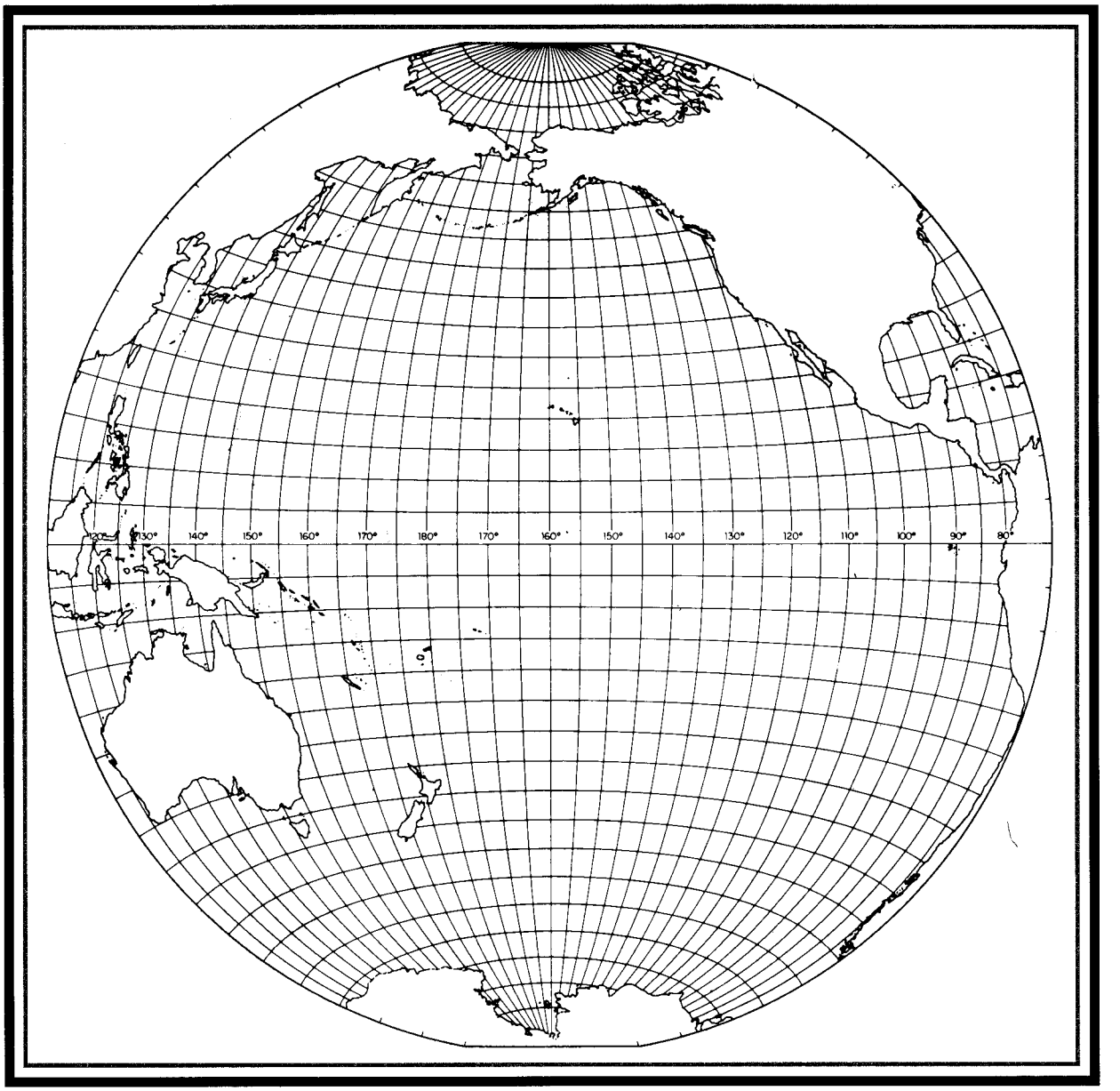

California Cooperative Oceanic Fisheries Investigations

Reports

VOLUME 35 INCLUDES INDEX FOR 1989–1993 OCTOBER 1994

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

Reports

VOLUME 35
January 1 to December 31, 1993

Cooperating Agencies:

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

CALCOFI COORDINATOR George Hemingway

EDITOR Julie Olfe

SPANISH EDITOR Jesús Pineda

Published October 1994, La Jolla, California
ISSN 0575-3317

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

Part 1

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

Now in its forty-fifth year of service to the state of California and to the community of scholars worldwide, the California Cooperative Oceanic Fisheries Investigations is pleased to be able to offer the largest-scale long-term data suite from any ocean ecosystem in the world. Thousands of horizontal and vertical profiles of physical, chemical, and biological variables, as well as the discrete data from which they were assembled, are published in hard-copy data reports of the Scripps Institution of Oceanography (SIO) Reference Series and are now available on-line via telnet to **nemo.ucsd.edu**; username: **info**. Typical of the kinds of syntheses that depend upon such a data suite is the paper by Hernández-Vázquez in this volume.

Anomalously warm temperatures have continued over much of the southern California sector of the California Current System, presenting further opportunities to study how large-scale variations in the ocean's climate affect marine life, from single-celled phytoplankton to marine birds and mammals. The report by Hayward et al. in this volume describes some of these oceanographic events. The electronic collection of environmental data has become standard on CalCOFI quarterly survey cruises: researchers measure surface properties while the ship is under way and assemble vertical profiles by using the CTD rosette at each station. We continue to benefit from the cooperation of non-CalCOFI scientists on the cruises, especially for bio-optical measurements in preparation for the launching of the next generation of satellite sensors for plant pigments, and for testing, in cooperation with personnel of the Woods Hole Oceanographic Institution, of a free-falling, fast-profiling instrument called the Fast Fish.

Sardine spawning biomass was estimated at the fourth and fifth annual Pacific Sardine Resource Assessment and Management workshops. Because estimates declined from 374,200 MT in 1991 to 71,700 MT in 1993, the recovery of the sardine resource appears to have slowed or leveled off. Factors contributing to this change may include environmental perturbations, excessive harvest, or natural fluctuations in abundance. It is clearly vital to both U.S. and Mexican interests that the sardine resource recover and that rational management models be elaborated, based on the best possible estimates of the condition of the population. In order to improve the accuracy of future estimates, scientists from the Southwest Fisheries Science Center (NMFS/SWFSC), the California Department of Fish and Game (CDFG), and the Mexican Secretariat of Fisheries (SEPESCA), using five research vessels—*McArthur, David Starr Jordan*, and *Mako* (U.S. vessels); *El Puma* and *BIP XII* (Mexican vessels)—initiated daily egg production method cruises ranging from San Francisco, California, to Punta Abreojos, Baja California Sur, in April of 1994. It is hoped that careful management will ensure the continued recovery of the resource.

The Coastal Pelagic Fisheries Management Plan was tabled indefinitely by the Pacific Marine Fisheries Commission (PMFC). Thus CDFG retains management responsibility, and plans to hold meetings for the purpose of streamlining quota-setting procedures for the fishery.

In addition to the sardine biomass cruises, 1993 activities aboard the R/V *Mako* included:

1. "Swept area" trawls to assess halibut stocks and to evaluate the effects of the recent gill net fishing closure (Proposition 132) within California waters south of Point Arguello
2. Diving assessments for withering syndrome in southern California abalone populations
3. Continued shark longline sampling and tagging studies with NMFS
4. Live-fish trapping to assess effects of the fishery on sheephead and to determine bycatch
5. Nearshore trawls to determine critical habitat for some marine sportfish including halibut, kelp bass, sand bass, croaker, surfperch, and corbina.

The SWFSC started a new project this year to evaluate the use of airborne lasers (lidar) for detecting and estimating the biomass of epipelagic schooling fishes—mackerel, sardine, anchovy, and others. A workshop has been held, and several cruises are planned.

Coastal Division scientists, in cooperation with the SWFSC Tiburon Laboratory, NOAA's National Undersea Research Program, and the Monterey Bay Aquarium Research Institute, continue to develop technology and procedures for using remotely operated underwater vehicles to estimate abundance of fish stocks. Traditional

swept-area methods may underestimate biomass in many cases. These studies are intended to develop new, cost-effective means for measuring biomass, to provide information about ecology of the slope community, and to improve trawl-based biomass estimates.

A new approach to measuring Dover sole biomass using egg and larval survey data was published in 1993. A paper dealing with a similar approach for estimating sablefish biomass is published in this volume.

The SWFSC's Coastal Division has conducted three FORAGE Program cruises in cooperation with Oregon State University to investigate how oceanographic processes affect groundfish recruitment. The cruises involved detailed measurements of oceanographic and biological variables stratified by area, depth, and season.

Several projects designed to improve management of thornyhead (*Sebastolobus* sp.) stocks are under way. The first project—a joint effort of scientists at SIO, Moss Landing Marine Laboratory, and the University of Hawaii—involves using radioisotope ratios to validate criteria used to age shortspine and longspine thornyhead. Coastal Division personnel are also participating in an effort by the Alaska Fisheries Science Center to update assessments for shortspine and longspine thornyheads north of Point Conception.

The molecular genetics project has focused on long- and shortspine thornyhead, but Dover sole and sablefish have also been sequenced. Mitochondrial DNA sequences from populations of thornyhead from Alaska, Oregon, and five sites in California have now been sequenced. The data show a high degree of site-specific variation, which indicates less mixing of populations than originally anticipated. The results suggest that, even though both thornyhead species have protracted larval and juvenile stages of longer than one year, they are retained to some degree in their natal regions. New genetic studies of rockfish (*Sebastes*) are being initiated in three areas: (1) determination of phylogenetic relationships among species, (2) development of genetic techniques for identifying eggs and early-stage larvae not identifiable by other means (by amplification and sequencing of larval DNA followed by comparison to adult sequences from phylogenetic studies), and (3) analysis of rockfish population structure based on microsatellite DNA allele frequencies. The symposium of the 1993 CalCOFI Conference, on the topic of the genetics of the fauna of the California Current, is published in this volume.

The CalCOFI Committee is pleased to announce the publication this year of CalCOFI Atlas 32, *Distributional Atlas of Fish Larvae and Eggs in the California Current Region: Taxa with Less than 1000 Total Larvae, 1951 through 1984*, by Geoff Moser and his team. We also look forward to the publication next year of CalCOFI Atlas 33, an identification guide to the eggs, larvae, and juveniles of about 500 species of fishes of the California Current region. The illustrations alone would make this work a classic, but the Moser team will also provide textual descriptions of the stages as well as morphometric, meristic, and life-history data for each species. The volumes will be hardbound for durability and Smythe-stitched to lie flat for bench use. Prepublication offerings will be announced early in 1995 for a hoped-for midyear press run.

The Committee thanks the officers and crews of the state of California vessel *Mako*, the NOAA ships *David Starr Jordan* and *McArthur*, and the University of California ship *New Horizon* for their continued support of the CalCOFI research program, and the Secretaría de Pesca, Government of Mexico, for its long-standing collegiality and cooperation. The Committee and the coordinator especially thank all those reviewers whose gift of time and thought has enriched the scientific community and served both the authors and the readers of this volume: Anne Hollowed, Robert Cowan, Nancy Lo, George Hunt, Elizabeth Venrick, Freda Reid, Teresa Chereskin, Loren Haury, Gregor Caillet, Doyle Hanan, Kurt Schaefer, William Lenarz, Steve Ralston, Jon Shenker, Larry Jacobson, Alec MacCall, Michael Domeier, Tim Barnett, Jon Govoni, Rick Methot, Irv Kornfield, Stewart Grant, Susan Picquelle, Stewart Hurlbert, John Butler, Lou Botsford, and George Hemingway. And finally, we thank the editor of *CalCOFI Reports*, Julie Olfe, and the Spanish language editor, Jesús Pineda.

The Committee notes the retirement of George Hemingway, long-time assistant to the director of MLRG and CalCOFI coordinator during several terms, including that at the time of his retirement. The Committee is grateful for his dedication to CalCOFI and for his skill at furthering its activities and purposes, and is very pleased that he has agreed to be recalled to active duty so that he may continue as coordinator. Thomas Hayward has been appointed academic administrator in MLRG to continue organizing the very successful research program that Mr. Hemingway has shepherded for so many years.

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1993

CALIFORNIA DEPARTMENT OF FISH AND GAME
Marine Resources Division
8604 La Jolla Shores Drive
La Jolla, California 92038-1508

Total landings of fishes, crustaceans, echinoderms, and mollusks increased by 5% from 1992—not enough to reverse a ten-year declining trend in reported landings.

Pelagic wetfish landings increased 18% from 1992, but the increase was mostly attributable to a threefold increase in market squid landings; Pacific sardine, Pacific mackerel, jack mackerel, and Pacific herring declined substantially (table 1).

Groundfish landings continued a ten-year decline, with a 19% decrease from 1992, including significant decreases of Dover sole, sablefish, and whiting; only widow rockfish, rex sole, and lingcod landings increased. California halibut landings also reflected the trend, declining by 24%.

California Dungeness crab landings surpassed the ten-year average. Spiny lobster landings continued a three-year decline, but were above the 1974–92 average. Sea urchin landings were 18% less than in 1992, and declined 38% in northern California. Continuing a long-term decline, total abalone landings were only 8% of the 1957 historic high.

Swordfish landings increased by more than 13%, and approximately 82% of the catch was taken in the drift gill net fishery. Six vessels used longline gear to fish outside U.S. waters and land fish in southern California. A significant portion (42%) of the swordfish catch was landed north of San Francisco because of persistent but weaker El Niño conditions. Statewide landings of live fish were estimated at 216 MT, a 17% increase over 1992. Catches were primarily with vertical longlines and troll longlines, although over 60% of live sheephead landings in southern California were made with trap gear.

Despite the lingering El Niño condition, 13% fewer anglers participated in the marine recreational fishery, and the total catch declined by 19%.

PACIFIC SARDINE

In 1986, spawning biomass estimates for the Pacific sardine (*Sardinops sagax*) exceeded the legally specified level for reestablishment of a commercial fishery in California. Each year since then, the California Department of Fish and Game (CDFG) has established a harvest quota based on an estimate of current spawning biomass. CDFG is required by law to include in the quota a directed fishery quota of at least 910 metric tons (MT) whenever the spawning biomass exceeds 18,200 MT.

At the fourth annual Pacific Sardine Resource Assessment and Management Workshop, the CANSAR (catch-at-age analysis of sardines) model estimated the 1992

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

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1973	68	118,391	25	9,201	1,259	5,383	134,326
1974	6	73,810	60	11,362	2,348	12,901	100,486
1975	3	141,486	129	16,415	1,086	10,542	169,661
1976	24	111,503	293	19,882	2,151	9,063	142,915
1977	5	99,504	5,333	44,775	5,200	12,605	167,424
1978	4	11,253	11,193	30,755	4,401	16,869	74,476
1979	16	48,094	27,198	16,335	4,189	19,660	115,493
1980	34	42,255	29,139	20,019	7,932	15,136	114,514
1981	28	51,466	38,304	13,990	5,865	23,132	132,785
1982	129	41,385	27,916	25,984	10,106	16,023	121,543
1983	346	4,231	32,028	18,095	7,881	1,786	64,367
1984	231	2,908	41,543	10,504	3,786	555	59,518
1985	583	1,600	34,053	9,210	7,856	10,110	63,410
1986	1,145	1,879	40,616	10,898	7,502	20,935	82,975
1987	2,061	1,424	40,961	11,653	8,264	19,662	84,025
1988	3,724	1,444	42,200	10,157	8,667	36,632	102,835
1989	3,845	2,410	35,548	19,477	9,046	40,235	110,560
1990	2,770	3,156	36,716	4,874	7,978	27,989	83,483
1991	7,625	4,184	30,459	1,667	7,345	37,388	87,203
1992	17,946	1,124	18,570	5,878	6,318	13,108	62,944
1993*	13,848	1,954	11,094	1,614	3,882	41,648	74,040

*Preliminary

TABLE 2
Pacific Sardine Quota Allocations (Metric Tons) for California, 1993

	Original allocations*			Revised allocations		
	Quota	Landings	Remainder	Quota	Landings	Remainder
Fishery						
Directed	15,875	12,385	4,640	18,145	16,000	2,900
Northern	5,290	650	4,640	3,570	670	2,900
Southern	10,585	11,735	0	14,575	15,330	0
Dead bait	455	872	57	455	872	57
Northern	57	0	57	57	0	57
Central	57	57	0	57	57	0
Southern	340	815	0	340	815	0
Live bait	910	1,320	0	910	1,650	0
Incidental reserve	2,720	60	2,660	450	70	380
Total allowable harvest	19,960	14,637	7,357	19,960	18,592	3,337

*Original allocations were in effect from January 1 to October 6, 1993; revised allocations were in effect from October 7 to December 31, 1993.

sardine spawning at 99,800 MT. During July 1993, this estimate was revised to 116,200 MT after all 1992 data were included. This increased biomass estimate was not enough to raise the harvest quota established for 1993.

Estimates of the sardine spawning biomass declined from 374,200 MT in 1991 to 116,200 MT in 1992. This decrease may have been caused by the relatively high combined catch of sardines in the United States and Mexico during 1992 (approximately 52,000 MT) or by a combination of high catch and the continued warm-water event (El Niño). El Niño may have displaced sardines to the north of Point Conception (beyond the range of CDFG data collection and thus not included in the biomass estimate).

Fishing industry concern about the lack of data collected north of Point Conception caused CDFG to base the 1993 total allowable harvest on three factors: (1) the upper 95% confidence limit from the CANSAR biomass estimate, (2) the tonnage landed during 1992, and (3) a trend projection from general linear models of previous estimates. The total allowable harvest was set at 19,960 MT and allocated among four categories: directed fishery, dead bait fishery, live bait fishery, and incidental catch in the mackerel fishery.

The directed fishery quota was divided geographically and opened on January 1, 1993 (table 2). The southern directed fishery quickly surpassed its quota and closed on April 22. Demand for sardines was low in the northern directed fishery because fish available were small; consequently, less than 15% of the northern quota was landed, and a local cannery was unable to can sardines because large fish are needed for the canning process.

The central and southern dead bait fisheries quickly filled their quotas. Both were closed early in the year, and no landings were accumulated for the northern dead bait quota (table 2).

In September, the live bait fishery exceeded its allocation because many sportfishing vessels used small sardines while there was a shortage of anchovies. The fishery was allowed to continue landing live bait because historically its landings decreased at the end of the year and because it appeared that the northern directed fishery would not use all of its allocation. The incidental take of sardines (35% by weight) in the commercial mackerel fishery did not exceed its allocation in 1993.

Early closure of the southern directed fishery and low landings in northern California prompted the fishing industry to propose legislation (AB14, passed October 1, 1993) to reallocate the remaining northern directed fishery and the remaining mackerel incidental reserve quotas between the southern and northern directed fisheries. October landings for the reopened southern directed fishery were high, but fishing slowed in November and December. Northern directed fishery landings remained low, and that quota was not filled by year's end (table 2).

At the fifth annual Pacific Sardine Resource Assessment and Management Workshop, the CANSAR model estimated the 1993 spawning biomass to be 71,700 MT. Industry representatives were concerned with the low estimate because most data in the model still came from southern California. To correct this bias, CDFG conducted a cooperative Daily Egg Production Method cruise in April 1994 with the National Marine Fisheries Service (NMFS) and Mexico's Instituto Nacional de Pesca. The cruise ranged from San Francisco to Punta Abreojos, Baja California.

PACIFIC MACKEREL

By January 1 of the 1992–93 fishing season (July 1, 1992, through June 30, 1993) 10,671 MT of Pacific mackerel (*Scomber japonicus*) had already been landed.

Regulations authorize an open fishery when the Pacific mackerel biomass exceeds 136,080 MT, and require a quota fishery (equal to 30% of the biomass above 18,144 MT) when the biomass is below 136,000 MT. The 1992–93 fishing season started with no quota in effect, but because total biomass estimates at midseason were below 136,000 MT, a 34,020 MT quota (based on a biomass estimate of 126,100 MT) was established at that time.

Pacific mackerel landings were 5,803 MT during the first quarter of calendar year 1993, slightly less than in the first quarter of 1992. In January, Pacific mackerel availability increased for the first time in four months, as fishing effort was also directed toward Pacific sardines (*Sardinops sagax*) and market squid (*Loligo opalescens*). Mackerel landings increased throughout February and March, even though fishing effort was diverted to Pacific sardines and market squid.

Second-quarter landings totaled 1,652 MT—half of the 1992 second-quarter landings. Consistent with seasonal patterns of the previous five years, landings were low during April and May. Landings began to increase in June, but continued El Niño conditions kept the catch at a low level. Fishing effort was concentrated on Pacific mackerel because the directed sardine quota fishery closed in April and the sardine dead bait fishery closed in May.

The 1992–93 fishing season ended on June 30, 1993, with a total catch of 18,312 MT, well below the 34,020 MT quota established at midseason, and 30% less than the previous season. The 1992–93 landings continue a downward trend that started with the 1989–90 season, and were the lowest seasonal catch of Pacific mackerel since 1978–79.

Although the Pacific sardine fishery was open and fish were available during most of the season, mackerel were preferred over sardines because mackerel brought a higher ex-vessel price ($100 to $120 per short ton compared with $80 to $100 per short ton for sardines). El Niño conditions displaced mackerel to the north, making them less available to southern California fishers. Evidence of displacement began in early May, when Pacific mackerel were sighted off Tofino, British Columbia; by late May the fish were sighted in the Barkley Sound, and by late June, along the west coast of the Queen Charlotte Islands.

The 1993–94 fishing season opened July 1, 1993 (third quarter of the calendar year) with a quota of 29,665 MT based on a biomass estimate of 117,029 MT. Third-quarter landings totaled 2,403 MT, representing only 27% of the previous year's third-quarter landings. During July and August, most large seiners fished tuna because the availability of Pacific mackerel was low; it remained low through September. Sightings of Pacific mackerel continued in British Columbia during July and August and spread from the southern Canadian border (48° N) to Yakutat, Alaska (59° N).

During October, Pacific mackerel landings increased, only to decline in November despite ex-vessel prices of $140–$150 per short ton. Some fishing effort was diverted to Pacific sardines when the directed sardine fishery opened in mid-October. Pacific mackerel landings increased in December as water temperatures cooled and El Niño conditions deteriorated. Landings totaled 2,268 MT in the fourth quarter of 1993, higher than fourth-quarter landings of 1992, but only 41% of the average fourth-quarter landings from the previous five years.

By fishing year's end, 4,833 MT of Pacific mackerel were landed, bringing landings for the 1993 calendar year to 12,391 MT, the lowest annual catch since 1978. Most of the Pacific mackerel were landed in southern California; 7% were landed in the Monterey Bay area. The declining trend may be attributed to a combination of a declining biomass since 1988, fish displacement to the north by El Niño, and a decreased market following the 1992 closure of a major cannery on Terminal Island. The cannery closure shifted a five-year wetfish landings pattern from 75% landed at Terminal Island canneries and 25% at San Pedro fish markets to 40% landed at Terminal Island canneries and 60% at the San Pedro markets during 1993.

PACIFIC HERRING

Annual statewide landings for Pacific herring (*Clupea pallasi*) roe were 4,350 MT in 1993, a decrease of 29% from the previous year. Statewide landings for the 1992–93 season (November to March) totaled 4,946 MT. The three gill net platoons (374 permittees) in the San Francisco Bay fishery landed 3,493 MT, which was 4% over their quota of 3,348 MT. Thirty-three round haul (purse seine and lampara) permittees fishing in San Francisco Bay landed 1,181 MT, 12% less than their 1,347 MT quota (figure 1). Tomales Bay was opened to commercial herring fishing for the first time since the 1988–89 season, and outer Bodega Bay was closed to commercial fishing. Tomales Bay permittees landed 201 MT, exceeding the 181 MT quota by 11%. Humboldt Bay permittees waited until mid-January to begin fishing. As a result, they missed several early spawning episodes and landed only 26 MT of the 54 MT quota. Crescent City permittees landed 28 MT of the 30 MT quota.

A prediction that record amounts of roe herring would be harvested in Alaska drove down the price of roe herring in California. Ex-vessel prices for gill net–caught herring with 10% roe recovery ranged from $500 to $600 per short ton during the 1992–93 season. The base ex-vessel price for round haul herring was $400 per short ton. As a result, the total ex-vessel value of California's roe fisheries was approximately $3.3 million—well below the ten-year average of nearly $10 million.

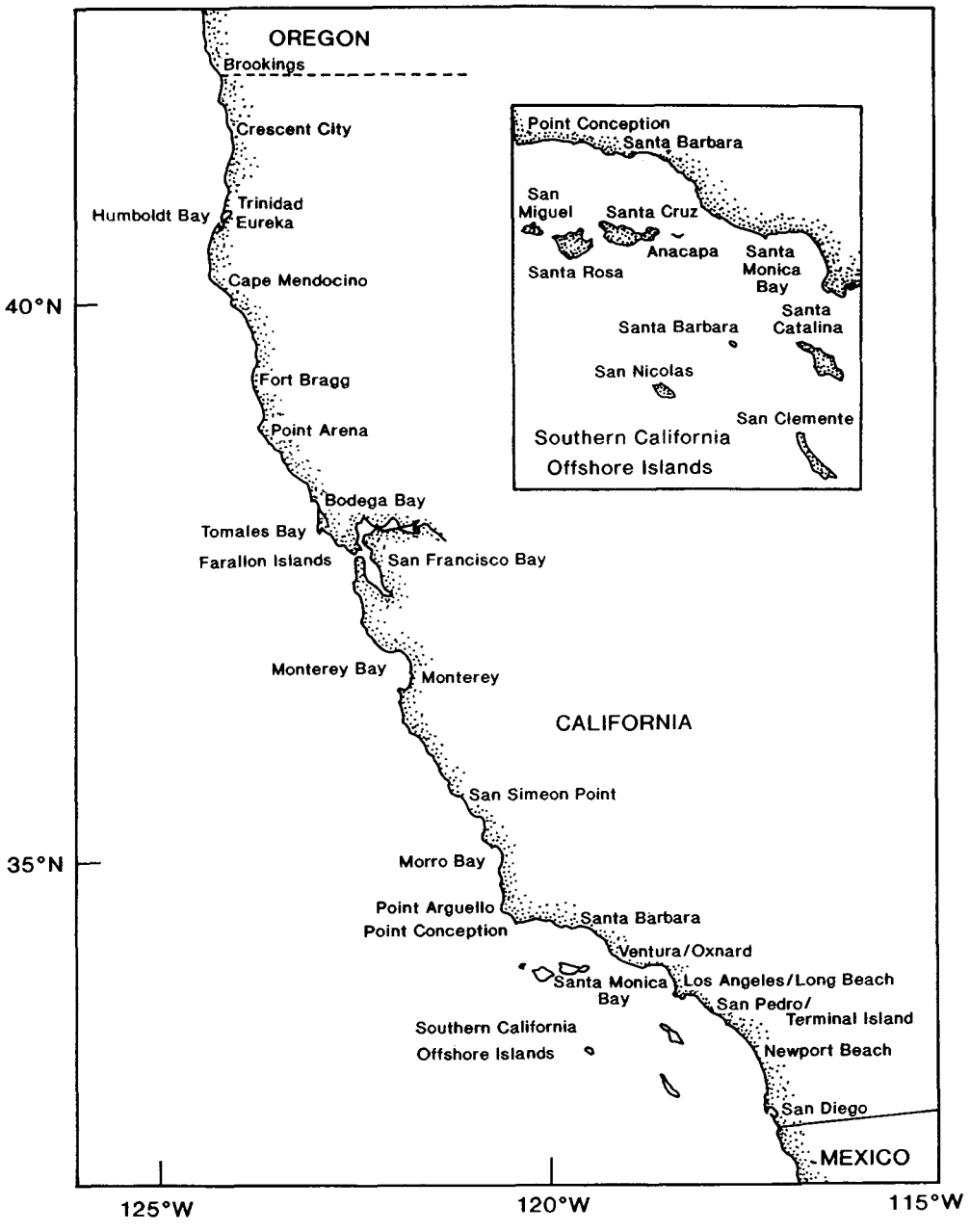

Figure 1. California ports and fishing areas.

Ten permittees in the San Francisco Bay herring roe-on-kelp fishery harvested 43 MT of roe-on-kelp, for 56% of the 77 MT quota. The estimated ex-vessel value of the roe-on-kelp fishery was $950,000, at prices ranging from $8 to $12 per pound.

CDFG biologists estimated spawning biomass for San Francisco Bay and Tomales Bay populations. No estimates were made for Bodega Bay, Humboldt Bay, or Crescent City Harbor. Hydroacoustic and spawn-deposition surveys were used to estimate spawning biomass in San Francisco Bay, and spawn-deposition surveys were used in Tomales Bay.

Estimated spawning biomass of San Francisco Bay herring declined significantly for the third consecutive season, to 19,500 MT for 1992–93, less than half of the previous season's estimate of 42,300 MT. This was the lowest biomass estimate in fifteen years and far below the long-term average of 49,900 MT. The decline could be partly attributed to the second consecutive season of poor recruitment of two-year-old herring. The San Francisco Bay young-of-the-year abundance indices for 1991, 1992, and 1993 were higher than the index for 1990, but still below the thirteen-year average for the index. This suggests that the 1991, 1992, and 1993

year classes will be stronger than the 1990 year class and that the biomass may increase.

The total spawning biomass estimate for Tomales Bay was 3,700 MT, more than a threefold increase from the 1991–92 season's estimate of 1,124 MT. This was the fourth consecutive season that the biomass has increased. After six years of drought, rainfall amounts were above normal during the 1992–93 spawning season. Spawning biomass levels in Tomales Bay may drop next season; historical data indicate that biomass usually declines in years following strong El Niño conditions.

GROUNDFISH

California's 1993 commercial groundfish harvest of 27,913 MT, with an ex-vessel value of approximately $23.5 million, represented approximately a 19% decrease (6,565 MT) from the 1992 landings. Dover sole (*Microstomus pacificus*), thornyhead (*Sebastolobus* spp.), sablefish (*Anoplopoma fimbria*), rockfish (*Sebastes* spp.), and Pacific whiting (*Merluccius productus*) were principal species harvested. Significant decreases were noted for Dover sole, sablefish, and whiting. Thornyhead and most other categories also declined but to a lesser degree (table 3). Widow rockfish (*Sebastes entomelas*), rex sole (*Glyptocephalus zachirus*), and lingcod (*Ophiodon elongatus*) landings increased moderately.

Distribution of 1993 landings by gear type did not differ significantly from recent years, although the bottom and midwater trawl component rose from 75.2% in 1992 to 77.9%, and the line portion of the catch dropped from 17.7% to 15.8%. Trap and setnet components were similar to 1992, at 1.0% and 5.3%, respectively.

For 1993, the Pacific Fishery Management Council (PFMC) set harvest guidelines off California for Dover sole, thornyhead, sablefish, widow rockfish, bocaccio rockfish (*Sebastes paucispinis*), and Pacific whiting. The PFMC instituted cumulative landing limits as well as trip limits during 1993, to meet annual harvest guidelines while providing a year-round groundfish fishery. Cumulative two-week limits were established for the *Sebastes* complex (including bocaccio rockfish) and DTS complex (Dover sole, thornyhead, and sablefish); a cumulative four-week limit was set for widow rockfish.

In 1993, within the Washington-Oregon-California (WOC) area, a harvest guideline of 140,000 MT for Pacific whiting was fully met (140,962 MT) by domestic catcher vessels and processors. A 10,000-pound trip limit was imposed before the unrestricted season opened on April 15 and was reimposed on September 4 after the unrestricted season was closed. All at-sea processing of whiting was restricted to waters north of California. California's shoreside whiting fishery landed and processed 3,144 MT, a 36% decline from 1992 landings (table 3).

TABLE 3
California 1993 Groundfish Landings (Metric Tons)

Species	1992	1993	Percent change
Dover sole	8,619	6,540	−24
English sole	564	470	−17
Petrale sole	528	457	−13
Rex sole	439	456	4
Other flatfish	520	479	−8
Widow rockfish	1,102	1,181	7
Bocaccio	1,467	1,254	−15
Other rockfish	7,396	6,061	−18
Thornyhead	4,328	4,101	−5
Lingcod	604	686	14
Sablefish	3,653	2,570	−30
Pacific whiting	4,930	3,144	−36
Other groundfish	328	514	57
Total	34,478	27,913	−19

Five midwater trawl vessels, fishing off Eureka and Crescent City, landed 98% of California's catch (at $0.05 per pound).

A whiting observation program was established in 1993 to monitor bycatch of salmon and other species in shoreside landings. To facilitate monitoring the entire landed bycatch, experimental fishing permits (EFPs) were issued to three Crescent City–based trawl vessels. The permits required delivery of unsorted whiting catches to selected shoreside plants. Rapid chilling at sea of unsorted whiting purportedly improved the quality of the product. Of the 76 EFP trips, 28 were observed. Salmon bycatch was 0.018 salmon per MT of Pacific whiting. All salmon observed were chinook (*Oncorhynchus tshawytscha*). The five most abundant species in the bycatch were jack mackerel (*Trachurus symmetricus*), Pacific mackerel (*Scomber japonicus*), widow rockfish, splitnose rockfish (*Sebastes diploproa*), and spiny dogfish (*Squalus acanthias*).

Sablefish management in the WOC area resembled that of 1992, with a trawl allocation of 58% and a nontrawl allocation of 42%. The 7,000 MT harvest guideline (including a tribal allotment of 300 MT) was, however, a sharp reduction from the 8,900 MT available in 1992. Total WOC sablefish landings in 1993 were 7,400 MT, and California accounted for 2,570 MT, or 35% of the total WOC catch.

The PFMC allowed unrestricted nontrawl sablefish fishing in the WOC area to begin on May 12, 1993, three days before the Alaska sablefish fishery. In contrast to 1992, the PFMC set a single nontrawl trip limit of 250 pounds before and after the unrestricted season. Landings under the 250-pound trip limit totaled 74 MT. In the WOC area, nontrawl landings of 2,792 MT were 1% less than the nontrawl allocation. California nontrawl gear caught 711 MT, about 25%, of the WOC nontrawl landings.

For the DTS complex, the two-week cumulative limit

was initially set at 45,000 pounds, of which no more than 20,000 pounds could be thornyhead and no more than 25% (or 1,000 pounds) per trip could be sablefish. On April 21, the DTS-complex cumulative limit was changed to 60,000 pounds per specified four-week interval to further reduce the catch of sablefish without increasing the potential for discard. In the WOC area, trawl sablefish landings were 4,608 MT, about 16% greater than the trawl allocation despite increasingly restrictive catch regulations, which were changed several times during the season. California trawl vessels landed 1,818 MT, or 39%, of this coastwide total.

The coastwide harvest rate of thornyhead in 1993 was lower than in 1992 because of a reduced thornyhead cumulative limit of 35,000 pounds per four-week period. Coastwide landings of 7,636 MT declined from 1992 landings but still exceeded the 7,000 MT harvest guideline by 636 MT. California landed 4,101 MT, or 54%, of the coastwide thornyhead catch.

The coastwide catch of Dover sole was 14,320 MT, a decrease of 1,689 MT from 1992. The continuing decline in production was the result of reduced market demand and increasingly restrictive landing limits. California landings of 6,540 MT were 46% of total coastwide landings, compared with a 54% share for 1992.

California's *Sebastes* complex landings declined from 8,863 MT in 1992 to 7,315 MT in 1993, and included nearly 1,254 MT of commercial bocaccio harvest and an estimated 200 MT from the recreational fishery. The California *Sebastes* fishery began with a 50,000-pound two-week cumulative limit including a 10,000-pound bocaccio limit. Midyear projections that 1993 bocaccio landings would be below the harvest guideline of 1,540 MT, and reports that bocaccio were discarded at the 10,000-pound limit caused the PFMC to increase the cumulative bocaccio limit within the *Sebastes* limit to 15,000 pounds.

The 1993 coastwide widow rockfish harvest guideline (HG) of 7,000 MT was unchanged from 1992. Widow rockfish harvest was projected to exceed the HG by early November, but the PFMC chose not to modify the cumulative limit of 30,000 pounds per four-week period and waited until December 1 to impose a 3,000-pound-per-trip limit. The total 1993 landed catch of 7,905 MT was 113% of the HG, of which California contributed 1,181 MT, or 15%.

The groundfish limited-entry plan, adopted by PFMC in 1991, was approved by NMFS in late 1992 for implementation on January 1, 1994. The plan requires permits for any trawl, longline, or pot vessel fishing in the limited-entry fishery. Non-permitted vessels will be allowed to fish in the "open-access" fishery. The limited-entry and open-access fisheries will be subject to separate quotas and trip limits.

In 1992, PFMC examined the feasibility of individual transferable quotas (ITQs) and chose to develop an ITQ program for nontrawl sablefish. In 1993, the PFMC continued to narrow the program options with the goal of adopting a plan in spring 1994.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1992–93 season were 4,567 MT, an increase of only 119 MT from the previous season, but well above the ten-year average of 3,643 MT.

The northern California season opened on December 1, 1992, with only a few fishers setting gear because of a price-related strike and poor (soft shell), postmolt crab condition. Fishers in Oregon and Washington agreed to an ex-vessel price of $1.00 per pound on December 1, and fishers from the border port of Brookings, Oregon, immediately set gear in California waters southward to Point Saint George. During the strike period, Oregon fishers harvested intensively from that area, arousing considerable hostility in California fishers and finally leading to altercations and vessel ramimings. Crab condition improved by January 1, 1993, but the price dispute continued despite a drop in the fishers' demand from $1.25 to $1.10 per pound. Fishing began in earnest on February 8 at $1.05 per pound, $0.30 per pound lower than the 1991–92 season price.

A fleet of 454 vessels landed approximately 4,357 MT at the northern California ports of Crescent City, Trinidad, Eureka, and Fort Bragg during the 1992–93 season. The port of Crescent City accounted for 2,500 MT of the total, followed by Eureka (1,436 MT), Trinidad (346 MT), and Fort Bragg (75 MT).

The San Francisco–area Dungeness crab season opened on November 10, 1992, with an ex-vessel price of $1.83 per pound. Total crab landings decreased by 326 MT from the previous season, to a 1992–93 total of 121 MT. Crab fishers landed 37 MT at Bodega Bay, and 84 MT at ports in the San Francisco area. Monterey and Morro Bay contributed 89 MT to the season total.

The 1992–93 season marked the first time that fishers were required to obtain a permit to participate in the California Dungeness crab fishery. Assembly Bill 3189 enacted a three-year moratorium on new entrants to the fishery, pending a study of the need to limit participation.

In September 1993, resource agency directors from California, Oregon, and Washington signed a memorandum of understanding recognizing the need for interstate cooperation in managing the Pacific Coast Dungeness crab fishery in general, as well as adjusting the fishing season if soft-shelled crabs were commonplace at the beginning of the winter season.

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

	Swordfish	Thresher shark	Shortfin mako shark
1983	1,183	783	147
1984	2,013	756	150
1985	2,362	700	103
1986	1,749	276	215
1987	1,246	239	274
1988	1,129	250	222
1989	1,296	295	177
1990	851	210	262
1991	711	344	151
1992	1,068	179	97
1993*	1,206	155	84

*Preliminary

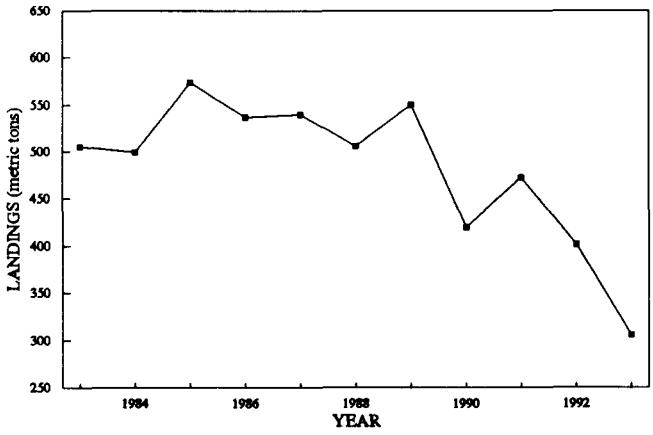

Figure 2. California landings of halibut, 1983–93.

SWORDFISH AND SHARKS

Swordfish (*Xiphias gladius*) landings increased to 1,206 MT in 1993, 13% more than in 1992 (table 4). About 82% of the catch was taken by the drift gill net fishery. Harpoon landings increased to 8%, and longline landings doubled to 10% of the catch. Six vessels (there were three in 1992) used longline gear outside of the U.S. Exclusive Economic Zone (EEZ) and landed fish in southern California. As in 1992, a significant portion (42%) of the swordfish catch was landed north of San Francisco because of persistent (but weaker) El Niño conditions. Typically, swordfish caught in drift gill nets or by longline sold for $2.25 to $4.35 per pound, whereas harpooned fish sold for $3.50 to $6.50 per pound.

Common thresher shark (*Alopias vulpinus*) landings declined to 155 MT in 1993, the lowest level in thirteen years. Landings at southern California ports sold predominantly at ex-vessel prices between $1.00 and $2.00 per pound. Nearly all of the thresher sharks were caught by the drift gill net fishery.

Shortfin mako shark (*Isurus oxyrinchus*) landings decreased by 13% to 84 MT (table 4). Most (70%) of the catch was landed in southern California ports, at ex-vessel prices between $0.75 and $1.50 per pound. Mako sharks are caught primarily by the drift gill net fishery, although hook and line gear accounted for approximately 14% of the mako catch, and almost 7% of the catch was landed by longline vessels operating outside the EEZ.

CALIFORNIA HALIBUT

California halibut (*Paralichthys californicus*) landings in 1993 were approximately 306 MT (table 5), a decline of 24% from the 401 MT landed in 1992 (figure 2). San Francisco accounted for 43% of total halibut landings; Santa Barbara accounted for 23%. Three factors may have contributed to low landings in Santa Barbara and other southern California ports. (1) The Marine Resource Protection Act of 1990 (Proposition 132) prohibited the use of gill and trammel nets in state waters south of Point Arguello after January 1, 1994, and entangling net fishers may have left the fishery to avoid increased permit fees ($1,000). (2) Warmer-than-normal sea temperatures from the El Niño event may have shifted the halibut, and the fishery, northward. (3) Opportunistic feeding of harbor seal (*Phoca vitulina*) and California sea lion (*Zalophus californianus*) on southern California set and trammel nets reduced the catch.

TABLE 5
California Commercial Halibut Landings, 1993

Port	Pounds	Metric tons	Value	Percentage of total pounds
Unknown	947	0.4	$2,353	0.1
Eureka	732	0.3	$1,656	0.1
San Francisco	289,685	131.5	$676,601	42.9
Monterey	39,576	17.9	$79,842	5.9
Morro Bay	59,842	27.2	$150,443	8.9
Santa Barbara	152,162	69.1	$355,128	22.5
Los Angeles	72,956	33.1	$218,364	10.8
San Diego	58,898	26.7	$140,622	8.7
Totals	674,798	306.2	$1,625,009	99.9

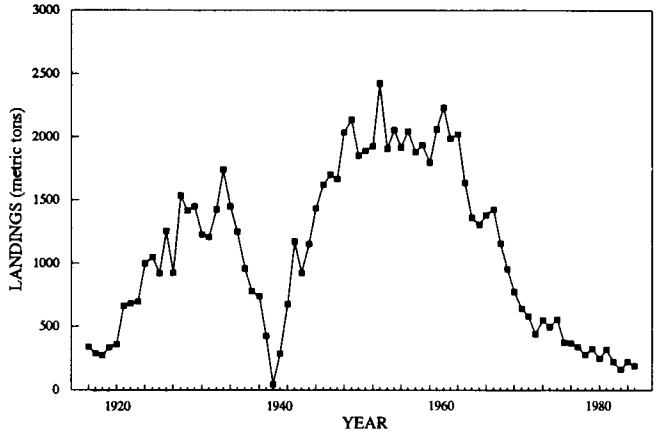

Figure 3. California abalone landings, 1916–93.

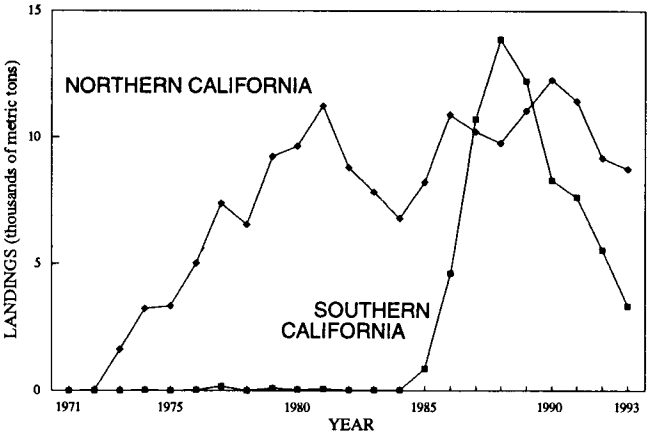

Figure 4. California sea urchin landings, 1971–93.

California halibut landings peaked in 1993 during March (51 MT) and July (50 MT). Landing-receipt data indicate that trawl nets accounted for 47% of the catch, followed by entangling nets (36%), hook and line (11%), and miscellaneous or unspecified gears (6%).

California halibut prices ranged from $1.00 to $6.75 per pound, averaged $2.68 per pound, and totaled $1.6 million for 1993.

ABALONE

Abalone (*Haliotis* spp.) historically have been harvested by both commercial and recreational fishers in California. Commercial landings were 200 MT in 1993, down from 235 MT in 1992 and third lowest since landing statistics began to be collected in 1916 (figure 3). The 1993 landings represented just 8% of the 1957 peak of 2,470 MT. Statewide recreational catch estimates were unavailable, but in 1989 the recreational catch of red abalone (*Haliotis rufescens*) in northern California was estimated to be 2.5 times larger than the statewide commercial abalone fishery.

Approximately 189 MT of red abalone, the principal species harvested, were landed by commercial fishers in 1993. These landings were 6% less than in 1992 and 80% less than the 1931–67 average of 953 MT. Red abalone was the only species taken commercially in northern California, off the San Mateo County coast and off the Farallon Islands.

Commercial catches of red abalone in southern California waters have declined over the past decade at all areas except San Miguel Island, where catches increased from 66 MT in 1982 to 133 MT in 1993, and constituted 71% of statewide abalone landings. During this same decade the statewide proportion of abalone landed in the Santa Barbara area declined from 20% to 3%; in the San Diego area, from 10% to 0.3%; at San Nicolas Island, from 10% to 0.2%; and at Santa Cruz Island, from 7% to 0.1%.

Pink, green, and black abalone were also landed commercially. All 1993 southern California landings reflect a continued decline from the previous year: pink abalone declined from 8 MT in 1992 to 7 MT; green abalone declined from 5 MT to 3 MT; and black abalone declined from 17 MT to 0.9 MT. Part of this decline was attributed to a statewide closure on sport and commercial take of black abalone. The closure was imposed in July 1993 to allow recovery for survivors of a disease known as withering syndrome, which continued to decimate black abalone populations at the Channel Islands and off the California mainland.

Average ex-vessel prices in 1993 increased by 29% from 1992 to $6.98 per pound, reflecting increasing worldwide demand. Thus the ex-vessel value of abalone landings rose to $3.1 million from $2.8 million in 1992 despite declining landings. Since 1983, ex-vessel prices have risen by 239%, while inflation grew by only 52% as measured by the California Consumer Price Index.

SEA URCHIN

In 1993, California landings of red sea urchin (*Strongylocentrotus franciscanus*) totaled 12,046 MT, 18% less than the 1992 total of 14,655 MT. Southern California landings decreased by 6% from the previous year, while northern California landings decreased by 38% (figure 4).

Catch per unit of effort (CPUE), in kilograms per diving hour, decreased in northern California from 144 kg per hour in 1992 to 112 kg per hour in 1993, and was dramatically less than the high rate of 311 kg per hour in 1988 (figure 5). Southern California CPUE decreased from 106 kg/hr in 1992 to 93 kg/hr in 1993, continuing a slow decline from the high rate of 149 kg/hr in 1989 (figure 5).

The number of sea urchin permits declined from 548 permittees and 84 apprentices in the 1992–93 season to 520 permittees and 77 apprentices during the 1993–94

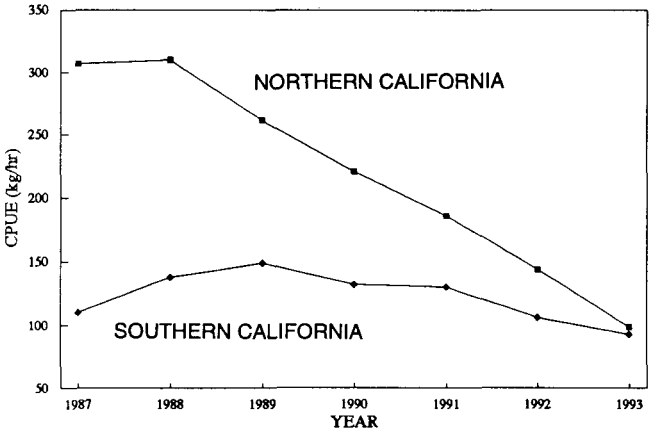

Figure 5. California sea urchin catch per unit of effort, 1987–93.

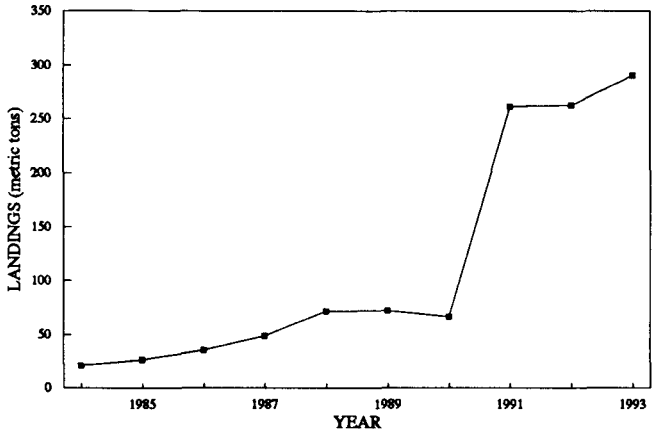

Figure 6. California sea cucumber landings, 1984–93.

season, a number considered too high, and well above the original target of 400 permits. The California Fish and Game Commission canceled the apprentice diver program in March 1994. Current apprentices will be granted full permit status, and no new permits will be issued until the number drops below the new target of 300.

The purple sea urchin (*Strongylocentrotus purpuratus*), a smaller species with less roe, is more difficult to process. Although interest in this species has increased in recent years, the market for purple urchins is still limited. Statewide, purple sea urchin landings decreased from 143 MT in 1992 to 49 MT in 1993. As the availability of red sea urchins continues to decline, harvest of purple sea urchins may increase, especially if harvesting and processing economics become favorable.

SEA CUCUMBER

Statewide, sea cucumber landings were 291 MT in 1993, an increase of 28 MT over 1992 landings. The catch comprised 12 MT of warty sea cucumber (*Parastichopus parvimensis*) and 279 MT of California, or giant red, sea cucumber (*P. californicus*). Commercial divers in southern California harvested the giant red sea cucumber by hand; trawlers harvested the warty cucumber. Most sea cucumbers were landed in the ports of San Pedro and Santa Barbara. The main fishing grounds for the giant red sea cucumber were the Santa Barbara Channel and the Santa Catalina Channel, at depths of 30 to 90 fathoms. Warty sea cucumbers were harvested as far south as San Diego, but most were taken from waters off the northern Channel Islands.

The average price for warty sea cucumbers was $0.66/lb and ranged from $0.30 to $0.90/lb; the average price for California sea cucumbers was $0.62/lb and ranged from $0.20 to $0.70/lb. The warty variety sold at a slightly higher average price because of a thicker, meatier body wall that yields a higher-quality food product. Most of the sea cucumbers were dried and exported to Hong Kong and Taiwan. The end product, called trepang, sold for $4.00 to $13.00/lb. A small portion of the harvest was distributed and sold within the United States.

The sea cucumber fishery began in California near Los Angeles around 1978, and averaged under 45 MT annually until 1982, when a trawl fishery developed near Santa Barbara. During the next ten years, annual landings increased gradually (figure 6). In 1991, an influx of trawlers, predominately out of the Los Angeles port area, greatly expanded the fishing effort and catch. From 1991 through 1993, sea cucumber landings exceeded 260 MT (figure 6). Since the 1992–93 season, the fishery has been a limited entry fishery based on a previous minimum sea cucumber landing of 50 pounds. There were 86 permittees in 1993. Landing receipt data indicate that 27 trawlers and 20 dive boats actively participated in the fishery during 1993.

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

Sea cucumbers have a short life span, low age of maturity, sporadic recruitment, and high natural mortality. Species with these characteristics can be vulnerable to overfishing, but it is expected that the southern California populations of warty and giant red sea cucumber can sustain current harvest levels, because of permit restrictions placed upon the fishery. Northern California dive fishery landings have leveled off and appear to be sustainable unless harvest restrictions for the northern

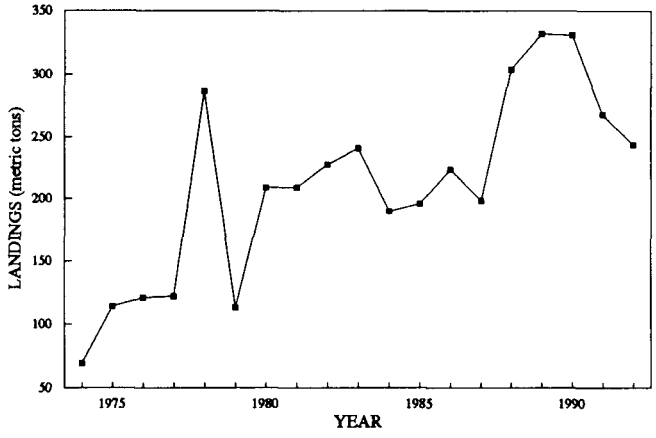

Figure 7. California spiny lobster landings, 1974–93.

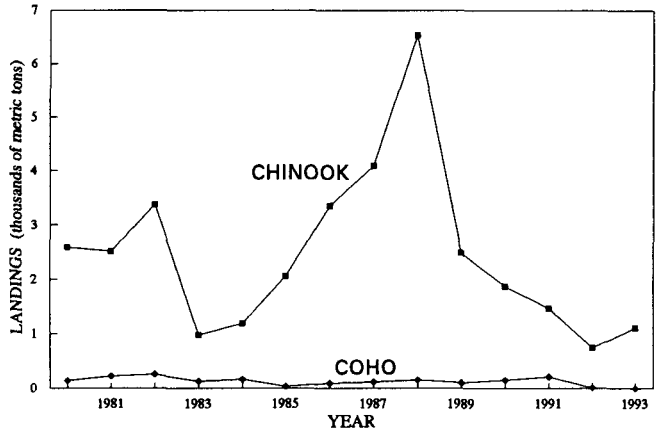

Figure 8. California commercial salmon landings, 1980–93.

California sea urchin fishery redirect that effort to the sea cucumber resource.

CALIFORNIA SPINY LOBSTER

During the 1992–93 commercial fishing season, spiny lobster (*Panulirus interruptus*) landings totaled 244 MT—24 MT (9%) less than the 268 MT landed in 1991–92 (figure 7). The 1992–93 landings were above the 1974 –92 average of 209 MT. The historic high catch of 500 MT was recorded during the 1949–50 season.

Since 1974, landings during the first two months of the season have consistently made up over 50% of the season's total. During the 1992–93 season 62% of the total was landed in the first two months.

Starting in 1965, permits were required for commercial lobster trapping, and the number of permits ranged from a low of 180 in 1970–71 (when a $100 fee was instituted) to 614 in 1968–69. For the 1992–93 season 329 permits were issued, representing a decrease of 8% from the previous season.

From 1952 to 1970, the total ex-vessel value of the fishery ranged between $250,000 and $500,000. Since then, total landings value increased to a high of $4 million in 1990. Ex-vessel prices in the fishery were $6.43 per pound for the 1992–93 season and totaled $3.3 million, a decrease of 17% from the previous season.

Spiny lobsters were also taken by recreational fishers, mostly scuba divers, but hoop netting was popular in a few areas, especially San Diego Bay. During the 1992–93 spiny lobster season, CDFG conducted dockside interviews (intercept program) and mailed survey questionnaires to recreational lobster fishers. Analysis of data from the intercept program, mail surveys, and commercial passenger dive boat (CPDB) logbooks for the 1992–93 season revealed that most recreational lobster fishers caught one lobster per trip. Catch and effort analysis for the recreational fishers revealed patterns similar to those observed in the commercial fishery, with decreasing catch

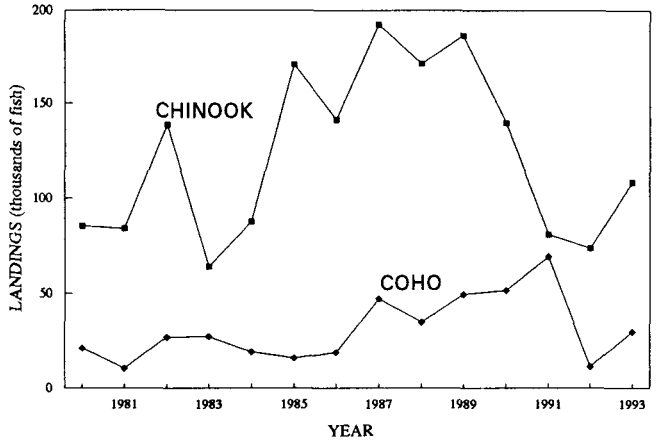

Figure 9. California recreational salmon landings, 1980–93.

and effort as the season progressed. Unlike the commercial fishery, however, the recreational fishing effort and subsequent catch increased during the final weeks of the season.

SALMON

During an estimated 24,800 days fished in 1993, the California commercial salmon fishery landed slightly over 2.4 million pounds of chinook salmon (*Oncorhyncus tshawytcha*; figure 8). No commercial landings of coho salmon (*Oncorhyncus ksutch*) were permitted. California recreational anglers caught 108,400 chinook and 29,700 coho salmon during 174,000 angler trips (figure 9).

Because six years of drought had reduced salmon availability, very restrictive commercial and recreational ocean salmon regulations were implemented to ensure annual escapement goals in the Klamath and Sacramento fall chinook stocks. These stocks represented most of California's ocean salmon landings. The Klamath fall chinook escapement goal was 35,000 natural spawners, and the Sacramento fall chinook goal was 122,00–180,000

spawners. The commercial fishery operated under various time and area closures between May 1 and September 30, 1993.

Ex-vessel prices for salmon, eviscerated and cleaned at sea, were $2.25 per pound, and total ex-vessel value was $5.4 million.

Recreational fishery regulations were less restrictive than in 1992, although a few restrictions north of Point Conception remained unchanged (barbless hooks, daily bag limit of two salmon, and a minimum size limit of 20 inches).

Recreational chinook landings at southern ports totaled 103,500 fish and were 46% higher than the 1992 landings of 71,000 fish. Recreational angler effort in the south totaled 140,300 angler trips, compared to 109,600 trips in 1992. The chinook catch per angler trip averaged 0.74 fish, compared to 0.65 fish in 1992. Recreational coho landings in the south totaled 15,400 fish, about three times more than the 1992 landings. The recreational chinook fishery opened with a catch quota of 12,000 fish, a daily bag limit of one salmon, and a closure of Sunday through Tuesday each week.

Northern recreational landings totaled 7,500 chinook and 19,000 coho, compared to 3,800 chinook and 8,200 coho in 1992. Angler effort was 51,300 trips in 1993, about 2.3 times greater than the 1992 effort of 21,900 trips. In September, 1,100 chinook and 1,400 coho were caught in the general area fishery, during 6,100 angler days.

LIVE-FISH FISHERY

The commercial fishery to catch and sell live fish continued to expand in California. In 1993, statewide landings for live fish were estimated at 216 MT, 17% more than in 1992 (table 6). The live-fish fishery began in 1988, mainly for the California Asian community. For this market, popular fishes are those that look attractive and can withstand the rigors of capture and transportation. Optimum weight ranges between 1 and 3 pounds, a suitable single entrée size at Asian restaurants. Ex-vessel prices ranged from $2.00 to $7.00 per pound. Larger fish were also sold live, but at a considerably reduced price. Prices fluctuated with market demand, fish size, fish condition, and weather conditions. Demand for live red rockfish increased toward the lunar New Year celebrations, and ex-vessel prices rose above $6.00 per pound.

Live-fish landings in southern California (Morro Bay south) totaled 190 MT, 23% more than in 1992 (figure 10). Most landings were made with hook and line gear until 1989, when finfish traps were used to catch sheephead. Use of traps grew rapidly; by 1993 over 60% of live sheephead were caught with trap gear. Traps used for finfish are constructed like lobster traps, but variations abound as this fishery continues to develop. Target species for both gear types included California sheephead; cabezon; California scorpionfish; treefish (*Sebastes serriceps*); and kelp (*S. atrovirens*), brown, grass (*S. rastrelliger*), and gopher rockfishes. Gill nets and trawls for live California halibut (*Paralichthys californicus*) were used near Ventura and Los Angeles, but total catch was not substantial.

TABLE 6
Preliminary 1993 Landings of Live Fish (Metric Tons)

	Southern California	Northern California
California sheephead	97	0
Cabezon	15	0
Rockfishes	68	25
All others	10	1
Total	190	26

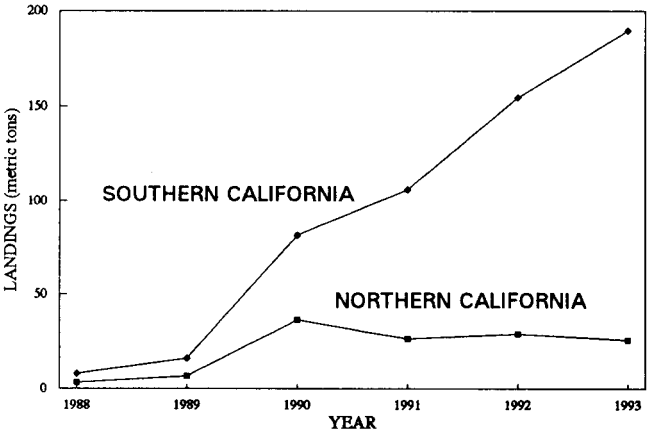

Figure 10. California live-fish landings, 1988–93.

Live-fish landings in northern California (north of Morro Bay) totaled 26 MT, 12% less than in 1992 (figure 10). Landings were made primarily by hook and line vessels using vertical longlines and troll longlines to harvest rockfish along nearshore rocky reefs and offshore banks. Principal rockfishes caught were canary (*Sebastes pinniger*), gopher (*S. carnatus*), brown (*S. auriculatus*), China (*S. nebulosus*), copper (*S. caurinus*), and quillback (*S. maliger*).

Monitoring and accurate data collection was difficult for this fishery because live-fish landings were not separated from dead-fish landings in the database. For this reason, CDFG developed and implemented new landing receipts that differentiate live fish from dead fish.

Management recommendations were drafted to regulate the live-fish trap fishery because of potential effects on sheephead populations. Proposed restrictions include a limited-entry program, limitations on number of traps, and construction requirements for traps.

RECREATIONAL FISHERY

California's large, diverse, marine recreational fishery includes skiff, beach-and-bank, pier, and commer-

TABLE 7
Commercial Passenger Fishing Vessel Landings

Species/Species-group	1993 Provisional Number of fishes*		Rank	1992 Final Number of fishes*		Rank
Rockfishes (misc.)	1,535,229	(23,271)	1	2,051,576	(28,710)	1
Pacific mackerel	396,950	(8,387)	2	327,747	(242)	4
Kelp bass	333,313	(4,115)	3	463,673	(12,838)	2
Barred sand bass	306,363	(4,199)	4	363,304	(3,047)	3
California barracuda	198,943	(4,122)	5	248,055	(6,198)	5
Pacific bonito	119,201	(6,934)	6	115,866	(5,410)	6
Salmon (misc.)	69,376	(1)	7	43,384	(1)	10
Spotted scorpionfish	64,194	(12,031)	8	77,290	(12,128)	7
Halfmoon	54,622	(11)	9	42,372	(1)	12
Ocean whitefish	38,247	(959)	10	40,702	(707)	14
Lingcod	33,760	(230)	11	43,251	(264)	11
Yellowtail	32,020	(16,546)	12	40,834	(32,986)	13
Yellowfin tuna	26,065	(26,015)	13	73,739	(58,282)	8
California sheephead	23,964	(983)	14	25,778	(1,367)	15
Skipjack tuna	20,454	(15,811)	15	52,302	(25,976)	9
White croaker	11,274		16	4,824		21
Bluefin tuna	9,964	(9,716)	17	8,586	(5,261)	17
Dolfinfish	8,035	(7,353)	18	22,727	(20,815)	16
Jack mackerel	7,198	(20)	19	1,806		26
Flatfishes (misc.)	6,319	(7)	20	7,365		18
Blacksmith	5,689		21	6,369		19
California halibut	5,083	(40)	22	4,341	(30)	22
Sharks (misc.)	3,766	(10)	23	3,518	(9)	24
Croakers (misc.)	3,682	(298)	24	2,315	(96)	25
Wahoo	3,207	(2,638	25	3,924	(3,736)	23
All others	13,923	(1,017)	—	15,121	(827)	—
Totals	3,330,841	(144,714)		4,090,769	(218,931)	

*Numbers in parentheses are fish caught in waters south of California (mainly off Mexico).

cial passenger fishing vessel (CPFV) modes. The CPFV fleet accounts for a substantial proportion of California's landings (table 7). In southern California, CPFVs fish for albacore (*Thunnus alalunga*), Pacific bonito (*Sarda chiliensis*), yellowtail (*Seriola lalandei*), California barracuda (*Sphyraena argentea*), yellowfin tuna (*T. albacares*), Pacific mackerel (*Scomber japonicus*), rockfishes (*Sebastes* spp.), barred sand bass (*Paralabrax nebulifer*), and kelp bass (*P. clathratus*). In central and northern California, CPFVs fish for salmon (*Oncorhyncus* spp.), striped bass (*Morone saxatilis*), rockfishes (*Sebastes* spp.), lingcod (*Ophiodon elongatus*), and white sturgeon (*Acipenser transmontanus*).

In 1992, above-normal sea-surface temperatures, caused by an El Niño event, and a six-year drought influenced fishing conditions by displacing some pelagic fish stocks northward. In 1993, fishing conditions were influenced by sea-surface temperatures that were returning toward normal and by a substantial rainy season. The more normal sea-surface temperatures had a negative effect on the CPFV industry, because some of the more desirable surface gamefish were less available, especially in southern California.

There were 13% fewer anglers (555,359) in 1993 than in 1992, and total catch declined by 19%, to 3,330,841 fish (table 7). Of the twenty-five most prominent fish species and species-groups ranked in the catch, fifteen had lower catches than during 1992. Most notably, yellowfin tuna and dolfinfish (*Coryphaena hippurus*) both declined by 65%, and skipjack tuna (*Euthynnus pelamis*) declined by 61%. Others with moderately lower landings in 1993 were kelp bass (28% decline), rockfishes (25%), yellowtail and lingcod (both 22%), and California barracuda (20%). On a positive note, ten species and species-groups had higher landings in 1993 than in 1992: jack mackerel (*Trachurus symmetricus*) increased by 75%; white croaker (*Genyonemus lineatus*) by 57%; salmon by 38%; and croakers (Sciaenidae) by 37%. Others with moderately higher landings in 1993 were halfmoon (*Medialuna californiensis*), which increased by 22%, Pacific mackerel, by 17%; California halibut (*Paralichthys californicus*), by 15%; and bluefin tuna (T. thynnus), by 14%.

Contributors:

R. Ally, CPFV
K. Barsky, shark/swordfish
T. Bishop, Pacific sardine
A. Grover, salmon
D. Hanan, editor
S. Harris, lobster
J. Hernandez, California halibut
K. Karpov, abalone
E. Konno, Pacific mackerel
K. McKee, live fish
D. Ono, sea cucumber
L. Quirollo, Pacific whiting
C. Ryan, Pacific herring
I. Taniguchi, sea urchin
D. Thomas, groundfish
R. Warner, Dungeness crab

THE STATE OF THE CALIFORNIA CURRENT IN 1993–1994

THOMAS L. HAYWARD, ARNOLD W. MANTYLA
Marine Life Research Group
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093

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

TERESA K. CHERESKIN
Marine Life Research Group
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093

ABSTRACT

This report is a summary and preliminary interpretation of recent shore-station and shipboard observations made of the coastal waters of California. The emphasis is upon data currently being collected by the CalCOFI (California Cooperative Oceanic Fisheries Investigations) program. The California Current was affected by El Niño conditions in 1992 and 1993, which were evident as elevated coastal sea level; widespread positive sea-surface temperature anomalies; a thicker mixed layer and deeper nutricline; and relatively low values of chlorophyll, primary production, and macrozooplankton biomass. A strong and broad inshore countercurrent was evident in January and February of 1992 and 1993. During 1992 and 1993, anomalies in coastal sea level and the circulation pattern were most pronounced during late winter to early spring, and structure during the remainder of the year was less extreme. A different pattern is developing in 1994. The inshore countercurrent was absent in January 1994, and coastal sea level was anomalously low. Mesoscale physical structure of the California Current was strong during the entire period described here. A particularly striking feature is the sharp coastal meander, which was first sampled during October 1993 and which remained evident through March 1994.

RESUMEN

Este reporte ofrece un resumen e interpretación preliminar de observaciones obtenidas en estaciones litorales y buques en aguas costeras de California. El enfoque es en los datos que estan siendo colectados por el programa CalCOFI ("California Cooperative Oceanic Fisheries Investigations"). Las condiciones El Niño en 1992 y 1993 influenciaron a la Corriente de California; estas condiciones se revelaron como un nivel del mar elevado, condiciones extendidas de anomalías positivas de temperatura del agua superficial, capa de mezcla más gruesa y nutraclina más profunda, y valores relativamente bajos de clorofila, producción primaria y macro-zooplancton. En Enero y Febrero de 1992 y 1993 hubo evidencia de una contra-corriente fuerte cercana a la costa. Du rante 1992 y 1993 las anomalías en el nivel del mar y el patrón de circulación costero fueron más pronunciados de finales de invierno a principios de verano, mientras que el resto del año la estructura fué menos marcada. En 1994 se está desarrollando un esquema distinto; en Enero no hubo contra-corriente cercana a la costa y el nivel del mar se mantuvo anormalmente bajo. Durante todo el intervalo aquí descrito, la estructura física de la Corriente de California en la meso-escala fué marcada. Una característica que llama la atención es un meandro costero bien definido que en un principio fué muestreado en Octubre de 1993 y que persistía hasta Marzo de 1994.

INTRODUCTION

This report summarizes recent coastal and shipboard observations of the physical, chemical, and biological state of the California Current system. Data collected from July 1992 through April 1994 on CalCOFI (California Cooperative Oceanic Fisheries Investigations) time-series survey cruises are emphasized. This is an introduction to the data being collected, and an attempt to make these timely observations more accessible to researchers and other users of the coastal ocean. This report follows a summary of the structure of the California Current region in 1991 and early 1992 (Hayward 1993). A brief interpretation of these data is presented in light of the impact of the 1992–93 El Niño event.

DATA SETS AND ANALYTICAL TECHNIQUES

Coastal sea level is measured continuously at several tide gauge stations. Data from La Jolla and San Francisco are used in this report as examples of southern and northern coastal sites. These stations have long time series which can be used for comparison with the recent data. The data shown in this report are corrected for the secular rise in sea level (Roemmich 1992). Anomalies from the monthly mean sea level were calculated by subtracting the long-term mean (1925–91 for La Jolla and 1900–90 for San Francisco).

Sea-surface temperature (SST) and salinity are also measured daily at several coastal stations (Walker et al. 1992). SST data from La Jolla (SIO Pier) and Pacific Grove are given in this report to complement the coastal sea-level data. SST and daily anomalies are calculated from the long-term harmonic mean temperature (1916–93 for La Jolla and 1919–93 for Pacific Grove).

The CalCOFI monitoring program started in 1949; a brief history and description of the program is given by Hewitt (1988). The present form of the sample grid (figure 1) and the program of quarterly sampling, (typically in January, April, July, and October) was

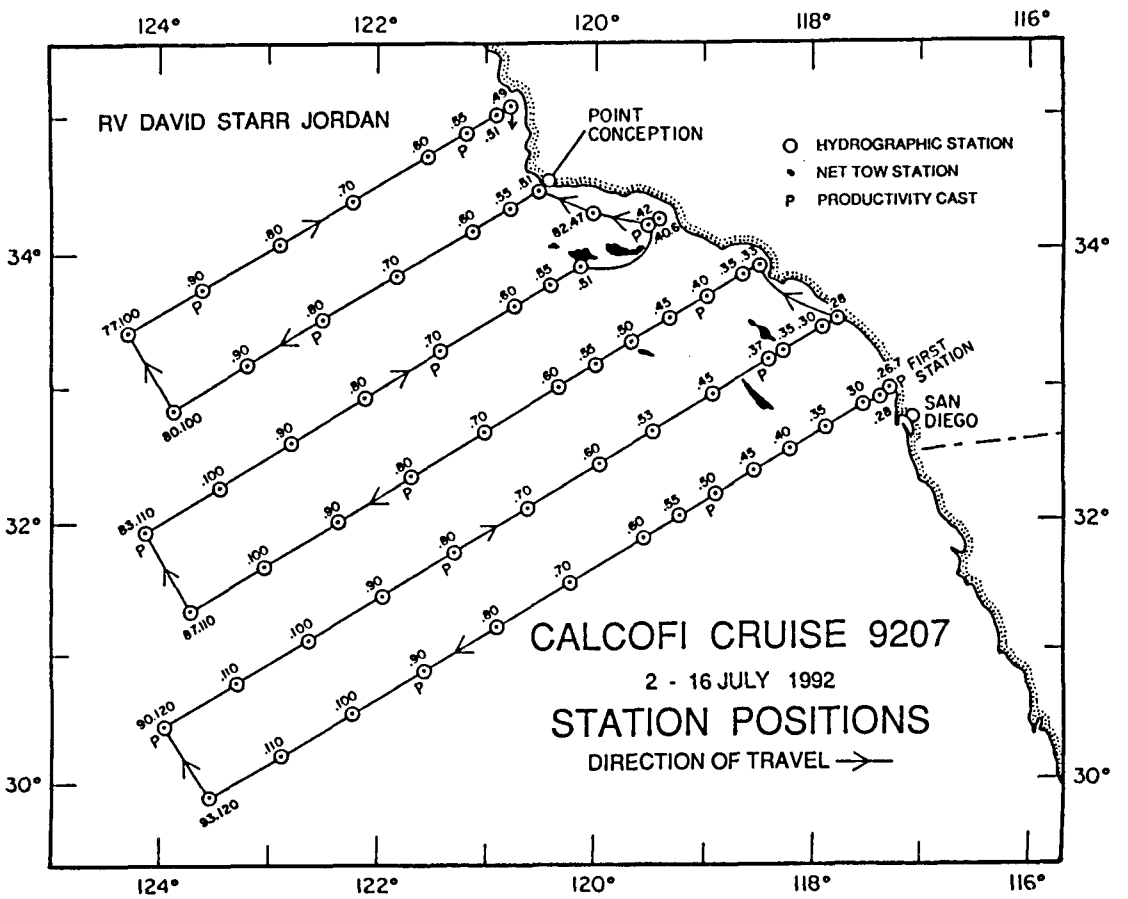

Figure 1. Cruise track for CalCOFI cruise 9207, July 1992, as an example of the present CalCOFI station plan. Core measurements at each station consist of a CTD/Rosette cast, an oblique bongo net tow, and a surface net tow. Continuous measurements of light, ADCP currents and backscatter intensity, as well as nearsurface temperature, salinity, chlorophyll fluorescence, and dissolved oxygen are made along the cruise track.

established in 1985. Lines are spaced at 40-nautical-mile (74 km) intervals, with stations spaced at 40 n. mi. intervals in the offshore region and at 8–20 n. mi. (15–37 km) intervals near the coast. This pattern has been occupied for the last ten years, and a set of "core" data has been collected with comparable techniques. Cruises are designated by year and month; e.g., cruise 9401 sampled in January 1994. Station locations are designated by a line and station number; e.g., 90.60 is station 60 on line 90, which is located due west of San Diego (figure 1). Descriptions of CalCOFI data given in this report discuss sections along a line (e.g., along line 90) as well as stations (e.g., inshore of station 60).

The core time-series data now collected at each CalCOFI station include a CTD/Rosette cast with sensors for pressure, temperature, salinity, dissolved oxygen, PAR (photosynthetically active radiation), fluorescence, and transmissivity. Water samples are collected with 10 l sample bottles on the rosette at 20 depths in the upper 500 m for determinations of salinity, dissolved oxygen, nutrients (NO_3, NO_2, PO_4, SiO_3), phytoplankton pigments (chlorophyll a and phaeophytin), and primary production (^{14}C uptake at one station per day). Oblique and surface (neuston) net tows (505 μm mesh) are taken at each station. Continuous near-surface measurements of temperature, salinity, dissolved oxygen, and chlorophyll fluorescence are made from water pumped through the ship, and the data are logged at one-minute intervals. Surface PAR and acoustic Doppler current profiler (ADCP) data are also recorded continuously. The ADCP data provide a measure of zooplankton biomass based upon acoustic backscatter, as well as a measure of upper-ocean currents. The most recent data presented here are preliminary, and some changes may be made after the final processing and quality control checks. The methods are described in more detail in the CalCOFI cruise data reports (e.g., Scripps Institution of Oceanography 1993a). Several cooperative research programs on recent CalCOFI cruises collected additional data, including bird observations, phytoplankton species composition, copepod egg production, full-depth CTD casts (FastFish), spectral light, physiological properties of the phytoplankton, and observations with an in situ optical particle counter.

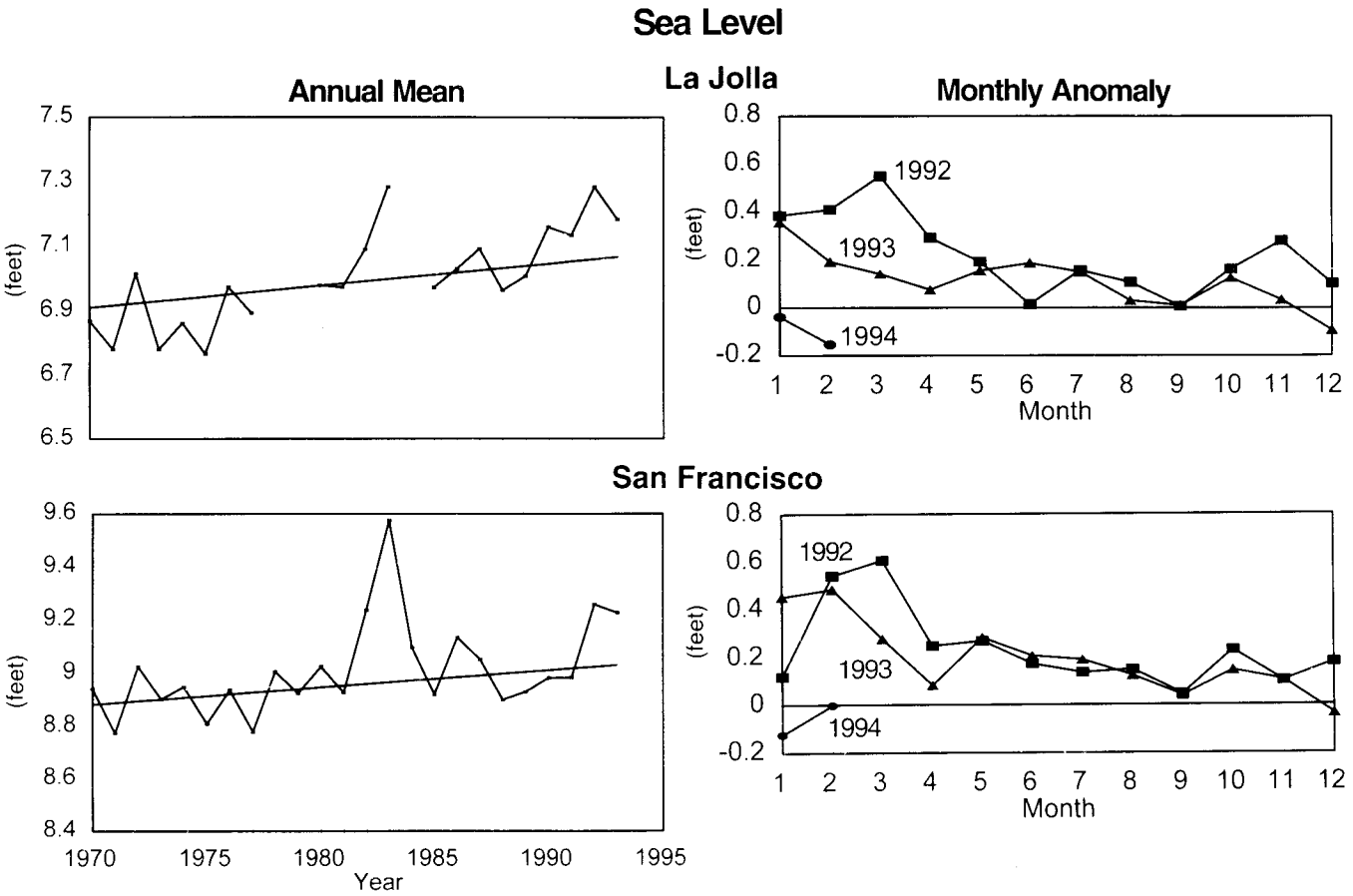

Figure 2. Coastal sea level at La Jolla and San Francisco. *Panels on the left* show the annual mean sea level; the *solid line* shows the linear regression for the secular rise in sea level for 1925–91 at La Jolla and 1900–90 at San Francisco. *Panels on the right* show the monthly anomalies in sea level for San Francisco and La Jolla for 1992–94. Monthly anomalies are the deviations from the long-term monthly mean, corrected for the secular rise.

Shipboard ADCP velocity data were collected and analyzed on CalCOFI cruises 9310 and 9401 as part of the pilot study for the WOCE time series station, PRS3. Velocities have been corrected for calibration (scale factor) and transducer misalignment (Kosro 1985; Pollard and Read 1989), and navigated from ship relative to absolute currents using GPS position measurements (Bahr and Firing 1989). Potential bias errors from noise and filter skew were minimized through selection of profiler parameters affecting filter tracking—bin and pulse length, signal-to-noise screening, low-pass filter bandwidth, and tracking parameters (Chereskin and Harding 1993). These data are preliminary in that no corrections or filtering for tides and inertial oscillations have been applied. For this report, velocities were vector averaged and gridded every 0.1 degree in latitude/longitude along the ship track.

Vertical profiles of temperature and salinity from hydrographic (CTD bottle trip) data are compared to the long-term mean distributions by comparing the observed values with the long-term (1950–92) harmonic means calculated at standard depths for the midpoint of the cruise (Lynn and Simpson 1987). These anomalies show how the structure during a cruise differed from the long-term mean pattern for that month. Monthly mean values (1951–84) for the station grid have also been calculated for macrozooplankton biomass. Chlorophyll and primary production were not measured in the early years of CalCOFI, so their time series is insufficient to properly estimate the monthly mean. Cruise mean values of chlorophyll and primary production are compared with the data taken since 1984.

The data, station plan, and methods for CalCOFI survey cruises are published in cruise data reports (Scripps Institution of Oceanography 1993a, b). CalCOFI hydrographic data are also available on the Internet via the Nemo hydrographic data server at Scripps Institution of Oceanography. These data can be accessed via telnet to **nemo.ucsd.edu**; using username: **info**. The cruise data reports can be cited as a source of data and methods.

EVOLUTION OF STRUCTURE

Coastal Shore Stations

The annual mean coastal sea level was anomalously high in 1992 and 1993 at La Jolla and San Francisco (figure 2). The high sea level in the annual means was mostly

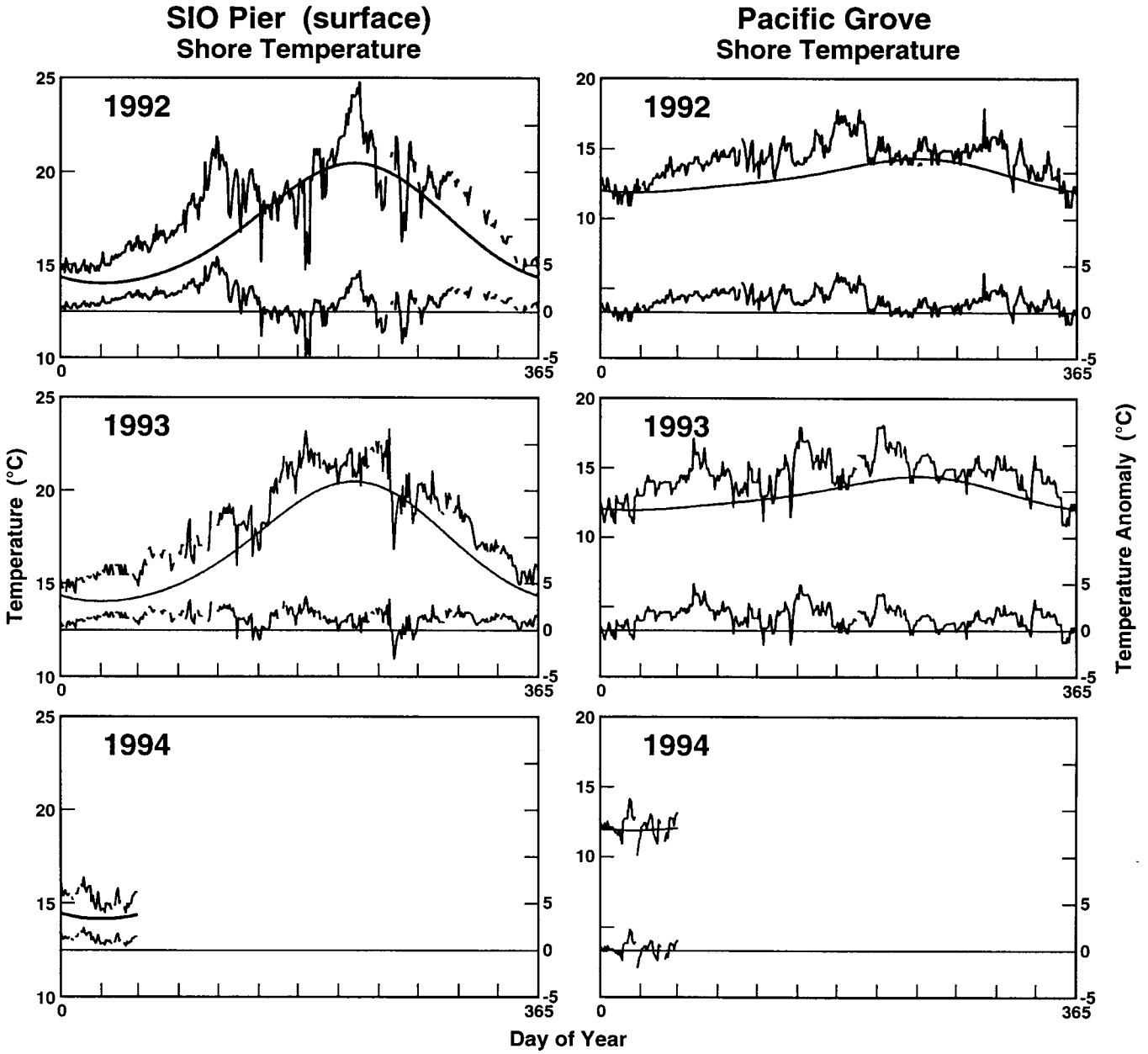

Figure 3. Sea-surface temperature at La Jolla (SIO pier) and Pacific Grove. The *upper curves* in each panel show the daily temperature and the long-term harmonic mean daily temperature for 1916–93 for La Jolla and 1919–93 for Pacific Grove. The *lower curve* shows the daily temperature anomaly from the harmonic mean.

due to large positive anomalies in the first few months of each year, with smaller positive values during the remainder of the year. The annual pattern was similar at both sites. Sea level in early 1994 was anomalously low at both sites.

Coastal surface temperatures at both La Jolla and Pacific Grove were anomalously high during most of 1992 and 1993 (figure 3). The exceptions were periods during summer 1992 when temperatures fluctuated about their seasonal norms. These coastal temperature records reflected large-scale and persistent anomaly patterns in the eastern North Pacific (Climate Diagnostic Bulletins, monthly). By March of 1992 positive SST anomalies developed along the western seaboard from central Mexico to the Alaskan border. The anomalies continued to increase in magnitude and to expand to the north to include Alaska and to the south to include the separately developing equatorial warming. The positive anomalies occupied the eastern third of the temperate North Pacific. By summer, magnitudes decreased but the overall pattern continued. Some coastal areas had below-normal SSTs only in September. Larger anomalies occurred again

in the early months of 1993, and widespread positive anomalies continued through to the latest observations in April 1994.

Cruise Data

Cruise means of vertically integrated chlorophyll, vertically integrated primary production, and macrozooplankton biomass generally fell within the scatter of the preceding years, but values during 1992–94 were on the low side of the range (figure 4). The main seasonal pattern in each property was a spring-summer maximum (which may be either absent or unsampled in some years). Fall and winter values were generally low. The quarterly CalCOFI cruises are too widely spaced to properly sample the annual cycle, and short-term seasonal blooms could easily be missed with this sampling scheme. Comparison with the 1951–84 monthly means shows that macrozooplankton biomass was anomalously low during the entire 1984–94 period (Roemmich and McGowan 1994).

Chronological Summary

The following is a chronological summary of the structure on each CalCOFI cruise, with emphasis upon the circulation pattern and its relation to biological patterns. These observations followed the early part of 1992—a period of El Niño conditions in the California Current characterized by anomalously warm water and elevated sea level (Hayward 1993). Chlorophyll and primary production were low. There was an anomalously strong inshore countercurrent. Conditions changed abruptly in April 1992, when the more typical pattern of strong southward flow of low-salinity water of the California Current returned, and chlorophyll and primary production increased. The positive anomalies of both coastal sea level and SST dropped markedly in April 1992.

9207. In July 1992, southward flow of the low-salinity core water of the California Current was split into two jets and altered by three cyclonic eddies (figure 5). Comparison with the harmonic mean dynamic height field shows that dynamic height was higher than normal, with the largest anomalies in the middle of the pattern. This suggests that there was weaker-than-normal southward flow in the outer part of the pattern, and stronger-than-normal flow around stations 50 and 60. Ten-meter temperature was lower than normal inshore of the main flow of the California Current along the coast from Santa Barbara to Del Mar. The mixed layer was warmer than normal over the remainder of the pattern. Ten-meter chlorophyll was also relatively high (values greater than 1 $\mu g\ l^{-1}$) in the entire coastal region.

9210. In October, there was a southeastward-flowing jet of low-salinity water in the middle of the pattern. The three cyclonic eddies observed during July appeared

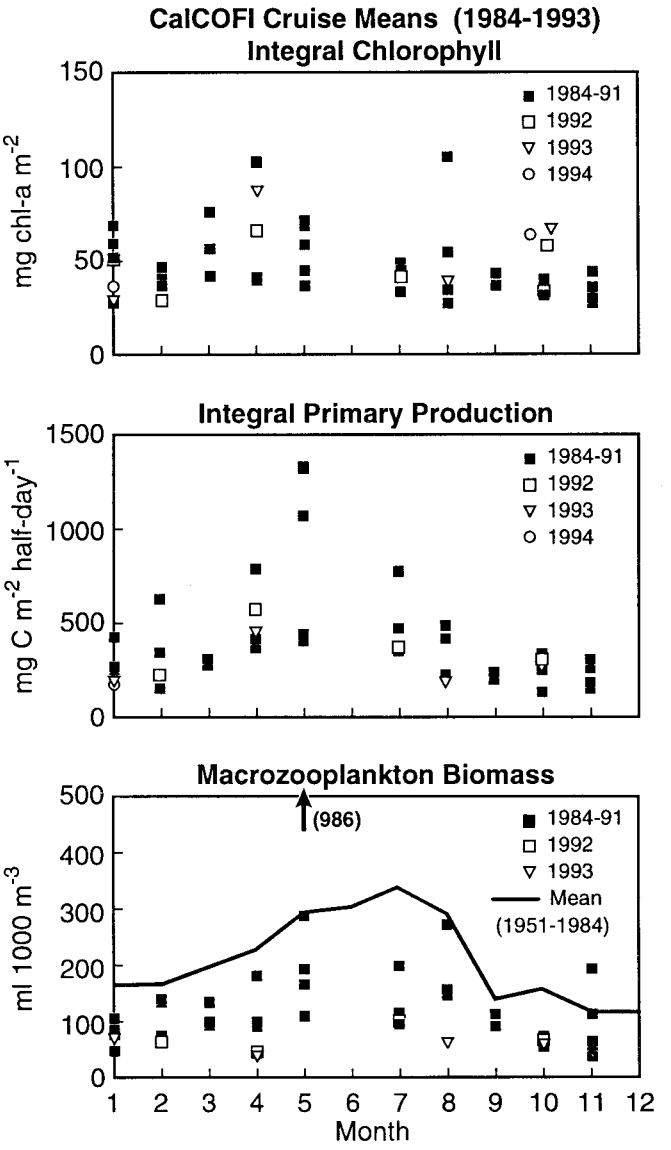

Figure 4. Cruise means of vertically integrated chlorophyll, vertically integrated primary production, and macrozooplankton biomass plotted versus the month of the cruise. Each point represents the mean of all of the measurements made on a single cruise. The *solid squares* show cruises that took place from 1984 to 1991; *open symbols* show values from 1992 to 1994. The monthly mean macrozooplankton biomass for the study area from 1951 to 1984 is shown as the *solid line*.

to still be present, but weaker than before (figure 6). Dynamic heights remained above normal, with maximum anomalies in the offshore region. The anomaly pattern is consistent with stronger-than-normal southward flow around stations 70 to 90, and stronger-than-normal northward flow in the inshore parts of lines 87 to 93. Ten-meter temperature was greater than normal over most of the grid, except for a band along the coast, where patches with large negative anomalies were observed. Ten-meter chlorophyll was generally low throughout the sample grid, with values greater than 1 $\mu g\ l^{-1}$ evident only in the coastal area near Point Conception.

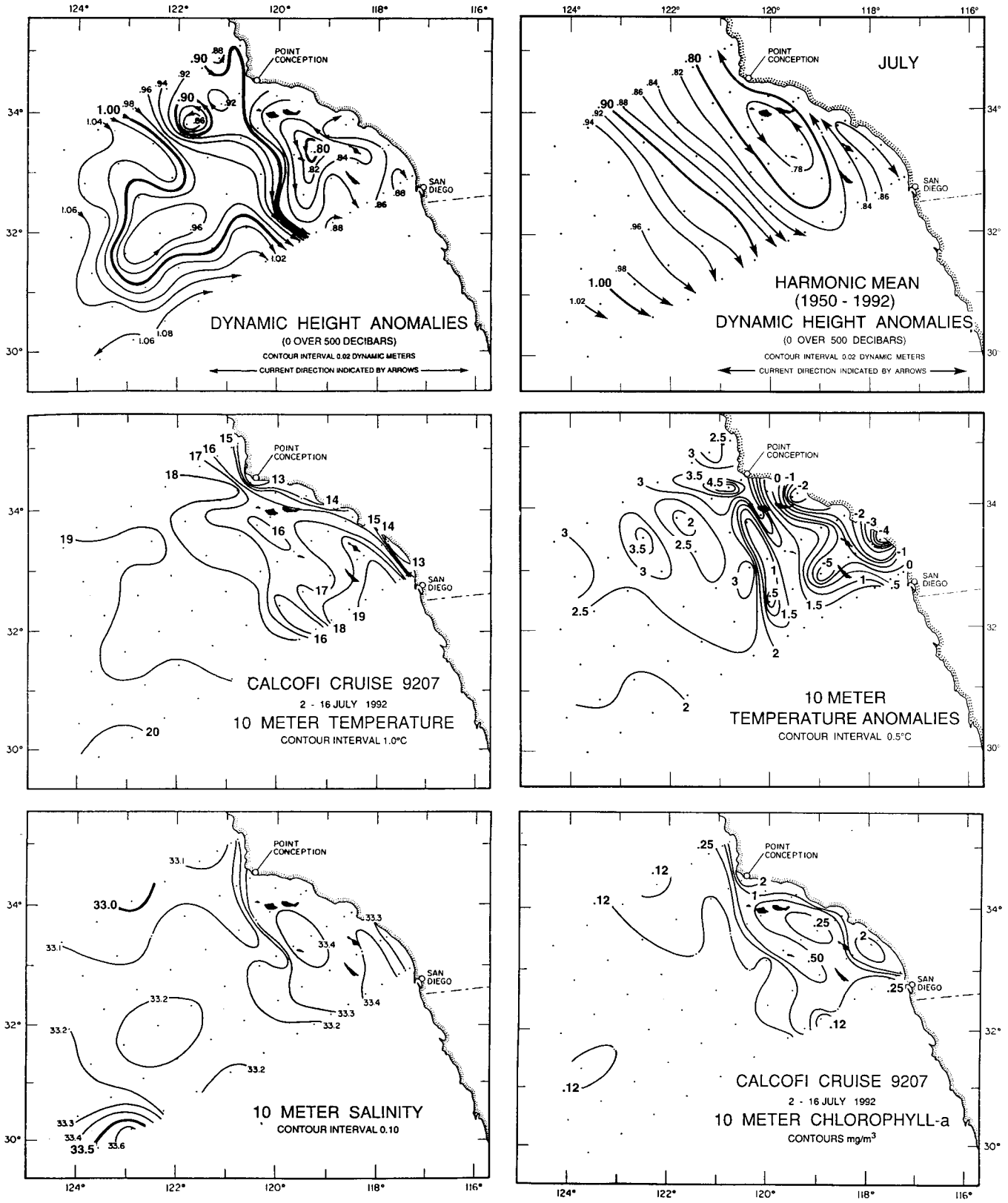

Figure 5. Spatial patterns for CalCOFI cruise 9207, 2–16 July 1992, including upper-ocean flow field derived from 0 over 500 m dynamic height anomalies, long-term (1950–92) harmonic mean 0 over 500 m dynamic height field calculated for 9 July, 10 m temperature, 10 m temperature anomalies, 10 m salinity, and 10 m chlorophyll.

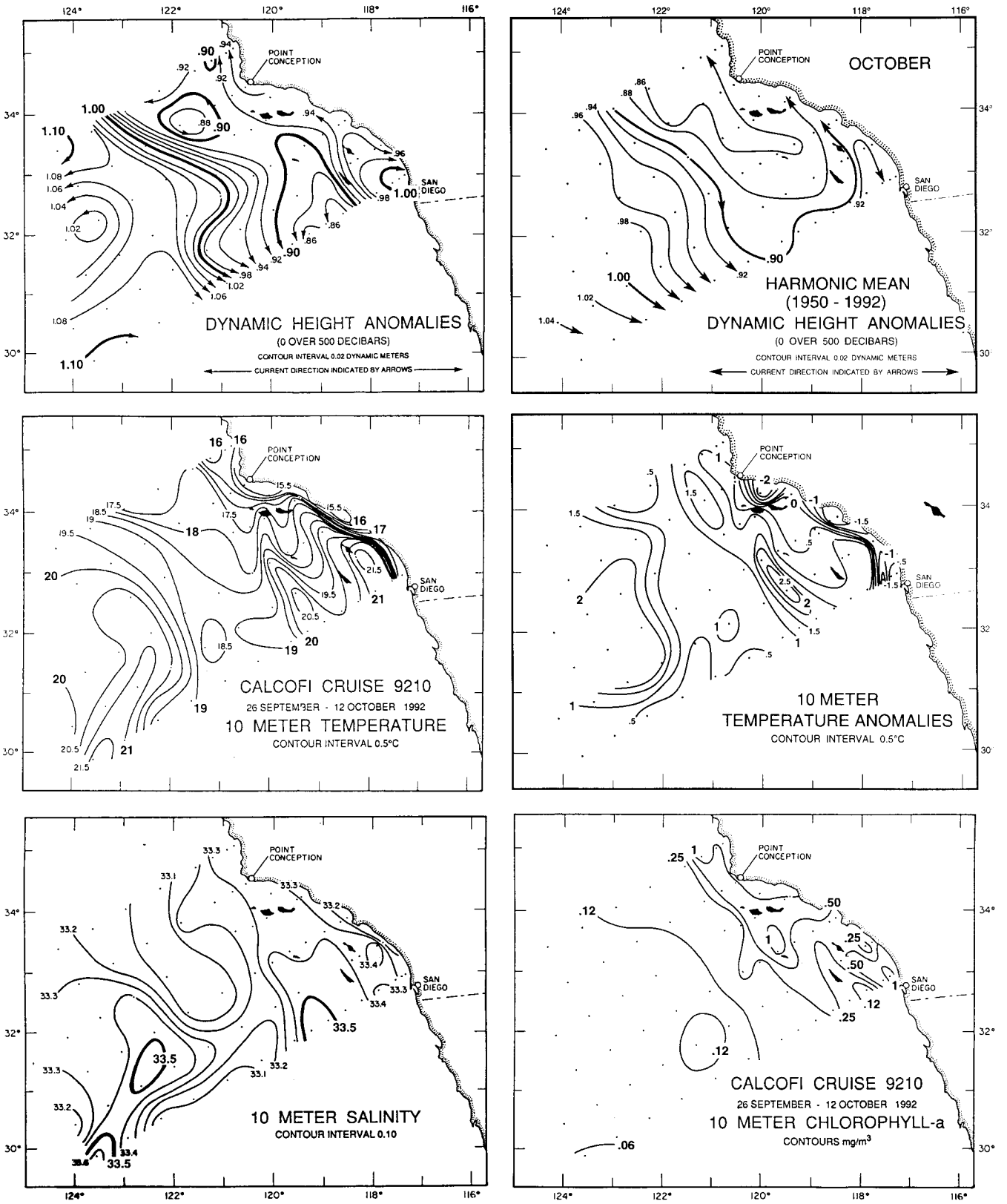

Figure 6. Spatial patterns (as described for figure 5) for CalCOFI cruise 9210, 26 September–12 October 1992. Harmonic mean dynamic heights and temperature were calculated for October 3.

9301. The January 1993 dynamic height field shows that there was a well-developed northward-flowing inshore countercurrent, and southward flow of the low-salinity water of the core of the California Current in the center of the grid (figure 7). The Southern California Eddy was broad, with a broad band of northward flow from the coast to offshore of the Channel Islands. This pattern was quite similar to the long-term mean field, although both the inshore countercurrent and the offshore flow of the California Current were stronger than normal. In contrast to other seasons, there is no southward flow on the Southern California Shelf. The pattern of a strong and broad inshore countercurrent was similar to that of January 1992 (Hayward 1993). Enhanced poleward flow in the coastal region in both years coincided with anomalously high sea level at La Jolla and San Francisco. The ten-meter temperatures were slightly above normal for most of the pattern. Mixed-layer chlorophyll was low throughout the grid, with values greater than 1 $\mu g\ l^{-1}$ evident at only a few coastal stations.

Sections of several properties along CalCOFI line 90 are given in the SIO cruise data report series. We calculated vertical sections of temperature and salinity anomalies from the long-term harmonic mean to complement a selection of these sections given in figure 8. The boundary between the coastal countercurrent and the southward flow of the California Current at station 90.70 is evident in these sections as a sharper slope in the thermocline and nutricline. Temperature was anomalously low in the upper thermocline at station 90.70 because of the shoaling of the thermocline. Temperature was anomalously high over most of the section, with the largest anomalies at the top of the thermocline (as is expected in conditions where the mixed layer is warmer and deeper than normal). Salinity was slightly lower than normal over most of the section.

9304. In April 1993 the inshore countercurrent was absent, as it is in the long-term mean for April, at which time the Southern California Eddy is weakly developed or absent (figure 9). The southward flow of the California Current was stronger than normal. Southward flow throughout the sample grid was perturbed by two mesoscale eddies in the offshore region. The strong southward flow near Point Conception was consistent with local upwelling in the region. Ten-meter temperature was anomalously high over most of the grid, except in the northern area along the coast. Chlorophyll levels were quite high on this cruise, with values greater than 8 $\mu g\ l^{-1}$ evident in the coastal region near Point Conception. Elevated chlorophyll was consistent with the return to a more normal circulation pattern because shoaling of the pycnocline and nutricline associated with southward flow brings nutrients closer to the euphotic zone.

The vertical sections along line 90 were strongly influenced by the mesoscale flow field. The strong eddy at station 70, and coastward flow inshore of this perturbed the normal onshore-offshore gradients in vertical structure (figure 10). East-west gradients in temperature, salinity, and nutrients were weak along the section. Temperature was anomalously high in the inshore region of the section, but there were anomalously cool pools in the upper thermocline in the offshore region where the thermocline had shoaled in association with the circulation pattern. Salinity was again anomalously low throughout the section.

9308. Values of dynamic height were approximately 9 dynamic cm higher in 9308 (figure 11) than in the long-term mean for July (figure 5), reflecting the generally thicker and/or warmer surface layer. Although roughly similar in pattern to the long-term mean, the inshore countercurrent was broader, and the Southern California Eddy was enlarged. A strong cyclonic eddy dominated the offshore edge of the California Current jet (along line 90), a pattern very similar to that found during the 9304 survey (figure 9). Ten-meter temperatures were above mean values along the southern California coast and in two offshore-tending E-W bands. Ten-meter temperature was well below normal in the Santa Barbara Channel and in the middle part of the pattern. Ten-meter chlorophyll was relatively high near Point Conception, and low over the remainder of the grid. The 100 m temperature field is sometimes used as a proxy to indicate pycnocline topography and the pattern of surface flow. Temperature data are usually available at an early stage of data processing. As in this example, the 100 m temperature pattern is usually a good indicator of the surface circulation pattern.

9310. As found in the long-term mean pattern for October (figure 6) there is a fully developed inshore countercurrent during October 1993 as well as the equatorward-flowing California Current jet (figure 12). The gradients are larger, however, indicating stronger flow both poleward and equatorward. A cyclonic eddy is partly resolved at the outer edge of the pattern (lines 87 and 90); perhaps this is the same feature found in the previous two surveys. The California Current jet is greatly distorted by a large shoreward meander. In the long-term mean there is a shoreward turn to the current immediately south of the present grid (Lynn et al. 1982). The position and strength of the feature found in 9310 is highly anomalous. Ten-meter temperature anomalies were mostly positive throughout the sample grid, with Santa Monica Bay having the greatest values of 2.3°C. Ten-meter chlorophyll was low over most of the grid, with values greater than 1 $\mu g\ l^{-1}$ evident only in the coastal area near Point Conception. Pattern in the flow field derived from dynamic height is compared with the

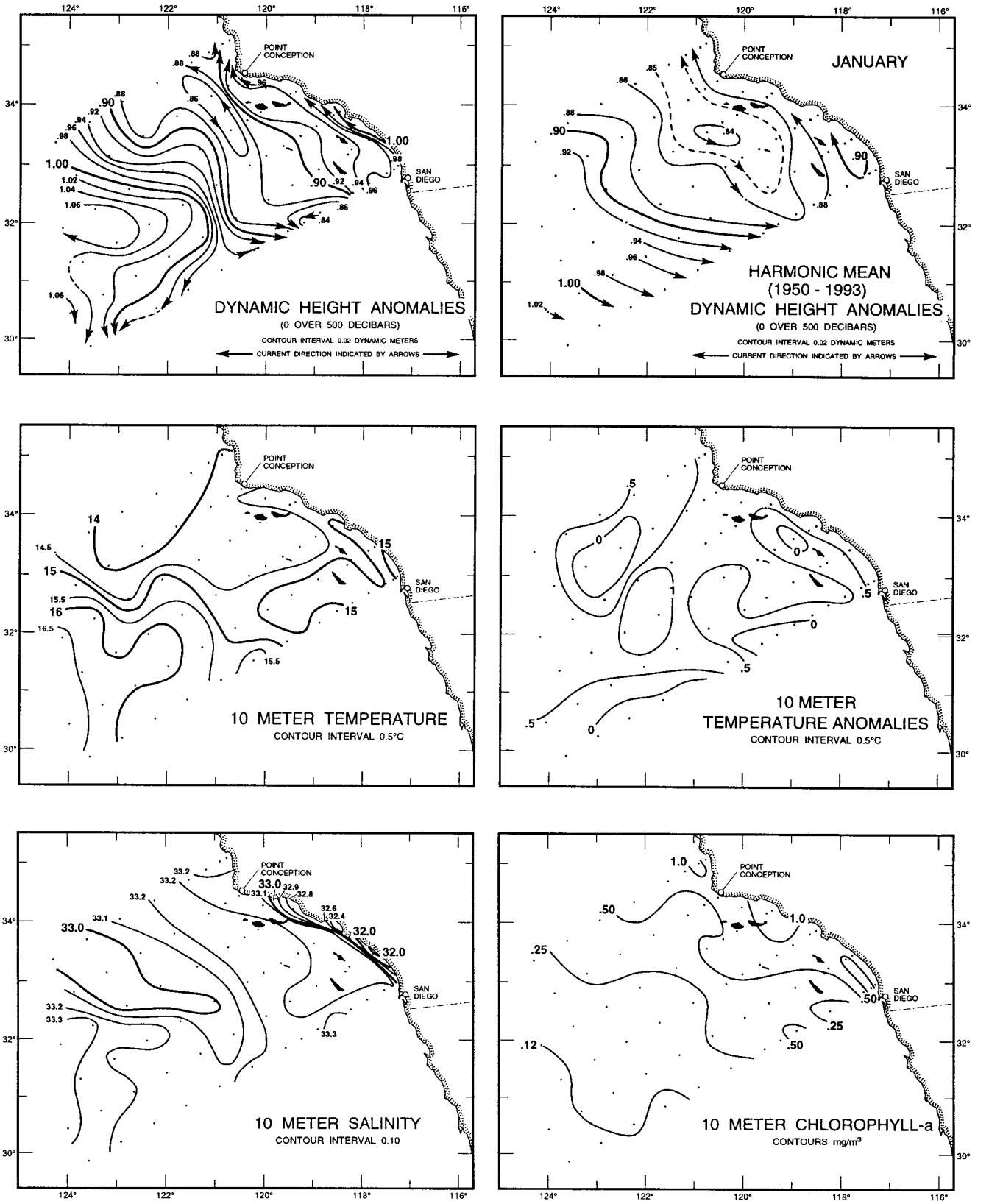

Figure 7. Spatial patterns (as described for figure 5) for CalCOFI cruise 9301, 12–27 January 1993. Harmonic mean dynamic heights and temperature were calculated for January 14.

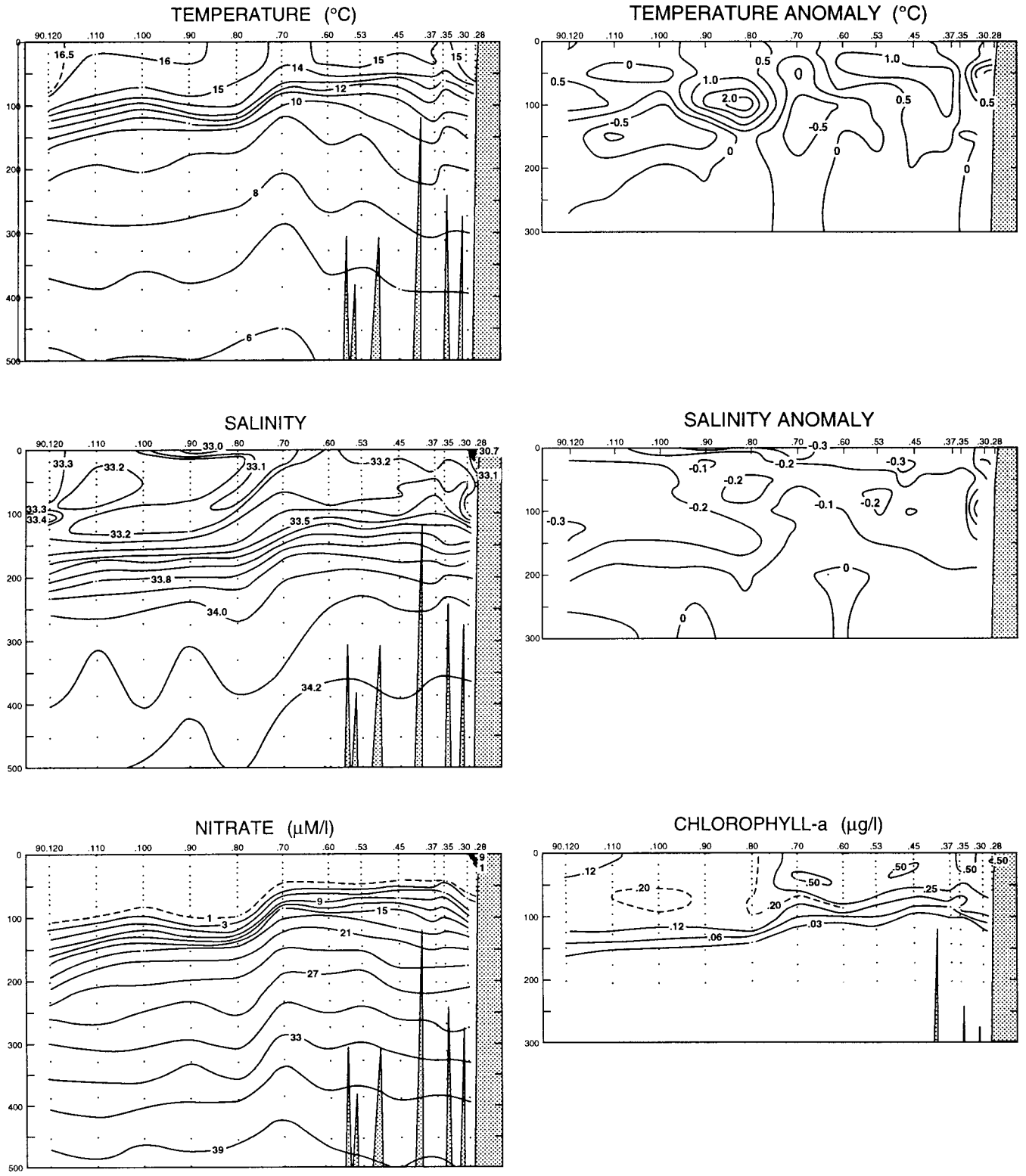

Figure 8. Vertical sections of temperature, temperature anomaly, salinity, salinity anomaly, nitrate, and chlorophyll along CalCOFI line 90 for cruise 9301.

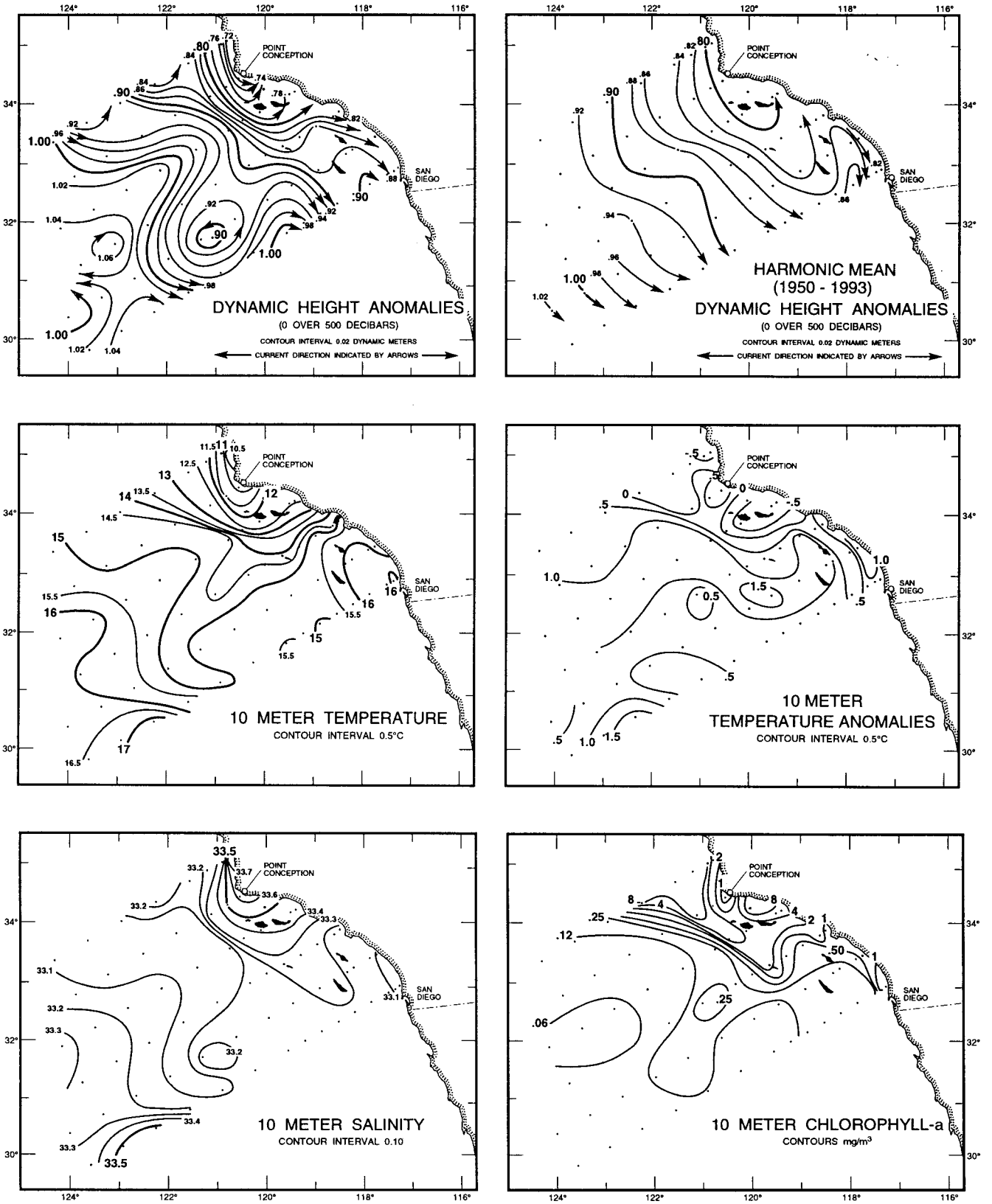

Figure 9. Spatial patterns (as described for figure 5) for CalCOFI cruise 9304, 30 March–15 April 1993. Harmonic mean dynamic heights and temperature were calculated for April 6.

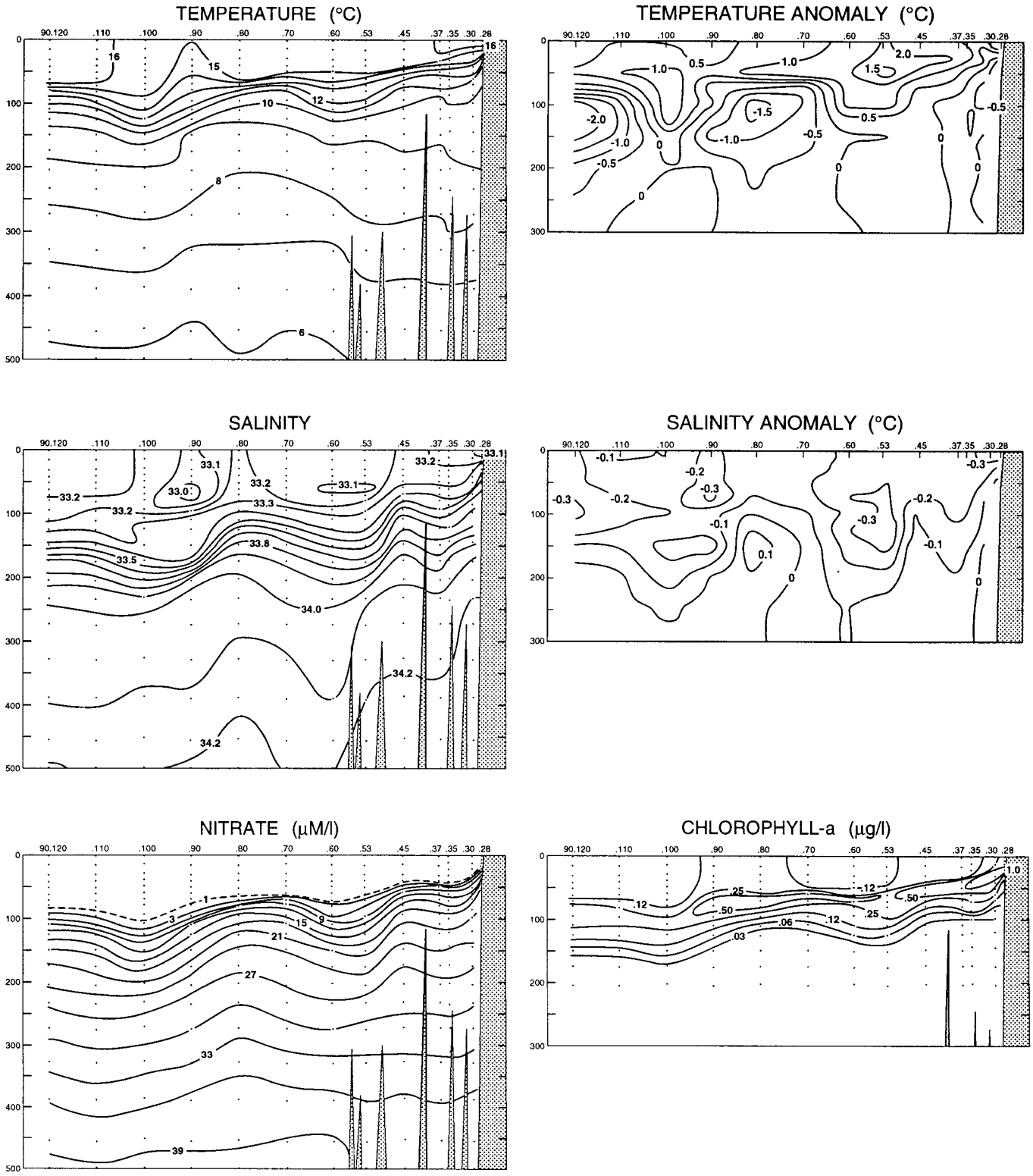

Figure 10. Vertical sections of temperature, temperature anomaly, salinity, salinity anomaly, nitrate, and chlorophyll along CalCOFI line 90 for cruise 9304.

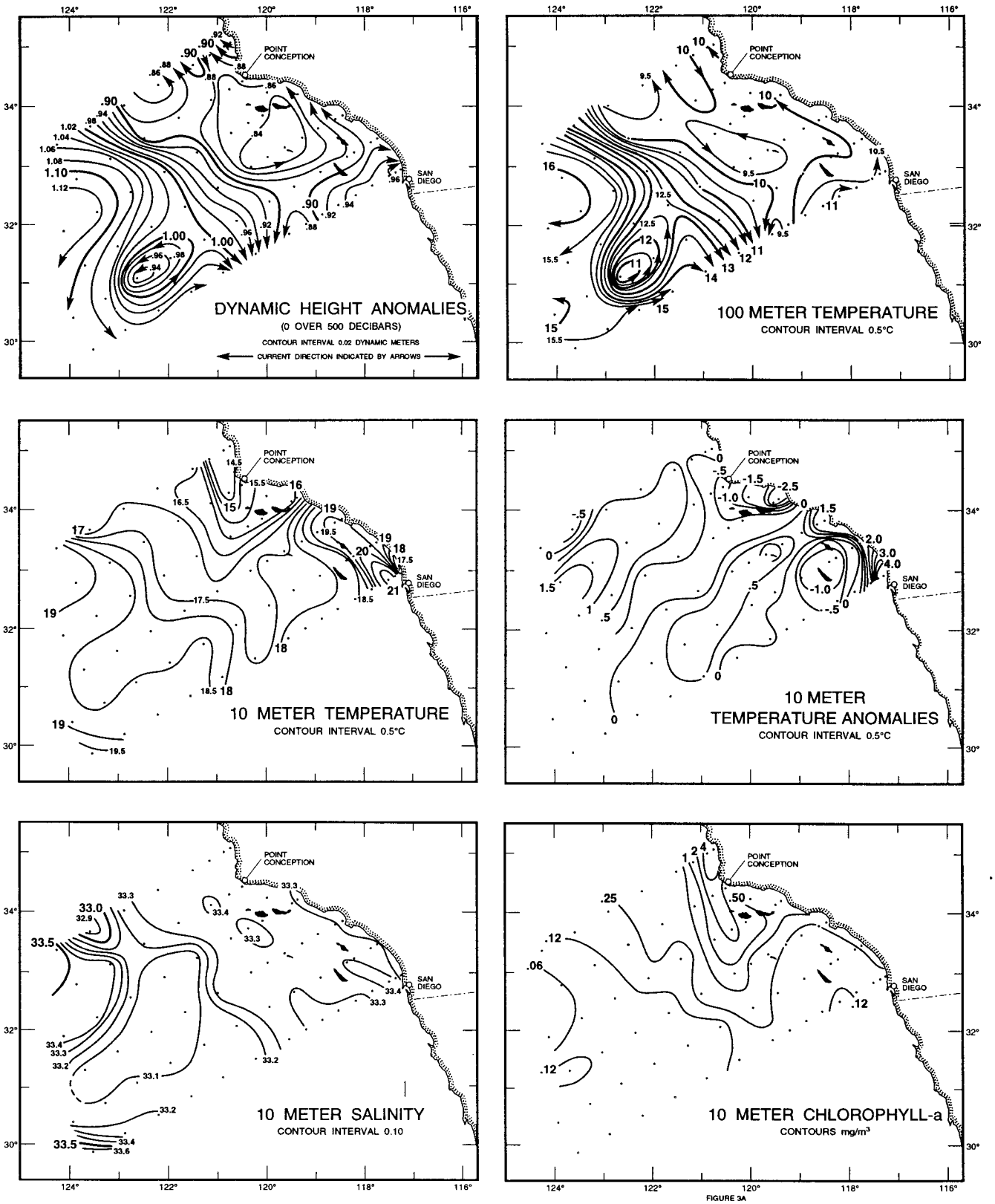

FIGURE 3A

Figure 11. Spatial patterns for CalCOFI cruise 9308, 11–27 August 1993, including upper-ocean flow field derived from 0 over 500 m dynamic height anomalies, 100 m temperature field as a proxy for the upper-ocean flow field, 10 m temperature, 10 m temperature anomalies, 10 m salinity, and 10 m chlorophyll.

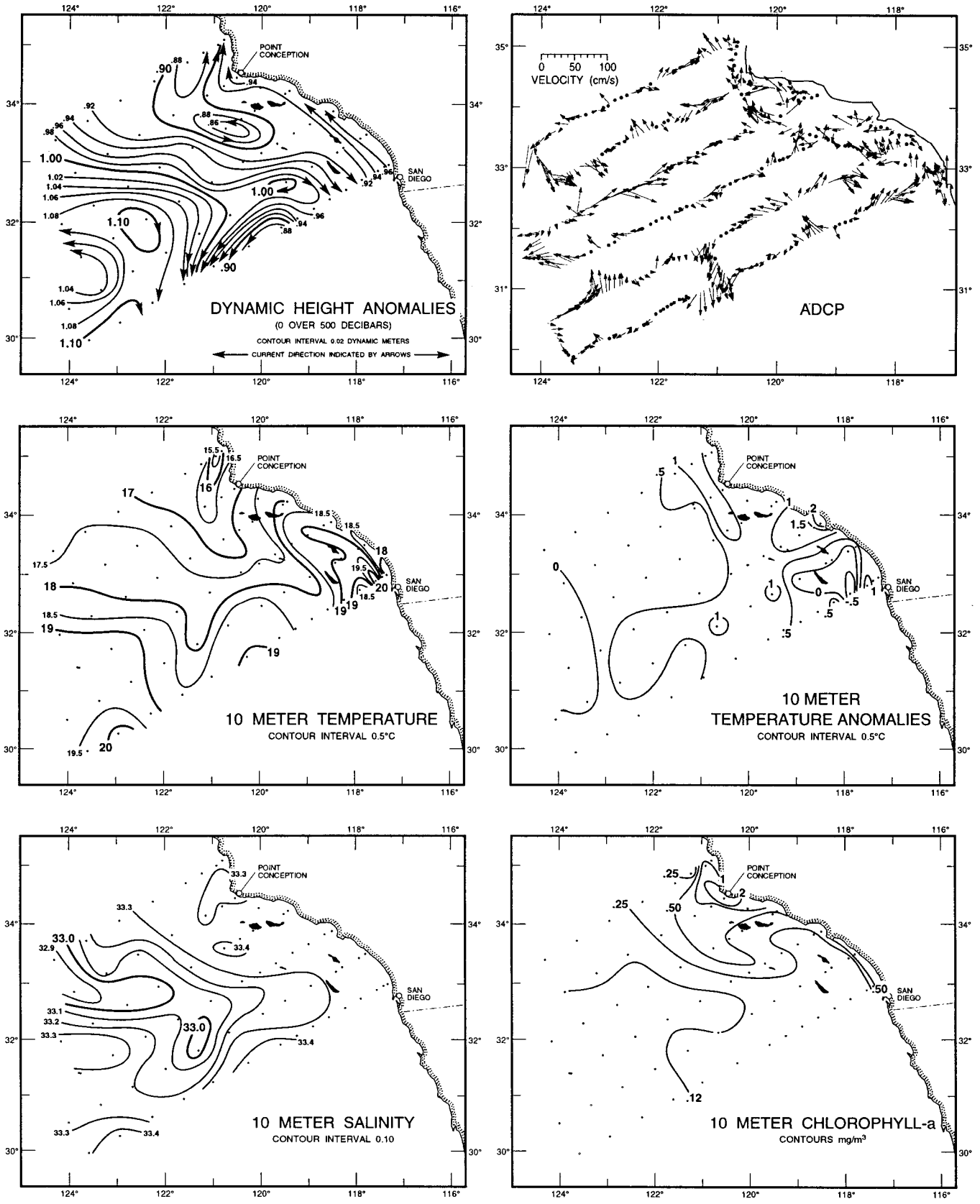

Figure 12. Spatial patterns for CalCOFI cruise 9310, 8–26 October 1993, including upper-ocean flow field derived from 0 over 500 m dynamic height anomalies, the 20–25 m flow field derived from ADCP, 10 m temperature, 10 m temperature anomalies, 10 m salinity, and 10 m chlorophyll.

upper-ocean flow field at 25 m derived from ADCP data. ADCP data provide point estimates of the actual flow in one depth zone in the upper ocean. The agreement throughout the grid is good.

9401. In January 1994, southward flow of the low-salinity core of the California Current was perturbed by a series of mesoscale eddies throughout the sample grid (figure 13). The flow field derived from dynamic heights was very much the same as given in the 20–25 m depth zone derived from ADCP data. The lack of a well-developed inshore countercurrent was anomalous when compared to the long-term mean pattern (shown in figure 7). Ten-meter temperature was generally between 1° and 2°C warmer than normal in the offshore region, and between 0.5° and 1°C warmer than normal near the coast. Ten-meter chlorophyll was generally low throughout the sample grid, with values less than 0.5 μg l^{-1}, except at several of the most nearshore stations, where high values were seen. The sharp eastward bend of the California Current between lines 83 and 87 was again a prominent feature of the flow field. This appeared to bring offshore water near to the coast in the southern California coastal region.

9403. The dynamic height data from March 1994 were not available as this manuscript was being prepared, so the 100 m temperature was used as a proxy to infer the flow field. The inferred flow was primarily to the south, with some indication of a weak coastal countercurrent. There was a cyclonic eddy located on the outer stations of line 87. The coastal bend of the California Current was still present in the middle of the sample grid (figure 14). The upper layers were still anomalously warm over much of the grid. Chlorophyll values were relatively high in the coastal region in the northern part of the sample grid, where surface waters were relatively cool.

DISCUSSION

A strong tropical El Niño episode began in the fall of 1991 and, after a return to near normal conditions in the summer of 1992, developed a second punch in late 1992 (Climate Diagnostic Bulletin numbers 91-9 to 92-12). El Niño conditions continued until the end of 1993 (Climate Diagnostic Bulletin numbers 93-1 to 93-12). The large-scale impact of El Niño upon coastal sea level and SST off North America was evident in January 1992 (Hayward 1993). The regional effects off California, Oregon, and Washington include changes in the large-scale atmospheric pressure pattern (and hence gradient winds), reduced upwelling or increased downwelling, anomalously high sea level and SST, thickened surface mixed layer, depressed nutricline, and episodic enhancement of the inshore countercurrent. SST and sea level were above seasonal norms during 1992 and 1993 at both La Jolla and San Francisco. The largest anom-

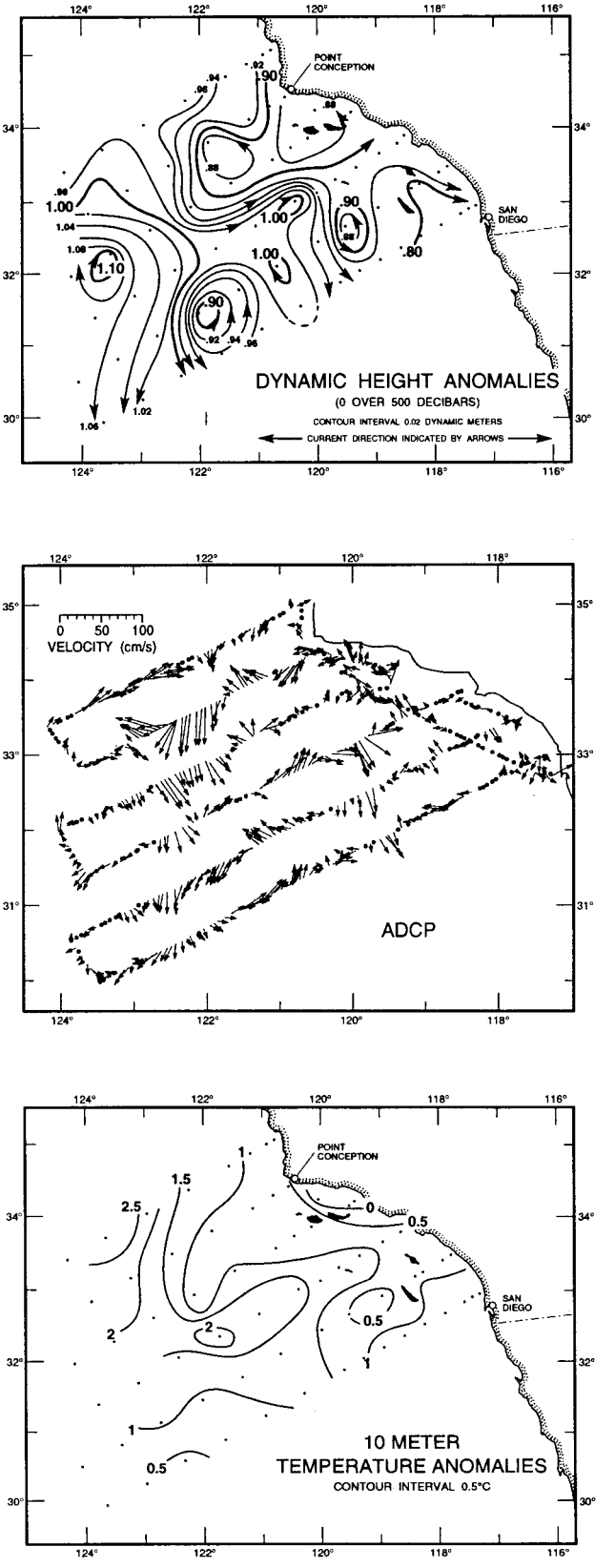

Figure 13. Spatial patterns for CalCOFI cruise 9401, 20 January–8 February 1994, including upper-ocean flow field derived from 0 over 500 m dynamic height anomalies, the 20–25 m flow field derived from ADCP, and 10 m temperature anomalies.

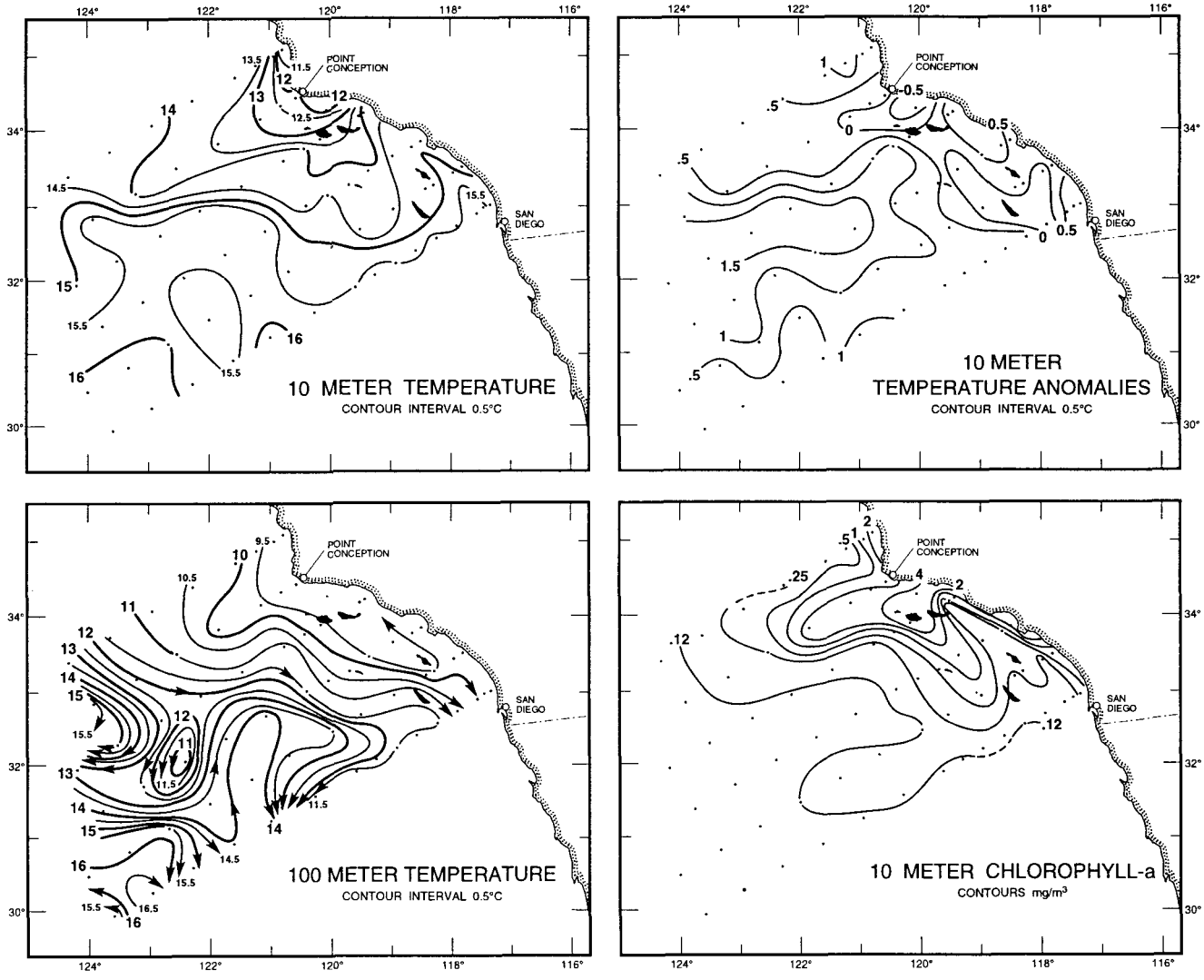

Figure 14. Spatial patterns for CalCOFI cruise 9403, 22 March–8 April 1994, including 10 m temperature, 10 m temperature anomalies, 100 m temperature as a proxy for the upper-ocean flow field, and 10 m chlorophyll.

alies in sea level and circulation occurred during late winter–early spring of both 1992 and 1993. Following a period of high coastal sea level and a broad inshore countercurrent in January of each year, sea level and the circulation pattern returned to much more typical patterns in March or April. The return to a typical circulation pattern was associated with a strong increase in primary production and plankton abundance. This spring increase could be called a spring bloom, but note that the cruise means in these properties were still below the higher values sampled in prior years, and macrozooplankton was well below the values of the prior decades throughout the period (Roemmich and McGowan 1994). Coastal sea-level anomalies are a useful indicator of anomalies in the large-scale circulation pattern of the California Current during the 1992–94 period (e.g., Reid and Mantyla 1976). SST remained anomalously high during most of 1992 and 1993, and it thus gives a somewhat different impression of structure than does coastal sea level. It may be that the temperature anomalies are related to oceanographic conditions on a longer time scale. Roemmich and McGowan (1994) observed a decline in macrozooplankton over the last decade, along with an increase in coastal temperatures.

The oceanographic structure in 1994 is developing differently than in the two prior years. Sea level was anomalously low in the early part of 1994 at both La Jolla and San Francisco. The strong and broad inshore countercurrent observed during the preceding Januaries was weak or absent in January 1994. SST at the shore stations was above normal at La Jolla and near normal at Pacific Grove. SST patterns in the coastal waters began to show evidence of returning toward seasonal norms in April 1994 (NOAA/SWFSC CoastWatch El Niño Watch

94-4). It is expected that properties influenced by the northward advection along the coast will be less strongly affected in 1994.

Similarities in mesoscale current structure from survey to survey suggest that some features evolve slowly and persist over periods of months in the California Current system. Although the spatial scale of the CalCOFI grid is marginal in resolving mesoscale features, large and strong features are evident. The eddies observed during July and October 1992, and the cyclonic eddy seen in the offshore region in April, August, and October 1993 are examples of features that appeared to persist. There is no certainty, however, that the same feature was sampled from cruise to cruise. It is known that mesoscale eddies are more common in some regions of the California Current than in others (Lynn and Simpson 1987; Hayward and Mantyla 1990), and that they persist for months (Koblinsky et al. 1984). The sharp coastward bend of the California Current first observed in October 1993 was another unusual feature of the circulation that persisted for several months. The meander can also be seen in the January 1994 dynamic height, and the March 1994 100 m temperature field. This meander will have the effect of transporting plankton and other water properties characteristic of the offshore regime of the California Current to more coastal areas.

It will be helpful to know more about the persistence of mesoscale circulation features because they also strongly affect biological structure (Simpson et al. 1984; Hayward and Mantyla 1990). If it can be demonstrated that such features commonly persist for periods of several months, our ability to predict future pattern based upon the present structure will be improved. Examination of satellite images may help to determine the persistence of mesoscale circulation features, especially after SeaWIFS satellite color-sensor data become available.

The observations presented here are examples of the timely data that are available for the coastal ocean. The data that are rapidly available are generally those which are frequently collected, easy to process, and for which there is a good processing and management scheme in place. These timely data can be used to address questions that reflect the broad range of interests of the scientific community and users of the coastal ocean. In many cases, however, application of such data to the questions at hand is difficult because the relation between the available data (e.g., temperature and sea level) and the questions at hand (e.g., understanding the causes and consequences of population fluctuations or detecting anthropogenic change) is highly complex or poorly known. Coastal data will be more widely applied to such questions as data collection, management, and distribution schemes improve, and as relations between the properties that can be measured and the questions of interest become more clear. Here we have described some of the data collected at coastal stations and on CalCOFI time series cruises, and we have attempted to show some of the relations between the properties that are measured and other aspects of coastal marine conditions.

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STATUS OF PACIFIC MACKEREL AND TRENDS IN BIOMASS, 1978–1993

LARRY D. JACOBSON
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

EDDY S. KONNO[1]
California Department of Fish and Game
330 Golden Shore, Suite 50
Long Beach, California 90802

JUAN P. PERTIERRA[2]
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

Estimates from virtual population analysis indicate that Pacific mackerel (*Scomber japonicus*) biomass increased during 1978–82 to the highest level on record (829,000 short tons), and then declined to less than 100,000 tons by 1993 (estimates for recent years are imprecise). High biomass in early years was due to the strong 1978 and 1980–82 year classes. The declining biomass after 1982 was due to lower recruitment. Current conditions appear similar to those in the mid 1940s, when Pacific mackerel declined after a period of high abundance. Abundance data and biomass indices during recent years were affected by ENSO conditions; more accurate estimates of biomass and assessment of ENSO effects will be possible after environmental conditions return to normal.

Recent catch levels (46,000 and 23,000 tons year^{-1} during 1992 and 1993) were large relative to biomass, and may have exceeded the target 30% total exploitation rate that is the basis for management in California. The economic condition of the fishery is poor, and resources available for management are at an all-time low because of changing priorities and financial constraints. Landings of Pacific mackerel increased in Mexico during recent years while California landings remained relatively constant, and biomass declined. Thus the future of the Pacific mackerel stock and fishery are uncertain.

RESUMEN

Estimaciones obtenidas por el análisis virtual de poblaciones indican que la biomasa de la macarela (*Scomber japonicus*) alcanzó durante 1978–82 los máximos niveles que hayan sido registrados (829,000 toneladas cortas), y subsecuentemente declinó a menos de 100,000 tons. cortas en 1993 (las estimaciones en años recientes son imprecisas). Los altos niveles de biomasa referidos se debieron a la fuerza de las clases de edad de 1978 y 1980–82, mientras que el decremento después de 1982 se debió a los bajos niveles de reclutamiento. Las condiciones actuales parecieran asemejarse a aquellas de mediados de los años 40, cuando la macarela declinó después de un periodo de alta abundancia. En años recientes, los datos de abundancia e índices de biomasa fueron afectados por condiciones El Niño-Oscilación Austral. Será posible obtener estimaciones mas exactas cuando las condiciones ambientales retornen a la normalidad.

Los niveles de captura recientes (46,000 y 23,000 tons. cortas año^{-1} en 1992 y 1993) fueron relativamente altos respecto a la biomasa, y podrían haber excedido los niveles fijados como meta, tasa de explotación de 30% del total, que es la base de la administración en California. La condición económica de la pesquería es mala, y debido a restricciones económicas y cambios de las prioridades, los recursos disponibles para la administración de la pesquería son mas escasos que nunca. En años recientes, se han incrementado los desembarcos de macarela en México, mientras que en California los desembarcos se han mantenido constantes, y la biomasa ha declinado. Por lo tanto, el futuro del stock y la pesquería de macarela son inciertos.

INTRODUCTION

Pacific mackerel (*Scomber japonicus*, also known as chub mackerel) are a mainstay of the southern California purse seine fishery (Konno and Wolf 1992; Thomson 1993). The purpose of this report is to document trends in Pacific mackerel biomass during 1978–93 and to extend the time series of estimates for 1929–84 in Prager and MacCall 1988. We obtained the biomass estimates by virtual population analysis (VPA), using the ADAPT procedure (Gavaris 1988), with fishery data stratified by quarter (see Jacobson et al. 1994 for data and analytical details).

There were three indices of relative abundance (table 1 and figure 1). The SPOTTER index was calculated from fish spotter logs in the same way as for northern anchovy (*Engraulis mordax*; Lo et al. 1992), except that data were aggregated by April–March annual periods. Thus we used data for April 1988–March 1989 as an index of relative abundance during the first quarter of 1989.

California Cooperative Oceanic Fisheries Investigations (CalCOFI) data for Pacific mackerel were used in two indices of relative abundance (table 1 and figure 1). The index DENSITY was the density of Pacific mackerel larvae per unit area calculated from catches in bongo nets. The index PROP+ was the proportion of bongo tows that were positive for Pacific mackerel larvae (Mangel

[1]Present address: California Department of Fish and Game, 34355 Rawson Road, Hemet, California 92543
[2]Present address: Instituto de Ciencias del Mar, Passeig Joan Borbo s/n, 08039, Barcelona, Spain
[Manuscript received April 26, 1994.]

TABLE 1
Indices of Relative Abundance for Pacific Mackerel

Year	SPOTTER (short tons block^{-1})	CV	DENSITY (larvae 10 m^{-2})	CV	PROP+	N (tows)
1978	21.93	0.44	9.9054	0.32	0.1377	247
1979	40.46	0.42	—	—	—	—
1980	31.44	0.42	—	—	—	—
1981	31.20	0.44	45.5338	0.36	0.3333	105
1982	32.42	0.42	—	—	—	—
1983	38.56	0.43	—	—	—	—
1984	32.25	0.47	2.1382	0.60	0.0536	112
1985	40.39	0.47	3.5956	0.46	0.1642	67
1986	21.21	0.48	2.8246	0.44	0.1000	70
1987	15.50	0.46	18.7083	0.66	0.0941	85
1988	6.50	0.51	4.5224	0.45	0.1282	78
1989	11.23	0.53	2.4788	0.45	0.0843	83
1990	3.04	0.60	0.3052	1.00	0.0130	77
1991	3.14	0.55	0.5695	0.59	0.0698	43
1992	4.40	0.52	0.2694	0.53	0.0430	93
1993	2.48	0.68	0.0603	1.00	0.0116	86

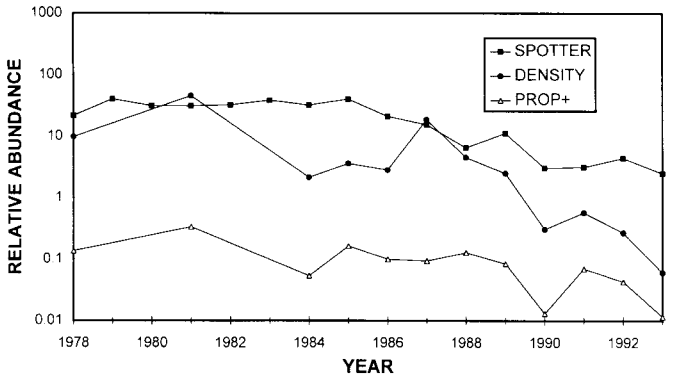

Figure 1. Indices of abundance for Pacific mackerel plotted in log scale for comparison.

and Smith 1990; Smith 1990). For purposes of standardization, CalCOFI indices were calculated with data from the current CalCOFI sampling grid (covering roughly the Southern California Bight; Hewitt 1988) that were collected during April–September of each year, when spawning is most common (MacCall and Prager 1988).

RESULTS

SPOTTER and DENSITY data (table 2 and figure 2) yielded VPA results that were generally similar to results from SPOTTER and PROP+ data (not shown; see Jacobson et al. 1994). Pacific mackerel biomass increased dramatically during 1978–82 to the highest level on record—829,000 tons (throughout this paper *tons* refers to short tons). VPA results and relative abundance data (table 1 and figure 1) indicate that biomass declined after 1982 to relatively low levels by 1993. High biomass in early years was due to the strong 1978 and 1980–82 year classes (MacCall et al. 1985). The decrease in biomass after 1982 was due to lower recruitment.

TABLE 2
Biomass and Recruitment Estimates (Age Zero Fish on July 1) for Pacific Mackerel, 1979–93, from the ADAPT Model Using SPOTTER with DENSITY Data

Year	Biomass (1,000 short tons)	CV[a]	Recruitment (million fish)
1978	78	0.01	1,985
1979	303	0.06	428
1980	363	0.08	1,987
1981	550	0.15	3,154
1982	829	0.19	1,366
1983	781	0.22	280
1984	691	0.24	234
1985	498	0.25	992
1986	504	0.31	795
1987	480	0.37	434
1988	442	0.50	911
1989	340	0.54	260
1990	269	0.67	267
1991	185	0.75	135
1992	71	1.21	30
1993	35	1.58	16

[a]Calculated using a parametric bootstrap procedure with 50 iterations.

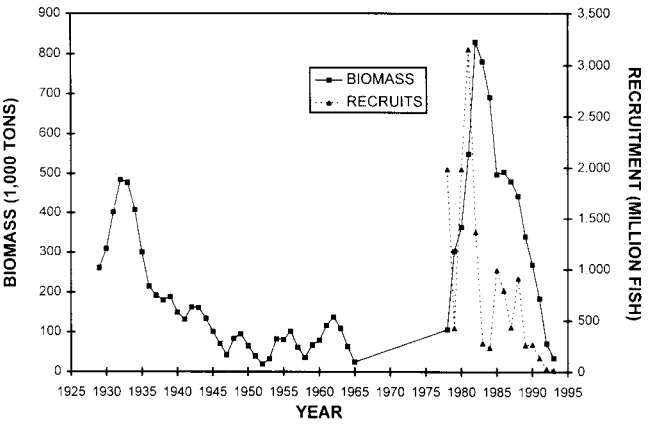

Figure 2. Biomass of Pacific mackerel during 1929–65 from Prager and MacCall 1988, and during 1978–93 from ADAPT (with SPOTTER and DENSITY data). Recruitment is the number of age zero fish on July 1.

Biomass estimates from ADAPT for Pacific mackerel during recent years (table 2 and figure 2) were probably too low because ENSO conditions during 1992–93 displaced pelagic fish to the north (Brodeur and Pearcy 1986) and away from the Southern California Bight area covered by CalCOFI and fish spotters. In 1993, for example, Pacific mackerel were sighted near the Queen Charlotte Islands, British Columbia—north of the normal limit of their distribution (California Department of Fish and Game 1994). Thus effects of ENSO and changes in biomass are confounded in the decline of SPOTTER and CalCOFI data during 1992–93, and in the resulting biomass estimates from the ADAPT procedure. It will be possible to more accurately measure 1992–93 biomass and assess the effects of ENSO on

TABLE 3
Pacific Mackerel Landings (Short Tons), 1978-93

Year	Calif. Commer.	Calif. Recr.	Mexican Commer.	Total
1978	12,448	1,898	9,309	23,655
1979	30,495	2,618	6,348	39,461
1980	32,544	2,997	4,668	40,209
1981	42,916	1,574	2,273	46,763
1982	31,759	1,841	4,977	38,577
1983	35,857	1,626	1,721	39,204
1984	46,422	1,573	2,345	50,340
1985	38,240	1,227	8,005	47,472
1986	45,560	1,092	10,340	56,992
1987	45,852	969	869	47,690
1988	48,072	838	4,926	53,837
1989	40,263	641	16,399	57,303
1990	41,959	1,065	39,400	82,423
1991	34,545	823	19,277	54,645
1992	21,700	738	24,001	46,439
1993	13,358	991	8,863[a]	23,212[a]

[a]Preliminary estimates.

abundance indices after environmental conditions return to normal.

Biomass estimates for Pacific mackerel were imprecise (CV > 30%) during 1986–93, and severely so (CV > 50%) after 1989 (table 2). This lack of precision was exacerbated by imprecise indices of abundance (table 1), low levels of fishing mortality in some years (Pope 1972), and by abundance data that were a "one way trip" (continuously decreasing; Hilborn and Walters 1992). It is likely, moreover, that we overestimated precision because we did not consider errors in landings and catch-at-age data, uncertainty about index and fishery selectivities, and effects of ENSO in our bootstrap variance calculations.

In view of the ENSO conditions, and considering all uncertainties, we estimate that Pacific mackerel biomass during 1993 was less than 100,000 tons. Thus current conditions appear similar to those in the mid 1940s, when Pacific mackerel declined to less than 100,000 tons after a period of high abundance (figure 2). After 1945, the stock varied around an average biomass of about 70,000 tons until the fishery collapsed in 1965.

Recent catch levels (46,000 and 23,000 tons year^{-1} during 1992 and 1993; table 3) were large relative to biomass estimates (<100,000 tons) and may have exceeded the target 30% total exploitation rate that is the basis for California management (quotas are set at 30% of the Pacific mackerel biomass above 20,000 tons). The California fishery is managed with quotas that make no allowance for Mexican harvests, and the Mexican fishery is not regulated by a quota. Thus, if current biomass is as low as we estimate or if recruitment is poor, catches in the next few years may be large enough to deplete the stock of Pacific mackerel.

The Pacific mackerel fishery in California is at a crossroad, and its future is uncertain. Economic conditions in the fishery are poor (Thomson et al. 1993; California Department of Fish and Game 1994). Resources available for management at state and federal levels are currently low because of changing priorities, low revenues from landings taxes, and other financial constraints. The CDFG lacked resources to age Pacific mackerel collected in port samples during 1994, and stock assessment may not be possible in 1995 because of a lack of personnel and data. Landings of Pacific mackerel increased in Mexico during recent years while California landings remained relatively constant, and biomass declined (tables 2 and 3). Thus the Pacific mackerel fishery in California, already beset with economic problems, faces reduced management during a period of increased total landings and potentially low biological productivity.

ACKNOWLEDGMENTS

W. Garcia (Instituto Nacional De Pesca, Ensenada, Baja California) provided landings data for the Mexican fishery in Ensenada. H. G. Moser, R. Charter, and staff (Southwest Fisheries Science Center, La Jolla) made a special effort to supply CalCOFI larvae data for 1986–93 for measuring relative abundance of Pacific mackerel (work funded by NOAA, Earth Systems Data Information Management Program). N. C. H. Lo (Southwest Fisheries Science Center, La Jolla) provided SPOTTER data. T. Barnes and P. Wolf (California Department of Fish and Game, Long Beach) gave technical advice. Alec MacCall (Southwest Fisheries Science Center, Tiburon) and John Hunter (Southwest Fisheries Science Center, La Jolla) gave editorial advice. J. P. Pertierra was supported by the Spaniard Ministerio de Educacion y Ciencia while resident at the Southwest Fisheries Science Center.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

Lake Arrowhead, California

November 2, 1993

GENETICS OF THE FAUNA OF THE CALIFORNIA CURRENT

The California Current is the dominant oceanographic feature on the west coast of North America. It profoundly affects the flora and fauna of the coast, from its influence on climate and upwelling to its effects on the transport and dispersal of organisms and their propagules.

A full understanding of the processes that promote or restrict the dispersal of organisms, and of the California Current's role in governing these processes, is necessary for the proper management of this ecosystem. We know that some genera contain dozens of species, and that others are represented by only a few species. Some species have distributions that separate obviously along known faunal breaks, whereas related species have continuous distributions along the coast. Some populations undergo great temporal cycles of expansion and contraction; others appear relatively stable over time.

Understanding spatial and temporal patterns of variation as they relate to physical and biological features of the California Current is a long-term goal of the CalCOFI program. Recently, a number of programs such as the joint NSF/NOAA GLOBEC (Global Ocean Ecosystem Dynamics) program have refocused interest on understanding the mechanisms that lead to patterns of variation in marine ecosystems, particularly larval transport processes and recruitment variation.

The purpose of this CalCOFI symposium was to examine the role that population genetics—specifically, emerging new techniques of molecular genetic analysis—can play in explaining the mechanisms that underlie observed patterns of spatial and temporal variation. In addition, we hoped to illustrate how population structure can be present but not readily detectable by other means. Finally, it was our intent to highlight the increasingly important role of genetic analyses in making management decisions about marine resources and protected species.

In the past, population geneticists (at least those with common sense!) investigated systems that had stable populations, well-defined barriers to gene flow (a mountain range or an isthmus would suffice), and well-determined times of separation (in the geologic past). Such conditions made it possible to identify population-level differences, and to make inferences about rates of movement among populations.

The study of genetic variability in oceanic populations has been problematic because these systems are inherently open and unstable. Barriers to migration (gene flow), if they exist, are often cryptic, incomplete, and intermittent. In addition, population size may vary by several orders of magnitude over periods of a few years, and the number of individuals that successfully contribute to a particular year class may be a small and nonrandom portion of the total population. These factors have made the application of traditional measures of genetic variation, and the statistical treatment of the data, difficult at best.

Initial studies of oceanic populations, primarily involving allozymes, often indicated no significant variation between putative populations. Quite likely this was because the time and degree of separation needed to produce divergence in allozyme frequencies by genetic drift were overwhelmed by the effects of continuous low levels of migration or by episodic mixing of populations.

Recently, investigators driven by curiosity—if not common sense—have begun to revisit the study of genetic variation in organisms that are influenced by complex and dynamic systems such as the California Current. The approach has been to use new genetic markers that evolve at faster rates, so that population-level differences can be observed in the face of higher levels of gene flow.

The organisms considered in the symposium ranged from marine mammals that forage in the current but are not subject to its physical transport effects, through benthic fish and invertebrates that rely on the current for dispersal of larvae, to calanoid copepods that are inti-

mately associated with the hydrographic processes of the current throughout their lives.

The papers in the symposium proceedings illustrate a variety of approaches for determining genetic population structure. They include novel approaches to revealing larval dispersal patterns by studying introduced species and hybridization zones. They also address temporal as well as spatial patterns of diversity. Several papers provide insights into the analysis of molecular genetic data, and into using power analysis to apply confidence limits to conclusions.

The symposium marks the beginning of what promises to be a new era of investigations into the California Current. Genetic approaches have much to offer toward investigating processes of larval dispersal, recruitment variability, and historic population structure. Genetic considerations are being used increasingly as a management tool, and the conservation of genetic diversity is becoming an explicit goal of management.

Biomedical technology will continue to provide new and innovative tools for the study of marine population genetics. However, a true understanding of the processes that determine genetic structure in oceanic populations will continue to rely on multidisciplinary studies of the physical and biological environment. The development of modeling and statistical procedures that are appropriate for the analysis of marine populations is a research priority.

Russell D. Vetter

Participants in the Symposium of the CalCOFI Conference: Genetics of the Fauna of the California Current. *Left to right:* Russell Vetter, Robin Waples, Dennis Hedgecock, Jennifer Nielsen, Andrew Dizon, Joseph Neigel, Ronald Burton, Jonathan Geller, Ann Bucklin, and student representative Axayacatl Olivares.

MOLECULAR GENETIC VARIATION OF *CALANUS PACIFICUS* (COPEPODA: CALANOIDA): PRELIMINARY EVALUATION OF GENETIC STRUCTURE AND SUBSPECIFIC DIFFERENTIATION BASED ON MTDNA SEQUENCES

ANN BUCKLIN
Ocean Process Analysis Laboratory and
Department of Zoology
University of New Hampshire
Durham, New Hampshire 03824

TODD C. LAJEUNESSE
Ocean Process Analysis Laboratory
University of New Hampshire
Durham, New Hampshire 03824

ABSTRACT

Molecular genetic data can reveal the systematic relationships among biological organisms and may be particularly useful for taxa that are morphologically indistinguishable. The copepod *Calanus pacificus* may include several subspecies, although no morphological characters diagnostic of each subspecies have been found. We use DNA sequence variation of a mitochondrial gene to investigate the degree of genetic differentiation associated with these systematic groupings and to begin a study of the evolutionary significance of geographic variation in the species. The DNA sequence of a 449 base pair portion of the mitochondrial 16S rRNA gene was determined for 27 individuals of *C. pacificus* collected from five sites in the North Pacific Ocean (Dabob Bay, Puget Sound, Wash.; three sites in the California Current; and the former Ocean Weather Station Papa). The molecular genetic differentiation between individuals of *C. p. oceanicus* and *C. p. californicus* (0.9% to 1.0% sequence difference) was greater than that between individuals of *C. p. californicus* from different geographic regions (0.2% to 0.5% difference), but less than that among species of *Calanus* (12% to 18% difference). The strongest evidence of subspecific differentiation is that the *C. p. oceanicus* individuals were grouped together and separate from *C. p. californicus* on a tree constructed by neighbor joining with 1000 bootstrapped subreplicates. Determination of the systematic significance of the molecular divergence will require further analysis of geographic and systematic patterns of intraspecific variation within *C. pacificus*, and analysis of additional genes.

RESUMEN

Las relaciones sistemáticas entre los organismos pueden ser reveladas con datos de genética molecular, que además pueden ser particularmente útiles para revelar taxa que son indistinguibles morfológicamente. El copépodo *Calanus pacificus* podría incluir varias subespecies, a pesar de que no se han encontrado caracteres diagnóstico para cada una de éstas. Usamos variación en la secuencia de ADN de un gen de la mitocondria para investigar el grado de diferenciación genética asociado con estos agrupamientos sistemáticos y para empezar a estudiar el significado evolutivo de la variación geográfica en la especie. Se determinó la secuencia de ADN en una porción de 449 pares de bases del gen del mitocondria 16S ARNr en 27 individuos de *C. pacificus* colectados en 5 sitios del Oceáno Pacífico Norte (Bahía Dabob, Puget Sound, Washington, tres sitios en la Corriente de California, y la antigua estación climatológica oceánica Papa). La diferenciación genética molecular entre los individuos de *C. p. oceanicus* y *C. p. californicus* (0.9% a 1.0% de diferencia en la secuencia) fué mayor que entre individuos de *C. p. californicus* de diferentes regiones (0.2% a 0.5% de diferencia), pero menor que entre especies de *Calanus* (12% a 18% de diferencia). La evidencia más fuerte de diferenciación subespecífica es que el análisis agrupó a los individuos de *C. p. oceanicus* y separó a los de *C. p. californicus* en un árbol construido por el método de unión de vecinos con 1000 muestras obtenidas por muestreo repetitivo automatizado ("bootstrapping"). La determinación del significado sistemático de la divergencia molecular requerirá más análisis de los patrones geográficos y sistemáticos de la variación intraespecífica en *C. pacificus* y análisis de más genes.

INTRODUCTION

Molecular Taxonomy

Where morphological or physiological evidence of systematic relationships is unclear, genetic characters may provide accurate and unambiguous indicators of the systematics of a group. Molecular characteristics have been used to identify and discriminate species (Wilson et al. 1985). But although genetic characteristics can frequently show patterns of relationship, they frequently do not indicate the level of taxonomic divergence between taxa. For example, there is no benchmark for differentiation at the genus, species, or subspecies level. Fixed differences between taxa for traits encoded by nuclear genes (especially allozymic variants of enzymes) are frequently considered to constitute sufficient evidence of distinction at the species level. It is essential that both intra- and interspecific variation of genetic characteristics are quantified and compared in order to understand the taxonomic significance of genetic differences.

Questions of the systematic significance of genetic differences within a species are especially difficult to re-

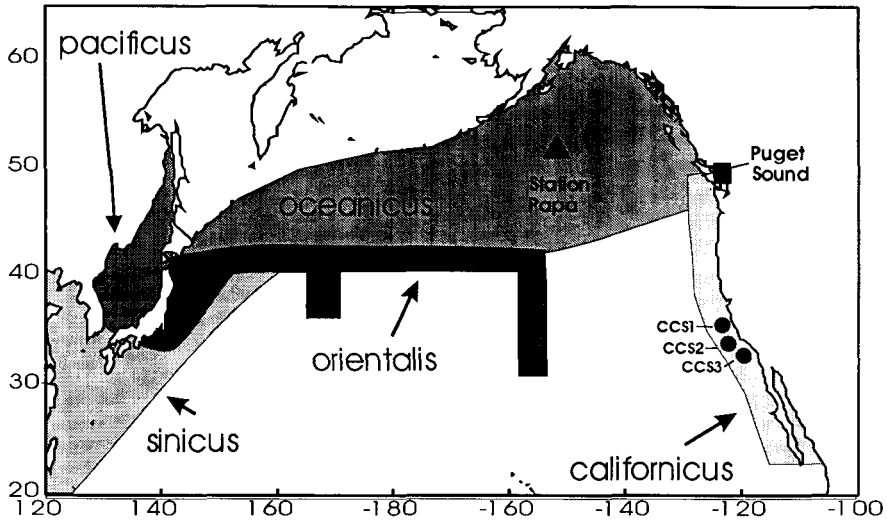

Figure 1. Geographic distribution of the subspecies of *Calanus pacificus* (also showing *C. sinicus*). Collection sites are shown as symbols. There are four sites within the range of *C. p. californicus*: Puget Sound (*square*) and CCS1, CCS2, and CCS3 (*circles*); one site, Station Papa (*triangle*), is within the range of *C. p. oceanicus*. (Distributions are derived from unpublished work by A. Fleminger.)

solve, since these groups may be so recently reproductively isolated that there may be no detectable genetic divergence. There are currently no established levels of genetic divergence associated with subspecies, sibling species, and semispecies. Intuitively, one might expect that these levels of genetic differentiation would be less than that between species and greater than that between conspecific populations.

Numerous researchers have quantified the genetic variation among conspecific populations by using mitochondrial DNA (mtDNA) (see review by Avise et al. 1987). The primary advantage of mtDNA for these studies is that it is inherited maternally; mtDNA may be expected to exhibit greater differences than nuclear DNA between lineages (Birky et al. 1989). Among marine invertebrates, several species have been shown to exhibit significant differentiation among conspecific populations (i.e., significant population genetic structure). The following species have been shown to be genetically structured on mesoscales to large scales (i.e., 100s to 1000s of km) by restriction fragment length polymorphisms of mtDNA: the horseshoe crab, *Limulus polyphemus* (Saunders et al. 1986); the oyster *Crassostrea virginica* (Reeb and Avise 1990); and the mussel, *Mytilus* spp. (Edwards and Skibinski 1987). Restriction fragment polymorphisms have also revealed significant genetic differentiation among geographic populations of marine fish, including herring (Kornfield and Bogdanowicz 1987), red drum (Gold and Richardson 1991), haddock (Zwanenburg et al. 1992), and plaice (Stott et al. 1992).

More recently, the nucleotide base sequence variation of mtDNA has been used to examine population structure in marine fish and invertebrates. The base sequence of a portion of cytochrome b discriminated populations of cod (Carr and Marshall 1991a, b) and blue marlin (Finnerty and Block 1992). Mitochondrial genes have revealed considerable intraspecific sequence variation in the sea urchins *Strongylocentrotus pallidus* (Palumbi and Kessing 1991) and *Heliocidaris tuberculata* (McMillan et al. 1992), and in the penaeid shrimp, *Penaeus stylirostris* (Palumbi and Benzie 1991); however, little or no geographic structuring was observed for these species. Two general principles emerge from the many studies: first, that both marine fish and invertebrates are quite variable at the protein and molecular level, and second, that this variability is resolved into genetically distinguishable, geographic populations in only some of the species (see Ovenden 1990 for a review of marine stock assessment using mtDNA).

Taxonomy of *Calanus* Species

Three subspecies of the calanoid copepod *Calanus pacificus* have been distinguished on the basis of the relative position of the spermathecae of females and the number of denticles and endopodite length of the fifth leg of males (Brodsky 1965). Intermediate forms for these characters exist, and neither the position of urosomal pores nor the shape of the fifth thoracic leg differs diagnostically among the subspecies (Fleminger and Hulsemann, unpublished data). Although the systematic significance of the morphological variation is in some doubt, the subspecies have been referred to in print repeatedly (Alldredge et al. 1984; Fleminger 1985; Fleminger and Hulsemann 1987).

The subspecies have distinct geographic distributions (figure 1). *C. p. californicus* is the only species of *Calanus*

found in the California Current between central California and the Gulf of California (Fleminger 1964). This subspecies exhibits complex behavioral reactions to hydrographic conditions (Cox et al. 1983) and marked migratory behavior (Alldredge et al. 1984) that is adaptive for life in the coastal upwelling region of the California Current. Another subspecies, *C. p. oceanicus*, has an oceanic distribution and may occur across the entire northern North Pacific (Brodsky 1965). The third subspecies, *C. p. pacificus*, is found in the temperate western Pacific, where it may overlap extensively with *C. sinicus*, from which it is morphologically distinguishable (Brodsky 1965).

In this preliminary analysis, genetic differences among samples of *C. pacificus* were determined in order to reveal the geographic and systematic patterns of molecular variation within the species. We present results based on sequencing a portion of the mitochondrial 16S rRNA gene. We chose this gene because it has been shown to vary sufficiently to make it possible to discriminate closely related species (e.g., Cunningham et al. 1992; Xiong and Kocher 1991). Also, previous studies have shown that there is considerable variation within several *Calanus* species and some evidence of population genetic structure (Bucklin and Kann 1991; Bucklin and Kocher, unpublished data).

MATERIALS AND METHODS

Sample Collection

Samples of each species were collected by net tow and preserved in 95% ethyl alcohol. One sample of *C. pacificus* from the California Current (CCS1) was collected in June 1992. Two other California Current samples of *C. pacificus* were collected during California Cooperative Fisheries Investigation (CalCOFI) surveys: one (CCS2) in November 1989 from CalCOFI station number 83.42, and the other (CCS3) in April 1992 from CalCOFI station 93.40. The locations of the sample sites were: CCS1 (34°54' N; 123°01' W); CCS2 (33°75' N; 121.9°9' W); and CCS3 (32°25' N; 118°10' W). The Ocean Weather Station Papa (PAPA) sample of *C. pacificus* was collected at 50° N; 145° W; the sample from Puget Sound, Wash. (PUGET) was collected at 47°45.5' N; 122°49.5' W (figure 1).

DNA Amplification

Mitochondrial DNA amplifications were performed on specimens preserved in 95% ethyl alcohol. The copepods were rehydrated in 0.4 ml of distilled deionized H_2O for 24 hrs prior to amplification. Each individual was then homogenized in a PCR buffer containing 77 µl dH_2O, 8 µl of 25 mg/ml $MgCl_2$, and 10 µl 10X PCR buffer (Promega Corp., Madison, Wis.) and refrigerated for 24 hrs. After incubation, the remainder of the PCR reaction mixture was added: 10 µl dNTP (Perkin-Elmer Corp., Norwalk, Conn.) 1 µl each of the 16SAR and 16SBR primers (100 µM concentration), and 1 µl Taq polymerase enzyme (Promega Corp.). The reaction volume was 100 µl; 2 drops of mineral oil were added on top to prevent evaporation.

The amplification primers used were 16SAR and 16SBR (Palumbi et al. 1991) based on the *Drosophila yakuba* sequence (Clary and Wolstenholme 1985). The sequences are:

16SAR 5' = CGCCTGTTTAACAAAAACAT = 3'
16SBR 5' = CCGGTTTGAACTCAGATCACGT = 3'

Amplification was carried out in a Perkin-Elmer thermal cycler, model 480. The amplification protocol was denaturation at 94°C for 1 min; annealing at 45°C for 2 min; and extension at 72°C for 3 min. The amplification was carried through 35 cycles and maintained at 4°C.

Amplification products to be sequenced were checked for size and purity by loading 10 µl on a 1% agarose gel containing ethidium bromide. Only amplification products showing bright, sharp bands were selected for sequencing. These products were purified by loading 45 µl onto a 1% Nusieve gel containing ethidium bromide, and electrophoresed at 50 volts. Product bands were cut from the gel and melted by heating to 65°C in 1.7 ml Eppendorf tubes. The temperature was lowered to 37°C, and 5–10 units of agarase (Sigma Chemical Corp., Chicago) were added. The samples were incubated overnight to ensure complete digestion of the agarose.

DNA Sequencing

The sequencing reaction was done in a Perkin Elmer thermal cycler, model 480, using a cycle-sequencing kit (Applied Biosystems, Inc., Foster City, Calif.). Fluorescently labeled dideoxynucleotides were incorporated during an asymmetrical amplification using the 16SBR primer. This primer was selected because it consistently produced good sequence data.

Nucleotide sequencing was carried out in an Applied Biosystems, Inc., automated DNA sequencer. The automated sequencer relies on an amplification reaction to produce strands terminated with fluorescently labeled dideoxynucleotides (Smith et al. 1986). The sequencer uses a 6% acrylamide gel; gels are electrophoresed for 11 hrs. The sequences are shown as fluorescent emission spectra for each base, resulting in a 4-color chromatogram. The sequence chromatogram is read by the computer

[1]Palumbi, S., A. Martin, S. Romano, W. O. McMillan, L. Stice, and G. Grabowski. 1991. The simple fool's guide to PCR (ver. 2). Unpublished manuscript.

software (SeqEd, version 2.0) and checked thoroughly for accurate machine reading.

Sequence Alignment and Data Analysis

The Genetics Computer Group (GCG) Sequence Analysis Software Package was used for alignments and preliminary analyses; the programs are based on those by Smithies et al. (1981) and are now commercially available as a package. The multiple-sequence alignment program PileUp (Devereaux et al. 1984) was used to align the sequences for each individual; PileUp is a simplification of the progressive alignment method of Feng and Doolittle (1987). Although the program has limitations, it is a safeguard against human subjectivity in the alignment process. Several parameters of the PileUp program can be altered: gap penalties used ranged from 0.5 to 5.0, and gap length penalties ranged from 0 to 0.5; the definitive alignment was done with a gap penalty of 5.0 and a gap length penalty of 0.3, which maximized the sequence identities.

A difference matrix was calculated for all pairwise comparisons of individual sequences. The mean and the standard error of the percent differences between individuals were determined for comparisons within and between samples.

Phylogeny Reconstruction

A tree was constructed by means of neighbor joining (Saitou and Nei 1987) in the software package MEGA (Molecular Evolutionary Genetics Analysis; Kumar et al. 1993) to show the molecular relationships among the 27 individuals. The neighbor-joining protocol first determines a distance matrix and then reconstructs the phylogeny. Tamura-Nei distances were used (Tamura and Nei 1993), based on both transitions and transversions. The resultant tree was tested for statistical significance by 1000 bootstrap replications.

RESULTS

Nucleotide base sequences for a 440-base-pair region of the mitochondrial 16S rRNA gene of *C. pacificus* was determined for 27 individuals (figure 2). There were 16 haplotypes among the 27 individuals. We found that 11 individuals were unique; 5 individuals shared the same haplotype; four other haplotypes were shared by 2–4 individuals.

Among the three samples of *C. pacificus* collected in the California Current (CCS1, CCS2, and CCS3), individuals differed by three or fewer bases among the 449 (≤0.7%). Among individuals within one sample, differences averaged considerably less than 1%: the mean difference between individuals within the PUGET sample was 0.20% and between individuals within the PAPA sample was 0.14% (figure 3). For comparisons between

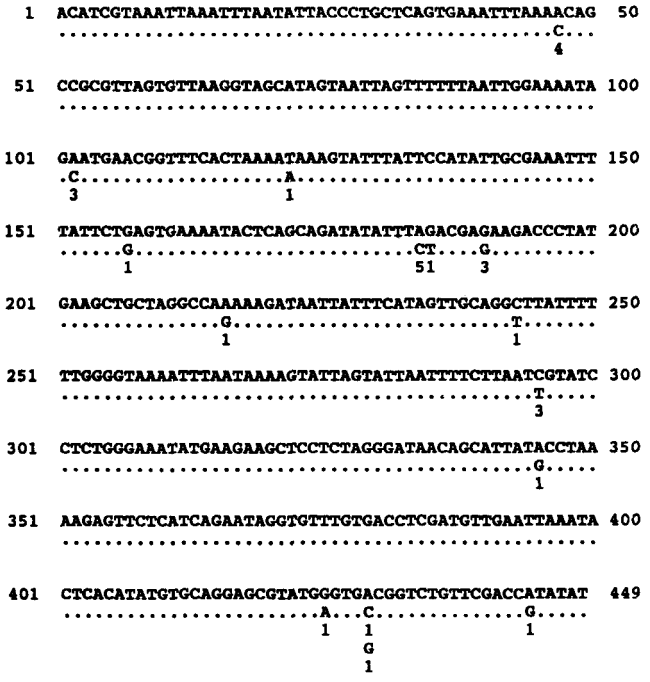

Figure 2. DNA base sequence for a 449 base pair region of the mitochondrial 16S rRNA gene for samples of geographic populations of *Calanus pacificus*. Only the sequence for the most abundant haplotype, shared by 5 of the 27 individuals sequenced, is shown. Substitutions are indicated just below each variable site; the number of haplotypes that exhibit each substitution is shown below the base substituted. The sequence alignment was done by the PileUp program of the GCG Software Package (Devereaux et al. 1984). Alignment was done with a gap weight of 5.0 and gap length weight of 0.3.

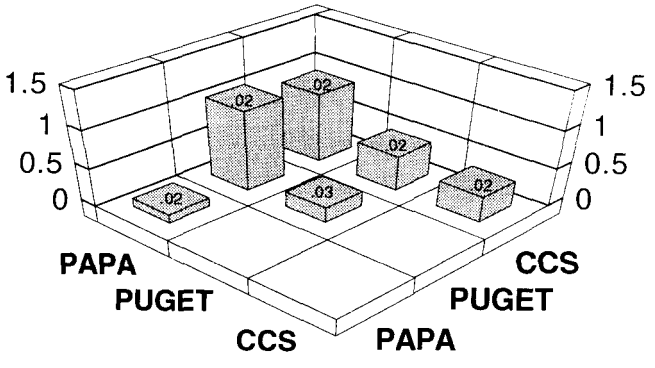

Figure 3. Percent DNA base sequence differences among samples of *C. pacificus*. The three samples collected in the California Current (CCS) have been pooled for comparison with the Puget Sound samples (PUGET) and the sample collected at Ocean Weather Station Papa (PAPA). Collection locations are given in figure 1 and the text. The bar height indicates the percent differences for pairwise comparisons within and between samples (or pools of samples). Numbers shown on top of the bars are the standard error; all bar heights differ significantly, except those of the CCS vs PAPA and PUGET vs PAPA comparisons, which are not different.

individuals in the CCS and PUGET samples (i.e., between individuals of *C. p. californicus*) the mean difference was 0.46%. In contrast, comparisons between *C. p. californicus* and *C. p. oceanicus* were 0.92% (for CCS vs PAPA samples) and 1.06% (for PUGET vs PAPA samples). The differences between *C. p. oceanicus* and *C. p.*

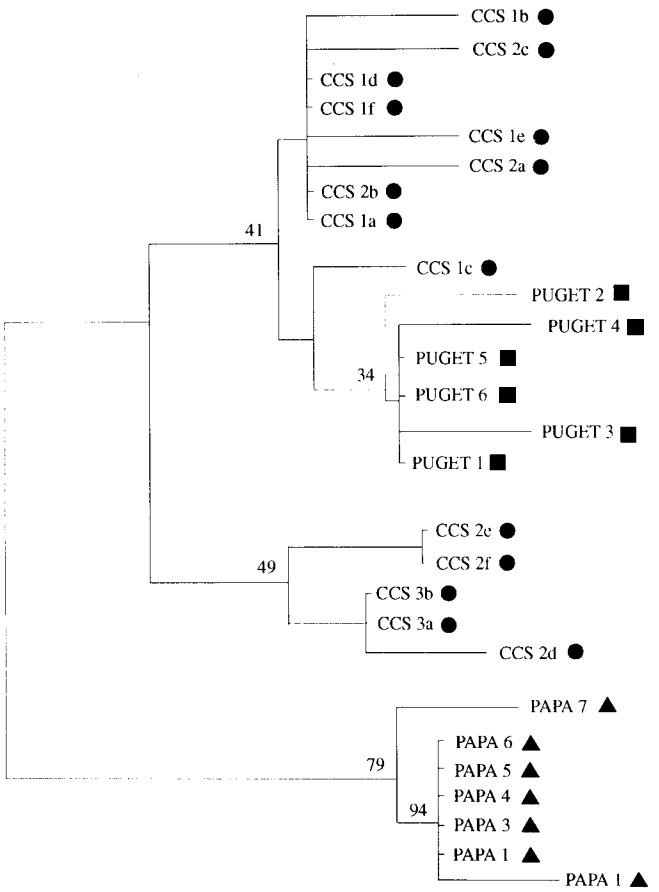

Figure 4. Neighbor-joining tree showing genetic differences among the 27 individuals of *Calanus pacificus*. Abbreviations are: California Current Collections (CCS), Puget Sound collection (PUGET), and O.W.S. Papa collection (PAPA). The symbols correspond to those used for the collection locations in figure 1. The tree is based on the neighbor-joining method, using Tamura-Jukes distances and considering both transitions and tranversions. Numbers on the branches are branch lengths; numbers in italics at branchpoints are the percentage of trees that show that branchpoint among 1000 bootstrapped replicates.

californicus individuals were significantly greater than the differences among individuals of the same subspecies (figure 3).

A phylogenetic analysis of the individuals of the five samples of *C. pacificus* further suggested that the *C. p. oceanicus* sample collected from Ocean Weather Station Papa was distinctive (figure 4). The tree topology was robust to the method of analysis: all trees indicated the distinctiveness of the individuals in the PAPA sample. The neighbor-joining tree (figure 4) has the *C. p. oceanicus* individuals clustered together and significantly distinct in 1000 bootstrapped subreplicates (Saitou and Nei 1987).

DISCUSSION

Previous studies of DNA sequence variation of the mitochondrial 16S rRNA gene have revealed differences in the sequences of a 450 bp region between species of *Calanus* on the order of 12% to 18% (Bucklin et al. 1992). Other studies comparing sequence data of the mitochondrial 16S rRNA gene between crustacean species have shown similar results. Between species of the shrimp *Penaeus*, 11% sequence differences were found by Machado et al. (1992) for this same region of the mitochondrial 16S rRNA gene. Palumbi and Benzie (1991) estimated interspecific differences between two *Penaeus* species at 11% (based on sequence data) and 9% (based on RFLP data). Brasher et al. (1992) showed that the mean mtDNA sequence divergence between three species of the rock lobster *Jasus* was 6.2%, whereas these species differed from a fourth by 14.9% to 16.7%. These divergences, and those of *Calanus* species, are typical of the congeneric species that have been studied (Avise et al. 1987).

Levels of mtDNA sequence variation within species of *Calanus* for the 16S rRNA gene ranged between 1.3% (between *C. helgolandicus* samples) and 2.6% (between *C. finmarchicus* samples) (Bucklin and Kocher, unpublished data). The characteristic pattern of intraspecific variation is that one haplotype is very common (approaching 50% of individuals sequenced), while there are many rare or unique haplotypes in each population. Intraspecific differences among individuals of *C. pacificus* are generally less than 1% (figure 3). Within the same subspecies, differences are on the order to 0.2%; between subspecies, the differences are approximately 1%.

Using the mitochondrial 16S rRNA gene, Xiong and Kocher (1993) measured differentiation within species of the black fly genus, *Simulium*, to be 0.47%, and within "complexes" (sibling species groups) to be 1.09%. For crustaceans, Silberman et al. (1994) found mtDNA sequence differences among conspecific populations to be between 1.2% and 1.7%, based on RFLP analysis. Another study by McLean et al. (1983) used restriction fragment length polymorphisms of mtDNA to establish levels of intraspecific variation of *Panulirus*, which they found to be similar to humans, deer mice, and *Drosophila*. These levels of intraspecific variation for the mitochondrial 16S rRNA gene may prove low in comparison with other mitochondrial and nuclear genes. Analysis of intraspecific variation of addition genes is important to determine whether the patterns described here are typical of all genes.

Although the sequence difference between the two subspecies of *C. pacificus* is far less than that between species, and similar to that between conspecific populations, these data cannot be said to "prove" that the geographic forms of *C. pacificus* do or do not deserve subspecific status. It is very difficult to determine the level of systematic distinctiveness using molecular characteristics, especially mtDNA. One problem is that no threshold levels of divergence of mtDNA sequences have

been associated with speciation events or subspecific differentiation, as has been done in some cases for nuclear genes. Rates of divergence of mtDNA appear to be rather variable from taxon to taxon. Also, recent divergences may not be reflected in the mtDNA characteristics, and newer taxa may show little or no sequence divergence.

In addition to the measures of sequence divergence, phylogenetic approaches are useful for identifying genetically distinct groups and for recognizing geographic structure (this approach has been called phylogeography; Avise et al. 1987). For example, despite little sequence differentiation between individuals of the different subspecies of *C. pacificus*, all individuals of *C. p. oceanicus* cluster together in the neighbor-joining tree (figure 4). This distinctive grouping is statistically significant according to the bootstrap test performed: 6 of the 7 individuals cluster 94% of the time, and the seventh individual is grouped with these 79% of the time. The 20 individuals of *C. p. californicus* are variable among themselves, but there are no statistically distinct groupings within the subspecies (other than a slight tendency of the individuals from Puget Sound to group together; figure 4). As found in an earlier study (Bucklin and Kocher, unpublished data), there was more intraspecific variation among 87 individuals of *C. finmarchicus* than among the *C. pacificus* individuals (the most divergent *C. finmarchicus* individuals were 2.7% different in sequence for this same gene region), but there was no distinctive clustering of individuals by geographic region or taxonomic subgroup.

In summary, mtDNA sequence data for 27 individuals yields some evidence of the differentiation of the open-ocean sample (O.W.S. Papa) of *C. pacificus*, which occurs within the geographic range of *C. p. oceanicus*. In contrast, there is no significant differentiation of any subgroup across the large latitudinal range of *C. p. californicus* (Puget Sound and throughout the California Current). The genetic differentiation of the *C. p. oceanicus* sample is apparent in the tree constructed by neighbor joining and is statistically sound according to a bootstrap test (figure 4). The tree construction provides the best evidence of the genetic distinctiveness of the subspecies of *C. pacificus*. The amount of sequence difference between individuals of the different subspecies (approximately 1%) is similar to that between conspecific individuals of other crustacean species (McLean et al. 1983; Silberman 1994), including other species of *Calanus* (Bucklin and Kocher, unpublished data). If the subspecies are reproductively isolated and thus genetically distinct, the divergence has been a relatively recent one. These subspecies may be too young to exhibit significant genetic divergence.

Molecular genetic traits of organisms may be a useful means for resolving long-standing, fundamental questions about the systematics and evolution of planktonic organisms. Questions having to do with the taxonomic significance of intraspecific variation are particularly problematical for species that show little intra- or interspecific variation, and may be particularly amenable to molecular analysis.

ACKNOWLEDGMENTS

A number of people have helped collect the *Calanus* samples for this project. Charlie Miller (Oregon State University) made collections in the California Current for this project. Mike Mullin (Scripps Institution of Oceanography) collected *Calanus pacificus* during a CalCOFI cruise. Bruce Frost (University of Washington) arranged for the O.W.S. Papa collection, and collected the sample from Puget Sound. Nancy Copley (Woods Hole Oceanographic Institution) provided invaluable assistance with copepod identification.

This project was supported by funding to A.B. from an NSF Research Fellowship in Biotechnology and the Ocean Sciences (OCE-9018528) and NOAA funding through the U.S. GLOBEC program (NA36GP0298-01).

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INFERRING THE GENETIC STRUCTURE OF MARINE POPULATIONS: A CASE STUDY COMPARING ALLOZYME AND DNA SEQUENCE DATA

RONALD S. BURTON
Marine Biology Research Division
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093-0202

ABSTRACT

The genetic structure of natural populations of marine organisms is frequently inferred from the distribution of alleles at gene loci. Until recently, most investigations relied entirely on protein electrophoretic techniques, with particular emphasis on polymorphic enzyme-coding gene loci (allozyme loci). Over the past few years, increasing use has been made of molecular techniques, including methods that allow the construction of gene genealogies. These later methods provide powerful insight into the evolutionary history of genetic variation and, under some conditions, provide valuable information concerning population structure. This paper compares results of both allozyme and DNA sequence studies for a set of populations of the intertidal copepod *Tigriopus californicus* along the California coast. The comparisons show that: (1) Allozyme frequencies distinguish almost all the study populations, whereas genealogies of the sampled DNA sequences do not. (2) Both nuclear and mitochondrial DNA sequences reveal strong population differentiation between central and southern California populations that is not apparent in the allozyme frequencies. (3) Allozymes and DNA sequences are not entirely concordant in the picture they present of population relationships. (4) The most complete analyses of population structure will require multiple genetic techniques.

RESUMEN

La estructura genética de poblaciones naturales de organismos se infiere a menudo a partir de la distribución de alelos en loci de genes. Hasta hace algunos años la mayoría de los estudios se basaban en técnicas de electroforésis de proteínas, con énfasis en loci de genes polimorfos que codifican enzimas (loci alocimos). En años recientes se ha incrementado el uso de técnicas moleculares, incluyendo el uso de métodos que permiten construir genealogías genéticas. Estos métodos ofrecen una perspectiva profunda de la historia evolutiva de la variación genética; en ciertas circunstancias, estos métodos proveen información importante de la estructura de la población. Este artículo compara los resultados obtenidos de alocimos y secuencias de ADN de un conjunto de poblaciones del copépodo intermareal *Tigriopus californicus* a lo largo de la costa de California. Las comparaciones produjeron varios resultados: (1) Las frecuencias de alocimos distinguieron a casi todas las poblaciones estudiadas, mientras que las genealogías de las secuencias de ADN no las demarcó. (2) Tanto las secuencias del ADN de las mitocondrias como las de los núcleos revelaron una marcada diferenciación poblacional entre California Sur y Central, mas este resultado no se repitió con las frecuencias de alocimos. (3) Los resultados de las secuencias de ADN y los alocimos no concuerdan en su totalidad en el esquema de las relaciones poblacionales. (4) Los análisis mas completos de la estructura de la población requerirán múltiples técnicas genéticas.

INTRODUCTION

Attempts to understand the genetic structure of marine invertebrate populations have long been hampered by our inability to directly track the dispersal of larval life stages that frequently spend substantial lengths of time in the plankton. Although current patterns and other physical factors may restrict or promote particular routes of dispersal, the oceans often appear to be barrier-free, and long-distance dispersal is clearly possible (e.g., Scheltema 1986). Despite this extensive potential for gene flow, population differentiation among marine invertebrates has now been widely documented through the use of biochemical and molecular genetic techniques (Burton 1983; Hedgecock 1986; Palumbi 1992). In particular, analyses of electrophoretically detected enzyme polymorphisms have made major contributions to our understanding of gene flow and recruitment in a diversity of marine species over the past two decades.

Several long-recognized problems arise from the use of allelic isozymes (allozymes) for the analysis of population structure. First, although protein electrophoresis allows the screening of many individuals, populations, and gene loci for analysis of population structure, its resolution is limited in that it detects only a subset of existing variants at a gene locus. Thus any putative allele may consist of multiple alleles that are indistinguishable, and differences between populations may frequently be underestimated. Second, as genetically different forms of the same enzyme, allozymes may differ in functional properties. Therefore, frequencies of alleles not only reflect patterns of gene flow and random genetic drift, but they may also result from the action of natural selection.

Finally, the evolutionary relationships among alleles are not necessarily reflected by similarity in their electrophoretic mobility; thus it is not possible to determine which alleles are derived by mutation from other alleles in the same population and which, if any, were introduced by immigrants from distant populations.

Recently, a variety of molecular techniques that assess variation in DNA sequence have supplemented or replaced allozyme techniques in the analysis of population structure (e.g., Avise 1992; Karl and Avise 1992). Of particular interest in the analysis of intraspecific population differentiation is the analysis of mitochondrial DNA (mtDNA). Unlike nuclear DNA, mtDNA is typically maternally inherited and not subject to recombination. Divergence between maternal lineages continues to increase through evolutionary time, and descendants can be assigned to lineages in nonreticulate gene genealogies (Avise 1991). In the case of nuclear genes, genealogies may be complicated by recombination between lineages, obscuring the true degree of evolutionary divergence among the sampled genes.

In addition to focusing on either nuclear or mitochondrial genomes, researchers can take two qualitatively different approaches to the use of molecular techniques for population analyses. One approach is to use restriction fragment length polymorphisms (RFLPs) or sequencing in order to find single polymorphic nucleotide sites, which are then studied in much the same way polymorphic enzymes are studied (i.e., frequencies of different alleles are determined in each study population). Although providing a wealth of markers for study, the data themselves are not qualitatively different from allozymes in that the frequencies of alleles can be estimated, but the allelic genealogies remain unknown. If restricted to nuclear markers, this approach presents nothing conceptually new to the study of population structure, and one can safely assume that the wealth of molecular markers will supplement (or replace) allozyme data in a straightforward manner.

The second approach focuses on obtaining sequences of specific fragments of DNA from relatively small numbers of individuals from each study population. In cases where a sufficient number of phylogenetically informative nucleotide sites are included in the study, sequence data can be used to infer the phylogenetic relationships among the sequenced alleles, or gene genealogy. In some cases, such information can give insight into population structure not available from allozyme frequencies. For example, the genealogical approach may reveal the ancestral lineage of an allele which may, in turn, suggest its geographic origin. The primary problem with DNA sequence data is cost—both in manpower and supplies. As a result, studies typically examine far fewer individuals, populations, and independent gene loci than do allozyme analyses. However, as discussed below, much of the power of sequence data derive from their high phylogenetic information content; depending on the types of questions to be addressed, DNA sequencing can be cost-effective.

Given the substantial differences in the nature of the data obtained from different genetic analyses, it is of great interest to carefully compare the different approaches within given study systems. In at least two marine systems, surprising results have come from comparing allozyme data with mtDNA and nuclear DNA data. In the American oyster, *Crassostrea virginica*, allozyme frequencies were found to be relatively uniform across broad geographic ranges (Buroker 1983). This result was interpreted as evidence of high levels of gene flow among populations until subsequent mtDNA data (Reeb and Avise 1990) and nuclear DNA data (RFLPs in anonymous single copy nuclear DNA; Karl and Avise 1992) revealed a region of sharp genetic differentiation where little allozyme differentiation had previously been apparent. Because of the concordance of the mtDNA and nucDNA genetic markers, it was concluded that gene flow was restricted across the phylogeographic break and that the similarity in allozyme frequencies across the break reflected the action of stabilizing natural selection favoring multilocus heterozygotes (Karl and Avise 1992).

The second study system is the focus of the current discussion. For the past fifteen years, my lab has focused attention on the population genetics of the supralittoral copepod, *Tigriopus californicus*. (Burton and Feldman 1981; Burton 1986). We have recently extended our work on the genetic structure of natural populations of this species from allozyme analyses to studies of DNA sequence variation at a mitochondrial gene (cytochrome oxidase I = COI) and a nuclear gene (histone H1) (Burton and Lee 1994). In the following paragraphs, I will review some aspects of each of our genetic data sets for California coast *T. californicus* populations. I will then attempt to draw some conclusions about the inferences of population structure that can be drawn from each type of genetic data either by itself or in conjunction with other data.

MATERIALS AND METHODS

Tigriopus californicus were collected from high intertidal rock pools at each of ten geographic sites along the central and southern California coast, including one site on the north side of Santa Cruz Island (figure 1). Population samples (typically 200–5,000 adults) were maintained in the laboratory as breeding populations in 400 ml beakers. Within two weeks of collection and before any mortality was observed among the field-collected animals, allozyme frequencies were determined

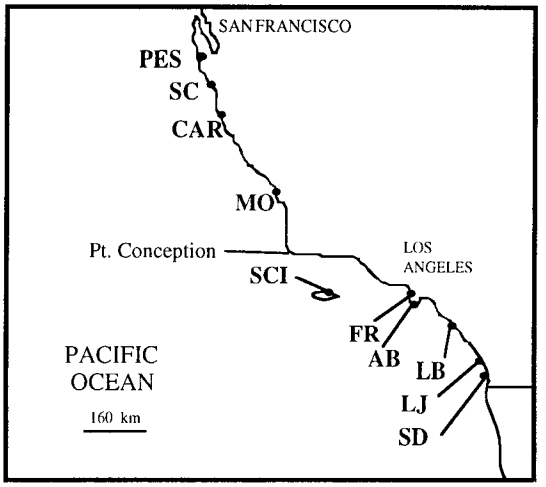

Figure 1. Map of *T. californicus* collecting sites along the central and southern California coast. PES = Pescadero Beach, SCN = Santa Cruz, CAR = Carmel, MO = Morro Bay, SCI = Santa Cruz Island, FR = Flatrock Point, AB = Abalone Cove, LB = Laguna Beach, LJ = La Jolla, SD = San Diego.

for seven gene loci by polyacrylamide gel electrophoresis, following Burton and Feldman (1981) and using stain recipes from Harris and Hopkinson (1976) and Bulnheim and Scholl (1981). A minimum of 35 individuals were scored per population for each gene locus.

Sequencing of both nuclear and mitochondrial genes was carried out on DNA extracted from 10–15 individuals from each of a number of isofemale lines established from the field-collected animals. This procedure was adopted after initial attempts to amplify COI alleles from DNA extracted from single adult *T. californicus* proved inconsistent. Because mitochondrial DNA is typically maternally inherited in animals, each isofemale line was expected to have only a single mtDNA haplotype. Although each line could contain as many as four alleles (two maternal and two paternal) for any nuclear gene, observed ambiguity in H1 sequences potentially due to multiple haplotypes segregating within isofemale lines was low, ranging from zero (13 lines) to five (2 lines) nucleotide positions per reported sequence. Since only three instances of ambiguity were observed at informative sites in the entire H1 data set (total 24 sequences with 51 informative sites), the impact of within-line polymorphism can, for the purposes of this study, be ignored.

With the exception of the Santa Cruz Island samples, the data discussed below have been previously published (see Burton and Lee 1994), so detailed protocols will not be presented here. In brief, we have used a variety of methods for DNA extraction and direct sequencing of DNA fragments amplified by the polymerase chain reaction. Our initial efforts focused on the COI gene and used total genomic DNA samples extracted by means of proteinase K digestion and phenol-chloroform extractions. Primer sequences for gene amplification and direct sequencing of the COI gene were as follows (position in the *Drosophila yakuba* mtDNA sequence [Clary and Wolstenholme 1985] are noted): primer COIK : (5'-GAGCTCCAGATATAGCATTCC-3'), 1730–1750; primer COIJ : (5'-CAATACCTGTGAGTCCTCCTA-3'), 2536–2516; primer COIL : (5'-TGAGAGAT-TATTCCAAATCC-3'), 2234–2213; primer COID: (5'-AAACCAACTGTGAACATGTG-3'), 2357–2338. Primers K and J were designed by R. Van Syoc, California Academy of Sciences. Biotinylated COIK was paired with either COID or COIJ for gene amplification by the polymerase chain reaction (PCR) using Perkin-Elmer's GeneAmp PCR Reagent Kit and the following thermocycle profile: 94°C, 1 min; 50°C, 1 min; 72°C, 2 min, for 35 cycles followed by 5 min at 72°C. PCR products were run on a 2% agarose gel and extracted from the agarose using Geneclean (Bio 101 Inc.). Solid-state sequencing (Ausubel et al. 1992) of the biotinylated strand with primers COIL and COID used Sequenase protocols (US Biochemical) following capture of the biotinylated strand on streptavidin-coated magnetic beads (Dynal, Inc.).

A previously published sequence of a histone H1 gene from *T. californicus* (Brown et al. 1992) was used to design primers for PCR amplification and sequencing of a fragment including the 5' end of the H1 coding region. Primers used were H1.5 (5'-ATATGTGTC-GAATCGAGGGC-3', position 137–156 in the published sequence) and H1.3 (5'-TCTCGACCAAGGACTTG-3', position 710–694). DNA samples used for H1 PCR were prepared by boiling 15 animals from a single isofemale line in 200 µl of 10% chelating resin (Sigma Chemical) for 8 minutes; after boiling, samples were vortexed for 10 sec and centrifuged (13,000 × g) for 2 minutes at 4°C (Walsh et al. 1991). Ten µl of the supernatant were used as template in the PCR reaction, which used the same thermocycle profile as COI PCR. We used Promega's Magic PCR Preps to purify PCR products, and carried out direct sequencing with the *f*mole Cycle Sequencing Kit (Promega) and manufacturer's protocols with ^{32}P-end-labeled primers. When possible, we analyzed the same isofemale lines for both COI and H1 sequence. Unfortunately, much of the COI sequencing had been completed and a number of the isofemale lines lost before the H1 sequencing project was initiated. We are currently trying to obtain COI sequences from the Santa Cruz Island site. As a result, both COI and H1 DNA sequences were obtained for only eight lines.

RESULTS

Allozyme data from ten population samples obtained in 1992–93 are presented in table 1. Despite the fact that each of the gene loci studied is polymorphic when the total data set is considered, within-population hetero-

TABLE 1
Allelic Frequencies for Six Polymorphic Allozyme Loci in 13 Populations of *T. californicus* along the California Coast

	Pgi					*Got2*				*ME*			
Population	F*	M	MS	S	VS	VF	F	S	VS	VF	F	S	VS
PES	0.46	0.54						1.00				1.00	
SCN		1.00						1.00				1.00	
CAR		1.00						1.00				1.00	
MO		1.00						1.00				1.00	
SCI-N		0.01	0.66	0.33				1.00				1.00	
SCI-S			0.02	0.95	0.03			1.00					
CO		1.00						1.00					
PD		0.58	0.31	0.11				1.00					
FR		1.00						1.00				1.00	
AB		1.00						0.99	0.01			0.98	0.02
LB	0.02	0.79		0.19		0.40	0.60			1.00			
LJ	0.06	0.94					1.00				1.00		
SD	0.22	0.78				1.00					1.00		

	Got1					*Gpt*			*Apk2*		*Apk1*	
Population	F	S	VS	ES	SS	F	S	VS	F	S	F	S
PES		1.00					1.00			1.00	1.00	
SCN	0.03	0.97				0.25	0.75			1.00	1.00	
CAR		0.98	0.02				1.00			1.00	1.00	
MO		0.80	0.20				1.00			1.00	1.00	
SCI-N	0.58	0.42					0.07	0.93		1.00		1.00
SCI-S		1.00					1.00			1.00	1.00	
CO		1.00					1.00			1.00	1.00	
PD		1.00									1.00	
FR	0.04	0.93	0.03				1.00			1.00	1.00	
AB		0.07		0.93			1.00			1.00	1.00	
LB	0.11	0.85			0.04		1.00		1.00		1.00	
LJ	0.19	0.79	0.02				1.00		1.00		1.00	
SD		0.88	0.12				0.94	0.06	1.00		1.00	

*Allelic designations VF, F, M, MS, S, VS, ES are in order of decreasing anodal mobility. Locus designations: Pgi = phosphoglucose isomerase, Got = glutamate-oxaloacetate transaminase, ME = Nadp-malic enzyme, Gpt = glutamate-pyruvate tranaminase, Apk = arginine phosphokinase.

TABLE 2
Nei's Genetic Distances (Standard Errors) Based on Seven Allozyme Loci and Calculated with the Jacknife Method of Mueller (1979)

	SCN	CAR	MO	SCI	FR	AB	LB	LJ	SD
PES	.043 (.006)	.032 (.005)	.039 (.006)	.586 (.057)	.033 (.005)	.178 (.025)	.647 (.064)	.686 (.065)	.664 (.065)
SCN		.009 (.001)	.014 (.002)	.593 (.058)	.009 (.002)	.146 (.023)	.626 (.061)	.649 (.063)	.669 (.064)
CAR			.004 (.001)	.621 (.059)	.000 (.000)	.133 (.022)	.582 (.059)	.608 (.061)	.627 (.062)
MO				.623 (.061)	.003 (.001)	.114 (.019)	.605 (.061)	.626 (.063)	.645 (.063)
SCI					.613 (.059)	.741 (.071)	2.44 (.20)	2.62 (.28)	2.59 (.20)
FR						.127 (.021)	.586 (.059)	.610 (.061)	.632 (.062)
AB							.819 (.078)	.820 (.078)	.878 (.081)
LB								.214 (.030)	.265 (.033)
LJ									.181 (.029)
SD									

zygosity is low ($H = 0.07 \pm 0.02$, mean $\pm$ SE), and many alleles are restricted in their distribution. Calculations of Nei's genetic distance (D) based on these relatively few loci are subject to considerable error but are useful as relative measures of population differentiation and are presented in table 2. Calculated D values range from zero (FR-CAR) to 2.62 (SCI-LJ); in the latter comparison the two populations share no alleles at four of seven loci. Although based on few loci, the observed D values are approximately an order of magnitude higher than typically encountered among conspecific populations (Thorp 1983). There is a striking lack of correspondence between the geographic distance between populations and genetic distance between the same populations (figure 2).

Twenty-one COI sequences (each was 500 base pairs long) were determined from isofemale lines of *T. californicus* derived from seven geographic populations (work on the Santa Cruz Island population is now being initi-

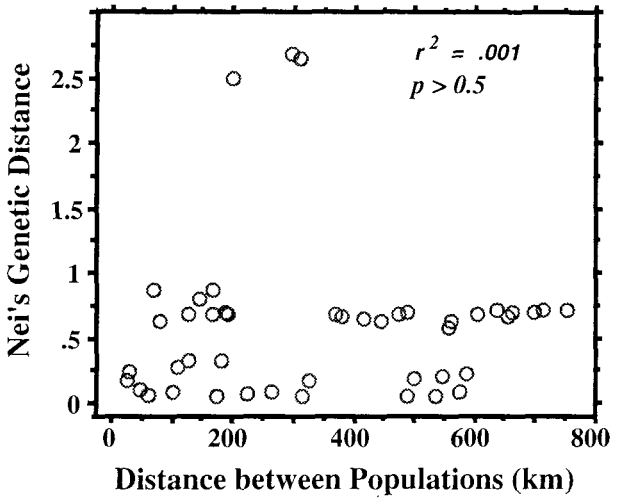

Figure 2. Relationship between geographic distance and Nei's genetic distance for all pairwise comparisons of populations in table 1. Although all points on the graph are not independent, no relationship between geographic distance and genetic distance is apparent from the allozyme data.

ated). The sequences were used to construct a maximum parsimony gene tree (Swofford 1989) that approximates the genealogical relationships among the sequences (figure 3A). Three results are apparent from the parsimony tree: (1) Extensive divergence exists between central and southern California COI sequences. Over 18% of all nucleotide sites were different in comparisons of any of the central (PES, SCN, CAR, MO) sequences to any of the southern (AB, FR, SD) sequences. (2) Although little variation was observed among isofemale lines derived from most of the natural populations, one strongly divergent haplotype was seen at SD; this cautions that additional data are needed before strong conclusions concerning population structure can be made on smaller geographic scales. (3) Bootstrap resampling of the data indicate that only the SCN population can be discriminated from other populations within a given (central or southern) region.

To assess whether or not the phylogeographic break observed in the COI data is reflected in the nuclear genome, we also sequenced approximately 500 bases of a histone H1 gene, including approximately 150 bases of the coding sequence and 350 bases of 5' flanking region (Burton and Lee 1994). In addition to the populations sampled for COI sequences, two sequences from Santa Cruz Island (SCI), two from La Jolla (LJ), and one from Laguna Beach (LB) have been obtained to date. The H1 PCR products showed a size polymorphism, with template DNA from all 11 isofemale lines from southern California sites (SD, LJ, LB, AB, FR) producing larger PCR products than that from the four central sites (MO, CA, SC, PES). PCR products from the SCI site were of the smaller size (i.e., consistent with being of the "central" type). Subsequent sequencing

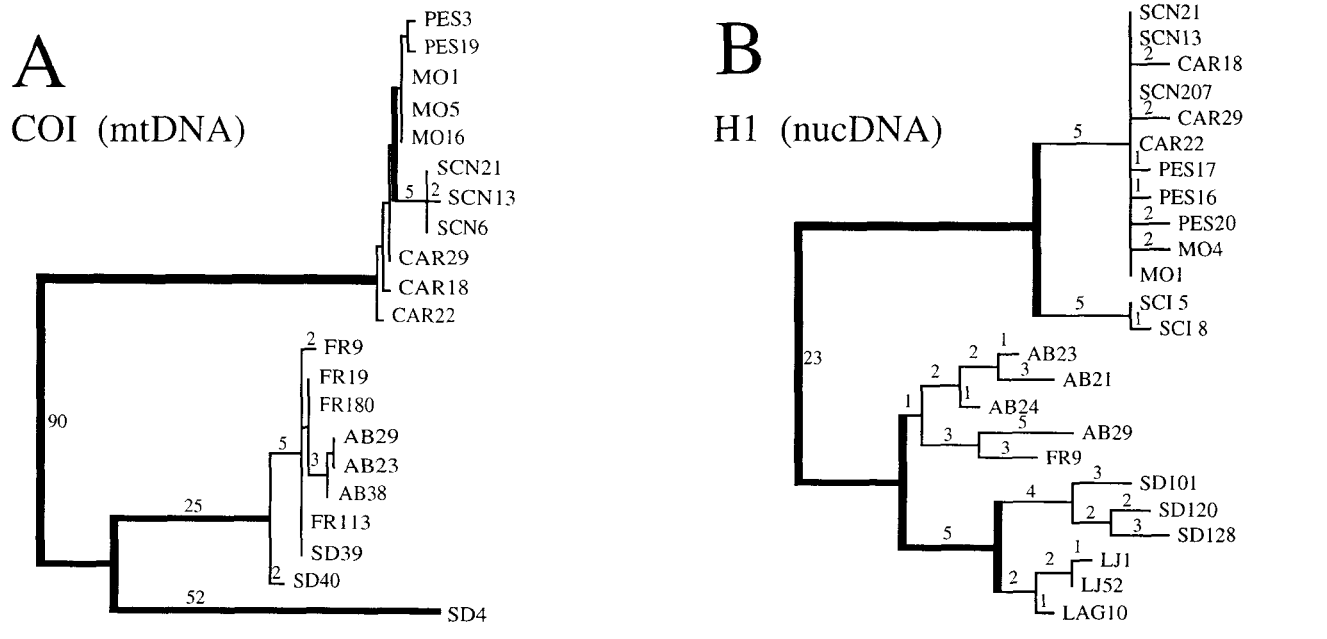

Figure 3. Genetic relationships along *T. californicus* isofemale lines. *A*, Unrooted maximum parsimony tree produced by the heuristic search procedure of PAUP 3.0r (Swofford 1989) for 21 COI sequences. Sequences are named according to source population, and numbers refer to the specific isofemale line. Branch lengths are the absolute number of nucleotide substitutions over the 500 base sequences. Tree shown is one of five equally parsimonious trees, all with similar topology. *Bold lines* indicate branches supported by bootstrap values >95%.
B, Unrooted maximum parsimony tree produced by the heuristic search procedure of PAUP 3.0r for 24 H1 sequences. Sequences are named as in *A*. Branch lengths are absolute number of nucleotide substitutions over the 425 bases sequenced (after exclusion of gaps). Tree is one of three similar, equally parsimonious trees. *Bold lines* indicate branches supported by bootstrap values >95%.

showed that two insertions (48 and 20 bases in length) in the 5' flanking region were found only in the southern samples. After these insertions/deletions are eliminated from the data set, an additional 23 of 425 bases (5.4%) distinguish between central and southern clades (figure 3B). The SCI sequences are differentiated from the central California populations, but clearly group with the central sequences in the parsimony tree; this topology is supported by 100% of bootstrap resamplings.

DISCUSSION

The Study System: *Tigriopus californicus*

The harpacticoid copepod *T. californicus* is a common inhabitant of high intertidal and supralittoral rock pools along the Pacific coast of North America, from Alaska to Baja California. The supralittoral distribution of *T. californicus* appears to result from heavy predation in the lower intertidal zone, and it is not commonly encountered in pools that harbor either fish or anemones (Dethier 1980). Restricted primarily to small ephemeral pools, *T. californicus* populations fluctuate dramatically in size; evaporative drying and extensive scouring during storms frequently lead to extinction of subpopulations inhabiting individual rock pools. The species has no resting or dormant stages capable of withstanding complete desiccation; newly refilled pools must be repopulated by immigrants. Although all life stages of *T. californicus* are free-swimming and potential dispersers, the means by which the species colonizes distant habitat is not known. Passive drifting of adults or larvae has not been documented; *T. californicus* has not (to my knowledge) been collected in plankton tows. Both larvae and adults tend to cling to the substrate in response to water turbulence, so rafting on debris washed out of inhabited pools as well as attaching to birds and crabs moving through pools are alternate means of dispersal.

Given its natural history, *T. californicus* is not representative of the ecology of species with extensive larval dispersal. However, it may provide a model system for the study of diverse benthic species that have direct development and show limited larval dispersal. In this light, many attributes of the *T. californicus* system make it particularly amenable to genetic analysis: (1) *T. californicus* is easily raised in the lab, with a generation time of about three weeks. (2) Controlled lab crosses are readily achieved, allowing formal genetic analysis of all markers employed in population studies. (3) *T. californicus* is easily collected at a variety of spatial scales, and the availability of habitat is simple to assess.

Allozymes

Although individual *T. californicus* are small (approximately 35 μg wet weight), we can consistently resolve a number of polymorphic enzyme loci on thin (0.8 mm) polyacrylamide gels. This work has demonstrated that populations inhabiting pools on a single rock outcrop are typically genetically homogeneous, whereas those separated by even short stretches of sandy beach (<500 meters) are often sharply differentiated (Burton and Feldman 1981). In fact, most of the 25 populations we have sampled along the California coast can be readily distinguished on the basis of allozyme frequencies. In many cases, alleles restricted to single populations ("private" alleles; Slatkin 1985) reach high frequency, strongly suggesting a lack of gene flow among the populations. In some cases, alleles fixed in one population have never been observed in other populations. Many of our study sites have been sampled at least five times (in some cases more than fifteen times) over periods of time extending up to 15 years; although some minor variation in allelic frequencies has been observed over this period, the geographic distribution of alleles and patterns of population differentiation have been essentially constant. For example, the Gpt^F allele has been found only in Santa Cruz County and has been consistently in the 20%–25% frequency range at the SCN site since 1979 (Burton and Feldman 1981; Burton 1986).

One striking feature of the *T. californicus* allozyme data is that, even when averaged across loci, no relationship between geographic distance and genetic distance is observed. This lack of correlation between geographic distance and genetic differentiation emphasizes a major limitation of the allozyme data: allozymes provide no phylogenetic information. When neighboring populations show one or more "private" alleles at high frequencies, it is difficult to determine whether the observed differentiation occurred *in situ* (over relatively long time periods), or if the initial immigrants colonizing the relevant geographic locales derived from already differentiated parent populations. Distinction between these hypotheses requires genealogical information. Along these lines, it is interesting to note that the SCI population appears to be equally divergent from its nearest neighboring populations to either the north or south. Was SCI colonized from northern or southern source populations? Again, resolution of this question requires genealogical information.

On the other hand, the speed and ease of allozyme analyses has allowed us to study population structure at a spatial and temporal scale that would not be practical using DNA sequencing techniques. Scoring allelic frequencies at several polymorphic gene loci with sample sizes of 50 individuals from each of ten populations can be completed in a week. The relatively few DNA sequences presented here required over a year to obtain.

Mitochondrial DNA Sequence

The most striking feature of the COI data is the great divergence between central and southern California clades. Minimum distance between sequences from the two clades exceeds 18%, a value that far exceeds any previously reported intraspecific value for a protein-encoding mitochondrial gene (Avise et al. 1987; Harrison 1989). Although we have no fossil record for establishing a molecular clock directly relevant to *T. californicus* populations, recent data on the COI gene in other crustacea yielded estimates of 2.2%–2.6% divergence per million years (Knowlton et al. 1993); at such a rate of sequence evolution, a conservative date for the split between central and southern COI clades is on the order of 7 million years. We also note that of 90 nucleotide substitutions (of the 500 bases sequenced) distinguishing the two major clades, only 3 result in diagnostic amino acid substitutions (6 amino acid residues are variable of the 165 inferred from sequence data).

A second remarkable feature of the COI data is the extreme divergence among the San Diego (SD) isofemale lines; the SD4 line differs from SD40 at 77 nucleotide sites (15.4%); notably, all these substitutions are synonymous. The existence of highly divergent mtDNA haplotypes within a population can be explained in two ways. First, it is possible that two maternal lineages have been maintained in the SD population long enough for the high level of divergence to have occurred *in situ*. The second possibility is that immigration from another population introduced divergent haplotypes into the SD population. Although neither hypothesis can be rejected, the extreme differentiation of the haplotypes argues against the former hypothesis. It seems unlikely that two lineages would have survived stochastic extinction ("lineage sorting") over millions of years in the ephemeral environment characteristically inhabited by *T. californicus* (Neigel and Avise 1986). Although more extensive within-population sampling is the subject of continuing work, the divergence at the SD site stands in marked contrast to the low levels of divergence (<1%) observed among isofemale lines from six other populations.

Nuclear DNA Sequence

An important (and perhaps unusual) feature of the H1 data presented here is the fact that no evidence for recombination between the sharply differentiated central and southern California clades has yet been observed. The simplest explanation for this lack of recombination is that the differentiation of the clades occurred allopatrically and, without subsequent gene flow, no opportunity for inter-clade recombination has existed (Burton and Lee 1994). This hypothesis seems entirely consistent with the other genetic data sets presented above. Attributes of the allozyme data (high-frequency private alleles) and the COI data (strong differentiation of central and southern clades) clearly suggest long periods of allopatric population differentiation.

The two sequences obtained from SCI suggest an answer to the question posed above concerning the origin of this population: H1 sequences from the SCI population are more closely related to those from central populations than to those from southern populations. The addition of COI sequence data may substantially strengthen support of this hypothesis. Although the SCI H1 sequences clearly group with the central clade, they are clearly differentiated from other members of the clade, as would be expected from the extensive allozyme differentiation between SCI and other central California populations.

Allozyme versus DNA Sequence Data

The relative value of the different types of genetic data discussed above depends primarily on the specific questions being asked. Many questions, some ecological and some evolutionary, can be addressed by population structure data. Neither allozyme nor sequence data alone can efficiently answer all commonly posed questions, although obviously any allozyme differentiation could ultimately be revealed at the DNA sequence level if the appropriate gene is sequenced.

One question of primary interest to both ecologists and fisheries managers is, "To what extent do geographically separated populations represent separate gene pools?" Analysis of population differentiation is inherently a one-sided experiment; i.e., although finding genetic differences between populations can often lead to strong conclusions, a lack of differentiation is typically ambiguous. This is because analysis focuses on only a tiny portion of the genome. Populations that appear to be identical on the basis of one sample of gene loci may later be found to be sharply differentiated at other loci. Because numerous loci can be surveyed quickly and with relative ease, allozyme studies remain a method of choice in assessing differentiation of geographic populations. In the *T. californicus* system, we have found allozymes to be remarkably sensitive in discriminating populations. Using from five to eight allozyme polymorphisms as markers, we can distinguish the great majority of over 20 California coast populations that we have studied over the past 15 years. In contrast with the results observed in a number of other species, most genetic diversity in *T. californicus* is revealed by between-population comparisons; heterozygosity within populations is relatively low. This might easily be explained by frequent population bottlenecks, as would be expected in an ephemeral habitat. However, closer inspection of the data adds one important feature: bottlenecks may explain why heterozygosity is low, but do not explain

the existence of high-frequency "private" alleles. Such a pattern of variation necessarily leads to the conclusion of highly restricted gene flow (Slatkin 1985).

Identification of discrete populations for ecological analysis or management purposes requires only that sufficient levels of genetic polymorphism be available for study. Morphological, allozyme, or DNA markers with simple Mendelian inheritance are potentially of equal value for addressing questions of gene pool continuity. From this perspective, the relative merits of allozyme and DNA approaches are apparent: allozymes are cheaper and faster, whereas DNA necessarily possesses a greater wealth of genetic variation. When beginning to analyze a new species or set of populations, some effort at the level of allozymes would seem a prudent methodological choice. If sufficient allozyme polymorphism is not found, a search for DNA sequence variation would be a next step. Once polymorphic nucleotide sites are identified, efficient methods for discriminating genotypes at particular nucleotide sites can be developed (see, e.g., Banks and Hedgecock 1993).

As mentioned above, two classes of hypotheses can be proposed to explain sharp differentiation of neighboring populations: (1) the populations were initially similar but have diverged via either random drift or selection *in situ* over a sufficient period of time to allow establishment of new mutant alleles; or (2) the original colonists were derived from already differentiated populations, so the present genetic differentiation simply reflects the indeterminate nature of the colonization process. Although conclusively demonstrating population differentiation, allozyme data alone cannot discriminate between these two very different explanations for the origin of the differentiation. Here, DNA sequence data clearly complement our allozyme studies. For example, the strong differentiation of the AB and FR populations (nearly fixed on alternate alleles at the *Got1* locus) appears to be the result of *in situ* differentiation, since COI and H1 DNA sequences from these populations are more closely related to each other than to those from any other population. In contrast to the lack of relationship between geographic distance and allozyme genetic distances, the DNA sequence data show clear geographic structure, with neighboring populations more similar than geographically distant populations.

When allozyme and DNA sequence data for the *T. californicus* system are compared, one striking discrepancy is immediately apparent: allozyme data suggest that Los Angeles area populations (AB and FR) are genetically similar to central California populations, whereas sequence data show exceptionally strong divergence between these same sets of populations. Although such discordance may provide insights into the natural history of conspecific populations (e.g., Reeb and Avise 1990; Karl and Avise 1992; Burton and Lee, in press), it simply emphasizes the fact that only weak inferences can be made from apparent population homogeneity. In *T. californicus*, DNA sequence data has dramatically changed our understanding of population structure by revealing a regional pattern of genetic variation that the allozyme data lacked. The geographic match between the two sets of sequence data suggests that population divergence has proceeded for enough time that concordant lineage-sorting of mitochondrial and nuclear genes has taken place (Neigel and Avise 1986; Avise and Ball 1990). The phylogeographic break in the historic distribution of the species lies somewhere between LA and the Morro Bay study sites, a region that includes Point Conception, a widely recognized zoogeographic boundary (Valentine 1966). The SCI population, lying south of Point Conception itself, appears to be derived from more northern populations based on H1 sequence data. However, the allozyme data show that SCI is highly divergent from populations to either the north or the south, indicating that the colonization of SCI occurred in the distant past and no ongoing gene flow is taking place. The genetic isolation of Santa Cruz Island was previously reported for the embiotocid fish, *Damalichthys vacca* (Haldorson 1980).

In summary, the *T. californicus* studies show that comparisons between allozyme and DNA sequence data can reveal a variety of surprises. First, despite the fact that protein electrophoresis is a relatively low-resolution technique compared to DNA sequencing, populations were generally more easily distinguished by allozyme data than by sequence data. Other molecular techniques, such as allele-specific PCR, could undoubtedly be developed to distinguish the populations based on nucleotide substitutions, but allozyme methodology has proven sufficient (and efficient) for simply demonstrating genetic isolation of populations in the *T. californicus* system. DNA sequence data, however, in revealing unprecedented levels of divergence between conspecific populations, provide a historical framework within which the allozyme data can be more fully understood.

ACKNOWLEDGMENTS

This work was supported by NSF grants BSR-8741308, DCB-8811227, and IBN-92-96185. I thank Cindy Lau and Linh Ngo for laboratory assistance.

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INTRASPECIFIC STRUCTURE OF THE NORTHERN RIGHT WHALE DOLPHIN (*LISSODELPHIS BOREALIS*): THE POWER OF AN ANALYSIS OF MOLECULAR VARIATION FOR DIFFERENTIATING GENETIC STOCKS

ANDREW E. DIZON, CARRIE A. LEDUC[1], AND R. GENE LEDUC
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

The northern right whale dolphin (*Lissodelphis borealis*) has experienced very high levels of fishery-induced mortality in international high-seas, large-scale driftnet fisheries, from about 38°N to 46°N, and 171°E to 151°W. Assessing the impact of these mortalities is difficult, however, because of the possible existence of a coastal population off California and the Pacific Northwest that is separate from offshore populations. To obtain quantitative measures of reproductive isolation between putative populations, a portion of the control region of the mitochondrial DNA (mtDNA) genome was sequenced in 65 geographically dispersed individuals, then analyzed in a nested ANOVA format. No evidence of geographically concordant population structuring was apparent. In addition, a Mantel test, examining pairwise correspondence between geographic and genetic distances among samples, failed to detect any evidence of isolation by distance. Because negative data such as these are often used in management decisions, a power analysis was conducted to determine the probability that a survey of comparable size would yield statistically significant results under a hypothetical but likely level of divergence between "bona fide" stocks. The analysis yielded an estimate of the rate of making a type II or beta error of about 10%.

RESUMEN

El delfín liso *Lissodelphis borealis* ha sufrido niveles de mortalidad muy alta en alta mar (alrededor de 38°N a 46°N y 117°E a 151°W) inducidos por una pesquería a gran escala que usa redes de deriva. Es difícil evaluar el impacto de esta mortalidad debio a que posiblemente existen poblaciones costeras frente a California y el Pacífico Noroeste que están separadas de las poblaciones de mar adentro. Con el fin de cuantificar el aislamiento reproductivo entre las supuestas poblaciones se obtuvo la secuencia de una porción de la región central del genoma del ADN de la mitocondria (ADNmt) en 65 individuos procedentes de varias regiones; estos datos se analizaron usando un análisis de varianza anidado. No se encontró evidencia de una estructura de la población con concordancia geográfica. Aun más, la prueba de Mantel, que examina correspondencia aparejada entre distancias geográficas y genéticas entre las muestras, tampoco detectó evidencia de aislamiento asociado al distanciamiento espacial entre los individuos. Debido a que datos negativos como los mencionados antes se usan para hacer decisiones en le manejo de las pesquerías, hicimos un análisis de potencia estadística; determinamos la probabilidad de que un reconocimiento de tamaño similar produzca resultados estadísticamente significativos con niveles de divergencia hipotéticos pero plausibles entre stocks (suponiendo diferenciación entre éstos). A partir del análisis, se estima que la frecuencia de producir errores del tipo II o beta es de alrededor 10%.

INTRODUCTION

Although the northern right whale dolphin (*Lissodelphis borealis*) is the most common cetacean species in the bycatch of the high-seas, large-scale driftnet fishery in the North Pacific (Hobbs and Jones 1993), its intraspecific (stock) structure is unknown. A separate coastal population off California and the Pacific Northwest may exist, but there are insufficient data to allow a rigorous test of this hypothesis even though the species has been the focus of considerable biological effort and expense.

Yet it is axiomatic that knowledge of the intraspecific (stock) structure is a critical component in determining the status and subsequent management of species impacted by human activities; stock, not species, is the unit on which management parameters such as optimal sustainable population and allowable biological removal estimates are based. Both the Marine Mammal Protection Act and the Endangered Species Act direct management efforts at taxa below the species level. The concern of the responsible manager is that if stock structure is arbitrarily subdivided too finely, population estimates and allowable removal levels may be so small that local fisheries may be unnecessarily closed down. On the other hand, if a species is too coarsely subdivided, evolutionarily significant local populations may be depleted or destroyed.

Knowledge of stock structure comes from four classes of information: distribution, demography, morphology, and genetics (Waples 1991a, b; Dizon et al. 1992). What

[1]Current address: Sequana Therapeutics, 11099 North Torrey Pines Road, La Jolla, CA 92037

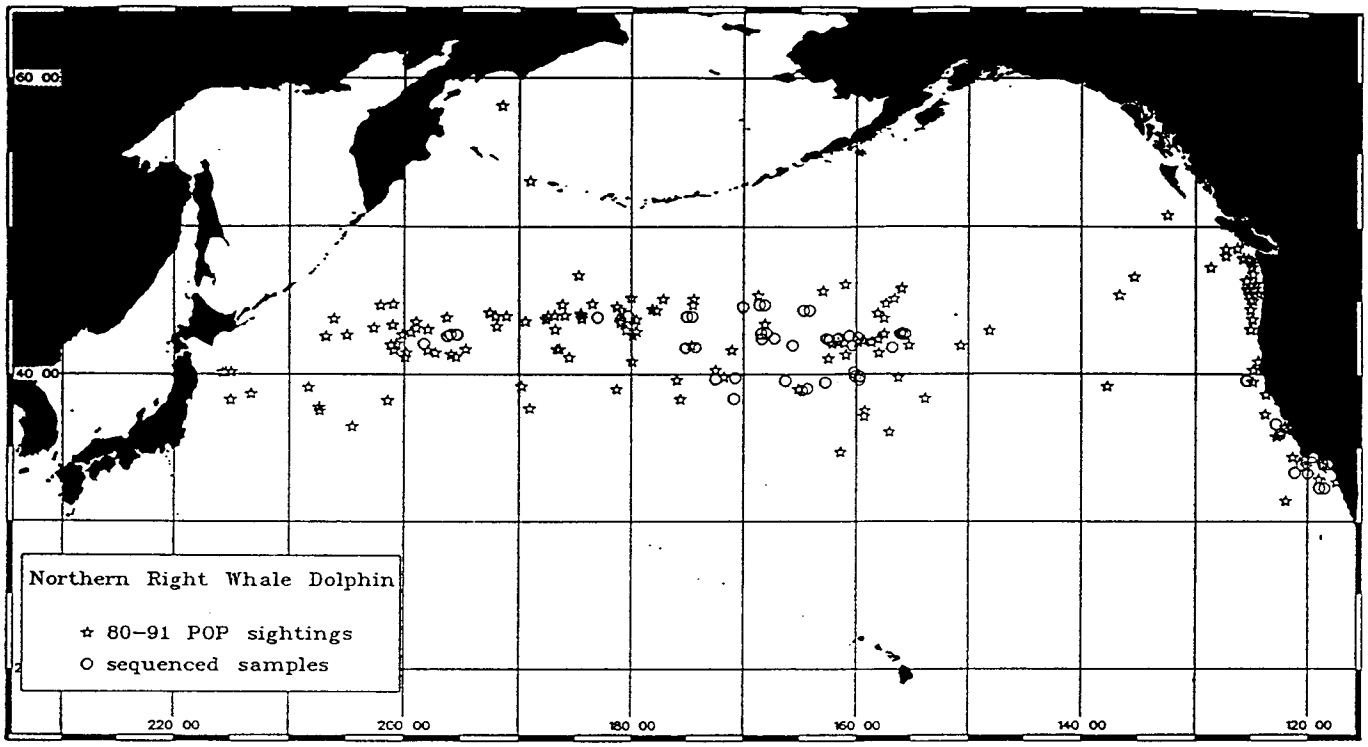

Figure 1. High seas sightings (*stars*) of northern right whale dolphins (*Lissodelphis borealis*). Data from the National Marine Mammal Laboratory's Platform of Opportunity Program (POP), 1980–91. *Circles* are sequenced sample collection locations.

few data are available from these sources for *L. borealis* are summarized in Leatherwood and Walker (1979), Baird and Stacey (1991), and Ferrero et al. (1993). Save for some distributional data that indicate an area of reduced density separating the potential coastal population and the offshore one (figure 1), there is no information in the literature regarding whether *L. borealis* exists as a single, panmictic population or is subdivided into two or more breeding populations. Although the tendency of delphinids to subdivide into coastal and offshore populations is well known (see Perrin et al. 1985; Dizon et al., in press), the stock structure of this species is an open question.

About 6,700 driftnet operations were observed between 1989 and 1990 (Hobbs and Jones 1993), and biological samples from the cetacean bycatch were collected. These, as well as samples collected off the U.S. west coast from beach-cast animals, cross-bow biopsies of bow-riding animals, and fishery mortalities were used in a molecular analysis of mtDNA.

Analyses based on molecular information derive their power from two properties (Vigilant et al. 1991): (1) the evolution of the molecule is dominated by selectively neutral substitutions, and (2) the changes occur at a reasonably constant rate, at least within fairly closely related taxa. The mtDNA molecule has the features of neutral and rate-constant mutation (Moritz et al. 1987). In addition, it is haploid and maternally inherited, eliminating recombination effects (Giles et al. 1980). These properties greatly simplify data analysis, and the relatively high rate of evolution (Moritz et al. 1987; Hoelzel et al. 1991) allows resolution of closely related forms. Analyses of mtDNA, primarily restriction fragment length polymorphism analyses, but also including direct sequencing, have been extensively used in the last several years to study intraspecific structure of marine mammals (e.g., see Baker et al. 1985, 1990, 1993; Lint et al. 1990; Dizon et al. 1991; Rosel 1992; Dowling and Brown 1993; Hoelzel et al. 1993).

Here we report on the results of a study examining the genetic diversity within and among three putative populations of *L. borealis* sampled from locations spanning their known range. We conduct a power analysis to estimate the probability of making a type II or beta error—i.e., incorrectly accepting the null hypothesis that the population is not subdivided into stocks. From a conservation standpoint, the costs of making such an error are perhaps higher than the costs of making a type I error—incorrectly rejecting the null hypothesis—because of the potential for destroying an undetected but evolutionarily significant population component of the species. Using genetic diversity studies from other species, we attempt to estimate the minimum genetic differences that separate closely related but "bona fide" stocks, and we use that estimate to determine the statistical power of our current study.

MATERIALS AND METHODS

Fifty-two individuals from the bycatch of the high-seas driftnet fisheries were obtained by National Marine Fisheries Service (NMFS) observers from the National Marine Mammal Laboratory (NMML). Of these, 16 were from west of the dateline (figure 1). The majority of samples obtained from NMML were clustered to the east of the dateline but west of 155°W latitude; of those, we sequenced 36. Note that the classification of animals east and west of the dateline into separate populations is arbitrary and not supported by any significant hiatus in distribution. We also obtained 13 samples from coastal U.S. waters. These samples came from incidental kills collected by fishery observers from Southwest Region (SWR, NMFS) accompanying set- or drift-net boats, dead beach-cast animals collected under the auspices of the California Marine Mammal Stranding Network organized by the SWR, or projectile biopsies of bow-riding dolphins collected under NMFS permit from a research vessel.

Our specific DNA procedures were as follows (see also Rosel 1992): tissue samples were preserved and stored in a saturated NaCl solution of 20% DMSO at room temperature (Amos and Hoelzel 1991). We extracted total cellular DNA (nuclear plus mtDNA) using established protocols (Hillis and Moritz 1990) modified for our particular needs. Double-stranded (symmetric) PCR amplification of approximately 0.1 μg template (sample) DNA was carried out in 100 μl reactions by means of standard reaction conditions and reagents supplied with the GeneAMP kit (Perkin Elmer Cetus, Inc). Chain elongation was initiated with the addition of 30 ρmoles of primers complementary to regions up- and downstream of the region of interest, the 5' end of the control region of the mtDNA genome—about a half of the control region. The upstream primer (anneals to heavy strand) was biotinylated at its 5' end to facilitate immobilization of the amplicon for later procedures. This primer is the so-called "universal primer" (slightly modified from Kocher et al. [1989] by Rosel [1992]). The downstream primer (anneals to light-strand), designed also by Rosel, anneals near similarity block B, a conserved region within the control region (Southern et al. 1988).

We used streptavidin-coated magnetic beads (Dynal Inc.; Hultman et al. 1989) to clean PCR-amplified samples and make them single stranded. The extremely high affinity of the streptavidin for the biotin moiety on the 5' end of the heavy-strand primer allowed the immobilization of the double-strand amplicon. A neodynmium-iron-boron permanent magnet was used to sediment the beads against a side of a 1.5 μl microcentrifuge tube for washing to remove unincorporated reaction products and for removal of the heavy strand itself by denaturization and subsequent elution.

We performed sequencing reactions on the light-strand DNA only, using standard conditions and reagents as supplied with the Sequenase, Version 2.0 sequencing kit (United States Biochemical Corporation) and 5 μCi of [α-^{35}S]dATP. Two internal primers, producing overlapping sequences, allowed us to routinely sequence about 500 bp's, about 80% of the amplicon. The sequencing reactants were then electrophoresed on 6% polyacrylamide wedge gels (0.4 to 0.8 mm) from 2 to 6 hours and read from autoradiographs exposed to the vacuum-dried gels. The individual sequences were aligned by eye in a spreadsheet format. Sequences will be submitted to GenBank.

Sequences were analyzed by means of distance methods, as opposed to parsimony methods. For our studies, parsimony methods were usually inappropriate for analyses of intraspecific structure. The number of taxa (individuals) far exceeded the number of phylogenetically informative sites (Stewart 1993), and a very large number of equally parsimonious trees were found, indicating the underlying lack of resolution of parsimony approaches for revealing intraspecific structure (Excoffier and Smouse 1994).

The genetic or evolutionary distance separating each pair of sequences was estimated using the Tamura-Nei method as implemented in Kumar et al.'s (1993) computer package, MEGA. The authors recommend this method as especially appropriate for mtDNA sequences. The derived matrix of 2,080 ($N[N\text{-}1]/2$ where $N = 65$) pairwise genetic distances was examined for evidence of a geographic structure, i.e., concordance between genetic distance and geographic strata, by means of an analysis of variance method modified for use with molecular sequence data (Excoffier et al. 1992). We used the computer program described by Excoffier et al. (AMOVA, analysis of molecular variance) and furnished by the senior author. The linear model employed assumes that individuals are arranged into populations, and populations nested into groups, defined by nongenetic criteria (sampling location). The program computes estimates of variance components and *F*-statistic analogues, designated Φ-statistics. The Φ-statistic is the correlation of random haplotypes drawn from within a stratum to random haplotypes drawn from among all the strata (Excoffier et al. 1992). The method also employs resampling methods to test the significance of the variance components and statistics, thus avoiding assumptions of normality. The method does not require specific assumptions regarding the evolution of sequences and, while not as powerful at detecting population subdivision as more rigorous models (e.g., Takahata and Palumbi 1985), is certainly more robust.

To ascertain if there was evidence of isolation by distance, we employed a Mantel test for matrix corre-

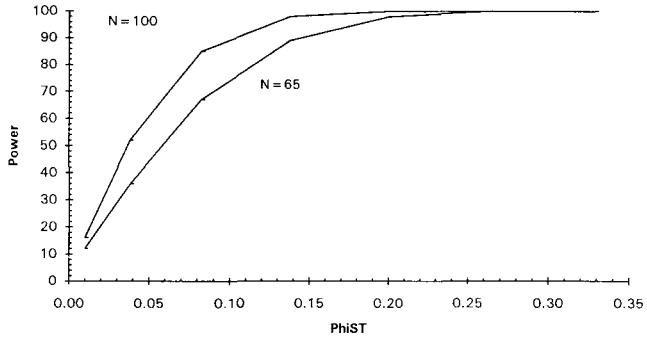

Figure 2. Power of an F (Φ) test at $\alpha = 0.05$ and 1 d.f. for a sample size of 100 and 65 (Cohen 1988). PhiST = Φ_{ST}.

spondence as implemented in the NT-SYS package (Rohlf 1990). A matrix of pairwise genetic distances was compared with a matrix of pairwise geographic distances. The geographic distances between samples were calculated as great circle distances in nautical miles. This program plots one matrix against the other in an element-by-element fashion and computes the Mantel statistic, Z, to measure the degree of relationship.

$$Z = \sum_{i,j}^{n} x_{ij} y_{ij},$$

where X_{ij} and Y_{ij} are the off-diagonal elements of matrices X and Y. If the matrices show similar relationships, Z will be larger than would be expected by chance alone. The Mantel test as implemented also uses resampling methods to test the significance of the variance components and statistics.

The variance estimates and the Φ-statistics from the AMOVA were used in a subsequent power analysis (Cohen 1988). We assume an alpha level of 0.05 with one degree of freedom and use the "Power of F" test tables in Cohen (1988) to construct a graph of the relationship between Φ_{ST} and power for two sample sizes ($N = 65$, $N = 100$; figure 2).

RESULTS

A total of 400 base pairs were sequenced in the control region plus the entire proline and a small portion of the threonine tRNA genes. The latter regions were eliminated from subsequent analysis. Of the 65 animals sequenced, one group of 5 and one group of 3 had identical haplotypes, and both groups contained animals from the coastal and the offshore populations. Seven other pairs each shared a unique sequence. For three pairs of the seven, both animals were sampled from the same school, so there is a potential that there were first- or second-order relations, but in the other four pairs, each member came from widely separate locations.

Of the 400 base pairs sequenced, there were 73 variable sites and 3 variable insertion/deletion events. Sixty-eight of these sites contained only transitional changes; three sites showed transversional changes, and two sites exhibited both. Average pair-wise Tamura-Nei genetic distances for the total sample were 0.020, or 2% ($N = 65$); for the inshore sample, 0.020 ($N = 13$); for the offshore sample east of the dateline, 0.021 ($N = 36$); and for the offshore sample west of the dateline, 0.022 ($N = 16$).

TABLE 1
ANOVA on Pairwise Genetic Distances between *Lissodelphis Borealis* mtDNA Sequences Stratified into Three Putative Populations: Inshore, Offshore East of the Dateline, and Offshore West of the Dateline

	Observed partition			
Component	Variance	% total	p	Φ-statistic
Among	0.000695	0.66	0.14	$\Phi_{ST} = 0.007$
Within	0.010388	99.34		

To analyze the effect of the relationship of geographic sampling location and genetic variation, we stratified the sequenced sample into three putative geographic populations: inshore, offshore west of the dateline, and offshore east of the dateline. The genetic distance measurements were then analyzed with the AMOVA program (table 1). The value p is the probability of having a more extreme variance component and Φ-statistic than the observed values by chance alone. The significance of the variance component and Φ-statistic is tested by permuting individuals to random populations. The within-population effect is tested by permuting individuals across populations without regard to either their original population or region.

It is apparent from table 1 that the main effect is due simply to variability among individual pairwise measurements and that there is no reduction in variance from stratification into populations. No other geographic stratifications of the data, including simple offshore and onshore populations, nor elimination of males from the analysis resulted in any significant effects. These results are consistent with lack of geographic structuring of the population.

Because of the disparity in size of geographic areas of the sampled populations (the offshore region spans in its east-west axis 1,862 n.mi., whereas the California region spans only 480 n.mi.), the AMOVA analysis may mask evidence of isolation by distance. Many offshore individuals are separated by larger distances than California samples are from some of the far eastern offshore samples. To examine this masking, we used the Mantel test (Rohlf 1990) to compare the same pairwise matrix of genetic distances used in the AMOVA analysis to a matrix of pairwise geographic distances. No correlation existed between genetic and geographic distance (normalized Mantel statistic $Z = -0.005$). Of 1000 permuted matrices, 49% demonstrated a larger Z value than the sample matrices, 51% a smaller value.

DISCUSSION

The degree of nucleotide variation within *Lissodelphis borealis* is somewhat higher than in other populations examined in our laboratory. In the portion of the control region sequenced, we found 76 variable sites. In the same region, Rosel (1992) found 43 variable sites in her sample of 29 *Delphinus delphis*, and those included individuals from two different ocean basins and two different morphotypes (long-beaked and short-beaked) that display fixed genetic differences and may be separate species. In her study, she estimated a genetic diversity of 1.2% for long-beaked samples and 1.6% for short-beaked samples.

For *Lissodelphis borealis*, the within-population diversity for the total sample was about 2.1% and not significantly different when calculated for either the offshore or California population alone. Neutral theory predicts a positive correlation between genetic diversity and population size (although this relationship can be profoundly altered by historical demography; Avise et al. 1988). The similarity in genetic diversity in the offshore and inshore samples is consistent with the hypothesis that the two samples were drawn from the same population or, alternatively, from populations of the same size. However, population abundance in the offshore region has been estimated to be about an order of magnitude larger than in the inshore region (Buckland et al. 1993; Barlow, in press; Barlow and Forney, in press).

Sequence divergence between *L. borealis* and other dolphin species seems reasonable when compared to values for closely related species pairs obtained in other similar studies. Sequence divergence between our study species and *Delphinus delphis* (Rosel 1992) is 6.7% and between our study species and *Stenella attenuata*, 7.5% (our data). Rosel (1992) estimated sequence divergence between *S. attenuata* and *D. delphis* of 6.0%.

Although the results of both the AMOVA and the Mantel tests, as well as the similarity of the genetic diversity values between the putative populations, are consistent with a lack of intraspecific structuring in *L. borealis*, it is negative evidence: Can a conservation manager develop policy from it? In other words, are these negative results of any value in deciding if the species should be managed as a single panmictic population or separately as an inshore and an offshore population? This is an important question because the putative offshore population was subject to high levels of fishing mortality and may well be depleted (Hobbs and Jones 1993), and the inshore population is currently exploited, albeit at a very low level (Forney, in press).

Mindful of the conservation dangers of incorrectly accepting the null hypothesis that the population is not subdivided into stocks, we attempted to estimate the power of our analysis to yield statistically significant results if the H_0 was indeed false. For this, we assume that given taxa levels, at least among closely related forms, are separated by roughly similar relative genetic distances; the higher the taxa level, the greater the genetic distance. If genetic distances are calculated from equivalent data sets, studies of genetic divergence between known stocks may be, at least as a first approximation, a way to "calibrate" stock differentiation, i.e., to estimate "effect size" (Cohen 1988).

We did this by determining the Φ_{ST} values obtained when comparisons are made of "bona fide" stocks examined experimentally in the same way as in our present study. However, here the reasoning becomes somewhat circular in that bona fide stocks are defined at least in part when they show statistically significant ($\alpha = 0.05$) Φ_{ST} values, but the biology and distribution of the two following stocks used to calibrate effect size make them likely calibration candidates. We use the Black Sea short-beaked common dolphins and eastern tropical Pacific (ETP) short-beaked common dolphins (Rosel 1992), $\Phi_{ST} = 0.15$, and the exclusively Washington–central California clade of northwestern Pacific harbor porpoise, which can be geographically separated into a northern and southern stock, $\Phi_{ST} = 0.18$ (Rosel 1992, and additional unpublished data from our laboratory). The harbor porpoise stocks are more differentiated than the common dolphin ones, although the common dolphin pair is clearly isolated by its extreme geographic separation. The harbor porpoise pair are less obviously separate stocks, but harbor porpoise are exclusively a coastal species, and recent contaminant analyses indicate little exchange between the two geographic regions (Calambokidis and Barlow 1991).

The question remains, however, is $\Phi_{ST} = 0.15$ a reasonable level to distinguish between biologically significant subdivisions and merely statistically significant ones? Although 0.15 is certainly arguable, it is not unreasonable to assume that some cutoff value for Φ_{ST} exists. The alternative is that any statistically significant value for Φ_{ST}, no matter how small, is evidence for restrictive gene flow, and any evidence of restrictive gene flow would be reason to subdivide a population for management purposes. This alternative would be a difficult one upon which to base management because no natural populations are likely to exhibit true panmixia. This would also mean that all genetic tests of stock have inherently low power because if the effect size for Φ_{ST} approaches zero, then the required sample size approaches infinity.

Rejecting the alternative, we for the moment consider the minimum value expected for Φ_{ST} for similar mtDNA analyses among similar taxa to be about 0.15. Then the statistical power of our present study ranges from 0.90 to 0.95 (figure 2). Put another way, the rate

of failing to reject a false null hypothesis of panmixia is 10%.

However, making a decision regarding stock structure of a species is a subjective one requiring considerable experience in order to weigh data from the four broad classes of information to infer the existence of evolutionarily significant populations, characterized by unique, adaptable but unmeasurable, genetic variation. In this study, genetic information from a neutral gene was sought as a proxy for evidence of adaptable population differentiation, and, like other biological information (Leatherwood and Walker 1979; Baird and Stacey 1991; and Ferrero et al. 1993), yielded no indication of population subdivision. And at the same time, we note that the power of our study was reasonably high.

But the validity of the interspecific calibration of stock differentiation, as well as the relatively small size of the coastal sample relative to the offshore sample size, warrants caution in accepting the null hypothesis of a single, panmictic stock for the northern right whale dolphin on the basis of the relatively high estimated power. In addition, an international moratorium on high-seas, large-scale driftnet fishery has reduced the urgency for such information. Perhaps the most important point of the study is the importance of considering power in stock designation studies. The nature of conservation management, with its need to balance conservation and economic interests, gives increased weight to negative results, which are usually dismissed in more academic investigations.

ACKNOWLEDGMENTS

We wish to acknowledge NMML (and especially Linda Jones and Rod Hobbs), Susan Chivers, and Robert Pitman for samples, as well as Kelly Peltier for DNA extractions, Tim Gerrodette for assistance with the power analysis, and Cristi Lux and Sean Costa for extraction and sequencing of some recently acquired samples.

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MARINE BIOLOGICAL INVASIONS AS MODELS OF DISPERSAL: TRACKING SECONDARY SPREAD AND INTROGRESSIVE GENE FLOW

JONATHAN B. GELLER
Department of Biological Sciences
University of North Carolina at Wilmington
Wilmington, North Carolina 28403

ABSTRACT

A major limitation of genetic approaches to the study of ongoing dispersal is that site- or population-specific markers are rarely available. Over spatial scales that encompass transport of propagules, newly generated neutral polymorphisms will have been spread by prior dispersal. Marine biological invasions provide an alternative approach to the study of larval dispersal in two ways. First, primary invasions generally occur in one or few sites. The sources of recruits in subsequent range extension can therefore be traced. Second, invading species can inject novel genetic markers into native populations when hybridization is possible. Similarly, when the distribution of native and invading species overlaps narrowly, dispersal can be traced by the movement of hybrid genotypes from the hybrid zone. Dispersal of the invading barnacle *Elminius modestus* in Great Britain, the crab *Carcinus maenas* in California, and the green alga *Codium fragile* in New England are examples of the first approach. The unidirectional introgression of the mitochondrial genome of the native northern mussel *Mytilus trossulus* into invading populations of *Mytilus galloprovincialis* in southern California is an example of the second approach. Marine biological invasions are increasing in frequency and in these ways provide population biologists and geneticists with useful model systems.

RESUMEN

Una de las limitantes mas importantes del estudio de la dispersión utilizando enfoques genéticos es que raramente se encuentran marcadores genéticos específicos, de sitios o de poblaciones. En escalas espaciales que abarcan el transporte de los disemínulos, los polimorfismos neutrales recientemente generados habrán sido diseminados por eventos de dispersión previos. Las invasiones biológicas en el medio marino proveen un enfoque alternativo al estudio de la dispersión; hay dos posibilidades. Primero, las invasiones empiezan generalmente en uno o pocos sitios, y las fuentes de reclutas pueden ser rastreadas después de una extensión del rango. Segundo, las especies invasoras pueden inyectar marcadores genéticos nuevos a las poblaciones nativas (siempre y cuando exista la posibilidad de hibridación). De la misma manera, cuando las especies nativas e invasoras traslapan de una manera marginal, la dispersión puede ser rastreada por el movimiento de genotipos híbridos provenientes de la zona híbrida. El primer enfoque es ejemplificado por la dispersión del cirripedio invasor *Elminius modestus* en Gran Bretaña, el cangrejo *Carcinus maenas* en California y el alga verde *Codium fragile* en Nueva Inglaterra, y el segundo por la introgresión unidireccional del genoma de la mitocondria del mejillón norteño nativo *Mytilus trossulus* en la población invasora del *Mytilus galloprovincialis* en el sur de California. Las invasiones biológicas en el medio marino han incrementado su frecuencia, y tal como se discutió anteriormente, proveen sistemas modelo útiles a los biólogos de poblaciones y genetistas.

INTRODUCTION

Dispersal is a key factor in the dynamics of marine populations because large numbers of marine species have planktonic life-history stages. Local populations are influenced by import and export of propagules, and it is insufficient to study local production and mortality. For this reason, there is great current interest in determining the fate of locally produced propagules and the source of recruits. Import and export of potential recruits will depend on transport mechanisms that operate over appropriate spatial scales (e.g., Farrell et al. 1991; Roughgarden et al. 1991).

Because variation in nucleic acids can resolve differences at individual, population, and species levels (Hillis and Moritz 1990), there has been much optimism that DNA-related approaches will allow population ecologists to uncover the sources of recruitment into local populations. However, a major limitation of genetic approaches to the study of ongoing dispersal is that site- or population-specific genetic markers are rarely available. Logically, newly generated neutral polymorphisms will have already been spread by prior dispersal over spatial scales that encompass transport of planktonic propagules. Current distributional patterns of genetic markers may indicate historical limits to dispersal (Avise et al. 1987) at large geographic scales, but will not provide sufficient resolution to discern patterns of dispersal among demographically linked populations. Direct oceanographic studies of movements of water masses offer one alternative to genetic approaches, but necessarily make simplifying assumptions about the behavior of larvae

(e.g., depth distribution and migration, duration of larval phase, time to competence to settle, etc.) that may vary in space, time, or across taxa. In this paper, I propose that marine biological invasions provide an alternative approach to the study of dispersal.

Marine biological invasions are the arrival and establishment of marine organisms in geographic regions where they were previously absent (Carlton 1985, 1987, 1989). In historical times, most marine invasions have been human-mediated, and various modes of transport or release have been involved, including the hulls of ships, releases of aquarium specimens, and releases of aquaculturally important species and their epibionts (Carlton 1985, 1989). Today, the most important mode of invasion is untreated seawater used as ballast in ocean-going ships (Carlton 1985; Williams et al. 1988; Carlton and Geller 1993). Ships routinely take seawater into dedicated tanks and holds for extra weight and stability. This water is unprocessed, and contains virtually all organisms in the water column at the time of ballasting that can pass through a coarse sieve (ca. 2 cm), including the larvae of larger organisms. A recent study by Carlton and Geller (1993) showed that ballast water arriving in Oregon from Japan in 159 ships over a five-year period contained all major marine phyla, with the absence of sponges and ctenophores (the latter have now been observed in ballast water [J. T. Carlton, pers. comm.]). A minimum of 367 distinctly identifiable taxa were observed, with molluscs, polychaetes, copepods, cirrepedes, and diatoms among the most abundant and most frequently released taxa. Because ballast water is carried from port to port, organisms can be entrained into a ship in coastal or estuarine waters, transported hundreds to thousands of kilometers (often to another continent), and released into other coastal or estuarine waters. In this way, natural biogeographic barriers are breached, and organisms may find themselves in environments physically and chemically similar to their home range.

Four characteristics of ballast-water-mediated transport make invasions an attractive alternative for the study of larval dispersal, because they make it possible to track range expansion of invading species, and to track genes introgressing into native populations. (1) Because of the association with shipping, initial invasions generally occur in one or few sites (ports). Therefore, subsequent range extensions of invading species can be easily traced to specific sources. (2) A broad taxonomic spectrum of marine organisms is transported in ballast water (Carlton and Geller 1993), so invading species that are similar to native species in terms of larval biology and reproductive phenology may be selected for study. (3) Invading species can inject novel genetic markers into native populations when hybridization is possible. Similarly, when the distribution of native and invading species overlaps narrowly, dispersal can be traced by the movement of hybrid genotypes from the hybrid zone. (4) Marine biological invasions appear to be increasing in frequency (Carlton et al. 1990; Carlton and Geller 1993). Thus if each invasion is considered an "experimental" release, new invasions serve to replicate the dispersal experiment.

In the following section, I first discuss three examples of range extension from an area of primary invasion to illustrate the utility of this approach to the study of dispersal patterns. Next, I discuss the results of current research on the spread of the mitochondrial genome of a native species into allopatric populations of an invading species through a narrow hybrid zone.

RANGE EXTENSION OF INVADING SPECIES

Elminius modestus

Scheltema and Carlton (1984) summarize the history of invasion and spread of the Indo-Pacific barnacle *Elminius modestus* into Great Britain and Europe. *Elminius* was not known in Britain before 1940, and Crisp (1958) suggests that it was introduced during World War II. Between 1940 and 1945, this species became established in southeastern Britain, and then spread rapidly northward and westward. From examination of reports of the presence of *Elminius*, Scheltema and Carlton (1984 and citations within) estimate that *Elminius* spread at a rate of 20 to 30 km per year. The larval phase of *Elminius* is estimated as 17–34 days, depending on temperature, which would have easily allowed spread at this rate. By 1956, the species had arrived in Scotland and as far as northern Germany along the European coast. In this example, the source of settlers to previously unoccupied shore could be rather precisely inferred.

Carcinus maenas

Ruiz and Grosholz (pers. comm. and submitted, 1994) have described the ongoing invasion of the European green crab, *Carcinus maenas*, in northern California. This crab, an important predator in its native range, was first discovered in 1989 in San Francisco Bay. *C. maenas* has planktonic zoea and megalopa larvae, as do other brachyuran crabs. Thus, this species may serve as a model for dispersal of native brachyuran species resident in San Francisco Bay. From 1989 to 1993, *Carcinus* were not observed outside of San Francisco Bay. But in January 1993, *Carcinus* were observed in Bodega Bay, north of San Francisco Bay. These sightings prompted Ruiz and Grosholz to investigate the intervening embayments of Drake's Estero, Bolinas Lagoon, and Tomales Bay, and crabs were found in each of these sites by the fall of 1993. Embayments north of Bodega Bay or south of San

Francisco Bay (Princeton Harbor, Monterey Bay) have apparently not yet been invaded by *Carcinus* as of the winter of 1993–94.

Several interesting points arise from these observations. First, a lag of four years occurred before crabs were observed outside of San Francisco Bay. This may be attributable to a period of local population increase preceding sufficient larval production for successful export, transport, and colonization outside San Francisco Bay. Second, the spread of *Carcinus* has been exclusively in the northward direction. Although details of the reproductive phenology of *Carcinus* in San Francisco Bay are lacking, this may indicate predominately northerly surface currents at the time larvae are produced.

In summary, the secondary spread of *Carcinus* after invasion of San Francisco Bay unambiguously demonstrates that propagules produced there are the source of recruitment in Bodega Bay.

Codium fragile

Carlton and Scanlon (1985) describe the arrival and spread in New England of *Codium fragile* ssp. *tomentosoides*, a large and conspicuous green alga native to western Europe. Using evidence from herbarium collections, direct observations, interviews of shellfishermen and shellfish wardens, and literature reports, Carlton and Scanlon infer that *Codium* arrived first in Long Island Sound in or about 1956, possibly transported on the hulls of ships. Subsequent dispersal in the northwestern Atlantic Ocean apparently involved both human-mediated and natural dispersal mechanisms. Human-mediated dispersal may have included transfer on ships' hulls, on oyster shells, in fishermens' nets, and in packing material for lobsters and baitworm.

In the present context, natural dispersal is of greater interest. Natural dispersal may have been through motile gametes ("swarmers"), thallus fragmentation and drift, or rafting of entire plants. After transplantation on oysters to Chatham, on Cape Cod, in 1961, over the next 10 years *Codium* spread by natural dispersal mechanisms along the southern shore of Cape Cod. Dispersal to the north led to populations on the outer Cape by 1967. From Buzzards Bay, *Codium* moved through the Cape Cod Canal, arriving in Cape Cod Bay by 1972. Reports of *Codium* in Cape Cod Bay followed a chronological sequence consistent with bidirectional spread from the mouth of the Cape Cod Canal. *Codium* reached Provincetown in the northeast by around 1975 and Duxbury Bay in the northwest by 1981. This analysis, summarized from Carlton and Scanlon (1985), suggests that dispersal on both sides of the Cape Cod peninsula is not directional, though rates of spread may vary. For example, spread to the northeast was apparently more rapid than to the northwest in Cape Cod Bay.

TABLE 1
Frequency of a Mitochondrial DNA Marker Indicative of *Mytilus trossulus* and *Mytilus galloprovincialis* in Populations from Alaska to Southern California

Site	*M. galloprovincialis*	*M. trossulus*	*N*
Shumagin Island, AK	0	100	20
Seattle, WA	0	100	23
Tillamook Bay, OR	0	100	54
Netarts Bay, OR	0	100	4
Yaquina Bay, OR	0	100	10
Coos Bay, OR	0	100	159
Humboldt Bay, CA	0	100	11
San Francisco Bay, CA	32.3	67.7	68
Monterey Bay, CA	72.4	27.6	58
Morro Bay, CA	51.6	48.4	31
San Diego Bay, CA	58.7	41.3	46
Japan (ballast water)	100	0	45

Data from Geller et al. 1994. For details on methods, see also Geller and Powers, in press.

GENETIC INTROGRESSION AS AN INDICATOR OF DISPERSAL

The mussel *Mytilus galloprovincialis* is native to southern Europe and the Mediterranean Sea and has been introduced to many regions globally, including Japan, Hong Kong, Singapore, South Africa, and southern California (McDonald et al. 1991; Seed 1992). On the North American west coast, *M. galloprovincialis* occur from at least San Diego to the San Francisco Bay region (McDonald and Koehn 1988; Sarver and Foltz 1993; Geller et al. 1994). Although larvae of this species are regularly released into ports of the Pacific Northwest from the ballast water of ocean-crossing ships (Carlton and Geller 1993), these larvae apparently do not survive, and only the native mussel *Mytilus trossulus* is found in these sites (Geller et al. 1994). Both species are found in the San Francisco Bay region, and will apparently hybridize where overlap occurs (McDonald and Koehn 1988; Sarver and Foltz 1993). Geller et al. (1994) showed (table 1) the occurrence of the mitochondrial genome of *Mytilus trossulus* in southern Calilfornia populations which analyses of allozymes indicated were purely composed of *Mytilus galloprovincialis* (McDonald and Koehn 1988; Sarver and Foltz 1993). This suggests the introgression of the mitochondrial genome across a species boundary, from native *M. trossulus* in the north to introduced *M. galloprovincialis* in the south.

One mechanism for mitochondrial introgression could be the production of hybrid larvae in the zone of overlap (San Francisco Bay), followed by transport to the south and backcrossing of settlers into pure *M. galloprovincialis* populations. Female hybrid larvae that are the product of male *M. galloprovincialis* and female *M. trossulus* will carry the *M. trossulus* mitochondrial genome. The mating of such hybrid larvae in a population of *M. galloprovincialis* will produce F_2 generation individuals that are

TABLE 2
Expected and Observed Percent Frequencies of Alleles at Three Partially Diagnostic Loci, and of a Mitochondrial DNA Marker for *Mytilus trossulus*[a]

Locus	Allele	*M.g.*[b]	*M.t.*[b]	Morro Bay	Mission Bay	Coos Bay
Gpi						
	86	0	0	0	0	0
	89	0	6	0	0	0
	93	0	24	0	0	5
	96	1	0	2	0	5
	98	0	56	2	7	45
	100	92	2	93	85	45
	102	0	10	4	9	0
	105	6	2	0	0	0
	107	0	0	0	0	0
Lap						
	92	0	6	3	0	5
	94	4	50	0	2	45
	96	69	28	70	56	45
	98	23	12	27	40	5
	100	4	4	0	2	0
Pgm						
	86	0	0	2	0	0
	89	5	0	0	2	0
	93	11	0	23	7	0
	100	54	10	48	64	10
	106	24	32	21	28	35
	111	4	52	4	0	50
	114	2	6	2	0	5
mtDNA marker				29	28	100

[a]Morro Bay $N = 28$; Mission Bay $N = 29$; Coos Bay $N = 10$.
[b]*M.g.* = *Mytilus galloprovincialis*; *M.t.* = *Mytilus trossulus*. Expected values are from McDonald and Koehn 1988.

mostly *M. galloprovincialis* in nuclear genotype, yet carry the *M. trossulus* mitochondrial genome. Actually, biparental inheritance and heteroplasmy of mitochondrial DNA has been shown in mussels (Fisher and Skibinski 1990; Hoeh et al. 1991; Zouros et al. 1992); thus the direction of crosses may not be important in determining whether hybrid larvae carry the *M. trossulus* mitochondrial genome. A test of this hypothesis is to characterize both nuclear and mitochondrial genotypes simultaneously from mussels from southern California populations. Table 2 presents preliminary data of this nature (J. B. Geller and D. Hedgecock, unpublished data). Populations from Morro Bay, Mission Bay (San Diego), and, for comparison, Coos Bay, Oregon, were surveyed for allelic frequencies at three enzyme-coding loci that are each partly diagnostic for *M. trossulus* and *M. galloprovincialis*. These mussels were also assayed for a mitochondrial marker diagnostic for *M. galloprovincialis* and *M. trossulus* (Geller et al. 1994; Geller and Powers, in press). As shown in table 2, around 28 percent of individuals from each of the southern California populations carried the mitochondrial genome of *M. trossulus*, while allelic frequencies for the populations were in general accordance with those reported by McDonald and Koehn (1988) for *M. galloprovincialis*. Coos Bay mussels all carried the mitochondrial genome of *M. trossulus* and also had allelic frequencies concordant with those reported by McDonald and Koehn (1988) for *M. trossulus*. These data support the hypothesis of mitochondrial introgression and have implications for the directionality of larval dispersal.

The direction of mitochondrial introgression is asymmetric, occurring only from *M. trossulus* to *M. galloprovincialis*. This can be explained in two ways: first, hybridization may be asymmetrical, in that F_1 hybrids may be viable only when they are products of a crossing between female *M. trossulus* and male *M. galloprovincialis*. If this were the case and if mitochondrial inheritance in mussels were mostly maternal, then transport of hybrid larvae could be bidirectional, but introgression detectable only in southern populations. Reports of biparental inheritance in crosses between *Mytilus galloprovincialis* and *M. edulis*, if extrapolated to crosses between *M. galloprovincialis* and *M. trossulus*, render this hypothesis unlikely (Hoeh et al. 1991; Zouros et al. 1992). An alternative explanation is that transport of hybrid larvae is predominately to the south. If so, the absence of *M. galloprovincialis* mitochondrial genomes in northern *M. trossulus* populations can be explained by the absence of a transport mechanism. Hybrid larvae carrying the mitochondrial genome of *M. trossulus*, *M. galloprovincialis*, or both, may be carried to southern populations, resulting in detection of the *M. trossulus* mitochondrial genome in those populations.

This proposed pattern of larval transport to the south seems contradictory to that seen in *Carcinus maenas*, described above, in which transport from San Francisco Bay appeared to be to the north. However, *Mytilus* from embayments immediately north of San Francisco were not sampled in the survey of mitochondrial genotypes, and analysis of allozymes indicates the presence of *M. galloprovincialis* in those populations (McDonald and Koehn 1988). Thus the distributions of *C. maenas* and *M. galloprovincialis* in the region north of San Francisco Bay are concordant. Neither species appears north of Bodega Bay. For *C. maenas*, insufficient time may explain its absence farther north, but *M. galloprovincialis* has been established in San Francisco Bay much longer, perhaps since the 1930s. The failure of *M. galloprovincialis* to spread north, or the failure of its mitochondrial genome to introgress into northern *M. trossulus* populations, suggests either lack of transport farther north, the lack of suitable habitat north of Bodega Bay, or a combination of both. If the introgression of the *M. trossulus* genome into southern *M. galloprovincialis* populations is mediated by southward movement of hybrid larvae, *Carcinus maenas* should eventually spread to the south.

CONCLUSION

These cases illustrate the utility of marine biological invasions for the study of ongoing dispersal over geo-

graphic scales relevant to population dynamics. Invasions involving large and easily identified organisms such as *Elminius modestus*, *Carcinus maenas*, or *Codium fragile* offer the most tractable systems for dispersal studies. However, many invading species are small, inconspicuous, or taxonomically understudied (Carlton and Geller 1993). Although these species are less attractive for dispersal studies, they are often highly abundant in the ballast water of ships. For these species, genetic characterization can allow study of their dispersal from an initial site of invasion. Some invading species are closely related to native species (i.e., congeners). In these cases, hybrid larvae produced in sites of invasion are "genetically marked" for their site of origin. Also, hybridization allows nonnative genes to introgress into native populations (Geller et al. 1994). Thus invasions can serve simultaneously as models of dispersal and gene flow.

Marine invasions appear to be on the increase: Carlton et al. (1990) estimate that there is currently at least one successful invasion of San Francisco Bay each year. Although invasions can be deleterious to native organisms and should not be encouraged or celebrated, the association with shipping will continue to propagate invasions for the foreseeable future. Population biologists and geneticists have an opportunity to gain useful knowledge from this inadvertant modification of native communities.

ACKNOWLEDGMENTS

I thank R. D. Vetter for the invitation to speak at the 1993 CalCOFI symposium on genetics of the California Current. I also thank J. T. Carlton, E. D. Grosholz, and G. M. Ruiz for providing prepublication drafts of their works on *Carcinus maenas* and for many discussions of marine biological invasions, and S. Bartl for critiquing earlier versions of this paper. Support for studies of invasion of mussels was provided by the National Science Foundation by a Marine Biotechnology Fellowship to J. B. G. Studies of marine biological invasions in Oregon were supported by a grant (R/EM-21) to J. T. Carlton by the National Oceanic and Atmospheric Administration Sea Grant (Oregon).

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TEMPORAL AND SPATIAL GENETIC STRUCTURE OF MARINE ANIMAL POPULATIONS IN THE CALIFORNIA CURRENT

DENNIS HEDGECOCK
University of California, Davis
Bodega Marine Laboratory
Bodega Bay, California 94923-0247

ABSTRACT

The hope that "biotechnology" will permit the identification of geographic sources of recruitment to most marine animal populations is not well supported either by logic or fact. First, population genetics tells us that dispersal among geographic populations is expected, at equilibrium, to eliminate the very molecular genetic differences that are supposed to permit identification of geographic provenance. Second, studies of allozymes and mitochondrial DNA have clearly shown that fish and invertebrate species with planktotrophic larvae are genetically quite similar over large regions, though not necessarily throughout their whole ranges. Genetic studies are, nevertheless, contributing new insights into the structure and biology of marine animal populations.

One new insight is that sharp genetic subdivisions can occur in continuously distributed species, particularly those spanning biogeographic boundaries. An even more widespread observation is of very slight but significant microgeographic genetic heterogeneity embedded within broad regions of genetically very similar populations. Examples of the latter from the California Current are presented for the barnacle *Balanus glandula* and the northern anchovy *Engraulis mordax*. Microgeographic heterogeneity holds interest for biological oceanographers and fisheries scientists because it contradicts the logic of population genetics as well as commonly held notions about the structure of zooplankton populations. Evidence suggests that genetic heterogeneity on microgeographic scales results from temporal variation in the genetic composition of recruits. This temporal variation could be a consequence of either selection on larval populations or large variance in the reproductive success of individuals, owing to chance matching of reproductive activity with windows of oceanographic conditions conducive to fertilization, larval development, retention, and recruitment. In support of the latter hypothesis, effective sizes for natural oyster populations are estimated to be only small fractions of breeding population numbers. The temporal aspect of population genetic structure forges a strong interdisciplinary bridge to oceanographic research aimed at elucidating the temporally and spatially varying factors affecting recruitment.

RESUMEN

Ni la lógica ni los hechos sustentan la expectativa de que la "biotecnología" permitirá identificar las fuentes geográficas de reclutamiento en la mayoría de las poblaciones de animales marinos. En primeras, la genética poblacional nos indica que en condiciones de equilibrio se espera dispersión entre poblaciones geográficas para eliminar las mismas diferencias moleculares genéticas que supuestamente permitirían la identificación del sitio geográfico de origen. En segundas, los estudios de alocimos y ADN de la mitocondria han mostrado claramente que las especies de peces e invertebrados con larvas planctotróficas son genéticamente muy similares a lo largo de grandes trechos (aunque no necesariamente a través de todo su rango). Sin embargo, los estudios genéticos están contribuyendo conocimientos nuevos de la estructura y biología de las poblaciones de animales marinos.

Una perspectiva nueva es que en especies distribuidas continuamente pueden ocurrir subdivisiones genéticas muy marcadas, particularmente en aquellas especies cuyos rangos incluyen fronteras biogeográficas. Otra observación aun más común es la sutil pero importante heterogeneidad microgeográfica genética que ocurre embebida dentro de regiones más extenidas de poblaciones muy similares genéticamente. Se presentan ejemplos de este último caso para el cirripedio *Balanus glandula* y la anchoveta norteña *Engraulis mordax*. La heterogeneidad microgeográfica es interesante para los oceanólogos biólogos y los investigadores pesqueros debido a que contradice tanto la lógica de la genética poblacional como nociones comunes de la estructura de las poblaciones de zooplancton. La evidencia sugiere que la heterogeneidad genética en escalas microgeográficas resulta de la variación temporal de la composición genética de los reclutas. Esta variación temporal podría ser resultado de selección en poblaciones de larvas o gran varianza en el éxito reproductivo de los individuos. Esto último podría ser debido a sincronización aleatoria de la actividad reproductiva con periodos de condiciones oceanográficas conducentes a la fertilización, desarrollo larval, retención y reclutamiento. En apoyo a esta última hipótesis, se estima que los tamaños efectivos de las poblaciones naturales de ostras son muy pequeños en relación a los tamaños de las poblaciones de criadores. El aspecto temporal de la estructura genética poblacional forja un fuerte vínculo interdisciplinario hacia la investigación oceanográfica que se enfoca en dilucidar los factores dinámicos temporales y espaciales que afectan el reclutamiento.

INTRODUCTION

Identification of the geographic sources of recruits to marine animal populations is important to understanding the coupling of physical and biological processes governing the distribution and abundance of zooplankton (GLOBEC 1991). The notion that genes or gene products might provide inborn markers or tags of provenance has thus proven attractive to oceanographers, particularly in light of the burgeoning promise of biotechnology for precision and accuracy of individual genetic identification (Cullen 1988; Morse 1990; Powers et al. 1990; Incze and Walsh 1991). Origins of recruits to marine animal populations may be more difficult to ascertain than anticipated, however, for both theoretical and empirical reasons.

Migration among populations is a potent, systematic means of homogenizing the gene pools of conspecific populations. For simplicity, assume migrants to a local population i are drawn at random from all other conspecific populations, and that p is the average frequency of an allele at a locus for this species. Over a single generation, then, the change in local allelic frequency, p_i, as a function of p and the proportion of immigrants into the population, m, is given by (Wright 1931):

$$\Delta p_i = m(p - p_i).$$

At equilibrium, $\Delta p_i = 0 = (p - p_i)$, so that allelic frequencies in a local population under constant migration pressure become indistinguishable from those in other conspecific populations. Of course, the effects of gene flow can be modeled more complexly, for example, by taking into account the stochastic effects of finite subpopulation size, the dimensionality and continuity of an organism's distribution, or the effects of selection, but migration remains a potent homogenizing influence unless diversifying selection at a locus is quite strong. For selectively neutral genes, one reproductively successful immigrant in each subpopulation every other generation is enough to maintain cohesiveness of allelic frequencies across all subpopulations (Wright 1931). Thus, marine animals that are either wholly pelagic or have planktonically dispersing larvae (i.e., zooplankton *sensu latu*) are expected to show little genetic differentiation over large geographic areas.

Spatial variance in allelic frequencies is typically quantified by Wright's (1931) standardized variance measure, $F_{ST} = \sigma^2/p(1-p)$, where p is the average frequency of an allele in the total population under consideration, σ^2 is the variance of p among localities within that total population, and the denominator $p(1-p)$ is the maximum variance that would obtain if localities were each fixed for one of the alternate alleles in a ratio of $p:(1-p)$. Most zooplankton species are expected to have $F_{ST} < 0.05$ over large regions.

A substantial number of studies of marine animals have confirmed the expectation of low spatial genetic variance (e.g., Berger 1973; Koehn et al. 1976; Winans 1980; Johnson and Black 1982, 1984; Graves et al. 1984; Watts et al. 1990; reviews or summaries by Burton 1983; Gyllensten 1985; Hedgecock 1986, 1987; Utter and Ryman 1993). Marine fish and invertebrates with planktonic larvae generally maintain very similar allelic frequencies over large regions (500–2000 km) so that geographic variation in allelic frequencies (F_{ST}) typically accounts for only a few percent of the total genetic diversity of these species. Fauna of the California Current are no exception to this generalization (mussels, Levinton and Suchanek 1978; pandalid shrimp, Berthélémy 1978; Dungeness crab, Nelson and Hedgecock 1980, Soulé and Tasto 1983; barnacles, Hedgecock 1982, unpubl. obs.; herring, Grant and Utter 1984; nine species of marine shore fishes, Waples 1987; sardines and anchovies, Hedgecock et al. 1989; sea urchins, Palumbi and Wilson 1990; dover sole, Vetter, data presented at CalCOFI Conference, 1993). With so little genetic variation among geographically widespread populations, it is impossible to ascertain the provenance of population samples (Utter and Ryman 1993), much less of individuals. The hope that detecting individual DNA differences will rectify this is futile because dispersal ensures that all genetic variants are eventually broadly distributed.

However, two qualifications to the general rule that marine animals with planktonically dispersing life stages are genetically very similar over large regions must be discussed. The first qualification is that marine animal species, though genetically very similar over large areas, are not necessarily homogeneous over their entire ranges. Rather, zooplankton species may be genetically subdivided on macrogeographic scales, particularly if they range across boundaries between biogeographic provinces. The second qualification is that very slight but statistically significant and persistent heterogeneities of allelic frequencies have frequently been observed on microgeographic scales, embedded within the large regions over which dispersal maintains an otherwise high level of genetic similarity as described above. Such observations contradict the logic of population genetics that gene flow should prevent such heterogeneity, as well as commonly held notions about population mixing in the sea. Study of the causes of microgeographic variation provides a direct link between population genetics and the ecological and oceanographic processes affecting recruitment.

MACROGEOGRAPHIC SUBDIVISION AND PHYLOGEOGRAPHY

Evidence for genetic divergence among large geographic subpopulations has been reported for many marine animals with planktonically dispersing larvae (Mulley

and Latter 1981a,b; Buroker 1983; Grant and Utter 1984; Avise et al. 1987; Grant et al. 1987; Hedgecock 1987; Ovenden et al. 1990; Palumbi and Wilson 1990; Reeb and Avise 1990; Benzie and Stoddart 1992a,b; Karl and Avise 1992; Macaranas et al. 1992). The degree of subdivision depends on the genetic markers employed, and varies from a small proportion of total genetic diversity to substantial genetic differences suggesting ancient evolutionary separations, warranting in some cases systematic study and possibly taxonomic recognition. Very often the genetic divergence is associated with an obvious barrier to dispersal—land masses, divergent currents systems, impassible basins, etc.—but recent studies have revealed unexpectedly large genetic discontinuities in continuously distributed populations (Reeb and Avise 1990; Karl and Avise 1992; Burton 1994). These discontinuities are sometimes remarkably sharp, evidently reflecting long-standing barriers to dispersal and gene flow, and are often associated with known biogeographic boundaries. The ability to correlate intraspecific genetic variation, particularly DNA sequence divergence, with geography has given rise to a new discipline, phylogeography, which bridges population genetics, systematics, and biogeography (Avise et al. 1987; Avise 1989; Neigel 1994).

Phylogeographic studies of California Current fauna are likely to provide new insight into oceanographic constraints to dispersal across biogeographic boundaries, such as Points Conception and Eugenia (see Burton 1994). However, the depth of population history must be appreciated in these studies. Genetic divergence, which accumulates over an evolutionary time scale, may not necessarily accord well with present physical oceanographic conditions or shorter-term ecological processes.

MICROGEOGRAPHIC HETEROGENEITY—"CHAOTIC PATCHINESS"

An unsolved paradox concerning the genetics of marine animals that disperse by means of planktonic larvae is the occurrence of slight but significant local or microgeographic population structure despite apparently high gene flow (Johnson and Black 1982; Burton 1983). Lack of microgeographic patterning of allelic frequencies among population of the limpet *Siphonaria* sp. led Johnson and Black (1982) to describe this variation as "chaotic patchiness." Two striking examples of this phenomenon in the California Current are provided by allozyme studies of the barnacle *Balanus glandula* (Hedgecock 1982, 1986, unpubl.) and the northern anchovy *Engraulis mordax* (Hedgecock et al. 1989; Hedgecock 1991; Hedgecock et al. 1994).

Balanus glandula is among the most polymorphic of crustaceans that have been analyzed for allozyme variation. The proportion of loci polymorphic in a Bodega Bay, California, population is 19 of 27 loci (70%); the average number of alleles per locus is 2.41; and the average percentage of loci heterozygous per individual is 21.4% (Hedgecock et al. 1982). In order to assess the genetic consequences of larval dispersal—the larval phase of *B. glandula* lasts perhaps up to four weeks in the plankton (Barnes and Barnes 1956; Strathmann 1982; J. D. Standing, pers. comm.)—a survey of the most polymorphic allozymes was made for samples of 17 *B. glandula* populations, mostly from central California but including 1 from Alaska and 3 from the Southern California Bight.

Complete data are available for 5 allozyme loci and ten sampling localities, nine in north-central California and one in the Southern California Bight (table 1). A hierarchical population analysis was made by grouping sampling localities into four regions and calculating spatial variance components and *F*-statistics for comparisons of locality to region (F_{LR}), locality to total (F_{LT} equal to the F_{ST} statistic defined in the Introduction), and region to total (F_{RT}) (table 2A). There is little variance in the frequencies of alleles from north-central to southern California (mean $F_{LT} = 0.023$); variation among regions, which includes population samples from two biogeographic provinces and a substantial divergence of *Got-2* allelic frequencies (cf. locality 10 to the others in table 1), is no greater on average than variation among localities within regions ($F_{RT} = 0.011$, $F_{LR} = 0.012$). A similar analysis for twelve localities, including the Alaska sample and an additional sample from the Southern California Bight, but for only 3 of the 5 loci, gave similar results. Variation among individuals within single, 0.25 m^2 samples accounted for 96% of total genetic diversity in the species, whereas differences among population samples accounted for only 4% of total genetic diversity. On this basis, the population genetic structure of *B. glandula* fits the generalization that geographically distant populations are genetically very similar, most likely because of gene flow via larval dispersal.

Despite this picture of genetic similarity, statistical tests of the homogeneity of allelic frequencies at 4 polymorphic loci reveal slight, but significant differences in allelic frequencies (table 2B), sometimes over short distances (figure 1). As in *Siphonaria*, these slight but significant differences in allelic frequencies have no discernable pattern, and genotypes show no obvious microgeographic clustering in careful mapping studies (Standing and Hedgecock, unpubl.). If gene flow via larval dispersal makes gene frequencies from Alaska to southern California very similar, why does it not produce statistically homogeneous populations on a local or microgeographic level?

On the basis of meristic, morphometric and transferrin-electrophoretic data (Vrooman et al. 1981) and

TABLE 1
Allelic Frequencies for Five Loci in Ten Samples of *Balanus glandula* Populations

	Sampling localities[a]									
Locus	1	2	3	4	5	6	7	8	9	10
Got-1										
N[b]	38	48	31	45	48	45	48	14	47	48
109	.026	.010	.000	.044	.021	.022	.021	.000	.032	.000
104	.092	.104	.113	.100	.146	.156	.094	.000	.117	.083
100	.500	.583	.677	.556	.552	.522	.531	.393	.574	.521
94	.368	.281	.210	.289	.260	.289	.344	.607	.266	.396
89	.013	.021	.000	.011	.021	.011	.010	.000	.011	.000
Got-2										
N	48	48	36	48	48	45	48	90	48	48
104	.708	.615	.736	.625	.573	.578	.615	.539	.677	.135
100	.292	.365	.264	.354	.427	.422	.385	.461	.323	.667
Other[c]	.000	.021	.000	.021	.000	.000	.000	.000	.000	.198[d]
Gpi										
N	48	48	47	48	48	46	48	93	48	48
106	.031	.010	.064	.031	.021	.043	.083	.091	.042	.010
104	.042	.063	.074	.073	.042	.043	.052	.059	.063	.063
100	.490	.479	.457	.354	.521	.413	.438	.425	.469	.302
98	.375	.354	.330	.417	.344	.435	.365	.355	.375	.563
95	.031	.073	.043	.031	.042	.022	.063	.043	.052	.010
93	.031	.010	.021	.063	.031	.043	.000	.027	.000	.042
Other	.000	.010	.011	.031	.000	.000	.000	.000	.000	.010
Mdh										
N	48	48	48	48	48	48	48	92	48	48
106	.000	.000	.000	.000	.000	.000	.021	.011	.000	.000
100	.969	1.000	.969	.990	.958	.948	.969	.957	.958	1.000
95	.031	.000	.031	.010	.042	.052	.010	.033	.042	.000
Mpi										
N	48	48	48	48	48	46	48	92	48	48
110	.094	.083	.073	.073	.073	.141	.063	.076	.052	.073
107	.292	.292	.229	.229	.125	.283	.292	.245	.240	.146
103	.167	.177	.177	.250	.260	.152	.188	.272	.177	.260
100	.354	.313	.250	.344	.323	.326	.292	.337	.396	.365
95	.094	.115	.219	.396	.188	.087	.135	.065	.125	.125
93	.000	.010	.031	.000	.010	.000	.031	.000	.000	.000
Other	.000	.010	.021	.010	.021	.011	.000	.005	.010	.031

[a]Key to sampling localities (all in California): 1, Fort Bragg; 2, Point Arena; 3, Gualala Point; 4, Salt Point; 5, Bodega Harbor jetty, high intertidal; 6, Bodega Harbor jetty, mid intertidal; 7, Bodega Harbor jetty, low intertidal; 8, Bodega Harbor, Gaffney Point; 9, San Francisco Bay; 10, Point Latigo.
[b]Number of individuals studied.
[c]Some rare alleles are pooled as "Other."
[d]A unique *97* allele at *Got-2* was found at this frequency in Point Latigo.

by analogy to concepts of population structure for the California sardine *Sardinops sagax caeruleus* (Radovich 1982), the northern anchovy *Engaulis mordax* is thought to comprise three geographic stocks—a northern population spawning in the Columbia River plume, a central population spawning primarily in the Southern California Bight, and a southern population spawning off of Punta Eugenia and in Magdalena Bay, Baja California Sur. Allozyme and morphometric studies of aged and sexed specimens from the central stock, which were collected by NMFS spawning biomass cruises from 1982 to 1985 (a total of over 3000 fish), revealed substantial genetic polymorphism and morphometric and life-history variation (Hedgecock et al. 1989; Hedgecock 1991). Detailed analyses of the allozyme data and of the morphometric data for the larger collections in 1984 and 1985 are presented elsewhere in this volume (Hedgecock et al. 1994; Nelson et al. 1994).

Like other members of the Clupeiformes that have been analyzed by protein electrophoretic methods, the northern anchovy has substantial levels of genetic variation. In a survey of 39 protein-coding loci, about 40% of the loci were polymorphic, and individuals were heterozygous, on average, at 7.5% of loci (Hedgecock et al. 1989). An initial survey of genetic variation for the 11 most polymorphic loci, among samples taken from Half Moon Bay to Santa Monica Bay in early 1982, revealed a typically small allele-frequency variance (mean $F_{ST} = 0.032$). Nevertheless, log-likelihood ratio tests of the independence of allele-frequencies and locality indicated that 5 loci (*Gpi*, *Hbdh-2*, *Lgg*, *Pgm*, and *Xdh*) had significantly heterogeneous allele-frequencies.

Similar results—low F_{ST} values but statistically significant heterogeneity of allelic frequencies—were obtained in each of four subsequent population surveys made in December 1982 and the winters of 1983, 1984,

TABLE 2
Spatial Variation for Five Loci among Samples from 10 Populations of *Balanus glandula*

A. Variance components and *F*-statistics for hierarchical analysis

X	*Y*	Variance component	F_{XY}
Locality	Region	.02924	.011
Locality	Total	.06023	.023
Region	Total	.03099	.012

B. Contingency chi-square analysis for each locus

Locus	Number of alleles	Chi-square	d.f.	*P*
Got-1	5	38.165	36	0.375
Got-2	3	215.295	18	0.0
Gpi	7	76.091	54	0.021
Mdh	3	24.665	18	0.105
Mpi	7	105.96	54	0.0
Totals		460.176	180	0.0

Variance components are corrected for sampling error. Regions are: (1) northern California coast, north of Russian River (four localities); (2) Bodega Harbor, Calif. (four localities); (3) San Francisco Bay (one locality); (4) Southern California Bight (one locality). Probabilities for contingency chi-square estimated from 1000 Monte Carlo runs of resampled matrix (Zaykin and Pudovkin 1993).

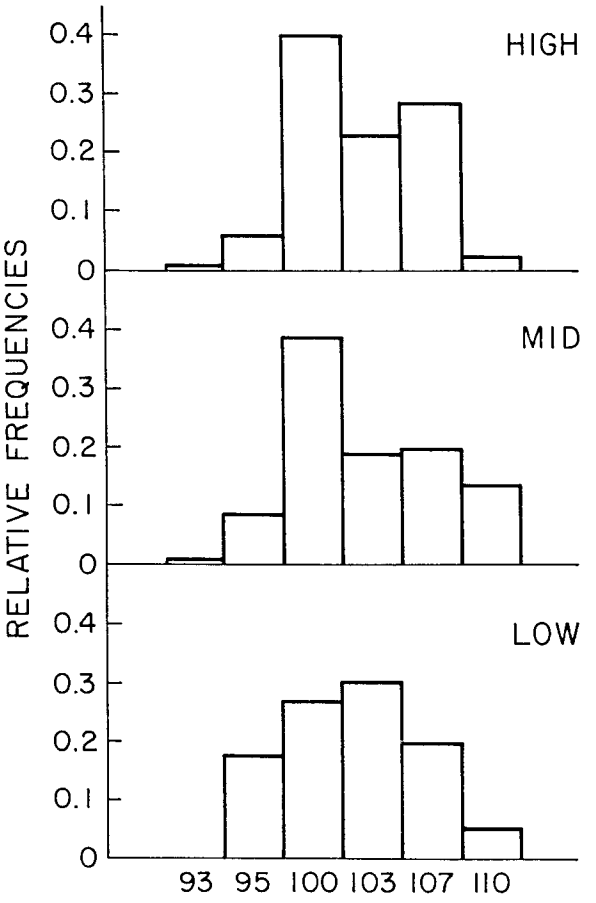

Figure 1. An example of microgeographic genetic heterogeneity in the barnacle *Balanus glandula*. Frequencies of six electrophoretically detectable alleles at the mannose-phosphate isomerase gene, *Mpi*, across an intertidal transect. Samples of 48 individuals were collected from each of high, mid, and low positions in the barnacle zone, spanning about 1 m of intertidal height, on the jetty at Bodega Harbor, California. These samples were collected one year before samples 5–7, table 1, with which they can be compared. Allelic frequencies are very significantly heterogeneous over this local transect (χ^2 = 24.644, 10 d.f., $p < 0.003$ by pseudo-probability method of Zaykin and Pudovkin 1993).

and 1985 (Hedgecock et al. 1994). F_{ST} ranged from only 0.005 to 0.020 in these surveys, somewhat lower than that reported for the early 1982 survey, owing primarily to exclusion of two enzymes, HBDH and XDH, that appeared to be influenced by liver tissue degradation (Hedgecock et al. 1989). Still, in each of the five surveys, 4 or 5 loci show significant heterogeneity of allelic frequencies among samples, although the loci showing this heterogeneity are not necessarily the same from year to year. With the exception of *Idh-1*, which was studied in only four of the five surveys, each locus shows significant heterogeneity of allelic frequencies in at least one survey; conversely, each locus has homogeneous allelic frequencies in at least one survey. Lack of consistency in the loci contributing to heterogeneity, and lack of spatial patterning of allelic frequencies result in a picture of "chaotic patchiness" in the genetic structure of the central stock of northern anchovy.

Genetic differentiation of barnacle populations on a local scale, despite a potential for high gene flow by pelagic larvae, can be explained either by differential survival of genotypes after recruitment or by temporal variation in the genetic composition of recruits. The same two hypotheses might apply to northern anchovy, which can disperse at all life stages, but would require additional hypotheses concerning the long-term cohesion of schools or homing to natal waters. Although differential survival may account for clinal patterns of variation (e.g., Koehn et al. 1980), which may be consistent with environmental gradients and natural selection for appropriate physiological responses, it does not explain well the chaotic patchiness of most microgeographic genetic variation observed to date. On the other hand, temporal variation in the genotypes of recruits has been demonstrated as a cause of microgeographic heterogeneity in limpets (Johnson and Black 1982, 1984) and sea urchins (Watts et al. 1990). These studies show, moreover, that temporal variance in allelic frequencies is exceeded by spatial variance only on scales of several hundreds to thousands of kilometers.

Although Johnson and Black (1984) believe that temporal genetic variance arises from temporally and spatially varying selection on larvae, an alternative explanation is that temporal genetic variance is a by-product of a large sampling error engendered by sweepstakes reproductive success on the part of a minority of individuals (Hedgecock 1994). The high fecundities and mortalities of early life stages of most marine animals create

the potential for a large variance in the number of offspring that individuals contribute to the next generation of reproducing adults. Such variance in reproductive success would, in turn, limit the effective population sizes of these species by several orders of magnitude, according to the relationship (Crow and Kimura 1970; Crow and Denniston 1988):

$$N_e = (4N-4)/(V_k + 2),$$

where N_e is the effective population size, N is the number of breeding adults, V_k is the variance in offspring number per parent, and the population is assumed to be dioecious and demographically stable. Whereas in terrestrial animals V_k is often binomial or Poisson and the ratio N_e/N is nearly 1.0, in marine species V_k may be orders of magnitude larger than binomial or Poisson, and the N_e/N ratio may be a small fraction.

This hypothesis makes two testable predictions. First, random genetic drift, which is a function of the effective population size, ought to be measurable if N_e is limited by large V_k. Second, to the extent that specific cohorts of larvae or new recruits represent the reproductive output of a minority of individuals, they should have less genetic diversity than that which exists in the total adult population. Thus, studies of temporal genetic change in adult populations and of the genetic composition of pelagic larval populations are promising approaches to testing alternative explanations of chaotic patchiness and temporal genetic change in marine animal populations.

TEMPORAL GENETIC CHANGE AND OCEANOGRAPHY

Analysis of temporal genetic change is a powerful means of measuring random genetic drift, estimating effective population numbers, and testing hypotheses about population genetics. The method is particularly robust over intervals of two to ten generations and when N_e is truly finite (Waples 1989) and has proved illuminating in the study of isolated, hatchery-propagated stocks of fish and shellfish (Hedgecock and Sly 1990; Waples and Teel 1990; Hedgecock et al. 1992). Application of the temporal method to natural populations now appears useful in testing the hypothesis that variance in reproductive success limits effective population numbers of many marine animals.

The analysis is based on the inverse relationship between observed temporal change in the frequencies of alleles and the effective size of an isolated population, N_e:

$$E(F) = t/(2N_e) + 1/(2S_0) + 1/(2S_t),$$

where $E(F)$ is the expected variance, owing to random drift of allelic frequencies, between an initial sample (taken without replacement) of S_0 individuals and a second sample of S_t individuals taken (without replacement) after an interval of t generations. Estimates of temporal variance are made from data (Pollak 1983), standardized to eliminate the effect of differences in initial allelic frequencies, and then averaged across loci, weighted by the number of independent alleles at each locus, to yield an estimate, $\hat{F}_K$ of $E(F)$ (see Hedgecock et al. 1992). Rearrangement of this equation yields an estimator, $\hat{N}_K$, of the effective population number:

$$\hat{N}_K = t/(2[\hat{F}_K - 1/(2S_0) - 1/(2S_t)]).$$

The terms $1/(2S_0)$ and $1/(2S_t)$ are harmonic mean sample sizes per locus, weighted by numbers of independent alleles per locus; temporal variance is thus corrected for sampling error.

Temporal genetic analysis has been applied to data from several natural populations of oysters (table 3). The Dabob Bay, Washington, population of Pacific oysters is a semi-isolated, naturalized population, which was established by repeated introductions from Japan over several decades. Mean effective size of this population over a period of 19 years is estimated to be about 400, in contrast to annual harvests on the order of 10^7–10^8 oysters. Estimating temporal variance and effective size for local populations of the American oyster appears to violate a basic assumption of temporal genetic analysis that the population under study be isolated so that immigration plays no role in changing allelic frequencies. Nevertheless, temporal genetic variance over two generations (corrected for sampling error) in three Delaware and Chesapeake Bay localities is as large as or larger than spatial genetic variance along the entire Atlantic seaboard (F_{ST} = 0.029; calculated from data of Buroker 1983). Actual temporal variance for the Chesapeake Bay site, 0.067, is greater than spatial genetic variance over the range of the species, from Canada to Mexico (F_{ST} = 0.039; Buroker 1983). Partial isolation of these oyster populations cannot be explained by immigration and are better explained by random genetic drift in partially isolated estuarine populations maintained by larval retention (cf. Hedgecock 1982). Partial isolation of major estuarine populations would help explain the evolution of local physiological races of oysters (Loosanoff and Nomejko 1951; Hedgecock and Okazaki 1984). Lack of temporal change for the Long Island site may be attributed to relatively greater gene flow into the more oceanic Long Island Sound.

Another major assumption of temporal genetic analysis is that the genetic markers are not affected by natural selection, so that changes of allele-frequencies over time are attributable strictly to random genetic drift. The validity of this assumption for allozymes can be verified in two ways. If allozymes are selectively neutral, then $n\hat{F}/E(\hat{F})$ is distributed as a chi-square variable with n

TABLE 3
Mean Temporal Variances in Allelic Frequencies, F_K, and Estimated Effective Population Numbers, N_K, for Populations of Pacific and American Oysters

A. Pacific oysters *Crassostrea gigas* from Dabob Bay, Washington (after Hedgecock 1994)

t	l	F_K	Sampling variance	Actual variance	lCL	N_K	uCL
1	6	0.0234	0.0114	0.0120	13.4	41.7	218.8
2	11	0.0192	0.0172	0.0020	63.6	511.6	∞
6	5	0.0237	0.0148	0.0089	68.0	336.7	∞
7	5	0.0206	0.0136	0.0070	93.0	501.9	∞
9	6	0.0340	0.0141	0.0199	77.1	226.0	804.7
9.5	6	0.0252	0.0139	0.0113	115.0	418.7	9293

B. Four populations of the American oyster *Crassostrea virginica* sampled two generations apart (after Hedgecock et al. 1992)

Locality	l	F_K	Sampling variance	Actual variance	lCL	N_K	uCL
Long Island	6	0.0158	0.0162	−0.0004	62.3	∞	∞
Delaware Bay	6	0.0424	0.0127	0.0296	13.8	33.8	79.4
Chesapeake Bay	4	0.0974	0.0304	0.0670	4.5	14.9	48.2
James River	6	0.0433	0.0100	0.0333	13.5	30.0	60.8

Interval length in generations is t; l is the number of loci studied; sampling variance is the harmonic mean of sample sizes per locus in the two populations compared; actual variance is F_K minus sampling variance; and lCL and uCL are the lower and upper 95% confidence limits on N_K.

degrees of freedom corresponding to the number of independent loci sampled. Agreement of the observed distribution with the chi-square distribution provides a test of the assumption of selective neutrality, as well as a means for calculating confidence limits on $\hat{N}_K$ (Waples 1989; table 3). An independent test of selective neutrality compares the actual loss of alleles over time to that predicted by population genetic theory assuming $N_e = \hat{N}_K$. Both tests have indicated that temporal genetic change in these oyster populations is caused by random genetic drift (Hedgecock et al. 1992; Hedgecock 1994).

These observations of random genetic drift confirm the first prediction of the hypothesis that variance in reproductive success is large enough in certain marine animal populations to limit effective population numbers to fractions of actual abundance. The observations are also consistent with the studies of Johnson and colleagues, indicating that temporal genetic change is not unusual in marine animal populations. Still, many more temporal genetic studies are needed to confirm the generality of these observations.

A second prediction of the hypothesis is for lower genetic diversity in particular cohorts of larvae or newly recruited juveniles than exists in the spawning adult stock. This prediction may be verified in the future by detailed comparisons of genetic diversities among adults, larvae, and juveniles. Because mitochondrial DNA appears to be predominantly maternally inherited in animals, polymorphisms in this genome may be ideal genetic markers for studies of larval broods. Advances in molecular biology, particularly in the development of enzymatic amplification of DNA by the polymerase chain reaction (PCR), now make possible population genetic studies of marine larvae (Banks et al. 1993), which have not generally been amenable to allozyme analysis. We are presently carrying out a detailed genetic study of oyster larvae in Dabob Bay, an ideal locality because temporally well-separated larval cohorts can be readily identified in plankton samples during a spawning season.

As can now be appreciated from satellite imagery (Roughgarden et al. 1988, 1991), oceanographic processes and conditions that affect the reproduction of marine animal life vary not only among years but also within and among seasons and over mesoscale distances. Temporal and spatial oceanographic variability has been correlated broadly with community structure (Parrish et al. 1981) and more narrowly with overall or regional recruitment success for a variety of taxa (Ebert and Russell 1988; Roughgarden et al. 1988). Nevertheless, the extent to which variability of the marine environment might also enhance variance in offspring numbers among conspecific individuals must now be considered.

To the extent that large variance in reproductive success in marine animals is mediated by oceanographic conditions and processes, there is a strong and direct linkage between population genetics and oceanography. This linkage must be forged if we are to understand broader questions about marine populations, such as their responses to global climate change (Incze and Walsh 1991). At the operational level, detailed studies of genetic diversities within and between cohorts of larvae might provide useful information, for example, on the spatial and temporal dimensions of windows of oceanographic conditions conducive to reproduction and recruitment. Such studies will require sample sizes of thousands of indi-

viduals, however, so that appropriate molecular methods will have to be developed for rapid and efficient processing of population samples. This almost certainly means going beyond the tedious direct sequencing of PCR products in every individual to the application of secondary methods for mass screening of particular nucleotide polymorphisms (e.g., Stoneking et al. 1991) or length variants at simple repeat-sequence loci (Weber and May 1989; Frégeau and Fourney 1993).

Within populations, large V_k might make population responses to selection pressures more complex and indeterminate than is presently appreciated by modelers of population dynamics. On the other hand, adaptive divergence among populations with the potential for gene exchange via dispersing pelagic larvae might be facilitated by a coupling of large V_k with mechanisms of larval retention, as perhaps illustrated by the evolution of physiological races of American oysters along the eastern U.S. seaboard. Finally, speciation in the sea may be more understandable if effective numbers of marine organisms are orders of magnitude smaller than abundance and if marine species are therefore subject to shifting-balance evolutionary processes.

ACKNOWLEDGMENTS

The barnacle studies were done in collaboration with J. D. Standing, M. R. Hemer, and K. Nelson, and assisted by W. Borgeson, R. Cimberg, J. Simmons, and J. Smiley. Studies of northern anchovy were made in collaboration with K. Nelson, E. Hutchinson, G. Li, and F. Sly and were funded in part by the California Sea Grant College Program (projects R/F-82 and R/F-98).

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ANALYSIS OF RAPIDLY EVOLVING MOLECULES AND DNA SEQUENCE VARIANTS: ALTERNATIVE APPROACHES FOR DETECTING GENETIC STRUCTURE IN MARINE POPULATIONS

JOSEPH E. NEIGEL
Department of Biology
University of Southwestern Louisiana
Lafayette, Louisiana 70504

ABSTRACT

Rapidly evolving genetic markers, such as mitochondrial DNA (mtDNA) sequence variants, provide novel opportunities for the study of natural populations, but not without presenting special challenges in analysis and interpretation. For many species of marine organisms, it has been difficult to detect geographic structure in the distribution of genetic markers. In allozyme studies, geographic structure was sought in the frequencies of alleles among populations or locales. However, theoretical considerations suggest that nearly complete demographic isolation over long periods of time may be required to produce detectable differences in allele frequencies. Thus, past connections or demographically insignificant levels of migration may have obscured ecologically significant divisions within species.

Genetic markers that evolve rapidly are now being used, with the expectation that they will provide greater sensitivity for the detection of genetic structure. In some cases, mtDNA surveys appear to have fulfilled this expectation by revealing genetic differentiation on a finer geographic scale than allozyme surveys. However, in addition to evolving at a faster rate, mtDNA can be analyzed in terms of genealogical relationships among sequences. In this paper, theoretical models are used to evaluate methods that use rapidly evolving markers and genealogical information for the analysis of genetic population structure.

RESUMEN

Los marcadores genéticos que evolucionan rápidamente, tales como secuencias variables de ADNmt, proveen oportunidades novedosas para el estudio de poblaciones naturales, aunque su análisis e interpretación representan un reto. Para muchas especies de organismos marinos ha sido difícil detectar una estructura geográfica de la distribución de marcadores genéticos. En estudios de alocimos, la estructura geográfica se ha buscado en la frecuencia de alelomorfos entre poblaciones o lugares. Sin embargo, consideraciones teóricas sugieren que para generar diferencias en frecuencias de alemorfos que sean detectables, es necesario un aislamiento demográfico casi completo durante largos periodos de tiempo. De esta manera, conexiones en el pasado o niveles demográficos insignificantes de migración podrían haber opacado divisiones ecológicas importantes entre especies.

Hoy en día se usan marcadores genéticos que evolucionan rápidamente con la expectativa de que provean una mayor sensibilidad para la detección de patrones genéticos. En algunos casos, estudios de ADNmt parecen llenar esta expectativa, revelando diferencias genéticas en una escala geográfica mas fina que las reveladas por los alocimos. Además de evolucionar rápidamente, el ADNmt se puede analizar en términos de relaciones genealógicas entre secuencias. En este artículo, se usan modelos para evaluar métodos que usan marcadores genéticos que evolucionan rápidamente e información genealógica para el análisis de la genética de la estructura de la población.

INTRODUCTION

Species are generally viewed as composed of loosely connected populations. Populations are thought of as demographic units, and most individuals enter the population as the immediate descendants of others from the same population. But some migration between populations is expected, and it is natural to consider the magnitude of migration in terms of the proportion of individuals that are migrants. This proportion is defined as the migration rate. Thus we might consider a population in which less than one percent of the individuals arrive as migrants (a migration rate of less than 0.01) as a well-defined demographic unit; another population, which receives half of its individuals as migrants (a migration rate of 0.5) might simply be considered as part of a larger demographic unit. Populations are also thought of as genetic units, in the sense that most of the gene pool originates from within the population.

Recently developed techniques, such as DNA fingerprinting, have received much attention because they can be used to determine first-order relationships (e.g., paternity) with a high degree of confidence (Jeffreyes et al. 1985). A simple thought experiment suggests that it should be possible to extend this approach to identify demographic units and assess levels of migration. First, using genetic markers, individual paternity could be established with a high degree of confidence. Once paternity relationships were known, it would be a simple matter to distinguish individuals that were migrants from the progeny

of the residents. In practice, however, we usually cannot trace individual paternity in natural populations. Instead, we sample individuals from multiple populations, and attempt to relate the distribution of genetic variation among these samples to patterns of migration among populations. This approach demands the use of models that predict how demographic processes, such as migration, will affect the distribution of genetic variation.

In this paper, I will briefly review some theoretical models that relate migration to the distribution of genetic variation, and then consider some of the special problems that can be anticipated when we attempt to put these models to use in marine systems. I will then explore alternative approaches with rapidly evolving genetic markers, and offer some predictions on what we can expect from them.

BASIC THEORY

The basic theory that relates migration to the distribution of genetic variation was developed by Wright (1951, 1965). Detailed reviews of more recent extensions of this theory, and their relevance to fisheries management are included in Ryman and Utter (1987). Fertilization is viewed as a process in which pairs of gametes are sampled to form zygotes. If each gamete is represented as a random variable with a value determined by its ancestry, then a correlation coefficient can be defined for the pairs of gametes that combine to form zygotes. Only gametes that trace to a common ancestor, and are thus identical by descent, have the same value. When gametes combine at random, the correlation coefficient is zero. Positive correlation coefficients result when gametes of common ancestry combine more frequently than expected. Wright (1951) defined a set of correlation coefficients ("F-statistics") in terms of the correlations between gametes. Of particular interest here is F_{ST}, defined as "the correlation between random gametes within a population, relative to gametes of the total population" (Wright 1965). Thus if gametes drawn from the same population are more likely to have a common ancestor than gametes drawn from different populations, F_{ST} is positive. It is important to note that "the correlation between gametes" makes no reference to genetic variation, it is based on the ancestry of gametes.

Before the development of molecular genetic markers, the usual way to calculate F_{ST} was from pedigree data (e.g., Wright 1965). But in many situations, including studies of natural populations, pedigree information is not available, and genetic markers are used as an indication of ancestry. If gametes can be distinguished by the alleles they carry, then gametes with a common ancestry will be more likely to carry the same alleles. This is the basis for estimating F_{ST} from genetic data. If allele frequencies vary among populations, this implies that gametes within an individual population are correlated, and F_{ST} has a positive value.

A variety of theoretical models indicate a very robust relationship between F_{ST} and two other parameters: effective population size and migration rate (the proportion of individuals that enter a population as migrants). Here I'll follow the usual convention, and consider the migration rate to be based on individuals that not only physically move between populations, but also are successful at reproduction as well. In these models, the equilibrium value of F_{ST} represents a balance between the process of genetic drift and migration.

Genetic drift occurs when some gametes are by chance overrepresented among those that form zygotes, and the pairing of these correlated gametes increases F_{ST}. The magnitude of this sampling error is inversely related to the "effective population size." The effective population size is generally smaller than the actual number of individuals in the population, because differences in the reproductive contributions of individuals increase the sampling variance for gametes.

The effect of migration is opposite to that of genetic drift. By adding gametes that originated from outside the population to the sample, migration lowers F_{ST}. If both genetic drift and migration are taking place among a large group of populations, F_{ST} will approach an equilibrium value, $\hat{F}_{ST}$:

$$\hat{F}_{ST} = \frac{1}{4N_e m+1} \qquad (1)$$

where N_e is the effective size of each population, and m is the proportion of individuals in each population that are migrants.

There has been some confusion over how F_{ST} should be estimated from actual data, and how it should be interpreted (see Weir and Cockerham 1984). For example, real populations are unlikely to be of uniform size or to exchange migrants equally; thus an "average" F_{ST} must be defined to accommodate this heterogeneity. A more workable quantity, G_{ST}, was introduced by Nei (1973), with provisions for multiple alleles and multiple loci. However, as exemplified by Cockerham and Weir's analysis (1993), it is useful to retain the somewhat abstract definition of F_{ST}, so that it remains independent of the method used for its estimation. In this way, F_{ST} can provide a standard basis for comparison of different methods and approaches. If F_{ST} is defined as a purely demographic parameter—i.e., Wright's (1951) "correlation between gametes"—then, in theory, an accurate estimate of F_{ST} from allozyme data should agree with an estimate based on DNA sequence data. If these estimates did not agree, then it would indicate that at least one of the estimates was wrong. F_{ST} is thus widely used because it should be possible to compare independent

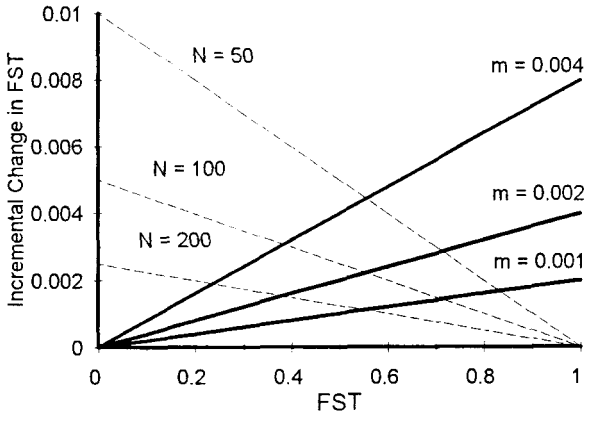

Figure 1. An equilibrium for F_{ST} occurs at the point where the increase due to genetic drift (*dashed lines*) is balanced by the decrease due to migration (*solid lines*). The lines cross over the equilibrium values of F_{ST} for particular combinations of effective population size and migration rate. Several of these combinations yield an equilibrium F_{ST} of 0.56. Because genetic drift is dependent on population size, less migration is needed to achieve this value in larger populations.

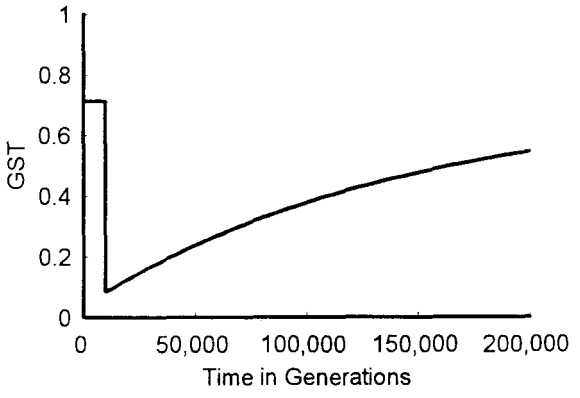

Figure 2. Among large populations, a brief episode of migration can have a long effect on G_{ST}. In this numerical example, the migration rate among populations of 100,000 was raised from zero to 0.1 at generation 10,000, then returned to zero after ten generations. In this example, the equilibrium value of G_{ST} reflects a balance between genetic drift and a mutation rate of 10^{-6}.

measurements of F_{ST} and relate them all to underlying demographic processes. In this paper, I will use F_{ST} to refer to the theoretical demographic parameter, and G_{ST} to refer to statistics that are based on genetic data. Although this convention is not universally applied, it reflects the original definitions of these quantities and avoids the introduction of additional terminology.

F_{ST} AND ESTIMATES OF MIGRATION

Equation 1 implies that the migration rate among a group of populations can be estimated from F_{ST}. However, there are several limitations to this approach. First, the equilibrium value of F_{ST} represents a balance between the opposing effects of genetic drift and migration. But whereas the effect of migration is dependent only on the migration rate, the effect of drift is inversely proportional to population size. Thus in larger populations, the effect of genetic drift is reduced, and a lower migration rate can achieve the same equilibrium value of F_{ST} as would be reached in smaller populations with higher migration rates (figure 1). For example, populations of 100 individuals that exchanged 50% of their individuals as migrants would reach the same F_{ST} as populations of one million with only 0.005% migration. As a consequence of this dependency on population size, very little migration is needed between large populations to keep F_{ST} close to zero.

In the above example, the equilibrium value of F_{ST} would be 0.005. Such small values of F_{ST} are difficult to estimate accurately from population genetic data because they require the detection of small differences in allele frequencies. To further complicate matters, the effective population size, N_e, cannot simply be equated with the number of individuals in the population, but must be adjusted for various factors that would affect the process of genetic drift. These include the sex ratio, the variance in number of offspring per individual, and fluctuations in population size over time. In practice, effective population size can seldom be estimated with much confidence.

A second problem with the interpretation of F_{ST} is the possibility that the populations have not reached an equilibrium between genetic drift and migration. Crow and Aoki (1984) showed that the number of generations, t, for F_{ST} to be near an equilibrium value is:

$$t \approx \frac{1}{2m + \frac{1}{2N_e}} \qquad (2)$$

In most instances, one of the two terms in the denominator will tend to be the major determinant of t. If the migration rate, m, is small relative to $1/2N_e$, populations will slowly diverge under the process of genetic drift, and F_{ST} will approach its maximum value of one. It takes genetic drift approximately $2N_e$ generations to approach this equilibrium. If, on the other hand, the migration rate is relatively high, migrants and residents will quickly become mixed, and F_{ST} will approach zero. Migration requires only about $1/2m$ generations to approach this equilibrium. This behavior implies that although F_{ST} can be rapidly lowered by a high migration rate, the elevation of F_{ST} by a reduction in migration will occur very slowly (see figure 2). Thus observations based on F_{ST} cannot distinguish between the immediate effects of ongoing migration and the residual effects of past migration.

F_{ST} AND MARINE POPULATIONS

Allozyme surveys of marine species with nektonic or extended planktonic life stages have typically shown very

little genetic divergence between geographic locales (for example, see the reviews by Gyllensten 1985, on non-anadromous marine fish, and Burton 1983, on marine invertebrates). Furthermore, reports of genetic divergence with low F_{ST} (or G_{ST}) values should be treated with caution.

There are two components to the variance in allele frequencies among population samples. One is the actual variance in allele frequencies among the populations; the other is the variance due to sampling a limited number of individuals from each population. If corrections are not applied for the latter component of variance, the estimate of F_{ST} will be upwardly biased, and it will appear that there is some population structure when there is actually none.

For example, imagine a group of populations, among which there is a very high level of migration, so that allele frequencies are exactly the same in each population. Samples of 15 individuals are taken from each population, and the frequencies of two alleles at one locus are determined for the samples. The actual allele frequencies in the populations are 0.5, but because of sampling error, the allele frequencies in the samples will vary around 0.5. The expected variance in allele frequencies among the samples would be about 0.008, corresponding to an uncorrected G_{ST} value of 0.03. With equation 1, the estimate for N_em would be 7.25. Thus regardless of how much migration was actually occurring, it would appear that migration was limited to about 7 individuals per generation. For large populations, this would erroneously suggest a very low migration rate (7.25 divided by the population size).

Methods for obtaining unbiased estimates of F_{ST} and related quantities have been developed by Nei and Chesser (1983) and Weir and Cockerham (1984). The latter method also corrects for the sampling error associated with a small number of populations. Unless such methods have been used, small values of G_{ST} cannot be considered good evidence of population structure.

An obvious explanation for the absence of discernible population structure in a marine species is that the potential for dispersal, provided by either passive transport in currents or active swimming, allows sufficient migration to prevent divergence among populations. Marine invertebrates without extended pelagic stages often do exhibit significant population structure (Hedgecock 1994). But lack of population structure can also be explained as an effect of large effective population sizes. Among large populations, the level of migration required to prevent genetic divergence is lowered. Furthermore, the effects of a past migration event would last longer in a large population, again because genetic drift would operate more slowly. Thus when we examine large populations that have the potential for high rates of gene flow, even if this occurs only rarely, it is not surprising to find little evidence of genetic divergence. Unfortunately, we cannot assume that such populations are strongly linked in a demographic sense. For example, consider a group of isolated populations with effective sizes of 100,000. An episode of migration, with a migration rate of ten percent for only ten generations, would eliminate nearly all of the divergence among them. However, if these populations then became completely isolated again, with no migration, it would take hundreds of thousands of generations for genetic divergence to be restored (figure 2). Thus the absence of genetic evidence for stock structure does not imply that such structure does not exist.

ALTERNATIVE APPROACHES

With the availability of new and more powerful molecular tools, more sensitive methods for detecting population genetic structure should be found. We cannot assume, however, that detection of more variation will, by itself, reveal more population structure. For although more sensitive molecular techniques can reveal additional genetic differences between individuals from different populations, the background level of genetic differences between individuals from the same population will also be increased. Our ability to detect population structure depends on finding, on average, more differences between individuals from different populations than between individuals from the same population.

The basic theory described above implies that if the correlation between gametes within a population is weak, it should be equally weak when measured with either moderately polymorphic or highly polymorphic genetic markers. Thus if we cannot differentiate populations with moderately polymorphic markers, highly polymorphic markers may do no better. This is not to say that detecting additional genetic variation isn't of any help at all. For those cases in which earlier attempts have failed to find any genetic polymorphisms, or for those in which the polymorphisms that were found were inadequate for statistical reasons, more suitable markers can probably be found by using molecular techniques.

The best hope for the development of more sensitive methods for analyzing population structure may lie not with the detection of more genetic variation, but rather with the detection of different kinds of variation. The first indication of this came about with studies of mitochondrial DNA variation in animal populations. In some cases, surveys of mtDNA appeared to provide a much more detailed picture of geographic variation than had allozymes (Avise et al. 1987; Moritz et al. 1987). This could be due in part to the maternal inheritance of mtDNA. Because females pass on a single mtDNA genotype to progeny, the effective population size for mtDNA is probably smaller than that for nuclear genes,

including those encoding most allozymes, which are present in two copies per individual and subject to biparental inheritance. A smaller effective population size would accelerate genetic drift, and thus increase divergence among populations. But even without this presumed effect of maternal inheritance, the very nature of mtDNA data would provide a different view of genetic population structure than that seen with allozyme data. This is because the polymorphisms detected in mtDNA molecules can be used to infer genealogical relationships (Avise et al. 1987).

The genealogical dimension of mtDNA data makes it possible to apply methods of analysis that could not be used with allozyme data. For example, the principles of cladistics can be applied to mtDNA variation within a species or population. In the cladistic approach to systematics, "characters" shared among groups of organisms are used to place them into hierarchical groups, or "clades." This hierarchy of groups is represented as a phylogenetic tree. One of the major tools of cladistics, parsimony analysis, identifies the phylogenetic tree that requires the least number of character transformations.

Slatkin and Maddison (1989) developed a method to estimate the product of effective population and migration rate (N_em) from a phylogenetic tree of the mtDNA within a species. This method treats the geographic location of each individual as a character, and uses a parsimony analysis to determine the minimum number of migration events that could reconcile this location "character" with the mtDNA phylogeny. Computer simulations provide a simple function to convert the minimum number of migration events to an estimate of N_em.

Neigel et al. (1991) observed that in many animal species, mtDNA variants (referred to as haplotypes) do not appear to have reached equilibrium distributions across the species' range. Groups of related mtDNA haplotypes, which represent maternal lineages, are often clustered geographically. Whereas geographic clustering of individual haplotypes could be explained by drift, the clustering of multiple related haplotypes implies that the association is historical. A model was proposed in which each new mtDNA lineage begins with a single individual at a specific location, and then disperses from that point over multiple generations. Dispersal is not limited to movements between distinct populations, but is limited by absolute distance. Individual haplotypes represent the youngest lineages; older lineages are composed of groups of related haplotypes. The model predicts that if dispersal is constant over time, the variance of a lineage's geographic distribution should be proportional to its age.

Furthermore, if the ages of mtDNA lineages can be estimated in generations, a standardized single-generation dispersal distance can be estimated from mtDNA data.

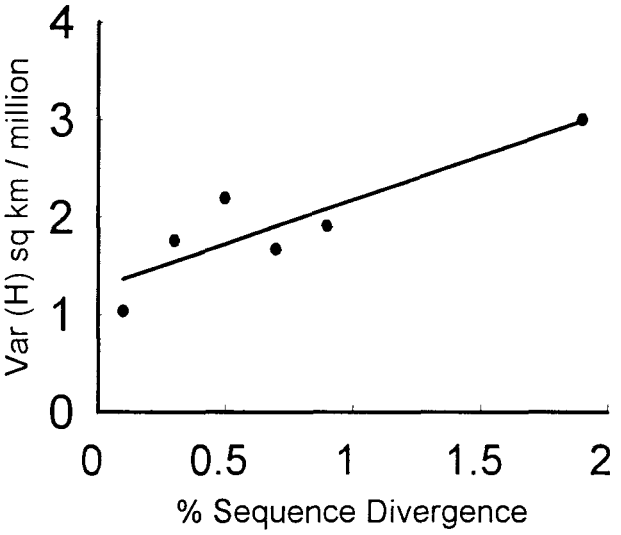

Figure 3. The relationship between the ages of mtDNA lineages and the variances of their geographic distributions in the American oyster, *Crassostrea virginica*. The positive slope of this relationship indicates that younger lineages have not achieved equilibrium distributions, and corresponds to a single-generation dispersal distance of 3.3 km.

This concept was tested further by Neigel and Avise (1993), who analyzed nine mtDNA data sets, including data from the American oyster, *Crassostrea virginica*; the American eel, *Anguilla rostrata*; and the hard-head catfish, *Arius felis*. Of these three marine species, only the American oyster showed evidence of nonequilibrium distributions. As shown in figure 3, the geographic distributions of older lineages have higher variances. The slope of this relationship corresponds to a single-generation dispersal distance of 3.3 km.

In retrospect, it is not surprising that the genealogical nature of mtDNA variation has suggested new approaches for the analysis of genetic population structure. The basic theory represented by the use of F_{ST} as a population structure parameter has now been extended to include maternally transmitted mtDNA (Takahata and Palumbi 1985) as well as genealogical relationships among DNA sequences (Slatkin 1991). However, these alternative methods of analysis still require that the frequencies of genetic variants have diverged between populations, and thus the methods are of no help if divergence is lacking.

What is more surprising is that some populations that exhibited very little divergence in allozyme allele frequencies have been found to differ sharply in mtDNA. One of the most dramatic examples is provided by studies of the American oyster, *Crassostrea virginica*. The contrast between the results of an allozyme study conducted by Buroker (1983) and a mtDNA study conducted by Reeb and Avise (1990) are shown in figure 4. Although allozyme frequencies at most loci are similar among these populations, there is a sharp division in mtDNA variation that separates Atlantic and

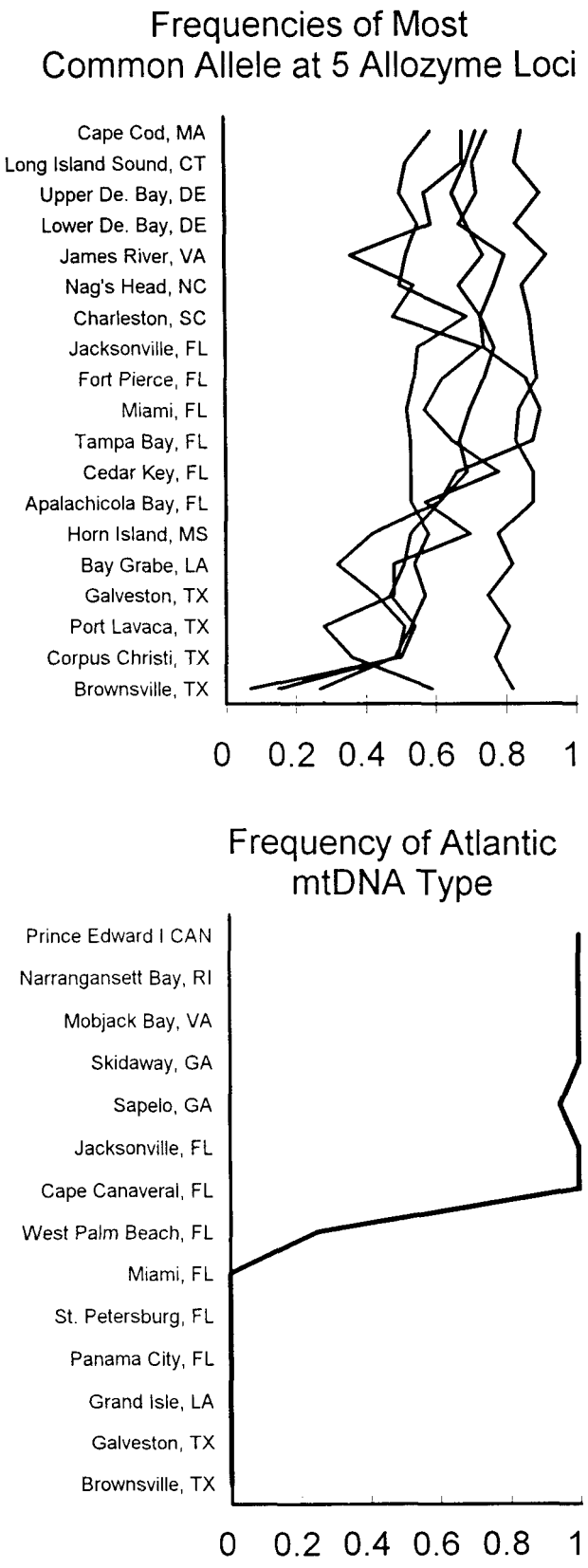

Figure 4. Geographic variation in frequencies of allozyme alleles and mtDNA haplotypes in the American oyster, *Crassostrea virginica*. *Upper panel*, frequencies of most common allele at 5 allozyme loci (Buroker 1983). *Lower panel*, frequency of Atlantic mtDNA type (Reeb and Avise 1990).

Gulf of Mexico populations. This difference in resolution is clearly not due to the greater variability of mtDNA. Even if only the two major lineages of mtDNA were distinguished, the pattern would still be very clear. It also seems unlikely that a difference in effective population size could produce such a dramatic difference between allozyme and mtDNA distributions. The difference in F_{ST} for these data sets corresponds to over a hundredfold difference in Nm. In the case of the American oyster, it appears that either allozymes, mtDNA, or both are not behaving as predicted by the basic theory that links migration to genetic divergence. Because this theory assumes that the genetic markers in question are not subject to natural selection, one possibility is that the frequencies of allozyme alleles are held constant by natural selection, while mtDNA variants are subject to genetic drift.

Support for this interpretation was recently provided by a study of nuclear DNA sequence polymorphisms in the American oyster. Karl and Avise (1992) examined variation in "anonymous" nuclear single copy DNA sequences, which for the most part do not appear to encode proteins, and would therefore not be subject to the same forms of selection that would act upon genes that encode allozymes. Although these nuclear DNA sequences were only moderately polymorphic, they clearly separated Gulf of Mexico and Atlantic populations and therefore corroborated the mtDNA pattern.

The complete replacement of one form of mtDNA with another, as well as the extent of mtDNA sequence divergence between Atlantic and Gulf of Mexico populations of American oyster, suggests a long period of complete demographic isolation, such as would be expected of distinct species. This is a crucial point, because although mtDNA proved to be a better tool than allozymes, it was not by virtue of detecting weak population structure. Apart from the major Gulf/Atlantic division, the mtDNA survey of Reeb and Avise (1990) revealed very little population structure. For example, it did not distinguish oysters from individual embayments. This is consistent with other surveys of mtDNA in marine species, many of which have failed to reveal any significant population structure (Ovenden 1990).

CONCLUSIONS

Two basic approaches can be followed in future applications of molecular markers to detect and quantify the weak genetic population structure expected in marine systems. First, more refined estimates of F_{ST} could be made by increasing both the number of polymorphic loci and the number of individuals sampled. As discussed above, it is not enough to find differences in the frequencies of genetic markers among population samples;

these differences must be shown to be statistically significant. For this approach, nuclear DNA markers may be superior to mtDNA. Although it is not a trivial matter to identify nuclear DNA polymorphisms (see Karl and Avise 1993), the sampling of multiple independently segregating loci is only possible with nuclear markers. Furthermore, there is no clear benefit to using an extremely polymorphic molecule. Excessive polymorphism can actually obscure genetic population structure if the markers fail to reveal similarities as well as differences. Development of new technologies for screening DNA polymorphisms, such as denaturing gradient gel electrophoresis (Myers et al. 1986), should allow larger numbers of individuals to be sampled, perhaps in the range of several thousand. Such large sample sizes would extend the statistical power of conventional approaches to the detection of genetic population structure.

A second, more daring approach is to experiment with novel genetic markers, with the hope that some may prove especially good at detecting genetic population structure. If mtDNA has occasionally revealed previously unseen population structure, other markers may do so as well. Recently, Turner and co-workers (1991) reported a highly repetitive DNA sequence in pupfishes (*Cyprinodon variegatus*) that exhibits extreme uniformity within populations, but marked divergence between populations along the Atlantic coast of North America. In contrast, allozyme surveys have not differentiated these populations (Darling 1976; Duggins et al. 1983). One possibility is that, as suggested for the American oyster, allozyme alleles in pupfish populations are maintained at nearly constant frequencies by selection. The divergence of repetitive sequences may then simply represent normal genetic drift. Another, more tantalizing, possibility also exists. Other repetitive sequences, such as those that code for globin genes, are known to exhibit a phenomenon called "concerted evolution" (Zimmer et al. 1980), in which copies of a sequence within a lineage diverge more slowly than homologous sequences in different lineages. If concerted evolution occurs at the level of populations, it is conceivable that an unusually high proportion of variation in repetitive sequences may be partitioned among populations.

It has often been difficult to detect genetic differences between populations of marine species that have planktonic larvae. If genetic differences are in fact present, molecular methods that can increase sample sizes and identify novel kinds of markers may help to surmount this hurdle. Once genetic differences between populations are detected, the new statistical tools that have been developed from theoretical population genetics can be used to analyze these differences, and should provide new insights into the biology and history of marine populations.

ACKNOWLEDGMENTS

Discussions with John Avise, Marty Ball, and Bob Zink have contributed to my ideas about gene flow and mitochondrial DNA. I am also indebted to Monty Slatkin for valuable advice, criticism, and encouragement. Comments by Dennis Hedgecock and an anonymous reviewer about an earlier draft of this paper were most helpful. Support for my work has been provided by grants from the NSF EPSCoR program, and the Louisiana Education Quality Support Fund.

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PHYLOGEOGRAPHIC PATTERNS IN CALIFORNIA STEELHEAD AS DETERMINED BY MTDNA AND MICROSATELLITE ANALYSES

J. L. NIELSEN
Hopkins Marine Station
Stanford University
Pacific Grove, California 93950

USDA US Forest Service
Pacific Southwest Research Station
800 Buchanan Street
Albany, California 94710

C. GAN
USDA US Forest Service
Pacific Southwest Research Station
800 Buchanan Street
Albany, California 94710

J. M. WRIGHT
Marine Gene Probe Laboratory
Department of Biology
Dalhousie University
Halifax, Nova Scotia B3H 4J1
Canada

W. K. THOMAS
Department of Molecular and Cell Biology
401 Barker Hall
University of California
Berkeley, California 94720

School of Biological Science
University of Missouri
510 Rockhill Road
Kansas City, Missouri 64110-2499

EXTENDED ABSTRACT

Polymerase chain reaction (PCR) and direct sequencing of mtDNA and microsatellites were used to test genetic diversity and biogeographic distributions in putative wild (N = 32) and hatchery (N = 6) populations of steelhead trout (*Oncorhynchus mykiss*) in California. Total genomic mtDNA was extracted nonintrusively from fin tissue (2 mm^2) taken from 426 wild fish and 66 hatchery fish throughout California. Extraction, amplification, and visualization of mtDNA followed methods given in Nielsen et al. (1994). Mitochondrial types were derived from analysis of base pair differences found in a highly variable region of the 3' end of the salmonid mtDNA control region (196 bp) and a 5 bp section of the adjacent phenylalanine tRNA. Nucleotide variation was found at nine sites (4.5%), and 13 different steelhead mtDNA types were identified in California (table 1). Distribution of steelhead mtDNA types in wild fish captured along the coast of California showed a distinct biogeographic frequency gradient, with different mtDNA types dominating broad geographic areas (figure 1). Hatchery populations in the same geographic areas lacked any similar biogeographic cline (Nielsen et al. 1994).

A subset of the same wild individuals used for mtDNA analysis (N = 144) was investigated for dispersed repetitive nuclear DNAs by means of PCR amplification and

TABLE 1

Steelhead (*Oncorhynchus mykiss*) mtDNA Types Found in 32 Streams and 6 Hatcheries throughout California, 1990–1993

		Variable sites								
mtDNA type	N	63	86	94	96	130	148	151	154	194
ST1	161	T	G	T	T	T	A	A	G	G
ST2	33	C	G	T	T	T	A	A	G	G
ST3	88	T	G	T	T	T	A	A	A	G
ST4	7	T	G	T	T	C	G	A	G	G
ST5	59	T	G	T	T	C	G	*	G	A
ST6	10	T	G	C	T	C	G	*	G	A
ST7	9	T	G	T	T	C	A	A	G	A
ST8	69	T	G	T	T	C	A	*	G	A
ST9	9	T	G	T	T	T	A	A	G	A
ST10	1	T	G	T	C	T	A	A	A	G
ST11	0	T	A	T	T	T	A	A	G	G
ST12	30	T	G	T	T	C	A	*	G	G
ST13	15	T	G	T	T	C	G	*	G	G
ST14	1	C	G	T	T	T	A	A	A	G
TOTAL	492	California steelhead: hatchery and wild								
	426	California steelhead: wild stocks only								

The number of fish (N) found in this study is given for each type. An asterisk (*) represents a nucleotide deletion. Type #11 was found only in steelhead outside of California.

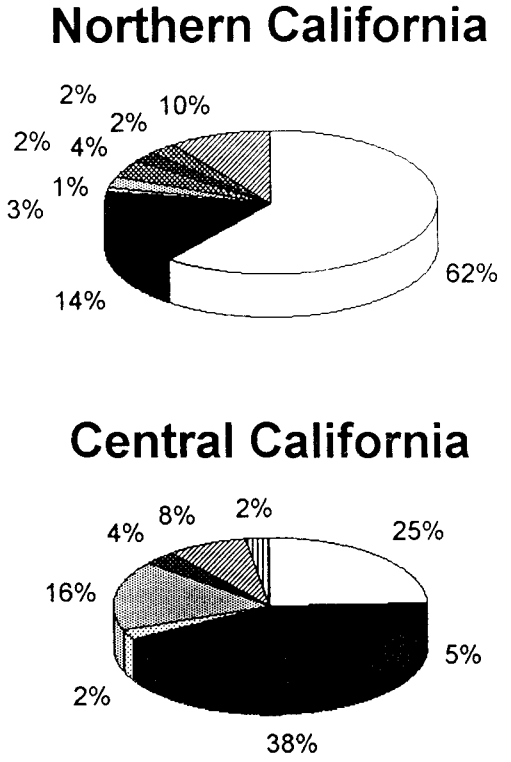

Figure 1. Frequency distributions of wild steelhead mtDNA types found throughout California. The northern range extends from the mouth of the Eel River (Humboldt County) to the Navarro River (Mendocino County); the central range is from the Russian River (Sonoma County) to the Carmel River (Monterey County); the southern range runs from Santa Rosa Creek (San Luis Obisbo County) to Malibu Creek (Los Angeles County).

a microsatellite probe (OMY77) developed in the Marine Gene Probe Laboratory at Dalhousie University by J. M. Wright. This probe disclosed twenty microsatellite alleles, ranging in size from 80 to 141 bp, in California steelhead (J. L. Nielsen, unpublished data). The bimodal

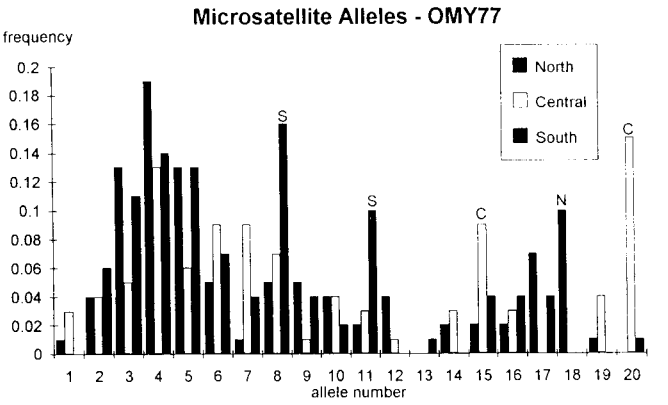

Figure 2. Frequency distribution of microsatellite alleles (given sequentially by size) obtained from analysis of 144 wild California steelhead, using the microsatellite probe OMY77, developed at Dalhousie University by J. M. Wright. Geographic ranges used to compare frequencies were the same as those given in figure 1. The letters indicate alleles where southern (S), central (C), or northern (N) frequencies were significantly different from those calculated with chi-square analysis ($p < 0.05$) for the other geographic areas.

frequency distribution of nuclear alleles, amplified by OMY77, was biogeographically distinct for alleles and geographic location (figure 2; likelihood chi2 = 129.7; d.f. = 38, $p < 0.001$). Chi-square analysis of frequency distributions within each microsatellite allele showed five alleles that occur at significantly different frequencies (contingency chi-square, $p < 0.05$) for different geographic areas. Further nuclear biogeographic resolution may be gained with additional microsatellite probes under investigation in our laboratory.

Parsimony analysis of the anadromous steelhead populations (PAUP V3.0) showed no significant geographic monophyletic relationships and supported significant gene flow between steelhead populations along the California coast (J. L. Nielsen, unpublished data). Some mtDNA types (#5, #6, and #8), however, remain relatively isolated in southern California. An area cladogram using character compatibility was run on 17 anadromous steelhead streams in California (CAFCA; M. Zandee, Dept. Theoretical Biology, P. O. Box 9518, 2300 RA Leiden, Netherlands.) This program combines a maximum parsimony tree with a presence-absence matrix based on geographic location. CAFCA added resolution to the hypothesis of recent reproductive isolation of southern steelhead populations by portraying all the southern steelhead streams as a single biogeographic clade (figure 3).

Ocean conditions contributing to the relative reproductive isolation of California steelhead genotypes leading to the mtDNA biogeographic cline remain speculative. An aquatic biogeographic species boundary running southwest from around Point Conception into the Pacific Ocean (Hedgecock et al. 1992) parallels the northern division of steelhead genotypes found primar-

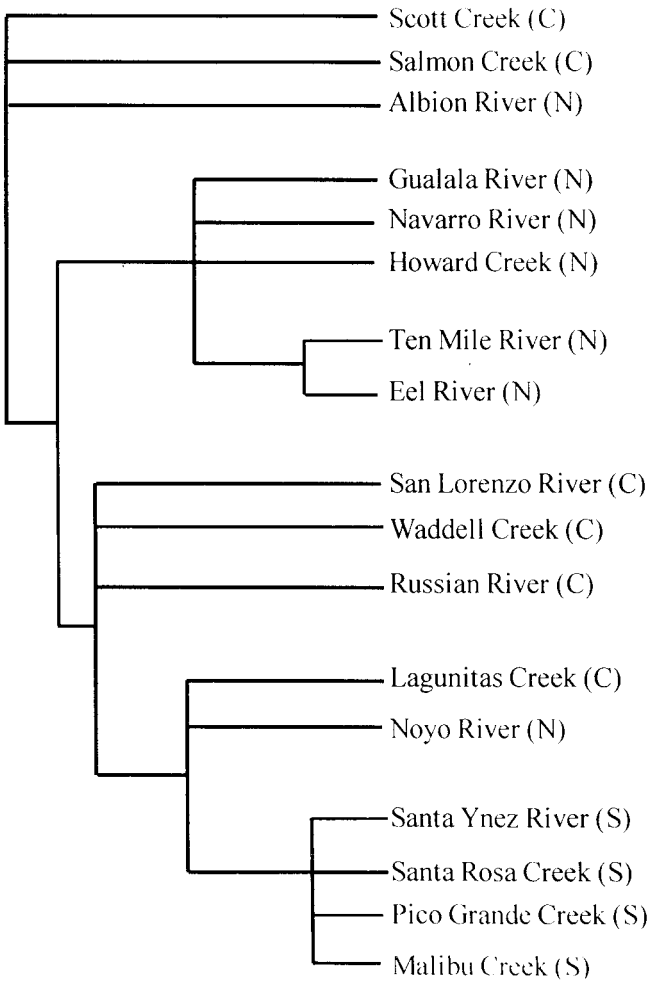

Figure 3. Area cladogram showing biogeographic character compatibility in 17 California steelhead streams from different geographic areas. Results were plotted after analysis of a maximum parsimony tree using PAUP V3.0 and the biogeographic function of CAFCA (available from M. Zandee, see text for address). Geographic stream locations are given as letter codes: N = northern; C = central; S = southern.

ily in southern California. This suggests that ocean currents along the southern California coast may have played a role in the distribution of southern steelhead lineages found in this study. At about 32° N the California Current turns eastward, flowing into the Southern California Bight, creating an oceanic gyre that ends in a strong oligotrophic front (the Ensenada Front) at the center of the bight (Lynn and Simpson 1987; Thomas and Strub 1990). Unique southern steelhead mtDNA types are found in streams that enter the ocean from about 36°30' N (Santa Rosa Creek) to 34° N (Malibu Creek); however, their historic distribution extended farther south into Baja California (about 32° N). Their distribution remains within the richer nutrient areas of the gyre along the southern California coast (Strub et al. 1991). Spring and summer nearshore movements of steelhead smolts as they enter the ocean environment in southern California may remain localized in these areas. Subsequent adult oceanic migration behavior based on prevailing oceanic currents may also have contributed to the isolation of southern steelhead genotypes in California. The presence of northern genotypes, in low frequencies, in most southern anadromous steelhead populations suggests continued gene flow from north to south along the coast following the general direction of the California Current.

Putative relic steelhead populations, separated from the ocean by water impoundment dams built at the turn of the century, were found in our study to have genotypes endemic to their local geographic range as shown in contemporary anadromous stocks (Santa Ynez River, Sespe Creek, Matilija Creek). This suggests that southern steelhead stocks are not the result of recent anthropomorphic manipulation, and must be viewed in an evolutionary context.

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Part III

SCIENTIFIC CONTRIBUTIONS

DISTRIBUTION OF EGGS AND LARVAE FROM SARDINE AND ANCHOVY OFF CALIFORNIA AND BAJA CALIFORNIA, 1951–1989

SERGIO HERNANDEZ-VAZQUEZ
Centro de Investigaciones Biologicas del Noroeste, S.C.
Km. 1 Carr. San Juan de La Costa "El Comitan"
Apartado postal 128
La Paz, B.C.S., México 23000

ABSTRACT

The CalCOFI data set for sardine and anchovy eggs and larvae from 1951 to 1989 formed the basis of this analysis. The seasonal pattern is described on a monthly basis; for the geographical analysis the CalCOFI area was divided into alongshore regions and offshore-onshore regions. The percentage of positive stations was used to describe the seasonal and geographical patterns of sardine and anchovy eggs and larvae. Two seasonal spawning patterns for sardine are described: one associated with the Southern California Bight area (northern pattern) and another located off Punta Eugenia, Baja California Sur (B.C.S.), Mexico (southern pattern). The northern pattern takes place from February to June–July; the southern pattern occurs from August to October. The transition zone between patterns could be Punta Baja, Baja California, Mexico. In contrast, the spawning pattern described for anchovy shows no geographical variations from Point Conception, California, to Magdalena Bay, B.C.S., and takes place from December to April, with high numbers of eggs and larvae in the Southern California Bight; there is, however, a secondary spawning center in the Punta Eugenia region.

RESUMEN

El presente análisis se fundamenta en la base de datos de "CalCOFI" de huevos y larvas de sardina y anchoveta de 1951 a 1989. Se describen los patrones estacionales sobre una base mensual. Para el análisis geográfico, se usaron diversos criterios: el área total abarcada por los muestreos "CalCOFI", y subdivisiones de ésta área, por región a lo largo de la costa, y por regiones costeras *vs.* regiones en mar adentro. Se usó el porcentaje de estaciones con presencia de huevos y larvas de sardina y anchoveta para describir los patrones estacionales y geográficos. Se describen dos patrones estacionales de desove para la sardina. El patrón "norteño" ocurre de febrero a junio–julio al sur de California, mientras que el "sureño" ocurre de agosto a octubre en Punta Eugenia, Baja California Sur (B.C.S.), México. La zona de transición entre ambos patrones podría ser Punta Baja, Baja California, México. En contraste, el patrón de desove de la anchoveta no varía geográficamente desde Point Conception, California, hasta Bahía Magdalena, B.C.S., y ocurre de diciembre hasta abril con máximos de huevos y larvas en el sur de California. Existe asimismo un punto de desove secundario en el área de Punta Eugenia.

[Manuscript received January 15, 1994.]

INTRODUCTION

The distribution and abundance of sardine (*Sardinops sagax*) and anchovy (*Engraulis mordax*) eggs and larvae in the California Current system have been intensely studied since the end of the 1940s, when the California Cooperative Oceanic Fisheries Investigations Program (CalCOFI) was established. This program was designed to obtain information about the causes of the great decline in sardine catches (Chelton et al. 1982). CalCOFI carried out oceanographic/biológical cruises on a monthly basis from Cape Mendocino, California, to Cabo San Lucas, Baja California Sur (B.C.S.), Mexico, to more than 200 nautical miles offshore.

In this paper I use the extensive CalCOFI data set to describe the distributional and abundance patterns of sardine and anchovy eggs and larvae observed during the 1951–89 period. Moser et al. (1993) presented a global analysis of the whole CalCOFI area; here I explore detailed area/time windows to find seasonal trends. No interannual variations are accounted for because they are the subject of a second paper in preparation. The seasonal variation is described, and its possible causes are discussed.

Sardine and Anchovy Fishery/ Population Fluctuations

Even a superficial review of catch statistics of the small pelagic fishes of eastern boundary currents shows one feature: great fluctuations in their catches (and certainly in their abundance) on annual and decadal scales. The years considered in this analysis (1951–89) do not include the period when great concentrations of sardine existed in the northern half of the CalCOFI area (California). In the 1930s and 1940s, the sardine catches in California were more than 500,000 tons in some years, but the fishery dramatically decreased at the beginning of 1950s. In the 1960s the California sardine fishery virtually disappeared, but a small Mexican fishery, less than 50,000 tons per year, was maintained on the west coast of Baja California. Barnes et al. (1992) present data on

the fluctuations of sardine biomass off California and northern Baja California from 1933 to 1991, and show that the sardine population began to decline in the early 1940s and reached its lowest levels in the mid 1970s. Thus it must be realized that the information described in this paper was primarily taken while the sardine population off California and northern Baja California (B.C.) was low.

The highest catches for the California anchovy fishery were made in the mid 1970s, with a maximum of 141,000 tons in the 1975–76 season. In the last ten years (1982–92), the annual average California catches were not over 3,000 tons; the Mexican fishery at Ensenada, B.C., fluctuated between 170,000 and 100 tons.

Sardine and Anchovy Spawning Range and Seasonality

It is known that in the 1930s, when a large Canadian sardine fishery existed, sardines spawned during summer as far north as British Columbia (Walford and Moser 1941). But sardines have been virtually absent from the region north of California since the 1950s and have only recently reappeared there. Clark (1934) showed that sardines spawn off California from February to August, with a peak in April–May. Scofield (1934) reported that the main areas of spawning were located between San Diego and Point Conception, with sporadic spawning as far north as San Francisco and as far south as Magdalena Bay, B.C.S. The cruises analyzed by Scofield were carried out during spring and early summer in 1929–32; only a few stations were located along the Mexican coast. The importance of the Scofield study is that it was made when sardine populations were at a high level in California. Before the development of the CalCOFI program, several authors suggested that sardine spawning off California was concentrated during spring and summer (Tibby 1937; Janssen 1937; Sette and Ahlstrom 1948).

Based on the more extensive coverage of the CalCOFI program, Ahlstrom (1954) described two main spawning areas for the sardine. The first is an area of intensive spawning off the central part of the Baja California peninsula. In this area spawning peaks from February to May, but eggs appear throughout the year in the Vizcaino, B.C., region. The second, larger area includes the Southern California Bight (SCB) and northern portion of the Baja California peninsula. In this region spawning peaks in April–June. Ahlstrom (1954) reported that during 1950–51 more than 80% of sardine spawning was concentrated off of central Baja California.

Ahlstrom (1960) suggested that a group of sardines spawns in the Southern California Bight from April to June, and from January to June in warmer years; another group spawns off the central and southern part of Baja California throughout the year, with peaks in both winter and summer. Also, he mentioned sporadic sardine spawning north of Point Conception from May to August.

Kramer and Smith (1971) used the CalCOFI 1951–60 data set for sardine eggs and larvae to suggest that "Two major centers of spawning are evident first in January in small areas off central Baja California and southern California . . . With the passage of time the southern groups spread northward and seaward; then in May and June, they intermix with the northern group, which spreads somewhat southward. In July, the two groups are separate again and, in October, heavy spawning occurs only off central Baja California."

Lluch et al. (1992) analyzed sardine spawning during the 1950s off California and Baja California and found that spawning started early in the year near Punta Eugenia, B.C.S. During spring, sardine populations expand both northwards and southwards; in the north they reach the Southern California Bight from March to July. When spawning ceases there, sardine distribution contracts again to the Punta Eugenia area, where spawning takes place year-round. Moser et al. (1993) present the patterns for sardine eggs and larvae for 1951–84. Moser et al. found a major spawning area in the Punta Eugenia region, where spawning occurs throughout the year, with a maximum from January to September. Moser et al. also show a spawning center in the Southern California Bight area during April–June, although some eggs are present there all year. Off central Baja California eggs are concentrated in the first ten nautical miles; in the northern part of the peninsula and in the Southern California Bight eggs have a broader offshore distribution.

Regarding anchovy, Ahlstrom (1966) showed that larvae are distributed from Oregon to Punta San Juanico, B.C.S. A number of researchers have described the seasonal pattern of anchovy spawning in the southern California and northern Baja California region, using the presence of eggs and larvae in the CalCOFI data set, and gonad maturity information from adult anchovies. Lasker and Smith (1977), Chavez et al. (1977), Parrish et al. (1986), and Moser et al. (1993) state that anchovy spawning is concentrated from February to April in the Southern California Bight, although anchovy eggs and larvae and actively spawning adults are present throughout the year. Chavez et al. (1977) found mature anchovies during February–May in the Ensenada region.

Several authors have postulated environmental mechanisms that may explain the distribution and timing of sardine and anchovy spawning in the California Current. Parrish et al. (1983) suggested a strong relationship between the sea-surface temperature, turbulence and transport, and reproductive success. Lluch-Belda et al. (1991) proposed a hypothesis relating the upwelling index and

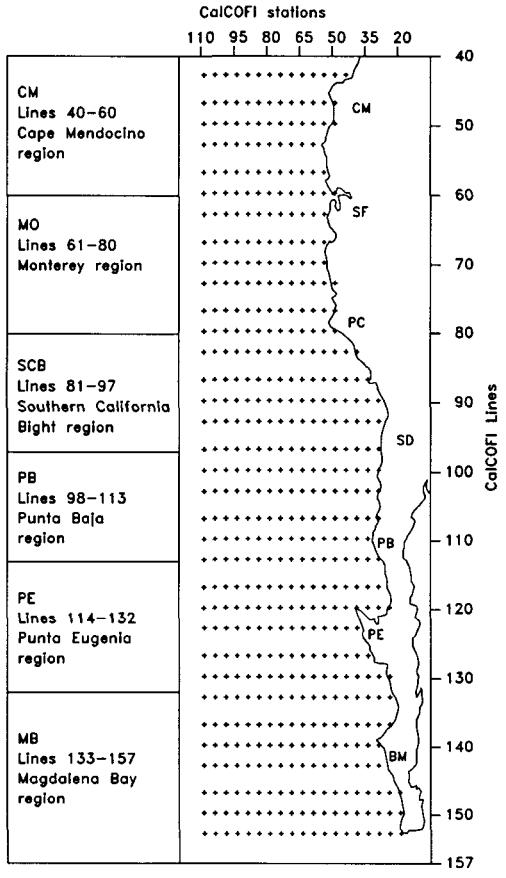

Figure 1. Basic CalCOFI grid, with the geographic areas used in this analysis (1951–89). CM = Cape Mendocino, Calif.; SF = San Francisco; PC = Point Conception; SD = San Diego; PB = Punta Baja, B.C.; PE = Punta Eugenia, B.C.S.; and MB = Magdalena Bay).

sea-surface temperature to the distribution of sardine eggs and larvae on a yearly basis.

DATA AND METHODOLOGY

The CalCOFI data set for sardine and anchovy eggs and larvae for the 1951–89 period formed the basis of this analysis. The CalCOFI basic grid consists of an array of lines and stations (Eber and Hewitt 1979). Lines are perpendicular to the coast at intervals of 40 nautical miles (n.mi.). Stations are parallel to the coast, and separated by 4 n.mi. (figure 1). For each CalCOFI station the data base includes the date (year, month, and day), time, geographical position (CalCOFI line/station code), sea-surface temperature (0–10 m), and the number of sardine and anchovy eggs and larvae (standardized to 10 m^2 of sea surface).

For the purpose of this paper the seasonal pattern is described on a monthly basis, and the geographical analyses utilize four different criteria as follows (figure 1):

1. All CalCOFI stations combined (global analysis).
2. The CalCOFI area divided by alongshore regions: Cape Mendocino (CM) region, 40–60 lines; Monterey (MO) region, 61–80 lines; Southern California Bight (SCB) region, 81–97 lines; Punta Baja (PB) region, 98–113 lines; Punta Eugenia (PE) region, 114–132 lines; and Magdalena Bay (MB) region, 133–157 lines.
3. By CalCOFI line.
4. Cross-shelf analysis: distance to the coast.

The CalCOFI line analysis used the standard CalCOFI lines (90, 93, 97 . . . .) because these lines were systematically sampled, whereas the intermediate lines—91, 92, 96—were omitted (of all stations sampled during the 1951–89 period only 5.6% were located in these intermediate CalCOFI lines). The other three analyses included all CalCOFI lines.

The percentage of positive stations was used to describe the seasonal and geographical pattern of occurrence of sardine and anchovy eggs and larvae for each of the four criteria. Some authors have used egg and larval density (the average number per station); others, however, have expressed doubts, because density may be biased if a sample is taken near a spawning adult. Nevertheless, both indices are very well correlated; to be certain, I analyzed all of the series and found them to be correlated beyond the 0.01 level.

The geographical and temporal coverage of the CalCOFI surveys varied widely during the 1951–89 period covered by this analysis. From 1951 to 1960, surveys were made monthly (only 6 months were not covered) and the latitudinal coverage was best from the north of Magdalena Bay (CalCOFI line 133) to Point Conception (CalCOFI line 80). Only 25% of surveys extended to the north and/or south of this area. Hewitt (1988) graphically described the temporal and spatial coverage surveys for the 1949–87 CalCOFI period. In summary, the geographical and seasonal coverage of the CalCOFI surveys is best from the Punta Eugenia area to the Monterey area and in the months from January to July; data are poorest in the Cape Mendocino region and in the months of September, November, and December.

The number of stations sampled per month was greatest in the first part of the year (table 1). From January to July more than 2,500 stations were sampled each month, whereas from August to December (except October), no more than 1,300 stations were sampled per month. The number of stations per CalCOFI line, in general, was less than 100 from August to December (except October), but lines 90–93 (located in the Southern California Bight region) had more than 100 stations sampled per line. From January to July, more than 100 stations per line were sampled from line 80 (Point Conception) to line 130 (Punta Eugenia).

The surveys generally occupied stations as far offshore as station 90 (150 to 300 n.mi., depending on CalCOFI

TABLE 1
Number of Stations Sampled in the CalCOFI Area, by Line and Month, 1951–1989

CalCOFI line	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total line	Areas*	Total areas
40	11	6		9	18	8	23	6		7	2		90		
43	10	1		6	4	3	15	3		6			48		
47	8	1	2	3	3	3	14	2					36		
50	8	9		7	17	19	26	5		7	7		105		
53	6	8		4	3	11	13	3		3			51		
57	6	8		4	3	12	15	3		3			54		
60	113	37	44	144	72	64	147	30	25	67	40	13	796		
63	72	46	37	95	61	43	87	23	5	40	20	11	540		
67	73	53	39	101	57	50	88	25	6	41	22	12	567		
70	118	47	50	129	96	69	125	33	17	54	38	12	788		
73	72	58	63	88	68	43	76	21	5	44	21	10	569		
77	88	88	84	105	105	63	97	47	16	65	42	14	814		
80	177	125	122	171	140	97	145	84	70	104	68	52	1355		
83	156	142	119	175	179	122	164	57	56	131	69	45	1415		
87	159	208	127	212	203	139	189	67	68	148	69	71	1660		
90	234	216	192	251	258	191	222	125	135	192	103	108	2227	CM	1204
93	201	237	221	230	245	205	220	101	127	201	94	91	2173	MO	4771
97	167	185	167	208	121	223	202	57	50	169	39	61	1649	SCB	9746
100	182	172	149	224	140	195	208	73	52	167	49	64	1675	PB	7218
103	137	153	110	221	119	186	172	49	39	126	17	53	1382	PE	6242
107	120	144	106	205	122	158	184	45	39	125	17	60	1325	MB	2716
110	141	174	138	187	157	148	183	96	50	131	44	65	1514	Sum*	31897
113	99	154	105	191	119	137	172	54	49	117	3	61	1261		
117	111	163	114	199	136	127	207	62	62	114	17	58	1370		
120	136	196	164	208	170	134	215	112	72	160	49	79	1695		
123	57	111	90	115	79	58	129	57	33	83	20	43	875		
127	46	122	81	117	81	58	124	67	27	90	19	39	871		
130	64	153	100	132	105	68	124	95	37	115	41	44	1078		
133	65	124	79	137	74	53	107	79	22	95	19	34	888		
137	70	120	79	120	85	56	105	65	22	89	31	27	869		
140	35	50	18	36	10	20	6	15	7	7	21	6	231		
143	36	29	17	24		9		10	3	7		6	141		
147	34	33	13	34		5		9	4	9		6	147		
150	35	33	18	17		22		9	10	9	14	6	173		
153	34	29	7	28		9		2	3	12		3	127		
157	37	28	9	12		20			2		11	3	122		
Total*	3338	3580	2788	4224	3137	2936	3903	1679	1234	2821	1050	1207			

*Includes intermediate CalCOFI lines (41, 42, . . . , 55, 56, . . . , 98, 99, . . . etc.)

line), but 14% of the surveys did not extend beyond CalCOFI station 80 (table 2).

RESULTS

The results are presented for four geographical perspectives, from a global CalCOFI view to regional cross-shelf views for both sardine and anchovy; each perspective includes a seasonal analysis. The larvae/egg ratio for the global and subarea analyses is also presented.

Global Analysis for Entire CalCOFI Area

For both sardine and anchovy, larvae were taken at more stations than were eggs. The total number of sampled stations during 1951–89 was 31,897; 2,089 (6.5%) were positive for sardine eggs; 2,877 (9.0%) for sardine larvae; 7,147 (22.4%) for anchovy eggs; and 15,012 (47.0%) for anchovy larvae. The corresponding values for the mean number of eggs and larvae per station were

TABLE 2
Frequency of Occurrence of Each Station as the Most Offshore Location Sampled, 1951–1989

CalCOFI station	Percent
40	1.47
50	1.10
60	3.68
70	4.04
80	3.68
90	30.51
100	23.16
110	3.68
120	12.87
130	1.47
140	3.68
150	0.74
160	1.47
170	0.37
180	1.10
190	0.00
200	6.99

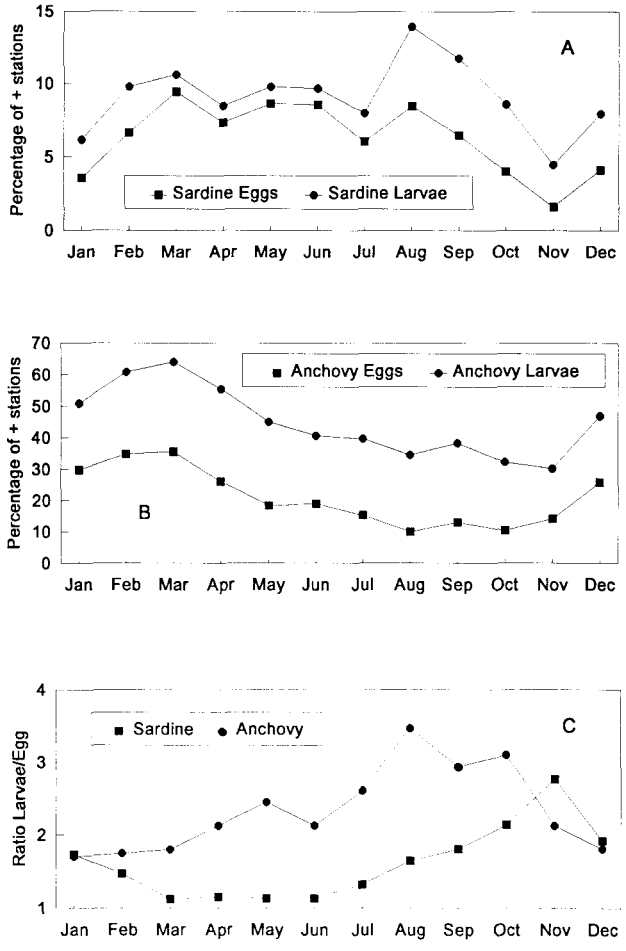

Figure 2. Monthly percentage of positive stations for eggs and larvae of (*A*) sardine and (*B*) anchovy. *C*, larvae/egg ratio for global analysis.

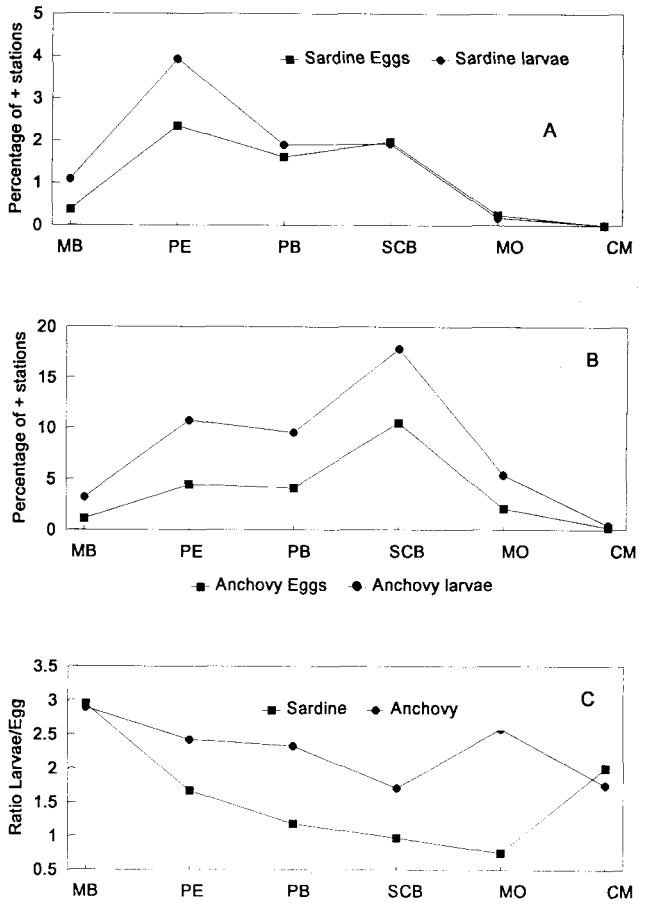

Figure 3. Percentage of positive stations for eggs and larvae of (*A*) sardine and (*B*) anchovy. *C*, larvae/egg ratio for analysis of areas (MB = Magdalena Bay; PE = Punta Eugenia; PB = Punta Baja; SCB = Southern California Bight; MO = Monterey; CM = Cape Mendocino).

13.86, 2.63, 65.81, and 64.82. Anchovy eggs and larvae occurred at more stations than sardine eggs and larvae.

Sardine eggs and larvae. As described by earlier workers, sardine eggs and larvae are present throughout the year along Baja California and California (figure 2A), but it appears that the spawning season along the whole coast is more extended than that described in earlier studies, because the percentage of positive stations for sardine eggs remains in the 6% to 9% range from February until September. The percentage decreases to less than 4% in October, to an annual low of 1.7% in November, and then rises to almost 4% in December and January. The highest percentages for sardine larvae are during August (14%) and September (12%). During the earlier peak of eggs and larvae (February to July), the percentage of positive stations is only slightly higher than that for eggs, but starting in August and continuing into the winter there are about twice as many positive stations for larvae as there are for eggs. As shown below, general patterns for the entire coast are due to complex seasonal patterns in different areas.

The larvae/egg ratio for sardine (figure 2C) shows low values from March to July (i.e., less than 1.5 larvae per egg), but the ratio increases to a maximum in November (highest ratio: 2.7).

Anchovy eggs and larvae. Both anchovy eggs and larvae are present throughout the year along the whole coast, with a peak from December to April (i.e., 28%–35% for eggs and 48%–65% for larvae; figure 2B). Percentages decline to a minimum of about 10% for eggs in August to October and about 30% for larvae in November. High larvae/egg ratios occur from July to October (highest value in August: 3.4). The ratio declines to less than 2 from November to March. From April to June the ratio again increases above 2 (figure 2C).

Analysis by Areas

This section describes latitudinal stratification of the seasonal patterns for sardine and anchovy eggs and larvae. It appears that sardine and anchovy larvae have quite different geographical patterns (figure 3). The highest values of occurrence of sardine larvae were in the Punta

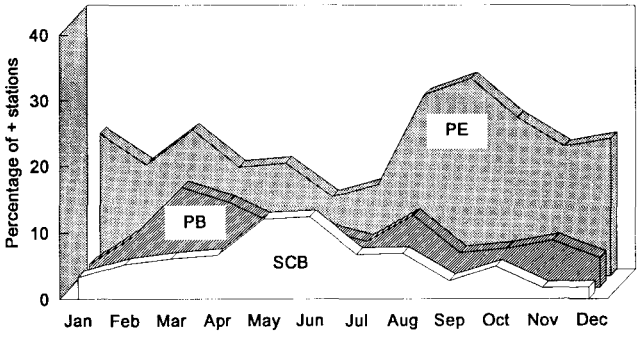

Figure 4. Monthly percentage of positive stations for sardine larvae, by area (PB = Punta Baja; SCB = Southern California Bight; PE = Punta Eugenia).

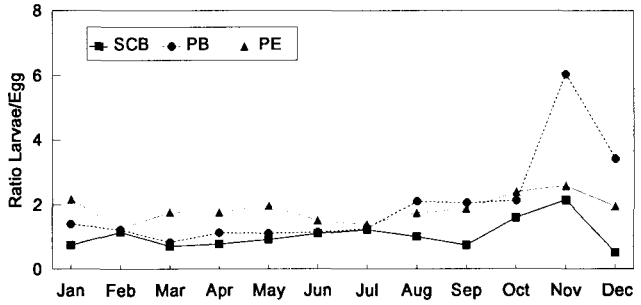

Figure 5. Monthly larvae/egg ratio for sardine, by area (SCB = Southern California Bight; PB = Punta Baja; PE = Punta Eugenia).

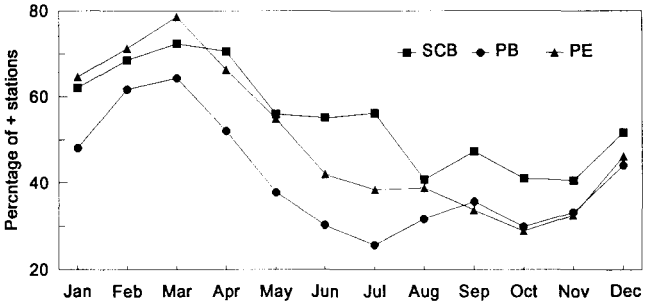

Figure 6. Monthly percentage of positive stations for anchovy larvae, by area (SCB = Southern California Bight; PB = Punta Baja; PE = Punta Eugenia).

Eugenia region, whereas for anchovy the highest values were in the Southern California Bight region. The occurrence of sardine eggs from the Southern California Bight to the Punta Eugenia region varied little except for diminishing northward and southward. However, the occurrence of sardine larvae in the Punta Eugenia region was almost twice that in the Punta Baja region and the SCB. Geographical patterns were similar for anchovy eggs and larvae, but larvae had higher percentages by region, except for Cape Mendocino, where the percentages were similar.

The lowest sardine larvae/egg ratios were in Monterey, with an increase toward the south (figure 3C). The ratio for the CM region is undoubtedly biased because of the low number of stations sampled. The ratios for anchovy increase both to the south and the north from SCB.

Sardine eggs and larvae. The seasonal patterns for eggs and larvae were similar for the three regions selected; I present only the data for larvae (figure 4). The Southern California Bight region shows the typical pattern described in the earlier papers; that is, the spawning season for the sardine begins in February and ends in June–July; some larvae, however, are present throughout the year. The adjacent Punta Baja region has its spawning peak two months earlier (March) than the SCB peak (May–June); there is also a small increase in positive stations during August. The Punta Eugenia region shows high values for all months except May and June. The maximum values of occurrence in the Punta Eugenia region (August–October) are much higher than those observed elsewhere.

The larvae/egg ratios for sardine have low values (with little variation) from February to September in the SCB region, and highest values during October and November (figure 5). The Punta Baja region has a sharp peak in November and a decline from December to July, when ratios show the lowest values and variability. Punta Eugenia also has a maximum ratio in November, and lower ratios from February to September.

Anchovy eggs and larvae. Because anchovy, like sardine, have the same seasonal patterns for eggs and larvae, again I present only the data for larvae (figure 6). In general, the three regions with maximum abundance of anchovy larvae (SCB, PB, and PE) have a similar seasonal pattern: the principal spawning season extends from December to July, as described by previous researchers. The Southern California Bight region shows a high number of positive stations from December to April, with a small decrease from May to July. The lowest values for the SCB region occur during October and November. The spawning seasons for anchovy in PB and PE are shorter than in the SCB (i.e., peak occurrence from December to March), but there were higher occurrences in PE than in PB. A comparison of monthly values of the percentage of positive stations among regions indicates that PB had lower values, while the SCB and PE had similar values.

Seasonally, the larvae/egg ratios for anchovy vary less for the SCB than for PE and PB (figure 7). For the SCB, ratios are lower from December to April, increase slightly from May to September, and decrease once again to November. PB has the lowest ratios from November to March, but there is a sustained increase from April to October. The seasonal pattern found for PE shows some similarity to that for PB, but instead of a sustained increase, there is a higher variability.

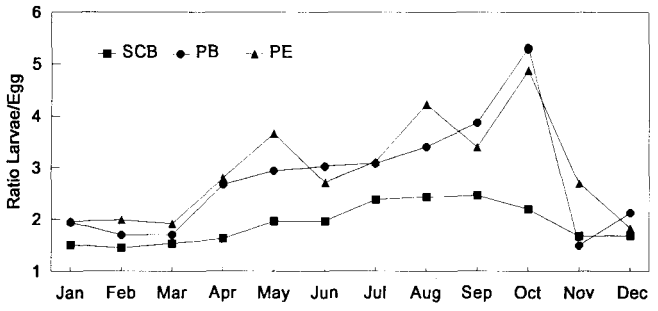

Figure 7. Monthly larvae/egg ratios for anchovy, by area (SCB = Southern California Bight; PB = Punta Baja; PE = Punta Eugenia).

Analysis by CalCOFI Lines

The geographical analysis by CalCOFI line may be biased from CalCOFI line 140 (Magdalena Bay) to the south, as well as from line 77 (north of Point Conception) to the north, since fewer than 300 stations were sampled per line, whereas from Point Conception to the north of Magdalena Bay, from 800 to 2,200 stations were sampled per line (table 1).

The percentage of positive stations by CalCOFI line for sardine and anchovy eggs and larvae differs considerably for the two species (figure 8). The occurrence of sardine eggs is even from just south of Point Conception (line 80) to just north of Magdalena Bay (line 140), except for a sharp peak in the Punta Eugenia region (line 120). Occurrence is very low to the north of Point Conception and south of Magdalena Bay. Sardine larvae have a similar latitudinal pattern, but from the Magdalena Bay region to the south the percentage of positive stations increases, suggesting an additional important spawning area; this pattern could, however, be due to the low number of stations sampled in this region (not more than 240 stations per line).

Sardine larvae/egg ratios show an increasing trend from north to south, with a sharp increase in the Punta Eugenia area (figure 9). In the northern areas the ratios vary from 0.77 to 1.11 (lines 80 to 97); the ratios observed at the northern portion of Baja California (lines 100 to 115) range from 0.84 to 1.6, whereas the values observed at the Punta Eugenia region (lines 117 to 130) vary from 1.36 to 2.52. The highest ratios (3.57 to 23) come from the southern part of the CalCOFI area (south of the Magdalena Bay region); again, the highest values might be biased because of the low number of stations taken in this region.

The percentage of positive stations for anchovy eggs and larvae indicates two areas of increased spawning: the Southern California Bight region and northern Baja California (figure 8). A second, broader peak occurs in the region from north of Punta Eugenia to north of Magdalena Bay. Between these two spawning areas, in the Punta Baja area, there is a small decrease. Anchovy

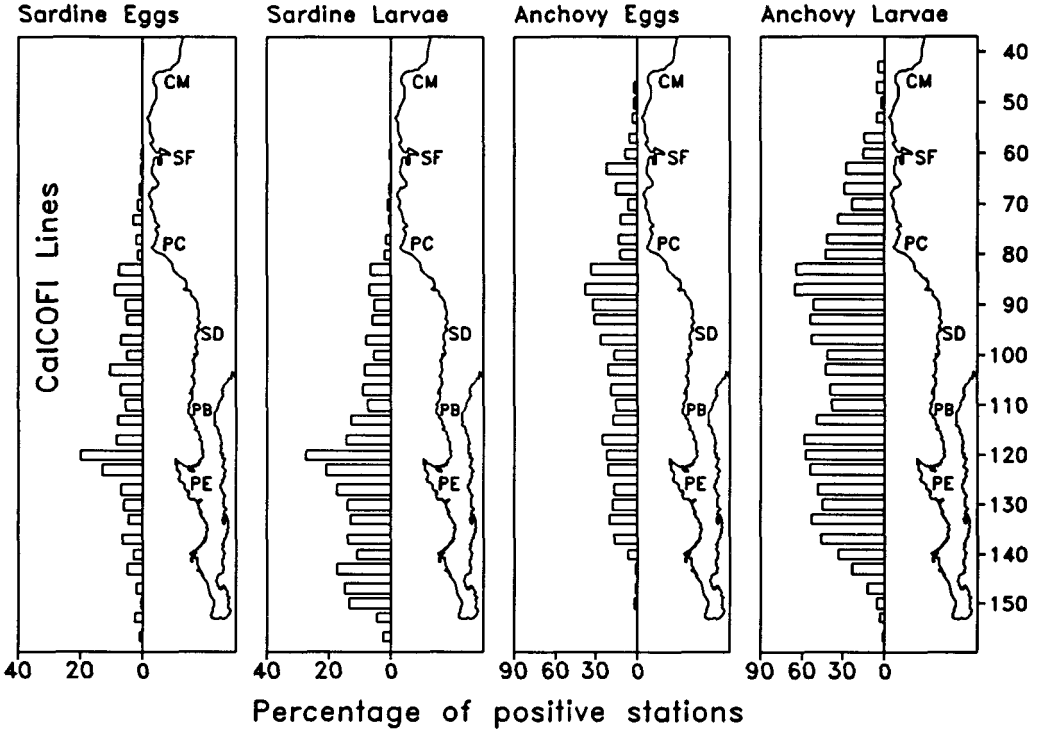

Figure 8. Percentage of positive stations for sardine and anchovy eggs and larvae per CalCOFI line.

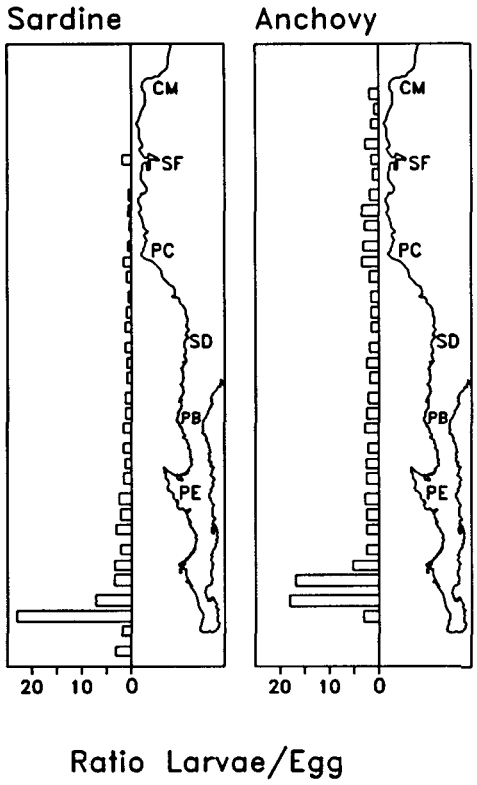

Figure 9. Larvae/egg ratio for sardine and anchovy per CalCOFI line.

eggs and larvae occur more frequently than those of sardine in the Point Conception area and extend into the northern areas (as far as Cape Mendocino).

The anchovy larvae/egg ratios, like the sardine ratios, diminish from south to north, except for CalCOFI lines 61–80, north of Point Conception (figure 9). Also, the ratios increase markedly (3.0 to 18.01) south of Magdalena Bay (where sample sizes were small).

Sardine eggs and larvae. Because the geographical and monthly percentages of positive stations for eggs and larvae by CalCOFI line exhibit essentially the same pattern, I present only the data for larvae (figure 10). The region to the north of Punta Baja shows the same seasonal pattern that was described by earlier workers; the highest occurrence of sardine larvae is from February to July. But the peak appears about two months earlier in the Mexican portion of this area (April) than in the California portion (June). The region south of Punta Baja shows very little seasonal variation in the percentage of sardine larvae, with only a moderate decrease in November and December. The strong peak that was previously shown for the Punta Eugenia region is obvious throughout the year. The Magdalena Bay region appears to be an important spawning area, with high occurrences during winter months and June, but the low number of stations taken in this region does not allow definitive conclusions (see table 1).

Anchovy eggs and larvae. Seasonal patterns for eggs and larvae are similar, therefore I show only those for larvae (figure 11). Anchovy larvae are present throughout the year from San Francisco (line 67) to Magdalena Bay (line 140). From January to May there are two modes, one in the Southern California Bight and one in the Punta Eugenia region. From June to November the southern mode shifts northward to the Punta Baja area, while the northern mode remains in the same location. In general, the seasonal pattern of larval occurrence shows higher values from December to July over the entire study area.

Inshore-Offshore Analysis

Offshore, more sardine and anchovy larvae are found than eggs, but in general the highest values appear near the coast for both eggs and larvae off California and Baja California (first 20 n.mi.; figure 12). The offshore occurrence of sardine eggs and larvae varies considerably among areas. The Magdalena Bay and Punta Eugenia regions show high percentages of positive stations for sardine eggs in the first 20 n.mi. The Punta Baja area seems to be a transitional region, since there is a moderate presence off 80–100 n.mi. In the Southern California Bight and central California areas there are only minor inshore peaks and little other variation within the first 100 n.mi.; values are quite low in the central California area. The few positive stations in the Cape Mendocino region exhibit little pattern. The offshore patterns for sardine eggs and larvae are different only in the Punta Eugenia region: there larvae have a high occurrence out to 80–100 n.mi., but the eggs are more concentrated in the first 20 n.mi.

Anchovy eggs and larvae are found more frequently within the first 40 n.mi. for all areas except Magdalena Bay, where more eggs are found in the 20 n.mi. fringe (figure 12, right side). In general, there are two offshore patterns. In the first—from the Southern California Bight to the north—the occurrence of eggs and larvae decreases as far as 100 n.mi. offshore. In the second pattern—from Punta Baja to the south—there is higher occurrence as far as 60 n.mi.

In order to demonstrate the seasonal offshore patterns for sardine and anchovy eggs and larvae, I use contour plots to show the percentage of positive stations by months and by distance offshore for each geographical region.

Sardine eggs and larvae. The seasonal offshore patterns for eggs and larvae are similar in all regions, but because larval occurrence is higher than that of eggs, I illustrate only the pattern for larvae (figure 13). The few stations in the Cape Mendocino area do not exhibit any pattern. Two general patterns are present off California and Baja California: the first corresponds to the Southern California Bight, in which high occurrence of sardine

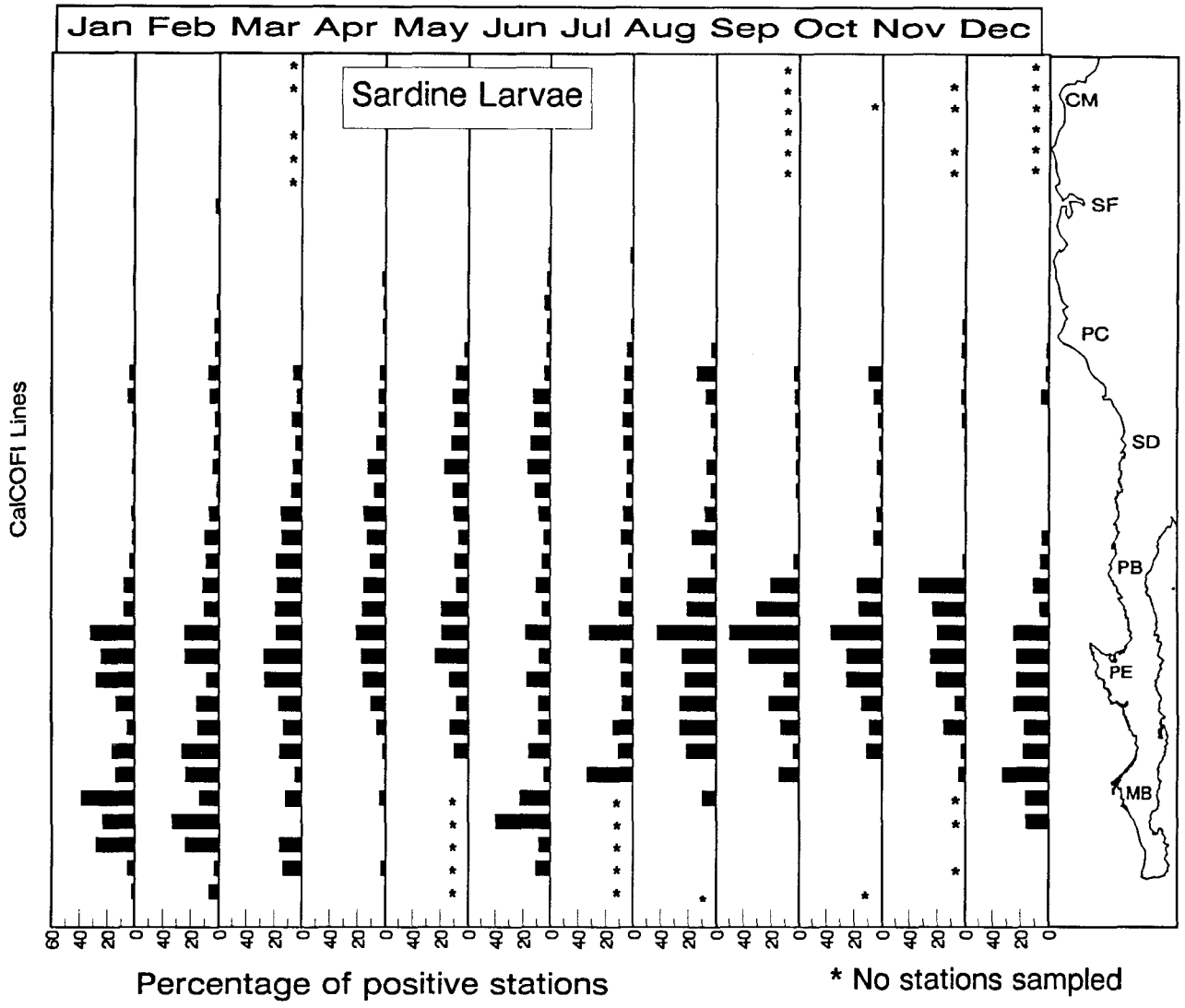

Figure 10. Monthly percentage of positive stations for sardine larvae per CalCOFI line.

larvae begins in April and extends until August, with the highest values during May and June. This region also shows a relatively homogenous offshore occurrence during those months. After August, low percentages (less than 5%) of positive stations extend as far as 90 n.mi. offshore in the SCB. In contrast, the Punta Eugenia area exhibits a high inshore occurrence of sardine larvae from August to February (more than 50%). From March to July moderate occurrence is evident (less than 30%), but the offshore distribution is homogenous as far as 90 n.mi. for this region.

The Punta Baja region seems to be a transitional area between the southern (Punta Eugenia region) and the northern patterns (SCB area), since features of both patterns are present: nearshore occurrence is highest from July to September, and there is a secondary, smaller, peak in February–March (associated with the northern pattern).

In the Magdalena Bay area the low number of offshore stations sampled did not allow a comparison with the Punta Eugenia region. In the Monterey area, there are high offshore values during June and July and low inshore values during the winter.

Anchovy eggs and larvae. Anchovy larvae are present throughout the year in all areas. Highest concentrations are nearshore from February to March (figure 14). Larvae show, in general, a more oceanic distribution than eggs for each area. In the area from Monterey to Magdalena Bay, high concentrations of anchovy larvae begin in November–December (near the coast) with a rapid increase until February–March. From April to May–June the presence of larvae decreases, reaching the lowest values in September and October. Regarding the inshore-offshore monthly distribution of larvae, the 50% contour shows higher offshore values from January to April (corresponding to the spawning peak), whereas in

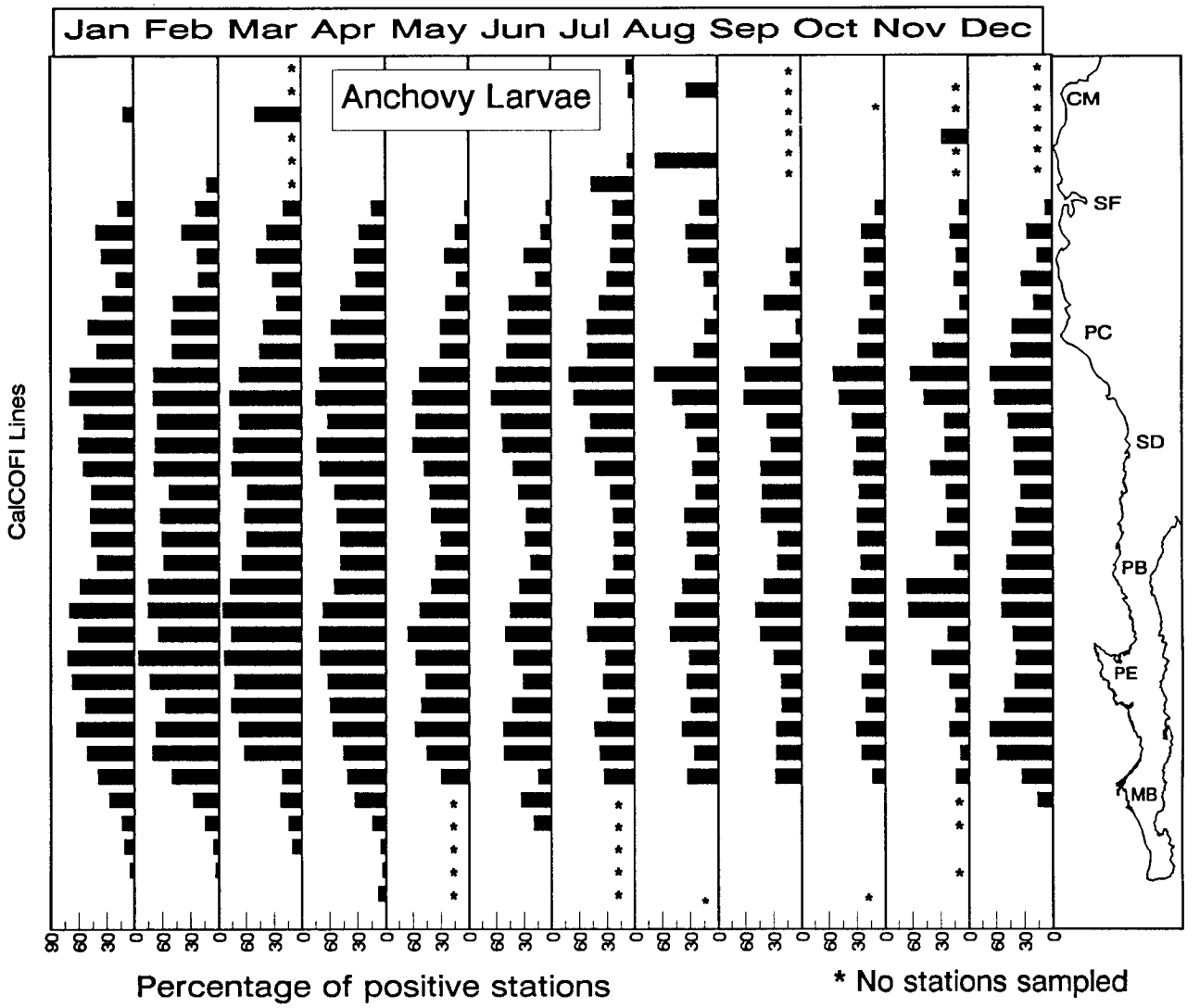

Figure 11. Monthly percentage of positive stations for anchovy larvae per CalCOFI line.

September and October the larvae are concentrated nearshore.

For particular regions, some specific features can be observed. There is a homogenous offshore distribution during June and July for the Monterey region. Offshore of Cape Mendocino, a high concentration nucleus at 70 n.mi. is evident during July.

DISCUSSION

In order to describe the long-term average geographic and seasonal distributions for sardine and anchovy eggs and larvae off California and Baja California it is important to briefly discuss several considerations. First, sardine and anchovy live in a highly productive and variable habitat. In the California Current they extend over three coastal zoogeographic provinces, an entire coastal upwelling zone, and three oceanic water masses (Moser et al. 1993). The large geographic range where these fishes live places them in regions with different seasonal and geographic patterns of abiotic and biotic parameters (SST, productivity, zooplankton biomass, etc.). The different patterns of these parameters along the extended range of sardine and anchovy could be a major factor in determining these fishes' reproductive behavior on a geographical/monthly basis. On the other hand, during the period studied (1951–89), the California Current experienced a series of warm and cold events. Also, natural fluctuations in abundance (on a decadal basis) of these populations, as well as the fisheries on them, could have altered the population structure and hence their reproductive processes.

Sardine Eggs and Larvae

The CalCOFI line and subarea analysis clearly demonstrates that sardine eggs and larvae are most concentrated in the southern portion of the range, from south of Punta

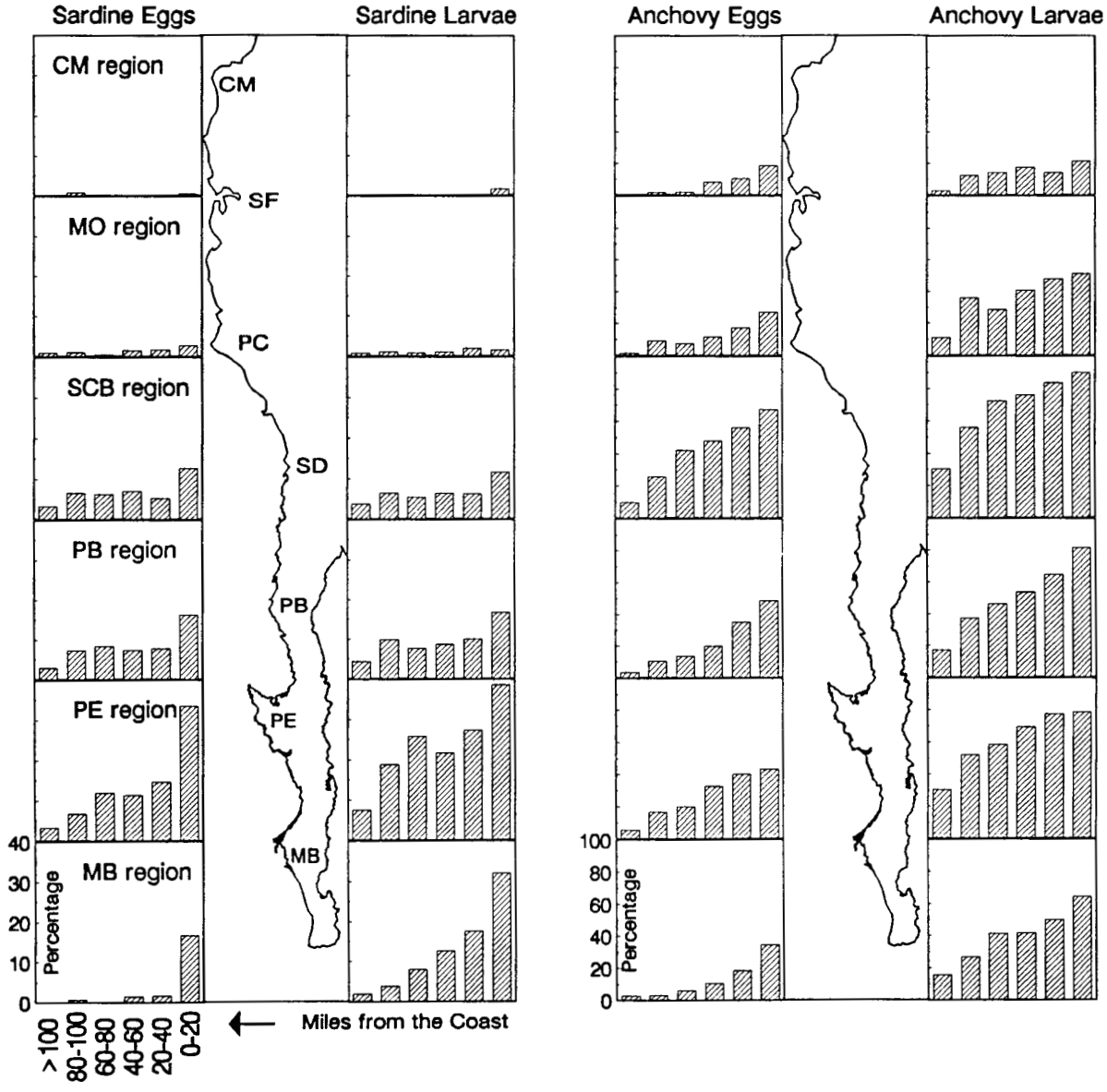

Figure 12. Inshore-offshore patterns for sardine and anchovy eggs and larvae by geographic region.

Baja, B.C., to north of Magdalena Bay, B.C.S. Eggs and larvae occur over the entire area studied, from San Francisco to Cabo San Lucas, B.C.S., but south of Magdalena Bay and north of Point Conception their values are relatively low. This geographic pattern agrees, in part, with the findings of Ahlstrom (1960) and Kramer and Smith (1971) that the Punta Eugenia region and the Southern California Bight are important spawning centers. Moser et al. (1993) also show that the Punta Eugenia area has the highest concentration of eggs and larvae.

The slight southward increase in the larvae/egg ratio (increasing southward) observed in analyses by CalCOFI line and subareas could be associated with higher SSTs observed in the south. Also the higher larvae/egg ratio from July to November could be associated with the high SST during these months. These patterns can be observed, generally, from Punta Eugenia to southern California. Incubation time is shorter at high SST (Lasker 1965).

The global seasonal analysis, which is very similar to that described in Moser et al. (1993) presents a misleading picture of the seasonality of sardine spawning. Both analyses are a composite of the two quite different seasonal patterns in the southern California–northern Baja California region and the central–southern Baja California region. In the northern pattern, spawning takes place from February to July, whereas the southern pattern shows two spawning peaks: a strong one from August to September and a small one in March.

The results presented in this paper have established that sardine eggs and larvae can be observed during any

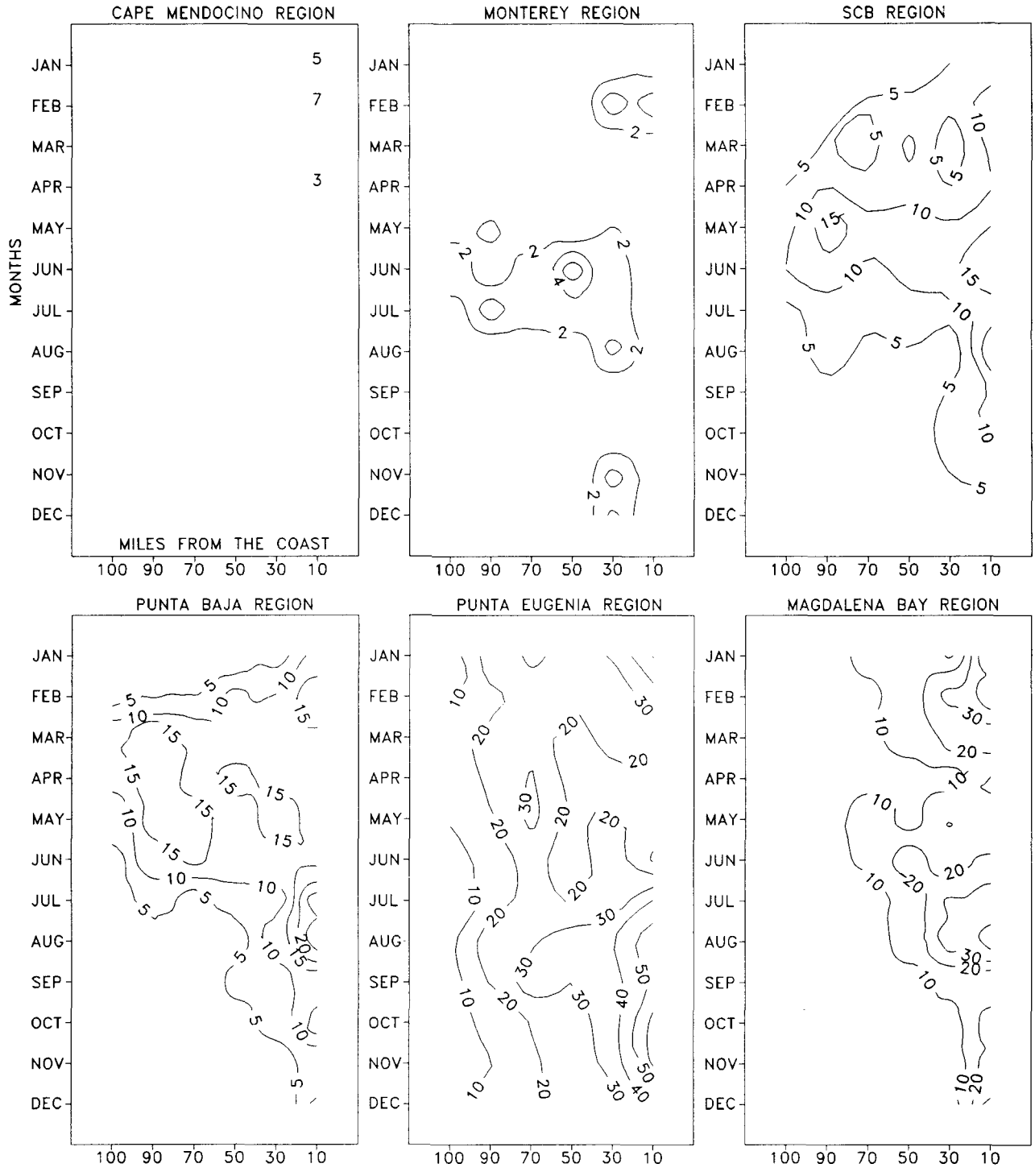

Figure 13. Monthly percentage of positive stations for sardine larvae by area and offshore.

month in at least one place off California and Baja California. The geographical-temporal analysis indicates in which months and areas high or low concentrations are found.

The analyses by CalCOFI line (geographical/seasonal) and subarea suggest that the Punta Baja region is a transition zone between the Punta Eugenia region and the Southern California Bight, because the Punta Baja seasonal pattern shows higher occurrence of larvae from February to March (as in southern California) and a small peak of spawning in August (the Punta Eugenia pattern).

The results for the geographical offshore analyses agree with those of Moser et al. (1993). High inshore

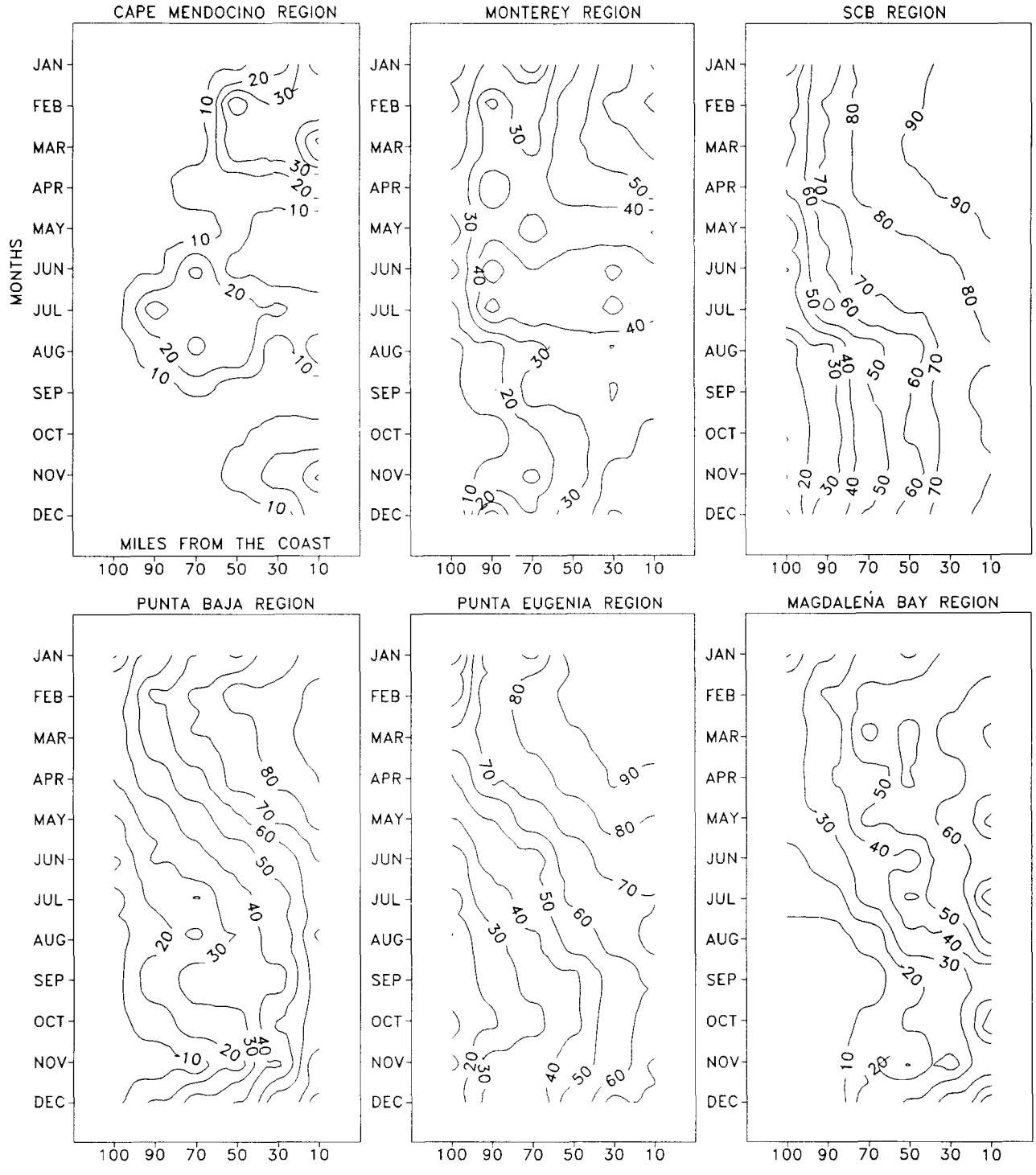

Figure 14. Monthly percentage of positive stations for anchovy larvae by area and offshore.

concentrations of sardine eggs and larvae are observed in the southern areas (Punta Baja south), and broader offshore presence of spawning is observed from southern California to the north. In the geographical/seasonal offshore analyses the pattern changes seasonally. From March to July, there is a homogenous presence of eggs and larvae from the coast to 100 n.mi. (from southern California to the Punta Eugenia region), which could be associated with upwelling processes during those months. From August to February, the offshore occurrence virtually disappears in the southern California and Punta Baja regions, but not in the Punta Eugenia area.

It can be concluded that the patterns found in the southern areas (Magdalena Bay and Punta Eugenia) are

different from those found in the northern areas (Punta Baja and the Southern California Bight).

Anchovy Eggs and Larvae

The main anchovy spawning center is clearly located in the Southern California Bight, but there is a secondary center in the Punta Eugenia area. As observed for the sardine, the higher larvae/egg ratio for anchovy from July to October could be associated with higher SSTs during these months, but the geographical effect on the ratios is not clear.

The spawning peak stretches from December to April in the global seasonal analyses, as has been previously described by several workers. The results of subarea and CalCOFI line analyses suggest no latitudinal differences for anchovy; the same seasonal pattern could be seen from southern California to the Punta Eugenia region.

It is evident that sardine and anchovy have different geographical and seasonal patterns in spawning. Although the sardine has its main spawning center in the Punta Eugenia region, anchovy are located in the Southern California Bight area. The main spawning season of the anchovy is restricted in time (December to April), whereas that of the sardine differs geographically.

ACKNOWLEDGMENTS

I wish to thank the CalCOFI staff, especially Izadore Barrett, for allowing me to use their data base. I thank Richard H. Parrish for his help and careful reviews and critical comments. I also thank the PFEG-SWFC staff for their hospitality during my stay at the Monterey lab. Principal support for this work was provided by the Centro de Investigaciones Biologicas del Noroeste at La Paz, B.C.S., Mexico. Finally, I also thank Daniel Lluch B. for the guidance and criticism that improved this paper.

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VARIATION IN LIFE HISTORY AND MORPHOLOGY IN NORTHERN ANCHOVIES (*ENGRAULIS MORDAX*)

KEITH NELSON, ELMARIE S. HUTCHINSON, GANG LI, FREDERIC L. SLY, AND DENNIS HEDGECOCK
University of California, Davis
Bodega Marine Laboratory
Bodega Bay, California 94923-0247

ABSTRACT

Individual, geographic, and interannual variation in morphometric and life-history traits was examined and related to environmental variables. In the winters of 1984 and 1985, 1,836 otolith-aged northern anchovies (*Engraulis mordax*) were obtained from 16 California–northern Baja California stations. Life-history characters were age, size (mean of logs of 11 morphometric measures), condition, and gonadosomatic index (GSI). Principal components analysis of 11 log-transformed morphometric traits adjusted for size and sex revealed five factors that summarized variation in (1) length of body, (2) length of jaw and operculum, (3) length of anal-fin base, (4) body depth, and (5) length of orbit and preorbital region. Independent variables used in further analyses were age, sex, size, year of sampling, year-class, distance offshore, CalCOFI line, depth of bottom, and sea-surface temperature at station. Within-station age-classes containing more than 13 fish were treated as independent subsamples (a total of 37).

Morphometric factors, although independent of size, were found to reflect condition. Although GSI and condition were negatively correlated among ages within years, they were independent among subsamples. Only 0.7% of individual variation in GSI was attributable to sex. Although there was overall positive correlation of GSI and size, the allometric relationship of GSI with size within a subsample (GSI slope) was negatively correlated with subsample mean GSI, signifying individual variation in reaction-norm allometry.

Spatial heterogeneity was unexpectedly large for all life-history and morphometric characters. Two temperature-correlated, mesoscale spatial patterns were found: (1) of size, GSI, and GSI slope; and (2) of condition, body depth, and body length. Pattern 2 resembled published satellite images of a recurrent pattern of phytoplankton-pigment concentration, reflecting primary production. A third pattern of negative correlation of jaw length with condition and body depth was independent of temperature, year, and other independent variables. Year-class- and temperature-related differences between 1984 and 1985 samples suggested expected effects of the 1982–84 El Niño, but these were not cleanly separable from the much larger contributions of geographic variation. Heterogeneity within and among subsamples, particularly in jaw and anal-fin-base lengths, suggested heterogeneity of early environment, both among ages from the same station and within certain subsamples.

[Manuscript received February 14, 1994.]

RESUMEN

Se examinó la variación individual, geográfica e interanual de los caracteres morfométricos y de las fases de vida de la anchoveta norteña y se buscó relacionar esta variabilidad con variables ambientales. Se obtuvieron 1836 *Engraulis mordax* y se determinó la edad por medio de sus otolitos; los especímenes se obtuvieron en los inviernos de 1984 y 1985 en 16 estaciones de Baja California (México) y California. Los caracteres de la fase de vida que se consideraron fueron edad, tamaño (el promedio de los logarítmos de 11 medidas morfométricas), condición e índice gonadosomático ("IGS"). El análisis por componentes principales de 11 caracteres morfométricos ajustados por tamaño y sexo revelaron 5 factores que resumen la variación en (1) talla, (2) longitud del maxilar y opérculo, (3) longitud de la base de la aleta anal, (4) profundidad del cuerpo y (5) longitud de la región orbital y preorbital. Otras variables independientes que se analizaron fueron edad, sexo, tamaño, año de muestreo, clase anual de edad, distancia hacia mar abierto, transecto establecido por el programa "CalCOFI", profundidad, y temperatura del agua superficial por estación. Las estaciones donde las clases de edad incluyeron mas de 13 especímenes fueron tratadas como submuestras independientes (resultando en un total de 37).

Los factores morfométricos reflejaron la condición, a pesar de que fueron independientes del tamaño. A pesar de que la correlación entre IGS y condición fué negativa entre las edades para los distintos años, estas variables fueron independientes entre las submuestras. El sexo sólo explica 0.7% de la variación individual del IGS. Hubo una correlación positiva entre IGS y tamaño. Sin embargo, hubo una correlación negativa entre la relación alométrica IGS—tamaño dentro de cada submuestra (pendiente del IGS) con el promedio del IGS por submuestra, lo que significa que hubo variación individual en la alometría de la norma de reacción.

La heterogeneidad espacial fué sorprendentemente alta para todos los caracteres morfométricos y de las fases de vida. Se encontraron dos patrones relacionados con la temperatura en la meso-escala: (1) de tamaño, IGS y pendiente del IGS, y (2) de condición, profundidad del cuerpo y talla. El patrón no. 2 se asemejó a imagenes de satélite ya publicadas de un patrón recurrente de un pigmento de fitoplancton que refleja la producción primaria. Un tercer patrón, correlación negativa entre longitud del maxilar con condición y profundidad del cuerpo, fué independiente de la temperatura, el año, y otras variables independientes. Debido a diferencias en las clases anuales así como en temperatura entre las muestras de 1984 y 1985, se esperarían efectos debidos al evento El Niño 1982–84. Sin embargo, estos efectos no se pudieron demarcar claramente de la contribución mas substancial de la variación geográfica. La heterogeneidad dentro y entre las submuestras, particularmente en la longitud del maxilar y de la base de las aletas anales, sugirió heterogeneidad del ambiente que los peces encuentran a edad temprana, tanto entre edades en la misma estación, como dentro de algunas submuestras.

INTRODUCTION

The responses of a species to changes in its environment determine where it can persist. A free-ranging animal such as a pelagic fish may encounter environmental variation with both temporal and spatial components, each with a wide spectrum of frequencies. Response to this variation may be behavioral, physiological, and morphological, with resulting modifications in life history. Certainly the most important among such norms of reaction (Schmalhausen 1949) are those to variations in temperature and food supply, including variation in growth rate and, in fishes, such reproductive traits as fecundity and age- and size-at-maturity (Miller 1979; Nelson and Soulé 1987; Nelson, 1993). In the marine coastal environment in particular, variations in water movements, temperature, and production are linked, although not in any simple way (references in Roesler and Chelton 1987). Responses of different morphological and life-history variables to such variations are also likely to be correlated with one another. Patterns of environmental correlation and effects upon population structure will be correspondingly more complex.

Anchovies are a characteristic and key forage species for other pelagic fishes in all eastern boundary current systems (Reid 1966). Because of CalCOFI, the northern anchovy (*Engraulis mordax*) and its California Current habitat are probably the best-known of these systems. Yet, how northern anchovy morphology and life history respond to spatial and temporal changes in the environment remains a mystery (cf. Fiedler et al. 1986).

Two subspecies of *Engraulis mordax* have been described (Hubbs 1925; cf. McGowan 1984): the wide-ranging nominate subspecies and another that inhabits San Francisco Bay and about which little is known. *Engraulis mordax mordax* Girard has been considered to be further subdivided into northern, central, and southern subpopulations, based on meristic, morphometric, and transferrin electrophoretic phenotypes (McHugh 1951; Vrooman et al. 1981). The central subpopulation was supposed to range from San Francisco Bay to northern Baja California, approximately the area shown in figure 1A. Vrooman et al. found electrophoretic evidence for a certain amount of geographic overlap with the northern subpopulation. Although the central and southern subpopulations were believed to be nonoverlapping, each may occupy an area off north central Baja California at a different time of year; anchovies belonging to the southern subpopulation are distinguished by their smaller maximum sizes (Parrish et al. 1985).

Previously, we found significant geographical heterogeneity for 5 of 11 electrophoretic allozyme loci among samples collected from the central subpopulation range by the 1982 CalCOFI winter (spawning biomass) cruise (Hedgecock et al. 1989); we have confirmed this with anchovies collected in four subsequent cruises (Hedgecock et al. 1994). In an attempt to understand the biological basis of this geographic variation, we expanded our study of 1984 and 1985 winter-cruise material to include much larger samples and analysis not just of allelic variation but also of morphometric and life-history variation. We report here the results of these latter analyses; the relationship of this variation to allozyme heterogeneity is presented elsewhere in this volume (Hedgecock et al. 1994). The different year classes represented in the material from the two winter cruises differ in the amount and ontogenetic timing of their experience of the 1982–84 major California El Niño event, and we sought in their morphological responses to that experience an "El Niño signature." Such effects have been reported previously for anchovies (Fiedler et al. 1986; Butler 1989) and other fishes (references in DeMartini 1991).

Thus, the objectives of this study are to ascertain the relative contributions of interannual and geographic differences to individual variation in size, morphometrics, and somatic and reproductive condition, and to the covariation of these variables. We find unanticipated correlations of morphometrics with somatic condition, and of reproductive condition with size and reproductive allometry. For all variables, geographic variation is unexpectedly great but of variable spatial scale. Although there are signs of pervasive influence of temperature, evidence for an El Niño signature is equivocal.

TABLE 1
Station Data for Northern Anchovy Collection

Year	Station[a] Symbol	Station[a] No.	CalCOFI coord.	n[b]	Percent female	Age, SD[c]	Standard length, SD
1984	A	4612	65:50.5	117	15.4	1.598, 0.901	111.5, 11.1
	B	4655	90:28	48	81.2	0.917, 0.539	100.3, 11.0
	C	4665	91.7:27	70	27.1	0.414, 0.551	84.1, 6.7
	D	4662	91.7:33	120	44.2	1.017, 0.389	104.7, 6.1
	E	4660	90:56	120	37.5	1.183, 0.518	118.3, 6.2
	F	4671	93.3:41	179	33.5	1.017, 0.326	107.3, 5.5
	G	4689	105:30	116	14.7	0.828, 0.622	101.4, 9.0
1985	H	4707	76.7:54	116	60.3	0.871, 0.880	96.0, 6.0
	I	4708	76.7:56	119	47.9	1.975, 1.298	98.9, 6.2
	J	4719	85:38	120	43.3	1.058, 0.781	103.9, 5.2
	K	4729	87.5:34	118	46.6	1.017, 0.795	95.9, 8.7
	L	4722	85.8:43	118	70.3	0.576, 0.821	117.0, 7.2
	M	4725	87.5:55	119	49.6	0.328, 0.489	105.9, 6.6
	N	4726	87.5:53	120	59.2	0.358, 0.515	109.3, 6.0
	O	4763	96.7:50	117	54.7	1.675, 0.981	118.9, 6.9
	P	4766	98.3:39	119	55.5	1.319, 0.882	108.2, 5.7
Totals				1836	45.1	1.028, 0.872	106.2, 10.7

[a]Letter symbols and CalCOFI coordinates for stations as in figure 1A.
[b]The number of fish for which data were complete.
[c]Age, SD is the average otolith score and its standard deviation.

MATERIALS AND METHODS

Samples

Samples were obtained at a total of 16 midwater-trawl stations in the winters of 1984 and 1985 by CalCOFI cruises 8403 and 8502 aboard the RV *David Starr Jordan* of the NOAA Southwest Fisheries Center (La Jolla). Localities are shown in figure 1A, and sample details are given in table 1; other station information including sea-surface temperature and depth of bottom are available on request. Whole fish were frozen individually aboard ship at −70°C and then shipped in plastic bags by air to the Bodega Marine Laboratory, where they were held at −70°C until dissection.

Specimens were partially thawed a few at a time and held under ice until measured. This procedure prevented undue warming of tissue samples removed subsequently for allozyme electrophoresis and minimized uncontrolled morphometric variation from differential thawing. All measurements and counts of any one type were made by the same person.

Measurements

Standard length (from snout to end of hypurals) was measured to the nearest mm with a mounted rule, and the following other morphometric characters were measured to the nearest 0.1 mm with vernier calipers: six lengths from the snout to (1) the anterior margin of the orbit (preorbit), (2) the posterior edge of maxilla, (3) the posterior edge of the operculum, (4) the supraoccipital border, (5) the dorsal fin origin, and (6) the vent; followed by measurement of the anteroposterior orbit diameter, the maximum head width, the minimum body depth at pectoral girdle, and the length of the anal-fin base.

Total wet weight was recorded to the nearest 0.1 g. After removal of tissues for electrophoresis, otoliths were removed for ageing, and sex and gonad wet weight (to the nearest 10 mg in a tared dish) recorded. Gonads were oven-dried to crispness, reweighed, and the tare rechecked. Somatic wet weight was entered into the data set as total wet weight minus gonad wet weight.

Sagittal otoliths were cleared overnight in 2% KOH, rinsed in deionized water for one or more days, air-dried, and stored by pairs in individual gelatin capsules in envelopes labeled by station. Each pair was placed under water in a separate well (1 cm diameter, painted black) drilled in plexiglass. Otolith annuli (age) were counted under a binocular dissecting microscope with incident illumination, following the methods of Collins and Spratt (1969). Comparison of early counts with those by an experienced California Department of Fish and Game scorer showed 92% overall agreement, dropping to 75% for a selected sample of older fish (Allen Grover, pers. comm.). Anchovies with age = 0 are approaching one year old; a derived variable—year class—was calculated as (year of sampling) − (age + 1).

Analysis

The BMDP multivariate statistical software package (Dixon et al. 1988) was employed for all analyses. Screening of outliers was done with bivariate plots of

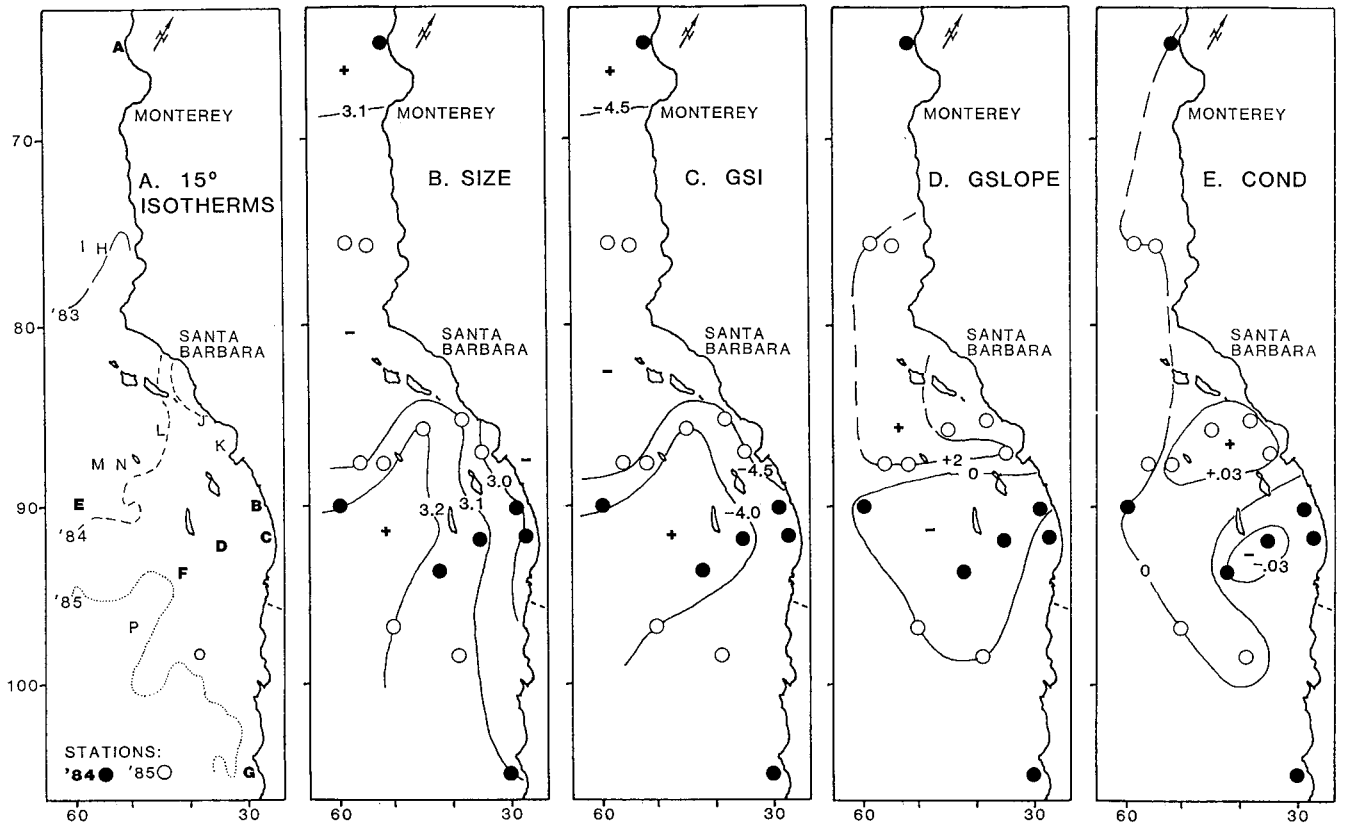

Figure 1. *A*, 1984 (*bold*) and 1985 CalCOFI winter cruise anchovy sample stations and 15°C sea-surface isotherms for winter 1983–85 (from Fiedler et al. 1986). *B–E*, contours of equal subsample (age classes within stations) means for life-history variables. *Filled circles* represent 1984 stations. In *B*, contours of mean size (table 1) are at approximately 10% intervals for unlogged morphometric variables; 3.1 corresponds roughly to an average fish of grand geometric mean standard length = 105 mm. In *C*, a difference in mean gonadosomatic index, GSI, of 0.1 again represents a difference of 10% in the unlogged ratio. In *D*, GSI slope (GSLOPE) = 0.0 corresponds to an allometric coefficient of 1.0. In *E*, contours of subsample-mean condition are residuals of regression of ln(somatic wet weight) on ln(standard length). Ordinate is CalCOFI coordinate cardinal line; abscissa is CalCOFI station line (for relationship to longitude and latitude see Eber and Hewitt 1979).

variables on standard length and sometimes other variables. Treatment of outliers, except for the variables anal-fin-base length and gonad wet weight, was based on a branching protocol. Very short anal fin bases noted at the time of measurement were remeasured and retained in the data set after incidence of short anal fin base was found to vary geographically. Residuals from regression of female gonad wet weight on gonad dry weight were bimodally distributed; the upper, smaller mode contained females with obviously hydrated oocytes.

For each fish with a complete set of 11 morphometric measurements (n = 1,912), residuals for analysis were obtained from predictive multivariate regression of the natural log of each trait on sex and size. Size was defined as the mean of the logs of the 11 morphometric traits (Mosimann 1987). The pooled regression slope rather than the common within-sample slope was used (cf. Reist 1986), because the average difference between the two slopes was small and unbiased. Four other derived variables are used in the analyses: (1) condition—the residual of the predictive regression of ln(somatic wet weight) upon ln(standard length); (2) gonadosomatic index, GSI = ln(gonad dry weight) − ln(somatic wet weight); (3) a gonad hydration index, GHI = ln(gonad wet weight) − ln(gonad dry weight); and (4) a measure of reproductive allometry—GSI slope, the coefficient from the regression of GSI upon ln(somatic wet weight). This regression was done separately for each age-class within each station. Ponderal measures of reproductive condition were employed because of the impracticality of histological examination on so large a collection of fish. **Throughout the remainder of this paper the names of traits will refer to the logged and otherwise adjusted variables described in this paragraph, not to the raw measurements themselves.**

Principal components analysis (PCA) of the 11 morphometric residuals was followed by both orthogonal and oblique (direct quartimin) rotations, with parameters suggested by Frane et al. (1988). Orthogonal and oblique rotation yielded similar sets of factors; only the results of orthogonal rotation are reported herein.

Mixed-model maximum-likelihood analyses of vari-

ance (ANOVAs; Jennrich and Sampson 1988) were performed to analyze effects of year, age, temperature, station, and interactions upon the dependent variables, size, condition, GSI, and morphometric factors obtained from PCA.

Bivariate plots of pairs of factor scores, etc., segregated by sex where appropriate, were made for 64 subsamples consisting of each age-class within each station. The distribution of numbers of individuals (n) among subsamples was multimodal, with one gap between $n = 11$ and 14, separating peaks at $n = 9$ and 17. There were 37 subsamples with $n > 13$; means and other statistics from subsamples with smaller n were much more variable. Throughout this paper, subsample means are for those subsamples with $n > 13$. The question of within-subsample heterogeneity was addressed by Levene's test for heterogeneity of variance within year class and by intercorrelations of variances of factor scores and size.

A new data set was constructed of subsample means of factor scores and size, condition, GSI, GSI slope, as well as other variables. These included year, sea-surface temperature, year class, age, depth of the bottom under station, distance from nearest mainland, and the longshore CalCOFI line coordinate (figure 1A). ANCOVA of subsample means among stations after correction, where appropriate, for year, age, size, and the five morphometric PCA factors tested equality of differences among subsamples within and among stations.

Spatial distributions of GSI slope and mean size, GSI, condition, and morphometric PCA factors for subsamples were examined with the aid of contours fitted by eye (figures 1 and 4). A contour passing through a station indicates that at least one subsample mean at that station lay on either side of that contour. Dashed lines indicate conjectural contour positions. As a control on this contouring procedure, subsample means were randomized over stations, and the resultant random contour maps were compared with the original contour maps. Spatial autocorrelation (Rossi et al. 1992) of paired 1985 subsample means, classified into distance categories, was also employed to estimate the spatial scale of geographic variation for each dependent variable.

RESULTS

Sex, Age, Year, and Station Information

Among individuals, sex and age were uncorrelated. Age and year (of sampling) were uncorrelated as well, but a significantly higher proportion of females was found in 1985. Sex ratios and age statistics by station are given in table 1. Among the 1984 stations were those with both highest and lowest sex ratios; conversely, those with both lowest and highest mean age were from 1985. Sea-surface temperature among stations was significantly lower in 1985 than in 1984 (13.7 vs 15.2°C; $t = 3.27$, d.f. 14; $p < 0.005$). As expected, temperature was correlated with CalCOFI line ($r = +0.701$), and distance offshore with depth ($r = +0.749$).

Size and Condition

Initially we used raw standard length as a measure of size, for detecting outliers and comparison with earlier studies. Subsample-mean standard length varied from 83 mm (station C, age 0, figure 1A) to 123 mm (station P, age 2). Within stations, different subsamples often had distributions with one or more similar modes of standard length. Within a subsample, standard length was unimodally distributed with a minimum coefficient of variation of 4%–5%, but occasionally the distribution was obviously bimodal with a correspondingly larger coefficient of variation, suggesting heterogeneity of such subsamples (see below).

For subsequent analyses we used the consensus measure of size defined in Materials and Methods, as suggested by Mosimann (1987). Sex differences accounted for 1.8% of the total variance among individuals in size, attributable to a higher proportion of females in some of the samples of larger anchovies. Within a subsample there was little difference in size between the sexes, and they were combined for analysis. Somatic wet weight was nearly isometric with the cube of standard length. Condition was weakly correlated with sex (1.9% of variance). Interannual and geographic variation in these and other dependent variables is described below.

Reproductive State

In mature females, the gonad-hydration index GHI can double during the day prior to ovulation (figure 2A; Hunter et al. 1985). For this reason we used dry gonad weight for the gonadosomatic index (GSI). Oocyte hydration was only seen among females with GSI > -4.6, which was close to the grand mean GSI in the population (corresponding to a [gonad dry weight]/[somatic wet weight] ratio of 0.01). Despite the difference in behavior of GHI between females and males (figure 2A), there was little difference between sexes in GSI (sex accounting for 0.7% of total variance) or GSI slope, and the sexes were combined for further analysis of reproductive state. Subsample GSI slope showed great heterogeneity. GSI slope, the measure of dry gonad allometry, was negatively correlated with subsample-mean size and especially with mean GSI, even becoming negative at high GSI (figure 2B); correlations with temperature are discussed below.

Principal Components Analysis (PCA) of Morphometrics

PCA of morphometric measures adjusted for sex and size yielded five components with eigenvalues greater

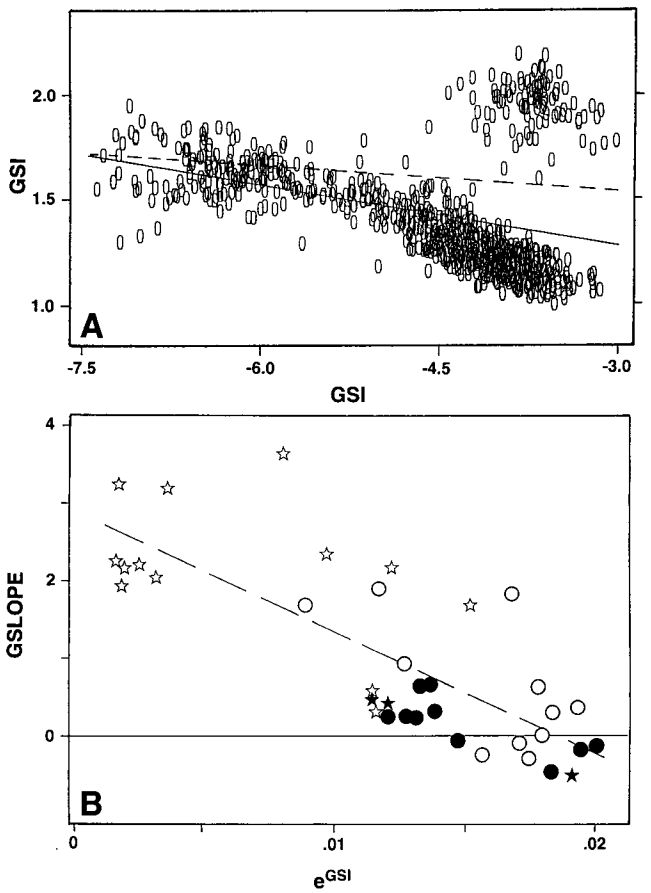

Figure 2. *A*, gonad hydration index, GHI, as a function of dry gonadosomatic index, GSI, for individual female anchovies. *Solid lines* are regressions for all females; *broken lines* are regressions for all males. Relative water content of gonad decreases more rapidly with maturation among females; cluster of points at upper right represents females with obviously hydrated oocytes. *B*, GSLOPE, slope of regression of GSI upon ln(somatic wet weight), as a function of subsample mean GSI, given here on the abscissa as its antilog to linearize the relationship. 1984 subsample points are filled; *circles* and *stars* differentiate subsamples with and without females with hydrated oocytes, respectively. An ordinate of 0 corresponds to GSI isometry.

than 1.0, which together accounted for 72% of total variance. Orthogonal rotation yielded five easily interpretable factors (table 2):

1. *Body length* (MI), with high positive loadings by standard length and lengths from snout to dorsal fin origin and from snout to vent
2. *Jaw length* (MII), with positive loadings primarily by lengths from snout to maxillary tip and from snout to operculum border
3. *Anal-fin-base length* (MIII), with a negative contribution from length from snout to supraoccipital border
4. *Body depth* (MIV), with positive loading by that trait alone
5. *Orbit/preorbit length* (MV), expressing positive correlation with orbit diameter and a complementary negative loading by length from snout to the front of the orbit

Analyses of Variance (ANOVAs)

Maximum-likelihood ANOVAs with age as fixed effect, and year and the interaction age × year as random effects indicated a significant age effect for GSI; year effects for condition, GSI, body length, and anal-fin-base length; and age × year effects for size, jaw length, and body depth. Figure 3 illustrates these differences between age classes by year of collection. However, when station (nested in year) is added to the model as a random effect, station alone remains as a highly significant effect; only for size are age and age × year accorded any significance. The large differences in figure 3 may represent station sampling effects. Table 3 summarizes likelihood-ratio tests of maximum-likelihood ANOVAs with age and temperature as fixed effects, and station within

TABLE 2
Loadings on Five Factors from Principal Components Analysis of Adjusted Measurements of Morphometric Traits, after Orthogonal Rotation

	Morphometric PCA factors					
Trait	Body length (MI)	Jaw length (MII)	Anal-fin-base length (MIII)	Body depth (MIV)	Orbit/preorbit length (MV)	Comm.[a]
Vent	0.809*	−0.011	−0.047	0.014	−0.014	0.657
Dorsal fin origin	0.737*	−0.007	0.001	−0.120	−0.061	0.561
Standard length	0.761*	−0.210	0.264	0.148	−0.059	0.718
Operculum	0.039	0.828*	−0.100	0.015	0.063	0.701
Maxillary	−0.215	0.786*	−0.094	−0.041	0.009	0.674
Anal-fin base	−0.164	−0.349	0.862*	−0.067	−0.002	0.897
Supraoccipital	−0.318	−0.043	−0.607	−0.164	0.005	0.498
Body depth	−0.075	−0.005	0.038	0.865*	−0.182	0.789
Orbit diameter	−0.269	0.067	−0.124	−0.267	0.837*	0.864
Preorbit	−0.386	0.027	−0.257	−0.537	−0.611	0.877
Head width	−0.021	−0.463	−0.448	0.442	0.164	0.637
VP[b]	0.199	0.150	0.136	0.126	0.105	

*Loadings greater than 0.7.
[a]The communality or squared multiple correlation of a trait with the factors.
[b]The proportion of total variance explained by each factor.

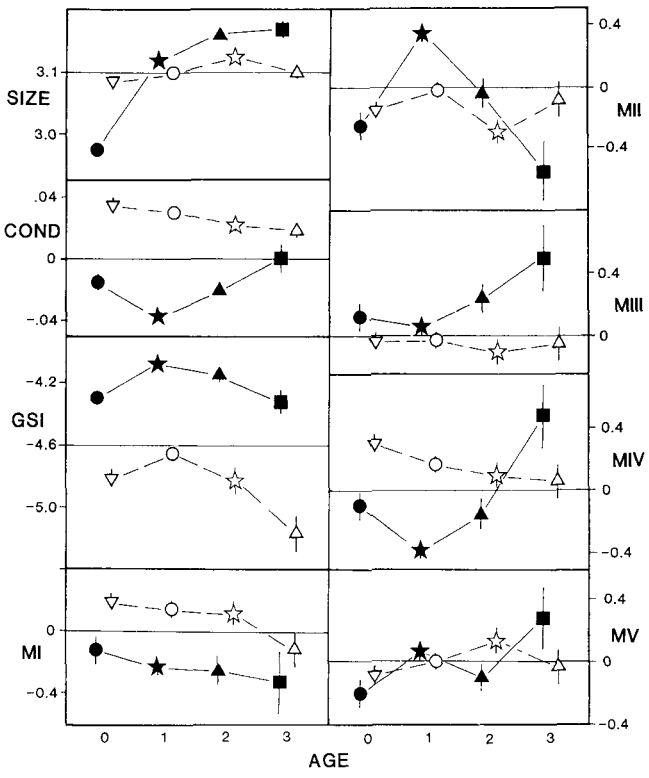

Figure 3. Dependent variable means for year classes within years. Year classes are as follows: 1980, *squares*; 1981, *triangles*; 1982, *stars*; 1983, *circles*; 1984, *inverted triangles*. *Solid line* connects 1984 ages (*filled symbols*); *dashed line* connects those from 1985. SIZE = consensus size measure; COND = condition factor; GSI = gonadosomatic index. PCA factors, MI–MV, are body length, jaw length, anal-fin-base length, body depth, and orbit/preorbital length. Dimensions are described in text and figures 1 and 4. Standard error bars are misleadingly small; differences between years may be station sampling effects (see Results, ANOVAs).

temperature as a random effect. The overwhelming effects of station can be seen, yet temperature retains some effect on GSI, body length, and body depth.

Correlation Analysis

Correlations of subsample means of dependent variables, among themselves and with independent variables, are presented in table 4. Two general patterns are seen: (1) condition is positively correlated with body length and body depth, and negatively correlated with jaw length and orbit/preorbit length; and (2) GSI slope is negatively correlated with size and GSI, which are themselves positively correlated. Body length, body depth, GSI slope, and condition subsample means are similarly correlated positively with year and negatively with temperature; mean GSI shows the opposite pattern. Jaw length and orbit/preorbit length are uncorrelated with the independent variables, but jaw length is highly significantly negatively correlated with body depth as well as with condition. Anal-fin-base length is negatively correlated with CalCOFI line, depth, and perhaps temperature; size is positively correlated with distance offshore, depth, and age. Notwithstanding their mutual (but opposite) correlation patterns with year and temperature, GSI and condition were negligibly correlated. Nevertheless, figure 3 suggests a high degree of negative correlation between reproductive and somatic condition among age-classes within years, which is so ($r = -0.847$; d.f. 6, $p < 0.01$).

Spatial patterns

The spatial distribution of subsample-mean size is shown in figure 1B; the contours, at approximately 10% increments in linear dimensions, reflect highly significant differences among subsample means. As noted by earlier workers (references in Parrish et al. 1985), anchovies are generally somewhat larger offshore and over deeper water (table 4), but in contrast to earlier findings, our samples showed no gradient of increasing size from southeast to northwest.

Spatial pattern for GSI subsample-means was similar to that of size (compare figures 1B,C). Notwithstanding the correlations of GSI slope with GSI and size, its spatial pattern was somewhat different (figure 1D). GSI slope >2 (figure 2B) was seen only in a northern group

TABLE 3
Maximum-Likelihood Analyses of Variance for Traits and Factor Scores of 1,836 Northern Anchovies

	Age (d.f. 3)		Temperature (d.f. 3)		Station (temp) (d.f. 1)	
Trait or factor	χ^2	p	χ^2	p	χ^2	p
Size	159.75	0.000	1.68	0.642	1432.46	0.000
Condition	1.16	0.762	6.13	0.106	742.75	0.000
GSI	9.96	0.019	8.58	0.035	922.80	0.000
Body length	5.17	0.160	18.14	0.000	11.57	0.001
Jaw length	11.99	0.007	2.25	0.522	245.19	0.000
Anal-fin-base length	1.54	0.673	4.65	0.200	64.15	0.000
Body depth	2.45	0.485	8.41	0.038	171.69	0.000
Orbit/preorbit length	2.24	0.525	1.22	0.749	56.34	0.000

Age (otolith score) and temperature (rounded to nearest degree) are fixed effects, and station within temperature is a random effect in mixed-model ANOVAs. χ^2 is the difference between log-likelihood estimates ($-2 \cdot \ln$[maximum likelihood]) for the full model and for the model with that effect set to zero; p is the associated probability, given the assumptions of the ANOVA. Variables are size, condition, GSI, and five PCA orthogonally rotated morphometric factors (table 2).

TABLE 4
Correlations among Mean Traits or PCA Factor Scores and Independent Variables for Subsamples of Northern Anchovy

	Body length (MI)	Jaw length (MII)	Anal-fin-base length (MIII)	Body depth (MIV)	Orbit/preorbit length (MV)	Size	Condition	GSI	GSI slope
MII	−0.099								
MIII	0.070	0.027							
MIV	0.228	−0.470*	0.200						
MV	0.002	0.169	−0.275	−0.187					
Size	−0.014	−0.037	−0.124	0.268	0.139				
Cond	0.401*	−0.512*	−0.143	0.524*	−0.354*	0.019			
GSI	−0.163	−0.050	−0.149	0.286	−0.129	0.556*	0.008		
Gslope	0.399*	−0.010	0.047	0.021	−0.130	−0.495*	0.209	−0.726*	
Year	0.566*	−0.093	−0.222	0.374*	0.091	0.005	0.504*	−0.371*	0.554*
Dist	0.410*	0.071	−0.191	−0.074	0.314	0.570*	−0.174	0.227	−0.059
Line	−0.149	0.091	−0.522*	−0.300	−0.167	0.043	−0.031	0.464*	−0.277
Depth	0.254	−0.048	−0.387*	0.021	0.321	0.492*	−0.115	0.284	−0.100
Temp	−0.435*	0.129	−0.346*	−0.483*	0.209	0.031	−0.472*	0.465*	−0.598*
Age	−0.202	−0.015	0.131	−0.057	0.271	0.362*	−0.089	−0.025	−0.273
YC	0.436*	−0.030	−0.215	0.222	−0.191	−0.309	0.311	−0.151	0.491*

Means are for 37 subsamples with more than 13 fish. Variables are: five orthogonally rotated morphometric PCA factors, size, condition, GSI, GSI slope, year (of sampling), distance offshore, CalCOFI line, depth of bottom, sea-surface temperature, age, year class (YC). With 35 d.f., r outside the range $-0.325 < r < 0.325$ (asterisks) is associated with $p < 0.05$ when the distribution is bivariate normal.

TABLE 5
Analysis of Covariance of Subsample Means for Traits or Factor Scores

Trait or factor	V%	F	p
Size	91.7	30.75	0.000
Condition	94.2	38.84	0.000
GSI	92.0	22.11	0.000
Body length	73.7	3.54	0.014
Jaw length	70.7	2.22	0.078
Anal-fin-base length	61.4	1.36	0.287
Body depth	79.3	6.11	0.001
Orbit/preorbit length	77.7	3.61	0.013

Variables corrected for year, age, size, and PCA factors, where appropriate. V% is percent of total variance among subsample means attributable to station differences; F is ratio of station mean square to subsample-within-station mean square; p is probability that differences among stations are similar to differences among ages within stations. Numerator degrees of freedom are 12; denominator d.f. are 19 (size), 18 (condition, GSI), and 14 (PCA factors).

of 1985 subsamples of maturing anchovies lacking females with hydrated oocytes. All but one of the negative GSI slopes were observed in subsamples containing females with hydrated oocytes, and these GSI slopes did not appear to be random deviations from zero; they formed a compact cluster (figure 1D).

Geographic patterns in subsample means for the five morphometric factors are shown in figure 4. The contours are in standard deviations (SD) from the grand mean (=0) of the standardized factor; 0.5 SD is equivalent to $p < 0.05$ for a t test of subsample mean with $n > 17$. The pattern for body depth (MIV, figure 4D) is strikingly similar to that for condition (cf. figure 1E).

Autocorrelation of subsample means for 1985 declined with distance, from a within-station r of +0.6 to +0.95 to an r near zero at 100–200 km for size, condition, GSI, GSI slope, body depth, and orbit/preorbit length. For morphometric factors body length, jaw length, and anal-fin-base length, within-station correlation was lower (cf. table 5), and r declined to zero within the first 100 km. For all variables, randomization of subsample means over stations resulted in more complex contour maps, usually with several equally likely alternative configurations; spatial autocorrelation was negligible, as expected.

Heterogeneity within Stations

The null hypothesis of the ANCOVAs of subsample means (table 5) is that even though differences between stations may be large, they are no greater than differences between subsamples within stations. F-statistics were highly significant for size, GSI, and especially condition; they were less so for body length, body depth, and orbit/preorbit length; and they were not significant for jaw length and anal-fin-base length. Since significant differences between stations do exist (table 3), these results indicate that some heterogeneity among subsamples within stations also exists for jaw length and anal-fin-base length.

For the 1982 year class, Levene's tests for heterogeneity of variance among subsamples were significant for size ($p < 0.001$) and the principal components body length, jaw length, body depth, and orbit-preorbital length ($p < 0.05$). For the 1983 year class, Levene's tests were significant for size ($p < 0.001$) and anal-fin-base length ($p < 0.01$). For the 1984 year class, Levene's tests were significant for size and jaw length ($p < 0.001$) and body length ($p < 0.05$). Thus, of 18 such tests (excluding year classes before 1982 for which sample sizes were small), 10 were associated with $p < 0.05$. Heterogeneity within certain subsamples was further suggested by positive cor-

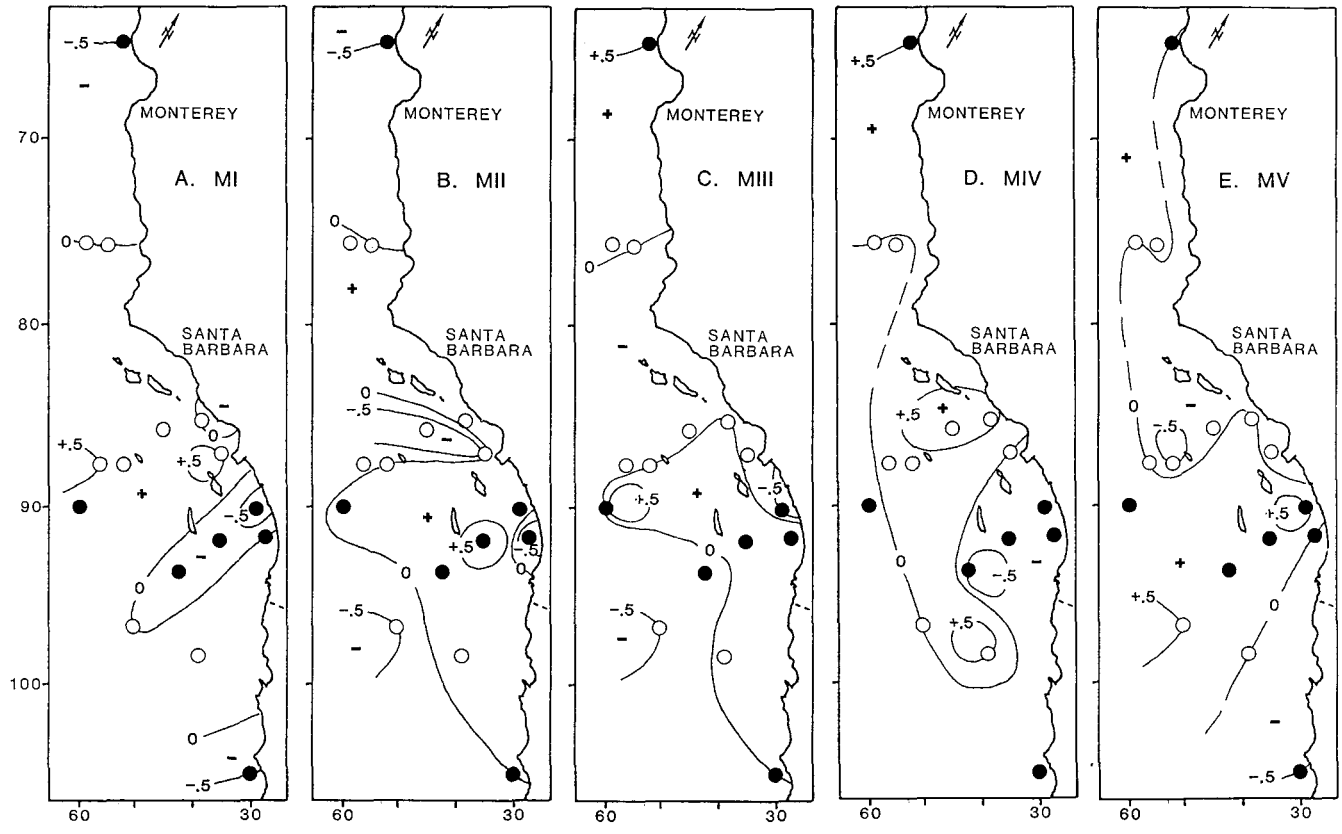

Figure 4. Contours of equal subsample means for orthogonally rotated morphometric factors MI–MV (body length, jaw length, anal-fin-base length, body depth, and orbit/preorbital length), in standard deviations of the standardized factor. Coordinates are CalCOFI coordinate cardinal and station lines as in figure 1. *Filled circles* are 1984 stations; *open circles* are 1985 stations.

relation of subsample variances between factors and between factors and size. Of 15 such intercorrelations of subsample variances, 12 were positive ($\chi^2 = 5.40$, $p < 0.025$; the mean of z-transformed intercorrelations was significantly greater than zero by t test, $p < 0.01$). Correlation was hardly reduced when subsample variances were adjusted for sex differences, nor did it appear to result from differences in subsample size.

DISCUSSION

Morphometrics and Condition

We chose the mean of the logs of the 11 morphometric measures as a general size variable, as suggested by Mosimann (1970, 1987). Because we were interested in variation in different parts of a continuously distributed population (rather than among isolated populations; Strauss and Bond 1990), we removed by regression as much as possible of the variance due to size before extracting principal components. To reduce variance introduced by the radical changes in shape accompanying sexual ripening, particularly the hydration of oocytes, we measured body depth at the pectoral girdle, rather than at a more representative pelvic location. We hoped thereby to recover from each anchovy measures of "shape" independent of size. We were indeed successful in avoiding substantial correlation of morphometric factors with size and with gonadal condition as measured by GSI.

However, subsample means of at least three of the five factors were each significantly correlated with somatic condition (table 4). That body depth was so correlated is reasonable; variation in the body-length factor, comprising, in part, measures of both length and depth, may be similarly explained. Negative correlation of condition with jaw length (table 4) has no such easy interpretation; jaw length was also negatively correlated with body depth, and these correlations of jaw length were in no case weakened after regression upon age, distance offshore, CalCOFI line, depth, temperature, and/or year (unpublished results).

The engraulids' elongate maxillae and opercula are associated with their unique filter-feeding method, in which the buccal and pharyngeal chambers are greatly expanded. Northern anchovies either attack prey individually or filter feed, depending upon prey size and abundance (Leong and O'Connell 1969); one might speculate that the temperature-independent association between

jaw length and condition and body depth is somehow trophic in origin. Part of the covariance discussed in the preceeding paragraph arises from similarities among the three neighboring Southern California Bight subsamples, which together constitute most of the 1984, age 1 group (figure 1A, stations B, D, and F; figure 3, filled stars). These fish share a combination of low mean condition, short and slender body, long jaw, and large orbits (figures 1 and 4), which we call the "lean and hungry look" (cf. Blaber et al. 1981 for a similar case in a clupeid).

Size and Shape

Much theoretical and practical effort has been expended in pursuit of precise differentiation of variables of size and shape (cf. Sampson and Siegel 1985; Bookstein et al. 1985; Reist 1986; Mosimann 1987; Strauss and Bond 1990). In light of the findings discussed above, we perceive a certain futility in this, at least in the study of individual variation in continuously distributed populations, growing and reproducing in spatially and temporally variable environments. However they are defined, size and shape of anchovies, both of which include aspects of somatic and reproductive condition, fluctuate greatly during the course of the year and from place to place and year to year. Size and shape are dynamic and all of a piece, and cannot be rigorously separated.

Therefore, we have no illusions that size and our morphometric factors measure absolutely distinct attributes of anchovies. Nevertheless, particularly in correlations with condition and GSI, they reflect different patterns of individual, temporal, and spatial variation. Condition was independent of size but was associated with body length, jaw length, body depth, and orbit/preorbit length (table 4). GSI was highly correlated with size (as was GSI slope, negatively), but was independent of condition and the morphometric factors. Inclusion of pelvic points among the morphometric measures probably would have reunited GSI with morphometrics and helped to provide a better picture of the complex exchanges between somatic and reproductive condition.

Somatic and Reproductive Condition

There is currently both theoretical and practical concern over the nature of trade-offs between reproductive investment and somatic condition and growth, particularly with respect to individual variation (Dygert 1986; Rijnsdorp 1990; Nelson 1993). Although significant *negative* covariance of GSI and condition among age classes within years (figure 3) seemingly supports a trade-off hypothesis, there is little correlation of the two either among individuals (unpublished analyses) or among subsample means.

It is remarkable that—notwithstanding the positive slopes of GSI on somatic wet weight in subsamples with lower mean GSI—negative GSI slopes are found when GSI is high (figure 2B). The negative correlation of GSI slope with GSI may be caused by temperature (table 4). It appears that with colder temperatures, maturation, especially of the smaller anchovies in a year class, is delayed and perhaps prevented entirely. When temperatures are such that all may mature, relative gonad size may be larger in smaller fish. Our analysis of data collected in the Los Angeles Bight in the winters of 1978 and 1979 (Hunter and Macewicz 1980, table 4) suggests that batch fecundity obeys a similar rule. The slope of the regression of log(number of hydrated eggs divided by somatic weight) upon log(somatic weight) in 1978 is -0.176, significantly different ($p < 0.002$) from the slope of $+0.401$ in the distinctly cooler winter of 1979 (12°–13° vs 14°–15°C; Hewitt and Methot 1982). Such size-dependent responses are examples of individual variation in reproductive reaction-norm allometry (Nelson, in press), with consequences for demographic response to temperature and trophic change. Puzzling and misleading patterns of response may result from lumping samples from different years or places (e.g., Parrish et al. 1986, figures 4B, 4C, 10).

Heterogeneity within and among Stations

In this paper, age classes within stations (subsamples with $n > 13$) have been treated as independent samples. For a sedentary species this would often be untenable. But the northern anchovy is a pelagic species capable of moving great distances (Haugen et al. 1969) and not known to return to localized spawning grounds as herring do. Common natal locality or even similar later experiences among different year classes spawning in the same area remain hypotheses to be tested. A priori, one might expect less similarity among anchovies of different ages from the same station than among members of the same year class from nearby stations.

For size, condition, GSI, and body depth, anchovies of different ages are more homogeneous within than among stations (table 4). This might result from assortative grouping, such as by swimming speed, or it might reflect common experience among year classes found at the same locality. There is evidence for both processes. On the one hand, at several stations, different ages displayed similar bimodal distributions of size. Also, heterogeneity of variance among subsamples within a year class was coupled with covariation of subsample variances for morphometric factors and size. These findings all imply that certain midwater-trawl hauls sampled several homogeneous groups with disparate size and morphometric characteristics. Such contiguous but dissimilar groups may have formed by assortative clustering, and may represent the "elementary populations" hypothesized by Lebedev (1969). On the other hand is the ev-

idence of mesoscale spatial autocorrelation (100–200 km for size, condition, GSI, GSI slope, body depth, and orbit/preorbit length). Such similarities among neighboring stations are more difficult to explain by assortative grouping, and therefore imply common experience.

Contours on maps of subsample means randomly reassigned to stations were more complex than those in figures 1 and 4 and often not topologically uniquely determined. Usually such randomized maps had several stations with more than one contour passing through them, signalling heterogeneity among the subsample means reassigned there. Such stations are seen only twice in the observed contour maps: for jaw length at station K and for anal-fin-base length at station E (figures 4B,C). For these factors, variance in subsample means was little different within and among stations (table 5), and within-station means were not highly autocorrelated. If differences in jaw length or anal-fin-base length are established early in life, they may reflect variation in larval or juvenile experience, not just among natal localities, but also among year classes from the same area that are later captured together. Thus, within-station heterogeneity for these factors could imply low spawning-site fidelity, and heterogeneity of origin of the different year classes at a station. These disparate year classes, through common environment and assortative grouping, later come to resemble one another in other ways (size, condition, GSI, body depth).

Spatial and Temporal Variation in the California Current System

Spatiotemporal patterns in anchovy life-history and morphometric characters must be related somehow to variation in the oceanographic regime along California and northern Baja California. This regime (Hickey 1979) is dominated by the southward-flowing California Current, which moves offshore at Point Conception (CalCOFI line 80) and returns onshore near line 100–110 (figure 1A). Inshore of this in the Southern California Bight is a semipermanent counterclockwise gyre. A northward-flowing countercurrent over the continental slope reaches the surface inshore north of Point Conception in fall and winter, as the Davidson Current (McLain and Thomas 1983). In spring and summer north of Point Conception, and most of the year south of line 100, northwest winds cause cold and nutrient-rich upwelled water to spread out locally offshore. Recent evidence suggests incursion of nutrient-poor warm water from the southwest into the bight during the second half of the year (Pelaez and McGowan 1986). Interannual variation of concern is the California El Niño that began in late 1982 and abated somewhat during the 1984 spawning season, but which may have had the largest positive temperature anomalies in summer 1984 (Fiedler et al. 1986; figure 1A shows 15°C winter isotherms for 1983–85). These changes may have been associated with northward advection, even at several hundred meters' depth (Norton et al. 1985), although there are certain problems with this hypothesis (McGowan 1985).

Variation in production may be related to these annual and interannual patterns of water movement. Fiedler (1983) and Pelaez and McGowan (1986) find correspondences between episodic zones of high surface phytoplankton-pigment concentration seen in satellite images and infrared images of areas of cold (upwelled) water. The latter include an inappropriately named "hot spot" over the submarine peninsula extending south-southeast from Point Conception along CalCOFI offshore coordinate 50 to the latitude of San Diego. Although El Niño events are associated with reduced nutrients, the biological response is likely to be complex and nonuniform and to involve delays at each point (McGowan 1985). Certain subtropical plankton and nekton appear far to the north (Pearcy et al. 1985). Again, there is room for interpretation about how much of this reflects northward advection vs *in situ* response by plankton (cf. Roesler and Chelton 1987) and active "following of isotherms" by certain nektonic species.

For each dependent variable in our analysis, spatial variation accounted for a much greater proportion of the variance than did interannual variation. Within a station, ages tended to have similar means (although occasional large differences were found with jaw length and anal-fin-base length in particular), and this was often true of neighboring stations as well (e.g., those sharing the "lean and hungry look"). Some or all of the effects of year of sampling may be artifacts of discrete sampling from a geographically variable population, but some of them may be real, reflecting interannual differences in temperature in particular.

We discern two seemingly independent temperature-correlated patterns, one shared by size, GSI, and GSI slope, and another related to condition, body depth, and body length (figures 1 and 4; cf. table 4). Neither consists of a simple cline such as that of temperature with CalCOFI line. Association with temperature accounts for less than 40% of the variance in any of these dependent variables, but sea-surface temperature at capture may be a poor proxy for the physiologically relevant thermal history of an anchovy. The temperatures likely to have significant impact on winter somatic condition and gonadal maturation are those in the previous growing season, which may not be related to temperatures at capture time. And if anal-fin-base length reflects temperature-dependent meristic differences established early in life (McHugh 1951), the connection with station sea-surface temperature is even more remote.

One might argue, then, that the significant correlations we see between morphological and reproductive traits and temperature are a minimum estimate of temperature-associated direct and indirect influences upon those variables. Signs of these influences may be found in the spatiotemporal distributions of subsample means (figures 1 and 4). The similar patterns of condition and body depth in particular resemble Pelaez and McGowan's (1986; cf. also Fiedler 1983) patterns of phytoplankton-pigment concentration and sea-surface temperature, differing mainly in offshore extent. One notices a similar "hot spot" of positive values trending southeastward of Point Conception, and inshore of this a northward "incursion" of negative values, including those subsamples characterized by the "lean and hungry look." We surmise that the correlation pattern here is with temperature as an indicator of prior trophic conditions, whereas the influence of temperature upon gonadal maturation, GSI, and GSI slope is more direct. However, the "incursion" also coincides well with sampling in 1984, and the "hot spot" with sampling in 1985. We cannot completely resolve the correlates of interannual and geographic variation in temperature, although we suspect the geographic differences are more important. Thus we conclude that although an "El Niño signature" may be discoverable in adult anchovies, it may be buried amid the disparate causes of geographic variation.

Fidelity to Locality and Water Mass

Fiedler et al. (1986) find "obvious discontinuities" in Department of Fish and Game (DFG) growth data, a sharp drop in size between October 1982 and February 1983, and a corresponding increase between September and November 1984. They suggest that the smaller anchovies caught during this period may have grown more slowly or have been of southern provenance, moving north with El Niño as certain other nekton is known to do (Pearcy et al. 1985). Our data agree in suggesting a small size for the 1983 year class, age-0 fish caught in 1984 (cf. Butler 1989). Otherwise, we detect no interannual differences in size, although 1984 and 1985 year-class means differed for the size-adjusted principal component MI, a measure of *relative* body length (figure 3).

Whether anchovies change their location during an El Niño or other warming event depends upon the degree to which they move independently of the water mass, as opposed to either active migration with it or passive advection. The outcome of a warming event will depend upon two sets of alternative conditions: (1) whether there is indeed mass water transport from the south or west or both during a warming event, or rather an *in situ* increase in water temperature; and (2) whether movements are oriented by geographically fixed features, or alternatively by prey density or some correlated environmental variable. The relative importance of these alternative but not necessarily exclusive possibilities will determine whether winter-cruise samples from the same location are of different provenance in different years, or whether their origins may be the same.

The available evidence suggests both that anchovies can move quite independently of the water mass, and that they possess a degree of spawning-site fidelity. The Sea of Azov population of the European anchovy *Engraulis encrasicolus* spawns in the Sea of Azov, then migrates through Kerch' Strait to winter in the Black Sea; its distribution within the Black Sea evidently varies with winter temperature (Chashchin 1985, and references therein). Thus their movements appear to reflect both environmental tracking and site fidelity, depending upon season. Adults of the northern race of *Engraulis mordax* may winter inshore with the juveniles, then segregate and move offshore for their summer spawning season (Laroche and Richardson 1980). A similar pattern but of opposite phase—southward and offshore movement for winter spawning—has been described for the central subpopulation in the Southern California Bight (Mais 1974). Haugen et al. (1969) interpret northern California recaptures of southern California anchovies and vice versa as implying movement northward in summer and southward in winter, which if true would be counter to seasonal flows of the California and Davidson Currents, respectively.

We do not know to what extent northern anchovies "follow the isotherms," nor to what extent they might combine summertime foraging flexibility with fidelity to winter spawning locality (but see MacCall 1990). But if anchovies captured in 1984 and 1985 had been of greatly different provenance, we would anticipate more pronounced temperature-influenced differences between them, on the order of the geographic variation we have described. Aside from the slower growth of age-0 fish in 1984, we found no appreciable differences in size. The morphometric differences observed between years would certainly have been exaggerated had El Niño presented us in the winter of 1984 with a different kind of anchovy from the south.

ACKNOWLEDGMENTS

The authors thank R. D. Methot for obtaining the samples of anchovies used in this study, Mary Simmons for her help with data entry, and Lynne Stenzel for her roles in data organization and analysis. This research was funded in part by a grant (R/F 98) from the California Sea Grant College Program.

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THE CENTRAL STOCK OF NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) IS NOT A RANDOMLY MATING POPULATION

DENNIS HEDGECOCK, ELMARIE S. HUTCHINSON, GANG LI, FREDERIC L. SLY, AND KEITH NELSON
University of California, Davis
Bodega Marine Laboratory
Bodega Bay, California 94923-0247

ABSTRACT

Allozyme variation at ten polymorphic loci is reported for a total of 2,628 northern anchovies from 32 midwater trawl samples of the central stock taken by the CalCOFI spawning biomass survey cruises of December 1982, and the winters of 1983, 1984, and 1985. Frequencies of genotypes at these loci conform to those expected on the basis of random mating, according to the Hardy-Weinberg (HW) principle and goodness-of-fit tests. Yet goodness-of-fit tests have low power for detecting failure of the HW principle or its assumptions and are here contradicted by evidence for significant heterogeneity of allelic frequencies among stations within years and within the total sample. Wright's F_{ST} statistic, a relative measure of allele-frequency variance among stations that ranges from 0.005 to 0.020, indicates little differentiation and relatively high gene flow among stations. Absolute total variance of allelic frequency among stations, however, is twice as large as the binomial sampling variance for a single, randomly mating population. Moreover, chi-square contingency tests of allele-frequency homogeneity among stations are highly significant over all loci for each of the four years. These results falsify the hypothesis that the central stock is a randomly mating population.

Several lines of evidence suggest that the genetic heterogeneity of the central stock is geographically unpatterned, or "chaotic," giving no indication of spatially distinct panmictic units. The loci that contribute to heterogeneity differ from year to year. Allelic frequencies are correlated weakly or not at all with latitude (CalCOFI line coordinate) or distance offshore. Spatial autocorrelation of allelic frequencies is weak among age subsamples within stations and declines to nonsignificant levels within 100 km. Correlations among genotypes at different loci, which can be nonzero in mixtures of genetically differentiated populations, are not significantly different from zero. Finally, cluster analysis of genetic distances among all 32 stations joins samples from different years and disparate latitudes at high levels of similarity.

Variation in allelic frequencies is significantly correlated with morphometric variation but not with measures of condition or reproductive state, suggesting that observed genetic heterogeneity is associated with substantial, perhaps heritable, morphological variation within the central stock. Genetic and morphometric variance may be generated by processes governing reproductive success, larval survival, and recruitment to first schools. How this variance is maintained through the adult stages is a matter for speculation, but it does permit natural selection to act among groups as well as among individuals.

[Manuscript received March 3, 1994.]

RESUMEN

Se reporta la variación de alocimos en diez loci polimorfos de 2,628 anchovetas norteñas del stock central obtenidas de 32 arrastres a media agua. Las muestras fueron obtenidas por el programa "CALCOFI" en los cruceros de evaluación de la biomasa de ponedores en diciembre de 1982 y los inviernos de 1983, 1984 y 1985. La distribución de frecuencias de los genotipos en estos loci se ajusta a las frecuencias esperadas en base a una suposición de apareamiento aleatorio, de acuerdo al principio Hardy-Weinberg (HW) y de acuerdo a pruebas de bondad de ajuste. Sin embargo, las pruebas de bondad de ajuste tienen poca potencia para detectar las fallas del principio HW o sus suposiciones. Y estas pruebas son contradichas por evidencia significativa de heterogeneidad de frecuencias de alelos tanto entre estaciones para un mismo año, como dentro del total de las muestras. El estadístico Wright $F_{ST,}$ que es una medida relativa de varianza de frecuencia de alelos entre estaciones con rango de 0.005 a 0.020, indicó poca diferenciación así como alto flujo genético entre las estaciones. Sin embargo, la varianza total absoluta de la frecuencia de los alelos entre las estaciones es el doble de la varianza de muestreo binomial para una sola población con apareamiento aleatorio. Aun mas, la prueba de contingencia Ji-cuadrada de homogeneidad de frecuencia de alelos entre estaciones es altamente significativa en todos los loci para cada uno de los 4 años. Estos resultados falsan la hipótesis que el stock central es una población con apareamiento aleatorio.

Varios indicios sugieren que la heterogeneidad genética del stock central carece de un patrón geográfico o que es "caótica", sin mostrar indicios de unidades en estado de panmixia separadas espacialmente. Los loci que contribuyen a la heterogeneidad difieren de año a año. La correlación entre las frecuencias de los alelos con la la-

titud (transectos de CALCOFI) o la distancia hacia mar adentro son bajas o nulas. La autocorrelación espacial de frecuencias de alelos es baja entre las submuestras de edad dentro de las estaciones y declina a niveles no significativos en un rango de 100 km. Las correlaciones entre los genotipos en loci distintos, que pueden ser diferentes de cero en mezclas de poblaciones diferenciadas genéticamente, no son estadísticamente diferentes de cero. Por último, un análisis de agrupamiento de distancias genéticas entre las 32 estaciones agrega muestras de años diferentes y latitudes distantes en niveles de similitud altos.

La variación de frecuencias de alelos está correlacionada significativamente con la variación morfométrica, mas no con medidas de condición o estados reproductivos, lo que sugiere que la heterogeneidad genética observada está asociada con variación morfológica importante, quizá hereditaria, dentro del stock central. La varianza genética y morfométrica podrían estar generadas por los procesos que gobiernan el éxito reproductivo, la sobrevivencia de larvas y el reclutamiento inicial al "primer" cardúmen. El cómo se conserva esta varianza en los estadíos adultos es motivo de especulación, mas esta varianza permite que la selección natural actúe entre grupos así como entre individuos.

INTRODUCTION

> In trying to identify and measure the causes of fluctuations in the abundance and distribution of a species of fish, it is essential that the number and identity of subpopulations, if any, within the species be established, since each subpopulation may have its own characteristic distribution, fecundity, natural mortality rate, growth rate, etc. This statement is axiomatic in the field of fisheries biology; and yet, there is some misunderstanding arising in part from semantic difficulties and in part from the lack of agreed definitions of problems. (Marr 1957)

On the basis of meristic and morphometric data and frequencies of electrophoretically detectable allelic forms of the serum protein transferrin (McHugh 1951; Vrooman et al. 1981), the northern anchovy *Engraulis mordax* Girard is considered to comprise a northern subpopulation spawning primarily in summer in the Columbia River plume, a central subpopulation spawning primarily in winter and spring in the Southern California Bight, and a southern subpopulation spawning off of Punta Eugenia and in Magdalena Bay, Baja California Sur, Mexico. The central subpopulation ranges from just north of San Francisco Bay (38°N) to Punta Baja (29°N) in northern Baja California (MacCall et al. 1983); it overlaps geographically but not temporally with the northern subpopulation in north central California (Vrooman et al. 1981) and perhaps likewise with the southern subpopulation in northern Baja California. Anchovies belonging to the southern subpopulation are morphologically distinguished from those in the central subpopulation by their smaller maximum sizes, longer heads, and larger eyes (Mais 1974; Vrooman et al. 1981; Parrish et al. 1985).

The central subpopulation of the northern anchovy has been regarded as both a stock, or unit of fishery management (MacCall et al. 1983), and a population of individuals that interbreed more or less at random with each other, and not at all or only infrequently with individuals from the other two subpopulations (Vrooman et al. 1981). Tagging studies show that adult anchovies can certainly traverse the range of the central subpopulation (Haugen et al. 1969). Frequencies of transferrin electrophoretic alleles are statistically homogeneous among samples from the central subpopulation, and proportions of transferrin phenotypes in the total subpopulation conform to those expected under random mating, according to the Hardy-Weinberg principle (Vrooman et al. 1981). Whether this is sufficient evidence that the central stock of northern anchovy is indeed a randomly mating population is an important practical and fundamental question.

On the practical side, assumption of random mating justifies application of the egg production method for estimating northern anchovy spawning biomass (Lasker 1985). In its most basic form the egg production method assumes that there is one true sex ratio, one true fraction of spawning females, and one true batch fecundity in the central stock. In practice, modifications of the basic method are necessary to account for regional variation in life-history characteristics and the catchability and vulnerability of spawning adults (Picquelle and Stauffer 1985; Smith and Hewitt 1985) and interannual variation in batch fecundity (Hunter et al. 1985). The demography of natural populations, however, is a complex summation of underlying, genetically heterogeneous, individual life histories (e.g., Brooks et al. 1994), so that finer-scale spatial and temporal heterogeneity within the central subpopulation might be confounded in estimates of spawning biomass. In a companion paper we demonstrate a surprising degree of spatial and interannual variation in the morphology and life history of northern anchovy within the central subpopulation (Nelson et al. 1994). In this paper, we present evidence that genetic heterogeneity among individual northern anchovies in the central stock is greater than that expected within a randomly mating population.

Previously, we reported significant heterogeneity of allelic frequencies among samples collected from within the range of the central subpopulation by the winter 1982 CalCOFI spawning biomass cruise (Hedgecock et al. 1989). Here we present comparable allozyme data for anchovies collected in four subsequent cruises. Samples collected in 1984 and 1985 were larger and were ana-

lyzed not just for genetic variation but for variation in morphometric and life-history traits as well. A preliminary analysis of a portion of the 1985 data was made by Hedgecock (1991), but we now present a complete analysis of correlation of morphometric, life history, and environmental variation with allozyme variation.

MATERIALS AND METHODS

Samples

Samples were collected at a total of 32 midwater trawl stations in December 1982, and early 1983, 1984, and 1985, by CalCOFI survey cruises 8212, 8302, 8403, and 8502 of the NOAA Southwest Fisheries Center, La Jolla, California. Localities, sample details, and alphabetic symbols for the 1984 and 1985 stations are given in figure 1A and table 1 of Nelson et al. (1994); comparable information for the 1982 and 1983 stations is given in table 1. With exceptions noted in these tables, sample sizes per station were 48 in the first two years and 120 in the last two years. Altogether 2,628 individuals were studied. Whole fish were frozen individually aboard ship at −70°C and then shipped in plastic bags by air to the Bodega Marine Laboratory, where they were held at −70°C until dissection.

Measurements

Specimens were partially thawed a few at a time and held on ice until measured and dissected. For the 1982 and 1983 samples, standard length (from snout to end of hypurals) was measured to the nearest mm with a mounted rule; more extensive morphological measurements were made on the 1984 and 1985 specimens, as described by Nelson et al. (1994). We dissected out tissues for electrophoresis, and otoliths for aging, and recorded the sex of each fish. Methods for determining ages from otolith followed those of Collins and Spratt (1969), as described by Hedgecock et al. (1989) and Nelson et al. (1994).

Allozyme Electrophoresis

Electrophoretic methods were described by Hedgecock et al. (1989). Eye, heart, liver, and skeletal (epaxial) muscle tissues were dissected from specimens, kept chilled during dissection, then stored at −70°C for no more than several days before electrophoresis. Tissue samples were thawed the day before electrophoresis, homogenized on ice in equal volumes of 0.5 M Tris-HCl, pH 7.1 buffer, and refrozen at −70°C overnight. Electrophoretic protocols for the ten polymorphic loci used for this study—*Est-5* (esterase), *Fum* (fumarate hydratase), *Gpi* (glucose-6-phosphate isomerase), *Hbdh-1* (3-hydroxybutyrate dehydrogenase), *Idh-1* (isocitrate dehydrogenase), *Ldh-1* (lactate dehydrogenase), *Lt-1* (leucyl-tyrosine dipeptidase), *Lgg* (leucyl-glycyl-glycine tripeptidase), *6pgdh* (6-phosphogluconate dehydrogenase), and *Pgm* (phosphoglucomutase)—are given in table 1 of Hedgecock et al. 1989. Two loci were dropped from this study: *Hbdh-2* because of the electrophoretic artifacts described previously (Hedgecock et al. 1989) and *Xdh* because of difficulty in scoring its closely migrating allozymes. All gels were scored independently by D. Hedgecock and G. Li or E. Hutchinson, and discrepancies resolved by joint re-examination and consensus.

Analysis

Individual genotypes were coded as paired alphabetical characters and analyzed with the BIOSYS-1 program (Swofford and Selander 1981; release 1.7 for the PC, Swofford 1989), to yield estimates of allelic frequencies, tests of Hardy-Weinberg (HW) equilibrium genotypic proportions, Wright's (1978) *F*-statistics, and Nei's (1972) minimum genetic distance in pairwise comparisons among all 32 stations. Fit to HW-expected proportions was tested by an exact probability method, after pooling of alleles into common and rare categories. Because most polymorphisms comprised two major alleles (see appendix tables A–D), there appears to be little loss of information by pooling. Comparable results were obtained by chi-square goodness-of-fit tests—with Levene's (1949) correction for small sample sizes—for loci with an expected number of at least 1.0 in each genotypic class. Log-likelihood analyses of allelic frequencies cross-classified by sex and age within locality (Fienberg 1980) were used to evaluate the homogeneity of station samples. The significance of contingency chi-square tests of locality × allele-frequency independence was evaluated for each locus by the pseudo-probability method and algorithm of Zaykin and Pudovkin (1993). We used minimum genetic distance and the unweighted pair-group method for cluster analysis of all stations.

We analyzed a subset of the 1985 samples, the six stations considered by Hedgecock (1991)—i.e., H, I, K, L, O, P in table 1 in Nelson et al. 1994—for evidence of population mixture. Using the methods and computer program PANMIX described by Waples and Smouse (1990), we calculated genotypic correlations (gametic phase disequilibria) for all pairwise combinations of loci studied in these samples and tested the null hypothesis that all interlocus correlations were zero. This was done both for individual and pooled stations, after collapsing all loci to two-allele cases.

Because morphometric measurements varied among ages, both within and among stations, Nelson et al. (1994) treated age classes within stations as independent subsamples of the 1984 and 1985 midwater trawl collections. For analysis of the 1984 and 1985 genetic data, we likewise selected 31 subsamples having more than 24

TABLE 1
Collection Localities and Samples of Northern Anchovy

Coll. no.	Date	CalCOFI Line; Station	Age (*N*>12) range	*N*	Standard length (cm) Mean	SD	Percent female*
A. 1982 cruise 8212							
4520	12/14	56.2; 50.0	0	19	8.31	1.65	54.5
			1	25	10.69	2.00	52.4
			0–2	48	9.73	2.16	51.4
4518	12/12	61.7; 52.0	0	14	8.09	0.91	54.5
			1	30	8.67	0.67	55.2
			0–3	48	8.61	0.91	51.2
4515	12/11	65.0; 50.5	1	36	8.43	0.78	37.1
			0–3	48	8.28	0.99	38.1
4522	12/15	73.8; 49.8	0	32	9.65	0.61	41.4
			0–2	48	10.41	1.40	50.0
4523	12/15	74.4; 49.3	0	20	9.74	0.92	73.3
			1	20	10.06	0.86	50.0
			0–3	48	9.91	0.95	58.6
4524	12/15	74.8; 49.0	0	16	10.26	0.79	25.0
			1	26	10.13	0.57	46.2
			0–2	48	10.28	0.76	41.7
4510	12/05	75.0; 49.0	1	28	11.97	0.99	64.3
			2	13	12.58	0.66	76.9
			0–3	48	11.93	1.12	68.8
B. 1983 cruise 8302							
4532	02/06	75.0; 49.0	0	41	8.95	0.71	46.2
			1	22	10.08	1.04	57.1
			0–3	72	9.67	1.36	50.7
4538	02/10	80.0; 53.0	1	18	10.81	0.82	33.3
			2	14	12.22	0.75	50.0
			0–4	48	11.23	1.11	37.5
4546	02/16	85.0; 51.0	0	22	9.90	0.47	71.4
			1	13	10.12	0.75	69.2
			0–3	48	10.36	0.96	69.8
4573	03/17	94.1; 34.0	0	24	9.00	0.42	70.8
			1	24	9.30	0.45	91.7
			0–1	48	9.15	0.46	87.0
4576	03/18	95.8; 38.0	0	15	9.93	0.41	26.6
			1	31	10.18	0.60	61.3
			0–2	48	10.15	0.68	52.1
4582	03/22	100.0; 36.0	0	13	10.02	0.45	69.2
			1	24	10.50	0.66	78.3
			0–3	48	10.71	0.95	74.5
4584	03/24	101.7; 34.0	0	40	9.10	0.53	55.0
			0–2	48	9.16	0.53	56.2
4586	03/28	105.0; 34.0	0	15	9.38	0.48	26.7
			1	33	9.30	0.57	36.4
			0–1	48	9.32	0.54	33.3
4590	03/30	110.0; 35.0	0	27	9.27	0.57	29.6
			1	18	9.92	0.72	38.9
			0–2	48	9.64	0.82	33.3

*Percent female is 100 times the number of females divided by the total number of fish with identifiable sex. Sex could not be determined for 27.0%, 10.4%, 12.5%, 8.3%, 39.6%, 0%, and 0% of fish collected in seven 8212 stations, respectively. Sex was indeterminate for only 1% of fish collected on cruise 8302.

individuals each. Subsamples were similarly selected from the 1982 and 1983 collections, although smaller sample sizes per station required a less stringent criterion: 25 subsamples with 11 or fewer fish (weighted mean = 4.6) were omitted, and 29 subsamples with 13 or more fish (weighted mean = 23.1) were retained.

The BMDP multivariate statistical software package (Dixon et al. 1988) was employed for additional analyses. Principal components analysis (PCA) was done without rotation on arcsine-square root transformed frequencies of the most common allele at each locus, for both stations and subsamples. Allele-frequency data for the 1982 and 1983 cruises were combined and analyzed separately from data for the 1984 and 1985 cruises, which had larger mean sample sizes and accompanying morphometric data. Correlations of genetic PCA factors with CalCOFI line coordinates, age, mean standard lengths, and—for the 1984 and 1985 samples—mean

measures of size, condition, gonadosomatic index, and five morphometric PCA factors were also obtained from BMDP (Nelson et al. 1994). We used autocorrelation (Rossi et al. 1992) of genetic factor scores (GII) for paired 1985 subsamples classified into distance categories to examine the spatial scale of genetic heterogeneity and to compare it with the spatial scales of variation in morphometric and life-history traits (Nelson et al. 1994).

RESULTS

Goodness-of-fit to Hardy-Weinberg Genotypic Proportions

Goodness-of-fit between observed numbers of genotypes at each of ten polymorphic allozyme loci and those expected under the Hardy-Weinberg principle for randomly mating populations was tested for each station sampled in each of the four surveys. Of the grand total of 313 exact probability tests, only 9 showed discrepancies significant at a nominal 5% significance level, fewer than the 16 expected by chance alone. The 9 significant tests, indicated by superscripts in the F_{IS} column of table 2, are spread over six loci, with *Est-5*, *Hbdh-1*, and *Ldh-1* accounting for two each and *Fum*, *Idh-1*, and *Lgg*, one each. Likewise, the 9 discrepancies are distributed across seven stations. Adjusting levels of significance for simultaneous testing of the hypothesis of random mating at ten loci per station (Cooper 1968; Rice 1989) leaves only one test significant at the 5% level (*Lgg* in 1984, station 4660). Agreement of observed and expected genotypic proportions is also evident for pooled data from each cruise. Means for Wright's (1978) F_{IS} statistic, which can be interpreted as a measure of average departure from random mating, fluctuate closely around zero, indicating no departure (table 2), and no significant departures from HW genotypic proportions were detected by exact probability tests for each locus in pooled cruise data.

Heterogeneity among Sexes and Age Classes within Stations

Loglinear models were fit to allele-frequency data tabulated by sex and age class for each of the 32 stations to determine whether these three factors were independent. Each of eight possible loglinear models (Fienberg 1980) were fit to the 190, frequency × age × sex, 3-way tables. Sex was found to be independent of age in 17 of 32 station samples but was significantly dependent on age in the remaining 15 stations; females were on average older than males at 11 stations. Allelic frequency was independent of sex and age, whether or not there was interaction of sex and age, in 174 (91.6%) of the 3-way tables.

In 16 cases, loglinear models involving interactions of allelic frequency with age or sex or both provided the best fits to the cross-classified data. Over all samples, dependence of frequency on age, and dependence of frequency on sex were each found in 9 stations. Because a model of frequency independent of age but conditional on sex fit data for two loci in one station (*Fum* and *Pgm* in station L, 1985), three subsamples for this station were considered in further analyses of allelic frequencies and morphometrics: age 0 females, age 1 females, and age 0 males. Interactions of allelic frequency with sex or age were spread over eight of the ten allozyme loci, led by *Pgm* with six; followed by *Est-5*, *Fum*, and *Ldh-1* with three each; *Hbdh-1* and *Lt-1* with two each, and *Idh-1* and *Lgg* with one each.

Heterogeneity among Stations

Allelic frequencies for 10 loci in each of 32 stations are given in appendix tables A–D. Heterogeneity of allelic frequencies among stations within years is measured by Wright's (1978) F_{ST} statistic, which standardizes the variance of allelic frequencies among samples against the maximum variance that would obtain if localities were fixed for alternate alleles in proportion to the mean allelic frequency for the total population. The F_{ST} values given in table 2 suggest that, relative to this maximum variance, genetic variance among stations ranges from less than 1% in 1984 and 1985 to 2.0% in December 1982. Combining all stations from the four cruises into a hierarchical analysis of genetic diversity, we find that standardized variance among stations within cruises, F_{SC}, is equal to variance among stations within the total, F_{ST} = 0.006, and that variance among cruises, F_{CT}, is zero.

Nevertheless, divergence of allelic frequencies among stations is highly significant for each of the four population surveys, as shown by the summed chi-square tests of heterogeneity (table 2). In each of the four surveys, four of ten loci yield significant heterogeneity chi-square values; but which loci are heterogeneous varies from year to year, resulting in a distribution of significant chi-square values over loci as follows: *Est-5*, 4; *Fum*, 1; *Gpi*, 3; *Hbdh-1*, 3; *Idh-1*, 0; *Ldh-1*, 1; *Lt-1*, 1; *Lgg*, 2; *6pgdh*, 1; *Pgm*, 0. Eight of the ten loci are significantly heterogeneous in at least one survey, and only two loci are homogeneous in all four surveys.

There is no correspondence of loci showing departures from Hardy-Weinberg genotypic proportions and loci showing heterogeneous allelic frequencies among localities; four loci with significant departures from random mating within stations show heterogeneity of allelic frequencies among stations, but five other loci with departures show no such heterogeneity (table 2). Likewise, loci showing interactions of allelic frequency with sex or age within station are not those showing spatial heterogeneity in the 1982, 1983, and 1984 surveys, although three of four loci showing spatial heterogeneity in the

TABLE 2
F-Statistics and Contingency Chi-Square Analyses for Northern Anchovy Samples from Four NMFS Cruises

Locus	F_{IS}[a]	F_{IT}	F_{ST}	No. of alleles	Heterogeneity among samples: Chi-square	d.f.	P[b]
A. December 1982 (8212); 7 samples							
Est-5	0.073[1]*	0.137	0.069	6	98.996	30	0.000*
Fum	0.000	0.014	0.014	3	18.116	12	0.092
Gpi	0.014	0.023	0.010	5	38.207	24	0.032*
Hbdh-1	0.094	0.102	0.009	5	39.860	24	0.019*
Idh-1	0.033	0.056	0.024	6	31.466	30	0.347
Ldh-1	−0.015	−0.008	0.007	2	4.772	6	0.573
Lt-1	0.152	0.155	0.004	5	20.584	24	0.808
Lgg	−0.065	−0.042	0.022	4	37.881	18	0.001*
6pgdh	0.020	0.031	0.011	3	14.656	12	0.251
Pgm	−0.057	−0.040	0.016	4	21.577	18	0.226
Mean	−0.006	0.014	0.020	Sum	326.115	198	0.000*
B. February–March 1983 (8302); 9 samples							
Est-5	0.020	0.074	0.055	5	72.176	28	0.000*
Fum	0.012	0.025	0.013	3	16.851	16	0.330
Gpi	−0.062	−0.035	0.025	4	43.254	21	0.009*
Hbdh-1	0.014	0.027	0.012	6	63.069	40	0.009*
Idh-1	−0.008	0.025	0.033	4	20.219	24	0.471
Ldh-1	0.016[1]*	0.022	0.005	2	4.961	8	0.762
Lt-1	−0.069	−0.059	0.009	5	37.256	32	0.222
Lgg	0.028	0.037	0.009	4	34.811	24	0.075
6pgdh	0.060	0.075	0.016	4	42.710	24	0.010*
Pgm	0.078	0.087	0.010	5	31.567	32	0.471
Mean	0.020	0.035	0.015	Sum	367.858	256	0.000*
C. February–March 1984 (8403); 7 samples							
Est-5	0.074	0.090	0.017	6	55.042	30	0.008*
Fum	−0.049[1]*	−0.047	0.002	4	18.615	18	0.398
Gpi	−0.016	−0.011	0.005	5	46.207	24	0.006*
Hbdh-1	0.063	0.067	0.004	7	32.952	36	0.596
Idh-1	0.007[1]*	0.010	0.003	6	31.898	30	0.316
Ldh-1	−0.072	−0.051	0.020	3	26.896	12	0.003*
Lt-1	−0.031	−0.019	0.011	7	78.057	36	0.000*
Lgg	−0.034[1]*	−0.028	0.006	4	23.470	18	0.164
6pgdh	−0.003	0.001	0.004	5	19.636	24	0.753
Pgm	−0.014	−0.002	0.012	4	25.556	18	0.094
Mean	−0.024	−0.015	0.008	Sum	358.330	246	0.000*
D. January–March 1985 (8502); 9 samples							
Est-5	0.034[1]*	0.041	0.007	7	68.397	48	0.023*
Fum	0.062	0.068	0.007	6	55.591	40	0.025*
Gpi	−0.034	−0.031	0.003	5	34.171	32	0.344
Hbdh-1	0.062[2]*	0.068	0.007	7	64.558	48	0.030*
Idh-1	−0.012	−0.008	0.003	5	34.233	32	0.326
Ldh-1	−0.022[1]*	0.024	0.002	4	18.612	24	0.892
Lt-1	−0.036	−0.033	0.003	6	35.073	40	0.726
Lgg	0.012	0.017	0.005	6	53.513	40	0.047*
6pgdh	0.021	0.025	0.004	6	47.741	40	0.150
Pgm	−0.050	−0.043	0.006	6	43.660	40	0.298
Mean	0.014	0.019	0.005	Sum	455.548	384	0.007*

[a]Superscripts with asterisks in the F_{IS} column indicate number of significant deviations from random-mating genotypic proportions.
[b]Asterisks in P column indicate significant among-sample heterogeneity χ^2 values.

1985 survey—*Est-5*, *Fum*, and *Hbdh-1*—show interactions with sex or age for stations I, L, and O. Finally, six 1985 stations that differed substantially in mean standard length and allelic frequencies (Hedgecock 1991) were tested for evidence of population mixture. Genotypic correlations between pairs of loci (gametic phase disequilibria), either for individual-station or pooled-station data, were not significantly different than zero.

Principal Components Analysis (PCA) of Allelic Frequencies

Using frequencies of the most common alleles at ten allozyme loci, we performed two PCAs of data from the 1982 and 1983 surveys—one for the 16 stations and the other for 29 age-class subsamples. The station data yielded four factors with eigenvalues greater than 1.0, accounting cumulatively for 69.5% of total variance in allelic frequencies. The subsample data yielded five factors with eigenvalues greater 1.0, accounting cumulatively for 74.1% of total variance. The patterns of contributions by individual loci to factors were quite different for the two analyses. Factor 2 for the station data (accounting for 18.5% of total variance) resembled factor 1 for the subsample data (accounting for 21.1% of total variance) in having high positive loadings by *Pgm* (≈0.7) and high negative loadings by *Idh-1* (≈−0.6); however, the latter was also positively loaded by *Gpi* and *Hbdh-1* (both >0.6), whereas the former was positively loaded not by these loci but by *Fum* (0.69). The third factor extracted in the subsample PCA, which accounted for 14.1% of total variance and later yielded correlation with age (see below), was loaded positively by *Fum* (0.83) and negatively by *6pgdh* (−0.51).

A comparable PCA for the 31 age-class subsamples selected from the 1984 and 1985 collections yielded four factors with eigenvalues greater than 1.0, accounting cumulatively for 67.3% of total variance in allelic frequencies. Factor 1, which accounted for 23.9% of total variance, was loaded positively (>0.7) by *Idh-1* and *Hbdh-1* and negatively by Gpi (−0.7). Factor 2, which accounted for 20.3% of variance, was loaded positively but weakly (≈0.5) by *Lgg*, *Fum*, and *Est-5* and negatively by *6pgdh* (−0.65) and *Lt-1* (−0.56).

Correlation of Genetic, Morphometric, and Environmental Factors

For the 1982 and 1983 data, genetic factor scores could be correlated with CalCOFI line coordinate, mean standard length, and—for subsamples—age (table 3). For the station data, only one of eight correlations, that between GII factor scores and CalCOFI line, was significant (r = 0.814, 14 d.f., $p < 0.01$). For the subsample data, two of 15 correlations were significant—GI factor scores vs CalCOFI line (r = 0.457, 27 d.f., $p < 0.05$) and GIII factor scores vs age (r = −0.478, 27 d.f., $p <$ 0.01). Mean standard length and age were not correlated with CalCOFI line, but age was positively correlated with mean standard length (r = 0.638, 27 d.f., $p < 0.01$), as expected (table 3).

For the 1984 and 1985 data, subsample scores for four genetic factors were correlated with subsample means for a total of 15 morphometric, life-history, and environmental variables: five morphometric factors (characterized as body depth, jaw length, anal-fin-base length, body depth, and orbit/preorbit length); a consensus measure of size; condition factor; gonadosomatic index (GSI); the coefficient from the regression of gonadosomatic index on ln(somatic wet weight) or GSI slope; distance of station from shore; CalCOFI line coordinate of station; year of capture; sea-surface temperature at capture; depth of bottom at station; and year class or estimated year of birth (see Nelson et al. 1994 for details). No correlation was observed among any of the genetic factors and condition, GSI, GSI slope, distance offshore, CalCOFI line, year of capture, sea-surface temperature, or year class. Single correlations between a genetic factor and each of the seven remaining variables—the five morphometric factors plus size and depth of bottom—exceed the critical significance value of 0.355 for $\alpha_{0.05}$ and 29 d.f. (table 4). The observation that 7 of 60 correlations are significant at the $\alpha_{0.05}$ level differs significantly from the expectation that 3 correlations might be significant by chance (χ^2 = 5.614, 1 d.f., p = 0.018); one correlation significant at the $\alpha_{0.01}$ level—0.456—is not different from the 0.6 expected by chance.

TABLE 3
Correlations of Genetic Factors with CalCOFI Line, Age, and Mean Standard Length for 1982 and 1983 Northern Anchovy Samples

	Stations		Subsamples		
	Line	Length	Line	Age	Length
Line	1.000		1.000		
Age	—	—	−0.131	1.000	
Length	0.047	1.000	0.024	0.638*	1.000
GI	0.131	−0.397	0.457*	−0.113	−0.068
GII	0.814*	0.065	−0.074	−0.057	−0.317
GIII	0.036	0.065	0.347	−0.478*	−0.221
GIV	0.384	0.167	−0.035	−0.113	0.036
GV	—	—	−0.049	−0.142	−0.046

Stations and subsamples (within-station age classes having 13 or more fish) are listed in table 1. Line is the CalCOFI coordinate for the station; length is the mean standard length for station or subsample; and age is the otolith age class. GI through GV represent principal components of allelic frequencies at ten allozyme loci; only four genetic factors were extracted from station data. *Correlations exceeding critical values for significance at the 5% level.

Spatial Pattern

Autocorrelation of 1984 and 1985 subsample scores for factor GII declines with distance, from a within-station r of 0.452 (N=16), significant only at the $\alpha_{0.05}$ level for a one-tailed test, to nonsignificant r values of 0.140 (N=61), −0.153 (N=103), 0.100 (N=133), and −0.078 (N=120) for distances of up to 100, 200, 300, and >300 km, respectively. This spatial pattern resembles that found for the morphometric factors body length, jaw length, and anal-fin-base length (Nelson et al. 1994).

TABLE 4
Correlations of Genetic Factors with Morphometric Factors and an Environmental Variable for 1984 and 1985 Northern Anchovy Samples

	Body length (MI)	Jaw length (MII)	Anal-fin-base length (MIII)	Body depth (MIV)	Orbit/preorbit length (MV)	Size	Depth of bottom
GI	0.023	0.091	−0.080	0.193	−0.124	0.438*	0.170
GII	−0.471*	0.409*	0.121	−0.363*	−0.010	−0.224	−0.424*
GIII	−0.024	0.289	−0.069	−0.095	0.379*	−0.130	−0.056
GIV	−0.102	0.138	−0.399*	−0.079	0.266	−0.129	0.002

Morphometric factors are described by Nelson et al. (1994). MI through MV are mean subsample scores for principal components of variation for 11 morphometric traits; size is a consensus measure based on these 11 traits. Depth of bottom is at station. GI through GIV represent genetic factor scores for 32 subsamples described by Nelson et al. (1994).
*Correlations exceeding the critical value for significance at the 5% level.

DISCUSSION

Is the Central Stock a Randomly Mating Population?

The central stock of the northern anchovy *Engraulis mordax* is commonly assumed, implicitly if not explicitly, to be a randomly mating population. This assumption is based primarily on long-term spatial and temporal distribution of eggs and larvae in CalCOFI samples (Kramer and Ahlstrom 1968; Hewitt 1980), recaptures of tagged adult fish (Haugen et al. 1969), meristic and morphometric studies (McHugh 1951; Vrooman et al. 1981), and agreement of transferrin genotypic frequencies with proportions expected on the basis of random mating and the Hardy-Weinberg (HW) principle (Vrooman et al. 1981). However, chi-square goodness-of-fit or exact probability tests of genotypic data have very low power to detect failure of the HW null hypothesis (Lewontin and Cockerham 1959; see review by Lessios 1992). In view of the potential significance of subpopulations for fishery biology and management so succinctly stated by Marr (1957), it may be important to question whether the assumption of random mating within the geographically defined central stock of northern anchovy has been sufficiently tested.

In our study of allozyme variation in 2,628 northern anchovies sampled at 32 stations within the range of the central stock, we too have found statistical agreement between observed distributions of genotypes at ten polymorphic loci and those expected according to the HW principle. Only 9 of 313 tests of agreement within stations showed discrepancies significant at a nominal $\alpha_{0.05}$ level; once significance is adjusted for simultaneous multiple testing of the hypothesis (Cooper 1968; Rice 1989), only one of these departures remains significant, which is expected by chance. Even after pooling data for all stations within each of the four survey cruises, we find no significant departures from HW genotypic proportions at any locus and no significant deviation of the mean fixation index from zero. Thus testing of HW genotypic proportions, either within or over all stations, offers no evidence against the assumption that the central stock of northern anchovy is a randomly mating population. Neither, however, does agreement with HW genotypic proportions prove the assumption true.

Having failed to reject the null hypothesis of random mating, we next examine evidence for heterogeneity of allelic frequencies among stations. The measure of population differentiation most often employed by population geneticists, Wright's F_{ST} statistic, ranges in this study from 0.005 to 0.020 over four survey cruises and was 0.032 in our previous analysis of data from an early 1982 cruise (Hedgecock et al. 1989). Such low values are typical for marine fishes (Gyllensten 1985), including the southern African anchovy, *Engraulis capensis*, for which mean F_{ST} was found to be 0.0015 (Grant 1985), and are generally regarded as indicative of only slight differentiation and relatively high rates of gene flow among localities. "Differentiation is, however, by no means negligible if F is as small as 0.05 or less" (Wright 1978).

In this case, the absolute variance of allelic frequencies among population samples, especially in comparison to the variance of sampling from a randomly mating population, is more informative than F_{ST} itself, which is among-population variance relative to its maximum value at complete fixation. For all ten loci and 32 stations sampled in this study, the expected binomial sampling variance of allelic frequencies is 0.00177. Absolute variance in allelic frequency among stations, which is obtained by subtracting the binomial sampling variance from total observed variance among stations, is 0.00131. Thus the total variance of allelic frequencies that we have measured among samples from the central stock is about twice what should have been observed were we sampling from a randomly mating population. That genetic differentiation among samples from this stock is not negligible is further demonstrated by chi-square tests of allele-frequency heterogeneity across all ten loci, in each of the four surveys (table 2). These tests consistently reveal highly significant heterogeneity of allozyme fre-

quencies, which is incompatible with the hypothesis that samples were drawn from a randomly mating population.

Our samples were drawn from a single, readily identified stock of northern anchovies living in a prescribed area of the California Current. If this stock is not a randomly mating population, then how should it be described? At the risk of becoming entangled in the "semantic difficulties" and "lack of agreed definitions" referred to by Marr (1957), we offer the following description. The central stock of northern anchovy is a geographic subpopulation which itself comprises a hierarchy of population units, the lowest ones in the hierarchy being the panmictic units within which mating is at random. Whether it is possible to partition this subpopulation into its individual panmictic units or to determine the causes of genetic heterogeneity within the central stock remain important questions.

Chaotic Spatial Pattern of Genetic Heterogeneity

Spatial patterning of allelic frequencies might suggest differential spatial distribution of panmictic units within the central stock. A number of lines of evidence indicate, however, that genetic heterogeneity within the central stock of northern anchovy is geographically unpatterned or "chaotic" (Johnson and Black 1982).

First, the loci contributing to heterogeneity differ from year to year. Including results previously reported for the early 1982 survey (Hedgecock et al. 1989), nine of ten polymorphic loci show significant heterogeneity of allelic frequencies in at least one of the five surveys taken, and all ten loci have homogeneous allelic frequencies in at least one survey. Moreover, the contributions of loci to factors extracted by various principal components analyses differ considerably from analysis to analysis. Comparing PCA factors for the 1982 and 1983 subsample data to those obtained for the 1984 and 1985 data, we find absolute loadings of loci, or the signs of the loadings, or both to be completely different. Comparing PCAs of stations vs subsamples for the 1982 and 1983 surveys, we find factor GII for stations to resemble factor GI for subsamples, in having positive loading by *Pgm* and negative loading by *Idh-1* and positive correlation with CalCOFI line coordinate (see below); nevertheless, there are major differences between the two factors in loadings by other loci. The contributions of particular loci to genetic heterogeneity are not consistent over groupings (station vs subsamples) or between years.

Second, although significant correlations between CalCOFI line coordinate and genetic factors from the 1982 and 1983 station and subsample PCAs suggest a cline in allelic frequencies with latitude, this correlation accounts for only a small percentage of allele-frequency variance for any one locus. In the station analysis, for example, correlation with CalCOFI line explains 66% of the variance in GII (table 3). This factor, in turn, explains only 18.5% of total variance in allelic frequencies and at most 55% of the variance contributed by any one locus (i.e., the squared loading of GII by *Pgm*, the largest contributor to that factor). Thus correlation of GII with CalCOFI line coordinate explains only 36.6% of among-station variance in the frequency of the Pgm^{100} allele. Correlation of CalCOFI line and GI from the subsample PCA (table 3) similarly explains only 10.7% of among-subsample variance in Pgm^{100} frequency; proportions of variance explained for other loci by this correlation are smaller still. Moreover, the direction of the cline implied by this correlation—increasing frequency of Pgm^{100} to the south—is opposite to the significant negative correlation between latitude and Pgm^{100} frequency reported for samples from early 1982 (Hedgecock et al. 1989). There is little evidence in these data for significant or persistent associations of allelic frequency with latitude.

Third, spatial autocorrelation of the second principal component, GII, for the 1984 and 1985 subsample data indicates that weak positive genetic correlation among ages within a station grades off to even weaker correlations among subsamples within 100 km.

Fourth, correlations of genotypes among loci (gametic phase disequilibria) are not significantly different from zero for six 1985 stations that differed obviously in mean standard length at age and allelic frequencies, providing no evidence that stations represent mixtures of genetically discrete populations (Waples and Smouse 1990).

Finally, a cluster analysis of minimum genetic distance among all 32 trawl samples shows collections from different years and diverse CalCOFI line coordinates joined at high levels of genetic similarity (figure 1). Heterogeneity of allelic frequencies in the central stock shows little spatial patterning, giving no indication of spatially distinct panmictic units.

Correlations of Genetic and Morphometric Traits

Having found heterogeneity of allelic frequencies both within and between station samples in 1982 (Hedgecock et al. 1989), we increased sample size per trawl collection and obtained data on 11 morphometric traits, age, sex, and reproductive status for each fish in the 1984 and 1985 surveys in order to look for morphological and life-history correlates of genetic heterogeneity. A preliminary analysis found a strong positive correlation of factor scores from a PCA of allelic frequencies at five loci with mean standard length for six 1985 stations (Hedgecock 1991). We have presented here, for 31 subsamples of the 1984 and 1985 trawl samples, a complete correlational analysis among genetic factor scores for ten loci and subsample means for 15 morphological, life-

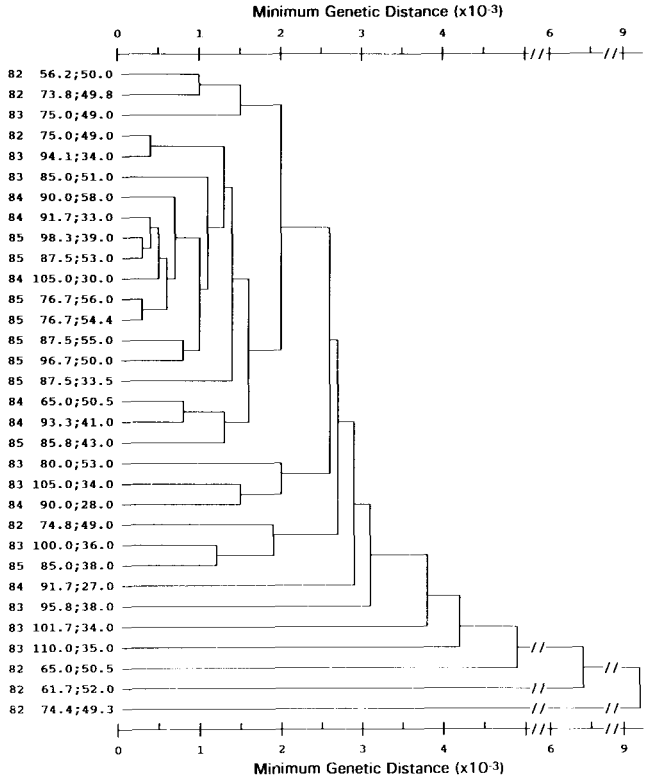

Figure 1. Cluster analysis of Nei's (1972) minimum genetic distance among 32 midwater trawl samples of northern anchovy. Samples are labeled with the year of collection (two digits, corresponding to CalCOFI cruises 8212, 8302, 8403, and 8502) followed by CalCOFI station coordinates. Samples from different years and disparate latitudes are joined at high levels of genetic similarity (low values of genetic distance).

history, and environmental descriptors (Nelson et al. 1994).

Four genetic factors (GI–GIV) were extracted by PCA of the frequencies of the most common alleles at ten loci in 31 age-class subsamples. Although no correlation was observed among any of the genetic factors and condition or gonadosomatic index—traits which may be involved in physiological responses to spatial patterns of productivity and temperature, respectively, in the California Current (Nelson et al. 1994)—each of these factors shows modest but significant correlation with at least one of six morphological variables, five morphometric factors (MI–MV), and a consensus measure of body size (table 4). Except for the correlation of GII with depth of bottom at station, none of the genetic factors is correlated with environmental variables, CalCOFI line coordinate, distance of station offshore, or sea-surface temperature at time of capture. The number of correlations significant at the $\alpha_{0.05}$ level, 7 out of a total of 60, is itself significant. GII is responsible for 4 significant correlations: with body size (MI), jaw length (MII), body depth (MIV), and depth of bottom. GI is correlated with size, GIII with orbit-preorbital length (MV), and GIV with anal-fin-base length (MIII). A correlation of GII with year class, $r = -0.325$, falls just short of the critical value of significance, 0.355.

Whereas no correlation was found between genetic factors for 1984 and 1985 samples and CalCOFI line coordinate, this correlation was significant for the 1982 and 1983 data. This may be attributable to the greater latitudinal range spanned by the 1982–83 collections, from 38°31.1'N to 29°47.3'N (effectively the entire range of the central subpopulation) compared to the more limited latitudinal range represented in the 1984–85 samples, 37°3.9'N to 30°49.2'N, which were also more concentrated in the Southern California Bight (see figure 1, Nelson et al. 1994). The nearly significant correlation of GII with year class in the 1984–85 data may be similar to the significant correlation of GIII with age in the 1982–83 data; loadings of several loci on these two factors are similar in size and sign: *Fum*, 0.51 vs 0.83; *6pgdh*, −0.65 vs −0.51; *Est-5*, 0.52 vs 0.35; and *Lt-1*, −0.56 vs −0.25, respectively. Finally, the correlation between a genetic factor and mean standard length reported in a preliminary analysis of six 1985 stations (Hedgecock 1991) appears to be subsumed in the subsample correlations of GI with size and of GII with MI, judging from the loadings of loci on the respective principal components.

The general conclusion that the central subpopulation is not a randomly mating population is reinforced by evidence of substantial morphological and life-history variation in the same samples (Nelson et al. 1994). Significant correlations between genetic and morphometric factors but not condition or reproductive state suggest that genetic heterogeneity is not a statistical artifact, but is associated with biologically meaningful, perhaps heritable, morphological variation. We wish to emphasize that we do not believe that these correlations are causal, i.e., that differentiation of the allozyme frequencies is directly responsible for the divergence of morphological traits. Rather, we regard the genetic-morphometric correlations as a reflection of spatial covariance between two sets of multivariate traits that show significant heterogeneity within the central stock of northern anchovy. How this heterogeneity arises and is maintained within a geographical area that is readily traversed by individual adults and is the major spawning ground for the species is unclear.

Causes of Heterogeneity within the Central Stock

One hypothesis for the genetic and morphological heterogeneity that we have observed within the central stock is that southern subpopulation fish migrated into the range of the central stock during the California El Niño of 1982–84. We believe that this hypothesis can be rejected on both genetic and morphological grounds. We observed similar among-station genetic heterogene-

ity in surveys taken before, during, and after the El Niño event, which commenced in late 1982 and lasted until summer of 1984. The southernmost samples taken in the winters of 1983 and 1984 at Cape Colnett and Punta Baja (CalCOFI lines 105 and 110) do not have distinctive allozyme frequencies, and cluster with more northerly samples of the central stock (figure 1). Moreover, the standard lengths of fish in these southerly samples, especially the age 0 and age 1 fish, are intermediate to those for other stations (table 1; table 1 of Nelson et al. 1994), not significantly smaller as would be expected if they had originated from the southern subpopulation (Mais 1974; Vrooman et al. 1981; Parrish et al. 1985). Likewise, fish sampled in 1984 are not appreciably smaller than those sampled in 1985 despite exposure to the elevated temperatures of El Niño (Nelson et al. 1994).

If we exclude immigration of the southern subpopulation into the Southern California Bight as the source of the genetic and morphological heterogeneity observed in the central subpopulation, we must then regard this heterogeneity as a property or feature of the central subpopulation itself. How does this heterogeneity arise within the geographical and oceanographical confines of what appears to be a single spawning stock?

Slight but significant genetic heterogeneity—chaotic genetic patchiness (Johnson and Black 1982)—embedded within broad areas of great genetic similarity has been observed of many marine animal species capable of planktonic or pelagic dispersal (Hedgecock 1994). This paradox may be resolved by the hypothesis that slight differences in allelic frequencies could arise as a consequence of variance in the reproductive success of spawning adults and subsequent sampling errors in the recruitment of larval fish to their first schools. That this may be the case for northern anchovy is suggested by significant correlations, in the 1982 and 1983 subsample data, of genetic factor GIII with age (table 3). Correlations, in the 1984 and 1985 subsample data, of genetic factors GII and GIII with morphometric factors MII (jaw length) and MIII (anal-fin-base length) respectively (table 4)—morphological features that may be established early in life (McHugh 1951)—are also consistent with this hypothesis. The pattern of spatial autocorrelation shared by MII, MIII, and GII—low within-station correlation grading off to insignificant correlation within the first 100 km—may reflect variation in larval or juvenile experience, not just among natal localities, but also among year classes from the same area that are later captured together. Within-station heterogeneity for these factors would imply low spawning-site fidelity and heterogeneity of origin of the different year classes at a station. These disparate year classes later come to resemble one another in size, body depth, condition, and reproductive state, possibly through common environment and assortative grouping (Nelson et al. 1994).

Despite the existence of some within-station heterogeneity, most of the genetic variance is among stations, as reflected by significant contingency chi-square values in all years (table 2) and correlations of genetic factors with CalCOFI line coordinates in the 1982–83 data and with morphometric factors that show spatial autocorrelation on a scale of 100–200 km (size and body depth) in the 1984–85 data (table 4; Nelson et al. 1994). Maintaining these differences among adult anchovy populations would appear to require one or more of the following: life-long fidelity to schools, assortative movements and grouping, or homing to natal spawning grounds. None of these behaviors is known for northern anchovies. Current understanding of the biology of this and other pelagic fishes is too rudimentary to specify alternative explanations of the phenomenon that we have recorded.

Finally, the similarity of our results to those of Altukhov et al. (1969) and Spanakis et al. (1989) for *Engraulis encrasicholus* indicates that genetic and morphological heterogeneity may be a general feature of anchovy populations. In some respects our data conform to the elementary population concept of Lebedev (1969). Variation in genetic and certain morphological traits may be linked to processes (variance in adult reproductive success) or environments acting early in the life of the northern anchovy, as required if "elementary populations are formed as 'intra-age' groups at the birthplaces of the young" (Altukhov et al. 1969). Unlike reports in the Russian literature on elementary fish populations, however, genetic, morphological, and life-history variation in northern anchovy appears not to be stable over time or space but chaotic in spatial pattern and ephemeral in its expression. The only feature that remains constant is the heterogeneity itself.

CONCLUSIONS

We can conclude only what the central stock of northern anchovy is not: it is not a randomly mating subpopulation. How genetic, morphological, and life-history variation are generated and maintained throughout the adult stages of this subpopulation are matters about which we can only speculate. The central stock appears to be a geographic subpopulation comprising "virtual" panmictic units, which produce cohorts of offspring that deviate in random fashion from the subpopulation's genotypic and phenotypic norms. These among-group deviations, which may be wholly or partially preserved through the lifetime of an individual cohort—either by homing to natal localites, assortative grouping with other cohorts on the basis of swimming speed or common experience, or both—are probably not transmitted to the succeeding generation, owing to substantial mixing and

gene exchange among cohorts spawning in the Southern California Bight. Although such variation cannot accumulate over generations, the processes that generate and sustain it may nevertheless play important roles in the adaptation and evolutionary potential of this subpopulation and perhaps other pelagic fishes as well. By continually generating greater phenotypic and genotypic variation than would otherwise be presented by a single, randomly mating population, the central subpopulation of northern anchovy permits natural selection to act not only among individuals but among groups as well.

ACKNOWLEDGMENTS

The authors thank R. D. Methot for obtaining the samples of anchovies used for this study, M. Simmons for help with data collection, and L. Stenzel for help with data organization and preliminary analysis. This research was funded in part by grants (R/F 82 and R/F 98) from the California Sea Grant College Program.

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APPENDIX

TABLE A

Allelic Frequencies in Seven Samples of Northern Anchovy from Cruise 8212

	Sample						
Locus	1	2	3	4	5	6	7
Est-5							
N	42	42	46	33	38	38	43
96	.000	.000	.011	.000	.000	.000	.000
98	.012	.036	.011	.030	.276	.026	.047
100	.917	.940	.870	.909	.684	.921	.919
101	.024	.000	.054	.045	.039	.013	.023
102	.048	.012	.054	.015	.000	.039	.012
103	.000	.012	.000	.000	.000	.000	.000
Fum							
N	48	48	48	48	48	48	48
96	.000	.000	.000	.000	.000	.010	.021
100	.469	.458	.458	.490	.594	.604	.510
104	.531	.542	.542	.510	.406	.385	.469
Gpi							
N	48	48	48	48	48	48	48
96	.000	.000	.010	.052	.010	.000	.000
98	.000	.000	.000	.000	.000	.021	.010
100	.938	.969	.979	.927	.948	.938	.948
103	.063	.021	.010	.021	.031	.042	.031
105	.000	.010	.000	.000	.010	.000	.010
Hbdh-1							
N	48	48	48	48	48	48	48
92	.021	.000	.000	.010	.021	.010	.000
94	.010	.031	.010	.042	.021	.000	.031
96	.010	.000	.010	.010	.000	.021	.021
100	.958	.927	.979	.938	.958	.969	.948
103	.000	.042	.000	.000	.000	.000	.000
Idh-1							
N	44	13	43	40	36	39	37
95	.000	.000	.012	.013	.014	.013	.000
100	.977	1.000	.965	.913	.903	.936	1.000
106	.022	.000	.012	.076	.084	.052	.000
118	.000	.000	.012	.000	.000	.000	.000
Ldh-1							
N	48	48	48	48	48	48	48
96	.177	.125	.125	.208	.188	.146	.135
100	.823	.875	.875	.792	.813	.854	.865
Lt-1							
N	48	48	48	48	48	48	48
94	.000	.000	.000	.000	.000	.000	.010
96	.000	.010	.010	.021	.021	.000	.000
97	.000	.000	.000	.000	.000	.000	.010
100	.958	.938	.958	.948	.969	.958	.938
103	.042	.052	.031	.031	.010	.042	.042
Lgg							
N	48	48	47	48	48	48	48
97	.010	.010	.011	.052	.052	.063	.010
100	.563	.781	.543	.563	.604	.635	.583
104	.396	.208	.404	.385	.302	.302	.385
107	.031	.000	.043	.000	.042	.000	.021
6pgdh							
N	48	48	48	48	48	48	48
98	.042	.063	.083	.031	.083	.031	.052
100	.948	.917	.917	.958	.875	.958	.948
104	.010	.021	.000	.010	.042	.010	.000
Pgm							
N	48	48	48	48	48	48	48
96	.010	.000	.000	.010	.000	.010	.010
100	.750	.750	.667	.760	.823	.813	.802
103	.240	.250	.333	.229	.167	.156	.177
106	.000	.000	.000	.000	.010	.021	.010

Key to samples: 1, 56.2;50.0. 2, 61.7;52.0. 3, 65.0;50.5. 4, 73.8;49.8. 5, 74.4;49.3. 6, 74.8;49.0. 7, 75.0;49.0.
N is the number of individuals sampled.
Idh-1^{106} is a composite category for alleles *104*, *106*, and *108*.

TABLE B
Allelic Frequencies in Nine Samples of Northern Anchovy from Cruise 8302

	Sample								
Locus	1	2	3	4	5	6	7	8	9
Est-5									
N	32	—	28	8	27	23	9	45	48
98	.047	—	.018	.063	.000	.000	.000	.011	.000
100	.891	—	.893	.938	.833	.957	1.000	.967	.885
101	.063	—	.036	.000	.167	.043	.000	.000	.000
102	.000	—	.054	.000	.000	.000	.000	.022	.115
Fum									
N	69	46	43	48	48	47	48	48	48
96	.007	.000	.000	.000	.000	.000	.000	.010	.000
100	.507	.478	.523	.531	.542	.638	.573	.583	.438
104	.486	.522	.477	.469	.458	.362	.427	.406	.563
Gpi									
N	60	46	43	12	48	44	—	47	43
98	.075	.000	.000	.000	.010	.000	—	.011	.000
100	.875	.967	.988	.958	.938	.943	—	.979	.965
103	.042	.033	.012	.042	.052	.057	—	.011	.035
105	.008	.000	.000	.000	.000	.000	—	.000	.000
Hbdh-1									
N	69	46	43	48	48	47	47	48	48
92	.000	.000	.000	.021	.000	.000	.000	.000	.000
94	.022	.000	.000	.031	.010	.000	.032	.010	.010
96	.022	.033	.035	.021	.021	.011	.053	.042	.000
98	.000	.000	.023	.000	.000	.000	.000	.000	.000
100	.935	.967	.930	.927	.958	.989	.915	.948	.990
103	.022	.000	.012	.000	.010	.000	.000	.000	.000
Idh-1									
N	39	42	30	—	29	24	—	39	48
95	.013	.000	.017	—	.000	.000	—	.000	.010
100	.974	.940	.900	—	.948	.958	—	.923	.865
106	.013	.048	.083	—	.052	.042	—	.077	.125
118	.000	.012	.000	—	.000	.000	—	.000	.000
Ldh-1									
N	69	46	41	48	48	47	48	48	48
96	.181	.130	.146	.146	.167	.181	.104	.115	.135
100	.819	.870	.854	.854	.833	.819	.896	.885	.865
Lt-1									
N	69	46	43	47	48	47	48	48	48
94	.000	.000	.012	.000	.000	.000	.000	.000	.000
96	.000	.000	.000	.000	.000	.000	.000	.010	.010
97	.022	.011	.035	.000	.000	.011	.010	.000	.000
100	.920	.978	.942	.936	.938	.947	.917	.917	.906
103	.058	.011	.012	.064	.063	.043	.073	.073	.083
Lgg									
N	69	44	43	46	48	46	37	48	46
97	.065	.011	.058	.022	.021	.076	.014	.031	.087
100	.514	.636	.535	.554	.635	.543	.635	.625	.630
104	.413	.352	.395	.380	.323	.359	.351	.344	.283
107	.007	.000	.012	.043	.021	.022	.000	.000	.000
6pgdh									
N	69	46	43	48	48	47	48	48	48
96	.014	.000	.000	.000	.010	.043	.000	.000	.000
98	.043	.022	.081	.031	.031	.032	.115	.083	.042
100	.920	.978	.907	.969	.948	.904	.885	.906	.958
104	.022	.000	.012	.000	.010	.021	.000	.010	.000
Pgm									
N	69	46	43	47	48	47	48	48	48
96	.000	.011	.000	.000	.000	.000	.000	.000	.000
98	.000	.000	.000	.000	.000	.000	.010	.000	.000
100	.775	.837	.837	.830	.802	.862	.740	.875	.854
103	.217	.152	.163	.170	.198	.138	.240	.125	.146
106	.007	.000	.000	.000	.000	.000	.010	.000	.000

Key to samples: 1, 4532, 75.0:49.0. 2, 4538, 80.0:53.0. 3, 4546, 85.0:51.0. 4, 4573, 94.1:34.0. 5, 4576, 95.8:38.0. 6, 4582, 1000.0:36.0. 7, 4584, 101.7:34.0. 8, 4586, 105.0:34.0. 9, 4590, 110.0:35.0.
N is the number of individuals sampled.
Idh-1^{106} is a composite category for alleles *104*, *106*, and *108*.

TABLE C
Allelic Frequencies in Seven Samples of Northern Anchovy from Cruise 8403

	Sample						
Locus	1	2	3	4	5	6	7
Est-5							
N	120	94	111	105	118	40	64
97	.000	.005	.023	.029	.034	.000	.000
98	.033	.011	.045	.005	.030	.013	.039
100	.929	.957	.847	.929	.860	.962	.930
102	.033	.027	.081	.033	.076	.025	.023
Other	.004	.000	.005	.005	.000	.000	.000
Fum							
N	120	120	120	120	120	48	72
96	.004	.000	.000	.025	.013	.010	.014
100	.575	.538	.525	.521	.546	.510	.556
104	.421	.463	.471	.450	.442	.479	.431
Other	.000	.000	.004	.004	.000	.000	.000
Gpi							
N	119	120	120	120	120	48	72
96	.000	.000	.000	.000	.000	.021	.000
100	.962	.962	.933	.967	.954	.948	.972
103	.034	.038	.067	.029	.046	.031	.021
Other	.004	.000	.000	.004	.000	.000	.007
Hbdh-1							
N	120	120	120	120	120	45	72
92	.013	.004	.004	.004	.008	.000	.000
94	.013	.004	.004	.017	.017	.022	.035
96	.013	.017	.025	.004	.004	.011	.021
100	.950	.971	.958	.962	.967	.967	.938
Other	.012	.004	.008	.013	.004	.000	.007
Idh-1							
N	120	77	117	120	119	43	65
95	.000	.006	.000	.004	.013	.023	.008
100	.942	.922	.940	.917	.937	.942	.908
106	.058	.071	.056	.071	.046	.035	.062
118	.000	.000	.004	.004	.004	.000	.015
Other	.000	.000	.000	.004	.000	.000	.008
Ldh-1							
N	120	120	120	120	120	48	72
96	.150	.125	.158	.108	.158	.115	.271
100	.850	.871	.842	.892	.842	.885	.729
Other	.000	.004	.000	.000	.000	.000	.000
Lt-1							
N	120	120	120	120	120	48	72
96	.000	.000	.042	.000	.000	.010	.000
97	.004	.017	.004	.004	.013	.021	.007
100	.929	.917	.896	.950	.946	.875	.951
103	.058	.067	.058	.029	.038	.094	.021
105	.004	.000	.000	.008	.004	.000	.014
Other	.004	.000	.000	.008	.000	.000	.007
Lgg							
N	117	118	117	120	120	48	72
97	.026	.042	.034	.042	.042	.010	.035
100	.547	.568	.560	.558	.512	.646	.597
104	.385	.386	.393	.387	.433	.302	.347
107	.043	.004	.013	.013	.013	.042	.021
6pgdh							
N	120	120	120	120	120	48	72
98	.063	.050	.050	.063	.063	.031	.035
100	.929	.942	.933	.929	.933	.969	.965
104	.004	.008	.017	.004	.004	.000	.000
Other	.004	.000	.000	.004	.000	.000	.000
Pgm							
N	120	120	120	120	119	48	72
100	.842	.796	.742	.825	.786	.875	.854
103	.154	.196	.254	.171	.214	.115	.146
Other	.004	.008	.004	.004	.000	.010	.000

Key to samples: 1, 4660, 90.0:58.0. 2, 4662, 91.7:33.0. 3, 4612, 65.0:50.5. 4, 4689, 105.0:30.0. 5, 4671, 93.3:41.0. 6, 4655, 90.0:28.0. 7, 4665, 91.7:27.0.
N is the number of individuals sampled.
Alleles with frequencies less than 0.01 in all stations are pooled as "other."
Idh^{106} is a composite category for alleles *104*, *106*, and *108*.

TABLE D
Allelic Frequencies in Nine Samples of Northern Anchovy from Cruise 8502

	Sample								
Locus	1	2	3	4	5	6	7	8	9
Est-5									
N	112	180	109	119	117	120	119	117	114
97	.000	.008	.018	.004	.004	.008	.008	.021	.013
98	.018	.022	.009	.004	.004	.017	.021	.021	.022
100	.938	.894	.899	.950	.919	.887	.945	.885	.921
101	.013	.017	.005	.017	.013	.004	.000	.038	.018
102	.027	.056	.064	.025	.056	.083	.025	.034	.022
Other	.004	.003	.005	.000	.004	.000	.000	.000	.004
Fum									
N	119	180	120	120	120	120	120	120	120
96	.008	.008	.004	.004	.000	.000	.000	.013	.004
100	.529	.519	.525	.521	.517	.496	.642	.492	.525
104	.462	.472	.467	.463	.483	.504	.354	.488	.471
Other	.000	.000	.004	.013	.000	.000	.004	.008	.000
Gpi									
N	119	179	120	119	120	120	120	120	120
96	.000	.003	.000	.000	.004	.013	.004	.004	.000
100	.958	.958	.971	.975	.958	.954	.938	.946	.946
103	.042	.039	.029	.021	.029	.033	.058	.050	.054
Other	.000	.000	.000	.004	.008	.000	.000	.000	.000
Hbdh-1									
N	120	180	120	120	120	120	120	120	120
92	.004	.011	.004	.000	.004	.004	.004	.000	.000
94	.017	.008	.013	.008	.017	.013	.004	.004	.004
96	.008	.011	.046	.008	.008	.021	.008	.038	.017
100	.958	.944	.929	.979	.954	.958	.983	.954	.979
103	.008	.022	.008	.004	.017	.004	.000	.004	.000
Other	.004	.003	.000	.000	.000	.000	.000	.000	.000
Idh-1									
N	116	178	114	120	115	118	120	120	116
93	.000	.011	.009	.004	.009	.008	.004	.008	.004
100	.905	.924	.943	.904	.922	.928	.938	.904	.931
106	.086	.062	.039	.092	.065	.064	.054	.067	.047
118	.009	.003	.009	.000	.004	.000	.004	.021	.017
Ldh-1									
N	119	180	120	120	120	120	120	120	120
96	.155	.139	.188	.142	.175	.142	.167	.158	.150
100	.845	.858	.813	.858	.825	.854	.833	.842	.846
Other	.000	.003	.000	.000	.000	.004	.000	.000	.004
Lt-1									
N	120	180	120	120	119	120	120	120	120
97	.017	.008	.004	.004	.013	.004	.017	.008	.000
100	.917	.933	.946	.917	.937	.938	.921	.958	.950
103	.058	.050	.046	.067	.042	.058	.050	.033	.046
105	.008	.003	.000	.013	.008	.000	.013	.000	.000
Other	.000	.006	.004	.000	.000	.000	.000	.000	.004
Lgg									
N	119	179	120	117	118	120	117	120	119
97	.059	.022	.042	.038	.034	.058	.021	.004	.050
100	.601	.570	.538	.590	.589	.525	.526	.525	.567
104	.328	.388	.383	.346	.352	.375	.423	.454	.366
107	.013	.020	.038	.026	.021	.042	.021	.013	.017
Other	.000	.000	.000	.000	.004	.000	.008	.004	.000
6pgdh									
N	120	180	120	114	120	120	119	118	120
98	.038	.047	.038	.026	.025	.021	.042	.017	.042
100	.950	.944	.950	.947	.967	.979	.954	.983	.946
104	.008	.008	.000	.018	.008	.000	.000	.000	.004
Other	.004	.000	.012	.008	.000	.000	.004	.000	.008
Pgm									
N	119	180	120	120	120	120	120	120	120
100	.832	.806	.825	.754	.837	.867	.796	.796	.808
103	.155	.183	.175	.242	.158	.121	.192	.192	.175
Other	.012	.012	.000	.004	.000	.012	.012	.012	.016

Key to samples: 1, 4708, 76.7:56.0; 2, 4766, 98.3:39.0; 3, 4725, 87.5:55.0; 4, 4729, 87.5:33.5; 5, 4707, 76.7:54.0; 6, 4763, 96.7:50.0; 7, 4719, 85.0:38.0; 8, 4722, 85.8:43.0; 9, 4726, 87.5:53.0.

N is the number of individuals sampled. Alleles with frequencies less than 0.01 in all stations are pooled as "other."

Idh^{106} is a composite category for alleles *104*, *106*, and *108*.

SEABIRDS AS INDICATORS OF IMPORTANT FISH POPULATIONS IN THE GULF OF CALIFORNIA

ENRIQUETA VELARDE
Centro de Ecología
Universidad Nacional Autónoma de México
Apartado Postal 70-275
México, D.F. 04510
México

MARIA DE LA SOLEDAD TORDESILLAS
Instituto Tecnológico y de Estudios Superiores de Monterrey
Plantel Guaymas
Apartado Postal 484
Guaymas 85400, Sonora
México

LETICIA VIEYRA, ROCIO ESQUIVEL
Centro de Ecología
Universidad Nacional Autónoma de México
Apartado Postal 70-275
México, D.F. 04510
México

ABSTRACT

We monitored the diet of the Heermann's gull (*Larus heermanni*) and the elegant tern (*Sterna elegans*) between 1983 and 1992 and compared the proportion of each fish species in the diet, through a correlation analysis, with the proportion of each of these same fish species in the commercial landings. We found strong positive correlations between the proportion of sardine (*Sardinops sagax caeruleus*) in the seabirds' diet and sardine landings. Strong negative correlations were found between the proportion of sardine in the seabirds' diet vs the proportion of anchovy (*Engraulis mordax*) in the birds' diet and anchovy landings. The proportion of sardine landings was negatively correlated with the proportion of anchovy in the seabirds' diet and with the proportion of the landings of both anchovy and mackerel (*Scomber japonicus*). The proportion of anchovy in the seabirds' diet was positively correlated with anchovy landings. A low, marginally positive correlation was found between the proportion of mackerel in the diet and the proportion of mackerel landed. Dietary studies of these seabirds provide reliable data on species composition of fish stocks, estimates of relative abundance, and availability of fish populations to higher trophic levels in this area. They also provide real-time, predictive, catch-independent data and complement commercial and research catch information.

RESUMEN

Entre 1983 y 1992 registramos la dieta de la gaviota ploma (*Larus heermanni*) y de la golondrina-marina elegante (*Sterna elegans*). Comparamos la proporción promedio de cada especie de pez en la dieta con la proporción de cada una de las mismas especies de pez en la descarga comercial por medio de un análisis de correlación. Se encontró una fuerte correlación positiva entre la proporción de sardina Monterrey (*Sardinops sagax caeruleus*) en la dieta y en la descarga comercial. Se encontraron fuertes correlaciones negativas entre la proporción de sardina en la dieta vs la proporción de anchoveta norteña (*Engraulis mordax*) en la dieta y en la descarga comercial. La proporción de sardina en la descarga comercial presentó una correlación negativa con la proporción de anchoveta en la dieta y con la descarga, tanto de anchoveta como de macarela (*Scomber japonicus*). La proporción de anchoveta en la dieta presentó una correlación positiva con la proporción en la descarga comercial. Se encontró una correlación baja y marginalmente significativa entre la proporción de macarela en la dieta y la desembarcada. Estos resultados indican que los estudios de la dieta de estas aves marinas proveen datos confiables acerca de la composición específica de la comunidad de pelágicos menores, así como estimaciones de la abundancia relativa y la disponibilidad de poblaciones de peces hacia otros niveles tróficos en esta región. Estos datos también proporcionan información en tiempo real y de valor predictivo que complementan la información obtenida por las capturas de la flota comercial y la exploratoria.

[Manuscript received February 4, 1994.]

INTRODUCTION

At a worldwide level, small pelagic fish (sardines, anchovies, etc.) represent a significant percentage of total fishery landings (25%). Numerous attempts to reach a sustainable use of these resources, and the equally numerous failures that have resulted in the collapse of many fisheries (Murphy 1981; Paulik 1983; Radovich 1982; Rothschild 1983) have evidenced the need for an ecosystemic approach to the analysis of these commercially important fish populations.

In Mexico, up to 1990, the landings of small pelagic fish represented 30% of the national total, 80% of which came from the Gulf of California. Species present in the catch were Pacific sardine (*Sardinops sagax caeruleus*), thread herring (*Opisthonema libertate*), Pacific mackerel (*Scomber japonicus*), round herring (*Etrumeus teres*), anchoveta (*Cetengraulis mysticetus*), and northern anchovy (*Engraulis mordax*) (Cisneros et al. 1991). The Gulf of California produced 70% of Mexico's commercial fishery, and Pacific sardine contributed 33% of the volume (Cisneros et al. 1991).

The Gulf of California is a subtropical sea with extremely complex hydrodynamics and a productivity comparable to the highest of any ocean, particularly in its northern portion (Alvarez-Borrego 1983). Strong upwelling, mainly of tidal origin, particularly in the Midriff Island region (figure 1), as well as a complex underwater topography are the principal factors that result in the

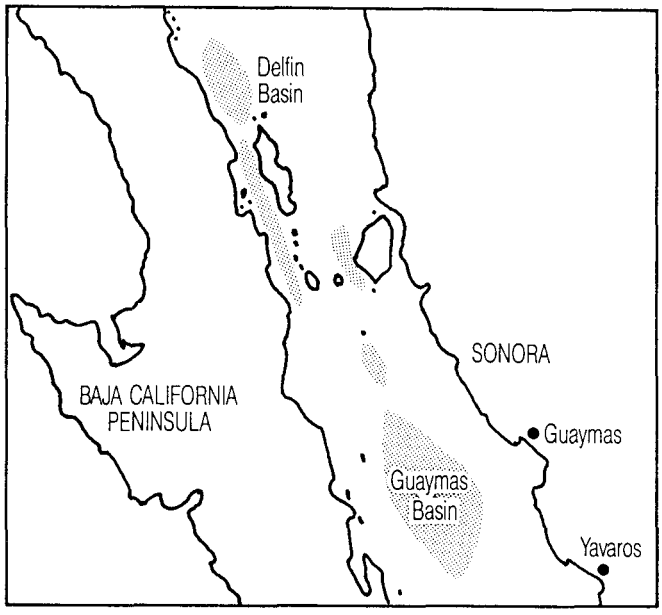

Figure 1. Section of the Gulf of California, showing the islands and the basins from the Midriff Island region to Conception Bay, Baja California, and the port of Yavaros, Sonora.

high productivity of the Gulf of California (Alvarez-Borrego 1983). Because of its high productivity and its geographic location in the border zone between the temperate and the tropical Pacific, the Gulf of California supports over half a million piscivorous seabirds. A large portion of the world population of several species breeds in the Gulf of California. For example, 99% of the world population of yellow-footed gull (*Larus livens*); 90% of Craveri's murrelet (*Synthliboramphus craveri*) and least petrel (*Oceanodroma microsoma*); 95% of Heerman's gull (*L. heermanni*) and elegant tern (*Sterna elegans*); and smaller but significant proportions (50%–70%) of other species, including the California brown pelican (*Pelecanus occidentalis*), blue-footed and brown boobies (*Sula nebouxii* and *S. leucogaster*), and black storm petrel (*Oceanodroma melania*) (Anderson 1983).

Until 1991, the Pacific sardine was the most abundant small pelagic fish in the gulf. This species is distributed along the Sonora and Baja California coasts, from the Guaymas and Carmen basins in the winter (Maluf 1983; figure 1), when the spawning peak occurs, to the Delfin Basin, where it migrates in summer (Cisneros et al. 1991; Hammann 1991; Hammann et al. 1991).

The northern anchovy, a species that has been recently reported to have occupied the Gulf of California, is restricted, like the Pacific sardine, to the low-temperature waters, mainly around the Midriff Islands (Cisneros et al. 1991). This species could have invaded the area as a consequence of a "La Niña" phenomenon during 1985 (Hammann and Cisneros-Mata 1989), but local fishermen believe that it has always been in the gulf, although in much lower abundances than at present. The northern anchovy population has increased steadily in recent years (Hammann et al. 1991).

Sardine catches by the fishing fleet in the Gulf of California from 1969 to 1990 increased at an average rate of 53% per year (estimated from data in Cisneros et al. 1991). Data from the Centro Regional de Investigación Pesquera of the Instituto Nacional de Pesca in Guaymas revealed that the Pacific sardine population of the Gulf of California began to show symptoms of overexploitation in the late 1980s: for example, a reduction in average size of individuals in the catches, and a smaller size at first reproduction (see Cisneros et al. 1990). These were the same signs shown by the Pacific sardine population when the northern anchovy began to replace it and before the sardine fishery collapsed in the California Current during the 1940s (Cisneros et al. 1990).

Generally, fish stocks are difficult to monitor; as a result, quick and wise management decisions are difficult to reach (Cushing 1988). Seabirds are valuable as sampling agents of the fish populations on which they feed (Ashmole and Ashmole 1967; Anderson et al. 1980, 1982; Sunada et al. 1981; Cairns 1987; Montevecchi et al. 1987; Montevecchi and Berruti 1991; Hamer et al. 1991). Their values are derived from the low cost of the sampling method, relative to the use of oceanographic research vessels, especially since seabird food studies can be combined with studies of breeding biology. The data obtained are catch-independent, complement commercial and research catch information, and provide real-time indices of relative abundance and availability of unsurveyed, commercially exploitable pelagic fish (Montevecchi and Berruti 1991).

The Heermann's gull and the elegant tern colonies in Isla Rasa total 240,000 and 45,000 birds, respectively (Velarde 1989; Tobón 1992). Their breeding season extends from late March to early July, and is both intra- and interspecifically synchronous, and constant from year to year (Velarde 1989; Tobón 1992).

In the Gulf of California, Heermann's gulls nesting in Isla Rasa were shown to be consuming mostly sardines during 1983 and 1984 (88.9% and 63.6% respectively; Velarde and Urrutia, unpublished data). In this paper we analyze the diets of two seabird species: the Heermann's gull and the elegant tern, and we compare the diet of these seabirds with the catches of small pelagic fish by the commercial fleet, in order to investigate potential correlations between them and to answer the following question: Do studies of the diets of seabirds feeding at certain areas and times of the year provide fishery-independent estimates on the species composition of fish stocks?

METHODS

The description of the diet of gulls and terns was made through the analysis of fresh regurgitations collected during the nesting season, from April through June, between 1983 and 1992 (except for 1987, a year in which data were not collected). Regurgitations were obtained from adult birds returning to the colony within a period of about three hours after dusk. Birds were captured with a mist net 9 m long by 2 m wide, with a 70 mm mesh. The net was placed 0.5 m above the ground and 200–300 m from the colony to avoid disturbing the nesting birds. In order to capture a substantial number of birds per sampling effort, the net was placed at a site where there was a relatively constant flux of birds going in and out of the colony.

Upon encountering the net and becoming entangled, most of the birds regurgitated the contents of their crop and, in the case of terns, also dropped the fish being carried in the bill for their chicks. Each regurgitation was placed in a plastic bag and assigned a number for subsequent reference. For each sample, the number of fish was estimated as the number of whole fish plus the number of heads or tails (whichever was greatest). Whole fish were numbered progressively within each sample. Whole fish and heads were identified to the species level whenever possible. The taxonomic determination was carried out with the help of field guides (Roedel 1948; Miller and Lea 1972; Thompson and McKibbin 1981) or through the examination of otoliths. When field determination was not possible, the sample was preserved in alcohol (30%) and identified with the help of specialists from the Centro Regional de Investigación Pesquera of the Instituto Nacional de Pesca in Guaymas, Sonora, and the Centro Interdisciplinario de Ciencias Marinas in La Paz, Baja California Sur. During 1983 and 1984, fish were identified only to the family level. For the purpose of comparison with samples from later years, Clupeoideae were assumed to be Pacific sardine, and Engraulidae to be northern anchovy, since no other Clupeoideae or Engraulidae species have been found in the seabirds' diet.

In April 1985, 1986, and 1989, when a high proportion of the samples were in an advanced state of digestion (because no chicks were hatched yet and food in the crop of the adult birds was only for the parent itself), only samples in a good state were used for the analysis.

Since most of the regurgitations contained only a single species of fish, the diet composition was determined through the frequency method, in which the number of regurgitations with a certain type of prey was divided by the total number that constituted the sample and was expressed as a percentage (Tordesillas 1992 and references therein).

Information on commercial catches of the species contained in the seabirds' diet, and landed in the ports of Guaymas and Yavaros, was obtained through the records kept and published by the National Fisheries Institute (Cisneros et al. 1991 and pers. comm.). These statistics were compared to those we obtained from the seabirds' diets. Yearly percentages of Pacific sardine, northern anchovy, and Pacific mackerel in commercial landings, in metric tons, were compared to yearly average proportions of these same species in the diet of seabird species studied by means of a Speerman rank correlation test (Zar 1974).

TABLE 1
Composition of the Diet of *Larus heermanni* and *Sterna elegans* in Isla Rasa, Baja California, Showing Sample Size (*N*) and Percentage of the Different Species

	Larus heermanni		*Sterna elegans*		Average
	N	%	*N*	%	%
1983					
Ss	43	97			97
Em	1	3			3
1984					
Ss	73	64			64
Em	42	36			36
1985					
Ss			10	31	31
Em			14	44	44
Sj			8	25	25
1986					
Ss			32	59	59
Em			19	35	35
O			3	6	6
1988					
Ss			49	54	54
Em			42	46	46
1989					
Ss	2	13	4	6	9
Em	13	87	67	94	91
1990					
Ss			1	2	1
Em	36	100	2	98	99
1991					
Em	90	98	110	96	97
O	2	2	5	4	2
1992					
Ss	1	2	5	9	6
Em	48	96	42	76	86
Sj			4	7	4
O	1	2	4	7	4

Ss = *Sardinops sagax*, Em = *Engraulis mordax*, Sj = *Scomber japonicus*, and O = others.

RESULTS

Annual use of small pelagic fish by seabirds is shown in table 1 and figure 2. Pacific sardine in the elegant tern's diet decreased abruptly between 1988 and 1989—from over 50% to 6%—and stayed under 10% thereafter. At the same time, northern anchovy increased from under 50% to almost 100%, staying over 75% thereafter. Pacific mackerel was fairly abundant (25%) in 1985 and disappeared thereafter until 1992, when it represented 7% of the diet.

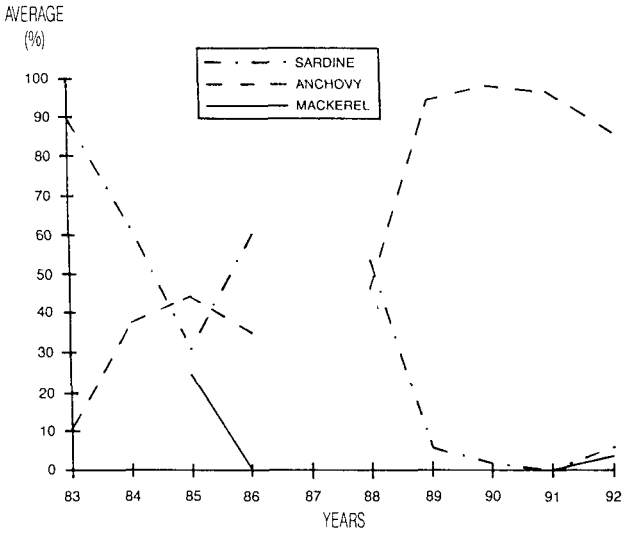

Figure 2. Yearly average percentage of three small pelagic fishes in the diet of seabirds in the Midriff Island region of the Gulf of California.

A similar pattern was apparent for the Heermann's gull. In 1983 Pacific sardine constituted almost 100% of the diet, and decreased steadily thereafter, disappearing completely in 1990. Anchovies increased in the gull's diet from under 37% before 1989 to 87% in 1989 (a change representing 50% of the diet), and over 95% thereafter (a change of almost 60% of the diet) (table 1).

Landings (and the percentage) of Pacific sardine, Pacific mackerel, and northern anchovy by the commercial fleet of the Gulf of California, in the ports of Guaymas and Yavaros, are shown in table 2. There was a positive correlation between the seabirds' relative consumption of sardines and their proportion in the catch (figure 3). Negative correlations were found between the proportion of sardine in the diet and the proportion of anchovies in both the seabirds' diet and the commercial landings. The proportion of sardine landings was negatively correlated with the proportion of anchovy in the seabirds' diet and with the landings of both anchovy and mackerel. Finally, the proportion of anchovy in the seabirds' diet was positively correlated with anchovy landings (figure 4). A low ($R = .63$) and marginal ($P = .0562$) correlation was found between the proportion of mackerel in the seabirds' diet and the proportion of mackerel landed by the commercial fleet (figure 5). Other correlations were low and/or not significant (table 3).

DISCUSSION

Many seabirds feed mainly on commercially important fish (Anderson et al. 1980, 1982; Sunada et al. 1981; Schaffner 1982). This is not surprising, since the typical shoaling distribution of small pelagic fishes, which renders them commercially exploitable, makes them easily exploitable to certain seabirds. This suggests a po-

TABLE 2
Percentage of Pacific Sardine, Northern Anchovy, and Pacific Mackerel Landed at Guaymas and Yavaros, Sonora, (from Cisneros et al. 1991) and Percentage of These Species in the Diet of the Seabirds

	Pacific sardine		Northern anchovy		Pacific mackerel	
Year	% Tons	% Diet	% Tons	% Diet	% Tons	% Diet
1983	99	97	0	3	1	0
1984	98	64	0	36	2	0
1985	93	31	0	44	7	25
1986	97	59	1	35	2	0
1988	99	54	0	46	1	0
1989	96	9	3	91	1	0
1990	77	1	13	99	10	0
1991	84	0	10	97	6	0
1992	28	6	22	86	50	4

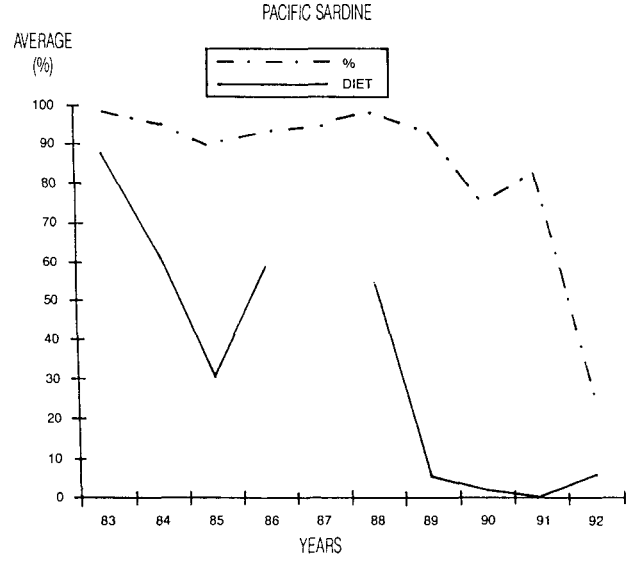

Figure 3. Percentage of Pacific sardine in commercial landings and in the diet of seabirds, 1983–92.

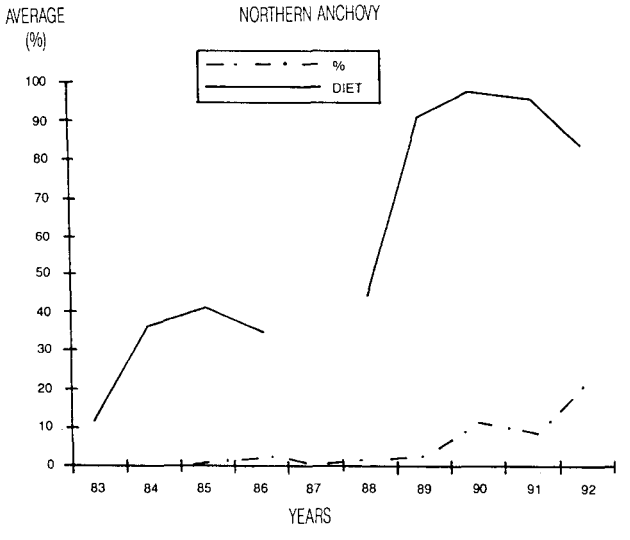

Figure 4. Percentage of northern anchovy in commercial landings and in the diet of seabirds, 1983–92.

TABLE 3
Results of Speerman Rank Correlation Analysis

		Pacific sardine		Northern anchovy		Pacific mackerel	
		Diet	Landing	Diet	Landing	Diet	Landing
Sardine diet	R =	.8452		−.9330	−.8008	−.1826	−.6044
	N =	(9)		(9)	(9)	(9)	(9)
	P =	.0168		.0083	.0235	.6056	.0874
Sardine landing				−.7029	−.8566	−.4813	−.8805
				(9)	(9)	(9)	(9)
				.0468	.0154	.1734	.0128
Anchovy diet					.7224	−.0228	.4341
					(9)	(9)	(9)
					.0410	.9485	.2195
Anchovy landing						.0834	.6268
						(9)	(9)
						.8135	.0662
Mackerel diet							.6061
							(9)
							.0865
Mackerel landing							

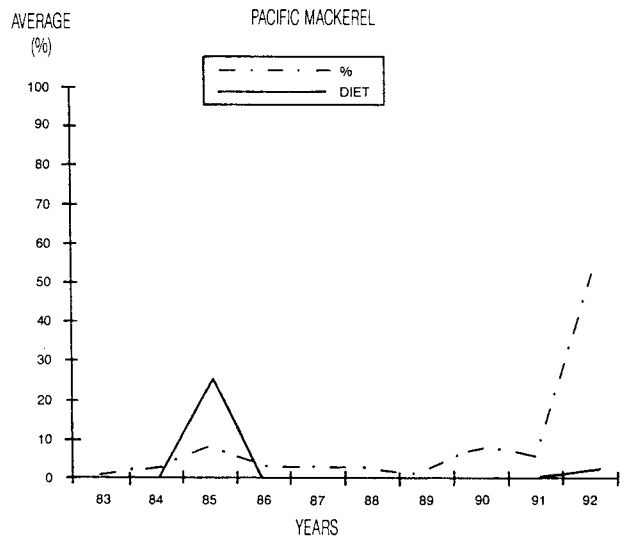

Figure 5. Percentage of Pacific mackerel in commercial landings and in the diet of seabirds, 1983–92.

tential competition between seabirds and fisheries for the same resource. In certain zones this relationship has temporarily benefitted fisheries, but has greatly diminished the seabird population. This has happened in Peru (Idyll 1973; Tovar 1978) and in South Africa (Crawford and Shelton 1978) among other places, where seabirds that specialized on a particular prey suffered reduced breeding success or did not breed at all (Cairns 1987; Hamer et al. 1991; Furness and Nettleship 1991). In the case of generalist-feeding seabird species, a change in prey stock may result in a change in diet (Montevecchi et al. 1987; Furness and Nettleship 1991).

The breeding season of most seabirds is markedly linked to seasonal fluctuations in the food supply (Perrins 1970; Kirkham and Morris 1979) and, during the nesting period, distribution and abundance of food are some of the most important factors that determine breeding success (Anderson et al. 1980, 1982; Cairns 1987; Hamer et al. 1991). Fisheries reports for the gulf (tables VIII and XI in Cisneros et al. 1991) indicate that Pacific sardines are most likely to be captured in the Midriff Island region between February and July. This coincides with the approximate time of the seabirds' nesting season in this area, indicating a likely coupling of the breeding season with the presence of the main food source.

The proportion of sardine in the seabirds' diets is positively correlated to total sardine landings in Sonora, and negatively correlated to proportion of anchovy in the diet and in the catch, showing that the first is a good indicator of the latter three. The proportion of anchovy in the seabirds' diets is negatively correlated to sardine landings and positively correlated to anchovy landings, which is expected from the above-mentioned correlations; it also shows that the first correlation is a good indicator of the latter two. Also expected from the above results is the negative correlation between sardine landings and anchovy landings. The negative correlations between the sardine landings and both the anchovy and the mackerel landings indicate that there is a tendency for the fleet to take these two latter species in the absence or reduction of the main target species, the Pacific sardine.

Whereas anchovy landings increased slowly but fairly steadily, at least until 1990, sardine landings suffered two distinct collapses: one in the 1989–90 fishing season and another in 1991–92 (figure 3). Landings were fairly stable between 1990 and 1991. An explanation for these observations may be that birds preferred anchovies over sardines, or that fishermen directed their effort toward sardines, and catches did not reflect the ongoing decline of the sardines.

As reported to the authors by fishermen, until 1989, most boats were equipped with sardine purse seine nets, and equipment in fishmeal factories was adapted for processing sardines, so fishing for and processing anchovies was avoided because of severe problems in handling the species (Doode 1992). Thus the fishing fleet avoided anchovy schools and actively searched for sardine, or else for schools of the larger mackerel, seldom catching a shoal of anchovies. This selective fishing for sardines created a proportionately larger pressure on the dwindling sardine population; this pressure was sustained for two seasons: 1989 through 1991. More opportunistic foragers—gulls and terns—most likely fed on pelagic fish according to their relative proportions in the environment. The proportion of sardines in the seabirds' diets was negatively correlated both to anchovy in the diet and anchovy landings, as would be expected from a more

opportunistic or random process, the species composition being less biased in the diet.

Also evident from the data (figures 3–5) is the fact that birds detected changes in the composition of the small pelagic fish community in a more pronounced way and, sometimes, at an earlier date. For the sardine, for example, a reduction in the seabirds' diet of almost 70% in 1985 was reflected in only a less than 10% reduction in the catch, whereas a major reduction in the seabirds' consumption of sardine in 1989 was reflected by a similar reduction in the catch only in 1992, a three-year lag.

In the case of the anchovy, a 30–40% increase in the seabirds' diet, peaking in 1985, was reflected by a 5% increase in the catch, peaking in 1986. Furthermore, the anchovy landings do not surpass 10% of the total small pelagic fish landings until 1990, six years after this species had reached over 30% in the seabirds' diet, in 1984.

For mackerel, an almost 50% increase of consumption by the seabirds was reflected by a catch increase of less than 10% in 1985. However, this does not hold for this species after 1989, when a 7% increase in the diet was reflected by a 50% increase in the catch. This may be due to the lack of the main target species for fisheries—the Pacific sardine—and to the fact that mackerel are preferred by fishermen over anchovies because anchovies create some problems both during capture and during processing for reduction. Furthermore, anchovies are not suitable for canning.

In conclusion, studies of the diets of these seabirds provide useful data on the species composition of fish stocks in the area studied, and probably provide a more reliable index of changes in forage-fish populations than do data derived from commercial landings. Evidently, Heermann's gulls and elegant terns, among other seabirds (Anderson 1983; Velarde and Anderson, in press), have coupled their breeding season with food availability in their nesting area (Cisneros et al. 1991; Hammann et al. 1991; Velarde et al., in press). This coincidence in time and space makes these seabirds valuable sampling agents and indicators of food supply within their foraging range during the nesting season. These birds sample small pelagic fish at precisely the time when both juvenile and adult populations of several species of the fish arrive at the Midriff Island region (Cisneros et al. 1991; Hammann 1991; Hammann et al. 1991). Therefore, these seabirds constitute useful indicators of ecological changes related to their food source, such as the succession or alternation of small pelagic fish species in the ecosystem.

ACKNOWLEDGMENTS

Through the years, field work has been supported by Instituto de Biologia–Universidad Nacional Autónoma de México, Consejo Nacional de Ciencia y Tecnologia, the Mexican Navy, Agrupación Sierra Madre, World Wildlife Fund, The Nature Conservancy–International Program, International Council for Bird Preservation, and Cementos Mexicanos. We thank the Dirección General de Conservación Ecológica de los Recursos Naturales from the Secretaria de Desarrollo Urbano y Ecología for granting the permits for field work in the Reserve of Isla Rasa. We acknowledge H. Montiel, Director of the Centro Regional de Investigación Pesquera in Guaymas, for his constant interest and support, as well as all the people in that institution involved in the Programa de Pelágicos Menores. We thank M. I. Ramirez for her advice and help with the data analysis. We are grateful to D. W. Anderson, M. A. Cisneros, G. Hamman, G. T. Hemingway, and two anonymous reviewers for the valuable critical review of the manuscript.

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EARLY LIFE HISTORY OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, OFF WASHINGTON, OREGON, AND CALIFORNIA, WITH APPLICATION TO BIOMASS ESTIMATION

H. GEOFFREY MOSER, RICHARD L. CHARTER, PAUL E. SMITH, NANCY C. H. LO, DAVID A. AMBROSE, CYNTHIA A. MEYER, ELAINE M. SANDKNOP, AND WILLIAM WATSON

Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

In January–February 1987 we conducted a cruise over the central California continental slope to sample the eggs and larvae of sablefish (*Anoplopoma fimbria*). Sablefish eggs were taken in 35% of the bongo and MOCNESS nets towed through the entire water column. Discrete depth tows showed that eggs were distributed between 200 and 800 m and were most concentrated between 240 and 480 m. On surveys off Oregon in February–April 1989 (slope region) and in January 1990 (slope region and offshore to ca. 170 n. mi.) we employed oblique bongo tows to sample the entire water column to a maximum depth of 1500 m. The inshore limit of eggs was at about 500 m bottom depth, and they were found seaward to about 150 n. mi. Eggs at the most seaward positive stations were four or five days old, suggesting that they were produced by an offshore segment of the sablefish population and did not represent eggs advected from the continental slope. Estimation of sablefish biomass by the egg production method is possible since we now have a quantitative method for sampling the pelagic eggs and simultaneously recording temperature throughout the tow. For the method to be successfully employed in the northeast Pacific, the sampling pattern would have to extend at least 200 n. mi. offshore, and the survey vessel would have to be capable of operating in the heavy seas encountered during the sablefish spawning season (January–March).

RESUMEN

Durante Enero–Febrero de 1987 hicimos un crucero por el talúd continental frente de California central para colectar muestras de huevos y larvas del bacalao negro (*Anoplopoma fimbria*). Encontramos huevos del bacalao negro en 35% de los arrastres hechos por toda la columna de agua con redes "bongo" y "Mocness." Arrastres a profundidades fijas mostraron que los huevos se distribuían entre 200 y 800 m, concentrandose entre 240 y 480 m. Frente a Oregon, hicimos arrastres oblicuos con redes "bongo" por toda la columna de agua hasta una profundidad máxima de 1500 m. En Febrero–Abril de 1989 estos arrastres se hicieron en la zona del talúd, mientras que en Enero de 1990 se hicieron en la zona del talúd y en mar abierto, hasta aprox. 315 km de la costa. El límite de la distribución de los huevos fué de aprox. 280 km hacia mar adentro, mientras que hacia la costa el límite coincidió con la zona de profundidad de aprox. 500 m. Los huevos encontrados en las estaciones en mar abierto tenían 4–5 días de edad, sugiriendo que éstos fueron producidos por un segmento de la población encontrada en mar abierto y nó debidos a la deriva de huevos producidos en el talúd continental. Es posible calcular la biomasa del bacalao negro por el método de producción de huevos, dado a que ahora contamos con un método cuantitativo para obtener muestras de huevos pelágicos y, de manera simultánea, el registro de temperatura durante el arrastre. Las condiciones para que este método tenga éxito en el Pacífico noreste incluyen que los muestreos deben extenderse hasta por lo menos 370 km hacia mar adentro, y que el buque de investigación sea capaz de operar en mares picados, una condición común en la época de desove (Enero–Marzo) del bacalao negro.

[Manuscript received January 22, 1994.]

INTRODUCTION

The sablefish, *Anoplopoma fimbria*, inhabits continental shelf and slope waters of the north Pacific and Bering Sea from Cedros Island, Baja California, Mexico, to the east coast of central Honshu, Japan (Allen and Smith 1988). Off the United States, sablefish is a member of the commercially important "deepwater complex" that includes Dover sole (*Microstomus pacificus*), shortspine thornyhead (*Sebastolobus alascanus*), and longspine thornyhead (*S. altivelis*). Annual U.S. commercial landings of sablefish for the ten-year period from 1982 to 1991 averaged 12,700 MT, with an ex-vessel value of $14.3 million in 1991 (Pacific Fishery Management Council 1992; Silverthorne 1992). Catch limitations imposed on the fishery (Methot 1992) point to the need for more information on the biology of sablefish; such information could lead to improved methods for assessing biomass.

The early life history of sablefish is unusual. The eggs and yolk-sac larvae are found almost exclusively at depths >200 m; at the end of the yolk-sac period the larvae migrate to the surface and are neustonic for the remaining larval period (Mason et al. 1983; Kendall and Matarese 1987). Early juveniles also inhabit surface waters, where

they can grow as much as about 2 mm per day (Boehlert and Yoklavich 1985; Shenker and Olla 1986). The neustonic larvae and juveniles are broadly distributed and may be found farther than 200 n. mi. from the coast (Kendall and Matarese 1987). Little is known of the movements of surface-living juveniles and of the means by which they return to shelf waters for settlement.

The study reported herein is an integral part of an overall research program of the Coastal Fisheries Resources Division (CFRD), Southwest Fisheries Science Center (SWFSC), directed to the commercial groundfishes of the continental slope. Dover sole biology, including ichthyoplankton-based biomass estimation, has been a major focus of this work, and the data presented here were collected on cruises designed principally to that end. But because adult sablefish habitat, spawning season, and egg and larval distributions broadly overlap those of Dover sole, data derived from the samples could be used to evaluate ichthyoplankton methods for estimating biomass of sablefish. The objectives of this paper are (1) to provide baseline information needed for evaluating ichthyoplankton methods for estimating sablefish biomass, and (2) to illustrate this application by using existing data to make a preliminary biomass calculation.

Sablefish is a promising candidate for egg production biomass estimation because it is a determinant spawner with a short spawning season (Hunter et al. 1989). Egg production methods require precise information on the areal boundaries of egg distribution and on the vertical distribution of eggs in the water column (Lo et al. 1992). Also required are criteria for staging the eggs, from fertilization to hatching, to determine mortality rates during the egg stage (Lo et al. 1992, 1993). Lastly, a minimum level of spawning activity is required for an ichthyoplankton-based method to be successful. Sablefish are unusual in that the adult spawning habitat spans a huge latitudinal range. The species has been fished commercially from Cedros Island, Baja California, Mexico, to the Bering Sea, but it is unlikely that it spawns successfully throughout this range. Thus knowledge of latitudinal changes in reproductive success is critical for evaluating biomass methods, and also has important implications for fishery management. Abundance of larval stages is the best historic indicator of reproduction because the eggs are too deep to have been taken in routine plankton surveys.

This paper addresses the above topics as follows. First, we compare relative abundance of sablefish larvae in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton time series with data from the Alaska Fisheries Science Center (AFSC) ichthyoplankton time series in the northern California Current region (Kendall and Matarese 1987; Doyle 1992a, b) to determine the change in abundance with decreasing latitude, to define the southern limits of sablefish reproduction, and to provide background information for designing egg production survey cruises. Next, we present the results of CFRD cruises that yielded data on (1) the areal limits of egg distribution, (2) the abundance of eggs over and seaward of the slope, and (3) the vertical distribution of sablefish eggs. Next, we estimate daily egg production of sablefish off Oregon and central California by using abundance-at-age data and egg mortality rates generated from CFRD groundfish cruises. Finally, we estimate spawning female biomass for central California and central Oregon slope regions by using our daily egg production estimates and the daily weight-specific fecundity data listed by Hunter et al. (1989) and Macewicz and Hunter (1994).

MATERIALS AND METHODS

CalCOFI surveys provided information on the distribution and abundance of sablefish larvae in the mid and southern regions of the California Current (table 1). During 1951–84, 9,802 oblique plankton tows were taken in February–April, when sablefish larvae appear in the plankton in this region. Most annual surveys covered a grid of stations that extended from San Francisco, California, to San Juanico Bay, Baja California, and seaward to 160–250 n. mi. Details of CalCOFI sampling methods and laboratory procedures are described in Moser et al. 1993 and in a series of 24 data reports that list the ichthyoplankton and associated station data for each CalCOFI survey conducted from 1951 (Ambrose et al. 1987) to 1984 (Stevens et al. 1990). Information from CalCOFI surveys on the distribution of sablefish larvae in the neuston was obtained from 572 Manta net samples taken in 1980–84 during February–April.

Plankton survey cruises of the AFSC provided comparative information on the distribution of sablefish larvae north of the CalCOFI survey. This time series consists of data from ten cruises off the coasts of Washington, Oregon, and northern California during 1980–87 (Kendall and Clark 1982; Savage 1989; Doyle 1992a, b). Survey lines extended from the shelf to farther than 200 n. mi. offshore, with the number of stations per survey ranging from 91 to 125. Oblique bongo tows to 200 m depth and neuston tows were taken on each station. Neuston tows were made with a "Sameoto" sampler with a mouth opening 0.3 m deep by 0.5 m wide (Sameoto and Jaroszynski 1969). Mesh size for oblique and neuston tows was 505 μm.

Four types of plankton tows were made on the CFRD groundfish cruises: Manta (neuston), CalBOBL (shallow bongo oblique), DBOBL (deep bongo oblique), and MOCNESS (discrete depth strata) (table 1). Mesh size for all nets was 505 μm. The Manta net sampled the upper 15.5 cm of the water column; tow duration was

TABLE 1
Summary of Plankton Collections Made on CalCOFI Surveys and CFRD Groundfish Research Cruises Used in This Study, and Number of Occurrences of Sablefish Eggs (in Parentheses) and Larvae (in Brackets)

				Number of tows			
Cruise	Date	Locality	Plankton stations	Manta (neuston)	Shallow bongo	Deep bongo	MOCNESS-1
CalCOFI surveys	1951–84	Calif. Current region	31,214	1,702 [8]	31,214 [5]	—	—
CFRD groundfish cruises							
8701 JD	1/11–2/15 1987	Central Calif., slope	75	73 [6]	54	42 (15) [2]	20 (9) [2]
8803 JD	2/23–4/9 1988	Central Calif., slope	62	62 [6]	62	44	—
8903 JD	2/21–4/1 1989	Central Oregon, slope	60	54 [15]	59 (5) [2]	46 (32) [18]	—
9001 JD	1/12–1/24 1990	Southern & central Oregon, slope and offshore	33	33	33 (4)	28 (15)	—

15 min at ca. 1 knot. CalBOBL tows were made to a maximum depth of 210 m; DBOBL and MOCNESS tows were made to a maximum of 1500 m or to near-bottom depths over the continental slope. Pay-out (50 m/min) and retrieval (20 m/min) rates and wire angles (45°) were similar for CalBOBL and DBOBL tows. A temperature-depth sensor attached to the DBOBL permitted monitoring and immediate adjustment of the tow trajectory and provided a temperature profile of each tow (Lo et al. 1993). A MOCNESS with a mouth opening of 1 m^2 (Wiebe et al. 1985) was used in 1987 off central California to determine the vertical distribution of the eggs. The MOCNESS tow profiles were similar to those employed during DBOBL tows. The first MOCNESS net sampled the entire water column during pay-out. During retrieval, sequential nets sampled segments of the water column, usually in 80 m depth increments. In most tows the upper 160 m was sampled by a single net, since sablefish eggs were not expected to be found there.

Egg and larval abundance is expressed either as number per 1000 m^3 of water filtered or number per 10 m^2 of surface area. Usually, number per unit volume is used for Manta tows. Abundance of eggs or larvae in oblique unstratified tows is expressed as the number per 10 m^2 of surface area, obtained by multiplying the number of eggs or larvae captured in a tow by a standard haul factor (*SHF*). The equation for *SHF* is:

$$SHF = \frac{10D}{V}$$

where, D = depth (m) of haul and V = total volume (m^3) of water filtered (Smith and Richardson 1977). In MOCNESS tows, egg or larval abundance for individual strata is presented as number per 1000 m^3 or as number per 10 m^2 of surface area. In the latter case, "surface area" refers to the upper limit of the stratum, and abundance is estimated for a discrete section of the water column. In one instance (larval length-frequency analysis), we expressed abundance for Manta tows as the number per 10 m^2 of surface area, computed from the *SHF*.

CFRD groundfish cruises off central California occupied stations over the continental slope and employed bottom trawls and a suite of plankton samplers (figure 1). Cruise 8701 JD (January–February 1987) consisted of a series of transects from Point Sur to just north of Point Conception, California. Cruise 8803 JD (February–April 1988) surveyed the same area using a stratified random station pattern (three bottom-depth strata).

Two CFRD groundfish cruises were conducted off Oregon. Cruise 8903 JD (February–April 1989) was a combined plankton sampling/bottom trawling cruise consisting of nine transects over the central Oregon continental slope (figure 1). Cruise 9001 JD (January 1990) consisted of four evenly spaced transects from Cape Blanco to Newport, Oregon, with stations beginning at the shelf edge and extending seaward to a maximum distance of about 170 n. mi. Station spacing was at 10 n. mi. intervals over the slope and at 20 n. mi. intervals seaward of the slope.

Sablefish eggs were distinguished from those of other species according to characters described by Kendall and Matarese (1987), and by additional features described herein. Larvae were identified by means of the descriptions of Kobayashi (1957), Ahlstrom and Stevens (1976), Kendall and Matarese (1987), and Matarese et al. (1989).

The following staging criteria for the eggs were modified from those used for northern anchovy, *Engraulis mordax* (Moser and Ahlstrom 1985) and for Dover sole (Lo et al. 1993):

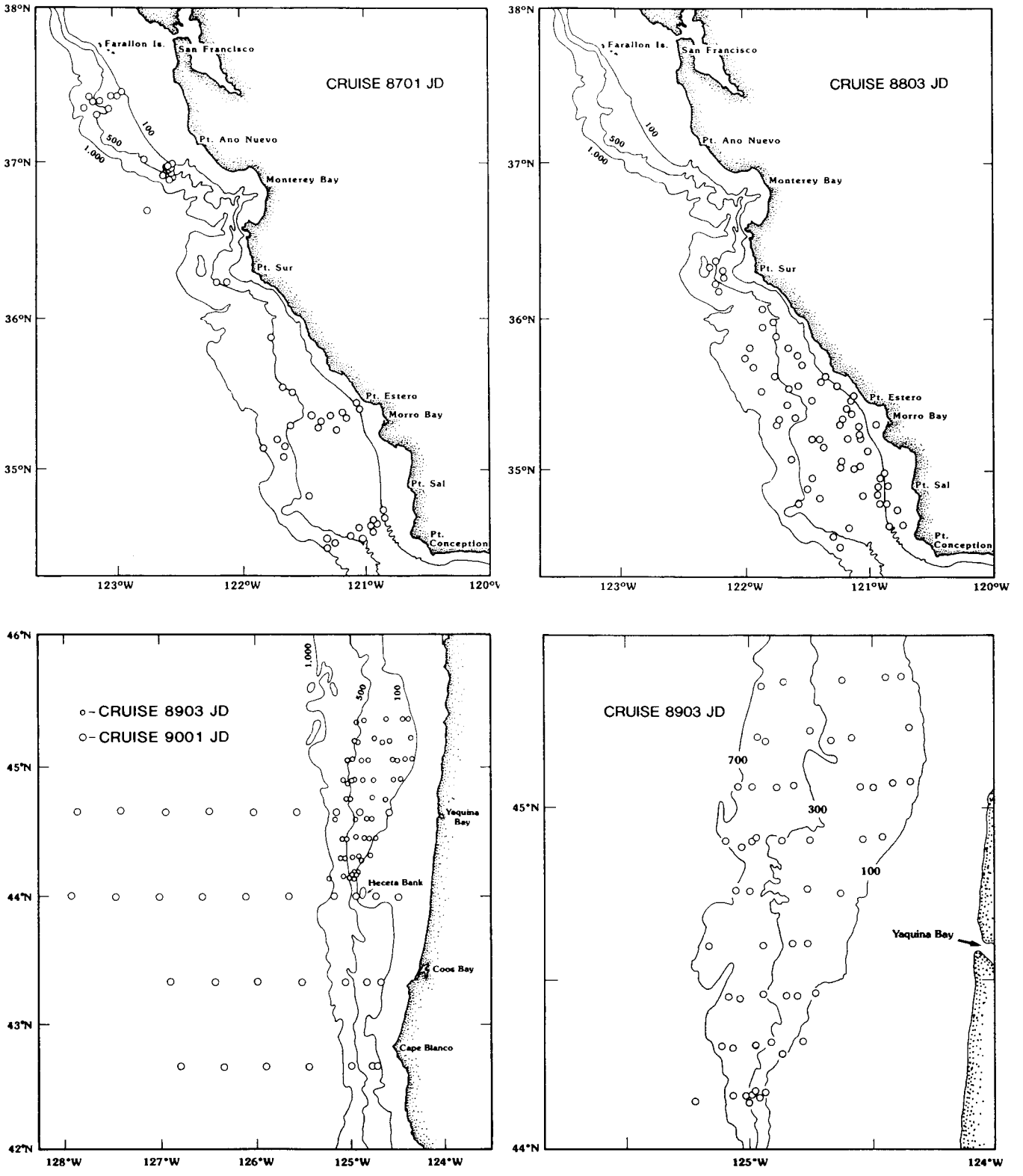

Figure 1. Stations (*circles*) occupied on Coastal Fisheries Resources Division (CFRD) groundfish research cruises. Isobaths are in fathoms.

St. I Prior to the first cell division of embryo.
St. II First cell division and subsequent blastodisc formation.
St. III Blastomeres are minute, and blastodisc has the appearance of tissue.
St. IV Germ ring extends 1/3 of the way around yolk sac (i.e., the blastoderm encloses 1/3 of yolk sac).
St. V Germ ring extends 2/3 of the way around yolk sac (i.e., the embryo encloses 2/3 of the yolk sac).
St. VI Blastopore closed.
St. VII Tail has a rounded tip separated from yolk mass.
St. VIII Free length of tail equals 1/2 head length (head length = distance from tip of snout to posterior edge of cerebellum).
St. IX Free length of tail equals full length of head.
St. X Tip of tail extends to 1/2 yolk-sac diameter.
St. XI Tip of tail extends to 3/4 yolk-sac diameter.

Assignment of age to staged eggs required information on the temperature-dependent development rate for each stage. Data on developmental rates for sablefish eggs were reported by Alderdice et al. (1988a, b), who incubated field-collected sablefish eggs in aquaria. Because Alderdice's staging criteria were different from ours and because his temperature range was lower, we used the temperature-development relationship for Dover sole, a species with similar egg (yolk) size developing at similar temperatures[1]; rate constants in the model were adjusted for the faster development time of sablefish (see Elliot et al. 1987; Pauly and Pullin 1988).

For Dover sole, the time required to reach stage XI, the hatching stage of sablefish, is 29 days at 5°C. Since sablefish reach this stage in 14 days, we assumed that the developmental rate for sablefish eggs at any stage is twice the rate of Dover sole. We checked the accuracy of our assumptions and model by comparing the time to yolk-plug closure, a stage criterion used by Alderdice and by us. At 5°C, sablefish eggs reached this stage in 151 hr in Alderdice's (1988a) experiment and in 144 hr in our model.

Eggs from both DBOBL and MOCNESS tows were used in egg production biomass calculations for central California; only DBOBL tows were available for Oregon. For the MOCNESS samples, the temperature at mid-stratum depth was used in the equation to estimate age of each staged egg. Temperature at depth for each DBOBL tow was obtained from the continuous temperature-depth record. We used the temperature at mid-depth of each tow for aging eggs from these tows.

[1]Moser, H. G., R. L. Charter, P. E. Smith, N. C. H. Lo, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, and W. Watson. Distribution and abundance of eggs and larvae of Dover sole, *Microstomus pacificus*, in the California Current region and their application to biomass estimation. In prep.

RESULTS

Egg Identification

Early planktonic eggs of sablefish are large, have a homogeneous, transparent yolk; a narrow perivitelline space; a smooth shell surface; and no oil globule (Mason et al. 1983; Kendall and Matarese 1987; Matarese et al. 1989). Dover sole eggs are similar to those of sablefish, and there was a size overlap in our samples. In a sample of 200 Dover sole eggs from southern California to Oregon, egg diameter ranged from 1.96 to 2.64 mm. Egg diameter in a sample of 152 sablefish eggs from the same region ranged from 1.90 to 2.22 mm, with a mean of 2.09 mm (SD = 0.06 mm). Usually, the perivitelline space is narrower in sablefish eggs than in Dover sole eggs, and the yolk of sablefish eggs is yellow to orange, in contrast to the pale yellow yolk of Dover sole eggs. Moreover, the yolk of sablefish eggs develops small vesicles of varying size, particularly after epiboly is completed, in contrast to the homogeneous yolk of Dover sole. At hatching, sablefish have a large yolk sac and are at a developmental stage similar to that in northern anchovy, even though the two species differ greatly in size.

Distribution

CalCOFI and AFSC time series. Sablefish eggs were not found in oblique plankton tows taken in the upper 200 m on CalCOFI surveys, because the eggs usually occur deeper than 200 m and because much of the CalCOFI survey area is south of the principal reproductive range of sablefish. Also, sablefish larvae are rare in these tows; of 9,802 oblique plankton tows taken off California and Mexico during 1951–84 in February–April, only five contained sablefish larvae (table 1; figure 2). Occurrence in neuston tows was only slightly greater in the same region: of 668 Manta net tows taken during 1980–84 in February–April, occurrence was 5.7% off central California (202 tows, including 96 tows taken during CFRD cruises 8701 JD and 8803 JD); 0.9% off southern California (216 tows); and 0% off Mexico (250 tows).

Decrease in occurrence and abundance of sablefish larvae from north to south in the California Current region is apparent when AFSC neuston tow data are compared with data from CalCOFI surveys and CFRD groundfish cruises (figure 3).[2] Mean abundance decreased by one-half from Washington to northern Oregon and again from northern Oregon to southern Oregon, then decreased by about 80% from southern Oregon to north-

[2]Comparisons of the performance of the "Sameoto" sampler and the Manta net have not yet been done, thus we are not able to evaluate their relative effectiveness in capturing sablefish larvae. Although the quantities in the two samplers are not strictly comparable and the abscissa in figure 3 is not metric, the results for each net show that incidence and abundance decrease equatorward.

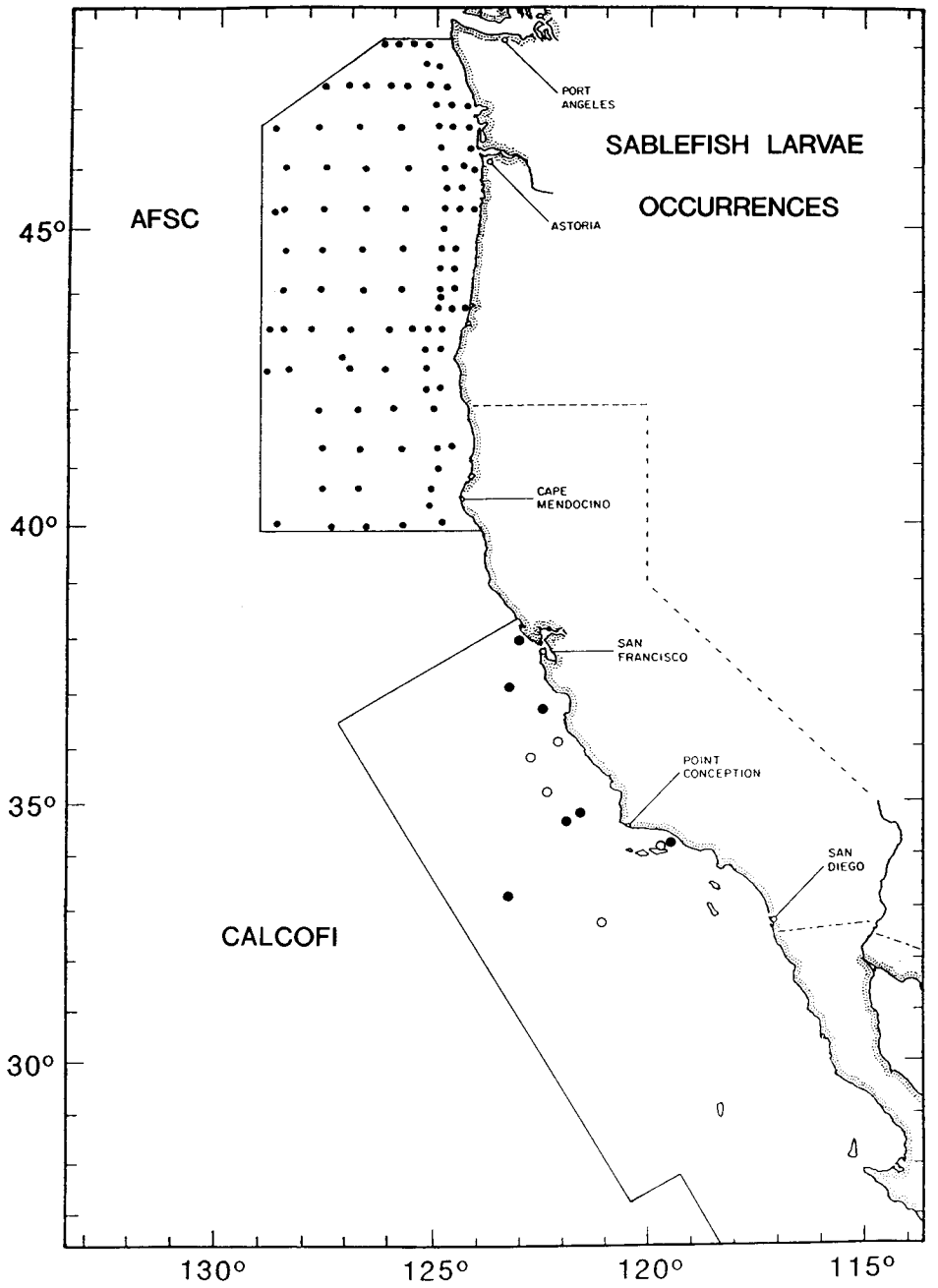

Figure 2. Sablefish larvae taken in plankton surveys of the Alaska Fisheries Science Center (AFSC) and in CalCOFI survey samples. The boundaries of both surveys are outlined. In the AFSC survey region, *solid circles* indicate positive stations for neuston samples. In the CalCOFI survey region, *solid circles* indicate positive stations for neuston (Manta) net samples; *open circles* indicate positive stations for oblique net samples.

ern and central California and by almost 100% from central California to southern California. Larvae have not been captured in neuston tows south of the U.S.-Mexican border. The trend for percentage occurrence shows a similar steep decline from north to south (figure 3).

Latitudinal shifts in peak larval abundance suggest that spawning progresses seasonally from south to north. Mean larval abundance (number per 1000 m^3 for all tows in the region) is highest in February off central California (table 2). Abundance is highest in March off northern California and southern Oregon (probably the peak month, although data are not available for February). Abundance peaks sharply in April off northern Oregon and even more sharply off Washington (table 2). Also, the offshore extent of sablefish larvae diminishes with decreasing latitude (figure 4). In AFSC neuston tows, mean larval abundance was high off Washington and Oregon in successive offshore zones; off northern

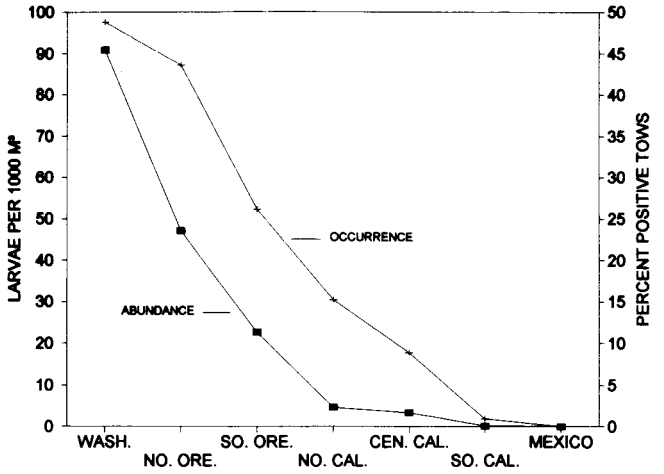

Figure 3. Mean occurrence (percent positive tows) and abundance (number/1000 m^3) of sablefish larvae in neuston samples. Data from Washington to northern California are based on samples taken during March–May on cruises conducted in 1982–87 by the AFSC. Data from central California to Mexico are based on Manta net samples from CalCOFI plankton surveys in 1980–84 during February–April. The central California data include Manta tows taken on CFRD groundfish cruises 8701 JD and 8803 JD. Wash. = Washington; No. Ore. = northern Oregon (north of Newport); So. Ore. = southern Oregon (south of Newport); No. Cal. = northern California (south to Point Delgada); Cen. Cal. = central California (south to Point Conception); So. Cal. = southern California (south to U.S.–Mexico border); Mexico (south to San Juanico Bay, Baja California).

TABLE 2
Seasonal Abundance (Mean No./1000 m^3 for All Tows in Each Region) of Sablefish Larvae in Surface Tows (Number of Tows in Parentheses) from Washington to Central California

	Month				
Region	Jan.	Feb.	Mar.	Apr.	May
Washington	0	—	37.8	158.1	16.4
	(18)	(0)	(27)	(81)	(54)
Northern	0	—	25.4	87.9	20.9
Oregon	(21)	(0)	(30)	(68)	(81)
Southern	0	—	45.2	22.4	17.8
Oregon	(21)	(0)	(30)	(8)	(142)
Northern	0	—	21.9	11.4	2.1
California	(28)	(0)	(16)	(22)	(173)
Central	0	5.2	1.4	1.1	0
California	(102)	(107)	(59)	(36)	(55)

Data from Washington to northern California are based on neuston net samples taken during 1980–87 by the Alaska Fisheries Science Center (Kendall and Clark 1982; Doyle 1992b).

Data from central California are based on Manta net samples from CalCOFI plankton surveys in 1980–84 and CFRD groundfish cruises 8701 JD and 8803 JD.

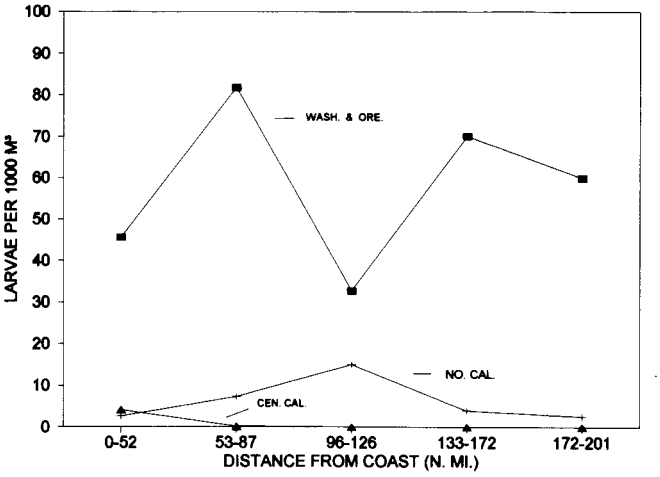

Figure 4. Mean abundance (number/1000 m^3) of sablefish larvae in AFSC and CalCOFI neuston tows for various offshore zones. See figure 3 caption for region boundaries.

California abundance peaked between 96 and 127 n. mi. from the coast. In our Manta net samples off central California, larvae were found only in water over or adjacent to the slope (figure 4).

CFRD groundfish cruises. On Cruise 8701 JD, abundance of sablefish eggs was low in DBOBL and MOCNESS tows on the four major transects, with nearly all eggs taken at stations between the 500 fath. (915 m) and 1000 fath. (1830 m) isobaths (table 3; figure 5a). The inshore limits of egg distribution were defined, but the offshore limits were not. Few yolk-sac larvae were collected in two DBOBL and two MOCNESS tows along the 500 fath. isobath on three of the four major transects (table 3; figure 5b). Neustonic larvae occurred, also in relatively low abundance, only in the southern region of the survey pattern between the 500 fath. and 100 fath. (183 m) isobaths (table 3; figure 5b). On Cruise 8803 JD, no sablefish eggs or yolk-sac larvae were taken in any of the DBOBL tows; neustonic larvae were taken in six Manta tows in the southern region of the pattern (table 3). Five of the six positive tows were made along the 100 fath. (187 m) bottom contour.

On Cruise 8701 JD, twenty MOCNESS tows taken over the midslope region yielded information on the vertical distribution of sablefish eggs. Of the nine MOCNESS tows positive for sablefish eggs, five sampled equivalent depth strata and could be compared directly (table 4; figure 6). In these tows, eggs were taken between 160 and 800 m; abundance was highest between 240 and 400 m (ca. 2 eggs/1000 m^3). Mean abundance was slightly lower (ca. 1.3 eggs/1000 m^3) in the 400–480 m stratum and fell off sharply below 480 m. Mean temperatures for the three strata of highest abundance ranged from 6.0° to 7.7°C (table 4). A similar pattern is apparent when stratum mid-depth is plotted against mean egg abundance for all nine MOCNESS tows positive for sablefish eggs (figure 7a). A plot of individual egg age against stratum mid-depth for all positive tows shows that eggs were not stratified according to age (figure 7b). Two larvae were captured in these samples—a 4 mm yolk-sac larva in a 280–360 m sample and a 7 mm larva in a 0–160 m sample.

On Cruise 8903 JD, sablefish eggs were taken in DBOBL tows on all transects, with nearly all positive

TABLE 3
Mean Abundance (All Tows) of Sablefish Eggs and Larvae in Plankton Tows Taken on CFRD Groundfish Cruises off Central California and Oregon

	Eggs		Larvae		
	Shallow bongo (no./10 m^2)	Deep bongo and MOCNESS (no./10 m^2)	Manta (neuston) (no./1000 m^3)	Shallow bongo (no./10 m^2)	Deep bongo and MOCNESS (no./10 m^2)
Central California					
8701 JD	0	2.6	4.3	0	0.2
8803 JD	0	0	3.7	0	0
Oregon					
8903 JD	0.6	30.1	17.6	0.3	4.3
9001 JD	0.7	3.8	0	0	0

Larvae taken in deep bongo and MOCNESS tows were yolk-sac stage; those taken in shallower samples were later-stage.

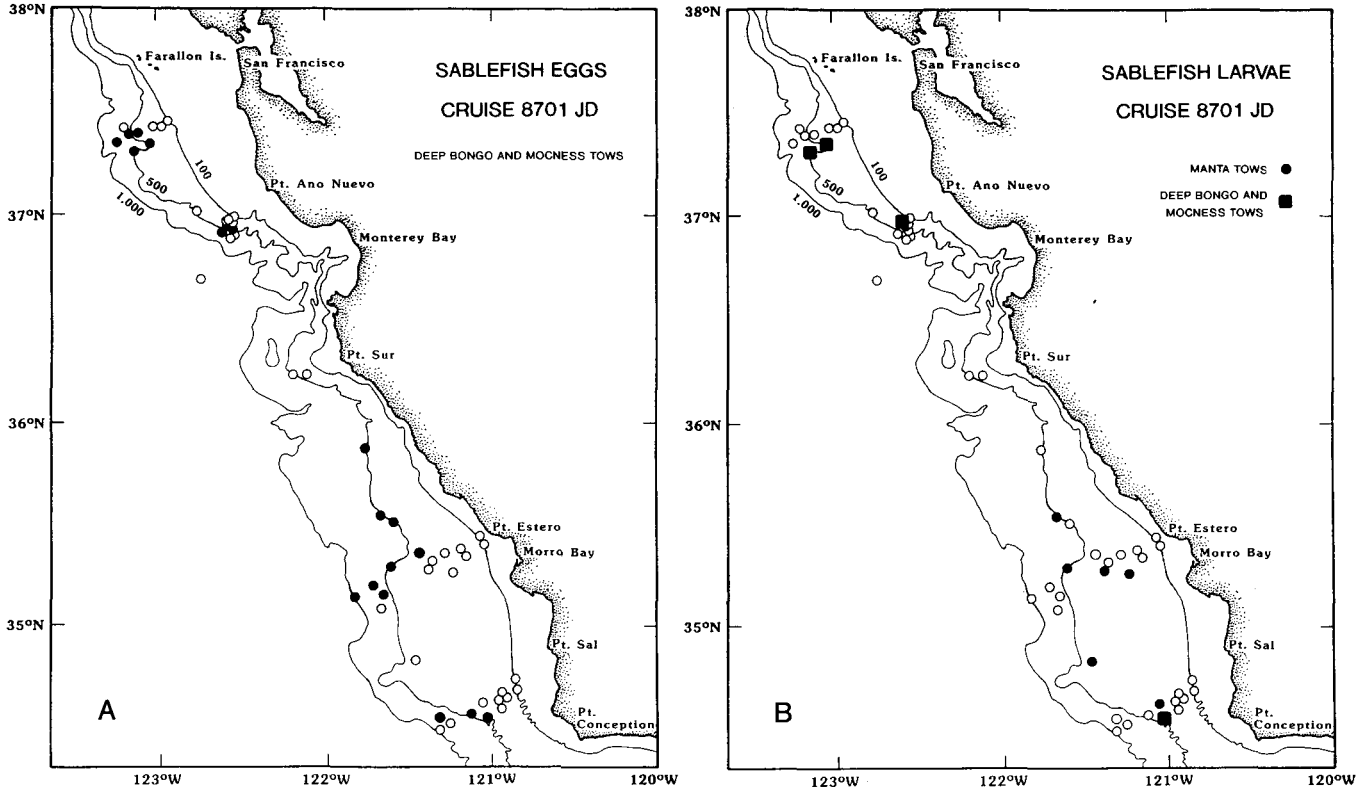

Figure 5. Sablefish eggs and larvae taken on CFRD Cruise 8701 JD. *Open circles* indicate sampling stations. In *A*, *solid circles* indicate stations where deep bongo tows (DBOBL) and MOCNESS tows were positive for eggs. In *B*, *solid circles* indicate stations where Manta tows were positive for larvae; *solid squares* indicate stations where DBOBL tows were positive for larvae. Isobaths are in fathoms.

stations between the 300 fath. (550 m) and 700 fath. (1280 m) isobaths (figure 8a). Mean egg abundance in DBOBL tows was ten times greater than for Cruise 8701 JD off central California (table 3).

Some characteristics of the dispersion of sablefish eggs are apparent when data are stratified according to egg age and bottom depth (table 5). No day "0" or day "1" eggs were captured in this set of samples. Either these eggs were not in the sampled volume at all or were so compact at the time of fertilization that they had not dispersed sufficiently to be encountered in this small sample set. The lower incidence of sablefish eggs of all ages in the shallowest zone (0–456 m) indicates that either there was little drift of eggs into the water over that zone or egg mortality was virtually total for eggs which drifted shoreward into that zone. It is unlikely that any spawning occurred in the shallow zone, since no reproductively active females were captured in trawls from those depths during the cruise (John Hunter, pers. comm.). In zone 2 (457–1004 m) and zone 3 (1005–1280 m), the abrupt rise to a maximum incidence at day 3 may be attributed to dispersal after spawning and fertilization. The gradual decline in occurrence from days 3 to 8 may be attributed to continued dispersion and

TABLE 4
Vertical Distribution of Sablefish Eggs from Five MOCNESS Tows Containing Sablefish Eggs on CFRD Groundfish Cruise 8701 JD, off Central California, January 26–30, 1987

Stratum (m)	Mean no. eggs/1000m^3	Standard deviation	Mean temperature (°C)	Temperature range (°C)	Total volume filtered (m^3)
0–160	0	—	10.9	8.6–13.3	7317
160–240	0.39	0.88	8.5	7.9–9.3	4493
240–320	2.11	1.30	7.7	6.9–8.5	4665
320–400	2.02	2.18	6.7	6.2–7.3	4432
400–480	1.29	1.92	6.0	5.6–6.4	5038
480–560	0.22	0.50	5.5	5.0–6.0	4488
560–640	0	—	5.1	4.7–5.5	3841
640–800	0.11	0.26	4.8	4.3–5.1	7691

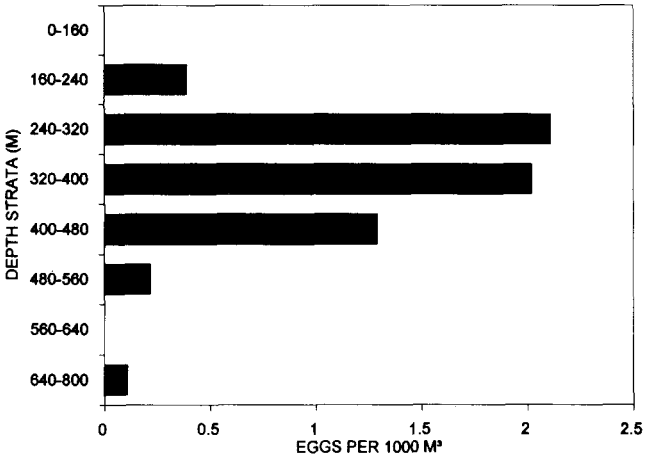

Figure 6. Vertical distribution of sablefish eggs in five MOCNESS tows that sampled equivalent depth strata off central California during CFRD Cruise 8701 JD. Mean egg abundance (number/1000 m^3) is shown for eight strata associated with each tow.

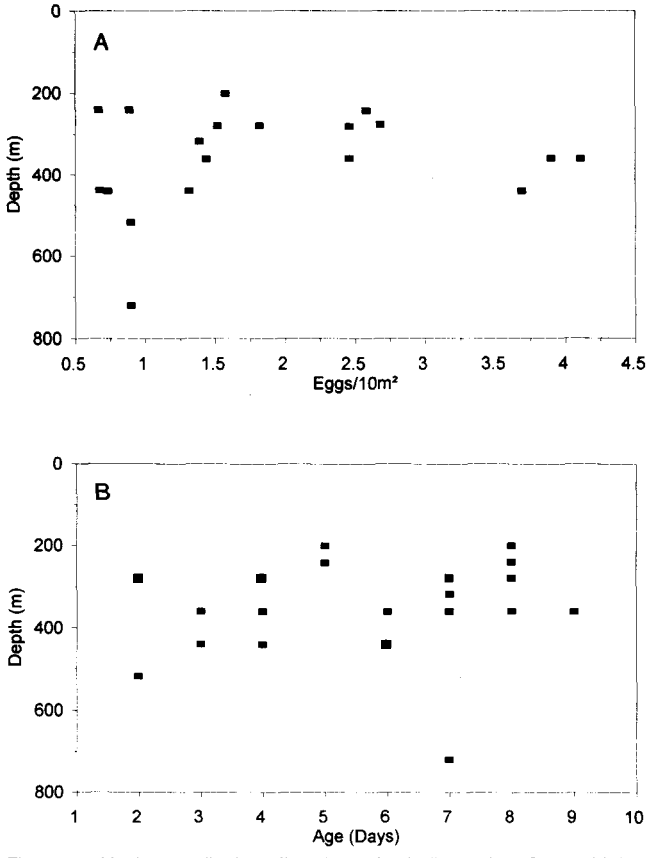

Figure 7. Vertical distribution (*A*) and age/depth distribution (*B*) of sablefish eggs captured on nine positive MOCNESS tows taken off central California during CFRD Cruise 8701 JD. In *A*, egg abundance (number/10 m^2) is plotted against the mid-stratum depth of each positive net; in *B*, ages of eggs are plotted against mid-stratum depth of each positive net. Some points may represent more than one egg.

mortality; the virtual disappearance at 13 days results primarily from mortality and hatching. A better description of spawning time and early stages of dispersal would require more samples.

Eggs were taken in shallow bongo tows at four stations, all in the southern part of the survey area near Hecate Bank, where complex currents might be responsible for their presence in the upper 200 m (figure 8b). Each of these tows captured only single eggs.

The distribution of yolk-sac larvae from DBOBL tows was similar to that of the eggs, and mean abundance was >40 times higher than off central California (table 3; figure 8c). Two shallow bongo tows contained sablefish larvae; these larvae, at the end of the yolk-sac stage (8–9 mm size), were in transit to the surface. Neustonic larvae were found at stations scattered over the entire survey area, and had a mean abundance four times greater than off central California (table 3; figure 8d). Size-frequency distributions of sablefish larvae differ for the three types of sampling gear (figure 9). Larvae captured in deep oblique tows were in the yolk-sac stage and ranged from 5 to 8 mm; larvae from surface nets were 8–18 mm; and the few larvae captured in shallow bongo nets were 8–9 mm—the size overlap for the other two nets (figure 9). All yolk-sac larvae captured were in poor condition; the greatest degree of disintegration appeared in the earliest yolk-sac stages. Disintegration and extrusion of the fragile early yolk-sac larvae are the most likely explanation for their low abundance. Early yolk-sac larvae

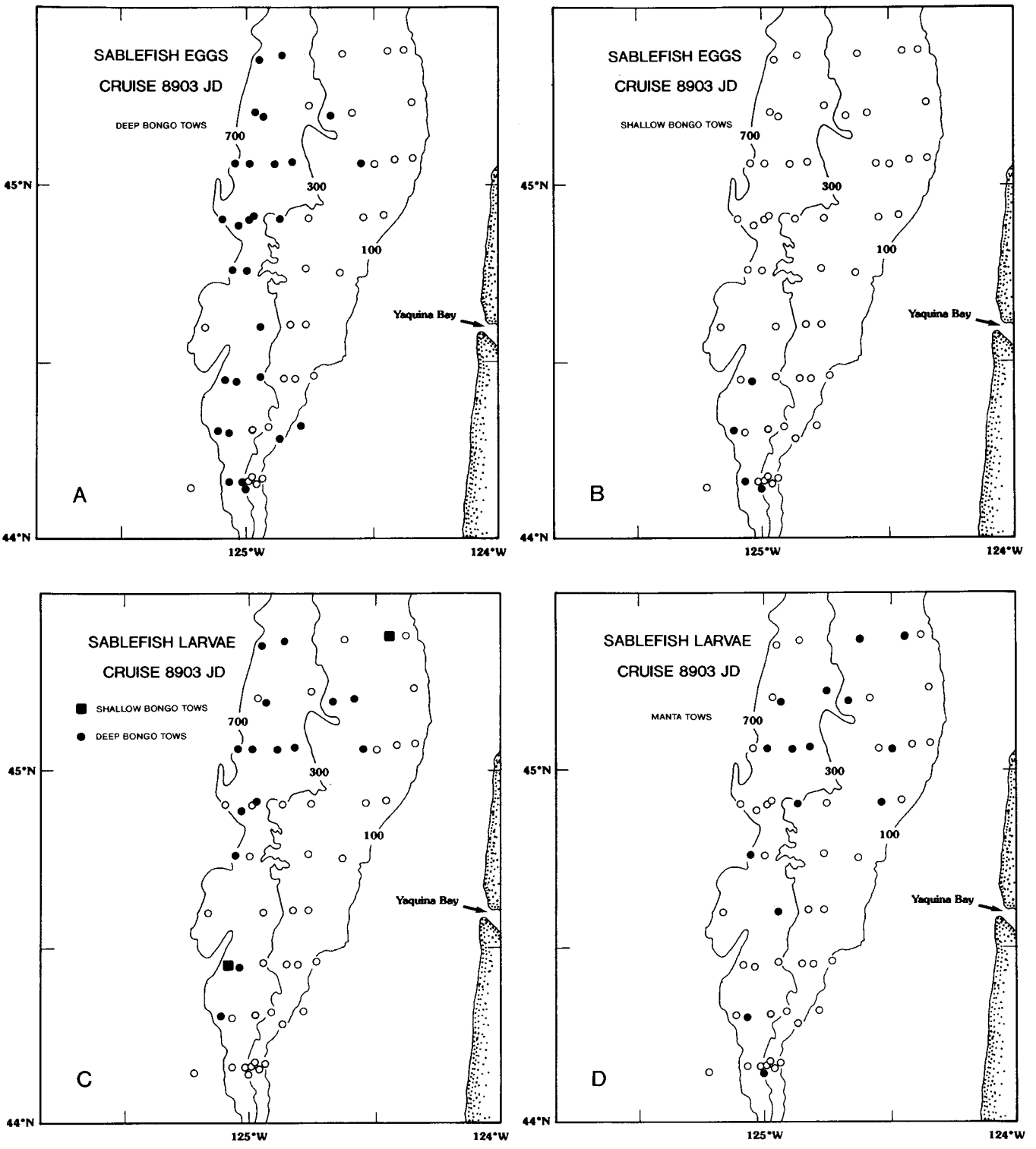

Figure 8. Sablefish eggs and larvae taken on CFRD Cruise 8903 JD. *Open circles* indicate sampling stations. In *A*, *solid circles* indicate stations where deep bongo (DBOBL) tows were positive for eggs. In *B*, *solid circles* indicate stations where shallow bongo (CalBOBL) tows were positive for eggs. In *C*, *solid circles* indicate stations where DBOBL tows were positive for yolk-sac larvae; *solid squares* indicate stations where CalBOBL tows were positive for post-yolk-sac larvae. In *D*, *solid circles* indicate stations where Manta tows were positive for post-yolk-sac larvae. Isobaths are in fathoms.

TABLE 5
Relative Frequency of Occurrence of Sablefish Eggs of Various Ages in Deep Bongo Oblique Plankton Tows on CFRD Groundfish Cruise 8903 JD off Central Oregon, February 22 to March 31, 1989

Age (days)	Zone 1 (0–456 m)	Zone 2 (457–1004 m)	Zone 3 (1005–1280 m)	All zones
0	0	0	0	0
1	0	0	0	0
2	0	0.16	0.05	0.10
3	0.07	0.33	0.36	0.31
4	0.07	0.25	0.11	0.18
5	0.00	0.24	0.20	0.19
6	0.00	0.22	0.18	0.18
7	0.07	0.16	0.11	0.13
8	0.00	0.09	0.07	0.07
9	0.00	0.07	0.05	0.05
10	0.07	0.11	0.00	0.06
11	0.00	0.02	0.05	0.03
12	0.00	0.02	0.05	0.03
13	0.00	0.00	0.02	0.01
Total	0.13	0.67	0.57	0.56

Data are stratified into three zones based on the bottom depth of the tow locality.

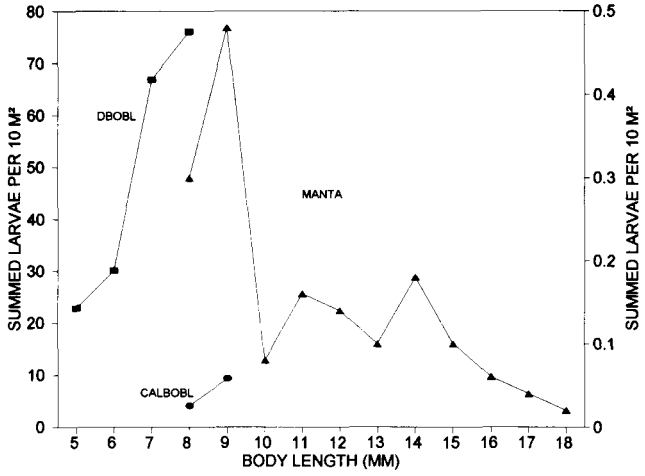

Figure 9. Length frequencies of sablefish larvae captured in Manta (*solid triangles*), deep bongo (*solid squares*), and shallow bongo (*solid ellipses*) nets on CFRD Cruise 8903 JD. Numbers on the left ordinate are summed abundance (larvae/10 m^2) in bongo tows; numbers on the right are summed abundance (larvae/10 m^2) in Manta tows.

should be fully vulnerable to the sampling gear and should be more numerous than more advanced yolk-sac stages.

Cruise 9001 JD examined offshore distribution; sablefish eggs were taken in DBOBL tows at slope stations of all transects and seaward to the next-to-last station (ca. 150 n. mi. offshore) on all but the southernmost transect (figure 10). Mean abundance of eggs over the slope was more than twice that of tows seaward of the slope: ca. 7 eggs/10 m^2 versus ca. 3 eggs/10 m^2. Eggs from samples over the slope ranged in age from 2 to 9 days, with 2- and 3-day-old eggs predominating; eggs seaward of the slope ranged from 3 to 7 days old, with 5- and 6-day-old eggs slightly more abundant. Eggs were taken in shallow bongo tows at five stations scattered over the survey pattern (figure 10). Mean abundance in DBOBL tows was one-eighth that of DBOBL tows made exclusively over the slope the previous year (table 3). No yolk-sac or neustonic larvae were captured in any tows.

Biomass Estimation

Mean abundance at age (eggs/10 m^2/day) was calculated for Cruise 8701 JD off central California and for the two cruises off Oregon (8901 JD and 9001 JD). A mortality curve was fitted to these data to estimate the daily production of newly spawned eggs (P_0/10 m^2/day) for each cruise (figure 11; table 6). The data were fitted to a nonlinear regression equation: $P_t = P_0 \cdot e^{(-Z \cdot t)}$, where P_t = daily egg production at age t; P_0 = daily egg production at age 0; and Z = instantaneous daily egg mortality. P_0 was highest (7.3) for cruise 8903 JD off Oregon and lowest (1.1) for the winter cruise off Oregon (figure 11). P_0 for central California was midway between these (3.5). Instantaneous mortality rates (Z) were similar for the two Oregon cruises: 0.25 for 8903 JD and 0.28 for 9001 JD. The rate was considerably higher (0.47) for central California. Variation was relatively low for Cruise 8903 considering the small sample size.

Egg production data from Cruise 8903 JD can be used for a rough estimation of spawning biomass for this section of the central Oregon coast. According to the calculations above, the daily production rate of newly spawned sablefish eggs is 7.3/10 m^2/day, or 0.73/1 m^2/day. From Macewicz and Hunter (1994), the potential annual fecundity for a 2,500 g female sablefish is 276,346 eggs, or 111 eggs/g/year. The exact length of the spawning season is unknown, as is the seasonal distribution of spawning rate, but available data suggest that the spawning season lasts from 90 to 120 days (John Hunter, pers. comm.). For convenience, in our preliminary biomass calculation we assumed that the spawning season was 111 days and that the fecundity was decreasing linearly at the time of the survey. Given these assumptions, the estimated daily egg production rate by sablefish females is 1 egg/g of female/day. Thus, under each m^2 of sea surface there are 0.73 g of spawning female sablefish, or 0.73 tons/km^2. The survey area was 56 × 170 km, or 9520 km^2. This would give about 6950 tons of female biomass for the central Oregon survey area.

DISCUSSION

Evaluation of Egg Production Methods for Sablefish

Our estimate of about 0.73 tons/km^2 of female sablefish in the central Oregon area surveyed during 1989 may be compared with trawl-based estimates of sable-

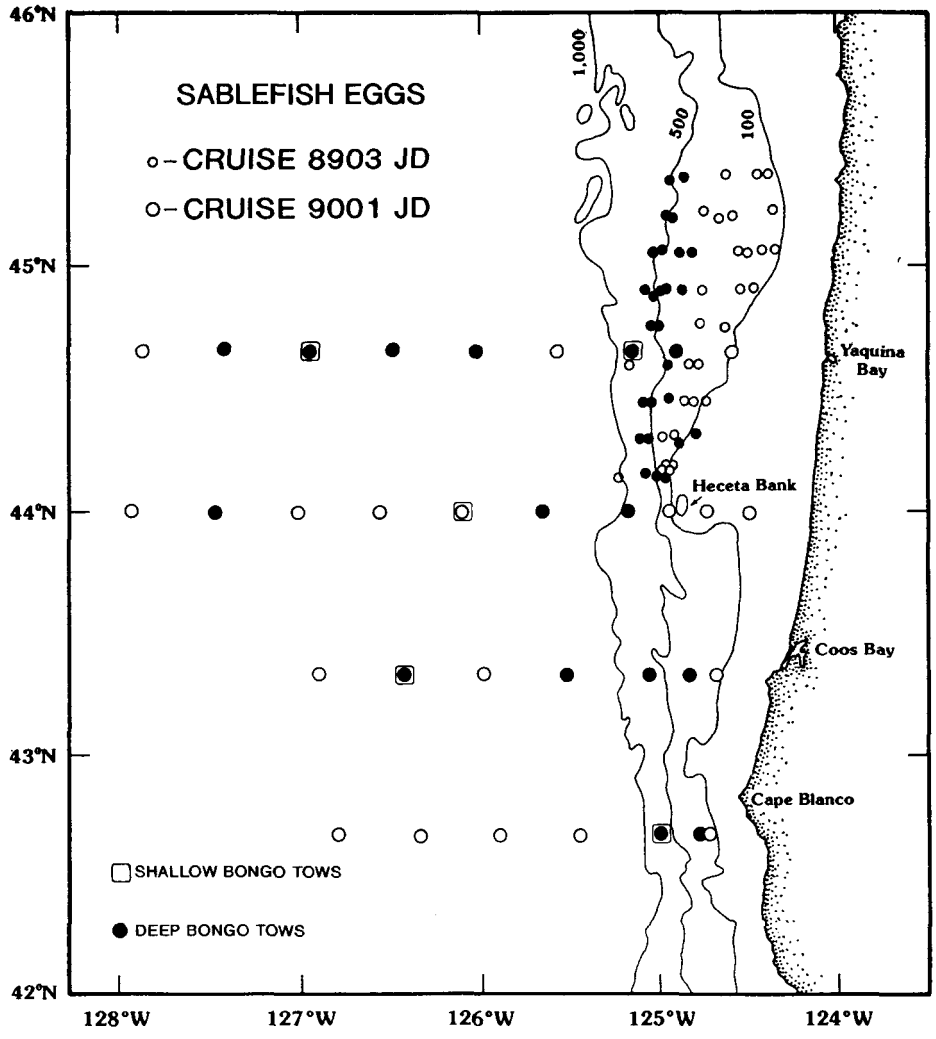

Figure 10. Sablefish eggs taken on CFRD Cruises 8903 JD (*small circles*) and 9001 JD (*large circles*). *Open circles* indicate sampling stations where deep bongo tows were negative. *Solid circles* indicate stations where deep bongo tows were positive; *open squares* enclose stations where shallow bongo tows were positive. Isobaths are in fathoms.

fish biomass densities for regions along the west coast of the United States and Canada. Methot (1992) estimated 3.87 tons/km^2 for the Vancouver-Columbia area (International North Pacific Fisheries Commission statistical area) and 1.41 tons/km^2 for the Eureka area. These estimates represent age 2+ males and females. Butler et al. (1989) gave an estimate of 1.33 tons/km^2 of adult and subadult males and females for the 250–549 fath. (458–1005 m) depth zone off central California. Our biomass density estimate for the central Oregon coast seems reasonable, especially if it were adjusted to account for males and subadults.

The reproductive biology and early life history of the sablefish make it ideally suited for egg production biomass estimation. Simultaneous sampling of planktonic and ovarian eggs is not necessary because potential annual fecundity can be estimated in the fall, before the spawning season (Hunter et al. 1989; Macewicz and Hunter 1994). Planktonic eggs are distinct and readily identifiable. The unique vertical distribution of the eggs below the zone of high primary and secondary production makes it possibile to use discrete depth sampling to reduce sorting time. Despite their relatively low fecundity, sablefish produce eggs that can be sampled effectively with plankton nets. This is a consequence of their dispersion and persistence in the water column and is in sharp contrast with the considerable patchiness of clupeoid eggs (Smith 1973; Smith and Hewitt 1984, 1985; Mangel and Smith 1990).

The fact that the eggs disperse within a confined vertical range may contribute to their availability to plankton tows. Low ambient temperatures in this stratum and a 2-week incubation period certainly contribute to the persistence of the eggs. The high incidence of eggs and

TABLE 6
Daily Egg Production (P_0) and Daily Instantaneous Mortality Rate (Z) for Sablefish Eggs from Three CFRD Groundfish Research Cruises

Parameter	Estimate	Standard error	Coefficient of variation
Cruise 8701 JD			
Central Calif.			
$P_0/10$ m^2	3.50	1.19	0.34
IMR (Z)	0.47	0.10	0.22
Cruise 8903 JD			
Oregon			
$P_0/10$ m^2	7.34	1.04	0.14
IMR (Z)	0.25	0.04	0.16
Cruise 9001 JD			
Oregon			
$P_0/10$ m^2	1.14	0.43	0.38
IMR (Z)	0.28	0.12	0.43

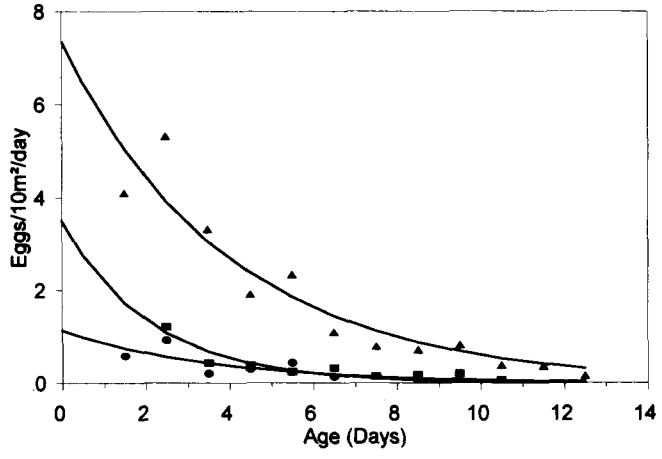

Figure 11. Mortality curve for sablefish eggs captured in deep bongo and MOCNESS tows during CFRD Cruise 8701 JD (*squares*) and in deep bongo tows during Cruise 8903 JD (*triangles*) and Cruise 9001 JD (*ellipses*). Daily egg production (eggs/10 m^2/day) is plotted against egg age (days) for the three cruises. The data were fitted to a nonlinear regression equation, $P_t = P_0 \cdot e^{(-Z \cdot t)}$, where P_t = daily egg production at age t, P_0 = daily egg production at age 0, and Z = instantaneous daily egg mortality.

the relatively low variance for estimates of daily egg production and mortality are remarkable considering the relatively small sample size and low egg abundance.

Most of the information required to plan an egg production biomass estimation survey for sablefish is available. We know that the inshore boundary of egg distribution corresponds approximately to the slope/shelf break. Since the minimum depth for eggs is about 200 m, any eggs over the shelf would be near or on the substrate and probably would not survive. We need to establish the offshore limits of egg distribution and to determine how far from the slope the eggs from slope-living females can be expected to appear. To adequately sample the offshore eggs, we need to establish the proper density for survey stations seaward of the slope.

Plankton sampling for a sablefish egg production survey off Oregon and Washington should be conducted during the peak spawning period (February–March), a time when storms frequently sweep through the region. Off Alaska, the survey would be slightly later in the spring (Kendall and Ferraro 1988). The survey vessel would have to be large and seaworthy to complete the extensive station pattern. Only a limited section of the coast could be surveyed unless more than one vessel was used.

Clearly, our estimate of biomass is heuristic, and some of the methods of calculation are not recommended if one were to embark on a formal estimate of sablefish biomass. For example, the assumption of linear reduction of population fecundity is particularly weak. Despite these reservations, the central conclusion to be drawn from the analysis is that sablefish is an ideal candidate for egg production biomass estimation.

Early Life History Adaptations

The results of this study and of preceding ones (see Mason et al. 1983; Kendall and Matarese 1987; McFarlane and Beamish 1992) reveal the uniqueness of sablefish early life history and invite discussion about the potential adaptive nature of these specializations. The deep, vertically constrained distribution of the eggs is unusual, if not unique, among coastal fishes. Intuitively, one would suspect that this part of the water column would have fewer egg predators and, consequently, that egg mortality rates would be reduced. On the contrary, egg mortality is 2.5 to 5 times higher than in Dover sole, a member of the "deep-water complex" whose similar-sized eggs are found in the upper water column (Lo et al. 1992, 1993; Moser et al.[3]). There appear to be no copepods in the 200–700 m depth stratum that are likely to specialize on fish eggs of this size (M. D. Ohman, Scripps Institution of Oceanography, pers. comm.), but recent findings (Bailey et al. 1993) that gammarid amphipods prey at a high rate on eggs and yolk-sac larvae of walleye pollack (*Theragra chalcogramma*) suggest that invertebrate predators may contribute significantly to sablefish egg and posthatching mortality. Other likely predators are mesopelagic fishes, such as members of the family Myctophidae, that may be able to locate patches of newly spawned eggs as they rise in the water column, and feed on the eggs as they disperse.

Some questions remain to be answered about the duration of the yolk-sac larval period and the vertical distribution of the yolk-sac larvae. McFarlane and Beamish (1992) have hypothesized from laboratory experiments that newly hatched yolk-sac larvae sink to a depth of 1000 m and begin to ascend gradually within about a week after hatching. They estimate that 50% of the yolk is used at about 2 weeks after hatching and that the yolk is fully used at about 40 days after hatching, when the

[3]See footnote 1 on page 148.

larvae have ascended to about 200 m. This scenario has yet to be confirmed by discrete-depth sampling. We know that larvae ascend rapidly through the upper 200 m, since they are extremely rare in time series of oblique plankton tows from this depth zone. The deep distribution of yolk-sac larvae hypothesized by McFarlane and Beamish (1992) may be adaptive from the standpoint of reduced predation, as would rapid passage through the upper mixed layer to the neustonic habitat.

Potential adaptive advantages of inhabiting the neuston have been discussed thoroughly (e.g., Zaitsev 1970; Hempel and Weikert 1972; Moser 1981; Doyle 1992a). Certainly, the high growth rates reported for sablefish larvae and early juveniles (Boehlert and Yoklavich 1985) support the notion that the neuston is a favorable trophic environment. The mesoscale patchiness of sablefish larvae apparent from our observations, from the AFSC time series (Kendall and Matarese 1987), and from the research of McFarlane and Saunders (in press) suggests that sablefish may be aggregating in response to prey concentrations associated with frontal features such as convergence zones and slicks (see Doyle 1992a). Indeed, the possibility of such adaptive contagious distribution prompted the CFRD to develop a research plan to study the fine-scale distribution of sablefish larvae in relation to the Columbia River plume.[4] The hypothesized association of sablefish larvae with this plume might also provide a mechanism for shoreward movement of larvae in concert with the seasonal shoreward progression of the plume.

Sablefish occupy a variety of habitats along the continental slope of the north Pacific; if both latitude and bathymetry are considered, sablefish are the most widely distributed commercial groundfish in the north Pacific. Virtually every habitat in this region is occupied by some ontogenetic stage of the species. Certainly the evolution of a highly vagile neustonic larva has contributed to the widespread distribution of the species. In fact, this vagility characterizes later ontogenetic stages. Pelagic juveniles, up to about 30 cm, have been captured in large numbers at considerable distance from the coast (Brodeur and Pearcy 1986), and recoveries of tagged sablefish on isolated seamounts (Alton 1986; Parks and Shaw, in press) suggest that adult sablefish may migrate great distances in mid-water or over the abyss. The tolerance of this species for low oxygen concentrations has permitted it to colonize the oxygen minimum zone along the entire slope region of the north Pacific arc. Emerging information suggests that this is but one facet of the remarkable adaptive repertoire of sablefish.

[4]A coordinated NOAA plan for fishery oceanography and recruitment research on West Coast groundfishes (FORAGE). Coastal Fisheries Resources Division, Southwest Fisheries Science Center, December 1989.

Latitudinal Range and Reproductive Competency

The time series data for surface-living larvae indicate that mortality of eggs and larvae increases markedly south of Oregon and that there is little or no survival of eggs or larvae south of the Southern California Bight. Substantial populations of sablefish occur along the coast of California north of Point Conception (Methot 1992), in the Southern California Bight (Cross 1987), and off the Pacific coast of Baja California, south to Cedros Island (Silva and Garcia 1988). We know that sablefish achieve sexual maturity and develop reproductively active gonads off southern California (Sullivan 1982) and Baja California (Olivia T. Vasquez, Instituto Nacional de la Pesca, Ensenada, Baja California, Mexico, pers. comm.). Tagging studies indicate little or no southward movement of demersal adults or subadults and, instead, show a tendency for movement to the north (McFarlane and Saunders, in press; Parks and Shaw, in press). Sablefish off Mexico appear to have a very long and tenuous connection to the reproductively successful fraction of the population to the north. It is likely that virtually all recruitment to sablefish populations off Mexico is from larger pelagic juveniles that avoid surface-towed plankton nets. Such large pelagic juveniles of northern origin may also contribute a substantial fraction of recruits to southern California.

An interesting management implication is that there may be limited need to regulate sablefish catch south of Point Conception, since the fraction of the population south of there has little or no reproductive potential. Moreover, sablefish fisheries south of Point Conception may be very unstable and subject to boom-or-bust conditions, since recruitment is dependent on larvae or juveniles that are transported great distances. The meager information we have on these fisheries appears to bear this out (Silva and Garcia 1988).

Drift algae provide a mechanism for the survival and transport of sablefish juveniles in the southern region of the range. Juvenile sablefish are known to associate with drifting seaweed off the coasts of southern California and Mexico. Using a miniature purse seine, Hunter and Mitchell (1970) made 50 collections of fishes associated with drifting seaweed (primarily giant kelp, *Macrocystis pyrifera*) from the Southern California Bight to Cedros Island, Baja California. Sablefish juveniles (66–149 mm SL) appeared in 15% of the samples and were the fourth most abundant species sampled. Kelp-associated sablefish juveniles were taken in samples from June and July, well offshore, where they would be subject to entrainment in the Southern California Eddy or in the southerly flow of the California Current. Drift-algae masses are common in the central and southern regions of the California Current and provide (1) an environment conducive to survival of sablefish juveniles and (2) a means

of southerly transport for presettlement individuals. Hunter and Mitchell's (1970) suggestion that drift algae reduced predation was supported by the results of their laboratory experiment in which fishes associated with algae were pursued less often, for shorter periods, and were captured less frequently by predators than were free-living fishes.

Little is known about the biology and distribution of late larvae and pelagic juvenile sablefish in their principal geographic range. Extensive sampling with surface nets (Pacific Northwest—Kendall and Matarese 1987; Canada—McFarlane and Beamish 1983; Gulf of Alaska—Kendall and Ferraro 1988) has not revealed the offshore limits of larval distribution, if indeed there are limits. How these broadly dispersed larvae reach the coast for settlement is unknown. Surface collections with neuston trawls (Shenker 1988) and purse seines (Brodeur and Pearcy 1986) indicate that large pelagic juveniles appear in the vicinity of the shelf break in the summer and fall off Oregon and Washington. Neuston net surveys off British Columbia show a similar seasonal onshore movement of larvae (McFarlane and Beamish 1983; McFarlane and Saunders, in press). How the broadly dispersed larvae and pelagic juveniles reach the coast for settlement is unknown. It is likely that this movement is aided by dynamic hydrographic processes, but such transport mechanisms have yet to be demonstrated.

ACKNOWLEDGMENTS

Many people contributed to this study. W. Flerx served as cruise leader for most of the field work and was ably assisted by R. Dotson, S. Manion, and D. Abramenkoff. The skill and cooperation of the ships' crews were essential to the success of the field collections. The samples were processed by L. Dunn, J. Haddox, and F. Pocinich. B. MacCall and E. Stevens helped identify sablefish eggs and larvae. A. Hays and M. Klaymann provided valuable assistance in data processing. Data from the AFSC were generously provided by A. Kendall, Jr., and J. Clark helped transfer those data. J. Hunter, G. Boehlert, A. Kendall, Jr., J. Butler, M. Ohman, and S. Ralston read the manuscript and offered valuable comments.

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FECUNDITY OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, FROM OREGON COASTAL WATERS

BEVERLY J. MACEWICZ AND J. ROE HUNTER
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038-0271

ABSTRACT

During November–December 1988 and February–March 1989, sablefish females were collected off Oregon's coast. Potential annual fecundity for a 2.5 kg sablefish female (without ovary) was about 276,000 oocytes, or 110 oocytes per gram of weight. The annual stock of oocytes is spawned in three or four batches. The ovaries of sablefish used to estimate potential annual fecundity showed no histological evidence of past spawning. The maturity window for estimating annual fecundity of sablefish was determined to be when the average diameters of advanced-yolked oocytes between 0.74 mm and 1.17 mm. Atretic losses of advanced-yolked oocytes were detected, but they seemed to have little effect on potential annual fecundity of the population. Fifty percent of the females off Oregon's coast (November–December 1988) were sexually mature when they reached 548 mm in fork length.

RESUMEN

Se colectaron hembras del bacalao negro frente a la costa de Oregon en Noviembre–Diciembre de 1988 y Febrero–Marzo de 1989. La fecundidad anual potencial de un bacalao negro hembra de 2.5 kg (sin ovarios) fué de 276,000 ovocitos, o 110 ovocitos por gramo de peso. El stock anual de ovocitos se desova en 3 o 4 puestas. Los ovarios usados para estimar la fecundidad potencial anual no mostraron evidencia histológica de desoves previos. Se determinó que el periodo de madurez oportuno para estimar la fecundidad anual es cuando el diámetro promedio de un ovocito en estado de vitelo avanzado es de entre 0.74 y 1.17 mm. Se observaron pérdidas de ovocitos en estado de vitelo avanzado con condición de atresia, pero las pérdidas parecieron tener poco impacto en la fecundidad anual de la población. El 50% de las hembras frente a la costa de Oregon (Noviembre–Diciembre, 1988) se encontraban sexualmente maduras cuando alcanzaron una longitud furcal de 548 mm.

INTRODUCTION

The annual fecundity of sablefish, *Anoplopoma fimbria*, appears to be determinate; that is, the stock of advanced-yolked oocytes before spawning is equivalent to the potential annual fecundity (Hunter et al. 1989). The other extensive measure of potential annual fecundity of sablefish comes from Mason (1984), who studied fish from off British Columbia, Canada. Other studies of sablefish reproduction include those by Phillips and Imamura (1954), Mason et al. (1983), Norris et al. (1987), Cailliet et al. (1988), and Fujiwara and Hankin (1988). The main objective of the study reported here was to estimate the potential annual fecundity for sablefish captured off the Oregon coast.

Estimates of potential annual fecundity depend upon four key assumptions: (1) fecundity is determinate; (2) oocytes are identifiable and fully recruited into the advanced stock; (3) the females have not spawned; and (4) potential fecundity estimated early in the season is nearly the same as the actual annual fecundity. In this paper, we review past evidence for determinate fecundity provided by Hunter et al. (1989) and, for the first time, evaluate assumptions 3 and 4. In addition, we use data from Oregon and central California to update the present information on spawning rates and batch fecundity, and we provide an estimate of the length at which 50% of the Oregon females are mature.

METHODS

Sablefish were collected in bottom trawls off Oregon's coast between Heceta Head and Cape Lookout (appendix table A) as part of two cooperative groundfish research surveys made in 1988–1989 by the Alaska Fisheries Science Center's (AFSC) Resource Assessment and Conservation Engineering Division, the Southwest Fisheries Science Center's (SWFSC) Coastal Fisheries Resource Division, and the SWFSC Tiburon Laboratory. The trawl used was either an AFSC-modified 5-inch mesh, 90/120, high-rise "poly Nor'Eastern" bottom trawl (fishing dimensions: ~4.6 m high and 13.5 m wide at wing tips), or a 5½-inch mesh, 75/90, high-rise Aberdeen bottom trawl. Trawls were towed on the bottom for 0.5 hour at depths shallower than 732 meters (400 fathoms) and for 1 hour at depths from 732 to 1,247 meters.

In both surveys, the total catch of sablefish in each haul was weighed. A random subsample of up to 100 sablefish was sexed and measured to the nearest millimeter (fork length). Ovaries were assigned to one of three classes: no yolked oocytes present, yolked oocytes present, or translucent (hydrated) oocytes present.

[Manuscript received January 22, 1994.]

Some fish, immediately after capture, were weighed to the nearest gram because their otoliths were saved (in 50% ethanol) or because ovarian tissue was removed and preserved. Females selected for ovarian preservation were taken randomly from the trawl catch; the whole ovary was preserved only when it contained yolked or hydrated oocytes. Any remaining sablefish not individually weighed in the random sample were grouped (male, active female, or inactive female), and the groups were weighed to the nearest pound. Individual weights were added to group weights to provide the combined total weight and number of individuals per reproductive class (appendix table B).

Ovaries with hydrated oocytes or other yolked oocytes were considered to be reproductively active and sexually mature, whereas ovaries in which observers saw no yolked oocytes were considered to be inactive (not capable of spawning at the time of capture or in the near future). To estimate size at maturity (length at 50% mature), inactive ovaries were considered sexually immature, since we used only specimens taken early in the spawning season (November–December 1988). We calculated the fraction of active ovaries for each fork length class (in 50 mm increments). Size at maturity was estimated by means of logistic regression (BMDPLR, Dixon et al. 1988).

Ovarian tissue samples and whole ovaries were preserved in 10% neutral buffered Formalin, and whole ovaries were subsequently weighed to the nearest 1/100 gram in the laboratory. A piece of each sablefish ovary was dehydrated and embedded in paraffin. Histological sections were cut at 5–6 μm and stained with Harris hematoxylin, followed by eosin counterstain (H&E). Each ovary was classified histologically in the manner developed for northern anchovy, *Engraulis mordax*, by Hunter and Goldberg (1980) and Hunter and Macewicz (1980, 1985a, b), with a few modifications appropriate for sablefish ovarian structure (Hunter et al. 1989). In the ovary, we identified the presence or absence of the following: oocytes in the first vitellogenic stages, advanced-yolked oocytes, migratory-nucleus-stage oocytes (precursor to hydration), hydrated oocytes, postovulatory follicles, and two stages of atresia (α and β). The rate at which postovulatory follicles degenerate and are absorbed in sablefish is unknown, so we did not assign ages to postovulatory follicles. At the end of the season, spent ovaries usually contained two groups of postovulatory follicles, distinguished by differences in their degree of deterioration, which indicated two past spawnings. Postovulatory follicles in one group were small, and the extent of their resorption indicated that they were older than 48 hours because in northern anchovy (Hunter and Macewicz 1985a) and chub mackerel (Dickerson et al. 1992) postovulatory follicles reach this stage of deterioration in 48 hours at habitat temperatures about 10°C higher than temperatures in the sablefish habitat.

Total fecundity (F_T) is defined as the total number of advanced-yolked oocytes in the ovary, including all hydrated oocytes. We estimated total fecundity gravimetrically: fecundity (F_T) is the product of the gonad weight (G) and oocyte density (C). Oocyte density is the number of oocytes per gram of ovarian tissue and is determined by counting the number of advanced oocytes in a weighed sample of ovarian tissue. Hunter et al. (1989) found no difference in oocyte density between the right and left ovary in sablefish off central California. They defined advanced-yolked oocytes as those in which the yolk is dense enough to occlude, or reduce, the visibility of the nucleus when the oocyte is viewed on a video screen; most of the oocytes larger than 0.6 mm in diameter met this criterion. We removed two tissue samples from the right ovary and counted all the advanced-yolked oocytes in both weighed samples.

In one of the samples, we also measured the diameter of 30 randomly selected (nonhydrated) advanced-yolked oocytes, to determine mean diameter of the advanced oocyte stock. Mean diameter of advanced oocytes (exclusive of hydrated oocytes) is a measure of the extent of yolking of the advanced oocytes in the ovary and, as a consequence, is an index of a female's readiness to hydrate and spawn a batch. The mean diameter is not an accurate measure of the degree of yolking if hydrated oocytes are included in the measurement. Advanced oocytes were identified, counted, and measured with a digitizer linked to a personal computer and a video camera system mounted on a dissection microscope.

Of sablefish captured off Oregon in November–December 1988, we estimated total fecundity for 130 active females containing advanced oocytes. Histological analysis of the ovaries indicated that three females had spawned already (postovulatory follicles present) and one female had extensive α atresia of yolked oocytes (≥50%); these four females were not used for analysis of potential annual fecundity but were used for other analyses. Near the end of the spawning season off Oregon (March 1989), we used 12 females with active ovaries for estimating total fecundity (appendix table C).

The number of hydrated oocytes in an ovary is equivalent to the batch fecundity (F_B), that is, the number of oocytes released during one spawning. Hydrated oocytes are easily identified because of their large diameter (about 2 mm) and translucent appearance. We estimated batch fecundity by counting the number of hydrated oocytes in two tissue samples per ovary. We estimated the number of nonhydrated advanced oocytes present in the same ovary by using the procedure described for estimating total fecundity. None of the ovaries collected in 1988 had hydrated oocytes. In 1989, 11

females with ovaries containing hydrated oocytes were taken, but 9 of these had begun spawning and were not suitable for estimating batch fecundity. Total fecundity (F_T) for females with hydrated ovaries is the sum of the hydrated and advanced-yolked oocytes.

To measure atretic losses anatomically (whole oocyte method), we counted the number of atretic oocytes (α atresia of advanced-yolked oocytes) occurring in the random sample of 30 advanced-yolked oocytes for each female for which we estimated a total fecundity. For Formalin-preserved ovaries, we also estimated the amount of α atresia of the advanced-yolked oocytes in a section of the ovary on the H&E slide (histological method) and grouped the ovaries into three classes by incidence of α (none; $0 < \alpha < 50\%$ of the advanced-yolked oocytes; and $\alpha \geq 50\%$ of the advanced-yolked oocytes).

RESULTS AND DISCUSSION

Maturity Window

An optimal range of ovarian maturity (a maturity window) exists for counting the oocytes constituting the potential annual fecundity (Hunter et al. 1992). If one counts the advanced stock of oocytes too early in the maturation period, not all of the oocytes destined to become part of the annual stock will be recruited. But if one counts too late, some oocytes may have been lost due to spawning. Other than the presence of hydrated or migratory-nucleus-stage oocytes, the best indicator of a female's readiness to spawn is the average diameter of the oocytes making up the advanced stock (Hunter et al. 1989). Thus the average diameters of the advanced, nonhydrated oocytes can be used to define the upper and lower bounds of the maturity window.

The diameter of the (nonhydrated) advanced-yolked oocytes of sablefish increases steadily during early maturation, and it continues to increase well into the spawning season (Hunter et al. 1989). Thus if oocytes are being recruited into the advanced stock, total fecundity would be expected to increase with mean oocyte diameter and would be positively correlated, whereas if spawning has begun, fecundity would be expected to decrease with mean oocyte diameter and would be negatively correlated. This point is illustrated diagrammatically for a single female in figure 1.

Hunter et al. (1989) examined the lower bound of the maturity window and concluded that, in sablefish, all oocytes were probably recruited into the advanced stock by the time their average diameter was above 0.7 mm, when the separation of the advanced mode was nearly complete. This conclusion was based on visual inspection of the oocyte frequency distributions of six sablefish ovaries. Since nearly all the ovaries of the active sablefish females analyzed from November–December

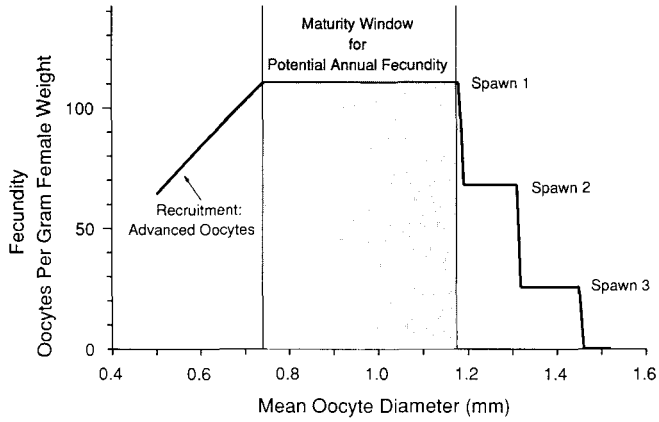

Figure 1. Hypothetical cycle of oocyte maturation in a single female, showing initial maturation of oocytes and the subsequent loss of oocytes due to spawning. The hydrations of oocytes are not indicated (these would be brief events just before each spawning). The diagram indicates changes in the standing stock of advanced oocytes (exclusive of hydrated oocytes) as a function of their average diameter. The diagram begins after some oocyte maturation has occurred, when the diameter of the advanced stock averages 0.5 mm (a condition probably prevalent in late summer or early fall in Oregon); the diagram ends after all advanced oocytes are spawned. The level segment of the line is the maturity window, a range of average oocyte diameters where estimates of the potential annual fecundity can be made without bias from oocyte recruitment or spawning losses. The maturity window for most, but not all, Oregon females occurs in early December.

1988 were well developed, 0.74 mm was set as the lower maturity bound for females to be included in the estimation of potential annual fecundity, because it was the smallest observed mean diameter above 0.7 mm for the advanced oocyte stock (appendix table C). There were too few females with ovaries containing mean oocyte diameters of the advanced stock between 0.6 mm and 0.9 mm to permit a quantitative analysis of oocyte recruitment such as the one carried out for Dover sole by Hunter et al. (1992).

The upper bound of the maturity window is the level of ovarian maturity (mean diameter of the advanced oocytes) at which spawning and oocyte losses begin. Multiple regression analysis indicated that ovaries of some sablefish taken in November–December 1988 exceeded the upper limit of the maturity window. The evidence was that total fecundity was negatively correlated with mean diameter of the advanced oocytes as well as being correlated with female weight (table 1). To determine the upper bound of the maturity window, we conducted a series of stepwise multiple regression analyses by successively removing data by 0.01 mm decrements of mean oocyte diameter, starting with the largest class (1.38 mm). This analysis indicated that the threshold for a significant effect of diameter on total fecundity was between mean oocyte diameters of 1.17 mm and 1.18 mm (table 2). The multiple regression coefficient for oocyte diameter was negative and significant when females containing ovaries with mean oocyte diameters equal to or larger than 1.18 mm were included, but insignificant when

TABLE 1
Total Fecundity (F_T) of Sablefish, *Anoplopoma fimbria*, and Female Weight (W, without Ovary) and the Average Diameter of the Advanced Oocytes (D) Based on Stepwise Regression with Analysis of Variance

Stepwise regression		
Step	1	2
Constant	−147,802	56,461
Weight (W)	162.1	163.9
t*	22.49	23.42
Diameter (D)		−192,244
t*		−3.07
S	89,416	86,518
r^2	80.31	81.72

Analysis of variance					
Source	D.F.	SS	MS	F	P
Regression	2	4.11×10^{12}	2.06×10^{12}	274.87	< 0.001
Error	123	9.21×10^{11}	7.85×10^{9}		
Total	125	5.04×10^{12}			

Source	D.F.	Sequential SS
Weight	1	4.04×10^{12}
Diameter	1	7.70×10^{10}

*For $P = 0.005$, $2.860 < t < 2.807$, d.f. ≥ 120.
Specimens from off Oregon November–December 1988.

only those having a diameter of 1.17 mm or less were considered. Thus the upper bound of the maturity window for estimating potential annual fecundity using our multiple regression method is 1.17 mm (mean diameter of the advanced oocyte stock).

We also used a spawning-rate index (fraction of all active females having ovaries containing postovulatory follicles, hydrated oocytes, or migratory nucleus oocytes) to examine the upper bound of the maturity window. When the index was calculated for each 0.1 mm interval of mean oocyte diameter, the index increased from 0 to 0.027 (1/31) at a diameter of 1 mm, and reached 0.11 (5/46) at a diameter of 1.2 mm (figure 2, lower panel). Thus about 10% of active females had ovaries showing histological signs of past or imminent spawning when the advanced but nonhydrated oocytes averaged 1.2 mm diameter. Of course no female showing signs of past or imminent spawning would ever be used in our estimate of potential annual fecundity. The maturity window question under discussion is: What fraction of the fecundity data should be discarded because it may contain females that spawned undetected by our histological analysis?

Depending on the criteria, the upper bound of the window varies between 1.0 mm (spawning activity detected in 2.7% of population) to 1.2 mm (11% of the population). These estimates are similar to the one based on multiple regression of 1.18-mm diameter. We prefer the multiple regression method because it provides a well-defined selection criterion, deals directly with fecundity decrements, and takes into account the fecundity of all females.

Estimate of Potential Annual Fecundity

An important aspect of this paper and of an earlier paper on Dover sole (Hunter et al. 1992) is that accu-

TABLE 2
Results of Stepwise Multiple Regression of the Total Fecundity (F_T) of Sablefish, *Anoplopoma fimbria*, on Female Weight (W, without Ovary) and Mean Oocyte Diameter (D) for a Succession of Oocyte Diameter-Classes with the Model $F_T = a + b_1W + b_2D$

Oocyte diameter class (mm)	Sample size N	Constant	Multiple regression coefficients and their t-ratios for: Female weight		Oocyte diameter		
		a	b_1	t	b_2	t*	r^2
0.74–1.38	126	56,461	163.9	23.42	−192,244	−3.07	0.817
0.74–1.31	125	38,781	164.0	23.49	−175,403	−2.75	0.819
0.74–1.26	120	55,083	160.2	18.77	−181,762	−2.64	0.753
0.74–1.24	116	51,841	161.4	18.44	−181,595	−2.50	0.751
0.74–1.22	113	78,566	159.6	17.77	−203,843	−2.72	0.743
0.74–1.20	104	46,489	165.7	18.49	−187,223	−2.42	0.772
0.74–1.18	95	45,728	165.2	17.86	−185,199	−2.18	0.776
0.74–1.17	89	32,608	166.2	16.44	−174,357	−1.86	0.759
0.74–1.16	85	36,894	163.9	15.87	−172,557	−1.74	0.754
0.74–1.14	81	16,431	163.6	15.39	−150,338	−1.42	0.753
0.74–1.12	75	12,267	165.0	15.77	−149,791	−1.40	0.776
0.74–1.10	65	16,517	165.6	14.96	−156,029	−1.26	0.783
0.74–1.08	56	−13,905	172.4	14.06	−141,132	−0.97	0.793
0.74–1.06	49	−112,959	178.8	15.16	−49,071	−0.33	0.839
0.74–1.04	45	−212,363	180.3	14.75	57,923	0.37	0.845
0.74–1.02	36	−195,118	168.7	8.71	69,487	0.36	0.712
0.74–1.00	30	−321,284	171.2	8.22	208,859	0.90	0.738

*For $P = 0.05$, t is 1.979 for d.f. = 125, 1.987 for d.f. = 88, and 2.014 for d.f. = 45.
Specimens taken along Oregon coast November–December 1988. Line separates oocyte diameter-classes where diameter is a significant variable from those where it is not.

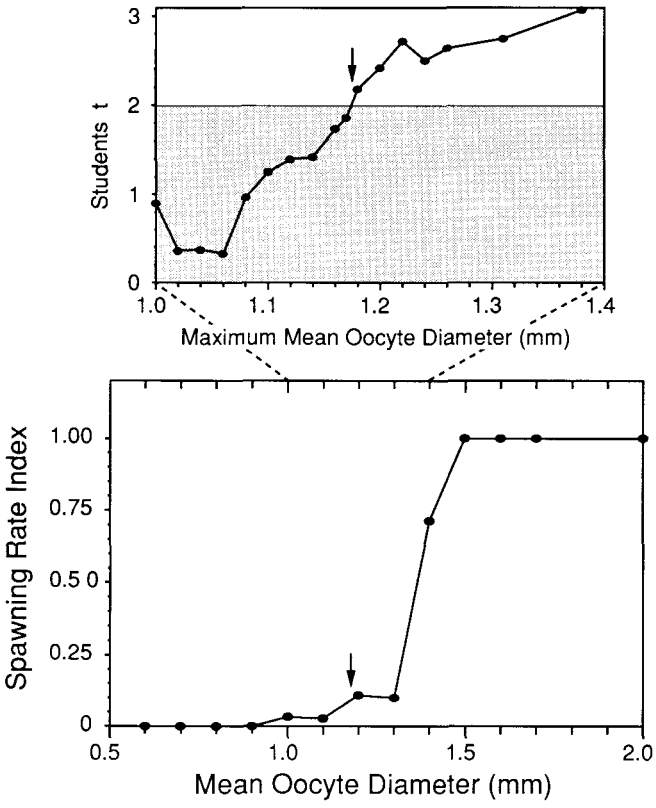

Figure 2. *Upper panel*, Student's $|t|$ as a function of maximum mean oocyte diameter from stepwise multiple regression analyses of fecundity as a function of female weight and oocyte diameter for Oregon sablefish taken during November–December 1988. When $|t| \geq 2$, the mean oocyte diameter has a significant negative correlation with fecundity, indicating a loss of oocytes from the advanced oocyte stock. *Lower panel*, Spawning rate index as a function of oocyte diameter: index = 0 when no females show signs of past or imminent spawning; index = 1 when all females show one of these signs. Arrow indicates point (1.17 mm) selected as the upper bound of the maturity window for estimating potential annual fecundity.

rate estimates of potential annual fecundity are much more difficult to make than is generally believed. A female sablefish was considered to be suitable for estimation of potential annual fecundity when the mean diameter of the advanced-yolked oocytes fell within the boundaries of the maturity window we have described (0.74–1.17 mm). In addition, females must also show no histological evidence of recent, past, or imminent spawning (no postovulatory follicles or hydrated oocytes within their ovaries) to be included in our estimate of potential annual fecundity.

Using only specimens that met these specifications, we regressed total fecundity on female weight (without ovary) for female sablefish captured off Oregon during November–December 1988; also using these specifications, we reevaluated the females from off central California (Hunter et al. 1989). The two linear regression equations for females from off central California and Oregon were quite similar (table 3). When the data were truncated so that the range in female weight was about the same for both regions, an analysis of covariance indicated that neither the difference of the intercepts between regions ($F_{1, 108} < 0.001$, $P = 0.992$) nor the difference between slopes ($F_{1, 108} = 0.15$, $P = 0.701$) was statistically significant. Combining all data, we obtained the following general equation:

$$Y_F = -126{,}654 + 161.2W$$

where Y_F is the estimated potential annual fecundity from the regression line, and W is female weight in grams without the ovary (figure 3). Thus the potential annual fecundity of a 2.5 kg sablefish female is about 276,000 oocytes (table 3), which is equivalent to about 110 oocytes per gram of female weight.

Mason et al. (1983) and Mason (1984) estimated the fecundity of sablefish taken off British Columbia, Canada. They used an exponential model and expressed fecundity (F) as a function of fork length (L, in cm). Both papers dealt with the same data, but showed small differences in the coefficients for the fecundity equation. We used the equation from Mason 1984, because that paper presented the original data:

$$F = 0.73L^{2.94}.$$

To compare results, we fit a weighted exponential equation (BMDPAR, Dixon et al. 1988) to our data for

TABLE 3
Relationship between Total Fecundity (F_T) and Female Weight (W, without Ovary) for Oregon and California Sablefish, *Anoplopoma fimbria*, Females with No Histological Evidence of Past or Imminent Spawning

State	Oocyte diameter class (mm)	Linear equation $F_T = a + bW$					Estimate for for 2500 g female	Female weight (g)	
		a	b	r^2	F	N		Mean	Range
California	0.78–1.16	−115,501	164.0	0.590	7.27	37	294,499	2,259	1,165–3,275
	0.78–1.30	−45,223	125.1	0.486	6.52	45	267,527	2,347	1,165–4,327
Oregon	0.74–1.17	−141,550	164.1	0.746	16.10	89	268,700	2,630	1,349–7,303
	0.74–1.38	−147,802	162.1	0.802	22.49	126	257,448	2,651	1,282–9,487
	1.18–1.38	−172,904	161.1	0.879	16.17	37	229,596	2,702	1,282–5,094
California + Oregon	0.74–1.17	−126,654	161.2	0.726	18.22	126	276,346	2,521	1,165–7,303

Females meeting specifications for potential annual fecundity estimation (average oocyte diameter between 0.71 and 1.17 mm) are compared to those that may have begun to spawn (average oocyte diameter larger than 1.17 mm).

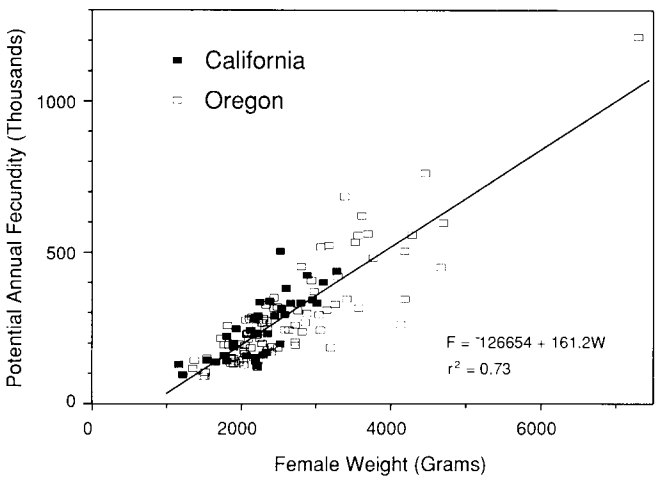

Figure 3. Potential annual fecundity as a function of body wet weight in grams (without ovary) for sablefish females taken off Oregon (November–December 1988) and off central California (October 1986).

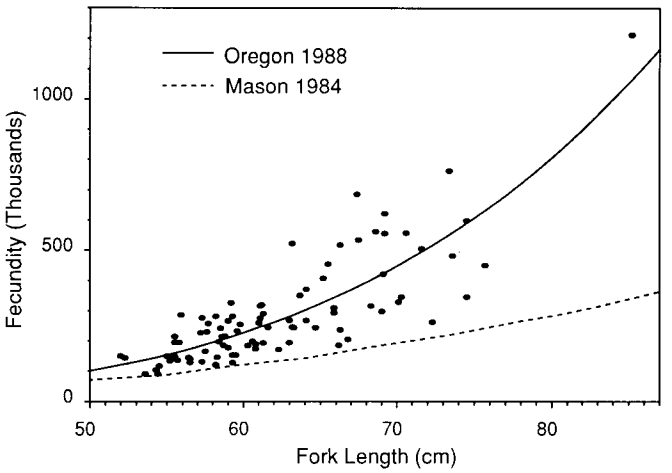

Figure 4. Potential annual fecundity of Oregon sablefish as a function of fork length (L) in cm (*solid circles* and *solid line*, $Y_F = 0.0033L^{4.4074}$) compared to Canadian females from Mason 1984 (*dashed line*, $F = 0.73L^{2.94}$).

potential annual fecundity from Oregon as a function of fork length, yielding the following relation:

$$Y_F = 0.0033L^{4.4074}$$

where L is fork length in cm and where the weights are the inverse of the variance of fecundity because the variance of the fecundity of females less than 63 cm was significantly smaller than the variance of fecundity for females ≥63 cm. The fecundity-length function for sablefish off Canada is distinctly lower than nearly all our Oregon data, regardless of the length of the female (figure 4).

After we selected females within the same length range (57–86 cm), an analysis of covariance applied to log-transformed data indicated that the two locations were significantly different for both of the intercepts ($F_{1, 112} = 5.78$, $P = 0.018$) and the slopes ($F_{1, 112} = 7.24$, $P = 0.008$). In fact, for a 67-cm female, the adjusted mean for potential fecundity from Oregon sablefish (358,613 oocytes) was about twice the Canadian sablefish fecundity estimate (171,099 oocytes). We believe the lower estimate of potential annual fecundity for the Canadian sablefish most likely results from loss of oocytes due to spawning. The Canadian sablefish females contained ovaries with large, advanced oocytes, which had peaks in distribution from 1.0 to 1.2 mm (Mason et al. 1983), indicating that some ovaries were probably above the upper bound of the maturity window. Additionally, the fish were taken off Canada during the spawning season, when up to 45% of female sablefish were spawning (Mason et al. 1983).

Evidence for Determinate Fecundity

Perhaps the most telling evidence for determinate annual fecundity is the decline in the standing stock of advanced oocytes during the spawning season. We combined Oregon data with central California data and examined the decline in the standing stock of advanced oocytes during the spawning season (figure 5). The standing stock of advanced oocytes in October–December (line for potential annual fecundity) is elevated above the line for females collected during the spawning season (January–March). Additional support for determinate annual fecundity in sablefish, but not unequivocal proof, is the existence of the hiatus in the oocyte distributions illustrated in Hunter et al. (1989) and Mason (1984), and the increase in the mean diameter of the advanced oocytes during the season for both California and Oregon sablefish (table 4).

A key issue affecting fishes with determinate annual fecundity is whether atretic losses during a season con-

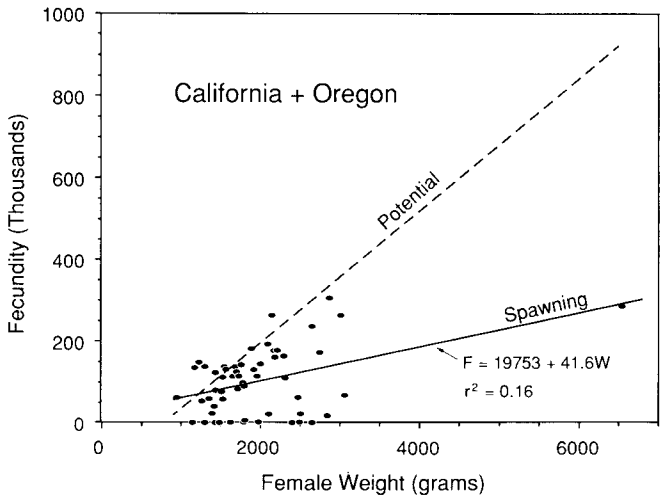

Figure 5. Total fecundity (number of advanced oocytes) as a function of weight (without ovary) for sablefish females collected off central California and Oregon during the spawning season (*solid circles* and *solid line*) compared to the potential annual fecundity (*dashed line*, $Y_F = -126{,}654 + 161.2W$) of California and Oregon females taken before spawning had begun.

TABLE 4
Mean Size and Standard Deviation of the Average Diameter of the Standing Stock of Advanced-Yolked Oocytes in Sablefish Used to Estimate Total Fecundity per Cruise

Cruise mean date and locality	Average diameter (mm) of advanced-yolked oocytes		Number of females
	Mean	S.D.	
October 25, 1986 California	1.00	0.17	51
December 6, 1988 Oregon	1.09	0.12	130
January 22, 1987 California	1.35	0.15	38
March 23, 1989 Oregon	1.32	0.23	6

stitute an important fraction of the potential annual fecundity. Although the fraction of α atretic oocytes varied between 0 and 0.72 when we used the whole-oocyte method (figure 6), the average fraction of advanced oocytes that were atretic was low (≤0.018) in both Oregon and California females (table 5). A stepwise multiple regression of female weight, elapsed time, and fraction of atretic oocytes on total fecundity indicated that the relation between fecundity and the proportion of atretic oocytes was not significant ($t = -1.88$, d.f. = 235, $P = 0.062$), but the coefficient for the fraction of oocytes atretic (−174,356) was negative, as would be expected. We conclude that atretic losses were not sufficiently high to produce a measurable decrement in total fecundity calculated from a regression model.

Histological methods revealed similar rates of α atresia of advanced-yolked oocytes in the ovaries of sablefish females in the two regions; α was detected histo-

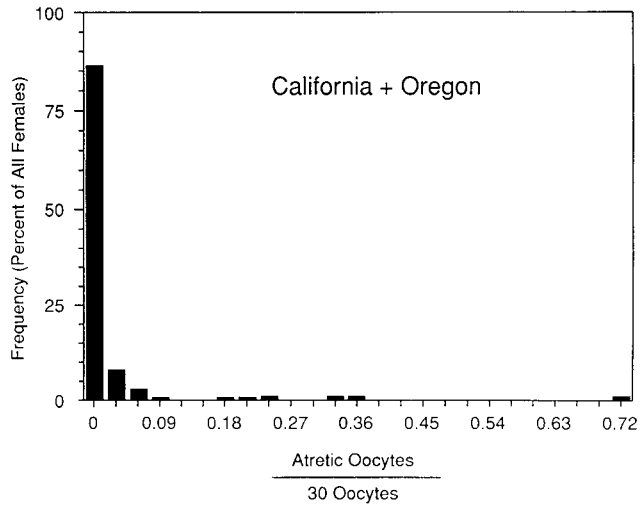

Figure 6. Percentage of sablefish (N = 236 females from California and Oregon) having various levels of atretic advanced-yolked oocytes (α stage), where the levels are the fraction of the 30 advanced-yolked oocytes that were atretic.

TABLE 5
Two Methods for Analyzing the Effect of Alpha-Stage Atresia of Advanced-Yolked Oocytes in Sablefish Collected off Central California and Oregon over the Spawning Season

Whole-Oocyte Method				
State	Percent of females with atretic advanced-yolked oocytes	Mean percent of yolked oocytes affected per female		Number females analyzed
		Mean	SD	
California	12.8	1.2	4.5	94
Oregon	14.8	1.8	7.8	142

Histological Method				
	Percent of females with various percentages of advanced-yolked oocytes affected by atresia (α)			Number females analyzed
	None	$0 < \alpha < 50\%$	$\alpha \geq 50\%$	
California	65.0	35.0	0.0	43
Oregon	70.5	23.0	6.5	139

logically in the ovaries of 35% of the California females and in 30% of the Oregon females (table 5). Highly atretic ovaries—ones in which 50% or more of the advanced-yolked oocytes were undergoing alpha-stage atresia—were rare. None of the ovaries from California sablefish were highly atretic, and only 6.5% of those from Oregon were classed as such (table 5).

In summary, a variety of evidence indicates that atretic losses of potential fecundity were low in sablefish. The standing stock of atretic oocytes was low regardless of the method of assessment; the low temperature of adult sablefish habitat (3–7°C; Hunter et al. 1989) would prolong the duration of α atresia, and no significant relation existed between fecundity and atresia when the whole-oocyte method was used. This conclusion must be tempered with the knowledge that inferring a rate from knowledge of only the standing stock is inherently risky.

Alpha atresia of the advanced oocytes was detected in about twice as many females when we used the histological method rather than the whole-oocyte method. The histological method was more sensitive because it allowed us to detect more subtle changes in oocyte structure and because we scanned about 150 oocytes per ovary, compared to 30 oocytes in the whole-oocyte method. Despite the lack of sensitivity, the anatomical method was valuable because it made it easy to compare the standing stock of atretic and nonatretic oocytes and to infer losses due to atresia.

Batch Fecundity and Spawning Frequency

Samples of sablefish females in Oregon were taken either too early in the spawning season (November–December 1988) or too late (February–March 1989) to capture many females with hydrated oocytes. Only two

TABLE 6
Relative Fecundity (Number of Advanced-Yolked Oocytes per Gram Female Weight, without Ovary) of 19 Sablefish with Hydrated Oocytes Taken off Central California and Oregon

Potential spawnings ≥2			Potential spawnings = 1		
Not hydrated	Hydrated	Total	Not hydrated	Hydrated	Total
72	34	106	0.64	44	45*
55	28	83	0.64	25	26*
39	50	89	0.09	10.3	10*
37	35	72	0.07	43	43*
37	29	66	0.03	0.72	0.75*
12	36	48	0	16	16*
12	36	48*	0	22	22*
8	48	56	0	29	29*
5	39	44*	0	6.0	6*
4	35	39*			
Mean relative hydrated batch fecundity	37.1			21.8	
SD	7.3			15.2	

*Postovulatory follicles present from previous spawning(s).
Females were separated into two classes: those likely to spawn two or more batches because, in addition to the hydrated batch, substantial numbers of advanced oocytes existed in the ovary; and those in which the hydrated oocytes may have been the last spawning batch because, other than the hydrated batch, few or no advanced oocytes existed in the ovary.

of the Oregon females with hydrated oocytes were suitable for batch fecundity estimates. We added the data for these two fish to that provided by Hunter et al. (1989) for California sablefish females and recomputed the estimates of relative batch fecundity. The results were similar to those in the original report: the last spawning batch was about 22 hydrated oocytes per gram of female weight, whereas the previous spawning batches averaged 37 oocytes/g (table 6). A t test showed significant difference in the means ($P = 0.019$, $t = 2.76$, d.f. = 11). Using the revised data of relative batch fecundity and our current estimate of potential annual fecundity for a 2.5 kg female (276,346 oocytes, or 110 oocytes/g female weight), we calculated that, on the average, a 2.5 kg female sablefish would be expected to spawn 3.37 times per year (3 spawnings would equal 96 oocytes/g [37 + 37 + 22]).

Maturity of Females

Maturity of sablefish females from off Oregon's coast was estimated from fish taken early in the spawning season (November–December 1988), when anatomical classification yields a reasonably accurate assessment of maturity. The percentage of mature sablefish females ($P \times 100$) as a function of fork length was estimated with the following logistic regression equation (BMDPLR, Dixon et al. 1988):

$$P = \frac{e^{a+bx}}{1+e^{a+bx}}$$

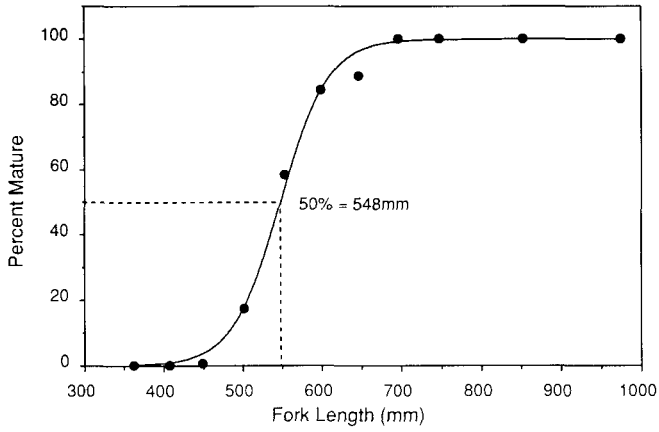

Figure 7. Percentage of mature sablefish (identified by active ovaries) within each 50 mm length class for females taken off Oregon in November–December 1988 (logistic curve parameters: $a = -18.072$; $b = 0.033$).

where x = fork length in mm; $a = -18.072$, SE(a) = 1.179, $t(a) = -15.32$; $b = 0.033$, SE(b) = 0.00214, $t(b) = 15.40$; and d.f. = 969; thus length at 50% mature was calculated as 548 mm FL with 95% CI of 546–592 mm (figure 7) for the sablefish taken off Oregon during November–December 1988. Our estimate of female length at 50% mature was about the same as the value of 55.3 cm estimated by Parks and Shaw (1987) for 569 female sablefish captured off Oregon and Washington early in the spawning season (August–September 1985).

We previously reported a value of 602 mm (Hunter et al. 1989) for sablefish taken off central California. The estimate was based on data from four or five observers using various multiple-stage anatomical criteria. By combining the stages differently, we obtained various values for the length at 50% mature ranging from 478 mm to 602 mm, depending on our interpretation of the criteria used to classify the ovaries (juvenile or early mature, spent or juvenile, immature or senescent). We believe a simple anatomical criterion (yolked oocytes visible) for maturity is preferable, with sampling being done just before the onset of the spawning season. These criteria were met by our estimate for Oregon sablefish, and thus we feel it is more reliable. The general issue of criteria for sexual maturity of females is discussed at length in Hunter et al. 1992.

ACKNOWLEDGMENTS

R. Dotson, E. Lynn, and W. Flerx collected samples on shipboard. All others who served on the scientific crews and the crews of NOAA ships *David Starr Jordan* and *Miller Freeman* contributed greatly to the success of the cruises. W. Kicklighter processed laboratory specimens and assisted with fecundity estimates. N. C. H. Lo gave considerable statistical advice. R. Allen improved the illustrations.

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APPENDIX

TABLE A

Position, Date, Mean Bottom Depth, and Time of Trawl for Each Survey Period

Coll. no.	Haul no.	Latitude Deg.	Latitude Minute N	Longitude Deg.	Longitude Minute W	Month	Day	Depth (fath.)	Time (hrs)
November–December 1988									
1228	1	44	08.85	124	56.47	11	28	106	0044
1229	2	44	08.84	124	58.08	11	28	186	0555
1230	3	44	08.58	124	59.12	11	28	230	1006
1231	4	44	07.91	125	00.13	11	28	322	1417
1232	5	44	06.43	125	01.45	11	28	447	2118
1233	6	44	11.26	125	01.83	11	29	558	0232
1234	7	44	06.71	125	03.27	11	29	660	0829
1235	8	44	19.35	125	06.70	11	29	662	1910
1236	9	44	20.63	125	04.62	11	30	583	0310
1237	10	44	19.85	125	02.07	11	30	458	0904
1238	11	44	18.58	124	59.17	11	30	373	1315
1239	12	44	18.31	124	54.71	11	30	262	2053
1240	13	44	17.11	124	53.77	12	1	121	0112
1241	14	44	26.19	124	45.23	12	1	106	0801
1242	15	44	27.45	124	49.47	12	1	180	1249
1243	16	44	27.03	124	51.59	12	1	211	1720
1244	17	44	27.02	124	57.22	12	1	365	2043
1245	18	44	24.71	125	03.00	12	2	445	0454
1246	19	44	25.53	125	04.51	12	2	529	0938
1247	20	44	25.25	125	06.67	12	2	673	1437
1248	21	44	36.04	125	03.20	12	3	673	0135
1249	22	44	35.83	125	00.02	12	3	531	1057
1250	23	44	35.67	124	57.65	12	3	456	1511
1251	24	44	38.40	124	54.31	12	3	350	2053
1252	25	44	38.78	124	52.53	12	4	236	0344
1253	26	44	35.16	124	48.39	12	4	193	0743
1254	27	44	36.09	124	46.51	12	4	186	1357
1255	28	44	44.45	124	38.21	12	4	146	2027
1256	29	44	46.29	124	44.38	12	5	194	0036
1257	30	44	44.06	124	46.69	12	5	227	0349
1258	31	44	41.58	124	55.84	12	5	353	0844
1259	32	44	44.86	124	59.66	12	5	477	1556
1260	33	44	46.00	125	00.49	12	5	523	2037
1261	34	44	42.50	125	04.16	12	6	650	0131
1262	35	44	59.16	125	02.12	12	6	635	1244
1263	36	44	55.16	125	02.37	12	6	535	2118
1264	37	44	54.22	124	59.01	12	7	463	0302
1265	38	44	55.79	124	54.91	12	7	354	0829
1266	39	44	54.40	124	53.12	12	7	230	1517

continued on next page

TABLE A (continued)
Position, Date, Mean Bottom Depth, and Time of Trawl for Each Survey Period

Coll. no.	Haul no.	Latitude		Longitude		Month	Day	Depth (fath.)	Time (hrs)
		Deg.	Minute N	Deg.	Minute W				
1267	40	44	53.75	124	47.81	12	7	150	2123
1268	41	44	54.31	124	33.64	12	8	216	0054
1269	42	44	54.61	124	28.75	12	8	140	0629
1270	43	45	03.63	124	21.32	12	8	129	1354
1271	44	45	02.67	124	26.14	12	8	173	1812
1272	45	45	03.64	124	30.91	12	8	207	2245
1273	46	45	03.28	124	33.82	12	9	220	0345
1274	47	45	03.99	124	49.35	12	9	355	0909
1275	48	45	02.00	124	52.54	12	9	422	1534
1276	49	45	00.66	125	02.17	12	9	563	2138
1277	50	45	05.60	125	00.15	12	10	615	0326
1278	51	45	09.30	125	01.64	12	10	682	1649
1279	52	45	13.99	124	56.56	12	11	543	0221
1280	53	45	10.28	124	56.86	12	11	462	0720
1281	54	45	12.11	124	46.18	12	11	353	1303
1282	55	45	11.09	124	39.84	12	11	293	1935
1283	56	45	11.64	124	35.37	12	11	222	2301
1284	57	45	12.12	124	27.05	12	12	224	0211
1285	58	45	12.70	124	21.00	12	12	186	0600
1286	59	45	22.04	124	23.67	12	12	157	1221
1287	60	45	20.01	124	26.92	12	12	212	1805
1288	61	45	21.00	124	37.48	12	12	232	2244
1289	62	45	21.75	124	46.11	12	13	313	0233
February–March 1989									
1298	1	44	07.64	124	54.54	2	21	93	0845
1299	2	44	10.52	124	59.19	2	21	176	1919
1300	3	44	09.46	124	58.47	2	22	229	2021
1301	4	44	10.10	125	00.80	2	23	350	0322
WH*	5	44	07.38	125	03.47	2	23	660	1805
WH	6	44	20.02	125	08.57	2	26	670	1048
WH	7	44	23.09	125	06.86	2	26	589	1912
WH	8	44	19.25	124	47.95	2	26	85	2355
1302	9	44	21.03	124	48.26	2	27	106	1203
WH	10	44	22.37	124	51.28	2	27	279	2003
WH	11	44	22.46	124	51.43	2	27	277	2219
1303	12	44	22.67	124	51.44	2	28	273	0037
WH	13	44	18.61	124	59.29	2	28	364	0806
1304	14	44	17.84	124	59.23	2	28	367	1026
1305	15	44	23.48	124	47.12	3	1	111	0729
1306	16	44	27.26	124	48.63	3	1	176	1231
1307	17	44	27.28	124	51.09	3	1	207	1845
WH	18	44	27.30	124	56.00	3	2	360	0135
1308	19	44	54.62	124	28.88	3	8	142	1607
1309	20	44	54.41	124	32.83	3	9	199	0013
1310	21	44	53.61	124	46.89	3	9	144	0632
1311	22	44	52.31	124	52.32	3	10	240	1626
WH	23	44	56.40	124	59.80	3	22	515	0055
1312	24	44	56.73	124	59.78	3	22	514	0415
1313	25	45	04.18	124	59.19	3	22	610	1756
1314	26	44	58.94	125	01.21	3	23	567	0200
1315	27	45	05.87	124	55.51	3	23	430	1018
WH	28	45	02.60	124	50.03	3	23	348	1638
1316	29	45	02.62	124	49.99	3	23	350	1855
1317	30	45	01.66	124	30.87	3	24	217	0109
1318	31	45	11.88	124	35.63	3	24	217	0436
1319	32	45	09.71	124	39.66	3	24	292	1005
1320	33	45	12.51	124	46.33	3	24	351	1809
1321	34	45	15.44	124	51.27	3	25	462	0202
1322	35	45	11.24	124	57.86	3	25	535	0934
1323	36	45	24.71	124	55.20	3	25	600	2123
1324	37	45	23.33	124	52.02	3	26	473	0632
1325	38	45	23.64	124	24.28	3	31	152	0011
1326	39	45	21.81	124	26.12	3	31	209	0720
1327	40	45	19.85	124	36.32	3	31	234	1708
1328	41	45	12.62	124	20.87	3	31	182	2355

*No collection number was assigned to waterhauls (WH) containing no fish.

TABLE B

Total Weight, Mean Fork Length, and Number of Sablefish Randomly Selected from Trawl Catches for Various Survey Periods in Oregon Coastal Waters

November–December 1988

			Males				Females							
							Inactive				Active			
	All specimens				Length (mm)				Length (mm)				Length (mm)	
Coll. no.	N	Weight (lb)	N	Weight (lb)	Mean	SD	N	Weight (lb)	Mean	SD	N	Weight (lb)	Mean	SD
1228	0	0.0	0	0.0	—	—	0	0.0	—	—	0	0.0	—	—
1229	1	1.2	1	1.2	388	—	0	0.0	—	—	0	0.0	—	—
1230	32	77.3	15	25.6	419	39	14	25.5	434	42	3	26.2	685	61
1231	94	353.3	70	260.5	519	54	13	35.4	490	44	11	57.4	576	73
1232	97	413.5	73	283.7	550	35	3	13.9	588	31	21	115.9	604	57
1233	25	120.9	16	67.2	568	47	0	0.0	—	—	9	53.7	624	43
1234	39	212.7	18	88.4	576	44	1	3.2	521	—	20	121.1	613	56
1235	9	54.1	4	21.2	584	30	0	0.0	—	—	5	32.9	638	47
1236	40	199.9	18	76.8	564	35	5	24.7	593	50	17	98.4	616	36
1237	74	289.5	57	207.3	550	35	6	23.7	557	33	11	58.5	605	58
1238	100	349.8	66	218.7	520	39	22	62.1	504	38	12	69.0	584	53
1239	100	163.1	62	104.0	426	26	38	59.1	422	28	0	0.0	—	—
1240	33	47.9	17	24.7	413	30	16	23.2	416	31	0	0.0	—	—
1241	0	0.0	0	0.0	—	—	0	0.0	—	—	0	0.0	—	—
1242	20	51.3	8	15.0	439	33	11	31.2	495	74	1	5.1	593	—
1243	71	148.0	35	57.4	429	30	32	66.9	448	52	4	23.7	618	36
1244	100	317.8	67	214.7	513	47	25	64.0	496	42	8	39.1	582	36
1245	64	241.4	52	181.7	533	35	1	2.6	515	—	11	57.1	595	54
1246	71	271.6	46	156.8	528	29	6	18.8	521	22	19	96.0	585	49
1247	29	149.2	12	60.0	589	59	0	0.0	—	—	17	89.2	593	40
1248	41	185.8	20	79.8	549	37	1	2.9	528	—	20	103.1	586	34
1249	69	288.8	48	179.5	546	35	5	22.7	577	56	16	86.6	598	56
1250	100	256.0	77	143.5	541	28	6	22.4	555	6	17	90.1	595	58
1251	90	325.1	70	238.3	529	38	9	25.4	502	56	11	61.4	604	48
1252	25	59.3	10	18.3	438	44	14	31.1	462	48	1	9.9	716	—
1253	4	9.9	2	4.1	458	52	2	5.8	517	54	0	0.0	—	—
1254	7	32.7	1	2.3	474	—	3	7.0	484	57	3	23.4	652	71
1255	50	82.8	23	35.1	416	29	26	39.0	422	28	1	8.7	675	—
1256	4	28.0	0	0.0	—	—	2	3.0	412	6	2	25.0	746	149
1257	20	114.0	7	30.9	537	133	5	13.9	496	73	8	69.2	689	45
1258	100*	352.2	83	288.9	528	37	11	34.0	522	27	6	29.3	573	73
1259	68	264.0	48	171.9	542	39	4	13.8	542	68	16	78.3	590	59
1260	25	107.8	19	76.0	553	32	2	9.1	579	92	4	22.7	629	78
1261	59	290.4	32	124.6	553	46	3	14.3	584	35	24	151.5	628	60
1262	65	348.6	40	189.5	582	45	1	2.3	457	—	24	156.8	637	67
1263	21	80.0	18	66.5	544	30	0	0.0	—	—	3	13.5	573	25
1264	100	344.9	87	291.3	529	36	3	10.4	546	59	10	43.2	572	43
1265	78	270.9	60	197.5	524	43	12	32.7	496	50	6	40.7	639	63
1266	36	150.7	26	100.8	546	39	5	15.8	522	56	5	34.1	630	63
1267	10	23.7	5	7.6	419	20	4	8.5	459	70	1	7.6	632	—
1268	100	288.3	42	66.3	419	32	46	134.7	497	74	12	87.3	637	44
1269	1	1.6	1	1.6	427	—	0	0.0	—	—	0	0.0	—	—
1270	5	6.4	1	1.0	377	—	4	5.4	404	34	0	0.0	—	—
1271	7	13.4	5	7.5	413	14	2	5.9	506	112	0	0.0	—	—
1272	9	17.8	5	8.9	438	23	4	8.9	465	87	0	0.0	—	—
1273	24	52.6	10	16.0	422	30	13	31.1	475	62	1	5.5	592	—
1274	100	303.0	80	243.5	511	39	18	49.4	500	28	2	10.1	602	9
1275	100	333.7	89	281.9	519	28	0	0.0	—	—	11	51.8	581	61
1276	26	114.7	17	66.5	556	36	1	6.1	630	—	8	42.1	595	43
1277	21	98.6	12	48.1	560	47	2	8.8	570	44	7	41.7	620	34
1278	7	39.6	2	13.2	668	42	0	0.0	—	—	5	26.4	584	26
1279	100	394.3	70	264.2	541	40	2	6.7	540	14	28	123.4	568	55
1280	80	289.1	61	207.8	526	30	6	21.7	538	29	13	59.6	576	52
1281	88	300.4	65	220.2	530	40	16	46.3	509	36	7	33.9	576	44
1282	63	166.2	34	78.8	468	44	24	55.4	470	43	5	32.0	619	60
1283	11	19.2	8	13.2	433	26	3	6.0	456	10	0	0.0	—	—
1284	2	3.6	1	1.8	450	—	1	1.8	443	—	0	0.0	—	—
1285	8	23.9	3	6.1	452	32	5	17.8	525	93	0	0.0	—	—
1286	34	76.3	14	44.3	418	22	20	32.0	412	30	0	0.0	—	—

*In addition, a nonrandom active female of 974 mm and 25.6 lbs was sampled.

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TABLE B (continued)
Total Weight, Mean Fork Length, and Number of Sablefish Randomly Selected from Trawl Catches for Various Survey Periods in Oregon Coastal Waters

November–December 1988														
							Females							
			Males				Inactive				Active			
	All specimens				Length (mm)				Length (mm)				Length (mm)	
Coll. no.	N	Weight (lb)	N	Weight (lb)	Mean	SD	N	Weight (lb)	Mean	SD	N	Weight (lb)	Mean	SD
1287	12	33.9	3	4.2	403	13	8	24.9	509	79	1	4.8	585	—
1288	27	91.8	11	28.3	489	37	11	29.1	486	64	5	34.4	640	48
1289	100	240.8	78	188.8	479	40	22	52.0	482	32	0	0.0	—	—
February–March 1989														
1298	5	3.1	4	2.5	315	7	1	0.6	323	—	0	—	—	—
1299	0	0.0	0	—	—	—	0	—	—	—	0	—	—	—
1300	12	17.6	7	9.2	409	29	5	8.4	441	25	0	—	—	—
1301	1	1.6	1	1.6	443	—	0	—	—	—	0	—	—	—
1302	8	4.8	3	1.7	315	—	5	3.1	320	16	0	—	—	—
1303	100	144.1	50	67.7	405	21	50	76.4	416	34	0	—	—	—
1304	0	0.0	0	—	—	—	0	—	—	—	0	—	—	—
1305	17	10.3	9	5.0	314	12	8	5.3	323	42	0	—	—	—
1306	100	134.0	47	58.2	397	28	53	75.8	406	26	0	—	—	—
1307	51	73.6	21	29.7	416	24	30	43.9	420	25	0	—	—	—
1308	7	7.1	4	3.6	345	55	3	3.5	397	8	0	—	—	—
1309	5	14.8	2	3.7	449	11	3	11.1	519	167	0	—	—	—
1310	98	152.9	41	59.3	416	19	57	93.6	433	31	0	—	—	—
1311	4	9.9	2	4.6	487	7	2	5.3	505	4	0	—	—	—
1312	69	242.8	44	136.7	524	30	24	100.7	575	46	1	5.4	597	—
1313	27	114.3	23	96.2	574	40	3	12.7	579	27	1	5.4	633	—
1314	50	186.6	45	151.7	542	36	5	34.9	670	57	0	—	—	—
1315	64	197.6	56	167.5	517	32	8	30.1	550	66	0	—	—	—
1316	15	56.5	11	37.8	536	50	4	18.7	563	31	0	—	—	—
1317	3	9.5	1	1.9	455	—	2	7.6	558	36	0	—	—	—
1318	2	3.4	2	3.4	438	5	0	—	—	—	0	—	—	—
1319	27	95.8	10	31.4	518	64	17	64.4	545	91	0	—	—	—
1320	15	53.0	11	38.8	538	74	4	14.2	550	29	0	—	—	—
1321	14	56.5	6	23.4	550	36	8	33.1	575	38	0	—	—	—
1322	45	149.5	38	115.0	524	29	7	34.5	584	59	0	—	—	—
1323	100†	324.7	93	293.1	527	29	6	26.9	588	33	1	4.7	531	—
1324	58	167.1	53	150.1	513	28	5	17.0	537	28	0	—	—	—
1325	6	5.6	3	2.9	379	50	3	2.7	363	37	0	—	—	—
1326	3	4.3	3	4.3	420	39	0	—	—	—	0	—	—	—
1327	12	40.6	4	14.7	545	8	8	25.9	522	69	0	—	—	—
1328	2	3.0	1	1.5	423	—	1	1.5	420	—	0	—	—	—

†More than 100 sampled; only first 100 used for analyses.

TABLE C

Standing Stock of Oocytes in Sablefish Ovaries in Order of Female Weight (without Ovary) within a Survey Period

November–December 1988

Coll. no.	Fish no.	Wet weight (g)	Fork length (mm)	Ovary weight (g)	Standing stock of advanced oocytes	Advanced oocyte diameter (mm)	
						Mean	SD
1280	204	1281.76	487	92.24	57422	1.21	0.038
1279	204	1323.53	512	57.47	49471	1.18	0.048
1260	204	1349.37	545	87.63	117804	0.97	0.048
1237	205	1371.28	523	91.72	144697	1.00	0.073
1263	216	1468.54	545	155.46	145643	1.21	0.041
1251	201	1489.89	544	59.11	92182	0.95	0.031
1266	201	1511.53	536	68.47	92065	1.04	0.064
1233	202	1513.58	547	155.42	129306	1.28	0.056
1264	219	1517.28	543	114.72	105521	1.10	0.063
1231	202	1541.83	520	80.17	151302	0.84	0.055
1258	241	1591.68	521	141.32	130273	1.22	0.034
1232	207	1595.43	539	132.57	106757	1.26	0.049
1261	201	1703.67	560	144.33	142350	1.24	0.059
1244	252	1725.52	555	173.48	216567	1.09	0.040
1280	220	1745.19	550	122.81	109741	1.18	0.045
1258	252	1751.94	565	173.06	161527	1.19	0.039
1265	222	1762.75	554	187.25	153742	1.25	0.043
1248	206	1768.08	555	122.92	196335	0.96	0.053
1288	213	1806.32	577	111.68	258684	0.92	0.069
1281	239	1825.92	558	189.08	195681	1.12	0.050
1264	218	1846.90	550	148.10	150581	1.12	0.035
1278	203	1852.65	552	124.35	135561	1.07	0.034
1274	204	1858.71	595	151.29	153408	1.16	0.048
1248	202	1886.68	573	63.32	132565	0.89	0.069
1244	223	1890.82	588	185.18	181299	1.18	0.057
1277	209	1894.19	555	130.81	149456	1.09	0.048
1279	208	1905.16	565	165.84	142007	1.17	0.032
1245	203	1906.26	570	133.74	130913	1.21	0.051
1280	205	1959.11	567	153.89	142173	1.19	0.034
1276	201	1963.82	584	192.18	198220	1.13	0.052
1259	202	1964.25	557	112.75	136680	0.97	0.140
1250	206	1995.50	576	211.50	172573	1.24	0.044
1263	218	2017.33	580	181.67	159706	1.26	0.033
1279	202	2022.19	583	130.81	147292	1.06	0.051
1250	204	2029.13	608	198.87	174518	1.16	0.051
1234	203	2029.58	565	160.42	130089	1.10	0.039
1275	218	2042.14	613	124.86	194514	1.04	0.040
1262	202	2042.19	575	116.81	166726	0.98	0.053
1282	225	2057.95	573	135.05	277740	0.92	0.107
1235	204	2068.24	576	198.76	230776	1.10	0.042
1245	202	2081.06	596	148.94	233221	1.01	0.060
1263	210	2085.23	594	218.77	157134	1.31	0.049
1264	207	2089.65	586	179.35	215439	1.04	0.041
1281	253	2098.97	593	218.03	281991	1.03	0.055
1244	235	2099.10	598	186.90	164364	1.20	0.042
1236	201	2106.61	584	163.39	143125	1.21	0.054
1246	204	2119.68	587	192.32	186391	1.11	0.040
1287	205	2120.01	585	71.99	243002	0.74	0.053
1238	210	2133.29	559	101.71	287712	0.82	0.051
1276	202	2157.18	562	189.82	146655	1.31	0.041
1275	217	2162.02	593	162.98	153656	1.12	0.045
1247	204	2201.51	598	207.49	255574	1.02	0.046
1242	209	2206.81	593	131.19	128330	0.95	0.040
1243	201	2211.62	572	74.38	227696	0.81	0.060
1278	206	2212.66	582	130.34	122464	1.17	0.049
1238	204	2223.98	564	138.02	146224	1.09	0.034
1259	207	2245.32	588	147.68	216796	1.07	0.051
1234	204	2271.62	590	202.38	266856	1.12	0.048
1261	203	2275.66	606	182.34	200147	1.09	0.039
1235	202	2280.98	641	226.02	268166	1.07	0.049
1258	208	2288.17	582	191.83	281858	1.04	0.042
1273	224	2323.67	592	186.33	326963	0.94	0.046
1288	206	2335.00	611	106.00	275506	0.88	0.070

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TABLE C (continued)
Standing Stock of Oocytes in Sablefish Ovaries in Order of Female Weight (without Ovary) within a Survey Period

November–December 1988

Coll. no.	Fish no.	Wet weight (g)	Fork length (mm)	Ovary weight (g)	Standing stock of advanced oocytes	Advanced oocyte diameter (mm)	
						Mean	SD
1278	201	2346.13	590	214.87	178505	1.12	0.034
1276	203	2346.21	632	163.79	248286	1.01	0.047
1236	204	2373.81	593	180.19	173997	1.18	0.055
1277	201	2392.96	611	289.04	236958	1.20	0.035
1274	278	2401.78	608	192.22	189929	1.17	0.039
1230	232	2402.10	623	76.90	172461	0.81	0.078
1266	217	2428.17	611	141.83	316590	0.84	0.058
1268	227	2432.21	637	175.79	350705	0.97	0.054
1243	208	2460.65	613	145.35	291572	0.97	0.061
1254	206	2477.19	612	239.81	320185	1.10	0.043
1232	204	2485.08	603	194.92	185176	1.15	0.039
1247	202	2572.86	630	254.14	173382	1.29	0.043
1248	201	2575.78	616	209.22	245790	1.05	0.040
1237	210	2637.80	633	244.20	243895	1.12	0.034
1237	208	2712.98	637	263.02	258215	1.21	0.042
1249	205	2716.93	668	228.07	205498	1.15	0.048
1250	205	2717.68	640	166.32	150693	1.20	0.065
1254	202	2717.94	610	180.06	260752	1.01	0.029
1246	216	2718.75	630	170.25	194841	1.06	0.072
1265	207	2757.15	659	184.85	309520	0.93	0.067
1288	205	2802.49	655	313.51	454950	1.03	0.057
1259	201	2813.62	663	183.38	238025	1.03	0.056
1268	219	2856.00	630	225.00	268702	1.07	0.035
1260	201	2877.27	690	236.73	298836	1.01	0.048
1251	205	2940.82	652	216.18	407804	0.89	0.075
1256	201	2971.33	641	133.67	371095	0.82	0.068
1277	202	3000.63	658	274.37	177216	1.38	0.035
1233	206	3026.84	669	277.16	283363	1.18	0.033
1243	218	3044.41	659	100.59	294290	0.82	0.080
1233	203	3057.59	647	237.41	243932	1.14	0.098
1238	206	3062.41	663	319.59	518580	1.12	0.039
1262	210	3148.31	659	243.69	310222	1.02	0.046
1249	217	3164.58	647	360.42	391366	1.19	0.043
1267	210	3172.94	632	291.06	523498	1.00	0.056
1231	213	3197.41	662	104.59	185875	0.96	0.044
1247	205	3227.66	647	297.34	256887	1.25	0.047
1282	205	3250.71	678	277.29	247440	1.21	0.040
1260	215	3256.73	701	265.27	328736	1.07	0.044
1231	205	3292.98	691	275.02	421292	1.03	0.052
1275	220	3355.37	673	236.63	229323	1.20	0.049
1282	213	3382.20	674	414.80	686743	1.00	0.082
1265	208	3394.10	701	558.90	492978	1.19	0.043
1245	201	3410.57	703	315.43	346096	1.13	0.089
1255	207	3525.60	675	429.40	534972	1.08	0.038
1251	209	3558.50	692	516.50	557040	1.14	0.057
1235	203	3567.94	683	307.06	316702	1.12	0.047
1257	204	3610.60	692	585.40	622620	1.13	0.061
1266	206	3621.30	683	558.70	552828	1.21	0.043
1230	203	3690.50	686	530.50	563099	1.17	0.042
1257	203	3760.59	736	359.41	482601	1.11	0.057
1257	220	3963.00	722	547.00	552886	1.19	0.047
1249	206	4131.28	723	233.72	262975	1.08	0.043
1234	201	4159.47	717	223.53	174829	1.21	0.044
1252	213	4176.93	716	313.07	506350	0.99	0.043
1261	204	4185.30	745	330.70	346537	1.14	0.062
1268	231	4275.81	706	303.19	559389	0.99	0.079
1254	203	4456.20	734	537.80	764413	1.00	0.089
1257	205	4507.70	755	710.30	686548	1.23	0.064
1232	206	4667.40	757	405.60	451441	1.09	0.148
1230	208	4693.80	745	517.20	599378	1.05	0.068
1250	220	5093.80	774	598.20	647755	1.18	0.122
1256	204	7303.40	852	947.60	1213591	1.03	0.059
1258	301	9486.60	974	1676.40	1438854	1.28	0.053

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TABLE C (continued)
Standing Stock of Oocytes in Sablefish Ovaries in Order of Collection Number within the Survey Period

February–March 1989

Coll. no.	Fish no.	Wet weight (g)	Fork length (mm)	Ovary weight (g)	Standing stock oocytes			Advanced oocyte diameter (mm)	
					Yolked	Hydrated	Total	Mean	SD
1312	214	2169.27	597	262.730	177724	0.0	177724	1.33	0.040
1312	225*	1794.70	581	50.302	0	1230.7	1231	0.00	0.000
1312	240	2491.29	662	55.709	81	1792.7	1874	0.00	0.000
1313	225*	2396.34	633	53.655	352	286.5	638	1.23	0.044
1313	226*	1977.61	587	43.391	151	1295.6	1446	1.24	0.047
1315	214*	1436.52	532	23.485	0	173.8	174	0.00	0.000
1315	225*	1146.24	487	31.759	0	240.2	240	0.00	0.000
1315	226*	1622.54	532	16.460	296	573.6	870	0.99	0.082
1321	201*	2645.97	640	48.035	24	23.7	47	0.00	0.000
1321	203*	1301.38	532	21.618	0	63.8	64	0.00	0.000
1321	214*	1483.67	549	31.334	553	46.7	599	1.67	0.210
1323	270	1683.80	531	439.200	92657	46400.2	139057	1.45	0.041

*These females with ovaries containing hydrated oocytes were not used for batch fecundity analyses because the ovaries showed histological evidence of new postovulatory follicles, which indicated that some hydrated oocytes had been lost to spawning.

THE DISTRIBUTION OF PELAGIC JUVENILE ROCKFISH OF THE GENUS *SEBASTES* IN THE UPWELLING REGION OFF CENTRAL CALIFORNIA

RALPH J. LARSON
Department of Biology
San Francisco State University
San Francisco, California 94132

WILLIAM H. LENARZ AND STEPHEN RALSTON
National Marine Fisheries Service
3150 Paradise Drive
Tiburon, California 94920

ABSTRACT

Many species of central California rockfishes conclude their pelagic stage during the spring–summer upwelling period, when advection of surface waters could carry them away from nearshore postpelagic habitats. We examined the distributions of late-stage pelagic juvenile rockfish in April and May/June of 1987 and 1988, based on midwater-trawl surveys between Point Reyes and Monterey Bay, California. Distributional patterns were complex, and changed rapidly with changing oceanographic conditions and with changes in species and size composition. The smallest pelagic juveniles often appeared offshore, in the region of the upwelling front, which suggested that they had been advected offshore at some time during upwelling. However, few pelagic juveniles were found offshore of the upwelling front. Larger pelagic juveniles were often found close to shore, even when upwelling was active. This suggests that later-stage pelagic juveniles undergo behavioral changes that enable them to move toward shore or remain there in spite of upwelling. We also found evidence of more passive advection and retention of pelagic juveniles of all sizes, including onshore movement during relaxation of upwelling. It appears that relaxation of upwelling may be a sufficient but not necessary aspect of the settlement of juvenile rockfish from pelagic to postpelagic habitats. If so, advection during upwelling may not have a negative effect on the settlement and ultimate recruitment of rockfish.

RESUMEN

Muchas especies de rocot del centro de California concluyen su estadio pelágico durante el periodo de surgencias de primavera–verano, cuando la advección de las aguas superficiales podría transportarlos lejos de los hábitats post-pelágicos cercanos a la costa. Examinamos los patrones de distribución de los estadios tardíos de los juveniles pelágicos de los rocot durante abril y mayo/junio de 1987 y 1988. Los ejemplares fueron obtenidos por medio de arrastres a media agua en un área comprendida entre Punta Reyes y la Bahía de Monterey, California. Los patrones de distribución encontrados fueron complejos y cambiaron rápidamente de acuerdo a las condiciones oceanográficas y de acuerdo a cambios en la composición por especies y tallas. Los juveniles pelágicos mas pequeños se encontraron a menudo alejados de la costa, en la región asociada al frente de la surgencia, lo que sugiere que fueron transportados por la corriente de surgencia. Sin embargo, pocos juveniles pelágicos fueron encontrados del lado hacia mar adentro del frente de la surgencia. Los juveniles pelágicos de mayor tamaño se encontraron a menudo próximos a la costa, aun en los periodos de actividad de la surgencia. Lo anterior sugiere que los juveniles pelágicos cambian su comportamiento durante sus fases tardías, lo que les permite desplazarse hacia la costa, o bien, permanecer allí a pesar de la surgencia. Asimismo encontramos evidencia de un proceso mas pasivo de advección y retención de juveniles pelágicos de todas las tallas, incluyendo movimiento hacia la costa durante periodos de aflojamiento de la surgencia. Este aflojamiento podría ser un aspecto importante pero no determinante para el establecimiento de los juveniles del rocot del hábitat pelágico al post-pelágico. En tal caso, la advección durante la surgencia podría no tener un efecto negativo en el asentamiento y reclutamiento final del rocot.

INTRODUCTION

The problems of drift and retention in marine animals with pelagic larval stages are widely recognized (e.g., Norcross and Shaw 1984; Bakun 1985, 1986; Sinclair 1988). To complete their life cycles, pelagic individuals must either remain in areas suitable for the next stage in the life cycle, or travel from the pelagic zone to these areas. Coastal upwelling systems pose a particular problem in this respect, since surface waters are transported offshore, possibly carrying propagules away from the areas inhabited by postpelagic juveniles. Parrish et al. (1981), Bakun and Parrish (1982), and Bakun (1985) suggested that the potential for offshore advection of larvae has selected for reproductive patterns that minimize the exposure of larvae to upwelling conditions, and Roughgarden et al. (1988) described the negative effect of offshore advection in barnacles.

Dozens of species of rockfish in the genus *Sebastes* inhabit the shelf and coastal zones in the region of maximum upwelling between Cape Blanco, Oregon, and Point Conception, California (Chen 1971). Many of these species bear young in winter and early spring, before upwelling begins (Kendall and Lenarz 1987; Wyllie

[Manuscript received January 22, 1994.]

Echeverria 1987). However, the larvae and juveniles of many species remain pelagic well into the spring–summer upwelling period (Kendall and Lenarz 1987; Moser and Boehlert 1991), so that juveniles of these species must settle from the pelagic zone when upwelling is active (Anderson 1983; Carr 1983, 1991). Thus, while viviparity and winter spawning in rockfishes could be seen as adaptations to the negative effects of offshore advection during upwelling (Parrish et al. 1981; Ainley et al. 1993), the late pelagic stages of many rockfish are exposed to upwelling at the time they settle. If this offshore advection does affect rockfish, spatial and temporal variation in upwelling could have important effects on both year-class strength and the geographical structure of rockfish populations.

Some evidence suggests that upwelling does have an advective effect on pelagic-stage rockfish. Moser and Boehlert (1991) noted the offshore distribution of some *Sebastes* larvae, and their figures indicate relatively greater offshore distributions off northern California, where seaward jets are common. Simpson (1987) also illustrated the offshore distribution of *Sebastes* larvae in a filament of advected water associated with an offshore eddy. Brodeur et al. (1985) found *Sebastes* larvae unusually close to shore during the El Niño spring of 1983, but much farther offshore soon after an upwelling event later that summer. Hobson and Howard (1989) found that mass strandings of juvenile shortbelly rockfish near shore in northern California were correlated with onshore transport, suggesting that the usual offshore distributions were maintained by normal offshore transport. Finally, Norton (1987) has suggested that year-class strength of widow rockfish is correlated with onshore transport, and Ainley et al. (1993) found that year-class strength in the suite of species found off central California (dominated by shortbelly rockfish) was affected negatively by strong upwelling in January–February.

In this paper we examine the distribution of late-stage pelagic juvenile rockfishes off central California. Our purpose is to infer the effects of upwelling on these fish by comparing their distributions with oceanographic features associated with upwelling.

BACKGROUND

Species

The species of *Sebastes* covered in this study extrude larvae a few millimeters long in areas ranging from coastal kelp forests to the edge of the continental shelf. Most of the central California species release larvae between November and March, but the principal period of parturition varies among species, and some species have extended periods of parturition (Wyllie Echeverria 1987).

At least several species of *Sebastes* are pelagic for 3–5 months, and appear to grow at a rate of about 0.5 mm per day (Woodbury and Ralston 1991). They transform into pelagic juveniles at least 20 mm long before leaving the pelagic zone for juvenile habitats. The juvenile habitats vary among species at several scales (Love et al. 1991). Species of *Sebastes* commonly leave the pelagic zone for habitats that are shallower than those occupied by adults, often recruiting to areas quite near shore (Love et al. 1991). Observations by divers demonstrate that nearshore species show considerable specialization of microhabitats (Carr 1983, 1991; Love et al. 1991). Some deepwater species make extensive surface-to-bottom migrations (Boehlert 1977); these species were not commonly encountered as pelagic juveniles in this study. Although many species clearly leave the pelagic zone for association with the benthos, the distinction between pelagic and benthic habitat may be less clear in species such as shortbelly and chilipepper rockfish, whose postpelagic juveniles and adults form schools that associate more loosely with the bottom. Nevertheless, these species become invulnerable to midwater trawls, presumably by shifting habitat. Essentially all of the species covered in this study settle from the pelagic zone to more benthic habitats that are shoreward of their pelagic distributions.

Several aspects of the ecology of pelagic juveniles vary among species. The timing and duration of parturition, along with the duration of the pelagic stage, influence the timing and duration of their appearance as pelagic juveniles in midwater trawls and their recruitment to postpelagic habitats. A preliminary overview of the seasonal occurrence of pelagic and newly settled juveniles of species encountered frequently in our study is presented in table 1. Some species are taken in midwater trawls for limited periods; others are taken over longer periods of time. The peak seasonal occurrence of pelagic juveniles varies by a month or more from year to year.

The size of pelagic juveniles also varies among species (appendix), and the relative sizes of pelagic and settled individuals are concordant (comparing data in the appendix with Anderson 1983). Data in the appendix also show that some species are present in relatively small ranges of size while others have wider size ranges as pelagic juveniles. Because size may itself be significant in the movements of pelagic juveniles or because size may be a proxy for age and ontogeny (Woodbury and Ralston 1991), we divided the size range of each species into categories (table 2). The categories were based upon the range of sizes present and the abundance of the species. Some species were too uncommon for division into size groups, and others were common enough for only two size classes. Abundant species were typically divided into three size classes, in hopes of distinguishing distributional characteristics at the extremes of size

TABLE 1
Summary of the Relative Seasonal Occurrence of Pelagic and Newly Settled Young-of-the-Year Juvenile Rockfish off Central California

	Relative duration of occurrence		
Relative peak in occurrence	Brief	Extended	Variable or not assessable
Early (April)	Pygmy		
	Copper[a]		
		Chilipepper	
	Stripetail		
		Canary	
		Shortbelly	
			Darkblotched
Intermediate (May–early June)	Blue		
	Squarespot		
			Cowcod
		Bocaccio	
	Widow		
			Black
	Yellowtail		
Late (June or later)			"Copper complex"[b] "Rosy complex"[c]
Variable or not assessable			Brown

[a]Members of the "copper complex" (a group of species that are difficult to distinguish as pelagic juveniles) that occur early in the season are most likely copper rockfish (*S. caurinus*), which appear in kelp forests the earliest of similar-appearing species (Anderson 1983).
[b]Members of the "copper complex" occurring later in spring are probably gopher rockfish (*S. carnatus*), black and yellow rockfish (*S. chrysomelas*), or kelp rockfish (*S. atrovirens*), which settle in kelp forests in June through August (Anderson 1983).
[c]The "rosy complex" contains members of the subgenus *Sebastomus*.

and age. For the analysis of distributions in any particular set of samples, size classes may have been pooled, based on abundance (see below).

Different species of *Sebastes* also have different depth distributions as pelagic juveniles (Lenarz et al. 1991). Bocaccio are found shallower than most other species, and yellowtail, blue, and pygmy rockfish are found deeper.

Physical System

Our study area, from Point Reyes to Monterey Bay (figure 1), is oceanographically complex. During the spring–summer period, when rockfish are completing their pelagic phase, episodic northwesterly winds lead to pulses of upwelling on a scale of days. Two centers of upwelling are located within the region: a strong upwelling center at Point Reyes, and a weaker center north of Monterey Bay, off Davenport (Schwing et al. 1991). Filaments of upwelled water from these centers carry cool water offshore and to the south, and the edges of these filaments are often marked by strong frontal regions (Schwing et al. 1991). The filaments and associated fronts are frequently associated with eddies and meanders. These eddies and meanders serve to mix upwelled water with offshore water and with older mixes of upwelled and offshore waters. Freshwater outflow from San Francisco Bay enters the Gulf of the Farallons and often extends to the south. Monterey Bay frequently contains upwelled water from the Davenport upwelling center, warmed as it recirculates. Cessation of northwesterly winds leads to relaxation of upwelling, accompanied by onshore movement of offshore waters and further mixing of upwelled and other waters. Changes in circulation take place on a scale of days to weeks.

METHODS

Field

This study is based on data gathered in cruises on the R/V *David Starr Jordan* off central California during 1987 and 1988. Part of a long-term survey, these cruises sampled pelagic juvenile rockfish with a midwater trawl and gathered hydrographic data. Pelagic juveniles of many species of rockfish were relatively abundant in these years.

Fish were sampled at night with a modified Cobb midwater trawl (nominally square mouth 14 m on a side, and 9.5 mm stretched mesh cod-end liner) which was towed at depth for 15 min. at 5 kmh^{-1} (Wyllie Echeverria et al. 1990). The typical targeted depths were 37 m at most stations and 13 m at bottom depths shallower than 91 m (figure 1). Hauls at some stations were carried out at two or more depths, usually selected from 13, 37, and 117 m. The usual sampling plan was to cover a standard set of stations within a 10-night "sweep," and to sample additional sites if time permitted within the 10-day period. Typical standard stations and some extra stations are illustrated in figure 1. In 1987 and 1988, cruises were carried out in April and again in May–June. One sweep of the study area was carried out in April, and three sweeps were carried out in May–June (table 3). Rockfish and other animals were identified and enumerated, and the standard length of all rockfish or a 100-fish subsample of each species was measured.

Two sets of hydrographic data were gathered. CTD casts were made with a Sea-Bird Electronics SEA-CAT-SBE-19 profiler at each trawl station and at sets of locations interspersed between trawl stations. Raw temperature and conductivity data were processed to remove outliers and were smoothed; salinity and density were computed and then smoothed, as described in Schwing et al. (1990).

Near-surface temperature and salinity were also recorded on a 5–15 min. basis continuously during most of each cruise. Ideally, the shipboard thermosalinograph continuously measured temperature and salinity of water drawn from a through-hull connection, and the ship computer's CAMAC system periodically captured these data and information on location and other variables. When totally operational, this system provided data on

TABLE 2

Definitions of Size Classes, and the Mean Sizes, Number of Areas Occupied, and Mean Abundances of Pelagic Juvenile Rockfish (Genus *Sebastes*) Captured in Midwater Trawls, 1987–1988

		APRIL 1987			JUNE 1987									APRIL 1988			JUNE 1988					
					SWEEP 1[a]			SWEEP 2			SWEEP 3						SWEEP 1			SWEEP 2		
Species	Size Class[b] (range)	Mean SL[c]	No. of areas[d]	Mean abund. (SD)[e]	Mean SL	No. of areas	Mean abund. (SD)	Mean SL	No. of areas	Mean abund. (SD)	Mean SL	No. of areas	Mean abund. SD	Mean SL	No. of areas	Mean abund. (SD)	Mean SL	No. of areas	Mean abund. (SD)	Mean SL	No. of areas	Mean abund. (SD)
Black rockfish	All	—	—	—	40.3	5	0.117	37.3	7	0.187	34.3	4	0.099	—	—	—	—	—	—	—	—	—
S. melanops (BLK)							(0.166)			(0.308)			(0.186)									
Blue rockfish	S+M	38.9	4	0.093	—	—	—	—	—	—	—	—	—	41.6	10	0.870	—	—	—	—	—	—
S. mystinus (BLUE)	(<54.5)			(0.159)												(0.567)						
	Medium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48.3	14	1.450	—	—	—
	(31–54)																		(1.102)			
	M+L	—	—	—	48.7	13	1.062	49.8	13	0.773	—	—	—	—	—	—	—	—	—	48.2	10	0.905
	(>30.5)						(0.501)			(0.835)												(1.005)
Brown rockfish	All	23.0	8	0.271	—	—	—	—	—	—	—	—	—	24.4	5	0.288	—	—	—	—	—	—
S. auriculatus (BRWN)				(0.303)												(0.365)						
Bocaccio	Small	—	—	—	—	—	—	28.7	5	0.164	26.4	5	0.215	31.8	5	0.152	—	—	—	—	—	—
S. paucispinus (BOC)	(<35.5)									(0.345)			(0.318)			(0.200)						
	S+M	42.6	4	0.249	43.1	4	0.147	—	—	—	—	—	—	—	—	—	45.4	9	0.454	—	—	—
	(<60.5)			(0.478)			(0.253)												(0.462)			
	Medium	—	—	—	—	—	—	44.0	9	0.286	—	—	—	—	—	—	—	—	—	—	—	—
	(36–60)									(0.420)												
	M+L	—	—	—	—	—	—	—	—	—	—	—	—	56.5	8	0.418	—	—	—	77.0	5	0.230
	(>35.5)															(0.371)						(0.398)
	Large	—	—	—	71.6	8	0.266	77.5	4	0.136	—	—	—	—	—	—	83.2	4	0.090	—	—	—
	(>60.5)						(0.348)			(0.281)									(0.193)			
Canary rockfish	Small	—	—	—	26.6	6	0.147	26.0	11	0.287	—	—	—	23.9	5	0.278	30.2	8	0.321	28.1	5	0.227
S. pinniger (CAN)	(<32.5)						(0.195)			(0.283)						(0.414)			(0.422)			(0.412)
	All	24.7	8	0.307	—	—	—	—	—	—	29.1	7	0.227	—	—	—	—	—	—	—	—	—
				(0.369)									(0.304)									
	Large	—	—	—	36.3	4	0.100	35.4	4	0.164	—	—	—	—	—	—	36.3	10	0.893	38.4	5	0.286
	(>32.5)						(0.185)			(0.336)									(1.028)			(0.595)
Chilipepper	Small	32.1	6	1.025	—	—	—	—	—	—	—	—	—	32.4	11	1.945	—	—	—	—	—	—
S. goodei (CHILI)	(<35.5)			(1.335)												(1.184)						
	S+M	—	—	—	53.0	12	1.071	53.7	6	0.253	—	—	—	—	—	—	—	—	—	—	—	—
	(<59.5)						(0.892)			(0.443)												
	Medium	38.2	7	0.749	—	—	—	—	—	—	68.0	3	0.241	42.0	11	2.316	53.4	10	1.318	—	—	—
	(36–59)			(1.298)							S+M+L		(0.520)			(1.787)			(1.810)			
	M+L	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60.4	6	0.360
	(>35.5)																					(0.935)
	Large	—	—	—	62.4	10	0.541	66.9	6	0.470	—	—	—	—	—	—	65.0	3	0.481	—	—	—
	(>59.5)						(0.672)			(0.847)									(1.035)			
"Copper complex"[f]	All	24.7	5	0.199	—	—	—	—	—	—	17.8	5	0.190	—	—	—	—	—	—	—	—	—
(COPPER)				(0.391)									(0.326)									
Cowcod	All	—	—	—	—	—	—	—	—	—	—	—	—	38.6	6	0.269	—	—	—	—	—	—
S. levis (COW)																(0.345)						
Darkblotched	All	33.0	5	0.132	—	—	—	—	—	—	—	—	—	42.7	3	0.125	—	—	—	—	—	—
S. crameri (DKBLT)				(0.191)												(0.278)						
Halfbanded rockfish	All	—	—	—	—	—	—	43.8	4	0.065	—	—	—	35.4	4	0.126	—	—	—	—	—	—
S. semicinctus (HLFBND)										(0.126)						(0.203)						
Olive rockfish	All	—	—	—	—	—	—	—	—	—	—	—	—	44.4	6	0.229	—	—	—	—	—	—
S. serranoides (OLIVE)																(0.326)						
Pygmy rockfish	All	30.3	6	0.191	—	—	—	—	—	—	—	—	—	32.2	10	0.836	—	—	—	—	—	—
S. wilsoni (PYGMY)				(0.260)												(0.646)						

Species	Size Class (range)	APRIL 1987 Mean SL[c]	No. of areas[d]	Mean abund. (SD)[e]	JUNE 1987 SWEEP 1[a] Mean SL	No. of areas	Mean abund. (SD)	SWEEP 2 Mean SL	No. of areas	Mean abund. (SD)	SWEEP 3 Mean SL	No. of areas	Mean abund. SD	APRIL 1988 Mean SL[c]	No. of areas[d]	Mean abund. (SD)[e]	JUNE 1988 SWEEP 1 Mean SL	No. of areas	Mean abund. (SD)	SWEEP 2 Mean SL	No. of areas	Mean abund. (SD)
"Rosy complex"	All	—	—	—	—	—	—	—	—	—	18.2	2	0.152	—	—	—	—	—	—	—	—	—
Sebastomus subgenus (ROSY)													(0.449)									
Shortbelly rockfish	Small	29.2	8	0.824	24.9	4	0.215	25.8	6	0.622	24.6	7	0.897	29.9	9	0.645	—	—	—	—	—	—
S. jordani (SBY)	(<32.5)			(1.124)			(0.393)			(0.962)			(1.122)			(0.501)						
	Medium	38.3	8	1.094	49.4	12	1.145	45.8	15	1.325	42.9	9	0.658	—	—	—	54.5	12	1.531	49.2	8	0.392
	(33–57)			(1.487)			(1.065)			(1.069)			(0.754)						(1.604)			(0.434)
	M+L	—	—	—	—	—	—	—	—	—	—	—	—	45.9	11	2.902	—	—	—	—	—	—
	(>32.5)															(1.546)						
	Large	—	—	—	63.5	12	1.908	67.9	15	2.528	72.1	8	0.584	—	—	—	66.4	13	2.789	67.2	8	2.204
	(>57.5)						(1.806)			(1.960)			(0.721)						(1.871)			(2.236)
Squarespot rockfish	S+M	30.3	5	0.177	49.1	9	0.753	—	—	—	—	—	—	43.2	8	0.984	—	—	—			
S. hopkinsi (SQSPT)	(<54.5)			(0.328)			(0.841)									(1.563)						
	Medium	—	—	—	—	—	—	50.7	11	0.474	—	—	—	—	—	—	51.5	10	0.539	—	—	—
	(31–54)							S+M+L		(0.432)									(0.450)			
	M+L	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	51.2	8	0.314
	(>30.5)																					(0.390)
	Large	—	—	—	56.3	6	0.145	—	—	—	—	—	—	—	—	—	57.1	5	0.304	—	—	—
	(>54.5)						(0.194)												(0.502)			
Stripetail rockfish	Small	25.7	6	0.331	—	—	—	—	—	—	—	—	—	29.4	9	0.820	—	—	—	—	—	—
S. saxicola (STRPTL)	(<32.5)			(0.497)												(0.861)						
	All	—	—	—	40.5	12	0.659	37.7	7	0.188	—	—	—	—	—	—	37.2	11	0.474	33.2	4	0.097
							(0.710)			(0.265)									(0.409)			(0.163)
	Large	36.2	5	0.209	—	—	—	—	—	—	—	—	—	35.3	8	0.947	—	—	—	—	—	—
	(>32.5)			(0.305)												(1.009)						
Widow rockfish	Small	29.5	4	0.123	—	—	—	28.3	2	0.140	—	—	—	—	—	—	—	—	—	—	—	—
S. entomelas (WID)	(<35.5)			(0.195)						(0.396)												
	S+M	—	—	—	54.0	11	0.834	—	—	—	—	—	—	40.9	7	0.298	—	—	—	—	—	—
	(<59.5)						(0.777)									(0.338)						
	Medium	40.9	4	0.100	—	—	—	53.1	15	1.133	—	—	—	—	—	—	51.0	13	0.986	50.1	9	0.790
	(36–59)			(0.199)						(0.894)									(0.897)			(0.877)
	M+L	—	—	—	—	—	—	—	—	—	51.5	6	0.232	—	—	—	—	—	—	—	—	—
	(>35.5)												(0.336)									
	Large	—	—	—	61.1	6	0.288	61.9	13	0.814	—	—	—	—	—	—	62.8	3	0.193	64.7	7	0.518
	(>59.5)						(0.489)			(0.731)									(0.497)			(0.713)
Yellowtail rockfish	Small	—	—	—	37.8	4	0.099	37.9	8	0.152	38.3	5	0.116	—	—	—	38.6	6	0.336	—	—	—
S. flavidus (YT)	(<42.5)						(0.169)			(0.174)			(0.163)						(0.652)			
	All	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	41.3	8	0.301
																						(0.347)
	Large	—	—	—	45.9	6	0.167	47.9	9	0.470	45.1	6	0.188	—	—	—	45.1	9	0.474	—	—	—
	(>42.5)						(0.282)			(0.643)			(0.258)						(0.554)			

[a]See table 3 for dates of sweeps. Readers interested in the abundances at each group of stations in a sweep can request these tables from the senior author.
[b]Adjacent size classes were combined when one or more size classes were not abundant. Mean lengths and abundances in different sweeps are presented, as employed in further analyses, only for those species/size classes (or combinations thereof) that were common enough to be analyzed.
[c]Sizes are in mm standard length.
[d]Areas occupied are the number of station groups (see description of each sweep) at which the species/size classes were present.
[e]Abundances are grand means and standard deviations of the average $\ln(x+1)$-transformed catches for each station group, averaged over all station groups.
[f]"Copper complex": *S. caurinus*, *S. chyrsomelas*, *S. carnatus*, *S. atrovirens*, and other related species.

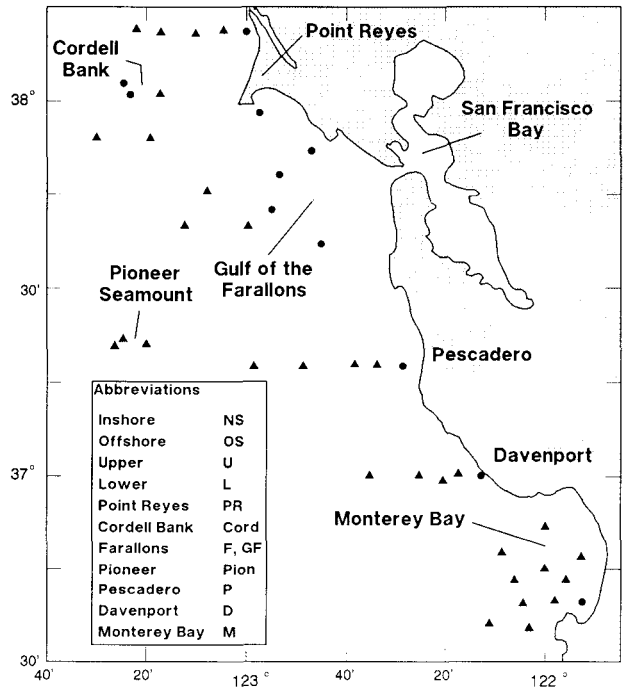


Figure 1. Map of the study area and typical midwater trawl stations. All but the stations at Cordell Bank and Pioneer Seamount were standard survey stations. The standard trawl depth was approximately 30 m at the stations marked with *triangles*, and approximately 10 m at stations marked with *circles*. Abbreviations of geographic terms that are used throughout the paper are defined in the box.

position, temperature, and salinity every 5 min. during the cruise. For use here, position was recalculated from recorded LORAN readings (rather than from SAT-NAV positions, which were subject to drift between satellite fixes), and the data set was edited to remove large blocks of data gathered when the vessel was not under way and to remove portions of the data stream that sampled trawled areas redundantly, before or after trawls actually took place. The entire system was not always operational. When the thermosalinograph was operating but the ship's computer was not, temperature and salinity from the thermosalinograph were recorded manually every 5–15 min., along with LORAN positions from the bridge. When the thermosalinograph was not working, temperature was measured by thermometer in the ship's running seawater system every 5–15 min., and 5 m salinity was determined from the CTD profiles. Temperatures and salinities thus gathered were cross-calibrated with thermosalinograph values and corrected before use.

Surface contours of temperature and salinity were computed with SURFER version 4.0 (Golden Software) using the kriging algorithm on the nearest three values in each octant surrounding smoothing points. In a continuous sweep of the study area, one pseudosynoptic map was made, but when a sweep was interrupted (particularly by strong winds that generated upwelling), contour maps were produced separately for each segment of the sweep and superimposed on each other.

TABLE 3
Dates of Sampling Cruises on the R/V *David Starr Jordan* in 1987 and 1988

Survey	Dates
April 1987	10–22 April
May/June 1987	
Sweep 1	23 May–1 June
Sweep 2	2–12 June
Sweep 3	12–21 June
April 1988	16–22 April
May/June 1988	
Sweep 1	22 May–2 June
Sweep 2	2–11 June
Sweep 3	11–18 June

Data Analysis

In overview, our objective was to infer the effects of upwelling and other oceanographic factors on pelagic juvenile rockfish by describing their distributions relative to sea temperature and salinity. Our general procedure for each sweep was to:

a. define regional groupings of surface temperatures and salinities, as an aid in displaying the range of conditions present,
b. combine trawl stations into small groups based upon geographical proximity and similarity of temperature and salinity,
c. determine which species and size classes of rockfish to include in the analysis, removing those that were too rare to be useful,
d. compute the average abundance of each species/size class of rockfish in each group of stations,
e. use an ordination procedure to find groups of species/size classes with similar distributional patterns,
f. compute the average, over species, of the standard score of abundance for each group of species in each area, and
g. plot these standardized deviations from mean abundance on contour maps of salinity or temperature.

Plots of temperature vs. salinity were useful in displaying the range of conditions present during a sweep and in defining groups of nearby trawl stations with similar hydrographic conditions. Such plots also often revealed geographically linked sets of points indicative of differing conditions, such as upwelled water off Point Reyes vs. Davenport, or warm, low-salinity water originating offshore vs. San Francisco Bay. To simplify our display, we therefore defined geographically related sets of temperature-salinity values, drew envelopes around these points, and used these envelopes in further displays. These envelopes are not meant to imply water masses in the classical oceanographic sense, although they often

work that way, but are intended to aid in the visualization of conditions. In the interest of space conservation, we present the derivation of only one set of envelopes, as an example. Curious readers may request other derivations from the senior author.

In our analysis, we used groups of nearby trawl stations with similar hydrography as our basic "sample" units, rather than individual stations. We had noted that such groups of stations typically had similar catches, but rarer species or size classes were better assessed if nearby stations were grouped. In addition, grouping nearby stations minimized the occurrence of sample units with no rockfish at all, which could not be included in ordinations. Stations were usually combined into latitudinal and onshore-offshore groups in which the latitudinal groupings normally corresponded with the sets of stations shown in figure 1: Point Reyes, Farallons (sometimes upper and lower), Pescadero, Davenport, and Monterey (sometimes upper and lower). Cordell Bank stations were usually incorporated into groups with Point Reyes or upper Farallons stations. The latitudinal groupings often differed oceanographically, but even when they did not, we kept them separate to preserve the possibility of detecting geographic variation.

Onshore and offshore groups of stations were normally defined on the basis of similarities of temperature and salinity. The temperature and salinity used to characterize each trawl station was defined as either the average of the CAMAC values recorded during a trawl (when the CAMAC system was operating), or the single measurements made at each station when the CAMAC system was not operating. Once identified, each group of stations was characterized by the average position, temperature, and salinity of stations within the group. This means of grouping stations meant that some stations changed groups when oceanographic conditions changed. We felt this appropriate, because the composition and abundance of organisms sampled in trawls at a particular station often changed with oceanographic conditions.

The abundance of various species and size classes differed seasonally and annually, so each species/size class was not always common. Species/size classes present in fewer than a third or so of the station groups were not treated separately in the analysis of distributions, because they offered little comparative information. Instead, size classes were combined when one or more adjacent size classes within a species were not common. Catches in each species/size class at each station were transformed to $\ln(x+1)$ and averaged over the stations in each station group. Hauls at standard depths (37 m, or 13 m at stations in shallow water [circles in figure 1]) were used in the main comparisons reported here.

Rather than attempting to describe the distribution of each species and size class separately, we hoped that some species and size classes would share distributional patterns that could be characterized together. We used the ordination method of detrended correspondence analysis (also known as detrended reciprocal averaging) to seek common distributional patterns. This procedure simultaneously ordinates taxa and areas, so that the relative positions of taxa on an ordination axis correspond with the relative positions of areas on the axis (Gauch 1982). The corresponding areas are those in which these taxa are relatively abundant, and the corresponding taxa are those that tend to co-occur in these areas. We used the detrended reciprocal averaging program of Pimintel and Smith (1985) to carry out the ordinations, employing the default program options and the downweighting of rare species. Jackson and Somers (1991) had found some instability of solutions with variation in one of the options in detrended correspondence analysis (the number of segments for detrending), but we found little evidence for such instability in ordination of three of our data sets in which we varied the number of detrending segments, so we used the default number of 27.

In addition to using the ordinations directly to examine distributional patterns, we used the proximity of taxa in the ordinations (supplemented by cluster analyses, which are not presented here) to group species/size classes with apparently similar distributions for further analysis of distributional patterns. We used an index of abundance for each group of species in which the index, I, was:

$$I = \frac{\sum_{i=1}^{n} \left(\frac{\bar{x}_{ij} - \bar{x}_{i\cdot}}{s_{i\cdot}} \right)}{n}$$

where $\bar{x}_{ij}$ was the average log-transformed abundance of species/size class i in the stations of station group j, $\bar{x}_{i\cdot}$ and $s_{i\cdot}$ were the average and standard deviation of the abundance of species i over all station groups, and n was the number of species/size classes in a group of species/size classes. These indices of abundance were plotted on contour maps of salinity to examine distributional patterns.

The above analyses were applied to each sweep of the study area except for sweep 3 of May/June 1988, when most pelagic juvenile rockfish had already settled. Additional analyses of specially sampled areas or of distinctive bathymetric distributions were carried out as appropriate.

RESULTS

April 1987

One sweep of the study area was completed between April 10 and April 20, 1987. A two-day seaward ex-

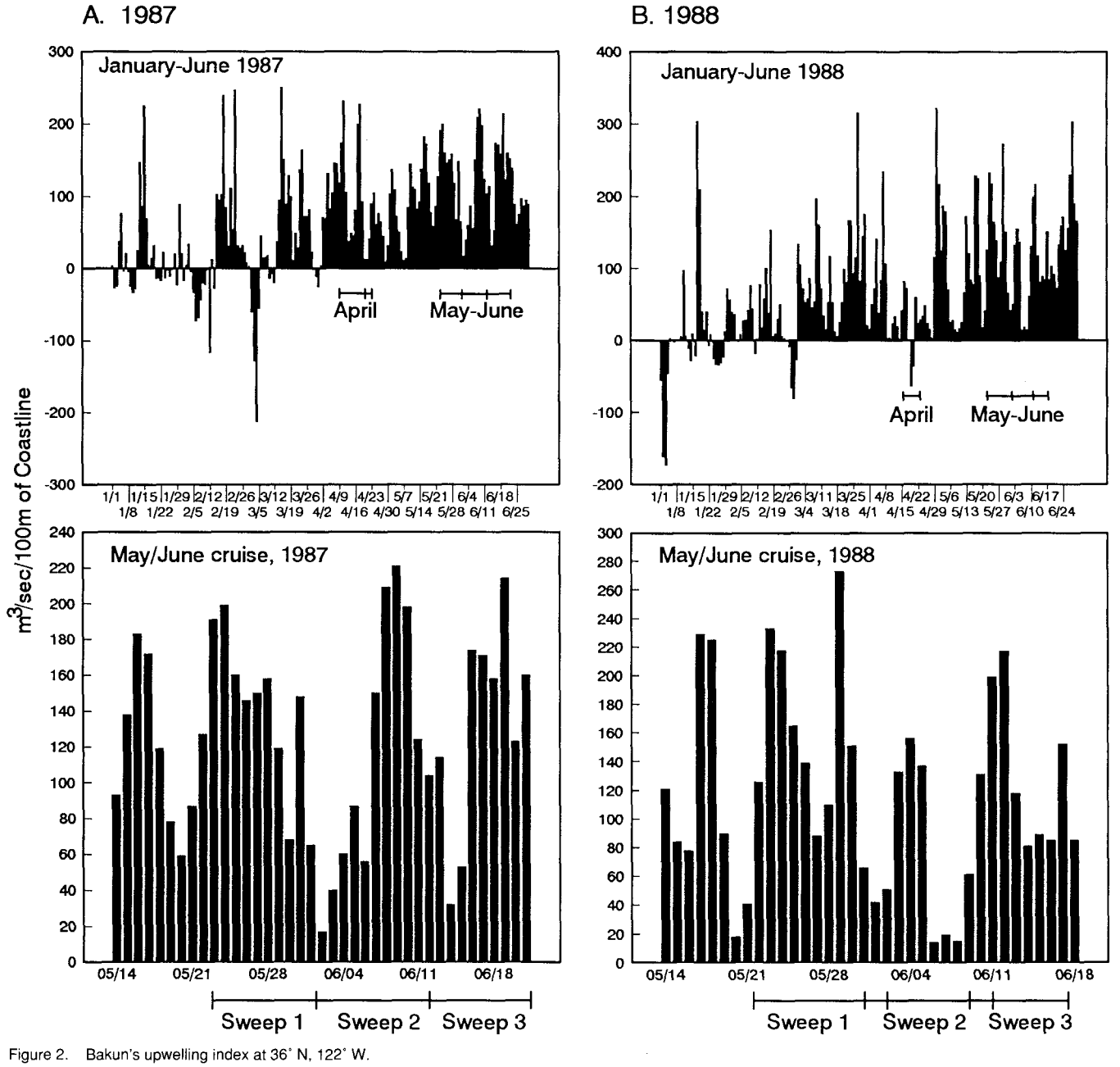


Figure 2. Bakun's upwelling index at 36° N, 122° W.

cursion was made following the regular sweep, in which one leg extended from the outer Pescadero stations past Pioneer Seamount, and the other offshore of Point Reyes.

Oceanography. Periods of upwelling-favorable winds had occurred intermittently for two months before this cruise (figure 2a). Upwelling conditions prevailed for several days immediately before the cruise and persisted for its first few days. After a short period of reduced winds, another brief windy period occurred before the end of the regular sweep (figure 2a).

Active upwelling was evident in the surface temperatures and salinities encountered during the regular sweep (figures 3 and 4). Tongues of cool, saline water extended from Point Reyes and Davenport, and relatively sharp fronts separated the recently upwelled water nearshore from warmer, less saline waters offshore in both areas. The larger Point Reyes plume extended in a convoluted pattern south of the Gulf of the Farallons, while the Davenport plume extended south in a less-pronounced pattern. Fresh water from San Francisco Bay was evident along the coast to Pescadero. The high salinities but warm temperatures in Monterey Bay suggested that the surface waters had been upwelled and subsequently warmed without mixing with offshore waters.

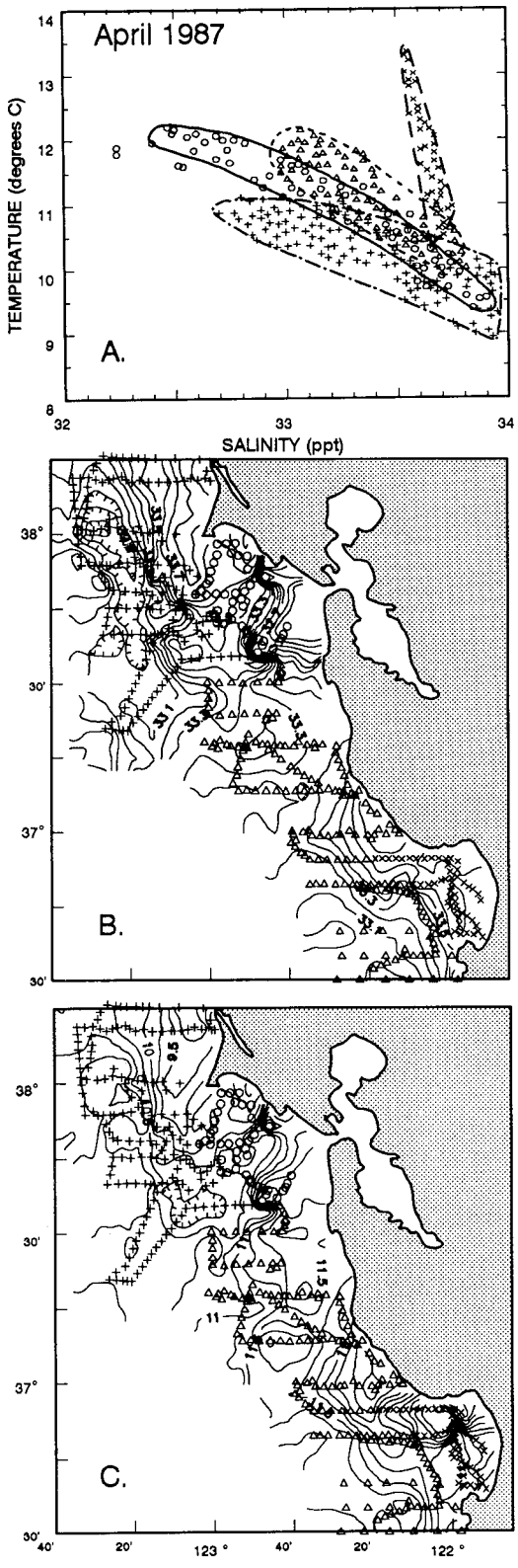


Figure 3. Oceanographic conditions and groups of temparature/salinity values in April 1987. *A*, temperature plotted against salinity for a representative subset of the surface temperature and salinity readings during the sweep, with different symbols representing geographically and hydrographically linked sets of points. The envelopes drawn around each set of points help display the range of conditions present during the sweep. The locations of the salinity and temperature readings are plotted on contour maps of salinity (*B*) and temperature (*C*).

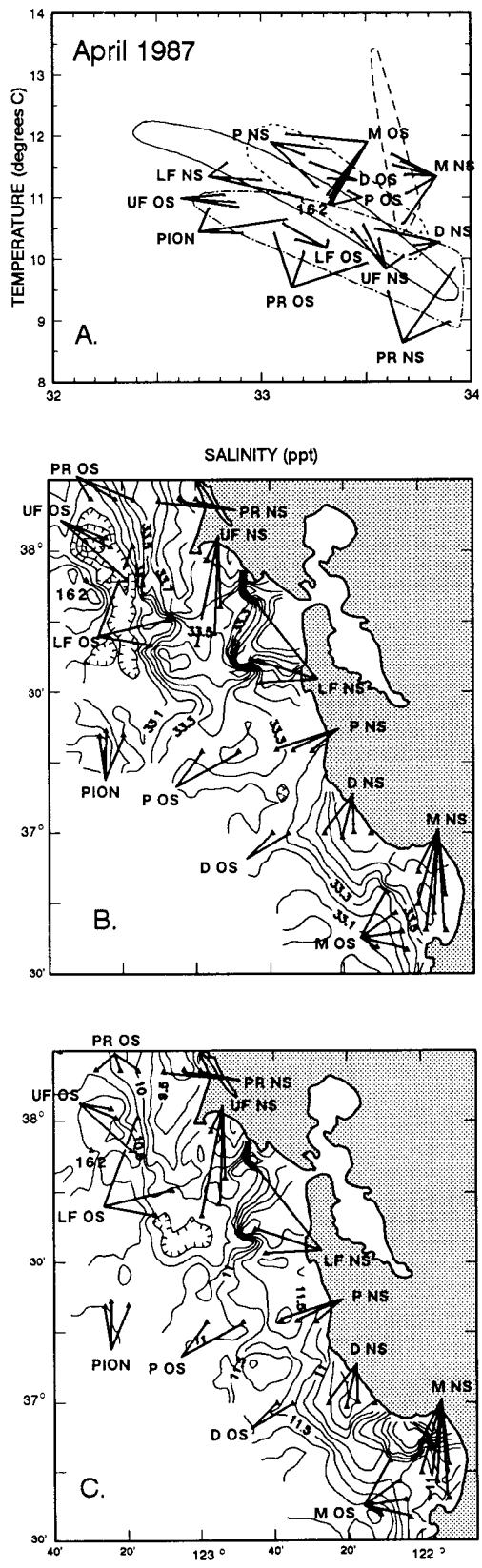


Figure 4. April 1987 trawl stations and their groupings, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Envelopes of temperature and salinity values in *A* are defined in figure 3. Abbreviations of place names are defined in figure 1.

We described four envelopes of temperature and salinity values (figure 3). Warm but saline Monterey Bay waters constituted one envelope (temperature and salinity points indicated by x's). Temperatures and salinities grading from freshly upwelled water to warmer, less-saline offshore water were defined for areas in the north (+'s) and south (triangles); northern waters were somewhat more saline at similar temperatures than the southern waters, and the most recently upwelled waters were more saline off Point Reyes than off Davenport. Waters in the Gulf of the Farallons (circles) ranged from cool and saline upwelled water to the warm, fresh outflow from San Francisco Bay. (Figure 3 and the above description illustrate the designation of temperature-salinity envelopes employed for each sweep. We will not present this procedure for the remaining sweeps, but interested readers may request diagrams similar to figure 3 for the remaining sweeps.)

We defined 13 groups of 2–6 trawl stations, based on latitudinal proximity and similarity of surface temperature and salinity (figure 4). Groups of nearshore stations tended to occur in recently upwelled water (Davenport nearshore, upper Farallons nearshore, and Point Reyes nearshore). Pescadero nearshore stations and lower Farallons nearshore stations were warmer and less saline, under the influence of the San Francisco Bay outflow. The nearshore Monterey stations reflected the insolated upwelled water characteristic of the bay. Groups of offshore stations occurred in warmer, less-saline water characteristic of the regions in which they were found.

Rockfish distributions—regular sweep. Because it took place early in the season, the April 1987 cruise yielded relatively small pelagic juvenile rockfish (table 2, appendix). Sixteen species/size classes were included in the analysis for this cruise; in only one species—the stripetail rockfish—was the large size class abundant enough to be analyzed separately, and the large size classes were absent for most species (table 2).

In the ordination of the 16 species/size classes and 13 areas, the second axis separated the Point Reyes areas from the others, based on the absence of species other than brown rockfish (figure 5). The first axis largely represented a gradient from nearshore to offshore in the areas south of Point Reyes. The upper Farallons nearshore area (UF NS) occurred at the extreme of the otherwise offshore end of axis 1 because the only taxon present there—small shortbelly rockfish—was also abundant in offshore areas. Species/size classes on the offshore end of axis 1 were relatively small: the small size classes of shortbelly, chilipepper, and widow rockfish, as well as canary rockfish and medium shortbelly rockfish, which were—on average—small in size (table 2). Little comparative size data are available for darkblotched rockfish. At the nearshore end of the gradient were the large

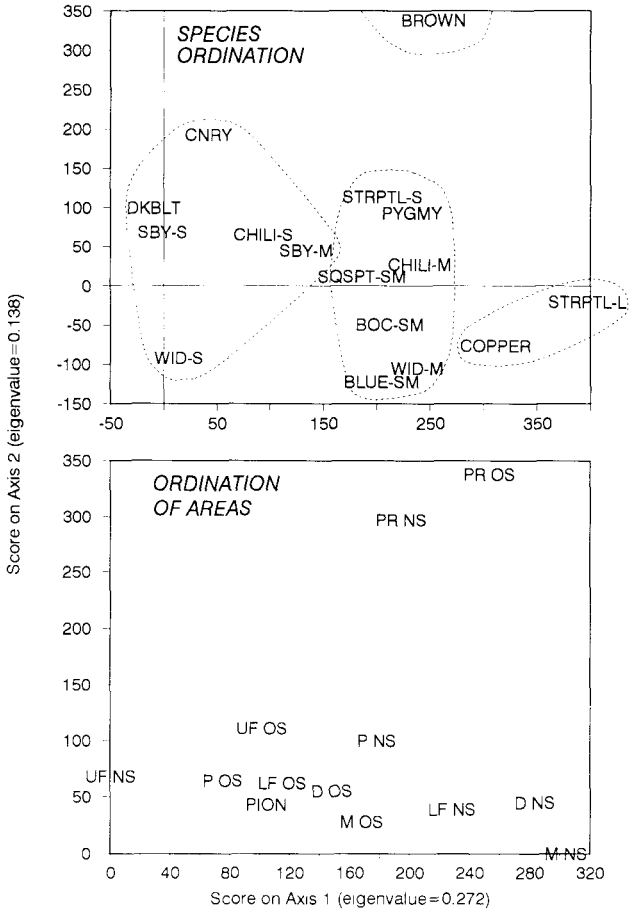


Figure 5. Ordination by detrended correspondence analysis of species and areas sampled during the April 1987 sampling cruise (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

size class of stripetail rockfish, and the copper rockfish complex. The latter fish were probably *S. caurinus*, which settle earliest among the complex of similar species (Anderson 1983). Stripetail rockfish also appear in midwater trawls relatively early in the season. Thus the species/size classes at the nearshore end of the gradient may have been ontogenetically advanced. In between were a mixture of medium and small size classes. The groupings of species/size categories for further analysis are indicated in figure 5. Brown rockfish will not be considered further.

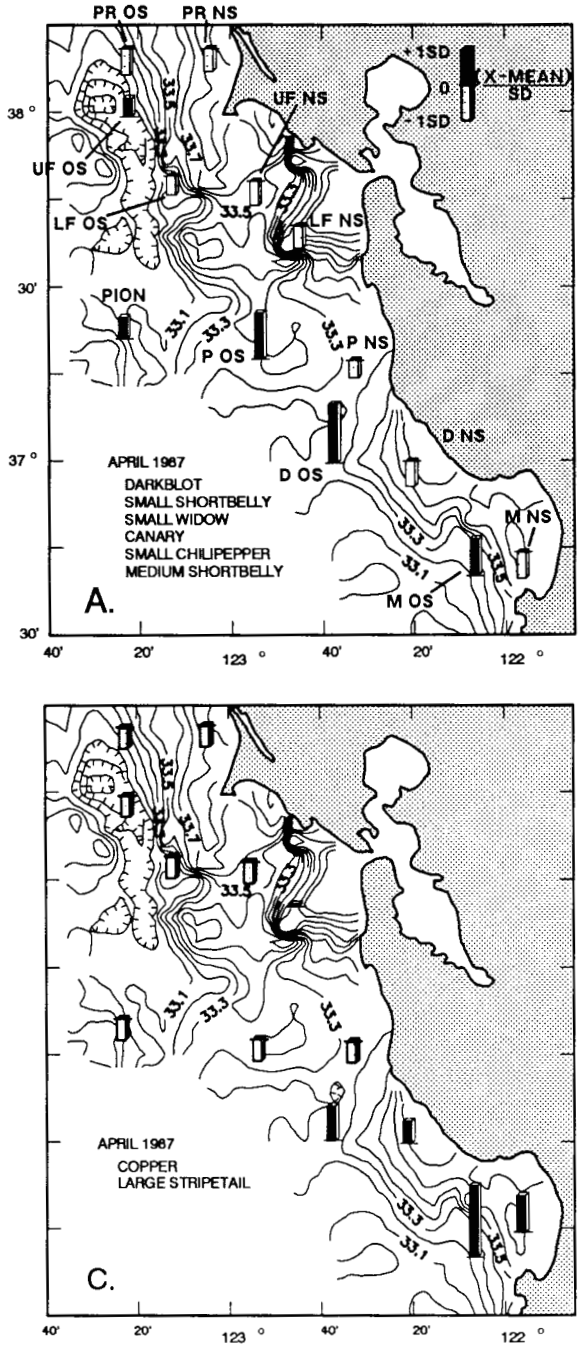
Overall, pelagic juvenile rockfish were the most abundant in the frontal regions off Monterey and Davenport (table 4). Other offshore areas in the southern part of the study area yielded relatively high catches of a variety of species/size categories, whereas the northern areas were largely devoid of pelagic juveniles. Some species were moderately abundant in the nearshore areas that scored high on axis 1 of the ordination.

The group of fish scoring the lowest on axis 1 of the ordination was abundant in offshore areas of relatively

TABLE 4
Abundance of Pelagic Juvenile Rockfish in Station Groups[a], 1987–1988

APRIL 1987				JUNE 1987										APRIL 1988				JUNE 1988							
				SWEEP 1				SWEEP 2				SWEEP 3						SWEEP 1				SWEEP 2			
Area[b]	Mean abund.[c]	Taxa prs.[d]	Taxa >avg.[e]	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.
M NS	0.135	5	3	M NS	0.478	13	4	M NS1	0.748	13	9	M NS	0.403	9	6	M NS	1.447	16	15	M NS	0.960	12	9	LM NS	1.056	7	6
								M NS2	0.361	10	6													UM NS	0.460	9	4
M OS	1.118	16	15	M OS	1.193	14	12	M OS1	0.145	8	0	M OS	0.310	4	3	M OS1	0.718	14	6	M OS	0.372	11	3	LM OS	0.669	7	4
								M OS2	0.604	9	7					M OS2	1.304	9	8					UM OS	0.405	11	4
D NS	0.110	6	3	D NS	0.645	10	8	D NS	0.937	13	12	D NS	0.072	4	0	D NS	0.827	14	9	D NS	1.508	9	9	D NS	0	0	0
																				D MID	0.528	13	3				
D OS	1.513	15	15	D OS	0.664	16	10	D OS	0.752	14	12	D OS	0.774	4	4	D OS	1.154	14	12	D OS	0.766	10	7	D OS	0.043	3	0
P NS	0.294	7	4	P NS1	0.656	7	5	P NS1	0.731	9	9	P NS	0	0	0	P NS	0.594	11	6	P NS	1.964	13	13	P NS	0.380	4	3
				P NS2	0.279	7	2	P NS2	0	0	0									P MID	0.099	3	0				
P OS	0.547	8	7	P OS	0.383	11	5	P OS	0.537	12	8	P OS	0.318	9	8	P OS	0.637	14	8	P OS	0.601	8	5	P OS	0.019	1	0
PION	0.510	13	10					PION	0.201	5	2																
LF NS	0.101	7	4	LF NS	0.479	13	7	LF NS	0.404	10	4	LF NS	0.236	5	4	LF NS	1.298	15	13	LF NS	0.462	10	1	GF	0.921	10	7
LF OS	0.095	4	1	LF OS	0.279	10	2	LF OS	0.311	13	4	LF OS	0.555	7	6	LF OS1	0.116	3	2	LF OS	0.666	11	5	LF OS	0.219	5	4
																LF OS2	0.660	10	8								
UF NS	0.022	1	0	UF NS	0.352	5	5	UF NS	0.688	12	9	UF NS	0.343	7	7	UF NS	0.622	6	5	UF NS	0.927	10	7				
UF OS	0.426	8	8	UF OS	1.133	14	14	UF OS	0.716	14	10	UF OS	0.457	4	4	UF OS	0.254	10	1	UF OS	1.506	12	12	UF OS	1.219	8	6
				CORD	0.435	10	5					CORD	0.392	8	7												
PR NS	0.052	2	1	PR NS	0.501	11	7	PR NS	0.913	7	7	PR NS	0.238	5	5					PR NS	0.285	6	2	PR NS	1.168	10	9
								PR MID	0.675	12	10																
PR OS	0.014	1	0	PR OS	0.039	2	0	PR OS	0.315	9	4	PR OS	0.019	1	0					PR OS	0.408	12	4	PR OS	0.614	8	5

[a]Station groupings differ from sweep to sweep, depending on conditions. The species/size groups used in each sweep are indicated in table 2.
[b]Each area is a group of stations defined by geographic proximity and hydrographic similarity (see descriptions of each sweep). See figure 1 for the definitions of the abbreviations for areas.
[c]Mean abundance (Mean abund.) is the grand mean, over species and size classes, of the average $\ln(x+1)$-transformed catches of each species/size class among the stations within each area.
[d]Taxa prs. is the number of species/size classes present in the group of stations.
[e]Taxa >avg. is the number of species/size classes present in an area at above-average abundance for all station groups within the entire sweep.



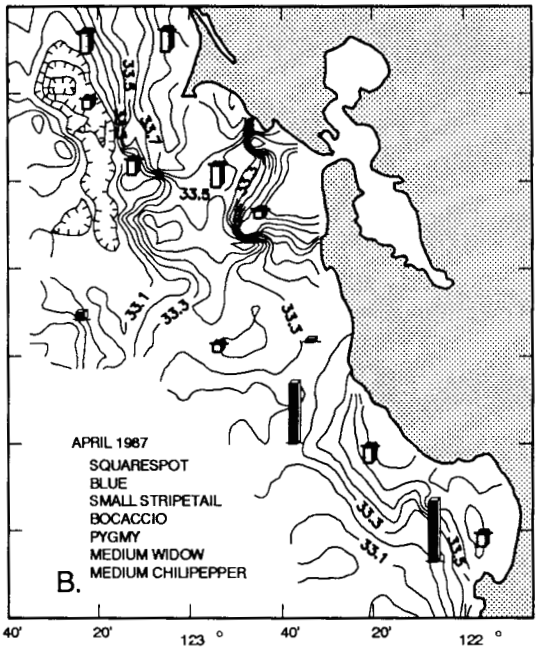


Figure 6. Relative distribution of species groups defined by ordination (figure 5), April 1987. Each bar represents the mean, over species, of the difference between the ln(*x*+1)-transformed abundance of a species in an area and its mean over all areas, divided by its standard deviation over areas. See figure 4 for station groupings. Contours are salinity (ppt).

low-salinity water, and absent in nearshore areas of recently upwelled water (figure 6a). The second ordination group, consisting of some medium size classes and earlier-settling species, was also abundant offshore in the south, and rare near shore, but it was somewhat less rare in the nearshore areas than the previous group (figure 6b). The copper–large stripetail group was abundant offshore of Davenport and Monterey, but was also above average in abundance closer to shore in these areas, in spite of upwelling. Thus the abundance patterns of these groups of species corresponded to their positions in the ordination.

Offshore Swing. A series of offshore stations was sampled after the regular sampling was completed. Beginning with the most offshore station in the Pescadero line and continuing past Pioneer Seamount, the first series of stations extended to the northwest (figure 7, line B). The second series of stations covered an east-west transect off Point Reyes (figure 7, line A). Profiles of density along each line were obtained from CTD casts. Catches of all three of the species groups tended to be above average for the entire cruise in the frontal zones separating coastal water from the more stratified offshore waters (figure 7). Catches declined offshore, especially for groups II and III (the species groups that scored higher on axis 1 of the ordination), and eventually dropped to zero for nearly all species. This indicates that pelagic juvenile rockfish may be concentrated near the upwelling front, and that the distribution of even the smallest size classes does not extend offshore indefinitely.

Summary. The absence of smaller size classes of pelagic juvenile rockfish in newly upwelled water and their presence in the fronts offshore in the April 1987 cruise suggests that earlier stages of pelagic juvenile rockfish are advected offshore during upwelling. But although earlier larvae may be distributed far offshore, the offshore swing conducted for this study suggests that the dis-

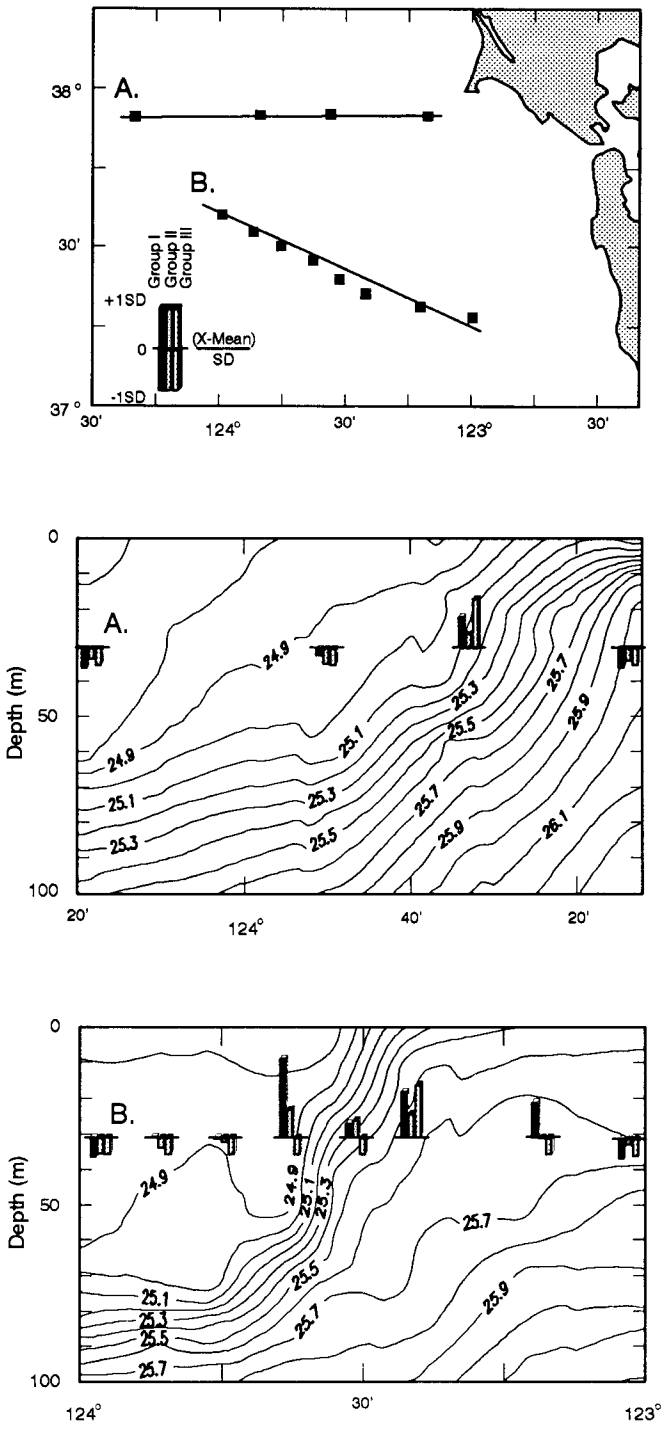


Figure 7. Distribution of pelagic juvenile rockfish offshore of the usual study area, April 1987. *Upper panel*, locations of trawl stations in northern offshore line (*A*) and southern offshore line (*B*). *Lower panels*, deviations from mean abundance of juvenile rockfish catches at stations in lines *A* and *B*, plotted on profiles of density (sigma t) as determined from CTD casts. Deviations from mean abundance were the mean among species within a group of the difference between each species' $\ln(x+1)$-transformed abundance at a station and its mean abundance in all trawls in April 1987, divided by its standard deviation over all trawls. Groups of species were defined in the ordination (figure 5). Group I: Darkblot, small shortbelly, small widow, canary, small chilipepper, and medium shortbelly rockfish. Group II: Small stripetail, pygmy, medium chilipepper, small and medium squarespot, small and medium bocaccio, medium widow, and blue rockfish. Group III: Copper and large stripetail rockfish.

tribution of pelagic juveniles does not extend offshore indefinitely. Despite the apparent offshore advection of many pelagic juveniles, distribution also seems to be related to size or ontogenetic stage. Larger size classes and early-settling species were found close to shore in some areas of quite recently upwelled water, suggesting that the later stages are not as affected by offshore advection as the earlier stages.

May/June 1987, Sweep 1

Oceanography. Upwelling-favorable conditions occurred fairly consistently during the few weeks before the May 22–June 2 sweep of the study area in 1987, but relaxed during the few days before the cruise (figure 2a). Upwelling-favorable conditions returned for most of the sweep, relaxing toward the end (figure 2a).

Surface temperatures varied widely during this sweep, but salinities were largely greater than 33.5 ppt (figure 8). Active upwelling was evident only off Point Reyes, but the high salinities generally prevalent in the region indicated that most of the waters in the study area had been upwelled, and that this water remained largely unmixed with offshore water. Little offshore water was evident during the sweep, but a complex front bordered the recently upwelled water off Point Reyes. The relatively fresh San Francisco Bay outflow was evident off Pescadero, yielding the lowest salinities of the cruise. The southern portion of the study area, which was visited shortly after the period of relaxed winds, contained relatively warm but also saline water, with a diffuse onshore-offshore gradient. This water likely had its origin in upwelling, and had not yet mixed greatly with offshore waters.

Trawl stations were combined into 14 groups (figure 8). Nearshore areas in the north (Point Reyes and the upper and lower Gulf of the Farallons) were in recently upwelled water, although some mixing and warming had occurred in the southern part of this area. The offshore Point Reyes and Cordell Bank stations were in or beyond the northern portion of the upwelling front, while the LF OS and UF OS stations were in increasingly warm and less saline water off the southern portion of the Point Reyes upwelling front. The offshore stations off Pescadero, Davenport, and Monterey Bay were in relatively warm but still saline water, while the most nearshore stations in these areas were in slightly more saline water. The most nearshore stations off Davenport and Pescadero (D NS and P NS1) were cooler, while the nearshore Monterey stations were warmed in the manner often characteristic of Monterey Bay. The intermediate stations off Pescadero (P NS2) were influenced by the San Francisco Bay outflow.

Rockfish distributions. Pelagic juvenile rockfish were much larger during this cruise than in April (table 2, ap-

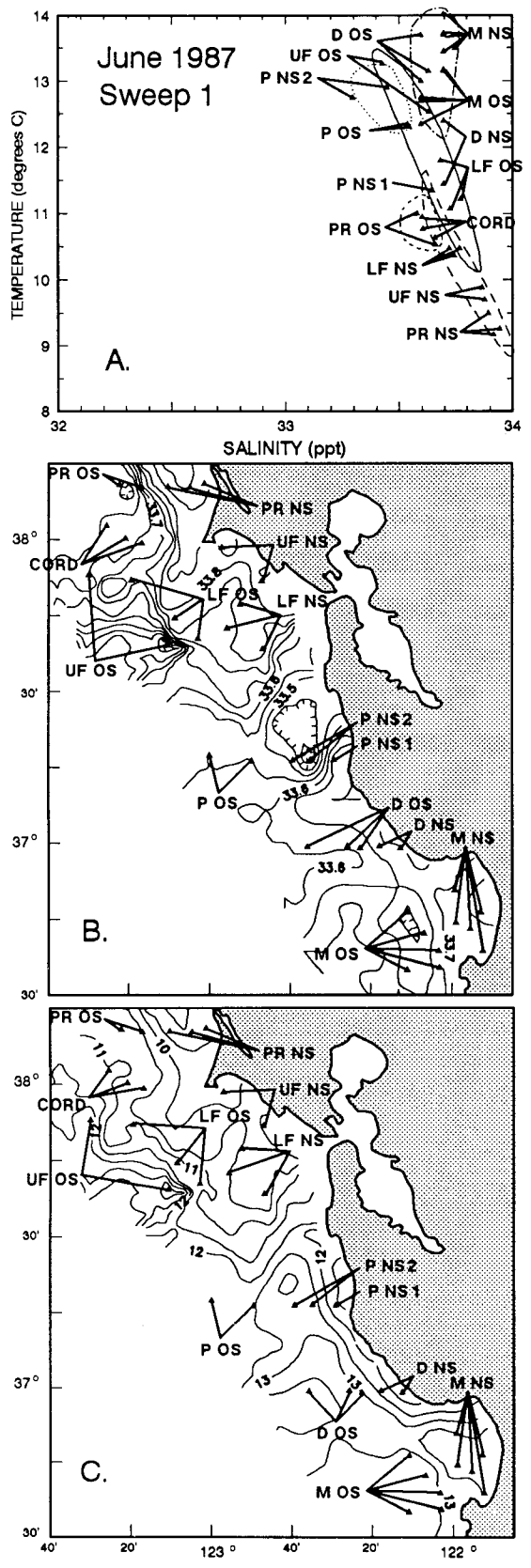


Figure 8. Trawl stations and their groupings from May/June 1987, sweep 1, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Abbreviations of place names are defined in figure 1.

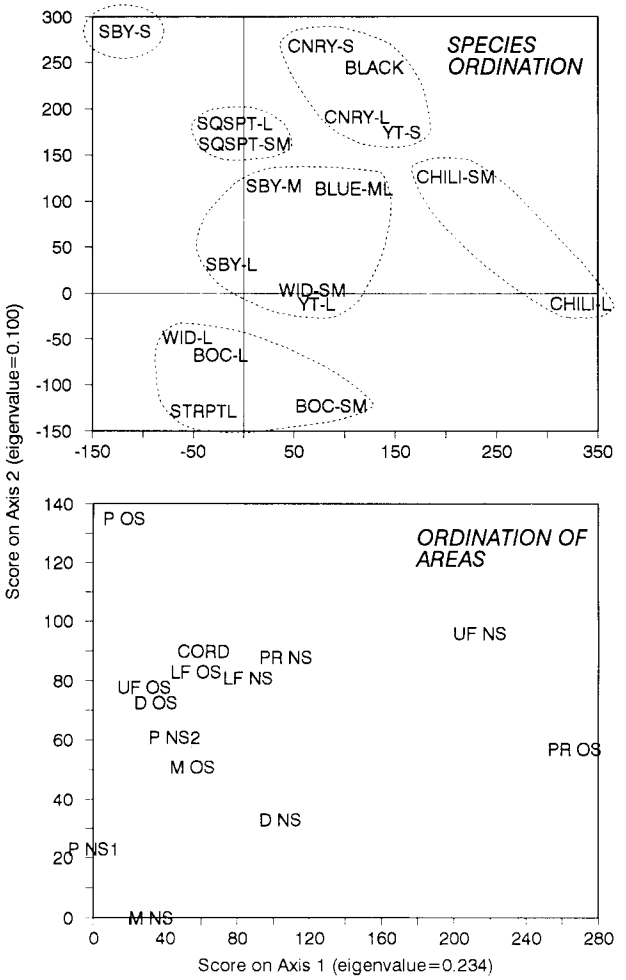


Figure 9. Ordination by detrended correspondence analysis of species and areas sampled during sweep 1 of May/June 1987 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

pendix). The large size classes of several species were abundant, and the small size classes of most species were rare or absent. Eighteen species/size classes were included in the analysis of this sweep (table 2).

Ordination of the 14 areas and 18 species/size classes resulted in a roughly triangular distribution of taxa and areas (figure 9). The high end of the first axis reflected taxa that occurred in some northern areas. The second axis reflected a roughly onshore-offshore gradient, with offshore areas scoring high and nearshore areas (particularly in the south) scoring low. Some smaller size classes, particularly small shortbelly rockfish, fell out at the offshore end of axis 2, while the predominant larger size classes occurred along the rest of axis 2. The two axes together yielded a triangular pattern with northerly, Point Reyes areas and their associated species on the right, offshore areas and their species in the upper left, and southerly nearshore areas in the lower left. Species/size categories did not fall into sharply distinctive groups. We

designated six groupings for use in further analysis (figure 9), recognizing that each group contained some heterogeneity.

Overall, species were most common and abundant offshore in the Monterey, upper Gulf of the Farallons, and Davenport areas (table 4). The fewest species and lowest overall abundance were in the offshore Point Reyes area. The most nearshore area off Pescadero (P NS1) and the nearshore area in the upper Gulf of the Farallons each had relatively few species, but those species present were abundant. Some of the remaining nearshore areas (Point Reyes, Monterey, and Davenport) had fair numbers of species but lower overall abundances, while the remaining offshore areas (Cordell, Pescadero, and lower Gulf of the Farallons) generally had fewer species and lower abundances.

Small shortbelly rockfish, which fell in the upper left corner of the ordination (figure 9), occurred in only four offshore areas of warm, lower-salinity water (figure 10a). The second group defined in the ordination included a mixture of sizes, and did not occur in many areas. They tended to be found toward the north, being absent in Monterey Bay (figure 10b). They were found in some offshore areas of warm, relatively low-salinity water, but were also abundant in recently upwelled water (figure 10b). Squarespot rockfish, including the large size class, were generally abundant offshore (figure 10c). The group consisting of medium and large shortbelly rockfish, medium/large blue rockfish, large yellowtail rockfish, and small/medium widow rockfish was somewhat heterogeneous in its distribution, but as a whole was relatively abundant in the south and in some nearshore areas, as well as offshore of the upper Gulf of the Farallons (figure 10d). The group consisting of stripetail rockfish, large widow rockfish, and medium and large bocaccio tended to be abundant in the south, and in that area the group was more abundant nearshore than the other groups (figure 10e). The last group, small/medium and large chilipepper rockfish, was abundant in the recently upwelled water off Point Reyes and two areas in the south (figure 10f).

The distributions of these groups, then, showed strong latitudinal differences, but less clear evidence of ontogenetically linked differences in onshore-offshore distributions. There was some indication of smaller size classes offshore in the first two groups, and larger size classes closer to shore in the last three groups, but small canary and yellowtail rockfish were found close to shore even in recently upwelled water, and some ontogenetically advanced fish (squarespot rockfish) were not abundant close to shore. The small size classes of some species (widow, chilipepper, and squarespot rockfish, as well as the "rosy complex"), which were too rare to be treated separately in the overall analysis, were found only in the upper Gulf of the Farallons offshore area, where many taxa were abundant.

Summary. Upwelling was strong only off Point Reyes during this sweep, and most of the study area contained upwelled water of less recent origin that was relatively unmixed with offshore water. Small size classes of most species were rare or absent, but medium and large size classes were abundant. There were strong north-south gradients in the distributions of pelagic juveniles, and some indications (with exceptions) of size-related differences in onshore-offshore distributional patterns across species. A number of species were abundant in some of the offshore areas (Monterey, Davenport, and Gulf of the Farallons), but only the latter area was in a frontal zone. Overall, there seemed to be a much smaller degree of commonality in distributional patterns across taxa and size classes than in April, and a greater degree of idiosyncrasy in species distributions.

June 1987, Sweep 2

Oceanography. Upwelling-favorable conditions appeared to relax considerably near the end of sweep 1, and these conditions continued into the first several days of the June 2–12 sweep of the study area (figure 2a). Upwelling-favorable conditions returned for a few days later in the sweep, but relaxed somewhat at the conclusion of the sweep.

Hydrographic conditions during sweep 2 seemed to reflect the absence of upwelling-favorable conditions (figure 11). The upwelling plume off Point Reyes appeared to weaken and move slightly offshore; warmer, slightly less saline water occurred inshore of the diffuse remnants of the Point Reyes upwelling plume, and the sharply defined front that was offshore of Point Reyes during sweep 1 disappeared or moved out of our sampling area (figure 11, cf. figure 8). A tongue of saline but not particularly cool water, probably the remnant of previous upwelling, occurred offshore of the San Francisco Bay outflow in the Gulf of the Farallons, and extended down the coast to Pescadero. The coolest, most saline water in the study area occurred in the upper Gulf of the Farallons, which was visited just after the period of upwelling-favorable winds. Warm, low-salinity water occurred offshore in the region south of the Gulf of the Farallons, separated from the more nearshore waters by a strong front. Warm, low-salinity water also appeared offshore of Davenport and Monterey Bay, separated from the coastal waters by a strong salinity gradient and less strong temperature gradient. There was little evidence of recent upwelling at Davenport, where the usual plume of cool, high-salinity water was absent. Instead, saline but relatively warm water remained pooled along the coast and in Monterey Bay.

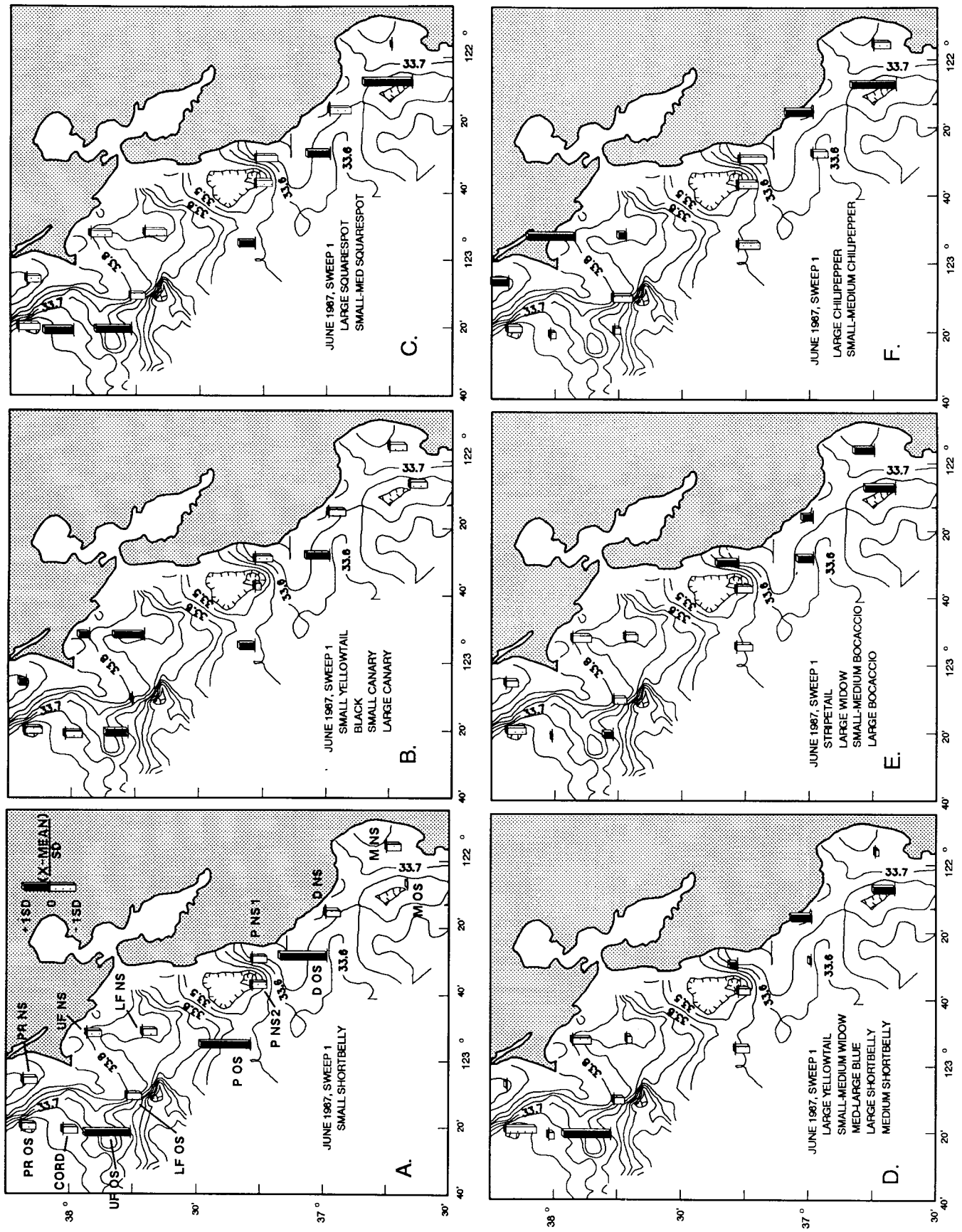


Figure 10. Relative distribution of species groups defined by ordination (figure 9), sweep 1 of May/June 1987. Explanations as in figure 6. See figure 8 for station groupings.

Trawl stations were combined into 17 groups of 1–4 stations (figure 11). Two stations in the upper Gulf of the Farallons occurred in the most recently upwelled water sampled. Other sets of stations off Point Reyes and the Gulf of the Farallons were in relatively cool water, grading to more offshore conditions in the UF OS stations. The middle stations off Point Reyes were in the core of the decaying plume, and the most nearshore station was in quite warm but moderate-salinity water. The offshore stations at Davenport, Pescadero, and Pioneer Seamount were in or beyond the frontal regions separating offshore from coastal water, and the different sets of offshore stations off Monterey Bay spanned the frontal region. Nearshore stations in the south were of moderate to high salinity, but also moderate to high temperature, indicating local warming. The middle station off Pescadero (P NS2) was in the tip of the decaying Point Reyes plume. No juvenile rockfish were captured at this station, so it was not included in the ordination analysis. However, it was included in the distributional analysis of species groups identified in the ordination.

Rockfish distributions. Overall, catches of pelagic juvenile rockfish increased during sweep 2 (table 4), and smaller size classes of several species appeared in greater abundance (table 2 and appendix). Twenty species/size groups were included in the analysis of this sweep (table 2).

The first ordination axis was very clearly an onshore-offshore gradient, and the second axis a north-south gradient (figure 12). Smaller size classes of juvenile rockfish fell to the offshore end of the first axis, and taxa falling toward the onshore end of the axis tended to be large, although not all large size classes scored low. Species/size classes were assigned to 6 groups for further analysis, as indicated in figure 12.

Overall, no single area yielded high catches of nearly all species/size categories (table 4). A number of areas had moderate to large catches of at least half the species/size categories, with the species mix varying from area to area. The nearshore area off Point Reyes had large catches of relatively few species; the LF OS area had small catches of relatively many species; and some areas (P NS2, Pioneer Seamount, and M OS1) had relatively small catches of few species (table 2).

Most of the species groups defined in the ordination had some internal heterogeneity in distribution, but the overall patterns reflected the positions of the groups and areas in the ordination. The group of relatively small fish scoring high on axis 1 had a predominantly offshore distributional pattern, well represented in the recently intruded offshore water of low salinity (figure 13a). Each of the species/size categories in this group increased in abundance from sweep 1 to sweep 2 (table 2).

The group consisting of small yellowtail, stripetail, large bocaccio, and black rockfish was ontogenetically

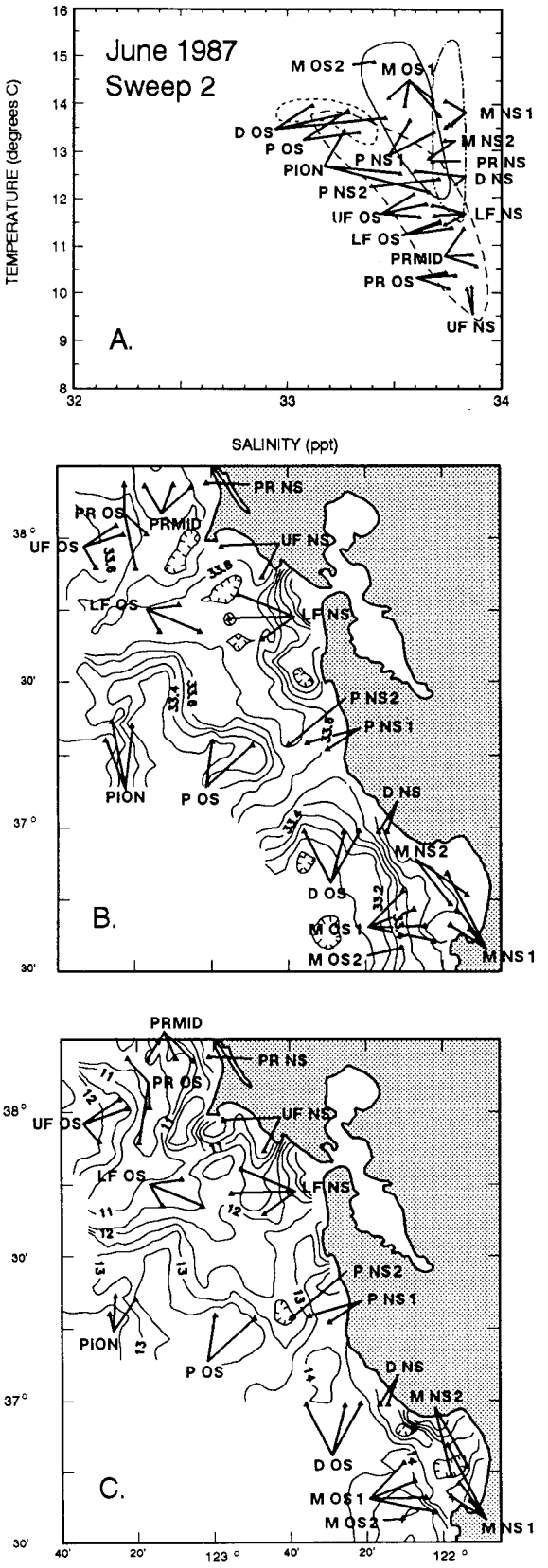


Figure 11. Trawl stations and their groupings from May/June 1987, sweep 2, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Abbreviations of place names are defined in figure 1.

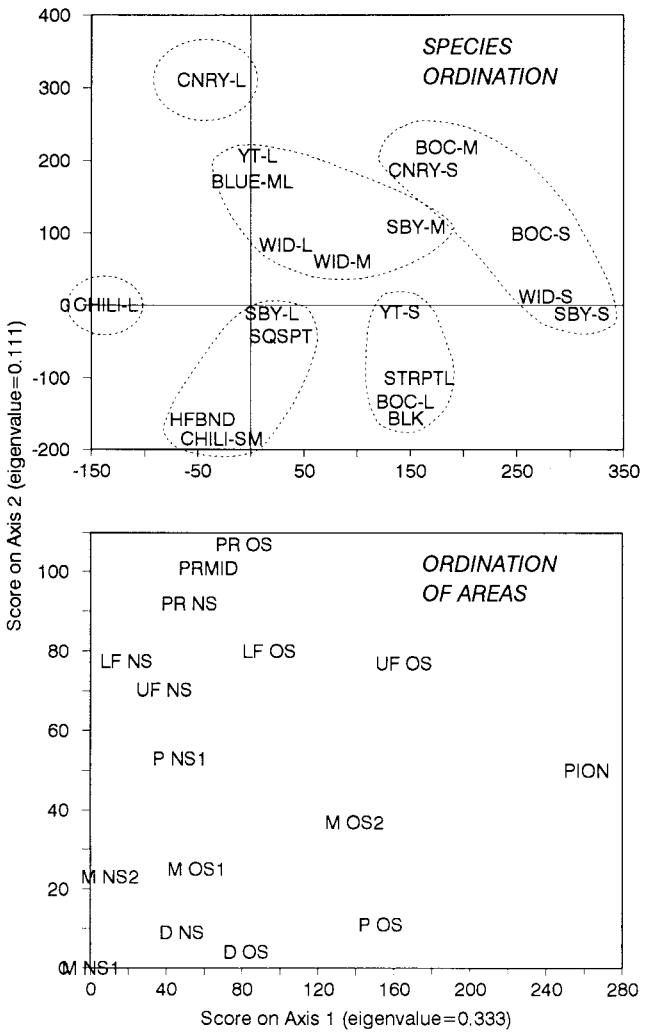


Figure 12. Ordination by detrended correspondence analysis of species and areas sampled during sweep 2 of May/June 1987 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

mixed. As a group, these taxa were abundant in the south (including nearshore areas off Monterey and Davenport), and abundant only in some offshore areas in the north (figure 13b). The distribution of the group showed no obvious relation to temperature and salinity, except for relatively low abundance in most areas of cool water in the northern part of the study area.

The group consisting of halfbanded, medium chilipepper, large shortbelly, and squarespot rockfish was relatively advanced ontogenetically. It was most consistently abundant nearshore and in the south (figure 13c). As a group, these taxa tended to be most abundant in some, but not all, of the nearshore areas of high salinity (figure 13c).

As a whole, the group consisting of medium and large widow rockfish, blue rockfish, large yellowtail rockfish, and medium shortbelly rockfish was relatively advanced ontogenetically. On average, this group tended to be abundant nearshore, except in Monterey, and only patchily present offshore (figure 13d). The areas showing near-average abundance for the group as a whole were internally heterogeneous. The offshore areas off Davenport, outside Monterey Bay, and the upper Gulf of the Farallons were notable in this respect. There was no particular relation between the abundance of this group and temperature and salinity, except that the group was relatively uncommon in low-salinity offshore waters (figure 13d).

Large canary rockfish were restricted to nearshore areas in the north with relatively cool, saline water (figure 13e). Large chilipepper rockfish were also found only in nearshore areas, but were most abundant in the south, in areas of relatively warm but saline water (figure 13f).

Summary. There was little active upwelling during or immediately before the sweep. Small size classes of several species became more abundant during this sweep, and appeared in offshore waters, often associated with an onshore intrusion of relatively warm, low-salinity water. Medium and large size classes of several species showed patchy and latitudinally separated distributional patterns, but were often abundant near shore.

Comparison of sweeps 1 and 2. The comparison of sweeps 1 and 2 suggests that relaxation of upwelling led to the onshore advection of some juvenile rockfishes, but the comparison was complicated by fish settling out between sweeps.

The increased temperatures and decreased salinities in several offshore areas (M OS2, D OS, and P OS) indicate the appearance of offshore water (figure 14a). The offshore displacement of the upwelling plume off Point Reyes led to an increase in salinity offshore, while the increase in temperature and decrease in salinity nearshore indicates advection to the nearshore region inside the plume (figure 14a).

From sweep 1 to sweep 2 several nearshore areas (PR MID, PR NS, UF NS, M NS1, P NS1, D NS) showed relatively large increases in abundance of juvenile rockfish (table 4). Several areas showed large turnovers in species composition. In several offshore areas of high species turnover (D OS, PR OS, LF OS, UF OS), average abundance increased, while in two nearshore areas (LF NS, M NS2) average abundance decreased slightly (table 4). The two offshore areas off Monterey showed large decreases in average abundance, and most species decreased. No rockfish were caught in the P NS2 area in sweep 2 (table 4).

Some early-settling species and large size classes (medium and large chilipepper, stripetail, blue, and large bocaccio) decreased in abundance from sweep 1 to sweep 2 (table 2). The difference was probably due to settlement. Some small stripetail rockfish did, however, ap-

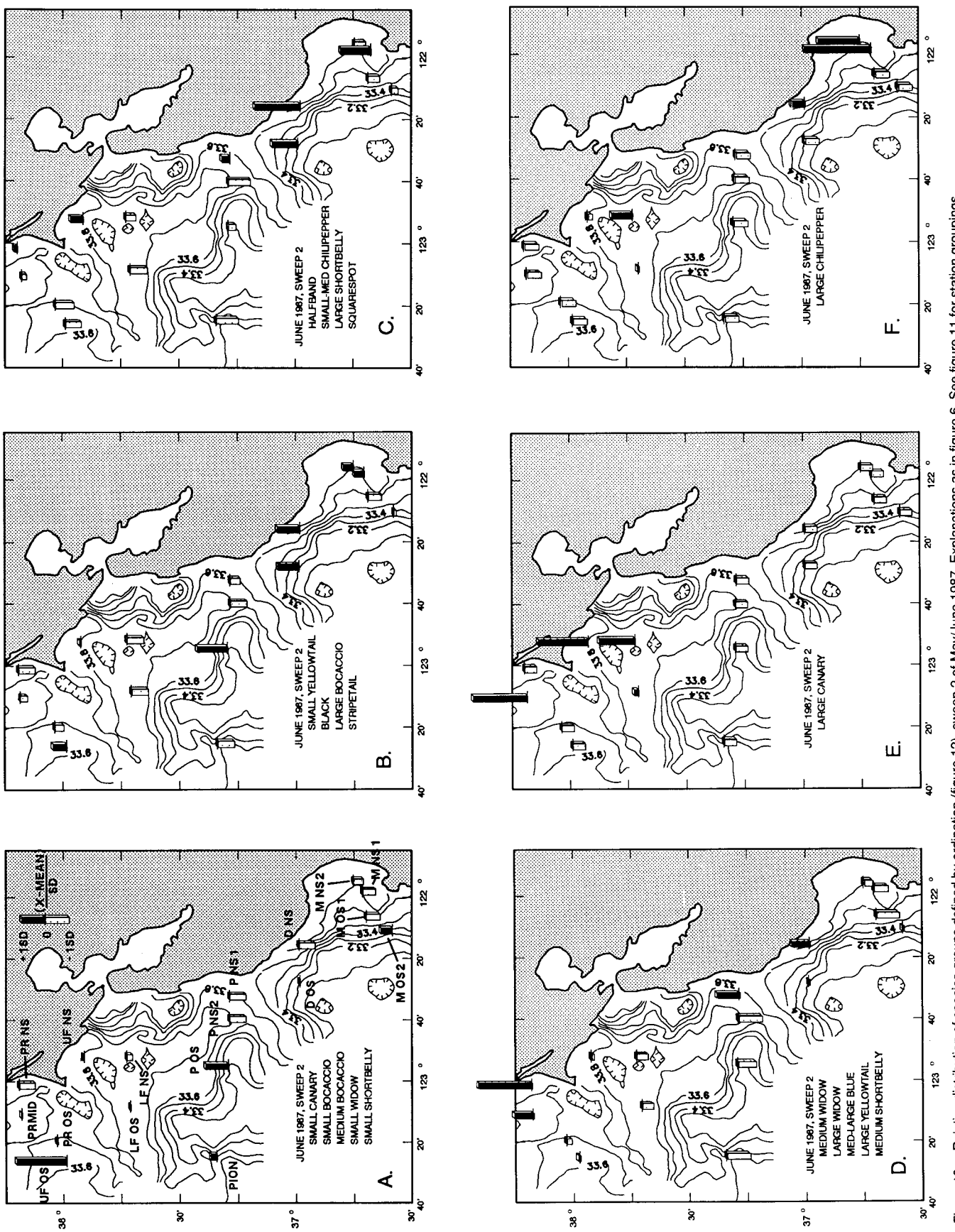


Figure 13. Relative distribution of species groups defined by ordination (figure 12), sweep 2 of May/June 1987. Explanations as in figure 6. See figure 11 for station groupings.

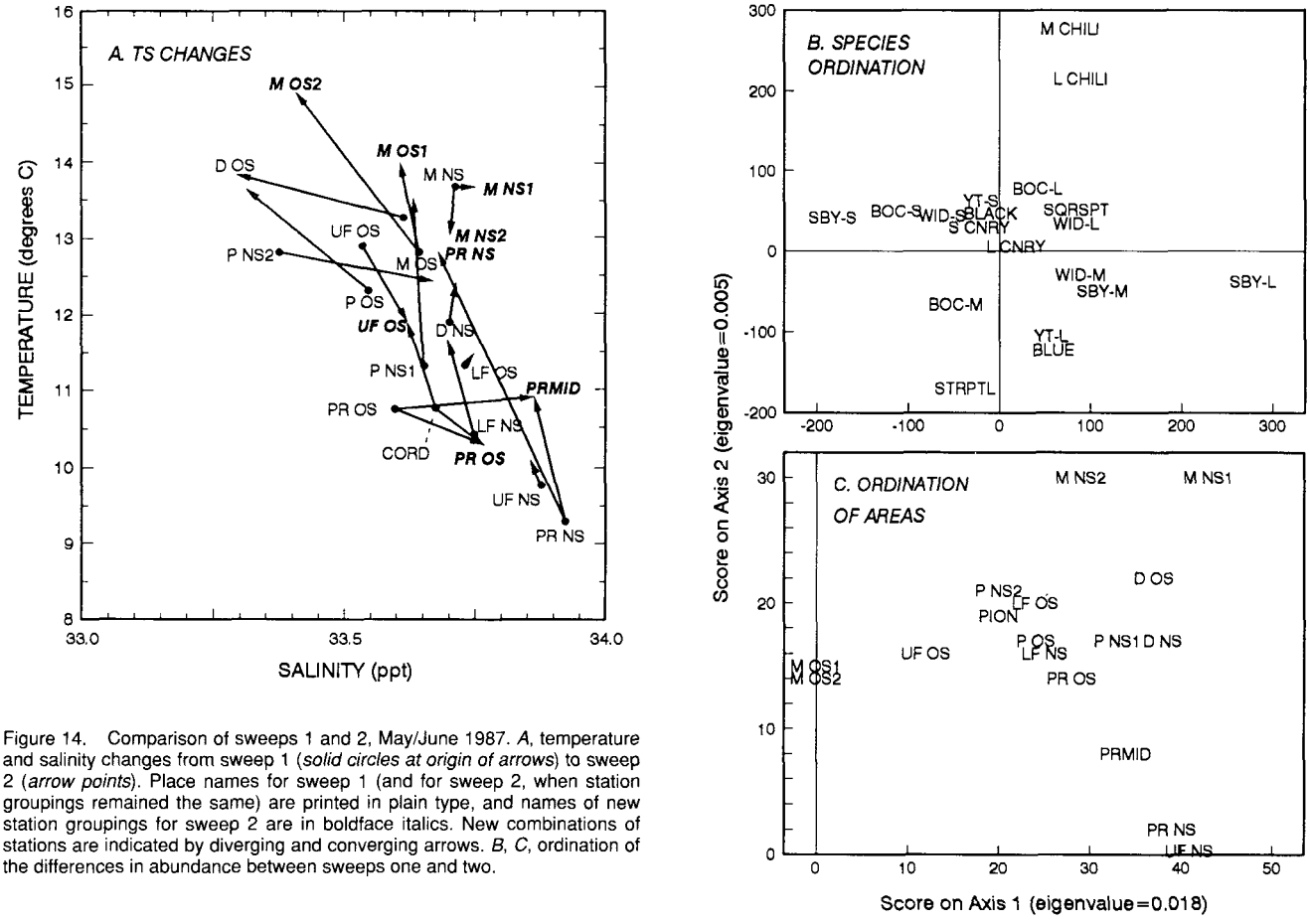


Figure 14. Comparison of sweeps 1 and 2, May/June 1987. *A*, temperature and salinity changes from sweep 1 (*solid circles at origin of arrows*) to sweep 2 (*arrow points*). Place names for sweep 1 (and for sweep 2, when station groupings remained the same) are printed in plain type, and names of new station groupings for sweep 2 are in boldface italics. New combinations of stations are indicated by diverging and converging arrows. *B, C*, ordination of the differences in abundance between sweeps one and two.

pear in offshore areas during sweep 2 (appendix g). Several species/size categories (large shortbelly, widow, yellowtail; medium widow, shortbelly; and small shortbelly) increased substantially in abundance between sweeps, while others (small bocaccio, widow, canary, yellowtail; medium bocaccio; large canary; and blue rockfish) increased but less substantially overall, either because they increased in fewer areas or because they were not present in many areas in either sweep (table 2). In general, then, most species/size groups other than early-settling species increased in abundance within the study areas between sweeps.

Differences in abundance between sweeps were ordinated to seek recurrent patterns of change in species abundance over areas (figure 14b,c). A cluster analysis was also carried out, giving similar results. Smaller size classes loaded low on axis 1 of the ordination, and larger size classes loaded high (figure 14b). Corresponding with the small size classes were offshore areas, where the small fish appeared and some larger fish declined in abundance (figure 14c). The second axis was largely a gradient from south to north. At the high end of the axis were species/size classes that either increased substantially in the Monterey nearshore areas or decreased (or did not increase) in the nearshore areas off Point Reyes, such as medium and large chilipepper and large bocaccio (figure 14b,c). These fish seemed to have settled out in the north, and perhaps moved inshore in the south. At the low end of axis 2 were species that increased (or did not decrease) in abundance in the nearshore areas off Point Reyes. Several species that were rare or absent off Point Reyes increased substantially in abundance in sweep 2 (large yellowtail, blue, medium and large widow, medium and large shortbelly, and squarespot rockfish). Some of these also increased nearshore in the south (squarespot, large shortbelly, and large widow).

The changes in abundance suggest three patterns of advection associated with relaxation of upwelling. First and most obvious was the appearance of small rockfish of several species in offshore areas, most often in areas where intrusion of offshore water was evident. Their appearance in these areas suggests that larvae or small juveniles had occurred offshore, and appeared in our catches as these offshore water masses moved into our study area and the fish grew to a size vulnerable to our sampling gear. The second pattern was the appearance of larger size classes of several species in nearshore areas off Point Reyes. Their increase was centered in the warm water

mass that appeared close to shore off Point Reyes during sweep 2. Water masses of similar characteristics were not present nearby within the study area during sweep 1 (figures 8, 11, 14a), suggesting that this water was advected into the area during sweep 2, perhaps from the north. Thus the appearance of these fish may have been associated with advection as well. Third, larger size classes of several species increased in abundance nearshore in Monterey or other southern areas between sweeps, often declining in offshore areas. Compression of the areas of relatively high-salinity, aged upwelled water toward shore when the offshore water appeared could indicate the onshore transport of these groups during the relaxation of upwelling.

Bathymetric distributions in relaxation area. Juvenile rockfish showed unusually shallow bathymetric distributions in southern Monterey Bay during sweep 2, and this was correlated with the development of a sharp, shallow thermocline (figure 15). Although thermal stratification was evident at four stations across southern Monterey Bay, there was no corresponding halocline at these stations (figure 15). Salinity throughout the water column was lower at the most offshore of these stations (figure 15), perhaps indicating a different water mass. A strong halocline was present only at CTD stations offshore of station D, corresponding to the offshore water mass that appeared off Monterey. Thus the shallow thermocline at the stations illustrated here was probably due to local warming, and could develop because vertical mixing and upwelling had subsided (as discussed in Send et al. 1987).

Several species of juvenile rockfish were unusually abundant above the thermocline (figure 15). When present at a station, four of the ordination groups (II–V) were usually abundant in tows at 10 m depth, often more abundant than at 32 m. In addition, several species were abundant in short surface tows made at stations B and D. These bathymetric distributions were among the most unusually shallow of the bathymetrically stratified tows made between 1983 and 1988. Of these species, bocaccio usually occur in shallow water, but the others are usually most abundant at 30 m (chilipepper, shortbelly, and squarespot rockfish), or even at 100 m (widow, blue, and yellowtail rockfish; Lenarz et al. 1991). In contrast to these four ordination groups, the small size classes in ordination group I were not abundant in shallow water. They were most abundant in middepths at offshore station D (figure 15).

In summary, several species/size groups were unusually shallow in this area. The smallest size classes were the major exception to this pattern. Although we have not scanned our data for other situations in which a similar shallow thermocline developed, it is interesting that these shallow distributions coincided with the devel-

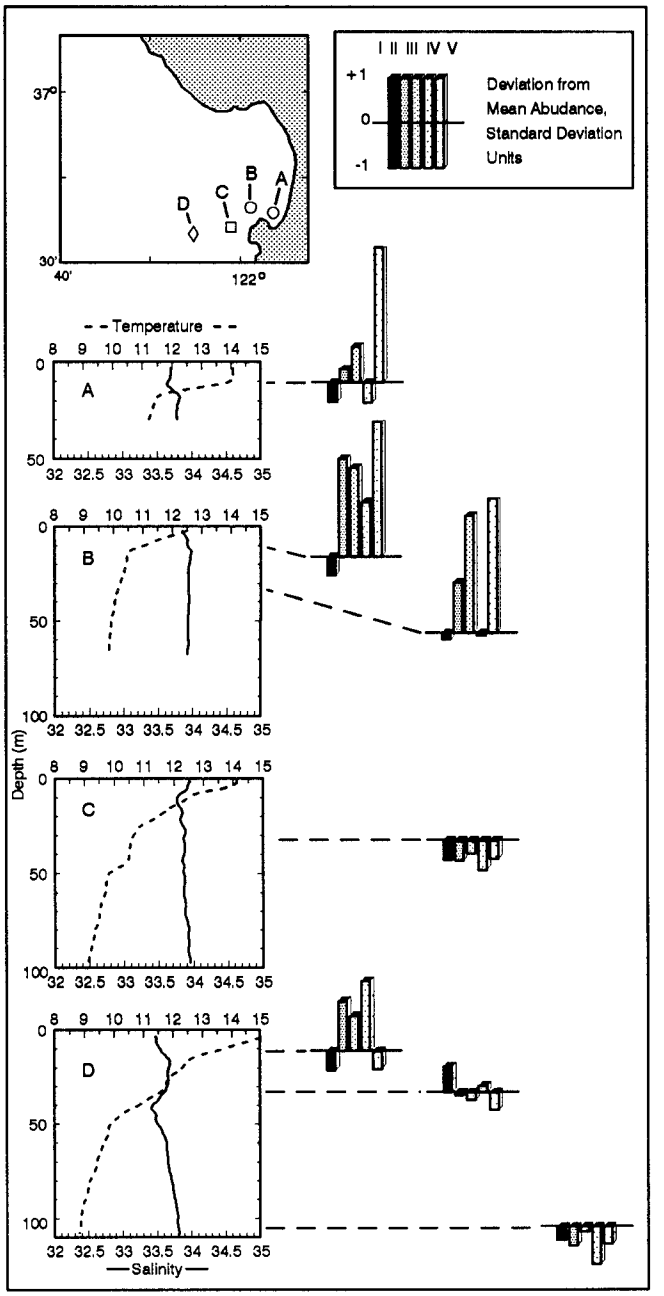


Figure 15. Horizontal and vertical distributions of pelagic juvenile rockfish in southern Monterey Bay during relaxation from upwelling, sweep 2 of May/June 1987. *Upper left*, map of stations. *Circles* indicate stations in the M NS1 group; the *square* indicates the M OS1 group; and the *diamond* indicates the M OS2 group (figure 11). *A–D*, CTD profiles at the corresponding stations, and comparative abundances of five groups of species identified in the ordination (figure 12). Bar graphs indicating abundance are aligned with the depth at which the trawls were made. Bars represent means (over species) of differences from the average abundance of each species in trawls carried out during sweep 2, scaled in standard deviation units. Group I: Small shortbelly and small bocaccio were present only at station D, and small canary rockfish were present only at station B. Group II: Small yellowtail (stations B,D), stripetail (station B), large bocaccio (stations A,B,D), and black rockfish (station B) were all absent at station C. Group III: Halfbanded (station B), medium chilipepper (stations A,B), squarespot (stations B,C,D), and large shortbelly (stations A,B,D). Group IV: Medium and large widow, medium shortbelly, blue, and large yellowtail rockfish were present mostly at stations B and D. Group V: Large chilipepper rockfish were present only at stations A and B.

opment of a sharp, shallow thermocline during the relaxation of upwelling and the apparent onshore movement of several taxa.

June 1987, Sweep 3

Oceanography. Upwelling-favorable conditions occurred during the middle of sweep 2, but declined at its conclusion and into the beginning of sweep 3, which took place between June 12 and 21 (figure 2a). After the relaxed conditions during the early part of sweep 3, quite strong winds and upwelling-favorable conditions occurred during the remainder of the sweep (figure 2a). Winds forced an interruption of sampling on June 16, in the middle of the Gulf of the Farallons. Sampling resumed on June 18, off Point Reyes. Because hydrographic conditions changed substantially within the same region before and after the interruption of sampling, temperature and salinity data were contoured separately in the periods before and after June 16 (labeled "before blow" and "after blow" in figure 16). In addition, failure of the shipboard CAMAC system during the period after June 18 forced us to rely on more widely spaced temperature and salinity data from CTD casts.

The occurrence of upwelling-favorable conditions during and before sweep 3 was reflected in hydrography (figure 16). A sharp onshore-offshore gradient in salinity occurred along the coast through most of the study area, while a similar temperature gradient was evident everywhere except in the central part of the study area (figure 16). Recent upwelling was most evident in the northern part of the study area, where salinities above 33.7 ppt and temperatures below 10°C occurred far offshore. The upwelling center off Davenport was evident, particularly in salinity, but water had evidently warmed close to shore, perhaps reflecting the passage of time since the most recent strong winds late in sweep 2 and the sampling early in sweep 3. Low-salinity offshore water masses were evident offshore of the upwelling front through much of the study area south of Point Reyes.

Trawl stations were combined into 13 groups of 1–6 stations (figure 16). Several sets of stations in the north were in recently upwelled water (PR NS, PR OS, UF NS), while others in the north were transitional (LF NS, LF OS, CORD). The UF OS and P OS stations were in offshore waters. Some groups of stations in the south were in mixed and insolated water masses (P NS, M OS, D OS); the others were in nearshore areas with high salinity and moderate temperature indicative of upwelled but insolated water (M NS, D NS). No fish were caught at either station in the P NS area, so this area was not included in the ordination of species and areas.

Rockfish distributions. Overall, catches of pelagic juvenile rockfish decreased between sweeps 2 and 3 (tables 2, 4). Several species disappeared or were found in

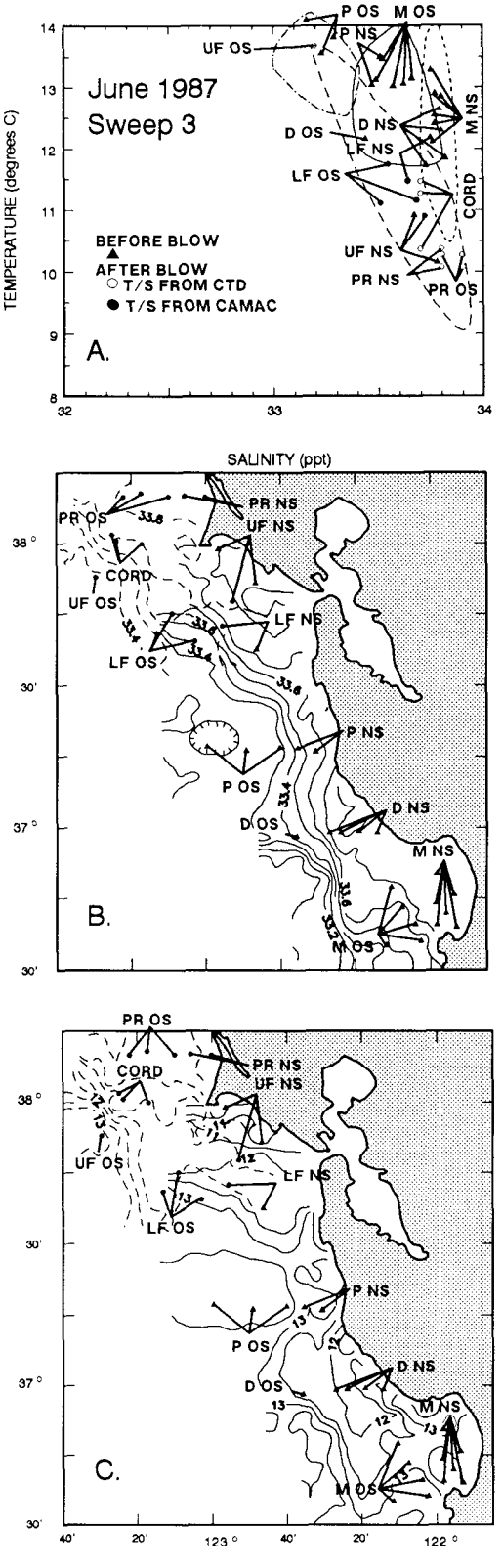


Figure 16. Trawl stations and their groupings from May/June 1987, sweep 3, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). "Before blow" stations were sampled before a windy period that forced a hiatus in sampling; "after blow" stations were sampled after, and some of the temperature and salinity data for these stations were taken from CTD rather than CAMAC. Abbreviations of place names are defined in figure 1.

only one area during sweep 3 (blue, squarespot, stripetail, and halfbanded rockfish), and several other species also decreased in abundance, particularly among larger size classes (black, bocaccio, canary, chilipepper, shortbelly, widow, and yellowtail rockfish). These declines likely indicate settlement of juveniles since sweep 2. Small size classes of several species either increased in abundance (rosy and copper complexes, and shortbelly rockfish), or stayed about the same (bocaccio, canary, chilipepper, yellowtail, and black rockfish), indicating an influx of younger fish (see appendix and table 2). Twelve species/size groups were included in the analysis of this sweep (table 2).

Ordination of the 12 taxa and 12 areas yielded an onshore-offshore gradient on axis 1 and a roughly north-south gradient on axis 2 (figure 17). Smaller taxa were associated with the offshore (high) end of the first axis, and several of the taxa falling at the other end were large (chilipepper, large shortbelly, large yellowtail), although some smaller size classes also scored low on axis 1 (mainly canary rockfish). The endpoints of axis 2 were determined by the unique distributions of canary and chilipepper rockfish. Species/size classes were grouped as indicated in figure 17 for further analysis.

No single area yielded large catches of many species (table 4). The UF NS and M NS areas, which fell out in the upper left quadrant of the ordination (figure 17), had moderate catches of a number of species in addition to those scoring high on ordination axis 1. The P OS, LF OS, and CORD areas also had a number of species in moderate abundance, but lacked some of the larger size classes and had some of the small species. The D OS, UF OS, and (to a lesser extent) M OS areas had large catches of just a few species. Of these, the M OS and UF OS areas in particular yielded mainly small species/size classes, and loaded high on axis 1. The LF NS, D NS, and PR OS areas had few species, and those in low abundance. These areas fell out in the lower left quadrant of the ordination (figure 17).

The group of small rockfish loading high on ordination axis 1 displayed an offshore distributional pattern, occurring largely at or beyond the front between high- and low-salinity water (figure 18a). Most members of this group were probably new to the study area since sweep 2. The copper and rosy complexes consisted of very small fish (table 2), and the small shortbelly rockfish and bocaccio were smaller on average than in sweep 2 (table 2, appendix b,e). It seems likely that most of these fish had occurred in offshore waters, and grew to a size retained by our gear by the time of this sweep. The species within the copper complex most likely to have been caught during this sweep were *S. chrysomelas*, *S. carnatus*, or *S. atrovirens*, the late-recruiting members of this group (Anderson 1983). Similarly,

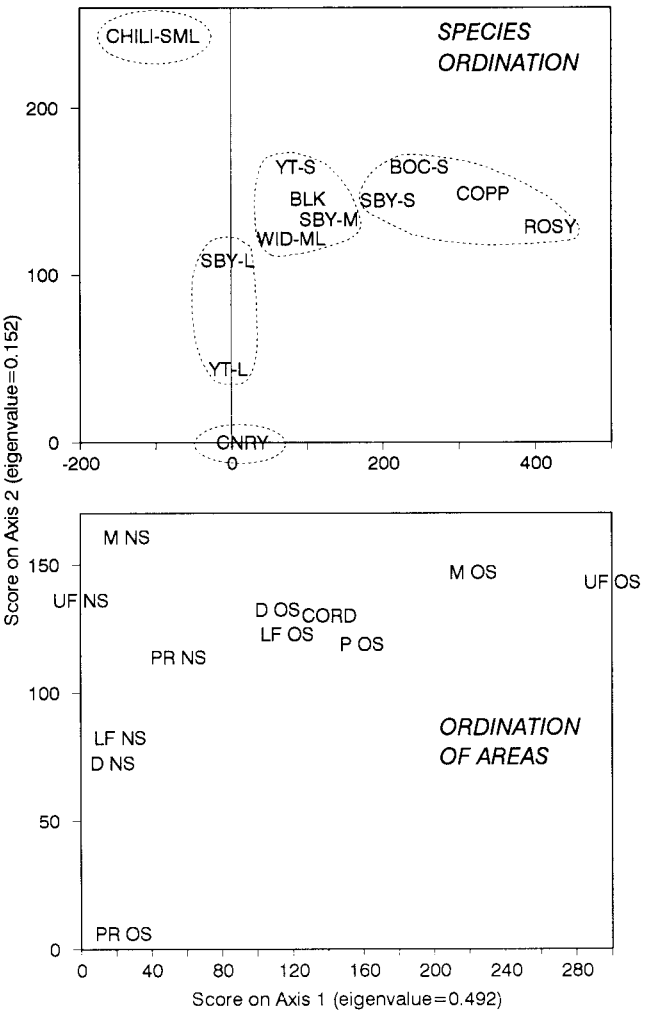


Figure 17. Ordination by detrended correspondence analysis of species and areas sampled during sweep 3 of May/June 1987 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

members of the subgenus *Sebastomus* (the rosy complex) are late spawners (Chen 1971). The small shortbelly rockfish and bocaccio captured here were probably the result of late spawning in these species.

The distribution of the second group defined by ordination—medium shortbelly, black, small yellowtail, and widow rockfish—was somewhat heterogeneous (figure 18b). Abundant in some offshore and transitional areas, at least some members of the group were also abundant in some nearshore areas of recent upwelling. The group was also heterogeneous with respect to size and ontogeny.

The large yellowtail–large shortbelly group occurred in some offshore areas, but as a whole these taxa were abundant near shore, especially toward the north (figure 18c).

The canary rockfish present during this sweep were relatively small (table 2, appendix d). This species was uncommon south of the Gulf of the Farallons, but in

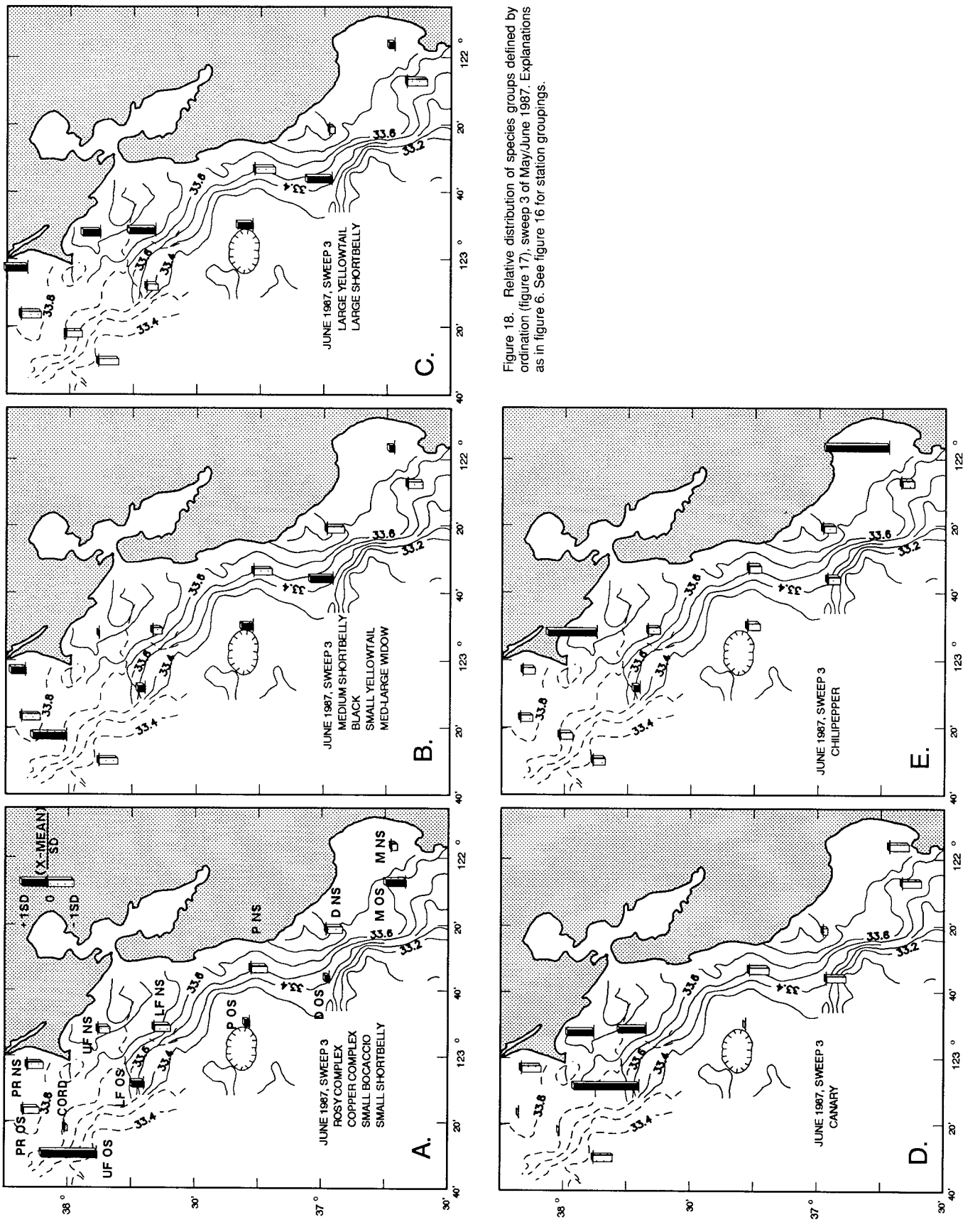


Figure 18. Relative distribution of species groups defined by ordination (figure 17), sweep 3 of May/June 1987. Explanations as in figure 6. See figure 16 for station groupings.

the north was common both offshore and nearshore, even in recently upwelled water (figure 18d).

The chilipepper rockfish present during this sweep were mostly medium to large in size (table 2, appendix c). This species was abundant mostly in the nearshore regions of the Gulf of the Farallons and Monterey Bay, in high-salinity water (figure 18e). The few small chilipepper rockfish present were at the LF OS area.

Summary. Sweep 3 was marked by a resumption of upwelling, the apparent settlement of large numbers of juvenile rockfish, and the appearance offshore of very small juveniles of some species. Remaining larger fish tended to be closer to shore, even in recently upwelled water. However, small juveniles of canary and yellowtail rockfish were not restricted to offshore distributions.

April 1988

The April 1988 cruise was relatively brief (six nights of sampling from April 16 to 22). As a result, the Point Reyes stations were not sampled, and other areas such as Cordell Bank and Pioneer Seamount were skipped as well, reducing the geographic coverage during this sweep. In addition, data from some stations were not used because of problems with the net.

Oceanography. Winds had been upwelling-favorable episodically through March and the first week of April, but these winds relaxed considerably during the week before the cruise, and downwelling-favorable conditions prevailed during much of the cruise (figure 2b).

Neither the ship's computer nor thermosalinograph was operational during this cruise, so surface temperature and salinity values were determined from CTD casts and measurements of water temperature with a thermometer. CTD readings (from the upper few meters of the water column) were obtained from about 80 points, including all trawl stations. The temperature of water in the ship's running seawater system was measured with a thermometer at each of these points, and at one or two points between each CTD station. Thermometer and CTD temperatures were cross-calibrated where both were measured, and the mean difference between the two was applied to all thermometer readings. In an additional difference from the treatment of previous sweeps, the temperature and salinity of each trawl station was determined from one value, the CTD reading, rather than from the average of 5-minute thermosalinograph values recorded during the trawl.

Because of both the limited geographic scope of sampling and the lack of recent upwelling, rather uniform oceanographic conditions were found during the April 1988 cruise (figure 19). Relatively high-salinity water (>33.6 ppt) occurred along the coast, even forming a plume-type structure off Davenport (figure 19), indicating that upwelling had occurred at some time before

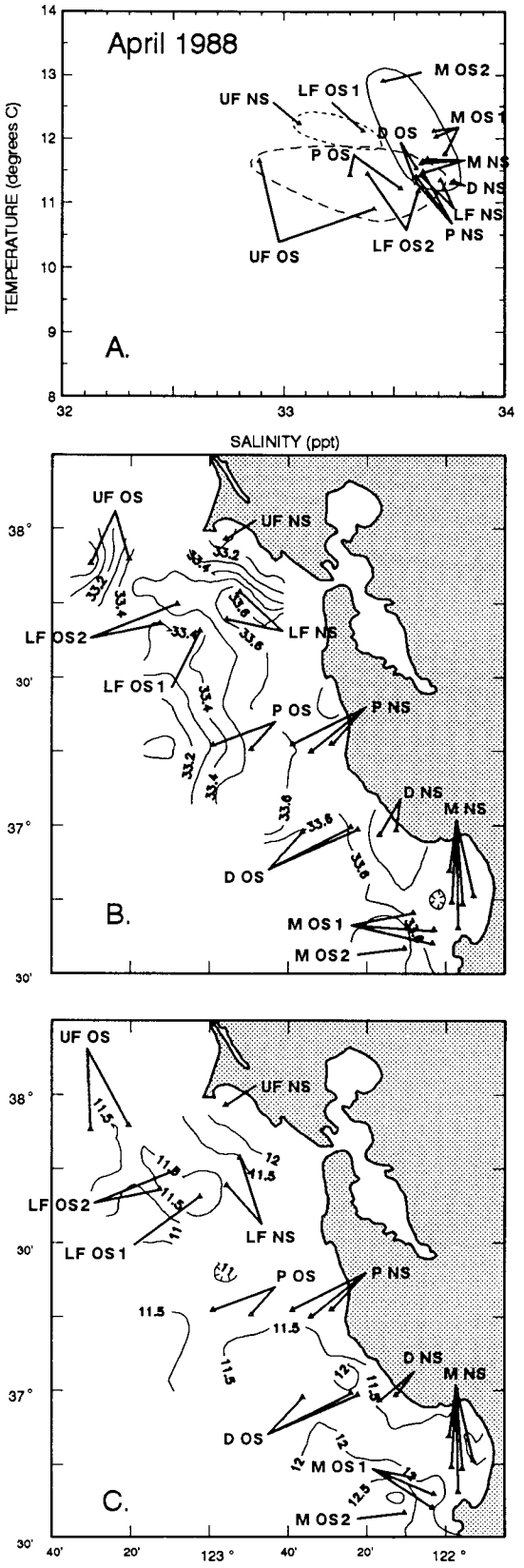


Figure 19. Trawl stations and their groupings from April 1988, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Abbreviations of place names are defined in figure 1.

the cruise. But the relatively warm temperature and rarity of very high salinities suggest that upwelling had not been recent, that the upwelled water had been warmed at the surface, and that little active advection due to upwelling was taking place during this cruise. There were some gradients to lower-salinity (but still cool) water offshore in the central and northern portions of the study area, but onshore-offshore fronts were not particularly strong. A tongue of somewhat warmer and lower-salinity water intruded from the south into the region offshore of Monterey Bay. The freshwater plume from San Francisco Bay was evident in the northern Gulf of the Farallons. These waters were underlaid (as were those of much of the study area) by cool, saline water typical of upwelling conditions.

Trawl stations were combined into 12 groups of 1–5 stations each (figure 19). Three of these contained only one station each—two because of unique oceanographic conditions (LF OS1 and M OS2), and one because hauls from a nearby, similar station were unusable (UF NS). Several of the areas had similar water characteristics: M NS, D NS, LF NS, P NS, and D OS were all in areas of relatively saline water at the lower range of temperatures present during the sweep, and were probably in slightly aged upwelled water that had not mixed to a great degree with offshore water (D OS showed the most mixing and D NS the least). M OS1 was in slightly warmer, but still saline, water, and M OS2 was in an apparent offshore intrusion of warmer, less saline water. P OS and LF OS2 were near a diffuse offshore front separating the more saline nearshore water from less saline offshore water, and the UF OS stations straddled a more pronounced offshore front in the northern portion of the study area. At the UF NS area, fresh San Francisco Bay plume waters overrode cool, saline waters below. The single LF OS1 station was difficult to classify. Its surface characteristics were most like the bay plume region, but more saline. It may have been located in a pocket of relatively warm offshore water.

Rockfish Distributions. Because it was early in the season, the April 1988 cruise yielded few of the large size classes of pelagic juvenile rockfish, and greater numbers of small and medium fish, but most species were larger than in April of 1987 (table 2, appendix). Eighteen species/size classes were included in the analysis of this sweep (table 2).

Seven of the 12 areas ordinated fell together in a rather tight cluster (figure 20). Three of the remaining areas were isolated in the ordination, forming three of the four axis extremes, and each of these (LF OS1, M OS2, and UF NS) consisted of only one station each. A weak onshore-offshore gradient ran diagonally from the lower left to the upper right of the ordination. This was slightly correlated with fish size, since some of the taxa scoring

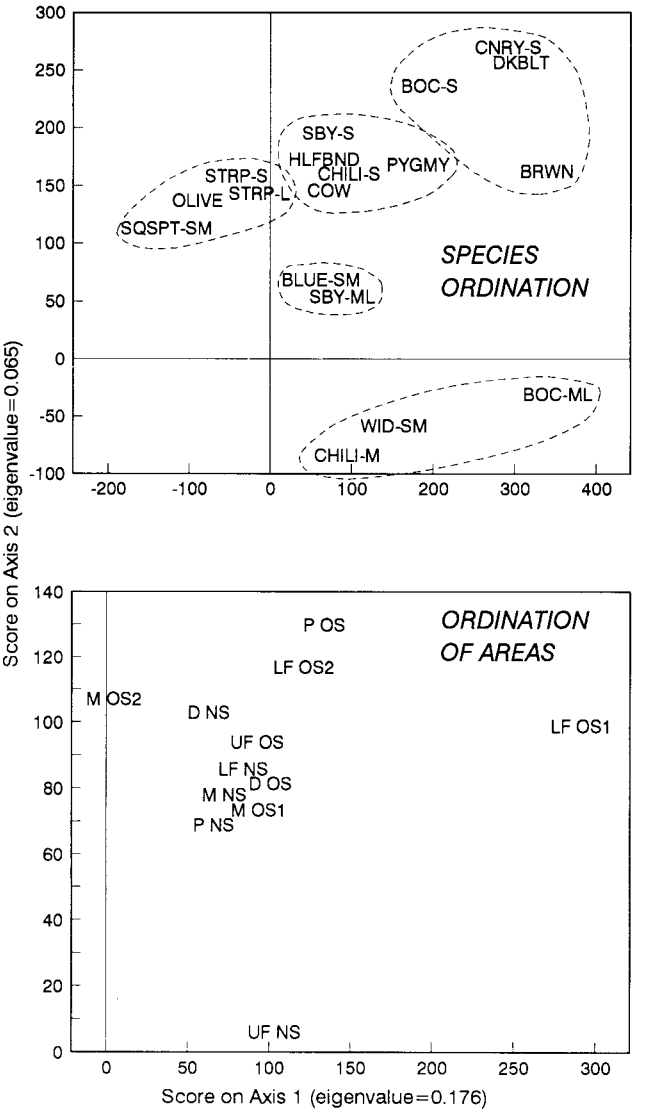


Figure 20. Ordination by detrended correspondence analysis of species and areas sampled during April 1988 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

low on axis 2 (medium chilipepper and medium-large bocaccio) were relatively large, and several of the smaller groups scored high on axes 1 and 2. However, much of the arrangement of species in the ordination was related to their occurrence in the areas lying at the extremes of the ordination axes. Thus, the ordination revealed little larger-scale structure in the assemblage of juvenile rockfish during this cruise. Five groups of taxa were defined for further analysis, as indicated in figure 20.

Three areas near the center of the ordination (M NS, LF NS, and D OS) had relatively high catches of several species/size classes (table 4). The M OS2 area, which was at the low end of ordination axis 1, had large catches of fewer species. The UF NS area, which was at the low end of axis 2, had few species, but most of those were

above average abundance for the study area. The LF OS1 area, which was the high extreme of axis 1, had low catches of very few species. The remaining areas had intermediate numbers of species, in low to moderate abundance. Among these were the P OS and LF OS2 areas that formed the other extreme to UF NS on axis 2 of the ordination.

The trio of medium chilipepper, small-medium widow, and medium-large bocaccio, which fell in the lower right corner of the ordination, was distinctive in its abundance in the UF NS area and its rarity in lower-salinity offshore areas (figure 21a). This group was among the larger fish present during the sweep. The group of small bocaccio, darkblotched, small canary, and brown rockfish included relatively small fish that fell in the upper right corner of the ordination. As a group, they were found in several of the lower-salinity offshore areas, and tended to be rare in nearshore areas (except LF NS, where many species were abundant; figure 21b). This group was better represented at the UF OS area than any other group. The group consisting of small and large stripetail, small-medium squarespot, and olive rockfish, which occurred low on axis 1 of the ordination, was abundant largely in the southern part of the study area (figure 21c). Members of this group were abundant at M OS2 in the tongue of warmer, less saline water, but were also abundant in the higher-salinity areas of D NS and M NS. This group represented a mix of sizes. The group consisting of small shortbelly, halfbanded, cowcod, small chilipepper, and pygmy rockfish included some small size classes (as well as the early-recruiting pygmy rockfish), but was found in the higher-salinity areas in the southern part of the study area and in the LF NS area (figure 21d). It was rare in lower-salinity offshore areas. The last group (medium-large shortbelly and small-medium blue rockfish) was widespread, and unusual in its abundance at both the UF NS and M OS2 areas (figure 21e). This group may have had a north-south bipolarity in its pattern of abundance, but showed no distinctive onshore-offshore pattern of distribution nor any particular relation to temperature and salinity.

Summary. The April 1988 cruise was unusual in the narrow ranges of geography, oceanographic conditions, and size classes encountered. The cruise took place during a major relaxation period that followed an extended period of upwelling. This, in combination with the reduced set of stations sampled, led to a rather tight clustering of stations with regard to oceanographic conditions. Because the cruise was early in the season, large size classes of juvenile rockfish were rare. However, the timing of the recruitment season seems to have been earlier in 1988 than in 1987, so small pelagic juveniles were not particularly abundant either. Most areas had similar catches of species and size classes, perhaps related to their similar oceanographic conditions. Where catches and conditions differed, there was some indication of onshore-offshore differences in distribution that were related to size and ontogeny among taxa. But there was no strict segregation of small size classes offshore and large size classes onshore.

June 1988, Sweep 1

The first sweep of the study area in May/June 1988 was carried out between May 22 and June 2. Sampling at the regular suite of stations was completed on the night of May 30–31. Following the regular sampling, two nights (5/31–6/1) were spent sampling an upwelling filament offshore of the Gulf of the Farallons.

Oceanography. Two periods of upwelling-favorable conditions occurred between the relaxed wind conditions of April and the initiation of this sweep (figure 2b). Immediately before this sweep, several days of upwelling-favorable conditions gave way to relaxed conditions, and these prevailed at the beginning of the sweep. But strong upwelling-favorable conditions returned shortly into the sweep, and reoccurred toward the end of the sweep (figure 2b).

The ship's thermosalinograph was operational during this sweep, but not its computer, so temperature and salinity readings were recorded manually at each CTD and trawl station, and at one or two points between these stations. The temperature and salinity values associated with each trawl station, then, were single points instead of averages of several values recorded during the trawl. Changing weather and other interruptions of the regular schedule led to discontinuities in the quasi-synoptic acquisition of oceanographic data, so the data from Monterey Bay and the Gulf of the Farallons were contoured separately.

The upwelling-favorable conditions present during this sweep were evident in the temperature and salinity patterns observed (figure 22). Salinity exceeded 33.7 ppt in most nearshore areas, and temperatures below 11°C were common, all indicating recent, active upwelling. Upwelling centers were evident off Davenport and below Point Reyes (figure 22). Upwelled water from Davenport formed a front with less-recently upwelled water to the north, and spread across Monterey Bay to the south. The nearshore portion of Monterey Bay, which was sampled before the first upwelling-favorable period during the sweep (figure 2b), was characterized by relatively warm but saline water, which presumably originated with earlier upwelling (figure 22). A lens of relatively fresh water from San Francisco Bay extended downcoast to the vicinity of Pescadero. Recently upwelled water occurred in the Gulf of the Farallons and off Point Reyes, with a filament extending offshore south of Point Reyes. The only truly offshore water was found off Point Reyes,

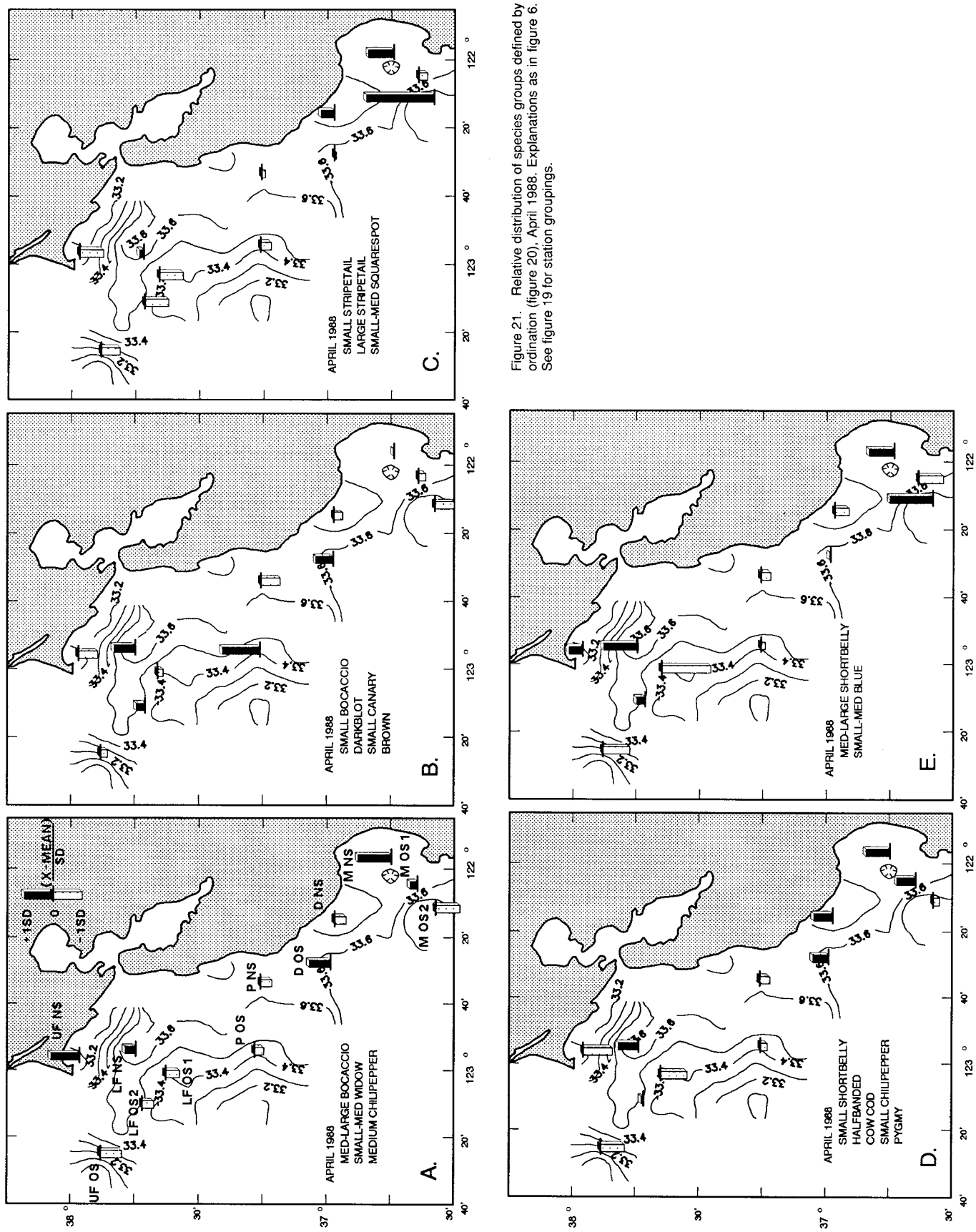


Figure 21. Relative distribution of species groups defined by ordination (figure 20), April 1988. Explanations as in figure 6. See figure 19 for station groupings.

where a very strong front separated upwelled water inshore from quite low-salinity, warm water offshore.

Trawl stations were combined into 14 groups of 1–6 stations each (figure 22). The M NS stations in Monterey Bay were in upwelled but insolated water, which was cooler in the south. The M OS stations were in saline but cooler water that had likely been advected south across Monterey Bay in the most recent episode of upwelling. The D NS, D MID, and D OS groups graded from very recently upwelled water inshore to less-recently upwelled water offshore. The P NS station was in somewhat recently upwelled water north of the Davenport center. Offshore, this graded into the San Francisco Bay plume (P MID), and then into somewhat mixed coastal/offshore water (P OS). In the Gulf of the Farallons, the LF NS stations were at the edge of the most recently upwelled water from Point Reyes, and the UF NS stations were in very recently upwelled water. The LF OS stations graded from somewhat recently upwelled water to mixes with lower-salinity offshore water south of the filament off Point Reyes, while the UF OS station was nearly in the center of this filament. The PR NS stations were in recently upwelled water along the coast, while the PR OS stations were at and beyond the front separating upwelled water from the low-salinity water mass offshore.

Rockfish distributions. Small size classes of pelagic juvenile rockfish were rare during this sweep, and medium and large size classes were abundant for many species (table 2, appendix). Even in species such as canary and yellowtail rockfish, where small size classes were abundant enough to analyze, the mean size of small fish was large (table 2). Sixteen species/size classes were included in the analysis of this sweep (table 2).

Ordination of the 14 areas and 16 taxa suggested a triangular arrangement, with southerly nearshore areas at the apex on the right, offshore areas in the upper left, and northerly areas (mostly nearshore) in the lower left (figure 23). Larger size classes of several species clustered at the right of the ordination, associated with the southern nearshore areas. Several widespread taxa, many of which were of medium size, occurred in the center of the ordination. Three other taxa, small to medium in size, occurred in the upper left of the ordination, associated with some offshore areas. Two other taxa (large canary and small yellowtail rockfish) had idiosyncratic distributions, both being below average in abundance in the southern nearshore areas and some offshore areas, but relatively abundant in some of the northern areas.

Overall patterns of abundance among areas influenced the ordination. The three nearshore areas in the south had large catches of a large subset of the species present (including some species that occurred nowhere else), while the UF OS area, which was near another corner

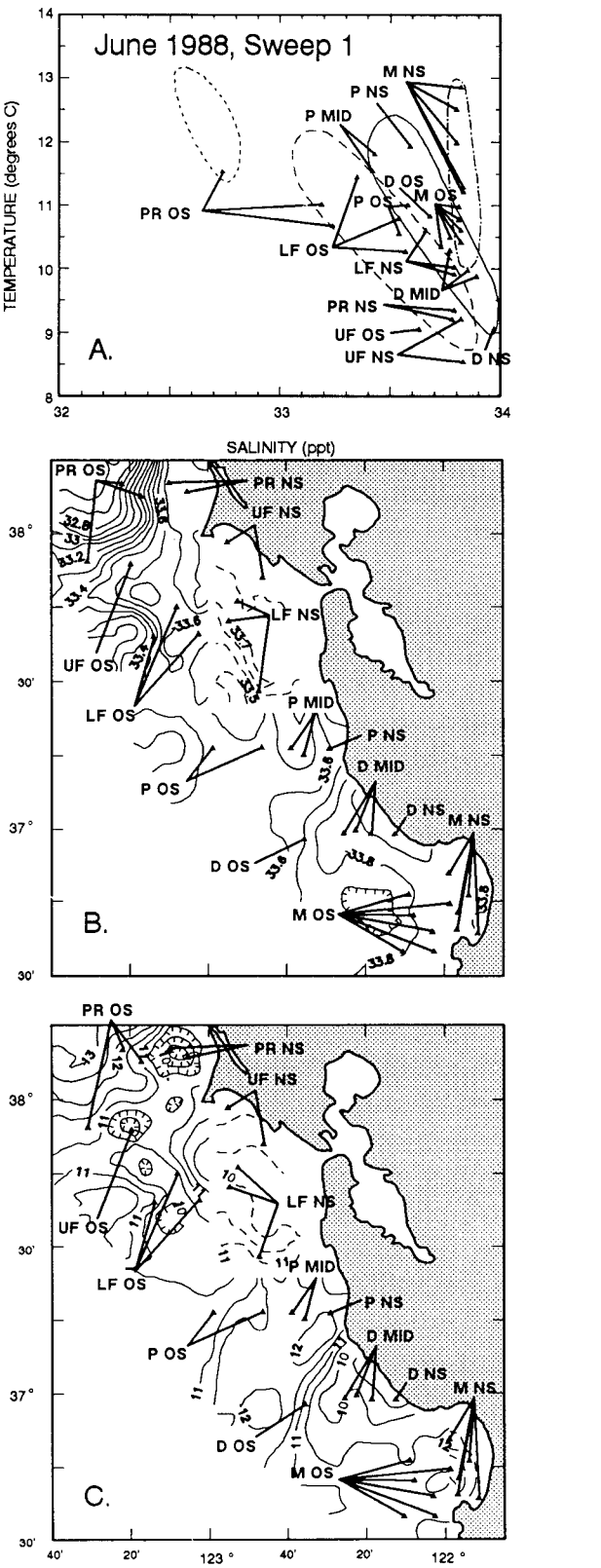


Figure 22. Trawl stations and their groupings from May/June 1988, sweep 1, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Monterey Bay and the Gulf of the Farallons were contoured separately (*dashed contour lines*) because of interruptions in sampling. Abbreviations of place names are defined in figure 1.

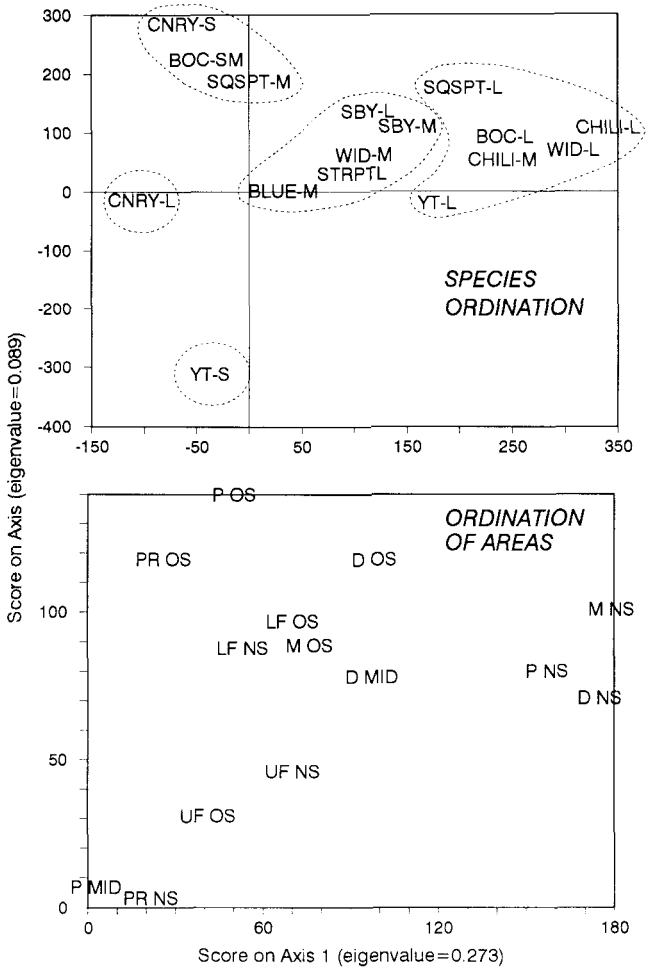


Figure 23. Ordination by detrended correspondence analysis of species and areas sampled during sweep 1 of May/June 1988 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

of the ordination, had large catches of another large subset of the species present (table 4). The P OS area, which was at the upper left apex of the ordination, yielded fewer species, but of those, most were relatively abundant. The P MID and PR NS areas had relatively small catches of few species. The presence of two somewhat uncommon taxa (large canary rockfish and small yellowtail rockfish) in one or both of these areas probably led to the prominent position of these areas in the ordination. We should note here that the most-inshore station off Point Reyes was not sampled during this sweep. The most-nearshore stations in other areas often had large catches, and we believe that the most-nearshore station off Point Reyes may also have yielded large catches, had we sampled it. We identified five groups of species/size classes for further analysis (figure 23).

The group of mostly large (or early-settling) taxa falling on the right of the ordination was most abundant in the nearshore areas to the south, both in less recently upwelled waters off Pescadero and Monterey, and at the very base of the active upwelling center off Davenport (figure 24a). Some, but not all, of the members of this group were also present farther offshore in the Davenport upwelling plume. The group in the center of the ordination, which included medium and large size classes and an early-settling species (stripetail rockfish), typically occurred in a large number of areas (table 2). As a group, however, they were most abundant in nearshore areas north of Monterey, and in the upwelling filament off Point Reyes (figure 24b). They were abundant near shore in the upwelling center off Davenport, and all but the stripetail rockfish were abundant in the newly upwelled water below Point Reyes. Thus their onshore-offshore distribution was similar to that of the first group, but this group occurred farther north. The group in the upper left corner of the ordination consisted of smaller size classes (two medium size classes and one small), and occurred largely in lower-salinity waters located offshore (figure 24c). Large canary rockfish were most abundant in the northern portion of the study area, both within the upwelling filament offshore of Point Reyes and in the more recently upwelled water above and below the point (figure 24d). Small yellowtail rockfish were also most abundant in the north, particularly in the upwelling filament off Point Reyes (figure 24e). Unlike other small fish, the small yellowtail rockfish were abundant in some nearshore areas, even in recently upwelled water below Point Reyes.

Summary: main sweep. Current upwelling was quite evident during this sweep of the study area. Despite this, large size classes of several species were found close to shore, even in the most recently upwelled water. We think that large catches of pelagic juveniles may also have been made at the most nearshore station off Point Reyes. Some of the smaller size classes were found farther offshore, in more oceanic water or in mixed water that had been upwelled less recently. The results of this sweep suggest that under some conditions large size classes can either maintain station close to shore, or move closer to shore in spite of upwelling.

In contrast to the idea that offshore transport in upwelling does not affect late-stage pelagic juveniles, larger size groups of a few species (most notably canary rockfish) were abundant in the plume of upwelled water extending off Point Reyes (figure 24). A similar effect did not seem to occur in the Davenport upwelling center, since the offshore areas within this plume (D OS at the edge of the plume, and M OS within) did not generally yield large catches of larger size groups, particularly in comparison to the inshore areas (figure 24).

Distributions in Point Reyes upwelling plume. Portions of two days and nights (5/31 and 6/1) were spent conducting hydrographic surveys and trawl samples near the

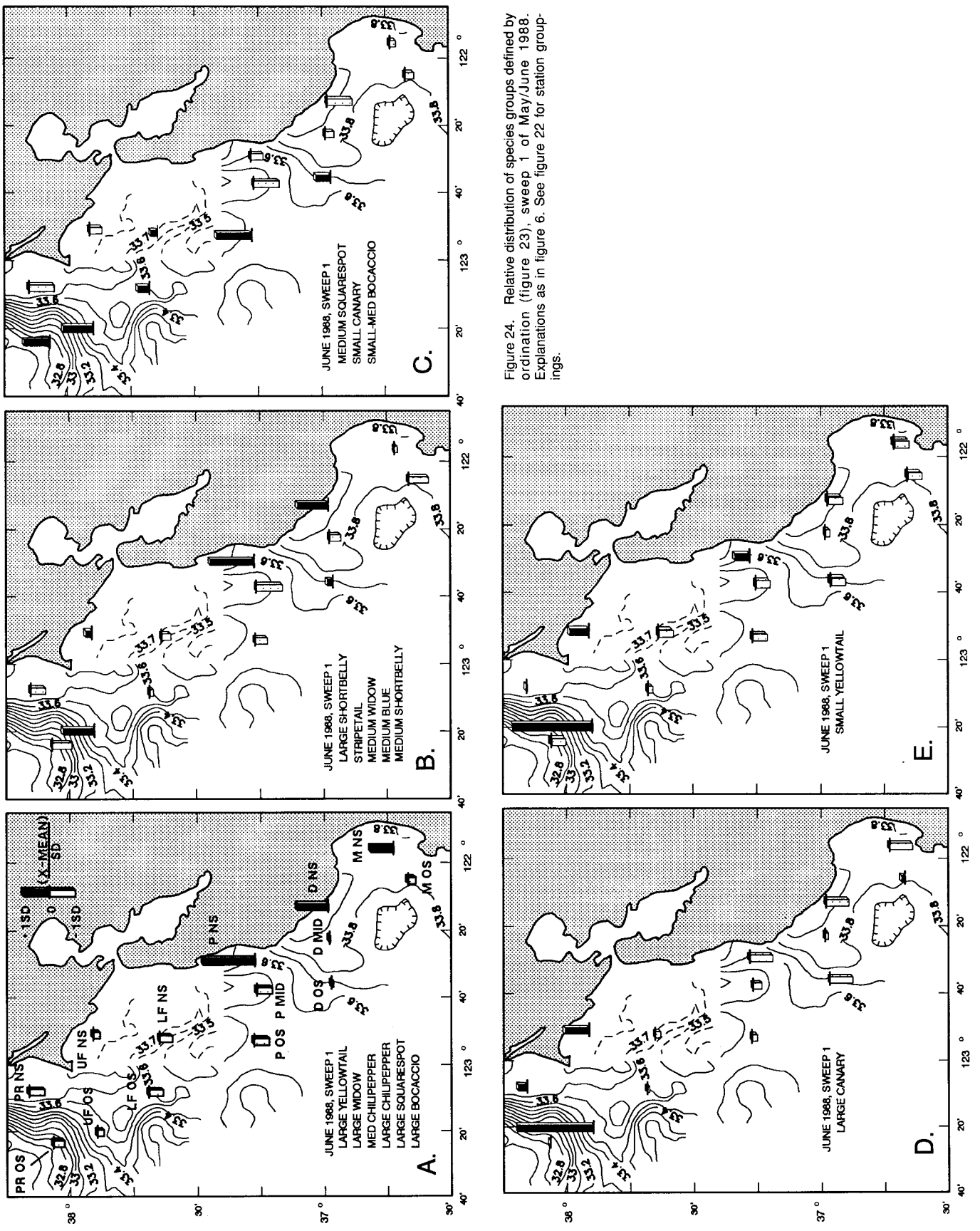


Figure 24. Relative distribution of species groups defined by ordination (figure 23), sweep 1 of May/June 1988. Explanations as in figure 6. See figure 22 for station groupings.

offshore end of the upwelling filament off Point Reyes. A core of cool, saline water extended over 55 km offshore of the Farallon Islands, and over 35 km offshore of the UF OS station sampled during the regular sweep (figure 25). Sharp gradients in temperature and salinity separated these waters from warmer, less saline waters on the south side of the plume (figure 25). On the north side of the plume, salinities dropped rapidly, but cool temperatures extended more broadly north. CTD casts in the core of the plume (figure 26, cast F) indicated only slight thermal stratification above 20 m. Nearer the southern edge of the plume (figure 26, cast E), salinity in the upper 50 m was much lower than in the core, and temperatures were slightly warmer, with sharp thermal stratification above 10 m. South of the plume (figure 26, casts A,B), the water column was strongly stratified, with a pycnocline at 40 m. Here, temperature converged with the core of the plume below 60 m, and salinity converged at about 100 m. To the north, (figure 26, cast D), complex thermal stratification with a sharp thermocline at 10 m yielded cooler temperatures above 50 m than found in the same depth range south of the plume; warmer temperatures below 50 m; and consistently lower salinities than south of the plume. This area bordered the low-salinity, offshore water mass evident off Point Reyes in the main part of the sweep. The core of the plume showed many indications of high productivity: green water, large amounts of krill, and abundant pinnipeds. Waters to the south of the plume were especially different: quite blue, and lacking the other indications of productivity.

Pelagic juvenile rockfish were sampled at three bathymetrically stratified stations on the night of 5/31–6/1 (figure 25, stations A, E, and F), and in single, standard-depth trawls at three stations on the night of 6/1 (stations B, C, and D). Station F was at the core of the plume; station E was at its southern edge; stations A and B were in blue water south of the plume; and stations C and D were north of the plume's core.

Catches of pelagic juvenile rockfish were highest in the core of the plume, and the three species/size groups that had been abundant in the northern portion of the study area during the regular sweep were also the most abundant in the plume (figure 25, station F). Catches of the two other species/size groups were at or just below average for the rest of the sweep. In the three abundant groups, catches were highest at 30 m and 110 m of depth. Catches of all groups were lower at the southern edge of the plume (figure 25, station E), and no juvenile rockfish were caught in the four trawls made in blue water south of the plume (figure 25, stations A and B). Catches were near to above average at the two stations north of the plume core (figure 25, stations C and D), where only small yellowtail rockfish were abundant.

These trawls suggest two main points. First, at least some pelagic juvenile rockfish can be advected offshore during upwelling. In fact, one adult olive rockfish was caught in trawls at the core of the plume; we think it lost contact with reefs off the Farallon Islands and was carried away. This advection is apparently not just a surface phenomenon, because pelagic juveniles were found well into the water column. Second, as found in the April 1987 survey, pelagic juveniles large enough to be captured in our gear may be rare in offshore water masses beyond the influence of some coastal processes. No pelagic juvenile rockfish were found in the blue water mass to the south of the plume, just as pelagic juveniles declined in abundance offshore of the coastal/offshore fronts in April of 1987.

June 1988, Sweep 2

The second sweep of the study area was carried out between June 2 and June 11. The regular portion of the sweep was completed on the night of June 8–9. Some offshore stations were sampled on the night of June 10–11.

Oceanography. Following the largely upwelling-favorable conditions during the regular portion of sweep 1, relaxed conditions prevailed immediately before sweep 2 (figure 2b). A brief period of moderately favorable conditions for upwelling occurred near the beginning of sweep 2, followed by relaxed conditions during the remainder of the regular portion of sweep 2 (figure 2b). Thus this sweep was largely characterized by conditions unfavorable for upwelling.

The thermosalinograph was operating during most of this sweep, but the ship's computer never was. When the thermosalinograph was operating, temperatures and salinities were recorded manually as in sweep 1. The thermosalinograph was not operating for a portion of this sweep, during which time near-surface temperature and salinity values were determined from CTD casts at trawl and CTD stations, and temperature was recorded by thermometer in the ship's running seawater system at points between trawl and CTD stations. Temperatures recorded by thermometer were calibrated to CTD readings (as in the April 1988 cruise).

Overall, oceanographic conditions during sweep 2 reflected the relaxation of upwelling. Evidence of previous upwelling could be found in the high-salinity waters present along the coast south of Point Reyes during sweep 2 (figure 27). But the absence of water cooler than 10°C (figure 27a,c) reflected the rarity of upwelling during the sweep. The coolest and most saline water was found in the northern, offshore portion of Monterey Bay, which was sampled during the period of the sweep that was most favorable for upwelling. The tongue of newly upwelled water present off Davenport during the first sweep (figure 22) was not evident during sweep 2,

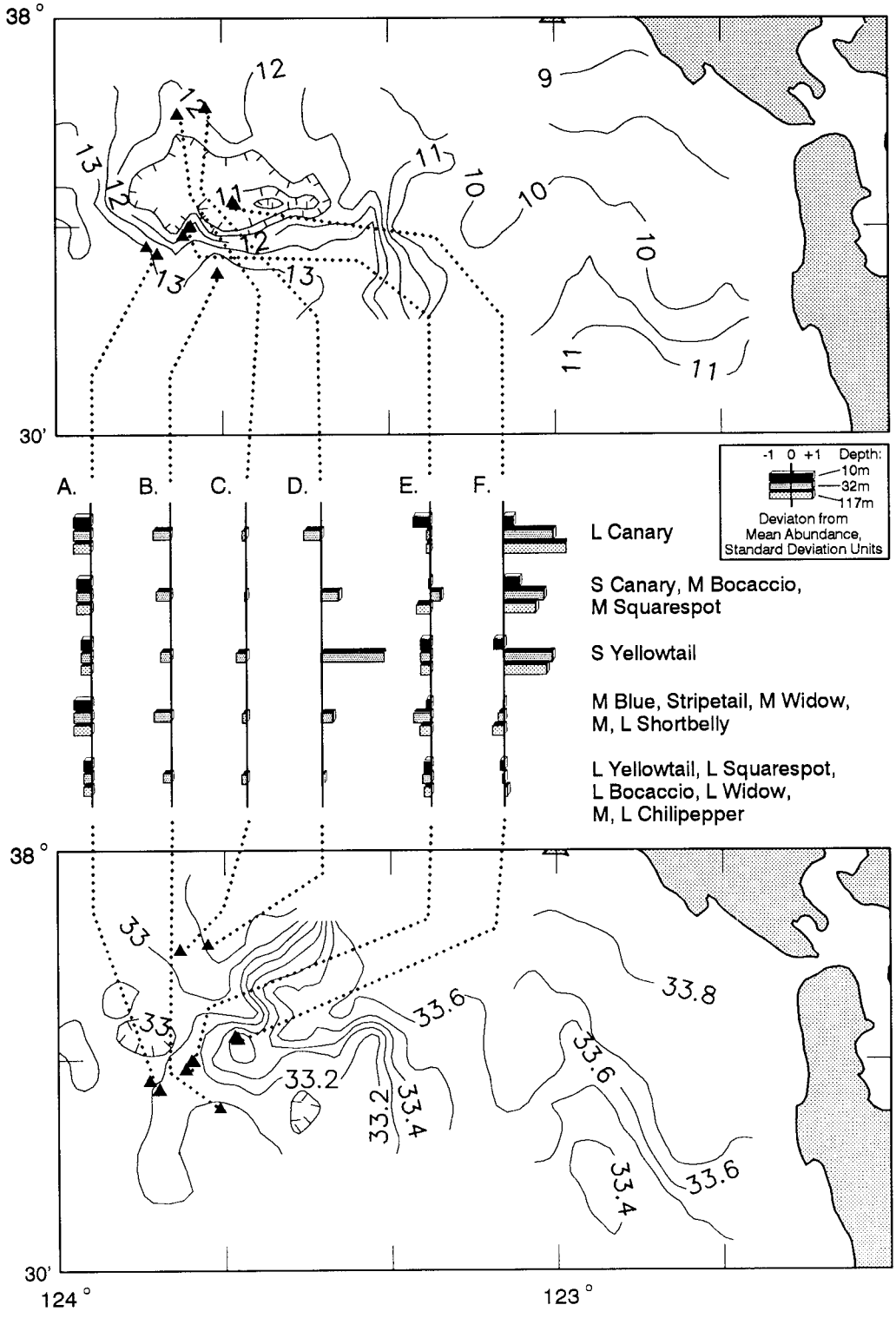


Figure 25. Distribution of pelagic juvenile rockfish in an upwelling plume, sweep 1 of May/June 1988. Positions of trawl and CTD stations are indicated by *triangles* on contour maps of surface temperature (*upper panel*) and salinity (*lower panel*). Comparative abundances of pelagic juvenile rockfish are presented in *bar graphs*, in which species are grouped according to the ordination of species and areas during the regular sweep (figure 23). The size of each bar is the average (over species in that group) of the difference between the $\ln(x+1)$-transformed abundance of a species at that station and the mean of that species over all stations in sweep 1, divided by its standard deviation over stations. Bars in groups of 3 represent bathymetrically stratified trawls at a station.

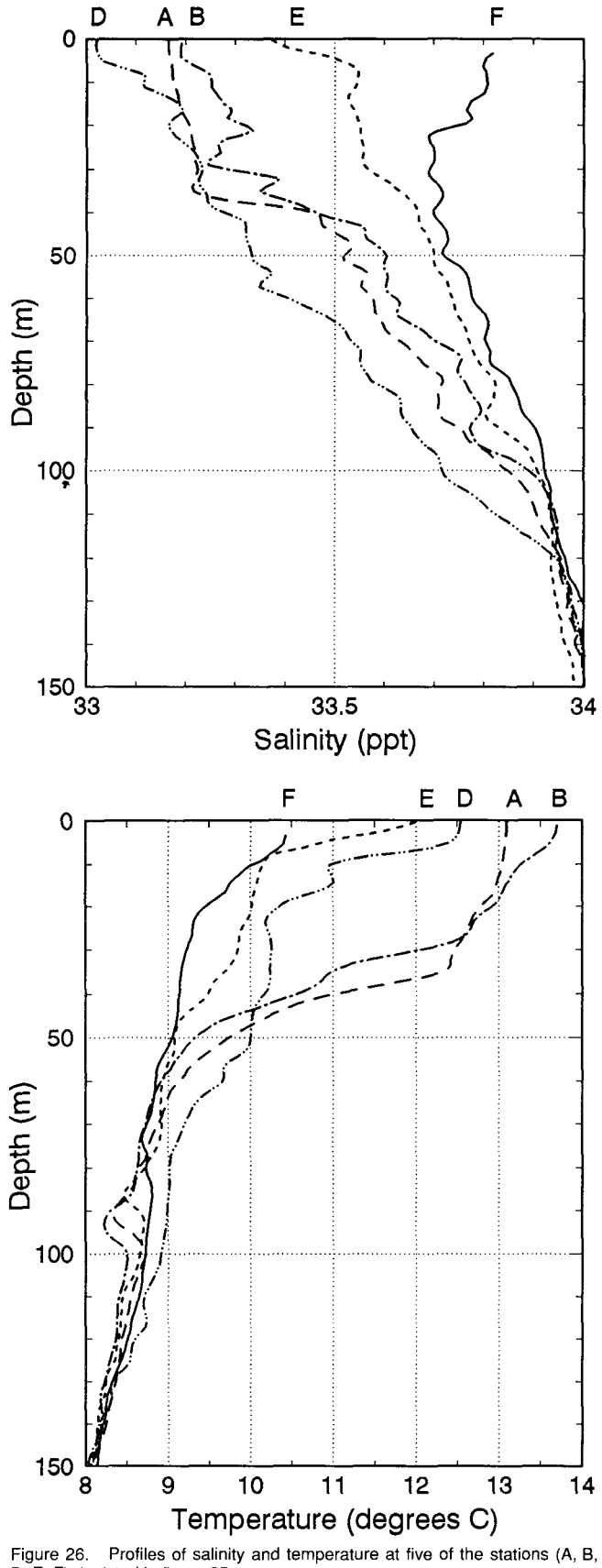


Figure 26. Profiles of salinity and temperature at five of the stations (A, B, D, E, F) depicted in figure 25.

and may have drifted across and into Monterey Bay. Local warming was evident in southern Monterey Bay (figure 27). The newly upwelled water present south of Point Reyes during sweep 1 (figure 22) likewise seems to have drifted south by sweep 2, as the most extensive mass of high-salinity water above Monterey Bay ranged from Pescadero into the southern Gulf of the Farallons (figure 27). This water had also warmed since sweep 1. The tongue of upwelled water present offshore of Point Reyes during sweep 1 was less extensive during sweep 2. The body of warm, low-salinity water present in the offshore area north of Point Reyes during sweep 1 was again present during sweep 2, but was closer to shore (figures 22, 27). Fronts indicating intrusion of offshore water were also evident from the Gulf of the Farallons to Pescadero, and offshore of Davenport (figure 27).

Trawl stations were combined into 13 groups of 1–4 stations each (figure 27). The stations within Monterey Bay (LM NS and UM NS) were in saline water that had warmed. The outer Monterey Bay stations were slightly less saline, but as cool as (LM OS) or cooler than (UM OS) the nearshore stations. The UM OS stations in particular may have been associated with the decaying plume of upwelled water from Davenport. The D NS station was in cool and saline water similar to the UM OS stations. The D OS stations were in waters of moderate salinity and temperature, indicating mixing of upwelled and nonupwelled water and local warming. The P NS station was on the inshore side of the mass of upwelled water that apparently had drifted south from the Gulf of the Farallons, and the P OS stations were near the offshore edge of this mass. The stations in the Gulf of the Farallons similarly were in coastal waters of moderately high salinity but moderate temperature. One station was at the edge of the freshwater outflow from San Francisco Bay. The LF OS stations were at and beyond the offshore front, and the UF OS stations were in the remnants of the Point Reyes upwelling plume. The PR NS stations were in mixed coastal waters, and the PR OS stations in the front and offshore water mass.

Rockfish distributions. All species except widow rockfish decreased in abundance from sweep 1 to sweep 2 (table 2), a decline that we attribute to settlement. As in sweep 1, individuals of most species were relatively large, with few small size classes present (table 2, appendix). Mean size of most taxa increased from sweep 1 to sweep 2, due to growth, appearance of larger fish within the study area, loss of smaller fish, or some combination of these factors. Mean size decreased only in squarespot, canary, and yellowtail rockfish (appendix d,i; table 2). Twelve species/size classes were included in the analysis of this sweep (table 2).

Although 13 groups of trawl stations were designated on the basis of oceanographic and geographic similarity,

one of these areas yielded no pelagic juvenile rockfish and two others yielded very small catches. These three areas (D NS, P OS, and D OS) were not included in the ordination, but were included in further analyses. Ordination of the remaining 10 areas and 12 species/size classes showed little general pattern, but instead seemed to be determined by the idiosyncratic distributions of different taxa (figure 28). Areas in the center of the ordination (UM NS, UM OS, GF, and PR NS) contained most species and size classes, at moderate to high relative abundances (table 4). Extreme areas in the ordination were characterized by the presence of one or a few particular species, with little concordance in the variation of species composition over areas. Areas at the right of the ordination (P NS and LF OS) were distinctive in the abundance of canary and yellowtail rockfish, which were uncommon or absent in other areas (figure 28). The upper left corner of the ordination was determined by the restriction of chilipepper rockfish to the LM NS area. The lower left corner of the ordination was determined by the abundance of three large size classes in three offshore areas (LM OS, UF OS, and PR OS). Unlike other sweeps, in this sweep larger taxa seemed to be associated with offshore areas. Species/size classes were assigned to four groups for further analysis, as indicated in figure 28.

The group of taxa on the right of the ordination (small and large canary rockfish, and yellowtail rockfish), were somewhat heterogeneous in their distributions, but shared a tendency to occur in the northern portion of the study area, particularly in the LF OS area (figure 29a). Large canary rockfish and yellowtail rockfish were also unusually abundant in the P NS area. As a group, they were also abundant in the PR NS and GF areas, where many species were found. The distribution of this group showed little relation to oceanography, except a tendency to be rare in the most saline waters and in the southern portion of the study area (figure 29a). The group in the middle of the ordination was abundant along with most other species in the PR NS, GF, and UM NS areas, and also in the PR OS and UF OS areas (figure 29b). The group seemed to have a disjunct distribution, being most consistently abundant in the northern portion of the study area, but also inside Monterey Bay. Its distribution bore no obvious correlation with oceanography: it was abundant both in low-salinity offshore waters and in high-salinity nearshore waters. This group consisted of medium to large size classes. The mostly large taxa in the lower left corner of the ordination were abundant with other taxa in the PR NS area, but were unusual in their abundance in the UF OS and LM OS areas (figure 29c). Two of these taxa (large widow and shortbelly rockfish) were also somewhat abundant in the PR OS area (where bocaccio also were taken, but in shal-

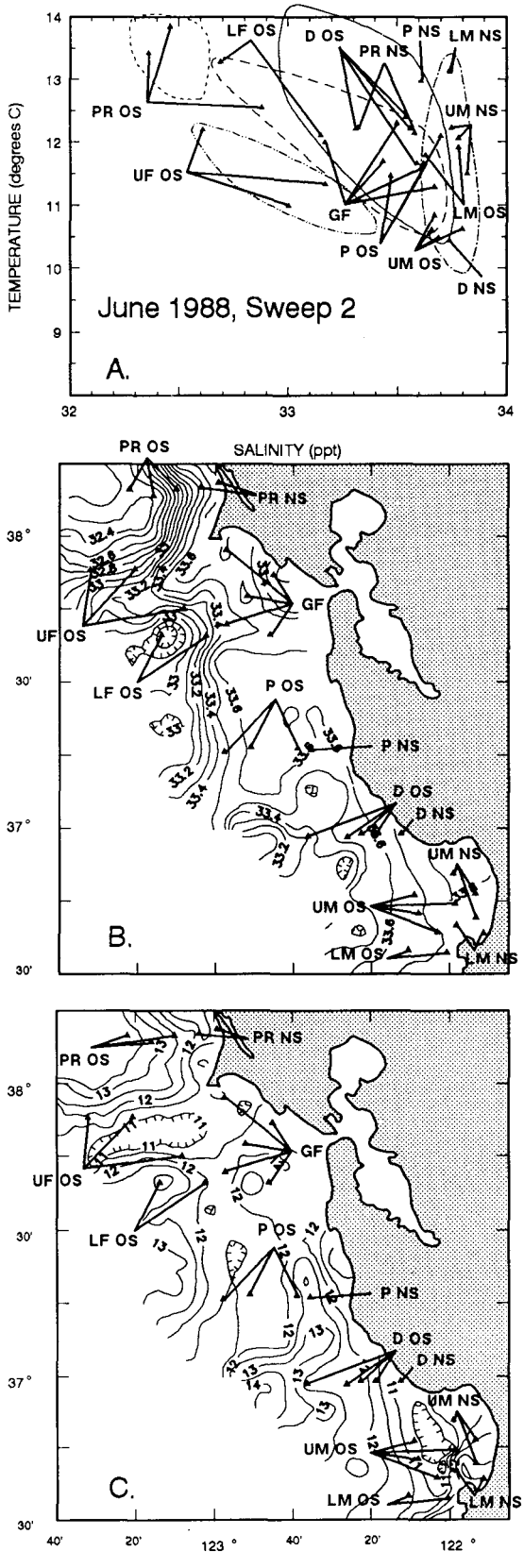


Figure 27. Trawl stations and their groupings from May/June 1988, sweep 2, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Abbreviations of place names are defined in figure 1.

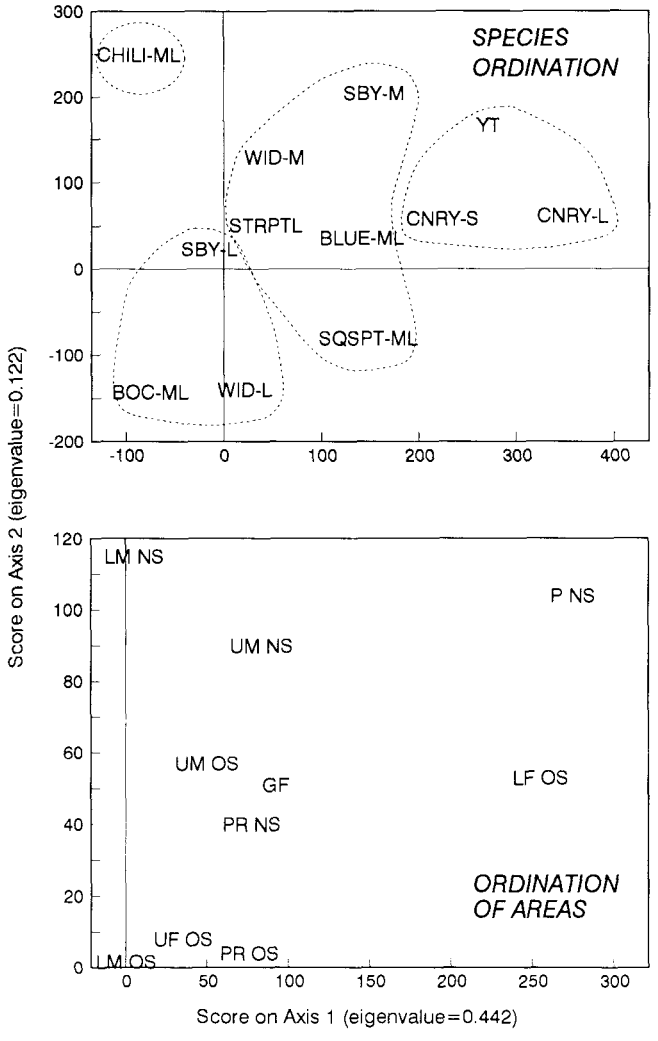


Figure 28. Ordination by detrended correspondence analysis of species and areas sampled during sweep 2 of May/June 1988 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

low trawls). This group, then, did not follow the pattern evident in other sweeps, and was relatively abundant offshore. However, it was also abundant in some areas of higher salinity, such as LM NS and LM OS. The final group, chilipepper rockfish, was abundant only in the LM NS area (figure 29d).

In some cases, more sense can be made of the distributions of fish during sweep 2 by comparing them to sweep 1 (figure 30). Both yellowtail and canary rockfish decreased greatly in abundance between sweeps (figure 30). Each had been only moderately abundant in the most southern portion of the study area during sweep 1, and both species decreased even more in sweep 2, presumably settling. Both species had been common in the northern part of the study area during sweep 1, and some fish remained in the general region. Small canary rockfish may have appeared in the PR NS area. We have no particular explanation for the unique occurrence of these species in the LF OS and P NS areas. In general, we see these species as having settled in large numbers between sweeps, leaving the remaining pelagic fish distributed patchily.

Members of the next group (blue, squarespot, medium shortbelly, and medium widow rockfish) had typically been present but not abundant off Point Reyes, and abundant to varying degrees in the offshore and inshore areas in the Gulf of the Farallons region, particularly in the Point Reyes plume (UF OS) during sweep 1 (figure 30). Most had been abundant in the nearshore areas off Pescadero and Davenport, and were present but not abundant nearshore and offshore in Monterey Bay. All of these taxa decreased in abundance by sweep 2—medium widow the least, and medium shortbelly the most. Typically they disappeared from the area of offshore intrusion at LF OS and disappeared or decreased substantially in the Pescadero and Davenport areas. Advection may have been responsible for the decline at LF OS, and advection or settlement at Davenport and Pescadero. Some members remained in Monterey Bay (particularly the cool water mass in upper Monterey Bay), perhaps advected from Davenport and not yet settled. Most members of this group apparently increased in abundance off Point Reyes, particularly in the nearshore area, and most remained abundant in the UF OS area. Thus the main pattern in this group was a decrease in abundance in the southern nearshore areas except Monterey Bay, and an increase in abundance off Point Reyes.

Large shortbelly, large widow, and bocaccio rockfish tended to show similar patterns of change (figure 30). Bocaccio decreased in abundance substantially between sweeps, while large shortbelly decreased less and large widow actually increased slightly in overall abundance. Like the previous group, members of this group disappeared in the area of the offshore intrusion at LF OS, and declined greatly off Pescadero and Davenport. They remained in some of the Monterey Bay areas. All increased, to greater or lesser degrees, off Point Reyes, and remained abundant in the remnants of the Point Reyes plume (UF OS).

Chilipepper rockfish essentially disappeared from the study area, apparently settling in most regions, particularly off Pescadero and Davenport (figure 30). Chilipepper rockfish remained abundant in large shoals (along with large shortbelly rockfish) in southern Monterey Bay.

Thus several groups that had been abundant off Pescadero and Davenport during sweep 1 had settled or been advected. We think that most had settled, but that remnants may have been advected into Monterey Bay (particularly those in the cool water masses in the northern portion of the bay) and remained pelagic. Large

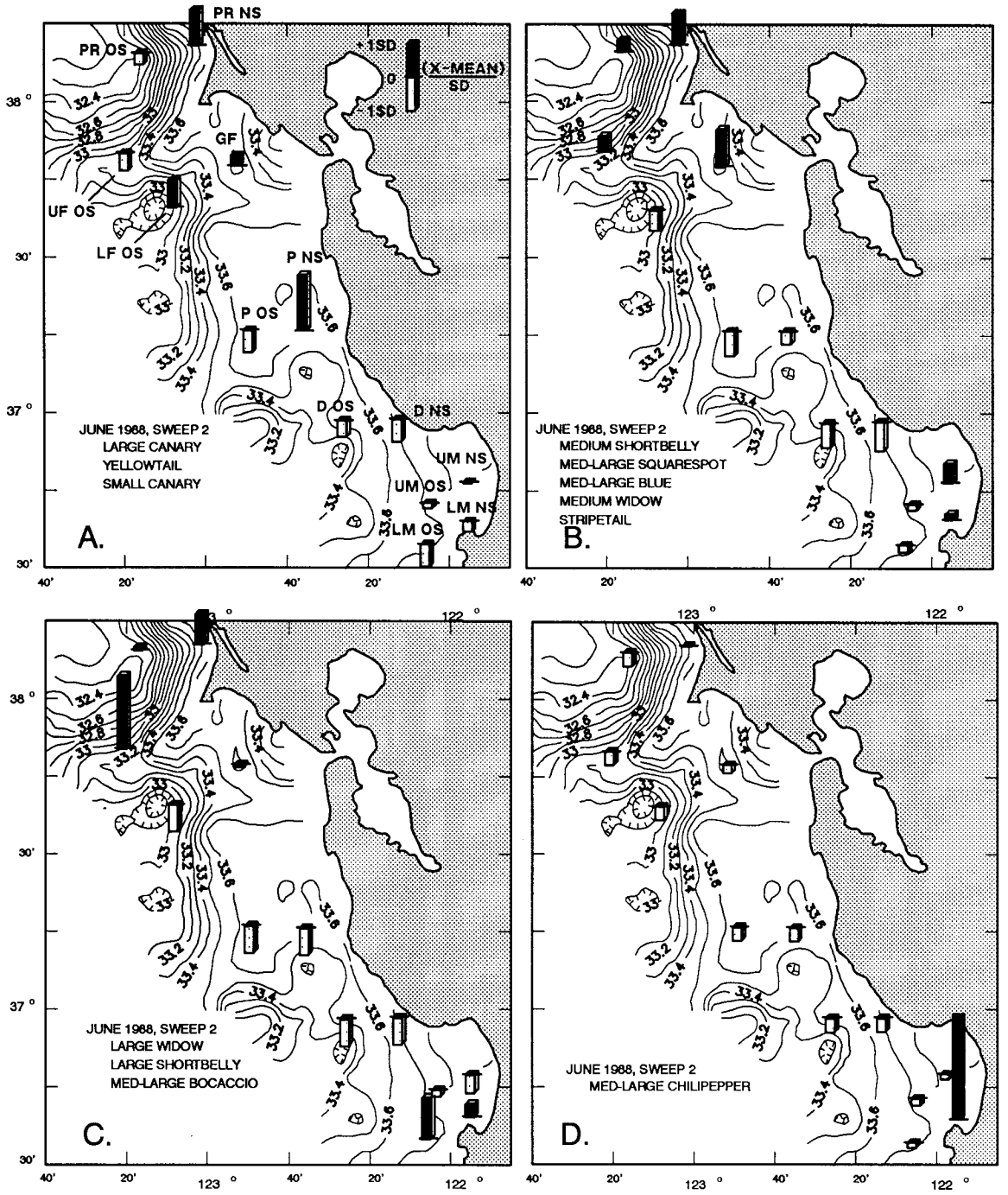


Figure 29. Relative distribution of species groups defined by ordination (figure 28), sweep 2 of May/June 1988. Explanations as in figure 6. See figure 27 for station groupings.

chilipepper and shortbelly rockfish formed large shoals in southern Monterey Bay during both sweeps. Perhaps this area is a nursery for postpelagic shortbelly and chilipepper rockfish. Many taxa remained abundant in the Point Reyes plume, indicating either a preference for conditions in this region or retention in an eddylike feature. Some increase in the abundance of large size classes in this area may have been due to growth of smaller fish. Several species increased in abundance off Point Reyes, both in the coastal waters nearshore and in the low-salinity water mass offshore. Nearshore, it is possible that the increase was more apparent than real, because the most shoreward station there was not sampled during sweep 1 (when many of the most shoreward stations yielded large catches) and had large catches in sweep 2. But this does not explain the increased catches

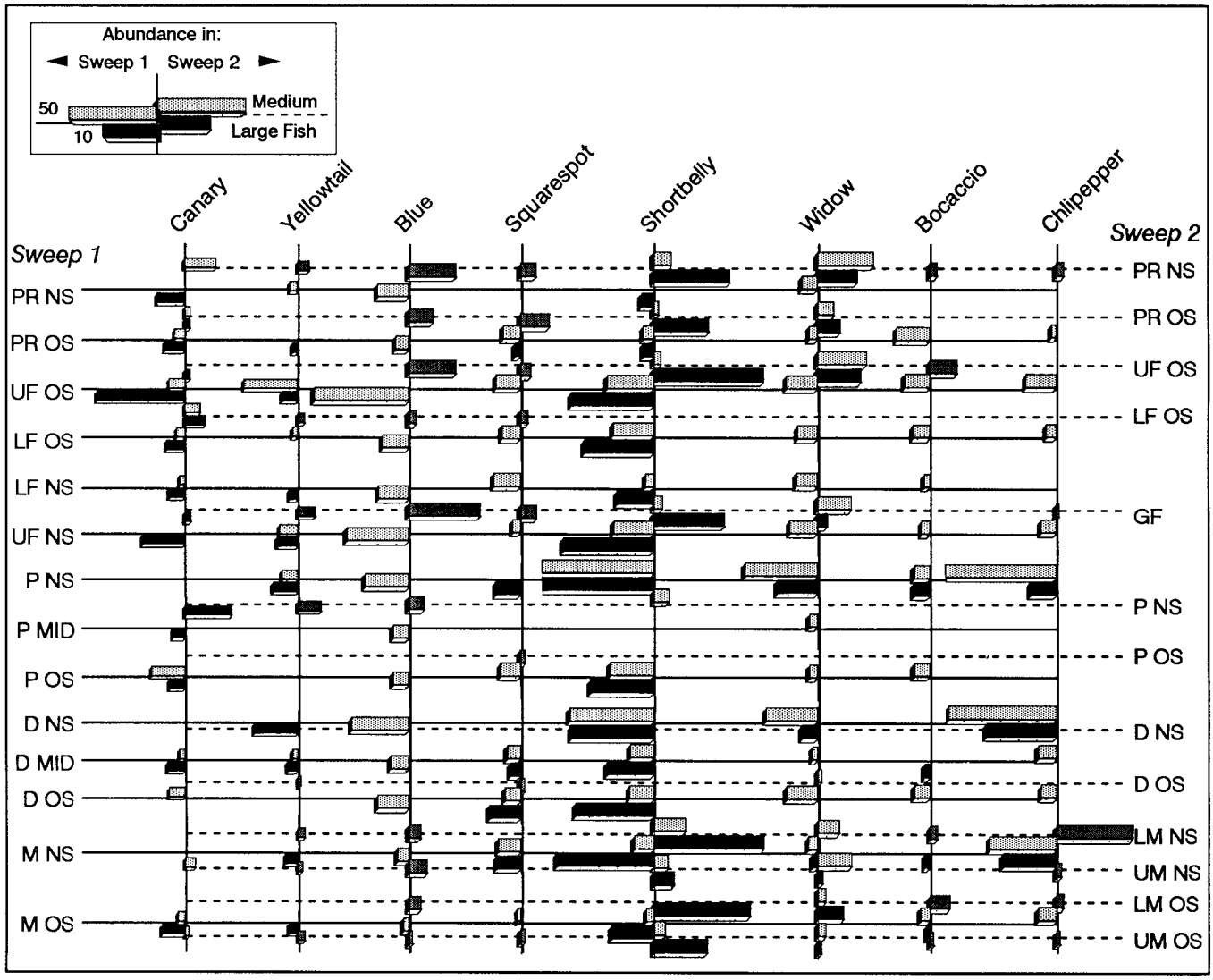


Figure 30. Comparison of pelagic juvenile rockfish abundances in sweeps 1 and 2 of May/June 1988. Station groups for sweep 1 are listed on the left, and the *aligned bars* (along the *solid horizontal lines*) extending to the left beneath each species indicate the species' abundance in the corresponding area. Station groups for sweep 2 are listed on the right. *Bars extending to the right* beneath each species (along the *dashed horizontal lines*) indicate the species' abundance in the corresponding area in sweep 2. *Pairs of bars* for one species indicate the smaller (*shaded upper bar*) and larger (*solid lower bar*) size classes for that species, if present, in that sweep. Species represented by only one size class are indicated with *one bar of intermediate shading*, aligned directly with the *horizontal line* linking areas. See table 2 for size classes. Scale is in number of fish per trawl, as transformed by $\ln(x+1)$.

offshore. In fact, the most offshore station had the largest catches, and these high catches occurred throughout the water column. We do not have a ready explanation for the apparently increased abundance of large fish in this offshore area.

Several stations were sampled offshore of the UF OS station during the two nights following the regular sweep, at longitudes between 123° 40' W and 124° 00' W. These were in an offshore water mass of low salinity and warm temperature (see figure 27 for nearby water mass characteristics). Like some of the other samples taken offshore of the upwelling front (April 1987; June 1988, sweep 1), these stations yielded few to no pelagic juvenile rockfish.

Summary. Because upwelling was not active and most pelagic juvenile rockfish were relatively large, gradients of oceanography and ontogeny were not large during sweep 2 of 1988. The size-related distributional patterns seen in some of the other sweeps were not evident at this time. In fact, little cohesive distributional pattern was found. In general, the 1988 year class was ontogenetically advanced: pelagic juveniles were relatively large in April and June, and their birthdates were earlier than in the previous 5 years (Woodbury and Ralston 1991). Many of the pelagic juveniles present during sweep 1 (often close to shore) seem to have settled by sweep 2, leading to large reductions in abundance in some areas (particularly Pescadero and Davenport). Pockets of pelagic

TABLE 5
Summary of Major Patterns in the Distribution of Pelagic Juvenile Rockfish, 1987–1988

Sweep	Range of oceanographic conditions	Range of fish sizes	North-south gradient?	Nearshore-offshore gradient?	Other notes
April 1987	Large gradient. Newly upwelled water to offshore water.	Most fish small; some advanced.	Some. Most species in south.	Yes. Small fish offshore; some early settlers nearshore.	Even small fish rare offshore of fronts.
June 1987 Sweep 1	Little gradient. Active upwelling in north; little offshore water.	Mostly medium–large fish; few small size classes.	Yes. A gradation.	Some. Smallest size group offshore, but mixed differences in some other species.	
June 1987 Sweep 2	Relaxation of upwelling; intrusion of offshore water.	Large gradient. Remaining large fish; appearance of small fish.	Yes. A gradation.	Yes. Smallest size classes in newly intruded offshore water; larger size classes near shore.	Increased abundance of larger fish near shore; shallow depth distributions in these areas.
June 1987 Sweep 3	Gradient from upwelled to offshore water.	Large gradient. Remaining large fish; appearance of small fish.	Yes.	Yes. New small fish offshore; larger fish near shore. Some small fish also near shore.	
April 1988	Small. No recent upwelling; little offshore water.	Mostly small to medium fish.	Did not sample northernmost areas.	Some differences within species, but some small fish nearshore.	
June 1988 Sweep 1	Active upwelling; little offshore water.	Mostly medium to large fish; few small fish.	Yes.	Large fish abundant near shore, even in recently upwelled water; some smaller size classes farther offshore.	Northerly-distributed juveniles abundant far offshore in upwelling plume off Point Reyes.
June 1988 Sweep 2	Relaxed upwelling; offshore intrusions.	Mostly medium to large fish; few small fish.	Yes, but some disjunct distributions in remains of upwelled water in north & south.	No. Idiosyncratic distributions of remnants of large year class.	

juveniles remained in the study area, in Monterey Bay and in the decaying upwelling plume off Point Reyes. Maybe these fish just had not settled yet, and it is possible that they were retained in areas unsuitable for settlement. The apparent increase in abundance of some species in nearshore and offshore areas of Point Reyes remains puzzling. The increase may have been (but was not necessarily) apparent rather than real in the nearshore area, since the most nearshore station was not sampled in sweep 1. However, the increase in the offshore area, which was very low-salinity offshore water, has no evident explanation. In general, we think that this sweep represents the remnants of a large year class that had mostly completed its pelagic stage.

DISCUSSION

The system we have studied is complex and dynamic. Physical conditions change in a matter of days; the propensity of the physical system to behave in certain ways changes seasonally; and the entire system changes from year to year. Furthermore, the pelagic juvenile rockfish we sampled are a transitional stage, which appeared in our sampling gear as a function of the timing of parturition and survival of larvae, and which left the pelagic zone as a function of ontogenetic changes. Because of these factors, each of our sampling sweeps was like a separate anecdote, offering different physical conditions and different size and species composition of pelagic juvenile rockfish.

In our survey of distributions in two years we found some patterns that we cannot account for on the basis of the data at hand, such as idiosyncratic distributions of some species. Perhaps this should be expected, because we did not know the spatial aspects of parturition and subsequent dispersal and survival of larvae, all of which may differ from species to species. However, we did find two recurrent patterns of differences in distribution among species and size classes that suggest consistent factors affecting the distribution of pelagic juvenile rockfish just prior to settlement (table 5).

First, at least some north-south gradient in species composition or abundance was evident in six of the seven sampling sweeps through the area, and the one sweep without such a gradient was abbreviated, lacking the most northerly stations (table 5). Second, clear gradients in fish size, from small fish offshore to larger fish nearshore, were present in four of the seven sweeps, with some indications of such a gradient in two additional sweeps (table 5). The sweeps with little onshore-offshore gradient in fish size (June 1987, sweep 1; April 1988; June 1988, sweep 2) either lacked strong onshore-offshore gradients in oceanographic conditions or lacked a wide range of fish sizes (table 5). We think that the north-south gradient may be either an effect of larger-scale

factors (such as the geographic ranges of species) or a manifestation of local effects. We think that the onshore-offshore gradient in fish size is due to offshore transport of small fish during upwelling, and to ontogenetic changes that make larger fish less susceptible to offshore transport or enable them to actually move toward shore. Our data also suggest that relaxation of upwelling conditions can affect the onshore-offshore distribution of fish.

Some species recurred in the northern portion of the study area, suggesting that some of the latitudinal differences in species composition observed in this study were the result of large-scale geographic factors. The most consistently northern species was the canary rockfish, which was often abundant in the northern part of the study area and was rarely abundant in the southern part. The yellowtail rockfish was also abundant in the north, but not to the same extent as canary rockfish. These patterns occurred in both 1987 and 1988, suggesting that the repeated observations were not due merely to serial correlation of consecutive samples. No species occurred as predominantly in the south, although stripetail rockfish and bocaccio were more abundant in the south during some sweeps from each year of sampling. Persistent geographical differences in the distribution of species as pelagic juveniles may reflect the geographical ranges of the parent populations. Both canary and yellowtail rockfish have northerly distributions, although other species occur to the north as well. Alternatively, different portions of the region may persistently support the survival or retention of the larvae and juveniles of particular species, due to recurrent local conditions.

Some of the differences in geographical distribution of pelagic juvenile rockfish did appear to be local effects. This was best illustrated by apparent changes in distribution observed between sweeps. For example, larger size classes of several species were most abundant near shore in the southern portion of the study area during sweep 1 of May/June 1988, and by sweep 2 had apparently settled in the south, but increased in abundance in the north, perhaps due to advection from other areas (figure 30). Thus the apparent northerly distribution during sweep 2 was an artifact of local settlement and advection, not an effect of large-scale geographical factors. Remnant patches of species that have mostly settled may also suggest geographical trends, but these distributions may really be due to local retention or to the proximity of postpelagic habitat, as illustrated by the distribution of chilipepper rockfish in sweep 3 of June 1987 (figure 18d) and in sweep 2 of June 1988 (figure 29d).

The apparent relationship between fish size and onshore-offshore distribution manifested itself in different ways. One manifestation was the restriction of most small fish to offshore regions, beyond the upwelling front. This was evident in the April 1987 cruise, and in sweeps 2 and 3 of June 1987. In these sweeps, very early-stage pelagic juveniles, some appearing for the first time in our trawls, occurred only offshore. As discussed below, we think that such distributions are the result of offshore advection of larvae and early juveniles of *Sebastes*. Another manifestation was the occurrence of larger size classes close to shore, even in upwelling centers. This was most evident in sweep 1 of May/June 1988. Observations like this suggest that later-stage individuals can reach the nearshore zone or remain there, even when upwelling is active. The last manifestation was the actual comparison of distributions within species, which often (but not always) showed that where the distributions of smaller and larger size classes differed, the larger size classes were closer to shore (or in more recently upwelled water), and the smaller size classes were farther from shore, in offshore water or mixes of offshore and upwelled water.

These size-related distributional patterns were not universal. In several sweeps, some species did not fit the general pattern (such as the offshore distribution of large size classes near Point Reyes during sweep 2 of June 1988, and several cases in which small size classes occurred close to shore). Cases such as these will conflict with the hypothesis we develop in this paper. Other exceptions to the general pattern occurred when ranges of fish size or oceanographic conditions were narrow, and in that sense may be exceptions that prove the rule (table 5). For example, little offshore water was present in the study area during sweep 1 of May/June 1987, and small size classes were not common, so size-related patterns were not the major type of variation in distribution found during the sweep. Similarly, large size classes were not common in April of 1988, and upwelling had not been active, so the absence of upwelling may have led to the lack of onshore-offshore differences in the distributions of size classes.

The occurrence of small size classes offshore, beyond the most recently upwelled water, suggests that larvae and early juveniles had been advected offshore during upwelling. The species of rockfish encountered in this study give birth to larvae from the shoreline (e.g., blue rockfish and the "copper complex") to the shelf break (e.g., shortbelly rockfish), so we would expect early larvae to occur in various areas over the shelf. But despite possible differences in the distributions of earlier larvae, the small pelagic juveniles sampled in this study showed similar distributions. These distributions suggest a common causal factor, which we think is offshore advection during upwelling. The appearance of new groups of small pelagic juveniles offshore, often near the upwelling front (as in April of 1987 and sweeps 2 and 3 of June 1987), suggests that they had not been present in the upwelled water that came to occupy surface wa-

ters over the shelf, and if they had been in waters over the shelf before upwelling, they were advected offshore.

The decline in abundance of even small pelagic juveniles offshore of the upwelling front suggests that factors such as habitat selection, passive advection, or differential survival of larvae or juveniles may occur offshore of the upwelling front. Our best data for the offshore decline in abundance came from April 1987, when small pelagic juveniles were abundant in and near the upwelling front, yet few were found in an extensive offshore excursion beyond the upwelling front. The absence of pelagic juveniles in the blue water mass south of the upwelling plume sampled after sweep 1 of May/June 1988 fits the same pattern, as does the rarity of pelagic juveniles in the offshore stations sampled in the same region after sweep 2 of June 1988. However, the general rarity of small pelagic juveniles during May/June of 1988 leaves open the possibility that small juveniles were not available. Nevertheless, there was a strong contrast in the abundance of juvenile rockfish within and without the upwelling front in that area. Larval surveys suggest that *Sebastes* larvae may occur dozens of kilometers offshore (Moser and Boehlert 1991), so the rarity of small juveniles offshore of the upwelling front is interesting. Since our sample size was small, perhaps the pattern is not general. If it is general, the pattern suggests that the upwelling front is important to larvae or early-stage pelagic juveniles. Larvae or juveniles may seek the conditions present in the front, or individuals away from the front may not survive.

The frequent occurrence of larger pelagic juveniles close to shore, even when upwelling is active, suggests that ontogenetic changes allow these fish to reach the nearshore zone, or to remain there once they are present, in spite of upwelling. Their distributions stand in contrast to those of smaller fish, which were often offshore during upwelling. Larger size classes were very abundant near shore in sweep 1 of May/June 1988, when upwelling was quite active. In April of 1987, when most of the pelagic juveniles were relatively small and distributed offshore, a few early-settling species were found closer to shore in recently upwelled water. It seems unlikely that these large fish were simply survivors of larvae and smaller juveniles retained near shore, since we rarely found small juveniles near shore.

We suspect that the changes in distribution in larger fish are not related to size per se, but to ontogenetic stage, since distributional differences occurred between size classes in most species, independently of differences in size across species. Furthermore, the relative sizes of pelagic and newly settled individuals are concordant over species. Thus, "copper," canary, and stripetail rockfish are relatively small as pelagic juveniles (table 2, appendix), and are also relatively small as newly settled individuals (Anderson 1983). Yellowtail and blue rockfish are larger as pelagic juveniles (table 2, appendix), and are also larger as newly settled individuals (Anderson 1983). This alone suggests that pelagic juvenile rockfish reach species-specific stages at which they become competent to settle. The nearshore distribution of larger pelagic juveniles further suggests that this "competence" brings behavioral changes that facilitate inshore movement or retention. We do not know what these behavioral changes are, but discuss possibilities below.

While the more nearshore distribution of larger pelagic juveniles suggests active, behaviorally influenced movements, some of our data suggest passive transport of even larger size classes. We have already discussed the apparent offshore transport of larvae and early-stage juveniles during upwelling. We also have some evidence, both specific and circumstantial, for passive movement during relaxation of upwelling, and for passive movement associated with apparent entrainment in frontal features.

Fish distributions changed with a substantial relaxation of upwelling near the beginning of sweep 2, 1987. An obvious change was the appearance of small size classes of several species with the intrusion of low-salinity offshore water masses into the study area. While Send et al. (1987) argued for little cross-shelf transport during relaxation from upwelling, we think that the apparent onshore displacement of the upwelling front and appearance of low-salinity water was due to relaxation of factors forcing the front offshore. This shift apparently brought with it small pelagic juveniles that had been offshore of our study area. We also observed apparent alongshore advection of water and associated pelagic juveniles. With the decay and offshore displacement of the cool, recently upwelled water off Point Reyes, a new body of warmer but still saline water appeared near shore, and apparently carried with it large numbers of some species of rockfish. The association of alongshore advection with relaxation of upwelling was documented by Send et al. (1987). Finally, we saw apparent increases in nearshore abundance of several larger size classes in the southern part of the study area. With the onshore movement of the upwelling front, the band of high-salinity water along the coast had narrowed, and we suspect that this may have concentrated some fish closer to shore. Also associated with some of this was the unusually shallow depth distribution of many taxa in the newly developed thermocline. In sum, these direct observations demonstrate three types of change in distribution of pelagic juvenile rockfish associated with relaxation of upwelling. The lack of marked on/offshore stratification of size classes during sampling periods without active upwelling (such as April 1988, and to a lesser extent sweep 1 of May/June 1987) provide some indirect evidence for the effect of

upwelling relaxation. The lack of offshore transport in upwelling, the mixing of offshore and nearshore water masses, and perhaps advection, may have created conditions that allowed the mixing of earlier- and later-stage pelagic juveniles.

We also have evidence suggesting that even large pelagic juveniles can become associated with or entrained in oceanographic features that are related to upwelling. We saw several instances in which a number of species were abundant in frontal areas, such as the Davenport-Monterey area during April of 1987. Our best-studied example of this was the upwelling plume offshore of Point Reyes during 1988. Several taxa were abundant near the base of this structure (but still 30 km offshore of Point Reyes) during both sweeps 1 and 2, and the same groups were abundant in the core of the plume another 25–30 km offshore after sweep 1. Many species abundant in the plume were also abundant near shore in the Gulf of the Farallons and off Point Reyes, so nearshore populations were not evacuated by offshore transport. However, the abundance of pelagic rockfish 50–60 km from shore suggests advection, and the persistence of part of this assemblage for at least one week suggests that the assemblage was retained. Incidentally, the correlation of rockfish distributions 100 m deep with the surface features we measured indicates that offshore advection of organisms during upwelling is not always limited to the classical 20–30 m Ekman layer, and in fact the features we observed at the surface were often evident to at least 30 m of depth (figure 7; Johnson et al. 1992). Advection and retention may have been an entirely passive process, in which fish were simply caught up in the current, or it may also have involved habitat selection by juveniles for conditions present in the advected water mass, but the result was nevertheless entrainment and retention of these fish. Without major changes in fish behavior (and perhaps even with behavioral changes), these fish would tend to travel with the structure.

The appearance of some taxa of pelagic juveniles near shore off Point Reyes in sweep 2 of June 1987 (described above) may illustrate the movement of entrained juveniles within a water mass, even though we do not know the source of the water mass or juveniles. On a different scale, the patchy and sometimes disjunct distributions of some species in sweep 2 of 1988, after many of the pelagic juveniles had settled, bear signs of the retention of nonsettled fish in particular water masses. For example, many species had been abundant in the newly upwelled water north of Monterey Bay during sweep 1, but essentially disappeared (mostly due to settlement, we assume) by sweep 2. However, remnants of these species' populations were found in Monterey Bay, where we have evidence for remnants of the cool, saline water mass that had been the Davenport upwelling plume during the previous sweep. We suggest that this water mass had drifted into Monterey Bay with the cessation of upwelling-favorable conditions, and carried with it some of the fish that had been present previously, but had not yet settled.

We have therefore found evidence both for the importance of passive entrainment and transport of pelagic juvenile rockfish and for ontogenetic changes in distribution that suggest a degree of independence from upwelling in later-stage individuals. It is apparent that younger pelagic juveniles may become aggregated near the upwelling front when upwelling has been active, and that later-stage pelagic juveniles may also be found in association with upwelling-related features. Distributions of pelagic juveniles may also move in association with changes in these features, and mixing may reduce onshore-offshore differences in fish abundance. These observations suggest that the fate of pelagic juveniles may depend on oceanographic conditions. The nearshore distribution of larger size classes, however, suggests that the fate of later-stage individuals does not depend on oceanographic conditions, at least in the same ways as implied above.

We think it would be useful to examine the distribution of rockfish larvae before and after the spring transition, which initially generates the distinction between the nearshore and offshore water masses seen in spring and summer (Send et al. 1987). The fate of larvae transported far offshore (up to hundreds of kilometers) remains unknown. Our smaller-scale data suggest that successful larvae either are associated with or come to be associated with the upwelling front, but we do not know whether this association is general, and we do not know when it begins. In addition, it would be interesting to know whether, and how, later larvae and early pelagic juveniles come to be associated with geographically restricted portions of the upwelling front, since these associations could influence the geographic extent of successful recruitment. In any case, we proceed with the working hypothesis that the larvae and early-stage pelagic juveniles of coastal *Sebastes* species are offshore of the upwelling front, and must move or be moved tens of kilometers closer to shore in order to find habitats suitable for the next stages in their life cycle.

Passive transport, often associated with relaxation of upwelling, may be sufficient for some nearshore movement of pelagic juveniles. This transport could occur in several ways. First, displacement of the upwelling front during relaxation may bring early-stage juveniles located in and beyond the front closer to shore, as we observed in sweep 2 of June 1987. Second, cessation of upwelling may also allow mixing of upwelled and offshore water, introducing pelagic juveniles to the coastal water mass,

where they may become mixed and remixed with additional pulses of upwelling and relaxation (which create new fronts between recently and less-recently upwelled water, as described by Send et al. 1987). Such changes could have accounted for the reduced onshore-offshore gradients in fish composition in April of 1988 and in May/June 1987, sweep 1. Third, plumes of upwelled water and the associated fronts themselves may be advected along and toward shore, as suggested by Schwing et al. (1991) and inferred for barnacle larvae by Farrell et al. (1991) and Roughgarden et al. (1991). Finally, relaxation may bring about direct cross-shelf transport of mixed coastal water, as suggested in the southern portion of our study area in sweep 2 of June 1987. Hobson and Howard (1989) suggested that cross-shelf transport during relaxation was responsible for mass strandings of juvenile rockfish in June of 1988. In a sense, the spatial and temporal heterogeneity of the coastal upwelling system may provide opportunities for pelagic juveniles to move into the nearshore region more or less passively. However, the effect of upwelling relaxation may be different in rockfish than in barnacles, where successful recruitment seemed to occur during periods of relaxation from upwelling that lasted weeks (Farrell et al. 1991; Roughgarden et al. 1991). Since the pelagic stage of barnacles lasts only a few weeks, successful recruitment might depend on periods of relaxation that encompass most of the pelagic stage, so that larvae are never advected far from shore. In contrast, the extended pelagic stage of rockfish may allow larvae and juveniles to be transported offshore but still experience several relaxation events during their late pelagic existence.

But although passive transport may be sufficient to account for the nearshore transport and settlement of juvenile rockfish, it may not be necessary, or it may not be the entire story. The onshore-offshore differences in fish size that we observed strongly suggest that ontogenetic changes in behavior influence distribution and may allow for settlement even in the absence of relaxation of upwelling. Regardless of the role passive transport may play in the onshore movement of pelagic juveniles, the abundance of late-stage pelagic juveniles close to shore even under intense upwelling conditions strongly suggests that later-stage individuals are affected by upwelling differently from earlier-stage individuals. Thus we do not believe that settlement of juvenile rockfish is as dependent on movement of the upwelling front as it is in larval barnacles (Farrell 1991; Roughgarden et al. 1988, 1991).

We do not know what behavioral changes take place in later-stage pelagic juveniles. An obvious possibility is movement deeper into the water column, where transport may be onshore rather than offshore (Bakun 1986). Later metamorphic stages of the flatfishes *Citharichthys sordidus* and *C. stigmaeus* both occupy deeper positions in the water column and are found closer to shore than earlier metamorphic stages off central California in spring and early summer (Sakuma 1992). But although the ontogenetic changes in depth distributions that Sakuma observed were quite clear, Lenarz et al. (1991), using data from the same sampling survey as Sakuma, were unable to find specific evidence for increasing depth distributions in larger rockfish (although they found deeper distributions in May/June than in April).

Another possibility is that later-stage pelagic rockfish undergo behavioral changes that allow them to take advantage of frontal structures or conditions associated with relaxation in a way that facilitates shoreward transport. One such mechanism may have been illustrated by the unusually shallow distribution of later-stage pelagic juveniles above the thermocline off Monterey during the relaxation event in sweep 2 of June 1987. In such a bathymetric position, individuals may be carried closer to shore in cross-shelf transport, if it occurs, or may be subject to shoreward transport in internal waves (Shanks 1983). Shenker (1988) and Doyle (1992) have noticed large numbers of pelagic juvenile rockfish in the neuston, raising the possibility that a shift to shallow water may be a regular part of the late pelagic existence of rockfish. But this behavior would only be successful when upwelling is not active, and we know that later-stage pelagic juveniles are found close to shore even when upwelling is active. Furthermore, we have not observed any widespread tendency for shallow distributions in late-stage pelagic juveniles (Lenarz et al. 1991). Clearly, however, surveys of the depth distributions of different-stage individuals under a variety of circumstances would be a valuable area for future study. Other behavioral changes are also possible (including young fish swimming toward shore, if they have a means of determining the direction of shore), some of which may not have occurred to biologists yet. We recommend recognizing the problem and focusing some direct study on obvious alternatives like changes in depth distribution, but keeping an open mind and conducting studies of sufficient generality to detect the unexpected. The entire process of settlement may be multistage, requiring fish first to move into the nearshore region and then to actually find shore and suitable settlement habitats. The process is likely to be imprecise, depending on sensory cues that are available in the immediate environment of the fish and that trigger simple changes in swimming activity. It is also likely that the behaviors will differ among species.

At this point, then, we are unable to determine the relative roles of passive transport processes and more active behavioral changes in the onshore movement of pelagic juvenile rockfish. At one extreme, entrainment,

transport, and mixing associated with fronts and other upwelling-related features could be of primary importance in the recruitment of rockfish, much as these processes seem to be important in barnacles (Farrell et al. 1991; Roughgarden et al. 1991). At the other extreme, advection and entrainment in upwelling-related features may indeed happen in rockfish, but most fish manage to settle anyhow. Here, association with upwelling-related structures may influence the geography of settlement and may entrain a few unlucky individuals, but may not have a large negative effect on settlement. We suspect that the latter case may be nearer the truth, particularly since unpublished data so far seem to indicate a good correlation over years between the abundance of pelagic juveniles and settled juveniles (S. Ralston and D. F. Howard, unpublished; D. venTresca, pers. comm.). Continued analysis of the pelagic stage, particularly the distribution of larvae and early juveniles around the spring transition, and the horizontal and vertical changes in distribution of later-stage pelagic juveniles, will be valuable in distinguishing the effects of passive and active factors in rockfish settlement. Another useful approach might be to compare the timing of settlement with oceanographic conditions, perhaps using settlement marks on rockfish otoliths (Haldorson and Richards 1987; Amdur 1991).

ACKNOWLEDGMENTS

We thank two anonymous reviewers for their comments on the manuscript, the captains and crew of the R/V *David Starr Jordan*, and David Woodbury and the rest of the scientific staff on the rockfish cruises, who did the hard work for this study. Manuel Gallardo-Caballo kindly translated the abstract.

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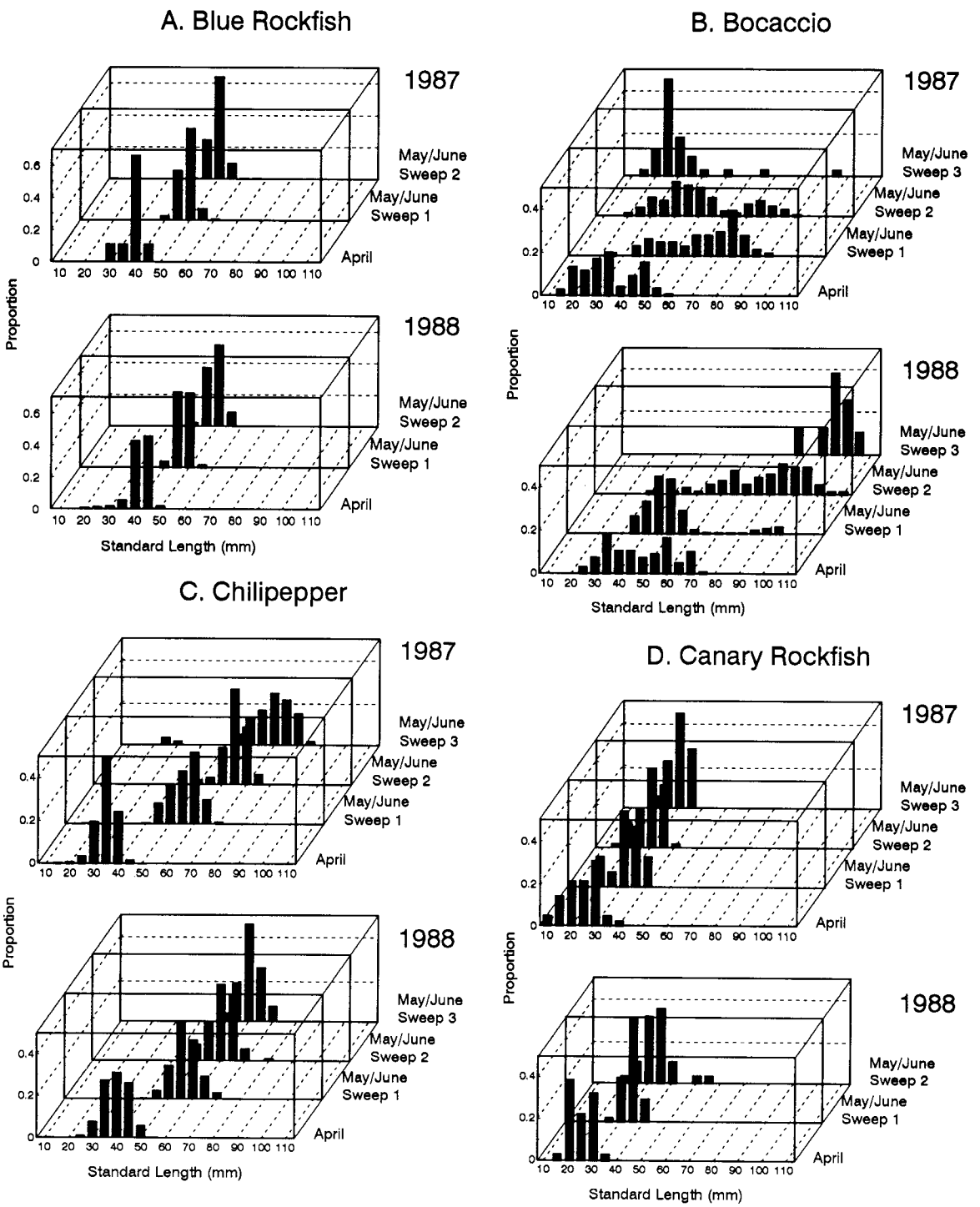
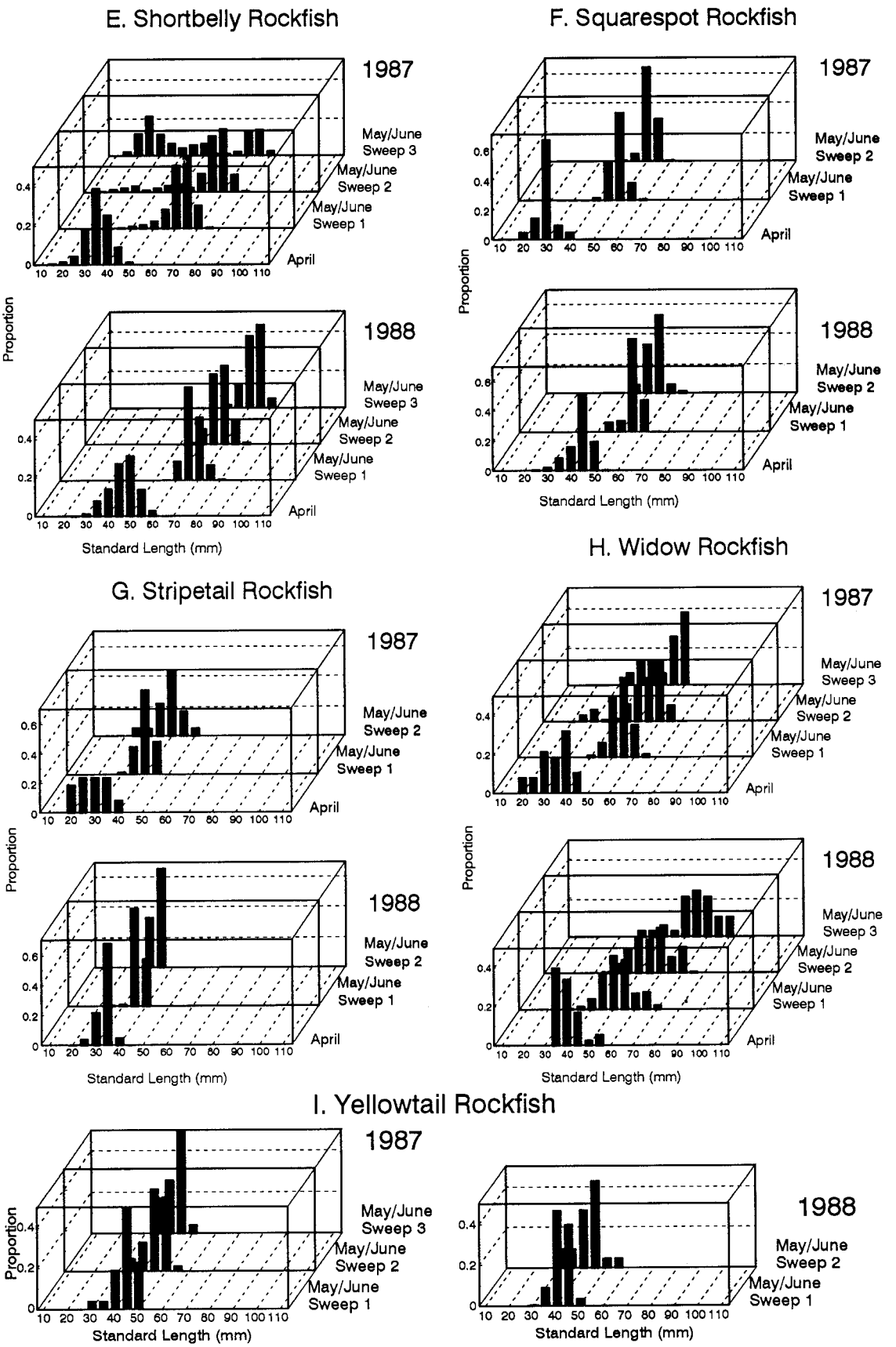
APPENDIX

Length-frequency distributions of pelagic juvenile rockfish in midwater trawls, 1987-1988. See table 3 for dates of cruises and sweeps of the study area.




E. Shortbelly Rockfish
F. Squarespot Rockfish
G. Stripetail Rockfish
H. Widow Rockfish
I. Yellowtail Rockfish
1987
1988
May/June Sweep 3
May/June Sweep 2
May/June Sweep 1
April
Proportion
Standard Length (mm)
10 20 30 40 50 60 70 80 90 100 110

A REVIEW OF THE SOUTHERN CALIFORNIA EXPERIMENTAL DRIFT LONGLINE FISHERY FOR SHARKS, 1988–1991

JOHN W. O'BRIEN AND JOHN S. SUNADA
California Department of Fish and Game
330 Golden Shore Drive, Suite 50
Long Beach, California 90802

ABSTRACT

In 1988 the California Fish and Game Commission authorized an experimental drift longline fishery with a number of restrictions to a select group of commercial longline fishermen. Target species were shortfin mako shark (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*).

During the first two years of this fishery, Department of Fish and Game personnel observed 19% of all fishing operations. Blue sharks and shortfin mako sharks accounted for approximately 91% of the catch, with blue sharks approximately twice as common as shortfin mako sharks. Shortfin mako shark catch per unit of effort (CPUE) changed little during the first two seasons, declined in the third season, then increased sharply in the fourth season. CPUE generally peaked in July and August. No striped marlin (*Tetrapturus audax*) were observed in the catch, and bycatch of other species was minimal. Length-frequency distributions of shortfin mako sharks exhibited two primary modes believed to represent ages two and three, indicating that the fishery harvested mostly juveniles.

RESUMEN

En 1988 la Comisión de Pesca y Caza de California autorizó una pesquería experimental de palangre a la deriva a un grupo selecto de pescadores; se impusieron varias restricciones. El objetivo de la pesquería fueron los tiburones marrajo (*Isurus oxyrinchus*) y azul (*Prionace glauca*).

Durante los primeros dos años de la pesquería, personal del Departamento de Caza y Pesca pudo observar el 19% de todas las maniobras de pesca. Los tiburones azul y marrajo contribuyeron el 91% de la captura y la razón de tiburones azul a marrajo fué de aproximadamente dos a uno. La captura por unidad de esfuerzo (CPUE) del tiburón marrajo cambió poco durante las primeras dos estaciones, declinó en la tercera, e incrementó marcadamente en la cuarta. La CPUE generalmente alcanzó los máximos valores en Julio y Agosto. No se observaron marlin (*Tetrapturus audax*) en la captura, y la captura de otras especies fué mínima. Hubo dos modas en las distribuciones de frecuencia de la longitud de los tiburones marrajo, y se piensa que éstas representan las edades dos y tres; ésto indicaría que la pesquería atrapó principalmente juveniles.

[Manuscript received February 1, 1994.]

INTRODUCTION

Commercial shark fishing operations have increased in recent years. During the late 1970s, a drift gill net fishery targeting swordfish (*Xiphias gladius*) and common thresher shark (*Alopias vulpinus*) developed off the southern California coast (Hanan et al. 1993). In the Santa Barbara Channel, a set gill net fishery for Pacific angel shark (*Squatina californica*) also began in the late 1970s (Herrick and Hanan 1988). Beginning in the mid 1980s, a shark fishery using drift longline gear developed in southern California, and by 1987, as interest continued to increase, the California Department of Fish and Game (the Department) determined that this gear was illegal, and prohibited its use within state waters. Participating fishermen applied to the California Fish and Game Commission (the Commission) for an experimental gear permit to continue fishing with drift longline gear. They stated that their methods were based on techniques developed by the National Marine Fisheries Service and would target shortfin mako sharks (*Isurus oxyrinchus*) and blue sharks (*Prionace glauca*).

Because of concern over potential incidental catch of striped marlin (*Tetrapturus audax*), an at-sea observer program was required to monitor the catch. The Commission issued ten permits in 1988 and 1989, and observers were assigned to vessels to document the species composition taken by longline gear. The Commission allowed the experimental fishery to continue during 1990 and 1991, but in 1992, on the Department's recommendation, denied the renewal of these permits.

Dockside and at-sea sampling results, as well as analysis of logbook information documenting species composition, size distribution, and CPUE data were compiled for the four years this fishery was authorized and are presented in this paper. This information is vital for proper management of fishery-sensitive species such as sharks, which are increasingly targeted by commercial and recreational fisheries.

THE FISHERY

Conditions and Regulations

The Commission authorized a limited experimental drift longline fishery in 1988 with a number of conditions regulating gear, seasons, areas, and harvest quotas (table 1). The Commission limited the number of ves-

TABLE 1
Summary of Main Conditions and Regulations Imposed on the Experimental Longline Fishery

	1988	1989	1990	1991
Permittees	10	10	6	8
Quota (lbs)	None	240,000	175,000	175,000
Maximum length of longline (miles)	5	4	4	4
Observers	Present	Present	Not present	Not present
Blue shark minimum catch	0	0	40,000	0
Season	April 1–Nov. 10	May 1–Sept. 15	May 1–Sept. 15	May 1–Dec. 31

sel permits issued, ranging from ten the first year to six in 1990. The initial ten permits were issued to longline fishermen who had (1) landed a minimum of 10,000 pounds of shortfin mako shark during 1987 and (2) been selected through a random lottery draw. Although there was no catch quota in 1988, quotas were imposed for the remaining three years of the fishery. The use of the longline gear was seasonally restricted in the area from Point Vicente and Santa Catalina Island in Los Angeles County to Point Loma in San Diego County (figure 1). The purpose of the closure was to minimize conflicts between other commercial shark and sport shark fisheries. Permittees were also required to notify the Department when and where they would land their catch so that Department personnel could sample the catch for information about length, weight, and sex.

Fleet and Gear Description

Longline vessels varied in length from 9 to 15 meters and typically carried a crew of two. The standard gear was restricted to a single drift longline not longer than 6.4 kilometers and constructed of stainless steel cable. Hooks were suspended from stainless steel leaders (gangions) not longer than 4 m, and spaced at approximately 16 m intervals (figure 2). The main line was suspended by buoys set at every fifth or sixth hook. Buoy lines were rarely longer than 10 m, resulting in fishing depths of 10–20 meters. Unlike set longline vessels, which disengage from the gear, drift longline gear remains attached to the vessel during fishing operations. Gear was normally deployed during daylight. Soak times ranged from 30 minutes to 10 hours, and averaged approximately 5 hours.

METHODS

Landing Data

The dressed weight (head, fins, and viscera removed) of shortfin mako and blue sharks was compiled by the Department's Marine Fisheries Statistics Unit from landing receipts, and is reported in pounds. Landing receipts must be completed by commercial fish buyers for each landing purchased. Estimates from the hook and line sport fishery for shortfin mako sharks for 1980 through 1989 were obtained from the Marine Recreational Fisheries Statistics Survey (MRFSS), and included creel census of private boats and commercial passenger fish-

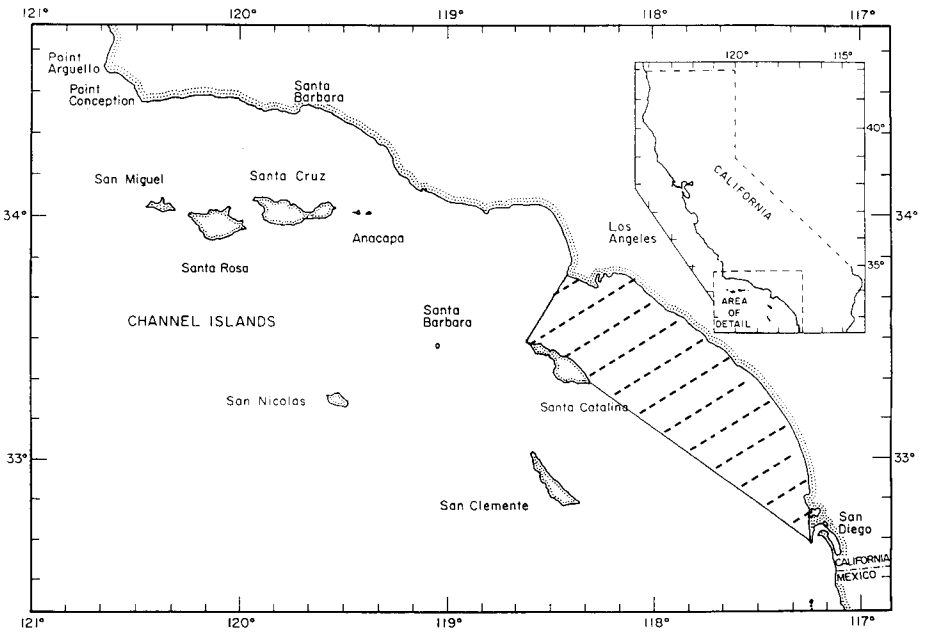


Figure 1. Area closed to experimental drift longline fishery from August 1 to September 15 (*dashed lines*).

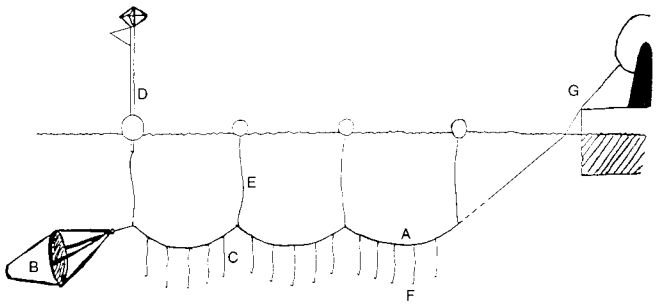


Figure 2. Diagram of typical drift longline gear in operation. *A*, mainline (stainless steel cable); *B*, sea anchor; *C*, gangion (wire, 6–12 ft); *D*, buoy with radar reflector; *E*, buoy line (10 ft); *F*, stainless steel hooks; *G*, fishing vessel.

ing vessel (CPFV) anglers. Sport-caught estimates for 1990, 1991, and 1992 are from the CPFV logbooks only, because the MRFSS was discontinued after 1989.

Observer Data

During the first two years of the fishery, vessels were required to carry Department personnel as observers, whose function was to determine species composition of the catch. Trips to be sampled were selected at random. Observers boarded boats before they left the dock and remained on board for the duration of the trip. Observers identified and enumerated all species captured by the longline gear. The observer program was discontinued by the Commission after 1989 because of the low bycatch of state and federally prohibited species and because of funding restrictions.

Concerns over possible high incidental catch and mortality of released blue sharks led the Department to establish qualitative criteria for assessing the condition of these sharks upon release (table 2).

TABLE 2
Qualitative Criteria Used to Assess Condition of Released Blue Sharks

1. Good: only slight signs of stress
   a. Minor wounds
   b. Cuts to lip or jaw
   c. Little to no bleeding
   d. Jaw not severed
   e. Physically active
2. Poor: alive but showing signs of severe stress
   a. Moderate wounds, cuts close to gill slits
   b. Jaw severed completely
   c. Injuries in pharynx, but vital organs, branchial arteries, or veins not injured
   d. Moderate bleeding
   e. Little physical activity
3. Moribund: dead or severely wounded
   a. Severe injuries from hook removal extend beyond pharynx into gill slits
   b. Pectoral or other fins removed
   c. Bleeding from severed branchial arteries and veins
   d. No physical activity

Dockside Sampling Data

Permittees were required to notify the Department at least 24 hours before landing their catch. Department personnel then attempted to sample each landing for length, weight, and sex during each year of the fishery. Because sharks were dressed at sea, alternate lengths and dressed weights were recorded.

Logbook Data

Each permittee was required to maintain a daily record of fishing activities on a logbook form issued by the Department. The four-year average rate of compliance was estimated at approximately 75%. For each set, the numbers and estimated weight of all sharks caught, the start and finish time, the start and finish location, depth and length of the main line, the number of hooks used, and water temperature were required to be recorded.

Calculation of CPUE and total effort. Total CPUE values were calculated from logbook data, for shortfin mako sharks only. CPUE was defined as the number of shortfin mako sharks caught per hook-hour.

CPUE = (N/H)

where:

N = total number of sharks reported in logbooks

H = total number of hooks multiplied by the total hours fished as reported in logbooks

CPUE was calculated by month, year, and Fish and Game block area (10-minute latitude-longitude blocks).

Total effort (H) was measured in hook-hours and summed by year and Fish and Game block.

CPUE analysis. Since the variances were heterogenous and the data were not distributed normally (even after transformation), a nonparametric one-way procedure was run on SAS to test for differences in total CPUE among years (SAS Institute Inc. 1987). The Kruskal-Wallis test was used with CPUE as the independent factor.

RESULTS

Landing Data

Shortfin mako shark landings decreased steadily from 270,000 pounds in 1988 to 110,000 pounds in 1991. Blue shark landings increased to 42,800 pounds in 1990, then dropped to 0 pounds in 1991 (table 3).

TABLE 3
Shortfin Mako Shark and Blue Shark Drift Longline Landings (lbs), 1988–1991

	1988	1989	1990	1991
Shortfin mako shark	269,604	177,928	174,215	110,513
Blue shark	2,462	10,818	42,818	0
Total	272,066	188,746	217,033	110,513

Source: California Department of Fish and Game landing receipts (landings from experimental fishery exclusively).

TABLE 4
Number and Percentage of Species Captured on Drift Longline Gear, 1988 and 1989

	1988		1989	
Species	No.	%	No.	%
Blue shark	1,900	62.1	1,320	62.0
Shortfin mako shark	883	28.9	610	28.7
Pelagic stingray	265	8.7	194	9.1
Ocean sunfish	1	—	2	0.1
California sea lion[a]	3	0.1	2	0.1
Hammerhead shark	2	0.1	0	0
Finescale triggerfish	1	—	0	0
Giant sea bass	1	—	0	0
Pacific mackerel	2	0.1	0	0

Source: observer data (no observer program in 1990 and 1991).
[a]Released alive

Observer Data

Department observers sampled approximately 19% of the total longline fishing effort during 1988 and 1989, and documented over 5,100 animals in the catch. Species composition was similar in both years. Blue sharks made up 62% of the total catch, shortfin mako sharks 29%, and pelagic stingrays (*Dasyatis violacea*) nearly 9% (table 4). The rest of the catch (less than 1%) consisted of California sea lions (*Zalophus californianus*), green sea turtles (*Chelonia mydas*), giant seabass (*Stereolepis gigas*), common thresher shark (*Alopius vulpinus*), ocean sunfish (*Mola mola*), pacific mackerel (*Scomber japonicus*), and finescale triggerfish (*Balistes polylepis*).

During 1988, Department observers recorded that 52% of the blue sharks released were judged in "good" condition, and likely to survive. Observers estimated that 88% of the blue sharks returned to the water were in "good" condition during 1989.

Dockside Sampling Data

A total of 3,719 shortfin mako sharks were measured over the four-year period. Alternate length (AL) ranged from 19 to 102 cm. Mean length of males ranged from 47.0 cm AL in 1988 to 50.0 cm in 1991, while mean lengths of females ranged from 47.0 cm in 1988 to 49.7 cm in 1991. Two distinct modes (42 and 53 cm AL) were present during each year of the fishery (figure 3).

The sex ratio for shortfin mako sharks was fairly consistent by year (1.3 males per female in 1988 and 1990, and 1.2 males per female in 1989 and 1991).

Logbook Data

The highest CPUE values were concentrated in a band of water located from 10 to 30 miles from the mainland between the southeast end of Santa Cruz Island and the southeast end of San Clemente Island (figure 4). Higher CPUE values were generally located farther offshore from 1988 through 1990, whereas during 1991 high CPUE values were located both offshore and inshore. Although no clear trend in CPUE values was observed from year to year, several areas exhibited high CPUE throughout the fishery, particularly an area approximately 10 miles north of Santa Catalina Island and another area 10–20 miles southeast of San Clemente Island.

Over the four years, monthly patterns of CPUE were similar; CPUE was low in April and May, steadily increased to a peak in July and August, then generally decreased in September (figure 5).

The highest effort values were also associated with the area of highest CPUE values (figure 4). Moderate-to-high effort values were concentrated in areas adjacent to the southeast ends of Santa Catalina and San Clemente islands, throughout the four years of the fishery.

Total effort decreased sharply from 609,026 hook-hours in 1988 to 377,382 hook-hours in 1989. Total effort increased moderately to 461,524 hook-hours in 1990, then fell dramatically to 157,720 hook- hours during 1991. Among years, differences in total CPUE were significant ($p = 0.035$). CPUE was 0.0157 fish/hook-hour in 1988 and 0.0156 fish/hook-hour in 1989. CPUE declined in 1990 to 0.0114 fish/hook-hour, then increased to 0.0163 fish/hook-hour in 1991.

DISCUSSION

Landing Data

Decreasing landings of shortfin mako sharks resulted from several factors: (1) quotas of 240,000 pounds for the 1989 season and 175,000 pounds for the 1990 and 1991 seasons were established as additional controls on the fishery; (2) unfavorable market conditions due to increased imports and decreased demand from East Coast buyers negatively influenced fishery effort in 1991, when the price for shortfin mako sharks dropped from $1.65 per pound to $0.80 per pound in July (Department landing data). For the remainder of that season, permittees had difficulty finding markets for their catch.

The longline fishery was not the sole source of shortfin mako shark landings from southern California waters: a commercial drift gill net and hook and line sport fishery also landed substantial numbers of these sharks (table 5). From 1988 to 1991, the experimental drift longline fishery accounted for 41% of the total commercial landings (Department landing data). The remaining 59% was landed by the drift gill net fishery. The sport fishery, which appears to be increasing in southern California, holds several annual tournaments targeting shortfin mako sharks (Bedford 1992). Estimates from the Marine Recreational Fisheries Statistics Survey (MRFSS) indicate that sport landings accounted for 25% of the total combined sport and commercial shortfin mako shark

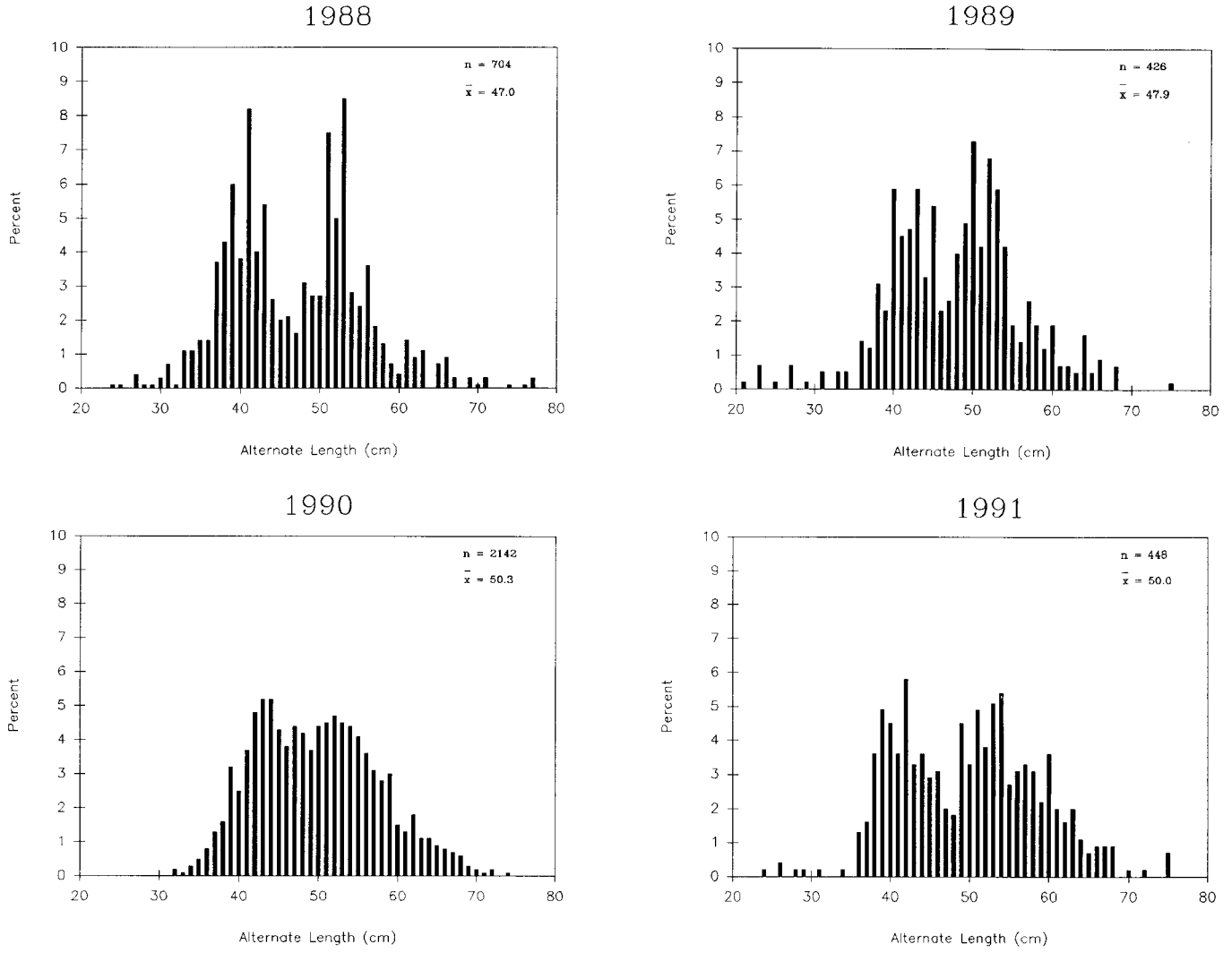


Figure 3. Length-frequency distribution of shortfin mako sharks taken by drift longlines, 1988–91.

landings during 1988 and 1989 (U.S. Dept. Commerce 1984–92).

Because of the high incidental catch of blue sharks and the successful experimental fishery for blue sharks in southern California during 1979 and 1980 (West Coast Fishery Development Foundation 1981), the Commission required permittees to develop a market for blue sharks during the 1989 and 1990 fishing seasons. In 1989, several wholesalers attempted to market blue shark for human consumption, for leather, and for crab bait, but there were no return buyers for those markets. Despite these difficulties, the Commission required that a minimum quota of 40,000 pounds of blue shark be marketed for human consumption for the 1990 season, but few wholesalers were willing to buy the 43,000 pounds landed (table 3) because no retail demand existed. Permittees resisted further attempts to develop a market for blue sharks because of low value relative to shortfin mako sharks and costly processing to prevent spoilage (high content of blood urea quickly converts to ammonia when a fish dies, making the meat unpalatable). Responding to this situation, the Commission did not set a minimum quota for blue sharks in 1991, and no landings were recorded.

Observer Data

The high percentage of blue sharks in the catch was not surprising. Department shark-tagging studies with hook and line gear in the late 1980s indicated that blue sharks were much more abundant than shortfin mako sharks in the Southern California Bight (Dennis Bedford, California Department of Fish and Game, pers. comm.). Strasburg (1958) found a 35 to 1 ratio of blue sharks to shortfin mako sharks in the central Pacific Ocean during the 1950s.

The large increase (52% vs 80%) from 1988 to 1989

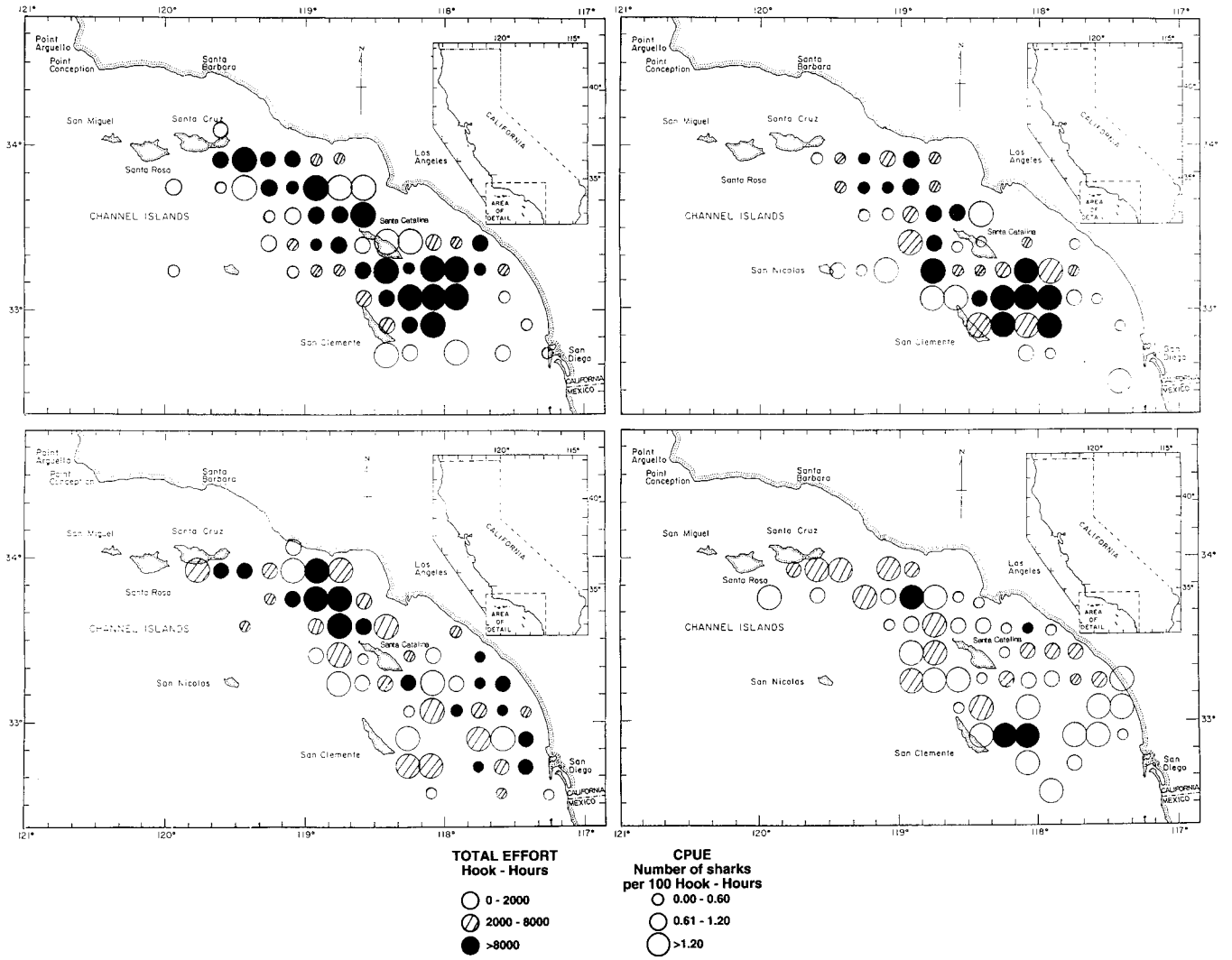


Figure 4. Total effort and catch per unit of effort for shortfin mako sharks by Fish and Game blocks for 1988 (*upper left*), 1989 (*upper right*), 1990 (*lower left*), and 1991 (*lower right*).

in released blue sharks judged to be in "good" condition was due to the development and wide use in the fishery of long-handled hook-removal pliers. Use of these pliers reduced injury and improved release condition because hooks could usually be removed without cutting the sharks' tissues. Interviews with longline permittees indicated that the pliers were also widely used in 1990 and 1991.

Additional concerns expressed by the Department about this fishery included incidental catches of commercially prohibited species such as striped marlin (*Tetrapturus audax*), as well as state and federally protected species such as sea turtles and marine mammals. Although sport anglers commonly use monofilament line to take striped marlin with bait and lures, no marlin were observed in the catch, and less than 1% of the total catch consisted of other prohibited species during 1988 and 1989. Perhaps this gear's steel cable construction deterred marlin from taking the bait despite their common occurrence in the Southern California Bight.

Pelagic stingrays, the third most abundant species captured, are found throughout tropical seas, as far north as Point Dume in southern California. Until recently, stingrays were considered rare off southern California (Miller and Lea 1972), but they appear to be vulnerable to both drift longline and drift gill net gear (Hanan et al. 1993).

This drift longline gear appeared to bring in less bycatch than the California drift gill net fishery. Observers recorded a total of 9 species captured on drift longline gear, whereas 71 species were documented from the drift gill net fishery (Hanan et al. 1993). Unlike fish caught in drift gill nets, most of the longline bycatch can be released alive.

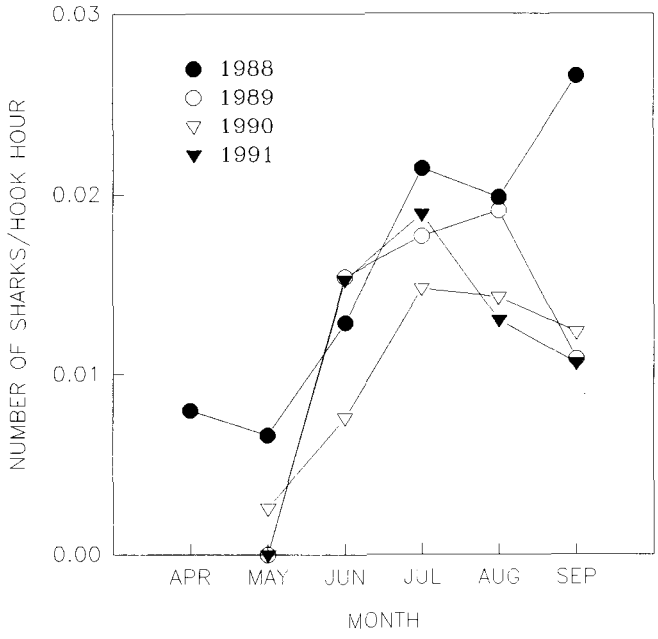


Figure 5. Monthly longline catch per unit of effort for shortfin mako sharks, 1988–91.

Dockside Sampling Data

Length distributions of shortfin mako sharks varied little throughout the four years of the fishery, and available information indicates that this fishery harvested primarily juvenile shortfin mako sharks. Length-at-age calculations by Cailliet et al. (1983) indicate that the two primary modes (42 and 53 cm AL) correspond to two- and three-year-old sharks, although it has also been suggested that these modes represent one- and two-year-old sharks (Dennis Bedford, pers. comm.). Cailliet et al. (1983), using vertebral analysis, state that shortfin mako sharks do not reach maturity until age seven, whereas Pratt and Casey (1983)—using vertebral analysis, tag return data, and modal analysis—found that Atlantic shortfin mako sharks matured at age three for males and age seven for females. Length-at-age estimates from Cailliet et al. (1983), and size-frequency data from this fishery indicate that approximately 81% of the shortfin mako shark catch was three years old or younger and likely to be immature. If shortfin mako sharks do not begin to mature until age seven, then it would take at least five years for the effects of harvesting large numbers of juvenile sharks to manifest themselves in the reproductive capacity of the stock and in future stock productivity.

Length-frequency data for shortfin mako sharks captured in the drift gill net fishery were very similar to data from the drift longline fishery (Hanan et al. 1993). The predominance of juvenile shortfin mako sharks in the catch from these two fisheries suggests that the Southern California Bight serves as a nursery area for shortfin mako sharks.

TABLE 5
Annual California Landings (lbs) of Shortfin Mako Shark, 1980–1992

Year	Commercial longline gear[a]	Commercial gillnet gear[b]	Total commercial landings	Sport landings	Total landings
1980		155,336	155,336	9,886	165,222
1981		277,345	277,345	236,259	513,604
1982		533,839	533,839	17,703	551,542
1983		330,260	330,260	23,885	354,145
1984		242,837	242,837	73,410	316,247
1985		226,695	226,695	196,192	422,887
1986	1,875	471,809	473,684	73,444	250,128
1987	64,077	547,943	612,020	452,148	1,064,168
1988	269,604	219,613	489,217	207,418	696,635
1989	177,928	210,394	388,322	92,314	480,636
1990	174,215	385,970	560,185	9,360[c]	569,545
1991	110,513	204,588	315,101	5,560[c]	320,661
1992	587	213,255	213,842	5,360[c]	219,202

[a]Includes all reported landings.
[b]Includes drift gill net, set gill net, and purse seine landings.
[c]1990–92 CPFV sport landings only.

Logbook Data

From 1988 through 1991, CPUE increased overall, with a sharp drop in 1990. However, because of a number of unknown variables that could affect CPUE (e.g., nonrandom distribution of fishing effort, emigration and immigration of animals, increased fishing skill of permittees), it is not clear whether CPUE represents an accurate index of shortfin mako shark abundance. CPUE data from a greater span of years and number of permittees may be required to identify the relationship between CPUE and abundance.

As in the drift longline fishery, catches of shortfin mako sharks from the drift gill net fishery peaked in August (Hanan et al. 1993). Because shortfin mako sharks are distributed within the warmer ocean waters of the Pacific (Cailliet and Bedford 1983), it seems probable that peak CPUEs would occur during July and August, when surface water temperatures are highest in coastal waters of the Southern California Bight. Shortfin mako sharks may be moving into the Southern California Bight during the summer to feed on Pacific mackerel, which are more available in the summer (Konno and Wolf 1992).

CONCLUSION

In summary, caution should be taken before allowing any fishery to develop which harvests predominately juveniles, especially slow-growing, late-maturing, low-fecund species such as elasmobranchs. Species possessing these characteristics are most vulnerable to overfishing (Holden 1973, 1974). Basic biological information such as age and growth, age and length at first maturity, fecundity, and gestation period must be validated. Information on juvenile and adult migratory patterns also

must be acquired. Until this information is obtained for shortfin mako sharks, it would seem unwise to encourage further exploitation of this species in the Southern California Bight.

ACKNOWLEDGMENTS

Funding was provided by the Interjurisdictional Fisheries Act of 1977 (formerly Bartlett Project). We thank all members of the California Drift Longliners Association for their help and cooperation in gathering data. Special thanks goes to Tim Athens, Larry Derr, and Scott Honeker for their assistance and advice. We thank Kent Smirl and Raul Rodriguez, who were the first observers and developed much of the criteria for assessing blue shark condition upon release. Joe Weinstein and Chuck Valle assisted with data analysis. Dennis Bedford provided advice and comments; Kris Rager helped prepare figures; and Juan Hernandez translated the abstract. Finally, thanks to Dave Parker and two anonymous reviewers for critically reviewing and measurably improving the manuscript.

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OCCASIONAL AVAILABILITY OF DOLPHIN, *CORYPHAENA HIPPURUS*, TO SOUTHERN CALIFORNIA COMMERCIAL PASSENGER FISHING VESSEL ANGLERS: OBSERVATIONS AND HYPOTHESES

JERROLD G. NORTON
Pacific Fisheries Environmental Group
Southwest Fisheries Science Center
P.O. Box 831
Monterey, California 93942

STEPHEN J. CROOKE
California Department of Fish and Game
330 Golden Shore, Suite 50
Long Beach, California 90802

ABSTRACT

Records from California-based commercial passenger fishing vessels (CPFV) show that dolphin, *Coryphaena hippurus*, catch off southern California was more than 8% of the total southern and Baja California CPFV catch in 1983, 1984, 1990, 1992, and 1993. The major portion of the catch is made off northern Baja California. Record catches for southern and Baja California were recorded in 1990 and 1992. Dolphin enter California waters under conditions that include elevated ocean temperatures and increased onshore and poleward coastal ocean transport. Large-scale environmental events, which apparently increase dolphin abundance off southern California, appear related to regional decrease in eastern Pacific high-pressure systems. When the high-pressure system is less intense, there is less southward wind along the coast. Consequently, California Current southward transport and coastal upwelling decrease, and the inshore countercurrent brings anomalously warm water into the Southern California Bight. Local kelp mat cover and local ocean processes are also likely to be important in aggregating dolphin and making them available to CPFV anglers.

RESUMEN

Los registros de la Flota Comercial de Pesca Deportiva ("FCPD") demuestran que la captura del dorado *Coryphaena hippurus* frente a la costa del sur de California rebasó el 8% de la captura de la FCPD de Baja California (B.C.) y B.C. Sur (México). La mayor parte de la captura se realiza frente al norte de Baja California. En 1990 y 1992 hubo capturas record en B.C. y B.C. Sur. El dorado entra en aguas de California en condiciones que incluyen temperaturas elevadas del oceáno e incremento del transporte hacia el norte (en la zona costera) y hacia la línea de costa. Los eventos a gran escala que aparentemente produjeron un incremento en la abundancia del dorado frente al sur de California parecen estar relacionados con un decremento regional en el sistema de alta presión del Pacífico oriental. Cuando el sistema de alta presión afloja, también afloja el viento hacia el sur a lo largo de la costa. Y en consecuencia tanto el transporte hacia el sur debido a la corriente de California como la surgencia costera decrementan, y la contracorriente cercana a la línea de costa acarrea aguas anormalmente cálidas a la Cuenca del sur de California. La disponibilidad local de frondas de algas pardas ("kelp") así como otros procesos oceánicos locales también podrían ser importantes para concentrar dorados y ponerlos a disposición de la FCPD.

[Manuscript received February 10, 1994.]

INTRODUCTION

Dolphin (*Coryphaena hippurus*), also known in the United States as dorado and mahimahi, are epipelagic predatory fish found in the world's tropical and subtropical oceans (Palko et al. 1982). Off southern California, dolphin are caught by commercial passenger fishing vessel (CPFV) anglers in the warm months of warmer years (tables 1 and 2).

Dolphin commonly reach sexual maturity and lengths exceeding 100 cm in their first year (Oxenford and Hunte 1986). Individuals may live longer than five years, but in both commercial and sport fisheries fewer than 5% of the fish taken are thought to be older than two years

TABLE 1
Number of Dolphin Caught by Commercial Passenger Fishing Vessels off California and Baja California

Year	Calif.	Total, Calif. and Baja Calif.	% Calif.[a]	Avg. temp.[b]
1979	1	9,184	0	18.9
1980	2	8,840	0	19.0
1981	35	1,281	3	19.8
1982	0	1,099	0	18.1
1983	1,258	4,992	25	18.9
1984	527	6,532	8	20.1
1985	3	1,307	0	19.3
1986	31	1,866	2	19.2
1987	0	3,518	0	18.1
1988	1	3,349	0	18.6
1989	3	2,341	0	18.7
1990	7,216	31,548	23	19.3
1991	0	1,301	0	17.6
1992	1,882	22,727	8	20.1
1993	707	8,574	8	18.8
Total	11,665	108,459	11	

[a]California percentage of total catch.
[b]Average 10 m temperature (°C) of a 3° × 3° area containing the California catch.

TABLE 2
Seasonal Dolphin Catch Expressed as Percentage of Annual Catch by Month

A. Southern California

Month	1983	1984	1990	1992	1993	Average
Jan.	0	0	0	0	0	0
Feb.	0	0	0	0	0	0
Mar.	0	0	0	0	0	0
Apr.	0	0	0	0	0	0
May	0	0	0.0	0	0	0.0
June	0	0	0.3	0	0	0.1
July	6.3	1.5	1.3	42.8	35.2	17.4
Aug.	69.0	36.2	86.4	40.9	21.4	50.8
Sept.	22.7	62.2	3.1	15.3	21.9	25.0
Oct.	2.0	0	8.8	1.1	21.2	6.6
Nov.	0	0	0	0	0	0
Dec.	0	0	0	0	0	0
No. of fish	1,258	527	7,216	1,882	707	11,590

California percentage of total during 1983, 1984, 1990, 1992, 1993 = 15.6%

B. Southern and Baja California

Month	1983	1984	1990	1992	1993	Average
Jan.	0	0.3	0.1	0.1	0	0.1
Feb.	0	0	0	0	0	0.0
Mar.	0	0	0	0	0	0.0
Apr.	0	0	0	0	0	0.0
May	0	0	1.7	0	0	0.3
June	0	0	0.1	0.5	0	0.1
July	9.8	1.0	9.0	28.5	53.1	20.3
Aug.	52.0	46.5	51.4	41.2	20.1	42.2
Sept.	32.2	31.6	21.7	20.1	6.3	22.4
Oct.	2.7	6.1	14.3	8.3	9.7	8.2
Nov.	1.8	14.1	1.2	0.9	9.1	5.4
Dec.	1.4	0.4	0.4	0.4	2.0	0.9
No. of fish	4,992	6,532	31,548	22,727	8,574	74,373

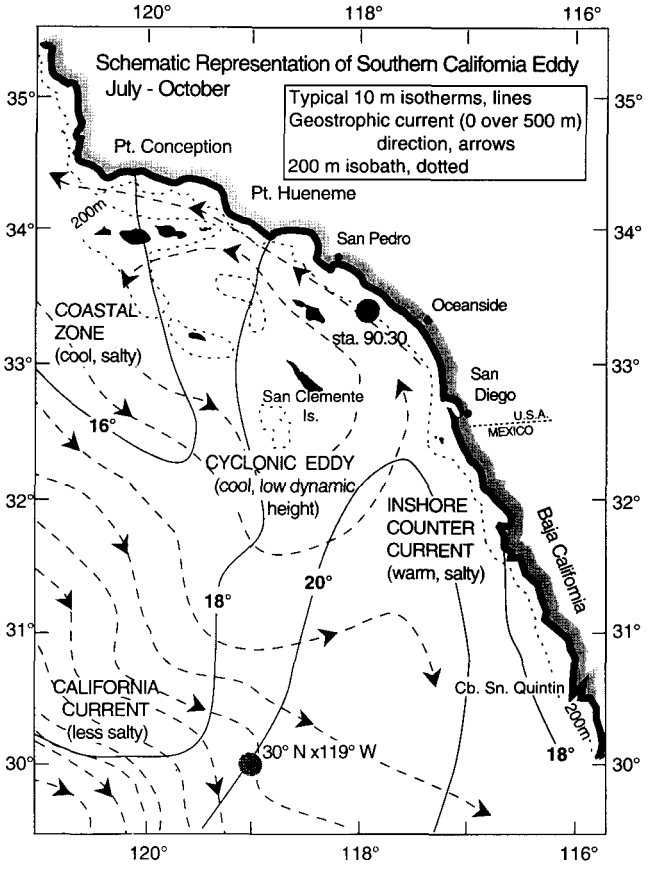

Figure 1. Composite diagram of the Southern California Eddy. *Dashed lines* show contours of surface dynamic height anomaly at an average spacing of 0.02–0.04 dynamic meters. *Shaded circles* show locations referred to in the text. Adapted from Reid et al. 1958; Lynn et al. 1982; Peláez and McGowan 1986; and Lynn and Simpson 1987.

(Kojima 1964; Beardsley 1967; Palko et al. 1982). About 85% of the dolphin taken by southern California CPFV anglers are less than one year old.

In the northeastern Pacific, the largest concentrations of all dolphin life stages are in the tropical biogeographic zone (Palko et al. 1982), which extends from the equator north to the southern end of the Baja California Peninsula at 22.8° N (Ekman 1953; Parrish et al. 1981); Bakus 1986; McGowan 1986). Poleward migration into the northern subtropical biogeographic zone appears limited by factors associated with the 20°C sea-surface isotherm (Kojima 1964; Palko et al. 1982). Biogeographic zones would be expected to be plastic for wide-ranging nektonic species such as dolphin. It is probable that the migrations of dolphin and other nektonic species reflect changing physical oceanographic conditions (Squire 1987). Throughout the dolphin's range, peak catch is seasonal, suggesting annual migrations (Patterson and Martinez 1991; Hamm et al. 1992).

Since 1979, total annual catch from southern and Baja California waters has varied thirtyfold (table 1). Catch off southern California is episodic. Off Baja California catch is more consistent; more than 1,000 dolphin are caught each year. When the total catch exceeds 4,000 fish, 75%–85% of the dolphin are taken north of Cabo San Quintin (figure 1) on 20- to 24-hour CPFV trips from San Diego and Oceanside. Usually CPFVs are pursuing yellowfin tuna (*Thunnus albacares*), skipjack (*Euthynnus pelamis*), or yellowtail (*Seriola lalandi*) on these excursions. Dolphin are a desirable bycatch. If dolphin fishing is successful, the CPFV will not abandon it to search for other species.

Dolphin are most frequently taken from beneath free-floating kelp mats composed of tangled *Macrocystis* sp. stipes and blades (fronds). Locating the fish depends on the CPFV operator's ability to find floating kelp mats.

Many studies have focused on the basin-scale environmental events of seasonal to several-years' duration (Norton et al. 1985; Ebbesmeyer et al. 1991; Norton and McLain 1994) and their possible biological consequences (Uda 1961; Norton 1987; Parker 1989; Lluch-Belda et al. 1992; Hollowed and Wooster 1992). The

best-known environmental events of this scale are the ENSO, or El Niño/Southern Oscillation, and its global teleconnections (Rasmusson and Wallace 1983; Simpson 1992; Norton and McLain 1994).

Because global anomalies associated with ENSO appear to be triggered by tropical Pacific events, it may be useful to compare tropical indicators of ENSO activity to physical conditions associated with the subtropical biogeographic zone (Longhurst 1967; Brinton and Reid 1986; Squire 1987) and to dolphin catch by southern California CPFV anglers.

The objective of this paper is to compare variation in CPFV dolphin catch off southern and Baja California to several scales of variation in the physical environment and to use the results of these comparisons to develop scenarios describing conditions that allow dolphin to enter the Southern California Bight. Comparisons begin with processes that may last several years and include the entire north Pacific, then proceed to smaller scales, concluding with seasonal and spatial variation of processes within the Southern California Eddy (figure 1).

DATA

Dolphin catch records (tables 1 and 2) were obtained from the California Department of Fish and Game database of CPFV logbook information, which provides numbers of each species caught per 0.1° geographical square off southern California. The origin of dolphin catch from Mexican waters is not as specific. When dolphin are available within 40 km of southern California ports, they are heavily fished by private boats (carrying two to six anglers) that may catch as many dolphin as the CPFVs. This suggests that when many fish are caught—as in 1990 and 1992; table 1—the CPFV logbook records underestimate abundance.

Commercial passenger fishing vessels are believed to be thorough as they search the coastal ocean for desirable pelagic species, especially within 70–120 km of their home ports. CPFV operators maintain radio contact with one another, commercial fish-spotting planes, commercial fisherman, and private boat operators. Radar and sonar devices aid the search.

Between San Pedro and San Diego more than 80 CPFVs (more than half from San Diego and Oceanside) search the coastal ocean each day from July through September. Each boat carries about 30 fishermen, so there are more than 2.0×10^5 angler days per season. Dolphin catch per angler day was about 0.15 during 1990, the year of greatest abundance (table 1).

The CPFV anglers use labor-intensive methods, unsuitable for commercial exploitation, that involve presenting live anchovies (*Engraulis mordax*) and sardines (*Sardinops sagax*) as bait. Many fish entering the Southern California Bight may not encounter CPFV activities, but it is unlikely that high concentrations of desirable fish occur within CPFV range without being sampled (caught) by CPFV anglers.

When fishing is good, increased fishing effort may be directed toward catching the more available species. This "target homing" by CPFVs may lead to negative and positive feedback bias in the catch records. That is, total catch values might be relatively deflated during years of low catch, and inflated for years of high catch. For dolphin, these biases are reduced by two related factors: (1) other pelagic species (see above) have been available and pursued during years of high dolphin catch, and (2) dolphin are usually taken as desirable bycatch during excursions for other species. Dolphin are not specifically sought, and they are not specifically rejected. Each factor reduces bias introduced by CPFV target homing.

Monthly mean sea temperature at 10 m depth was interpolated from vertical temperature profiles in the U.S. Navy Fleet Numerical Oceanography Center's (FNOC) Master Oceanographic Observations Data Set (MOODS5). Temperature profiles were extracted, checked for consistency, and plotted with the programs of McLain et al. (1985).

California Cooperative Oceanic Fisheries Investigations (CalCOFI) temperature-salinity-depth data were obtained from the Scripps Institution of Oceanography, Marine Life Research Group. Historical and mean (1950–78) station data were obtained from the Southwest Fishery Science Center (NMFS/NOAA). CalCOFI data are published in data reports of Scripps Institution of Oceanography (UCSD) along with parameter distribution maps. Maps from CalCOFI cruises of July 1990 (9007) and October 1992 (9210) have been adapted for use in our figures.

Seasonal mean values for the Southern Oscillation Index (SOI) were obtained from the Climate Analysis Center (NMC/NOAA). These are the five-month running mean of the difference between the standardized sea-level-pressure anomalies at Tahiti (17.53° S, 149.57° W) and Darwin (12.47° S, 130.85° E).

SOI values correlate well with atmospheric, oceanic, and biological (ENSO) anomalies throughout the world. Tropical atmospheric oscillations as measured by the SOI may be connected with the region of dolphin catch off southern and Baja California via the atmosphere and the ocean (Rasmusson and Wallace 1983; Baumgartner and Christensen 1985; Kope and Botsford 1990; Simpson 1992; Clarke 1992; Norton and McLain 1994).

Monthly mean values of SLP and an upwelling index at 30° N, 119° W were derived from the FNOC 63 × 63 grids of northern hemisphere analyzed fields (Bakun 1975). The SLP is a general atmospheric parameter that reflects changes in air-sea heat exchange, wind stress and wind-curl forcing, and wind-forced mixing. The up-

welling index is computed from SLP gradient at 30° N, 119° W. Although the interpretation of the upwelling index may be more complex than the terminology would imply, it is more closely related to Ekman transport and coastal upwelling than to SLP. However, SLP series are probably more indicative of combined large-scale forcing (Norton and McLain 1994).

RESULTS

Although the catch record is too short for detailed statistical analysis, some patterns are evident and will help form hypotheses to be tested as additional data become available.

Off southern California, significant dolphin catch (≥8% of the combined catch) was reported in 1983, 1984, 1990, 1992, and 1993, along with an apparent increase in dolphin availability to southern California CPFV anglers since 1990 (table 1). These observations may represent dolphin response to the environment on two temporal scales. First, there is considerable year-to-year variation ranging over three orders of magnitude in California catch and one order of magnitude in the total catch. Second, a multiyear population response is evident. The high total catch (>8,000) recorded in 1979 and 1980 was not observed again for nine years. Then in 1990, 1992, and 1993 high catches were again recorded (table 1).

When the best years for California dolphin catch are compared, the highest percentage of the catch is made in August (table 2). Off California, the catch is limited to July, August, and September. Off Mexico there is frequently good catch in October, with at least some fish being taken during the next three months.

Large-Scale Events and Dolphin Availability

The occasional availability of dolphin to CPFV anglers may represent an anomalous northward shift of physical conditions characterizing the subtropical biogeographic zone. In this section we use an oceanic indicator series and three atmospheric indicator series to examine how large-scale physical events of seasonal and longer scale relate to a northward subtropical biogeographic zone shift and subsequent dolphin fishing success.

The three atmospheric series are compared to total CPFV catch in figure 2. The period since 1990 (thick dashed lines) is especially striking because there is coincident downward trend in all the atmospheric variables at the same time that dolphin became more available to CPFV anglers.

Dolphin migration into southern California waters is also related to the large-scale events. The extreme 1982–83 perturbation in SOI corresponded to a reduction in SLP annual-cycle amplitude and an unusually high fraction (25%) of the total dolphin catch being made

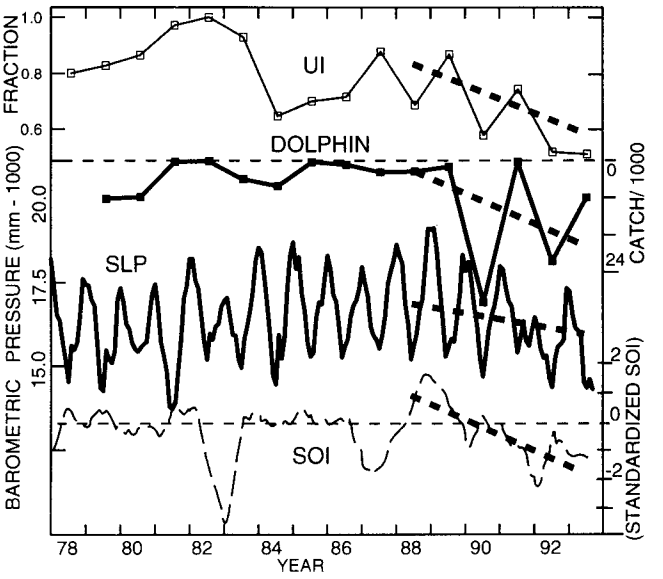

Figure 2. Comparison of atmospheric indices to total dolphin catch (*filled squares*). The scale giving numbers of dolphin caught per year, *upper right*, is inverted. *Lower dashed line* gives the five-month running mean of the standardized Southern Oscillation Index (SOI). Five-month running means of sea-level atmospheric pressure (SLP) at 30° N, 119° W are shown by the *lower solid line*. The *top line* gives average July–August upwelling index (UI) at 300° N, 119° W as a fraction of the highest value in the 1978–93 series. The endpoints of the *thick dashed lines* marking multiyear trend were determined by averaging all available values for 1987–89 and 1990–92.

off southern California in 1983 (table 1). Both total and southern California catch were anomalously large in 1990, a period of conspicuous drop in both the SOI and the average SLP at 30° N, 119° W (figure 2).

Relationships between the SOI and local SLP suggest that large-scale atmospheric adjustments are reflected in both measurements. Downward trends, or generally decreasing values of SOI [$\delta(SOI)/\delta t < 0$], corresponded to shortening of the annual range in SLP fluctuation. That is, the atmosphere off northern Baja California has a more tropical aspect (Gordon 1953) when $\delta(SOI)/\delta t < 0$, as shown in 1979–80, 1982–83, and 1990–93 (figure 2). The lower annual maximum SLP during these periods suggests that the anticyclonic subtropical high is locally reduced in magnitude and that southward wind and consequent California Current forcing and coastal upwelling may be reduced (Reid et al. 1958; Parrish et al. 1981).

The upwelling index is more of a local atmospheric indicator than SOI and SLP because of local differencing (Bakun 1975), but some of the same features appear in all three atmospheric series (figure 2). There is a downward trend in upwelling index during 1989–93, coincident with a similar trend in the SLP and SOI series. Also note that two of the three lowest upwelling index values correspond to two of the best years of dolphin fishing. The upwelling index shows an overall drift to lower values, which is not evident in the other series.

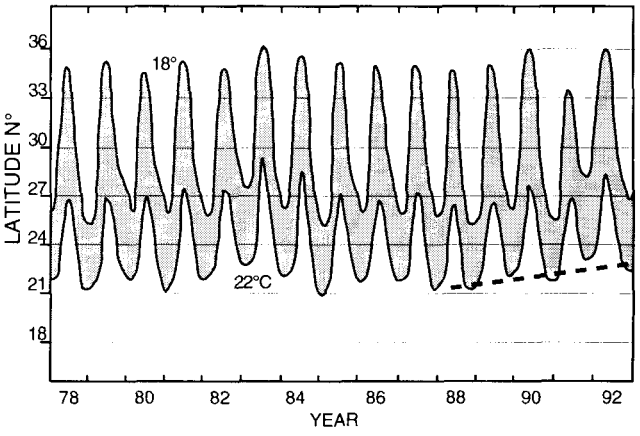

Figure 3. Smoothed envelope bounded by the 18°–22° isotherms at 10 m depth. Available temperature values from coastal areas extending up to 300 km offshore were smoothed with a five-point median filter (McLain et al. 1985). The *dashed line* marks an apparent multiyear trend beginning in 1988.

Regional oceanic effects of the oceanic and atmospheric connections from the equatorial atmosphere to the California coast are indicated in figure 3, which shows annual excursions of the 18°–22°C temperature envelope at 10 m depth. The latitude spanned by this envelope includes the 20°C isotherm and the northernmost edge of dolphin availability (Palko et al. 1982). The envelope may also be a good indicator of the fluctuating northern boundary of the subtropical biogeographic zone. Spatial scales up to three times the size of the Southern California Eddy are represented in figure 3.

Note that the three years when late-summer extension of the 18°C isotherm reached 36° N were the three years of the greatest California dolphin catch (compare figure 3 and table 1). In addition, the apparently decreasing southern excursion of the 22°C isotherm suggests the same multiyear event shown in figure 2. This trend is probably related to decreased California Current transport and coastal upwelling forced by the regional atmosphere and possibly an increase in downwelling, coastally trapped, wave energy emanating from the tropics (Clarke 1992; Norton and McLain 1994).

The anomalous features shown in figure 2 are reflected in figure 3. Statistical relationships among similar sets of parameters are given by Norton and McLain (1994).

Ocean Temperature and Salinity (T-S) Relationships in the Southern California Bight during Dolphin Presence

When temperature and salinity values from hydrocasts are graphed with salinity as a function of temperature, the position and shape of the resulting curve—developed by connecting the points representing discrete depths—often identifies water sources. Temperature is on the vertical axis increasing upward

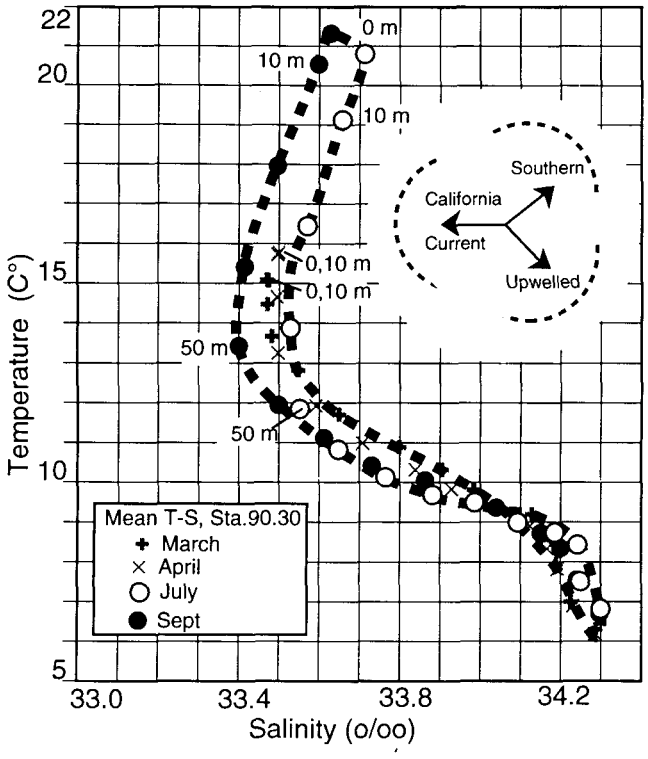

Figure 4. Mean temperature-salinity (T-S) curves at CalCOFI station 90.30. The *dotted line* encloses a mean seasonal T-S reference range. Selected depths are given in meters. The depths plotted, starting from highest temperature, are 0, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250, 300, 400, 500 meters.

so that the shallowest depths are plotted toward the top (figure 4).

In this section we discuss T-S curves at station 90.30 (figure 1) during seasons of high dolphin catch, to see how local T-S characteristics relate to availability off southern and Baja California. Average (1950–78) T-S plots for March, April, July, and September are shown in figure 4. Selected depths are labeled. The dotted line enclosing all four curves gives a reference T-S range of monthly means. Note that above 14°C on the temperature scale, July has the highest salinity and is the right boundary of the mean T-S space. September has the lowest salinity and is the left boundary of the mean T-S space.

The diagram in the upper right of figure 4 shows the expected displacement of T-S curves when southern water, upwelled water, or water from the core of the California Current is brought into the vicinity of station 90.30 (compare to figure 1). The dashed arcs suggest considerable variation and even overlapping of T-S characteristics in water from the three sources. This diagram indicates that between April and July there is normally an influx of southern water at the surface, as shown by upward, to-the-right movement of the 0 and 10 m points. As fall approaches, this water is mixed with modified California Current water of lower salinity and higher

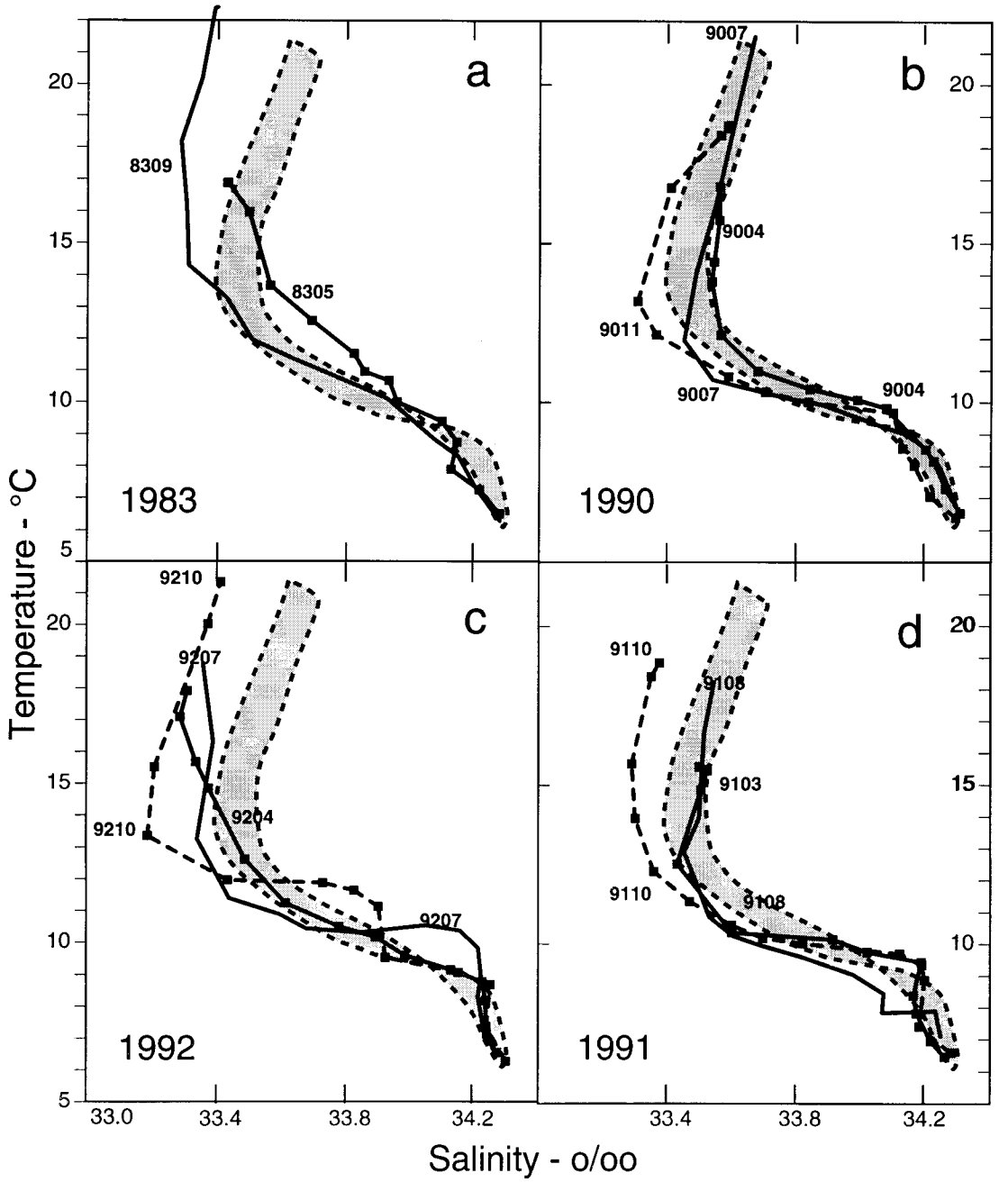

Figure 5. Temperature-salinity relationships derived from available CalCOFI data for station 90.30. Each curve is labeled with the CalCOFI cruise number (year and month). The *dotted line* encloses the mean T-S reference range shown in figure 4.

temperature, shifting the upper portion of the curve up and to the left. Local and regional insolation and evaporation are also important in the upper 10 m during summer and fall (Nelson and Husby 1983).

Temperature-salinity curves for 1983, 1990, and 1992—the best years for CPFV dolphin catch in southern California—are shown in figure 5.

In each year of good catch, the T-S curve shifts out of the top of the reference envelope during the July–September season. Part of this change is due to local heat gain by water resident in the eddy, but the large-scale analysis shown in figures 2 and 3 suggests that other processes may be involved.

In 1983 and 1992 lower-salinity California Current water was transported to station 90.30 in the late summer. Summer and fall transport from the south is also indicated during years of high catch, as shown in the movement of the T-S curves (above 15°) from April to July in 1990 and 1992.

Figure 5d is representative of T-S curves at station

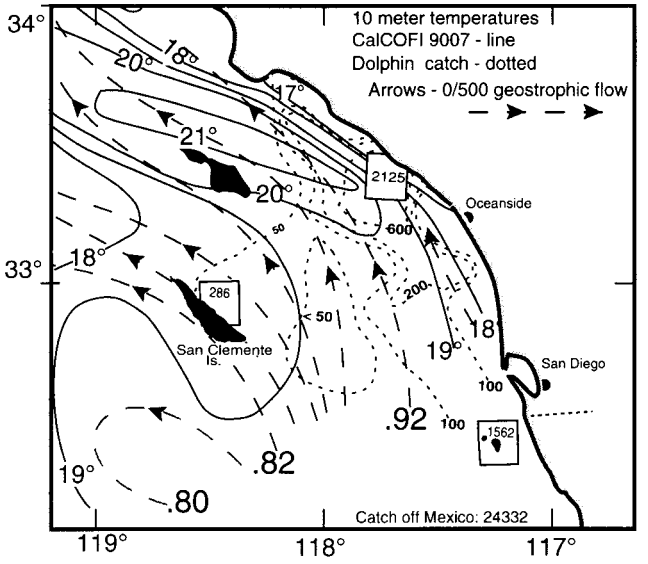

Figure 6. Spatial distribution of CPFV dolphin catch in 1990 (*dotted lines*), ocean temperature at 10 m (*solid lines*), and geostrophic flow (*arrows*) in the southern California catch area. Boxes show 0.1° areas with catch greater than 30 fish that were not contoured by standard conventions. Temperature at 10 m and dynamic height anomaly (*dashed*) are from CalCOFI survey 9007. The dynamic height anomaly contours are at 0.02 dynamic-meter intervals. Maximum geostrophic velocity was about 20 cm/sec.

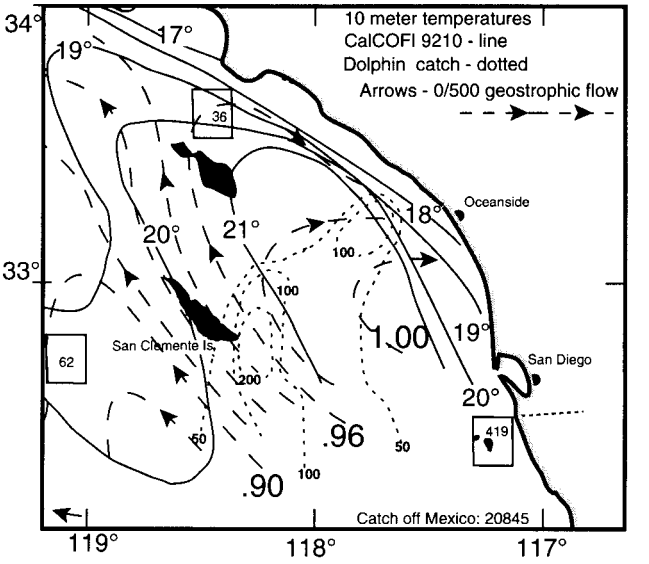

Figure 7. Spatial distribution of CPFV dolphin catch in 1992 (*dotted lines*), ocean temperature at 10 m (*solid lines*), and geostrophic flow (*arrows*) in the southern California catch area. Boxes show 0.1° areas with catch greater than 30 fish that were not contoured by standard conventions. Temperature at 10 m and dynamic height anomaly (*dashed*) are from CalCOFI survey 9210. Maximum velocity was about 22 cm/sec.

90.30 during a year of low dolphin availability (1991). There was little influx of low-salinity California Current water at mid-depths until late in the season and no evidence of southern water in the surface layers from March through August. All near-surface points were well below the average temperature.

Distribution of Catch and Physical Processes within the Southern California Bight

During 1990 the greatest catch of dolphin off southern California was along the coast near Oceanside. It appears that water of high temperature (20°–22°C) and high dolphin concentration was maintained in the bight by advection from the south (figure 6).

California dolphin catch in 1992 was less than one-third the catch in 1990. Fish that were caught came from the vicinity of San Clemente Island. The catch area during 1992 coincided with maximum northward geostrophic flow at the surface (computed over 500 m reference level: 0/500) around San Clemente Island (figure 7). Geostrophic flow (0/500) in the channel between the islands and the mainland was greater in 1990. This may be related to dolphins' being closer to the mainland in 1990.

In 1990 and 1992 there were pools of 21°C water thicker than 10 m in the bight. In 1990 the 20° and 21° isotherms were closed on the south, which suggests that cooler water from the west side of the eddy was intermittently transported toward the coast, concentrating the dolphin near shore. Dolphin were apparently less concentrated in 1992, when the isotherms were open to the south and the 19°C isotherm was removed to the northwest (compare figures 6 and 7). During 1992, there may have been higher concentrations of dolphin in less-well-searched areas offshore.

The T-S data from station 90.30 are consistent with figures 6 and 7 in showing different hydrographic patterns during 1990 and 1992. Low-salinity California Current water was available to the bight in 1992, but the higher salinity of 1990 shows that the California Current was then less directly available to the bight.

The data are less complete for 1983 and 1993, but certain conditions of the fishery and hydrography are worth noting. The catch pattern for 1983 was similar to that of 1990. Channel and mainland fishing areas appeared most important. From mid-July 1983 through the first week in August, the 10 m sea temperature at station 90.30 increased from 18.2° to 21.7°C. During 1993, geostrophic flow (0/500) into the channel between San Clemente Island and the mainland from the south was weak (~7 cm/sec), and the 21°C isotherm intruded to about 33° N. In August 1993, eastward geostrophic flow (0/500) was pronounced; T-S curves from April through October were 0.4‰ salinity to the left of the mean reference space; and the most dolphin were caught early in the fishing season (table 2).

DISCUSSION

The years preceding and following 1991 were good catch years, but in 1991 only 1,301 dolphin were caught (table 1). Because the capacity of the fishing fleet was

comparable in these three years (1990, 1991, and 1992), it is of interest to examine physical variability during 1991. The atmospheric indices (figure 3) do not suggest a cool period of anomalously strong high-pressure systems, which would extend the cool eddy plume southward and push the subtropical biogeographic zone to the south. However, the cool 1991 period is clearly shown in figure 3 and in the T-S curves for 1991 (figure 5d). We might speculate that poleward-propagating, upwelling, coastally trapped waves were important in maintaining this cool period.

Upwelled water appeared to characterize the inshore limb of the eddy during the 1991 dolphin fishing season (figure 5d), leading to flatter dynamic topography. Maximum northward geostrophic flow at the surface was about a fourth of the maximum velocity shown in figures 6 and 7. Consequently, neither temperature nor northward current strength were conducive to dolphin entry into California waters.

Since more than 85% of the CPFV catch comprises dolphin less than one year old, it can be proposed that year-class success of the locally sampled population contributes significantly to CPFV dolphin catch. Thus 1983 is listed as a good catch year because of the relatively high catch in California waters (1,258), but the total catch during 1983 was relatively low (4,992). Certainly, many conditions of the subtropical biogeographic zone were shifted to the north during 1983 (Fiedler 1984; Brinton and Reid 1986; Squire 1987). The low overall dolphin availability during the 1983 season may have resulted from local reproductive failure during the previous year. Note that the southern excursion of the temperature envelope shown in figure 3 is reduced during winters preceding good dolphin catch (1980, 1983, 1984, 1990, and 1992), but it is also reduced for 1986 and 1987, which were not particularly good catch seasons. The atmospheric indicator series (figure 2) also suggest that 1986 and 1987 might have been good dolphin fishing seasons if the fish had been available to migrate northward. It is possible that the low availability of dolphin during 1986 and 1987 also resulted from reproductive failure in the locally sampled population.

The local importance of the 20°C sea-surface layer is verified by this study (figures 6 and 7). However, July–September mean surface temperatures at station 90.30 exceed 20°C (figure 4). From this it might be expected that dolphin would be more frequently found off southern California. The source and path of the warm water appears to be important. To import large numbers of dolphin, the continuity of the advective path from the region of dolphin presence to the waters off southern California must be continuous and temporally uninterrupted by periods (areas) of cooler water. In the eddy system, cool water (<19°C) during the dolphin fishing season may result from a more intense California Current on the large scale and increased coastal upwelling on the local scale. Both processes are intensified by increased development of high-pressure systems in the eastern Pacific, and resulting southward winds along the coast (Reid et al. 1958; Hickey 1979).

The most productive CPFV dolphin fishing tactic is to cast live bait around floating objects, mainly kelp mats. Concentration and distribution of mats throughout the bight may be important in making dolphin available to CPFV anglers. During warm-water years (e.g., 1990) free-floating kelp fronds may be more abundant because of grazing by kelp bed invertebrates as the thermocline and nutricline are displaced deeper than the holdfasts, thus reducing the overall productivity of the kelp bed (Zimmerman and Robertson 1985; Tegner and Dayton 1991). Aggregations of drifting fronds (mats) will be found in areas of hydrographic convergence, which may be important in aggregating dolphin (Uda 1961) and bringing drifting kelp and feeding fish together.

Increased generation of eastern Pacific tropical cyclones is associated with the waning ENSO (Chan 1985). Increased tropical cyclone activity causes more frequent periods of swell (long gravity waves) that dislodge holdfasts and generate floating mats at kelp beds near the mainland and Channel Islands. These mats concentrate dolphin and may be a factor in the apparent greater abundance during ENSO periods.

CONCLUSION

Dolphin availability to southern California CPFV anglers will depend on near (small-scale, $<2 \times 10^2$ km) and distant (large-scale, $>1.0 \times 10^3$ km) effects. Pacific basinwide perturbations, which weaken or displace the eastern Pacific high-pressure system and lead to less-intense California Current forcing and coastal upwelling, appear important in allowing dolphin to enter California waters from the south and west. Less-intense southward advection of California Current water will allow the subtropical biogeographic boundary to shift northward, opening the Southern California Bight to dolphin migration. Seasonal accumulation of warm water near shore and resulting increased northward geostrophic flow facilitates dolphin migration into the bight. Once dolphin enter the bight, upwelling conditions around the seaward banks and islands may be important in producing a cool plume that will limit the dolphins' westward movement and concentrate them in warm water near the mainland. An alternate but not exclusive scenario involves partial breakdown of the cool central portion of the eddy, which allows warmer, less-saline California Current water to enter from the west. When dolphin are found in this water, they may be less concentrated. Coastally trapped long waves emanating from the south

may be important in forcing local ocean processes and displacing biogeographic boundaries. Local factors affecting the production and distribution of free-floating kelp mats may also be important in making dolphin available to CPFV exploitation.

ACKNOWLEDGMENTS

We thank Doug McLain and Art Stroud of the Ocean Applications Group (NOS/NOAA) for their help in obtaining MOODS5 data; Sherry Gripp of Scripps Institution of Oceanography for sending CalCOFI temperature-salinity-depth data at early stages of processing; Bob Lea and Paul Gregory of the California Department of Fish and Game for providing dolphin catch data; and Larry Eber and Cindy Meyer of the Southwest Fishery Science Center (NMFS/NOAA) for providing historical and mean CalCOFI station profiles. We also thank Heather Parker and Debra Losey for helping with initial literature searches. In addition, special thanks are due Jan Mason, Sue Smith, Bob Lea, Mary Yoklavich, Frank Schwing, Doug McLain, Dave Husby, Richard Parrish, Robert Paquette, and two reviewers for reading various versions of the manuscript and making suggestions that led to substantial improvement.

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COMPARISON OF CROSS-SHELF TRENDS IN ACOUSTIC DOPPLER CURRENT PROFILER AMPLITUDE AND ZOOPLANKTON DISPLACEMENT VOLUME IN SOUTHERN CALIFORNIA

MICHELE L. G. LYONS, PAUL E. SMITH, AND H. GEOFFREY MOSER
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038-0271

ABSTRACT

Simultaneous insonification and net sampling of the plankton in a discrete volume of water is the preferred field method for calibrating acoustic devices. The problem with this technique for the acoustic Doppler current profiler (ADCP) is that the volume insonified is too large for any plankton net. This causes error because of small-scale patchiness. The ADCP may be calibrated over large spatial scales by comparing the cross-shelf gradient in zooplankton volume to the cross-shelf gradient in the ADCP amplitude. We accomplished this by comparing ADCP amplitude data from transects off southern California in spring and summer during 1991 with zooplankton volumes from oblique net tows taken in the same seasons and area during 1991. The cross-shelf trends are similar, showing that measuring zooplankton with ADCP is possible. Although the ADCP may not be accurate for estimating the integrated zooplankton volume, it does describe the vertical distribution of the zooplankton and the scale and intensity of mesoscale patchiness as well as the amount of zooplankton, furnishing information not available from integrated net tows.

RESUMEN

El método preferido para calibrar aparatos acústicos en el campo es obtener simultáneamente muestras de plancton con redes y la respuesta sónica en un volumen aislado de agua. Para el Medidor de Perfiles Acústicos de Corrientes Doppler (MPACD), esta técnica tiene la desventaja de que el volumen de donde se obtiene la respuesta sónica es demasiado grande para las redes. Esto causa error debido as los patrones de agregación a pequeña escala. El MPACD podría calibrarse a escalas mayores comparando los gradientes perpendiculares a la línea de costa de volumen de zooplancton con los de la amplitud del MPACD. Comparamos datos de la amplitud del MPACD en transectos efectuados frente a las costas de California en primavera y verano de 1991 con datos de volumen de zooplancton colectado por arrastres oblicuos en las mismas estaciones y en la misma zona, en 1991. Las tendencias de los datos en dirección perpendicular a la costa son similares, lo que mostró que es factible medir el zooplancton con el MPACD. A pesar de que el MPACD no estima con exactitud el volumen integrado de zooplancton, sí describe la distribución vertical del zooplancton, la escala e intensidad de los patrones de agregación en la meso-escala, y la cantidad de zooplancton; esta información no puede obtenerse a partir de arrastres integrales de la columna de agua hechos con redes.

INTRODUCTION

The 50-year zooplankton time series of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has produced many advances in our knowledge of zooplankton distribution, ecology, and life history (e.g., Roesler and Chelton 1987 and references therein). One use of this large base of knowledge is to calibrate new methods of studying zooplankton distribution and ecology. One of the newest methods is the acoustic Doppler current profiler (ADCP).

The ADCP improves on traditional methods of studying zooplankton pattern because in addition to detecting patches, it also relates them to currents in the sea. Standard net tows show only the intensity of patchiness; they do not show the scale of patches or their location. Echo sounders can find the patches and define their vertical distribution, but they do not measure the currents along with the zooplankton. The ADCP does both (Smith et al. 1989).

Previous studies have calibrated the ADCP by comparing net tows directly to the backscattering intensity examined by the ADCP. Flagg and Smith (1989a, b) compared the results of moored and ship-mounted ADCPs against the results of MOCNESS tows and found very high correlations, but they took few net samples. They suggested several techniques for increasing the accuracy of the zooplankton index: calibrating the transducers' signal in a temperature bath, changing the geometric average to an arithmetic average, and measuring the initial signal intensity along with the returned sound (Flagg and Smith 1989a). Plueddemann and Pinkel (1989) used an acoustic Doppler system, similar to an ADCP, to describe and measure the speed of zooplankton vertical migration. Heywood (et al. 1991) used an ADCP without Flagg and Smith's corrections, like the one we used for this study, to measure the amount of zooplankton

[Manuscript received February 1, 1994.]

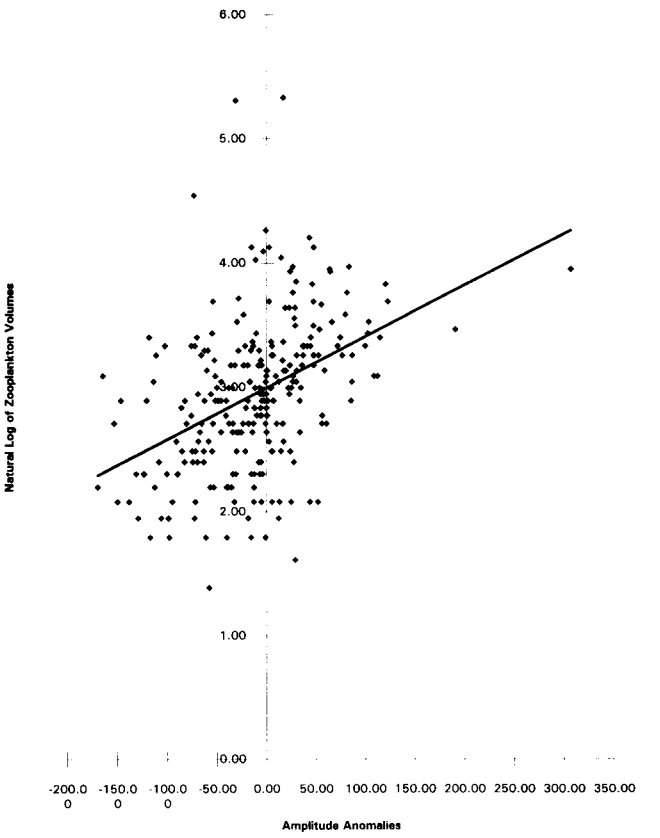

Figure 1. Correlation of MOCNESS net samples and ADCP results (R = 0.26, N = 255, $p < 0.001$). From Lyons, poster presented at CalCOFI meeting, 1992.

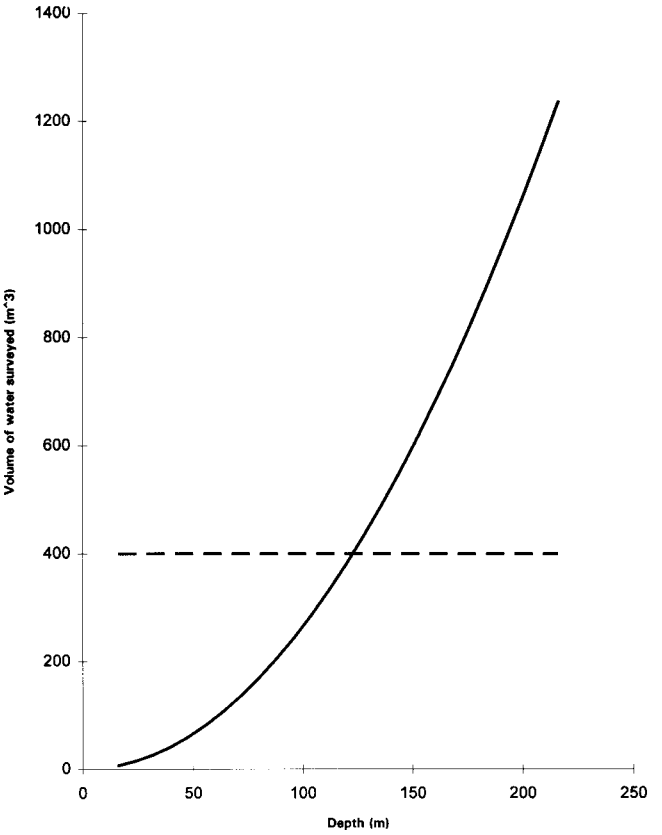

Figure 2. Comparison of volume surveyed by ADCP with volume from CalCOFI standard oblique tow. The *straight line* represents ADCP survey volumes at each depth; the *dashed line* represents the total volume surveyed by one whole net tow.

around an island in the Indian Ocean. Calibrations for the Heywood study came from 200-meter integrated net tows.

Previous research done by the first author compared ADCP data from off central California with zooplankton volumes from MOCNESS tows done simultaneously (figure 1). For each depth range, an anomaly was calculated. The anomaly was the difference between the raw ADCP data and an average for each depth. The average corrected for spherical spreading and attenuation. The anomalies were summed up over the volume the net sampled. The correlation between the MOCNESS tows and the ADCP results was significant (R = 0.26, N = 255). The low variance explained by this relationship may have been caused by the presence of several outliers, but there was no evidence that any should be removed.

The problem with calibrating the ADCP at this small scale is that an ADCP samples far more water than nets sample (figure 2). At 125 meters, an ADCP samples more water in each 8-meter bin than a net would in its entire 200-meter deep tow. In a region of small-scale patchiness, an ADCP will estimate an amount of zooplankton that will differ from that estimated by nets, even though both are correct.

In this paper we calibrated the ADCP at a large scale by using a comparison of the 650 km inshore-offshore trend in zooplankton abundance. Every parameter in the California Current, including zooplankton biomass, changes as one measures it farther offshore. The rate of this change may be expressed as the inshore-offshore slope. Comparing the slopes of ADCP amplitude data and zooplankton net tows makes it possible to calibrate the ADCP on a much larger scale than can be done when each tow is compared to each ADCP amplitude. This calibration against nets will allow the ADCP to provide absolute zooplankton volumes rather than the relative measure that is all that is available when there is no comparison with nets.

METHODS

The ADCP uses sound to measure current speeds. The one we used, manufactured by RDInstruments, emits 150 kHz sound pulses from a hull-mounted transmitter (figure 3). A ping is transmitted in four beams, each pointing into the water at an angle of 30 degrees

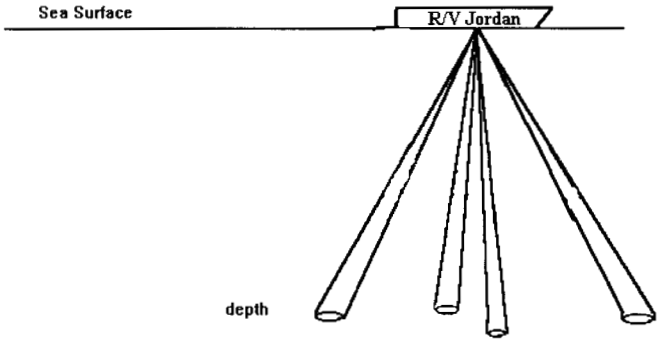

Figure 3. Diagram showing the arrangement of ADCP beams under the research vessel. One beam is directed toward the bow, one toward the stern, and two toward the sides of the ship.

off vertical. These pulses scatter off particles in the water. The frequency of the reflected sound is related to the current speed. The amount of reflected sound (the amplitude) that returns to the transmitter is proportional to the amount of particles in the water and their target strength. After the raw amplitude has been received by the ADCP, the amplitudes are averaged into minute-long (60-ping) ensembles. The data are also grouped by depth into 8-meter-deep bins. The amplitude, proportional to the amount of zooplankton in that volume of water, is recorded as "counts." The counts are related to decibels by a temperature-dependent conversion factor. Converting to decibels did not seem necessary for this work. The four bins closest to 50 m, 100 m, 150 m, and 200 m were chosen from two CalCOFI survey cruises conducted in March and August 1991 (table 1). The areas from which we obtained data are shown in figure 4.

Zooplankton were collected by CalCOFI standard oblique tows (Smith and Richardson 1977). A paired bongo net with 505-micron mesh was towed approximately 200 meters to the surface. We present only the volume of small plankton (no organisms larger than 5 ml), not the total plankton displacement volume, although the results were similar for both. We transformed the data by using logarithms to match the ADCP data, which were already log-transformed. The zooplankton volume from the same cruises as the ADCP were used for this study (table 1).

Because of net avoidance, the zooplankton volumes from the nets were very different between day and night.

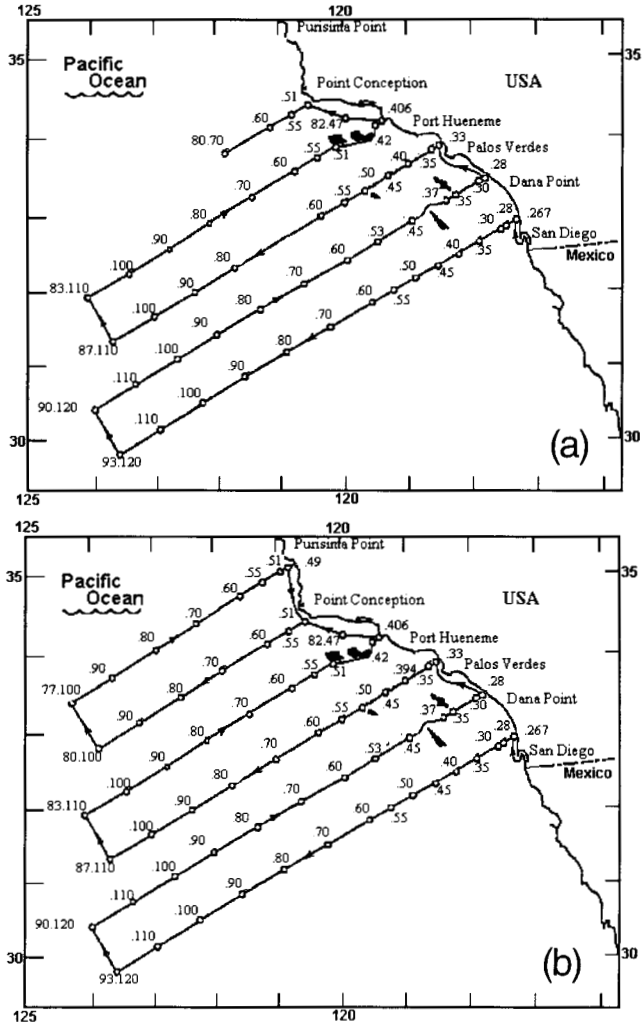

Figure 4. CalCOFI survey station pattern with area sampled in this study outlined for the March (*a*) and August (*b*) cruises in 1991.

The average volume for a nighttime tow was more than twice that of a daytime tow. This was not aliased into the spatial trend because each cross-shelf transect took at least two days to complete. The difference between the nighttime and the daytime zooplankton volumes for the nets would contribute to the variability around the slope, but would not contribute systematically to the trend itself.

These data were examined three ways—the averages in each 50 or 100 km block from shore were compared;

TABLE 1
Source of Data

Cruise	Ship	Date	Number of net tows	ADCP ensembles*
9103JD	R/V *David Starr Jordan*	26 Feb.–11 Mar. 1991	48	5173
9108JD	R/V *David Starr Jordan*	24 Jul.–9 Aug. 1991	58	3007

*Units are minutes of data gathered (ensembles) at each of the four different depths.

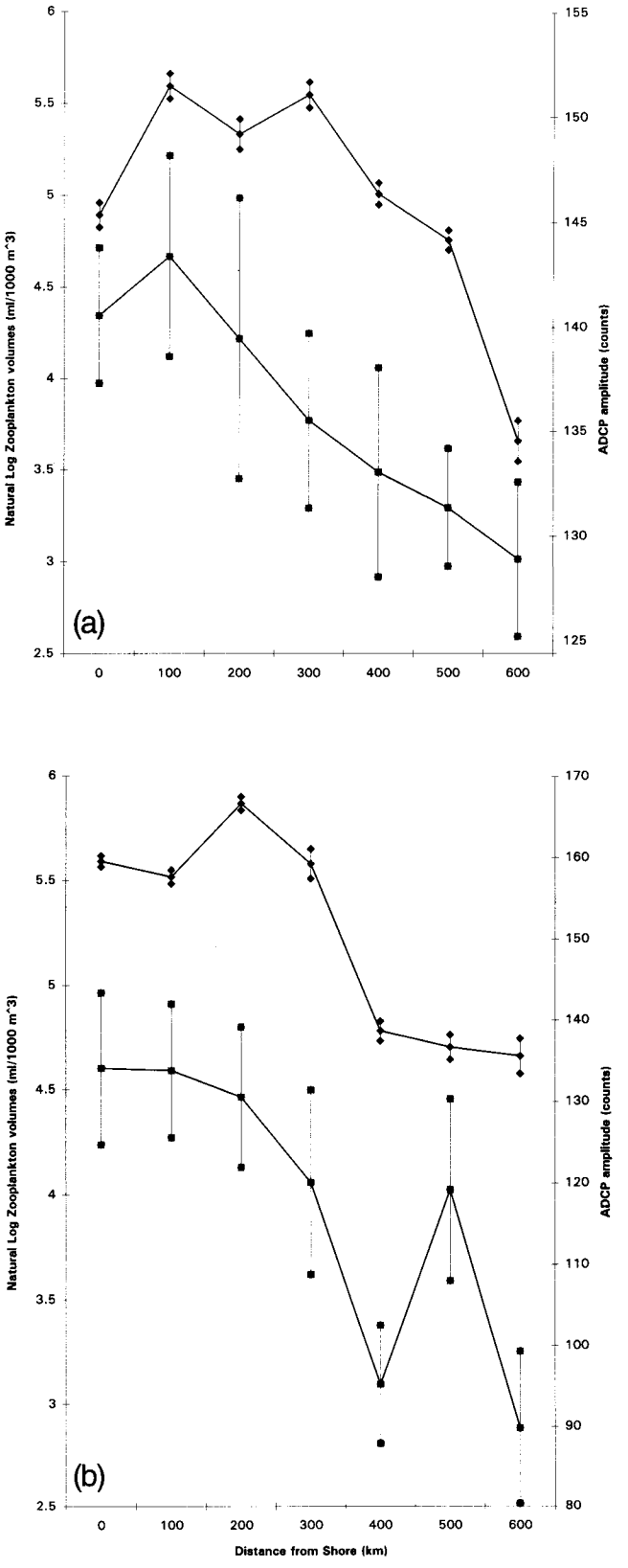

Figure 5. Inshore/offshore trends of the ADCP data (*diamonds*) at 50 m depth, and the net tow results (*squares*) for spring (*a*) and summer (*b*). The lines connect the means; confidence limits (± 2 SE) are shown by symbols above and below each mean.

the data were regressed with the distance from shore (Zar 1984); and the averages of the 50 m ADCP were compared to the net tow averages. We chose to average over 50 km for the ADCP to compare the different depths to show the greater detail that the ADCP can provide. We had to use the 100 km block for the net tows because the smaller block was imprecise. Figures 5 and 6 present the averages of the data for blocks 50 or 100 km from shore, graphed against distance from shore, with confidence intervals of two standard errors.

To simplify the calculations and avoid dealing with the irregularities of the California coastline, we calculated the distance from shore by changing the latitude and longitude, recorded from the Global Positioning System for the ADCP for each ensemble, to CalCOFI line and station (Eber and Hewitt 1979). The station for each line corresponding to the shore is known. Using this information, we calculated the number of stations between the study point and shore for the ADCP and the net data. The number of stations was translated into the distance offshore for each data point.

As an additional confirmation, we graphed the averages over the 100 km blocks for the ADCP versus the net tows. Correspondent averages would show that the ADCP agrees with the net tows over a large range of zooplankton abundances.

RESULTS

The main trend in zooplankton abundance across the shelf declines (figure 5). Both the ADCP and the net results show the same major trend. The spring patterns show a peak at 100 km and a relatively gradual decline to 600 km for the net data. The ADCP results show a broader maximum, from 100 to 300 km offshore before the decrease. The summer pattern shows a shallower slope.

Comparing the trend across shelf for the four different depths of the ADCP shows that the trend is constant between depths in summer, but not in spring (figure 6). Because the signal amplitude decays with depth, the return from zooplankton diminishes as the signal goes deeper. This reduction in signal amplitude explains the large decrease between depths. The reduced amplitude can be corrected by calculating spherical spreading and attenuation. We did not make such corrections because our emphasis was on comparing different trends, not comparing the absolute value of different depths together.

The spring patterns for each depth are not similar (figure 6a). The placement of the fluctuations in the trend varies between the depths. All depths do show the same general declining trend.

The summer profiles for the separate depths are very similar (figure 6b). All four depths show a broad maximum before a decrease. They also show a minimum at

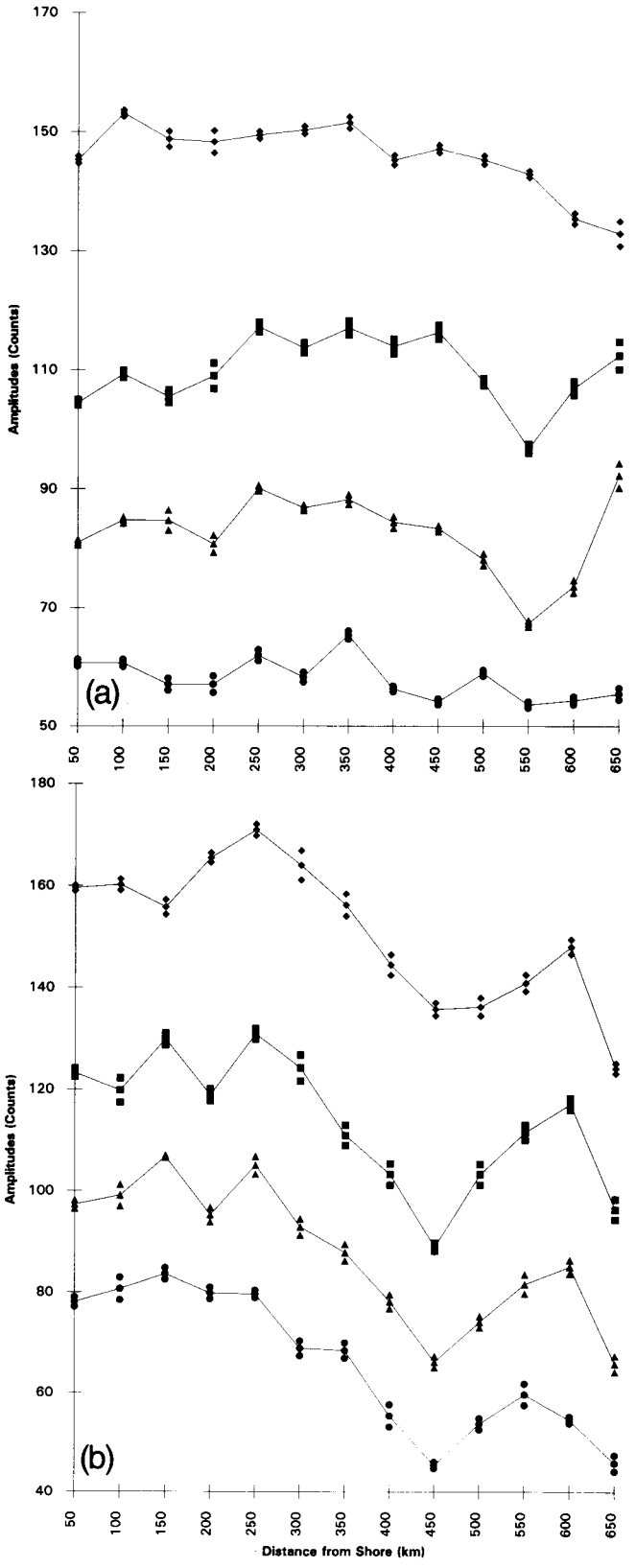

Figure 6. Depth-stratified ADCP results for spring (*a*) and summer (*b*) divided into 50 m (*diamonds*), 100 m (*squares*), 150 m (*triangles*), and 200 m (*circles*) depth intervals. Means and confidence limits are the same as those described for figure 5.

TABLE 2
Results of Regression

	Spring			Summer		
	Slope	N	r^2	Slope	N	r^2
CalBOBL data						
	−2.4	48	32.8%	−2.2	58	30.2%
ADCP data						
50 meters	−13.7	5173	7.6%	−47.4	3007	25.2%
100 meters	4.7	5173	0.8%	−47.9	3007	23.7%
150 meters	−7.8	5173	2.4%	−54.3	3007	36.0%
200 meters	−10.1	5173	6.0%	−61.0	3007	42.3%

450 km with a secondary maximum at 550–600 km. This pattern is reflected in the net tow trend for this season as well (figure 5b).

The slope calculated from the regression of the net tows generally agrees with the slope from the ADCP (table 2). The complicated patterns in figures 5 and 6 are not easily reduced into one number. The spring ADCP trend varies between depths and between the ADCP and the net tows. The low variability explained by the ADCP's slope shows that the spring trend was much more variable than the summer one. The summer ADCP trends are all similar and compare well with the slope of the net tow.

There is a strong relationship between the averages of the ADCP and the net tows for the 100 km blocks from shore (figure 7). Both the spring and the summer averages appear to fall onto the same line. There is less variance in the ADCP average in spring. Unfortunately, we do not have enough net tow data to use smaller averaging blocks, and thus more points in this figure.

DISCUSSION

The trends exhibited by the ADCP and the zooplankton data for both spring and summer demonstrate the extreme variability in the California Current. It is difficult to apply only one meaningful number to the slope. Thus, the most valid means of comparing the two instruments across the shelf is to compare the pattern of the ADCP across-shelf trend to the trend of the net tows (figure 5).

The spring pattern shows an offshore maximum for both instruments (figure 5a). The offshore maximum is broader for the ADCP, perhaps because of the greater resolution of the ADCP in detecting changes in the trend. Nets do not sample these changes because they reflect single points along the trend. The ADCP continuously measures the trend. Thus it detects the whole trend, including any fluctuations. This is apparent in figure 6a. Each depth has its own significant peaks and valleys, some of which, such as the peak at 250 km, cross depths. Some of the peaks and valleys are only on one depth, like the decrease at 650 km for the 50 m depth.

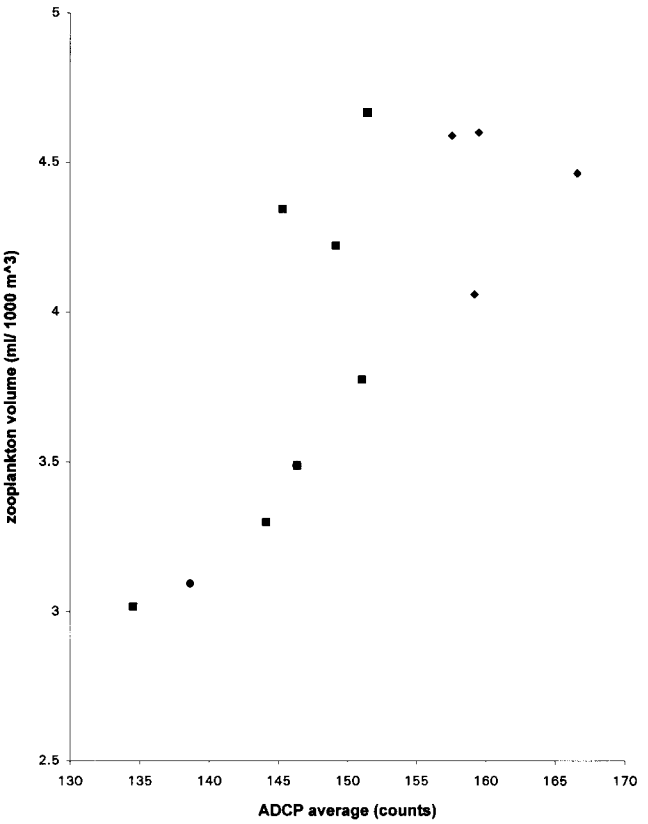

Figure 7. The averages of the 100-kilometer blocks from shore for spring (*diamonds*) and summer (*squares*) for the net tows against the ADCP averages at 50 meters.

The nets provide an overall estimate of the trend, but the ADCP follows the trend more precisely.

The summer pattern compares even better between different depths of the ADCP (figures 5b, 6b). When the ADCP is averaged over the same scale as the net tows, the patterns are not similar. When the ADCP is averaged less, over 50 km blocks, the patterns at each depth match each other and the trend of the net tows as well. This better match shows how averaging smooths fluctuations in the trend.

The slopes from the regression of the onshore-offshore trends of the ADCP and the net tows match to within an order of magnitude (table 2). This small correlation is adequate, considering the amount of error in each number. The net results present problems because of net avoidance by zooplankton and because the net samples all depths. The ADCP is not an exact measure of zooplankton volume and summarizes over a larger volume of water. Thus this agreement, weak though it is, supports the hypothesis that ADCP amplitude offers a means of measuring the absolute zooplankton volume in the ocean.

In fact, the ADCP's precision is probably higher than that of a net. Thousands of ADCP profiles can be recorded in one cruise (table 1). But time constraints on four cruises do not even allow 100 net tows. The smaller standard error for the ADCP curves is a result of averaging many more values together (figure 5). Given the results of a normal cruise, the ADCP will give more precise data than net tows. Further research will ascertain the ADCP's accuracy compared to nets.

ADCP data can augment standard plankton data by estimating, continuously and relatively accurately, the scale, intensity, and depth of plankton patches. The CalCOFI standard oblique tow provides one number for the whole water column; the ADCP furnishes a result every 8 meters. It also makes it possible to map zooplankton, a great benefit to investigations of zooplankton. These advantages demonstrate why the ADCP will help us understand the distribution of zooplankton in the California Current.

ACKNOWLEDGMENTS

We wish to thank Rich Charter for organizing the cruises, and his seagoing staff for conducting them. We especially thank Dave Griffith and Cindy Myers for their help. We thank Amy Hayes, who measured the plankton volumes. We also thank two anonymous reviewers, whose comments much improved the manuscript.

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LEVEL OF SIGNIFICANCE AND POWER OF TWO COMMONLY USED PROCEDURES FOR COMPARING MEAN VALUES BASED ON CONFIDENCE INTERVALS

NANCY C. H. LO
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

Confidence intervals (CIs) are frequently used to compare true means of two populations in the following ways: (A) If two 95% CIs are overlapping, then it can be concluded that the two population means are the same. (B) When only one CI is available, it can be concluded that two means are equal if one sample mean is within the 95% CI of the other mean. But the level of significance (α) of these two procedures does not always equal the intended 5%. The statistical power of these two procedures is unknown. This paper recommends another statistical procedure: (C), which is based on the CI of the difference (d) of two population means: CI(d). In this simulation study, the actual level of significance and the statistical power of these three procedures are computed for equal sample sizes. Statistical distributions considered are normal, Poisson, gamma, and lognormal. The simulation results indicate that the α value is 0.005 averaged over three continuous distributions (for Poisson, it is 0.06) for procedure A; 0.17 for procedure B; and 0.05 for CI(d). Thus, when the true means are indeed different, B is the most powerful procedure, and A is the least powerful procedure.

RESUMEN

Los intervalos de confianza (IC) para comparar la media verdadera de dos poblaciones se usan frecuentemente de dos maneras. (A) Si dos IC al 95% traslapan, se puede concluir que la media de las dos poblaciones no es la misma. (B) Cuando sólo se dispone de un IC, puede concluirse que las dos medias son iguales si una de éstas se encuentra dentro del IC de 95% de la otra media. Sin embargo, el nivel de significancia (α) de estos dos procedimientos no siempre es igual al 5% deseado. La potencia estadística de estos dos procedimientos es desconocida. Esta contribución recomienda otro procedimiento estadístico: (C), basado en los IC de las diferencias (d) de dos medias poblacionales: CI(d). En este estudio, usamos simulaciones y calculamos el nivel de significancia real y la potencia estadística de estos tres procedimientos (para muestras de tamaño igual). Se usaron distribuciones normal, Poisson, gama y lognormal. Los resultados de las simulaciones indicaron que para el procedimiento A los valores α promediados en tres distribuciones contínuas fué de 0.005 (0.06 para la distribución Poisson), 0.17 para el procedimiento B y 0.05 para el procedimiento C. Consecuentemente, cuando las medias verdaderas son diferentes, el procedimiento con mayor potencia es el B, mientras que el de menor potencia es el A.

[Manuscript received February 7, 1994.]

INTRODUCTION

In the scientific literature, summary statistics such as averages and standard errors are often used to construct confidence intervals (CIs) for the true mean under the assumption of the normal distribution of the sample mean. Frequently, CIs are used to compare means of two populations in the following ways; (A) If two 95% CIs are overlapping, it can be concluded that the two population means are the same. (B) When only one CI is available, it can be concluded that two means are equal if one sample mean is within the 95% CI of the other mean. Although these two procedures are convenient and popular ways of making inferences about population means, their level of significance (α) does not always equal the intended 5%.

The correct statistical procedures should be those based on the difference of two sample means: for example, t statistics and the CI for the difference of population means: CI(d). When CI(d) is used, and if the CI(d) contains zero, it can be concluded that the two population means are the same. Thus there are actually three procedures to be considered: procedure A is the overlapping of two CIs; procedure B is the inclusion of one sample mean in the CI from the second sample; and procedure C is the CI(d) based on the difference of two sample means assuming normal distribution.

The procedure used is important because it affects conclusions. Take, for example, Hunter and Leong's (1981) comparison of the mean batch fecundity of northern anchovy (15–19g) that matured in the laboratory and in the sea (figure 1):

Locality	n	Mean	(2SE)	95% CI
Laboratory	38	8910	(1210)	(7700, 10120)
Sea	17	6800	(1150)	(5650, 7950)
Difference		2110	(1669)	(441, 3779)

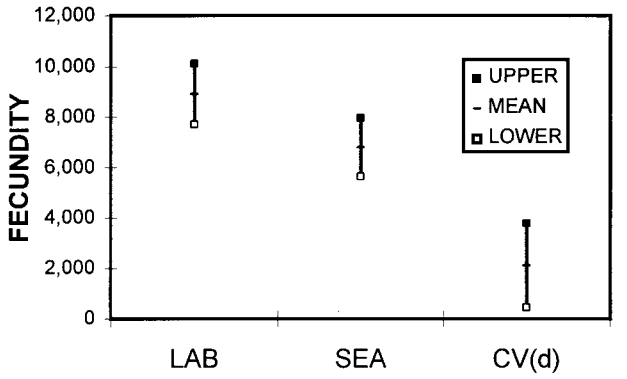

Figure 1. Confidence intervals based on the individual sample mean fecundity of anchovy that matured in the laboratory and in the sea. The CI(*d*) is the confidence interval based on the difference of two sample mean fecundities. Low and high are the lower and upper 95% confidence limits.

The two mean batch fecundities are not significantly different if procedure A is used, but they are significantly different if B or C is used. Clearly, procedure C is the preferred choice, since it is known that the confidence level is 95%. If A or B must be used, however, the investigator should be aware that the level of significance can affect the result.

The purpose of this paper is to compare these three procedures. A simulation study was conducted to compute the actual confidence level ($1-\alpha$), and the power of procedures A and B was compared to that of procedure C. Note that the level of significance (α) is the probability of claiming that the two population means are different by rejecting the null hypothesis that two population means are equal when, in fact, they are the same. This is a wrong conclusion and is the so-called type I error. The power is also the probability of rejecting the null hypothesis that two means are equal, when the two population means are indeed different. Thus the power is the probability of making the right decision at the expense of α value. While the α value is normally predetermined, the power of a procedure depends not only on the α value, but also on the magnitude of the difference between two population means and the sample size. Statistical power has been recognized as an important element in evaluating fishery population estimation procedures (Peterman 1990; Solow and Steel 1990). But the power must be considered together with the level of significance.

In the simulation, all 95% CIs were computed on the assumption of normally distributed sample means for four underlying distributions: normal, Poisson, gamma, and lognormal. The density functions are given in the appendix. Different statistical distributions for various sample sizes ranging from 5 to 100 were included in the simulation to check the robustness of the CI(*d*). The CI(*d*) is based on the normal assumption, which is valid only for large sample size. Here, CI(*d*) is robust if it maintains a 95% confidence level as intended.

In this paper I do not provide the optimal CI of the difference of population means for each distribution. I refer the reader to Barr 1969 and Nelson 1989 for normal; Casella and Robert 1989 for Poisson; Withers 1991 for gamma; Land 1988 for lognormal; Douglas 1993 and Weerahandi 1993 for a generalized CI; and Beal 1989 for CI and sample size in general. Barr (1969) and Nelson (1989) dealt with the overlapping problems for the normal case only. Ideally, distribution-specific CIs should be sought, but some of the procedures are complex and difficult to apply. Although the normal-based CIs are convenient, their limitation should be recognized. They should be used with caution, particularly when sample size is small.

METHODS

Suppose that one sample of size (n_i) is taken from each of two populations with mean (μ_i) and standard deviation (σ_i), $i = 1, 2$. The goal is to determine whether the population means are equal, i.e., $\mu_1 = \mu_2$. Each of the three procedures would lead to the conclusion that the two averages are not significantly different if:

A. CI_1 and CI_2 are overlapping, where $CI_i =$

$$\bar{x}_i \pm t_{df_i,\alpha/2} s_{\bar{x}_i} \text{ for } i = 1, 2 \qquad (1)$$

where df_i (degree of freedom) $= n_i - 1$, and $s_{\bar{x}_i}$ is the standard error of the sample mean.

B. The sample mean from one data set is within the CI computed from the other data set (CI_2).

$$\bar{x}_1 \in CI_2 = \bar{x}_2 \pm t_{df_2,\alpha/2} s_{\bar{x}_2} \qquad (2)$$

C. The CI(*d*) of the difference of the population means contains zero. The CI(*d*) was computed from the difference of two sample means and the standard error of the difference. This is the confidence interval based on the normal distribution of the sample mean. The 95% CI for $d = \mu_1 - \mu_2$ is

$$CI_d = (\bar{x}_1 - \bar{x}_2) \pm t_{df,\alpha/2} s_{\bar{x}_1 - \bar{x}_2} \qquad (3)$$

where df $= (n_1 - 1 + n_2 - 1)$ if variances are equal. If variances are not equal, the formula for the d.f. is available from statistics books (Zar 1984).

The formulas related to the standard error of the sample mean have not been given because they can be found in any statistics reference. Equations 1 to 3 are used for three underlying distributions. In all cases, sample sizes were set to be equal, i.e., $n_1 = n_2$.

In the simulation, data are generated from each of the distribution functions for sample sizes ranging from 5 to 100 (actual sample size may differ for different distri-

TABLE 1
Mean (μ) and Standard Deviation (σ) for Each Distribution Used in the Simulation

Distribution	Parameters*
Normal	μ_1 = 1, and μ_2 = 1, 1.5, 2, 3, 4, and 5 $\sigma_1 = \sigma_2 = 2$
Poisson	mean = variance: μ_1 = 0.5, and μ_2 = 0.5, 1, 2, 5, and 10
Gamma	b(scale parameter) = 1 $\mu_1 = bc = 3$ and μ_2 = 0.5, 1, 1.5, 2, 2.5, and 3 where c is the shape parameter
Lognormal	μ_1 = 0 and μ_2 = 0, 0.5, 1, and 2 $\sigma_1 = \sigma_2 = 1$

*μ_1 is the mean under the H_0 and μ_2 is the mean under the H_a.

butions). To compute the α values, two independent samples were generated from distributions with same mean value. To compute β values, two independent samples were generated from two distributions with different mean values. One thousand iterations (m) were run for each comparison, and the actual level of significance (α) under the null hypothesis H_0: $\mu_1 = \mu_2 = \mu$ was computed for various μ values as:

$$\alpha_A = (\text{number of two CIs not overlapping})/m \quad (4)$$

$$\alpha_B = (\text{number of } \bar{x}_1 s \text{ is not contained in CI}_2)/m \quad (5)$$

and

$$\alpha_C = (\text{number of CI}(d)\text{s not containing zero})/m \quad (6)$$

The power of the three procedures was also computed for various sample sizes under the alternative (H_a): $\mu_2 \neq \mu_1$, where μ_1 was kept constant and μ_2 varied. The confidence level for each individual CI was 95%. Under H_a: $\mu_2 \neq \mu_1$, data were generated from two populations, one with mean μ_2, and one with μ_1. I computed β_A, β_B, and β_C in the same way as the α values (equations 4–6).

The parameters for each distribution are given in table 1. The α values were computed from two samples, each taken from populations with identical mean values indicated by μ_2 in table 1. Samples from the population with mean values equal to μ_2 are compared with samples from the population with mean values equal to μ_1 to compute the power.

RESULTS

Normal Distribution

The α values for $\mu_1 = \mu_2$ = 1, 1.5, 2, 3, 4, and 5 were computed for sample sizes 5 to 100, even though the difference of μ_1 and μ_2, not the actual values of μ_1 and μ_2, is relevant. The standard deviation is set at 2 (table 2). For procedure A, the computed α values are less than 0.05, with an average of 0.005. For procedure B, the opposite is true, and the computed α values are greater than 0.05, with an average of 0.15. For procedure C, the α values are close to 0.05, as expected. In procedure A, the true α values are not affected by the sample sizes, as they are in procedure C. In procedure B, however, the level of significance is affected by the sample size. The α values for sample sizes ≤10 ranging from 0.12 to 0.14 are smaller than those ranging from 0.14 to 0.17 for larger sample sizes.

TABLE 2
Level of Significance (α), Confidence Level ($1-\alpha$), and Overall Power for Three Procedures, for Each Statistical Distribution

	Procedures			
	A	B	C	Hypothesis
Normal				
α	0.005	0.15	0.05	H_0: $\mu_1 = \mu_2$
$1-\alpha$	0.995	0.85	0.95	
Power relative to option C	low	high		H_a: $\mu_2 \neq \mu_1$
Poisson				
α	0.06	0.17	0.05	H_0: $\mu_1 = \mu_2$
$1-\alpha$	0.94	0.83	0.95	
Power relative to option C	low	high		H_a: $\mu_2 \neq \mu_1$
Gamma				
α	0.006	0.16	0.05	H_0: $\mu_1 = \mu_2$
$1-\alpha$	0.994	0.84	0.95	
Power relative to option C	low	high		H_a: $\mu_2 \neq \mu_1$
Lognormal				
α	0.004	0.19	0.05	H_0: $\mu_1 = \mu_2$
$1-\alpha$	0.996	0.81	0.95	
Power relative to option C	low	high for $n < 30$		H_a: $\mu_2 \neq \mu_1$

The power values were computed for μ_2 = 1, 1.5, 2, 3, 4, and 5, compared to μ_1 = 1. Again, σ = 2 and sample size = 10, 20, . . . , 50, 100. Procedure B is the most powerful of the three, and A is the least powerful, regardless of sample sizes, if the population means are different (table 2 and figure 2). For example, when μ_2 = 2, compared to μ_1 = 1, for sample size 30, the power is 0.18 for procedure A, 0.69 for procedure B, and 0.5 for procedure C. The difference in power among the three distributions is more pronounced for a small sample size and a small difference in mean values.

Poisson Distribution

The Poisson distribution (equation A2) is often used to model the distribution of counts of rare events that are randomly distributed in time and space, e.g., the number of fish schools in a certain area during a certain season. The Poisson distribution has only one parameter: μ = mean = variance. The shape of the distribution depends on μ; for large μ, the distribution tends to be symmetric and close to the normal distri-

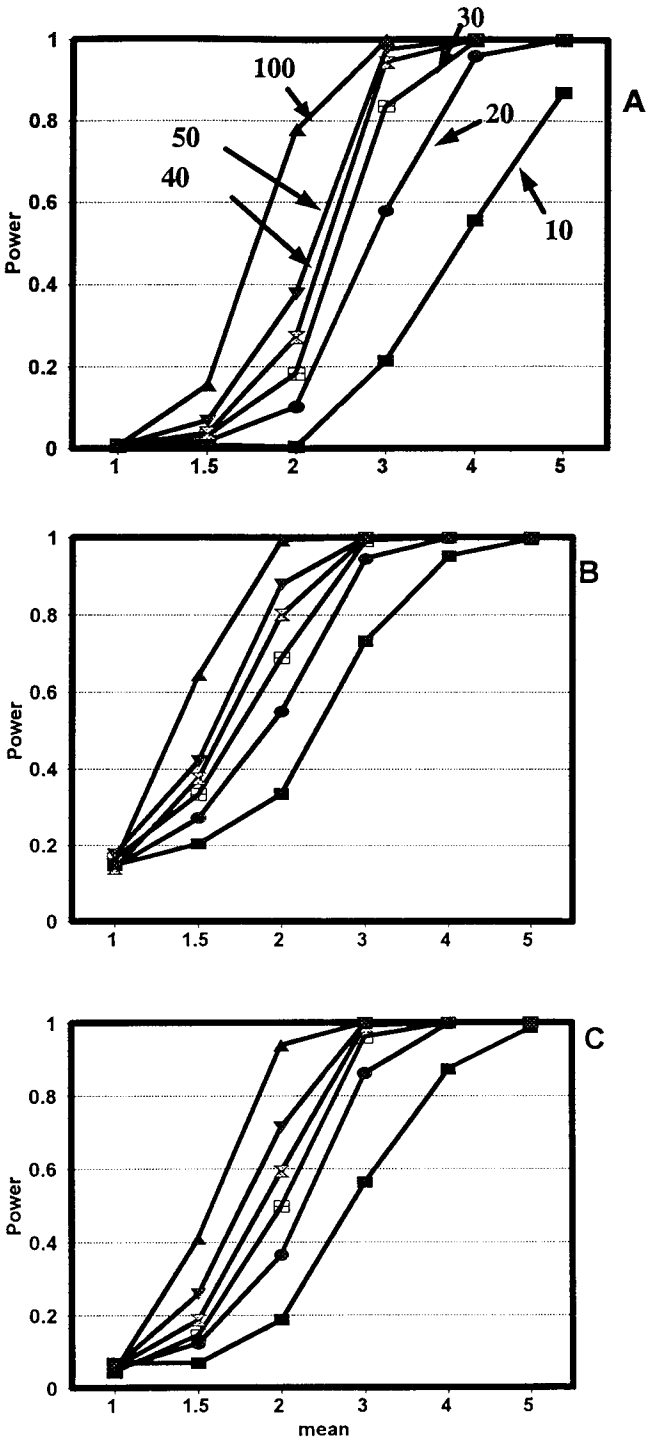

Figure 2. Power for procedures A, B, and C at different mean values (μ_2) compared to $\mu_1 = 1$; $\sigma = 2$ for sample sizes ranging from 10 to 100 for normal distribution.

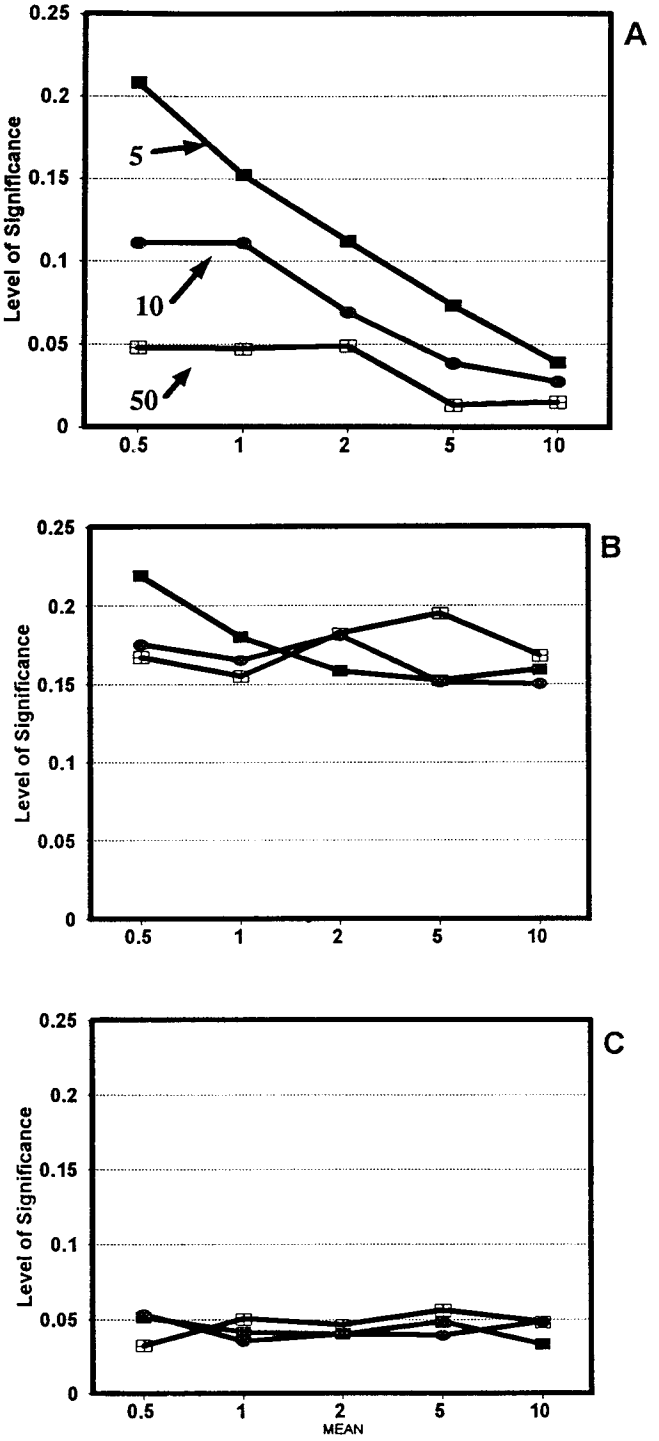

Figure 3. Level of significance (α) for procedures A, B, and C at different mean values for sample sizes 5, 10, and 50 for Poisson distribution.

bution. In the simulation, the α values were computed for μ = 0.5, 1, 2, 5, 10 and sample sizes 5, 10, and 50 (figure 3). Procedures A and B are sensitive to the sample size and mean values: the level of significance (α) decreases as the sample size and the mean values increase. But for procedure C, the α values (slightly less than 0.05) are independent of sample size and the mean values.

The α value averaged over all sample sizes and mean values was 0.06 for procedure A, 0.17 for procedure B, and close to 0.05 for procedure C (table 2 and figure 3).

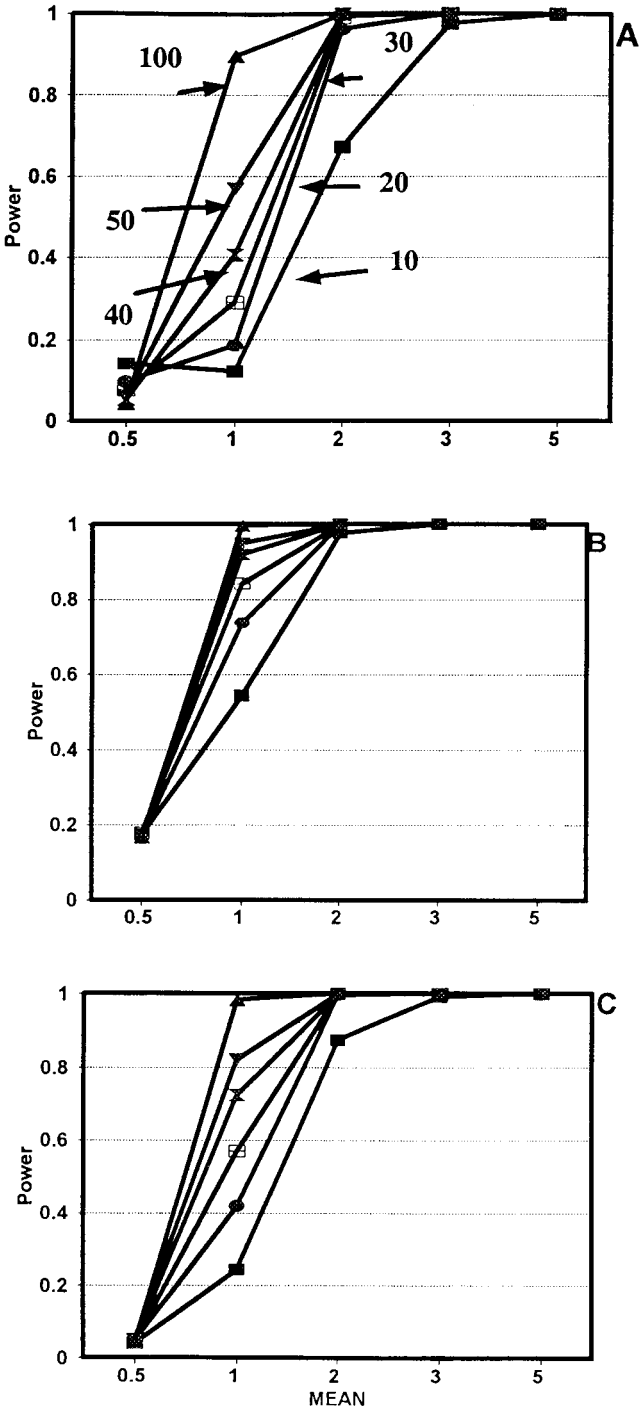

Figure 4. Power values for procedures A, B, and C at different mean values (μ_2) compared to μ_1 = 0.5 for sample sizes ranging from 10 to 100 for Poisson distribution.

Although the α values for sample sizes >10 are similar for procedures A and C, A is less powerful than C, regardless of sample sizes (figure 4). For example, for $\mu_2 = 1$ compared to $\mu_1 = 0.5$ for sample size 30, the power is 0.3 for procedure A, 0.84 for procedure B, and 0.57 for procedure C.

Gamma Distribution

The gamma distribution (equation A3) has two parameters (b,c) with mean = bc, and variance = b^2c. Without loss of generality, the scale parameter, b, was set at 1 (this is the exponential distribution). The shape of the gamma distribution tends to be symmetric as parameter c increases. Data were generated from six populations in which $b = 1$, and c = 0.5, 1, 1.5, 2, 2.5, or 3 compared to samples from one population with $b = 1$ and $c = 3$ (or $\mu_1 = 3$).

For procedures A and C, the computed α values are independent of the mean values, with an average of 0.006 for A and 0.05 for C. For procedure B, the computed α values decrease as the sample size and the mean values increase (figure 5). The average of all the α values is 0.16 (table 2). Procedure B is the most powerful procedure, and A is the least powerful, regardless of sample size and mean values (figure 6). For example, for $\mu_2 = 2$ compared to $\mu_1 = 3$, with a sample size = 30, the power is 0.41 for procedure A, 0.85 for procedure B, and 0.72 for procedure C.

Lognormal Distribution

The lognormal distribution is often used to describe abundance per unit area (Meyers and Pepin 1990; Lo et al. 1992; equation A4). A random variable, y, follows lognormal if $x = \ln(y)$ is normal (μ, σ^2).

For each of three procedures, α was computed for $\mu_1 = \mu_2 = 0$, 0.5, 1, and 2; $\sigma_1 = \sigma_2 = 1$; and sample size n = 5, 10, 30, and 50. The α values are independent of sample size, with an average of 0.004 for procedure A, 0.19 for B, and 0.05 for C. For procedures A and B, the variation of α values increases as mean value increases (table 2, figure 7).

Procedure A is the least powerful of the three. For sample sizes <30, procedure B is most powerful. For sample sizes ≥30, procedure C is most powerful (figure 8). For example, for sample size = 30 and $\mu_2 = 1$ compared to $\mu_1 = 0$, the power is 0.63 for procedure A, 0.81 for procedure B, and 0.96 for procedure C.

CONCLUSIONS

Table 2 summarizes the simulation results for the level of significance and overall power for each of the four distributions.

The α value of procedure A is 0.005 for normal, gamma, and lognormal distributions. Thus procedure A probably leads to the conclusion that two means are the same even though they are different. But if the two CIs do not overlap, one can be much more than 95% sure that the population means are different. The α value of procedure A is not sensitive to sample size and mean values except for the Poisson distribution. For the Poisson,

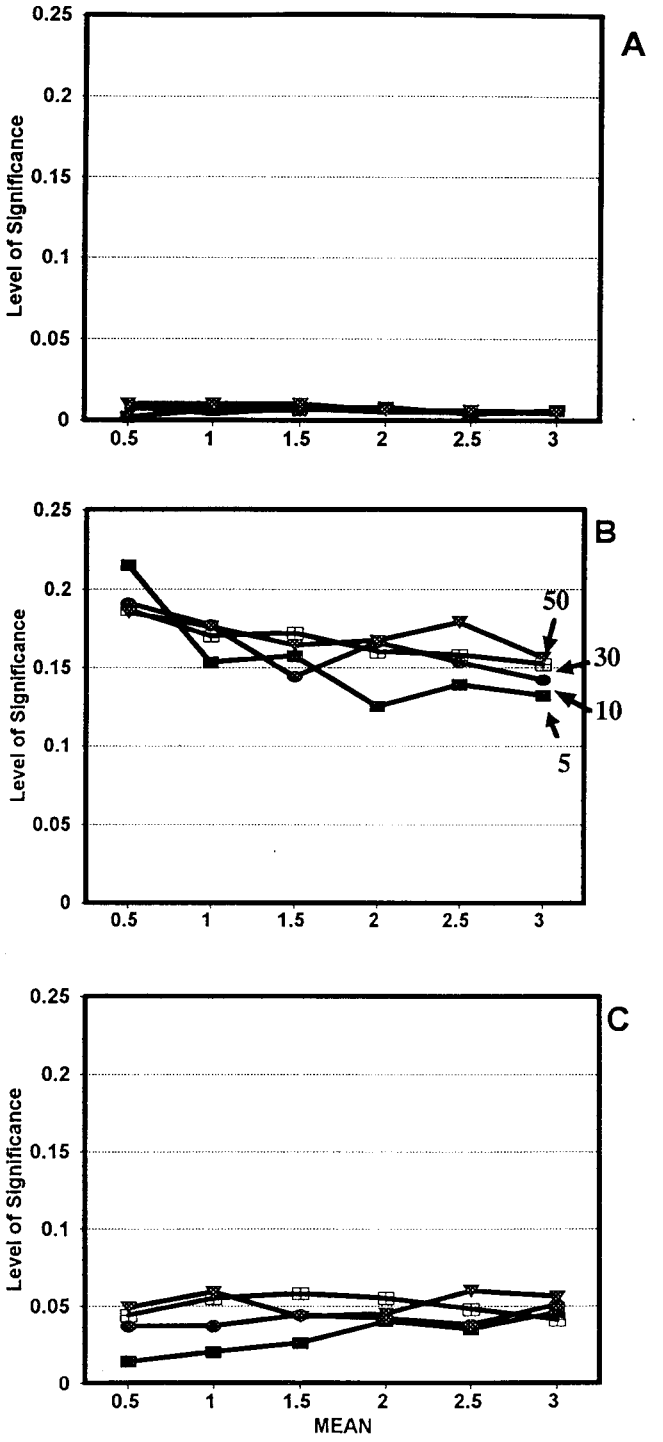

Figure 5. Level of significance (α) for gamma distribution (b = 1) for procedures A, B, and C at different mean values for sample sizes ranging from 5 to 50.

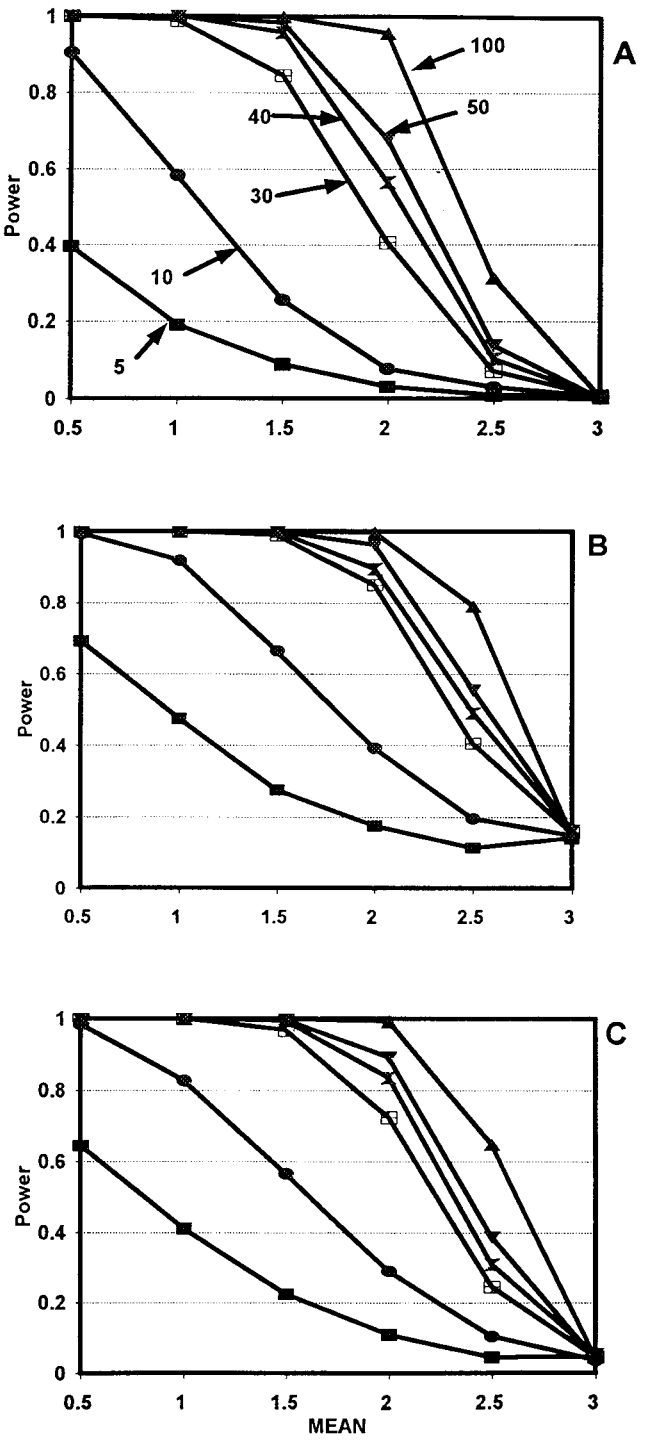

Figure 6. Power for procedures A, B, and C at different mean values (μ_2) compared to μ_1 = 3 for sample sizes ranging from 5 to 100 for gamma distribution.

the α is large for small sample size and small mean values; it decreases as the sample size or the mean values increase, with an overall average equal to 0.06 (figure 3).

The α value of procedure B is 0.17 averaged over all the distributions. Thus procedure B invites one to conclude that two population means are different when, in fact, they are the same. For the normal distribution, the α values differ for sample size < or > 10, and are not affected by the mean values. For Poisson distribution, α values decrease as the mean values increase for

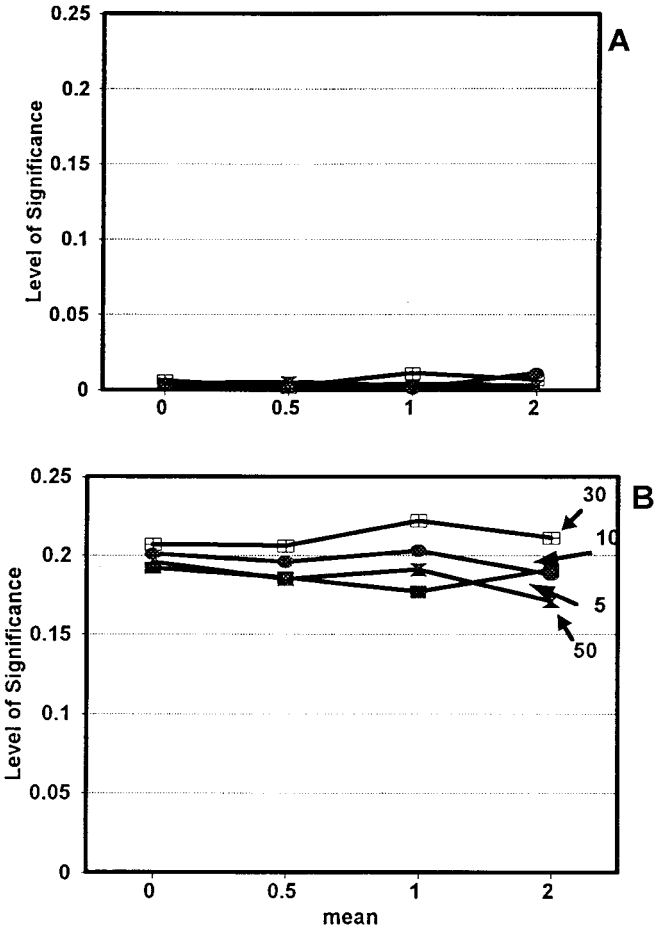

Figure 7. Level of significance (α) for procedures A and B at different mean values for sample sizes ranging from 5 to 50 for lognormal distribution (α values for procedure C are close to 0.05 and were not plotted.)

small sample size (n = 5). For gamma distribution, the α value of procedure B decreases as the sample size or the mean value increases, particularly for a sample size equal to 5.

Of the three procedures, B is most powerful, and A is least powerful if the population means are indeed different. The difference in the power values between procedures A and B results from the difference in α values; thus one should not conclude that procedure B is "better" than A based on power unless both A and B have the same α value. As expected, power increases with sample size and the difference between the means for all procedures.

Procedure C maintains the assumed confidence level for the four distributions when the sample size is greater than 10. Therefore, CI(d) is a robust procedure that can be used for these three nonnormal distributions if the sample size is moderate.

In the example of comparing the mean fecundity of anchovy, the fact that procedures A and B indicated different conclusions is not surprising now that we know

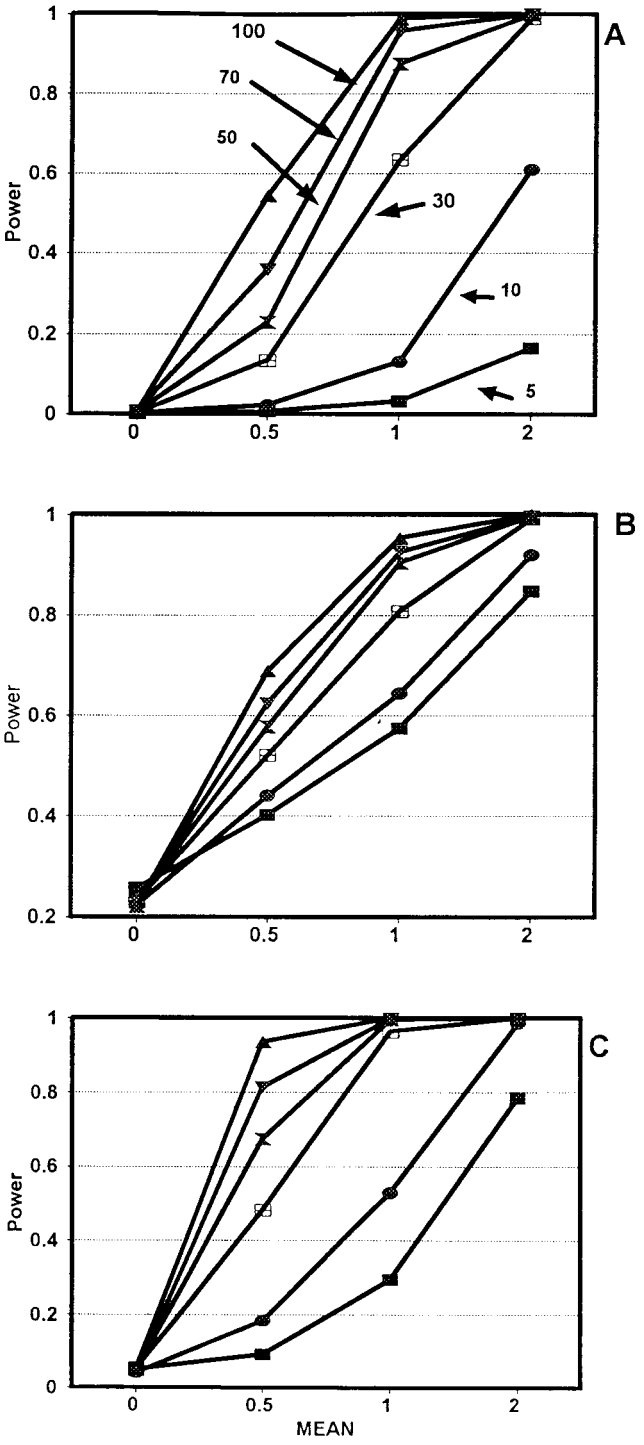

Figure 8. Power for procedures A, B, and C at different mean values (μ_2) compared to μ_1 = 0; σ = 1 for sample sizes ranging from 5 to 100 for lognormal distribution.

that procedure A has a low level of significance which leads to claiming that the two means are not statistically different, whereas procedure B does the opposite.

For the lognormal distribution, if the variances are not equal, variance should be included in the compu-

tation of the CI because the mean of y is equal to $\exp(\mu+\sigma^2/2)$. The CI should be one for $\exp(\mu+\sigma^2/2)$. The latter expression is in terms of the mean and variance of x.

For future research, it would be useful to

- obtain the level of significance of the original CI to achieve a 5% level of significance for procedures A and B for other distributions as reported by Nelson (1989) for the normal case
- investigate the effect of unequal sample sizes on the level of significance and power of the three procedures
- develop procedures for comparing two population means when the standard error is given but not the sample size.

ACKNOWLEDGMENTS

I thank Susan Picquelle of Northwest Fisheries Science Center, Seattle; Alfredo Julian, Larry Jacobson, and Paul Smith of Southwest Fisheries Science Center; and C. J. Park of San Diego State University for reading the manuscript and providing constructive comments.

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APPENDIX

Density functions used in the simulation analysis

Normal

$$f(x;\mu,\sigma) = \frac{1}{\sigma\sqrt{2\pi}}\, e^{-(x-\mu)^2/(2\sigma^2)} \qquad \text{(A1)}$$

for $-\infty < x < \infty$; $0 < \sigma$, $-\infty < \mu < \infty$

Poisson

$$f(x;\lambda) = \lambda^x e^{-\lambda}/x!$$

for $x = 0, 1, 2, 3, \ldots$; $0 < \lambda$ (A2)

Gamma

$$f(x;b,c) = \frac{1}{\Gamma(c)\, b}\, (x/b)^{c-1} e^{-(x/b)} \qquad \text{(A3)}$$

for $0 < x$; $0 < b,c$

Lognormal

$$f(y;\mu,\sigma) = \frac{1}{y\,\sigma\sqrt{2\pi}}\, e^{-(\ln(y)-\mu)^2/(2\sigma^2)} \qquad \text{(A4)}$$

for $0 < y$; $0 < \sigma$, $-\infty < \mu < \infty$.

Part IV

INDEX TO CALCOFI REPORTS 1989–1993

This index contains two parts: author and subject. The index was generated from the publications listed on the right. The year following the volume number is the publication date. Two previous indexes have been published: in volume 24 for the years 1950–1982 and in volume 30 for 1983–1988.

California Cooperative Oceanic Fisheries Investigations Reports:
Volume 30; 1989
Volume 31; 1990
Volume 32; 1991
Volume 33; 1992
Volume 34; 1993

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SUBJECT INDEX

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(book):
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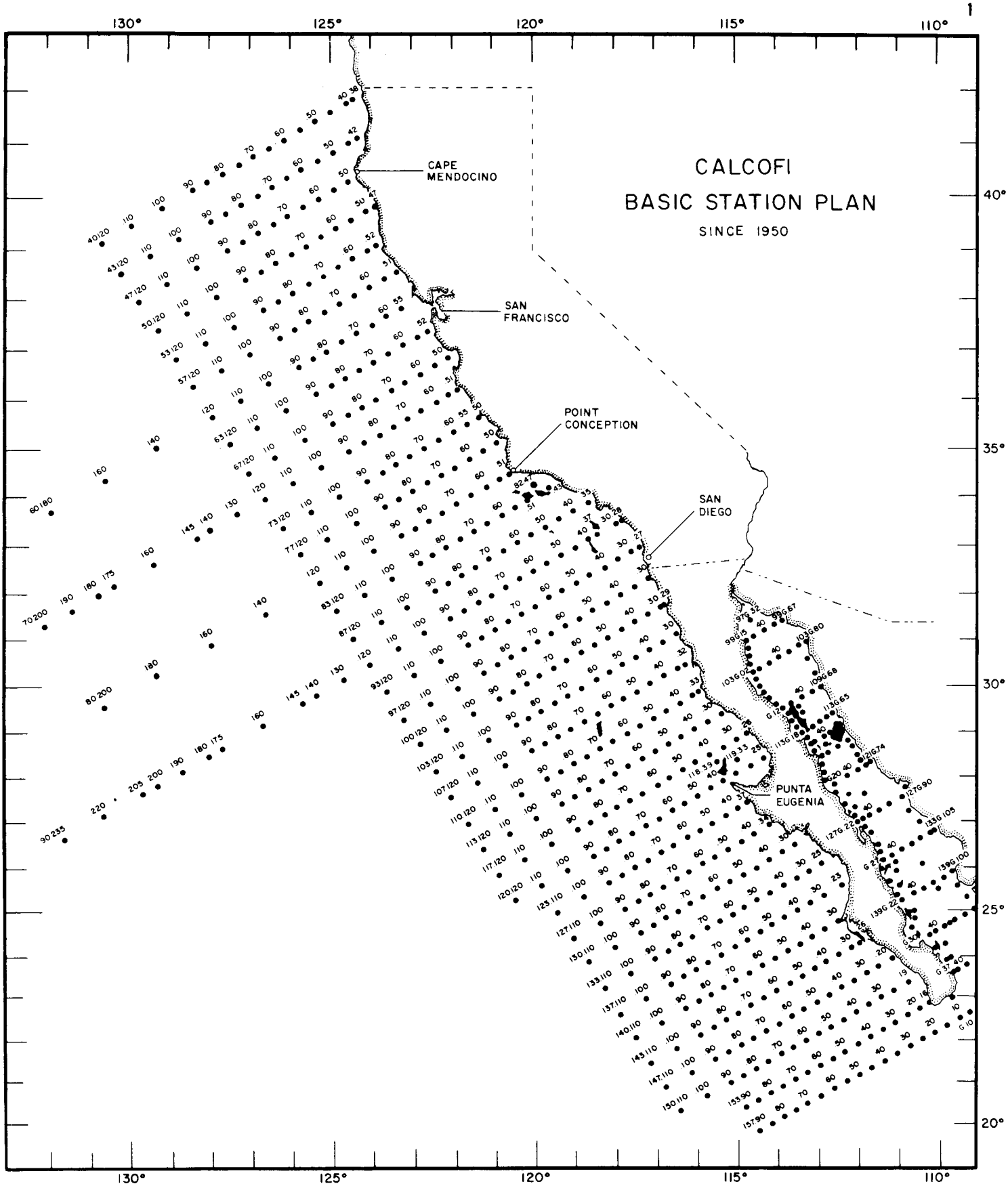

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