples are reduced because samples are taken once a year in the peak reproductive season, whereas LCM surveys must be conducted throughout the entire year. (2) Biomass estimates are based on biological parameters and are independent of stock assessment models that require indices of relative abundance. (3) The precision of parameters and biomass estimates can be determined (Hewitt 1985b).

The purpose of this study is to estimate the spawning biomass of anchovy (*Engraulis mordax*) in the Gulf of California during the spawning season of 1991 with the daily egg production method.

METHODS

Survey Design

Data used in previous studies for larval census estimates and commercial catch data were used to estimate

the distribution of eggs, larvae, and adult northern anchovy in the Gulf of California, where the peak spawning season is January–February (Green-Ruiz and Aguirre-Medina 1990). Northern anchovy in the gulf spawn until April, and spawning adults have been observed near shore (Cisneros-Mata et al. 1991; Nevárez-Martínez et al. 1993).

Most pelagic fish eggs in the California Current and on the west coast of Baja California are found between the surface and 70-m depth (Hewitt 1983; Smith et al. 1985). The maximum depth of anchovy eggs is related to depth of the thermocline (Ahlstrom 1959).

There have been no studies of vertical distribution of anchovy eggs in the Gulf of California, but the thermocline is at about 100 m in winter (Robinson 1973). All the above-mentioned factors were considered in designing the sampling program for anchovy in the gulf.

Study Area

In 1991, two simultaneous surveys were conducted in the Gulf of California to estimate the spawning biomass of northern anchovy with the DEPM. Two ships (the RV BIP[1] XI and RV BIP XII) were used from January 24 through February 14, 1991.

The survey followed a station plan established by the National Program of Small Pelagics for the Gulf of California. The ichthyoplankton survey started in the north (line 140) and continued south (to line 440) in 30 perpendicular lines separated by 10 nautical miles (n mi). Sampling stations were 5 n mi apart along each line (figure 1).

A total of 352 plankton samples were taken with a CalVET net of 25-cm diameter, 333-micron mesh, and 1.5-m length, retrieved vertically from a depth of 100 m (Smith et al. 1985). Ichthyoplankton samples were taken during both day and night. Samples were fixed with 3% neutral buffered formalin (Moser and Ahlstrom 1985). A Nansen bottle and deep-sea reversing thermometers were used to record temperatures at the surface and at 10-m depth.

Adult Survey

Midwater trawls intended to sample spawning adults were made at 70 stations along both coasts of the Gulf of California (figure 2), with a 4-panel, 47-m-long midwater trawl of 2.5-cm mesh and a vertical and horizontal opening of 27 m. Trawls lasted 30 minutes, mostly at night. Trawls were made when anchovy schools were detected by video echo sounder, following the sampling criteria described by Picquelle (1985) and Smith and Hewitt (1985). The sea-surface temperature was recorded for each trawl.
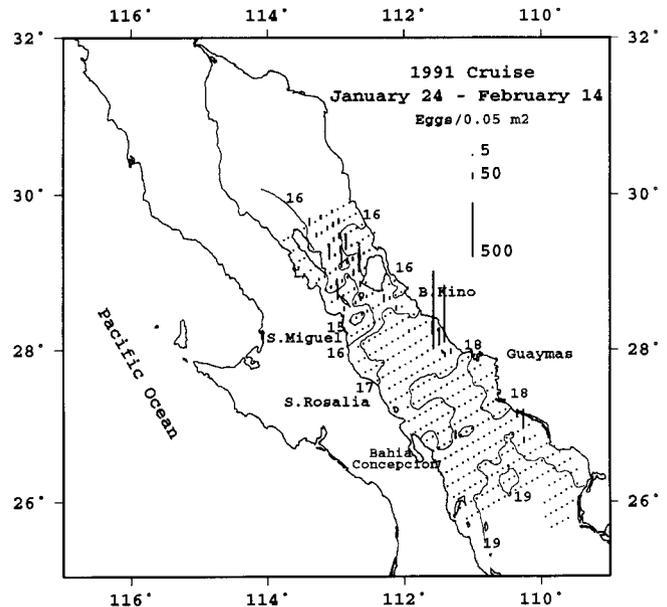
Figure 1. Station plan of the 1991 ichthyoplankton survey and geographic distribution of northern anchovy (*Engraulis mordax*) from CalVET samples, and 10-m isotherms.
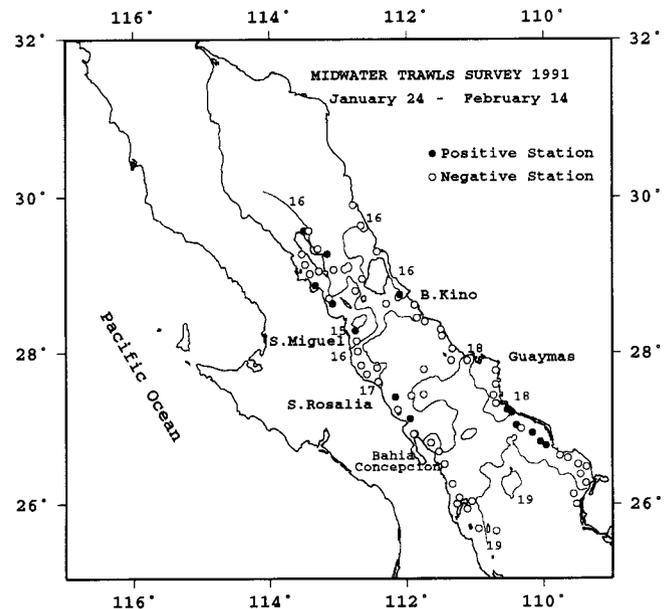

Figure 2. Geographic distribution of trawl stations, positive stations, and 10-m isotherms.

Anchovy were randomly sampled from the trawl catches. The first 50 fish were sexed and measured (standard length). The total weight, gonad-free body weight, and maturity were determined by macroscopic examination. In most cases, gonad-free body weight and maturity were determined from the first 25 mature females (Picquelle and Hewitt 1983). Sometimes additional hydrated females were selected to increase the number of females for fecundity estimates, but these additional samples were not included in the estimate of spawning fraction.

BIOMASS ESTIMATE MODEL

Spawning biomass was estimated with the model developed by Parker (1980) and modified by Stauffer and Picquelle (1980). The spawning biomass is defined as the quotient of the daily production of eggs in the sea and the daily fecundity (per ton of spawners) of the population:

$$B = \frac{kP_0AW}{RSF} \tag{1}$$

Where B = spawning biomass estimate in metric tons;

P_0 = daily egg production rate in number of eggs per day per 0.05 m^2 of sea surface;

A = area of survey in m^2;

W = average weight of mature females in grams;

R = female fraction of the population by weight;

F = batch fecundity in number of eggs;

S = fraction of mature females spawning per day;

k = conversion factor from grams to metric tons (10^{-6} t/g).

An estimate of variance for the biomass assessment was derived with the delta method (Picquelle and Hewitt 1983; Parker 1985; Bindman 1986):

$$\hat{Var}(B) \cong B^2 \left\{ \frac{Var(P_0)}{P_0^2} + \frac{Var(W)}{W^2} + \frac{Var(R)}{R^2} + \right.$$

$$\frac{Var(F)}{F^2} + \frac{Var(S)}{S^2} + 2 \left[\frac{Cov(P_0W)}{P_0W} - \frac{Cov(P_0R)}{P_0R} - \right.$$

$$\frac{Cov(P_0F)}{P_0F} - \frac{Cov(P_0S)}{P_0S} - \frac{Cov(P_0WR)}{WR} -$$

$$\frac{Cov(WF)}{WF} - \frac{Cov(WS)}{WS} + \frac{Cov(RF)}{RF} +$$

$$\left. \left. \frac{Cov(RS)}{RS} + \frac{Cov(FS)}{FS} \right] \right\} \tag{2}$$

where Cov(RS), for example, is the covariance between female fraction and the fraction mature.

DATA PROCESSING

Temperature-Dependent Anchovy Egg Development

Daily egg production was determined from ichthyoplankton samples and the embryonic developmental stage of each egg. Developmental stages were determined by microscopic inspection (Moser and Ahlstrom 1985),

and ages were assigned on the basis of sea temperature at 10-m depth at the sampling station where the eggs were collected, according to a model for temperature-dependent northern anchovy egg development (Lo 1985).

The standard length of preserved larvae (SLP) was measured to the nearest 0.5 mm with a micrometrical ocular. Only larvae smaller than 7.0 mm were included in egg production estimates. Because representative samples of larger larvae cannot be taken with a CalVET net (Lo 1983), age of yolk-sac larvae was estimated from a temperature-dependent growth curve (Zweifel and Lasker 1976).

Egg Production (P_0) and Egg Mortality (Z)

In order to estimate daily egg production and mortality rate, a single equation model (SEM) was fit to the age and the daily production of eggs and larvae (Lo 1986). The SEM integrates the information about eggs and larvae, assuming that eggs and yolk-sac larvae (larvae <5 mm SLP; Zweifel and Lasker 1976) have the same mortality rate. Before the SEM was applied, numbers of eggs and larvae were corrected for duration, retention, extrusion, and avoidance (Lo 1983).

The single equation model is

$$E(\bar{y}i) = P_0 e^{\alpha x_{1i}} \left(\frac{x_{2i}}{u_i} \right)^{-\beta} \tag{3}$$

Where P_0 = daily egg production;

α = daily embryonic mortality rate;

x_{1i} = independent variable

$$x_{1i} = \frac{t_i \quad \text{for} \quad t_i \leq u_1}{u_1 \quad u_1 \leq t_i \leq 20};$$

x_{2i} = independent variable

$$x_{2i} = \frac{u_1 \quad \text{for} \quad t_i \leq u_1}{t_i \quad u_1 \leq t_i \leq 20};$$

t = age of eggs and yolk-sac larvae;

u_1 = maximum age of mortality stanza, when larvae absorbed the yolk sac;

β/t = daily larval mortality rate between 5.5 and 10 mm (fixed length).

For egg samples, the survey area was poststratified into stratum 1 (the area containing positive tows) and stratum 0 (devoid of eggs). Stratum 1 covered 74% and stratum 0 covered 26% of the total area (figure 1).

Adult Parameters

In the laboratory, preserved gonads from both sexes were weighed to the nearest milligram. A sample was taken from the central part of each for histological examination. The samples were dehydrated in alcohol

in gradual steps at concentrations from 70% to 100%. Next, they were soaked in xilene and acetone, and embedded in Amerafin. They were then cut into 5–7-micron sections. The tissue samples were stained with the traditional hematoxylin and eosin histotechnique (Humason 1979).

Each gonad was analyzed and classified histologically in order to estimate the fraction of females and males that were mature, and to measure spawning rate for histological classification (Hunter and Goldberg 1980; Hunter and Macewicz 1985; Macewicz et al. 1996; Cotero-Altamirano 1987).

Batch Fecundity

The number of eggs spawned by spawning batch—the batch fecundity—was estimated from the number of hydrated oocytes in the ovary (Hunter et al. 1985). All hydrated females from the adult survey were used to estimate batch fecundity. Both ovaries from each female were examined histologically to identify females that had begun to ovulate and spawn (ovaries with hydrated oocytes and new postovulatory follicles). We eliminated these females to avoid underestimating batch fecundity. We tested for how location of tissue sample affected batch fecundity estimates, but found that fecundity estimates were not affected by sampling location. We estimated mean batch fecundity from data for 63 hydrated females and then determined the relation between batch fecundity and gonad-free weight by linear regression.

We estimated adult parameters: female weight (W), batch fecundity (F), spawning fraction (S), and sex ratio (R) from anchovy caught by midwater trawl. We used weighted sample mean variance estimators (Picquelle and Stauffer 1985):

$$\bar{\bar{y}} = \frac{\sum_{i=1}^{n} m_i \bar{y}_i}{\sum_{i=1}^{n} m_i} \qquad (4)$$

$$\text{Vâr } \bar{\bar{y}} = \frac{\sum_{i=1}^{n} m_i^2 (\bar{y}_i - \bar{\bar{y}})^2}{\left(\sum_{i=1}^{n} \frac{m_i}{n}\right)^2 n(n-1)} \qquad (5)$$

Where m_i = number of fish subsampled from the ith trawl;

n = number of positive trawls;

$\bar{y}_i$ = average for the ith trawl = $\sum_{j=1}^{mi} \frac{y_{ij}}{mi}$;

y_{ij} = observed value for the jth fish in the ith trawl.

RESULTS

Oceanography and Distribution of Anchovy Eggs

During the survey, temperature at 10 m ranged from 14.5° to 19°C. We observed two cold-water masses, one in the north from Angel de la Guarda Island to Cape San Miguel and the other near the Sonora coast in front of Punta Kino (figure 1).

The ichthyoplankton survey took 382 samples; 92 were positive for anchovy eggs. The principal spawning region was in the north around the large islands. Anchovy eggs were also found in two smaller regions close to Guaymas in the south (figure 1).

Daily Egg Production

The estimated daily egg production (P_0) was 7.8 eggs/0.05/m²/day (CV = 0.33), and the estimated daily embryonic mortality rate (Z) was 0.35/day (CV = 0.17; figure 3, table 1).

Adult Distribution

The adult survey consisted of 70 midwater trawls; 14 were positive for anchovy. Adults were found where surface temperatures ranged from 15.4° to 17.8°C. The greatest abundance of adults was in the north around large islands, and southward near Guaymas (figure 2). The distribution of schools of spawning anchovy coincided with the distribution of eggs (figures 1, 2).

Length and Maturity

The length of female adults in the samples ranged from 90 to 125 mm, mean 105 mm (CV = 0.25). Length of male adults ranged from 93 to 124 mm, mean 103
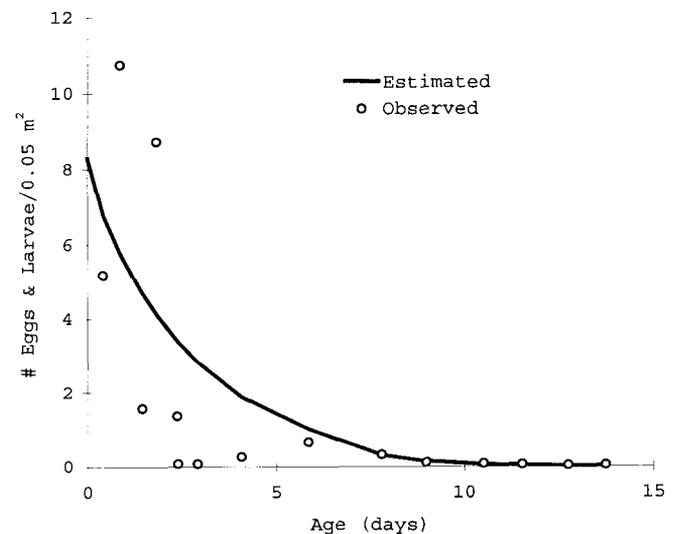

Figure 3. Embryonic mortality curve for northern anchovy (*Engraulis mordax*) eggs and yolk-sac larvae from the 1991 daily egg production method survey.

TABLE 1
Abundance by Size and Age of 1991 Field-Caught Anchovy Eggs (E) and Larvae, Used to Estimate Daily Egg Production (P_0) and Instantaneous Mortality Rate (z)

Size[a] (mm)	Age (days)	No. of eggs or larvae/0.05 m²
E	0.409	5.1900
E	0.853	10.7500
E	1.448	1.5790
E	1.834	8.7300
E	2.369	1.3610
2.67	2.380	0.0765
3.12	2.900	0.0701
3.69	4.070	0.2745
4.24	5.860	0.6643
4.79	7.800	0.3294
5.32	8.990	0.1148
5.85	10.510	0.0842
6.37	11.530	0.0517
6.89	12.750	0.0348
7.4	13.740	0.0310

[a]Fixed length (corrected)

Figure 4. Standard length distribution for northern anchovy (*Engraulis mordax*) taken in all trawls. Females (*open bars*); males (*filled bars*).

mm (CV = 0.19; figure 4). We defined "first maturation" as "when 50% of the famales are mature." We used logistic regression to determine the length at 50% mature. Females taken in the survey were 50% sexually mature at a standard length of 104.7 mm; males at 102 mm (figure 5). The length at 50% maturity for the anchovy in the Gulf of California was less than that estimated for the Pacific coast (table 2).

Female Weight

Before estimating average female weights, we corrected the weight of hydrated females in the sample for bias due to the presence of females with hydrated ovaries (Picquelle and Stauffer 1985). We adjusted weights with a regression of whole-body weight on ovary-free weight estimated for females without hydrated ovaries,

$$W = -0.7369 + 1.155\omega \qquad (6)$$

where ω is the ovary-free weight ($R^2 = 94.2\%$). The estimated average female weight was 13.4, with a variance of 0.0643.

Batch Fecundity

The batch fecundity for each mature female was estimated by regression of batch fecundity on ovary-free
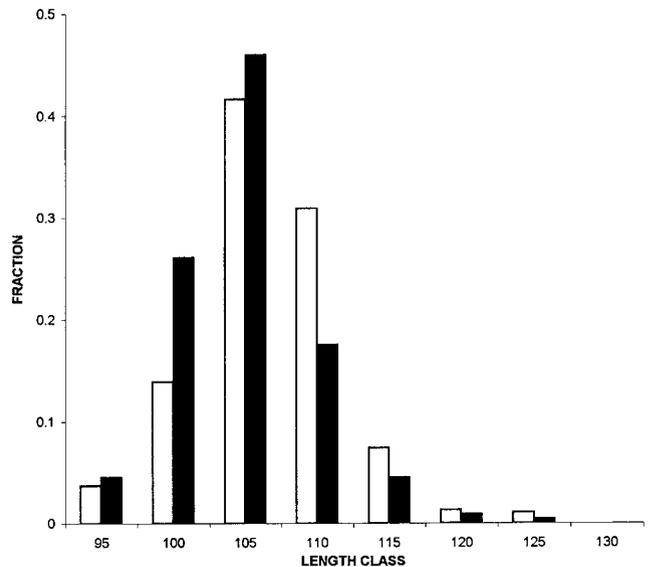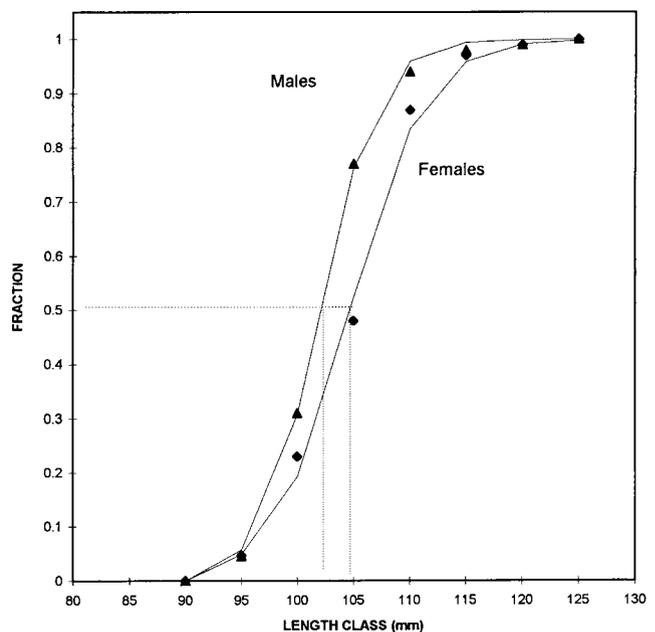

Figure 5. Fraction of northern anchovy (*Engraulis mordax*) females and males that were sexually mature as a function of standard length. *Dotted lines* are estimated length at which females (104.7 mm) and males (102 mm) were mature.

TABLE 2
Length at Maturity of *Engraulis mordax* off the California and Baja California Coasts and in the Gulf of California

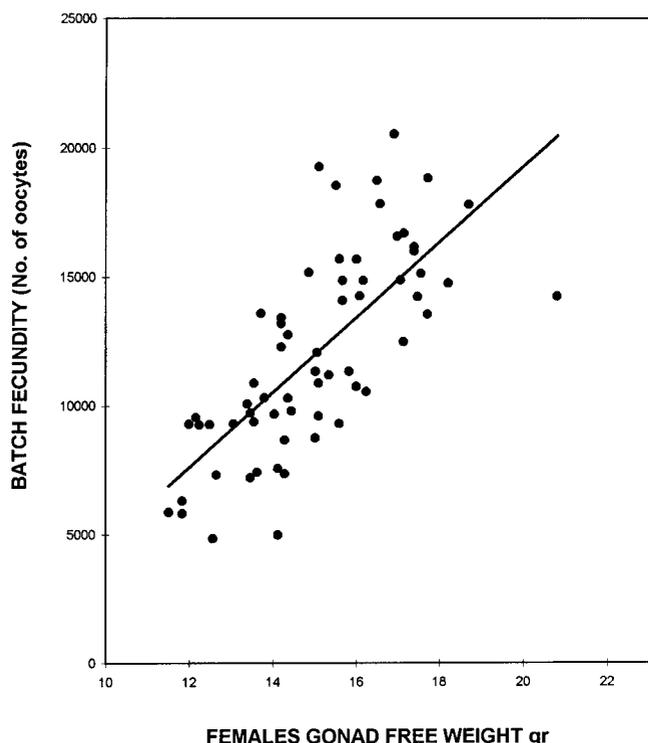|	Length at maturity (mm)			
	Female	Male	Both	Authority
Baja California west coast			130	Clark and Phillips 1952
Oregon, Washington	107	104		Laroche and Richardson 1980
Central California			96	Hunter and Macewicz 1980
Ensenada, B.C.	111	98		Cotero-Altamirano 1987
Gulf of California	104.7	102		Authors' survey

FEMALES GONAD FREE WEIGHT gr

Figure 6.   Linear regression of batch fecundity on ovary-free weight fitted to females with hydrated eggs.

weight as estimated for a sample of 63 hydrated females (without new postovulatory follicles) taken during the survey.

The relation between female ovary-free weight (W) and batch fecundity (F) was:

$$F = -9897 + 1458W \qquad (7)$$

where $R^2 = 53\%$, and the female ovary-free weight ranged from 11.5 to 20.8 g (figure 6).

We used equation 7 to estimate batch fecundity for all mature females from each trawl. The mean batch fecundity for mature females in trawl samples was estimated to be 8,220 oocytes (CV = 0.079).

Spawning Fraction

The average fraction of females spawning per day was 0.174/day (CV = 0.20), estimated from females that spawned the night before capture.

Sex Ratio

Sex ratio is the fraction of females in the anchovy stock based on fish weight. For northern anchovy in the gulf during our survey, the estimated sex ratio was 0.68 (CV = 0.027).

Biomass Estimate

The spawning biomass estimate was 105,079 metric tons (CV = 0.44). Estimates of the rate of egg mortality and adult reproductive parameters are summarized in table 3.

DISCUSSION

Peak spawning time was estimated to be 2200 hours, based on 1991 data similar to that for the anchovy off California (Picquelle and Hewitt 1983). To estimate the peak spawning time, we followed the procedures used by Lo et al. (1996) for Pacific sardine, in which the 50th percentile of the cumulative proportions of stage 2 eggs since sunset (1800) was assumed to be the peak capture time for stage 2 eggs (figure 7). The peak spawning time was computed as: 50th percentile of capture time from sunset − the age of stage 2 eggs + the sunset time = $11 - 7 + 18 = 2200$ hrs.

In 1991, the temperature of the sea at 10-m depth ranged from 14.5° to 19.0°C (average 17.6°). Green-Ruiz and Hinojosa-Corona (in press) found that *Engraulis mordax* spawns at higher temperatures in the Gulf of California than off the California coast, and found the highest abundance of eggs at 17°.

We compared spawning biomass estimates from our survey with values obtained in 1987 by means of the larval census method (Green-Ruiz and Aguirre-Medina

TABLE 3
Estimates of Daily Egg Production and Adult Reproductive Parameters for Spawning Biomass of
E. mordax in the Gulf of California for 1991, from Daily Egg Production Method

| Parameters		Mean	Variance	Coefficient of variation
Daily egg production (10^{12} eggs/day)	P_0A	7.49	4.9×10^6	0.44
Average female weight (g)	W	13.64	0.06425	0.019
Batch fecundity (eggs/batch/mature female)	F	8220	4.2×10^5	0.079
Spawning fraction (spawning females/total females)	S	0.174	1.28×10^{-3}	0.206
Sex ratio (females/total)	R	0.68	3.31×10^{-4}	0.027
Daily specific fecundity (eggs/g biomass/day)		72		
Spawning biomass (metric tons)	B	105,079	2.18×10^9	0.445
Egg mortality rate	z	0.35	3.54×10^{-3}	0.17
Average temperature (°C)		17.6		
Average temperature of positive stations (°C)		16.4		
Positive stations (%)		21.0		
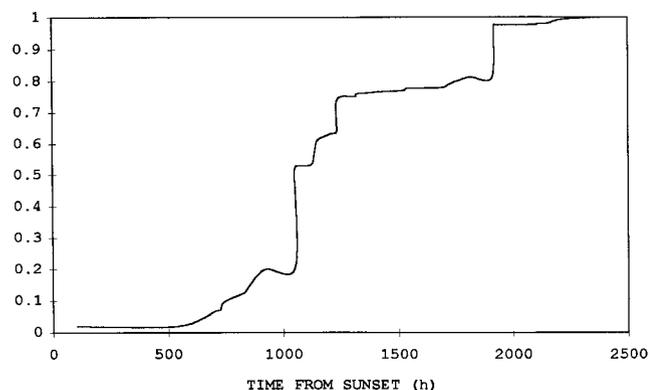
Figure 7. Cumulative proportion of time from sunset (1800) for stage 2 northern anchovy (*Engraulis mordax*) eggs during survey.

1990). The difference (106,000 t vs 421,000 t) indicates that the two methods yield comparable results, but detailed comparison is not possible because the estimates were for different years.

The coefficient of variation (0.44) for our biomass estimate was high, mainly because our estimate of egg mortality (z) was relatively imprecise (CV = 0.17), partly because it came from a single-equation model where both egg and larval data were used. Otherwise, the estimate of the mortality rate may have a higher variance because the distribution of eggs in the sea is patchy, and too few eggs in early stages were caught (Smith 1981).

Comparisons between Gulf and West Coast Stocks

Anchovy in the Gulf of California are less abundant than off California. Biomass in the gulf ranged from 12% to 34% lower than estimates for the Pacific coast. The egg mortality rate for anchovy in the Gulf of California was higher than that estimated for anchovy along the Pacific coast of California during 1981–85. Only in 1980 was the California estimate higher. Adult parameters for anchovy in the gulf were generally similar to estimates for anchovy off California (table 4).

The small pelagic fishes in the Gulf of California vary

in abundance. It is therefore necessary to continue assessing the anchovy population in order to understand the dynamic behavior of this important species in the Gulf of California.

ACKNOWLEDGMENTS

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TABLE 4

Time Series of Egg Production Parameters for Estimating Spawning Biomass of *E. mordax* in the California Current (1980–85)[a] and in the Gulf of California (1991)

Parameters		1980	1981	1982	1983	1984	1985	1991
Daily egg production (10^{12}) eggs/day)	P_0A	26.34	20.96	13.51	17.25	12.98	16.95	7.49
Egg mortality rate	Z	0.45	0.14	0.16	0.18	0.17	0.29	0.35
Average female weight (g)	W	17.44	13.37	18.83	11.20	12.02	14.50	13.64
Batch fecundity (eggs)	F	7,751	8,329	10,845	5,297	5,485	7,343	8,220
Spawning fraction	S	0.142	0.106	0.120	0.094	0.160	0.120	0.174
Sex ratio	R	0.478	0.501	0.472	0.549	0.582	0.609	0.68
Daily specific fecundity (eggs/g)	F/W	444	623	576	473	456	501	603
Spawning biomass (10^3 t)	B	870	635	415	652	309	522	105

[a]Bindman 1986.

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INSHORE SOFT-BOTTOM FISHES OF TWO COASTAL LAGOONS ON THE NORTHERN PACIFIC COAST OF BAJA CALIFORNIA

JORGE A. ROSALES-CASIÁN[1]
Grupo de Ecología Pesquera
Departamento de Ecología
División de Oceanología
CICESE
Apartado Postal 2732
Ensenada, B.C.
México

ABSTRACT

Two series of monthly trawls were made: from May 1992 to April 1993 at Estero de Punta Banda and during 1994 in Bahía de San Quintín, Baja California (Mexico). Seasonal samplings in both places were made during 1994 only. The stations in the two embayments were situated at 5 and 10 m; four replicate beam-trawl tows were made per station. A total of 160 tows was made, and 45 fish species were collected. The most important species in the ichthyofaunal community of Estero de Punta Banda differed from those in Bahía de San Quintín. In Estero de Punta Banda, three economically important species were dominant by the index of community importance (ICI) ranking (relative abundance and frequency of occurrence): *Paralichthys californicus*, *Paralabrax clathratus*, and *Paralabrax nebulifer*. In Bahía de San Quintín, the 5-m-depth catches were dominated by (ICI rank) *Syngnathus leptorhynchus*, *P. californicus*, and *Symphurus atricauda*; at 10 m *S. atricauda* was most important, followed by the other two species in the same order. Total annual catches were highest at 5 m and intermediate at 10 m in San Quintín, and lowest at 5 m in Punta Banda. The abundance by trawl and the standing crop were high during November and December in Punta Banda. In San Quintín, upwelling influence on fish abundance and biomass distribution is indicated by high abundance at 5 m when the temperature decreases, and low abundance when the temperature increases. At 10 m, abundance and biomass follow the same pattern of change as temperature. The low density (annual 558 fish/ha) in Estero de Punta Banda contrasted with the highest standing crop, both annual (17,355 g/ha) and monthly (November, 50,387 g/ha), compared to San Quintín at 5 m (annual 916 fish/ha; annual standing crop 10,002 g/ha; monthly standing crop 33,621 g/ha in November, too). In the seasons of 1994, no differences between areas and depths were found in catch parameters, except in the standing crop. Differences may be due to interannual variability. Owing to the nearly pristine condition of Estero de Punta Banda and Bahía de San Quintín, and their potential as nursery grounds

and for dispersion of ecologically and economically important fishes to repopulate to the north, both areas should be protected.

INTRODUCTION

The Pacific coast of Baja California is important to a number of fish communities. It is considered a transition zone between southern and northern ichthyofauna; it is a spawning zone for transboundary species; and it is frequented by commercial and recreational fisheries (Hubbs 1960; Escobar-Fernandez and Arenillas-Cuetara 1987; Moser and Watson 1990; Love 1991; Danemann and De la Cruz-Aguero 1993; Moser et al. 1993; Arenas et al. 1996; CDFG 1996). Many species found in California waters are also abundant in Baja California and, in fact, may have their centers of distribution there (Moser et al. 1993). Baja California may serve as a source of larvae, juveniles, and adults for California waters. The sparse development of the Baja California coastline and the relative paucity of fish studies contrasts markedly with the situation for southern California.

Coastal lagoons serve as nurseries for many fish species. High food production, a relatively higher temperature, and decreased predation risk are some of the benefits to fish in these areas (Kneib 1987; Kramer 1990). The lagoons are often dominated by species that move into estuaries for feeding, growth, or protection (Yañez-Arancibia 1985) during specific stages of their lives, and then move offshore (Monaco et al. 1990). Thus fishes represent an important link between estuaries and coastal zones (Deegan 1993).

Along the northern Pacific coast of Baja California, Estero de Punta Banda and Bahía de San Quintín are the two most extensive lagoons. The estero was a nearly pristine environment until 1984, when a dike built by an oil company isolated an area of 0.21 km² from the tidal regime; fortunately the main channel was not dredged and the main circulation was not disrupted before the activities were stopped. In 1987, a hotel was developed on the sand bar, and together with the dike modified 2.2 km² of the area's total 21 km². Nonetheless, the estero persists as an ecologically important place for invertebrates, fishes, and birds (Ibarra-Obando and Escofet 1987; Ibarra-Obando and Poumian-Tapia 1991, 1992).

In Bahía de San Quintín, an oyster culture has been developed for years, mainly situated in Bahía Falsa. The arm named Bahía de San Quintín includes a few houses and the Old Mill Hotel, but no drainages empty into the bay. Development pressure persists: a marina was proposed for the whole Estero de Punta Banda, and a tourist resort was proposed for the western sand bar of San Quintín. Fortunately, both projects were abandoned.

While the seagrass (Ballesteros-Grijalva and García-Lepe 1993; Poumian-Tapia 1995), invertebrate (Barnard 1970; Calderón-Aguilera 1992; Buenrostro-Lopez 1996), and bird communities (Sounders and Sounders 1981; Wilbur 1987; Ward et al. 1991; De la Cueva and Fernandez 1996; Fernandez-Aceves 1996) of these lagoons have been studied, very few studies on fishes have been published. Works on the fish fauna of Bahía de Todos Santos and Estero de Punta Banda were reviewed by Hammann and Rosales-Casián (1990). Except for the record of an endemic species, *Paraclinus walkeri* (Hubbs 1952; Rosenblatt and Parr 1969), and a recent species checklist (Rosales-Casián 1996), nothing has been published on the fishes of San Quintín.

The objective of this study was to describe the fish assemblages of the shallow, soft-bottom habitat of these two northern Baja California coastal lagoons.

STUDY AREAS

Estero de Punta Banda (31°40'–31°48'N, 116°04'–116°40'W), is an L-shaped coastal lagoon (figure 1) covering 21 km^2, with a narrow mouth (<200 m) and a natural channel (<8 m deep). It is situated in the southeast margin of Bahía de Todos Santos–Ensenada (123 km south of U.S. border), and is separated from the bay by a 7.5-km-long sand bar. It is a protected habitat containing *Zostera* and *Spartina* beds (3.3 km^2), mud and sand flats, and small channels (Ibarra-Obando and Poumian-Tapia 1991, 1992). The nearest coastal upwelling from Estero de Punta Banda is located about 15 km away (Cota 1971; Chavez de Ochoa 1975).

Bahía de San Quintín is 200 km south of Ensenada, 30°24'–30°30'N and 115°57'–116°01' W (figure 1). This bay has an area of 4,000 ha, and is divided into a western arm called Bahía Falsa, and an eastern arm, Bahía de San Quintín. The bay communicates with the sea through a mouth less than 1,000 m wide and 2–7 m deep (Contreras 1985; Ballesteros-Grijalva and García-Lepe 1993). Both arms are protected by sand bars. However, during high tides and high waves, the water can cross the narrow part of the Bahía Falsa sand bar. A third zone is the head of Bahía de San Quintín; divided by a breakwater, it creates shallow (<2 m), warm, and saline waters (Alvarez-Borrego et al. 1975). This backwater exhibits a lesser tide amplitude and height, and low current velocity (Del Valle-Lucero and Cabrera-
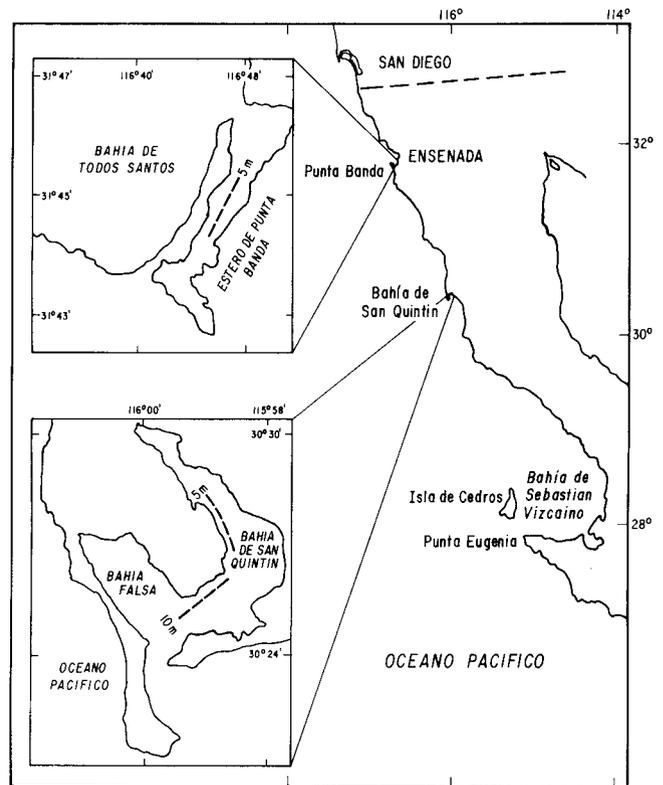

Figure 1. Beam-trawl sampling sites (Estero de Punta Banda and Bahía de San Quintín) in northern Pacific off Baja California, México.

Muro 1981a, b). A strong upwelling occurs throughout much of the year close to the mouth (Dawson 1951).

Because there is little rainfall, salinity and temperature values increase from the mouth toward the head of each lagoon (Chavez de Nishikawa and Alvarez-Borrego 1974; Celis-Ceseña and Alvarez-Borrego 1975; Ballesteros-Grijalva and García-Lepe 1993). Both lagoons are strongly influenced by tides (Alvarez-Borrego et al. 1977; Pritchard et al. 1978).

MATERIALS AND METHODS

Sampling Methods

In the Estero de Punta Banda, samplings were made monthly from May 1992 to April 1993; in Bahía de San Quintín they were made throughout 1994. Additional seasonal samplings in the estero were made during February (winter), May (spring), July (summer), and November (fall) of 1994. Collections were made with a beam trawl (Kramer and Hunter 1987; Kramer 1990; Allen and Herbinson 1990, 1991) on the soft bottom of Punta Banda and in the San Quintín channels (figure 1). The beam trawl (1.6 m by 0.4 m, 3-mm mesh netting) was towed at 1.5 knots for five minutes. Four replicate tows were made parallel to shore at 5 m in Punta Banda and

at 5 and 10 m in San Quintín. A wheel with a revolution counter recorded the distance. When possible, distance was measured with a second wheel counter on the beach, by following the boat.

All fish were identified (Miller and Lea 1972; INP 1976), and family Clinidae was determined by the descriptions of Rosenblatt and Parr (1969). Fish biomass was recorded to ±0.1 g for fishes weighing up to 150 g, and to ±1.0 g for heavier fishes. At each trawl end, temperature (°C) was measured at the surface and near the bottom.

Data Analysis

The distance was based on the average attained by all "good" tows according to distances along the beach; low or high readings caused by fouling or damage to the meter were discarded. The sampled area was computed as the product of the distance towed and the beam-trawl width (1.6 m; Allen and Herbinson 1990; Kramer 1990; Allen and Herbinson 1991). The average area per tow in Punta Banda was 341 m^2; in San Quintín it was 429 m^2 (5 m), and 421 m^2 (10 m).

For each site, I computed the total fish caught and their biomass; total numbers caught per species; relative abundance; frequency of occurrence, abundance, and biomass per trawl; density (no./ha); and standing crop (g/ha).

To determine differences in catch patterns with time and between depths and areas, I transformed the data from each replicate monthly trawl to log (x+1) prior to ANOVA analysis. I used the simple linear Pearson correlation between temperature (bottom and surface) and abundance to measure the degree of association (Zar 1984). To estimate the contribution of each species to its assemblage, I used the index of community importance (ICI; Stephens and Zerba 1981; Love et al. 1986). The ICI was obtained by the sum of the percent of abundance and frequency-of-occurrence rankings; afterwards, I reranked the species. I used Kendall's rank correlation to compare the top ten species (abundances and ICI ranking) from each assemblage (Siegel 1956).

RESULTS

Temperature

In Estero de Punta Banda (1992–93), temperatures at 5 m were highest in August (24.1°C, ±SD 0.3) and lowest in December (14.5°C ±0.6; figure 2A), with an overall mean of 18.9° (±2.7). Seasonal mean temperatures in 1994 were 16° (February), 17.2° (May), 22.8° (July), and 14.7° (November), with an overall mean of 17.7°, ±3.2.

In contrast, in Bahía de San Quintín there were two temperature maxima and minima; at 5 m, a first peak
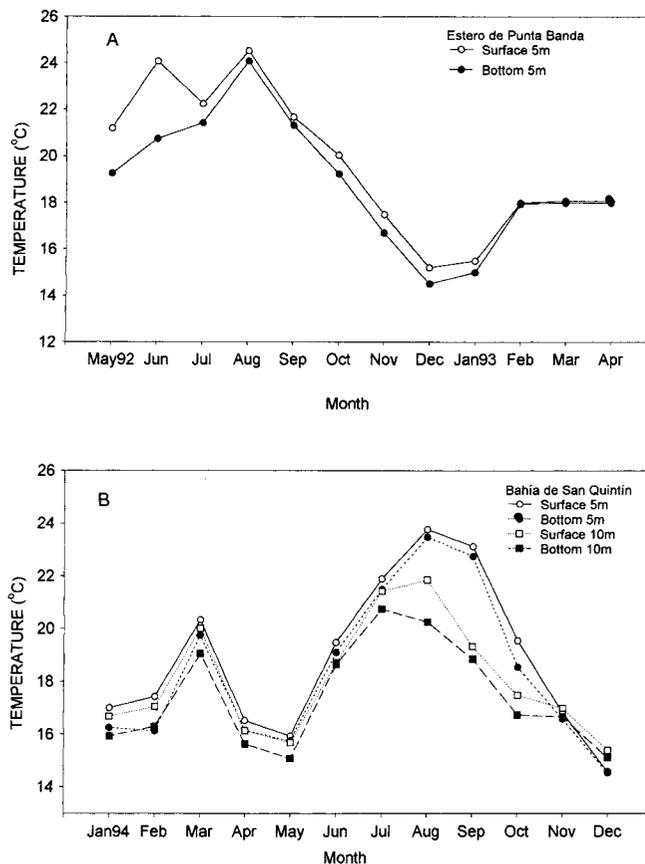

Figure 2. Mean monthly temperatures at sites surveyed. May 1992–April 1993 in Estero de Punta Banda (A), and 1994 in Bahía de San Quintín (B).

occurred in March (19.8°, ±0.2), and a second in August (23.5°, ±0.2). At 10 m, the first peak also occurred in March (19.1°, ±0.2), the second in July (20.8°, ±0.6). Lowest temperatures (figure 2B) were observed first during an upwelling event in May (15.1°, ±0.3), and during the cold month of December (15.1°, ±0.1).

Sampling Effort

Forty-eight trawls were taken during 1992–93 in Estero de Punta Banda (5 m only), and sixteen trawls as seasonal samplings during 1994. In Bahía de San Quintín, ninety-six trawl samplings (5 and 10 m) were taken in 1994.

Species Composition by Areas

In Punta Banda (1992–93), a total of 926 fish was caught belonging to 25 species (table 1). Most common species were kelp bass (Paralabrax clathratus), bay blenny (Hypsoblennius gentilis), bay pipefish (Syngnathus leptorhynchus), and California halibut (Paralichthys californicus). The halibut had the highest occurrence, 87.5%, and ranked highest by the ICI, followed by kelp bass and barred sandbass (Paralabrax nebulifer).

At 5 m in Bahía de San Quintín (1994), 1,929 fishes were caught from 30 species (table 2). Bay pipefish were abundant, appearing in 77% of the tows. Shiner perch (*Cymatogaster aggregata*) were second, followed by cheek-spot goby (*Ilypnus gilberti*) and California tonguefish (*Symphurus atricauda*). California halibut were fifth in abundance, but they were taken in 68.8% of the tows. These species composed 76.6% of the total catch, and occurred in more than 40% of the tows. Bay pipefish, California halibut, California tonguefish, and cheekspot gobies dominated this isobath by ICI (table 2). We took one specimen of the endemic *Paraclinus walkeri*.

At 10 m in Bahía de San Quintín, a total of 1,125 fishes were collected, belonging to 28 species (table 3). The California tonguefish and bay pipefish were the most abundant species. The slough anchovy (*Anchoa delicatissima*) was taken infrequently but in relatively large numbers. These three species, comprising 57% of the total, were caught in one-third to more than one-half of the tows, and constituted the top ICI rankings; California tonguefish was first. Four specimens of the endemic *P. walkeri* were also collected at this depth (table 3).

Rank correlation tests between assemblages indicate a high similarity between depths in Estero de Punta Banda (5 m) and Bahía de San Quintín (5 and 10 m on the basis of the relative abundances of species (Kendall's tau = 1.0, $p = 0.000$), and the top ten ICI-ranking species (Kendall's tau > 0.977, $p = 0.000$).

Abundance and Biomass

In Punta Banda (1992–93), abundances increased in October and peaked in December (62 fish/trawl, ±SE 8). Otherwise they ranged from 1.5 to 15 fish/trawl (figure 3). The overall mean was 19 fish/trawl (±4). Abundance varied significantly with time (ANOVA, $p = 0.000$). No correlation between abundances and bottom temperature ($r = -0.225$, $p = 0.124$) was found. Overall biomass was 593 g/trawl ±364, and was highest in November (1,720 g/trawl ±635), lowest (29 g/trawl ±3) in April (figure 4) and varied significantly with time ($p = 0.001$). No significant correlation was found between biomass and temperature ($r = -0.225$, $p = 0.124$).

In San Quintín (1994), abundances were highest at 5 m in May (91 fish/trawl ±SE 37) and November (84 fish/trawl), and lowest (5 fish/trawl ±2) in January (figure 5). The bay pipefish (*S. leptorhynchus*) constituted 48.3% of total abundance in May and 63.4% in November. The overall mean was 39 fish/trawl (±6). Abundance varied with time (ANOVA, $p = 0.000$), and no significant correlation was found with bottom temperature ($r = -0.114$, $p = 0.441$). Biomass was highest (1,442 g/trawl ±512) in November, and lowest (3 g/trawl ±3) in January (figure 5). The overall mean was 429 g/trawl (±80). Biomass at 5 m varied significantly with time ($p = 0.000$), and was not significantly correlated with bottom temperature ($r = -0.000$, $p = 0.998$).

TABLE 1

Composition of Beam-Trawl Catches (5-m Depth) by the Index of Community Importance (ICI) in Estero de Punta Banda, B.C., México (May 1992 to April 1993)

Species	Number	% Relative	Rank	% FO	Rank	ICI
Paralichthys californicus	105	11.34	4.0	87.50	1.0	5.0
Paralabrax clathratus	353	38.12	1.0	33.33	5.0	6.0
Paralabrax nebulifer	58	6.26	5.0	45.83	2.0	7.0
Pleuronichthys ritteri	56	6.05	6.0	41.67	3.0	9.0
Hypsoblennius gentilis	119	12.85	2.0	29.17	7.0	9.0
Syngnathus leptorhynchus	107	11.56	3.0	14.58	8.0	11.0
Hypsopsetta guttulata	23	2.48	8.0	35.42	4.0	12.0
Paralabrax maculatofasciatus	32	3.46	7.0	31.25	6.0	13.0
Cymatogaster aggregata	22	2.38	9.0	12.50	9.0	18.0
Xenistius californiensis	13	1.40	10.0	8.33	11.0	21.0
Heterostichus rostratus	11	1.19	11.0	8.33	11.0	22.0
Anisotremus davidsonii	6	0.65	12.0	6.25	12.0	24.0
Symphurus atricauda	4	0.43	13.5	8.33	11.0	24.5
Seriphus politus	2	0.22	15.5	4.17	13.0	28.0
Oxyjulis californica	4	0.43	13.5	2.08	19.0	32.5
Anchoa compressa	2	0.22	15.5	2.08	19.0	34.5
Hypsoblennius jenkinsi	1	0.11	21.0	2.08	19.0	40.0
Girella nigricans	1	0.11	21.0	2.08	19.0	40.0
Hypsypops rubicundus	1	0.11	21.0	2.08	19.0	40.0
Menticirrhus undulatus	1	0.11	21.0	2.08	19.0	40.0
Plathyrinoidis triseriata	1	0.11	21.0	2.08	19.0	40.0
Scorpaena guttata	1	0.11	21.0	2.08	19.0	40.0
Atractoscion nobilis	1	0.11	21.0	2.08	19.0	40.0
Porichthys myriaster	1	0.11	21.0	2.08	19.0	40.0
Leptocottus armatus	1	0.11	21.0	2.08	19.0	40.0
Totals	926	100.0				

TABLE 2
Composition of Beam-Trawl Catches (5-m Depth) by the Index of Community Importance (ICI)
in Bahía de San Quintín, B.C., México (January to December 1994)

Species	Number	% Relative	Rank	% FO	Rank	ICI
Syngnathus leptorhynchus	790	40.95	1.0	77.08	1.0	2.0
Paralichthys californicus	137	7.10	5.0	68.75	2.0	7.0
Symphurus atricauda	162	8.40	4.0	56.25	3.0	7.0
Ilypnus gilberti	183	9.49	3.0	47.92	5.5	8.5
Cymatogaster aggregata	205	10.63	2.0	39.58	8.0	10.0
Hypsoblennius gentilis	87	4.51	7.0	54.17	4.0	11.0
Embiotoca jacksoni	127	6.58	6.0	41.67	7.0	13.0
Hypsopsetta guttulata	55	2.85	8.0	47.92	5.5	13.5
Hypsoblennius jenkinsi	40	2.07	9.0	33.33	9.0	18.0
Porichthys myriaster	33	1.71	10.0	25.00	10.0	20.0
Heterostichus rostratus	28	1.45	11.0	22.92	11.0	22.0
Paraclinus integripinnis	19	0.98	12.0	18.75	12.5	24.5
Clevelandia ios	15	0.78	13.0	18.75	12.5	25.5
Pleuronichthys ritteri	7	0.36	15.0	12.50	14.0	29.0
Urolophus halleri	8	0.41	14.0	6.25	17.0	31.0
Squalus acanthias	5	0.26	16.5	8.33	15.5	32.0
Scorpaena guttata	4	0.21	18.0	8.33	15.5	33.5
Gillichthys mirabilis	5	0.26	16.5	4.17	18.5	35.0
Paralabrax nebulifer	2	0.10	21.0	4.17	18.5	39.5
Porichthys notatus	3	0.16	19.5	2.08	25.0	44.5
Paralabrax clathratus	3	0.16	19.5	2.08	25.0	44.5
Pleuronichthys verticalis	2	0.10	21.5	2.08	25.0	46.5
Syngnathus californiensis	2	0.10	21.5	2.08	25.0	46.5
Citharichthys sordidus	1	0.05	26.0	2.08	25.0	51.0
Synodus lucioceps	1	0.05	26.0	2.08	25.0	51.0
Engraulis mordax	1	0.05	26.0	2.08	25.0	51.0
Xystreuris liolepsis	1	0.05	26.0	2.08	25.0	51.0
Gobionellus longicaudus	1	0.05	26.0	2.08	25.0	51.0
Paraclinus walkeri	1	0.05	26.0	2.08	25.0	51.0
Leptocottus armatus	1	0.05	26.0	2.08	25.0	51.0
Totals	1,929	100.0				

TABLE 3
Composition of Beam-Trawl Catches (10-m Depth) by the Index of Community Importance (ICI)
in Bahía de San Quintín, B.C., México (January to December 1994)

| Species	Number	% Relative	Rank	% FO	Rank	ICI
Symphurus atricauda	349	31.02	1.0	52.08	1.0	2.0
Syngnathus leptorhynchus	168	14.93	2.0	35.42	3.5	5.5
Paralichthys californicus	64	5.69	5.0	43.75	2.0	7.0
Ilypnus gilberti	95	8.44	4.0	35.42	3.5	7.5
Hypsopsetta guttulata	55	4.89	6.0	31.25	5.0	11.0
Hypsoblennius gentilis	53	4.71	7.0	25.00	6.5	13.5
Porichthys myriaster	31	2.76	9.0	25.00	6.5	15.5
Citharichthys sordidus	25	2.22	11.0	22.92	8.0	19.0
Hypsoblennius jenkinsi	42	3.73	8.0	12.50	11.5	19.5
Cymatogaster aggregata	23	2.04	12.0	14.58	9.5	21.5
Pleuronichthys ritteri	14	1.24	14.0	14.58	9.5	23.5
Anchoa compressa	28	2.49	10.0	6.25	14.0	24.0
Clevelandia ios	21	1.87	13.0	12.50	11.5	24.5
Anchoa delicatissima	125	11.11	3.0	2.08	23.5	26.5
Heterostichus rostratus	7	0.62	15.0	6.25	14.0	29.0
Embiotoca jacksoni	5	0.44	16.0	6.25	14.0	30.0
Paraclinus walkeri	4	0.36	17.0	4.17	17.0	34.0
Scorpaena guttata	2	0.18	20.0	4.17	17.0	37.0
Pleuronichthys verticalis	2	0.18	20.0	4.17	17.0	37.0
Citharichthys stigmaeus	2	0.18	20.0	2.08	23.5	43.5
Atherinops affinis	2	0.18	20.0	2.08	23.5	43.5
Parophrys vetulus	2	0.18	20.0	2.08	23.5	43.5
Plathyrinoidis triseriata	1	0.09	25.5	2.08	23.5	49.0
Paralabrax clathratus	1	0.09	25.5	2.08	23.5	49.0
Urolophus halleri	1	0.09	25.5	2.08	23.5	49.0
Zapteryx exasperata	1	0.09	25.5	2.08	23.5	49.0
Xystreuris liolepis	1	0.09	25.5	2.08	23.5	49.0
Paraclinus integripinnis	1	0.09	25.5	2.08	23.5	49.0
Totals	1,125	100.0				
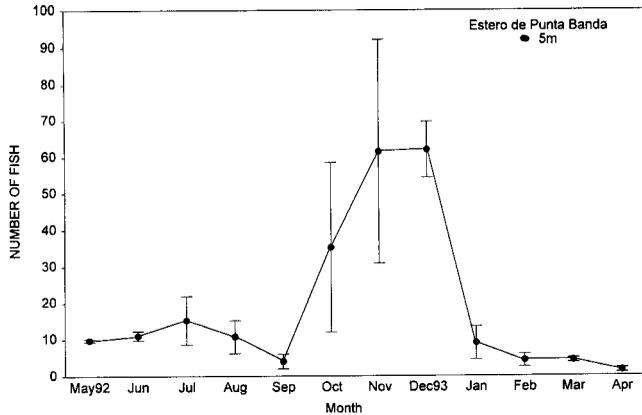
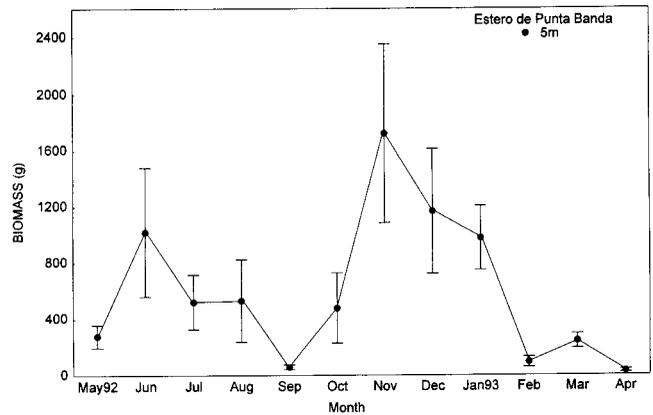Figure 3. Mean abundance per beam-trawl tow at Estero de Punta Banda. *Bars* represent standard error (±SE).

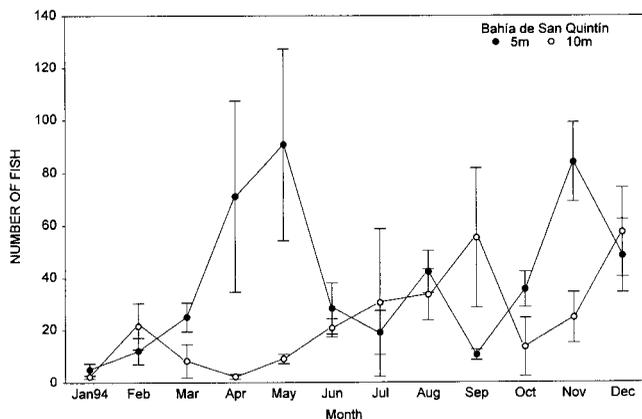Figure 4. Mean biomass (g) per beam-trawl tow at Estero de Punta Banda. *Bars* represent standard error (±SE).

Figure 5. Mean abundance per beam-trawl tow (5- and 10-m depths) at Bahía de San Quintín. *Bars* represent standard error (±SE).

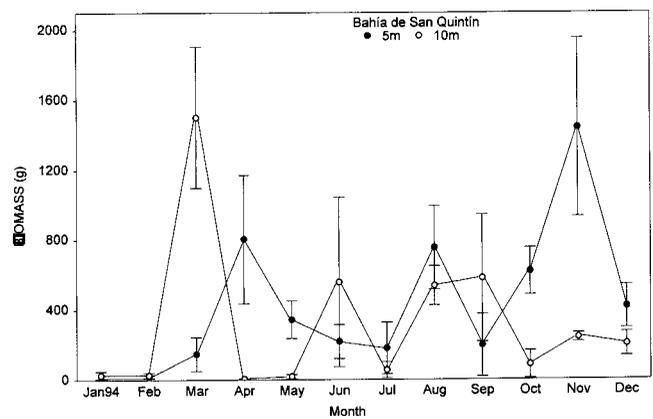Figure 6. Mean biomass (g) per beam-trawl tow (5- and 10-m depths) at Bahía de San Quintín. *Bars* represent standard error (±SE).

Along the 10-m isobath, catches were highest in September (55 fish/trawl ±SE 27) and December (57 fish/trawl ±17), and lowest (2 fish/trawl ±0.6) in January (figure 6). The annual mean was 23 fish/trawl (±4). Catch per trawl varied significantly with time ($p = 0.000$), but was not significantly correlated with temperature ($r = 0.056$, $p = 0.705$). Biomass per trawl at 10 m was highest in March (1,501 g ±404; figure 6). The minimum biomass (6.4 g/trawl ±2) was collected in April. The overall mean was 320 g/trawl ±81. Biomass differed significantly with months ($p = 0.000$), and was significantly correlated with bottom temperature ($r = 0.361$, $p = 0.012$).

Density and Standing Crop

In Punta Banda (1992–93), the annual mean density was 558 (±SE 430) fish/ha (table 4). High densities occurred from October to the peak (1,816 fish/ha ±227) in December. Low densities occurred during the rest of the year, with the lowest (44 fish/ha ±19) in April. The overall standing crop was 17,355 g/ha (±3,073), and peaked in June and in November (50,387 g/ha

±18,612). Again, the lowest density was in April (852 g/ha ±348; table 4). Fish density ($p = 0.001$) and standing crop ($p = 0.003$) changed significantly over the year at 5 m.

In Bahía de San Quintín, the annual mean density at 5 m was 916 fish/ha (±SE 137). Highest densities occurred in May (2,116 fish/ha ±854) and November, and the lowest in January (117 fish/ha ±55; table 5). Density varied with time (ANOVA, $p = 0.000$). The mean standing crop for the entire survey (5 m) was 10,002 g/ha (±1,871), with the highest peak (33,622 g/ha ±11,936) in November, and the minimum in January (74 g/ha ±SE 60). The standing crop differed significantly over the year (ANOVA, $p = 0.000$).

At 10 m, the annual density was 552 fish/ha ±SE 102. Two moderate peaks occurred in September (1,313 fish/ha) and December (1,361 fish/ha ±404), with the lowest density (54 fish/ha) in January and April (table 5). Density varied significantly with time (ANOVA, $p = 0.014$). The overall standing crop was 7,608 g/ha (±1,935), and the highest (March, 35,677 g/ha ±9,602), was three times those found in June, August, and

TABLE 4

Monthly Mean Density (no./ha) and Standing Crop (g/ha) of Beam-Trawl Tow (5-m Depth) at Estero de Punta Banda, B.C., México (May 1992 to April 1993)

Month	no./ha	±SE	g/ha	±SE
May	285.6	14.02	8,130.3	2,399.63
June	322.2	37.81	29,858.1	13,409.77
July	446.6	195.88	15,269.9	5,686.33
August	314.8	132.81	15,533.5	8,610.49
September	117.2	58.58	1,724.3	507.50
October	1,032.4	680.94	13,990.7	7,320.33
November	1,801.2	896.71	50,386.6	18,612.11
December	1,815.8	226.86	34,136.3	13,057.11
January	263.6	130.43	28,562.1	6,663.00
February	124.5	49.84	2,745.0	1,024.43
March	124.5	18.43	7,068.6	1,522.06
April	43.9	18.91	852.3	348.36
1992–93	557.7	429.66	17,354.8	3,073.18

September. The lowest mean (152 g/ha ±42) occurred in April (table 5). The standing crop varied significantly with time ($p = 0.000$).

Between-Area Comparisons

Total catch was highest (1,929 fish) at 5 m in Bahía de San Quintín, intermediate at 10 m (1,125 fish) in Bahía de San Quintín, and lowest (926 fish) in Estero de Punta Banda (tables 1–3). Bay pipefish, inhabiting the submerged seagrass beds, was most abundant (1,065 ind., 26.8%) primarily from the 5-m isobath of San Quintín. Tonguefish contributed 12.9% (515 ind.) of the total catch and was an important inhabitant of the mud bottom (10 m) of San Quintín. Kelp bass was abundant in Punta Banda and scarce in San Quintín, with a contribution of almost 9%. The cheekspot goby was fifth in overall abundance, contributing 7% of the catch. These five species accounted for 63.4% (2,521 fish) of the total catch from the two areas and depths. In spite of pro-

ducing the lowest total catch (926), Estero de Punta Banda had the greatest total biomass (28,443 g) and the highest monthly mean biomass (November, 1,720 g ±SE 635.5), indicating that it contained some larger fishes. Abundance and biomass from Punta Banda and San Quintín varied significantly with depth (ANOVA, $p < 0.006$).

The lower annual density found at 5 m in Estero de Punta Banda (558 fish/ha ±SE 430), compared to 5 m (916 fish/ha ±137) in San Quintín, contrasted with the larger annual standing crop (17,355 g/ha ±3,073) and the greater monthly standing crop (November, 50,387 g/ha ±18,612; tables 4, 5). The difference was attributed to high numbers of small bay pipefish in San Quintín. There were significant differences in density ($p = 0.0033$) and standing crop ($p = 0.0026$) between depths in Punta Banda (5 m) and Bahía de San Quintín (5 and 10 m).

Seasonality

In Estero de Punta Banda (1992–93), 350 fish were caught from 15 species (table 6). *Paralabrax clathratus* was the most abundant (46.3%), and *P. californicus* the most frequent (68.8%) in tows; along with *Pleuronichthys ritteri*, these topped the ICI, with the halibut ranked first. In 1994, 593 fish from 17 species were collected; the most abundant were *I. gilberti* (57.2%), *S. atricauda* (15.5%), and *P. californicus* (6.8%). The most frequently caught species was *S. atricauda* (68.8%) with the highest ICI rank, followed by the cheekspot goby and California halibut (table 6).

In San Quintín and during the seasons of 1994, a total of 822 fishes belonging to 24 species were collected at 5 m; *S. leptorhynchus* was the most abundant (38.4%), the most frequent in collections (81.3%), and first in the ICI rank (table 7). *Symphurus atricauda* and *C. aggregata* showed a high frequency of occurrence and ranked second and third in ICI.

TABLE 5

Monthly Mean Density (no./ha) and Standing Crop (g/ha) of Beam-Trawl Tow (5- and 10-m Depth) at Bahía de San Quintín, B.C., México (January to December 1994)

Month	5 m				10 m			
	no./ha	±SE	g/ha	±SE	no./ha	±SE	g/ha	±SE
January	116.6	54.69	74.0	60.15	53.5	14.95	679.7	510.41
February	279.9	116.22	484.5	230.98	510.9	209.99	636.3	369.92
March	583.0	128.79	3,452.7	2,229.07	196.1	150.73	35,677.3	9,601.83
April	1,655.8	848.95	18,762.8	8,583.83	53.5	22.49	152.1	42.44
May	2,116.4	853.49	8,027.6	2,508.55	213.9	42.29	462.8	285.07
June	658.8	228.17	5,097.4	2,261.58	493.1	83.10	13,264.6	11,498.37
July	443.1	196.97	4,191.9	3,451.68	724.8	670.09	1,317.7	1,078.95
August	985.3	188.35	17,577.0	5,566.26	796.1	231.52	12,754.9	2,629.16
September	244.9	47.13	4,577.3	4,181.45	1,313.0	632.58	13,770.8	8,632.72
October	827.9	157.16	14,434.5	3,137.42	320.8	265.78	2,044.3	1,876.67
November	1,959.0	352.78	33,621.7	11,936.11	588.2	231.09	5,732.0	582.40
December	1,125.2	325.01	9,727.7	2,875.24	1,360.5	403.45	4,808.1	1,643.41
1994	916.3	137.25	10,002.4	1,870.95	552.0	102.43	7,607.6	1,934.97

TABLE 6
Composition of Beam-Trawl Catches (5-m Depth) by the Index of Community Importance (ICI) in Estero de Punta Banda, B.C., México, by Seasons, 1992–93 and 1994

Species	1992–93						Species	1994					
	Total	% Relative	Rank	% FO	Rank	ICI		Total	% Relative	Rank	% FO	Rank	ICI
Paralichthys californicus	46	13.14	2.0	68.8	1.0	3.0	*Symphurus atricauda*	92	15.51	2.0	68.8	1.0	3.0
Pleuronichthys ritteri	38	10.86	3.0	31.3	2.5	5.5	*Ilypnus gilberti*	339	57.17	1.0	56.3	4.0	5.0
Paralabrax clathratus	162	46.29	1.0	18.8	4.5	5.5	*Paralichthys californicus*	40	6.75	3.0	62.5	2.5	5.5
Paralabrax nebulifer	19	5.43	4.0	18.8	4.5	8.5	*Hypsopsetta guttulata*	12	2.02	8.0	62.5	2.5	10.5
Hypsopsetta guttulata	11	3.14	8.0	31.3	2.5	10.5	*Pleuronichthys ritteri*	19	3.20	6.0	50.0	5.0	11.0
Hypsoblennius gentilis	18	5.14	5.0	12.5	8.0	13.0	*Paralabrax maculatofasciatus*	22	3.71	5.0	37.5	6.0	11.0
Paralabrax maculatofasciatus	14	4.00	6.0	12.5	8.0	14.0	*Xenistius californiensis*	32	5.40	4.0	12.5	10.0	14.0
Cymatogaster aggregata	13	3.71	7.0	12.5	8.0	15.0	*Paralabrax clathratus*	15	2.53	7.0	12.5	10.0	17.0
Heterostichus rostratus	6	1.71	10.5	12.5	8.0	18.5	*Syngnathus leptorhynchus*	4	0.67	10.5	18.8	7.0	17.5
Anisotremus davidsonii	5	1.43	12.0	12.5	8.0	20.0	*Paralabrax nebulifer*	5	0.84	9.0	12.5	10.0	19.0
Syngnathus leptorhynchus	8	2.29	9.0	6.3	13.0	22.0	*Anisotremus davidsonii*	4	0.67	10.5	12.5	10.0	20.5
Xenistius californiensis	6	1.71	10.5	6.3	13.0	23.5	*Hypsoblennius gentilis*	3	0.51	12.0	12.5	10.0	22.0
Symphurus atricauda	2	0.57	13.0	6.3	13.0	26.0	*Heterostichus rostratus*	2	0.34	13.0	6.3	15.0	28.0
Scorpaena guttata	1	0.29	14.5	6.3	13.0	27.5	*Hypsoblennius jenkinsi*	1	0.17	15.5	6.3	15.0	30.5
Atractoscion nobilis	1	0.29	14.5	6.3	13.0	27.5	*Urolophus halleri*	1	0.17	15.5	6.3	15.0	30.5
							Synodus lucioceps	1	0.17	15.5	6.3	15.0	30.5
							Porichthys myriaster	1	0.17	15.5	6.3	15.0	30.5
Totals	350	100.0						593	100.0				

The seasonality in Punta Banda (1992–93) showed an overall mean of 26 fish/trawl (±SD 36). Abundances increased from lowest in winter (4 fish/trawl) to highest in fall (61 fish/trawl; figure 7A). Abundances did not vary with seasons (ANOVA, $p = 0.078$). In 1994, the estero had the lowest mean (6 fish/trawl) in winter and the highest (96 fish/trawl) in spring, with an overall mean of 46 fish/trawl (±55). A similar pattern was found for 5 m in San Quintín (1994), with the lowest mean (12 fish/trawl) in winter and the highest (91 fish/trawl) in spring (figure 7A); the highest overall mean (51 fish/trawl ±52) occurred at this site and depth. The abundance at 5 m varied with seasons in 1994 in the estero (ANOVA, $p = 0.023$) and in San Quintín ($p = 0.008$). At 10 m in San Quintín, the highest abundance (33.3 fish/trawl) was in summer, and the lowest in spring. An inverse trend was found: a spring increase at 5 m and decrease at 10 m, and vice versa in summer (figure 7A). Seasonal abundances (5 m) in Punta Banda (1992–93, 1994) and San Quintín (1994) did not differ significantly (ANOVA, $p = 0.237$), nor did San Quintín abundances at 10 m ($p = 0.130$).

In Punta Banda, the lowest seasonal biomass (1992–93) was in spring (356 g/trawl) and the highest (813 g/trawl) in fall (figure 7B), with an overall of 701 g/trawl (±SE 407). In 1994, the overall mean was 555 g/trawl, ±296, with the lowest (356 g/trawl) in spring and highest (813 g/trawl) in fall. In Bahía de San Quintín (1994), the lowest biomass (5 m) occurred in winter (21 g/trawl), and highest in fall (1,442 g/trawl). At 10 m, biomass was low during all seasons (lowest, 6 g/trawl, in fall; highest, 56 g/trawl, in summer). The overall biomass for 5 m was
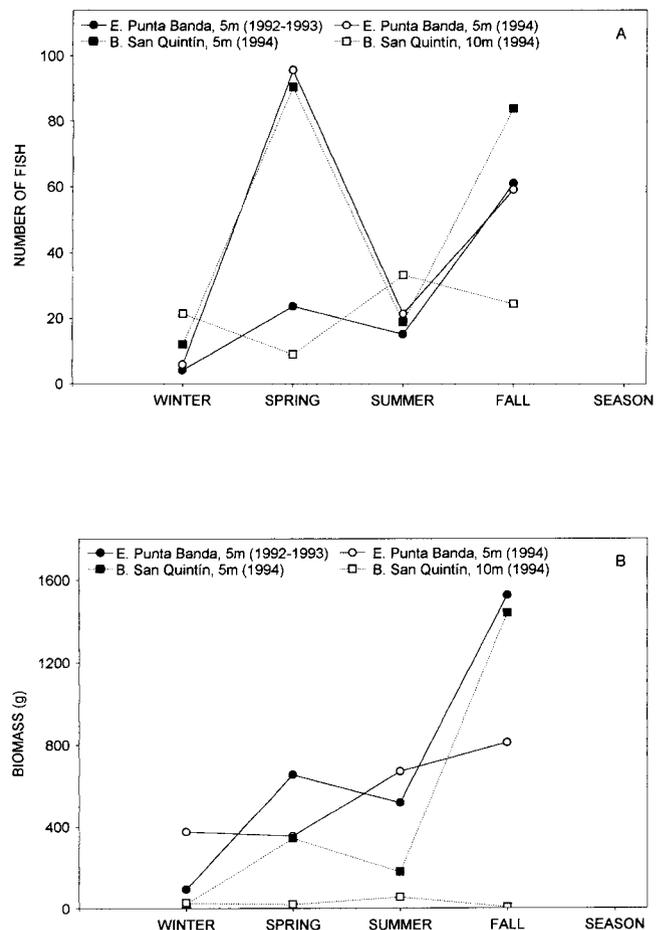
Figure 7. Seasonal mean abundance (*A*) and biomass (*B*) in Estero de Punta Banda (5 m) during 1992–93 and 1994, and in Bahía de San Quintín (5 and 10 m) in 1994.

TABLE 7
Composition of Beam-Trawl Catches (5-m and 10-m Depth) by the Index of Community Importance (ICI) in
Bahía de San Quintín, B.C., México, by Seasons (February, May, July, and November), 1994

| Species | 5-m depth | | | | | | Species | 10-m depth | | | | | |
	Total	% Relative	Rank	% FO	Rank	ICI		Total	% Relative	Rank	% FO	Rank	ICI
Syngnathus leptorhynchus	316	38.4	1.0	81.3	1.0	2.0	Symphurus atricauda	113	53.3	1.0	68.8	1.0	2.0
Symphurus atricauda	55	6.7	5.0	75.0	2.0	7.0	Citharichthys sordidus	25	11.8	2.0	43.8	2.0	4.0
Cymatogaster aggregata	106	12.9	3.0	50.0	5.5	8.5	Paralichthys californicus	11	5.2	4.5	31.3	3.0	7.5
Embiotoca jacksoni	56	6.8	4.0	50.0	5.5	9.5	Porichthys myriaster	15	7.1	3.0	18.8	7.5	10.5
Ilypnus gilberti	138	16.8	2.0	43.8	8.0	10.0	Syngnathus leptorhynchus	7	3.3	7.0	25.0	4.5	11.5
Hypsopsetta guttulata	22	2.7	8.0	56.3	3.0	11.0	Hypsopsetta guttulata	4	1.9	9.0	25.0	4.5	13.5
Paralichthys californicus	40	4.9	6.0	50.0	5.5	11.5	Pleuronichthys ritteri	10	4.7	6.0	18.8	7.5	13.5
Hypsoblennius gentilis	28	3.4	7.0	50.0	5.5	12.5	Parophrys vetulus	11	5.2	4.5	12.5	10.0	14.5
Hypsoblennius jenkinsi	15	1.8	9.0	25.0	9.0	18.0	Hypsoblennius gentilis	4	1.9	9.0	18.8	7.5	16.5
Paraclinus integripinis	10	1.2	10.0	18.8	10.5	20.5	Ilypnus gilberti	3	1.4	11.0	18.8	7.5	18.5
Gillichthys mirabilis	5	0.6	12.5	18.8	10.5	23.0	Synodus lucioceps	4	1.9	9.0	6.3	13.0	22.0
Urolophus halleri	6	0.7	11.0	12.5	13.5	24.5	Cymatogaster aggregata	2	0.9	12.0	6.3	13.0	25.0
Clevelandia ios	4	0.5	14.0	12.5	13.5	27.5	Pleuronichthys verticalis	1	0.5	14.0	6.3	13.0	27.0
Pleuronichthys verticalis	2	0.2	17.5	12.5	13.5	31.0	Pleuronichthys decurrens	1	0.5	14.0	6.3	13.0	27.0
Pleuronichthys ritteri	2	0.2	17.5	12.5	13.5	31.0	Scorpaena guttata	1	0.5	14.0	6.3	13.0	27.0
Heterostichus rostratus	5	0.6	12.5	6.3	20.0	32.5							
Porichthys myriaster	3	0.4	15.5	6.3	20.0	35.5							
Paralabrax clathratus	3	0.4	15.5	6.3	20.0	35.5							
Gobionellus longicaudus	1	0.1	21.5	6.3	20.0	41.5							
Synodus lucioceps	1	0.1	21.5	6.3	20.0	41.5							
Paralabrax nebulifer	1	0.1	21.5	6.3	20.0	41.5							
Scorpaena guttata	1	0.1	21.5	6.3	20.0	41.5							
Citharichthys sordidus	1	0.1	21.5	6.3	20.0	41.5							
Paraclinus walkeri	1	0.1	21.5	6.3	20.0	41.5							
Totals	822	100.0					Totals	212	100.0				

TABLE 8
Seasonal Mean of Density (fish/ha) and Standing Crop (g/ha) in Estero de Punta Banda (1992–93 and 1994),
and Bahía de San Quintín, B.C., México (1994)

| | Density (fish/ha) | | | | Standing crop (g/ha) | | | |
| | Punta Banda | | San Quintín | | Punta Banda | | San Quintín | |
Season	1992–93 (5 m)	1994 (5 m)	1994 (5 m)	1994 (10 m)	1992–93 (5 m)	1994 (5 m)	1994 (5 m)	1994 (10 m)
Winter	124.6	176.0	279.7	21.5	93.7	376.1	20.8	26.8
Spring	696.4	2,808.0	2,109.6	9.0	657.4	355.9	344.2	19.5
Summer	447.2	630.5	442.9	33.3	521.4	673.6	179.8	55.5
Fall	1,796.2	1,737.5	1,958.0	24.5	1,529.4	813.1	1,441.7	5.8
Overall	766.1	1,338.0	1,197.6	22.1	700.5	554.6	496.6	26.9
±SE	266.2	402.1	303.1	7.9	203.5	147.8	124.2	12.1

497 g/trawl (±377), and for 10 m, 27 g/trawl (±24). The mean biomass varied with the seasons at 5 m in San Quintín only (ANOVA, $p = 0.001$).

The highest overall density (1,338 fish/ha ±SE 402) and seasonal density (2,808 fish/ha, spring) were observed in Punta Banda in 1994 (table 8). In San Quintín, low densities were found at 10 m during all seasons of 1994, including the lowest for all periods, depths, and places (9 fish/ha, spring). At 5 m, low densities coincided with winter and summer, and the highs with spring and fall (table 8).

In Estero de Punta Banda, there was no difference in density between seasons in 1992–93 (ANOVA, $p = 0.081$), but density differed significantly with seasons during 1994 ($p = 0.023$). In San Quintín (1994), density also

differed with season at 5 m ($p = 0.009$), but not at 10 m ($p = 0.445$).

As density, the overall mean standing crop was highest at Punta Banda in 1992–93 (701 g/ha ±SE 204), and lowest in 10 m of San Quintín during 1994 (27 g/ha ±12; table 8). The highest seasonal standing crop (1,529 g/ha) was found at 5 m in Punta Banda during fall of 1992–93, and the lowest (6 g/ha) at 10 m during fall in San Quintín (table 8). The only place where differences in mean standing crop were found between seasons (ANOVA, $p = 0.000$) was at 5 m of Bahía de San Quintín (1994).

Seasonal density did not vary significantly between sites, depths, and years (ANOVA, $p = 0.095$), but the standing crop varied significantly ($p = 0.000$).

DISCUSSION

Small-meshed beam trawls have been used in some studies of demersal assemblages in California nearshore coast and bays (Allen 1985; Kramer and Hunter 1987; Allen and Herbinson 1990, 1991; Kramer 1990). Until this study, such studies had not been made off Baja California. Between 1992 and 1994, we sampled fishes living on or over mud or mud-sandy substrata in Estero de Punta Banda and Bahía de San Quintín. This survey indicates that these fish assemblages are quite dynamic from year to year, with different species dominant in each area and depth, and with differences in total catches, abundances by trawl, density (fish/ha), and standing crop. However, seasonal catches in 1994 in both areas and depths differed only in the standing crop.

The study shows that both lagoons serve as nursery grounds for a number of species. Three species (California halibut, kelp bass, and barred sand bass) are of major commercial and recreational importance in both Mexico and the United States. In Estero de Punta Banda, small California halibut were the dominant species in the trawls. A previous study (Rosales-Casián and Hammann 1993) showed that while few large halibut are found inside Estero de Punta Banda, substantial numbers of larger individuals are found just outside, in Bahía de Todos Santos. It appears that metamorphosing halibut larvae settle in Estero de Punta Banda, then migrate to Bahía de Todos Santos as they grow (Castro-Longoria and Grijalva-Chon 1988; Hammann and Rosales-Casián 1990; Rosales-Casián and Hammann 1993).

In Estero de Punta Banda, newly settled kelp bass were abundant in seagrass beds from August to December. Their presence was probably due to good annual reproductive success in Bahía de Todos Santos, because they had not been previously reported from the Estero (Estrada-Ramírez 1985; Navarro-Mendoza 1985; Beltrán-Félix et al. 1986; Castro-Longoria and Grijalva-Chon 1988). This bay–lagoon–bay movement of larvae and juvenile kelp bass was described by Rosales-Casián (1995). Juvenile barred sand bass were also common in this lagoon, again in association with the abundant seagrass beds. In the same habitat, we caught fair numbers of another economically important serranid, the spotted sand bass (*Paralabrax maculatofasciatus*); the catch for this species (in contrast to that for the other two species) included adults as well as immature fish. The high density of seagrass in Estero de Punta Banda indicates the relatively pristine environment (Ibarra-Obando and Poumian-Tapia 1991) and appears to be a major factor in the abundance of juveniles of a number of species.

Few beam-trawl studies of California lagoons have been made. However, Allen and Herbinson (1991), working in bay habitats of southern California, found that topsmelt (*Atherinops affinis*), cheekspot goby, bay pipefish,

staghorn sculpin (*Leptocottus armatus*), and arrow goby (*Clevelandia ios*) were all important. Kramer (1991) studied flatfishes in shallow waters of San Diego, California, and found more California halibut and diamond turbot in bays than in coastal habitats. The most abundant species from that study was the speckled sanddab (*Citharichthys stigmaeus*; 78.6% of total), caught mostly on the open coast off San Diego. California halibut ranked second in abundance. The tonguefish was reported as poorly estimated because it is nocturnally active (Kramer 1991), and its diel pattern of activity affects availability to trawling (DeMartini and Allen 1984). However, in our 10-m-depth samples from Bahía de San Quintín, tonguefish was the dominant species in abundance, frequency of occurrence, and ICI ranking. The turbid water of the tidal current probably accounts for this change.

Some bias can be expected when sampling with a beam trawl, mainly because it has a small open mouth, but the estuarine environments of Punta Banda and San Quintín offer similar conditions (turbidity, seagrasses, tidal current), and the absence of some fish species in the samples can be due to interannual variation, rather than to the beam trawl. This gear does capture small halibut (*P. californicus*) fairly efficiently (Kramer 1990), and also primarily small fishes.

In Bahía de San Quintín, seagrasses at 5 m led to high abundances of bay pipefish. These plants contain large quantities of the small invertebrates eaten by pipefish and many other species. An analysis of the diets of juvenile kelp bass, barred sand bass, and spotted sand bass in Estero de Punta Banda showed a notable amount (up to 12.9% by weight), and frequency of occurrence (up to 47%) of *Zostera marina* fragments (Mendoza-Carranza 1995). This probably results from the fishes' biting leaves as they eat their prey.

The major fish species in Estero de Punta Banda and Bahía de San Quintín differ. California halibut, kelp bass, barred sand bass, hornyhead turbot, and bay blenny dominated the 5-m depth trawls of Punta Banda. At the same depth in San Quintín, pipefish, California halibut, tonguefish, cheekspot goby, and shiner perch dominated, as they did at 10 m, except that diamond turbot replaced shiner perch.

Temperature and tidal current can significantly influence the abundance and distribution of fishes. During this study, there was considerable upwelling in April–June off San Quintín. As first reported by Dawson (1951), this cold water is positioned very near the lagoon's mouth. When temperatures fell during May, fish abundances at 5 m increased. When temperatures increased from June to September, abundances decreased. At 10-m depth, the abundance patterns were reversed. Our data (5 m) showed a more than 8°C difference between May and August. Our unpublished data from outside the bay

reveal within-month differences of more than 12°C. These low temperatures can produce an unfavorable environment for some species, and fishes probably respond by moving from deeper and colder water into the warmer shallows. The barred sandbass (*Paralabrax maculatofasciatus*) inhabits a broad range of temperature regimes and was abundant in Estero de Punta Banda. Its absence from Bahía de San Quintín may be due to its inability to survive the seasonally low temperatures in this lagoon.

Other differences in the fish species from Punta Banda and San Quintín can be explained by El Niño. In 1992–93, a strong event influenced our samplings in the estero; 1994, however, is considered a cold year, and some species (e.g., cheekspot gobies, *Ilypnus gilberti*) that were absent in 1992–93 became most abundant. This species is a major prey for juvenile California halibut in coastal and bay habitats of San Diego (Drawbridge 1990) and in Estero de Punta Banda (Sandoval-Muy 1995).

Estero de Punta Banda, despite being a smaller and less productive lagoon (Alvarez-Borrego et al. 1977; Millán-Nuñez and Alvarez-Borrego 1978) had a greater annual total biomass and a higher standing crop than did Bahía de San Quintín. This implies that Estero de Punta Banda is not only a nursery ground, but also a feeding place for larger fishes. This may be because Estero de Punta Banda is connected with Bahía de Todos Santos, another fish-rich environment (Hammann and Rosales-Casián 1990), while San Quintín connects to the relatively depauperate open coast. This trend has also been noted on the coast of southern California for flatfishes and for nearshore assemblages in general (Kramer 1990; Allen and Herbinson 1990, 1991).

The density at 5-m depth in San Quintín was nearly twice that found at 10 m in the same place, and in Estero de Punta Banda. In contrast, the standing crop of fish in Estero de Punta Banda was greater than that collected at either depth in Bahía de San Quintín. This difference was due to the presence of some larger fishes (California halibut, spotted sand bass, barred sand bass) in the estero, and great numbers of bay pipefish in the bay.

The clinid *Paraclinus walkeri* is an interesting species, apparently endemic to Bahía de San Quintín (Hubbs 1952; Rosenblatt and Parr 1969; Rosales-Casián 1996). We caught a few individuals of this species but did not sample around the pier pilings of the Old Mill Hotel, where previous collections had shown them to be quite abundant (Richard Rosenblatt, SIO, pers. comm.).

Some change in the fish species assemblage at Punta Banda seems to have occurred over time. In a 1982–83 study, Beltrán-Félix et al. (1986) found spotfin croaker (*Roncador stearnsii*) and diamond turbot to be very abundant. In our study, diamond turbot were less important, and spotfin croakers were absent. It is unclear what has led to these changes, though decade-long oceanographic changes, noted in several studies, may be responsible (Roemmich and McGowan 1995; MacCall 1996).

Protected areas have been identified as nursery grounds along the southern California coast (Allen and Herbinson 1990, 1991; Kramer 1991). These habitats, however, are not only relatively rare along the California coast, but are also severely impacted by human activities, and have been reduced by up to 90% of their original size (Kramer 1990). On the other hand, because the bays and coastal lagoons along Pacific Baja California are relatively pristine, they have a great potential for reproduction, feeding, and refuge for fish species of ecological and economic importance. They may be major nursery sites and an important source of fishes for southern California. Little information exists about the coastal ichthyofauna of Baja California, but many species are distributed from Baja California to the Southern California Bight. It seems apparent that the ecological role of both Estero de Punta Banda and Bahía de San Quintín should be maintained through careful preservation.

CONCLUSIONS

This study in Estero de Punta Banda and Bahía de San Quintín showed that these soft-bottom habitats differ between years in dominant species, total and per-trawl catch, density, and standing crop. By areas, the seasonality of 1994 showed differences in standing crop only.

In Punta Banda three economically important species were dominant by ICI: *P. californicus*, *P. clathratus*, and *P. nebulifer*. In San Quintín the dominant species were *S. leptorhynchus*, *P. californicus*, and *S. atricauda* at 5 m; at 10 m this order changed to *S. atricauda*, *S. leptorhynchus*, and *P. californicus*.

Total catch of fishes was highest in Bahía de San Quintín (5 m), intermediate there at 10 m, and lowest in Estero de Punta Banda.

Bahía de San Quintín presented the highest mean abundance during May at 5 m, and the lowest mean at 10 m. The May low temperatures, caused by an upwelling close to the bay mouth, probably influenced this pattern. The only notable increase in Punta Banda was during October and November, mainly because of the presence of juvenile *P. clathratus*.

Overall, the density was lowest in Punta Banda and at 10-m depth in San Quintín; it was highest at 5 m in San Quintín. In contrast, the highest standing crop was found in Punta Banda, both annual mean and monthly mean (during November).

Estero de Punta Banda and Bahía de San Quintín both need protection and regulation.

ACKNOWLEDGMENTS

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SPATIAL AND TEMPORAL PATTERNS OF ZOOPLANKTON BIOMASS IN MONTEREY BAY, CALIFORNIA, DURING THE 1991–1993 EL NIÑO, AND AN ASSESSMENT OF THE SAMPLING DESIGN

CHERYL L. BADUINI[1]
Moss Landing Marine Laboratories
P.O. Box 450
Moss Landing, California 95039

ABSTRACT

To estimate spatial and temporal zooplankton bio-mass, and the appropriateness of the sampling design, eighteen surveys were conducted in Monterey Bay, California, between November 1991 and August 1993. Vertical tows were taken to estimate zooplankton bio-mass in six regions of the bay on each survey day. In year 1, when 100-m vertical tows were made, zooplankton biomass peaked in January, March, and August; in year 2, when 50-m vertical tows were made, biomass peaked in April, August, and October. Mean zooplankton bio-mass differed significantly among seasons for both years, but trends differed between years. In year 1, mean bio-mass measured in the Davidson and oceanic seasons was significantly greater than in the upwelling season. In year 2, mean biomass measured in the upwelling and oceanic seasons was significantly greater than in the Davidson period. The seasonal trends in zooplankton biomass dur-ing this study were representative of similar trends for the phytoplankton cycle in Monterey Bay, which had a spring and an autumn bloom and decreased biomass in winter. Low zooplankton levels recorded in Monterey Bay during February and April 1992 and January and March 1993 were probably related to an El Niño–Southern Oscillation warm-water event (ENSO) in 1991–93. The sampling regime adequately revealed large-scale spatial (tens of km) and temporal (seasonal) differences in zooplankton biomass, but probably does not adequately describe smaller spatial and shorter temporal processes.

INTRODUCTION

Zooplankton occupy an important ecological role in the transfer of energy from primary producers to higher trophic levels of the Monterey Bay ecosystem (Baltz and Morejohn 1977; Chu 1982). They are primary prey for numerous vertebrates in Monterey Bay (Scheonherr 1989; Baduini 1995). Nevertheless, there is little un-derstanding of the distribution, abundance, and seasonal cycles of zooplankton in the bay. In contrast, there is ex-tensive information about the seasonal cycles of phyto-plankton abundance in the bay (Bolin and Abbott 1963;

Garrison 1976; Silver and Davoll 1976; Waidelich 1976; Schrader 1981). Silver and Davoll (1976, 1977) and Waidelich (1976) conducted net tows for zooplankton during their phytoplankton surveys, but recorded only displacement volume (ml/1,000 m^3) and collected few zooplankton samples. It is difficult to determine season-ality or spatial differences in zooplankton abundance with the few samples collected for these reports; it is also difficult to design a sampling scheme that adequately detects the appropriate scale of spatial and temporal pat-terns. For these reasons, I sampled zooplankton to esti-mate seasonal variation of biomass in Monterey Bay from November 1991 to August 1993. An additional objec-tive of the study was to assess the ability of the sam-pling design to detect spatial and temporal patterns in zooplankton biomass.

Monterey Bay spans approximately 44.3 km and is exposed to the open ocean and the California Current system (figure 1). Its most prominent bathymetric fea-ture is the submarine canyon that begins approximately 100 m offshore of Moss Landing Harbor and reaches a depth of 1,830 m. Hydrographic seasons include an up-welling season from March to August, an oceanic pe-riod from September through October, and the Davidson Current period from November to February (Skogsberg 1936; Bolin and Abbott 1963; Abbott and Albee 1967; Smethie 1973).

Coastal upwelling is driven by persistent northwest winds that characterize spring and early summer. The length of the upwelling season varies annually, and up-welling events may be sporadic at the end of the sea-son. Upwelling also may occur after any period of persistent northwest winds; for example, Smethie (1973) documented an unseasonal upwelling event during the Davidson period in December 1971. With the relax-ation of upwelling, the oceanic period is characterized by onshore flow of offshore waters. Oceanic periods are not always well marked (Bolin and Abbott 1963) and may be obscured by sporadic upwelling after the end of the upwelling season. During the Davidson Current pe-riod, the California Countercurrent surfaces between the coast and the California Current system and flows north. This results in onshore water flow, downwelling, and deep mixing along the coast (Smethie 1973).

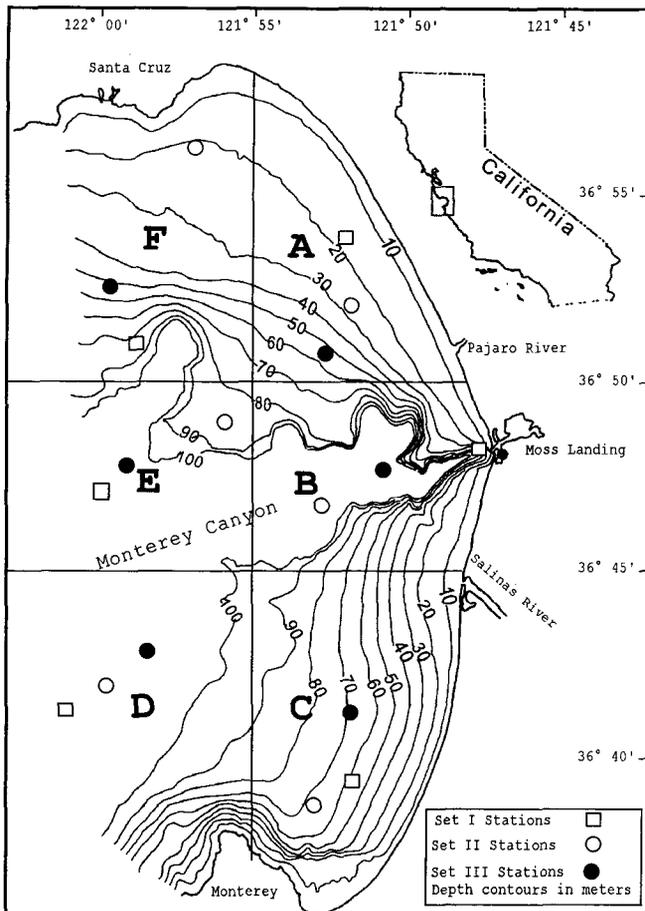Phytoplankton cycles generally follow a pattern

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Figure 1. The six regions of the Monterey Bay study area: A, nearshore north; B, nearshore central; C, nearshore south; D, offshore south; E, offshore central; and F, offshore north.
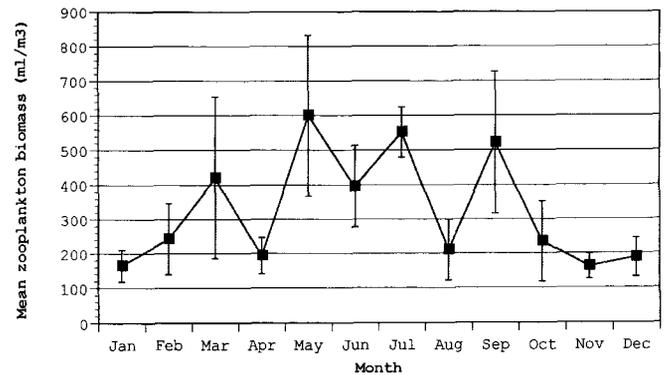

Figure 2. Seasonal cycle of zooplankton biomass (displacement volume) from data collected in Monterey Bay, Oct. 1971–Aug. 1972 (Waidelich 1976) and July 1975–July 1977 (two stations, #4 and #5; Silver and Davoll 1976, 1977). Error bars represent standard error.

mean from 1987 to 1992 in the same region (Sakuma et al. 1994a, b).

METHODS

Sampling Design

Eighteen zooplankton surveys were conducted in Monterey Bay from November 11, 1991, to August 17, 1993, with a vertically towed 335-μm, 0.5-m-diameter, 3-m-long, Puget Sound opening/closing plankton net (Research Nets). A precalibrated flowmeter (General Oceanics Model #2030) was mounted inside the mouth of the net to estimate water volume filtered per tow, except on five occasions when length of wire deployed and wire angle were used to calculate the volume filtered. Six regions of Monterey Bay were sampled on each cruise: A, nearshore north bay; B, nearshore central bay; C, nearshore south bay; D, offshore south bay; E, offshore central bay; and F, offshore north bay (figure 1).

One station was sampled per region (six stations total) on each survey day. Three sets of stations were chosen randomly and sampled throughout the study period: Sets I, II, and III (table 1). The offshore central station in Set I was chosen because it had been sampled historically (Bolin and Abbott 1963). To study temporal variability in zooplankton biomass, six fixed stations were sampled on every other survey throughout the study period (Set I stations). Six alternate stations were sampled one to two times per season in 1991–92 (Set II stations) and one to two times per season in 1992–93 (Set III stations). The additional sets (II and III) were added to increase the area sampled to determine spatial variability in zooplankton biomass. Because each survey event sampled a different water column at the same station than the previous survey, each sample was treated as a random sample (Cassie 1968).

Vertical zooplankton tows were collected as representative samples of seasonal zooplankton biomass in the

similar to the hydrographic seasons, with low winter abundance due to low light levels and a well-mixed water column, a spring bloom associated with increasing light and enhanced nutrient concentrations, and an autumn bloom resulting from reduced zooplankton grazing (Waidelich 1976).

Zooplankton also follows a pattern similar to the hydrographic seasons, but is less well marked (figure 2; Silver and Davoll 1976, 1977; Waidelich 1976). In 1972, Waidelich (1976) observed a zooplankton maximum one month before the maximum of the phytoplankton spring bloom. This observation differs from those in other mid-latitude marine ecosystems, where the zooplankton bloom lags the phytoplankton bloom by about one month. Waidelich (1976) attributed this discrepancy to sampling error.

This paper reports the spatial and temporal patterns of zooplankton biomass in Monterey Bay, California. Samples were collected during the El Niño–Southern Oscillation event of 1991–93. This period was characterized by surface temperatures 1°–4°C greater than the

TABLE 1
Dates and Station Sets Sampled (X) for Zooplankton Surveys in Monterey Bay, November 1991 to August 1993

	Station set sampled		
Survey date	A	B	C
11/11/91	X		
11/21/91		X	
2/4/92	X		
2/18/92		X	
4/10/92	X		
4/28/92		X	
5/28/92		X	
7/23/92	X		
10/12/92	X		
11/5/92			X
12/16/92	X		
1/11/93			X
3/3/93	X		
4/19/93			X
8/4/93	X		
8/12/93		X	
8/17/93			X

upper water column. In 1991–92 (year 1), two replicate vertical tows per station were conducted from 100 m to the surface. In 1992–93 (year 2), two replicate vertical tows were conducted from 50 m to the surface. Because of differences in the sampling regime between years, each year was analyzed separately.

Samples were preserved in 10% buffered formalin in seawater (Salonen and Sarvala 1985). Large coelenterates were removed. Subsamples were taken with a Stempel pipette, filtered, rinsed with deionized water, and dried in an oven (Blue M) at 60°C ± 10° (Omori and Ikeda 1984) for at least 48 hrs. Aliquots were weighed with an electronic balance to the nearest 0.001 g. Total weight of the sample was then determined, and biomass was standardized to mg/m^3 on the basis of volume of water filtered.

Year 1 (November 1991 through September 1992) and year 2 (October 1992 through August 1993), consisting of 100-m and 50-m vertical tows, respectively, were analyzed individually because of a significant difference in biomass with depth. Each year was analyzed to determine the significance of differences in mean zooplankton biomass among seasons, regions, and sites (Underwood 1981; Zar 1984; SYSTAT 1992). Biomass estimates were logarithmically transformed to normalize data. Three oceanographic seasons were differentiated: upwelling (March to August), oceanic (September to November), and Davidson (December to February; Skogsberg 1936; Bolin and Abbott 1963; Abbott and Albee 1967; and Smethie 1973). Regions were north, central, and south, and sites were nearshore and offshore areas of the bay (figure 1). Tukey multiple comparison tests were used to determine the differences among significantly different seasons (Day and Quinn 1989).

Assessment of Sampling Design

Two pilot projects were conducted to assess the power of the sampling design. Ten replicate zooplankton tows were collected at one central nearshore station on March 31, 1992, to determine optimal replicate size. Precision (measured as standard error/mean) versus sample size was plotted along with cost per unit sample. Cost was measured as time required to complete an additional tow. Optimal replicate size was determined by calculating where the product of cost and standard error/mean was least.

Similarly, ten random samples were collected in the central nearshore region on March 31, 1992, to assess regional variability in zooplankton biomass and to determine an optimal number of tows per region. Precision and cost versus sample size were graphed to determine the optimal number of stations per region. The variability among stations in the central nearshore region was calculated to determine minimum detectable effect size of the regional replicate size used during this study.

RESULTS

Patterns of Zooplankton Biomass

The three random surveys per season (table 1) revealed that in year 1 (100-m vertical tows) zooplankton biomass peaked in January, March, and August; in year 2 (50-m tows) biomass peaked in April, August, and October (figures 3, 4).

Mean zooplankton biomass differed significantly among seasons for both years (year 1, $F = 4.26$, $n = 53$, $p = 0.020$; year 2, Kruskal-Wallis statistic $= 6.02$, $n = 96$, $p = 0.049$), but the trends differed between years (figure 5). In year 1 (100-m tows), mean biomass measured during the Davidson and oceanic seasons was significantly greater than during the upwelling season
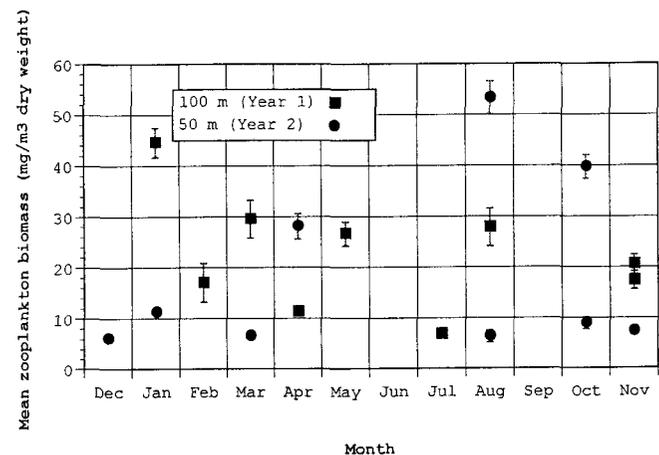

Figure 3. Mean zooplankton biomass estimates (mg/m^3 dry weight) per sampling date from November 1991 to August 1993 in Monterey Bay, California. Each point denotes mean biomass for all tows collected on each survey. Error bars represent standard error.
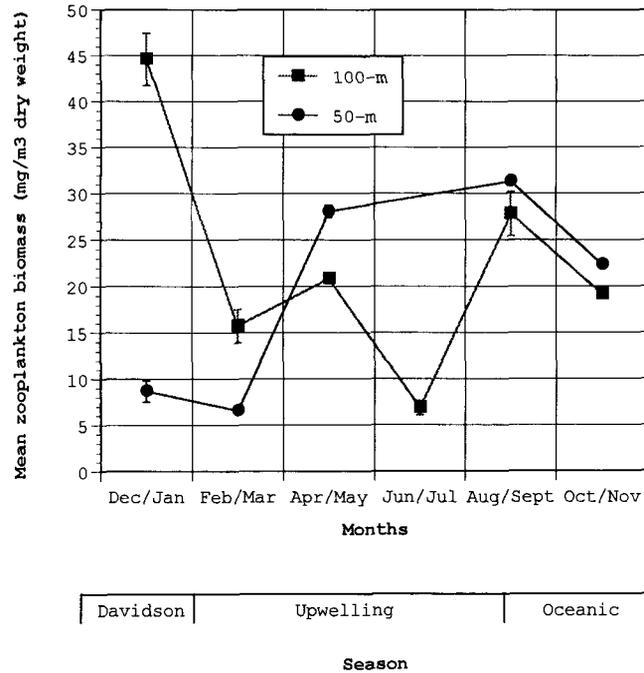
Figure 4. Mean bimonthly zooplankton biomass estimates (mg/m³ dry weight) from November 1991 to August 1993 in Monterey Bay, California. Error bars represent standard error.

(Tukey statistic = −0.24, n = 53, p = 0.015 for Davidson; Tukey statistic = −0.26, n = 53, p = 0.020 for oceanic; figures 4, 5). In year 2 (50-m tows), mean biomass measured during the upwelling and oceanic seasons was significantly greater than during the Davidson period (Tukey statistic = 0.25, n = 96, p = 0.040 for upwelling, and Tukey statistic = 0.29, n = 96, p = 0.032 for oceanic; figures 4, 5a).

There were no significant differences among regions of the bay within each year (figure 5b). Also, there were no significant differences between nearshore and offshore regions of the bay within each year, but the trend in biomass differs between years (figure 5c). In year 1, biomass was greater nearshore than offshore; in year 2, however, biomass was greater offshore.

Sampling Design

Precision (SE/mean) increased and stabilized after five replicate tows were sampled at a central nearshore station in Monterey Bay (figure 6a). Cost (time/unit tow) increased linearly with increasing number of samples. Optimal replicate size (where product of cost and precision was least) was three replicates per station. Only two replicates were conducted per station in this study.

Precision fluctuated and decreased as sampling effort increased within regional stations (figure 6b). Cost increased linearly with increasing sample size per region. Optimal sample size per region was two stations per region.
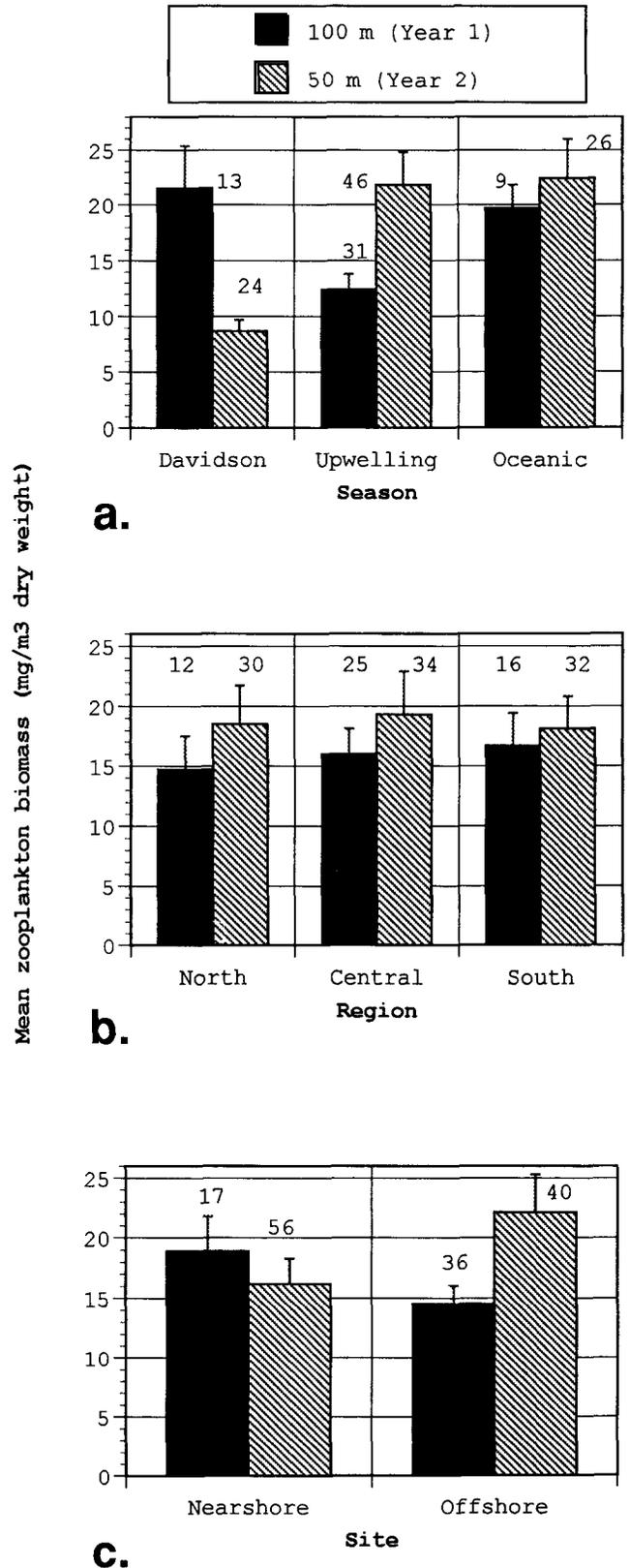
Figure 5. Mean zooplankton biomass estimates (mg/m³ dry weight) for 100-m (year 1) and 50-m (year 2) vertical tows: (a) by season; (b) by region; and (c) in nearshore and offshore areas of Monterey Bay, California. Error bars represent standard error. Sample sizes are indicated above bars.
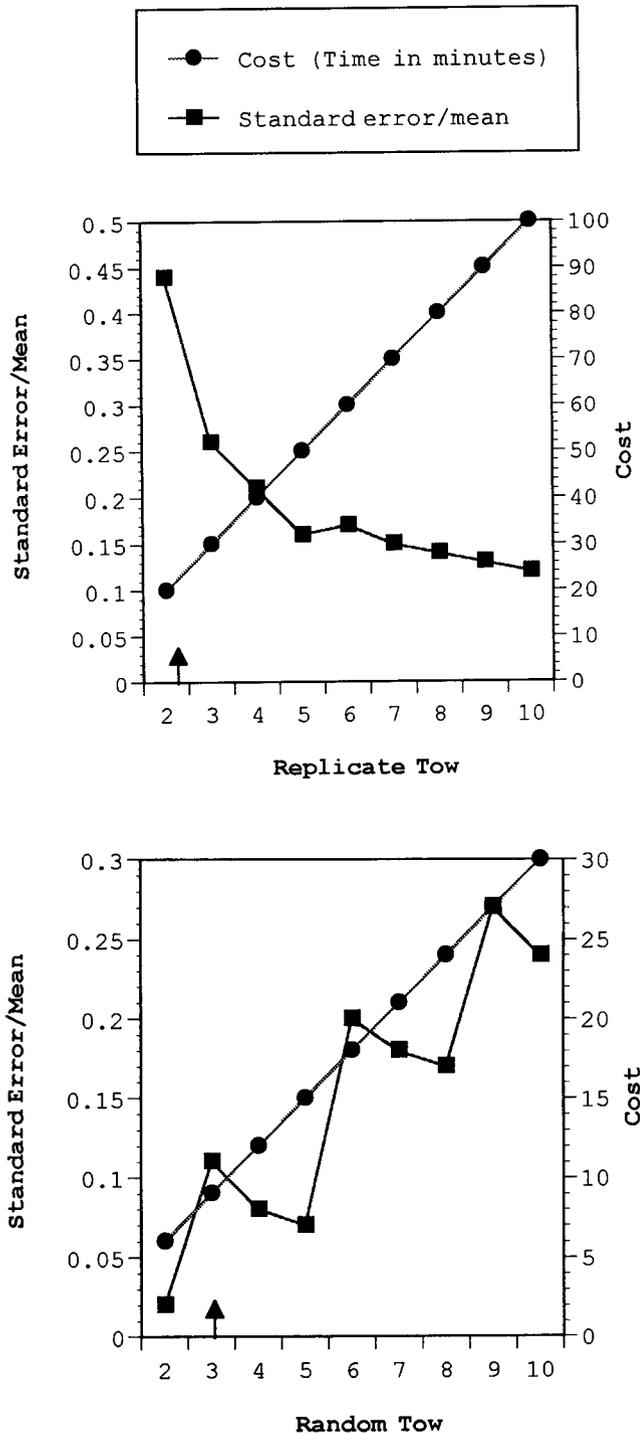
Figure 6. Estimates of precision (SE/mean) for zooplankton tows in Monterey Bay: *top*, ten replicate tows at one central nearshore station; *bottom*, ten random tows within the central nearshore region. *Arrows* indicate actual number of tows made during the study.

Assuming that the variability of the central nearshore region was representative of all six regions of this study, 3.3 samples per region were required to detect a doubling in zooplankton biomass. Three samples per region effectively detected a 2.6 increase in biomass.

DISCUSSION

Spatial and Temporal Distribution of Zooplankton Biomass

The seasonal trends in zooplankton biomass observed during both years of this study were representative of similar trends observed for the phytoplankton cycle in Monterey Bay, with a spring and autumn bloom and decreased zooplankton abundance in winter. A surprising result, however, was the high biomass collected in January of year 1 (figure 4). This may have resulted from a local upwelling event that may have occurred in the bay during that time.

Additionally interesting are the different seasonal trends observed between years. The different trends may have resulted because zooplankton were collected at different depths in the two years, and because this difference was statistically significant. Although the 100-m and 50-m tows were not collected in the same year, we will assume for comparison that trends would be similar between years for each tow depth. The greater biomass during the upwelling and oceanic seasons of year 2 may have resulted from upwelling events that brought greater biomass into surface waters, where it was detected in the relatively shallow, 50-m tows. This trend was not observed in year 1, possibly because biomass was calculated over a greater depth range (100 m) and thus the greater productivity in surface waters went undetected. However, two peaks in biomass occurred during the upwelling season of year 1, in May and August.

The low zooplankton levels recorded in Monterey Bay during February and April 1992 and January and March 1993 (figure 3) were probably related to an El Niño–Southern Oscillation warm-water event (ENSO) in 1991–93. Water temperatures were 1°–4°C higher near the surface in May–June 1992 compared with the mean for May–June 1987–92 (Sakuma et al. 1994a). Salinities were, on average, 0.8 ppt lower near the surface. Movement of California Current water inshore was the most likely explanation for the hydrography in 1992. Conditions during February to March 1993 off central California were characterized as a continuation of the ENSO that developed in early 1992 (Sakuma et al. 1994b). Temperatures throughout the water column (to 500 m) were cooler than for a similar period in 1992 (Sakuma et al. 1994b), but remained substantially warmer than the region's long-term average in the CalCOFI database. Surface temperatures were 1° to 3°C higher than the mean for 1983–93. The distribution of surface salinities and temperatures in May–June 1993 indicated an onshore displacement of California Current water similar to that seen in 1992 (Sakuma et al. 1994b). Additionally, female *Calanus* were less abundant in southern California waters in February and April 1992 than in 1989–91 (Mullin 1994).

Although there were low levels of zooplankton in the bay during several months in 1992–93, there was a large increase in zooplankton biomass from February to March and April to May 1992. There was a similar increase in biomass from March to April 1993 (figure 3). This may have been the period when the dampening El Niño effects were overcome by a pulsed upwelling event in the bay.

Sampling Design

Eighteen stations represented the spatial distribution of zooplankton biomass over the 550-km² area of Monterey Bay. This limited sampling scheme, however, revealed large-scale spatial differences in zooplankton biomass (the greater nearshore mean zooplankton biomass measured in 1991–92). The low precision determined for the central nearshore region also indicates that spatial resolution was limited. The precision curve never stabilized when ten random zooplankton tows were conducted over a 74-km² area.

Two to three surveys per season were conducted to determine temporal differences in zooplankton biomass. This sampling regime revealed large-scale temporal differences in zooplankton biomass (the seasonal differences within years), but probably does not adequately describe shorter temporal processes that may occur over days or weeks.

Although this study quantified the seasonal and spatial abundance of zooplankton biomass in Monterey Bay, there is little information about the seasonal diversity of zooplankton taxa in the bay. Calanoid copepods, particularly *Calanus pacificus*, dominated zooplankton samples collected at the surface in February and December 1991. Other taxa, such as zoea crab larvae, were abundant in autumn. It is unknown how the cycling of particular zooplankton communities affects the distribution and abundance of their vertebrate predators. Thus the effects of predation on the distribution and abundance of zooplankton taxa in Monterey Bay are incomplete and require further examination.

ACKNOWLEDGMENTS

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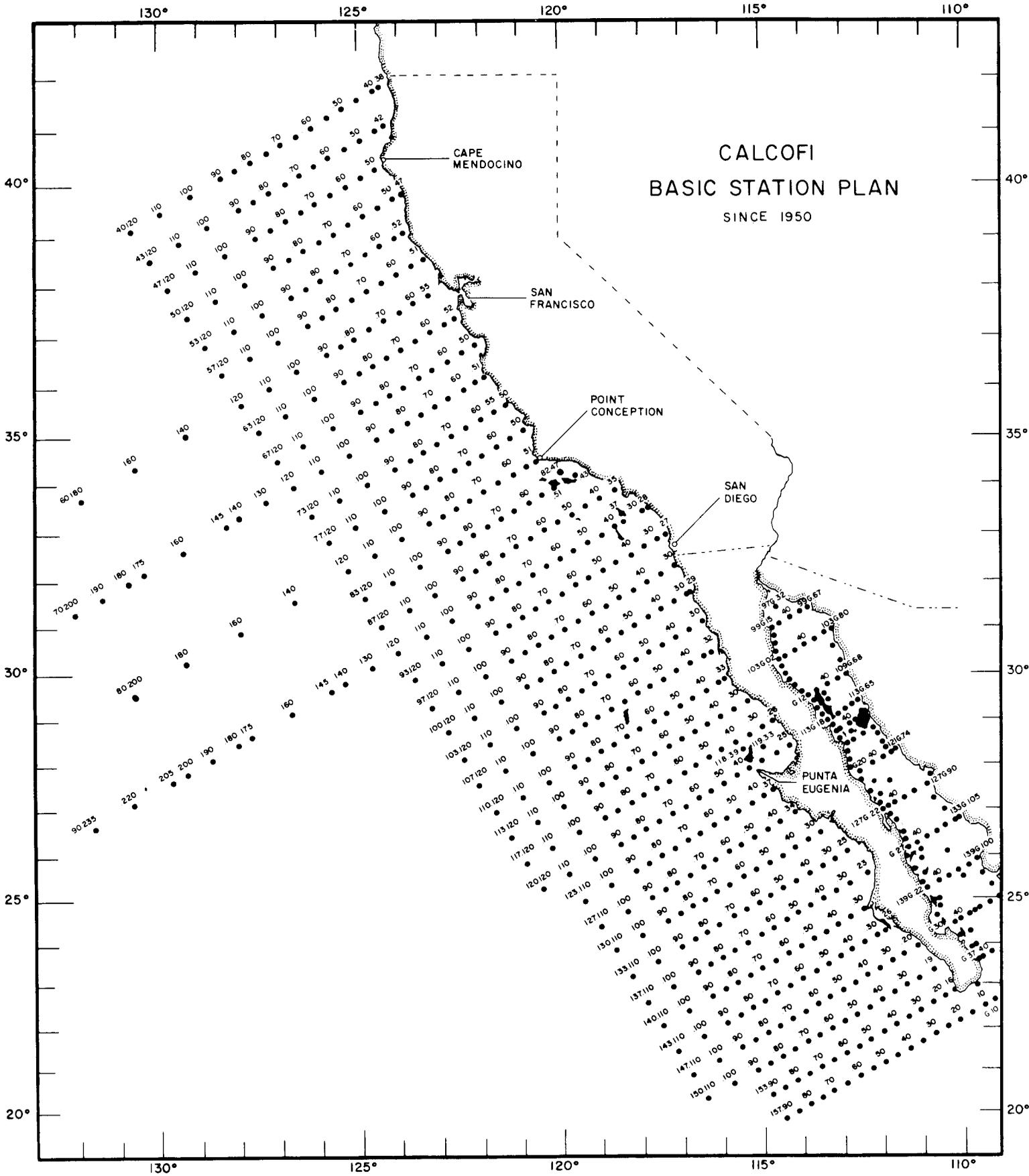(chapter):
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