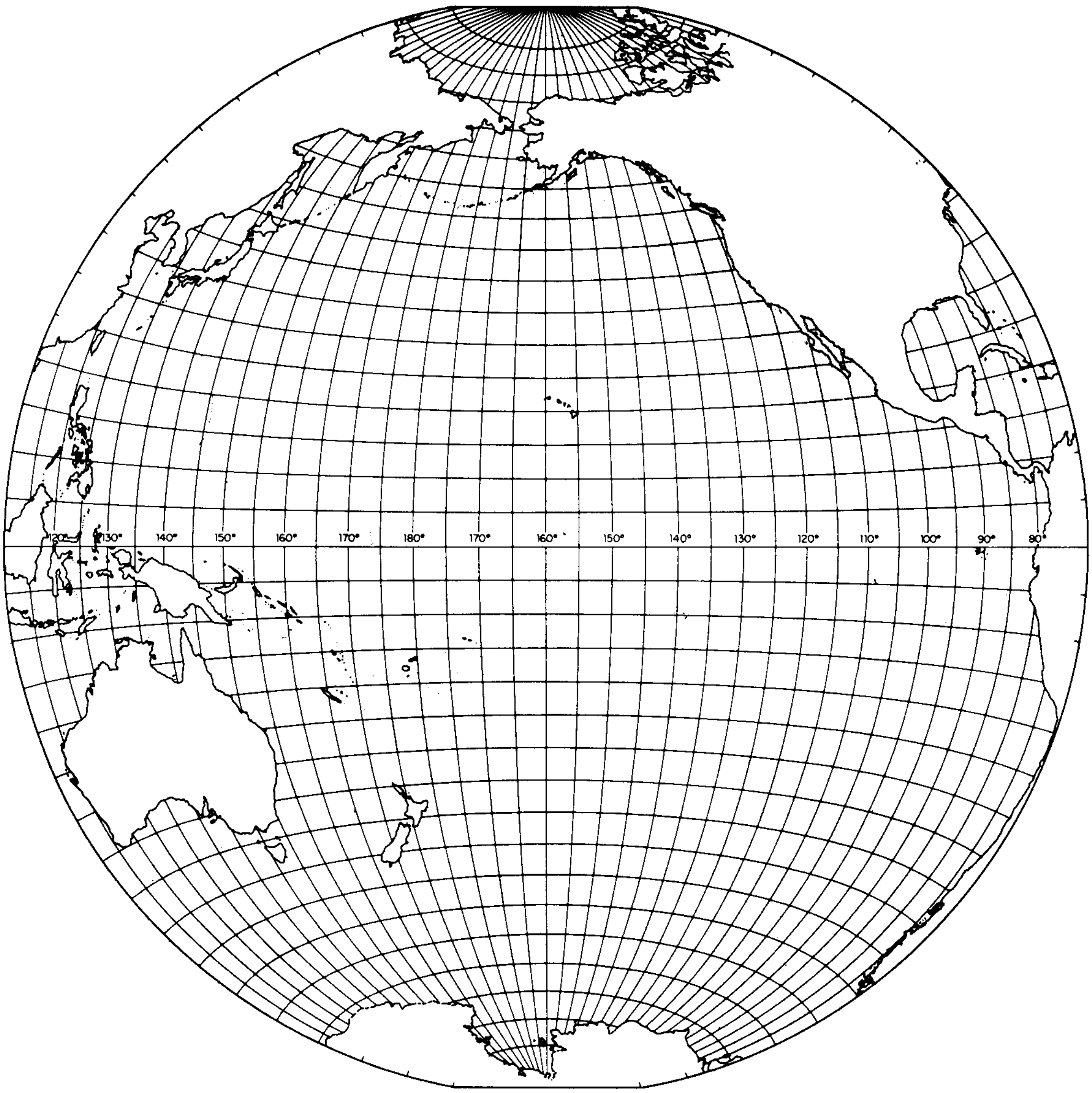

California Cooperative Oceanic Fisheries Investigations

Reports

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CALIFORNIA
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CALIFORNIA DEPARTMENT OF FISH AND GAME
UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL MARINE FISHERIES SERVICE

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

The CalCOFI agencies continued their collaborative investigations of marine systems. Serious budget shortfalls in 1990 impacted programs, particularly for CalCOFI's state organizations. In dealing with current fiscal constraints, we gave top priority to continuing oceanographic and fisheries measurements in the California Current. All four quarterly CalCOFI cruises surveying the southern California sector of the California Current were completed. Maintaining the seagoing time series, for which the CalCOFI program is world famous, is especially critical in view of the emerging importance of global change.

The sardine resource continued to recover, and the CalCOFI agencies continued to monitor its status. At a sardine management workshop involving state, federal, industrial, and Mexican federal biologists, various sources of information, including data from aerial surveys (fish school spotters) and CalCOFI surveys, led participants to conclude that the spawning biomass had increased to about 100,000 tons, a level similar to that of the early 1960s. A draft policy for sardine management during recovery and postrecovery phases was outlined. As a result of this information, the California Department of Fish and Game (CDFG) opened a 2,499-ton fishery quota on January 1, 1991; the southern allocation (1,666 tons) was landed in two days, completing the shortest season to date. This was the first time the quota had been increased above 1,000 tons since sardine fishing was reopened in 1986. A reexamination of the workshop information led to a second quota increase and a total 1991 quota of 6,150 tons. The 2,434 tons added to the southern allocation were landed in four 24-hour fishing periods.

A 30-day sardine egg survey was conducted to assess the spawning biomass and trends in sardine abundance. No other cruises were conducted by the CDFG because of budget constraints.

The annual groundfish survey was conducted off the coast of Oregon in January and February to define the offshore limits and distribution of sablefish eggs, to relate sablefish egg distribution to oceanographic features, and to determine the feasibility of estimating sablefish biomass by the egg production method. It was determined that a successful egg production survey for sablefish off Washington and Oregon would have to extend seaward at least 200 nautical miles, and would require a vessel capable of sampling in heavy seas. Additional groundfish work included a larval production assessment survey, age and stock assessment of thornyheads, and assessment of juvenile rockfish recruitment. We continue to use the CalCOFI collections to describe early life stages and life strategies of various groundfish species.

We used 1990 CalCOFI collections of anchovy eggs and larvae to estimate daily egg production, which was incorporated into a stock synthesis estimate of anchovy spawning biomass. Results indicated that the biomass was greater in 1990 than in 1989. Efforts to improve the stock synthesis estimates continue: in 1990 we confirmed that including aerial survey data yields more precise spawning biomass estimates for anchovy. National Marine Fisheries Service (NMFS) and CDFG scientists revised an amendment to the anchovy Fishery Management Plan to include a description of anchovy habitat, an analysis of how anchovy management affects vessel safety, and a definition of overfishing.

On the quarterly CalCOFI cruises, we have begun comparing data collected with a newly purchased CTD (with a rosette for water bottles) and data from the standard hydrographic casts, with the intent of shifting entirely to the CTD. Also, data on temperature, salinity, and chlorophyll are now collected electronically from the seawater system while the vessel is under way. An acoustic Doppler current profiler, which allows measurements of zooplankton volume and current speed, depth, and direction, was installed on the *David Starr Jordan*. Data are summarized once per minute while the vessel is under way, resulting in a complete profile averaged over 300 meters. A 1-m^2 multiple opening/closing net environmental sampling system (MOCNESS), which will be used for Dover sole egg production surveys, was purchased. Studies on how continental slope fishes adapt physiologically to the oxygen minimum zone, and on the genetic differences among groundfish stocks and other marine species will be conducted at a new NMFS physiology-genetics laboratory in La Jolla. The CDFG 80-ft RV *Mako* was added to the CalCOFI fleet in July, but is not expected to be fully staffed and operational until the beginning of 1992. With the addition of the *Mako*, the CDFG will regain the ability to do offshore work, which was lost with the sale of the RV *Alaska* in 1980.

International cooperation remained an important aspect of CalCOFI. At the fourth annual meeting of MEXUS-Pacifico, the focus of our cooperative fisheries research agreement was expanded to include work on marine mammals and sea turtles. We continued our routine exchange of fisheries and biological data; in the future we plan to share additional information, including data from CalCOFI, aerial, and Scripps Pier temperature surveys. A second workshop on aging pelagic fishes was held in Ensenada, Baja California. CalCOFI continued to support the Spanish-Portuguese Sardine Anchovy Recruitment Program (SARP). We assisted with the application of egg production technology, and enjoyed a visit by a SARP scientist. Also, plans were made for a cooperative NMFS-Soviet cruise in 1991 to collect information about the reproduction of jack mackerel.

In 1990 the CalCOFI Conference was held at Asilomar Conference Center in Pacific Grove for the first time. As we had hoped, more scientists and students from northern locations attended. In the future, we plan to alternate the location of our annual conferences between the south and the north. The conference symposium focused on a wide range of recent and developing applications of oceanography to fisheries problems. Some of the papers from that symposium are printed in this volume.

The Committee wishes to acknowledge the recent retirement of Herbert W. Frey from the CDFG. Amid his accomplishments and responsibilities over the last three decades, Herb found time to serve CalCOFI as coordinator, *Reports* editor, and committee member. He also served as an executive secretary for the Marine Resources Committee, which was established by the same legislation that provided the initial funding for the California Cooperative Sardine Research Program, the forerunner of CalCOFI. We wish Herb a long and busy retirement.

Many thanks to the officers and crews who help us with our work on the University of California RV *New Horizon*, the National Oceanic and Atmospheric Administration ship *David Starr Jordan*, and the Southern California Ocean Studies Consortium RV *Yellowfin*. The Committee also wishes to thank everyone who contributed to Volume 32 of *CalCOFI Reports*: editor Julie Olfe for her patient assistance, gracious accommodation of numerous delays — which were beyond her control — in the manuscript process, and diligent efforts to keep publication of the *Reports* on track in spite of a changing schedule; Spanish editor Maria Vernet; George Hemingway for technical assistance at the conference; Mary Larson and Diana Watters for assistance with conference registration; and Coordinator Patricia Wolf. The reviewers and editorial consultants for this volume were Larry Allen, Dan Anderson, William Balch, George Boehlert, Edward Brinton, Mark Carr, David Checkley, Calvin Chun, Jeff Cross, John Cullen, Edward DeMartini, Thomas Hayward, Michael Horn, John Hunter, Larry Jacobson, Richard Klingbeil, Sharon Kramer, Ralph Larson, Alec MacCall, Kathleen Matthews, Richard Parrish, William Pearcy, Stephen Ralston, Jeff Runge, Donald Schultze, Paul Smith, Erik Thuesen, and Elizabeth Venrick.

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REVIEW OF SOME CALIFORNIA FISHERIES FOR 1990

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Total landings of fishes, crustaceans, echinoderms, and mollusks decreased 19% from 1989. This is the second consecutive year that California has experienced a decline in total landings. The 1990 landings exceeded the 1985 low by only 7%, and are 33% below the 10-year average.

Pelagic wetfish landings declined 29% from last year. This marked the first drop since the recent upward trend in wetfish landings began in 1985, and the lowest total since 1986. Landings decreased for all species except northern anchovy (table 1).

Groundfish landings declined slightly, but the species composition was similar to last year's. California halibut landings were the lowest in ten years.

Landings of swordfish declined to an 8-year low, and landings of the common thresher shark to a 12-year low, but the mako shark catch increased about 33%. Albacore landings increased slightly over last year's record low, but were still only 12% of the 25-year average.

The red sea urchin fishery continued as one of the major fisheries in the state; landings in northern California decreased 17% from 1989, while southern California landings increased.

The sport catch increased slightly from 1989, with record high catches of dolphinfish, yellowtail, and tropical tunas. The high availability of these fish was related to the warmer oceanic conditions that prevailed off southern California for the latter part of the year.

PACIFIC SARDINE

In 1989 the California Department of Fish and Game (CDFG) conducted two sea surveys to assess the spawning biomass of the Pacific sardine (*Sardinops sagax*). The egg production area method (EPAM) was used to determine if the observed spawning area exceeded the critical spawning area of 2,300 nautical miles^2 (n.mi.^{2}), which is considered indicative of a 20,000-ton spawning biomass. The presence of sardine eggs indicated spawning in an area of 3,280 n.mi.^{2} Because current state regulations allow a directed sardine fishery when the spawning biomass exceeds 20,000 tons, the survey results made possible the January 1, 1990, opening of the fifth consecutive 1,000-ton directed fishery since the current sardine management law went into effect in 1974.

The 1,000-ton quota was divided between northern California (20% reserved for landings north of Point Buchon; figure 1) and southern California (80% reserved for landings south of Point Buchon).

TABLE 1
Landings of Pelagic Wetfishes in California (Short Tons)

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1971	149	44,853	78	29,941	120	15,759	90,900
1972	186	69,101	54	25,559	63	10,080	105,043
1973	76	132,636	28	10,308	1,410	6,031	150,489
1974	7	82,691	67	12,729	2,630	14,453	112,577
1975	3	158,510	144	18,390	1,217	11,811	190,075
1976	27	124,919	328	22,274	2,410	10,153	160,111
1977	6	111,477	5,975	50,163	5,827	14,122	187,570
1978	5	12,607	12,540	34,456	4,930	18,899	83,437
1979	18	53,881	30,471	18,300	4,693	22,026	129,389
1980	38	47,339	32,645	22,428	8,886	16,957	128,293
1981	31	57,659	42,913	15,673	6,571	25,915	148,762
1982	145	46,364	31,275	29,110	11,322	17,951	136,167
1983	388	4,740	35,882	20,272	8,829	2,001	72,112
1984	259	3,258	46,531	11,768	4,241	622	66,679
1985	653	1,792	38,150	10,318	8,801	11,326	71,040
1986	1,283	2,105	45,503	12,209	8,405	23,454	92,959
1987	2,309	1,595	45,890	13,055	9,258	22,028	94,135
1988	4,172	1,618	47,278	11,379	9,721	41,040	115,208
1989	4,308	2,700	39,825	21,820	10,134	45,076	123,863
1990*	3,445	3,528	35,047	5,144	8,938	31,304	87,406

*Preliminary

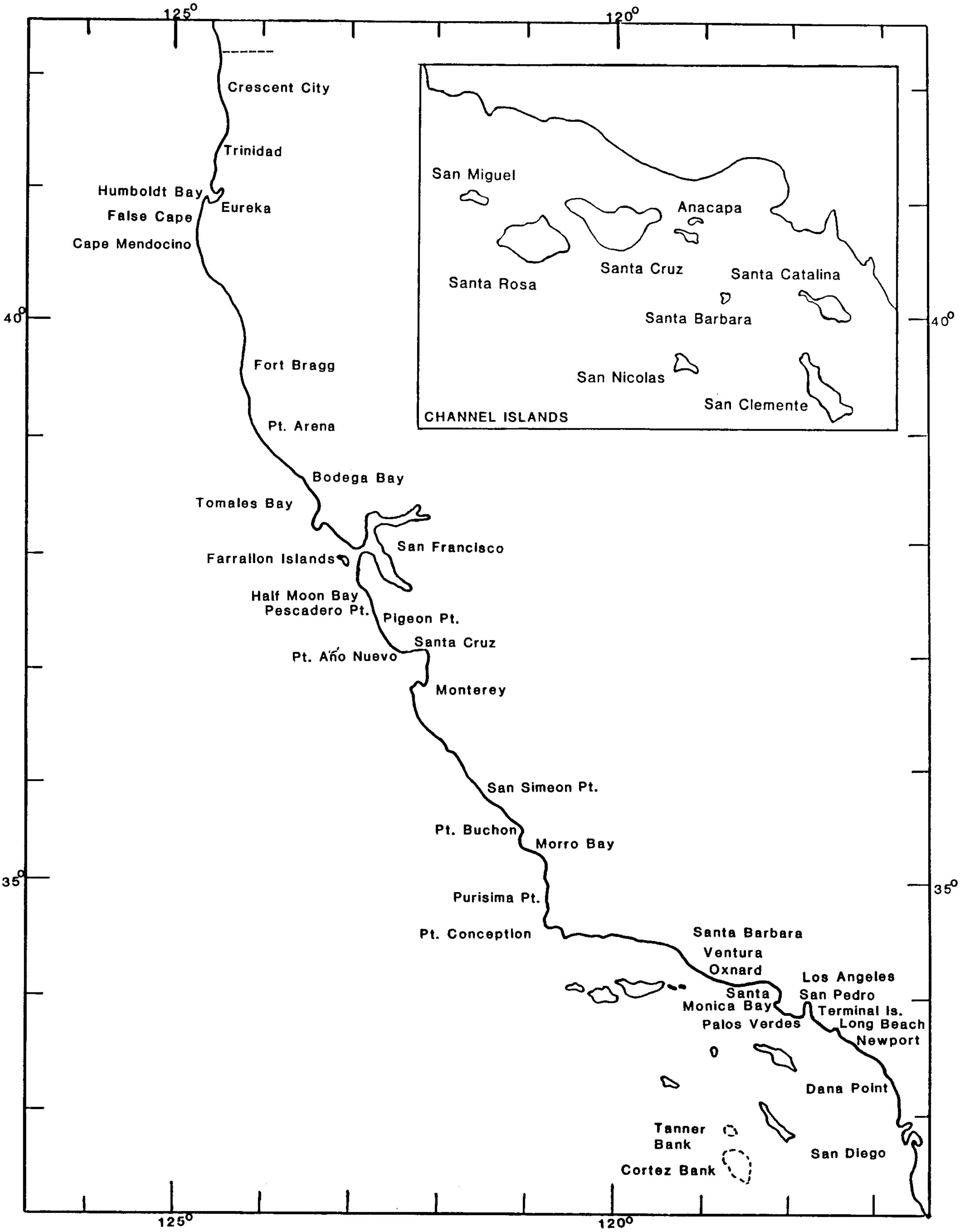

Figure 1. California ports and fishing areas.

In addition to the directed fishery, there was a 350-ton quota for live bait (opened January 1, 1990) and a 250-ton quota for dead bait (opened March 1).

The southern California allocation of the directed fishery was landed in six days, and the fishery was closed on January 6, six days earlier than in 1989. The period was shortened because many sardines were caught close to the Los Angeles Harbor. The catch totaled 1,181 tons, with 84% of the landings consisting of pure loads of sardines. In 1989, only 34% of the landings contained 100% sardines. Most of the catch was used for human consumption, the remainder for dead bait and pet food.

The northern California directed fishery began in late January and was closed on April 25. The catch totaled 217 tons. The proportion of pure loads of sardines in the catch (88%) was lower than during the 1989 fishery, when almost all landings were pure loads.

The dead bait fishery quota is allocated among three geographic areas: 75 tons are reserved for landings north of Pescadero Point, 50 tons for landings between Pescadero Point and Point Buchon, and the remaining 125 tons for landings south of Point Buchon. The southern dead bait fishery was closed on March 2, 1990, after two days of fishing. Most of the catch (188 tons) comprised pure loads of sardines. The central dead bait allocation was met on April 10, and the landings (50 tons) consisted entirely of pure loads. No landings were made toward the northern dead bait allocation in 1990.

The occurrence of sardines in the live bait fishery, as estimated from bait haulers' monthly logbooks, amounted to 595 tons. Sardines represented 10.5% of the total take for live bait. Approximately 90% of the sardine live bait catch was landed in July, August, and September, with young-of-the-year sardines most abundant during July. Total landings exceeded the annual 350-ton live bait quota by 70% because of an error in tallying the logbook catch.

The tolerance limit for sardines landed incidentally in the mackerel fishery remained at 35% by weight throughout the year. The incidental sardine catch totaled 1,214 tons, and represented 2.9% of total mackerel fishery landings. This was the third consecutive year that the proportion of sardines in the mackerel catch decreased. In 1989, sardines made up 4.5% of the mackerel catch; in 1988, 5.5%. Incidental sardine landings decreased 65% from 1989.

The total 1990 landings of sardines from all sources (directed, dead bait, live bait, and incidental) was 3,445 tons (table 1). This was the second year in which total landings of sardines declined. The decrease in 1990 was largely due to a 34% decline in total mackerel landings (mackerel were unavailable to southern California fishermen during the first part of the year, and there was also a lengthy price dispute).

In July 1990, the CDFG conducted an EPAM survey to evaluate the sardine spawning biomass. The survey covered the waters off southern California from Purisima Point to the Mexican border, from close to shore to as far out as 200 miles. The observed spawning area of 1,480 n.mi.^{2} was 62% smaller than the area observed in 1989. During 1990, spawning occurred along the coast from Santa Barbara to Long Beach, and inshore of the Santa Barbara Channel Islands. No spawning was observed at the Tanner and Cortez banks (figure 1). The absence of spawning at the banks, and decreases in overall spawning may be due in large part to an early (before the survey) increase in water temperature in the Southern California Bight.

A sardine management workshop involving state, federal, industrial, and Mexican federal biologists was held by the CDFG in September 1990. A review of the status of the sardine resource led to an estimate that the current biomass of age two and older fish is 100,000 tons, and to a recommended harvest level of 5% (including all sources of catch). As a result, a 2,499-ton directed quota (with about 3,000 tons reserved for other sardine quotas and incidental landings) was scheduled for 1991.

Legislation was enacted in 1990 to change the allocation of the directed fishery quota: one-third is reserved for landings north of San Simeon Point, and the remaining two-thirds are reserved for landings south of the point. Additionally, the northern portion may not be taken until August 1; this provision was included because sardines are usually not available in that area until later in the year.

PACIFIC MACKEREL

At the start of 1990, there were 15,447 tons of Pacific mackerel (*Scomber japonicus*) already landed towards the total for the 1989–90 fishing season (July 1 through June 30). There were no quota restrictions, since the biomass was estimated at 263,000 tons. Current legislation allows an open fishery when the biomass exceeds 150,000 tons.

Landings were low during the first three months of the year, totaling only 5,633 tons. The presence of bluefin tuna (*Thunnus thynnus*) off Santa Barbara, the directed sardine (*Sardinops sagax*) fishery, and a call for squid (*Loligo opalescens*) by the southern California canneries accounted for decreased effort and low catch during the month of January. Landings remained low in February and March despite fishing effort being directed back to mackerel. Unpredictable weather in March, coupled with complaints from fishermen of a high abundance of incidental sardines (over 35%), which prevented them from landing their catch, and low availability of mackerel, kept the total landings small.

Rough weather and the high incidence of sardines continued to keep the landings low during the first two months of the second quarter. Few vessels left port during May, but those that did brought in several landings of large (300–500 mm FL) Pacific mackerel. In June more Pacific mackerel were available, and fishing effort increased, raising the catch over the previous months. Mostly large mackerel were caught, and 4,100 tons were landed during this quarter.

The 1989–90 season closed on June 30, with a total catch of 25,908 tons of Pacific mackerel. The 1989–90 landings decreased 44% from the previous season. The species composition of the total statewide mackerel landings was 54% Pacific mackerel, 41% jack mackerel, and 5% Pacific sardines. During the 1988–89 season, the total landings had comprised 80% Pacific mackerel, 16.5% jack mackerel, and 3.5% Pacific sardines. Landings in northern California made up only 0.3% of the total, compared with 1% during the 1988–89 season.

The 1990–91 season opened on July 1, 1990, with no quota restrictions, since the biomass was estimated to exceed 150,000 tons. In fishery samples from January through June 1990, the 1989 year class made up 14% of the landings, the 1988 year class, 48%. From July through December 1990 these two year classes dropped to 8% and 21% of the landings. Many Pacific mackerel continued to be available during the third quarter, and landings totaled 17,395 tons. Most of the landings were pure Pacific mackerel.

High landings continued through October, with 5,313 tons landed for the month. The catch decreased in November, due in part to rough seas and a maintenance shutdown of the United Food Processors cannery. In addition, the fleet actively fished for mackerel for only two days in December before directing its effort to squid. The holiday season may also have reduced the fishing effort at the end of the quarter. Only 7,190 tons were landed during the quarter.

By year's end, 24,586 tons of Pacific mackerel had been landed toward the 1990–91 season total. Pacific mackerel landings for 1990 totaled 35,047 tons (table 1), with 93% of the landings made in southern California. The total was a 12% decrease from 1989. When compared to the average landings over the previous five years, the 1989 catch decreased 20%. The reduced availability of Pacific mackerel during 1990 may have been due to warmer-than-usual water conditions that displaced mackerel farther to the north, particularly during the first half of the year.

MARKET SQUID

Market squid (*Loligo opalescens*) landings in 1990 were 31,304 tons (table 1): 22,451 tons (72%) were from the southern California fall-winter fishery, and 8,710 (28%) were from the central California (Monterey Bay area) spring-summer-fall fishery (table 2). The remainder (143 tons) came from areas north of the Monterey Bay area. This is a 31% decrease in statewide landings from the 45,076 tons landed in 1989. Southern California landings in 1990 were 40% below those in 1989; landings in the Monterey Bay area were 11% higher; and landings from north of Monterey Bay were up dramatically from the 4 tons landed in 1989. The total 1990 ex-vessel value was approximately $4.3 million, 27% below the $5.9 million ex-vessel value recorded in 1989.

Ex-vessel prices typically fluctuate from year to year and during the year. In 1990, prices in southern California remained lower than those paid in central and northern California. Southern California prices ranged from $110 to $150 per ton and averaged about $130 per ton. Monterey Bay area ex-vessel prices ranged from about $130 to $200 per ton and averaged $160 per ton. In the past twenty years the ex-vessel price has been as high as $600 per ton.

TABLE 2

California Market Squid Landings (Tons)

Year	Monterey	Southern California	Other	State total
1970	4,314	7,982	0	12,296
1971	8,323	7,435	trace	15,758
1972	6,129	3,950	0	10,079
1973	620	5,410	0	6,030
1974	7,248	7,205	0	14,453
1975	2,495	9,316	trace	11,811
1976	2,511	7,642	0	10,153
1977	2,234	11,887	1	14,122
1978	10,326	8,571	trace	18,897
1979	14,183	7,842	1	22,025
1980	7,856	9,100	1	16,957
1981	14,134	11,779	2	25,915
1982	11,670	6,276	5	17,951
1983	542	950	509	2,001
1984	431	84	107	622
1985	4,202	7,039	85	11,326
1986	6,049	16,488	917	23,454
1987	5,269	16,665	94	22,028
1988	5,329	34,634	426	40,389
1989	7,877	37,195	4	45,030
1990*	8,710	22,451	143	31,304

*Preliminary

Most squid were frozen for human consumption, while some were sold fresh or used for dead and live bait. The squid live bait fishery is centered in southern California. Much of the squid processed in California is exported.

Annual squid landings since 1970 have averaged 17,748 tons. Landings during years characterized by El Niño Southern Oscillations (ENSO), such as 1973, 1983, and 1984, were unusually low. However, large increases in southern California landings in recent years, and increased fishing effort in other areas suggest that the resource has been underutilized.

During 1970–85, southern California landings averaged 54% of total statewide landings. Since 1986, they have risen dramatically, averaging nearly 79% of total landings. But in 1990, southern California landings decreased for the first time in six years. This may be because many of the squid landed in 1990 were very small, averaging over 15 per pound. Some dealers had difficulty marketing these small squid and set trip limits for their boats, or quit buying small squid altogether. Squid landings were 11,650 tons in the Santa Barbara area in 1990, very close to the post-ENSO annual average of 11,700 tons. Thus the overall decrease in southern California landings was primarily at Terminal Island and San Pedro ports.

Since the 1983–84 ENSO, annual landings in Monterey Bay have averaged approximately 6,240 tons, slightly above the 20-year average of 6,213 tons, but well below average annual landings of 11,600 tons during the peak period of 1978–82. Of the 8,710 tons landed in Monterey Bay in 1990, 978 tons were landed at Santa Cruz. Most of these squid were caught north of Santa Cruz near Año Nuevo Island, an area that has been fished only sporadically since the ENSO years.

Attracting lights were approved for southern Monterey Bay in 1989 and are used by most of the Monterey Bay fleet. However, they continue to be controversial. Fishermen opposed to the lights contend that they disrupt squid spawning and that small boats cannot compete with large boats with large light systems. Those in favor of the lights note that southern California fishermen have used them for many years without any apparent adverse effects on spawning. They also claim that lights allow them to use shallower nets that can be fished off the bottom, thus protecting squid eggs attached there.

Continuing low ex-vessel squid prices and difficulties in finding enough crew have heightened interest in half-purse drum seines in the Monterey Bay area. Only a few boats switched to half-purse drum seines when they were first allowed in 1989, primarily because major capital outlay that year was for powerful and expensive systems of attracting lights. In 1990, however, more boats switched to half-purse drum seine gear.

PACIFIC HERRING

Annual statewide landings for the 1990 roe herring fishery (*Clupea harengus*) were 8,938 tons, a 10.8% decrease from 1989 (table 1). Statewide landings for the 1989–90 season (November to March) totaled 8,962 tons. San Francisco Bay gill net permittees landed 6,723 tons, approximately 6% over the established quota of 6,321 tons. Round haul permittees fishing in San Francisco Bay landed 2,239 tons, which was roughly 82% of the 2,736-ton quota. In Bodega Bay, permittees landed 95 tons (200-ton quota); Humboldt Bay permittees landed 61 tons (60-ton quota); and Crescent City landings totaled 33 tons (30-ton quota). Ex-vessel prices for roe herring ranged from $800 to $1,400 per ton.

San Francisco Bay eggs-on-kelp permittees had a very good 1989–90 season. They processed 107 tons (110-ton quota) of eggs-on-kelp; in 1988–89, landings were 47 tons (64-ton quota). The number of permittees allowed in this fishery increased from six to ten for the 1989–90 season.

Spawning biomass estimates were determined for San Francisco, Tomales, and Bodega bays. The 1989–90 season estimate for San Francisco Bay was 64,500 tons, a 2% decline from the previous season. The Tomales Bay spawning biomass was estimated at 345 tons from spawning-ground surveys. Hydroacoustic surveys in Bodega Bay resulted in a biomass estimate of 350 tons. Tomales Bay and Bodega Bay herring are considered one stock; therefore the total spawning biomass, including the catch missed by hydroacoustic surveys (95 tons), is estimated at 790 tons. This is roughly double the 1988–89 estimate of 380 tons.

This was the third consecutive poor season in Tomales Bay. However, the age structure of the sampled catch has remained relatively stable, which does not suggest a population in decline. Drought conditions, which have persisted for four years and have resulted in low freshwater runoff into Tomales Bay, may be the primary reason why herring have not spawned near historic levels in the bay.

Results of young-of-the-year (YOY) surveys in San Francisco Bay suggest a weak 1990 year class. Very few YOY herring were found in midwater trawl tows at stations located throughout the bay.

The 1990–91 roe herring quotas statewide remained unchanged from the 1989–90 season. The current regulations will continue while the Department of Fish and Game is complying with California Environmental Quality Act requirements to assess the fishery's effects on other resources.

GROUNDFISH

California's 1990 commercial groundfish harvest was 38,849 metric tons (MT), with an ex-vessel value of approximately $30,347,000. All-species 1990 landings decreased approximately 4%, or 1,661 MT, from the 1989 level (table 3). Rockfish (*Sebastes* spp.), Dover sole (*Microstomus pacificus*), sablefish (*Anoplopoma fimbria*), and thornyheads (*Sebastolobus* spp.) were the principal species harvested in 1990. Increases in harvest were noted for rockfish and thornyheads, while decreases occurred in most of the other categories.

The general historical pattern of landings by gear changed during 1990. Bottom and midwater trawl landings continued to dominate total landings, but their contribution dropped from 86% in 1989 to 77% in 1990. While the trap component remained about the same (2%), both the line and setnet components almost doubled, to 12% and 8%.

Federal and state regulations for 1990 affected the harvest of widow rockfish (*Sebastes entomelas*), sablefish, Dover sole, and thornyheads. Trip limits were again used as the primary means of limiting landings. At current levels of fishing effort, trip limits offer the most viable method of meeting the Pacific Fishery Management Council (PFMC) objective of a year-round groundfish fishery.

In late 1989, the PFMC set the 1990 Washington-Oregon-California (WOC) widow rockfish quota at 9,800—10,000 MT, with the intention to manage for 9,800 MT. The allowed catch represented a considerable drop from the 1989 quota of 12,000 MT. Trip limits of 10,000 pounds per week or 25,000 pounds per two weeks were the most restrictive ever imposed. On October 11, the trip limit was reduced to 3,000 pounds, and on December 12 the fishery closed. Because of a late-season surge in effort, the total 1990 landed catch of 10,533 MT in the WOC area was 8% over the quota. California landings of 1,975 MT were 19% of the WOC total.

TABLE 3
California Groundfish Landings (Metric Tons)

Species	1989	1990	Percent change
Dover sole	7,713	6,419	−17
English sole	1,015	912	−10
Petrale sole	840	691	−18
Rex sole	735	570	−22
Other flatfish	858	1,429	67
Widow rockfish	1,566	1,975	26
Other rockfish	9,978	11,019	10
Thornyheads	5,319	5,391	1
Lingcod	1,262	1,118	−11
Sablefish	3,583	3,531	−1
Pacific whiting	7,302	5,519	−24
Other groundfish	339	275	−19
Total	40,510	38,849	−4

Nontrawl sablefish management underwent several changes in 1990. The PFMC initially recommended revising the trawl:nontrawl allocation from 58%:42% to 62%:38%, and delaying the opening of the nontrawl season from January 1 to April 1. The secretary of commerce did not approve these management measures before the fishery opened on January 1. Therefore the nontrawl trip limit in effect at the end of 1989 remained in effect until the PFMC recommendations were formally disapproved. On January 31 the trip limit was rescinded, and nontrawl fishing was unrestricted. The 1990 nontrawl allocation, using the 1989 ratio of 58%:42%, was 3,612 MT. A trip limit went into effect in June and was adjusted in July and again in September. The total landed catch of sablefish by nontrawlers in 1990 was 3,519 MT, approximately 3% less than the quota. California landings accounted for 1,329 MT, or 38% of the nontrawl total.

The 1990 trawl quota for sablefish was 4,998 MT, and landings were restricted to 1,000 pounds or 25% per trip of the deepwater complex (sablefish, Dover sole, thornyheads, and arrowtooth flounder—*Atheresthes stomias*). Fleet size was similar to that of 1989 except that substantial effort from the shrimp fishery shifted to the groundfish fishery in August and September. This caused an increase in the deepwater complex fishery where effort targeted on thornyheads. However, the landings of trawl-caught sablefish also increased, and in September the PFMC was notified that sablefish would become a prohibited species as early as November 8, 1990, if landings were not reduced by 50% during the last quarter. The PFMC responded by changing the definition of the deepwater complex (removing arrowtooth flounder) and placing a 15,000-pound trip limit on the deepwater complex while retaining the sablefish restrictions. The total landed WOC catch of sablefish by trawl in 1990 was 5,199 MT, which exceeded the quota by 4%. California trawl sablefish landings of 2,202 MT made up approximately 44% of WOC landings.

Despite 1990 limits on trip poundage and frequency for the deepwater complex, thornyhead landings were considerably higher than last year, increasing from 7,925 MT to 10,126 MT. The increase resulted from a continuing Asian demand for headed and gutted longspine thornyheads (*Sebastolobus altiveli*). In response to this increase, the PFMC set a 1991 harvest guideline of 7,900 MT and a weekly trip limit of 7,500 pounds. California landed 5,391 MT, or 53%, of the WOC catch. The coastwide catch of Dover sole was 15,795 MT, a decrease of 1,328 MT, which reflects both additional regulations and reduced demand. California landings of 6,419 MT were 41% of total WOC landings. A harvest guideline of 22,500 MT was established for 1991.

A stock assessment of bocaccio rockfish, completed in 1990, indicated a declining resource. Trawl landings of bocaccio were about 2,000 MT annually during the late 1970s. Landings increased to about 4,700 MT by 1981 with the recruitment of the large 1977 year class, but have fallen to just over 1,000 MT since 1985. In 1989 the total landed catch of about 1,800 MT comprised about two-thirds trawl catch, one-sixth setnet catch, and one-sixth recreational catch. The model used in the assessment indicated that the biomass had decreased from about 75,000 MT in 1978 to 7,000 MT in 1990. A significant fraction of the observed decline is due to poor recruitment since 1978. In response to concerns for bocaccio, the PFMC set a 1991 harvest guideline of 1,100 MT and established a trip limit for rockfish of 25,000 pounds with no more than 5,000 pounds of bocaccio south of Coos Bay, Oregon.

PACIFIC WHITING

The combined U.S. and Canadian coastal whiting (*Merluccius productus*) catch for 1990 was 269,500 MT, down from a high of 309,000 MT in 1989. The U.S. portion of the harvest for 1990 was about 183,200 MT: 171,000 MT were taken by domestic joint venture (JV) trawlers; 4,100 MT were taken by domestic at-sea catcher/processors; and 8,100 MT went to shoreside processors. An estimated 68,000 MT of the JV catch were taken off California.

Figure 2. California landings of Pacific whiting, 1977–90.

California shore-based landings of Pacific whiting totaled 5,519 MT in 1990, a 24% decline from the 7,302 MT landed in 1989 (figure 2). The California total accounted for 69% of all shore-based whiting landings made in Washington, Oregon, and California during 1990. The most significant portion of the California catch (5,516 MT) was harvested by five targeting midwater trawl vessels, which delivered whiting at Eureka (1,033 MT) and Crescent City (4,483 MT) over a four-month period (April through July). Five northern California midwater trawlers also took most of the 1989 California harvest, but over a six-month period (March through August). Domestic shore-based processing of whiting in 1990 accounted for only 4% of the U.S. share of the allowable catch for the year.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1989–90 season totaled 4.6 million pounds, slightly less than half of the 1988–89 landings of 9.6 million pounds.

The northern California ports of Crescent City, Trinidad, Eureka, and Fort Bragg (figure 1) received 2.34, 0.54, 0.78, and 0.06 million pounds, respectively, for a total of 3.72 million pounds. This is 4.25 million pounds below the catch of the previous season.

The season opened December 1 in northern California, with the price per pound set at $1.25, similar to the year before. Catch per trap declined rapidly after the first week, and by the middle of the month many fishermen had quit. Most of the landings (86%) were made in December. The season ended on July 15; approximately 375 vessels participated in the fishery.

Reports from trawlers and from fishermen examining stomachs of fishes caught in nearshore waters indicate that the 1989 year class of Dungeness crab is strong. This year class should begin recruiting to the fishery in the 1991–92 season.

The San Francisco area Dungeness crab season opened on November 14. Landings for Bodega Bay were 0.34 million pounds; San Francisco, 0.19 million pounds; and Half Moon Bay, 0.20 million pounds, for a total of 0.73 million pounds. This is less than half of the previous season's total of 1.5 million pounds. Seventy-nine percent of the total landings were taken in November and December. Approximately 200 vessels participated in the fishery.

The ports of Monterey and Morro Bay contributed 0.10 million pounds to the total statewide landings.

PACIFIC OCEAN SHRIMP

For the first time in seven years the statewide landings of Pacific Ocean shrimp (*Pandalus jordani*) declined. The 1990 landings of 8.6 million pounds decreased 35% from the 13.3 million landed in 1989 (table 4). In spite of this decrease, the 1990 landings were still the fifth largest on record. Areas of production were Area A (Oregon border to False Cape) and Area B-1 (False Cape to Point Arena) (figure 1). Area C (Pigeon Point to the Mexican border) reported no catch for the first time since 1978.

Shrimp landings at Area A ports totaled 8.2 million pounds, a 4.3 million-pound decrease from 1989. Like the statewide landings, Area A's landings were the fifth largest ever. Total Area A landings comprised 7.4 million pounds from Area A waters, 18,000 pounds from Area B-1 waters, and 730,000 pounds from Oregon waters. The season opened April 1, with fishermen receiving $.45 per pound. The price paid to the shrimpers increased $.05 per pound approximately every two months until the price reached $.60 per pound, where it remained.

A total of 58 boats (39 single-rigged and 19 double-rigged) delivered shrimp to Area A ports during 1990, an increase of two boats over 1989. Single-rigged vessels had an average seasonal catch rate of 350 pounds per hour, a decrease of 193 pounds per hour from 1989. Double-riggers averaged 634 pounds per hour, down from 842 pounds per hour in 1989.

TABLE 4
California Pacific Ocean Shrimp Landings (1,000s of Pounds)

Year	Area A	Area B-1	Area B-2	Area C	Total
1974	1,674	517	166	5	2,362
1975	3,395	348	1,188	62	4,993
1976	2,674	721	<1	5	3,400
1977	13,026	585	2,029	0	15,640
1978	12,473	2,061	0	0	14,534
1979	4,236	0	4	865	5,105
1980	3,340	174	<1	1,582	5,096
1981	2,945	41	2	1,112	4,100
1982	3,967	12	0	437	4,416
1983	232	0	0	945	1,177
1984	1,340	0	0	154	1,494
1985	3,373	0	0	23	3,396
1986	5,876	0	0	840	6,716
1987	6,599	653	0	671	7,923
1988	10,272	379	0	380	11,031
1989	12,458	833	0	24	13,315
1990*	8,165	519	0	1**	8,685

*Preliminary
**Landed in Area C, but caught in Area A-1.

The 1990 catch exhibited several biological anomalies that seemed to be in response to an extremely weak 1989 year class. Two-year-old males made up 62.7% of the males in the 1990 catch, although they averaged only 0.1% of the males during the previous 10-year period. The 1990 landings had only 18.8% one-year-old shrimp, compared to the 1980–89 average of 80.5%. Primary females (one-year-olds) constituted an average 39.5% of the females during the 1980–89 period but were totally absent from the 1990 catch.

Area B-1 landings were 519,000 pounds, down 38% from 1989. Over 50% of the season's landings occurred in the first two months of the season, and one vessel accounted for 44% of the total. During the 1990 season, 62% of the catch was sold at an ex-vessel price of $0.45 per pound, with the balance bringing $0.50 to $0.60 per pound.

A total of 72 landings were made by six single-rigged vessels. These vessels had an average seasonal catch rate of 441 pounds per hour. The CPUE started at 607 pounds per hour in April and declined to 175 per hour in August. Count per pound was below 100 for the first three months of the season and slightly over for the remainder. One-year-old shrimp made up 21% of the sampled catch in April, and steadily increased to 80% by August. No samples were taken in September or October. The percentage of females declined from a high of 35% in April to 17% in August. Gravid females made up 3% of the females in April and 29% in May.

SWORDFISH AND SHARKS

Landings of swordfish (*Xiphias gladius*) in 1990 fell to 1.9 million pounds, a 32% decline from the previous year's total, and the lowest level in eight years (table 5). Since swordfish are highly migratory and occur off Baja California, this species is harvested by both Mexican and American fishermen. The decline in recent landings may be the cumulative effect of increased effort from both fishing groups, although current Mexican landing data are unavailable. Harpoon fishermen again reported a dismal year, with only 410 fish taken; this catch nearly equals last year's. Drift gill netters saw the catch drop to 9,000 fish, a decline from 11,000 in 1989.

Catch-per-unit-effort (CPUE) for gill net gear declined slightly from 2 fish per day in 1989 to 1.6 fish per day in 1990, while CPUE for harpoon gear remained unchanged at 0.3 fish per day. Major fishing areas were similar to last year: the three main ones were off San Francisco, Morro Bay, and San Diego.

TABLE 5
Landings of Selected Shark Species and Swordfish (Pounds)

Year	Shortfin mako shark	Swordfish	Common thresher shark	Pacific angel shark
1977	19,911	511,388	129,522	366
1978	26,765	2,604,233	302,054	82,383
1979	35,079	586,529	735,726	128,295
1980	154,529	1,197,187	1,805,978	110,037
1981	274,217	1,142,897	1,973,411	268,640
1982	527,006	1,677,020	2,396,960	317,953
1983	322,854	2,601,600	1,722,056	351,344
1984	239,687	4,429,540	1,662,587	632,937
1985	225,535	5,196,685	1,540,770	1,237,810
1986	473,608	3,845,932	606,583	1,241,130
1987	602,718	2,741,015	525,076	940,187
1988	488,136	2,484,428	549,516	487,278
1989	388,322	2,850,734	649,174	268,252
1990*	576,428	1,872,910	466,217	250,810

*Preliminary

TABLE 6
California Halibut Landings (Metric Tons)

Year	North of Pt. Conception	South of Pt. Conception	Total
1977	25	186	211
1978	34	165	199
1979	54	205	259
1980	90	231	321
1981	163	409	572
1982	206	339	545
1983	256	248	504
1984	153	345	498
1985	144	429	573
1986	240	312	552
1987	192	347	530
1988	229	276	505
1989	305	245	550
1990*	189	230	419

*Preliminary

Common thresher shark (*Alopias vulpinus*) landings in California totaled 466,000 pounds, a decline of 28% from 1989 totals and a twelve-year low. Thresher sharks were taken all along the California coast, with more than 53% of the landings in southern California. Market sampling data indicate that the fishery continues to harvest juvenile fish, but very few adults.

Shortfin mako shark (*Isurus oxyrinchus*) landings increased by 33% over last year's figures, reaching over 576,000 pounds. Of this total, 30% (173,000 pounds) was taken by the experimental drift longline fishery, and 70% (403,000 pounds) by the drift gill net fishery. The experimental drift longline fishery targets directly on shortfin mako shark, while the drift gill net fishery captures these fish incidentally with swordfish and thresher sharks. Drift longline length-frequency data indicate that the catch consists of one-, two-, and three-year-old fish. Because of CDFG fiscal problems, the drift gill net fishery was inadequately sampled for a length-frequency distribution.

Pacific angel shark (*Squatina californica*) landings were 251,000 pounds, the lowest level in ten years. Landings continued to be affected by a number of factors, including low market demands, reduced availability, and a minimum size limit. The Santa Barbara–Ventura area continued to be the major fishing location.

CALIFORNIA HALIBUT

California halibut (*Paralichthys californicus*) landings in 1990 were 419 MT, 24% below the 550 MT recorded in 1989 (table 6). The 1990 landings are 6% below the 14-year average of 446 MT and are the lowest recorded since the 1980 landing of 321 MT. During 1990, 55% of the landings were made south of Point Conception. The remaining 45% were made north of Point Conception, a 38% decrease from 1989. This large decrease in central and northern California landings is most likely due to increased restrictions on the use of entangling (gill and trammel) setnets, and more restrictive seasonal and landing conditions for the nearshore experimental trawl fishery for California halibut. The experimental trawl fishery began in 1986 as an effort to mitigate the effects of increasing nearshore closures on the use of setnets in central California.

The highest landings of California halibut in 1990 occurred during July (29 MT) and August (33 MT). Entangling nets brought in 62% of all halibut taken, followed by trawl (27%), hook-and-line (10%), and less than 1% for remaining miscellaneous and unspecified gears. Most of the trawl-caught halibut (84%) and hook-and-line-caught halibut (89%) were taken off central California. Most of the halibut caught in entangling nets (79%) were taken off southern California. Ex-vessel prices for California halibut typically ranged from $1.00 to $3.50 per pound and averaged $2.37 per pound. Total ex-vessel value was approximately $2.2 million, compared to $2.7 million in 1989.

CALIFORNIA SPINY LOBSTER

The southern California spiny lobster (*Panulirus interruptus*) fishery landed 729,000 pounds during the 1989–90 season (first Wednesday in October to first Wednesday after March 15), making it the highest season since 1955–56, when 790,000 pounds were landed.

The highest recorded landings of lobster from California waters were 1.1 million pounds, taken in the 1949–50 season. Seasonal landings generally declined over the next 25 years, reaching a low of 152,000 pounds in 1974–75. Since then, there has been a general upward trend.

Landings were fairly stable for the first eight of the past ten seasons, ranging between 400,000 and 500,000 pounds. The catch then increased to 668,000 pounds for the 1988–89 season, and this season was 61,000 pounds (9.1%) greater, raising the 10-year average to 511,000 pounds.

A special permit is required to fish commercially for lobsters. The number of permittees peaked at 440 during the 1984–85 season and then declined to 303 in 1988–89. Last year there was a slight increase, to 341 permittees. The average number for the past ten seasons has been 361.

Although the number of permittees has declined, there are indications that fishing efforts have increased. According to CDFG wardens, the average number of traps per fisherman has been increasing. Also, the bulk of the catch is being made earlier in the season, which suggests an abundance of fishing gear. Since 1980–81, the portion of the catch taken in the first two months of each season has increased from 51% to 68%.

In 1989–90, the ex-vessel price averaged $5.50 per pound. With landings of 729,000 pounds, the fishery was worth $4 million to the fishermen; this was a $400,000 (12%) increase over the previous season.

ALBACORE

In 1990, albacore (*Thunnus alalunga*) landings in California totaled 971 tons. This was a 6% increase from 1989's record low of 914 tons, but only 12% of the 25-year average (7,997 tons). The number of California boats participating in the 1990 fishery decreased by 30% from 1989. However, fishing success for the fleet was good: 63 out of 157 boats landed over one ton of albacore during the season.

The 1990 season had a false start in late April when an intrusion of warm water created a corridor along the coast and brought albacore up from the Guadelupe Islands. By mid-May, albacore were being caught as far north as Bodega Bay. Unfortunately, strong winds developed, the corridor collapsed, and fishing stopped at the end of May. As in recent years, the true start occurred in July, when sport boats located albacore off northern Baja California, primarily around Geronimo Island and Cape Colnett. The fish ranged in size from 10 to 16 pounds, with 25-pound fish taken occasionally. In addition, a number of purse seine vessels caught albacore, as well as subtropical species such as skipjack and bluefin tuna, around the Coronado Islands and Sixty-Mile Bank. Although a good sport fishery developed in southern California, and several commercial fishing boats had limited success, there was clearly not enough albacore to maintain a strong commercial effort south of Point Conception. In August, most albacore boats were working between Newport, Oregon, and the Columbia River, and offshore 400 miles. In September, jig boats worked farther north to the Queen Charlotte Islands, British Columbia, and stayed in the vicinity until weather drove most of them south in October. Vessels that headed south in September and October ran across large schools of albacore between Fort Bragg and Cape Mendocino, and caught 50 to 100 fish per day. But these schools were transitory, and disappeared after a day or two.

Pan Pacific Cannery and the Western Fishboat Owners Association (WFOA) set the 1990 price for albacore at $1,100 per ton for fish 7–9 pounds and $1,700 per ton for fish greater than 9 pounds. The WFOA also agreed to a $100 per ton shipping fee for fish landed at buying stations. The 1990 agreement increased last year's prices by $100 and $200 per ton. The increase may have resulted partly from a decreased catch by the Japanese longline fleet, and, in turn, the uncertainty of albacore availability in the eastern Pacific.

Although the 1990 season was slightly better than the 1989 season, total California landings fell short of the historically high numbers experienced before 1985 (figure 3). The causes for this were two-fold. First, the migration path seems to have shifted, moving most albacore into northern Pacific waters and shifting fishing effort and landings away from California. Second, the albacore population on both sides of the Pacific seems to be declining, as evidenced by the lack of three- and four-year-old fish. These fish normally make up most of the commercial catch.

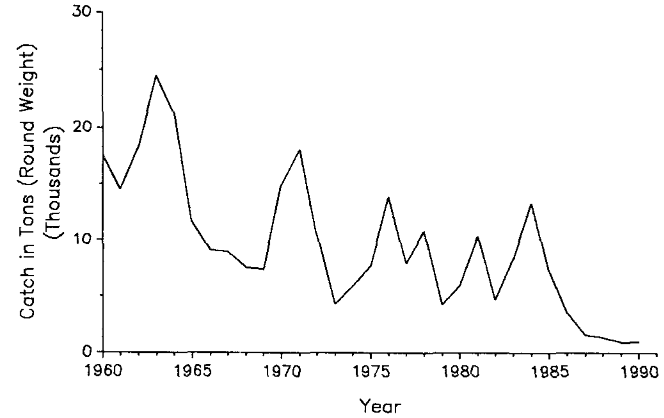

Figure 3. Annual albacore landings for California, 1960–90.

RIDGEBACK AND SPOT PRAWN

Ridgeback prawn (*Sicyonia ingentis*) are taken primarily with trawl nets. Trawling is allowed by permit from October 1 through May 31. An incidental catch of 50 pounds per load is allowed during the closed period. Landings for 1990 were approximately 82,800 pounds, or one-half the previous year's catch (figure 4). Most of the catch came from the Santa Barbara Channel. Log data showed a CPUE of 30 pounds per hour in the first part of the year, and 70 pounds per hour at the end of 1990. The CPUE for the previous two years was 66 pounds per hour. The ex-vessel price in the Santa Barbara region was $1.30 to $1.40 per pound.

Spot prawn (*Pandalus platyceros*) used to be caught mainly by trawl gear, but are now taken primarily with traps. By permit, spot prawns may be harvested year-round by trap. They may also be taken by trawl with a permit from February 1 through October 31; an incidental catch of 50 pounds per load is allowed during the closed season. Landings for 1990 were approximately 314,600 pounds, about 66% more than last year. This represents an increased demand for live product, rather than increased abundance of spot prawn. Trapping took place in the Santa Barbara Channel and Santa Monica Bay, and off Los Angeles, Santa Catalina Island, and San Diego (figure 1). The spot prawn is a much larger shrimp than the ridgeback, and brings a significantly higher price. Ex-vessel prices in the Santa Barbara region ranged from $3.50 (dead) to $5.00 (live) per pound.

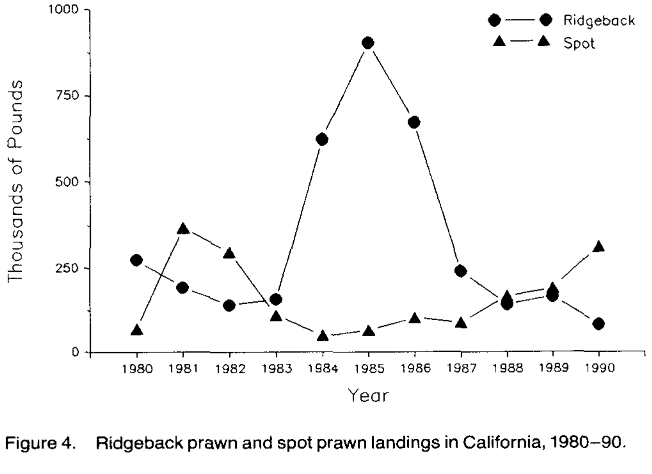

Figure 4. Ridgeback prawn and spot prawn landings in California, 1980–90.

TABLE 7
Sea Urchin Landings (1,000s of Pounds)

Year	Northern California	Southern California	Total
1971	0	<1	<1
1972	<1	76	76
1973	18	3,594	3,612
1974	51	7,056	7,107
1975	3	7,323	7,326
1976	95	11,012	11,107
1977	386	16,208	16,594
1978	34	14,394	14,428
1979	237	20,307	20,544
1980	103	21,196	21,299
1981	194	24,720	24,914
1982	92	19,347	19,439
1983	61	17,207	17,268
1984	59	14,920	14,979
1985	1,921	18,074	19,995
1986	10,174	23,957	34,131
1987	23,600	22,500	46,100
1988	30,525	21,463	51,988
1989	26,745	24,168	50,913
1990*	18,627	23,370	41,997

*Preliminary

SEA URCHIN

In 1990 the red sea urchin (*Strongylocentrotus franciscanus*) fishery continued as one of the major fisheries in the state. Landings for 1990 were estimated to be over 42 million pounds, a 17% decrease from 1989 (table 7). Northern California landings were down 30.4% from 1989, while those from southern California increased 10.4%. The northern California ports of Fort Bragg, Point Arena, and Bodega Bay had 16%, 11%, and 10% of the statewide landings, respectively. In the south, Oxnard-Ventura had 22% of the statewide total; Santa Barbara had 16%; and San Pedro–Los Angeles, 12%. The decrease in northern California is attributed to the continued reduction of high-density virgin stocks, more restrictive regulations, reduced effort, and poor weather. The increase in southern California resulted from effort shifts from the north, strong market prices, and prolonged periods of mild weather.

Divers, using surface-supplied air, harvest sea urchins by raking them into mesh bags, which are airlifted to the surface and winched aboard the vessel. CPUE is measured as pounds harvested per diving hour as reported on daily harvesting logbooks. The northern California average was 507 pounds per hour in 1990, compared to 570 pounds per hour in 1989. In southern California the 1990 average CPUE was 294 pounds per hour, ranging from 166 at the Palos Verdes Peninsula to 407 at San Nicolas Island; in 1989, the average was 323 pounds per hour and ranged from 166 to 516.

Size distributions of sea urchins landed in northern California in 1990 have changed somewhat, with a mean of 106 mm (103 mm in 1989). This reflects the larger minimum size of 90 mm that was adopted for northern California in June 1990. The mean size of sampled sea urchins from the southern California fishery was 96 mm (94 mm in 1989). The percentage of sea urchins below the 76-mm minimum size in southern California declined to 6% (from 10% in 1989, and 17% in 1988), reflecting a change in harvesting practices in response to the minimum size regulations.

The sea urchin fishery is likely to come under added restrictive management in 1991. The objective of the new measures will be to further reduce harvesting pressure, especially in southern California. Resource surveys and fishery monitoring programs will continue to be important for evaluating management changes.

RECREATIONAL FISHERY

Catches from the California commercial passenger fishing vessel (CPFV, or partyboat) fleet (table 8) can generally be considered indicative of nearshore and offshore sport angler success. The CPFV fleet can locate and catch any species available within the fishing area. Catches can vary widely for latitudinally migratory species such as barracuda (*Sphyraena argentea*) and yellowtail (*Seriola lalandei*), and for highly migratory transoceanic species like albacore. Catches of resident species in nearshore areas may also show fluctuations associated with warmer oceanic regimes.

Partyboat landings for 1990—4.7 million fish—were 3% higher than in 1989. The 1990 year was a bonanza for the fleet, with tropical tunas coming well within overnight range of San Diego, and some other migratory species like yellowtail (68,308 fish, ninth ranked) and barracuda (196,000 fish, sixth ranked) abundant. In addition, dolphinfish (also known as dorado) catches were at a record high of 31,000, ranking fifteenth. A sailfish was caught off Dana Point in late summer, representing a northerly range extension of about fifty nautical miles.

TABLE 8
1990 Commercial Passenger Fishing Vessel Catch

Species/species group	Thousands of fish	Rank
Rockfish	2,272	1
Pacific mackerel	468	2
Kelp bass	438	3
Sand bass	423	4
Bonito	260	5
Barracuda	196	6
Sculpin	159	7
Salmon	88	8
Yellowtail	68	9
Lingcod	60	10
Yellowfin tuna	47	11
Halfmoon	46	12
Ocean whitefish	45	13
Sheephead	34	14
Dolphinfish	31	15
Skipjack tuna	16	16
Flatfish (misc.)	15	17
Jack mackerel	8	18
California halibut	6	19
Albacore	3	20
Others	57	—
Total	4,740	

The rockfish complex ranked first, with 2.27 million fish, followed by Pacific mackerel, with just under a half million logged. Kelp bass ranked third, with catches increasing 64% over 1989; sand bass followed, with a slightly higher catch than last year.

The bonito catch was off 23% from 1989. Sculpin catches were about the same as last year. Salmon fishermen registered a moderate season of 87,000 fish. The lingcod take ranked tenth with 60,000 fish, a 22% decrease from last year. The yellowfin tuna catch was excellent (47,000 fish), ranking eleventh and making 1990 the second highest year on record for this species. The catch of highly desirable albacore was poor (3,600 fish) and just made the top twenty list. The striped bass sport fishery had another poor year (2,356 fish), with almost 200 fish over 1989 but far below the 10,000 fish in 1988. The catch of popular California halibut retained nineteenth place, although it declined 27%.

The high dolphinfish catch, the proximity of tropical tunas, and good catches of barracuda and yellowtail undoubtedly were related to a warmer oceanic climate. Sea-surface temperature anomalies were consistently positive off southern California from April through the end of the year, and coupled with negative upwelling indices, may partially account for the biological phenomena in the CPFV fishery of 1990.

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Part II

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FISHERY OCEANOGRAPHY

SOME INTERACTIONS BETWEEN YOUNG WALLEYE POLLOCK AND THEIR ENVIRONMENT IN THE WESTERN GULF OF ALASKA

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ABSTRACT

Surveys in Shelikof Strait, Alaska, show that large concentrations of walleye pollock (*Theragra chalcogramma*) enter the sea valley each March and spawn early in April. Surveys for eggs and larvae have disclosed dense regions of eggs that become patches of larvae. Processes that transport larvae to nursery grounds or to the open ocean seem important to recruitment. Early results suggested that larvae could be rapidly removed (in 14 days) from the shelf by the vigorous, varying flow of the Alaska Coastal Current (ACC). In the upper 100 m, however, most of the volume transport remains on the shelf. Baroclinic instability between the ACC and coastal waters can create eddies (first observed in infrared satellite images) at the exit of Shelikof Strait. Eddies frequently contain the highest concentrations of larvae. The phasing and location of eddies, the ACC, and hatching determine how a given mechanism will affect retention of larvae on the shelf. Year-class size seems largely determined by the end of the larval period, although events during the following summer may also reduce the year class. Storms during the early larval period may be particularly detrimental to survival, although the mechanism is not yet clear. An index of storminess in the Gulf of Alaska may provide a way of predicting year-class size. Studies of physical and biological conditions in larval patches and adjacent shelf waters are being made to determine whether growth and mortality rates differ in these areas.

RESUMEN

Estudios en el Estrecho de Shelikof, Alaska, muestra que grandes concentraciones de *Theragra chalcogramma* entran el valle marino en marzo y desovan a principios de abril. Estudios sobre la distribución de huevos y larvas han indicado la existencia de densas regiones de huevos que se convierten en manchas de larvas luego de la eclosión. Los procesos que transportan las larvas a las zonas de cría o al mar abierto dominan el reclutamiento. Resultados anteriores sugieren que las larvas pueden desaparecer rápidamente de la plataforma continental (en 14 dias) debido al flujo rápido y variable de la Corriente Costera de Alaska (CCA). Sin embargo, la mayor parte del volumen transportado en los 100 m superficiales se queda en la plataforma. Inestabilidades baroclínicas entre la CCA y aguas costeras pueden crear remolinos (observados por imágenes de satélite infrarrojas) en la boca del Estrecho de Shelikof. Estos remolinos contienen, con frecuencia, las concentraciones más altas de larvas. La fase y ubicación de los remolinos, la CCA, y la eclosión determinan la manera que un cierto mecanismo influye en la retención de larvas sobre la plataforma. El tamaño de las clases de edad parecen enteramente determinadas hacia el final del período larval, aunque sucesos que ocurren durante el verano subsiguiente pueden reducir también la clase de edad. Tormentas durante el principio del período larval pueden afectar negativamente la supervivencia, aunque el mecanismo no está todavía claro. Un índice relacionado a las tormentas del Golfo de Alaska podría proveer una forma de predicción de la clase de edad anual. Se están haciendo estudios sobre las condiciones físicas y biológicas en las manchas de larvas y en aguas vecinas de la plataforma para determinar si las tasas de crecimiento y de mortalidad entre estas areas son distintas.

INTRODUCTION

An important scientific challenge during the remainder of this and the beginning of the next century is to understand natural fluctuations in fish populations. This is especially true for fishes that constitute a major portion of the total annual catch and are thus commercially valuable. Knowledge of recruitment dynamics will improve management of exploited marine fish populations. Traditional approaches have to be changed. "A better understanding of the population dynamics process requires more interdisciplinary research among fisheries scientists and oceanographers" (Beamish et al. 1989), and this will occur only through dedicated, long-term research efforts. The Fisheries Oceanography Coordinated Investigations (FOCI) program is a long-term, cooperative effort between scientists at

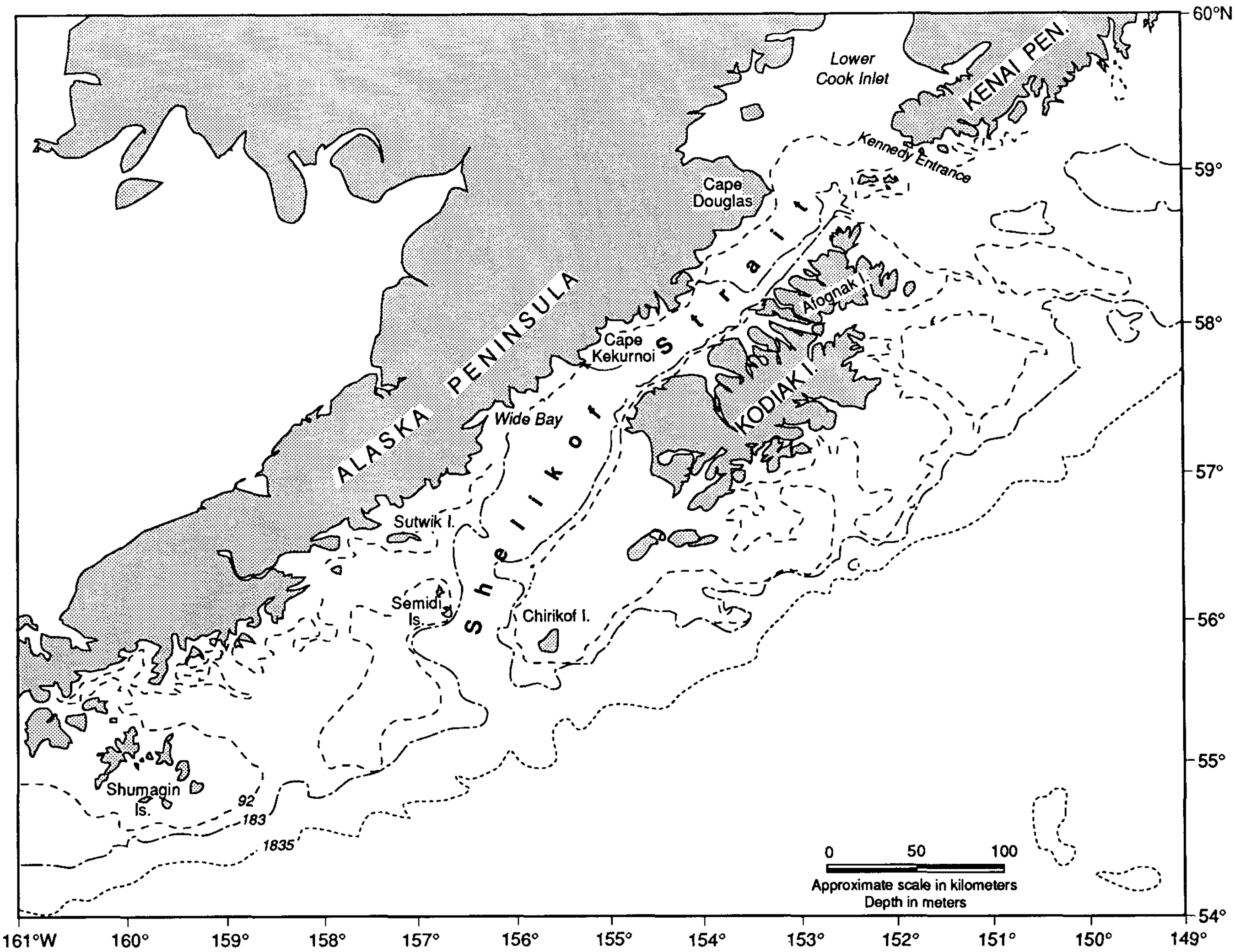

Figure 1. Map of the FOCI study region in the Gulf of Alaska. Depth contours are in meters.

the Pacific Marine Environmental Laboratory of the Oceanic and Atmospheric Research component of the National Oceanic and Atmospheric Administration (NOAA) and the Alaska Fisheries Science Center of the National Marine Fisheries Service. The goal of FOCI is to understand how the environment affects recruitment to commercially valuable fish and shellfish stocks in Alaskan waters.

Some of the largest fisheries in the world exist in the North Pacific Ocean and the Bering Sea. Walleye pollock (*Theragra chalcogramma*) is an important commercial species along both the Asian and North American coasts. Although exploited since the turn of the century, walleye pollock became a target species in 1964 when the Japanese developed shipboard methods for producing surimi. Between 1970 and the mid 1980s, world catches varied between 5 and 6 million metric tons (Fishing News International 1985). In the 1980s, walleye pollock was the single most important species in the world fish catch by weight (Bakkala et al. 1987). Since the mid 1980s pollock catches have increased dramatically and averaged between 6 and 7 million MT annually (FAO 1990).

FOCI research was initiated in 1984 to understand processes determining recruitment of walleye pollock in Shelikof Strait, Alaska (figure 1). Large concentrations of the fish aggregate each March in a limited area of the strait. The fish spawn in early April, producing dense patches of eggs. By late April, the eggs hatch, and patches of yolk-sac larvae form. Currents transport the larvae to their nursery grounds along the Alaska Peninsula (Kim 1989). The early life history of walleye pollock in Shelikof Strait provides a tractable problem for a commercially important species (Kim and Gunderson 1989). We originally believed that larvae and juveniles that remain along the Alaska Peninsula are more likely to survive than those that leave the continental shelf.

Our field studies have demonstrated that in most years larvae are found mainly in patches on the shelf. We have not been able to test our original transport hypothesis directly, because it would require sampling over a large area where we expect larval abundance to be very low. Numerous studies have shown that other fishes whose early life pattern is closely tied to an advective system suffer increased mortality when transport is abnormal (Norcross and Shaw 1984). Also, fewer copepods, which serve as larval prey, are found in oceanic waters of the Gulf of Alaska than in coastal areas (Cooney 1987). We have focused our research on the physical and biological environment, especially on processes within the larval patch.

BACKGROUND

Physical Setting and Features of the Physical Environment

The study area is dominated by a high, nearly continuous mountain chain along the Alaska Peninsula, and a deep (>250 m) sea valley between Kodiak Island and the peninsula (figure 1). The mountains perturb geotriptic winds (geostrophic winds adjusted in speed and direction to account for friction). Ageostrophic winds are typical in Shelikof Strait (Schumacher et al. 1989). Numerous gaps in the mountains cause spatial variability on the scale of tens of kilometers. The sea valley forms a natural guide for shelf circulation, a conduit connecting the continental slope to the inner shelf. Immediately east of Sutwik Island and the Semidi Islands, the sea valley becomes more orthogonal to the continental slope. The sill between the valley and continental slope has a minimum depth of approximately 225 m. The shelf between the Semidi and Shumagin islands is generally deeper than 150 m, but there is a shoal region (< 100 m) southwest of the Semidi Islands. The many embayments along the Alaska Peninsula provide a nursery ground for young walleye pollock.

Much of the variability in the Gulf of Alaska is due to large-scale atmospheric phenomena. An annual cycle in the number of low-pressure centers crossing the region results from global patterns in upper-level atmospheric pressure (Niebauer 1988). The consistent passage of storms along the Aleutian Island chain, a feature known as the Aleutian Low, dominates atmospheric circulation over the Gulf of Alaska in winter and plays a crucial role in the hydrological cycle. To provide a time series representation of atmospheric circulation, Emery and Hamilton (1985) defined the Northeast Pacific Pressure Index (NEPPI: the difference between surface pressure at Reno, Nevada, and 50°N, 170°W). This index is a measure of the strength, frequency, and location of storm passage (a measure of the Aleutian Low). There is correlation between NEPPI and sea-level temperature and height observed along the coast of British Columbia. Because gradients in coastal sea level generate currents, coastal circulation should also be related to NEPPI. Analysis of NEPPI and nearly 5 years' worth of current data from the Shelikof Strait region indicate a statistically significant relation between fluctuations in NEPPI and in the current (Roach and Schumacher 1991). Frequent storms along the mountainous coastline of Alaska produce much precipitation (>330 cm yr^{-1}). The hydrological cycle has a maximum discharge rate in October and a minimum in August, reflecting seasonal variations in air temperature, precipitation, runoff, and freshwater storage from the previous winter (Royer 1981).

The dominant circulation feature over the continental shelf is the Alaska Coastal Current (ACC). The ACC extends more than 1,500 km along the south coast of Alaska (Reed and Schumacher 1987). It is identifiable by its low salinity, which results from the large freshwater input (Royer 1981, 1982). This is one of the most vigorous coastal currents in the world, with surface speeds of 25 to 175 cm s^{-1}. Volume transport results from the addition of fresh water along the entire coastline and is perturbed by the alongshore wind through both confinement of the fresh water and alteration of coastal sea level (Schumacher and Reed 1980; Royer 1981; Reed and Schumacher 1981). Between Kodiak Island and the peninsula, differential Ekman pumping also appears to generate fluctuations in transport (Reed and Schumacher 1989a). Estimates of volume transport computed from observations of water property along the Kenai Peninsula exceed $10^6\ \mathrm{m}^3\,\mathrm{s}^{-1}$; maximum values occur in fall, when freshwater flux is greatest (Schumacher and Reed 1980; Royer 1981).

Circulation in Shelikof Strait and the western Gulf of Alaska is complex. Baroclinic instability is evident in satellite images and in analysis of current energy (Mysak et al. 1981). Satellite imagery (Reed et al. 1988; Schumacher et al., in press) and tracked buoys (Incze et al. 1990) show eddies. The observed mean transport in the sea valley is $0.85 \times 10^6\ \mathrm{m}^3\,\mathrm{s}^{-1}$; wind-forced pulses exceed $3.0 \times 10^6\ \mathrm{m}^3\,\mathrm{s}^{-1}$ (Schumacher et al. 1989). The ACC bifurcates east of Sutwik Island; one branch flows along the Alaska Peninsula, and the other transports about 75% of the total volume seaward through the valley (Schumacher et al. 1989). Few observations have been col-

TABLE 1
Annual Abundance Estimates of Several Life Stages of Walleye Pollock from Shelikof Strait, Gulf of Alaska

	Numbers of fish			Cohort abundance from spawning year						
Source	Blend	Hydro	Blend	Blend	Plankton	Plankton	Plankton	Trawl	Trawl	VPA
Stage	3–10 adults	All adults	3–10 spawners	Spawned eggs	Eggs	Early larvae	Late larvae	Age-0 juveniles	Age-1 juveniles	3-yr-old juveniles
Date	1 Apr	1 Apr	1 Apr	10 Apr	7 Apr	22 May	10 Jun	15 Sep	15 Sep + 1	1 Apr + 3
Age of cohort	1	1	1	10	7	52	71	168	533	1095
Log age	0.00	0.00	0.00	1.00	0.85	1.72	1.85	2.23	2.73	3.04
Authors*	H&M	W	H&M	H&M	R&P	R&P	B&S	B&S	B&S	H&M
Exponent	9	9	9	14	†	†	†	†	†	9
Year										
1972	—	—	—	—	—	—	—	—	—	1.6505
1973	—	—	—	—	—	—	—	—	—	0.3765
1974	—	—	—	—	—	—	—	—	—	0.2665
1975	2.393	—	0.367	0.828	—	—	—	9.76	—	1.4895
1976	1.889	—	0.417	1.091	—	—	—	18.19	—	2.3790
1977	1.405	—	0.394	1.230	—	—	—	19.44	—	1.8855
1978	2.302	—	0.447	1.309	—	—	—	11.96	—	3.2715
1979	3.796	—	0.634	1.594	—	114.7	298.9	—	10.74	1.6800
1980	4.298	—	0.824	2.181	—	—	—	2.90	3.74	0.5645
1981	6.016	7.881	1.130	2.896	52.82	458.1	2064.6	10.90	3.18	0.5025
1982	5.467	—	1.265	3.491	9.32	3.8	29.9	3.83	—	0.2460
1983	4.056	4.593	1.180	3.657	—	20.8	849.4	—	2.65	0.4550
1984	2.954	2.987	0.966	3.255	16.00	—	83.5	11.92	1.25	0.8570
1985	1.872	1.015	0.658	2.373	10.73	2.9	986.0	22.08	3.84	0.8120
1986	1.393	0.782	0.423	1.534	5.69	—	82.2	6.21	0.29	0.1355
1987	1.702	—	0.394	1.286	2.44	38.5	56.7	9.76	0.48	—
1988	1.880	1.231	0.412	1.221	0.93	—	307.2	14.91	—	—
1989	1.322	1.018	0.377	1.189	—	—	—	—	—	—
Sum	42.745	19.507	9.8892	29.135	97.93	638.8	4758.4	141.86	26.17	16.5715
Minimum	1.322	0.782	0.367	0.828	0.93	2.9	29.9	2.9	0.29	0.1355
Maximum	6.016	7.881	1.265	3.657	52.82	458.1	2064.6	22.08	10.74	3.2715
Max/min	4.551	10.078	3.447	4.417	56.796	157.966	69.050	7.614	37.034	24.144
n	15	7	15	15	7	6	9	12	8	15
Mean	2.850	2.787	0.659	1.942	13.990	106.467	528.711	11.822	3.271	1.105

*H&M = Hollowed and Megrey, NMFS, Seattle, pers. comm.; B&S = Bailey and Spring, in press; W = Williamson, NMFS, Seattle, pers. comm.; R&P = Rugen and Picquelle, NMFS, Seattle, pers. comm.
†Indices of abundance

lected between the Semidi and Shumagin islands, but it appears that some of the water flowing seaward in the valley returns to the shelf (Schumacher and Reed 1986).

Early Life History of Walleye Pollock

Before 1981 little was known of the early life history of walleye pollock in the Gulf of Alaska; until then it was not even possible to separate their larvae from those of other gadids in field samples (Dunn and Matarese 1987). Annual hydroacoustic/midwater trawl surveys through the 1980s showed that large concentrations of prespawning walleye pollock migrate from the southwest end of Shelikof Strait to the area near Cape Kekurnoi. The fish spawn mainly in the deep sea valley, between late March and mid-April (Kim and Nunnallee 1990). The spawning population has varied between 1.3 and 6.0 billion fish during the 1980s (A. B. Hollowed and B. A. Megrey, NMFS, Seattle, pers. comm.: see table 1). Each female produces hundreds of thousands of free-floating planktonic eggs in a series of about ten batches over 2–3 weeks. Laboratory observations have shown that the fish spawn primarily in pairs and mainly in the evening (Baird and Olla 1991). Egg diameter (ca. 1.3 mm) decreases with time but is not related to female size (Hinckley 1990).

The eggs are found deep in the water column (nearly all below 150 m, and many within 25 m of the bottom) and hatch in about 2 weeks, depending on temperature (Matarese et al., in press). Because of the large spawning population, the localized spawning area, the short season, and generally the lack of strong spatial differences in the deep currents, a large "patch" of eggs is produced that can be recognized through plankton surveys of the region (Kendall and Picquelle 1990).

The larvae are about 3–4 mm standard length (SL) at hatching and are relatively undeveloped, without functioning mouths or eyes. They quickly rise from their deep hatching depth to the upper 50 m of the water column, where they drift in the prevailing currents from late April into June. They generally remain as a large identifiable patch, and grow about 0.2 mm d^{-1} during this time. Their diet consists mainly of copepod nauplii, and the size range of prey increases as the larvae grow. They are visual feeders, and eat mostly during the day (Kendall et al. 1987).

By the end of May the patch of larvae is usually near the Semidi Islands, and the larvae have reached 8–11 mm SL (Kendall and Picquelle 1990). The biology of young-of-the-year walleye pollock after May is poorly known. During June and July they have reached about 20–30 mm and remain as a patch that drifts to the area of the Shumigan Islands (Hinckley et al. 1991). They remain planktonic during this period, and do not seem to form schools. By the end of their first summer, at least some of them are found in bays along the Alaska Peninsula (Bailey and Spring, in press).

APPROACH

It is generally accepted that physical oceanic processes influence and may even primarily determine the eventual recruitment of fish. Predation on eggs and larvae and the condition of larvae during transport to nursery grounds are believed to be the most important factors in determining recruitment (Rothschild 1986). Survival is affected by two broad categories of physical mechanisms: turbulence of the water column, which influences food availability, and fluctuations in the currents that transport eggs and larvae to nursery areas. How physical conditions affect predation is less well known. Water properties, particularly temperature, affect growth rate, thus affecting phasing between stage of development (through late larvae) and transport. By the time fish become juveniles, they are no longer planktonic and thus are less affected by transport. Where they spend their first summer, however, results from their transport since spawning (Norcross and Shaw 1984).

A research plan developed at the Alaska Fisheries Science Center and the Pacific Marine Environmental Laboratory is reviewed and updated annually. Four program advisors act as independent reviewers. The primary forum for evaluating the quality of the research is scientific publications (presently there are 147 publications, nearly half in refereed journals) and presentations. Initially, research focused on field observations to determine transport, water properties, and egg and larval distributions. Laboratory work centered on immunoassays and growth studies of larvae. As the program matured, it became apparent that two additional types of research were needed: process-oriented studies of mortality within and outside the larval patch, and examination of various indices of climate and abundance of animals versus estimates of three-year-olds. Many of the physical and biological data are being put into a model of dispersion of larvae (Stabeno et al. 1990). This model includes advective, diffusive, and biological source/sink terms and has been used to simulate larval distributions.

The success of FOCI results from effective interdisciplinary research. The program melds theoretical and observational scientists with backgrounds in meteorology, physical and biological oceanography, and fishery biology from government, private laboratories, and universities. Developing and maintaining communication and cooperation among researchers with varying backgrounds has been a necessary condition for success. A report presenting our managerial and administrative techniques is available on request.

RECENT RESULTS

Egg and Larval Distributions

Kendall and Picquelle (1990) analyzed the seasonal and geographic distribution of walleye pollock eggs and larvae (1,929 samples collected during 32 ichthyoplankton cruises in the Gulf of Alaska from 1972 to 1986). They found eggs primarily in April, and larvae in late April and May. Most eggs are found in Shelikof Strait, in a small area off Cape Kekurnoi (figure 1). In most years larvae drift southwestward in a large patch (Kim and Kendall 1989). The number of larvae decreases, and their size increases during this drift. Significant interannual differences in location of the patch and size of the larvae become apparent by late May.

To determine the vertical distribution of the eggs, we studied incubated eggs in a density gradient water column and analyzed vertically discrete plankton tows (Kendall and Kim 1989). During the 2-week incubation period, a complex pattern of interaction between stage of egg development and local water density determines depth; many of the eggs are located below 200 m. As the eggs begin to develop, they rise in the water column until they reach a level of neutral buoyancy at about 150 m. Later in development the eggs sink, then rise again just before hatching. Recent studies (Kendall et al., in press) have confirmed this pattern with more extensive sampling in different areas and years. Sampling with an epibenthic sled has revealed that some eggs are even found within 1 m of the bottom (A. C.

Matarese, NMFS, Seattle, pers. comm.). Interannual differences in water density in the spawning area may affect the vertical distribution of the eggs, which may in turn affect their hatching location because of vertical shear of the currents. Below about 150 m, currents are fairly weak, and on the south side of the sea valley they flow toward the northeast; above 150 m, currents are generally stronger and flow to the southwest (Schumacher et al. 1989).

By late May the larvae have reached a mean length of 11 mm SL and live between about 15 and 50 m. They follow a diel pattern of limited vertical migration (Kendall et al. 1987). Current shear decreases exponentially from approximately 0.005 s^{-1} at 15 m to a nearly constant value of only 0.002 s^{-1} between 20 and 50 m (figure 2). Given the observed mean shear, the daily difference between transport of plankton at 15-m and 45-m depths is <1 km. The larvae follow a crepuscular pattern of activity, and are concentrated between 14 and 28 m during twilight. At night they are more dispersed, and during the daytime they are concentrated in the lower portion of their depth range.

Recent studies (Kendall et al., in press) have shown that larvae over a considerable size range (4–11 mm SL), and throughout the season in Shelikof Strait have a similar pattern of vertical distribution. In the laboratory, walleye pollock larvae swim upward in low light and darkness, and downward at high light intensities, when they are also more active (Olla and Davis 1990). These changes in activity are not endogenous, but rather are responses to the daily light cycle. The larvae also change their vertical distribution to avoid low temperature and turbulence. Only a few larvae, mainly smaller than 4 mm SL, are found deep in the water column, as would be expected from the vertical location of late-stage eggs (Kendall et al., in press). Apparently the eggs hatch deep, but the larvae quickly swim to the upper layers (<50 m) and remain there during development. Under laboratory conditions walleye pollock larvae react positively to light within 24 hours of hatching (Olla and Davis 1990).

Water Properties

Three classes of water exist in the study area: Lower Cook Inlet, Alaska Coastal Current, and bottom water. From April to June, water in lower Cook Inlet is generally colder and less saline than water in the ACC; the differences are about 0.5°C and 0.5 psu. The interannual variation of bottom-water properties is striking: off Cape Kekurnoi salinity has varied from <32.5 to >33.5 psu while temperature varied between <3.8° and >5.8°C (Reed and Schumacher 1989a). During spring, however, the bottom waters are always warmer and more saline than ACC water above them. The bottom waters also provide nutrients for primary production (Reed et al. 1987). The juxtaposition of ACC and Lower Cook Inlet water accounts for baroclinic instability (Mysak et al. 1981), which leads to formation of eddies.

Water temperatures in the upper 150 m follow a clear seasonal pattern: the warmest values occur in August–September and the coldest values in March–April (Reed and Schumacher 1989a; Roach and Schumacher, in press). The largest standard deviations occur in May when walleye pollock eggs hatch and develop into first-feeding larvae. There

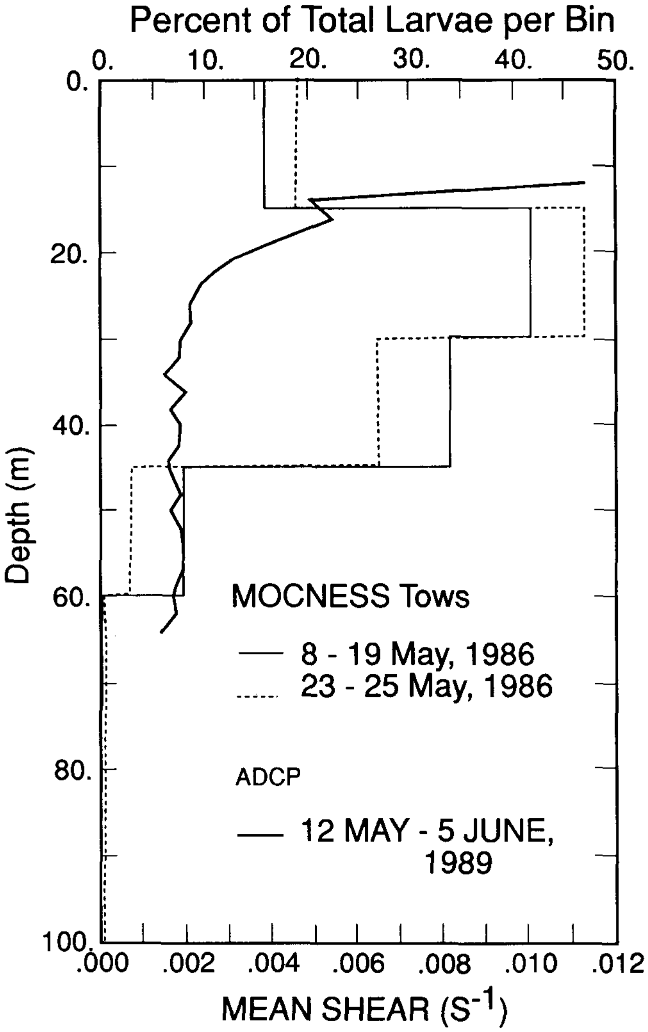

Figure 2. Observed vertical mean velocity shear (s^{-1}) and percent of larvae caught per 15-m bin.

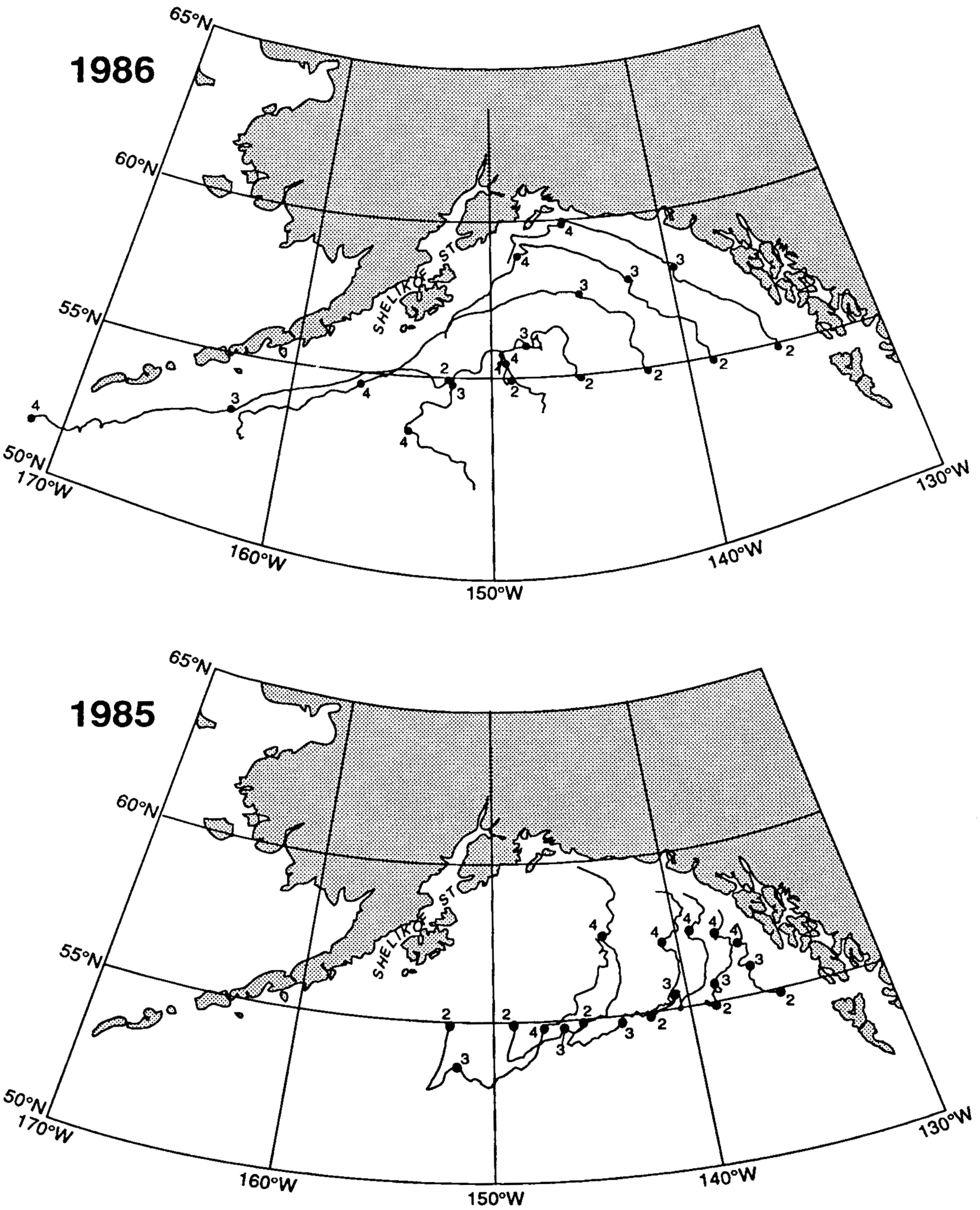

Figure 3. Trajectories from a wind-driven circulation model with a steady baroclinic field: *upper panel*, conditions during a typical year (1986); *lower panel*, anomalous trajectories (1985).

are also interannual variations in the bottom-water temperature: during spring 1986, bottom waters were more than 0.5°C colder than in other years.

A wind-driven model with a density field that varies in space but is constant with time has been used to examine interannual variations of water-parcel trajectories in the North Pacific Ocean (Ingraham and Miyahara 1989). In some years the typical flow into the head of the Gulf of Alaska is weakened (1979, 1982, 1985), and the westward intensification of the Alaska Stream is minimal (figure 3). The anomalies in flow trajectories coincide with anomalies in the NEPPI index. During these years, more saline water is found at depth in the sea valley (Ingraham et al. 1991). This information links local water properties to large-scale processes, and strengthens the

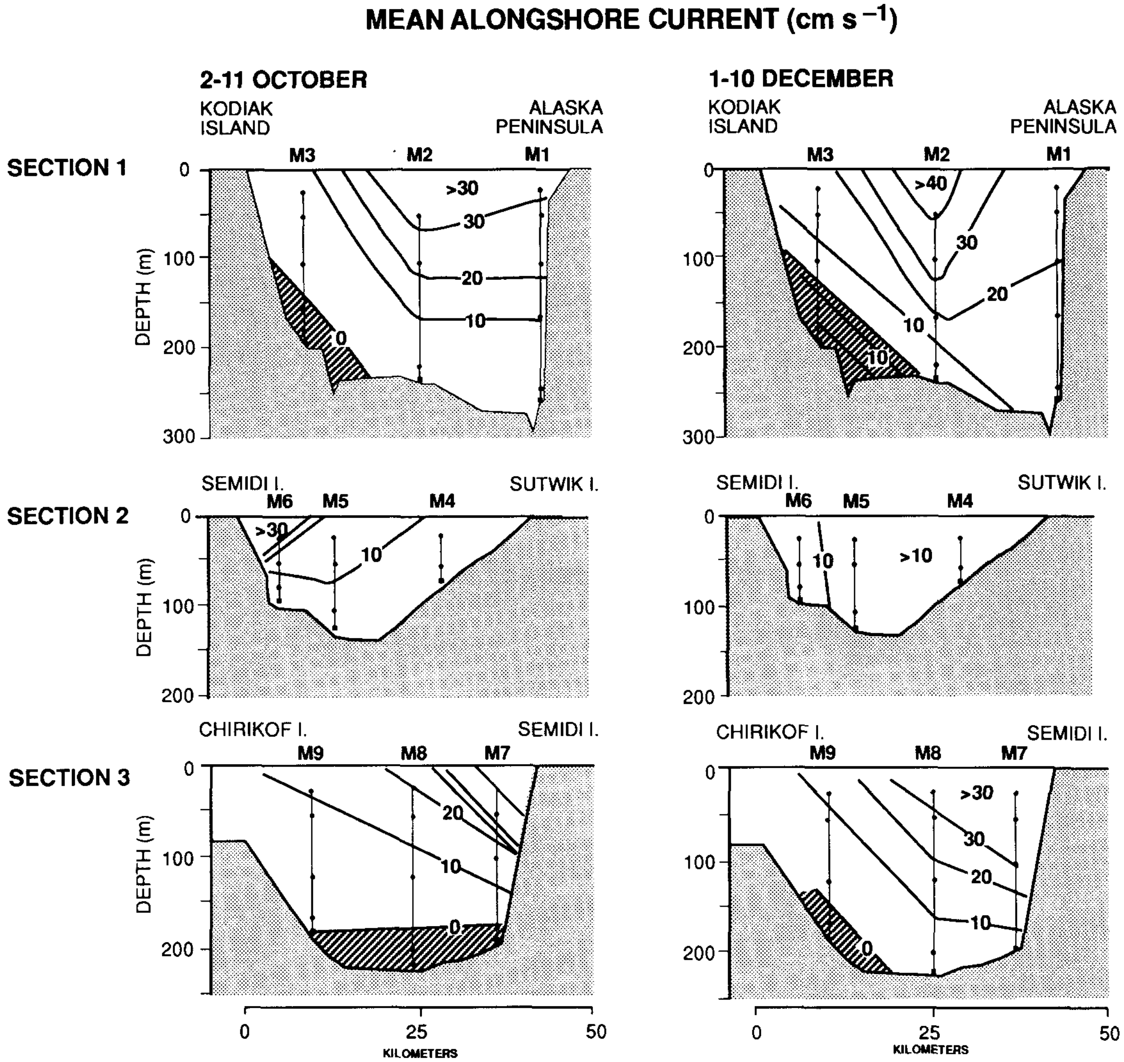

Figure 4. Structure of mean current speed (cm s^{-1}) from measurements (current meters are shown as dots on moorings) over the sea valley (*sections 1 and 2*) and over the shallower shelf (*section 3*) during two 10-day events (after Schumacher et al. 1989). These are examples of the estuarine-like flow over the sea valley; the region with flow into the valley is shaded.

use of NEPPI as an index of conditions in the study area. The occurrence of different water in the sea valley may indicate that the composition of the zooplankton community varies interannually.

No direct impact of the temperature and salinity variations has been observed on early stages of walleye pollock. Secondary effects, however, may be important in the chain of events that dictates year-class success. For example, when bottom temperatures are significantly lower, incubation time is increased. Similarly, differences in salinity (at the ambient temperatures, salinity dominates the equation of state of seawater and hence dictates density) would affect the depth of eggs in the water column, altering when and where the eggs hatch. The importance of hatching location to eventual transport and retention on the shelf is a function of phasing between biological and physical processes.

Transport and Mesoscale Features of Circulation

The FOCI hypothesis is focused on transport of planktonic life stages to nursery grounds; before FOCI, however, little was known about volume transport in the study area. An experiment was conducted between 1984 and 1985 to measure volume transport and to examine its temporal variability (Schumacher et al. 1989). Estuarine-like flow (flow is seaward in the upper 150 m and reverses below this depth [Reed and Schumacher 1989a]) was found in the sea valley, with warmer, more saline water from the continental slope entering on the southeastern side of the valley (figure 4). Mean volume transport of the Alaska Coastal Current was measured at 0.85×10^6 m^3 s^{-1}. This is in good agreement with estimates of transport from CTD data, provided that the level of no motion is carefully selected to approximate the two-layered velocity field over the sea valley (Reed and Schumacher 1989a). Approximately 75% of the mean transport was through the sea valley, with the remaining flux along the Alaska Peninsula. Wind-related changes in volume transport can be as large as four times the mean value. During such extreme events, transport of eggs could alter the usual pattern of hatching location and eventual transport of larvae to coastal nursery grounds.

The ACC does not span the sea valley, and estimates from current records of coherence become insignificant for separations >10 km (Reed and Schumacher 1989b). Thus where walleye pollock eggs hatch relative to the ACC is important. Larvae hatched shoreward of the ACC remain in coastal waters and drift toward the southwest. Larvae that are advected with the portion of volume transport that flows along the peninsula also remain on the shelf. Larvae transported in the ACC can be removed from the sea valley within a few weeks (Incze et al. 1989). The fate of animals transported out of the sea valley is uncertain, because dynamics and patterns of shelf-slope exchange are not well known. It has been suggested that some of the flow out of the sea valley enters the next valley to the southwest (Schumacher and Reed 1986), giving larvae a pathway back onto the shelf. Estimates of how flow affects larval distribution suggest that horizontal advection, divergence, and turbulent diffusion are all important (Reed et al. 1989). To further address questions of larval dispersion, a slab model of the change in concentration with time of larvae has been used to simulate observed data (Stabeno et al. 1990). Although preliminary results from this model are encouraging, our ability to input advection at the necessarily small length scales is limited.

Since 1986, twenty-five satellite-tracked buoys (drogued at 40 m) were deployed in the study area. Most of the deployments have been in spring, near Cape Kekurnoi. The circulation inferred by averaging all independent buoy trajectories in a spatial grid (8×8 km) provides the most comprehensive description of circulation available (figure 5). There is good agreement between velocities as measured by buoys and moored instruments (comparisons were made at 20 locations). To date, 25% of the buoys have continued along the peninsula. The rest flowed seaward past the Semidi Islands, but most turned southwest immediately past the islands or returned to the shelf downstream, eventually becoming part of the flow along the peninsula. Only 25% of the buoys left the shelf permanently and became incorporated in the Alaskan Stream (Stabeno and Reed, in press).

Satellite imagery (Reed et al. 1988; Schumacher et al., in press) has greatly enhanced knowledge of variability and spatial scales of the velocity field. Estimates of sea-surface flow are made from measurements of sea-surface temperature pattern displacements between sequential images by means of an interactive visualization algorithm (Vastano and Borders 1984). Whenever possible, surface flow vectors have been compared to Eulerian measurements and flow estimates from a drift-current model; there is good agreement throughout the upper 60 m of the water column (A. C. Vastano, Texas A&M Univ., College Station, TX, pers. comm.).

Eddies and patches of walleye pollock larvae are sometimes congruent (figure 6). Eddies have been identified in both Advanced Very High Resolution Radiometer (AVHRR) and synthetic-aperture radar (SAR) images, as well as in data about water properties (figure 7). Most eddies observed so far have been at the exit of the strait proper and off Wide Bay (Incze et al. 1990) and may result from baroclinic instability. All of these features appear to translate toward the southwest with the dominant current. A sequence of images from May 1987 shows that an eddy remained quasi-stationary off Wide Bay for at least two weeks. In May 1990, three satellite-tracked buoys were deployed in a region where high concentrations of larvae were observed. These buoys define an eddy that remained nearly stationary for approximately two weeks (figure 8). The eddy had a radius ~10 km, and the mean current speed increased from ~20 cm s^{-1} near the center to >30 cm s^{-1} at a radius of 10 km. The measured speeds were greater than baroclinic speeds calculated from water properties, suggesting a significant barotropic component of velocity. After two weeks, the eddy moved southwest.

A second mechanism has been identified that affects transport and can cause formation of larval patches. In the vicinity of Kodiak Island, complex wind patterns develop as storms interact with mountains. As low-pressure systems approach Shelikof Strait from the southwest, the surface atmospheric pressure field is perturbed. Wind data collected from a research aircraft show convergence of geotriptic and ageostrophic winds in the region off Wide Bay (Macklin et al. 1984). The potential effect of this wind pattern on surface flow has been modelled (figure 9). Based on direct wind measure-

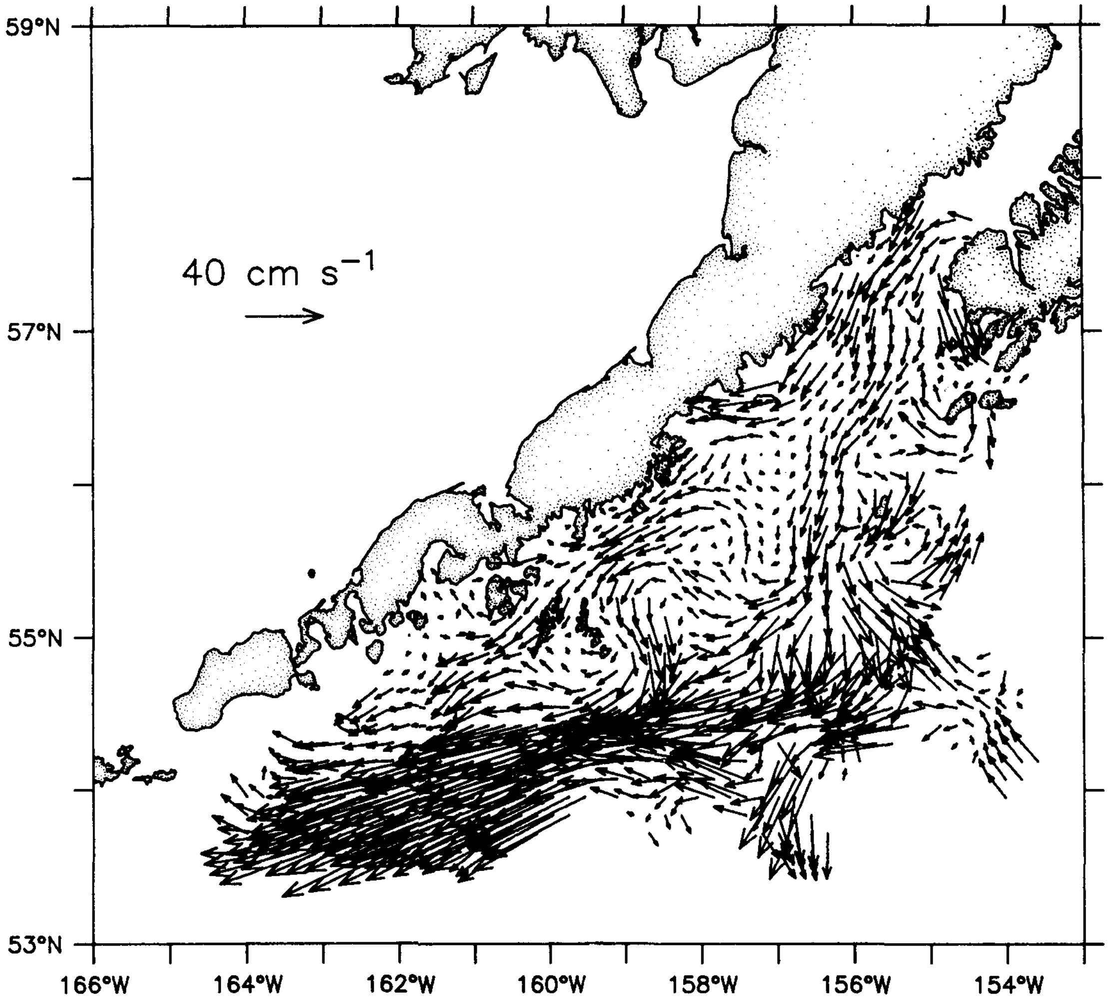

Figure 5. Mean circulation vectors based on satellite-tracked buoys.

ments made at five locations around the open-shelf region southwest of Kodiak Island (Lawrence et al. 1991) and on surface pressure charts, a "standard" wind pattern was developed. This wind field was used with a simple algorithm to generate surface current vectors that indicate a region of convergence off Wide Bay. High atmospheric pressure southwest of Shelikof Strait generates offshore winds over the open shelf and northeastward winds in Shelikof Strait (Schumacher et al. 1989). This wind pattern causes divergent and offshore currents. Under these conditions, plumes of cold coastal water have been observed leaving Wide Bay and extending across the shelf. As the plumes interact with bathymetry and currents in the sea valley, they may form eddies. Both eddies and wind-driven convergence zones can contribute to the observed patterns of larval distribution.

Growth and Condition of Larvae

Much of our work has been devoted to measuring growth rates and condition of larvae. Daily increment deposition on the otoliths was verified by laboratory experiments (Bailey and Stehr 1988), and techniques to determine the age of juveniles were developed (Brown and Bailey, in press). Several techniques to measure larval condition were investigated, and use of RNA/DNA was found most satisfactory. Bioenergetic requirements of the larvae were established through laboratory experiments (Bailey and Stehr 1986; Yamashita and Bailey 1990). These studies were related to environmental conditions through studies of the prey field (primarily copepod nauplii).

Growth rates (determined from otolith analysis) of young larvae showed no year-to-year differences. But there were geographic variations: growth rate

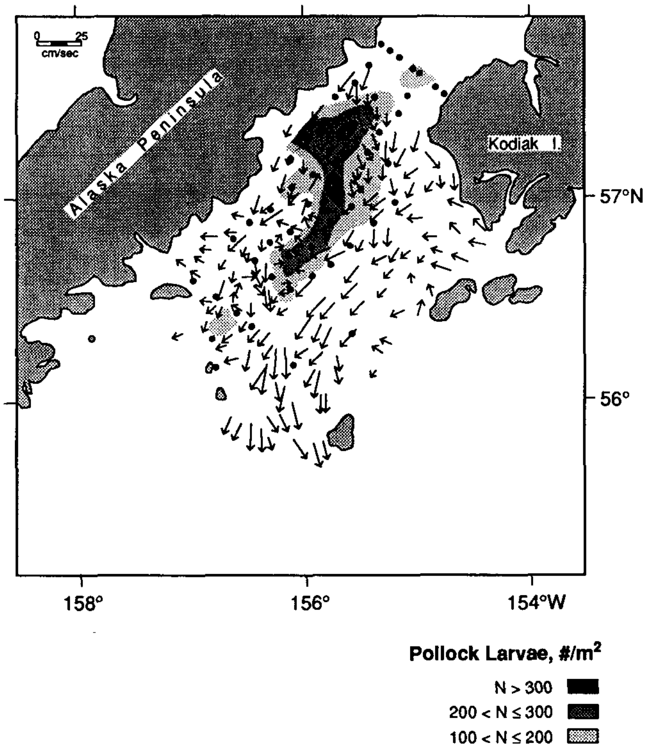

Figure 6. Surface velocity field inferred from AVHRR images of sea-surface temperature and contours of larval abundance. The contours are in units of m⁻². The pattern of surface currents was developed by tracking features on images between 28 and 29 April 1986.

increased from southwest to northeast along the Alaska Peninsula (Yoklavich and Bailey 1990). Time of maximum larval occurrence varied among the years, possibly because of changes in time of spawning, differential mortality, or drift out of the area. Decreases in numbers of larvae (from each day of spawning) between May and June–July 1987 surveys were used to determine daily mortality rates of 0.10–0.14 for young larvae and 0.01–0.02 for older larvae (integrated over a month between surveys).

Analysis of RNA/DNA from field samples shows that early in the season larvae are not in as good condition as later in the season. This may indicate that first-feeding larvae from early in the spawning season may sometimes be present before the spring bloom has brought copepod naupliar abundance to levels sufficient for larval growth. Also, larval condition varies spatially, and we are examining how this relates to hydrographic conditions and zooplankton distributions (M. F. Canino, NMFS, Seattle, pers. comm.). Laboratory experiments have shown that first-feeding larvae require 76 copepod nauplii per day for metabolism and growth, indicating that lack of food may sometimes limit growth (Yamashita and Bailey 1990).

Determinants of Year-Class Strength

Although most of our studies have focused on the early stages of walleye pollock, we have also investigated factors, including environmental indices, that may correlate with year-class strength. One of the first questions is, When is year-class strength first established? We have concentrated on the egg and larval stages, following the traditional paradigm that this is when year class is determined. As an attempt to validate this, we compared indices of abundance of late larvae, and age-0 and age-1 juveniles with level of recruitment (age 3) determined by cohort analysis (Bailey and Spring, in press). Age-0 and age-1 abundance was correlated with age-3 recruitment. It appears from the limited time series available that high larval abundance is a prerequisite for strong year classes, and low numbers of larvae always result in low numbers of recruits. Low recruitment, however, also results in some years when late larvae and age-0 juveniles are abundant. It seems that sometimes events after the larval period adversely affect juvenile survival.

Abundance estimates of the walleye pollock that spawn in Shelikof Strait have been made over the last several years at various life stages (table 1). Although data are not available for all stages in all years, and some are indices rather than absolute population estimates, these data do help establish ranges of variation and suggest relationships between interannual trends in abundance at various stages. Estimates of the adult population are available from 1975 through 1989. The estimates used here are based on a blend of hydroacoustic and bottom trawl surveys and commercial catches (A. B. Hollowed and B. A. Megrey, NMFS, Seattle, pers. comm.). The number of spawned eggs has been derived from the annual estimates of adult abundance and age structure and an age/fecundity relationship (B. A. Megrey, NMFS, Seattle, pers. comm.). Indices of abundance of eggs and early larvae are based on analysis of plankton collections in Shelikof Strait over several years (W. C. Rugen and S. J. Picquelle, NMFS, Seattle, pers. comm.). Numbers of late larvae are estimated from larval surveys conducted in late May. Because these surveys have been made at slightly different times over the years, the numbers here are estimated numbers of larvae of the year class reaching 15 mm SL, given a certain mortality and growth rate (Bailey and Spring, in press). Such estimates are available for every year from 1979 through 1988, except 1980. The numbers of age-0 and age-1 juveniles are indices based on late-summer trawl surveys, which did not always encompass the entire area occupied by the year classes (Bailey and Spring,

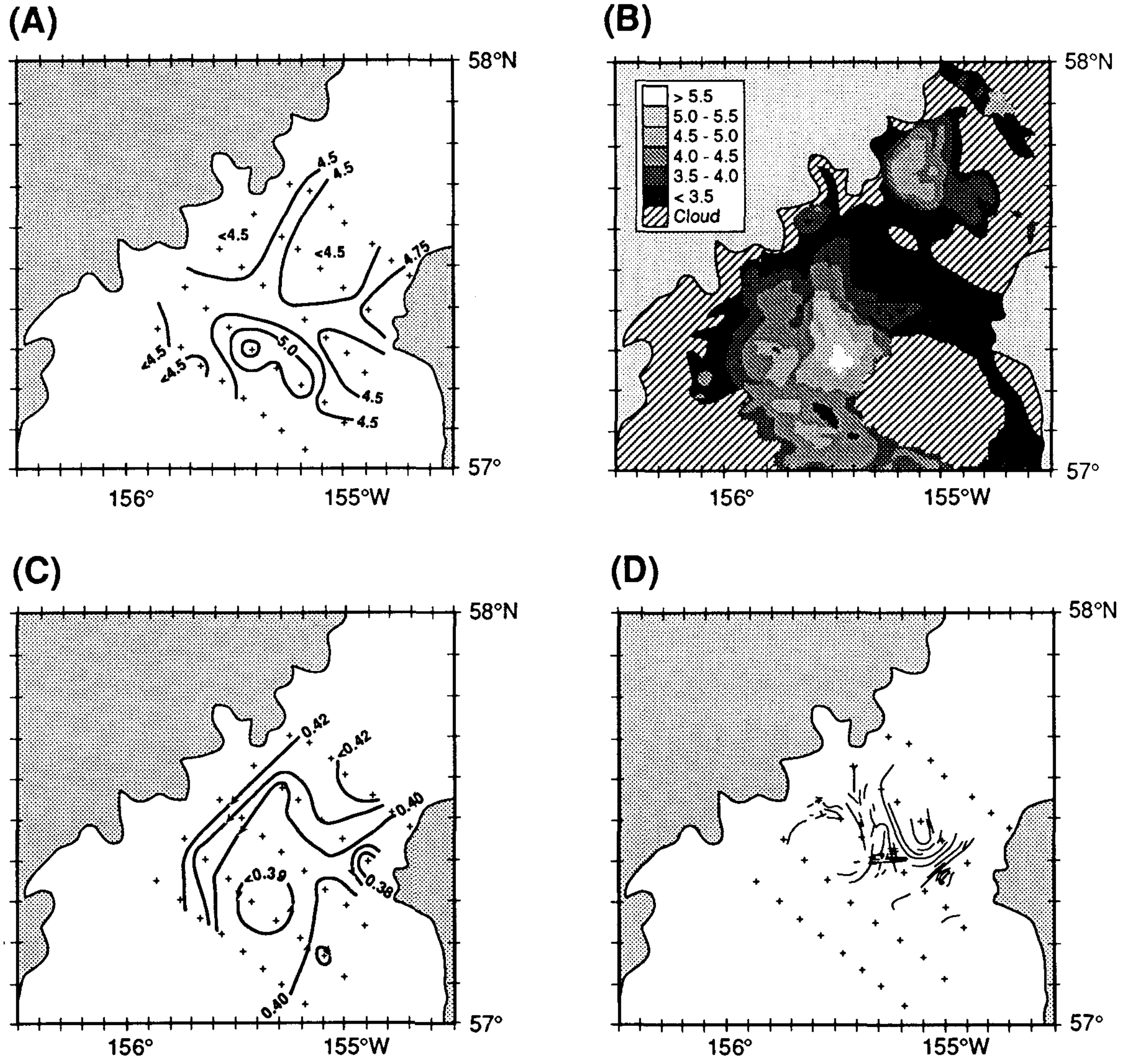

Figure 7. (*A*) Sea-surface temperature contoured from a 38-station CTD survey occupied between 27 and 29 April 1988; (*B*) AVHRR image of Shelikof Strait obtained on 29 April 1988; (*C*) geopotential topography; (*D*) sketch map of detectable current features seen in an SAR image from July 1978.

in press). Age-0 indices are available for all but two years from 1975 through 1988, and age-1 indices are available from 1979 through 1987, except 1982. Recruitment to the fishery is at age 3, and this is the basis for the cohort analysis of year-class size, results of which are given here for 1972 through 1986 (A. B. Hollowed and B. A. Megrey, NMFS, Seattle, pers. comm.).

From 1975 through 1989 the adult population had a 4.6-fold range of variation. Abundance of adjacent years is highly correlated. The population had a single peak abundance in 1981, with lesser and approximately equal numbers of fish at the beginning and end of the series. This distribution was due primarily to the passage of several adjacent moderate-to-very-strong year classes through the population (1975–79).

Because the age structure of the population changed markedly during this period, the number of eggs produced lagged behind the trend in population abundance. Numbers of eggs produced had a 4.2-fold range of variation. Over 2×10^{14} eggs were produced every year from 1980 through 1985; the most eggs were produced in 1983 (figure 10). The indices for eggs in the plankton between 1981 and 1988 showed a 57-fold variation. The early larvae

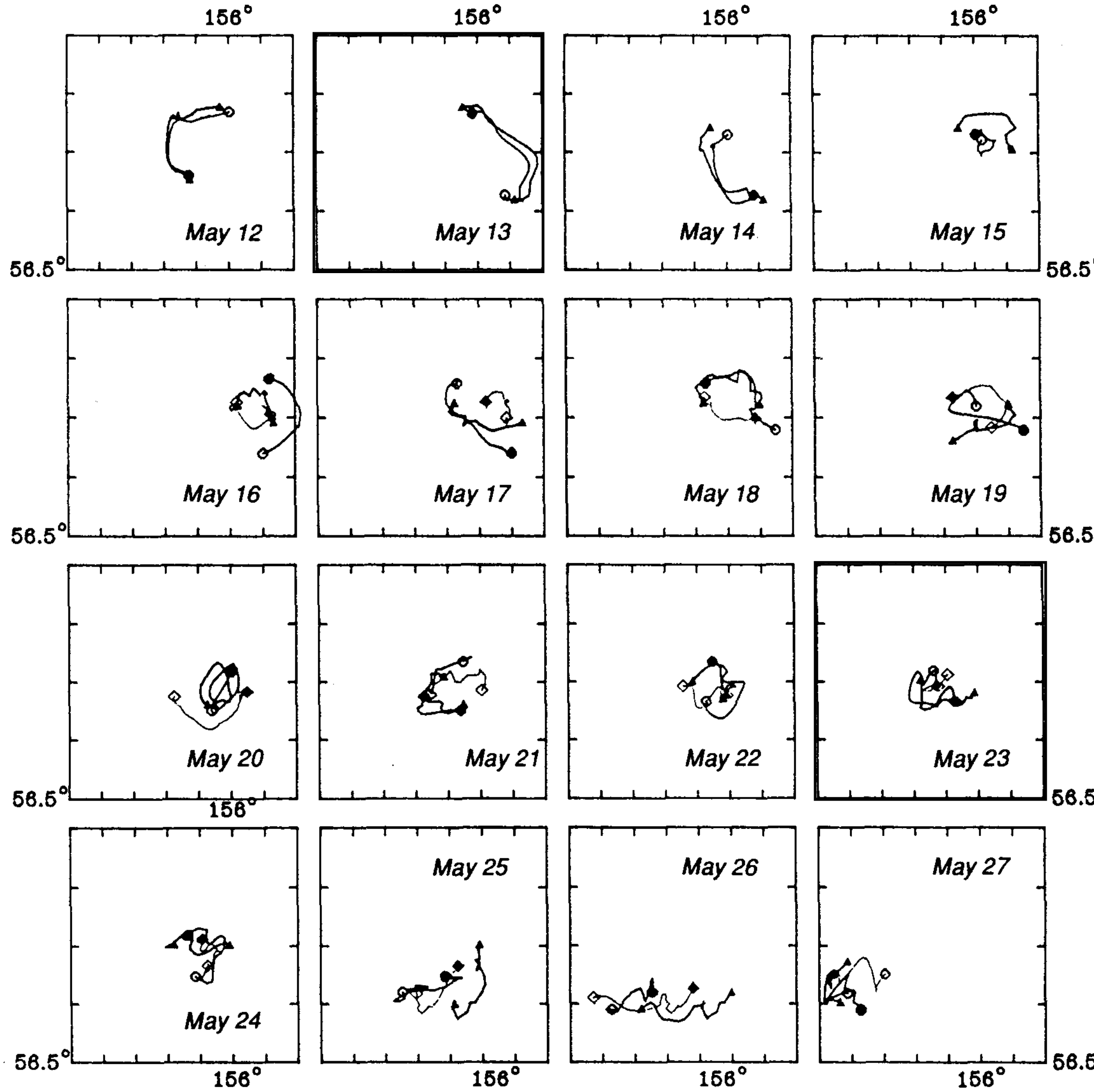

Figure 8. Satellite-tracked buoys in an eddy during May 1990.

varied more than any of the other stages, 158-fold, from 1979 through 1987.

The numbers of late larvae had a 69-fold range of variation among the 9 years for which there are data. The indices of abundance of age-0 juveniles showed a 7.6-fold range of variation among the 12 years for which there are data. Eight years of data for the age-1 juveniles produced indices of abundance with a 37-fold range of variation. The time series for 3-year-old recruits is 15 years long and has a range of variation of 24.1. The recruitment time series is dominated by five successive strong year classes (1975–79). When the adult population was at its height (1980–83), weak year classes were produced (figure 10).

We compared annual abundance estimates between stages by ranking the abundance of each stage through the time series for that stage. For each pair of stages, we used only those years when estimates of both stages were available. We did not consider the indices for planktonic eggs and early larvae because the time series were so short. When the ranked abundances of two stages are plotted against each other, an indication of their relationship can be seen, and this is probably the limit to which these data can be analyzed (figure 11). The number of adults is related to the number of eggs produced, but there is considerable scatter in the data because of changes in the age composition, and thus the egg-producing capacity of the adults (figure 11A). Numbers of eggs

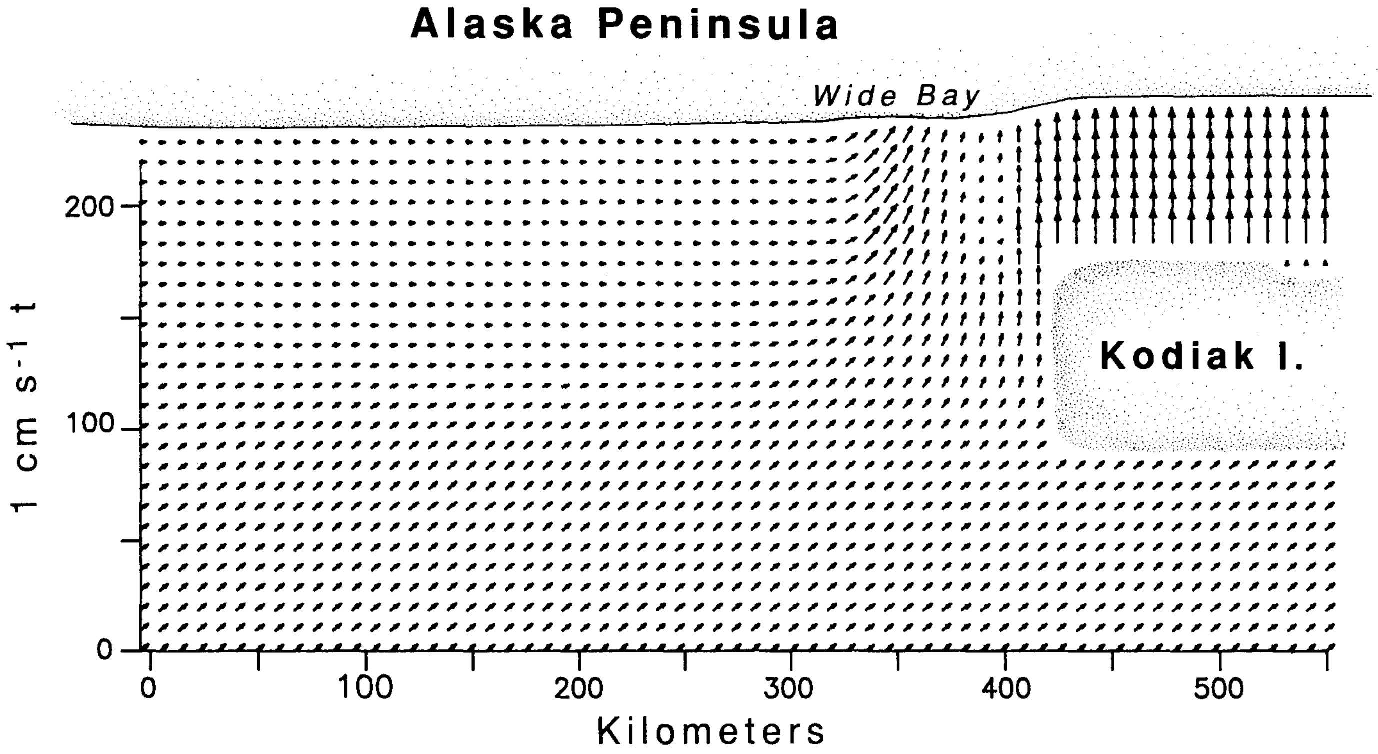

Figure 9. Surface velocity field as generated by a wind-driven model. Note the region of convergence off Wide Bay.

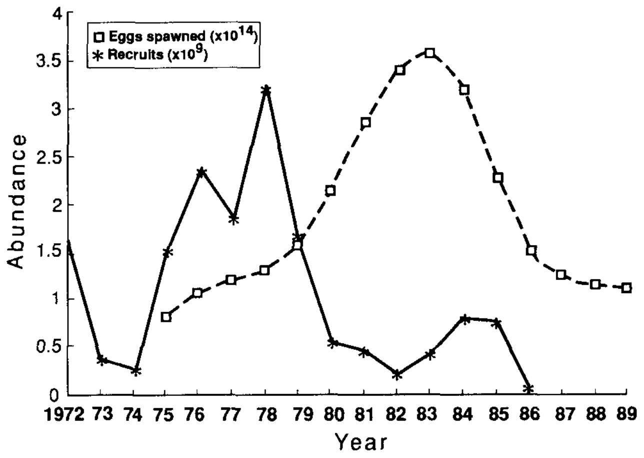

Figure 10. Numbers of eggs produced and number of recruits for the Shelikof Strait, Gulf of Alaska, walleye pollock population.

produced are considered in subsequent diagrams as a measure of the relationship between spawning stock size and year-class abundance. When the numbers of eggs produced are plotted against the numbers of late larvae, no pattern of relationship can be seen (figure 11B). High numbers of eggs resulted in low and high numbers of late larvae, and low numbers of eggs also resulted in low and high numbers of late larvae. A positive relationship is indicated between the numbers of late larvae and the numbers of age-0 juveniles, for the 7 years with the data (figure 11C). The numbers of age-0 and age-1 juveniles also seem to be positively related, but there are only 6 years of data. An exception was the 1980 year class, which seemed very low as age-0 juveniles, but high as age-1 juveniles (figure 11D).

Combined with the above, plots of year-class size at various life stages against ranks of 3-year-old recruits can indicate when year class is established (figure 12). When numbers of late larvae are plotted against 3-year-old recruits, little indication of relationship is seen (figure 12B). Very high numbers of recruits resulted when there were moderate and low numbers of late larvae. In the two years when there were few larvae, few recruits were produced. It appears that in years when few larvae survive to reach 15 mm, the numbers of recruits will be low; however, high numbers of late larvae do not always produce high numbers of recruits. Therefore, interannual variation in survival sometimes occurs after the late larval stage. Age-0 and age-1 juvenile abundance both showed a positive relationship to numbers of recruits (figures 12C and 12D). Except for 1984, the numbers of age-1 juveniles gave a very good indication of how many recruits there would be.

We calculated daily rates of change between successive stages (late larvae to age-0 juveniles, age-0

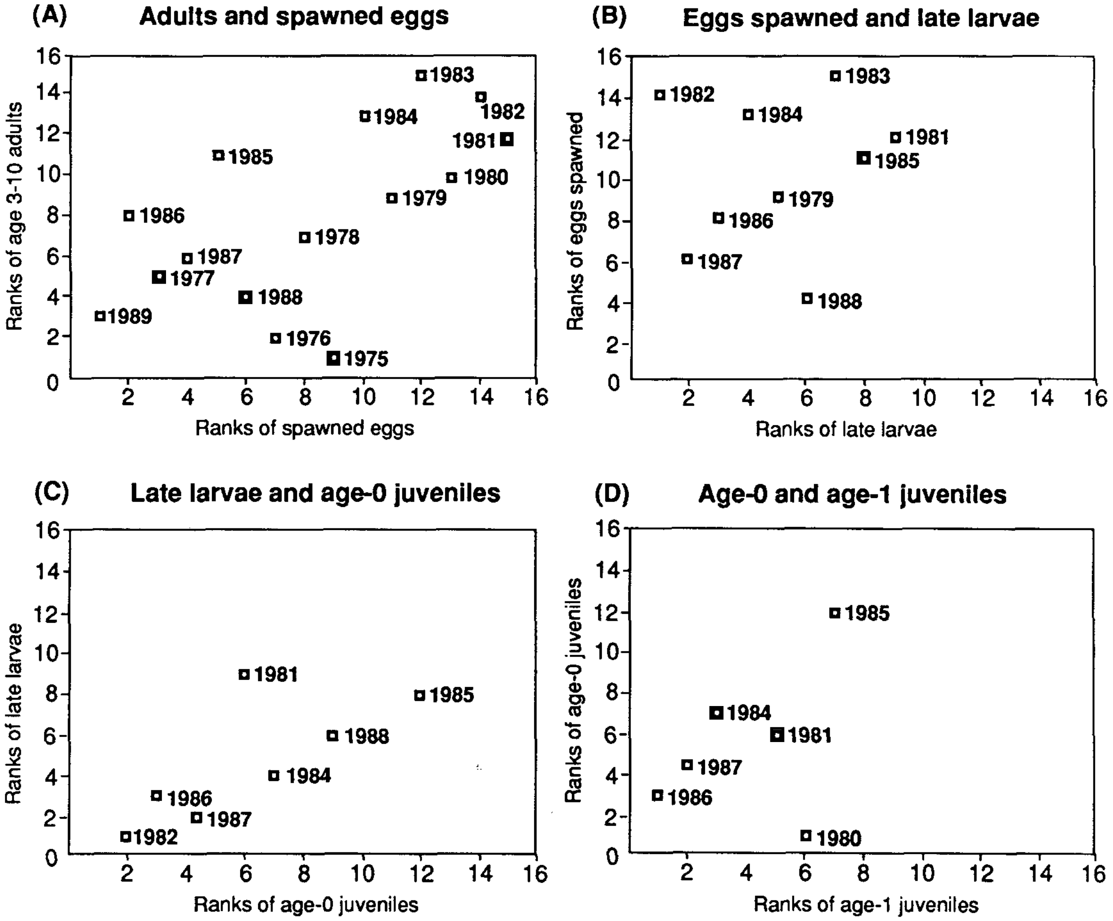

Figure 11. Comparisons of ranks of annual abundance estimates of walleye pollock from Shelikof Strait, Gulf of Alaska, at various stages. Positive relationships are indicated by values on a diagonal from the lower left to the upper right; negative relationships are indicated by values on the diagonal from upper left to lower right. Random scatter of values throughout a diagram indicates no relationship between abundance of the two stages.

to age-1 juveniles, and age-1 juveniles to age-3 recruits) for years when abundance estimates of both stages were available (figure 13). Because only indices of abundance of age-0 and age-1 juveniles were available, the "mortality" rates cannot be considered absolute, but rather a means of comparison among years. These rates were plotted against the abundance of the year class at the beginning of the time interval from which the rate was derived. A positive relationship on these plots would indicate that higher mortality occurs in years when abundance is high (density-dependent mortality). The plots of age-0 and age-1 juveniles showed no pattern, but the plot of the late larvae indicated that density-dependent mortality may occur between the late larval and age-0 stages. Sources of such mortality should be investigated but may include increased predation on young walleye pollock when they are exceptionally abundant, or reduced food levels because the feeding requirements of the walleye pollock exceed the production capacity of their prey.

Overall, a weakly negative relationship is indicated between the numbers of eggs produced and the resulting numbers of recruits (figure 12A). Earlier studies have also revealed this relationship (Megrey 1989). This indicates that some density-dependent mechanism affected the prerecruits. With the intense nature of the spawning, egg cannibalism was a plausible mechanism. However, examination of stomach contents of adults in the spawning area during the time of spawning and egg presence over a three-year period revealed that no more than 10% of the eggs were eaten by adults (Brodeur et al. 1991). Another mechanism would be a decrease in egg size—and thus size of larvae at hatching—at large stock sizes. Indeed it was found that size at hatching was dependent on egg size, but also that interannual variations in egg size were not correlated

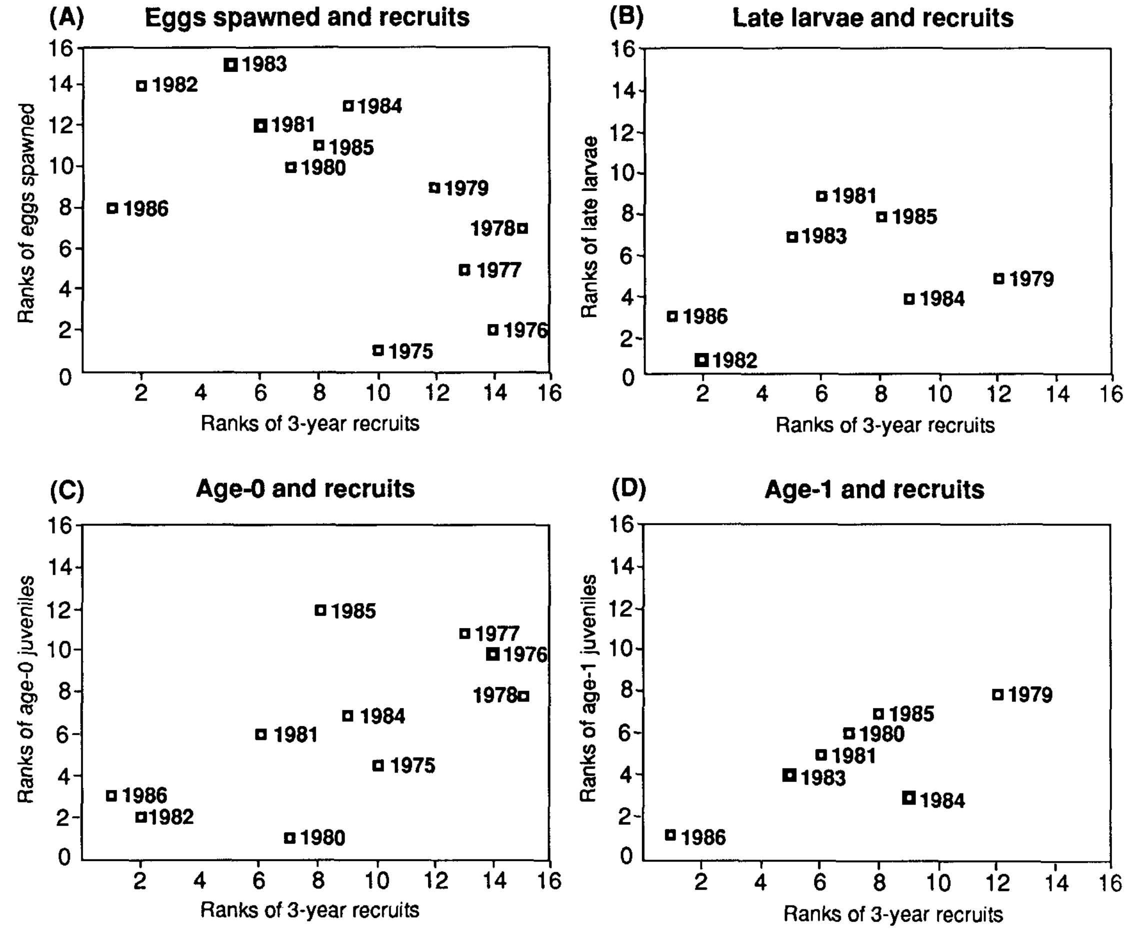

Figure 12. Comparisons of ranks of annual abundance estimates of 3-year-old recruits and various other stages of walleye pollock from Shelikof Strait, Gulf of Alaska. Positive relationships are indicated by values on a diagonal from the lower left to the upper right; negative relationships are indicated by values on the diagonal from upper left to lower right. Random scatter of values throughout a diagram indicates no relationship between abundance of the two stages.

with size of the spawning stock (Hinckley 1990). Given the short time series of data available, it is possible that the observed relationship of spawners and recruits is spurious. This is indicated by the fact that the numbers of late larvae bore no relationship to numbers of eggs produced.

Walleye pollock recruitment also seems to be negatively related to the large-scale climatic indicator NEPPI, which indicates storminess in the Gulf of Alaska. High NEPPI values are produced when the Aleutian Low is intense; low values indicate that the low is weak, absent, or displaced. Thus low recruitment seems to result from stormy years (Schumacher and Kendall 1989). On a smaller scale, birthdate distributions have shown increased mortality following April and May storms in the area of larval occurrence. Good larval survival occurs when there is calm weather during the week after hatching (K. M. Bailey, NMFS, Seattle, and S. A. Macklin, ERL, Seattle, pers. comm.). Olla and Davis (1990) have shown in the laboratory that larvae avoid turbulence. Storms may increase mortality by decreasing food availability, destroying food patches, or decreasing insolation required for phytoplankton production. Incze et al. (1990) followed a patch of larvae marked by a drogue during the passage of a storm and investigated the storm's effects on microzooplankton's vertical distribution and abundance. Although the mixed layer and level of maximum microzooplankton deepened during the storm, quantities of prey remained >30 organisms per liter (well above a successful feeding threshold of 10 per liter) somewhere in the upper 45 m of the water column. Birthdate distributions of larvae collected later that year showed minimal survival of the first-feeding larvae that were present during the storm (K. M. Bailey, NMFS, Seattle, and S. A. Macklin, ERL, Seattle, pers. comm.), so some factor other than food availability may contribute to storm-related larval mortality.

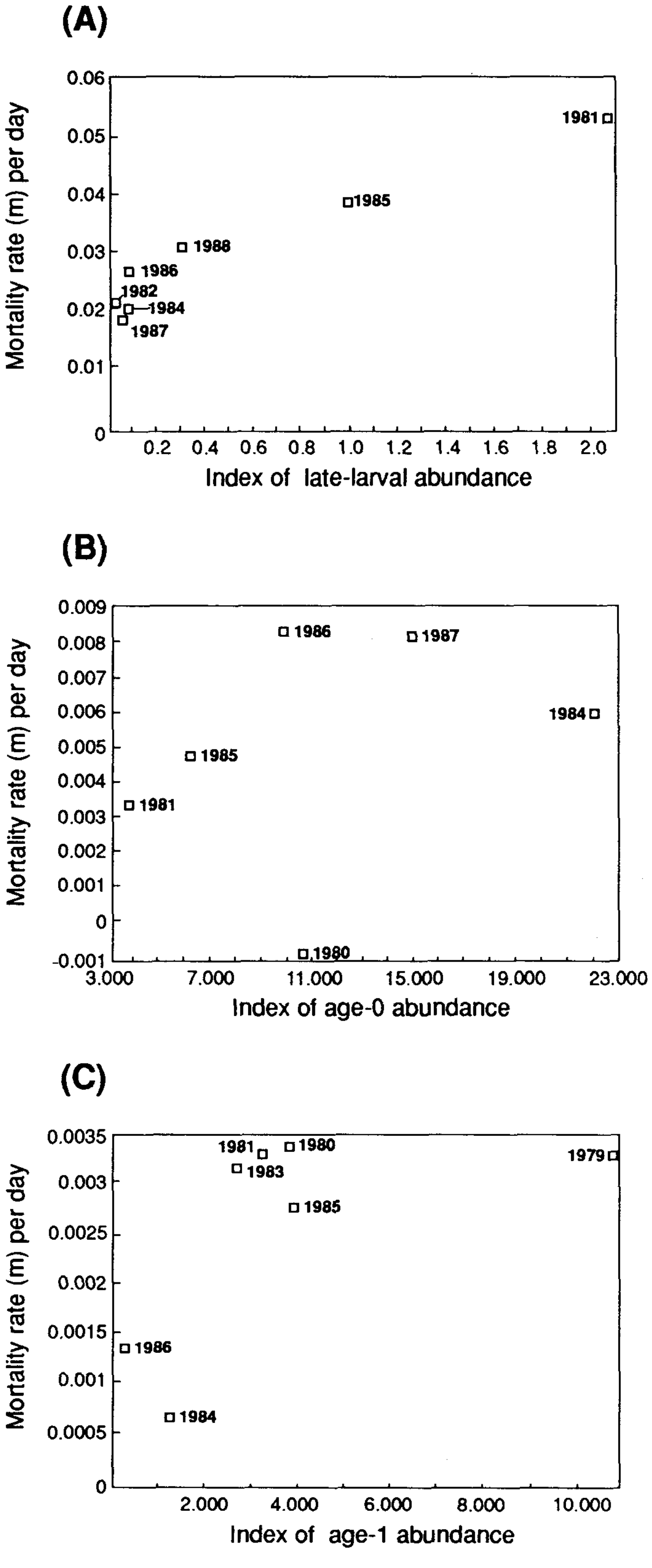

Figure 13. Estimates of daily mortality rates between successive stages and abundance estimates of the initial stage for walleye pollock from Shelikof Strait, Gulf of Alaska. (*A*) Late larvae to age-0 juveniles; (*B*) age-0 juveniles to age-1 juveniles; (*C*) age-1 juveniles to age-3 recruits.

SUMMARY

Since 1984, the FOCI program has been conducting fisheries oceanographic research in order to understand how the environment affects recruitment to the walleye pollock stock in Shelikof Strait, Alaska. This research was based on fundamental knowledge of the physical environment and, to a lesser degree, knowledge of fisheries biology. We have focused on transport of the planktonic stages toward nursery grounds, and processes affecting mortality as the animals are transported. We consider the following observations to be of major importance in understanding how the environment is related to recruitment of walleye pollock.

1. Circulation is dominated by the Alaska Coastal Current, which is one of the strongest and most persistent currents along the coasts of North America. Although most volume transport throughout the water column is directed seaward through the Shelikof sea valley, approximately 75% of the water in the upper 50 m appears to stay on the continental shelf.

2. A persistent, relatively weak flow of slope water into the sea valley provides a nutrient source under and (at the near surface) to the south of the ACC. Interannual variations in bottom-water properties have been related to circulation anomalies in the Gulf of Alaska.

3. Baroclinic instability and wind-driven flow out of Wide Bay form features that tend to concentrate and retain larvae on the shelf. The role of these features in larval retention, and the potential impact on secondary production and larval mortality are ongoing topics of research.

4. Strong spatial variations in the wind field can cause an area of convergence of the surface-layer currents. The scale of this feature is consistent with the observed size of the patch of walleye pollock larvae.

5. During the 1980s, several adjacent strong year classes (1975–79) moved through the Shelikof Strait population of walleye pollock, causing a variation in numbers of adults from 6.0 to 1.3 billion. Only weak or moderate year classes have occurred since 1979. Thus during our studies we have not had the opportunity to observe conditions leading to a strong year class: interannual variations in the physical environment, and in the early life history of walleye pollock have resulted in only minor changes in year-class size.

6. There is little interannual variation in the timing and location of walleye pollock spawning and egg and larval development within the Shelikof Strait system. The fish spawn primarily in early April over the deep trench near Cape Kekurnoi. The

eggs stay mainly below 150 m in the water column and are advected little during their two-week incubation period. The larvae develop in the upper 50 m of the water column and are advected to the southwest as they grow at about 2 mm d^{-1} during late April and May. During this time the larvae are often in large patches and have been found entrained in eddies, which increase their residence time in the area and lessen their chances of being advected offshore.

7. Observable growth of surviving larvae varies little. Condition of larvae varies with season and location. Insufficient food may be available early in the spawning season. Larvae in eddies seem to be in better feeding condition that those outside eddies.

8. Events during the egg and early larval stages are important in establishing year-class size, which is unrelated to the number of eggs spawned. Year-class size seems largely determined by the end of the larval period, although events during the following summer may also reduce the year class. Storms during the early larval period may be particularly detrimental to survival, but the mechanism is not yet clear. An index of storminess in the Gulf of Alaska may provide a way of predicting year-class size.

Although much has been discovered about pollock, their environment, and processes that link the fish to their environment, there are many gaps in our observations and understanding of recruitment. Some important questions that FOCI research will attempt to address include: How beneficial is it for larvae to be within an eddy; is it a relatively food-rich safe haven or does it provide a concentrated source of food for predators? What mechanisms generate eddies; how often are they formed; what is their time history and relation to the general circulation? What processes are involved in the relation between wind mixing and survival of early larvae? What are the important survival processes during late larval and early juvenile life, and are these density dependent? How well are local wind, current, and mixing related to NEPPI? The answers to these questions will greatly enhance our understanding of environmental influences on the early stages of walleye pollock in the western Gulf of Alaska.

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DEPTH DISTRIBUTIONS OF LATE LARVAE AND PELAGIC JUVENILES OF SOME FISHES OF THE CALIFORNIA CURRENT

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ABSTRACT

The vertical distribution of pelagic young-of-the-year larval and juvenile fishes in the California Current is reviewed. New data from synoptic midwater trawls conducted at depths of 13, 37, and 117 m along the central California coast are presented. Data for 15 species of rockfish, Dover and rex soles, northern anchovy, and Pacific whiting show that most species tend toward a uniform distribution among the three sampled depths. Notable exceptions include bocaccio (most abundant at 13 m) and blue, yellowtail, and pygmy rockfishes (most abundant at 117 m). With the advent of persistent upwelling during May and June, pelagic juvenile rockfish tend to occur deeper in the water column than in March–April. Data about shortbelly rockfish support the view that during periods of intense upwelling (May–June) relatively small fish stay deep, presumably to avoid advection offshore. There was not a clear relationship between depth distribution of fish and depth of the thermocline.

RESUMEN

Se revee la distribución vertical de larvas y juveniles de peces nacidos en el año en la Corriente de California. Se presentan datos nuevos de estudios sinópticos con redes de arrastre conducidos a profundidades de 13, 37, y 117 m a lo largo de la costa de California central. Datos de 15 especies de rocotes (*Sebastes* spp.), lenguados como *Microstomus pacificus* y *Glyptocephalus zachirus*, anchoveta norteña (*Engraulis mordax*), y merluza del Pacífico (*Merluccius productus*) demuestran que la mayoría de las especies tienen distribución uniforme entre las tres profundidades muestreadas. Excepciones notables incluyen *Sebastes paucispinis* (más abundante a 13 m) y *S. mystinus*, *S. flavidus*, y *S. wilsoni* (más abundantes a 117 m). Debido a la persistente surgencia de aguas, los juveniles pelágicos de rocotes tienden a ocurrir a mayores profundidades en la columna de agua durante mayo y junio que en marzo y abril. Datos sobre *S. jordani* apoya la noción que los peces pequeños se mantienen a profundidad durante períodos de intensa surgencia, presumiblemente tratando de evitar transporte hacia mar abierto. No se encontró una clara relación entre la distribución por profundidad de los peces y la profundidad de la termoclina.

INTRODUCTION

Knowledge of the vertical distribution of pelagic early life stages of fish is needed to understand transport and biological processes. Fish may adapt their behavior to take advantage of vertical shears in currents that might either retain the fish in or transport them to favorable areas (Bakun 1986; Sinclair 1988). After reviewing pertinent literature, we present results on the vertical distribution of rockfish (*Sebastes* spp.) and other species from our surveys of pelagic young-of-the-year rockfish off the coast of California from Monterey to Point Reyes.

Small rockfish larvae, which are only identified to genus because diagnostic characteristics are not known for most species, have generally been found at relatively shallow depths. Ahlstrom (1959) published the most detailed study on rockfish larvae off the coast of southern and Baja California. The larvae were found mostly in the upper mixed layer and thermocline. All but 3% of the rockfish larvae were collected in strata shallower than 80 m. Moser and Boehlert (1991) obtained similar results at two stations off southern California. Both studies indicated that the depth distribution of rockfish larvae is directly related to the depth of the thermocline. Rockfish larvae were found even shallower off Oregon (Richardson and Pearcy 1977; Boehlert et al. 1985). Barnett et al. (1984) found rockfish larvae in the neuston layer off southern California; Shenker (1988) found them in the neuston layer off Oregon. The data collected off southern California indicated that larvae were more abundant in the water column than in the neuston and epibenthic layers.

Ahlstrom (1959) found Pacific whiting (*Merluccius productus*) larvae deeper than rockfish and usually within or below the thermocline. Only 5% of the whiting were caught above 43 m, whereas 56% of the rockfish larvae were taken there.

Northern anchovy (*Engraulis mordax*) larvae are found at very shallow depths. For a 1959 study, Ahlstrom caught about 48% of anchovy between the surface and 48 m; less than 1% came from deeper than 88 m. Boehlert et al. (1985) did not catch any anchovy larvae deeper than 10 m. Shenker (1988) caught anchovy larvae in the neuston layer off Oregon. Barnett et al. (1984) tended to catch more anchovy larvae in the water column than in the neuston and epibenthic layers off southern California.

Larvae of the two species of flatfish in our study differ in their depth distribution. Pearcy et al. (1977) found that almost all Dover sole (*Microstomus pacificus*) larvae occurred in the upper 600 m of water off Oregon. Best catch rates were made in the 0–50-m depth stratum, but high rates also occurred in the 100–150-m stratum. Boehlert et al. (1985) caught rex sole (*Glyptocephalus zachirus*) larvae between the surface and 30 m; the highest catches occurred between 10 and 20 m. Shenker (1988) caught rex sole larvae in the neuston layer off Oregon.

Juveniles of several species of rockfish, including splitnose (*S. diploproa*) and bocaccio (*S. paucispinis*), have been captured at the surface associated with drifting kelp (Mitchell and Hunter 1970; Boehlert 1977). Shenker (1988) captured unidentified juvenile rockfish and juvenile black (*S. melanops*), blue (*S. mystinus*), and canary (*S. pinniger*) rockfish in the neuston layer. Juveniles of many species of rockfish have been captured with midwater trawls and purse seines in the upper 100 m (Brodeur and Pearcy 1986; Kendall and Lenarz 1987, and papers reviewed by them), but the vertical distribution of these species in the upper water column has not been published. Moser and Ahlstrom (1978) found juvenile blackgill rockfish (*S. melanostomus*), and a few other species that we rarely capture in our surveys, between 200 and 250 m.

METHODS

We collected juvenile fish at night with a modified Cobb midwater trawl off the coast between Monterey (36°35′N) and Point Reyes (38°10′N). The net, which is described by Wyllie Echeverria et al. (1990), nominally has a square mouth, but acoustic measurements showed that although the height of the mouth was 14 m, the width varied from 8 m (when the center of the net was at 13-m depth) to 13.5 m (at 117-m depth).

Acoustic measurements also showed that the net was not always at targeted depths, but precision was sufficient to separate tows taken at different targeted depths. We assume here that all tows were at their targeted depths. During the survey the targeted depth was usually 37 m but was set at 13 m for shallow stations. When time and depth allowed we towed at 13 m, 37 m, and 117 m to obtain data on the vertical distribution of fish. Since we did not use an opening-closing net, some contamination by specimens from nontargeted depths was possible. The net was dropped to the targeted depth as rapidly as possible while the vessel maintained steerage, was towed for 15 minutes at about 5 km per hour, and was then retrieved as rapidly as possible while the vessel maintained steerage. We do not believe that contamination is a serious problem. We used a cod end with 9.5-mm stretched mesh width that retained only some of the largest larvae and did not retain all of the smaller juveniles encountered. We did most of the work from mid-May through June, and from late March through mid-April, between 1983 and 1990.

We standardized catches for net mouth width by dividing by the width. For each station with tows at 13, 37, and 117 m, we calculated average depth for each captured species. We calculated average depths both as simple averages of individual station averages (unweighted) and from the sums of catches made at each depth over all stations (weighted). If the fish were equally abundant at the three sampled depths, the average depth would be 55.7 m. If the fish and samples were evenly distributed between 0 and 117 m, the average depth would be 58.5 m. Thus under the even-fish-distribution assumption, the uneven depth distribution of our samples had little effect on our estimates of average depth between the surface and 117 m. However, if there were relatively high densities of fish in unsampled strata, our estimates of average depth could be biased. We tested null hypotheses that catch rates for two depths were equal by using the paired *t* test and the sign test (Dixon and Massey 1957).

RESULTS

Results are presented for 15 species of rockfish — bocaccio, darkblotched rockfish (*S. crameri*), bank rockfish (*S. rufus*), black rockfish, shortbelly rockfish (*S. jordani*), squarespot rockfish (*S. hopkinsi*), canary rockfish, stripetail rockfish (*S. saxicola*), chilipepper (*S. goodei*), halfbanded rockfish (*S. semicinctus*), yellowtail rockfish (*S. flavidus*), brown rockfish (*S. auriculatus*), widow rockfish (*S. entomelas*), blue rockfish, and pygmy rockfish (*S. wilsoni*); 2 species of flatfish — Dover and rex sole; Pacific whiting; and northern anchovy (table 1). We also caught Pacific and speckled sanddabs (*Citharichthys sordidus* and *C. stigmaeus*), but the depth distribution data on these two species are being used for a thesis by graduate student Keith Sakuma at San Francisco State University and are not included in this paper. We collected at least one specimen at 61 stations with tows at 13, 37, and 117 m; 83 stations with tows at 13

TABLE 1
Number of Positive Stations, Average Depth (m) and Standard Error of the Average Depth for Pelagic Young-of-the-Year Fish off Central California during May–June

		Unweighted		Weighted	
Species	Number of stations	Average depth	Standard error	Average depth	Standard error
Bocaccio	29	30.4	3.0	26.2	3.6
Darkblotched rockfish	9	33.7	11.7	24.7	5.3
Dover sole	10	39.0	11.8	28.8	9.1
Northern anchovy	9	41.8	12.2	25.0	17.8
Bank rockfish	4	52.3	26.5	15.4	12.1
Black rockfish	7	53.0	18.4	43.9	21.7
Shortbelly rockfish	43	53.6	5.0	36.2	8.2
Squarespot rockfish	27	54.7	7.6	39.4	27.6
Pacific whiting	59	54.8	3.3	27.8	9.1
Canary rockfish	20	55.2	6.2	80.3	38.3
Stripetail rockfish	11	56.9	6.5	51.1	17.6
Chilipepper	22	58.5	8.6	39.1	10.9
Halfbanded rockfish	5	60.5	17.6	40.7	32.3
Rex sole	24	63.5	7.4	42.5	6.7
Yellowtail rockfish	21	64.8	9.1	66.2	18.4
Brown rockfish	5	69.0	21.9	60.2	28.4
Widow rockfish	31	70.2	7.0	45.6	14.1
Blue rockfish	30	82.0	7.3	57.8	20.9
Pygmy rockfish	13	83.0	13.4	75.9	23.5
Average		56.7	10.8	43.5	17.1

Weighted averages are weighted by catches. Species are arranged by unweighted average depth.

and 37 m; 77 stations with tows at 37 and 117 m; and 64 stations with tows at 13 and 117 m. We captured more than 150,000 rockfish, 125,000 Pacific whiting, 1,250 northern anchovy, and 500 flatfish.

The unweighted average depth of most species was close to the average expected (55.7 m) when densities are equally distributed at the three sampled depths (table 1 and figure 1). The unweighted average over all species was 56.7 m. Weighted average depths were shallower than the unweighted averages for 17 of the 19 species. The average over species of weighted average depths was 13 m less than the unweighted average. Very large catches tended to occur at shallow depths. Weighted standard errors were about 50% greater than unweighted.

The results indicate that bocaccio were more common at shallow than at deep depths; densities of canary and halfbanded rockfish were lower at 13 m than at 37 m; and yellowtail, blue, and pygmy rockfish were most abundant at 117 m (table 2 and figure 2). Weighted 13-m densities of Pacific whiting were greater than 37-m densities, but the converse was true for unweighted densities. Catch rates of Pacific whiting appeared to be lowest at 117 m. Weighted and unweighted depth comparisons differed for widow rockfish.

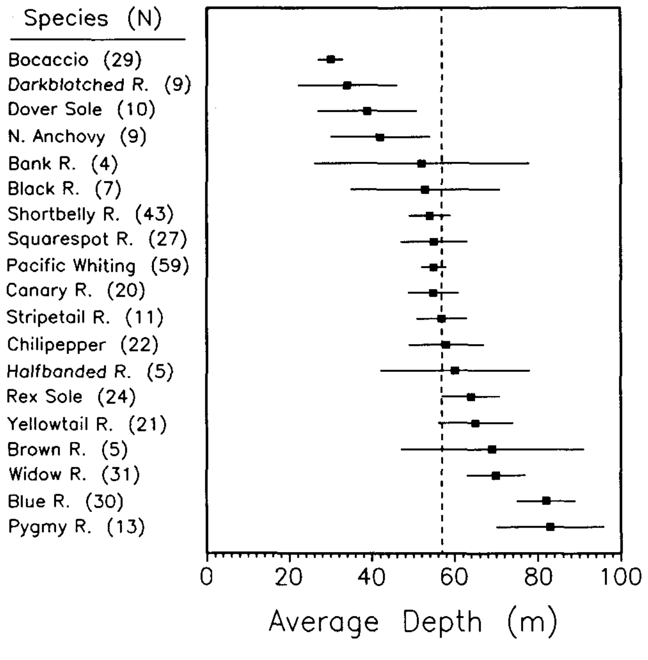

Figure 1. Unweighted average depths (*solid squares*), standard errors (*horizontal lines*), and number of stations with at least one positive tow at 13, 37, or 117 m (N) for pelagic young-of-the-year off central California during May–June. The overall average is shown as a *dashed vertical line*. (R. = rockfish)

There is evidence that average depth changes as the season progresses. We compared average depth in March and April with May and June for bocaccio, chilipepper, and blue, shortbelly, and widow rockfish in 1987, 1988, and 1990. Our data were insufficient to make such comparisons for other species. Unweighted average depth between the two time periods increased in all cases except for bocaccio in

TABLE 2

Results of Sign and Paired *t*-Tests That Catch Rates of Young-of-the-Year Fish Are Independent of Depth of Tow off Central California during May–June

	Probability of greater difference due to chance alone								
	13 and 37 m			37 and 117 m			13 and 117 m		
Species	*n*	Sign	*t*	*n*	Sign	*t*	*n*	Sign	*t*
Bocaccio	31	<0.10	>0.10	22	<0.01	<0.01	12	<0.05	<0.01
Darkblotched rockfish	12	>0.10	>0.10	5	>0.10	>0.10	6	>0.10	<0.05
Dover sole	11	>0.10	>0.10	9	>0.10	>0.10	8	>0.10	>0.10
Northern anchovy	14	>0.10	>0.10	12	>0.10	>0.10	3	>0.10	>0.10
Bank rockfish	6	>0.10	>0.10	4	>0.10	>0.10	4	>0.10	>0.10
Black rockfish	12	>0.10	<0.10	7	>0.10	>0.10	4	>0.10	>0.10
Shortbelly rockfish	63	>0.10	>0.10	53	>0.10	<0.10	40	>0.10	>0.10
Squarespot rockfish	26	>0.10	>0.10	30	>0.10	>0.10	24	>0.10	>0.10
Pacific whiting	73	<0.10	<0.01	68	<0.05	>0.10	58	>0.10	<0.05
Canary rockfish	19	<0.05	<0.05	16	<0.10	>0.10	6	>0.10	>0.10
Stripetail rockfish	14	>0.10	>0.10	11	>0.10	>0.10	6	>0.10	>0.10
Chilipepper	27	>0.10	>0.10	29	>0.10	>0.10	14	>0.10	>0.10
Halfbanded rockfish	9	<0.05	<0.10	6	>0.10	>0.10	3	>0.10	>0.10
Rex sole	26	>0.10	>0.10	30	>0.10	>0.10	24	>0.10	>0.10
Yellowtail rockfish	29	>0.10	>0.10	23	<0.10	<0.10	15	>0.10	>0.10
Brown rockfish	5	>0.10	>0.10	11	>0.10	>0.10	—	—	—
Widow rockfish	35	>0.10	>0.10	32	<0.10	<0.05	31	<0.10	<0.10
Blue rockfish	33	>0.10	>0.10	36	>0.10	<0.10	32	<0.05	<0.10
Pygmy rockfish	6	>0.10	>0.10	13	<0.10	<0.05	12	>0.10	>0.10

Results with probabilities less than 0.10 are underlined. *n* is the number of positive stations. Cases with fewer than three positive stations are not included.

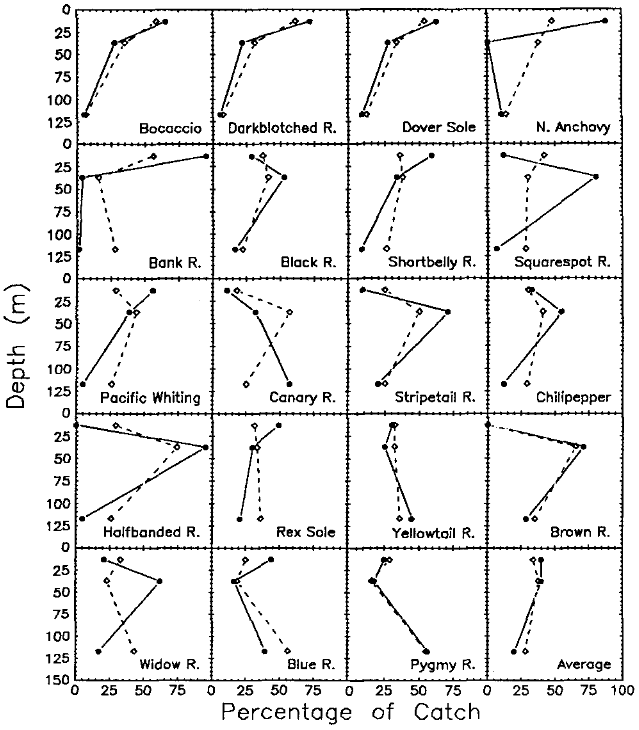

Figure 2. Weighted (*solid circles and lines*) and unweighted (*open diamonds and dashed lines*) depth distributions for pelagic young-of-the-year fish off central California during May–June. (R. = rockfish)

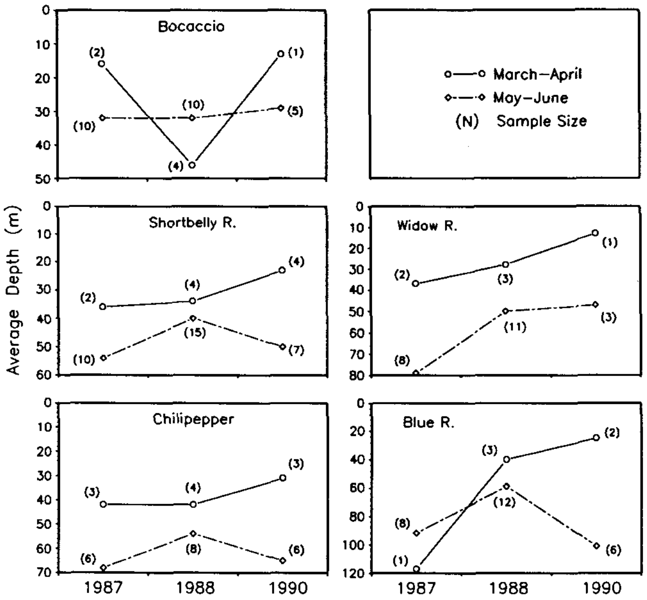

Figure 3. Unweighted average depths for pelagic young-of-the-year bocaccio, chilipepper, and shortbelly, widow, and blue rockfish off central California during March–April and May–June. Sample size is the number of stations with at least one positive tow at 13, 37, or 117 m. (R. = rockfish)

1988 and blue rockfish in 1987 (figure 3). Catches of these five species at 117 m were typically quite low in March–April. Similar results were obtained for weighted average depths. The unweighted overall average depth increased 19 m between the two periods, and weighted average increased 9 m.

Data were also available to compare size compositions of shortbelly rockfish in paired 13- and 37-m tows from 1987–90, and from unpaired 13- and 37-

m tows in 1987 and 1988. During May–June, small shortbelly rockfish (<50 mm) tended to be deeper than larger fish (figure 4). This was true both when the data were unweighted, as in the figure, or weighted by catch.

DISCUSSION

The vertical distribution of late larval and juvenile rockfish that we found in March–April is similar to that of rockfish larvae (Ahlstrom 1959; Richardson and Pearcy 1977; Boehlert et al. 1985; Moser and Boehlert 1991). Our catches were relatively low in tows deeper than 37 m. By May–June the average depth of capture increased by 9–19 m, and catch rates for 117-m tows were seldom significantly less than rates for shallow tows (table 2 and figure 2). Also, reported distributions of larval northern anchovy (Ahlstrom 1959; Boehlert et al. 1985) and rex sole (Boehlert et al. 1985) were shallower than we found for young-of-the-year of the same species in May–June. In contrast, our May–June catch rates for juvenile Pacific whiting indicated greater relative abundance at shallow depths than was reported for larvae by Ahlstrom (1959).

Perhaps the different pattern for Pacific whiting is related to their habit of spawning at depths of 130–500 m in midwater, up to 400 km off the coast (Bailey et al. 1982). Except for northern anchovy, the other species spawn relatively close to shore. Northern anchovy spawn at midwater (sometimes far offshore) in fairly shallow depths. Bailey et al. (1982) present data showing that large catches of Pacific whiting eggs and larvae often occur in areas where northward geostrophic flow at 200 m would tend to advect the fish onshore.

The young-of-the-year fish in our study inhabit a greater depth range in the water column than other investigators found for earlier life stages. The larger fish that characterize our samples may be adapted to searching the water column for optimal feeding conditions, low predation rates, or favorable currents, while the smaller fish tend to occupy depths that, on the average, are favorable. We found that, even though shortbelly rockfish tend to be closer to the surface in March–April than in May–June, the smaller fish were often deeper than the larger fish in May–June. Offshore transport of surface waters due to upwelling is more prevalent in May–June than in March–April. Perhaps the smaller fish are adapted to avoid the surface waters, and thus reduce the risk of offshore advection, during May–June.

We often found bocaccio at very shallow depths in May–June. Bocaccio grow very rapidly compared to other rockfish and can reach 20 cm in their first year (Phillips 1964). In order to realize their rapid growth, very young bocaccio may need to remain in the upper water column to encounter higher temperatures and food densities. The time spent in the upper water column may subject them to increased offshore advection. Other studies indicate that such advection may occur, because larvae of bocaccio are found farther offshore than the more abundant larvae of shortbelly rockfish (MacGregor 1986; Moser and Boehlert 1991).

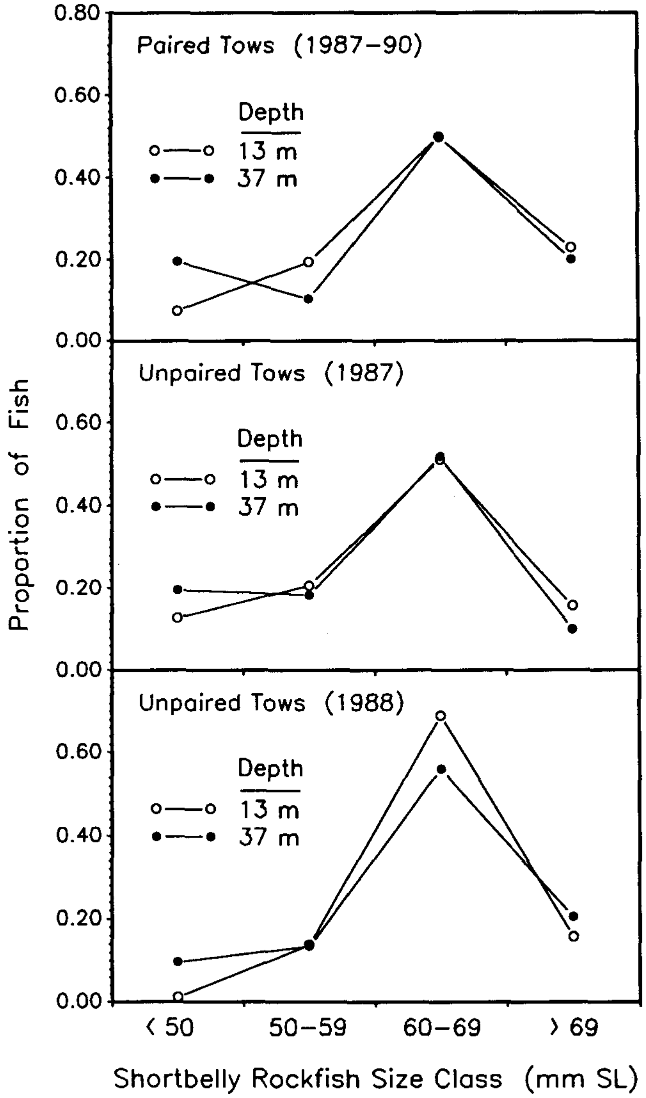

Figure 4. Size class compositions unweighted by catch for pelagic young-of-the-year shortbelly rockfish off central California during May–June.

Depth distributions were often shallower when observations were weighted by catches than when not weighted (tables 1 and 2 and figure 2). This was because very large catches tended to occur at shallow depths. It is possible that the fish school when at shallow depths, or avoid shallow depths unless conditions are particularly advantageous. Attempts to relate depth distributions at individual stations to oceanographic conditions have not produced convincing results. We did not find a clear relationship between depth distribution and the depth of the thermocline, as Ahlstrom (1959) and Moser and Boehlert (1991) found for rockfish larvae. However, large catches of juveniles often occur near to and offshore of upwelling fronts. We will continue to explore these relationships.

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MESOSCALE OCEANIC RESPONSE TO WIND EVENTS OFF CENTRAL CALIFORNIA IN SPRING 1989: CTD SURVEYS AND AVHRR IMAGERY

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ABSTRACT

Analysis of hydrographic data obtained during juvenile groundfish surveys, in relation to local wind forcing and AVHRR sea-surface temperature imagery, reveals that the oceanic region off central California between Point Reyes and Point Sur in spring 1989 was characterized by complex circulation patterns and considerable temporal and mesoscale variability. The "spring transition" to upwelling-favorable winds is most clearly evidenced by rapid, large decreases in SST (up to 4°–5°C) measured at four meteorological buoys. Daily-averaged winds are spatially coherent and oscillate between upwelling-favorable and relaxation conditions at 3–10-day intervals.

Persistent upwelling centers near Point Reyes and Point Año Nuevo were characterized by relatively cool, salty (8°–10°C, 33.6–34.0 psu) water in the upper 50 m, which is derived from offshore water at depths of 50–100 m. Water-mass analysis reveals that upwelled water is advected equatorward from its source. Some upwelled water is transported into shallow coastal areas and warmed. Alongshelf fronts between relatively warm, low-salinity (>13°C, <33.5 psu) offshore water and cool, higher-salinity upwelled water are advected onshore in response to wind relaxation or reversal events; frontal gradients intensify at these times. AVHRR imagery verifies the spatial patterns and complex mesoscale variability of the near-surface patterns observed in the CTD survey data. Eddylike hydrographic features are noted with horizontal scales on the order of the station spacing (10 km). How the complex circulation patterns and intense mesoscale spatial and temporal variability affect the survival and subsequent recruitment of juvenile groundfish is discussed.

RESUMEN

Análisis de datos hidrográficos con relación a la fuerza del viento local y a imágenes infrarrojas de satélite (AVHRR SST), obtenidos durante las campañas de investigación de juveniles de peces de fondo, muestra que la región oceánica de la parte central de California, entre Punta Reyes y Punta Sur, en la primavera de 1989, estaba caracterizada por patrones de circulación complejos y una considerable variabilidad temporal y espacial de mediana escala. La "transición de primavera" hacia vientos favorables a la surgencia de aguas es claramente evidente en las grandes y rápidas reducciones en salinidades y temperaturas superficiales (SST), de hasta 4°–5°C, medidas entre cuatro boyas meteorológicas. Los promedios diarios de los vientos son coeherentes en el espacio y varían entre condiciones favorables a la surgencia y períodos de relajamiento en intervalos de 3 a 10 dias.

Centros de surgencia persistentes cerca de Punta Reyes y Punta Año Nuevo estaban caracterizados por aguas relativamente frías y saladas (8°–10°C, 33.6–34.0‰) en los 50-m superficiales. Esta agua se deriva del mar abierto a profundidades de 50–100 m. Análisis de masas de aguas muestran que el agua de surgencia se desplaza hacia el ecuador desde su punto de origen. Algo de agua de surgencia es transportada hacia zonas costeras poco profundas donde se calienta. Frentes a lo largo de la plataforma continental, que separan aguas de mar abierto relativamente cálidas y de baja salinidad (>13°C, <33.5‰) y aguas de surgencia frías y de más alta salinidad, son desplazados hacia la costa en respuesta al relajamiento de los vientos (o sucesos revertidos); los gradientes a través del frente se intensifican en estos momentos. Imágenes de satélite infrarrojas verifican los patrones espaciales y la compleja variabilidad de las aguas superficiales observada en escalas intermedias con sonda de temperatura, salinidad, y profundidad (CTD) durante las campañas. Se observaron rasgos hidrográficos parecidos a remolinos con escalas horizontales del orden de la distancia entre estaciones (10 km). Se discute la influencia de los patrones complejos de circulación y la intensa variabilidad temporal y espacial a escalas intermedias con relación a la supervivencia y reclutamiento de los juveniles de los peces de fondo.

INTRODUCTION

The oceanic region off central California between Point Reyes (38°N) and Point Sur (36.3°N) (figure 1) is characterized by several important dynamic processes and features that contribute to an ap-

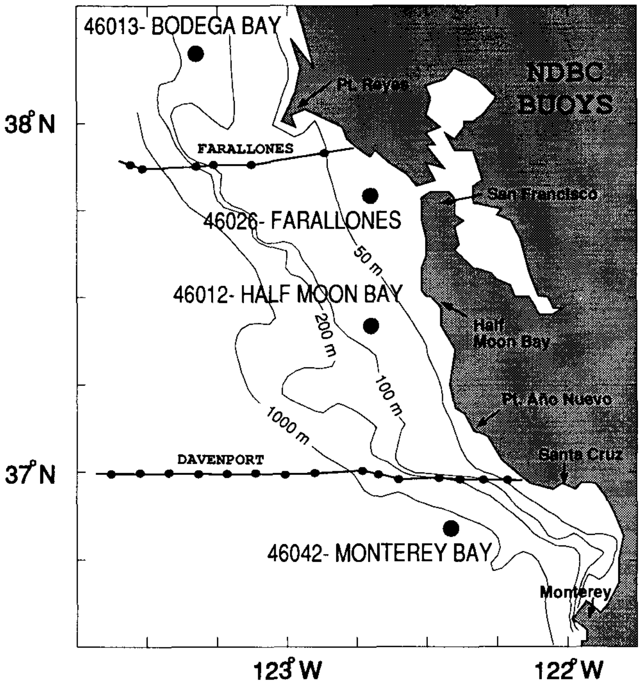

Figure 1. Area map of the juvenile rockfish recruitment survey region, showing location of NDBC meteorological data buoys (*large solid circles*) and cross-shelf CTD sections.

parently complex circulation. Significant physical processes include wind-forced motions (e.g., upwelling, horizontal advection, vertical mixing), tides, the circulation of the large-scale California Current system, flow/bathymetry interactions, and buoyancy effects (e.g., heat exchange with the atmosphere, freshwater inflow). Bathymetric features on a range of scales that could profoundly influence the circulation appear throughout the region. These include submarine canyons, banks, seamounts, headlands and embayments of various dimensions, and a wide range of continental shelf and slope widths. Water masses of unique characteristics may enter the region via local upwelling, advection onshelf or alongshelf due to changes in wind stress, and freshwater discharge, primarily from San Francisco Bay. Given this complex arrangement of forces and processes, a circulation that varies greatly in time and space should be expected over this portion of the California shelf.

This coastal environment is also a transition zone between two major biogeographical provinces, resulting in the presence of more species than are found either in the cold-temperate north (Oregonian Province, 35°–55°N) or in the warm-temperate south (California Province, 25°–35°N) (Briggs 1974). The area around Monterey Bay is believed to be a distributional barrier for a variety of marine organisms, including algae (Murray et al. 1980), molluscs (Valentine 1966), and fish (Horn and Allen 1978). The rich biological diversity may be enhanced further by the complex circulation patterns and by the diverse physical processes and variety of water types and ocean conditions in the region. At least, the flow regime must greatly influence the location, temporal variability, and ultimate success of larval and juvenile dispersal and recruitment into the adult groundfish population.

The region features numerous commercially and recreationally important species of groundfish, including the *Sebastes* complex — a major component of the West Coast groundfish fishery (Gunderson and Sample 1980), with annual landings from 1981–88 averaging over 45,000 MT/yr (PFMC 1989). Since 1983, the Southwest Fisheries Science Center (SWFSC) of NOAA NMFS has conducted a systematic midwater trawl field survey of the coastal ocean between Point Reyes and Point Sur each spring. The goals of the survey are to describe variations in groundfish recruitment, and to define the environmental conditions that lead to variability within the fishery. Data obtained during these annual surveys provide information on distribution and abundance patterns of young-of-the-year pelagic juveniles in this area (Wyllie-Echeverria et al. 1990). The Groundfish Analysis Group of SWFSC Tiburon Laboratory, under the direction of William Lenarz, is developing a recruitment index for rockfish based on this information.

The physical oceanographic component of these annual studies includes repeated surveying of the central California coastal region's hydrography via conductivity/temperature/depth (CTD) vertical casts and continuous surface mapping of temperature and salinity. CTD data from three spring 1989 sweeps (NOAA R/V *David Starr Jordan* cruise DS89-04) are used to define and describe the predominant hydrographic features present in the near-surface coastal ocean off central California following the spring transition. Selected Advanced Very High Resolution Radiometer (AVHRR) satellite sea-surface temperature (SST) images are used to verify and test the synopticity of the maps constructed from near-surface ship observations and to detail surface hydrographic features occurring beyond the sampling region.

We will discuss two key hypotheses. First, hydrographic and circulation features off central California, on scales on the order of 100 km, occur persistently during the upwelling season. Second, substantial spatial (10–50-km) and temporal (1–2-day) variations occur in the position and extent of these features. We focus on defining persistent hydrographic features and their variability on synoptic (<10-day) time scales. These should relate to natural fluctuations within the physical processes (e.g., upwelling) that control the circulation and, ultimately, the distribution and eventual settlement of larval and juvenile groundfish.

METHODS

Juvenile Rockfish Survey Design

Annual 30-day cruises aboard the NOAA R/V *David Starr Jordan* began in 1983 and have been conducted annually during late spring (May–June), a time when most pelagic stage juvenile rockfishes are identifiable to species, but before they settle to nearshore and benthic habitats. The sampling design presently permits three consecutive sweeps through a study area from 38°10′N (near Point Reyes) and 36°35′N (near Monterey), and from the coast to about 75 km offshore (figure 1). A CTD cast is made at each trawl station. Beginning in 1987, daytime activities were restructured to permit sampling of a more extensive grid of CTD stations. Each sweep is sampled south to north, and takes approximately ten days (seven nights of scheduled work plus three nights of additional discretionary sampling).

Collection and Processing of CTD Data

All CTD data obtained during the 1989 juvenile rockfish surveys were collected with a Sea-Bird Electronics SEACAT-SBE-19 profiler. At each CTD station, the profiler was lowered to its maximum rated depth (200 m), or to a depth 10 m off the bottom if water was less than 200 m deep. Only data collected on the downcast were ultimately preserved for analysis. A total of 380 acceptable CTD casts were obtained during the 1989 survey. One hundred thirty-five acceptable casts were obtained during sweep 1 (14–22 May); 153 casts during sweep 2 (23 May–3 June); and 92 casts during sweep 3 (4–13 June). Schwing et al. (1990b) provide a detailed description of the data collection and the reduction and processing procedures for this cruise, together with a full suite of data.

Meteorological Time Series

Meteorological data were obtained for selected sites in the survey region (figure 1). These sites include the region's four National Data Buoy Center (NDBC) moored buoys — 46013 (Bodega Bay: 38.2°N, 123.3°W); 46026 (Farallones: 37.8°N, 122.7°W); 46012 (Half Moon Bay: 37.4°N, 122.7°W); and 46042 (Monterey Bay: 36.8°N, 122.4°W) — and a land station at Monterey (Monterey Bay Aquarium; 36.6°N, 121.9°W). Daily averages of several surface meteorological characteristics, including air and sea temperature, wind speed and direction, and barometric pressure, were calculated for the period that includes the 1989 *Jordan* rockfish survey. The principal axis components of each buoy's wind, which is the compass heading along which variance is maximized, were also derived.

AVHRR Imagery

Sea-surface temperature (SST) images for the study region were produced from the data of the AVHRR carried aboard TIROS-N/NOAA polar-orbiting satellites (McClain et al. 1985). The calculated SST values and the blackbody brightness temperatures were registered to the surface temperature at NDBC 46042. Additional processing details are found in Tracy 1990.

RESULTS

Meteorological Conditions Preceding and During the DS89-04 Cruise

Meteorological time series of the daily vector mean wind, the principal axis component of the wind, and SST are presented for the four NDBC buoys (figures 2 and 3). All four NDBC wind series display very similar signals. Daily winds at Monterey Bay Aquarium are included to demonstrate the relative difference in wind speed over land and ocean. Until about 1 May, there were frequent (every 3 to 10 days) reversals or reductions in the principal wind component; however, the mean alongshore wind was about zero. After 1 May, winds at all sites were predominantly southward to southeastward (i.e., upwelling-favorable), until 30 June and beyond. This dramatic change in the region's wind patterns, called the spring transition (Huyer et al. 1979; Lentz 1987; Strub et al. 1987b), marks the onset of the upwelling season. However, numerous wind-relaxation events (reductions in the speed of upwelling-favorable wind) and wind-reversal events occurred during the upwelling season (Send et al. 1987). Two notable reversals occurred near the beginning of sweeps 2 (23 May) and 3 (4 June). Although the principal component at the three southern buoys is nearly alongshore, thus optimal for upwelling, the principal axis at Bodega is nearly normal to the coast (figure 2).

The synoptic variability of the wind field is reflected in SST at the buoys as well (figure 3). Changes in SST were relatively minor before the spring transition, and were associated with wind

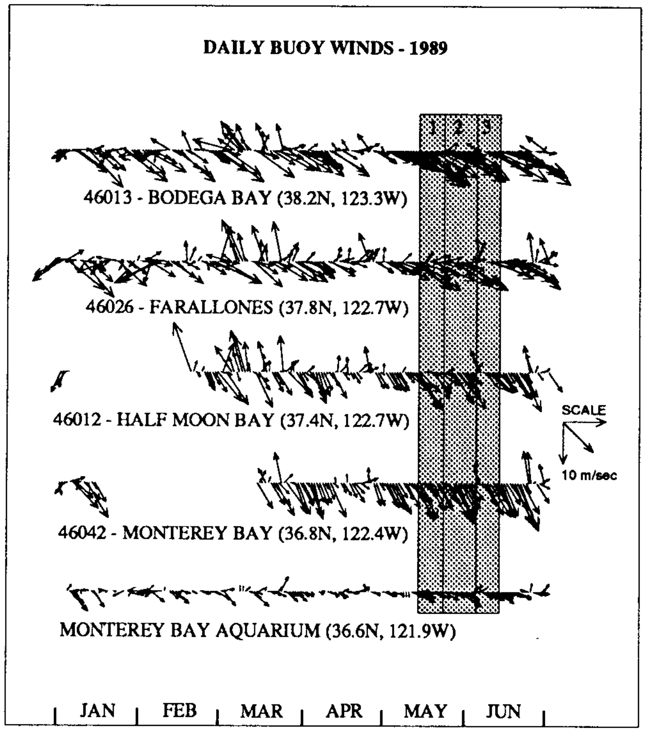

Figure 2. Vector time series of daily average winds from NDBC buoys and Monterey Bay Aquarium, January–June 1989. *Arrows* point in direction to which wind was blowing. *Shaded area* denotes period of groundfish cruise.

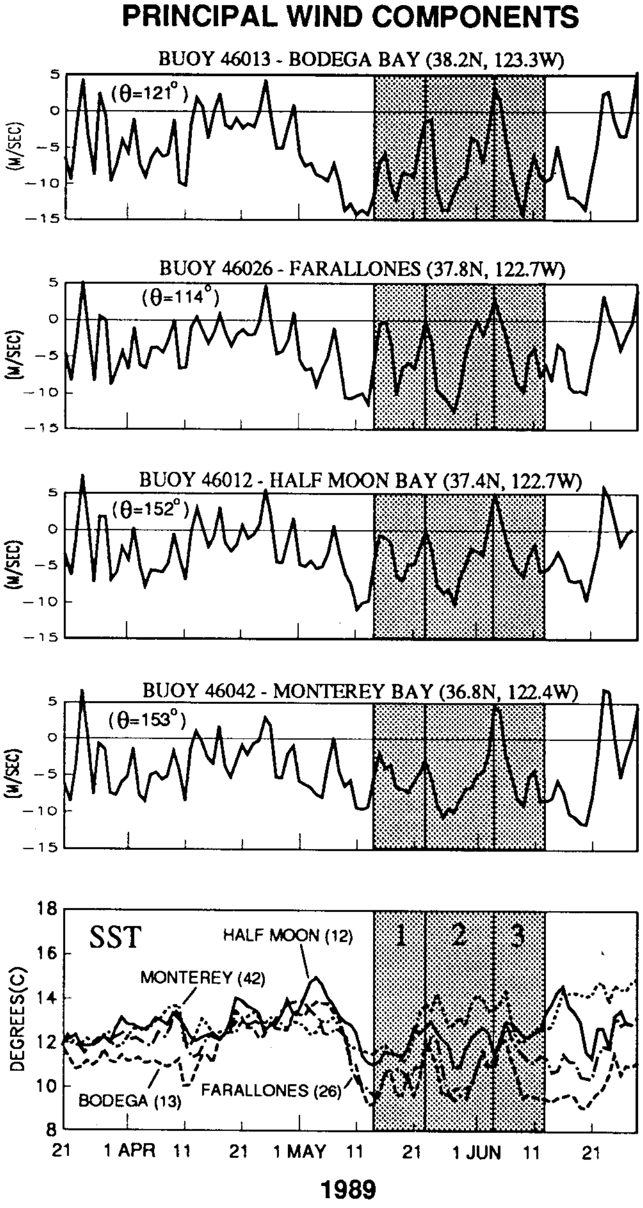

Figure 3. Time series of principal-axis wind component and sea-surface temperature (SST) from NDBC buoys for 21 March–29 June 1989. Negative wind speeds are in the direction of the principal axis, defined by θ at each buoy. *Shaded areas* denote period of groundfish cruise.

reversals. SST was also positively correlated with air temperature (not shown) at each site. The onset of upwelling, however, resulted in a dramatic decrease in SST of up to 4°–5°C at the buoys. Wind reversals and relaxations are reflected as warming events in the SST signals. Although SST at all four buoys responded similarly to wind forcing, the magnitude of the response, as well as the mean temperature for the upwelling season, varied with location. Monterey SST is generally the warmest; Bodega is generally the coolest.

In summary, both wind and SST from NDBC buoy time series varied widely on scales less than 10 days; i.e., less than the period of one sweep. For example, buoy SSTs changed by as much as 3°C during a single sweep. Such variability must be kept in mind for interpretations of the "synoptic" horizontal property maps from a single sweep—especially near-surface conditions, which are most influenced by meteorological forcing.

Horizontal Maps of Temperature, Salinity, and Density

Near-surface (5-m-depth) temperature and salinity throughout the groundfish survey region is summarized, by sweep, in a series of horizontal maps (figures 4–6). These maps were objectively contoured from the CTD cast data. The NDBC SST and principal wind-component time series, shown as inserts in the temperature maps, clearly demonstrate that conditions changed substantially during the course of each sweep. We will consider day-to-day environmental changes when describing the hydrography, rather than interpret the contour maps in a synoptic sense, i.e., as if the entire survey was made instantaneously.

Sweep 1 surface hydrography. Near-surface conditions during sweep 1, 14–22 May (figure 4), reflect

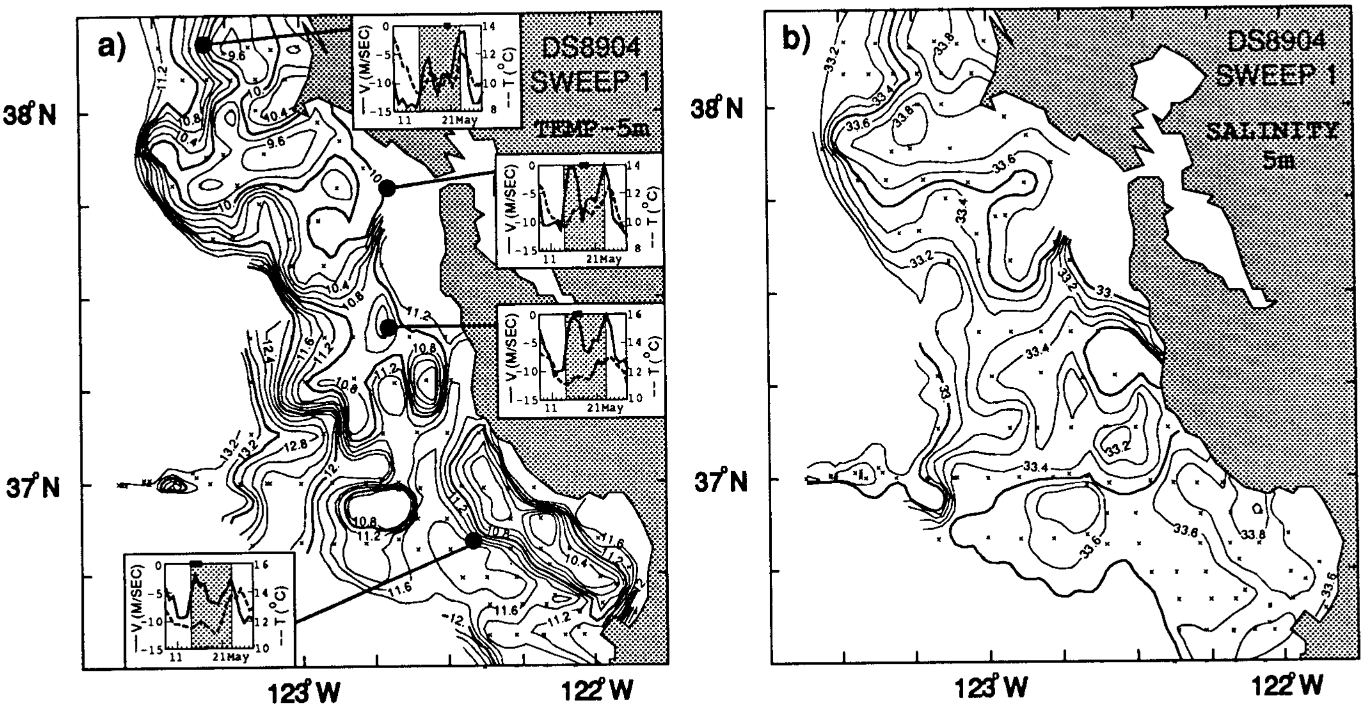

Figure 4. *a*, Temperature at 5-m depth during sweep 1 (14–22 May 1989), from CTD data. Location of CTD stations denoted with an x. Contour interval is 0.2°C; *bold contours* denote 1°C intervals. Time series of principal-axis wind components and SST at the four NDBC buoys, whose positions are denoted by *large solid circles*, are also shown. *Shaded areas of buoy records* define sweep duration; *short bold bars* mark period when stations in the area of each buoy were occupied. *b*, Salinity at 5-m depth during sweep 1. Contour interval is 0.1 psu; *bold contours* denote 0.5-psu intervals.

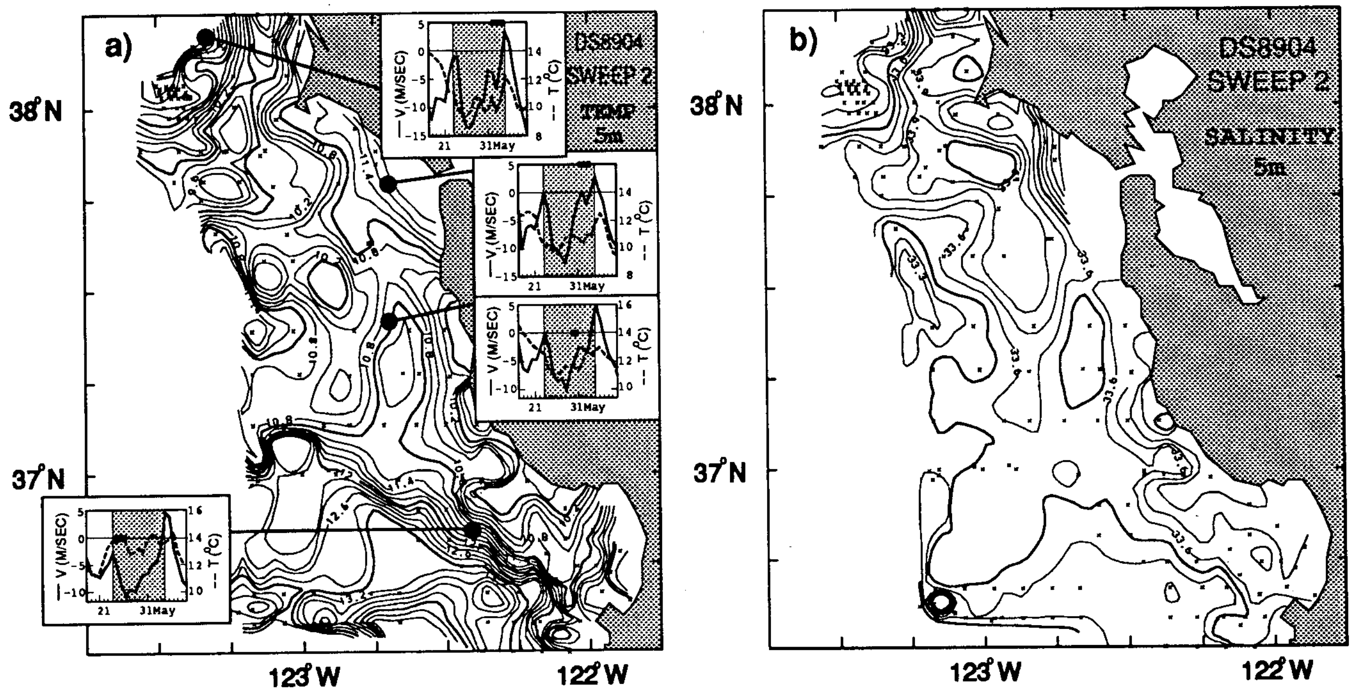

Figure 5. *a*, Temperature at 5-m depth during sweep 2 (23 May–3 June 1989), from CTD data. Contour interval is 0.2°C; *bold contours* denote 1°C intervals. See figure 4a for further details. *b*, Salinity at 5-m depth during sweep 2. Contour interval is 0.1 psu; *bold contours* denote 0.5-psu intervals.

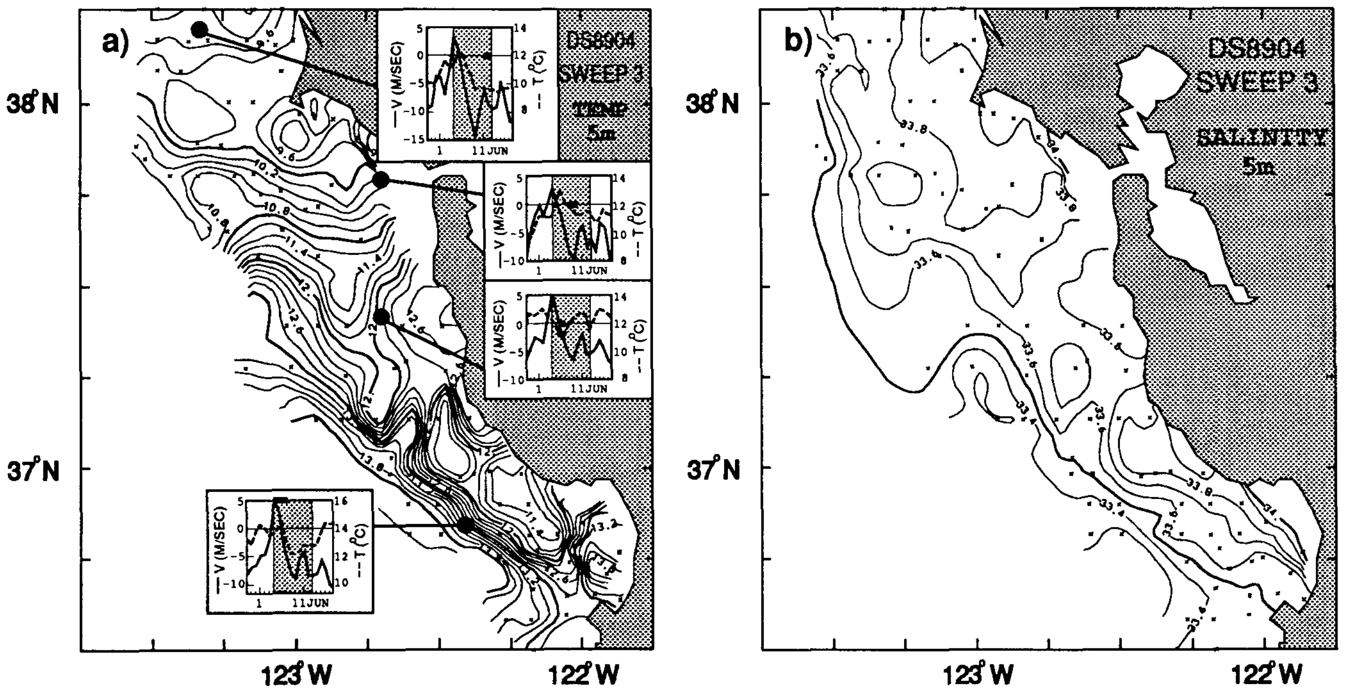

Figure 6. *a*, Temperature at 5-m depth during sweep 3 (4–13 June 1989), from CTD data. Contour interval is 0.2°C; *bold contours* denote 1°C intervals. See figure 4a for further details. *b*, Salinity at 5-m depth during sweep 3. Contour interval is 0.1 psu; *bold contours* denote 0.5-psu intervals.

the presence, position, and extent of several features of water mass and circulation typically seen in this region during spring. Two relatively cool (<10.5°C) and saline (>33.7 psu) areas of recently upwelled surface water appear near Point Reyes (38.0°N) and Point Año Nuevo (37.2°N). These areas of upwelled water contrast with the much warmer (>13°C) and less saline (<33.0 psu) surface water seen offshore. A warm feature that appears persistently west of Monterey Bay in CTD maps and AVHRR SST imagery (Tracy 1990) is composed of this water type. A strong alongshelf front often develops between these two water types. A second source of warm, fresh water appears to be the San Francisco Bay plume; however, CTD coverage is limited in the area where the bay's effluent is most evident. The plume is more apparent in AVHRR imagery.

Situated within these larger water masses are numerous mesoscale eddylike features whose horizontal dimensions are on the order of 10 km. They are much smaller than previous hydrographic sampling in the region (e.g., CalCOFI) could reveal, and are barely resolvable at the station spacing of the rockfish surveys. The existence and size of these features are confirmed with continuous surface mapping (Schwing et al. 1990b) and AVHRR imagery.

The coolest and most saline water was observed during sweep 1 off Point Reyes, and featured a minimum temperature of about 9.5°C and a maximum salinity of over 33.9 psu. This water was bounded offshore by a very strong front. Surface water gradually increased in temperature and decreased in salinity from Point Reyes to Half Moon Bay. A second relatively cool, saline feature extended along the shelf from Point Año Nuevo to near Monterey, crossing the mouth of Monterey Bay. Tracy (1990) demonstrated the existence of a persistent upwelling center off Point Año Nuevo with AVHRR imagery. His results imply that upwelled water is subsequently advected south in a relatively shallow (<50 m) surface layer toward Monterey Bay. The position and extent of the elongated cool, salty feature seen in figure 4 is consistent with those findings. A similar process, associated with an upwelling center north of the survey region, is probably responsible for the cool, saline water seen near Point Reyes.

Although the highest salinities within these recently upwelled features were observed at sites nearest the coast, the coolest water was actually found about 20–25 km offshore. Thus the shallowest portions of the shelf adjacent to these upwelling sources feature relatively warm and saline water at the surface. The discrepancy is more extreme off Point Año Nuevo and in Monterey Bay. In contrast, temperatures at 30 m (not shown) were coolest at the most nearshore sites, corresponding to the salinity maximum at this depth. The character of this coastal water suggests that it was upwelled, then warmed over the shallow (<50 m) areas of the shelf. Aside from this difference in shallow shelf regions, the surface hydrographic features seen in all three sweeps extended to 50 m and deeper.

Sweep 2 surface hydrography. Near-surface temperature and salinity patterns during sweep 2, 23 May–3 June (figure 5) are similar to those seen during sweep 1. The coolest and most saline water masses were located off Point Reyes and Point Año Nuevo; warmer, fresher water was noted again in the offshore and southern portions of the region and immediately seaward of San Francisco Bay. Again the fine scale of the sampling design reveals several mesoscale hydrographic features. However, temperature, salinity, the position and extent of these water types, and the location and intensity of the fronts that separate them all vary substantially from sweep 1. For example, the offshore front during sweep 1 was sharper north of 37°N than to the south. During sweep 2 this front was much more distinct south of 37°N. The Point Año Nuevo upwelling center featured a cooler minimum temperature (<10°C) during sweep 2, and was constrained to the shallowest stations along the coast. The maximum salinity near Point Año Nuevo was also higher (>34 psu) during sweep 2.

Stations off Point Año Nuevo and Half Moon Bay were occupied after a significant wind-relaxation event during sweep 1, but after relatively strong upwelling-favorable winds during sweep 2. Stations off Monterey, on the other hand, were surveyed after the upwelling-favorable conditions that preceded the first survey, but immediately following the significant wind-relaxation event of 23 May. Thus it appears that a stronger offshore front develops during relaxation events, in contrast with the findings north of Point Reyes (Send et al. 1987).

Sweep 3 surface hydrography. Conditions during sweep 3, 4–13 June (figure 6), display even more dramatic differences from the first two sweeps, although the same water masses and eddylike features are again apparent. The alongshelf front separating upwelled and offshore water masses is sharpest off Monterey Bay; essentially no cross-shelf gradient is seen north of 37.5°N. Surface water south of 37°N was 1°–2°C warmer during sweep 3, with the coolest water (11.5°C) away from the coast once again. Stations in the southern half of the survey were occupied after a strong wind reversal; northward wind components up to 5 m/s were observed at all buoys on 4 June. As a result, the offshore front was most distinct during this sweep.

Temperature-Salinity Relationships

A temperature-salinity diagram composed of CTD observations taken south of 37.25°N during sweep 2 clearly defines the differences between the offshore, upwelled, and nearshore water masses, and reveals some of the region's vertical structure (figure 7). Surface offshore water (*triangles*; >13°C, 33.2–33.4 psu) contrasts with water at upwelling centers north of Monterey Bay (*circles*; <10.5°C, 33.6–33.9 psu). These two masses are separated by an alongshore front, represented by *diamonds*. Frontal water comprises a linear mixture of offshore and upwelled water. Upwelled water at the surface displays the characteristics of offshore water at 50-m depth. In addition, upwelled water at 50 m is similar to the 100-m offshore water; i.e., water is vertically advected by about 50 m near the coast. Nearshore water, confined to Monterey Bay in this area, features salinities identical to those measured at upwelling centers, but is 1°–2°C warmer. The range of temperature and salinity, defined at the surface, 50 m, 100 m, and 200 m within dashed lines, decreases with depth. The large temperature range observed at the surface is probably due to greater short-term variability in surface heating.

Individual profiles of temperature, salinity, and density from stations representing offshore, upwelled, nearshore, and frontal locations (figure 8) further reveal the distinct characteristics of these water masses. Although the temperature of nearshore water to about 60 m was between that at offshore and upwelling sites, its salinity was clearly that of the upwelling centers. At greater depths, the salinity in Monterey Bay is increasingly that of an offshore source. Frontal water, in contrast, is some mixture of offshore and upwelled water to at least 150 m.

AVHHR SST

Four SST images (figure 9) collected during the survey period provide an excellent illustration of how quickly the position, extent, and intensity of surface water masses can change. Both the persistence of features and the variability of their relative locations are demonstrated in these data. The observed patterns correspond closely with those described from the hydrography. All are presented with the same grey scale, which is linear between 8° and 13°C. Waters cooler than 8°C are uniformly light; waters warmer than 13°C are uniformly dark.

The first image, from 11 May, shows the SST pattern three days before the beginning of sweep 1. This image was collected just before the peak of a fairly strong period of upwelling-favorable winds. Cool

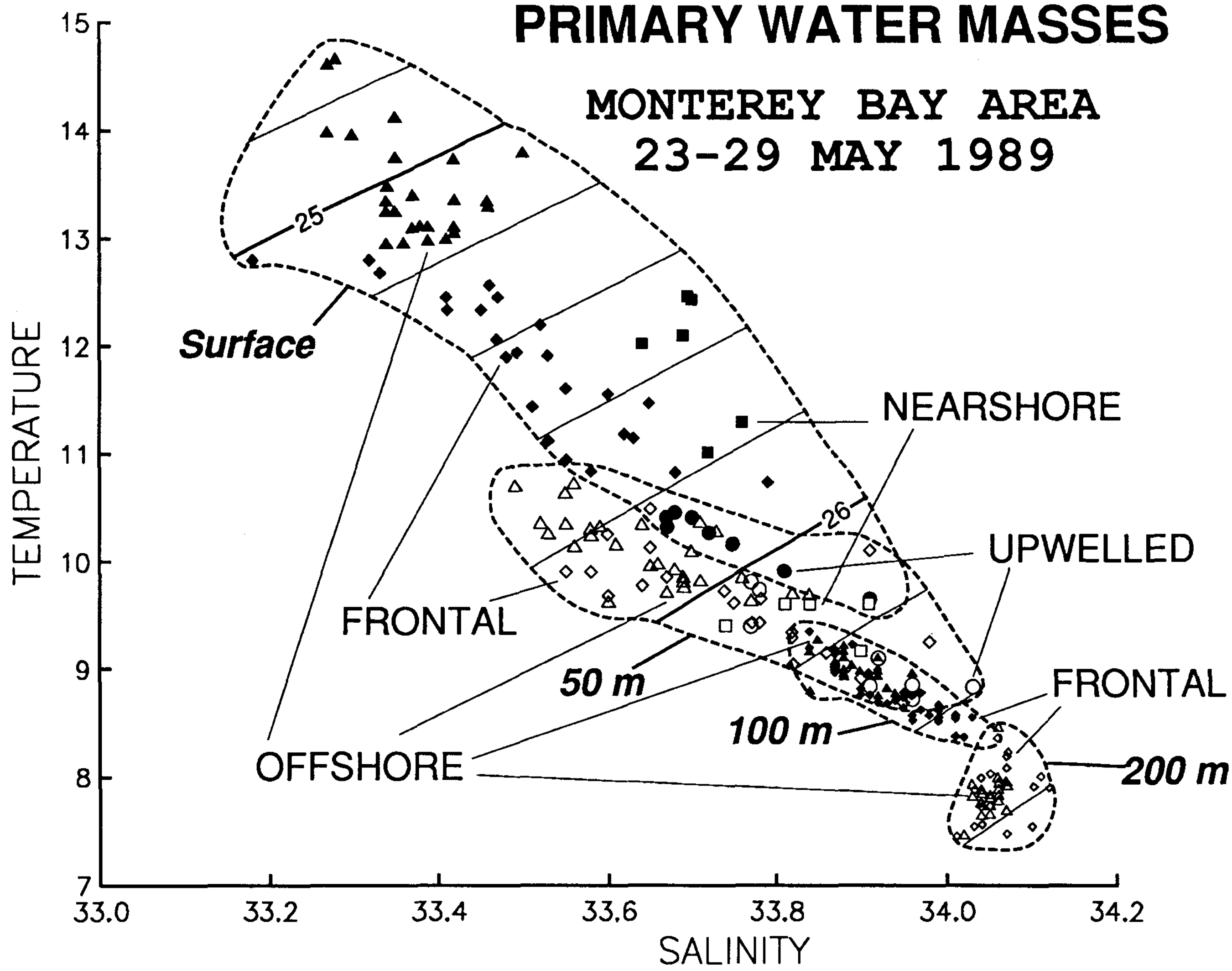

Figure 7. Temperature-salinity (T-S) diagram from CTD observations taken south of 37.25°N during sweep 2. *Dashed lines* enclose T-S ranges at surface (*large solid symbols*), 50-m depth (*large open symbols*), 100-m depth (*small solid symbols*), and 200-m depth (*small open symbols*). *Triangles* represent T-S pairs at offshore stations; *circles* represent stations in upwelling centers; *squares* represent nearshore (Monterey Bay) stations; and *diamonds* represent frontal stations. Sigma-t isolines are shown at 0.2 kg/m³ intervals.

water (lighter shade) extends south past Point Reyes to about 37.25°N. It appears that this streamer comprises cool water upwelled from two sources. The majority is an extension of cool water from the north, flowing past Point Reyes, and augmented by water upwelled locally near the point. South of 37.5°N, the streamer separates, one portion going approximately alongshelf southeast of 123°W, the other passing offshore to the southwest. Warmer water (darker shade) is located between these streamers.

A warm streamer, with maximum temperature offshore of the Golden Gate, extends to the south, leaving the coast around Half Moon Bay. Cool water, suggestive of coastal upwelling, appears along the coast from Half Moon Bay to Santa Cruz and again to the south of Monterey Bay. This cool water band appears separated from the Point Reyes cool water by the Golden Gate warm band.

The cool upwelling streamer near Point Año Nuevo has offshore and alongshore components and the suggestion of a warm feature between them, similar to the streamer off Point Reyes. The alongshore streamer extends south from Santa Cruz about halfway across Monterey Bay. Surface temperature inside the bay is fairly uniform, with the suggestion of some warm water right along the coast. Clouds obscure the southwest corner of the image.

This image corresponds well with the sweep 1 surface map (figure 4a). The Point Reyes streamer and the downstream split are clearly seen, as well as

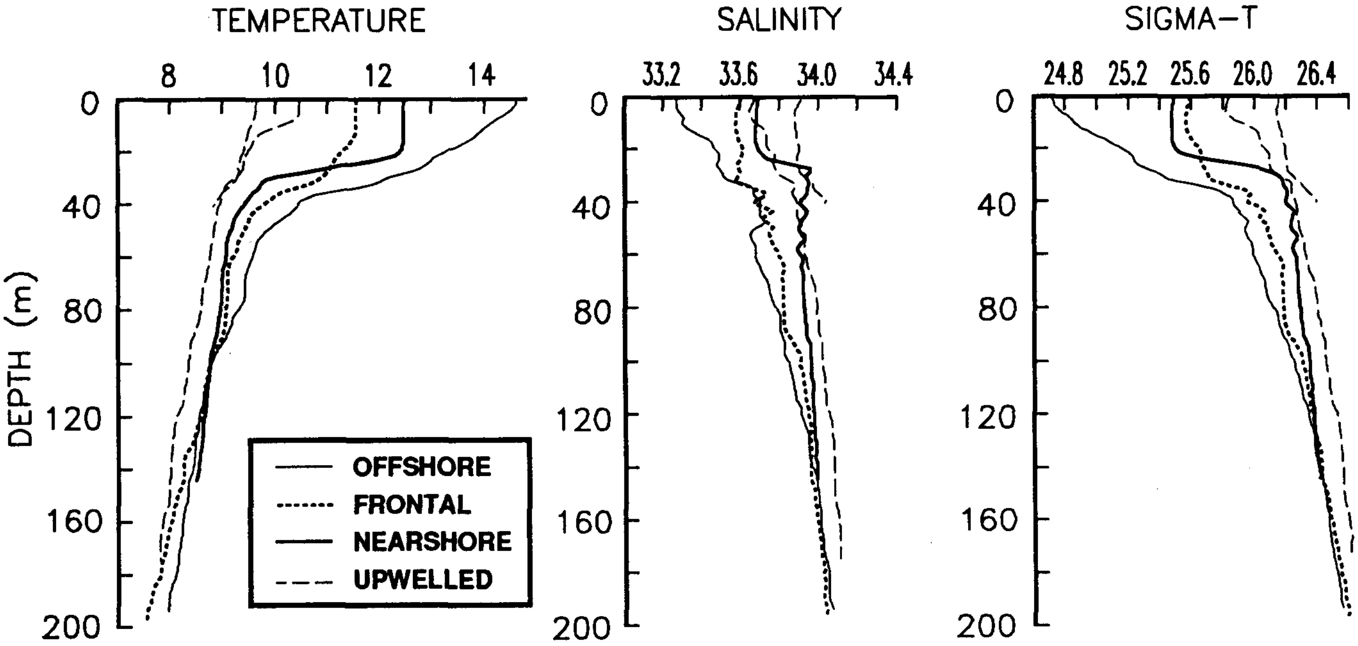

Figure 8. Individual profiles of temperature, salinity, and sigma-t at CTD stations representative of offshore, upwelled, nearshore, and frontal locations during sweep 2.

the Point Año Nuevo streamer extending across Monterey Bay, and the relatively warm water inside the bay. The position of the alongshelf front separating upwelled and offshore water is also approximated. Although the eddylike features seen in the CTD near-surface maps appear in the AVHRR imagery as complex but connected flow features, the small spatial scales of variability noted in the hydrographic data are reflected in the satellite observations.

The date of the second image, 25 May, is closer to the time of the northern sampling during sweep 1 (19–21 May) than sweep 2 (1–3 June). The southern portion of the study area was surveyed during sweep 2 at the time of this image, thus that portion of figure 5a has a slightly stronger correspondence to figure 9b. Upwelling-favorable winds began blowing on 24 May, following a significant wind reversal. Although the general pattern is the same, the SST field on 25 May differs from that on 11 May (figure 9a) in two significant ways. The most noticeable change from sweep 1 is the presence of a distinct warm feature just west of Monterey Bay. Although this feature looks like a meander or eddy at this scale, the full-scale image (not shown) suggests that it is best described as a warm segment of the variegated eastern boundary of the California Current. In addition, the whole region appears slightly warmer relative to two weeks earlier.

The Point Reyes streamer is still well defined on 25 May, extending south to the edge of the warm feature off Monterey Bay (figure 9b). However, it is not as cool as that seen after several days of upwelling-favorable wind (*cf.* figure 9a). The streamer is no longer divided, although the offshore edge shows evidence of complex small-scale interaction with the warmer oceanic water to the west. The Golden Gate warm streamer again extends south, separating the Point Reyes streamer from the cool coastal water present from Half Moon Bay to Santa Cruz. Distinct cool water centers are seen along this portion of the coast. Cool water extends across Monterey Bay; the separation of warm coastal (Monterey Bay) water from the warm offshore feature is more distinct than noted previously. As in the sweep 2 surface-temperature map (figure 5a), the strongest front is associated with the north-to-southeast edge of this feature. There are no strong fronts in the northern part of the study area, although remnants of the different water masses are seen.

By 28 May (figure 9c) the coastal oceanic response to the upwelling event that began about 24 May is well established. There is strong upwelling both north and south of Point Reyes, near Point Año Nuevo, and near Point Sur. Water from these upwelling centers has spread both offshore and generally southward. The coastal-oceanic boundary has retreated offshore. This is demonstrated by the

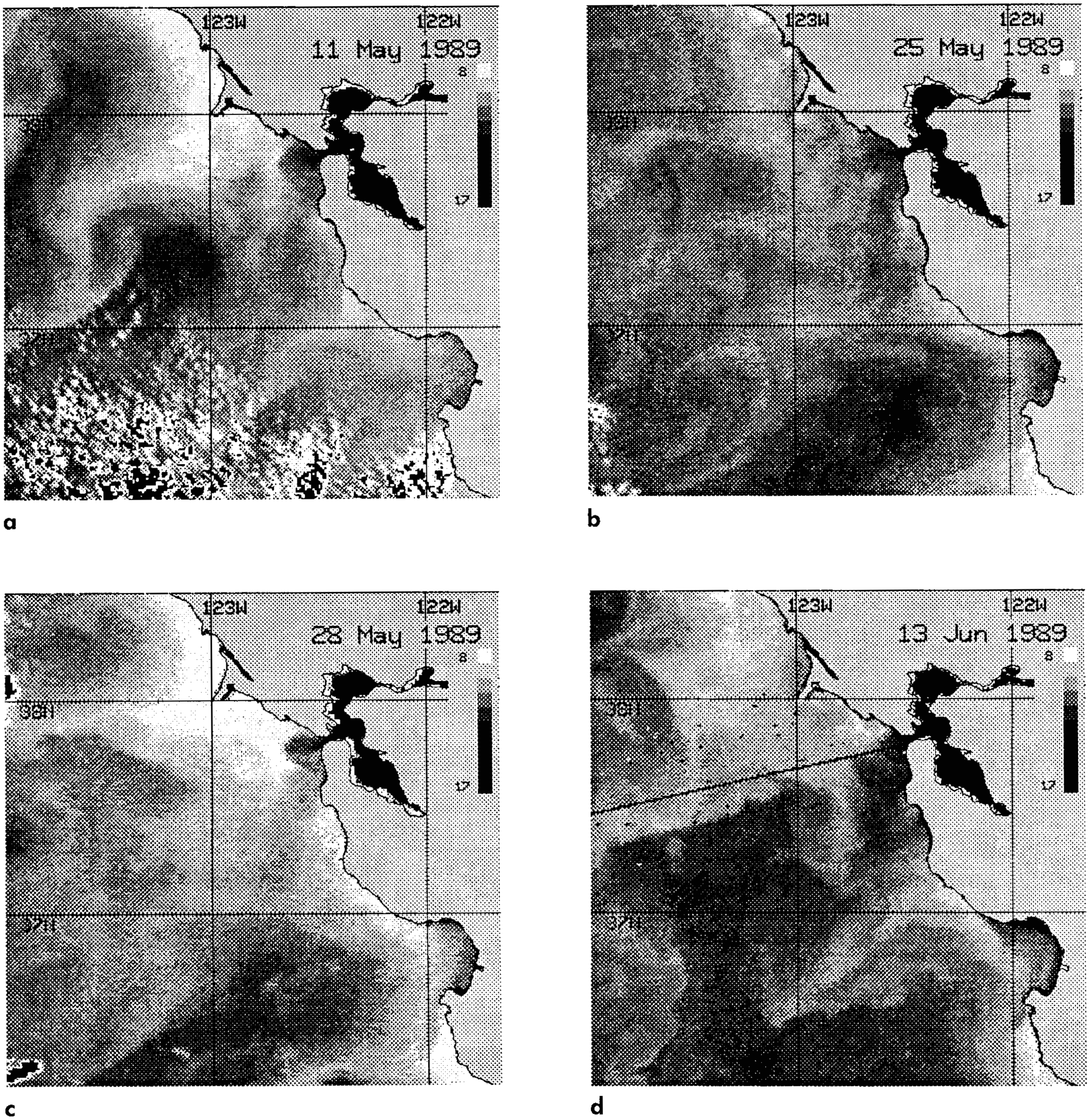

Figure 9. AVHRR sea-surface temperature (SST) images of the survey region from 11 May, 25 May, 28 May, and 13 June 1989. Linear grey scale for SST is shown. Lighter shades denote cooler temperatures. Speckled pattern at bottom of image from 11 May is scattered cloud. Latitude and longitude are shown at 1° intervals.

westward displacement of the warm water off Monterey Bay. A comparison of the images in figures 9b and c, taken only three days apart, clearly shows how suddenly and dramatically coastal ocean conditions can change during the upwelling season.

About two weeks later, 13 June, the imagery reveals more warm water closer to shore, with coincident warming and possible constriction of the southward-flowing Point Reyes cool streamer (figure 9d). Winds at this time were light and upwelling-favorable, but varied substantially from north to south (figures 2 and 3). There is again an offshore streamer of cool water west of Point Año Nuevo, possibly comprising both Point Año Nuevo and

Point Reyes cool waters. But the offshore extent of this cool water is limited, relative to that during upwelling periods. During strong wind reversals, such as on 29 June (figures 2 and 3), surface evidence of upwelling is hidden as the entire coastal region warms to greater than 13°C (Tracy 1990).

The Point Reyes streamer appears ~2°C warmer than the Point Año Nuevo coastal upwelling streamer on 13 June, probably because the northern portion of the survey region was under wind-relaxation conditions while the southern part was experiencing stronger southward wind (figure 2). The warm feature off Monterey Bay is still present, and is connected with a region of warm water extending northward, west of 123°W. This image further indicates the complexity of the boundary between the coastal and offshore water masses. The warmest water is seen again off the Golden Gate and in Monterey Bay. Figure 9d corresponds well with the CTD temperature map from sweep 3 (figure 6a), even though the image was taken on the last day of the sweep.

The impression gained from a series of satellite images of the study area is that several general water masses, indicated by surface temperature, are present at all times, but their relative and absolute location can change on short subsynoptic time scales not detected by traditional ship-survey methods. These changes could profoundly affect the biota in the region, as discussed below.

Both the persistence of these water masses during the upwelling season, and their variability on synoptic time scales is reflected in the CTD surface maps (figures 4–6) as well as the NDBC SST time series (figures 2 and 3). The consistently coolest buoy site, off Bodega, is located near the core of the southward-flowing upwelling streamer off Point Reyes. Buoy SST increases to the south, as this streamer mixes with warmer surrounding water. The warmest buoy, off Monterey, lies in the warm feature that separates the two Point Año Nuevo upwelling streamers.

Vertical Cross-Shelf Sections

The vertical distribution of density along two representative cross-shelf sections (figure 1), extending offshore from Davenport (37°00′N) and through the Farallones (37°53′N), are presented for each sweep in figures 10 and 11. These figures display the vertical structure and extent of the features defined previously from the near-surface CTD and AVHRR data. They also show the pronounced spatial and temporal variability of the coastal ocean associated with upwelling/relaxation events. The time series of the principal-axis wind component from the NDBC buoy nearest each section is included.

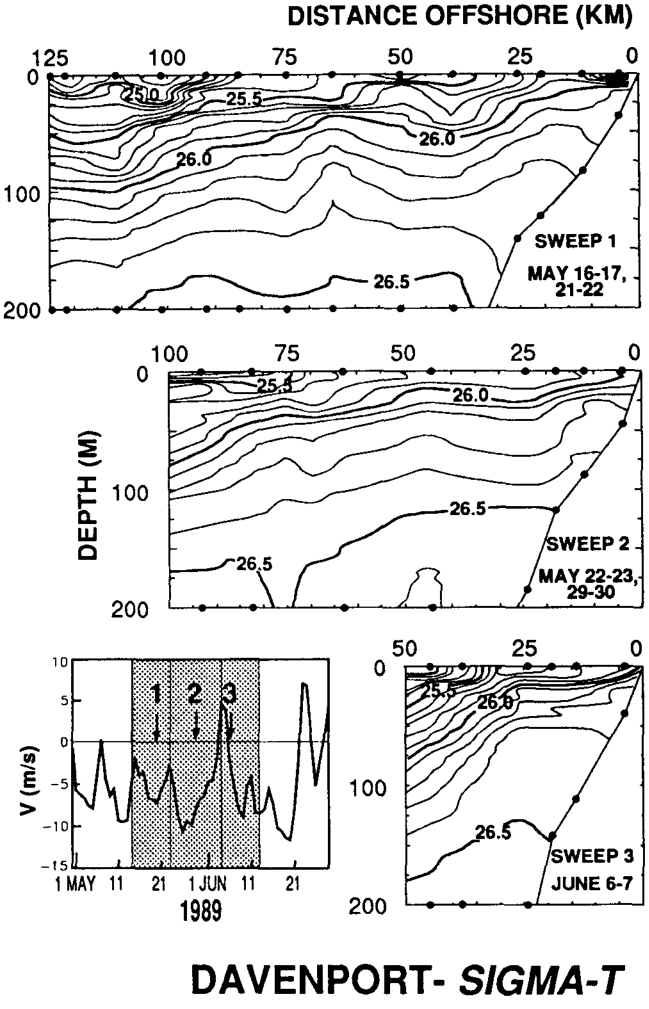

Figure 10. Vertical distribution of density along Davenport cross-shelf section (37°00′N), by sweep. Time series of the principal-axis wind component at NDBC buoy 46042 is included. *Bold arrows above the wind records* indicate the start of each survey.

Changes in the density structure off Davenport (figure 10) are representative of the temporal variability that existed during the survey period, and show the close relationship between ocean structure and coastal wind conditions. Wind during sweeps 1 and 2 was upwelling-favorable. The hydrographic structure appears similar during these sweeps as well.

Isopycnal doming near the coast, to depths as great as 100 m, defines the local upwelling center seen in the horizonal maps (figures 4–6) and AVHRR images (figure 9), and affirms the idea, based on the temperature-salinity relationship (figure 7), that water upwells from about 50 m to the surface. Doming off Davenport is confined to within 10–20 km of the coast (figure 10), consistent with estimates of the Rossby baroclinic radius of deformation based on these CTD data.

Between sweeps 1 and 2, all isopycnals to depths of at least 200 m, the maximum depth of the CTD casts, shoaled in response to increasing southward wind. The 26.0 isopycnal actually surfaced during sweep 2. Over the same interval, the outcropping of the 25.5 isopycnal moved from 35 km to 75 km offshore. The generally higher densities during sweep 2 indicate more recently upwelled water, in agreement with the stronger southward wind.

Possibly the most striking temporal variability is associated with the position, strength, and slope of the offshore front that separates less dense (warm, fresh) offshore water from denser (cool, salty) water nearer the coast. The front was located about 90 km offshore during sweep 1. Following the strong wind reversal at the onset of sweep 3, this front intensified, steepened, and moved to within about 35 km of the coast. The ocean response was rapid, within a few days of the wind reversal. Near-surface stratification also increased after the reversal (i.e., the mixed-layer depth decreased). The pattern of increased near-surface stratification during periods of weak wind was also noted elsewhere in the survey region.

It is thought that low wind speed results in reduced vertical mixing, which allows heat entering the ocean from the atmosphere to be trapped in a relatively thin surface layer. Reversals also bring warmer air into the region: the air temperature at NDBC buoy 46042, off Monterey, increased by 3°C during the reversal at the beginning of sweep 2 (figure 3). The large excursions in the position and strength of the offshore front, and the general change in the region's surface temperature are evident in the SST images (figure 9).

The position of the offshore front near the Gulf of the Farallones (figure 11) also moved between sweeps, suggesting that the relative contribution of upwelling varies on time scales of 10 days or less. However, the source of upwelled water over this portion of the shelf does not appear to be "local." Although isopycnal doming is again evident over the continental shelf break and slope (>50 km offshore), isopycnals are relatively flat over the shelf. No upwelling within a Rossby radius of the coast is apparent. Thus most of the upwelled water in the gulf is probably advected from the north, as implied from the near-surface hydrographic maps (figures 4 and 5) and satellite SST images (figure 9). Contrast this with the Davenport section (figure 10), where there is significant isopycnal tilting up to the coast.

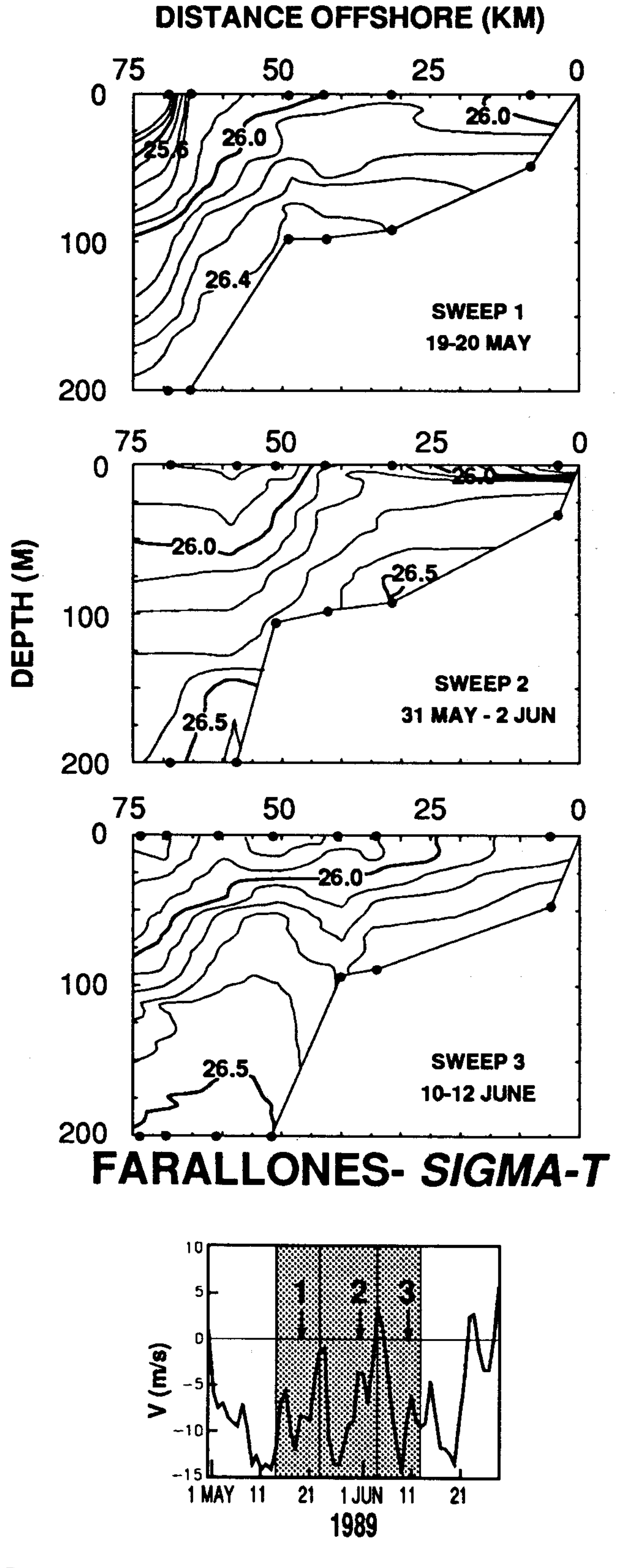

Figure 11. Vertical distribution of density along Farallones cross-shelf section (37°53′N), by sweep. Time series of the principal axis wind component at NDBC buoy 46026 is included. *Bold arrows above the wind records* indicate the start of each survey.

Although some of the isopycnal tilting over the slope off the Farallones may have been due to true upwelling, the structure is probably an artifact of the front that separates warm, fresh, offshore water from cool, saline, upwelled water. A density maximum is seen about 30–40 km offshore at this latitude, corresponding to the core of the cool water advecting south past Point Reyes. This mass of dense water appears even more distinct in contrast to the less-dense lens of water over the inner 20 km of the section, the source of which was probably San Francisco Bay outflow.

DISCUSSION

The hydrographic observations from the spring 1989 rockfish survey define a physical environment off central California that comprises several persistent and distinct water masses. The general locations of these masses are consistent throughout the 30-day survey period, and during the spring of other years as well (Schwing et al. 1990a). Most notable are two recently upwelled water masses off Point Reyes and Point Año Nuevo, which are separated from warmer and less saline offshore water by a distinct alongshelf front. Other distinct masses include the outflow from San Francisco Bay, and nearshore water, which is upwelled, advected onto the shallow portions of the shelf, and then warmed. Because much of this nearshore area is fairly sheltered from the wind, vertical mixing is reduced, and heat accumulates rapidly in the surface mixed layer. Nearshore areas also receive greater radiation because they are less susceptible to fog.

The location of each water mass, and of other circulation features described here, is linked to the physical processes characteristic of the site (e.g., wind forcing, flow/bathymetry interaction). The forces that contribute to the region's dynamics are the same everywhere; it is the *relative balance* of these forces — which varies (possibly greatly) with position — that leads to the seemingly incoherent arrangement of upwelling centers, fronts, and other dynamic features. For example, the proper combination of wind forcing and bathymetry is needed for upwelling to occur at a specific site. Given the rich environmental complexity off central California, it is not surprising that the coastal ocean displays such high mesoscale variability.

Despite their persistence, these water types vary substantially in extent and relative importance from sweep to sweep. Although wind direction during late spring is predominantly equatorward, or upwelling-favorable, the wind typically weakens or reverses direction at 3–10-day intervals (figures 2 and 3). The coastal ocean responds to such meteorological changes within 1–2 days. The strength of the offshore front that separates cool, salty shelf water from warmer, less saline offshore water seems directly linked to wind-relaxation events. Sharper fronts are observed immediately after relaxations or reversals of upwelling-favorable wind. The fronts also migrate closer to the coast after wind-relaxation events.

The dynamics behind this pattern may be relatively straightforward. During upwelling, an offshore flow in the surface Ekman layer sets up a cross-shelf pressure gradient and isopycnal doming within a Rossby radius of the coast. These gradients are balanced by an equatorward geostrophic current. Under steady upwelling conditions, the offshore surface flow is mass balanced by along-isopycnal flow toward the coast at depth. The resulting counterclockwise vertical cell (looking north) is confined inshore of the upwelling front.

A decrease or reversal in wind stress creates an unbalanced situation. An onshore flow develops to adjust the cross-shelf gradient. This flow is revealed by the rapid onshore movement of the offshore front. The circulation of the inshore cross-shelf cell is opposite the circulation during upwelling. Whereas the seasonal upwelling flow is controlled primarily by the density field, the 3–10-day variations in upwelling are largely barotropic (Mooers et al. 1978). Another effect of episodic upwelling periods separated by relaxation events is a long-term circulation that is a hybrid of these two regimes (Smith et al. 1971; Send et al. 1987). This highly complex residual circulation may maintain larvae and their prey near the highly productive upwelling centers. Direct velocity measurements are needed to confirm this conceptual model of the upwelling/relaxation circulation based on hydrographic and satellite data.

Our observations reveal that recently upwelled water flows offshore and equatorward as two distinct streamers separated by a warm, less saline water mass. Some unknown dynamic process exists that either (1) forces warm offshore meanders near the shelf or (2) forces separate upwelling streamers to the west and south, and causes the subsequent complex frontal interaction between these masses. We are examining this phenomenon in more detail. Some recent studies describing the behavior of filaments as they flow offshore, and in some cases retroflect (Strub et al. 1991) may shed light on this problem. The mechanism responsible for the variegated offshore front is also not known. Several possibilities exist: barotropic or baroclinic instabilities, spatial wind variability (wind curl), or variations in bathymetry.

Of particular interest to fisheries oceanographers is how the important coastal processes, water masses, and features off central California affect fisheries recruitment in the region. In the paragraphs below, we discuss some of the key physical processes associated with the rockfish survey results, and speculate on their biological implications. Larval and juvenile groundfish may take advantage of these oceanographic processes to enhance development, avoid predators, and position themselves for favorable settlement as preadults.

1. *General transport patterns.* Consider first the typical, persistent circulation of the region during spring. The mean flow generally parallels the near-surface isotherms, with cooler water on the left when looking downstream. The hydrographic structure in the upper 200 m implies a predominantly equatorward surface current over the entire region. Previous current-meter studies between the Farallones and Monterey Bay have measured predominantly southward velocities, typically 20–30 cm/s, during the upwelling season (Strub et al. 1987a; Chelton et al. 1988). Superimposed on this pattern are numerous eddylike features, whose horizontal scales are typically 10 km, that extend as deep as 100 m. The circulation is typically clockwise around a warm feature, and counterclockwise around a cool-water mass.

Species with long larval stages are likely to be transported a substantial distance southward by the mean flow. In the absence of any other transport mechanism or behavioral strategy that precludes long-distance transport, recruitment within a central California population will probably be provided by a stock to the north. Mesoscale features, which appear to be somewhat persistent, may be one mechanism for maintaining larvae near their source, or at least aggregating them before settlement. These features may also concentrate and enhance primary and secondary production, which could attract larvae and promote their development (Hayward and Mantyla 1990). Finally, the well-defined and persistent alongshelf front that separates offshore and shelf water may also separate areas of high and low biological productivity (Hood et al. 1990).

2. *Discrete, persistent upwelling centers.* Our observations suggest that upwelling does not occur uniformly along the central California coast, but is confined to several discrete upwelling centers. The dominant centers in this region appear to be somewhere north of Point Reyes, near Point Año Nuevo, and at Point Sur, to the south of the survey region. The three-dimensional structure of these centers is associated with variations in alongshelf and vertical flow, which are due to spatial differences in the wind field, bathymetric irregularities, and coastline irregularities (Smith 1983). Variable coastal upwelling and advection produces a complex hydrography and circulation near the coast, and numerous cross-shelf as well as alongshelf fronts. Thus certain locations along the coast associated with this variability may be more favorable for the aggregation and development of groundfish larvae and their prey. Closely spaced physical and biological sampling is required to properly resolve this complexity *in situ*.

Frequency of wind reversals. Wind forcing is not continuously upwelling-favorable in time, but relaxes or reverses direction every three to ten days. As our results demonstrate, an onshore surface flow develops in response to each relaxation event. This flow, which is evidenced by the rapid onshore movement of the offshore front, may also transport nutrient-rich water, plankton, and larval fish back toward the coast, or at least maintain their position fairly close to the coast. A poleward component of flow also develops during relaxation (Send et al. 1987) and may limit the extent that larvae are transported alongshore before settlement. At least, the absence of continuous upwelling precludes upwelled water and its contents from being transported far offshore, and into the southward-flowing California Current. Episodic upwelling regularly provides nutrients to the coastal environment while it maintains material, including larval and juvenile fish, relatively close to the source of high productivity.

4. *Frontal position, strength, and variability.* The offshore front moves rapidly onshore and strengthens during wind reversals. As it moves onshore, it probably transports and accumulates material in the frontal zone. Preliminary analysis suggests that the largest hydrographic variability in this region is along fronts (Schwing et al. 1990a). This variability probably is associated with the 3–10-day wind variability described in this paper. Evidence suggests that plankton biomass is maximized relative to offshore filaments (Abbott and Zion 1987; Hood et al. 1990). Larger organisms may be able to detect these variations and position themselves in productive frontal zones. Future analyses will correlate larval and juvenile abundance with frontal position, to test the hypothesis that fronts aggregate fish. Aggregation may be either active (fish are transported with the front) or passive (higher prey concentrations within the front attract larvae and juveniles).

5. *Aging of upwelled water.* Some time lag exists between the initial upwelling of nutrient-rich water, the peak in primary production, and the peak in secondary production. "Aged" upwelled water may

be a more productive trophic environment for larval and juvenile groundfish. Episodic upwelling events bring pulses of productive water to the surface, where — under the right environmental conditions — energy is sequentially passed up trophic levels to the groundfish. Again the importance of the offshore front as a mechanism for concentrating nutrients and plankters is evident. If offshore flow is continuous or too strong, these materials will disperse rapidly, creating a relatively unproductive environment for larval growth. Another potentially productive environment is upwelled water trapped in cyclonic eddies (Hayward and Mantyla 1990).

It is still not known how, and to what degree, larval and juvenile groundfish respond to these physical factors to maintain a position that best helps them grow rapidly, avoid predators, and settle in optimal sites. The complexity of the region's physical oceanography is reflected in the temporal and spatial variability of phytoplankton (Hayward and Mantyla 1990; Hood et al. 1990) and zooplankton (Abbott and Zion 1987). This complexity may selectively fractionate biological organisms by size or taxonomic group as well (Hood et al. 1990). For example, a phytoplankter's position is totally controlled by the current regime, whereas zooplankton can modify their position with their behavior to abet or minimize their transport. Smaller groundfish larvae are much more at the mercy of the flow than are juveniles and preadults. Thus when considering how the processes and features of circulation affect a region's biological variability, the behavioral capabilities of the organism in question must be addressed specific to its life history and trophic level. One intriguing prospect is that dynamic features act as "trophic traps" for fish; i.e., eddies and fronts that concentrate plankton ultimately may attract fish, concentrating them as well.

We have provided a conceptual model of the spring circulation off central California, and speculated how it may directly and indirectly affect fish distribution and abundance. But there is still much to be learned about this coastal environment. This will require more detailed synoptic field measurements that combine physical and biological sampling; the development of refined process models; and, ultimately, coupled physical-biological models that realistically account for behavioral effects.

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Part III

SCIENTIFIC CONTRIBUTIONS

PRODUCTION OF EGGS BY THE COPEPOD *CALANUS PACIFICUS* IN THE SOUTHERN CALIFORNIA SECTOR OF THE CALIFORNIA CURRENT SYSTEM

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ABSTRACT

Production of eggs by female *Calanus pacificus* during two years was determined by shipboard incubations in ambient seawater plus seston and in seawater enriched with cultured phytoplankton to detect the extent of food limitation. In all seasons, there was some production in the unenriched water at some stations. In winter and spring, production exceeded 30 eggs·(female·day)$^{-1}$ near Point Conception and along the southern California coast and the Santa Rosa–Cortes Ridge; in summer and fall, however, this rate was less widespread, or attained only by females with enriched food. At the stations farthest offshore, production was frequently <10 eggs·day^{-1} even after two days of supplemental food. The geographic patterns of the ratio of production in ambient and in food-supplemented water also indicated seasonality in food limitation. Although egg production was generally correlated with concentrations of chlorophyll, this relation was quite imprecise.

RESUMEN

La producción de huevos por hembras de *Calanus pacificus* fue determinada durante dos años en incubaciones a bordo de barco, empleando agua de mar con concentraciones ambientales de seston y agua de mar enriquecida con cultivos de fitoplanton, con el fin de detectar el grado de limitación alimentaria. Durante todas las estaciones del año se encontró producción de huevos en algunas estaciones no enriquecidas. En invierno y primavera una producción >30 huevos (hembra día)$^{-1}$ fue observada en Point Conception y a lo largo de la costa del sur de California y de la cadena de Santa Rosa–Cortés. En verano y otoño, este nivel de producción fue menos extendido, o alcanzado solamente por hembras con refuerzo alimentario. En las estaciones más alejadas de la costa, la producción fue generalmente de <10 huevos (hembra día)$^{-1}$, incluso despues de dos días de comida suplementaria. Los patrones geográficos de la proporción de producción en aguas ambientales con respecto a la producción en aguas con comida suplementaria también indicaron estacionalidad en la limitación de comida. Aunque la producción de huevos se correlacionó en términos generales con las concentraciones de clorofila, esta relación fue bastante imprecisa.

INTRODUCTION

Varying sizes of planktonic populations (as biomasses or abundances) can result from changes in the physical processes influencing an area (frequently the ultimate, and sometimes also the proximate, cause) plus ecological responses or readjustments of the populations themselves. Such variability is particularly well documented in the California Current because of the venerable California Cooperative Oceanic Fisheries Investigations (CalCOFI). For example, there is now clear evidence (e.g., Reid 1962; Chelton et al. 1982) that the biomass of zooplankton responds coherently on the interannual scale throughout the California Current to variations in southward transport, and Colebrook (1977) showed that the biomasses of most major planktonic groups — copepods, euphausiids, and particularly salps and doliolids — changed coincident with an extreme climatic event: the 1958–59 El Niño. By more closely examining the timing of maximal zooplanktonic biomass relative to maximal southward flow, Roesler and Chelton (1987) concluded that off northern California such interannual variations in biomass are caused by variations in direct advection of biomass from more northern regions (where biomass is high). Off Baja California, a time lag in response suggests that variations in advection of nutrients from the north, translated via the food chain into zooplanktonic biomass (probably after recycling within the euphotic zone), may be more important. Whether this is equally true for all taxa, or whether some vary more as a direct result of advection and others more as a result of biotic interactions, is not known.

Even when physical variation in a region includes advection of exotic species, physiological and demographic rate processes (proximate causes for biomass variation) of indigenous species may also be

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altered. Particularly on smaller spatial-temporal scales, such alterations may be correlated with food or predators. For example, Hakanson (1987) has shown that the lipid contents of copepodite stage V *Calanus pacificus* are geographically positively correlated in the California Current with chlorophyll (though on smaller scales or at other times this may not be so [Ohman 1988]). The immediacy of demographic response to variations in food probably varies with species (Dagg 1977), but at some scales any species will vary in growth or reproductive rate per capita. Reproductive variation, times the abundance of females, results in variation in the rate of population increase. Even for an indigenous, planktonic population there can be ambiguity as to cause, however; demographic rates in a particular area can change because of physiological response to environmental changes, or because another population of the same species but with different properties has been advected into the area.

The rate at which females produce eggs has been widely used to indicate secondary production for particular species; to determine how production varies in response to food, temperature, etc.; and particularly to test for food limitation of growth rate (e.g., Ambler 1986; Beckman and Peterson 1986; Bellantoni and Peterson 1987; Borchers and Hutchings 1986; Checkley 1980a,b; Dagg 1978; Durbin et al. 1983; Hirche and Bohrer 1987; Kimmerer 1984; Kiørboe et al. 1985; Peterson 1985; Runge 1985a,b; Smith and Lane 1987). Applying this approach to assess a coastal front's effect on rate processes as well as abundances, Kiørboe and Johansen (1986) showed that per capita egg production was higher on the unstratified side of the front, where the chlorophyll concentration was elevated, than on the stratified side, but the abundances of late copepodites and adults were independent of the front, indicating that the pattern of abundance alone did not reveal "where the action was."

In my assessment, this body of literature has shown both the utility of this means of efficiently assessing ecological relations, and the (probably real) complexities: the immediate response depends on past history of the females, the season, and the size or quality of the food. To put the last point another way, the biomass of food should best be assessed in terms of the nutritional factor that most limits egg production (though, in fact, this is seldom known).

For an example of variation in a zooplanktonic population's demographic rates, I investigated the seasonal and mesoscale spatial variability in the production of eggs by an important pelagic copepod, *Calanus pacificus*, in the southern California sector of the California Current. I designed the study to make inexpensive use of sampling, and of data generated concurrently, by the ongoing CalCOFI cruises, and to be eventually interpretable in the context of the historical record of interannual variations in zooplanktonic biomass and physical processes already established by this program.

METHODS

CalCOFI cruises on the *New Horizon* and *David Starr Jordan* cover a sector of the California Current off southern California quarterly; these cruises are designated *XXYY*, where *XX* represents the year and *YY* the month. Each cruise includes stations in the coastal zone, in the relatively oligotrophic Southern California Bight, in the relatively eutrophic tongue extending SSE from Point Conception along the Santa Rosa–Cortes Ridge, and in the offshore California Current beyond (see Mullin 1986 for summaries of the Southern California Bight, and Peláez and McGowan 1986 and McGowan 1985 concerning areas farther offshore). Each station is sampled whenever the ship arrives at it, so there is no purposely maintained relation between a particular station and time of day.

CalCOFI sampling includes water bottle casts for particulate and dissolved properties at standard depths, typically with seven samples within the euphotic zone. Temperature was determined from reversing thermometers; I have plotted temperature at 10 m, based on data reports for each cruise (published in the SIO Reference Series). Because the vertical distribution of the copepods used in experiments was unknown, both within the upper 200 m (the region sampled) and below this depth, and probably differed between stations, the temperature at 10 m should not be interpreted as that experienced by the copepods *in situ*. Rather, it indicates the geographical pattern of temperature over the sampled region, and is approximately the temperature relevant to incubations that I set up on ship to measure egg production.

The biomass of phytoplankton was determined at the standard depths by extraction of chlorophyll from cells retained on a GF/C or GF/F glass fiber filter, followed by fluorometric analysis (Venrick and Hayward 1984). Because the concentration of chlorophyll is correlated with other properties of the seston (Eppley et al. 1977), I have assumed that it represents, or at least is linearly proportional to, the food for the copepod *Calanus pacificus*, even though this genus is known to ingest nonphytoplanktonic

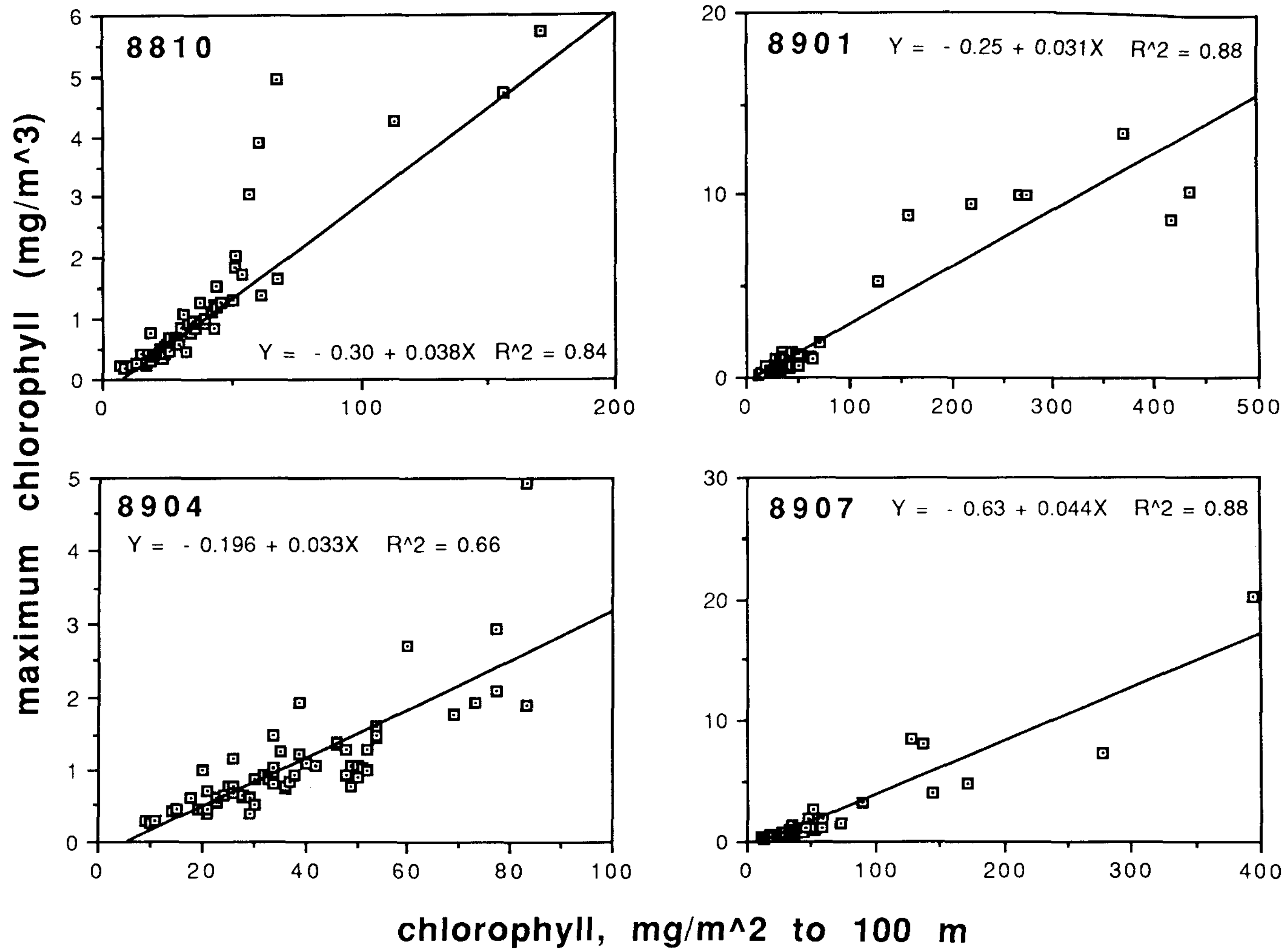

Figure 1. Relations between phytoplanktonic biomass as chlorophyll in mg·m^{-2} to 100 m (integrated from concentrations at seven standard depths) and maximum concentration of chlorophyll (mg·m^{-3}) actually measured at each station, for four cruises. All correlations are significant at $p << 0.01$.

particles and to feed inefficiently, if at all, on the smallest particles (1–2-μm) nominally retained by the filters. Also, the depth range within which there is significant biomass of phytoplankton, the variability in concentration within this range (notably, the degree of a subsurface maximum), and the distribution of types and sizes of particles at each depth vary seasonally and with location offshore (Eppley et al. 1977; Reid 1983). Thus the concentration of food as perceived by the copepods depends on their depth distribution relative to that of the particles they eat. Arguably, the maximal concentration of particles of suitable types may be more significant to *Calanus* than is the biomass of total chlorophyll per unit of sea surface if this maximum is where feeding occurs (e.g., Napp et al. 1988a). Nevertheless, I have mapped total chlorophyll as mg·m^{-2}, from the surface to 100 m or the bottom, based on the concentrations measured or interpolated at 0, 10, 20, 30, 50, 75, and 100 m (published in the SIO Reference Series). This estimate of biomass correlates closely with the maximal concentration of chlorophyll actually measured at the same stations, however, and the relation was similar for different cruises (figure 1).

CalCOFI sampling at each station also includes an oblique net tow from 200 m to the surface with paired nets of 505-μm mesh, only one of which is used for a quantitative, Formalin-preserved sample. After briefly narcotizing the catch from the other net, or the catch from a 1-m-diameter, 505-μm-mesh net, in seawater plus methane tricaine sulfonate, I picked out living female *Calanus* for incubation.

If egg production varies vertically, females from specific depths should be incubated in water (and food) from those depths to assess production. However, because stations are occupied at whatever time of day they are reached; because *Calanus* migrates dielly in some seasons; and because the depth at which eggs are laid may not match the daytime depth at which females are found (because of nocturnal egg laying and diel migration [cf. Peterson 1985]), I simplified by using water (and seston) from 10–20 m at each station for incubations.

At selected stations, I placed female *Calanus* in each of three shaded containers, which were placed in seawater flowing from the ship's through-hull intake. Each container was a plastic cylinder with a mesh screen and a funnel attached to the bottom so that eggs could fall through the mesh (reducing cannibalism) and be drawn off without removing females from the container (cf., e.g., Hirche and Bohrer 1987). I filled each cylinder with seawater and natural seston from the euphotic zone at the station; one cylinder ("unfed") had only this. The copepods, because they were more concentrated in the containers than *in situ*, were able to graze down the natural seston during the incubation. To test for maximal egg production without food limitation, I added excess food as the diatom *Thalassiosira weisflogii* (maintained in nutrient-enriched cultures on shipboard) to a second cylinder ("fed") at the start of the incubations (cf. Durbin et al. 1983), as well as to a third cylinder after 24 hours. I removed eggs (and nauplii, if any) for counting after 24 and 48 hours, and preserved, recounted, and retained the female copepods after the second assessment to verify identity and measure size with an ocular micrometer.

I assumed that any difference between the initial and final number of copepods in a container was due to linear change during the experiment. However, if fewer than 33% of the copepods were recovered alive at the end of an experiment, I assumed that damage during capture or toxicity during incubation had affected egg production severely enough to reject the results. In fact, in 89% of 375 48-hour incubations, at least 67% of the copepods survived.

I modified the basic design in simple ways to examine the two critical issues of interpretation in this experiment: (1) Is the production of eggs in the containers of ambient seawater ("unfed") during the first 24 hours equal to the daily rate of reproduction *in situ*? (2) Is the production of eggs in water enriched with *T. weisflogii* a suitable measure of the maximal rate, unlimited by food?

The first issue results from the following assumptions: (a) that the rate is not altered by either temperature or light during the incubation, nor because the containers prevent diel vertical migration, nor as a result of stresses imposed on the females by the sampling and sorting; (b) that all the eggs counted are viable (nauplii were often present in addition to eggs, but I did not test for viability of all eggs); (c) that the concentration of natural food in the container is the same as that experienced *in situ* by the "typical" copepod, i.e., that the copepods do not preferentially produce eggs at depths where food is more concentrated (see above); and (d) that egg production in the first 24 hours is not depressed by reduction of food in the containers because of the unnaturally elevated concentration of copepods (reduction surely occurs, but egg laying may not be immediately inhibited), nor are eggs removed by unnaturally high cannibalism. Grazing down of food in experimental containers could lead either to an underestimation of overall reproductive rate (i.e., equivalent underestimation at all stations) or to an accentuation of real differences in rates between females from moderately oligotrophic and eutrophic regions. In many ways, this issue is similar to concerns over the potential artifacts in measuring primary production by incubations in containers (e.g., Peterson 1980).

Limitation of station time and the complexity of communities of copepods from which female *Calanus* (which were sometimes quite rare) had to be selected dictated my methods of sampling (standard CalCOFI tow) and sorting (narcotizing with MS222, removal by forceps). Nevertheless, to assess the possibility that these procedures adversely affected egg laying, I used a 2-way ANOVA to compare egg production in the presence of *Thalassiosira* by females collected in a standard tow to that of females captured in a shorter, slower tow. I also compared the production of those sorted under a microscope after narcotization to that of females picked by pipette from a beaker without narcotization. I repeated each collection-sorting combination four times.

There were no significant differences between these treatments ($p >> 0.1$ in all cases). This does not mean that collection had no adverse effect (see Results below), merely that reasonable alternative procedures caused no difference in the rate of egg laying, given the variability within each treatment.

I tested the effect of the size of experimental container (influenced by convenience) and the concentration of female copepods. Females lay clutches (batches) of eggs, and the rate of production of clutches by an individual is at least as variable as the number of eggs per clutch (Runge 1985a; Peterson 1988). Therefore, if an experiment is shorter than the interval between clutches, having a larger number of females in a container will yield a more precise estimate of mean rate of egg production through averaging over more individual vagaries in whether or not a clutch was produced. (This also means that average clutch size will be underestimated by the average rate, unless all females produce clutches.) However, the more females there are in a given volume, the faster they eat the suspended particles in the water. This can affect the number of eggs recovered (relative to the number of females) either if the rapid depletion of food causes egg laying to stop in less than one day, or if the females eat eggs. If either problem is serious, the apparent rate of egg production per female should decrease as the concentration of females increases.

At three stations on cruise 8901, I placed various concentrations of female *Calanus* in the 500-ml containers of unenriched (ambient) seawater, and measured the production of eggs over 24 hours. The trends varied among the individual experiments (figure 2A), and none of the correlation coefficients was high. When I standardized the data by adjusting the rates for stations 90.53 and 87.35 to match those of station 93.30 (by assuming that 20 females per 500 ml produced eggs at the same mean rate at all stations), there was no discernable relation between egg production per female and concentration of females (figure 2B). I repeated the experiments at three stations on cruise 8904, except that the lowest concentrations of females were established in 1-l containers. In this case, the apparent rate of egg production decreased with increasing concentrations in all experiments (figure 2C), and the production standardized to station 90.30 also showed a significant ($p < 0.01$) depression (figure 2D). Egg production tended to be greater in 1-l than in 500-ml containers when the concentration of copepods was the same (tested separately on cruise 8907), but the difference was nonsignificant ($0.05 < p < 0.10$, 2-tailed).

The result shown in figure 2D, and the augmentation of egg production within 24 hours which almost always resulted from adding *T. weisflogii* (see Results), suggest that assumption d might be incorrect, so I examined it further. To directly test how fast egg laying declined after depletion of food, I compared in three experiments the 24-hour egg production of 5–7 groups of female *Calanus* in ambient water with or without added *T. weisflogii*. All of the females had already been maintained in excess *T. weisflogii* for 24 hours (cf. Borchers and Hutchings 1986; Peterson 1988). The interesting alternative to the null hypothesis (no difference) would be reduced egg laying by the females that had been returned to ambient water.

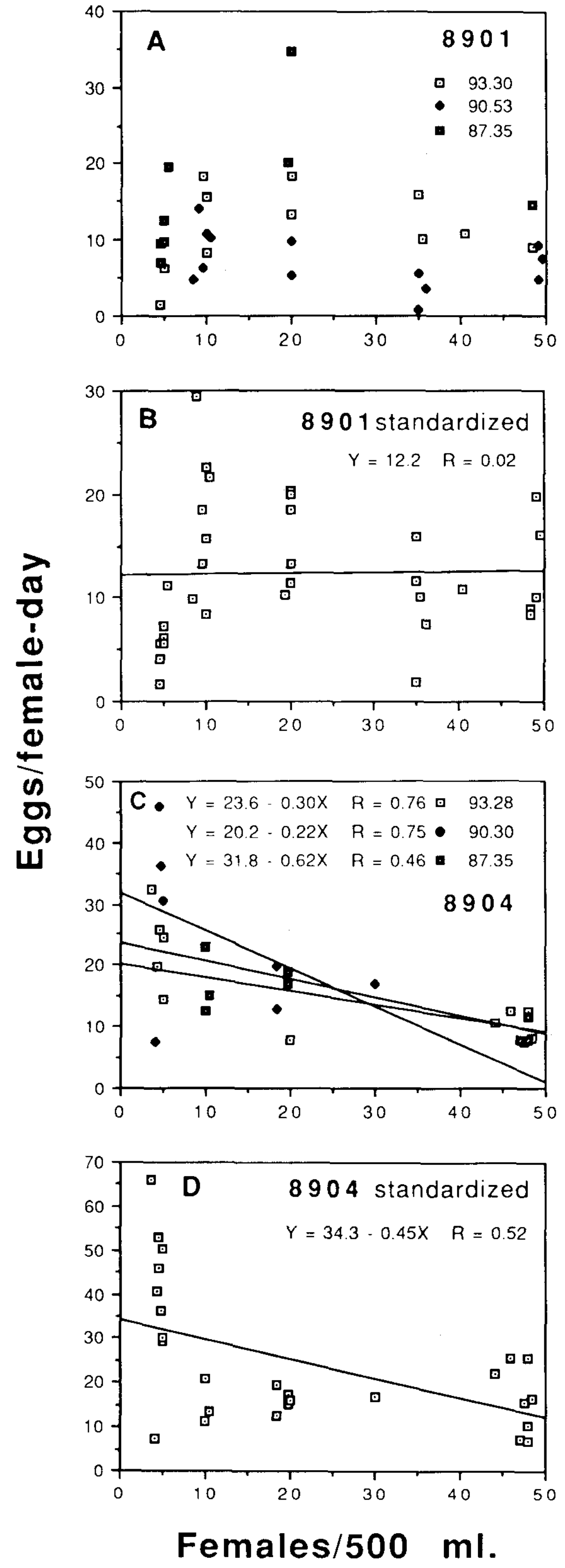

Figure 2. Rate of daily egg production per female in ambient seawater as a function of concentration of females in experimental containers, for three stations on each of two cruises (*A*, *C*). Rates were standardized (*B*, *D*) by assuming that at all three stations the mean rates at 20 females (500 ml) ' equalled that at station 93.30 of cruise 8901 or 90.30 of cruise 8904. Linear fits are presented only to illustrate negative relations, not to imply linearity throughout the range measured.

In all three cases, the median production of females deprived of *T. weisflogii* on the second day was significantly reduced ($p < 0.05$ by rank sum test) relative to those continued in the enriched water. The overall reduction in the combined tests was significant at $p << 0.01$. Therefore, drastic change from a plentitude of available food caused production to be reduced from 32 to 20 eggs·(female-day)$^{-1}$. Whether this would also happen when food was reduced more gradually at natural concentrations by grazing during the first day of an experiment is not proven, nor is it clear whether reduced production or increased cannibalism when females are deprived of *T. weisflogii* is the cause, but the results at least indicate that a problem exists.

Overall, there eventually was enough evidence to conclude that the concentration of females in experimental containers can, when ambient seston is not enriched, apparently reduce the rate of egg production by some amount with respect to that when females are dilute enough that they do not deplete the food supply. Therefore, although I had incubated approximately 20 females in each 500-ml cylinder during cruises 8810–8907, I conducted the incubations on cruises 8911–9008 in 1-l rather than 500-ml cylinders, with no more than 15 *Calanus* per cylinder. The rates of egg production reported below for the "unfed" cases may underestimate the natural rates, particularly for cruises 8810–8907 (figures 3–6). In principle, chemostats could obviate this difficulty in the experimental design.

The assessment of how food limits egg production also deserves comment. If *T. weisflogii* had failed to increase egg production, this would not necessarily rule out food limitation (since it may not be a "satisfactory" food, though *Calanus* has been cultured through its life cycle on this food alone: Mullin and Brooks 1970); enhancement of production is, however, strong evidence for some sort of food limitation.

I used rank sum tests to compare the 48-hour egg production per female for incubations in which *Thalassiosira weisflogii*; brine shrimp (*Artemia*) nauplii; the chrysophyte flagellate *Monochrysis lutheri*; the coccolithophorid *Emiliania huxleyi*; the smaller diatom *Thalassiosira pseudonana*; or a senescent culture of the large diatom *Lauderia borealis* was provided as food. *T. weisflogii* and *Artemia* resulted in similar production rates ($p > 0.1$, 2-tailed); for both, production exceeded that in unsupplemented water. But *Monochrysis*, *Emiliania*, *T. pseudonana*, and the senescent *Lauderia* were significantly inferior to *T. weisflogii* ($p < 0.01$), though *Emiliania*, *T. pseudonana*, and *Lauderia* were themselves superior to natural seston. Other foods may be superior to *T. weisflogii* in stimulating egg production, but I have not found them.

The absolute magnitudes of egg production rates provide some information on the extent of limitation by food, but are also affected by temperature, size of females, etc. Therefore, I tested several ratios of rates as indicators of food limitation, as described in table 1.

The ratio of rates of unfed and fed females is a measure of realized production relative to potential production over the short (ratio a) or medium (ratio b) term. Ratio c would be high, and ratio d low, if food limitation was so severe that females needed a full day's feeding before beginning to lay eggs at the maximal rate. These ratios are mapped for each cruise. Ratio e would be close to 1.0 only in the absence of food limitation.

The calculation of several ratios would be redundant if ratios a, b, d, and e were strongly positively intercorrelated, and all were strongly negatively correlated with ratio c. However, correlations among these ratios were weak (though of the right sign); either the different ratios correspond to different aspects of limitation by food, or some of them are meaningless. In fact, production of eggs on the second day in unsupplemented seston was sufficiently rare (except in January) that ratio e proved of little discriminatory use.

RESULTS

Figures 3–10 are maps covering two years (October 1988; January, April, July, and November 1989; and March, April, and August 1990) of temperature at 10 m, chlorophyll in the water column, daily production of eggs by female *Calanus* in natural and

TABLE 1

Ratios Used to Assess How Severely Food Limitation Affects Egg Production by *Calanus*

Ratio	Interpretation
a. (unfed females)/(fed females), egg production rate on 1st day	The *greater* the ratio, the less severe is food limitation (unless both rates are 0, when females are unripe, spent, or extremely food-limited).
b. (unfed females)/(fed females), total egg production on both days	Same as above
c. (2nd-day rate)/(1st-day rate) fed females.	The *less* the ratio, the less severe is food limitation.
d. (females fed 2nd day only)/(females fed both days), 2nd-day rate	The *greater* the ratio, the less severe is food limitation.
e. (2nd-day rate)/(1st-day rate), unfed females	The *greater* the ratio, the less severe is food limitation.

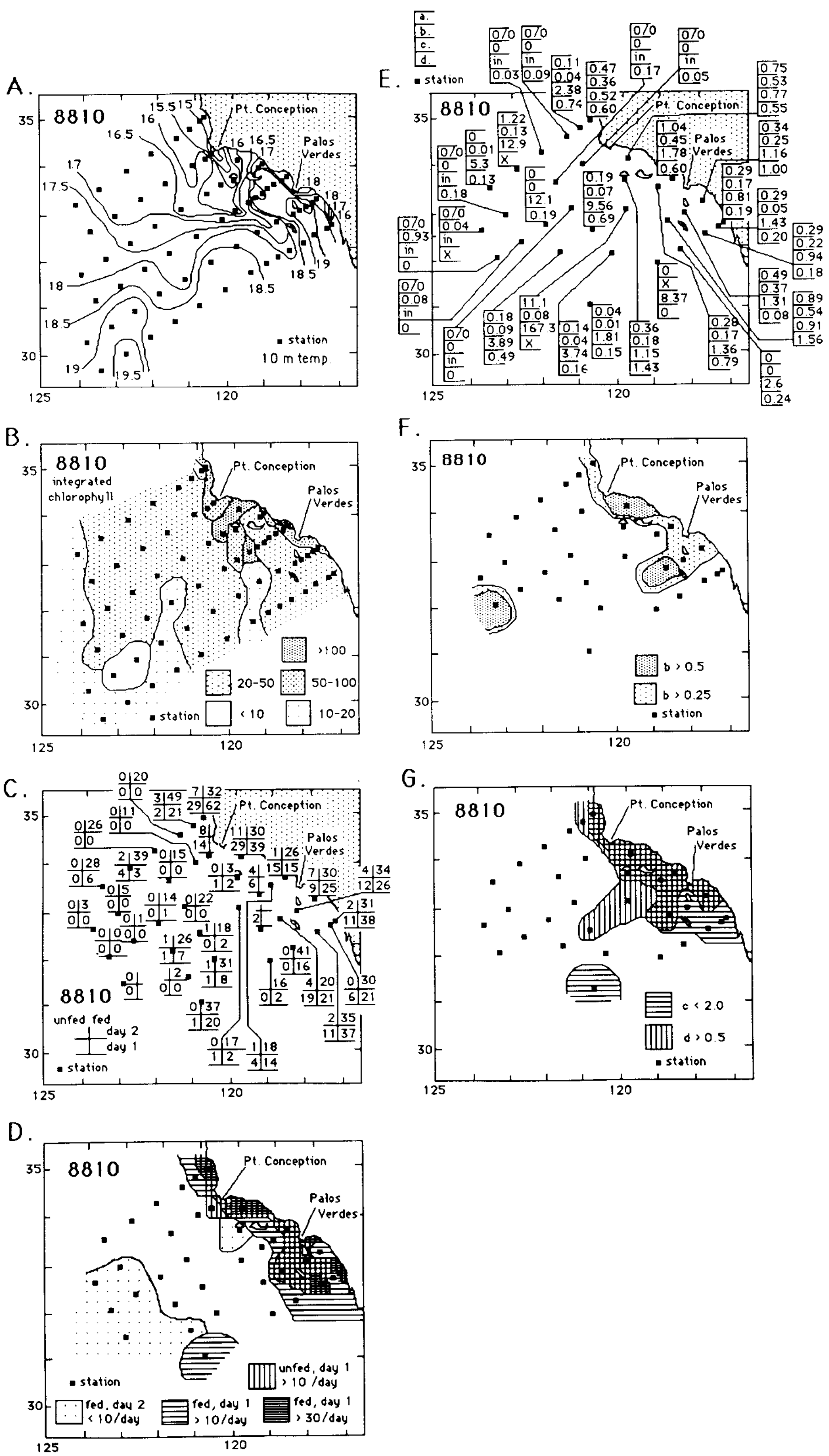

Figure 3. Maps for cruise 8810. *A*, Temperature (°C) at 10 m. *B*, Integrated chlorophyll, mg·m^{-2}. *C*, Eggs produced per female on first and second days in ambient and food-enriched conditions (blank means no data). *D*, Contours of daily egg production (no shading means <10·day^{-1} on day 1). *E*, Ratios a–d (see Methods text for definitions and interpretations): 0/0 means numerator and denominator 0; "in" means only denominator 0; X means no data. *F*, Contours of ratio b, higher values meaning less food limitation of production. *G*, Areas of low food limitation of production as shown by relatively low values of ratio c and high values of ratio d.

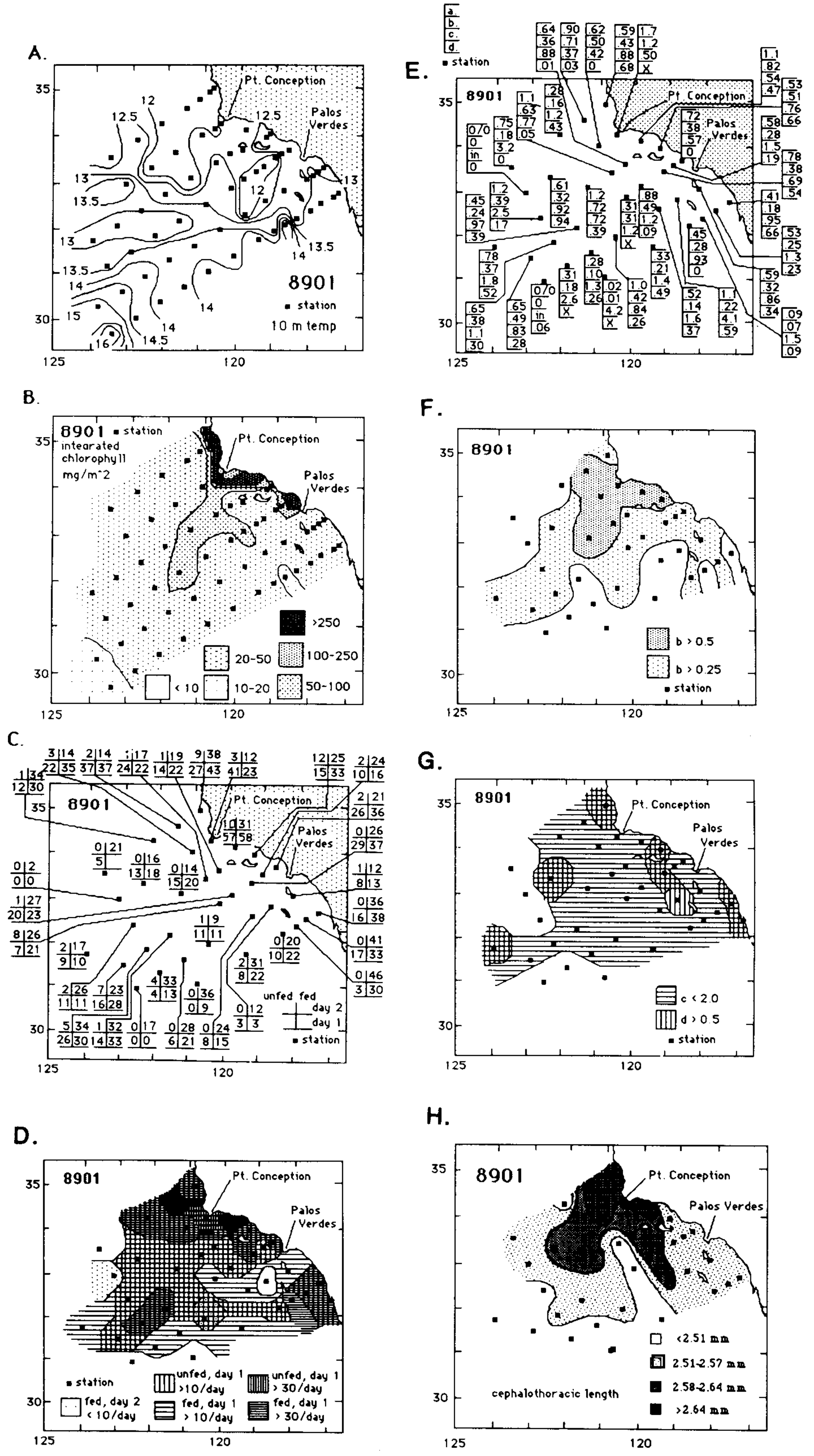

Figure 4. Maps for cruise 8901. See figure 3 for explanation of *A–G*. *H*, contours of cephalothoracic (prosomal) length of female *Calanus* from stations where experiments were conducted.

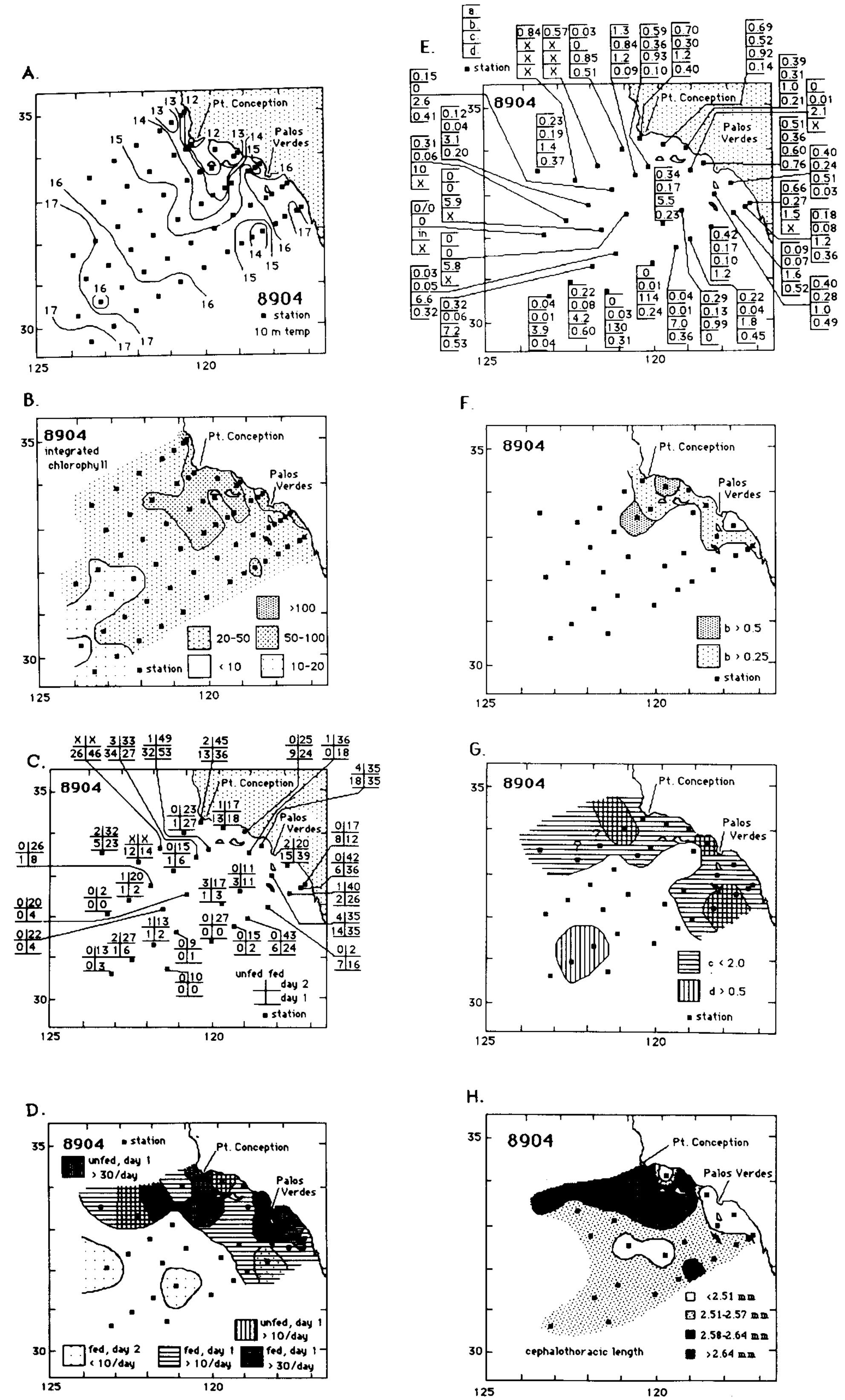

Figure 5. Maps for cruise 8904. See figures 3 and 4 for explanation. Note that there are no stations north of Point Conception.

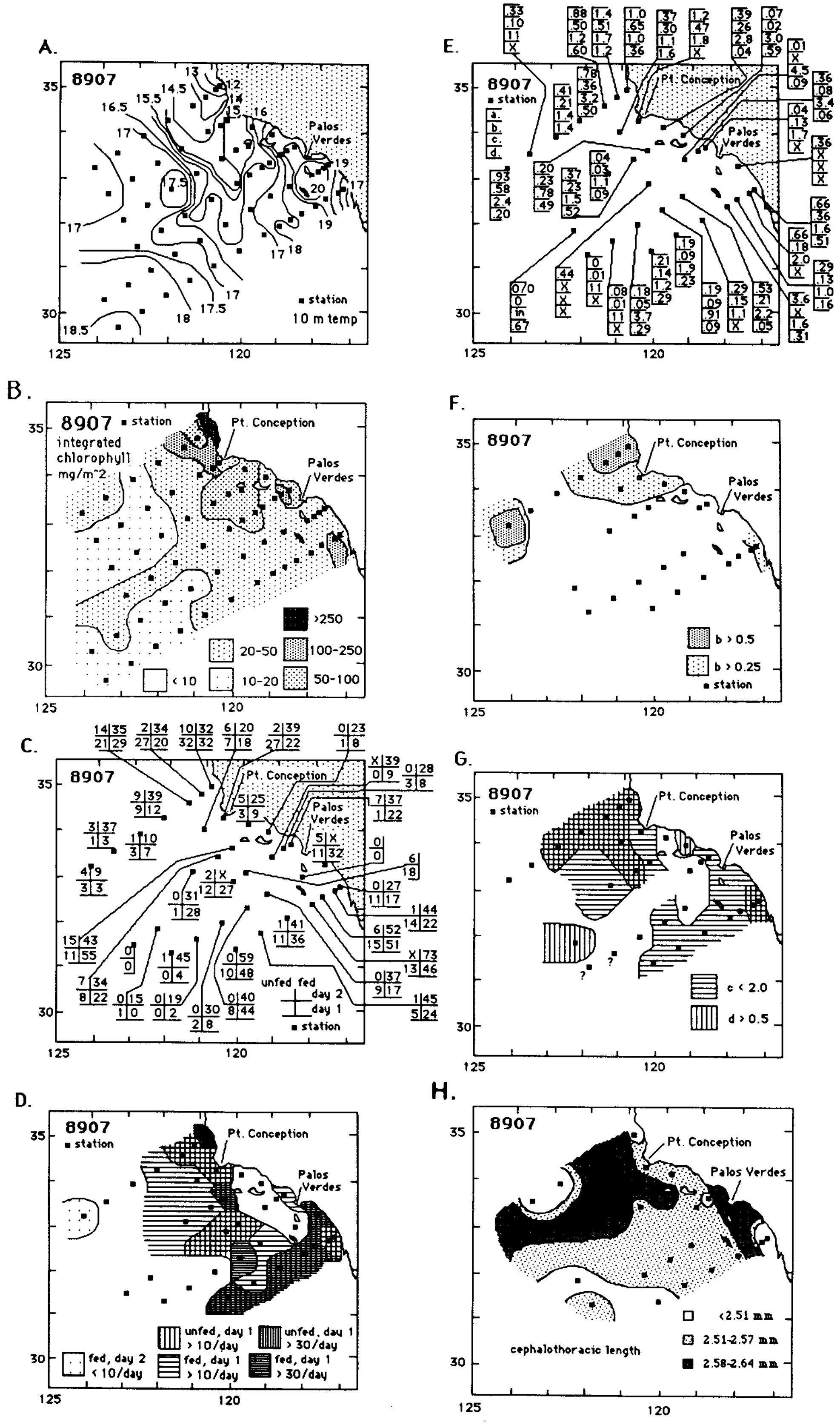

Figure 6. Maps for cruise 8907. See figures 3 and 4 for explanation.

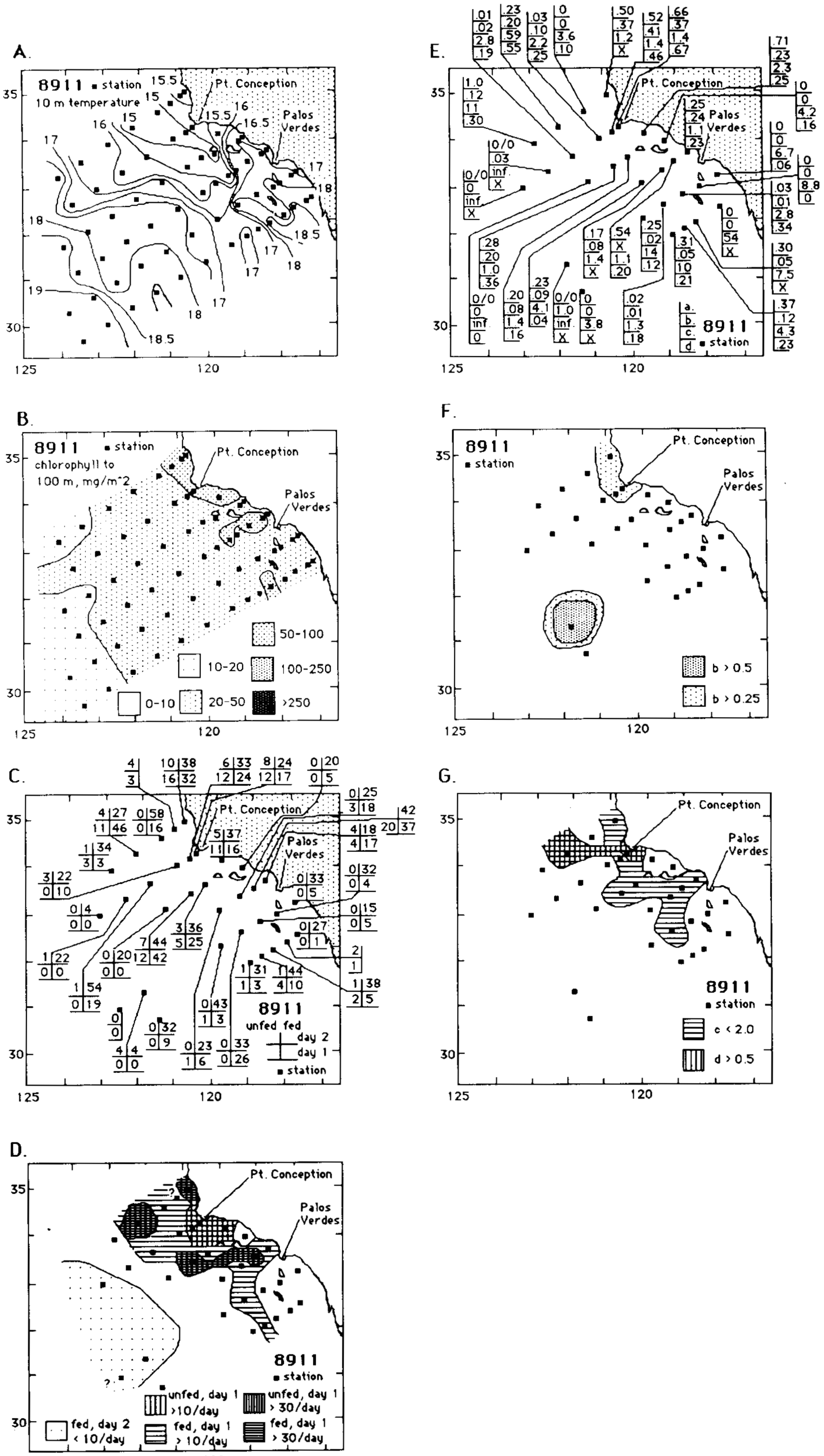

Figure 7. Maps for cruise 8911. See figure 3 for explanation.

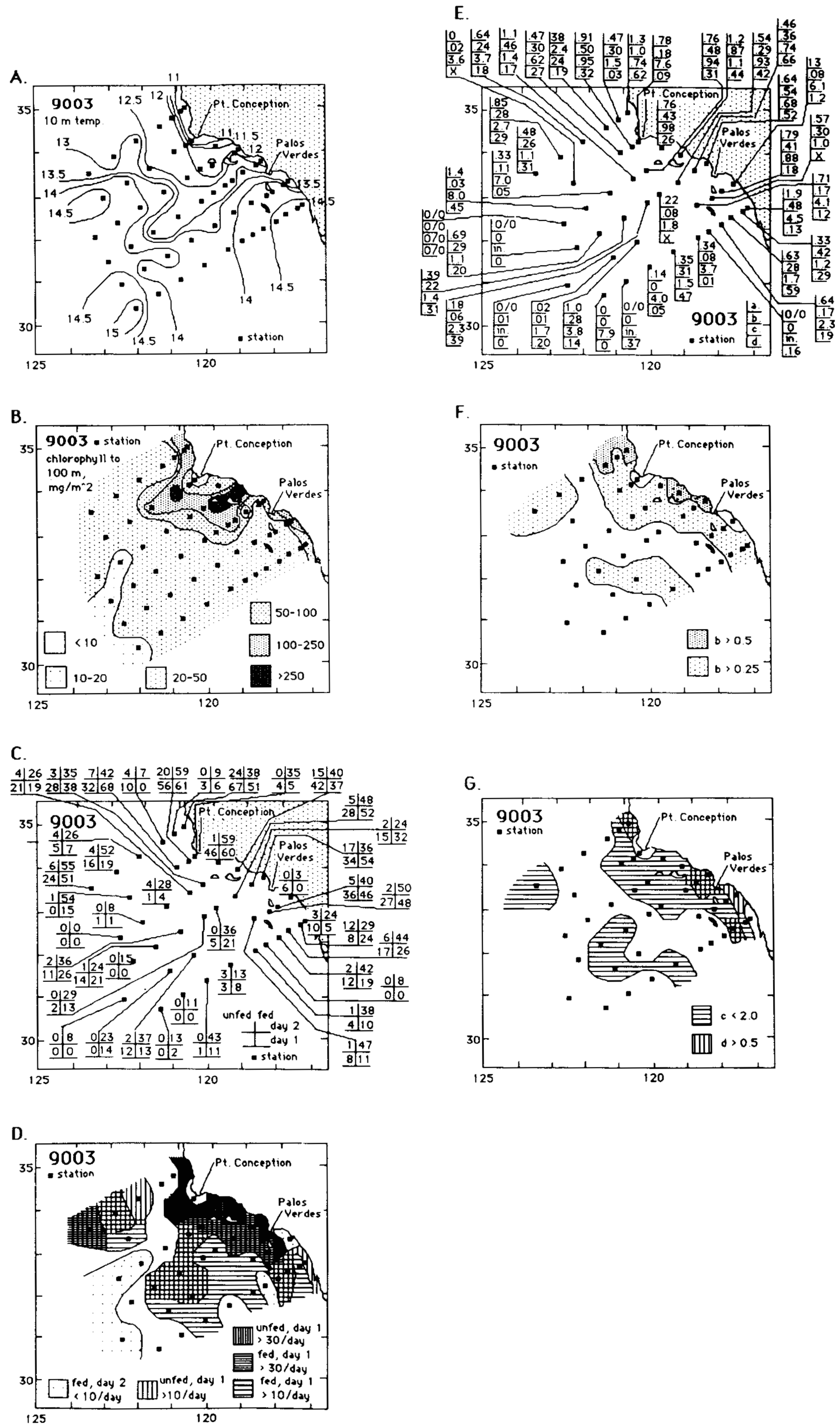

Figure 8. Maps for cruise 9003. See figure 3 for explanation.

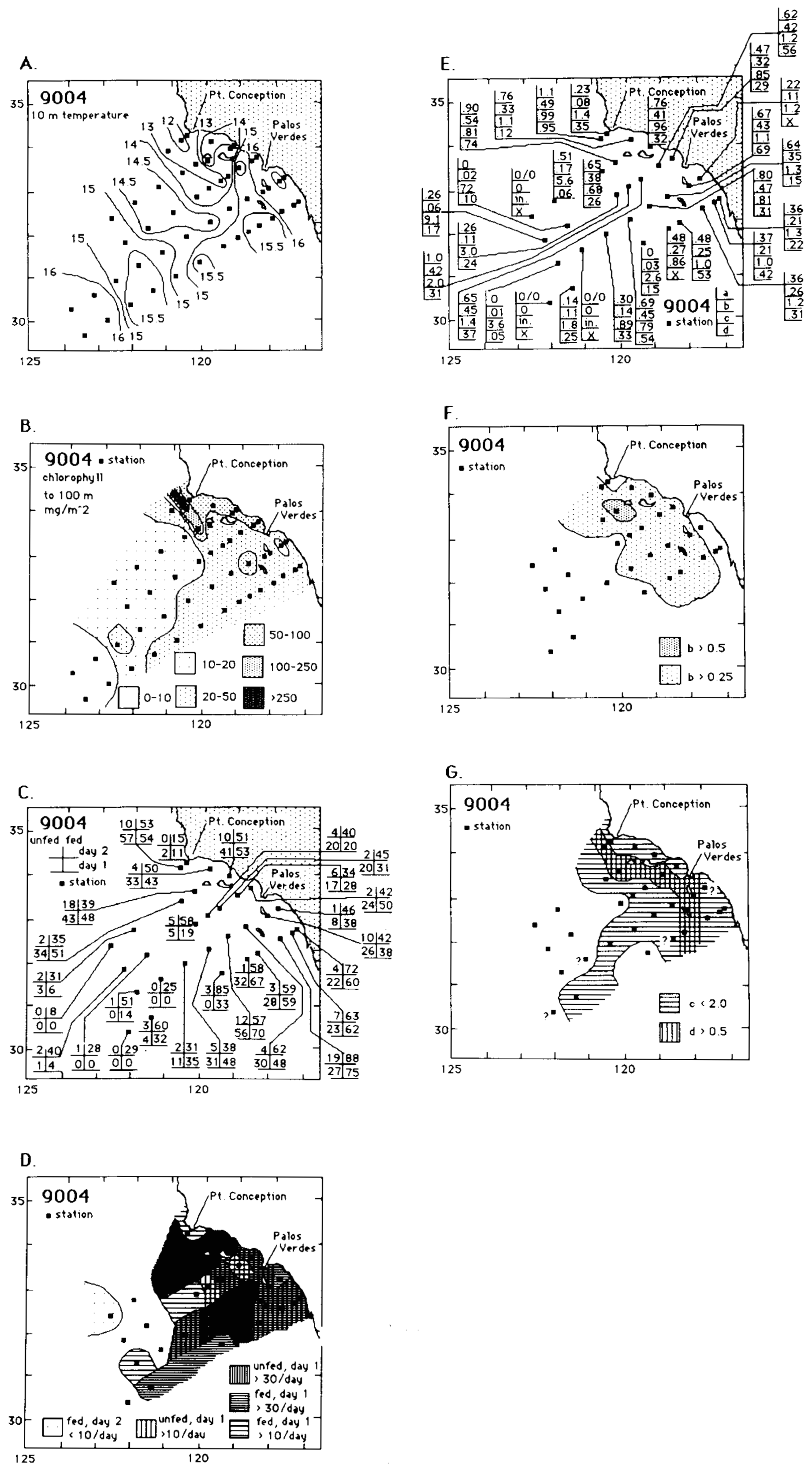

Figure 9. Maps for cruise 9004. See figure 3 for explanation. Note lack of northerly stations.

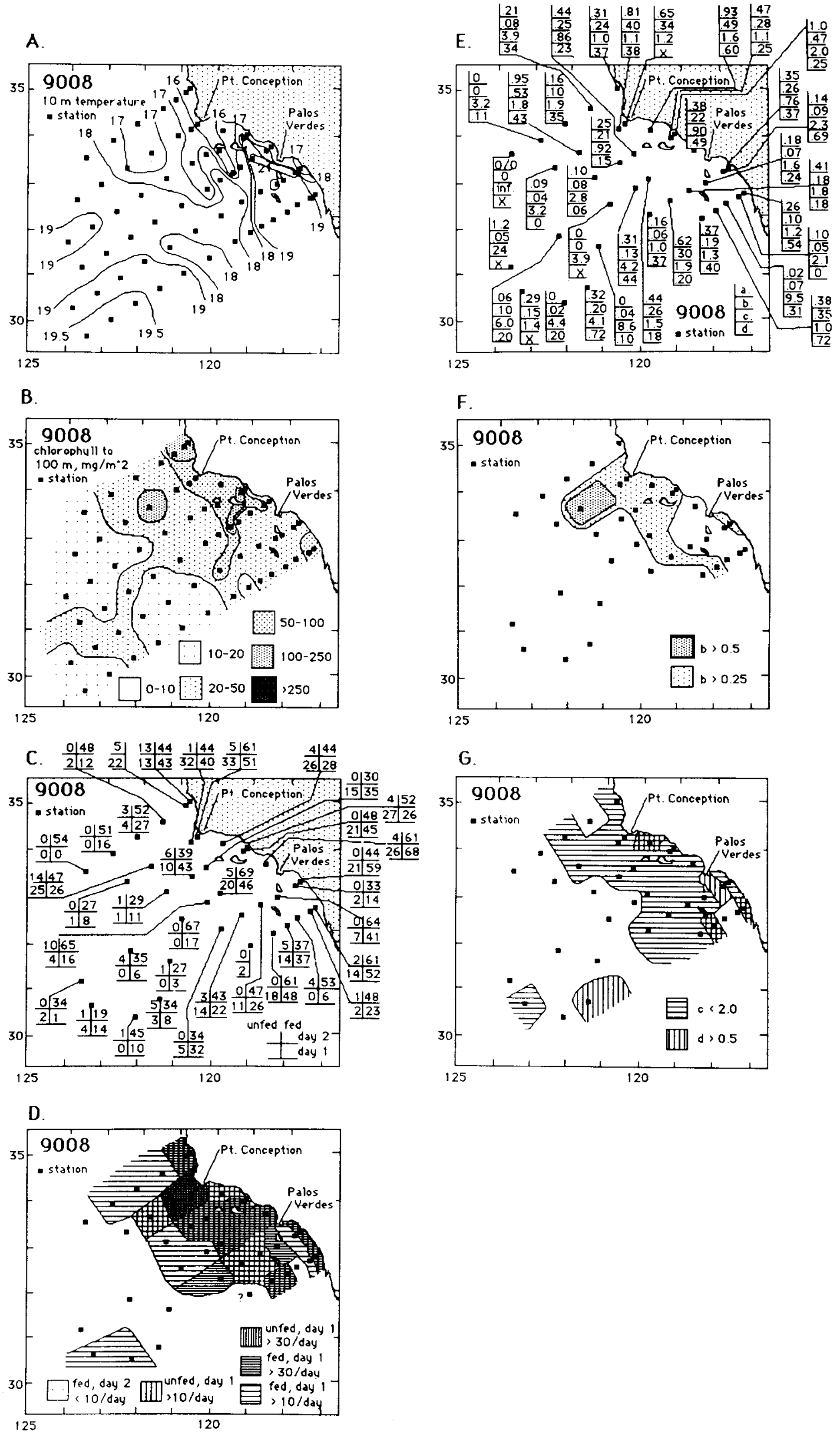

Figure 10. Maps for cruise 9008. See figure 3 for explanation.

Thalassiosira-enriched seawater on each of the two days of incubation, and ratios a–d (see Methods), together with more easily comprehended contour maps of the egg production and ratios b, c, and d. The sizes of females, as cephalothoracic (prosomal) lengths, are also shown for three 1989 cruises.

Large-scale features appearing on most cruises include the following.

1. The coolest water was in the northern, nearshore region and (on 8901) in the Southern California Bight; the warmest water was in the southwestern, offshore region and (in summer–fall) in the Southern California Bight (A in each figure).
2. The biomass of chlorophyll was consistently high nearshore in the vicinity of Point Conception (except immediately off Point Conception on 8901 and 9003); this relatively eutrophic region often extended southward along the nearshore and offshore edges of the northern half of the bight (B in each figure).
3. Both realized (in ambient seston) and potential (in *Thalassiosira*-enriched incubations) production of eggs were greatest nearshore and to the north, except on 8907 and 9004, when potential production was also high in the south. Perhaps the most variable region was the southern portion of the bight. Greatest absolute limitation by food (i.e., low production even on the second day with supplemented food [dotted areas of D in each figure]) occurred offshore; only on cruise 8810 were there more than four such stations (though three such stations represented a large area on 8911), meaning that there are few locations or seasons where females occur in the upper 200 m but are unable to reproduce because of infertility or exhaustion of oocytes or sperm. Only a more prolonged exposure to augmented food would reveal whether low fecundity on cruise 8810 was due to severe limitation by food or to infertility.
4. Egg production was consistently least limited by food nearshore, in relative terms (shaded areas in F and G of each figure); areas of only modest food limitation (as indicated by ratio b) extended far offshore on 8901 because of high reproductive rate even in unenriched water, and sporadically on other cruises because of poor production even when food was added.

Generalizations 3 and 4 mean that there is a pattern, though a variable one, to per capita reproductive rate of *Calanus* in the California Current off southern California; figures 3–10 (D, F, and G) are not random mosaics. Qualitatively, the patterns are related to the mesoscale distributions of phytoplanktonic biomass (figures 3–10, B), though there are some interesting differences.

There are also some clear differences, which may be seasonal, between cruises. For example, absolute production was poorest, and relative food limitation most widespread, on 8810; on 8901, both strong production and regions approaching food-independence were the most widespread (figures 11–13). (8904 and 9004 are difficult to compare to the other cruises because of the paucity of data along the northernmost line.) Compared to the seasonality of reproduction of *Calanus* spp. in more polar latitudes, however, the year-round reproduction off southern California is the interesting feature (cf. Mullin and Brooks 1967, figure 2).

Egg production of unfed females was significantly, positively correlated with that of females from the same stations provided with *Thalassiosira* (figure 14). This is because there were some stations on each cruise where even fed females produced few eggs on the first day (i.e., food limitation was sufficiently severe that at least a day's active feeding was necessary to elevate the rate of production, so ratio c was much greater than 1.0), and other stations where even ambient seston sustained relatively high rates, and where fed females also had high rates. The interesting variability is in the middle range, where fed females frequently produced eggs at moderately high rates, but unfed females did not.

Though the patterns of egg production qualitatively resembled those of the distribution of chlorophyll, on all cruises the rate of production by both unfed and fed females varied considerably with respect to chlorophyll (figure 15). The expected relations should include (1) increasing production with increasing biomass of chlorophyll, quasi-linearly at small biomasses and asymptotically at large ones (i.e., a saturation of the rate at large biomasses); (2) some "maintenance level"—a minimal biomass of chlorophyll at which no production by unfed females occurs (i.e., a positive abscissal intercept); (3) at any biomass below saturation, production by fed females exceeding that by unfed ones; and (4) stronger correlation between the production and biomass of chlorophyll, and a more pronounced difference in production between "poor" and "rich" stations, for unfed females than for fed ones.

Expectation 3 was met in all cases. Data from 8901 and 8907 failed to meet expectation 1, in the sense that egg production was not significantly correlated with integrated chlorophyll ($p > 0.01$ by 1-tailed test, this probability level chosen because of the multiple tests) for these two cruises. Expectation 4 was met in the sense that R^2 values for relations of

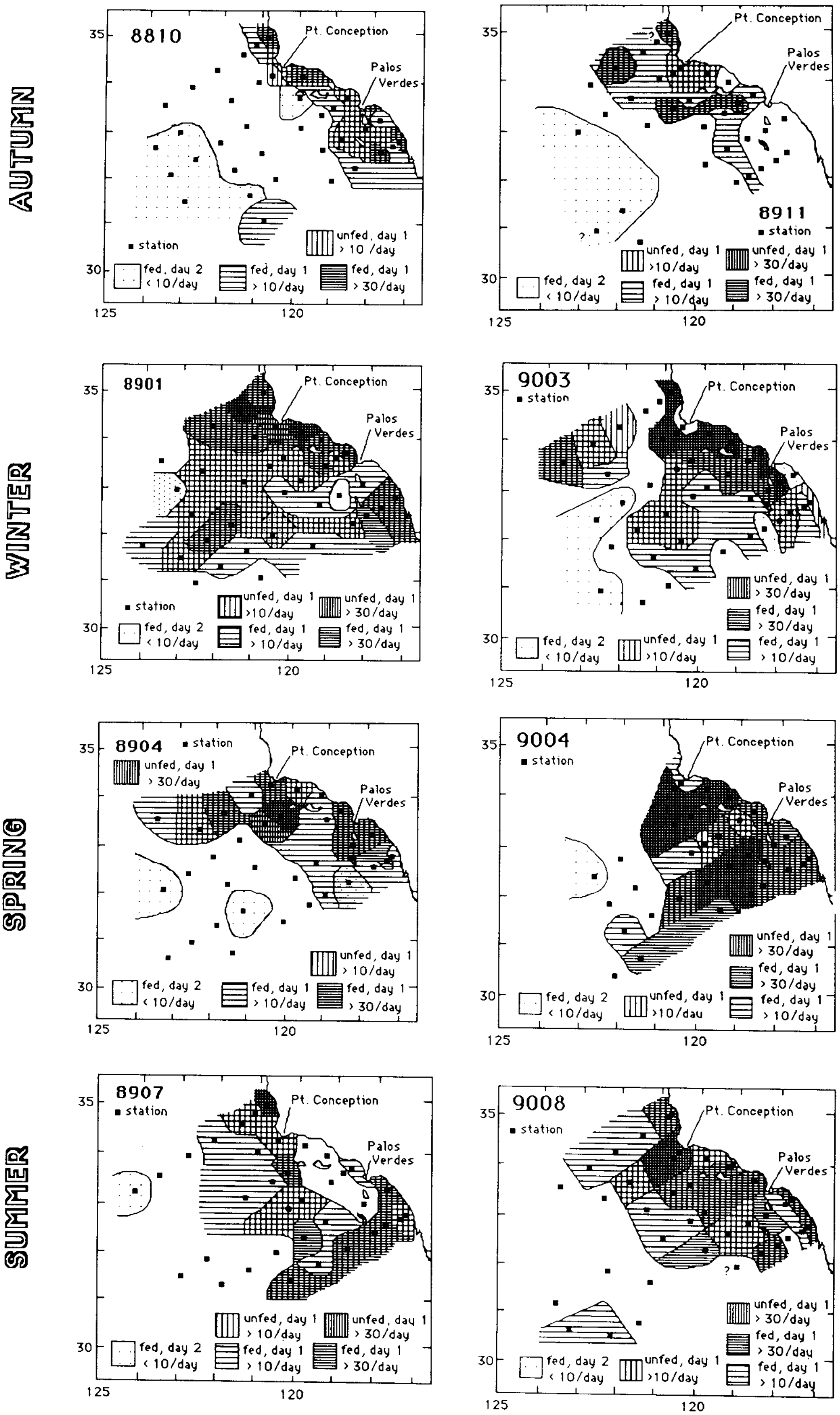

Figure 11. Maps of egg production for all cruises, arranged seasonally.

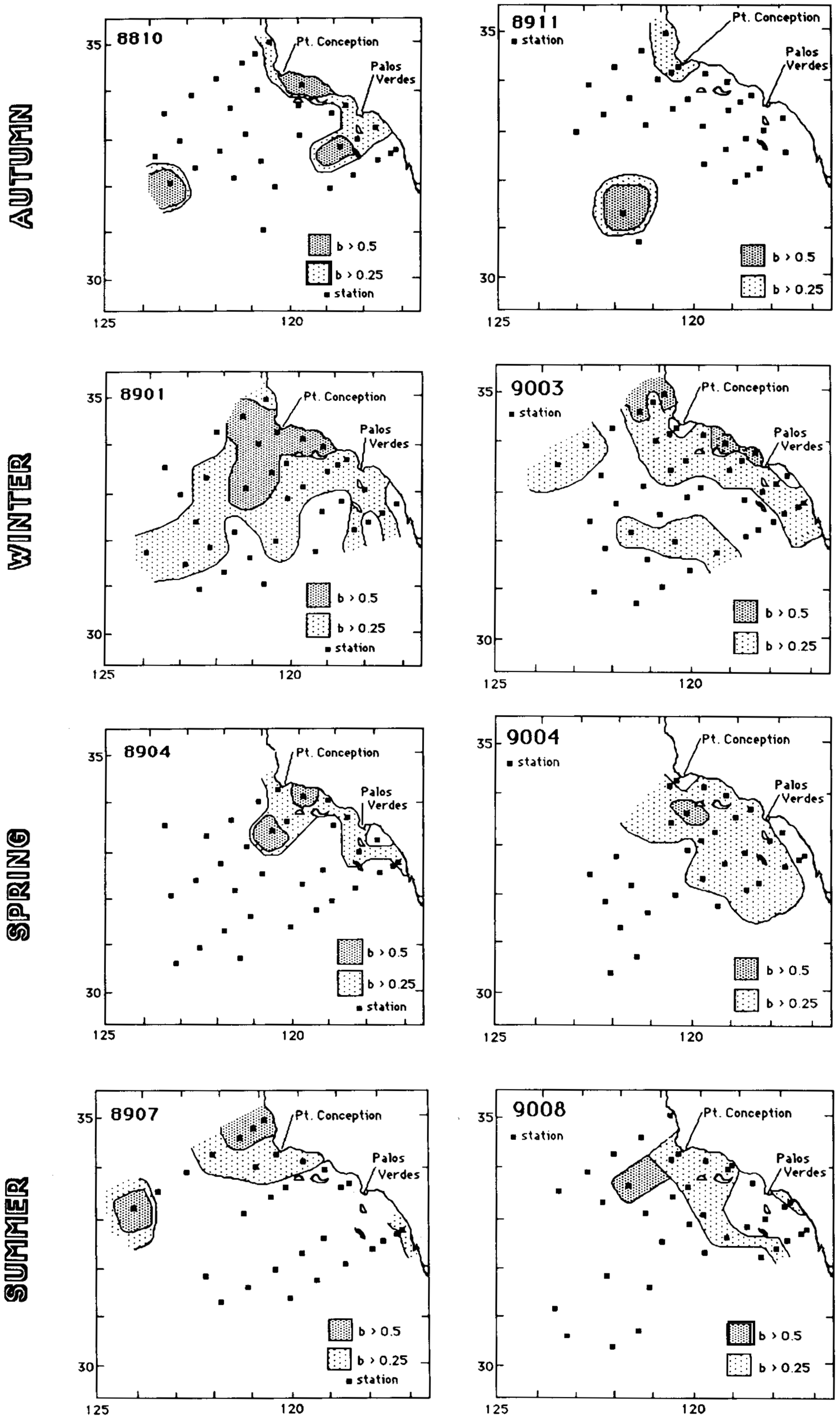

Figure 12. Maps of ratio b (2-day egg production, unfed:fed females), arranged seasonally.

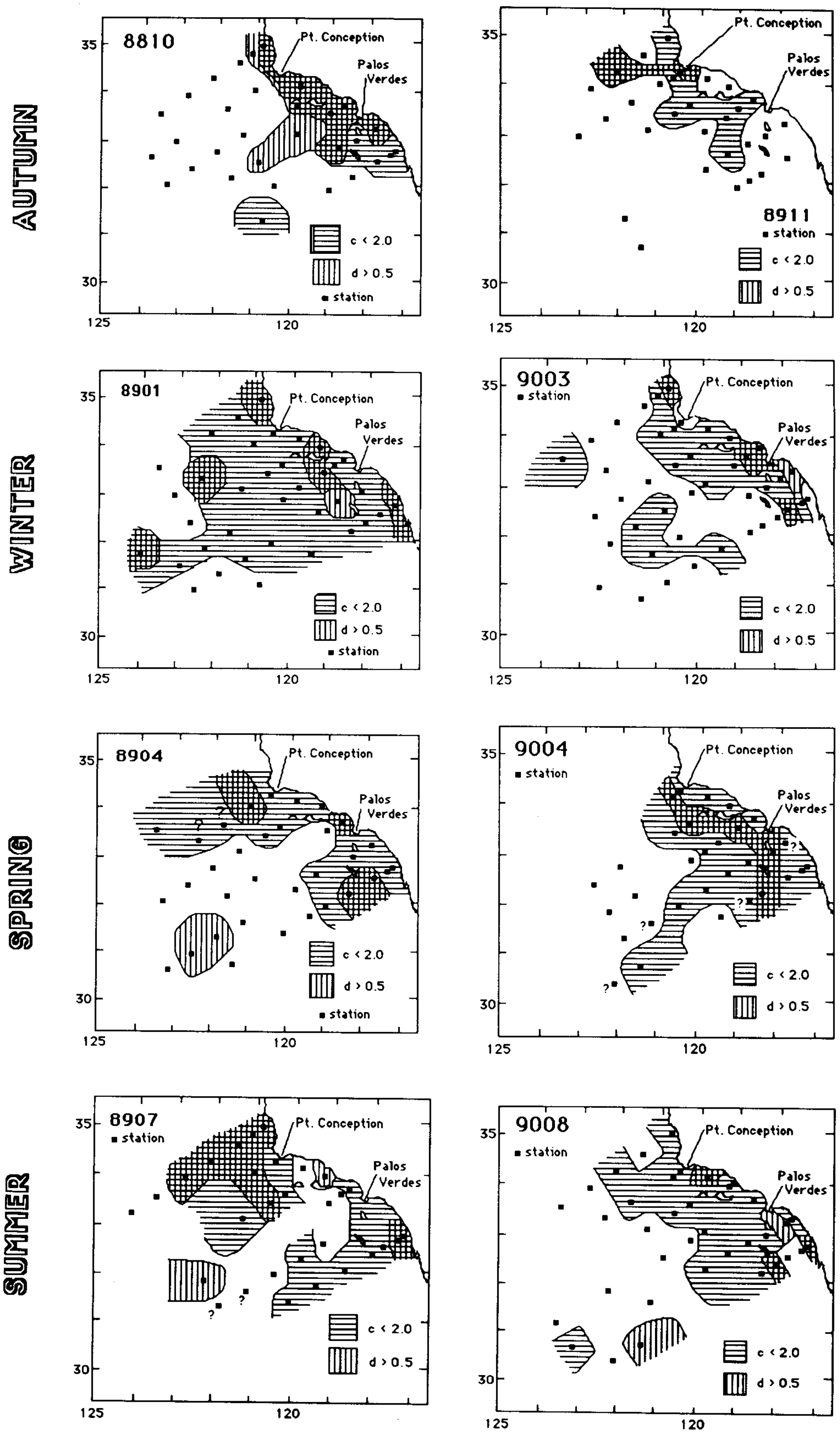

Figure 13. Maps of ratios c and d, arranged seasonally.

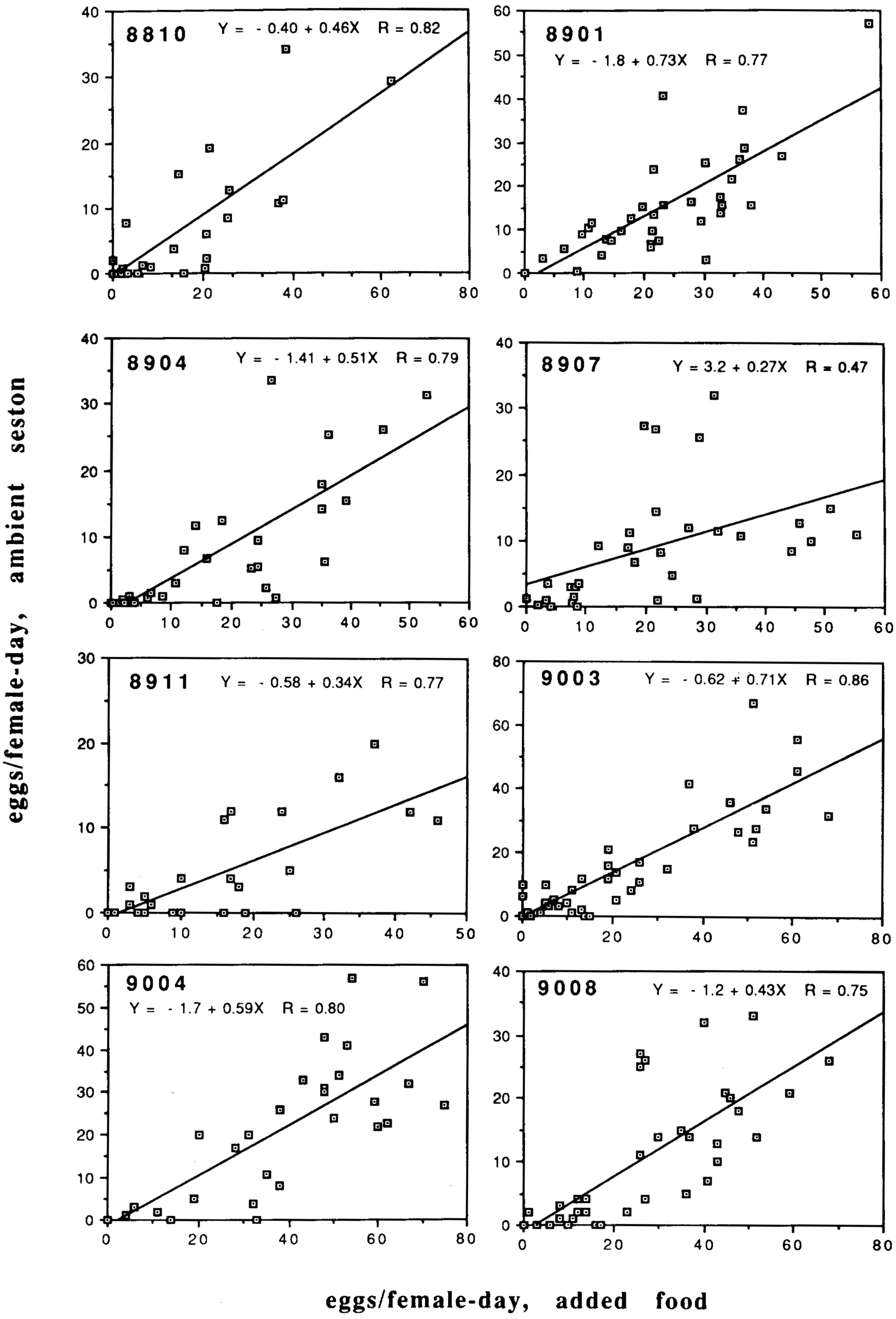

Figure 14. Rates of egg production of female *Calanus* for first 24 hours with excess phytoplankton added as food, and in unsupplemented seawater and seston from each station, for eight cruises. All correlations are significant at $p < 0.01$.

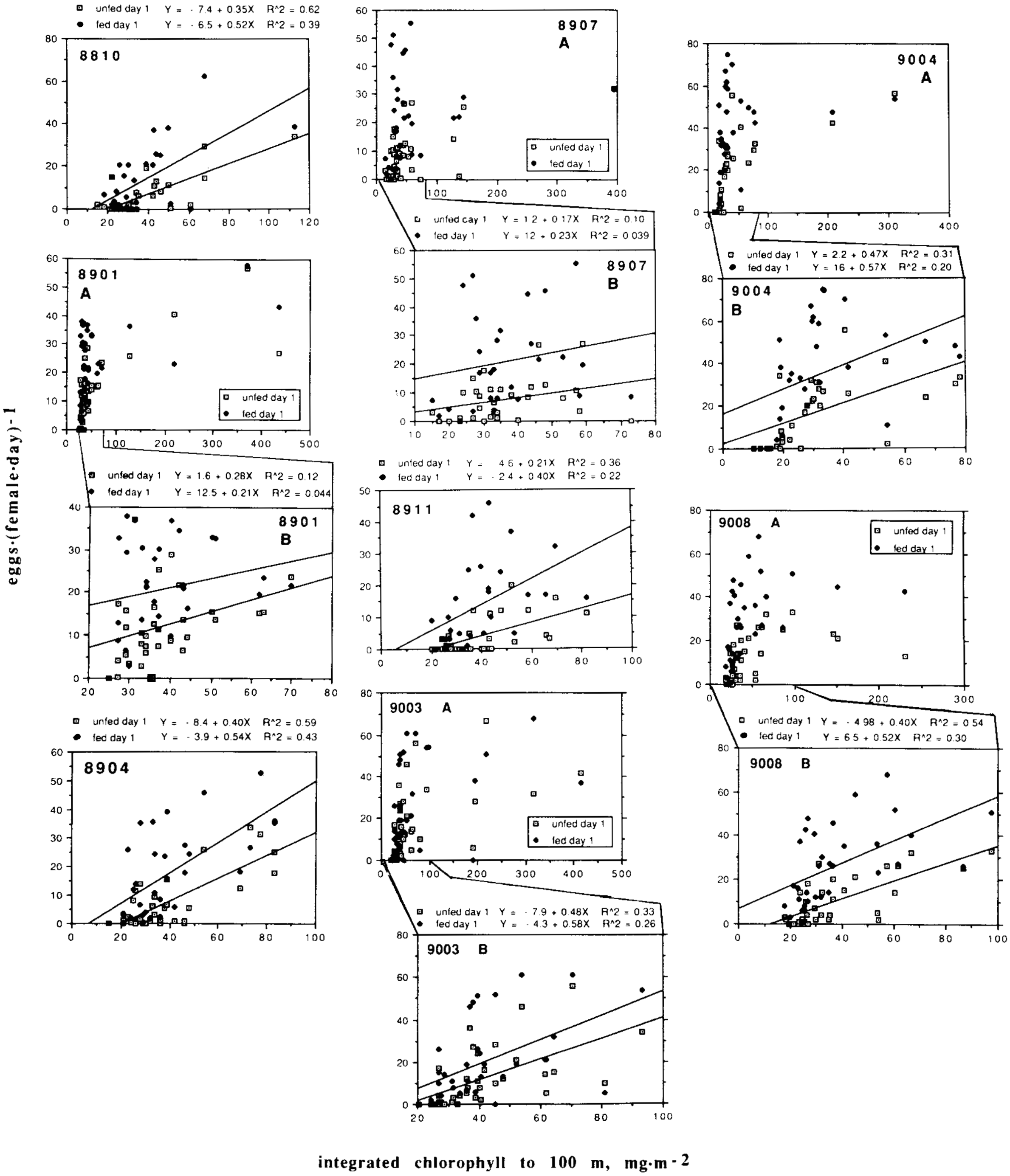

Figure 15. Rates of egg production over the first 24 hours for unfed (i.e., ambient seston) and fed (seston augmented with *Thalassiosira*) female *Calanus* as functions of chlorophyll biomass. October 1988: both correlations are significant at $p < 0.01$.
January 1989: *A*, all data; *B*, data for stations where biomass of chlorophyll was <100 $mg \cdot m^{-2}$, and linearity might be expected. The correlation for unfed females is marginally significant ($0.025 < p < 0.05$, 1-tailed), and the correlation for fed females is not significant ($p > 0.05$, 1-tailed).
April 1989: both correlations are significant at $p < 0.01$.
July 1989: *A*, all data; *B*, data for stations <100 $mg \cdot m^{-2}$. The correlation for unfed females is marginally significant ($0.025 < p < 0.05$, 1-tailed), and the correlation for fed females is not significant ($p > 0.05$, 1-tailed).
November 1989: both correlations are significant at $p < 0.01$, 1-tailed.
March 1990: *A*, all data; *B*, data for stations <100 $mg \cdot m^{-2}$. Both correlations are significant at $p < 0.01$, 1-tailed.
April 1990: *A*, all data; *B*, data for stations <100 $mg \cdot m^{-2}$. Both correlations are significant at $p < 0.025$, 1-tailed.
August 1990: *A*, all data; *B*, data for stations <100 $mg \cdot m^{-2}$. Both correlations are significant at $p < 0.01$, 1-tailed.

unfed females exceeded those for fed females (i.e., the regression explained more of the variance in production by unfed females than by fed ones). I expected that production of unfed females would range from 0 to some maximum as a function of chlorophyll, while that of fed females would range from low (but >0) to the same maximum. Thus the former would have the greater slope. However, contrary to this expectation, the slopes for the regressions of egg production against ambient chlorophyll were generally greater for fed than for unfed females. (I did not determine the statistical significance of these differences.) Further, the expectation (2) that the abscissal intercept for data from unfed females would be positive (i.e., that the ordinal intercepts in the regression equations would be negative) was not met by the data from cruises 8901, 8907, and 9004. It is conceptually possible that production of eggs could occur in the absence of chlorophyll, fueled by ingestion of detritus or heterotrophs. However, the extrapolations indicating slight egg production by unfed females at 0 chlorophyll are more likely to be artifacts resulting from the linear regression fit to (probably) curvilinear relations (even though I restricted the analyses to stations where concentration of chlorophyll was low enough that linearity should pertain). In summary, the relations of production to chlorophyll met some but not all of the expectations for the relations between a food-limited reproductive rate and the biomass of usable food.

In principle, the best measure of potential production rate (a rate not limited by food) should be the production by females during the second day of feeding, and an effect of the size of the females on the rate of production might be detectable. For example, Runge (1984) showed that the clutch size of *C. pacificus* increased approximately from 22 to 50 eggs·female^{-1} as prosomal length increased from <2.1 to 2.8 mm. In my incubations, *Calanus* produced approximately 38 eggs·(female·day)$^{-1}$ on the second day when provided with *Thalassiosira*, suggesting that clutches are produced daily, but there was still considerable variation, and no significant increase for larger females within the range of sizes I encountered (figure 16). Analysis of variance showed that temperature at each station explained little of this variability.

It is possible that production of eggs by copepods injured during capture, anesthesia, or sorting is inhibited (or stimulated before the incubation, leaving the females spent), though the tests of capture and anesthesia reported above did not demonstrate this. If the incidence of such injury varied between stations, and if it reduced survival as well as egg production, there might be a positive correlation between production by well-fed females (i.e., those on the second day in supplemented food) and their survivorship in the incubations. I examined data from all eight cruises for such correlations; there were significant (1-tailed $p < 0.025$), positive correlations for cruises 8904, 8907, and 8911. This may indicate that injury contributed to variable production of eggs, but the evidence is still ambiguous, since such positive correlations might also exist because of naturally variable states of health, even without injury.

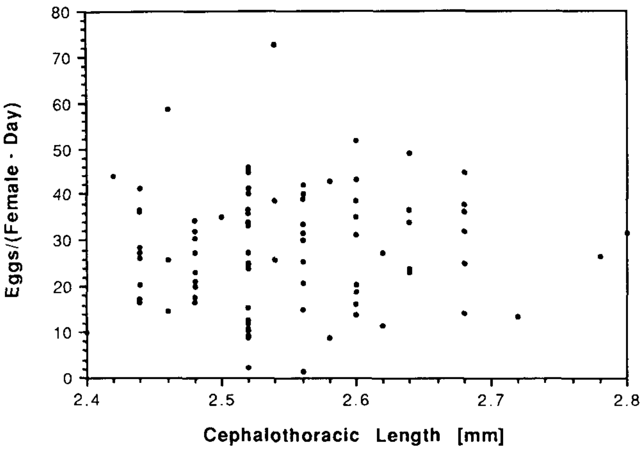

Figure 16. Production of eggs during the second day by female Calanus fed Thalassiosira, as a function of cephalothoracic (prosomal) length, in mm, for three 1989 cruises. The relation is nonsignificant.

As noted in Methods, ratio b should increase, and ratio c decrease, as limitation of egg production by the ambient food supply becomes less severe. Figure 17 shows that variation in these ratios supports the hypothesis that chlorophyll in the water column generally relates to the effective supply of food, but that the variability is again considerable. This means that either the experimental manipulations caused great variability as an artifact, or else that there are sources of food limitation (and its alleviation) which are poorly related to the areal distribution of total chlorophyll.

DISCUSSION

The mesoscale geography of growth rates of the *Calanus* population is the product of the maps in figure 11 and maps of the abundance of females. This geography is significant with respect to the locations of food production for larval fish (many of which rely on copepod nauplii for much of larval life), to the areas and seasons where the population

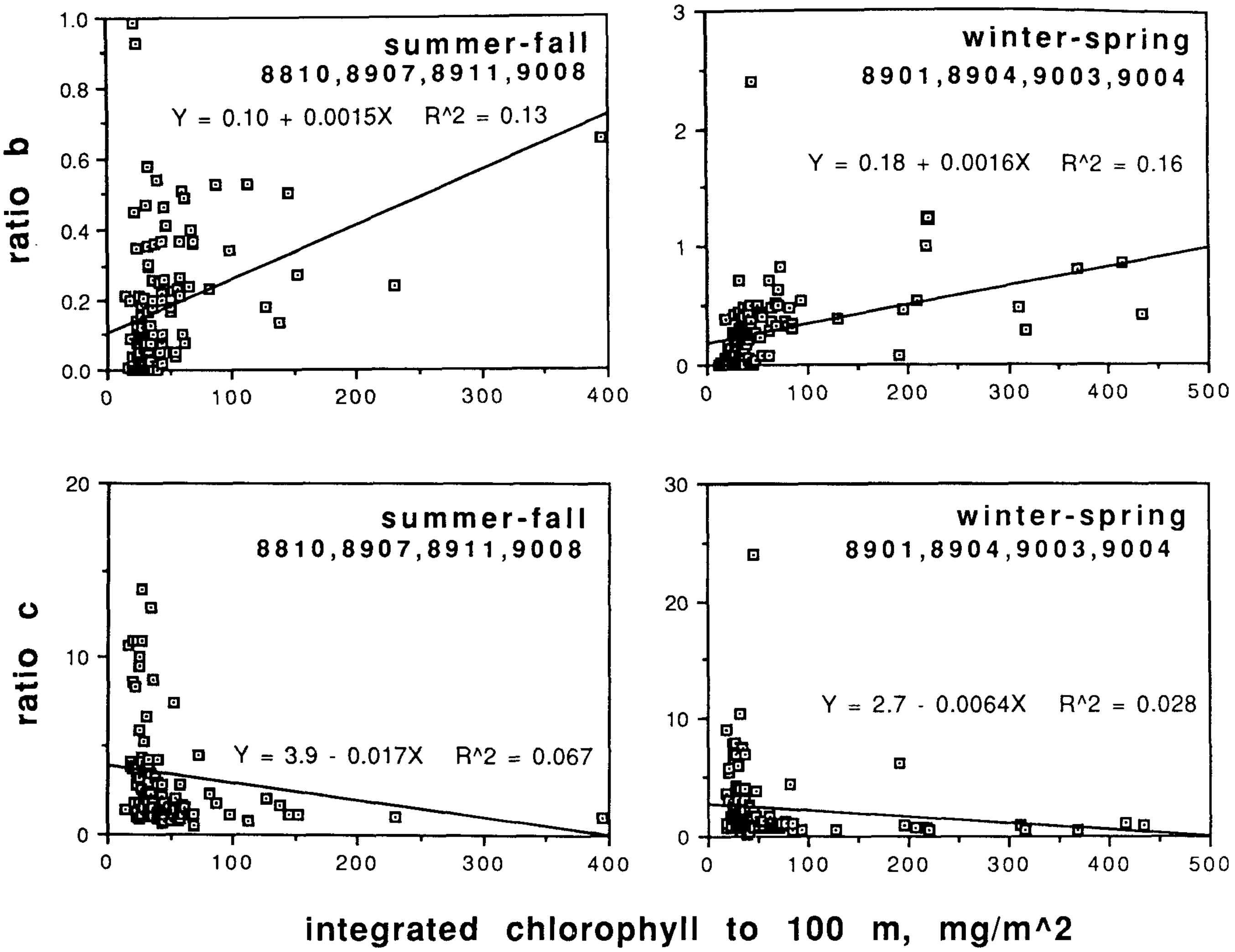

Figure 17. Ratios b (*top*) and c (*bottom*) versus integrated chlorophyll, for cruises grouped by season (four cruises per season). See Mullin 1991 concerning the relations for ratio b on four individual cruises. For ratio c, two summer-fall and three winter-spring values >50 have been eliminated; curvilinear (logarithmic and exponential) fits explained approximately twice as much of the variability. In all of the four cases, $p < 0.05$, 1-tailed.

will wax or wane (natality–mortality), and to the relative importance of immigration and emigration by advection, which also has a mesoscale structure (e.g., Roemmich 1989).

The great areal extent of egg production in January 1989, and the generally high rates in the northern and inshore regions on other cruises indicate that low temperature near the surface is not the rate-limiting factor for reproduction in the studied area. If anything, per capita reproductive rates are low in the areas and seasons of elevated temperatures, though because these are also areas of low biomass of chlorophyll the actual cause is ambiguous. *Calanus pacificus* ranges as far south as Cabo San Lázaro in Baja California (Fleminger 1964, as *C. helgolandicus*), but is most abundant south of Point Conception in nearshore regions, and the southern limit of reproduction is not known. Cool temperatures, but not phytoplanktonic food, can be found below the euphotic zone, and much of the population of late copepodite stages of *Calanus* off southern Baja California is deep-living and nonmigratory, at least at times (Longhurst 1967).

Some mesoscale relations are suggested, in spite of the coarseness of the pattern of sampling. On cruise 9003 (figure 8) in particular, the station immediately adjacent to Point Conception was characterized by low temperature, moderately low chlorophyll concentration, and low egg production. These are probably symptoms of, and responses to, intense localized upwelling, since near-surface O_2 concentration was only about 50% of saturation, and salinity was 0.2–0.4 ‰ higher than at adjacent stations.

On both conceptual and empirical grounds, the relation between per capita rate of egg production and concentration of food should be quasi-hyperbolic (the rate increasing with increasing concentration until some other environmental or physiological limit becomes crucial), possibly with a positive abscissal intercept (a threshold concentration necessary to initiate egg release). Figure 4 of Mullin 1988 summarizes most of the relevant measurements that have previously been reported. Within the range of natural concentrations of seston in the open ocean, however, saturating concentrations may seldom be approached, so a linear increase in rate with increasing biomass of seston might adequately describe such data.

Runge (1984) found experimentally that the relation between rate of egg production of *Calanus pacificus* (from Washington waters) and food indicated saturation above approximately 250 mg $C \cdot m^{-3}$. This is approximately 4 mg chlorophyll$\cdot m^{-3}$; as shown in figure 1, such concentrations were present at only a few stations — those where the integrated biomass exceeded 100 mg chlorophyll$\cdot m^{-2}$. In Runge's study, egg production ceased if the concentration of phytoplankton was less than 50 mg $C \cdot m^{-3}$, or 0.8 mg chlorophyll$\cdot m^{-3}$. Peterson (1988) found experimentally that still higher concentrations of phytoplankton were necessary to saturate egg production of the related species *Calanus marshallae*, from Oregon.

Comparison of figure 15 with Runge's and Peterson's data is inexact for two major reasons. First, non-phytoplanktonic organic seston is available to *Calanus* throughout the California Current, and some fraction of this, such as microzooplankton and some part of the detrital carbon, is likely to be nutritious (e.g., Eppley et al. 1977). Second, at least half of the total chlorophyll is likely to be in phytoplankters too small to be grazed readily by *Calanus* (e.g., Mullin and Brooks 1976), and this fraction is likely to be greater offshore and where total biomass is low than nearshore where it is high (Eppley et al. 1977; Reid 1983). Because of these opposing problems, the biomass of chlorophyll could either overestimate or underestimate the concentration of food as perceived by *Calanus* (or both, in different locations or times), even if the copepods were distributed uniformly through the upper 100 m so that the vertical structure was unimportant.

If other measures of seston were available for these cruises, it would be interesting to attack this problem "in reverse," by determining the size category or measure of sestonic biomass with which the rate of egg production was most tightly correlated (cf. Mullin and Brooks 1970; Checkley 1980b). Based on the experimental studies with other species of copepods (Checkley 1980a; Kiørboe 1989), particulate nitrogen would be a particularly valuable addition, since it is more limiting to egg production than is carbon when phytoplankton cultured so as to differ in C/N ratio is used as food. However, Eppley et al. (1977) reported that ratios of organic carbon to nitrogen were relatively invariant in the seston of the Southern California Bight, and close to the ratio that, when phytoplankton is the food, results in maximally efficient use of ingested carbon as well as nitrogen in production of eggs. Thus particulate nitrogen may covary so closely with chlorophyll that distinguishing it as a more precise predictor of egg production by goodness of fit (rather than by controlled experiments) would be difficult (though Checkley [1980b] concluded that food limitation was better estimated by phytoplanktonic than by total particulate nitrogen).

Because there was a strong relation between integrated chlorophyll per unit surface area and the maximal concentration in the water column (figure 1), the relations of reproductive rate to maximal chlorophyll were no more precise than those to integrated chlorophyll: in only three of the eight cruises (8901, 8907, and 9008) did a regression against the maximal concentration of chlorophyll account for more of the variability in egg production rate than did the regression against integrated chlorophyll. Moreover, Napp et al. (1988b) showed that at stations in the Southern California Bight there was little vertical variation in the nutritional quality per unit biomass of the seston, at least as indicated by analysis of protein, carbohydrate, and lipid. Thus it is difficult to argue that a strong vertical association between female *Calanus* and a particularly nutritious layer, obscured by the vertically integrated sampling, caused the scatter observed in figure 15.

Even assuming that the biomass of chlorophyll is correlated with what a female copepod perceives as food, a relevant question is the degree to which the chlorophyll biomass measured at a single station is representative of the surrounding area, and therefore also of the recent past biomasses experienced by the copepods captured there. If horizontal patches of chlorophyll of high intensity but small spatial scale (and therefore small temporal persistence) were characteristic, females captured at different stations with similar concurrent chlorophyll biomasses could have had quite different nutritional histories, and hence reproduce at quite different rates in both ambient and food-enriched incubations.

There are several reasons for believing that this is not the dominant source of variability shown in figure 15. First, there is large-scale pattern to the chlorophyll distribution (panel B in figures 3–10); the maps are not mosaics of different individual stations, and regions of similar biomasses tend to be contiguous. Second, horizontal patchiness within the distance integrated by a net tow, which might create variability between the females within one incubation, can be almost as great as that between adjacent stations. For instance, Mullin (1979, figure 2) found relatively little increase in horizontal, longshore heterogeneity of chlorophyll in the euphotic zone of the Southern California Bight on scales from 100 m to 10 km in March, and Star and Mullin (1979, 1981) found that horizontal patchiness of near-surface chlorophyll in the coastal zone (in the longshore direction), offshore California Current, and North Pacific Central Gyre in July was either relatively minor or not statistically detectable. Certainly there are some fronts or other steep gradients in the horizontal distribution of chlorophyll in the region surveyed, but the results summarized above, though limited to specific times, imply that such fronts are not common enough to cause great variability in rate of egg production between females from stations with similar biomasses of chlorophyll at the time of sampling.

Finally, figure 2 (upper panels) shows that reproductive rates estimated from parallel incubations of females from the same station in the same unsupplemented seawater can vary considerably. This variability is unexplained, but patchiness of chlorophyll around a station could play a role only if it caused female copepods of differing nutritional states to be present (this is certainly possible because of the integrative nature of the collecting tow) *and* if these different states were quite unevenly distributed among the replicate incubations. Alternatively, artificial differences between incubations in the incidence of injured females, or chance differences in the proportion of females releasing batches of eggs, could be responsible.

In a larger-scale study, Hakanson (1987) compared the wax ester and triglyceride contents of CV *Calanus* to chlorophyll in the water column of the California Current system; he found that these two lipid types (representing long- and short-term storage, respectively) were strongly correlated. *Calanus* could be lipid-rich or lipid-poor where the concentration of chlorophyll was relatively small (the lipid-rich copepods presumably having recently grazed down larger concentrations of chlorophyll, or fed on non-plant food), but were always lipid-rich where concentrations of chlorophyll were large. This would not be likely if the patches of elevated concentration were very small. Nor did the variability in lipid content of *Calanus* at a station relate to the vertical variability of chlorophyll there, again suggesting that small-scale patchiness of chlorophyll is not reflected in storage lipids.

Variation in per capita reproduction by *Calanus* within the Southern California sector of the California Current suggests that limiting factors vary geographically. The poor correlations between reproduction by unfed females and ambient biomass of chlorophyll (figure 15) and between ratios b and c and chlorophyll (figure 17) therefore mean either that chlorophyll is an imprecise measure of the rate-limiting food (though, as noted above, it is strongly correlated on some scales with other possible "bulk" measures), or that there are factors other than concurrent nutrition which also affect reproductive rate but vary geographically quite differently from chlorophyll. Even after a day of feeding in excess food, when all females might be expected to produce eggs at nearly the same rate, there is a large scatter (figure 16), which supports the latter explanation.

If the source of variability was food limitation that could be negated by a day's feeding, one would expect egg production during 24–48 hours in excess food to be either uncorrelated with that during 0–24 hours (i.e., variability during the second period removed by one day's feeding) or negatively correlated with it (well-nourished animals would produce eggs during the first 24 hours and be spent during the second 24, while poorly nourished ones would not produce eggs until the second period). In fact, the per capita egg production of well-fed animals during the second 24 hours was positively correlated with their production during the first 24 (figure 18, $p << 0.01$), and had almost as great a range (though failure to lay any eggs was much more common on the first than on the second day). This persistence of variability again suggests that small-scale patchiness of food around a station is not the sole cause of the variability shown in figure 15. Though there was a geographic pattern to body size (panels H in figures 4–6), this did not explain variability in maximal reproductive rate (figure 16). Analysis of the geographical pattern of population genetics might be revealing, but the possible role of injury on egg production must be assessed first.

In any case, a consequence is that maps of integrated chlorophyll concentrations, whether derived from shipboard or remotely sensed data, may be of little value in predicting the per capita reproduction by *Calanus* at particular stations. Such maps will also

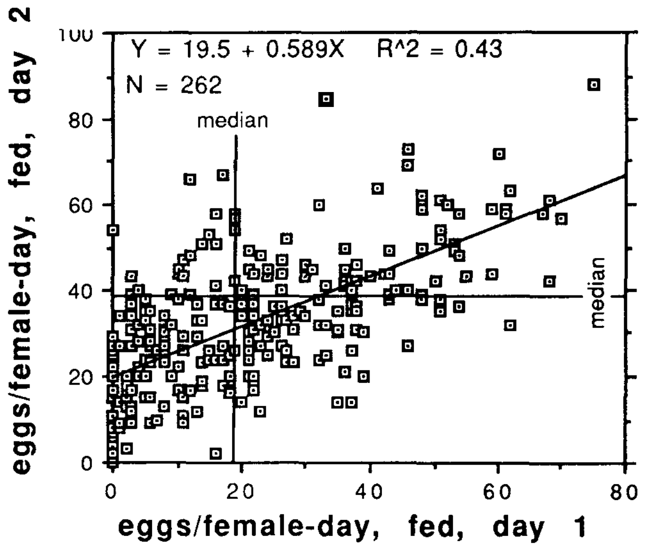

Figure 18. Production of eggs during the second day by female *Calanus* fed *Thalassiosira*, as a function of that on the first day, for all eight cruises. Medians for each day are shown. The correlation is significant at $p << 0.01$, 2-tailed.

not help predict the population's reproductive rate unless the abundances of females are more strongly correlated with chlorophyll than are the per capita rates. Other species will differ in geographical pattern, of course; if the per capita reproductive rate of females represents secondary productivity per unit biomass generally (reproduction plus somatic growth), it is possible that total secondary production by mesozooplankton (those large enough to be retained in the 500-μm mesh) is correlated with biomass of chlorophyll (which is often correlated with primary production: e.g., Hayward and Venrick 1982; Eppley et al. 1985; Mullin 1991). It would be rash, however, to conclude from present evidence that rates of primary and secondary production are tightly linked, except on the largest scales.

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RELATIVE ASSIMILATION NUMBERS OF PHYTOPLANKTON ACROSS A SEASONALLY RECURRING FRONT IN THE CALIFORNIA CURRENT OFF ENSENADA

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ABSTRACT

Higher surface chlorophyll *a* concentrations (Chl *a*) and integrated primary productivity (PP) have been reported for the cold side of a seasonally recurring front in the California Current. To test the hypothesis that greater PP at the cold side may partially be due to higher assimilation numbers (mgC·mgChl $a^{-1}\cdot h^{-1}$) of phytoplankton than those on the warm side, we generated photosynthesis-irradiance (P-I) curves for whole communities sampled across the front. Our data do not support the hypothesis. No differences were evident between our relative assimilation number values from both sides of the front. Higher PP values at the cold side seem to be due to the shallower subsurface Chl *a* maximum, which causes less limitation of light for the phytoplankton.

RESUMEN

Se han reportado valores más altos de concentración superficial de clorofila (Clf *a*) y productividad primaria integrada (PP) para el lado frío de un frente estacionalmente recurrente en la Corriente de California. En julio de 1985 generamos curvas fotosíntesis-irradiancia de comunidades de fitoplancton muestreadas a través del frente para probar la hipótesis de que la mayor PP en el lado frío se debe parcialmente a que los números de asimilación (mgC·mgClf $a^{-1}\cdot h^{-1}$) son mayores que los del lado caliente. Nuestros datos no apoyan la hipótesis. Los valores de números de asimilación relativos de ambos lados no muestran una diferencia evidente. Los valores más altos de PP del lado frio parecen deberse a una posición más somera del máximo subsuperficial de Clf *a*, lo cual causa una menor limitación de luz para el fitoplancton.

INTRODUCTION

Studying satellite images of phytoplankton pigments off California, Peláez and McGowan (1986) described a latitudinally oriented, sharp front just south of San Diego. This front starts about 160 km off the coast and extends some 500 km offshore. It is a persistent feature of the region. According to these authors, its phytoplankton pigment content changes approximately threefold over a distance of some 50 kilometers. The front retains its identity throughout the year, though it may wobble, tilt, or change position. In addition, the pigment gradient across the boundary changes markedly with time. During summer, the boundary shifts slowly to the south, reaching its southernmost position by mid- or late summer (off Ensenada, Baja California). The boundary is sharp and distinct in spring and early summer. By late summer, however, it is distinctly less intense (the pigment gradient is not as steep), and its outer edge erodes and ruptures. Peláez and McGowan (1986) also indicated that the large-scale phytoplankton pigment patterns for a given season tended to reappear from one year to another in the three years analyzed. Thomas and Strub (1990) reported similar dynamics at a zonally oriented frontal region within the California Current north of 33°N.

In order to describe the vertical structure and dynamics of the physical, chemical, and biological properties associated with the persistent, seasonally recurring feature studied by Peláez and McGowan (1986), the FRONTS cruise aboard RV *New Horizon* of the Scripps Institution of Oceanography (SIO) was carried on in July 1985 (Haury et al. 1986). As part of this project, we studied the photosynthesis-irradiance relationship of phytoplankton communities sampled across the front.

Simultaneous to our cruise, an independent study was being made by Prézelin et al. (1987) and Smith et al. (1987) across a coastal front in the Southern California Bight. Prézelin et al. (1987) reported on the diurnal patterns of size-fractionated photosynthetic parameters and on the algal groups dominating the phytoplankton communities across the front. Their data showed that either nannoplankton or netplankton can dominate natural phytoplankton assemblages in coastal frontal regions. Their study documents the range of variability possible in diurnal patterns of size-fractionated photosynthesis and illustrates that a general view of the size-dependency in assimilation numbers and diurnal patterns of photosynthesis cannot be supported.

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The purpose of our work was to report on the changes of assimilation numbers (P_m^B), or maximum photosynthetic rates in per unit chlorophyll *a* at optimum irradiance, of whole phytoplankton communities sampled across the Ensenada front described by Peláez and McGowan (1986). To generate the P-I curves, incubation experiments were performed only at noon; thus we describe only spatial changes of assimilation numbers. The hypothesis to be tested is that greater primary productivity at the cold side of the front may partially be due to higher assimilation numbers of phytoplankton. This will help to explain the strong changes of pigment concentrations and primary productivity across the front.

METHODS AND MATERIALS

The FRONTS cruise was divided into two legs. During the first leg, from 1 to 11 July 1985, an intensive series of CTD casts was made to find the boundary. A strong cold frontal area was also detected in satellite AVHRR images sent to the ship (Haury et al. 1986). During this leg we performed ^{14}C incubations to describe the vertical distribution of P_m^B for three hydrographic stations (A, B, and C; figure 1). Vertical profiles of photosynthetically active radiation (PAR) were obtained with a Biospherical Instruments quantum scalar irradiance meter, model QSP 170BR. We monitored PAR from the sun and sky with a solar hemispherical sensor (BIQSIM, model QSR-240).

Samples were collected, in special casts, from depths corresponding to 100%, 50%, 25%, 10%, and 1% of irradiance incident just below the surface (E_0). Samples were obtained with 7-l Niskin bottles with clear neoprene rubber closures. Sixteen subsamples were drawn from each depth into 125-ml incubation glass bottles, which were inoculated with ^{14}C as $NaHCO_3$. Two replicate samples from each depth were incubated on board, in sunlight, at each of eight irradiances: 88%, 60%, 45%, 22%, 5.5%, 4%, 3%, and 1% of solar irradiance measured on deck. The incubator consisted of acrylic tubes with black plastic filter screens to control irradiance. Incubation irradiances were measured inside empty bottles and tubes. Incubations were done between 1100 and 1400 hrs. After about 2 hours of incubation, samples were filtered onto 0.45-μm-pore membrane filters and placed in scintillation vials. One-half ml of 10% HCl was added to each sample, which was then allowed to sit uncovered at room temperature for 12 hours (after Lean and Burnison 1979). Then 10 ml of scintillation fluor were added to each sample, and the samples were taken to SIO where the radioactivity was determined with a scintillation Beckman LS 100 counter.

During the second leg, 12 to 23 July, we ran eight ^{14}C incubation experiments to determine P_m^B for samples from depths corresponding to 100% and 50% E_0 (stations D through K, figure 1). Incubations were done at noon, as in the first leg, but instead of two replicate samples from each depth we used five at each incubation irradiance. Two incubation experiments of the first leg and four of the second were done for stations at the warm side of the front, the other five experiments were done for stations at the cold side (figure 1).

Two transects across the front were sampled during the second leg. The southwest-to-northeast transect was covered three consecutive times, while the northwest-to-southeast transect was covered only once, with a total of 37 hydrographic stations for both transects (Haury et al. 1986). Besides these 37 stations, we occupied 8 more for our incubation experiments, so that our sampling was done around 1000 hrs. For each sampled depth, we also measured dissolved oxygen concentration (O_2), nutrients (PO_4, NO_3, NO_2, and SiO_2), chlorophyll *a* (Chl *a*), phaeopigments, and phytoplankton abundance.

We determined O_2 by the Winkler method as modified by Carpenter (1965), using the equipment

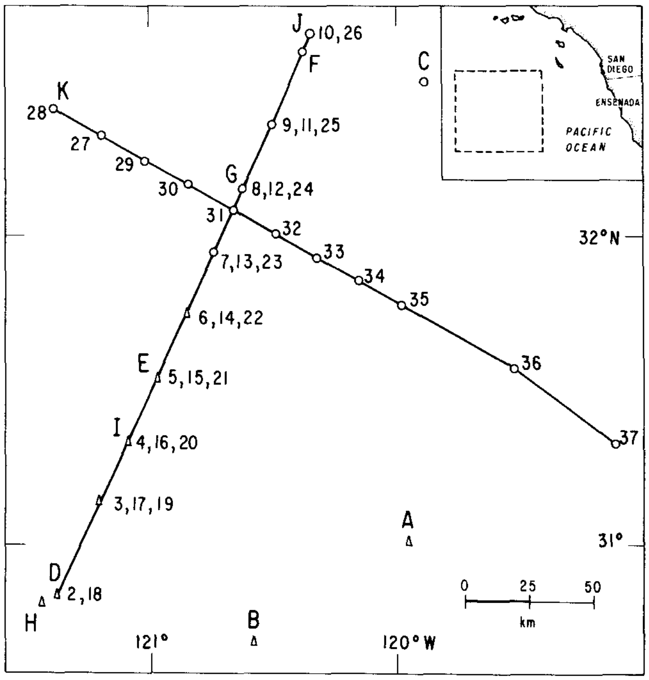

Figure 1. Station locations for second leg of FRONTS cruise. Letters indicate the positions of our incubation experiment stations. Data reported by Haury et al. (1986) are from stations represented by numbers. *Triangles* represent stations from the warm side of the front; *circles* represent those from the cold side.

and procedure outlined by Anderson (1971). We used an automated analyzer at sea to determine nutrients, with procedures similar to those described in Atlas et al. (1971). Chlorophyll was measured with a fluorometric technique (Yentsch and Menzel 1963; Holm-Hansen et al. 1965). Chl *a* samples were obtained with 0.45-μm-membrane filters. We extracted pigment following Venrick and Hayward (1984): we placed the filters in scintillation vials containing 10 ml of 90% acetone, and refrigerated them for 24 hours. The samples were then brought to room temperature; their fluorescence was determined, before and after acidification, with a Turner Designs fluorometer. Phytoplankton abundance was determined by the Utermöhl (1958) inverted microscope technique, and cells greater than 8 μm were counted apart from the smaller ones.

Photosynthesis data (per m^3) were normalized per unit Chl *a* to obtain assimilation ratios (P^B). Photosynthesis-irradiance curves were drawn, and assimilation numbers (P^B_m) were estimated by eye-fitting, in each case, with the mean of P^B's for the replicates at the optimum irradiance. Then, all P^B_m's were divided by the largest one of our data set (2.88 $mgC \cdot mgChl\ a^{-1} \cdot h^{-1}$) to obtain relative assimilation numbers ($RP^B_m = \frac{P^B_m}{P^B_m(\max)}$). The ^{14}C activity added to the incubating samples was constant, but unfortunately its absolute value is uncertain, which is why we use relative assimilation numbers instead of absolute values.

RESULTS

The temperature front was detected at station 6, 31°44.8′N, where the 18°C isotherm was almost vertical from the surface to 35-m depth (figure 2a). Across the front, measured sea-surface temperatures ranged from more than 19°C at the south, to less than 16.5°C at the north, in a distance of about 160 km. Surface Chl *a* values ranged from less than 0.08 $mg \cdot m^{-3}$ at the warm side of the front to more than 0.25 $mg \cdot m^{-3}$ at the cold side (figure 2b).

The isopleths showing the vertical distribution of Chl *a*, O_2, NO_3, PO_4, and SiO_2 sloped upward from the warm to the cold side, mainly at the front itself (figure 2b–f). The subsurface Chl *a* maximum changed depth from about 90 m at the south to near 10 m at the north, and its concentration changed slightly from about 0.30 $mg \cdot m^{-3}$ at the south to about 0.25 $mg \cdot m^{-3}$ at the north. The two northernmost stations had a homogeneous vertical distribution of Chl *a* from the surface to 70 m, with values between 0.20 and 0.30 $mg \cdot m^{-3}$. The subsurface O_2 maximum did not coincide with the Chl *a* maximum: the O_2 maximum was between 50 and 60 m at the south of the front and between 30 and 40 m at the north.

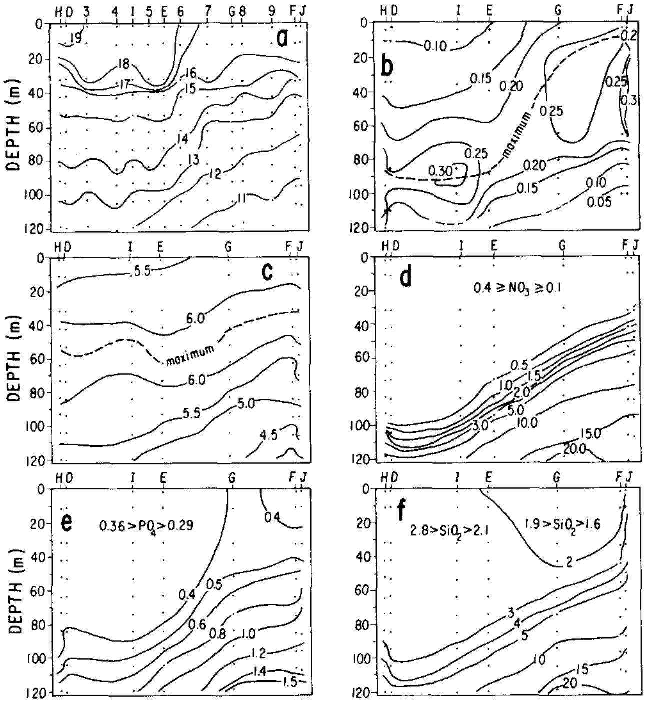

Figure 2. Vertical distributions of *a*, temperature; *b*, chlorophyll *a* ($mg \cdot m^{-3}$); *c*, oxygen ($ml \cdot l^{-1}$); *d*, nitrate (μM); *e*, phosphate (μM); and *f*, silicate (μM).

Surface values of NO_3 were relatively low along the whole transect, but greater than 0.1 μM. The 0.5-μM NO_3 isogram was deeper than 90 m at the southernmost station, and only 30 m deep at the northernmost station; below this isogram, there was a steep NO_3 vertical gradient, with the 5-μM isogram only 20 m deeper (figure 2d). PO_4 surface values were slightly greater at the cold side of the front, with concentrations of 0.4 μM, compared to values between 0.30 and 0.35 μM at the south. Conversely, SiO_2 surface values were slightly greater at the warm side of the front, with concentrations as high as 2.8 μM, compared to values as low as 1.6 μM at the north (figure 2). PO_4 and SiO_2 presented steep vertical gradients like NO_3, starting at the same depth (figure 2d–f). NO_2 surface values varied from undetected to 0.03 μM; its values at the nutricline were between 0.05 and 0.20 μM, with maximum values at depths changing from 105 m at the southernmost station to 60 m at the northernmost one (data not presented).

The depth corresponding to 1% E_0 was greater at the warm side of the front than at the cold side: 82–88 m at the warm side, and 59–65 m at the north

TABLE 1

RP_m^B Values for Communities of Phytoplankton Sampled from the Indicated Light Levels, Total Phytoplankton Abundance (cells•ml^{-1}), and Abundance of the <8-µm Size Fraction

STA.	z (m)	% E_0	RP_m^B	PHYTOPLANKTON	
				TOTAL	<8µm
A 83 4	0	100	0.25		
	8	50	0.29	111	97
	16	25	0.26	85	72
	36	10	0.39	74	62
	83	1	0.07	89	77
B 82 6	0	100	1.00	114	68
	2	50	0.75	184	173
	14	25	0.65	142	117
	32	10	0.66	112	98
	82	1	0.24	116	106
C 59 9	0	100	0.39	136	126
	4	50	0.28	104	91
	10	25	0.46	77	55
	24	10	0.39	114	101
	59	1	0.18	142	124
D 85 14	0	100	0.74	173	131
	2	50	0.90	138	120
E 88 15	0	100	0.53	216	175
	3	50	0.61	242	209
F 65 16	0	100	0.36	117	94
	2	50	0.20	98	75
G 64 17	0	100	0.33	147	128
	2	50	0.28	26	22
H 86 18	0	100	0.43	156	136
	3	50	0.35	43	32
I 85 19	0	100	0.58	113	97
	3	50	0.51	72	54
J 61 20	0	100	0.49	115	91
	3	50	0.37	46	23
K 61 21	0	100	0.34	125	108
	2	50	0.28	64	32

Numbers under station letters are the 1% E_0 depth in meters (e.g., 83), and the sampling date in July (e.g., 4).

(table 1). This is a less steep gradient than the one shown by the nutrient isograms across the front, so that the 1% E_0 depth is much farther into the nutricline at the cold side of the front than at the south. The 50% E_0 depth varied from 2 to 8 m, usually falling at 2–3 m.

Although only cells larger than about 2.5 µm are counted with our inverted microscope, nannoplankton was always the most abundant fraction (table 1). Counted cells smaller than 8 µm were between 50% and 95% of total counts, mostly falling between 75% and 85%. There was no difference in either total abundance or percent abundance of nannoplankton between the warm and the cold side of the front. Microflagellates were the dominant counted group in all cases.

All of our samples showed photoinhibition at high irradiances. Because we only had four discrete high irradiances in our incubation experiments, it was not possible to precisely determine the values of optimum or saturating light. But our data show that in most cases light saturation was reached at about 250 micro-Einsteins·m^{-2}·s^{-1} (figure 3). Although there were some higher values of RP_m^B at the warm side of the front with respect to those on the cold side, there was no clear spatial pattern. No difference was evident for RP_m^B values from one side to the other of the front, or between the 100% and 50% E_0 depths (table 1). One standard deviation of RP_m^B values for the 100% E_0 depth of cold stations was 0.06; that of warm stations was 0.26. For the 50% E_0 depth it was 0.06 for the cold stations and 0.23 for the warm stations. For stations A, B, and C, RP_m^B was relatively constant from the sea surface to the 10% E_0 depth, but its values were lower at the 1% E_0 depth.

DISCUSSION

The front has a clear effect on the spatial distribution of seawater properties down to more than 100 m. At 120 m, temperature (°C), Chl *a*, and O_2 were clearly lower, and nutrients were higher at the north than at the south of the front (figure 2). The

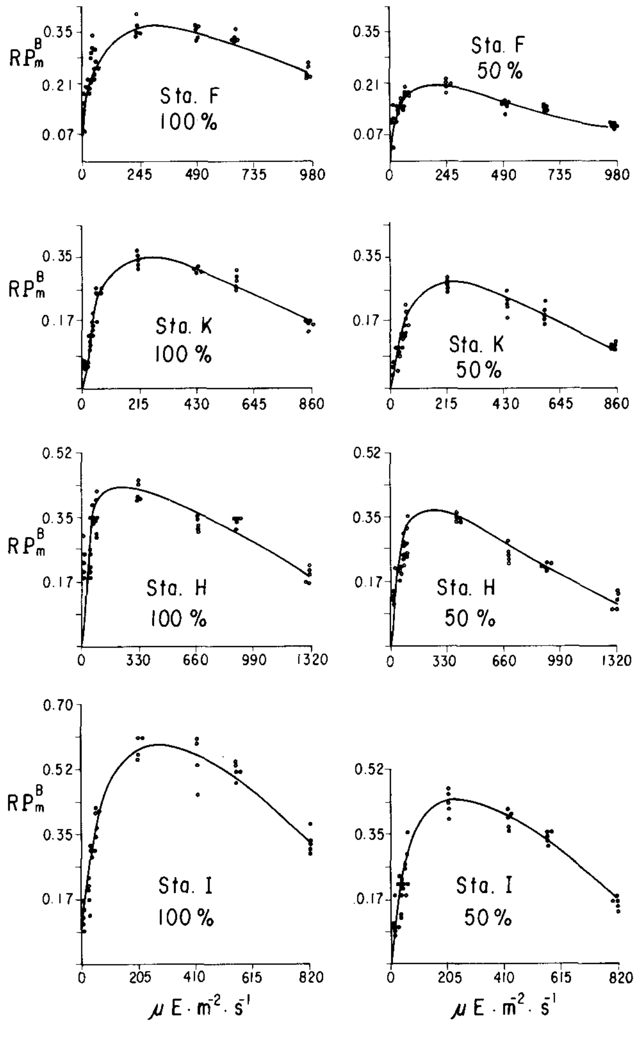

Figure 3. Examples of photosynthesis-irradiance curves for two stations at the cold side of the front (F and K), and two at the warm side (H and I). Sampled light levels (percentages) are beneath the station letters. μE means micro-Einsteins (micromoles of photons).

subsurface Chl *a* maximum is a widespread feature mainly present in summertime, but often also found during winter (Shulenberger and Reid 1981; Alvarez-Borrego and Gaxiola-Castro 1988; J. J. Cullen, Bigelow Laboratory, pers. comm.). It does not seem to occur so deep in the coastal waters of the California Current (Venrick et al. 1973). South of the front, salinity presented a subsurface minimum (Haury et al. 1986), closely coinciding with the Chl *a* maximum. South of the front, surface salinity was 33.6‰, and it was 33.3‰ at the minimum. North of the front, S‰ values were very uniform, around 33.3‰, from the sea surface to 60 m. This uniformity, a weaker thermocline, and the homogeneous vertical Chl *a* distribution at stations G, F, and J, and also from the sea surface to around 70 m all indicate relatively stronger mixing processes at the north of the front than at the south.

Integrated primary productivity for the water column was between two and three times greater to the north of the front than to the south, although integrated Chl *a* was only slightly higher at the north (data from Haury et al. 1986). The highest Chl *a* values were distributed from the sea surface to 70-m depth at the north, whereas at the south they were distributed between 70 and 120 m (figure 2b). Thus, greater integrated primary productivity at the north resulted from more light being available to phytoplankton there. Surface Chl *a* values at the north side of the front were an order of magnitude lower than those considered to be characteristic of coastal conditions. Conditions at the south of the front were similar to those reported for the central North Pacific by Hayward (1987). The subsurface O_2 maximum had values up to 0.3 ml·l^{-1} higher at the north of the front than at the south, and this also indicates higher primary productivity at the north. This O_2 maximum is a summer feature arising from the photosynthetic production of oxygen, which accumulates because the overlying density cap retards its equilibration with the atmosphere (Shulenberger and Reid 1981).

Our data do not support the hypothesis that higher primary productivity at the north was due to a higher photosynthetic potential per unit of chlorophyll. Relative assimilation numbers were practically the same at both sides of the front. Thus differences in primary productivity across the front are not due to differences in light adaptation of the phytoplankton communities. At the north, the 1% E_0 depth was well into the nutricline. However, this greater nutrient availability did not cause higher RP^B_m's.

Light saturation, or optimum light, for samples from 50% and 100% light levels was reached in most cases at 22%–28% E_0 (figure 3). This indicates phytoplankton's adaptation to relatively low light levels, and, in turn, its relatively long residence times at depths higher than those from which it was sampled. The phytoplankton sampled from 0–8-m depth may have moved up and down the water column to depths at least greater than 20 m. Falkowski (1983) examined the hypothesis that the recent light history of phytoplankton contains information about vertical mixing processes in the euphotic zone. He used a model to estimate vertical displacement rates of phytoplankton in the New York Bight. Lewis et al. (1984) concluded that the vertical mixing induced by turbulence largely controls the photosynthetic performance of algae in nature. RP^B_m

values of the 1% E_0 depth at stations A, B, and C (table 1) were lower than those of shallower depths. This was due to phytoplankton's greater residence time at depth in the first case. When phytoplankton become conditioned to lower irradiances, assimilation numbers decrease (Prézelin and Matlick 1980; Falkowski 1981).

Prézelin et al. (1987) studied the diurnal changes of assimilation numbers for phytoplankton communities sampled from the 80%, 10%, and 1% E_0 depths, across a coastal front in the Southern California Bight. Our results agree with those of Prézelin et al. in that, contrary to previous reports of netplankton flagellates dominating frontal boundaries, the nannoplankton was the most abundant size fraction.

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HOLOPLANKTONIC POLYCHAETES FROM THE GULF OF CALIFORNIA: AUGUST–SEPTEMBER 1977

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ABSTRACT

This study is based on zooplankton samples collected by Instituto Nacional de Pesca, México (August–September 1977) with a standard open net, at 41 stations in the epipelagic region of the Gulf of California. The seventeen species of holoplanktonic polychaetes that were determined represent new records from this region. *Tomopteris planktonis*, with a relative abundance of 73%, and 85% of occurrence, was the dominant species.

With respect to their biogeographical affinities, most species belong to a subtropical-tropical pattern, three species are true cosmopolitans, and two have warm-water affinities. The data agree with the general patterns of distribution recorded for other groups of zooplankton in the epipelagic region of the Gulf of California.

RESUMEN

Este estudio se basó en las muestras de zooplancton recolectadas por el Instituto Nacional de Pesca, México, en agosto-septiembre de 1977, con una red estandar, en 41 estaciones en la región epipelágica del Golfo de California. Se determinaron diecisiete especies de poliquetos holoplantónicos, que constituyen nuevos registros para esta región. *Tomopteris planktonis* fue la especie dominante, con una abundancia relativa de 73% y una ocurrencia de 85%.

Por sus afinidades biogeográficas la mayoría de las especies pertenecen al patrón subtropical-tropical, tres especies son verdaderamente cosmopolitas, y dos tienen afinidad por aguas cálidas. Estos datos coinciden con los patrones generales de distribución observados en otros grupos del zooplancton en la región epipelágica del Golfo de California.

INTRODUCTION

Little information is available on the distribution of the pelagic polychaetes from the Gulf of California. Of the pelagic forms of benthic species, species of the families Nereidae and Syllidae were recorded by Gravier (1901), who described a Heteronereid form collected by Diguet between Loreto and Carmen islands; Treadwell (1929) described *Ceratonereis singularis* from San José and Carmen islands; and Steinbeck and Ricketts (1971) recorded pelagic forms of *Ceratonereis tentaculata*, *Platynereis polis-calma*, *P. agassizi*, *Perinereis* sp., *Neanthes* sp., and a pelagic form of *Amblyosyllis* sp. from La Paz and Cabo San Lucas.

No records of holoplanktonic species of the families Tomopteridae, Alciopidae, Lopadorhynchidae, Typhloscolecidae, Pontodoridae, and Iospilidae have been found.

In general, knowledge of the pelagic polychaetes in the Pacific Ocean is contained in a few papers. Dales (1957) included literature records and reported the distribution of the species in the northeast Pacific, from Cape Disappointment, Oregon (about 47°N), to Punta Eugenia, Mexico (about 27°N). Tebble (1962) analyzed the distribution of these animals in the North Pacific, and Fernández (1983) in the Eastern Tropical Pacific. The purpose of this report is to extend our knowledge of the distribution patterns of these annelids to the Gulf of California.

METHODS

The plankton samples examined were collected from the R/V *Antonio Alzate*, Instituto Nacional de Pesca, México, between August 27 and September 6, 1977, on Cruise AA-77-04 in the Gulf of California. The locations of the stations from which samples were collected are shown in figure 1. Oblique net tows were taken from the epipelagic region (0–200 m) with a standard open net (1-m diam., 0.5-mm mesh size) fitted with a flowmeter in its mouth. The samples were preserved in 4% seawater Formalin and neutralized with a borax-saturated solution. The pelagic polychaetes were sorted out from the total sample, identified, and counted. Estimates of abundance were standardized to 1000 m^3 of water strained; ranges of abundance follow Frontier (1969): 1–3, rare; 4–18, low; 19–80, intermediate; and 81–350, high.

A report containing hydrographic data has been issued for *Antonio Alzate* Cruise AA-77-04 by Alvarez (1988). The distribution of temperature and salinity isolines at 10-m and 50-m depths are shown in figures 2 and 3.

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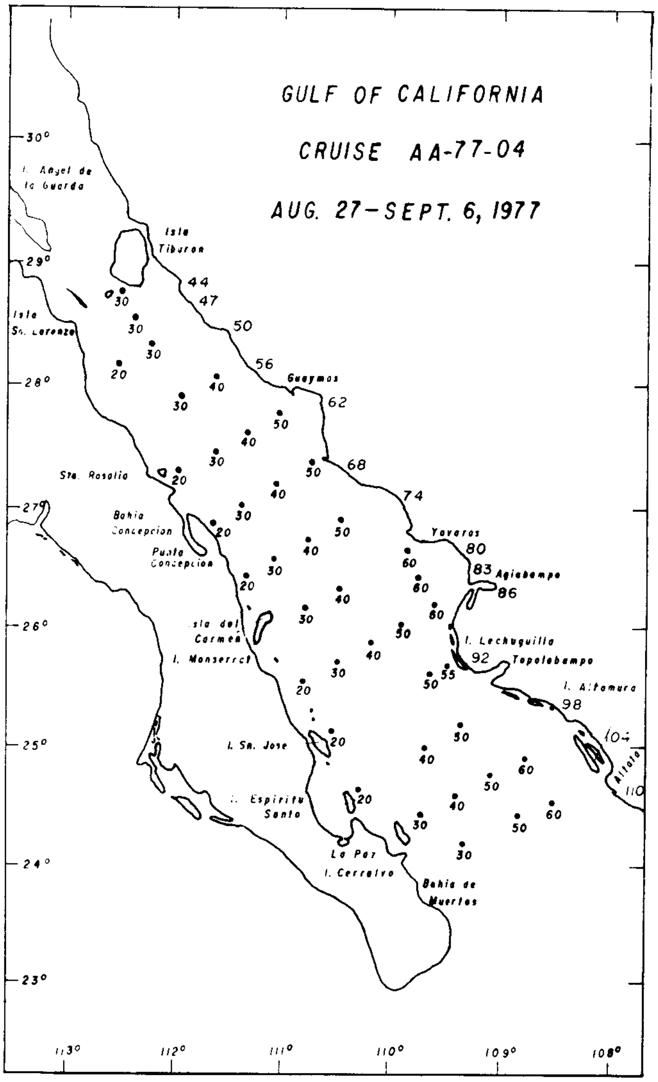

Figure 1. Locations of stations for zooplankton sampling. Numbers along the coast designate latitudinal transects.

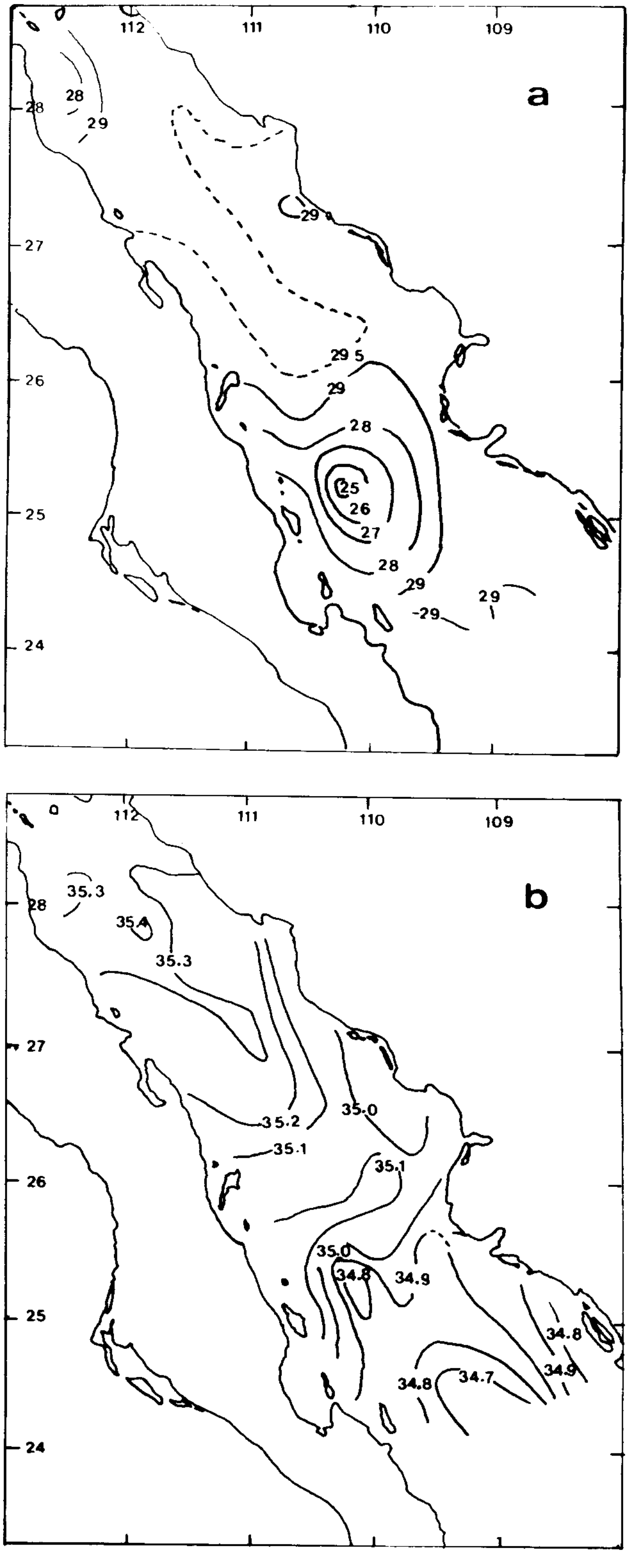

Figure 2. Distribution of isolines at 10-m depth in the Gulf of California: *a*, temperature; *b*, salinity (from Alvarez 1988).

RESULTS

Seventeen species were determined from the samples; they belong to twelve genera and five families of holoplanktonic polychaetes, which are listed in table 1. Dales and Peter (1972) provide a synopsis of the species belonging to these families. These species had not been previously recorded from the Gulf of California; their ranges of distribution have now been extended to this biogeographically important region.

One species, *Tomopteris planktonis*, clearly dominated in the survey area, being the most abundant and widespread; it showed an overall relative abundance of 73%, and an occurrence of 85% (figure 4). In most samples *T. planktonis* had intermediate abundance, but at four localities in the center of the middle region of the gulf, it had high abundance (figure 5).

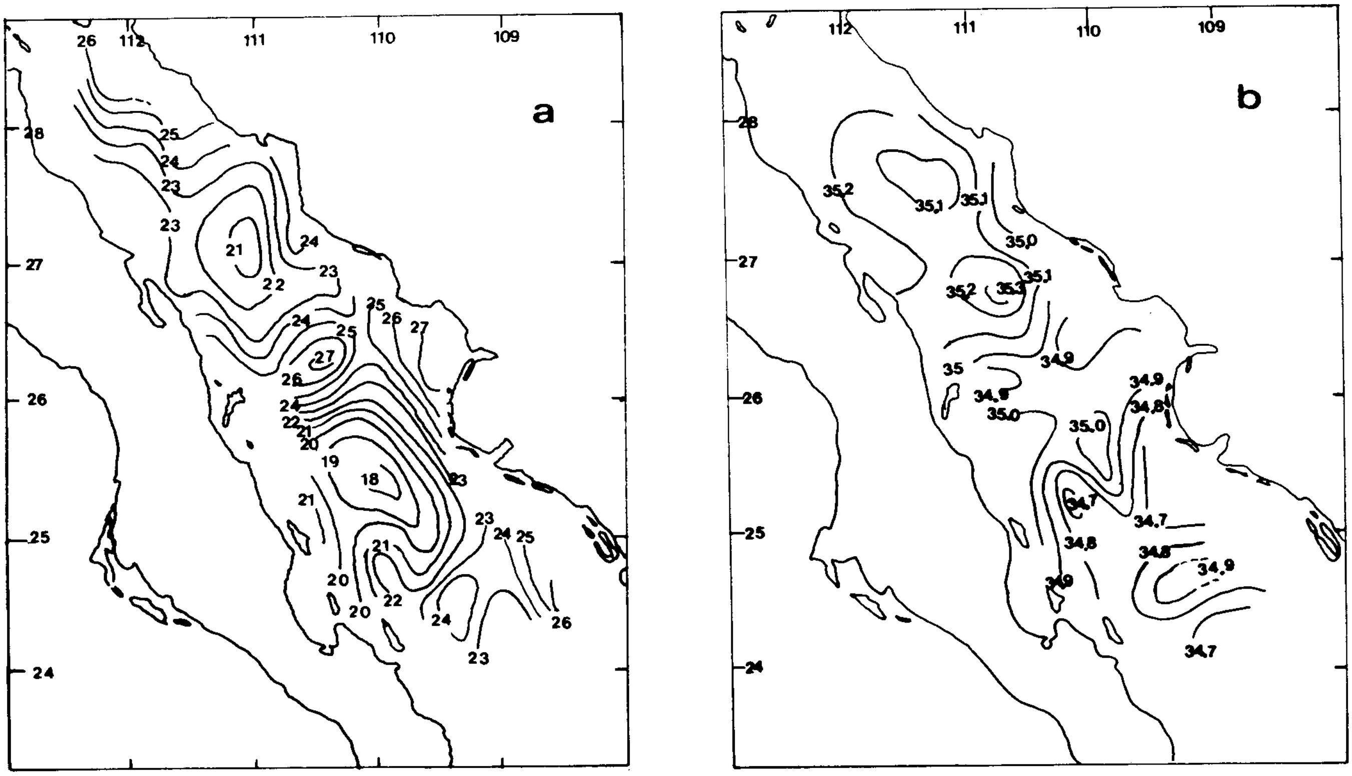

Figure 3. Distribution of isolines at 50-m depth in the Gulf of California: *a*, temperature; *b*, salinity (from Alvarez 1988).

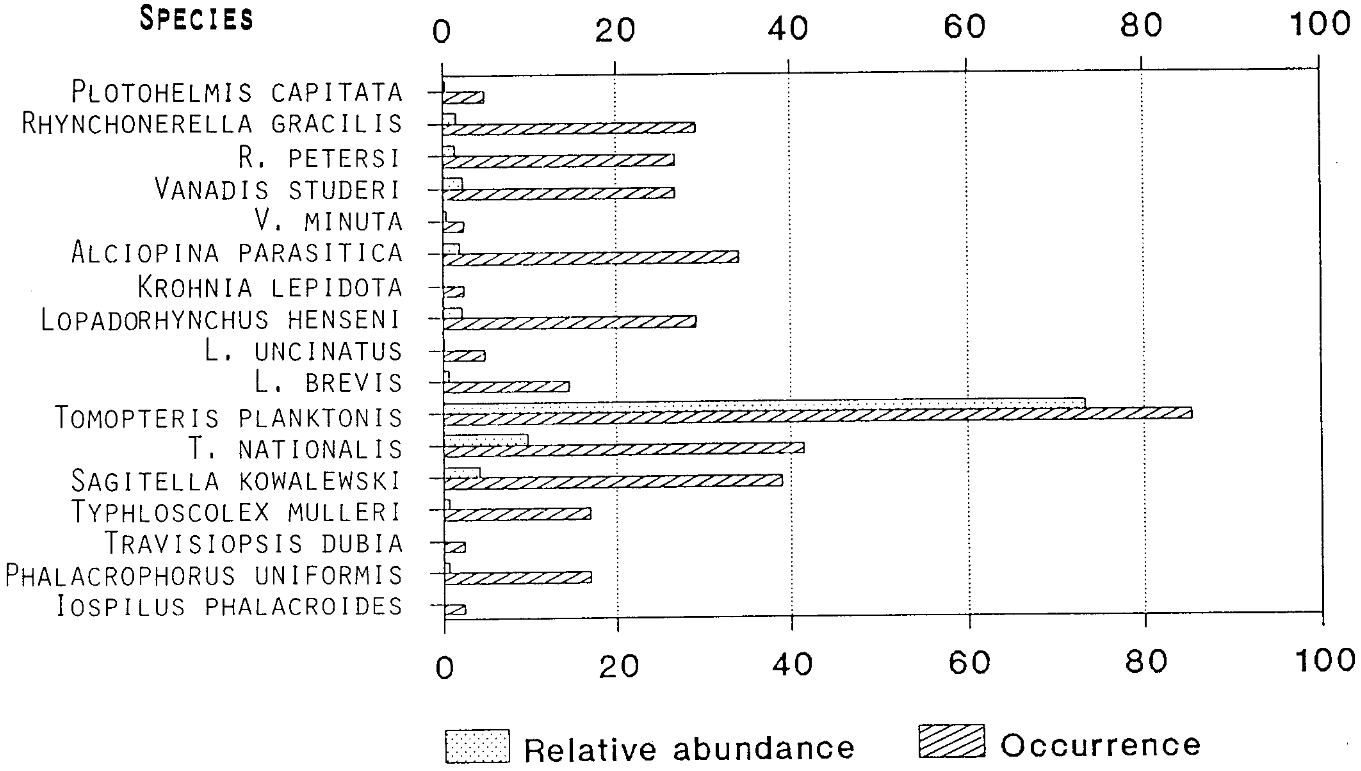

Figure 4. Relative abundance and occurrence of the species of holoplanktonic polychaetes from the Gulf of California during August–September 1977.

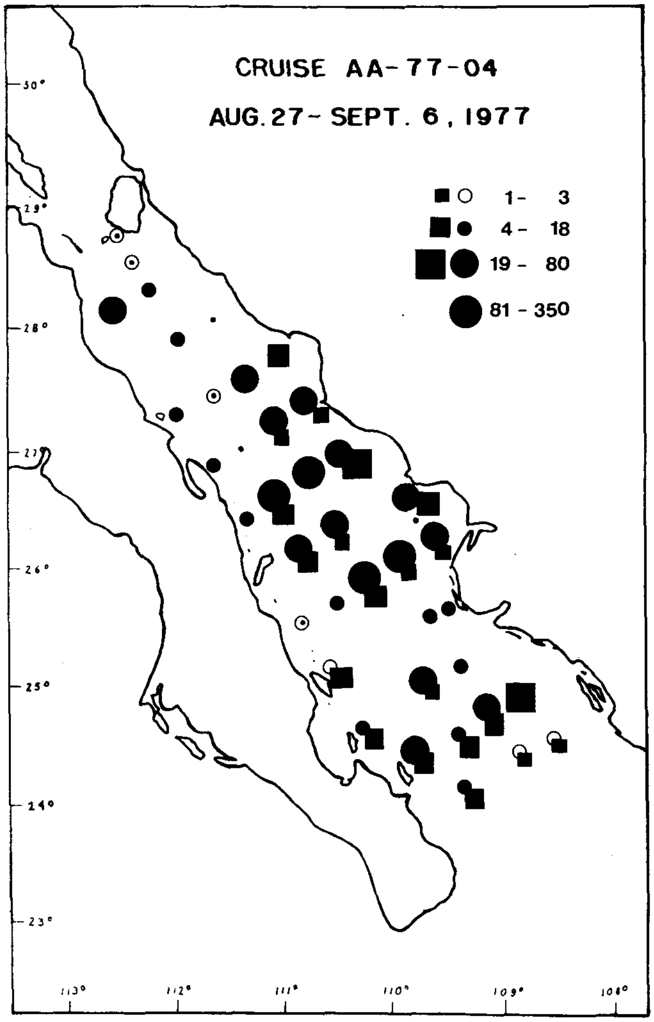

Figure 5. Distribution and density (individuals/1000 m³) of *Tomopteris planktonis (circles)* and *T. nationalis (squares)*.

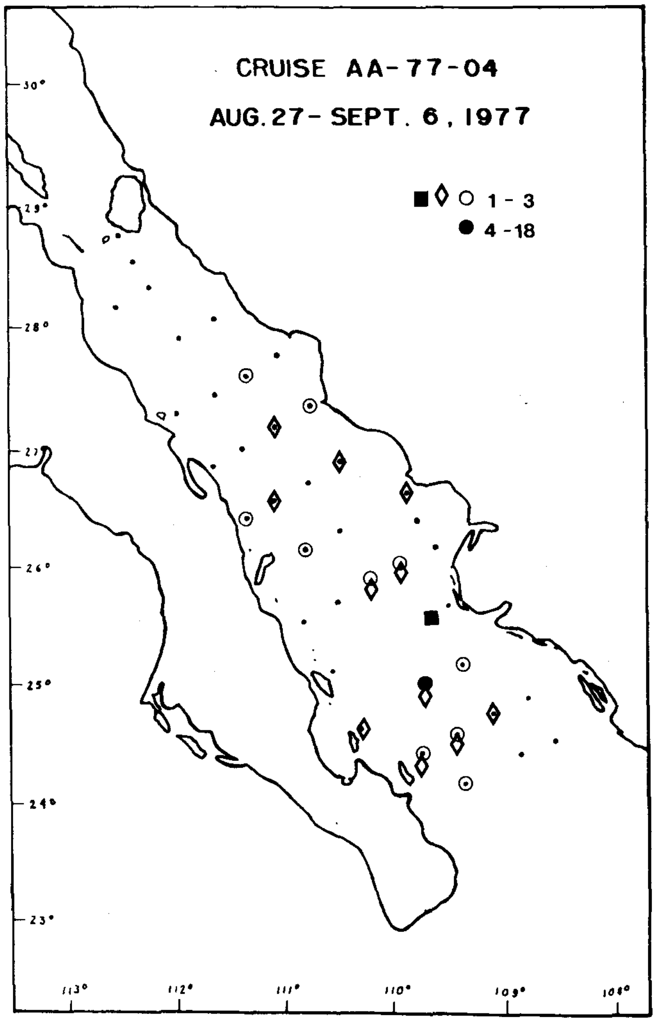

Figure 6. Distribution and density (individuals/1000 m³) of *Sagitella kowalewski (circles)*, *Typhloscolex mulleri (diamonds)*, and *Travisiopsis dubia (squares)*.

TABLE 1
New Records of Holoplanktonic Polychaeta from the Gulf of California

Family Tomopteridae
Tomopteris planktonis
T. nationalis
Family Typhloscolecidae
Typhloscolex mulleri
Sagitella kowalewski
Travisiopsis dubia
Family Alciopidae
Alciopina parasitica
Rhynchonerella petersi
R. gracilis
Vanadis studeri
V. minuta
Plotohelmis capitata
Krohnia lepidota
Family Lopadorhynchidae
Lopadorhynchus henseni
L. brevis
L. uncinatus
Family Iospilidae
Iospilus phalacroides
Phalacrophorus uniformis

Second in order of abundance and of occurrence (50%) was another species of Tomopteridae, *T. nationalis* Apstein, 1900; this was found between Guaymas (28°N, eastern side of gulf), and the southernmost transects of the survey area (across the gulf, more or less between 23°40′ and 24°40′N) where it was consistently present. Abundance was low at most stations, but at an eastern locality—offshore of Altamura Island (25°N)—it had an intermediate abundance (figure 5). Although most Pacific Ocean records treat *T. nationalis* as *T. apsteini* Rosa, 1908, Day (1967) has stated that *T. apsteini* is probably synonymous with *T. nationalis*, and Fernández (1983) has agreed with this opinion.

Third in order of occurrence (39%) in the study region was *Sagitella kowalewski*. This species had a distribution similar to that of *T. nationalis* and was usually present in low abundance; it was somewhat more abundant at a few stations from the mid-gulf region (figure 6).

The following species had a range of occurrence between 15% and 31%, and were low in abundance:

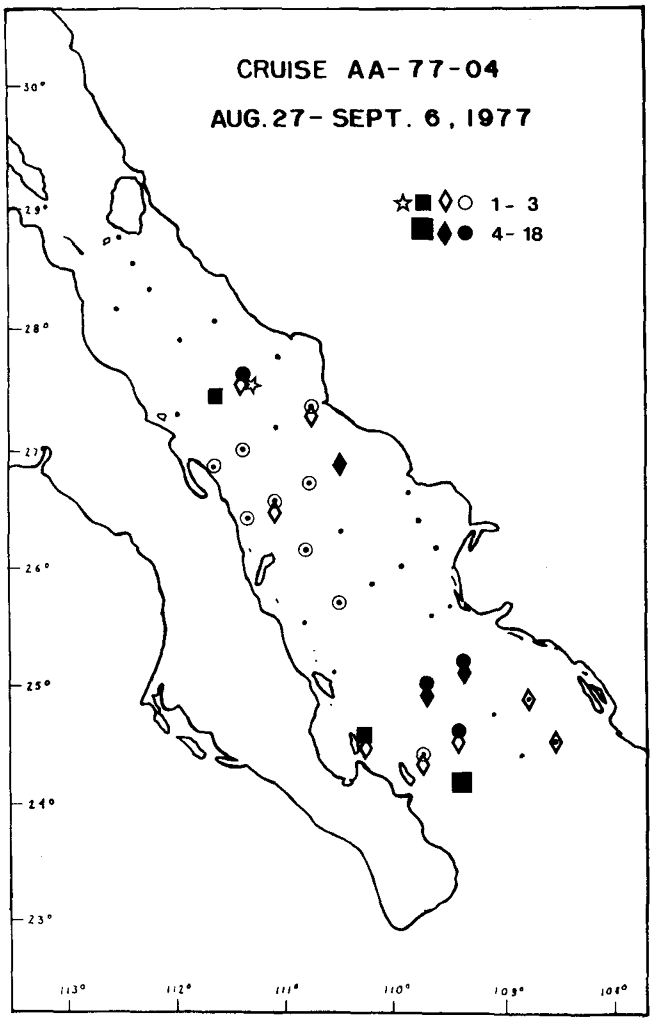

Figure 7. Distribution and density (individuals/1000 m^3) of *Alciopina parasitica* (circles), *Plotohelmis capitata* (squares), *Vanadis studeri* (diamonds), and *Krohnia lepidota* (star).

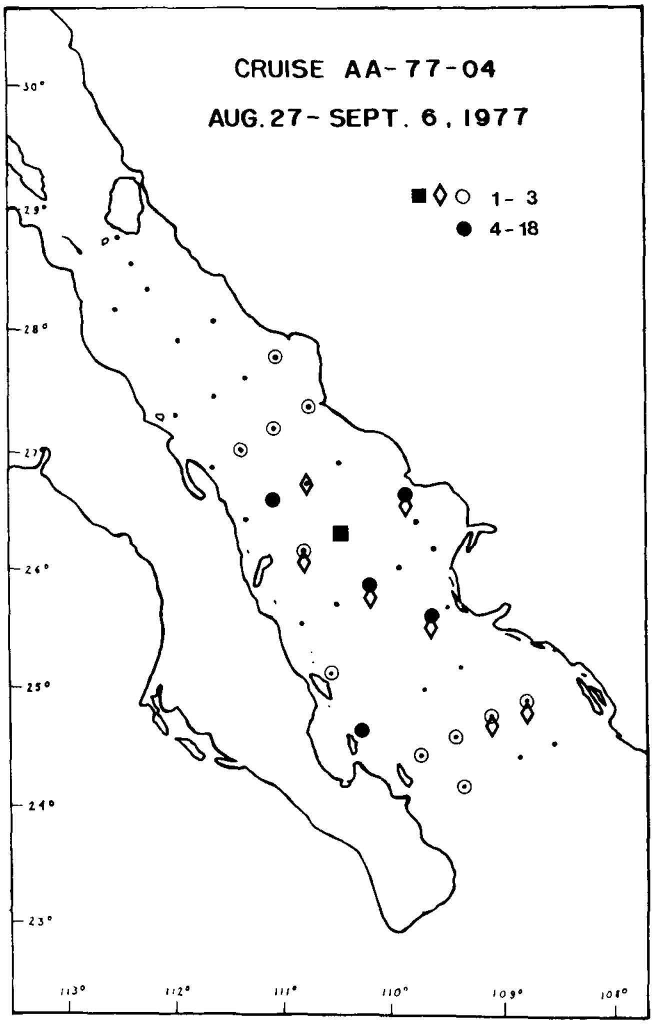

Figure 8. Distribution and density (individuals/1000 m^3) of *Rhynchonerella gracilis* (circles), *R. petersi* (diamonds), and *Vanadis minuta* (square).

Alciopina parasitica, *Lopadorhynchus henseni*, *Rhynchonerella petersi*, *R. gracilis*, *Vanadis studeri*, *Phalacrophorus uniformis*, *Typhloscolex mulleri*, and *Lopadorhynchus brevis*. Some of these were distributed mainly in two areas: the middle region of the gulf (26°–27.5°N) over the Guaymas Basin, and the southern region (24°–25.5°N) encompassed by lines of stations between Espíritu Santo and San Ignacio islands and between Cerralvo and Altamura islands (figures 7–9). The intermediate area between these two regions showed significant temperature variations at 10-, 30-, and 50-m depths, as compared to the generally warmer temperatures of the rest of the survey region during the sampling period (figures 2 and 3). In this study *T. mulleri* and *Alciopina parasitica* were restricted to the two southern thirds of the survey area (figures 6 and 7).

Plotohelmis capitata, with low abundance, was found at three stations: the first was midway between Santa Rosalía and Guaymas; the others were in the southwestern part of the gulf (figure 7). This species was first recorded in the Pacific Ocean as *Rhynchonerella fulgens* (Izuka 1914).

Lopadorhynchus uncinatus, *Vanadis minuta*, *Krohnia lepidota*, *Iospilus phalacroides*, and *Travisiopsis dubia* were each found at one or two localities, in low abundance. Of these five species, only *K. lepidota* was present in the northern region, in one sample collected west of Guaymas (figure 7). The rest of the above species were mainly restricted to the southern two-thirds of the survey area (figures 6–9).

DISCUSSION

Tomopteris planktonis is a cosmopolitan species known from all explored water masses in the world. However, in the North Pacific Ocean, Tebble (1962) found it only in the Subtropical and Transition zones, restricted in the latter to the southern bound-

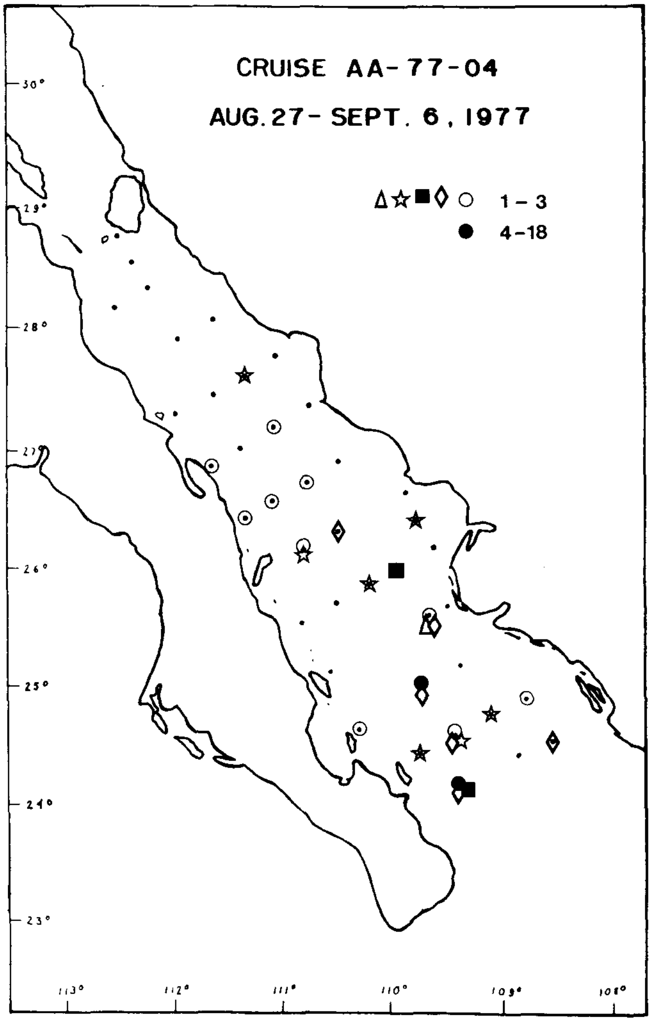

Figure 9. Distribution and density (individuals/1000 m^3) of *Lopadorhynchus henseni (circles)*, *L. brevis (diamonds)*, *L. uncinatus (squares)*, *Phalacrophorus uniformis (stars)*, and *Iospilus phalacroides (triangles)*.

ary of the Subarctic zone. It is also interesting to note that he found it to be absent from the California Current region. However, Tebble (1962) stated that the first record of *T. planktonis* from the North Pacific was made by Dales (1955), as *T. cavalii* from Monterey Bay; under the same name, Dales (1957) reported it as being sparsely distributed in surface waters throughout the California Current, generally most common 400–500 km offshore. Fernández (1983) found *T. planktonis* widely distributed in the Eastern Tropical Pacific during all bimonthly working periods (1967–68) of the EASTROPAC Program. It was most abundant in the equatorial region, especially near the Galápagos Islands.

Tomopteris nationalis was first recorded from the Pacific Ocean by Dales (1957). He reported a single specimen from the California Current, at 28°40.5′N and 122°46′W. In that paper he did not report *T. apsteini*, but noted that it was found by Rosa (1908) off the Mexican coast. However, in Rosa's report the name "*Tomopteris apsteini* nom. nov." was used only to redescribe specimens from Messina, Italy, belonging to the Hamburg Museum. Rosa (1908) had recorded *Tomopteris (Johnstonella) Aloysii Sabaudiae* Rosa, 1907, from off Acapulco, Mexico (13°24′N and 97°22′W) indicating that "questa specie sembra affine alla *T. nationalis*, forma atlantica". Tebble (1962) also mistakenly attributed to Rosa (1908) the first record of *T. apsteini* in the North Pacific on the basis of the collection from off Mexico. He found this species in few stations across the North Pacific in the Subtropical zone, between 135°W and the Japan coasts. Izuka (1914) reported *T. apsteini* from Misaki, Japan, but his description does not mention particular diagnostic characters (rosettes, spur gland on the ventral side of the neuropodia). Because of this, Imajima and Hartman (1964) questioned the specific identity of Izuka's specimens. Fernández (1983) found *T. nationalis* in the Eastern Tropical Pacific during the five bimonthly working periods of the EASTROPAC Program, with scattered distribution and moderate abundance.

Sagitella kowalewski is a true cosmopolitan species, and has been reported from the Pacific Ocean by Berkeley (1930), Okuda (1937, 1938 as *Plotobia paci-chaeta*), Treadwell (1943), Uschakov (1955, 1957a, 1972), Dales (1957), Berkeley and Berkeley (1960), Tebble (1962), and Fernández (1983).

Typhloscolex mulleri is a cosmopolitan species recorded from all regions of the world. It is widespread in the Pacific Ocean (Treadwell 1943; Uschakov 1952, 1955, 1957a, 1957b; Berkeley and Berkeley 1948, 1957, 1960; Dales 1951; Tebble 1962; and Fernández 1983).

Alciopina parasitica has also been found in the Pacific Ocean, mainly in the tropical region; in the subtropical region it is only known from extensions of warm waters. Chamberlin (1919) recorded it (as *Corynocephalus paumotamus*) from the Eastern South Pacific Ocean. Treadwell (1943) reported a wider distribution, between 40°N and 40°S. Uschakov (1972) cited four localities off Japan and at 45°N, 165°E, possibly in an extension of the Kuroshio Current. Recently, Fernández (1983) showed that it has a wider distribution in the Eastern Tropical Pacific. This species was not recorded in the California Current by Dales (1957) or in the North Pacific by Tebble (1962).

Rhynchonerella petersi, *R. gracilis*, *Phalacrophorus uniformis*, and *Lopadorhynchus brevis* are widely distributed in tropical and subtropical regions of the Pacific Ocean. Several authors have recorded them from various locations: *R. petersi*, Uschakov (1957a, as *Callizona setosa*), Tebble (1962), and Fernández (1983); *R. gracilis*, Izuka (1914, as *Callizona japonica*), Uschakov (1957a, as *C. nasuta*), Berkeley and Berkeley (1960), Tebble (1962), and Fernández (1983); *P. uniformis*, Treadwell (1943, as *P. attenuatus*), Tebble (1962), and Fernández (1983); *L. brevis*, Chamberlin (1919, as *L. parvum*), Dales (1957), Berkeley and Berkeley (1958), Tebble (1962), and Fernández (1983).

Because *Vanadis studeri* may have been confused with *V. minuta* (Orensanz y Ramírez 1973), and because *Lopadorhynchus henseni* may resemble *L. krohni* (Kim 1967), their geographical distributions should be examined more carefully. However, they may have warm-water affinities.

Plotohelmis capitata is a common species in the Malacca Strait (Fauvel 1939). Also it has been reported as *P. capitata* (Dales 1960) from the Malacca Strait and South China Sea, and as the most common species off Peru (Berkeley and Berkeley 1961, 1964). It has a wide distribution in the Eastern Tropical Pacific (Fernández 1983). As in the case of *A. parasitica*, it was not recorded from the California Current by Dales (1957) or from the North Pacific by Tebble (1962).

In general, there are few records for the following species in the Pacific Ocean: *Lopadorhynchus uncinatus* was reported by Treadwell (1943, as *L. varius*), Dales (1955, 1957), Berkeley and Berkeley (1958, 1960), Tebble (1962), and Fernández (1983); *Vanadis minuta* by Treadwell (1906), Dales (1957), Tebble (1962), and Fernández (1983); *Krohnia lepidota* was recorded by Chamberlin (1919, as *Rhynchonerella cincinnata*), Treadwell (1943, as *Callizona pigmenta*), Tebble (1962), and Fernández (1983); *Travisiopsis dubia* was reported by Dales (1960), Tebble (1962), and Fernández (1983). There are few records of *Iospilus phalacroides*, and its world distribution is not well known.

The biogeographical affinities of the taxa are those to be expected for the Gulf of California. Most species show a subtropical-tropical pattern; three are truly cosmopolitan taxa; and two are warm-water species. No species from cold or temperate water were recorded (table 2). Species with a subtropical-tropical pattern are also prominent among the gulf's foraminifera, chaetognaths, calanoid copepods, hyperiid amphipods, and euphausiids (Brinton et al. 1986).

Tomopteris planktonis was the dominant polychaete and the only widely distributed species within the area of study. Its distribution extended northward in the gulf to at least Tiburón Island, where sharp annual temperature gradients are developed. Its distribution is probably due to broad ecological tolerance, as inferred from its cosmopolitan pattern. The remaining sixteen species were distributed from the Santa Rosalía–Guaymas transect southwards.

TABLE 2

Relative Abundance, Occurrence, and Biogeographical Affinities of Holoplanktonic Polychaetes from the Gulf of California

Species	Relative abundance	Occurrence (%)	Biogeogr. types
Tomopteris planktonis	73.0	85	Cosmopolitan
T. nationalis	10.0	50	Subtropical-tropical
Sagitella kowalewski	4.5	39	Cosmopolitan
Alciopina parasitica	2.0	34	Tropical
Lopadorhynchus henseni	2.0	29	Tropical ?
Rhynchonerella gracilis	1.5	29	Subtropical-tropical
R. petersi	1.4	27	Subtropical-tropical
Vanadis studeri	2.3	27	Tropical ?
Phalacrophorus uniformis	2.0	17	Subtropical-tropical
Typhloscolex mulleri	2.0	17	Cosmopolitan
Lopadorhynchus brevis	1.5	14	Subtropical-tropical
Plotohelmis capitata	0.5	7	Tropical
Lopadorhynchus uncinatus	0.1	4	Subtropical-tropical
Vanadis minuta	0.1	4	Subtropical-tropical
Krohnia lepidota	0.1	4	Subtropical-tropical
Travisiopsis dubia	0.1	4	Subtropical-tropical

The warm-water species *Alciopina parasitica* and *Plotohelmis capitata* were found nearly to 28°N, near Guaymas. This distribution may be explained by the summer circulation pattern, in which tropical water moves inwards from the Eastern Pacific Ocean (Roden 1958; Roden and Groves 1959; Alvarez-Borrego and Schwartzlose 1979). Both species are widely distributed in the Eastern Tropical Pacific (Fernández 1983). Similar summer intrusions have been observed among other zooplanktonic taxa such as tropical species of euphausiids (Brinton and Townsend 1980).

Summer water temperatures could be responsible for the complete absence of cold- and temperate-water species in these samples; temperatures in the epipelagic zone are highest during the summer (Robinson 1973; Alvarez 1988). Temperate species may be replaced in surface water by tropical taxa and submerge to deeper layers as do certain calanoid copepods (Fleminger, in Brinton et al. 1986).

An interesting feature of the general distribution of most members of the family Alciopidae is their absence from stations along the transect San José Island–Punta San Ignacio (25°N). Their distribution is apparently interrupted (figures 7 and 8). In this area water temperatures have a strong gradient (18°–27°C in the 50–0-m layer), according to data from Alvarez (1988), as shown in figures 2 and 3.

All seventeen species collected in the Gulf of California have also been recorded from the Eastern Tropical Pacific Ocean (Fernández 1983); twelve are known from the subtropical, transition, and subarctic regions of the North Pacific (Tebble 1962); and seven are reported from the California Current (Dales 1955, 1957). These data are in agreement with those for a number of other pelagic animals when the Gulf of California is defined as part of the Tropical Eastern Pacific faunistic region (e.g., Walker 1960).

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SARDINE AND ANCHOVY SPAWNING AS RELATED TO TEMPERATURE AND UPWELLING IN THE CALIFORNIA CURRENT SYSTEM

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ABSTRACT

Sardine and anchovy spawning was analyzed regarding its relation to sea-surface temperature and upwelling, using CalCOFI cruise data and Bakun's upwelling indices.

Previous reports of temperature ranges for sardine and anchovy spawning have not taken into account the distribution of SST and have mostly referenced the cooler spawning area of the species. By obtaining the proportion of positive stations to total sampled stations for each tenth of a degree Celsius in the SST distribution, we were able to discriminate the ranges of preferred temperatures of spawning for both species. Sardines spawn in a much wider temperature range (13°–25°C) than anchovy (11.5°–16.5°C). Two maxima of spawning occur in the California Current: at 15°C and 23°C. An additional peak is present in the Gulf of California at about 19°C. Only one maximum is evident for anchovy spawning, at about 14°C.

The distribution of spawning as a function of upwelling was also analyzed for both species. There is a maximum for sardines at intermediate values of upwelling. There are two maxima for anchovy: a minor one at low levels of upwelling and a major one at the maximum values of upwelling. We conclude that sardines are eurythermic as compared to anchovies, but spawn only at intermediate values of upwelling, whereas anchovies are stenothermic but spawn at much wider ranges of upwelling, particularly at low and high values. The differences suggest exclusive competition, but more detailed analyses are needed.

RESUMEN

Se analizó el desove de sardina y anchoveta con respecto a su relación con la temperatura superficial del mar y las surgencias, utilizando los datos de los cruceros CalCOFI y los índices de surgencia desarrollados por Bakun.

Los intervalos de temperaturas de desove de sardina y anchoveta que se habían señalado anteriormente no tuvieron en cuenta la distribución de la temperatura superficial; además, se habían referido mayormente al área más fría de la distribución del desove. Mediante la obtención de la proporción de las estaciones positivas a las totales por cada décima de grado en la distribución de frecuencias de la temperatura superficial, fué posible discriminar los intervalos de temperaturas preferentes para el desove de ambas especies. Las sardinas desovan en un intervalo de temperatura mucho más amplio (13° a 25°C) que el de anchoveta (11.5° a 16.5°C). Se presentan dos máximos de desove de sardina en la Corriente de California: uno a 15°C y otro a 23°C. Otro máximo adicional se presenta en el Golfo de California a 19°C. Sólo se registró un máximo de desove en la anchoveta, alrededor de 14°C.

La existencia de tres máximos no es, proponemos, un fenómeno inherente de la especie, sino una característica inducida ambientalmente. Creemos que algún factor relacionado con las surgencias puede ser el responsable de esta desusual distribución.

Se analizó también la distribución del desove de ambas especies en función de las surgencias; hay un máximo para la sardina a niveles intermedios de surgencia. Hay dos máximos para la anchoveta: uno menor que se localiza a niveles bajos de surgencia, y el más importante, que ocurre a niveles máximos de surgencia.

Concluimos que las sardinas son euritérmicas en comparación con las anchovetas, pero que desovan a niveles intermedios de surgencia, mientras que las anchovetas son estenotérmicas pero desovan en una amplitud mayor de valores de surgencia, particularmente a valores bajos y altos. Los resultados sugieren exclusión competitiva, pero se necesitan análisis más detallados.

INTRODUCTION

Environmental temperature has long been considered the most important factor affecting marine organisms; their geographical distribution is closely associated with the latitudinal temperature gradient. Temperature affects the rate of metabolic processes. Cold winter temperatures can depress the activity of

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poikilotherms to a point where there is no possibility for acclimation. Conversely, summer temperatures can increase oxygen consumption to an extent that metabolic demands exceed energy reserves. Thus, tolerance to temperature is an important factor regulating the distribution of fishes (Levinton 1982).

Massive stocks of pelagic fishes are possible only in areas where productivity is high. Upwelling areas (including the California–Baja California coast) are among the most productive in the world, with upwelling being recognized as a fundamental cause (Nelson 1979).

Sardines (*Sardinops*) and anchovies (*Engraulis*) are both subtropical species, coexisting particularly in areas of subarctic and tropical mixing, where they constitute some of the most voluminous fisheries species in the world. Recent papers have emphasized their ample and synchronous fluctuations of abundance and geographical extension (Lluch et al. 1989; Parrish et al. 1989). The connection of these changes to temperatures has been hypothesized (Crawford et al., in press; Lluch et al., in press). In this paper, we analyze temperature ranges associated with the spawning of both species off the west coast of North America.

Adult sardines' tolerance for temperature seems to be very wide. On the cold side, Smith (1978) states that sardines feeding during the summer off British Columbia may have been at temperatures "far colder" than 13°C. On the other hand, temperatures higher than 25°C are commonly associated with sardine catches in Magdalena Bay (Casas 1987), and there are unpublished reports of 28° temperatures associated with sardine catches. Parrish et al. (1989) state the range of 7° to 27° as the temperature tolerance of adult *Sardinops*.

Regarding spawning temperatures, Tibby (1937) concluded that the optimum for sardines lies between 15° and 18°, with an implied peak at 16°. Ahlstrom (1965) found similar temperature limits, with peaks between 14.7° during the 1951–56 season and 15.3° in 1958. Earlier, Ahlstrom (1954) had found that the relation between temperature and spawning was complex, pointing to a 3-degree temperature range of 13.5° to 16.5° during the season, but higher than 19° during the "off-season." He also pointed out that the minimum spawning temperature for sardines is 13°. This temperature was confirmed in his 1965 paper and by Smith (1978). Parrish et al. (1989) stated that most spawning occurs within the 13°–17° range, following Ahlstrom (1965). At the warm-water limits, Saldierna et al. (1987) reported a minimal temperature of 16.1° and a maximum of 25.6° associated with eggs and larvae in Magdalena Bay.

Hammann (in press) analyzed the temperatures associated with positive stations for sardine eggs in the Gulf of California. He found that the average SST was 19.9°, and stated that 50% of the positive stations were between 17.75° and 20°.

Data on anchovy tolerance to environmental temperature are scarce. Smith and Lasker (1978) pointed out that temperatures representative for anchovies commonly vary 4° to 6°C. Ahlstrom (1966), however, reported temperature ranges for anchovy eggs from 9.9° to 23.3°, and pointed out that most anchovy eggs were taken within a 7° range, from 12° to 18.9°; indeed, the adult limits of tolerance for temperature should be wider.

The relationship between sardine abundance and upwelling is controversial. Although the high productivity induced by nutrient-rich subsurface waters is a fundamental component of the system, many authors have pointed to the lack of relation between abundance of sardines and productivity (Ahlstrom 1965) or even to upwelling's deleterious effects on sardine abundance, operating either through offshore transport of larvae (Parrish et al. 1981) or increased water turbulence (Lasker and MacCall 1983).

DATA AND METHODS

We used data from CalCOFI cruises from 1951 through 1989, which comprise some 19,500 samples from stations shown in figure 1. Data for each sample include surface or 10-meter temperatures (as available), and number of sardine and anchovy eggs and larvae. Positive samples are those containing eggs or larvae of these species. Averaged upwelling indices were taken from Mason and Bakun (1986) and updated with data supplied by them for the points marked in figure 1.

Sardine and anchovy eggs and larvae percent frequency distributions were each divided by the corresponding overall percent SST frequency distribution.

Average upwelling indices were estimated for all of the SST range. To obtain them, we used Bakun's monthly averaged upwelling indices. We then estimated the average SSTs for the subareas shown in figure 1, compared the monthly index with the average SST in that month, and finally estimated the average for all the indices in each SST interval (0.1°C).

Average sardine egg abundance as a function of upwelling was estimated with the same monthly averaged indices mentioned above, and relating to

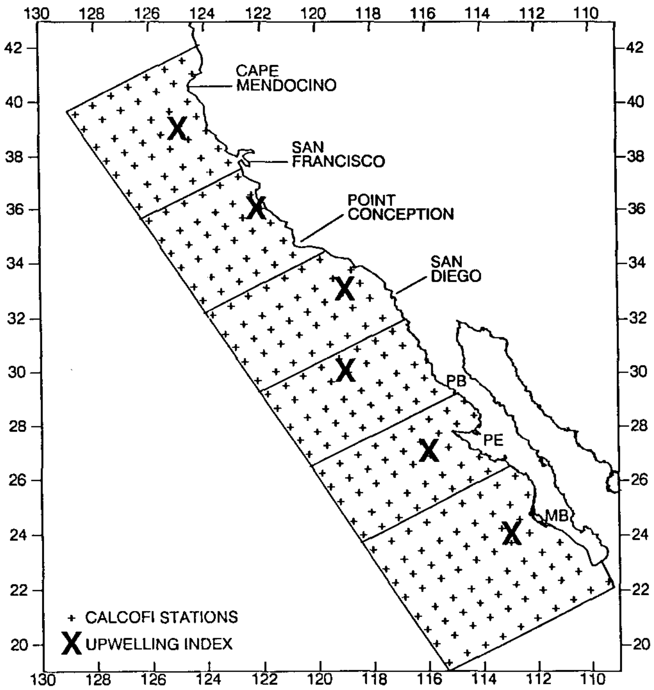

Figure 1. Area of study. The CalCOFI grid is shown as small crosses for the principal stations sampled. Large X's are locations of monthly averaged upwelling indices. Subareas were used to average SST measurements to relate them to upwelling indices. PB = Punta Baja; PE = Punta Eugenia; MB = Bahía Magdalena.

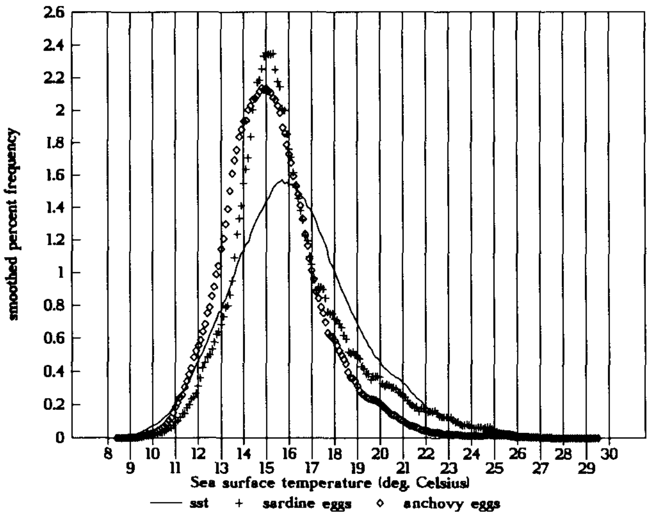

Figure 2. Percent frequency distribution of overall sea-surface temperature measurements, percent number of positive stations for sardine eggs, and percent number of positive stations of anchovy eggs. Series smoothed by 11-term running means, centered on the sixth datum.

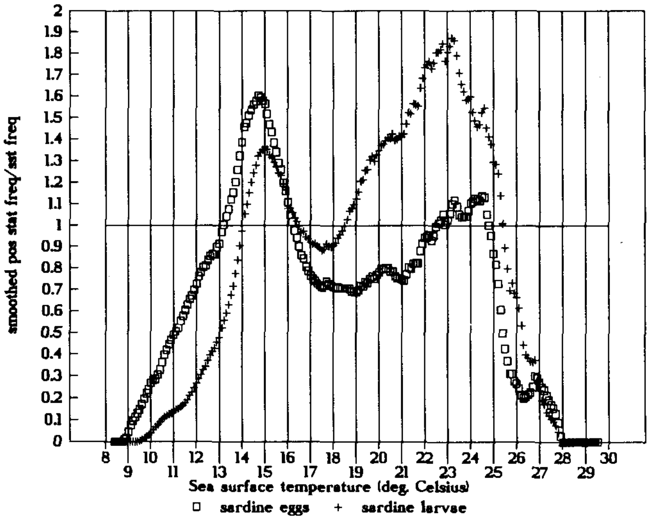

Figure 3. Quotients of the percent frequency distribution of positive stations for sardine eggs and larvae and the general SST percent frequency distribution. Series smoothed by 11-term running means, centered on the sixth datum. Horizontal line denotes baseline.

them (in intervals of 10 units) the average number of positive stations. The overall average number was estimated for each upwelling interval.

All of the series were smoothed for improved presentation, since there is high interpoint variability. We mostly used 11-term running averages centered in the sixth datum. However, we used Spencer's method (in a commercial statistical software) to smooth the upwelling indices series because of the need to preserve the extreme points. We also estimated the percent distribution of each of the series to avoid scaling problems when showing them in the same graph.

RESULTS

The percent frequency distribution of SST is shown in figure 2, together with eggs-associated percent temperature distribution (i.e., the frequency distribution of the temperature of positive stations) for both sardines and anchovy.

Figures 3 and 4 show the quotients of the percent distribution of sardine and anchovy eggs and larvae divided by the percent distribution of SST. Points above 1.0 (the baseline) are preferred temperatures for spawning, since their frequency is larger than the one expected as a function of overall SST distribution; values less than one are less frequent than the overall SST distribution.

With this transformation, differences between species become very apparent. First, the sardines' preferred spawning range is much wider, from roughly 13.5° to 25°, whereas that of anchovies is restricted to 11.5° to 16.5°. Second, sardine spawning shows two different peaks, the first at 15° and the second at 23°, whereas there is only one peak (14°) for anchovies.

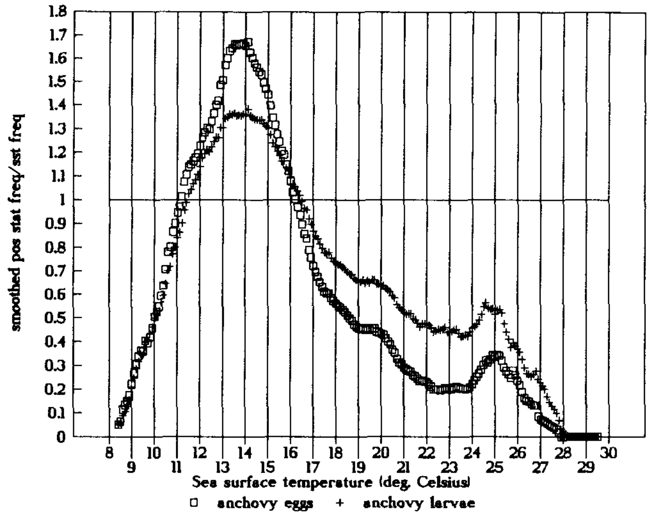

Figure 4. Quotients of the percent frequency distribution of positive stations for anchovy eggs and larvae and the general SST percent frequency distribution. Series smoothed by 11-term running means, centered on the sixth datum. Horizontal line denotes baseline.

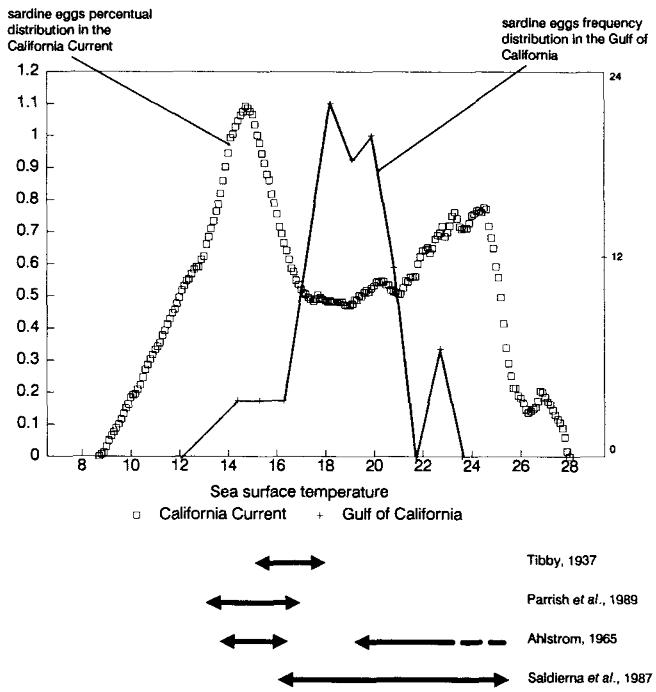

Figure 5. Summary of sardine spawning temperature ranges as reported by several authors. *Upper section*, sardine spawning in the California Current (this paper) and in the Gulf of California (from Hammann, in press). *Lower section*, temperature ranges of sardine spawning as reported by several authors.

Regarding the differences between egg and larval distributions for both sardines and anchovies, it seems evident that sardine eggs spawned below 14.5° have a diminished rate of survival. Even though there is spawning from 9° up, there seems to be a great loss under 14°. The peak distribution for this range is 14.6° for eggs, but 15° for larvae. On the contrary, anchovy eggs and larvae seem to match very closely at this cooler limit, with similar peaks for both.

Figure 5 shows the percent distribution of sardine spawning as a function of SST in the California Current and the Gulf of California (after Hamman, in press), as well as ranges as mentioned by Tibby (1937), Ahlstrom (1954, 1965), Parrish et al. (1989) and Saldierna et al. (1987).

Although there is very little information on anchovy spawning temperatures, the available reports are summarized in figure 6.

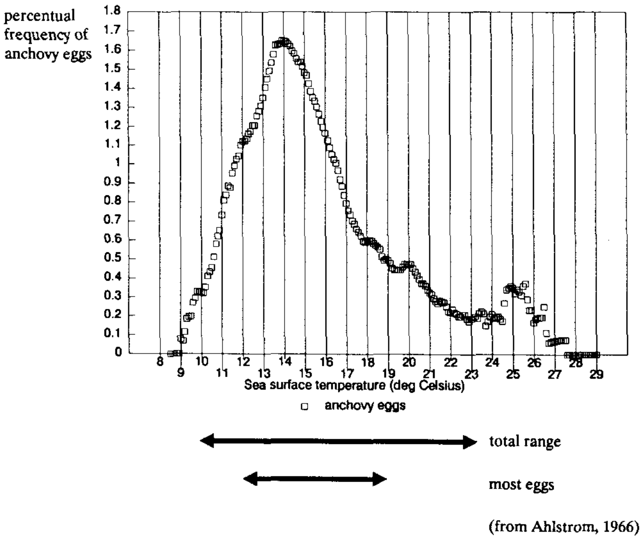

Figure 6. Summary of anchovy spawning temperature ranges. *Upper section*, anchovy spawning percent frequency distribution (this paper). *Lower section*, temperature ranges as reported previously.

Average upwelling indices as a function of SST are shown in figure 7, both as the scatter diagram and the smoothed series. The major peak occurs at 12.5°C, but the 16° peak is the most extended. High upwelling indices are associated with the 15°–18.5° range. The decline in upwelling intensity also shows the north-south gradual decline in productivity, as temperatures rise.

Spawning of both sardine and anchovy as a function of upwelling are presented in figure 8; spawning is represented by the proportion of positive to total stations associated with each of the upwelling indices. The differences are striking. There is a clear maximum for sardine spawning at intermediate values, below or above which spawning declines markedly, but there are two peaks for anchovy — a minor one at very low levels of upwelling and a major one at the higher indices.

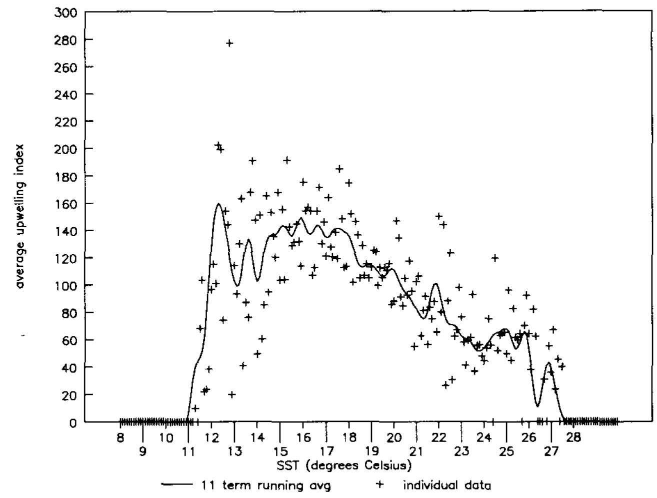

Figure 7. Average upwelling indices in the temperature domain (+) and smoothed series by Spencer's method.

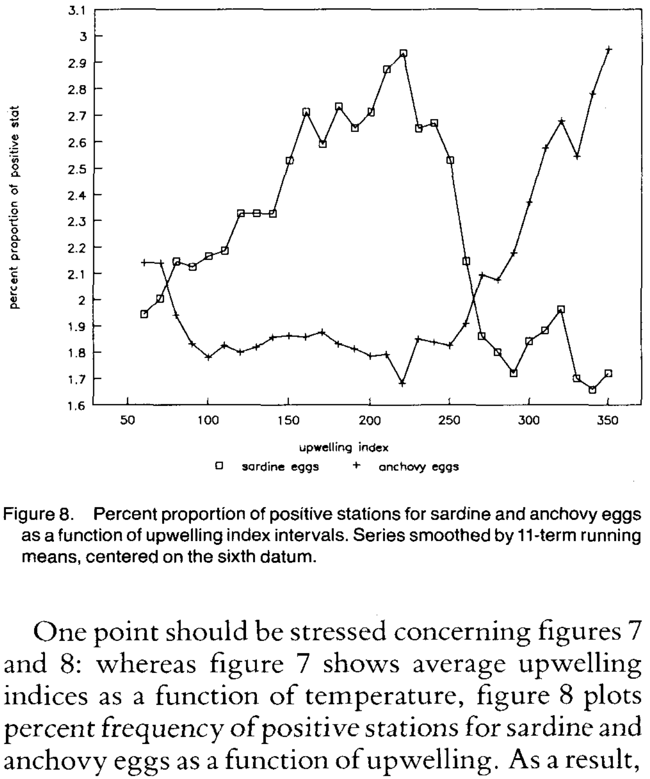

Figure 8. Percent proportion of positive stations for sardine and anchovy eggs as a function of upwelling index intervals. Series smoothed by 11-term running means, centered on the sixth datum.

One point should be stressed concerning figures 7 and 8: whereas figure 7 shows average upwelling indices as a function of temperature, figure 8 plots percent frequency of positive stations for sardine and anchovy eggs as a function of upwelling. As a result, the upwelling indices scales are quite different, and the graphs only indicate general trends within their total amplitude. No comparison between them would be meaningful.

DISCUSSION

It is always difficult to define absolute temperature limits for organisms, whether breeding or not, since in nature there tends to be an ample variation. It is evident that sardines and anchovies spawn through a very wide temperature range: there are positive stations from less than 10°C to more than 28°C for both sardines and anchovies (figure 2). There are no clear-cut limits within these distributions.

On the other hand, the maxima for both species appear very close (15° for anchovy and 15.3° for sardine), and are very much the same as the general SST distribution, whose peak is around 15.5°. However, the general SST distribution has a definitive influence on the apparent distribution of sardine and anchovy spawning: the absolute number of positive stations depends on the total number of stations at a particular temperature. Thus it is the proportion of positive stations at each temperature that interests us; that is, the quotient between the relative temperature distribution of eggs and larvae and the general SST frequency distribution (figures 3 and 4).

The relative proportion of larvae to eggs increases from north to south for both species. This could mean either that survival of larvae increases toward the warm side of the ranges or that the higher proportion is an effect of the shorter development time of the egg as a function of higher temperatures. Another possibility (suggested by one of our reviewers) is that larvae grow slower in the south. Existing data are not sufficient to indicate which of these options — alone or combined — apply.

Most previous authors have worked with sardine spawning in the cooler temperature range. Tibby (1937), Ahlstrom (1954, 1965), Smith (1978), and Parrish et al. (1989) refer to temperature ranges that closely agree with the first peak reported in this paper. The warmer temperature range has seldom been reported, and only at its southern end, around Magdalena Bay (Saldierna et al. 1987). However, Ahlstrom (1954) referred to this second range as the "off-season" and reported temperatures "higher than 19°C."

The results reported by Hammann (in press) show that in the Gulf of California the temperature range for sardine spawning (14°–23°) is located between the two peaks reported in this paper for the California Current. It is unusual that there may be three different temperature ranges for sardine spawning, as presented here. Normally, the optimum spawning temperature would be expected around the midpoint between the extremes. The spawning temperatures in the Gulf of California are around this midpoint of the total range. Thus, we believe that the hiatus found between the two major peaks in the California Current is not an inherent phenomenon, but a different, environmentally caused feature.

We believe that the environmental factor responsible for the gap in the sardine spawning range is somehow related to upwelling. Low upwelling (and induced productivity) limit the abundance of sardines, as is evident from the fact that there are no sardines where there is no upwelling — as in the area between Ensenada and Bahía Sebastián Vizcaíno, except during the upwelling season. On the other hand, limits to sardine spawning at high upwelling indices can be assumed from the reports of several authors: Ahlstrom (1965) reported that no clear relation existed between productivity and sardine abundance; Lasker (as summarized by Lasker and MacCall 1983) proposed that intense upwelling could negatively affect the survival of larvae because of turbulence and instability of the water column. Another way in which intense upwelling could negatively influence sardine abundance is by the offshore transport of larvae (Parrish et al. 1981).

Both mechanisms — egg and larvae loss from turbulence, and offshore transport of larvae — would operate after spawning. We find that spawning itself is influenced by upwelling. It is clear from figure 8 that there is a maximum of spawning at intermediate values of upwelling; at lower and higher values, spawning decreases considerably. There must be some way for sardines to select appropriate upwelling conditions for spawning.

We suggest that sardines spawn preferably at (1) the range of temperatures with intermediate upwelling values (figure 7: temperatures between 14° and 15°C) that is found between the lower temperature range with high values of upwelling (12°–13°) and the warmer temperature range with high values of upwelling (15°–18°); and (2) at temperatures higher than 18.5°, as average upwelling indices decline to intermediate values. These two ranges correspond to the two peaks of spawning as a function of temperature shown in figure 3. The gap between the two peaks corresponds to the high upwelling values and a temperature range between 15° and 18°.

SST is a good indicator of spawning only at the limits, particularly at the lower one; otherwise, it is a poor indicator, since there is a very wide range of appropriate temperatures. However, the combination of temperature and upwelling appears to determine time and space of sardine spawning.

Anchovies, on the other hand, seem to behave the opposite way: a narrow range of spawning (figure 4) combines with the capability of spawning at low or high upwelling indices (figure 8). We suggest that the peak of anchovy spawning is somehow related to the high values of upwelling that occur at the low temperature range (12° to 13°) as shown in figure 7.

Figure 8 suggests competitive interaction between both species, with sardines showing ecological dominance. However, other factors may determine anchovies' preference for upwelling, and further analysis of this possible relationship is required.

We conclude that sardines may be considered as eurithermic and preferring warmer temperatures for spawning than anchovies, which are stenothermic and prefer cooler temperatures, as indicated in the formerly reported observations. Anchovies seem much more adapted for cooler spawning than sardines. This point is supported further by the importance of the warmer peak for sardines.

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BEAM-TRAWL SURVEY OF BAY AND NEARSHORE FISHES OF THE SOFT-BOTTOM HABITAT OF SOUTHERN CALIFORNIA IN 1989

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ABSTRACT

Small-meshed (2.5-mm) beam trawls have been used in several recent surveys to examine the distribution of newly settled California halibut (*Paralichthys californicus*). However, information on the entire fish assemblage collected in these surveys has not previously been reported. The objective of this study was to describe the bay and shallow coastal ichthyofauna of southern California as sampled by small-meshed beam trawls. Areas off Los Angeles, Orange, and San Diego counties were surveyed from April to September 1989. Three stations were sampled at each of four coastal sites (Hermosa Beach, Long Beach, San Onofre, and Carlsbad) and two bay sites (Anaheim Bay and Agua Hedionda Lagoon). A 1.0-m beam trawl was used in bays and a 1.6-m beam trawl along the coast. A total of 288 samples was collected at depths of 0–3 m in bays and 6–13 m along the coast. The total collection of 48,994 fish comprised 72 species of 31 families. The catch was dominated by newly transformed (10–15-mm-long) fish.

Fish density decreased from bays to the exposed coast. However, standing crop was highest on the semiprotected coast and lowest in bays. Density decreased with increasing depth, but standing crop increased with depth. Fish density was much higher in May than in the other months. Standing crop was much lower in April than in the other months. The fish fauna included some species characteristic of either bay or coastal habitats, but other species occurred in both; some coastal species preferred either semiprotected or exposed habitats.

RESUMEN

Las redes de arrastre de fondo de malla fina (2.5 mm) han sido utilizadas en varios estudios por examinar la distribución de los individuos del lenguado de California (*Paralichthys californicus*) recientemente establecidos. Sin embargo, información sobre el conjunto de peces no ha reportada previamente. El objetivo del este estudio fue describir la ictiofauna de las bahías y las áreas costeras de poca profundidad del sur de California muestradas por las redes de arrastre de fondo de malla fina. Siendo así, se estudiaron algunas áreas costeras de los condados de Los Angeles, Orange, y San Diego, entre abril y septiembre de 1989. Se tomaron muestras en cuatro localidades costeras (Hermosa Beach, Long Beach, San Onofre, y Carlsbad) y en dos lagunas costeras (Anaheim Bay y Agua Hedionda Lagoon). Se muestrearon tres estaciones en cada localidad utilizando una red de arrastre de fondo de 1.0 m en las lagunas y una red de 1.6 m en las áreas costeras. Se colectaron 288 muestras en total, a profundidades de 0–3 m en las lagunas y de 6–13 m a lo largo de la costa. En este estudio se colectaron un total de 48,994 peces, representando 72 especies de 31 familias. La captura total fue dominada por individuos recientemente transformados (con longitudes de 10–15 mm).

La densidad de individuos decreció desde las bahías hacia la costa expuesta. Sin embargo, la densidad de biomasa fue más elevada en la costa semiprotegida y más baja en las bahías. La densidad de individuos decreció con la profundidad, pero la biomasa aumentó con la profundidad. La densidad de individuos fue más elevada en mayo que en las otros meses. La densidad de biomasa fue más baja en abril que en los otros meses. La ictiofauna incluyó algunas especies típicas de las bahías o de los habitats costeros, pero otras especies occurrierron en ambas áreas. Algunos especies de costa preferieron áreas semiprotegidas o áreas expuestas.

INTRODUCTION

The earliest surveyors of the soft-bottom ichthyofauna of southern California (Gilbert 1890, 1892, 1896, 1915; Ulrey and Greeley 1928) used beam trawls as a sampling device. However, since the 1950s small otter trawls have been preferred (Mearns and Allen 1978) because they capture more species of fish and are less cumbersome to use. The soft-bottom ichthyofauna of the southern California shelf has been extensively sampled during the past thirty-five years by otter trawls with 4.9–7.6-m headrope and 12-mm cod-end mesh (Carlisle 1969; M. J. Allen and Voglin 1976; M. J. Allen 1982; Moore et al. 1982; L. G. Allen 1985; Love et al. 1986).

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For most shelf species, 12-mm mesh in the cod end was sufficient to collect fish as short as 20–25 mm (Sherwood 1980; M. J. Allen 1982), and thus newly transformed juveniles of many species were captured (Moser et al. 1984). However, many nearshore and bay species transform at a smaller size (Ahlstrom et al. 1984; Kramer 1990). Thus newly transformed individuals of these species may pass through the mesh openings of the nets used in otter trawls.

Among the species that transform at a small size is California halibut (*Paralichthys californicus*), which undergoes metamorphosis and settles at 7–9 mm in length (Ahlstrom et al. 1984; L. G. Allen 1988). A number of surveys conducted since 1983 have examined settlement patterns of California halibut because of its importance to fisheries (Kramer and Hunter 1987, 1988; L. G. Allen 1988; M. J. Allen and Herbinson 1990; Kramer 1990; MBC 1990, 1991; L. G. Allen et al., in press). Some of these surveys (Kramer and Hunter 1988; M. J. Allen and Herbinson 1990; Kramer 1990; MBC 1990; L. G. Allen et al., in press) found extensive coastal settlement of halibut in some years. Previous studies (Haaker 1975; M. J. Allen 1982; Plummer et al. 1983) had suggested that settlement probably occurred only in bays. Thus the use of fine-meshed nets revealed a previously unknown distribution pattern of the smallest juveniles of this species.

Because the emphasis of most of the studies was on settlement patterns of California halibut, the catch of other fish species was either ignored or not reported. Although the distribution of larval fishes in nearshore waters of southern California is relatively well known (Barnett et al. 1984; Walker et al. 1987), little is known about this benthic microichthyofauna. This fauna consists largely of newly transformed juveniles of larger fishes but also includes many fishes with small adult sizes. Many species use bay and nearshore areas temporarily as nurseries before moving to deeper habitats as larger juveniles and adults. But the relative use of bays and shallow coastal areas for nurseries is not known for many species.

The main objective of this survey was to determine settlement patterns of California halibut. The results of the halibut portion of this survey are given in M. J. Allen and Herbinson 1990 and MBC 1990. The objective of this portion of the study was to describe the distribution and abundance of the ichthyofauna of the shallow soft-bottom habitat of bay and nearshore coastal areas of southern California from fine-meshed beam-trawl collections.

METHODS

Study Area

The study area was the same as that of M. J. Allen and Herbinson (1990) and MBC (1990). It extended about 130 km north to south from Hermosa Beach (Los Angeles County) to Carlsbad (San Diego County), California. Within this area, surveys were conducted at Hermosa Beach, Long Beach, Anaheim Bay, San Onofre, Carlsbad, and Agua Hedionda Lagoon (figure 1).

Anaheim Bay and Agua Hedionda Lagoon are bays; Hermosa Beach and Long Beach are semiprotected coastal sites; and San Onofre and Carlsbad are exposed coastal sites (M. J. Allen and Herbinson 1990). The bay sites are fully protected from offshore swells. The Hermosa Beach site is protected from swells from the south or southwest by the Palos Verdes Peninsula and offshore islands but is exposed to western swells. Southern swells occur most frequently during the summer, and western swells primarily during the winter (Maloney and Chan 1974). Thus exposure is variable but semiprotected during the period of this survey (April–September). The Long Beach site is protected from swells from the northwest, west, and southwest by the Palos Verdes Peninsula, breakwaters, and offshore islands. The San Onofre site is fully exposed to swells from the south and southwest; the Carlsbad site is exposed to swells from the west and south.

Stations at all sites were randomly sampled within blocks stratified by depth. The water depth of the blocks ranged from 0.0 to 0.8 m, 1.0 to 1.5 m, and

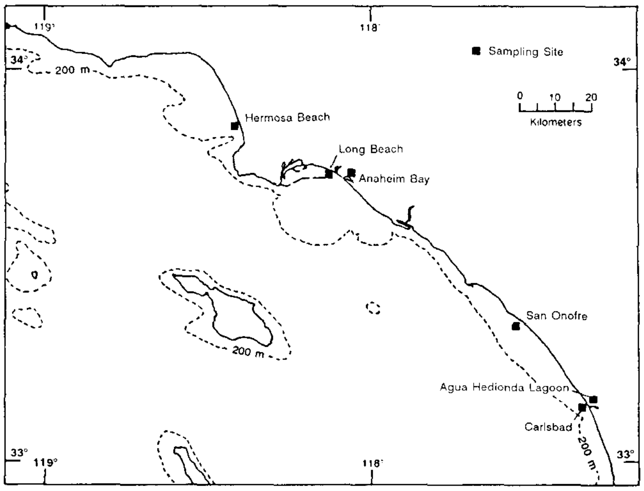

Figure 1. Locations of beam-trawl surveys in southern California, April–September 1989.

3.0 to 3.5 m in bays, and from 6 to 8 m, 8 to 11 m, and 11 to 15 m along the coast. Maps of the station locations are given in M. J. Allen and Herbinson 1990 and MBC 1990. Station coordinates are given in MBC 1990.

Sampling Methods

The fish were collected with the same nets used by Kramer (1990) and M. J. Allen and Herbinson (1990). Along the coast, samples were collected with a 1.6-m-by-0.4-m beam trawl, but in bays, a 1.0-m-by-0.3-m beam trawl was used. Both trawls were lined with 2.5-mm mesh netting. The beam trawls were equipped with a wheel and revolution counter (meter wheel), which recorded the distance trawled along the bottom. At coastal stations loran C coordinates (longitude and latitude) were recorded at the beginning and end of each haul. In the bays, 200-m trawl paths were measured and marked with buoys to separately indicate towing distance, in case the meter wheel fouled. Depth was measured with sonar at coastal sites and with a sounding line at bay sites.

Coastal trawling was done from the *Westwind*, a 14.6-m research vessel. Bay trawling at 1.0- and 3.0-m stations was done from a 5.2-m Boston whaler. At 0.5-m stations the beam trawl was pulled by two field technicians on foot.

The sites were sampled from April to September. Three 10-min (coast) or 200-m (bay) replicate hauls were attempted during daylight hours at each site's three stations, for a total of nine samples per site. Physical characteristics of each tow are given in MBC 1990.

All fish captured were retained for identification and measurement. Most were returned to the laboratory for processing, but large specimens were identified to species, measured, weighed, and released in the field. Only large debris was discarded in the field; the remaining debris and invertebrates were returned to the laboratory for closer examination. Specimens and debris samples were fixed in 10% buffered Formalin-seawater.

In the laboratory the samples were rinsed of Formalin after about a week and transferred to 70% isopropyl alcohol. Samples were then sorted to separate fish from invertebrates and debris. Fish were identified to species, measured, and weighed. The standard length (SL) of each bony fish or total length (TL) of each cartilaginous fish was measured to the nearest millimeter. For abundant species, subsamples of up to 200 fish were measured. Each species in a sample was weighed on a Mettler balance to the nearest 0.01 g.

After the last haul at each station, near-bottom water samples were collected with Van Dorn bottles. Temperature and hydrogen ion concentration (pH) of these samples were measured in the field with a Horiba analyzer. Station values are given in MBC 1990.

Data Analysis

The bottom area actually sampled in each tow was calculated from meter wheel readings or distances measured in the field. When fouling had occurred or the meter wheel reading was obviously too low, the distance traveled was estimated. This estimate was 200 m in bays and 315 m along the coast. The coastal estimate was based on the average distance attained by all "good" tows. The area sampled was computed as the product of the distance towed and the width of the trawl — 1.0 m for bays and 1.6 m for the coast. Estimated areas for replicates with extremely low readings were 200 m^2 for bays and 504 m^2 for the coast.

Fish catch parameters were summarized for number of individuals, density (number of individuals per hectare), biomass, standing crop (biomass per hectare), numbers of species, and Shannon-Wiener diversity (H'). The equation for H' is

$$H' = -\sum_{j=1}^{S} \frac{n_j}{N} \ln \frac{n_j}{N}$$

where n_j = number of individuals in the jth species; S = total number of species; and N = number of individuals. H' is an index of the relative distribution of individuals among species but is also influenced by the number of species.

Catch parameters were summarized by habitat (bay, semiprotected coast, exposed coast), site, depth, and month. Frequency of occurrence, abundance, density, biomass, and standing crop were summarized for all species by habitat. Mean lengths and length ranges were summarized for each species. A complete summary is given in MBC 1990.

RESULTS

Sampling Effort

From April to September 1989, 36 to 52 trawl samples were taken each month, for a total of 288 samples. All stations were sampled, but fewer than three replicates were obtained at some stations because of fouling by algae or sand. Totals of 190 samples were collected along the coast and 98 in the bays;

of the coastal samples, 95 were collected at semiprotected and 95 at exposed stations. From 47 to 50 samples were collected at each site, 29 to 35 at each depth in the bays, and 60 to 64 at each depth along the coast.

Physical Oceanography

Means and ranges of temperatures and pH by month for bay and coastal habitats are given in M. J. Allen and Herbinson (1990). Temperatures ranged from 13.8° to 24.7°C and were always greater in bays than on the coast. Temperatures and pH by station and survey are given in MBC 1990.

Spatial and Temporal Variation of Catch Parameters

Entire survey. A total of 48,994 fish, weighing 243.3 kg and representing 72 species was collected. On average, 170 fish (SD = 464), 0.8 kg (SD = 1.2 kg), and 7 species (SD = 3) were taken per replicate; mean H' per replicate was 1.05 (SD = 0.49). Mean fish density for the entire survey was 6,289 individuals/ha (SD = 22,850 individuals/ha); mean standing crop was 19 kg/ha (SD = 24 kg/ha).

Habitat. Fish density was about five times greater in the bays than along the coast. In bays, the mean density was 13,346 fish/ha (SD = 37,453 fish/ha), whereas along the coast it was 2,649 fish/ha (SD = 5,309 fish/ha). Mean density in the bays was about four times greater than along the semiprotected coast (3,310 fish/ha; SD = 7,067 fish/ha) and seven times greater than along the exposed coast (1,988 fish/ha; SD = 2,355 fish/ha) (figure 2). Along the coast, the mean density was about 1.5 times greater in the semiprotected habitat than in the exposed habitat.

The mean standing crop of fish along the coast (23 kg/ha; SD = 26) was about twice as great as in the bays (11 kg/ha; SD = 16 kg/ha). The mean standing crop on the semiprotected coast (27 kg/ha; SD = 25 kg/ha) was about 1.4 times that of the exposed coast (19 kg/ha; SD = 27 kg/ha) and 2.5 times that of the bays (figure 2).

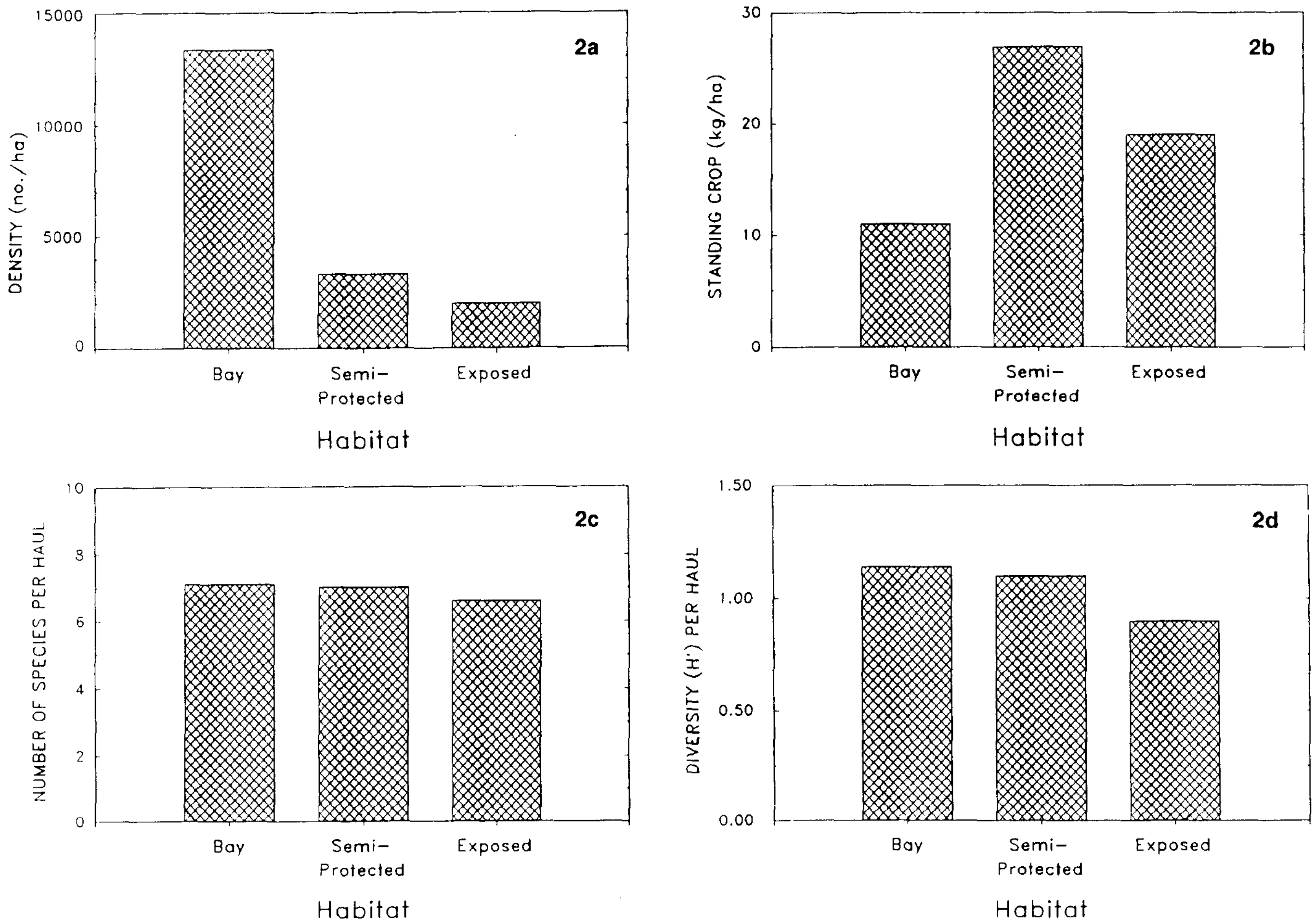

Figure 2. Variation in catch parameters from beam-trawl surveys of the southern California coast, April–September 1989, by habitat: *a*, density; *b*, standing crop; *c*, species richness; *d*, Shannon diversity.

Sixty species were taken along the coast and 43 in the bays; 48 were collected on the exposed coast and 44 on the semiprotected coast. However, the mean number of species per haul ranged from 6.6 (SD = 3.2) on the exposed coast to 7.1 (SD = 2.8) in bays (figure 2). Mean *H′* per haul for bays was 1.14 (SD = 0.54), and that for the coast was 1.00 (SD = 0.46). The mean *H′* for the semiprotected coast (1.10/haul; SD = 0.47/haul) was similar to that of bays (figure 2); both were somewhat higher than that of the exposed coast (0.90/haul; SD = 0.42/haul).

In summary, fish density decreased from bays to exposed coast. Standing crop was highest on the semiprotected coast and lowest in bays. Mean numbers of species and diversity were similarly high in bays and semiprotected coasts and were slightly lower on exposed coasts.

Site. Fish density was about twelve times greater in Anaheim Bay than at San Onofre, the site with the lowest density (figure 3); at Anaheim Bay the mean density was 23,121 fish/ha (SD = 51,436), whereas at San Onofre the density was 1,913 fish/ha (SD = 2,834). Densities were moderately low at Long Beach and Agua Hedionda Lagoon, and were very low at Carlsbad and Hermosa Beach.

Fish standing crop was about three times greater at Hermosa Beach than at Agua Hedionda Lagoon (figure 3); at Hermosa Beach, mean standing crop was 32 kg/ha (SD = 26 kg/ha), whereas at Agua Hedionda Lagoon it was 10 kg/ha (SD = 13 kg/ha). Standing crop was moderate at Carlsbad and Long Beach, but low at San Onofre and Anaheim Bay.

The number of species taken per site ranged from 28 at Long Beach to 40 at San Onofre. The mean number of species per haul ranged from 4.6 (SD = 3.4) at San Onofre to 7.0 at Carlsbad (SD = 3.6) and Hermosa Beach (SD = 2.2) (figure 3). Numbers of species were also high at Anaheim Bay and Agua Hedionda Lagoon, but were moderate at Long Beach. Mean *H′* per haul ranged from 0.79 (SD = 0.41) at San Onofre to 1.36 (SD = 0.46) at Agua Hedionda Lagoon (figure 3). *H′* was relatively low

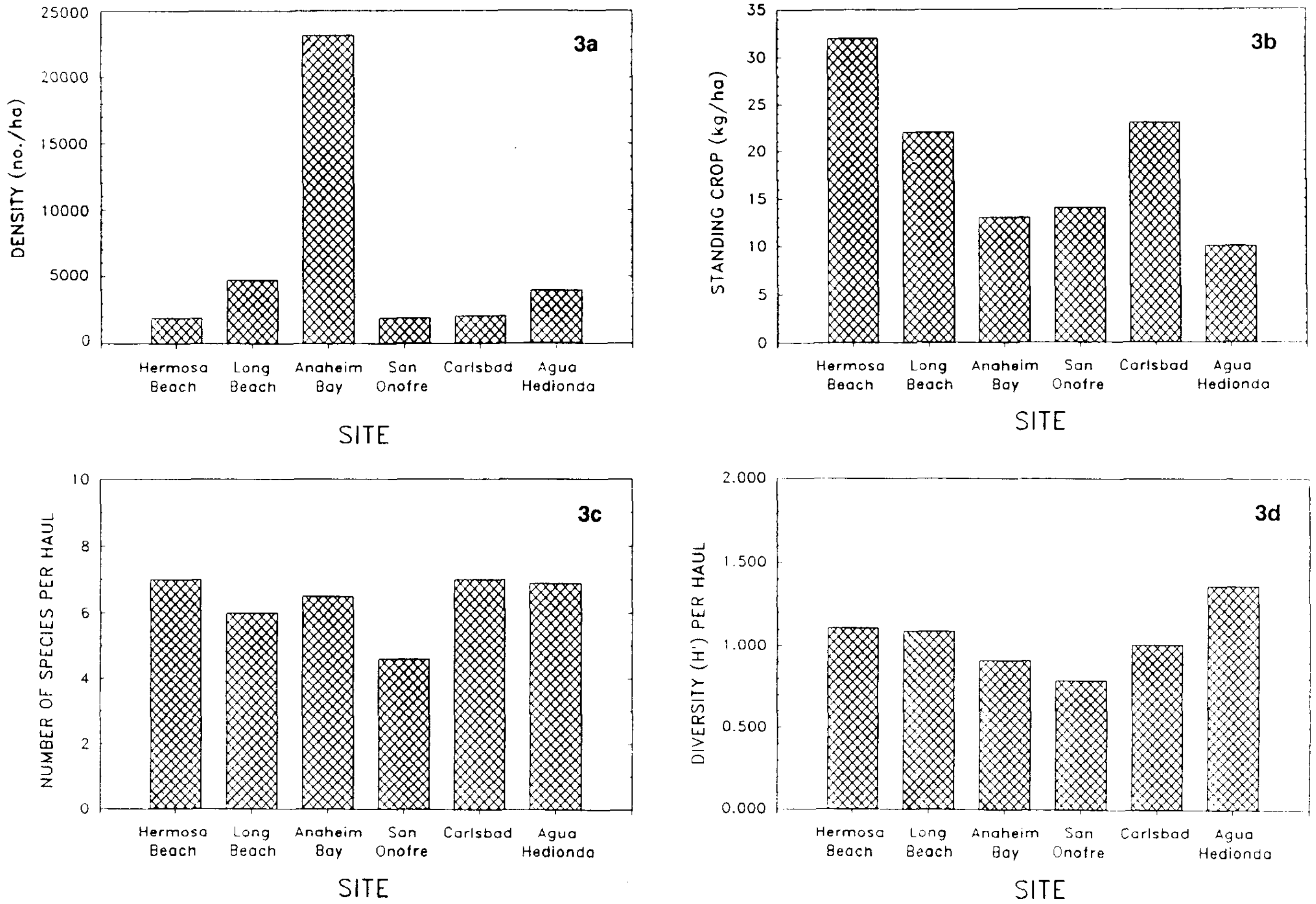

Figure 3. Variation in catch parameters from beam-trawl surveys of the southern California coast, April–September 1989, by survey site: *a*, density; *b*, standing crop; *c*, species richness; *d*, Shannon diversity.

at Anaheim Bay and moderate at the other coastal sites.

In summary, fish density was much greater at Anaheim Bay than at the other sites, which had similar low densities. Standing crop was highest at Hermosa Beach and other coastal sites, but was low in the two bays. Number of species and diversity were low at San Onofre but high at Agua Hedionda Lagoon. Carlsbad and Hermosa Beach had the highest mean number of species.

Depth. Fish density generally decreased with increasing depth (figure 4). The mean density at 0.5 m (29,265 fish/ha; SD = 59,800 fish/ha) was about 26 times greater than at 13.0 m (1,139 fish/ha; SD = 1,000) and 3.5 times greater than at 1.0 m (8,258 fish/ha; SD = 9,851), the depth with the next highest density. In turn, the mean density at 1.0 m was about seven times greater than that at 13.0 m. The density at 3.0 m was lower than that at 6.0 and 10.0 m.

Standing crop generally increased with depth (figure 4). Mean standing crop at 13.0 m (25.9 kg/ha; SD = 28.0 kg/ha) was about five times greater than at 0.5 m (4.9 kg/ha; SD = 3.9). The standing crop at 10.0 m was less than that at 6.0 m.

The mean number of species per haul ranged from 8.2 (SD = 2.8) at 1.0 m, to 5.6 (SD = 2.6) at 13.0 m (figure 4). Mean *H'* per haul ranged from 0.83 (SD = 0.51) at 0.5 m to 1.44 (SD = 0.33) at 3.0 m. No obvious depth-related trend was apparent for number of species or for diversity.

In summary, fish density decreased with increasing depth, and standing crop increased with depth. Number of species and diversity per haul showed no depth-related trends.

Month. Mean fish density in May (18,206 fish/ha; SD = 52,887) was about 6.5 times higher than in September (2,811 fish/ha; SD = 3,542 fish/ha). Densities in June and July were only slightly higher than in the other months, including September (figure 5).

The mean standing crop in August (23 kg/ha; SD = 37) was about three times greater than in April (8

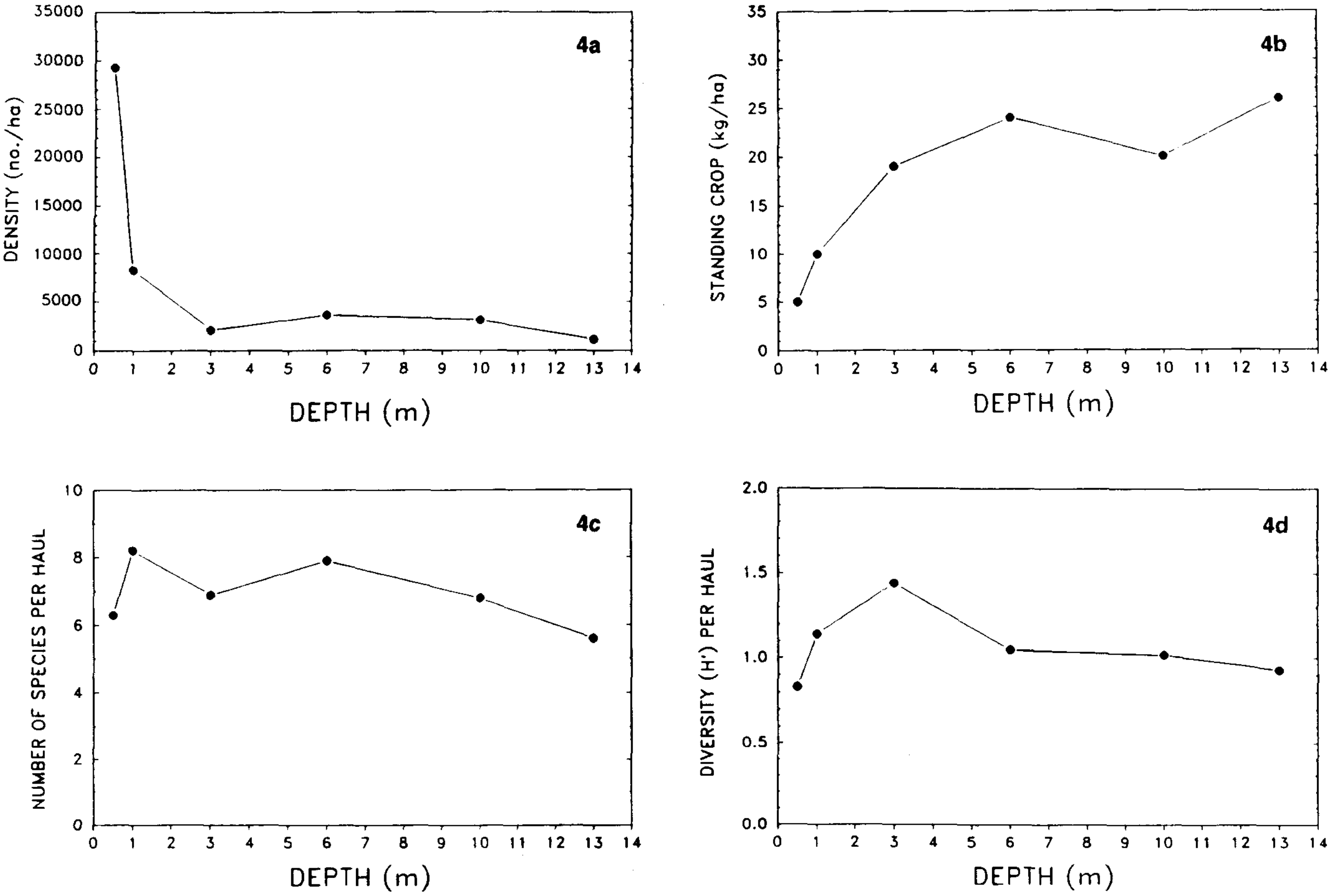

Figure 4. Variation in catch parameters from beam-trawl surveys of the southern California coast, April–September 1989, by water depth: *a*, density; *b*, standing crop; *c*, species richness; *d*, Shannon diversity.

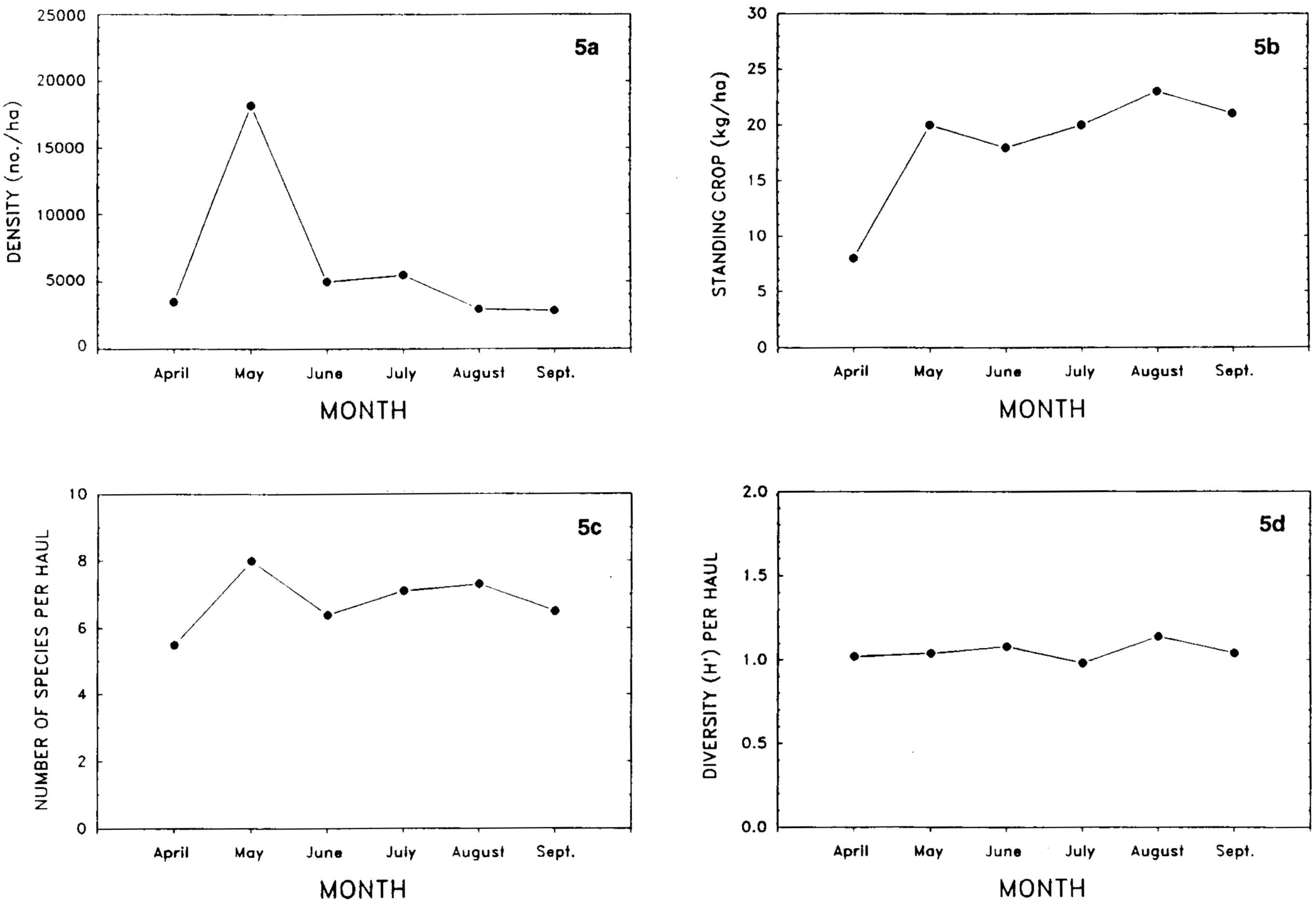

Figure 5. Variation in catch parameters from beam-trawl surveys of the southern California coast, April–September 1989, by month: *a*, density; *b*, standing crop; *c*, species richness; *d*, Shannon diversity.

kg/ha; SD = 10). The standing crop was high from May to September (figure 5).

The mean number of species per haul ranged from 5.5 (SD = 2.4) in April to 8.1 (SD = 2.9) in May. Numbers of species per haul were moderate from June to September. The mean diversity per replicate showed little monthly variation, ranging from 0.98 (SD = 0.42) in July to 1.14 (SD = 0.47) in August (figure 5).

In summary, fish densities were much higher in May than in other months. Standing crop was much lower in April than in other months. Number of species showed no obvious monthly trend, and diversity showed little monthly variation.

Composition of Catch

Taxonomic composition. The 72 species of fish collected represented two classes and 30 families (table 1). Bony fishes (Osteichthyes) were represented by 24 families and 65 species; cartilaginous fishes (Elasmobranchiomorphi) were represented by 6 families and 7 species. The most diverse families were the Syngnathidae (pipefishes), Embiotocidae (surfperches), Gobiidae (gobies), and Pleuronectidae (righteye flounders), with 6 species each.

Frequency of occurrence. Eleven species occurred in 20% or more of the 288 samples (table 2). Overall, speckled sanddab (*Citharichthys stigmaeus*) and California halibut were the only species that were found in more than 50% of the samples; speckled sanddab occurred in 60% of the samples and California halibut in 55%. However, species occurrence differed between bay and coastal habitats (table 2). Four species occurred in 50% or more of the bay samples: cheekspot goby (*Ilypnus gilberti*), bay pipefish (*Syngnathus leptorhynchus*), giant kelpfish (*Heterostichus rostratus*), and California halibut. Three species occurred in 50% or more of the coast samples: speckled sanddab, spotted turbot (*Pleuronichthys ritteri*), and California halibut.

TABLE 1

Common and Scientific Names of Fishes Captured during Beam-Trawl Surveys off Southern California at Depths of 0.5 to 13.0 m, April–September 1989

Taxon	Common name
Elasmobranchiomorphi	
Carcharhinidae	
Mustelus californicus	gray smoothhound
Torpedinidae	
Torpedo californica	Pacific electric ray
Rhinobatidae	
Platyrhinoidis triseriata	thornback
Rhinobatos productus	shovelnose guitarfish
Rajidae	
Raja inornata	California skate
Dasyatidae	
Gymnura marmorata	California butterfly ray
Urolophidae	
Urolophus halleri	round stingray
Osteichthyes	
Engraulidae	
Engraulis mordax	northern anchovy
Synodontidae	
Synodus lucioceps	California lizardfish
Ophidiidae	
Ophidion scrippsae	basketweave cusk-eel
Batrachoididae	
Porichthys myriaster	specklefin midshipman
Porichthys notatus	plainfin midshipman
Gobiesocidae	
Gobiesox rhessodon	California clingfish
Rimicola eigenmanni	slender clingfish
Rimicola muscarum	kelp clingfish
Cyprinodontidae	
Fundulus parvipinnis	California killifish
Atherinidae	
Atherinops affinis	topsmelt
Syngnathidae	
Cosmocampus (= Bryx) arctus	snubnose pipefish
Syngnathus auliscus	barred pipefish
Syngnathus californiensis	kelp pipefish
Syngnathus euchrous	chocolate pipefish
Syngnathus exilis	barcheek pipefish
Syngnathus leptorhynchus	bay pipefish
Scorpaenidae	
Scorpaena guttata	California scorpionfish
Cottidae	
Icelinus quadriseriatus	yellowchin sculpin
Leptocottus armatus	Pacific staghorn sculpin
Orthonopias triacis	snubnose sculpin
Scorpaenichthys marmoratus	cabezon
Agonidae	
Agonopsis sterletus	southern spearnose poacher
Cyclopteridae	
Liparis mucosus	slimy snailfish
Serranidae	
Paralabrax clathratus	kelp bass
Paralabrax maculatofasciatus	spotted sand bass
Paralabrax nebulifer	barred sand bass
Haemulidae	
Anisotremus davidsonii	sargo
Xenistius californiensis	salema
Sciaenidae	
Atractoscion nobilis	white seabass
Cheilotrema saturnum	black croaker
Genyonemus lineatus	white croaker
Menticirrhus undulatus	California corbina
Seriphus politus	queenfish
Kyphosidae	
Girella nigricans	opaleye
Embiotocidae	
Brachyistius frenatus	kelp perch
Cymatogaster aggregata	shiner perch
Embiotoca jacksoni	black perch
Hyperprosopon argenteum	walleye surfperch
Micrometrus minimus	dwarf perch
Phanerodon furcatus	white seaperch
Labridae	
Oxyjulis californica	senorita
Clinidae	
Gibbonsia elegans	spotted kelpfish
Gibbonsia metzi	striped kelpfish
Heterostichus rostratus	giant kelpfish
Blenniidae	
Hypsoblennius gentilis	bay blenny
Hypsoblennius gilberti	rockpool blenny
Hypsoblennius jenkinsi	mussel blenny
Gobiidae	
Acanthogobius flavimanus	yellowfin goby
Clevelandia ios	arrow goby
Gillichthys mirabilis	longjaw mudsucker
Ilypnus gilberti	cheekspot goby
Lepidogobius lepidus	bay goby
Quietula y-cauda	shadow goby
Bothidae	
Citharichthys stigmaeus	speckled sanddab
Citharichthys xanthostigma	longfin sanddab
Hippoglossina stomata	bigmouth sole
Paralichthys californicus	California halibut
Xystreurys liolepis	fantail sole
Pleuronectidae	
Hypsopsetta guttulata	diamond turbot
Pleuronectes (= Parophrys) vetulus	English sole
Pleuronichthys coenosus	C-O sole
Pleuronichthys decurrens	curlfin sole
Pleuronichthys ritteri	spotted turbot
Pleuronichthys verticalis	hornyhead turbot
Soleidae (= Cynoglossidae)	
Symphurus atricauda	California tonguefish

Common and scientific names follow Robins et al. 1991.

Thirty species were found in both bay and coastal habitats. The most common of these were California halibut, spotted turbot, and cheekspot goby. Thirty species occurred only along the coast: the three most common were speckled sanddab, hornyhead turbot (*Pleuronichthys verticalis*), and thornback (*Platyrhinoidis triseriata*). Twelve species occurred only in the bays. The three most common of these were bay pipefish, topsmelt (*Atherinops affinis*), and bay blenny (*Hypsoblennius gentilis*).

Species abundance and density. Twelve species accounted for 95% of the total catch (table 3). Topsmelt, queenfish (*Seriphus politus*), cheekspot goby, and white croaker (*Genyonemus lineatus*) together accounted for 76% of the catch. Topsmelt constituted 56% of the bay catch, whereas queenfish and white

TABLE 2
Species Occurring in 20% or More of Beam-Trawl Samples Taken off Southern California, April–September 1989

		Frequency of occurrence (%)		
		Bay	Coast	Total
Species	Common name	(n = 98)	(n = 190)	(n = 288)
Citharichthys stigmaeus	speckled sanddab	0	91	60
Paralichthys californicus	California halibut	53	56	55
Pleuronichthys ritteri	spotted turbot	16	66	49
Ilypnus gilberti	cheekspot goby	67	33	45
Seriphus politus	queenfish	11	44	33
Heterostichus rostratus	giant kelpfish	58	17	31
Pleuronichthys verticalis	hornyhead turbot	0	42	28
Leptocottus armatus	Pacific staghorn sculpin	46	17	27
Genyonemus lineatus	white croaker	4	36	25
Syngnathus leptorhynchus	bay pipefish	65	0	22
Engraulis mordax	northern anchovy	2	29	20

n = number of samples
See MBC 1990 for complete listing of species.

TABLE 3
Fish Species Accounting for 95% of the Total Fish Taken by Beam Trawl in Bay and Coastal Habitats of Southern California, April–September 1989

		Number of fish					(%)	
			Coast					
Species	Common name	Bay	Semiprotected	Exposed	Total	Study total	Total	Cum.*
Atherinops affinis	topsmelt	13,759	0	0	0	13,759	28	28
Seriphus politus	queenfish	84	4,142	4,771	8,913	8,997	18	46
Ilypnus gilberti	cheekspot goby	6,959	285	65	350	7,309	15	61
Genyonemus lineatus	white croaker	17	6,666	517	7,183	7,200	15	76
Citharichthys stigmaeus	speckled sanddab	0	1,640	2,599	4,239	4,239	9	85
Engraulis mordax	northern anchovy	2	928	843	1,771	1,773	4	88
Paralichthys californicus	California halibut	305	348	109	457	762	2	90
Syngnathus leptorhynchus	bay pipefish	747	0	0	0	747	2	91
Leptocottus armatus	Pacific staghorn sculpin	604	6	59	65	669	1	93
Pleuronichthys ritteri	spotted turbot	25	409	68	477	502	1	94
Heterostichus rostratus	giant kelpfish	338	20	30	50	388	1	95
Clevelandia ios	arrow goby	372	1	0	1	373	1	95

*Cumulative
See MBC 1990 for complete listing of species abundances.

croaker together made up 65% of the coastal catch. White croaker and queenfish constituted 72% of the catch from the semiprotected coast; queenfish were 50% of the catch from the exposed coast.

The species with the greatest overall densities were topsmelt, cheekspot goby, and queenfish, with means of 2,575, 1,243, and 701 fish/ha. However, topsmelt did not occur on the coast. In bays, the species with the greatest densities were topsmelt, cheekspot goby, and bay pipefish (table 4). On the semiprotected coast, the three dominant species were white croaker, queenfish, and speckled sanddab. On the exposed coast, the three dominant species were queenfish, speckled sanddab, and northern anchovy (*Engraulis mordax*).

Among the 11 species with mean densities of 50 fish/ha or greater, topsmelt and bay pipefish were found only in bays, and speckled sanddab only along the coast. Speckled sanddab were more abundant on the exposed coast than on the semiprotected coast. Of species found in both bay and coastal habitats, 5 were most abundant in bays. These were cheekspot goby, Pacific staghorn sculpin (*Leptocottus armatus*), California halibut, arrow goby (*Clevelandia ios*), and giant kelpfish. Of these, cheekspot goby, California halibut, and arrow goby were next most abundant on the semiprotected coast, whereas Pacific staghorn sculpin and giant kelpfish were next most abundant on the exposed coast. Three species (queenfish, white croaker, and northern anchovy) were most abundant along the coast. All had highest densities on the semiprotected coast, followed by the exposed coast, and then bays.

Species biomass and standing crop. Twenty species accounted for 95% of the total fish biomass catch in the study (table 5). Spotted turbot, California halibut, hornyhead turbot, and thornback together accounted for 56% of the biomass. Spotted sand bass

TABLE 4
Top Ten Species by Density in Habitats Sampled by Beam Trawl off Southern California, April–September 1989

Rank	Species	Common name	Density (no./ha) Mean	SD
Bay			(n = 98)	
1	*Atherinops affinis*	topsmelt	7,726	35,150
2	*Ilypnus gilberti*	cheekspot goby	3,653	6,629
3	*Syngnathus leptorhynchus*	bay pipefish	408	744
4	*Leptocottus armatus*	Pacific staghorn sculpin	333	873
5	*Clevelandia ios*	arrow goby	211	813
6	*Heterostichus rostratus*	giant kelpfish	187	262
7	*Paralichthys californicus*	California halibut	158	275
8	*Paralabrax clathratus*	kelp bass	120	365
9	*Paralabrax nebulifer*	barred sand bass	114	226
10	*Paralabrax maculatofasciatus*	spotted sand bass	61	116
Semiprotected coast			(n = 95)	
1	*Genyonemus lineatus*	white croaker	1,354	6,111
2	*Seriphus politus*	queenfish	1,050	3,324
3	*Citharichthys stigmaeus*	speckled sanddab	320	399
4	*Engraulis mordax*	northern anchovy	209	941
5	*Paralichthys californicus*	California halibut	94	184
6	*Pleuronichthys ritteri*	spotted turbot	81	82
7	*Ilypnus gilberti*	cheekspot goby	61	113
8	*Symphurus atricauda*	California tonguefish	24	41
9	*Pleuronichthys verticalis*	hornyhead turbot	22	25
10	*Syngnathus exilis*	barcheek pipefish	11	34
Exposed coast			(n = 95)	
1	*Seriphus politus*	queenfish	1,008	2,120
2	*Citharichthys stigmaeus*	speckled sanddab	555	646
3	*Engraulis mordax*	northern anchovy	136	441
4	*Genyonemus lineatus*	white croaker	104	284
5	*Paralichthys californicus*	California halibut	25	44
6	*Syngnathus exilis*	barcheek pipefish	25	46
7	*Pleuronichthys ritteri*	spotted turbot	15	22
8	*Pleuronectes vetulus*	English sole	14	37
9	*Ilypnus gilberti*	cheekspot goby	14	32
10	*Pleuronichthys verticalis*	hornyhead turbot	13	27

n = number of samples
See MBC 1990 for complete listing of fish densities by habitat.

TABLE 5
Fish Species Constituting 95% of the Fish Biomass Taken by Beam Trawl off Southern California, April–September 1989

		Biomass (kg)					(%)	
			Coast					
Species	Common name	Bay	Semiprotected	Exposed	Total	Study total	Total	Cum.*
Pleuronichthys ritteri	spotted turbot	0.5	49.8	10.2	60.0	60.5	25	25
Paralichthys californicus	California halibut	0.9	20.8	15.9	36.7	37.7	15	40
Pleuronichthys verticalis	hornyhead turbot	0.0	14.3	5.7	20.1	20.1	8	49
Platyrhinoidis triseriata	thornback	0.0	5.7	12.9	18.6	18.6	8	56
Citharichthys stigmaeus	speckled sanddab	0.0	3.5	11.8	15.3	15.3	6	63
Gymnura marmorata	California butterfly ray	0.0	0.0	11.4	11.4	11.4	5	67
Hypsopsetta guttulata	diamond turbot	1.5	6.1	1.5	7.6	9.2	4	71
Torpedo californica	Pacific electric ray	0.0	6.8	0.0	6.8	6.8	3	74
Xystreurys liolepis	fantail sole	0.0	4.1	2.3	6.4	6.4	3	76
Porichthys myriaster	specklefin midshipman	0.0	6.2	0.0	6.3	6.3	3	79
Heterostichus rostratus	giant kelpfish	4.5	0.5	0.3	0.8	5.4	2	81
Paralabrax maculatofasciatus	spotted sand bass	5.2	0.0	0.0	0.0	5.2	2	83
Urolophus halleri	round stingray	1.4	1.8	1.8	3.6	5.0	2	85
Genyonemus lineatus	white croaker	0.0	4.5	0.2	4.7	4.7	2	87
Citharichthys xanthostigma	longfin sanddab	0.0	0.0	4.0	4.0	4.0	2	89
Scorpaena guttata	California scorpionfish	0.0	1.5	2.2	3.7	3.7	2	90
Leptocottus armatus	Pacific staghorn sculpin	1.5	0.1	1.7	1.8	3.3	1	92
Symphurus atricauda	California tonguefish	0.0	2.8	0.5	3.2	3.2	1	93
Rhinobatos productus	shovelnose guitarfish	0.0	0.5	2.7	3.2	3.2	1	94
Synodus lucioceps	California lizardfish	0.0	0.8	0.9	1.7	1.7	1	95

*Cum. = cumulative
See MBC 1990 for complete list of species.

(*Paralabrax maculatofasciatus*), giant kelpfish, and diamond turbot (*Hypsopsetta guttulata*) constituted 54% of the bay biomass. Spotted turbot, California halibut, and hornyhead turbot as a group accounted for 53% of the coastal biomass. Spotted turbot and California halibut accounted for 53% of the biomass on the semiprotected coast, whereas California halibut, thornback, speckled sanddab, and California butterfly ray (*Gymnura marmorata*) constituted 58% of the exposed-coast biomass.

Spotted turbot, California halibut, and thornback had the greatest overall standing crops, with means of 4.1, 2.9, and 1.4 kg/ha. In bays, the species with the greatest standing crops were the spotted sand bass, giant kelpfish, and Pacific staghorn sculpin (table 6). On the semiprotected coast, the three dominant species were spotted turbot, California halibut, and hornyhead turbot. On the exposed coast, the three dominant species were the California halibut, thornback, and speckled sanddab.

Among the 10 species with mean standing crops of 0.5 kg/ha or greater overall, spotted sand bass was found only in the bays, whereas thornback, hornyhead turbot, speckled sanddab, and California butterfly ray were found only along the coast; thornback, speckled sanddab, and California butterfly ray had highest standing crops on the exposed coast, and hornyhead turbot on the semiprotected coast. Of species collected in both bay and coastal habitats, three (spotted turbot, California halibut, and diamond turbot) had highest standing crops on the semiprotected coast. Spotted turbot and California halibut had next highest standing crops on the exposed coast, whereas diamond turbot had its next highest standing crop in bays. Giant kelpfish and round stingray (*Urolophus halleri*) had highest standing crops in bays; giant kelpfish was next highest on the semiprotected coast; and round stingray was next highest on the exposed coast.

Length. Fish collected in the study ranged in

TABLE 6
Top Ten Fish Species by Standing Crop in Habitats Sampled by Beam Trawl off Southern California, April–September 1989

Rank	Species	Common name	Standing crop (kg/ha) Mean	SD
Bay			(n = 98)	
1	*Paralabrax maculatofasciatus*	spotted sand bass	2.8	8.8
2	*Heterostichus rostratus*	giant kelpfish	2.5	6.0
3	*Leptocottus armatus*	Pacific staghorn sculpin	0.8	1.6
4	*Hypsopsetta guttulata*	diamond turbot	0.8	2.1
5	*Urolophus halleri*	round stingray	0.7	3.8
6	*Embiotoca jacksoni*	black perch	0.6	3.4
7	*Paralabrax clathratus*	kelp bass	0.6	1.7
8	*Paralichthys californicus*	California halibut	0.5	1.3
9	*Paralabrax nebulifer*	barred sand bass	0.4	0.9
10	*Atherinops affinis*	topsmelt	0.2	1.0
Semiprotected coast			(n = 95)	
1	*Pleuronichthys ritteri*	spotted turbot	9.8	11.2
2	*Paralichthys californicus*	California halibut	4.8	9.0
3	*Pleuronichthys verticalis*	hornyhead turbot	2.5	4.2
4	*Platyrhinoidis triseriata*	thornback	1.4	5.2
5	*Porichthys myriaster*	specklefin midshipman	1.4	4.2
6	*Torpedo californica*	Pacific electric ray	1.3	12.2
7	*Hypsopsetta guttulata*	diamond turbot	1.2	2.7
8	*Genyonemus lineatus*	white croaker	1.0	4.2
9	*Xystreurys liolepis*	fantail sole	0.8	3.1
10	*Citharichthys stigmaeus*	speckled sanddab	0.7	0.8
Exposed coast			(n = 95)	
1	*Paralichthys californicus*	California halibut	3.3	6.1
2	*Platyrhinoidis triseriata*	thornback	2.6	5.7
3	*Citharichthys stigmaeus*	speckled sanddab	2.6	2.5
4	*Gymnura marmorata*	California butterfly ray	2.4	22.4
5	*Pleuronichthys ritteri*	spotted turbot	2.3	4.2
6	*Pleuronichthys verticalis*	hornyhead turbot	1.3	3.1
7	*Citharichthys xanthostigma*	longfin sanddab	0.8	2.6
8	*Rhinobatos productus*	shovelnose guitarfish	0.5	2.0
9	*Scorpaena guttata*	California scorpionfish	0.5	2.2
10	*Xystreurys liolepis*	fantail sole	0.4	1.3

n = number of samples
See MBC 1990 for complete listing of standing crops by habitat.

length from 3 to 810 mm. The species with the longest mean lengths were Pacific electric ray, *Torpedo californica* (one specimen only); California skate, *Raja inornata* (one specimen only); and shovelnose guitarfish, *Rhinobatos productus* (table 7). The longest individual fish in the study were a Pacific electric ray (810 mm TL); California skate (539 mm TL); and California halibut (503 mm SL). The species with the shortest mean lengths were queenfish, black croaker (*Cheilotrema saturnum*), and kelp clingfish (*Rimicola muscarum*). The smallest individual fish were larval queenfish, white croaker, and cheekspot goby, which were 3 mm long.

The three most abundant species (topsmelt, queenfish, and cheekspot goby) were dominated by 10–15-mm fish. About 21% (2,931 of 13,759) of the topsmelt were measured: they ranged from 5 to 72 mm SL, with a mean length of 15 mm (table 7) and a mode of 10 mm. Topsmelt was collected only in bays, and most of the fish measured were 10–20 mm SL. About 64% (5,761 of 8,997) of the queenfish were measured; they ranged from 3 to 64 mm SL with a mean of 11 mm. Queenfish were found in all three habitats, but more than 60% of those measured were from the exposed coast. The length-frequency distribution was similar in all three habitats, with a mode of 10 mm in each. About 72% (5,259 of 7,309) of the cheekspot goby were measured; they ranged from 3 to 50 mm SL, with a mean of 16 mm. Cheekspot goby was found in all three habitats, but about 93% of those measured were from the bays. The length-frequency distribution had a mode of 15 mm in all three habitats, but the 10-mm length-class was almost as abundant on the exposed coast.

DISCUSSION

Small otter trawls have been used for extensive studies of demersal fish assemblages along the nearshore coast and bays (L. G. Allen 1985). In general, studies were restricted to either bays or the nearshore coast. Only limited comparisons have been made between habitats. Although beam trawls were used for deeper surveys along the shelf and slope in the past (Gilbert 1896; Ulrey and Greeley 1928), they have not been used recently until the late 1980s (Kramer and Hunter 1987, 1988; L. G. Allen 1988; M. J. Allen and Herbinson 1990; Kramer 1990; MBC 1991; L. G. Allen et al., in press).

These studies have emphasized California halibut; the entire fish catch of these studies has not yet been described. However, Kramer (1990) described the flatfish catch of beam-trawl surveys along the San Diego County coast during 1987–88. Of the studies mentioned, all surveyed both bays and coast except L. G. Allen et al. (in press), which covered only the nearshore coast. Thus this study (which is a summary of the gray report, MBC 1990) is the first to examine the entire ichthyofauna of the bays and the

TABLE 7

Lengths of the Ten Largest and Smallest Fish Species Collected in Beam-Trawl Surveys off Southern California, April–September 1989

			Length (mm)				Number of fish	
Rank	Species	Common name	Min.	Max.	Mean	SD	Measured	Total
	Largest species							
1	*Torpedo californica*	Pacific electric ray	—	—	810.0	—	1	1
2	*Raja inornata*	California skate	—	—	539.0	—	1	1
3	*Rhinobatos productus*	shovelnose guitarfish	217	501	334.8	97.6	13	13
4	*Platyrhinoidis triseriata*	thornback	83	450	291.9	82.4	77	77
5	*Urolophus halleri*	round stingray	195	396	287.9	61.2	15	15
6	*Mustelus californicus*	gray smoothhound	—	—	275.0	—	1	1
7	*Menticirrhus undulatus*	California corbina	—	—	267.0	—	1	1
8	*Gymnura marmorata*	California butterfly ray	166	337	238.0	88.6	3	3
9	*Ophidion scrippsae*	basketweave cusk-eel	192	241	225.5	18.3	6	6
10	*Pleuronichthys decurrens*	curlfin sole	—	—	214.0	—	1	1
	Smallest species							
1	*Seriphus politus*	queenfish	3	64	11.3	5.5	5,761	8,997
2	*Cheilotrema saturnum*	black croaker	—	—	12.0	—	1	1
3	*Rimicola muscarum*	kelp clingfish	6.5	16	12.4	4.3	4	4
4	*Icelinus quadriseriatus*	yellowchin sculpin	11	18	13.3	4.0	3	3
5	*Liparis mucosus*	slimy snailfish	9	18	13.5	6.4	2	2
6	*Rimicola eigenmanni*	slender clingfish	—	—	14.0	—	1	1
7	*Genyonemus lineatus*	white croaker	3	208	14.7	20.8	2,411	7,200
8	*Atherinops affinis*	topsmelt	5	72	14.7	8.8	2,931	13,759
9	*Ilypnus gilberti*	cheekspot goby	3	50	15.9	3.6	5,259	7,309
10	*Atractoscion nobilis*	white seabass	5	65	16.0	15.7	22	22

Min. = minimum; Max. = maximum
See MBC 1990 for complete list of species.

nearshore coast off southern California using a beam-trawl survey.

Like any other net, a beam trawl is better suited for sampling some species and sizes of fish than others. Because of the small net mouth, beam trawls probably underestimate the density of large fish and of fast-swimming fishes. Thus actual fish densities are probably higher than the values presented here. Kramer (1990) examined the selectivity of the beam trawls used in this survey for different size classes of California halibut. The 1.0- and 1.6-m beam trawls were equally effective at capturing halibut <80 mm SL, but the 1.6-m beam trawl was better at capturing larger halibut. However, the 1.6-m beam trawl captured more halibut <200 mm SL than did a 7.6-m otter trawl. Both the 1.0- and 1.6-m beam trawls probably have collection efficiencies of near 100% for 10-mm halibut (S. H. Kramer, MBC Applied Environmental Sciences, Costa Mesa, Calif, pers. comm.). The nets are probably similarly efficient for the small fish (10–15 mm) of other species that numerically dominate the catch for this study. However, efficiencies are likely to vary by size class and mobility of each species, and net-specific selectivities have not been established.

Estuaries and bays are important nursery grounds for some species of marine fishes (Moyle and Cech 1982), with juveniles of noncommercial species dominating southern California bays (L. G. Allen 1982). Fish density in the present study was about four times greater in the bays than on the semiprotected coast, and seven times greater than on the exposed coast; however, standard deviations were large. Density also varied greatly between the two bays examined. Fish density at Anaheim Bay was about six times greater than at Agua Hedionda Lagoon, where density was only slightly lower than that at the highest coastal site (Hermosa Beach).

In contrast, fish standing crop on the semiprotected coast was about 2.5 times greater than in the bays, and 1.4 times greater than on the exposed coast. Some of this difference may be due to the inclusion of more large fish in the catch of the 1.6-m net (as indicated by Kramer 1990). But it may be that most of the difference is due to a real reduction in the standing crop of larger fish in bays. Although standing crops were generally higher at semiprotected coastal sites than at exposed sites, the standing crop at Carlsbad (an exposed site) was slightly higher than that at Long Beach (a semiprotected site). It should be noted that a single large ray or flatfish can greatly influence the standing crop estimate for an area. For instance, the single Pacific electric ray taken in this survey weighed 6.8 kg (table 5) whereas the 13,759 topsmelt collected weighed 0.4 kg (MBC 1990). Because the beam trawl is less effective at capturing large fish (Kramer 1990), the standing crop of an area is probably greatly underestimated.

Thus the bay assemblage consisted of many small fish (mostly juveniles of larger species), whereas the nearshore coastal assemblage included more large fish. Although bays are apparently the best habitat for many small fish, and the coast the best place for larger fish, the semiprotected coast had the highest combined values of density and standing crop. Protection from swells is apparently important for small and juvenile fish, whereas many larger fish or species prefer (or at least are more abundant in) exposed habitats. The coast in general and the semiprotected habitat in particular had the highest number of species; however, the number of species and diversity per haul was similar in all habitats. In general, the exposed habitat appears to be a harsher environment that is suitable primarily for larger fishes.

Fish density was much greater at 0.5-m and 1.0-m stations than at deeper stations. This was due largely to the presence of topsmelt and cheekspot goby at these depths (MBC 1990). Topsmelt were found almost exclusively at 0.5 m, and cheekspot goby were most abundant at 0.5 and 1.0 m. Because topsmelt occur primarily in the upper few centimeters of the water column, the 0.5-m stations were the only ones that consistently included this portion of the water column in the sample (the 1.0-m beam trawl had a mouth opening that was 0.3 m high). Removal of these two species from the catch would reduce the fish density in shallow water to levels found at greater depths. The low standing crops at these shallow depths suggest that depths less than 1.0 m are unsuitable for larger fish.

Fish density was much greater in May than in the other months surveyed. This was primarily because there were large densities of topsmelt and white croaker in that month. Walker et al. (1987) noted a high abundance of atherinid larvae in coastal waters off San Onofre in spring 1978–80, with lower abundances in summer. In Anaheim Bay, peak spawning of topsmelt occurs in April and May (Klingbeil et al. 1975). Thus the high abundance of newly transformed topsmelt at this time is expected. However, Walker et al. (1987) noted highest abundances of white croaker larvae in winter or early spring, before the period sampled in this study.

The ichthyofauna of this study included species that appear only in bays and only along the coast, in addition to those that occupy both habitats. The primary bay assemblage (based on frequency of occurrence) consisted of cheekspot goby, bay pipefish, giant kelpfish, and California halibut. Topsmelt had the highest density, and spotted sand bass had the highest standing crop. The primary coastal assemblage consisted of speckled sanddab, spotted turbot, and California halibut. Dominant species in the semiprotected habitat were white croaker by density and spotted turbot by standing crop. Dominant species in the exposed habitat were queenfish by density and California halibut by standing crop.

In the bays, California halibut populations consisted primarily of juveniles, whereas cheekspot goby, bay pipefish, and giant kelpfish populations included the entire size range of the species. Giant kelpfish and bay pipefish are ambushing species that are probably associated primarily with eelgrass (*Zostera marina*) beds; bay pipefish has a syringelike feeding mechanism and eats amphipods and copepods (Hart 1973), whereas giant kelpfish can eat crustaceans and fish (Feder et al. 1974). Cheekspot goby and California halibut live primarily on the bottom. Cheekspot goby prefers sandy bottoms (Brothers 1975) and feeds on small crustaceans. California halibut generally has a larger mouth and probably eats larger prey. Small halibut feed on amphipods and cumaceans (L. G. Allen 1988).

Although occurring less frequently than some species in this study, juvenile topsmelt constituted most of the fish in bays. Topsmelt are generally the most abundant bay species in southern California (L. G. Allen 1982). All topsmelt captured in this survey were age-0 fish, the largest being 72 mm SL; topsmelt measure 65–100 mm SL by the end of the first year (L. G. Allen 1980). Age-0 topsmelt feed primarily on detritus and planktonic crustaceans (Klingbeil et al. 1975).

The high standing crop of spotted sand bass indicates that the bay is an important habitat for larger juveniles and adults of this species. It is a permanent resident of bays (Dixon and Eckmayer 1975; Klingbeil et al. 1975) and a cruising generalist that eats fish and crustaceans (Feder et al. 1974).

Along the coast, the most common species were flatfishes, represented by both juveniles and adults. Speckled sanddab, the most common species, is a generalist that feeds on benthic and nektonic prey (Ford 1965; M. J. Allen 1982); spotted turbot feeds on sessile anemones and polychaetes (Luckinbill 1969); and California halibut ambushes nektonic prey (Haaker 1975; M. J. Allen 1982). Both spotted turbot (a benthic feeder) and California halibut (an ambusher) had high standing crops on the coast.

Although not common, larval and small juvenile queenfish and white croaker were the most abundant fishes captured along the coast. Larvae of both species are most abundant near the bottom in the depth range sampled in this survey (Barnett et al. 1984). The beam trawl probably underestimated the density of white croaker and queenfish because it only samples to 0.4 m above the bottom. The number caught might have been much greater if the net sampled to 1.0 m above the bottom. Larvae and juveniles of these species probably eat copepods.

The cheekspot goby and California halibut were relatively abundant in both bay and coastal habitats; along the coast they were most abundant in semiprotected coastal areas. The cheekspot goby apparently does not occur widely in Anaheim Bay, being found primarily near the entrance (Klingbeil et al. 1975). In this study it was most abundant in enclosed bays but was moderately abundant in southeastern Santa Monica Bay at Hermosa Beach, a semiprotected coastal habitat (MBC 1990). Larvae of this species are known to be abundant along the nearshore coast (Barnett et al. 1984), but benthic juveniles have not been previously reported from the coast.

Although small juvenile California halibut are generally most abundant in bays (Haaker 1975; L. G. Allen 1988; M. J. Allen and Herbinson 1990; Kramer 1990), relatively high densities are sometimes found in southeastern Santa Monica Bay (M. J. Allen and Herbinson 1990; L. G. Allen et al., in press). Cheekspot gobies are considered to be an important food for juvenile halibut in bays (Drawbridge 1990). The absence of these gobies along the coast has been suggested as a possible reason for poor survival of juvenile California halibut on the coast (Kramer 1990). The relatively high coastal densities of these typical bay forms in southeastern Santa Monica Bay suggest that this semiprotected region shares some characteristics of the enclosed embayments of southern California. Because natural semiprotected coasts are rare along the mainland of southern California, the physical environment and microichthyofauna of southeastern Santa Monica Bay should be studied further. As bay and lagoon habitats of southern California become depleted, semiprotected coastal habitats may become increasingly important as alternative nursery grounds for some species.

Soft-bottom habitats along the coast generally do not have attached algae or seagrasses. However, eelgrass is often abundant in bays. As noted above, some bay species (e.g., giant kelpfish, bay pipefish) were probably associated with eelgrass beds. Along the coast, the dominant vegetation on soft bottoms is drift algae, consisting largely of red algae and kelp. Beds of drift algae are often extensive along the bottom of the nearshore coast, but they are only temporary. Along the coast, barcheek pipefish (*Syngnathus exilis*) was the primary species associated with drift-algae beds. But these beds probably provide cover for many transforming juveniles of other species, including white seabass, *Atractoscion nobilis* (L. G. Allen and Franklin 1988; Donoho 1990). Thus coastal drift-algae beds are a potentially important nearshore habitat on soft bottoms, and warrant further examination.

CONCLUSIONS

A beam-trawl survey of the southern California coast indicated that bay and nearshore coastal soft-bottom habitats differ in fish densities, standing crops, and species composition; semiprotected coastal habitats share some biological and physical attributes of bay and exposed coastal habitats.

Fish density decreased from bays to the exposed coast; however, standing crops were highest in semiprotected coastal areas and lowest in bays.

Fish density decreased with increasing depth, whereas standing crops increased with increasing depth; high densities at 0.5 and 1.0 m were primarily due to high densities of topsmelt and cheekspot goby.

Although standing crops increased from May to September, density was much higher in May than in any other month, because of large numbers of juvenile topsmelt and white croaker.

The ichthyofauna generally consisted of species that were characteristic of either bay or coastal habitats, but some species occurred in both areas; some coastal species were substantially more abundant in semiprotected habitats, whereas others were more abundant in exposed habitats.

In constrast to coastal fishes, bay fishes were typically small. Several species were probably associated with eelgrass beds. Drift-algae beds along the coast probably provide cover for newly transformed juveniles of some species.

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THE SHALLOW-WATER FLATFISHES OF SAN DIEGO COUNTY

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ABSTRACT

Seven species of flatfish live in the shallow marine waters (depth 14 m) of San Diego County: California halibut, *Paralichthys californicus*; fantail sole, *Xystreurys liolepis*; speckled sanddab, *Citharichthys stigmaeus*; spotted turbot, *Pleuronichthys ritteri*; hornyhead turbot, *Pleuronichthys verticalis*; diamond turbot, *Hypsopsetta guttulata*; and California tonguefish, *Symphurus atricauda*. Speckled sanddab was most abundant, representing 79% of the flatfish catch. California halibut had the highest biomass, and represented 46% of the catch.

Only California halibut and diamond turbot used bays as nursery areas; they had distinct ontogenetic distributions, with length increasing with depth. The remaining species settled on the open coast but were not found together during early juvenile stages; they settled at different depths, and at different times of the year. Older juveniles and adults partitioned the habitat by eating different foods and by living at different depths and locations.

Life histories of nearshore flatfishes varied widely: speckled sanddab settled at a large size on the open coast and matured rapidly, whereas California halibut settled at a small size, used bays as nurseries, and delayed maturity.

RESUMEN

Siete especies de lenguados viven en aguas marinas someras (profundidad de 14 m) en el condado de San Diego: *Paralichthys californicus, Xystreurys liolepis, Citharichthys stigmaeus, Pleuronichthys ritteri, P. verticalis, Hypsopsetta guttulata,* y *Symphurus atricauda. Citharichthys stigmaeus* fué la especie mas abundante representando un 79% de la captura de lenguado. *Paralichthys californicus* presentó la mayor biomasa y un 46% del lenguado capturado.

Solamente *Paralichthys californicus* y *Hypsopsetta guttulata* utilizaron bahías como zonas de cría. Estas dos especies presentan distribuciones características durante la ontogénesis, con aumento de longitud del individuo con profundidad. Las otras especies se establecieron en la costa pero no coincidieron durante los períodos juveniles más tempranos: se establecieron a diferentes profundidades, y en tiempos del año diferentes. Los juveniles más viejos y los adultos dividieron el habitat comiendo alimento diferente y viviendo a profundidades y localidades diferentes.

Los ciclos de vida de los lenguados en aguas de poca profundidad variaron ampliamente: *Citharichthys stigmaeus* se estableció después de alcanzar tamaño grande y maduró rapidamente, mientras que *Paralichthys californicus* se estableció con tamaño pequeño, utilizó las bahías como áreas de cria, y demoró la maduración.

INTRODUCTION

Flatfishes (order Pleuronectiformes) have complex life histories of pelagic eggs and larvae and demersal adults. Larvae are symmetrical, but transform into asymmetrical juveniles (both eyes on one side of the head) that settle to the bottom. The duration of the pelagic larval stage and the size at transformation vary among flatfishes, but the general trend is toward longer pelagic larval stage and larger settlement size with increasing depth of adult habitat (Moser 1981).

Interspecific differences in morphology among flatfishes result in interspecific differences in soft-bottom resource use. For example, flatfishes can be divided into two groups: species that have large, symmetrical mouths and feed on fish and large crustaceans living on or above the bottom, and species that have small, asymmetrical mouths and feed on worms and small crustaceans living on or in the substrate (Allen 1982).

Off southern California, Pleuronectiformes are the most abundant soft-bottom fishes caught in otter trawls (Allen 1982). Reports of bottom-trawl surveys off southern California lack information on size-specific abundance of soft-bottom species (Allen 1982; DeMartini and Allen 1984; Love et al. 1986). Most of these surveys sampled depths greater than 12 m.

The objective of this paper is to describe the size-specific distribution and abundance of the seven most abundant flatfish species found along the shallow open coast and bay habitats of southern California. The organization and dynamics of the flatfish assemblage will be discussed in light of these findings.

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MATERIALS AND METHODS

Monthly collections were taken on the open coast and in bays from September 1986 to September 1988, and followed a stratified random design (for details see Kramer 1990a). Four blocks were sampled that represented 40 n.mi. of the open coast between Mission Bay and San Onofre: San Onofre, offshore of Agua Hedionda Lagoon, Torrey Pines, and Mission Beach (figure 1).

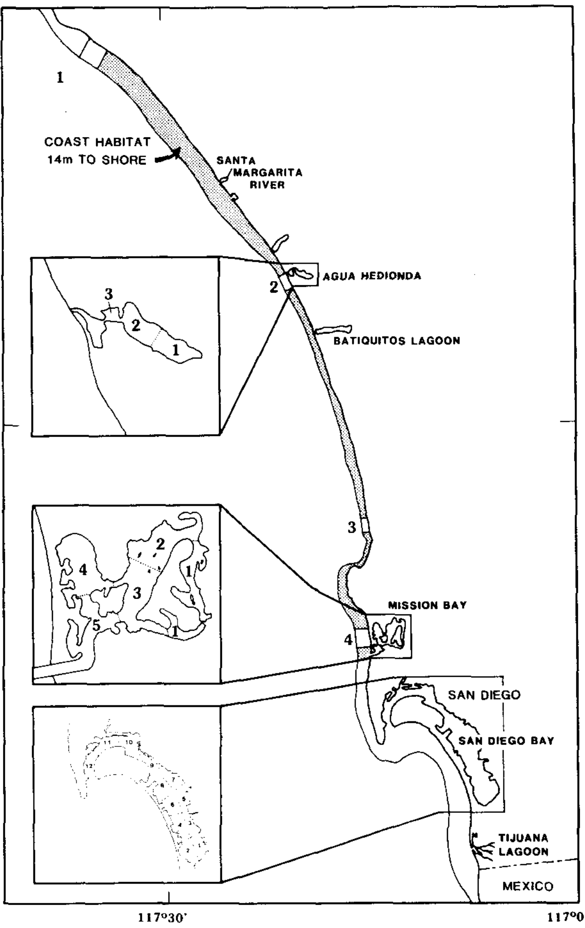

Figure 1. Map of location of sampling blocks. Open-coast blocks are (*1*) San Onofre, (*2*) adjacent to Agua Hedionda Lagoon, (*3*) Torrey Pines, and (*4*) Mission Beach. The two bays routinely sampled were Agua Hedionda Lagoon and Mission Bay, with sampling in San Diego Bay in June–July 1988.

The two bays sampled were Mission Bay and Agua Hedionda Lagoon. Each was divided into blocks of similar habitat (five blocks in Mission Bay, three in Agua Hedionda Lagoon) (Kramer 1990a). Three to four randomly selected isobaths were sampled within three depth strata for each block. On the open coast, the three depth strata were from about 5 m (near the first breaker line) to 8 m, 9 to 11 m, and 12 to 14 m. In bays, strata ranged from "shoreline" (<1 m) to "open water" strata of 1–2-m and 2–4-m depths. San Diego Bay was sampled in June and July 1988, by means of a similar design but with 12 blocks (figure 1). The area of each habitat was computed from navigational charts (Kramer 1990a).

Gear consisted of two beam trawls with mouth openings of 1.6 and 1.0 m, and a 1-by-6-m beach seine. Gear was lined or made of 3-mm mesh netting. A meter wheel was mounted on the trawls to track distance traveled along the bottom, and to allow estimation of the area swept by each trawl (Krygier and Horton 1975).

The 1.6-m beam trawl was fished from a small (15-m) vessel, and the 1.0-m beam trawl was fished from a skiff (5 m) or pulled by hand in shallow water (<1 m). The beach seine and 1.0-m beam trawl were pulled parallel to shore at depths <1 m, for a distance of 20–50 m.

All flatfishes taken in trawls and seines were measured (standard length [SL] in mm), and fish were selected at random and frozen for later analysis in the laboratory (Kramer 1990b). At the laboratory, each fish was thawed, measured (SL in mm), and weighed (wet weight in g). Biomass was estimated by converting standard lengths into wet weight using allometric equations describing the relationship between standard length and wet weight (Kramer 1990b).

Mean density (no./ha) was determined for flatfish species and their length classes by season, location, and depth. Five length classes were used for speckled sanddab: SL ≤40 mm, 41–60 mm, 61–80 mm, 81–100 mm, and >100 mm. Six 50-mm length classes were used for California halibut: SL ≤50 mm, 51–100 mm, 101–150, 151–200, 201–250, and >250 mm. For the remaining species, five 50-mm length classes were used: SL ≤50 mm, 51–100, 101–150, 151–200, and >200 mm. No corrections were made for bias due to gear type.

Seasonality of settlement was determined by the temporal pattern of settlement. For each species, "newly settled" individuals were classified by length; maximum was 10 mm above the minimum estimated transformation length in published literature (Ahlstrom et al. 1984).

Analysis of variance (ANOVA) was used to describe the variability in density by length class (density in no./ha) with respect to location (four open-coast blocks and two bays), season (fall 1986 through summer 1988), and depth (<5 m, 5–8 m, 9–11 m, 12–14 m). An accepted significance level of $P \leq 0.05$ was used for all analyses except where noted. Abundance was determined by multiplying the mean density for each habitat by the area of each habitat. Abundance estimates were summed for open coast and bay habitats.

RESULTS

Thirteen flatfish species representing three families were captured. Seven species belonged to the family Paralichthyidae (Hensley and Ahlstrom 1984): California halibut, *Paralichthys californicus*; fantail sole, *Xystreurys liolepis*; speckled sanddab, *Citharichthys stigmaeus*; Pacific sanddab, *Citharichthys sordidus*; longfin sanddab, *Citharichthys xanthostigma*; gulf sanddab, *Citharichthys fragilis*; and bigmouth sole, *Hippoglossina stomata*. Five species were of the family Pleuronectidae: spotted turbot, *Pleuronichthys ritteri*; hornyhead turbot, *Pleuronichthys verticalis*; curlfin turbot, *Pleuronichthys decurrens*; English sole, *Parophrys vetulus*; and the diamond turbot, *Hypsopsetta guttulata*. California tonguefish, *Symphurus atricauda*, was the only member of the family Cynoglossidae.

The total number of flatfishes caught was 32,546; seven of the thirteen species accounted for >99% of the catch (California halibut, speckled sanddab, spotted turbot, hornyhead turbot, fantail sole, diamond turbot, and California tonguefish). Paralichthyidae represented 91.9% of the catch, followed by by Pleuronectidae with 7.7%, and Cynoglossidae with 0.4%. Three species of paralichthyid flatfishes accounted for 91.89% of the catch (California halibut, speckled sanddab, and fantail sole), and three species of pleuronectid flatfishes accounted for 6.9% (spotted, hornyhead, and diamond turbots).

Total biomass of the seven most abundant flatfish species was estimated at 662 kg. Paralichthyidae represented 68.3% of the total biomass, followed by Pleuronectidae with 31.3%, and Cynoglossidae with 0.4%.

The sampling design covered only a portion of the depth range of many species, and the beam trawls undersampled California halibut and probably other flatfishes >250 mm SL relative to otter trawls (Kramer 1990a). For example, speckled sanddab is small (maximum length = 144 mm SL) and is probably sampled effectively by the gear; however, the species is abundant at greater bottom depths than those sampled (depths of maximum abundance 5 to 40 m; figure 2). Thus abundance estimates did not fully represent the entire population of any species.

Density, abundance, and distribution of tonguefish were poorly estimated in this study because of their diurnal behavior. Tonguefish is nocturnally active: it remains buried in the sand or mud during the day and feeds at night. Tonguefish is the only flatfish in southern California coastal waters that has diel behavior that affects availability to trawling (DeMartini and Allen 1984).

Size Range (Figure 2)

Speckled sanddab was the smallest flatfish species captured (5–135 mm SL), followed by California tonguefish (21–208 mm). Spotted turbot (7.5–237 mm), diamond turbot (7–266 mm), and hornyhead turbot (10–265 mm) were similar in size: spotted turbot and diamond turbot have a maximum recorded length of 375 mm SL, whereas hornyhead turbot has a maximum recorded length of 290 mm (Miller and Lea 1972).

The largest flatfishes were California halibut and fantail sole. Fantail sole ranged from 7.5 to 340 mm SL, but has a maximum recorded length of 423 mm (Miller and Lea 1972). California halibut was the largest flatfish taken in this survey; standard length ranged from 6.1 to 600 mm, which is considerably less than the maximum recorded length of about 1,300 mm (Miller and Lea 1972).

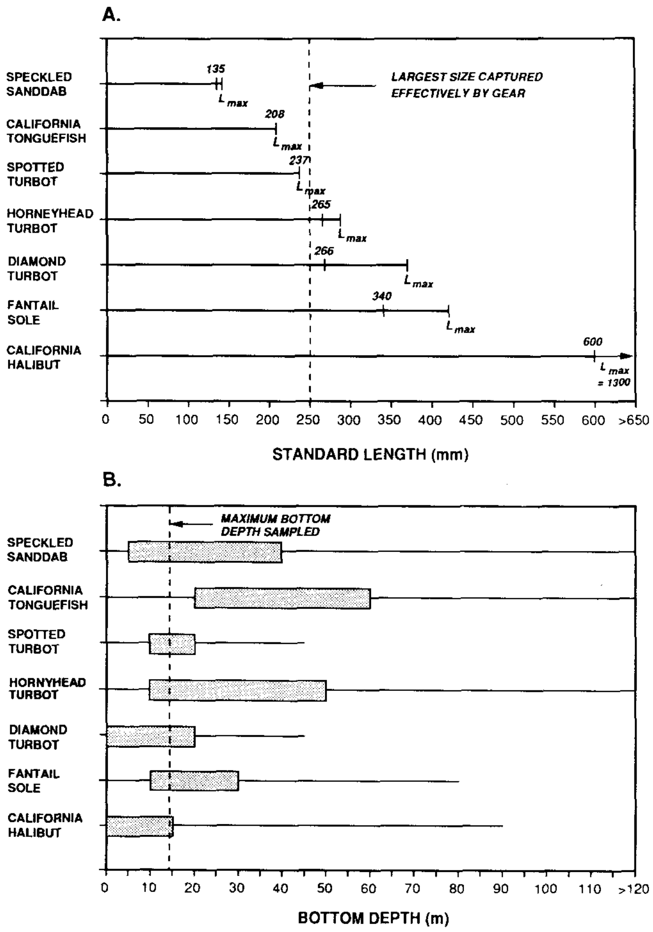

Figure 2. *A*, Maximum standard length and range captured effectively by sampling gear. *B*, Maximum depth, depths of maximum abundance, and outer bound of sampling depth. Lengths and depths obtained from literature (Ford 1965; Miller and Lea 1972; Allen 1982; DeMartini and Allen 1984; Love et al. 1986).

Catch Statistics (Figure 3)

Numbers captured. Speckled sanddab was the most abundant flatfish (25,298 fish), and represented 78.6% of the flatfish catch. Distribution of speckled sanddab varied in both space and time; 45% were caught at Torrey Pines, and 27.1% were caught in spring 1988. Almost all (99.6%) speckled sanddab were found on the open coast, and most were caught deeper than 10 m.

California halibut ranked second in number captured (4,085), and represented 12.6% of the flatfish catch. Most halibut were caught in bays: 60.2% came from Mission Bay and Agua Hedionda Lagoon, and 46.2% from Mission Bay alone. The total number of halibut captured decreased with depth.

Spotted turbot followed California halibut (956), and represented 2.9% of the flatfish catch. Greatest numbers (36.3%) were caught at Mission Beach. Most spotted turbot were caught on the open coast (83.9%); some were taken in the outer areas of Mission Bay.

Diamond turbot was fourth in number taken (848), representing 2.6% of the flatfish catch. Most diamond turbot were caught in bays — 43% in Mission Bay and 40% in Agua Hedionda Lagoon. The number captured decreased with depth.

Hornyhead turbot ranked fifth in number (423), and represented 1.3% of the flatfish catch. Most hornyhead turbot (33.3%) were caught at Torrey Pines. Only four were caught in bays (0.9%), all in the entrance channel to Mission Bay. Hornyhead turbot increased in abundance with depth.

Fantail sole ranked seventh in numerical abundance (228), and represented 0.7% of the flatfish catch. Most (99.1%) fantail sole came from the open coast, and 45% were taken offshore of Agua Hedionda Lagoon.

California tonguefish ranked seventh in numerical abundance (129), and represented 0.4% of the flatfish catch. Mission Bay yielded 48% of the California tonguefish catch.

Biomass. California halibut had the highest biomass at 307.0 kg, or 46.4% of the flatfish biomass. Highest biomass was on the open coast offshore of Agua Hedionda Lagoon (67.3 kg, or 21.9% of the halibut biomass, and 10.2% of the flatfish biomass). Total biomass increased with depth to 11 m, and then declined.

Spotted turbot was second highest, at 117.5 kg, or 17.8% of the flatfish biomass. Highest biomass was at Mission Beach (46 kg, or 39.2%), followed by Carlsbad (29.4 kg, or 25%). Biomass was highest in the 9–11-m depth stratum on the open coast.

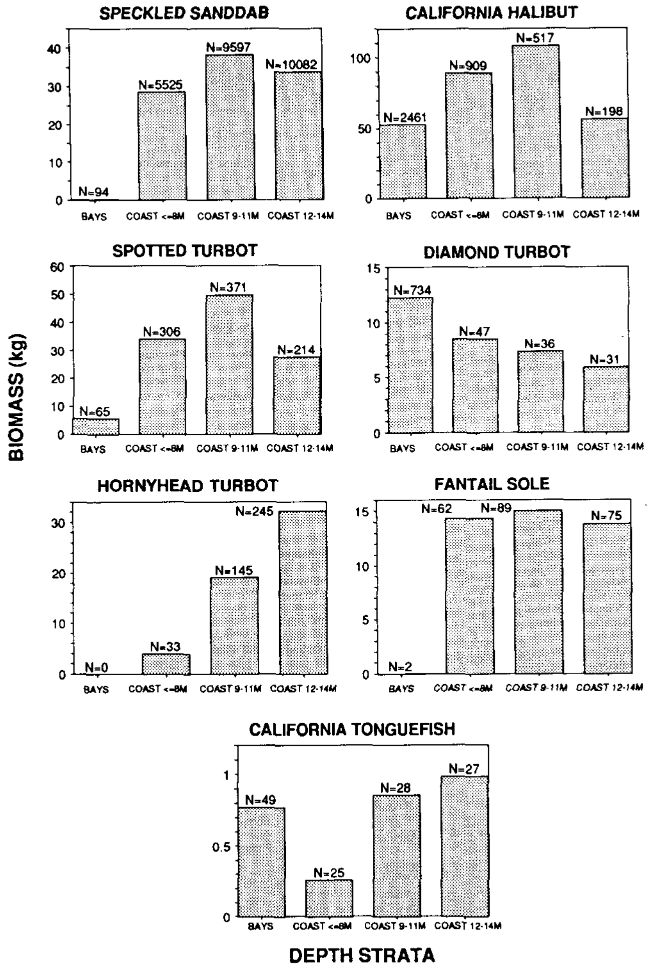

Figure 3. Total biomass and number captured by depth stratum for seven flatfish species.

Biomass of speckled sanddab was 101.0 kg, and ranked third (15.3%) in flatfish biomass, followed by hornyhead turbot with 55.4 kg, or 8.4% of flatfish biomass. Hornyhead turbot biomass increased with increasing bottom depth.

Fantail sole ranked fifth in biomass, with a total of 43.3 kg, or 6.6% of the flatfish biomass. Biomass was relatively constant across all open-coast depth strata, and ranged from 14 to 16 kg.

Diamond turbot had the sixth highest total biomass, at 34.3 kg, or 5.2% of the total biomass. Biomass was highest in bays (12.5 kg, or 36.5%), and decreased with depth.

Biomass of tonguefish was the lowest, at 2.9 kg, or 0.5% of the flatfish biomass. Greatest biomass was in Mission Bay (1.0 kg, or 35%). Biomass on the open coast increased with depth.

Variations in Density[2]

Depth. Density of speckled sanddab and hornyhead turbot varied significantly with depth (F = 387.1, df = 3, 3516, $P < 0.01$; and F = 52.7, df = 3, 3516, $P < 0.01$, respectively), and increased with depth. Speckled sanddab density increased from a mean of 272.5/ha (SE = 17.5) in the shallowest open coast stratum (5–8 m) to 630.8/ha (SE = 50.7) in the deep stratum (12–14 m). Hornyhead turbot increased from 1.24/ha (SE = 0.36) in the shallowest open-coast stratum to 16.2/ha (SE = 1.36) in the deepest stratum.

Density of California halibut also differed significantly with depth (F = 37.6, df = 3, 3516, $P <$ 0.01). The smallest length class ($\leq$50 mm) was most dense in bays (mean = 46.7, SE = 4.5), and decreased with depth on the open coast (shallowest coastal stratum mean = 11.7, SE = 2.7; deepest coastal stratum mean = 1.9, SE = 1.0). Density of the larger classes increased with depth; the largest class (>250 mm) was least dense in the bays (mean = 0.5, SE = 0.1) and most dense in the deepest coastal stratum (mean = 5.7, SE = 0.6). Halibut <150 mm were found primarily in the bays; larger halibut were found on the open coast.

Density of spotted turbot differed significantly with depth (F = 12.9, df = 3, 3516, $P < 0.01$). Spotted turbot was most dense in the shallow and mid-depth strata (5–11 m) on the open coast ($\text{mean}_{\text{shallow}}$ = 20.7/ha, SE = 1.9; $\text{mean}_{\text{middle}}$ = 21.5/ha, SE = 1.5), with the lowest open-coast density in the deep stratum ($\text{mean}_{\text{deep}}$ = 14.5, SE = 1.1). Lowest densities were found in bays, with a mean of 2.1/ha (SE = 0.4). Spotted turbot were found in shallow coastal habitats, but not in bays (figure 4).

Density of tonguefish in the 151–200-m class varied significantly with depth (F = 5.7, df = 3, 3516, $P < 0.01$). However, the smallest (<50 mm) and the largest (151–200 mm) tonguefish were caught in deeper coastal waters (9 m), with intermediate length classes in shallow coastal water (<7 m) and in the bays (figure 4).

Density of fantail sole did not vary significantly with depth for any of the length classes (F = 2.2, df = 3, 3516, $P > 0.05$).

Location. Densities of California halibut and diamond turbot differed significantly with location (F = 33.0, df = 5, 3516, $P < 0.01$; and F = 47.0, df = 5, 3516, P < 0.01, respectively). These fish were most dense in bays, where there were seasonally high concentrations of juveniles. The highest density of diamond turbot occurred during the period of peak settlement of juveniles, with a maximum of 864/ha (SE = 248) in Agua Hedionda Lagoon in winter 1987, and 51.8/ha (SE = 20) in Mission Bay in spring 1987. Halibut was also most dense during settlement of juveniles, with a maximum of 188/ha (SE = 15.7) in Mission Bay in spring 1987, and 797/ha (SE = 410) in Agua Hedionda Lagoon in winter 1987.

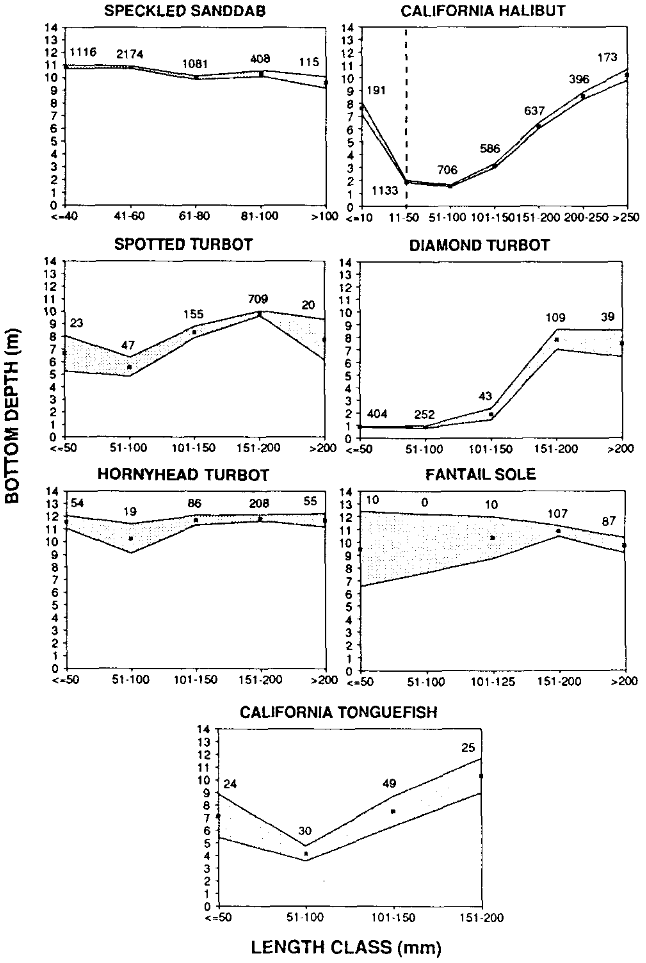

Figure 4. Mean bottom depth of standard length classes for seven flatfish species.

There were more California halibut and diamond turbot at open coast locations adjacent to bays than in areas far from bays. Density in bays ranged from 36.5/ha (SE = 2.9) offshore of Agua Hedionda Lagoon to 12.1/ha (SE = 1.3) at San Onofre. Maximum coastal densities of diamond turbot were at Mission Beach, ranging from 1.3/ha (SE = 0.85) in fall 1986 to 12.7/ha (SE = 3.6) in fall 1987. Density of diamond turbot in the >250-mm class did not vary significantly with location (F = 0.6, df = 5, 3516, P = 0.71).

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[2] Tables of density for each species by sample block, quarter, and length class are available in Kramer 1990b.

Density of spotted turbot differed significantly with location ($F = 66.0$, df = 5, 3516, $P = 0.01$). There were more spotted turbot on the open coast than in bays, with highest density at Mission Beach (mean = 28.5/ha, SE = 2.0) and lowest at Agua Hedionda Lagoon (mean = 0.30/ha, SE = 0.30). The open coast offshore of Agua Hedionda Lagoon had the second highest density (mean = 17.8/ha, SE = 1.4), with lowest open-coast densities at the two locations farthest from bays ($\text{mean}_{\text{Torrey Pines}} = 9.1$/ha, SE = 1.2; $\text{mean}_{\text{San Onofre}} = 7.2$/ha, SE = 0.9).

Density of speckled sanddab also differed significantly between coastal locations ($F = 138.4$, df = 3, 1004, $P < 0.01$); highest density was at Torrey Pines (overall mean = 948.3/ha, SE = 73.0); the lowest was at San Onofre (mean = 180.9/ha, SE = 13.5). Highest density obtained in a single tow was 8,463/ha, or nearly $1/\text{m}^2$, and was taken in the deep stratum at Torrey Pines in summer 1988.

Density of hornyhead turbot, fantail sole, and California tonguefish also varied significantly with location, except for the following rare length classes: hornyhead turbot 51–100 mm; fantail sole juveniles ≤50 mm; and tonguefish 51–100 mm. Like speckled sanddab, hornyhead turbot was most dense on the open coast at Torrey Pines (mean density = 12.7/ha, SE = 1.42), and least at San Onofre (mean = 1.65/ha, SE = 0.38). The highest density of >200-mm fantail sole was also at Torrey Pines, with a mean of 2.58/ha (SE = 0.5). Tonguefish was most dense on the open coast offshore of Agua Hedionda Lagoon (mean = 3.1/ha, SE = 0.62), and least at Torrey Pines (mean = 0.24/ha, SE = 0.17).

Seasonality. Density of speckled sanddab, California halibut, diamond turbot, and hornyhead turbot varied significantly with season. Most of the seasonal variability was due to settlement of juveniles in the smallest length classes. Highest densities of speckled sanddab were obtained in spring and summer of 1988 (overall mean summer = 630.8, SE = 50.7). These high densities were due to large numbers of small juveniles in the ≤40-mm length class ($\text{mean}_{\text{spring}} = 495.2$, SE = 41.9; $\text{mean}_{\text{summer}} = 405.3$, SE = 49.3). Lowest density occurred in winter 1987 (overall mean = 102.5, SE = 11.4).

California halibut ≤50 mm had maximum densities in winter (mean = 63.9/ha, SE = 17.6) and spring of 1987 (mean = 96.9/ha, SE = 13.6), and in spring (mean 43.5/ha, SE = 6.2) and summer 1988 (mean = 34.0/ha, SE = 5.1).

Density differed significantly with season only for diamond turbot ≤50-mm, and did not differ significantly for the larger classes ($P_{\text{SL101–150 mm}} = 0.07$, $P_{\text{SL151–200 mm}} = 0.75$, $P_{\text{SL201–250 mm}} = 0.52$, and $P_{\text{SL>250 mm}} = 0.39$). Overall density was greatest in winter and spring, with mean densities ranging between 40.0/ha (SE = 8.75) in spring 1988 to 56.0/ha (SE = 13.4) in spring 1987. These peaks were due to settlement of juveniles.

Density of hornyhead turbot varied significantly with season for the ≤50-mm, 101–150-mm, and 151–200-mm length classes. The 51–100-mm and >200-mm classes did not differ significantly with season ($P_{\text{SL50–100 mm}} = 0.61$, $P_{\text{SL>200 mm}} = 0.14$), and were relatively rare, with maximum seasonal densities of 0.82/ha (SE = 0.55) for the 51–100-mm class and 2.47/ha (SE = 0.77) for the >200-mm class.

Density of large fantail sole (>151 mm) also differed significantly with respect to season. No fantail sole between 51 and 100 mm were caught. The fish were relatively uncommon, with overall densities ranging from 0.82/ha (SE = 0.23) in summer 1988 to 2.96/ha (SE = 0.53) in fall 1986.

There were no seasonal patterns in density of spotted turbot or California tonguefish. Spotted turbot ranged from a low mean density of 5.2/ha (SE = 1.1) in winter 1987 to a high of 11.9/ha (SE = 1.7) in spring 1987. The 151–200-mm class was most dense, regardless of season, and ranged from 2.7/ha (SE = 0.6) in winter 1987 to 7.8/ha (SE = 1.2) in spring 1987.

Relationship between Size and Depth (Figure 4)

There were insignificant or weak linear relationships between length and depth of capture for speckled sanddab, hornyhead turbot, fantail sole, tonguefish, and spotted turbot. California halibut length was positively correlated with depth, which suggests ontogenetic changes in depth distribution (Allen 1982; Plummer et al. 1983). The relationship between standard length (mm) and depth of capture (m) is:

$$\text{SL} = 14.87 \star \text{DEPTH} + 48.19$$

(SE slope = 0.29, $r^2 = 0.40$, $n = 3898$). Transforming stages (SL ≤ 10 mm) were found on the open coast, with small juvenile halibut in bays at depths of 4 m and less, and larger halibut in the deeper coastal strata (>12 m).

Diamond turbot had a similar ontogenetic depth distribution to halibut, with the smallest individuals in the shallowest habitats. The linear regression describing standard length at depth of capture is:

$$\text{SL} = 15.12 \star \text{DEPTH} + 41.27$$

($r^2 = 0.59$, SE slope = 0.43, $n = 848$). Like halibut, small juvenile diamond turbot use bays as nursery areas.

Size and Season of Settlement (Figure 5)

Diamond turbot larvae are the smallest of the flatfishes at transformation, ranging from 4.4 to 8.8 mm SL (Ahlstrom et al. 1984). Juveniles of $\leq$14 mm were considered "newly settled"; 51 newly settled juveniles were caught—45 (88%) in winter 1988. All settlement occurred in bays, in the blocks farthest from the entrances.

Length at transformation of California halibut ranges from 7.5 to 9.4 mm SL (Ahlstrom et al. 1984). Juveniles $\leq$17 mm were considered newly settled. A total of 398 newly settled halibut was caught from February to May 1987 and from January to September 1988. Most newly settled halibut (271) were caught on the open coast in 1988, with over 50% (144) at Torrey Pines, followed by offshore of Agua Hedionda Lagoon (41, or 15%). Fewer newly settled halibut (127) were caught in 1987, and nearly all (124, or 97.6%) were in the bays. Of these, most settled in the blocks between the entrance and the middle of the bays.

Speckled sanddab larvae are the largest of the flatfish group at transformation, ranging in length from 24 to 35.5 mm SL (Ahlstrom et al. 1984). Juveniles of $\leq$35 mm were considered newly settled, and 7,456 newly settled speckled sanddab were caught in the survey. Although some settlement occurred throughout both years, peak settlement was between May and October in 1987, and from February until the end of the sampling program in September 1988. Speckled sanddab settlement was greatest in 1988, with over 50% at Torrey Pines (n = 2,920), followed by the open coast offshore of Agua Hedionda Lagoon (n = 1,614).

Newly settled juveniles of the remaining species were relatively rare. Spotted turbot, hornyhead turbot, and fantail sole all transform at a small size (Ahlstrom et al. 1984), and were considered newly settled at $\leq$17 mm SL. Only 4 newly settled spotted turbot were caught, in May and June 1988. Five newly settled hornyhead turbot were captured in August 1988 on the open coast offshore of Agua Hedionda Lagoon and at Torrey Pines. From March through September 1988, 4 newly settled fantail sole were captured: 2 in Mission Bay, and 2 on the open coast at Torrey Pines.

California tonguefish transform at a relatively large size (19–24.2 mm; Ahlstrom et al. 1984), with juveniles of $\leq$ 29 mm considered newly settled. Ten newly settled tonguefish were caught on the open coast at depths $\geq$9 m: 7 in fall 1986, and 3 from December 1987 through March 1988.

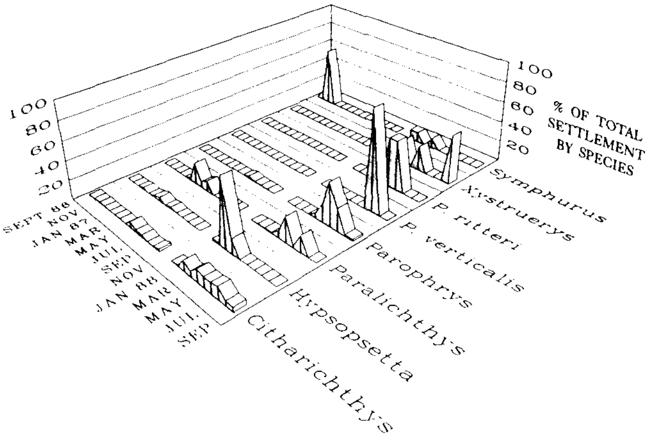

Figure 5. Settlement seasonality (percentage of newly settled fish by species each month) for eight flatfishes: speckled sanddab, *Citharichthys stigmaeus* (n = 7,456); California halibut, *Paralichthys californicus* (n = 398); spotted turbot, *Pleuronichthys ritteri* (n = 4); diamond turbot, *Hypsopsetta guttulata* (n = 51); hornyhead turbot, *Pleuronichthys verticalis* (n = 5); fantail sole, *Xystreurys liolepis* (n = 4); California tonguefish, *Symphurus atricauda* (n = 10); and English sole, *Parophrys vetulus* (n = 159).

Abundance Estimates

Speckled sanddab. Speckled sanddab was most abundant in 1988 (figure 6). Total abundance estimated for both spring and summer 1988 by location was: San Onofre, 1,562,539 (SE = 183,131), Agua Hedionda, 833,415 (SE = 71,099), Torrey Pines, 1,293,550 (SE = 154,833), and Mission Beach, 1,036,291 (SE = 98,419). Estimated abundance for spring and summer 1987 was significantly less than that for 1988. For example, abundance at Torrey Pines for both spring and summer 1987 was 372,317 (SE = 69,400), which is about one quarter of the abundance in 1988.

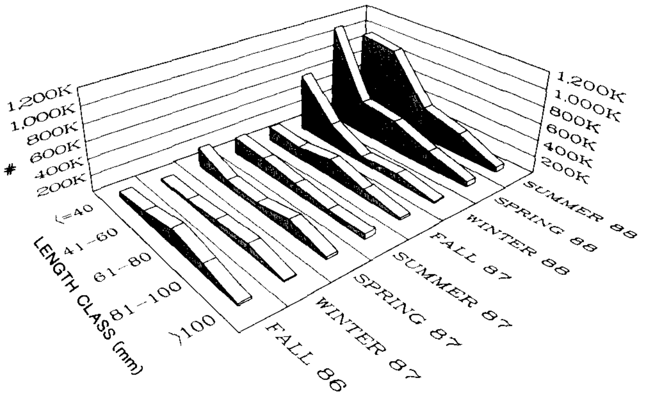

Figure 6. Total abundance of speckled sanddab estimated by season for the open coast.

California halibut. Nearly all halibut in the 51–100-mm length class were found in the bays, whereas most of the halibut in the 201–250-mm class were found on the open coast (figure 7).

In 1987, 50-mm juveniles were more abundant in bays than in 1988; conversely, they were more abundant on the coast in 1988 than in 1987. Abundance of halibut <50-mm summed over all habitats for both years differed significantly, being higher in 1987 than 1988 (n_{1987} = 227,055, SE = 17,623; n_{1988} = 155,407, SE = 16,966). Although settlement occurred on the open coast in 1988, juvenile halibut in the 51–100-mm length class were not found on the open coast.

Spotted turbot. Lack of small spotted turbot on the shallow open coast suggests that they did not use shallow habitats as a nursery area (figure 8). Density of spotted turbot in all except the 150–200-mm class appears to be underestimated or incompletely sampled.

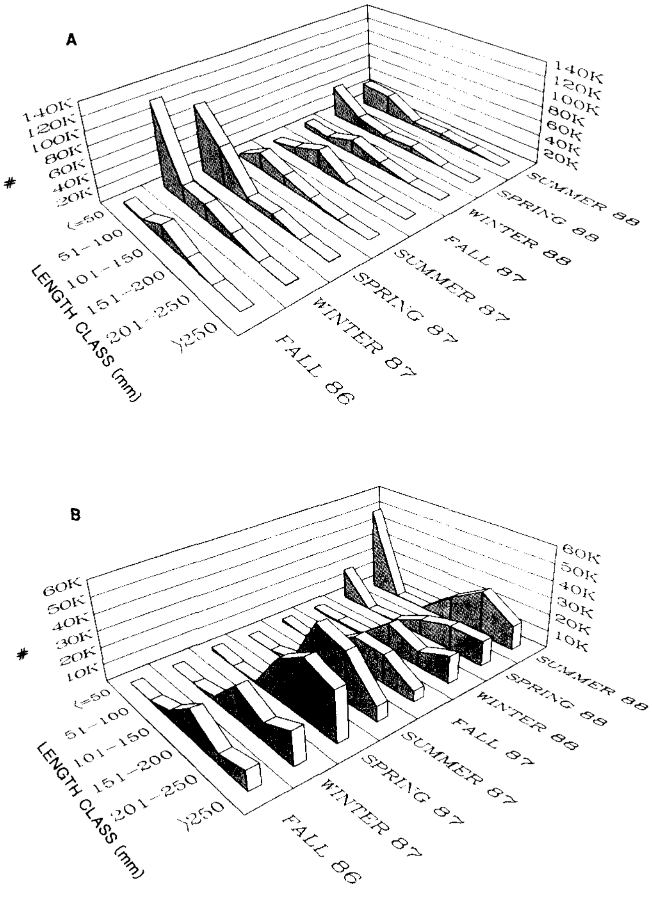

Figure 7. Total abundance of California halibut estimated by season for (*A*) bays and (*B*) open coast.

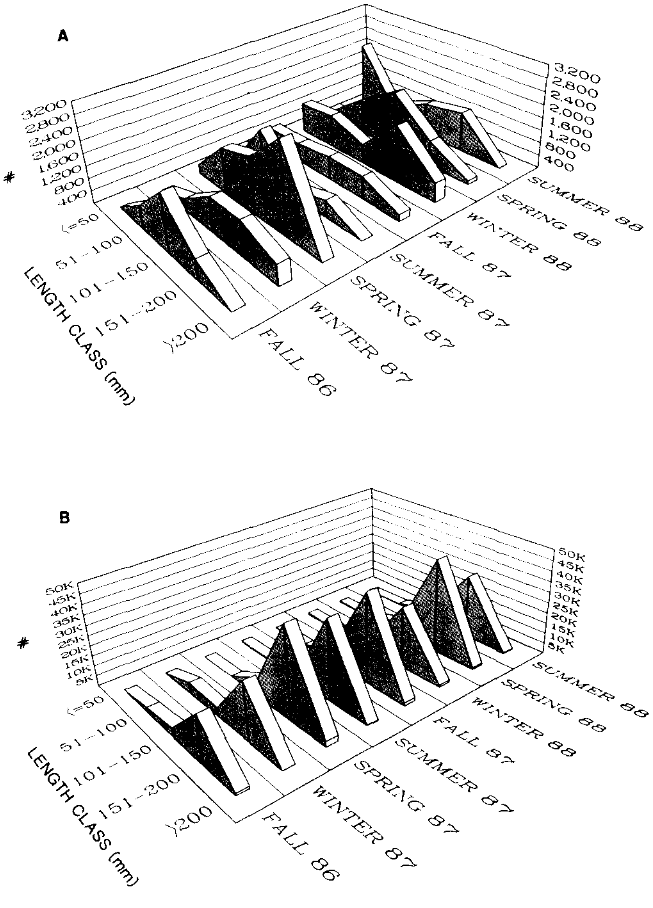

Figure 8. Total abundance of spotted turbot estimated by season for (*A*) Mission Bay and (*B*) open coast.

The most juvenile spotted turbot in the three smallest size classes (≤50, 51–100, and 101–150 mm) were found in the entrance channel to San Diego Bay during the June and July 1988 survey. Density of spotted turbot ≤50 mm ranged from 214 to 739/ha (mean = 473/ha, SE = 88), and was much higher than that at any other location.

Abundance of spotted turbot ≤50 mm at the San Diego Bay entrance (area = 600 ha) was 164,632 (SE = 53,433). Abundances of the 51–100, 101–150, and 151–200-mm length classes at the entrance to the bay were 12,432 (SE = 8,580), 35,640 (SE = 17,670), and 82,320 (SE = 26,452). These accumulations of small spotted turbot suggest that they may prefer the habitat at the entrance to San Diego Bay.

Total abundance of adults in the 151–200-mm class on the open coast ranged from a low of 23,000 (SE = 8,178) during fall 1986 to 45,264 (SE = 10,776) during spring 1988. Abundance was lower in the fall and winter than in the spring and summer (figure 8).

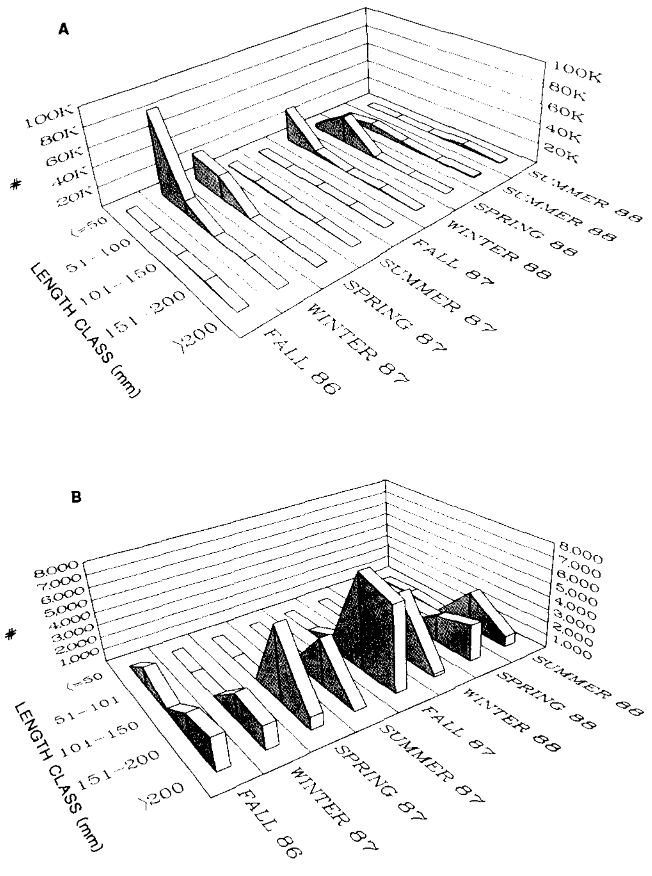

Figure 9. Total abundance of diamond turbot estimated by season for (*A*) bays and (*B*) open coast.

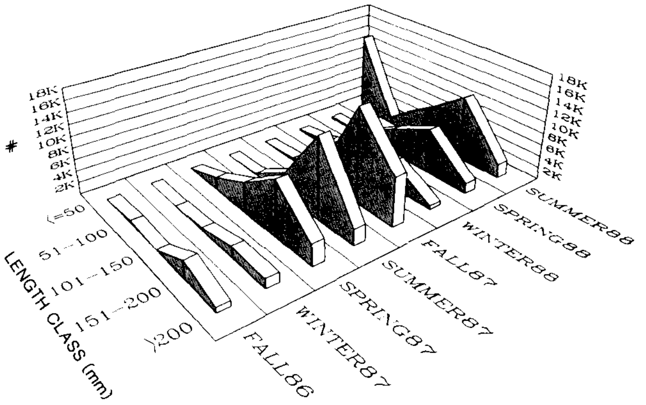

Figure 10. Total abundance of hornyhead turbot estimated by season for the open coast.

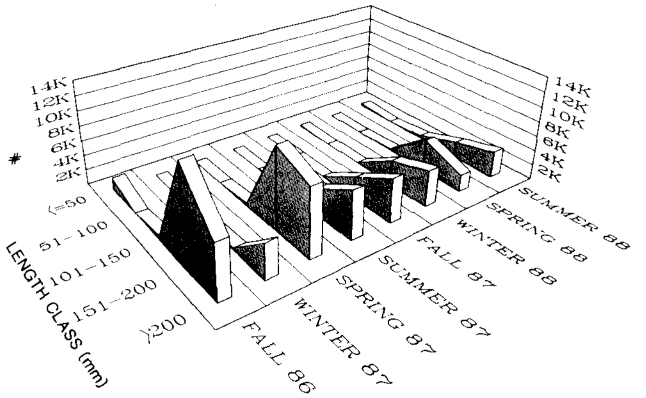

Figure 11. Total abundance of fantail sole estimated by season for the open coast.

Diamond turbot. The number of juvenile diamond turbot in bays appeared sufficient to support the adult population on the open coast (figure 9). Diamond turbot of 51–100 mm SL were most abundant in bays in spring, with 24,164 (SE = 554) in 1987 and 28,108 (SE = 580) in 1988. Maximum abundance of adults (151–200 mm) on the open coast was 7,632 (SE = 573) in fall 1987—considerably lower than the estimated production of juveniles from bays.

Hornyhead turbot. Hornyhead turbot ≤50 mm were most abundant on the open coast in summer 1988, with an estimated abundance of 13,853 (SE = 5,116) (figure 10). No small juveniles were caught on the open coast in 1987. Hornyhead turbot do not appear to use bays as nursery areas.

The 151–200-mm length class was most abundant, with greatest numbers in summer and fall of 1987: there were 14,006 (SE = 5,312) in summer and 16,210 (SE = 7,519) in fall on the open coast. Abundance was lower in winter, with 1,973 (SE = 1,973) in 1987 and 4,567 (SE = 2,151) in 1988. Winter lows and summer-fall peaks in abundance were consistent for both years of the survey, and may represent seasonal movements of adults across the shelf.

Fantail sole. Juvenile fantail sole <100 mm were rare or missing in collections, indicating that they did not use shallow habitats as nursery areas. Their nursery area is probably deeper than 15 m.

Abundance of adults on the open coast was comparable to abundance of diamond turbot and hornyhead turbot. Fantail sole in the 151–200-mm length class were most abundant in 1986 and 1987, with maximum seasonal abundance of 13,191 (SE = 1,161) in fall 1986, followed by 11,084 (SE = 791) in spring 1987 (figure 11). The abundance of >200-mm fantail sole ranged from 2,280 (SE = 360) in spring 1988 to 9,155 (SE = 755) in summer 1987. The fish appeared in the study in low numbers, without any obvious seasonal trends.

California tonguefish. Although density and abundance are underestimated, trends in the data are probably valid. Greatest density of tonguefish on the open coast was off Agua Hedionda Lagoon, with seasonal means ranging from 0 to 5.8/ha (SE = 2.35) for the 101–150-mm class and from 0 to 4.7/ha (SE = 1.79) for the 151–200-mm class (figure 12).

San Diego Bay had the highest density of tonguefish. Like spotted turbot, tonguefish were found primarily at the entrance of the bay (blocks 10–12, figure 1). The 51–100-mm class was most dense in the outermost block (block 12), with density ranging from 474 to 1,089/ha (mean = 705.9/ha, SE = 248.3). Density decreased farther into the bay, and was lower at block 10 (mean = 301.6/ha, SE = 143.5).

Estimated abundance of tonguefish in the 51–100-mm class from San Diego Bay was 368,303 (SE = 71,826). Tonguefish in the 51–100-mm class were caught in both Mission Bay and San Diego Bay, but not on the open coast.

Other Flatfish Species

Six additional flatfish species captured include *Citharichthys sordidus, C. xanthostigma, C. fragilis, Hippoglossina stomata, Pleuronichthys decurrens,* and *Parophrys vetulus*. Of the *Citharichthys* sp., *C. sordidus* and *C. fragilis* were rare, with only 6 fish captured along the open coast. Numbers captured and range in standard length were: *C. sordidus* (1; 21.5 mm) and *C. fragilis* (5; 18.3–24 mm). Longfin sanddab, *C. xanthostigma*, was more abundant: 96 were caught on the open coast. They ranged from 19.5 to 233 mm: 5 were <40 mm, and 91 were 129–233 mm. Only 1 *Hippoglossina stomata* (204 mm), and 8 *Pleuronichthys decurrens* (143–180 mm) were caught, all on the open coast.

English sole (*Parophrys vetulus*) was relatively uncommon: 262 were captured, and ranged from 10 to 295 mm. Most (159, or 61%) were newly settled, with standard length ≤30 mm (transformation length ca. 20 mm; Ahlstrom et al. 1984). Settlement occurred between May and September (figure 5). English sole were most abundant in summer 1988, when 134 fish, representing 51% of the English sole catch, were taken. Combined catch in spring and summer 1988 was 247, or 94% of the total catch of English sole.

There was no relationship between standard length and depth of capture; the mean bottom depth was 10.82 m for 50-mm fish (n = 207, SD = 2.48) and 10.81 m for 51–100-mm fish (n = 52, SD = 2.02). Only one English sole was taken from a bay, which suggests that in southern California, the open coast serves as a nursery.

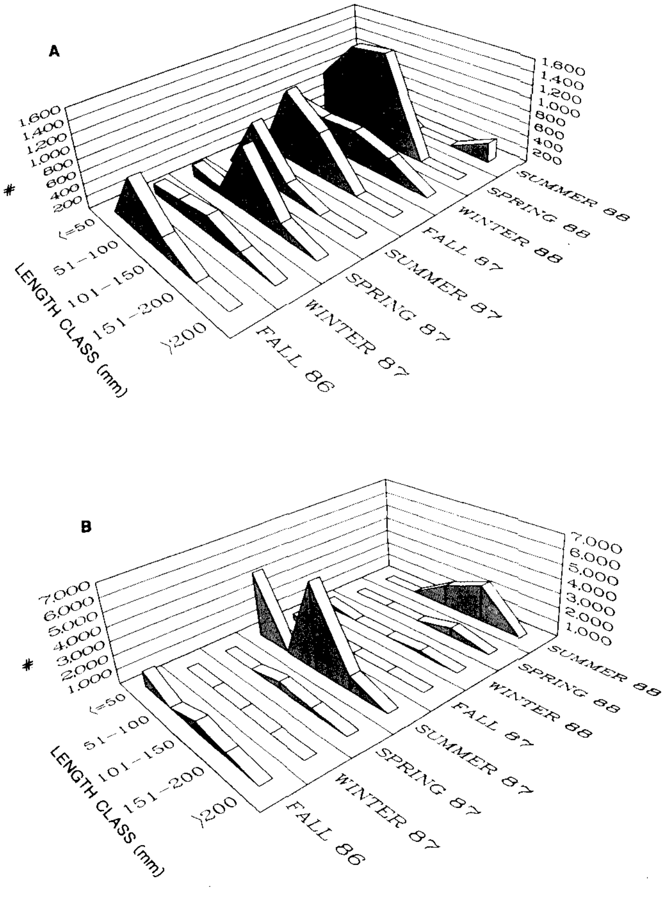

Figure 12. Total abundance of California tonguefish estimated by season for (*A*) Mission Bay and (*B*) open coast.

DISCUSSION

Season and Location of Settlement

Only California halibut and diamond turbot used bays as nursery areas, but timing and location of settlement were slightly different. Diamond turbot settled between January and March in back bays, whereas halibut settled primarily between March and September, either on the open coast or closer to the entrance in bays (figure 5). Both species settle at a small size (table 1) and spend little time in the plankton, perhaps as a strategy to decrease dispersal away from the nearshore habitats where adults spawn. Diamond turbot adults probably spawn in or near bays (Lane 1975), and halibut larvae are known to be distributed nearshore (Gruber et al. 1982; Barnett et al. 1984; Lavenberg et al. 1986; Moser and Watson 1990).

Tonguefish settled in the late fall and winter of both years, whereas spotted turbot settlement was observed only in May and June 1989 (figure 5). Spotted turbot and tonguefish both use nearshore nursery areas, probably including the entrance to San

TABLE 1
Key Life-History Characteristics of Inshore Flatfishes

A. Juveniles

Species	Size at settlement	Settlement location*	Settlement depth Mean	Settlement depth SD	Settlement depth *N*	Ontogenetic distribution
California halibut	≤17	B, C	5.05	3.67	398	Yes
Diamond turbot	≤14	B	1.25	0.46	51	Yes
Speckled sanddab	≤35	C, B	11.02	2.25	773	No
Fantail sole	≤17	C	6.35	5.91	4	No
Hornyhead turbot	≤17	C	8.84	2.54	5	No
Spotted turbot	≤16	C	9.19	4.35	4	No
California tonguefish	≤29	C, B	11.37	1.20	10	?

B. Adults

	Size at 1st maturity (a)	Maximum SL (mm)	Depth distribution	Major prey	Season of spawning†
California halibut	300 +	1274	≤15 (d,e,j,k)	Anchovies (b,e)	W,Sp,Su
Diamond turbot	160	373	≤20 (d,j,k)	Polychaetes (c)	W,F
Speckled sanddab	70	144	5–40 (d,e,j,k)	Mysids (d,e)	Sp,Su,F (g)
Fantail sole	160	423	10–30 (d,e,j,k)	Crabs (e)	Su,F
Hornyhead turbot	140	290	10–50 (d,e,j,k)	Polychaetes (e,f)	W,Sp,Su?,F? (h)
Spotted turbot	140	237	10–20 (d,j,k)	Anemones (e,f)	Sp,Su,F?,W?
California tonguefish	120	208	20–60 (d,e,j,k)	Amphipods (e)	Su,F? (i)

(a) Miller and Lea 1972; (b) Plummer et al. 1983; (c) Lane 1975; (d) Ford 1965; (e) Allen 1982; (f) Luckinbill 1969; (g) Goldberg 1987; (h) Goldberg 1982a; (i) Goldberg 1981; (j) Love et al. 1986; (k) DeMartini and Allen 1984.
*B = bays; C = coast
†W = winter; Sp = spring; Su = summer; F = fall

Diego Bay. High abundance there suggests that the bay may be an optimal habitat for spotted turbot and tonguefish, or that it is an area of increased susceptibility to capture with the beam trawl. The entrance is dredged to about 15 m and has a sandy bottom similar to the open coast. The channel is protected from large swells, but is influenced by tidal currents. The bottom was populated with sea pens, *Stylatula* sp., and was the only location where dense stands of sea pens were found. *Stylatula* has been found in the stomachs of spotted turbot, and may be an important food (Ford 1965).

Fantail sole, hornyhead turbot, speckled sanddab, and English sole did not depend on shallow-water nursery habitats. Newly settled fantail sole and hornyhead turbot were caught from March to September 1989, whereas speckled sanddab settled throughout both 1989 and 1990 but were caught in greatest numbers from March to September 1989 (figure 5).

Juvenile English sole were found only on the open coast, although they use bays as nursery areas in northern California, Oregon, and Washington (Toole 1980; Krygier and Pearcy 1986; Rogers et al. 1988). The English sole settled on the open coast between April and September, at about the same time as halibut, but in deeper water and at a larger size (figure 5; table 1).

The seasonal spawning pattern is winter and spring for species using bays and the shallow open coast as nursery areas (diamond turbot, California halibut). But species that settle in deeper waters of the open coast spawn throughout the entire year or in other seasons (table 1).

Annual Variation in Settlement

Variability in rates of settlement could be caused by differences in larval survival due to food availability or predation, variability in reproductive effort and abundance of adults, or variability in oceanographic conditions influencing the transport of larvae to the nearshore. Newly settled and small juveniles of all species were more abundant in 1988 than 1987, suggesting that the factors influencing settlement success affect the entire nearshore environment. Ford (1965) also found considerable variability in population estimates for speckled sanddab in 1962 and 1963, which suggests that there is high interannual variability in speckled sanddab abundance.

Spatial patterns in settlement were also evident, with most of the coastal settlement of speckled sanddab and California halibut at Torrey Pines in 1988. It seems unlikely that increased egg production would account for the spatial and temporal settlement patterns for all species; therefore the increased settlement may be due to differential larval mortality or transport on the coast.

Oceanographic conditions can lead to variability in the transport of larvae and juveniles to their prospective nearshore nursery habitats (Nelson et al. 1977; Mearns 1979; Cohen 1985; Boehlert and Mundy 1988). Currents in the Southern California Bight are characterized by minimal offshore Ekman transport and a gyral geostrophic flow pattern, resulting in minimal seaward dispersion (Owen 1980; Parrish et al. 1981).

Fish larvae can be transported onshore by internal waves, which occur when the water column is thermally stratified in spring, summer, and fall (Winant and Bratkovich 1981; Shanks 1983, 1988). Postflexion diamond turbot and California halibut are neustonic, and are distributed within 2–3 km of shore (Barnett et al. 1984; Moser and Watson 1990). Most of the nearshore coastal flatfishes have relatively short-lived planktonic larvae and settle at a small size, which may decrease the risk of dispersal to unfavorable areas.

Comparison of Life Histories

Size at settlement increases with settlement depth: diamond turbot settle at the smallest size in the shallowest habitats, and speckled sanddab settle at a larger size in deeper water (figure 13; table 1). Smaller size at settlement suggests shorter duration of pelagic stages and less dispersal, which may be advantageous for species using bays as nursery areas.

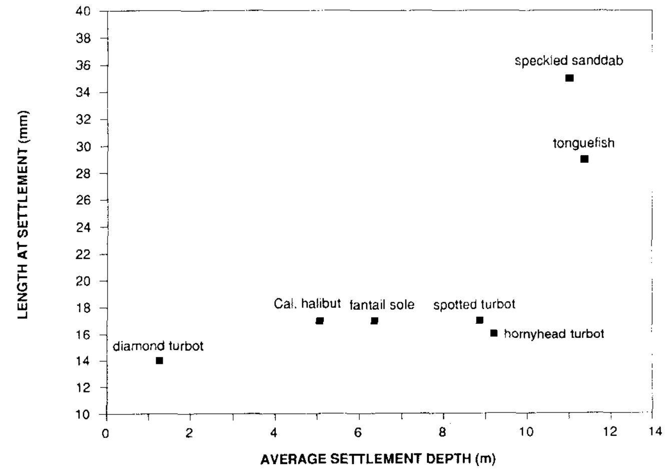

Figure 13. Size at settlement versus settlement depth.

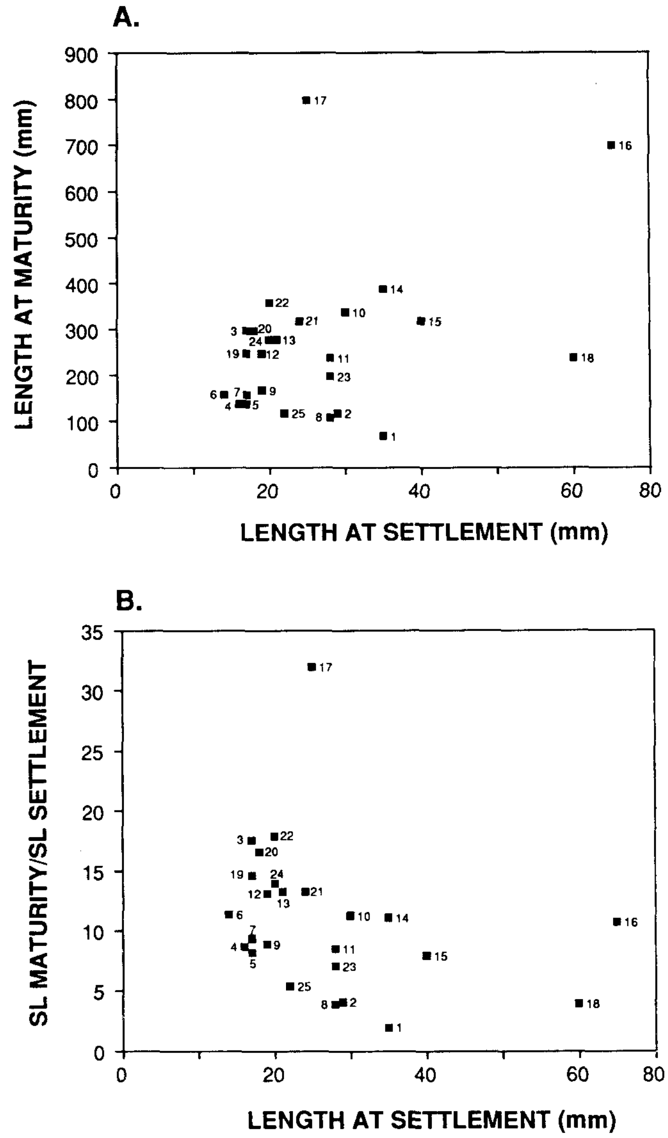

Figure 14. *A*, Length at maturity versus length at settlement for 25 species of flatfishes. *B*, Ratio of size at maturity/size at settlement versus length at settlement for 25 species of flatfishes. Length at settlement determined by adding 10 mm to smallest size at transformation (Ahlstrom et al. 1984). Size at maturity was obtained from Kramer 1990, or referenced below. Numbers in figure refer to fishes listed as follows: 1. *Citharichthys stigmaeus*; 2. *Symphurus atricauda*; 3. *Paralichthys californicus* (Haaker 1975); 4. *Pleuronichthys verticalis*; 5. *Pleuronichthys ritteri*; 6. *Hypsopsetta guttulata*; 7. *Xystreurys liolepis*; 8. *Citharichthys xanthostigma* (Goldberg 1982b); 9. *Hippoglossina stomata* (Goldberg 1982a); 10. *Parophrys vetulus* (Roff 1981); 11. *Microstomus kitt* (Roff 1981); 12. *Platichthys flesus* (Roff 1982); 13. *Pleuronectes platessa* (Roff 1982); 14. *Glyptocephalus cynoglossus* (Roff 1982); 15. *Microstomus pacificus* (Roff 1982); 16. *Reinhardtius hippoglossoides* (Roff 1982); 17. *Hippoglossus stenolepis* (Roff 1982); 18. *Glyptocephalus zachirus* (Hosie and Horton 1977); 19. *Pseudopleuronectes americanus* (Klein-MacPhee 1978); 20. *Platichthys stellatus* (Orcutt 1950); 21. *Limanda ferruginea* (Royce et al. 1959); 22. *Paralichthys dentatus* (Smith and Daiber 1977); 23. *Hippoglossoides platessoides* (Roff 1982); 24. *Limanda aspera* (Roff 1981); 25. *Limanda limanda* (Roff 1982).

After settlement, juveniles of some species allocate energy to growth, and others to reproduction. However, there is no apparent relationship between size at maturity and size at settlement (figure 14; table 1). Sizes at maturity and at settlement of 25 flatfish species indicate the range in these life history characteristics; speckled sanddab mature at the smallest size, and Pacific halibut (*Hippoglossus stenolepis*) at the largest (figure 14).

The ratio of size at maturity to size at settlement indicates the relative amount of energy put into growth or reproduction after settlement. This ratio is lowest for speckled sanddab; they settle and begin to reproduce soon afterwards, investing energy primarily in reproduction, not growth. The ratio is highest for Pacific halibut, which settle and then grow to a large size before reproducing.

Community Structure

Size-structured distribution patterns. Several species have size-structured distribution patterns, including California halibut and diamond turbot (figure 4). Separation of small juveniles from large adults may reduce the risk of cannibalism: large California halibut have been found with smaller halibut in their stomachs (Drawbridge 1990).

Juvenile halibut and diamond turbot both use bays as nursery areas, but there is little overlap in diet. Small diamond turbot eat primarily polychaetes and clam siphons, whereas small halibut eat crustaceans and small fish (Lane 1975; Haaker 1975; Peterson and Quammen 1982; Allen 1988; Drawbridge 1990). Potential juvenile competitors with diamond turbot include English sole, spotted turbot, and hornyhead turbot, but these three species do not use bays as nursery areas.

Speckled sanddab of all sizes are found together on the open coast. Risk of cannibalism is low, because sanddab settle at a size larger than the largest prey consumed by adults (most adult prey are 20 mm or shorter; Ford 1965). Species that do not segregate by size (including hornyhead turbot) may not have the risk of mortality due to cannibalism.

Habitat partitioning. Seven flatfish species inhabit shallow inshore habitats, but do not occur at the same size in the same habitats and do not eat the same prey (table 1). For example, halibut and speckled sanddab do not occur together over the same size range (20–130 mm SL); the halibut live in bays, speckled sanddab on the open coast (figure 4). Halibut's change in distribution suggests that movement from the bays to the open coast occurs when the fish are between 100 and 200 mm (Kramer 1990a). Larger halibut (>250 mm) are primarily piscivorous, and have been found with speckled sanddab in their stomachs (Ford 1965; Allen 1982; Plummer et al. 1983; Hobson and Chess 1986; Drawbridge 1990). Ford (1965) estimated that predation by California halibut could account for 78% of the total monthly mortality of speckled sanddab. Speckled sanddab may also prey upon newly settled halibut, which settle at a size small enough to be within the range (<20 mm) eaten by sanddab (Ford 1965).

Speckled sanddab and juvenile English sole both inhabit the open coast, and settle at about the same size (≤35 mm). They both eat copepods and mysids as small juveniles (<50 mm), but speckled sanddab continue to feed on mysids while English sole switch to a predominately polychaete diet by the time they reach 70 mm (Ford 1965; Toole 1980). Juvenile English sole and speckled sanddab have been found in Humboldt Bay, but not in the same habitats; English sole occur in the intertidal zone, speckled sanddab in deeper channels (Toole 1980).

California halibut and fantail sole are morphologically similar yet eat different prey. Larger juveniles (>200 mm) occur together on the open coast, but halibut eat fish and mysids, and fantail sole eat primarily decapods and other crustaceans (Ford 1965; Allen 1982; Plummer et al. 1983). Newly settled juveniles do not occur together; fantail sole settle in much deeper water (12–15 m; Moser and Watson 1990) than halibut.

Large juvenile and adult spotted turbot, hornyhead turbot, diamond turbot, and English sole occur together on the open coast, but have different diets: all of them eat polychaetes, but each eats different species. About 40% of the hornyhead turbot's diet by weight is the polychaete *Owenia fusiforma*, and 50% of spotted turbot's diet is anemones that are attached to the basal disc of the sand tube of polychaetes (Ford 1965; Luckinbill 1969). Diamond turbot also eat polychaetes, but clam siphons compose nearly 40% of the diet by weight (Ford 1965; Lane 1975; Peterson and Quammen 1982). English sole also eat polychaetes, but brittle stars compose 16% of the diet by volume (Ford 1965; Allen 1982). Although these species coexist, they partition the habitat by eating different prey.

Dietary overlap is probably greatest between newly settled and small juvenile stages of flatfish; food resources are partitioned during later juvenile and adult stages. Newly settled juveniles were found in different habitats, with very little overlap in distribution. Most species, including fantail sole, tonguefish, hornyhead turbot, and spotted turbot, probably settle at depths greater than those surveyed (>14 m). Speckled sanddab settled deeper than halibut, and both settled deeper than diamond turbot. Time of settlement also differed, with diamond turbot settling primarily in winter, halibut in spring, and speckled sanddab in late spring and summer (figure 5). Small juvenile stages (<50 mm) were also found in different habitats: diamond turbot in back bays, halibut in the middle sections of bays out to the open coast at depths <8 m, and speckled sanddab on the open coast at greater bottom depths (figure 4).

In conclusion, the flatfish species found in shallow-water habitats (≤14 m) do not occur together during early juvenile stages; they settle at different depths, have ontogenetic depth distributions, and settle at different times of the year. Older juveniles and adults partition the habitat by partitioning food resources and by living at different depths and locations. Life histories of nearshore flatfishes vary widely, from that of speckled sanddab, which settle at a large size on the open coast and mature rapidly, to that of California halibut, which settle at a small size, use bays as nurseries, and delay maturity.

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VARIATIONS IN THE CATCH OF JACK MACKEREL IN THE SOUTHERN CALIFORNIA PURSE SEINE FISHERY

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ABSTRACT

Jack mackerel landings from southern California sampled by the California Department of Fish and Game show a high degree of variability in recruitment success. The period from 1947 to 1983 is examined for variations in landings due to changes in fishing effort of the multispecies purse seine fishery. Fishing effort for jack mackerel has been affected by the availability of alternative species such as Pacific sardine and Pacific mackerel, and by economic factors including cannery capacity and the price of imported mackerel. Significant variations in recruitment success are apparent. Above-average recruitment for jack mackerel and Pacific mackerel, both pelagic species in southern California waters, often occurs in the same years.

The age composition of jack mackerel landings has changed noticeably during this period. Before 1965, fish three years old or older contributed significantly to the fishery, but after 1965 the fishery was dominated by one- and two-year-old fish. The seasonal nature of the multispecies fishery and the decreased contribution of older fish from the fall fishery are reflected in this change in age composition. Other factors include economic effects, the frequency of relatively strong year classes, shifts in the areas fished, and possible changes in fish behavior.

RESUMEN

Los desembarcos de la macarela (*Trachurus symmetricus*) del sur de California muestreada por el Departamento de Pesca y Caza de California muestra un alto grado de variabilidad en reclutamiento. Se examina el período de 1947 a 1983 con el fin de detectar variaciones en desembarco con respecto al esfuerzo de la pesquería de red de cerco multiespecífica. El esfuerzo de pesca de macarela ha sido afectado por la disponibilidad de especies alternativas como la sardina del Pacífico (*Sardinops sagax*) y la macarela del Pacífico (*Scomber japonicus*), y por factores económicos tales como la capacidad de las enlatadoras y el precio de la macarela importada. Se encontraron variaciones significativas en el éxito del reclutamiento. Reclutamiento por arriba del promedio de la macarela y la macarela del Pacífico, ambas especies pelágicas de las aguas del sur de California, ocurren a menudo en el mismo año.

La composición en edad de la macarela ha cambiado notablemente durante este período. Antes de 1965, peces de tres años de edad o mayores contribuían significativamente a la pesquería, pero después de 1965 la pesquería ha sido dominada por peces de uno y dos años. La estacionalidad de la pesquería multiespecífica y una menor contribución de los peces más viejos de la pesquería de otoño se reflejan en este cambio en composición de edad. Otros factores incluyen factores económicos, la frecuencia relativa de clases de edad fuertes, cambios en las áreas de pesca, y posibles cambios en el comportamiento de los peces.

INTRODUCTION

Jack mackerel, *Trachurus symmetricus*, has been an economically important species for the southern California purse seine fleet since 1947, averaging nearly $2 million in landings per year since 1947 (values not adjusted for inflation; MacCall et al. 1980). The population ranges from Baja California to the Gulf of Alaska and far offshore. MacCall and Stauffer (1983) estimated the total biomass to be 1.48 to 1.81 million MT. Most of the jack mackerel landed (over 90%) are caught by purse seiners in southern California waters, with smaller sporadic landings to the north at Monterey, California, and to the south at Ensenada, Mexico (MacCall et al. 1980). The purse seine (wetfish) fleet harvests jack mackerel from only a small portion of its range and captures only young fish.

Canneries started packing jack mackerel as a substitute for Pacific mackerel, *Scomber japonicus*, and Pacific sardine, *Sardinops sagax*, during the collapse of the sardine population and the decline of the Pacific mackerel population in the late 1940s (Roedel 1953). Jack mackerel are taken by the fleet from nearshore waters along the coast between Point Conception and the Mexican border, around islands in the

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[Manuscript received January 30, 1991.]

Southern California Bight, and offshore at Tanner and Cortez banks. Schools of mackerel are sometimes species specific, but often consist of a mixture of jack mackerel, Pacific mackerel, and Pacific sardine. The jack mackerel caught in the purse seine fishery are primarily small (about 100–350 mm fork length, FL) and young (0–5 years old). They are canned at Terminal Island and Port Hueneme for human consumption and pet food (MacCall et al. 1980).

Jack mackerel have been sampled by the California Department of Fish and Game at the Terminal Island canneries since 1947 (Knaggs 1974a). Length is measured; sex is recorded; and otoliths are removed for age determination. The validity of otolith age determinations for this population was examined by Knaggs and Sunada (1974), and maturation and growth were documented by Wine and Knaggs (1975).

The purposes of this paper are to review the factors that have affected the jack mackerel landings, examine the age composition of the catch, and look at the pattern of recruitment.

MULTISPECIES ASPECTS OF THE FISHERY

Large fluctuations in the volume of jack mackerel landings have resulted from a number of factors related to the variables present in a multispecies fishery. The southern California wetfish fleet developed in the 1930s to harvest Pacific sardine and Pacific mackerel, but took small amounts of jack mackerel (then called horse mackerel) incidentally to the target species. The history of the jack mackerel fishery up to 1951 was reviewed by Roedel (1953).

In the 1930s and 1940s Pacific sardine was by far the leading species landed by the fleet, with Pacific mackerel second (figure 1). Both Pacific mackerel and sardines were canned, but sardines commanded the highest price because they were also processed for fish oil and meal, and fish oil was in demand at that time. Canneries paid a much lower price for jack mackerel: in 1935 jack mackerel brought $6 per ton while Pacific mackerel brought $15 per ton. Northern California sardine landings declined in the mid-1940s, and many of the purse seiners went south, increasing the fishing pressure on Pacific mackerel and sardines in southern California waters (Fitch 1952). The sardine catch dropped in 1947 despite the increased effort, but revived briefly in southern California in 1949 and 1950 (figure 1).

In 1947, when Pacific mackerel and sardines became so scarce that fishermen could not fill the canneries' demands, large quantities of jack mackerel were first accepted. The name was changed from horse mackerel to jack mackerel in 1948 to enhance consumer appeal, and canneries developed a marketable product. The jack mackerel catch, therefore, did not increase gradually as the fishery developed, but started with nearly the highest landings ever recorded for the species.

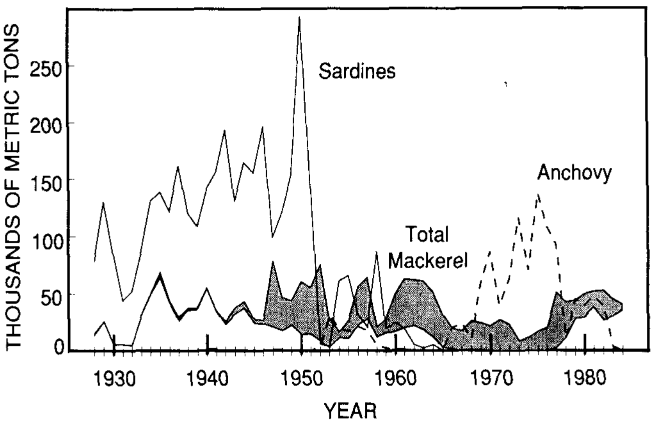

Figure 1. Annual landings of wetfish in southern California. Total mackerel comprises two species: Jack mackerel (*shaded area*) and Pacific mackerel (*area below shading*).

Northern anchovy, *Engraulis mordax*, has been an important species to the wetfish fleet since the beginning of the anchovy reduction fishery in late 1965. Within four years anchovy had topped jack mackerel landings and, except for 1978, continued to lead landings from 1969 to 1982 (Anon. 1984). Anchovy are fished by the same boats, but with nets with smaller mesh than the nets used for the other three species; so boats are not likely to fish for both anchovy and jack mackerel in the same trip. Anchovy are reduced to fish meal, but have a lower oil content than sardines. Anchovy do not command as high a price as jack mackerel, but fishing boats may shift between anchovy and jack mackerel when availability or marketability changes, or when the anchovy season opens or closes.

The fishing season for anchovy in southern California opens on September 15 and is limited to a quota on reduction landings. Fishing often starts a few weeks later, because the fishermen use the first few weeks of the season to negotiate prices with the canneries. Through 1978, the season closed on May 15 or as soon as the quota was filled. Since 1979, the closure date has been June 30, with an additional closed period on reduction landings in February and sometimes March. During the 1973 and 1974 seasons the increased cost of fuel kept boats nearer shore where jack mackerel could not be found, but anchovy were available. Anchovy fishing diverted effort away from jack mackerel fishing and contributed to reduced jack mackerel landings in 1973, 1974, 1977, and 1980 (Mason 1989).

The resurgence of Pacific mackerel in the 1970s, and regulations restricting its harvest have considerably affected jack mackerel landings. From the mid-1920s through the early 1960s, the Pacific mackerel fishery was unregulated and was one of the most important commercial fisheries in California (Klingbeil 1983), but by the mid-1960s the fishery had collapsed. Virtually no Pacific mackerel were caught for the next ten years. Because of the reduced biomass, a moratorium on Pacific mackerel took effect in August 1970 (Klingbeil 1983). Regulations allowed up to 18% Pacific mackerel in loads of jack mackerel to minimize the negative impact a recovering Pacific mackerel population might have on the jack mackerel fishery. As the population started to recover in 1977, mixed catches with Pacific mackerel in excess of this limit occurred, interfering with the landing of jack mackerel (Klingbeil 1983).

When the 1977 spawning biomass of Pacific mackerel was assessed at 30,000 tons, the moratorium was lifted, and a quota system was implemented. When a season's quota was filled, "interseason" regulations took effect. These restricted the percentage of Pacific mackerel that could be landed with jack mackerel until fishing on the next Pacific mackerel quota began. The allowable percentage of Pacific mackerel changed several times over the next few years, ranging from 18% to 50%. In the 1977–79 seasons, daily or weekly landing limits were imposed on mixed mackerel catches with high percentages of Pacific mackerel to delay reaching the quota. This shifted the effort of the larger vessels toward jack mackerel as long as they were available in relatively pure schools. Pacific mackerel landings increased to the point of dominating combined mackerel landings by the 1979 season and continued to dominate them for the next four seasons (figure 1).

Details on the remarkable recovery of the Pacific mackerel and the regulations governing it have been covered by Klingbeil (1983). The overall effect of these regulations on jack mackerel landings is hard to assess. Although tolerance levels were intended to keep pressure off the Pacific mackerel population, the restrictions may have also limited jack mackerel landings during periods when jack mackerel could not be found schooling as a single species. Overall, the regulations probably slowed the redirection of fishing effort from jack to Pacific mackerel.

ECONOMIC CONSIDERATIONS

Jack mackerel are sold almost exclusively to canneries, and these canneries often limit the volume of landings they will accept (MacCall and Stauffer 1983). Canning capacities, stock on hand, and competition from other mackerel products, both foreign and domestic, have affected the volume of jack mackerel landed. Cannery orders limited landings in 1954, 1955 (Knaggs 1974a), 1959, 1960 (Knaggs 1974b), and 1977 (Mason 1989). Cannery capacity was reduced during the 1973–75 seasons after one cannery burned (Mason 1989). Cannery capacity in 1979 was estimated to be 80,000 MT (MacCall et al. 1980). Jack mackerel landings have not reached this level, partly because other species such as Pacific bonito (*Sarda chiliensis*) are also packed by these canneries, and partly because of the limited market for canned mackerel. Combined jack and Pacific mackerel landings since 1978 have only slightly exceeded the 45,000 MT of jack mackerel landed in 1977 (figure 1). Pacific mackerel are often found closer to shore than jack mackerel, decreasing fuel costs and making Pacific mackerel a more profitable target, as happened in the 1978 season (Mason 1989).

Purse seiners catch various species of pelagic fish. The selection of target species is one economic factor in which fishermen have some control. Profits are maximized by shifting effort among a variety of pelagic schooling fish as availability, marketability, and the opening and closing of fishing seasons and quotas allow. The fleet fished for sardines in the 1954 and 1955 seasons when availability increased and the price of jack mackerel was down, and in 1958 when sardines were again available and jack mackerel were unavailable. When other more profitable species such as Pacific bonito (in 1967, 1971) and both bonito and bluefin tuna, *Thunnus thynnus*, (in 1972, 1973, 1974, and 1980) became more available, fishermen shifted their effort for weeks or months to these species. In the fall of 1967, the fishing effort of the purse seine fleet was directed toward bonito, but price disputes over bonito and anchovy stopped all fishing by the fleet for three months (Fleming and Knaggs 1977). Thus the availability of different species to the purse seine fleet enhances fishermen's income, but confuses the interpretation of jack mackerel catch statistics as representative of availability.

There have been other causes for the fluctuations in catch during the history of the jack mackerel fishery (figure 2). Scarcity of fish was blamed for the reduced catches in 1953 (Knaggs 1974a), 1957, 1958 (Knaggs 1974b), 1966 (Knaggs and Barnett 1975), 1972–74, 1979, and 1983 seasons (Mason 1989).

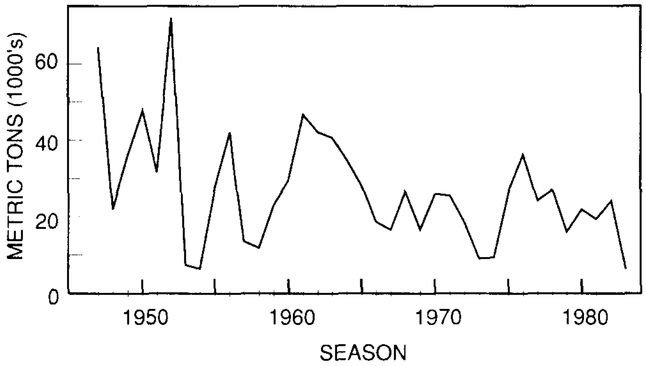

Figure 2. Landings of jack mackerel in southern California by season (1 August to 31 July).

These were many of the seasons with the lowest catches. Other factors had noticeable effects in certain seasons. In 1969, high levels of the pesticide DDT were found in jack mackerel, making it unfit for human consumption. Only pet food could be produced for six months until fish with lower DDT levels were caught (Fleming and Knaggs 1977). Several months of bad weather may have been one factor in reducing the jack mackerel catch in the 1972, 1973, and 1982 seasons (Mason 1989); however, weather conditions severe enough to prevent fishing lasted only a few months, so it was not rough weather alone that caused severe drops in seasonal landings. During the 1983 El Niño, however, jack mackerel were unavailable in southern California throughout the fall; the wetfish fleet moved north to Monterey, where most of the season's jack mackerel landings were made (Mason 1989).

In summary, the following factors have affected the jack mackerel landings by season:

- Landings of sardines: 1954, 1955, 1958
- Landings of anchovy: 1973, 1974, 1977, 1980
- Landings of Pacific mackerel: 1979–83
- Landings of bonito and/or bluefin tuna: 1967, 1971, 1973, 1974, 1977, 1980
- Market conditions: 1954, 1955, 1959, 1960, 1977
- Reduced cannery capacity: 1973–75
- Scarcity of schools of jack mackerel: 1953, 1957, 1958, 1966, 1972–74, 1979, 1983
- El Niño events: 1958, 1983
- DDT levels: 1969

POPULATION ASSESSMENT

Sampling Methods

The California Department of Fish and Game samples jack mackerel at the Terminal Island canneries. There is no closed season on jack mackerel fishing, so for reporting purposes, the season has been 1 August to 31 July of the following calendar year (Knaggs 1974a). The sampling plan has changed several times since 1947. Sampling methods for various periods are presented in a series of technical reports published by the California Department of Fish and Game (Knaggs 1974a,b; Knaggs and Barnett 1975; Fleming and Knaggs 1977; Mason 1989). The reports include estimates of numbers of fish landed for each month, and age composition.

Age Composition

The fish caught by the southern California purse seine fleet are less than 400 mm FL and under 8 years old. Fish larger than 400 mm FL are rarely caught by the purse seine fleet, but are taken incidentally by the salmon and albacore troll fisheries off California and Oregon, and by the offshore whiting trawl fishery (MacCall et al. 1980). Some of these larger fish have been over 30 years old (Fitch 1956). Thus the purse seine fishery harvests jack mackerel from a limited segment of the total population.

The age composition of the jack mackerel landings has not been consistent throughout the history of the fishery. The average age of the fish caught by the wetfish fleet has decreased markedly. In the first decade of the jack mackerel fishery (1947–56) the catch was dominated by fish age 3 or older (figure 3). Younger fish contributed no more than 16,000 MT (35 million pounds) to the fishery per season. The next eight seasons (1957–64) appear to be a transition period when the weight of younger fish reached a level of about 18,000 MT (40 million pounds) per season, but older fish still contributed significantly to the catch in some years. In the final period (1965–83) fish younger than age 3 continued

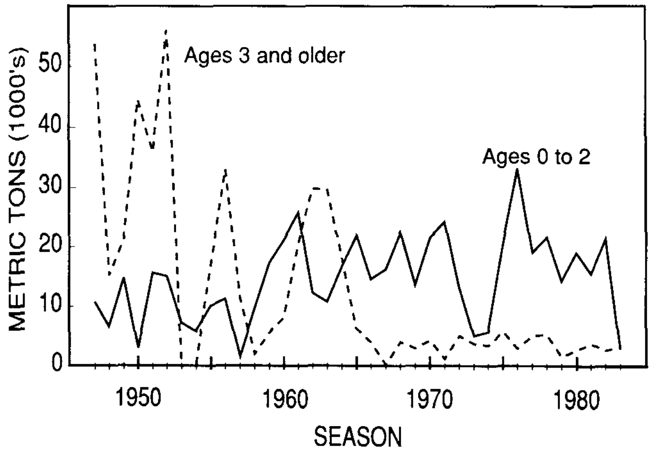

Figure 3. Jack mackerel landings divided into two age groupings: 0–2 (*solid line*) and 3 and older (*dashed line*).

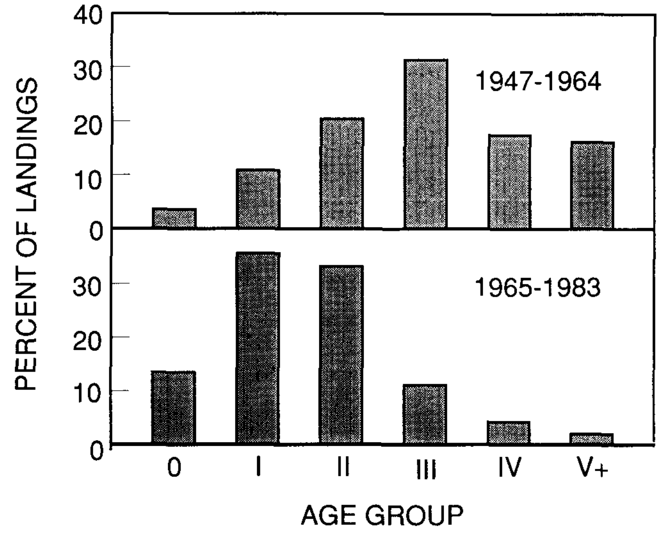

Figure 4. Age composition of jack mackerel landings from two time periods.

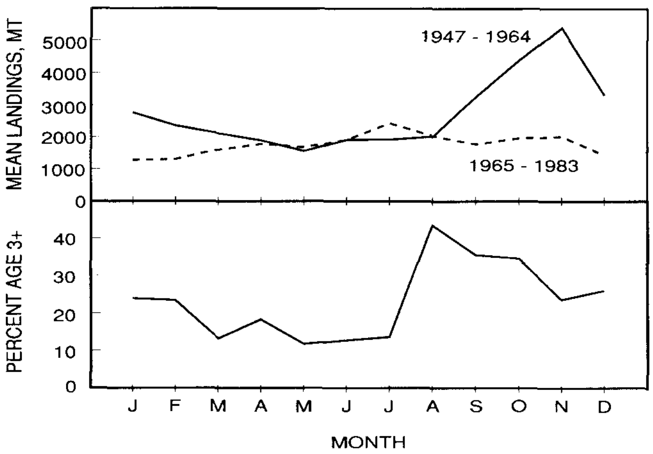

Figure 5. Seasonality of jack mackerel in southern California. *Upper panel*, mean seasonal landings from 1947 to 1964 (*solid line*) and 1965 to 1983 (*dashed line*). *Lower panel*, landings of fish age 3 and older from 1972 to 1983 as a percentage of each month's landings.

to be caught at about the 18,000-MT (40-million-pound) level, consistently dominating the catch, while older fish dropped out of the fishery, contributing less than 7,000 MT (15 million pounds) per season. Thus the catch shifted from older to younger fish during the middle 1960s.

A comparison of the age composition of the 1947–64 period with the 1965–83 period (figure 4) reveals that the earlier period was dominated by age-3 fish, whereas the later period was dominated primarily by age-1 fish and secondarily by age-2 fish. During the earlier period, fish of age 3 or older composed 65% of the catch; in later years those age groups contributed only 18%.

Seasonality in Age Composition

During the early period (1947–64), when older fish appeared in the fishery, the highest landings were made during the late fall, and the lowest landings during spring and summer (figure 5). This pattern reflected increased fishing effort at the opening of the sardine season (October 1) from boats looking primarily for sardines, but prepared to catch Pacific mackerel or jack mackerel if they could not find sardines (Roedel 1952). The lower catches of jack mackerel in the spring of these earliest years were associated with decreased fishing effort in the late spring when the sardine season was closed and Pacific mackerel was seasonally unavailable (Roedel 1953). However, by 1950 the fleet discovered that jack mackerel did not always disappear in the spring, and fishing continued year-round. More recently, from 1965 to 1983, seasonality was reduced, with only a slight peak in July. During this period, anchovy was the alternate fishery available to the purse seine fleet, and the closure of the anchovy reduction season, in May or June, increased fishing pressure on jack mackerel during the summer.

A seasonal pattern also appears in the age composition of the catch. Landings from 1972 to 1983 were examined on a monthly basis for age composition (data for earlier years were unavailable). Even during this period, when older fish were less commonly caught, fish age 3 and older composed more than one-third of the catch from August through October (figure 5). They contributed less than 25% of the catch during the rest of the season, and less than 15% during May, June, and July.

The age composition of the catch was undoubtedly influenced by the interaction of two seasonal factors: (1) larger fish were most often caught in the fall, and (2) the fall fishery contributed less after 1964. Using the monthly age composition data from the later period (1972–83) on mean monthly landings from the earlier period (1947–64) to estimate the contribution of fish of age 3 and older in the earlier period gives an expected 25% of the season's catch as age 3 or older. However, age 3 and older fish actually composed 65%, not 25%, of the catch in the earlier period. Therefore changes in the seasonality of fishing effort explain only a small proportion of the change in age composition.

Recruitment

The relative strength of different year classes has varied widely throughout the history of the jack mackerel fishery. To minimize confusion with variations in seasonal cannery production, comparisons of different year classes are based on the relative virtual year-class strength as described by MacCall and Stauffer (1983). These strengths are produced by summing the percentage contribution of a year class (from numbers of fish) to each season it appeared in the fishery. For example, the 1970 year class contributed 30% of the season's catch as young-of-the-year in 1970, 65% of the 1971 catch as 1-year-olds, 37% as 2-year-olds, 17% as 3-year-olds, 14% as 4-year-olds, and 3% as 5-year-olds, for a total index of 165. An average year class would contribute about 100%, and an above average class would contribute more by providing a higher percentage of the catch than surrounding year classes. Year classes are effectively compared only with other year classes occurring simultaneously in the fishery.

The series of year classes can broken into three periods with different patterns of strength. During the first period, from the first fully represented year class in 1947 until 1958, strongly represented jack mackerel year classes in 1947, 1952, 1953, and 1958 (figure 6) were separated by strings of weakly represented year classes. The second period (1959–73) had clusters of strongly and weakly represented year classes, with the dominant 1958 year class being followed by two strong ones in 1959 and 1960. The next four year classes (1961–65) contributed much less to the catch, and stronger classes followed from 1966 to 1970 (especially 1967 and 1970), with less-dominant year classes in 1971–73 (figure 6). The third period (1974–80) features a remarkable series of alternating strong and weak year classes. The 1974, 1976, 1978, and 1980 classes were all relatively strong, whereas those of 1973, 1975, 1977, and 1979 were relatively weak. A scarcity of young fish in southern California during the 1982–83 El Niño enhanced the relatively high year-class strength of 1980.

Variability in year-class strength is an important factor in the age composition of the catch. In the early period of the fishery (1947–58) relatively strong year classes were separated by strings of four much weaker classes. Fish from the more prominent year classes dominated the catch until another strong class appeared five years later. Only a strong year class could contribute large numbers of fish for several seasons. As the relatively strong 1958, 1959, and 1960 year classes disappeared from the fishery (in 1964), and there were not any strong year classes to provide large numbers of older fish, the catch became limited to ages 0 to 3. After the 1966 season, relatively strong year classes appeared frequently, usually every two to three years, so younger fish were readily available. If younger fish were easier to catch, they might have been expected to dominate the catch as long as there was a ready supply of them. However, if older fish were still present, one would expect to have seen older fish during the 1973 and 1974 seasons, when young jack mackerel were hard to find. The catch during this period, although reduced, remained ages 0 to 2. The relatively strong 1970 year class did not appear strongly in the catch after age 2 (Mason 1989, table 18). To some extent, the frequency of relatively strong year classes may have contributed to the shift toward younger fish in the fishery.

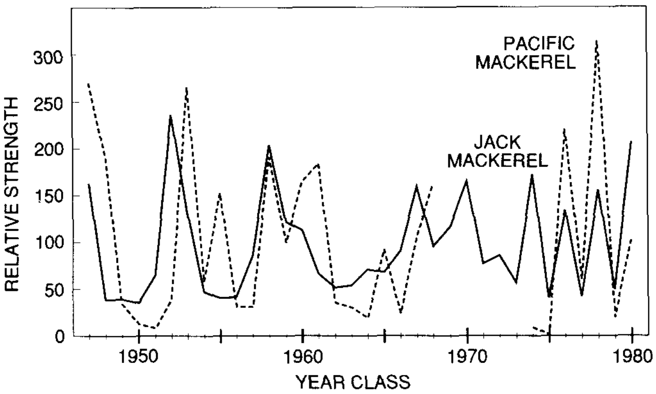

Figure 6. Recruitment strength of year classes of jack mackerel (*solid line*), and Pacific mackerel (*dashed line*), as measured by the sum of the percentage contribution of each year class to seasonal landings in southern California.

DISCUSSION

Decline in Age Composition

The decline in the abundance of older fish in the catch stands out as an important change in the fishery. What has produced this change? Two factors presented above have contributed to this decline. First, the distribution of fishing effort during the season combined with the pattern of large fish being available in the fall accounts for part of the change in age composition. Second, the higher frequency of relatively strong year classes since 1965 may explain some of the decline in abundance of older fish.

But these factors don't appear to account for all of the change observed. Overfishing should be examined to see if it contributed to the change. Economic factors have both enhanced and reduced fishing pressure at different times, affecting the ages at which particular year classes were caught. Shifts in effort from one species to another may have added complications in fishing techniques and spatial distribution. Environmental factors may have affected different ages in different ways. By examining these factors we may be able to tell which ones have contributed to the change in the age composition of the catch.

The decreased abundance of older fish in the catch between the early years of the fishery and the post-1965 period could reflect a true reduction of older fish in the population, or only a decline in their contribution to the southern California fishery. It is not possible to assess changes in the age composition of the whole population, since only young jack mackerel are harvested, and the fishery operates over a small portion of the total range. Although it is likely that some of the change in the age composition in the very earliest years (1947–51) is attributable to the presence of older fish from year classes unexploited before the fishery began, these fish disappeared from the landings by 1953 (Knaggs 1974a, table 17). They do not account for older fish present from 1954 to 1964. MacCall and Stauffer (1983) estimated that fish age 8 or younger compose less than two-thirds of the population, and that the purse seine fleet harvests only a small percentage (13%–20%) of the potential yield of this age group. If this is true, then the decline in older fish in the catch reflects a change in what is caught by the fishery, not a decline in the population due to overfishing.

Depressed market conditions were an economic factor that affected the age at which jack mackerel were caught in some seasons. During the 1953 and 1954 seasons the low price of imported mackerel protected the 1952 year class from exploitation as 1- and 2-year-olds (Knaggs 1974a), so more fish from this year class were caught at older ages in 1955–57. However, the 1958–60 year classes did not have this protection as young fish (except in the 1958 season, when sardines were being caught) but still contributed large amounts to the catch as 3- and 4-year-olds. Thus depressed market conditions had a limited effect on age composition.

Although it is possible that some undocumented changes in fishing tactics caused by the shift in fishing effort from sardines to anchovy may have contributed to the decline in age composition, I could find no evidence to support this theory. It appears that the change in age composition truly reflects the age of fish available to the purse seine fleet.

Another factor that may have contributed to the change in apparent age composition is related to the areas fished. Before 1965, sardines were the most desirable species to the purse seine fleet, followed by Pacific mackerel; therefore, boats fished where they expected to find sardines or Pacific mackerel. Most of the jack mackerel landed before 1965 came from the Channel Islands area off Santa Barbara or the area near San Pedro harbor (Clothier and Greenwood 1956; Duffy 1968). Boats rarely fished the more southern areas around San Clemente Island and Tanner and Cortez banks. However, from 1964 to 1971, when sardines and Pacific mackerel were absent, most of the catches were from these offshore southern areas (MacCall et al. 1980). This leads to the assumption that more fish from older age groups are caught in the Channel Islands area or the area near San Pedro harbor than on Tanner and Cortez banks. This assumption cannot be rigorously examined because information about catch locations is inadequate. The assumption does not hold true for the 1952 season, when older fish composed 79% of the catch, and 78% of the catch came from San Clemente Island and Tanner and Cortez banks (Knaggs 1974a, tables 2 and 15). In addition, since the return of Pacific mackerel in 1977, the fleet has spent more of its effort inshore, in search of Pacific mackerel (Anon. 1980), but the large jack mackerel once caught inshore have not reappeared in the catch.

The fact that small jack mackerel are found in shallow schools fishable by southern California purse seiners, and that fish larger than 400 mm FL are found in other areas, either offshore or farther north (MacCall et al. 1980), suggests that the fish may have altered their behavior since 1965. Increases in sea-surface temperature or changes in ocean circulation patterns in southern California could have caused some jack mackerel to move to more northern, or deeper cool waters at an earlier age.

It seems that the change in the age composition of the jack mackerel landings between the 1947–64 period and the post-1964 period cannot be ascribed to just one cause, but is probably due to several factors: (1) changes in the seasonal pattern of the fishery, (2) the frequency of relatively strongly recruited year classes, (3) economic factors, (4) shifts in the areas fished, and (5) changes in fish behavior.

Recruitment Variability

Both jack mackerel and Pacific mackerel have shown a high degree of recruitment variability from year to year. Because both species are taken by the same fleet and are of similar ecological type, it is very likely that environmental conditions might have correlated effects on recruitment. To compare the recruitment success of the two species, relative virtual population estimates were developed for Pacific mackerel. Catch by age and season, from table 6 of Parrish and MacCall (1978), was used to calculate relative year-class strengths in Pacific mackerel from 1947 to 1967. Similar data from table 3 of MacCall et al. (1985) were used to calculate relative year-class strength for 1974 to 1980. There is a gap in the time series from 1969 to 1973 because there was no fishery for Pacific mackerel (and therefore no data) for the years when the fishery had collapsed. A correlation significant at the $p < 0.05$ level exists between the reproductively successful year classes for Pacific mackerel and successful year classes of jack mackerel ($r = .385$, df = 29). A comparison of jack and Pacific mackerel (figure 6) shows that both species had relatively successful year classes in 1947, 1953, 1958–60, 1967, 1976, 1978, and 1980. The 1974 year classes were also relatively successful for both species; however, the Pacific mackerel success is not apparent from figure 6, because it was this year class that started the recovery of the Pacific mackerel population (Anon. 1979), and its relative strength is underestimated because the moratorium was not lifted until 1977.

It is also interesting to note that these successfully recruited year classes for both Pacific and jack mackerel are opposite to (and alternating with) successfully recruited year classes for combined rockfish species (*Sebastes dalli* and *S. saxicola*) taken as juveniles in quarterly trawl surveys in southern California. Mearns et al. (1980) indicated that the peak catch years for juveniles of these species were 1971, 1973, 1975, and 1977—all very poor years for mackerel recruitment (figure 6). These years for the Santa Monica Bay and Orange County coastline had cool or cooling water with decreasing clarity. Thus conditions favorable for demersal rockfish recruitment may be very different from those supporting good pelagic mackerel recruitment.

CONCLUSIONS

The high variability in landings seen in the southern California jack mackerel catch is due in some years to a lowered availability of jack mackerel and in other years to interspecific interactions within the wetfish fishery, as well as to economic factors. The decline in abundance of older fish in the catch after 1964 is partially caused by a decline in fall fishing effort. The increased frequency of relatively strong year classes after 1964 increased the availability of young fish. Changes in the areas fished by the wetfish fleet may have also contributed to catching younger fish. Nevertheless, the disappearance of older fish cannot be explained solely by fishery interactions, and may reflect a real change in the availability of these age groups to the purse seine fishermen. Pacific mackerel recruitment has also varied, and in most cases jack and Pacific mackerel have shown similar patterns in relative year-class strength.

ACKNOWLEDGMENTS

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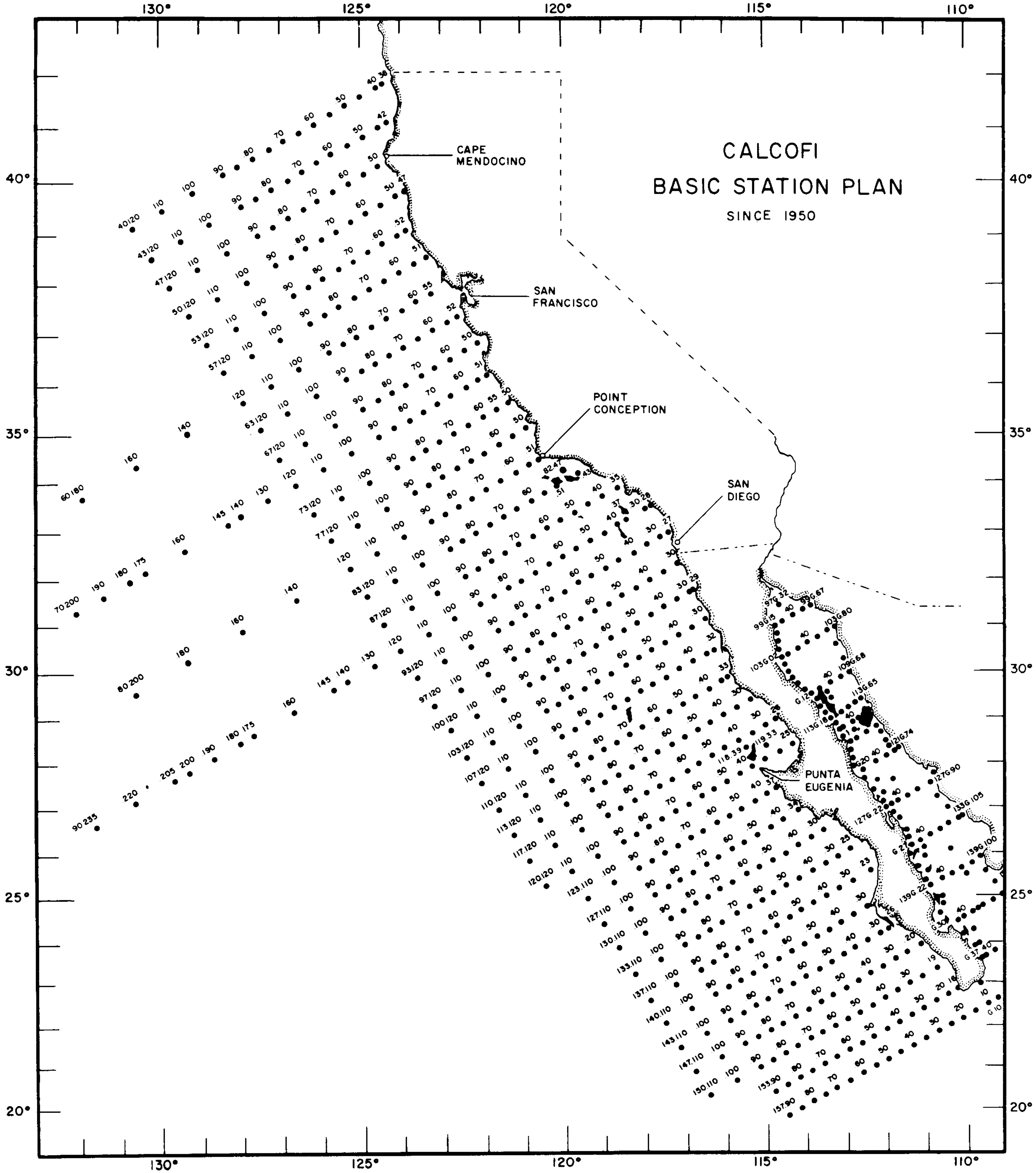

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